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Reassessment of *Prejanopterus curvirostris*, a Basal Pterodactyloid Pterosaur from the Early Cretaceous of Spain

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Abstract: *Prejanopterus curvirostra*, from the Early Cretaceous of La Rioja province, was the first pterosaur genus and species described from Spain. The material comprises disarticulated cranial and postcranial remains from several individuals. The fossil-bearing bed is assigned to the lacustrine Leza Formation (eastern Cameros Basin, NW margin of the Iberian Range). This unit is regarded as either Berriasian-Valanginian or Barremian-Aptian. *Prejanopterus curvirostris* (specific name emended) was originally diagnosed on the basis of several characters of which the most significant was a lateral curvature of the rostrum. Re-examination of the holotype (rostrum) and paratype (partial rostrum with teeth) indicates that there is no genuine sideways bend of the preserved premaxilla-maxilla segments, but a slight dorsal curvature. *Prejanopterus* is characterized by a unique combination of characters: an emended diagnosis is provided. In contrast with previous estimates, the wing span of *Prejanopterus* was probably not much (if ever) in excess of 2 m. A phylogenetic analysis suggests that *Prejanopterus* is a basal pterodactyloid positioned between *Pterodactylus* and *Cycnorhamphus-Gallodactylus*. *Prejanopterus* represents the first evidence of Pterodactylidae in the Early Cretaceous of the Iberian Peninsula.

Key words: Pterosauria, *Prejanopterus*, Leza Formation, Early Cretaceous, La Rioja, Spain

1 Introduction

The fossil record of Spanish pterosaurs consists of skeletal remains and footprints (Barrett et al., 2008; Lockley et al., 2008; Holgado et al., 2011). Pterosaurian tracks are known from the Late Jurassic of Asturias (Lockley et al., 2008), the Jurassic-Cretaceous transition of Soria (Sánchez-Hernández et al., 2009 and references therein) and the Early Cretaceous of La Rioja (Moratalla and Hernán, 2009). With the exception of a wing phalanx from the Late Jurassic of Asturias, all other skeletal remains come from the Early and Late Cretaceous. Pterosaur sites are located in different basins of the Iberian Range and the Basque-Cantabrian Region (Holgado et al., 2011 and references therein). Ornithocheirids and the azhdarchid *Europejara olcadesorum* have been described from the Barremian Konservat-Lagerstätte of Las Hoyas in Cuenca province (Vullo et al., 2009b, 2012). Ornithocheirid remains are also known in the Albian of Castellón province (Company, 2007) and the Cenomanian of Asturias (Vullo et al., 2009a). Finally, azhdarchid material is present in the Campanian-Maastrichtian of Condado de Treviño and Valencia (Buffetaut, 1999; Company et al., 1999). Additional Cretaceous localities have yielded indeterminate pterodactyloid remains (see references in Holgado et al., 2011).

In Spain, the first pterosaur genus and species described was *Prejanopterus curvirostra* Fuentes Vidarte and

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Meijide Calvo (2010) from the Early Cretaceous of Préjano, in La Rioja province. This taxon was first mentioned, as "*Prejanopterus curvirrostra*" (with two r's), in an unpublished report (Fuentes Vidarte et al., 1999) and the name was used in a popular science book (Pérez-Lorente et al., 2001) and also in pamphlets (e.g., Grande, 2002). The fossils and a life restoration of the animal were exhibited in the Centro Paleontológico de Enciso (Pérez-Lorente et al., 2001: fig. 41); subsequent exhibitions toured several places of Spain, including La Rioja and Burgos provinces. After being a *nomen nudum* for a decade, the specimens were finally published by Fuentes Vidarte and Meijide Calvo (2010) as *Prejanopterus curvirostra*.

Following the Article 34.2 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999), the ending of the specific name *curvirostra* (feminine) should be corrected to make it agree in gender with the generic name *Prejanopterus* (masculine). Accordingly, the emended form *Prejanopterus curvirostris* is used herein; both the authors and date of the name remain unchanged (International Commission on Zoological Nomenclature: art. 50.3.2).

This taxon was described on the basis of disarticulated cranial and postcranial remains, housed in the Centro Paleontológico de Enciso, Enciso, Spain. Fuentes Vidarte and Meijide Calvo (2010) regarded *Prejanopterus curvirostris* as a member of Pterodactyloidea mainly characterized by a lateral curvature of the rostrum. The aim of this work is to reassess the diagnostic features of *Prejanopterus* and discuss its phylogenetic relationships.

Institutional abbreviation: CPE, Centro Paleontológico de Enciso, Enciso, Spain.

2 Geological Setting

The fossil remains of *Prejanopterus curvirostris* were discovered in 1980 and collected during 1993 and 1994 by a team of the Instituto de Estudios Riojanos conducted by Félix Pérez-Lorente (Universidad de La Rioja, Logroño) (Pérez-Lorente et al., 2001; Fuentes Vidarte and Meijide Calvo, 2010). The site, which is called Fuente Amarga, is located near the village of Préjano in La Rioja Province, Spain (Fig. 1).

Geologically, the Fuente Amarga site is assigned to the Leza Formation and lies within the northern sector of the eastern Cameros Basin (NW margin of the Iberian Range). The Cameros Basin was one of the several highly subsiding basins of the Mesozoic Iberian Rift System formed during Late Jurassic-Early Cretaceous times in response to extensional tectonics (Salas et al., 2001). The basin has been subsequently filled by several depositional sequences ranging from Tithonian to Albian, which consist predominantly of alluvial and lacustrine deposits (Mas et al., 2002; Doublet et al., 2003). The carbonate-dominated deposits of the Leza Formation are interpreted as coastal lacustrine systems with intermittent marine incursions from the Tethys Sea (Alonso and Mas, 1993). Indeed, in the Préjano sector, the limestones, dolostones and marls of the Leza Formation reflect a coastal-lake paleoenvironment filled with brackish water, as is indicated by the coexistence of abundant marine microfossils, such as dasycladal algae and benthic foraminifera, and charophytes (Suárez-González et al., 2011).

The pterosaur remains were found in the lower part of the Préjano section of the Leza Formation (facies association 2 in Suárez-González et al., 2011: fig. 2), which

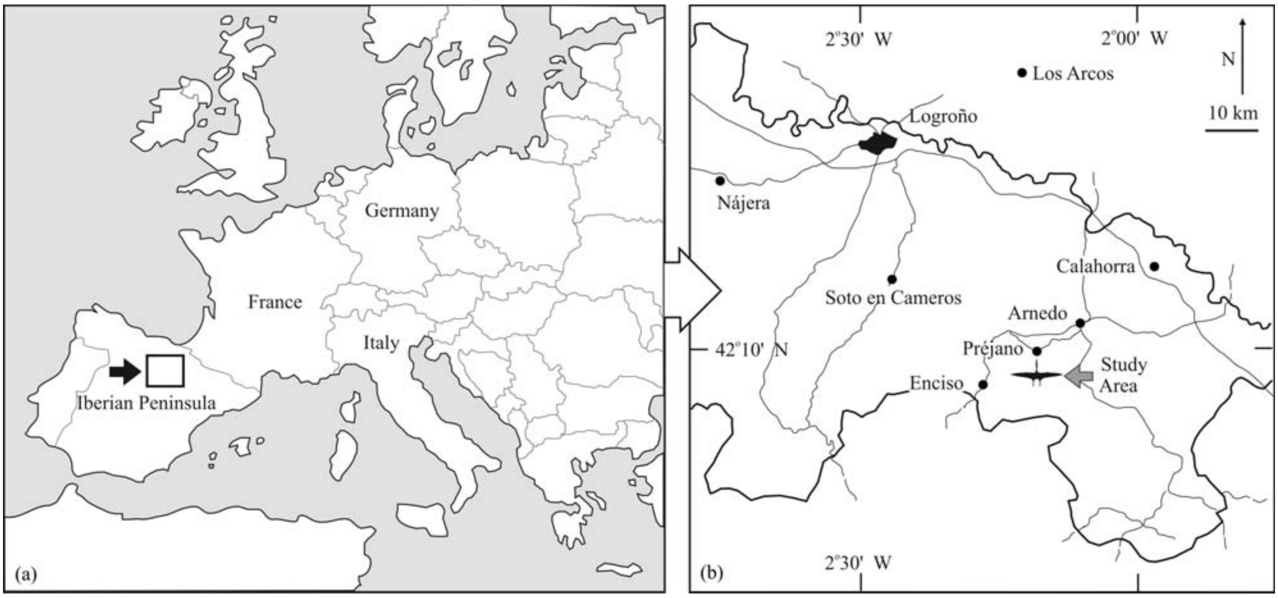

Fig. 1. Location map.

(a), general area of provenance of *Prejanopterus curvirostris* in La Rioja, Spain. Inset shows the position of the detailed map. (b), sketch map of La Rioja province showing the location of the collecting site (Fuente Amarga locality) in the vicinity of the village of Préjano.

is composed of black limestones and marls, organised into shallowing upward-coarsening sequences ranging from 2 to 4 m in thickness. The micritic limestones contain charophytes, ostracods, dasycladals, gastropods, remains of actinopterygian fishes, crocodyliforms and pterosaurs. Some reptile eggshell fragments have also been found (Suárez-González et al., 2011). The fossils are located at the bottom of a limestone bed.

The Leza Formation is generally regarded as Late Barremian-Early Aptian in age as part of the Enciso Group (SD7 of Mas et al., 2002, 2011) on the basis of the presence of the dasycladal species *Salpingoporella urladanasi* Conrad, Peybernès and Radoičić, 1977 (Suárez-González et al., 2011). However, the age of this formation remains controversial as the palaeontological content is rather poor. An older age has been suggested for the Leza Formation on the basis of both biostratigraphic (Hernández-Samaniego et al., 1990) and stratigraphic evidences (Doublet, 2004). On the basis of charophytes, Hernández-Samaniego et al. (1990) regarded this unit as Malm-Berriasian in age and consequently it was included in the Purbeck. According to S. Doublet (pers. comm. 2011), an angular discordance separates the Leza Formation from the Enciso Group in the Soto de Cameros sector and the Leza valley. Doublet (2004) interpreted the Leza Formation as forming part of the earlier Oncala Group and assigned to it a Berriasian-Valanginian age. Recently, Clemente (2011:108) also pointed out that the "stratigraphic position [of the Leza Formation] together with the facies associations and sedimentary environments, clearly favours an attribution to the Oncala Group". She dates the Oncala Group (made up of a total of eight formations including the Leza Formation) as Early-Middle Berriasian on the basis of its ostracod assemblage (Clemente, 2011: 115, 130).

3 Material

The Préjano material consists of a mixed assemblage of disarticulated cranial and postcranial remains from several pterosaur individuals. Most of the bones are preserved as incomplete or fragmentary elements. The fossils are preserved in a number of limestone blocks, with the exception of two of them (FA 185, paratype; and FA 29), which have been extracted from the rock. Although the bones show some degree of crushing, they are three-dimensionally preserved.

We interpret that the holotype, paratype and referred specimens of *Prejanopterus curvirostris* belong to a single species. The pterosaur remains from the Fuente Amarga site are quite homogeneous in size and the duplicate elements (mandible, metacarpal IV, femur) possess a similar or identical anatomy, with very little osteological variation. This indicates that the bones probably belong to the same species.

Fuentes Vidarte and Meijide Calvo (2010: appendix) identified 118 bones from a total of 186. However, some of the identifications made by these authors should be taken with considerable caution. For instance, Fuentes Vidarte and Meijide Calvo (2010) recognized at least four distinct individuals in the assemblage based on the presence of four left ulnae, but we were unable to confirm this. On the basis of the number of mandibles (three: FA 3, 160, 163) and the fact that they are comparatively smaller than the two incomplete rostrums (FA 185, paratype, being larger than FA 112, holotype), we estimate that the minimal number of individuals represented in the Préjano assemblage is five. The degree of ossification of the epiphyseal regions of the wing phalanges and pelvic elements of *Prejanopterus* suggests that the bones are those of subadult to adult individuals (Bennett, 1993; Kellner and Tomida, 2000), which is consistent with the results of a paleohistological analysis (see below).

4 Systematic Paleontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Pterodactylidae Bonaparte, 1838 *sensu* Knoll, 2000
Prejanopterus Fuentes Vidarte *et* Meijide Calvo, 2010

Type and only species: *Prejanopterus curvirostra* Fuentes Vidarte *et* Meijide Calvo, 2010

Prejanopterus curvirostris Fuentes Vidarte *et* Meijide Calvo, 2010 (specific name emended; International Commission on Zoological Nomenclature: art. 34.2)

Figs. 2-5

Chresonymies:

1999 *Prejanopterus curvirrostra* Fuentes Vidarte et al.: 28
2001 *Prejanopterus curvirrostra* Pérez-Lorente et al.: 49
2009 *Prejanopterus curvirrostra nomen nuda* (sic) Moratalla and Hernán: 71
2010 *Prejanopterus curvirostra* n. gen. et sp. Fuentes Vidarte and Meijide Calvo: 313

Holotype: FA 112, rostrum (Fig. 3; Fuentes Vidarte and Meijide Calvo, 2010: fig. 3a) on slab CPE/242-20a (see Appendix 1).

Paratype: FA 185, fragmentary rostrum (Fig. 4; Fuentes Vidarte and Meijide Calvo, 2010: figs. 4b-d), isolated from the matrix (slab CPE/242-22a+22c; see Appendix 1).

Referred material: see Appendix 1 (also Fuentes Vidarte and Meijide Calvo, 2010: Appendix II).

Type locality and horizon: Fuente Amarga site, near Préjano (La Rioja Province, Spain); Leza Formation, Lower Cretaceous, Upper Barremian-Lower Aptian

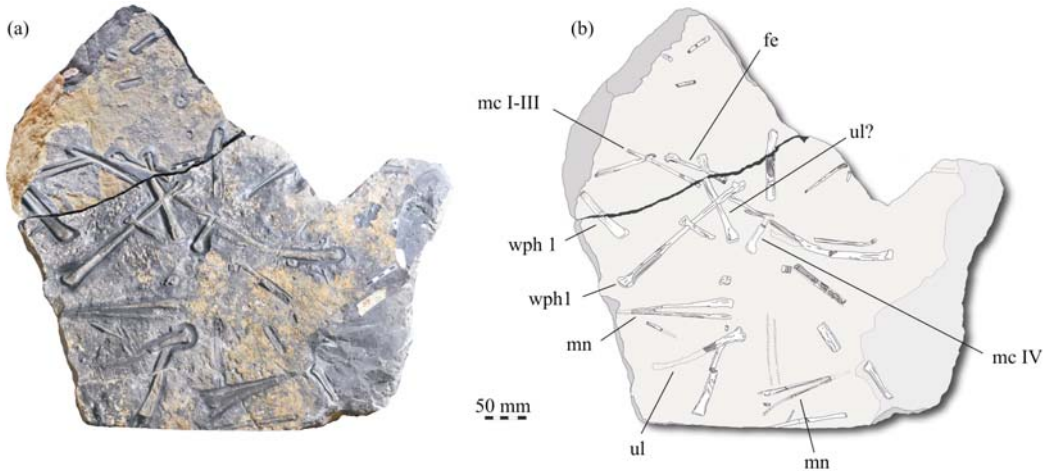

Fig. 2. *Prejanopterus curvirostris* from Fuente Amarga locality, La Rioja province, Spain.
(a), composite figure of slabs CPE/242-6a and CPE/242-6b showing the association of lower jaws and several appendicular elements. (b), schematic drawing. Abbreviations: fe: femur; mn: mandible; ul: ulna; ul?: possible ulna; mc IV: metacarpal IV; mc I-III: metacarpal I, II, or III; wph 1: wing phalanx 1. The remaining elements are mostly fragmentary limb bones, including wing phalanges. Scale bar = 50 mm.

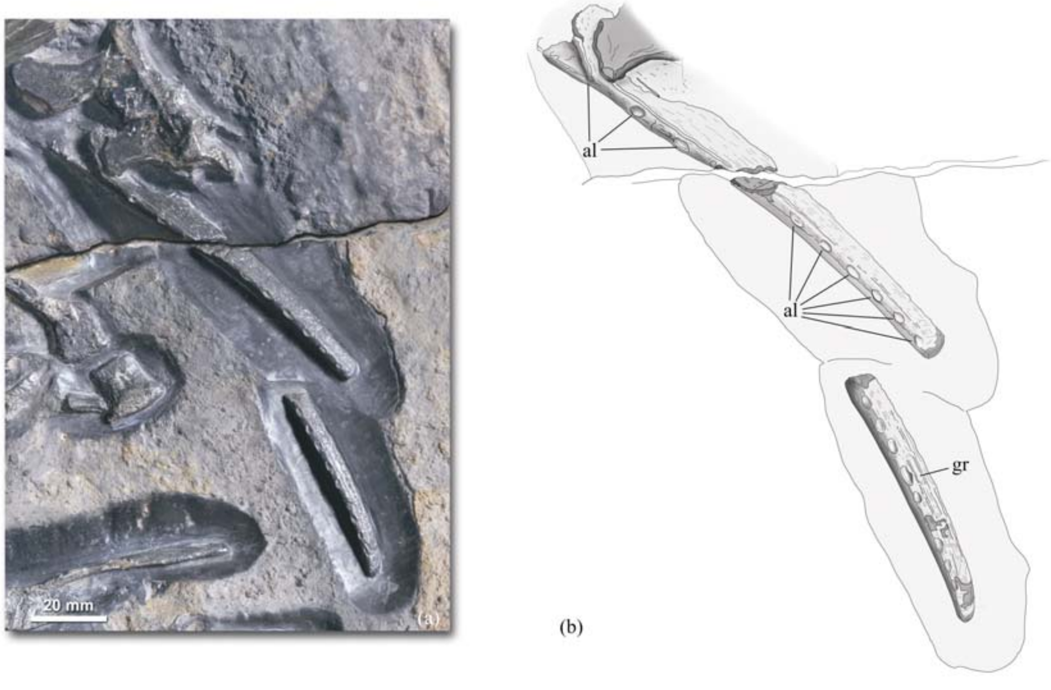

Fig. 3. *Prejanopterus curvirostris* from Fuente Amarga locality, La Rioja province, Spain.
Enlarged photograph (a) and interpretative drawing (b) of the slab CPE/242-20a containing the holotype rostrum (FA 112) in lateral-occlusal view. Abbreviations: al: alveoli; gr: groove. Scale bar = 20 mm.

(Enciso Group: Alonso and Mas, 1993; Suárez-González et al., 2011; Mas et al., 2011) or Berriasian-?Valanginian (Oncala Group: Doublet, 2004; Clemente, 2011; see also Hernández-Samaniego et al., 1990).

Revised diagnosis: Medium-sized pterodactyloid (wing span ranges from 1.5 to 2 m in adults) with the following unique combination of characters: upper jaw with a toothless tip (the edentulous region seems to be slightly greater than the space between two of the most rostral alveoli); small, subequal-sized and widely-spaced alveoli bearing blunt teeth (FA 185); subrectangular, longer than wide sternum; very elongate and spatulate prepubis; appendicular bones with relatively thick bone walls (radius/thickness of femoral cortex approximately 3.8 at midshaft).

5 Description

Cranial skeleton

Skull Skull remains consist of an incomplete rostrum (FA 112, holotype), a fragmentary rostrum (FA 185, paratype), and a fragment of braincase (FA 133). The quadrate and quadratojugal described by Fuentes Vidarte and Meijide Calvo (2010: fig. 4a) are actually a coracoid and a fragment of scapula (see below).

Rostrum (Figs. 3, 4). FA 112 consists of three fragments (preserved length 140 mm). The upper jaw is low and very elongate, with a gently dorsally concave outline. The length/maximum depth (or rostral index; see Martill and Naish, 2006) is greater than 14. At least 19 pairs of alveoli are preserved in the rostrum; the total number of alveoli is unknown as the caudal segment is distally damaged. As preserved, the rostral end of the rostrum is dorsoventrally compressed and laterally unexpanded. The tooth row does not extend to the tip of the rostrum (there is a small edentulous region, which seems slightly greater than the space between two of the rostralmost alveoli). The suture between the premaxilla and the maxillae is not obvious, so the occurrence of four premaxillary teeth, as described by Fuentes Vidarte and Meijide Calvo (2010), cannot be confirmed. The alveoli are small, oval, and widely spaced. The largest ones (between 3 and 4 mm in diameter) are located in the mid and caudal regions of the tooth row, whereas the smallest ones (approximately 2 mm in diameter) are those of the most rostral portion of the tooth row. Ventrally, there is a median, longitudinal groove.

FA 185 is a caudal fragment of rostrum (Fig. 4). In cross-section, the bone is triangular, more compressed laterally than dorsoventrally. As in FA 112, the dorsal margin is rounded and there is no evidence of a crest. A lateral groove indicates the suture between the maxilla and the premaxilla. A median groove is marked ventrally in the caudal portion. FA 185 preserves seven alveoli (with six *in situ* teeth, two of them hardly visible) in the right row and six alveoli (with two teeth) in the left row. The teeth are small, unicusped, and laterally compressed. As preserved, the teeth are conical and blunt. They are projected ventrolaterally.

FA 133 is considered to be the caudal portion of a braincase, including the occipital condyle. Other elements found in close proximity to FA 133 may be cranial remains as well, but an accurate identification is difficult because of the very fragmentary nature of the specimens.

Mandible (Figs. 2, 5a). Three mandibles have been recovered (FA 3, 160, 163). They are visible in ventral view. The mandibular symphysis is not preserved, but can be appraised due to impressions in the slabs (Fig. 5a). The symphysis is well-developed and forms at least 30% of the total length of the best preserved lower jaw (preserved length: 172 mm). The mandible is not expanded laterally and lacks a sagittal crest. No teeth were found associated to the lower jaws.

Axial skeleton

Vertebrae. Several vertebrae are known in the assemblage, but most of them are damaged or incompletely preserved (e.g., FA 80, which is a small dorsal vertebra, 18 mm in height). Some specimens described by Fuentes Vidarte and Meijide Calvo (2010) as carpal bones may actually be vertebral centra observed in ventral view (FA 26, 128, 129) or in lateral view (FA 71).

Pectoral girdle

Scapula and coracoid (Fig. 5b). A complete left coracoid (FA 114) and a fragment of scapula are known; these elements were originally interpreted as a quadrate and a fragment of quadratojugal (Fuentes Vidarte and Meijide Calvo, 2010: fig. 4a). As preserved in caudal view, the coracoid (length: 47.5 mm) is a slender bone that lacks a well-developed brachial flange. The articulation surface with the sternum is flattened, without a caudal expansion.

Sternum (Fig. 5c). FA 20 is the only known sternal bone. As preserved, it is remarkable in its subrectangular outline, much longer than wide (preserved length: 53 mm). The sternum bears a well-marked ventral keel. The cristospine is not preserved.

Forelimb

Humerus (Fig. 5c). FA 21 is an incomplete right humerus (preserved length: 80 mm). The proximal end and most of the deltopectoral crest are broken. The humeral shaft is straight and the distal end is D-shaped in articular view. An incomplete left humerus (FA 12), on the same slab as FA 21, has a relatively well-developed deltopectoral crest.

Radius and ulna. Fragmentary ulnae (FA 151, 161) have been recognized, but they are too incomplete for a detailed description. No radius was recognized with certainty.

Carpals and metacarpals. The presence of carpal bones cannot be confirmed. The metacarpus is represented by three metacarpals IV (FA 14, 69 and 158; see Figs. 2, 5e); all of them are incomplete (preserved length of the largest one: 190.5 mm). In addition, there are two incomplete metacarpals I/II/III (FA 148, preserved length: 133.5 mm; and FA 173).

Wing phalanges (Figs. 5d, e). At least four first phalanges of digit IV are present in the assemblage (FA 33, FA 47, from the right wing; FA 13, 154 from the left wing), but only one is complete (FA 154, length 235 mm; Fig. 5d). A complete fifth specimen (FA 99; preserved length: 228 mm) could be a second wing phalanx. In all specimens the extensor tendon process is fused to the proximal end (Fig. 5e), indicating that the phalanges belong to ontogenetically mature individuals (Kellner and Tomida, 2000). There is no evidence of a pneumatic opening on the proximal part. Other specimens possibly correspond to the second, third and fourth wing phalanges (Fig. 2), but the fragmentary nature of the fossils makes an accurate identification

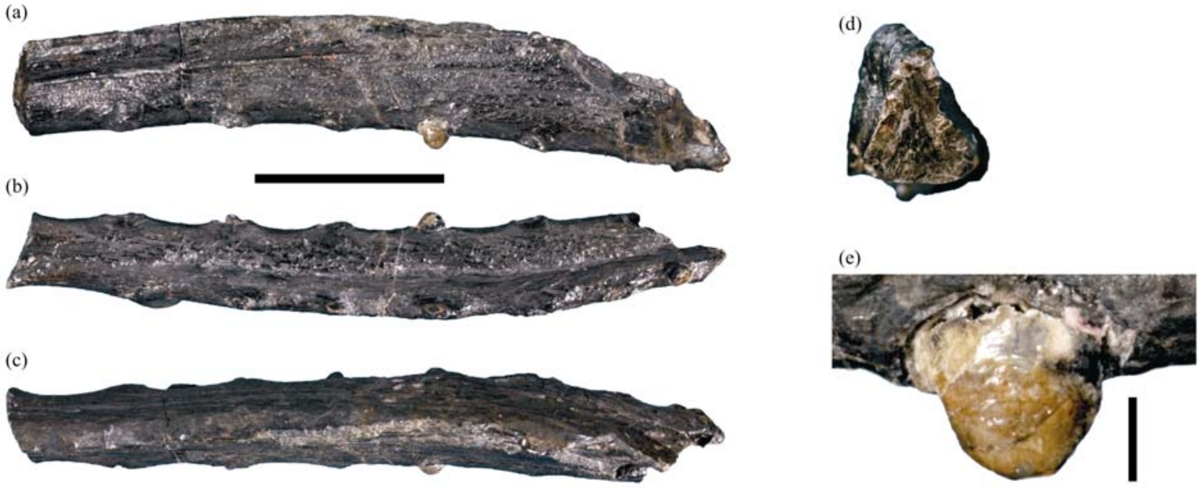

Fig. 4. *Prejanopterus curvirostris* from Fuente Amarga locality, La Rioja province, Spain.
Fragment of rostrum with teeth (FA 185) in left lateral (a), ventral (b), dorsal (c) and rostral cross-section (d) views. (e), detail of the largest preserved tooth. Scale bars = 20 mm (a-d) and 1 mm (e).

Fig. 5. *Prejanopterus curvirostris* from Fuente Amarga locality, La Rioja province, Spain.
(a) mandible (FA 163) in ventral view; (b) left coracoid and fragment of scapula (FA 114) in caudal view; (c) sternum (FA 20) in ventral view and right humerus (FA 21) in medial view; (d) phalanx 1 of wing digit IV (FA 154) in ventral view; (e) distal end of metacarpal IV (FA 14) in dorsal/ventral view, proximal end of phalanx 1 of left wing digit IV (FA 13) in ventral view, and left pelvic girdle (FA 50) in lateral view; (f) right femur (FA 29) in cranial and medial views and in cross-section; (g) left wing metacarpal (FA 69, misidentified as a tibia in Fuentes Vidarte and Meijide Calvo 2010: fig. 4E) in craniolateral view; (h) prepubis (FA 137) in lateral/medial view. Scale bars = 10 mm.

difficult. The phalanges lack a longitudinal ventral ridge.

Pelvic girdle and hindlimb

Ilium, ischium and pubis (Fig. 5e). A damaged left pelvis is preserved in lateral view (FA 50). All elements of the pelvis are fused together (preserved length: 48 mm). The preacetabular process of the ilium is oriented craniodorsally. Although incomplete, it appears to be longer than the postacetabular process. The postacetabular process of the ilium is short and relatively deep, with a convex dorsal margin and a concave ventral margin. The acetabulum is large and subcircular. The relationships between the pubis and ischium are difficult to discern; the presence of an ischiopubic plate is likely, but cannot be confirmed because of breakage. The cranial profile of the pubis in lateral view is slightly concave.

The pelvis of *Prejanopterus* is very distinctive, with a large acetabulum and a distinct pubis and ischium. On these features, it resembles that of “*Pterodactylus*” *longicollum* (Plieninger, 1907: fig. 33; Wellnhofer, 1970: fig. 11c). However, they differ in the morphology of the postacetabular process of the ilium, which is more prominent in *Prejanopterus*. The subtriangular form of this process is reminiscent of that of *Tapejara wellnhoferi* (Eck et al., 2011: fig. 9, pl. 4; labeled as a prepubis).

Prepubis (Fig. 5h). The only known prepubis (FA 137; length: 38.5 mm) is a flat bone, with a long and slender peduncle, which expands cranially in a spatulate fashion. The prepubis of *Prejanopterus* is remarkably elongate as compared to many other pterosaurs.

Femur (Figs. 5f). Three femora are known (FA 29, 84 and 150), but only one is complete (Fig. 5f). The femoral shaft is relatively straight in cranial/caudal view and gently bowed in lateral view. The neck is not constricted but relatively robust. There is no evidence of a foramen in the caudal surface of the femur neck. The femoral head is directed medially at about 140º to the long axis of the shaft. In FA 29, the major trochanter seems to be pointed. However, this is probably due to an artifact of preparation because the two other femora lack such morphology. As for other limb bones, the femur of *Prejanopterus curvirostris* shows a relatively thick bone wall compared to other pterosaurs but dsungaripterids (see Fastnacht, 2005). The radius/thickness (R/t) ratio of the cortex in cross-section of femur FA 29 (incorrectly labelled FA 84 by Fuentes Vidarte and Meijide Calvo, 2010: fig. 4d) is approximately 3.8 at midshaft. Pterosaur bones are usually thin-walled with a typical cortical thickness of about 1 mm and a R/t ratio that ranges from nearly 4 to 20 (Fastnacht, 2005: fig. 12).

Tibia, fibula, tarsals, metatarsals and pedal phalanges. These elements have not been recognized for sure in the assemblage.

6 Paleohistology

The histological section of appendicular bones (wing phalanx I FA 47, femur FA 29) of *P. curvirostris* display a thick cortex (about 0.6-0.8 mm in thickness), composed mostly of highly vascularized primary fribrolamellar bone tissue (Fig. 6). The vascular network consists of randomly oriented simple primary vascular canals, which are broad and frequently anastomose, resulting in a plexiform pattern (Francillon-Vieillot et al., 1990). Vascular density slightly reduces outwardly, resulting in a sparse arrangement of longitudinal vascular canals in the periphery of the bone, organized in circular rows. This histological pattern is indicative of a moderate to fast growth rate followed by a late decline in bone deposition. In the examined samples, the medullary cavity is endosteally coated by a narrow layer of avascular bone, centripetally deposited. This layer is separated from the periosteal bone by a resting line and marks the maximum expansion of the marrow cavity. Such structure usually indicates skeletal maturity and cessation of effective growth (Ricqlès et al., 2000; Steel, 2008), but the absence of a peripheral lamella of avascular in the outermost cortex bone might suggest that the individual did not reached asymptotic size (see Chinsamy et al., 2009). No LAGs or other histological structures of periodical growth have been observed. Therefore, the bone microstructure suggests a continuous, uninterrupted growth strategy for *Prejanopterus curvirostris*.

7 Phylogenetic Relationships

Fuentes Vidarte and Meijide Calvo (2010) discussed the systematic position of *Prejanopterus curvirostris*. They included this taxon in the Pterodactyloidea based on the following characters: (1) long and compressed rostrum, triangular in section; (2) mandible triangular in dorsal view; (3) long metacarpus; (4) wing finger phalanges without caudal striations (Fuentes Vidarte and Meijide Calvo, 2010: 319). Of these characters only the long metacarpus is a valid synapomorphy of the clade Pterodactyloidea (see e.g., Kellner, 2003: 118; Unwin, 2003: 159) and, indeed, several significantly long metacarpals IV (and two long metacarpals I-III) have been found together with the holotype of *P. curvirostris* (Fig. 2). Fuentes Vidarte and Meijide Calvo (2010) did not assign *P. curvirostris* to any subgroup within Pterodactyloidea.

In order to assess with more accuracy the relationships of *Prejanopterus curvirostris*, a cladistic analysis was conducted. With this end in view, the most comprehensive character/taxon matrix available to date (Lü et al., 2010) was completed with the scoring for *Prejanopterus curvirostris* (2/3 of which are missing data). The matrix

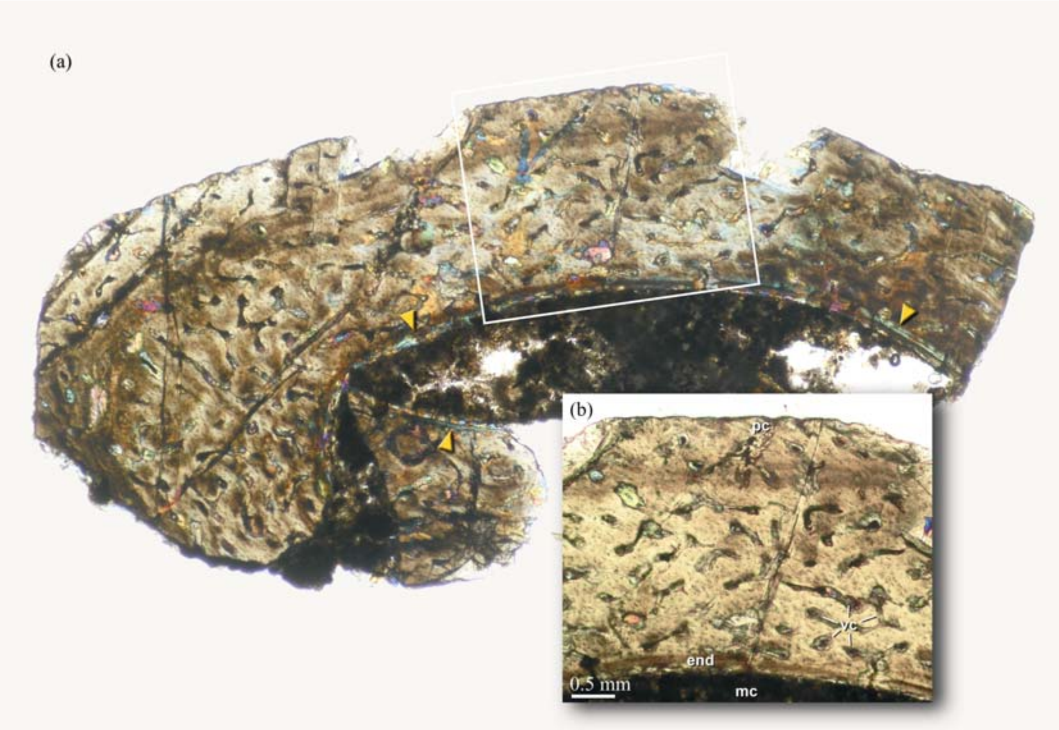

Fig. 6. Bone histology of *Prejanopterus curvirostris* from Fuente Amarga Locality, La Rioja province, Spain. (a), transverse cross section of phalanx 1 of wing digit IV (FA 47) showing a well-vascularized bone with plexiform vascularity surrounded by a woven fibred matrix. Inset area show location of detailed figure (b). The presence of a thin layer of secondary lamellar bone coating the perimedullary cortex (arrow) indicates cessation of expansion of the medullar cavity. The absence of avascular tissue in the peripheral region of the compacta suggests active bone deposition in the periosteal circumpherence at the time of death. Abbreviations: end: endosteal bone; mc: medullary cavity; pc: peripheral cortex; vc: vascular canals. Scale bar = 0.5 mm (a) and 0.1 mm (b).

(Appendix 2) was processed using TNT (Goloboff et al., 2008). A "traditional search" (heuristic) was performed based on 1000 replicates using TBR branch swapping. 752 most parsimonious trees (376 steps long) have resulted. Their characteristics are: C.I. = 0.434 and R.I. = 0.797. The strict consensus tree shows a topology that is consistent with that obtained by Lü et al. (2010). However, our strict consensus tree shows a lesser amount of polytomies than theirs (compare Fig. 7a with Lü et al., 2010: fig. 4a).

Prejanopterus is positioned between *Pterodactylus* and *Cycnorhamphus* within Pterodactylidae (Figs. 7a, b). To judge from Unwin (2003: 179), the scoring of the operational taxonomic unit *Pterodactylus* in Lü et al. (2010) is probably based on *P. antiquus* and *P. kochi*, whereas that of *Cycnorhamphus* was done on the basis of both *C. suevicus* and *Gallodactyllus canjuersensis* (which are close, but probably distinct species). The node "*Pterodactylus* + more derived taxa" (= Pterodactylidae *sensu* Knoll, 2000) is supported by five synapomorphies: (1) a rounded occipital region; (2) a squamosal that is entirely ventral to the orbit; (3) a ventrally facing occiput; (4) a subhorizontal quadrate; and (5) a pubis whose rostral profile is slightly concave in lateral view. The node "*Prejanopterus* + more derived taxa" is based on a single synapomorphy: a dorsoventrally compressed rostrum tip. The node "*Cycnorhamphus* + more derived taxa" (= Ctenochasmatoidea *sensu* Unwin, 2003) is supported by two synapomorphies: (1) a semicircular sternum, (2) a coracoid with a well-developed brachial flange.

8 Discussion

Fuentes Vidarte and Meijide Calvo (2010) diagnosed *Prejanopterus curvirostris* as follows (translated from Spanish): "long, pointed and crestless rostrum that curves toward the left from the middle third and with a very pronounced median groove extending along the palate; the premaxilla has 4 pairs and the maxilla bears 16 pairs of alveoli; alveoli 1 to 5 and 10 to 11 are smaller than the alveoli 6 to 9 and 12 to 20; unicusped teeth of elliptical section; the lower jaw is slender, straight, pointed and lacks a crest; mandibular symphysis approximately 35% of the length of the lower jaw". These characters are not regarded here as autapomorphies of *Prejanopterus* because they are also known in other pterosaurs. For example, the presence of a relatively elongate rostrum and mandibular symphysis and the absence of a premaxillary crest are known in several lineages of Pterodactyloidea (Unwin, 2003; Andres

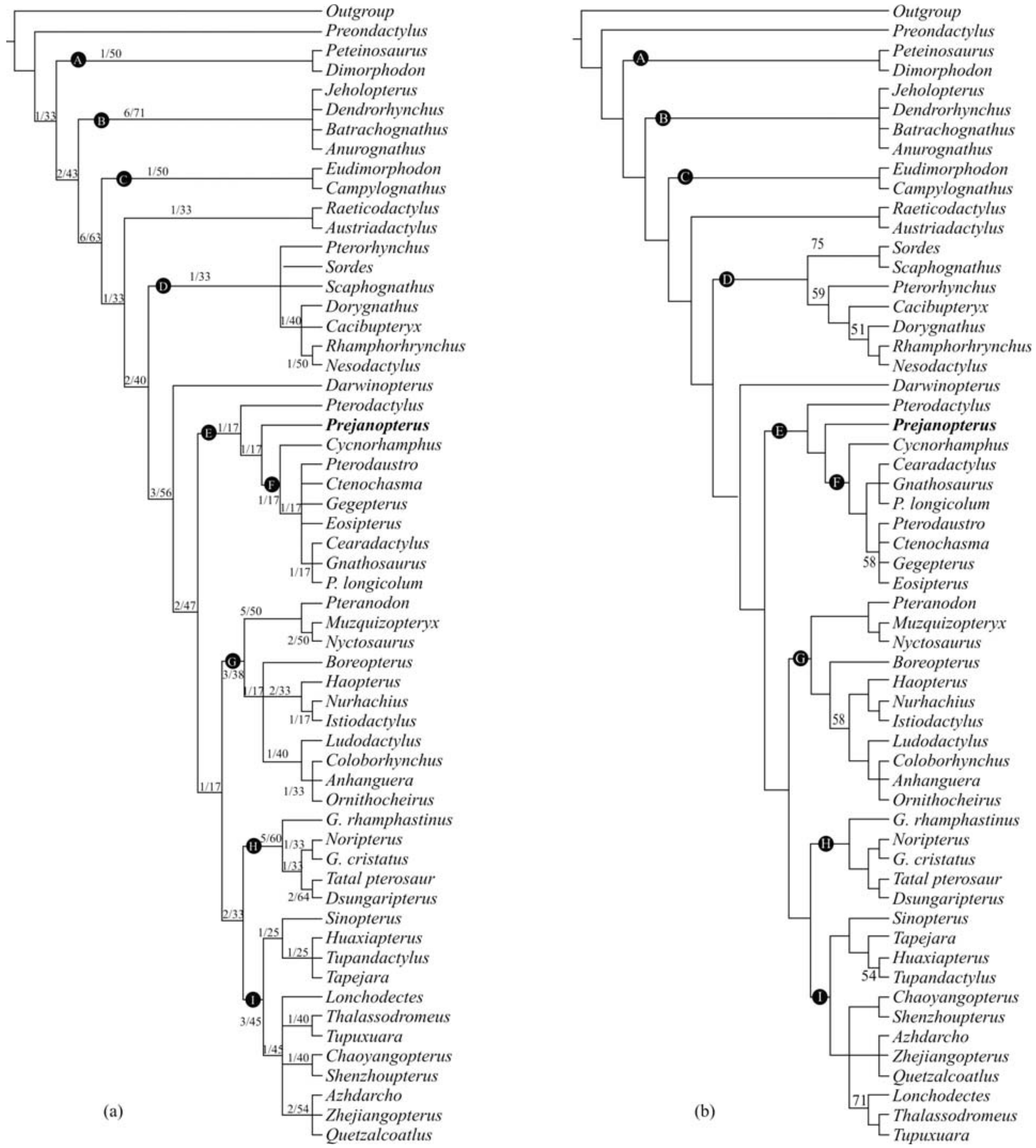

Fig. 7. Consensus trees generated by the cladistic analysis of the Pterosauria performed in this paper (scoring of *Prejanopterus curvirostris* in Appendix 2).

(a), Strict consensus tree; Bremer and relative Bremer indices are showed at the appropriate nodes (Bremer, 1994; Goloboff and Farris, 2001); (b), majority-rule consensus tree; numbers at nodes indicate the percentage of equally parsimonious trees in which these forks occur. Nodes: A: Dimorphodontidae[1]: <*Dimorphodon macronyx* and *Peteinosaurus zambellii*, B: Anurognathidae[1]: <*Anurognathus ammoni* and *Batrachognathus volans*, C: Campylognathoididae[2]: <*Campylognathoides zitteli* and *Eudimorphodon ranzii*, D: Rhamphorhynchidae[2]: <*Rhamphorhynchus longicaudus* and *Scaphognathus crassirostris*, E: Pterodactylidae[3]: <*Pterodactylus antiquus* and *Ctenochasma elegans*, F: Ctenochasmatoidea[1]: <*Cycnorhamphus suevicus* and *Pterodaustro guinazui*, G: Ornithocheiridae[2]: <*Anhanguera blittersdorffi* and *Pteranodon longiceps*, H: Dsungaripteridae[4]: <*Germanodactylus rhamphastinus* and *Dsungaripterus wei*, I: Azhdarchidae[2]: <*Tapejara wellnhoferi* and *Quetzalcoatlus northropi*. All definitions are node-based and are taken from the papers that first phylogenetically defined them: 1: Unwin (2003), 2: Knoll (2001), 3: Knoll (2000), 4: Knoll and Bouveur (2001).

and Ji, 2008; Lü et al., 2010). Among them, pterodactylids (*Pterodactylus*, *Cycnorhamphus*), ornithocherids (*Istiodactylus*, *Haopterus*) and azhdarchids (like *Lonchodectes*) have unicusped, spaced teeth in the jaws. In addition, some representatives of these clades, e.g. *Pterodactylus* (Wellnhofer, 1970, 1978) have teeth similar to that of *Prejanopterus*. The occurrence of four premaxillary teeth cannot be confirmed in *Prejanopterus* on the basis of the available material. From the original diagnosis of *P. curvirostris*, the most significant character is the lateral curvature of the rostrum as compared to the straight mandible. Fuentes Vidarte and Meijide Calvo (2010) noted that such a curvature is present in both the holotypic rostrum (FA 112) and a second incomplete specimen with teeth (FA 185). However, there is no genuine lateral bend in the holotype (Fig. 3) and the apparent lateral curvature of the fragmentary rostrum is probably due to deformation (Fig. 4).

As is typical in Pterodactylidae, *Prejanopterus* has an elongated rostrum and the dorsal margin of the skull was probably concave (Lü et al., 2012). *Prejanopterus* resembles *Pterodactylus* and *Cycnorhamphus* in many aspects, such as the presence of a low upper jaw that lacks a crest (see above). However, it differs from these taxa in having a slightly upturned rostral end of rostrum (straight in *Pterodactylus* and *Cycnorhamphus*; Wellnhofer, 1970; Fabre, 1976). Moreover, *Prejanopterus curvirostris* differs from *Pterodactylus antiquus* and *P. kochi* in the presence of a dorsoventrally compressed tip of rostrum (see above), from *Cycnorhamphus suevicus* in the presence of more than 11 pairs of teeth in the upper jaw that are not strongly recurved, from *Gallodactylus canjuersensis* in having a much less robust coracoid, and from *Gladocephaloideus jingangshanensis* in a greater number of teeth in the upper jaw (19 versus 15). Besides, the teeth of the latter species have sharp tips (Lü et al., 2012).

At first sight, the jaws of *Prejanopterus* looks also like those of the germanodactylid *Normannognathus wellnhoferi* from the Kimmeridgian of Normandy, France (Buffetaut et al., 1998). However, the latter differs from *Prejanopterus* in having the first premaxillary alveolus at the tip of the jaws and by the presence of long, slender teeth with slightly recurved crowns. *Prejanopterus* shares with the azhdarchid *Lonchodectes compressirostris* from the Albian Cambridge Greensand of England (Unwin, 2001) the presence of small, widely spaced and subequal-sized alveoli. However, *Prejanopterus* differs from *Lonchodectes* in lacking a midline, ventral ridge in the upper jaw.

Prejanopterus shows a unique combination of characters: (1) upper jaw with a toothless rostral end; the edentulous space is slightly greater than that between two of the rostral alveoli (Fig. 3) (the dentition extends to the very tip of the rostrum in most pterodactyloids, including all known pterodactylids); (2) small, blunt, and widely-spaced teeth (the teeth of *Prejanopterus* appear to be comparatively shorter than those of other pterodactyloids and do not show a tapering distal tip, see Fig. 4; however, this character should be taken with caution because of the fragmentary nature of the available specimens); (3) subrectangular, longer than wide sternum (Fig. 5c) (*Prejanopterus* is the only known pterodactylid with a subrectangular sternum; other pterodactyloids may exhibit this character, i.e. *Tapejara* and some specimens of *Pteranodon*; see Wellnhofer, 1978: fig. 8; Frey et al., 2003: fig. 1e); (4) very long and spatulate prepubis (the prepubis of pterodactyloids is commonly a fan-shaped or triradiate bone, while that of *Prejanopterus* is battledore-shaped and remarkably elongate; compare Fig. 5h with Wellnhofer, 1978: fig. 15; Lü et al., 2011: fig. 5); 5) appendicular bones with relatively thick bone walls: radius/thickness of femoral cortex approximately 3.8 at midshaft (Fig. 5f) (only dsungaripterids have a thicker cortex; see Fastnacht, 2005).

Finally, Fuentes Vidarte and Meijide Calvo (2010) estimated to 4.26 m the wing span of *Prejanopterus*, but this is probably an overestimation. Based on the dimensions of complete long bones, such as the femur (FA 150, length: 113 mm) and the first phalanx of digit IV (FA 154, length: 235 mm), subadult to adult individuals of *Prejanopterus curvirostris* are comparatively larger in size than the holotypes of *Cycnorhamphus suevicus* (77 mm and 141 mm, respectively) and *Gallodactylus canjuersensis* (ca. 101 mm and 154 mm, respectively; see Fabre 1976), which are both considered to be immature individuals (Bennett, 1996). According to these measurements and considering the mixed nature of the Préjano assemblage (see above), a conservative estimate of the wing span of *Prejanopterus curvirostris* ranges from 1.5 to 2.2 m. *Prejanopterus* was therefore a medium-sized pterodactyloid.

9 Conclusions

The pterosaur material of *Prejanopterus curvirostris* Fuentes Vidarte and Meijide Calvo, 2010, which includes a mixed assemblage of disarticulated cranial and postcranial remains from a number of individuals found in the Lower Cretaceous Leza Formation of La Rioja (Spain), was re-examined. This taxon was originally mainly diagnosed on the basis of the lateral curvature of the rostrum as compared to the straight mandible. However, we cannot confirm the presence of a genuine lateral bend in the holotypic material. Additional supposed autapomorphies of *Prejanopterus* are rejected because they are also known in other pterosaurs. However, the species is valid as it is based on material that shows a unique combination of characters: upper jaw with a toothless tip; low, blunt and widely-spaced teeth; subrectangular, longer than wide sternum; very elongate and spatulate prepubis; and limb bones with relatively thick bone walls (radius/thickness of the femoral cortex is 3.8 at midshaft). A cladistic analysis based on the data matrix of

Lü et al. (2010) indicates that *Prejanopterus* is placed phylogenetically between *Pterodactylus* and *Cycnorhamphus*.

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Appendix 1 List of material of *Prejanopterus curvirostris*

The pterosaur remains are preserved on several slabs; only two bones are free of matrix (the fragmentary rostrum FA 185, paratype, and the femur FA 29). Slabs are numbered CPE/242-5 to CPE/242-36 (CPE/242-32 is a cast of slab CPE/242-7b). Several slabs are unprepared (CPE/242-7a, 18, 21, 25) and others do not contain identifiable pterosaur bones, but fragments or long and hollow bones lacking epiphyses (CPE/242-6c, 7b, 7c, 7d, 8, 9, 10, 11, 12, 13a, 13b, 14, 16, 19b, 19c, 19d, 22b, 23, 24a, 26, 27, 33, 35, 36). Besides pterosaur, a few actinopterygian and crocodyliform remains (scales and osteoderms, respectively) are also present on these slabs and many fragmentary bones, probably pterosaurian but unidentified. Only identifiable pterosaur remains are listed below:

Slab **CPE/242-31**:	FA 3: mandible;
Slab **CPE/242-5a+5b**:	FA 12: incomplete left humerus; FA 13: incomplete phalanx 1 of left wing digit IV (Fig. 5e, left); FA 14: incomplete metacarpal IV (Fig. 5e, lower left); FA 20: sternum (Fig. 5c, left); FA 21: incomplete rigth humerus (Fig. 5c, right); FA 50: left pelvic girdle (Fig. 5e, right);
Slab **CPE/242-17**:	FA 23: phalanx 1 of wing digit I/II/III; FA 26, vertebral centrum?;
Slab **CPE/242-30**:	FA 29: right femur (free of matrix) (Fig. 5f);
Slab **CPE/242-19e**:	FA 31: two vertebral centra; FA 33: incomplete phalanx 1 of right wing digit IV;
Slab **CPE/242-34+35**:	FA 47: proximal phalanx 1 of rigth wing digit IV;
Slab **CPE/242-19a:**	FA 56: two vertebral centra;
Slab **CPE/242-24b:**	FA 69: incomplete metacarpal IV (Fig. 5g);
Slab **CPE/242-28:**	FA 71: dorsal vertebra; FA 80: dorsal vertebra;
Slab **CPE/242-15:**	FA 84: left femur;
Slab **CPE/242-20a+20b**:	FA 99: phalanx 2 of wing digit IV?, FA 110: skull fragment?; FA 112: rostrum (holotype; Fig. 3); FA 114: left coracoid and fragment of scapula (Fig. 5b); FA 125: cervical vertebra; FA 128: vertebral centrum?; FA 129: vertebral centrum?; FA 133: fragment of braincase; FA 137: prepubis (Fig. 5h);
Slab **CPE/242-6a+6b** (Fig. 2):	FA 148: metacarpal I/II/III; FA 150: rigth femur, FA 151: incomplete ulna?; FA 152: distal end of phalanx 1of wing digit IV; FA 154: complete left phalanx 1 of wing digit IV (Fig. 5d); FA 158: distal end of metacarpal IV; FA 160: mandible; FA 161: incomplete left ulna; FA 163: mandible (Fig. 5a);
Slab **CPE/242-29a+29b**:	FA 173: metacarpal I/II/III;
Slab **CPE/242-22a+22c**:	FA 185: fragmentary rostrum (paratype, free of matrix; Fig. 4).

Abbreviations: CPE: Centro Paleontológico de Enciso, Enciso, Spain; FA: Fuente Amarga locality.

Appendix 2 Scoring of *Prejanopterus curvirostris* for the 117 characters in the data matrix by Lü et al. (2010) (see Fig. 7)

1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60
0011?	2??0?	?????	?????	?????	?????	?????	?0??0	?10?0	0?000	00??0	00010
61–65	66–70	71–75	76–80	81–85	86–90	91–95	96–100	101–105	106–110	111–115	116–117
00???	?????	??1??	00??0	????0	?????	?????	???00	??11?	1?00?	00???	??