



A new toothless pterosaur (Pterodactyloidea) from Southern Brazil with insights into the paleoecology of a Cretaceous desert

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Abstract: The first pterosaur bone bed from Brazil was reported in 2014 at the outskirts of the town Cruzeiro do Oeste, Paraná State, in the Southern region of the country. Here named ‘cemitério dos pterossauros’ site, these outcrops were referred to the Goio-Erê Formation (Turonian-Campanian) of the Caiuá Group (Bauru Basin) and revealed the presence of hundreds of isolated or partially articulated elements of the tapejarine pterosaur *Caiuajara* and fewer amounts of a theropod dinosaur. Here we present a new tapejaromorph flying reptile from this site, *Keresdrakon vilsoni* gen. et sp. nov., which shows a unique blunt ridge on the dorsal surface of the posterior end of the dentary. Morphological and osteohistological features indicate that all recovered individuals represent late juveniles or sub-adults. This site shows the first direct evidence of sympatry in Pterosauria. The two distinct flying reptiles coexisted with a theropod dinosaur, providing a rare glimpse of a paleobiological community from a Cretaceous desert.

Key words: Paleoecology, Pterosauria, Pterodactyloidea, *Keresdrakon vilsoni*, Paraná, Cretaceous.

INTRODUCTION

Pterosaurs are the first vertebrates to conquer the air by developing powered flight (e.g., Kellner 2006).

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* Contribution to the centenary of the Brazilian Academy of Sciences.

Despite having been recovered in all continents (Hammer and Hickerson 1994, Barrett et al. 2008), their fossil record can be considered as patchy, with only few deposits having presented complete or nearly complete skeletons (e.g., Eaton 1910, Tischlinger and Frey 2002, Barrett et al. 2008, Bantim et al. 2014, Kellner 2017). Even in the stratigraphic units that have yielded large quantities

of these volant archosaurs, there is a general lack of pterosaur bone beds (e.g., Wellnhofer 1975, Wild 1978, Saraiva et al. 2008, Dalla Vecchia 2014, Cheng et al. 2017, Pinheiro and Rodrigues 2017), so far restricted to only three occurrences: the Lagarcito Formation (Lower Cretaceous, Albian) in San Luis, Argentina (Yrigoyen 1975, Chiappe et al. 1998), the Lower Cretaceous deposits of the Tugulu Group in Hami, Xinjiang, China (Eberth et al. 2001, Wang et al. 2014), and the strata of the Upper Cretaceous Goio-Erê Formation (Bauru Group) that outcrop at Cruzeiro do Oeste, Paraná State, Brazil (Basilici et al. 2012, Manzig et al. 2014). The latter is the first occurrence of pterosaurs in the Bauru Group that has yielded a comparatively large number of other fossil vertebrates such as dinosaurs (e.g., Brusatte et al. 2017, Bandeira et al. 2018) and crocodylomorphs (e.g., Riff et al. 2012).

The outcrops at the region of Cruzeiro do Oeste have a peculiar history (Fig. 1). The site, here named 'cemitério dos pterossauros' (pterosaur graveyard), was discovered some 40 years ago by the Dobruski family. No fieldwork was carried out in the area over these years until it was rediscovered in 2011, when some specimens that had been eroding on the surface were collected without fine stratigraphic control (see Manzig and Weinschütz 2012). Later (October/ 2012) one of the authors (AWAK) was invited by LCW and Paulo C. Manzig (at that time associated with CENPALEO - Centro Paleontológico of the Universidade do Contestado) to examine this material and recognized the presence of at least two pterosaur taxa and one theropod dinosaur. He has encouraged CENPALEO to organize fieldwork in the region, which was carried out in cooperation with the Museu Nacional/UFRJ during July/2012, January-February/2013, July/2013, and July/2014. This activity resulted in thousands of fossil bones, mostly found isolated that were split between CENPALEO and the Municipality of Cruzeiro do Oeste by a written agreement signed some years

later. Some blocks (still unprepared) are housed in the Museu Nacional and were not affected by the recent fire that has consumed the main building of the institution (e.g., Zamudio et al. 2018). Training for the preparation of the material was performed by the Museu Nacional, first at CENPALEO (July/2012) and then at Cruzeiro do Oeste (August/2016).

The more numerous bones recovered so far belong to a small tapejarine pterosaur that was named *Caiuajara dobruskii* Manzig et al. 2014. The previously identified dinosaur was recently named *Vespersaurus paranaensis* Langer et al. 2019, also known by hundreds of isolated elements. An acrodont lizard, *Gueragama sulamericana* Simões et al. 2015, which was described based on fragmentary material (Simões et al. 2015), complete the known reptilian fauna from this site. Lizard remains tend to be quite incomplete (e.g., Chavarría-Arellano et al. 2018), for all those representing ancient desertic environments.

In this study we present the description of the second toothless pterosaur taxon from this deposit, *Keresdrakon vilsoni* gen. et sp. nov., which is known by far less specimens than *Caiuajara* and *Vespersaurus*. We also explore the paleoecological relationships of the known taxa of this Cretaceous desert environment, which has the potential for unveiling many new findings (Kellner 2012).

GEOLOGICAL SETTING

The stratigraphic assignment of the deposits in the outskirts of Cruzeiro do Oeste has been put under dispute recently (Figs. 1-2). The 'cemitério dos pterossauros' site was originally regarded by Manzig et al. (2014) as belonging to the Caiuá Group, more specifically to the Goio-Erê Formation. Langer et al. (2019) agreed with the assignment to the Caiuá Group but argued that the site is located in an area already mapped as the Rio Paraná Formation (Fernandes 2004).

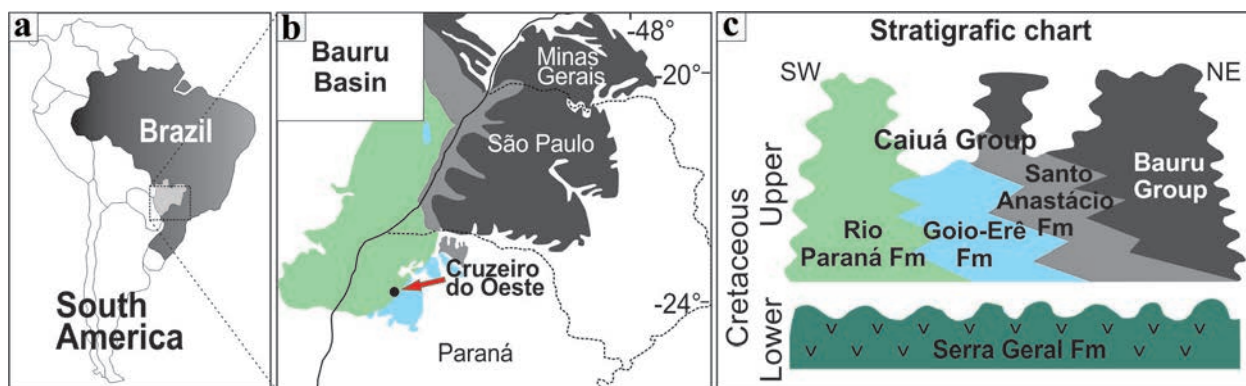


Figure 1 - Map showing the location of the ‘cemitério dos pterossauros’ site in Cruzeiro do Oeste (red arrow), Paraná State, southern Brazil. (a) The outcrops of the Bauru Basin (light grey) in Brazil, (b) detail of the Bauru basin with the Rio Paraná (light green), Goio-Erê (light blue), Santo Anastácio (grey) formations, and the Bauru Group (dark grey), and (c) stratigraphic chart showing the relations of the former, including the underlying Serra Geral Formation (green).

The Bauru Basin is formed by the Bauru and the Caiuá groups (Fernandes and Coimbra 2000) and has its development linked to the isostatic compensation related to the large basaltic lava accumulation of the Eocretaceous Serra Geral magmatic event (Fernandes 2004). Batezelli (2010) showed that the Caiuá Group was formed by a depocenter located in the southernmost part of the basin (in relation to the Bauru Group) directed towards the Paraná State and whose northern limit extended to the southeastern part of the Minas Gerais State. Based on the eolian sedimentary rocks, the paleoclimate at that time of deposition is regarded as arid (Fernandes 2004).

The Caiuá Group is characterized by predominantly desert-type red beds and divided into the Rio Paraná, Goio-Erê and Santo Anastácio formations (Fernandes and Coimbra 2000). All three units are interpreted as chronocorrelated and interdigitated, whose limits are transitional (Fernandes 2004). Their contact with the basalts of the underlying Serra Geral Formation is marked by an unconformity (Fig. 1).

The Rio Paraná Formation is composed of fine to very fine to medium grained sandstones, forming large eolian structures with medium to large cross stratification that, according to Fernandes (2004), correspond to the central region of the ‘sand sea’.

The Goio-Erê Formation consists of fine and very fine (sometimes medium) grained sandstones, rich in quartz and whose color ranges from reddish brown to purplish gray. These rocks are mineralogically and textually supermature. They form tabular layers with cross-stratification, sometimes with flat-parallel lamination, and deposits that correspond to wet interdunes (Fernandes and Coimbra 2000). Lastly, the Santo Anastácio Formation fills shallow troughs of the valleys formed by the Paraná river tributaries. The deposits constitute massive tabular sandstones and correspond to sand sheets present on the extensive desertic marginal plains of the former ‘sand sea’ (Fernandes 2004).

Although the ‘cemitério dos pterossauros’ site is showed to correspond to the Rio Paraná Formation in the current geologic map encompassing the region of Cruzeiro do Oeste, the lithological characteristics of the outcrop with the bonebeds are more consistent with the description of the deposits of the Goio-Erê Formation. The fossils themselves indicate the presence of humid inter-dunes where life could thrive. Therefore, we interpret the ‘cemitério dos pterossauros’ site as a non-mappable occurrence of the Goio-Erê Formation. Otherwise, it would indicate the presence of interdune deposits within the Rio do Paraná Formation, which contradicts its original interpretation.

The age of those layers is also controversial. Basilici et al. (2012) favor a Turonian - Campanian age, with the lower limits even being considered as Coniacian by Milani et al. (2007), while Batezelli (2015) argues for a lower Cretaceous age (Aptian-Albian). No definitive conclusion can be reached at the present stage of knowledge, particularly concerning the 'cemitério dos pterossauros' site.

Regarding the bonebeds, they occur on a secondary road floor leading from the center of the town Cruzeiro do Oeste to the rural areas nearby, as well as on the right ravine (direction city - rural areas). As pointed out before (Manzig et al. 2014), there are three distinct lithological units formed by massive, fine to very fine sandstones (Fig. 2). The surface of the grains is opaque and covered with iron oxide. On the top of the sequence there are very fine sandstones. Four bonebeds have been observed, with the lower one bearing many disarticulated remains of pterosaurs (*Caiuajara* and *Keresdrakon*) and one theropod dinosaur (*Vespersaurus*). The same fossil assembly was recovered in the subsequent two other bonebeds, although elements tend to be sparser. The last bonebed consists mainly of hundreds of very small bones attributed to *Caiuajara*.

MATERIALS AND METHODS

PHYLOGENETIC ANALYSIS

In order to determine the phylogenetic position of *Keresdrakon vilsoni* gen. et sp. nov., we performed a phylogenetic analysis using the software TNT 1.5 (Goloboff and Catalano 2016). This analysis is based on Holgado et al. (2019 - see data matrix there). We have used all taxa of that study (144) adding only the new species. All characters are discrete and the original coding was maintained. Search for the most parsimonious trees (MPTs) was conducted via Traditional Search (TBR swapping algorithm), 10,000 replicates, random seed, and collapsing trees after search. We also conducted the

analysis via New Technology using Sect. Search, Ratchet (parameters: 20 substitutions made, or 99% swapping completed, 6 up-weighting prob., 6 down-weighting prob., and a total number of iterations of 10), Tree fusing, Driven search (15 initial addseqs., 15 times of min. length), random seed, and without collapsing trees after search. Subsequently, the results of the New Technology were analyzed via Traditional Search (TBR swapping algorithm), starting trees for RAM, and without collapsing trees after search.

The coding of *Keresdrakon vilsoni* in the data matrix published by Holgado et al. (2019) is as follows:

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101????????????????00?120000-00?0--00--
??0-????????????2????????????000???13200
101?30-00010000--0000?111?00?????
00020011?0?01520??1???????????????
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SLIDE PREPARATION

Two bones of *Keresdrakon vilsoni* gen. et sp. nov. were sectioned for a preliminary histological analysis (CP.V 2077 and CP.V 2374). All elements were measured, photographed and described for bone microstructure investigation before they were sectioned, according to the methodology proposed by Lamm (2013). Bones were sectioned in the diaphysis portion, and a sample of about 1 cm thick from each was obtained for histological slide preparation. These specimens were immersed in clear epoxy resin Resapol T-208 catalyzed with Butanox M50, cut with the aid of a micro rectify (Dremel 4000 with extender cable 225) coupled to a diamond disk. The section assembly side was ground and polished in a metal polishing machine (AROPOL-E, AROTEC LTDA) using AROTEC abrasive grit (grit size 60 / P60, 120 / P120, 320 / P400, 1200 / P2500). Finally, the sections were examined and photographed in a light microscope (Zeiss Inc. Barcelona, Spain) equipped with an AxioCam camera with Axio Imager, after the

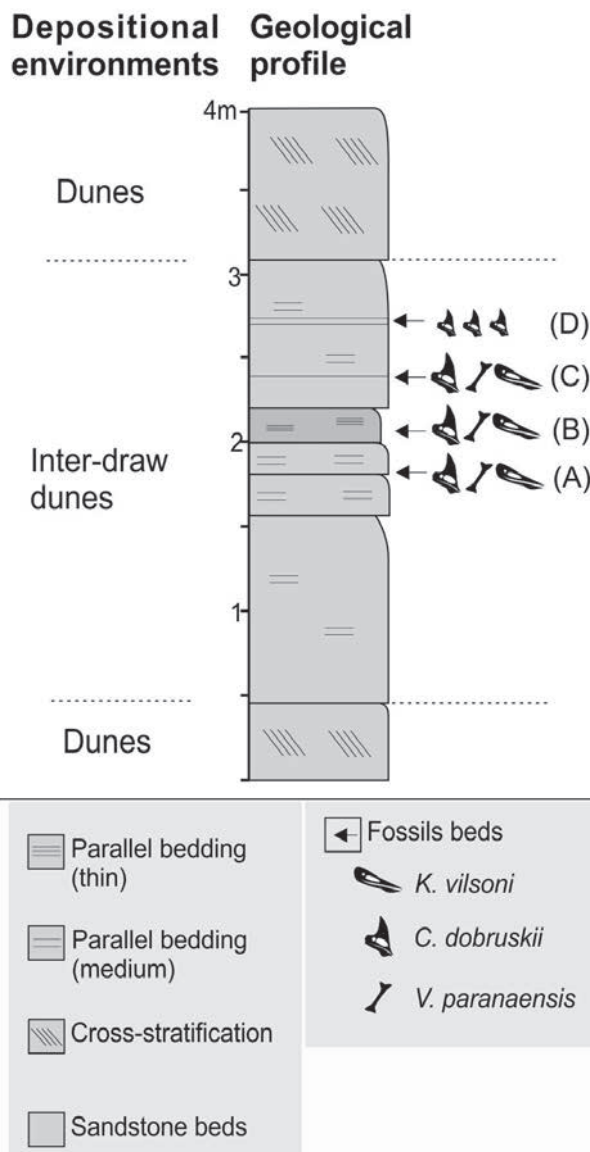


Figure 2 - Stratigraphic sequence of the 'cemitério dos pterossauros' site, showing the recorded taxa (*Caiuajara dobruskii*, *Vespersaurus paranaensis* and *Keresdrakon vilsoni*) in the four (A-D) bonebeds, the correspondent depositional environments, and the sedimentary structures. Note that in bonebed D only small individuals of *Caiuajara* were collected.

histological slides were prepared. The M2 imaging software was used in the examination procedure.

NOMENCLATURAL ACTS

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the

International Code of Zoological Nomenclature. The Zoobank Life Science Identifiers (LSIDs) to the prefix <http://zoobank.org/>. The LSID for this publication is urn:lsid:zoobank.org:pub:C4E8E040-D158-42C3-A91F-E432CDEAB424, and the LSIDs for the new erected groups and taxa are: urn:lsid:zoobank.org:act:E26A65E0-2859-4CD3-B773-B99D568D366C (*Keresdrakon*) and urn:lsid:zoobank.org:act:8358C917-6C12-4390-AAB8-37D82723BBBCD (*Keresdrakon vilsoni*).

The following pterosaur genera and species are mentioned in this study: *Argentadraco* Kellner and Calvo 2017, *Caiuajara dobruskii* Manzig et al. 2014, *Caupedactylus* Kellner 2013, *Eurazhdarcho* Vremir et al. 2013, *Hamipterus* Wang et al. 2014, *Pteranodon* Marsh 1876, *Quetzalcoatlus* Lawson 1975, *Tapejara* Kellner 1989, *Thalassodromeus* Kellner and Campos 2002, *Tupuxuara leonardii* Kellner 1994, and *Zhejiangopterus linhaiensis* Cai and Wei 1994.

SYSTEMATIC PALEONTOLOGY

- PTEROSAURIA Kaup 1834
- PTERODACTYLOIDEA Plieninger 1901
- AZHDARCHOIDEA Nesov 1984
- TAPEJAROMORHA Andres et al. 2014

***Keresdrakon* gen. nov.**

Etymology: A combination of Keres, death-spirits who personified violent death in Greek mythology and are associated to doom and/or plunder; and drakon, which is the Ancient Greek word for dragon or huge serpent.

Type species: *Keresdrakon vilsoni*, type by monotypy.

Diagnosis: The same as for the type species.

***Keresdrakon vilsoni* gen. et sp. nov.**

Etymology. In honor to Mr. Vilson Greinert, a volunteer who dedicated hundreds of hours preparing most of the specimens from 'cemitério dos pterossauros' site housed in CENPALEO and in the town of Cruzeiro do Oeste.

Holotype. Partial skeleton including the anterior portion of the skull, quadrate, almost complete lower jaw, two cervical vertebrae, four dorsal vertebrae, sternum, elements of the gastralia, right scapula, incomplete humeri, proximal portion of a radius, incomplete femora, incomplete tibia, left ilium, right pubis, left ischium and other fragmentary elements (CP.V 2069) housed at the Centro Paleontológico (CENPALEO) of the Universidade do Contestado, Mafra, Santa Catarina, Brazil (Fig. 3, Table I). It was recovered from bonebed C (Fig. 2).

Paratypes. Rostral end of a skull, including the anterior part of the nasoantorbital fenestra (CP.V 2068, Fig. 4) and the rostral end of lower jaw (CP.V 2070, Fig. 4); incomplete mid-cervical vertebra (CP.V 2445); mid-cervical vertebra, tibia (shaft) and rib (CP.V 2317); scapulae (CP.V 2004 - right, 2075 - left, 2339 - right); coracoid (CP.V 2083 - left); humerus (CP.V 1011 - right); ulnae (CP.V 2073 right, 2074 left, 2077 right, the latter used for osteohistological analysis), radii (CP.V 2251 and 2247); and first phalanges of the fourth wing finger (CP.V 2242 right, 2248 left, 2373 right) (Table II).

Referred specimens. Fragment of two jaws (CP.V 2254; CP.V 2343); two incomplete mandibular rami (CP.V 2071); one mid-cervical vertebra (CP.V 2398), incomplete dorsal vertebrae (CP.V 4181, CP.V 2234, 2316); elements of a large wing (CP.V 5797); femora (CP.V 2081, 2245); tibia (CP.V 2246); one large incomplete long bone interpreted as the first wing phalanx (CP.V. 2374) used for osteohistological purposes (see osteohistology section) (Table III).

Type locality, horizon and age. `Cemitério dos pterossauros' site (53° 03' 53,4"W; 23° 45' 34,5"S - contra Langer et al. 2019), Cruzeiro do Oeste, Paraná State, Brazil; Bauru Basin, Caiuá Group, Goio-Erê Formation Cretaceous (Milani et al. 2007, Basilici et al. 2012, Batezelli 2015).

TABLE I

Measurements (in mm) of the holotype (CP.V 2069) of *Keresdrakon vilsoni* nov. gen., nov. sp.

skull	278*mm
mandible	361* mm
cervical vertebra, centrum	52 mm
sternum, sternal plate	82 mm
sternum, cristospine	36** mm, 17*** mm
scapula (right)	146* mm
femur (left)	189* mm

*preserved;

**anteroposterior;

***dorsoventral.

Diagnosis. Azhdarchoid pterodactyloid with the following autapomorphies: short blunt ridge on the dorsal surface of the posterior end of the dentary; foramen on the ventral surface at the anterior half of the proximal articulation of the first phalanx of digit IV; and foramen on lateral surface of the ischium.

The new species can be further distinguished from other azhdarchoid pterosaurs by the following combination of characters: dorsal margin of the premaxillae above the nasoantorbital fenestra rounded; sagittal groove on the dorsal surface of the premaxillae above the nasoantorbital fenestra; ridge on the medial surface of the splenial; ventral bar of the nasoantorbital fenestra thick; lateral pneumatic foramen on mid-cervical vertebra large; and strongly asymmetrical sternal articulation of the coracoid.

DESCRIPTION AND COMPARISON

The material of *Keresdrakon vilsoni* is preserved in a red coarse and friable sandstone (Figs. 3-9, Tables I-III). The bones show different degrees of compression, but most maintain at least some three-dimensionality, an uncommon condition regarding pterosaurs. Although some specimens were damaged due to weathering, there are several elements with breakages that have occurred prior or during the

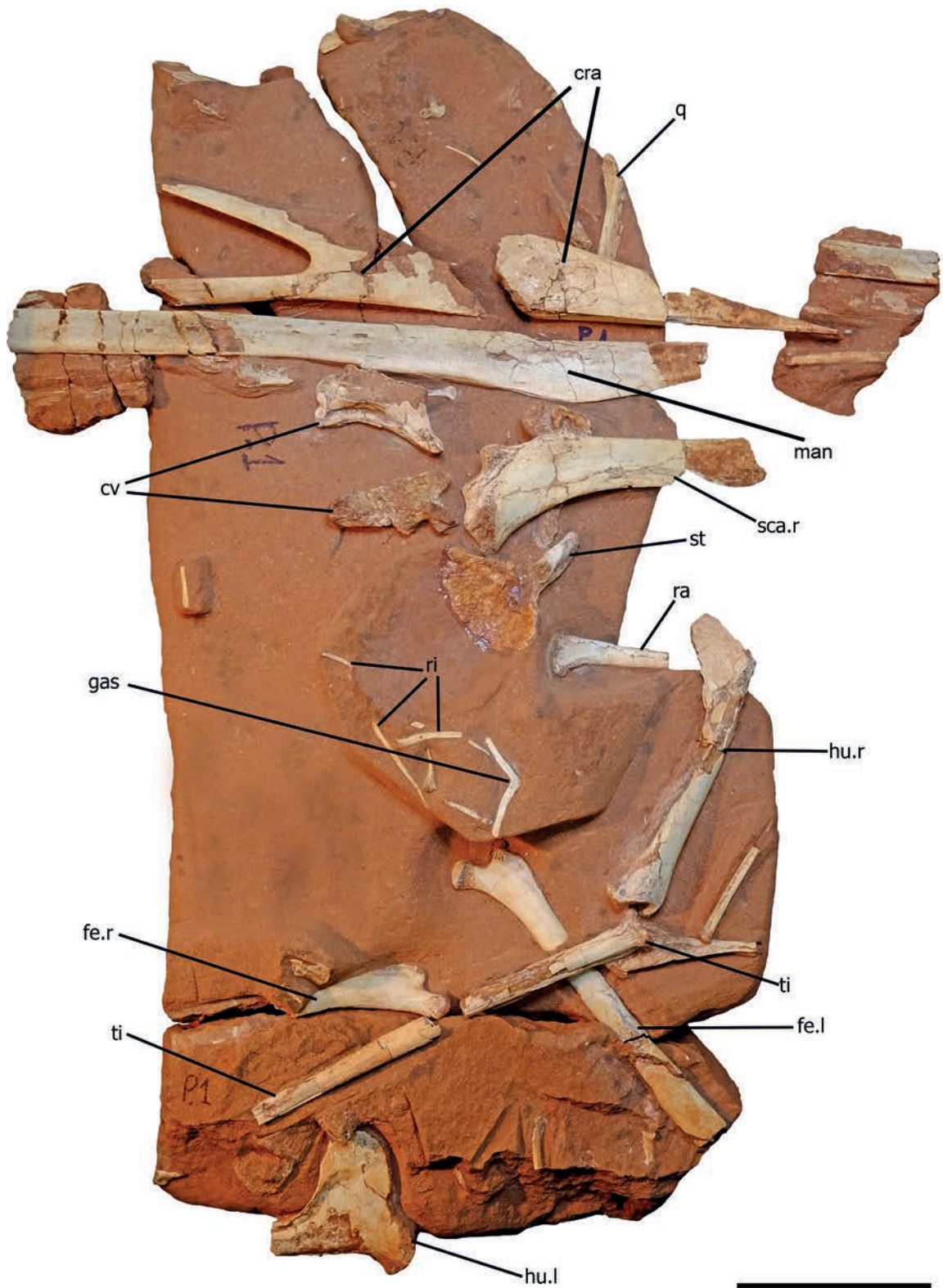


Figure 3 - Holotype of *Keresdrakon vilsoni* gen. et sp. nov. (CP.V 2069). Skull and lower jaw are presented in right lateral view. Abbreviations: cra - skull, cv - cervical vertebra, fe - femur, gas - gastralia, hu - humerus, man - mandible, q - quadrate, ra - radius, ri - ribs, sca - scapula, st - sternum, ti - tibia; l - left, r - right. Scale bar = 100mm.

TABLE II
Measurements (in mm) of the paratypes of *Keresdrakon wilsoni* nov. gen., nov. sp.

skull, rostral end	CP.V 2068	197* (length)
lower jaw, mandibular symphysis	CP.V 2070	183* (length)
mid-cervical vertebra, centrum	CP.V 2445	56 (length)
scapula (right)	CP.V 2004	163 (length)
coracoid (left)	CP.V 2083	109** (length)
humerus (right)	CP.V 1011	173 (length)
ulna (right)	CP.V 2073	224 (length)
ulna (left)	CP.V 2074	223 (length)
ulna (right)	CP.V 2077	227 (length)
Radius	CP.V 2251	196 (length)
Radius	CP.V 2247	213 (length)
1st wing phalanx (right)	CP.V 2242	228* (length), 36*** (width)
1st wing phalanx (left)	CP.V 2248	367 (length), 37*** (width)
1st wing phalanx (right)	CP.V 2373	242* (length), 39*** (width)

*preserved;

**from tubercle to sternal articulation;

***width medial articulation proximal.

Obs. scapulae (2075 and 2079) and ulnae (2073 & 2074) might belong to the same individual.

fossilization process. Based on the skulls and the first wing phalanges, at least three individuals are recognized so far but the actual number must be higher, particularly due to the fact that elements of the new pterosaur were found in three different levels throughout the section (Fig. 2).

The holotype (CP.V 2069) is the most complete specimen (Fig. 3). The bones were found associated but not articulated except for the upper and lower jaw. Most elements are not fused such as the scapula (found isolated and not fused to the coracoid), the distal epiphysis of the right humerus, and the pelvic elements. The following bones are fused: premaxillae with each other and with the maxillae, the splenial with the dentary, the opposing dentaries, and the centrum with the neural arch of the preserved mid-cervical vertebrae. As far as we know from pterosaur ontogeny, CP.V 2069 likely

represents an animal that was between ontogenetic stage (OS) 2 and 3 *sensu* Kellner (2015).

The holotype (CP.V 2069) also shows the best preserved skull of the new species, formed by the rostral end until part of the nasoantorbital fenestra and a lower jaw that lacks the most distal portion of the mandibular rami (Figs. 3-4a, c). Additional cranial material consists of the anterior portion of an upper jaw (CP.V 2068, Fig. 4a) and part of a mandibular symphysis (CP.V 2070, Figs. 4d, e). Two additional jaw fragments (CP.V 2254; CP.V 2343) and incomplete mandibular rami (CP.V 2071) are also tentatively referred to this species.

Based on these specimens, *Keresdrakon wilsoni* is toothless and bears a low skull. The rostrum is elongated, longer than that of any tapejarid (Wang and Zhou 2003a, Lü et al. 2006, Kellner and Campos 2007, Pinheiro et al. 2011, Kellner 2013), chaoyangopterid (Wang and

TABLE III
Measurements (in mm) of the referred specimens of *Keresdrakon vilsoni* nov. gen., nov. sp.

femur	CP.V 2245	83* (length), 93** (length)
tibia	CP.V 2246	154* (length)
1st wing phalanx	CP.V 5797	322* (length) , 55*** (width)
mid-cervical vertebra, centrum	CP.V 2398	38 (length)

*preserved;

** estimated;

***width medial articulation proximal.

Zhou 2003b, Lü et al. 2008) and the azhdarchid *Zhejiangopterus linhaiensis* Cai and Wei 1994, but shorter than that of the azhdarchid *Quetzalcoatlus* sp. (Kellner and Langston 1996). The rostrum ends in a pointed tip. The dorsal margin of the rostrum until the anterior half of the nasoantorbital fenestra is slightly sigmoid, differing in this respect from all other pterodactyloids. The ventral margin is slightly curved downwards but not as in tapejarines (Kellner and Campos 2007). It lacks the large quantities of foramina that are commonly observed in tapejarids, including *Caiuajara* (Manzig et al. 2014). Occlusion of jaws form no gap, a different condition from tapejarines (Kellner and Campos 2007).

The anterior angle of the nasoantorbital fenestra (CP.V 2068 ~19.3°; CP.V 2069 ~22.5°) is more acute than in other azhdarchoids except for *Quetzalcoatlus* sp. (~15.8°, see Kellner and Langston 1996). In lateral view, the ventral bar of this opening formed by the premaxillae/maxillae is thicker than in other azhdarchoids, except in *Thalassodromeus* (Kellner and Campos 2002, Pêgas et al. 2018). Although not complete, it is unlikely that this cranial opening is as large as observed in the tapejarids (Kellner and Campos 2007) or high as in chaoyangopterids (Lü et al. 2008).

There is no evidence of a premaxillary sagittal crest until the anterior margin of the nasoantorbital fenestra, and it is unknown if such a structure, which is a common feature among azhdarchoids (Kellner and Langston 1996, Wang

and Zhou 2003a, Kellner and Campos 2007, Lü et al. 2008), was present more posteriorly. Above the anterior portion of the nasoantorbital fenestra, the premaxillae have a rounded dorsal margin and display a sagittal groove (Figs. 3-4a). Inside this cranial opening, the premaxillae are fused, have laterally raised borders and form medially a flat surface, lacking the ridge present in *Caiuajara* (Manzig et al. 2014). No suture with the maxillae is visible. The palate is slightly concave and gets more flattened posteriorly, lacking any ventral ridge as in thalassodromines (Kellner and Campos 2007) or an expansion close to the anterior opening of the nasoantorbital, which is diagnostic for tapejarines (Kellner and Campos 2007). On the lateral side, a longitudinal groove is observed.

An incomplete right quadrate (CP.V 2069) is preserved, showing that it is a long rod-like bone that has a thin medial flange (incomplete) and laterally shows an elongated groove probable the articulation for the quadratojugal.

The lower jaw is long and ends in a pointed tip (Figs. 3, 4). As common in pterodactyloids, the main element is the dentary, which fuses into a symphysis. The occlusal (=dorsal) surface is pierced by several foramina, which are more than those of the upper jaw, but much fewer than those in tapejarines (Kellner and Campos 2007, Andres et al. 2014, Manzig et al. 2014) and similar to the low number present in basal tapejarines (Kellner 2013, Pêgas et al. 2016). The ventral surface of the symphysis is blunt and bears a small and thick

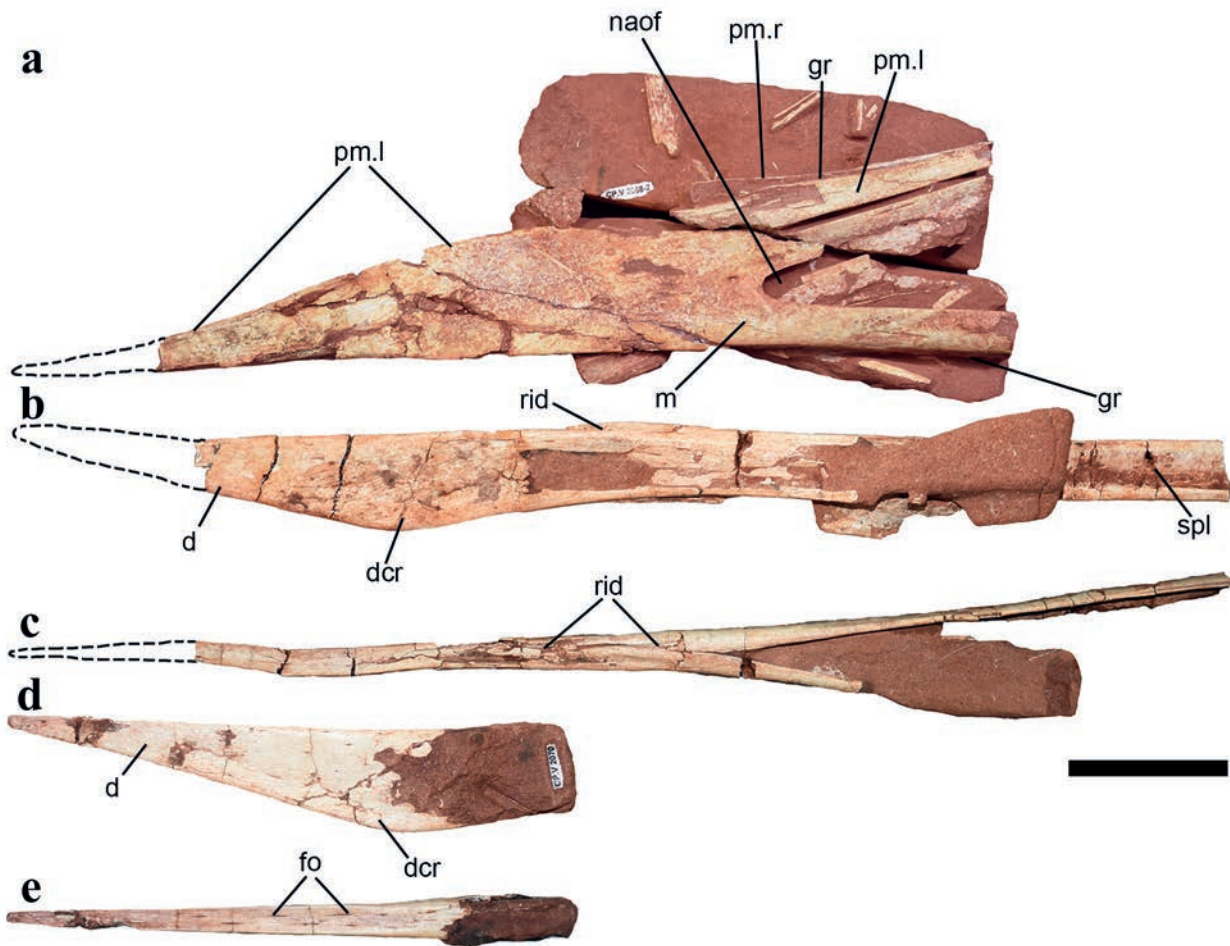


Figure 4 - Skull and lower jaws of *Keresdrakon wilsoni* gen. et sp. nov. (a) Incomplete skull showing the rostral part, in left lateral view (CP.V 2068), (b) incomplete lower jaw (CP.V 2069 part of the holotype) in left lateral and (c) dorsal views, (d) anterior portion of a dentary (CP.V 2070) in left lateral and (e) dorsal views. Abbreviations: d - dentary, dcr - dentary crest, fo - foramina, gr - groove, m - maxilla, naof - nasoantorbital fenestra, pm - premaxilla, rid - ridge, spl - splenial; l - left, r - right. Scale bar = 50mm.

dentary crest. It differs from the deeper lower jaw at the posterior end of the mandibular symphysis of *Argentadraco* (Kellner and Calvo 2017). The occlusal surface is anteriorly flattened and becomes slightly concave posteriorly. A medial ridge starts at the region corresponding to the end of the dentary crest and runs at least for 40 mm (up to 65 mm) until almost reaching the posterior dorsal end of the symphysis. Such a dentary dorsal ridge has never been reported before in pterosaurs so far. *Argentadraco* bears two mandibular ridges separated by a depression and laterally boarded by a sulcus, differing from the condition of *Keresdrakon*.

Although the mandible is not complete, the symphysis in the holotype (CP.V 2069) has reached about 220 mm and corresponded up to 46% of the estimated mandible length (~470mm). Despite the fact that the exact posterior limit of the dorsal portion of the mandibular symphysis cannot be established, it seems not to extend further posteriorly relative to the ventral end, neither to develop a symphyseal shelf, differing from several azhdarchoids (Kellner and Langston 1996, Vullo et al. 2012, Kellner 2013, Pêgas et al. 2016). The typical tapejarine step-like dorsal margin of the mandibular symphysis (Kellner and Campos 2007) is absent. At the most posterior

preserved end of the right mandibular ramus (CP.V 2069), the medial portion of the lower jaw can be observed showing the splenial. This bone is very thin and shows a blunt longitudinal ridge that does not extend anteriorly.

Few cervical vertebrae are preserved and might belong to distinct individuals (Fig. 5). The elements from the middle series are sub-equal in length, with the centrum longer than wide but not to the same degree as in archaeopterothyrids, chaoyangopterids and azhdarchids (Nesov 1984, Howse 1986, Kellner 2003, Andres and Ji 2008, Lü et al. 2008, Leal et al. 2018). They bear developed postexapophyses and hypapophysis. On each side of the hypapophysis, small projections - the preexapophysis - are present but not as developed as in the azhdarchid *Eurazhdarcho* (Vremir et al. 2013). This structure corresponds to a ridge identified in an azhdarchid middle cervical vertebra from Morocco (Rodrigues et al. 2011) and the preexapophyseal articulations reported in the pteranodontoid *Pteranodon* (Bennett 2001). Although not reported, they are present in at least some tapejarines, including *Tapejara* (Wellnhofer and Kellner 1991) and *Caiuajara* (Manzig et al. 2014) (AWAK pers. obs.). They have not been reported in thalassodromines (Aires et al. 2013) and anhanguerids (Wellnhofer 1985, 1991).

The neural spine is tall and blade-like (Fig. 5). The centrum is laterally pierced by a pneumatic foramen, which is absent in chaoyangopterids (Lü et al. 2008) and azhdarchids (Howse 1986). The size of this pneumatic foramen is comparable to the one found in anhanguerids (Wellnhofer 1985, 1991, Buchmann and Rodrigues 2019), and is much larger than that in the pteranodontoid *Pteranodon* (Bennett 2001) and tapejarids (e.g., Aires et al. 2013). There are also three pneumatic openings on the anterior and posterior articulation surfaces in some vertebrae – one above and one on each side of the neural canal (CP.V. 2445, CP.V 2317; Fig. 5g). In one mid-cervical element, the lateral

pneumatic openings at the anterior articulation are reduced or absent (Fig. 5d). In CP.V 2445, the neural arch on the left side is broken, revealing that the inner part of the vertebra is hollow and has the neural canal encased by a bony tube supported by trabeculae (Fig. 5f). Such a construction has been previously observed in one undescribed tapejarid (Kellner 2006) and might be a general feature of at least derived pterosaurs. This vertebra (CP.V 2445) also displays one foramen on each side of the hypapophysis. No cervical rib was found in the mid-cervical elements.

The sternum (CP.V 2069) is a large plate-like and thin quadrangular bone (Figs. 3, 6). During the collecting process the sternal plate (Fig. 6a) was separated from the anterior portion of the sternum (Figs. 6b, c). The cristospine is shallow and elongated, with a blunt anterior and ventral margin. At the base of the cristospine on the dorsal surface is a large foramen (Figs. 6b, c). Several elements of the thin “V” shaped gastralia are preserved. The scapula is an elongated bone with a straight shaft and a flattened and elongated proximal articulation (Fig. 7j). It shows a well-developed tuberculum at the lateroposterior margin, similar to that of *Caupedactylus* (Kellner 2013). On the lateral surface above the glenoid this bone shows a marked depression. The sole coracoid (CP.V 2083) attributed to this species is incomplete, lacking the glenoid portion (Figs. 7h-i). The developed coracoidal flange as the one reported in some azhdarchids (Kellner and Langston 1996) is absent. However, there is a broad tubercle on the ventroposterior margin (Fig. 7h), a feature commonly observed in tapejarids (Kellner 2013). The articulation with the sternum is dorsoventrally flattened, lacks a posterior expansion and is strongly concave. It further has the posterior portion more developed than the anterior one, giving it an asymmetric outline that, to our knowledge, has not been reported in any other pterosaur before (Figs. 7h-i).

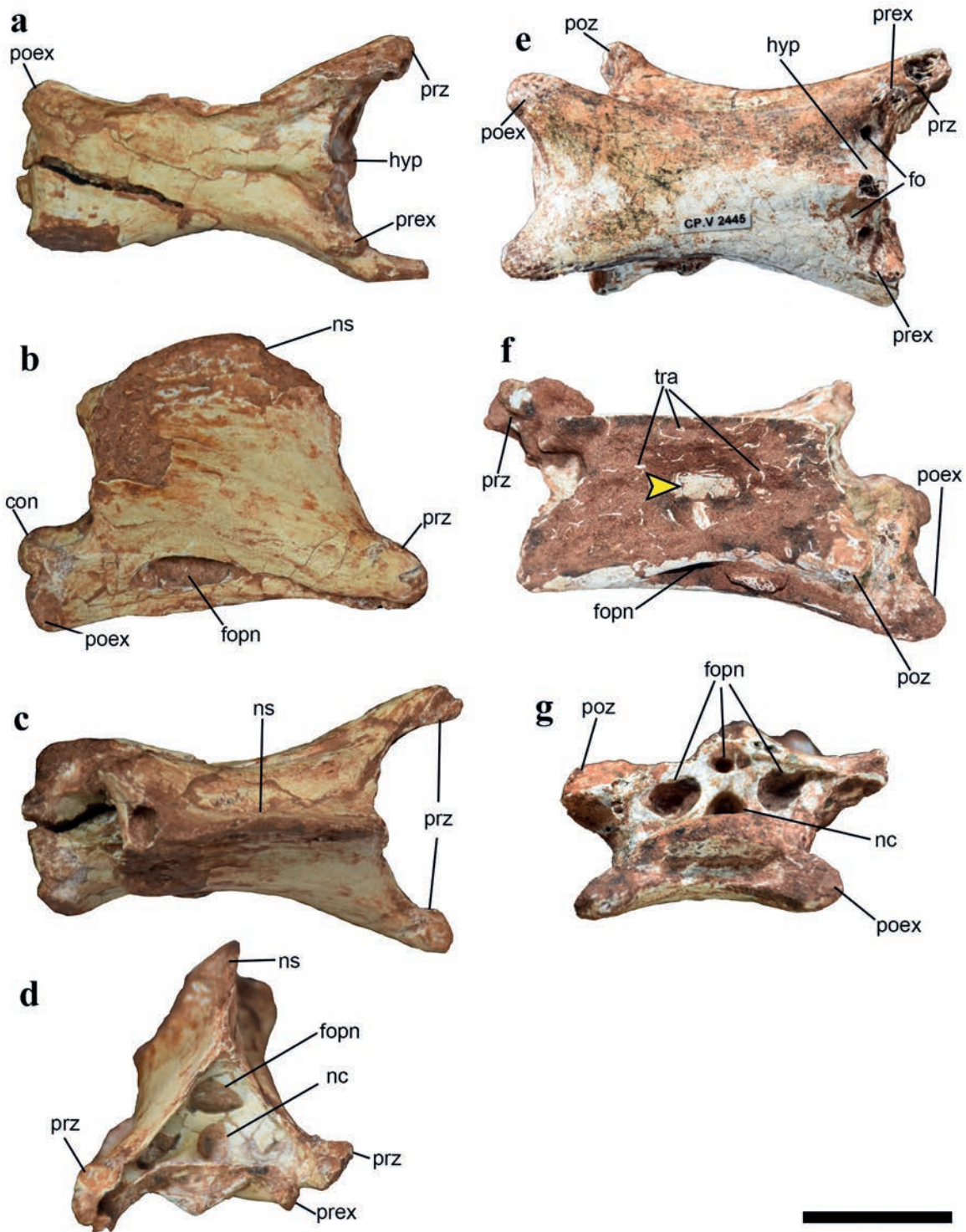


Figure 5 - Cervical vertebrae of *Keresdrakon vilsoni* gen. et sp. nov., CP.V 6495 in (a) ventral, (b) right lateral, (c) dorsal and (d) anterior views; CP.V 2445 in (e) ventral, (f) dorsolateral, (g) posterior views. Note the ossified tube that encloses the neural canal in (F) marked by an arrow. Abbreviations: con - condyle, fo - foramen, fopn - foramen pneumaticum, hyp - hypapophysis, nc - neural canal, ns - neural spine, poex - postexapophysis, poz - postzygapophysis, prex - preexapophysis, prz - prezygapophysis, tra - trabeculae. Scale bar = 20mm.

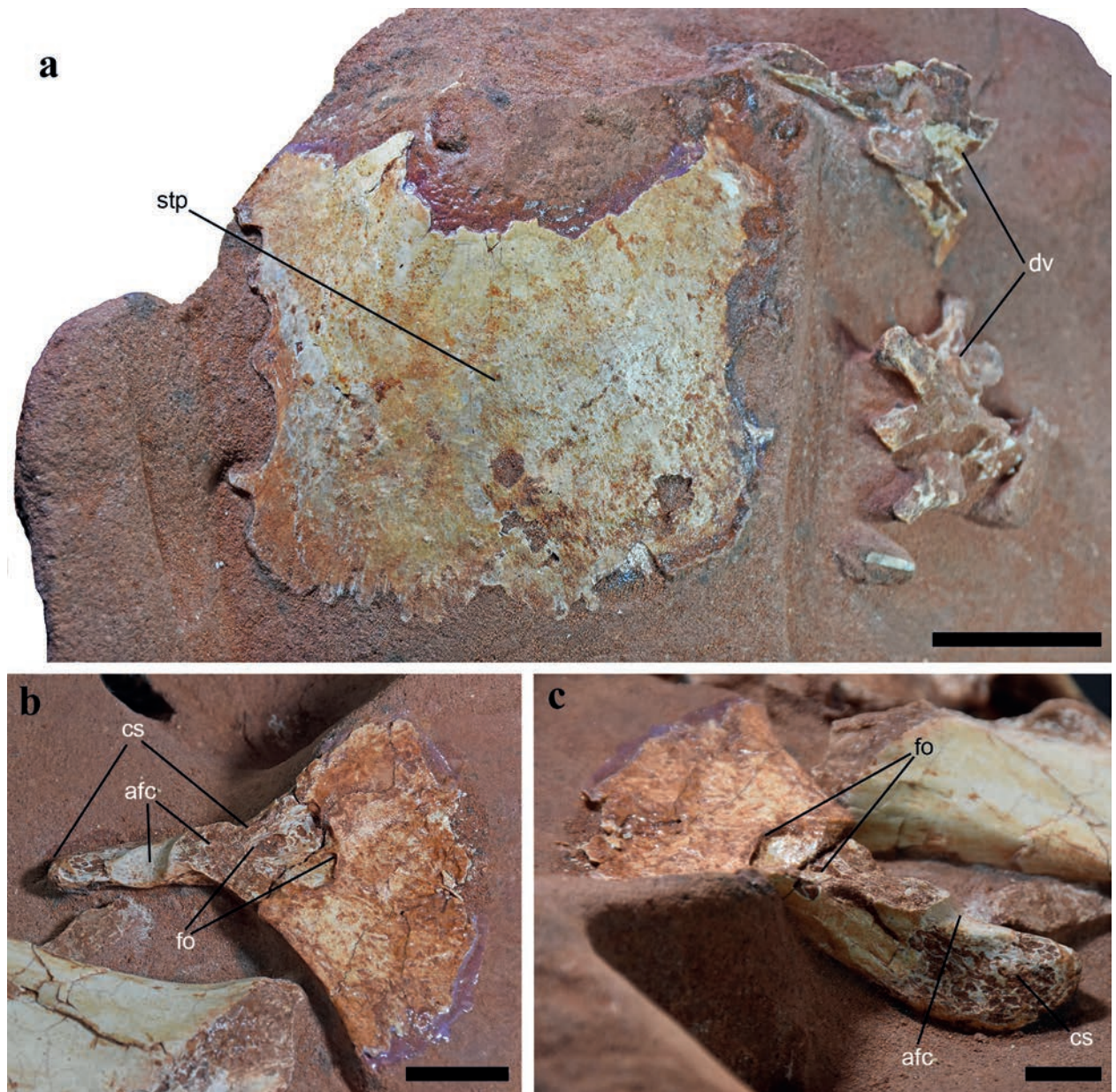


Figure 6 - Sternum of *Keresdrakon wilsoni* gen. et sp. nov. (CP.V 2069, part of the holotype). (a) ventral, cristospine in dorsal (b) and (c) right lateral views. Abbreviations: afc - articular facet for coracoid, cs - cristospine, fo - foramen, stp - sternal plate Scale bars = (a) and (b) 50mm, (c) 20mm.

Overall, the humerus (Figs. 7d-g) shows a similar shape to the one of *Caupedactylus* (Kellner 2013). The deltopectoral crest (CP.V 1011) is long and quadrangular in lateral view, with parallel margins. It is proximally placed and directed ventrally, curving gently inwards. While there is no pneumatic foramen on the dorsal surface of

the proximal portion, a large one can be found piercing the ventral surface, placed at the base of the deltopectoral crest (Fig. 7f), which is more developed than in *Caupedactylus* (Kellner 2013).

The ulna is a long bone with the proximal and distal articulations slightly twisted relative each other. In all of these elements attributed to

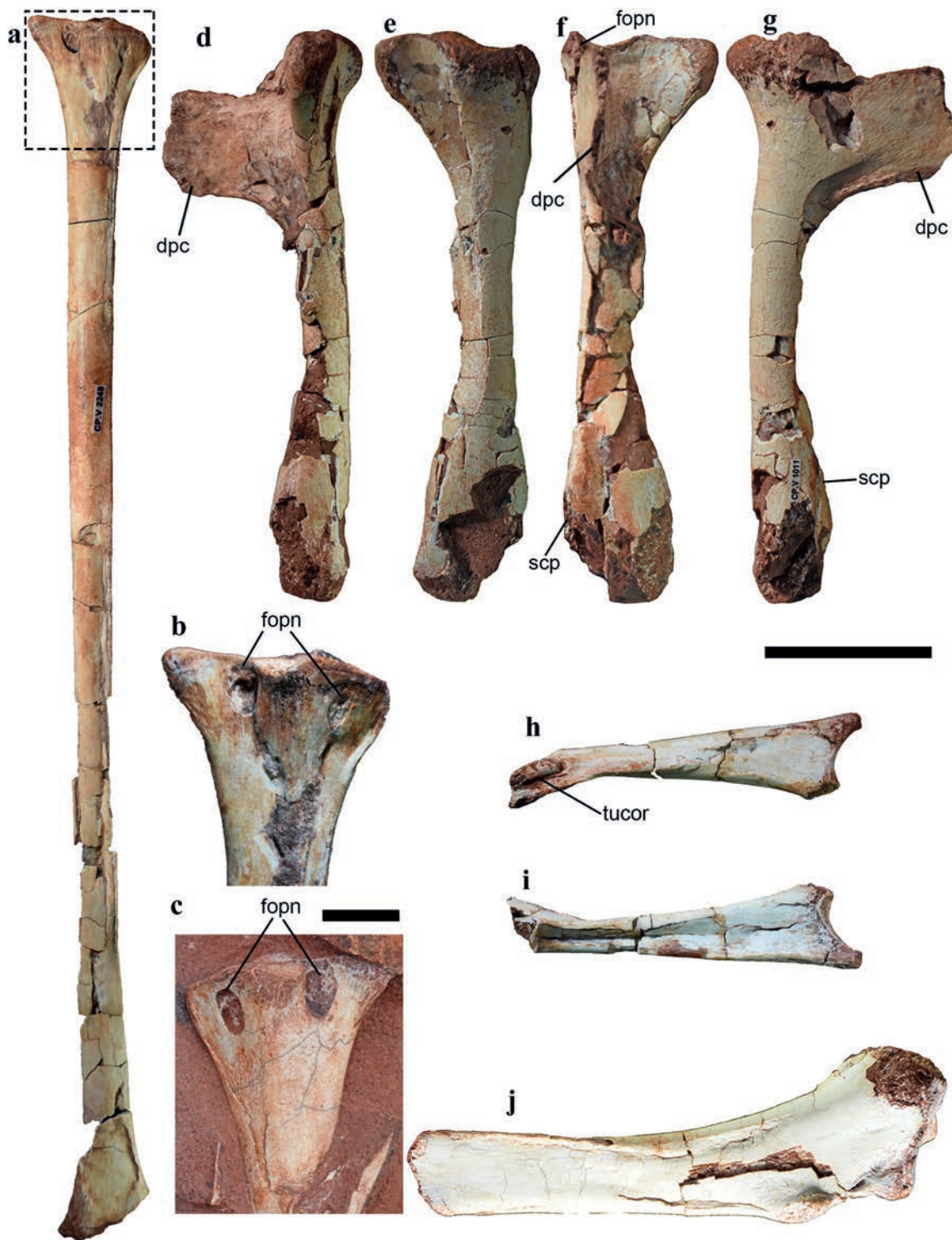


Figure 7 - *Keresdrakon vilsoni* gen. et sp. nov. (a) complete left first phalanx of manual digit IV (CP.V 2248), (b) proximal articulation of left first phalanx of manual digit IV (CP.V 2248), (c) proximal articulation of right first phalanx of manual digit IV (CP.V 2373); right humerus (CP.V 1011) in (d) medial, (e) dorsal, (f) ventral and (g) lateral views; left incomplete coracoid in (h) ventral and (i) dorsal views, (j) scapula in dorsal view. Abbreviations: dpc - deltopectoral crest, fopn - foramen pneumaticum, tucor - coracoidal tuberculum. Scale bars = (b) and (c) 10mm, all others 50mm.

this species, there is a marked depression on the posterior surface at the proximal articulation (CP.V 2073, CP.V 2077) showing that the ulnar epiphysis was unfused in these specimens (Fig. 9c). A developed foramen pierces the anterior surface of the proximal articulation. The distal articulation is flattened anteroposteriorly and shows a small ridge along the dorsal margin of the anterior surface. Although no radius and ulna can be confidently attributed to the same individual, in those specimens where both bones have about the same length, the diameter of the radius is about half that of the ulna, a common feature within azhdarchoids (Kellner 2003). The distal articulation of the radius has a flattened posterior surface, which is pierced by a pneumatic foramen, and a more irregular anterior surface that shows a long blunt ridge (anterior tubercle) at the lower ventral portion.

The first phalanges of the fourth wing finger that are attributed to *Keresdrakon* lack the extensor tendon process, which shows that it was unfused in all specimens (CP.V 2242, 2248, 2373; Figs. 7a-c). The shaft of the phalanges is slightly bowed anteriorly, with a concave anterior margin and a convex posterior one (Fig. 7a), a feature that has been observed in dsungaripterids (Wellnhofer 1978) and some tapejarines (Eck et al. 2011). These elements show a pneumatic foramen on the ventral side of the proximal articulation situated close to the posterior margin. All three also show a second pneumatic foramen closer to the anterior margin (Figs. 7b, c), which has never been reported in any pterosaur before. In some specimens this foramen is quite clear, while in others it is more difficult to observe due to compression.

The holotype (CP.V 2069) also shows the remains of a pelvic girdle (Fig. 8). The ilium is an elongated bone with a developed postacetabular process that has the anterior projection particularly expanded, as observed in some tapejarids (AWAK pers. obs.). This bone forms most of the acetabulum, a common feature in derived pterosaurs (Fig. 8a).

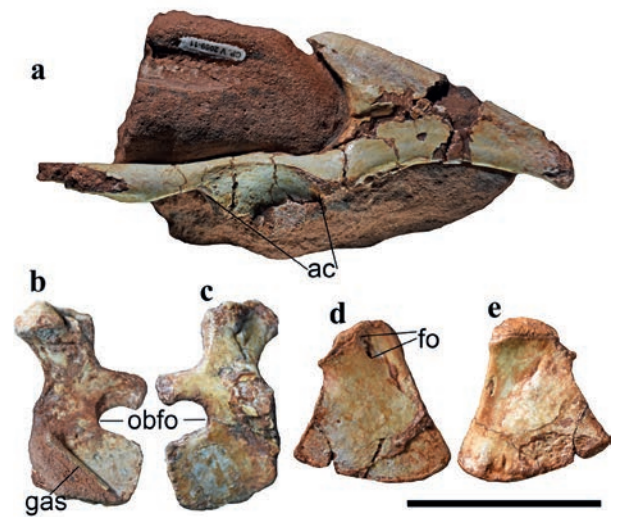


Figure 8 - *Keresdrakon wilsoni* gen. et sp. nov., pelvis (CP.V 2869, part of the holotype), (a) left ischium in lateral view; right pubis in (b) medial and (c) lateral views; right ischium in (d) lateral and (e) medial views. Abbreviations: ac - acetabulum, fo - foramen, gas - gastralia, obfo - obturator foramen. Scale bar = 50mm.

The pubis is a dorsoventrally elongated bone with a stout dorsal portion that contacts the ilium, followed by a thin bony plate that gently curves medially (Figs. 8b, c). The anterior portion of this bony plate further bends laterally to form the anterior opening of the pelvic canal. The ventral margin of the pubis is concave, while the posterior margin that forms the contact surface with the ischium is gently convex. This bone is perforated by a well-developed oval obturator foramen whose distal margin is formed by the ischium. Dorsal to this foramen the pubis forms a comparatively thick bony bar that has a convex posterior articulation where it joins the ischium. The obturator foramen in this species is similar in size at least to some tapejarines (Eck et al. 2011), but larger compared to most other groups of pterosaurs as, for example, anhanguerids and pteranodontids (Wellnhofer 1978, 1991, Bennett 2001, Naish et al. 2013). The ischium is a subtriangular plate that gently curves medially (Figs. 8d, e). The anterior and posterior margins are almost straight, while the ventral border is slightly concave. The anterodorsal corner has a

concave articulation surface that receives the dorsal part of the pubis, while the posterodorsal corner is displaced medially. On the lateral surface there is a small foramen, which has not been reported in other pterosaurs (Wellnhofer 1978, 1991, Bennett 2001, Naish et al. 2013).

The femur is bowed anteriorly (Fig. 3). Its proximal articulation is made by a well-developed femur head with a constricted neck that is set from the shaft at $\sim 135^\circ$. The femur head forms a convex rounded surface with a suboval outline and lacks a medial notch observed in some pterodactyloids. A pneumatic foramen is present on the posterior surface between the femur head and the triangular greater trochanter. The tibia is a long and much thinner element than the femur. No fibula was found suggesting that this bone was not fused in the material recovered from the new species.

OSTEOHISTOLOGY

In order to assess a preliminary histological analysis of *Keresdrakon vilsoni*, two bones were sectioned: one ulna (CP.V 2077) and one incomplete portion of a large element lacking articulations (CP.V 2374), interpreted as the first wing phalanx (Fig. 9). Overall, the osteohistological pattern is very similar in both samples, showing fibrolamellar primary tissue, a feature observed in most pterosaurs (de Ricqlès et al. 2000, Prondvai et al. 2012, Eleutério et al. 2016). The cortex thickness varies from 410 μm in the first wing phalanx (CP.V 2374) to 850 μm in the ulna (CP.V 2077). Bone microstructure shows dispersed osteocytes lacunae in the cortex with some plexiform and anastomosed canals randomly deposited.

The ulna (CP.V 2077) shows some vascular canals accessing the periosteal surface (Fig. 9d), a specific condition for juvenile to sub-adult individuals (Steel 2008). There are no structures throughout the entire bone circumference that point to an advanced maturity of this individual, such as

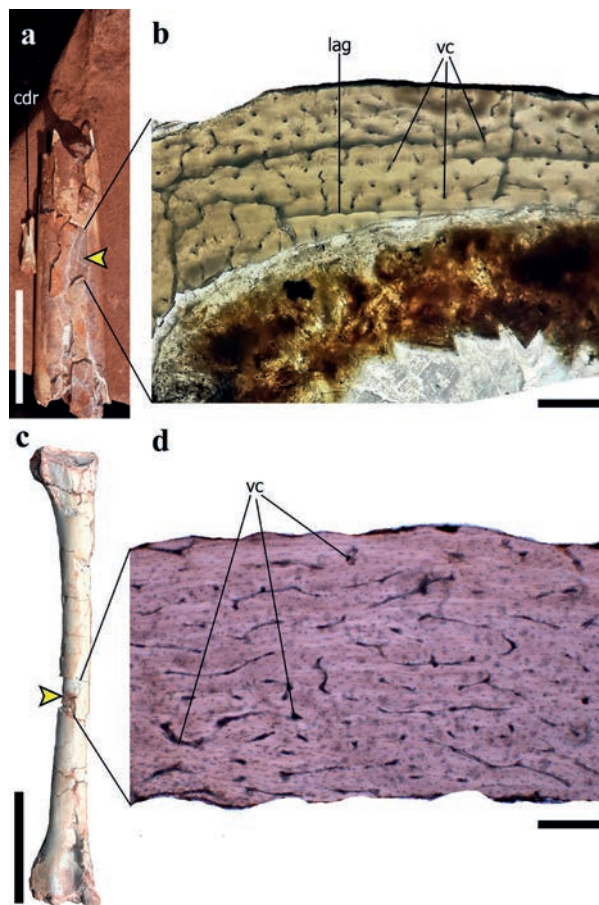


Figure 9 - Osteohistological sections of *Keresdrakon vilsoni* gen. et sp. nov. appendicular elements. Incomplete first wing phalanx of digit four (CP.V 2374) (a) and osteohistological cross section of the diaphysis; left ulna (CP.V 2077) (c) and respective osteohistological cross section of the diaphysis. Abbreviations: lag - line of arrested growth, vc - vascular canal. The yellow arrows point where the samples were taken. Scale bar = (a) and (c) 50mm, (b) and (d) 200 μm .

growth marks, bone remodeling structures or an external fundamental system (Steel 2008, Kellner et al. 2013, Andrade et al. 2015). Furthermore, the absence of the endosteal lamella suggests that this bone belongs to a juvenile. In *Hamipterus* and some anhanguerid pterosaurs the size variation is reflected in the osteohistological pattern of each bone (Sayão 2003, Eleutério et al. 2015, Wang et al. 2014), which establishes a correlation between size difference and ontogenetic development (Wang et al. 2014, 2017). The osteohistological features of this specimen are consistent with a juvenile but not

a neonate (see Wang et al. 2017 for histological structures of neonates and embryos). Several grains of silica and quartz fill the inner medullary cavity. These grains have possibly been deposited during the bone transport process, pointing to bone fragmentation prior to fossilization.

The most different pattern among samples belongs to the first wing phalanx (CP.V 2374), which has a unique growth mark located in the deep portion of the cortex (Fig. 9b). The presence of cyclical growth marks is continuous and partly caused by endogenous physiological processes (Eleutério et al. 2015), with lines of arrested growth being common in vertebrates as general. However, these marks are hardly found in pterosaurs, but have been recorded in Cretaceous anhanguerids (Sayão 2003, Eleutério et al. 2015) and Jurassic pterosaurs (Padian et al. 2004). The presence of these growth marks suggests that this bone belongs to an ontogenetically less developed individual compared to others.

PHYLOGENETIC RESULTS

Phylogenetic analysis resulted in 6 most-parsimonious trees (MPTs), with 341 steps, a consistency index of 0.66 and retention index of 0.87. Azhdarchoidea is supported by the following synapomorphies: character state 7(2) - a dorsoventrally elongated orbit (piriform); 12(3) - slit-like lower temporal fenestra; 56(2) - a cranio-mandibular articulation under the anterior margin of the orbit; and 75(3) - a long extension of the contact surface of opposing dentaries, up to 55% the mandible length. Furthermore, *Keresdrakon wilsoni* gen. et sp. nov. was recovered as a sister taxon of the Tapejaridae (Fig. 10), which would enable to recognize a non-tapejarid lineage within the Tapejaromorpha (Andres et al. 2014). Tapejaromorphs are characterized by two synapomorphies: character state 79(1) - a dentary ossified sagittal crest; and 118(1) - coracoid with

developed tuberculum on the posteroventral margin. The Tapejaridae (*sensu* Kellner 2003) is supported by character state 27(1) - anterior portion of the rostrum forming a high ossified plate, which is absent in *Keresdrakon*.

DISCUSSION

Two species are considered sympatric when they show the same or overlapping geographical distribution, irrespective of their macrohabitat (Rivas 1964), and there are several examples in modern environments (e.g., Leal and Fleishman 2002, Luiselli 2006, Pigot and Tobias 2015). Even though sympatry is normally used for closely related species and associated with speciation (e.g. Mayr 1942, Diamond 1975, Van Valen 1976, Pigot and Tobias 2015), there are cases in which this concept is applied to phylogenetically more distant taxa (e.g., Magnusson 1985, Rao and Choudhury 1990, Soler and Møller 1990, Choudhary et al. 2018).

Sympatry in the fossil record, particularly considering extinct vertebrates, is difficult to be established since different individuals that have never shared the same habitat might be preserved together in the same deposit as a result of time averaging (e.g., Behrensmeyer et al. 2000). Bone beds or the occurrence of specimens in close associations are occasionally used as indication of coexistence (e.g., Cabreira et al. 2016), although caution is always needed (e.g., Rogers and Kidwell 2000). This situation is even more complicated in pterosaurs due to the lack of bonebeds (e.g., Kellner 2017). So far, some authors assume sympatry for these flying reptiles if species or genera occur in the same stratigraphic unit (e.g., Upchurch et al. 2015, Longrich et al. 2018), but direct and more conclusive evidences are difficult to obtain.

The bonebeds of Cruzeiro do Oeste, however, represent a particular case that provides, to our knowledge, the first direct evidence for sympatry in Pterosauria. Young (1973) has reported the

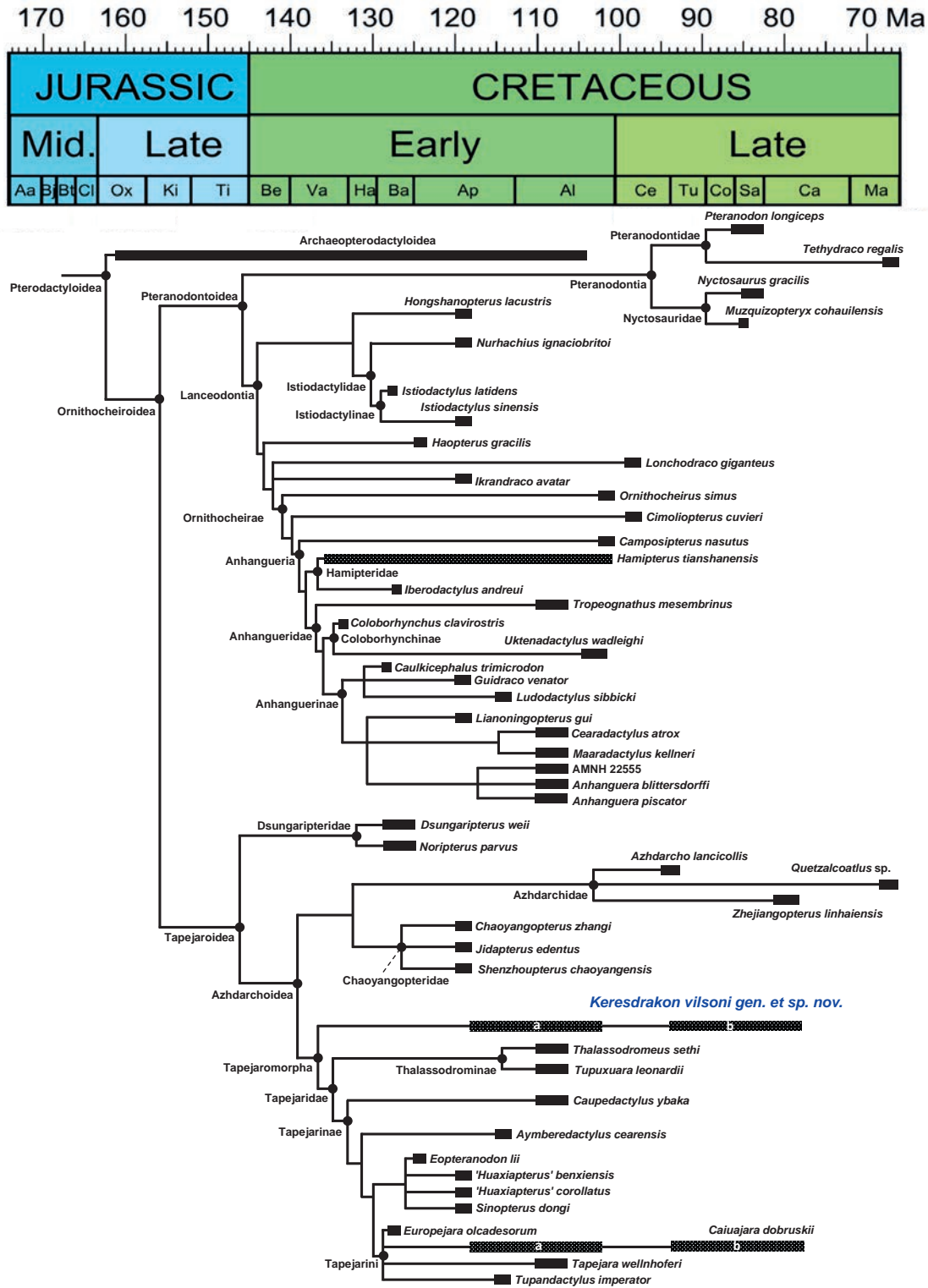


Figure 10 - Time-calibrated phylogenetic tree showing the relationships of *Keresdrakon vilsoni* gen. et sp. nov. within the Pterodactyloidea. Intermittent bars show uncertain temporal range. Letters in intermittent bars indicate controversial age hypotheses of the Goio-Erê Formation: (a) Albian-Aptian; (b) Turonian-Campanian. Outgroup relationships are not shown (see Holgado et al. 2019 - Supplementary Information for further details). Stratigraphic chart modified from Cohen et al. (2013).

occurrence of two taxa in the same deposits in two localities in Wuerhe, but it is not clear if they actually came from the same horizon, as is the case of the material studied here. The 'cemit rio dos pterossauros' site also shows the co-occurrence of a theropod dinosaur and two flying reptile species that can confidently be regarded as part of the same paleobiological community (e.g., Figs. 11-16).

The majority of bones collected at the 'cemit rio dos pterossauros' site was found isolated, and only very few can be assigned to the same individual. This is also the case of *Caiuajara dobruskii*, with only one articulated specimen and few others presenting skeletal elements in close association. The same condition is observed for the dinosaur *Vespersaurus*, for which at least 12 individuals have been discovered. Except for some feet, two arms and few pelvic elements, all specimens known to us were found disarticulated, albeit in close association (AWAK and LCW pers. obs., specimens housed in CENPALEO and in Cruzeiro do Oeste). The holotype of *Vespersaurus paranaensis* is no exception, for which the assignment to the same individual of a few vertebrae from different parts of the body, pelvic elements and pes seems to be unlikely.

The material of *Keresdrakon vilsoni* also shows this taphonomic pattern: most elements were found isolated and only a few were associated. The great exception is the holotype (CP.V 2069). In terms of paleoecological interpretations, the disarticulated state of the material suggests that pterosaurs and dinosaurs died around an oasis, with their skeleton exposed for some time that led to disarticulation, and then accumulated due to episodic events of high energy such as desert storms.

At least four of such events could be identified and resulted in bone beds. In three of them (from base to top, A, B, and C, Fig. 2), the pterosaurs *Caiuajara dobruskii* and *Keresdrakon vilsoni*, as well as the dinosaur *Vespersaurus paranaensis*, were found in close association (Figs. 11-16). The repeating pattern of this close association argues

that *Keresdrakon*, *Caiuajara* and the dinosaur were coeval. As was pointed out before (e.g., Kellner 2010, 2017), several pterosaurs were found in the same deposit such as the Solnhofen Limestone (Wellnhofer 1975, Bennett 1996), Yixian and Jiufotang Formations (e.g., Wang and Zhou 2006), Crato and Romualdo formations (e.g., Maisey 1991, Kellner 2006, Unwin and Martill 2007, Vila Nova et al. 2011), Cambridge Greensand (e.g., Unwin 2001, Rodrigues and Kellner 2013), and Niobrara Chalk (Bennett 2001, 2003, Kellner 2010). However, the lack of stratigraphic control and the absence of specimens showing more than one individual preserved in close association, conclusively demonstrating that different pterosaurs were recovered from the exact same level within these deposits, is a problem that has hampered several biological questions regarding these flying reptiles (e.g., Kellner 2010, Wang et al. 2014).

Still considering taphonomy, the number of elements referable to *Caiuajara* by far outnumber all others. There are well over 100 individuals identified from this small pterosaur and although some specimens clearly show the orientation of elements indicating the action of water currents, there is no specific predominance of one bone over another. Only pelvic elements are scarcer, to which there is no particular explanation.

The second more common fossil is *Vespersaurus*, known by at least 12 individuals (based on stratigraphy and number of elements of the hind limb). Contrary to *Caiuajara*, most specimens of this dinosaur recovered so far belong to the hind limb (including feet) and the pelvis, with rare remains of the skull and arms. Metatarsals II and IV, which in the original description were described based on pictures (Langer et al. 2019) indicating that the specimen is lost or was destroyed, are very compressed lateromedially (Fig. 13). There are also many caudal vertebrae, several articulated (Figs. 11, 12). The amount of elements of *Vespersaurus*



Figure 11 - Sample (CP.V 6559) from bonebed A of Figure 2, showing on the left (a) side a partial skeleton of the pterosaur *Caiuajara dobruskii* and on the right (b) the remains of the dinosaur *Vespersaurus paranaensis*. White line shows the limits between the two specimens. Scale bar = 100mm.

paranaensis that occurs in three bonebeds, suggests that this species might have been gregarious.

Bones of *Keresdrakon vilsoni* are the rarest of the three species. Referring isolated bones to a specific taxon can be difficult, as well as distinguishing diagnostic from ontogenetic features, which is a problem not restricted to pterosaurs (e.g., Müller 2017). Due to the morphological similarity of postcranial elements of pterosaur groups in general (e.g., Kellner 2003, Unwin 2003, Vila Nova et al. 2015), it is possible that difficulties might arise in separating larger individuals (sub-adults) of *Caiuajara dobruskii* from smaller ones (juveniles) of *Keresdrakon vilsoni*. The anatomical differences

in the cranial anatomy between both pterosaurs of the 'cemitério dos pterossauros' site are striking, but the main differences in the postcranial skeleton are primarily restricted to the presence of pneumatic foramina. While *Keresdrakon vilsoni* possesses an additional pneumatic foramen on the ventral surface at the anterior half of the proximal articulation of the first wing phalanx (absent in *Caiuajara dobruskii*), it lacks a pneumatic foramen at the dorsal surface of the proximal articulation of the humerus (present in tapejarine pterosaurs, including *Caiuajara*). Both species show the lateral surface of the mid-cervical vertebrae pierced by a pneumatic foramen (sometimes two in *Caiuajara*),



Figure 12 - Sample (CP.V 7228) from bonebed A of Figure 2 showing the close association of a femur of *Caiuajara dobruskii* (a) and the incomplete tail and forelimb (including partial manus) of *Vespersaurus paranaensis* (b), separated by the white line. Scale bar = 100mm.

which in *Keresdrakon* is much larger. Another difference is the strongly asymmetrical sternal articulation of the coracoid in *Keresdrakon vilsoni*, not observed in several coracoids recovered from *Caiuajara dobruskii*. Nonetheless, the minimum number of *Keresdrakon* individuals recorded so far is three. Based on the distribution of the bones throughout the section the actual number must be higher. Despite the small sample, no preservation bias of any particular portion of the skeleton is detectable, with cranial and postcranial elements being recovered. There is also no specific taphonomic reason for the comparatively low number of preserved elements of this pterosaur, which might have been the least represented of the three species that occurred in this environment (not including the lizard *Gueragama*). Based on the present number of specimens, *Keresdrakon vilsoni* might have had a solitary behavior and

was not gregarious as inferred for the dinosaur and *Caiuajara*.

Lastly, the lizard *Gueragama sulamericana*, known from two fragmentary specimens only (Simões et al. 2015), is the sole other taxon recognized so far from the 'cemitério dos pterossauros' site. Even though the exact stratigraphic level from where this material came from is unknown, this lizard was most likely part of the same paleobiological community of the dinosaur and the pterosaurs.

Sedimentological data supports the interpretation that the Goio-Erê Formation was formed in a desert environment with interdunal wetland (Milani et al. 2007, Fernandes et al. 2009). Whilst *Caiuajara dobruskii* most likely was a frugivore, a feeding behavior suggested for tapejarines in general (Kellner 1989, Wellnhofer and Kellner 1991, Wang and Zhou 2003a, Vullo



Figure 13 - Paratype of *Caiuajara dobruskii* (CP.V 1003) (a) and a partial articulated hind limb of *Vespersaurus paranaensis* with tibia, fibula, tarsals (including astragalus) and metatarsals on the upper right corner (b). This specimen was collected from bonebed C of Figure 2. White line shows the limits of the two specimens. Scale bar = 100mm.

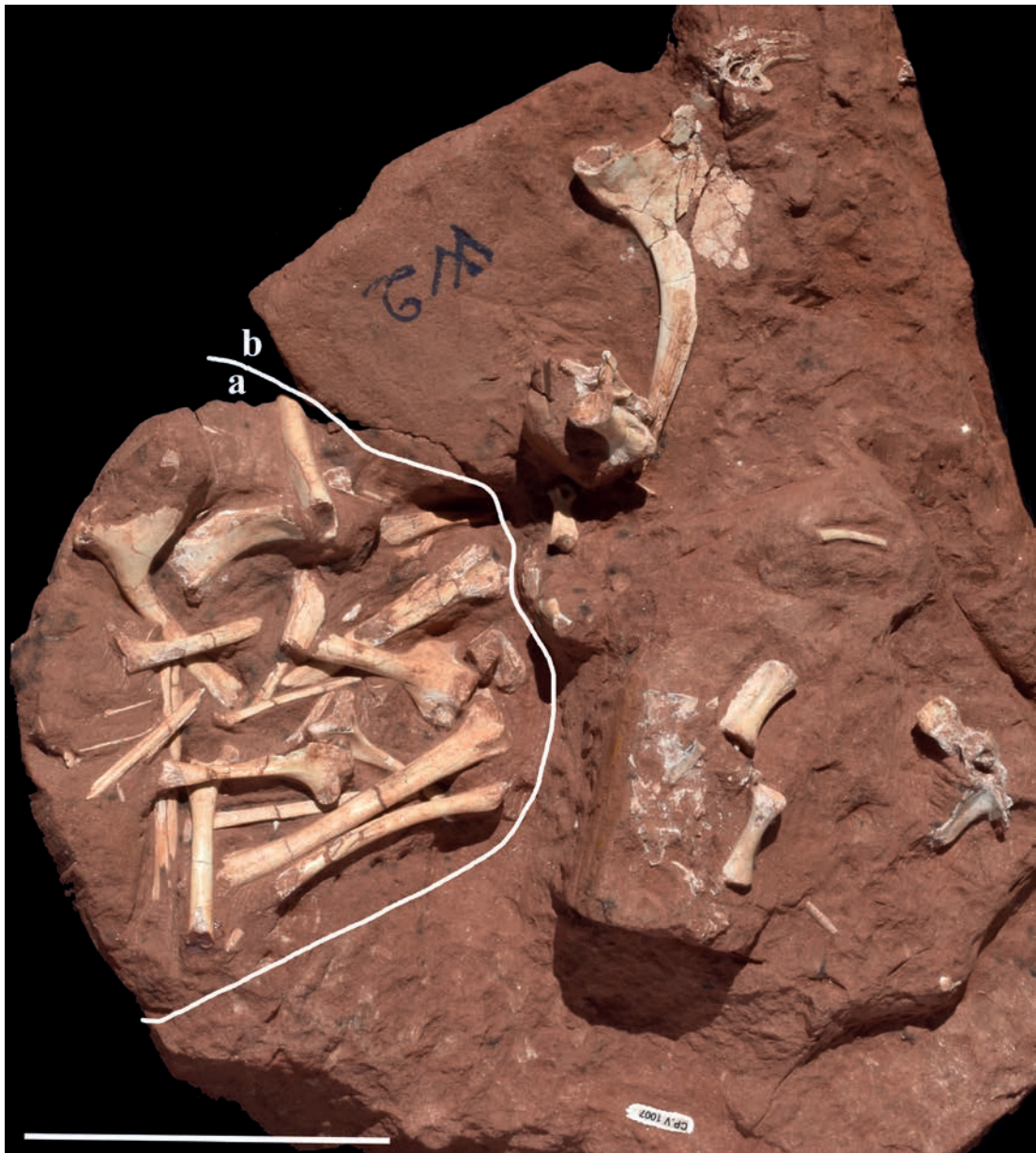


Figure 14 - Sample (CP.V 1007) from bonebed level C of Figure 2, showing the close association of *Caiuajara dobruskii* (a) and *Vespersaurus paranaensis* (b) separated by the white line. Scale bar = 100mm.

et al. 2012), this does not seem to have been the case of *Keresdrakon vilsoni*. Taken into account that deserts tend to have limited resources, niche partitioning concerning these pterosaurs would be feasible, particularly if they were sympatric, which is considered here. Therefore, we can infer that *Keresdrakon vilsoni* might have behaved as an opportunistic predator or a scavenger (Fig. 17).

According to previous studies, a long and laterally flattened rostrum like the one of *Keresdrakon* is appropriate to support low bite pressures restricted to the jaw tips and the straight jaw margins, as has been proposed for azhdarchids (Witton and Naish 2008). Therefore, subjugation of larger prey, such as the dinosaur *Vespersaurus*, might have been more difficult for this pterosaur despite its larger

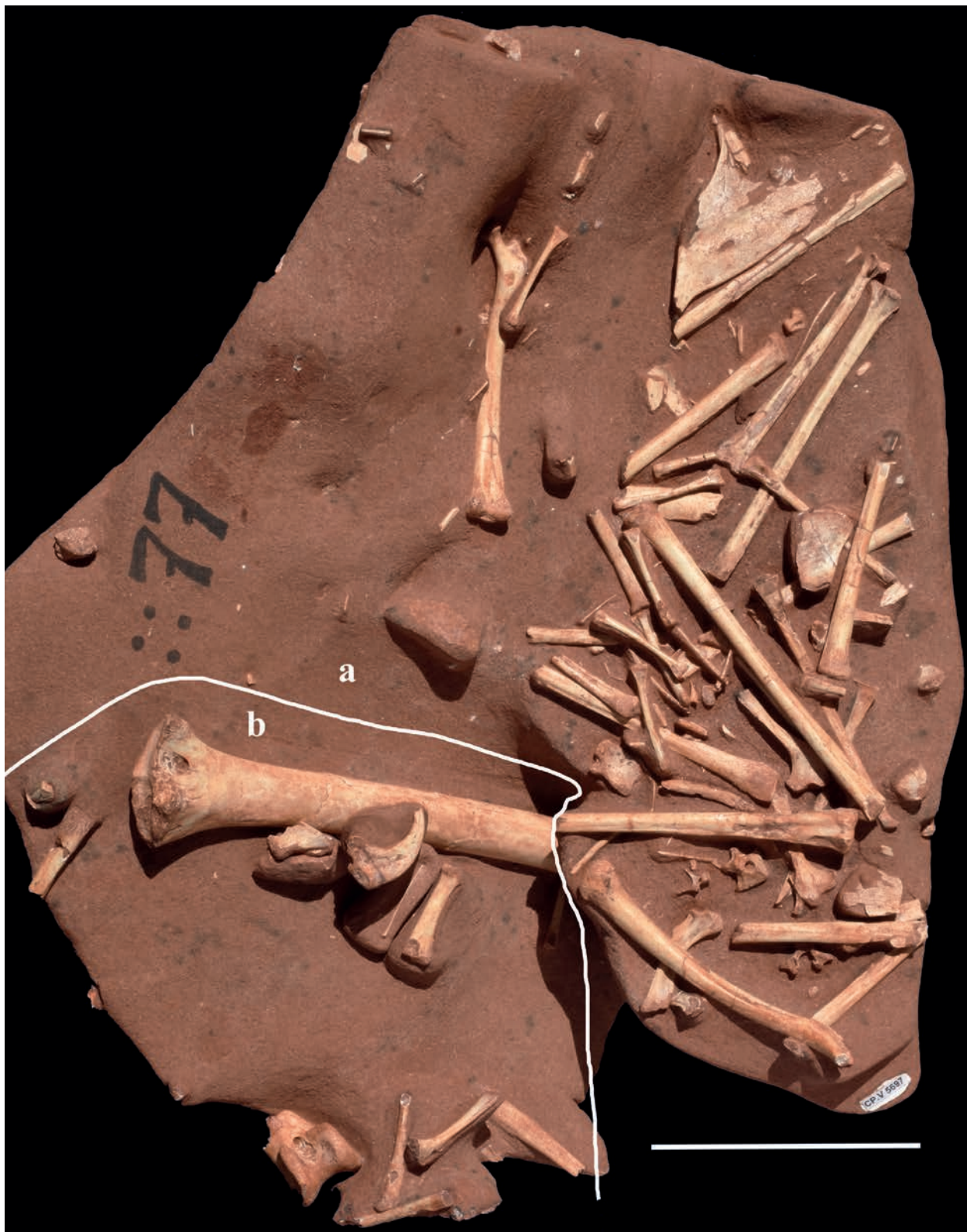


Figure 15 - Sample (CP.V 5697) from bonebed C of Figure 2, showing on the right (a) a partial skeleton of the *Caiuajara dobruskii* the left (b) elements of *Keresdrakon vilsoni* gen. et sp. nov. separated by the white line. Scale bar = 100mm.

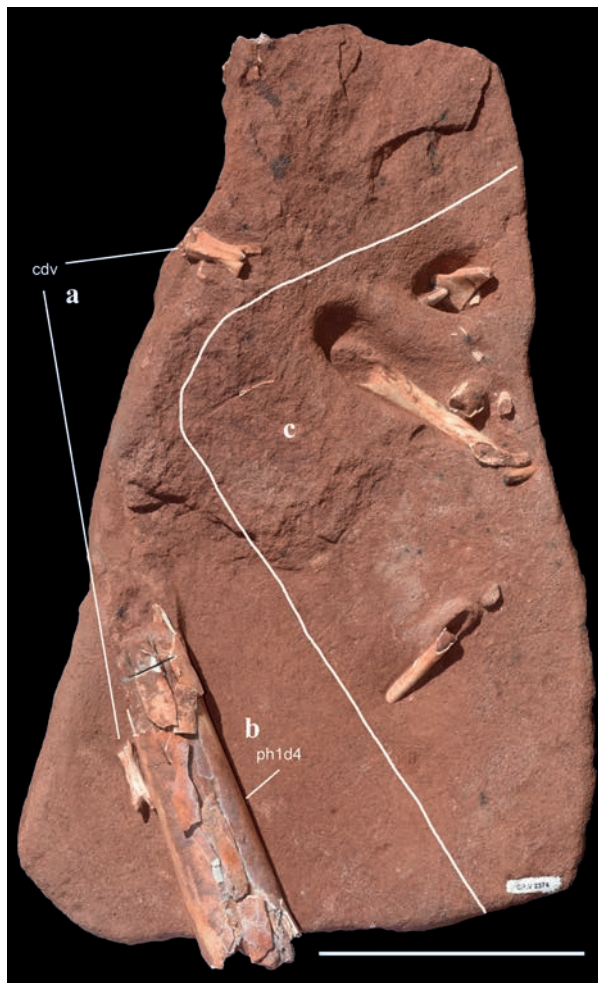


Figure 16 - Sample (CP.V 2374) from bonebed C of Figure 2, showing two caudal vertebrae from *Vespersaurus paranaensis* (a), the diaphysis of a large first phalanx of manual digit IV of *Keresdrakon vilsoni* gen. et sp. nov. (b), and bones of *Caiuajara dobruskii* (c), separated by the white line. Abbreviations: cdr - caudal vertebrae, ph1d4 - first phalanx of manual digit IV. Scale bar = 100mm.

size, which could better handle smaller or immobile food items such as carcasses. This feeding behavior is observed in the extant marabou stork (Kahl 1966) *Leptoptilos crumenifer* (Lesson, 1831). The feeding preference of this bird comprises mainly carrion and scraps, but it will opportunistically eat almost any animal matter that it can swallow, including small mammals and reptiles such as crocodile hatchlings and eggs (Hancock et al. 1992). Considering the little diverse fossiliferous record of the Caiuá

Group at the 'cemitério dos pterossauros' site, *Keresdrakon* could probably prey on small lizards such as *Gueragama sulamericana*. According to Simões et al. (2015) the latter is assigned to have presented the same habit as that of modern agamid lizards in arid regions, which is to live in burrows to avoid the arid weather. Additionally, *Keresdrakon* might have also feed on eggs, younglings or even juveniles of *Caiuajara dobruskii*, which was the predominant species in this region during part of the Cretaceous.

Regarding carrion feeding hypothesis, so far there have been only *Caiuajara* and *Vespersaurus* coming from these layers. Although admittedly speculative, it is most likely that *Keresdrakon* might have fed on their carcasses, particularly on that of the dinosaur. As for *Vespersaurus*, its primary food resource might have been *Caiuajara*, which is found in large numbers in this deposit.

The lateral surface of the rostral end of the skull of CP.V 2068 is quite rough (unlike the mild condition observed in CP.V 2069), suggesting that this specimen could have been exposed before burial. The roughness aspect of the bone surface is considered as an indicator of ontogeny in pterosaurs (Bennett 1993, Steel 2008). In the *Pteranodon* specimens, this roughness (grain pattern for Bennett 1993) is only present in some specimens with non-ossified epiphyses, reinforcing the hypothesis that this characteristic is present in juveniles. Both samples analyzed for histological studies in *Keresdrakon* had open vascular canals in the periosteal region (CP.V 2077 and CP.V 2374), which is also an osteohistological characteristic pointing to juveniles (de Ricqlès et al. 2000, Steel 2008). Therefore, features such as open canals in the periosteum and the roughness or granulation patterns endorse the interpretation of these specimens between ontogenetic stages OS2 and OS3 of Kellner (2015).

The few elements of *Keresdrakon vilsoni* analyzed show a distinct osteohistological pattern



Figure 17 - Reconstruction of the paleoenvironment showing the possible interaction of the vertebrate fauna recovered from the 'cemitério dos pterossauros' site. See text for details. Artwork by Maurilio Oliveira.

from that of *Caiuajara dobruskii*. The latter present a highly vascularized plexiform tissue (Sayão et al. 2018), absent in the bones of *Keresdrakon* studied here, which have a low vascularized cortex, with few vascular canals connected (anastomosed). Although both taxa present fibrolamellar complexes, the plexiform tissue of *Caiuajara* has additional radial connections between vascular canals. Both types of histological features are indicative of fast growth rates (Chinsamy-Turan 2005), although the plexiform tissue is considered to have slightly denser vascular canals than those of the laminar tissue (Francillon-Vieillot et al. 1990). Thus, it is not possible to establish differences in growth rates between the specimens analyzed of both pterosaur species based only on their vascular arrangement. In any case, the bones studied here indicate high growth rates for both species.

Regarding bone maturity, *Caiuajara* shows some signs of remodeling (Sayão et al. 2018) represented by secondary osteons in the fourth metacarpal (CP.V 2061), which are absent in both *Keresdrakon* samples. Although this difference may be related to a sampling problem, it suggests that the population of *Caiuajara* may present individuals slightly more ontogenetically developed than *Keresdrakon*. Fused scapulocoracoids and several first wing phalanx with the extensor tendon process fused agrees with this supposition. Further osteohistological analyzes are needed to support this observation.

Comparisons with *Tupuxuara leonardii* (Iwaki specimen) and *Caupedactylus* (Kellner 2013), particularly regarding the humerus length, suggest that *Keresdrakon vilsoni* had a wingspan of approximately 3 m, quite larger than that of *Caiuajara dobruskii* (Manzig et al. 2014: 0.65 to 2.35 m). Taking into account that they are young individuals this proportion could be even higher.

CONCLUSIONS

The coexistence of fossil vertebrates, including pterosaurs, are hard to be proven in the fossil record, specially cases of sympatry. Regarding pterosaurs, there must have been several places along deep time where closely related species might have overlapped and shared similar geographic distribution. The challenge is to find direct evidences of this. The 'cemitério dos pterossauros' site represents the co-occurrence of distinct pterosaur species in the same bone beds, showing that *Keresdrakon* and *Caiuajara* were coeval. This site also shows that the dinosaur *Vespersaurus paranaensis* shared this ancient desert environment with these two flying reptiles. While *Caiuajara*, despite being small and therefore potentially having a more fragile skeleton, by far outnumber the other taxa and is one of the few examples in the fossil record that might argue for gregarious behavior in pterosaurs, *Keresdrakon vilsoni* was scarcer and apparently represents a species with solitary behavior. We advocate that both specialized in different feeding items of this most likely depauperate environment. *Caiuajara* is regarded as being frugivorous and *Keresdrakon* might have been an opportunistic predator or a scavenger feeding at small animals or carcasses such as that of *Vespersaurus*. The latter might have made a living by hunting individuals of *Caiuajara dobruskii* that were abundant. All three were part of a paleobiological community that existed in this region during part of the Cretaceous.

As has been pointed out before (Kellner 2012), the outcrops in the region of Cruzeiro do Oeste, more specifically deposits from the Caiuá Group as the Goio-Erê formation, might turn out to become the 'Brazilian Mongolia' in terms of fossil vertebrates. The hundreds of fossils from two pterosaur species and one theropod dinosaur, as well as the occurrence of a lizard, endorse this potential. It is also likely that the future might show additional taxonomic groups like mammals and other reptiles.

More fieldwork and careful collection of specimens might contribute to a better understanding of the ecosystem of ancient Cretaceous deserts that, despite its general depauperate conditions, had areas where life could prosper.

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AUTHOR CONTRIBUTIONS

AWAK and LCW conceived and designed the study and performed fieldwork that resulted in the collection of the material housed in CENPALEO and in Cruzeiro do Oeste; AWAK, BH and JMS wrote the main manuscript; LCW conducted the geological study; BH and AWAK performed the phylogenetic analysis; RAMB and JMS did the osteohistological analysis. All authors contributed and reviewed the manuscript.

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