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2003
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A definite prosauropod dinosaur from the Lower Elliot Formation (Norian: Upper Triassic) of South Africa

Adam M. Yates

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Johannesburg, Private Bag 3, WITS, 2050 South Africa.
E-mail: yatesa@geosciences.wits.ac.za

Received 3 June 2003. Accepted 10 September 2003

A new sauropodomorph dinosaur specimen is described and identified as a prosauropod. It is tentatively placed as the sister taxon of *Riojasaurus incertus* from Argentina. The systematic position of all commonly accepted sauropodomorph dinosaurs from the Lower Elliott Formation of South Africa is reviewed and it is found that none can be positively identified as prosauropod. *Euskelosaurus browni* is a *nomen dubium* based on material that cannot be identified further than Sauropodomorpha. *Blikanasaurus cromptoni* and *Antetonitrus ingenipes* are basal sauropods. *Melanorosaurus readi* is probably another basal sauropod but opinion remains divided. *Plateosauravus cullingworthi* presents conflicting character data and at present is classified as Sauropodomorpha *incertae sedis.* Consequently the specimen described here represents the only prosauropod specimen currently recognized in the Lower Elliot Formation of South Africa.

Keywords: Triassic, Lower Elliot Formation, South Africa, Sauropodomorpha, Prosauropoda.

INTRODUCTION

Prosauropod dinosaurs in the broad sense, that is any basal sauropodomorph that is not a member of the derived, columnar-limbed sauropod clade (i.e. *Vulcanodon* + Eusauropoda), have long been known from the Lower Elliot Formation (Upper Triassic, Karoo Supergroup) of South Africa. Indeed, the unit contains a moderate diversity of such dinosaurs, with three taxa, *Euskelosaurus browni, Melanorosaurus readi* and *Blikanasaurus cromptoni,* commonly being accepted as valid (e.g. Galton 1990). Another taxon, *Antetonitrus ingenipes,* has recently been added to the list but this was explicitly described as a basal sauropod, rather than a prosauropod (Yates & Kitching 2003). The previous three taxa are frequently referred to the Prosauropoda but recent phylogenetic work (Yates 2003, in press; Yates & Kitching 2003) suggests that none of them can be confidently placed in the Prosauropoda *sensu stricto* (i.e. the clade containing all sauropodomorphs that share a more recent common ancestor with *Plateosaurus* than with the sauropod *Saltasaurus*; Sereno 1998). The phylogenetic position of each of these taxa is briefly discussed below before the presence of true prosauropods in the Lower Elliot Formation is examined.

Euskelosaurus browni Huxley, 1866

Euskelosaurus browni is based on some fragmentary postcranial remains (BMNH R1625) of which a proximal right femur is most informative. It has been distinguished from *Melanorosaurus readi* on the basis of its sinuous femoral shaft, the placement of the lesser trochanter well away from the lateral margin of the femur in anterior view and the proximally placed fourth trochanter (Galton 1985). These are plesiomorphic features within Sauropodomorpha and there are at least two different taxa in the Lower Elliot Formation that display them. In addition, the holotype does not display any synapomorphies that would allow it to be identified as either prosauropod, basal sauropod or basal sauropodomorph. Consequently the name should be discarded as a *nomen dubium.* The name *Plateosauravus cullingworthi* (Haughton, 1924) becomes the next available species name for the diagnostic material (SAM 3341–3356, 3602–3603, 3607–3609) that was referred to *Euskelosaurus browni* by Van Heerden (1979). This species was originally described as a new species of *Plateosaurus* but Huene (1932) erected the new genus *Plateosauravus* to accommodate it. *Plateosauravus cullingworthi* does not display any obvious, unique autapomorphies but can be diagnosed by an unusual combination of characters not found in any other sauropodomorph. These include: moderately large size (femur length of at least 545 mm); anterior dorsal neural spines with distal, lateral swellings; tall posterior dorsal neural spines reaching a height that is more than twice the length of their base; a relatively slender humerus where the width of the distal end is less than one third of the total length of the bone; a strongly sinuous deltopectoral crest that is only 42% of the length of the humerus; the postacetabular process of the ilium is square-ended; the ischial peduncle of the ilium has a posterior 'heel'; a femur that is sinuous in both lateral and anterior views; the fourth trochanter located entirely in the proximal half of the femur and placed centrally on the posterior surface of the femur, well away from the medial edge; the descending process of the distal tibia extends as far laterally as the anterolateral process. Unfortunately, the specimens of *P. cullingworthi* lack the critical anatomical regions that are rich in useful characters (e.g. the skull and manus). Consequently, it cannot be placed with any certainty in the Prosauropoda, Sauropoda, or in a position basal to these two. A cladistic analysis by the author (Yates 2003) has found weak support for this taxon (called '*Euskelosaurus*' in that analysis) as a basal sauropod, based largely on its tall dorsal neural spines (greater than 1.5 times the length of the base) and the reduced deltopectoral

crest of its humerus (less than 50% of the length of the humerus). However, its position became highly labile just one step away from the most-parsimonious tree. The distal end of the neural spine of the single known anterior (pectoral) dorsal vertebra possesses lateral swellings. This character was not included in the analysis of Yates (2003) but subsequent analyses by the author (Yates, in press; Yates & Kitching 2003) have interpreted this character state as a synapomorphy of the Prosauropoda. Thus further work may yet support the placement of this species within the Prosauropoda but at the moment the data are inconclusive and it should be classified as Sauropodomorpha *incertae sedis.*

Melanorosaurus readi Haughton, 1924

This species was originally based on a composite collection of postcranial bones (SAM 3449, 3450), from which the femur (SAM 3450) is the most informative and it has been treated as the lectotype (Galton 1985; Van Heerden & Galton 1997), although this designation has not been formally proposed.

This species was also found to be a basal sauropod in the analysis by Yates (2003) and this has been strongly corroborated in subsequent analyses by the author (Yates, in press; Yates & Kitching 2003). Character states that support this position are the tall dorsal neural spines, dorsoventrally deep hyposphenes (equal to the diameter of the neural canal) on the dorsal vertebrae, the presence of four sacral vertebrae, a deep radial fossa on the ulna, and the failure of the descending process of the distal tibia to extend laterally to the craniolateral corner of the distal tibia. Only the last of these character states is actually visible in the syntype series, all of the others are gleaned from a set of referred specimens (two individuals both catalogued as NM R1551) (Van Heerden & Galton 1997). However, another recent analysis of early sauropodomorph relationships retains this taxon within the Prosauropoda (Galton & Upchurch, in press). This position is based on femoral character states that *Melanorosaurus readi* shares with the prosauropod *Riojasaurus incertus.* These include a straight femur in anterior view and a crest-like lesser trochanter that is shifted laterally. However, these characters are also present in basal sauropods such as *Antetonitrus ingenipes* and *Vulcanodon karibaensis* (Yates & Kitching 2003; Raath 1972; Cooper 1984). Thus, the identification of *Melanorosaurus readi* as a prosauropod is not compelling.

Blikanasaurus cromptoni Galton & Van Heerden, 1985

This specimen is based solely on a left epipodium, tarsus and pes (SAM K403). No other specimens have been referred to it.

All recent cladistic analyses of early sauropodomorph relationships that have included *Blikanasaurus cromptoni* have found that it is a basal member of the Sauropoda (Yates 2003, in press; Yates & Kitching 2003; Galton & Upchurch, in press). Character states supporting this position include the smoothly rounded posteromedial margin of the astragalus in dorsal view, and a shortened third metatarsal (40% of the length of the tibia).

So are there any incontrovertible prosauropods in the Lower Elliot Formation at all? A partial set of remains (BP/1/4953) from Hamelneuskop on the farm Nova Barletta, Clocolan district, Free State, cannot be referred to any of the taxa listed above and would appear to represent the first definite prosauropod remains to be recognized from the Lower Elliot Formation. The specimen was found in a horizon of large concretions near the top of the Lower Elliot Formation (Kitching & Raath 1984). It was initially identified as *Euskelosaurus* sp. (Kitching & Raath 1984) but at the time this name was simply used as a catch-all for large sauropodomorphs from the Lower Elliot Formation.

DESCRIPTION

An articulated series of ten dorsal vertebrae (probably the 3rd to the 12th dorsal vertebrae) and a right femur comprise the specimen. The quality of the preservation is not good. Indeed the first, second, and last vertebrae of this series are so distorted by explosive deformation that they yield no useful information. The positional identification of the vertebrae is based on the morphology of the first well-preserved vertebra (the third in the series) in comparison with the dorsal series of *Massospondylus carinatus* (pers. obs. of BP/1/5241), *Plateosaurus engelhardti* (Huene 1926) and *Riojasaurus incertus* (pers. obs. of PVL 3808). The third vertebra of BP/1/4953 possesses a neural spine that is cranio-caudally shorter and transversely broader than those following it and has strongly upturned transverse processes indicating that it derives from the anterior end of the dorsal column (dorsals 1–5 in *Plateosaurus engelhardti*; Huene 1926). The fourth vertebra of the series lacks these features, indicating that the first three vertebrae in BP/1/4953 represent dorsals 3–5.

All of the vertebrae have simple, hourglass-shaped centra with weakly defined pleural depressions. The neural arches are low (about equal to the height of the centrum), as are the neural spines. The anteroposterior length of the square-shaped neural spine of the 5th dorsal is short (half the total length of the vertebra). The transverse width of this neural spine is noticeably thicker than in the following vertebrae. In the following vertebrae (dorsals 6–8) the neural spine bases are much longer (three quarters of the total length of the vertebra) and almost twice as long as they are high. The posterior margin of these is strongly concave so that the caudodistal corner of the neural spine forms a triangular projection in lateral view. The neural arches are laminated as in most other saurischians (Wilson 1999) but these laminae resemble those of *Riojasaurus incertus* in being short, low and thick, especially those posterior to the 7th dorsal where they form such low ridges that the appellation 'lamina' is barely warranted. The 7th dorsal has a prezygodiapophyseal lamina but the vertebrae caudal to it do not (nomenclature of the laminae follows Wilson 1999). The paradiapophyseal lamina is present on all of the vertebrae that are well-preserved enough to retain their laminae except on the 12th dorsal where it is not present due to the proximity of the parapophysis to the diapophysis. The transverse processes are markedly short and thick. Those of the 5th dorsal are strongly upturned, whereas those

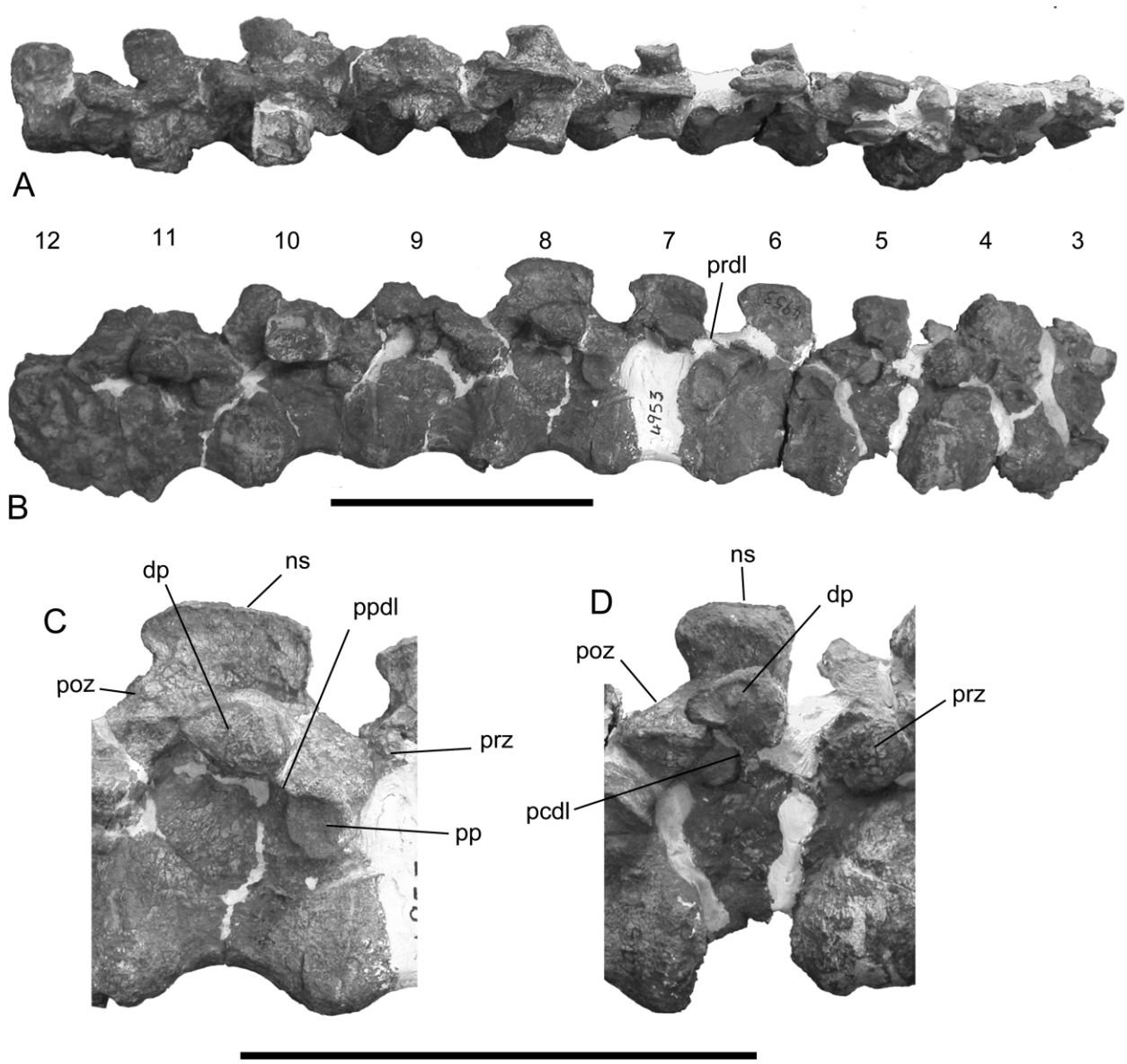


Figure 1. Articulated series of dorsal vertebrae of Prosauropoda indet. (BP/1/4953) in (**A**) dorsal and (**B**) right lateral views. **C**, 8th dorsal vertebra in right lateral view. **D**, 5th dorsal vertebra in right lateral view. Scale bars = 200 mm. Abbreviations: dp, diapophysis; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pp, parapophysis; ppdl, paradiapophyseal lamina; podl, postzygodiapophyseal lamina; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis.

posterior to it are only slightly upturned.

The femur closely resembles that of *Plateosaurus engelhardti* from Trossingen and lacks any of the femoral specializations listed by Galton (1985) as diagnostic for 'Melanorosauridae'. The medial inturning of the femoral head is not complete so that the long axis of the head lies at 45° to the transverse axis of the distal femur. The shaft is sigmoid in both lateral and anterior views. The anteroposterior diameter of the shaft is equal to the mediolateral diameter at the midlength of the femur. The lesser trochanter is a low, rounded ridge that is well removed from the lateral margin of the shaft in anterior view. The large fourth trochanter is placed entirely in the proximal half of the bone and is well removed from the medial margin of the shaft in caudal view. All of these features are found in more basal sauropodomorphs (e.g. *Thecodontosaurus antiquus* and *Efraasia minor*) and are primitive for Prosauropoda. Poor preservation makes it impossible to determine if there was any sort of extensor depression on the anterior distal surface.

DISCUSSION

The presence of laminated dorsal vertebrae and the lack of ornithischian synapomorphies, such as a long, finger-like lesser trochanter and a 'hooked' fourth trochanter, clearly identify BP/1/4953 as a saurischian dinosaur. Amongst saurischians it can be clearly referred to the Sauropodomorpha by the proximodistally elongate lesser trochanter that is not separated from the shaft of the femur by a cleft, and by the absence of prezygodiapophyseal laminae from the mid dorsal vertebrae. Diagnosis of the Prosauropoda is somewhat problematic, with little agreement between workers over the content of the clade or its diagnostic characters. Sereno (1999) diagnosed Prosauropoda with a long list of mainly cranial and manual characters, although some cervical, pelvic and

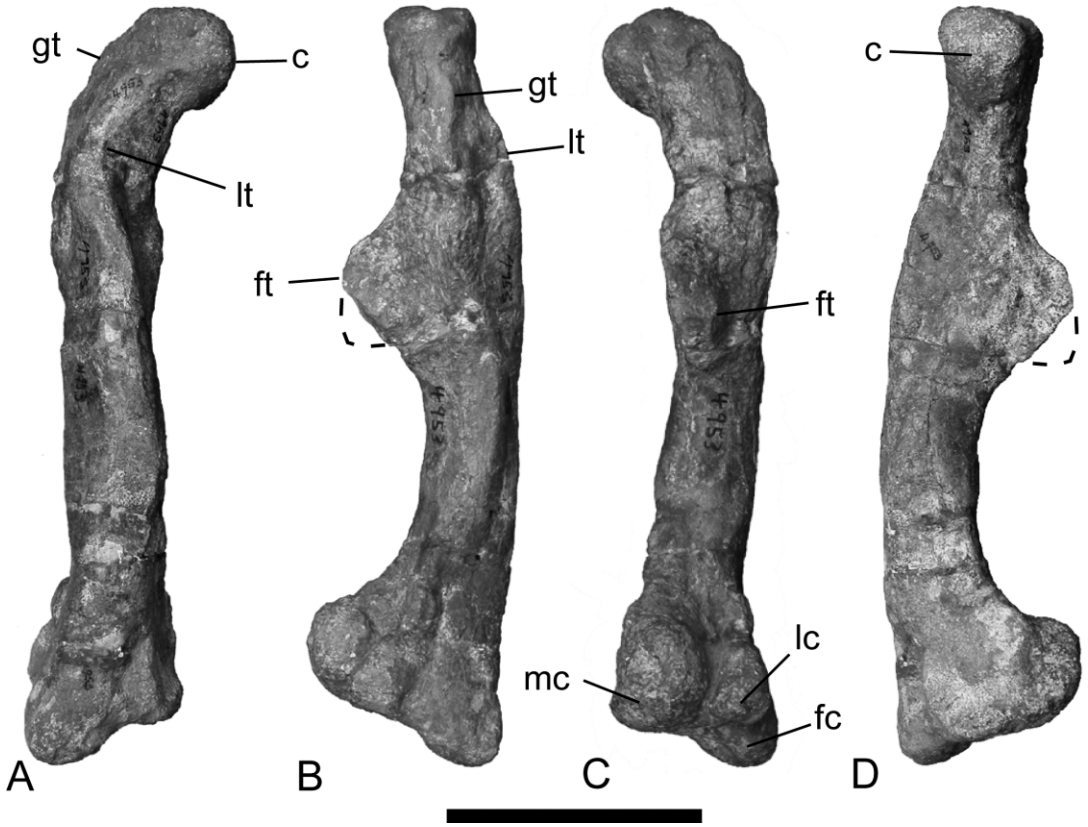


Figure 2. Right femur of Prosauropoda indet. (BP/1/4953) in (**A**) cranial, (**B**) lateral, (**C**) caudal and (**D**) medial views. Scale bar = 200 mm. Abbreviations: c, caput; fc, fibular condyle; ft, fourth trochanter; gt, greater trochanter; lc, lateral condyle; lt, lesser trochanter; mc, medial condyle.

pedal characters were also included. Yates (2003) has demonstrated that many of these character states are actually plesiomorphic for Prosauropoda because they are present in the taxa *Saturnalia tupiniquim, Thecodontosaurus antiquus* and *Thecodontosaurus caducus,* which are basal to the Prosauropoda + Sauropoda clade. In any case, none of the characters that Sereno (1999) used to diagnose the Prosauropoda can be determined in BP/1/4953. Of the character states used by Yates (in press) and Yates & Kitching (2003) to diagnose the Prosauropoda, only one could potentially be determined with the limited set of remains at hand. This is the presence of lateral swellings of the distal ends of the neural spines of the vertebrae in the pectoral region (dorsals 1–4 in *Riojasaurus incertus*; pers. obs. of PVL 3808). Unfortunately even this character cannot be determined with any certainty in BP/1/4953 because the neural spine of the presumed 3rd and 4th dorsals have been severely affected by explosive, pedogenic deformation. Nevertheless, the morphology of the 5th dorsal neural spine suggests that the derived condition was present in this specimen. In *Plateosaurus engelhardti* and *Riojasaurus incertus* the first vertebra following those with the lateral swellings is itself transversely expanded in comparison to all following vertebrae even though it lacks distinct swellings. Similarly, the neural spine of the 5th dorsal vertebra of BP/1/4953 is transversely expanded in comparison to those behind it, suggesting that the neural spines preceding it may have borne lateral expansions. It should also be noted that the derived condition for this character is also present in the theropod *Dilophosaurus wetherilli* (Welles 1984, fig. 13). At present this is simply regarded as a convergence but as the sampling of larger, early saurischians improves, this character may be found to be more widespread. A more useful character state that can be used to diagnose BP/1/4953 as a prosauropod is the presence of mid-dorsal neural spines with concave posterior margins in lateral view (Fig. 3). This character has not yet been employed in cladistic analyses of sauropodomorph relationships but it can be seen to be well developed in *Riojasaurus incertus* (Bonaparte 1972, fig. 57a), in *Lufengosaurus huenei* (Young 1941, fig. 6), and to a lesser extent in *Plateosaurus engelhardti* (Huene 1926, plate 2, fig. 2). The condition is also present, but weakly developed, in *Massospondylus carinatus* (Galton 1976, fig. 4). In contrast, outgroups to Prosauropoda, or at least the clade *Riojasaurus* + Plateosauria, have neural spines with straight posterior margins and no projecting posterior distal corner. These include herrerasaurids (e.g. *Herrerasaurus ischigualastensis*; Novas 1994, fig. 1), theropods (e.g. *Dilophosaurus wetherilli*; Welles 1984, figs 14 & 15), sauropods (e.g. *Kotasaurus yamanpalliensis*; Yadagiri 2001, fig. 4g) and *Efraasia minor* (pers. obs. of SMNS 12354).

Further evidence supporting the position of BP/1/4953 can be gleaned from a derived character that the specimen shares with *Riojasaurus incertus,* suggesting that these two taxa might have a sister-group relationship within Prosauropoda. *Riojasaurus incertus* is remarkable amongst sauropodomorphs in having poorly developed lamination of the neural arches of the dorsal vertebrae, especially those from the middle and posterior end of the series. Instead of forming tall, thin webs of bone, the laminae of

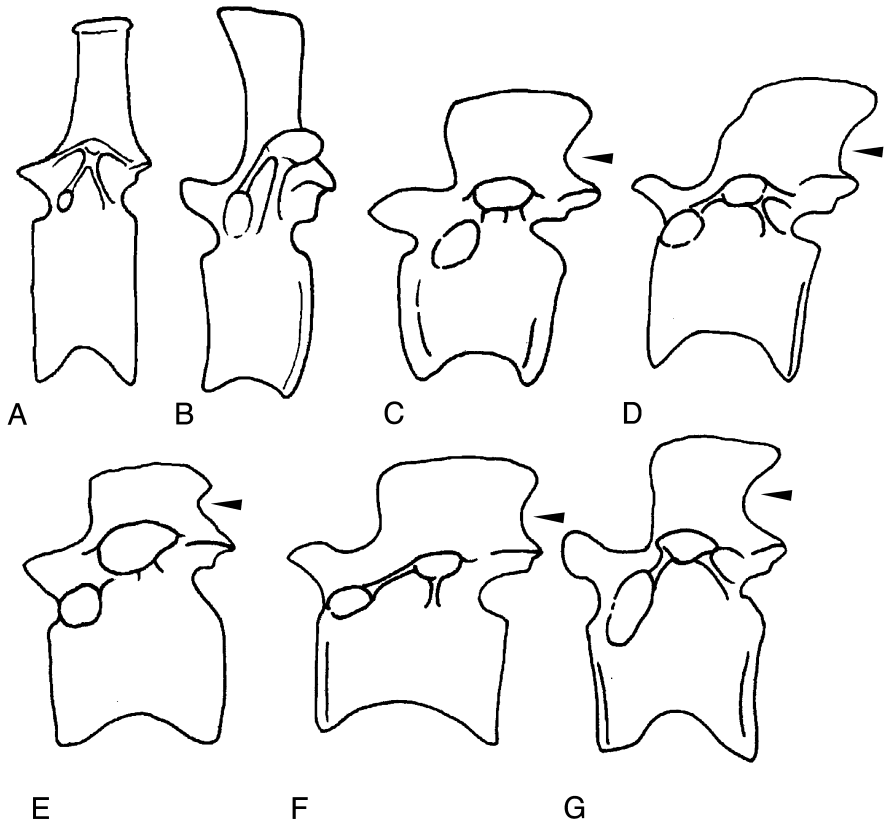


Figure 3. Middle to posterior dorsal vertebrae of various saurischians. **A**, *Herrerasaurus ischigualastensis,* redrawn from Novas (1994). **B**, *Kotasaurus yamanpalliensis,* redrawn from Yadagiri (2001). **C**, *Riojasaurus incertus*, redrawn from Bonaparte (1972). **D**, *Plateosaurus engelhardti,* redrawn from Huene (1926). **E**, Prosauropoda indet. (BP/1/4953). **F**, *Massospondylus carinatus,* redrawn from Galton (1976). **G**, *Lufengosaurus huenei,* redrawn from Young (1941). Arrows indicate the derived concavity in the posterior margin of the neural spine of prosauropods.

R. incertus are low, short, thick ridges which in the posterior dorsals are as wide as they are high (pers. obs. PVL 3808). The middle dorsals of BP/1/4953 display the same condition. Although explosive deformation may have accentuated the thickness of the laminae in BP/1/4953 it does not explain their lack of height and the character is accepted as having a biological rather than diagenetic origin.

The low neural spines of BP/1/4953 (where the height is less than length of the base) distinguish this specimen from *Plateosauravus cullingworthi.* In the latter taxon the middle and posterior neural spines are at least twice as high as they are long at the base (Van Heerden, 1979, pl. 9–12). The same character distinguishes BP/1/4953 from *Melanorosaurus readi* and *Antetonitrus ingenipes,* but these taxa can also be distinguished from BP/1/4953 on the basis of femoral morphology. In the latter taxa the femur is straight in cranial view, the lesser trochanter is crest-like and has shifted towards the lateral margin of the shaft, and the fourth trochanter straddles the boundary between the proximal and distal halves of the bone. BP/1/4953, on the other hand, retains the primitive condition for these characters with a sinuous femoral shaft in cranial view, a low, ridge-like lesser trochanter that is placed well away from the lateral margin of the shaft, and a fourth trochanter that is placed entirely in the proximal half of the bone.

Although BP/1/4953 is clearly distinct from the named, valid sauropodomorph taxa of the Lower Elliott Formation, it is not prudent to create a new name based on such incomplete material. The potential of the Lower Elliott Formation to yield good dinosaur remains is far from exhausted, as has been demonstrated by the recent discovery of a complete, but largely undescribed, sauropodomorph skull and skeleton (NM R3314; Welman 1999). The erection of new names based on low-quality types will only lead to taxonomic confusion in the future, as has been the case for dinosaurs from the Elliot Formation in the past.

The apparent close relationship between BP/1/4953 and *Riojasaurus incertus* from the Norian Los Colorados Formation of Argentina supports the hypothesis that the Lower Elliot Formation can be correlated with this unit (Lucas & Hancox 2001). *Antetonitrus ingenipes* from the Lower Elliot Formation is very similar to *Lessemsaurus sauropodoides* from the Los Colorados Formation. Both taxa are large and have tall neural arches and neural spines (general features widespread amongst sauropods) but also share the derived character of dorsal neural spines that expand transversely towards the distal end. An undescribed first metacarpal (almost certainly belonging to *Lessemsaurus sauropodoides*) from the Los Colorados Formation shares with *Antetonitrus ingenipes* the derived condition of being wider than it is long (pers. obs. of unregistered PVL material). Thus these taxa add further evidence of faunal similarity between the two formations and suggest that they are close to, if not actually coeval.

INSTITUTIONAL ABBREVIATIONS

BP, Bernard Price Institute for Palaeontological Research, Johannesburg; BMNH, Natural History Museum, London; NM, National Museum, Bloemfontein; PVL, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; SAM, South African Museum, Cape Town; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

The late L. Huma collected the specimen described here. R. Damiani helped in the handling of the heavy specimens and made comments on an earlier draft of this work. P. Barrett and P. Galton reviewed the paper. E. Bordy provided invaluable discussions on the stratigraphy of the Lower Elliot Formation. This research was supported by a NRF postdoctoral fellowship.

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