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A New Crested Pterosaur from the Early Cretaceous of Spain: The First European Tapejarid (Pterodactyloidea: Azhdarchoidea)

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Abstract

Background: The Tapejaridae is a group of unusual toothless pterosaurs characterized by bizarre cranial crests. From a paleoecological point of view, frugivorous feeding habits have often been suggested for one of its included clades, the Tapejarinae. So far, the presence of these intriguing flying reptiles has been unambiguously documented from Early Cretaceous sites in China and Brazil, where pterosaur fossils are less rare and fragmentary than in similarly-aged European strata.

Methodology/Principal Findings: *Europejara olcadesorum* gen. et sp. nov. is diagnosed by a unique combination of characters including an unusual caudally recurved dentary crest. It represents the oldest known member of Tapejaridae and the oldest known toothless pterosaur. The new taxon documents the earliest stage of the acquisition of this anatomical feature during the evolutionary history of the Pterodactyloidea. This innovation may have been linked to the development of new feeding strategies.

Conclusion/Significance: The discovery of *Europejara* in the Barremian of the Iberian Peninsula reveals an earlier and broader global distribution of tapejarids, suggesting a Eurasian origin of this group. It adds to the poorly known pterosaur fauna of the Las Hoyas locality and contributes to a better understanding of the paleoecology of this Konservat-Lagerstätte. Finally, the significance of a probable contribution of tapejarine tapejarids to the early angiosperm dispersal is discussed.

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Introduction

In the Early Cretaceous (145–99 million years ago), a peak occurred in the morphological disparity of Pterosauria, suggesting that new ecological niches were exploited [1–4]. One of the most striking adaptations in the evolutionary history of several groups of pterosaurs is the development of distinctively crested skulls. The Tapejaridae [5,6] is one of the groups that have appeared during this period and that have acquired these important ecomorphological innovations. This clade of pterodactyloids is represented by peculiar forms, which are subdivided into two groups: the long-faced and large Thalassodrominae and the short-faced and smaller Tapejarinae [6,7]. Both bear well-developed cranial crests [6–8], making the tapejarids a bizarre-looking and enigmatic group of pterosaurs.

The subfamily Tapejarinae comprises the oldest known edentulous pterosaurs [9,10]. It has been interpreted that the acquisition of a suite of ecomorphological novelties was key to develop the behavior and feeding strategies (i.e., frugivory) that helped tapejarines exploit unexplored ecological niches. Due to their short skull with a particular downturned rostrum and unusually shaped toothless beak, tapejarines have most consistently been suggested to have been seed and/or fruit eaters [9,11,12].

This group of peculiar pterodactyloids is uncommon in the fossil record, occurring mainly in some late Early Cretaceous (Aptian–Albian stages, 125–99 million years ago) fossil Konservat-Lagerstätten of Brazil (e.g. *Tapejara*, *Tupandactylus*) [7] and China (e.g. *Sinopterus*) [9]. In addition, a single jaw fragment from the early Late Cretaceous (Cenomanian stage, 99–93 million years ago) of Morocco has been tentatively referred to as an indeterminate tapejarid [6,13,14]. Despite the diversity and

richness of the European Cretaceous pterosaur faunas [15–17], tapejarids have not been reported from this continent so far.

Here, we report an incomplete skull and lower jaw of a new tapejarid pterosaur, *Europejara olcadesorum* gen. et sp. nov., from the mid-Early Cretaceous (Barremian stage, 130–125 million years ago) La Huérguina Formation laminated limestone of Las Hoyas (Cuenca) in eastern Spain. This new taxon is the oldest known tapejarid and the first found in Europe, thus extending the stratigraphic and geographical distribution of the group. It differs from all other known tapejarids by bearing a well-developed caudally recurved sagittal crest (autapomorphy) on the lower jaw. *Europejara* sheds new light on the evolutionary history of the group based upon a new phylogenetic analysis, suggesting that the origin of these toothless pterosaurs took place in Eurasia near the beginning of the Early Cretaceous. The late Barremian age of the Las Hoyas beds [18] also makes *Europejara* the oldest hitherto known toothless pterosaur, slightly older than *Eopteranodon* from the earliest Aptian of the Yixian Formation, China [19–21]. As in some groups of non-avian theropod dinosaurs [22] and early birds [23], the acquisition of complete edentulism, which appears to have occurred independently twice [24] or more likely at least three times [20,25,26] during the evolutionary history of Pterosauria, could be correlated with the development of new feeding strategies [9]. Within the Azhdarchoidea (i.e. the clade grouping chaoyangopterids, tapejarids, and azhdarchids), the complete tooth loss as well as some other morphological adaptations observed in the jaws of tapejarines could indicate herbivorous habits and be linked to the early angiosperm diversification [11]. However, such an assumption is based essentially on rostral morphology and lacks direct support from the fossil record that could be conclusively provided by gut contents only. In addition, although a co-existence in time and space of tapejarids and early flowering plants can be qualitatively observed, the fossil record and distribution of these pterosaurs are too scarce to provide any convincing quantitative evidence for an interaction between both groups. In this context, the hypothesis arguing that tapejarine tapejarids were frugivorous pterosaurs and significant long-distance dispersal vectors during the first radiation of flowering plants is here briefly discussed on the basis of the data available. Given the widespread geographical distribution and the particular adaptations of tapejarids (e.g. for possible frugivory), we discuss why studies should consider them a distinct component part of the Cretaceous Terrestrial Revolution [27].

Materials and Methods

Institutional Abbreviations

AMNH: American Museum of Natural History, New York, USA; BSP: Bayerische Staatssammlung für Paläontologie, Munich, Germany; CPCA: Centro de Pesquisas Paleontológicas da Chapada do Araripe, Crato, Brazil; GMN: Geological Museum of Nanjing, Nanjing, China; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCCM-LH: Las Hoyas collection of the Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain.

The Las Hoyas Fossil Site

The Las Hoyas subbasin is located in the Serranía de Cuenca, southwestern Iberian ranges, eastern Spain [28]. The sequence including the Las Hoyas fossiliferous deposits is composed of laminated limestone and rare marlstone levels (La Huérguina Formation, upper Barremian) [18]. These deposits were produced in the context of a continental subtropical, wet and forested environment overlying a low-relief karstic terrain [29].

The Konservat-Lagerstätte of Las Hoyas has yielded a rich floral and faunal continental assemblage [18,30,31]. The Las Hoyas biota mainly consists of obligate aquatic organisms (e.g. osteichthyan fishes, decapod crustaceans, belostomid insects, charophytes, the aquatic plant *Montsechia*) [29,31]. The amphibious forms (i.e. crocodyliforms, turtles, and lissamphibians) are much less abundant, and the facultative ones (i.e. terrestrial/arboreal forms such as insects, lizards and basal birds) are rather rare. Large animals such as dinosaurs (e.g. *Concavenator*) [32] are exceptional in the assemblage, and correspond to the incidental ecological category [33]. Pterosaurs are rare in the Las Hoyas assemblage, with only a few teeth indicating the presence of a rather large ornithocheirid (= anhanguerid) and a small basal istiodactylid [34]. The terrestrial macroflora is dominated by conifers (Cheirolepidiaceae) and ferns (Matoniaceae and Schizaeaceae), although angiosperm remains are present and relatively diverse [31].

Among the most significant taphonomic features of the vertebrate specimens of this site are their articulation and preservation (e.g. mineralization of soft tissue) [32,35]. However, the Las Hoyas beds also contain numerous isolated vertebrate remains, such as teeth, ribs, feathers and fish scales.

Phylogenetic Analysis

In order to access the phylogenetic position of *Europejara olcadesorum* gen. et sp. nov., we performed a phylogenetic analysis using PAUP 4.0b10 for Microsoft Windows [36] using the TBR heuristic searches performed using maximum parsimony (see Appendix S1 for character list and data matrix). Characters were given equal weight and treated unordered (ACCTRAN setting). This analysis is based on previous studies (e.g. [1,20,24–26,37]). The search conducted by PAUP, with *Ornithosuchus longidens* and *Herrerasaurus ischigualastensis* as outgroups, produced 135 equally parsimonious trees (205 steps; consistency index = 0.7561; retention index = 0.8538; rescaled consistency index = 0.6456), from which a strict consensus cladogram was obtained.

Although a discussion of previous phylogenetic analyses is not the scope of this paper, we did also score *Europejara olcadesorum* in the phylogenetic analysis published by Andres & Ji [20] and obtained a similar result.

Nomenclatural Acts

The electronic version of this document does not represent a published work according to the International Code of Zoological Nomenclature (ICZN), and hence the nomenclatural acts contained in the electronic version are not available under that Code from the electronic edition. Therefore, a separate edition of this document was produced by a method that assures numerous identical and durable copies, and those copies were simultaneously obtainable (from the publication date noted on the first page of this article) for the purpose of providing a public and permanent scientific record, in accordance with Article 8.1 of the Code. The separate print-only edition is available on request from PLoS by sending a request to PLoS ONE, 1160 Battery Street, Suite 100, San Francisco, CA 94111, USA along with a check for \$10 (to cover printing and postage) payable to “Public Library of Science”.

In addition, this published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/”. The LSID for this

publication is: urn:lsid:zoobank.org:pub:60DF87C8-E4CA-4021-877F-0EF6FA78B1BC.

Results

Systematic Paleontology

Systematic hierarchy:

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Azhdarchoidea Nessov, 1984 (*sensu* [24])

Tapejaridae Kellner, 1989

Tapejarinae Kellner, 1989 (*sensu* [7])

Europejara olcadesorum gen. et sp. nov.

ZooBank Life Science Identifier (LSID) for genus.

urn:lsid:zoobank.org:act:69302E4D-F4BF-472F-9C72-2105BE44A227.

ZooBank LSID for species.

urn:lsid:zoobank.org:act:AED2386E-16C6-40B1-9E75-1EE06579AD95.

Etymology. Genus name formed by the combination of Europe and *Tapejara*, the internal specifier of the Tapejarinae [5,7]; species named after the Olcades, Celtiberians who were the first inhabitants of the Cuenca region.

Holotype. MCCM-LH 9413, jaws and post-orbital elements of the skull preserved on part and counterpart slabs (Figures 1, 2, 3, 4). Specimen housed in the Museo de las Ciencias de Castilla-La Mancha (MCCM), Cuenca, Spain.

Locality and Horizon. Las Hoyas (Cuenca, Spain), upper Barremian laminated limestone of the La Huérguina Formation (Lower Cretaceous) [18,28].

Diagnosis. Tapejarine tapejarid with the following combination of characters that distinguish it from other members of the clade (autapomorphies marked with an asterisk*): dentary bony sagittal crest caudally recurved*; dentary crest more developed dorsoventrally than anteroposteriorly*; high dentary crest height/mandibular ramus height (DCH/MRH) ratio* (found to be about 4 whereas it ranges from 1.5 to 3 in other tapejarid species); presence of a lingual bulge developing medially along the dorsal border of the dentary; presence of some shallow but well marked depressions on the medial surface of the mandibular rami.

Description and Comparisons

The skull is incomplete, crushed, and flattened dorsoventrally, whereas the mandible is preserved in lateral view (Figure 1). The bones of the left post-orbital region of the skull (jugal postorbital process, postorbital, quadrate, and squamosal) are crushed and displaced. Some small bones, including a fragmentary lacrimal and a possible postfrontal, were preserved around the orbital region and have been removed from the matrix during the acid preparation. No integumentary structures (e.g. soft tissue, keratinous rhamphotheca) are preserved.

Both maxillae are incomplete. They are exposed dorsally and form an angle of about 12°. The posterior end of the right maxilla is apparently still in contact with the anterior process of the jugal, but no suture can be observed. Only the left jugal, missing its anterior and ascending processes, can be unambiguously identified. Its preserved part corresponds to the process that is in contact with the postorbital. This robust process separates the orbit from the lower temporal fenestra. It decreases in width from its base to the contact area with the postorbital. Some longitudinal folds are present at its base. The incomplete element that is interpreted as a fragmentary lacrimal is thin and fenestrated, a typical feature of tapejarine pterosaurs (e.g. [6]).

The postorbital is roughly triangular, and no suture can be observed between this bone and the underlying process of the jugal (Figure 3A). The left quadrate is located posterior to the preserved process of the jugal, thus determining the approximate position of the narrow lower temporal fenestra. The quadrate bears medially a thin bony lamella, as well as a few longitudinal folds. The mandibular articulation of the quadrate shows two rounded condyles. The squamosal appears as a bony mass whose outline is poorly defined. It is in connection with the quadrate.

The palate, exposed in dorsal view, shows two narrow and elongate choanae separated by a thin vomer (Figure 3B). The sutures between the palatine, pterygoid, ectopterygoid and maxilla are poorly visible. A process of the pterygoid–ectopterygoid complex projects anterolaterally and connects to the posterior process of the maxilla. It separates two oval-shaped fenestrae posterolaterally to the choanae (Figure 3C). A shallow depression is present on the anterior surface of this pterygoid–ectopterygoid complex process.

Some trapezoidal-shaped scleral plates are also preserved. Most of these thin bony elements, now removed from the matrix, were originally preserved in the orbital region of the skull. A few other scleral plates are scattered on the slab surface.

The mandible is nearly complete with a preserved length of 230 mm and an estimated total length of 255 mm. Although most of the preserved portion of the mandible corresponds to the dentaries, some posterior elements can be identified as the surangular and the retroarticular process. The mandibular rami (22 mm in height) are robust and show parallel dorsal and ventral borders. The lateral surface of the ramus is smooth whereas the medial surface displays some shallow but well-marked depressions. A lingual bulge is present medially along the dorsal border of the dentaries. In lateral view, the cutting edge of the dentaries is slightly sigmoid at the symphyseal area, being convex posteriorly and concave anteriorly. The dorsal surface of the symphysis is concave in cross-section. The mandible of *Europejara* bears a deep dentary bony sagittal crest that is recurved caudally. The estimated height of this crest is about 90 mm, giving a DCH/MRH ratio of about 4 (Figure 5A).

The hyoid apparatus, represented by the ossified first pair of rod-like ceratobranchials, lies adjacent to the ventral margin of the mandible. The branches are about 135 mm in length and less than 2 mm in diameter, and are slightly curved in their posterior half (Figure 3A).

Europejara is mainly distinguished from the Chinese tapejarines by having a larger size and in having a more developed, deeper dentary sagittal crest. In *Sinopterus dongi*, the DCH/MRH ratio is between 1.5 (value based on the specimen IVPP V 13363 [12]) and 2.2 (value based on the specimen GMN-03-11-001, the holotype of *Huaxiaopterus jii* [38], itself a junior synonym of *S. dongi* [39]) (Figure 5D, 5E). The dentary sagittal crest is even less developed in both “*Huaxiaopterus*” *corollatus* and “*Huaxiaopterus*” *benxiensis* (two species still needing a new generic name) than in *Sinopterus dongi* [40,41]. Finally, the rare Chinese genus *Eopteranodon* has a skull which remains poorly known. Judging from the figures provided by Lü & Zhang [19], the dentary sagittal crest seems to be similar to that of *Sinopterus*.

The mandible of *Europejara* differs from that of *Tapejara* in displaying a dorsal border less sigmoid at the symphyseal area in lateral view and in having less robust and relatively thinner rami. The DCH/MRH ratio is 2.5 in *Tapejara* (value based on the reconstructed mandible of the specimen AMNH 24440 [11]) (Figure 5C). In juvenile individuals in which the dentary crest is less pronounced [42,43], this ratio tends to be lower (around 2).

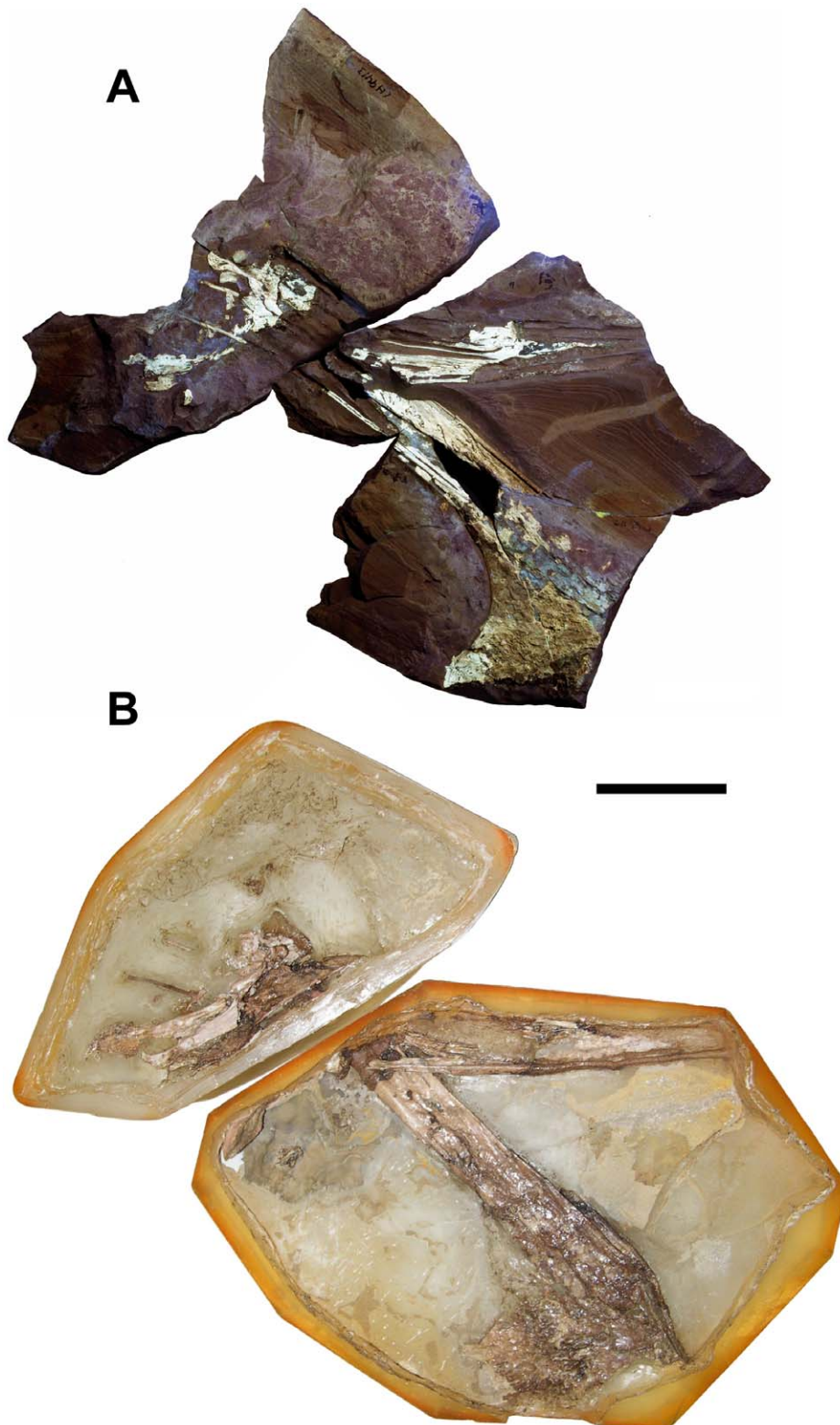


Figure 1. Photographs of the holotype of *Europejara olcadesorum* gen. et sp. nov. (MCCM-LH 9413). (A) Main slab under ultraviolet light. (B) Acid-prepared counterslab. Scale bar: 50 mm.
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The dentary crest is more developed anteroposteriorly in *Tapejara*, occupying approximately the anterior half of the mandible.

The mandibles of *Europejara* and *Tupandactylus* are rather similar in size and proportions, with slender mandibular rami and a deep sagittal crest [44]. However, the DCH/MRH ratio is lower in

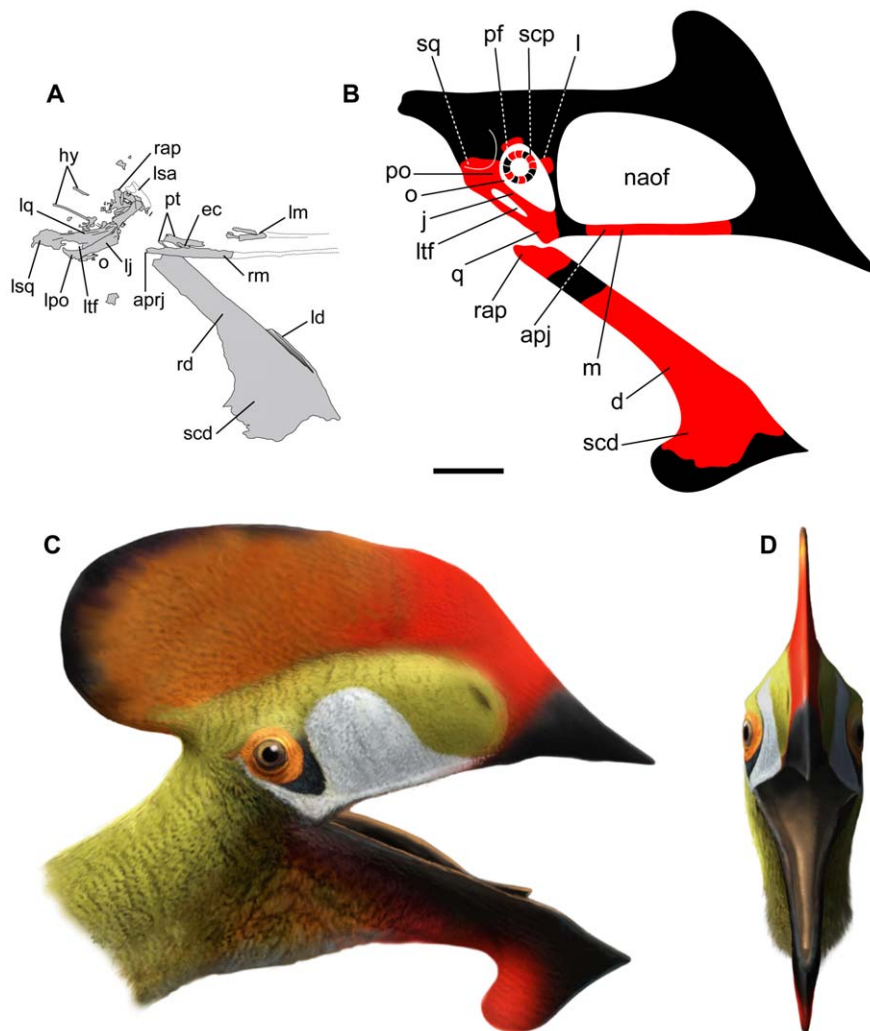


Figure 2. Line drawing of the holotype of *Europejara olcadesorum* gen. et sp. nov. and life restoration. (A) Interpretative line drawing of the skull as observed on the acid-prepared counterslab. (B) Reconstruction of the skull (based in part on *Tapejara*) showing preserved parts in red. Life restoration of the head of *Europejara* in lateral (C) and frontal (D) views. apj, anterior process of the jugal; aprj, anterior process of the right jugal; d, dentary; ec, ectopterygoid; hy, hyoids; j, jugal; l, lacrimal; ld, left dentary; lj, left jugal; lm, left maxilla; lpo, left postorbital; lq, left quadrate; lsa, left surangular; lsq, left squamosal; ltf, lower temporal fenestra; m, maxilla; naof, nasoantorbital fenestra; o, orbit; pf, postfrontal; po, postorbital; pt, pterygoid; q, quadrate; rap, retroarticular process; rd, right dentary; rm, right maxilla; scd, sagittal crest of the dentary; scp, scleral plates; sq, squamosal. Scale bar: 50 mm.

doi:10.1371/journal.pone.0038900.g002

Tupandactylus, with a value of 3 (value based on the specimen CPCA 3590 [44]) (Figure 5B). The dentary sagittal crest of *Tupandactylus* is more developed anteroposteriorly and markedly different in shape, with a more abrupt anterior margin than the posterior one. In addition, the dorsal border of the mandible of *Tupandactylus* is only slightly convex at the symphyseal area, and thus not displaying the sigmoid shape observed in *Europejara*.

The condition of the specimen BSP 1997 I 67 from the early Cenomanian Kem Kem beds in Morocco is too fragmentary for a significant comparison with the mandible of *Europejara*. The Kem Kem specimen corresponds only to the anterior portion of the mandibular symphysis [13]. However, the development of a deep dentary sagittal crest [6,13] would indicate that this specimen is a tapejarine. Based on the mandible of *Tapejara*, a reconstruction suggests that the lower jaw of the Moroccan tapejarine may have been larger (about 450 mm in length), and the tip of the rostrum much more pointed than in *Europejara* (Figure 5F).

Among other azhdarchoids, *Europejara* clearly differs from chaoyangopterids (i.e., *Chaoyangopterus*, *Jidapterus*, *Shenzhoupterus*), thalassodromine tapejarids (i.e., *Thalassodromeus*, *Tupuxuara*), and azhdarchids (i.e., *Azhdarcho*, *Bakonydraco*, *Zhejiangopterus*, *Quetzalcoatlus*) by the presence and the shape of the dentary sagittal crest. The lower jaw of the latter three groups is more elongate (i.e., with a higher length/height ratio) and has a dentary sagittal crest which is very low or apparently absent.

A strict consensus cladogram of the phylogenetic analysis is shown in Figure 6. Our results place *Europejara* as a member of the Tapejaridae. This group is currently divided into two clades: the Thalassodrominae and the Tapejarinae (*sensu* [7]). *Europejara olcadesorum* can clearly be distinguished from the thalassodromines which are large pterosaurs (wingspans around 4 meters) with peculiar large premaxillary crests and straight beaks. The new taxon, on the contrary, is comparatively smaller (estimated wingspan around 2 meters, based on proportions of other tapejarines) and shares derived features present in the Tapejarinae,

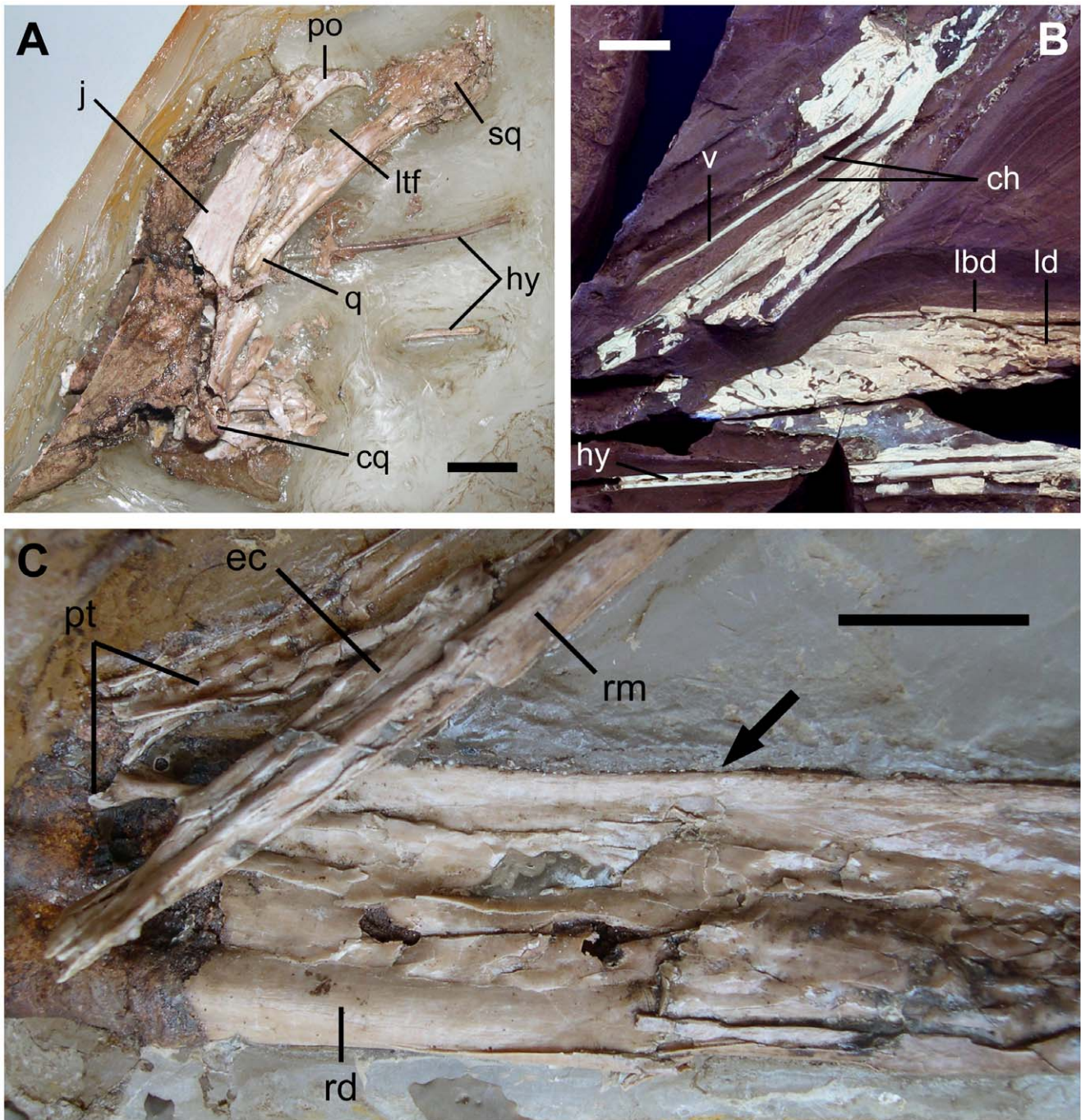


Figure 3. Skull of *Europejara olcadesorum* gen. et sp. nov. (A) Close-up of the crushed left post-orbital region of the skull (acid-prepared counterslab) in lateral view showing the narrowness of the lower temporal fenestra (ltf), the mandibular condyle of the quadrate (cq) and the distal extremities of the hyoid apparatus (hy). (B) Close-up of the posterior area of the palate (main slab under ultraviolet light) in dorsal view showing the thin, elongated vomer (v) septum separating the two choanae (ch). Note the medial surface of the left dentary (ld) and the hyoid apparatus (hy), adjacent to the ventral margin of the mandible. (C) Detail of the posterior area of the palate (acid-prepared counterslab) in dorsal view showing the pterygoid (pt), the ectopterygoid (ec), and the right maxilla (rm). Note the robustness of right mandibular ramus (in lateral view) and its thin, edentulous dorsal edge (arrow). ch, choanae; cq, mandibular condyle of the quadrate; ec, ectopterygoid; hy, hyoid apparatus; j, jugal; lbd, lingual bulge of the dentary; ld, left dentary; ltf, lower temporal fenestra; po, postorbital; pt, pterygoid; q, quadrate; rd, right dentary; rm, right maxilla; sq, squamosal; v, vomer. Scale bars: 10 mm.
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including the presence of a bony dentary sagittal crest. Furthermore, *Europejara* possesses an unambiguous tapejarine synapomorphy: a peculiar step-like, sigmoid dorsal dentary edge at the symphyseal area. However, its relationships within the clade

Tapejarinae (*sensu* [7]) remain poorly resolved (Figure 6). *Europejara* differs from *Sinopterus* (regarded as the senior synonym of *Huaxiaopterus*; see [39]) from the Jiufotang Formation [12,38] and *Tapejara* from the Santana Formation [5,11] in having a visibly

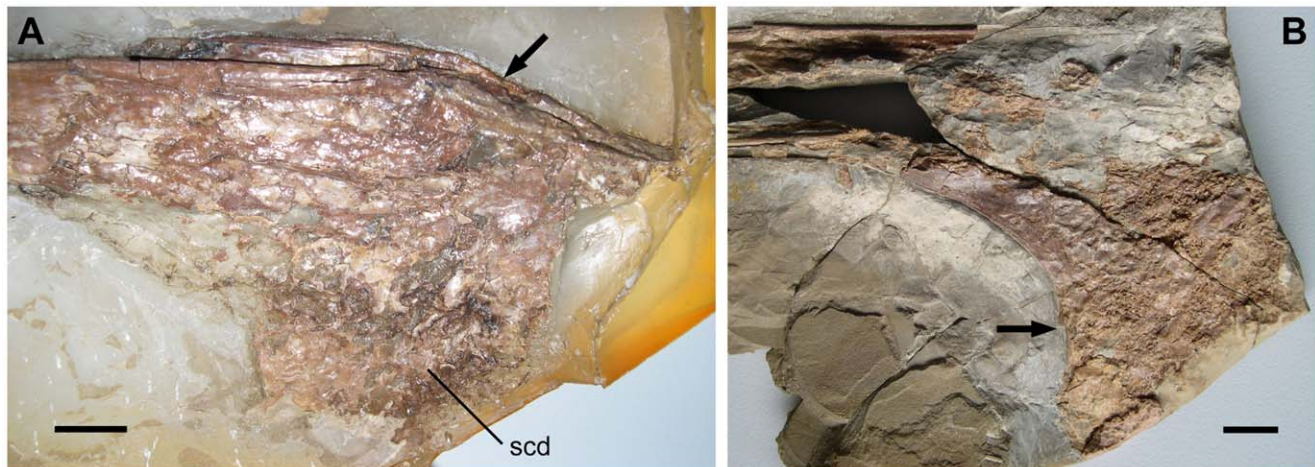


Figure 4. Lower jaw of *Europejara olcadesorum* gen. et sp. nov. (A) Close-up of the symphyseal area (acid-prepared counterslab) in right lateral view showing the typical step-like dorsal margin of the dentary in tapejarines (arrow). Note the strong lateral compression of the mandible and the trabecular structure of the sagittal crest of the dentary (scd). (B) Close-up of the best preserved margin of the dentary crest (main slab). Note the concave posterior border (arrow) giving the peculiar recurved aspect of the dentary crest of *Europejara*. scd, sagittal crest of the dentary. Scale bars: 10 mm.

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deeper dentary bony sagittal crest that is recurved caudally. The length of the palate and mandible indicates that the skull of *Europejara* was relatively more elongate than that of *Tapejara*, but shorter than that of *Tupandactylus* from the Crato Formation [7,11,44].

The mandibular crest of *Europejara* displays a unique shape never before observed in previously described pterosaurs. The purpose of such a deep and recurved dentary sagittal crest remains unclear but it may have served multiple functions (e.g. aerodynamics, thermoregulation, social behavior, and/or gular pouch supportive structure). While well-developed cranial bony crests have been reported for various groups of pterosaurs, mandibular crests are only known in ornithocheirids (= anhanguerids) and tapejarids [15,45], in addition to some primitive non-pterodactylid pterosaurs [46]. Among Tapejaridae, both premaxillary and dentary crests are low in *Sinopteris* and “*Huaxiapterus*”, whereas they are well-developed in *Tapejara* and *Tupandactylus* [44]. It can thus be inferred that the dimensions of both crests were roughly correlated in tapejarids. Accordingly, the deep dentary crest of *Europejara* suggests the presence of a relatively high premaxillary sagittal crest (Figure 2 B–D), as in *Tapejara* and *Tupandactylus*. Such a premaxillary sagittal crest might also have been caudally recurved, mimicking the condition of the dentary crest.

Discussion

The presence of a tapejarid in the Barremian of Spain stresses that the distribution of this group was scattered throughout the Gondwanan and Laurasian landmasses bounded by the Tethyan Ocean, from Brazil to the Iberian Peninsula and China (Figure 7). Although *Europejara* is definitively a tapejarid, the information provided by the fossil to resolve its phylogenetic affinities is partially incomplete. Notwithstanding this, the phylogenetic result does not reject the hypothesis of *Europejara* being the sister group of a clade grouping the Brazilian and Chinese taxa. In fact, this would be the most stratigraphically congruent result; proposing any of the Brazilian taxa as the closest relatives of clade grouping *Europejara* plus the Chinese tapejarines would be inconsistent unless older taxa were found in the Gondwanan masses. Furthermore, the fact that the earliest known members of the Tapejaridae

correspond to the forms found in the late Barremian of the La Huérguina Formation (this study) and around the Barremian–Aptian boundary of the Yixian Formation [9,10] reinforces the view that the group may well have originated in Eurasia, rather than in Gondwana [9]. Later, in the Aptian, tapejarids may have extended their geographic distribution, reaching the northeastern parts of Brazil. Lastly, the occurrence of a tapejarid in the Cenomanian of North Africa (Morocco) [6,13,14] suggests a possible Gondwanan diversification during the mid-Cretaceous. However, the knowledge of the evolutionary and paleobiogeographic history of Tapejaridae is affected by an uneven fossil record sampling [2,47]. Indeed, their apparent absence in the Aptian–Albian deposits of North America, Europe and Africa may be due to the lack of pterosaur-bearing Konservat-Lagerstätten of this age in those continents.

During the evolutionary history of Pterosauria, total edentulism (i.e. the complete loss of teeth) occurred twice [24] or most likely at least three times [20,25,26]. All members of Azhdarchoidea reported to date and known by cranial and mandibular material, ranging from the Aptian to the Maastrichtian, were toothless forms. In addition, some edentulous lineages evolved among non-azhdarchoid pterodactylids (e.g. *Pteranodon*, *Geostenbergia*, *Nyctosaurus*) during the Late Cretaceous [24,25,39]. Thus, the Barremian tapejarid *Europejara olcadesorum* represents the oldest known unambiguous toothless pterosaur as directly evidenced by the edentulous jaws preserved in MCCM-LH 9413. An isolated humerus from the Barremian part of the Wessex Formation in southern England was assigned to an indeterminate non-azhdarchoid azhdarchoid pterosaur [48], and therefore may also correspond to a toothless form. Recently, the genus *Aurorazhdarcho* from the Late Jurassic Solnhofen Limestone (Tithonian) of southern Germany was described as the oldest known azhdarchoid, but the only known specimen is a postcranial skeleton [49].

Tapejarines had well-developed flying skills and an excellent visual system [42], and have mostly been regarded as frugivorous or seed-eating forms on the basis of the shape and of their edentulous jaws [4,9,11,12]. Furthermore, there is evidence that their beak may have been covered rostrally by a rhamphotheca [8,44]. Although the rhamphotheca would have been basically

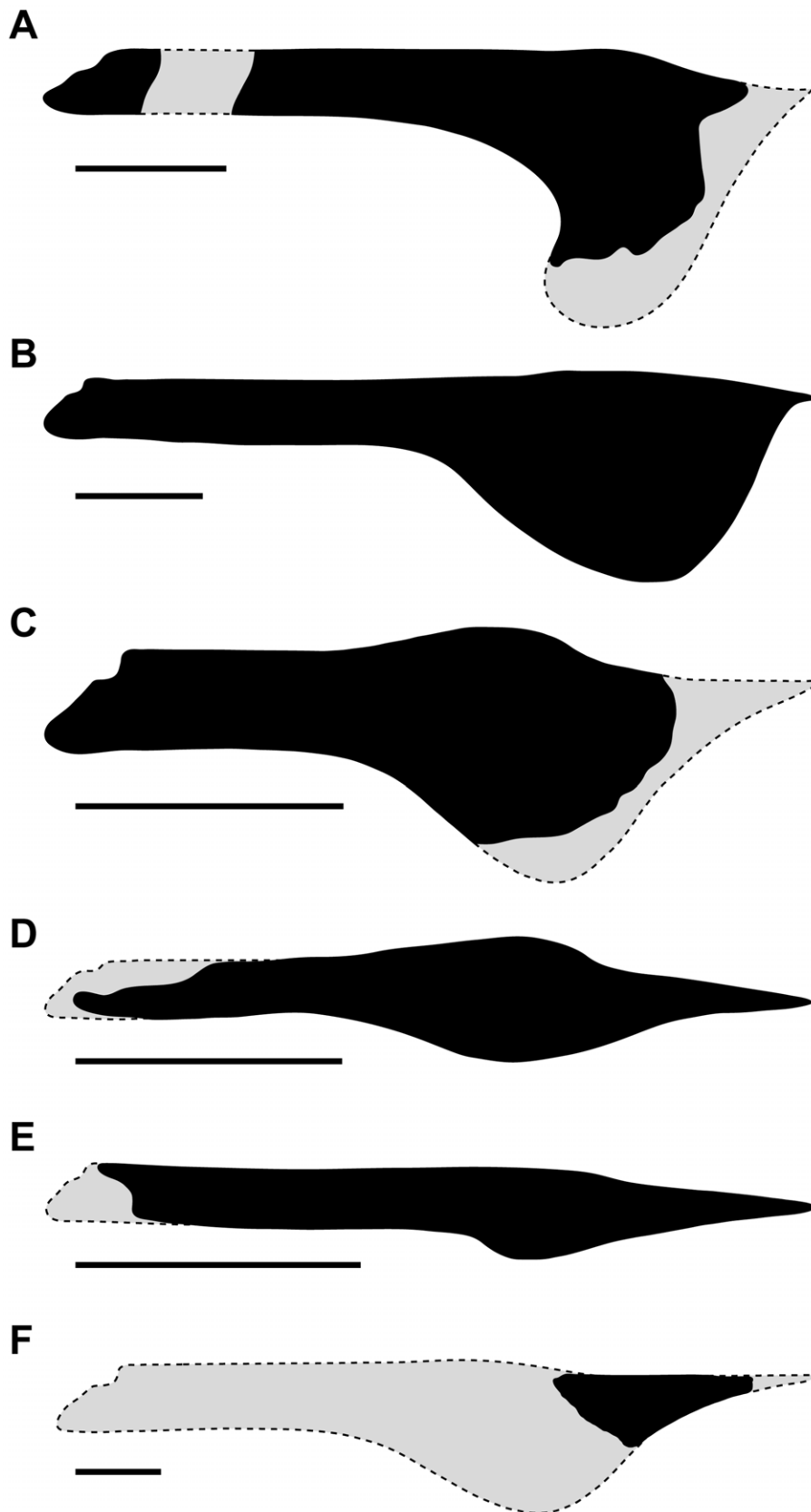


Figure 5. Comparisons of tapejarine lower jaws. (A) *Europejara olcadesorum* gen. et sp. nov. (specimen MCCM-LH 9413): dentary crest height/mandibular ramus height (DCH/MRH) ratio = 4. (B) *Tupandactylus imperator* (specimen CPCA 3590): DCH/MRH ratio = 3. (C) *Tapejara wellnhoferi* (specimen AMNH 24440): DCH/MRH ratio = 2.5. (D) *Sinopterus dongi* (specimen GMN-03-11-001, holotype of *Huaxiapterus jii*): DCH/MRH ratio = 2.2. (E)

Sinopterus dongi (specimen IVPP V 13363): DCH/MRH ratio = 1.5. (F) Kem Kem tapejarine (specimen BSP 1997 I 67): DCH/MRH ratio unknown. Gray areas indicate missing parts. Scale bars: 50 mm.
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shaped by the underlying bones, like in modern birds, the cutting edges of the keratinous bill of some tapejarines might have borne one or more pointed projections as in the omnivorous rhamphastid birds (i.e. toucans) [50,51]. Despite the fact that this analogy is not supported by direct fossil evidence, this suggests that, if not fully herbivorous, an omnivorous diet including seeds and/or fruits, insects and small vertebrates can be addressed for tapejarines.

The concept of a Cretaceous Terrestrial Revolution (KTR, a period of major reorganization of ecosystems in the Cretaceous, as termed by Lloyd et al. [27]) associates the diversification of angiosperms with that of insects, birds and mammals, but does not integrate pterosaurs within this macroevolutionary event. As far as

the vertebrate–angiosperm interactions are concerned, an efficient and successful dispersal mode would have been a key mechanism at the origin of the rapid Early Cretaceous cosmopolitanism of angiosperms. In this sense, the internal vertebrate dispersal mode [52,53] would have favored the colonization by flowering plants of new, distant areas.

The fossil assemblages of the Early Cretaceous localities of the La Huérguina Formation in Spain and the Yixian and Jiufotang formations in northeastern China contain organisms which may have inhabited mosaic of subtropical wet, forested and lacustrine environments [28,31,54,55]. The presence and abundance of early angiosperms in these regions [56–58] would support the hypothesis that frugivorous–granivorous pterosaurs have existed in such paleoecosystems and thus could have been angiosperm seed dispersers [59], together with insects and birds. Tapejarines not only were members of the trophic networks throughout the KTR, but their morphological innovations, in turn, may have been tied to the dispersal of early angiosperms. In fact, tapejarines and early flowering plants display synchronic radiation events and similar patchy geographic distributions that appear to covary (i.e. temporal and spatial congruence). In light of this, the Barremian–Aptian distribution of tapejarines might be partially associated with the first radiation phase of the early angiosperm plants occurring at that time in both hemispheres [60–62] (Figure 7A, 7B).

This first phase of the early angiosperm diversification is particularly well documented in the Iberian Peninsula with about 50 taxa recently being recognized from the late Barremian–early Aptian of Portugal [63]. In the late Aptian–early Albian mesofossil flora of the Portuguese Famalicão locality, about 110 species of angiosperms have been identified, with a high proportion of fleshy-fruited forms [53,63]. Dispersal systems of such species have been interpreted as endozoochorous (i.e. berries and drupes). Palynomorph assemblages from the La Huérguina Formation show a varied spectrum of early angiosperm pollen grains (Figure 7E, 7F). Although most terrestrial plant microfossils collected in this formation belong to pteridophytes and gymnosperms, there is a significant amount of angiosperm pollen grains (*Afropollis*, *Clavatipollenites*, *Retimonocolpites*, *Stellatopollis*, *Transitoripollis*). In addition, angiosperm leaf macrofossils are relatively common at Las Hoyas [64] (Figure 7C). Moreover, the Aptian–Albian Crato and Santana formations from which the Brazilian tapejarines have been recovered are also famous for their rich and diverse early angiosperm assemblages [65,66]. Thus, all this evidence provides a spatial and temporal congruence between the early radiation of angiosperms and tapejarines, although further analyses are necessary to address if this association involved the co-evolution of these groups (see [67]), or whether tapejarines were more likely incidental vectors.

In conclusion, *Europejara* is the first tapejarid pterosaur described from Europe and represents the oldest known edentulous pterosaur. This discovery documents an important stage in the evolutionary history of pterodactyloids, in which the great cranial morphological disparity observed during the Early Cretaceous may reflect a broadening of feeding habits. From a paleoecological point of view, it can reasonably be assumed that herbivorous pterosaurs (most likely including tapejarines) existed and were one of the biological vectors involved in the dispersal of early angiosperms between the different landmasses of the Early Cretaceous world. However, this hypothesis will need to be tested

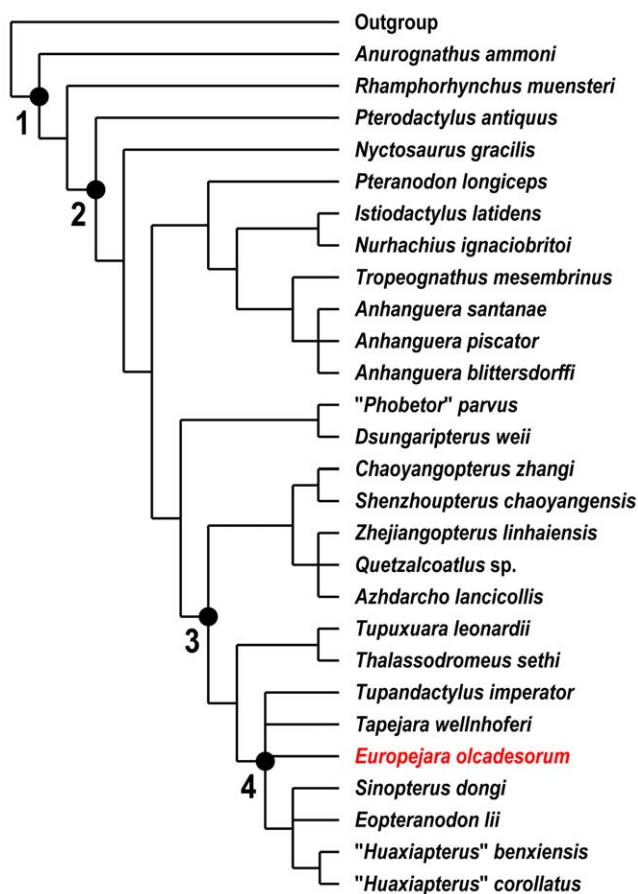


Figure 6. Strict consensus cladogram showing the relationships of *Europejara olcadesorum* gen. et sp. nov. to other Pterodactyloidea. *Europejara olcadesorum* was found to be a member of the clade Tapejarinae (*sensu* [7]). Tree length = 205, consistency index = 0.7561, retention index = 0.8538, rescaled consistency index = 0.6456 (see Appendix S1 for character list and data matrix). Nodes: 1, Pterosauria; 2, Pterodactyloidea; 3, Azhdarchoidea; 4, Tapejarinae (*sensu* [7]). As indicated by its toothless condition, *Europejara* is included within the clade Azhdarchoidea (synapomorphy: character 57, state 3). *Europejara* shares with other tapejarines the apomorphic feature consisting of the presence of a step-like dorsal margin of the dentary in lateral view (synapomorphy: character 52, state 1).

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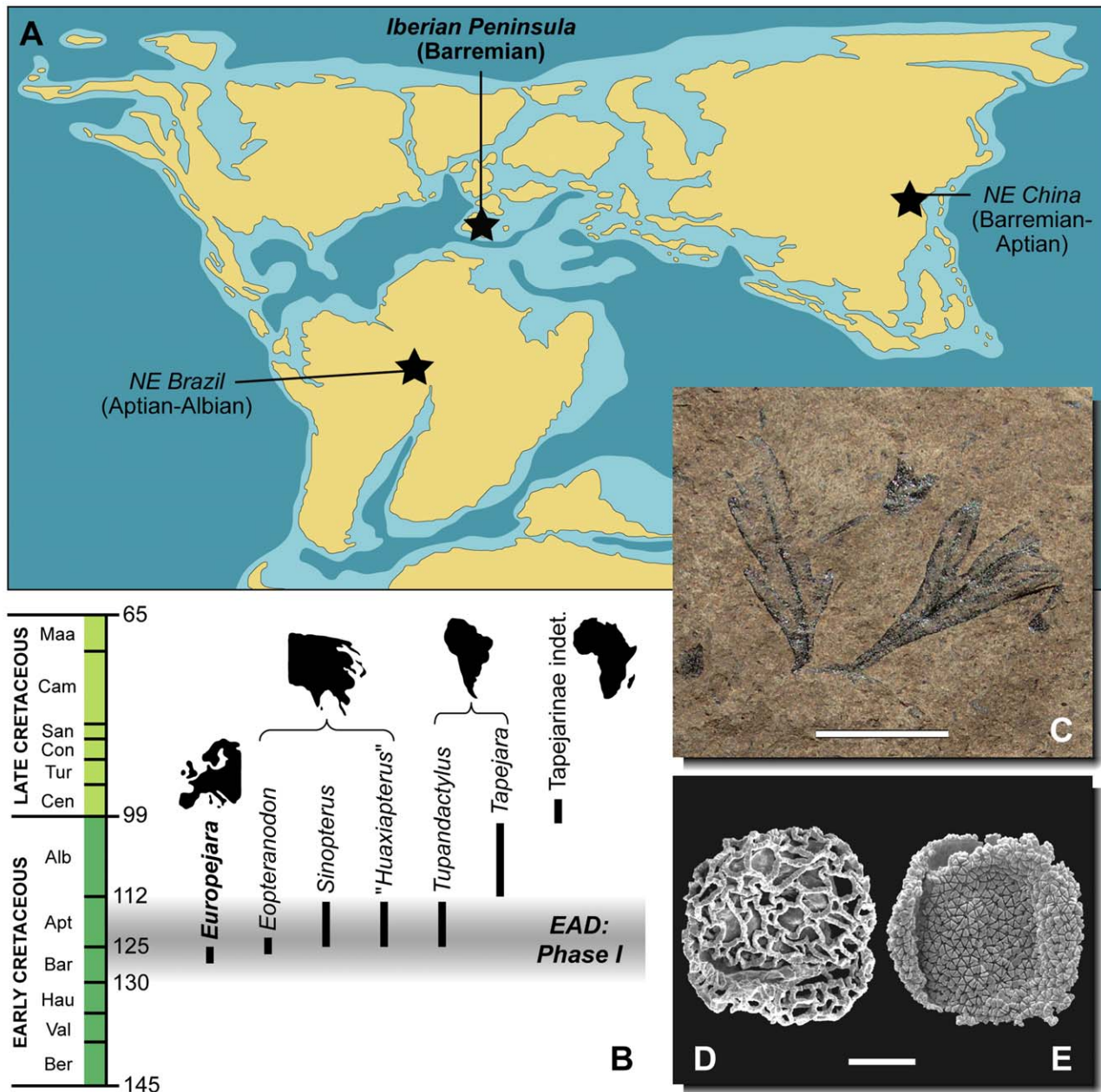


Figure 7. Distribution through time and space of tapejarine pterosaurs and early angiosperms. (A) Early Cretaceous (Aptian) paleogeographical map showing the three main areas where tapejarids co-occur with early angiosperms (black stars). (B) Stratigraphic distribution of the different tapejarid taxa (silhouettes above each taxon denote geographical occurrences); note that the diversification of tapejarids coincides with the Phase I of the early angiosperm diversification (EAD) [60–62]. (C) Leaves of an early angiosperm (cf. *Jixia*) from the late Barremian of Las Hoyas (MCCM-LH 30351), one of the oldest known macrofossil of a terrestrial flowering plant. Early angiosperm pollen grains *Afropollis* (D) and *Stellanipollis* (E) from the La Huérguina Formation, both worldwide distributed during the Barremian–Aptian interval. Ber, Berriasian; Val, Valanginian; Hau, Hauterivian; Bar, Barremian; Apt, Aptian; Alb, Albian; Cen, Cenomanian; Tur, Turonian; Con, Coniacian; San, Santonian; Cam, Campanian; Maa, Maastrichtian. Scale bars: 10 mm (C) and 10 µm (D,E).
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and confirmed when more quantitative (i.e. further occurrences) and qualitative (i.e. gut contents) data are available.

Supporting Information

Appendix S1 Phylogenetic Analysis: Character List, Data Matrix. (DOC)

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Author Contributions

Conceived and designed the experiments: ADB. Performed the experiments: RV JML AWAK ADB. Analyzed the data: RV JML AWAK ADB.

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