

Archosaurian anatomy and palaeontology. Essays in memory of Alick D. Walker. Edited by D. B. Norman and D. J. Gower

***Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland**

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Erpetosuchus, a small archosaurian reptile from the Late Triassic of Scotland and North America, has often been implicated in the ancestry of crocodylians. A restudy of the type specimen, using new high-fidelity casts, as well as examination of new, hitherto undescribed material, allows a detailed description and restoration of *Erpetosuchus granti* from the Lossiemouth Sandstone Formation (late Carnian, Late Triassic). This small reptile is known only from the front end of its body; a complete skull, cervical vertebral column, anterior dorsals and ribs, shoulder girdle, and forelimb. The skull shows a number of unusual features: a reduced row of only 4–5 teeth on the anterior part of the maxilla, a large antorbital fenestra set in a deep fossa whose margins are marked by distinct sharply angled ridges, a jugal that is divided into a lateral and a ventral portion by a sharp ridge, a deeply recessed tympanic area, the angular and surangular marked by a strong ridge running back from the ventral margin of the mandibular fenestra, and teeth oval in cross-section and lacking anterior and posterior carinae and marginal serrations. The remains suggest that *Erpetosuchus* was a light, cursorial animal that may have fed on insects. A cladistic analysis of crurotarsan archosaurs indicates that *Erpetosuchus* is the closest sister group of Crocodylomorpha among known basal archosaurs. It shares with them a deep recess in the cheek region framed by the quadrate and quadratojugal which slope forward side-by-side at an angle of 45° above horizontal, and reach the upper margin of the lower temporal fenestra. In *Erpetosuchus* the recess is entirely lateral, while in crocodylomorphs, the recess penetrates medially as well, since the quadrate/quadratojugal bar meets the side wall of the braincase. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, 136, 25–47.

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INTRODUCTION

When Newton (1894) described the new reptile *Erpetosuchus granti* from the Lossiemouth Sandstone Formation (Late Triassic) of Lossiemouth, near Elgin, in north-east Scotland, he presented something of an enigma to the world. Newton clearly recognized that *Erpetosuchus* was an archosaur, perhaps close to the phytosaurs and the aetosaurs, but also showing some similarities with crocodylians. The phylogenetic position of this reptile has been debated ever since (Broom, 1906; Watson, 1917; Huene, 1936; 1956; Romer, 1956; Walker, 1968, 1970; Krebs, 1976; Olsen *et al.*, 2000),

and its affinities have remained uncertain, to the extent that it is generally assigned to its own family, Erpetosuchidae. The recent report of a specimen of *Erpetosuchus* from North America (Olsen *et al.*, 2000) indicates that a re-study of the original material, and some previously unpublished specimens from Lossiemouth, will be timely.

Alick Walker began to study the type specimen of *Erpetosuchus granti*, housed in the Natural History Museum, London in 1963, and he continued to accumulate notes and sketches from that time until the 1980s. He published preliminary restorations of the skull in lateral view (Walker, 1970; Benton & Walker, 1985), but did not complete his planned re-description of the material. M.J.B. has re-examined all the material, including Newton's casts and A.D.W.'s casts and notes, and the present paper is a collaborative effort.

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Institutional abbreviations: AMNH, American Museum of Natural History, New York; BGS GSM, Geological Survey Museum, Keyworth; BMNH, Natural History Museum, London; NMS, National Museums of Scotland (formerly Royal Scottish Museum, RSM).

STUDYING THE ELGIN REPTILES

Most of the fossil reptiles from the Permian and Triassic sediments at Elgin are preserved as hollows in the rock (Benton & Walker, 1981, 1985). Bone material is occasionally present, but it is usually soft and poorly preserved, and is sometimes heavily mineralized. Early studies, from the 1840s to the 1880s, relied on traditional preparation methods; the sandstone was removed mechanically, so far as was possible, to expose the bones, or the remnants of the bones. Then, in the 1890s, E. T. Newton at the Geological Survey Museum in London pioneered the use of effective casting materials. Earlier and later efforts using plaster of Paris were not hugely successful, since the natural rock moulds are complex, and a flexible material has to be used.

Newton (1894: 574) described the original appearance of the type specimen of *Erpetosuchus* when he received it (Fig. 1A):

When the block first came to me it had been broken across in two directions, and one piece was wanting. The two portions remaining formed an irregular cube, showing on one side some small cavities, which proved to be parts of the vertebral column that had been broken across. Another surface... exhibited several holes... and an outline which seemed to indicate a transverse section of the skull... After carefully probing to find in which direction the bones lay,... it was decided to split the smaller block from end to end, so as, if possible, to open longitudinally a cavity which seemed to be part of a skull. This operation was successful beyond expectation...

Newton revealed the entire skull and mandible, with the associated cervical and anterior dorsal vertebral column and ribs, some rows of dorsal scutes above, and the entire pectoral girdle and forelimb on each side, an 'exceedingly pretty little reptile'.

For cast-making, Newton chose gutta percha, a rubber-like hydrocarbon that is obtained from the latex of Malaysian trees of the Family Sapotaceae (*Palaquium*, *Payena*, etc.). In his day, gutta percha (the name is derived from the Malay words *getah*, gum, and *percha*, a tree producing it) was used for making golf balls, but it was its toughness that attracted Newton. He found he could pour the latex into the cavities in the rock, let it harden, and then remove it while it was still flexible. In time, it hardened to a firm, if somewhat delicate, cast, which retained enough flexibility that he could, for example, manipulate processes of the skull to look

inside. Newton had his casts coloured, brown for the bone and pink for intervening rock. Newton's casts are still in superb condition, over 100 years after they were made, and they show remarkably fine detail, such as the sculpturing on the frontal bone, sutures between skull bones, and the microscopic sculpture of the tiny scutes (Figs 1B–D, G, 4A). Newton also had some plaster models of the skull and mandible of *Erpetosuchus* sculptured, for purposes of display and exchange (Fig. 1E, H), but the illustrations in his paper (Newton, 1894) were taken directly from the gutta percha casts, and they are accurate.

Later, when A.D.W. began his studies of the Elgin reptiles in the 1950s and 1960s, he used synthetic materials, polyvinyl chloride (PVC) and Vinagel, to take further casts from the natural rock moulds (Figs 1F, I, 4B). PVC has the advantage over gutta percha of not going hard, and it retains its flexibility. In comparisons of Newton's casts made in the 1890s with those made by A.D.W. in the 1960s, it is clear that some fine detail has been lost in the rock moulds, probably as each cast is taken. For example, some of the PVC casts of the cervical scutes show less detail of the sculpture patterns than is shown by the gutta percha casts. However, A.D.W. worked carefully to gain access to areas of the skeleton of *Erpetosuchus* that Newton had not reached, and by careful cleaning of the hollows, he was able to obtain more detail of the vertebrae, for example. In addition, a clean PVC cast shows better detail of suture lines and surface sculpturing when examined under the microscope than one of the older gutta percha casts.

It should be noted that the remark made by Olsen *et al.* (2000: 635), that 'most of the cranial sutures shown in Walker's reconstruction are not evident on the casts examined by us' is a reflection on their casts, and not on Newton's or A.D.W.'s casts or interpretations. Recently made casts are tenth- to fifteenth-generation, and the holotype mould has demonstrably lost some of the subtleties of detail that are clearly recorded in Newton's original gutta percha casts and A.D.W.'s PVC casts. In this work, we have used the original casts.

DESCRIPTION

SUBDIVISION ARCHOSAURIA COPE, 1869
 INFRADIVISION AVESUCHIA BENTON, 1999
 ORDER CRUROTARSI SERENO & ARCUCCI, 1990
 SUBORDER SUCHIA KREBS, 1976
 FAMILY ERPETOSUCHIDAE WATSON, 1917
ERPETOSUCHUS GRANTI NEWTON, 1894

1894 *Erpetosuchus granti* Newton; Newton, pp. 574–586, pl. 53.

1895 *Erpetosuchus granti* Newton; Traquair, p. 276.

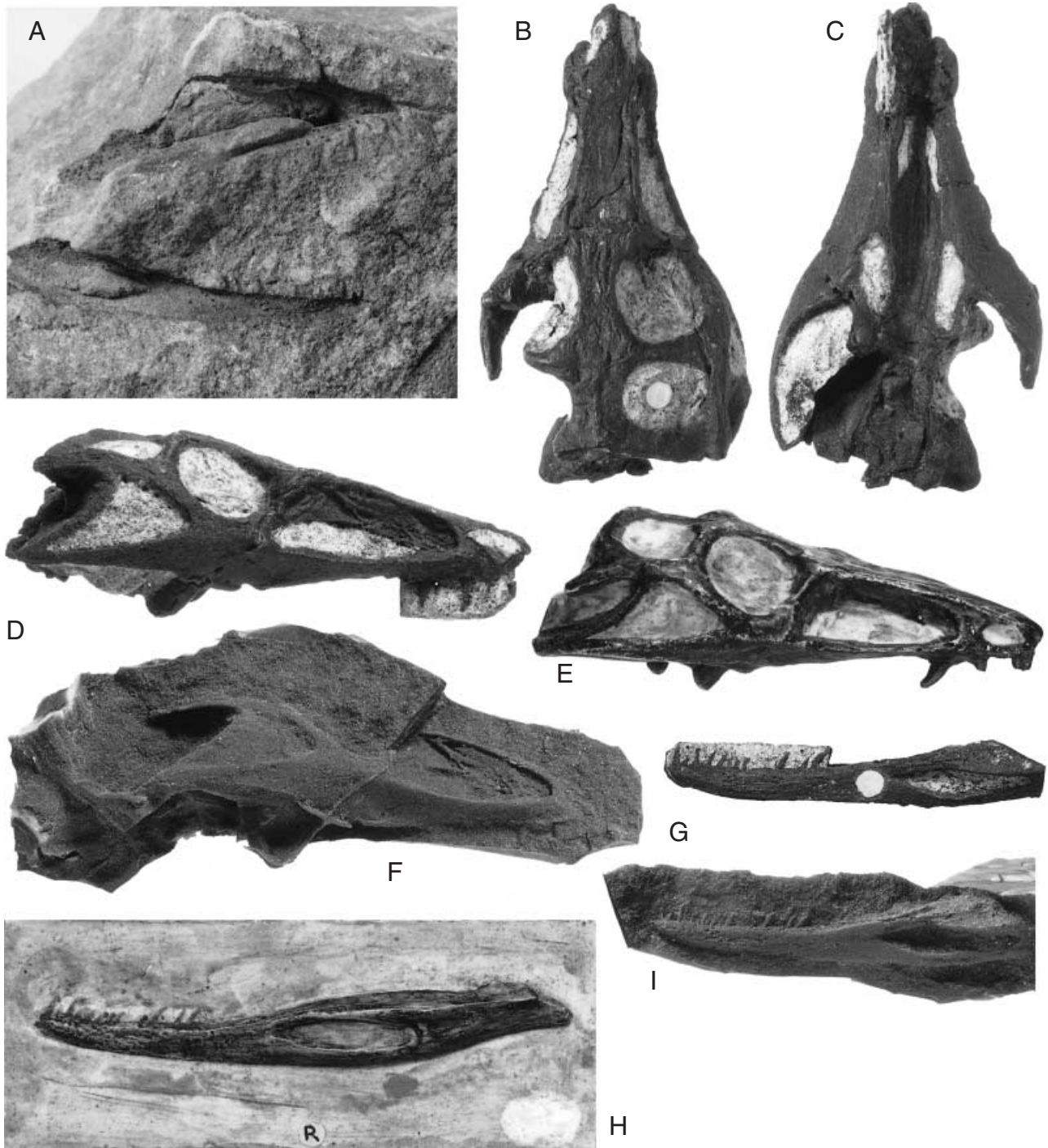


Figure 1. Moulds, casts and models of the skull and mandible of *Erpetosuchus granti* Newton (1894) (BMNH R3139). (A) Natural rock mould of the left side of the anterior part of the articulated skull and mandible; other sandstone blocks fit on to this one to complete the three-dimensional mould of the entire head; the small black marks in the moulds are cubic crystals of iron oxide mineral. (B–D) Gutta percha cast of the skull, made by E. T. Newton in the 1890s, in dorsal (B), ventral (C), and right lateral (D) views. (E) Plaster model of the skull, made by Newton in the 1890s, in dorsal view. (F) PVC cast of the skull, made by A.D.W. in the 1960s, in lateral view. (G) Gutta percha cast of the left mandible, made by Newton in the 1890s, in lateral view. (H) Plaster model of the left mandible, made by Newton in the 1890s, in lateral view. (I) PVC cast of the left mandible, made by A.D.W. in the 1960s, in lateral view. Scale: all photographs are natural size ($\times 1$).

- 1906 *Herpetosuchus* Newton; Broom, pp. 188, 189.
 1914 *Erpetosuchus granti* Newton; Huene, p. 22, fig. 35.
 1913 *Herpetosuchus granti* Newton; Broom, p. 626.
 1917 *Erpetosuchus granti* Newton; Watson, p. 180.
 1956 *Erpetosuchus granti* Newton; Huene, p. 451.
 1956 *Erpetosuchus granti* Newton; Romer, p. 594.
 1961 *Erpetosuchus granti* Newton; Reig, p. 92, fig. 3B.
 1961 *Erpetosuchus granti* Newton; Walker, pp. 183, 185.
 1968 *Erpetosuchus granti* Newton; Walker, pp. 12, 13.
 1970 *Erpetosuchus granti* Newton; Walker, pp. 365, 367–368, fig. 12d.
 1976 *Erpetosuchus granti* Newton; Krebs, pp. 87–89, fig. 32.
 1985 *Erpetosuchus granti* Newton; Benton and Walker, p. 211, fig. 3D.
 2000 *Erpetosuchus granti* Newton; Olsen *et al.* p. 634.

Type specimen: BMNH R3139, a virtually complete skull and mandible, cervical and anterior dorsal vertebrae, shoulder girdle, and forelimbs. Collected by Robert Grant from the breakwater at Lossiemouth. Newton's gutta percha casts are BGS GSM 91029–91051, and A.D.W.'s PVC and Vinagel casts are located with BMNH R3139.

Locality and horizon: Original provenance uncertain; either from Lossiemouth East Quarry (National Grid Reference, NJ 236707) or from Spynie Quarries (NJ 223657, etc.). In either case, from the Lossiemouth Sandstone Formation (late Carnian, Late Triassic).

Other material: (1) NMS 1966.43.4A, B, part and counterpart of a small area of the dorsal region, with some articulated scutes and associated ribs; part of the Stollery collection, from Mr E. Stollery of Sandend (Cullen), a former dealer in rocks and minerals. (2) NMS 1992.37.1, portion of the cervical vertebral column and scutes, collected by Neville Hollingworth from the shore located between the diverging piers just south of the old railway station at Lossiemouth (NJ 239713), so probably not *in situ*, but part of the quarry rubble dumped on the shore from Lossiemouth quarries in the nineteenth century. (3) BMNH R4807, a block with impressions of 16 vertebrae in series, presented by the Rev. Dr George Gordon in July, 1885. Labelled as coming from Lossiemouth.

Generic diagnosis: Characters differentiating *Erpetosuchus* from all other known archosaurs are: (1) reduced maxillary tooth row (4–5 teeth), restricted to the zone in front of the midpoint of the antorbital fenestra; (2) large antorbital fenestra set in a deep fossa whose margins are marked by distinct sharply angled ridges; (3) jugal forms a pair of surfaces below the orbit separated by a distinct longitudinal ridge, one facing dorsolaterally, and the other essentially

ventrally and slightly laterally; (4) deep 'otic notch' below an overhanging squamosal, formed by the quadrate and quadratojugal running up and forward, but not medially to the side wall of the braincase; (5) angular and surangular marked by a strong ridge running back from the ventral margin of the mandibular fenestra; (6) teeth oval in cross-section, lacking anterior and posterior carinae and lacking marginal serrations.

SKULL

General

Erpetosuchus has a long, low skull when seen in lateral view (Fig. 2A), with a low snout, and only a few teeth well to the front of the jaws. The lower jaw is also slender, and bears limited numbers of teeth at the front. The posterior portion of the skull is considerably expanded laterally, when seen from above (Fig. 2B); the narrow snout contrasts with a square skull roof. The skull is lightweight, being pierced by moderately large nares, long deeply recessed antorbital fenestrae, large circular partially dorsally facing orbits, and large temporal fenestrae, the lower being somewhat triangular and laterally facing, and the upper being circular and dorsally facing. The high position of the orbit, with the long antorbital fenestra, and elongate triangular lower temporal fenestra partially beneath, is a striking feature.

The type specimen preserves the skull in full three-dimensional detail, and virtually undistorted, so the reconstruction (Fig. 2) may be given with some confidence. In the specimen, only the left-hand posterior sector of the skull is not preserved, and the braincase is somewhat displaced and fragmented. Our restoration (Fig. 2) differs from that of Newton (1894: pl. 53) in relatively minor details: the upper margin of the snout is slightly arched dorsally, and is not straight, in lateral view; the rear tip of the squamosal does not curve downwards; the quadrate/quadratojugal are fully visible from above, and not obscured by the squamosal; the pterygoids do not end in a midline posterior point, but a midline V-shape running anteriorly, and the braincase is set further forward than is shown by Newton who leaves it in its slightly displaced location. Walker (1970: fig. 12d) gave a preliminary version of the present restoration, in lateral view.

Dermal bones of the skull roof

The *premaxilla* is a short element, restricted to the anteriormost tip of the snout, surrounding the anterior, ventral, and posterior margins of the naris, and bearing four small teeth. The lower, tooth-bearing, margin of the premaxilla is offset from the line of the maxilla by a small notch and step up (Fig. 2A). In

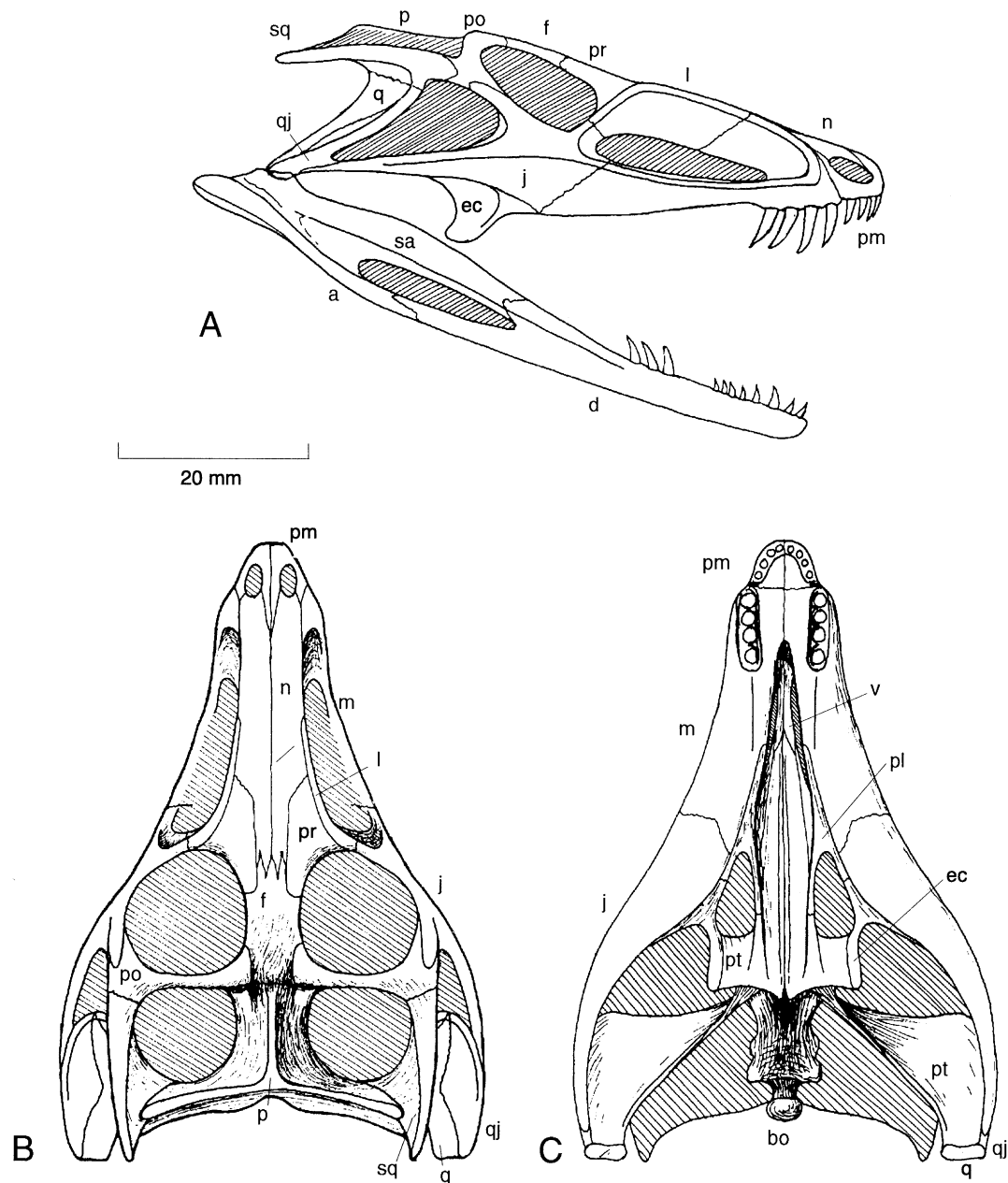


Figure 2. Restoration of the skull of *Erpetosuchus granti* Newton (1894) (BMNH R3139), in right lateral (A), dorsal (B), and ventral (C) views. Drawing by A.D.W. Abbreviations: a = angular, d = dentary; f = frontal; j = jugal; l = lacrimal; m = maxilla; n = nasal; p = parietal; pl = palatine; pm = premaxilla; po = postorbital; pr = prefrontal; pt = pterygoid; q = quadrate; qj = quadratojugal; sa = surangular; sq = squamosal; v = vomer.

dorsal view (Fig. 2B), the premaxillae meet along a straight suture, and a tapering process runs between the anterior tips of the nasals. In ventral view (Fig. 2C), the premaxillae also meet in the midline, and contact the maxillae in a small secondary palate along straight sutures.

The *maxillae* are complex elements that make up most of the side of the snout, and which contribute substantially to an anterior secondary palate. Behind

the contact with the premaxilla, the lower margin of the maxilla extends backwards as a remarkably straight edge, but strikingly toothless, except for two (of four) slender fang-like teeth, well spaced apart, towards the front (Fig. 2C). This lower branch of the maxilla contacts the jugal along a broad ventro-medially directed suture (Fig. 2A, C), and its dorsal margin forms a deep recess for the antorbital fenestra. A distinct longitudinal ridge separates the ventral, pal-

atal portion of the maxilla from the lateral portion. In front of the antorbital fenestra, the maxilla sweeps round the anterior part of the recess and back to meet the lacrimal and the nasal. In palatal view (Fig. 2B), the maxilla bears four closely spaced alveoli on a flattened platform, the individual teeth being more than twice the diameter of the premaxillary teeth. Behind the alveolar platform is a narrow crest, on the lateral side of which the mandibular teeth pass as the jaw closes, and on the medial side of which the maxilla descends to form a short secondary palate at the front, and the lateral margin of the choana behind.

The *nasals* are paired midline elements that form most of the roof of the snout, running from the dorsal margin of the nares, where they contact the premaxillae laterally and medially (Fig. 2A, B). The two nasals contact each other along a long straight midline suture. Laterally, each nasal contacts the premaxilla anteriorly, then the maxilla and lacrimal, which exclude the nasal from the border of the antorbital fossa, then the prefrontal, and finally the frontal along a short zig-zag suture posteriorly. The surface of the nasal bones is smooth and unpitted.

The *frontal* is a short single element, less than half the length of the nasals; there is no sign of a suture in the midline. The frontal contacts the nasal and prefrontal anteriorly, enters the border of the orbit for a short distance, and is bounded posteriorly by the postorbital/postfrontal and the parietal. The surface of the frontal is marked by irregular pits which become short ridges and grooves anteriorly; these rugosities appear to be restricted to the frontal.

The *parietal* is a broad T-shaped element, again fused from two parietals, but leaving no trace of the midline suture and no hint of a parietal foramen (Fig. 2B). The upper surface, strictly defined, is a very narrow T-shaped structure, little more than a 'sagittal crest', and the remainder of the parietal sweeps ventrally on deep curved surfaces into the margins of the upper temporal fenestra on each side. The lateral wings of the parietal stand broadly at right angles to the midline branch, and bend slightly backwards at their distal ends. These lateral wings form essentially the entire posterior margin of the upper temporal fenestrae, as well as marking the entire upper margin of the occiput. The parietal meets the frontal and postfrontal/postorbital anteriorly along a straight suture, and the lateral wings contact the squamosal.

The *lacrimal* is a large element, forming much of the dorsal and posterior portion of the antorbital fossa (Fig. 2A), and extending as a thin lateral strip of bone on to the dorsal surface of the skull (Fig. 2B). Below the lateral contact with the nasal and prefrontal, the lacrimal forms a sharp angle between the dorsal and lateral aspects of the snout. Below this, the lacrimal

meets the maxilla anteriorly and the jugal posteroventrally in the deep margin of the antorbital fossa. In this deep part of the antorbital fossa, both the maxilla and the lacrimal bear numerous pits and wrinkles, and this is seen in Newton's casts (BGS GSM 91029, 91030) as in A.D.W.'s.

The *prefrontal* is smaller than the lacrimal, forming the antero-dorsal margin of the orbit (Fig. 2A, B). The prefrontal contacts the nasal and frontal medially and the lacrimal laterally, but is excluded from contact with the jugal by the lacrimal.

Behind the orbit, the *postorbital/postfrontal* is a straight, narrow bar of bone that contacts the frontal and parietal medially, and the jugal and squamosal laterally (Fig. 2A, B). It divides the large orbit from the almost equally large upper temporal fenestra. No trace of a suture between the postorbital and the postfrontal can be seen, so the two elements are evidently fused. Some pitting is seen in the postfrontal area of the element, close to the frontal.

The *jugal* is a complex, five-branched structure, forming margins to the antorbital fenestra, the orbit, the lower temporal fenestra, and much of the posterior ventral skull margin (Fig. 2A–C). It is divided into an essentially lateral and a ventral portion by a sharp ridge running antero-posteriorly. Above this ridge, the jugal forms the ventral margin of the orbit, contacting the postorbital with a slender overlapping process. The two anterior branches of the jugal contact the lacrimal and the maxilla, respectively, and they form the narrow postero-ventral angle of the margin of the antorbital fenestra. The posterior branch of the jugal is long and tapering, forming a slightly recessed anterior margin to the lower temporal fenestra, and meeting the quadratojugal far posteriorly. In ventral view (Fig. 2B), the ventral portion of the jugal, below the ridge, is as broad as the maxilla anteriorly and, in this portion, also contacts the palatine and the ectopterygoid.

The *squamosal* is a slender curved element, located between the two temporal fenestrae. Behind its anterior contact with the postorbital, the squamosal divides into a superficial and a deep portion. The former is a tapering, curved element that projects far posteriorly above the otic notch (Fig. 2A) and bounds the dorsal margin of the lower temporal fenestra. Below this, a deep scalloped portion of the squamosal meets the quadrate laterally (Fig. 2A), and the parietal medially (Fig. 2B).

The *quadrate* and *quadratojugal* together form a remarkable deep otic notch, recessed well below the superficial lateral skull surface, and protruding far forward dorsally, distorting the shape of the lower temporal fossa (Fig. 2A). The two elements take equal part in the otic notch, the quadratojugal being located laterally, forming the posterior margin of the lower

temporal fenestra, and contacting the jugal on a short suture at the extreme posteroventral corner of the fenestra. The quadrate bears a small mandibular articular condyle, and the plate-like pterygoid process sweeps far forward at an angle of about 60° above horizontal (Fig. 2C).

Dermal bones of the palate

In the palate (Fig. 2C), the premaxilla and maxilla form together a short secondary palate, as noted above. The maxillae and jugals provide broad strong margins to the palate, which is consequently narrow and elevated above the level of the tooth-bearing jaw margins. The vomers are slender paired structures that contact each other along a straight suture in the midline, and form a sharp vertical wall between the choanae, disappearing anteriorly above the secondary palate.

Behind the vomers, the *palatines* and *pterygoids* form an elongate narrow palate, the latter meeting their counterparts along a straight midline suture, with no sign of an interpterygoid vacuity. The palatines do not meet in the midline, but contact the vomers anteriorly, and have a long medial suture with the pterygoids. The palatine also contacts the maxilla and jugal along a long lateral suture, where it forks around the anterior margin of the suborbital fenestra. The pterygoid is more extensive, forming the bulk of an elongate antero-posterior trough on either side of the somewhat elevated midline suture. Behind the palatine, the pterygoid forms the medial and posterior margins of the suborbital fenestra, and contacts the ectopterygoid laterally. Behind the suborbital fenestra, the pterygoid forms a rather square lateral ectopterygoid ramus that is marked by a deep trough extending behind the fenestra, and does not appear to bear teeth. The quadrate ramus extends posterolaterally as a narrow tapering element that meets the equally sheet-like pterygoid ramus of the quadrate. Medially, the posterior margins of the ectopterygoid rami of the pterygoids are nearly straight, and there is only a short V-shaped notch between them, marking the much-reduced interpterygoid vacuity. The dorsal contacts of the pterygoid with the basiptyergoid processes of the braincase and with the epiptyergoids cannot be seen in the specimens.

The *ectopterygoid* is a small element that forms the posterolateral margin of the suborbital fenestra, and contacts the jugal anterolaterally and the pterygoid medially.

Braincase

The braincase is not well preserved. In the type specimen, it has obviously been shifted downwards and back, and when restored (Fig. 2C), is located somewhat anteriorly, just in front of a line between the

quadrate condyles. In Newton's casts (BGS GSM 91029, 91030), the outline of the braincase is well displayed in ventral view, showing its elongate slender shape, the small occipital condyle and the short basioccipital, bearing two square lateral tubera. The basisphenoid is longer, and it bears two long basiptyergoid processes that diverge from the midline, and descend some 4 mm. They are disarticulated from their life position, in close contact with the pterygoids.

In posterior view, the rounded occipital condyle lies below the foramen magnum, on either side of which the triangular exoccipitals pass into the paroccipital processes. Indications of the supraoccipital, above the foramen magnum, may also be seen. On the left side, the paroccipital process appears to fit distally into a small ledge on the posterior surface of the squamosal, set in below the parietal. A relatively large post-temporal opening would then exist between the posterolateral wings of the parietal and the paroccipital process.

LOWER JAW

Both lower jaws are present, but the left is seen best at the anterior end (Fig. 1G–I), the right at the posterior end, and the reconstruction (Fig. 2A) is a composite from both sides. The lower jaw is a long, low element in which the dentary makes up just more than the anterior half. The mandibular fenestra is elongate, and set in a shallow fossa bounded by an elongate ridge above, on the surangular and the dentary. There is a marked retroarticular process.

The *dentary* has a gently rounded anterior tip and a slightly flexed upper margin, in lateral view (Fig. 2A). In cross-section, the dentary forms a thick lateral wall to the anterior half of the lower jaw, bearing the teeth on a broad dorsal platform, and thickening ventrally to form a relatively flat base to the mandible. Dentary teeth are present in two clusters, eight small teeth at the front, roughly equally spaced, and ranging in size, with number three from the front the largest. These teeth interlocked with those of the premaxilla and maxilla. Behind them, and separated by a gap equivalent in length to some four teeth, follow three larger, markedly recurved fang-like teeth. Posteriorly, the dentary meets the surangular on a slightly V-shaped suture line, then forms the anteroventral margin of the mandibular fenestra, and meets the angular ventrally on a short suture. The anterior section of the dentary bears small grooves and pits, evidently passages for nerves and blood vessels.

The *splenial*, not seen in lateral view, is a deep, flat, thin plate of bone that covers the entire medial face of the mandible in its anterior half, starting from just below the base of the teeth and ending just above the ventral margin of the jaw, contacting the dentary at

both levels (BGS GSM 91032). In this cast, the splenial does not extend to the front of the mandible, but stops 15 mm short, exposing a shallow trough along the ventral half of the medial side of the dentary. This trough in the dentary is presumably for reception of the splenial, and perhaps lies behind the symphysis, which is not seen in the cast. The *coronoid* cannot be distinguished, although it may be represented by a long thin medial plate visible in casts of the left lower jaw. In any case, the coronoid, if present, did not project dorsally as a major element. The surangular forms the entire dorsal and posterior margins of the mandibular fenestra, behind which is a depressed trough-like zone, bounded above by a sloping and overhanging portion of the bone. The *surangular* sweeps around the articulation point with the quadrate, and the *articular* lies mainly medially, excluded from lateral view by the surangular. The *angular* forms the ventral margin of the mandible below the posterior portion of the mandibular fenestra, and the *prearticular* can be seen at the very back, where it runs round beneath the retroarticular process from the medial face of the mandible.

DENTITION

All teeth are slender, conical, and recurved, although they vary considerably in size. They do not show any sign of the normal anterior and posterior carinae, nor of the serrations on those carinae, which are typical of most archosaurs. The teeth evidently sit in sockets, as Newton (1894: 580) assumed (BGS GSM 91032).

The assumption that there were four small teeth on the premaxilla is based on the presence of two small teeth, each about 2 mm long, on the right-hand side,

and four alveoli lacking teeth on the left-hand side. On both right and left sides there are two long teeth on the maxilla, each 5–6 mm long and 2 mm in diameter, and additional gaps between these two indicate that the maxilla bore four teeth in all on each side. It cannot be said whether the sequence of tooth implantation meant that there were only two maxillary teeth in place on each side at a time, or whether the missing two had been broken off in the specimen. The latter suggestion is more probable, since the mandible seems to have a fuller complement of teeth.

The left lower jaw element bears 11 small conical recurved teeth that vary in size (Fig. 1A, G–I). Two small anterior teeth, each 2.5 mm long, are followed by a larger tooth, 3 mm long, and then five smaller ones, each about 2 mm long. Behind a gap follow three larger, distinctly backwards-directed teeth, each about 2.5 mm long.

AXIAL SKELETON AND SCUTES

The anterior 12 vertebrae are preserved, mainly in articulation, but with the 7th rotated out of sequence, and with a gap between the 11th and 12th (Fig. 3). Cervicals and dorsals cannot be distinguished unequivocally, although most basal archosaurs had seven cervicals. Details of the vertebrae are obscured in places by the fact that the separate blocks broke along the line of the vertebral column. Elements of the atlantal system are preserved in the occipital region of the skull, somewhat disarticulated, and hard to distinguish from offset portions of the braincase. The axis is more clearly visible, on the right-hand side, where its expanded neural spine and small postzygapophysis are evident, but the prezygapophysis, and details

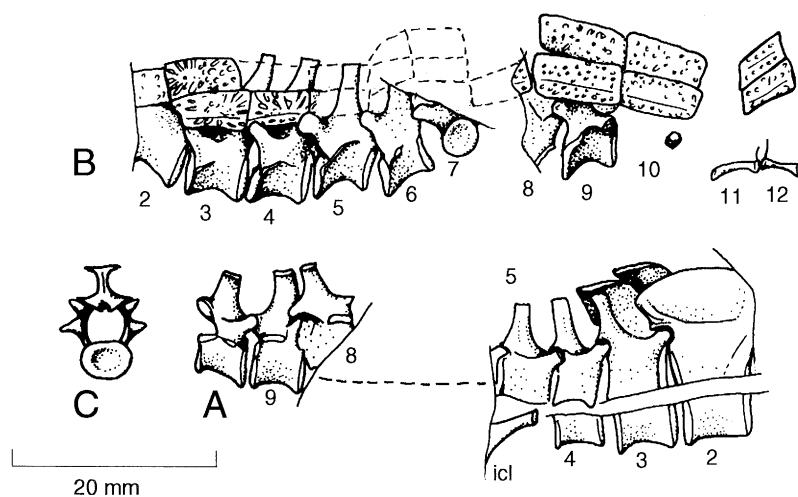


Figure 3. Cervical and anterior dorsal vertebral series of *Erpetosuchus granti* Newton (1894) (BMNH R3139). (A, B) Presacral vertebrae 2–12, seen in right lateral (A) and left lateral (B) views, with associated dorsal midline scutes. (C) Posterior view of presacral vertebra 10. Abbreviations: icl = interclavicle; 2–12 = presacral vertebrae 2–12.

of the deep, smooth-walled centrum are unclear (Fig. 3A).

Cervicals 3–5 are seen relatively well on the right-hand side (Fig. 3A), showing their high, short overall shape (centrum 5 mm long and 4 mm wide; vertebra 16 mm high, but perhaps 14 mm because of casting gap). The centra are deeply laterally compressed, with high-arched ventral margins that bear a sharp ventral keel. The zygapophyses are short, and the neural spines anteroposteriorly narrow. On the left-hand side (Fig. 3B), there is a low diagonally backwards-running ridge from the anteroventral margin of the centrum to the short transverse process, the parapophysis and diapophysis in continuum. Vertebra 7 is rotated out of position, showing the circular concave anterior face of the centrum and a transverse process.

Vertebrae 8–10, on a separate block, are reasonably well preserved, but 11 and 12 are obscure. The centrum is 6 mm long, 5 mm broad, concave, and with a marked ventral keel. The neurocentral suture may be seen in vertebra 10 on each side. The short prezygapophysis expands back into the short transverse process. The neural spine is shorter, and anteroposteriorly expanded, in comparison with more anterior vertebrae. At the top is a clear spine table in vertebrae 8, 9, and 10 (Fig. 3A, C). In posterior view, the centrum of vertebra 10 is low, the neural canal wide and high, and the poszygapophyses located high on the neural arch (Fig. 3C).

Cervical ribs cannot be found in the specimen. Two long slender dorsal ribs are associated with vertebrae 10–12 in the region of the left scapula, but they do not show the proximal heads.

Scutes are present in association with vertebrae 2–10. Pairs of scutes may be seen in association with each of these vertebrae in Newton's casts (BGS GSM 91034–91036; Newton, 1894: pl. 53, figs 5, 6), but some of these scutes (those associated with vertebrae 2, 5–8, 11, 12) are much less clear in more recent casts by A.D.W. Each scute is roughly 8 mm long and 5 mm wide, and covered with a finely pitted radiating sculpture pattern (Fig. 4). There is a straight ridge, or inflection, only slightly elevated, running longitudinally on each scute, but off-centre and closer to the lateral than the medial margin. Towards the anterior margin of the scute above vertebra 9 there is a short, smooth zone, some 2 mm long, which in life may have been overlain by the scute immediately in front. Above vertebrae 3–6, and 9 and 10, sets of four scutes in association (Figs 3B, 4A) show that there were at least two parallel rows of paramedian scutes running from the back of the head along the midline of the body. A possible additional lateral row of scutes is hinted at by an obscure scute impression lying laterally of two upturned midline scutes; perhaps this row begins about vertebra 11 or 12.

The total length of the scutes (8 mm) exceeds the length of the centrum in the first 12 vertebrae (5–6 mm), so there was probably an overlap between scutes of approximately 2 mm, based on the assumption that there was essentially one column of scutes per vertebra, and confirming the anterior smooth zone seen in scute 9.

APPENDICULAR SKELETON

Pectoral girdle

The pectoral girdle is preserved approximately *in situ* on either side of the vertebral column, and a combination of evidence from both sides allows a reasonably detailed reconstruction of all elements. The right scapula and coracoid are seen best from inside and from the front, while the left scapula may be seen best in lateral view.

The *scapula* (Fig. 5A–C) is a slender strap-like element, some 33 mm long, which passes from a basal width of 9 mm to a mid-shaft width as little as 2.5 mm, and with a maximum distal blade width of 7 mm. There is a distinctive projection on the medio-anterior margin, possibly marking the upper limit of the attachment of the clavicle. The lower portion of the scapula expands posteriorly into a broad plate which curves over laterally on its dorsal margin. The contact between the scapula and the coracoid is substantial posteriorly through the glenoid region, but there is a narrow notch anteriorly between the two elements. The short, angled glenoid is seen in Newton's casts (BGS GSM 91037, 91038), but it lies close to the proximal head of the humerus, and is less clear in A.D.W.'s casts.

The *coracoid* (Fig. 5A–D) is seen on the right side, although Newton (1894: 581) mentions both right and left elements. The curved interior aspect of the right coracoid lies over the lateral branch of the interclavicle and below the proximal head of the humerus. In medial/dorsal view (Fig. 5A, D), the coracoid is a rounded concave element, about 10 mm long and 7 mm wide, with a clear expanded longitudinal medial margin presumably for contact with the side of the interclavicle. There is no sign of a coracoid foramen, nor is there a posterior process. As with the scapula, the glenoid portion is somewhat obscured.

The *interclavicle* is beautifully exhibited, in dorsal view (Fig. 5D), on the right side of the vertebral column, beginning from beside vertebra 5 (Fig. 3A). The element has evidently been disarticulated and shifted up and forwards. The interclavicle is essentially complete, and some 39 mm long. The anterior tip is a short rod, behind which the element is flat and slightly concave in dorsal view. Clavicles may have attached to the anterior tip, and the coracoids may have fitted into the slightly curved anterolateral edges of the interclavicle.

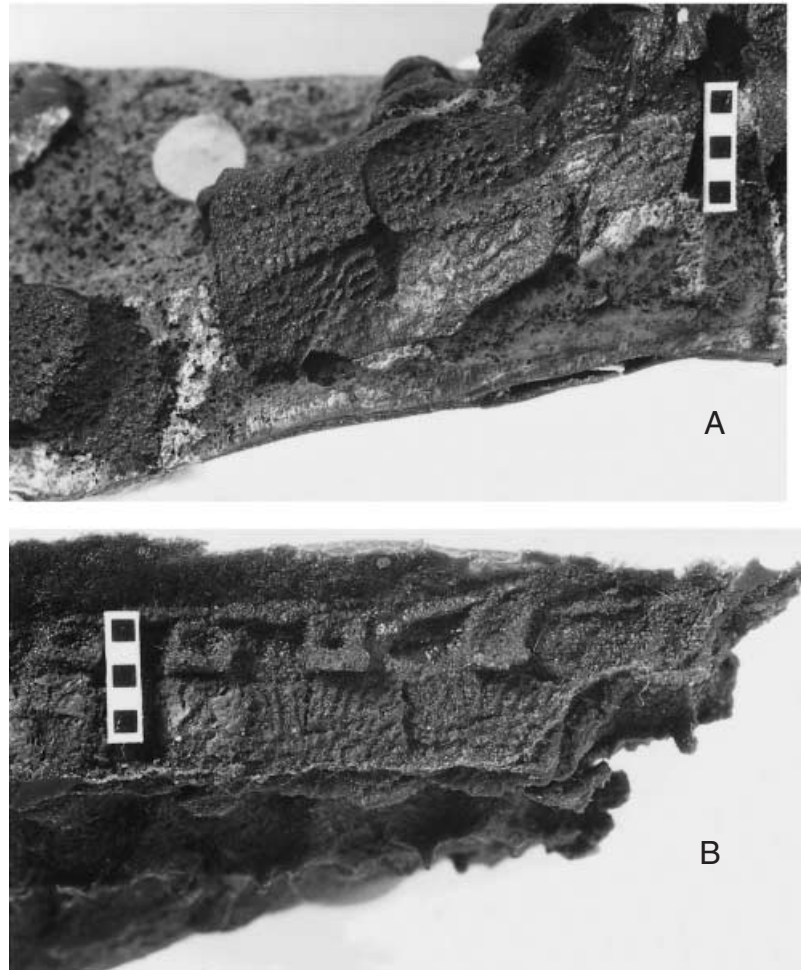


Figure 4. Photographs of scutes of *Erpetosuchus granti* Newton (1894). (A) Paired scutes above presacral vertebrae 9 and 10 in BMNH R3139 (cf. Figure 3B), from E. T. Newton's gutta percha cast. (B) Lateral scutes above presacral vertebrae 6 and 7 in NMS (1992).37.1 (cf. Figure 3B, D), from A.D.W.'s PVC cast. Scale: both $\times 3$.

The anterior portion expands laterally about 11 mm back from the tip, but the full length of the lateral projections is obscured by the vertebral column on the left and the coracoid on the right. Behind the coracoids, the interclavicle extends a long posterior process that narrows gradually to a point. The possible *clavicle* noted by Newton (1894: 581) is a rib.

Forelimb

The forelimb is preserved on both sides. Both the right (BGS GSM 91046, 91047; Fig. 6A–D) and the left *humerus* (BGS GSM 91040, 91041; Fig. 6E) were cast in three dimensions by Newton. In both cases, the distal end is incomplete. The humerus is 38 mm long, slender, almost straight, but with slight lateral bowing at mid-shaft length. Its proximal end is 10 mm across at the broadest point and shows a heavy posterior articular ball that fitted into the glenoid, and a nar-

rower, curved, sheet-like deltopectoral crest in front that extends to just less than halfway down the length of the element. The shaft is roughly circular in cross section, some 2 mm in diameter, and it twists so that the distal end expands in a different plane from the proximal. The distal end is triangular, with a shallow intercondylar area.

The *radius and ulna* (Fig. 6F) are best seen on the left side and, as far as preserved, they both measure 21 mm long. The proximal ends are not visible, and there is a gap of some 9 mm between the distal end of the left humerus and the forearm elements, so indicating an original length of 30 mm for both. The radius and ulna are both somewhat flattened, and relatively straight. The ulna is 2 mm across, the radius 1.5 mm. The distal ends of both elements are not much expanded, and the terminations are slightly curved.

The *wrist and hand* are present on both sides. On the right, the elements are somewhat disarranged, but

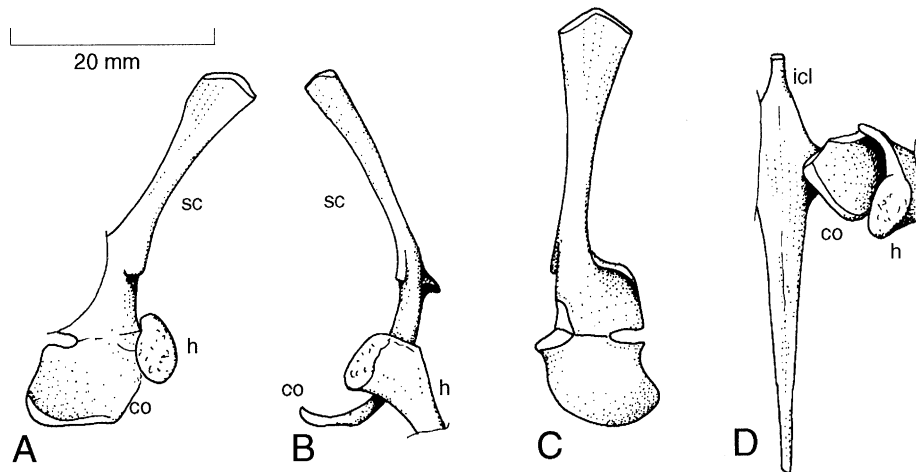


Figure 5. Elements of the shoulder girdle of *Erpetosuchus granti* Newton (1894) (BMNH R3139). (A–C) Right scapulo-coracoid, with associated humerus, in medial (A) and anterior (B) views, and resoration in lateral view (C). (D) Dorsal (interior) view of the interclavicle, coracoid, and proximal humerus. Abbreviations: co = coracoid; h = humerus; icl = interclavicle; sc = scapula.

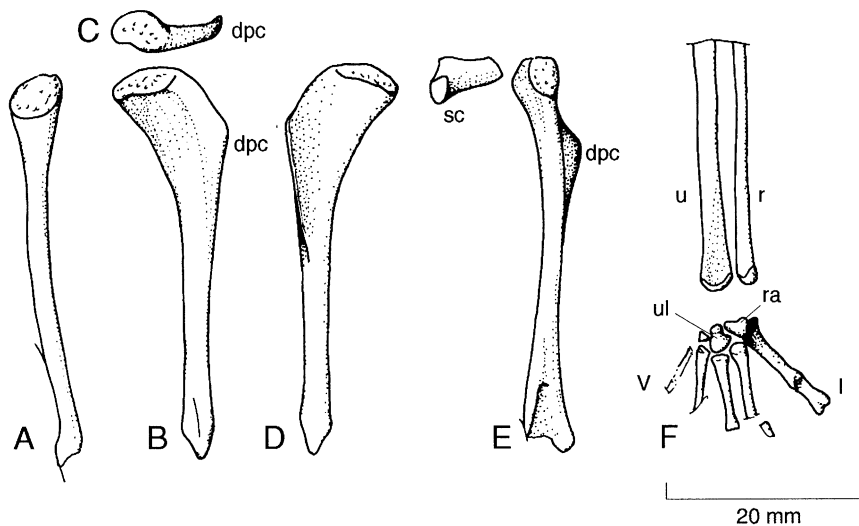


Figure 6. Elements of the forelimb of *Erpetosuchus granti* Newton (1894) (BMNH R3139). (A–D) Right humerus in anterior (A), lateral/dorsal (B), proximal (C), and medial/ventral (D) views. (E) Left humerus in posterior view. (F) Left lower forelimb in ventral/posterior view. Abbreviations: dpc = deltopectoral crest; hu = humerus; r = radius; ra = radiale; sc = scapula; u = ulna; ul = ulnare; I, V = toes I and V.

the left hand is remarkably well preserved and seen in ventral view, bent and removed a short distance (2 mm) from the distal ends of the radius and ulna (Fig. 6F). The gap could permit insertion of elongate crocodylian-like carpals, but this is contradicted by the facts that the left hand has a full array of small carpals in any case, and the right hand shows no such gap. At least three carpal elements may be seen in the left hand, but their identification must remain somewhat tentative. The large proximal one is presumably the radiale, and beside it is the possible ulnare. An

additional small element is probably a distal carpal, presumably the fourth. Another distal carpal may be in close association with the proximal end of metacarpal II, but that is not clear.

Traces of all five digits of the hand are present. Digit one is the most robust. The metacarpal, 6.5 mm long, is broader than the others, and its proximal end lies partly below the putative radiale. The distal end shows two distinct condyles, and the first phalanx of the digit, 4 mm long, is in close contact, and it too bears two distal condyles. Digit 2 is represented by a metacarpal

lacking its distal end, and a possible displaced first phalanx. Digits 3 and 4 are represented only by the metacarpals, and the remains of digit 5 are too poorly preserved to distinguish individual elements.

ADDITIONAL SPECIMENS

NMS (1966).43.4A, B

The specimen, preserved as part and counterpart, shows five sets of scutes and associated ribs. Vertebrae are present, deeper in the slab, but their condition is too poor for further preparation and study.

Eight scutes can be seen in dorsal view (Fig. 7A), five broad squarish elements in the midline, and at least three associated smaller, lateral scutes. The two anterior midline scutes are hard to make out in detail, but may be measured as 6 and 5 mm long, respectively. They measure 4 mm wide. The third scute is 5 mm long and 4 mm wide, the fourth and fifth 5 mm long and 5 mm wide. Beside the third, fourth, and fifth midline scutes are narrower lateral ones, each 5 mm long, but 2.5 or 3 mm wide. Each scute has a longitudinal flexure, or slight ridge, running down the middle, and there is a sculpture of small irregular pits.

In ventral view (Fig. 7B), the undersurfaces of midline scutes b, c, and d may be seen, somewhat concave from side to side, and with squared corners. The narrow structures to the right are probably pegs on the medial margins of the scutes. To the left of scute 'a' is an indication of a further scute (Fig. 7A).

The scutes match those of the type specimen of *Erpetosuchus granti* well in terms of shape and sculpture, the length of 5 mm corresponding to the mean vertebral length. Probably these scutes were in total 7–8 mm long, as in the type specimen, but they are arranged here in life position, and hence the anterior 2–3 mm is concealed by the next scute in front. These scutes are relatively wider, however, being roughly

square, so they may come from further dorsally than those in BMNH R3139, but not too far back since the ribs are still two-headed. It is possible that the larger scutes are the central row, and the smaller lateral ones could then represent the second lateral row of paramedian scutes indicated as beginning in the anterior dorsal region.

Broad, sweeping dorsal ribs may be seen on the right-hand side of the scute rows (Fig. 7A, B). The most anterior rib is complete, and 32 mm long. This rib, and the others, appear to have two-branched heads, the capitulum branching ventrally 4 mm before the termination of the tuberculum. In this case, it is likely that these are anterior dorsal ribs.

NMS (1992).37.1A, B

A third specimen of *Erpetosuchus* consists of a part of the cervical vertebral column with associated scutes, preserved in two larger and two smaller blocks. Based on comparisons with BMNH R3139, the first partial vertebra is the 3rd, so cervicals 3–8 are preserved in the block (Fig. 8). The centra are laterally constricted, and some 7 mm long. The zygapophyses are broad and set at an angle of about 20° above horizontal. The neural spine is tall, measuring 2 mm from back to front in cervicals 3–6, and 2.5 mm in cervicals 7 and 8. In dorsal view (Fig. 8B), the spine table is clear. It measures 5 mm from side to side in cervicals 7 and 8, and is essentially rectangular in shape, but with rounded corners, and it is somewhat concave in the centre. In posterior view (Fig. 8C), the extent of the spine table is clear, set on top of the narrow neural spine.

Two scutes are well preserved, and two in front of those are more obscure. The two well-preserved scutes, associated with cervicals 6 and 7, are 6 mm long and 5 mm wide, slightly larger than those in the cervical region in BMNH R3139, but corresponding to

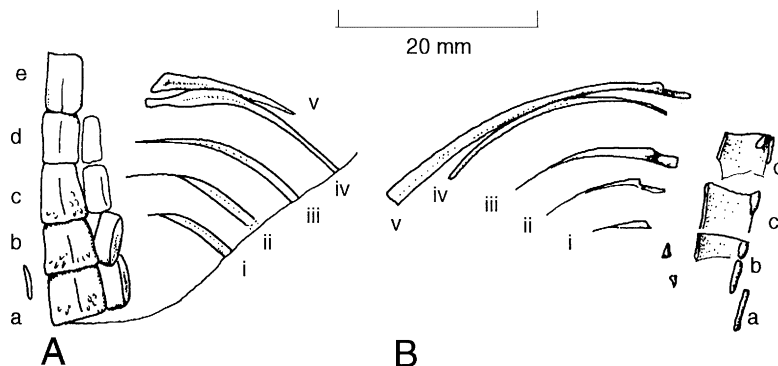


Figure 7. Section of the dorsal vertebral column of *Erpetosuchus granti* Newton (1894), and associated ribs and scutes (NMS 1966.4.3), in dorsal (A) and ventral (B) views. Scutes are lettered a–e, and ribs are numbered i–v for descriptive purposes.

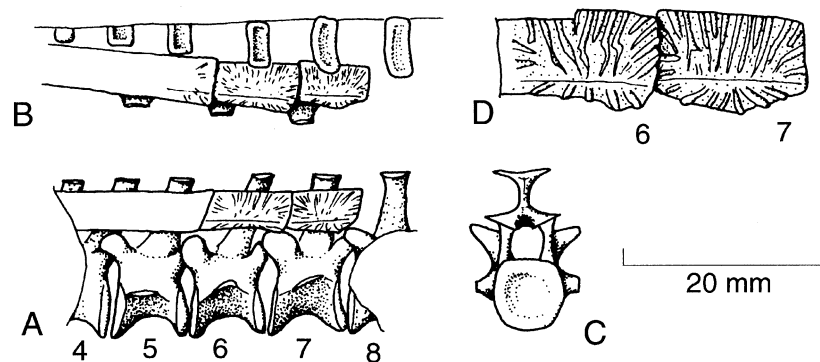


Figure 8. Short series of cervical vertebrae 4–8 of *Erpetosuchus granti* Newton (1894) (NMS 1992.37.1). (A, B) Cervical vertebrae 4–8, with associated scutes, in left lateral (A) and dorsal (B) views. In the latter, the spine tables are very clear. (C) Cervical vertebra 8 in posterior view. (D) Scutes 6 and 7 in enlarged view (cf. Figure 4C).

the slightly longer vertebrae in the present specimen. In detail (Figs 4B, 8D), these two scutes are much better preserved than those of the type specimen. They bear an off-centre low longitudinal ridge which divides the sculpture cleanly. Radiating low, rounded ridges and grooves extend laterally from the ridge, and these trend forwards and backwards in the anterior and posterior parts of the scute, respectively. The margins of the scute appear to be thin, forming in places scallops between the heavier ridges which project slightly.

Further obscure traces at the back of the blocks include some ribs and perhaps fragments of the pectoral girdle, but they are hard to cast adequately. On the larger block, the back of the (?) left lower jaw is also present.

The present specimen differs from BMNH R3139 in the lower and longer cervical vertebrae, the larger zygopophyses, the larger scutes, and the apparently more deeply etched sculpture on the scutes. These differences are ascribed to sexual dimorphism or individual variation in a specimen of *Erpetosuchus granti*.

BMNH R4807

The block with 16 small vertebrae has remained undescribed in the BMNH collections since it was donated in 1885. It is labelled ‘*Herpetosuchus*’, Broom’s (1906, 1913) misspelling of *Erpetosuchus*, but identity with that genus has never been assessed. Unfortunately, the sandstone in which this specimen is preserved is coarser than usual (quartz grains 0.5–1.0 mm across are abundant, and a 10-mm quartz pebble is also present), so preservation of detail is poor. There are no ribs or scutes, and only rather obscure traces of putative appendicular elements. The specimen is not illustrated here.

The vertebrae are in a straight line, but slightly disarticulated, with a space of 2–3 mm between adjacent elements. Some show distinctly amphicoelous termi-

nations of the centra. One vertebra at the beginning of the series indicates the antero-posterior orientation, and that the series consists of vertebrae exposing their left lateral, and partially ventral, aspects. This anteriormost vertebra has a centrum 7 mm long, with a broad transverse process, whose termination measures 4 mm anteroposteriorly, near the posterior margin of the neural arch. The neural spine and zygopophyses are obscure. If this vertebra is numbered 1 in the series, 4–6 also show traces of a similarly broad transverse process, as well as a deep ventral excavation of the centrum, and hints of a narrow, backwards-sloping neural spine. Vertebrae 2, 3 and 7–16 show little beyond the outline of the centrum. Centrum length diminishes from 7 mm in vertebrae 1–8 to 6 mm in vertebrae 9–11, and 5 mm in vertebrae 12–16.

The series of vertebrae could represent the proximal part of the tail of a reptile, presumably an archosaur, and possibly *Erpetosuchus*.

RECONSTRUCTION

The reconstruction of the anterior half of *Erpetosuchus* (Fig. 9) is based mainly on the type specimen, BMNH R3139. The skull and vertebral column back to vertebra 12 are preserved almost complete and in good association. The pectoral girdle and forelimb are based on a combination of evidence from the right and left elements which, although complete, are visible to different extents in the specimen and the casts. The ribs and scutes are based on evidence of isolated elements as described above. There are two rows of elongate paramedian scutes from the head backwards, one on each side of the midline, and a lateral, narrower row is shown beginning about vertebra 11.

The relatively slender pectoral girdle and forelimb suggest that *Erpetosuchus* may have been a facultative biped. Clearly, without the hindlimbs, it is impossible to be sure, but *Erpetosuchus* shows similar proportions

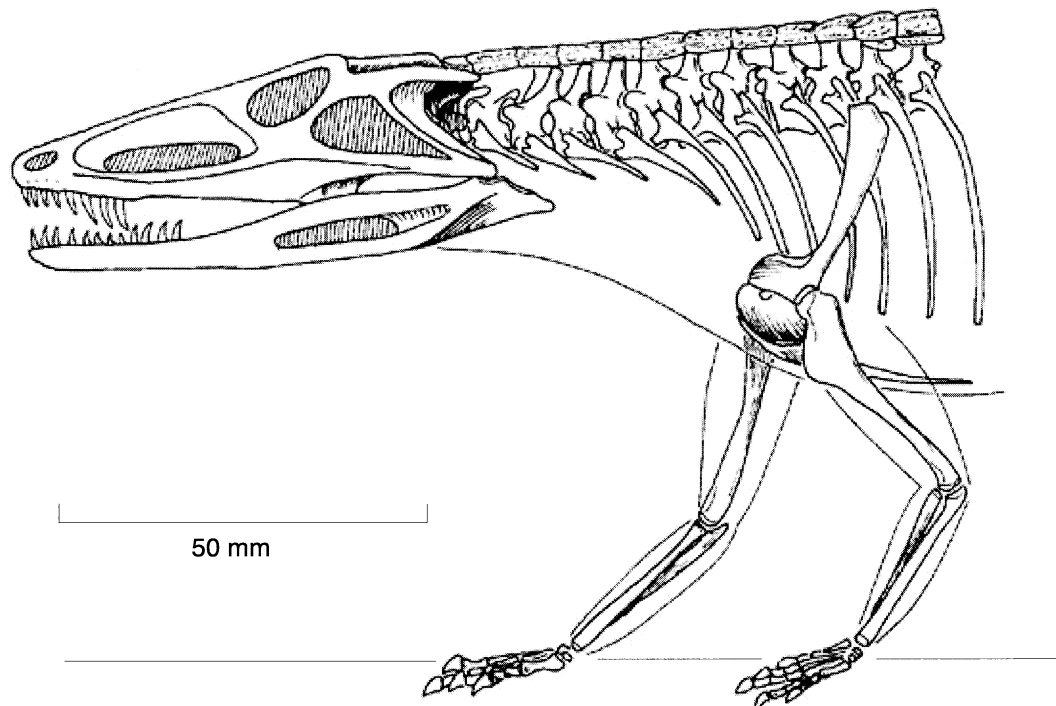


Figure 9. Restoration of the anterior part of the skeleton of *Erpetosuchus granti* Newton (1894), in left lateral view, based mainly on BMNH R3139.

of the skull, neck and forelimbs to the facultatively bipedal sphenosuchian crocodylomorph *Terrestri-suchus* (Crush, 1984), as well as to *Scleromochlus*, the dinosauromorphs *Lagerpeton* and *Marasuchus*, and basal dinosaurs (Serenó & Arcucci, 1994a,b; Benton, 1999). If *Erpetosuchus* were a cursor, it may not have used its forelimbs in running, since the radius is shorter than the humerus (in cursors, the distal limb element is often longer than the proximal (Hildebrand, 1974)).

The long slender recurved and pointed teeth confirm that *Erpetosuchus* was a carnivore, while its small size points to a diet of insects and other small prey. The concentration of teeth at the front of the mouth suggests that *Erpetosuchus* snatched at its prey, secured it as it struggled, and swallowed it whole, with no further oral processing. Sadly no invertebrates are preserved as fossils in the Elgin sediments, but cockroaches, bugs, beetles, grasshoppers, dragonflies, spiders, scorpions, millipedes, and many others existed in the northern hemisphere in the Late Triassic.

AFFINITIES

Previous ideas

Over the past century, *Erpetosuchus* has been ascribed many places in the phylogenetic tree of the archosaurs, although generally close to the crocodil-

ian clade. Newton (1894: 584–6) noted that the skull was similar to that of the Early Jurassic marine crocodylian *Teleosaurus*, especially in the long snout, the square skull table, and the locations and shapes of the various skull openings. However, he noted also that the palate of *Erpetosuchus* was distinctly uncrocodylian, especially in having only a short secondary palate, and that it closely resembled the palates of the aetosaur *Stagonolepis* and the phytosaur *Phytosaurus*. The vertebrae and forelimbs Newton thought were extremely crocodylian in appearance, while the pectoral girdle was much more like that of *Stagonolepis* and *Phytosaurus*. In the end, Newton (1894: 586) argued that *Erpetosuchus* was most closely allied to the phytosaurs, which, at that time, were still retained as a subdivision of Crocodylia by some authors.

Subsequent authors (e.g. Broom, 1906, 1913; Huene, 1911; 1936; 1956; Watson, 1917; Romer, 1956, 1966; Walker, 1961; Krebs, 1976) generally sustained this viewpoint, regarding *Erpetosuchus* as some kind of basal archosaur, allied either to the phytosaurs, the ornithosuchids, or the aetosaurs, and often implicated in the ancestry of crocodylians.

Walker (1968: 12, 13) actually argued that *Erpetosuchus* was a basal crocodylomorph, which he placed in a distinct Suborder Erpetosuchia, based on his assumption that the coracoid had an extended poste-

rior process and that there was a space between the forearm and the hand that might have been occupied by elongate carpals. Bonaparte (1982) followed this interpretation, placing *Erpetosuchidae* within *Crocodylomorpha*, as a family of *Sphenosuchia*. Later, Walker (1970: 367–8) indicated that he had been mistaken in assuming crocodylomorph characters of the coracoid and wrist, and he identified *Erpetosuchus* again as a pseudosuchian, meaning a derived basal archosaur, somewhere in the ill-defined group that gave rise in the Late Triassic to dinosaurs, pterosaurs, and crocodylians, perhaps equivalent to the basal part of the clade *Avesuchia* of Benton (1999). Krebs (1976: 87–90) followed this view. The crocodylian-like characters (low skull, long snout, broad square posterior skull roof, obliquely upwards-directed orbits, narrow frontal and parietal regions, deep otic notch with elongate oblique quadrate and quadratojugal running anterodorsally) were then interpreted simply as convergences.

Phylogenetic background

The broad outline of the phylogeny of the basal archosaurs is well established as a result of cladistic analysis (Benton, 1984, 1985, 1990, 1999, 2002; Gauthier, 1986; Benton & Clark, 1988; Sereno, 1991; Parrish, 1993; Juul, 1994; Gower & Wilkinson, 1996). The clade *Archosauria* consists of a number of basal branches below the major clade *Avesuchia* (= 'Archosauria' of Gauthier [1986], a crown-clade reassignment of the term previously applied to the more inclusive clade; we prefer to follow traditional usage of the term *Archosauria*, and Benton, [1999] introduced the term *Avesuchia* for the 'crown-clade *Archosauria*'). *Avesuchia* falls into two branches, the 'bird branch', *Avemotarsalia*, and the 'crocodylian branch', *Crurotarsi*. Note that the 'bird branch' of *Avesuchia* has generally been termed *Ornithosuchia* or *Ornithodira*, names introduced by Gauthier (1986). Gauthier & de Queiroz (2001) reject the term *Ornithosuchia*, explaining that it was named after *Ornithosuchus*, on the assumption that the latter was a basal member of the 'bird line'. Since the switch of *Ornithosuchus* definitively to the *Crurotarsi*, the term *Ornithosuchia* cannot be redefined in its original context. Gauthier & de Queiroz (2001) do not consider the term *Ornithodira*, but they reject its usage simply for the 'bird branch'. *Ornithodira* was given a phylogenetic nomenclature (PN) node-based definition, as consisting of *Pterosauria*, *Dinosauromorpha*, their most recent common ancestor and all descendants (Benton, 2002). A new term for the 'bird line', in some ways to replace *Ornithosuchia*, was introduced by Benton (1999), the *Avemotarsalia* (= 'bird feet'), with a stem-based PN definition as the clade consisting of all *avesuchians* closer to *Dinosauria* than to *Crocodylia*.

Within this accepted scheme, *Erpetosuchus* is clearly an archosaur (possession of antorbital fenestra; postfrontal reduced to half or less the size of the postorbital; possession of lateral mandibular fenestra). It is also a derived archosaur (possession of antorbital fossa; parietal foramen absent; postaxial intercentra absent; lateral processes of interclavicle reduced; scapula length more than twice its maximum width), an *avesuchian* (teeth on palatine and vomer absent), and a *crurotarsan* (possession of 'spine tables' on neural spines of dorsal vertebrae; scapulocoracoid notch at anterior junction of scapula and coracoid). *Erpetosuchus* lacks all apomorphies of *Avemotarsalia* and *Ornithodira*, and of subclades within *Ornithodira*. Hence, it is reasonable to restrict the cladistic analysis to *crurotarsans*.

Olsen *et al.* (2000) have already provided a preliminary cladistic analysis of the phylogenetic position of *Erpetosuchus*. Using a small subset of *crurotarsan* archosaurs, they found that *Erpetosuchus* was more derived in the crocodylomorph direction than *Stagonolepis*, *Gracilisuchus* and *Postosuchus*, but less derived than the basal crocodylomorph *Sphenosuchia* and the crocodylians *Protosuchus* and *Alligator*.

Olsen *et al.* (2000) coded *Erpetosuchus* for most of their 33 characters, but study of the type material has shown five errors in their codings. We note below where our codings, given first, differ from those of Olsen *et al.* (2000), which are noted in squared brackets:

Character 11: 0 [?]: there is a descending process of the squamosal anterior to the quadrate (Fig. 2A).

Character 13: 1 [0]: the quadratojugal extends anterodorsally, but does not contact the postorbital (Fig. 2A).

Character 14: 0 [?]: the quadrate does not contact the prootic, remaining laterally placed (Fig. 2A, B).

Character 24: 0 [?]: the basipterygoid processes of the basisphenoid are present.

Character 25: 0 [?]: it cannot be said whether the basipterygoid processes are simple and without a large cavity (0), or greatly expanded, with a large cavity (1).

On re-running the analysis using the data matrix in Olsen *et al.* (2000), we were able to retrieve their result, a single most parsimonious tree (MPT) showing the relationships as indicated earlier. Nine of their characters were uninformative (nos. 6, 7, 9, 22, 25, 26, 29, 31, 32), being either autapomorphies or constant throughout, so excluding those, and re-coding *Erpetosuchus* as indicated above, we re-ran the analysis. This yielded two MPTs of length 38, with a consistency index (CI) of 0.737, a Retention Index (RI) of 0.706, and a Rescaled consistency index (RC) of 0.520. The uncertainty concerned the placement of *Postosuchus*, whether as sister-group of *Gracilisuchus* or as sister-group of *Erpetosuchus* + *Crocodylomorpha*. Runs of 1000 bootstrap replicates for both analyses showed

Table 1. Character-taxon matrix showing the distribution of states of 56 characters (see Appendix) for 14 crurotarsan archosaurs. Character-state codings are: 0, plesiomorphic state; 1 and 2, apomorphic states; ?, unknown; N, inapplicable as a result of transformation. In the analyses, characters coded ‘?’ and ‘N’ are all treated as unknown. Codings for characters 1–33 for *Stagonolepis*, *Gracilisuchus*, *Postosuchus*, *Sphenosuchus*, *Protosuchus* and *Alligator* are taken from Olsen *et al.* (2000)

	10	20	30	40	50							
<i>Parasuchus</i>	00000	00000	00000	00000	00000	00000	00000	20000	00000	00000	00000	0
<i>Ornithosuchus</i>	01001	00000	00000	000??	??000	00000	00000	10020	00100	10100	01111	1
<i>Stagonolepis</i>	00000	00000	00000	00100	00000	00000	00000	22000	11100	10000	10101	0
<i>Ticinosuchus</i>	?????	?????	?????	?????	?????	??000	001??	?????	?????	??110	1000?	1
<i>Batrachotomus</i>	01111	00000	00?00	0000?	??000	00???	????11	11111	0000?	10???	?????	?
<i>Prestosuchus</i>	01?1?	?0000	00000	000??	??0??	??0?0	0011?	11111	00001	1011?	1000?	1
<i>Saurosuchus</i>	01101	?1000	00000	000?0	00000	00??0	00?11	10111	01001	10???	10001	1
<i>Fasolasuchus</i>	01???	?????	?????	?????	?????	00??0	00?01	1?0??	?????	??0??	?????1	1
<i>Gracilisuchus</i>	?1?10	??000	01001	000??	??0??	000?0	0?100	10000	11100	110??	00???	0
<i>Postosuchus</i>	01000	??000	1?100	11000	00000	00000	0??10	10011	00000	11010	01111	0
<i>Erpetosuchus</i>	0110?	??100	01002	011??	??0??	000??	?0100	00020	01010	11??0	?????	1
<i>Sphenosuchus</i>	00111	01111	11012	11111	11001	011??	???00	20000	00010	11011	01111	0
<i>Protosuchus</i>	11111	0?101	10112	10121	2211?	012?1	01100	20000	00010	11011	01111	0
<i>Alligator</i>	1?1?1	10101	10112	10121	2011?	00201	00000	2?00?	00010	11011	01111	0

that the positions of *Sphenosuchus*, *Protosuchus* and *Alligator* were robust, yielding values of 88–95%. The placements of *Postosuchus* and *Erpetosuchus* were less certain, being supported in 59–76% of bootstrap replicates.

Cladistic analysis

In a more comprehensive cladistic analysis of the phylogenetic position of *Erpetosuchus*, the seven taxa and 33 characters of Olsen *et al.* (2000) are re-used. Their codings are accepted, except for *Erpetosuchus* which was re-coded as described above. In addition, one of their characters (no. 13) was re-coded so that the outgroup taxon was coded ‘0’. Additional taxa were added, as follows (with mention of the main references used): the phytosaur *Parasuchus* (Chatterjee, 1978), the ornithosuchid *Ornithosuchus* (Walker, 1964; Bonaparte, 1972), the rauisuchians *Ticinosuchus* (Krebs, 1965), *Batrachotomus* (Gower, 1999), *Prestosuchus* (Huene, 1942; Barberena, 1978), *Saurosuchus* (Sill, 1974; Alcober, 2000) and *Fasolasuchus* (Bonaparte, 1981). Additional codings for the new characters were obtained as follows: *Stagonolepis* (Walker, 1961), *Gracilisuchus* (Romer, 1972; Brinkman, 1981), *Postosuchus* (Chatterjee, 1985; Long & Murry, 1995), *Sphenosuchus* (Walker, 1990; Clark *et al.*, 2000), *Protosuchus* (Colbert & Mook, 1951), *Alligator* (Iordansky, 1973), and from specimens. In all cases, the genus represents the family or larger clade.

The 23 additional characters, numbered 34–56, are listed in Appendix 1. These characters are derived from

a larger database used in Benton (2002). Some are original, but most are based on characters introduced in earlier studies by Gauthier (1986), Benton & Clark (1988), Sereno (1991), Parrish (1993), Juul (1994), Benton (1999), Gower (1999, 2000), and Alcober (2000), which vary among various crurotarsans, and might be helpful in distinguishing clades. The problems in achieving this, especially in differentiating the various ‘rauisuchians’ and *Postosuchus*, and in finding the place of ornithosuchids and *Gracilisuchus* with respect to each other and to phytosaurs and stagonolepidids, are notoriously difficult (Benton & Clark, 1988; Sereno, 1991; Parrish, 1993; Juul, 1994; Gower, 1999, 2000).

The data matrix (Table 1) lists codings so far as they could be determined for all 56 characters across 14 taxa. This was run on PAUP 4.0b8 (Swofford, 2000), with a branch and bound search (characters treated as unordered; characters unweighted; outgroup defined as *Parasuchus*; rooted on outgroup). Ten characters were uninformative, and these were excluded (nos. 6, 9, 22, 25, 29, 32, 46, 55 were autapomorphies; 26 and 31 were invariant in all taxa sampled). A permutation tail probability (PTP) test indicated, with high confidence ($P = 0.01$), that the null hypothesis that the data contain no phylogenetic signal could be rejected.

From the first run, involving all 14 taxa, 82 most parsimonious trees (MPTs) were obtained (tree length, 86; CI, 0.616; RI, 0.703, RC, 0.433). Much of the variation among the 82 MPTs concerned the positions of *Ticinosuchus* and *Fasolasuchus*, which were then excluded from re-runs of the analysis. Both are coded for relatively few characters, and those that can

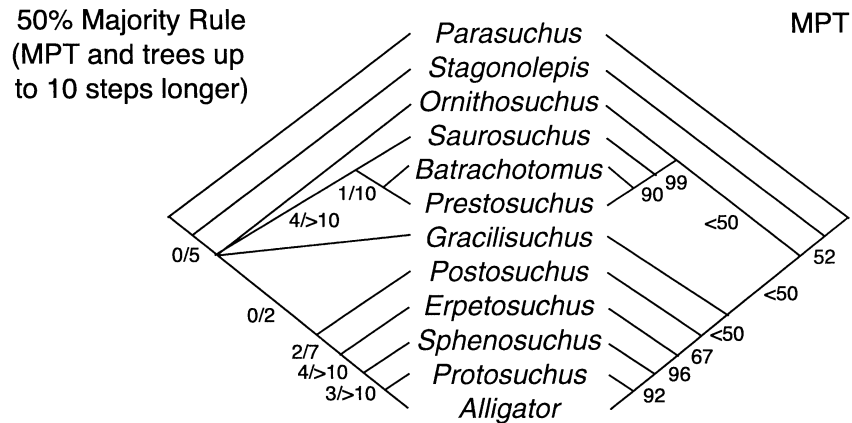


Figure 10. Cladograms showing putative relationships of *Erpetosuchus*, showing the most parsimonious tree (MPT), with bootstrap measures for each node (10 000 replicates) on the right, and 50% majority-rule tree, based on the MPT and trees up to 10 steps longer, with Bremer support values from the strict/50% majority-rule consensus trees indicated at each node.

be coded are essentially identical to *Batrachotomus*, *Saurosuchus*, and *Prestosuchus*.

This reduced data matrix, consisting of 12 taxa, yielded one MPT (length, 85, CI, 0.624; RI, 0.692; RC, 0.432; Fig. 10, Appendix 2). Bootstrap assessment (10 000 replicates) confirmed this tree. The pairing of *Protosuchus* and *Alligator* (Crocodylia) was present in 92% of replicates, *Sphenosuchus* + Crocodylia (Crocodylomorpha) in 96% of replicates, and *Erpetosuchus* + Crocodylomorpha in 67% of replicates. Among the rauisuchians, *Batrachotomus* and *Prestosuchus* are paired in 90% of replicates, and *Saurosuchus* + those two (Rauisuchia) in 99% of replicates. The positions of *Ornithosuchus*, *Gracilisuchus*, and *Postosuchus* cannot be determined with certainty, being associated variously with Rauisuchia or with *Erpetosuchus* + Crocodylomorpha. *Stagonolepis* is confirmed as outgroup to the taxa already named, but only weakly (52% of bootstrap replicates).

Decay analysis was performed in PAUP by saving trees longer than the MPTs step-by-step, and by calculating strict and 50% majority rule consensus trees. The decay index according to each method indicates the robustness of nodes, low values corresponding to poorly supported nodes, high values to robust nodes. The decay indices from the strict consensus tree agree with the bootstrap values (Fig. 10), that the basal position of *Stagonolepis* is weakly supported, as is the outgroup relationship of *Postosuchus* and *Gracilisuchus* to the (*Erpetosuchus* + Crocodylomorpha) clade, and *Ornithosuchus* to the Rauisuchia.

Discussion of cladistic analysis

The present cladistic analysis, like so many others of the Crurotarsi and Suchia, is far from adequately

convincing. Much more detailed anatomical work is required on the various 'rauisuchians' and the basal crocodylomorphs. Many key taxa, including *Erpetosuchus*, are woefully incomplete, and hence hard to characterize adequately. As a result, the present analysis is plagued by low decay indices and low bootstrap values, indicating that many parts of the tree are not robustly supported, and could well be modified by new finds and new anatomical study.

The present result is consistent with some earlier findings, but not others. For example, the close linkage of *Erpetosuchus* to the Crocodylomorpha (Olsen *et al.*, 2000) is confirmed, an observation that has long been proposed in one form or another (Newton, 1894; Walker, 1961, 1968). The clade consisting of *Erpetosuchus* and Crocodylomorpha is marked by a striking apomorphy, the anteriorly sloping quadrate and quadratojugal that form a deep embayment behind the lower temporal fossa and below the squamosal. In Crocodylomorpha, this otic recess becomes deeper, as the quadrate and quadratojugal together slope anteromedially as well as anterodorsally. The low bootstrap value for the clade (67%), however, precludes giving it a name.

In relation to this cladistic analysis, it is appropriate that the Crocodylomorpha, consisting of crocodylians and their closest relatives, be given a stem-based phylogenetic definition, using *Ornithosuchus*, *Erpetosuchus* and Eusuchia (living crocodylians and their fossil relatives) as specifiers. Two outgroup specifiers are selected since the cladistic relationships of nearest outgroups to Crocodylomorpha are unresolved, but also to clarify that *Erpetosuchus* is excluded from Crocodylomorpha. A stem-based diagnosis is necessary, because there are a number of basal forms (e.g. *Triolestes*, *Pseudhesperosuchus*, *Saltoposuchus*) that are

very close to the origin of the clade, but are incompletely known, and new finds and studies might alter our understanding of the cladogram.

Crocodylomorpha Walker (1968) consists of all archosaurs closer to Eusuchia than to *Erpetosuchus* or *Ornithosuchus*.

There is no unequivocal evidence here that *Postosuchus* is closer to Crocodylomorpha than to Rausuchia, as suggested by Benton & Clark (1988), Benton (1990), Parrish (1993), and Olsen *et al.* (2000). *Postosuchus* shares a number of possible synapomorphies of the skull with crocodylomorphs, but shares others with rausuchians, leaving this issue still unresolved (Parrish, 1993; Benton, 1999; Gower, 2000). Rausuchia, at least, does stand apart as a well-defined clade, although the precise arrangement of taxa within the clade found here differs from previous suggestions (Parrish, 1993; Gower, 2000).

Ornithosuchus and the ornithosuchids have had a chequered phylogenetic history, and the current analysis fails to resolve their proper location. Ornithosuchids have been classified as theropod dinosaurs (Walker, 1964), as basal archosaurs close to *Scleromochlus* and the sphenosuchid crocodylomorphs (Bonaparte, 1972, 1975), as outgroup to the Avemetatarsalia on the dinosaurian and avian branch of evolution (Gauthier, 1986; Benton & Clark, 1988; Benton, 1990), and finally as crurotarsans, definitively on the line to crocodilians (Serenó, 1991). This latter view has been accepted by most since 1991, but the position of ornithosuchids within Crurotarsi has been disputed: Parrish (1993) placed Ornithosuchidae basal to all other crurotarsans (the Crocodylotarsi), while Juul (1994) found Ornithosuchidae were outgroup to the clade (Crocodylomorpha + *Gracilisuchus* + *Postosuchus*), and Benton (1999) tentatively found that Ornithosuchidae were sister group to Rausuchia + *Postosuchus*, the situation found here also.

Gracilisuchus has also had a somewhat chequered phylogenetic history, having been identified as a basal ornithosuchid by Romer (1972), a view followed by Bonaparte (1975). Brinkman (1981) could not accept this, arguing that *Gracilisuchus* showed resemblances to some basal crocodylomorphs. Benton & Clark (1988) found that *Gracilisuchus* was second most basal member of the Crocodylotarsi, lying between Parasuchia below and Stagonolepididae above. Parrish (1993) found that *Gracilisuchus* was sister group to a clade consisting of Popsauridae + Crocodylomorpha. Juul (1994) made *Gracilisuchus* the sister group of *Postosuchus*, while Gower & Wilkinson's (1996) consensus presented an unresolved trichotomy among Crocodylomorpha, *Postosuchus* and *Gracilisuchus*. Results in the current analysis are equivocal, with *Gracilisuchus* being either outgroup to the clade consisting of *Postosuchus* + *Erpetosuchus* + Crocodylomor-

pha, or part of an unresolved polytomy with those taxa (Fig. 10).

Stagonolepis, representing the stagonolepidids (or aetosaurs), is found here to be basal to the other taxa included in the analysis, although support is weak (Fig. 10). Previous cladistic analyses tended to confirm this view, with aetosaurs forming part of the Crurotarsi, lying between Parasuchia below and the Rausuchia + Crocodylomorpha above (Gauthier, 1986; Benton & Clark, 1988; Benton, 1990, 1999; Gower & Wilkinson, 1996). Parrish (1993), however, placed the aetosaurs as sister group to the clade (Rausuchidae + Popsauridae + Crocodylomorpha), but more derived than Prestosuchidae, which other analysts have found to form part of a larger Rausuchia (Gower & Wilkinson, 1996; Alcober, 2000; Gower, 2000). Juul (1994) actually paired Stagonolepididae with Prestosuchidae. Walker (1961: 183–185), following a suggestion of Huene (1920), noted strong similarities between the aetosaurs and the erpetosuchids. He was partly misled since he included in the Family Erpetosuchidae the forms *Dyoplax* and *Stegomus*, which were later assigned to Crocodylomorpha (see below).

The phytosaurs, termed variously Phytosauridae or Parasuchia, are the outgroup taxon here, following the findings of virtually all cladistic analyses of Crurotarsi to date (e.g. Gauthier, 1986; Benton & Clark, 1988; Benton, 1990, 1999; Sereno, 1991; Juul, 1994; Gower & Wilkinson, 1996). Parrish (1993) placed the Parasuchia higher in the cladogram than the Ornithosuchidae, but his result has not been confirmed.

Other erpetosuchids

Walker (1970: 368) and Krebs (1976: 87–90) included the poorly represented form *Parringtonia gracilis* from the Manda Formation (Anisian) of Tanzania in the Family Erpetosuchidae, based on the joint possession of an extremely slim, forwards-curved scapula. The maxillary fragment and the vertebrae are not inconsistent with this assignment, but the evidence is too slender for clear determination of *Parringtonia*. Certainly, the African taxon (BMNH R8646) shows some general resemblances to *Erpetosuchus*: it is of similar size, there appear to be only five teeth on the maxilla (but only the anterior part is preserved, so this cannot be asserted confidently), the scapula is broadly similar in general shape, and the scutes are comparable in shape and sculpture. However, these characters could all *Parringtonia* with any number of other small archosaurs (it is an archosaur at least, as indicated by the deeply recessed anterior margin of the antorbital fenestra on the maxillary fragment), and it does not display any of the six apomorphies of *Erpetosuchus* noted earlier.

In addition, Walker (1961: 183–5; 1970: 368) included *Dyoplax* from the Schilfsandstein (Carnian,

southern Germany) in the *Erpetosuchidae*, but this taxon has been reassigned to the *Sphenosuchia*, as a genuine basal crocodylomorph (Lucas *et al.*, 1998), a view questioned by Clark *et al.* (2000). Walker (1961: 183–5) also included *Stegomus longipes* (= *Stegomusuchus*), an Early Jurassic form from the Portland Formation (Hettangian-Sinemurian, Connecticut Valley, USA), in his *Erpetosuchidae*, but he later (Walker, 1968, 1970) realized it was a protosuchid crocodylian.

A second occurrence of the genus *Erpetosuchus* has been reported (Olsen *et al.*, 2000) from the New Haven Formation (?early to mid Norian) of Connecticut, USA. The specimen (AMNH 29300) is a partial skull and mandible associated with poorly preserved vertebrae. Similarities to *Erpetosuchus granti* are the generally long and low skull, its small size (length, 65–70 mm), the outline shapes of the lower margin of the antorbital fenestra, the deep fossa around the lower margin of the antorbital fenestra, the triangular shape of the lower temporal fenestra associated with a forwards-sloping quadrate/quadratojugal process, the disposition and shape of the maxillary teeth, the overall shape of the mandible, and the long sausage-shaped mandibular fenestra. In addition, and more significantly, the American specimen shares all six diagnostic characters of *Erpetosuchus* noted earlier. Differences from the Scottish specimen are the indications of five or six maxillary teeth, not four, the more gently rounded lower margin of the orbit, and the relatively smaller antorbital fenestra. These might indicate no more than specific or individual variations.

CONCLUSIONS

1. *Erpetosuchus granti* Newton (1894), a small archosaur reptile from the Lossiemouth Sandstone Formation (late Carnian, Late Triassic) of Scotland, is redescribed. The type specimen represents only the front end of the body; a complete skull, cervical vertebral column, anterior dorsals and ribs, shoulder girdle, and forelimb. The type material has been restudied, based on the natural rock mould, the gutta percha casts made by Newton in the 1890 s, and new PVC casts. Three additional specimens have also been described.
2. *Erpetosuchus* shows a number of autapomorphies of the skull: a reduced row of only 4–5 teeth on the anterior part of the maxilla, a large antorbital fenestra set in a deep fossa whose margins are marked by distinct sharply angled ridges, a jugal that is divided into a lateral and a ventral portion by a sharp ridge, a deeply recessed tympanic area formed by the quadrate and quadratojugal running up and forward but not medially, the angular and surangular marked by a strong ridge running

back from the ventral margin of the mandibular fenestra, and teeth oval in cross-section and lacking anterior and posterior carinae and marginal serrations.

3. The remains suggest that *Erpetosuchus* was a light, cursorial animal that fed on small prey, perhaps insects.
4. A cladistic analysis of crurotarsan archosaurs indicates that *Erpetosuchus* is the closest sister group of Crocodylomorpha among known basal archosaurs. It shares with them a deep recess in the cheek region framed by the quadrate and quadratojugal which slope forward side-by-side at an angle of 45° above horizontal, and reach the upper margin of the lower temporal fossa. In *Erpetosuchus* the recess is entirely lateral, while in crocodylomorphs, the recess penetrates medially as well, since the quadrate/quadratojugal bars meets the sidewall of the braincase.

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34. Slit-like subnarial fenestra between premaxilla and maxilla, above and behind the maxillary-premaxillary kinetic joint: absent (0), present (1) (Benton & Clark, 1988; Juul, 1994; Alcober, 2000).
35. Maxillary-premaxillary kinetic joint, with a peg on the maxilla fitting into a socket on the premaxilla, lying below the subnarial fenestra: absent (0), present (1) (Parrish, 1993; Gower, 1999; Alcober, 2000).
36. Nares separated by: posterior processes of premaxillae (0), processes of premaxillae and nasals (1), anterior processes of nasals (2).
37. Naris shorter than (0), equal to (1), or longer than (2) antorbital fenestra.
38. Antorbital fenestra shape: elliptical or circular (0), triangular, and with elongate narrow anterior point (Benton & Clark, 1988; Alcober, 2000).
39. Orbit shape: circular or elliptical (0), tall and narrow (the 'keyhole-shaped orbit'; maximum width is less than half the maximum height) (1), or with distinct ventral point surrounded by V-shaped dorsal processes of jugal (2) (Benton & Clark, 1988; Parrish, 1993; Gower, 2000).
40. Postorbital/jugal bar behind orbit: curved or straight (0), 'stepped', with distinct anterior projection (1) (Benton & Clark, 1988; Juul, 1994; Alcober, 2000).
41. Lower temporal fenestra size: equal to, or larger than (0), or smaller than (1) upper temporal fenestra (modif. Benton & Clark, 1988).
42. Lower temporal fenestra shape: elliptical (0), triangular (1) (modif. Benton & Clark, 1988).
43. Squamosal ventral process and quadratojugal dorsal process slope forward to form a distinct triangular projection into the lower temporal fenestra: absent (0), present (1).
44. Quadrate and quadratojugal orientation: roughly vertical, and do not reach the upper margin of the lower temporal fenestra (0), run side-by-side and slope forward at an angle of 45° above horizontal, or less, reaching the upper margin of the lower temporal fenestra (1).
45. Separate anterior process on ventral ramus of squamosal, projecting into lower temporal fenestra: absent (0), present (1) (Alcober, 2000).
46. Parietal foramen: present (0), absent (1).
47. Quadrate foramen: present (0), absent (1).
48. Accessory laminar rectangular process on anterior face of neural spine of mid-caudal vertebrae: absent (0), present (1) (Benton & Clark, 1988; Sereno, 1991; Juul, 1994).
49. Clavicle: present (0), rudimentary or absent (1) (Gauthier, 1986).
50. Proximal carpals (radiale, ulnare): equidimensional (0), elongate (1).
51. Acetabulum: mainly laterally orientated (0), mainly ventrally deflected (1) (Benton & Clark, 1988).
52. Acetabulum: imperforate (0), semiperforated (1), extensively perforated (2) (Gauthier, 1986).

APPENDIX 1

Characters used in the analysis of relationships of *Erpetosuchus* among crurotarsans. Characters 1–33 are as listed in Olsen *et al.* (2000). Additional characters are derived from analyses in Benton (1999, 2002), with sources as cited individually.

34. Slit-like subnarial fenestra between premaxilla and maxilla, above and behind the maxillary-premaxillary kinetic joint: absent (0), present (1) (Benton & Clark, 1988; Juul, 1994; Alcober, 2000).

53. Pubis: shorter (0) or longer (1) than ischium.
 54. Pubis length: less (0) or more (1) than three times width of acetabulum (Serenó, 1991).
 55. Pubic acetabular margin, posterior portion: continuous with anterior portion (0), recessed (1) (Serenó, 1991).
 56. Osteoderm sculpture: present (0), absent (1) (Parrish, 1993).

APPENDIX 2

Characters diagnosing the clades in the cladogram shown in Figure 10. The apomorphic condition (1) is normally not indicated, but for multistate characters (numbers 15, 19, 21, 22, 28, and 36), the derived condition (1, 2) is shown. Character state reversals are indicated by a minus sign. Equivocal character placements are indicated with an asterisk (*) at each possible node. The verbal clade diagnoses include only the unequivocal characters.

Stagonolepis + *Ornithosuchus* + *Rauisuchia* + *Gracilisuchus* + *Postosuchus* + *Erpetosuchus* + *Crocodylomorpha*: 43, 46, 53, 55

Squamosal ventral process and quadratojugal dorsal process slope forward to form a distinct triangular projection into the lower temporal fenestra; parietal foramen absent; pubis longer than ischium; posterior portion of pubic acetabular margin recessed.

Ornithosuchus + *Rauisuchia* + *Gracilisuchus* + *Postosuchus* + *Erpetosuchus* + *Crocodylomorpha*: 2, 33, 36(1), 49, 54

Facial portion of maxilla anterior to anterior edge of antorbital fenestra shorter than posterior portion to anterior edge of fenestra; paramedian dorsal osteoderms with distinct longitudinal bend near lateral edge; nares separated by processes of premaxillae and nasals; clavicle rudimentary or absent; pubis more than three times width of acetabulum.

Ornithosuchus + *Rauisuchia*: 5*, 39(1)*, 48, 56*

Accessory laminar rectangular process on anterior face of neural spine of mid-caudal vertebrae.

Rauisuchia: 3*, 34*, 35, 38, 40*, -43*, 45, 51*, -53, -54.

Maxillary-premaxillary kinetic joint, with a peg on the maxilla fitting into a socket on the premaxilla, lying below the subnarial fenestra; antorbital fenestra triangular, and with elongate narrow anterior point; separate anterior process on ventral ramus of squamosal, projecting into lower temporal fenestra; pubis shorter than ischium (reversal); pubis less than three times width of acetabulum (reversal).

Batrachotomus + *Prestosuchus*: 4*, 37(1)

Naris equal in length to antorbital fenestra.

Gracilisuchus + *Postosuchus* + *Erpetosuchus* + *Crocodylomorpha*: 12, 47

Squamosal with ridge on dorsal surface along edge of upper temporal fenestra; quadrate foramen absent.

Postosuchus + *Erpetosuchus* + *Crocodylomorpha*: 11, 16, 17, -43*, 52*

Descending process of squamosal anterior to quadrate absent; posteroventral edge of parietals extends less than half the width of occiput; medial extent of upper temporal fenestra on lateral surface of parietal separated in midline by 'sagittal crest'.

Bathytotica (*Erpetosuchus* + *Crocodylomorpha*): 3*, 5*, 8, 15(2), 18*, 19(1)*, 20*, 21(1)*, 30*, -36, 44

Postfrontal absent; interparietal suture absent; nares separated by posterior processes of premaxillae (reversal); quadrate and quadratojugal side-by-side slope forward at an angle of 45° above horizontal, or less, reaching the upper margin of the lower temporal fenestra.

Crocodylomorpha: 5*, 10, 14, 19(1)*, 20*, 21(1)*, 27, 28(1), 30*, 50

Squamosal with broad lateral expansion overhanging lateral temporal region; quadrate contacts prootic; articular with dorsomedial projection; coracoid with elongate postcoracoid process; proximal carpals elongate.

Crocodylia (*Protosuchus* + *Alligator*): 1, -12, 13*, -17, 19(2), 21(2), 23, 24, 28(2), 30*, 36(2)

Dorsal process of premaxilla vertical and strongly sutured to maxilla; squamosal without ridge on dorsal surface along edge of upper temporal fenestra; medial extent of upper temporal fenestra on lateral surface of parietal separated in midline by broad flat area (reversal); exoccipitals contact each other below supraoccipital; depression for mastoid antrum enters into prootic and connects with opposite through supraoccipital; paroccipital process narrower dorsoventrally with only slightly expanded distal end; basiptyergoid processes of basisphenoid absent; coracoid with elongate ventromedial process expanded ventrally; nares separated by anterior processes of nasals.

Stagonolepis [*Stagonolepididae*]: 18*, 37(2), 41*, 42*, 51*

Naris longer than antorbital fenestra.

Ornithosuchus [*Ornithosuchidae*]: -33*, 39(2)*, -49, 52*

Clavicle present (reversal).

Saurosuchus: 7*, 42*

Gracilisuchus: 4*, 15(1), 41*, 42*

Interparietal suture partially obliterated.

Postosuchus: 13*, 34*, 39(1)*, 40*

Erpetosuchus: -11, -16, 39(2)*, 42*, 56*

Descending process of squamosal anterior to quadrate present (reversal); posteroventral edge of parietals extends more than half the width of occiput (reversal).

Sphenosuchus: -2, 7*

Facial portion of maxilla anterior to anterior edge of antorbital fenestra equal in length to, or longer

than, portion posterior to anterior edge of fenestra (reversal).

Alligator: -27, -33*

Articular without dorsomedial projection posterior to the glenoid fossa (reversal).