A new specimen of the sauropodomorph dinosaur *Ignavusaurus rachelis* from the Early Jurassic of Lesotho

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The upper Elliot Formation (?Rhaetian–Sinemurian) of South Africa and Lesotho has yielded a rich fauna of non-avian dinosaurs, which has generally been considered to be dominated by the massopodan sauropodomorph *Massospondylus carinatus*. However, re-evaluation of the abundant sauropodomorph collections from this unit suggests that the species-richness of upper Elliot sites has been underestimated. Here, we describe a series of cervical and dorsal vertebrae collected from Likhoele Mountain, Lesotho, which are referred to the rare upper Elliot sauropodomorph taxon *Ignavusaurus rachelis*. This material represents only the second-known specimen of this taxon, extending its geographic range, and underscores the value of undertaking detailed re-assessments of neglected historical collections.

Keywords: Sauropodomorpha, Massospondylidae, upper Elliot Formation, taxonomy.

INTRODUCTION

The Stormberg Group (Late Triassic–Early Jurassic) of the main Karoo Basin has yielded abundant dinosaur remains from numerous localities in South Africa and Lesotho (e.g. Kitching & Raath 1984; Knoll 2004, 2005). Diverse faunas have been recovered from both the Upper Triassic lower Elliot Formation (Norian–Rhaetian) and the Upper Triassic–Lower Jurassic (?Rhaetian–Pliensbachian) upper Elliot and Clarens formations (e.g. Knoll 2004, 2005; Viglietti *et al*. 2020a,b). In each case, sauropodomorph dinosaurs are the numerically dominant tetrapod taxa (Kitching & Raath 1984).

Until recently, almost all of the sauropodomorph dinosaur specimens recovered from the upper part of the Stormberg Group were assumed to be referable to the massospondylid *Massospondylus carinatus* (e.g. Kitching & Raath 1984; Knoll 2005). However, taxonomic re-appraisals, new discoveries and stratigraphic revisions have demonstrated that the upper Elliot and Clarens formations hosted a much more diverse sauropodomorph fauna (McPhee *et al*. 2017). In addition to *M. carinatus*, this included at least one small-bodied ?non-massopodan (*Arcusaurus pereirabdalorum*), three other likely massospondylids or putative massospondylids (*Ignavusaurus rachelis*, *M. kaalae* and *Ngwevu intloko*), and four sauropodiforms (*Aardonyx celestae*, *Antetonitrus ingenipes*, *Ledumahadi mafube* and *Pulanesaura eocollum*) (Yates & Kitching 2003; Barrett 2009; Knoll 2010; Yates *et al*. 2010, 2011; McPhee *et al*. 2015, 2018; Chapelle *et al*. 2019). Consequently, new discoveries can no longer be assumed to represent *Massospondylus* but must be assessed more rigorously to demonstrate their taxonomic affinities. Moreover, large historical collections of sauropodomorph material from the upper Stormberg Group, which have generally been referred to *Massospondylus* spp. solely on the basis of provenance, now require extensive re-evaluation in order to build a more accurate picture of the species-richness and palaeoecology of upper Stormberg dinosaur faunas (see also Barrett *et al*. 2019).

One such collection is housed at the Natural History Museum, London, which includes specimens acquired in the late nineteenth century (e.g. the holotype of '*Massospondylus browni*': Seeley 1895). However, the bulk of this material was collected by a series of Anglo-South African expeditions to South Africa and Lesotho in the 1960s that were led jointly by either the Natural History Museum/ Birkbeck College or University College London (UCL), both in collaboration with the Iziko South African Museum (e.g. Crompton 1968). Although many of the ornithischian dinosaurs collected by these expeditions were described relatively promptly (e.g. Thulborn 1970, 1972, 1974; Santa-Luca *et al.* 1976), the majority of the sauropodomorph material recovered remains undescribed and unprepared (but see Barrett & Yates 2006). Here, we report a new specimen of the rare upper Elliot Formation sauropodomorph *Ignavusaurus rachelis* that was collected during one of the UCL expeditions to Lesotho in July–August 1968, which was led by the late Prof. Kenneth Kermack. This represents only the second-known specimen of *Ignavusaurus* and underscores the importance of unlocking the information stored in historical museum collections.

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SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen, 1842
Saurischia Seeley, 1887 (*sensu* Baron *et al*. 2017)
Sauropodomorpha von Huene, 1932
?Massospondylidae von Huene, 1914 (*sensu* Sereno 1998)

Ignavusaurus rachelis Knoll, 2010, Figs 1 & 2

Material. NHMUK PV R37375, an articulated series of five neural arches (representing one cervical, two cervicodorsals and two dorsals), also including one centrum (forming part of the posterior-most articulated vertebra), and one isolated partial ?dorsal neural arch. This specimen was collected on the 1968 UCL expedition and was originally given the field number 'C.10' in K.A. Kermack's unpublished field notes (held at NHMUK) and identified as 'dinosaur vertebrae' therein.

Locality and horizon. Likhoele Mountain, near Mafeteng, Mafeteng District, Lesotho, from a quarry named 'Dinosaur exposure' (K.A. Kermack, unpubl. field notes). No stratigraphic information is recorded in the field notes. However, a continuous section of upper Stormberg Group sediments is exposed at this site, including the lower Elliot, upper Elliot and Clarens formations (Sciscio & Bordy 2016), leaving open the possibility that any of these units could have been the source of this specimen. An elevation of '6,680 feet' (2035 m) was recorded for the quarry (K.A. Kermack, unpubl. field notes), which would place the source of this material within the Clarens Formation, as the upper Elliot/Clarens formation contact is at 1967 m (Sciscio 2016). However, the Clarens Formation at Likhoele Mountain forms sheer vertical cliffs and it is unlikely that the specimen could have been recovered from this part of the section; moreover, the red, fine-grained sandstone encasing the specimen is identical to that occurring at several levels within the upper Elliot Formation at Likhoele Mountain (Sciscio & Bordy 2016; L. Sciscio, pers. comm.). Consequently, we regard the source horizon for NHMUK PV R37375 as the upper Elliot Formation, which is of ?Rhaetian–Sinemurian age (Sciscio *et al*. 2017; Bordy *et al*. 2020; Viglietti *et al*. 2020b).

Description. All of the articulated vertebrae are visible in dorsal, ventral and lateral views (Fig. 1), with the exception of the disarticulated neural arch, which is partially covered by matrix. The anterior-most and posterior-most vertebrae, as well as the isolated neural arch are also visible in anterior and posterior views, respectively. Each vertebra exhibits moderate crushing and deformation, with this being particularly pronounced on their right-hand sides. The presence of matrix and damage to the neural arches prevents description of some anatomical features. Measurements are provided in Table 1.

Table 1. Measurements for NHMUK PV R37375. All measurements are in mm. Measurements marked with an asterisk are minima due to breakage. No measurements were possible for the cervical vertebra; in other cases extensive breakage or the presence of matrix and/or overlapping elements prevented measurement.

	ACH	ACW	CL	NSH	NSL	NSW	PCW
Cervicodorsal 1	–	–	–	29.8	22.5	19.34	–
Cervicodorsal 2	–	–	–	23.1	23.1	15.2	–
Dorsal 1	–	–	–	24.8	28.9	9.1	–
Dorsal 2	27.8*	24.1	52.8*	–	–	–	18.9*
Isolated neural arch	–	–	–	15.1*	29.5*	8.1	–

Comparisons with other well-known Early Jurassic sauropodomorphs, such as *Adeopapposaurus mognai* (Martínez 2009) and *Massospondylus carinatus* (Barrett *et al.* 2019), indicate that the anterior-most vertebra of the articulated series is a posterior cervical, due to its extreme neural arch elongation, whereas the next two vertebrae share features with both posterior cervical and anterior dorsal vertebrae, notably an anteroposteriorly short neural spine with a rectangular or square transverse cross-section. The lack of parapophyses on the more complete third vertebra in the series suggests that these two vertebrae are at the neck-trunk junction and are considered to be 'cervicodorsals' herein. The fourth and fifth vertebrae have parapophyses that are situated on the neural arch, as well as mediolaterally flattened neural spines, so are identified as dorsals, as is the isolated partial neural arch. Neural arch terminology follows Wilson (1999) and Wilson *et al*. (2011).

The cervical neural arch (vertebra 1 in the series) lacks its neural spine, prezygapophyses, most of the transverse processes and the ventral parts of the neural arch pedicels (Figs 1–3). Although the prezygapophyses and neural spine are damaged, there are broken surfaces indicating that spinoprezygadiapopyseal laminae (SPRLs) were present, framing a deep prespinal fossa. In lateral view, the postzygapophyses are oriented horizontally and are extremely elongate, so it is likely that they would have overhung the posterior margin of the centrum (Figs 1A,C, 2A,C). In dorsal view, the postzygapophyses taper posteriorly to a rounded apex, diverging from each another at an angle of approximately 30°. A blunt, ridge-like, low epipophysis is present, which terminates anterior to the posterior tip of the postzygapophysis (Figs 1A,C, 2A,C). Breakage prevents determination of the size or shape of the neural spine or the presence/absence of spinopostzygapophyseal laminae (SPOLs). The portion of the neural arch ventral to the level of the zygapophyses is dorsoventrally tall and several laminae and fossae are present on its lateral surfaces (Figs 1A,B, 2A,B, 3A). All of the laminae are prominent and robust, framing correspondingly deep fossae. The paradiapophyseal lamina (PPDL) is short, broad and extends posterodorsally from the anteroventrolateral corner of the neural arch to the diapophysis, forming an angle of approximately 90° with the posterior centrodiapophyseal lamina (PCDL). The PCDL forms a pronounced, rounded buttress, whose dorsal part (on the right-hand side) bears a shallow depression. Together, the PPDL and PCDL frame a deep, triangular centrodiapophyseal fossa (cdf). There is some evidence for a thin, horizontally inclined postzygodiapophyseal lamina (PODL) and this, together with the PCDL and a strut-like centropostzygapophyseal lamina (CPOL), forms the boundary of a large, triangular postzygopophyseal centrodiapophyseal fossa (pocdf).

The cervicodorsals (vertebrae 2 and 3 in the series) are represented by partial neural arches that include the neural spine, parts of the prezygapophyses, postzyg-

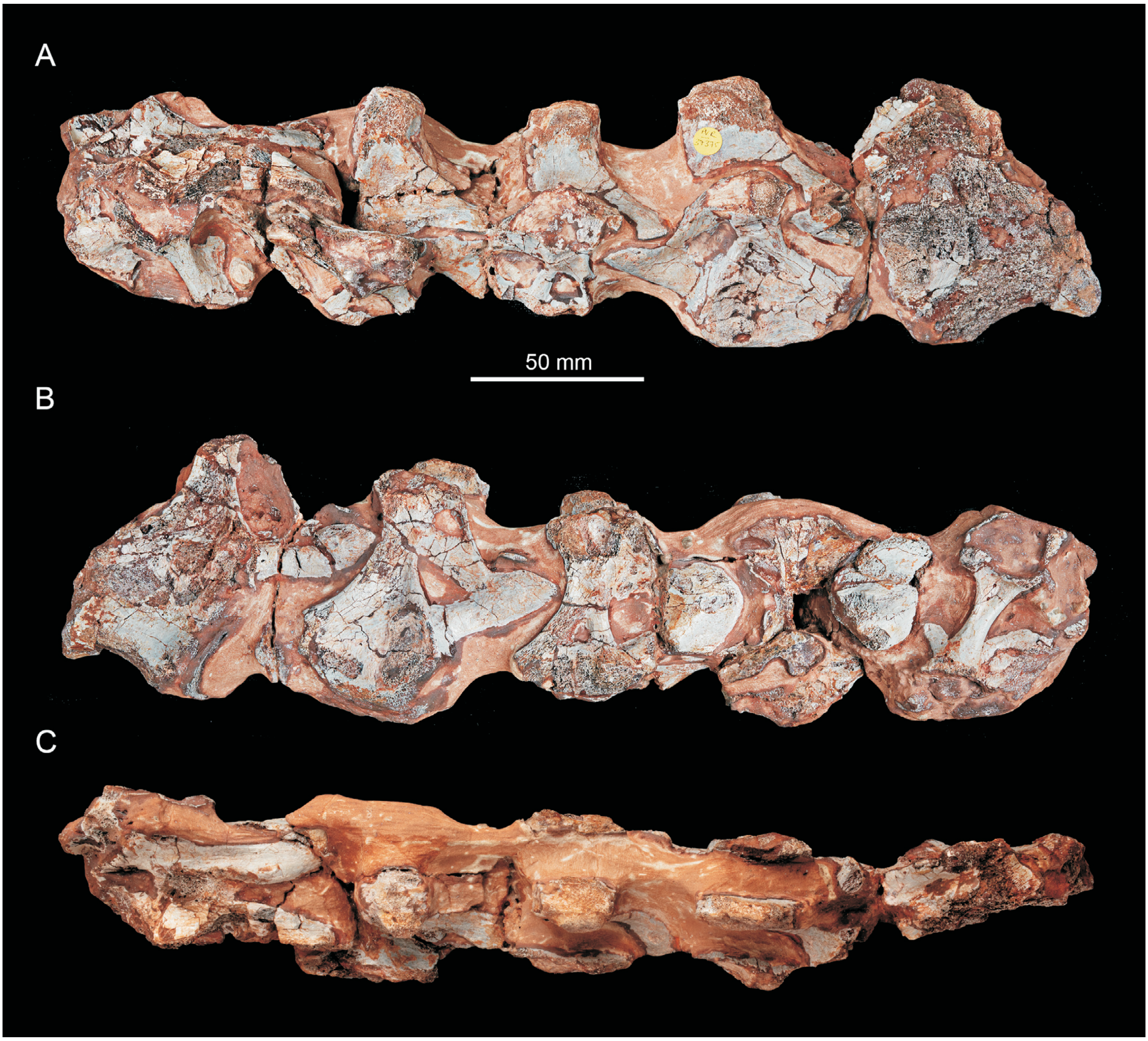

Figure 1. Partial axial column referred to *Ignavusaurus rachelis* Knoll, 2010 (NHMUK PV R37375) from the upper Elliot Formation of Likhoele Mountain, Lesotho, in left lateral (**A**), right lateral (**B**) and dorsal (**C**) views (with anterior to the left).

apophyses and diapophyses (the latter are best preserved in vertebra 3). In lateral view, the prezygapophyses possess an unusual, rounded, globular outline, rather than forming the tapered triangular processes that are typical of other sauropodomorphs (Figs 1A,B, 2A,B, 3A). This is due to anteroventral expansion of the ventral margin of the process, and it terminates in a broad, semicircular apex. A short prezygodiapophyseal lamina (PRDL) extends horizontally and posteriorly. This provides the dorsal margin of a deep prezygopophyseal centrodiapophyseal fossa (prcdf), whose other margins are formed by a robust prezygoparapophyseal lamina (PRPL) anteroventrally and the almost vertically inclined and prominent PPDL posteriorly. As in the cervical neural arch, the PCDL is robust, although it is more steeply inclined so that the PCDL and PPDL meet at an angle of approximately 80°. These two laminae enclose a small cdf. The postzygapophyses are largely obscured, but thin spinopostzygapophyseal laminae form the boundaries of what appears to be a deep and extensive (but matrix-filled) postspinal fossa. No epipophysis is present. The diapophyses extend dorsolaterally, so that they are strongly angled and project well above the horizontal (Figs 1 & 2). Although this has been accentuated by crushing (so that the right diapophyses form an angle of approximately 20° with the neural spine), all preserved diapophyses project strongly dorsally, suggesting this is a genuine feature (and the neural spines are not distorted strongly either, contrary to the expected condition if the entire neural arch had been extensively deformed). The neural spines are transversely broad and anteroposteriorly short relative to those in the dorsal vertebrae, with square to sub-rectangular transverse cross-sections (Figs 1A,C, 2A,C). In lateral view, the anterior margins of neural spine are slightly convex, whereas the posterior margin is concave (Fig. 1B). The dorsal surface of the neural spine is flat to slightly convex and slopes gently in a posteroventral direction.

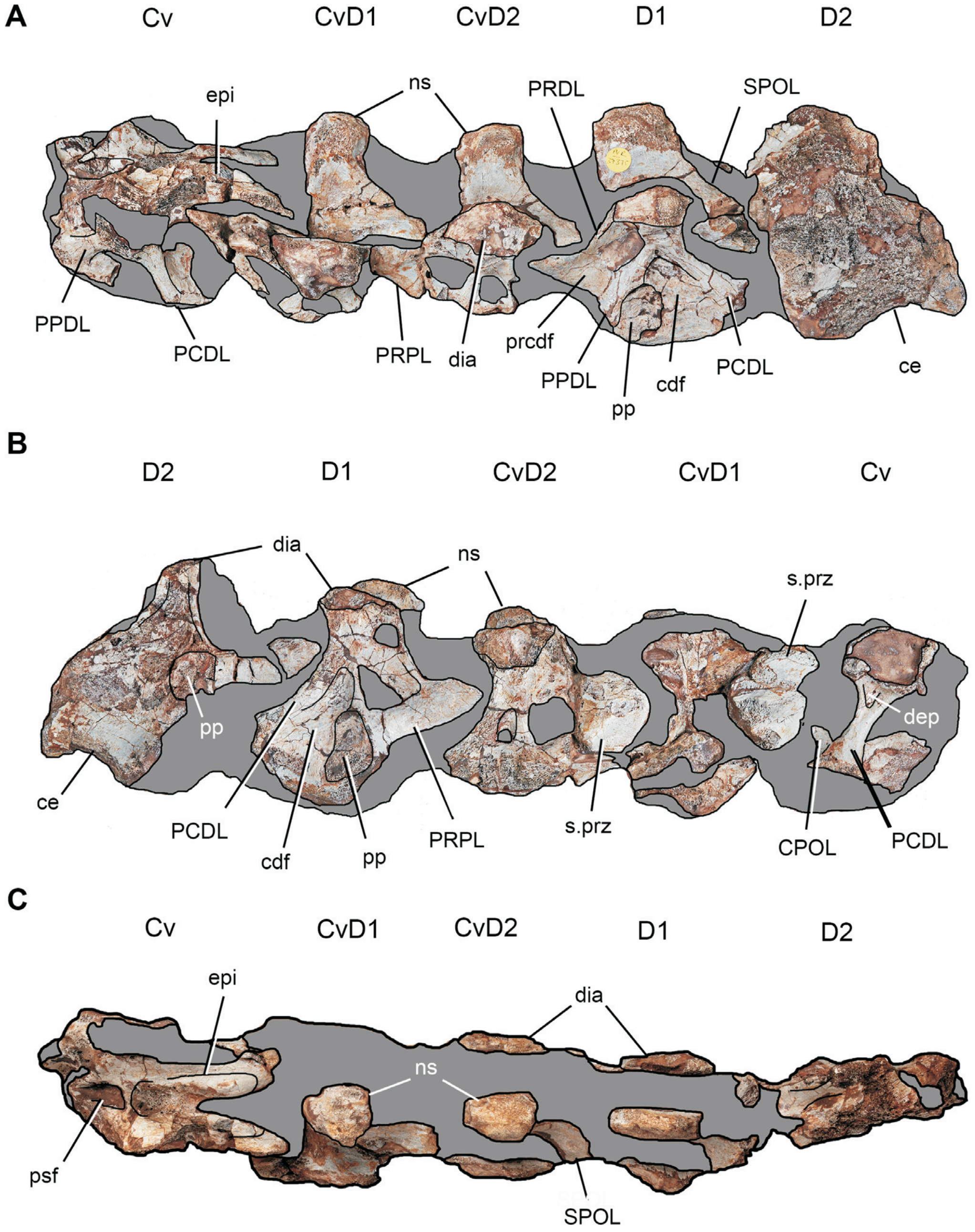

Figure 2. Annotated diagram of a partial axial column referred to *Ignavusaurus rachelis* Knoll, 2010 (NHMUK PV R37375) from the upper Elliot Formation of Likhoele Mountain, Lesotho, in left lateral (**A**), right lateral (**B**) and dorsal (**C**) views (with anterior to the left).

Dorsals 1 and 2 (vertebrae 4 and 5 in the series) are the most completely preserved in the series and dorsal 2 includes a weathered, but almost complete centrum, as well as the neural arch (Figs 1, 2, 3B,C). The neural arch of dorsal 1 is almost complete, although its prezygapophyses are largely obscured, and parts of the right-hand side of the neural arch are available for dorsal 2, but its left-hand side is uninformative. In lateral view, the neural arch pedicles of dorsal 1 are dorsoventrally expanded, so that a considerable distance separates the base of the arch from the base of the prezygapophysis, forming a distinct pedestal (Figs 1A,B, 2A,B, 3B). A large, oval parapophysis, with its long axis oriented dorsoventrally, is situated on the anteroventral surface of the neural arch and has a shallowly concave surface surrounded by a distinct raised lip of bone (Figs 1A,B, 2A,B, 3B). In lateral view, the prezygapophyses have an elongate, triangular outline that contrasts markedly with the semicircular outline seen in the cervicodorsals (see above). A broad, rounded PRPL forms the anteroventral border of an extensive, deep prcdf, the dorsal margin of which is composed of a sharp PRDL. A short, but distinct, PPDL forms the posteroventral marking of the prcdf and the anterior border of a tall, narrow and shallow cdf. It is not possible to determine if an anterior centrodiapophyseal lamina (ACDL) was also present. The posterior margin of the cdf is formed by a long, prominent PCDL. A small circular perforation present in the right PRDL of dorsal 1, close to the tip of the diapophysis, is probably a preservational artefact, as it has rugose, unfinished bone margins (Figs 1B, 2B, 3B). As in the cervicodorsals, the transverse processes are oriented strongly dorsolaterally (Figs 1C, 2C, 3C). Their distal ends are slightly expanded anteroposteriorly. The neural spine of

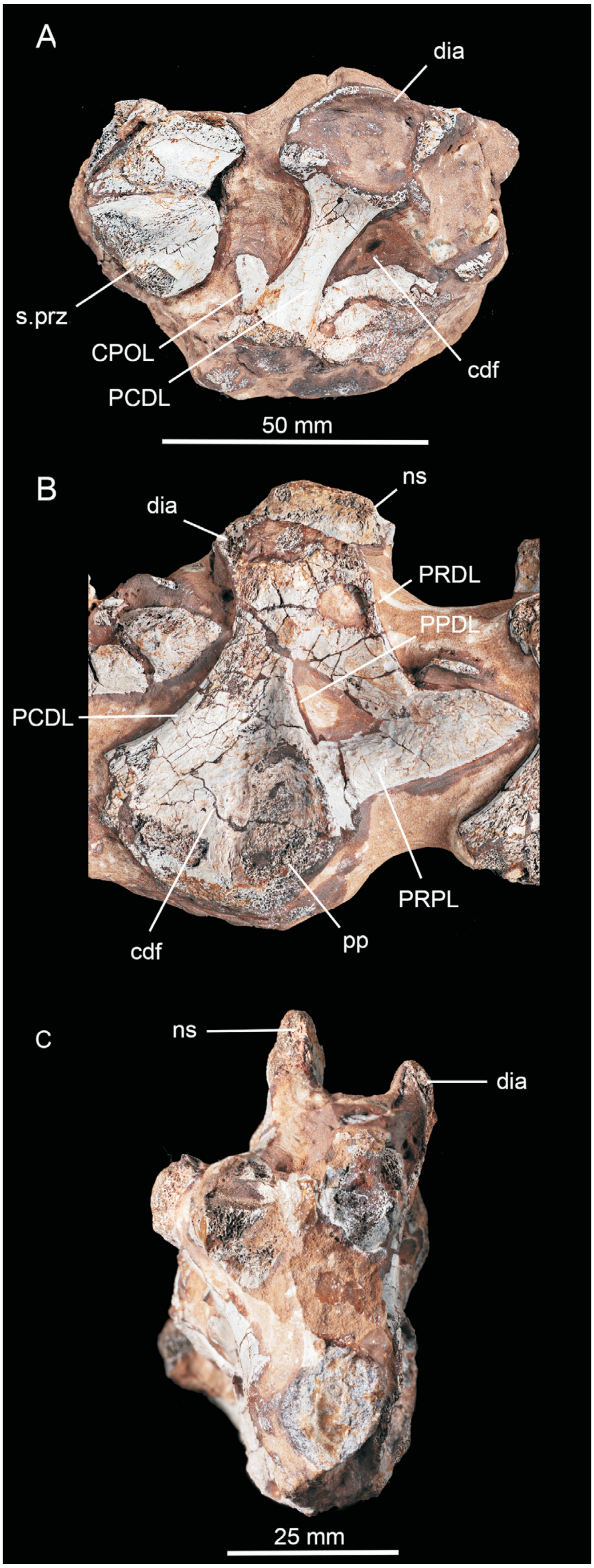

Figure 3. Close-up views of individual vertebrae referred to *Ignavusaurus rachelis* Knoll, 2010 (NHMUK PV R37375) from the upper Elliot Formation of Likhoele Mountain, Lesotho. **A**, posterior-most cervical in right lateral view; **B**, dorsal vertebra 1 in right lateral view; **C**, dorsal vertebra 2 in anterior view (taken when detached temporarily from the main vertebral series).

dorsal 1 is of comparable dorsoventral height to that in the cervicodorsals but is substantially narrower mediolaterally and is greater in length anteroposteriorly, forming a plate-like morphology. In lateral view, the neural spine margins are straight anteriorly, slightly convex dorsally and slightly concave posteriorly, although all of the margins are slightly abraded. Prominent, ridge-like SPOLs frame a mediolaterally wide and deep postspinal fossa.

In dorsal 2, the posterior, ventral and left-lateral surfaces of the centrum are damaged, with its anterior surface largely being covered by matrix (Figs 1A,B, 2A,B). The lateral surfaces of the centrum are anteroposteriorly and dorsoventrally concave ('saddle-shaped') and lack ridges or pneumatic features. Ventrally, the lateral surfaces merge and the ventral surface of the centrum is not offset by distinct ridges or breaks in slope. In lateral view, the centrum has a gently concave ventral margin; the ventral surface is too poorly preserved to determine if either a midline keel or groove was present. The anterior articular surface of the centrum is dorsoventrally taller than it is mediolaterally wide, is elliptical in outline (with the long axis of the ellipse extending dorsoventrally) and has shallowly concave articular surface. The centrum is elongate, with a centrum length/anterior centrum height ratio of *c*. 1.9 (see measurements in Table 1). Damage prevents determination of whether the neurocentral junction was open or closed. Where comparisons are possible, the neural arch of dorsal 2 is identical to that of dorsal 1. Finally, the isolated, fragmentary neural arch yields little useful information, but is consistent in morphology with the other dorsal vertebrae.

DISCUSSION

The taxonomic validity of *Ignavusaurus rachelis* was questioned by Yates *et al.* (2011), who proposed that it shared many features with *Massospondylus* and might represent a damaged juvenile specimen of the latter taxon (see also McPhee *et al.* 2017). In addition, Yates *et al.* (2011) stated that the differences used by Knoll (2010) to distinguish *Ignavusaurus* and *Massospondylus* were subtle and potentially within the range of variation of the *Massospondylus* hypodigm, but they provided no specific comparisons to support this assertion. Indeed, all of the features that Yates *et al.* (2011) noted as shared by the two taxa (e.g. weakly constricted tooth crown bases, marginal denticles restricted to the tooth apices) are either regarded as synapomorphic for Massospondylidae or are found in many other members of the clade, rather than suggesting a particularly close relationship with *Massospondylus* itself (e.g. Apaldetti *et al.*, 2011; Chapelle *et al.*, 2019). Recent phylogenetic analyses have usually recovered *Ignavusaurus* and *Massospondylus* within Massospondylidae but they have not been identified as sister taxa in any of these treatments (e.g. Apaldetti *et al.* 2011; Chapelle *et al.* 2019), lending some support to the idea that they should be regarded as distinct. Countering this, both Yates *et al.* (2011) and McPhee *et al.* (2017) noted that the juvenile status of the *Ignavusaurus* holotype might affect its phylogenetic position: however, neither of these papers test this assertion. By contrast, detailed comparisons between the postcranial skeletons of *Massospondylus* and *Ignavusaurus* have revealed numerous differences between these taxa (Knoll 2010; Barrett *et al*. 2019). Moreover, the combination of features present in *Ignavusaurus* does currently distinguish it from other valid Elliot sauropodomorphs (Knoll 2010; Barrett *et al*. 2019). Consequently, we regard it as a distinct taxon herein (*contra* Yates *et al*. 2011; *contra* McPhee *et al*. 2017) pending a more thorough revision.

Knoll (2010) identified 18 characters in his differential diagnosis of *Ignavusaurus*, of which one is shared with NHMUK PV R37375 to the exclusion of the other small to medium-sized sauropodomorphs from the upper Elliot and Clarens formations. This is the presence of diapophyses that are almost dorsally directed (Figs 1C, 2C, 3C), which are present in NHMUK PV37375 and *Ignavusaurus* (Knoll 2010) but absent in *Massospondylus carinatus* (BP/1/4934) and *Ngwevu intloko* (BP/1/4779), which each possess transverse processes that project almost horizontally (Barrett *et al*. 2019; Chapelle *et al*. 2019; K. Chapelle, pers. comm.). In addition, as noted by Knoll (2010), but not listed in his diagnosis, the dorsal neural arches of *Ignavusaurus* are tall relative to their centra, due to the elevated positions of the zygapophyses, which produces an expanded, parapet-like area below them (Figs 1 & 2). This feature is also present in NHMUK PV R37375, but in *M. carinatus* (BP/1/4934) the distance between the base of the neural arch and the bases of the zygapophyses is relatively smaller (Knoll 2010; Barrett *et al*. 2019). Finally, Barrett *et al*. (2019) noted that the dorsal centra of *Ignavusaurus* are unusually elongate (with centrum length/centrum height ratios of ~1.72–2.0) and potentially diagnostic, a feature that also occurs in NHMUK PV R37375 (ratio of ~1.9). This contrasts with the conditions in *M. carinatus* (BP/1/4934) and *Ngwevu* (BP/1/4779) where the dorsal centra are relatively short (ratios of ~1.1–1.5; Barrett *et al*. 2019; K. Chapelle, pers. comm.).

Unfortunately, the holotype specimen of *Ignavusaurus* lacks cervical vertebrae and one or two anterior dorsal vertebrae (Knoll 2010), limiting comparisons with NHMUK PV R37375. However, NHMUK PV R37375 can be further distinguished from *Massospondylus carinatus* and *Ngwevu*, adding circumstantial support for its referral to a different sauropodomorph taxon. For example, the posterior-most cervical vertebrae of *M. carinatus* and *Ngwevu* lack epipophyses (BP/1/4934 – Barrett *et al*. 2019; BP/1/4779 – Chapelle *et al*. 2019), whereas these structures are present in NHMUK PV R37375. In addition, the diapophyseal laminae of the posterior cervical and cervicodorsals of NHMUK PV R37375 are extremely prominent and robust (Figs 1 & 2), whereas those of *M. carinatus* (BP/1/4934) are relatively weakly developed, in spite of the much larger size of the neotype specimen (Barrett *et al*. 2019). Finally, both *M. carinatus* (BP/1/4934; Barrett *et al*. 2019) and *Ngwevu* (BP/1/4779; Chapelle *et al*. 2019) lack the unusual semicircular prezygapophyses present in NHMUK PV R37375.

The foregoing comparisons focus on other upper Stormberg Group sauropodomorphs, as these are the most likely taxa for the reception of NHMUK PV R37375. However, this specimen can also be distinguished from other putative massospondylids, including *Adeopapposaurus*, *Coloradisaurus* and *Lufengosaurus*, on the basis of the same features. For example, all of these taxa have relatively short dorsal vertebral centra, with centrum length/centrum height ratios of ~0.96–1.5 (see ratios given in Barrett *et al*. 2019). In addition, the transverse processes of the dorsal vertebrae in all of these taxa project almost strictly horizontally (Young 1941; Martinez 2009; Apaldetti *et al*. 2013; IVPP V15, PSVJ 610, PMB, pers. obs.), whereas those of NHMUK PV R37375 are steeply inclined. Finally, the posterior cervicals and anterior dorsals of *Adeopapposaurus* lack the semicircular prezygapophyses seen in NHMUK PV R37375 (Martinez 2009; PSVJ 610, P.M.B., pers. obs.; NB, these areas are not preserved in *Coloradisaurus* or *Lufengosaurus*).

Given the detailed similarities between NHMUK PV R37375 and the holotype of *Ignavusaurus*, as well as the many differences between these two specimens and other Elliot Formation massospondylids, we formally refer this specimen to *Ignavusaurus rachlis*. NHMUK PV R37375 represents only the second-known specimen of this taxon and its discovery provides a direct faunal link with the type locality at Qacha's Nek (Quacha's Nek District, Lesotho), which is approximately 140 km west of Likhoele Mountain. It also provides new information on the cervicodorsal transition in this taxon and possesses a potential new autapomorphy for *Ignavusaurus*, namely the unusually shaped, semicircular prezygapophyses seen in the cervicodorsals, although confirmation of this will require the discovery of additional material.

The identification of this specimen provides another example of how new taxonomic records can be generated through the re-evaluation of undescribed or poorly surveyed historical museum collections. Together with other recent work, such as the description of *Ngwevu intloko* (Chapelle *et al*. 2019), it also underscores the fact that systematic reappraisal of the material historically referred to *Massospondylus* might yield previously hidden new information on the species-richness and palaeoecology of upper Stormberg Group dinosaur faunas.

ABBREVIATIONS

Institutional

BP	Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), Johannesburg, South Africa
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, People's Republic of China
NHMUK	Natural History Museum, London, U.K.
PVSJ	Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Anatomical

ACH	anterior centrum height
ACW	anterior centrum width
cdf	centrodiapophyseal fossa
ce	centrum
CL	centrum length
CPOL	centropostzygapophyseal lamina
Cv	cervical vertebra
CvD	cervicodorsal vertebra
D	dorsal vertebra

dep	depression
dia	diapophysis
epi	epipophysis
ns	neural spine
NSH	neural spine height
NSL	neural spine length
NSW	neural spine width
PCDL	posterior centrodiapophyseal lamina
PCW	posterior centrum width
pp	parapophysis
PPDL	paradiapophyseal lamina
prcdf	prezygopophyseal centrodiapophyseal fossa
PRDL	prezygodiapophyseal lamina
PRPL	prezygoparapophyseal lamina
psf	prespinal fossa
SPOL	spinopostzygapophyseal lamina
s.prz	semicircular prezygapophysis

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