New abelisaurid remains from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina

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ABSTRACT

New theropod remains with abelisaurid affinities from the Upper Cretaceous (Anacleto Formation, lower Campanian), NW Patagonia, Argentina, are here described. The specimen (MPCN-PV 69) consists of a partial premaxilla, fragmentary vertebrae, proximal portion of both humeri, distal portion of the pubis, and an incomplete pedal ungual. Characters linking with Abelisauridae are a premaxilla with a sub-quadrangular body, externally ornamented, and paradental plates with a striated surface; and humerus with bulbous proximal head, conical internal tuberosity, and reduced greater tubercle. The humerus is similar to those of *Carnotaurus* and *Aucasaurus*, due to the presence of a bulbous head and a discontinuity between the head and the internal tuberosity, but also differs from both taxa in the more distal location of the greater tubercle with respect to the internal tuberosity. *Aucasaurus* also comes from Anacleto Formation, but differences in the humeri suggest that MPCN-PV 69 is a different taxon. The phylogenetic analysis performed supports the affiliation to Abelisauridae, but fails to determinate a more precise relationship with others abelisaurids. However, a majority rule consensus of the analysis shows a position within Brachyrostra. Despite being fragmentary, MPCN-PV 69 probably represents a new abelisaurid from the Anacleto Formation, thus increasing the knowledge and diversity of Late Cretaceous South American abelisaurids.

1. Introduction

The deposits of the Anacleto Formation (Campanian), in Patagonia, are renowned for their rich content of fossil continental tetrapods, standing out the record of an abundant dinosaur fauna. Sauropods are the most diverse dinosaurs in this unit, which are represented by *Antarctosaurus wichmannianus* (von Huene, 1929), *Neuquensaurus australis* (Lydekker, 1893; Powell, 1986; Salgado et al., 2005), *Barrosasaurus casamiquelai* (Salgado and Coria, 2009), *Rinconsaurus caudamirus* (Calvo and González Riga, 2003), *Overosaurus paradasorum* (Coria et al., 2013), among others. In sedimentary rocks of this formation were also found the extensive nesting sites of sauropods from Auca Mahuevo, together with many eggs with embryonic remains, some of them with casts of the skin (Chiappe et al., 1998, 2000, 2001, 2004; Garrido et al., 2001; Chiappe and Coria, 2004). Ornithischians are represented so far by the ornithopod *Gasparinisaura cincosaltensis* (Coria and Salgado, 1996). On the other hand, unlike many sauropods found in this formation, the record of theropods is scarcer, and only includes the neovenatorid megaraptoran *Aerosteon riocoloradensis* (Sereno et al., 2008) and the abelisaurid *Aucasaurus garridoi* (Coria et al., 2002). Despite the well-known *Abelisaurus comahuensis* (Bonaparte and Novas, 1985) has been considered as belonging to the Anacleto Formation after the inclusion of all dinosaur bearing deposits of the Lago Pellegrini to that unit, it is locally known that the specimen actually comes from the Allen Formation at the Sr. Fernández field, close to Salitral Moreno, Río Negro Province (F. Fernández, pers.

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comm.). Since no witnesses are alive and no field notes were taken, more information is necessary to assess the stratigraphic provenance of this taxon.

In the present contribution we describe the partial skeleton of an abelisaurid theropod that comes from the Anacleto Formation, at the Verdecchia's family field, close to Fisque Menuco (General Roca), Río Negro Province, Argentina. Despite these remains are fragmentary, they probably represent a new taxon, thus increasing the record of abelisaurid theropods from this geological unit.

Abelisauroids are between the most peculiar predatory dinosaurs that lived during the Late Cretaceous in southern continents. They are represented by two morphologically distinct groups (Bonaparte, 1991a). One of them is the still poorly known medium to small-sized noasaurids (Bonaparte and Powell, 1980). These are represented by *Noasaurus leali* (Bonaparte and Powell, 1980), *Masiakasaurus knopfleri* (Sampson et al., 2001), *Laevisuchus indicus* (Huene and Matley, 1933), and *Ligabueino andesi* (Bonaparte, 1996), among other taxa. The second group includes the medium to large-sized abelisaurids, including *Abelisaurus comahuensis* (Bonaparte and Novas, 1985), *Carnotaurus sastrei* (Bonaparte, 1985), *Aucasaurus garridoi* (Coria et al., 2002), *Ekrixinatosaurus novasi* (Calvo et al., 2004a), *Ilokelesia aguadagrandensis* (Coria and Salgado, 1998), *Skorpiovenator bustingorryi* (Canale et al., 2009), *Pycnonemosaurus nevesi* (Kellner and Campos, 2000), *Rugops primus* (Sereno et al., 2004), *Majungasaurus crenatissimus* (Depéret, 1896), *Indosaurus matleyi* (Huene and Matley, 1933), *Rajasaurus narmadensis* (Wilson et al., 2003), *Rahiolisaurus gujaratensis* (Novas et al., 2010), and *Arcovenator escotae* (Tortosa et al., 2013), among others. Some of them are represented by nearly complete skeletons that document extensively the anatomy of the group.

Abelisauroids have been recorded from South America, Africa, Australia, Europe, Asia, Madagascar and India (Carrano and Sampson, 2008) and, despite being recorded from the Middle Jurassic to the Late Cretaceous, they are especially abundant in the Upper Cretaceous strata of southern continents. The deposits of the Anacleto Formation illustrate the last endemic stage of a South American fauna with an exclusive Gondwanan signature (Apesteguía, 2002; Leanza et al., 2004) and thus a high diversity of abelisaurids is expected.

The survey in the study site was performed in a joint effort between the PANGEA Network of Italian Museums, the Agencia Cultura of Río Negro Province, the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', and the 'Félix de Azara' Foundation. Later, when founded, the Museo Patagónico de Ciencias Naturales, where materials are now deposited, replaced the last two institutions in the fieldworks.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; FMNH PR, Field Museum of Natural History, Chicago, USA; GSI, Geological Survey of India, Calcutta, India; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MCF-PVPH, Museo Carmen Funes, Plaza Huincul, Neuquén, Argentina; MNN, Musée National du Niger, Niamey, Niger; MPCA, Museo Provincial 'Carlos Ameghino', Cipolletti, Río Negro, Argentina; MPCM, Museo Paleontologico Cittadino di Monfalcone, Gorizia, Italy; MPCN-PV, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina; UA, Université d'Antananarivo, Antananarivo, Madagascar; UCPC, University of Chicago Paleontological Collection, Chicago, USA; UNPSJB-PV, Universidad Nacional de la Patagonia "San Juan Bosco", Comodoro Rivadavia, Argentina.

2. Systematic paleontology

Theropoda Marsh, 1881
Neotheropoda Bakker, 1986
Ceratosauria Marsh, 1884
Abelisauroidea Bonaparte, 1991
Abelisauridae Bonaparte and Novas, 1985
Genus et sp. indet.

3. Material

The specimen MPCN-PV 69 (Fig. 1) consists on a small to mid-sized theropod skeleton composed by a partial premaxilla, three probable dorsal vertebrae, fused sacral vertebrae, the proximal half of both left and right humeri, the distal portion of the pubis, and an incomplete pedal ungual phalanx, plus some indeterminate fragments. Due to the grade of fusion of the neural arches to the centra, the specimen corresponds probably to an adult or at least to a subadult. The total length of the skeleton is difficult to specify because it is highly fragmented, but is estimated to be between 3 and 5 m long.

Most of the material was found on surface in a single 4 m² area at the bottom of a creek along three different years in which the specimen bones were subsequently added by weathering of the origin site. The premaxilla, however, comes from several meters toward the top of the hill, but we consider it as belonging to the same specimen since it was found in the same erosive line and further the preservation is identical to the other bones. No systematic excavation was made in the place and the site of origin was not discovered. Whereas only this area provided theropod remains, the whole fossiliferous area provided the remains of numerous adult and juvenile specimens of titanosaurid sauropods that were not studied yet (Apesteguía et al., 2012).

4. Locality and horizon

Verdecchia family field is located 20 km SW from Fisque Menuco (General Roca), Río Negro Province, Argentina (Fig. 1A). The outcrop, found and described by Héctor Leanza in the Geologic Chart General Roca (Hugo and Leanza, 1999), represents a limited exposure with amphitheater structure where outcrops the Anacleto Formation (Río Colorado Subgroup) considered as lower Campanian, Upper Cretaceous (Dingus et al., 2000; Leanza et al., 2004; Garrido, 2010).

The Anacleto Formation is composed by a sequence of continental deposits, mainly sandstones, claystones and concretional limestones (for more detailed geological data see Supplementary Information). The exposed level within this geological unit is not well determined, but was suggested as corresponding to its basal levels (H. Leanza, pers. comm.). The presence of fossil vertebrates in the area was noticed by C. Hugo and H. Leanza during the geological prospection.

The site presents a rich bonebed belonging probably to cf. *Laplatasaurus araukanicus* (Huene, 1929) or *Bonitasaura salgadoi* (Apesteguía, 2004). Turtle shells and a dipnoan tooth plate were also found in the area. The theropod material here studied was found by Mr. Raúl Ortíz in the context of a fieldtrip lead by one of the authors (S. A.) in coordination with the Group Pangea. All the material is housed in the MPCN, at General Roca, Río Negro.

5. Results

5.1. Description
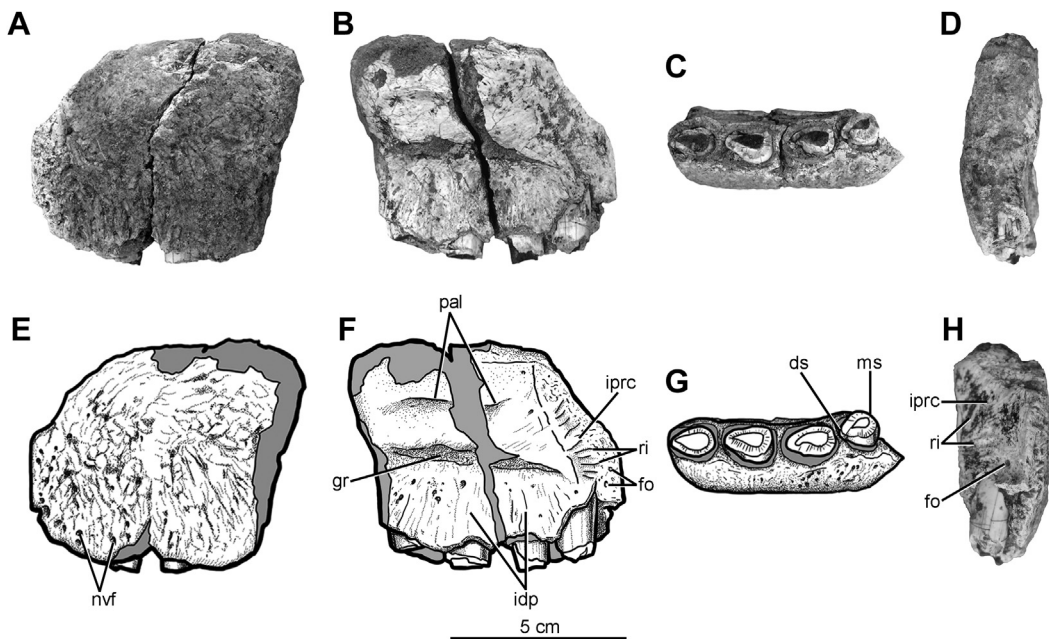
5.1.1. Premaxilla

The only cranial material recovered belongs to a fragmentary premaxilla, with four teeth preserved still inserted in the corresponding alveoli (Fig. 2). The preserved portion is approximately
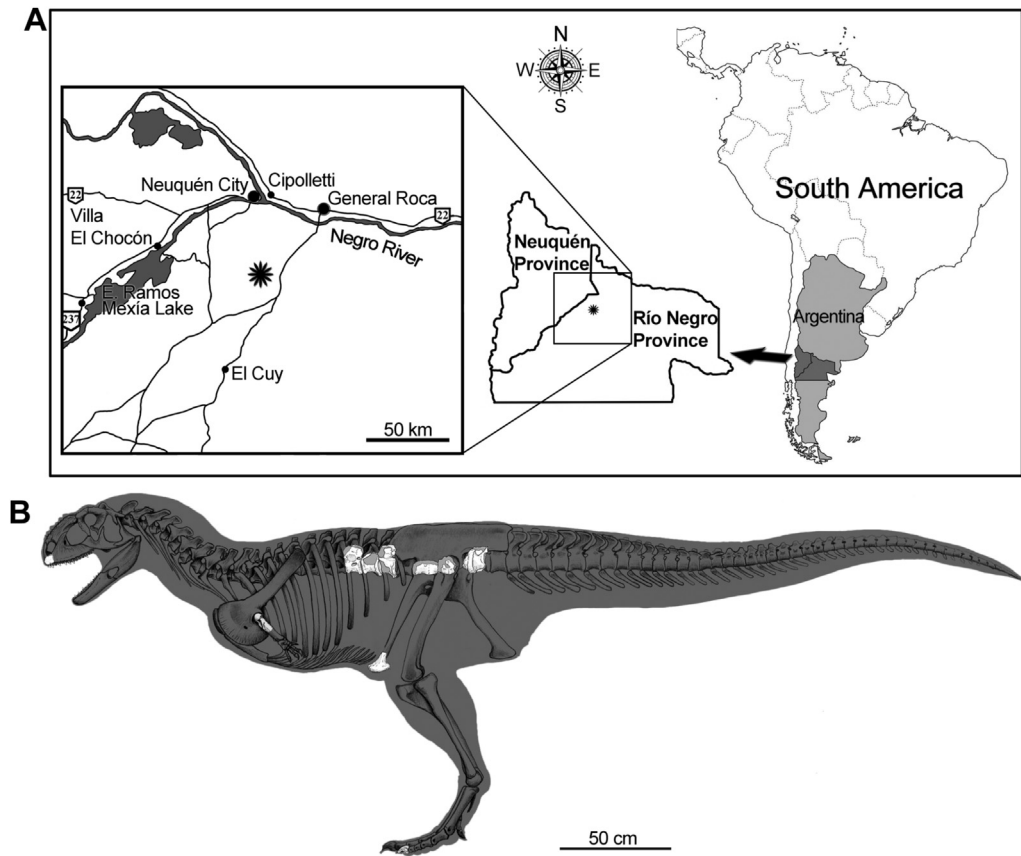
Fig. 1. Geographic provenance of MPCN-PV 69. (A) Locality where were found the materials here studied, at the Verdecchia family field (indicated with a star), 20 km SW from General Roca, Río Negro Province. (B) Preserved remains of MPCN-PV 69, highlighted in their positions on the skeleton (positions of vertebrae are tentative).

quadrangular and slightly more elongated than high, although the dorsal and posterior parts are eroded. Both the narial zone and the articular surface with the maxilla are not preserved. Although the premaxillary body is incomplete, we consider that only a small part

of the posterior part was eroded (i.e., the posterior edge); conversely, the erosion was stronger on the dorsal portion, so the body probably had a greater height. Despite this, the general shape is common for the premaxillary body of abelisaurids reported so far

Fig. 2. Left premaxilla of MPCN-PV 69. (A, E) Lateral view; (B, F) medial view; (C, G) occlusal view; (D) posterior view; (H) anterior view. Abbreviations: ds, distal surface of the crown; fo, foramina; gr, groove on the medial surface; idp, interdental plates; iprc, interpremaxillary contact; ms, mesial surface of the crown; nvf, neurovascular foramina; pal, palatal process; ri, ridges. Drawings by Jorge González.

(e.g., Bonaparte et al., 1990; Sampson et al., 1996; Sampson and Witmer, 2007; Canale et al., 2009; Novas et al., 2010). Anteriorly, a flat surface is observed, obliquely oriented respect to the medial side of the bone and inclined in lateral direction, being rugose and pierced by small foramina (Fig. 2B, F, H). This possibly represents the surface of interpremaxillary contact. A series of sub-parallel ridges is observed, especially on the ventral part of the surface, which are arranged perpendicular to the anterior end, acquiring dorsally a more oblique distribution. Similar features are present in the interpremaxillary contact of *Majungasaurus* (FMNH PR 2100), especially in the foramina piercing the surface and the rugose aspect with the presence of ridges (Sampson and Witmer, 2007). However, in FMNH PR 2100 the surface is substantially more rugose than in MPCN-PV 69, a feature probably related with an advanced ontogenetic stage in FMNH PR 2100 (Sampson and Witmer, 2007). In other specimens of *Majungasaurus* (i.e. FMNH PR 2008, UA 8716, and UA 8717) the contact surface is less rugose and crossed by striae roughly parallel to the anterior end of the bone (Sampson et al., 1996; Sampson and Witmer, 2007), thus being different from the perpendicular striae of MPCN-PV 69. Moreover, in all named specimens of *Majungasaurus* the ventral part of the articular surface bears parallel, obliquely directed ridges (Sampson and Witmer, 2007), resembling those observed in MPCN-PV 69.

The premaxilla of MPCN-PV 69 is compressed transversely and has a slight curvature, resulting in a convex lateral surface and a concave medial one. The lateral surface is ornamented with a rough texture consisting of grooves and channels (Fig. 2A, E), which is a characteristic feature of the skull bones of abelisaurids, including the premaxilla (Bonaparte et al., 1990; Sampson et al., 1996; Sampson and Witmer, 2007; Canale et al., 2009; Novas et al., 2010). The grooves become wider and more conspicuous near the alveolar edge, where the presence of foramina, possibly neurovascular, is also observed.

The medial surface is characterized by having a horizontal groove filled with sedimentary deposits, separated from the alveolar ridge (Fig. 2B, F). It is possible that this groove contained a series of foramina within, in a similar way to the premaxillae of other abelisaurids (Sampson et al., 1996; Sampson and Witmer, 2007). This groove is ventrally inclined towards the anterior zone of the bone and closer to the alveolar edge, thus differentiating from the more horizontally disposed groove with foramina present in the maxilla, as can be observed in several abelisaurid specimens (e.g., UNPSJB-PV247, Lamanna et al., 2002; UCPC 10, Mahler, 2005; FMNH PR 2100, Sampson and Witmer, 2007; MNN GAD1-1, Sereno and Brusatte, 2008). Between this groove and the alveolar ridge, the medial surface is formed by fused interdental plates, which are crossed by vertical striations and also are pierced by foramina (Fig. 2B, F). The presence of fused interdental plates is a feature observed in abelisaurids, although is also seen in noasaurids as *Masiakasaurus* (Carrano et al., 2002), in more primitive theropods as *Ceratosaurus* (Madsen and Welles, 2000), and also in allosauroids as *Allosaurus* (Madsen, 1976) and others basal tetanurans as *Torvosaurus* (Galton and Jensen, 1979). On the other hand, dorsally to the horizontal groove, the medial wall of bone protrudes medially, reaching a plane more internally located. In a more dorsal position, a rise is observed in the form of a shallow ridge, also located horizontally, which loses height towards the anterior side, disappearing close to the most anterior preserved edge (Fig. 2B, F). This ridge corresponds to a palatal process, which is similar to that present in *Majungasaurus* (FMNH PR 2008, FMNH PR 2100, UA 8716; Sampson et al., 1996; Sampson and Witmer, 2007) *Rahiolisaurus* (Novas et al., 2010), and other materials from India (AMNH 1733 and GSI-IM K27/710; Sampson et al., 1996), especially in the poor development. Even a reduced palatal process of the premaxilla was found as sinapomorphic for Abelisauridae by previous authors (Canale et al., 2009).

Four teeth are preserved in situ, as mentioned above, but none is complete (Fig. 2C, G). This teeth count also is present in other abelisaurids as *Majungasaurus*, *Carnotaurus*, *Rahiolisaurus* and *Rugops* (Bonaparte et al., 1990; Sereno et al., 2004; Sampson and Witmer, 2007; Novas et al., 2010), but it is widely present in the premaxillae of theropods, with some exceptions (Rauhut, 2003; Sampson and Witmer, 2007), and also is considered a primitive state in theropods (Currie and Zhao, 1993; Rauhut, 2003). All of the teeth are broken at the base of the crown, so that the morphology of the latter is unknown. However, due to fracture, the shape of the section of the teeth can be observed. The crowns have a section approximately oval or teardrop-shaped, resembling the cross-section of the teeth of *Rahiolisaurus* (Novas et al., 2010). The teeth located at the anterior end has a strongly convex shape toward the lateral side (the labial side), whilst the surface located toward the lingual side is convex but to a lesser degree. The second tooth has a similar shape, but the two following teeth, more posteriorly located, have the mesial side much more expanded while the distal end is sharpened. Furthermore, the lingual surface has a slight concavity in its central zone. Thus, the two posterior teeth acquire a subtriangular or teardrop shape (Fig. 2C, G). The shape of these teeth in section is far from the morphology observed for maxillary teeth of other abelisaurids, since in the latter the maxillary teeth are labiolingually compressed and have a symmetrical section, with both lingual and labial sides with a similar degree of convexity (Lamanna et al., 2002; Mahler, 2005; Sampson and Witmer, 2007; Smith, 2007). Marked carinae are not visible in any of the teeth, but in the two anterior teeth the mesial and distal ends are sharp and protrude slightly, which may indicate the presence of shallow carinae. Among abelisaurids, teeth are characterized by marked and serrated carinae, which cross the crown from its base to the apex (Smith et al., 2005; Sampson and Witmer, 2007; Smith, 2007; Sereno and Brusatte, 2008). Despite the teeth of MPCN-PV 69 are incomplete they show a general shape consistent with the premaxillary teeth of other abelisaurids (Smith, 2007).

5.1.2. Vertebrae

Three probably fragmentary dorsal vertebrae and two groups of fused sacral vertebra have been preserved. The three considered as dorsals consist in the centrum and scarce portions of the neural arches (Fig. 3A–C, F–H). The correct anatomic position of these three vertebrae is difficult to precise, mainly due to the poor preservation of the material especially at the neural arches. The centra are spool-shaped, i.e. with expanded anterior and posterior articular faces and constricted middle portion, and the articular surfaces are gently amphicoelous. They have some similarities with caudal vertebrae of other abelisaurids, mainly after the ventrally expanded posteroventral border of the centrum, a feature observed in anterior caudals of *Carnotaurus* (MACN-CH 894, Persons and Currie, 2011), *Rahiolisaurus* (Novas et al., 2010), and an isolated vertebra from Patagonia (MACN-PV-RN 1012, Ezcurra and Méndez, 2009). In *Carnotaurus* and MACN-PV-RN 1012 these expansions bear articular facets for the hemal arches, but in MPCN-PV 69 no facets are observed. The ventral surface of these vertebrae is nearly smooth and there is no evidence of a longitudinal groove or keel. In some abelisaurids as *Majungasaurus*, *Ilokelesia*, and MACN-PV-RN 1012 was reported the presence of a longitudinal groove on the ventral surface of the anterior caudal centra (Coria and Salgado, 1998; O'Connor, 2007; Ezcurra and Méndez, 2009). However, in some abelisaurids, like *Carnotaurus*, the groove is not present (Rauhut, 2003), and therefore this is not a reliable character to ensure that the studied vertebrae are not caudals. Two of the vertebrae present portions of the neural arches, but lacking neural spines, zigapophyses, and the zone between the centra and the diapophyses; only is visible the base of the latter, which is robust
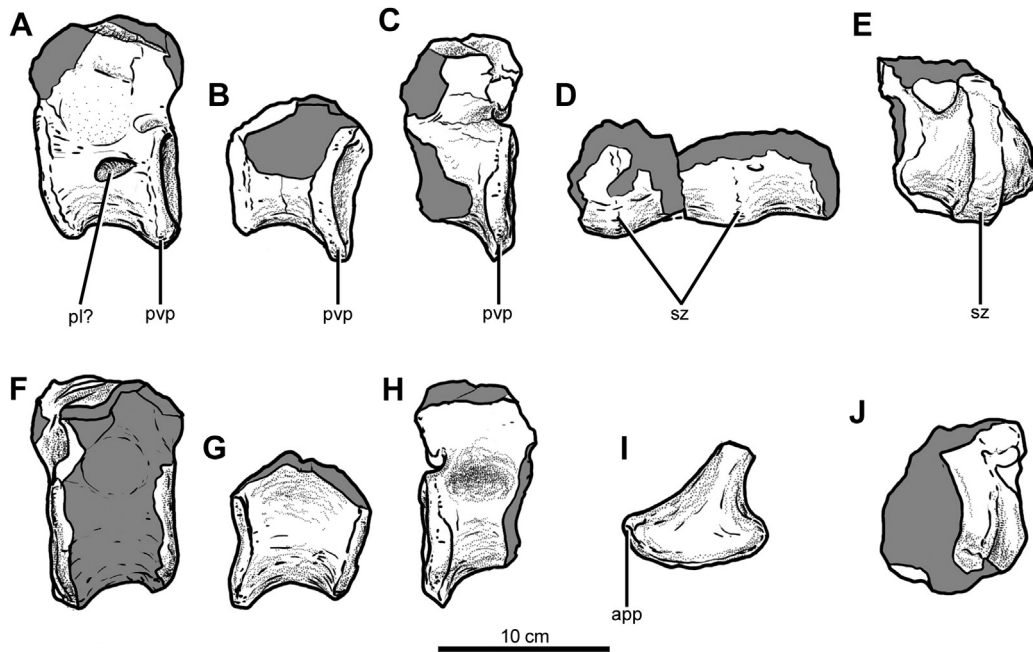
Fig. 3. Vertebrae and pubis preserved of MPCN-PV 69. (A—C, F—H) Supposed dorsal vertebrae: (A—C) left view; (F—H) right view. (D) Fused sacral centra in undetermined view. (E, J) Fused sacral centra: (E) left? view; (J) right? view. (I) Distal portion of the left pubis, in lateral view. Abbreviations: app, anterior process of the distal pubis; pl?, possible pleurocoel; pvp, posteroventral projection of the centrum; sz, suture zone between sacral vertebrae. Drawings by Jorge González.

and well-developed. Unfortunately, the morphology of the transverse processes, so characteristic in abelisaurid vertebrae, especially in the caudals, cannot be observed. Based on the absence of articular facets for the hemal arches and the absence of a ventral sulcus on the centrum, we consider these vertebrae as possible dorsals but, as was explained above, these characters are not sufficient to state this assignment.

Due to the absence of parapophyses in the centrum they probably represent posterior dorsals. In fact, the posterior dorsal vertebrae in abelisaurids exhibit a migration of the parapophyses from the centrum to the neural arch, reaching a close association with the diapophyses (Bonaparte et al., 1990; Coria and Salgado, 1998; Coria et al., 2006; O'Connor, 2007). Two of them present a complete centrum, which has a length similar to their maximum height, a condition similar to that observed in dorsal vertebrae of *Carnotaurus* and *Majungasaurus* (Bonaparte et al., 1990; O'Connor, 2007), but different to that observed in *Ilokelesia*, where de centrum is longer than its height (Coria and Salgado, 1998; Coria et al., 2006). One vertebra presents an excavation on the lateral side of the centrum, relatively large and oval-shaped (Fig. 3A). This opening can represent a pleurocoel and related with pneumatic foramina, but the nature of the structure cannot corroborate due to lack of preservation. Pneumaticity has been reported in centra of dorsal vertebrae of other abelisaurids, such as *Majungasaurus* and *Carnotaurus*, the first two with little foramina only on anterior dorsal centra (Bonaparte et al., 1990; O'Connor, 2007), and also in isolated vertebrae from Patagonia (Martínez et al., 2004) and in *Dahalokely* (Farke and Sertich, 2013). .

Three sacral centra have been preserved, which are completely fused to each other (Fig. 3D), and also are two other very incomplete centra (Fig. 3E, J). It is not possible to check if both groups of fused vertebrae were articulated to each other or if they represent parts of the same centra. The fusion of the sacral centra is a feature present in other abelisauroids, as *Masiakasaurus*, *Carnotaurus*, *Majungasaurus* and *Berberosaurus* (Bonaparte et al., 1990; Carrano et al., 2002, 2011; Allain et al., 2007; O'Connor, 2007). These

centra are compressed in the central zone and expanded in the zone of co-ossification. Pneumatic foramina are not visible, as is common in the sacral centra of abelisauroids (Bonaparte et al., 1990; Carrano et al., 2002; Allain et al., 2007; O'Connor, 2007), although this absence of pneumaticity is also observed in other ceratosaurs, as *Ceratosaurus* (Madsen and Welles, 2000), and in tetanurans as *Allosaurus* (Madsen, 1976; Rauhut, 2003). Conversely, in carcharodontosaurids pleurocoels are present in sacral centra (e.g., *Acrocanthosaurus*, Harris, 1998) and also in some coelurosaurs, as oviraptorosaurs (e.g., *Khaan*, Balanoff and Norell, 2012).

5.1.3. Humeri

Both humeri preserved only their proximal portion and, although fragmentary, have many morphological similarities with humeri of other abelisaurids. The preserved part of the right humerus measures approximately 10 cm long, and the portion of the left humerus around 11 cm. In both bones the estimated total length is around 25 cm, and therefore they are probably shorter than the humeri of *Carnotaurus*, *Aucasaurus* and *Majungasaurus*.

The proximal articulation head is hemispherical and prominent (Fig. 4C, F), as is observed in *Elaphrosaurus* (Galton, 1982) and the abelisaurids *Aucasaurus*, *Carnotaurus*, *Rahiolisaurus* and *Majungasaurus* (Bonaparte et al., 1990; Coria et al., 2002; Carrano, 2007; Méndez et al., 2010; Burch and Carrano, 2012). In *Eoabelisaurus* the humeral head is well-developed but it is not bulbous and is more compressed anteroposteriorly, whereas in other abelisauroids, e.g. *Masiakasaurus*, the head is hemispherical but not so anteroposteriorly expanded and is less bulbous than in abelisaurids, (Carrano et al., 2002, 2011; Pol and Rauhut, 2012). Conversely, this surface of articulation is transversely broad and kidney-shaped in proximal view in *Ceratosaurus*, *Allosaurus* and coelurosaurs (Madsen, 1976; Madsen and Welles, 2000; Rauhut, 2003; Novas et al., 2006; Méndez et al., 2010). In MPCN-PV 69 the head is separated from the diaphysis by a distinct neck, similarly to the condition present in *Carnotaurus* and *Majungasaurus*.
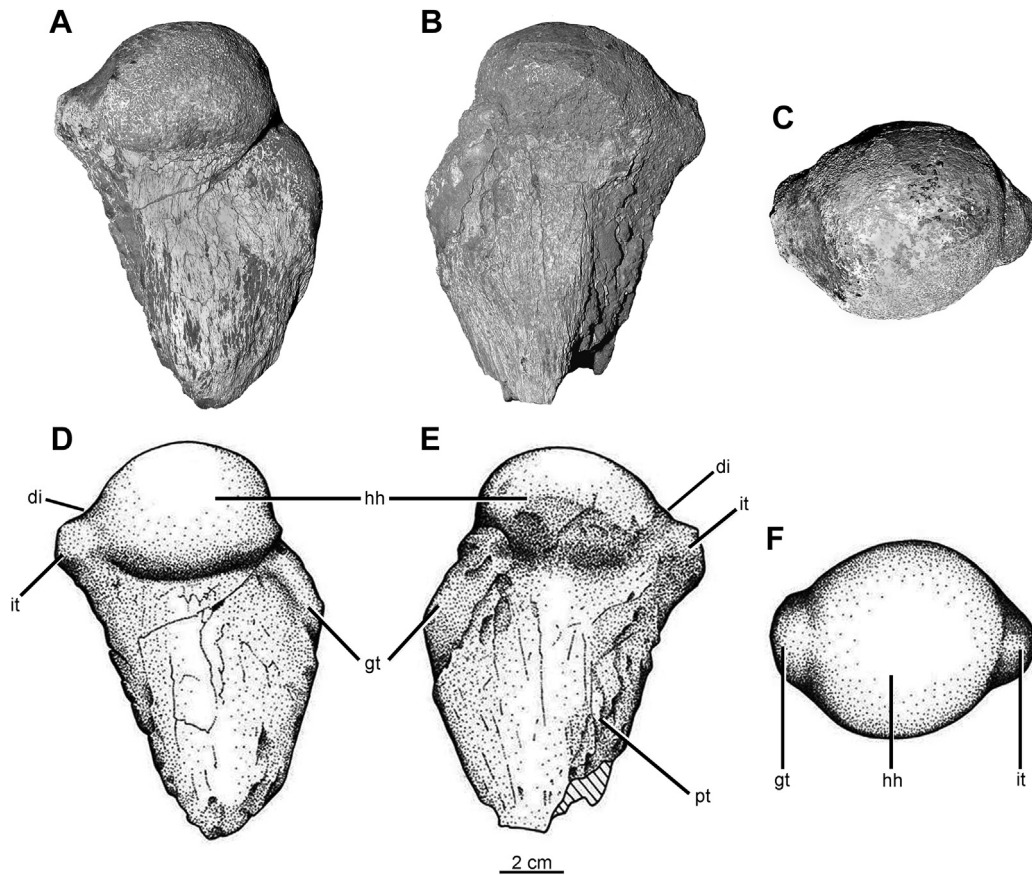
Fig. 4. Proximal portion of the left humerus of MPCN-PV 69. (A, D) Anterior view; (B, E) posterior view; (C, F) proximal view. Abbreviations: di, discontinuity between the humeral head and the internal tuberosity; gt, greater tubercle; it, internal tuberosity; hh, humeral head; pt, posterior tuberosity. Drawings by Jorge González.

The internal tuberosity is well-developed in both humeri, conical in shape and medially projected (Fig. 4), in a similar way to that of the humerus of *Carnotaurus*, *Aucasaurus*, *Rahiolisaurus* and *Majungasaurus* (Figs. 5, 6), but differing from the most reduced
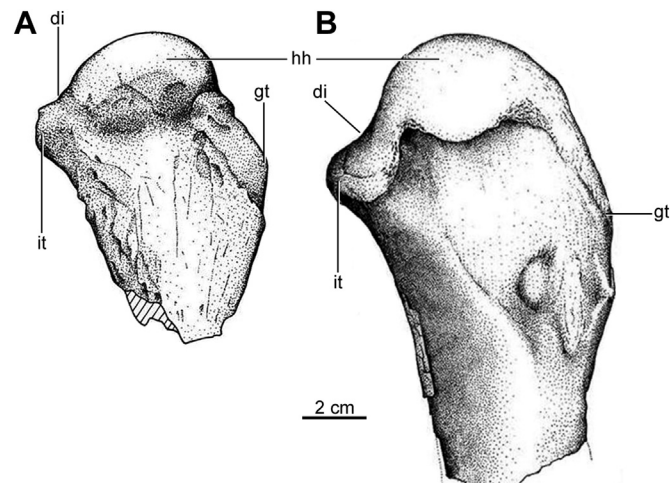
Fig. 5. Comparison between the humeri of MPCN-PV 69 and *Aucasaurus garridoi*. (A) left humerus of MPCN-PV 69, in posterior view (reversed for better comparison). (B) Right humerus of *Aucasaurus garridoi*, in posterior view (from Coria et al., 2002). Abbreviations: di, discontinuity between the humeral head and the internal tuberosity; gt, greater tubercle; it, internal tuberosity; hh, humeral head. Drawings by Jorge González.

and more anteroposteriorly compressed internal tuberosity of *Masiakasaurus* (Carrano et al., 2002; Novas et al., 2006; Méndez et al., 2010). In other theropods, e.g. *Dilophosaurus*, *Ceratosaurus*, *Elaphrosaurus*, and basal tetanurans as *Allosaurus* and *Acrocanthosaurus*, this structure is also medially projected and triangular in anterior and posterior view, but is more anteroposteriorly compressed and not conical, and is continuous with the proximal articular head (Madsen, 1976; Galton, 1982; Welles, 1984; Currie and Carpenter, 2000; Madsen and Welles, 2000). On the other hand, in *Majungasaurus*, *Carnotaurus*, *Aucasaurus*, and MPCN-PV 69, there exists an interruption between the internal tuberosity and the humeral head (Figs. 4, 5, 6). However, this may be a plesiomorphic character, since in *Herrerasaurus* a deep trough separates both structures (Sereno, 1993), and a discontinuity is observed also in *Ceratosaurus* (Madsen and Welles, 2000). Nevertheless, the presence of an interruption between the base of the internal tuberosity and the surface of the head could be a character distinguishing derived abelisaurids from other abelisauroids with known humerus anatomy, as *Eoabelisaurus*, *Masiakasaurus*, and a material reported by Novas et al. (2006), in which the two structures are continuous. However, a more detailed observation of the humerus of *Eoabelisaurus* is necessary to confirm this, due to the degree of preservation in this specimen may obscure anatomical interpretation. Nevertheless, the phylogenetic position of *Eoabelisaurus* may be doubtul (Novas et al., 2013), and possibly this taxon represents a basal ceratosaur. In this context, the evolution of this character in the humerus between ceratosaurs would need more resolved phylogenetic relationships to be better understood.
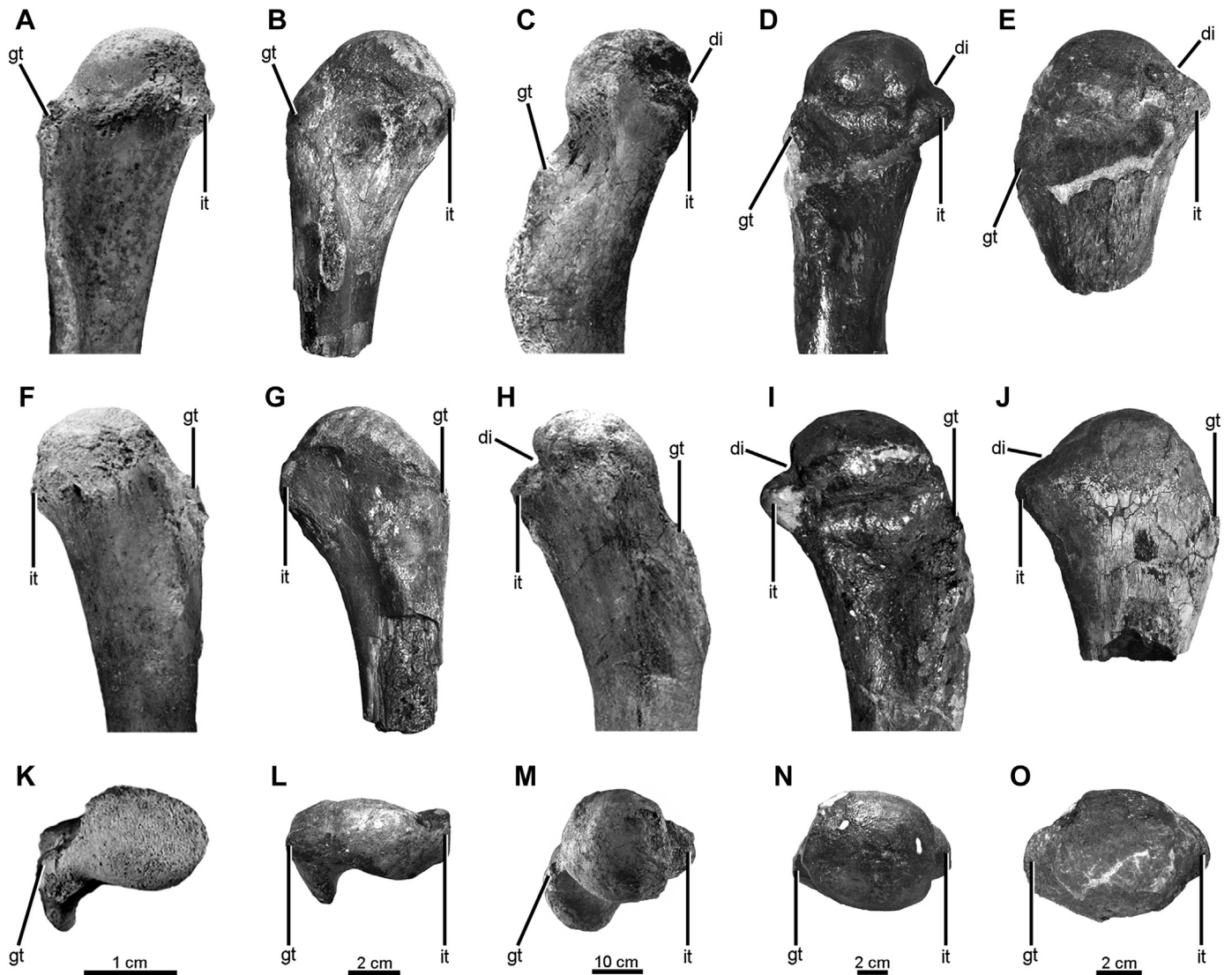
Fig. 6. Comparison between the proximal portions of humeri of several abelisauroids. (A, F, K) *Masiakasaurus* (FMNH PR 2143, from Carrano et al., 2002): (A) anterior view; (F) posterior view; (K) proximal view. (B, G, L) MCF-PVPH 53, an abelisauroid humerus from the Upper Cretaceous of Patagonia (photographs courtesy of Ariel Méndez): (B) anterior view; (G) posterior view; (L) proximal view. (C, H, M) *Majungasaurus* (FMNH PR 2423, from Carrano, 2007): (C) anterior view; (H) posterior view; (M) proximal view. (D, I, N) *Carnotaurus* (MACN-CH 894) (photographs courtesy of Ariel Méndez): (D) anterior view; (I) posterior view; (N) proximal view. (E, J, O) Right humerus of MPCN-PV 69: (E) anterior view; (J) posterior view; (O) proximal view. Abbreviations: di, discontinuity between the humeral head and the internal tuberosity; gt, greater tubercle; it, internal tuberosity.

On the lateral surface of both humeri is noted the greater tubercle, which is reduced and conferring a convex aspect to the lateral border in anterior and posterior view (Fig. 4A, B, D, E). It is located slightly distally respect to the internal tuberosity, as in *Majungasaurus* and *Rahiolisaurus*, but differing from *Carnotaurus*, *Aucasaurus*, *Masiakasaurus*, and other abelisauroid humeri found in Patagonia (i.e., MCF-PVPH 53, Novas et al., 2006), where the greater tubercle is located at level of the internal tuberosity (Figs. 5, 6). On the other hand, in *Dilophosaurus*, *Ceratosaurus*, *Elaphrosaurus*, *Allosaurus* and coelurosaurs the greater tubercle is proximally located respect to the internal tuberosity (Madsen, 1976; Galton, 1982; Welles, 1984; Madsen and Welles, 2000; Novas et al., 2006). Another difference observed with respect to the humerus of *Aucasaurus* is that in the latter the humeral head is almost continuous with the greater tubercle, whereas in MPCN-PV 69 the two structures are separated by a little interruption (Fig. 5).

On the posterior surface is observed an elongated tuberosity, better preserved in the left humerus, like a ridge, distally located

respect to the level of the greater tubercle (Fig. 4B, E), which is similar to that observed in the humerus of *Majungasaurus* and *Rahiolisaurus* (Carrano, 2007; Méndez et al., 2010; Burch and Carrano, 2012). The total extension of this structure is not possible to see, due to lack of the distal portion of the bone. This prominence has been considered as a probable synapomorphy of Abelisauroidea by previous authors (Novas et al., 2006; Méndez et al., 2010) and as a point of muscle insertion (i.e., *M. latissimus dorsi* and part of the *M. deltoideus*; Jasinoski et al., 2006; Carrano, 2007; Méndez et al., 2010).

5.1.4. Pubis

MPCN-PV 69 includes an isolated distal portion of the left pubis (Fig. 3I). The distal end is anterior and posteriorly expanded, constituting a well-developed pubic boot, with a convex distal surface in lateral view, resembling the condition observed in *Carnotaurus* (Bonaparte et al., 1990). Conversely in *Eoabelisaurus* there is no evidence of any anteroposterior expansion (Pol and Rauhut,

2012), whereas in *Masiakasaurus* the pubic boot is more developed, with a long posterior projection, but with a straight and slightly concave distal surface (Carrano et al., 2011).

In MPCN-PV 69 the posterior process is eroded, but probably was longer and positioned in acute angle respect to the diaphysis, conversely to the anterior expansion which is shorter and positioned forming an obtuse angle with the diaphysis. In this way the morphology resembles the pubic boot of *Carnotaurus*. In allosauroid tetanurans, e.g., *Allosaurus*, *Aerosteon*, *Megaraptor*, and *Giganotosaurus*, a more developed anterior expansion is common, although in these theropods the pubic boot is massive and very anteroposteriorly expanded (Madsen, 1976; Coria and Salgado, 1995; Calvo et al., 2004b; Sereno et al., 2008).

5.1.5. Pedal ungual phalanx

This ungual phalanx is robust, tall, gently curved, and devoid of a flexor tubercle (Fig. 7). The lateral surface bears two vascular grooves which describe a Y-shaped pattern, surrounding a triangular bumped area located toward the posterior end of the lateral side of the claw. This is characteristic for Abelisauroidea (Novas and Bandyopadhyay, 2001; Carrano et al., 2002; Carrano and Sampson, 2008; Novas et al., 2013). The ventral aspect is excavated, as in pedal ungual phalanges of *Majungasaurus* (FMNH PR 2434), MPCA 56, K27/634, and MPCM 13573 (Novas and Bandyopadhyay, 2001; Novas et al., 2005; Carrano, 2007). Except for the noasaurid *Masiakasaurus*, which bears a ventral keel, the feature seems to be common for Abelisauroidea (Novas et al., 2013). Its posterodorsal process is poorly developed (Fig. 7) as in large, robust abelisaurids (e.g., MPCA 56; K27/634; FMNH PR 2434), but differing from the noasaurids *Masiakasaurus knopfleri* (Carrano et al., 2002) and *Velocisaurus unicus* (Bonaparte, 1991b), which present a markedly elongated process.

6. Discussion

6.1. Phylogenetic analysis

Despite the fragmentary condition of MPCN-PV 69, a phylogenetic analysis was performed in order to assess its phylogenetic position. The codings of this specimen were added to a previously published character matrix (see Suppl. Inf.) including several ceratosaur taxa (Farke and Sertich, 2013), which in turn is based on previous matrices (Carrano and Sampson, 2008; Canale et al., 2009; Pol and Rauhut, 2012). A new character was added to this matrix,

Fig. 7. Pedal ungual phalanx of MPCN-PV 69, in lateral view. Abbreviations: pdp, posterodorsal process; vg, vascular grooves. Drawing by Jorge González.

which refers to the kind of separation observed between the proximal articular head of the humerus and the internal tuberosity (Suppl. Inf.). This addition was made with the intention of emphasize the differences noted between derived abelisaurids and others abelisauroids. We follow the reinterpretations of character codings of some abelisauroid taxa conducted by Farke and Sertich (2013), i.e. for character 6 in *Ekrixinatosaurus*, *Rugops*, *Masiakasaurus*, and *Noasaurus*, and for character 25 in *Ilokelesia* (for more detail see Farke and Sertich, 2013). For the codifications of *Ilokelesia* was considered not only that published by Coria and Salgado (1998) which is damaged (Carrano and Sampson, 2008; Novas et al., 2013), but especially the morphology of the other two assigned postorbitals preserved. Moreover, most of characters and codifications for the postorbital were obtained from the matrix performed by Carrano and Sampson (2008), while the remaining characters for this bone in *Ilokelesia* were revised using photographs. The codifications of *Kryptops* were made considering only the maxilla of the holotype (MNN GAD1-1), because the postcranial elements present allosauroid affinities which suggest a partial chimaera (Carrano et al., 2012; Novas et al., 2013). *Camarillasaurus* was removed from the analysis due that it presents dubious evidence of being a ceratosaur. Thus, a total of 30 taxa and 193 characters were analyzed. The analysis was performed using TNT 1.1 (Goloboff et al., 2008), considering the same weight for all the characters. The heuristic search of the most parsimonious topologies was carried out from 1000 replicates of Wagner trees obtained from RAS (random addition sequences), which later were submitted to the TBR (tree bisection and reconnection) swapping algorithm, saving 10 trees per replication. Branches with a minimum length of zero were collapsed during the analysis.

A total of 8120 equally parsimonious trees of 332 steps were recovered from the analysis. The strict consensus shows a massive polytomy at the base of Ceratosauria, with only a resolved node that includes *Ceratosaurus* and *Genyodectes*, and other polytomy including all the abelisaurid taxa (Suppl. Fig. 1). Despite these unsolved relationships MPCN-PV 69 is held in Abelisauridae. Unfortunately, the addition of a new character did not influence the results obtained, so the differences in the kind of separation between the articular head and the internal tuberosity appears to be not significant.

The application of the method for identification of unstable taxa (Pol and Escapa, 2009) revealed that *Velocisaurus* and *Berberosaurus* are between the most unstable taxa that collapse nodes. In effect, pruning the two taxa generates a significantly more resolved strict consensus, where the major clades are identified, i.e. Ceratosauria, Abelisauroidea, Noasauridae and Abelisauridae (Fig. 8). Unfortunately Abelisauridae remains as a great polytomy, including MPCN-PV 69.

In their analysis Farke and Sertich (2013) removed *Indosaurus* and *Kryptops*, based on TAXEQ3 software (Wilkinson, 2001), and also they removed *Velocisaurus* because pruning this taxon pre- and post-analysis showed no difference in topology. However, in the analysis here performed the pruning of *Velocisaurus* post-analysis demonstrated different results, whereas the removal of *Indosaurus* and *Kryptops* does not affect the relationships obtained. Only when MPCN-PV 69 is removed (together with *Kryptops* and *Indosaurus*) the clade Abelisauridae is totally resolved (Suppl. Fig. 2), with *Rugops* as the most basal taxon, and the Indo-Malagasy *Rajasaurus* and *Majungasaurus* differentiated from the South American taxa, which constitute the Brachyrostra.

More resolved phylogenetic relationships of MPCN-PV 69 are achieved in the majority rule consensus, after the removal of *Velocisaurus*, *Berberosaurus*, *Kryptops* and *Indosaurus*. In this case MPCN-PV 69 is recovered between the South American abelisaurids, forming a polytomy at the base of Brachyrostra (Fig. 9).
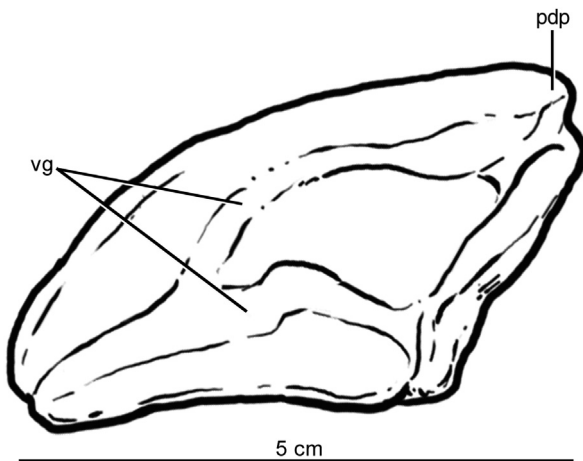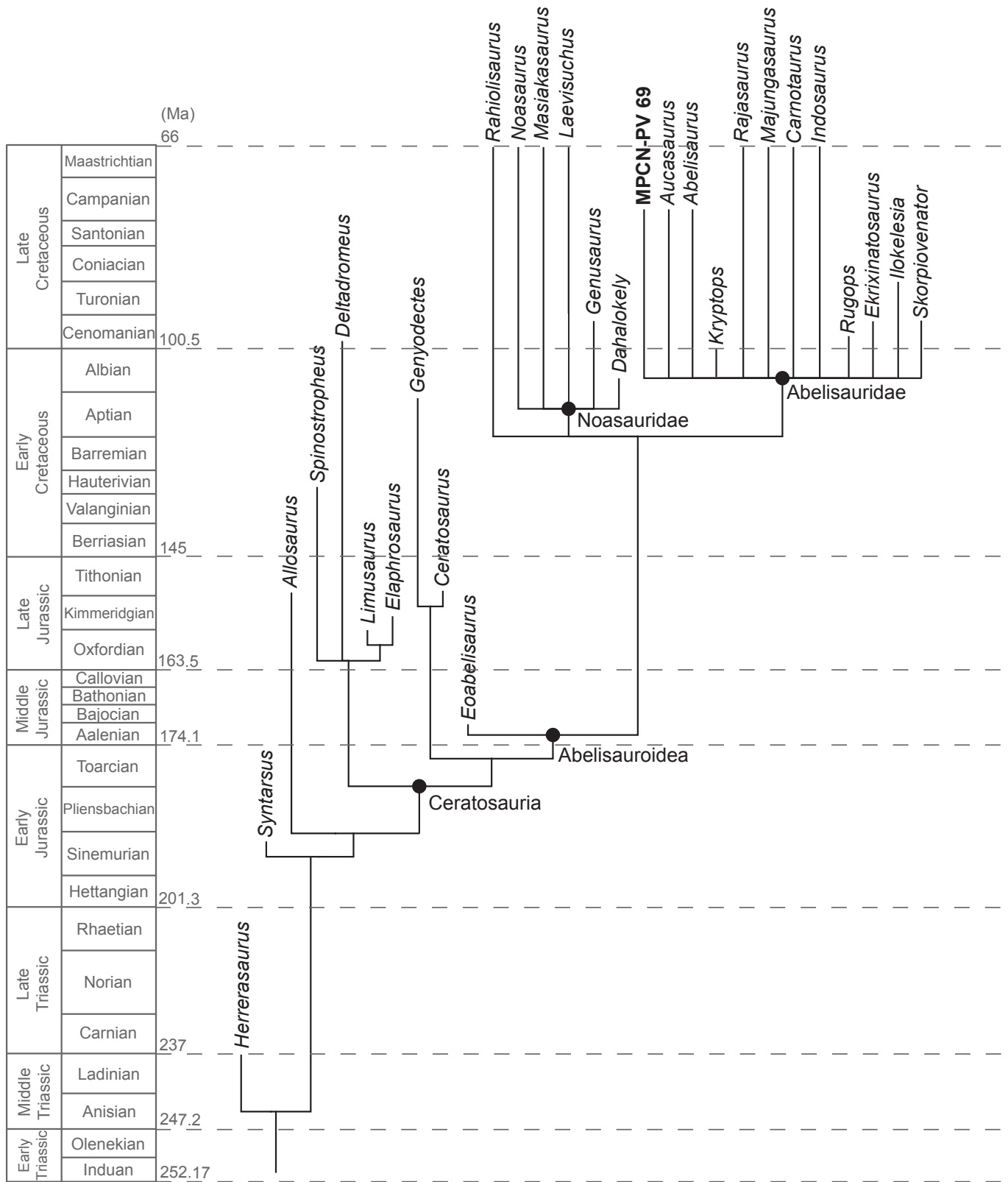
Fig. 8. **Phylogenetic relationships of ceratosaurian theropods, including MPCN-PV 69**. Strict consensus tree of the MPTs from the phylogenetic analysis, on a stratigraphic framework, and after the pruning of *Velocisaurus* and *Berberosaurus*.
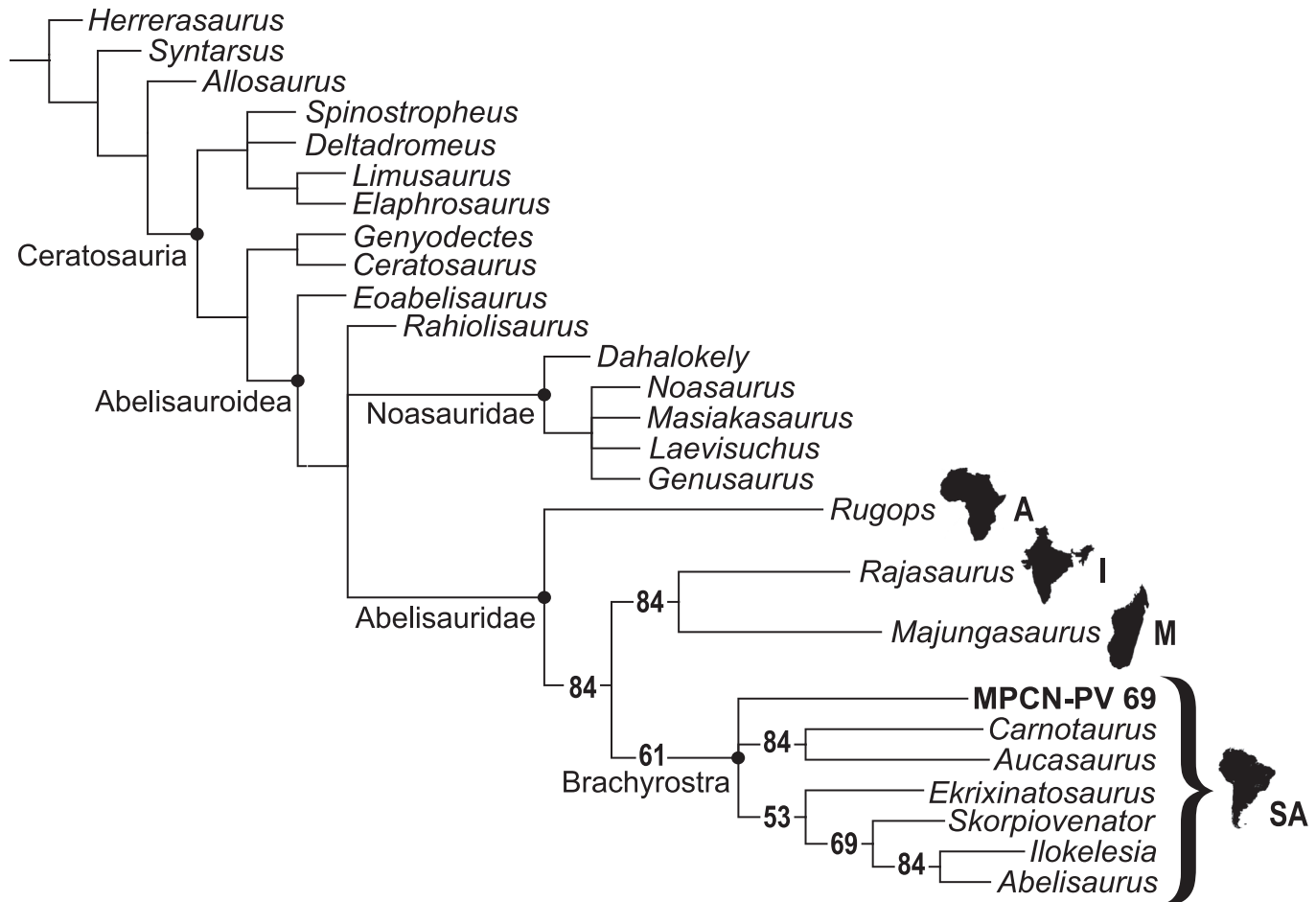
Fig. 9. Majority rule consensus tree obtained from the phylogenetic analysis after the removal of *Velocisaurus*, *Berberosaurus*, *Kryptops* and *Indosaurus*. Numbers on branches within Abelisauridae indicate the percentage of times in which these branches were obtained between the MPTs (cut-off: 50). The percentages of branches outside Abelisauridae not have been indicated because all of them are 100. For abelisaurids the geographical provenance of different taxa is shown. Abbreviations: A, Africa; I, India; M, Madagascar; SA, South America.

6.2. Morphological characters linking MPCN-PV 69 with abelisaurids and some considerations about the clade of South American abelisaurids Brachyrostra

The fragmentary nature of MPCN-PV 69 does not preclude the recognition of diagnostic characters that allow the assignment of this specimen to Abelisauroidea: humerus with inflated proximal head and tuberosity on caudal surface of the shaft (Novas et al., 2006); pedal ungual phalanx without flexor tubercle, ventral groove, and Y-shaped lateral vascular grooves (Novas and Bandyopadhyay, 2001). Furthermore, MPCN-PV 69 can be assigned to Abelisauridae based on the presence of a sub-quadrangular premaxillary body with an ornamented external surface, and a surface texture of paradental plates vertically striated (Sampson and Witmer, 2007; Carrano and Sampson, 2008); humerus with very anteroposteriorly expanded and bulbous proximal head, conical internal tuberosity, and reduced greater tubercle (Novas et al., 2006; Méndez et al., 2010).

The humerus shows many similarities with that of the only two Patagonian Cretaceous abelisaurids with this bone preserved: *Carnotaurus* and *Aucasaurus*; i.e. the bulbous head and the conical internal tuberosity separated from the articular head by an interruption (Figs. 5, 6). However, as was noted above, this character of the humerus does not allow emphasizing similarities or differences between abelisauroids in the phylogenetic analysis. On the other

hand, the more distal location of the greater tubercle with respect to the internal tuberosity differentiates the humerus of MPCN-PV 69 from that of *Carnotaurus* and *Aucasaurus*. Another difference with *Aucasaurus* is the presence of an interruption between the humeral head and the greater tubercle (Fig. 5). Taking into account these discrepancies and that MPCN-PV 69 and *Aucasaurus* both come from the Anacleto Formation, is probable that at least two abelisaurid species were present in that geological unit. Notwithstanding these discrepancies and common characters they are not enough to adjust the phylogenetic position of MPCN-PV 69. Undoubtedly, the degree of incompleteness of this specimen, and consequently the scarcity of information of its anatomy affect the results of the phylogenetic analysis.

Although in the majority rule consensus MPCN-PV 69 is linked with the brachyrostran abelisaurids, it did not preserved any of the diagnostic characters of Brachyrostra, as this clade was defined by Canale et al. (2009). The main reason of this is MPCN-PV 69 lacks a great percentage of the bones from the diagnostic characters of Brachyrostra were recovered. Although the phylogenetic analysis shows that MPCN-PV 69 can be positioned among the abelisaurid theropods, it was not capable to indicate a tighter resolution of the relationships of this specimen with the other abelisaurids. However, we must highlight the anatomical similarities between the humerus of the studied specimen and that of Patagonian brachyrostrans, as *Carnotaurus* and *Aucasaurus*.

Concerning the phylogenetic relationships within the Brachyrostra some considerations should be taken into account, mainly with respect to the position of *Abelisaurus*. Described in 1985 by Bonaparte and Novas, the holotype of *Abelisaurus comahuensis* consists only in cranial remains, including bones from the rostrum, the orbital and post-orbital zones, the skull roof, and the occipital area. In previous studies where phylogenetic relationships between ceratosaurs and abelisauroids were analyzed, this taxon was obtained as a basal abelisaurid, and as the sister taxon of the node including the Indo-Malagasy and the brachyrostran abelisaurids (e.g., Canale et al., 2009; Pol and Rauhut, 2012). Other authors (e.g., Novas, 2009) noted that *Abelisaurus* has plesiomorphic features supporting a basal position within the Abelisauridae, i.e. the absence of a dorsally projected supraoccipital prominence, a structure that is well-developed in other abelisaurids as *Carnotaurus* and *Majungasaurus*. On the other hand, in other analyses *Abelisaurus* appears in a more derived position, linked with other South American and with Indo-Malagasy abelisaurids in the same node (Carrano and Sampson, 2008) or obtained as part of Brachyrostra (e.g., Farke and Sertich, 2013; Tortosa et al., 2013; and in the analysis here performed, Fig. 9). Taking into account these latter results about the phylogenetic position of *Abelisaurus* some considerations concerning morphological similarities between this taxon and other abelisaurids should be discussed. The analysis of Farke and Sertich (2013), in which is based the analysis performed in this work, links *Abelisaurus* with *Ilokelesia*, *Skorpiovenator*, and *Ekrixinatosaurus*, within the sister clade of Carnotaurini. The relationship between *Abelisaurus* and these abelisaurids, especially with *Skorpiovenator* and *Ilokelesia*, is based mainly in the morphology of the postorbital bone. *Abelisaurus* shares with both taxa a posterior process of the postorbital representing more than half, but less than the total length of the anterior process (character 28, see Suppl. Inf. and Farke and Sertich, 2013), whereas it shares with *Ilokelesia* a posterior margin of the ventral process of the postorbital straight or slightly concave over its entire length (character 32), and a lateral depression on the posterodorsal part of the junction of the anterior, posterior, and ventral postorbital processes (character 33). In the analysis performed by Tortosa et al. (2013) the relationships between *Abelisaurus* and the other Brachyrostra are different, because *Abelisaurus* is nested within Carnotaurini. Despite this discrepancy, in this latter analysis the characters linking *Abelisaurus* with Brachyrostra are also related with the postorbital, being two of them the same characters of Farke and Sertich (2013) already explained (28 and 32), and the presence of a suborbital flange with a strongly anteroposteriorly expanded jugal process (see Tortosa et al., 2013). The latter feature also can be considered for non-brachyrostran abelisaurids, as *Majungasaurus*, although in this taxon the posterior process of the postorbital is shorter, i.e. less than half of the length of the anterior process (Sampson and Witmer, 2007). Nevertheless, relationships based only in characters of the postorbital may be poorly supported, especially when the morphology of the postorbital of *Ilokelesia* is considered doubtful. In fact, the other two referred postorbitals of this taxon show a ventral process with a convex posterior margin, differing from the postorbital described originally by Coria and Salgado (1998) which has a straight margin. Thus, the true morphology of the ventral process is uncertain and the character shared with *Abelisaurus* (a straight or slightly concave posterior margin, character 32) is called into question. Even if this character is recoded in *Ilokelesia* the relationships between the abelisaurids are drastically modified, where Brachyrostra is not recovered and where *Abelisaurus* is not directly related with South American abelisaurids (Suppl. Figs. 4, 5). In this case, the position of MPCN-PV 69 in the strict consensus is the same, within Abelisauridae, but in the majority rule consensus is included in a polytomy together with almost all abelisaurids, but not directly related with other South American taxa (Suppl. Fig. 6). Here we continue encoding the ventral process of the postorbital of *Ilokelesia* with a straight posterior margin, because the originally published postorbital seems more complete. Although it should be noted that phylogenetic relationships among South American abelisaurids should not be based in characters of a single bone with questionable morphology.

The postorbital of *Abelisaurus* also shows similar morphological features with that of other abelisaurids, both from South America and Madagascar. Thus, it shares with *Carnotaurus* a knob-like dorsalmost postorbital–squamosal contact, whereas in *Ilokelesia* and *Skorpiovenator* this contact is smooth (Carrano and Sampson, 2008; Farke and Sertich, 2013). With the Malagasy *Majungasaurus* the shared character consists in an anteroventral portion of ventral process of the postorbital confluent with the remaining process, differing from the ventral process of the postorbital of *Ilokelesia*, *Carnotaurus* and *Skorpiovenator* which is 'stepped' medially, forming a broadly open fossa (Carrano and Sampson, 2008). Other characters of the postorbital are widely distributed between abelisaurids, including *Abelisaurus*, and are more representative of the whole clade (e.g., external surface of postorbital sculptured; presence of a postorbital suborbital flange; among others, see Carrano and Sampson, 2008). Unfortunately, the postorbital in Indian taxa as *Rajasaurus* and *Indosaurus* was not preserved, precluding any comparison.

There are other characters in common between *Abelisaurus* and other abelisaurids not involving the postorbital. Some of these characters are shared with Indo-Malagasy taxa, specifically with *Indosaurus*, *Majungasaurus* and *Rajasaurus*, i.e. a nasal-frontal contact placed just above the highest point of the orbit (obtained as a synapomorphy of the clade constituted by *Indosaurus*, *Majungasaurus* and *Rajasaurus*, by Carrano and Sampson, 2008). However, this character was not possible to code in many brachyrostrans as *Aucasaurus*, *Ekrixinatosaurus*, *Ilokelesia* and *Skorpiovenator*, and therefore is quite possible to represent a synapomorphy of a more inclusive clade, i.e. Indo-Malagasy abelisaurids + Brachyrostra. Among other cranial synapomorphies of the Indo-Malagasy abelisaurids obtained by Carrano and Sampson (2008) and in the analysis here performed are: (1) the presence of a wide dorsal groove on occipital condyle, and (2) a skull roof ornamentation in the midline; but both are not shared by *Abelisaurus*. Regarding the two cranial synapomorphies that support Brachyrostra (characters 30 and 72), one of them is not present in *Abelisaurus* (ch. 30: ventral process of the postorbital 'stepped' medially and forming a broadly open fossa), and the presence of the other is unknown in this taxon due to the lack of preservation of the dentary (ch. 72: ventral margin of the dentary deeply convex along its entire length). About the second synapomorphy uncertainty will remain until obtain new information of the dentary of *Abelisaurus*.

In the original description of *Abelisaurus* Bonaparte and Novas (1985) reconstructed the skull of this taxon with an elongated shape, sharply differing from the abbreviated skulls observed in brachyrostrans. However, it is possible that the reconstruction have overestimated the real length of the skull, considering that the rostral bones were found separated from the bones of the orbital zone. Furthermore, it has been noted that taphonomic effects have altered the proportions of the skull and several contacts between bones are missing (González, 2007; Carrano and Sampson, 2008). Thus, taking into account that: (1) the premaxilla should be unfused; (2) the maxilla should be shortened according to dental alveoli; (3) a nasal ventral keel demonstrated that the bone is single and posteriorly incomplete; (4) the quadrate was originally reconstructed as sloping strongly laterally and posteroventrally, and badly positioned respect to the basal tubera; (5) the contacts

between the jugal and surrounding bones, especially the maxilla and the quadratojugal were misinterpreted, resulting in an excessively elongated jugal; and (6) a distorted quadrate-articular contact, the skull of *Abelisaurus* should be substantially shorter and wider, as already proposed for that of *Carnotaurus* (González, 2002; Carrano and Sampson, 2008).

Thus, it can be said that there exists morphological evidence suggesting the inclusion of *Abelisaurus* and the other South American abelisaurids in Brachyrostra. However, the phylogenetic relationships between *Abelisaurus* and the brachyrostrans are supported only by characters of postorbitals and are very unstable. Furthermore, and as was explained above, *Abelisaurus* also shares characters with the Indo-Malagasy abelisaurids.

Many abelisaurids are fragmentary or with missing data and thus the stability of relations between taxa is low in many cases. This can be evidenced with the low values of Bremer supports obtained from the phylogenetic analysis (Suppl. Fig. 3), which show the poor stability of the nodes conforming Abelisauridae. A more detailed survey of the anatomy and the correct disposition of the bones of the skull of *Abelisaurus* and a more extensive phylogenetic study are necessary to understand the relationships between the abelisaurids and to adjust the phylogenetic position of *Abelisaurus*, but these questions fall outside the scope of this work.

On the other hand, and despite the lack of robustness that can present the phylogenetic results here obtained, they support previous biogeographic hypotheses about the evolution of Abelisauridae (e.g., Carrano and Sampson, 2008; Ezcurra and Agnolín, 2012a,b; Pol and Rauhut, 2012; Tortosa et al., 2013). In these hypotheses the South American abelisaurids were immerse in an endemic evolutionary frame, after the separation of South America and Africa during the Late Cretaceous. In such a context is feasible that Late Cretaceous South American abelisaurids, including *Abelisaurus*, have evolved as a unique endemic group, i.e. Brachyrostra.

6.3. Comments about evolutionary trends and the function of the forelimb in abelisaurids

The hemispherical proximal articular head of the humerus of derived abelisaurids was related to a wider range of mobility of the shoulder (Bonaparte et al., 1990; Senter and Parrish, 2006; Carrano, 2007; Burch and Carrano, 2007). For other theropods, specifically *Tyrannosaurus*, also was proposed a greater mobility of the humerus at the shoulder joint (Carpenter and Smith, 2001; Carpenter, 2002). In this taxon the humeral head also has been described as hemispherical (Brochu, 2003), but, although it is rounded and more circular in proximal view when compared to other theropods, is actually not hemispherical and substantially less developed than in abelisaurids (Senter and Parrish, 2006). On the other hand, the range of mobility also depends on the morphology of the glenoid fossa, specifically in the development of the dorsal and ventral lips that are part of the rim of the fossa, which can restrict the movement of the humeral head. In *Tyrannosaurus* these lips are poorly developed, which enabled a greater capacity of protraction and retraction of the humerus in comparison with other theropods (Carpenter, 2002). Conversely, in derived abelisaurids, as *Majungasaurus* and *Carnotaurus* (Bonaparte et al., 1990; Carrano, 2007; Burch and Carrano, 2012), the dorsal and ventral lips are relatively well-developed, more than in *Tyrannosaurus*, so the mobility of the humerus in the sagittal plane may have been more restricted. Thus, although the humerus of abelisaurids may have a higher mobility, the range of motion was different than in *Tyrannosaurus*, being probably higher in the lateromedial component (i.e. abduction-adduction movements), as is also suggested by previous studies in the forelimb mobility of *Carnotaurus* (Senter and Parrish, 2006).

A rounded head of the humerus can also be observed in other abelisauroids, as in the basal form *Rahiolisaurus*, in noasaurids like *Masiakasaurus*, and even in non-abelisauroid ceratosaurs as *Elaphrosaurus* (Galton, 1982; Carrano et al., 2002, 2011; Méndez et al., 2010). Though rounded, in all these taxa the humeral head does not reach the markedly hemispherical form of derived abelisaurids. Despite these differences is possible to say that the well rounded humeral head shows a widespread distribution in Ceratosauria. For it, it could be considered as a character plesiomorphically retained in derived taxa (Senter and Parrish, 2006).

This morphology was maintained and slightly enhanced beyond the extreme reduction of the forelimb in derived abelisaurids. Moreover, *Elaphrosaurus* and *Masiakasaurus* have unreduced forelimbs, so the rounded humeral head is not directly linked with a forelimb reduction. A greater range of mobility in the humerus possibly had a functional benefit in these ceratosaurs with unreduced forelimbs, but in derived abelisaurids this greater mobility may not be necessarily related to any particular function. Furthermore, the reduction of the forelimb along the abelisauroid evolution seems to have occurred in a modular fashion, starting at the distal elements (i.e., the autopodium), and only later affected the more proximal elements (Pol and Rauhut, 2012). Even this reduction seems to have started already in basal ceratosaurs, since in *Ceratosaurus* and *Limusaurus* the hand shows shorter metacarpals than in more basal theropods (Ruiz et al., 2011). In this context, the last element affected is the humerus, so this bone would have a more conservative morphology even in the derived abelisaurids with a vestigial manus.

The modular fashion in the reduction of the elements can also explain the presence of a well-developed pectoral girdle in abelisaurids. In these theropods the coracoid exhibit an extensive surface for muscle attachment, which together with the large deltopectoral crest in the humerus (Bonaparte et al., 1990; Carrano, 2007; Burch and Carrano, 2012), suggests the presence of large and powerful adductor muscles, as also occur in *Tyrannosaurus* (Carpenter, 2002), though at a different degree. This unreduced condition on the scapula and coracoid also can be explained as because the retaining of the support muscles that held the shoulder girdle to the axial skeleton and for mobility of the girdle and the ribcage (Senter and Parrish, 2006). In this evolutionary context is expected that other abelisauroids also present a well-developed pectoral girdle, which occur in *Masiakasaurus*, where the coracoid also shows a great area for muscle attachment (Carrano et al., 2011).

For the forelimb of tyrannosaurids several functional hypotheses have been proposed (Middleton and Gatesy, 2000, and references herein). Some authors claim that the forelimbs of *Tyrannosaurus* were actively used in predation, probably to clutch preys close to the body (e.g., Carpenter, 2002). Moreover, despite the overall reduction of the forelimb of this taxon, the manus in *Tyrannosaurus* preserved well-developed phalanges and sharp claws, which would have helped to clutch the prey. However, more detailed morphofunctional studies are necessary for abelisaurids, especially considering the evident anatomical (e.g., glenoid fossa borders) and probably functional (e.g., range of mobility) differences with tyrannosaurids. In abelisaurids, the lower arms are extremely reduced, the elbow joint became immobile, the manual phalanges underwent a great reduction and simplification, forming stubby fingers, which probable loss the independent movement and grasping capabilities, as well as the complete loss of manual unguals (Agnolín and Chiarelli, 2010; Senter, 2010; Burch and Carrano, 2012). All these features made their manus incapable of clutch a prey during predation activities, stabilization of the female during mating, or any of the functions proposed for tyrannosaurids, thus becoming a truly vestigial structure (Senter, 2010). Based on the evolutionary trends in this group of theropods, which have

suffered an extreme reduction of their hands and forearms, it is quite reasonable to say that the complete vestigial forelimbs of abelisaurids probably had no evident, recognizable functions. However, it is still intriguing the vast distribution of these highly mobile short arms and why species completely devoid of forelimbs didn't appeared yet.

6.4. Patagonian dinosaur fauna at the Late Cretaceous

After the extinction of the rebbachisaurids, the last diplodocoid sauropods, during the Turonian-Coniacian event (Salgado, 2001; Apesteguía, 2002; Gallina and Apesteguía, 2005), the othertimes vast clade diversity of Patagonia (e.g., Gallina et al., 2014) became reduced to a high number of species belonging to a single clade: the titanosaurs (e.g., *Antarctosaurus wichmannianus*, von Huene, 1929; *Neuquensaurus australis*, Lydekker, 1893; Powell, 1986; Salgado et al., 2005; *Barrosasaurus casamiquelai*, Salgado and Coria, 2009; *Rinconsaurus caudamirus*, Calvo and González Riga, 2003; *Overosaurus paradasorum*, Coria et al., 2013).

Conversely, the analyses of the Late Cretaceous theropod fauna in north Patagonia, and the recognition of the purported Maastrichtian carcharodontosaurids (Candeiro et al., 2008; Apesteguía et al., 2004; Martinelli and Forasiepi, 2004), represented by isolated teeth, as actually brachyrostran abelisaurids (Apesteguía et al., 2013), depict a panorama in which, although a high number and diversity of small to mid-sized theropods remained present, brachyrostran abelisaurids became the top southern predators after the extinction of the Carcharodontosauridae at the Coniacian boundary (Apesteguía, 2002; Leanza et al., 2004; Novas et al., 2013).

Furthermore, they still remained as such even after the late Campanian-early Maastrichtian contact with North America during the FABI (First American Biotic Interchange) (Goin et al., 2012), when Maastrichtian North American herbivores entered massively into South America (e.g., Bonaparte and Rougier, 1987). In this context, is quite possible that the large and stocky pedes which produced the symmetrical tracks with parallel digits seen in the Maastrichtian trackway fields of Bolivia could be made exclusively by brachyrostran abelisaurids. Moreover, the presence of these theropods in the Maastrichtian of Bolivia can be also documented by isolated teeth with abelisaurid affinities (Gianechini and Apesteguía, 2012).

The Anacleto Formation (lower Campanian) can be considered the last endemic stage of a South American fauna with an exclusive Gondwanan signature (Apesteguía, 2002; Leanza et al., 2004). No hadrosaurids or North American clades traveled southward and southern lineages reached their maximum time in isolation. For instance, a high diversity of abelisaurids should be expected. However, the only recorded species of abelisaurids are *Aucasaurus garridoi* (Coria et al., 2002), perhaps *Abelisaurus comahuensis* (Bonaparte and Novas, 1985), if not belonging to the Allen Formation, and MPCN-PV 69, accompanied by the mid-sized neovenatorid megaraptoran *Aerosteon riocoloradensis* (Sereno et al., 2008).

In order to have a wider view of the so called Coloradoan fauna (Leanza et al., 2004; from the Río Colorado Subgroup, which includes the successive Bajo de la Carpa and Anacleto Formations), we could consider the theropod taxa provided by the Bajo de la Carpa Formation. In the last years new abelisaurid remains from this unit were reported (Ezcurra and Méndez, 2009; Gianechini et al., 2011; Filippi et al., 2014), increasing the abelisaurids diversity for the Coloradoan fauna. Among other theropod taxa from this formation would add the noasaurid *Velocisaurus unicus* (Bonaparte, 1991b), the alvarezsaurid *Alvarezsaurus calvoi* (Bonaparte, 1991b), neovenatorids (Gianechini et al., 2011), and birds (Alvarenga and Bonaparte, 1992; Bonaparte, 1991b).

The peculiar Coloradoan stage of southern Neuquen Basin, chronologically restricted to the lower Santonian−lower Campanian, can be compared in South America with part of the Adamantina and Uberaba formations, in Brazil (Dias-Brito et al., 2001), providing the former only one large abelisaurid, *Pycnonemosaurus nevesi* (Kellner and Campos, 2002), and the later only isolated teeth (Bertini et al., 1993), some of them referable to unenlagine deinonychosaurs (Apesteguía et al., 2013).

7. Conclusions

The specimen here presented, MPCN-PV 69, despite being very fragmentary, has morphological characters that allow diagnose it as an abelisaurid, probably a new taxon. The characters that it shares with Abelisauroidea are a humerus with inflated proximal head and tuberosity on caudal surface of the shaft; and a pedal ungual phalanx without flexor tubercle, ventrally grooved, and Y-shaped lateral vascular grooves. Moreover, the specimen can be referred to Abelisauridae based in the presence of a subquadrangular premaxillary body with an ornamented external surface, and a surface texture of paradental plates vertically striated; and a humerus with anteroposteriorly expanded and bulbous proximal head, conical internal tuberosity, and reduced greater tubercle. The phylogenetic analysis supports the affiliation to Abelisauridae, but fails to determine a more precise relationship with others abelisaurids, possibly due to the fragmentary nature of the specimen. However, the majority rule consensus of the analysis shows a possible phylogenetic position within Brachyrostra. The humerus shares some characters with those of other Late Cretaceous Patagonian abelisaurids, as *Aucasaurus* and *Carnotaurus*, specifically the bulbous proximal articular head and the presence of a discontinuity between the head and the internal tuberosity. On the other hand, differences are observed with these two Patagonian taxa, i.e. the more distal location of the greater tubercle with respect to the internal tuberosity, and furthermore with *Aucasaurus*, i.e. the presence of an interruption between the humeral head and the greater tubercle. The stratigraphic provenance of MPCN-PV 69 and *Aucasaurus* is the same (Anacleto Formation, lower Campanian), but anatomical differences between both forms allow to suggest that likely MPCN-PV 69 represents a different taxon.

Previous phylogenetic analyses show a clade Brachyrostra constituted by the majority of the South American abelisaurids (Canale et al., 2009; Pol and Rauhut, 2012), but resulting in a more basal position for *Abelisaurus*, outside Brachyrostra. However, in more recent analyses (Farke and Sertich, 2013; Tortosa et al., 2013) *Abelisaurus* was located within Brachyrostra, relationships supported mainly by characters of the postorbital. But the linking between *Abelisaurus* and the brachyrostrans still needs more conclusive evidence, mainly because the materials of some taxa show a doubtful morphology and because materials of *Abelisaurus* are very fragmentary and some characters are shared with Indo-Madagascan taxa. Nevertheless, the phylogenetic results support previous biogeographic hypotheses related with the endemic evolution of Late Cretaceous South American taxa. Additional analyses with larger samples of characters and more complete materials would help to adjust the relationships between South American abelisaurids.

While the forelimb of derived abelisaurids shows a marked tendency to an extreme reduction of the manus and forearm, the humerus is well-developed and with a hemispherical proximal articular surface. This feature would have conferred great mobility at the level of the shoulder joint, however the complete forelimb would have had no recognizable function.

MPCN-PV 69, although fragmentary, probably represents a new brachyrostran abelisaurid, the second or third for the Anacleto

Formation, thus increasing the diversity of these group of theropods for this unit. In other studied regions and ages from South America no more than one abelisaurid taxon each was recorded up to now. After 50 million years from the established separation of African abelisaurids by the opening of the Atlantic Ocean, and about 10 my after the extinction of carcharodontosaurids, South American abelisaurids reached their peak on diversity in isolation. 10 my later, they'd have to share this space with large deinonychosaurs and perhaps North American theropods which we didn't found yet. Though still weak, the evidences show that the Coloradoan stage, the last endemic moment for exclusively Gondwana-originated fauna, enjoyed a larger abelisaurid diversity than other moments of the Late Cretaceous of South America.

Acknowledgments

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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.2014.11.009.