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A new theropod dinosaur from the Early Jurassic of South Africa and its implications for the early evolution of theropods

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A new theropod, *Dracovenator regenti*, from the upper Elliot Formation is described, based upon a fragmentary skull. It can be diagnosed on the basis of a bilobed fossa on the lateral surface of the premaxilla that is connected to the alveolar margin by a narrow channel, the presence of a deep, oblique, lateral notch on the articular and hypertrophied dorsal processes on the articular. Other aspects of its morphology display a mosaic of coelophysoid and advanced theropod characteristics. A cladistic analysis of basal Theropoda, including the new taxon finds that the new taxon is closely related to *Dilophosaurus wetherilli* and *Zupaysaurus rougieri* although the clade formed by these three taxa is not robustly supported. It also finds that Coelophysoidea *sensu lato* is paraphyletic with respect to Ceratosauria + Tetanurae but that this topology is not a significantly better explanation of the data than an inclusive, monophyletic Coelophysoidea.

Keywords: Theropoda, Coelophysoidea, *Dracovenator,* upper Elliot Formation, South Africa.

INTRODUCTION

Prior to Gauthier's classic (1986) monograph, our understanding of the interrelationships of theropod dinosaurs could be described as murky at best. Most works still adhered to the old notion of a coelurosaur versus carnosaur dichotomy that separated small gracile forms from the larger, more robust, taxa. Nevertheless many had expressed doubts as to the 'naturalness' (monophyly in modern parlance) of these groupings. Gauthier established a basal dichotomy in Theropoda that cut across the big versus small division. The two branches were the Ceratosauria and the Tetanurae. Gauthier's Ceratosauria included the former carnosaur *Ceratosaurus nasicornis* and the small, gracile coelophysoids, while the Tetanurae, included the true carnosaurs and the true coelurosaurs. The monophyly of the Tetanurae as constituted by Gauthier has never been seriously questioned since and it is supported by a number of synapomorphies of the cranial and postcranial anatomy, although the exact node at which these synapomorphies fall on varies between analyses, depending on the basal topology of the Tetanurae and which basal tetanuran taxa are included (Holtz 1994; 2000; Sereno *et al.* 1994, 1996, 1998; Rauhut 2003). The monophyly of Gauthier's Ceratosauria has not been so widely accepted, with suggestions that the larger *C. nasicornis* and its close relatives, the newly recognized Abelisauroidea, share a more recent common ancestor with tetanurans than they do with coelophysoids (Bakker 1986; Forster 1999). However, the closer relationship of *C. nasicornis* to Coelophysoidea than to Tetanurae continued to find support form phylogenetic analyses through the 1990s and into the early years of the new millennium. Several recent analyses that have incorporated substantial amounts of new information have overturned these results (Carrano *et al.* 2002, Rauhut 2003, Sereno *et al.* 2004). It is now the majority view amongst theropod systematists that Ceratosauria contains *Ceratosaurus* spp. and Abelisauroidea and that this clade is more closely related to Tetanurae than it is to Coelophysoidea although Tykoski & Rowe (2004) continue to support the inclusion of Coelophysoidea within Ceratosauria.

The break-up of Ceratosauria is carried further in Rauhut's (2003) comprehensive study of early theropod relationships. He found that, despite a relatively distinctive morphology, the monophyly of the broader coelophysoid assemblage (*Dilophosaurus wetherilli*, *Liliensternus* spp. and Coelophysidae) was questionable. In particular *Dilophosaurus wetherilli* was found to share a number of derived characteristics with Ceratosauria and Tetanurae not present in other coelophysoids. Nevertheless the position of *D. wetherilli* was unstable and depended upon the inclusion of the enigmatic taxon *Shuvosaurus inexpectatus* which may or may not be a dinosaur (Long & Murry 1995). When *S. inexpectatus* was included *Dilophosaurus wetherilli* formed a clade with Ceratosauria + Tetanurae but when *Shuvosaurus inexpectatus* was excluded it became equally as parsimonious for *Dilophosaurus wetherilli* to be included within Coelophysoidea as for it to form a clade with Ceratosauria + Tetanurae. Other analyses have continued to support the inclusion of *D. wetherilli* within Coelophysoidea (Sereno *et al.* 2004; M.T. Carrano, pers. comm.) but the support for this clade is very weak (M.T. Carrano, pers. comm.). If *D. wetherilli* really does share a more recent common ancestor with Ceratosauria + Tetanurae then it would imply that its coelophysoid-like characteristics such as its elongate and acutely pointed premaxilla, subnarial gap, elongate skull, expanded dentary tip and possibly tall, paired naso-lacrimal crests on the snout were symplesiomorphies of basal Theropoda. In other words, theropods might have passed through a 'coelophysoid'

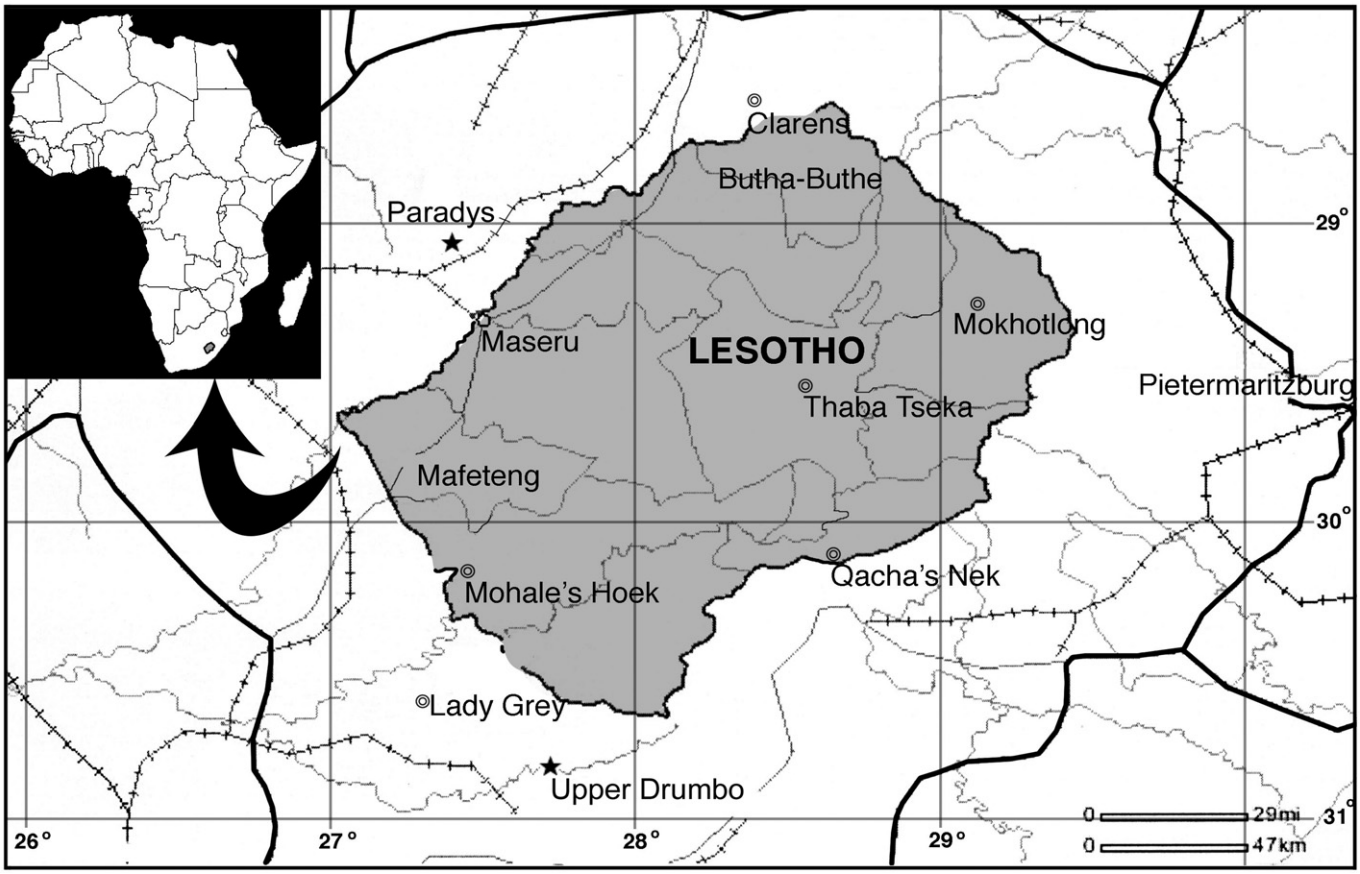


Figure 1. Locality Map for the farms Upper Drumbo and Paradys.

stage in their early evolution. In this respect, the recently described *Zupaysaurus rougieri* from the Late Triassic of Argentina is particularly interesting (Arcucci & Coria 2003). Described as the oldest tetanuran, it shares many characteristics with coelophysoids (most noticeably *Dilophosaurus*-like paired naso-lacrimal crests) as well as sharing some derived characters with ceratosaurian and tetanuran theropods. *Z. rougieri* might add further support to the hypothesis that the broader coelophysoid assemblage is a paraphyletic grade at the base of Neotheropoda. '*Dilophosaurus*' *sinensis* is yet another taxon that might support this hypothesis (Hu 1993), as it has a number of tetanuran-like characters (Lamanna *et al.* 1998) but it has not yet received an adequate description that allows its phylogenetic position to be accurately assessed.

Here I describe a new taxon of medium-sized (estimated skull length of 500 mm) theropod from the Early Jurassic of South Africa that also displays a mosaic of characteristics.

MATERIAL

J.W. Kitching found the holotype in a sandstone bed in the upper Elliot Formation (*Massospondylus* Range-Zone, Kitching & Raath 1984) on the farm Upper Drumbo in the Barkly East district of Eastern Cape, South Africa (Fig. 1). It consists of a fragmentary, disarticulated skull including both premaxillae, the posterior section of the right maxilla, fragments of the right and left dentary, the right angular, a partial right prearticular, the posterior end of the right mandibular ramus (in two pieces) and numerous unidentified fragments of bone.

A theropod snout (BP/1/5278), also from the upper Elliot Formation (farm Paradys, Ladybrand District, Free State), was described as a South African specimen of *Coelophysis* (= *Syntarsus* Raath) *rhodesiensis* (Munyikwa & Raath 1999) but it might represent a juvenile specimen of the new taxon.

The upper Elliot Formation is Early Jurassic in age but, like most intercontinental deposits of this age, finer resolution than this has proved difficult. It may lie anywhere between the Hettangian and the Toarcian, though a date closer to the younger end of this range is preferred here for reasons given in Yates *et al.* (2004).

SYSTEMATIC PALAEONTOLOGY

Theropoda Marsh, 1881
Neotheropoda Bakker, 1986, *sensu* Sereno 1998

***Dracovenator regenti* gen. et sp. nov.**

Etymology. Draco, dragon (Latin); *venator,* hunter (Latin), refers to both its probable habit of preying on prosauropod dinosaurs and its location in the foothills of the Drakensberg (Dutch: Dragon's Mountain) Range. Species name honours the late Regent 'Lucas' Huma, Prof. Kitching's long-term field assistant and friend.

Diagnosis. A theropod with the following autapomorphic characters: a large bilobed fossa surrounding a large lateral premaxillary foramen that is connected to the alveolar margin by a deep narrow channel; a deep, oblique notch on the lateral surface of the articular, separating the retroarticular process from the posterior

Table 1. Cranial material used in the comparison with *Dracovenator regenti* gen. et sp. nov. Additional information on *Coelophysis rhodesiensis* was obtained from a series of close-up colour photographs of the cranial specimens held at QG. Comparisons with other taxa are based on the literature and are referenced in the text.

Taxon	Specimens
Massospondylus carinatus	SAM PK1314
Liliensternus liliensterni	MB R. 2175
Coelophysis bauri	Unnumbered Ghost Ranch specimens held at the Science Center, Monash University, Melbourne, CM 31374 (cast)
Coelophysis rhodesiensis	QG165 (currently held at the BP)
Dilophosaurus wetherilli	UCMP 37302, 37303, 77270

margin of the glenoid; and particularly well-developed dorsal, tab-like processes on the articular, one on the medial side, just posterior to the opening of the chorda tympanic foramen and the other on the lateral side on the anterolateral margin of the fossa for the m. depressor mandibulae.

It most closely resembles *Dilophosaurus wetherilli* (Table 1) and *Zupaysaurus rougieri* but can be further distinguished from the former (apart from the presence of the autapomorphies described above) by: the presence of a raised ventral margin of the antorbital fossa placed close to the alveolar margin of the maxilla; the presence of unfused, triangular interdental plates on the maxilla; and the lack of a large transversely arched diastema behind the premaxillary row of teeth. It can be further distinguished from *Z. rougieri* by the probable presence of a rectangular anterior ramus of the maxilla offset from the ascending ramus by a prominent inflection. Considering other taxa of coelophysoid grade it can be distinguished from: *Procompsognathus triassicus, Segisaurus halli, Coelophysis bauri, C. rhodesiensis* and *'Syntarsus' kayentakatae* by its greater adult body size; from *Liliensternus liliensterni, Coelophysis bauri* and *C. rhodesiensis* by its probable rectangular anterior ramus of the maxilla; and from *C. bauri, C. rhodesiensis* and *'Syntarsus' kayentakatae* by its buccolingually compressed and serrated premaxillary teeth. It can be distinguished from the unusual, and poorly described, theropod *'Dilophosaurus' sinensis* by the elongate acutely angled body of the premaxilla, the retraction of the external naris to a level posterior to the last premaxillary tooth and the presence of only four premaxillary teeth.

Holotype. BP/1/5243, fragmentary skull.

DESCRIPTION OF THE HOLOTYPE

Premaxilla (Fig. 2)

The right premaxilla is more complete than the left. The main body consists of a subtriangular block of bone that is longer than it is high. In lateral view, the long axis of the nasal process, and the posterior part of the dorsal margin, forms an acute angle of approximately 25° with the horizontal alveolar margin. Anterior to this the dorsal margin curves smoothly downward to meet the alveolar margin and form a rounded anterior margin. A horizontal, elongate, triangular spike forms the posterolateral process. Its dorsal margin forms the ventral margin of the external naris. There is a markedly sharp bend between the ventral margin of this process and the rest of the posterior margin of the premaxillary body unlike *Coelophysis bauri, C. rhodesiensis* and *Dilophosaurus wetherilli* where the two margins are confluent in lateral view. The anterior ramus of the maxilla would fit into the space defined by these two margins and thus was probably rectangular and elongate as it is in basal tetanurans such as *Afrovenator abakensis* (Sereno *et al.* 1994, fig. 3a). An exceptionally long, slender nasal process forms the dorsal margin of the external naris. The nasal process, which has a D-shaped cross-section, maintained a union with its partner up to a point level with the posterior tip of the posterolateral process (about 53 mm along the length of the nasal process). Thereafter the nasal process diverges from the midline and continues for a further 45 mm. The posterior extension of the nasal process is seen in other coelophysoid-grade taxa (e.g. *Dilophosaurus wetherilli, Coelophysis rhodesiensis*). The divergence from the midline indicates that a wedge of the nasal pair was inserted between the left and right nasal processes. The posterior end of the nasal process becomes mediolaterally compressed and a sharp, low dorsolateral crest is developed at its tip. A similar but far deeper crest is developed on the nasal process of the premaxilla in *Dilophosaurus wetherilli* where it is the anteriormost extension of the naso-lacrimal crest. Thus it is probable that *Dracovenator regenti* had a nasolacrimal crest that was lower than that of *Dilophosaurus wetherilli.*

The lateral surface of the premaxillary body bears a distinctive set of foramina that are symmetrical on the left and right premaxillae. There is an especially large bilobed fossa surrounding the foramen above the second alveolus. The foramen is connected to the alveolar margin by a narrow channel, which cuts across the floor of the anterior lobe of the fossa. A large fossa surrounding a foramen in this position is also present in *Dilophosaurus wetherilli* and *Coelophysis rhodesiensis* but this fossa is not bilobed or connected to the alveolar margin by a channel. In front of this fossa there are two smaller foramina, placed vertically above the first alveolus. A fourth small foramen exits above the large bilobed foramen and a fifth above that one, near the dorsal margin. A shallow, subtriangular narial fossa lies anterior the external naris. Dorsal to this fossa there is a distinctive slot-shaped foramen piercing the base of the nasal process as there is in *Dilophosaurus wetherilli.*

The medial symphysis with the opposite premaxilla is extensive and takes up most of the medial surface of the premaxillary body but does not occupy the posteroventral region or the medial side of the posterolateral process.

A narrow medial shelf projects from the ventromedial

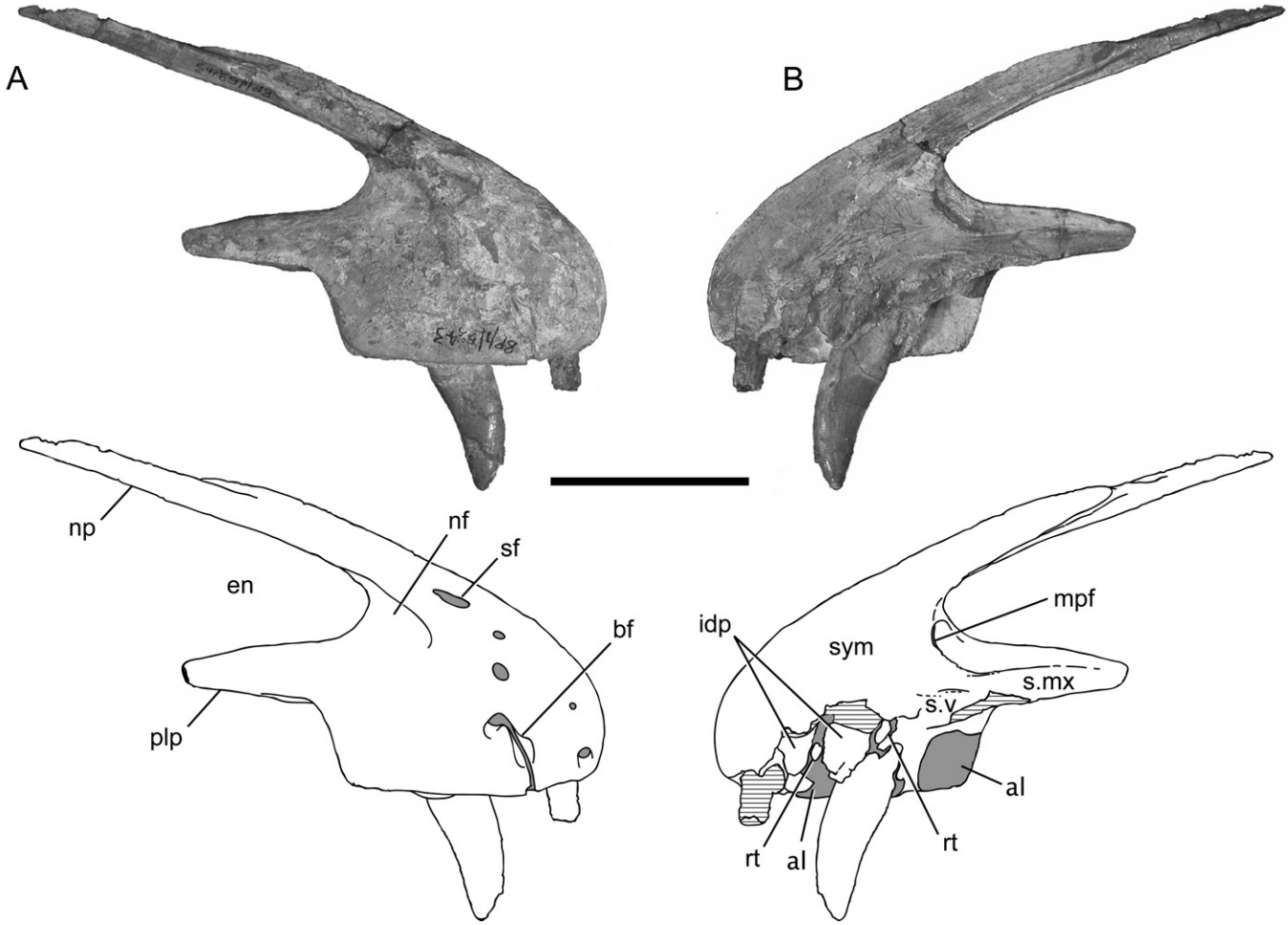


Figure 2. Left premaxilla of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) lateral and (**B**) medial views. Grey areas represent patches of matrix or glue, hatched areas represent broken bone or tooth surfaces. Scale bar = 50 mm.

margin of the base of the posterolateral process. A narrow slot-like foramen pierces the ventrally facing surface created by this shelf. This shelf is presumably homologous with the larger, protrusive posteromedial process observed in many saurischians (e.g. *Massospondylus carinatus; Coelophysis rhodesiensis,* Rauhut 2003, fig. 8; *Sinraptor dongi,* Currie & Zhao 1993, fig. 4). Above this shelf at a point about half way along the posterolateral process is a low ridge. The ridge extends anteriorly and stays parallel to the margin of the external naris. As it curves dorsally, around the anterior rim of the external naris, it defines the anterior rim of the medial premaxillary foramen and the posterior margin of the medial symphysis. The area between horizontal section of this ridge and the ventral margin of the posterolateral process is concave and lightly striated. This is the articular surface for the anteromedial process of the maxilla. A second, much shorter, horizontal ridge begins between the ventromedial shelf and the first ridge, at about the level where the first ridge curves dorsally. The area between the second ridge and the shelf is also striated and probably represents the articulating surface for the anterior end of the vomers.

The premaxilla bears four alveoli, the first of which is smaller than the others. Erupted teeth are present in the first and third alveoli of the right premaxilla, but the first is badly damaged. Both the first and the third teeth have labio-lingually compressed crowns, unlike those of other coelophysoids, where at least the first tooth has a subcircular cross-section (Tykoski & Rowe 2004). The first tooth has a mesiodistal basal length of 10.6 mm and a labiolingual width of 5.1 mm. The crown is directed more or less vertically. The crown of the third tooth is 32.3 mm high and has a mesiodistal basal length of 14.5 mm while the labiolingual width is 7.3 mm. The crown is procumbent and gently curved distally along its length. It has well developed serrations on the distal carina with a density of 14 per 5 mm. The serrations have rounded tips in lateral view and are subrectangular in distal view. The carina begins just a few millimetres above the base of the crown. The mesial margin of the tooth has a weakly developed carina that occupies the apical third of the crown. It has only a few poorly developed, faint serrations.

Maxilla (Fig. 3)

Only a fragment of the right maxilla containing six alveoli is present. Judging from the proximity of the ventral margin of the antorbital fossa to the alveolar margin and the reduction in size of the alveoli towards its posterior end, this fragment comes from the posterior end of main maxillary body, with at most two alveoli missing from the posterior tip. The presence of the attachment scar for the palatine on the medial side also supports this position for the fragment. Interestingly, the depth does not decrease greatly along the length of this fragment,

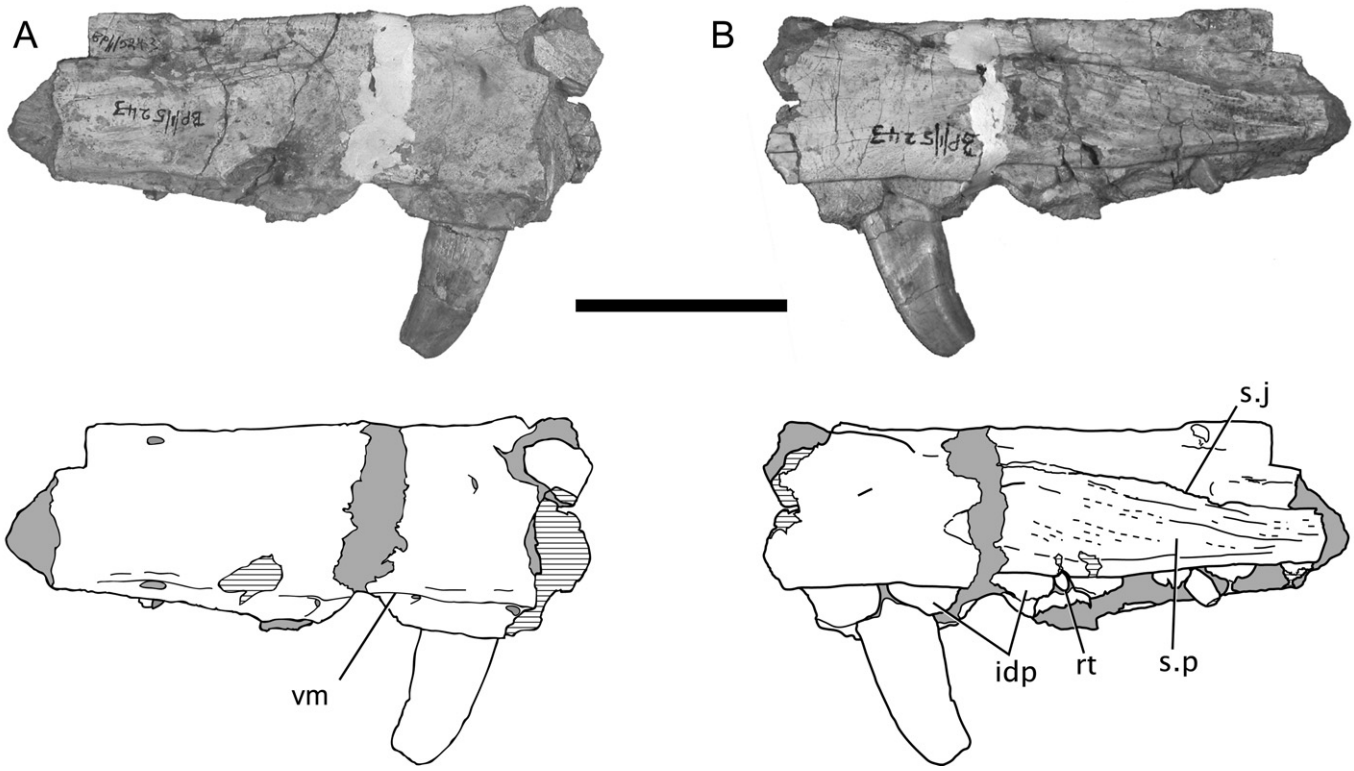


Figure 3. Posterior part of right maxilla of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) lateral and (**B**) medial views. Scale bar = 50 mm.

indicating that the maxilla did not taper to a point at its posterior end.

The lateral surface is shallowly impressed with the antorbital fossa. The ventral margin of the fossa is placed close to the alveolar margin so that the antorbital fossa occupies most of the depth of the maxilla (between 87% and 94%). The ventral margin is also raised into a rounded ridge above the level of the lateral surface of the maxilla, matching the 'alveolar ridge' that is seen in most coelophysoid-grade taxa (Rowe 1989, e.g. *Liliensternus liliensterni, Coelophysis bauri, C. rhodesiensis* and *'Syntarsus' kayentakatae*) except *Dilophosaurus wetherilli* (Welles 1984).

The medial surface is excavated so that there is a thin dorsally projecting lamina on the lateral side that is bounded medially by a shelf that forms the dorsal surface of the main body of the maxilla. The shelf slopes from the dorsal margin, at the anterior end of the fragment to a level just above the posteroventral corner of the maxilla. The dorsal surface of the shelf would have received the anterior end of the jugal. The shelf becomes shallower and less pronounced, with rounder margins, towards the anterior end of the fragment. Below the posterior two thirds of the shelf there is an elongate area of oblique striations that forms the articulating surface for the lateral margin of the palatine. A deep and narrow paradental sulcus extends along the ventral margin, separating the interdental plates from the rest of the medial surface. The interdental plates are unfused, low, sub-triangular plates, unlike the fused, rectangular plates seen in ceratosaurs (e.g. *Ceratosaurus dentisulcatus,* Madsen & Welles 2000; Abelisauridae, Lammana *et al.* 2002) and *Dilophosaurus wetherilli.*

The single erupted maxillary tooth is strongly labiolingually compressed with a mesiodistal basal length of 18.0 mm and a labiolingual basal width of 6.4 mm. The estimated crown height is 40 mm. The apical region is gently curved distally. It has serrated carinae on both the mesial and distal margins. The mesial carina starts 21 mm above the base and has a density of 34 serrations per 10 mm. The serrations are simple, appearing subcircular in mesial view and lacking deep grooves between them. The distal carina starts at the base itself and bears coarser (28 serrations per 10 mm), more strongly developed serrations. The serrations are separated by deeper, broader grooves than those of the mesial carina. The tips of the serrations are rounded in labial or lingual view.

Dentary (Fig. 4)

There are two dentary fragments, one from each dentary. The larger of the two fragments comes from the mid section of the left dentary. It preserves three alveoli but no erupted tooth crowns. A tooth root with strong labiolingual compression is present in the anterior alveolus. The tips of replacement teeth are visible in the anterior and posterior alveoli. These show that the mesial and distal carinae of the dentary teeth were serrated and that the serrations continue over the tip of the tooth. As in the maxilla, the triangular interdental plates are unfused. A narrow and shallow paradental sulcus separates the base of the interdental plates from the medial surface of the dentary. The meckelian sulcus is broad and shallow with rounded margins. It extends along the ventral half of the medial surface. On the lateral side there is a narrower longitudinal sulcus that is located 18 mm down from the alveolar margin. The lateral sulcus fades towards the anterior end of the dentary fragment. Its ventral margin is steep and sharp while its dorsal margin slopes gradually.

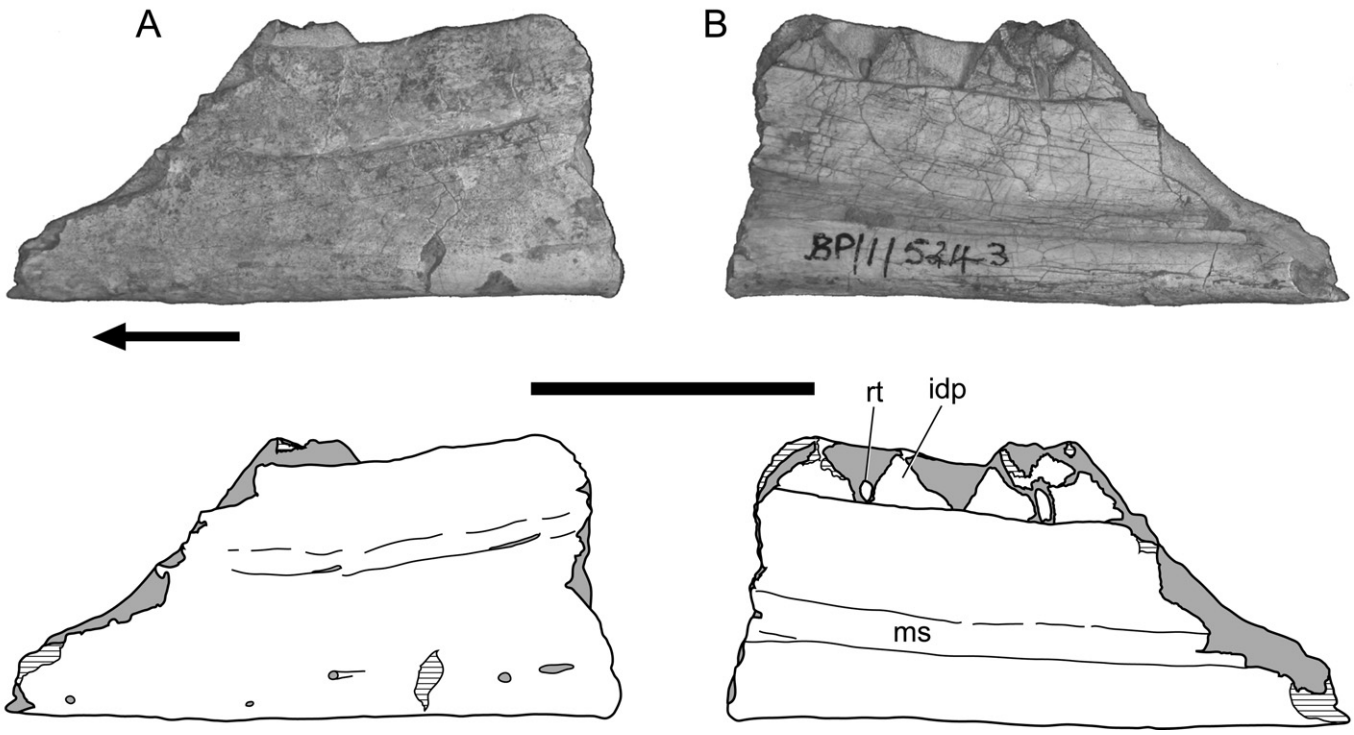


Figure 4. Middle part of left dentary of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) lateral and (**B**) medial views. Arrow in (**A**) points to the anterior. Scale bar = 50 mm.

Elongate neurovascular foramina are placed at irregular intervals along the floor of the lateral sulcus. The smaller right dentary fragment provides no further details.

Prearticular (Fig. 5C,D)

There is a short fragment from near the posterior end of the right prearticular. The fragment consists of a dorsoventrally shallow anterior region that would have formed the ventromedial margin of the adductor fossa and a dorsoventrally expanded posterior region that would have met the glenoid-retroarticular complex; however, the two fragments can no longer be joined.

The lateral surface bears two, tall, sharp-edged ridges, that extend across the length of the fragment, although their height decreases towards the posterior end. At the anterior end these ridges are closely spaced creating a deep, V-shaped sulcus between them. Towards the posterior end they diverge creating a broad, triangular fossa. The upper ridge is placed at the dorsal margin itself, thus creating a laterally projecting shelf that floors the adductor fossa.

The ventral margin of the prearticular fragment widens towards the anterior end. At about the midlength of the fragment a thin, ventrally directed crest arises from the ventromedial margin. This creates a ventrolaterally facing, elongate fossa for the reception of the angular.

Angular (Fig. 5A,B)

The mid-section of the right angular is present. It is a relatively simple, flat bone with a gently convex ventral margin in lateral view. The strongly concave dorsal margin forms the ventral border of the external mandibular fenestra. The ventral margin suggests that the entire fenestra would have been large and ovoid in shape. At its narrowest, the ventral margin of the external mandibular fenestra is just 19 mm from the ventral margin of the angular, and hence the mandible itself. The dorsoventral depth of the angular increases both posteriorly and anteriorly as it does in *Dilophosaurus wetherilli.* More derived theropods (e.g. *Ceratosaurus dentisulcatus,* Madsen & Welles 2000, pl. 13e,f; and *Sinraptor dongi,* Currie & Zhao 1993, fig. 10 e, f) differ in having an anteriorly tapering angular. The articular surface for the dentary is a smooth, flat triangular area on the anterior half of the lateral surface. Its ventral margin is depressed below the level of the lateral surface of the bone. The ventral margin of the angular curves medially to form a sharp-edged medially facing shelf in the posterior half of this fragment. The prearticular would have articulated with the dorsal surface of this shelf. The shelf narrows and disappears at the level that the posterior tip of the dentary would have extended. Anterior to the shelf is a sharp, narrow ridge that extends across the anterior medial surface. A shallow elongate fossa is present between the ridge, which forms its dorsal margin, and the bulging ventral margin of the angular. This fossa would have fitted the posterior end of the splenial. Thin pieces of the posterior-most region of the angular are present on the lateral side of the glenoid-retroarticular complex.

Mandibular glenoid and retroarticular process (Figs 6 & 7)

The posterior end of the right mandibular ramus is preserved. It is a complex of four bones, the articular, surangular, angular and prearticular, preserved in two fragments. The main fragment includes the glenoid fossa and the retroarticular process, while the smaller fragment preserves the ventral crest and a small portion of the

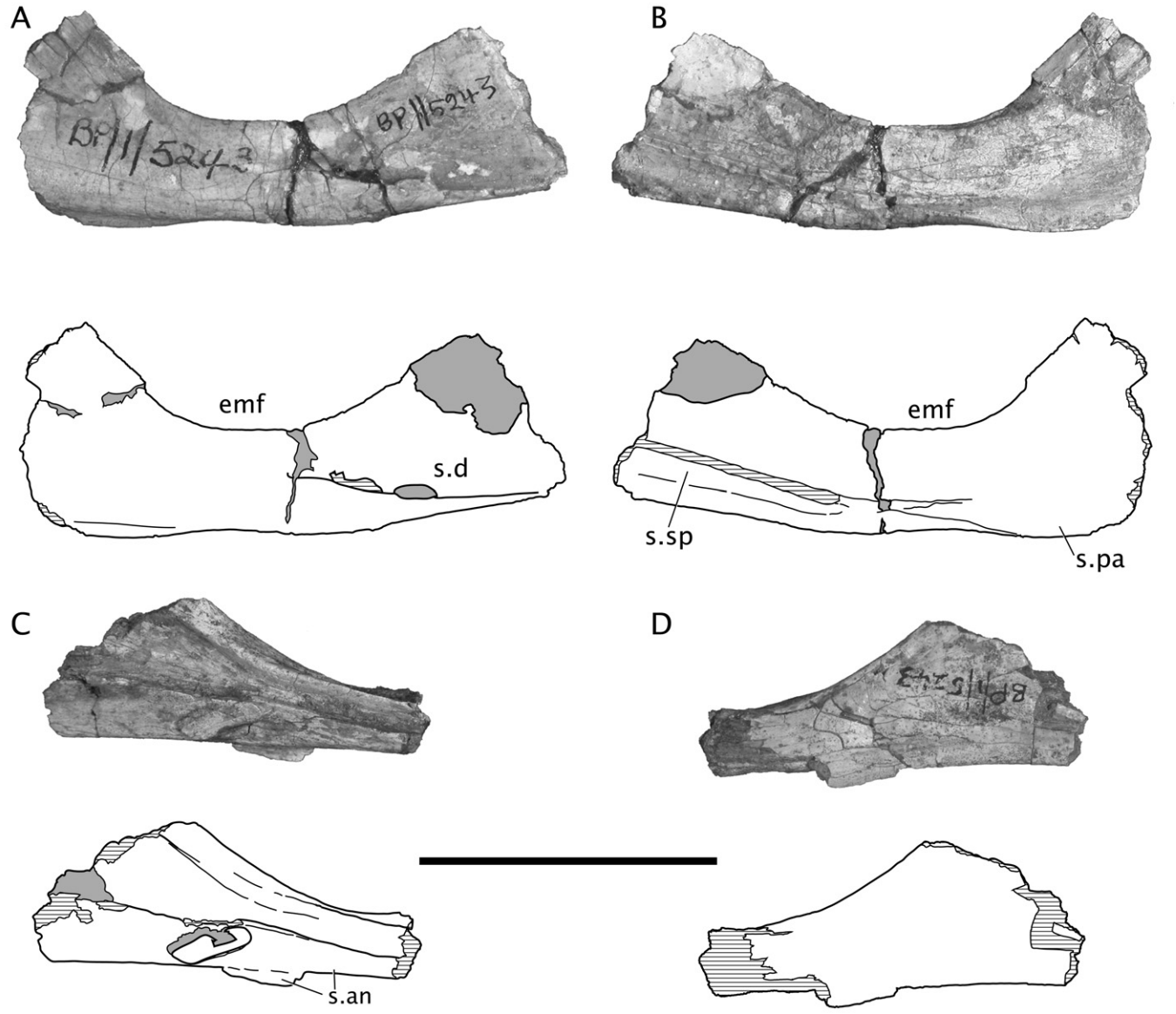


Figure 5. Post dentary bones of *Dracovenator regenti* gen et sp. nov. (BP/1/5243). Middle section of the right angular in (**A**) lateral and (**B**) medial views. Posterior fragment of the right prearticular in (**C**) lateral and (**D**) medial views. Scale bar = 50 mm.

posterior medial wall of the adductor fossa. The angular is represented only by a few thin flakes of bone on the lateral surface of the smaller fragment, anteroventral to the glenoid. It forms part of the deep thin crest that protrudes ventrally. The contact between the angular and the surangular is missing due to a large break along which the bone surface has flaked away. Like much of the damage to this fragmentary specimen, this break appears to have occurred before, or during, burial. The surangular covers much of the ventrolateral surface. It also forms a thick, rounded, laterally protruding ridge that extends forward from the anterolateral corner of the glenoid. A similar ridge is also present in *Dilophosaurus wetherilli* where it extends forward to form a shelf-like ridge on the lateral surface of the surangular (Welles 1984). There is a medial extension of the surangular that forms the anterolateral part of the glenoid and lateral wall of the adductor fossa. The dorsal margin of the lateral wall of the adductor fossa is a rounded ridge that is inset from the lateral ridge described above. Directly ventral to the lateral rim of the glenoid the surangular forms a small fossa. The sharp lateral lip of the glenoid socket forms the dorsal margin of this fossa. Dorsal and posterior to the fossa, the posterior rim of the glenoid forms a laterally protruding, vertically oriented, rectangular process. The surangular–articular suture is difficult to see in this region but it appears to lie close to the ventral end of this process indicating that most of the process is formed by the articular. Posterior to the lateral articular process there is a broad, rounded notch that curves posterodorsally. The suture between the surangular and articular is evident as it traverses the ventral part of this notch. Behind the lateral notch the dorsal margin of the surangular lies close to the rim of the fossa for the m. depressor mandibulae. The surangular terminates just a few millimetres in front of the posterior tip of the retroarticular process. The broad lateral notch mentioned above curves smoothly up onto the dorsal surface of the retroarticular process. The posterior part of the retroarticular process forms an ovoid concave region that faces posterodorsally, as it does in *Dilophosaurus wetherilli* and most tetanurans (Rauhut 2003), where the m. depressor mandibulae would have attached.

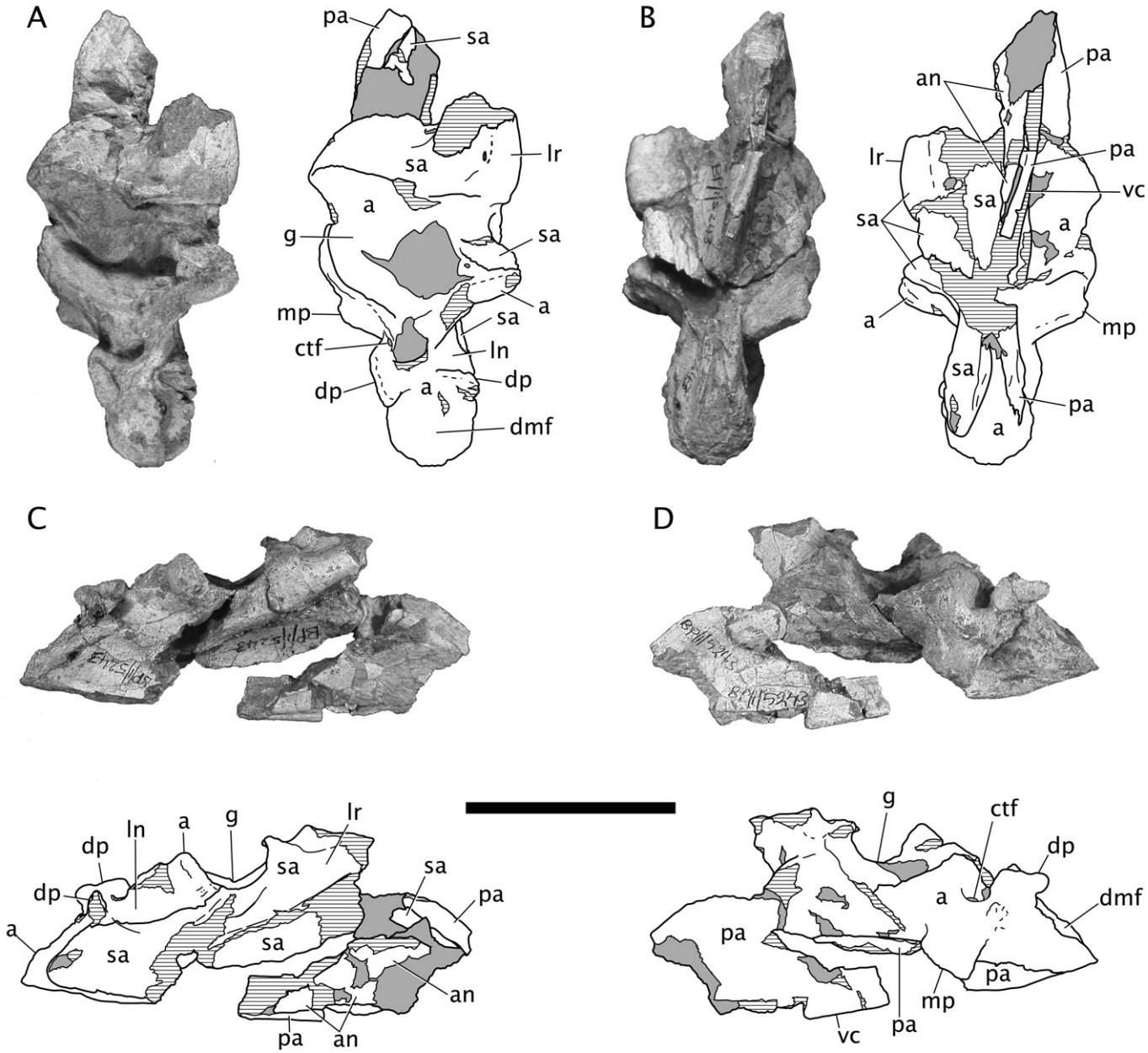


Figure 6. Posterior end of the right mandibular ramus of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) dorsal, (**B**) ventral, (**C**) lateral and (**D**) medial views. Scale bar = 50 mm.

However, unlike most tetanurans the fossa for the m. depressor mandibulae remains primitively narrow (its transverse width is 45% of that of the glenoid). The anterolateral rim of this fossa is produced dorsally into a tab-shaped process, with a transverse long axis. A much weaker version of this process is present in *D. wetherilli.* On the opposite, anteromedial corner of the posterodorsal fossa, there is a second, larger tab-like dorsal process. In this case, however, the long axis is oriented obliquely, extending posterolaterally to anteromedially. Again, a weaker version of this process can be observed in *D. wetherilli.* The chorda tympanic foramen opens from the dorsomedial surface of the articular in front of the anteromedial edge of the medial dorsal process. A deep fossa is present in the region enclosed by the chorda tympanic foramen, the medial dorsal process, the lateral notch and the posterior rim of the glenoid. However, this fossa is not floored by finished bone, instead it is largely matrix and scraps of cancellous bone. It is likely that this fossa represents a damaged area that was hollowed out during preparation. The medial surface of the retroarticular process bears a rugose fossa ventral to the medial dorsal process. A large rectangular process, that is directed medioventrally, arises from the space between the rugose fossa and the posteromedial corner of the glenoid, ventral to the chorda tympanic foramen. A similar process, usually described as a pendant process, is also present in allosauroid tetanurans (e.g. *Sinraptor dongi,* Currie & Zhao 1993, fig. 11f) and *Dilophosaurus wetherilli* (where the process itself has broken away but its base is clearly present). The anterior edge of the medioventral process is connected to the posterior wall of the glenoid by a short, thick web of bone. A deep sulcus separates the ventromedial process from the ventral crest. A narrow pointed sliver of the prearticular can be seen on the medial surface of the ventral crest, below the posterodorsal

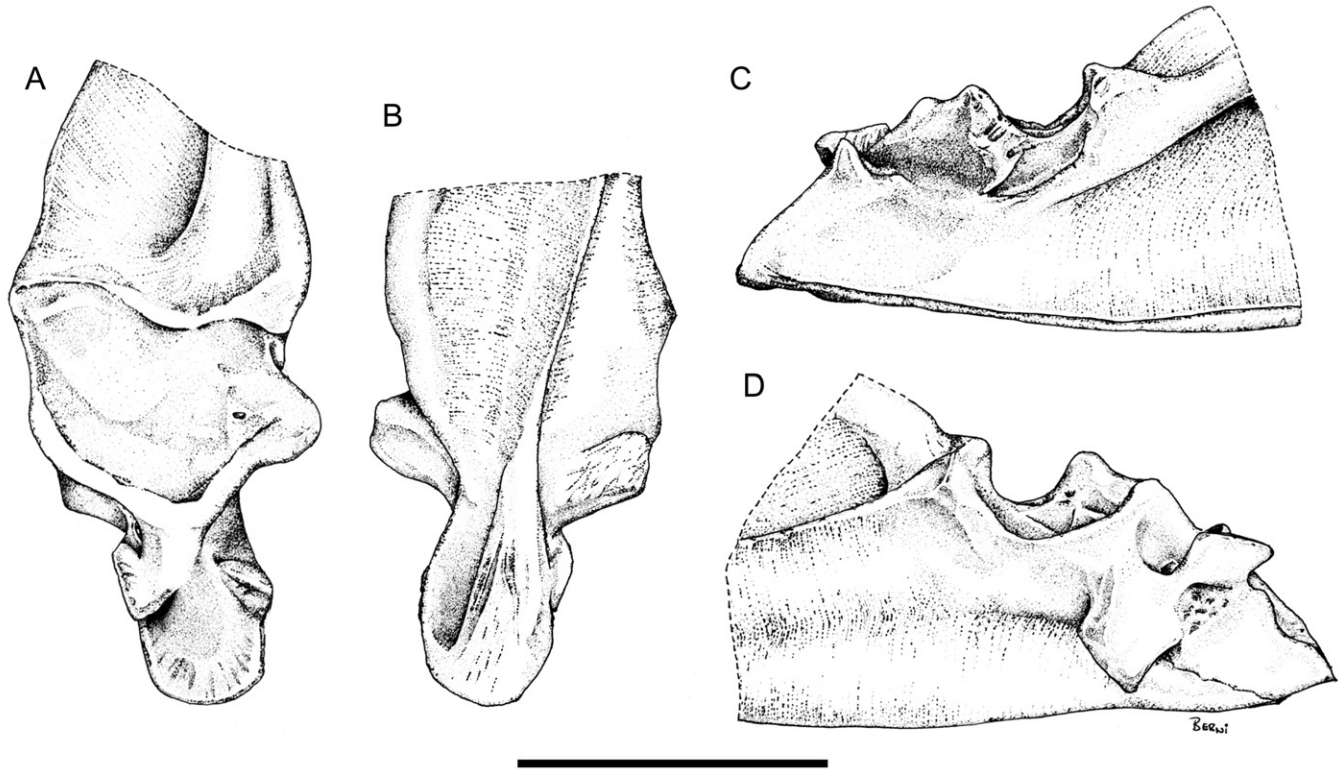


Figure 7. Reconstruction of posterior end of right mandibular ramus of *Dracovenator regenti* gen et sp. nov. (BP/1/5243) in (**A**) dorsal, (**B**) ventral, (**C**) lateral and (**D**) medial views. Scale bar = 50 mm.

articular fossa. It is impossible to trace the articular–prearticular contact anterior to the ventromedial process. In ventral view, the prearticular and the surangular approach each other anteriorly, so that the ventral exposure of the articular is pinched out at the level of the ventromedial process. The ventral crest becomes narrower at this point, with the ventral margin being formed entirely by the prearticular, and the angular being restricted to its lateral surface.

DESCRIPTION OF BP/1/5278 (Fig. 8)

An articulated set of premaxillae, maxillae, nasals and dentaries comprise BP/1/5278. The posterior maxillae, nasals and dentaries are missing. The left side is generally better preserved than the right, though some details are clearer on the right side. Munyikwa & Raath (1999) described the specimen but there are some details and reinterpretations that need to be added to their description.

The nasal processes of the premaxillae extend as far back as the posterior rim of the external naris, thus they extend beyond the posterior tips of the posterolateral processes of the premaxilla. These processes diverge from each other at their posterior ends and are clasped on each side by the bifurcated tips of the premaxillary processes of the nasals. Thus, a w-shaped premaxilla–nasal suture is formed. The shape of the premaxilla–maxilla suture is not well preserved on the left side. It appears that many of margins of the bones have been lost, perhaps due to invasive hematite mineralization. This can be clearly seen along the ventral margin of the maxilla, where the strip of bone below the ventral rim of the antorbital fossa is absent between the third and eighth maxillary tooth. The ventral margin of the anterior ramus of the maxilla, on the left side, slopes anterodorsally to meet the premaxilla. This enhances the appearance of a subnarial notch. However, it appears from the right side that the complete anterior ramus of the maxilla was more rectangular in shape. The ventral margin of the premaxilla is incomplete on both sides, though the slightly better preserved (though less complete) right premaxilla indicates that there was a bend between the ventral margin of the posterolateral process and the posterior margin of the premaxillary body.

The left maxilla displays two small oval fossae on the medial wall of the antorbital fossa, in front of the antorbital fenestra. These match the position of the maxillary and promaxillary fenestra of tetanuran theropods well and are here called the promaxillary and maxillary fossae, respectively. A raised rim along the dorsal margin of the antorbital fenestra curves ventrally at the anterior end of the antorbital fenestra to form a sharp posterior and posteroventral margin to the maxillary fossa – indeed there is a slight recessing of the fossa posteroventrally. The sharp, raised rim is present in coelophysids, although the promaxillary and maxillary fossae are only present as vague shallow depressions. The promaxillary fossa appears to pierce the maxilla but this could easily be a puncture of the extremely thin bone created during preparation. A second hole pierces the medial wall of the antorbital fossa near its anteroventral corner but the rim of this hole is sharp and not depressed as in the fossae described above, so this feature is certainly caused by damage incurred during preparation. Furthermore, the medial wall of the right antorbital fossa shows no foramen in this region. The right maxilla has an extensively damaged external surface making it impossible to observe the fossae. The antorbital fossa is also deeply

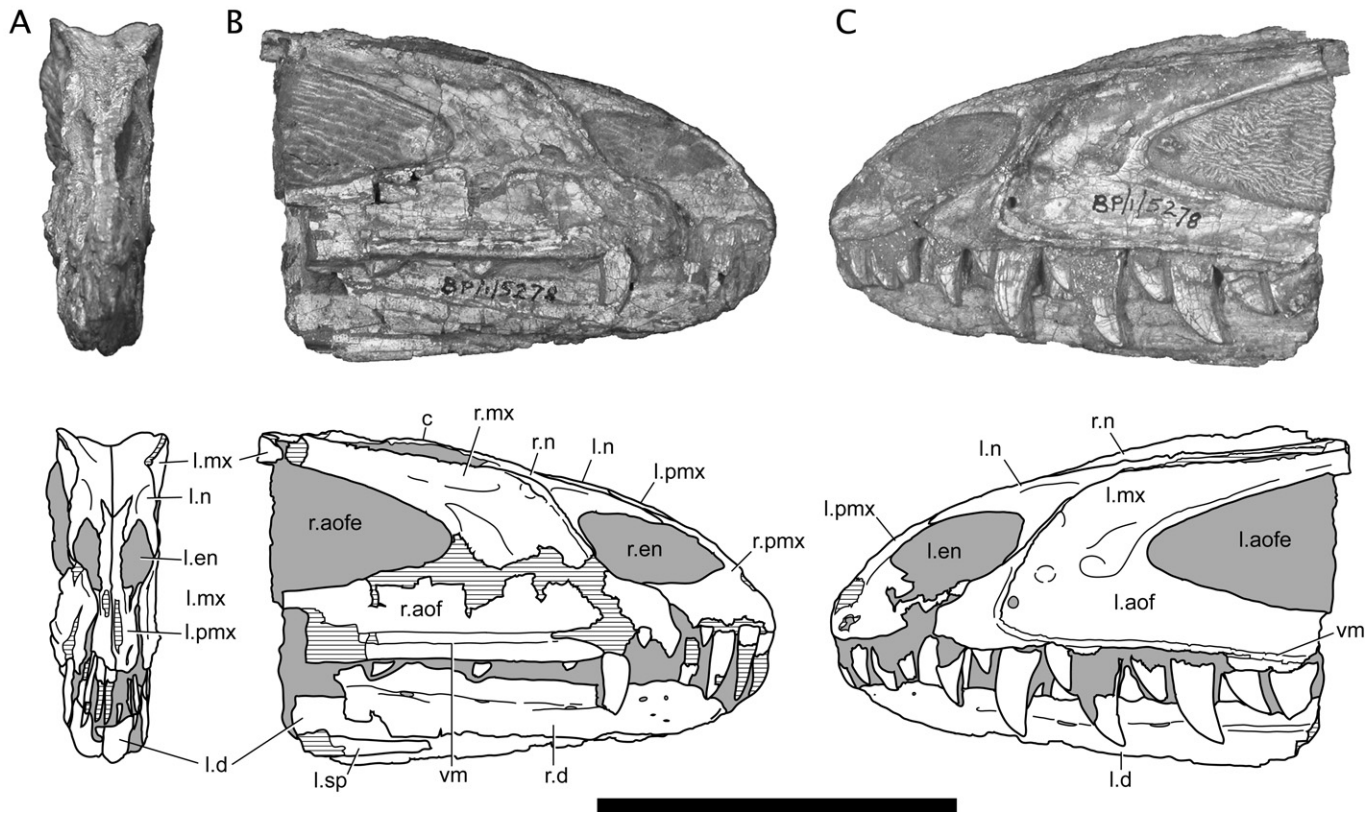


Figure 8. Snout of juvenile ?*Dracovenator regenti* gen. et sp. nov. (BP/1/5278) in (**A**) anterior, (**B**) right lateral and (**C**) left lateral views. Scale bar = 50 mm.

recessed under the anterior rim at the level of the promaxillary fossa.

The anteroventral processes of the nasals are bowed slightly laterally so that the posterior rim is set lateral to the anterior rim. This feature resembles that of ceratosaurs (Rauhut 2003; e.g. *Ceratosaurus magnicornis,* Madsen & Welles 2000, plate 3a) but it is less strongly developed in BP/1/5278 than in these taxa. The dorsolateral margin of the nasals forms a rounded ridge above the posterolateral processes, but posterior to these, where the nasal–maxilla suture reaches the dorsolateral margin of the skull, the nasal flares into a thin, sharp-edged crest that protrudes above the maxilla. This crest is absent on the left side but it is clear that the lateral margin of the nasals is broken here. The crest, which is only two millimetres high, is an incipient version of the crest seen in *Zupaysaurus rougieri, Coelophysis kayentakatae* and *Dilophosaurus wetherilli.*

CLADISTIC ANALYSIS

Dracovenator regenti was included in a modified version of Rauhut's (2003) character-taxon matrix (using only data from the holotype), the most comprehensive analyses of early theropod relationships published to date. Modifications include the collapsing of Coelurosauria more derived than *Proceratosaurus bradleyi* into a single terminal taxon (the interrelationships of this well-corroborated group are of no concern to this work), the separation of '*Syntarsus' kayentakatae* from *Coelophysis rhodesiensis, Acrocanthosaurus atokensis* from Carcharodontosauridae, the addition of 28 new characters and four new taxa in addition to *Dracovenator regenti*. These taxa are the recently described (or re-described) *Masiakosaurus knopfleri* (Carrano *et al.* 2002), '*Poekilopleuron' valesdunensis* (Allain 2002) *Tugulusaurus faciles* (Rauhut & Xu 2005) and *Zupaysaurus rougieri* (Arcucci & Coria 2003). New *Coelophysis* (= *Syntarsus* Raath) *rhodesiensis* material has shown that the supposed clade *Coelophysis rhodesiensis* + '*Syntarsus' kayentakatae* clade cannot be diagnosed by the presence of a postnasal fenestra (Bristowe & Raath 2004). Thus there is little to support the monophyly of *Syntarsus* Raath, or rather its replacement name *Megapnosaurus,* and the two species are treated as separate terminals in this analysis. The synonymy of *Megapnosaurus* and *Coelophysis* (Bristowe & Raath 2004) is provisionally accepted here, while *'Syntarsus' kayentakatae* has a number of unusual character states and deserves a new genus name. Although an exclusive clade *Coelophysis bauri* + *C. rhodesiensis* is not supported by the topology of the most-parsimonious tree found in this analysis (see below) it only takes one extra step to produce such a result. Since the Rauhut's codings for his composite OTU *'Syntarsus'* were based almost entirely on *Coelophysis rhodesiensis* this terminal taxon was simply relabelled for this analysis (with appropriate modifications listed below) and a new terminal for *'Syntarsus' kayentakatae* was created.

The outgroups follow Rauhut (2004) and consist of *Euparkeria, Marasuchus* and Ornithischia. These taxa were included in the analysis in order to polarize the characters but no characters that resolve relationships between the outgroups were considered.

The new characters are as follows (numbers follow on from the character list in Rauhut 2003).

225. Skull length less than (0), or greater than (1), three

times the occipital height of the skull (Sereno 1999).

226. Absence (0), or presence (1), of a foramen on the medial side of the premaxillary body, below the narial margin (Sereno *et al.* 2004).

227. Absence (0), or presence (1), of a slot-shaped foramen at the base of the nasal process of the premaxilla.

228. Posterior tip of the nasal process of the premaxilla level with (0), or extending posterior to (1), the posterior tip of the posterolateral premaxillary process.

229. Posterolateral premaxillary process at least one and a half times longer (0), or subequal (1), to the dorsoventral depth at its base (modified from Carrano *et al.* 2002).

230. Absence (0), or presence (1), of a transversely arched diastema posterior to the premaxillary row of teeth. This character is distinct from the 'subnarial gap' (Rowe 1989). That character refers to an arch or notch at the premaxilla–maxilla contact that is visible in lateral view. This character refers to the transversely concave toothless region behind the premaxillary tooth row. Taxa that have a notched premaxilla–maxilla contact in lateral view do not necessarily display this structure (e.g. baryonychines, Sereno *et al.* 1998, fig. 2a,b).

231. Premaxillary teeth with elliptical (0), or subcircular (1), cross-sections (Tykoski & Rowe 2004).

232. Premaxillary tooth crowns are labiolingually symmetrical (0) or asymmetrical (1) (Sereno *et al.* 1994).

233. Premaxilla–nasal suture on internarial bar is v-shaped (0) or w-shaped (1) (Sereno *et al.* 2004).

234. Subnarial foramen on the premaxilla–maxilla suture is absent (0), present but no larger than the lateral nutritive foramina of the maxilla and located outside the narial fossa (1), or present and larger than lateral nutritive foramina of the maxilla and located on the border of, or inside the narial fossa (2) (Yates 2003a, modified from Sereno & Novas 1993).

235. Promaxillary recess is shallow to absent (0) or extends into the anterior ramus of the maxilla (Sereno *et al.* 1994).

236. Depth of the ventral antorbital fossa less than, subequal (0), or many times greater (1) than the depth of the maxilla between the alveolar margin and the ventral margin of the antorbital fossa (modified from Rauhut 2003).

This character was subsumed into Rauhut's character 15, which described the presence, or absence, of an alveolar ridge. The alveolar ridge is not a neomorphic feature: it is the ventral margin of the antorbital fossa that has become raised above the level of external surface of the maxilla. Although most taxa that have such a raised ventral margin of the antorbital fossa also have a ventrally located margin (the derived state for this character) some taxa with this condition (e.g. *Eoraptor lunensis*) show a plesiomorphic placement of the ventral margin. Thus the two characters are not necessarily correlated and should be coded separately in a matrix.

237. Frontal pair in articulation is longer than wide (0) or wider than long (1) (Allain, 2002).

238. Spur of bone from basisphenoid projecting anteriorly into basisphenoid recess absent (0) or present (1) (Tykoski & Rowe 2004)

239. Dorsoventral expansion of the dentary tip absent (0) or present (1) (Sereno 1999).

240. Pendant medial process of the articular absent (0) or present (1) (Sereno *et al.* 1994).

241. Absence (0), or presence (1), of erect, tab-like dorsal processes on the articular, one immediately posterior to the opening of the chorda tympanic foramen and the other on the anterolateral margin of the posterodorsal fossa.

242. Transversely convex (0) or concave (1) attachment area for the m. depressor mandibulae on dorsal surface of articular. This character was subsumed into Rauhut's (2003) character 73, which describes the width of the attachment area for the m. depressor mandibulae. *Dracovenator regenti* has a concave attachment area, conforming to Rauhut's definition for the derived state for character 73 but it remains narrower than the mandible in front of the mandibular joint, which conforms to his definition of the plesiomorphic state. Clearly the width of the area can be independent of whether or not it is concave. In this analysis, character 73 describes only the width of the attachment area (0 = narrower than the mandible in front of the mandibular joint, 1= wider) whereas character 242 describes the transverse shape of this area.

243. Anterior tip of the axial neural spine in front of (0), level with, or behind (1), the axial prezygapophyses (Tykoski & Rowe 2004).

244. Cervical vertebrae 3–6 subequal to (0), or greater than 10% longer than (1), the length of the axis (Yates 2003a).

245. Cervical vertebrae 7–9 subequal to (0) or greater than 10% longer than (1) the length of the axis (Yates 2003a, modified from Gauthier 1986).

246. Sharp epipophyseal-prezygapophyseal ridge in cervical vertebrae absent (0) or present (1) (Sereno *et al.* 2004).

247. Distal humeral condyles are highly convex (0), or nearly flat (1) (Carrano *et al.* 2002).

248. Distal carpal 1 less than (0), or greater than (1), 120% of the transverse width of distal carpal 2 (Yates 2003a, modified from Sereno 1999).

249. Absence (0), or presence (1) of a distal ischial expansion (Yates 2003a, modified from Sereno 1999)

250. Width of the distal end of metatarsal IV subequal to (0), or less than 50% of (1), of the width of the distal end of metatarsal II (Sereno *et al.* 2004).

251. Astragalus and calcaneum separate (0), or fused (1), in adults (modified from Rowe 1989).

252. Proximal ends of metatarsals II and III separate (0), or fused (1), in adults (modified from Rowe 1989)

Codings for these characters are given in Appendix 1. Codings for characters 1–224 of *'Syntarsus' kayentakatae, Acrocanthosaurus atokensis,* derived coelurosaurs, Carcharodontosauridae, *Dracovenator regenti, Masiakosaurus knopfleri, 'Poekilopleuron' valesdunensis* and *Zupaysaurus rougieri* are given in Table 1.

Further changes include the following modifications to the following characters.

2. Premaxillary body in front of external nares: shorter than body below the nares and angle between anterior margin and alveolar margin more than 75° (0); longer than body below the nares and angle less than 70° (1).

The derived state is divided into two states in this analysis: external naris overlapping with some of the premaxillary body (1) and external naris entirely posterior to premaxillary body (2). *Coelophysis bauri, C. rhodesiensis, Dilophosaurus wetherilli,* Spinosauridae (= Baryonychidae in Rauhut 2003) *'Syntarsus' kayentakatae* and *Dracovenator regenti* are coded as having state 2, otherwise codings are unchanged from Rauhut (2003). Because state 2 is an extreme form of state 1, the character is treated as ordered.

22. Pronounced lateral rims of the nasals, sometimes bearing lateral cranial crests: absent (0); present (1).

As noted by Rauhut (2003) the derived state of this character displays some variability with some taxa exhibiting tall, naso-lacrimal crests. These crests are treated here as a second derived state of this character. *Dilophosaurus wetherilli, 'Syntarsus' kayentakatae* and *Zupaysaurus rougieri* are coded as having state 2. All other codings remain as in Rauhut (2003). As state 2 represents a hypertrophied form of state 1 the character is treated as ordered.

142. Deltopectoral crest: prominent and extending over at least one third of the humerus and well developed (0); strongly reduced in size, extending for much less than one third of the humerus (1).

Rauhut (2003) utilized both size and shape criteria to distinguish state 1 (deltopectoral crest strongly reduced to a small triangular eminence). In practice dinosaurian deltopectoral crests are neither strictly rectangular nor triangular and the difference between the two shape states is rather subjective. I prefer to restrict this character to a simple description of the size differences. Consequently *Deltadromeus agilis* is recoded as having a reduced deltopectoral crest (state 1).

145. Radius: more than half of the length of the humerus (0); less than half the length of the humerus (1).

As it stands, Rauhut's character differentiates the extremely shortened radii of abelisaurids and various basal tetanurans from those of other theropods. However, it fails to distinguish between the moderately short radii of most neotheropods and sauropodomorphs and those of several basal taxa that have radii that approach the humerus in length. Thus the original state 0 is divided into two states: those taxa with a radius more than 80% of the length of the humerus (*Euparkeria capensis, Marasuchus lilloensis, Eoraptor lunensis* and *Herrerasaurus ischigualastensis*) are assigned state 0; while all taxa with a radius that is between 50% and 80% of the length of the humerus (Ornithischia, Sauropodomorpha, *Coelophysis bauri, C. rhodesiensis, Liliensternus liliensterni, Dilophosaurus wetherilli, Piatnitzkysaurus floresi, 'Szechuanosaurus' zigongensis, Allosaurus fragilis, Ceratosaurus* spp., *Acrocanthosaurus atokensis,* and derived coelurosaurs) are coded as having state 1. Those taxa originally coded as having state 1 in Rauhut's (2003) matrix (*Torvosaurus tanneri,* Spinosauridae and Abelisauridae) are now coded as having state 2 (a radius less than 50% of the length of the humerus). The modified character is treated as ordered.

184. Strongly expanded pubic boot: absent (0); present (1).

There are two issues regarding this character. Firstly there is controversy over the state present in Herrerasauridae. Sereno *et al.* (1993) and Rauhut (2003) code herrerasaurids as having a pubic boot whereas Langer (2004) argues, and I agree, that the appearance of a distal expansion in herrerasaurids is caused by the posterior folding of the distal lateral margins of the pubic apron, not the proximodistal expansion of the distal end itself. Secondly Rauhut's character only distinguishes those taxa that have a particularly enlarged boot (at least twice the anteroposterior length of the pubic shafts) from all others. Yet the primitive condition is to have no anteroposterior expansion of the distal end at all, while some taxa coded as 0 in Rauhut's matrix have a small distal expansion. Consequently *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei* are recoded as unknown for this character, reflecting that the transformation by caudal folding has rendered the character indeterminate in these taxa. All other taxa originally coded as 1 are now recoded as having state 2 (a large pubic boot over twice the anteroposterior length of the pubic shafts). Sauropodomorpha, *Coelophysis bauri* and *Liliensternus liliensterni* are recoded from 0 to 1 (a small distal pubic expansion less than twice the anteroposterior length of the pubic shafts).

Finally, the following coding changes were made to the following characters. Changes based upon new evidence have references to that evidence; those that are not referenced represent simple differences of opinion.

4. The posteroventral process of the premaxilla is more widespread amongst early saurischians than Rauhut appreciated. It is certainly present in basal Sauropodomorpha (e.g. *Thecodontosaurus caducus, Massospondylus carinatus*) and Sinraptoridae (Currie & Zhao 1993) so these taxa are recoded as having state 1. Because the process passes medial to the maxilla it cannot be seen in specimens where the premaxilla and maxilla are in articulation. Consequently the following taxa that were previously coded as not having the process (state 0): *Eoraptor lunensis, Herrerasaurus ischigualastensis* and *Monolophosaurus jiangi,* are recoded as being unknown.

6. *Eoraptor lunensis* is recoded as having state 0.

11. *Liliensternus liliensterni* is recoded as having state 0.

22. *Neovenator saleri* is recoded as having state 1 following the discovery of the nasals of this taxon (Naish *et al.* 2001).

23. Rauhut (2004) coded *'Syntarsus'* as having a bluntly

squared anterior tip of the jugal on the basis of QG 278, a specimen of *Coelophysis rhodesiensis.* However, this specimen is probably damaged and a newly prepared specimen shows that the anterior tip of the jugal tapers to a sharp point in this taxon (Bristowe & Raath 2004, fig. 5). Consequently *C. rhodesiensis* is recoded as having state 0.

24. There are no specimens of *Coelophysis rhodesiensis* with a jugal in natural articulation with the maxilla and the lacrimal consequently it is impossible to determine what state is present in this taxon and it is recoded as being unknown (the original coding was based on *'Syntarsus' kayentakatae*).

46. Rauhut (2004) coded *'Syntarsus'* as lacking a squamosal–quadratojugal contact on the basis of *'Syntarsus' kayentakatae.* Since this region is not articulated in any specimen of *Coelophysis rhodesiensis* the character is recoded as unknown in this taxon. Furthermore I disagree with Rauhut's assessment of *'Syntarsus' kayentakatae* and code it as having a squamosal–quadratojugal contact (state 0).

49. New skull material of *Coelophysis rhodesiensis* (Bristowe & Raath 2004) shows that the quadrate foramen is deeply recessed and partly encircled by the quadrate and so it is recoded as having state 1.

67. The basal sauropodomorph *Thecodontosaurus caducus* has a ventral fossa on its ectopterygoid (state 1), although this feature is not present in more derived members of this group (Yates 2003a). Consequently Sauropodomorpha is recoded as polymorphic (states 0 and 1).

102. The basal sauropodomorphs *Plateosaurus engelhardti, Thecodontosaurus caducus* and *Thecodontosaurus antiquus* have large cervical epipophyses that overhang the rear margins of the postzygapophyses (Yates 2003a,b). Consequently Sauropodomorpha is recoded as polymorphic (states 1 and 2).

130. *Deltadromeus agilis* is recoded as having state 0.

131. *Coelophysis bauri, C. rhodesiensis, 'Syntarsus' kayentakatae* and Spinosauridae are recoded as having state 1 following the discovery of furculae in these taxa (Downs 2000; Tykoski *et al.* 2002; Lipkin & Sereno 2002).

140. *Deltadromeus agilis* is recoded as having state 1.

153. The basal sauropodomorph *Thecodontosaurus antiquus* has reduced phalangeal formula for the outer digits of its manus. The fourth finger supports just two phalanges while the fifth finger has none (Benton *et al.* 2000). Consequently Sauropodomorpha is recoded as polymorphic (states 0 and 1).

155. The basal sauropodomorph *Thecodontosaurus antiquus* has a well developed extensor pit on the distal end of at least metacarpal II and a weaker one on metacarpal III (pers. obs. of YPM 2195 and BRSUG material). Consequently Sauropodomorpha is recoded as polymorphic.

165. Several sauropodomorph skin impressions are known and these indicate a scaly skin (Mantell 1852; Czerkas 1994; Chiappe *et al.* 1998), thus the taxon is recoded as having state 0.

204. Rauhut (2003) coded this character as polymorphic for *'Syntarsus'* while noting in the text that it displays a cnemial crest that is confluent with the fibular condyle in proximal view (i.e. state 0) based upon a specimen of *Coelophysis* (= *Syntarsus*) *rhodesiensis.* Since the condition is the same in *'Syntarsus' kayentakatae* (Tykoski & Rowe 2004, fig. 3.9n) Rauhut's coding probably represents a simple typographical error in the data matrix. In any case, both *Coelophysis rhodesiensis* and *'Syntarsus' kayentakatae* are coded as 0 in this analysis.

Procompsognathus triassicus, Ligabueno andesi and *Velocisaurus unicus* were included in Rauhut's complete matrix but were excluded from the analysis for reasons of taxonomic redundancy and they are likewise omitted from this analysis. Rauhut also deleted *Xuanhanosaurus qilixiaensis, Siamotyrannus isanensis* and *'Chilantaisaurus' maortuensis* after an initial analysis because these poorly known taxa greatly increased the number of most-parsimonious trees without changing the relationships between the other taxa in the tree. Consequently, they are also omitted from this analysis. A further poorly known taxon, *Poekilopleuron bucklandi* that Rauhut kept in his analysis (but pruned from the tree he described), is omitted from this analysis for the same reasons. Lastly this analysis excludes the enigmatic taxon *Shuvosaurus inexpectatus* because it probably represents the skull of *Chaterjeea elegans,* a suchian archosaur (Long & Murry 1995).

Collapsing the Coelurosauria into a single terminal taxon (with the exceptions of the basal *Proceratosaurus bradleyi* and *Tugulusaurus faciles*) rendered 62 characters parsimony-uninformative (41 one of these are constant). Nevertheless, these characters are retained so that the character numbering system remains comparable to Rauhut's.

Analysis of this matrix (heuristic search, TBR branch swapping, random addition sequence with 20 replicates) using PAUP 4.0b (Swofford 2002) produced 810 most parsimonious trees that were 522 steps long. The strict consensus of these trees is highly resolved (Fig. 9). Herrerasauridae and *Eoraptor lunensis* are found to be non-eusaurischian saurischians. Coelophysoids in the broad sense are paraphyletic with true Coelophysoidea (*Liliensternus liliensterni, L. airelensis, Coelophysis bauri, C. rhodesiensis, Gojirasaurus quayi, Segisaurus halli* and *'Syntarsus' kayentakatae*) being the sister group of all other theropods. *Dilophosaurus wetherilli* forms a clade with *Zupaysaurus rougieri* and *Dracovenator regenti* which is the sister group of Ceratosauria + Tetanurae. This clade is supported by: paired nasolacrimal crests; a slot-shaped foramen at the base of the nasal process of the premaxilla; a pendant medial process on the articular; and tab-like dorsal processes on the medial and lateral sides of the articular. The basal topology of Tetanurae differs strongly from Rauhut's original analysis. As in that analysis, *'Szechuanosaurus' zigongensis* and *Piatnitzkysaurus floresi* form a basal trichotomy with a clade consisting of all other

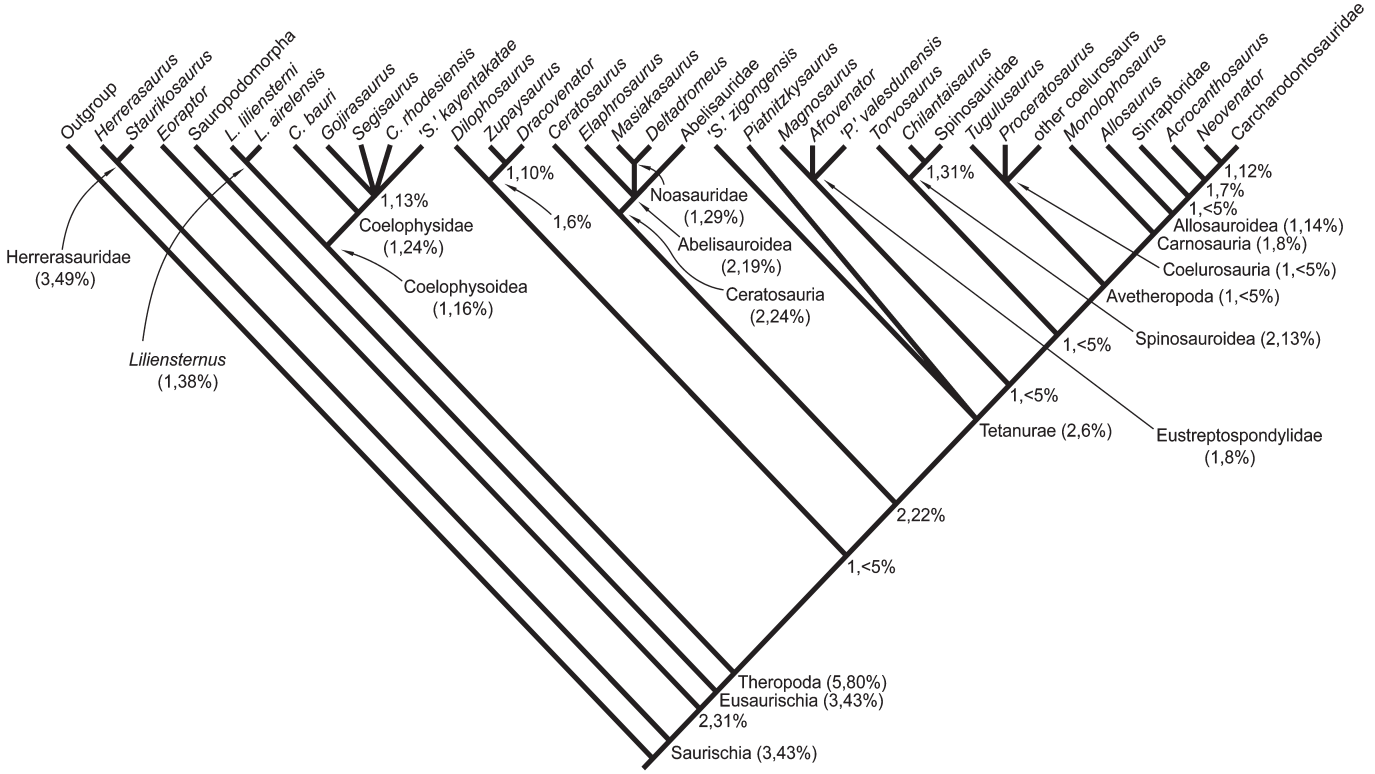


Figure 9. Strict consensus of 54 most-parsimonious trees. Only ingroup relationships are shown, the outgroup taxa (*Euparkeria, Marasuchus,* Ornithischia) are omitted. Numbers at each node indicate support measures, the left is the decay index and the right is the bootstrap support. Tree Length = 513, CI = 0.4893, HI = 0.5107, RI = 0.7152, RCI = 0.3499.

Tetanurae. Unlike Rauhut's analysis, all other non-coelurosaurian taxa do not form a single, highly inclusive, monophyletic Carnosauria. Instead Eustreptospondylidae (consisting of *Afrovenator abakensis, Magnosaurus* spp. and *'Poekilopleuron' valesdunensis*) and Spinosauroidea (*Torvosaurus tanneri, Chilantaisaurus tashuikouensis* and Spinosauridae) form serially closer outgroups to the Avetheropoda (Carnosauria and Coelurosauria). It is interesting to note that *Afrovenator abakensis, Magnosaurus* (as *Eustreptospondylus*) and *'Poekilopleuron' valesdunensis* were also found to form a clade exclusive of all other theropods in a recent analysis of basal tetanuran relationships (Holtz *et al.* 2004).

Very few nodes are robustly supported as can be seen from the generally low decay indices and very low bootstrap supports (Fig. 9). Theropoda is the only strongly supported clade (decay index = 5 steps, bootstrap = 80%) although Saurischia, Herrerasauridae and Eusaurischia are better supported than other nodes in the analysis. This low degree of support is not unexpected given the inclusion of several poorly known taxa (not least of which is *Dracovenator regenti* itself). As the position of *D. regenti* and the relationships of Coelophysoidea are the main questions of this work, a single Templeton test was performed that compared a tree from the set of most-parsimonious trees with one of the shortest trees where *Dilophosaurus wetherilli, Zupaysaurus rougieri* and *Dracovenator regenti* were included in an expanded, monophyletic Coelophysoidea. The difference in length between these two topologies was just one step, and it is unsurprising that the test found that there was no significant difference between them ($P = 0.858$).

DISCUSSION

The holotype of *Dracovenator regenti* clearly displays a number of synapomorphies of the neotheropod clade (*Coelophysis bauri* + Neornithes and all descendants of their most recent common ancestor, Sereno 1998) despite its incompleteness. Synapomorphies include: anteromedial processes of the nasals that separate the posterior ends of the nasal processes of the premaxilla (creating a w-shaped premaxilla–nasal suture on the internarial bar); a horizontal posterolateral process of the premaxilla that fails to contact the nasal; and a shallow antorbital fossa bordered by a low rounded ridge. Within this clade the specimen displays an intriguing melange of character states. Certain features closely resemble coelophysoids while others are found only in more derived theropods. Coelophysoid-like characteristics of *Dracovenator regenti* include: the low angle between the anterior and alveolar margins of the premaxilla; the retraction of the external nares (also in spinosaurids); the raised ventral margin of the antorbital fossa and its placement immediately above the alveolar margin of the maxilla. Characters found in Ceratosauria + Tetanurae, or included clades are: loss of the posteroventral process of the premaxilla; the probable presence of a rectangular anterior ramus of the maxilla offset from the ascending ramus by an inflection in the anterior profile of the maxilla; a concave attachment area for the depressor mandibulae on the dorsal surface of the retro-articular process; and a pendant medial process on the articular. The shape of the anterior ramus of the maxilla is inferred from the near right-angled bend in the posterior margin of the premaxilla between the main body and the posterolateral process. The pendant medial process of the

articular has an intriguing distribution. Its presence in the avetheropod tetanuran clade Allosauroidea has been previously documented but its presence in *Dilophosaurus wetherilli* has remained unnoticed. Nevertheless examination of the referred material (UCMP 77270) shows that the base of a broken pendant process is present. In the present analysis the process is regarded as a synapomorphy of *Dilophosaurus wetherilli* + (*Dracovenator regenti* + *Zupaysaurus rougieri*) that is convergent with Allosauroidea. However, its presence in the basal tetanuran *Cryolophosaurus ellioti* (Sereno *et al.* 1996, table 2) alludes to a broader distribution and the character could diagnose a more inclusive clade.

The cladistic analysis suggests that the broader coelophysoid assemblage may not be monophyletic but this topology is not a significantly better explanation of the data than one where *Dilophosaurus wetherilli, Dracovenator regenti* and *Zupaysaurus rougieri* are included in a broad, monophyletic Coelophysoidea. It is unfortunate that key taxa such as *Dracovenator regenti* and *Zupaysaurus rougieri,* which show a tantalizing mix of typical coelophysoid characters with more derived theropod features, are so poorly known. Hopefully future discoveries of *Dracovenator regenti* will help decide the matter conclusively.

Although the small snout (BP/1/5278) is strikingly similar to *Coelophysis rhodesiensis,* it does display some differences that indicate its referral to that taxon is doubtful. Most noticeably it has compressed, blade-shaped premaxillary teeth with serrations on their posterior carinae (Munyikwa & Raath 1999), as do those of *Dracovenator regenti,* whereas those of *Coelophysis rhodesiensis* do not (Raath 1977). If the anterior ramus of the maxilla is correctly interpreted as being rectangular with an associated sharp bend in the premaxilla–maxilla suture then this would be a further point of agreement between BP/1/5278 and *Dracovenator regenti. Coelophysis rhodesiensis,* like most coelophysoid grade taxa, has an anteroventrally directed first maxillary tooth (Tykoski & Rowe 2004) but in BP/1/5278 it is directed fully ventrally. This character cannot be determined in *Dracovenator regenti* but it does indicate that BP/1/5278 is not referable to *Coelophysis rhodesiensis.* Further differences between BP/1/5278 and *C. rhodesiensis* are subtler. These include more sharply defined fossae within the antorbital fossa, anterior to the antorbital fenestra, the lack of a dorsoventral expansion at the anterior tip of the dentary and the development of a tiny dorsolateral nasal crest. It is telling to note that in all of these features BP/1/5278 resembles *Zupaysaurus rougieri* which is found to be the sister taxon of *Dracovenator regenti* in the cladistic analysis. If BP/1/5278 does belong to *Dracovenator regenti* then it would represent a juvenile individual that is approximately 20% of the size of the holotype individual. Probably the nasal crests would grow into larger structures in adult individuals. Unfortunately the BP/1/5278 lacks the posterior end of the skull, so we cannot determine if the diagnostic features of the articular of *D. regenti* were present, neither is the preservation of the external surface of the premaxillae sufficient to determine if the bilobed fossa was present. The specimen differs from *D. regenti* by having an external naris that is not fully retracted posterior to the premaxillary tooth row and having a nasal process of the premaxilla that does not protrude far beyond the level of the posterior tip of the posterolateral process. However, if BP/1/5278 is truly a juvenile individual then we might expect these features to develop with ontogeny. In any case, there is no unequivocal autapomorphy linking BP/1/5278 to *Dracovenator regenti* and the referral is left as a plausible, but unproven, suggestion.

Dracovenator regenti is the first recorded body-fossil of any theropod, other than *Coelophysis rhodesiensis,* from the *Massospondylus* RZ of southern Africa. However, it has long been known from footprint evidence that theropods larger than *C. rhodesiensis* were present in this biozone. Ellenberger (1970) reported theropod footprints (as *Kainotrisauropus moshoeshoei*), referable to the ichnotaxon *Eubrontes* sp. (Olsen & Galton 1984), that were 34 cm long from the upper Elliot Formation. There is also a large theropod trackway from the overlying Clarens Formation (Raath & Yates 2005). The Clarens Formation contains taxa typical of the *Massospondylus* RZ (Kitching & Raath 1984). These traces come from a theropod similar in size to *Dilophosaurus wetherilli.* The holotype skull of *Dracovenator regenti* is estimated to have been about 500 mm long, and individual elements are comparable in size to those of *Dilophosaurus wetherilli,* so *Dracovenator regenti* is a plausible trackmaker for the large theropod traces of the *Massospondylus* RZ.

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ABBREVIATIONS

Institutional

BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg
CM	Carnegie Museum of Natural History, Pittsburgh
MB	Museum für Naturkunde der Humboldt Universität, Berlin
QG	Zimbabwe Natural History Museum, Bulawayo
SAM	South African Museum, Iziko Museums, Cape Town
UCMP	University of California, Museum of Palaeontology, Berkeley

Anatomical

a	articular
al	alveolus
an	angular
aof	antorbital fossa
aofe	antorbital fenestra
bf	bilobed fossa
c	cranial crest
ctf	chorda tympanic foramen
d	dentary
dmf	fossa for the attachment of the m. depressor mandibulae
dp	dorsal process of the articular
emf	external mandibular fenestra
en	external naris
g	glenoid
idp	interdental plate

j	jugal
l.	left
ln	lateral notch
lr	lateral ridge of the surangular
mp	medial process of articular
mpf	medial premaxillary foramen
ms	meckelian sulcus of the dentary
mx	maxilla
n	nasal
nf	narial fossa
np	nasal process of premaxilla
p	palatine
pa	prearticular
plp	posterolateral process of premaxilla
pmx	premaxilla
r.	right
rt	replacement tooth
s.	surface for articulation of
sa	surangular
sf	slot-like foramen
sp	splenial
sym	symphyseal surface
v	vomer
vc	ventral crest
vm	ventral margin of antorbital fossa

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APPENDIX 1. Character codings for the new characters (225–252) added to this analysis. For polymorphic character states, A = 0,1.

Euparkeria	00000	00000	000?0	00000	000?0	000
Marasuchus	?????	?????	000??	???00	00??0	000
Ornithischia	00000	00000	000?0	00010	00000	000
Eoraptor	0?0?0	00001	000??	0???1	000?0	000
Herrerasaurus	00000	00001	000?1	00011	00000	000
Staurikosaurus	?????	??0??	????0	?0???	0?0?0	0??
Sauropodomorpha	00000	00002	000?0	00011	10011	000
C. bauri	11010	11010	01001	00001	10011	010
Gojirasaurus	?????	?????	??0??	?????	?????	???
L. airelensis	?????	?????	?????	????1	?????	0??
L. liliensterni	?????	??0??	?10?1	????1	1???1	000
Dilophosaurus	11110	11010	00001	11101	100?1	0??
Segisaurus	?1???	?????	??0??	?????	1?0?1	0??
C. rhodesiensis	11010	11010	01011	0000?	10011	011
Magnosaurus	0?0?1	001??	000?0	?????	????1	0??
Monolophosaurus	0?000	00012	10??1	?0?11	1???1	0??
Piatnitzkysaurus	?????	?????	?0000	?????	?00?1	0?0
Proceratosaurus	????0	000??	?0??0	?????	?????	???
'S.' zigongensis	?????	?????	?0???	????1	100?1	???
Allosaurus	01001	00012	10000	10111	10011	000
Ceratosaurus	01001	00012	00000	00?01	111??	010
Elaphrosaurus	?????	?????	??0??	????1	111?1	010
Sinraptoridae	01001	00012	10000	10111	100?1	0?0
Torvosaurus	?1001	0011?	?00?0	?????	?00?1	000
Afrovenator	?????	?????	000??	????1	1?011	0?0
Chilantaisaurus	?????	?????	?????	?????	?????	???
Neovenator	??001	000??	?00?0	?????	????1	??0
Deltadromeus	?????	?????	??1??	?????	?11??	?00
Acrocanthosaurus	0?001	00012	100?0	?0111	10011	000
Abelisauridae	01001	00012	00000	00101	111?1	010
Spinosauridae	1?010	01000	10001	0?111	100?1	0?0
Carcharodontosauridae	0???1	0001?	100?0	?????	???11	??0
other coelurosaurs	01000	00012	10000	00111	1001A	000
'P.' valesdunensis	0?0??	001??	00??0	?????	?????	???
Masiakosaurus	?????	??0??	?01?0	?????	?11??	110
Zupaysaurus	1????	??01?	01??0	?????	?????	?1?
'S.' kayentakatae	1?010	110?0	01011	000??	?????	?11
Tugulusaurus	?????	?????	?????	?????	?????	00?
Dracovenator	?1110	0001?	?1???	111??	?????	???

APPENDIX 2. Character codings (characters 1–224) for the new, or significantly modified, taxa added to this analysis. For polymorphic character states: A = 0,1; B = 1,2; C = 0,2; D = 0,2,3.

Acrocanthosaurus

10?01 10000 01001 11011 01221 10110 11010 00010 00001 00010 020?? ?????
????1 02?12 001?1 01??? 00?00 00111 12101 20010 02100 20110 ???01 0?001
1?101 00111 ?1000 10000 00001 20011 10210 10211 ???1? 1???? ????? ????
01220 00101 00001 01210 011?? 202?? ????1 ????0 ?220

Carcharodontosauridae

?0??? 20?01 11000 10111 10221 10110 1101? 00011 01001 ????? 1B0?? 01111
?000? ????2 0???? 0???? ?00?0 00111 ????1 20010 12100 201?0 ????? ??001
1?10? ?01?? ???00 ????? ????? ????? ????? ????? ????? 101?0 ???00 0?001
01220 00101 00101 01210 011?? 20201 100?? ????0 ????

'S.' kayentakatae

02??1 20110 11101 10000 02110 00110 000?0 10000 00000 000?0 0100? ?????
??0?? ????0 00000 00??? 00?10 00100 0?000 000?? ????? ????? ????? ?????
????? ????? 10000 000?? ????? ????? ??1?? ????? ????? ????? ????? ?????
?0?0? ????? ??000 01100 01001 ?0?10 ???00 000?0 ?1??

Other coelurosaurs

0A0A1 20001 01010 11000 A0021 00110 10010 0A000 00C0A 01100 01110 01111
10AA1 03112 00111 0111A 00010 00111 1B0A0 21011 0B100 101A0 11200 0AA01
01010 00111 11000 10010 00001 D011A 10210 10212 00000 10110 10001 0101B
01021 00100 00CA1 012B0 A1111 2220B 10112 11010 0220

'P.' valesdunensis

010?1 200?? 21100 11??? ????1 1011? ????? 00?00 10001 ?0??? ?1000 0???0
0000? ?2??? 0???? 0121? 00000 00??? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????

Masiakosaurus

????? ???0? 00001 00??? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? 0000? ?01?0 00AA1 ????0 ?1010 12100 000?? ?2200 0???1
?1110 00??? ????? ????1 011?? ????? ????? ????? ????? ????? ????? ????0
00120 01??? ???00 00200 11111 102?? ???01 10110 ????

Zupaysaurus

????? ????0 01001 1?000 02020 00110 10000 0?000 00001 0001? 0???? ?????
????? ????1 00?10 00??? ?00?? 00??? ??0?0 ????? ????? ????? ????? ?????
????? ????? ????? 1???? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ?0??? ?01?? ??000 0001? ????

Tugulusaurus

????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
?1??? ????? ????? ????? ????? ??11? ????0 ??2?? ?001? ????? ????? ?????
????? ????? ???00 012B0 01101 212?? ???01 1101? ????

Dracovenator

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