



A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur

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ABSTRACT

A unique site at the northern area of Patagonia (Neuquén, Argentina) reveals a terrestrial ecosystem preserved in a detail never reported before in a Late Cretaceous deposit. An extraordinary diversity and abundance of fossils was found concentrated in a 0.5 m horizon in the same quarry, including a new titanosaur sauropod, *Futalognkosaurus dukei* n.gen., n.sp, which is the most complete giant dinosaur known so far. Several plant leaves, showing a predominance of angiosperms over gymnosperms that likely constituted the diet of *F. dukei* were found too. Other dinosaurs (sauropods, theropods, ornithomorphs), crocodylomorphs, pterosaurs, and fishes were also discovered, allowing a partial reconstruction of this Gondwanan continental ecosystem.

Key words: Dinosauria, Titanosauria, ecosystem, taphonomy, Upper Cretaceous, Gondwana, Patagonia, Argentina.

INTRODUCTION

In March 2000 a very large sauropod cervical vertebra was found in the northern shore of Lake Barreales, some 90 km northwest of Neuquén city, Northwestern Argentina (Fig. 1A). Since then, over 1000 specimens (including 240 fossil plants and 300 teeth) have been collected in an area of about 400 m² that is called the Futalognko site. The importance of this region led to the establishment of a study center – the Centro Paleontológico Lago Barreales (CePaLB) – that carries out controlled excavations. The sedimentary rocks at this site represent the lower portion of the Upper Cretaceous (Turonian-Coniacian) Portezuelo Formation of the Neuquén Group (Leanza and Hugo 2001) and they are composed mainly of siltstones and sandstones. Fossils are

found associated and partially articulated in the same quarry, particularly in a 0.5 m level of siliciclastic fluvial facies (Fig. 1B,C).

Here we describe a new sauropod dinosaur which is the most complete of the giant dinosaurs, and provide information about the Cretaceous terrestrial ecosystem present in this region of former Gondwana.

SYSTEMATIC PALEONTOLOGY

Saurischia Seeley 1887

Sauropodomorpha Huene 1932

Sauropoda Marsh 1878

Titanosauria Bonaparte and Coria 1993

Lognkosauria new taxon

ETYMOLOGY

Lognko from the Mapuche language meaning chief + *saurus*, from the Greek language meaning lizard.

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DEFINITION

Lognkosauria is phylogenetically defined as the most recent common ancestor of *Mendozasaurus neguyelap* and *Futalognkosaurus dukei* and all its descendants.

Futalognkosaurus dukei gen. et sp. nov.

ETYMOLOGY

From the Mapuche indigenous language: *Futa* meaning giant and *lognko* meaning chief; *saurus* from the Greek language meaning lizard; and *dukei*, in honor of the Duke Energy Argentina Company that sponsored the excavation (2002-2003).

HOLOTYPE

Atlas, axis, five anterior, four middle, and three posterior cervicals; 10 dorsals; ribs; complete sacrum; both ilia; right pubis and ischium; and one anterior caudal. All material is housed at the CePaLB-Universidad del Comahue, Neuquén, Argentina (MUCPv-323; Fig. 2).

HORIZON, AGE AND LOCALITY

Portezuelo Formation, Rio Neuquén Subgroup, Neuquén Group, Late Cretaceous, Turonian-Coniacian (Leanza and Hugo 2001). The material comes from the northern coast of the Lake Barreales, 90 km northwest of Neuquén City, Neuquén Province, Patagonia, Argentina.

DIAGNOSIS

Neurapophysis of the atlas laminar and rectangular, and posteriorly directed; neural spine of the axis high and triangular; posterior border of the neural spine on middle cervical elements concave; ventral depression between parapophyses on middle cervical centra; anterior dorsal vertebrae with horizontal and aliform diapophyses; pre- and postzygapophyses of anterior dorsal vertebrae horizontal; first caudal vertebra with prespinal lamina bifurcated on its base forming two small infraprespinal laminae; supraspinal cavity in first caudal vertebra bordered by the prespinal and lateral laminae; 2nd and 3rd sacral ribs fused; wide and well developed iliac peduncle on ischia.

DESCRIPTION AND COMPARISON

Futalognkosaurus dukei is the most complete giant sauropod ever found, with an estimated length between 32

to 34 meters (Calvo 2006). The atlas has a laminar, rectangular neurapophysis that expands upward and curves medially. The axis has a high and robust neural spine with triangular shape. The centrum lacks pleurocoels differing in this respect from *Saltasaurus* (Powell 2003) and *Alamosaurus* (Lehman and Coulson 2002). All cervicals have a triangular shaped neural spine that is compressed lateromedially and elongated anteroposteriorly. Like in *Malawisaurus dixeyi* (Jacobs et al. 1993) and *Gondwanatitan faustoi* (Kellner and Azevedo 1999), the cervicals lack pleurocoels. Middle cervicals bear high and sail-shaped neural spines as in *Malawisaurus* and *Rapetosaurus* (Rogers and Forster 2001). *Futalognkosaurus* shares with *Rapetosaurus* neural arches three times higher than the centra in anterior and middle cervicals. In lateral view, the spinoprezygapophyseal border is straight and the spinopostzygapophyseal margin is concave, a feature not generally observed in other members of the Titanosauria. Posterior cervicals have neural arches at least three times higher than the centrum and neural spines compressed proximodistally and expanded laterally as in *Mendozasaurus neguyelap* (González Riga 2003, 2005). No prespinal lamina as the one reported in *Isisaurus* (Jain and Bandyopadhyay 1997) is present. A well-developed and deep supradiapophyseal cavity (or fossa) is present in *Futalognkosaurus dukei* and *Mendozasaurus neguyelap* (González Riga 2005). *Sauroposeidon proteles* (Wedel et al. 2000) differs from *Futalognkosaurus dukei* because it has cervical centra extremely elongated with low neural arches.

The dorsal vertebrae of *Futalognkosaurus dukei* lack hyosphene-hypantrum, which are present in the giant *Argentinosaurus huinculensis* (Bonaparte and Coria 1993). Diapophyses are laminar, planar and directed laterally. Anterior dorsals have neural spine formed by a spinodiapophyseal and a spinopostzygapophyseal laminae; no spinoprezygapophyseal lamina is present. Prezygapophyses are placed almost horizontally, differing from the inclined condition observed in *Mendozasaurus* and *Argentinosaurus*. *Futalognkosaurus* has the 2nd and 3rd sacral ribs fused unlike any other Titanosauria. The 1st caudal is strongly procoelous with tip of the neural spine expanded. The prespinal lamina is strongly developed and bifurcate on its base forming two small infraprespinal laminae. On anterior view, there are two deep supraspinal cavities on the neural spine. The right

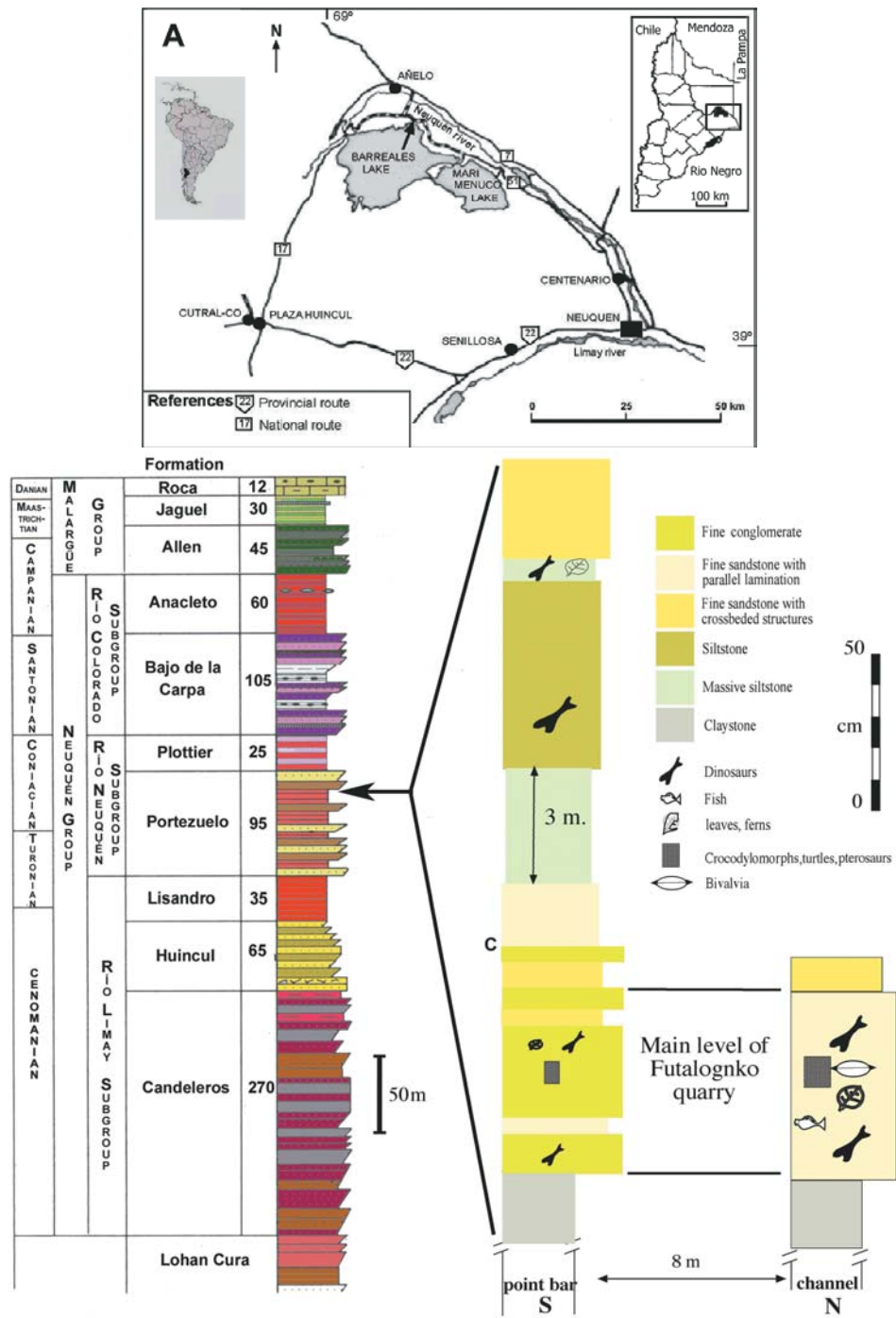


Fig. 1 – Localization and geologic details of the Futalognko quarry. A – Map of Neuquén Province (northwest Patagonia), indicating the new locality. B – Geologic column of the Neuquén Group with the position of the layers of the Futalognko quarry. C – Detail indicating the layers where fossils have been collected in the point bar and channel of a meandering river system. Note that most of the fossils are concentrated in a layer of 50 centimeters.

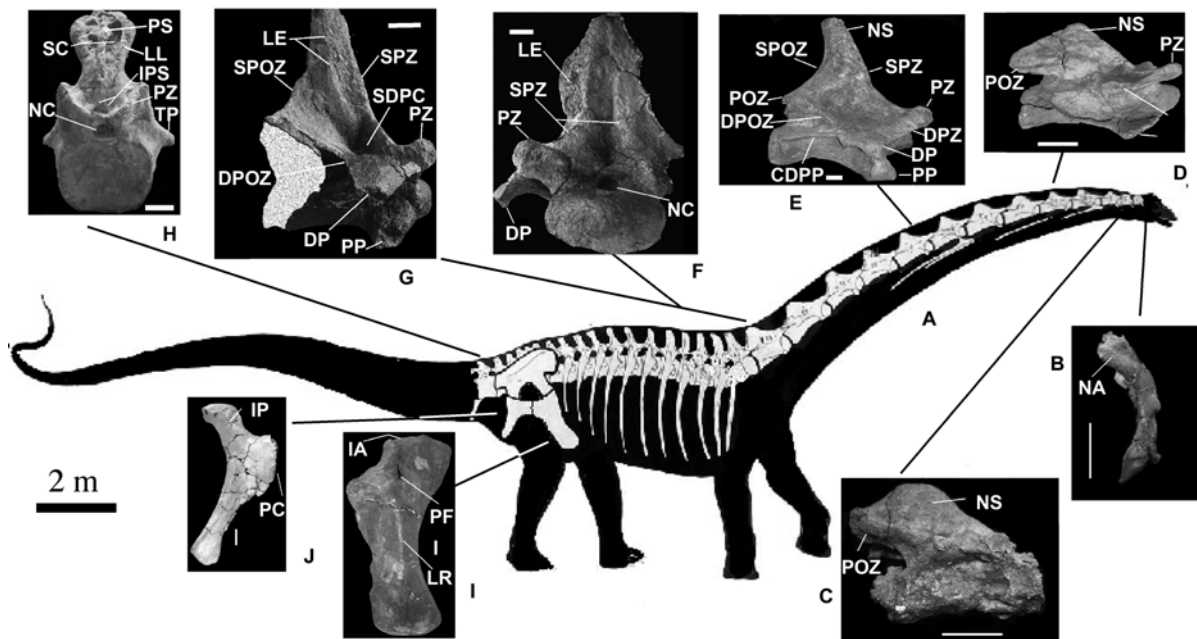


Fig. 2 – *Futalognkosaurus dukei* gen. et sp. nov, a new giant sauropod dinosaur from Cretaceous strata of Patagonia (Argentina). A – Skeletal reconstruction showing the preserved elements. B – Atlas in lateral view. C – Axis in lateral view. D – Anterior cervical in lateral view. E – Middle cervical in lateral view. F – Posterior cervical in anterior view. G – Posterior cervical in lateral view. H – First caudal in anterior view. I – Pubis in lateral view. J – Ischium in lateral view. Scale bars (B–J), 10 cm. Abbreviations: CDPP = centrodiapophyseal posterior lamina; DP = diapophysis; DPOZ = diapopostzygapophyseal lamina; DPZ = diapoprezygapophyseal lamina; IA = iliac articulation; IP = iliac peduncle; IPS = infraprespinal lamina; LE = lateral expansion; LL = lateral lamina; LR = longitudinal ridge; NA = neurapophysis; NC = neural canal; NS = neural spines; PC = pubis contact, PF = pubic foramen; POZ = postzygapophysis; PP = parapophysis; PS = prespinal lamina; PZ = prezygapophysis; SC = supraspinal cavity (or fossa); SDPC = supradiapophyseal cavity; SPOZ = spinopostzygapophyseal lamina; SPZ = spinoprezygapophyseal lamina; TP = transverse process.

pubis (137 cm long) is a robust bone, more than in most other titanosaurids.

PHYLOGENETIC RELATIONSHIPS

The ingroup relationships of the Titanosauria have been extensively discussed in the last years (Salgado et al. 1997, Wilson and Sereno 1998, Upchurch 1998, Wilson and Upchurch 2003, Wilson 2006, among others). Some anatomical features such as the procoelic condition of the caudal vertebra, allows the allocation of *Futalognkosaurus dukei* in the Titanosauria. In order to assess the phylogenetic position of *Futalognkosaurus dukei* relative other titanosaurs, we have used a data matrix (65 characters) proposed by Calvo et al. (in press). In this study we analyze the relation of *Futalognkosaurus* with 18 taxa using the program PAUP, version 3.0 (Swof-

ford 1989). *Camarasaurus grandis* Cope 1877 was assigned as outgroup (Fig. 3) and all multi-state characters were considered unordered (see appendices). The application of the heuristic method with delayed transformation optimization produced one most parsimonious tree (Fig. 3) with a length of 108 steps and high consistency and retention index (C.I. = 0.722; R.I. = 0.780).

The analysis supports the Titanosauria *sensu* Bonaparte and Coria (1993), defined as the most recent common ancestor of *Andesaurus delgadoi* and Titanosauridae and all its descendants (Salgado et al. 1997). *Futalognkosaurus* can be clearly diagnosed as a Titanosauridae (*sensu* Salgado et al. 1997) or Lithostrotia (*sensu* Wilson and Upchurch 2003). The present phylogenetic analysis also shows *Malawisaurus* as the sister group of *Mendozasaurus* (*sensu* González Riga 2003). *Mendozasaurus* is the sister group of *Futalognkosaurus*, forming

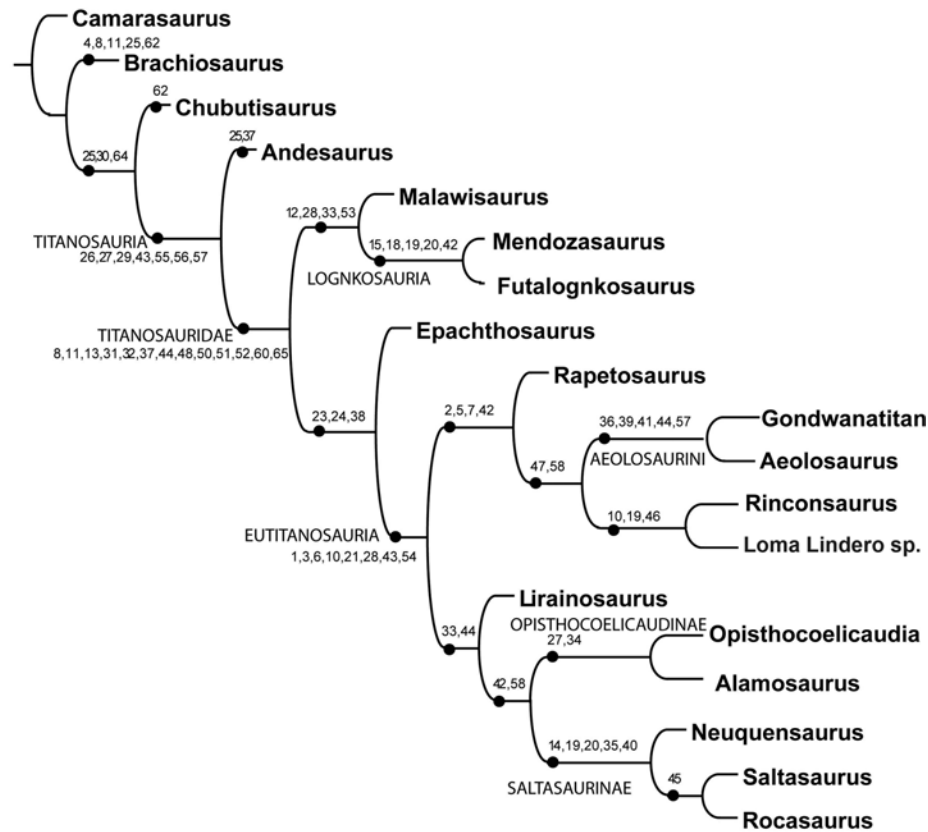


Fig. 3 – Cladistic analysis of titanosaurid sauropod dinosaurs, showing the phylogenetic position of *Futalognkosaurus dukei*. Numbers at the nodes indicate synapomorphies (see appendices). The new giant dinosaur is closely related to *Mendozasaurus*, forming a new clade called Lognkosauria. Data matrix after Calvo et al. (in press).

a new clade named Lognkosauria nov., which is supported by five synapomorphies (see character list): (15.1) presence of a laterally expanded posterior cervical neural spines, wider than the centra, (18.1) posterior cervical vertebrae, with a height 1.5 the length of the centra, (19.2) deep and extended supradiapophyseal cavity in posterior cervical vertebrae, (20.2) posterior cervical centra proportions: ratio anteroposterior length/height of posterior face less than 1,5, and (42.1) anteriormost caudal vertebrae with neural spines transversely elongated. This node has a high bootstrap value (88%) and it is well supported.

DISCUSSION

Futalognkosaurus dukei n.gen, n.sp. has a size comparable to *Argentinosaurus huinculensis* (Bonaparte and Coria 1993) and *Puertasaurus reuili* (Novas et al. 2005), up to date, considered the largest of all sauropods but,

unfortunately, known by few and incomplete elements. The discovery of *Futalognkosaurus* and *Mendozasaurus* indicates the presence of a new lineage of titanosaurs, with strong and huge necks, differing from the remaining members of this group, increasing the diversity of those large dinosaurs that once roamed the Earth.

Besides *Futalognkosaurus*, other sauropod dinosaur remains that represent two additional yet undescribed taxa were also found in the Futalognko site, but none was articulated or nearly as complete. Theropod specimens were also unearthed and indicate the presence of several species, two of which were formally described. One represents *Megaraptor namunhuaiquii*, previously recovered in the Sierra del Portezuelo, around 80 km South from the Futalognko site, in levels of the Portezuelo Formation (Novas 1998). The material of *Megaraptor* collected at the Futalognko site consists of a complete and articulated arm (Fig. 4E), showing that

the bones originally interpreted as a foot of this taxon (Novas 1998) are, in fact, the hand (Calvo et al. 2004b). The new specimen demonstrates that *Megaraptor* is not a member of the Coelurosauria, but a basal tetanuran that developed a unique elongated hand with very large sickle-shaped claws, more so than the ones of spinosaurids (Charig and Milner 1997).

The second theropod belongs to the genus *Unenlagia* that was also first described from the Sierra del Portezuelo (*U. comahuensis*). This genus has been regarded as the sister group of Avialae (*Archaeopteryx* + modern birds) (Novas and Puerta 1997) while others suggest that it was a more basal dromaeosaurid (Norell et al. 2001). The new species recovered from the Futalognko quarry, named *Unenlagia paynemili*, belongs to a more slender species that has a small anterior process in the pubis (not present in *U. comahuensis*) and indicates that those enigmatic *Unenlagia*-type maniraptoran dinosaurs were more common (Calvo et al. 2004a, Fig. 4F). Additional theropod material consists of isolated bones and over 250 teeth that show several morphotypes, suggesting the presence of a rather diverse theropod fauna in this quarry (study in progress). Most are very similar to those reported in dromaeosaurids (Fig. 4B) but some show wrinkled enamel close to the margin of the teeth which are typical of carcharodontosaurids (Serenio et al. 1996, Kellner and Campos 2000) (Fig. 4C).

Remains of ornithischian dinosaurs were also collected in the quarry and consist of isolated bones (dorsal vertebra, femur, and ilium) that are referable to Ornithopoda, which are rare in South America (Fig. 4G). Based on the separated distal condyles of the femur, they are referable to the Iguanodontia.

Other fossil reptiles are crocodylomorph teeth, some referable to Peirosauridae (Fig. 4D), which were found in the Neuquén Group (Digregorio 1972), Morocco (Buffetaut 1994) and Brazil (Price 1955). Recently a lower jaw of a tiny individual was also recovered (Fig. 4L) and belongs to a new species closely related to *Comahuesuchus*. The new specimen shows that those rare and unusual notosuchid crocodylomorphs have a large posterior tooth that shows coarse serrations similar to theropod dinosaurs, increasing the groups of crocodylomorphs with “theropod-like” teeth (Campos et al. 2001). Among the pterosaur bones recovered is the proximal part of an ulna referable to the *Azhdarchoidea*

sensu Kellner (2003), with an estimated wing span of around 6 m (Kellner et al. 2007, Fig. 4H). Histological sections show the presence of reticular fibro-lamellar bone, with numerous vascular canals, indicating that it was still growing at time of death and therefore can be considered the largest pterosaur recovered from the former Gondwana. Remains of pelomedusoid turtles and undetermined reptilian eggshells were also found.

Unexpectedly, the Futalognko quarry has also yielded delicate fish specimens; the first from the Neuquén Group reported so far (Fig. 4I). There are six specimens representing three different taxa: a small Euteleostei and two clupeomorphs (Gallo et al. 2003). Despite not being complete, all preserved elements are articulated. Ganoid scales of semionotid fishes and freshwater bivalves were also collected.

Lastly, about 240 plant specimens were recovered. Leaves are well preserved, with the majority corresponding to dicotyledonian angiosperms that are shown to have been abundant in this area (Fig. 4J,K). Some gymnosperm leaves, fructifications and remains of conifers were found too. In this wide diversity of foliar structures there are indications of herbaceous habit for some specimens as well as signs of caducity. Therefore, in this complex association, angiosperms seem to constitute the main element of the ancient flora in this region, and this material consists the first record of those derived plants in the Upper Cretaceous of the Neuquén Basin (Passalia et al., in press).

The fossil content in this region is not limited to the Futalognko quarry. In a range of 1500 m, there are three more quarries at the same level, that have also yielded a variety of specimens, including an articulated partial skeleton of a new theropod (Fig. 4M) and isolated remains of ornithopods, including jaws (Fig. 4N). Very well preserved pleurodiran turtles (including skull) were also found. Two other sites have been discovered in the Plottier Formation that overlies the Portezuelo layers, only 25 m above the Futalognko quarry and also contain large quantities of dinosaur bones, particularly sauropods, bivalves and plant remains, albeit in lower diversity.

Other terrestrial important and rich Cretaceous ecosystems such as the Jehol Biota of China (Chang et al. 2003) and the Santana Formation of Brazil (Maisey 1991, Kellner et al. 1994, Kellner and Campos 1999), have

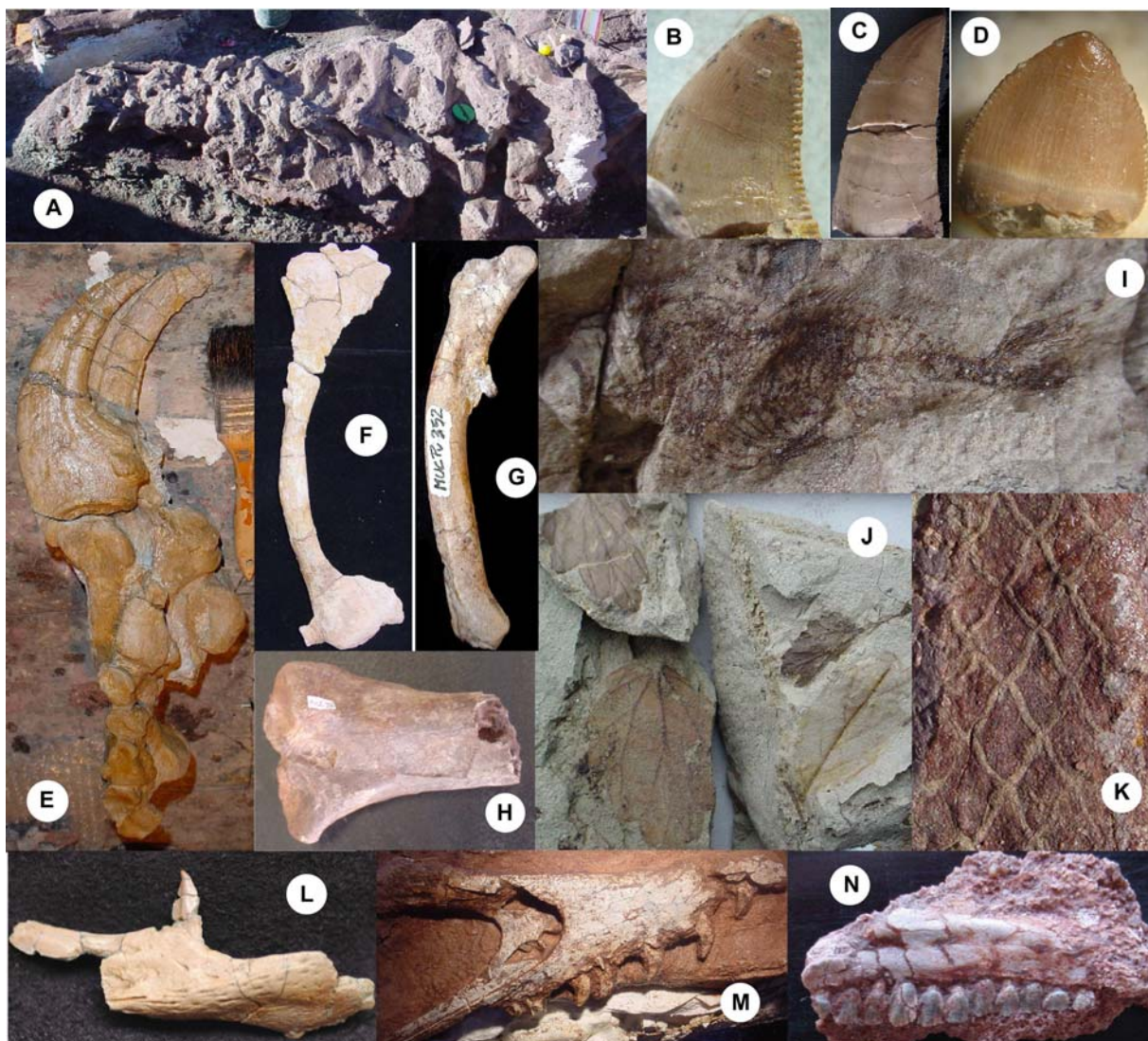


Fig. 4 – Selected fossils from the newly discovered Futalognko locality. A – Articulated vertebral column of *Futalognosaurus dukei* gen. et sp. nov.; B – Tooth of a dromaeosaurid theropod; C – Tooth of a carcharodontosaurid theropod; D – Tooth of a Mesoeucrocodylia, Peirosauridae indet.; E – Manus of *Megaraptor namunhuaiquii*; F – Pubis of *Unenlagia paynemili*; G – Femur of an Iguanodontia indet.; H – Proximal end of large azhdarchoid pterosaur ulna; I – Clupeomorph fish; J – Selected Magnoliopsida angiosperm leaves; K – undetermined plant stem; L – Lower jaw of a new *Comahuesuchus*-like notosuchid crocodylomorph; M – Skull of a new Maniraptoran theropod; N – Lower jaw of a new Iguanodontian ornithomorph.

been reconstructed based on fossils collected in large areas and from different layers whose outcrops sometimes are hundreds of meters apart and possible represent a time span of a few million years. The excavated part of the Futalognko site is restricted to a small area (400 m²) and due to a controlled collecting program in which all specimens are plotted on a quarry map, it can be demon-

strated that the fossils were found in a bed about 0.5 m thick, representing a time span in the scale of years. We were also able to reconstruct the taphonomic history of this unusual deposit.

Based on geological data, the Portezuelo Formation was deposited in a flat landscape as most of the stratigraphic units of the Neuquén Group. A detailed sedi-

mentological facies analysis (Sánchez et al. 2005) shows that an active and wide meandering river system was installed in this area during the late Cretaceous (Turonian-Coniacian). Moreover, the cyclic deposition of different fluvial facies suggests that the climate was warm and humid, intercalated with short dry seasons.

Three different sedimentological facies deposits that are associated to this meandering system could be recognized: channel, point bar and small lake deposits, the later corresponding to an abandoned meander. Our sedimentological and paleontological studies show that all three facies are present at the Futalognko site (Fig. 1C). The point bar deposits were formed first. During the dry season, fine-grained sediments (that latter one become sandstones and show well preserved fossils) were deposited latter. The wet seasons were responsible for flooding events that carried the animal remains downstream the river channel and deposited them in fine conglomerates. Those fossil remains usually are crushed with signs of erosion indicating a moderate transportation.

Regarding the remains of *Futalognkosaurus dukei* we hypothesize that it died of unknown causes on a floodplain, near the margins of a river. The carcass was possibly partially dismembered by theropod dinosaurs present in this area such as *Megaraptor* and small dromaeosaurids (and, perhaps also some crocodylomorphs like peirosaurids). A short time after its death, a single flooding event of great intensity washed the carcass of this giant sauropod dinosaur into the river channel. Due to its giant size the carcass likely acted as a barrier, reducing the competency of the currents generated by subsequent smaller flooding events that are very common in the wet seasons. This resulted in the deposition of additional organic remains around this huge carcass. At some point, the river changed its course laterally, leaving an oxbow lake behind. Surprisingly some tiny fish skeletons were found together with the dinosaur elements. Since they are complete, the only explanation for their presence along with the large bones is that they were trapped when this lake was formed. The few bivalves preserved in the same horizon were trapped too.

Subsequently wind and rain carried sediments, leaves and branches from the nearby vegetation inside the small lake. Most of the plant material is carbonized indicating that a reducing environment was installed in

this lake and that the original connection with the river was broken. These fossil plants are preserved in laminated and rippled siltstone around the dinosaur bones resulting in this very unusual combination of fossils. The events that lead to this accumulation must have happened in a comparatively short time otherwise, the bones of *Futalognkosaurus* would have been decomposed.

All this sedimentological and paleontological data make us confident to regard the plants and animals found and preserved in the Futalognko site as part of the same terrestrial ecosystem which can be reconstructed as follows. During the Late Cretaceous (Turonian-Coniacian), Patagonia had a warm and humid climate with dry seasons, and a meandering river system crossed a forest formed mainly by angiosperms, with few subordinated gymnosperms. This region was home to small ornithomorphs, small and large theropods (e.g., *Megaraptor*, *Unenlagia*), and giant sauropod dinosaurs such as *Futalognkosaurus*. Other reptiles present in this ecosystem were peirosaurid and notosuchid crocodylomorphs, pleurodiran turtles and large azhdarchoid pterosaurs. This large diversity of specimens with different potential preservation (e.g., leaves, invertebrates, delicate fish skeleton and large dinosaur bones) associated in one quarry at the same horizon was never reported in Gondwana. This unique site consists a rare occasion where a Late Cretaceous terrestrial ecosystem can be confidently reconstructed.

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RESUMO

Um depósito fóssil na região norte da Patagônia (Neuquén, Argentina) revela um ecossistema nunca antes registrado a este nível de detalhes em depósitos do Cretáceo Superior. Uma diversidade e abundância extraordinária de fósseis encontrase concentrada em uma camada de 0,5 m no mesmo sítio, incluindo um novo saurópodo titanossaurídeo, *Futalognkosaurus dukei* n. gen. n. sp., que é o mais completo dinossauro gigante encontrado até a presente data. Foram descobertas várias folhas de plantas indicando a predominância de angiospermas sobre gimnospermas que possivelmente formavam a base da dieta de *F. dukei*. Outros dinossauros (saurópodes, terópodes, ornitópodes), crocodilomorfos, pterossauros e peixes foram também encontrados possibilitando a reconstrução parcial deste ecossistema continental do Gondwana.

Palavras-chave: Dinosauria, Titanosauria, ecossistema, tafonomia, Cretáceo Superior, Gondwana, Patagônia, Argentina.

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APPENDIX 1

Character List

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01. Frontal contribution to the supratemporal fossa: absent (0); present (1).
 02. Parietal occipital process, dorsoventral height: deep, nearly twice the diameter of the foramen magnum (0); short, less than the diameter of the foramen magnum (1).
 03. Parietal, contribution to post-temporal fenestra: absent (0); present (1).
 04. Parietal, distance separating supratemporal fenestrae: less than (0); or twice (1); the long axis of supratemporal fenestra.
 05. Supraoccipital, height: twice (0); subequal (1) than height of foramen magnum.
 06. Paroccipital process, ventral non-articular process: absent (0); present (1).
 07. Longitudinal groove on the supraoccipital: absent (0); present (1).
 08. Tooth shape: spoon-like (0); compressed cone chisel-like (1); pencil chisel-like (2).
 09. Wear facets of teeth sharply inclined: absent (0); present (1).
 10. Tooth crowns, cross-sectional shape at mid-crown: D-shaped (0); subcylindrical with smooth crest (1); cylindrical (2).
 11. Cervical vertebrae, number: 12 (0); 13 (1); 14 or more (2).
 12. Pleurocoels in anterior and middle cervical vertebrae: present (0); absent (1).
 13. Cervical pleurocoels divided by lamina or septa: present (0); absent (1).
 14. Cervical prezygapophyses, relative length: articular facets that surpass (0); or not surpass (1) the centra.
 15. Posterior cervical neural spines, laterally expanded and wider than the centra: absent (0); present (1).
 16. Neural spines in cervical vertebrae: tall (0); short (1).
 17. Anterior cervical neural spines: bifid (0); single (1).
 18. Posterior cervical vertebrae, proportions – ratio total height / centrum length: less (0); or more (1) than 1.5.
 19. Supradiapophyseal cavity (or fossa) in posterior cervical vertebrae: absent (0); shallow or reduced (1); deep and extended (2).
 20. Posterior cervical centra, proportions: ratio anteroposterior length / height of posterior face: >3 (0); between 2,5 and 1,5 (1); less than 1,5 (2).
 21. Dorsal vertebrae, number: 12 (0); 11 (1); 10 or fewer (2).
 22. Anterior dorsal neural spines, shape: bifid (0); single (1).
 23. Anterior dorsal neural spines inclined posteriorly more than 20 degrees: absent (0); present (1).
 24. Posterior dorsal neural spines, dorsal development: more (0); or less (1); than 20% of the total height of the vertebra.
 25. Prespinal lamina in dorsal vertebrae: absent (0); present in the distal end of neural spine (1); present all along the neural spine (2).
 26. Centroparapophyseal lamina in posterior dorsal vertebrae: absent (0); present (1).
 27. Ventrally widened or slightly forked centroparapophyseal laminae in posterior dorsal vertebrae: absent (0); present (1).
 28. Hyposphene-hypantrum articulation in dorsal vertebrae: present (0); absent (1).
 29. Pleurocoels in dorsal vertebrae, shape: circular or elliptical (0); posteriorly acuminate (1).
 30. Camellate or somphospondylous types of internal structures of presacral vertebrae: absent (0); present (1).
 31. Sacral vertebrae, number: five (0); six (1).
 32. First caudal vertebrae, type: platycoelous (0); procoelous (1); opisthocoelous (2); biconvex (3).
 33. Wide and deep interzygapophyseal cavity: absent (0); present (1).
 34. Caudal transverse processes: disappear by caudal 15 (0); disappear by caudal 10 (1).
 35. Anterior and middle caudal centra, proportions: as high as wide (0); depressed (1).
 36. Mid caudal centra, posterior articular face: vertical (0); strongly inclined posteriorly (1).
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APPENDIX 1 (cont.)

37. Articular face shape on anterior caudal centra: non-procoelous (0); slightly procoelous (1); strongly procoelous with prominent condyles (2).
 38. Articular face shape on middle caudal centra: non-procoelous (0); slightly procoelous with reduced condyles (1); strongly procoelous with prominent condyles (2).
 39. Neural arch in anterior caudal vertebrae: placed in the middle of the centrum(0); anteriorly (1); on the anterior border (2).
 40. Anterodorsal border of neural spine in middle caudal vertebrae located posteriorly with respect to anterior border of the postzygapophyses: absent (0); present (1).
 41. Anteriorly directed neural spine on anterior caudal vertebrae: absent (0); present (1).
 42. Shape of the section of neural spines in most anterior caudal vertebrae in dorsal view: axially elongated (0); transversely elongated (1); quadrangular (2).
 43. Neural spine in middle caudal vertebrae, shape: short anteroposteriorly (0); laminated and anteroposteriorly elongated (1).
 44. Length proportions of prezygapophyses with respect to the centrum length in middle caudal vertebrae: shorter than 50% (0); between 40 to 50% (1); longer than 50% (2).
 45. Ventral depression divided by a longitudinal septum in anterior and middle caudal vertebrae: absent (0); present (1).
 46. Postzygapophyseal process in middle caudal vertebrae: absent (0); present (1).
 47. Well developed interprezygapophyseal lamina in middle caudal vertebrae: absent (0); present (1).
 48. Scapular glenoid orientation: relatively flat (0); strongly beveled medially (1).
 49. Humerus, breadth of proximal end with respect to the total length: less (0); or more (1) than 50%.
 50. Humerus, type of proximal border: strongly curved (0); straight or slightly curved (1); sigmoidal (2).
 51. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1).
 52. Sternal plates, shape: suboval (0); semilunar (1).
 53. Sternal plate with straight posterior border: absent (0); present (1).
 54. Coracoid, shape: suboval (0); quadrangular (1).
 55. Metacarpals, distal phalangeal articular facets: present (0); absent (1).
 56. Pubis, length with respect to ischium: shorter or equal (0); longer (1).
 57. Ischium, posterior process twice or more the length of pubic articulation: present (0); absent (1).
 58. Ischium, iliac peduncle: short and poorly developed (0); slender and well developed (1); wide and well developed (2).
 59. Shape of preacetabular lobe of ilium: moderately expanded (0); broadly expanded and directed upward (1).
 60. Orientation of preacetabular lobe of ilium: nearly vertical (0); nearly horizontal and laterally projected (1).
 61. Relative orientation of the pubic peduncle of ilium: angled (0); perpendicular with respect to the sacral axis (1).
 62. Humerus / femoral ratio of 0.90 or more: absent (0); present (1).
 63. Lateral bulge of femur, below the greater trochanter: absent (0); present (1).
 64. Distal end of tibia broader transversely than anteroposteriorly: absent (0); present (1).
 65. Osteoderms: absent (0); present (1).
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APPENDIX 2

Data Matrix

<i>Camarasaurus</i>						
0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	00000
<i>Brachiosaurus</i>						
0001000110	1000001001	0100100000	0000000010	0000000000	0000000010	11100
<i>Chubutisaurus</i>						
??????????	??????????	???2?0001	?0?00001?	???0???00	???0?????	?111?
<i>Andesaurus</i>						
??????????	??????????	?1?0111011	?0?0001010	0010000?0?	???1110??	?01??
<i>Malawisaurus</i>						
??????210	?11000?00?	?1?0111111	?10002010	0?11000???	1110??10??	???11
<i>Mendozasaurus</i>						
??????????	?1010?122	?10?2??111	?110002110	0111000101	111?1?????	?0111
<i>Futalognkosaurus</i>						
??????????	2110101122	210?2??111	111?0?2?1?	?1?0?0???	?????11211	1????
<i>Epachthosaurus</i>						
??????????	??????????	?111211011	11?0002210	0011000101	11??11??11	1011?
<i>Rapetosaurus</i>						
1110111212	201000100?	1111211111	1?00002210	010?000101	110??11011	101?1
<i>Lirainosaurus</i>						
??????21?	??????????	?1?1211111	?11?002210	0000000?01	?101??????	?1?1?
<i>Rinconsaurus</i>						
??????211	?010001011	?111211111	1??002210	0101011101	1101111111	101??
Loma del Lindero sp.						
1110111211	?11000?011	?111211111	1?0?002210	0201011101	110?111111	1011?
<i>Gondwanatitan</i>						
??????????	??????????	?111211111	11??112220	1002001?0?	??????0111	???1?
<i>Aeolosaurus</i>						
??????212	??????????	?1??2?????	?30?012220	1102001?01	?10?1101??	???1?
<i>Opisthocoelicaudia</i>						
??????????	??????????	1011210111	1211000010	0200000111	1101111111	1011?
<i>Alamosaurus</i>						
??????2?2	?010001001	?1?1200111	1311002210	0200000101	1111111211	1011?
<i>Neuquensaurus</i>						
??????????	?011001012	?111211111	131?102211	0200000101	11011?1211	1?111
<i>Saltasaurus</i>						
1?10010212	?001011012	?111211111	110?102211	0200100112	1101111211	10111
<i>Rocasaurus</i>						
??????????	??????01?	?111211111	????102211	0?00100???	?????11211	1?1??