Reinterpretation of a Chilean pterosaur and the occurrence of Dsungaripteridae in South America

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Abstract – A fragmentary specimen of pterosaur originally assigned to the genus *Pterodaustro* Bonaparte, 1970 is reassessed. The presence of a sagittal dorsal cranial crest on a fragment of nasopreorbital arcade with linear vertical trabeculae and the occurrence of alveolar protuberances on the *os dentale* indicate the new specimen has similarities with crested pterodactyloid pterosaurs of the family Ctenochasmatidae, and with members of the Dsungaripteridae. The presence of alveolar protuberances allows us to assign the specimen to the Dsungaripteridae. It forms the basis of a new genus and species, *Domeykodactylus ceciliae*.

1. Introduction

Outside the Brazilian Cretaceous, pterosaurs are rare in South America (Campos & Kellner, 1985; Price, 1953; Wellnhofer, 1991) and are restricted to a few occurrences in Argentina (Bonaparte, 1970, 1971; Gasparini, Leanza & Garata Zubillaga, 1987; Montanelli 1987; Sanchez, 1973; Unwin 1996), Chile (Bell & Padian, 1995) and Peru (Bennett, 1989). Casamiquela & Diaz (1978) described some fragmentary skull remains from the supposed Late Jurassic of northern Chile, which they assigned to the Cretaceous pterosaurian genus *Pterodaustro* Bonaparte, 1970. The material was originally identified as pterosaurian on account of the thin nature of the wall of the mandible, and as pterodactyloid partly on account of its size. It is now considered to belong within the pterodactyloidea, on account of its similarity with dsungaripteroid pterosaurs (see below). New preparation of this material shows that structures previously interpreted as fine, elongate teeth of a mandible are in fact vertical linear trabeculae of a medial cranial crest. The two pieces do not fit together, and so it is not absolutely certain that the two bones pertain to the same individual. However, the matrix of the two pieces is the same, the preservational style of the bone is the same, and both are from the same locality, where, in 1997, a search failed to yield any more bones in this deposit.

The material is accessioned in the collection of the Departmento de Ciencias Geológicas at the Universidad Católica del Norte, Antofagasta as specimen number 250973. Replicas of the specimen are held at the Staatliches Museum für Naturkunde Karlsruhe.

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2. Locality and stratigraphy

The specimen was collected from outcrops of purple-coloured arkose in the deeply incised valley of the Quebrada la Carrea, (GPS reading 25° 25.830′ S/69° 20.969′ W) and was discovered by one of us (GChD) during routine stratigraphic fieldwork. This locality is in the southernmost part of the Sierra Candeleros, Cordillera de Domeyko, Segunda Región de Antofagasta, northern Chile (Fig. 1).

The age of the outcrop yielding the specimen cannot be determined with precision, due to a lack of diagnostic fossils, but there are arguments suggesting a Late Jurassic to Early Cretaceous age. Marls with concretions at the base of the sequence here are correlated with similar lithologies of Oxfordian age in nearby exposures. An overlying horizon yields abundant fishes, and a sandstone yields remains of the plant *Brachyphyllum*. Specimens of *Williamsonia* have been obtained from above the arkoses. Nearby, outcrops of red sandstones overlie marine sediments that yield the bivalves *Megatrigonia* and *Pterotrigonia* (*Scabrotrigonia*), which are of Lower Cretaceous age. Thus an Early Cretaceous age is considered more likely than a Late Jurassic one (Chong, 1976; Casamiquela & Diaz, 1978).

These outcrops occur within a thick sequence of sandstones, tuffs, conglomerates and breccias, as well as finer-grained sediments, and interfinger with andesitic volcanic rocks. Lithological facies and sedimentary structures suggest a coastal environment, probably associated with estuaries (Chong, 1976).

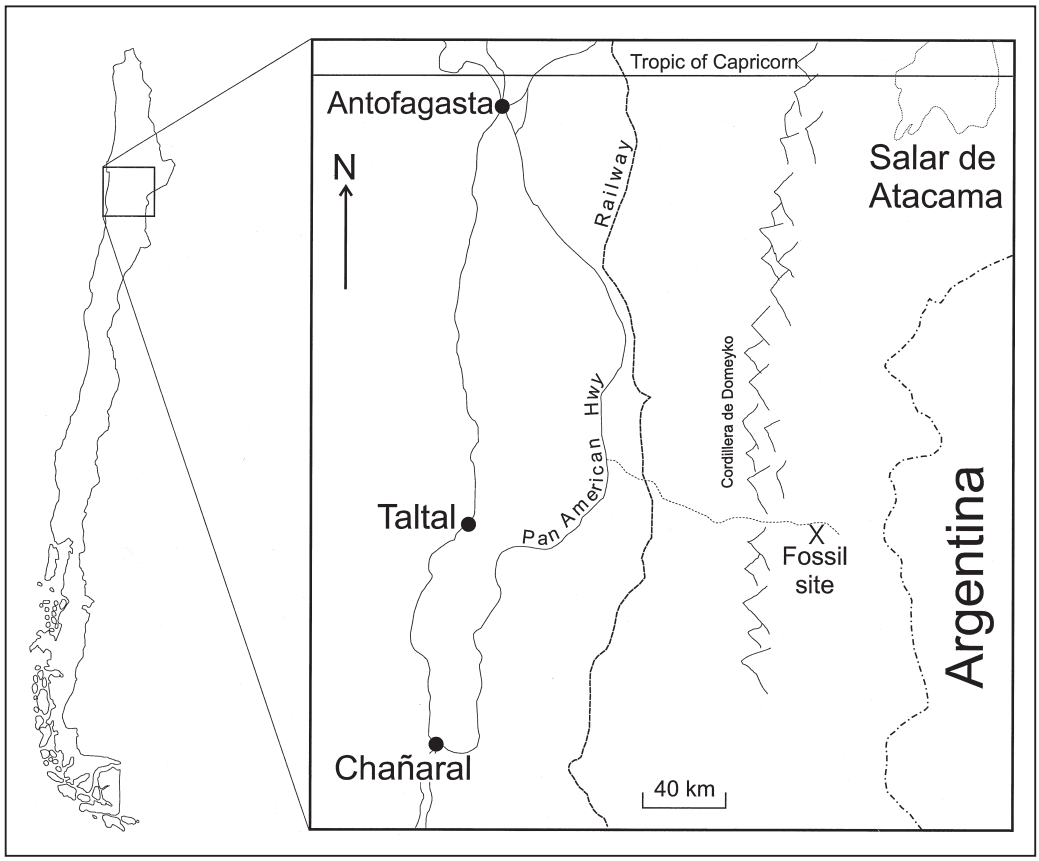

Figure 1. Map showing the location of the Quebrada La Carreta and the approximate position of the pterosaur locality.

The bones are enclosed in indurated, purple-coloured, poorly sorted, immature polymictic arkose with a carbonate cement. The bones are white or bluish white, and are stained in places with an unidentified pale-yellow mineral and black pyrolusite. Cracking of the bone has been intense, and some severe distortion has occurred. The piece bearing the mandible fragment has been cut to a wedge-shaped tablet of rock approximately 130×26×33 mm, with a maximum depth of 18 mm. The fragment of medial cranial crest lies on a cuboid piece of rock approximately 120×50×19 mm. The reverse face of this slab has been coated with a filler material that resembles car body filler. Presumably, this was added to strengthen the rock after the repair of three fractures.

3. Systematic palaeontology

Order PTEROSAURIA Kaup, 1834
Suborder PTERODACTYLOIDEA Pleininger, 1901
Superfamily DSUNGARIPTEROIDEA Young, 1964
Family DSUNGARIPTERIDAE Young, 1964
Genus *Domeykodactylus* nov.

Diagnosis. Crested pterosaur in which each mandible bears at least 16 low and narrow protuberant dental alveoli that decrease in size and spacing from caudal to rostral.

Etymology. Domeyko, from the Cordillera de Domeyko, where the specimen was discovered.

Species *Domeykodactylus ceciliae* sp. nov.

Holotype. Incomplete mandible with portions of the left and right rami and symphysis; (Figs 2, 3).

Referred material. Portion of premaxilla found in the same piece of rock and in very close proximity to the holotype (Figs 2, 5).

Type locality. Quebrada La Carreta, Sierra da Candeleros, Segunda Región de Antofagasta, Chile.

Etymology. After Cecilia Demargasso, who was so kind to us.

Diagnosis. As for the genus (see above).

4. Description of the specimen and osteology

4.a. Lower jaw

Only fragments of both rami of the mandible are preserved. The lower jaw is distorted by oblique compaction, such that the right mandible is seen from a ventrolateral aspect and the left mandible from a ventral aspect. The latter underwent vertical compaction.

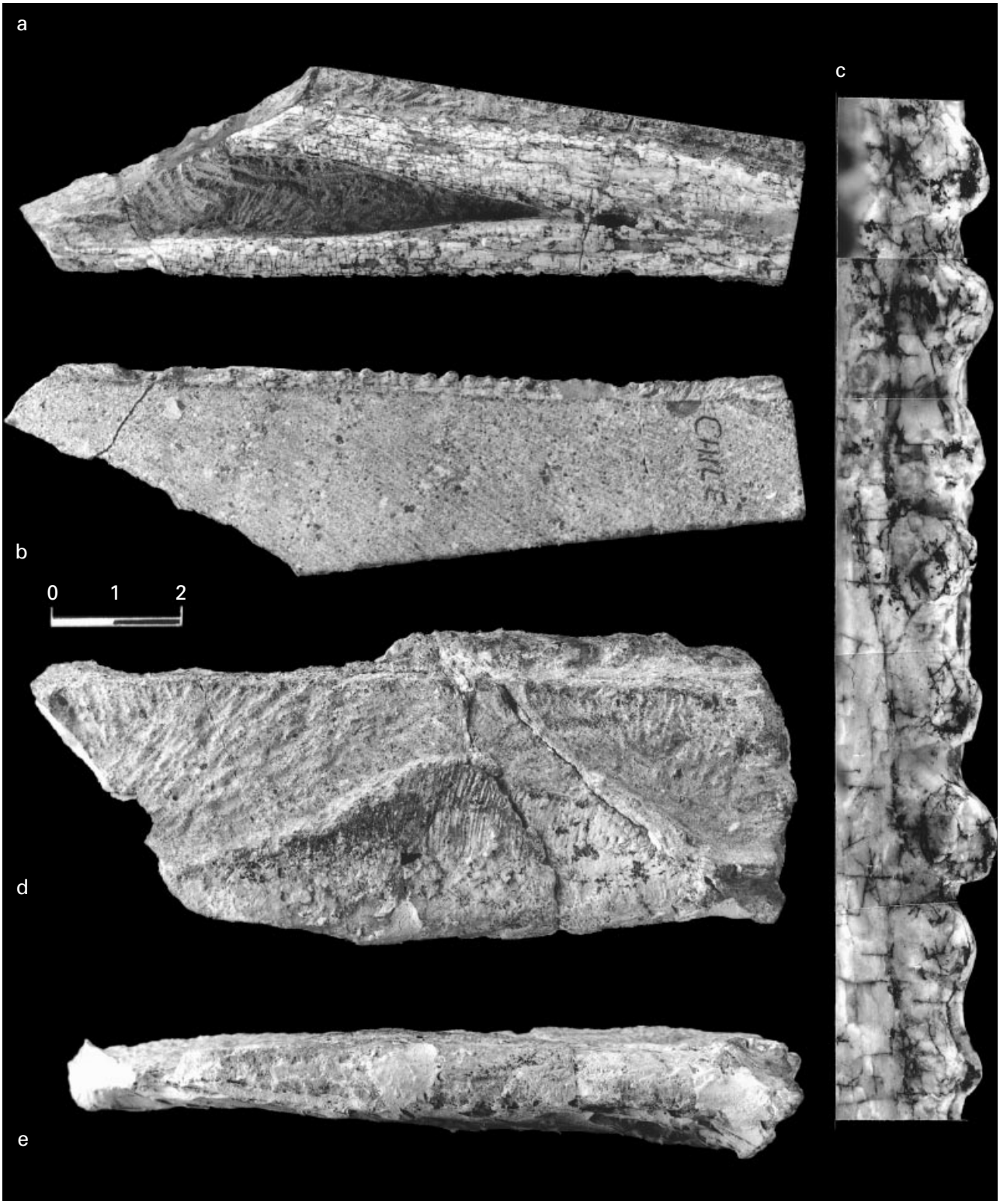

Figure 2. Bones of *Domeykodactylus ceciliae* gen. et sp. nov. from the Quebrada La Carreta, Sierra da Candeleros, Segunda Región, Chile. (a) Ventral view of the dentary. (b) Dorsal view of the left ramus of the dentary, showing the dental border with expanded alveolar margins. (c) Detail of the expanded alveolar margins, approx. × 6.5. (d) Portion of the dorsal margin of the antorbital opening (most probably a portion of premaxilla), with a striated sagittal crest. The dorsal surface is uppermost. (e) The same bone as (d), viewed ventrally. The scale bar is in centimetres.

Most of the *facies buccalis* is obscured by matrix. Only a 5 mm wide area of *facies buccalis* of the left ramus has been cleaned in order to expose the row of protuberances. The rostral end of the mandible is missing, as are both articular ends, with the right ramus being the more complete. The only bones that can be identified are both *ossa splenialia* and both *ossa dentalia*.

Parallel to the rostral fracture line, a section of bone

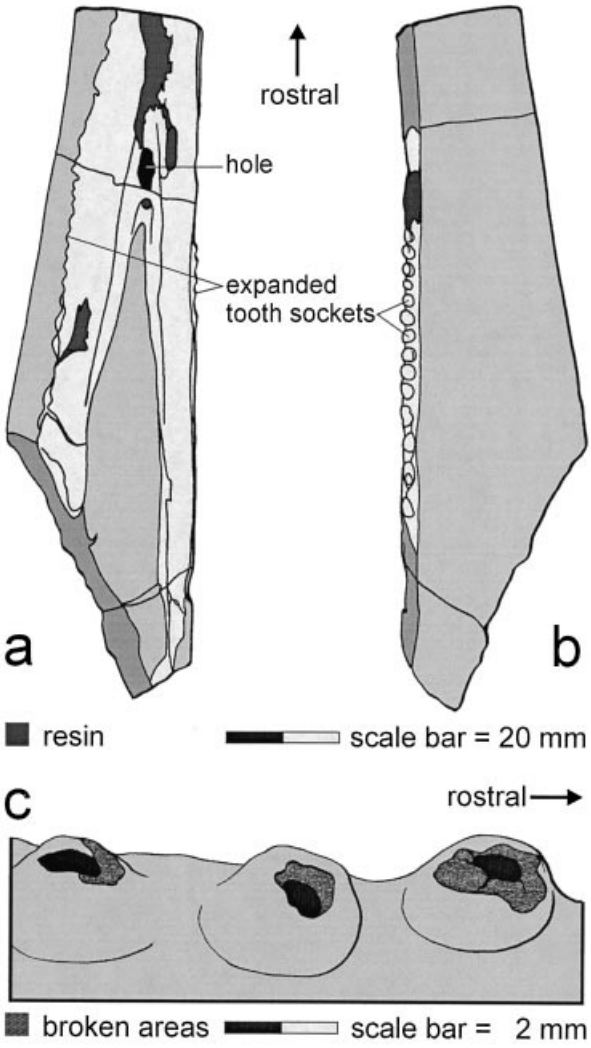

Figure 3. Portion of mandible of *Domeykodactylus ceciliae* gen. et sp. nov. from the Quebrada La Carreta, Chile. (a) Ventral view of the mandible on a slab of arkosic sandstone. (b) View of the other side of the slab, showing the dental border of the left side of the mandible. (c) Sketch illustrating the expanded nature of the dental alveolar borders. The black shading represents broken-off teeth.

and sediment has been removed for thin-section petrographic and histological analyses. On the cut surface, the cross-section of the right third of the *rostrum mandibulae* is seen. The left two thirds are modelled by pale-yellow-coloured resin. Prior to preparation at the Staatliches Museum für Naturkunde Karlsruhe, the specimen was impregnated with this resin, which is of unknown composition and covers some areas of the specimen. Unfortunately, it obscures the region of the *symphysis mandibulae*, which extends over one third of the specimen. Due to weathering and fracturing, the superficial layers of the compacta have flaked off. Consequently, sutures are not easily identifiable. Adjacent to the caudal end of the *symphysis mandibulae*, there is a longitudinally oval cavity (four times longer than wide) with uneven margins. The specimen was broken transversally, adjacent to the caudal margin of the cavity .

Caudally, the preserved segment of the right *os dentale* is about 10 mm shorter than that of the medially adjacent *os spleniale*. A suture between both bones is preserved on the medioventral edge of the right ramus, but, due to weathering, this does not necessarily represent the original course of the *sutura dentalosymphisialis*. From the cavity anterior to the sulcus, a stair-like fracture extends caudolaterally, and terminates in a patch of resin. Only the *facies lateralis*, with the protuberances on the *margo dorsolateralis* of the *os dentale*, is visible. Of the adjacent splenial, only a short portion of the *margo ventralis* caudal to the *symphysis mandibulae* is exposed.

The left *ramus mandibulae* is compacted in a dorsoventral direction, so that the *facies lateralis* of the posterior half of the preserved part of the left *os dentale* forms a sharp, laterally directed fold running subparallel to the *margo dorsolateralis* of the *os dentale*. A longitudinal depression is seen lateral to the *symphysis mandibulae*. On the *facies medialis* of the left *ramus mandibulae*, a suture is preserved that might represent the *sutura dentalosymphysialis*. However, some parts of the *margo medialis* of the *os dentale* are broken. The protuberances on the *margo dorsolateralis dentalis* are visible from all sides, after having been prepared at the Staatliches Museum für Naturkunde Karlsruhe.

Due to the distortion and compaction of the bone tissue, a reconstruction of the anatomy of the *mandibula* is problematic. In cross-section, the *rami mandibulae* were most likely caudally inclined, approximately 60° against the vertical plane, from a dorsolateral to a ventromedial direction. This inclination possibly decreased toward the rostrum, but the evidence is equivocal. Caudal to the mandibular symphysis, the fragments of the *rami mandibulae* include an angle of about 20°. Due to the resin impregnation, it is not possible to identify the nature of the *symphysis mandibularis*. However, a sulcus is present at the caudal fifth of the preserved part of the *symphysis mandibularis*. Lateral to this sulcus, two blunt ridges, extending about 15 mm caudally, indicate a ventral reinforcement of the mandible in the postsymphysial area. The rostral part of the preserved segment is straight.

On the *margo dorsolateralis* of the right dentary, 15 protuberances are preserved. The 16 protuberances of the left dentary are better preserved: while the caudalmost of these protuberances are prominent and well spaced, they gradually become smaller and more densely spaced rostrally; where the protuberances are uncrushed, they show a long oval (caudally) to subcircular (rostrally) cross-section. As seen on the left dentary, the row of protuberances begins rostral to the caudal break of the *ramus mandibulae*, and ends 10 mm rostral to the caudal end of the *symphysis*

mandibulae. The cranial part of the rostrum must therefore have been a toothless beak (Fig. 4).

Binocular microscopy of the apices of the protuberances at a magification of ×116 reveals that protuberances 4, 5, 8, 9, 10, 11, 12 and 16 each contain a tooth root. The crowns of these teeth have broken off. The protuberances therefore represent the inflated margins of the *alveoli dentalis*. Buccal to the *spatia interalveolares*, 1–3 small depressions are visible on the *facies dorsalis* of the left dentary, which might represent receptacles for the corresponding teeth of the upper jaw.

4.b. Sagittal cranial crest

The specimen comprises a fragment of the nasofrontal arcade of a skull, including the basal portion of a medial cranial crest. The matrix adjacent to the dorsal margin of the crest fragment has been prepared away. Under binocular examination, it becomes evident that the preserved dorsal margin does not represent the *margo dorsalis* of the crest. Only the left side of the specimen is exposed. The right side is obscured by the matrix, which is reinforced by a material resembling car body filler. The compacta of the dorsal border of the *fenestra nasoantorbitalis* has partly flaked off. Only single patches are preserved where the bone surface bends medially. Along the ventral margin of the fragment, three triangular pieces have broken out, the gaps of which have been filled with the filler. The gaps are continuous, with three cracks running obliquely through the specimen and converging at a point dorsal to the skull fragment.

The crest fragment shows vertical subparallel striation. The striae most likely consist of linear trabeculae that support the crest internally. They may have been encased between two layers of compacta that were lost during diagenesis and/or preparation of most of the lateral surface of the crest. Only on the rostral part of the fragment is a patch of the compacta of the crest preserved. The linear trabeculae of the crest are slightly curved. We assume that the curvature of the trabeculae indicates the cranial direction; no exceptions to this have been reported for pterosaurian head crests. This means that the exposed surface is the right

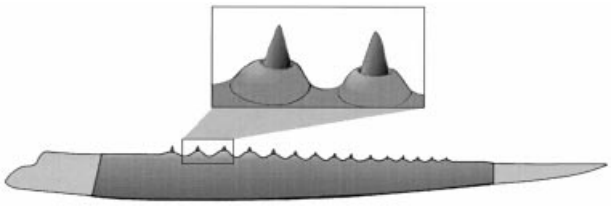

Figure 4. Reconstruction of a portion of dentary of *Domeykodactylus ceciliae* gen. et sp. nov. showing the well-spaced, expanded alveolar borders with (assumed) low-crowned teeth.

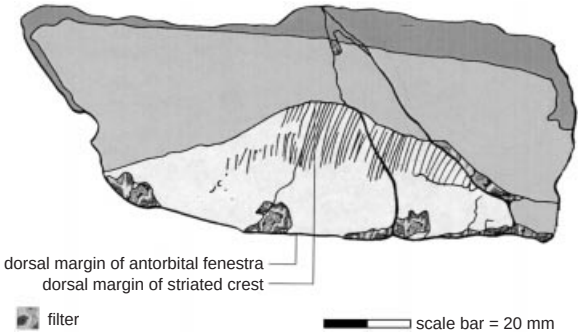

Figure 5. Slab of arkosic sandstone with a small portion of the dorsal margin of the antorbital fenestra (most probably a portion of premaxilla), with a striated sagittal crest. The striations were previously interpreted as teeth. The top of the image is dorsal.

facies lateralis. The maximum preserved height of the exposed trabeculae is 15 mm, and there are between 12 and 14 trabeculae per 10 mm. The widths of individual trabeculae are variable, but none is greater than 1.0 mm. The bone fragment of the nasofrontal arcade is not identifiable. The diameter of the arcade was ventrally rounded, with a median sulcus.

5. Discussion and conclusions

The structures previously identified as teeth on a bone, thought to be a fragmentary mandible by Casamiquela & Diaz (1978), are shown to be vertically oriented linear trabeculae on a medial cranial crest dorsal to the antorbital opening. This misidentified feature was the only criterion by which the specimen was assigned to *Pterodaustro* Bonaparte, 1970, and thus the specimen can no longer be assigned to this genus, or indeed to the family Pterodaustridae. The presence of alveolar protuberances on the dental border of the mandible give the dentary a serrated dorsolateral margin, which is similar to the condition in the Asiatic Cretaceous pterosaurs *Dsungaripterus* Young, 1964 and the Tatal pterosaur previously called *Phobetor* (a preoccupied name; Bakhurina, 1982), both of which are included in the family Dsungaripteridae (Wellnhofer, 1991). An increase of tooth size posteriorly and toothless jaw tips are apomorphies of Dsungaripteroidea (Unwin, 1995; Unwin & Lü, 1997), but the expanded alveoli allow us to be more precise in our placement, because these are apomorphic for Dsungaripteridae (see below). Similarly, the striated crest is also a feature found in Dsungaripteridae, but it is not clear if it is apomorphic for the group. The Chilean specimen differs from *Dsungaripterus* in the degree of prominence of the alveolar protuberances: they are high and rounded in *D. weii*, and number only eight on each side of the dentary. In *Domeykodactylus*, there are 16 alveolar protuberances, and each is low and narrow. In the Tatal

pterosaur, the alveoli appear not to be expanded into protuberances. There are similar small tooth roots to those seen in *Domeykodaktylus* in the expanded alveolar regions of *Dsungaripterus* (P. Wellnhofer, pers. comm. 1996).

The medial crest of *Domeykodactylus* is characterized by slightly curving, subparallel trabeculae, commencing approximately halfway up the lateral margin of this bone at a position where the ventral margin forms the border of the antorbital opening. A similarly grooved crest is seen in the Tatal pterosaur, *Dsungaripterus* and in the ctenochasmatids *Gnathosaurus* and *Huanhepturus*. In these ctenochasmatid genera, the crest is low and only weakly grooved, and in addition, none of these genera has dentaries bearing expanded alveoli. The Germanodactylidae, including *Germanodactylus* and the recently described *Normannognathus* from the Late Jurassic of northern France (Buffetaut, Lepage & Lepage, 1998), also have a sagittal crest, but in these genera the teeth are short and the alveolar borders are not expanded; they are thus distinct from *Domeykodactylus*. *Domeykodactylus* therefore cannot be assigned to the Ctenochasmatidae or the Germanodactylidae. It is placed within the Dsungaripteridae because of the possession of fine teeth in expanded alveolar borders and the possession of a prominently grooved sagittal crest.

There remains, however, an Upper Cretaceous pterosaur described by Owen (1874) as *Ornithocheirus sagittirostris* from the Wealden Group of Sussex, southern England. The mandible of this taxon also has expanded alveoli, and is similar in this respect to *Domeykodactylus*. However, the teeth do not expand posteriorly, and this species must therefore lie outside of Dsungaripteridae.

Assignment of *Domeykodactylus* to Dsungaripetridae is of palaeobiogeographical significance, as *Domeykodactylus* becomes the first reliable record of the Dsungaripteridae in South America. Until now, records of this family of distinctive pterosaurs have been restricted mainly to China, Mongolia (Wellnhofer, 1991) and Japan (Unwin *et al*. 1996), with a possible record in Romania (Jurcsák & Popa, 1984) in the northern hemiphere.

There have been several rather tentative claims for Dsungaripteridae in the southern hemisphere. Galton (1981) referred some fragmentary post-cranial remains, previously assigned to *Pterodactylus brancai* from the Upper Jurassic of East Africa, to the Dsungaripteridae, although Unwin & Heinrich (in press) have recently demonstrated that this material belongs within Germanodactylidae. The Argentinian pterosaur *Puntanipterus globosus* Bonaparte & Sanchez, 1975 was also tentatively referred to Dsungaripteridae by Galton (1981), while Bennett (1989, 1994) considers *Santanadactylus spixi* from the Romualdo Member of the Santana Formation, Brazil to be dsungaripterid. Although the placing of *Santanadactylus* within dsungaripterids appears to have been accepted by Wellnhofer (1991, p. 145), this was brought into question by Unwin & Lü (1997), and its present higher taxonomic status remains to be established. Unwin (1996) also noted that the late Middle Jurassic *Herbstosaurus pigmaeus* from Argentina showed some similarities to the dsungaripteroid pterosaurs.

The distinctively striated sagittal crest is similar to a feature seen in the Brazilian Lower Cretaceous Tapejaridae (E. Frey & D. M. Martill, unpub. data). In some Tapejaridae, these bony crests suppport extensive soft-tissue extensions, which may have been several times higher than the skull (Campos & Kellner, 1997; Martill & Frey, 1998). We suggest that the striated surfaces in Ctenochasmatidae and Dsungaripteridae form the insertion loci for a fibre-strengthened soft-tissue extension of the premaxillary crest, the function of which remains unknown.

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