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A brief history of *Massospondylus*: its discovery, historical taxonomy and redescription of the original syntype series

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Massospondylus carinatus Owen, 1854 is one of the first dinosaurs to have been described from outside Europe and was based on material collected from what is now the upper Elliot Formation of the Free State province, South Africa. The species was included in various taxonomic reviews during the late nineteenth and early twentieth centuries but no additional material was referred beyond the original syntype series and it remained poorly known. This was exacerbated by the destruction of the syntypes during World War II. From the 1970s onward, fieldwork in the upper Stormberg Group of South Africa, Lesotho and Zimbabwe led to the discovery of many new sauropodomorph dinosaur specimens that have been referred to the taxon (often uncritically) that have been used to shed further light on the anatomy, palaeobiology and biostratigraphical utility of *Massospondylus carinatus*. Here, we review the taxonomic history of this species, provide updated descriptions of the syntypes (based on surviving casts) and use apomorphies to identify these specimens more accurately.

Keywords: *Massospondylus carinatus*, Dinosauria, Sauropodomorpha, Orpen Collection, upper Elliot Formation, historical taxonomy.

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INTRODUCTION

Massospondylus carinatus Owen, 1854 is one of the most fully documented Early Jurassic sauropodomorph dinosaurs. The anatomy of several key specimens has been described in detail (Gow 1990; Sues *et al*. 2004; Chapelle & Choiniere 2018; Barrett *et al*. 2019), and it has been the focus of numerous studies on growth rate (Chinsamy 1993; Erickson *et al*. 2001), ontogeny (Gow 1990; Gow *et al*. 1990; Reisz *et al*. 2005, 2010; Chapelle *et al*. 2020a, 2021), reproductive behaviour (Kitching 1979; Grine & Kitching 1987; Zelenitsky & Modesto 2002; Reisz *et al*. 2012; Stein *et al*. 2019), feeding and tooth replacement (Raath 1974; Barrett 2000; Barrett & Upchurch 2007; D'Emic *et al*. 2013) and locomotion (Bonnan & Senter 2007; Neenan *et al*. 2019; Chapelle *et al*. 2020b), providing an exemplar for work on other early sauropodomorph taxa. Referred specimens have been considered so abundant that *Massospondylus* forms the basis of an eponymous biostratigraphical assemblage, the *Massospondylus* Assemblage Zone, which has been used for intra- and interbasinal correlations across southern Africa (e.g. Bond 1965, 1973; Cooper 1981; Kitching & Raath 1984; Bordy *et al*. 2020; Viglietti *et al*. 2020) and elsewhere (Attridge *et al*. 1985; Apaldetti *et al*. 2011).

However, our current familiarity with *M. carinatus* masks a lengthy taxonomic history, and the taxon was poorly characterized and rarely discussed until relatively recently (see reviews in Cooper 1981; Sues *et al*. 2004; Yates & Barrett 2010; Barrett *et al*. 2019). This neglect was due, at least in part, to the poor quality of the original syntype series, which consisted of isolated, and often broken, elements of uncertain association that were destroyed during World War II. Here, we re-evaluate the collection of material that yielded the syntypes of *M. carinatus* Owen, 1854, *Leptospondylus capensis* Owen, 1854 and *Pachyspondylus orpenii* Owen, 1854, as well as the material that Richard Owen and others referred to each of these taxa historically, based on the plaster casts of these specimens that survive in museum collections in London and Cape Town. We also review the history of this formerly obscure, but now well-known, early dinosaur taxon.

A HISTORY OF *MASSOSPONDYLUS CARINATUS* AND ASSOCIATED TAXA

For most of the nineteenth century, South Africa was a British colonial possession (then known as the 'Cape Colony'): consequently, many of the fossils found in the region at this time were transported back to London, where they were deposited in the British Museum (now the Natural History Museum), the Hunterian Museum of the Royal College of Surgeons and other U.K. collections.

In 1846, four brothers relocated from Ireland to settle in South Africa. They were the sons of Charles Edward Herbert Orpen (1791–1856), an Edinburgh-trained physician and eye surgeon (https://www.geni.com/people/

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Dr-SV-PROG-Charles-Edward-Orpen/60000000156715538 05): Francis (Frank) Henry Samuel Orpen (1824–1893), Charles Sirr Orpen (1826–1887), Joseph Millerd Orpen (1828–1923), and Richard John Newenham Orpen (1830–1913). Joseph Orpen (Fig. 1) became a British government official, working first as a land surveyor and later holding various administrative posts across southern Africa (South Africa, Lesotho and Zimbabwe) (Orpen 1964): https://www.geni.com/people/Joseph-Millerd-Orpen/6000000018953033632). During his surveying work, Joseph and his brothers acquired a series of 56 postcranial bones '… in the Drakenberg [*sic*] range of mountains near Harrismith …' from '… a secondary formation, probably of the age of the New Red Sandstone in Europe' (Owen 1854, p. 97) in either 1853 (J.M. Orpen in Seeley 1895a) or 1854 (Owen 1854). These specimens were sent to their father, then based in East London (Eastern Cape, South Africa), who forwarded them to Richard Owen, then curator of the Hunterian Museum (Charles Orpen, a fellow of the Royal College of Surgeons, is noted as the donor of the material with his sons as the collectors: Owen 1854). Given Joseph Orpen's long life, he was able to provide a further account of these discoveries to Harry Govier Seeley in a letter written in 1889, noting that 'The spot where I obtained some large bones of a saurian about 1853, which my father sent home, was on a hill capped by sandstone on the east boundary of the farm Beaucherf, in the district of Harrismith, on the watershed of the Drakensberg. Below the sandstone is a chocolate-coloured shale. I think more of the bones would be found on the spot by excavating. The fossils were on the east face of the beacon-hill which is northwest of Beaucherf House' (Orpen in Seeley 1895a, p. 102).



Figure 1. Portrait of Joseph Millerd Orpen (from Orpen 1964).

Although the locality name 'Beaucherf' was used in some historical accounts (e.g. Haughton 1924), the farm is currently known as Beauchef Abbey 215 (Kitching & Raath 1984; Sues *et al*. 2004; Yates & Barrett 2010) and is located within the administrative district of Harrismith, Free State province, South Africa at 28°30′9.91″S and 29°9.1′29″E (Kitching & Raath 1984; P. Viglietti, pers. comm., 2021). Following additional stratigraphic work, the 'New Redstone' units mentioned by Owen (1854) were subsequently allocated to the 'Stormberg Series', being mentioned first as the 'Red Beds' (e.g. Haughton 1924) but later formalized as the Elliot Formation of the Stormberg Group (see review in Viglietti *et al*. 2020). Although these deposits were formerly regarded as Late Triassic in age (e.g. Haughton 1924; Kermack 1974), it was later recognized that they straddle the Triassic–Jurassic boundary (Olsen & Galton 1984; Olsen & Sues 1986). Kitching & Raath (1984) reported that the only exposures visible at Beauchef Abbey were from the upper Elliot Formation, which is currently regarded as latest Triassic (Rhaetian) to Early Jurassic (Hettangian–Sinemurian) in age, with most of its known fossil localities situated in the Early Jurassic portions of the unit (Sciscio *et al*. 2017; Bordy *et al*. 2020; Viglietti *et al*. 2020).

Owen (1854) registered the Orpen Collection at the Hunterian Museum (Figs 2, 3A), assigning the specimens to a continuous series of catalogue numbers (No[s].): Nos. 331–386. One of these (No. 386) was compared closely with the jaw of a gavial, but no formal referral was made to any taxon, although Owen's comparative observations (1854, p. 106) make it clear that he regarded it as crocodile-like; however, Seeley (1895a) later suggested that this specimen was a saurischian chevron. Huene (1906) proposed that No. 386 represented conjoined ischial shafts, which seems plausible on the basis of his figure, but as this specimen was not referred to any particular taxon, has no type status, and is no longer available (neither the original nor a cast exists), is it not considered further herein.

By contrast, Nos. 331–385 formed the basis for three new taxa – *Massospondylus carinatus* Owen, 1854, *Pachyspondylus orpenii* Owen, 1854 and *Leptospondylus capensis* Owen, 1854 (given in order of page priority) – providing the syntype series of each and a list of specimens that were referred to the three species with varying degrees of confidence (Table 1). Owen (1854) refrained from referring his new taxa to any of the reptile groups recognized at the time, noting instead that they combined features seen in lizards, crocodiles and dinosaurs.

Massospondylus carinatus was named based on five cervical vertebrae (Nos. 331–335) that Owen (1854: pp. 97–98) identified unambiguously as belonging to the taxon and that should be regarded as its syntype series (Yates & Barrett 2010). Many other specimens from the Orpen Collection (Nos. 336, 337, 349, 350, 352, 354–356, 358–364),

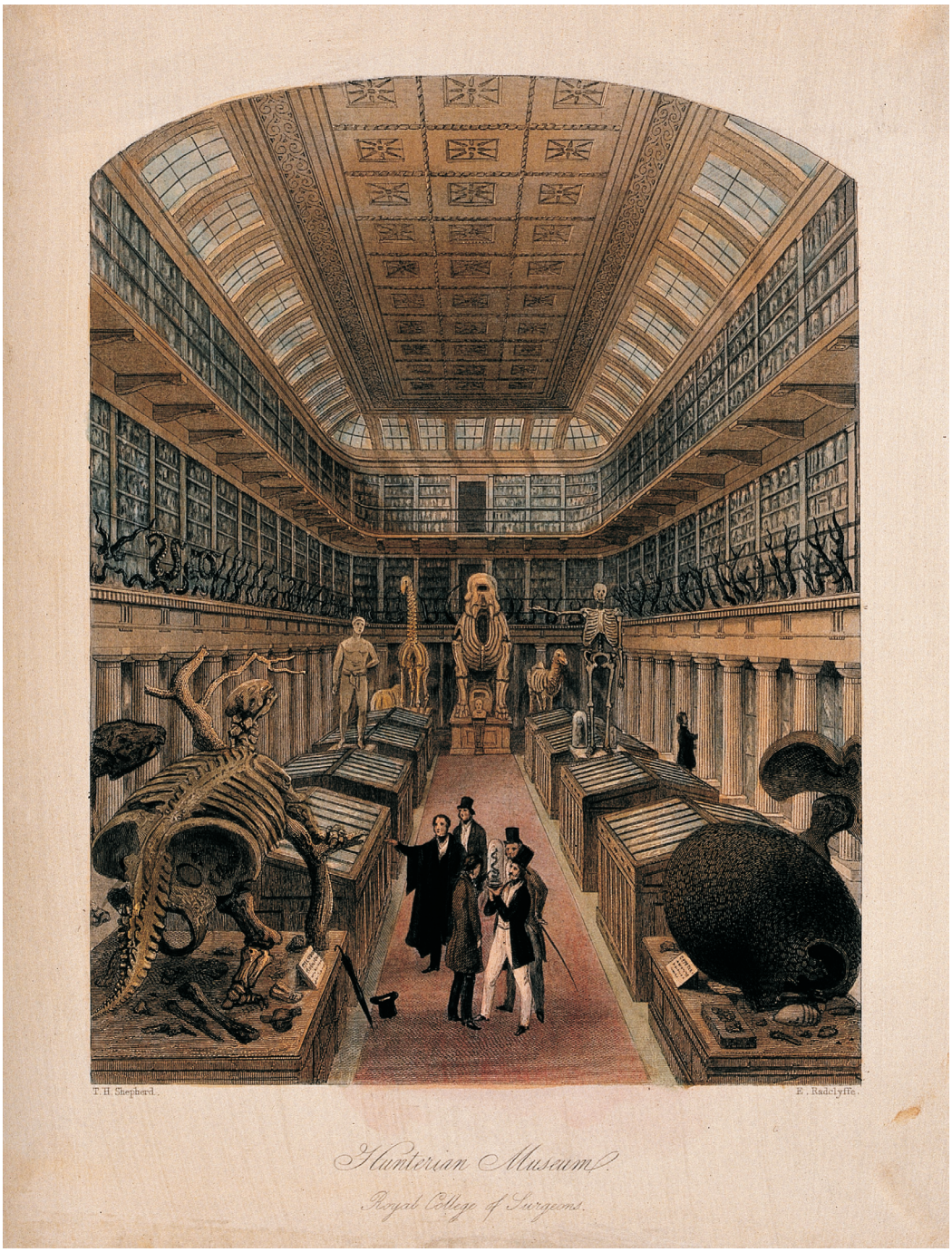


Figure 2. Colour lithograph of the palaeontological gallery at the Hunterian Museum in the Royal College of Surgeons of England, London. Artists, T.H. Shepherd and E. Radclyffe. This file comes from Wellcome Images, a website operated by Wellcome Trust, a global charitable foundation based in the United Kingdom (© Wellcome Trust: https://wellcomeimages.org/indexplus/image/V0013494.html).

including dorsal vertebrae, scapulae, humeral fragments, an ilium, a pubis (misidentified as a coracoid, see below), femora and tibiae, were also mentioned by Owen (1854: 98, pp. 101–103) as either *Massospondylus carinatus*?, *Massospondylus* or *Massospondylus*? (no species designation in either of the latter cases) and these should be regarded as referrals (Yates & Barrett 2010), rather than part of the type series (Table 1). Owen (1854) mentioned that his new genus name referred to the elongation of the cervical vertebrae (*'masson'* Gr. = longer [comparative of *makros*]; *'spondylos'* Gr. = vertebra) and it seems likely that the species name refers to the well-developed keel (carina) present on their ventral surfaces (although Owen did not mention its etymology).

The second new taxon, *Pachyspondylus orpenii*, was also based on a set of vertebrae, in this case one dorsal, one sacral and five caudals (Nos. 338–342, 345, 346), which form the syntype series (Owen 1854: pp. 99–100). Other specimens (Nos. 343, 344, 351, 353, 357, 366–384), including caudal vertebrae, a humerus, a pubis (misidentified as a scapula, see below), an ischium (misidentified as a coracoid, see below) and an assortment of metacarpals, metatarsals and phalanges, were referred to either *Pachyspondylus* or *Pachyspondylus*? (with no species designation in either case) and should be regarded as referrals (Owen 1854, pp. 100–105; Table 1). Owen's (1854) genus name refers to the stoutness of the vertebrae (*'pachys'* Gr. = thick; *'spondylos'* Gr. = vertebra) and the species name



Figure 3. Historical image of the Hunterian Museum in the building of the Royal College of Surgeons of England. **A**, lithograph of the exterior of the Royal College of Surgeons, London. Engraving after T. H. Shepherd. This file comes from Wellcome Images, a website operated by Wellcome Trust, a global charitable foundation based in the United Kingdom (© Wellcome Trust: https://wellcomeimages.org/indexplus/image/V0013491.html). **B**, photograph of the Royal College of Surgeons after a WWII bombing raid on the night of May 10th/11th 1941. The museum was directly struck by a high-explosive bomb which hit Room V and adjacent areas, destroying the osteological collections, including the Orpen Collection. Courtesy of Westminster City Archives (with permission).

presumably honours one or more members of the Orpen family.

Finally, *Leptospondylus capensis* was based on a syntype series consisting of only two caudal vertebrae (Nos. 347 and 348; Owen 1854, p. 100) and a single ungual phalanx was referred to *Leptospondylus*? (no species designation: No. 385; *ibid*., p. 105; Table 1). In this instance, Owen's (1854) genus name refers to the slenderness of the syntype vertebrate ('*leptos*' Gr. = slender; '*spondylos*' Gr. = vertebra) and, although he omitted the etymology, his species name clearly reflects their provenance.

Owen (1854) provided no illustrations of these specimens nor any detailed justifications for dividing them among the three taxa that he had erected, noting only that

Table 1. Catalogue of the Orpen Collection formerly held in the Hunterian Museum of the Royal College of Surgeons, London. This shows the original catalogue number, Owen's (1854) taxonomic statements and his original anatomical identifications. The taxonomic status of each element is shown, along with the NHMUK and SAM catalogue numbers for the surviving casts corresponding to the original specimens.

Catalogue	Owen taxonomy	Status	Owen identification	NHMUK No.	SAM No.
331	*Massospondylus carinatus*	Syntype	Caudal vertebra	PV R3027	SAM-PKC-958
332	*Massospondylus carinatus*	Syntype	Caudal neural arch	PV R3028 (*partim*)	SAM-PKC-959
333	*Massospondylus carinatus*	Syntype	Caudal vertebra	PV R3028 (*partim*)	SAM-PKC-960
334	*Massospondylus carinatus*	Syntype	Partial centrum	PV R3028 (*partim*)	SAM-PKC-961
335	*Massospondylus carinatus*	Syntype	Caudal centrum	PV R3028 (*partim*)	SAM-PKC-962
336	*?Massospondylus carinatus*	Referred	Dorsal centrum	PV R1312	SAM-PKC-963
337	*?Massospondylus carinatus*	Referred	Dorsal centrum	NA	NA
338	*Pachyspondylus orpeni*	Syntype	Caudal vertebra	PV R3035 (*partim*)	NA
339	*Pachyspondylus orpeni*	Syntype	Caudal centrum	NA	NA
340	*Pachyspondylus orpeni*	Syntype	Caudal centrum	NA	NA
341	*Pachyspondylus orpeni*	Syntype	Caudal neural arch	NA	NA
342	*Pachyspondylus orpeni*	Syntype	Caudal vertebra	PV R3035 (*partim*)	NA
343	*?Pachyspondylus*	Referred	Caudal vertebra	PV R3035 (*partim*)	NA
344	*?Pachyspondylus*	Referred	Caudal vertebra	NA	NA
345	*Pachyspondylus orpeni*	Syntype	Dorsal vertebra	PV R3035 (*partim*)	NA
346	*Pachyspondylus orpeni*	Syntype	Sacral	PV R3035 (*partim*)	NA
347	*Leptospondylys capensis*	Syntype	Caudal centrum	PV R3025	NA
348	*Leptospondylys capensis*	Syntype	Caudal vertebra	NA	NA
349	*Massospondylus*	Referred	Left scapula	PV R3029 (*partim*)	SAM-PKC-964
350	*Massospondylus*	Referred	Left scapula	PV R3029 (*partim*)	SAM-PKC-965
351	*Pachyspondylus*	Referred	Left scapula	PV R3036 (*partim*)	NA
352	*Massospondylus*	Referred	Right coracoid	PV R3030	SAM-PKC-966
353	*?Pachyspondylus*	Referred	Coracoid	PV R3036 (*partim*)	NA
354	*?Massospondylus*	Referred	Humerus	PV R3031 (*partim*)	SAM-PKC-967
355	No name given	NA	?Humerus	NA	NA
356	*?Massospondylus*	Referred	Humerus	PV R3031 (*partim*)	SAM-PKC-968
357	*Pachyspondylus*	Referred	?Humerus	NA	NA
358	*?Massospondylus*	Referred	Ilium	PV R3032 (*partim*)	SAM-PKC-969
359	*Massospondylus*	Referred	Ischium	PV R3032 (*partim*)	SAM-PKC-970
360	*?Massospondylus*	Referred	Right femur	PV R3033 (*partim*)	SAM-PKC-971
361	*Massospondylus*	Referred	Left femur	PV R3033 (*partim*)	SAM-PKC-972
362	*Massospondylus*	Referred	Right femur	PV R3033 (*partim*)	SAM-PKC-973
363	*Massospondylus*	Referred	Right tibia	PV R3034 (*partim*)	SAM-PKC-974
364	*Massospondylus*	Referred	Tibia	PV R3034 (*partim*)	NA
365	No name given	NA	Left tibia	NA	SAM-PKC-975
366	*?Pachyspondylus*	Referred	Tarsal	PV R3037 (*partim*)	NA
367	*?Pachyspondylus*	Referred	Metatarsal	PV R3037 (*partim*)	NA
368	*?Pachyspondylus*	Referred	Metatarsal	PV R3037 (*partim*)	NA
369	*?Pachyspondylus*	Referred	Metatarsal	PV R3037 (*partim*)	NA
370	*?Pachyspondylus*	Referred	Metatarsal	NA	NA
371	*?Pachyspondylus*	Referred	Metatarsal	NA	NA
372	*?Pachyspondylus*	Referred	Metatarsal	NA	NA
373	*?Pachyspondylus*	Referred	Metatarsal	PV R3037 (*partim*)	NA
374	*?Pachyspondylus*	Referred	Metatarsal	PV R3037 (*partim*)	NA
375	*?Pachyspondylus*	Referred	Phalanx	PV R3037 (*partim*)	NA
376	*?Pachyspondylus*	Referred	Phalanx	NA	NA
377	*?Pachyspondylus*	Referred	Phalanx	NA	NA
378	*?Pachyspondylus*	Referred	Phalanx	PV R3037 (*partim*)	NA
379	*?Pachyspondylus*	Referred	Phalanx	PV R3037 (*partim*)	NA
380	*?Pachyspondylus*	Referred	Phalanx	PV R1312a	SAM-PKC-976
381	*?Pachyspondylus*	Referred	Phalanx	NA	NA
382	*?Pachyspondylus*	Referred	Ungual phalanx	PV R3037 (*partim*)	NA
383	*?Pachyspondylus*	Referred	Ungual phalanx	PV R3037 (*partim*)	NA
384	*?Pachyspondylus*	Referred	Ungual phalanx	NA	NA
385	*?Leptospondylus*	Referred	Ungual phalanx	PV R3026	NA
386	No name given	NA	?Dentaries	NA	NA

these decisions were based on size, proportions and preservational features. Indeed, as noted by Sues *et al*. (2004, p. 240), many of his referrals seem to have been made 'somewhat arbitrarily', especially as most of these additional specimens have no anatomical overlap with those in the aforementioned syntype series. Moreover, it is unknown if any of the specimens were originally associated or articulated, whether they were all found in close proximity, or if they were recovered from the same stratum. Owen (1854) suggested that some of the individually catalogued fragments might originally have been parts of the same bone (for example, he proposed that Nos. 354–356 were parts of the same humerus) but he offered no further comments on the number of individuals represented.

Following Owen's establishment of these taxa, they were mentioned only rarely during the remainder of the nineteenth century, with brief, scattered references appearing in the literature (see below). Given the intense interest in other extinct reptiles at this time, it is tempting to speculate that this lack of engagement reflects Owen's (1854) rather perfunctory descriptions and his decision to gloss over the affinities of these taxa (he later referred *Massospondylus* to Crocodylia but provided no reasons for doing so; e.g. Owen 1860a, p. 271; Owen, 1860b, p. 164). The fragmentary nature of the material might have contributed to this ambivalence but, given the large number of similarly poorly preserved specimens of other taxa that were mentioned frequently in the early palaeontological literature, this seems unlikely. Huxley (1867) mentioned *Massospondylus*, *Pachyspondylus* and *Leptospondylus* in his first paper on South African dinosaurs, noting in passing that they differed from his new taxon '*Euskelesaurus*' [*sic*] (now considered a *nomen dubium*; Yates 2003a; Yates & Kitching 2003), without offering further comment on their relationships, while Jones (in Tate 1867) included them in a faunal list alongside other Stormberg taxa. Owen (1880) referred to all three taxa in comparisons with dicynodont material, and this seems to have been his last publication to mention them.

Lydekker (1888) re-examined the Orpen Collection in order to compare these specimens with new fossil reptile material from the 'Maleri Beds' of central India. He appears to have been the first to recognize the dinosaurian nature of *Massospondylus* and *Pachyspondylus* and suggested that these taxa were probably theropods and members of Anchisauridae (N.B., many early discoveries of non-sauropod sauropodomorph taxa were originally regarded as members of various theropod sub-groups until the mid-twentieth century). This classification was accepted by later authors (e.g. Zittel 1887–90; Marsh 1889a, b). Lydekker (1888) figured two of the specimens (No. 336, a cervical vertebra; No. 380, a pedal phalanx) and opined that *Massospondylus* and *Pachyspondylus* might be synonymous, giving priority to the former, although his discussion omitted *Leptospondylus*. Finally, Lydekker suggested that Owen's (1854) description was taxonomically invalid and proposed instead that his own publication should: 1) be regarded as the official source of the binomen; and 2) that the two specimens he figured (Lydekker 1888, fig. 3) be designated as the types of *Massospondylus carinatus*. However, Owen's (1854) publication and descriptions are clearly valid under the rules of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) so Lydekker's proposals are invalid (and were ignored by the majority of later workers). Subsequently, the same figures of the vertebra (No. 336) were republished (Lydekker in Nicholson & Lydekker 1889, fig. 1067; Lydekker 1890a, fig. 58) alongside affirmations of the anchisaurid affinities of *Massospondylus* and the type status of the vertebra (No. 336: with the phalanx, No. 380, being relegated to referred specimen status). The saurischian affinities of *Massospondylus* were elaborated upon by Seeley (1892) who compared it further to '*Euskelesaurus*' [*sic*] (Seeley 1894a,b). An isolated vertebra (IM G.281/1-u) and tooth (NHMUK PV R4190) from the 'Maleri Beds' and 'Tikli Beds', respectively, were assigned to *Massospondylus* around this time, leading to the erection of two new species – *M. hislopi* Lydekker, 1890b and *M. rawesi* Lydekker, 1890b – which extended the distribution of the genus to India (see also Lydekker in Nicholson & Lydekker 1889, fig. 957).

Seeley (1895a) was the first to provide a detailed, illustrated account of the Orpen Collection, as well as a critical evaluation of Owen's earlier conclusions. Following his examination of the material, Seeley (1895a) concluded that: 1) at least three individuals were represented; 2) that most of the individual bones belonged to a single taxon – *Massospondylus carinatus*; and 3) that *Massospondylus* was a 'megalosaurian saurischian' (*ibid*., p. 103). Seeley (1895a) corrected several of Owen's anatomical misidentifications and suggested that the names *Pachyspondylus* and *Leptospondylus* should be '… held for the present in abeyance …' (*ibid*.: pp. 103–104), as he presumably regarded them as indistinguishable from *Massospondylus*. Indeed, Seeley referred most of the Orpen Collection to the latter taxon, simplifying Owen's (1854) complex scheme of syntypes and referred specimens. Seeley (1895a) did not designate a lectotype specimen or comment on Owen's proposed taxonomy but regarded the elements that he described as parts of an extended syntype series for *M. carinatus*. Seeley's revision of *M. carinatus* was published alongside an account of several other bones collected from the 'Stormberg beds' of '… the Telle River, north of the Witte Bergen in the Mattisi country …' by Alfred Brown, which included several vertebrae, a pair of femora and phalanges. These specimens (NHMUK PV R3302) were used as the basis for a new species, *Massospondylus browni* Seeley, 1895b. (NB, although this binomen was first used in Seeley [1892] it was published without an accompanying description, illustration or diagnosis, so was a *nomen nudum* prior to 1895). Nopcsa (1901) listed *M. carinatus* and *M. browni* in his synopsis of known dinosaur species and followed Lydekker and Seeley in regarding them as 'anchisaurid megalosaurs'.

Huene (1906) was the next to tackle the relationships of *Massospondylus* and provided many new figures of the Orpen specimens (based on casts held in the University of Tübingen), gave additional descriptions and corrected

several of Seeley's anatomical mistakes. Although he did not discuss the taxonomy of Owen's Stormberg species, Huene clearly considered them as synonyms, as he listed all of the specimens as *M. carinatus*. Following comparisons with other early dinosaurs, Huene (1906) grouped *Massospondylus*, *Thecodontosaurus* and *Anchisaurus* into the Thecodontosauridae, which he considered to be a theropod subgroup. He also commented on the status of *M. browni* (referring the material to two species of *Thecodontosaurus*) and suggested that neither *M. hislopi* nor *M. rawesi* were dinosaurs. Consequently, Huene (1906) restricted the genus to the original Orpen Collection material. Broom (1911) suggested that that Orpen Collection represented two individuals, one of which was *M. carinatus* and the other potentially referrable to his new species *M. harriesi* (see below). He also agreed with previous authors that *Pachyspondylus* and *Leptospondylus* were likely invalid and in referring *M. browni* to *Thecodontosaurus* (Broom 1911).

The next two decades witnessed the discovery of many other dinosaur specimens from the Stormberg Group of South Africa, leading to the naming of two new species of *Massospondylus*. The first of these, *M. harriesi* Broom, 1911, was based on material collected from the upper Elliot Formation of Foutanie Farm, near Fouriesburg in the Free State province (cadastral unit 331), whose type material included incomplete fore- and hind limb elements (SAM-PK-3394) (Broom 1911; Kitching & Raath 1984). An isolated pes (Huene 1911) and several partial skeletons, one with skull material (SAM-PK-5135), were referred to this species (Haughton 1924). A partial postcranial skeleton originally referred to *M. browni* by Van Hoepen (1920) was also included in *M. harriesi* (Haughton 1924). The second new species, *M. schwarzi* Haughton, 1924, was based on a partial hind limb (SAM-PK-5134) from the Elliot Formation of Makomoreng, Eastern Cape province (Haughton 1924; Kitching & Raath 1984). Haughton (1924) provided a brief review of *M. carinatus*, based on Huene's (1906) account and the plaster casts held in the Iziko South African Museum, but despite having extensive new collections of dinosaur material at his disposal he did not refer any new specimens to the taxon. During this period, Huene (1914) erected the new family Massospondylidae for *M. carinatus*, *M. harriesi* and another South African taxon *Aetonyx palustris* Broom, 1911. Haughton (1924) added a further Stormberg taxon, *Dromicosaurus gracilis* Van Hoepen, 1920, to this group. In his benchmark review of saurischian dinosaur taxonomy and systematics, Huene (1932) retained *M. carinatus*, *M. schwarzi* and *M. harriesi* as valid species, but abandoned Massospondylidae and placed them within Thecodontosauridae, along with *Thecodontosaurus* (= *Massospondylus*) *browni* and several other taxa. Otherwise, *Massospondylus* was not much discussed during the mid-twentieth century, although it was consistently included in taxonomic compilations (e.g. Lull 1910; Williston 1925; Romer 1956, 1966; Steel 1970; White 1973).

Perhaps the most famous event in the history of *Massospondylus carinatus* is the destruction of the original syntype series, although only a few details have been provided in the palaeontological literature (Attridge 1963; Steel 1970; Sues *et al*. 2004; Yates & Barrett 2010). As noted previously, the Orpen Collection, and many other palaeontological specimens, were housed in the Hunterian Museum of the Royal College of Surgeons (Owen 1854), where six conjoined galleries and other associated facilities functioned as multipurpose teaching, research and collections spaces (Keith 1910; Allen 1974; Figs 2, 3A). The fossil reptile specimens formed part of the comparative osteological collection, most of which was stored in Room V of the museum, with the other rooms being dedicated to various aspects of human anatomy (Keith 1910; Cave 1941). Most of the fossil reptile specimens were held in a series of wall-mounted cases around the north and west sides of Room V, close to examples of modern reptile skeletons; other significant specimens of recent and fossil mammals, birds and fish were stored nearby (Keith 1910; Cave 1941; Fig. 2). Following the onset of World War II, precautions were taken to protect the collections in the event of bombing raids, including the removal of some collections to remote locations and strengthening of the museum basements for on-site storage underground (Cave 1941; Wakeley 1965). However, many specimens could not be moved due to either a lack of sufficient storage space or their large size (Cave 1941). Between October 1940 and April 1940 shell fragments from German bombing raids damaged the roof of the museum but did not lead to any losses from the collection (Cave 1941). On 11 October 1940 a bomb exploded on Portugal Street, immediately adjacent to the museum and directly outside Room V, shattering many of the windows and roofs around the building but causing only minor damage to the osteological specimens, although details of the specimens affected were not recorded (Cave 1941). Just a few days later, on 16 October 1940, a land mine exploded in nearby Lincolns Inn Fields, which caused considerable structural damage to the building and affected specimens in the human anatomical collections (Cave 1941). Other bombing incidents in October 1940 and February 1941 caused only minor building damage or temporary closures of the building (Cave 1941). However, on the night of May 10th/11th 1941, the museum was struck directly by a high-explosive bomb that hit Room V and adjacent areas, destroying this part of the building and most of its contents, while incendiary bombs gutted other areas (Cave 1941; Wakeley 1965; Fig. 3B). Falling debris broke through into the basement storage rooms, leading to the destruction of the osteological collections, which were stored in this area, a problem exacerbated by heavy rainfall, which flooded the site (Cave 1941; Wakeley 1965). The material affected included all the fossil reptile material catalogued by Owen (1854) as well as many other scientifically important specimens that had been integral to the development of medicine, anatomy and zoology. As noted by Cave (1941, p. 8): 'The magnitude of this disaster to the College, to the nation and to the medical and scientific worlds needs no emphasis'. Among these casualties were *Massospondylus*, *Pachyspondylus* and *Leptospondylus*. Of the 550 reptile specimens included in the comparative collection, only 23 survived (Cave 1941). Fortunately,

casts of selected specimens from the Orpen Collection remained in the Natural History Museum (London, U.K.), Iziko South African Museum (Cape Town, South Africa) and the Institut und Museum für Geologie und Paläontologie, Universität Tübingen (Tübingen, Germany). These casts, and the line-drawings provided by Seeley (1895a), Huene (1906) and others, are the only surviving records of this material (see below).

Subsequent to the work of Broom, Haughton and Van Hoepen, no significant discoveries of *Massospondylus* material were reported from South Africa for many years, although it is likely that material continued to accumulate in Cape Town, Pretoria and Bloemfontein during the mid-twentieth century. It is tempting to speculate that work on South African dinosaurs was overshadowed by work on the abundant and important synapsid material from the Karoo Basin, which formed the primary research focus for many palaeontologists in the region at this time. However, material continued to be referred to *Massospondylus* from other southern African countries with reports from the Karoo-aged sediments of the mid-Zambezi, Mana Pools and Tuli basins of Zimbabwe (e.g. Attridge 1963; Bond 1965, 1973; Raath *et al*. 1970; Raath 1974; Cooper 1981; Munyikwa 1997) and from the Stormberg Group of Lesotho (Ellenberger *et al*. 1964; Attridge & Charig 1967; Anonymous 1969; Kermack 1974). Many of the Zimbabwean specimens, which consist almost exclusively of postcranial remains, were described by Cooper (1981) in a detailed, well-illustrated monograph. By contrast, the material collected from Lesotho, which is housed in collections in Cape Town, Paris and London, has not yet been described in detail, with the exception of a complete but crushed skull (SAM-PK-K1314), which has been figured on many occasions (e.g. Attridge & Charig 1967; Attridge *et al*. 1985; Norman 1985) but only described in part (Barrett & Yates 2006).

Galton & Cluver (1976) provided a taxonomic review of many southern African sauropodomorph species in which they proposed a wide-ranging series of synonymies and shuffled genera between two of the family-level taxa that were in use at this time: Anchisauridae ('narrow-footed prosauropods') and Plateosauridae ('broad-footed prosauropods'). They referred *Massospondylus* to Plateosauridae, in contrast to previous authors, but followed Huene, Haughton and others in restricting *Massospondylus carinatus* to its syntype series and in regarding *Pachyspondylus orpeni* and *Leptospondylus capensis* as its junior subjective synonyms. Similarly, Galton & Cluver (1976) regarded *M. harriesi* as a valid taxon and referred many other taxa and specimens to its hypodigm, including *Aetonyx palustris*, *Gryponyx africanus*, *Dromicosaurus gracili*, *Thecodontosaurus dubius* and a referred specimen of *M. browni*. However, no rationale was given for these decisions other than noting superficial resemblances in foot anatomy. By contrast, the type specimen of *M. browni* was regarded as a *nomen dubium* (Anchisauridae *incertae sedis*) and was excluded from *Massospondylus*. Based on these taxonomic changes, Galton & Cluver (1976) noted that *Massospondylus* was the most widely distributed genus of sauropodomorph in southern Africa.

Alongside his description of the Zimbabwean material, Cooper (1981) performed a comprehensive review of upper Stormberg 'prosauropod' species and agreed with Galton & Cluver (1976) that the taxonomy was oversplit. Cooper (1981) compared the Zimbabwean sample with the type specimens of South African taxa and noted that none of them differed substantially. He concluded that the minor differences noted by earlier authors were not taxonomically informative and could be regarded as either taphonomic, geographic, individual or ontogenetic variation. Moreover, following the principle of date priority he regarded *Massospondylus carinatus* as the valid binomen for all this material, leading him to refer a vast number of specimens to this taxon for the first time in its long history. Many species became junior subjective synonyms of *Massospondylus*, including not only those taxa listed by Galton & Cluver (1976), but also *M. browni*, *M. harriesi*, *Gryponyx taylori*, *Gr. transvalensis*, *Aristosaurus erectus*, *Thecodontosaurus minor* and *Gyposaurus capensis*. In addition, Cooper (1981) suggested that *Lufengosaurus* and *Yunnanosaurus* should also be referred to *Massospondylus*. This resulted in a trans-continental distribution covering South Africa, Lesotho, Zimbabwe and China. Cooper (1981) also reinstated *Massospondylus* to Anchisauridae and provided the first in-depth palaeobiological analysis of the taxon, envisaging it as an active, bipedal, endothermic carnivore, although most recent authors regard it as either herbivorous or facultatively omnivorous (Galton 1985; Barrett 2000).

Cooper's (1981) detailed descriptions superceded the earlier descriptions of Seeley (1895a) and Huene (1906), and his monograph became a standard reference on *Massospondylus* postcranial anatomy for anatomical and phylogenetic studies. However, this work was limited by several factors: 1) the lack of cranial material that could be referred confidently to the genus; 2) the fact that few associated skeletons were available to him; and 3) the assumption that the Zimbabwean material was conspecific with the South African taxon named by Owen (1854). Cooper (1981) did not provide a new diagnosis of the taxon nor use unique features to refer specimens to the hypodigm, relying instead on overall similarity to build his taxonomic framework. This led to a situation in which it was generally assumed that all lightly-built sauropodomorph remains from the upper Stormberg Group were referrable to *Massospondylus* (e.g. Kitching & Raath 1984; Gow 1990; Gow *et al*. 1990) and there were no further assessments of upper Elliot sauropodomorph taxonomy until the 2000s. As a result, hundreds of sauropodomorph specimens collected from the upper Elliot and Clarens formations between the 1970s–2000s were simply assumed to be *Massospondylus*, labelled as such in collections in Cape Town, Johannesburg, Pretoria, Grahamstown and Bloemfontein, and largely ignored: many of these specimens require re-examination. However, a strong case was never made for referring *any* of these specimens to *M. carinatus* based on comparisons with the syntypes: rather, a set of nested inferences was built by Cooper (1981) and others that linked the priority of this name (over others) with stratigraphic and geographic overlap

and general anatomical similarity. It is entirely possible that the set of specimens now considered referrable to this taxon are in no way related to the specimens of the syntype series, but that habitual usage of the name shifted understanding of the taxon's hypodigm. As a result, the application of the name *M. carinatus* to all of this more recently recovered material might have been more serendipitous than taxonomically justified.

Systematic collecting efforts in the 1970s–1980s, led by Alfred Crompton (SAM), James Kitching (BPI), Christopher Gow (SAM then BPI) and Roger Smith (SAM), resulted in the recovery of many new sauropodomorph specimens from the upper Elliot Formation of the Free State and Eastern Cape provinces, with crucial discoveries of skeletons including complete skulls. Preliminary descriptions of these specimens referred all of them to *M. carinatus* (Cooper 1981; Kitching & Raath 1984; Gow 1990; Gow *et al*. 1990), a conclusion followed by all subsequent authors (e.g. Sues *et al*. 2004). A clutch of eggs was also referred to the genus (Kitching 1979) although its significance was not fully appreciated until later (Grine & Kitching 1987; Zelenitsky & Modesto 2002; Reisz *et al*. 2005, 2010, 2012; Stein *et al*. 2019; Chapelle *et al*. 2020a). Although these new specimens offered the opportunity for a thorough re-assessment of the genus, Gow (1990; Gow *et al*. 1990) did not comment on the diagnosis of the taxon but simply accepted the prior conclusions of Cooper (1981) and others. Sues *et al*. (2004) were the first authors to provide a character-based diagnosis of *M. carinatus*, based on cranial anatomy, and these authors also highlighted the need to stabilize its taxonomy further, as well as providing the first thorough description of four well-preserved skulls. Building on this work, Barrett & Yates (2006) provided more details of another referred skull and proposed BP/1/4934 as the neotype of *M. carinatus* (Yates & Barrett 2010). The latter specimen includes a skull and almost complete postcranial skeleton, enabling it to serve as a more useful exemplar than the unavailable, unassociated and fragmentary syntypes described by Owen (1854) thereby improving its taxonomic stability. During this period, a referred partial skull was shown to differ from other examples known and was established as the type specimen of a second species, *M. kaalae* (Barrett 2009). Subsequently, more detailed studies of the neotype postcranium (Barrett *et al*. 2019) and a referred skull (Chapelle & Choiniere 2018) permitted the development of stricter, character-based diagnoses.

In parallel with these South African discoveries, new material from other countries was also referred to *Massospondylus*. These included specimens from the Lower Jurassic Kayenta Formation of the U.S.A. (Attridge *et al*. 1985) and Cañón del Colorado Formation of Argentina (Martínez 1999), and from the Late Triassic Upper Maleri Formation of India (Kutty *et al*. 1987), all of which suggested a trans-continental distribution and a possible use for the genus in global stratigraphic correlations. However, re-assessment of the Indian specimen identified it as guibasaurid sauropodomorph (Novas *et al*. 2011), and the Argentinean material was later recognized as a distinct (but closely related) taxon, *Adeopapposaurus mognai* (Martínez 2009). For several years the Kayenta Formation specimens were used as exemplars for the genus in biomechanical and taxonomic studies (e.g. Crompton & Attridge 1986; Galton 1990), but additional work has shown that they also represent a different taxon, *Sarahsaurus aurifrontalis* (Rowe *et al*. 2011; Marsh & Rowe 2018). Cooper's (1981) suggestion that *Lufengosaurus* and *Yunnanosaurus* were junior subjective synonyms of *Massospondylus* has not been supported by any other study (e.g. Galton 1990; Galton & Upchurch 2004) and the historical referrals of the Indian specimens '*M. rawesi*' and '*M. hislopi*' (see above) have also been rejected (Huene 1906; Galton & Upchurch 2004; Carrano *et al*. 2010). Consequently, the distribution of *Massospondylus sensu stricto* is considered restricted to southern Africa.

More rigorous character-based taxonomic approaches, and a clearer understanding of the composition of the *Massospondylus* hypodigm, have also allowed the description of two new sauropodomorph taxa from the upper Elliot Formation of South Africa and Lesotho based on material formerly referred to *Massospondylus* – *Ignavusaurus rachelis* (Knoll 2010) and *Ngwevu intloko* (Chapelle *et al*. 2019).

In addition to basic anatomical and taxonomic work, the discovery of this new, more complete material stimulated phylogenetic work and *Massospondylus* has been included in numerous cladistic studies on sauropodomorph systematics (e.g. Galton 1990; Sereno 1999; Benton *et al*. 2000; Yates 2003b, 2004, 2007; Yates & Kitching 2003; Galton & Upchurch 2004; Kutty *et al*. 2007; Smith & Pol 2007; Upchurch *et al*. 2007; Martínez 2009; Knoll 2010; Sertich & Loewen 2010; Apaldetti *et al*. 2011, 2013; Novas *et al*. 2011; Pol *et al*. 2011, 2021; Yates *et al*. 2011; Otero & Pol 2013; McPhee *et al*. 2015, 2018; Peyre de Fabrègues & Allain 2016, 2020; Wang *et al*. 2017; Chapelle & Choiniere 2018; Müller *et al*. 2018; Chapelle *et al*. 2019; Rauhut *et al*. 2020; Regalado Fernández & Werneburg 2022). Its inferred relationships have varied through time, dependent on the size of the dataset, the taxa included in the analysis and the source material for scoring anatomical characters. For example, many earlier studies relied on Cooper's (1981) descriptions for postcranial characters, but the lack of associated material and doubts on its conspecificity render these scores problematic. Similarly, the holotype skull of *Ngwevu intloko* would have been conflated with those of *Massospondylus* in many analyses. Early non-numerical analyses identified *Massospondylus* as an early-diverging member of a monophyletic Prosauropoda and led to the resurrection of Massospondylidae as a distinct monotypic family (e.g. Galton 1990). Subsequently, numerical analyses have generally recovered *Massopondylus* in a massospondylid clade whose composition varies but that most frequently includes *Adeopapposaurus*, *Coloradisaurus*, *Leyesaurus* and *Lufengosaurus* as close relatives (e.g. Smith & Pol 2007; Upchurch *et al*. 2007; Yates 2007; Apaldetti *et al*. 2011, 2013; Otero & Pol 2013; Wang *et al*. 2017; Peyre de Fabrègues & Allain 2020; Rauhut *et al*. 2020; Pol *et al*. 2021).

In spite of this work, much remains to be done. It remains far from clear if all the specimens currently referred to *Massospondylus* genuinely pertain to the taxon (as currently

defined) or if other taxa remain hidden within its hypodigm. Moreover, the exact dating of these specimens is often uncertain and needs to be re-assessed in light of new constraints on the chrono- and lithostratigraphy of the upper Stormberg Group (e.g. Bordy *et al*. 2020; Viglietti *et al*. 2020). This is important as it has consequences for the use of this material in biostratigraphical correlations (both within and between basins) as well as its impact on palaeobiological studies (as the large sample size currently available might be a chimera). For convenience, key events in the history of *Massospondylus* are summarized in Fig. 4.

THE ORPEN COLLECTION: DESCRIPTIONS AND COMPARISONS

Here, we present descriptions of the Orpen Collection based on the surviving casts in the collections of NHMUK and SAM (we did not have the opportunity to examine those at GPIT firsthand). Sadly, these represent only part of the original collection, and, in the absence of published figures, the other specimens originally listed by Owen (1854) are now completely lost to science. None of these institutions appears to hold much archival information on these casts, and it is not clear how or why they were procured. In the case of the NHMUK set, the registers record the fact that two of the casts (NHMUK PV R1312, R1312a) were made in the museum sometime in 1888 whereas the others were purchased in April 1902 from C.B. Firth. The casts housed in SAM were obtained around 1906 from R.F. Damon (Z. Skosan, pers. comm.), the owner of a Dorset-based fossil dealership and natural history cast-making business. Those in GPIT were acquired by Friedrich von Huene (I. Werneburg, pers. comm.). Although the casts represent the original syntype series of these taxa, these 'plastotypes' cannot act as name-bearing type specimens as artificial physical replicas are ineligible for nomenclatural acts (see International Code on Zoological Nomenclature 1999, Article 72.5; see also Yates & Barrett 2010).

A summary of the current identifications of each of these specimens is provided in Table 2.

Axial skeleton

Cervical vertebrae

Owen (1854, pp. 97–98) regarded Nos. 331–335 as caudal vertebrae, but Seeley (1895) correctly noted that they are from the cervical series. Seeley (1895, pp. 104–106, fig. 1) provided an accurate description of No. 331 (updated herein), which he retained within *Massospondylus carinatus*. By contrast, Seeley (1885) excluded Nos. 332–335 from *M. carinatus* and regarded these vertebrae as referable to a different taxon, although no evidence was provided to support this proposal (nor were they referred to any other named taxon). Huene (1906, p. 133) dismissed Seeley's suggestion and reinstated the vertebrae in the type series, provided further descriptions and figured Nos. 331–335 (*ibid*., figs 44, 45, pl. XIII [XX], figs 6–8). Measurements of the cervical vertebrae are provided in Table 3.

The centrum of No. 331 (NHMUK PV R 3027; SAM-PKC-958; Fig. 5A–F) is complete but is slightly deformed and its articular surfaces have been damaged. The anterior articular surface is sub-circular in outline and is gently concave (Fig. 5A); the posterior articular surface is also shallowly concave but has a more shield-shaped outline that is taller than wide, with a straight dorsal margin and lateral margins that descend in a straight line for a short distance before merging ventrally (Fig. 5C). In lateral view, the ventral margin of the centrum is strongly concave and the lateral surfaces are anteroposteriorly concave and convex dorsoventrally (Fig. 5B, D). A distinct break-in-slope, marked by a thin ridge divides the lateral surfaces into larger dorsal and smaller ventral portions. There are no pneumatic openings. A low, sub-triangular parapophysis is present on the anterior-most part of the lateral centrum surface, at approximately mid-centrum height. The lateral surfaces merge ventrally to form a sharp midline keel that extends for the full length of the centrum (Fig. 5F). The centrum has a total length/anterior articular surface height ratio of 2.43.

A robust, posterior centrodiapophyseal lamina (PCDL) is present, which arises from the posterodorsal corner of the centrum and merges with the posterior margin of the transverse process to create a rounded ledge that overhangs the lateral surface of the centrum (Fig. 5B, D). This ledge is almost horizontal, rising only slightly dorsally as it extends anteriorly. There is some indication of a low, ridge-like paradiapophyseal lamina (PPDL). The PPDL and PCDL form the boundaries of an extensive, shallow, triangular centrodiapophyseal fossa (CDF).

The neural arch extends for the full length of the centrum (Fig. 5B, D, E). It is almost complete but lacks the right prezygapophysis, left transverse process and left postzygapophysis. In anterior view, the neural canal opening is sub-circular (Fig. 5A), but posteriorly it is sub-elliptical, with the long axis of this ellipse oriented transversely (Fig. 5C). The prezygapophysis extends anterior to the anterior articular surface for a short distance. Its articular surface is ovate, flat to very gently convex and is bevelled to face dorsomedially at an angle of approximately 45° to the horizontal (Fig. 5B, D). The base of the prezygapophysis has a narrow triangular cross-section. An interprezygapophyseal lamina (TPRL) links the two prezygapophyses and forms the floor of a shallow concavity that is confluent with an incipient prespinal fossa posteriorly (Fig. 5E). Low, ridge-like spinoprezygapophyseal laminae (SPRL) extend from the dorsal margins of the prezygapophyses to the anterior margin of the neural spine (Fig. 5E). A low lamina (epipophyseal-prezygapophyseal lamina: EPRL) extends posterodorsally from the prezygapophysis to meet the anterior margin of the postzygapophysis, dividing the lateral surface of the neural arch into distinct dorsal and ventral portions (Fig. 5B, D).

A short, wing-like transverse process is present, which is situated just anterior to the midpoint of the vertebra. It has a flattened, elliptical cross-section and a short, rounded triangular outline in dorsal view (Fig. 5E).

The postzygapophyses extend for a short distance beyond the centrum posteriorly and have flat, elliptical

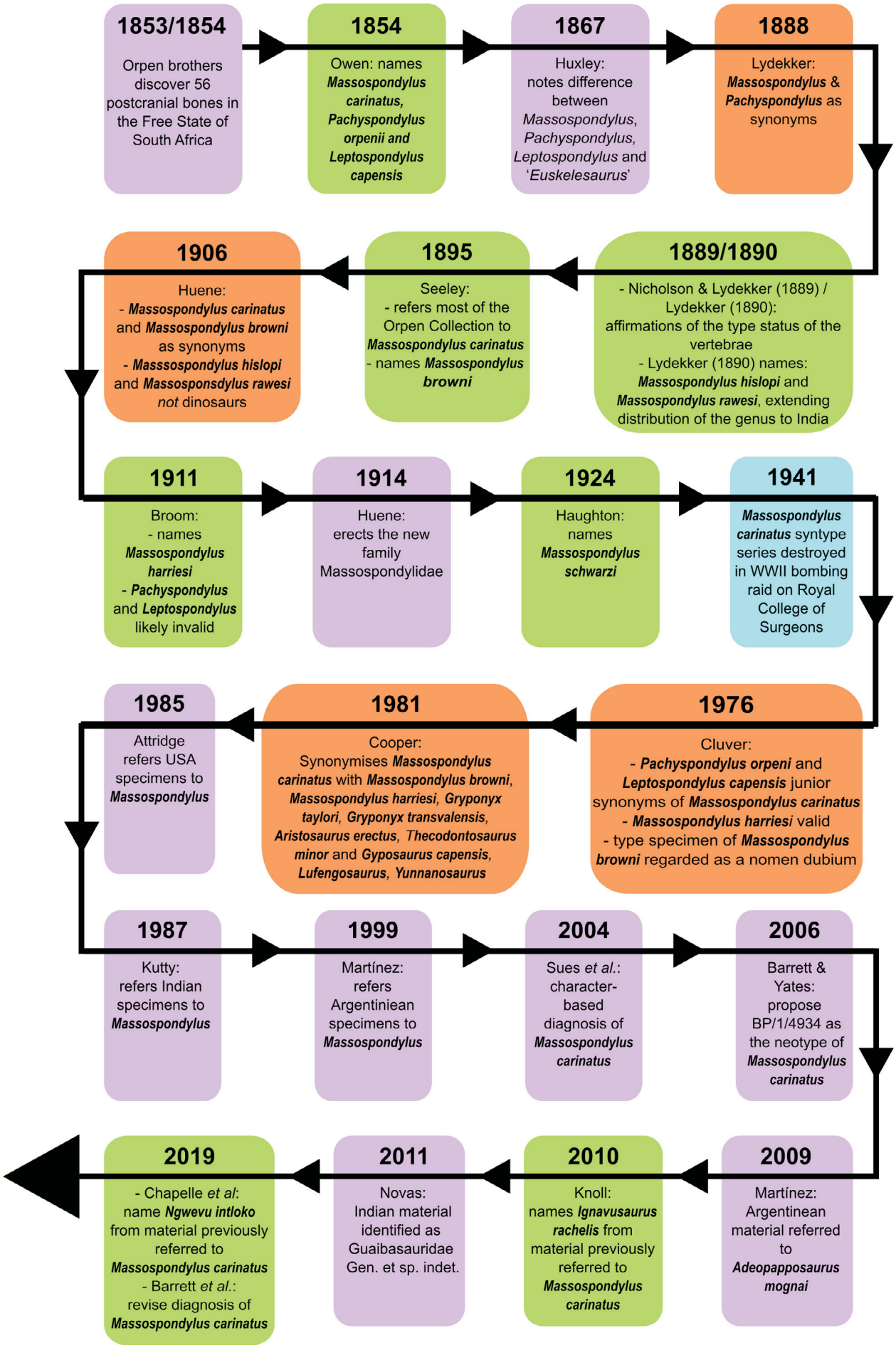


Figure 4. Chronological timeline summarising the taxonomic history of *Massospondylus* spp.

Table 2. Current identifications of the specimens within the Orpen Collection (see text for further details). As some of the specimens are not represented by casts, Huene's (1906) identifications of these specimens are retained for now (indicated with '*').

Catalogue	NHMUK No.	SAM No.	GPIT No.	Current identification	Current taxonomic identification
331	PV R3027	SAM-PKC-958	GPIT-PV-60058	Mid-cervical vertebra	Massopoda indet.
332	PV R3028 (*partim*)	SAM-PKC-959	GPIT-PV-60055	Mid-cervical neural arch (partial)	?Massospondylidae indet.
333	PV R3028 (*partim*)	SAM-PKC-960	GPIT-PV-60057	Mid-cervical vertebra (posterior part only)	Massopoda indet.
334	PV R3028 (*partim*)	SAM-PKC-961	GPIT-PV-60051	Partial cervical centrum	Massopoda indet.
335	PV R3028 (*partim*)	SAM-PKC-962	GPIT-PV-60056	Mid-cervical centrum	Massopoda indet.
336	PV R1312	SAM-PKC-963	GPIT-PV-60082	Dorsal centrum	Dinosauria indet.
337	NA	NA	NA	Dorsal centrum*	Unknown (insufficiently described)
338	PV R3035 (*partim*)	NA	GPIT-PV-60053	Proximal caudal vertebra (with partial arch)	Theropoda or Sauropodomorpha indet.
339	NA	NA	NA	Caudal vertebra*	Unknown (insufficiently described)
340	NA	NA	NA	Caudal vertebra*	Unknown (insufficiently described)
341	NA	NA	NA	Caudal vertebra*	Unknown (insufficiently described)
342	PV R3035 (*partim*)	NA	NA	Proximal caudal vertebra (with partial arch)	Dinosauria indet.
343	PV R3035 (*partim*)	NA	GPIT-PV-60054	Middle caudal vertebra (with partial arch)	Dinosauria indet.
344	NA	NA	NA	Caudal vertebra*	Unknown (insufficiently described)
345	PV R3035 (*partim*)	NA	GPIT-PV-60059	Middle caudal centrum	Dinosauria indet.
346	PV R3035 (*partim*)	NA	GPIT-PV-60063	Sacral centrum	Dinosauria indet.
347	PV R3025	NA	GPIT-PV-60088	Proximal caudal vertebra	Dinosauria indet.
348	NA	NA	NA	Dorsal centrum*	Unknown (insufficiently described)
349	PV R3029 (*partim*)	SAM-PKC-964	GPIT-PV-60072	Left scapula (proximal end)	Sauropodomorpha indet.
350	PV R3029 (*partim*)	SAM-PKC-965	GPIT-PV-60062	?Left scapula (distal end)	Sauropodomorpha indet.
351	PV R3036 (*partim*)	NA	GPIT-PV-60085	Right pubis (proximal)	Sauropodomorpha indet.
352	PV R3030	SAM-PKC-966	GPIT-PV-60037	?Right pubis (proximal end)	Sauropodomorpha indet.
353	PV R3036 (*partim*)	NA	GPIT-PV-60094	?Right ischium (shaft only)	?Sauropodomorpha indet.
354	PV R3031 (*partim*)	SAM-PKC-967	GPIT-PV-60071	Right humerus (proximal end)	Sauropodomorpha indet.
355	NA	NA	NA	?Humerus (following Owen 1842)	Unknown (insufficiently described)
356	PV R3031 (*partim*)	SAM-PKC-968	GPIT-PV-60060	Right humerus (distal end)	Sauropodomorpha indet.
357	NA	NA	NA	Left scapula (proximal end)*	Unknown (insufficiently described)
358	PV R3032 (*partim*)	SAM-PKC-969	GPIT-PV-60076	Left ilium	?Massospondylidae indet.
359	PV R3032 (*partim*)	SAM-PKC-970	GPIT-PV-60081	Left scapula (proximal end)	Sauropodomorpha indet.
360	PV R3033 (*partim*)	SAM-PKC-971	GPIT-PV-60078	Right femur (proximal end)	Sauropodomorpha indet.
361	PV R3033 (*partim*)	SAM-PKC-972	GPIT-PV-60042	Left femur (distal end)	Sauropodomorpha indet.
362	PV R3033 (*partim*)	SAM-PKC-973	GPIT-PV-60080	Right femur (missing proximal-most end)	Sauropodomorpha indet.
363	PV R3034 (*partim*)	SAM-PKC-974	GPIT-PV-60079	Right tibia (proximal end)	Indet. non-anchisaurian sauropodomorph
364	PV R3034 (*partim*)	NA	GPIT-PV-60061	Left tibia (distal end)	Indet. non-anchisaurian sauropodomorph
365	NA	SAM-PKC-975	NA	Tibia	Indet. non-anchisaurian sauropodomorph
366	PV R3037 (*partim*)	NA	GPIT-PV-60089	?Left metacarpal V	Sauropodomorpha indet.
367	PV R3037 (*partim*)	NA	GPIT-PV-60077	Left metatarsal II (proximal end)	Sauropodomorpha indet.
368	PV R3037 (*partim*)	NA	GPIT-PV-60086	Right metatarsal III (distal end)	Dinosauria indet.
369	PV R3037 (*partim*)	NA	GPIT-PV-60093	Right metatarsal II (proximal end)	Sauropodomorpha indet.
370	NA	NA	NA	Metatarsal II (proximal end)*	Sauropodomorpha indet.
371	NA	NA	NA	Metacarpal I IV (distal end)*	Dinosauria indet.
372	NA	NA	NA	Metacarpal I IV (distal end)*	Unknown (insufficiently described)
373	PV R3037 (*partim*)	NA	GPIT-PV-60099	Metatarsal (distal end)	Dinosauria indet.
374	PV R3037 (*partim*)	NA	GPIT-PV-60087	Right manual metacarpal 1	Massopoda indet.
375	PV R3037 (*partim*)	NA	GPIT-PV-60052	Right pedal phalanx	Dinosauria indet.
376	NA	NA	NA	Phalanx (following Owen 1842)	Unknown (insufficiently described)
377	NA	NA	NA	Left manual phalanx*	Unknown (insufficiently described)
378	PV R3037 (*partim*)	NA	NA	Left pedal phalanx	Dinosauria indet.
379	PV R3037 (*partim*)	NA	GPIT-PV-60113	?Left pedal phalanx	Dinosauria indet.
380	PV R1312a	SAM-PKC-976	NA	Phalanx	Dinosauria indet.
381	NA	NA	NA	Manual phalanx*	Sauropodomorpha indet.
382	PV R3037 (*partim*)	NA	GPIT-PV-60090	Ungual phalanx	Sauropodomorpha indet.
383	PV R3037 (*partim*)	NA	GPIT-PV-60096	Ungual phalanx	Sauropodomorpha indet.
384	NA	NA	NA	Right pedal ungual, digit 1*	Unknown (insufficiently described)
385	PV R3026	NA	GPIT-PV-60097	Ungual phalanx	Sauropodomorpha indet.
386	NA	NA	NA	Ischia*	Dinosauria indet.

Table 3. Vertebral measurements in millimetres. Asterisks (*) indicate incomplete bones; dashes ('–') indicate inapplicable or substantially incomplete measurements.

Cervical vertebrae					
NHMUK catalogue number:	PV R3027	PV R3028 (*partim*)	PV R3028 (*partim*)	PV R3028 (*partim*)	PV R3028 (*partim*)
Owen (1854) catalogue number:	331	332	333	334	335
Centrum, length	102	–	–	–	88
Centrum, anterior height	42	–	–	–	46
Centrum, anterior width	44	–	–	–	44
Centrum, posterior height	46	–	39	?54	42
Centrum, posterior width	46	–	37	?44	38
Neural arch, total height (including spine)	58	–	–	–	–
Neural spine, anteroposterior length	47	124*	–	–	–
Dorsal vertebra					
NHMUK catalogue number:	PV R1312				
Owen (1854) catalogue number:	336				
Centrum, length	70				
Centrum, anterior height	50				
Centrum, anterior width	41				
Centrum, posterior height	53				
Centrum, posterior width	44				
Sacral vertebra					
NHMUK catalogue number:	PV R3035 (*partim*)				
Owen (1854) catalogue number:	346				
Centrum, length	50*				
Centrum, posterior height	29				
Centrum, posterior width	44				
Caudal vertebrae					
NHMUK catalogue number:	PV R3035 (*partim*)	PV R3035 (*partim*)	PV R3035 (*partim*)	PV R3035 (*partim*)	PV R3025
Owen (1854) catalogue number:	338	342	343	345	347
Centrum, length	68	43	50*	56	48
Centrum, anterior height	59	50	–	54	59
Centrum, anterior width	49*	38	–	42	52
Centrum, posterior height (including chevron facet)	63	50	30	53	57
Centrum, posterior width	61	38	31	38	53

articular surfaces that face ventrolaterally, forming an angle of approximately 45° with the horizontal (Fig. 5B, D). A low, ridge-like epipophysis is present on the dorsal surface of the postzygapophysis and extends for approximately half to two-thirds of its length but does not reach the tip of the process (Fig. 5D). The base of the postzygapophysis has a flattened cross-section. Very short spinopostzygapophyseal laminae (SPOL) are present. A dorsoventrally elongate, slit-like postspinal fossa is situated at the junction of the postzygapophyses (Fig. 5C).

The neural spine has a sub-rectangular outline in lateral view, with a straight, dorsally inclined anterior margin, a gently convex and horizontally extending dorsal margin and a short, posteroventrally sloping posterior margin (Fig. 5B, D). It is laterally compressed and lacks a spine table.

Seeley (1895) did not describe or figure Nos. 332–335 as he regarded them as uninformative and potentially referrable to a different species. No. 332 (NHMUK PV R3028 *partim*; SAM-PKC-959; Fig. 5H) consists of a broken neural arch lacking the tips of the prezygapophyses, the transverse processes and the summit of the neural spine. It is dorsoventrally lower than the neural arch of No. 331 and more elongate, but its poor preservation prevents description of many features. It differs from No. 331 in lacking epipophyses, having a proportionately longer neural spine and in possessing a more rounded, prominent EPRL. No. 333 (NHMUK PV R3028 *partim*; SAM-PKC-960; Fig. 5G) consists of the posterior part of a vertebra, including a partial neural arch. The preserved part of the neural arch is essentially identical to that of No. 332, with the exception that a ridge-like epipophysis is present. Its centrum is low and elongate, with a rounded, horizontally inclined PCDL extending anteriorly from its posterodorsolateral corner. In ventral view, the centrum is strongly constricted transversely and its ventral surface is smoothly rounded transversely, lacking a ventral midline keel. In posterior view, the articular surface is slightly taller than wide and is deeply concave. No. 334 (NHMUK PV R3028 *partim*; SAM-PKC-961; Fig. 5I–K) is a fragment of a spool-like centrum, consisting of the ?posterior part only. Its preserved articular surface is shield-shaped in outline and shallowly concave (Fig. 5I). A prominent midline keel is present on its ventral surface (Fig. 5K;

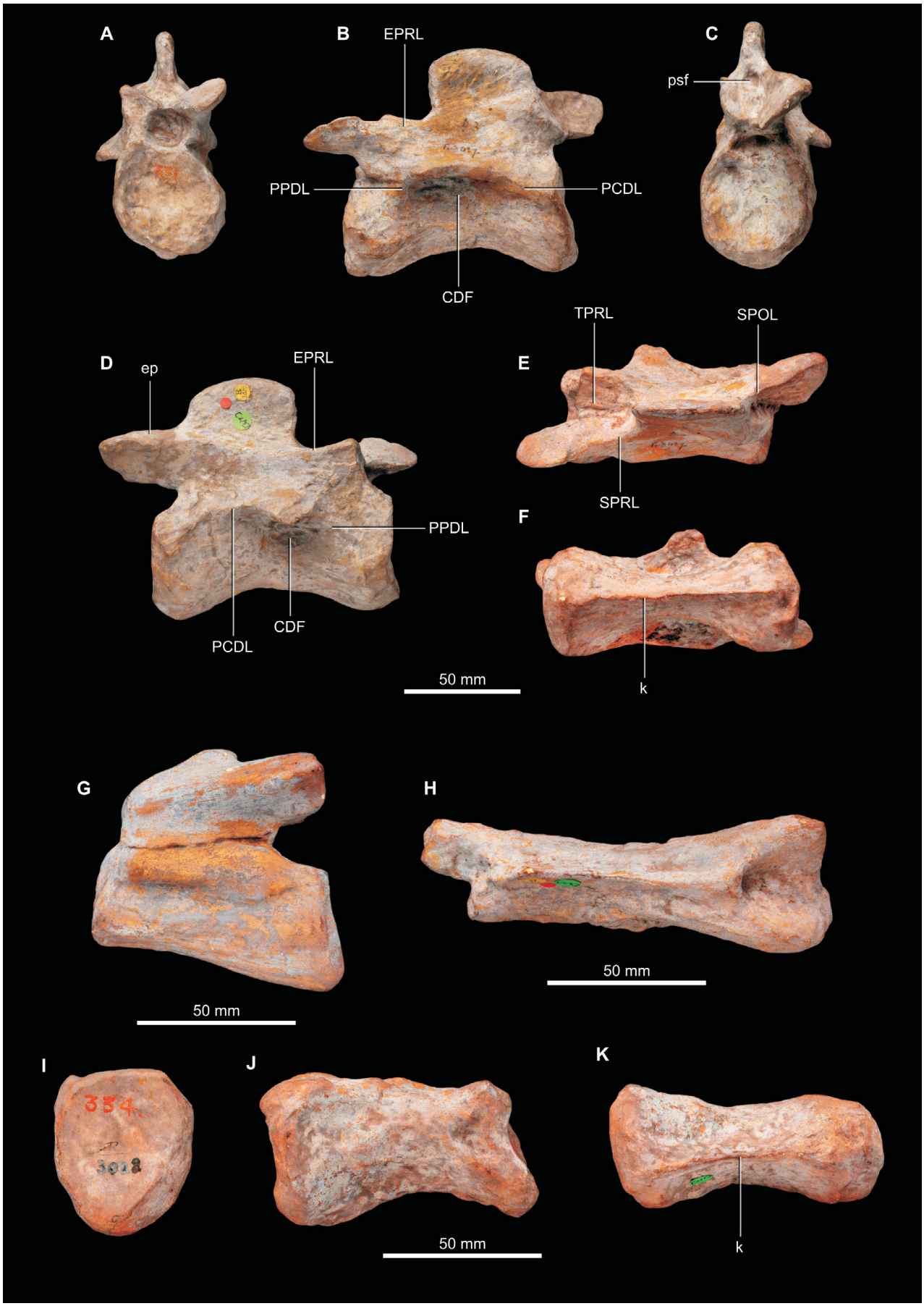


Figure 5. Casts of cervical vertebrae from the Orpen Collection. These represent the original syntype series of *Massospondylus carinatus*. **A–F**, NHMUK PV R3027, catalogue number 331, mid-cervical vertebra in anterior (**A**), left lateral (**B**), posterior (**C**), right lateral (**D**), dorsal (**E**) and ventral (**F**) views. **G**, NHMUK PV R3028, catalogue number 333, mid-cervical vertebra in left lateral view. **H**, NHMUK PV R3028, catalogue number 332, partial mid-cervical neural arch in dorsal view. **I–K**, NHMUK PV R3028, catalogue number 334, mid-cervical centrum in anterior (**I**), right lateral (**J**) and ventral (**K**) views.

incorrectly identified as a dorsal vertebra by Huene [1906]). Finally, No. 335 (NHMUK PV R3028 *partim*; SAM-PKC-962; not figured) consists of a small, badly preserved centrum. Both the anterior and posterior articular surfaces are slightly taller than they are wide, are shallowly concave and have shield-shaped outlines. The lateral surfaces of the centra are longitudinally concave and dorsoventrally convex and merge ventrally, meeting to form a sharp midline keel that extends for the full length of the vertebra. Mound-like swellings on the lateral surfaces that are situated a short distance posterior to the anterior margin might represent parapophyses. The centrum has a length/anterior height ratio of 1.91.

None of the cervical vertebrae display any of the features currently regarded as autapomorphic for *M. carinatus*, namely centrum length/height ratios >7.0 (for anterior cervical vertebrae) and neural spines of anterior cervical vertebrae bearing hook-like expansions anteriorly (Barrett *et al*. 2019) (although the latter feature might be ontogenetically variable: K.E.J.C., pers. obs.). Nevertheless, the neural arch of No. 332 does bear a strong resemblance to those of *M. carinatus* (Barrett *et al*. 2019) and *Ngwevu intloko* (Chapelle *et al*. 2020), suggesting that it might pertain to an indeterminate massospondylid. However, none of the other cervicals bear features synapomorphic of Massospondylidae, such as possessing centrum length/height ratios >3.0 (e.g. Yates 2007; Apaldetti *et al*. 2013). No. 331 bears several features diagnostic of Sauropodomorpha and several slightly more exclusive clades therein (following Yates, 2007; Apaldetti *et al*., 2013), some of which are also present in Nos. 333–335, notably: epipophyses forming tall ridges (Sauropodomorpha); anterior cervical vertebrae with centrum length/height ratios >2.5 (*Efraasia*+more derived sauropodomorphs); ventral midline keel present on anterior cervicals (*Sarahsaurus*+more derived sauropodomorphs); and a concave anterior articular facet on centrum (excluding it from Sauropoda). This combination of features suggests that Nos. 331 and 333–335 represent indeterminate massopodan sauropodomorphs, but further identification is not possible with the available material.

Dorsal vertebra

A single dorsal vertebral centrum is preserved among the casts (No. 336; NHMUK PV R1312; SAM-PKC-963; Fig. 6A), which was retained in *Massospondylus carinatus* by Seeley (1895, p. 106) and was figured by Lydekker (1888, fig. 3; 1890a, fig. 58). Lydekker (1890a) deemed this specimen the type as he suggested that Owen's original description was inadequate; however, Owen (1854) clearly established the name on the basis a syntype series without designating a holotype (see above). Huene (1906, pl. XIII [XX], fig. 9) figured this element and noted four other dorsal vertebrae in the collections of the Hunterian Museum (Nos. 337, 348 [a syntype of *Leptospondylus capensis*], and two unnumbered specimens; *ibid*. fig. 46), but casts of these do not survive (see Table 1). Huene's (1906) descriptions and figures are not sufficient to comment further on the identification of these four specimens. Measurements of the dorsal vertebrae are provided in Table 3.

In lateral view, the centrum has lateral surfaces that are anteroposteriorly concave and dorsoventrally convex (Fig. 6A). It has a concave ventral margin, and no foramina or fossae are present. The lateral surfaces are separated from the ventral surface by distinct breaks of slope, but these do not form strong bounding ridges. The ventral surface is strongly concave anteroposteriorly but almost flat mediolaterally. It is smooth and bears neither a ventral keel nor a ventral groove. The anterior and posterior articular surfaces are both flat to very shallowly concave. Each is dorsoventrally taller than mediolaterally wide and has a sub-elliptical outline with its long axis trending dorsoventrally. The basal part of the neural arch is also preserved and its anterior part flares slightly laterally (in the region of the parapophyses) but few other details are preserved. The transverse cross-section through the base of the neural arch produces a neural canal with an elongate, hourglass-shaped outline in dorsal view. The neural canal excavates the dorsal surface of the centrum slightly.

The centrum anterior height/length ratio of 1.4 is within the range seen in *M. carinatus* but excludes it from *Ignavusaurus* (Barrett *et al*. 2019). The vertebra possesses no useful diagnostic features, although its size does suggest that it is from a dinosaur, so No. 336 is regarded as Dinosauria indet. herein.

Sacral vertebra

No. 346 (NHMUK PV R3035 *partim*: Fig. 6B, C) is a sacral centrum missing its ?anterior articular surface. Although it is one of the syntypes of *Pachyspondylus orpenii* (see Owen 1854), it was referred to *Massospondylus carinatus* by Seeley (1895, p. 106, fig. 2) and Huene (1906, p. 133, pl. XIV [XXI], fig. 1). Measurements of the sacral vertebrae are provided in Table 3.

In lateral view, the ventral margin of the centrum is only slightly concave so that it has a sub-rectangular outline (Fig. 6C). The lateral surfaces are dominated by large sub-triangular processes, situated centrally, which represent the broken bases of the sacral ribs; the rest of the lateral surface is shallowly concave longitudinally. The lateral and ventral surfaces are separated by a gentle break-of-slope, rather than distinct ridges and the ventral surface is mediolaterally constricted with respect to the articular ends. There is neither a groove nor a keel on the ventral surface, which is gently convex mediolaterally and shallowly concave anteroposteriorly. The posterior articular surface has a kidney-shaped outline, with a dorsal margin that is gently invaginated and with straight to slightly convex lateral and ventral margins (Fig. 6B). The articular surface is shallowly concave and does not appear to be broken, so it either represents the posteriormost sacral or a sacral from an individual in which sacral fusion was incomplete.

The specimen possesses no diagnostic features and is referred to Dinosauria indet., though based solely on its size and its general resemblance to other dinosaur sacral vertebrae.

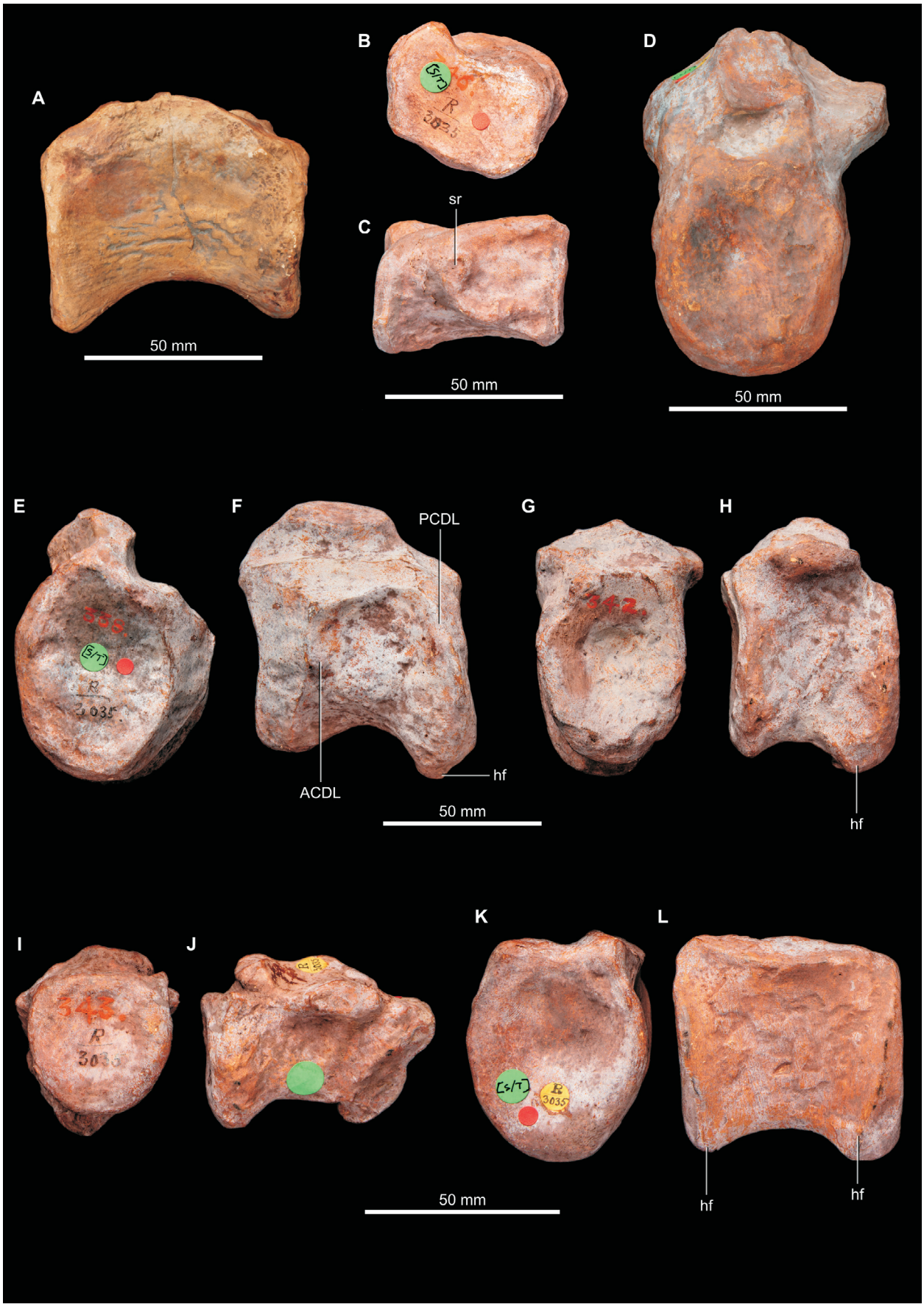


Figure 6. Casts of dorsal, sacral and caudal vertebrae from the Orpen Collection. **A**, NHMUK PV R1312, catalogue number 336, dorsal vertebra centrum in left lateral view. **B**–**C**, NHMUK PV R3035 (*partim*), catalogue number 346, sacral vertebra in posterior (**B**) and left lateral (**C**) views. **D**, NHMUK PV R3025, catalogue number 347, proximal caudal vertebra in anterior view. **E**–**F**, NHMUK PV R3035 (*partim*), catalogue number 338, proximal caudal vertebra in anterior (**E**) and left lateral (**F**) views. **G**–**H**, NHMUK PV R3035 (*partim*), catalogue number 342, proximal caudal vertebra in anterior (**G**) and left lateral (**H**) views. **I**–**J**, NHMUK PV R3035 (*partim*), catalogue number 343, middle caudal vertebra in anterior (**I**) and left lateral (**J**) views. **K**–**L**, NHMUK PV R3035 (*partim*), catalogue number 345, middle caudal vertebra in anterior (**K**) and left lateral (**L**) views.

Caudal vertebrae

Seeley (1895, p. 107) transferred the caudal vertebrae that formed the syntype series of both *Pachyspondylus orpenii* and *Leptospondylus capensis* (see Owen 1854) to *Massospondylus carinatus* but regarded them as representing the remains of more than one individual. Many of the caudal vertebrae listed by Owen (1854) do not appear to have been cast (Nos. 339–341, 344, 348) and as they were not figured are known only from Owen's and Huene's (1906) brief descriptions. Owen (1854) identified No. 345 as a dorsal centrum, but its large haemal arch facets identify it as a caudal, whereas Huene (1906) regarded No. 348 as a dorsal (see above). Of the five available casts, three are proximal caudals (Nos. 338, 342, 347) while the other two are from the middle or distal part of the tail (Nos. 343, 345). Seeley (1895, fig. 3) figured only one caudal (No. 338); Huene (1906) figured Nos. 338, 343, 345, 347 (*ibid*., pl. XIV [XXI], figs 2–5) as well as four unnumbered vertebrae that are otherwise unknown and are presumably lost (*ibid*., fig. 47). Measurements of the caudal vertebrae are provided in Table 3.

The proportions of the proximal caudals vary slightly, reflecting their different sizes (as noted by Seeley [1895]) and/or slightly different positions within the tail, although they are otherwise similar (Fig. 6D–L). No. 347 (NHMUK PV R3025; Fig. 6D) is the most complete, consisting of a centrum and partial neural arch; No. 338 (NHMUK PV R3035 *partim*; Fig. 6E, F) includes only a small section of the neural arch base; and No. 342 (NHMUK PV R3035 *partim*; Fig. 6G, H) is similarly preserved to the latter. No. 347 lacks large haemal arch facets and might represent caudal 1 or 2, though the positions in the caudal series of all the other preserved vertebrae are unknown.

Nos. 342 and 347 have centra that are approximately square-shaped in lateral view (Fig. 6H), whereas that of No. 338 is more elongate and rectangular (Fig. 6F). All three proximal caudals have lateral surfaces that are anteroposteriorly concave and dorsoventrally convex and that generally lack foramina, ridges or other features. However, two short, stout vertebral laminae are present in No. 338: a sub-vertical anterior centrodiapophyseal lamina (ACDL) and obliquely-inclined PDCL. The lateral surfaces blend into the ventral surfaces around gentle breaks-in-slope, without forming distinct ridges. In ventral view, the centra have a slightly constricted hourglass-shaped outline and the ventral surface is longitudinally concave and mediolaterally convex. Nos. 342 and 347 lack any ventral keel or groove; No. 338 possesses a short midline buttress that is confluent with the anterior articular surface, but that only extends posteriorly for a short distance before merging into the ventral surface. The articular surfaces of all three vertebrae are shallowly concave and have sub-elliptical outlines with their long axes oriented vertically (Fig. 6D, E, G). None of the vertebrae bear prominent anterior haemal arch facets, but Nos. 338 and 342 exhibit well-developed posterior facets, so the posterior margin of the centrum is extended much farther ventrally than its anterior margin in lateral view (Fig. 6F, H). In posterior view, the haemal arch facets have a crescentic outline.

Neural canal openings are visible in No. 347 and are sub-circular anteriorly and elliptical posteriorly (with the long axis of this ellipse oriented transversely; Fig. 6D). The bases of the transverse processes are preserved in Nos. 342 and 347: these are dorsoventrally compressed, sheet-like and situated centrally on the neural arch. They appear to have extended horizontally, rather than dorsolaterally, although that of No. 347 seems to have been rotated so that its dorsal surface faced anterodorsally. All other neural arch processes are broken and offer no information.

No. 343 (NHMUK PV R3035 *partim*; Fig. 6I, J) is a partially complete middle to distal caudal lacking its anterior end and most of the neural arch; No. 345 (NHMUK PV R3035 *partim*; Fig. 6K, L) is a middle caudal centrum. In most respects the centra are similar to those of the proximal caudals, differing only in their proportions, as the middle caudals are more elongate and are longer than they are tall. The lateral surfaces of the centra are saddle-shaped and blend gradually into the ventral surfaces (Fig. 6J, L). In ventral view, the centra are constricted and there is some indication of a shallow ventral midline groove in No. 345. The articular surfaces are shallowly concave (Fig. 6I, K): those of No. 345 are taller than wide and have a sub-elliptical outline, whereas the posterior articular surface of No. 343 is sub-circular (the anterior facet is not preserved). No. 345 possesses a small anterior haemal arch facet and much larger posterior facet, both of which have a crescentic outline. Haemal arch facets are absent in No. 343 suggesting that it is from a more distal part of the tail. However, although broken, transverse processes were still present in No. 343: these were dorsoventrally flattened and extended laterally.

With one exception (No. 338), none of the caudal vertebrae possess features that are synapomorphic for any clade although their overall morphology and size is consistent with identification as a dinosaur, and they are regarded as Dinosauria indet. herein. The presence of prominent vertebral laminae in No. 338 is consistent with identification as either a theropod or sauropodomorph dinosaur (Wilson 1999; Galton & Upchurch 2004).

Pectoral girdle and forelimb

Scapula

At least three of Owen's (1854, pp. 101–102) specimens represent portions of scapulae (Nos. 349, 350 and 359) although one was incorrectly identified as a left ischium (*ibid*., p. 102). Seeley (1895, pp. 103 and 109–110, fig. 5) incorrectly identified all three specimens as ischial fragments, but this was corrected by Huene (1906). Owen (1854, p. 101) correctly noted that that No. 349 is the proximal part of a left scapula and he, Seeley (1985, p. 103) and Huene (1906, p. 135, pl. XIV [XXI], figs 8, 9) opined that Nos. 349 and 350 represented different parts of the same individual element; however, although this is plausible on the basis of size, the mixed nature of the assemblage prevents confirmation of this suggestion. No. 359 was figured by Huene (1906, fig. 49). A further specimen, No. 357, which was originally listed as a ?humerus

of *Pachyspondylus* (Owen 1854), was identified as a left scapula by Huene (1906, p. 135) but was not figured and no cast is available. The chimeric nature of the assemblage is exemplified by the presence of several proximal scapulae (Nos. 349, 357, 359), which not only differ in size (see Table 4 for measurements) but are all left scapulae, thus representing a minimum of three individuals.

The scapulae are described with their long axes oriented horizontally. In lateral view, the proximal end of the scapula forms a dorsoventrally expanded plate with a sub-pentagonal outline (No. 349 [NHMUK PV R3029 *partim*; SAM-PKC-964; Fig. 7A]; No. 359 [NHMUK PV R3032 *partim*; SAM-PKC-970; Fig. 7B]). Both scapulae are lacking the anterodorsal corner of the proximal plate, which could account of their earlier identification as ischia. The lateral surface of the proximal plate is smoothly concave both anteroposteriorly and dorsoventrally and the posterior margin of this concavity is formed by a distinct, rounded rim that is confluent with the acromial ridge dorsally and that expands to buttress the glenoid ventrally. This rim also separates the lateral surfaces of the proximal plate and scapula shaft. The concavity is deeper in the dorsal part of the proximal plate than ventrally. As preserved, the proximal plate expands further ventrally than dorsally with respect to the margins of the scapula shaft but given the damage to the anterodorsal region it is possible that the dorsal part of the plate was originally more extensive. The base of the acromion process forms an obtuse angle of approximately 120° with the dorsal margin of the shaft. The anterior margin of the proximal plate forms the articular surface for the coracoid and is straight and vertically inclined. It is separated from the ventral margin of the proximal plate, which is very slightly concave and represents the glenoid, by an angle of approximately 120° (No. 349; Fig. 7A) or 150° (No. 359; Fig. 7B).

Table 4. Pectoral girdle, forelimb and manus measurements in millimetres. Asterisks (*) indicate incomplete bones; dashes ('–') indicate inapplicable or substantially incomplete measurements.

Scapula			
NHMUK catalogue number:	PV R3029 (*partim*)	PV R3029 (*partim*)	PV R3032 (*partim*)
Owen (1854) catalogue number:	349	350	359
Proximal plate, maximum dorsoventral height	105*	–	88*
Proximal plate, maximum anteroposterior length	74	–	58
Proximal plate, maximum mediolateral width (at dorsal margin of glenoid fossa)	39	–	29
Shaft, dorsoventral height	53	–	34
Distal expansion, maximum dorsoventral height	–	71*	–
Humerus			
NHMUK catalogue number:	PV R3031 (*partim*)	PV R3031 (*partim*)	
Owen (1854) catalogue number:	354	356	
Length (as preserved)	140*	78*	
Proximal expansion, maximum mediolateral width	100	–	
Distal expansion, maximum mediolateral width	–	89	
Radial (lateral) condyle, maximum anteroposterior	–	35	
Metacarpal I			
NHMUK catalogue number:	PV R3037 (*partim*)		
Owen (1854) catalogue number:	374		
Length, dorsal margin	36		
Length, ventral margin	53		
Proximal end, dorsoventral height	45		
Proximal end, maximum mediolateral width (ventral margin)	33		
Distal end, dorsoventral height	36		
Distal end, maximum mediolateral width	18		
Metacarpal V			
NHMUK catalogue number:	PV R3037 (partim)		
Owen (1854) catalogue number:	366		
Length	34		
Proximal end, maximum dorsoventral height	25		
Proximal end, maximum mediolateral width	25		
Distal end, maximum dorsoventral height	20		
Distal end, maximum mediolateral width	21		
Manual unguals			
NHMUK catalogue number:	PV R3037 (partim)	PV R3037 (partim)	PV R3026
Owen (1854) catalogue number:	382	383	385
Length	47*	55*	32*
Proximal articular surface, height	36	40	20



Figure 7. Casts of pectoral girdle, forelimb and manus bones from the Orpen Collection. **A**, NHMUK PV R3029 (*partim*), catalogue number 349, left proximal scapula in lateral view. **B**, NHMUK PV R3032 (*partim*), catalogue number 359, left proximal scapula in lateral view. **C**, NHMUK PV R3029 (*partim*), catalogue number 350, left distal scapula in lateral view. **D**–**F**, NHMUK PV R3031 (*partim*), catalogue number 354, right proximal humerus in anterior (**D**), posterior (**E**) and proximal (**F**) views. **G**–**I**, NHMUK PV R3031 (*partim*), catalogue number 356, right distal humerus in anterior (**G**), posterior (**H**) and distal (**I**) views. **J**–**L**, NHMUK PV R3037 (*partim*), catalogue number 374, right metacarpal V in dorsal (**J**), left lateral (**K**) and distal (**L**) views. **M**, NHMUK PV R3037 (*partim*), catalogue number 366, ?left metacarpal V in dorsal view. **N**, NHMUK PV R3026, catalogue number 385, ungual phalanx in lateral view. **O**, NHMUK PV R3037 (*partim*), catalogue number 382/383, ungual phalanx in lateral view. **P**, NHMUK PV R3037 (*partim*), catalogue number 382/383, manual ungual phalanx in lateral view.

In medial view, the proximal plate is shallowly concave dorsoventrally in its dorsal part but becomes flat to slightly convex ventrally. There is some indication of a short, horizontally directed groove that would have been confluent with the articular surface for the coracoid, situated immediately dorsal to the expanded glenoid region. The surface of the proximal plate merges smoothly with the shaft surface. In anterior view, the proximal plate is strongly expanded mediolaterally in its ventral part to form the articular surface for the coracoid and the glenoid fossa. The glenoid surface has a sub-triangular outline, with the apex of this triangle extending ventrolaterally and the surface is gently concave. it is separated from the articular surface for the coracoid by a marked ridge of bone and distinct break-in-slope. The coracoid articulation has a rounded, sub-elliptical outline with its long axis trending dorsoventrally, but is broken dorsally. The preserved surface is shallowly concave. Dorsally, the proximal plate thins considerably in mediolateral thickness and its medial margin describes a shallow sinusoidal curve.

In both Nos. 349 and 359 the base of the scapular shaft is dorsoventrally narrow and its dorsal and ventral margins converge to extend parallel to each other over their preserved lengths (Fig. 7A, B). The lateral surface of the shaft is strongly convex dorsoventrally, whereas the medial surface is either weakly convex (No. 349) or flat (No. 359), imparting either a narrow elliptical or 'D'-shaped transverse cross-section, respectively.

No. 350 (NHMUK PV R3029 *partim*; SAM-PKC-964; Fig. 7C) is a badly preserved fragment of a scapula blade missing parts of its dorsal and ventral margins. Its medial and lateral surfaces are both gently convex so that anteriorly it has a tall, narrow elliptical cross-section. This distal part of the blade was clearly expanded with respect to the anterior part of the scapular shaft, but its incompleteness prevents determination of whether this expansion was symmetrical or not, or the relative degree of expansion with respect to either the anterior shaft or proximal plate.

Nos. 349, 350 and 359 are superficially similar to the neotype of *M. carinatus* (Barrett *et al*. 2019) but similar scapulae are also present in a variety of other sauropodomorphs (e.g. *Adeopapposaurus*, *Lufengosaurus*: Young 1941; Martínez 2009). Moreover, although *M. carinatus* has been diagnosed on the basis of having an asymmetrically expanded distal scapula blade (with a large ventral and smaller dorsal expansion; see Barrett *et al*. 2019) the presence/absence of this feature cannot be assessed in No. 350. The overall appearance and size of the specimens suggests that they pertain to a sauropodomorph (Galton & Upchurch 2004), but their generalized morphology and poor preservation excludes a definitive referral to any other known upper Stormberg Group taxon (none of which possess diagnostic features of their scapulae: Knoll 2010; Chapelle *et al*. 2019) or to any particular sauropodomorph clade (Yates 2007; Apaldetti *et al*. 2013). They are regarded as Sauropodomorpha indet. herein.

Humerus

The collection includes proximal (No. 354; SAM-PKC-967; Fig. 7D–F) and distal (No. 356; SAM-PKC-968; Fig. 7G–I) parts of right humeri (registered together as NHMUK PV R3031). Owen (1854, pp. 101–102) suggested that these were parts of the same bone, a conclusion followed by Seeley (1895, p. 116, fig. 12) and Huene (1906, pl. XIV [XXI], figs 6, 7). However, although this is plausible, as the two fragments match well in terms of size, this cannot be confirmed. A third specimen (No. 357) thought to be a humerus by Owen (1854, p. 101) was re-identified as an ischium by Seeley (1895, pp. 103 and 109) and as a scapula by Huene (1906; see above). Measurements are provided in Table 4.

In anterior or posterior view, the proximal expansion of the humerus (No. 354) consists of a large internal tuberosity, the humeral head and the deltopectoral crest (Fig. 7D, E). The internal tuberosity has a sub-triangular outline, with a bluntly rounded apex that extends medially. It is positioned ventral to the humeral head and the dorsal surface of the internal tuberosity merges with the latter along a smooth curve. The humeral head forms the proximal-most point of the humerus but is rather poorly developed and its articular surface does not extend onto the anterior surface of the humerus. Instead, it forms a low lip that overhangs it. Lateral to the humeral head, the proximal margin of the humerus descends ventrally to merge with the deltopectoral crest. A shallow, 'U'-shaped notch separates the dorsal margin of the crest from the remainder of the proximal margin. This notch lies at a level just ventral to the ventral margin of the internal tuberosity. The deltopectoral crest is incomplete, but the preserved portion is prominent, has a narrow, sub-rectangular outline and extends from the humerus anteriorly and slightly laterally. Its lateral margin is straight. The anterior surface of the proximal humerus is dorsoventrally flat but mediolaterally concave due to the curvature of the deltopectoral crest.

The proximal humerus is strongly convex mediolaterally and slightly concave dorsoventrally in posterior view. The posterior surface of the internal tuberosity bears a low pyramidal swelling. A shallow sulcus separates this swelling from the articular surface of the humeral head, which forms a larger sub-elliptical boss that slightly overhangs the rest of the posterior surface. The long axis of this boss extends mediolaterally. No other features, such as intramuscular lines, can be discerned clearly though it is unclear whether this is due to surface damage of the original bone or the introduction of casting artefacts.

In proximal view, the humerus has a slightly sinuous outline (Fig. 7F). The internal tuberosity and humeral head are the most strongly expanded parts of the bone anteroposteriorly (with the humeral head showing the greater expansion) and the proximal margin tapers as it extends laterally from the region of the head, giving rise to the thin, sheet-like deltopectoral crest. None of the humeral shaft is preserved and the broken base of the proximal end has a narrow sub-triangular cross-section that tapers strongly laterally.

A shallow sulcus covers most of the anterior surface of the distal humerus (No. 356; Fig. 7G), covering the area dorsal to and between the ulnar and radial condyles. The radial and ulnar condyles are similar in size and form

rounded sub-ovate bosses that project anteriorly. In anterior view, the dorsal margin of the radial condyle is confluent with a robust, low, rounded crest that extends for a short distance before merging into the surface of the bone. A prominent, triangular entepicondyle is present on the medial margin of the distal end, dorsal to the ulnar condyle, producing a strongly bevelled and medioventrally facing surface between it and the distal humeral surface. The posterior surface of the distal end is flat and featureless (Fig. 7H). In distal end view, the humerus has a dumbbell-shaped outline and the two condyles project both anteriorly and posteriorly for approximately the same distance (Fig. 7I). The broken base of the shaft has a stout, elliptical cross-section, with a long axis that trends mediolaterally.

Both these specimens differ from the humeri preserved in the neotype of *M. carinatus*. In BP/1/4934 the humeral head is prominent and extends for a considerable distance dorsal to the internal tuberosity (Barrett *et al*. 2019) but in No. 354 the apex of the humeral head is substantially lower. Moreover, *M. carinatus* possesses a well-defined olecranon fossa (Barrett et al. 2019), as does *Adeopapposaurus* (Martínez 2009), but this feature is absent in No. 356. An olecranon fossa is also absent in *Arcusaurus*, *Ignavusaurus* and *Ngwevu* (Knoll 2010; Yates *et al*. 2011; Chapelle *et al*. 2019). Other differences in both humeral shape or intramembral ratios (such as the relative length of the deltopectoral crest, which is diagnostic for *M. carinatus*: Barrett *et al*. 2019) cannot be assessed due to incompleteness or uncertainly over the association between Nos. 354 and 356. Given their similarity to other sauropodomorphs (e.g. Galton & Upchurch 2004) these specimens are here regarded are Sauropodomorpha indet.

Metacarpal I

No. 374 (NHMUK PV R3037 *partim*; Fig. 7J–L) was listed by Owen (1854, p. 104) as a fifth metatarsal and by Seeley (1895, pp. 114–115) as a first metatarsal; Huene (1906, p. 135, fig. 61, pl. XVI [XXIII], fig. 3) was the first to identify it correctly as a right metacarpal I. Here, it is described in life position (assuming that the hand was held in a supinated position, with the long axes of the central digits extending anteroposteriorly). Measurements are provided in Table 4.

Metacarpal (Mc) I has a sub-trapezoidal outline in lateral view and both its proximal and distal ends are expanded dorsoventrally with respect to the short, stout shaft that connects them. The proximal expansion is the larger of the two and is developed asymmetrically, so that it expands further dorsally than ventrally. The posterior and anterior margins (articular surface margins) are very gently concave in lateral view, the ventral margin (ventral margin of the shaft) is slightly arched and the dorsal margin of the shaft is deeply notched. The ventral margin of Mc I is considerably longer than the dorsal margin contributing further to the asymmetry of the element. The lateral surface of Mc I between the two articular expansions is almost flat dorsoventrally, but gently concave anteroposteriorly. By contrast, the medial surface of the shaft is slightly convex dorsoventrally and deeply concave anteroposteriorly, due to the torsion of the distal end with respect to the rest of the bone (see below).

The articular surface of the proximal expansion has an elongate, triangular outline in posterior view, whose rounded apex points dorsally and whose lateral, medial and ventral margins are all straight to very slightly concave. A dorsoventrally extending ridge traverses the articular surface and is slightly offset towards the lateral margin of the bone, dividing this surface into two shallowly concave facets of different sizes (a large triangular facet medially, and smaller, strip-like facet laterally). The long axis of the proximal end extends dorsoventrally.

In anterior view, the distal expansion is divided into dorsal and ventrally positioned ginglymi, which give it a dumbbell-shaped outline with strongly concave medial and lateral margins and weakly convex dorsal and ventral margins. The articular surface is saddle-shaped (dorsoventrally concave and strongly convex mediolaterally). In anterior view, the long axis of the distal end is oriented ventrolaterally–dorsomedially, so that Mc I exhibits subtle torsion between its distal and proximal ends with the two long axes offset by approximately 30°. The dorsal and ventral margins of the distal expansion each bear incipient collateral ligament pits.

When viewed dorsally, the proximal and distal expansions are approximately equal in mediolateral width and are connected to each other by a narrow ridge. By contrast, in ventral view the proximal articulation is much more greatly expanded than the distal one, with most of this expansion extending medially, contributing further to the overall asymmetry of the bone. The ventral surface of the proximal end is covered by a large shallow sulcus that represents the articular surface for Mc II.

Torsion between the proximal and distal ends of Mc I and its marked asymmetry are features that characterize a wide variety of sauropodomorph dinosaurs (Galton & Upchurch 2004). Moreover, in No. 374 the ratio between the length of the metacarpal and the maximum height of its proximal articular surface is approximately 0.85, which is regarded as synapomorphy of Massospondylidae + more derived sauropodomorphs (e.g. Yates 2007; Apaldetti *et al*. 2013). No. 374 possesses no other features that distinguish it from the first metacarpals of many other sauropodomorph taxa (e.g. *Lufengosaurus*, *M. carinatus*, *Ngwevu*: Young 1941; Barrett *et al*. 2019; Chapelle *et al*. 2019), so it is identified as that of an indeterminate massopodan herein.

Metacarpal V

Owen (1854, p. 103) described No. 366 (NHMUK PV R3037 *partim*; Fig. 7M) as a tarsal, noting similarities to the calcaneum of crocodiles, but as noted by Huene (1906, pl. XVI [XXIII], fig. 6) this element is an Mc V. As with the preceding description, this element is described as though held in life position. Measurements are provided in Table 4.

In both lateral and dorsal views, Mc V consists of strongly expanded proximal and distal articular regions, which are connected by a short, stout shaft. Both the

articular regions are expanded mediolaterally and dorsoventrally with respect to the shaft, but the proximal expansion is the larger of the two. The proximal articular region has a pyramidal shape with a sub-quadrate outline and four flat, obliquely inclined surfaces facing dorsally, ventrally, posteromedially and posterolaterally. These surfaces converge posteriorly to form a low ridge that is displaced towards the medial side of the bone. The proximal articular surface is mediolaterally widest along its dorsal margin and narrow ventrally; the medial and lateral margins are subequal in length. The shaft has a sub-circular to elliptical transverse cross-section. The distal articular region forms a rounded, globose surface that is almost equally expanded dorsoventrally and mediolaterally. In dorsal or ventral view, Mc V is slightly asymmetrical with the long axis of the distal end set at a small angle with respect to the proximal end.

Although No. 366 does not possess any features considered synapomorphic for any sauropodomorph clade, it closely resembles the Mc V in a wide variety of sauropodomorphs (Galton & Upchurch 2004) and is referred to Sauropodomorpha indet. herein.

Manual unguals

Casts of three ungual phalanges of varying sizes are available (Nos. 382, 383, 385; NHMUK PV R3026, R3037 *partim*; Owen 1854, p. 105). Owen (1854) did not attribute these to either the manus or pes but Seeley (1895, pp. 115–116) regarded them as part of the foot and figured No. 383 (*ibid.*, fig. 11). Huene (1906, figs 63, 64, 68) considered Nos. 383 and 385 as manual unguals, whereas he regarded No. 382 as part of the pes. For ease of comparison, the unguals are described as though held horizontally (i.e. with their recurved tips directed ventrally). Measurements are provided in Table 4.

In lateral view, the unguals are tallest proximally (Fig. 7N–P). The dorsal margin is strongly convex, whereas the ventral margin is strongly concave and the ungual tapers as these margins converge distally, to form a narrow, strongly recurved point (the tip is missing in all three examples). The proximal articular surface is strongly concave dorsoventrally, due in part to a large lappet that overhangs this surface dorsally. The articular surface has a sub-ovate outline, with its long axis is oriented dorsoventrally. In dorsal view, the ungual is compressed mediolaterally and tapers anteriorly. The lateral and medial surfaces each bear grooves for claw sheaths positioned either at or slightly ventral to ungual mid-height.

Seeley (1895) regarded these as pedal unguals but all three are identified as manual unguals herein. In sauropodomorphs, manual unguals exhibit strong recurvature and are mediolaterally compressed, whereas pedal unguals are proportionally wider and lack marked recurvature (Galton & Upchurch 2004). Although these unguals bear no synapomorphies of any particular clade they are indistinguishable from those of many sauropodomorphs (Galton & Upchurch 2004) and are referred to Sauropodomorpha indet.

Pelvic girdle

Ilium

A left ilium (No. 358; NHMUK PV R3032 *partim*; SAM-PKC-969; Fig. 8A) was included among the material described by Owen (1854, 102; see also Seeley 1895, p. 108, fig. 4; Huene 1906, p. 137, pl. XV [XXII]). It is almost complete but is lacking the pubic peduncle. Measurements are provided in Table 5. In lateral view, the dorsal margin of the ilium is gently convex anteriorly, but this becomes straight posteriorly. The preacetabular process is anteroposteriorly short and has an almost equitriangular outline that tapers to a blunt, rounded tip in lateral view. It is mediolaterally compressed with a very narrow, sub-triangular transverse cross-section. This process is separated from the base of the pubic peduncle by a broad, 'U'-shaped sulcus. Although the pubic peduncle is missing, the shape and orientation of its broken surface indicates that it would have extended further anteriorly than the preacetabular process.

The main blade of the ilium dorsal to the acetabulum is divided into two surfaces in lateral view, by a subtle break-in-slope that occurs approximately level with the ventral margin of the preacetabular process (Fig. 8A). Consequently, the dorsal part of the iliac blade is strongly concave anteroposteriorly and dorsoventrally, whereas its ventral part is weakly convex in both directions. A poorly developed supraacetabular crest separates the lateral surface of the ilium from the acetabular articular surface. The postacetabular process is well-developed and has a sub-quadrate outline with a flat to convex dorsal margin, a short, flat posterior margin and an anteroventrally sloping, straight ventral margin (Fig. 8A). The latter is very slightly offset from the otherwise straight posterior margin of the iliac blade by a very subtle inflection. The postacetabular process is mediolaterally expanded with respect to the rest of the iliac blade and has a broad, sub-triangular transverse cross-section with the apex of this triangle oriented laterally.

In lateral view, the acetabulum is almost fully open, with only its dorsal-most part slightly overhung laterally by a ventral extension of the iliac blade and its medial part formed from a shallow sheet of bone (Fig. 8A). Viewed ventrally, the acetabulum is strongly expanded mediolaterally with respect to the dorsal part of the ilium. It is widest anteriorly and tapers slightly posteriorly. The acetabular surface is strongly concave both mediolaterally and anteroposteriorly.

In medial view, the ventral margin of the ilium forms a mediolaterally expanded buttress that lies dorsal to the acetabulum. Anteriorly, this buttress probably forms the ventral margin of the area that would have been occupied by the sacral rib attachments. A short, but well-defined ridge that extends for a short distance anteriorly along the base of the postacetabular process would also have contributed to the ventral margin of the sacrum attachment area. Sadly, the cast is not detailed enough to reveal details of either the number or shape of the sacral rib facets, although Seeley (1895) estimated that three or four sacrals would have been likely. The dorsal part of the



Figure 8. Casts of pelvic girdle bones from the Orpen Collection. **A**, NHMUK PV R3032 (*partim*), catalogue number 358, left ilium in lateral view. **B**–**C**, NHMUK PV R3030 (*partim*), catalogue number 352, ?right proximal pubis in lateral (**B**) and proximal views (**C**). **D**–**E**, NHMUK PV R3036 (*partim*), catalogue number 351, right proximal pubis in lateral (**D**) and proximal views (**E**). **F**–**G**, NHMUK PV R3036 (*partim*), catalogue number 353, ?left ischial shaft in lateral (**F**) and posterior views (**G**).

Table 5. Pelvic girdle, hindlimb and pes measurements in millimetres. Asterisks (*) indicate incomplete bones; dashes ('–') indicate inapplicable or substantially incomplete measurements.

Ilium				
NHMUK catalogue number:	PV R3032 (*partim*)			
Owen (1854) catalogue number:	358			
Length, anteroposterior	224			
Blade, height dorsal to acetabulum	89			
Preacetabular process, anteroposterior length of	34			
Postacetabular process, anteroposterior length of	39			
Ischiac peduncle, anteroposterior length of	33			
Ischiac peduncle, mediolateral width	39			
Acetabulum, maximum mediolateral width	55			
Pubis				
NHMUK catalogue number	PV R3036 (*partim*)	PV R3030		
Owen (1854) catalogue number	351	352		
Proximal end, anteroposterior length	101	83		
Proximal end, maximum mediolateral width	32	24		
Ischium				
NHMUK catalogue number**:**	PV R3036 (*partim*)			
Owen (1854) catalogue number:	353			
Length (as preserved)	95*			
Maximum anteroposterior length (as preserved)	58*			
Femora				
NHMUK catalogue number:	PV R3033 (*partim*)	PV R3033 (*partim*)	PV R3033 (*partim*)	
Owen (1854) catalogue number:	360	361	362	
Length as preserved	159*	181	245	
Proximal end, maximum mediolateral width	83*	–	–	
Proximal end, maximum anteroposterior length	52	–	–	
Distal end, maximum mediolateral width	–	102	104	
Distal end, maximum anteroposterior length	–	84	83	
Shaft, mediolateral diameter	–	53	50	
Shaft, anterolateral diameter	–	51	51	
Tibiae				
NHMUK catalogue number:	PV R3034 (*partim*)	PV R3034 (*partim*)		
Owen (1854) catalogue number:	363	364		
Length (as preserved)	142*	135*		
Proximal end, maximum anteroposterior length	109	–		
Proximal end, maximum mediolateral width	77	–		
Cnemial crest, dorsoventral length	73	–		
Distal end, maximum anteroposterior length	–	66		
Distal end, maximum mediolateral width	–	42		
Shaft, anteroposterior diameter	48	42		
Shaft, mediolateral diameter	38	35		
Metatarsal II				
NHMUK catalogue number:	PV R3037 (*partim*)	PV R3037 (*partim*)		
Owen (1854) catalogue number:	367 (left Mt II, proximal)	369 (right Mt II, proximal)		
Proximal end, maximum anteroposterior length	59	56		
Proximal end, maximum mediolateral width	43	36		
Distal shaft, maximum anteroposterior length	21	27		
Distal shaft, maximum mediolateral width	21	19		
Maximum length (as preserved)	77*	77*		
Metatarsal III				
NHMUK catalogue number:	PV R3037 (*partim*)	PV R3037 (*partim*)		
Owen (1854) catalogue number:	368 (right Mt III, distal)	373 (Mt?, distal)		
Distal end, maximum anteroposterior length	29	18		
Distal end, maximum mediolateral width	42	31		
Shaft, maximum anteroposterior length	19	–		
Shaft, maximum mediolateral width	24	–		
Length (as preserved)	86*	–		
Phalanges				
NHMUK catalogue number:	PV R3037 (*partim*)	PV R3037 (*partim*)	PV R3037 (*partim*)	PV R1312a
Owen (1854) catalogue number:	375	378	379	380
Length	60	40	42	32
Proximal end, maximum width	40	33	25	24
Proximal end, maximum height	30	27	23	22
Distal end, maximum width	38	30	23	22
Distal end, maximum height	23	18	15	17

ilium's medial surface is strongly convex anteroposteriorly (so that in dorsal view, the ilium is bowed medially), as is the area immediately adjacent to the ventral buttress. The triangular area posterior to the ventral buttress and ventral to the postaceabular process is smooth and shallowly concave.

In either lateral or medial view, the ischiac peduncle forms a short, posteroventrally directed process with a sub-quadrate outline. In ventral view, it has a sub-triangular outline with a long anterior margin (forming the posterior border of the acetabulum), an almost equally long posterolateral margin and a short medial margin.

Various features of the ilium allow its identification as that of a sauropodomorph, such as the absence of a buttress between the preacetabular process and the acetabular margin and the presence of an almost fully open acetabulum (Galton & Upchurch 2004). The rounded to slightly pointed overall outline of the postacetabular process (rather than a more angular or square-ended process) is consistent with referral to Massospondylidae. Overall, the ilium is very similar to that of *Adeopapposaurus* (Martínez 2009), *M. carinatus* (Barrett *et al*. 2019) and *Ignavusaurus* (Knoll 2010), suggesting that referral to Massospondylidae is likely, but attribution to a particular taxon is not possible given the absence of clear autapomorphies.

Pubis

The proximal parts of two ?right pubes are preserved (Nos. 351 and 352). Owen (1854, p. 101) originally identified these as parts of a coracoid (No. 352; NHMUK PV R3030; SAM-PKC-966; Fig. 8B, C) and scapula (No. 351; NHMUK PV R3036 *partim*; Fig. 8D, E), respectively, but this error was corrected by Seeley (1895, pp. 103 and 110) and Huene (1906, p. 138, fig. 51). Seeley (1895, fig. 6) provided a reconstruction of the entire pubis based on No. 351 and '… several specimens, some of which have hitherto escaped attention, and remain … without numbers' (*ibid*., p. 110), but the whereabouts of these additional specimens is unknown (see also Huene 1906). As both preserved pubes are from the same side and differ substantially in size, these specimens provide additional support for the mixed nature of the assemblage from which they came, although they are morphologically similar. The following description is based on No. 351 noting differences from No. 352 where appropriate. Descriptions assume that the elements are held in life position. Measurements are provided in Table 5.

The proximal part of the pubis has an elongate oval outline in dorsal view, with a rounded anterior margin, slightly convex medial and lateral margins and an almost straight posterior margin (Fig. 8C, E). The anterior two-thirds of the dorsal surface is flat and represents the iliac articular surface. Posterior to this the dorsal surface is gently excavated, so that it is anteroposteriorly and mediolaterally concave, forming the pubic contribution to the acetabular margin. In No. 351, the dorsal surface of the pubis maintains an almost constant mediolateral width along its entire length, whereas in No. 352 the acetabular region is slightly waisted with respect to the iliac articulation.

In lateral view, the ischial articulation is offset from the rest of the dorsal surface, forming an angle of approximately 120° with the latter (Fig. 8B, D). In both specimens, the ischial articular surface is flat and faces posteriorly, but it differs slightly in outline as it is sub-quadrate in No. 351 but sub-triangular in No. 352. The lateral surface of the proximal portion of the pubis is weakly convex anteroposteriorly but becomes flatter as the pubis begins to extend into the ventral shaft. The corresponding areas on the medial surface are slightly convex: as a result, the proximal-most part of the shaft has a flattened 'D'-shaped transverse cross-section. A large, obturator foramen was present, but its overall shape and relative size is unknown as the bar of bone that would have closed it posteriorly is missing from both specimens.

Although only a short portion of the shaft is preserved in both specimens, it is clear there was substantial torsion with respect to the proximal end, with the long axis of the shaft inclined ventromedially at its proximal-most end. The 'medial' surface of the shaft is twisted to face anteromedially, which would presumably have enabled to the formation of the pubic apron ventrally as the pubis articulated with its antimere.

Both pubes possess an iliac articulation whose anterior margin overhangs the pubic apron, which is considered a synapomorphy of *Plateosauravus* and more derived sauropodomorphs (Yates 2007; Apaldetti *et al*. 2013). Although the neotype of *M. carinatus* includes both pubes, their proximal ends are largely obscured by other elements (Barrett *et al*. 2019), and the pubis of *Ngwevu* is fragmentary (Chapelle *et al*. 2019) precluding useful comparisons. Moreover, the incompleteness of Nos. 351 and 352 limit comparisons with other taxa, although they are similar to those of both *Ignavusaurus* (Knoll 2010) and *Adeopapposaurus* (Martínez 2009), as well as other non-massospondylid taxa (e.g. *Yunnanosaurus*: Young 1942). Both specimens are regarded as Sauropodomorpha indet. herein.

Ischium

Owen (1854, p. 101) identified No. 353 (NHMUK PV R3036 *partim*; Fig. 8F, G) as a partial coracoid, but the morphology of this element is comparable to the proximal part of a ?left ischial shaft, representing the region just ventral to the proximal plate and dorsal to the ischial symphysis. This specimen was not mentioned by Seeley (1895) but was identified correctly by Huene (1906, p. 137, fig. 52). Huene's identification of No. 386 as conjoined ischial shafts seems reasonable based on his figures (1906, fig. 53), but no cast of this specimen survives. Measurements are provided in Table 5.

In lateral view, No. 353 has a broad dorsal margin, but tapers ventrally as the anterior and posterior borders converge (Fig. 8F). The anterior margin of the ischial shaft is convex along its preserved length, while the posterior margin is shallowly concave. In its proximal part, the anterior part of the ischial shaft is pinched-out into an anteromedially extensive but mediolaterally thin flange, whereas the posterior part of the shaft is mediolaterally broader, with most of its mediolateral expansion occur-

ring laterally rather than medially. As a result, the lateral surface of the proximal shaft is concave anteriorly, but a strong change in slope that gives its posterior part a strongly convex profile, leading to a sinuous transverse cross-section at this point. The corresponding medial surface of the shaft is flat. In dorsal view, the shaft has a narrow, elongate elliptical cross-section. Ventrally, the shaft narrows in lateral view, but thickens mediolaterally so that the ventral part of the preserved shaft is rod-like. In distal view, the shaft has a sub-circular cross-section. The posterior surface of the shaft bears a conspicuous midline groove that extends for the full length of the preserved fragment (Fig. 8G).

Given the incompleteness of the preserved element, meaningful comparisons with other taxa are not possible, although it is similar to the ischia of many other early sauropodomorphs (Galton & Upchurch 2004) and is so considered Sauropodomorpha indet. herein.

Hind limb

Femora

Three partial femora were listed by Owen (1854, pp. 102–103; NHMUK PV R3033) including the proximal end of a right femur (No. 360; SAM-PKC-971; Fig. 9A–E) and the distal ends of a left (No. 361; SAM-PKC-972; Fig. 9F–I) and right femur (No. 362; SAM-PKC-973; Fig. 9J–N). Owen (1854) considered Nos. 360 and 361 to be parts of the same bone and that No. 362 was from the same individual. This is plausible, as all three elements are consistent in size, but cannot be determined definitively based on the available material. Seeley (1895, pp. 111–112, fig. 7) agreed with Owen's identifications and also mentioned a partial femoral shaft, which was presumably an unnumbered (and now lost) fragment in the collections of the Hunterian Museum. No. 360 is broken at the level of the anterior trochanter and includes only a splint of the femoral shaft. A large crack covers much of its posterior surface. Figures of the femora and some additional descriptive details were also provided by Huene (1906, p. 138, fig. 54, pl. XV [XXII], fig. 2 and pl. XVI [XXIII], figs 1, 2). Measurements are provided in Table 5.

The proximal articular surface of the femur is subelliptical in dorsal view (Fig. 9E). Its anterior margin is smoothly convex and blends into the convex medial margin of the femoral head. By contrast, the posterior margin is sinuous, as a small notch separates the head from the posteromedial tuber. The articular surface is anteroposteriorly longest in the region of the posteromedial tuber and tapers slightly laterally to form the greater trochanter. This surface is mediolaterally and anteroposteriorly convex and lacks a distinct trochanteric fossa, so there is no clear separation between the femoral head and the greater trochanter. In medial view, the femoral head is globose with a flat to slightly convex articular surface.

Viewed anteriorly, the femoral head is oriented medially and very slightly dorsally (Fig. 9A). Its medial margin is almost straight and oriented vertically and it is offset from the shaft ventrally by a distinct notch. Only the dorsal-most part of the anterior trochanter is preserved, positioned toward the lateral margin of the shaft ventral to the greater trochanter. The apex of the anterior trochanter is a sharp, triangular crest whose tip lies ventral to the femoral head.

The posteromedial tuber forms a small but distinct boss on the posterior surface of the proximal end (Fig. 9C, E). It forms the dorsolateral border of a broad, shallow, dorsoventrally open sulcus, that covers most the posterior surface of the femoral head.

In Nos. 361 and 362, the shafts have sub-circular transverse cross-sections at femoral midlength. The distal ends are anteroposteriorly and mediolaterally expanded, with the greatest expansion occurring mediolaterally (Fig. 9F, H, J, L). When viewed medially or laterally, the shafts are bowed slightly anteriorly (Fig. 9G, K, M). A sharp intramuscular line extends along the shaft lateral margin but fades away before it reaches the distal end of the bone. A broad, shallow, ventrally opening sulcus lies on the midline of the anterior surface immediately dorsal to the distal margin (Fig. 9H, L).

The distal articular surface is gently concave mediolaterally and slightly convex anteroposteriorly. A deep, 'U'-shaped notch separates the tibial and fibular condyles in distal view (Fig. 9I, N). Both condyles and the crests arising from them extend for approximately the same distance posteriorly, but the tibial condyle is approximately twice the width of the fibular condyle. The medial margin of the tibial condyle is straight and its posterior margin is broadly rounded. By contrast, the fibular condyle is slightly inset from the lateral margin of the distal end and it tapers to a rounded triangular apex. The apex is directly slightly curved laterally, giving it a sinuous appearance.

The notch between the distal condyles is confluent with a deep sulcus on the posterior surface of the shaft (Fig. 9H, L). This sulcus is bounded medially and laterally by stout crests arising from the dorsal surfaces of the tibial and fibular condyles, respectively. The tibial condylar crest is broad, low and dorsoventrally short, whereas that originating from the fibular condyle is tall, narrow and extends as a distinct ridge for a considerable distance dorsally before merging into the shaft surface.

Possession of a fully inturned femoral head clearly identifies No. 360 as a dinosaur and all the preserved femora are very similar to those of sauropodomorphs (Galton & Upchurch 2004). The large size of these specimens is also consistent with referral to Sauropodomorpha. However, Nos. 360–362 do not possess any features that are currently considered to be synapomorphic for any sauropodomorph clade (Yates 2007; Apaldetti *et al*. 2013). No. 360 is similar to the partial femur preserved in the neotype of *M. carinatus* (Barrett *et al*. 2019), but femora with comparable features are also known in a variety of other taxa (e.g. Young 1941; Martínez 2009). All three specimens are regarded as Sauropodomorpha indet. herein.

Tibiae

Owen (1854, p. 103) mentioned the proximal end of a right tibia (No. 363; NHMUK PV R3034 *partim*; SAM-

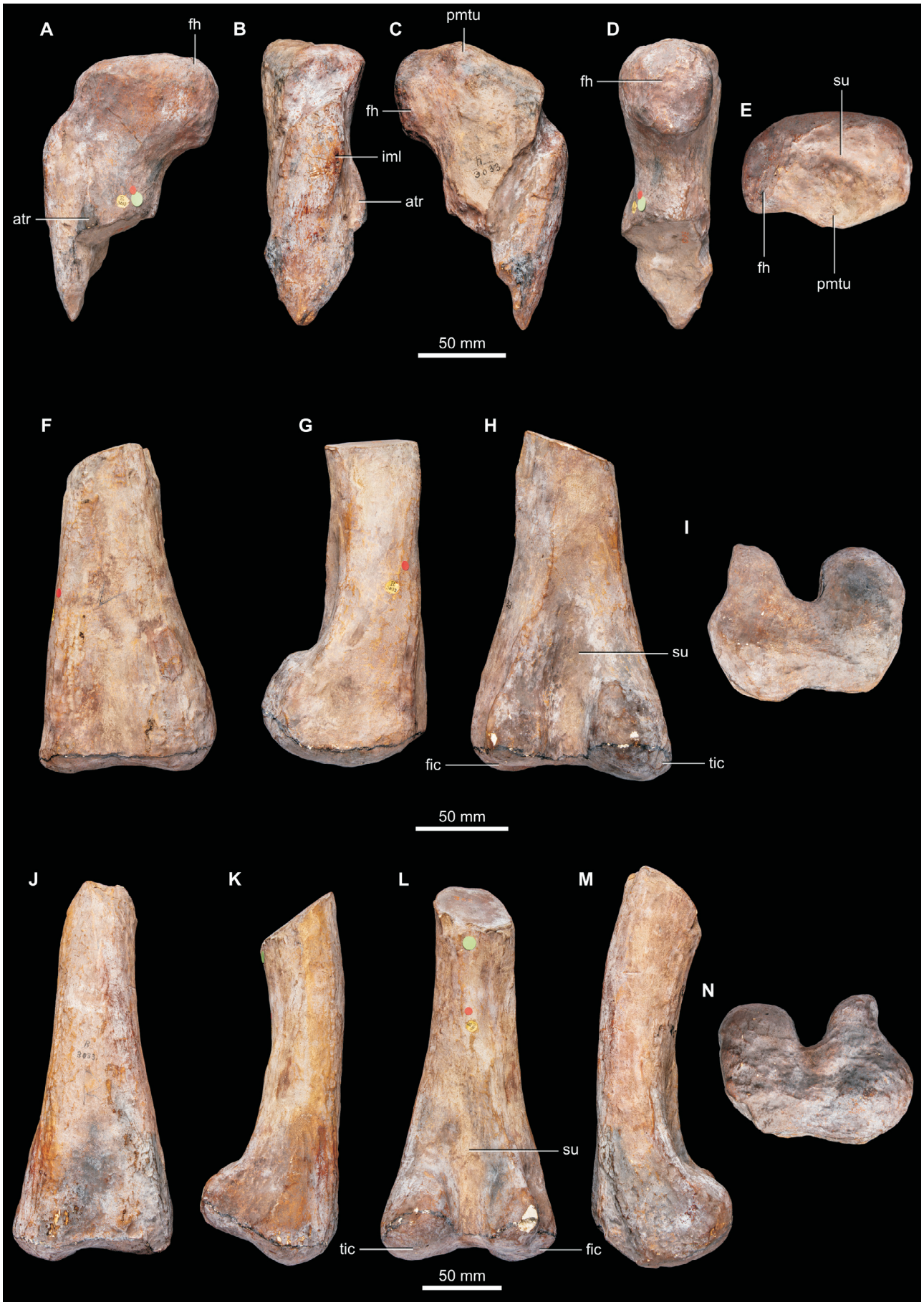


Figure 9. Casts of femora from the Orpen Collection. **A**–**E**, NHMUK PV R3033 (*partim*), catalogue number 360, right proximal femur in anterior (**A**), lateral (**B**), posterior (**C**), medial (**D**) and proximal (**E**) views. **F**–**I**, NHMUK PV R3033 (*partim*), catalogue number 361, left distal femur in anterior (**F**), medial (**G**), posterior (**H**), distal (**I**) views. **J**–**N**, NHMUK PV R3033 (*partim*), catalogue number 362, right distal femur in anterior (**J**), lateral (**K**), posterior (**L**), medial (**M**) and distal (**N**) views.

PKC-974; Fig. 10A–E) and the distal end of a left tibia (No. 364; NHMUK PV R3034 *partim*; Fig. 10F–J), which he regarded as being from the same individual. A third partial tibia was also mentioned (No. 365; SAM-PKC-975), which Owen (1954, p. 103) listed as the proximal end of a left tibia from a second, smaller individual. Seeley (1895, p. 113, figs 8, 9) also mentioned all three specimens, but regarded Nos. 364 and 365 as parts of the same bone. However, No. 365 is the distal end of a right tibia (P.M.B., pers. obs.). As the field relationships of all three specimens are unknown, and there is no anatomical overlap between the preserved proximal and distal ends, it is unclear if any of these separate pieces represent parts of the same individual element or indeed the same individual. Nos. 363 and 364 were figured by Huene (1906, figs 55, 70, pl. XV [XXII], figs 3, 4). Measurements are provided in Table 5.

The right tibia (No. 363; Fig. 10A–D) consists of the proximal articular surface and a short section of shaft. The proximal end is expanded anteroposteriorly and mediolaterally with respect to the shaft, although the degree of anteroposterior expansion is greater. In dorsal view, the proximal articular surface has an irregular 'D'-shaped outline, with prominent cnemial, fibular and posterior crests (Fig. 10E). The cnemial crest projects anteriorly and tapers to a broad, rounded apex. The medial margin of the proximal end, including that of the cnemial crest, forms a continuous convex curve, which is interrupted in its anterior part by crushing (which is more clearly visible in medial view). The lateral margin of the cnemial crest is straight and separated from the anterolateral margin of the fibular condyle by a broad, open notch (forming an angle of approximately 120°). The laterally and slightly posteriorly projecting fibular condyle has a hemispherical outline in dorsal view and is substantially larger than the cnemial crest. A small inflection separates the posterior margin of the fibular condyle from the short, rounded, sub-triangular and posteriorly projecting posterior crest. The dorsal surface of the proximal articular surface is generally flat, but a shallow, mediolaterally oriented trough separates the cnemial and fibular crests.

In lateral view, the dorsal margin of the tibia is bevelled so that its long axis extends slightly anterodorsally-to-posteroventrally (Fig. 10B). The cnemial crest is short, but prominent, and extends ventrally before merging into the anterior margin of the shaft a short distance below the proximal end. The fibular condyle swells to form a distinct elliptical boss in lateral view whose long axis extends anteroposteriorly. A broad ridge supports this boss ventrally before merging into the shaft, extending to the same point as the cnemial crest. A broad, shallow, dorsoventrally extending sulcus separates the ridges arising from the cnemial and fibular crests. The posterior crest has a blunt triangular outline in lateral view, which overhangs the posterior surface of the shaft. In medial view, the proximal expansion has a smoothly convex surface anteroposteriorly, which is interrupted by a large depression that is interpreted as damage due to crushing (Fig. 10D). The shaft has convex lateral and medial margins. These merge anteriorly and posteriorly to produce a sub-elliptical transverse cross-section that is longer anteroposteriorly than wide mediolaterally.

Of the two preserved distal tibiae, No. 364 is the best preserved and thus forms the basis for the following description (Fig. 10F–J); No. 365 is essentially identical in most respects. The distal end of the tibia is expanded both mediolaterally and anteroposteriorly with respect to the shaft, with the greatest expansion occurring mediolaterally (Fig. 10F–I). The shaft has a 'D'-shaped transverse cross-section, with a straight medial margin and anterior, lateral and posterior margins that merge along one continuous curve. Further ventrally, the shaft acquires a sub-quadrate cross-section just dorsal to the distal expansion. The distal end is divided into two distinct processes, the antero- and posterolateral processes, which are separated by a deep notch that would have received the astragalus (Fig. 10F). In anterior view, the ventral margin of the anterolateral process is oriented obliquely, so that its articular surface is oriented ventrolaterally. A stout ridge arises from the lateral-most tip of the anterolateral process and extends dorsally for a short distance before merging into the shaft. As the posterolateral process extends further ventrally than the anterolateral process, its anterior surface is exposed in anterior view. Both processes extend for approximately the same distance laterally. The posterolateral process is anteroposteriorly longer than the anterolateral process in lateral view. In posterior view, a low rounded intramuscular line arises from the midpoint of the ventral margin and extends dorsally until it eventually merges with the rest of the shaft surface. Another similarly extensive intramuscular line forms the anteromedial margin of the shaft and distal end. In ventral view, the distal articular surface has a sub-trapezoidal outline whose anterior margin is the longest (Fig. 10J). The anterior margin is gently concave; the lateral margin bears a shallow notch that is confluent with that separating the antero- and posterolateral processes; the short posterior margin is straight; and the medial margin is canted to face posteromedially.

In addition to a strong overall resemblance to the tibiae of sauropodomorphs (Galton & Upchurch 2004), No. 364 bears one unambiguous synapomorphy that unites most post-Carnian members of the clade, namely that the distal portion of the tibia is mediolaterally broader than it is long anteroposteriorly (Yates 2007; Apaldetti *et al*. 2013). In addition, as the antero- and posterolateral processes extend for similar distances laterally, No. 364 can be excluded from Anchisauria (Yates 2007; Apaldetti *et al*. 2013). Comparisons with *M. carinatus* are hampered by the lack of tibiae in the neotype specimen (Barrett *et al*. 2019), but there are no significant differences between Nos. 363–365 and the tibiae of *Ngwevu* (Chapelle *et al*. 2019) or *Ignavusaurus* (Knoll 2010). We regard all three of these specimens as belonging to an indeterminate non-anchisaurian sauropodomorph.

Metatarsal II

Nos. 367 and 369 (both NHMUK PV R3037 *partim*; Fig. 10K–N) represent the proximal ends of a left and right metatarsal (Mt) II, respectively (correctly identified as



Figure 10. Casts of hindlimb and pes bones from the Orpen Collection. **A**–**E**, NHMUK PV R3034 (*partim*), catalogue number 363, right proximal tibia in anterior (**A**), lateral (**B**), posterior (**C**), medial (**D**) and proximal (**E**) views. **F**–**J**, NHMUK PV R3034 (*partim*), catalogue number 364, left distal tibia in anterior (**F**), lateral (**G**), posterior (**H**), medial (**I**) and distal (**J**) views. **K**–**L**, NHMUK PV R3037 (*partim*), catalogue number 369, right proximal metatarsal II in medial (**K**) and proximal (**L**) views. **M**–**N**, NHMUK PV R3037 (*partim*), catalogue number 367, left proximal metatarsal II in lateral (**M**) and proximal (**N**) views. **O**, NHMUK PV R3037 (*partim*), catalogue number 368, right distal metatarsal III in anterior view. **P**, NHMUK PV R3037 (*partim*), catalogue number 373, distal metatarsal in anterior view. **Q**–**S**, NHMUK PV R3037 (*partim*), catalogue number 375, right pedal phalanx in dorsal (**Q**), medial (**R**) and proximal (**S**) views. **T**–**V**, NHMUK PV R3037 (*partim*), catalogue number 378, left pedal phalanx in dorsal (**T**), lateral (**U**) and proximal (**V**) views. **W**–**Y**, NHMUK PV R3037 (*partim*), catalogue number 379, ?left pedal phalanx in dorsal (**W**), lateral (**X**), and proximal (**Y**) views. **Z**–**ZZ**, NHMUK PV R1312a (*partim*), catalogue number 380, pedal phalanx in dorsal (**Z**) and medial/lateral (**ZZ**) views.

metatarsals by Owen [1854, p. 103], Seeley [1895, p. 116] and Huene [1906, p. 139, fig. 57]). Huene (1906, p. 139, fig. 56) listed a third specimen (No. 370) as the proximal end of a left Mt II, which seems likely based on his figure, although no cast survives. Measurements are provided in Table 5.

In proximal view, the Mt IIs have a sub-rectangular outline whose long axis trends anteroposteriorly (assuming that the metatarsals were held vertically in life; Fig. 10L, N). The medial and lateral margins of the proximal end are subequal in length and deeply concave, giving the proximal articular surface an hourglass-shaped outline. By contrast, the posterior and anterior margins are much shorter (with the posterior margin slightly broader than the anterior margin) and both are shallowly concave. The articular surface is very gently concave anteroposteriorly and flat to slightly convex mediolaterally, giving a subtle saddle-shaped morphology. Each corner of the articular surface is confluent with a stout, well-defined ridge that descends ventrally, each of which divides the shaft into distinct anterior, medial, lateral and posterior surfaces.

The anterior surface of Mt II is narrow and maintains a constant mediolateral width as it descends ventrally. The dorsal-most part of the shaft is overhung slightly by the articular surface, creating a shallow concavity, but the remainder of the shaft surface is flat. In medial or lateral view, the shaft is broadest dorsally and tapers ventrally as its anterior and posterior margins converge. Assuming that the shaft is held vertically, the proximal margin of the metatarsal (articular surface) is not horizontal but angled slightly anteroventrally. The proximal part of the shaft's lateral surface is shallowly concave anteroposteriorly, forming an articular surface for the reception of Mt I. This concavity becomes weaker ventrally so that the rest of the shaft surface becomes flat.

In posterior view, Mt II is broadest dorsally and this area is mediolaterally concave. Ventrally, the shaft narrows and becomes slightly convex mediolaterally. Finally, the medial surface of the shaft is strongly convex in its proximal part, forming a deep sulcus to accommodate the proximal end of Mt III, but below this the shaft surface becomes gently convex. The shaft transverse cross-section is 'D'-shaped (flat medially and convex around its other surfaces).

Although the preserved Mt IIs are similar to those associated with the neotype of *M. carinatus* (Barrett *et al*. 2019), the hourglass-shaped outline of the proximal end is found in the majority of early sauropodomorphs and is widely regarded as a synapomorphy of the group (Galton & Upchurch, 2004; Yates, 2007; Apaldetti *et al*. 2013). As these elements possess no other diagnostic features they are regarded as Sauropodomorpha indet. herein.

Metatarsal III

The distal end of a right Mt III is included in the collection (No. 368; NHMUK PV R3037 *partim*; Owen [1854, p. 103]; Huene [1906, p. 139, fig. 58]; Fig. 10P). Measurements are provided in Table 5. The shaft of Mt III is slender and straight in both anterior and lateral views. The shaft surfaces are continuous and merge smoothly into each other giving it an elliptical transverse cross-section, whose long axis trends mediolaterally. Ventrally, the shaft expands both anteroposteriorly and mediolaterally to form the articular region. In either lateral or medial view, the anteroposterior expansion of the distal end is asymmetrical, with all the expansion occurring posteriorly. The anterior surface of the distal expansion bears a shallow fossa, but it is unclear if this is a taphonomic artefact. Its lateral and medial surfaces each bear deep, well-defined collateral ligament pits that are open dorsally but bounded by a raised rim anteriorly, ventrally and posteriorly. The anteromedial corner of the distal expansion bears a low ridge that would have buttressed the ventral part of Mt II. In posterior view, a shallow sulcus invaginates the ventral margin of the distal expansion. The distal articular surface is strongly convex anteroposteriorly, but very slightly concave mediolaterally, giving it a subtle saddle-shaped morphology. In distal view, Mt III has a sub-rectangular outline, whose long axis trends mediolaterally, with a slightly convex anterior margin, straight to slightly concave medial and lateral margins and a concave posterior margin.

This element possesses no diagnostic features that enable it to be referred to any particular taxon, although its size and general morphology are consistent with identification as a dinosaur (Galton & Upchurch 2004), so it is regarded as Dinosauria indet.

Metatarsal IV

Nos. 371 and 372 were identified as partial 'metacarpal IV[s]' in Huene (1906, p. 139, fig. 59), although it seems likely this was a typographic error for Mt IV as they are listed in his description of the foot. Huene's (1906) figure of No. 371 is consistent with his identification, but as no cast survives these elements are not discussed further.

Indeterminate metatarsals

No. 373 (NHMUK PV R3037 *partim*; Owen 1854, p. 104; Fig. 10O) represents the distal end of a metatarsal, but it is too poorly preserved to identify further (though Huene [1906, p. 139, fig. 60] suggested it might be Mt II). The distal end is mediolaterally and anteroposteriorly expanded with respect to the shaft and the medial and lateral surfaces of this expansion exhibit evidence of shallow collateral ligament pits. In distal view, the articular surface has a rectangular outline with its long axis extending mediolaterally. The articular surface is saddle-shaped (mediolaterally concave and anteroposteriorly convex). The distal condyles are of approximately equal size, though in anterior or posterior view they are situated asymmetrically with respect to the long axis of the shaft. The shaft has a narrow elliptical cross-section, with its long axis oriented mediolaterally. The general morphology and size of No. 373 supports its likely referral to Dinosauria, but this specimen lacks other features that would allow attribution to any particular clade.

Non-ungual phalanges

Casts of four non-ungual phalanges are available (Nos. 375, 378–380; NHMUK PV 1312a and R3037 *partim*;

SAM-PKC-976; Owen 1854, pp. 104–105; Seeley 1895, pp. 114–115; Fig. 10Q–ZZ) and are likely from the pes, though it is possible that some of these elements might be from a manus (see Huene 1906). Nos. 375 and 379 have been figured (Seeley 1895, fig. 10; Huene 1906, figs 65, 67). All four specimens are similar, differing only in size, stoutness and the outline of the proximal articular surface. The following are described as though they are held horizontally. Three other non-ungual phalanges were mentioned by Owen (1854: Nos. 376, 377, 381) and No. 381 was figured by Huene (1906, fig. 62), but no cast of these survives. Measurements are provided in Table 5.

Each phalanx has mediolaterally expanded proximal and distal expansions in dorsal view, and these are connected via a narrower shaft (Fig. 10Q, T, W, Z). The shaft has concave lateral and medial margins, so that these elements all have hourglass-shaped outlines. In lateral or medial view, the articular areas are expanded dorsoventrally with respect to the shaft, with most of this expansion occurring ventral to the long axis of the bone; the proximal articulation is more strongly expanded in both dimensions than the distal one (Fig. 10R, U, X, ZZ).

In Nos. 375, 378 and 379 the proximal articular surface is strongly concave dorsoventrally, but flatter mediolaterally (Fig. 10S, V, Y). By contrast this surface is divided into medial and lateral concavities by a dorsoventrally extending midline ridge in No. 380. All four phalanges possess a proximal articular surface with a 'D'-shaped outline (straight ventral margin, straight lateral or medial margin and a continuously curved lateral or medial + dorsal margin). No. 380 bears a small, 'V'-shaped dorsal lappet; incipient versions of the same feature are also present on Nos. 375 and 379, but this is absent in No. 378.

The shaft has an elliptical transverse cross-section at midlength in all specimens. In lateral view, the ventral margin of the shaft is arched strongly dorsally whereas its dorsal margin is straight or very slightly concave. The distal end of each phalanx is divided into two subequally sized ginglymi, all of which bear distinct collateral ligament pits. In distal view, the articular surface has sub-trapezoidal outline and is saddle-shaped, being dorsoventrally convex and mediolaterally concave.

None of the non-ungual phalanges exhibit any features that allow them to be referred to any particular taxon or clade, but their general size and shape is consistent with referral to Dinosauria.

CONCLUSIONS

Although the original syntype series of *Massospondylus carinatus* Owen was destroyed in World War II, these specimens are represented (in part) by a series of casts and illustrations. Examination of the casts, many of which are figured in detail for the first time, reveals that none possess any features that are currently considered to be diagnostic for the taxon: instead, they represent a collection of indeterminate sauropodomorph and dinosaur remains (see Table 2). Some of these elements also differ in morphology from the more complete specimens that are now generally considered to represent *M. carinatus* (e.g. the neotype, BP/1/4934).

Specimens referred to *Pachyspondylus orpenii* Owen and *Leptospondylus capensis* Owen share no features that allow them to be referred to *M. carinatus* nor are they sufficiently distinctive to regard them as distinct taxa and they represent taxonomically indeterminate material. Hence, rather than considering them as junior subjective synonyms of *M. carinatus*, these binomina should be regarded as *nomina dubia*.

Finally, *Massospondylus carinatus* provides an excellent example of how changing taxonomic opinions and the discovery of new material can affect the fortunes of a species throughout its taxonomic history. Originally an obscure taxon limited to its syntype series, *M. carinatus* was neglected for most of the late nineteenth and early twentieth centuries, and later revisions either synonymized it with other species or regarded it as distinct but poorly known. Later, the discovery of new specimens provided fresh impetus to include it in phylogenetic and palaeobiological analyses and to provide fuller descriptions, although the referrals of these specimens to *Massospondylus* were made on a weak foundation. Moreover, the practice of identifying new material as *Massospondylus* led to the uncritical referral of other specimens to the taxon (e.g. BP/1/4779) that have been shown to represent distinct species. Although it is unclear if the more complete material now used as exemplars of the taxon represent the same species as Owen's original syntypes, the designation of a neotype has helped to stabilize the situation. Further study is required to assess how many of the numerous referred specimens are genuinely referable to what we now regard as *M. carinatus*, not least as the ontogenetic and intraspecific variation of this material is poorly understood, especially if we are to determine the true species-richness of the Early Jurassic dinosaur faunas from southern Africa in which it (purportedly) occurs.

ABBREVIATIONS

Anatomical

ACDL	Anterior centrodiapophyseal lamina
acr	Acromion process
alp	Anterolateral process
atr	Anterior trochanter
b	Boss
CDF	Centrodiapophyseal fossa
clp	Collateral ligament pit
cnc	Cnemial crest
dpc	Deltopectoral crest
ent	Entepicondyle
ep	Epipophysis
EPRL	Epipophyseal-prezygapophyseal lamina
fh	Femoral head
fic	Fibular condyle
ficr	Fibular crest
gr	Groove
hf	Haemal facet
hh	Humeral head
ilas	Iliac articular surface
iml	Intramuscular line
isas	Ischial articular surface
it	Internal tuberosity
isp	Ischial peduncle
k	Keel
lclp	Lateral collateral ligament pit
Mc	Metacarpal
mclp	Medial collateral ligament pit
Mt	Metatarsal
pap	Preacetabular process

PCDL	Posterior centrodiapophyseal lamina
pcr	Posterior crest
plp	Posterolateral process
pmtu	Posteromedial tuber
pop	Postacetabular process
PPDL	Paradiapophyseal lamina
psf	Postspinal fossa
puac	Pubic contribution to the acetabular margin
pup	Pubic peduncle
rc	Radial condyle
SPOL	Spinopostzygapophyseal lamina
SPRL	Spinoprezygapophyseal lamina
sac	Supraacetabular crest
sr	Sacral rib
su	Sulcus
tic	Tibial condyle
TPRL	Interprezygapophyseal lamina
uc	Ulnar condyle

Institutional

BPI	Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa
GPIT	Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Tübingen, Germany
IM	Indian Museum, Kolkata, India
NHMUK	Natural History Museum, London, U.K.
SAM	Iziko South African Museum, Cape Town, South Africa

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