

A new ornithopod (Dinosauria, Ornithischia) from the Upper Cretaceous of Antarctica and its palaeobiogeographical implications



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ARTICLE INFO

Article history:

Received 29 May 2015

Received in revised form

14 August 2015

Accepted in revised form 7 September 2015

Available online xxx

Keywords:

Ornithopoda

Euiguanodontia

Palaeobiogeography

Antarctica

Gondwana

Weddellian Province

ABSTRACT

A new ornithopod dinosaur from the Upper Cretaceous (Maastrichtian) Snow Hill Island Formation, at James Ross Island, Antarctica is here described. This new taxon, named as *Morrosaurus antarcticus* gen. et sp. nov., is represented by a fragmentary right hind limb belonging to a medium-sized individual. Our phylogenetic analysis nests the new taxon in a monophyletic clade of Southern Hemisphere ornithopods that includes most Patagonian and Antarctic ornithopods. Several members of this group share a slender and bunched foot with narrow metatarsal IV, expanded chevrons, and bowed humerus without deltopectoral crest. Several features indicate that these ornithopods exhibit adaptations for a specialized cursorial mode of life. The recognition of Patagonian and Antarctic Ornithopoda belonging to a monophyletic clade reinforces palaeobiogeographical signals indicating that Patagonia, Antarctica and Australia shared a common Late Cretaceous terrestrial fauna.

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1. Introduction

The Cretaceous fossil record of non-avian dinosaurs in Antarctica is strongly patchy and biased (Reguero, Goin, Hospitaleche, Dutra, & Marenssi, 2013). Up to now, scarce remains of titanosaurs, basal theropods, dromaeosaurids, and birds have been described (Case et al., 2000; 2007; Cerda et al., 2011; Chatterjee, 1989; 2002; Clarke, Tambussi, Noriega, Erickson, & Ketchum, 2005; Covacevich & Rich, 1982; Gasparini, Pereda–Suberbiola, & Molnar, 1996; Hammer & Hickerson, 1994; Hooker, Milner, & Sequeira, 1991; Milner & Hooker, 1992; Olivero, Gasparini, Rinaldi, & Scasso, 1991; Rich, 1996; Rich & Rich, 1989; Rich, Vickers–Rich, & Gangloff, 2002; Salgado & Gasparini, 2006). On the other hand, ornithischian remains are relatively frequent, and indicate the presence of basal ankylosaurs and several ornithopods, including hadrosaurian and basal iguanodontians (Barrett, Milner, & Hooker, 2014; Novas, Cambiaso, Lirio, & Núñez,

2002; Case et al., 2000; Coria, Moly, Reguero, Santillana, & Marenssi, 2013; Hooker et al., 1991). This striking abundance was interpreted by Novas et al. (2002) as indicative of the existence of some kind of provincialism among Gonwanan biota. The basal ornithopods are represented by an incomplete and still undescribed skeleton belonging to a taxon of uncertain affinities (Hooker et al., 1991). The specimen comes from the López de Bertodano Formation (Maastrichtian) from James Ross Island (Fig. 1). More recently, Coria et al. (2013) described the new genus and species *Trinisaura santamartaensis*, coming from Snow Hill Island Formation (Campanian) of James Ross Island. A preliminary phylogenetic analysis of *Trinisaura* carried out by Coria et al. (2013) resulted in a stem-iguanodontian position for this taxon.

In Novas and colavorators reported the incomplete hindlimb of a new relatively large iguanodontian coming from the López de Bertodano Formation (Maastrichtian) at James Ross Island. The aim of the present paper is to describe the specimen mentioned by these authors and to analyse its phylogenetic relationships within Ornithopoda, and with taxa known from other localities of the Southern Hemisphere.

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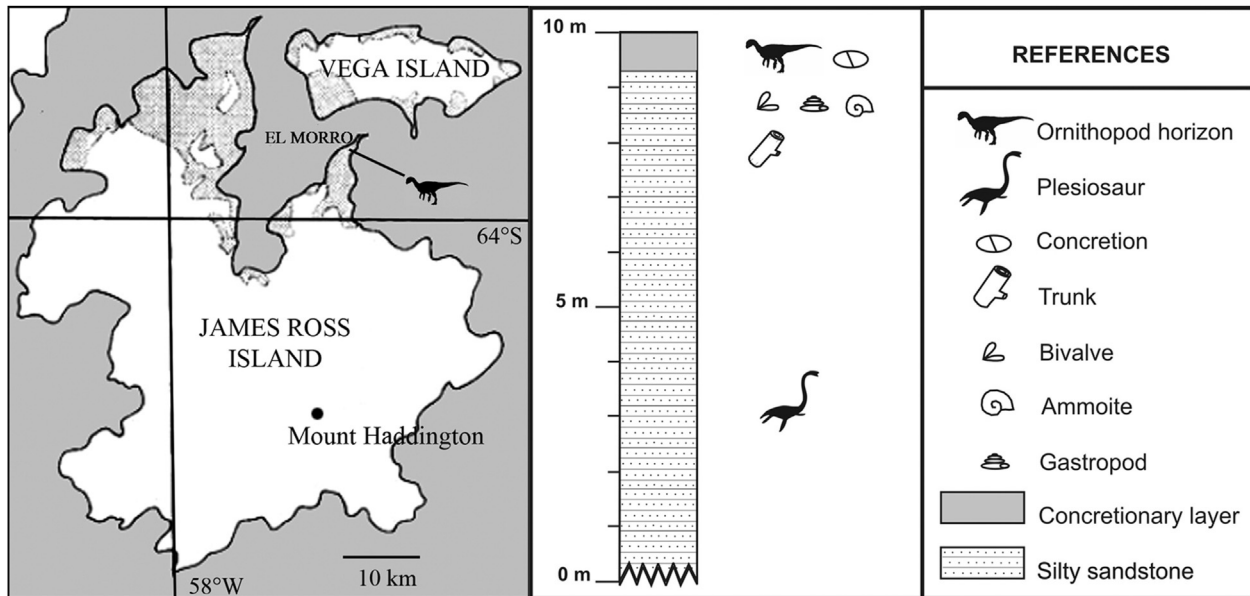


Fig. 1. Map showing the fossiliferous locality and the stratigraphic column of the site. The locality is indicated by an ornithopod silhouette.

2. Materials and methods

2.1. Stratigraphical setting

The specimen here described was found at Cape Lamb Member, Snow Hill Formation, around 30 m below the Theropod found by Case, Martin, Chaney, and Reguero (2003, 2007). The horizon could be correlated with the first lower 15 m of the section studied by Di Pasquo and Martin (2013) at the North part of El Morro (The Naze) Peninsula, James Ross Island.

The ornithopod bones were found on green sandstones, in association with plesiosaur bones, and abundant marine invertebrates. They come from locality 3 of Del Valle, Fourcade, and Medina (1982) in levels characterized by *Gunnarites antarcticus*, *Gunnarites kalika*, *Eupachydiscus grossouvrei* and *Diplomoceras lambi*. The presence of *Gunnarites antarcticus* allow to correlate the Ornithopod level, according to Olivero (2012), to Snow Hill Island Formation, Cape Lamb Member, NG Sequence, *Gunnarites* Assemblage 10, referring it to an early Maastrichtian age. This age agrees with the global stratigraphic ranges of selected palynomorphs studied by Di Pasquo and Martin (2013) at El Morro (The Naze).

The Cretaceous outcrops in Península El Morro (The Naze) were assigned to the López de Bertodano Formation by Del Valle et al. (1982). The López de Bertodano Formation was introduced by Rinaldi, Massabie, Morelli, Rosenman, and del Valle (1978) for the Cretaceous strata exposed on Seymour (Marambio) Island, and subsequently identified widely throughout the James Ross Basin. Because of this, previous works (Cambiaso, 2007; Novas et al., 2002; Motta, Rozadilla, Gentil, Aranciaga Rolando, & Muñoz, 2012) assigned this age for the ornithopod remains. However, Pirrie, Crame, Lomas, and Riding (1997) restrict the spatial occurrence of this stratigraphic unit to Seymour (Marambio) Island and eastern Spath Peninsula, Snow Hill (Cerro Nevado) Island. In this way, the Cretaceous outcrops of Cape Lamb, False Island Point, Humps Island, El Morro (The Naze) peninsula, and the vicinity of St. Martha Cove were reassigned by Pirie et al. (1997) to the Snow Hill Island Formation.

According to Di Pasquo and Martin (2013) the Cretaceous terrestrial environments surrounding the deposit were represented by *Nothofagus* rainforests, under highly humid and temperate to cool-temperate climate, frost-free and high-rainfall conditions.

Well-defined growth rings within fossil wood samples recovered from Lachman Crags and Naze Peninsula (James Ross Island) show that the climate was markedly seasonal (Francis, 1986, 1991).

Institutional abbreviations. MACN Pv, Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina.

Systematic palaeontology

DINOSAURIA Owen, 1842.

ORNITHISCHIA Seeley, 1888.

ORNITHOPODA Marsh, 1881.

EUIGUANODONTIA Coria & Salgado, 1996

ELASMARIA Calvo, Porfiri, & Novas, 2007.

Morrosaurus antarcticus gen. et sp. nov.

2.1.1. Derivation of name

The generic name *Morrosaurus* is due to the “El Morro”, the place where the dinosaur remains were recovered. The specific name *antarcticus* is in reference to the Antarctic continent.

2.1.2. Holotype

MACN Pv 19777, fragmentary right hind limb belonging to a single individual, including proximal and distal end of femur, proximal and distal end of the tibia, proximal ends of metatarsals II, III, IV and proximal end of phalanx 1-III.

2.1.3. Locality and horizon

Locality: Lat 63° 55' 40" S Long. 57° 30' 15" W, close to the shore, at 10 m above sea level, at NW of Fortress Hill, El Morro (The Naze) Peninsula, James Ross Island, Antarctica (Fig. 1). Horizon: Cape Lamb Member of the López de Bertodano Formation (Maastrichtian).

2.1.4. Diagnosis

Mid-sized ornithopod diagnosable on the basis of the following combination of characters (autapomorphies marked by an asterisk): 1) femur with lesser trochanter positioned anterolaterally to the greater trochanter; 2) in proximal view, femur with the lateral margin of greater trochanter sigmoidal in shape, with

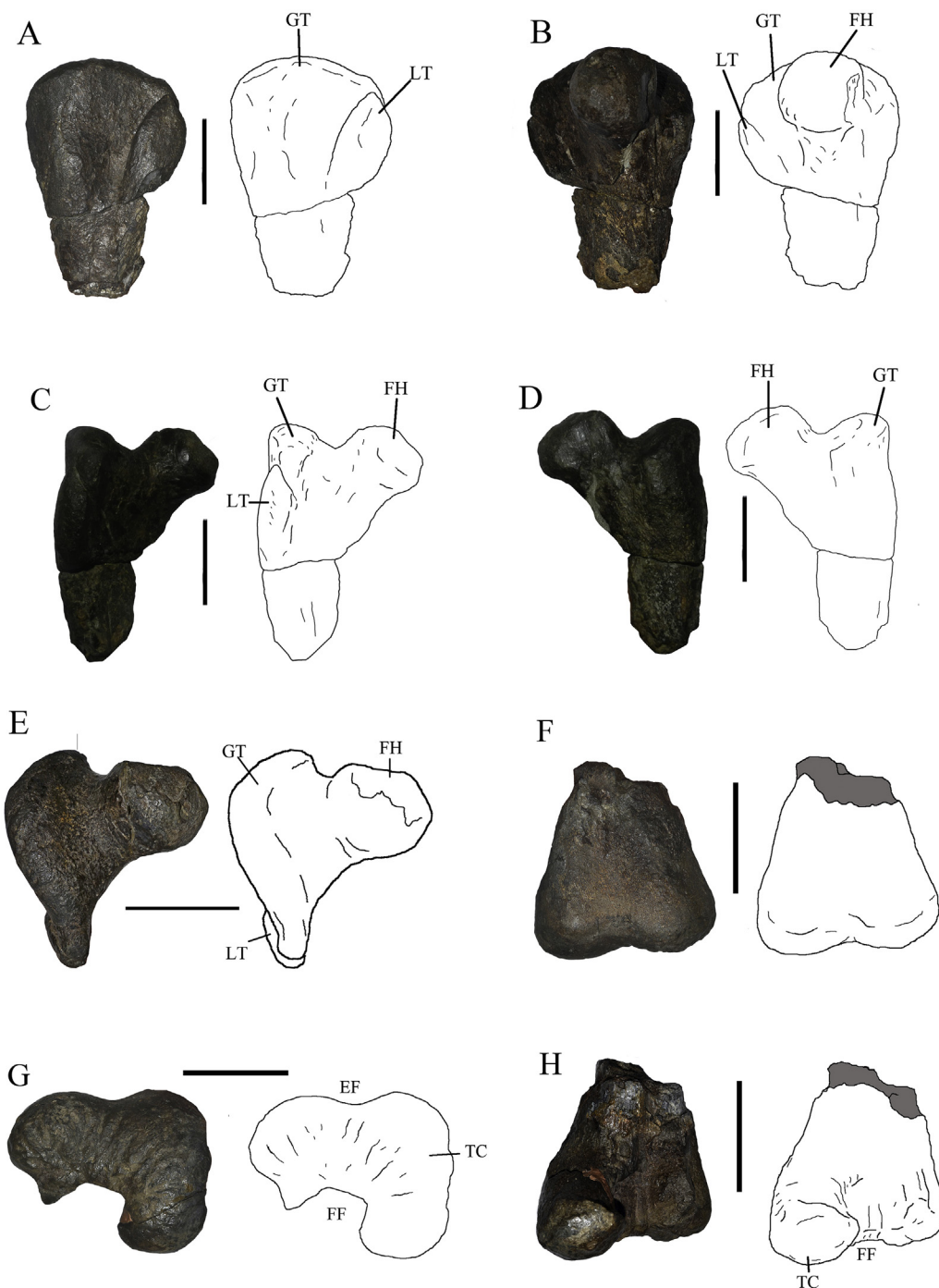


Fig. 2. Right femur of *Morrosaurus antarcticus* (MACN Pv 19777). Proximal end in: A, lateral; B, medial; C, anterior; D, posterior; and E, proximal views. Distal end in: F, anterior; G, distal; and H, posterior views. Abbreviations: GT, greater trochanter; LT, lesser trochanter; FH, femoral head; EF, extensor fossa; FF, flexor fossa; TC, tibial condyle. Scale bar: 5 cm.

transversely thick posterior edge, and a very thin anterior one*; 3) tibia with medial malleolus subtriangular in contour in anterior view and showing a concave anterior surface; and 4) proximal end of metatarsal IV in proximal view, with a thick and very well developed posterior process that medially wraps the metatarsal III*.

2.2. Description

The femur is only represented by its proximal and distal ends (Fig. 2). Nevertheless, the preserved portion of shaft indicates that it was probably a gracile element. The proximal end shows in

proximal view, the greater trochanter that extends anteroposteriorly, and shows a strong sigmoidal profile (Fig. 2E). This results from the transversely thick posterior end, that becomes abruptly narrow towards the anterior edge of the bone, a character shared with *Anabisetia* (Coria & Calvo, 2002), *Gasparinisaura* (Coria & Salgado, 1996), and *Notophysilophodon* (Martínez, 1998) (Fig. 3). However the sigmoidal proximal contour is more developed in *Morrosaurus* than in other taxa. In fact, in this taxon, the anterior margin of the trochanter is strongly transversely thin and shows its medial and lateral surfaces slightly concave, a condition unknown in other Ornithopoda.

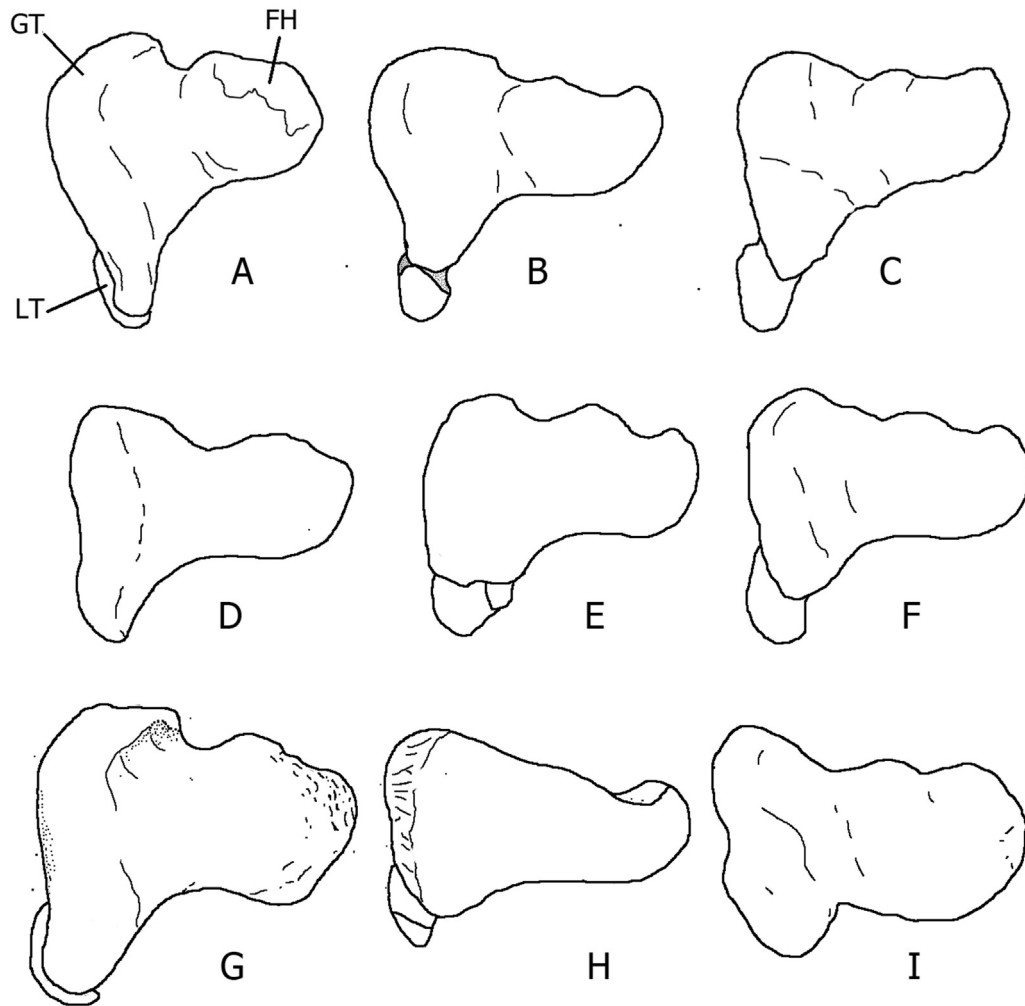


Fig. 3. Comparison of the proximal view of right femur of selected ornithopods. A, *Morrosaurus* (MACN Pv 19777); B, *Anabisetia* (modified from Coria & Calvo, 2002); C, *Nothohypsilophodon* (modified from Ibiricu et al., 2014); D, *Gasparinisaura* (modified from Coria et al., 1996); E, *Dryosaurus* (modified from Galton, 2009); F, *Dysalotosaurus* (modified from Galton, 2009); G, *Kangnasaurus* (modified from Cooper, 1985); H, *Hypsilophodon* (modified from Galton, 1980) I, *Camptosaurus* (modified from Carpenter & Wilson, 2008) Abbreviations: GT, greater trochanter; LT, lesser trochanter; FH, femoral head.

The lesser trochanter is transversally flattened and is anterolaterally placed. It is strongly attached to the greater trochanter, being separated by a deep proximodistal cleft between them, as occurs in *Hypsilophodon* (Huxley, 1869), *Dryosaurus* (Marsh, 1878), *Kangnasaurus* (Cooper, 1985), as for example. The proximal end of lesser trochanter is broken off, but it probably does not reach the proximal edge of the major trochanter (Fig. 2A–D).

The femoral head is strongly weathered, and thus, its total size and shape are not known. It is separated from the greater trochanter by a well defined neck (Fig. 2C–E).

The distal end of the bone shows well-developed distal condyles and is not fused with proximal tarsals like *Heterodontosaurus* and its kin (Crompton & Charig, 1962; Sereno, 2012). In distal view, the tibial condyle, shows a quadrangular contour and is transversally three times wider than the fibular condyle. These condyles delimitate a wide and deep flexor fossa, a character present in most non-hadrosaurid ornithopods, whereas in hadrosaurs both condyles conform a tubular structure (Norman, Sues, Witmer, & Coria, 2004). The anterior face of the bone shows a shallow extensor fossa such as in most basal Ornithopoda, whereas in other taxa (e.g., *Fulgurotherium* (Huene, 1932), *Thescelosaurus* (Gilmore, 1913), *Othnielosaurus* (Galton, 1977), *Hypsilophodon* (Huxley, 1869),

Gasparinisaura (Coria & Salgado, 1996), *Nothohypsilophodon* (Martinez, 1998)), this groove is totally absent. The articular surface is crossed by numerous grooves and rugosities, suggesting the presence of a very large cartilage bursa (Fig. 2F).

The proximal and distal ends of the tibia are very fragmentary, and most anatomical data are obscured due to weathering. It shows a well-developed cnemial crest, showing a wide and deep concavity on its medial face (Fig. 4A and B).

The distal end presents a subtriangular-shaped medial malleolus. In distal view it is anteriorly curved, and shows a concave anterior surface and a convex posterior one (Fig. 4C and D).

Only the proximal end of the fibula is preserved. It is transversally narrow, with a slight concavity on its medial face. In lateral view, the proximal end shows equally expanded posterior and anterior processes. The preserved portion of the shaft is transversally narrow (Fig. 4E and F). The proximal articular surface is slightly concave and shows a strongly rugous surface, indicating the existence of a cartilage cap.

The distal medial tarsal is disc-like, strongly dorsoventrally flattened and transversely wide. In proximal view is ovoidal in shape and covers the proximal end of metatarsals II and III. Along its midline shows two shallow and poorly defined concavities (Fig. 5D).

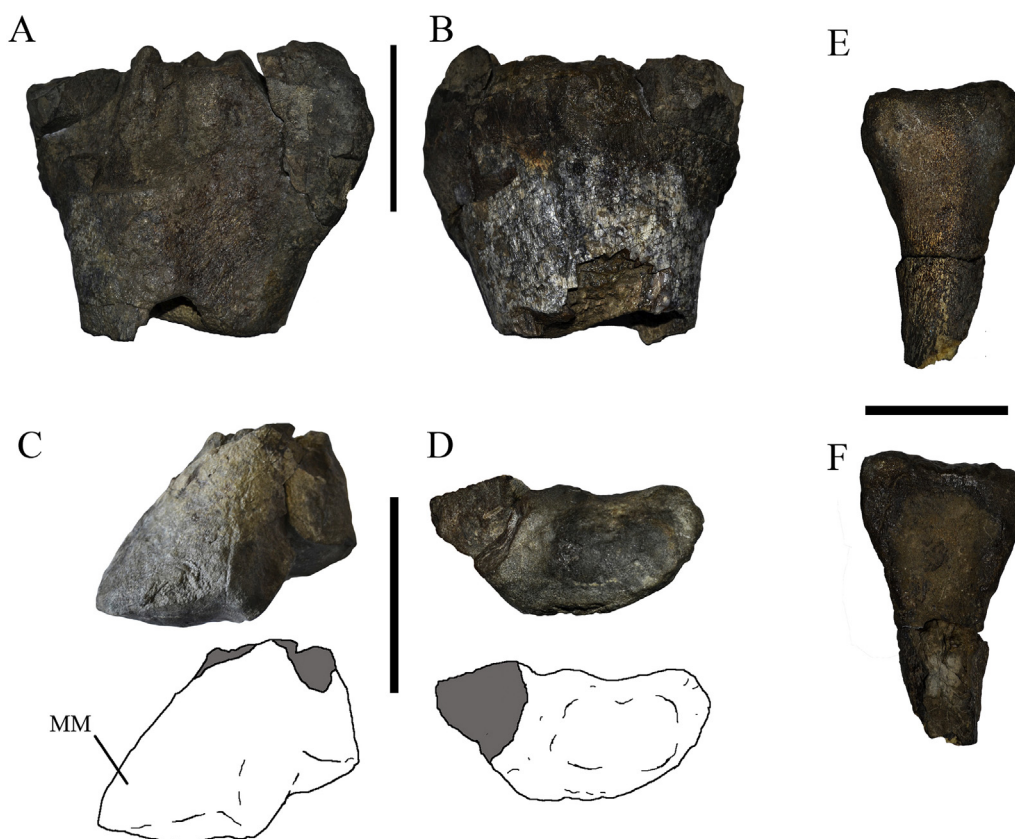


Fig. 4. Right tibia of *Morrosaurus antarcticus* (MACN Pv 19777). Proximal end in: A, medial; and B, lateral views. Distal end in: C, posterior; and D: distal views. Proximal end of right fibula in: E, lateral; and F: medial views. Abbreviation: MM, medial malleolus. Scale bar: 5 cm.

Nearly complete metatarsals II, III and IV are preserved. The elements are gracile and indicate a bunched and elongate pes (Fig. 5B).

In lateral view, the proximal end of metatarsal II is anteroposteriorly expanded and in proximal view is more transversely compressed than other metatarsals. It shows a subrectangular contour that becomes narrower towards the anterior margin of the bone. The medial face shows a proximodistally extended groove for the articulation of metatarsal III. The distal end of the bone shows a strongly concave medial margin and a slightly concave lateral one. The lateral collateral pit is not well defined. The distal gynglimous is not well developed and the articular surface is nearly flat, lacking an articular groove. It shows a rugose surface suggesting presence of cartilage.

The metatarsal III is the stouter bone of the metapodium. In proximal view shows a subtriangular contour with a strongly anteroposteriorly extended lateral surface. It contacts with the metatarsal II by means of a flat and wide articular face (Fig. 5A). Distally, the shaft becomes quadrangular in contour, and expands to conform a distal trochlea with deep extensor and flexor grooves (Fig. 5C).

Metatarsal IV is subtriangular in contour when viewed proximally. It shows a strong anterolateral expansion that posteriorly wraps the metatarsal III (Fig. 5A). In *Kangnasaurus* (Cooper, 1985) and *Gasparinisaura* (Coria & Salgado, 1996) a similar process is present, but is much less prominent. In cross section, the shaft of the metatarsal is suboval in contour, with its main axis transversely oriented.

Only the proximal end of the phalanx 1-III was recovered. Its articular surface shows a dorsoventrally depressed ovoid profile, and shows a more concave medial surface to receive the medial

condyle of the metatarsal III (Fig. 6).

3. Comparisons

Because of geographical position, detailed comparisons between *Morrosaurus* and other Southern Hemisphere ornithopods are carried out in some detail. Among these ornithopods, *Muttaburrasaurus* (Bartholomai & Molnar, 1981) differs in a very large number of features, including its robust and columnar femur, with small and distally located lesser trochanter (Molnar, 1996). *Morrosaurus* differs from *Anabisetia* (Coria & Calvo, 2002) on its larger size, a more robust femur, and a strongly sigmoidal proximal end of greater trochanter, which lacks an anterolateral concavity (Fig. 3). *Morrosaurus* differs from *Gasparinisaura* (Coria & Salgado, 1996) in a large number of features, including larger size and more robust proportions, femur with unfused lesser and greater trochanters, greater trochanter with a longitudinal shallow groove on its midline, distal end of femur with a deep extensor groove, and lateral condyle not laterally displaced (Coria & Salgado, 1996; Salgado, Coria, & Heredia, 1997) (Fig. 2). From *Notohypsilophodon* (Martínez, 1998) differs by its larger size, the femur with the lesser trochanter more distally placed and that do not reaches the level of the greater trochanter, and the distal end of femur with a deep extensor groove and with the lateral condyle not laterally displaced (Ibircu, Martínez, Luna, & Casal, 2014; Martínez, 1998). Although represented by a nearly complete skeleton, direct comparisons with *Talenkauen* (Novas, Cambiaso, & Ambrosio, 2004) are difficult to assess (Novas et al., 2007). However, some differences are noted. In *Morrosaurus* the distal end of the tibia is anteroposteriorly robust, whereas in *Talenkauen* (Novas et al., 2004) is much narrower (Cambiaso, 2007). The metatarsals of *Talenkauen* (Novas et al.,

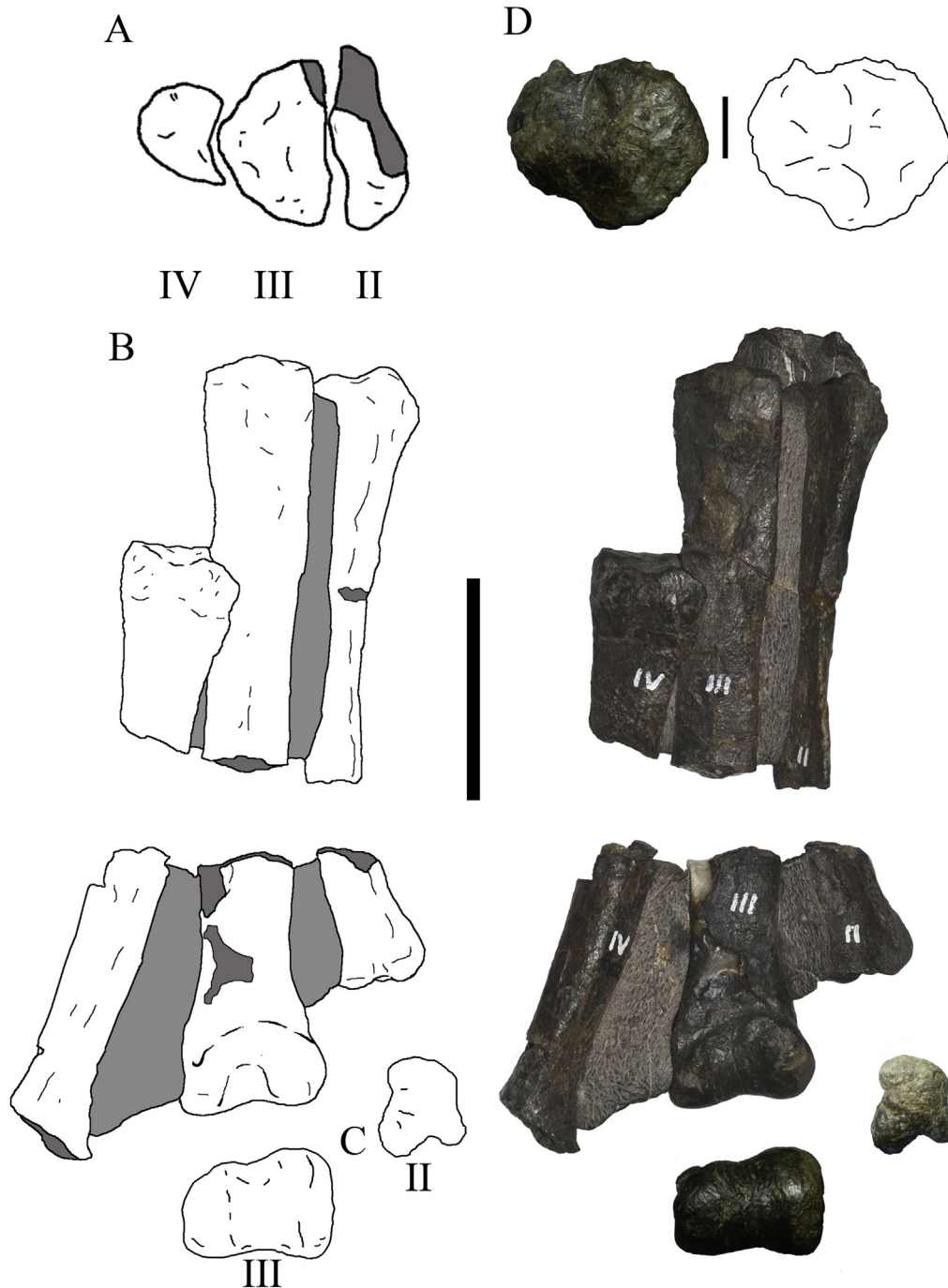


Fig. 5. Metatarsals of *Morrosaurus antarcticus* (MACN Pv 19777) in: A: proximal; B, anterior view; and C, distal views. D: distal tarsal in proximal view. Scale bar: A–C, 7 cm; D, 2 cm.

2004) are stouter and robustly built. The proximal end of metatarsal II is anteroposteriorly narrower and transversely wider, with a drop-shaped contour, very different from the condition of *Morrosaurus*, as indicated above. In *Talenkauen* (Novas et al., 2004) the proximal end of metatarsal III is sub-quadrangular in contour, whereas in *Morrosaurus* it is subtriangular (Cambiaso, 2007).

Dysalotosaurus (Janensch, 1955), coming from the Upper Jurassic of Tendaguru, differs from *Morrosaurus* in a large amount of features, including its smaller size, more gracile elements, and in having a deep and wide cleft separating the major and lesser trochanters of proximal femur (Fig. 3).

Because *Trinisaura* (Coria et al. 2013) is the only named ornithopod from Antarctica, special comparisons are made above. In *Trinisaura* (Coria et al. 2013), the lesser trochanter of the femur is anteroposteriorly expanded, representing one third of the anteroposterior proximal end of the bone when viewed laterally. In *Morrosaurus*, as occurs in other ornithopods, the trochanter is more transversely compressed and spike-like (Fig. 2D). The extensor groove in *Morrosaurus* is deeper and more well defined that the condition in *Trinisaura* (Coria et al., 2013). Finally, the femur and tibia of *Morrosaurus* are much stouter, very different from the gracile-limbed *Trinisaura* (Coria et al. 2013).

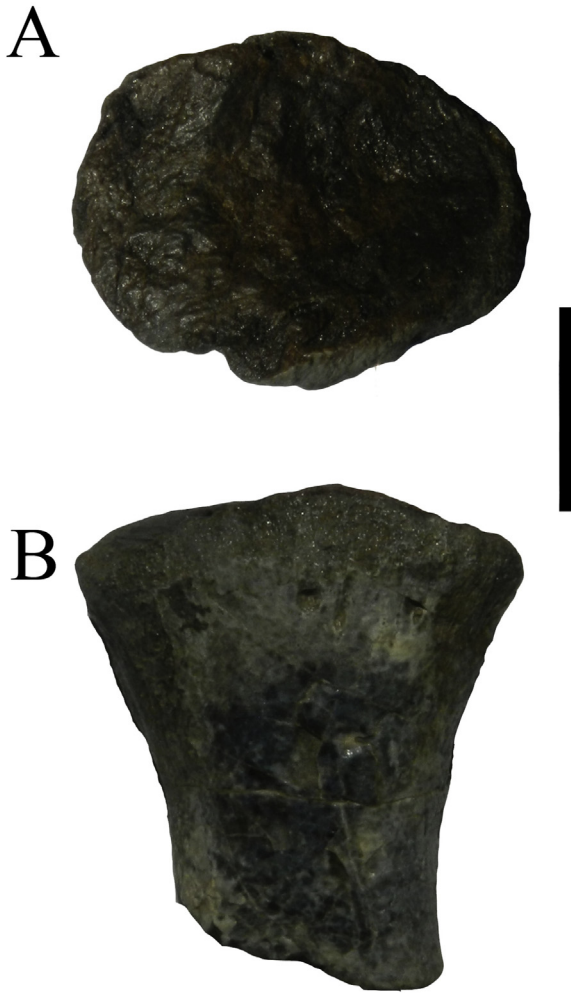


Fig. 6. Phalanx 1–III of *Morrosaurus antarcticus* in: A, proximal; and B, dorsal views. Scale bar: 2 cm.

Similarities in the general morphology and proportions of the postcranial skeleton of *Morrosaurus* are evident with the African Cenomanian species *Kangnasaurus koetzeei* (Cooper, 1985). Nevertheless, in *Morrosaurus* the lesser trochanter extends along the

anterolateral margin of the greater trochanter, whereas in *Kangnasaurus* (Cooper, 1985) it is only laterally exposed (Cooper, 1985). The greater trochanter in *Morrosaurus* is sigmoidal when viewed proximally, whereas in *Kangnasaurus* (Cooper, 1985) the major trochanter is transversely thicker and shows a nearly straight lateral surface (Fig. 3). The medial malleolus of *Morrosaurus* is subtriangular in contour in anterior view, and shows a concave anterior surface. On the other hand, in *Kangnasaurus* (Cooper, 1985) the malleolus is ovoidal in shape and the anterior surface is flat. In addition, in *Morrosaurus* the proximal end of metatarsal IV in proximal view is subtriangular in contour (Motta et al., 2012), and the posteromedial process is very thick, whereas in *Kangnasaurus* (Cooper, 1985) the proximal end of metatarsal IV is subquadrangular in shape, and the posteromedial process is less developed.

Due to the absence of comparable materials, comparisons with *Macrogyphosaurus* (Calvo et al., 2007) are not possible. However, because both taxa are geographically and stratigraphically distant each other, it is highly unlikely that *Morrosaurus* may belong to the latter taxon.

3.1. Phylogenetic analysis

The phylogenetic relationships of the new ornithopod were analyzed using a modified version of Butler et al. (2009) data matrix as modified by Pol et al. (2011). The data matrix of Pol et al. (2011) includes 52 taxa and 230 characters, to which we added 5 new taxa (*Trinisaura* (Coria et al., 2013), *Kangnasaurus* (Cooper, 1985), *Macrogyphosaurus* (Calvo et al., 2007), *Notohypsilophodon* (Martinez, 1998), and the new taxon) and 9 new characters (231–239) (Appendices A and B, in Supplementary material).

Present phylogenetic analysis was performed using TNT 1.1 (Goloboff et al., 2008). All characters were equally weighted and treated as unordered. Heuristic searches were performed after 1000 pseudoreplicates of WAG + TBR search strategy, with 10 random addition sequences after each search and 100 trees were saved at each replicate.

The phylogenetic analysis resulted in the recovery of 50 most parsimonious trees of 633 steps, with a consistency index of 0.425, and a retention index of 0.695 (Fig. 7).

Relationships between stem-ornithopods and other ornithischians resulted in an unresolved polytomy. However, because present analysis focuses on derived ornithopods, and thus,



Fig. 7. Strict consensus tree showing derived iguanodontian interrelationships.

relationships of more basal taxa are not discussed nor tested here.

The strict consensus of the shortest trees resulted in a clade formed by most Gondwanan ornithopods with *Gasparinisaura* (Coria et al., 1996) as the sister group of a polytomy including remaining Patagonian and Antarctic non-hadrosaurid ornithopods (see Appendix C). Different tree lengths were obtained depending on forced alternative position of each Gondwanan ornithopod. If *Gasparinisaura* (Coria et al., 1996) is excluded from the clade and is included at the base of Laurasian iguanodontians it results in a tree of 640 steps (+6 extra steps). If *Macrogyphosaurus* (Calvo et al., 2007) is included at the base of Laurasian iguanodontians it results in a tree of 639 (+5 extra steps), and if *Notohypsilophodon* (Martinez, 1998) is included within Laurasian iguanodontians it results in a tree of 644 steps (+10 extra steps).

With the aim to test the robusticity of tree topology, we calculated the Bremer support for each node. Nesting of the new taxon within the Gondwanan ornithopods clade is poorly supported (Bremer support = 1), as the monophyly of the entire clade (bremer support = 1). However, as noted by the authors of the matrix (Butler et al., 2009), these low values along most of the phylogenetic tree are due to the presence of large number of homoplasies among most taxa. Present results are concordant with Butler et al. (2009) analysis and main conclusions.

4. Discussion

4.1. Phylogenetic relationships of *Morrosaurus antarcticus*

The vast majority of ornithischians found in Gondwanan landmasses belong to non-Hadrosaurid ornithopods. Among them, the Patagonian taxa *Notohypsilophodon* (Martínez, 1998), *Macrogyphosaurus* (Calvo et al., 2007), *Gasparinisaura* (Coria & Salgado, 1996), *Talenkauen* (Novas et al., 2004), *Anabisetia* (Coria et al., 2002) comprises genera that show some common anatomical features, noted since their original descriptions. In this way, many authors (e.g., Barrett et al., 2014; Calvo et al., 2007; Coria & Calvo, 2002; Coria and Cambiaso, 2007; Ibiricu et al., 2010; Novas et al., 2004) have raised the hypothesis that some of these ornithopods may conform an endemic gondwanian clade. However, most of these studies were unable to recognize a monophyletic Gondwanan clade. In this regard, Calvo and collaborators (2007) were the first recognizing a group of Southern Hemisphere taxa, composed by *Talenkauen* and *Macrogyphosaurus*. This grouping was based on two shared features, namely the well-developed epiphyses on the third cervical vertebra, and thin ossified plates on thorax. Other authors noted anatomical similarities between sparse Southern Hemisphere ornithopods, including strong posteroventral expansions of the middle posterior chevrons, anteroproximally-posterodistally elongate tibial cotyle of the calcaneum, reduced humeral deltopectoral crest, proximally mediolaterally compressed metatarsal II (Ibiricu et al., 2010; Novas et al. 2004).

In the present phylogenetic analysis, we find a monophyletic clade of Southern Hemisphere ornithopods, as suspected by those authors (Fig. 7). This group includes the Patagonian *Gasparinisaura* (Coria & Salgado, 1996) as the most basal member, and an unresolved sister-group composed by *Notohypsilophodon* (Martinez, 1998), *Anabisetia* (Coria & Calvo, 2002), *Talenkauen* (Novas et al., 2004), *Macrogyphosaurus* (Calvo et al., 2007), and the Antarctic ornithopods *Trinisaura* (Coria et al., 2013) and *Morrosaurus*. The lack of resolution of this clade may be due to the incomplete nature of several of these genera (Fig. 7).

Calvo et al. (2007) defined the clade Elasmaria as *Talenkauen santacruzensis* (Novas et al., 2004), *Macrogyphosaurus gondwanicus* (Calvo et al., 2007), their most recent common ancestor, plus all the

descendants. Present analysis found support to this clade, to which most Patagonian and Antartic non-hadrosaurian ornithopods are incorporated.

This clade is supported by three synapomorphies, including: 1) well developed epiphysis in the third cervical vertebra (Calvo et al., 2007; Ibiricu et al., 2010; Character 234), 2) subtriangular shaped chevrons (Calvo et al., 2007; Ibiricu et al., 2010; Character 144), and 3) lateral margin of greater trochanter of femur with a strongly transversely compressed anterior edge (Character 231). The clade including all Elasmarians with the exception of *Gasparinisaura* are the following: 1) rudimentary deltopectoral crest in the humerus (Novas et al., 2004; Ibiricu et al., 2010; Character 154), 2) strongly laterally bowed humeral shaft (Character 155), 3) intercostal mineralized plates (Calvo et al., 2007; Ibiricu et al., 2010; Character 235).

These synapomorphies are discussed as follows:

- 1) Rudimentary or absent deltopectoral crest in the humerus (Character 154). Plesiomorphically in Dinosauria, including Ornithischia, the humerus shows a relatively well-developed deltopectoral crest (Novas, 1996). This condition is also present in *Heterodontosaurus* (Crompton & Charig, 1962), basal ornithopods like *Hypsilophodon* (Huxley, 1869) and *Orodromeus* (Horner & Weishampel, 1988), and iguanodontians like (Gilmore, 1913), *Tenontosaurus*, and *Iguanodon* (Mantell, 1825). In the Patagonian taxa *Anabisetia* (Coria et al., 2002), *Notohypsilophodon* (Martinez, 1998), and *Talenkauen* (Novas et al., 2004), and the Antarctic *Trinisaura* (Coria et al., 2013), the deltopectoral crest is apomorphically reduced and is represented by a shallow thickening located on the lateral side of the proximal end of the bone. A similar condition was convergently evolved in Pachycephalosauria (Coria et al., 2012; Maryanska, Chapman, & Weishampel, 2004). In contrast with other South American ornithopods, *Gasparinisaura* (Coria & Salgado, 1996) shows a subtriangular and prominent deltopectoral crest (Coria & Salgado, 1996) (Fig. 8).
- The development of the deltopectoral crest is intimately related with the anchoring of pectoral musculature and retractor muscles of the arm (Carpenter & Smith, 2001; Dilkes, 2000, 2001; Jasinowski, Russell, & Currie, 2006). The reduction of this ridge of bone may be related with a partial loss of the arm movements or at least of musculature size.
- 2) Shaft of the humerus strongly bowed laterally (Character 155). Most dinosaurs, including the great majority of ornithopods show a nearly straight to slightly sigmoidal humerus. On the other hand, in *Thescelosaurus* (Gilmore, 1913) and Pachycephalosauria the humerus is slightly laterally bowed, a condition that is more extreme in *Trinisaura*, a trait that was considered as autapomorphic of this genus by Coria and collaborators (2013). However, the same morphology is also present in *Talenkauen* (Novas et al., 2004), *Anabisetia* (Coria & Calvo, 2002), and *Notohypsilophodon* (Martinez, 1998) (Fig. 8). Present paper results in the recognition of a laterally bowed humerus as a derived trait convergently acquired by *Thescelosaurus*, Elasmaria, and Pachycephalosauria.
- 3) Lateral margin of the greater trochanter of femur with strongly transversely compressed anterior edge (Character 231). The ancestral condition for ornithopod femur is to show a deep cleft that separates the greater and lesser trochanters, and the anterior edge of the greater trochanter is usually transversely thick, a morphology that occurs in *Heterodontosaurus* (Crompton & Charig, 1962), *Hypsilophodon* (Huxley, 1869), *Thescelosaurus* (Gilmore, 1913), *Tenontosaurus* (Ostrom, 1970) and

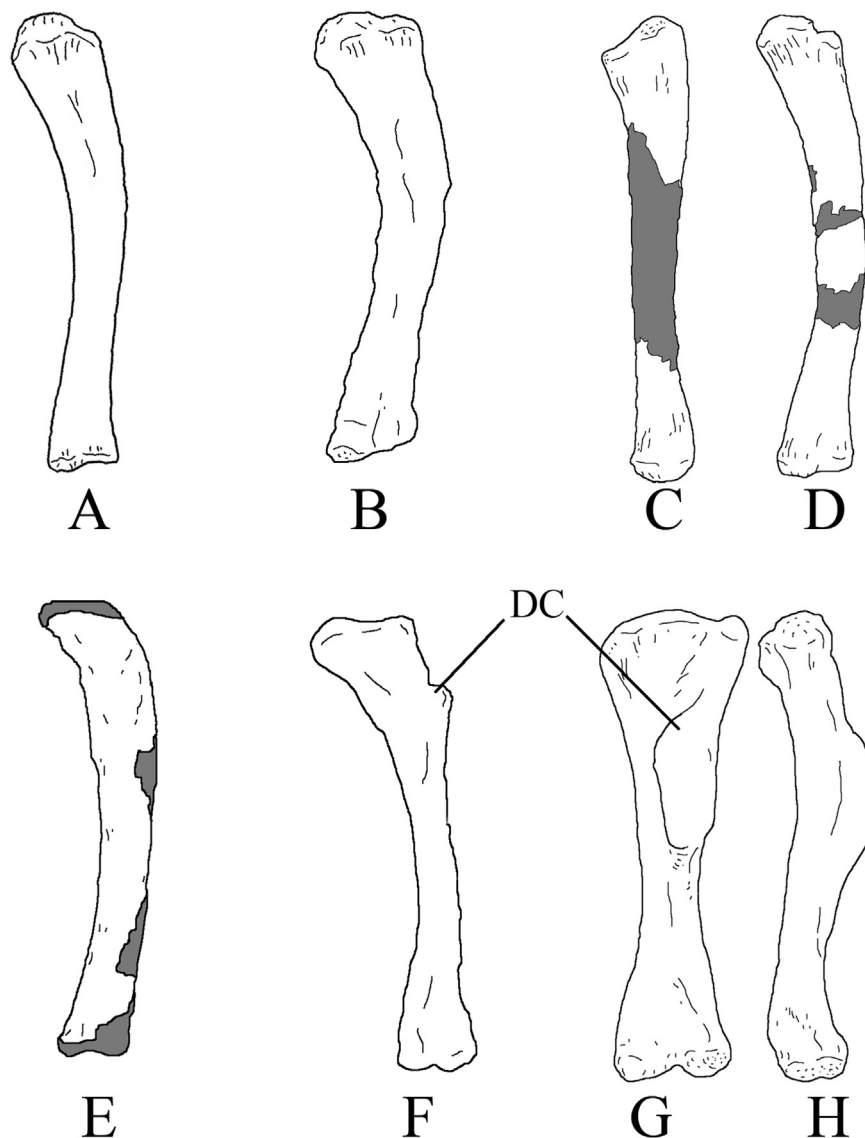


Fig. 8. Comparison between selected iguanodontian humerus of the left side. Note the absence of deltopectoral crest and the lateral bowing of shaft in Southern Hemisphere taxa. A, B, D–G, anterior, and C, H, lateral views. A, *Anabisetia* (modified from Coria & Calvo, 2002); B, *Talenkauen* (modified from Cambiaso, 2007); C–D, *Notohypsilophodon* (modified from Ibricic et al., 2014); E, *Trinisaura* (modified from Coria et al., 2013); F, *Gasparinisaura* (modified from Cambiaso, 2007); G–H, *Camptosaurus* (modified from Carpenter & Wilson, 2008). Abbreviation: DC, deltopectoral crest.

Dryosauridae, as for example. In *Morrosaurus* and the patagonian ornithopods *Gasparinisaura* (Coria & Salgado, 1996) and *Anabisetia* (Coria & Calvo, 2002), the greater trochanter becomes narrower towards the anterior edge. Furthermore, in *Morrosaurus* the anterior edge of greater trochanter is extremely compressed and its medial and lateral surfaces are slightly concave. In *Gasparinisaura* (Coria & Salgado, 1996), the lesser trochanter shows a marked reduction and it is strongly fused to the greater trochanter (Coria & Salgado, 1996). Nevertheless, the anterior margin of the greater trochanter shows a remarkable transverse narrowing. Thus, this condition should be considered as a character unique to Elasmaria (Fig. 3).

4) Subtriangular-shaped chevrons in caudal vertebrae, when viewed laterally (Character 144). The ancestral condition for Ornithopoda is that the chevrons from the mid caudal series are rod-like and only slightly posteriorly expanded. This condition is present in *Heterodontosaurus* (Crompton & Charig, 1962), and

many ornithopods, such as *Hypsilophodon* (Huxley, 1869), *Tenontosaurus* (Crompton, 1970), and *Iguanodon* (Mantell, 1825). Nevertheless in the patagonian taxa *Gasparinisaura* (Coria & Salgado, 1996) and *Macrogryphosaurus* (Calvo et al., 2007) the chevrons are strongly asymmetrical, with the posterior end caudally projected, a condition that was regarded as autapomorphic of *Gasparinisaura* in the original description of this taxon (Coria & Salgado, 1996). This morphology is also present in an unidentified Australian Cretaceous ornithopod (Vickers-Rich & Rich, 1999) and the Jurassic North American ornithopod *Parksosaurus* (Sternberg, 1937). This expansion increases along the chevron series from cranial to caudal vertebrae. The expanded ventral haemal tips probably provided enlarged insertion surfaces for the ischio-caudalis muscle, which is a key muscle in the control of lateral and ventral tail flexure (Persons, Funston, Currie, & Norell, 2015). Larger surface for muscle attachment could evidence stronger musculature. This

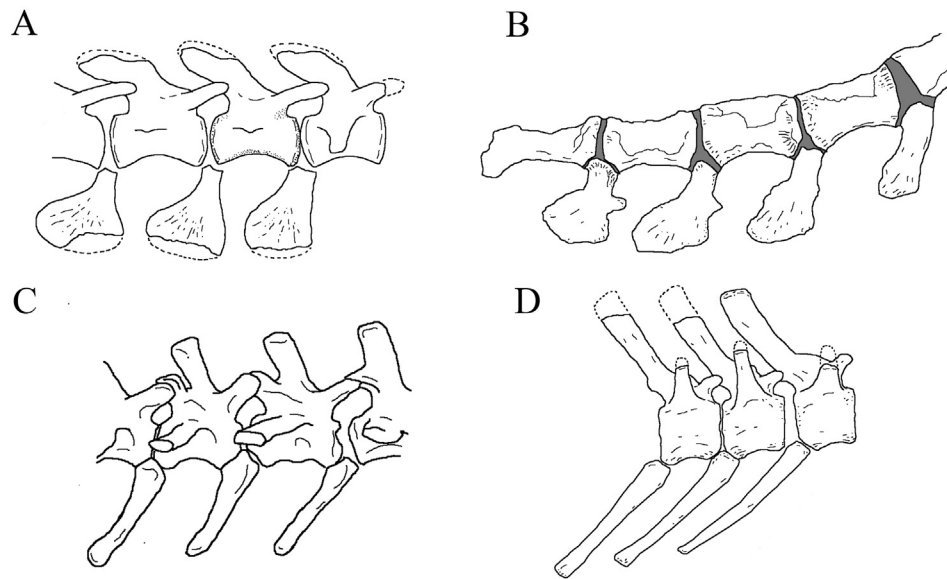


Fig. 9. Comparison of chevron shape in lateral view on the proximal tail of selected ornithopods. A, *Gasparinisaura* (modified from Coria & Salgado, 1996); B, *Macrogyphosaurus* (modified from Calvo et al., 2007); C, *Heterodontosaurus* (modified from Santa Luca, 1979); D, *Thescelosaurus* (modified from Gilmore 1915).

may imply an increasing control of tail movements, in contrast to taxa with rod-like chevrons (Fig. 9).

In this way, the presence of subtriangular chevrons is considered as a derived feature convergently acquired by *Parksosaurus* and *Elasmaria*.

5) Well-developed epiphysis in the third cervical vertebra (Character 234). This feature was considered by Calvo et al. (2007) as diagnostic for *Elasmaria*, being present in *Talenkauen* (Novas et al., 2004) *Macrogyphosaurus* (Calvo et al., 2007), and *Anabisetia* (Coria & Calvo, 2002). In fact, in *Macrogyphosaurus* (Calvo et al., 2007) the epiphyses on the third cervical vertebrae are posteriorly projected and surpassing the distal end of the postzygapophyses. On the other hand, in *Talenkauen* (Novas et al., 2004) the epiphyses are less developed and do not reach the level of the postzygapophyses. The strong development of cervical epiphyses appears to be related with a greater development of epiaxial musculature, and suggests the existence of increased maneuverability of the neck (Méndez, 2012).

Regrettably, remaining South American ornithopods do not preserved complete neck vertebrae, and thus, this condition is uncertain in other taxa. Nevertheless, present analysis resulted in the recognition of this feature as a derived trait diagnostic of *Elasmaria*.

6) Mineralized intercostal plates (Character 235). Plate-like structures considered as analogous to uncinat processes of living birds are found in the Patagonian *Talenkauen* (Novas et al., 2004) and *Macrogyphosaurus* (Calvo et al., 2007), as well as the Early Cretaceous ornithopod *Hypsilophodon* (Huxley, 1869), the Late Cretaceous *Thescelosaurus* (Gilmore, 1913), and Late Jurassic *Othnielosaurus* (Galton, 2006) (Butler & Galton, 2008). In *Talenkauen* (Novas et al., 2004), the plates are polygonal in contour and are located on both sides of the ribcage. In contrast, in *Macrogyphosaurus* (Calvo et al., 2007) the plates are sub-circular, and are not restricted to the lateral sides of the thorax, but are also present in the chest (Calvo et al. 2007). These thin

plates are strongly expanded and overlap the posterior ribs and plates.

Uncinate processes in other dinosaurs are represented by strip-like projections (Paul, 2002). Primary interpretations regard a protector function to the plates (Hulke, 1874), but its fragile nature dismisses this hypothesis (Butler & Galton, 2008; Novas et al., 2004). In birds, uncinat processes are involved in toracic movements that optimize lung ventilation (Fedde, 1987). The plates in the ribcage of *Talenkauen* (Novas et al., 2004) and *Macrogyphosaurus* (Calvo et al., 2007) could be related with the anchoring of well developed intercostal muscles (Novas et al., 2004). A third hypothesis proposes that these plates contribute to the stiffness of the ribcage (Boyd, Cleland, & Novas, 2011).

In any case, presence of ossified plates is considered as diagnostic of *Elasmaria*, and convergently acquired by *Thescelosaurus* and *Hypsilophodon*.

In addition to the above mentioned features, Ibiricu et al. (2010) propose the anteroproximally-posterodistally elonged tibial cotyle of the calcaneum, as a possible synapomorphy of Gondwanan ornithopods. This condition is present in *Gasparinisaura* (Coria et al., 1996), *Kangnasaurus* (Cooper, 1985), *Notohypsilophodon* (Martínez, 1998), and *Ouranosaurus* (Taquet, 1976), and contrast with the more reduced and nearly flat condition of remianng Ornithopoda. Nevertheless, in our phylogenetic analysis, this character was not here obtained as a synapomorphy, probably because the saltuary nature of the preservation of the calcaneum.

It is worth mentioning here, that the recovery of a highly abarcative *Elasmaria* is not very strongly supported phylogenetically. In fact, some taxa, particularly *Gasparinisaura* (Coria et al., 1996), show remarkable morphological differences with other Gondwanan ornithopods (as for example in the humeral shape), that may be indicative of different phylogenetic relationships. This hypothesis should be tested with more detailed and abarcative phylogenetic analyses.

Furthermore, the poor anatomical representation of several taxa (e.g., *Trinisaura* (Coria et al., 2013), *Notohypsilophodon* (Martínez, 1998), *Morrosaurus*) conspires against the inner resolution within the *Elasmaria* clade, were all taxa more derived than *Gasparinisaura* (Coria & Salgado, 1996) are represented by a polytomy. Future

discoveries of more complete specimens will increase our knowledge of the inner systematic and palaeobiogeographical implications of this clade.

Some anatomical features indicate that Elasmaria was a group of ornithopods that differed from other taxa in several aspects. Some characters show the Patagonian and Antarctic ornithopods as dinosaurs adapted to a strongly cursorial mode of life. The metatarsus shows a strong and thick, and cranially exposed metatarsal III, much stronger than metatarsals II and IV. The latter two embrace the metatarsal III in the proximal half of the length of the bone. These conform a long and slender metapodium that resembles the configuration of the pes present in other dinosaur clades, such as abelisauroids and rheids (Bonaparte, 1991). Other ornithopods, including *Tenontosaurus* (Ostrom, 1970), *Camptosaurus* (Marsh, 1885), *Iguanodon* (Mantell, 1825), and *Thescelosaurus* (Gilmore, 1913), show a stouter metatarsus of graviportal proportions (Galton, 1974a, 1974b). These bear relatively stout metatarsals II and IV, and neither show the close appressing of the metatarsals (Fig. 10).

Furthermore, as indicated above, the large uncinat process in *Talenkauen* (Novas et al., 2002) and *Macrogyphosaurus* (Calvo et al., 2007) could be also related with improved pulmonary dynamics, as indicated by previous authors (Boyd et al., 2011).

Elasmarians show subtriangular chevrons with an extended and posteriorly oriented distal ends, increasing the surface for muscles important for tail movements. Some theropods such as some Tyrannosauridae and Dromeosauridae present chevrons with a similar structure that could be related to better control of balance of tail (Persons et al. 2015).

Slender and compact metatarsus and expanded chevrons should be interpreted as adaptations for an efficient cursorial mode of life.

4.2. Palaeobiogeographical implications

Bonaparte (1984; 1986) proposed that during most of the Mesozoic, specially the Cretaceous period, Gondwanan and Laurasian landmasses experienced a deep faunistic isolation. However, as early recognized by several authors, the faunas on each landmass were far from homogeneous. In this regard, the Cretaceous continental vertebrate faunas from northern Africa and Brazil closely resemble each other (Calvo, 1999), and differ from those from Madagascar, India and Patagonia, the latter three being very similar in composition (Bonaparte, 1986, 1999). This suggests that some

kind of faunal provincialism was apparent in Southern continents (Benson, Rich, Vickers-Rich, & Hall, 2012; Novas, 2009; Novas, Agnolín, Ezcurra, Porfiri & Canale, 2013; Novas, de Valais, Vickers-Rich, & Rich, 2005). Among dinosaurs, Northern Africa and Brazil share spinosaurids and sigilmassasaurids, absent in other Gondwanan continents (Apesteguía, 2002; Novas, 2009; Novas, de Valais, Vickers-Rich, & Rich, 2005). Southern Gondwanan landmasses including Patagonia and Australia share among dinosaurs a strong abundance and diversity of megaraptorids (Agnolin, Ezcurra, Pais, & Salisbury, 2010; Novas et al., 2013; Smith et al., 2008). In spite of such similarities, Patagonia differs from Antarctica and Australia in having abundant abelisauroid theropods, and titanosaurs, that are absent or scarce in the latter two continents (Cerda et al., 2011; Coombs & Molnar, 1981; Hocknull et al., 2009; Novas et al., 2013).

In this regard, during the Cretaceous, Patagonia shows a large diversity and abundance of titanosaur sauropods, contrasting with Laurasian continents (Bonaparte & Kielan Jaworowska, 1987; Bonaparte, 1984; 1986, 1999; Novas, 2009). On the contrary, ornithischian dinosaurs were relegated to a background herbivorous ecological niche (Bonaparte, 1986; Coria & Cambiaso, 2007). Nevertheless, in Australia and New Zealand the record of sauropods is scarce and ornithischians appears to be abundant and diverse (Agnolin et al., 2010; Bartholomai & Molnar, 1981; Molnar & Galton, 1986; Rich & Rich, 1989; 1996; Rich & Vickers-Rich, 1999; 2003; Wiffen & Molnar, 1989).

In Antarctica, diverse ornithischian clades were described from Upper Cretaceous beds, including basal ornithopods of small (Coria et al., 2013; Milner & Hooker, 1992), medium (this paper), and large size (Rich & Rich, 1989). Furthermore, hadrosaur-like specimens were found (Case et al., 2000), and ankylosaurs constitute a remarkable component of the fauna (Gasparini et al., 1996; Salgado & Gasparini, 2006). On the contrary, sauropods are represented by a single incomplete caudal vertebra of a possible derived titanosaur (Cerda et al., 2012). In this aspect, Cretaceous dinosaur faunas from Antarctica are very similar to that of New Zealand and Australia, being remarkable different in composition to other southern landmasses, including Patagonia (Novas et al., 2004). In this regard, *Morrosaurus* is an important addition to such pattern, greatly increasing the diversity of Antarctic ornithopods known so far.

The land connection between Patagonia and Antarctica during the Late Cretaceous resulted in the presence of shared faunas and

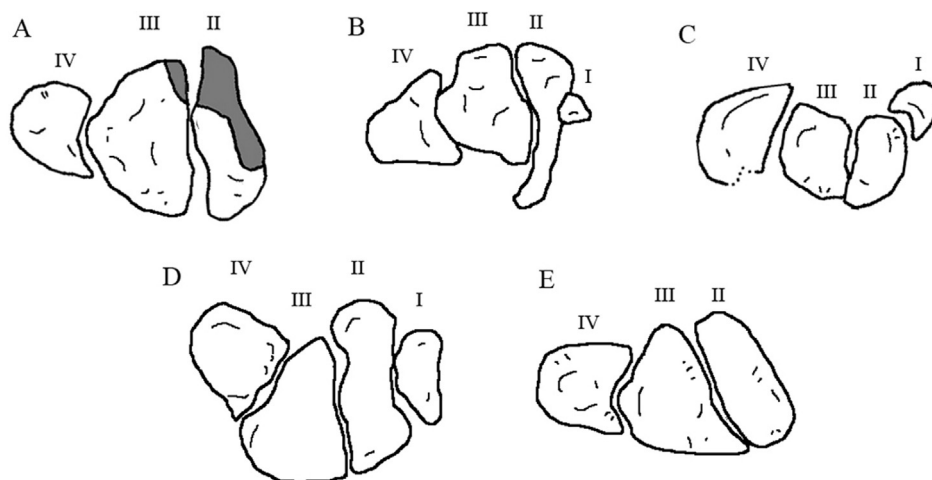


Fig. 10. Comparison of right metatarsals in proximal view of selected iguanodontians. A, *Morrosaurus*; B, *Anabisetia* (modified from Cambiaso, 2007); C, *Talenkauen* (modified from Cambiaso, 2007); D, *Camptosaurus* (modified from Galton & Powell, 1980); E, *Mantellisaurus* (modified from Galton, 2009).

floras between both continents. In this way, Zinmeister (1982) established the Weddellian Bioprovince for the marine invertebrate faunas shared during the Late Cretaceous and Paleogene of Patagonia, Antarctica, Australia and New Zealand. Novas et al. (2002) indicated that marine reptile faunas for these southern continents were also related to each other and were isolated from Laurasian taxa. In land, the Weddellian realm also includes plants, remarkably *Nothofagus* (Shen, 1994), and some metatherian clades (Case et al., 2000).

The recognition of several Patagonian and Antarctic ornithopods as belonging to the clade Elasmaria reinforces the palaeobiogeographical pattern defined for these taxa. In fact, the shared presence of elasmarians in Patagonia, Antarctica, and probably also Australia (see Agnolin et al., 2010) is in concordance with previous hypotheses suggesting some kind of shared faunistic components along the Weddellian marine coasts.

5. Conclusions

Present paper describes a new basal ornithopod from the Upper Cretaceous of Antarctica. The new taxon is named as *Morrosaurus antarcticus* gen. et sp. nov, and differs from previously known Antarctic ornithopods in several anatomical details, as well as in being a relatively robust and medium-sized animal.

In spite of that, a remarkable number of similarities between *Morrosaurus* and other Southern Hemisphere taxa are noted, particularly *Talenkauen*, *Anabisetia*, *Gasparinisaura*, and others. This results in that Patagonian, Antarctic, and possible Australian taxa conform a monophyletic ornithopod group: Elasmaria.

Elasmarians are characterized by bowed humerus with reduced deltopectoral crest, expanded ossified uncinat plates, elongate and tightly bunched foot, and expanded tail chevrons. The modifications of the foot and tail indicate improved locomotor capabilities for elasmarians, suggesting that they occupied an ecological niche different from that of other Gondwanan herbivorous dinosaurs.

The fact that Antarctic taxa like *Trinisaura* (Coria et al., 2013) and *Morrosaurus* could be closely related with Patagonian ornithopods to conform a monophyletic group, demonstrates that Elasmaria was widely distributed in southern Gondwana. In this regard, its recognition strengthens the faunistic similarities by terrestrial Weddellian faunas, as previously proposed by some authors. However, the abundance and diversification of ornithischians in Antarctica and Australia suggests that differences in composition with Patagonia were present, and some kind of provincialism may be present in those continents by Late Cretaceous times. Explanations for such differences could be related to the palaeolatitudinal position of each landmass and, consequently, to palaeoclimatic regimes (Novas, 2009).

Morrosaurus constitutes an important addition to the knowledge of Gondwanan ornithopods, particularly Antarctic taxa. Nevertheless, the ornithopods from Gondwana are still very poorly known and several are recorded by incomplete skeletons. In this regard, more detailed analyses as well as finding of new specimens will increase our knowledge of its systematics and palaeobiogeographic distribution.

Acknowledgements

We thank the Dirección Nacional del Antártico – Instituto Antártico Argentino for logistics support in Antarctica. To Adriel R. Gentil for his help in the early stages of this work and Nicolás R. Chimento, Federico Brison Egli, Julia S. D'Angelo, Gabriel L. Lio and Rodolfo A. Coria, for their comments and observations during the development of present contribution, and to Eduardo Koutsoukos, Andrew T. McDonald and an anonymous reviewer, who helped to

improve this work with their valuable comments and suggestions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2015.09.009>.