VOLUME 39
PART 3

MEMOIRS

OF THE

QUEENSLAND MUSEUM

Minister: Hon. J. Sheldon, MLA
Director: A. Bartholomai, MSc, PhD
Editor: F. A.NOVAS, PhD & R.E. MOLNAR, BSc, PhD

PUBLISHED BY ORDER OF THE BOARD 20 DECEMBER, 1996

AN ANTARCTIC CRETACEOUS THEROPOD

R.E. MOLNAR, ALEJANDRO LOPEZ ANGRIMAN & ZULMA GASPARINI

Molnar, R.E., López Angríman, A. & Gasparini, G. 1996 12 20: An Antarctic Cretaceous theropod. *Memoirs of the Queensland Museum* **39**(3): 669-674. Brisbane. ISSN 0079-8835.

The distal part of a theropod tibia has been recovered fromthe Coniacian-Santonian Hidden Lake Fm. near Cape Lachmann, James Ross Island. The piece closely resembles the corresponding region in *Megalosaurus* and, more closely, in *Piatnitzkysaurus*. This suggests that a persistently plesiomorphic tetanuran lineage inhabited the Antarctic. The relatively small size of the animal argues against a mean annual temperature below 15°C in its environment. ☐ *Antarctica, theropod, Late Cretaceous, biogeography, tetanuran.*

R.E. Molnar, Queensland Museum, P.O. Box 3300, South Brisbane, Queensland, 4101, Australia; Alejandro López Angríman, BRIDAS, Av. L. N. Alem 1180, (1001) Buenos Aires, Argentina; Zulma Gasparini, Depto. Paleontología de Vertebrados, Museo de La Plata, (1900) La Plata, Argentina; 5 July 1996.

During the summer of 1988 one of the authors (A.L.A.) discovered a small bone in the Cretaceous deposits 4km north of Col Crame, in the Cape Lachman region, northwestern James Ross Island (Fig. 1). In a basin in the northwestern sector of the Weddell Sea, the origin of the island is related to the opening of that sea during the breakup of Gondwanaland (Medína et al., 1992). The specimen derives from the middle section of the Hidden Lake Fm., Gustav Gr. (Ineson et al., 1986), referred to the Coniacian-Santonian (Buatois & López Angríman, 1992a). It is the first Cretaceous Antarctic theropod and the oldest Cretaceous tetrapod from Antarcica.

Prior to Angríman's discovery, ornithischians were the only Cretaceous dinosaurs known from Antarctica (Gasparini et al., 1987; Olivero et al., 1991; Hooker et al., 1991). The Late Cretaceous theropods from New Zealand (Molnar & Wiffen, 1994) imply that theropods also lived in Antarctica at that time (cf. Molnar, 1989) but this discovery verifies their occurrence and helps fill out our knowledge of Antarctic faunal evolution. A theropod is known from the Early Jurassic of Antarctica (Hammer & Hickerson, 1994).

Collection designations. ANSP, Academy of Natural Sciences, Philadelphia; MLP, Departamento de Paleontología Vertebrados, Museo de La Plata, La Plata.

DESCRIPTION

The specimen (MLP: 89-XII-1-1) is the distal end — representing probably 10-15% of the total length — of a left tibia. The piece is complete save for very small portions of the extremities of the medial malleolus and the flange that backs the fibula. In general form it is (Fig. 2) is similar to the corresponding part of the tibia in *Megalosaurus bucklandi*, *Piatnitzkysaurus floresi* and *Poekilopleuron bucklandii*. Seen from the front, the shaft is expanded laterally to form a broadly rounded post-fibular flange, and medially into an angularly truncate medial malleolus. A broad, flat-surfaced prominence proximomedially bounds the ascending process and dorsal face of the astragalus, extending proximolaterally across the anterior face from the medial malleolus. Its edges are marked by sharp angulations. This is termed the medial buttress. The posterior face is almost flat but with a slight longitudinal concavity laterally. Above the post-fibular flange the surface of this concavity abruptly slopes anteriorly to meet the anterior surface of the shaft at a sharp edge.

The broken end reveals a central cavity surrounded by relatively thin-walled bone (Fig. 2D). The shaft is tear-shaped in section at the break. Fragments of bone in the calcite fill of the central cavity suggest that the shaft was crushed just above the broken end before or shortly after burial. The distal end is slightly concave from the front and triangular when viewed distally, with the anterior surface forming the longest edge and the inclined lateral edge the shortest. The distal surface is shallowly concave in the middle, becoming mildly convex both medially and laterally.

The form of the anterior surface of the distal tibia (Fig. 2C) indicates that the ascending process of the astragalus was moderately low, relatively narrow and restricted to the lateral half of the tibial shaft. Thus the astragalus would have been unlike those of ornithomimosaurs or tyrannosaurs in form, but probably much like that of *Poekilopleuron bucklandii.*

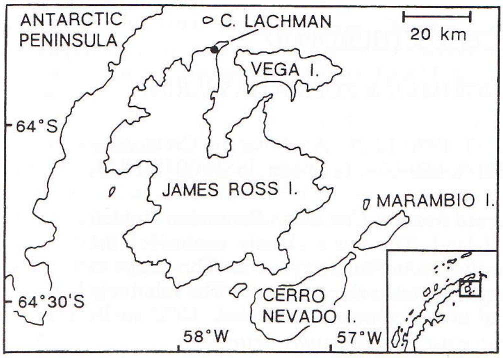

FIG. 1. Map of James Ross Island, showing where the theropod tibia was found (dot). C=Cape, I=Island.

IDENTIFICATION. The general form and relatively thin-walled hollow shaft indicate that this tibia derives from a theropod. Dryosaurs have also been reported with thin-walled limb elements (Chinsamy, 1995) and dryosaurs or similar forms are known from Late Cretaceous New Zealand (Wiffen & Molnar, 1989), hence probably inhabited Antarctica at this time. However no other dinosaurs have the astragalar ascending process set into a depression of the anterior face of the distal tibia, dorsomedially bounded by an abrupt step or offset in the anterior face. This feature is characteristic of neotheropods (Sereno et al., 1994), and isn't found in herrerasaurs (Fig. 3). The truncate medial malleolus also occurs in a restricted group of theropods (Table 1), but this probably represents a stage in the evolution of distal tibial form (Fig. 3).

The work on theropod astragali of Welles & Long, 1974, (with the correction of Carpenter, 1992) accords well with recent phylogenetic analyses of theropods (Holtz, 1994; Russell & Dong, 1993; Sereno et al., 1994). A general tendency toward increased height and breadth of the ascending process can be seen in the lineage leading to arctometatarsalians (Fig. 3). Furthermore, a survey of figured tibiae indicates that distal tibial form is reasonably distinctive for the recognised theropod groups (Table 1).

The distal tibia of ceratosaurs is variable because of the evolution of the ankle in this group. In distal view the tibia is not anteroposteriorly compressed in the Triassic and Early Jurassic forms, as it is in later ceratosaurs and tetanurans. The ascending process is absent or low and narrow, the medial buttress is absent in *Coelophysis* and *Syntarsus* but present in *Dilophosaurus*, and the medial malleolus is quite subdued or absent in *Coelophysis* and *Dilophosaurus* but present and angular in *Syntarsus* (Raath, 1969; Welles, 1984; Colbert, 1989). Early ceratosaurs, e.g., *Coelophysis*, (and herrerasaurs) lack an ascending process and the astragalus interlocks with an offset distal surface of the tibia, the offset being visible anteriorly (Padian, 1986, fig. 5.5).

The neoceratosaur distal tibia is known only in *Ceratosaurus* and *Xenotarsosaurus*, where the distal expansion is approximately symmetrical and the fossa for the ascending process low. In *Ceratosaurus* the medial buttress is broad with the 'step' extending nearly horizontally at least 2/3 of the way across the shaft (about halfway in the Hidden Lake specimen) and the medial malleolus does not extend as far proximally along the shaft, so is more pointed in anterior view (Gilmore, 1920); the distal tibia of *Xenotarsosaurus* is similar but with a broadly rounded malleolus (Martinez et al., 1987). Dromaeosaurs (i.e., *Deinonychus antirrhopus*) have a broad, high, ascending process, lack the medial buttress — probably correlated with the broadening of the ascending process — and have a broadly rounded medial malleolus (Ostrom, 1969). Arctometatarsalian theropods also have a broad, high ascending process and lack the medial buttress, and have a nearly symmetrical distal end (in anterior or posterior view) with no distinctive form to the medial malleolus (Welles & Long, 1974). Other coelurosaurs (e.g., *Calamosaurus*) similarly have a high, broad ascending process and no medial buttress but the medial malleolus is similar in silhouette, from in front, to that of the Hidden Lake tibia (Lydekker, 1891). There is little data available on oviraptorosaurs, but judging from *Chirostenotes* and *Microvenator*, the form is similar to that in arctometatarsalians, with the exception that the fibular flange seems truncate in the former genus (Ostrom, 1970; Currie & Russell, 1988). The segnosaur distal tibia remains unknown or undescribed. That of *Yangchuanosaurus* shows a low ascending process, a medial buttress different in form and an angular medial malleolus (Dong et al., 1983). In *Sinraptor* the ascending process is low and narrow, the medial buttress essentially similar to that of *Ceratosaurus*, and with an angular medial malleolus (Currie & Zhao, 1993). In distal view the tibia is more anteroposteriorly compressed. *Allosaurus* has a broader, higher ascending process, a narrower medial buttress, and a generally similar medial malleolus that is, however, more medially projecting and more rounded in outline (Gilmore, 1920; Madsen, 1976).

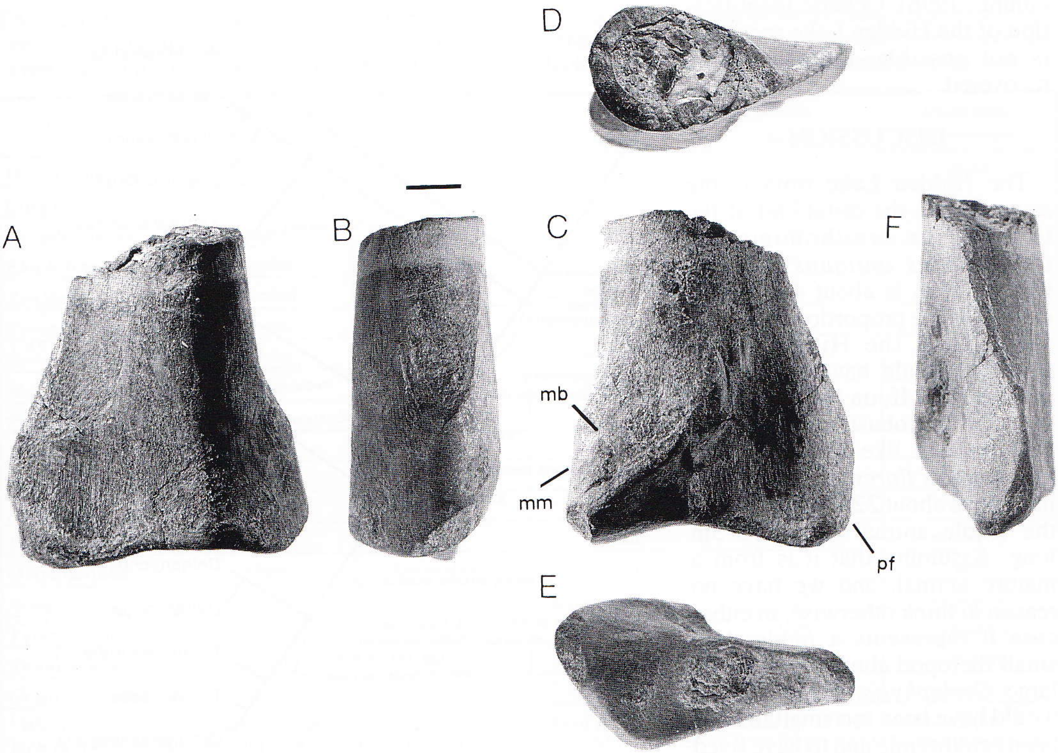

FIG. 2. The theropod distal tibia (MLP: 89-XII-1-1) from the Hidden Lake Fm., James Ross Island, in: A, posterior; B, medial; C, anterior; D, proximal; E, distal; and F, lateral views. mb=medial buttress, mm=medial malleolus, pf=flange behind fibula, scale = 1cm.

The distal tibiae of *Megalosaurus bucklandi* (Huxley, 1870; Hulke, 1879) and *Poekilopleuron bucklandii* (Eudes-Deslongchamps, 1837) — possibly related forms — *Erectopus superbus* (Sauvage, 1882) — of uncertain affinities — and *Piatnitzkysaurus floresi* (Bonaparte, 1986) — a plesiomorphic allosauroid — are the most similar. However, the tibiae of torvosaurids (specifically *Afrovenator abakensis*, *Eustreptospondylus oxoniensis* and *Torvosaurus tanneri*), animals similar in other ways to megalosaurs, differ in having an angular medial malleolus (e.g., Britt, 1991). Of those with similar distal tibiae, the most similar is that of *P. floresi*, which matches that of the Hidden Lake theropod in the forms of the medial malleolus and buttress — particularly the curve of the step adjacent to the facet for the astragalar ascending process — and the fibular flange. The distal tibiae of the previously noted megalosaurs, and of *Erectopus*, differ in that the fibular flange projects distally, forming the distalmost part of the tibia. This does not occur in *Piatnitzkysaurus* or the Hidden Lake tibia. There are slight differences: the Hidden Lake tibia is less compressed distally, its fibular flange projects less and its medial buttress is slightly broader than in *P. floresi*. Nonetheless, had the Hidden Lake tibia been found instead in the Cañadon Asfalto Fm. (Callovian-Oxfordian) of Argentina, it would likely have been attributed to an immature *Piatnitzkysaurus*.

The similarity of the Hidden Lake tibia to those of megalosaurs and *Piatnitzkysaurus*, all Middle Jurassic forms, and *Erectopus*, an Albian form, implies that the Hidden Lake theropod represents a lineage probably derived from relatively plesiomorphic megalosaur or primitive allosauroid (but not sinraptorid) stock, unrelated to the lineages culminating in the more or less contemporaneous arctometatarsalians. Interestingly, the only other known Antarctic theropod, the Early Jurassic *Cryolophosaurus ellioti* (Hammer & Hickerson, 1994), is also now thought to be a plesiomorphic allosauroid (Hammer, pers.

comm., 1996). Generic identification of the Hidden Lake specimen is not possible, unless more is recovered.

DISCUSSION

The Hidden Lake tibia is the same size as the distal end of the tibia of the ornithomimosaur *Coelosaurus antiquus* (ANSP 9222) which is about 40cm long overall. If the proportions were the same, then the Hidden Lake theropod would have been about 3-3.5m long. If, on the other hand it was more robust, with the tibia proportioned like those of *Piatnitzkysaurus floresi*, then it would have been about 22-23cm long and the whole animal about 2.5-3m long. Assuming that it is from a mature animal, and we have no reason to think otherwise, in either case it represents a moderately small theropod about the size of a large *Coelophysis*. This theropod would have been too small to have been ectothermic and to have lived under a climate with a mean annual temperature of less than 15°C (cf. Molnar & Wiffen, 1994; Spotila et al., 1991). This suggests that James Ross Island enjoyed a rather mild climate, at least in some places, during the Coniacian-Santonian. The specimen was found in the middle section of the Hidden Lake Fm., in the level of the calcareous sand with abundant carbonised material. Associated trace fossils include *Planolites* sp. and *Palaeophycus* sp., and remains of logs without the borings of *Teredolites* that are often found in the upper and lower levels of this formation (Buatois & López Angríman, 1992b). The environment of deposition was a developing distributary plain in the central fan of a fan delta depositional system (Buatois & López Angríman, 1992a) into which, we infer, the specimen had been transported after death.

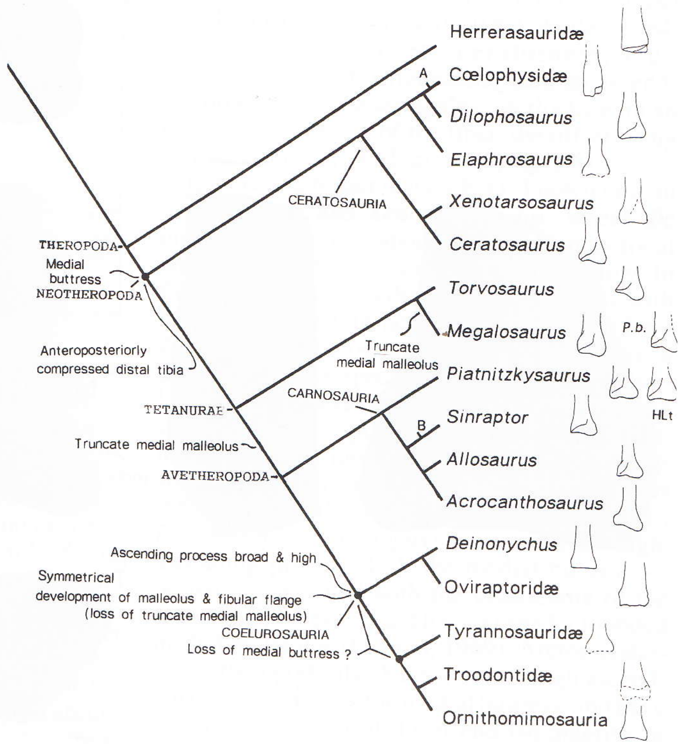

FIG. 3. Phylogenetic relationships among theropods, with astragalar and distal tibial characters discussed in text assigned to nodes. A and B indicate presumed reversals of character state: A, to uncompressed distal tibia; B, to angular (rather than truncate) medial malleolus. Along the right margin are diagrams of the distal tibiae of the genera included, with that for *Poekilopleuron bucklandii* (P.b.) added next to that for *Megalosaurus*, and that for the Hidden Lake theropod (HLt) next to *Piatnitzkysaurus*. Cladogram after Holtz (1994), with the positions of *Sinraptor*, following Sereno, et al. (1994), and *Piatnitzkysaurus*, following Molnar, et al. (1990), added. (Tibial diagrams redrawn from the literature, except for the Hidden Lake theropod and *Piatnitzkysaurus*).

This tibia suggests a more primitive theropod, or at least one with less advanced distal tibial structure, than was common in the Late Cretaceous Asiamerica or South America. Thus it suggests that lineages deriving from Middle Jurassic forms persisted in the Antarctic.

ACKNOWLEDGEMENTS

The specimen was collected with the kind logistical assistance of the Instituto Antártico Argentino, and the participation of Drs Christian Cherniglasov, Roberto Llorente and especially Luis Buatois. We also appreciate the help of Fernando Novas (Museo Nacional de Ciencias Naturales, Buenos Aires), Jaime Powell (Instituto Miguel Lillo, Tucumán), Alec Ritchie (Australian Museum, Sydney) and H. Phillip Powell (Oxford

TABLE 1. Theropod distal tibial form. In the last column, 'lateral' indicates that the lateral flange is more strongly developed than the medial malleolus; 'symmetric' that flange and malleolus are about equally developed and symmetrical in anterior view; 'both' that flange and malleolus are equally developed but not symmetrical .

Taxa	Medial malleolar development	Medial buttress	Astragalar ascending process		Distal tibial development
			width	height	
Herrerasauridae	slight	absent	narrow	low	slight
Coelophysidae	slight	absent	narrow	lows	light
Dilophosaurus	slight	present	narrow	low	lateral
Elaphrosaurus	angular	?	?[1]	?	symmetric
Xenotarsosaurus	rounded	?	moderate	low	symmetric
Ceratosaurus	angular	present	moderate	low	both
Torvosaurus	angular	present	moderate	low	lateral
Megalosaurus	truncate	present	moderate	low	lateral
Piatnitzkysaurus	truncate	present	?	?	lateral
Sinraptor	angular	present	moderate	low	lateral
Allosaurus	truncate	present	moderate	low	lateral
Acrocanthosaurus	truncate	present	?	?	both
Deinonychus	rounded	absent	broad	high	symmetric
Oviraptoridae	slight	low or absent	broad	?	both
Avimimus	slight	absent	broad	high	symmetric
Tyrannosauridae	rounded	absent	broad	high	symmetric
Troodontidae	slight	absent	broad	high	symmetric
Ornithomimidae	slight	absent	broad	high	symmetric

[1] Welles & Long (1974) describe the astragalar ascending process of *Elaphrosaurus bambergi* as high and broad, citing Janensch (1925). However it is not clear from Janensch that the ascending process is actually preserved so this may be an inference. Hence the proportions are here considered to be unknown.

University Museum, Oxford) who made available theropod material in their care, and Angela Milner (British Museum) for hypsilophodontian material. Don Baird (Princeton University) provided a cast of the tibia of *Coelosaurus* which washelpful and Jim Farlow (University of Indiana/Purdue University), William Hammer (Augustana College) and Tom Holtz, Jr (University of Maryland) all provided helpful comments. We much appreciate all their assistance.

LITERATURE CITED

BONAPARTE, J.F. 1986. Les Dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cóndor (Chubut, Argentine). (part 1). Annales de Paléontologie (Vert.-Invert.), 72: 247-289.

BUATOIS, L.A., & LOPEZ ANGRIMAN, A. 1992a. Evolución de sistemas deposicionales en el Grupo Gustav, Cretácico de la Isla James Ross, Antártida. Pp. 263-297. In, Rinaldi, C. (ed.) 'Geología de la Isla James Ross'. (Instituto Antártico Argentino: Buenos Aires).

BUATOIS, L.A. & LOPEZ ANGRIMAN, A. 1992b. Trazas fósiles y sistemas deposicionales del Grupo Gustav, Cretácico de la Isla James Ross, Antártida. Pp. 239-262. In, Rinaldi, C. (ed.) 'Geología de la Isla James Ross'. (Instituto Antártico Argentino: Buenos Aires).

BRITT, B.B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. Brigham Young University Geology Studies, 37: 1-72.

CARPENTER, K. 1992. Tyrannosaurids (Dinosauria) of Asia and North America. Pp. 250-268. In, Mateer, N. & Chen P.J. (eds) 'Aspects of Nonmarine Cretaceous Geology'. (China Ocean Press: Beijing).

COLBERT, E.H. 1989. The Triassic dinosaur *Coelophysis*. Bulletin of the Museum of Northern Arizona. 57: 1-174.

CURRIE, P. J., & RUSSELL, D.A. 1988. Osteology and relationships of *Chirostenotes pergracilis* (Saurischia, Theropoda) from the Judith River (Oldman) Formation of Alberta, Canada. Canadian Journal of Earth Sciences, 25: 972-986.

CURRIE, P. J. & ZHAO, X. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences, 30: 2037-2081.

DONG, Z., ZHANG, S. & ZHOU, Y. 1983. The dinosaurian remains from Sichuan Basin, China. Palaeontologia Sinica, 162: 1-145.

EUDES-DESLONGCHAMPS, J.-A. 1837. Mémoire sur le *Poikilopleuron* bucklandii, grand saurien fossile, intermédiare entre les crocodiles et les lézards. Mémoire de la société Linnéenne de Normandie, 6: 37-146.

GASPARINI, Z., OLIVERO, E., SCASSO, R. & RINALDI, C. 1987. Un ankylosaurio (Reptilia, Ornithischia) Campaniano en el continente Antartico. Anais do X Congresso Brasileiro de Paleontologia, 131-141.

GILMORE, C.W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. United States National Museum, Bulletin, 110: 1-159.

HAMMER, W.R. & HICKERSON, W.J. 1994. A crested theropod dinosaur from Antarctica. Science, 264: 828-830.

HOLTZ, T.R., Jr 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. Journal of Paleontology, 68: 1100-1117.

HOOKER, J.J., MILNER, A.C. & SEQUEIRA, S.E.K. 1991. An ornithopod dinosaur from the late Cretaceous of West Antarctica. Antarctic Science, 3: 331-332.

HULKE, J.W. 1879. Note on *Poikilopleuron bucklandi* of Eudes-Deslongchamps (pere) identifying it with *Megalosaurus bucklandi*. Quarterly Journal of the Geological Society of London, 35: 233-238.

HUXLEY, T.H. 1870. On the classification of the Dinosauria with observations of the Dinosauria of the Trias. Quarterly Journal of the Geological Society of London, 26: 31-50.

INESON, J., CRAME, J. & THOMSON, M. 1986. Lithostratigraphy of the Cretaceous strata of west James Ross Island, Antarctica. Cretaceous Research, 7: 141-159.

JANENSCH, W. 1925. Die Coelurosaurier und Theropoden der Tendaguru-Schichten Deutsch-Ostafrikas. Palaeontographica (Suppl. 7) 1: 1-99.

LYDEKKER, R. 1891. On certain ornithosaurian and dinosaurian remains. Quarterly Jounral of the Geological Society of London, 47: 41-44.

MADSEN, J. H., Jr 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological and Mineral Survey, Bulletin, 1091: 1- 163.

MARTINEZ, R., GIMENEZ, O., RODRIGUEZ, J. & BOCHATEY, G. 1987. *Xenotarsosaurus bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae), un nuevo Theropoda de la Formacion Bajo Barreal, Chubut, Argentina. Actas IV Congreso Argentino de Paleontología y Bioestratigrafía, 23-31.

MEDINA, F., BUATOIS, L., & LOPEZ ANGRIMAN, A. 1992. Estratigrafía del Grupo Gustav en la Isla James Ross, Antártida. Pp. 167-192. In, Rinaldi, C. (ed.) 'Geología de la Isla James Ross'. (Instituto Antártico Argentino: Buenos Aires).

MOLNAR, R.E. 1989. Terrestrial tetrapods in Cretaceous Antarctica. In, Crame, J.A. (ed.) 'Origins and Evolution of the Antarctic Biota', Geological Society Special Publication, 47: 131-140.

MOLNAR, R.E., KURZANOV, S.M. & DONG, Z. 1990. Carnosauria. Pp. 169-209. In, Weishampel, D.B., Dodson, P. & Osmólska, H. (eds) 'The Dinosauria'. (University of California Press: Berkeley).

MOLNAR, R.E. & WIFFEN, J. 1994. A Late Cretaceous polar dinosaur fauna from New Zealand. Cretaceous Research, 15: 689-706.

OLIVERO, E., GASPARINI, Z., RINALDI, C. & SCASSO, R. 1991. First record of dinosaurs in Antarctica (Upper Cretaceous, James Ross Island): palaeogeographical implications. Pp. 617-622. In, Thomson, M., Crame, J. & Thomson, J., (eds) 'Geological Evolution of Antarctica'. (Cambridge University Press: Cambridge).

OSTROM, J.H., 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Bulletin, Peabody Museum of Natural History, 30: 1-165.

1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. Bulletin, Peabody Museum of Natural History, 35: 1-234.

PADIAN, K. 1986. On the type material of *Coelophysis* Cope (Saurischia: Theropoda) and a new specimen from the Petrified Forest of Arizona (Late Triassic: Chinle Formation). Pp. 45-60. In, Padian, K. (ed.) 'The Beginning of the Age of Dinosaurs'. (Cambridge University Press: New York).

RAATH, M.A., 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. Arnoldia, 4: 1-25.

RUSSELL, D.A. & DONG, Z. 1993. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. Canadian Journal of Earth Sciences, 30: 2107-2127.

SAUVAGE, H.E. 1882. Recherches sur les reptiles trouvés dans le Gault de l'est du Basin de Paris. Mémoires de la Société géologique de France, (3), 4: 439-442.

SERENO, P.C., WILSON, J.A., LARSSON, H.C.E., DUTHEIL, D.B. & SUES, H.-D. 1994. Early Cretaceous dinosaurs from the Sahara. Science, 266: 267-271.

SPOTILA, J.R., O'CONNOR, M.P., DODSON, P. & PALADINO, F.V. 1991. Hot and cold running dinosaurs: body size, metabolism and migration. Modern Geology 16: 203-227.

WELLES, S.P. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. Palaeontographica, A, 185: 85-180.

WELLES, S.P. & LONG, R.A. 1974. The tarsus of theropod dinosaurs. Annals of the South African Museum, 64: 191-218.

WIFFEN, J. & MOLNAR, R.E. 1989. An ornithopod dinosaur from New Zealand. Geobios, 22:531-536.