

A primitive sauropodomorph from the upper Elliot Formation of Lesotho

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Abstract – A well-preserved, articulated dinosaur skeleton from southern Africa is described. The specimen comes from the upper Elliot Formation (?Hettangian) of Ha-Ralekoala (Lesotho) and represents a new species: *Ignavusaurus rachelis* genus et species nova. A cladistic analysis suggests that *Ignavusaurus* is more derived than *Thecodontosaurus–Pantydraco*, but more primitive than *Efraasia*. *Ignavusaurus* indeed shares a number of unambiguous synapomorphies with the taxa more derived than *Thecodontosaurus–Pantydraco*, such as a fully open acetabulum, but it is more plesiomorphic than *Efraasia* and more derived sauropodomorphs as shown by the evidence of, for instance, the distal extremity of its tibia that is longer (cranio-caudally) than wide (latero-medially). The discovery of *Ignavusaurus* increases the known diversity of the early sauropodomorph fauna of the upper Elliot Formation, which stands as one of the richest horizons in the world in this respect.

Keywords: dinosaur, Jurassic, phylogeny, Africa.

1. Introduction

The upper Elliot Formation of southern Africa is well known by vertebrate palaeontologists as one of the most important Lower Jurassic terrestrial tetrapod-bearing assemblages (Knoll, 2005; Irmis & Knoll, 2008). Nevertheless, complete or subcomplete specimens are generally rare, as are articulated remains.

In his revision of basal sauropodomorph systematics, Galton (1990) only recognized one valid species, based on several dozen partial skeletons, in the upper Elliot Formation: *Massospondylus carinatus* Owen, 1854. Galton & Upchurch (2004) added *Melanorosaurus thabanensis* Gauffre, 1993. Nevertheless, the holotype and unique specimen of the latter taxon (a femur) comes from the lower Elliot Formation (Knoll, 2005). Vasconcelos & Yates (2004) revived *Gryponyx africanus* Broom, 1911 as a basal massospondylid, while Yates, Hancox & Rubidge (2004) reported the presence of an upper Elliot Formation sauropod probably related to *Vulcanodon karibaensis* Raath, 1972. At the same time, Barrett (2004) documented the existence of an upper Elliot Formation basal sauropodomorph that he recently described in details and named *Massospondylus kaalae* Barrett, 2009. Preliminary results also point to a fairly diverse upper Elliot Formation sauropodomorph fauna (Yates, Bonnan & Neveling, 2007).

Knoll (F. Knoll, unpub. Ph.D. dissertation, MNHN, 2002) referred to the existence of a skeleton of a young ‘prosauropod’ individual from the upper Elliot Formation of Lesotho and figured the right ilium (F. Knoll, unpub. Ph.D. dissertation, MNHN, 2002, pl. 10).

The aim of this paper is to fully describe, compare and discuss this specimen.

Institutional abbreviations. BM – Lesotho National Museum, Maseru, Lesotho; BP – Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; MB – Museum für Naturkunde, Berlin, Germany; MNCN – Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN – Muséum National d’Histoire Naturelle, Paris, France; NM – Nasionale Museum, Bloemfontein, South Africa; QG – Queen Victoria Museum, Harare, Zimbabwe; SAM – Iziko South African Museum, Cape Town, South Africa; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany; UCR – University of Zimbabwe, Harare, Zimbabwe.

2. Systematic palaeontology

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Sauropodomorpha von Huene, 1932
Ignavusaurus genus novum

Etymology. From Latin *ignavus*, coward, and ancient Greek *σαύροϛ* (masc.), a lizard, because the type locality, Ha-Ralekoala, literally means ‘The place of the father of the coward’.

Diagnosis. As for type and only known species.

Ignavusaurus rachelis species nova
Figures 2–14

Etymology. In honour of the paleontologist Raquel López-Antoñanzas from the National Museum of Natural Sciences in Madrid (CSIC). The name Raquel comes from the Hebrew *רַחֵל* (ewe); its most common Latin form (Rachel) is a noun of the third declension, hence the genitive ending in ‘-is’.

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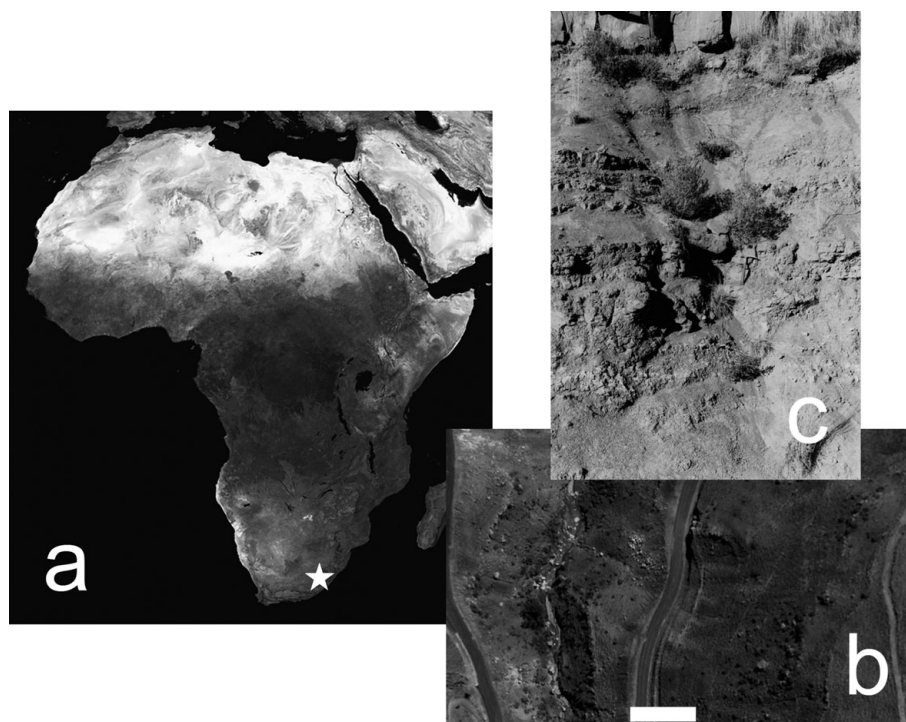


Figure 1. Discovery site of BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. (a) Situation in Africa; (b) aerial photograph of the area, scale bar equals 50 m; (c) excavation point (rock pick to right of photograph centre is about 33 cm long).

Holotype. BM HR 20, a partial, articulated skeleton. The specimen is provisionally housed in the National Museum of Natural History in Paris. It will eventually return to Lesotho as soon as the National Museum is built in Maseru.

Type locality. The specimen was found at a remote site in southern Lesotho, whose coordinates are S: 30°04'; E: 28°23' (Fig. 1a, b). It lay close to the place named Ha Ralekoala (Qacha's Nek district), not far from Sekake, at an elevation of approximately 1725 m.

Type horizon and age. The skeleton, which is largely articulated, was isolated in well-indurated reddish siltstone (Fig. 1c) of the upper Elliot Formation. A palynological study of the matrix has been carried out by R. Rauscher (Université de Strasbourg 1, Strasbourg) and E. Masure (Université Paris VI, Paris). It proved unsuccessful, but the upper Elliot Formation is most often thought to be Hettangian in age (Knoll, 2005 and references therein).

Diagnosis. A non-sauropod sauropodomorph dinosaur with the following unique combination of character-states: transverse width of the ventral ramus of the postorbital greater than its rostrocaudal width at midshaft; height of the postorbital rim of the orbit raised so that it projects laterally to the caudal dorsal process; first dentary tooth adjacent to symphysis; teeth linearly placed within the jaws; orientation of the dentary tooth crowns slightly procumbent; distribution of the serrations along the mesial and distal carinae of the tooth restricted to the apical half of the crown; 14 vertebrae between cervicodorsal transition and primordial sacral vertebrae; transverse processes of the dorsal vertebrae dorsally directed; caudal margin of middle dorsal neural spines concave in lateral view with a projecting caudodorsal corner; first caudal centrum shorter than high; shape of the metacarpal V about as wide as it is long with a strongly convex proximal articulation surface; caudal margin of the postacetabular process of the ilium bluntly pointed; lateral margins of the pubic apron concave in dorsal view; no longitudinal dorsolateral sulcus on

proximal ischium; roughly hemispherical femoral head with no sharp medial distal corner; subrectangular astragalus in proximal view; pyramidal process on the cranio-lateral corner of the proximal surface of the astragalus; transverse width of the proximal end of the fifth metatarsal 50% of the length of this bone. Although none of these features are proper to *Ignavusaurus rachelis*, they do not occur in this combination in any other taxon.

3. Description and comparisons

Numerous teeth (some of them associated) and many skull fragments, including the quadrate and the postorbital, have been retrieved. Much of the vertebral column is preserved, including most of the dorsal series and the proximal third or so of the tail (Fig. 2). The pectoral girdle is reduced to a fragment of scapula, whereas the pelvis is fairly complete. A substantial part of the left forelimb is present as well as a large portion of the right leg, a fragmentary left femur and phalanges of the left foot. Measurements are provided in Table 1.

Ignavusaurus rachelis was compared with the wealth of material of the Elliot Formation housed in the MNHN at first hand. Among these specimens, those studied by Gauffre (F.-X. Gauffre, unpub. Ph.D. dissertation, MNHN, 1996) are determined here as *Melanorosaurus readi* Houghton, 1924. All the material appears indeed to belong to a single species, whose femur is similar to that of *Melanorosaurus readi* (see Galton, Van Heerden & Yates, 2005), with a subrectangular, very tall, fairly vertical and straight fourth trochanter that is located near the medial border of the shaft. . . Dental comparison with this taxon was made on the basis of the observation of the skull of NM QR3314 and its published description (Yates, 2007b). Most of the remaining specimens kept in the MNHN were studied by Costedoat (D. Costedoat, unpub. D.E.S. dissertation, Univ. Paris, 1962) and are identified here as *Massospondylus* cf. *carinatus*. These

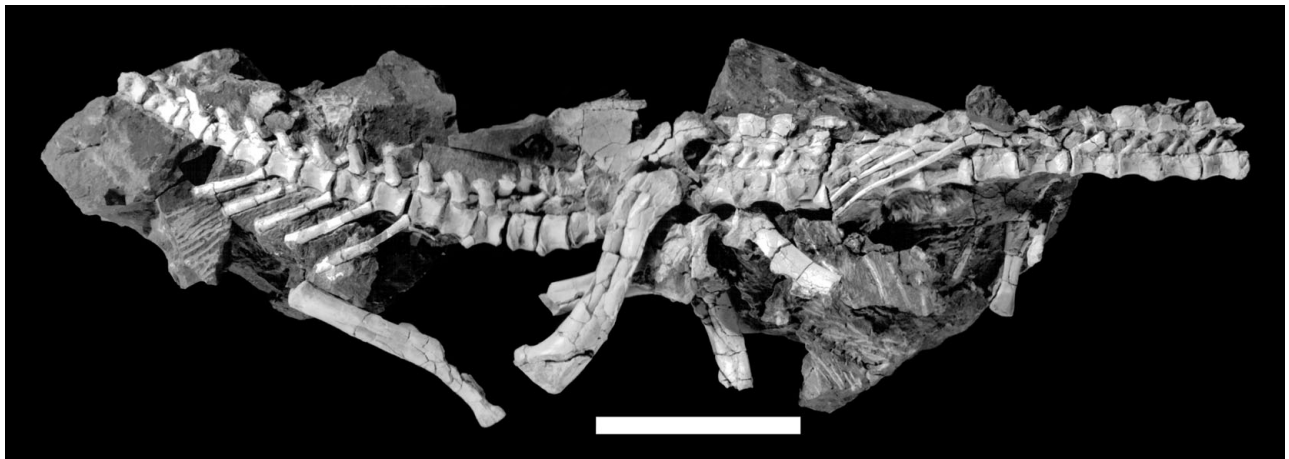


Figure 2. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Part of the specimen as exposed in the course of preparation. Scale bar equals 12 cm.

Table 1. Measurements of *Ignavusaurus rachelae* gen. et sp. nov.

Element	Measurement (mm)
Length of the dorsal centrum 3	29.5
Length of the dorsal centrum 14	22.7
Length of the dorsosacral centrum	26.6
Length of the sacral centrum 1	20.1
Length of the sacral centrum 2	24.3
Length of the caudal centrum 1	19.7
Length of the caudal centrum 14	20.1
Distal width of the left scapula	32.7
Proximal width of the left humerus	28.5
Length of the left ulna	66.2
Length of the left radius	60.3
Length of left metacarpal III	22.4
Length of left metacarpal IV	17.7
Length of left metacarpal V	10.8
Length of phalanx 1 of left manual digit III	9.6
Length of phalanx 2 of left manual digit III	8.1
Length of phalanx 3 of left manual digit III	7.7
Length of ungueal phalanx of left manual digit III	10.4
Length of phalanx 1 of left manual digit IV	6.8
Length of phalanx 2 of left manual digit IV	4.1
Length of phalanx 3 of left manual digit IV	3.6
Length of phalanx 1 of left digit manual V	6.9
Length of right ilium	95.3
Length of right ischium	105.7
Length of the left pubis	121.9
Length of the right femur	152.7
Distal width of the right tibia	18.8
Length of right metatarsal V	28.5
Length of phalanx 2 of right pedal digit II	12.7
Length of phalanx 2 of right pedal digit III	14.6
Length of phalanx 3 of right pedal digit III	12.0
Length of the phalanx 1 of right pedal digit V	6.4

latter observations were complemented by comparisons with the description of this taxa provided by Cooper (1981), as well as by observations of additional specimens of *M. carinatus* housed in the SAM. Comparisons with other taxa were essentially made through comprehensive material in the SMNS and MB (plateosaurids), a cast in the MNCN (*Mussaurus patagonicus*) and literature.

3.a. Skull and teeth

Unfortunately, the skull is fragmented in more than a hundred and twenty small bits, which limits comparisons. Among the largest fragments, the right quadrate and the

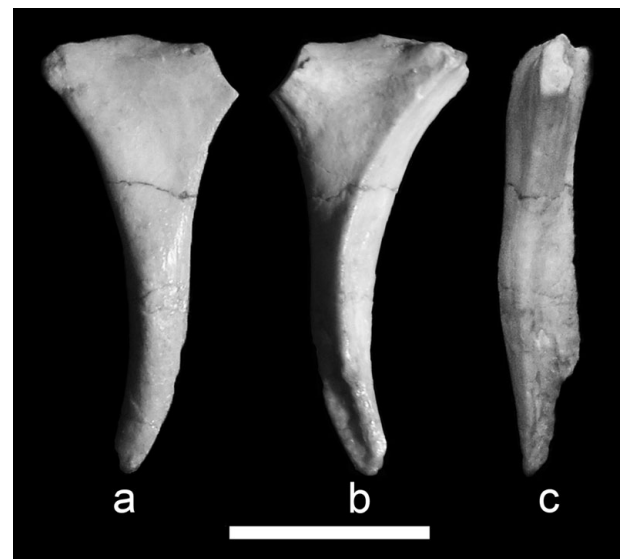


Figure 3. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Left postorbital: (a) lateral view; (b) medial view; (c) caudal view. Scale bar equals 1 cm.

left postorbital (Fig. 3) can be recognized. The quadrate is elongate with a strongly concave caudal margin in lateral and medial views. This latter makes an angle of about 80° with the condyle, which is simple and longer than wide. Although the rostradorsal and caudal branches have been broken, the postorbital no doubt displayed a typical Y-shape. Its latero-medial width decreases sharply caudally. In lateral view, the medial axes of the three branches cross over in a flat zone of the bone, which contrasts with the condition in *Plateosaurus longiceps* (MB.R.1937) in which the intersection of these axes takes place on a lateral eminence.

Some thirty complete or fragmentary teeth are present (Fig. 4). The height of most of the crowns does not reach 4 mm. All the teeth are narrow, labio-lingually compressed, and carinated. However, some are pointed and devoid of denticulation, whereas others are more spatulate, with a rather flat lingual surface and a convex labial one, and with a slight neck and up to five, relatively salient, apically directed denticles on each carina. Intermediate morphologies also occur, some teeth having in particular very attenuated denticles. The heterodonty of *Ignavusaurus rachelis* is fairly

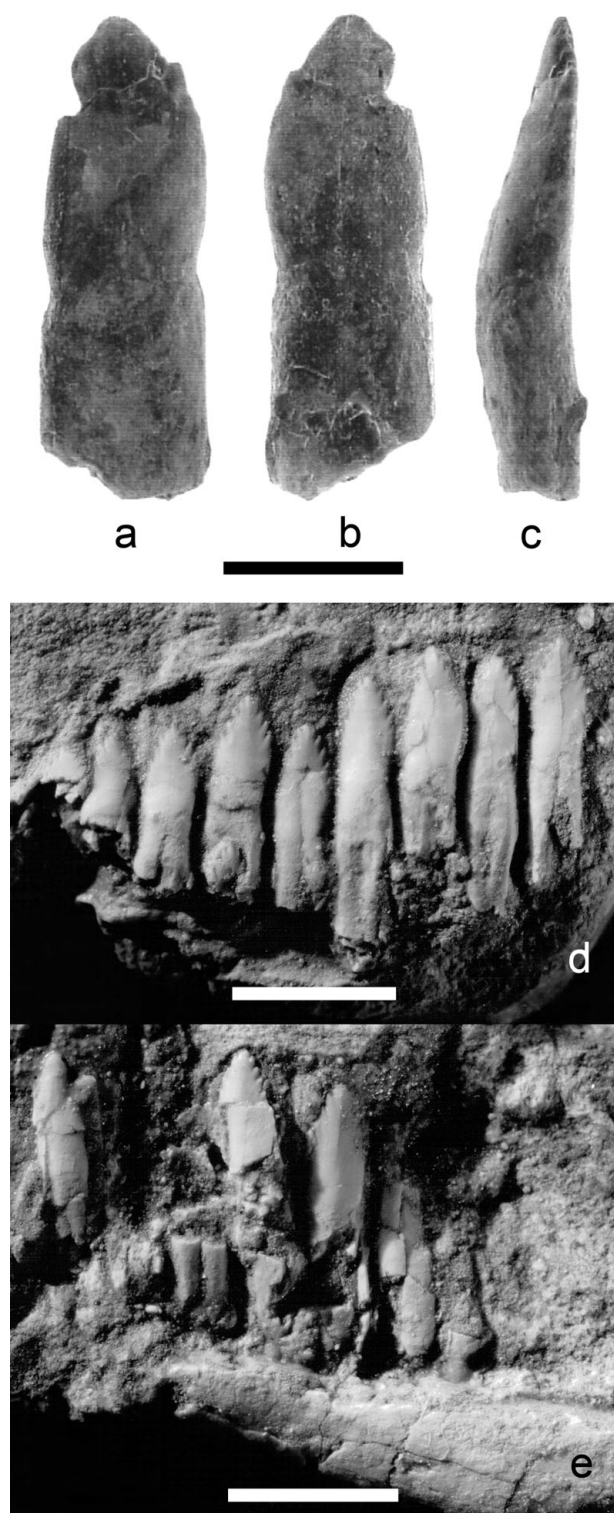


Figure 4. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Teeth and dentary: (a) labial view of an isolated tooth; (b) lingual view of the same tooth; (c) distal view of the same tooth; (d) labial view of a series of associated teeth; (e) labial view of left dentary with teeth. Scale bar equals 2 mm (a–c) and 5 mm (d, e).

remarkable since a dentition made of similar high-crowned teeth is the prevalent condition in basal sauropodomorphs. The single dentigerous bone found (a fragment of the left dentary; Fig. 4e) suggests that tapering teeth were rostrally positioned in the jaws and slightly procumbent.

The preservation of a series of nine teeth in their original respective position (Fig. 4d) suggests that the overlap was weak or non-existent. All in all, the dentition of *I. rachelis* suggests a more opportunistic diet than the possibly fairly herbivorous one that evolved in less basal sauropodomorph taxa such as *Plateosaurus* (see e.g. Barrett, 2000 and Barrett & Upchurch, 2007).

The skull and dentition of *Massospondylus carinatus* are relatively well known (see e.g. Gow, Kitching & Raath, 1990; Sues *et al.* 2004; Barrett & Yates, 2006). Without even invoking the difference in size, the teeth of *M. carinatus* differ from those of *Ignavusaurus rachelis* in their more marked neck and the shape and distribution of their denticles. The denticles of most of the teeth of *I. rachelis* are indeed very sharp and are distributed on the apical half of the crown, whereas, in general, they are quite rounded and present essentially on the apical third of the crown in *M. carinatus*.

The teeth of *Melanorosaurus readi* (Yates, 2007b; pers. obs.) are larger and relatively wider (mesiodistally) than those of *Ignavusaurus rachelis*. In addition, the denticles are serration-like in *M. readi*; they are more numerous and rather rounded than salient, in contrast with the condition in *I. rachelis*.

3.b. Vertebrae, ribs and hemal arches

Except for the most cranial preserved vertebra (namely the 2nd dorsal, which is reduced to the caudal half of the centrum) the following 29 vertebrae are fairly complete (Fig. 2). They constitute two articulated series disjointed in the sacral region. Based on the configuration (position of the parapophyses. . .) in a number of species belonging to the genera *Plateosaurus*, *Lufengosaurus*, *Yunnanosaurus* and *Riojasaurus* (Galton, 1990, 1999; pers. obs.), the series of 31 vertebrae of BM HR 20 comprises the last 13 dorsals (from the fragmentary 2nd to the 14th), 1 dorsosacral, 2 sacrals and the 15 first caudals. Breaks in several of the centra have made it possible to see that the cortical bone is very thin (less than 1 mm) and that it covered a very poorly ossified spongiosa.

The dorsal centra (Fig. 5) are slightly amphicoelous. Their ventral border becomes progressively more rounded caudally. They are more than twice as long as wide. In lateral view, the ventral borders appear concave as well as the lateral faces in ventral view. Numerous 'pleats' of the bone surface are present near the articular extremities. The neural arches are not fused to the centra. They are about twice as tall as the centra and their base is well developed, being about as high as the neural spine. They are relatively simply organized. The cranial centrodiaepophyseal lamina is similar in shape (thickness, roundness and straightness) and length to the caudal centrodiaepophyseal lamina. These laminae form a constant angle of 75° along the entire length of the dorsal series. A discrete migration of the parapophysis from the base of the neural arch toward the diapophysis can be observed in the series from the most cranial dorsal vertebra caudally. In the 3rd and 4th dorsals and possibly in the 5th also, the parapophysis involves a small part of the centrum. In all well-preserved dorsal vertebrae (namely all but the 2nd), the parapophysis is associated with the cranial centrodiaepophyseal lamina, which is therefore actually a paradiapophyseal lamina. The transverse processes of the dorsal vertebrae are dorsally directed, being at an angle of about 80° from one another. Although accounted for in part by preservational artifact (lateral crushing), this is likely a genuine character-state to some extent because this angle increases all along the vertebral series with the result that the last preserved caudals have almost horizontal

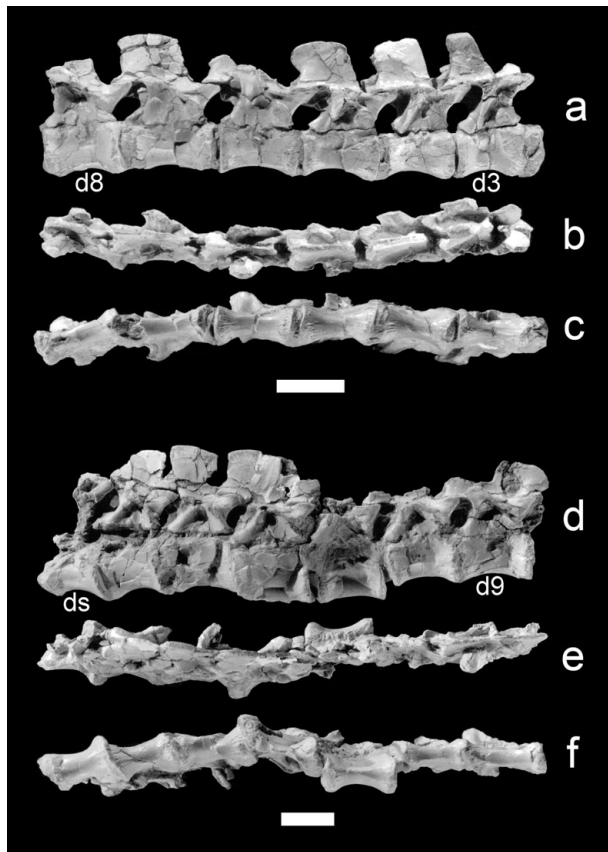


Figure 5. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Articulated dorsal vertebrae, plus dorsosacral (slightly reconstructed): (a) right lateral view of second to eighth dorsal vertebrae; (b) dorsal view of second to eighth dorsal vertebrae; (c) ventral view of second to eighth dorsal vertebrae; (d) right lateral view of ninth to fourteenth dorsal vertebrae, plus dorsosacral; (e) dorsal view of ninth to fourteenth dorsal vertebrae, plus dorsosacral; (f) ventral view of ninth to fourteenth dorsal vertebrae, plus dorsosacral. d3 – third dorsal vertebra; d8 – eighth dorsal vertebra; d9 – ninth dorsal vertebra; ds – dorsosacral vertebra. Scale bar equals 2 cm.

transverse processes. The caudal margin of the middle dorsal neural spines is concave in lateral view with a projecting caudodorsal corner. The dorsal portion of the vertebral series was associated with numerous ribs, which are fragmented and crushed along their length, but appear to be of the general basal sauropodomorph gross morphology (see Galton & Upchurch, 2004).

There is no coossification in the sacral region: there was no fusion between the sacrals and the sacral ribs and between these and the blade of the ilium, nor between the centra and the neural arches. The configuration of this zone is a bit uncertain due to imperfect preservation, but one dorsosacral and two sacrals appear to be present (in *Plateosaurus longiceps* and related species, there are generally two sacrals and a caudosacral; Galton & Upchurch, 2004). The first sacral is shorter than the dorsosacral and the second sacral, but otherwise all the three are rather similar. The facet for the articulation of the sacral rib is located cranially on the centrum (due to deficient preservation, no detail can be provided on the shape and position of the sacral ribs attachment on the ilium). The centrum is rounded ventrally. The centrum of the dorsosacral and of the first sacral shows a bilateral depression ventral to the pedicel of the neural arch.

The height/length ratio of the caudal centra (Fig. 2) decreases along the series: from the seventh caudal vertebra caudally, the centra are longer than high. The articular faces are ovular and the ventral faces of the centra are unobtrusively ‘carinated’. The poor ossification of the caudal vertebrae is visible in the absence of fusion of the neural arches with the centra and between the neural arches and the transverse processes. The latter are situated very low. The caudals bear a hemal arch from the second vertebra caudally. The length of the hemal arches is about a third greater than the height of the vertebra.

With respect to the dorsal vertebrae, differences with *Massospondylus carinatus* are found mostly in the neural arches. For instance, the relative height from the neurocentral suture to the level of zygapophyseal facets is much higher in *Ignavusaurus rachelis*. In the 13th dorsal vertebra of *I. rachelis* this height is more than 80% the height of the centrum, whereas it is about 60% in *M. carinatus* (Cooper, 1981, fig. 10). Important differences with *Melanorosaurus readi* are also present. In this taxon, the dorsal centra are more derived in being always proportionally shorter. The neural arch height/centrum height ratio is higher in *I. rachelis* than in *M. readi* and the plateosaurids. In the latter, the base of the neural arch is flat, the cranial centrodiapophyseal lamina tends to be thinner and shorter than the caudal one (especially in caudal dorsals) and they orientate differently than in *I. rachelis*.

The caudals of *Ignavusaurus rachelis* are very different from those of *Massospondylus carinatus* as figured by Cooper (1981, figs 15, 16c). For instance, in *M. carinatus* the articular surfaces of the midcaudals are not ovular, but rather heart-shaped. In contrast with the condition in *I. rachelis*, the caudal articular surfaces appear somewhat convex in lateral view. In *M. carinatus*, the ventral border of the caudals appears much more concave in lateral view than in *I. rachelis*. Moreover, the neural arch of the caudal vertebrae of *M. carinatus* covers only the cranial-central portion of the centrum versus almost all the dorsal surface in *I. rachelis*. In comparison with MNHN MAF 977 (a middle caudal vertebra of *Melanorosaurus readi*), some differences are also obvious. For instance, the articular surfaces are more rounded than ovular, the caudal articular apophyses are less elevated and, above all, the transverse processes are both situated and directed more ventrally. In plateosaurids, the length of the hemal arch is about equal to the height of the vertebra that bears it.

3.c. Gastralia

The gastralia are long ‘spaghetti-like’ rods that are ovoid in cross-section, instead of being rather cylindrical as in *Massospondylus carinatus* (Cooper, 1981).

3.d. Scapula

Unfortunately, only the distal extremity of the left scapula is preserved (Fig. 6a, b). It is gently, proximo-distally arched. The distal expansion is narrower than in *Massospondylus carinatus* (Cooper, 1981, fig. 23a, b) and might have been partly cartilaginous.

3.e. Humerus

Only about the distal third of the left humerus is present (Fig. 6c–f). In cranial view, both the longitudinal bulges are strongly convex. The intercondylar surface is roughly triangular. In caudal view, the concave surface (olecranon

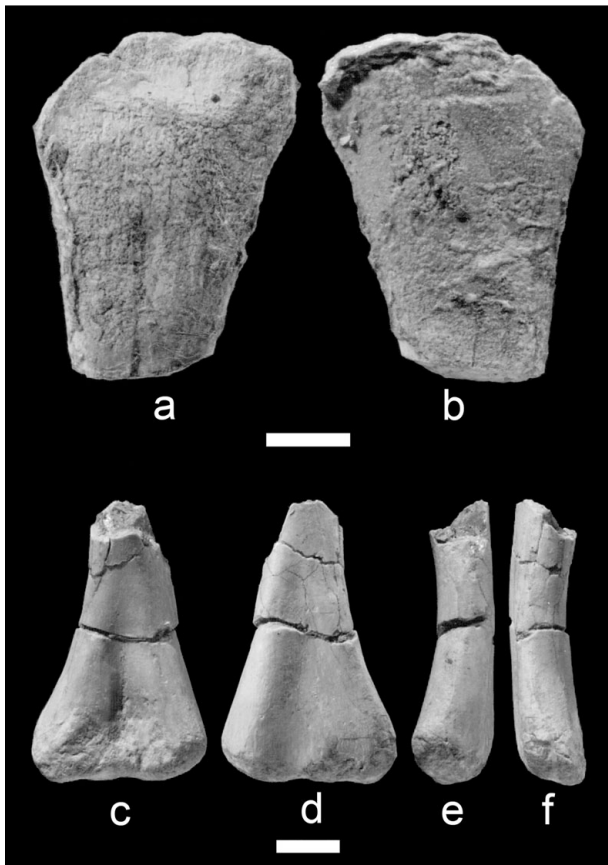


Figure 6. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Distal extremity of left scapula and distal end of left humerus: (a) lateral view of scapula; (b) medial view of scapula; (c) cranial view of humerus; (d) caudal view of humerus; (e) lateral view of humerus; (f) medial view of humerus. Scale bar equals 1 cm.

fossa) is limited laterally by a proximo-distally lengthened swelling. The medial condyle extends slightly more distally than the lateral one.

In cranial view, the distal condyles of the humerus of *Massospondylus carinatus* are separated by a rather deep semicircular fossa (Cooper, 1981, figs 26, 27), which is lacking in *Ignavusaurus rachelis*. In *Melanorosaurus readi* (MNHN MAF 981), the medial bulge of the cranial side is much flatter than in *I. rachelis*, approaching the condition in eusauropods.

3.f. Ulna

Only the left, quite well-preserved, ulna is present (Fig. 7a–d). The proximal articular surface is roughly triangular in proximal view. The olecranon process is moderately developed, but the coronoid process is prominent. The shaft has an elliptical cross-section. The distal epiphysis is relatively weakly transversally expanded and only slightly convex.

The extreme weakness of the intercotylar crest makes the ulna of *Ignavusaurus rachelis* strikingly different from that of a number of taxa such as *Plateosaurus longiceps*, *Massospondylus carinatus* and *Melanorosaurus readi* (MNHN MAF 765). In addition, the sigmoid notch is much more pronounced in *I. rachelis* than in *M. carinatus*, so that both the olecranon and coronoid process are more conspicuous in the former. In *I. rachelis*, the extremities are disposed at around 40° from one another. This is close to the condition

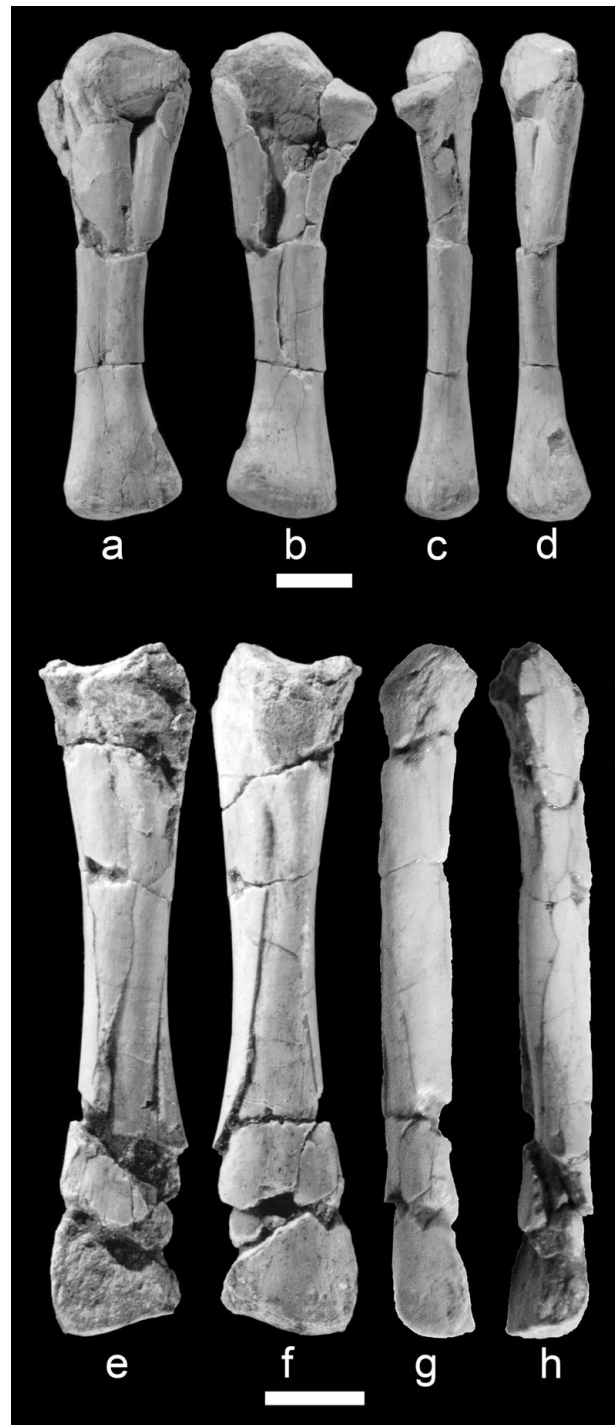


Figure 7. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Left ulna and left radius: (a) lateral view of ulna; (b) medial view of ulna; (c) cranial view of ulna; (d) caudal view of ulna; (e) lateral view of radius; (f) medial view of radius; (g) cranial view of radius; (h) caudal view of radius. Scale bar equals 1 cm.

in *Melanorosaurus readi*, but clearly lower than in *M. carinatus*, in which the twisting is about 60° (Cooper, 1981). In comparisons with *M. carinatus* (Cooper, 1981, p. 735, fig. 31), *I. rachelis* is also distinguished by the absence of a distal tubercle for the attachment of the radio-ulnar ligament. On the whole, the ulna of BM HR 20 clearly differs from the ulna of *M. carinatus*, as well as from that of larger Triassic forms.



Figure 8. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Left metacarpal III and phalanges of manual digit III: (a) dorsal view; (b) right lateral view. Scale bar equals 1 cm.

3.g. Radius

Only the left radius is present (Fig. 7e–h). In the matrix, it was positioned inside out at about 130° from the humerus and 135° from the ulna. It is a lightly built bone in which, as usual, the proximal extremity is concave and cranio-caudally expanded. The distal one, which is incomplete, is rather flat. The diaphysis is straight; the distal and proximal extremities are disposed at nearly 30° from one another.

The twisting of the diaphysis of the radius in *Ignavusaurus rachelis* is not far from that in *Plateosaurus cullingworthi* (van Heerden, 1979, pls 27, 28). However, it is much less than that in *Massospondylus carinatus* (about 45° according to Cooper, 1981; a difference whose amplitude can hardly be accounted for by crushing). Moreover, in comparisons with the radius of *M. carinatus* and *P. cullingworthi*, that of *I. rachelis* appears less broad at the level of the extremities, the articular surfaces of which are also different. This is especially true for *M. carinatus*, for which the distal condyle is said to be strongly convex (Cooper, 1981, fig. 29) and the proximal articular surface is also rounded.

3.h. Carpus

No element of the carpus can be determined with certainty. However, close to the distal extremity of the ulna (but possibly a little displaced), a small (diameter of almost 5 mm), somewhat lentil-like bone was uncovered. The identification of this bone is difficult. Its shape is different from the carpal bones of *Massospondylus carinatus* as figured by Cooper (1981, figs 32–36), but it recalls the possible remnant of radiale described by Broom (1911, p. 295) in *Gryponyx africanus*.

3.i. Metacarpal III and phalanges of manual digit III

Metacarpal III and the phalanges of manual digit III are well preserved (Fig. 8). Metacarpal III has strongly concave lateral margins. The ventral face is much flatter than the dorsal one. The proximal articular surface is flat, whereas the distal one is convex. The first phalanx is short, wider than deep in proximal view. The second phalanx is also short, but it is deeper. The third phalanx has a more elongate morphology. The unguis is weakly hooked, much deeper than wide in proximal view.

When compared with metacarpal III of *Massospondylus carinatus* (QG1282; Cooper, 1981, fig. 41), that of *Ignavusaurus rachelis* appears especially distinct in caudal view because of the strong concavity of the ventral side in the former. The phalanges of manual digit III of *I. rachelis* show

some morphological differences with the equivalents in the manus of *M. carinatus* (Cooper, 1981, figs 43, 45, 46), but they are unobtrusive. The unguis phalanx of digit III of *I. rachelis* appears more ovular than that of *M. carinatus* (QG1160; Cooper, 1981, fig. 43) in proximal view.

The collection of the MNHN contains several dissociated metacarpals and phalanges that are difficult to identify. Gauffre (F.-X. Gauffre, unpub. Ph.D. dissertation, MNHN, 1996, fig. 32B) only described as metacarpal III MNHN MAF 728, which shows a morphology that is on the whole similar to that of *Ignavusaurus rachelis*. However, some differences are noticeable. For instance, the ventral border of the distal articular surface is convex in metacarpal III of *Melanorosaurus readi*, whereas it is flat in that of *I. rachelis*. Moreover, the proximal articular surface makes a sharper angle with the longitudinal axis of the bone in *M. readi* than in *I. rachelis*.

3.j. Metacarpal IV and phalanges of manual digit IV

The metacarpal IV is similar to the metacarpal III, but it is only about 80% as large. The first phalanx is short and wide. The second phalanx has a close morphology, but it is much smaller. The third phalanx is a minuscule, short, slightly hooked bone.

In comparison with *Massospondylus carinatus* (Cooper, 1981, fig. 40h, i), the metacarpal IV of *Ignavusaurus rachelis* is wider at the extremities. The proximal articular surface of the two first phalanges appears more quadrangular in *I. rachelis* than in *M. carinatus* (Cooper, 1981, fig. 43). The third phalanx of the manual digit III is not hooked at all in *M. carinatus* (Cooper, 1981, fig. 45).

3.k. Metacarpal V and phalanx of manual digit V

The metacarpal V is a distinctive, short bone, wider proximally than distally. Both articular ends are convex. The medial, lateral, dorsal and ventral sides are more or less concave. The phalanx is small, wider than deep, with a simple proximal concavity.

The metacarpal V of *Ignavusaurus rachelis* is distinct from that of *Massospondylus carinatus* (Cooper, 1981, fig. 40a–d) in that its proximal extremity is much deeper than the distal one, instead of being about equally deep. The first phalanx of the manual digit V is remarkably less massive in *I. rachelis* than in *M. carinatus* as figured by Cooper (1981, fig. 45).

3.l. Ilium

Both ilia are preserved (Fig. 9). They are both incomplete but, fortunately, the unbroken parts of each are different so that one can have an accurate idea of the complete ilium. It is typical of the brachyliac condition (Colbert, 1964), which is characteristic of ‘prosauropods’. The blade is short and deep. Its dorsal margin is only weakly, but evenly, convex. The preacetabular process is pointed, about as long as deep. It does not project further cranially than the pubic peduncle and its depth is much less than that of the blade dorsal to the acetabulum. The postacetabular process is bluntly pointed. Its length is nearly equivalent to the distance separating the pubic and ischial peduncles. The pubic peduncle is elongated (about as long as the iliac blade is deep in its central part). The ischial peduncle does not bear any caudally projecting ‘heel’ at its articular end. The acetabulum is fully open.

The differences between the ilium of *Ignavusaurus rachelis* and that of *Massospondylus carinatus* (Cooper,

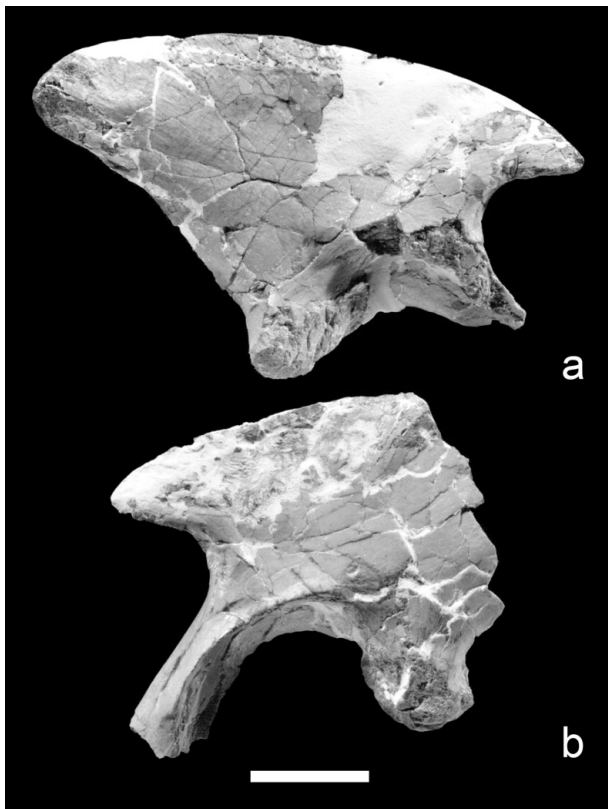


Figure 9. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Ilium (partly reconstructed): (a) right ilium, lateral view; (b) left ilium, lateral view. Scale bar equals 2 cm.

1981, figs 39, 51, 52) are numerous. Thus, the preacetabular process forms a much more open angle with the pubic peduncle in *I. rachelis* than in *M. carinatus*. There is generally a ridge ventral to the swollen surface of the postacetabular process that borders a rather deep depression for the origin of the *M. caudifemoralis brevis* in *M. carinatus* (Cooper, 1981, fig. 85). In *I. rachelis*, the *brevis* shelf is not so distinct. The pubic peduncle of the ilium of *I. rachelis* is straight, not curved in its midlength, and the ischiatic peduncle is more ventrally directed than in *M. carinatus*. The supra-acetabular buttress forms a more largely opened collar to the acetabulum on the ilium of *I. rachelis* than in *M. carinatus*.

The ilium of *Ignavusaurus rachelis* is distinguished from that of *Massospondylus carinatus* and *Melanorosaurus readi* by the dorsal border of the blade, from the preacetabular process to the postacetabular one, which generally does not form a regular curve. The shape of the postacetabular process of the ilium of *M. readi* is in between the thin and (moderately) pointed one of *I. rachelis* and the thick and blunt one of plateosaurids.

3.m. Pubis

A large part of the left pubis (proximal portion damaged), as well as fragments of the right, are preserved (Fig. 10a–d). This is a thin, relatively narrow bone. The whole of the dorsal surface is fairly flat, but there is a central longitudinal eminence on the ventral face in the proximal half of the pubic blade. The lateral edge is bowed toward the midline symphysis. The medial margin is marked by a small, badly preserved expansion proximally. The obturator notch is completely visible in dorsal view. Lateral to the obturator foramen, there is a shallow concavity on the ventral surface.

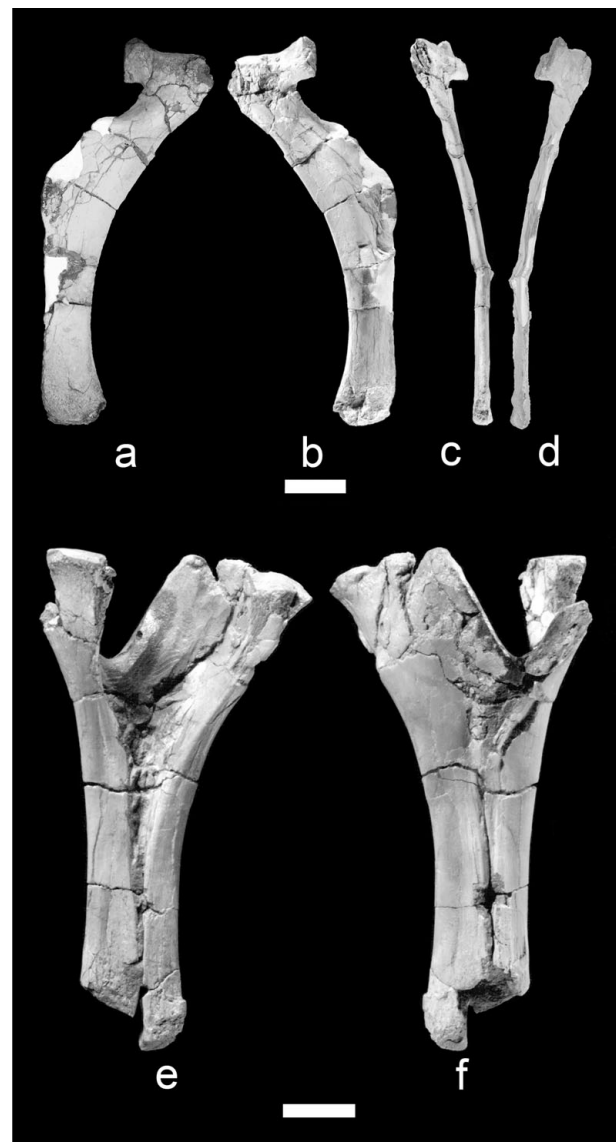


Figure 10. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Left pubis (partly reconstructed) and articulated ischia: (a) dorsal view of pubis; (b) ventral view of pubis; (c) lateral view of pubis; (d) medial view of pubis; (e) dorsal view of ischia; (f) ventral view of ischia. Scale bar equals 2 cm.

In comparison with *Massospondylus carinatus* (Cooper, 1981, figs 57, 58), the lateral border of the pubis of *Ignavusaurus rachelis* is clearly more curved. From this point of view, the pubis of *M. carinatus* appears intermediate between that of *I. rachelis* and that of *Melanorosaurus readi* (F.-X. Gauffre, unpub. Ph.D. dissertation, MNHN, 1996, fig. 36, pl. 17; Galton, Van Heerden & Yates, 2005, fig. 1.10c, e), which approaches the condition in plateosaurids (wide pubic blade with a rectilinear lateral border). Also, the ischium of *M. carinatus* bears a completely closed obturator foramen, whereas that of *I. rachelis* appears largely open as in '*Anchisaurus*' (Galton, 1976; Galton & Upchurch, 2004), but admittedly preservation of this zone is frequently imperfect (see e.g. Sereno, 2007).

3.n. Ischium

The ischia are articulated and rather well preserved, although a bit deformed and incomplete (Fig. 10e, f). In overall

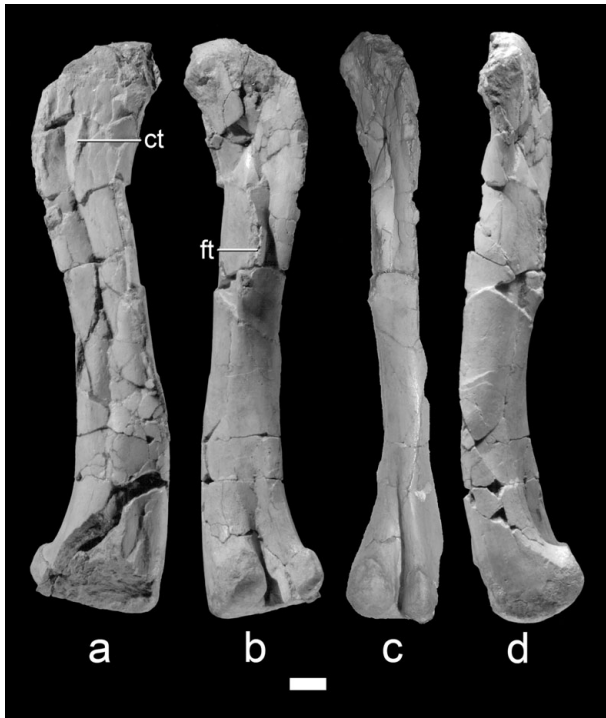


Figure 11. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Right femur: (a) cranial view; (b) caudal view; (c) lateral view; (d) medial view. ct – cranial trochanter; ft – fourth trochanter. Scale bar equals 1 cm.

morphology, the ischium shows two regions: a plate-like obturator section proximally and a rod-like distal shaft. The passage from the obturator plate to the shaft is very gradual. The ischial component of the acetabular rim is large and rectilinear. There is no longitudinal dorsal sulcus (for the origin of the ischio-femorals), but rather a barely noticeable groove. The distal extremity of the shafts, which was possibly cartilaginous, is lacking. In transverse section, the shaft is about as deep as wide and triangular in shape. No elongate interischial fenestra is present.

The ischium of *Ignavusaurus rachelis* differs in several respects from that of *Massospondylus carinatus* (Cooper, 1981, fig. 54). Thus, the participation of the ischial proximal plate to the acetabulum is well marked in *M. carinatus* by a widely open notch, which is absent in *I. rachelis*. The proximal shaft of the ischium of *M. carinatus* is somewhat heart-like in cross-section (Cooper, 1981, fig. 55) due to a deep dorsal groove, which is lacking in *I. rachelis*. The transverse width of the conjoined distal ischial expansions is much less in *M. carinatus* than in *I. rachelis*.

The morphological differences with the ischia of *Plateosaurus cullingworthi* (Van Heerden, 1979, fig. 14, pls 34, 35) are even more important. As a matter of fact, the lateral margin of the ischial shaft is continuously curved (concave) in this taxon, whereas the two margins are much more parallel in *Ignavusaurus rachelis*. Other differences include the more pronounced robustness of the area of articulation with the ilium in *P. cullingworthi*.

3.o. Femur

Both femora are present, but fractured. The left femur is much damaged proximally, the distal extremity is lacking and a histological examination revealed that the spongiosa is badly preserved as well. The right femur (Fig. 11) is in a much better state, even if both extremities are incompletely

preserved. In medial and lateral views, the longitudinal axis of the femur was strongly bent and the angle between the long axis of the femoral head and the transverse axis of the distal condyles is also pronounced (at least 30°). The femoral head is dorsomedially projected, not offset from the shaft on a neck and appears roughly hemispherical, but this condition might be due to the state of preservation of this zone. The cranial (= 'lesser') trochanter is positioned near the centre of the cranial face, so that it is not visible in caudal view of the femur. It is shaped like a proximo-distally lengthened raised process. The proximal tip of the cranial trochanter reaches about the level of the femoral head. There is no transverse ridge extending laterally from it. The fourth trochanter is positioned in the proximal half of the femur in a central location along the mediolateral axis. It is not perfectly preserved but, as far as can be determined, it is a low rugose ridge, whose length is about 1/5 the total length of the femur, and it is subtrapezoidal in profile, with a slightly steeper distal angle than the proximal slope. No extensor depression is well discernible on the cranial surface of the distal end of the femur.

The breakages, a small amount of deformation and the imperfect state of preservation of the femoral head limit the comparisons between the femur of *Ignavusaurus rachelis* and that of other taxa. The femur of *Massospondylus carinatus* has been well illustrated by Cooper (1981, figs 59, 60). It shows many differences with that of *I. rachelis*. In caudal view, the internal outline of the femur of *M. carinatus* (Cooper, 1981, fig. 60) shows a swelling at the level of the fourth trochanter. In this view, the internal outline of the femur is straight all along its length in *Ignavusaurus rachelis*. Moreover, the fourth trochanter of the femur of *I. rachelis* is slightly curved in caudal view, not sigmoidal like in *M. carinatus*. In cranial view, the cranial trochanter appears in a more central position in *I. rachelis* than in *M. carinatus*, although this difference could be in part due to deformation. The femoral shaft of *M. carinatus* is clearly more slender in its middle part, whereas the width of the shaft is nearly constant all along its length (in cranial and caudal views) in *I. rachelis*. With respect to the distal extremity, the differences are significant. For instance, it is not as caudally expanded in *I. rachelis* as it is in *M. carinatus*. In medial view, the distal articular surface in *I. rachelis* is not flat as in *M. carinatus*, but rather gently curved.

The femur of *Melanorosaurus readi* has been illustrated in particular by Gauffre (F.-X. Gauffre, unpub. Ph.D. dissertation, MNHN, 1996, pls 3–5; see also Galton, Van Heerden & Yates, 2005, figs 1.11e–h, 1.12a–d, 1.13a–c, g–i). The most obvious difference concerns the relative distance separating the femoral head from the fourth trochanter. Whereas the fourth trochanter is close to the femoral head in *Ignavusaurus rachelis* (a primitive character-state for sauropodomorphs), a deep neck makes the high fourth trochanter of *M. readi* extend onto the distal half of the bone. Moreover, in *M. readi* the fourth trochanter has a relatively shorter base than in *I. rachelis*. In cranial view, the cranial trochanter is rather lateral in *M. readi*, whereas it is central in *I. rachelis*. In medial and lateral views, the condyles of the femur of *M. readi* have a rounded caudal outline, whereas they become angular near the junction with body of the bone in *I. rachelis*.

3.p. Tibia

Only the right tibia is present in BM HR 20 (Fig. 12). Unfortunately, a great part of the cranio-proximal extremity is missing (the cnemial crest is not preserved) and the external region of the distal extremity is a bit damaged. The bone has an elongate shape, but it is still slightly shorter than the



Figure 12. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Right tibia: (a) cranial view; (b) caudal view; (c) lateral view; (d) medial view. Arrow points to posterior intercondyloid groove. Scale bar equals 1 cm.

femur (tibia/femur length ratio ≈ 0.95). The preserved caudo-proximal articular surface bears a characteristic groove, in continuity with the shaft of the bone, for part of the powerful caudal cruciate ligament. There is neither cranio-caudal nor significant transverse widening at the distal extremity, which is longer (cranio-caudally) than wide (latero-medially). The caudo-lateral process does not flare laterally. The distal articular surface is subrectangular.

In *Massospondylus carinatus* (Cooper, 1981, figs 65, 66), there is no groove on the proximal articular surface. Moreover, the malleoli show a greater difference (in lateral view) in their respective distal extension in *M. carinatus* than in *Ignavusaurus rachelis*. In medial view, the distal region widens more in *M. carinatus* than in *I. rachelis*.

A groove similar to that on the tibia of *Ignavusaurus rachelis* is not present on the tibiae of *Melanorosaurus readi* kept in the MNHN (MAF 927, 987, 1039, II LC, IV LC). Moreover, the distal extremity shows a straight border in *I. rachelis* in medial view, not a convex one as in MNHN MAF 987. Contrary to the condition in *M. readi*, the cranial malleolus was not clearly more expanded medio-laterally than the caudal malleolus in *I. rachelis*. In addition, the distal articular region in *I. rachelis* is not strongly convex (but rather flat), the cranial outline is convex (not concave) and the internal outline is rather concave (not convex). Noticeable differences also occur between the tibia of *I. rachelis* and that of *Plateosauravus cullingworthi* as illustrated by van Heerden (1979, fig. 17, pls 42–44), such as the widening of the distal extremity.

3.q. Astragalus

The astragalus of the right pes has been preserved almost completely (Fig. 13a, b). It is an angular, subrectangular bone.

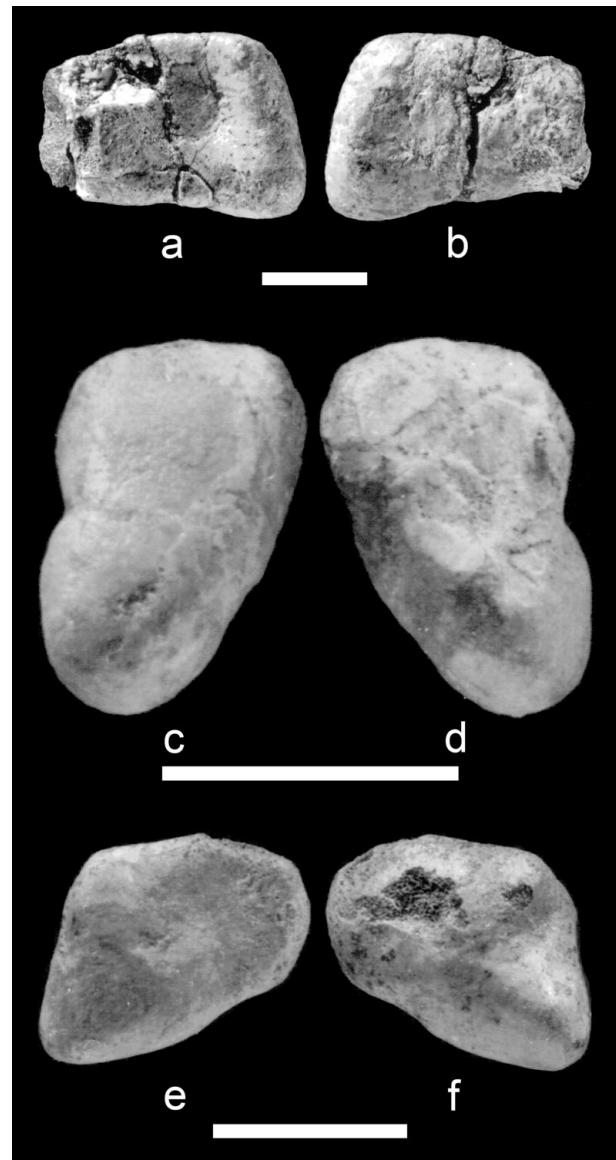


Figure 13. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Right astragalus, right distal tarsal III and right distal tarsal IV: (a) proximal view of astragalus; (b) distal view of astragalus; (c) proximal view of distal tarsal III; (d) distal view of distal tarsal III; (e) proximal view of distal tarsal IV; (f) distal view of distal tarsal IV. Scale bar equals 1 cm.

The distal side is weakly convex. The proximal one (about half of which is occupied by the medial cotylus) is concave, except for the ascending process. The latter provides an articular surface for the cranial malleolus of the tibia, whereas the caudal malleolus fitted in the small medial cotylus.

In general shape, the astragalus of *Ignavusaurus rachelis*, with its ‘interlocking’ tibial–astragalus articulation, looks like that of other basal sauropodomorphs such as *Saturnalia tupiniquim* (Langer, 2003, fig. 6a–f). Therefore, in comparison with the astragalus of *Massospondylus* (Cooper, 1981, figs 70a–f, 71a–d; MNHN unnumbered specimen from Ha Noosi, Lesotho), there are unmistakable resemblances. However, in proximal and distal views, the caudomedial margin of the astragalus of *Ignavusaurus rachelis* form a well-marked corner (approximately 105°), whereas this edge is more evenly rounded in *Massospondylus carinatus*.

The astragalus of *Melanorosaurus readi* (MNHN MAF1038; F.-X. Gauffre, unpub. Ph.D. dissertation, MNHN,

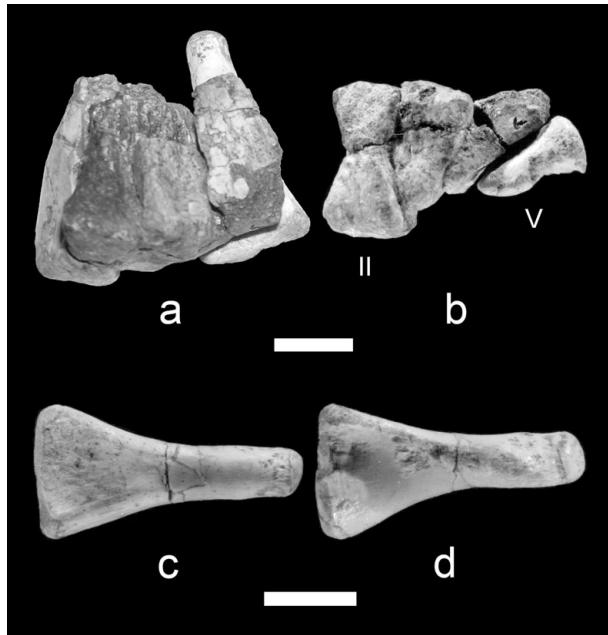


Figure 14. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Right metatarsals II to V (a) dorsal view of metatarsals II to V; (b) proximal view of metatarsals II to V; (c) dorsal view of metatarsal V; (d) ventral view of metatarsal V. II – metatarsal II; V – metatarsal V. Scale bar equals 1 cm.

1996, pl. 11.1) is easily distinguished from that of *Ignavusaurus rachelis*. In particular, it has a more latero-medially lengthened shape.

3.r. Distal tarsal III

Distal tarsal III is a small rounded bone that shows few characters (Fig. 13c, d). Fortunately, as it was found in association with distal tarsal IV and metatarsals II to IV, the orientation of this bone is known in *Ignavusaurus rachelis*. The lateral and dorsal margins are slightly convex, whereas the medial one is rather straight with a little depression at mid-length. The ventral corner is blunt. The proximal articular surface is much flatter than the distal one.

The distal tarsal III of *Ignavusaurus rachelis* is different from that of *Massospondylus carinatus* figured by Cooper (1981, fig. 70o–r) in a number of respects. In particular, it is fairly triangular in proximal and distal views, whereas that of *M. carinatus* is rather ovoid.

3.s. Distal tarsal IV

Distal tarsal IV is a subtrigonal bone (Fig. 13e, f). It is reminiscent of distal tarsal III, except that it is larger and more elongated medio-laterally.

Distal tarsal IV of *Ignavusaurus rachelis* is distinct from that of *Massospondylus carinatus* (Cooper, 1981, fig. 70k–n) in that its medial side is not concave. Also, the medio ventral corner extends much more ventrally in the latter than in the former.

3.t. Metatarsals II to IV

The proximal extremities of the right metatarsals II to IV were preserved together with distal tarsal III and IV, metatarsal V and the first phalanx of this digit (Fig. 14a, b). The proximal

articular surface of metatarsal II is hourglass-shaped, that of metatarsal III looks like an inverted isosceles triangle with a narrow base whose opposed angle is rounded and that of metatarsal IV is a very shallow triangle.

The proximal articular surface of the metatarsal II of *Massospondylus carinatus* (Cooper, 1981, fig. 72j) is clearly broader than that of *Ignavusaurus rachelis*. In addition, that of the metatarsal III is asymmetric (Cooper, 1981, fig. 72j). The articular surface of metatarsal III is also very different in *M. carinatus* due to the fact that its ventral side is strongly concave (Cooper, 1981, fig. 72j), instead of flat as in *I. rachelis*.

The proximal view of metatarsal III of *Melanorosaurus readi* (MNHN MAF 1037; F.-X. Gauffre, unpub. Ph.D. dissertation, MNHN, 1996, fig. 33) is roughly wedge-shaped like that of *Ignavusaurus rachelis*. The metatarsal IV of *M. readi* (MNHN MAF 1219) is similar to that of *I. rachelis* in proximal articular view.

3.u. Metatarsal V and first phalanx of pedal digit V

The metatarsal V of *Ignavusaurus rachelis* has a typical Eiffel-tower shape in dorsal and ventral views (Fig. 14a–d) with concave medial and lateral margins and a proximal half much wider than the distal one. In contrast with the ventral side, the dorsal side is slightly and evenly convex. The phalanx is a small, narrow bone. Its ventral border is slightly concave, whereas the dorsal one is strongly convex.

The metatarsal V of *Ignavusaurus rachelis* shows differences with that of *Massospondylus carinatus* (Cooper, 1981, figs 16b, 77). For instance, the medial border in *I. rachelis* is straighter than in *M. carinatus*, in which the proximal extremity is also wider. Moreover, the lateral border shows, in ventral view, a crest that continues up to the distal articular surface in *I. rachelis*, but not in *M. carinatus*. With respect to the first phalanx of the digit V, the differences between *I. rachelis* and *M. carinatus* (Cooper, 1981, figs 72e–g, 79–82) are insignificant.

The metatarsal V of *Melanorosaurus readi* (MNHN MAF 1178; F.-X. Gauffre, unpub. Ph.D. dissertation, MNHN, 1996, fig. 30) differs from that of *Ignavusaurus rachelis* in particular in that the lateral border is less convex, whereas the medial one is much more concave. Further comparisons based on the available material are difficult.

3.v. Second and unguinal phalanges of pedal digit II

The second phalanx of pedal digit II is well developed. Its proximal articular surface is biconcave. In dorsal view, the caudal border shows a central caudal extension, whereas in ventral view it is much more evenly convex. The unguinal is dorsoventrally deep and longer than the previous phalanx. Its proximal articular surface is biconcave and ovoid in shape, slightly deeper than wide.

3.w. Second, third and unguinal phalanges of pedal digit III

Only a fragment of the distal extremity of the first phalanx of pedal digit III has been preserved, still in articulation with the second phalanx. The latter is much stronger than the third phalanx, which is also much shorter than the unguinal. The unguinal is deeper than wide. No particular feature distinguishes these phalanges from those of other basal sauropodomorphs.

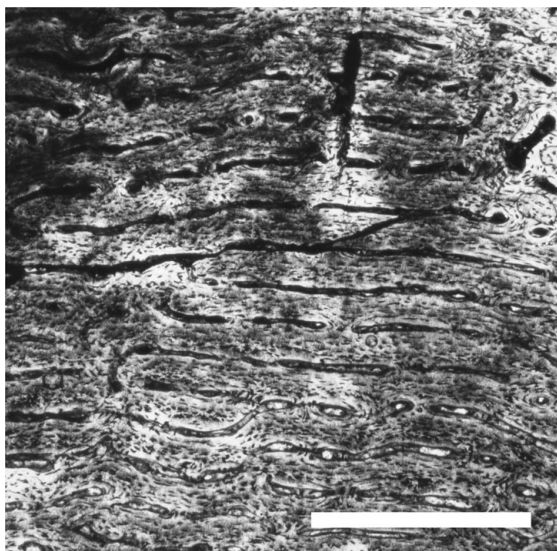


Figure 15. BM HR 20: *Ignavusaurus rachelis* gen. et sp. nov. Transverse section in the mid-shaft of the humerus showing highly vascularized, fibrolamellar bone without any growth interruption visible (azonal bone). The vascular canals are predominantly laminar and circular. Scale bar equals 500 μm .

3.x. First phalanx of pedal digit IV

Only a fragmentary proximal extremity of this bone has been recovered. It shows a simple concavity, which is convex in outline except for the ventral side, which is flat.

4. Discussion

4.a. Age determination

The holotype of *Ignavusaurus rachelis* probably had a body length of about 1.50 m. With an estimated humeral circumference of 31 mm and a femoral circumference of 69 mm, its weight would have been about 22.5 kg, according to the appropriate formula of Anderson, Hall-Martin & Russell (1985). This size, although moderate, suggests that BM HR 20 was not recently hatched (the hatchlings seem to have been very small in basal sauropodomorphs: Galton & Upchurch, 2004).

The morpho-anatomical examination of the specimen does not permit confident age estimation. No character positively suggests a non-adult state. For instance, the lack of fusion of the neural arch-centrum articulation can occur in large 'prosauropod' specimens (Moser, 2003; see also Irmis, 2007). Moreover, the femur of *Ignavusaurus rachelis* plots as from a fully grown individual in the graph of Callison & Quimby (1984, fig. 7; coordinates: $x = 1.19$; $y = 6.00$).

With the purpose of resolving the issue of the ontogenetic age of the holotype of *Ignavusaurus rachelis*, thin histological sections of the humerus and femur were made and examined (Fig. 15). The cortex shows a densely vascularized laminar to subplexiform fibrolamellar bone complex. There are no lines of arrested growth and no haversian reworking. There is generally active perimedullar erosion without remark-

able endosteal bone deposition, indicating diameter growth of the medullar cavity, and no sign of decrease of the subperiosteal growth. These features indicate that this specimen is a young, fast-growing individual, maybe less than a year old. The pattern appears close to that of *Thecodontosaurus* (C. Cherry, unpub. Masters thesis, Univ. Bristol, 2002; Ricqlès *et al.* 2008). A femur of *Massospondylus* (BP/1/4267a) studied by Chinsamy (1993) with a diameter similar to that of BM HR 20 had five growth rings. Likewise, a femur of this taxon with the same length as that of the holotype of *Ignavusaurus rachelis* would have about three growth rings according to Chinsamy (1993, fig. 7; see also Chinsamy-Turan, 2005, fig. 5.4). Interestingly enough, the postcranial skeleton of *Massospondylus* mainly changed in its proportion during ontogenetic development (Reisz *et al.* 2005).

4.b. Phylogenetic position

Ignavusaurus shows some derived traits, but overall a large number of primitive character-states. For instance, a distal tibia not wider (latero-medially) than long (cranio-caudally) is an uncommon condition in non-sauropod sauropodomorphs, recalling only the taxa more plesiomorphic than *Efraasia* (see e.g. Upchurch, Barrett & Galton, 2007; Yates, 2007b). Likewise, *Ignavusaurus* lacks a number of character-states that are generally present in the sauropodomorphs more derived than *Efraasia*, such as a distally placed fourth trochanter (see e.g. Langer *et al.* 2009).

In order to assess with more accuracy the relationships of *Ignavusaurus*, a cladistic analysis was conducted. Recently, some very thorough phylogenetic studies of basal sauropodomorphs have been made available, such as those of Barrett *et al.* (2007), Kutty *et al.* (2007), Upchurch, Barrett & Galton (2007), Upchurch *et al.* (2007) and Yates (2007a,b). Although all have considerable merit, those of Yates (2007a,b) bear a special interest in the context of the present study because they include both the basal sauropodomorphs *Thecodontosaurus* and *Pantydraco* (Yates, 2003; Galton, Yates & Kermack, 2007). The most recent of these two analyses (Yates, 2007b), with the moderate amendment and addition of Smith & Pol (2007), was therefore chosen for the phylogenetic analysis of *Ignavusaurus*. The matrix (Table 2) was processed using PAUP* ver. 4.0b10 (Swofford, 2001) using the PaupUp ver. 1.0.3.1. graphical interface (Calendini & Martin, 2005). The relatively high number of terminal taxa and characters precluded exact tree building, so a heuristic search by stepwise addition ('closest' option) was performed.

Sixty most parsimonious trees (1128 steps long) have resulted. Their characteristics are: C.I. = 0.370 and R.I. = 0.693. The insertion of *Ignavusaurus* in the matrix used by Smith & Pol (2007) did not perturb the topology of the strict consensus tree obtained by those authors, with polytomies mostly present in the relationships between taxa more derived than

Table 2. Full coding for *Ignavusaurus rachelis* gen. et sp. nov.

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01100?100??????????????0?0?00???????????????0010?????000?00001000310001001?1011001100100101?0
00?0111010000101?0??1?????010100??00111010?????110???11?012?10??000?0?0(0/1)0000001?

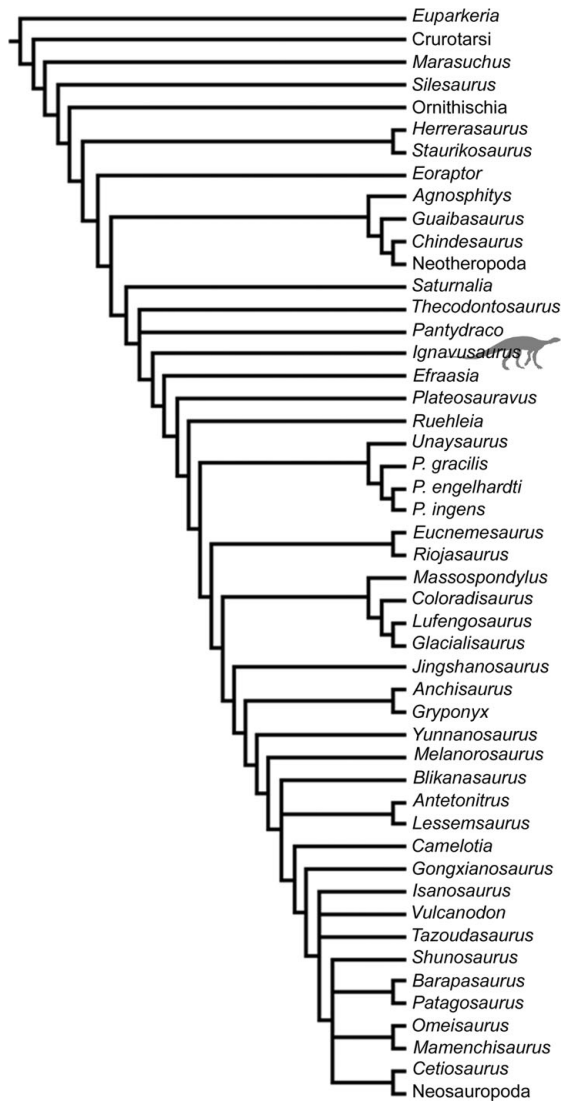


Figure 16. Phylogenetic relationships of *Ignavusaurus rachelis* gen. et sp. nov. within Sauropodomorpha. Strict consensus tree of 60 most parsimonious trees (L = 1128, C.I. = 0.370, R.I. = 0.693).

Vulcanodon (Eusauropoda). *Ignavusaurus* is positioned between *Thecodontosaurus*–*Pantydraco* and *Efraasia* (Fig. 16). As already suggested by the comparisons above, it does not appear especially closely related to the other taxa known in the Elliot Formation, such as the coeval *Massospondylus*. However, it should be noted that only one step is required to collapse *Thecodontosaurus*, *Pantydraco*, *Ignavusaurus*, *Efraasia* and a branch leading to the more derived taxa to the same node.

With respect to *Thecodontosaurus*–*Pantydraco*, *Ignavusaurus* and more derived taxa share the following

unambiguous synapomorphies: (1) one dorsosacral vertebra, (2) length of midcaudal centra less than twice the height of their cranial faces, (3) lack of deep distal extensor pits on the second and third metacarpals, (4) phalangeal formula of manual digits four and five greater than 2–0, respectively, (5) fully open acetabulum and (6) presence of a phalanx in pedal digit five. On the other hand, *Efraasia* and more derived taxa display the following unambiguous synapomorphies with respect to *Ignavusaurus*: (1) longest chevron less than twice the length of the preceding centrum, (2) entepicondyle of the distal humerus with a flat distomedially facing surface bounded by a sharp proximal margin, (3) transverse width of the distal tibia greater than its craniocaudal length and (4) femoral length of at least 400 mm. *Ignavusaurus* allows a reassessment of some character-states of the sauropodomorph systematics. For instance, a proximal metatarsal IV expanded transversely was considered a potential synapomorphy of a fairly diverse monophyletic Prosauropoda by Upchurch, Barrett & Galton (2007). However, this could not be coded for *Efraasia* and more basal taxa. Its presence in *Ignavusaurus* suggests that it is a basal synapomorphy of a more inclusive group than Prosauropoda *sensu* Sereno (1998).

If *Ignavusaurus* is one of the most primitive sauropodomorphs, being only more derived than the recently described *Panphagia protos* (Carnian, Argentina; Martínez & Alcober, 2009) and, as detailed above, *Saturnalia tupiniquim* (Carnian, Brasil), *Thecodontosaurus antiquus* (Rhaetian, United Kingdom) and *Pantydraco caducus* (?Rhaetian, United Kingdom), then it has to be compared with two recently described sauropodomorphs of possible similar phylogenetic position: *Lamplughosaura dharmaramensis* and *Pradhadania gracilis* (Sinemurian, India; Kutty *et al.* 2007). Whereas a basal nesting within Sauropoda is favoured for *Lamplughosaura* (Kutty *et al.* 2007, p. 1234), as supported by a number of characters such as the textured surface of tooth enamel (cf. Wilson & Sereno, 1998), the generally incomplete nature of the type specimen of *Pradhadania* prevents the phylogenetic position of this taxon from being decided. In any case, *Pradhadania* is clearly different from *Ignavusaurus*. For instance, whereas the mandibular symphysis of the latter tapers (Fig. 4e), that of *Pradhadania* is enlarged dorso-ventrally (Kutty *et al.* 2007, fig. 17.5–6), probably much as in *Riojasaurus incertus* (Bonaparte & Pumares, 1995, fig. 3) and even more derived sauropodomorphs. This suggests that *Ignavusaurus* may be more primitive than *Pradhadania*. The same difference occurs between

Ignavusaurus and *Mussaurus patagonicus* (Bonaparte & Vince, 1979; Pol & Powell, 2007; pers. obs. of cast of holotype). A cladistic analysis involving the extremely young material on which this species is based suggested a phylogenetic position between *Thecodontosaurus* and *Efraasia* (Upchurch, Barrett & Galton, 2007), as for *Ignavusaurus*. However, a parallel examination based on subadult individuals suggested a nesting among derived non-sauropod sauropodomorphs (Pol & Powell, 2005; see also Pol & Powell, 2007), as actually suspected by Upchurch, Barrett & Galton (2007).

At this point, it should be emphasized that the phylogenetic position of *Ignavusaurus rachelis* has to be taken with some reservation because of the ontogenetic stage of the holotype. Indeed, as for other tetrapods, juvenile basal sauropodomorphs may show more plesiomorphic characters than adults (Upchurch, 1997). However, the issue is compounded by the increasing evidence suggesting that major morphological features of the Sauropoda may have originated through paedomorphic processes from more basal sauropodomorphs (Bonaparte & Vince, 1979; Reisz *et al.* 2005; Pol & Powell, 2007).

5. Conclusions

Ignavusaurus rachelis is a non-graviportal (subcursorial), rather primitive, non-sauropod sauropodomorph that contributes to our knowledge of basal dinosaurs and their early diversification in Gondwana. It appears to be preceded in the basal sauropodomorph phylogenetic series only by *Panphagia*, *Saturnalia* and *Thecodontosaurus–Pantydraco*. If the latter two taxa are indeed Rhaetian in age (see Whiteside & Marshall, 2008), then their temporal separation with *Ignavusaurus* is possibly a gap of only a few million years.

This new species underlines how much the upper Elliot Formation, together with a few other strata such as those of the Lufeng Formation in China, constitutes a remarkable window into the early evolution and diversity of sauropodomorph saurischians and thereby into the origin of sauropods. At the time of formation of the upper Elliot Formation, southern Africa was inhabited minimally by one very primitive sauropodomorph (*Ignavusaurus*), some plateosaurians (*Massospondylus*, *Gryponyx*) and two sauropods (unnamed taxa) (Barrett, 2004; Vasconcelos & Yates, 2004; Yates, Hancox & Rubidge, 2004; Yates, Bonnan & Neveling, 2007). The discovery of *Ignavusaurus* confirms Barrett's (2009) suspicion of an overlooked upper Elliot Formation sauropodomorph diversity.

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