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A late Jurassic pterosaur (Reptilia, Pterodactyloidea) from northwestern Patagonia, Argentina

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Abstract

A small to medium-sized pterodactyloid pterosaur (wingspan approximately 1.10 m) from the Upper Jurassic (middle-late Tithonian) marine deposits of the Vaca Muerta Formation of Patagonia (Los Catutos area, central Neuquén Province, Argentina) is reported. The specimen lacks the skull but constitutes a nearly complete postcranial skeleton, which includes cervical and dorsal vertebrae; a few thoracic ribs; both pectoral girdles; the left pelvic girdle; a proximal right wing (humerus, ulna, and radius) and metacarpal IV; a left wing that lacks only wing phalanx four; and both hindlimbs, the right one without the foot. Ontogenetic features suggest that the new fossil corresponds to a relatively mature individual, probably a subadult. Observed characters support its assignment to the Archaeopteroactyloidea, a basal clade within the Pterodactyloidea. This specimen is the second pterosaur from Los Catutos and the most complete Jurassic pterosaur so far known from South America.

Keywords: Argentina; Middle–late Tithonian; Neuquén Basin; Pterodactyloidea; Pterosauria

1. Introduction

The record of Jurassic pterosaurs from South America is scant, with only a few incomplete specimens known from Patagonia. Recently, non-pterodactyloids have been reported from Cerro Cóndor, Chubut province (Argentina), in the Callovian Cañadón Asfalto Formation (Rauhut and Puerta, 2001; Rauhut et al., 2001; Unwin et al., 2004). These are the oldest pterosaurs recorded in South America; *Herbstosaurus pigmaeus* Casamiquela, 1975, a pterodactyloid pterosaur (Wellnhofer, 1991b; Unwin and Heinrich, 1999) of the southern sector of Arroyo Picún Leufú (Neuquén province, Argentina) comes from the middle–late Tithonian Vaca Muerta Formation (Codorniú and Gasparini, submitted). Two other specimens recovered from the Vaca Muerta Formation come from the Los Catutos area, also in the Neuquén province. One is a tibia of a pterodactyloid (Gasparini et al., 1987), and the other is the much more complete specimen described herein.

The institutional abbreviations used herein are as follows: BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, München; MHIN-UNSL-GEO, Museo de Historia Natural de la Universidad Nacional de San Luis, Geología, Argentina; MOZ, Museo Olsacher of Zapala, Neuquén, Argentina.

2. Geological setting

The Tithonian–Valangianian marine sediments of the Vaca Muerta Formation are widely exposed in the Neuquen Basin of northwestern Patagonia. The lithographic limestones of the Los Catutos Member of the Vaca Muerta Formation (Leanza, 1980; Leanza and Zeiss, 1990; Scasso et al., 2002) are restricted to the southern part of the Neuquén Basin. The area of Los Catutos is located 13 km northwest of the town of Zapala, Neuquén province (Fig. 1), on the southern end of the east limb of the Sierra de la Vaca Muerta anticline (Leanza and Zeiss, 1994). The type locality of the Los Catutos Member is a fossiliferous quarry called ‘El Ministerio’ (Cione et al., 1987; Leanza and Zeiss, 1990, 1992, 1994; Scasso and Concheyro, 1999). Sedimentological and structural analyses of Los Catutos area suggest that these limestones were deposited in a shallow sea (10–30 m) no more than 100 km from the eastern coast of

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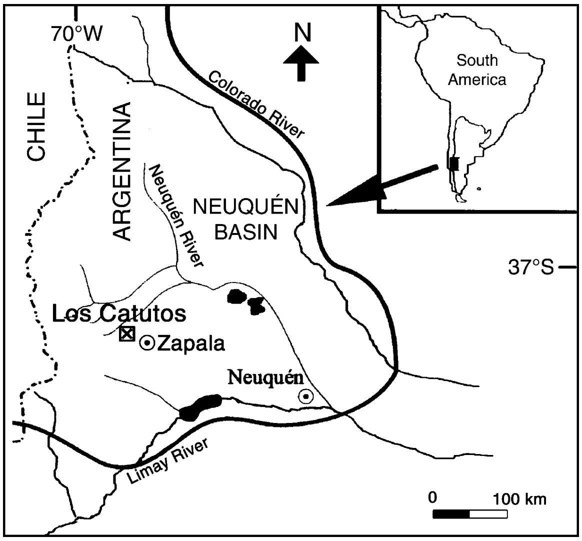

Fig. 1. Location map of the area of Los Catutos, Neuquén Province, Argentina.

the Neuquén Basin (Leanza and Zeiss, 1990; Scasso et al., 2002). The Los Catutos Member belongs to the *Windhauseniceras internispinosum* ammonite zone, which corresponds to the middle–late Tithonian (Leanza and Zeiss, 1990). This dating is confirmed by the association of calcareous nannofossils, particularly *Polycostella beckmanii* (Scasso and Concheyro, 1999). The same locality yields a diverse association of marine reptiles, consisting of ophthalmosaurian ichthyosaurs, pleurodiran and cryptodiran turtles, metriorhynchid crocodilians, and plesiosaurs (Gasparini et al., 1995).

3. Material

The specimen (MOZ 3625P) was collected as split slab and counterslab (Figs. 2 and 3). It lacks the skull but constitutes a nearly complete postcranial skeleton, with a wingspan approaching 1.10 m (Table 1). In addition, MOZ 3625P includes some cervical and dorsal vertebrae; a few thoracic ribs; both pectoral girdles exposed in anterior view; the left pelvic girdle displaced toward the lower portion of the specimen; a proximal right wing (humerus, ulna, and radius) and right metacarpal IV; a more complete left wing that only lacks the wing phalanx four; and both hindlimbs, the right one without the foot (Fig. 4). Most long bones are disarticulated and therefore exposed in different views; both humeri are in ventral view, and both metacarpal IV are in cranial view. The mostly complete left wing is exposed in the upper part of the specimen, and the metacarpal IV is displaced from its original position to a location near the bones of the right wing. The bad preservation and fragmentary state of the remains preserved in the middle and on the right side of the specimen (fb in Fig. 4) prevent a precise identification, but they likely belong to a portion of the proximal vertebral column. The pelvic girdle is displaced toward the lower region of the specimen. The right hindlimb lacks the foot. The left hindlimb is complete, and the femur is exposed in caudal view.

Fig. 2. Photograph of slab of the specimen MOZ 3625P.

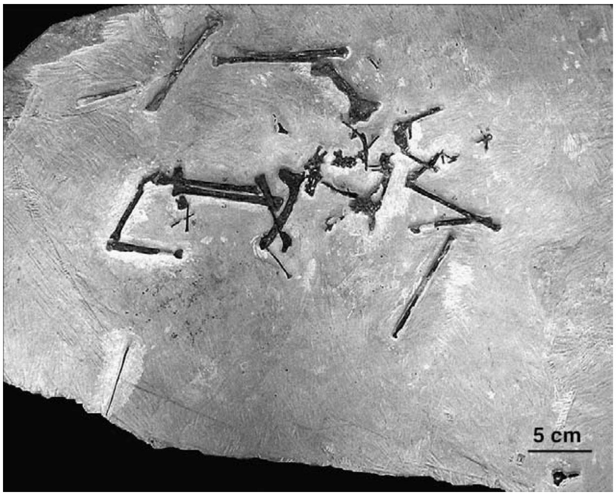

Fig. 3. Photograph of counterslab of the specimen MOZ 3625P.

4. Description

The identifiable bones are marked in the hypothetical reconstruction (Fig. 5).

Table 1
Measurements (maximum length in millimeter) of the most complete bones of MOZ 3625P

Middle cervical vertebrae (length)	16.00
Scapula	40.00
Coracoid	42.00
Humerus	65.00
Radius	87.00
Ulna	88.00
Metacarpal I	61.00
Metacarpal IV	67.00
WpI	95.00
Ilium	43.00
Femur	66.00
Tibia	85.00
Metatarsal II?	28.00

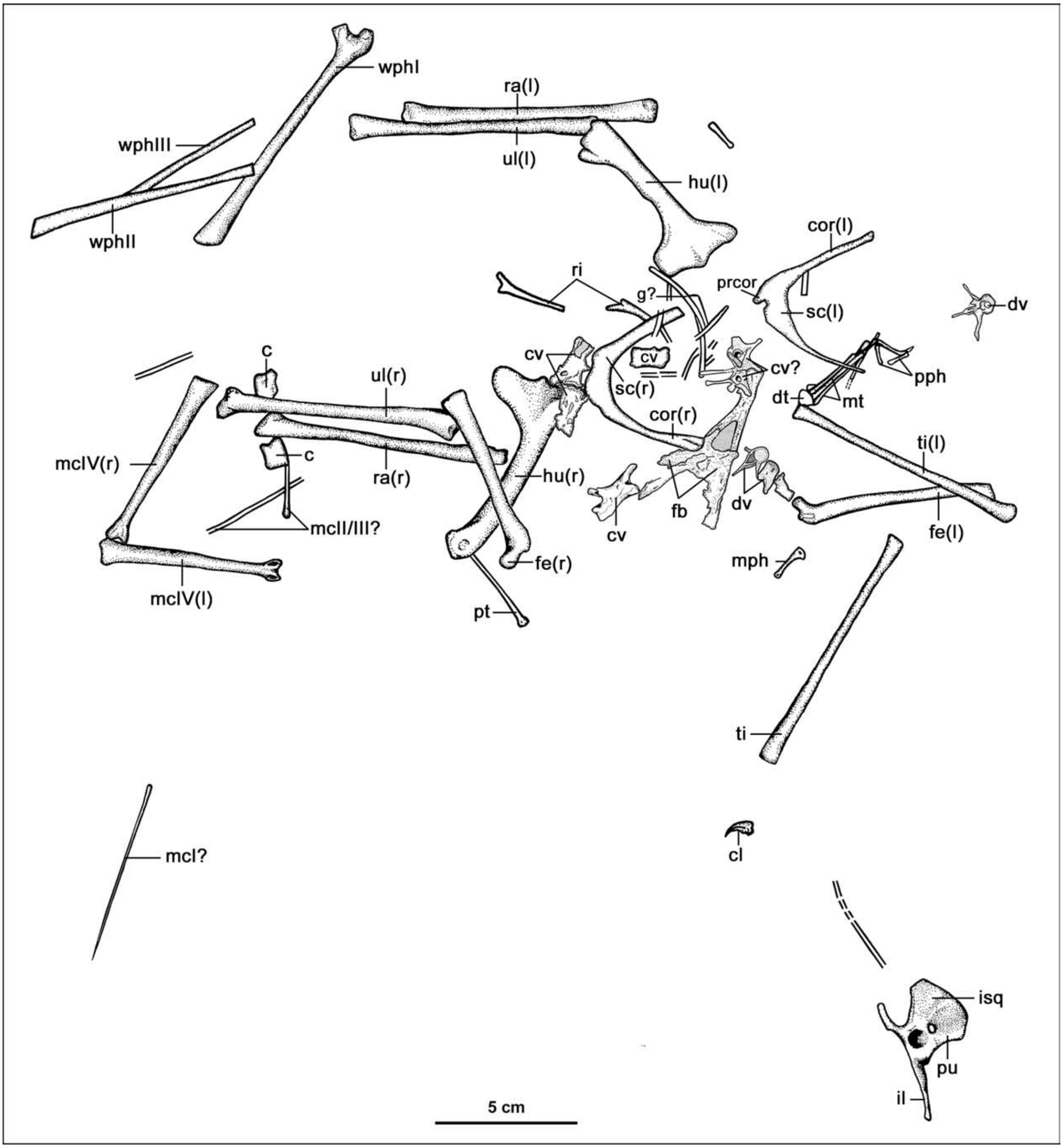

Fig. 4. Composite drawing of MOZ 3625P. Abbreviations: c, carpals; cl, manual claw; cor, coracoid; cv, cervical vertebrae; dt, distal tarsals; dv, dorsal vertebrae; fe, femur; fb, fragmentary bones; hu, humerus; il, ilium; isq, ischion; mcI, metacarpal I; mcII/III?, wing metacarpal II or III; mcIV, wing metacarpal IV; mph, manual phalanges; mt, metatarsals; pph, pedal phalanges; prcor, procoracoid; pu, pubis; pt, pteroid; ra, radius; ri, rib; sc, scapula; ti, tibia; ul, ulna; wph I–III, wing phalanges I–III r, right; l, left.

4.1. Axial skeleton

Small portions of the vertebral column, mostly disarticulated, were preserved from the axial skeleton. Among them are six incomplete dorsal ribs, which present double heads and curved, thin shafts; four cervical vertebrae, probably midseries cervicals, two articulate and badly preserved; and an isolated cervical vertebra exposed in lateral view on counterslab. The latter is well preserved and permits a more detailed description (Fig. 6A). The centrum is procelic and elongate and its length reaches, at most, three times the minimum height and probably the width. The prezygapophyses extend toward the anterior end of the centrum, and their articular surfaces point dorsomedially. The postzygapophyses are higher than the prezygapophyses and do not exceed the posterior end of the condyle. No postexapophyses appear ventrolaterally to the condyle. No pneumatic foramen is found. The neural arch is depressed with an apparently low neural spine. Two vertebrae preserved on slab in caudal view seem to correspond to the two last vertebrae of the midseries cervical, called dorsalized cervicals

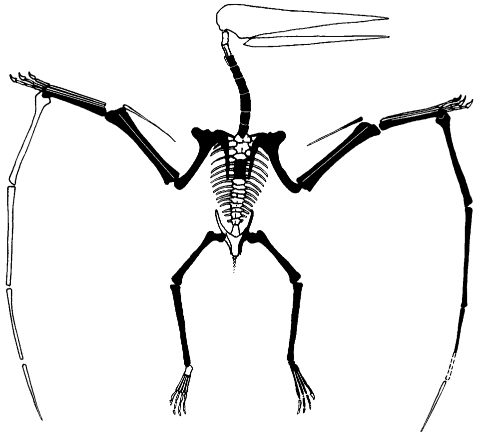

Fig. 5. Hypothetical pterodactyloid in which the bones preserved in MOZ 3625P are marked.

(Bennett, 2001). These latter are somewhat different from the middle cervicals—the posterior condyle is low and wide lateromedially, they have a higher neural spine, and the transverse processes bear short ribs. Probably, the length of the vertebral centrum is much shorter (Fig. 6B).

Three vertebrae from the dorsal series are preserved. An isolated dorsal vertebrae on slab is exposed in cranial view. The other dorsals on counterslab are contiguous, one exposed in cranial view and the other in lateral view. The centrum is procelic and subquadrangular in shape in lateral view and circular in cranial view. The neural arch is high and forms a high neural canal. In cranial view, the transverse processes are exposed in a laterodorsal angle of approximately 30° with respect to the neural spine. In one of the dorsal vertebrae of the series, exposed in lateral view, the neural arches are separated from their respective centra, suggesting immaturity.

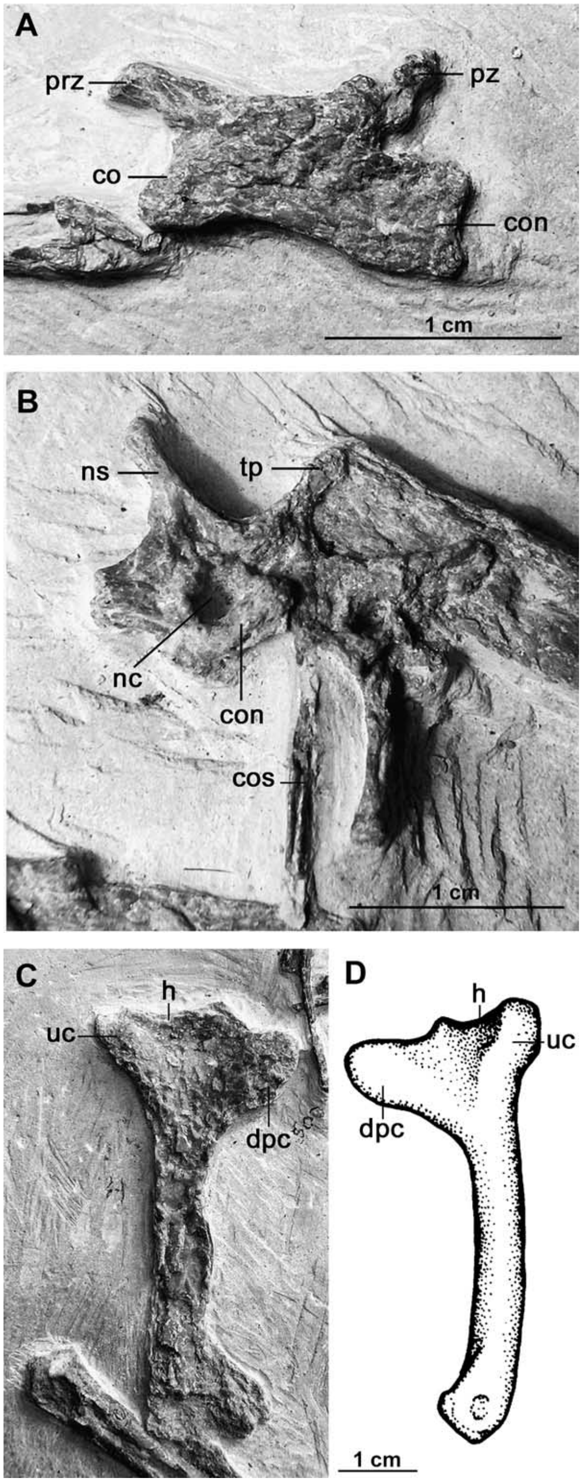

Fig. 6. (A) Detail of the midcervical vertebrae of MOZ 3625P; (B) detail of the last? vertebrae of the cervical series of MOZ 3625P; (C) photograph of the left humerus; (D) composite drawing of the right humerus. Abbreviations: co, cotyle; con, condyle; h, head; dpc, deltopectoral crest; nc, neural canal; ns, neural spine; prz, prezygapophysis; pz, postzygapophysis; tp, transverse process; uc, ulnar crest.

4.2. Appendicular skeleton

The appendicular skeleton is represented by portions of both fore- and hindlimbs, both scapulocoracoids, and the left pelvic girdle. The forelimbs are better preserved on slab.

4.2.1. Pectoral girdle and forelimb

Both left and right pectoral girdles are preserved on slab and counterslab. They are exposed in cranial view near the left and right humeri, respectively. The scapula is elongate with curved shaft. The distal end is strong and expanded and contacts the coracoid and forms the dorsal portion of the glenoid fossa. The proximal end of the scapula is also expanded but planed and thin, and its margin is slightly convex, in contact with the vertebral column. The coracoid is more robust than the scapula, and its shaft is almost straight. The distal end forms the ventral portion of the glenoid fossa. The proximal end of the coracoid is quite strong and has a concavity in the middle. On the anterior and dorsal end of the coracoid is the procoracoid (sensu Wellnhofer, 1991a), a conspicuous prolongation. The scapula and coracoid are fused, forming a strong, single bone, the scapulocoracoid, which is U-shaped (Bennett, 1996; Kellner and Tomida, 2000). The suture of the contact between both bones cannot be seen. In pterosaurs, these bones are usually subequal in size, with the scapula often longer. In only one clade, Pteranodontoidea (sensu Kellner, unpublished), the reverse is observed (Kellner and Moody, 2003). In MOZ 3625P, the coracoid is slightly longer than the scapula, but the difference is so small that they are considered equal in size.

The left humerus is complete on slab (Fig. 6C). Portions of the right one are preserved on slab and counterslab (Fig. 6D). Both humeri are exposed in ventral view. The deltopectoral crest of the humerus is D-shaped and curves slightly ventrally. The longest axis of the crest is parallel to the longitudinal axis of the humerus and occupies approximately 30% of the length of the humerus. The shortest portion of the crest is the distal end, which has rounded margins. These features approach that of basal pterodactyloids and dsungaripterids more than that of the much longer (∼40% of the humerus) and warped deltopectoral crest of Pteranodontoidea (sensu Kellner, 2003) and other ornithocheiroids (Bennett, 1989, 1994, 2001; Unwin, 1995, 2003). The diameter of the shaft remains uniform over the proximal two-thirds, then increases in width over the distal one-third (hu(l) in Fig. 4). This seemingly primitive condition differs from that of the ornithocheiroids, for which the diameter of the shaft increases from the base of the deltopectoral crest distalward (Bennett, 1989). The ulnar crest or posterior tuberosity is slightly curved ventrally, as is the deltopectoral crest. At the distal end of the humerus, the condyles are well ossified.

The right and left radius and ulna are complete and exposed in anteroventral view. These bones are straight, with midshafts of almost the same width (the ulna is slightly wider). These subequal diameters differ from advanced pterosaurs such as *Anhanguera piscator,* in which the radius diameter is less than half the ulna (Kellner and Tomida, 2000). The ulna is a long, straight bone with strong, expanded ends. The condyles of the proximal end are proximally directed (Fig. 4). The ulnae of archaeopterodactyloids (i.e. *Pterodactylus*) are not sufficiently known to make comparisons (Bennett, 1991, 2001). The radius is long and straight, with an almost constant diameter of the shaft for its length.

The right carpals are preserved on slab at both sides of the radius and ulna. The proximal carpals are fused to form a proximal sincarpal, and the distal series form the distal sincarpal. Owing to their size and preservation, not many features can be observed, but their shape is rectangular with rounded margins. Carpal bones are generally fused in osteologically mature individuals (Wellnhofer, 1978). The pteroid bone is incompletely preserved on slab, next to the distal end of the right humerus. It lacks the distal end, and its proximal end is expanded and rounded.

Metacarpals I–III are long, slender, toothpick-like bones. In MOZ 3625P, only one metacarpal, metacarpal I?, is completely preserved and is far from the rest of the wing bones. Its proximal end thins gradually and ends on a sharp point. Its distal end is somewhat expanded and rounded; it would articulate with the first manual digit. It is similar in length to metacarpal IV, for which, at least in this specimen, it is clear that one metacarpal articulated with the carpus. Probably the rest of the metacarpal, mc II and III, also articulated with the carpus. This character relates the new fossil to *Ctenochasma gracile* (*Pterodactylus elegans*), *P. antiquus, P. kochi,* and *Pterodaustro guinazui* (Codorniú and Chiappe, 2004), in which metacarpals I–III are almost equal in length to mcIV and the proximal end can articulate with the carpus (Wellnhofer, 1970). In contrast, in *Pteranodon,* these metacarpals do not articulate proximally with the carpus and are reduced to thin sticks only 30% the length of mcIV (Bennett, 2001).

Left metacarpal IV is displaced and preserved next to the right wing bones. Both mcIV are exposed in cranial view. As in all other pterosaurs, this bone is considerably stronger than the other three metacarpals (Wellnhofer, 1991b). The proximal end is expanded, and in the left metacarpal IV, a tubercle is observed. This tubercle is moderately developed and would articulate with the distal face of the distal sincarpus. The shaft of the metacarpus decreases from the proximal end toward the distal, forming a short neck near the distal articulation. The distal end is very characteristic in shape, and the articulation pulley-shaped, formed by two condyles separated by a medial furrow (Wellnhofer, 1978, 1991b). Both ventral and dorsal condyles are circular in shape; the dorsal is slightly longer than the ventral. Metacarpal IV of MOZ 3625P is longer than half of the forearm. This last character differentiates it from non-pterodactyloid pterosaurs, in which this bone is shorter than half the length of the forearm, and relates it to the Pterodactyloidea, in which it is longer than half the forearm. Likewise, it differs from the large Cretaceous forms because in these, metacarpal IV is longer than the whole forearm (Wellnhofer, 1978; Bennett, 2001). This general trend is seen in the relationships of several wing bones; mcIV tends to increase in size, reaching its maximum in nyctosaurids (Kellner, 2003).

The right wing on slab preserves the first phalanx of digit IV. Phalanx I consists of a strong proximal articulation formed by two cavities to receive the distal end, a distinctive pulley of mcIV (Wellnhofer, 1991b). At this end, the phalanx extends the extensor tendon process. This process develops from a secondary ossification center (Bennett, 2001) and commonly is not fused to the shaft of phalanx I in immature specimens; in adults, the fusion is complete, and all the suture traces are obliterated. In MOZ 3625P, this process is totally fused to the phalangeal shaft, suggesting that this specimen was osteologically mature. From the expanded proximal end of phalange I, the shafts decrease in diameter and are relatively constant toward the distal end. The distal end is convex and articulates with the concave face of phalanx II. The thin incomplete elements exposed on both slabs belong to wing phalanges II and III, probably of the left wing. The first three phalanges of the wing finger have straight shafts.

One phalanx of the manual digit I–III? is preserved in the counterslab. The proximal end is more expanded than the distal one, and its shaft is slightly curved. A strongly curved ungueal phalanx is also preserved isolated in the counterslab, though it is uncertain to which manual finger it belonged. This phalanx is lateromedially compressed and has a moderate flexor tubercle on the side. It is larger and stronger than the pedal phalanges preserved in the slab.

4.2.2. Pelvic girdle and hindlimb

The left pelvic girdle is preserved in the counterslab and exposed in lateral view. The ilium is anteroposteriorly elongate. The anterior end is very long and somewhat compressed dorsoventrally. Behind the anterior extension lies the middle region of the ilium, which forms the upper margin of the acetabulum. The postacetabular process is lateromedially compressed, and its dorsal margin is almost straight. This process is shorter, more robust, and higher than the preacetabular process.

The pubis, dorsoventrally elongate, lies anterior to the ischium. In lateral view, the dorsal margin of the pubis is robust and massive, articulating with the ventral margin of the ilium. It is slightly concave, and its ventral margin forms a narrow, convex surface for the articulation with the prepubis.

The ischium is larger than the pubis and forms most of the pelvic girdle. The posterodorsal margin is concave and caudally inclined. The ventral margin is very convex, ending in a caudally convex point. The pubis and ischium form a completely enclosed lateral puboischiadic plate without sutures, an ontogenetic character seen in mature pterosaurs (Wellnhofer, 1978, 1991b) except for a tapejarid pelvis (AMNH 22569) with a lateral opening. This feather, however, has been considered of systematic significance (Kellner, 1995; Kellner and Tomida, 2000). The fact that the right pelvic plate is preserved disarticulated suggests it was unfused from the sacrum, a condition that could indicate immaturity (Dalla Vechia, pers. obs.). The acetabulum, oriented laterally, is formed by the three bones of the pelvis. It is subcircular and not perforated, as in all pterosaurs (Wellnhofer, 1978). The obturator foramen lies ventral to the acetabulum. The prepubis has not been preserved.

The femur is a long, thin bone with a conspicuous head and short neck. The femoral head is well rounded and directed medially to articulate with the acetabulum (Bennett, 2001). The neck is oriented anteromedially some 110° with respect to the shaft of the femur. The shaft is straight in cranial view. The trochanter major is at the end of the neck, where it contacts the shaft. The trochanter minor is not clearly observed. At the distal end, the medial and lateral condyles seem well ossified.

The tibia has a straight shaft, wider proximally than distally. Its diameter becomes smaller for one-quarter of the length, and then is constant up to the distal end. The tibia and proximal tarsals are fused (Wellnhofer, 1978; Bennett, 2001); the fibulae are not preserved. In MOZ 3625P, the proximal tarsals seem fused to the tibia, but this region cannot be seen clearly. The distal tarsals are also badly preserved.

The left foot is incompletely preserved on slab. It lacks metatarsal V, and the other four metatarsals are heaped. One is complete and articulates with three delicate phalanges (including the ungueal); consequently, it is probably finger II. The ungueal phalanges are smaller than the manual and almost straight. They have no prominent flexor tubercles.

5. Discussion

The well ossified ends of the long bones (e.g. humerus, radio, ulna, femur, tibia); the proximal and distal carpals forming proximal and distal sincarpi, respectively; the extensor tendon process fused to the shaft of the wing phalange I; the scapula fused to coracoid without suture; and the pelvic elements co-ossified without suture all suggest that the specimen was osteologically mature. However, the presence of a pelvic plate that is not fused to the sacrum and open neurocentral sutures in at least one of the dorsal vertebrae indicate that MOZ 3625P still retained some juvenile traits at the time of its death. The incompleteness of wing phalanges II and III and absence of the wing phalange IV make direct measure of its wingspan impossible. This value was calculated using the wing phalanges of an adult specimen of *P. antiquus* (BSP 1968 I 95, whose wingspan is 510 mm; Wellnhofer, 1970). The phalange proportions of *P. antiquus* are 1.00:0.92:0.86:0.68, which suggest a wingspan of 1097.4 mm for MOZ 3625P. Similar extrapolations based on a relatively mature *Pterodaustro guinazui* individual (MHIN-UNSL-GEO-V 243, wingspan 1590 mm) result in similar wingspan values (i.e. 1057.5 mm) for MOZ 3625P. These data suggest that MOZ 3625P was a specimen whose wingspan approached 1.10 m.

The absence of ribs on the midcervical vertebrae, the metacarpal IV length more than 80% the humerus length, the ulna/metacarpal ratio (<2), and the femur/metacarpal IV ratio (≤ 1) all support the assignment of MOZ 3625P to the Pterodactyloidea (sensu Kellner, unpublished, 2003). Within this clade, MOZ 3625P is interpreted as closely related to the basal pterodactyloid clade Archaeopterodactyloidea (sensu Kellner, 2003) because of the presence of a proximally placed and ventrally curved deltopectoral crest of the humerus, elongated middle vertebrae (though not to the same degree as in azdarchids), and low and blade-like neural spines of the middle cervicals.

However, the precise systematic position of MOZ 3625P within basal pterodactyloids (*Pterodactylus*, *Ctenochasma*, *Pterodaustro*, *Cycnorhamphus*, *Germanodactylus,* and *Gallodactylus canjuersensis*) remains uncertain; key characters belonging to the skull and other parts of the skeleton are not preserved. Its affinities to other pterosaurs from the Neuquén Basin are also uncertain. MOZ 3625P shares with *Herbstosaurus pigmaeus* a very small angle of the head of the femur (approximately 100° with respect to the axis of the shaft in *Herbstosaurus*), but the latter is too incomplete to be able to establish additional comparisons, as is also the case for the isolated tibia (MOZ 2280P) reported by Gasparini et al. (1987, Fig. 1) from Los Catutos.

The discovery of MOZ 3625P adds significant new information to the poorly known record of South American Jurassic pterosaurs—the new fossil is the most complete Jurassic pterosaur known thus far from this continent.

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