

NEW INFORMATION ON *LESSEMSAURUS SAUROPOIDES* (DINOSAURIA: SAUROPODOMORPHA) FROM THE UPPER TRIASSIC OF ARGENTINA

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Abstract: Postcranial remains of *Lessemsaurus sauropoides* are described herein, including elements of the vertebral column, pectoral girdle, forelimb, pelvis and hindlimb. These remains were closely associated with the cervicodorsal neural arches previously described from this taxon. This assemblage of bones shows numerous derived characters, including some derived similarities exclusively shared with *Antetonitrus ingenipes* from the Upper Triassic of South

Africa. Additionally, this material reveals an unusual combination of plesiomorphic character states present in many non-eusauropod sauropodomorphs together with derived characters that suggest affinities with eusauropods and related taxa.

Key words: *Lessemsaurus*, Sauropodomorpha, Prosauropoda, Sauropoda, Triassic.

BASAL sauropodomorphs from the Villa Unión-Ischigualasto Basin (north-west Argentina; Stipanovic and Bonaparte 1972) are so far exclusively known from the upper section of the Los Colorados Formation (Groeber and Stipanovic 1953). Three different taxa have been described from this unit: *Riojasaurus incertus* (Bonaparte 1972; Bonaparte and Pumares 1995), *Coloradisaurus brevis* (Bonaparte 1978) and *Lessemsaurus sauropoides* (Bonaparte 1999). The original description of the last taxon focused on eight cervicodorsal vertebrae (PVL 4822–1), and several similarities with both non-eusauropod sauropodomorphs ('prosauropods') and basal sauropods ('cetiosaurids') were noted (Bonaparte 1986, 1999). Additional undescribed material (also catalogued under PVL 4822) consists of other vertebral elements and remains of the pectoral girdle, forelimb, pelvis and hindlimb. These elements are described and figured herein, providing a more complete understanding of the anatomy of *Lessemsaurus sauropoides*.

The undescribed remains are referred to *Lessemsaurus sauropoides* on the basis of their close association with the type material described by Bonaparte (1999) and the presence of numerous characters that distinguish this material from that of other non-eusauropod sauropodomorphs from the Los Colorados Formation. This assemblage of

bones (PVL 4822) includes material from more than one individual (based on the recovery of several duplicate elements in the collection). *Lessemsaurus sauropoides* is of interest because of the presence of a unique combination of apomorphic and plesiomorphic character states. These remains are compared with other non-eusauropod sauropodomorphs and their significance and phylogenetic relevance is discussed.

The comparisons made in this contribution are based on the examination of specimens of different taxa and relevant literature detailed in Table 1. Unless noted explicitly, all references to other taxa are based on the sources of data listed in this table.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BMNH, The Natural History Museum, London, UK; BPI, Bernard Price Institute, Johannesburg, South Africa; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, People's Republic of China; NGMJ, Nanjing Geological Museum, Nanjing, China; MB, Institut für Paläontologie, Museum für Naturkunde, Humboldt-Universität, Berlin, Germany; MCP, Museu Pontificia Universidade Católica, Porto Alegre, Brazil; MPEF, Museo Palaeontológico Egidio Feruglio, Trelew, Argentina; NM QR, National Museum, Bloemfontein, South Africa; PVL, Instituto Miguel Lillo, Tucumán, Argentina; SAM, Iziko – South African Museum,

Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; ULR, Museo Ciencias Naturales, Universidad La Rioja, La Rioja, Argentina; YPM, Yale Peabody Museum, New Haven, USA.

Anatomical abbreviations. 4t, fourth trochanter; I.1, phalanx 1 of first digit; I.u, ungual of first digit; a-I, concave articular surface for metatarsal I; a-II, articular surface for metacarpal II; acp, acromion process; agr, groove for ascending process of astragalus; alp, anterolateral descending process; ap, ascending process; apr, pubic apron; bcr, brevis crest; cn, cnemial crest; dac, hemispherical distal condyle; d.f., flexor fossa of distal humerus; dle, dorsolateral edge of asymmetrical ungual; dno, dorsal notch of ischial symphysis; dpc, deltopectoral crest; fdp, facet for descending process; fhe, femoral head; fpo, popliteal fossa; gl, glenoid cavity; ibl, iliac blade; ilp, iliac peduncle; isp, ischial peduncle; it, humeral internal tuberosity; lc, lateral condyle; lco, lateral concavity of pubic apron; ld, lateral depression; ldc, lateral distal condyle; lgr, unbifurcated lateral groove; lp, lunar lateral process; mb, astragalar main body; mc, medial condyle; mdc, medial distal condyle; mlp, medial collateral ligament pit; mtc I-II, metacarpals I through II; mtt I-V, metatarsals I through V; mwa, medial wall of acetabulum; ncs, neurocentral suture; of, obturator foramen; ol, olecranon; pa, parapophysis; paf, proximal articular facet; pap, preacetabular process; pdl, proximo-dorsal lip; pdp, posterior descending process of tibia; plp, proximolateral process; pmc, subrectangular posteromedial

TABLE 1. Source of comparative data used in this study. All comparative references to the following taxa have been observed in the specimens listed or taken from the respective bibliographic reference. Comparisons based on other specimens or taken from additional references are explicitly indicated in the text.

Taxon and source

Anchisaurus polyzelus, YPM 1883
Antetonitrus ingenipes, BPI/1/4952
Blikanasaurus cromptoni, SAM-PK-K403
Coloradisaurus brevis, PVL 5904
Efraasia minor, SMNS 12667
Ferganasaurus verzilimi, Alifanov and Averianov (2003)
Kotasaurus yamanpalliensis, Yadagiri (2001)
Lufengosaurus huenei, IVPP V15
Massospondylus carinatus, BPI/1/4934
Melanorosaurus readi, NM QR1551
Mussaurus patagonicus, PVL 4587
Omeisaurus maoianus, Tang *et al.* (2001)
Patagosaurus fariasi, PVL 4170
Plateosaurus engelhardti, SMNS 13200
Riojasaurus incertus, PVL 3808
Saturnalia tupiniquim, MCP 3844-PV
Tazoudasaurus naimi, Allain *et al.* (2004)
Tehuelchesaurus benitezi, MPEF-PV 1125
Thecodontosaurus antiquus, YPM 2195
Thecodontosaurus caducus, Yates (2003)
Vulcanodon karibaensis, Cooper (1984)
Yunnanosaurus huangi, NGMJ V116 [V20]

corner; pmf, proximomedial flange; pop, postacetabular process; ppl, proximal pubic plate; ppr, parapophyseal ridge; pup, pubic peduncle; pvh, proximoventral heel; rfo, radial fossa; rp, rounded proximal surface of humerus; sac, supracetabular crest; scb, scapular blade; stm, steep distal margin of 4th trochanter; tub, flexor tubercle; uap, anterior process of ulnar proximal end; umc, medial concavity on ulnar proximal end; vk, ventral keel of ischial shaft; vme, ventromedial edge of asymmetrical ungual.

SYSTEMATIC PALAEOLOGY

SAURISCHIA Seeley, 1887

SAUROPODOMORPHA von Huene, 1932

Genus LESSEMSAURUS Bonaparte, 1999

Type species. *Lessemsaurus sauropoides* Bonaparte, 1999

Diagnosis. As for type and only species.

Lessemsaurus sauropoides Bonaparte, 1999

Text-figures 1–13

1986 unnamed advanced prosauropod Bonaparte, p. 248, fig. 19.1–2.

1999 *Lessemsaurus sauropoides* Bonaparte, p. 133.

2000 *Lessemsaurus*; Buffet *et al.*, p. 73.

2003 *Lessemsaurus sauropoides*; Yates and Kitching, p. 1753.

2004 *Lessemsaurus sauropoides*; Galton and Upchurch, p. 234, fig. 12.6F–I.

2005 *Lessemsaurus*; Wilson, p. 403.

Holotype. PVL 4822–1. Bonaparte (1999) described and figured eight presacral neural arches. He mentioned additional presacral vertebrae and some appendicular elements as probably associated with this specimen. Owing to the lack of articulated remains, it cannot be determined which of the PVL 4822 elements belong to the same individual. Therefore, the holotype is now restricted to the eight presacral neural arches originally described and figured by Bonaparte (1999) and catalogued as PVL 4822–1. These eight neural arches are individually identified by the collection numbers (PVL 4822-1/1–4822-1/7 and PVL 4822-1/10).

Referred material. The rest of the elements in the assemblage originally catalogued as PVL 4822 have been given additional numbers to allow identification of each individual element (PVL 4822/8–4822/9 and 4822/11–4822/79). These elements include dorsal and sacral vertebrae, scapulae, coracoid, humerus, ulna and radius, metacarpals I and II, manual digit I, ilium, ischium, pubes, femur, tibia fragmentary metacarpals and pedal phalanges. All of these remains were found closely associated with each other by Bonaparte and others during the Lillo Palaeontologic Expedition of 1971. Bonaparte (1999) interpreted these remains as belonging to three different individuals.

Locality and horizon. La Esquina (8 km west of Provincial Road 26, at the 142 km mark), La Rioja Province, Argentina. Upper section of the Los Colorados Formation (Groeber and Stipanovic 1953). The age of this unit has been considered as Norian–Rhaetian (Bonaparte 1972) or the tetrapod-based biochron late Coloradoan (Bonaparte 1973). The horizon where these remains were found is located approximately 150 m below the upper limit of this unit (Bonaparte 1999).

Revised diagnosis. A large non-eusauropod sauropodomorph with the following unique combination of characters (autapomorphies indicated with an asterisk): dorsal and middle to posterior cervicals with high neural arches; strong neural arch constriction below the postzygapophyses; deep postspinal fossa; dorsoventrally high infrapostzygapophyseal depression; middle and posterior dorsals with neural spines higher than long (with a height/length ratio of 1.5–2.0); robust scapula, with its blade markedly expanded; metacarpal I extremely short, with a proximal end lateromedially wider than metacarpal length; acute lateral process on proximolateral corner of metacarpal II*; pubic peduncle of ilium with a medial flange, forming a narrow and marginal medial wall of the acetabulum*; brevis crest extending from the base of the ischial peduncle to the posterior tip of the postacetabular process*; and cross-section of the distal tibia subrectangular with its major axis orientated lateromedially and being twice as long as its anteroposterior extension.

DESCRIPTION

The neural arches that compose the holotype of *Lessem-saurus sauropoides* (PVL 4822–1) were described in detail by Bonaparte (1999) and will not be described further herein. Instead, we focus on the undescribed material, including the additional vertebral remains, the shoulder girdle, forelimb, pelvis and hindlimb.

Vertebral column

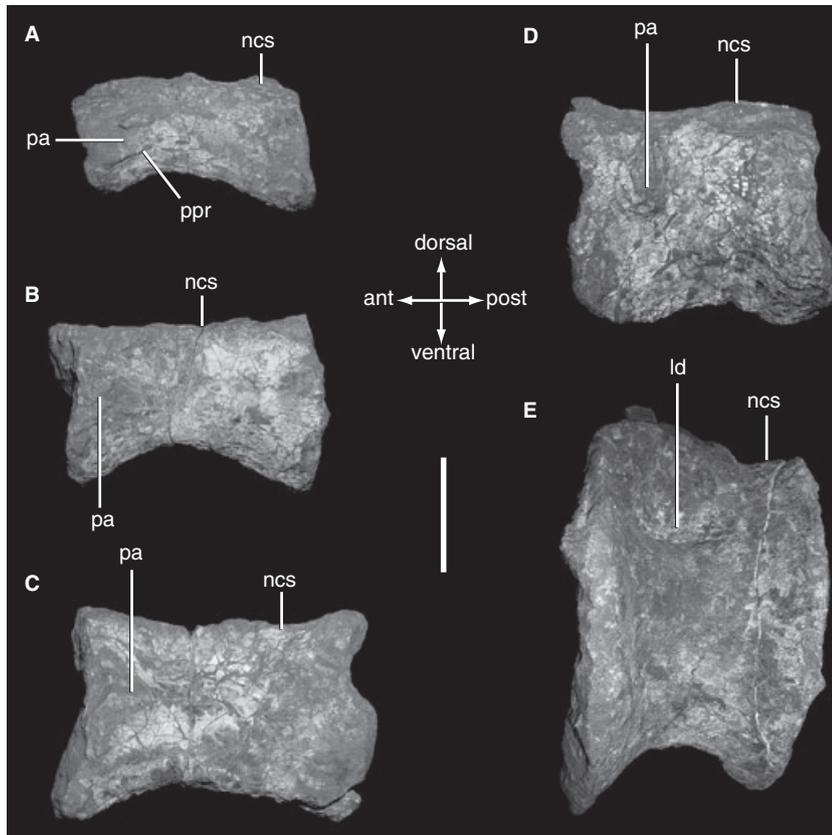
Cervical vertebrae. PVL 4822 includes three cervical vertebral centra (PVL 4822/20–4822/22; Text-fig. 1). The element 4822/20 is the most anterior centrum and probably belongs to a middle cervical. The anterior articular surface is dorsoventrally shorter than the posterior end of the centrum, the former being approximately 0.78 times as high as the latter (Text-fig. 1A). The anteroposterior length of the middle cervical centrum of *Lessem-saurus sauropoides* is approximately twice the dorsoventral height of its posterior articular surface and 2.27 times the height of its anterior articular surface. The middle cervicals of some non-eusauropod sauropodomorphs have similar proportions (e.g. *Rioja-saurus incertus*, ULR 56; *Kotasaurus yamanpalliensis*). However, most non-eusauropod sauropodomorphs [e.g. *Massospondylus*

carinatus, BPL/1/5241; *Coloradisaurus brevis*, PVL 3967; *Lufengosaurus huenei* (Young 1941); *Yunnanosaurus huangi* (Young 1942); *Plateosaurus engelhardti*, MB skelett 25] and derived sauropods have middle cervical vertebrae proportionately longer than those of *Lessem-saurus sauropoides*. The centrum is acamerate (*sensu* Wedel 2003) and amphicoelous, as in all non-eusauropod sauropodomorphs. The lateral surface of the centrum is only slightly concave and bears an elongated crest-like parapophysis close to its anterior edge (Text-fig. 1). The vertebral centrum PVL 4822/20 is notably constricted lateromedially with respect to its anterior and posterior ends and is approximately half the width of the articular surfaces. The ventral surface of this centrum is rounded and lacks the sagittal crest present in several non-eusauropod sauropodomorphs (e.g. *Massospondylus carinatus*, SAM-PK-K391; *Anchisaurus polyzelus*). A flat ventral surface is present in other non-eusauropod sauropodomorphs, however (e.g. *Plateosaurus engelhardti*, MB skelett 25; *Thecodontosaurus caducus*).

The centrum PVL 4822/21 probably belongs to a posterior cervical vertebra. In contrast to the middle cervical (PVL 4822/20), the anterior and posterior articular facets of this element are sub-equal in dorsoventral height (Text-fig. 1B). As in the middle cervical, this centrum is acamerate (*sensu* Wedel 2003) and amphicoelous. The lateral surface of the centrum is slightly more concave in this vertebra and the parapophysis is similarly located at the anterior edge of the centrum. The parapophysis of PVL 4822/21 is subcircular in shape, rather than an elongated crest. The lateromedial constriction between the anterior and posterior ends is extremely marked in this vertebra, with its width approximately 0.4 times that of the articular surfaces. As with the middle cervical, the ventral surface of this centrum lacks a sagittal crest.

The centrum PVL 4822/22 is either the last cervical or the first dorsal, based on its proportions, degree of lateromedial constriction and position of the parapophysis on the centrum. As in PVL 4822/21, the centrum is acamerate and amphicoelous, and its anterior and posterior articular facets are sub-equal in dorsoventral height (Text-fig. 1C). The parapophysis is located slightly more dorsally than in the preceding elements and is subtriangular in lateral view. The lateromedial constriction at centrum mid-length is even more developed than in the preceding vertebrae, its width being approximately 0.3 times the breadth of the anterior articular surface. In contrast to the rounded ventral surface of the preceding elements, the ventral surface of PVL 4822/22 has a sharp edge. This morphology is also present in several taxa that lack a sagittal crest in the anterior and middle cervical vertebrae (e.g. *Plateosaurus engelhardti*, MB skelett 25). Both articular surfaces are dorsoventrally deeper than lateromedially wide, in contrast to the subcircular shape seen in most other non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, MB skelett 25; *Riojasaurus incertus*, PVL 3844; *Lufengosaurus huenei*). In ventral view, the anterior articular surface is more lateromedially expanded than the posterior one, mainly because of the lateral projection of the cranially located parapophyses.

Dorsal vertebrae. Bonaparte (1999) described five dorsal neural arches belonging to PVL 4822–1. The material catalogued as



TEXT-FIG. 1. Cervicodorsal vertebral centra of *Lessemsaurus sauropoides* in lateral view. A, middle cervical PVL 4822/20. B, posterior cervical PVL 4822/21. C, posterior cervical-anterior dorsal PVL 4822/22. D, anterior dorsal PVL 4822/23. E, posterior dorsal PVL 4822/24. Scale bar represents 5 cm.

PVL 4822 also includes several dorsal centra (PVL 4822/23–4822/25). The centrum PVL 4822/23 probably belongs to the first or second dorsal vertebra (Text-fig. 1D). The height of the anterior articular surface is sub-equal to that of the posterior articular surface. However, in contrast to the cervical centra, the anterior articular surface is lateromedially narrower than the posterior articular surface. The anteroposterior length of PVL 4822/23 is only slightly greater than the dorsoventral height of its articular surfaces. The anterior dorsals of most non-eusauropod sauropodomorphs are proportionately longer than those of *Lessemsaurus sauropoides* (e.g. *Plateosaurus engelhardti*, MB skelett 25; *Massospondylus carinatus*, SAM-PK-K391). Other sauropodomorphs, however, have proportionately short and high centra, as in *Lessemsaurus sauropoides* (e.g. *Riojasaurus incertus*; *Kotasaurus yamanpalliensis*; *Patagosaurus fariasi*). The lateral surface of the centrum is concave and the centrum is acamerate and amphicoelous. The parapophysis is dorsoventrally taller than it is long anteroposteriorly and is located close to the dorsal corner of the vertebral centrum, but more posteriorly than in the preceding elements. Vertebral centrum PVL 4822/23 is notably constricted lateromedially, but its narrowest point is located on the anterior third of the vertebra, rather than at centrum mid-length, as in the cervical vertebrae. At this point, the vertebral centrum is approximately 0.5 times as wide as the anterior articular surface. As in PVL 4822/22, a sharp crest forms the ventral surface of the centrum.

The isolated dorsal centrum PVL 4822/24 and the three articulated centra PVL 4822/25 probably belong to posterior and middle dorsal vertebrae, respectively. These vertebral centra are more symmetrical than the anterior dorsals, with an anterior articular surface that is equal in depth and width to the posterior articular surface. The centra become less constricted lateromedially towards the posterior part of the dorsal series. This constriction is located at their midpoint, as in most non-eusauropod sauropodomorphs. The ventral surfaces of the centra are rounded and lack the sharp ventral edge seen in the centra around the cervicodorsal transition (except for some vertebrae that have a sharper ventral edge that may have resulted from post-mortem lateromedial crushing; PVL 4822/24). The lateral surfaces of the centra bear a central depression. This depression is deep and well delimited by sharp ridges on PVL 4822/24 (Text-fig. 1E).

Sacral vertebrae. Only two fragmentary sacral vertebrae are present in PVL 4822. These probably belong to the first and second primordial sacrals. Their centra are remarkably large and robust, with articular surfaces 108 mm wide. These vertebrae probably belong to an individual different from that pertaining to the majority of the cervicodorsal vertebrae (PVL 4822-1/1–25) owing to their significant size difference. The ventral surface is rather flattened and the lateral surface bears a notably deep small depression. Unfortunately, the transverse processes and sacral ribs are not preserved.

Pectoral girdle

Scapula. Two scapulae are included in PVL 4822: a left (PVL 4822/50) and a right (4822/51) element. These elements probably belong to different individuals as the left scapula is significantly smaller than the right and its dorsoventral extension is approximately 85 per cent of that of the right element. The small scapula (PVL 4822/50) probably belongs to the same individual as the cervicodorsal series (or a similarly-sized specimen).

The scapula of *Lessemsaurus sauropoides* is remarkably different from that of non-eusauropod sauropodomorphs. The following description is based on a vertical orientation of the scapula (Text-fig. 2). This element is strongly expanded ventrally and dorsally (Text-fig. 2). The dorsal end is approximately 0.59 times the dorsoventral extension of the scapular in the small element (PVL 4822/50), while this ratio is 0.54 in the larger left scapula (PVL 4822/51). The ventral expansion is only slightly smaller, its anteroposterior extension being approximately 0.52 times the dorsoventral length of the scapula (PVL 4822/51). PVL 4822/50 has an incomplete ventral end and cannot be precisely measured. Most non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, AMNH 6810; *Massospondylus carinatus*, BPI/1/5241; *Yunnanosaurus huangi*; *Riojasaurus incertus*, PVL 3663; *Isanosaurus attavipachi* (Buffetaut *et al.* 2000)). However, a few sauropodomorphs have a broadened scapular shaft, similar to that of *Lessemsaurus sauropoides* (*Melanorosaurus readi*; *Antetonitrus ingenipes*) and probably *Vulcanodon karibaensis*, as noted previously (Gauthier 1986; Yates and Kitching 2003). The scapula shaft of *Lessemsaurus sauropoides*, however, is notably restricted in its dorsoventral extent (Text-fig. 2), a character shared exclusively with *Antetonitrus ingenipes*. Due to its short extension and the broad ventral and dorsal ends, the anterior and posterior edges of the scapula shaft are markedly concave.

The dorsal blade of *Lessemsaurus sauropoides* is thin, laminar and has a convex dorsal margin. The posterodorsal corner of the scapula extends posteriorly as an acute process, exceeding the level of the caudal margin of the ventral expansion. The anterodorsal corner is less developed, not as acute, and is level with the anteroventral margin of the scapula.

The ventral end of the scapula of *Lessemsaurus sauropoides* expands anteriorly because of the acromion process, which is as reduced in the anteroposterior dimension as in most non-eusauropod sauropodomorphs. This condition contrasts with the markedly enlarged acromion process of derived sauropodomorphs (e.g. Neosauropoda; Wilson and Sereno 1998). The acromion process of *Lessemsaurus sauropoides* forms an angle of approximately 40 degrees with the dorsoventral axis of the scapula shaft (Text-fig. 2). This angle lies among those seen in non-eusauropod sauropodomorphs, which range between 40 and 50 degrees (e.g. *Riojasaurus incertus*, PVL 3663; *Plateosaurus engelhardti*, AMNH 6810; *Melanorosaurus readi*; *Antetonitrus ingenipes*). Other non-eusauropod sauropodomorphs (e.g. *Saturnalia tupiniquim*, *Coloradisaurus brevis*, *Lufengosaurus huenei*, *Massospondylus carinatus*) have angles varying between 65–80 degrees. This condition is also present in eusauropods (Yates and Kitching 2003). The ventral margin of the scapula has not been perfectly preserved in either of the scapulae referred to *Lessemsaurus sauropoides*. The lateral surface of the ventral expansion of the scapula, between the acromion process and the glenoid surface, is markedly concave, as in most sauropodomorphs. The glenoid region occupies the posterior half of the ventral expansion and is much thicker lateromedially than the rest of the scapula. The

scapula forms the dorsal half of the articular glenoid facet, which faces posteroventrally.

The scapular shaft is notably broad in comparison with other sauropodomorphs. The minimum anteroposterior width of the scapulae of *Lessemsaurus sauropoides* is approximately 0.24 times its dorsoventral extension (PVL 4822/51). In the smaller specimen (PVL 4822/50) this ratio is even larger (0.29). Most sauropodomorphs have narrower scapular shafts with ratios varying between 0.15–0.17 [e.g. *Saturnalia tupiniquim*; *Plateosaurus engelhardti*, AMNH 6810; *Massospondylus carinatus*, BPI/1/5241; *Yunnanosaurus huangi*; *Riojasaurus incertus*, PVL 3663; *Isanosaurus attavipachi* (Buffetaut *et al.* 2000)]. However, a few sauropodomorphs have a broadened scapular shaft, similar to that of *Lessemsaurus sauropoides* (*Melanorosaurus readi*; *Antetonitrus ingenipes*) and probably *Vulcanodon karibaensis*, as noted previously (Gauthier 1986; Yates and Kitching 2003). The scapula shaft of *Lessemsaurus sauropoides*, however, is notably restricted in its dorsoventral extent (Text-fig. 2), a character shared exclusively with *Antetonitrus ingenipes*. Due to its short extension and the broad ventral and dorsal ends, the anterior and posterior edges of the scapula shaft are markedly concave.

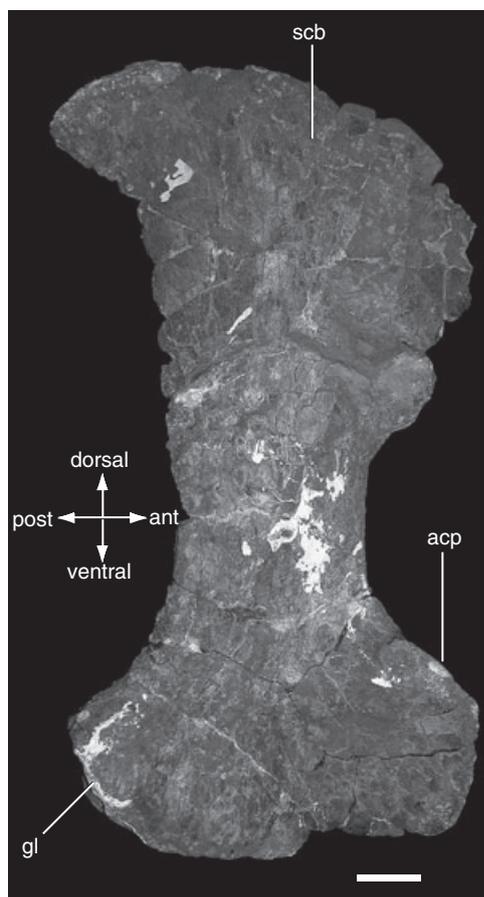
The dorsal blade of *Lessemsaurus sauropoides* is thin, laminar and has a convex dorsal margin. The posterodorsal corner of the scapula extends posteriorly as an acute process, exceeding the level of the caudal margin of the ventral expansion. The anterodorsal corner is less developed, not as acute, and is level with the anteroventral margin of the scapula.

Coracoid. Only one incomplete coracoid is preserved (PVL 4822/52). Although, the distal end of the posteroventral process is missing, the coracoid of *Lessemsaurus sauropoides* is rather small and subcircular in lateral view (as preserved), as in all other sauropodomorphs. The glenoid region is lateromedially thicker than the preserved region of the posteroventral process of the coracoid. Unfortunately, the coracoid tubercle has not been preserved, and therefore it cannot be determined if this tubercle was markedly reduced or lost as in derived sauropodomorphs (Wilson and Sereno 1998).

Forelimb

An almost complete forelimb is included in PVL 4822. These elements may belong to the smaller specimen, although the lack of comparative material precludes corroboration of this hypothesis.

Humerus. The humerus of *Lessemsaurus sauropoides* (PVL 4822/53) is particularly interesting owing to the unique combination of character states present. This element has symmetrically expanded proximal and distal ends separated by a short and narrow shaft, giving the element an hourglass shape in anterior and posterior views (Text-fig. 3). The proximal end of the humerus of *Lessemsaurus sauropoides* differs from that of non-eusauropod sauropodomorphs. The relative width of the proximal expansion with respect to humeral length is 0.4; similar to that of most non-eusauropod sauropodomorphs except for a few taxa with highly expanded proximal humeri



TEXT-FIG. 2. Right scapula of *Lessemsaurus sauropoides* PVL 4822/51 in lateral view. Scale bar represents 5 cm.

(e.g. *Massospondylus carinatus*, *Yunnanosaurus huangi*, *Coloradisaurus brevis*). The proximal surface of the humerus of *Lessemsaurus sauropoides* is markedly convex, with a moderately well-developed rounded articular head. A similar condition is also present in *Melanorosaurus readi*, *Antetonitrus ingenipes*, *Kotasaurus yamanpalliensis* and basal eusauropods (e.g. *Ferganasaurus verzilini*). In contrast, other non-eusauropod sauropodomorphs have a straight and transversely orientated proximal edge of the humerus (e.g. *Saturnalia tupiniquim*; *Plateosaurus engelhardti*, MB skelett 25; *Riojasaurus incertus*; *Yunnanosaurus huangi*). The medial region of the proximal end of the humerus bears a poorly developed internal tuberosity (Text-fig. 3). In contrast, some non-eusauropod sauropodomorphs have an extremely enlarged internal tuberosity (e.g. *Massospondylus carinatus*, *Coloradisaurus brevis*, *Lufengosaurus huenei*, *Yunnanosaurus huangi*). A less-developed internal tuberosity is a generalized feature among sauropodomorphs (e.g. *Saturnalia tupiniquim*; *Plateosaurus engelhardti*, MB skelett 25; *Melanorosaurus readi*; eusauropods).

The deltopectoral crest rises gradually from the rounded proximolateral corner of the humerus (Text-fig. 3A). This crest occupies 40 per cent of the length of the humerus. This proportion is slightly lower than that in most non-eusauropod sauropodomorphs, which have deltopectoral crests occupying 45–55

per cent of their humeral lengths (e.g. *Massospondylus carinatus*; *Lufengosaurus huenei*; *Plateosaurus engelhardti*, MB skelett 25; *Coloradisaurus brevis*; *Riojasaurus incertus*). The most basal sauropodomorph (i.e. *Saturnalia tupiniquim*), *Vulcanodon karibaensis*, *Kotasaurus yamanpalliensis*, and neosauropods have similarly reduced deltopectoral crests.

The deltopectoral crest is low, contrasting with the condition of most non-eusauropod sauropodomorphs in which this crest is remarkably high and sharp-edged. The condition of *Lessemsaurus sauropoides* is slightly less developed than in *Melanorosaurus readi* (SAM-PK-K3450) and *Antetonitrus ingenipes*. However, the deltopectoral crests of these taxa (including *Lessemsaurus sauropoides*) are not as low and reduced as those of eusauropod taxa (e.g. *Tehuelchesaurus benitezi*, *Ferganasaurus verzilini*), in which the crest is an extremely low ridge. In lateral view, the profile of the deltopectoral crest of *Lessemsaurus sauropoides* and *Antetonitrus ingenipes* is rounded and anteriorly convex. In contrast, other non-eusauropod sauropodomorphs have a subrectangular profile with a straight and vertically orientated anterior margin. In anterior view, the deltopectoral crest of *Lessemsaurus sauropoides* is slightly sinuous, being directed mediolaterally along its proximal half and laterodistally along its distal half (Text-fig. 3A). The condition seen in *Lessemsaurus sauropoides*, however, is not as marked as in other sauropodomorph taxa (e.g. *Riojasaurus incertus*, *Coloradisaurus brevis*, *Lufengosaurus huenei*). The deltopectoral crest of *Lessemsaurus sauropoides* lacks the proximodistal sulcus located lateral to the crest in other non-eusauropod sauropodomorphs (e.g. *Massospondylus carinatus*, *Lufengosaurus huenei*).

The humeral shaft is remarkably short, occupying less than 20 per cent of the total length of the humerus (Text-fig. 3). The shaft has a circular cross-section. The distal end of the humerus is lateromedially wide and anteroposteriorly narrow. The width of the distal expansion is approximately 0.43 times the total length of the humerus. This ratio indicates a notably enlarged ventral expansion, similar to those of a few other non-eusauropod sauropodomorphs (e.g. *Yunnanosaurus huangi*, *Coloradisaurus brevis*). Most other sauropodomorph humeri have less expanded ventral ends, with their width/length ratios varying between 0.30 and 0.36 [e.g. *Saturnalia tupiniquim*; *Plateosaurus engelhardti*, MB skelett 25; *Melanorosaurus readi* (Galton *et al.* 2005); *Kotasaurus yamanpalliensis*; *Tehuelchesaurus benitezi*; *Ferganasaurus verzilini*]. The anterior surface of the distal end has a deep fossa that broadens distally (Text-fig. 3A). This fossa is deep, as in some non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, MB skelett 25; *Massospondylus carinatus*, SAM-PK-K391), although it is not circular in outline and not sharply delimited.

Because of the diversity of sizes and the lack of clear association among the assemblage of elements catalogued as PVL 4822, the relative length of the hindlimb and forelimb elements cannot be determined for *Lessemsaurus sauropoides*. However, all of the humeral remains are notably long in comparison with the known femora.

Ulna. If the only known ulna (PVL 4822/54) belongs to the same individual as the humerus PVL 4822/53, the ulna would be approximately 0.58 times the length of the humerus (Text-

TEXT-FIG. 3. Right humerus of *Lessemsaurus sauropoides* PVL 4822/53. A, anterior view. B, posterior view. Scale bar represents 5 cm.

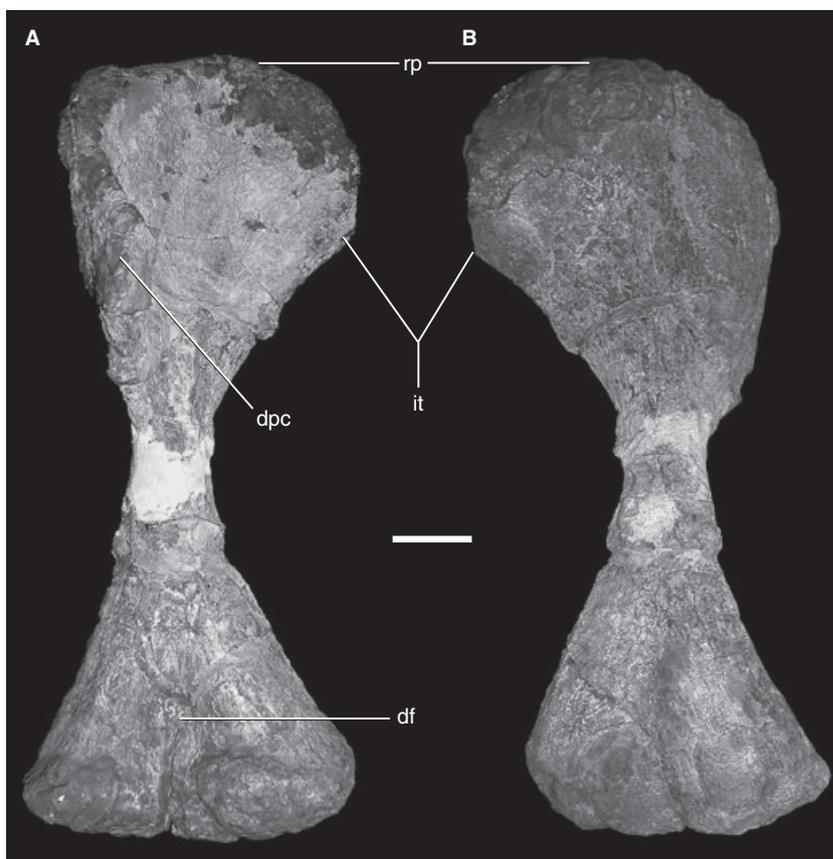
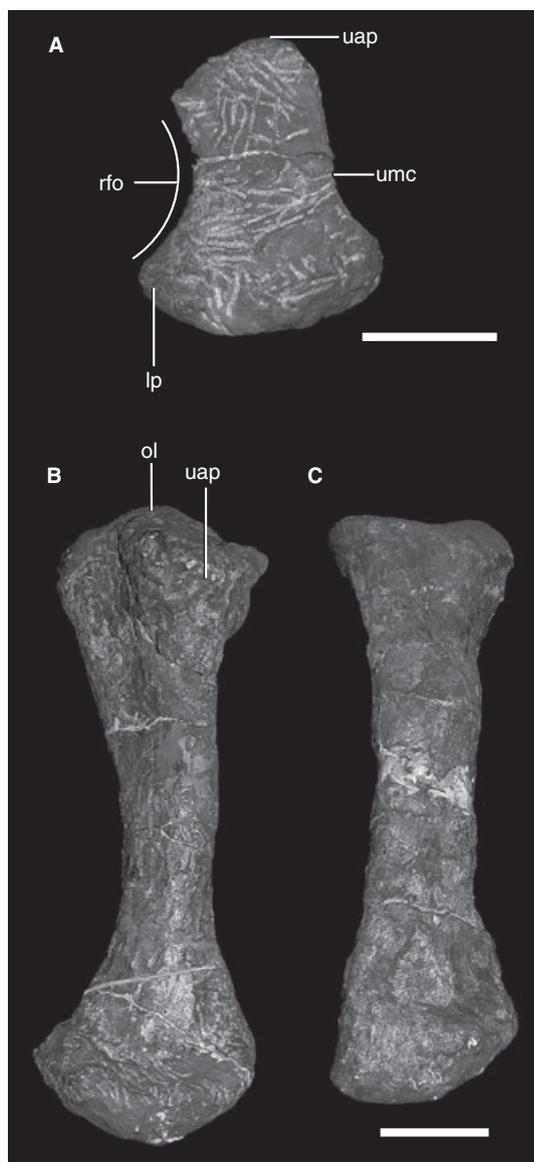


fig. 4). This ratio is similar to the condition in most non-eusauropod sauropodomorphs, with the exception of *Yunnanosaurus huangi* and *Massospondylus carinatus*, which have proportionately longer ulnae. The ulna is expanded lateromedially both proximally and distally (Text-fig. 4B). The lateromedial width of these expansions is approximately 0.35 times the length of the ulna, a proportion similar to that seen in *Yunnanosaurus huangi*, *Lufengosaurus huenei* and *Melanorosaurus readi* (SAM-PK-K3449). This metric is proportionately larger than that of *Antetonitrus ingenipes* and *Vulcanodon karibaensis*. The ulnar shaft, however, is not as lateromedially narrow as in non-eusauropod sauropodomorphs (e.g. *Yunnanosaurus huangi*, *Lufengosaurus huenei*, *Plateosaurus engelhardti*). The anteroposterior extension of the ulna shaft decreases gradually towards the distal end, where the ulna becomes anteroposteriorly flattened and lateromedially wide.

The proximal end of the ulna is expanded both lateromedially and anteroposteriorly (Text-fig. 4A). Thus, in proximal view the ulna is triradiate, as in most non-eusauropod sauropodomorphs. The anterior process of the proximal end is high and lateromedially broad, being slightly deflected laterally. This process delimits a relatively large radial fossa. In *Lessemsaurus sauropoides* this fossa is more concave than in most non-eusauropod sauropodomorphs. Some sauropodomorph taxa, however, have a similar degree of development (e.g. *Antetonitrus ingenipes*, *Yunnanosaurus huangi*). *Melanorosaurus readi* (Bonnar and Yates 2007), *Vulcanodon karibaensis*, and more derived sauropodomorphs have an even more strongly developed radial fossa (Wil-

son and Sereno 1998; Bonnar 2003; Yates and Kitching 2003). Ventrolateral to the radial fossa, the ulna of *Lessemsaurus sauropoides* has an incipiently developed lateral process that would articulate with the posterior edge of the proximal end of the radius (homologous to the 'anterolateral' process *sensu* Bonnar 2003). The posterior margin of the proximal end of the ulna of *Lessemsaurus sauropoides* is flat and extensive. The lateromedial length of this edge is approximately 0.85 times the anteroposterior length of the proximal articular surface of the ulna. The medial margin of the proximal ulna is also concave (Text-fig. 4A), although less so than the lateral edge (i.e. the radial fossa). This condition contrasts with that of most sauropodomorphs (e.g. *Yunnanosaurus huangi*, *Plateosaurus engelhardti*, *Vulcanodon karibaensis*, *Ferganasaurus verzilini*, *Tehuelchesaurus benitezi*), but is present in some of the ulnar material of *Antetonitrus ingenipes* and *Melanorosaurus readi* (SAM-PK-K3449 and NM QR 3314). The proximal end of the ulna has a poorly developed olecranon process, resembling the condition in eusauropods. The distal end of the ulna of *Lessemsaurus sauropoides* is markedly expanded lateromedially but flattened anteroposteriorly (Text-fig. 4C). The distal articular surface is subovoid in shape.

Radius. The only radius (PVL 4822/55) was probably associated with the ulna (PVL 4822/54). It is a stout and robust element (Text-fig. 4C) in comparison with most non-eusauropod sauropodomorphs. The proximal end is lateromedially narrow and anteroposteriorly elongated, as in most non-eusauropod



TEXT-FIG. 4. Left radius-ulna of *Lessemsaurus sauropoides*. A, ulna PVL 4822/54 in proximal view. B, ulna PVL 4822/54 in anterior view. C, radius PVL 4822/55 in lateral view. Scale bars represent 5 cm.

sauropodomorphs (including forms such as *Antetonitrus ingenipes*). Derived sauropodomorphs have a much broader proximal end of the radius, which is subtriangular in some taxa (e.g. *Camarasaurus*).

The shaft of the radius is ovoid in cross-section, with the major axis orientated anteroposteriorly. Thus, in lateral view, the shaft of the radius is poorly constricted with respect to the proximal and distal ends. This morphology contrasts with the slender, elongated, and rod-like shape of the radial shaft in most non-eusauropod sauropodomorphs (e.g. *Thecodontosaurus antiquus*, *Plateosaurus engelhardti*, *Lufengosaurus huenei*, *Riojasaurus incertus*). Some sauropodomorphs, however, have similar proportions to *Lessemsaurus sauropoides* [e.g. *Antetonitrus ingenipes*,

Jingshanosaurus xinwaensis (Zhang and Yang 1994)]. Interestingly, *Vulcanodon karibaensis* and eusauropods also have the radial shaft poorly constricted and subovoid in cross-section (e.g. *Ferganasaurus verzilini*, *Camarasaurus*). The distal end of the radius of *Lessemsaurus sauropoides* is slightly flattened lateromedially and moderately expanded anteroposteriorly (Text-fig. 4C), as in all basal saurischians. In contrast, neosauropods have a broad posterior surface that articulates with the ulna.

Manus. The manus of *Lessemsaurus sauropoides* is poorly represented in PVL 4822 and is restricted to a left metacarpal I (PVL 4822/56), a right metacarpal II (PVL 4822/57), a left phalanx I.1 (PVL 4822/58) and a left ungual of digit I (PVL 4822/59). Despite the fragmentary nature of the known remains, the manus is particularly interesting owing to its unique combination of plesiomorphic and apomorphic character states.

Although the first metacarpal is not articulated with a second metacarpal, its proximal end would probably have been proximally inset into the carpus, as in all non-eusauropod sauropodomorphs (Serenio 1999). This inference is based on the presence of a flat articular surface on the proximolateral corner of metacarpal I (Text-fig. 5A), which abuts the medial surface of distal carpal II in non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*; *Riojasaurus incertus*, PVL 3662).

The first metacarpal bears many of the unique characters present in non-eusauropod sauropodomorphs, although it is remarkably broad lateromedially and short proximodistally (Text-fig. 5A). The lateromedial width of the proximal end is approximately 1.18 times the maximum proximodistal length of metacarpal I (i.e. the distance between the proximolateral end and the distal lateral condyle). A similarly short and broad metacarpal I is also present in *Antetonitrus ingenipes* and a specimen referred to *Melanorosaurus readi* (NM QR 3314; Galton *et al.* 2005). A few non-eusauropod sauropodomorphs have a slightly more elongate metacarpal I, which is sub-equal in breadth and length (e.g. *Massospondylus carinatus*, *Lufengosaurus huenei*, *Yunnanosaurus huangi*). Most non-eusauropod sauropodomorphs, however, have significantly more gracile first metacarpals, with a maximum width to maximum length ratio ranging between 0.60 and 0.76 (e.g. *Thecodontosaurus antiquus*; *Plateosaurus engelhardti*; *Riojasaurus incertus*, PVL 3662; *Anchisaurus polyzelus*). Derived sauropods also have elongated first metacarpals, which are sub-equal in length to all other metacarpals. In this derived condition, metacarpal I is part of the characteristic semi-tubular arrangement of the sauropod manus, which is interpreted as being mechanically advantageous for graviportal locomotion, as shearing and tensile forces would be reduced and redistributed (Bonnar 2003). This condition has been considered to be a synapomorphy of either Neosauropoda (Wilson and Sereno 1998) or Eusauropoda (Upchurch 1998; Bonnar 2003). However, the outgroup condition for these clades is unknown [e.g. *Barapasaurus tagorei* (Jain *et al.* 1975); *Kotasaurus yamanpalliensis*; *Vulcanodon karibaensis*].

In proximal view, metacarpal I is subtriangular, as in all non-eusauropod sauropodomorphs. The lateral surface of the proximal end is flat and extensive. The medial end is much shallower, forming the tip of the triangular proximal surface. Because of the reduced proximodistal extension of metacarpal I, the shaft is extremely short and lateromedially wide.

The distal articular condyles of metacarpal I are highly asymmetrical (Text-fig. 5A), as in all non-eusauropod sauropodomorphs. The lateral and medial condyles are large and have articular surfaces that extend along an angle of approximately 180 degrees (Text-fig. 5). The distal end of the lateral condyle only slightly exceeds that of its medial counterpart. The lateral condyle is lateromedially narrow and much higher than the medial condyle. This condition is also present in *Antetonitrus ingenipes*, but contrasts with the condition of other non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*). Some derived neosauropods (e.g. *Shunosaurus*, *Brachiosaurus* and titanosauriforms) also lack this strong asymmetry (Wilson 2002). However, basal eusauropods have an asymmetrical distal end of metacarpal I (e.g. *Ferganasaurus verzilini*). The medial condyle is rather low, being approximately half of the lateral condyle's depth. Its lateromedial width is approximately twice the breadth of the lateral condyle. The ventral excursion of the articular surface of the medial distal condyle is larger than its dorsal counterpart. Thus, the entire articular surface is orientated ventrodistally rather than distally (the axis that joins the dorsal and ventral ends of the articular surface forms an angle of 50 degrees with the proximodistal axis of metacarpal I). The lateral surface of the medial condyle of metacarpal I bears a moderately well-developed ligament pit.

The second metacarpal (PVL 4822/57) is also a short and broad element (Text-fig. 5C). This metacarpal is much longer than metacarpal I, with its maximum proximodistal length approximately 1.78 times the length of the first metacarpal (PVL 4822/56). If these two elements belong to the same individual (or at least to specimens of similar size), their relative lengths would be remarkably dissimilar, a unique condition for *Lessemsaurus sauropoides*. All non-eusauropod sauropodomorphs have a metacarpal II that is only slightly longer than metacarpal I, with metacarpal II : metacarpal I length ratios varying between 1.2 and 1.4 (e.g. *Thecodontosaurus antiquus*; *Anchisaurus polyzelus*; *Plateosaurus engelhardti*; *Riojasaurus incertus*, PVL 3662; *Massospondylus carinatus*; *Lufengosaurus huenei*; *Yunnanosaurus huangi*; *Antetonitrus ingenipes*). Derived sauropodomorphs (e.g. eusauropods) have a relatively longer metacarpal I than basal forms.

The proximal end of metacarpal II is rather flattened and lateromedially broad (Text-fig. 5C). The dorsal surface bears a low crest that extends proximodistally along the proximal half of metacarpal II, being slightly displaced medially as in most non-eusauropod sauropodomorphs (e.g. *Massospondylus carinatus*; *Plateosaurus engelhardti*; *Riojasaurus incertus*, PVL 3662). The medial margin of the proximal end of metacarpal II is not perfectly preserved, making it impossible to determine the presence of the flat surface that abuts the proximolateral end of metacarpal I in some non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, *Massospondylus carinatus*, *Antetonitrus ingenipes*). The proximolateral corner of the second metacarpal of *Lessemsaurus sauropoides* has a short and acute process extending laterally. This process is either absent or only incipiently present in other sauropodomorphs (Text-fig. 5C).

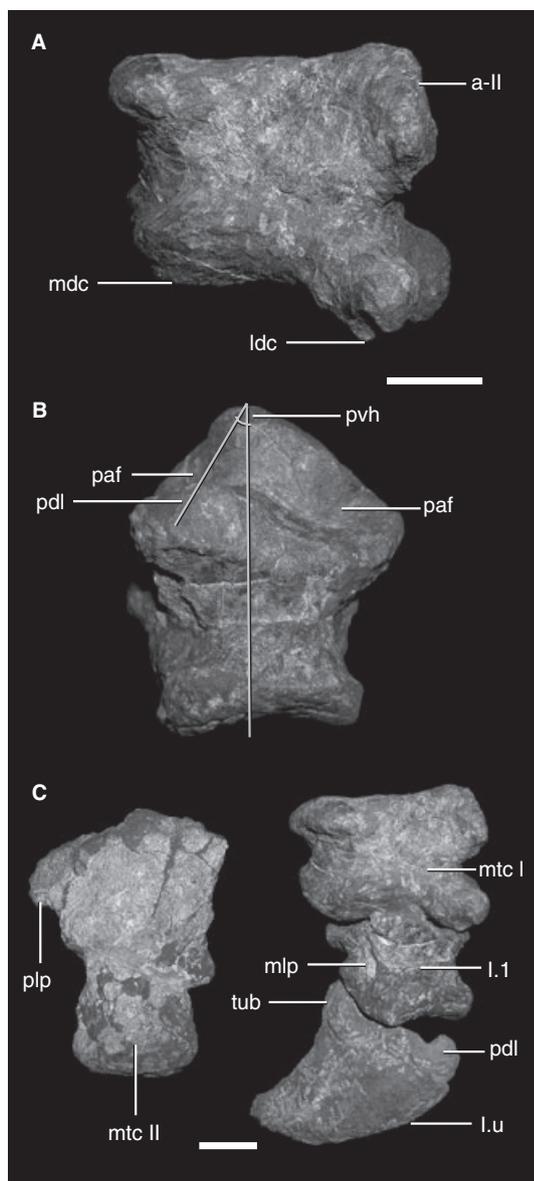
The shaft of metacarpal II is poorly constricted, dorsoventrally flattened, and extremely short proximodistally. The narrowest

point is located distal to the metacarpal mid-length. The sub-ovoid distal end is poorly preserved. Despite the poor preservation, it seems to lack both well-developed condyles and an intercondylar groove.

Remains of digit I include the first phalanx of manual digit I (PVL 4822/58), which was probably associated with the first metacarpal (PVL 4822/56). This element has the characteristic torsion along the proximodistal axis that is present in all non-eusauropod sauropodomorphs. In *Lessemsaurus sauropoides*, the torsion of phalanx I.1 is approximately 29 degrees (Text-fig. 5B). This relatively low degree of torsion is similar to that of most non-eusauropod sauropodomorphs (e.g. *Thecodontosaurus antiquus*; *Plateosaurus engelhardti*; *Riojasaurus incertus*, PVL 3362). This condition contrasts with the highly twisted phalanx I.1 of a few non-eusauropod sauropodomorphs, in which the torsion is approximately 45 degrees (e.g. *Massospondylus carinatus*, *Yunnanosaurus huangi*, *Lufengosaurus huenei*), as well as with the lack of torsion in derived sauropodomorphs (e.g. eusauropods).

Manual phalanx I.1 of *Lessemsaurus sauropoides* is remarkably short and broad, being slightly wider at its proximal end than proximodistally long (Text-fig. 5B). This character is also present in *Antetonitrus ingenipes*. All other non-eusauropod sauropodomorphs have either a subquadrangular phalanx I.1 (e.g. *Massospondylus carinatus*, *Lufengosaurus huenei*, *Yunnanosaurus huangi*), or a phalanx I.1 that is longer than wide (e.g. *Thecodontosaurus antiquus*; *Anchisaurus polyzelus*; *Efraasia minor*; *Plateosaurus engelhardti*; *Riojasaurus incertus*, PVL 3662). The proximal articular surface of phalanx I.1 has two concave facets divided by a well-developed ridge. This ridge ends dorsally at the well-developed proximodorsal lip and ventrally at the tip of the proximal heel of phalanx I.1 (Text-fig. 5B). The lateral articular facet is higher and faces proximolaterally, while the reduced medial facet faces proximomedially. The medial facet extends proximovertrally much more than the lateral facet, contributing to the development of the proximal heel of phalanx I.1. Thus, in medial view, this heel seems remarkably extensive while in lateral view it is as developed as in other basal saurischians. The differential development and extension of the proximal articular surfaces of manual phalanx I.1 is clearly correlated with the asymmetrical morphology of the distal condyles of metacarpal I.

Due to the short proximodistal length of phalanx I.1, its shaft is short and rather wide lateromedially, being approximately 0.6 times the width of the proximal end. The shaft of phalanx I.1 is high dorsoventrally, being sub-equal in height with respect to the distal and proximal ends (excluding the proximal heel of the latter). The distal end of phalanx I.1 bears an extensive articular surface, extending along an angle of 180 degrees. The lateral and medial condyles diverge ventrally, so that the dorsal surface of the distal end of phalanx I.1 is much narrower lateromedially than its ventral counterpart. This articular surface is ginglymoidal and the intercondylar groove is deep along the ventral half of this articular surface. The distal articular surface extends more ventrally than dorsally, as in other non-eusauropod sauropodomorphs. The axis that joins the dorsal and ventral ends of the medial articular surface forms an angle of 60 degrees with the proximodistal axis of phalanx I.1. The lateral pit for the collateral ligament is extensive, but shallow and poorly delimited. The



TEXT-FIG. 5. Manual remains of *Lessemsaurus sauropoides*. A, first left metacarpal PVL 4822/56 in dorsal view. B, left manual phalanx I.1 PVL 4822/58 in dorsal view. C, second right metacarpal PVL 4822/57 and left manual digit I (including the unguis PVL 4822/59) in dorsal view. Scale bars represent 2 cm.

medial pit is reduced in extent but is notably deeper and well-delimited (Text-fig. 5C). This depression is located close to the dorsal end of the distal articular condyle.

The unguis of digit one (PVL 4822/59) is robust, lateromedially flattened, and well developed (Text-fig. 5C), being sub-equal in length to the combined proximodistal lengths of metacarpal I and phalanx I.1. The proximal end of unguis I bears two concave articular facets divided by a sharp ridge. In lateral and medial views, these articular facets are not as concave as in most non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, *Yunnanosaurus huangi*, *Massospondylus carinatus*). The proximo-

ventral end of the first manual unguis of *Lessemsaurus sauropoides* has a weak flexor tubercle (Text-fig. 5C). This contrasts with the large flexor tubercle found in all basal saurischians, including all non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, *Yunnanosaurus huangi*, *Massospondylus carinatus*). Furthermore, some non-eusauropod sauropodomorphs have an extremely well-developed flexor tubercle (e.g. *Anchisaurus polyzelus*; *Thecodontosaurus antiquus*; *Efraasia minor*; *Melanorosaurus readi*, NM QR 3314). Basal eusauropods, in contrast, lack a well-developed flexor tubercle (e.g. *Ferganasaurus verziilini*). Unguis I also lacks the extensive proximodorsal lip present in most non-eusauropod sauropodomorphs (Text-fig. 5C).

The lateral and medial surfaces of unguis I are slightly convex and lack the characteristic groove that bifurcates proximally in all non-eusauropod sauropodomorphs (and sauropodomorph outgroups). Interestingly, the condition seen in *Lessemsaurus sauropoides* is also present in basal eusauropods (e.g. *Ferganasaurus verziilini*).

The distal half of unguis I is strongly recurved in most non-eusauropod sauropodomorphs (e.g. *Thecodontosaurus antiquus*, *Anchisaurus polyzelus*, *Plateosaurus engelhardti*, *Massospondylus carinatus*, *Lufengosaurus huenei*). In these forms, the tangents of the proximal and distal ends of the dorsal margin form an angle of approximately 90 degrees. In contrast, unguis I of *Lessemsaurus sauropoides* is significantly less recurved (Text-fig. 5C). The distribution of this character among basal eusauropods is poorly known, but all known eusauropod manual unguis from digit I are less recurved than those of non-eusauropod sauropodomorphs. The dorsoventral height of the first manual unguis of *Lessemsaurus sauropoides* tapers constantly and gradually along its length (Text-fig. 5C). In contrast, in some non-eusauropod sauropodomorphs, there is a steep reduction in the dorsoventral height at a point close to the mid-length of the first manual unguis (e.g. *Thecodontosaurus antiquus*, *Anchisaurus polyzelus*, *Efraasia minor*, *Yunnanosaurus huangi*; *Lufengosaurus huenei*).

Pelvic girdle

An almost complete pelvis is present in PVL 4822, including a right ilium (PVL 4822/60), a left and right pubis (PVL 4822/61–4822/62), and fragmentary remains of a distal ischium (PVL 4822/63).

Ilium. The ilium (PVL 4822/60) of *Lessemsaurus sauropoides* is similar to that of most non-eusauropod sauropodomorphs (Text-fig. 6). The iliac blade is dorsoventrally low and antero-posteriorly elongated. As in all non-eusauropod sauropodomorphs, the preacetabular process is short and subtriangular, with its apex directed anteriorly. A similar condition is also present in the basal sauropod *Kotasaurus yamanpalliensis*, although all eusauropods have an extensive, dorsoventrally high preacetabular process that extends anterior to the pubic peduncle (Seren 1999; Yates and Kitching 2003). The anterior end of the preacetabular process of *Lessemsaurus sauropoides* differs from that of other non-eusauropod sauropodomorphs. Firstly, its anterior end is straight, rather than ventrally deflected as in some taxa (e.g. *Yunnanosaurus huangi*). Secondly, the dorsal margin of the

preacetabular process is continuous with the dorsal margin of the iliac blade (Text-fig. 6). In other non-eusauropod sauropodomorphs, these two margins are separated by a moderately developed step (e.g. *Riojasaurus incertus*; *Lufengosaurus huenei*; *Yunnanosaurus huangi*; *Massospondylus carinatus*, BPI/1/4693).

As mentioned above, the iliac blade of *Lessemsaurus sauro-poides* is dorsoventrally low above the acetabulum (Text-fig. 6). The dorsal margin of the iliac blade is orientated subparallel to the longitudinal axis of the skeleton and is slightly convex. These characters represent the plesiomorphic condition for Sauropodomorpha and are strongly modified in eusauropods, which possess a high iliac blade with a strongly convex dorsal margin (McIntosh 1990).

The acetabular region is enlarged anteroposteriorly relative to the condition in most non-eusauropod sauropodomorphs. The acetabulum is rather high dorsoventrally, occupying half of the maximum dorsoventral height of the ilium (measured at the ischial peduncle). The supracetabular crest is slightly widened at the base of the pubic peduncle (Text-fig. 6). This crest forms a narrow shelf that extends anteroventrally along the dorsal half of the pubic peduncle (although the ventral end of the crest seems to be broken). The supracetabular crest represents an intermediate morphology between the condition of most non-eusauropod sauropodomorphs and eusauropods. All non-eusauropod sauropodomorphs (except *Saturnalia tupiniquim*) have a similarly located supracetabular crest, but it is significantly more developed than in *Lessemsaurus*. In ventral view, the supracetabular crest of non-eusauropod sauropodomorphs is a broad shelf with laterally convex margins. Derived sauropodomorphs (e.g. eusauropods) lack this large supracetabular crest. The acetabulum is completely open, as in all sauropodomorphs (except for *Saturnalia tupiniquim*; Langer 2003). However, the acetabulum of *Lessemsaurus sauro-poides* bears a unique condition among sauropodomorphs. The anterior articular surface of the acetabulum has a narrow medial flange that faces laterally, forming a narrow and marginal medial wall of the acetabulum (Text-fig. 6). This narrow medial wall extends along most of the dorsal margin of the acetabulum. The posterior articular surface of acetabulum, extending along the ischial peduncle, lacks this

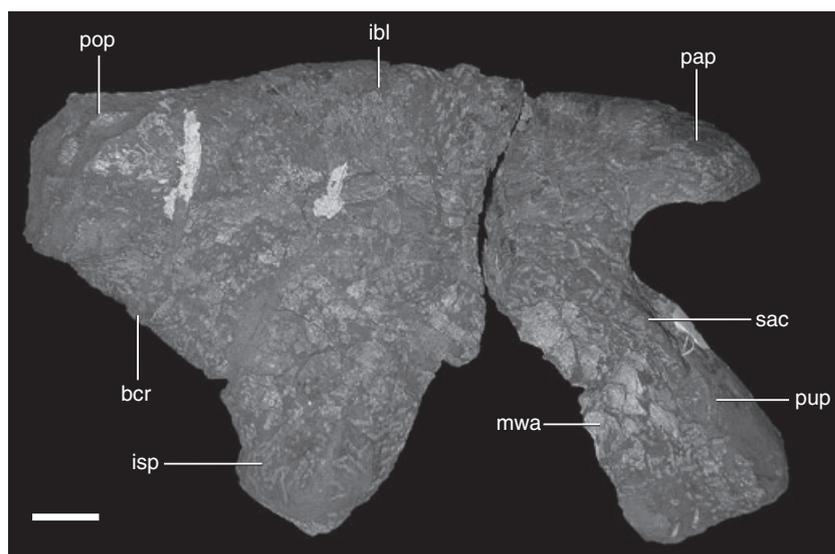
structure. The acetabular articular surface of the ischial peduncle is flat or slightly convex, while the anterior and dorsal surfaces are slightly concave.

The pubic peduncle is well developed and extends anteroventrally at an angle of approximately 50 degrees with respect to the longitudinal axis of the ilium (Text-fig. 6). In contrast to the condition in most non-eusauropod sauropodomorphs, the pubic peduncle expands anteroposteriorly towards its ventral end. Owing to the extension of the medial acetabular wall, the cross-section at the mid-point of the pubic peduncle is unique among non-eusauropod sauropodomorphs. Its anterior surface is convex, its extensive medial edge is flat and orientated anteroposteriorly, and its posterior surface (i.e. the acetabular surface) is posteriorly concave. The anterior and posterior surfaces meet at the sharp lateral edge of the pubic peduncle formed by the supracetabular crest. At the distal end of the pubic peduncle, this crest disappears and the cross-section becomes teardrop-shaped, tapering posteriorly from the convex anterior margin.

The ischial peduncle is only slightly shorter than the pubic peduncle as in several other taxa (e.g. *Thecodontosaurus caducus*, BMNH P77/1; *Efraasia minor*, SMNS 12354; *Plateosaurus engelhardti*; *Yunnanosaurus huangi*; *Riojasaurus incertus*). Other non-eusauropod sauropodomorphs have an ischial peduncle that is significantly shorter than the pubic peduncle (e.g. *Massospondylus carinatus*, BPI/1/4693; *Lufengosaurus huenei*). The latter condition is accentuated in *Kotasaurus yamanpalliensis*, *Vulcanodon karibaensis* and eusauropods, where the ischial peduncle is almost absent. The ischial peduncle has a subtriangular cross-section, with its base located anteriorly (on the acetabular surface). The posteroventral edge of the ischial peduncle lacks the distinct heel present in some non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, *Riojasaurus incertus*).

The postacetabular blade of the ilium of *Lessemsaurus sauro-poides* is slightly reduced anteroposteriorly in comparison with the elongated condition of most non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, *Riojasaurus incertus*). However, the condition present in *Lessemsaurus* (Text-fig. 6) does not reach the degree of reduction seen in the postacetabular blade of *Kotasaurus*. Derived eusauropods have an extremely

TEXT-FIG. 6. Right ilium of *Lessemsaurus sauro-poides* PVL 4822/60 in lateral view. Scale bar represents 5 cm.



reduced postacetabular blade (Yates and Kitching 2003). The dorsal margin of the postacetabular blade is slightly concave. The posterior end is blunt and dorsoventrally extensive, as in the basal sauropodomorph *Thecodontosaurus caducus*. The posterior margin of the postacetabular process of *Lessemsaurus* is not well preserved, however, and its blunt condition could be a result of preservational causes.

The ventral margin of the postacetabular process is entirely occupied by the posterior extension of the 'brevis crest' (i.e. the sharp ridge that connects the ventral surface of the brevis fossa with the posterior edge of the ischial peduncle). The degree of development of this crest is unique among sauropodomorphs (Text-fig. 6). It extends from the base of the ischial peduncle to a point that lies almost at the posterior tip of the postacetabular process. A similar crest is present in some non-eusauropod sauropodomorphs (e.g. *Riojasaurus incertus*), although in this taxon the crest is significantly reduced, originating at the dorsoventral midpoint of the ischial peduncle and disappearing well before the posterior end of the postacetabular process (close to the anterior end of the brevis fossa). Due to the posterior extension of the brevis crest of *Lessemsaurus*, the brevis fossa is short anteroposteriorly.

Pubis. A pair of articulated pubes (PVL 4822/62) is interesting owing to its unique combination of plesiomorphic and apomorphic sauropodomorph character states. The pubes are moderately elongated and narrow, and their maximum lateromedial width would have been approximately 0.65 times their maximum proximodistal length (Text-fig. 7). Several non-eusauropod sauropodomorphs have similar proportions [e.g. *Plateosaurus engelhardti*, *Massospondylus carinatus* (Cooper 1981), *Vulcanodon karibaensis*, *Tazoudasaurus naimi*]. Eusauropods, in contrast, have much wider and shorter pubes, as noted by Cooper (1984).

The pubic plate is extensive, occupying approximately 40 per cent of the entire length (Text-fig. 7). The proximal plate is relatively large, resembling the condition of *Vulcanodon karibaensis*, *Tazoudasaurus naimi* and basal eusauropods [*Kotasaurus yamampalliensis*, *Shunosaurus lii* (Zhang 1988), *Omeisaurus maoianus*], in which the proximal plate occupies 40–56 per cent of pubis length. Basal sauropodomorphs have a proportionately more restricted pubic plate that usually occupies less than 33 per cent of total pubic length. As in most sauropodomorphs, the lateral margin of the pubic plate lacks lateral pubic tubercles. These are present in basal saurischians (e.g. *Herrerasaurus ischigualastensis*; Novas 1993) and a few non-eusauropod sauropodomorphs (e.g. *Saturnalia tupiniquim*; *Efraasia minor*, SMNS 12354; *Plateosaurus engelhardti*, SMNS 12950). The margins of the obturator foramen of *Lessemsaurus sauropoides* are not well preserved, although this opening seems to be rather reduced, as in derived sauropodomorphs.

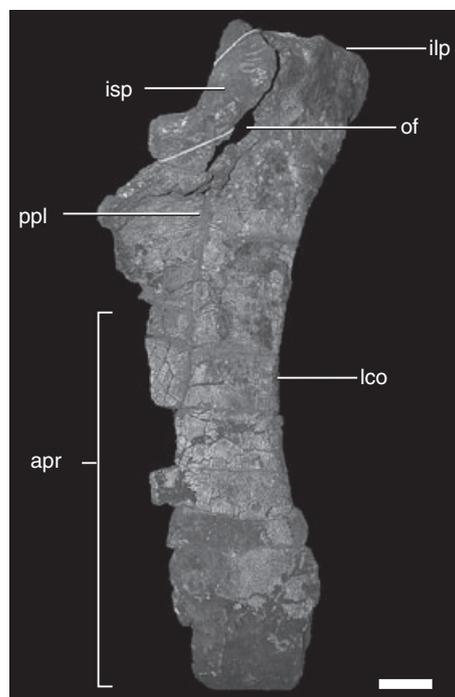
Distal to the pubic plate, the pubis is flat, lateromedially wide, and orientated transversely (Text-fig. 7). This orientation and morphology of the pubic apron is the plesiomorphic condition for Sauropodomorpha as it is present in sauropodomorph outgroups (*Herrerasaurus ischigualastensis*; Novas 1993) and all non-eusauropod sauropodomorphs (including *Vulcanodon karibaensis* and *Tazoudasaurus naimi*). The lateral margins of the pubic apron are slightly concave, as in some non-eusauropod

sauropodomorphs (e.g. *Coloradisaurus brevis*, *Massospondylus carinatus*, *Lufengosaurus huenei*, *Tazoudasaurus naimi*). However, in contrast to these forms, the pubic apron of *Lessemsaurus* tapers gradually along its distal end. The lateromedial width of the pubic apron is slightly more developed with respect to the pubic apron's length than in non-eusauropod sauropodomorphs. The minimum lateromedial width of the pubic apron of *Lessemsaurus* is approximately 80 per cent of its proximodistal length, while the maximum lateromedial width is sub-equal to its proximodistal length. The blade of the pubic apron is thick at its lateral margin and remarkably thin along its medial edges. The distal end of the pubes (Text-fig. 7) is less expanded than in most non-eusauropod sauropodomorphs.

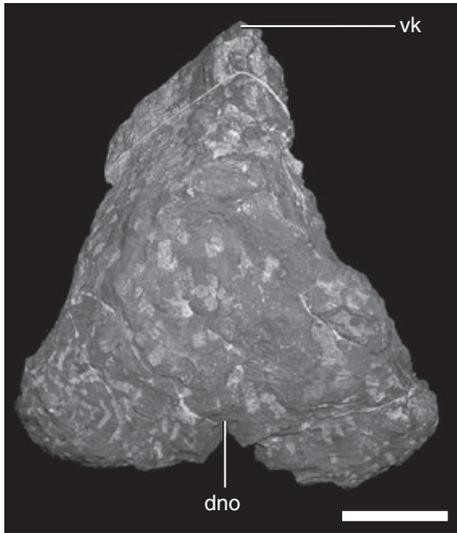
Ischium. The ischia are represented by two conjoined distal ends (PVL 4822/63; Text-fig. 8). As in all non-neosauropod sauropodomorphs, the preserved portion of the ischial shaft is subtriangular in cross-section. The distal end of the conjoined ischia is subtriangular, and its dorsoventral height is approximately 0.8 times its lateromedial width. A similar condition is present in *Vulcanodon karibaensis* and some non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*).

Hindlimb

Femur. Two femora are present: one is poorly preserved (PVL 4822/64), while a second (right) is complete (PVL 4822/65). The femur has a posteriorly bent distal end and is sigmoid in



TEXT-FIG. 7. Right pubis of *Lessemsaurus sauropoides* PVL 4822/61 in ventral view. Scale bar represents 5 cm.



TEXT-FIG. 8. Distal ischia of *Lessemsaurus sauropoides* PVL 4822/63 in ventrodistal view. Scale bar represents 5 cm.

lateral view (Text-fig. 9B) as in most non-eusauropod sauropodomorphs (Galton 1990). In posterior view, however, the femur of is straight (Text-fig. 9A) and lacks the lateral curvature of the femoral distal end that is present in some non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*). The femoral head is well developed, having its major axis perpendicular to the proximodistal axis of the femur and to the longitudinal axis of the skeleton.

TEXT-FIG. 9. Right femur of *Lessemsaurus sauropoides* PVL 4822/65. A, posterior view. B, posteromedial view. Scale bar represents 10 cm.



The fourth trochanter is a well-developed crest located at femoral mid-length (Text-fig. 9), as in *Antetonitrus ingenipes*, *Vulcanodon karibaensis* and eusauropods. In contrast, non-eusauropod sauropodomorphs have a fourth trochanter located on the proximal half of the femoral shaft. In medial view, the fourth trochanter has a straight profile. As in most non-eusauropod sauropodomorphs (Langer 2003), the proximal end of this ridge merges into the femoral shaft gradually while its distal end is remarkably steep (Text-fig. 9B). The fourth trochanter is located close to the medial margin of the femoral shaft, a character present in some non-eusauropod sauropodomorphs [*Riojasaurus incertus*, *Colo-radisaurus brevis*, *Anchisaurus polyzelus*, *Melanorosaurus readi* (Galton *et al.* 2005), *Antetonitrus ingenipes*] and eusauropods. In posterior view, the fourth trochanter has a sigmoid profile. The medial surface of the fourth trochanter bears a pronounced depression for the insertion of the m. caudofemoralis longus, as in *Melanorosaurus readi* and *Antetonitrus ingenipes*. Unfortunately, the lesser trochanter is poorly preserved in both preserved femora (PVL 4822/64–4822/65) and it cannot be determined if it was as well developed as in *Riojasaurus incertus* or *Melanorosaurus readi* or if it was reduced, as in other sauropodomorphs.

The femoral shaft is subovoid, being slightly wider latero-medially and anteroposteriorly (Text-fig. 9). This condition is intermediate between the subcircular femoral shaft of most non-eusauropod sauropodomorphs and the derived elliptical cross-section of *Antetonitrus ingenipes* and eusauropods. The distal end of the femur markedly expands lateromedially at the level of the condyles with respect to the lateromedial width of the femoral shaft. The popliteal fossa on the posterior surface of the distal femur is remarkably deep owing to the large posterior extension of the tibial and fibular condyles.

Tibia. Two tibiae are present (Text-fig. 10). The right tibia (PVL 4822/66) is slightly larger than the left one (PVL 4822/67): they probably belonged to different individuals. In comparison with the only complete femur of *Lessemsaurus sauropoides* (PVL 4822/65), the largest tibia is approximately 0.60 times the proximodistal length of the femur. However, these comparisons must be taken cautiously as these elements may belong to different-sized individuals and the femur/tibia length ratio is subject to strong ontogenetic variation in other non-eusauropod sauropodomorphs (e.g. *Mussaurus patagonicus*; Bonaparte and Vince 1979). It is interesting to note, however, that this ratio is similar to that of *Vulcanodon karibaensis* and eusauropods.

The proximal surface is subtriangular, having a remarkably large lateromedial extension along its posterior edge. The cnemial crest is lateromedially broad in the right tibia (PVL 4822/67) and lateromedially flattened in the larger left element (PVL 4822/66). These differences are probably the result of lateromedial crushing of PVL 4822/66. In both specimens, the cnemial crest does not project dorsally (Text-fig. 10), as in all non-eusauropod sauropodomorphs. The proximal half of the tibial shaft is subcircular in cross-section. Towards the distal end, however, the tibial shaft expands lateromedially. This expansion is present in all sauropodomorphs, except for basal forms (e.g. *Saturnalia*, *Thecodontosaurus caducus*). The distal portion of the tibial shaft of *Lessemsaurus* is uniquely flattened anteroposteriorly (Text-fig. 10). Thus, the cross-section of the distal tibia is subrectangular with its major axis orientated lateromedially and is twice as long transversely as anteroposteriorly.

The distal tibia has the articular socket for the ascending astragalar process characteristic of sauropodomorphs (Text-fig. 10B). This articular concavity extends proximodistally between the posterolateral and anterolateral processes of the distal tibia. In lateral view, the anterolateral flange exceeds distally the limit of the posterolateral process. Interestingly, the anterolateral descending process of the tibia is more laterally extensive than the posterolateral process (Text-fig. 10B). Thus, the articular socket of the tibia is visible in posterior view but is hidden in anterior view by the extensive anterolateral process. As noted by Yates (2004), this morphology only occurs in neosauropods and the non-eusauropod sauropodomorphs *Anchisaurus polyzelus* and *Antetonitrus ingenipes*. The medial surface of the distal tibia is markedly convex, whereas the anterior and posterior surfaces of the distal tibia are flat.

Astragalus. The astragalus of *Lessemsaurus* is only known from a single right element (PVL 4822/68; Text-fig. 11). In most respects, this element resembles the morphology seen in non-eusauropod sauropodomorphs. The main body of the astragalus is subrectangular, having its major axis orientated lateromedially. The lateral end of the astragalar body is slightly shorter anteroposteriorly (approximately 80 per cent) than the medial end (Text-fig. 11B). This condition is also present in some non-eusauropod sauropodomorphs (e.g. *Melanorosaurus readi*, *Mussaurus patagonicus*, *Coloradisaurus brevis*) and most basal eusauropods (Upchurch 1995, 1998; Wilson 2002). The posteromedial corner of the astragalus of *Lessemsaurus* is formed by straight medial and posterior edges that meet at a right angle (Text-fig. 11B), as in most non-eusauropod sauropodomorphs.



TEXT-FIG. 10. Tibiae of *Lessemsaurus sauropoides*. A, right tibia PVL 4822/66 in posterolateral view. B, left tibia 4822/67 in anterior view. Scale bar represents 10 cm.

In contrast, neosauropods have a medially tapering subtriangular astragalar body with an anteroposteriorly long lateral edge and an extremely short medial end (Upchurch 1995; Wilson and Sereno 1998). The condition of this character in the Early Jurassic *Vulcanodon karibaensis* and *Tazoudasaurus naimi* appears to be intermediate between the subrectangular astragalar body of non-eusauropod sauropodomorphs and the triangular-shaped astragalus of neosauropods.

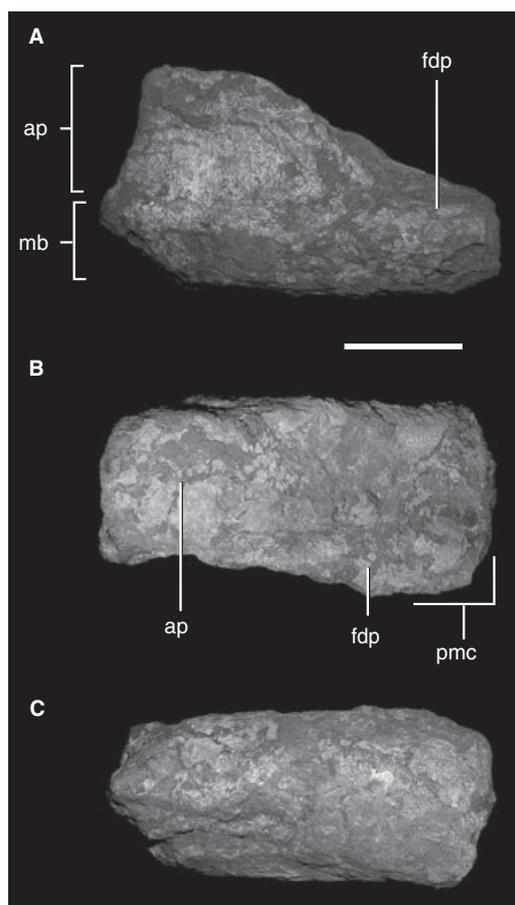
The proximodistal depth of the astragalar main body is approximately constant, as in other non-eusauropod sauropodomorphs. The distal surface of the astragalus of *Lessemsaurus* is slightly convex, similar to all non-eusauropod sauropodomorphs and basal eusauropods. Neosauropods, in contrast, have a strongly convex ventral surface of the astragalar body (Upchurch 1995; Wilson 2002).

The astragalar ascending process is remarkably extensive. It occupies approximately 70 per cent of the lateromedial extension of the astragalus and 83 per cent of its anteroposterior length. Thus, the posterior and medial basins of the astragalar dorsal surface are reduced in *Lessemsaurus* (Text-fig. 11B). Most non-eusauropod sauropodomorphs have smaller astragalar ascending processes and extensive posterior and medial concave surfaces (*Plateosaurus engelhardti*; *Riojasaurus incertus*, PVL 3663; *Coloradisaurus brevis*). Despite its reduction, the posterior concave facet of the astragalar dorsal surface still separates the ascending process from the astragalar posterior margin in *Lessemsaurus*, in contrast to the condition of *Mamenchisaurus* and neosauropods

(Wilson 2002). The posterior concave facet of *Lessemsaurus* bears small foramina but lacks the vertical crest present in *Barapasaurus* and more derived sauropods (Wilson 2002).

The proximal articular surface of the ascending process of *Lessemsaurus* faces proximomedially and is slightly deflected anteriorly. As in most non-eusauropod sauropodomorphs, the lateral and anterior surfaces of the astragalar ascending process are vertically orientated. The anterior surface of the ascending process has well-developed fossa (present in most non-eusauropod sauropodomorphs). This structure is present in *Blikanasaurus cromptoni*, but is lost in *Vulcanodon karibaensis* and Eusauropoda (Wilson and Sereno 1998).

Pes. Pedal remains are fragmentary, but include: a complete, poorly preserved, metatarsal I (PVL 4822/69); a proximal end of metatarsal II (PVL 4822/70); a complete metatarsal III (PVL 4822/71); proximal and distal ends of metatarsal IV (PVL 4822/72–4822/73); and a complete metatarsal V (PVL 4822/74). The metatarsus of *Lessemsaurus* is relatively broad and robust (Text-fig. 12A) in comparison with those of non-eusauropod sauropodomorphs, but it is more slender and elongate than in *Blikanasaurus cromptoni* or eusauropods.



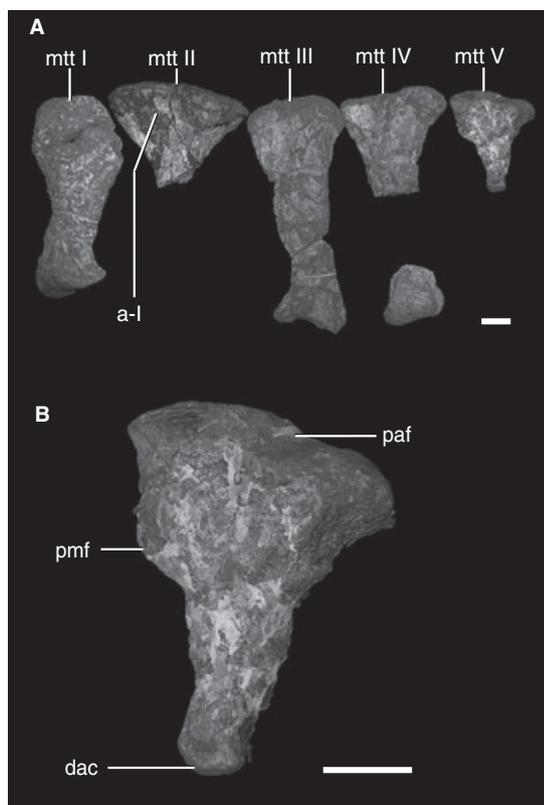
TEXT-FIG. 11. Left astragalus of *Lessemsaurus sauropoides* PVL 4822/68. A, posterior view. B, dorsal view. C, ventral view. Scale bar represents 5 cm.

Metatarsal I (PVL 4822/69) is a long and robust element that is poorly constricted at its midpoint (Text-fig. 12A). The proximodistal length of this metatarsal is approximately 0.79 times the length of the third metatarsal. In most non-eusauropod sauropodomorphs, the first metatarsal is significantly shorter, being approximately 0.60–0.65 times the length of metatarsal III. The condition in *Blikanasaurus cromptoni* and *Vulcanodon karibaensis* also falls within this range. However, more derived forms (e.g. *Omeisaurus maoianus*) have a metatarsal I that is enlarged and similar to that of *Lessemsaurus*. The proximal end of metatarsal I is slightly expanded lateromedially, but its preservation is extremely poor. The expanded proximal region of metatarsal I overlaps the proximal end of metatarsal II. The shaft of metatarsal I is only slightly constricted (Text-fig. 12A), but its lateromedial width is similar to that of metatarsal III (as in non-eusauropod sauropodomorphs). Derived sauropodomorphs generally have a first metatarsal that is much wider than the other elements (Wilson and Sereno 1998). The distal end of metatarsal I is also poorly preserved, although it can be noted that the articular condyles are asymmetrically developed. The surface of the distal end of metatarsal I is rather expanded and bears a shallow ligament pit. The medial articular surface is dorsoplantarly short as in most non-neosauropod sauropodomorphs.

The second metatarsal is known only from its proximal end (PVL 4822/70). As in all non-eusauropod sauropodomorphs (including *Blikanasaurus cromptoni*), the proximal articular surface has an hourglass shape in proximal view, with strongly concave lateral and medial margins for the articulation of metatarsals I and III (Sereno 1999). The lateral concavity is secondarily lost in *Vulcanodon karibaensis* and more derived sauropods. The proximal articular surface is flat and dorsoventrally elongated with straight dorsal and plantar edges (Text-fig. 12A).

The third metatarsal is complete but imperfectly preserved (PVL 4822/71). The proximal articular facet is subtriangular, having a broad plantar surface and a narrow dorsal apex. The metatarsal III of *Lessemsaurus sauropoides* tapers gradually along its shaft, reaching its minimum width close to its distal end (Text-fig. 12A). At this point, the third metatarsal of *Lessemsaurus sauropoides* is slightly flattened dorsoventrally. The distal end of the metatarsal III is slightly deflected medially with respect to its proximodistal axis. Although this could be accentuated by its preservation, a similar deflection is present in other sauropodomorphs (e.g. *Coloradisaurus brevis*; *Massospondylus carinatus*, BPI/1/4377; *Blikanasaurus cromptoni*; *Vulcanodon karibaensis*). Unfortunately, the distal articular surface of PVL 4822/71 is broken. The lateral and medial surfaces of the distal end of metatarsal III have shallow but clearly defined collateral ligament pits. The dorsal depression for the extensor ligament seems to be absent from the third metatarsal of *Lessemsaurus*, although as noted above, this region is poorly preserved so this could be a preservational artefact.

The fourth metatarsal is only represented by proximal (PVL 4822/72) and distal ends (PVL 4822/73). These two fragments might belong to the same element, as they have comparable sizes and preservational attributes (Text-fig. 12A). As in all non-neosauropod sauropodomorphs, metatarsal IV is remarkably broad at its proximal end but narrow distally. The dorsoventral height of the proximal end is low, as in other sauropodomorphs



TEXT-FIG. 12. Metatarsal elements of *Lessemsaurus sauropoides*. A, metatarsal I (PVL 4822/69), metatarsal II (PVL 4822/70), metatarsal III (PVL 4822/71), proximal and distal ends of metatarsal IV (PVL 4822/72–4822/73) and metatarsal V (PVL 4822/74) in dorsal view. B, detail of reduced metatarsal V PVL 4822/74. Scale bars represent 3 cm.

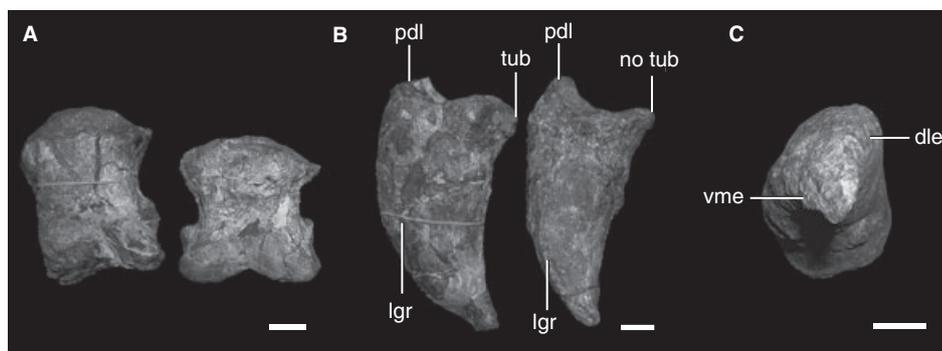
[e.g. *Plateosaurus engelhardti*; *Massospondylus carinatus*, BPI/1/4377; *Blikanasaurus cromptoni*; *Vulcanodon karibaensis*; *Omeisaurus tinafuensis* (Tang *et al.* 2001)]. The dorsal surface of the proximal end of metatarsal IV lacks a proximodistally orientated crest. The poor preservation of this region, however, precludes determining if this crest was truly absent in *Lessemsaurus* or if it is just missing in PVL 4822/72 because of incomplete preservation. The determination of this character with more material would be interesting as the crest of eusauropods is reduced in comparison with that of most non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*; *Massospondylus carinatus*, BPI/1/4377; *Coloradisaurus brevis*; *Riojasaurus incertus*, PVL 3526; *Blikanasaurus cromptoni*). The distal end of metatarsal IV (PVL 4822/73) is poorly expanded with respect to the proximal end (PVL 4822/72). Its articular surface is subtrapezoidal in cross-section, being much narrower than in metatarsal III (Text-fig. 12A). The dorsal half of the articular surface is markedly convex and lacks an intercondylar groove, as in *Riojasaurus* (PVL 3526). The ventral surface of the distal articular surface bears a broad groove between the articular condyles. The lateral condyle extends ventrolaterally in a well-developed flange, as in most non-eusauropod sauropodomorphs (including *Blikanasau-*

rus cromptoni). Derived sauropodomorphs (e.g. eusauropods), have a less prominent ventrolateral flange on the lateral distal condyle of metatarsal IV. As in most non-eusauropod sauropodomorphs, metatarsal IV of *Lessemsaurus* has a well-developed lateral ligament pit. The dorsal fossa for the extensor ligament is absent from metatarsal IV.

Metatarsal V (PVL 4822/74) is flat and triangular as in all non-eusauropod sauropodomorphs (Text-fig. 12A–B). It is remarkably short, being 0.44 times the length of metatarsal III. The reduced condition in *Lessemsaurus* is also present in all other non-eusauropod sauropodomorphs (including *Blikanasaurus cromptoni*). Derived sauropodomorphs (e.g. *Vulcanodon karibaensis*, *Omeisaurus maoianus*) have a much more elongated metatarsal V, which is approximately 0.7 times the length of metatarsal III. The proximal end is dorsoventrally low and lateromedially wide. Metatarsal V of *Lessemsaurus* tapers distally along its entire length. The medial margin of this element has a pronounced flange that extends medially and would have been overlapped by metatarsal IV (Text-fig. 12B). The distal end of metatarsal V bears a hemispherical terminal surface (Text-fig. 12B). It is unclear if this surface is indicative of the presence of an ossified pedal phalanx V.1. Several other non-eusauropod sauropodomorphs have similar distal ends of metatarsal V but were found without a phalanx in this digit (e.g. *Thecodontosaurus caducus*; *Anchisaurus polyzelus*; *Riojasaurus incertus*, PVL 3526; *Blikanasaurus cromptoni*).

Remains of the pedal digits of *Lessemsaurus* are also incomplete. These are restricted to three non-terminal phalanges (PVL 4822/75–4822/77) and two unguals (PVL 4822/78–4822/79). The three non-terminal pedal phalanges are probably proximal elements based on their size (relative to the metatarsals) and proportions (Text-fig. 13A). Two of these phalanges are subquadrangular in dorsal view, with marked lateromedial constriction in their shafts (PVL 4822/75–4822/76). These phalanges probably belong to pedal digits I and II based on the development of their ginglymoidal articular surface. The third non-terminal phalanx (PVL 4822/77) is slightly longer than wide and is less constricted at its proximodistal midpoint. Its distal end has two well-developed articular condyles, although the intercondylar groove is much shallower than in the two other phalanges. The morphology of this phalanx is most congruent with the first pedal phalanx of digit III of other non-eusauropod sauropodomorphs. If these interpretations are correct, the pedal digits of *Lessemsaurus* would resemble the short and broad condition present in some non-eusauropod sauropodomorphs (e.g. *Melanorosaurus readi*, NM QR 3314; *Blikanasaurus cromptoni*). Other non-eusauropod sauropodomorphs have a much more elongated pes (e.g. *Plateosaurus engelhardti*; *Coloradisaurus brevis*).

One of the pedal unguals (PVL 4822/78) is significantly taller dorsoventrally than the other (PVL 4822/79). These unguals are large, with their proximodistal height approximately 0.5 times the length of metatarsal III and 0.64 times the length of metatarsal I (Text-fig. 13B). The larger pedal unguis is lateromedially flattened with a narrow ventral surface. The two concave proximal articular facets are slightly asymmetrical and are divided by a sharp longitudinal ridge. The proximal flexor tubercle is present but small (Text-fig. 13). The flattened lateral and medial



TEXT-FIG. 13. Pedal phalanges of *Lessemsaurus sauropoides*. A, proximal pedal phalanges PVL 4822/75–4822/76 in dorsal view (ordered by number from right to left). B, pedal unguals PVL 4822/78–4822/79 in lateral view (ordered by number from left to right). C, pedal ungual phalanx II? (PVL 4822/79) in distal view. Scale bars represent 2 cm.

surfaces bear a shallow proximodistal groove. The ventromedial edge of this ungual phalanx is distinctly sharp. All of these characters are exclusively present in pedal ungual I of non-eusauropod sauropodomorphs (e.g. *Plateosaurus engelhardti*, MB skelett 25; *Massospondylus carinatus*, BPI/1/4377; *Blikanasaurus cromptoni*). However, in contrast to the pedal ungual I of these forms, the ungual PVL 4822/78 lacks a proximal bifurcation of the lateral and medial grooves. The second ungual (PVL 4822/79) is markedly asymmetrical, having a dorsomedially facing surface and a ventrolaterally facing surface separated by sharp ridges (Text-fig. 13B–C). The ventrolateral surface bears a shallow groove while the dorsomedial surface seems to be smooth. Its proximal articular surface is rather narrow lateromedially and lacks a flexor tubercle on its ventral surface. This combination of characters is present in the second digit ungual of some sauropodomorphs (e.g. *Antetonitrus ingenipes*). In contrast, most non-eusauropod sauropodomorphs have a rather symmetrical and ventrally flattened second pedal ungual. Interestingly, the condition in *Lessemsaurus* resembles the sickle shaped, asymmetrical unguals of some derived eusauropods in lacking a ventrally flattened surface.

DISCUSSION

Taxonomic identity of PVL 4822

The assemblage PVL 4822 was found in close association, but not in articulation. It includes elements from several individuals as demonstrated by the duplication of elements and size differences among the material. Nevertheless, we regard all of this material as referable to *Lessemsaurus* for the reasons given below.

Firstly, the assemblage of bones seems to be monospecific as none of the duplicate elements is distinguishable from each other (and some elements, such as the scapulae, bear apomorphic features). Secondly, many of the elements found in this association can be distinguished from those of other sauropodomorphs known from the Los Colorados Formation (*Riojasaurus incertus* and

Coloradisaurus brevis) owing to the presence of the numerous characters (characters observed in PVL 4822-1 were originally noted by Bonaparte 1999):

1. Dorsoventrally elongated cervicodorsal neural arches (PVL 4822-1).
2. Strong neural arch constriction below the postzygapophyses (PVL 4822-1).
3. Deep postspinal fossa (PVL 4822-1).
4. Dorsoventrally high infrapostzygapophyseal depression (PVL 4822-1).
5. Articular surface of cervicodorsal centrum higher than wide (PVL 4822/22).
6. Middle and posterior dorsals with neural spines higher than broad (PVL 4822-1).
7. Scapular dorsal blade and shaft expanded with respect to scapula dorsoventral height (PVL 4822/50).
8. Rounded proximal edge of humeral surface (PVL 4822/53).
9. Well-developed radial fossa on ulna (PVL 4822/54).
10. Radial shaft poorly constricted (PVL 4822/55); unknown in *C. brevis*.
11. Proximodistal length of metacarpal I sub-equal to its lateromedial width, and remarkably smaller than metacarpal II (PVL 4822/56); unknown in *C. brevis*.
12. Acute lateral process on proximolateral corner of metacarpal II (PVL 4822/57); unknown in *C. brevis*.
13. Manual phalanx I.1 wider than long (PVL 4822/58); unknown in *C. brevis*.
14. Manual ungual I poorly curved and lacking lateral grooves (PVL 4822/59); unknown in *C. brevis*.
15. Preacetabular process of ilium straight and with its dorsal margin continuous with the iliac blade (PVL 4822/60); unknown in *C. brevis*.
16. Pubic peduncle of ilium flaring distally, lacking a large supracetabular crest and forming a thin and marginal medial wall of the acetabulum (PVL 4822/60).
17. Brevis crest extending from the base of the ischial peduncle to the posterior tip of the reduced postacetabular process (PVL 4822/60); unknown in *C. brevis*.
18. Flat pubic apron with concave lateral margins (PVL 4822/62).

19. Distal end of femur straight in posterior view with fourth trochanter located at the midpoint of the diaphysis (PVL 4822/65).
20. Cross-section of the distal tibia subrectangular with its major axis orientated lateromedially and twice as long as its anteroposterior extension (PVL 4822/66–4822/67).
21. Subquadrangular pedal phalanges (PVL 4822/75–4822/76).
22. Narrow ventral surface of pedal unguals lacking a flattened surface (PVL 4822/78–4822/79).

Finally, the diagnostic postcranial characters of *Riojasaurus* (Bonaparte 1972) and *Coloradisaurus* (D. Pol, pers. obs.) are absent from the material catalogued under PVL 4822. Consequently, we refer all of this material to *Lessemsaurus sauropoides* on the basis of current data. However, future discoveries of articulated remains are necessary to test the taxonomic identity of the material described herein.

Affinities of *Lessemsaurus*

Lessemsaurus sauropoides was originally referred to the Melanorosauridae (Bonaparte 1999), a group of large, robust non-eusauropod sauropodomorphs of disputed monophyly (Galton 1985; Van Heerden and Galton 1997; Yates 2003, 2004; Galton and Upchurch 2004; Barrett *et al.* 2005). Bonaparte (1999) considered this form to be closer to sauropod origins than other non-eusauropod sauropodomorphs, such as *Plateosaurus* or *Riojasaurus*. More recently, Yates and Kitching (2003) noted the similarity in the distally flared dorsal neural spine present in the *Lessemsaurus* material described by Bonaparte (1999) and that of *Antetonitrus ingenipes*, a new taxon from the lower Elliot Formation (Norian) of South Africa.

Galton and Upchurch (2004) included *Lessemsaurus* in a cladistic analysis, which recovered it as the sister taxon of *Camelotia* on the basis of the shared presence of anteroposteriorly short posterior dorsal centra. This clade clustered with *Melanorosaurus* and *Riojasaurus* to form a monophyletic Melanorosauridae, but none of the synapomorphies of this more inclusive clade could be scored for *Lessemsaurus* (based on the information published at that time: PVL 4822-1). Owing to the large amount of missing data, the position of *Lessemsaurus* was weakly supported in the context of that dataset: only one extra step was necessary for it to become the sister-taxon of *Euskelosaurus*, *Massospondylus* or *Blikanasaurus*, or for it to become the most basal sauropodomorph.

The remains described herein offer new information on the anatomy of *Lessemsaurus*. Interestingly, they provide a suite of derived characters shared exclusively with *Antetonitrus*. These include: the presence of a scapula with a broad dorsal blade and shaft (with respect to scapula dorsoventral height); a short scapular shaft; the distal

lateral condyle of metacarpal I taller dorsoventrally than the medial condyle; and a manual phalanx I.1 that is slightly wider (at its proximodistal end) than proximodistally long. The absence of these derived conditions in all other sauropodomorphs suggests that these characters may be synapomorphies of a clade including these two taxa. This suggestion must be tested within the context of an inclusive phylogenetic analysis: however, the latter lies outside the scope of this contribution.

Lessemsaurus and the origin of eusauropod morphology

Bonaparte (1999) interpreted the anatomy of the cervico-dorsal neural arches of *Lessemsaurus* (PVL 4822-1) as displaying a morphology that was approaching the condition present in eusauropods (e.g. posterior cervical neural spines transversally wide; well-delimited depressions on anterior surface of neural arch pedicels of the cervicals; infrapostzygapophyseal constriction in cervicals; dorsal neural spine high, with the neural arch more than half the total height of the vertebra; and sharply delimited pneumatic fossa on posterior dorsal centra). The combination of these derived characters with the retained presence of sauropodomorph plesiomorphies (e.g. the absence of pleurocoels in cervical vertebrae; dorsal transverse process not deflected dorsally; dorsolateral surface of the diapophyseal lamina lacking a depression; absence of spinodiapophyseal lamina on middle and posterior dorsals) suggested that this taxon was potentially relevant for understanding the origin of the morphological features that traditionally characterized Eusauropoda. The new information provided herein identifies an additional set of plesiomorphic and derived characters in the rest of the skeleton that supports this view, placing *Lessemsaurus* as a particularly interesting form owing to the unique combination of character states.

The additional set of derived characters shared with eusauropods provides potential synapomorphies for a clade formed by *Lessemsaurus*, eusauropods and related forms, such as *Vulcanodon*. Several of the characters discussed below are also present in *Antetonitrus ingenipes*, but are absent in all 'prosauropods' (exceptions noted below):

1. Proportionately short and high dorsal centra (also present in *Camelotia borealis*: Galton 1998; Galton and Upchurch 2004).
2. Well-developed acromion process and ventral expansion of scapula.
3. Humerus with a low deltopectoral crest and markedly convex proximal surface.
4. Radial shaft that is poorly constricted and subovoid in cross-section.
5. Poorly curved manual ungual I with a reduced flexor tubercle and proximodorsal lip, and lacking a collateral groove.

6. Pubic plate occupying more than 40 per cent the total length of pubis.
7. Distal end of femur straight in posterior view.
8. Fourth trochanter located at femoral mid-length.
9. Anterolateral descending process of the tibia exceeds laterally the posterolateral descending process (also present in *Anchisaurus polyzelus*; Yates 2004).
10. Relatively long metatarsal I (being approximately 80 per cent of the length of metatarsal III).
11. Subquadrangular non-terminal pedal phalanges [also present in *Melanorosaurus readi* (NM QR 3314) and *Blikanasaurus cromptoni*].
12. Pedal ungual with narrow (instead of flattened) ventral surface and lacking a proximal bifurcation of the lateral and medial grooves.

As mentioned above, the new material described herein reveals that *Lessemsaurus sauropoides* lacks numerous derived characters present in basal eusauropods (some of which are also recorded in *Vulcanodon*). For these characters, *Lessemsaurus* (and in many cases *Antetonitrus ingeniipes*) possesses the plesiomorphic condition present in other non-eusauropod sauropodomorphs (or 'prosauropods'). Among these we can note the following:

1. Acamerate and amphicoelous centra.
2. Distal end of the radius lacking a broad posterior surface for articulation with the ulna.
3. Metacarpal I with a subtriangular proximal surface and which is reduced in length with respect to other elements of the metacarpus.
4. Iliac blade that is low and slightly convex.
5. Well-developed ischial peduncle of the ilium.
6. Moderately elongated pubes with a flattened and transversely orientated pubic apron.
7. Steep distal end of fourth trochanter.
8. Distal end of the femur bent posteriorly.
9. Subrectangular astragalar main body, with posterior and medial margins meeting at a right angle.
10. Distal surface of astragalus flattened or slightly convex.
11. Width of metatarsal I sub-equal to that of the other metatarsals.
12. Reduced triangular metatarsal V that is less than half the length of the other metatarsals.

Other characters, such as the degree of development of the radial fossa of the ulna, the supracetabular crest, the postacetabular process of ilium, and the width/length ratio of the metatarsus, seem to show an intermediate condition between the morphology present in non-eusauropod sauropodomorphs ('prosauropods') and that of eusauropods.

Lessemsaurus and the monophyly of Prosauropoda

The new material described herein also has a bearing on the debated monophyly of Prosauropoda, because of the presence of characters that have been considered as pro-

sauropod synapomorphies. The simultaneous presence in *Lessemsaurus* of such characters, together with those that suggest affinities of this taxon with eusauropods, is of particular interest because it provides relevant information for testing prosauropod monophyly. Among the proposed prosauropod synapomorphies of recent studies (Serenio 1999; Galton and Upchurch 2004), *Lessemsaurus* can be scored for the following characters:

1. Absence of prezygadiapophyseal lamina on caudal dorsals (Galton and Upchurch 2004).
2. Metacarpal I inset into the carpus, evidenced by the flat articular surface on the proximolateral corner of this element for the distal carpal II (Serenio 1999).
3. Metacarpal I basal width more than 65 per cent of the maximum length (Serenio 1999).
4. Twisted manual phalanx I.1 (Serenio 1999; Galton and Upchurch 2004).
5. Proximal heel in manual phalanx I.1 (Galton and Upchurch 2004).
6. Subtriangular preacetabular process of ilium (Serenio 1999).
7. Subtriangular ischial distal shaft in cross-section (Serenio 1999).
8. Metatarsal II proximal articular surface hourglass-shaped (Serenio 1999).

Four other characters proposed as prosauropod synapomorphies (Serenio 1999; Galton and Upchurch 2004) can be scored in the present material of *Lessemsaurus* but show a similar morphology to eusauropods: anteroposteriorly short caudal dorsal centra (length/height ratio < 1.0); deltopectoral crest orientated obliquely to the long axis through the distal humeral condyles; deltopectoral crest occupying less than 50 per cent of the humeral length; and reduced obturator foramen in pubis (less than 50 per cent of the acetabulum).

All of these sets of characters provide evidence for understanding the evolution of the characteristic morphology of eusauropods and testing prosauropod monophyly, owing to the presence of previously unrecorded combinations of morphologies present in 'prosauropods' and eusauropods. This will be discussed elsewhere, as integrating and testing this phylogenetic information lies outside the scope of this paper.

CONCLUSIONS

The remains of *Lessemsaurus sauropoides* described herein increase our knowledge of sauropodomorph diversity in the Late Triassic Los Colorados Formation (north-west Argentina). The similarities noted between *Lessemsaurus* and *Antetonitrus* suggest a possible close relationship between the South African and South American tetrapod faunas during the Late Triassic, which needs to be thoroughly tested following taxonomic revision of the abun-

dant material collected from the lower Elliot and Los Colorados formations.

This material adds information that will be useful in understanding several outstanding problems in the early evolutionary history of Sauropodomorpha. Some of these problems, such as understanding the evolutionary processes behind the origin of sauropod *bauplan*, the changes in diversity patterns (e.g. extinctions, radiations), and the evolution of character complexes, cannot be approached without an inclusive phylogenetic analysis of all relevant taxa. In particular, the outcome of these studies will be strongly dependent upon whether a monophyletic (Gauffre 1995; Sereno 1999; Galton and Upchurch 2004) or paraphyletic (Gauthier 1986; Yates 2003, 2004) Prosauropoda is supported. As discussed above, these remains, as well as those of the large sauropodomorphs from the lower Elliot Formation (Galton and Van Heerden 1998; Yates and Kitching 2003; Galton *et al.* 2005), will play a critical role in these analyses as they possess a particularly interesting combination of plesiomorphic and apomorphic sauropodomorph characters.

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