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New fossil record of a Jurassic pterosaur from Neuquen Basin, Vaca Muerta Formation, Argentina

Laura Codorniú[a,*], Alberto Garrido[b]

[a] CONICET – Departamento de Geología, Universidad Nacional de San Luis, Av. Ejército de Los Andes 950, San Luis 5700, Argentina
[b] Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher" – Dirección Provincial de Minería, Neuquén, Argentina

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ABSTRACT

Discoveries of Jurassic pterosaurs in the Southern Hemisphere are extremely unusual. In Argentina, pterosaurs from the Upper Jurassic (Tithonian) have only been found in the Northwest of Patagonia (Neuquén Basin). These come from marine deposits and three specimens have been discovered up to the present. In this paper, we report a new finding from the Neuquén Basin. This material is identified as a tibiotarsus, which probably belonged to an osteologically adult individual and represents a new species of a pterodactyloid pterosaur of medium size. This discovery provides new evidence that at least two different species of pterodactyloid pterosaurs may have coexisted in Los Catutos Member, Vaca Muerta Formation, from the shallow marine deposits of the Neuquén Basin.

1. Introduction

Discoveries of Jurassic pterosaurs are extremely rare in Southern Hemisphere. The oldest record in Gondwana comes from the Middle Jurassic, of Argentina. These fossils have been collected from the Cañadón Asfalto Formation (Rauhut et al., 2001; Unwin et al., 2004; Codorniú et al., 2010, 2011; Paulina–Carabajal et al., 2011). New data indicate that the lacustrine levels of the Cañadón Asfalto Formation in the vicinity of the village of Cerro Cóndor probably range from the uppermost Toarcian to the lowermost Bathonian (Cabaleri et al., 2010; Cúneo and Bowring, 2010).

In the East side of Gondwana, fragmentary remains are known from the finely laminated limestone from the Kota Formation of Kota, India (Rao and Shah, 1963). The age of this formation is controversial; it was previously assigned to the Early Jurassic (Jain, 1973; Yadagiri and Prasad, 1977), but now is regarded as late middle Jurassic to possibly Early Cretaceous (Prasad and Manhas, 2007). The fossils are isolated fragments assigned to "*Campylognathoides indicus*" (Jain, 1974). However, the interpretation of the type specimen of "*C. indicus*" has been questioned by Padian (2008), who suggested that the jaw most likely belongs to a fish. The postcranial bones merit restudies, given that they have no real affinity to *Campylognathoides* (Padian, 2008).

Regarding the last Epoch of the Jurassic, there is evidence of pterosaurs both in Africa and Argentina. The pterosaurs from Africa come from Tendaguru beds, Tanzania. All taxa named before Unwin and Heinrich (1999) had been established using isolated elements from the fore and hind limbs. These authors then conducted a revision of the record and concluded that all previously named pterosaur taxa from Tendaguru, "*Rhamphorhynchus tendagurensis*", "*Pterodactylus maximus*", "*Pterodactylus brancai*" and "*Pterodactylus arnigi*", should be considered *nomina dubia* (Unwin and Heinrich, 1999). They also claimed that this African sample comprised two pterosaurs, a "rhamphorhynchoid" and (following Galton, 1980) a dsungaripteroid pterodactyloid. They named the latter taxon *Tendaguripterus recki* (Unwin and Heinrich, 1999), based on an incomplete short section of the small mandibular symphysis. Subsequently new material from Tendaguru was described; one of these specimens is a proximal portion of a right humerus which was assigned to the Dsungaripteroidea (Costa and Kellner, 2009). The other is also a humerus, but it is complete and very small and was referred to the Archaeopterodactyloidea (Costa and Kellner, 2009). Recently two middle cervical vertebrae were considered as a possibly primitive azhdarchid pterosaur, the oldest record of azhdarchids of Africa (Sayão and Kellner, 2001; Costa et al., 2011).

In Argentina, pterosaurs from the Upper Jurassic (Tithonian) are restricted to the Northwest of Patagonia (Neuquén Basin). They come from marine deposits and four specimens have been discovered up to the present. One of them, *Herbstosaurus pigmaeus* (Casamiquela, 1975; Wellnhofer, 1978; Unwin, 1996) was found in the upper levels of the Tithonian in the Vaca Muerta Formation,

* Corresponding author. Tel.: +54 (0)266 4520324; fax: +54 (0)266 4430224.
E-mail addresses: lcodor600@gmail.com (L. Codorniú), algene@copelnet.com.ar (A. Garrido).

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southern sector of the Arroyo Picún Leufú (Fig. 1), and consists of postcranial remains and impressions of an incomplete specimen (Codorniú and Gasparini, 2007). The other three specimens were collected in the lithographic limestones of the Los Catutos Member (Vaca Muerta Formation), close to Zapala city (Fig. 1).

The first pterosaur from Los Catutos Member area was described in the late 1980's. It is an isolated bone from the hindlimb identified as a tibia from a small pterodactyloid (Gasparini et al., 1987), and is presently under revision (Codorniú and Gasparini, 2013). The second is a nearly complete articulated postcranial skeleton originally described and illustrated by Codorniú et al. (2006). It has been further prepared, which allowed the identification of additional postcranial bones. The revision of this pterodactyloid supports the determination of a new taxon *Wenupteryx uzi*, gen. et sp. nov. (Codorniú and Gasparini, 2012). The third pterosaur was recently discovered by one of the authors (A.G.), who collected a slab with an intact impression of a tibiotarsus from Los Catutos area. This new finding is described in this paper.

1.1. Institutional abbreviations

BMNH, British Museum (Natural History), London; **HMN**, Humboldt Museum für Naturkunde, Berlin; **MOZ–PV**, Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher" Zapala, Neuquén, Argentina. Colección de Paleontología de Vertebrados.

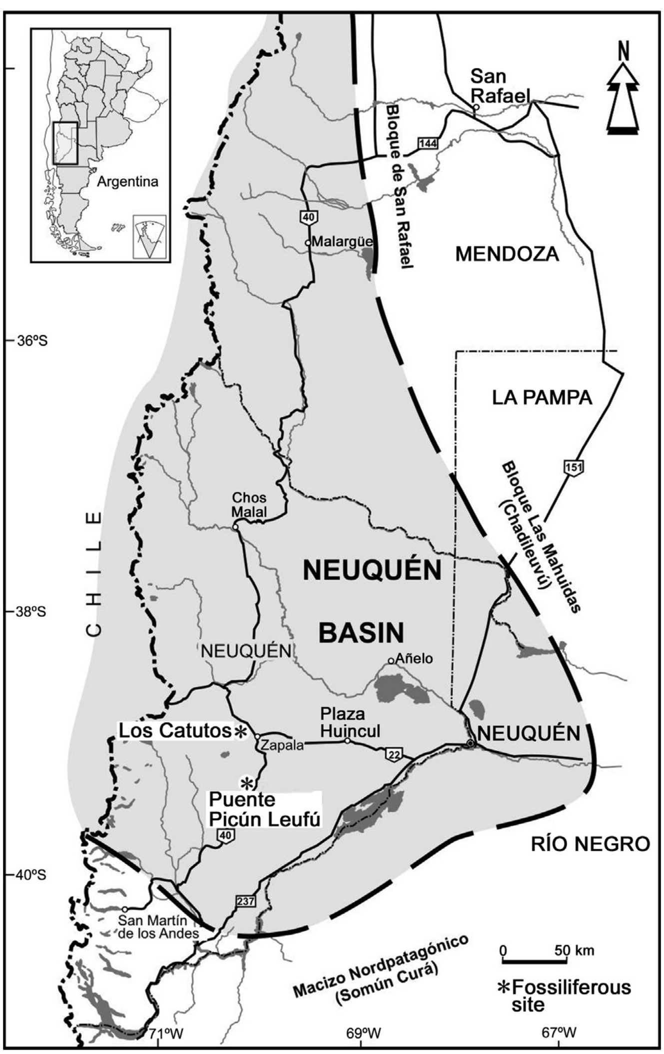

Fig. 1. Location map of Puente Picún Leufú and Los Catutos fossiliferous site, Neuquén Basin, Argentina.

2. Geological setting

The specimen MOZ–PV–094, was recovered from a flagstone of a walkway located in the downtown of the city of Zapala (Neuquén province, Argentina), close to the Museum of Natural Sciences (MOZ). Lithologically, the flagstone corresponds to a marly limestone (lithographic limestone type) coming from a mining quarry located in the Los Catutos locality, 15 km north of Zapala city (Figs. 1 and 2).

In this area a brachysyncline structure exposes Tithonian and Berresian marine deposits, corresponding to the Vaca Muerta and Picún Leufú Formations (Fig. 2). The Vaca Muerta Formation is characterized along the basin by the development of a thick succession of calcareous sandy shales and black shales along with subordinate amounts of interbedded calcareous sandstones, siltstones and limestones (Weaver, 1931; Leanza, 1973; Parent et al., 2011, 2013).

In the southern area of the Neuquén Basin, a 70 m thick succession of lithographic limestones and marls is intercalated in the middle part of the Vaca Muerta Formation, and has been identified by Leanza and Zeiss (1990) as the Los Catutos Member. According to Scasso et al. (2002) these limestones and marls can be classified as pelbiomicrites and biopelmicrites, developed in a low–energy, dysaerobic, openmarine environment.

Los Catutos Member rocks are rich in ammonites, with a minor presence of fish, crustacean, bivalve, gastropod and reptile remains (Leanza and Zeiss, 1990; Parent et al., 2013). In this last case a diverse herpetofauna composed of turtle, ichthyosaur, plesiosaur, crocodile, and pterosaur remains has been found (Fernández and de la Fuente, 1988, 1993; Gasparini, 1988; Gasparini et al., 1995; Gasparini and Fernández, 1997; Codorniú et al., 2006). The age of the Los Catutos Member has been dated on the basis of its ammonite fauna as surely 'mid to late' Tithonian (Zeiss and Leanza, 2010; Parent et al., 2013).

The locality of origin of the flagstone carrier of the specimen MOZ–PV–094, is justly registered in the archives of the Dirección Provincial de Minería (mining bureau) of the Neuquén province. Likewise, the petrological characteristic and composition of this rock, strongly supports this attribution to the deposits of Los Catutos Member.

3. Material

MOZ–PV–094 is an intact impression of an isolated bone, preserved in a slab. A cast was used to identify positive characters. This cast shows that the bone was slightly compressed in an anteroposterior direction. Thus, the detailed anatomical description is based on both the mold and cast (Figs. 3–5).

4. Description

MOZ–PV–094 consists of a large right tibiotarsus (proximal tarsals and part of the fibula are fused to the tibia), exposed in anterior view in the cast. The tibia is a long bone with a transversely elongate, suboval proximal surface and a notably straight shaft. The anterior surface of the proximal end of the tibia has a small V–shaped cnemial crest, with the apex directed anteriorly (Fig. 3B–C). This structure may have served for the attachment of muscles, particularly *M. triceps femoris* (Bennett, 2001). The fibula is a long thin bone that articulates with the latero–posterior margin of the tibia (Bennett, 2001). This bone is well exposed in the proximal end and more distally is covered by the specimen

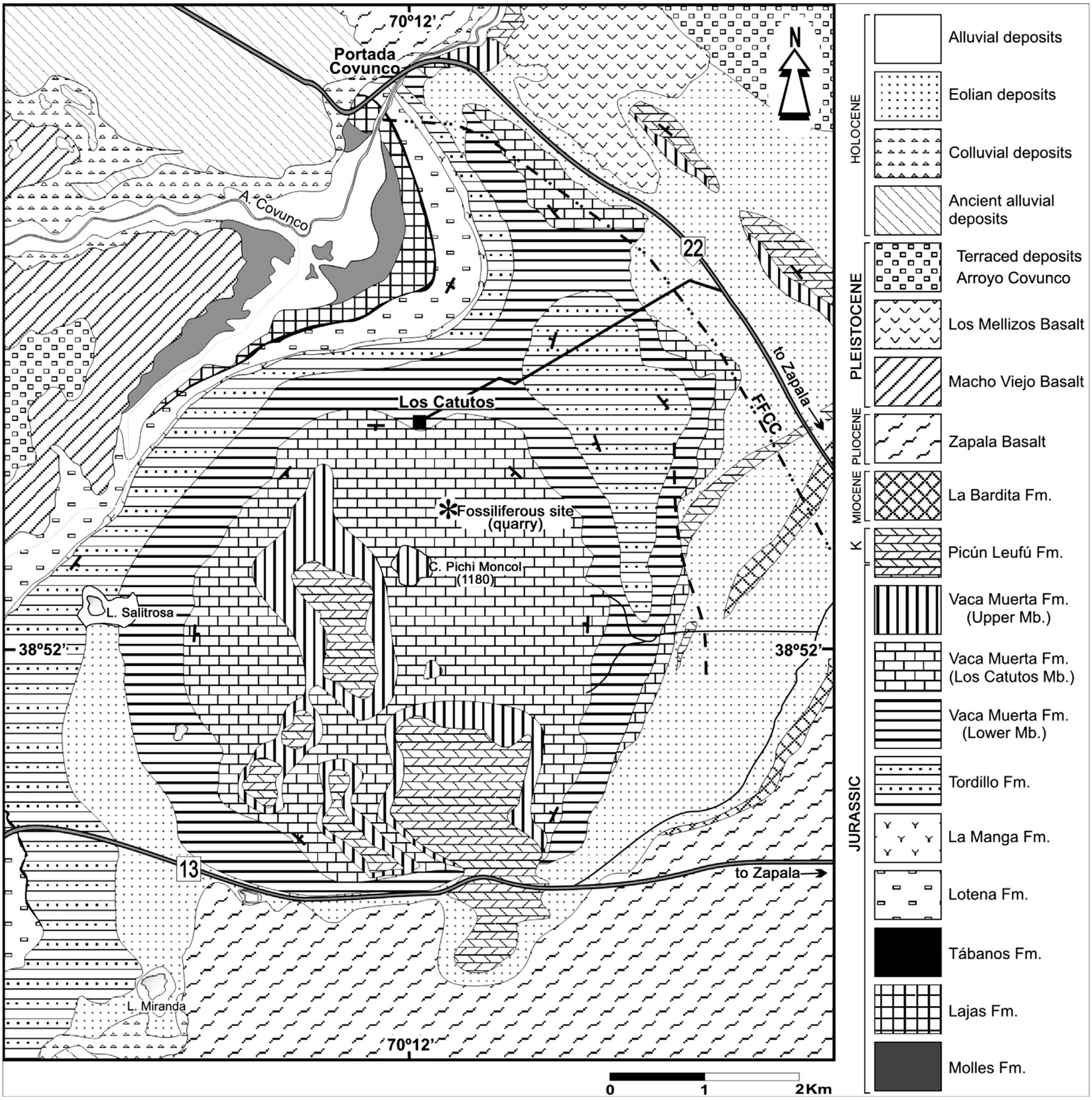

Fig. 2. Geological map of Los Catutos fossiliferous site, Neuquén Basin, Argentina (slightly modified after Leanza and Zeiss, 1990).

deformation (Figs. 3–5). It can be appreciated that the proximal end of the fibula is suboval and occupies about a third of the total area of the proximal surface of the tibiotarsus. It is not possible to determine the exact length of the fibula, but it clearly seen that this bone is distally fused to the shaft of the tibia and does not articulate with proximal tarsals.

The length of the tibiotarsus is 214 mm, it is slightly narrower at the proximal end (21.05 mm) than at the distal end (27 mm). Near the proximal end of the tibiotarsus, the width of the shaft slightly increases distally; this width remains constant for about 90 mm up before reaching the half of the total length of the bone. From this point it begins to narrow gradually until the minimum width (15 mm) of the bone is attained at about three quarters of its length. Near the distal end of the shaft it expands again to reach the maximum width at the level of the condyles.

The portion of the shaft where the diameter remains constant (approximately 90 mm) presents a bone alteration. This abnormality looks like a bone fracture involving both the tibia and the fibula. Most likely, the hematoma that occurred when the bone was broken in life was large and the healing occurred through periosteal calcification. Healed fractures were observed by Bennett (2003) in limb bones of *Pteranodon*. Another possibility that may account for this deformation is Osteomyelitis. Such an acute or chronic bone infection or Brodie's abscess of any bone may be precipitated by trauma to the affected area. A Brodie's abscess may be defined as a roughly spherical region of bone destruction, filled with pus or connective tissue, usually in the metaphyseal region of long bones and caused by bacteria. Evidence of this alteration is most clearly seen in the lateral or medial view, and the bulge is well developed in the anterior surface of the bone, in the metaphysis and in part of

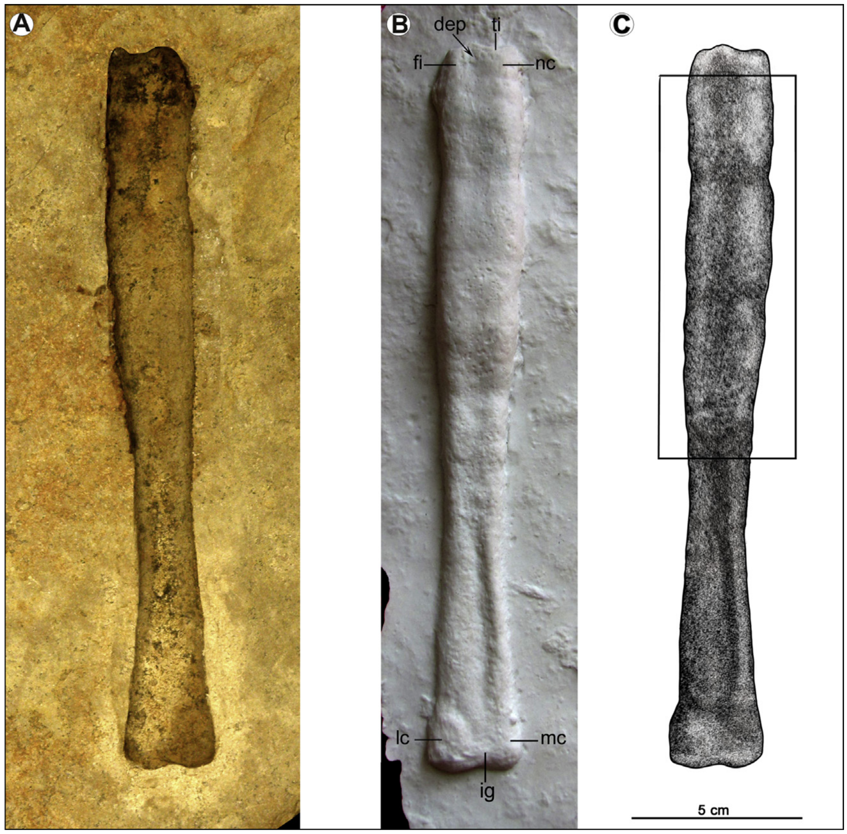

Fig. 3. A, Photograph of the original slab of the specimen MOZ–PV–094; B, Photograph of the cast showing right tibiotarsus in anterior view; C, Composite drawing of the cast. Abbreviations: dep, tibiofibular depression; fi, fibula; ig, intercondylar groove; lc, lateral condyle; mc, medial condyle; nc, cnemial crest; ti, tibia. Quadrangular line indicates the area of the bone alteration.

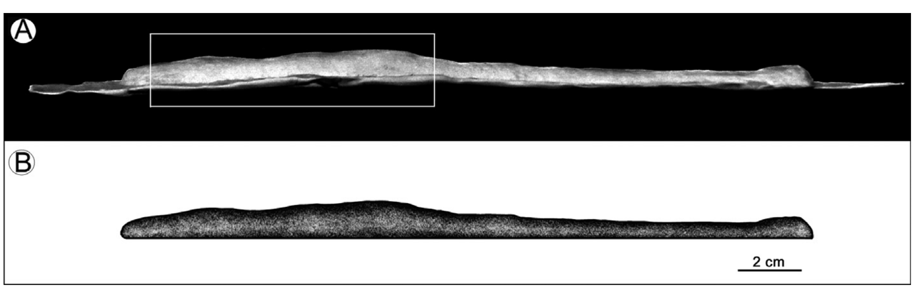

Fig. 4. Details of the cast in lateral view, showing the bulge of the alterated bone. A, Phothograph; B, Composite drawing. Quadrangular line indicates the area of the bone alteration.

the diaphysis, but does not affect the ephyfisis (Figs. 4 and 5). It is not possible to determine exactly the type of pathology, however, no erosional structure can be attributed to this form. The continuous, very fine lamination (rhythmites) that characterized the fossiliferous rock indicate a very low-energy conditions of sedimentation (Scasso et al., 2002), and no other evidence of high-energy or erosional structure is observed.

The proximal articular surface of the tibiotarsus is concave for the articulation of the distal condyles of the femur, and is slightly elongated in lateromedial view. The cast, observed in proximal view, shows the facet joints of the fibula and the tibia. In anterior view, and between the facet joints of fibula and tibia, there is a shallow depression to mark the contact of both bones (Fig. 5).

The distal end of the tibiotarsus consists of the lateral and medial condyles, which are well fused to the shaft of the tibia and which are formed by the proximal tarsals (astragalus and calcaneum). There is apparently no trace of the suture between the proximal tarsals and the tibia though it is difficult to determine due to the type of preservation. The fusion of the shaft of the tibia to the proximal tarsals, without evidence of suture, indicates that this pterosaur probably represents an osteologically mature individual, but not necessary adult size. For example in some basal pterosaurs these bones can be well fused before adult size is reached, as in *Dimorphodon* (Padian, 1983), *Dorygnathus*, and *Campylognathoides* (Padian, 2008). The condyles are convex, subcircular and the lateral condyle is slightly larger compared to the medial. Between the two condyles there is a narrow intercondylar "V"–shaped groove (Fig. 3B). We cannot determine whether this groove was deep or not, because the material is somewhat flattened. The groove on the distal end of the tibiotarsus could have functioned as a pulley for the tendons of *extensors* of the ankle and *flexors* of the pedal digits (Bennett, 2001). The distal condylar region projects anteriorly to the shaft (Fig. 4), probably also is projected posteriorly (but the specimen can observe only in anterior view, this projection is circular shaped.

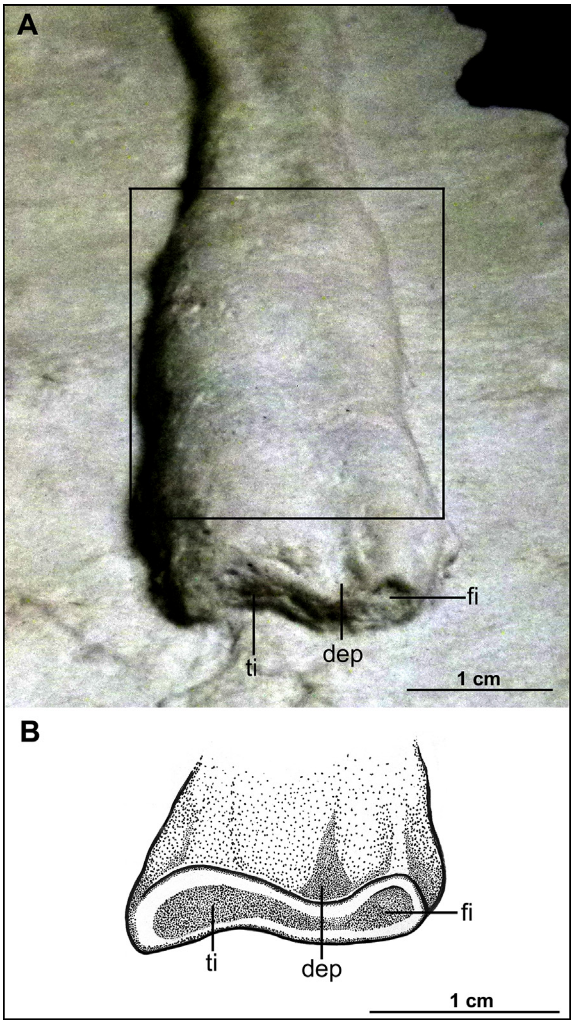

Fig. 5. A, Photograph of the cast showing right tibiotarsus in antero–proximal view; B, Drawing of the cast in proximal view. Abbreviations: dep, tibiofibular depression; fi, fibula; ti, tibia. Quadrangular line indicates the area of the bone alteration.

The combination of the features observed in this new specimen, especially in the proximal and distal ends allows its identification as a pterosaurian tibiotarsus.

5. Discussion

The identification of this specimen was not easy; however the combination of osteological characters observed in the proximal and distal ends, allowed its identification as a pterosaur tibiotarsus. It was not an easy assignment because it has a relative degree of crushing and an abnormality was observed in a portion of the shaft. However comparison with specimens from different parts of the fore and hind limbs with similar degree of crushing of the *Pterodaustro guinazui* collection, guide us in determining this specimen.

Furthermore, osteologic data from an isolated tibiotarsus, such as this one, are limited in terms of their allocation potential to one specific clade. This difficulty results from the scarce availability of features from this part of the skeleton in existing phylogenetic analyses (Kellner, 2003; Unwin, 2003; Lü et al., 2010; Rodrigues and Kellner, 2013). Up to the present, the available data refer to other elements of the axial skeleton. One character refers to relative proportions between the femur + tibia length relative to the length of dorsal + sacral vertebra [ch.107, Lü et al. (2010)]; the other trait refers to the proportional length between the tibiotarsus and the first wing phalanx; see for example Kellner (2003, ch. 67) and most recent analysis (Wang et al., 2012; Rodrigues and Kellner, 2013, ch. 87). Therefore this feature cannot be applied in this study due to lack of preservation of the rest of the skeleton.

On the other hand, the only character that can be seen partially in this specimen is referred to the relation between fibula and tibia length [ch.8, Unwin (2003) and ch.113, Lü et al. (2010)]. The state 0 of the last character shows that in the outgroup of Pterosauria and in “rhamphorhynchoids” of the Triassic and Lower Jurassic, for example *Peteinosaurus*, *Dimorphodon* and *Campylognathoides*, the fibula and tibia are separated bones and they are subequal in length. In these cases the fibula articulates with the proximal tarsals. In the new specimen from Los Catutos area, it can be clearly seen that the fibula is not a single element separated from the shaft of the tibia, but that both elements are fused distally and we cannot determinate the exact length of the fibula.

Pterosaurs exhibiting state 1, length of fibula less than 80 percent the length of the tibia [ch.8, Unwin (2003) and ch.113, Lü et al. (2010)], constitute the vast majority of the Pterosauria and involve both “rhamphorhynchoids” and pterodactyloids pterosaurs. The shortening of the fibula tends to increase in the Cretaceous pterosaurs, in which the fibula is reduced to a small splint (Wellnhofer, 1978, 1991). This character, state 2 of ch.113 of Lü et al. (2010) is distributed in both basal (*Boreopterus*, Istiodactylidae, Ornithocheiridae and Nyctosauridae) and in derived pterodactyloids (*Quetzalcoathlus* and *Zhejiangopterus*) (*sensu* Lü et al., 2010). Although, in particular the clade Ornithocheiridae has been recently restricted, see Rodrigues and Kellner (2013).

The tibiotarsus MOZ-PV-094 appears to comply with condition 1 of the character of Lü et al. (2010), which is present in a huge variety of species of “rhamphorhynchoids” and pterodactyloids pterosaurs.

Comparison of other Jurassic pterosaurs, specifically those registered in East Gondwana as stated in the introduction from India and Africa, is limited due to the scarcity of records. The isolated tibiotarsi previously referred as “*P. brancai*” (Reck, 1931), and as *Dsungaripterus*? *brancai* (Galton, 1980) are a very well tridimentionally materials. Four tibiotarsi have been located, the holotype of “*P. brancai*” (HMN Nr. 1), plus two others of about the same size, and the distal part of a larger specimen. Anteriorly, this material shows that the distal two thirds of the preserved part of the fibula merge almost imperceptibly with the shaft of the tibia. The shaft of the fibula tapers to a splint-like distal end, which is fused to the middle section of the shaft of the tibiotarsus (Galton, 1980). Traces of a sutural line are visible between the shaft of the tibia and the distal condylar region that is formed by the fused astragalus and calcaneus (Galton, 1980; Fig. 2M-P), this suture also is visible in the largest specimen (BMNH R9191). The distal condylar region of this African material described by Galton (1980) projects anteriorly and posteriorly to the shaft, with a pulley-like articular surface in between. This feature also is observed in MOZ-PV 094, but less evident because the compression, the anterior projection of the condylar region can appreciate in lateral view (Fig. 4). The tibiotarsus, (HMN Nr. 1, is about the half size (126 mm) of the new patagonian specimen. Both tibiotarsi share some features like a small cnemial crest, the fused tibia-fibula; and the lateral condyle larger than the medial condyle.

The only Late Jurassic pterosaur of Argentina, preserving the tibiotarsus is the almost complete pterosaur *W. uzi* (MOZ–PV 3625), coming from the same levels as the one from Los Catutos (Codorniú et al., 2006; Codorniú and Gasparini, 2013). In spite of its being small in size (85 mm), this tibiotarsus (Fig. 6) shows some morphological similarity in relation to the new specimen (MOZ–PV 094). Both tibiae present a straight shaft and both show the minimum width at about two thirds of their total length. Unfortunately, the bone surface of the proximal and distal ends of MOZ-PV 3625 is damaged, which does not allow an exact determination of the diagnostic features. Although it can be observed that one of the condyles, which is less damaged is rounded and it is fused with the shaft of the tibia. But, we cannot determinate if there is evidence of the traces of the suture between the bones because of the injury. Another condyle is broken in two parts, one portion remained with the tibiotarsus and the other portion is slightly shifted and inverted, as if a book is opened (Fig. 6). This small tibiotarsus belongs to a postcranial skeleton that presents many evidences of osteologically maturity, for example, well ossified ends of the long bones (humerus, radio, ulna, femur), proximal and distal carpals forming proximal and distal syncarpals [for other see Codorniú et al. (2006)], but with a few immature traits like a pelvic girdle not fused to the sacrum, and isolated prepubis, instead of both elements (right and left) fused through the medial margins. These features support the hypothesis that this specimen had not reached the adult stage and was sub-adult at the time of death, despite many features that indicate maturity. *W. uzi* (MOZ-PV 3625) represents a sub-adult individual of a small pterodactyloid pterosaur of approximately 1.10 m in wingspan and the new tibiotarsus is two and half times larger than that of *Wenupteryx*. The great difference in size between the specimens leads us to suggest that the new specimen belongs to another species of a medium size pterodactyloid pterosaur. Unfortunately it has no diagnostic features.

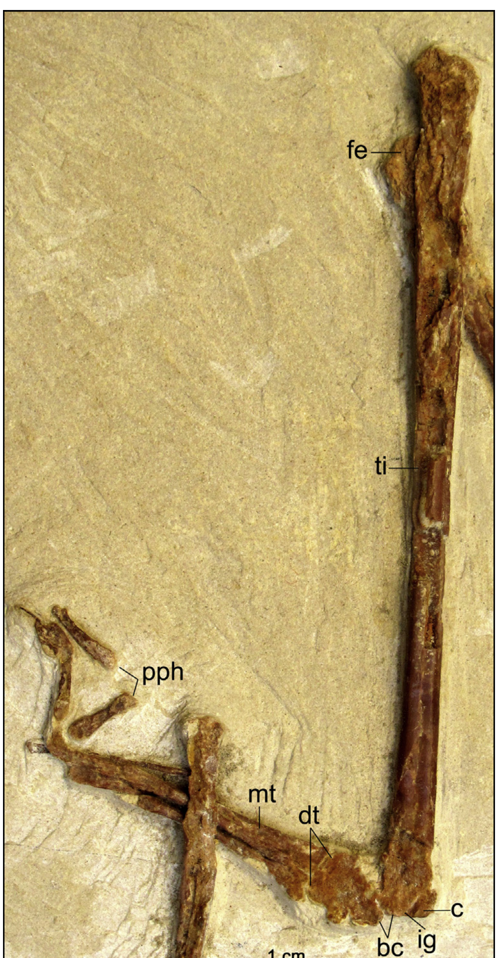

Fig. 6. Photograph of the tibiotarsus of MOZ–PV 3625. Abbreviations: bc, broken condyle; dt, distal tarsals; fe, femur; ig, intercondylar groove; c, condyle; mt, metatarsals; pph, pedal phalanges; ti, tibia.

This new record constitutes evidence of the fact that at least two different species of pterodactyloids pterosaurs coexisted in the marine sediments of the Tithonian from Los Catutos Member (Vaca Muerta Formation). In this brief exploration of Jurassic materials, this new finding of the Neuquén Basin from Los Catutos could represents the largest marine pterosaur known up to the present from the Upper Jurassic from Gondwana.

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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.jsames.2013.09.010.

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