Anatomy of a basal sauropodomorph dinosaur from the Early Jurassic Hanson Formation of Antarctica

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The anatomy of a basal sauropodomorph (Dinosauria: Saurischia) from the Early Jurassic Hanson Formation of Antarctica is described in detail. The material includes a distal left femur and an articulated right pes, including the astragalus, distal tarsals, and metatarsals I–IV. The material is referable to Sauropodomorpha and represents a non-eusauropod, sauropodomorph more derived than the most basal members of Sauropodomorpha (e.g., *Saturnalia*, *Thecodontosaurus*, *Efraasia*, and *Plateosaurus*) based on a combination of plesiomorphic and derived character states. Several autapomorphies present in both the femur and metatarsus suggest that this material represents a distinct sauropodomorph taxon, herein named *Glacialisaurus hammeri* gen. et sp. nov. Some of the derived characters present in the Antarctic taxon suggest affinities with *Coloradisaurus* and *Lufengosaurus* (e.g., proximolateral flange on plantar surface of metatarsal II, well-developed facet on metatarsal II for articulation with medial distal tarsal, subtrapezoidal proximal surface of metatarsal III). Preliminary phylogenetic analyses suggest a close relationship between the new Antarctic taxon and *Lufengosaurus* from the Early Jurassic Lufeng Formation of China. However, the lack of robust support for the taxon's phylogenetic position, and current debate in basal sauropodomorph phylogenetics limits phylogenetic and biogeographic inferences drawn from this analysis. The new taxon is important for establishing the Antarctic continent as part of the geographic distribution of sauropodomorph dinosaurs in the Early Jurassic, and recently recovered material from the Hanson Formation that may represent a true sauropod, lends support to the notion that the earliest sauropods coexisted with their basal sauropodomorph relatives for an extended period of time.

Key words: Dinosauria, Sauropodomorpha, Prosauropoda, phylogeny, paleobiogeography, Jurassic, Hanson Formation, Antarctica.

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Introduction

During the austral summer of 1990–1991, a field team led by William Hammer of Augustana College collected the partial remains of a sauropodomorph dinosaur (Hammer and Hickerson 1994). The material includes a partial left femur and several elements of the right ankle and metatarsus. These specimens were collected in the lower part of the Hanson Formation on Mt. Kirkpatrick in the Beardmore Glacier region of the Central Transantarctic Mountains (Fig. 1), and were tentatively referred to the sauropodomorph family Plateosauridae by Hammer and Hickerson (1996). Other vertebrate material collected with the sauropodomorph fossils include the relatively complete theropod dinosaur *Cryolophosaurus ellioti* (Hammer and Hickerson 1994; Smith et al. 2007), pelvic material from a possible sauropod dinosaur, a pterosaur humerus, and the tooth of a large tritylodont (Hammer and Hickerson 1994, 1996). All of this material has been collected from a single site, at approximately 4,100 meters on Mt. Kirkpatrick, with the exception of the possible sauropod material, collected in 2003–2004 from a new site approximately 100 meters higher in the Hanson Formation. The articulated right ankle and metatarsus was collected with other fossil material within five meters laterally, and a single meter stratigraphically (Hammer and Hickerson 1994). The left femur was collected as float from the base of the exposure (William R. Hammer, personal communicatin 2006). Though it is possible that the femur may have originated from further up in the section, the quality of preservation and associated matrix are consistent with elements from within the exposure. Furthermore, several cranial elements attributable to the skull of the theropod dinosaur *Cryolophosaurus*, which was weathering out of the exposure, were also found as nearby float (Hammer and Hickerson 1994). The relative size of the partial femur also matches well with what would be expected based on the size of the recovered metatarsus. The distal femur is not attributable to the holotype of *Cryolophosaurus*, as this specimen (FMNH PR1821) possesses both right and left elements. Furthermore, the distal femora of *Cryolophosaurus* are much more gracile in proportions,
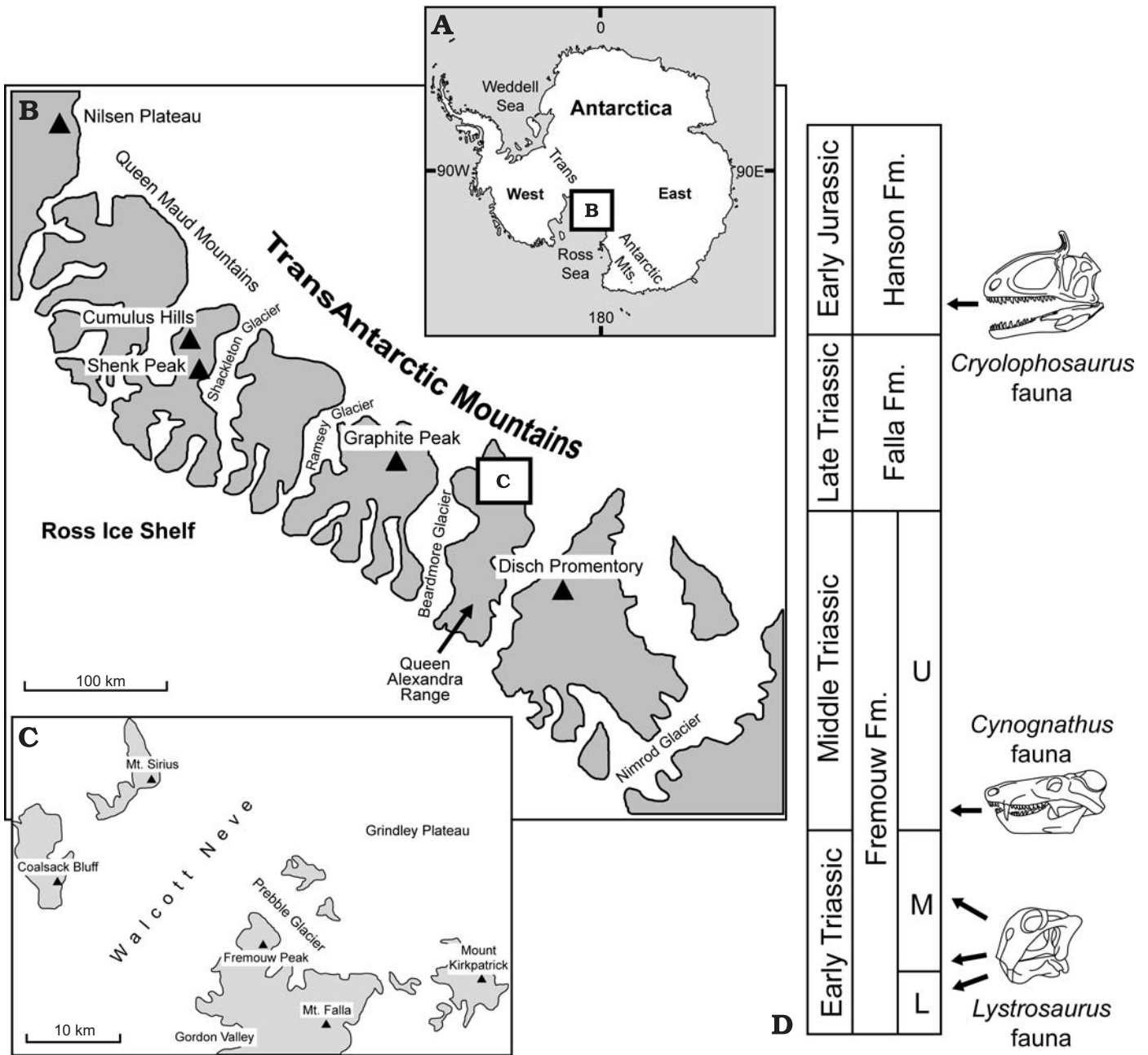
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Fig. 1. Map of Antarctica (**A**), with inset maps showing the Central Transantarctic Mountains (**B**), and the Beardmore Glacier area where the Mount Kirkpatrick dinosaur site is located (**C**). Age and generalized stratigraphy of Triassic and Jurassic portions of the Beacon Supergroup in the Beardmore Glacier area, with relative positions of Mesozoic vertebrate faunas indicated at right (**D**). Abbreviations: FM, Formation; L, lower member; M, middle member; U, upper member.

have midshafts which are less anteroposteriorly flattened, anteroposteriorly thinner medial epicondylar crests, and mediolaterally thinner tibiofibularis crests than the sauropodomorph distal femur. Hammer and Hickerson (1994) cautiously suggested that several articulated posterior cervical vertebrae collected near the skull of *Cryolophosaurus ellioti* in 1990–1991 may belong to the sauropodomorph as well. However, these cervicals retain well-developed postzygadiapophyseal laminae, which are conspicuously absent in the mid-posterior cervicals of most basal sauropodo-

morphs (Yates 2003b). Detailed examination of this material, in addition to the collection of the rest of the posterior cervical and anterior dorsal vertebral column in 2003–2004, has revealed that these posterior cervicals do indeed belong to the *Cryolophosaurus ellioti* specimen with which they are associated (Smith et al. 2007).

The Hanson Formation was deposited in an active volcano-tectonic rift system formed during the breakup of Gondwana, and is considered to be Early Jurassic in age (Elliot 1996). The presence of *Dicroidium odontopteroides*

in the Falla Formation 300 meters below the vertebrate bearing layers of the Hanson Formation, and pollen and spore assemblages from the middle part of the Falla Formation provide an upper bound of Carnian–Norian (Late Triassic) for the base of the Hanson Formation (Kyle and Schopf 1982; Farabee et al. 1989; Elliot 1996). A radiometric date of 177±2 Ma of the overlying Prebble Formation and Kirkpatrick Basalt (Heimann et al. 1994) gives a lower bound of Aalenian (earliest Middle Jurassic) for the top of the Hanson Formation. Additional radiometric dates from the top of the Hanson Formation, including a K-Ar date of 203±3 Ma (Barrett and Elliot 1972), and an Rb-Sr isochron date of 186±9 Ma (Faure and Hill 1973), suggest that the lower part of the Hanson Formation, which includes the vertebrate-bearing horizons, is probably middle Early Jurassic (Elliot 1996).

Basal sauropodomorph relationships are currently in a state of revision, as evidenced by the vastly different hypotheses of relationships currently proposed (Benton et al. 2000; Yates 2003a, b, 2004, 2007a, b; Yates and Kitching 2003; Galton and Upchurch 2004; Leal et al. 2004; Pol 2004; Barrett et al. 2005, 2007; Pol and Powell 2005, 2007b; Upchurch et al. 2007). New discoveries (Yates and Kitching 2003; Leal et al. 2004; Pol and Powell 2005; Reisz et al. 2005), reinterpretation of previously collected material (Benton et al. 2000; Yates 2003b, 2007a; Pol 2004; Barrett et al. 2005, 2007; Bonnan and Yates 2007; Fedak and Galton 2007; Galton et al. 2007; Pol and Powell 2007a), and a general desire for more detailed information concerning the early evolution of the sauropodomorph dinosaurs has fueled much of this increased interest. Accordingly, the new sauropodomorph material described here provides additional insight into the anatomy and systematics of the group. The material is also important for establishing the Antarctic continent as part of geographic distribution of the group, and may ultimately provide more detailed information on the biogeography of early sauropodomorph dinosaurs.

Institutional abbreviations.—BPI, Bernard Price Insitute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; FMNH, The Field Museum of Natural History, Chicago, USA; GPIT, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MB, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; MCP, Museu de Ciências e Tecnologia PUCS, Porto Alegre, Brazil; NGMJ, Nanjing Geological Museum, Nanjing, China; NMQR, National Museum, Bloemfontein, South Africa; PVL, Fundacíon Miguel Lillo, Tucumán, Argentina; SAM, South African Museum (Iziko Museums of Cape Town), Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCMP, University of California Museum of Paleontology, Berkeley, USA; YPM, Yale Peabody Museum, New Haven, USA.

Systematic paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Sauropodomorpha von Huene, 1932

Genus *Glacialisaurus* nov.

Derivation of the name: From the Latin *glacialis*, meaning "icy" or "frozen". In reference to the geographic location of the type species, which is from the Beardmore Glacier region in the Central Transantarctic Mountains.

Diagnosis.—Same as for only known species.

Glacialisaurus hammeri sp. nov.

Figs. 2–6, Table 1.

Holotype: FMNH PR1823, a partial right astragalus, medial and lateral distal tarsals, and partial right metatarsus preserved in articulation with each other.

Referred material: FMNH PR1822, a distal left femur.

Type locality: Mt. Kirkpatrick, Beardmore Glacier region, Central Transantarctic Mountains, Antarctica.

Type horizon: Approximately 4,100 meters, in the tuffaceous siltstones and mudstones of the lower part of the Hanson Formation, which is Early Jurassic in age (Elliot 1996).

Derivation of the name: In honor of Dr. William R. Hammer (Augustana College, Rock Island, USA), for his contributions to vertebrate paleontology and Antarctic research.

Diagnosis.—A robust non-eusauropod sauropodomorph dinosaur that can be distinguished from other sauropodomorphs by the presence of the following autapomorphies: (1) a robust medial epicondylar ridge on the distal femur (convergently present, though more gracile, in many basal theropod dinosaurs); (2) a robust adductor ridge extending from the proximal end of the femoral medial condyle; (3) a second metatarsal with an anterior border that is weakly convex in proximal aspect; (4) a hypertrophied lateral plantar flange on the proximal end of metatarsal II (present, but less developed in many basal sauropodomorphs, e.g., *Saturnalia*, *Plateosaurus*); (5) a second metatarsal that is gently twisted medially about its long axis at the distal end of its shaft; and (6) a second metatarsal with a medial distal condyle that is more robust and well-developed than the lateral distal condyle.

Anatomical description

Femur.—The only known femur is an incomplete left element (Figs. 2, 3). It is broken mid-shaft slightly above the level of the medial epicondylar crest. The preserved portion of the femur has also been broken transversely and slightly obliquely below the level of the preserved proximal portion of the medial epicondylar crest and above the adductor ridge extending from the medial condyle. This break has been repaired, but the proximal portion of the femur is now shifted anteriorly slightly relative to the distal portion. This damage may have occurred post-mortem, but pre-fossilization, as the
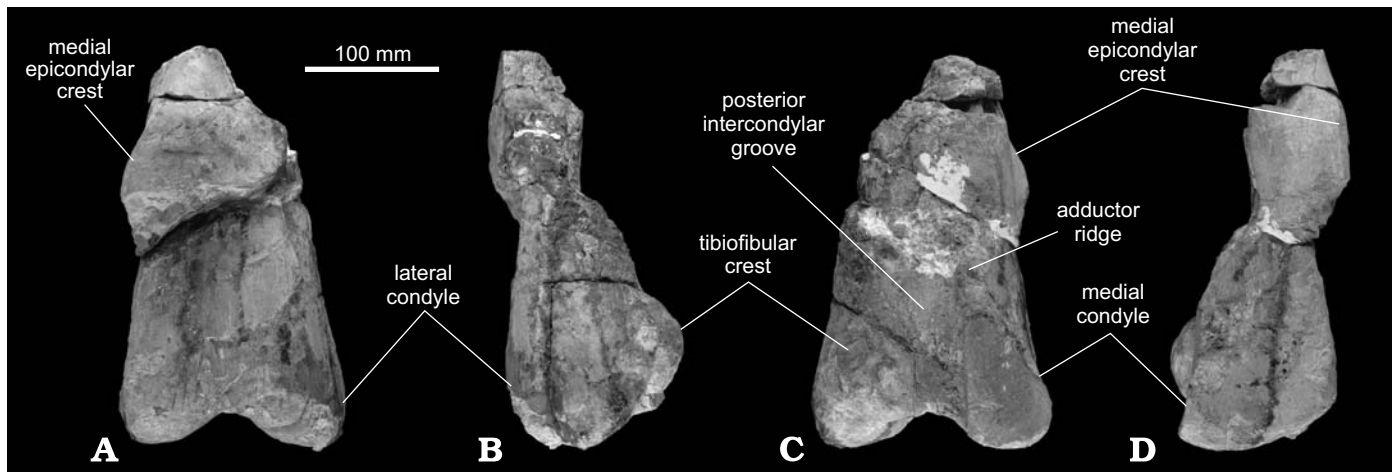
Fig. 2. Sauropodomorph dinosaur *Glacialisaurus hammeri* gen. et sp. nov. from the Early Jurassic Hanson Formation at Mt. Kirkpatrick, Beardmore Glacier region, Antarcticac. Distal left femur (FMNH PR1822) in anterior (**A**), lateral (**B**), posterior (**C**), and medial (**D**) views.

posterior and medial portions of the break have been in-filled with calcite. The length of the partial femur is 300 mm, and the inferred length of the entire element would have been at least 600 mm. The cross section of the femoral shaft is slightly wider transversely than anteroposteriorly, but is not as elliptical as in eusauropods. The proximal portion of a robust medial epicondylar crest is preserved (Fig. 2). It extends smoothly from the medial surface of the distal femoral shaft. The anterior surface of the femur is flat, and not transversely convex as in the basal sauropodomorphs *Saturnalia tupiniquim* (MCP 3844-PV; though the degree of convexity appears weaker in the paratype specimens: MCP 3845-PV, and MCP 3846-PV), and *Pantydraco* (Yates 2003b; Galton et al. 2007); and sauropodomorph outgroups, such as *Chindesaurus byransmalli* (Langer 2004: fig. 2.8; Long and Murry 1995), and *Silesaurus opolensis* (Dzik 2003). There is no trace of an anterior extensor groove on the cranial surface of the distal femur (Figs. 2, 3). A large craniocaudal groove is present on the distal surface of the femur, separating the medial and lateral condyles (Fig. 3). It ends abruptly posteriorly and does not grade smoothly into the popliteal fossa. However, the lateral margin of the distal groove arcs postero-

medially to grade into the distal sulcus of the tibiofibular crest. The popliteal fossa is deep and mediolaterally wide. It becomes mediolaterally broader at its proximal end. There is no evidence of an infrapopliteal ridge, as in some coelophysoid theropods (Tykoski and Rowe 2004; Tykoski 2005). The distal femoral condyles are rounded and large. The lateral condyle is slightly more bulbous and circular than the medial condyle, which is an anteroposteriorly elliptical shape. The posterior portion of the medial condyle is broken off, though its base is preserved.

A robust ridge extends from the proximal end of the medial condyle, and probably represents the distal portion of the adductor ridge (Hutchinson 2001). The adductor ridge of the Antarctic sauropodomorph is more developed than in other non-eusauropod sauropodomorphs. A prominent tibiofibular crest is present on the posterior side of the lateral femoral condyle (Figs. 2, 3). This crest is kidney-shaped with its long axis running proximolateral-distomedially. The distal surface of the tibiofibular crest is mediolaterally broader than anteroposteriorly long, as in *Lufengosaurus huenei* (IVPP V15; Young 1947: figs. 6, 12; = *L. magnus*), *Antetonitrus* (BPI/1/4952) and *Melanorosaurus* (SAM-PK-K 3450), but differing from other basal sauropodomorphs (e.g., *Efraasia* SMNS 12354; *Anchisaurus* YPM 1883; *Coloradisaurus* PVL 5905; *Massospondylus* BPI/1/4377; and *Plateosaurus* SMNS 13200). The tibiofibular crest is only weakly excavated laterally and distally, though it is well defined and separated from the lateral femoral condyle.

Astragalus.—The right astragalus is preserved in articulation with several distal tarsals and portions of the right metatarsus (Figs. 4, 5). The distal tarsals and metatarsus are preserved in an extended position relative to the astragalus, such that their proximodistal axis is perpendicular to that of the astragalus (Fig. 5). Due to this, a small anterolateral portion of the astragalus is still connected to the distal tarsals and metatarsus by matrix and is not visible. The astragalus is a low, transversely elongate element. Though the tip of the medial border
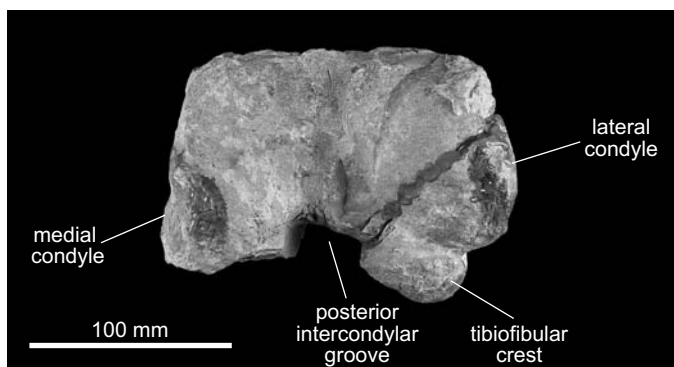

Fig. 3. Sauropodomorph dinosaur *Glacialisaurus hammeri* gen. et sp. nov. from the Early Jurassic Hanson Formation at Mt. Kirkpatrick, Beardmore Glacier region, Antarcticac. Distal left femur (FMNH PR1822) in distal view.
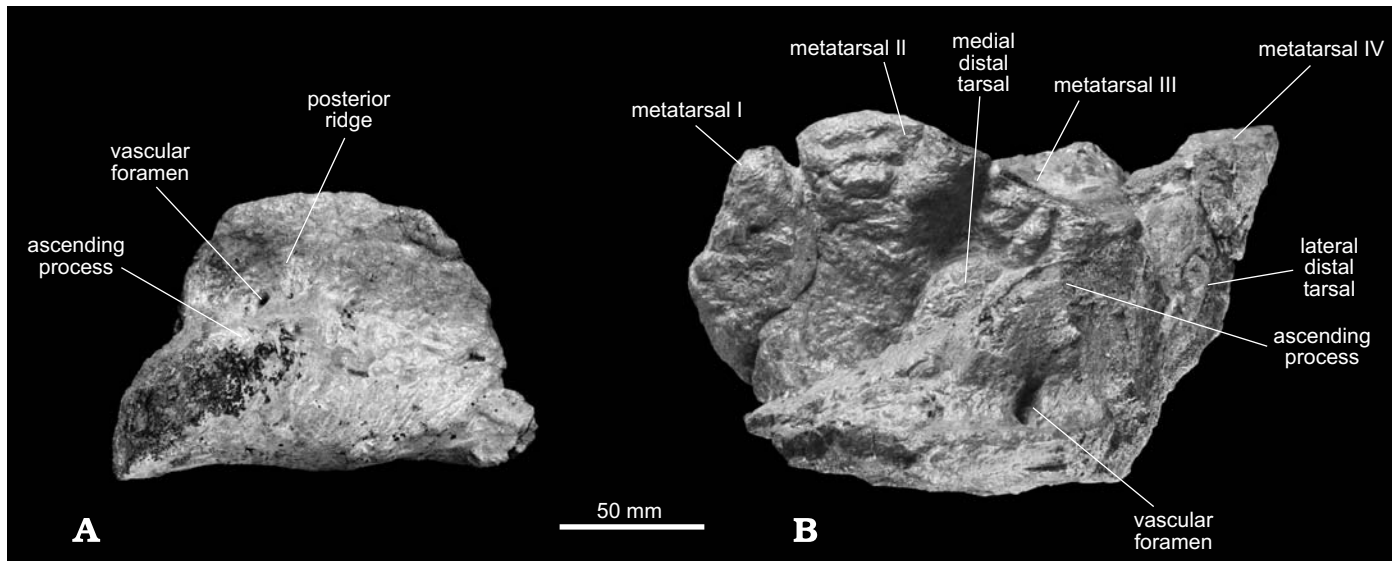
Fig. 4. Sauropodomorph dinosaur *Glacialisaurus hammeri* gen. et sp. nov. from the Early Jurassic Hanson Formation at Mt. Kirkpatrick, Beardmore Glacier region, Antarcticac. Right astragalus (FMNH PR1823) in dorsal (**A**), and posterior (**B**) views. Right distal tarsals and metatarsus have been digitally removed in A.

of the astragalus is broken, its medial portion is not broader craniocaudally than its lateral portion. In contrast, the astragali of most non-eusauropod sauropodomorphs are craniocaudally broader at their medial end than at their lateral end (e.g., *Saturnalia* [Langer 2003: 21]; *Thecodontosaurus antiquus* [Benton et al. 2000]; *Coloradisaurus* PVL 5904; *Riojasaurus* PVL 3663; *Melanorosaurus* NM QR1551; *Lessemsaurus* PVL 4822; and *Blikanasaurus* SAM-PK-K 403). The astragalus is weakly convex distally as in most basal sauropodomorphs, though the convexity is not as pronounced and "roller"-shaped as in *Blikanasaurus* (SAM-PK-K 403; Galton and Van Heerden 1998: fig. 4D), or *Lessemsaurus* (PVL 4822; Pol and Powell 2007a: fig. 11). The proximal surface of the astragalus is composed of a broadly concave surface for reception of the posterior descending process of the distal tibia, and the elevated astragalar ascending process that would articulate with the anterior region of the distal tibia. The posterior articular surface is anteroposteriorly extensive as in most non-eusauropod sauropodomorphs. Although the lateralmost region of the posterolateral articular surface is not preserved, the astragalus of FMNH PR1823 appears to lack the vertical crest present in *Barapasaurus* and most derived eusauropods (= "crest of posterior astragalar fossa" sensu Wilson and Sereno 1998). Two small pits are set in this region, within a small elliptical fossa at the base of the posterior surface of the ascending process (Fig. 4). This elliptical fossa is anteroposteriorly elongate, and the posteriorly located pit is deeper and more sharply rimmed than the anterior pit. Sauropodomorph workers have traditionally interpreted these structures as vascular foramina (Yates and Kitching 2003; Galton and Upchurch 2004; Pol and Powell 2007a), though in FMNH PR1823 both pits appear to be blind. The ascending process of the astragalus is robust and is most prominent at the anterolateral side of the astragalus (Fig. 4). As in most basal sauropodomorphs, it is mound-shaped with

its proximal articular surface (for the descending anterior process of the tibia) facing proximomedially, being slightly deflected anteriorly. The posterior edge of this ascending process articular facet extends posteromedially and projects a low ridge that divides the concave proximal articular surface of the astragalus into a medial tibial facet and a laterally positioned posterior astragalar fossa (Fig. 4). This low posterior ridge extends to the dorsal lip of the posterior border of the astragalus. No fossae or foramina are visible on the anterior side of the astragalus, but this portion of the bone is poorly preserved. The lateral edge of the astragalus is worn and damaged making any interpretation of the calcaneal and fibular articulations difficult.

Distal tarsals.—Two distal tarsals are preserved, capping the proximal ends of metatarsals III and IV (Figs. 4, 5). The medial distal tarsal is proximodistally flat and a mediolaterally elongate triangular shape in proximal aspect. Its corners are rounded with the posteromedial corner being the most robust and bulbous. The medial distal tarsal primarily caps the proximal surface of the third metatarsal, though the anteriormost several centimeters of metatarsal III are not covered in proximal view (Figs. 4B, 5A). The medial distal tarsal is not confined solely to metatarsal III, as in *Saturnalia tupinquim* (Langer 2003), but also caps a small portion of the posterolateral proximal end of metatarsal II (Figs. 4B, 5A, C). As in *Saturnalia tupinquim* (Langer 2003), the posterior portion of the medial distal tarsal is deeper than the rest of the bone, consisting of a triangular wedge between the posteroproximal tips of metatarsals II and III (Fig. 5C).

Part of the lateral distal tarsal is preserved, with half of it having been sheared off in the same plane as the lateralmost portion of the astragalus and metatarsal IV (Figs. 4, 5). Judging by the worn texture of the bone on the broken surface of
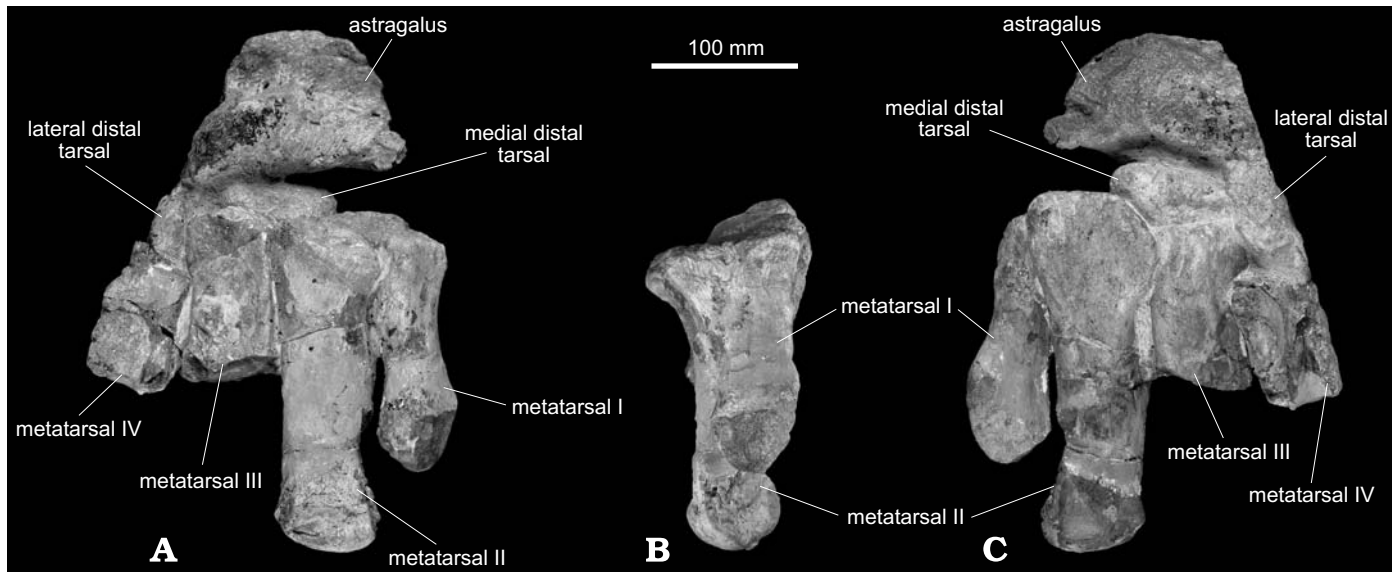
Fig. 5. Sauropodomorph dinosaur *Glacialisaurus hammeri* gen. et sp. nov. from the Early Jurassic Hanson Formation at Mt. Kirkpatrick, Beardmore Glacier region, Antarcticac. Right pes (FMNH PR1823) in anterior (**A**), medial (**B**), and posterior (**C**) views. Astragalus and distal tarsals have been digitally removed in B.

these three elements, this portion of the articulated pes may have been weathering out of the surrounding rock. The lateral distal tarsal caps the proximal surface of metatarsal IV, and both have shifted slightly distally relative to the rest of the metatarsus (Fig. 5). The lateral distal tarsal also appears to have rotated laterally approximately 90°, such that its posterior border still faces posteriorly, but its long axis (the mediolateral axis) is now oriented proximodistally (Fig. 5). This shifting would mean that it is actually the proximalmost portion of the lateral distal tarsal that has been sheared off along with the lateral portions of the astragalus and metatarsal IV. The preserved portion of the lateral distal tarsal is quadrangular and despite the loss of its proximalmost portion, was probably longer mediolaterally than proximodistally. The caudomedial prong of the lateral distal tarsal tapers to a point as in *Herrerasaurus*, *Saturnalia*, and most basal sauropodomorphs (Langer and Benton 2006). This caudomedial process would have articulated with the rounded posterolateral edge of the medial distal tarsal.

Metatarsal I.—A complete right metatarsal I is preserved in articulation with the rest of the metatarsus (Figs. 4, 5). It is rotated medially relative to the long axis of the rest of the metatarsus, such that its "anterior" border faces anteromedially. The distal end of metatarsal I is slightly twisted medially so that the transverse plane through the distal condyles forms an acute angle with the broad anteromedially facing surface of its shaft (and proximal end). A similar condition is found in other non-eusauropod sauropodomorphs such as *Plateosaurus* (FMNH UR 459) and *Lufengosaurus huenei* (Young 1947; = *L. magnus*), but contrasts with the straight metatarsal I of *Coloradisaurus* (PVL 5908) and *Massospondylus* (BPI/1/4377). The condition of FMNH PR1823 is also different from eusauropodomorph outgroups, where the shaft

of metatarsal I is markedly twisted about its long axis (*Vulcanodon* [Cooper 1984]; *Antetonitrus* BPI/1/4952; and *Blikanasaurus* SAM-PK-K 403), a morphology also present in the basal sauropodomorph *Pantydraco* (Yates 2003b: fig. 20A; Galton et al. 2007). The proximal outline of metatarsal I is an anteroposteriorly elongate diamond-shape with slightly sinuous medial and lateral borders (Fig. 4B). The proximal articular surface of metatarsal I is set at approximately 90° with respect to the proximodistal axis of the metatarsal shaft, as in all non-eusauropod sauropodomorphs. Proximally, metatarsal I reaches the same level as metatarsals II–IV and appears to have an extensive articulation with the tarsus, similar to most non-eusauropod sauropodomorphs, but unlike the condition in the basal sauropodomorph *Saturnalia tupinquim* (Langer 2003). Metatarsal I is roughly 3/4 the length of metatarsal II, as in most basal sauropodomorphs. Only the proximal half of metatarsal I is closely appressed to metatarsal II. The shaft of metatarsal I is elliptical in cross section and its midshaft width is subequal to that of metatarsal II or III (Table 1). The shaft of metatarsal I of FMNH PR1823 is relatively broad and short with respect to its length, making it more robust than that of many basal sauropodomorphs (e.g., *Saturnalia* MCP 3944-PV; *Pantydraco* [Yates 2003b; Galton et al. 2007]; *Anchisaurus* YPM 208; and *Coloradisaurus* PVL 5904), but similar in proportions to the first metatarsals of *Massospondylus* (BPI/1/4377), *Plateosaurus* (MB skelett 25; FMNH UR 459), and *Riojasaurus* (PVL 3526). Metatarsal I of FMNH PR1823 is not as stout as the first metatarsals of *Melanorosaurus* (NM QR1551), *Antetonitrus* (BPI/1/4952), and *Blikanasaurus* (SAM-PK-K 403), however. The distal end of metatarsal I is damaged, and the distal condyles are not completely preserved. Most of the lateral condyle is preserved, though much of the outermost bone has been worn away. The base of the

lateral collateral ligament pit is evident, facing anteromedially. The proximal portion of the small posterior groove separating the two distal condyles is preserved, with its long axis running proximolateral-distomedial as in *Plateosaurus* (FMNH UR 459). Most of the medial distal condyle has been broken off, but its base is preserved. It is clear that the medial distal condyle was less robust and more proximally positioned than the lateral condyle. This would have resulted in a medial displacement of the phalanges of the first digit, a morphology that is present in most saurischians (Langer 2003), including basal members such as *Herrerasaurus ischigualastensis* (Novas 1993), and *Guaibisaurus candelariensis* (Bonaparte et al. 1999; Langer 2003).

Metatarsal II.—The second right metatarsal is a robust element completely preserved in articulation with the other elements of the metatarsus (Figs. 4–6). Its proximal outline is anteroposteriorly elongate and hourglass-shaped, with concave medial and lateral borders for articulation with the proximal ends of metatarsals I and III (Fig. 4B). The medial concavity is well-developed, as in most sauropodomorphs with the exception of the group's basalmost members, where the concavity is absent (*Saturnalia* [Langer 2003]), or weakly developed (*Pantydraco* [Yates 2003b; Galton et al. 2007]). The lateral concavity of FMNH PR1823 appears to be less developed relative to the medial concavity, though the posterolateral border of the proximal articular surface of metatarsal II is ob-
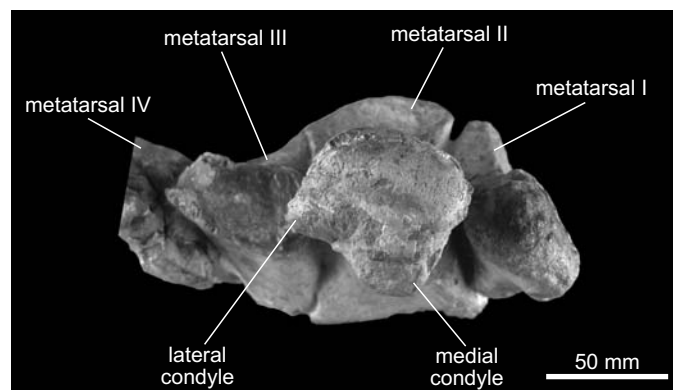

Fig. 6. Sauropodomorph dinosaur *Glacialisaurus hammeri* gen. et sp. nov. from the Early Jurassic Hanson Formation at Mt. Kirkpatrick, Beardmore Glacier region, Antarcticac. Right metatarsal II (FMNH PR1823) in distal view. Anterior is toward the top of the page. Note the medial twisting of the distal articular end, and the more robust development of the medial condyle.

scured by the medial distal tarsal. The anterior border of the second metatarsal is weakly convex in proximal aspect (Fig. 4B), in contrast to most non-eusauropod sauropodomorphs.

Posteriorly, the proximal end of the second metatarsal is expanded to cover the posterolateral and posteromedial corners of the proximal ends of metatarsals I, and III, respectively. This wing-like proximal expansion is more prominent on the lateral side where it also bears a small articular facet for

Table 1. Selected measurements of *Glacialisaurus hammeri* gen. et sp. nov. Values proceeded by an asterisk denote measurements of incomplete elements and thus represent minimums.

Measurement[1]	Value in mm[2]	Specimen
Femur length	300*	FMNH PR 1822
Femur width across distal condyles	170	FMNH PR 1822
Femur, distal anteroposterior length across popliteal fossa	91	FMNH PR 1822
Astragalus, mediolateral width, anteriorly	162*	FMNH PR 1823
Astragalus (anteroposterior length)	101	FMNH PR 1823
Medial distal tarsal, mediolateral width at widest point	88	FMNH PR 1823
Metatarsal I, length across anteromedial face	163	FMNH PR 1823
Metatarsal I, anteroposterior width at midshaft	58	FMNH PR 1823
Metatarsal I, mediolateral width at midshaft	62	FMNH PR 1823
Metatarsal II, length across anterior face	218	FMNH PR 1823
Metatarsal II, anteroposterior length at midshaft	52	FMNH PR 1823
Metatarsal II, mediolateral width at midshaft	62	FMNH PR 1823
Metatarsal III, length across anterior face	105*	FMNH PR 1823
Metatarsal III, anteroposterior length at midshaft	40	FMNH PR 1823
Metatarsal III, mediolateral width at midshaft	66	FMNH PR 1823
Metatarsal IV, length across anterior face	91*	FMNH PR 1823
Metatarsal IV, anteroposterior length at midshaft	23	FMNH PR 1823
Metatarsal IV, mediolateral width at midshaft	59*	FMNH PR 1823

[1] Measurements less than 150 millimeters were taken with a set of Mitutoyo calipers, while measurements exceeding 150 millimeters were taken with a standard tape measure.

[2] All measurements are rounded off to the nearest millimeter.

the medial distal tarsal, which faces proximolaterally (Fig. 5C). In plantar view, this articular facet is visible and extends distally along the proximal portion of the shaft as a well-developed, robust lateral flange that underlaps metatarsal III (Fig. 5C). A similar morphology of the proximal and plantar surfaces of metatarsal II is present in *Coloradisaurus* (PVL 5904), "*Gyposaurus sinensis*" (NGMJ V 108 [V43]; this specimen was originally referred to *Gyposaurus sinensis* by Young [1948], though it has been suggested to belong to a distinct taxon [Barrett et al. 2003; Upchurch et al. 2007]. Therefore, we refer herein to this specimen as "*Gyposaurus sinensis*"), *Lufengosaurus huenei* (Young 1947: fig. 7; = *L. magnus*), and *Massospondylus* (BPI/1/5241). Several other non-eusauropod sauropodomorphs have a more developed ventro-lateral wing of the proximal surface of metatarsal II (e.g., *Antetonitrus* BPI/1/4952; *Blikanasaurus* SAM-PK-K 403), though the well-developed articular facet for the medial distal tarsal on the proximolateral corner of the ventrolateral flange appears to be exclusively shared by the Antarctic sauropodomorph, *Coloradisaurus* (PVL 5904), "*Gyposaurus sinensis*" (NGMJ V 108 [V43]), and *Lufengosaurus huenei* (Young 1947: fig. 7; = *L. magnus*). In other basal sauropodomorphs (e.g., *Plateosaurus* skelett 25; SMNS 13200; *Melanorosaurus* NM QR3314), the ventrolateral flange of metatarsal II is weakly developed and not more robust than the ventromedial process.

A weak concavity on the anterior surface of the proximal end of the second metatarsal may represent part of the insertion area for the M. tibialis anterior (Dilkes 2000; Carrano and Hutchinson 2002), resembling the condition in *Saturnalia* (Langer 2003), *Plateosaurus* (MB skelett 25), *Anchisaurus* (YPM 208), *Coloradisaurus* (PVL 5904), *Massospondylus* (BPI/1/4377), and *Melanorosaurus* (NM QR3314). This concavity is more pronounced and proximodistally elongate on the anterior proximal surface of metatarsal III (Fig. 5A). The shaft of metatarsal II is relatively straight with a slight medial bow, similar to the condition in *Riojasaurus* (PVL 3526), *Anchisaurus* (YPM 208), *Lufengosaurus* (IVPP V 15), and *Blikanasaurus* (SAM-PK-K 403). The shaft of metatarsal II is subsquare in cross section, resembling the condition in *Massospondylus* (BPI/1/4377), *Antetonitrus* (BPI/1/4952), and *Blikanasaurus* (SAM-PK-K 403), and differing from the anteroposteriorly flat condition in *Plateosaurus* (FMNH UR 459), *Coloradisaurus* (PVL 5904), and the subcircular shafts of *Saturnalia* and *Melanorosaurus* (NM QR1551; NM QR3314). The distal end is expanded into well-developed articular condyles (Figs. 5, 6). The medial distal condyle is more robust and well-developed than the lateral condyle (Fig. 6), contrasting with the condition in most other non-eusauropod sauropodomorphs in which the lateral condyle is more developed. The expanded medial distal condyle results in a greater anteroposterior width of the medial side of the distal articular end of metatarsal II versus the lateral side. Posteriorly, the medial distal condyle also extends further proximally than the lateral distal condyle (Fig. 5C). The distal part of the shaft of metatarsal II is twisted

slightly medially (Fig. 6), as in *Blikanasaurus* (SAM-PK-K 403), but differing from other basal sauropodomorphs which have a straight or laterally twisted second metatarsal. The distal condyles of metatarsal II are separated posteriorly by a small groove, as in *Saturnalia* (Langer 2003), *Plateosaurus* (SMNS 13200), *Coloradisaurus* (PVL 5904), *Massospondylus* (BPI/1/4377), *Melanorosaurus* (NM QR1551), *Antetonitrus* (BPI/1/4952), and *Blikanasaurus* (SAM-PK-K 403). This groove in FMNH PR1823 is not as extensive as that of *Anchisaurus* (YPM 1883). Weak collateral pits appear to be present on the lateral and medial sides of the distal articular surface, though they are still partially filled with matrix.

Metatarsal III.—The third right metatarsal is broken mid-shaft and only the proximal portion is preserved (Fig. 5A, C). The posterior 3/4 of the proximal articular surface is capped by the medial distal tarsal. In proximal outline the third metatarsal is roughly trapezoidal, with a straight to slightly concave anterior border, a gently convex medial border for articulation with metatarsal II, an extensive posterolateral border that is overlapped by metatarsal IV, and a restricted and concave posterior border (Figs. 4, 5). The posterior edge is lateromedially narrower than the anterior border, but is not acute or rounded, thus the proximal outline of metatarsal III is subtrapezoidal. This morphology is similar to the condition in *Lufengosaurus huenei* (Young 1947: fig. 7; = *L. magnus*), "*Gyposaurus sinensis*" (NGMJ V 108 [V43]), and *Coloradisaurus brevis* (PVL 5904) in which the posterior edge of metatarsal III is expanded, resulting in a subtrapezoidal proximal outline. In contrast, most non-eusauropod sauropodomorphs have a subtriangular shaped proximal surface the third metatarsal in which the posterior edge is acute or rounded, and poorly exposed on the plantar surface of the metatarsus (e.g., *Sauturnalia* MCP 3844-PV; *Plateosaurus* MB skelett 25; *Melanorosaurus* NM QR 1551; *Antetonitrus* BPI/1/4952; *Vulcanodon* [Cooper 1984]). Other non-eusauropod sauropodomorphs also seem to have a relatively broad posterior margin of the proximal surface of metatarsal III, although their condition is either not as developed as in FMNH PR1823 and the above mentioned forms (e.g., *Massospondylus* BPI/1/4377; *Blikanasaurus* SAM-PK-K 403), or they are known from crushed, poorly preserved, and/or incompletely prepared specimens and their condition cannot be established with certainty (e.g., *Anchisaurus* YPM 1883; *Riojasaurus* PVL 3526; *Massospondylus* BPI/1/5241). Metatarsal IV has shifted distally revealing much of the proximal posterolateral articular surface of metatarsal III (Fig. 5C). As noted above, a broad fossa on the anterior surface of metatarsal III probably served as part of the insertion area of the M. tibialis anterior (Dilkes 2000; Carrano and Hutchinson 2002). This fossa is not very deep, but is proximodistally elongate. It begins on the lateral side of the anterior face of the third metatarsal and extends distally for probably at least 1/3 the length of the bone. The slight lateral orientation of the long axis of the fossa at its proximal end accords well with the hypothesized origin of the M. tibialis an-

terior on either the lateral femoral condyle, or the antero-lateral portion of the proximal tibial shaft (Carrano and Hutchinson 2002). The broken shaft of metatarsal III is elliptical in cross section, with the medial side being slightly broader anteroposteriorly than the lateral side.

Metatarsal IV.—As with metatarsal III, only the proximal portion of the fourth metatarsal is preserved (Fig. 5A, C). The lateral half has been broken off, and the bone has shifted distally (along with the lateral distal tarsal), relative to the rest of the metatarsus. In proximal outline the fourth metatarsal is similar in morphology to that of *Lufengosaurus huenei* (Young 1947: fig. 7; = *L. magnus*) in possessing a relatively broad anterior face and a finger-like posteromedial projection. This finger-like process is only slightly concave anteromedially for its articulation with the third metatarsal and meets the anterior surface of the fourth metatarsal at an obtuse angle, as in *Saturnalia* (MCP-PV 3844), *Lufengosaurus* (Young 1947: fig. 7; = *L. magnus*), *Coloradisaurus* (PVL 5904), and *Massospondylus* (BPI/1/4377). Posterolaterally, the fourth metatarsal is gently concave for its contact with metatarsal V (Fig. 5C). The shaft of the fourth metatarsal is anteroposteriorly compressed and even more transversely elongate than that of the third metatarsal. An expanded metatarsal IV with a lateral extension that overlaps the cranial surface of metatarsal V is also present in *Herrerasaurus* and most sauropodomorphs (Langer 2004).

Discussion

Comparative anatomy.— Despite their fragmentary nature, the specimens described here display several diagnostic features as well as a combination of plesiomorphic and derived characters. Within a general framework, *Glacialisaurus* can clearly be referred to Dinosauria based on the presence of a robust, pyramidal-shaped astragalar ascending process (Novas 1993; Benton 2004). The astragalus of FMNH PR1823 also possesses an elliptical basin posterior to the ascending process for articulation with the descending process of the tibia, and the caudomedial prong of the lateral distal tarsal tapers to a point, features that are both present in other sauropodomorphs and *Herrerasaurus* (Langer 2004; Langer and Benton 2006).

Glacialisaurus shares several anatomical features with sauropodomorph dinosaurs more derived than *Saturnalia tupiniquim*, *Pantydraco*, and *Efraasia* (Galton 1973; Yates 2003a; Galton et al. 2007). The kidney-shaped tibiofibular crest ("crista tibiofibularis" of Baumel and Witmer 1993) is well-separated from the femoral lateral condyle, in contrast to the condition in basal sauropodomorphs, including *Saturnalia tupiniquim* (MCP 3844-PV; Langer 2003), *Pantydraco* (Yates 2003b; Galton et al. 2007), and *Efraasia* (Galton 1973; Yates 2003a), and sauropodomorph outgroups such as *Herrerasaurus ischigualastensis* (PVL 2566), *Silesaurus opolensis* (Dzik 2003) and *Marasuchus lilloensis* (PVL 3872; Sereno and Arcucci 1994). However, the tibiofibular

crest is not as well excavated laterally and distally as it is in many coelophysoid theropods (Rauhut 2003; Tykoski and Rowe 2004; Tykoski 2005). The proximal surface of metatarsal I is diamond shaped, with its lateromedial expansion more developed than in *Pantydraco* (Yates 2003b; Galton et al. 2007b) and *Saturnalia tupiniquim* (Langer 2003), in which this surface is subelliptical. Metatarsals II and III are robustly developed with a width to length ratio greater than 0.25. As noted by previous authors (Benton et al. 2000; Galton and Upchurch 2004) this ratio represents a considerably more robust condition than the gracile metatarsal shafts typical of basal sauropodomorphs such as *Saturnalia* (Langer 2003), *Pantydraco* (Yates 2003b; Galton et al. 2007), *Efraasia* (SMNS 12354), and *Plateosaurus* (SMNS 13200; MB skelett 25; FMNH UR 459). The second metatarsal of *Glacialisaurus* is also more robust than those of *Riojasaurus* (PVL 3526), *Coloradisaurus* (PVL 5904), *Lufengosaurus* (IVPP V 15), *Massospondylus* (BPI/1/4377), and *Anchisaurus* (YPM 1883), though not as short and stout as the metatarsus of most eusauropod immediate outgroups, such as *Melanorosaurus readi* (Van Heerden and Galton 1997), *Antetonitrus ingenipes* (Yates and Kitching 2003; BPI/1/4952), and *Blikanasaurus cromptoni* (Galton and Van Heerden 1998; SAM-PK-K 403). The first metatarsal of *Glacilisaurus* is not closely appressed to the shaft of the second metatarsal throughout its length, unlike the condition in basal sauropodomorphs, such as *Thecodontosaurus caducus*, where the shaft of metatarsal I remains in contact with metatarsal II throughout its entire length (Yates 2003b). In more derived sauropodomorphs (e.g., *Anchisaurus* YPM 208; *Coloradisaurus* PVL 5904; *Plateosaurus* MB skelett 25; FMNH UR 459) metatarsals I and II are only appressed proximally, as in *Glacialisaurus*. Finally, FMNH PR1823 also possesses a second metatarsal with a concave lateral border in proximal aspect (Yates and Kitching 2003). A well-developed concave lateral facet on the proximal surface of metatarsal II is also present in most basal sauropodomorphs, with the exception of the basalmost forms (absent in *Saturnalia* [Langer 2003], and only slightly developed in *Pantydraco* [Yates 2003b; Galton et al. 2007]), and plateosaurids (Yates 2003b). As noted by previous authors, *Vulcanodon* and basal eusauropods lack a concave lateral facet for the articulation of metatarsal III (Cooper 1984; Yates 2003b). This morphology has traditionally been defined as the presence or absence of an "hourglass-shaped" proximal second metatarsal in most analyses (Sereno 1999; Benton et al. 2000; Galton and Upchurch 2004), thus incorporating information on the morphology of the medial border of the proximal second metatarsal as well. However, as noted by Yates (2003b: 30), the "prosauropod" *Plateosaurus* (FMNH UR 459; Huene 1926) possesses a second metatarsal that is concave medially, but relatively flat laterally in proximal aspect, suggesting that the "hourglass-shaped" metatarsal II morphology should be treated as two independent characters.

Additionally, several characteristics that have traditionally been interpreted as synapomorphies of Eusauropoda (and

some closely related forms such as *Lessemsaurus*, *Antetonitrus*, and *Vulcanodon*) are absent in *Glacialisaurus*. The cross section of the femur of *Glacialisaurus* is only slightly wider transversely than anteroposteriorly, differing from the strongly elliptical cross-section of the femora of *Antetonitrus* (BPI/1/4952) and eusauropods (Gauffre 1993; Wilson and Sereno 1998; Yates and Kitching 2003). Galton and Upchurch (2004) considered the femora of *Riojasaurus*, *Melanorosaurus*, and *Camelotia* as transversely widened relative to other "prosauropods", though the femora of these taxa do not have the extreme anteroposterior compression present in eusauropods (similar to the condition described above for *Glacialisaurus*). Two ossified distal tarsals are present in FMNH PR1823, which appears to represent the primitive condition for dinosaurs (Langer 2003: 23). As noted by previous authors (Gauthier 1986; Wilson and Sereno 1998), these elements are lost in *Vulcandon* and eusauropods. The posterior articular facet of the proximal surface of the astragalus of *Glacialisaurus* is well-developed in its anteroposterior length. This region (that includes the posterior astragalar fossa) is reduced in *Blikanasaurus* (SAM-PK-K 403) and *Lessemsaurus* (PVL 4822), and even more reduced in neosauropods (in which the posterolateral edge of the ascending process reaches the posterolateral astragalar margin; Wilson 2002). The absence of an extremely convex, "roller-like" astragalar distal surface in *Glacialisaurus* also distinguishes the Antarctic taxon from eusauropods and closely related taxa (e.g., *Vulcanodon*). The proximal articular surface of metatarsal I of *Glacialisaurus* is perpendicular to the proximodistal axis of this element, constrasting with the condition of most eusauropods in which the proximal surface is obliquely set with respect to the proximodistal axis of the metatarsal (Wilson 2002). Unfortunately, some potentially informative characters of the astragalus cannot be confidently assessed for *Glacialisaurus*, given the incomplete preservation of FMNH PR1823. These include the presence or absence of an anterior fossa on the astragalar ascending process. Many basal sauropodomorphs possess a small fossa on the anterior side of the astragalar ascending process (including derived forms such as *Lessemsaurus* [Pol and Powell 2007a], *Blikanasaurus*, and *Melanorosaurus* [Galton et al. 2005]). The morphology of this feature varies considerably among basal sauropodomorphs, though its absence is characteristic of eusauropods (and some of their most closely related taxa). In non-eusauropod sauropodomorphs the fossa can be deeply excavated and sharply rimmed, as in *Plateosaurus* (GPIT II), or very shallow with smooth edges, as in *Lufengosaurus huenei* (IVPP V 15), and "*Gyposaurus sinensis*" (NGMJ V 108 [V43]). Enough of the bone surface of FMNH PR1823 is preserved to suggest that a very deep, sharply rimmed fossa was not present, though the quality of preservation is not good enough to rule out the possibility of a small, shallow fossa. The caudomedial margin of the astragalus is extensive and right-angled in non-eusauropod sauropodomorphs, but is notably reduced in neosauropods (Upchurch 1995, 1998; Wilson 2002). Although a medially broad astragalus is clearly not present in FMNH PR1823, the

breakage of the medial edge of the astragalus prevents an assessment of the development of the astragalar posteromedial corner.

Hammer and Hickerson (1996) tentatively referred the Antarctic sauropodomorph specimens to the family Plateosauridae, though no detailed anatomical features besides the size and robustness of the material were cited as the basis for this referral. The present study reveals several morphological differences between the Antarctic sauropodomorph and *Plateosaurus*. First, the distal end of the tibiofibular crest of *Glacialisaurus* is lateromedially broader than anteroposteriorly long, whereas in *Plateosaurus* and other basal sauropodomorphs the opposite is present. Second, *Glacialisaurus* does not possess a deep, sharply rimmed anterior fossa on the astragalar ascending process as in *Plateosaurus* (GPIT II; though as noted above, the possible presence of a shallow fossa cannot be ruled out). Third, the Antarctic sauropodomorph differs from *Plateosaurus* (FMNH UR 459) in the possession of more robust, and less anteroposteriorly flattened metatarsals. Fourth, the proximal end of the second metatarsal of *Glacialisaurus* possesses a strongly concave medial margin with a well-developed ventrolateral flange, whereas that of *Plateosaurus* (FMNH UR 459) is almost straight in proximal aspect with a poorly developed ventrolateral flange. Finally, the proximal end of metatarsal III of *Glacialisaurus* has a relatively broad and flat posterior edge, whereas in *Plateosaurus* and other basal sauropodomorphs the proximal end is subtriangular with an acute posterior edge.

The Antarctic taxon described here shares several derived characters with *Lufengosaurus huenei* and related taxa (e.g., "*Gyposaurus sinensis*", *Massospondylus*, *Coloradisaurus*), mainly centered in their metatarsal morphology. First, the proximolateral region of the proximal end of metatarsal II bears an offset and well-developed articular facet for the medial distal tarsal in *Glacialisaurus* and the above-mentioned taxa. Distal to this articular face, on the plantar surface, the second metatarsal of *Glacialisaurus* bears a laterally projected flange that resembles the condition of *Lufengosaurus*, "*Gyposaurus sinensis*", *Massospondylus*, and *Coloradisaurus*. The proximal end of the fourth metatarsal of *Glacialisaurus* also resembles that of these sauropomorphs in the presence of a slightly concave facet for the third metatarsal. *Glacialisaurus* additionally shares with *Lufengosaurus* the presence of a relatively broad shaft of metatarsal I, being subequal in width to that of metatarsal II. This character is absent in "*Gyposaurus sinensis*", *Massospondylus*, and *Coloradisaurus*, though it is also present in other derived "prosauropods" such as *Melanorosaurus*, *Blikanasaurus*, and *Antetonitrus*.

Despite its differences and similarities with plateosaurids and other basal sauropodomorphs, *Glacialisaurus* is considered a distinct taxon based on several morphological features that distinguish it from most previously described "prosauropods". The presence of a robust medial epicondylar ridge on the distal femur is an autapomorphic feature for a sauropodomorph. This feature is convergently present in basal

theropods, though is much thicker anteroposteriorly in *Glacialisaurus* than the medial epicondylar flanges typical of many early theropod dinosaurs (Carrano et al. 2002; Rauhut 2003). This flange likely separated the distal portions of the two Mm. femorotibiales components (M. femorotibiales externus, and M. femorotibiales internus), and may also have served as the origin for a subdivision of M. femorotibialis externus (Carrano and Hutchinson 2002: 213–214). The femur also bears a well-developed adductor ridge above its medial condyle. The prominent development of the adductor ridge of *Glacialisaurus* differs from the morphology of other sauropodomorphs (e.g., *Anchisaurus* YPM 1883; *Antetonitrus* BPI/1/4952; *Coloradisaurus* PVL 5904; *Lessemsaurus* PVL 4822; and *Lufengosaurus* IVPP V15). Robust adductor ridges are convergently present in a variety of other dinosaurian taxa, including some theropods, ankylosaurs, and ornithopods (Paul M. Barrett, personal communication 2007).

Though several features in the referred femur of *Glacialisaurus* suggest possible theropod affinities (e.g., medial epicondylar crest, robust adductor ridge, deep intercondylar sulcus on distal end), FMNH PR1822 is clearly not attributable to *Cryolophosaurus* (see discussion in Introduction). Furthermore, several of the characteristics shared with theropods exhibit a different morphology in FMNH PR1822. For example, the medial epicondlyar ridge of *Glacialisaurus* is much thicker anteroposteriorly than the gracile, crest-like ridge of basal theropods (Rauhut 2003; Tykoski and Rowe 2004), and it lacks any well-defined fossa or excavation on its anterior surface, such as is present in several basal theropods (e.g., *Carnotaurus* MACN CH 894, *Dilophosaurus* UCMP 77270). Several other features of FMNH PR1822 (e.g., moderate anteroposterior compression of midshaft; mediolaterally wide tibiofibular crest) are only present in sauropodomorph taxa (e.g., *Melanorosaurus* SAM-PK-K 3450, *Lufengosaurus* IVPP V15). Finally, the relative size of FMNH PR1822 is consistent with what would be expected based on the size of the holotype metatarsus (FMNH PR1823), and both elements appear to possess congruent, albeit limited, phylogenetic information (see below).

Most of the diagnostic characters of *Glacialisaurus* are concentrated in the morphology of the second metatarsal. The proximal surface of this metatarsal displays the typical "hour-glass" shape present in most basal sauropodomorphs, though its anterior border is convex, whereas other forms have an anterior border that is straight or slightly concave (e.g., *Plateosaurus* SMNS 13200; *Lufengosaurus* (IVPP V15; Young 1947), *Melanorosaurus* NM QR 1551; *Blikanasaurus* SAM-PK-K 403; *Vulcanodon* [Cooper 1984]; and *Massospondylus* BPI/1/ 4377). The hypertrophied lateral flange on the proximolateral region of the plantar surface of metarsal II is also distinct in *Glacialisaurus* with respect to other basal sauropodomorphs. As noted above, this feature is present in some basal sauropodomorphs (*Coloradisaurus*, "*Gyposaurus sinensis*", *Lufengosaurus*, and *Massospondylus)*, though in these forms the flange is clearly less developed.

The second metatarsal is also unusual in being medially twisted along its proximodistal axis at the distal end of its shaft. This condition is otherwise only found (and slightly less developed) in *Blikanasaurus* (SAM-PK-K 403). It must be noted, however, that the distal shaft of the second metatarsal has been repaired during preparation, such that some of the medial twisting in FMNH PR1823 may have been artificially accentuated. Irrespective of the degree to which the second metatarsal of *Glacialisaurus* is medially twisted, its condition clearly differs from the untwisted metatarsal II of *Plateosaurus* (MB skelett 25) and *Saturnalia* (MCP 3844-PV), or the second metatarsals of *Antetonitrus* (BPI/1/ 4952) and *Massospondylus* (BPI/1/4377) that are slightly twisted laterally. Finally, the medial distal condyle of the second metatarsal is more robust and well-developed than the lateral distal condyle. The only other taxon that approaches this condition is *Blikanasaurus* (SAM-PK-K 403) in which the condyles are subequally developed. Other basal sauropodomorphs, such as *Antetonitrus* (BPI/1/4377), *Melanorosaurus* (NM QR1551), *Plateosaurus* (MB skelett 25), *Coloradisaurus* (PVL 5904), *Massospondylus* (BPI/1/4377), and *Saturnalia* (MCP 3844-PV), show the opposite condition in which the lateral condyle is more developed than the medial one.

Phylogenetic position.—Despite its fragmentary nature, the Antarctic taxon retains a combination of plesiomorphic and derived characteristics that imply somewhat of an intermediate position within sauropodomorph phylogeny, along with other sauropodomorphs traditionally classified as "prosauropods". Unfortunately, relationships in this part of the sauropodomorph tree are currently unstable and highly contested (Benton et al. 2000; Yates 2003b, 2004, 2007a, b; Yates and Kitching 2003; Galton and Upchurch 2004; Leal et al. 2004; Pol 2004; Barrett et al. 2005, 2007; Pol and Powell 2005, 2007b; Upchurch et al. 2007). A detailed analysis and revision of basal sauropodomorph phylogeny is beyond the scope of the present paper. However, in order to assess the relationships of the Antarctic sauropodomorph, a preliminary phylogenetic analysis was performed using one of the most exhaustive phylogenetic analyses of basal sauropodomorphs published to date (Yates 2007a, b). Several characters were added to the dataset (Appendix 1), and one character was recoded for *Melanorosaurus* (Character 243: 1→0; Adam M. Yates, personal communication 2006). The phylogenetic analysis was peformed using PAUP* 4.0b10 (Swofford 2002). 36 characters were treated as ordered, following Yates (2007a). A heuristic search was performed with 5,000 random addition sequence replicates to find the most parsimonious trees for the data matrix. Tree bisection and reconnection (TBR) was utilized as the branch swapping algorithm for the heuristic search. Character-state transformations were evaluated under both ACCTRAN and DELTRAN optimizations. Support for the resulting most parsimonious trees (MPTs) was quantified by performing a bootstrap analysis (Felsenstein 1985). Heuristic searches were performed on 2,000 pseudoreplicate datasets, with 10 random addition sequence replicates for each
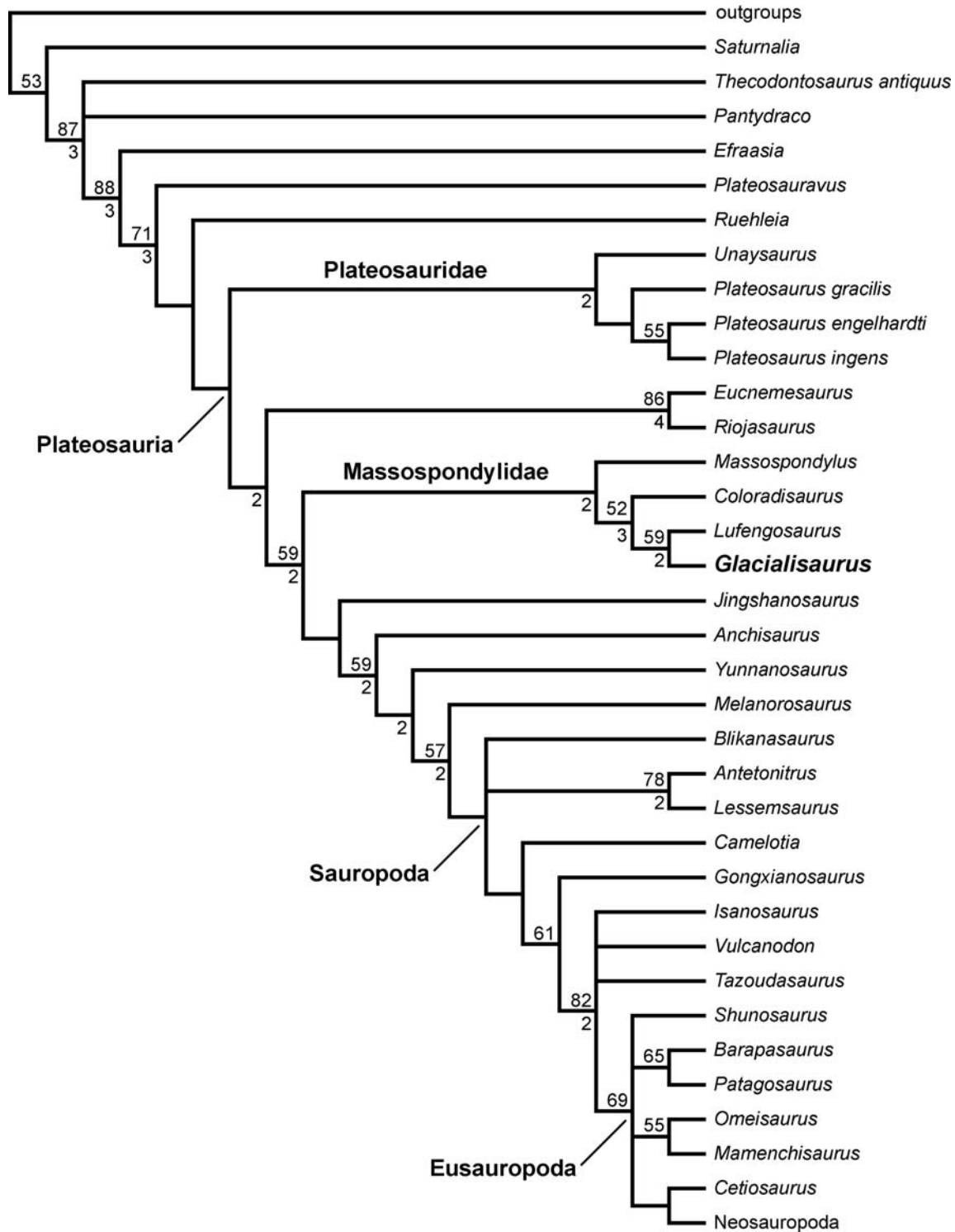
Fig. 7. Phylogenetic analysis of basal sauropodomorph dinosaurs based on Yates (2007a, b), and including *Glacialisaurus* and several novel characters (see Appendix 1). Bootstrap values greater than 50% are listed above nodes, and Bremer decay indices greater than 1 are listed below nodes. Relationships among non-sauropodomorph taxa (here collapsed into an "outgroup" lineage) are identical to those recovered in Yates (2007a, b). Several taxon labels (in bold) follow Yates (2007b).

search. The maximum number of trees saved for each random addition sequence replicate was set to 100 to prevent the searches from becoming stuck on a large island of MPTs during any particular random addition sequence replicate. While this strategy drastically reduces the amount of tree space explored for any given random addition sequence replicate, it does allow for a much larger number of bootstrap replicates to be performed. Bremer support values were also calculated

for each node in the strict consensus of all MPTs using TreeRot.v2c (Sorenson 1999).

The phylogenetic analysis resulted in the recovery of 60 MPTs, each of 1106 steps, with a consistency index of 0.378, and a retention index of 0.698. The strict consensus of the 60 MPTs and support values for each node are presented in Fig. 7. The Antarctic sauropodomorph is recovered as sister-taxon to *Lufengosaurus* from the Early Jurassic Lufeng Formation of China. This clade is supported by two unambiguous synapomorphies: a first metatarsal that is as wide or wider than metatarsal II (Character 331: 0→1; convergently present in *Jingshanosaurus, Yunnanosaurus, Melanorosaurus, Blikanasaurus Antetonitrus, Gongxianasaurus*, and most eusauropods); and the presence of a tibiofibular crest that is wider mediolaterally than deep anteroposteriorly (Character 356: 0→1; convergently present in *Melanorosaurus, Antetonitrus, Isanosaurus*, and Neosauropoda). *Coloradisaurus* is recovered as the sister-taxon of the *Glacialisaurus* + *Lufengosaurus* clade. This relationship is supported by six unambiguous synapomorphies, including: a well-developed ventrolateral plantar flange on the proximal end of metatarsal II that extends further laterally than the ventromedial plantar flange (Character 354: 0→1; convergently present in *Blikanasaurus, Antetonitrus, Lessemsaurus*, and *Tazoudasaurus*); and the presence of a well-developed postero-proximolaterally facing facet on the proximolateral corner of the ventrolateral plantar flange of metatarsal II for articulation with the medial distal tarsal (Character 357: 0→1). *Massospondylus* is recovered as the sister-taxon of the (*Coloradisaurus* [*Glacialisaurus* + *Lufengosaurus*]) clade, constituting a stem-based group Yates (2007b) designated Massospondylidae. This clade is diagnosed by eight unambiguous synapomorphies, but unfortunately, none of them can be assessed for the Antarctic taxon (e.g., Character 318: 0→1, presence of a pyramidal dorsal process on the posteromedial corner of the astragalus).

Though the phylogenetic analysis resulted in a completely resolved placement of *Glacialisaurus*, these results should be interpreted with caution for several reasons. First, very few characters can be reliably scored for the Antarctic taxon, resulting in little positive evidence for its phylogenetic placement. Also, the resolved position of *Glacialisaurus* as sister-taxon to *Lufengosaurus* is at least partially supported by several characters that are convergently present in many closely related eusauropods and their immediate outgroups (i.e., the absence of these features in *Massospondylus* and *Coloradisaurus* is crucial to them being interpreted as synapomorphies of a *Glacialisaurus* + *Lufengosaurus* clade, and not as diagnostic of a more inclusive group). Finally, basal sauropodomorph phylogeny is currently in a state of revision, and many vastly different hypotheses of relationships have recently been proposed (Benton et al. 2000; Yates 2003a, b, 2007a, b; Yates and Kitching 2003; Galton and Upchurch 2004; Pol 2004; Barrett et al. 2005, 2007; Pol and Powell 2005, 2007b). In particular, the taxonomy of Chinese sauropodomorphs, including *Lufengosaurus*, requires additional at-

tention (Barrett et al. 2005, 2007). Even accepting any particular author's hypothesis of relationships, few reliable morphological characters in the distal femur and metatarsus exist that are diagnostic of less inclusive sauropodomorph clades. Galton and Upchurch (2004: 257) observed this phenomenon in their phylogenetic analysis of basal sauropodomorphs, noting that synapomorphies of the more highly nested "prosauropod" clades are strongly biased toward cranial, rather than postcranial, modifications. Accordingly, though the results of the phylogenetic analysis presented here represent a useful initial test of the relationships of the new Antarctic taxon, they should be viewed as tentative, subject to further revision of the basal sauropodomorph record. Additionally, more complete remains of *Glacialisaurus* would greatly improve our knowledge of its phylogenetic affinities.

Temporal and biogeographic implications.—Though the recovery of *Glacialisaurus* as sister-taxon to *Lufengosaurus* from the Early Jurassic Lufeng Formation of China lends support to the interpretation of the sediments of the Hanson Formation as being Early Jurassic in age (Elliot 1996), the lack of robust support for the phylogenetic placement of the Antarctic taxon, and of current consensus on basal sauropodomorph relationships, limits its potential utility as a biostratigraphic control on the age of the Hanson Formation (Hammer and Hickerson 1996). Other vertebrate material collected from the Hanson Formation, including the theropod *Cryolophosaurus ellioti*, a partial pterosaur humerus and a tritylodont tooth (Hammer and Hickerson 1994), remain to be studied in more detail, though it is unlikely that detailed biostratigraphic information (i.e., Stage level or below) could be gleaned from this material. The primary age control on the Hanson Formation thus remains the relative stratigraphic position of this unit, and the few radiometric dates that have been recovered, which suggest that the Hanson Formation is Early Jurassic in age (reviewed in Elliot 1996).

Along with the partial remains of a possible sauropod dinosaur collected during the 2003–2004 field season (material currently still being prepared, William R. Hammer, personal communication 2006), the material described here constitutes the entirety of the sauropodomorph fossil record from the Antarctic continent. The paleolatitude of the Hanson Formation vertebrate locality was at least 55° South, and possibly as high as 65° South, during the Early Jurassic (~Pliensbachian) (Rees et al. 2000). This would make the Antarctic taxon one of the highest-paleolatitude sauropodomorphs known from the Jurassic. Basal sauropodomorphs appear to have attained a nearly worldwide distribution by the end of the Late Triassic (Galton and Upchurch 2004). Basal sauropodomorphs present in the Early Jurassic include *Glacialisaurus* from Antarctica; *Anchisaurus polyzelus* and several undescribed taxa from the Eastern and Western United States (Attridge et al. 1985; Galton and Upchurch 2004; Loewen et al. 2005; Fedak and Galton 2007); "*Gyposaurus sinensis*", *Jingshanosaurus, Lufengosaurus, Yimenosaurus*, and *Yunnanosaurus* from China (Young 1941a,b, 1942; Bai et al.

1990; Zhang and Yang 1994; Galton and Upchurch 2004); *Massospondylus*, *Gryponyx africanus*, and three new taxa from southern Africa (Cooper 1981; Gow 1990; Gauffre 1993; Barrett 2004; Galton and Upchurch 2004; Sues et al. 2004; Vasconcelos and Yates 2004; Yates et al. 2006); and undescribed remains from India (Galton and Upchurch 2004); suggesting that basal sauropodomorphs maintained a global distribution into the middle part of the Early Jurassic. The recent recovery of a possible sauropod dinosaur from the Hanson Formation lends additional evidence to the theory that the earliest sauropods coexisted with their basal sauropodomorph cousins during the Late Triassic–Early Jurassic (Buffetaut et al. 2000; Galton and Upchurch 2004; Barrett and Upchurch 2005, 2007). However, given the current lack of consensus on the phylogenetic relationships of basal sauropodomorph dinosaurs, as well as disagreements between authors on taxonomic content, it is difficult to determine if the geographic radiation of basal sauropodomorphs temporally preceded, or was contemporaneous with, the geographic radiation of the earliest sauropod dinosaurs.

Acknowledgements

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Appendix 1

Additional character descriptions and modifications to the data matrix of Yates (2007a, b).

354. Lateral extent of ventrolateral flange on plantar surface of MT II in proximal aspect: similar in development to ventromedial flange (0); well-developed, extending further laterally than ventromedial flange extends medially (1).

The emphasis here is placed on the relative lateral/medial extents of the ventrolateral and ventromedial plantar flanges of MT II in proximal aspect, and not necessarily the degree of development, or robustness of either flange. For example, *Massospondylus* (BPI/1/5241) possesses a robustly developed ventrolateral flange, but it does not extend significantly laterally relative to the medial extension of the ventromedial flange.

355. Distal articular surface of astragalus: relatively flat or weakly convex (0); extremely convex and "roller-shaped" (1)

Most basal sauropodomorphs retain an astragalus with a ventral surface that is flat or only slightly convex. Most sauropods and taxa traditionally refered to as "Melanorosaurids" possess an astragalus with an extremely convex, "roller"-like distal articular surface. These taxa include *Lessemsaurus* (PVL 4822; Pol and Powell 2007a: fig. 11), *Melanorosaurus* (NM QR1551; Van Heerden and Galton 1997: 48), *Blikanasaurus* (SAM-PK-K 403; Galton and Van Heerden 1998: fig. 4D), *Vulcanodon* (Raath 1972: 19; Cooper 1984: figs. 23, 25), and *Kotasaurus* (Yadagiri 2001: 249). Van Heerden and Galton (1998: 165) suggested that the convex morphology of the distal astragalar surface formed a "rolling joint" with the two distal tarsals. Though Galton (1976: 47) describes the ventral astragalar surface of *Anchisaurus polyzelus* as "gently convex", he also notes that this specimen (YPM 1883) has been "considerably compressed to form a thin, capping plate that is probably only about a third of its original thickness". Due to this proximodistal compression, the degree of convexity of the ventral articular surface of the astragalus of *Anchisaurus polyzelus* cannot be assessed with confidence, and this taxon is coded as missing data for this character. Similarly, the astragali of both specimens (YPM 208, 209) of *Ammosaurus major* (considered a junior synonym of *Anchisaurus polyzelus* by Yates 2004) are either compressed or incomplete (Galton 1976: 58, 66), preventing any assessment of the relative convexity of the ventral astragalar surface.

356. Distal surface of tibiofibular crest: as deep anteroposteriorly as wide mediolaterally or deeper (0); wider mediolaterally than deep anteroposteriorly (1).

In several large-bodied sauropodomorphs, including *Glacialisaurus* (FMNH PR1823), *Lufengosaurus huenei* (IVPP V15; Young 1947: figs. 6, 12; = *L. magnus*), *Melanorosaurus* (SAM-PK-K 3450), *Antetonitrus* (BPI/1/4952), *Isanosaurus*, and neosauropods, the tibiofibular crest is bulbous and mediolaterally wide relative to its anteroposterior depth.

357. Well-developed facet on proximolateral corner of plantar ventrolateral flange of MT II for articulation with medial distal tarsal: absent (0); present (1)

Many sauropodomorph taxa possess a well-developed ventrolateral flange on the plantar surface of the proximal end of

Table 2. Additional character codings for the taxa from Yates (2007a, b)[1].

Taxon	Characters 354–361
Euparkeria	????????
Crurotarsi	00–0??00
Marasuchus	????????
Silesaurus	00000?0?
Ornithischia	?000????
Herrerasaurus	00000000
Staurikosaurus	????????
Eoraptor	????????
Agnosphitys	????????
Guaibasaurus	0??0????
Chindesaurus	????????
Neotheropoda	00000?1?
Saturnalia	00000000
Thecodontosaurus antiquus	?0??????
Pantydraco	0??00000
Efraasia	??0???00
Plateosauravus	????????
Ruehleia	????????
Unaysaurus	????????
Plateosaurus gracilis	????????
Plateosaurus engelhardti	00000011
Plateosaurus ingens	????????
Eucnemosaurus	????????
Riojasaurus	????????
Massospondylus	0?00?011
Coloradisaurus	1?011?11
Lufengosaurus	10111011
Jingshanosaurus	????????
Anchisaurus	??0????1
Yunnanosaurus	?0???11?
Melanorosaurus	01100?11
Blikanasaurus	11?0?1?1
Antetonitrus	1?100??1
Lessemsaurus	11?????1
Camelotia	????????
Gongxianosaurus	????????
Isanosaurus	?110??1?
Vulcanodon	?1??00?1
Tazoudasaurus	1??0????
Shunosaurus	????????
Barapasaurus	????????
Patagosaurus	????????
Omeisaurus	????????
Mamenchisaurus	?1??????
Cetiosaurus	????????
Neosauropoda	?11???11

[1] Codings for characters 1–353 are as given in Yates (2007a) with the exception of character 243, which is recoded as "0" for *Melanorosaurus* (Adam M. Yates, personal communication 2006).

metatarsal II. This flange overlaps the proximal plantar surface of metatarsal III and also participates in an articulation with the medial distal tarsal. In several taxa, including the Antarctic sauropodomorph, *Coloradisaurus* (PVL 5904), *Gyposaurus siensis* (NGMJ V 108 [V43]), and *Lufengosaurus huenei* (Young 1947: fig. 7; = *L. magnus*), a well-defined facet is present on the proximolateral corner of the plantar ventrolateral flange of MT II for articulation with the medial distal tarsal. This facet can be seen as a small divot or depression on the proximolateral corner of MT II when viewed in plantar aspect. Thus, the facet faces postero-proximolaterally, as opposed to the rest of the proximal facing articular surface of MT II.

358. Proximal outline of metatarsal III: subtriangular with acute or rounded posterior border (0); subtrapezoidal, with posterior border broadly exposed in plantar view (1).

359. Angle formed by the anterior and anteromedial borders of metatarsal IV: obtuse (0); right angle, or acute (1).

The anteromedial border of metatarsal IV is the often concave in sauropopodomorphs and laps under the posterolateral edge of metatarsal III as an extended finger-like process. In most basal saurpodomorphs the angle formed between this border and the anterior border of metatarsal IV is relatively wide (e.g., *Plateosaurus* [MB skelett 25], *Massospondylus* [BPI/1/4377], *Saturnalia* [MCP-PV 3844], *Glacialisaurus* [FMNH 1823]).

In several sauropodomorph taxa, including *Yunnanosaurus* (Young, 1942) and *Blikanasaurus* (SAM-PK-K 403), the angle formed by the anterior and anteromedial borders of the fourth metatarsal is close to 90°, or even acute.

360. Well-developed tibiofibular crest on distal femur: absent (0); present (1).

Silesaurus opolensis (Dzik 2003), *Herrerasaurus ischigualastensis* (PVL 2566), *Saturnalia tupiniquim* (MCP 3844-PV; Langer 2003), *Pantydraco* (Yates 2003b; Galton et al. 2007), and *Efraasia* (SMNS 12354; Galton 1973; Yates 2003a) all possess a weakly defined tibiofibular crest. In most other sauropodomorphs the tibiofibular crest is distinctly kidney-shaped and its borders are well excavated. This morphology may be size-related, though many small coelophysoid theropods also possess a well-defined tibiofibular crest.

361. Shaft of metatarsal I: closely appressed to metatarsal II throughout its length (0); or only closely appressed proximally, with a space between metatarsals I and II distally (1).

Saturnalia tupiniquim (MCP 3844-PV; Langer 2003), *Pantydraco* (Yates 2003b; Galton et al. 2007), and *Efraasia* (Galton 1973; Yates 2003a) retain a slender first metatarsal that is closely appressed to metatarsal II throughout its length (Yates 2003b: fig. 20A). In more derived sauropodomorphs the first metatarsal splays medially from the second metatarsal at its distal end.

Table 3. Full coding for *Glacialisaurus hammeri*. Multiple codings in parentheses represent uncertainty between several states.

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