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Pterosaur Tracks from the Upper Cretaceous Anacleto Formation (Neuquén Basin), Northern Patagonia, Argentina: Insights into Campanian Pterosaur Diversity in Gondwana

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Abstract: The Campanian Anacleto Formation holds an abundant and diverse ichnofossil and body-fossil vertebrate record. Despite the striking diversity of this record, pterosaur fossils had never been described from the unit. Here, we report four pterosaur manus tracks from fluvial red beds cropping out in the Área Natural Protegida Municipal Paso Córdoba (Río Negro Province, northern Patagonia, Argentina). Tracks are longer than wide, tridactyl with digit impressions of different lengths (I < II < III), anteriorly directed and laterally asymmetrical. Being on loose slabs and lacking direct examination of pes morphology, the material is classified as undetermined pterosaur tracks. The new find represents the first occurrence of pterosaurs from the lower–middle Campanian of Argentina and one of the few evidences from South America for this time interval. In addition, it is one of the few ichnological pterosaur records from Gondwana, thus shedding light on the palaeobiogeography of this clade during the latest Cretaceous. Pterosaur tracks from the Anacleto Formation allow us to integrate the body-fossil record from the unit and to add a new component, along with birds, to the flying archosaur fauna coexisting with non-avian dinosaurs, notosuchians, chelonians, squamates and mammals in the Campanian of northern Patagonia.

Keywords: Pterosauria; South America; ichnology; Cretaceous; fluvial environment; Neuquén Group; vertebrate diversity

1. Introduction

The Neuquén Basin is, in origin, a back-arc, rift-related basin in southwestern South America that presents a Late Triassic–Early Cenozoic succession with a quite varied and abundant paleontological record [1] (and references therein). The Neuquén Group, developed during the early foreland phase of the Neuquén Basin [2], represents a succession of

Upper Cretaceous continental deposits (Cenomanian–middle Campanian), outstanding for its abundant and diverse fauna of terrestrial tetrapods [3–7]. The lower to middle Campanian Anacleto Formation is the uppermost unit of the succession [7] and preserves a vastly diverse paleontological record. The osteological vertebrate remains from this lithostratigraphic unit include fishes, lizards, snakes, chelids, mammals, dinosaurs and crocodylomorphs [7–15]. The ichnological record is represented by sauropod, theropod and avian tracks [5,16–21], while oological remains consist of thousands of eggs, some of which include embryos, from the Auca Mahuevo locality in Neuquén province [3,22–26].

Several vertebrate tracks have been recently recovered from the Anacleto Formation at the Área Natural Protegida Municipal (ANPM), Paso Córdoba, General Roca, Río Negro Province, Argentina (Figure 1).

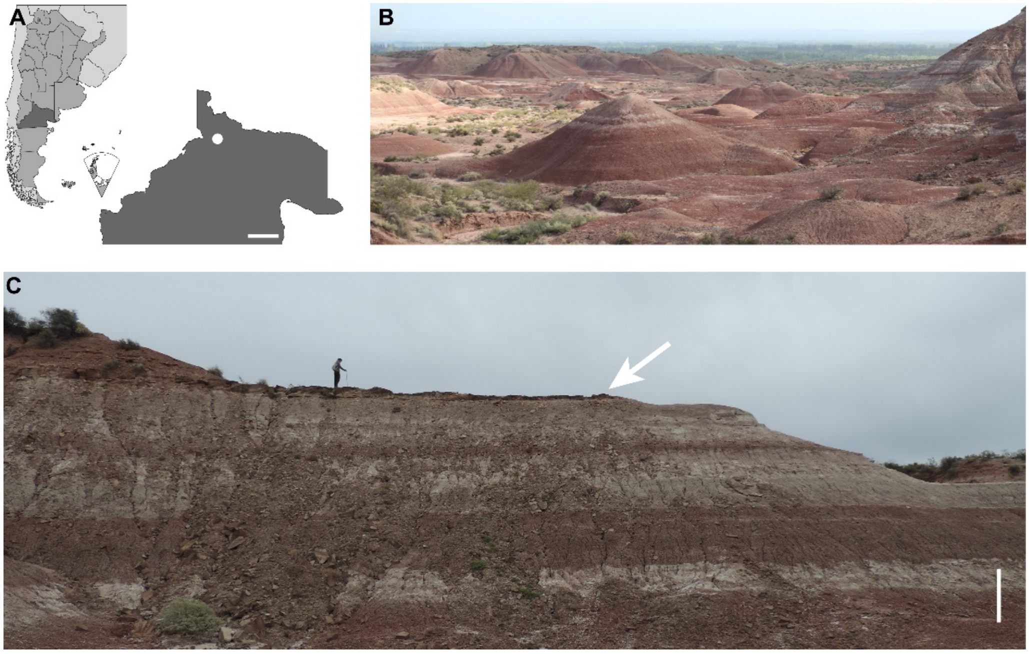

Figure 1. The new ichnological locality in the Área Natural Protegida Municipal Paso Córdoba, General Roca, Río Negro Province, Argentina. (**A**) Geographical map of the location of the site within the Río Negro province silhouette; the white dot indicates the General Roca area. Scale bar equals to 100 km; (**B**) Panoramic photography of Valle de la Luna Rojo, where the Anacleto Formation crops out; (**C**) Panoramic view of the Cañadón del Surgente (Anacleto Formation), where the site was found (white arrow). From the base, purple and reddish pelites alternate with whitish calcareous beds, above which fluvial red beds overlay. The arrow indicates the location of the ichnological material in a medium- to fine-grained sandstone bed. Scale bar equals 2 m.

The new ichnological locality, placed at the base of the informally called Cañadón del Surgente (from the English Upwelling Canyon) at the Valle de la Luna Rojo area, returned abundant sandstone slabs with invertebrate and vertebrate traces. Most of these remains are currently under study, and among these, four pterosaur manus tracks are the main goal of this contribution. The Gondwanan pterosaur ichnological record is still poorly documented [27–32], whereas the bone record is very abundant, especially in South America, and particularly in Argentina and Brazil, with some records in Chile, Peru and Venezuela [33–52]. The aims are to describe, compare and analyze the new pterosaur tracks found at the ANPM Paso Córdoba and then to discuss the important role that they have in the reconstruction of the paleocommunity of the Anacleto Formation and for the latest Cretaceous of Gondwana.

2. Geological and Paleontological Setting

2.1. Geology and Regional Context

The Neuquén Basin is located on the central–west region of Argentina and covers an area of more than 120,000 km^2 [53]. This basin has been defined as an ensialic back-arc basin resulting from thermal-tectonic collapse behind a stationary magmatic arc during the Late Triassic [54]. It comprises a continuous Jurassic–Cretaceous succession of up to 7000 m in thickness, including continental and marine siliciclastic, carbonate and evaporite deposits that accumulated under a variety of basin styles involving three main evolutionary stages [1].

The last stage of the basin (Late Jurassic–Late Cretaceous) led to the deposition of a continental to mainly marine sequence, represented in the Mendoza Group, and continental foreland successions in the Rayoso and Neuquén groups. The Neuquén Group forms a succession of non-marine deposits of fluvial, aeolian, lacustrine and deltaic origin developed between the lower Cenomanian and the middle Campanian. It is composed mainly of sandstones, mudstones and graywackes with minor conglomerates and subordinated tuffaceous and evaporitic deposits. The Neuquén Group reaches 1200 m of maximum thickness and includes three subgroups and nine formations [7,55]. The Río Limay Subgroup comprises the Candeleros and Huincul formations; the Río Neuquén Subgroup involves the Cerro Lisandro, Portezuelo, Los Bastos, Sierra Barrosa and Plottier formations; and finally, the Río Colorado subgroup consists of the Bajo de la Carpa and Anacleto formations [7] (Figure 2).

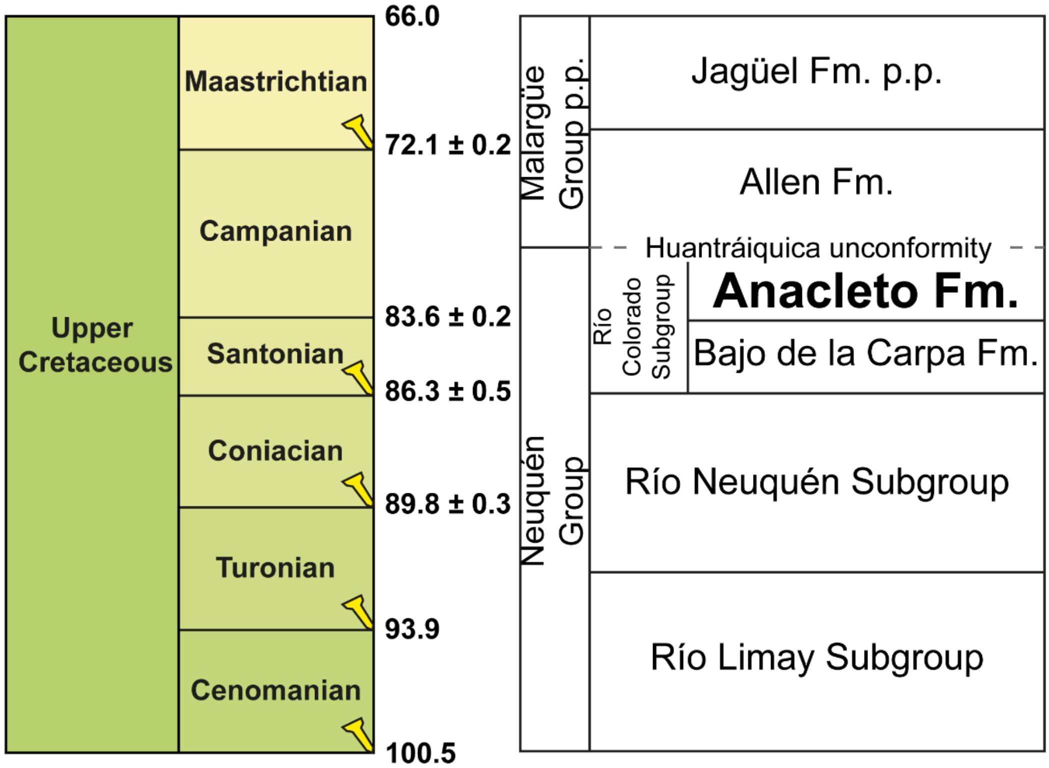

Figure 2. Chronostratigraphic scheme of the Upper Cretaceous units of the Neuquén Basin, showing the Neuquén Group and the Cretaceous portion of the Malargüe Group (redrawn and slightly modified from [7]). Absolute ages according to the International Chronostratigraphic Chart (version 2022/02 accessed on 1 February 2022; retrieved from www.stratigraphy.org).

The Anacleto Formation [56] is a succession of predominantly pelitic to fine-grained psamitic rocks [7], formed in a fluvial environment of low energy, with flowing streams in wide alluvial plains [57,58]. It lies in sharp, planar, erosional or transitional contact above the Bajo de la Carpa Formation [58,59] and is unconformably covered by the Allen Formation of the Malargüe Group [57,60,61]. The lower to middle Campanian age of the

Anacleto Formation is based on magnetostratigraphic analyses in the Auca Mahuevo area, Neuquén Province [7,62]. Recently, U–Pb detrital zircon ages from a sample of the Anacleto Formation in Paso Córdoba, Río Negro Province, gave a maximum depositional age of 78.6 ± 1.7 Ma (middle Campanian) [63].

2.2. Geology of the ANPM Paso Córdoba

In the ANPM Paso Córdoba the Mesozoic succession is represented by the Upper Cretaceous Bajo de la Carpa, Anacleto and Allen formations [57,64].

The Bajo de la Carpa Formation is predominantly formed by chestnut-gray, medium- to coarse-grained, poorly sorted, poorly lithified, quartz-rich sandstones organized in thick strata exhibiting cross-stratification associated with paleochannels. The deposits have been related to a fluvial paleoenvironment with alternating conditions of high and moderate energy [7,57].

The Anacleto Formation conformably and transitionally lies above the Bajo de la Carpa Formation [7,57]. The unit is mainly represented by purple and reddish (locally turning into greenish and gray), intensely bioturbated pelites rich in clay minerals, siltstones and fine sandstones alternating with whitish to pinkish calcareous beds [57,65]. Different authors interpreted these deposits as related to a meandering fluvial system transporting a mixed, siliciclastic and carbonate sediment load in a climate affected by strong seasonality through a wide alluvial plain [55,58,65], and the associated to lacustrine settings recorded in the upper portion of the unit [7,18,57,64].

The track-bearing slabs are reddish to pinkish, medium to coarse-grained sandstones, textural and compositionally immature. Clasts are mostly angular to sub-rounded, with low sphericity, and mostly composed of quartz, feldspar and lithic fragments with minor biotite. Using the Qt–F–L ternary diagram of [66], the rock was classified as a sub-litharenite. The slabs are most likely part of a 25 cm-thick, laminated sandstone bed with ripple marks alternating with red pelites whose stratal architecture is compatible with a floodplain setting (probably a sheetflood deposit) related to a major fluvial system [18] (Figure 1C). As it is suggested before, detrital zircons from the Anacleto Formation in ANPM Paso Córdoba were recently analyzed [63], giving a maximum U–Pb depositional age of 78.6 ± 1.7 Ma (middle Campanian). The stratigraphic levels where the pterosaur tracks were found are below this dating.

The boundary with the Allen Formation is expressed by a gradual transition in the study area [18,61,64,67], but see [57] for a contrasting interpretation. The Allen Formation is mainly constituted by pelites and heterolithic deposits with wavy and lenticular lamination, yellowish, fine- to medium-grained sandstones with parallel and wavy lamination, and medium-grained sandstones with tangential cross-bedding related to an aeolian system [64].

2.3. Paleontology of the ANPM Paso Córdoba

The ANPM Paso Córdoba is outstanding for its Cretaceous paleontological record. The Bajo de la Carpa Formation has yielded two species of notosuchid cocodriliforms, *Notosuchus terrestris* [68] and *Comahuesuchus brachybuccalis* [69]; an undetermined baurusuchid [70]; remains of the snake *Dinilysia patagonica* [71]; and three theropod dinosaurs, namely the alvarezsaurid *Achillesaurus manazzonei* [72], the abelisauroid *Velocisaurus unicus* [73] and the fragments of a large indeterminate carnotaurinae abelisaurid [74]. Additionally, paleosol levels with rhizoliths and galleries of small vertebrates, interpreted as dwelling and/or reproduction galleries, have been recently identified [75,76].

Regarding the Anacleto Formation, remains of the chelid *Yaminuechelys* cf. *gasparinii* and the titanosaur sauropod *Antarctosaurus wichmannianus* have been recovered from deposits exposed in the Valle de la Luna Rojo [77–79]. In addition, a mandibular fragment, tentatively assigned to a didelphoid marsupial, has been briefly mentioned [80]. In the transitional passage between fluvio-lacustrine pelites of Anacleto Formation and aeolian sandstones of Allen Formation, different indeterminate taxa of bivalve and gastropod mollusks, ostracods and charophytes were reported [81,82]. Moreover, a trampled area with undetermined vertebrate tracks preserved as negative relief with evidence of microbial mats [18], small tetradactyl and tridactyl avian tracks, and undetermined cross-section tracks were also found [19,83].

The Allen Formation also yields an almost complete titanosaur skeleton, associated with twelve abelisaurid teeth [84–88]. Almost at the same stratigraphic level, a second locality was identified, yielding the remains of a partially articulated titanosaur skeleton and two associated abelisaurid teeth [89,90]. The ichnological record of this unit is composed of titanosaur, hadrosaurid and bird tracks [18,19,91–95]. In addition, several intensely trampled areas found in other outcrops of the Allen Formation preserve numerous vertebrate tracks in both cross-section and on bedding planes. Interestingly, one of the tracks of these areas preserves skin traces, and others preserve wrinkled structures [18]. Finally, paleosols with abundant vertebrate burrows have been recorded in dune facies [96].

3. Material and Methods

The study material consists of four manus tracks identified as the imprint produced by the left hand of one or several pterosaurs. The collection numbers in the MPCN (Museo Patagónico de Ciencias Naturales "Juan Carlos Salgado", General Roca, Río Negro) are pending designation from the Río Negro Secretary of Culture, and here they are respectively referred to as track M1 to M4. They are preserved as convex hyporeliefs (natural casts) in four small, laminated sandstone slabs found as fallen blocks a few meters downhill from their original place. The measures used in the present contribution follow the standards of [97,98]. These measures are: length of manus impression (Lm), width of manus impression (Wm), length/width ratio (Lm/Wm), length of digit impressions I, II and III (LI, LII and LIII), and divarication angles between digit impressions I, II and III (DAI–II, DAII–III, DAI–III) (Figure 3). The ichnotaxonomy of pterosaur tracks follows the approaches of [30,99–101].

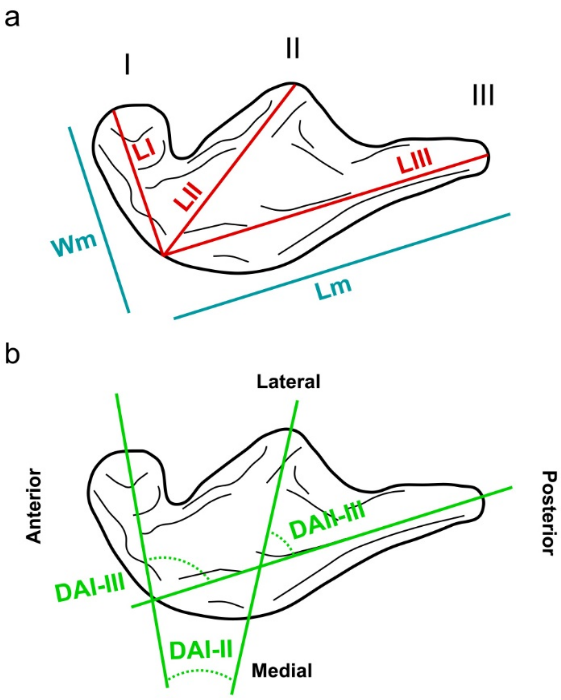

Figure 3. (**a**,**b**) Orientation of the tracks and measurements used in this work: Lm, length of manus imprint; Wm, width of manus imprint; LI, length of digit imprint I; LII, length of digit imprint II; LIII, length of digit imprint III; DAI–II, divarication angles between digit imprints I–II; DAII–III, divarication angles between digit imprints II–III; DAI–III, divarication angles between digit imprints I–III.

High-resolution digital photogrammetry was undertaken to achieve a more precise representation of three-dimensional (3D) morphology of the track, which was performed following the proposal of [102,103]. The photogrammetric process was performed using the Agisoft Metashape Professional software package (version 1.7.3). This software uses semi-automatic processing of images and automatically calculates camera calibrations with the final goal of creating 3D textured meshes. Photographs of track-bearing slabs were taken using two digital cameras, a reflex Canon EOS 80D of 24 Megapixel equipped with 50 mm focal length and a bridge camera Nikon Coolpix P520 of 18 Megapixel with 24–1000 mm focal length. In order to achieve a good image overlap, 45, 34, 44 and 39 images were acquired, for specimens M1, M2, M3 and M4, respectively. To correctly scale the final model, a metric reference marker was placed on the surface. Ground sampling resolution of about 0.03 mm/pix was obtained, while after the scaling process, a submillimetric mean error was achieved for each model. Three-dimensional meshes were converted to color topographic profiles using the open software Paraview (version 5.4.1).

4. Results

The four tridactyl imprints are longer than wide, rhombic in overall shape and laterally asymmetrical (Figure 4).

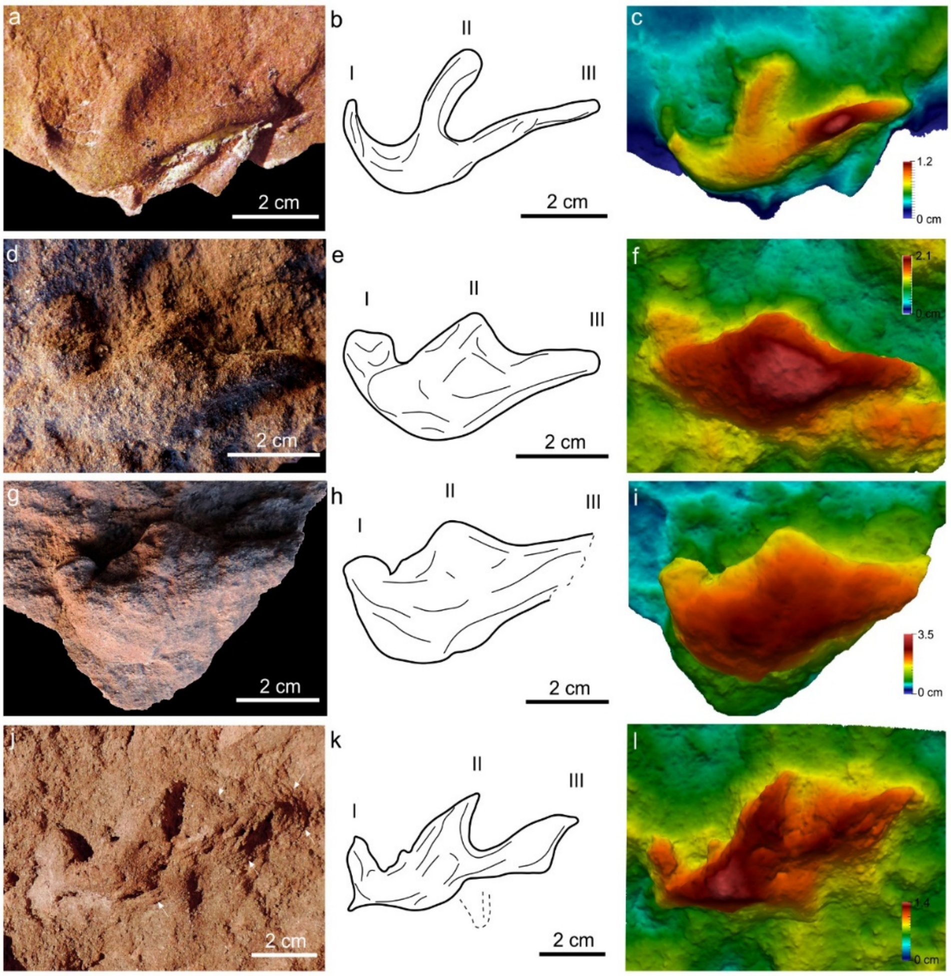

Figure 4. Details of the four pterosaur manus impressions: (**a**) photography of M1 impression; (**b**) interpretative drawing of M1; (**c**) false-color depth image of M1; (**d**) photograph of M2; (**e**) interpretative scheme of M2; (**f**) false-color depth image of M2; (**g**) photograph of M3; (**h**) interpretative scheme of M3; (**i**) false-color depth image of M3; (**j**) photograph of M4; (**k**) interpretative scheme of M4; (**l**) false-color depth image of M4. References: white arrows indicate striae.

The M1 material (Figure 4a–c) is the best-preserved, being 5.8 cm long and 2.8 cm wide (Lm/Wm = 2.1). The impression lengths of digits I, II and III are 2.0, 3.7 and 5.4 cm, respectively. The impression of digit III is the longest, being 2.7 times longer than the impression of digit I (Table 1).

Table 1. Measurements of the pterosaur left manus tracks. Abbreviations as in Section 3.

Track	Lm (cm)	Wm (cm)	Lm/Wm	LI (cm)	LII (cm)	LIII (cm)	DAI–II (°)	DAII–III (°)	DAI–III (°)
M1	5.8	2.8	2.1	2.0	3.7	5.4	62	39	101
M2	5.5	2.8	1.96	2.2	3.1	4.9	22	60	82
M3	6.0	3.2	1.88	2.4	3.6	5.7	22	58	80
M4	7.5	3.0	2.50	1.9	4.5	6.7	46	40	86
Average	**6.2**	**3**	**2.11**	**2.1**	**3.7**	**5.7**	**38**	**49**	**87**

Track M1 has the narrowest digit impressions of the four tracks studied here (Figure 4), where the impression of digit I is the narrowest of the three digits, and the impression of digit II is the widest. The impression of digit I is laterally oriented, recurved and narrowed distally and finishes in a sub-rounded to acuminate end; the impression of digit II is elongated, lightly recurved, laterally oriented and has a rounded distal end; and the impression of digit III is elongated, straight, posteriorly directed and presents a sub-rounded end. The outline at the hypex, the outline border between two contiguous digits at their bases, is wider between digits I and II and tighter between II and III. The divarication angles between the axis of two-digit impressions (Figure 3) are acute between digits I and II (62°) and between II and III (39°), whereas between digits I and III, the angle is obtuse (101°). These divarication angles show a wide-open angle between the impressions of digits I and II of almost two times (1.8) wider than between digits II and III. The thickest region of this track (deepest in the original concave track) corresponds to the mid-length area of digit III, being around 1 cm high (Figure 4c).

Track M2 (Figure 4d–f) is 5.5 cm long and 2.8 cm wide (Lm/Wm = 1.96). The lengths of digits I and II impressions are 2.2 cm and 3.1 cm, respectively, while the digit III imprint is the longest, with 4.9 cm long. The digit I impression is elongated, straight, laterally oriented and has a rounded distal end. The digit II impression is sub-triangular, straight, laterally oriented and has a roughly acute to rounded distal end. The digit III impression is elongated, nearly sub-triangular, straight, posteriorly directed and has a rounded distal end and a smooth concavity on the medial surface. The outline at the hypex between digits I and II is very tight, whereas between digits II and III, it is wide open. The divarication angles are acute between both digits I and II (22°) and II and III (60°) but where the aperture angle of the latter is 2.7 times larger than the former. On the other hand, a nearly right angle is present between digits I and III (82°). The thickest region of this track is the area where digits II and III converge (up to 1 cm high).

Track M3 (Figure 4g–i) has an incompletely preserved digit III impression, where the complete track is at least 6 cm long (Lm/Wm = 1.88). The impression of digit I is the shortest (2.4 cm); that of digit III is the longest (5.7 cm), which would have been longer due to its incomplete preservation; and digit II is intermediate (3.6 cm; III > II > I). The impression of digit I is elongated, straight, laterally oriented, with a rounded distal end; the digit II impression is straight, triangular in outline, laterally oriented, and roughly acuminate distally; the preserved impression of digit III is elongated, straight, posteriorly directed, with a smooth concavity in the medial surface. The hypex between digits I and II is poorly defined, but it is apparently somewhat tight, whereas between II and III, it is very wide and shallow. The divarication angles formed between the impressions of digits I and II and between II and III are acute (22° and 58°, respectively) but very different from each other, where the latter is 2.6 times larger than the former. The divarication angle between digits I and III is acute as well but closer to the right angle (80°). The thickest region of this track is the posteromedial area of the digits II and III impressions (up to 1.5 cm high), the digit I is the shallowest of the three digits, and the III is the thickest.

Track M4 (Figure 4j–l) is 7.5 cm long and 3.0 cm wide (Lm/Wm = 1.88). The digit I impression is the shortest of the three (2.4 cm long), elongated, straight, laterally oriented, with a roughly rounded end. The imprint of digit II is 4.5 cm long, sub-triangular in outline, posteriorly curved, with an acuminate end. The digit III impression is the longest of the three (6.7 cm), being elongated, straight, and posteriorly oriented, with an acuminate end. The border at both hypexes (between I–II and II–III) forms similar tight outlines. The divarication angles formed between digits I and II impressions and between II and III are very similar (46° and 40°, respectively), and the total divarication between I and III is almost a right angle (86°). The thickest region of this track occurs in the posterior area of digit II (up to 0.5 cm high), and digits II and III impressions are thicker than I and almost similar to each other.

5. Discussion and Conclusions

These manus tracks share such an overall morphology (e.g., tridactyl, asymmetrical, elongated digit III impression) that it suggests the probable trackmaker could have been a pterosaur [104]. Nevertheless, the tracks are slightly dissimilar from each other, very likely due to the differences in the substrate and the properties of the trampled sediment during track formation. Track M1 has the most detailed shape, considering the sum of morphological traits that best reflect the anatomy and dimensional proportions of the producer fore autopod. It displays a sharper outline compared with the other tracks, particularly that related to digit I and III as well as hypexes and proximal portion. Moreover, the track walls of track M1 are almost vertical, unlike the gently inclined track walls in the other cases. Tracks M2 and M3 are more deeply impressed than tracks M1 and M4; they have wider digit impressions (e.g., digit I in M2, digit III in M3), and both are characterized by a faint digit II impression that appears straight if compared with that of tracks M1 and, for a lesser extent, M4. Similarly, the hypex between digit II and III impressions in tracks M2 and M3 has a much milder outline than that of tracks M1 and M4, which differently are characterized by acuminate and laterally curved digits II and III impressions and a digit I impression thinner than that of tracks M2 and M3. Based on the greater thickness, the wider digit impressions and the morphology of the digit II impression of both tracks M2 and M3, it is considered that they would have formed on a substrate with high moisture content [105]. Conversely, track M1 would have formed in a more consistent, drier, substrate, as indicated by its almost vertical track walls. Track M4 is associated with thin parallel striae observed around digit II and III impressions (Figure 4k: white arrows) that could be the consequence of a small dislocation of soft sediments [105]. Therefore, considering that the morphological differences between the four manus tracks could be due to variations in the substrate consistency, and that the general morphological characters agree with the interpretation of a pterosaur manus as the trackmaker [104], the authors consider that all four tracks could have been produced by the same type of trackmaker autopod under different substrate conditions [104,105].

Pterosaur tracks are included in three ichnofamilies and four ichnogenera (sensu [101]): Pteraichnidae (ichnogenus *Pteraichnus* [104]); Agadirichnidae (ichnogenera *Haenamichnus* and *Agadirichnus* [29,106,107]); and Rhamphichnidae (ichnogenus *Rhamphichnus* [101]). The main differences among these ichnogenera are in pes track morphology [29], where the manus tracks are more conservative and similar in shape among almost all the ichnotaxa [97]. Except for *Rhamphichnus*, in which the digit manus impressions are subparallel and oriented anteriorly and digits I and II impressions are longer than that of III [101], other pterosaur ichnogenera have the impressions of digits I and II usually oriented laterally and digit III, as the longest, posteriorly. The Anacleto Formation material shares this last configuration of the digit impression. The manus tracks of *Haenamichnus* ichnospecies (i.e., *H. uhangriensis* and *H. gainensis* [107,108]), when impressed, are poorly preserved lacking clear diagnostic features, so they cannot be used in this comparison. *Agadirichnus*, besides differing from *Pteraichnus* in several features of the manus track, also contrasts in having a short and rounded manus digit I impression [29], which is also present in the tracks studied here. Even though some similarities are shared with the ichnogenus *Agadirichnus*, the authors consider that classifying pterosaur manus tracks without information of the pes impressions is not reliable from an ichnotaxonomic point of view [109]; therefore, they prefer to be cautious in the assignment and consider the analyzed material as an undetermined pterosaur track different from *Rhamphichnus*.

The pterosaurian track record, spanning from the Middle Jurassic to the Late Cretaceous [30], is relatively scarce in comparison with those linked to other groups of Mesozoic vertebrates such as dinosaurs ([110,111] but see [30] for a different opinion). This scarcity is particularly evident in Gondwana, where only five pterosaur track-bearing lithostratigraphic units were known before the present study, four in Morocco [28–31] and one in Argentina [27,32]. If they are described in chronological order, among the Moroccan sites, brief mentions about pterosaur tracks assigned to *Pteraichnus* are made in the Middle–?Upper Jurassic Isli Formation [31,112]. Some poorly preserved tracks putatively assigned to pterosaurs were identified in the Cenomanian Kem Kem beds [28], but the affinity of this material has subsequently been questioned [30]. In Argentina, two pterosaur track-bearing outcrops are present in the Cenomanian Candeleros Formation of Patagonia. The first one is located at the edge of the Embalse Ezequiel Ramos Mexía, Neuquén and Río Negro provinces, where some trackway segments and manus-pes sets were identified and classified as cf. *Pteraichnus* isp. and *Pteraichnus* isp. [19,27,113–115]. A second track site was recently reported from Aguada de Tuco, located in the central area of the Neuquén Basin (Neuquén Province); it has yielded several isolated manus and pes tracks preserved in fluvial deposits, which have been referred to cf. *Pteraichnus* isp. [32]. In the Coniacian–Santonian of the south of Morocco, a complete manus-only trackway, two isolated pes tracks and possibly an incomplete trackway were found and associated with doubts to *Agadirichnus elegans*, *Pteraichnus* or a new ichnogenus [30]. Also in Morocco, several isolated manus and pes pterosaur tracks were identified in the Maastrichtian Tagragra Formation and related to the *Agadirichnus elegans* and cf. *Pteraichnus* isp. [29,106]. According to the above exposed, the Anacleto Formation is the sixth unit in Gondwanaland and the second in South America with pterosaur tracks, and the material described here increases the knowledge of the ichnodiversity of the southern continents. Moreover, this finding provides new and valuable information to the worldwide scarce pterosaur ichnological Upper Cretaceous record, which is circumscribed to the Cerro del Pueblo Formation (uppermost Campanian, Mexico, [116]); North Horn Formation (Maastrichtian, USA, [117]); Cantwell Formation (Campanian–Maastrichtian, USA, [118]); Jinhua Formation (Turonian–Coniacian, China, [119]); and Uhangri Formation (Cenomanian–Campanian, South Korea, [107]).

Pterosaurs have historically been divided into two major groups on the basis of their anatomical characters and temporal distribution: the "rhamphorhynchoids", the early diverging and probably paraphyletic pterosaur group, and the pterodactyloids, more deeply nested and monophyletic clade within Pterosauria [120,121]. Some controversies lay behind the affinities of the pterosaurian taxa. Based on cladistic analyses, some consider the "rhamphorhynchoids" as non-pterodactyloid pterosaurs, whereas the monophyly of this group is supported by others. As the diversity of pterosaurs increased, the clades have been enlarged; thus, the two-group division of pterosaurs is not that accurate nowadays [120,121]. The earliest bone fossil remains of a pterodactyloid are recorded for the Callovian–Oxfordian boundary (Middle–Upper Jurassic boundary, [122]), while tracks are referred to the Aalenian (lower Middle Jurassic, [111]). On the other hand, the youngest osteological record of non-pterodactyloid pterosaur corresponds to the anurognathids from the lower Aptian Jiufotang Formation of China (upper Lower Cretaceous, [123]). Consequently, any pterosaur tracks younger than the latter age, including the entire Upper Cretaceous, and the Campanian age of the Anacleto Formation of the present study, cannot be supported by the non-pterodactyloid pterosaur record to date.

Skeletal remains of Campanian pterosaurs are scarce in South America, being only found in the Goio-Erê Formation of Brazil, dated as Turonian–Campanian [41,124]. Other outcrops in Gondwana were described in the Turonian–lower Campanian Lappur Sandstone of Kenya [125], the Campanian–Maastrichtian Mata Series of New Zealand [126] and the Santonian–Campanian Santa Marta Formation of Antarctica [124]. Consequently, the pterosaur tracks from Paso Córdoba provide valuable information to reach a more comprehensive understanding of the record of this clade in Gondwana at the end of the Cretaceous.

The Anacleto Formation is one of the best-known units from South America regarding its paleontological content showing a very diverse fauna of terrestrial vertebrates, such as theropods (*Aucasaurus* and *Aerosteon*, [127,128]); sauropods (e.g., *Barrosasaurus* and *Overosaurus*, [8,11,129]); ornithopods (*Gasparinisaura*, [4]); notosuchians (*Gasparinisuchus* and *Pehuenchesuchus*, [10,130]); chelids (*Yaminuechelys*, [13,79]); squamates (*Dynilisia*, [9,131]); and mammals [80]. Moreover, sauropod eggs with embryos have been identified as megaloolithid specimens [3,22]. The ichnological record is composed of tracks of non-avian theropods [16]; sauropods (including *Teratopodus malarguensis*, [17,20,21,132–136]); birds (*Barrosopus slobodai*, cf. *Ignotornis* isp., cf. *Aquatilavipes* isp., [5]); pterosaurs (this work); and undetermined vertebrates [18,19].

The Anacleto Formation can be labeled under Category 4 of [137], in which the ichnological and osteological remains co-occur in the same unit, but where the tracks are a small portion of the available evidence. This difference between both types of material is notable in the Anacleto Formation, probably because of the scarcity of suitable facies for the formation and preservation of tracks. Interestingly, the ichnological record of the studied formation reveals the presence of two vertebrate groups not represented osteologically, birds and pterosaurs (Figure 5). Therefore, the record in this formation can be classified as Category 4b of [137] in which the ichnological and osteological records are not mutually consistent. As it was profusely pointed out, the ichnological record is sometimes ahead of the osteological one [137–139]; thus, all the track material should be considered as relevant as the skeletal one, in order to determine the diversity of a particular unit.

Tetrapod group	Osteological record	Ichnological record	Oological record
Theropoda			
Sauropoda			
Ornithopoda			
Avialae			
Pterosauria			
Notosuchia			
Chelonia			
Squamata			
Mammalia			

Figure 5. Tetrapod osteological fossil and ichnofossil record of the Anacleto Formation. References: Dark grey with drawings, presence of the remains; white without drawings, absence of the remains. The figure is based on the works cited in the text.

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References

1. Howell, J.A.; Schwarz, E.; Spalletti, L.A.; Veiga, G.D. The Neuquén basin: An overview. *Geol. Soc. Spec. Publ.* **2005**, *252*, 1–14. [CrossRef]
2. Asurmendi, E.; Sánchez, M.L.; Fennell, L. Neuquén Group (Upper Cretaceous): A case of underfilled-overfilled cycles in an Andean foreland basin, Neuquén basin, Argentina. *J. S. Am. Earth Sci.* **2017**, *80*, 444–459. [CrossRef]
3. Chiappe, L.M.; Coria, R.A.; Dingus, L.; Jackson, F.; Chinsamy, A.; Fox, M. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature* **1998**, *396*, 258–261. [CrossRef]
4. Coria, R.A.; Salgado, L. A basal iguanodontian (Ornithischia: Ornithopoda) from the Late Cretaceous of South America. *J. Vertebr. Paleontol.* **1996**, *16*, 445–457. [CrossRef]
5. Coria, R.A.; Currie, P.J.; Eberth, D.; Garrido, A. Bird footprints from the Anacleto Formation (Late Cretaceous), Neuquén, Argentina. *Ameghiniana* **2002**, *39*, 453–463.
6. Leanza, H.A.; Apesteguía, S.; Novas, F.E.; de la Fuente, M.S. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cret. Res.* **2004**, *25*, 61–87. [CrossRef]
7. Garrido, A.C. Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (Argentina): Nueva propuesta de ordenamiento litoestratigráfico. *Rev. Mus. Arg. Cienc. Nat.* **2010**, *12*, 121–177. [CrossRef]
8. Filippi, L.S.; García, R.A.; Garrido, A.C. A new titanosaur sauropod dinosaur from the Upper Cretaceous of North Patagonia, Argentina. *Acta Palaeontol. Pol.* **2011**, *56*, 505–520. [CrossRef]
9. Filippi, L.S.; Garrido, A.C. Nuevo registro del género *Dinilysia* (Squamata, Serpentes) para la Formación Anacleto (Campaniano Inferior—Medio), Rincón de los Sauces, Neuquén, Argentina. *Ameghiniana* **2012**, *49*, 132–136. [CrossRef]
10. Martinelli, A.G.; Sertich, J.J.; Garrido, A.C.; Praderio, Á.M. A new peirosaurid from the Upper Cretaceous of Argentina: Implications for specimens referred to *Peirosaurus torminni* Price (Crocodyliformes: Peirosauridae). *Cret. Res.* **2012**, *37*, 191–200. [CrossRef]
11. Coria, R.A.; Filippi, L.S.; Chiappe, L.M.; García, R.; Arcucci, A.B. *Overosaurus paradasorum* gen. et sp. nov., a new sauropod dinosaur (Titanosauria: Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Zootaxa* **2013**, *3683*, 357–376. [CrossRef] [PubMed]
12. Cerda, I.A.; García, R.A.; Powell, J.E.; López, O. Morphology, microanatomy, and histology of titanosaur (Dinosauria, Sauropoda) osteoderms from the Upper Cretaceous of Patagonia. *J. Vertebr. Paleontol.* **2015**, *35*, e905791. [CrossRef]
13. de la Fuente, M.S.; Maniel, J.I.; Jannello, J.M.; Filippi, L.S.; Cerda, I. Long-necked chelid turtles from the Campanian of northwestern Patagonia with comments on K/P survivorship of the genus *Yaminuechelys*. *C. R. Palevol.* **2015**, *14*, 563–576. [CrossRef]
14. Gianechini, F.A.; Apesteguía, S.; Landini, W.; Finotti, F.; Valieri, R.J.; Zandonai, F. New abelisaurid remains from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. *Cret. Res.* **2015**, *54*, 1–16. [CrossRef]
15. Baiano, M.A.; Coria, R.A.; Canale, J.I.; Gianechini, F.A. New abelisaurid materials from the Anacleto formation (Campanian, Upper Cretaceous) of Patagonia, Argentina, shed light on the diagnosis of the abelisauridae (theropoda, ceratosauria). *J. S. Am. Earth Sci.* **2021**, *110*, 103402. [CrossRef]
16. Krapovickas, V.; Garrido, A.C. Sobre una huella de Theropoda de la Formación Anacleto (Campaniano Temprano), provincia del Neuquén, Argentina. *Ameghiniana* **2006**, *43*, 43R.
17. González Riga, B.J.; Ortiz David, L.D.; Tomaselli, M.B.; dos Anjos Candeiro, C.R.; Coria, J.P.; Prámparo, M. Sauropod and theropod dinosaur tracks from the Upper Cretaceous of Mendoza (Argentina): Trackmakers and anatomical evidences. *J. S. Am. Earth Sci.* **2015**, *61*, 134–141. [CrossRef]

18. Díaz-Martínez, I.; Cónsole-Gonella, C.; de Valais, S.; Salgado, L. Vertebrate tracks from the Paso Córdoba fossiliferous site (Anacleto and Allen formations, Upper Cretaceous), Northern Patagonia, Argentina: Preservational, environmental and palaeobiological implications. *Cret. Res.* **2018**, *83*, 207–220. [CrossRef]
19. de Valais, S.; Díaz-Martínez, I.; Citton, P.; Cónsole-Gonella, C. Vertebrate tracks of the Río Negro Province, Patagonia, Argentina: Stratigraphy, palaeobiology and environmental contexts. *Rev. Asoc. Geol. Argent.* **2020**, *77*, 1–63.
20. Tomaselli, M.B.; Ortiz David, L.D.; González Riga, B.J. Paleoenvironmental contexts of South American Cretaceous sauropod tracks. *J. S. Am. Earth Sci.* **2021**, *110*, 103393. [CrossRef]
21. Tomaselli, M.B.; Ortiz David, L.D.; González Riga, B.J.; Coria, J.P.; Mercado, C.R.; Guerra, M.; Sánchez Tiviroli, G. New titanosaurian sauropod tracks with exceptionally well-preserved claw impressions from the Upper Cretaceous of Argentina. *Cret. Res.* **2021**, *129*, 104990. [CrossRef]
22. Chiappe, L.M.; Coria, R.A.; Jackson, F.; Dingus, L. The Late Cretaceous nesting site of Auca Mahuevo (Patagonia, Argentina): Eggs, nests, and embryos of titanosaurian sauropods. *Palaeovertebrata* **2003**, *32*, 97–108.
23. Jackson, F.D.; Garrido, A.; Schmitt, J.G.; Chiappe, L.M.; Dingus, L.; Loope, D.B. Abnormal, multilayered titanosaur (Dinosauria: Sauropoda) eggs from in situ clutches at the Auca Mahuevo locality, Neuquén Province, Argentina. *J. Vertebr. Paleontol.* **2004**, *24*, 913–922. [CrossRef]
24. Jackson, F.D.; Schmitt, J.G.; Oser, S.E. Influence of vertisol development on sauropod egg taphonomy and distribution at the Auca Mahuevo locality, Patagonia, Argentina. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2013**, *386*, 300–307. [CrossRef]
25. Grellet-Tinner, G.; Chiappe, L.M.; Coria, R. Eggs of titanosaurid sauropods from the Upper Cretaceous of Auca Mahuevo (Argentina). *Can. J. Earth Sci.* **2004**, *41*, 949–960. [CrossRef]
26. Schweitzer, M.H.; Chiappe, L.; Garrido, A.C.; Lowenstein, J.M.; Pincus, S.H. Molecular preservation in Late Cretaceous sauropod dinosaur eggshells. *Proc. R. Soc. Lond. B Biol. Sci.* **2005**, *272*, 775–784. [CrossRef] [PubMed]
27. Calvo, J.O.; Lockley, M.G. The first pterosaur tracks from Gondwana. *Cret. Res.* **2001**, *22*, 585–590. [CrossRef]
28. Belvedere, M.; Jalil, N.E.; Breda, A.; Gattolin, G.; Bourget, H.; Khaldoune, F.; Dyke, G.J. Vertebrate footprints from the Kem Kem beds (Morocco): A novel ichnological approach to faunal reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2013**, *383*, 52–58. [CrossRef]
29. Masrour, M.; de Ducla, M.; Billon-Bruyat, J.P.; Mazin, J.M. Rediscovery of the Tagragra tracksite (Maastrichtian, Agadir, Morocco): *Agadirichnus elegans* Ambroggi and Lapparent 1954 is pterosaurian ichnotaxon. *Ichnos* **2018**, *25*, 285–294. [CrossRef]
30. Masrour, M.; Pascual-Arribas, C.; de Ducla, M.; Hernández-Medrano, N.; Pérez-Lorente, F. Anza palaeoichnological site. Late Cretaceous. Morocco. Part I. The first African pterosaur trackway (manus only). *J. Afr. Earth Sci.* **2017**, *134*, 766–775. [CrossRef]
31. Klein, H.; Lagnaoui, A.; Gierliński, G.D.; Saber, H.; Lallensack, J.N.; Oukassou, M.; Charrière, A. Crocodylomorph, turtle and mammal tracks in dinosaur-dominated Middle–? Upper Jurassic and mid–Cretaceous ichnoassemblages of Morocco. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2018**, *498*, 39–52. [CrossRef]
32. Heredia, A.M.; Díaz-Martínez, I.; Pazos, P.J.; de Valais, S. A new pterosaur tracksite from the Upper Cretaceous Candeleros Formation, Neuquén Province, Patagonia, Argentina. In XII Congreso de la Asociación Paleontológica Argentina, Buenos Aires, Argentina. *PE-APA* **2021**, *22*, R189. [CrossRef]
33. Bennett, S.C. A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *J. Paleontol.* **1989**, *63*, 669–677. [CrossRef]
34. Chiappe, L.; Rivarola, D.; Cione, A.; Fregenal-Martínez, M.; Sozzi, H.; Buatois, L.; Gallego, O.; Laza, J.; Romero, E.; López-Arbarello, A.; et al. Biotic association and palaeoenvironmental reconstruction of the "Loma del *Pterodaustro*" fossil site (Early Cretaceous, Argentina). *Geobios* **1998**, *31*, 349–369. [CrossRef]
35. Kellner, A.W.A.; Moody, J.M. Pterosaur (Pteranodontoidea, Pterodactyloidea) scapulocoracoid from the Early Cretaceous of Venezuela. In *Evolution and Palaeobiology of Pterosaurs*; Buffetaut, E., Mazin, J.M., Eds.; Geological Society of London, Special Publications: London, UK, 2003; Volume 217, pp. 73–77. [CrossRef]
36. Unwin, D.M.; Martill, D.M. Pterosaurs of the Crato Formation. In *The Crato Fossil Beds of Brazil: Window into an Ancient World*; Martill, D.M., Bechly, G., Loveridge, R.F., Eds.; Cambridge University Press: Cambridge, UK, 2007; pp. 475–524. [CrossRef]
37. Martill, D.M. First pterosaur remains from the Exu Formation (Cretaceous) of the Araripe Basin, Brazil. *Zitteliana* **2008**, *28*, 243–248.
38. Martill, D.M. A new pterodactyloid pterosaur from the Santana Formation (Cretaceous) of Brazil. *Cret. Res.* **2011**, *32*, 236–243. [CrossRef]
39. Haluza, A.; Canale, J.I. A partial pterosaur ulna from the Candeleros Formation (Neuquén Group), Late Cretaceous of Argentina. *Hist. Nat.* **2013**, *3*, 5–12.
40. Medeiros, M.A.; Lindoso, R.M.; Mendes, I.D.; de Souza Carvalho, I. The Cretaceous (Cenomanian) continental record of the laje do coringa flagstone (Alcântara Formation), northeastern South America. *J. S. Am. Earth Sci.* **2014**, *53*, 50–58. [CrossRef]
41. Manzig, P.C.; Kellner, A.W.; Weinschütz, L.C.; Fragoso, C.E.; Vega, C.S.; Guimarães, G.B.; Godoy, L.C.; Liccardo, A.; Ricetti, J.H.Z.; de Moura, C.C. Discovery of a rare pterosaur bone bed in a Cretaceous desert with insights on ontogeny and behavior of flying reptiles. *PLoS ONE* **2014**, *9*, e100005. [CrossRef]
42. Codorniú, L.; Gasparini, Z. The Late Jurassic pterosaurs from Northern Patagonia, Argentina. *Earth Environ. Sci. Trans. R. Soc. Edinb. Spec. Issue* **2013**, *103*, 399–408. [CrossRef]
43. Codorniú, L.; Carabajal, P.A.; Pol, D.; Unwin, D.; Rauhut, O.W.M. A Jurassic pterosaur from Patagonia and the origin of the pterodactyloid neurocranium. *PeerJ* **2016**, *4*, e2311. [CrossRef] [PubMed]
44. Codorniú, L.; Chiappe, L.M.; Rivarola, D. Neonate morphology and development in pterosaurs: Evidence from a ctenochasmatid embryo from the early Cretaceous of Argentina. *Geol. Soc. Spec. Publ.* **2017**, *455*, 83–94. [CrossRef]

45. Ortiz, L.D.; González Riga, B.J.; Kellner, A.W.A. Discovery of the largest pterosaur from South America. *Cret. Res.* **2018**, *83*, 40–46. [CrossRef]
46. Bellardini, F.; Codorniú, L. First pterosaur post-cranial remains from the Lower Cretaceous Lohan Cura Formation (Albian) of Patagonia, Argentina. *Ameghiniana* **2019**, *56*, 116–134. [CrossRef]
47. Kellner, A.W.A.; Calvo, J.O.; Sayão, J.M.; Porfiri, J.D. Pterosaur bones from the Portezuelo Formation (Cretaceous), Neuquén Group, Patagonia, Argentina. *Arq. Mus. Nac. Rio J.* **2006**, *64*, 369–375.
48. Kellner, A.W.; Weinschütz, L.C.; Holgado, B.; Bantim, R.A.; Sayao, J.M. A new toothless pterosaur (Pterodactyloidea) from Southern Brazil with insights into the paleoecology of a Cretaceous desert. *An. Acad. Bras. Cienc.* **2019**, *91*. [CrossRef] [PubMed]
49. Bantim, R.A.M.; de Andrade, R.C.L.P.; Ferreira, J.S.; Saraiva, A.Á.F.; Kellner, A.W.A.; Sayao, J.M. Osteohistology and growth pattern of a large pterosaur from the Lower Cretaceous Romualdo Formation of the Araripe Basin, Northeastern Brazil. *Cret. Res.* **2021**, *118*, 104667. [CrossRef]
50. Pêgas, R.V.; Holgado, B.; Ortiz, L.D.; Baiano, M.A.; Costa, F.R. On the pterosaur *Aerotitan sudamericanus* (Neuquén Basin, Upper Cretaceous of Argentina), with comments on azhdarchoid phylogeny and jaw anatomy. *Cret. Res.* **2022**, *129*, 104998. [CrossRef]
51. Alarcón-Muñoz, J.; Otero, R.A.; Soto-Acuña, S.; Vargas, A.O.; Rojas, J.; Rojas, O. First record of a Late Jurassic rhamphorhynchine pterosaur from Gondwana. *Acta Palaeontol. Pol.* **2021**, *66*, 571–583. [CrossRef]
52. Alarcón-Muñoz, J.; Codorniú, L.; González, E.; Suárez, M.E.; Suárez, M.; Vicencio-Campos, O.; Soto-Acuña, S.; Kaluza, J.; Vargas, A.O.; Rubilar-Rogers, D. A new locality with ctenochasmatid pterosaurs (Pterosauria: Pterodactyloidea) in the Atacama Desert, Northern Chile. *Cret. Res.* **2022**, *135*, 105173. [CrossRef]
53. Yrigoyen, M.R. Hydrocarbon resources from Argentina. In *World Petroleum Congress, Buenos Aires. Petrotecnia, 1991, 13*; Special Issue; Sage Publications: Thousand Oaks, CA, USA, 1991; pp. 38–54.
54. Mpodozis, C.; Ramos, V.A. The Andes of Chile and Argentina. In *Geology of the Andes and Its Relation to Hydrocarbon and Mineral Resources*; Ericksen, G.E., Cañas Pinochet, M.T., Reinemud, J.A., Eds.; Earth Sciences Series; Circum-Pacific Council for Energy and Mineral Resources: Menlo Park, CA, USA, 1989; Volume 11, pp. 59–90.
55. Cazau, L.B.; Uliana, M.A. El Cretácico superior continental de la Cuenca Neuquina. In *Congreso Geológico Argentino*; La Asociación: Surquillo, Peru, 1973; Volume 3, pp. 131–163.
56. Herrero Duclox, A. Estratigrafía y tectónica de los Estratos de Dinosaurios del Neuquén. *Bol. Inf. Pet.* **1939**, *16*, 16–17.
57. Hugo, C.A.; Leanza, H.A. *Hoja Geológica 3069-IV General Roca (Escala 1:250.000). Provincias de Río Negro y Neuquén. Instituto de Geología y Recursos Minerales*; SEGEMAR: Buenos Aires, Argentina, 2001; Boletín 308; pp. 1–65.
58. Rodríguez, M.F.; Leanza, H.A.; Salvarredy Aranguren, M. *Hoja Geológica 3969-II Neuquén, Provincias del Neuquén, Río Negro y La Pampa. Instituto de Geología y Recursos Naturales*; SEGEMAR: Buenos Aires, Argentina, 2007; Boletín 370; pp. 1–165.
59. Sánchez, M.L.; Gómez, M.J.; Heredia, S. Sedimentología y paleoambientes del Subgrupo Río Colorado (Cretácico Superior), Grupo Neuquén, en las bardas de la ciudad de Neuquén y alrededores. *Rev. Asoc. Geol. Argent.* **2006**, *61*, 236–255.
60. Uliana, M.A.; Dellapé, D.A. Estratigrafía y evolución paleoambiental de la sucesión maastrichtiana–eoterciaria del engolfamiento neuquino (Patagonia Septentrional). In *Congreso Geológico Argentino*; La Asociación: Surquillo, Peru, 1981; Volume 8, pp. 673–711.
61. Armas, P.; Sánchez, M.L. Sedimentología y arquitectura de las dunas costeras de la Formación Allen, Grupo Malargüe, cuenca Neuquina-Río Negro, Argentina. *Rev. Mex. Cienc. Geol.* **2013**, *30*, 65–79.
62. Dingus, L.; Clarke, J.; Scott, G.R.; Swisher, C.C., III; Chiappe, L.M.; Coria, R.A. Stratigraphy and Magnetostratigraphic/Faunal Constraints for the Age of Sauropod Embryo-Bearing Rocks in the Neuquén Group (Late Cretaceous, Neuquén Province, Argentina). *Am. Mus. Novit.* **2000**, *3290*, 1–11. [CrossRef]
63. Gómez, R.; Tunik, M.; Casadio, S.; Canale, N.; Greco, G.; Baiano, M.A.; Pino, D.A.; Báez, A.; Da Silva, S.P. Primeras edades U-Pb en circones detríticos del Grupo Neuquén en el extremo oriental de la Cuenca Neuquina (Paso Córdoba, Río Negro). *Lat. Am. J. Sedimentol. Basin Anal.* **2022**, *29*, 67–81.
64. Paz, M.; Baez, A.D.; Pino, D.A.; Yunes, Y.S.; Garat, L.M.; Ponce, J.J.; Tunik, M.A. Análisis sedimentológico de depósitos lacustres y eólicos del Cretácico Tardío en la localidad Paso Córdoba, cuenca Neuquina. *Rev. Asoc. Geol. Argent.* **2014**, *71*, 459–471.
65. Armas, P.; Moreno, C.; Sánchez, M.L.; González, F. Sedimentary palaeoenvironment, petrography, provenance and diagenetic inference of the Anacleto Formation in the Neuquén Basin, Late Cretaceous, Argentina. *J. S. Am. Earth Sci.* **2014**, *53*, 59–76. [CrossRef]
66. Folk, R.L.; Andrews, P.B.; Lewis, D.W. Detrital sedimentary rock classification and nomenclature for use in New Zealand. *N. Z. J. Geol. Geophys.* **1970**, *13*, 937–968. [CrossRef]
67. Armas, P.; Sánchez, M.L. Hybrid coastal edges in the Neuquén Basin (Allen Formation, Upper Cretaceous, Argentina). *Andean Geol.* **2015**, *42*, 97–113.
68. Woodward, A.S. On two Mesozoic crocodilians *Notosuchus* (genus novum) and *Cynodontosuchus* (genus novum) from the Red Sandstones of the Territory of Neuquén (Argentina Republic). *An. Mus. Plata* **1896**, *4*, 1–20.
69. Bonaparte, J.F. Los vertebrados fósiles de la Formación Río Colorado de Neuquén y cercanías, Cretácico Superior, Argentina. *Rev. Mus. Argent. Cienc. Nat. Bernardino Rivadavia Paleontol.* **1991**, *4*, 17–123.
70. Leardi, J.M.; Pol, D.; Gasparini, Z. New Patagonian baurusuchids (Crocodylomorpha; Notosuchia) from the Bajo de la Carpa Formation (Upper Cretaceous; Neuquén, Argentina): New evidences of the early sebecosuchian diversification in Gondwana. *C. R. Palevol* **2018**, *17*, 504–521. [CrossRef]
71. Woodward, A.S. On some extinct reptiles from Patagonia of the genera Miolania, Dinilysia, and Genyodectes. In Proceedings of the Zoological Society of London; Blackwell Publishing Ltd.: Oxford, UK, 1901; pp. 169–184.

72. Martinelli, A.G.; Vera, E.I. *Achillesaurus manazzonei*, a new alvarezsaurid theropod (Dinosauria) from the Late Cretaceous Bajo de la Carpa Formation, Río Negro Province, Argentina. *Zootaxa* **2007**, *1582*, 1–17. [CrossRef]
73. Brissón-Egli, F.; Agnolín, F.L.; Novas, F.E. A new specimen of *Velocisaurus unicus* (Theropoda, Abelisauroidea) from the Paso Córdoba locality (Santonian), Río Negro, Argentina. *J. Vertebr. Paleontol.* **2016**, *36*, e1119156. [CrossRef]
74. Ezcurra, M.D.; Méndez, A.H. First report of a derived abelisaurid theropod from the Bajo de la Carpa Formation (Late Cretaceous), Patagonia, Argentina. *Bull. Geosci.* **2009**, *84*, 547–554. [CrossRef]
75. Consolé-Gonella, C.A.; Díaz-Martínez, I.; de Valais, S.; Citton, P.; Paniceres, P. Presencia de excavaciones de vertebrados fósiles en la Formación Bajo de la Carpa (Santoniano), Paso Córdoba, Río Negro, Argentina. *PE-APA* **2019**, *20*, R7.
76. Fischer, G. Registro Fósil de la Formación Bajo de la Carpa (Cretácico Superior) en el Área Natural Protegida de Paso Córdoba (Río Negro, Argentina): Implicancias Paleoecológicas y Paleobiológicas e Inferencias Paleoambientales. Ph.D. Thesis, Universidad Nacional de Río Negro, General Roca, Río Negro Province, Argentina, 2022. Unpublished.
77. Wichmann, R. Las capas con Dinosaurios en la Costa sur del Río Negro, frente a General Roca. *Physis* **1916**, *11*, 258–262.
78. von Huene, F.R.F. Los Saurisquios y Ornitisquios del Cretáceo Argentino. *An. Mus. Plata* **1929**, *3*, 1–196.
79. de la Fuente, M.S.; Barbieri, R.; Chafrat, P. Una tortuga Chelidae (Testudines: Pleurodira) de cuello largo en el Grupo Neuquén, Río Negro, Argentina: Significado cronológico y paleobiogeográfico. *Andean Geol.* **2010**, *37*, 398–412. [CrossRef]
80. Goin, F.J.; Carlini, A.A.; Pascual, R. Un probable marsupial del Cretácico Tardío del norte de Patagonia, Argentina. In Proceedings of the 4º Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, Argentina, 23–27 November 1986; Volume 2, pp. 401–410.
81. Gigli, A.; Archuby, F.; Díaz-Martínez, I. Significación paleoambiental de las acumulaciones de moluscos del Campaniano de Paso Córdoba, General Roca, Río Negro. *PE-APA* **2019**, *20*, R38.
82. Gigli, A.; Díaz-Martínez, I.; Archuby, F. Análisis de facies y microfacies sedimentarias de los niveles ricos en invertebrados del Cretácico Superior de Paso Córdoba, General Roca, Río Negro. *PE-APA* **2019**, *20*, R11.
83. Díaz-Martínez, I.; de Valais, S.; Cónsole-Gonella, C.; Salgado, L.; Paniceres, P.; Citton, P. Nuevos hallazgos de huellas de vertebrados (formaciones Anacleto y Allen, Cretácico Superior) en Paso Córdoba, General Roca, Río Negro, Argentina. *Ameghiniana* **2017**, *54*, R4.
84. Álvarez, C.; Álvarez Soria, J.; Barbieri, R.; Brandt, E.; Canudo, J.I.; Capobianco, A.; Cárdenas, M.; Cruzado-Caballero, P.; de Valais, S.; Díaz-Martínez, I.; et al. Nuevos restos de Sauropoda (Titanosauria) de la Formación Allen (Cretácico Superior) en Paso Córdoba (General Roca, Provincia de Río Negro). *Ameghiniana* **2016**, *53*, R5.
85. Díaz-Martínez, I.; de Valais, S.; Yunes, Y.; Garat, L.M.; Salgado, L. Tafonomía y paleoecología de un nuevo yacimiento del Cretácico Superior (Formación Allen) con restos de dinosaurios en Paso Córdoba, Río Negro, Argentina. *Ameghiniana* **2016**, *53*, R16.
86. Meso, J.G. Dientes de Theropoda Asociados a un Esqueleto de un Saurópodo Titanosaurio Hallado en la Formación Allen (Campaniamo-Maastrichtiano) de la Provincia de Río Negro, Argentina. Ph.D. Thesis, Universidad Nacional de Río Negro, General Roca, Río Negro Province, Argentina, 2017. Unpublished.
87. Meso, J.G.; Salgado, L.; Canale, J. Dientes de Theropoda asociados a un esqueleto de un saurópodo titanosaurio hallado en la Formación Allen (Campaniano-Maastrichtiano) en la provincia de Río Negro, Argentina. *Ameghiniana* **2015**, *53*, R33.
88. Meso, J.G.; Hendrickx, C.; Baiano, M.A.; Canale, J.I.; Salgado, L.; Díaz-Martínez, I. Isolated theropod teeth associated with a sauropod skeleton from the Late Cretaceous Allen Formation of Río Negro, Patagonia, Argentina. *Acta Palaeontol. Pol.* **2021**, *66*, 409–423. [CrossRef]
89. López-Rodal, L.; Pino, D.; Cárdenas, M.; Montes, R.; Méndez, A.; Paniceres, P.; Díaz-Martínez, I.; Salgado, L. Estudio tafonómico preliminar de un nuevo dinosaurio saurópodo perteneciente a la Formación Allen (Cretácico Superior) en Paso Córdoba, General Roca, Río Negro. *PE-APA* **2019**, *19*, R21.
90. López-Rodal, L. Estudio Tafonómico de un Nuevo Dinosaurio Saurópodo de la Formación Allen (Cretácico Superior) en el Área Natural Protegida Paso Córdoba, General Roca, Río Negro, Argentina. Ph.D. Thesis, Universidad Nacional de Río Negro, General Roca, Río Negro Province, Argentina, 2021. Unpublished.
91. Calvo, J.O.; Ortíz, R.A. Nuevos registros de dinosauria en la Formación Allen (Cretácico Superior) en el área Natural Protegida Paso Córdoba. General Roca, Río Negro. *Ameghiniana* **2011**, *48*, R150.
92. Calvo, J.O.; Ortíz, R.A. Hadrosaur ichnites from Río Negro province (Upper Cretaceous). *Ameghiniana* **2013**, *50* (Suppl.), R38.
93. Ortíz, R.A.; Calvo, J.O. Icnofacies del Miembro Inferior de la Formación Allen, Grupo Malargüe (Campaniano superior-Maastrichtiano inferior), Paso Córdoba, Río Negro, Argentina. *PE-APA* **2017**, *54*, 39.
94. Ortíz, R.A.; Calvo, J.O.; Garrido, A.C. Primer registro de huellas de aves para la Formación Allen, Cretácico Superior, Paso Córdoba, Río Negro, Argentina. *Ameghiniana* **2013**, *50*, R64.
95. Urzagasti, S. Análisis de huellas avianas del Cretácico Superior del Cañadón del Laberinto (Valle de la Luna Amarillo, Paso Córdoba, Río Negro, Argentina). Ph.D. Thesis, Universidad Nacional de Río Negro, General Roca, Río Negro Province, Argentina, 2022. Unpublished.
96. Díaz-Martínez, I.; Cónsole-Gonella, C.A.; de Valais, S.; Citton, P.; Paniceres, P. Excavaciones de vertebrados asociadas a las facies eólicas de la Formación Allen (Cretácico Superior) en Paso Córdoba, Río Negro, Argentina. *PE-APA* **2019**, *20*, R76.
97. Pascual-Arribas, C.; Hernández-Medrano, N. Huellas de *Pteraichnus* en la Muela (Soria, España): Consideraciones sobre el icnogénero y sobre la diversidad de huellas de pterosaurios en la Cuenca de Cameros. *Rev. Soc. Geol. Esp.* **2016**, *29*, 89–105.
98. Hernández-Medrano, N.; Pascual-Arribas, C.; Pérez-Lorente, F. First pterosaur footprints from the Tera Group (Tithonian–Berriasian) Cameros Basin, Spain. *J. Iber. Geol.* **2017**, *43*, 245–255. [CrossRef]

99. Pascual-Arribas, C.; Canudo, J.I.; Pérez, E.S.; Hernández-Medrano, N.; Castanera, D.; Barco, J.L. On the validity of *Pteraichnus palacieisaenzi*, Pascual Arribas and Sanz Pérez 2000: New data from the Huérteles formation. *PalZ* **2015**, *89*, 459–483. [CrossRef]
100. Elgh, E.; Pieńkowski, G.; Niedźwiedzki, G. Pterosaur track assemblages from the Upper Jurassic (lower Kimmeridgian) intertidal deposits of Poland: Linking ichnites to potential trackmakers. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2019**, *530*, 32–48. [CrossRef]
101. Mazin, J.M.; Pouech, J. The first non-pterodactyloid pterosaurian trackways and the terrestrial ability of non-pterodactyloid pterosaurs. *Geobios* **2020**, *58*, 39–53. [CrossRef]
102. Mallison, H.; Wings, O. Photogrammetry in paleontology—A practical guide. *J. Paleontol. Tec.* **2014**, *12*, 1–31.
103. Falkingham, P.L.; Bates, K.T.; Avanzini, M.; Bennett, M.; Bordy, E.M.; Breithaupt, B.H.; Castanera, D.; Citton, P.; Díaz-Martínez, I.; Farlow, J.O.; et al. A standard protocol for documenting modern and fossil ichnological data. *Palaeontology* **2018**, *61*, 469–480. [CrossRef]
104. Lockley, M.G.; Logue, T.J.; Moratalla, J.J.; Hunt, A.P.; Schultz, R.J.; Robinson, J.W. The fossil trackway *Pteraichnus* is pterosaurian, not crocodilian: Implications for the global distribution of pterosaur tracks. *Ichnos* **1995**, *4*, 7–20. [CrossRef]
105. Milàn, J. Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks reflecting differences in walking pattern and substrate consistency: Ichnotaxonomic implications. *Palaeontology* **2006**, *49*, 405–420. [CrossRef]
106. Ambroggi, R.; De Lapparent, A.F. Les empreintes de pas fossiles du Maestrichtien d'Agadir. *Notes Serv. Géol. Maroc* **1954**, *10*, 43–57.
107. Hwang, K.G.; Huh, M.; Lockley, M.G.; Unwin, D.M.; Wright, J.L. New pterosaur tracks (Pteraichnidae) from the Late Cretaceous Uhangri Formation, southwestern Korea. *Geol. Mag.* **2002**, *139*, 421–435. [CrossRef]
108. Kim, J.Y.; Lockley, M.G.; Kim, K.S.; Seo, S.J.; Lim, J.D. Enigmatic giant pterosaur tracks and associated ichnofauna from the Cretaceous of Korea: Implication for the bipedal locomotion of pterosaurs. *Ichnos* **2012**, *19*, 50–65. [CrossRef]
109. Billon-Bruyat, J.P.; Mazin, J.M. The systematic problem of tetrapod ichnotaxa: The case study of *Pteraichnus* Stokes, 1957 (Pterosauria, Pterodactyloidea). *Geol. Soc. Lond. Spec. Publ.* **2003**, *217*, 315–324. [CrossRef]
110. Lockley, M.G.; Harris, J.D.; Mitchell, L. A global overview of pterosaur ichnology: Tracksite distribution in space and time. *Zitteliana* **2008**, *28*, 187–198.
111. Whyte, M.A.; Romano, M. First record of the pterosaur footprint *Pteraichnus* from the Saltwick Formation (Aalenian) of the Cleveland Basin, Yorkshire, UK. *Proc. Yorks. Geol. Soc.* **2014**, *60*, 19–27. [CrossRef]
112. Gierlinski, G.; Adach, L.; Lockley, M. First report of Jurassic pterosaur tracks from Africa. In Proceedings of the Society of Vertebrate Paleontology, 73rd Annual Meeting, Los Angeles, CA, USA, 30 October–2 November 2013; p. 133.
113. Calvo, J.O.; Moratalla, J.J. First record of pterosaur tracks in southern continents. In Proceedings of the III Encuentro Argentino de Icnología y I Reunión de Icnología del Mercosur, Resúmenes, Mar del Plata, Argentina, 28 April–3 May 1998; pp. 7–8.
114. Díaz-Martínez, I.; de Valais, S.; Citton, P.; Cónsole-Gonella, C.; Calvo, J.O.; Paniceres, P.J.; Fischer, G.; Urzagasti, S.; Caratelli, M.; Isasi, M.; et al. Huellas de dinosaurios y pterosaurios en el sector rionegrino del Embalse Ezequiel Ramos Mexía (Formación Candeleros, Cenomaniano). *PE-APA* **2022**, *22*, R255.
115. Rivera, C.J.; Avila, L.; Calvo, J.O. Nuevos hallazgos de huellas de pterosaurio de la Formación Candeleros (Grupo Neuquén) en el Depto de Picún Leufú, Neuquén, Argentina. *PE-APA* **2022**, *24*, R32.
116. Rodríguez-de la Rosa, R.A. Pterosaur tracks from the latest Campanian Cerro del Pueblo Formation of southeastern Coahuila, Mexico. *Geol. Soc. Lond. Spec. Pub.* **2003**, *217*, 275–282. [CrossRef]
117. Lockley, M.G. Pterosaur and bird tracks from a new Late Cretaceous locality in Utah. In *Vertebrate Paleontology in Utah*; Gillette, D.D., Ed.; Utah Geological Survey: Salt Lake City, UT, USA, 1999; pp. 355–359.
118. Fiorillo, A.R.; Kobayashi, Y.; McCarthy, P.J.; Wright, T.C.; Tomsich, C.S. Pterosaur tracks from the Lower Cantwell Formation (Campanian–Maastrichtian) of Denali National Park, Alaska, USA, with comments about landscape heterogeneity and habit preferences. *Hist. Biol.* **2015**, *27*, 672–683. [CrossRef]
119. Lü, J.C.; Chen, R.J.; Azuma, Y.; Zheng, W.J.; Tanaka, I.; Jin, X.S. New pterosaur tracks from the early Late Cretaceous of Dongyang City, Zhejiang Province, China. *Acta Geosci. Sin.* **2010**, *31*, 46–48.
120. Unwin, D.M. On the phylogeny and evolutionary history of pterosaurs. In *Evolution and Palaeobiology of Pterosaurs*; Buffetaut, E., Mazin, J.M., Eds.; Geological Society, Special Publications: London, UK, 2003; Volume 217, pp. 139–190. [CrossRef]
121. Martínez, R.N.; Andres, B.; Apaldetti, C.; Cerda, I.A. The dawn of the flying reptiles: First Triassic record in the southern hemisphere. *Pap. Palaeontol.* **2022**, *8*, e1424. [CrossRef]
122. Andres, B.; Clark, J.; Xu, X. 2014. The earliest pterodactyloid and the origin of the group. *Curr. Biol.* **2014**, *24*, 1011–1016. [CrossRef] [PubMed]
123. Lü, J.; Meng, Q.; Wang, B.; Liu, D.; Shen, C.; Zhang, Y. Short note on a new anurognathid pterosaur with evidence of perching behaviour from Jianchang of Liaoning Province, China. *Geol. Soc. Lond. Spec. Publ.* **2018**, *455*, 95–104. [CrossRef]
124. Kellner, A.W.; Rodrigues, T.; Costa, F.R.; Weinschütz, L.C.; Figueiredo, R.G.; Souza, G.A.; Brum, A.S.; Eleutério, L.H.S.; Muller, C.W.; Sayão, J.M. Pterodactyloid pterosaur bones from Cretaceous deposits of the Antarctic Peninsula. *An. Acad. Bras. Cienc.* **2019**, *91*, 1–16. [CrossRef]
125. O'Connor, P.M.; Sertich, J.J.; Manthi, F.K. A pterodactyloid pterosaur from the Upper Cretaceous Lapurr sandstone, West Turkana, Kenya. *An. Acad. Bras. Cienc.* **2011**, *83*, 309–315. [CrossRef]
126. Wiffen, J.; Molnar, R.E. First pterosaur from New Zealand. *Alcheringa* **1988**, *12*, 53–59. [CrossRef]
127. Coria, R.A.; Chiappe, L.M.; Dingus, L. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. *J. Vertebr. Paleontol.* **2002**, *22*, 460–465. [CrossRef]

128. Sereno, P.C.; Martínez, R.N.; Wilson, J.A.; Varricchio, D.J.; Alcober, O.A.; Larsson, H.C. Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS ONE* **2008**, *3*, e3303. [CrossRef]
129. Salgado, L.; Coria, R.A. *Barrosasaurus casamiquelai* gen. et sp. nov., a new titanosaur (Dinosauria, Sauropoda) from the Anacleto Formation (Late Cretaceous: Early Campanian) of Sierra Barrosa (Neuquén, Argentina). *Zootaxa* **2009**, *2222*, e16. [CrossRef]
130. Turner, A.H.; Calvo, J.O. A new sebecosuchian crocodyliform from the Late Cretaceous of Patagonia. *J. Vertebr. Paleontol.* **2005**, *25*, 87–98. [CrossRef]
131. Scanferla, C.A.; Canale, J.I. The youngest record of the Cretaceous snake genus *Dinilysia* (Squamata, Serpentes). *South Am. J. Herpetol.* **2007**, *2*, 76–81. [CrossRef]
132. González Riga, B.J.; Ordoñez, M.; Nasif, D.; Croce, C.; Crack, J. First record of dinosaur tracks from the Anacleto Formation in the Mendoza Province, Neuquén Basin, Argentina. In Proceedings of the Reunión Anual de Comunicaciones de la Asociación Paleontológica Argentina, Luján, Argentina, 23–25 November 2011; pp. 35–36.
133. González Riga, B.J.; Ortiz David, L.D.; Gutiérrez, P.; Martínez, L.; Pinto, L.; Resa, L.; Sánchez Tiviroli, G.; Pascual, M.; Pena, V.; Poblete, S. Huellas de saurópodos titanosaurios en la Formación Anacleto, Cretácico Superior de Malargüe, Mendoza, Argentina. *Ameghiniana* **2013**, *50*, R19.
134. González Riga, B.J.; Ortiz David, L.D.; Coria, J.P.; Sánchez Tiviroli, G.; Gutiérrez, P.; Pinto, L.; Spinelli, S.; Prieto, G.; Cartelone, F.; Pascual Tudanca, M. Huellas de dinosaurios en el sur de Mendoza (Argentina): Evidencias paleobiológicas y ambientes sedimentarios. In Proceedings of the 19° Congreso Geológico Argentino, Córdoba, Argentina, 2–6 June 2014.
135. Tomaselli, M.B.; Ortiz David, L.D.; González Riga, B.J.; Coria, J.P.; Mercado, C.R.; Guerra, M.; Sánchez Tiviroli, G. Análisis y discusiones en icnotaxonomía a partir del icnotaxón *Teratopodus malarguensis*. *PE-APA* **2022**, *22*, R220.
136. Tomaselli, M.B.; Ortiz David, L.D.; González Riga, B.J.; Coria, J.P.; Mercado, C.; Sánchez Tiviroli, G.; Giovanetti, M.P.; Guerra, M. Nuevas huellas de saurópodos titanosaurios en la Formación Anacleto (Cretácico Superior, Mendoza-Argentina). *PE-APA* **2019**, *19*, R40.
137. Lockley, M.G. *Tracking Dinosaurs: A New Look at an Ancient World*; Cambridge University Press: Cambridge, UK, 1991.
138. Buatois, L.A.; Gabriela Mángano, M. Ichnodiversity and ichnodisparity: Significance and caveats. *Lethaia* **2013**, *46*, 281–292. [CrossRef]
139. Thulborn, R.A. *Dinosaur Tracks*; Chapman and Hall: London, UK, 1990.