



FORELIMB POSTURE IN *CHILESAURUS DIEGOSUAREZI* (DINOSAURIA, THEROPODA) AND ITS BEHAVIORAL AND PHYLOGENETIC IMPLICATIONS

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Abstract. Many dinosaur skeletons show evidence of behavior, including feeding, predation, nesting, and parental care. The resting posture of the forelimbs has been studied in some theropod species, in relation to the acquisition of flight in advanced maniraptoran theropods. *Chilesaurus diegosuarezi* is a bizarre tetanuran recently described from the Toqui Formation (latest Tithonian) of southern Chile that is represented by multiple well-preserved and articulated specimens. The aim of the present work is to analyze the forelimb posture of four articulated specimens of *Chilesaurus diegosuarezi*, focusing on its anatomical description, and phylogenetic and behavioral implications. All the preserved specimens show strongly ventrally flexed arms with the hands oriented backwards, an arrangement that closely resembles those in dinosaur specimens previously described as preserving resting posture, such as *Mei long*, *Sinornithoides youngi* and *Albinykus baatar*. As a result, it seems that individuals of *Chilesaurus diegosuarezi* have been in passive activity (e.g. feeding, resting) when they were buried quickly, allowing their fossilization in life position and preserving the forelimb resting posture. The arrangement of the forelimb bones in *Chilesaurus* could show the first evidences of the structures linked to the muscles that flex the forearms, features related with the acquisition of flying control in advanced maniraptorans.

Key words. Forelimb resting posture, soft tissue, flexion, flight evolution.

Resumen. POSTURA DE LAS EXTREMIDADES ANTERIORES EN *CHILESAURUS DIEGOSUAREZI* (DINOSAURIA, THEROPODA) Y SUS IMPLICANCIAS FILOGÉNICAS Y DE COMPORTAMIENTO. Muchos esqueletos de dinosaurios muestran evidencias de comportamiento, incluyendo alimentación, depredación, anidación y cuidados parentales. La posición de reposo de los miembros anteriores ha sido estudiada en algunos terópodos, particularmente en relación con la adquisición del vuelo en maniraptores derivados. *Chilesaurus diegosuarezi* es un extraño tetanuro recientemente descrito, proveniente de la Formación Toqui (Titoniano superior) del sur de Chile, el cual se encuentra representado por varios especímenes bien preservados y articulados. El objetivo de este trabajo es analizar la postura de los miembros anteriores de cuatro especímenes articulados de *Chilesaurus diegosuarezi*, focalizando en su descripción anatómica, y las implicancias filogenéticas y de comportamiento. Todos los especímenes conservados muestran brazos fuertemente flexionados ventralmente, con las manos orientadas hacia atrás, una posición muy similar a la que ha sido reconocida como postura de reposo en ejemplares de dinosaurios descritos previamente, como *Mei long*, *Sinornithoides youngi* y *Albinykus baatar*. Como resultado, es posible que los individuos de *Chilesaurus* hayan estado en actividad pasiva (por ejemplo, alimentándose o descansando) cuando fueron sepultados rápidamente, permitiendo su fosilización en posición de vida y preservando una posición de reposo de los miembros anteriores. La disposición de los huesos de los miembros anteriores de *Chilesaurus* podría mostrar las primeras evidencias sobre la presencia de estructuras vinculadas a los músculos que flexionan los brazos, rasgos relacionados con la adquisición del control del vuelo en maniraptores derivados.

Palabras clave. Miembros anteriores, postura de reposo, tejido blando, flexión, evolución del vuelo.

MANY dinosaur skeletons show evidence of behavior, including feeding, predation, nesting, and parental care (Dong and Currie, 1995; Norell *et al.*, 1995; Varricchio *et al.*, 1997; Carpenter, 1998; Clark *et al.*, 1999; Zhou and Zhang, 2002; Grellet-Tinner *et al.*, 2006; Erickson *et al.*, 2007; O'Connor *et al.*, 2011). A unique kind of resting posture has been recognized as shared by living birds (Wing, 1956) and some non-avian theropods and basal dinosaurs (Xu and Norell, 2004; Nesbitt *et al.*, 2011; Agnolín and Martinelli, 2012). This interpretation was reached after analyses based mainly on the posture in which some fossil dinosaur skeletons have been preserved. Particularly, the resting posture of the forelimbs has been studied in theropod species, in relation to the acquisition of flight in advanced maniraptoran theropods (Sereno and Chenggang, 1992; Carpenter, 2002; Senter and Robins, 2005; Senter, 2006a, b; Fowler *et al.*, 2011; White *et al.*, 2015) and some of them focused on the relationship between bones with feathers or soft tissues (Garner *et al.*, 1999; Xu, 2006; Xu *et al.*, 2014, 2015).

Chilesaurus diegosuarezi Novas *et al.* (2015) is a bizarre tetanuran recently described from the Toqui Formation (latest Tithonian) of southern Chile (De la Cruz and Suarez, 2006; Salgado *et al.*, 2008). This species is represented by the holotype, which is a nearly complete skeleton, and several other partial skeletons. All these specimens are articulated and preserve evidence about the posture of the limbs. The aim of the present work is to study the posture of four articulated specimens of *Chilesaurus diegosuarezi*, focusing in the anatomical description of the resting pose of the forelimbs and their phylogenetic and behavioral implications.

MATERIALS AND METHODS

We analyze the resting posture of *Chilesaurus diegosuarezi* based on four specimens housed at the Servicio Nacional de Geología y Minería of Chile (SNGM): **SNGM-1935** (holotype), a nearly complete skeleton only lacking several skull bones, distal caudal series, and feet; **SNGM-1936**, complete and articulated forelimbs, nearly complete left ilium, incomplete right ilium, both pubes and ischia, right astragalus, and right metatarsals; **SNGM-1937**, associated forelimbs, left hindlimb, and incomplete right distal ends of tibia and fibula; and **SNGM-1938**, both forelimbs with incomplete hands, left and right scapula and coracoids, and

nearly complete dorsal vertebral series and articulated ribs.

All the specimens were collected in the lower beds of Toqui Formation, which crops out in the mountains flanked by the Maitenes and Horquetas rivers, south of Lago General Carrera (De la Cruz and Suárez, 2006; Salgado *et al.*, 2008). The specimens mentioned above were found and collected in natural articulation in the field. Here we describe these specimens of *Chilesaurus* as they were originally preserved in the field, before mechanical disarticulation, but the joint motion could not be analyzed in detail.

The relative position and orientation of the bones is described with respect to the main anteroposterior axis of the backbone (see Gatesy and Baier, 2005; Baier *et al.*, 2013), and is referred along the text as the “main body axis”.

DESCRIPTION

SNGM-1935. The holotype specimen lacks information of the posterior autopodial elements and some cranial bones. However, the rest of the skeleton is almost complete (see Figure 1). The preservation of each bone is affected by weathering and abrasive preparation techniques, but lacks any sign of post-mortem transport and taphonomical deformation is nearly absent. A slight taphonomical flattening is seen on the left anterior side, where the shoulder girdle is attached to the vertebral column. Indeed, the skeleton is relatively intact, with most of the bones preserved in tight articulation. The few cranial bones are preserved disarticulated, but associated to each other. The neck is almost complete, with several cervical vertebrae articulated. The forelimbs are flexed and laterally located with respect to the main body axis. The humerus and radius-ulna are in the same plane forming an angle of 80° between them. The right humerus is posterolaterally extended and the radius-ulna is anterolaterally oriented with respect to the main body axis. The right manus is medioventrally and posteriorly oriented. The hand is immediately ventral to the radius-ulna. The angle of flexion of the wrist with the forearm is very acute, nearly 20°. The left humerus and radius-ulna are in very similar position to the right forelimb. The hindlimbs are slightly flexed, and posteriorly directed, with the femora located sub-parallel to the pelvic girdle and the tibia-fibula dorsally flexed.

SNGM-1936. The pelvic girdle and hindlimb bones are associated but disarticulated. However, the elements of the left

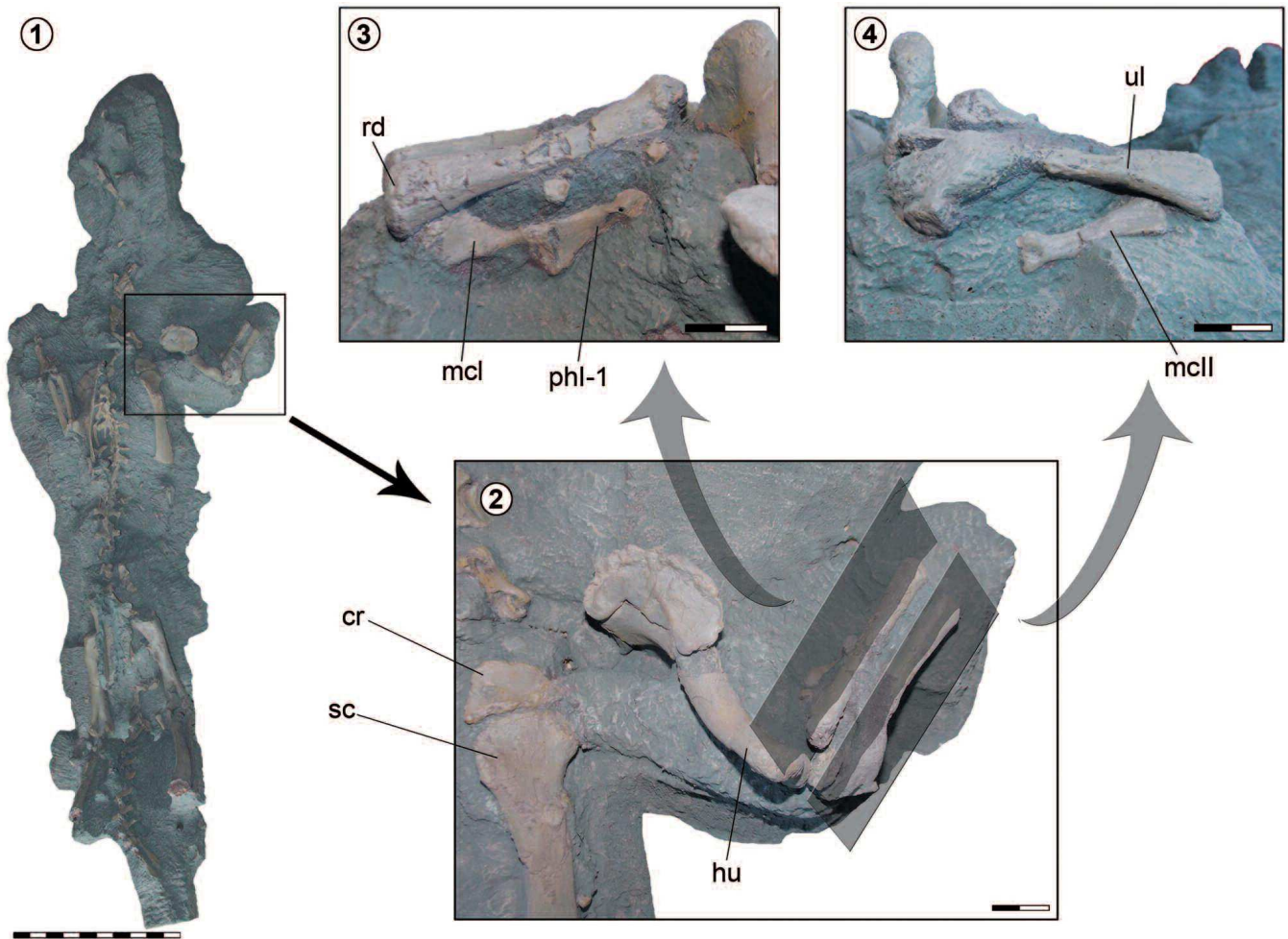


Figure 1. Cast of SNGM-1935 specimen (holotype) of *Chilesaurus diegosuarezi*. 1, Skeleton in dorsal view; 2, detail of the right forelimb in dorsal view; 3, detail of right hand in posterolateral view; 4, detail of right hand in anteromedial view. Abbreviations: cr, coracoid; hu, humerus; mcl, first metacarpal; mcll, second metacarpal; phl-1, first phalanx of the first digit; rd, radius; sc, scapula; ul, ulna. Scale bar in 1 = 200 mm; scale bar in 2, 3 and 4 = 20 mm.

forelimb are articulated and in life position, preserving their relationship with the dorsal column and allowing the orientation of the bones (Figure 2). Only the distal end of the humerus is preserved in articulation with the radius-ulna. The humerus is posterolaterally oriented in dorsal view, with respect to the main body axis. The elbow is more flexed than in the holotype. The radius-ulna is weathered and forms an angle of 70° with the humerus. These elements are anteroventrally oriented with respect to the body axis. As a result, the angle between the humerus and radius-ulna is observed in lateral view. In lateroventral view, the main axis of the metacarpus forms an acute angle (approximately 45°) with the radius-ulna. The main axis of the hand is posteriorly oriented relative to the main body axis, and as a consequence the palmar surface faces dorsally.

SNGM-1937. This specimen has only the coracoids and forelimbs preserved in articulation (Figure 3), but the right coracoid and humerus are twisted backwards. The left coracoid shows a posteriorly oriented scapular facet. The humerus is lateroventrally and posteriorly oriented with respect to the main body axis. In anterodorsal view, the angle between the humerus and radius-ulna is acute, near 40° . The elbow shows a stronger flexion than in the holotype and SNGM-1936. The radio-ulna is medioventrally and anteriorly oriented respect of the main body axis. The major axis of the hand is ventrally oriented relative to the main body axis. In this position, the wrist is not as flexed as in the above-described specimens, showing an angle of 60° . The palmar surface of the hand is posteriorly oriented, with respect to the main body axis.

SNGM-1938. This specimen preserves part of the dorsal vertebrae, ribs, shoulder girdle, and forelimbs in articulation. All elements show less weathering and post-mortem deformation than the holotype, and only a slight torsion of the

posterior dorsal vertebrae is observed (Figure 4). The dorsal vertebral column is parallel to each scapular blade. The left humerus is posterolaterally oriented respect of the main body axis and the radius-ulna are perpendicular to it. The elbow shows the same angle as the right forelimbs of the holotype. The left and right manus are incomplete, but the preserved metacarpals are placed parallel and ventral to the ulna, in the same position as the right manus of the holotype. This suggests that the hands would have been under the trunk and posteromedially oriented with respect to the main body axis, as in the holotype.

DISCUSSION

All the specimens of *Chilesaurus* showed a similar position and arrangement of the forelimb bones, being notably flexed. The position of the forelimb elements of *Chilesaurus* resembles previous descriptions for resting posture in some dinosaurs, mainly derived coelurosaur theropods, such as *Mei long*, *Sinornithoides youngi*, and *Albinykus baatar* (Xu and Norell, 2004; Nesbitt *et al.*, 2011). The resting posture has been described in coelurosaur theropods as the body resting on its symmetrically folded hindlimbs, the forelimbs vertically flexed and laterally extended with the elbows slightly displaced laterally, and the neck curved posterolaterally to the left side of the body (Xu and Norell, 2004). This posture was reported by the first time in a non-coelurosaurian dinosaur by Agnolín and Martinelli (2012) for the early saurischian *Guaibasaurus candelariensis*, and these authors also described a similar pattern in the non-dinosaurian ornithodirans *Saltopus* and *Scleromochlus*. In concordance with resting posture, the four specimens of *Chilesaurus* here described have the forelimbs ventrally flexed and with the hands oriented backwards, similar to the resting pattern of Aves (Wing, 1956) and the taxa mentioned above (Xu and Norell, 2004; Nesbitt *et al.*, 2011; Agnolín and Martinelli, 2012). However, the hindlimb position of *Chilesaurus* is inconsistent with this pattern, because the hindlimbs are posteriorly extended respect of the main body axis, rather than ventrally flexed. It is possible that the flexed position of the forelimbs in *Chilesaurus* not necessarily implies a sleeping behavior at the moment of death. Rather, this position seems to show a passive forelimb activity following previous studies of standard theropod resting posture (Senter and Robins, 2005; Milner

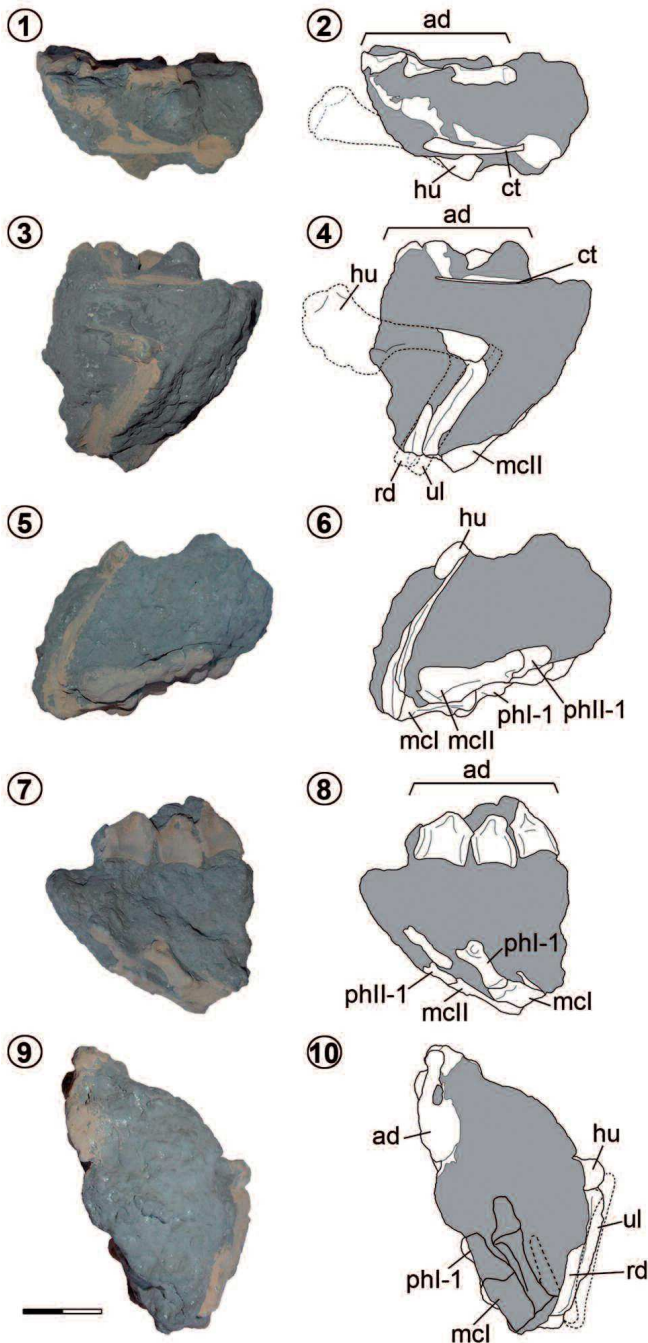


Figure 2. Cast of SNGM-1936 specimen of *Chilesaurus diegosuarezi* and drawings. 1–2, Dorsal view; 3–4, lateral view; 5–6, lateroventral view; 7–8, medial view; 9–10, anterior view. Abbreviations: **ad**, anterior dorsal vertebrae; **hu**, humerus; **mcl**, first metacarpal; **mcll**, second metacarpal; **phl-1**, first phalanx of the first digit; **phll-1**, first phalanx of the second digit; **rb**, rib; **rd**, radius; **ul**, ulna. Scale bar= 20 mm.



Figure 3. Cast of SNGM-1937 specimen of *Chilesaurus diegosuarezi*. 1, dorsal; 2, lateral; 3, anterolateral view. Abbreviations: cr, coracoid; ha, hand; hu, humerus; mcIII, third metacarpal; rd, radius; sc, scapula; ul, ulna. Arrows indicate anterior direction. Scale bar= 20 mm.

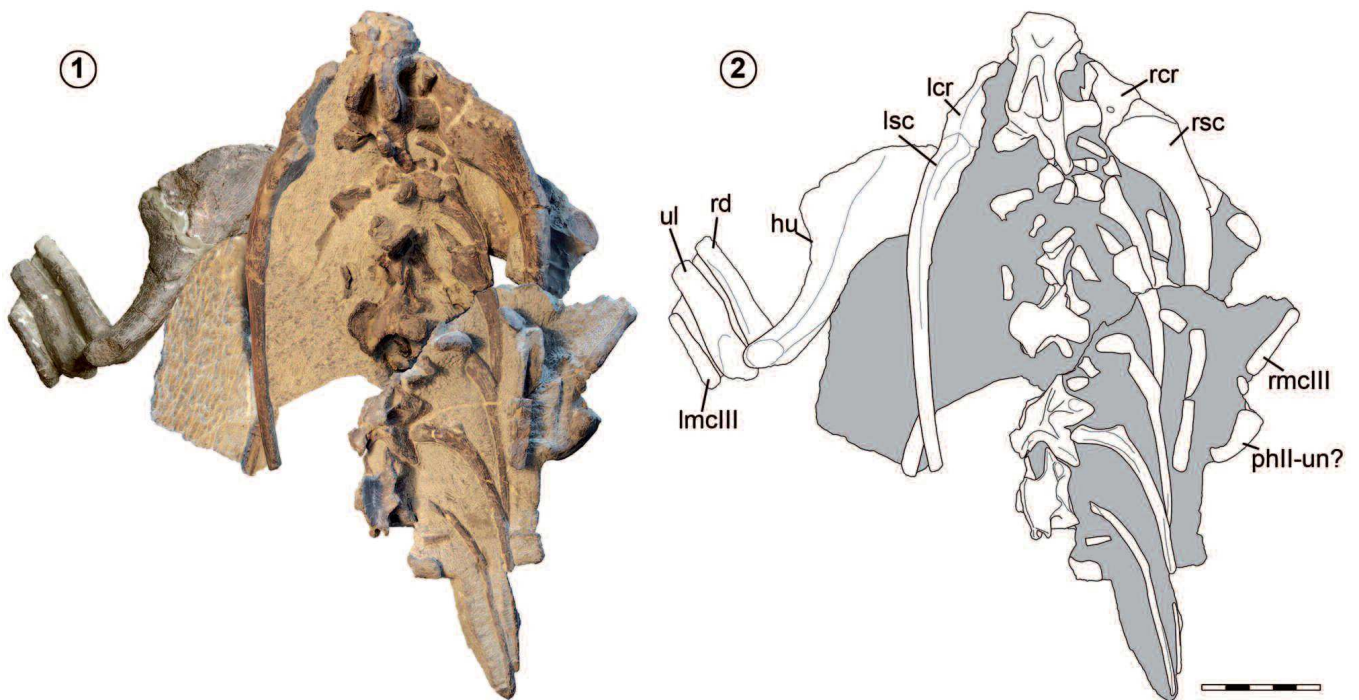


Figure 4. SNGM-1938 specimen of *Chilesaurus diegosuarezi* in dorsal view. 1, photograph; 2, drawing. Abbreviations: hu, humerus; lcr, left coracoid; lmcIII, left third metacarpal; lsc, left scapula; phII-un?, probable unguis phalanx of the second digit; rcr, right coracoid; rd, radius; rmcIII, right third metacarpal; rsc, right scapula; ul, ulna. Scale bar= 20 mm.

et al., 2009). In this aspect, the acute angles between the humerus and the radio-ulna and between the radio-ulna and manus could indicate the presence of a strong limitation to anterior extension of the forelimbs, as noted for other theropods (Senter and Robins, 2005). The specimen SNGM-1937 shows an angular relation in the wrist that resembles that in *Deinonychus* (Gishlick, 2001; Carpenter, 2002). In fact, numerous coelurosaurs have the same

resting position as the forelimbs of *Chilesaurus*, with the humerus and radius-ulna in perpendicular relation or elbow flexed in an acute angle, manus under the radius-ulna, and palmar surface posterodorsal and dorsomedial oriented with respect to the main body axis (e.g. *Balaur*, *Hexing*, *Sinornithosaurus*, *Sinosauropteryx*, *Anchiornis*, *Microraptor* and *Xiaotingia*, described by Xu *et al.*, 1999; 2000; 2011; Liyong *et al.*, 2012 and Brusatte *et al.*, 2013).

The position of folded versus extended forelimb is an interesting topic in theropod evolution. Several authors have suggested that the presence of many avian traits in the forelimb bones are related with soft structures, as patagial skin and muscles, present in several maniraptoran dinosaurs (Sereno and Chenggang, 1992; Xu *et al.*, 2014). Hopp and Orsen (2004) suggested that the forelimb folded structure in advanced theropods could be a consequence of the need to manage the evolving set of brooding forelimb feathers. Chatterjee and Templin (2004) related the swivel wrist joint with climbing behavior. Maniraptorans and some other tetanurans possess a relatively large degree of forearm flexion, though many appear to have been non-flying species (Novas and Puerta, 1997; White *et al.*, 2015), resembling the condition described here in *Chilesaurus* (see Figure 5). Xu *et al.* (2014) mentioned that a three-fingered hand (TFH) with initial laterally folding capability (LFC) may be a synapomorphy of Tetanurae, while the extended forelimbs were considered a plesiomorphic condition for Theropoda (see Sereno, 1993; Xu *et al.*, 2014). However, presence of partially folded forelimbs in *Guaibasaurus* may

suggest that such condition may be more widespread than previously thought (Agnolin and Martinelli, 2012). In this sense, folded limbs were also presumably present in crocodile-line archosaurs, as proposed by Hutson and Hutson (2014).

The cojoined flexion of wrist and elbow in living birds was studied in detail by Vazquez (1992, 1994). This author concludes that this flexion is mainly conducted by the action of a large number of tendons located within the propatagium. The existence of propatagium was considered unique to modern birds (Vazquez, 1994), but recently, Agnolin and Novas (2013) and Feduccia and Czerkas (2015) found that it was more widespread than previously thought among coelurosaurs. In this regard, Feduccia and Czerkas (2015) considered that because a propatagium must be exclusively linked with aerodynamic adaptations, its presence in non-volant taxa as *Caudipteryx* may necessarily represent a secondary derived flightless condition. Because the propatagium controls the flexion of wrist and elbow, the preserved flexed forearm in *Chilesaurus* may be also regarded as an indirect indication of the presence of propatagium in

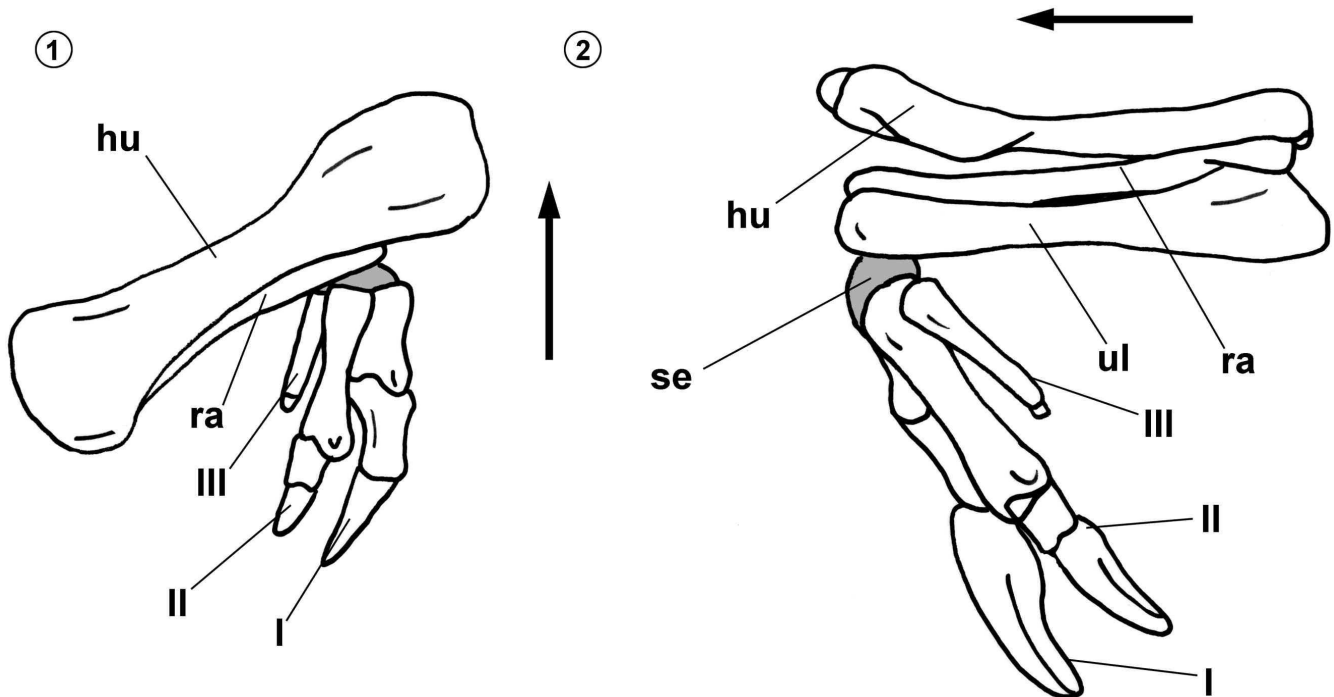


Figure 5. Illustration showing the degree of flexion of the left forelimb in *Chilesaurus diegosuarezi*. 1, dorsal view with the hand exposed in palmar view; 2, lateral view. The arrows points anteriorly. Abbreviations: hu, humerus; ra, radius; se, semilunar; ul, ulna.

this taxon. This suggests that presence of propatagium was not only more widespread than previously thought, but also that it is not uniquely related to flight capabilities. The propatagium and related structures have also been described for Pterosauria (Wang *et al.*, 2002; Frey *et al.*, 2003; Wilkinson, 2007; Bennet, 2008; Kellner *et al.*, 2010). More recently, Hutson and Hutson (2014) in a detailed analysis also sustained that crocodiles also exhibit automatic wrist folding guided mainly by soft tissues (see also Walker,

1972). These authors propose that the capability of automatic wrist folding was probably plesiomorphic for crocodile-line archosaurs. This opens interesting questions regarding the origin of forelimb folding in archosaurs. Summarizing, on the basis of evidence published by previous works and the present contribution, it is possible to infer that the presence of soft structures related to automatic folding of the forelimbs may be more widespread than suspected (Figure 6).

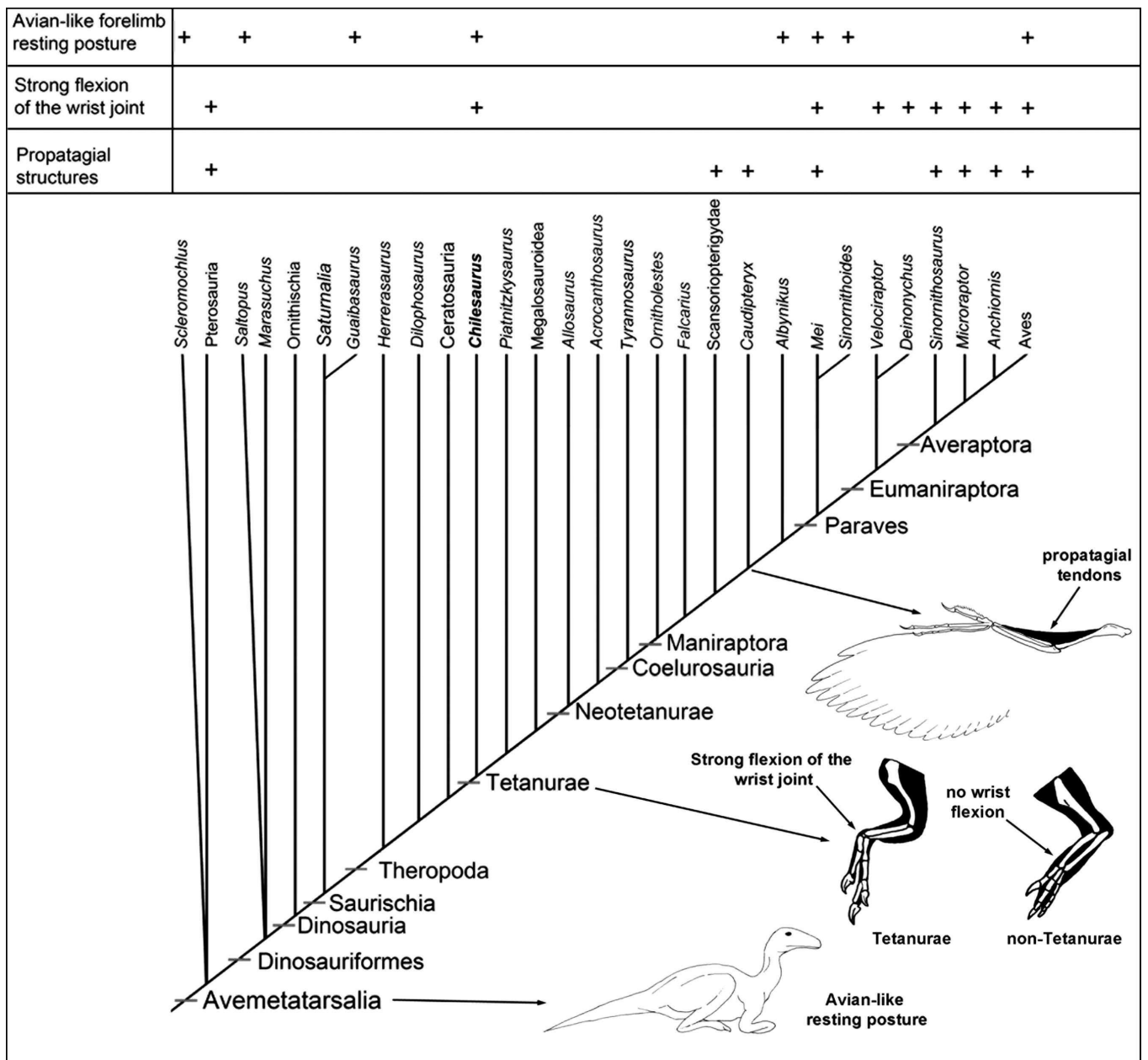


Figure 6. Phylogenetic relationships of *Chilesaurus diegosuarezi* within Avemetatarsalia showing the distribution of an avian-like forelimb postures and propatagial structures (modified from Martínez *et al.*, 2011; Porfiri *et al.*, 2014; Agnolin and Novas, 2013; Novas *et al.*, 2015).

CONCLUSIONS

All the specimens of *Chilesaurus diegosuarezi* described here present the forelimb elements arranged following a resting posture. Thus, it seems that the specimens of *Chilesaurus* were buried quickly and fossilized almost in life position during passive activity (e.g. feeding, resting). The position of the forelimb bones in *Chilesaurus* may show the first evidences of the structures linked to the muscles that flex the forearms, features related with the acquisition of flying control (Vazquez, 1994; Agnolín and Novas, 2013).

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