

Development and evolution of the notarium in Pterosauria

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Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: CNPq process141041/2015-3

Abstract

The notarium is the structure formed by fusion of the dorsal vertebrae which occurred independently in pterosaurs and birds. This ankylosis usually involves two to six elements and in many cases, also includes the last cervical vertebra. Fusion can occur in different degrees, uniting the vertebral centra, the neural spines, the transverse processes, the ventral processes, or a combination of these sites. A detailed assessment of the fusion process of pterosaur dorsal vertebrae is still lacking. Here we identify the fusion sequence of pterosaur notarial elements, demonstrating the order of ossification in vertebral bodies and neural spines based on fossils and extant birds. In both Pterosauria and Aves, the notarium generally develops in an antero-posterior direction, but the actual order of each fusion locus may present slight variations. Based on our data, we were able to identify seven developmental stages in the notarium formation, with broad implications for the prediction of ontogenetic stages for the Pterosauria. In addition, we report the occurrence of a notarium in *Ardeadactylus longicollum* (Kimmeridgian, Southern Germany), the oldest occurrence of this structure in pterosaurs.

KEYWORDS

Ardeadactylus, macroevolution, ontogeny, Upper Jurassic

1 | INTRODUCTION

The notarium (= 'Os Dorsale') is a rigid axial structure that results from the fusion of anterior to mid-dorsal vertebrae. It occurs in two of the three groups of flying vertebrates, the Pterosauria and Aves, but is absent in Chiroptera (Eyton, 1869; Storer, 1982; Wellnhofer, 1991; Baumel and Witmer, 1993). In Pterosauria, this fusion ranges from two to eight vertebrae, and in several cases, includes the last cervical vertebra (Figure 1). The structure is present in Archaeopterygiformes, and not only in large, more specialized Cretaceous pterodactyloids, which raises questions about its origin within the group. Despite its wide occurrence in pterosaurs and birds, no previous study provided a thorough evaluation of this structure in a complete morphological, functional or developmental sense.

Vertebrae are complex structures, with a reasonably conservative main body, the centrum, and a neural arch that is widely variable

among vertebrates (Romer, 1956; Hall, 2015). Fusion of vertebral structures is the key element in the characterization of the notarium, but it also involves ankylosis, closure of spaces/passages, as well as an additional articulation for the medial/distal end of the scapular blade on the lateral surface of neural spines. As structurally complex elements, the nature of the fusion between notarial vertebrae is highly diverse, in both birds and pterosaurs (Figure 2). Vertebral fusion can be observed among contiguous centra, neural spines, and transverse processes, sometimes forming a ventral plate (Storer, 1982; Samejima and Otsuka, 1984).

In birds, fully developed notaria are only displayed by mature individuals ("adult" *sensu* Heers *et al.*, 2016). Notarium formation has usually already begun in a moderately advanced ontogenetic stage, while the animal can fly competently, but is still undergoing skeletal maturation (McLelland, 1990). The notarium is absent in nestlings and young individuals (Hogg, 1982; McLelland, 1990; Thomas *et al.*,

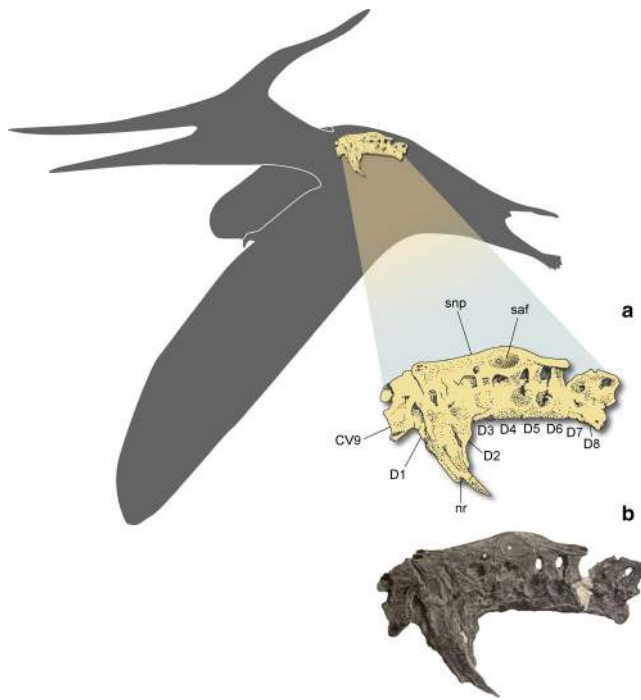


FIGURE 1 Left view of the notarium of *Pteranodon longiceps*, specimen YPM 2692; (a) Illustration with identification of its morphology, showing fused vertebrae and associated structures. (b) Photograph of notarium from Eaton (1910). Note the degree of ankylosis associated with the supraneural plate. CV, cervical vertebra; D, dorsal vertebra; NR, notarial rib; SAF, scapular articulation facet; SNP, supraneural plate; Not to scale; drawing by Luciano Vidal, silhouette by Rodrigo T. Müller based on the artwork by Julio Lacerda

2014). The expression and the evolution of the notarium is probably linked to HOX genes, as differential expression of these genes is responsible for the ontogenetic/embryological development of the vertebrae (James, 2009).

In light of the development progression of skeletal fusion elsewhere in the vertebrate body, variation in development of the notarium is likely attributable in part to ontogeny. Some studies focus on the development of bird notarium, in order to provide a map of key individual changes during growth (e.g. Rydzewski, 1935, Hogg, 1982, Storer, 1982, Samejima and Otsuka, 1984 and James, 2009). This is important because Aves is the only living group that can be used as a model in the understanding of the pterosaur notarium, as this structure is absent in other reptiles, preventing the use of the Extant Phylogenetic Bracket (EPB) protocols (Witmer, 1995).

Here we show the fusion patterns of the pterosaur notarium based on comparisons between several fossil specimens, extant birds and the literature. We recognize a series of developmental stages for the notarium in order to facilitate the identification of notarial ossification steps. In addition, the oldest record of a notarium from the Kimmeridgian (Upper Jurassic) of Baden-Württemberg (Germany), *Ardeadactylus longicollum* Von Meyer, 1854, is also recognized as such and described in detail for the first time.

1.1 | Institutional abbreviations

AMNH, American Museum of Natural History, New York; BSP, Bayerische Staatssammlung für Paläontologie, Munich; FHSM, Fort Hays Sternberg Museum, Fort Hays; IMCF, Iwaki Coal and Fossil Museum, Fukushima; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy, Beijing; MCN-FZB, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre; MCP-PUCRS, Museu de Ciência e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCNA, Museo de Ciencias Naturales de Alava, Vitoria; MPEG, Museu Paraense Emílio Goeldi, Belém; MHNT, Museu de História Natural de Taubaté, Taubaté; MN, Museu Nacional, Rio de Janeiro; NHMUK, Natural History Museum London; RGM, Nationaal Natuurhistorisch Museum (Naturalis), Leiden; SGU, Saratov State University, Saratov; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe; SMNS, Staatliches Museum für Naturkunde Stuttgart; "V", Paul Gigase Collection, Antwerpen; YPM, Yale Peabody Museum of Natural History, New Haven; ZIN PH, Zoological Institute, Russian Academy of Sciences, Paleoherpological Collection, Saint Petersburg.

2 | MATERIAL AND METHODS

Extensive data on axial morphology of Pterosauria was collected and revised from the literature, photographs, and first hand examination of specimens and casts. Data sampled from collections includes 74 pterosaur specimens (NHMUK: 34 spp; SMNS: 15; BSP: 15; AMNH: 10), most of them bearing a notarium. Additional data on the notarial structures of Aves were collected from MCP-PUCRS, MCN-FZB, MHNT, and MPEG (various genera of Tinamiformes, Galliformes, Gruiformes, Falconiformes, Pelecaniformes, Suliformes, Procellariiformes, Accipitriformes, and Passeriformes). Examination of specimens focused on the number of fused vertebrae, degree of fusion, structures fused, presence of sutures, intraspecific variation, and presence/absence of structures of high taxonomic value.

2.1 | Terminology

A standard nomenclature for a notarial formula is proposed here. Because the notarium is a structure that may incorporate cervical vertebrae, it is appropriate to refer to both cervical vertebrae and dorsal vertebrae whenever it is possible. Because pterosaurs have nine cervical vertebrae and posterior dorsal vertebrae are variable, a notarial formula then provides the type of vertebra (C = cervical; D = dorsal), followed by a number corresponding to the position of the element in the series. Coded items of the same type and number are homologous. The term "notarial vertebra" refers to the vertebrae that form the notarium (may be cervical or dorsal origin). Full fusions are represented through plus sign ('+'), while an en-dash ('-') indicates incomplete fusion, retaining a sutural line. Articulated

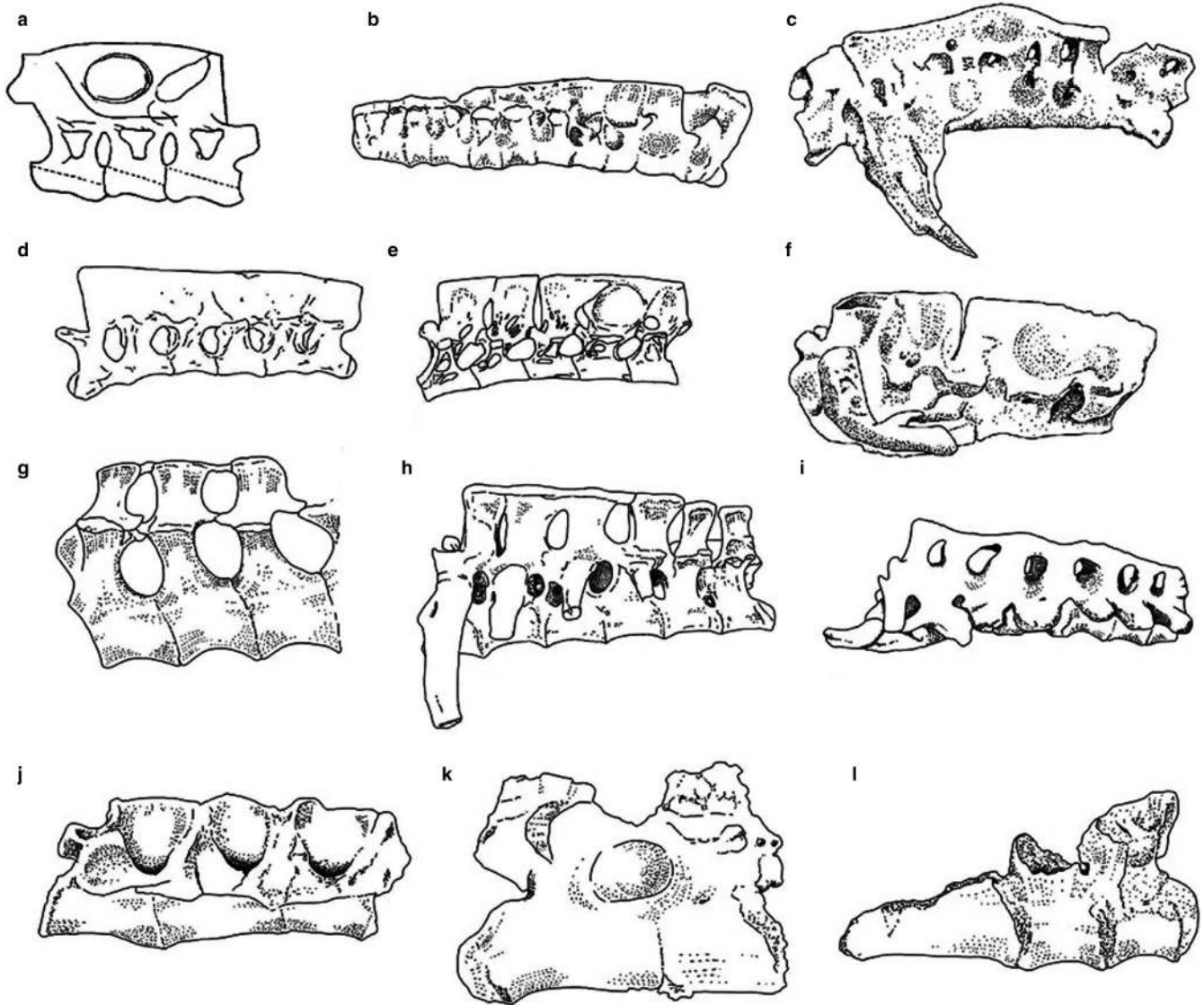


FIGURE 2 Diversity of notaria in pterosaurs, taken from the literature: (a) “*Ornithocheirus*” sp. (Seeley 1901), (b) *Istiodactylus latidens* NHMUK PVR 3867 (Hooley, 1913), (c) *Pteranodon longiceps* YPM 2692 (Eaton, 1910), (d) *Anhanguera spielbergi* RGM 401880 (Veldmeijer, 2003), (e) *Santanadactylus brasiliensis* V-201 (Wellnhofer *et al.*, 1983), (f) *Tropeognathus mesembrinus* MN 6594-V (Kellner *et al.*, 2013), (g) *Dsungaripterus weii* IVPP V.2777 (Young, 1964), (h) *Tupuxuara leonardii* IMCF 1052 (photo courtesy by Andre J. Veldmeijer), (i) *Thalassodrominae* indet. AMNH 22567 (Aires *et al.*, 2013), (j) *Azhdarchidae* indet. MCNA 8563 (Astibia *et al.*, 1990), (k) *Azhdarcho lancicollis* ZNPH 153/44 (Averianov, 2010), (l) *Volgadraco bogolubovi* SGU 49/104a (Averianov *et al.*, 2008). Notaria shown on left view, except for B (right view). Not to scale; drawings by Luciano Vidal

vertebrae that are preserved in the specimen but not incorporated into the notarial series, are represented separated by a comma (‘,’). A question mark (‘?’) is used whenever the nature of the connection is unknown (e.g., given poor preservation). A specimen described by the formula “C8, C9–D6, D7” preserves from the eighth cervical to the seventh dorsal, with a notarium that is formed through a continuous series from the ninth cervical to the sixth dorsal, without interruption. Neural plate is formed when occurs the complete fusion of all neural spines that form the notarium. Ossified tendons (or ossified ligaments) can occur along the lateral or apical regions of the neural spines, and in some circumstances, they can be united in a dense supraneural plate above the neural spines and not between them.

2.2 | Phylogenetic analysis

The phylogenetic analysis performed here employed the data matrix of Wang *et al.* (2012), with 106 characters. From the original analysis, a total of 21 operational taxonomic units (OTUs) were used, representing taxa with complete dorsal axial series, some specimens with the presence of notarium and some without this structure, thus proportionally reducing biases related to missing data. *Scleromochlus taylori* Woodward 1907 was used as outgroup, and the ingroup (Pterosauria) was a priori defined as monophyletic. The score for character 65 of *Tropeognathus mesembrinus* was altered to acknowledge the presence of a notarium in this taxon, following Kellner *et al.* (2013). *Ardeadactylus longicollum* SMNS 56603 was included in the

data matrix following our observations. Finally, *Germanodactylus cristatus* was also scored from references available on the type specimen BSP 1892 IV1 (Plieninger, 1901), including the presence of a notarium (reported by Vidovic and Martill, 2017). Full scores for *Tropeognathus mesembrinus*, *Ardeadactylus longicollum*, and *Germanodactylus cristatus* are displayed in the Supplementary Material.

The data matrix was analyzed using the software TNT (Goloboff *et al.*, 2008) through the heuristic search algorithm (TBR swapping; 10,000 replicates), under the option “traditional search”. Unless stated otherwise, procedures followed Wang *et al.* (2012).

3 | RESULTS

3.1 | The earliest pterosaur notarium

Description—The specimen SMNS 56603 (Figure 3) was originally described by Plieninger (1907) as *Pterodactylus longicollum*, a taxon erected by Von Meyer (1854). Much later, Wellnhofer (1970) designated the specimen as the neotype of the taxon, because the holotype was lost during the World War II. Bennett (2013), while revising the genus *Pterodactylus*, placed this specimen as *Ardeadactylus*

Bennett (2013) on the basis of the distinctive morphology of the skull, wing, and dentition. So far, the putative notarium has only been briefly mentioned as a series of eight connected dorsal vertebrae, by Plieninger (1907). This author recognized eight connected dorsal vertebrae (12–19, or dorsal vertebrae 1–8) exposed in left lateral view, with reasonably preserved neural spines. Herein, we describe this vertebral sequence in detail, describing the morphological features that allow its characterization as a notarium (Figure 3).

The notarial series in *Ardeadactylus* is comprised of eight preserved dorsal vertebrae, from the first to the eighth dorsal. The dorsal vertebra immediately posterior are not preserved. Cervical vertebrae C3–C8 are exposed and much longer than other vertebrae. The eighth cervical is also preserved and shares the morphology of the dorsal vertebrae, but displays no sign of fusion with adjacent vertebrae. Between the dorsal and most of the cervical series (C3–C8) there is a substantial gap, and C9 is positioned nearby (although disconnected) to the D1. This suggests that C9 disarticulated from the dorsal series as result of decay. Dorsal vertebra D4 and D8 are mostly damaged, hindering a precise description of their morphology. Despite taphonomic damage, it is possible to recognize several signs of fusion, suggesting that the series of eight dorsal vertebrae was fused into a single unit.



FIGURE 3 *Ardeadactylus longicollum* SMNS 56603 (a), showing detail of the dorsal region (b) and the notarium (c), partially preserved and exposed on left view. D, dorsal vertebra; OT, ossified tendon. Scale bar = 10 mm

Dorsal vertebrae centra are cylindrical, procoelous, and anteroposteriorly short. In the preserved dorsal series, centra, zygapophyses, and transverse processes are directly fused, through ankylosis. There is no sign of fusion between the D1 and the last cervical vertebra. The preserved neural spines are blade-like, expanding laterally at the distal end. These lateral expansions form a shelf-like structure that provides support and an improved anchor point for tendons (Bennett, 2003b). Neural spines are mostly fused apically, through supraneural ossified tendons, as seen in birds and some pterosaurs. However, ankylosis may extend ventrally along the surface of the neural spine (as in D5). Neural spines are mostly stabilized via ossified tendons, although in some neural spines it is possible to devise tendons from their shelves (D5–D7). In lateral view, neural spines are anteroposteriorly expanded at their base and apex, but constrained at the mid-height, which gives the spines an “hourglass” shape. Spaces between neural spines (“fenestration”) are elliptical (D1–D2) to subcircular, as the shape of the neural spine becomes more “hourglass-like” distally through the axial series.

Dorsal vertebrae D1–D2 preserve fused neural spines, united through their apices. Centra and zygapophyses are poorly preserved, but are clearly fused. Dorsal vertebrae 2–3 are also fully fused by centra (Figure 3).

D4 retains only part of the centrum, which is displaced from its original position, and has a highly deformed neural spine, inclined

posteriorly and dorsally as a preservational artifact. However, the ossified tendons can still be clearly recognized on top of the spine, showing that the structure was ossified in life and endured preburial damage, not being the byproduct of mineralization after the damage. D5 preserves the neural spine and most of the centrum. The apical part of the neural spine clearly displays a thin anterior projection, which is interpreted here as a part of a tendon shaft that would be connected to the neural spine of the fourth dorsal vertebra. Dorsal 6 is fused to D5 by their centra, zygapophyses, neural spines, and transverse processes (Figure 3).

Dorsal vertebra 7 has a slightly longer centrum than the other dorsal vertebrae, which is only partially fused to the centrum of D6. However, fusion between D6 and D7 also extends to the neural spines and zygapophyses. The posterior articulation surface of D7 is smoothly convex, bearing no evidence of fusion with D8. The left transverse process of D7 is present, deformed ventrally, as in D8.

The last element of the notarial sequence is D8, which preserves only part of the neural arch. Given that the centrum of D7 displays a convex articulation for D8, it seems reasonable to assume that D8 was procoelous, as the rest of the series. The neural spine of D8, although deformed, is in a better condition than the neural spine of D4 and shares the same spatulate morphology exhibited by the remaining dorsal vertebrae. The neural spine is

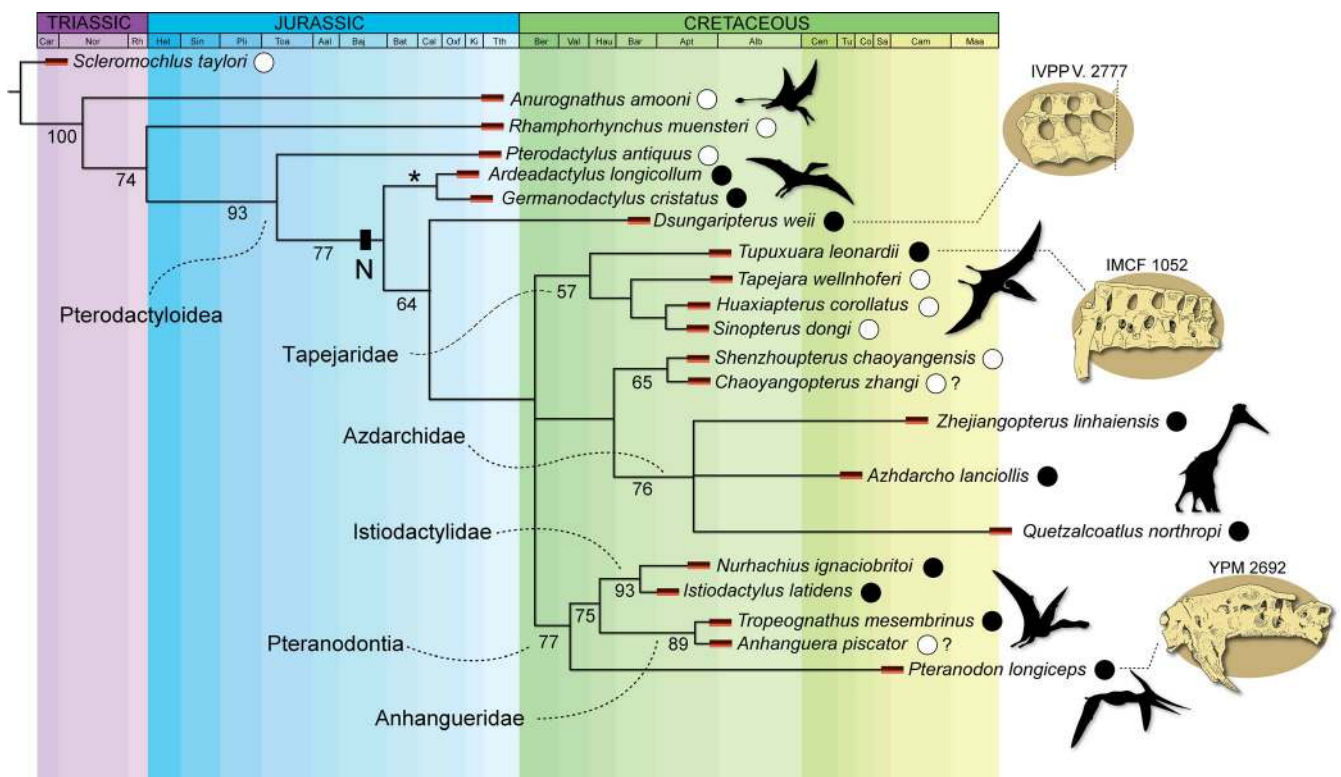


FIGURE 4 Strict consensus topology of two equally parsimonious trees (206 steps, $ci = 0.68$, $hi = 0.32$, $ri = 0.70$, $rc = 0.47$), produced in TNT (Goloboff *et al.*, 2008), from a modified matrix of Wang *et al.* (2012). The analysis positioned *Ardeadactylus longicollum* as sister group of *Germanodactylus*. Selected notaria on the right, along with silhouette of corresponding taxa; notaria and silhouettes not to scale; Black circle, presence of the notarium; white circle, absence of the notarium. Drawings by Luciano Vidal, silhouette by Rodrigo T. Müller based on the artwork by Raúl Martín, Júlio Lacerda and Mark Witton

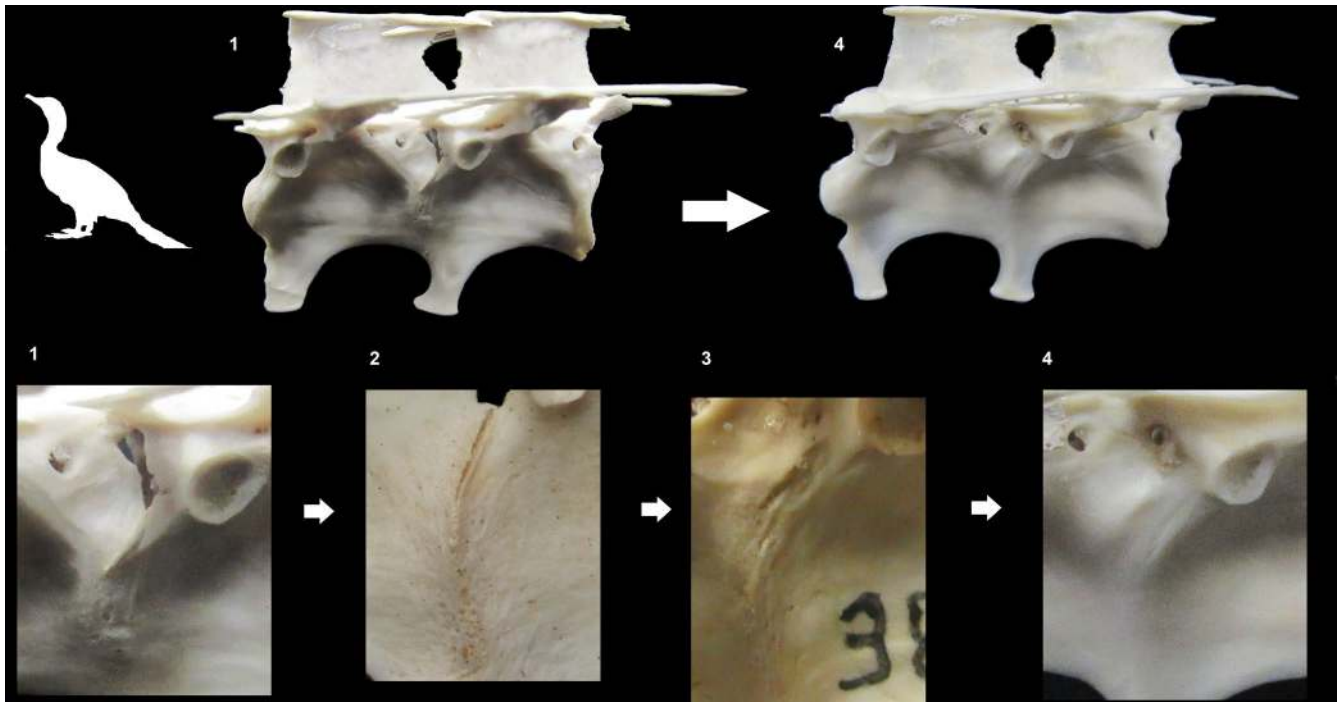


FIGURE 5 Sequence of ossification occurs in a ventro-dorsal direction of the notarial vertebral centra in different developmental stages of the cormorant bird *Phalacrocorax brasilianus* (Suliformes). Left to the right: MCP 1539 (1), MHNT 0823 (2), MCP 3836 (3) and MCP 01435 (4). Above, the notarium of MCP 1539 (1) and MCP 01435 (4). No scale. Silhouette by Alex Aires

also anteroposteriorly longer at its apex than at its base, following the same overall “hourglass” profile as the preceding dorsal vertebrae. Supraneural tendons are indistinct from the bony shelves of the top of the neural arch, and are probably continuous with D7. The left transverse process is fractured at midlength, and its lateral edge is lost. Zygapophyses between D7 and D8 are intimately connected, but do not display signs of fusion. Neither the supraneural tendons nor the zygapophyses display any sign that fusion progressed posteriorly to the next vertebra (D9) is not preserved. Their surfaces are round, without extensions or signs of broken structures.

Phylogenetic analysis—The heuristic search resulted in two most parsimonious trees of 206 steps (CI = 0.68; RI = 0.70), summarized through a strict consensus (Figure 4). Overall, the topology recovered by Wang *et al.* (2012) is retained, with azhdarchoids and pteranodontians forming monophyletic branches, united in an apical region of the topology to form the clade Ornithocheiroidea. *Ardeadactylus* is the sister taxon of *Germanodactylus*, representing the Archaeopterodactyloidea, and forming with ornithocheiroids a monophyletic Pterodactyloidea. The clade formed by *Ardeadactylus* and *Germanodactylus* lies outside Tapejaridae, Azhdarchoidea, and Pteranodontia. Most interestingly, the clade formed by *Ardeadactylus* and *Germanodactylus* is the earliest branch of Pterodactyloidea to present a notarium. Therefore, it is both the oldest and the most basal occurrence of such structure in the fossil record, predating all other instances of notarium by over 20 million years.

3.2 | The sequence of fusion in the pterosaur notarium

We used birds as guides to understand the fusion sequence in the notarium. The fusion sequence in notarial vertebrae of the bird *Phalacrocorax brasilianus* (specimens MHNT 357, MCP 0925, MCP 3836, MCP 1051, MCP 1539, and MCP 01435) (Figure 5) was observed. The beginning of the fusion between the first and second thoracic centra is clear, and if the formation of the notarium does not proceed in the subsequent vertebrae, only these two remain united. A similar pattern can be inferred for many species of Passeriformes (James, 2009). In *Gallus gallus*, the fusion is in the antero-posteriorly direction around 105 days after hatching, first in the neural spines, followed by vertebral centra, and after in zygapophyses and transverse processes, completing the notarium between 165 and 170 days after hatching (Hogg, 1982). The animal is considered as an adult when it reaches skeletal maturity at the same time when the complete notarial fusion in *G. gallus* occurs (Starck, 1992; Thomas *et al.*, 2014).

Observations on the fusion are present in Table 1, displaying the ossification between the vertebrae that compose the dorsal column in Pterosauria, where notarial fusions occur, and the presumed stages of development of the notarium specimens. Fusion patterns usually follow the scheme below (where N = notarial vertebra, “-” = incomplete fusion, with apparent suture line and “+” = complete fusion, with no apparent suture line):

(a) N2 – N3; (b) N2 – N3 – N4; (c) N2 + N4 – Nx; (d) N1 – N2 + Nx; (e) N1 + Nx.

A hypothetical sequence of notarium formation (NS or "notarium stage") here is proposed for Pterosauria based on what is available in the fossil record and present-day birds (Figure 6):

NS1—Notarium unfused. The vertebrae do not show any signs of co-ossification, but are very close to each other, joined by tendons, especially between the neural spines and on their sides and between the transverse processes. It occurs in juveniles of species that present a notarium in adulthood, and in some groups of birds that do not form the structure, as in some Anseriformes, Procelariiformes, Charadriiformes, Cathartiformes, and some Passeriformes (Storer, 1982). Among the pterosaurs, AMNH 22555 appears to fit this stage. About this specimen (traditionally assigned to "*Anhanguera santanae*", but see Pinheiro and Rodrigues, 2017), Veldmeijer *et al.* (2009) argue that there are no dorsal vertebrae forming a notarium, but our first hand observation revealed that some elements of the dorsal series are consistent with an immature "pre-notarium" phase, in which vertebral fusion had still not started. The apical portions of the AMNH 22555 neural spines present anterior and posterior margins directed toward the adjacent vertebrae, making them very close to each other, that would possibly facilitate a posterior connection through tendon ossification (Personal Observation). The neural spine of the fifth vertebra is enlarged, providing the space for the articulation facet with the scapula, indicating that if the animal were alive longer, it would most likely form a notarium. This may have phylogenetic implications, since in many phylogenetic studies, a notarium is coded as absent for this specimen.

NS2—Beginning of co-ossification of tendons, which are united in a broad straight beam at the top of the neural spines, anchoring and serving as the basis for a posterior fusion of the spinal processes. The articular facet with the scapula appears on the sides of the fourth dorsal vertebra (fifth notarial) in Ornithocheiroidea and related forms. BSP 1991 I27 (*Brasileodactylus* sp.—personal observation) appears to be in the interval between this stage and the subsequent stage, because it presents only the second and third dorsal vertebra fused by their centra. This is an example that the fusion begins between the first two "true dorsal vertebrae", similar to condition in *G. gallus* (Hogg, 1980, 1982). In addition, the presence of a joint surface with the scapula is noticeable on the sides of the neural spine of the fifth notarial vertebra. The fourth dorsal vertebra is absent in this specimen. These features suggest an early developmental stage of the notarium.

NS3—Beginning of the fusion between the vertebral bodies and at the top of the neural spines. Fusion is more advanced between the first and second dorsal and less between the third and fourth dorsal vertebra. The vertebral centra of D2 and D3 starts the co-ossification in ventral portion. The well preserved IMCF 1052 (*Tupuxuara leonardii*) (personal observation) is in this phase (Figure 7), with six fused vertebrae, and it shows some fusion patterns common to Azhdarchidae, such as the absence of a supraneural plate connecting the neural spines; instead these are united solely by ossified tendons at their ends. This specimen shows such union only between the first to the fourth notarial vertebrae, and the last two are still free. Between the first and second dorsal vertebrae, fusion occurs

over about one-third of the length of the spinous processes. IMCF 1052 has fusion only between the first three notarial vertebrae spines with a thin band of ossified tendons between the third and the fourth, which suggests it is at an immature stage of the notarium, when compared with AMNH 22567 (*Thalassodrominae* indet.—personal observation). This scenario leads to the interpretation that fusion occurs in the anteroposterior direction and is independent between the spinous processes and centra. The last notaries of IVPP V.2777 (*Dsungaripterus weii*) (Young, 1964) have a similar morphology to IMCF 1052 (*Tupuxuara leonardii*), only extending as far as the final third of the spines and never the whole length as in the mature Pteranodontia and the MCNA 8563 (*Azhdarchidae* indet.) (Astibia *et al.*, 1990).

NS4—Ossification advances in the neural spines in all the dorsal vertebrae that form the notarium. Ossification is observed between the first two and between the third, fourth, and fifth notarial vertebrae, exactly in the zone of the facet for scapular articulation and less between the second and third dorsal ones. The vertebral centra are well advanced in the fusion, especially in D1+D2–D3. Sutures remain in the centra of the last dorsal vertebrae and less fusion between C9–D1. The specimens "V-201" (*Santanadactylus brasiliensis*) (Wellnhofer *et al.*, 1983), IVPP V-2777 (*Dsungaripterus weii*) (Young, 1964) and AMNH 22567 (*Thalassodrominae* indet.) (Aires *et al.*, 2013), may represent this stage. The fusion of the neural spines can be observed between the second and third and between the fourth, fifth, and sixth dorsal vertebrae in V-201 (see Wellnhofer *et al.*, 1983). The fusion is most pronounced between the fourth and fifth neural spines (Wellnhofer *et al.*, 1983). The preserved vertebral centra of this specimen are not exposed, but the neural spine region shows well-defined articulation surfaces for the scapula, with most of the facet located on the lateral surface of the fifth notarial neural spine.

NS5—First and second dorsal vertebrae are completely fused, both in their centra and in the neural spines. The scapular facet increases, extending from the fourth dorsal to the third and a little in the fifth element till the beginning of the ossification at the top of the spine between the last cervical and the first dorsal. Tenuous sutures are seen in last vertebral centra and more in C9–D1. The specimens MN 6594-V (*Tropeognathus mesembrinus*) and SMNK PAL 1133 (assigned to *Anhanguera robustus*, but see Pinheiro and Rodrigues, 2017) are close to this stage. MN 6594-V (Kellner *et al.*, 2013), displays a similar notarial development stage as V-201 (*S. brasiliensis*), because both display a partial union between the neural spines of the second and third notarial vertebrae, absence of union between the third and fourth, and again, a more prominent fusion between the fourth, fifth, and sixth notaries, in the zone of the scapular facet. However, the union of the neural spines at this zone in *T. mesembrinus* is more advanced than in *S. brasiliensis*. Elgin (2014) noted that the notarium of the specimen SMNK PAL 1133 appears to be in juvenile stage when compared to other anhanguerids due to the semi-fused state of the neural spines.

NS6—The spinal plate is almost completely fused. Only a few spaces with a third of the total length of the neural spines exist, close to the zygapophyses. The ossification between the last

TABLE 1 The pterosaur dorsal column with notarium reported in literature

Taxon	Specimen	Vertebral column formula	Fused centra	Neural spines	References
<i>Ardeadactylus longicollum</i>	SMNS 56603	C9, D1+D2+D3,?, D5+D6,D8	5	Fused	Plieninger (1907), this study
<i>Germanodactylus cristatus</i>	BSP1892 IV1	D1+D2+D3	3	?	Vidovic and Martill (2017)
<i>Nyctosaurus gracilis</i>	FHSM 2148	D1+D2	2	?	Williston (1903)
<i>Muzquizopteryx coahuilensis</i>	IGM 8621	C9+D1+D2+D3+D4+D5,D6,D7,D8,D9, D10,D11,S	6	Fused	Frey et al. (2006)
Nyctosauridae indet	KJ2	D1+D2+D3+D4+D5,D6,D7	5	Fused	Bennett (2003a)
Nyctosauridae indet	FMNH P 25026	D1+D2+D3,D4,D5	3	?	Williston (1903)
Nyctosauridae indet (juvenile)	CM 11422	D1,D2,D3,D4,D5,D6,D7	0	?	Bennett (2003b)
Nyctosauridae indet (juvenile)	YPM 2527	D1,D2,D3,D4,D5,D6,D7	0	Fused	Bennett (2001)
<i>Pteranodon</i> sp.	KUVP 16487	D1+D2+D3+D4+D5+D6,D7,D8,D9	6	Fused	Bennett (2001)
<i>Pteranodon</i> sp.	UALVP 24238	D1+D2+D3+D4+D5,D6,D7,D8,D9,D10+ D11+D12+S	4	?	Bennett (2001)
<i>Pteranodon</i> sp.	YPM 2692	D1+D2+D3+D4+D5+D6, D7+D8, D9	8	Fused	Bennett (2001)
<i>Pteranodon</i> sp.	UNSM 50036	D1+D2+D3+D4+D5,D6+D7,D8,D9,D10 +D11+D12+S	5	?	Bennett (2001)
<i>Pteranodon</i> sp.	UNSM 50128	D1+D2+D3+D4,D5,D6,D7,D8,D9,D10, D11	4	?	Bennett (2001)
<i>Pteranodon</i> sp.	NHM R2931	D1+D2+D3+D4+D5-D6	5	?	Eaton (1910), Bennett (2001)
<i>Pteranodon</i> sp.	NHM R3299	D1-D2-D3+D5	3	inside matrix	This study
<i>Pteranodon</i> sp.	YPM 2699	D1+D2+D3+D4+D5	5	?	Bennett (2001)
<i>Istiodactylus latidens</i>	NHMUK 3877	C9, D1+D2+D3+D4+D5+D6,D7,D8,D9	6	Fused	This study
<i>Istiodactylus sinensis</i>	NGMC 99-07-011	D1+D2+D3+D4+D5,D6,D7	5	?	Andres and Ji (2006)
<i>Nurhachius ignaciobritoi</i>	IVPP V-13288	D1+D2+D3+D4+D5+D6,D7+D8,D9,D 10,D11	?	Fused	Wang et al. (2005)
<i>Zhenyuanopterus longirostris</i>	GLGMV 0001	D1+D2+D3,D4,D5,D5,D6,D7,D8,D9,D1 0,D11,D12	3	Fused	Lü (2010)
<i>Arthurdactylus conandoylei</i>	SMNK PAL 1132	D1+D2+D3+D4+D5,D6,D7,D8,D9,D10+ D11+D12+S	5	Fused	Frey and Martill (1994)
<i>Barbosania gracilirostris</i>	MNHS/00/85	D2+D3+D4+D5	4	Fused	Elgin and Frey (2012)
<i>Santanadactylus brasiliensis</i>	V-201	C9,D1+D2,D3+D4+D5,D6,D7,D8,D9,D10	?	Fused	Wellnhofer et al. (1983)
<i>Brasileodactylus</i> sp.	BSP 1991 I 27	C9, D1,D2+D3,D4,D5,D6,D7,D8,D9,D10	2	?	Veldmeijer et al. (2009)
<i>Tropeognathus mesembrinus</i>	MN 6594-V	C8, D1+D2+D3+D4+D5,D6,D7,D8,D9,D 10,D11,D12	5	Fused	Kellner et al. (2013)
<i>Anhanguera spielbergi</i>	RGM 401 880	C7,C8, C9+D1+D2+D3+D4+D5,D6,D7,D 8,D9,D10,D11,D12	6	Fused	Veldmeijer (2003)
<i>Anhanguera robustus</i>	SMNK PAL 1133	C8, C9-D1+D2+D3+D4+D5,D6?,D7?,D8?	4	Fused	Elgin (2014)
Anhangueridae indet.	AMNH 22571	C9+D1+D2+D3+D4+D5	5	Fused	This study
<i>Ornithocheirus</i> sp	?????	D3+D4+D5	0	Fused	Seeley (1901)
<i>Noriopterus complicidens</i>	GIN 125/1010	D1+D2+D3+D4+D5?	5	Fused	Lü et al. (2009a)
<i>Noriopterus complicidens</i>	IVPP 4059	Dx+Dy?	2	?	Hone et al. (2017)
<i>Dsungaripterus weii</i>	V.2777	D5+D6+D7,D8,D9,D10,D11,S	3	Fused	Young (1964)

(Continues)

TABLE 1 (Continued)

Taxon	Specimen	Vertebral column formula	Fused centra	Neural spines	References
<i>Chaoyangopterus zhangii</i>	IVPP V-13397	Dx+Dy?	?	Fused?	Wang and Zhou (2003)
Tapejaridae indet.	MN 6588-V	C9,D1+D2+D3+D4,D5,D6,D7,D8,D9,D10+D11+S	4	Fused	Sayão and Kellner (2006)
<i>Tupuxuara leonardii</i>	IMCF 1052	C9,D1+D2+D3+D4,D5,D6	4	Fused	Kellner and Hasegawa (1993), this study
Thalassodrominae indet.	AMNH 22567	C7,C8,C9,D1+D2+D3+D4+D5+D6+D7	5	Fused	Aires <i>et al.</i> (2013)
<i>Bennettazhia oregonensis</i>	USNM 11925	D5+D6?	2	?	Gilmore (1928)
<i>Azhdarcho lancicollis</i>	ZIN PH 153/44	Dx+Dy+Dz?	3	?	Averianov (2010)
<i>Azhdarcho lancicollis</i>	ZIN PH 6/44	D5+D6?	2	?	Averianov (2010)
<i>Azhdarcho lancicollis</i>	CCMGE 7/11915	D1+D2+D3?	3	?	Averianov (2010)
<i>Zhejiangopterus linhaiensis</i>	M1325	D1+D2+D3+D4+D5+D6,D7,D8,D9,D10,D11,D12	6	?	Cai and Wei (1994)
<i>Zhejiangopterus linhaiensis</i>	M1328	C7,D1+D2+D3+D4+D5+D6,D7,D8,D9,D10,D11,D12,S	6	?	Cai and Wei (1994)
<i>Volgadraco bogolubovi</i>	SGU 49/104a	D3+D4+D5+D6?	4	?	Averianov <i>et al.</i> (2008)
Azhdarchidae indet.	RBCM. EH.2009.019.001	Dx+Dy+Dz?	3	Fused	Martin-Silverstone <i>et al.</i> (2016)
Azhdarchidae indet.	MCNA 8563	Dx+Dy+Dz?	3	Fused	Astibia <i>et al.</i> (1990)
<i>Hatzegopteryx thambema</i>	FG GUB R 1083	????	?	?	Vremir <i>et al.</i> (2011)
<i>Quetzalcoatlus northropi</i>	?????	????	?	?	Kellner (2003)

(-) = partial fusion between vertebrae; (,) = absence of fusion between vertebrae; (+) = total fusion between vertebrae. Underlined = fused vertebrae forming the notarium; Dx + S = dorsal vertebrae fused in the synsacrum.

Abbreviations: C, cervical vertebra; D, dorsal vertebra; S, synsacrum.

cervical vertebra (C9) spine and the other notarial vertebrae advances more slowly. Few signs of sutures can be verified. SMNS 56603 (*Ardeadactylus longicollum*) (Figure 3), NHMUK PVR 3867 (*Istiodactylus latidens*), AMNH 22571 (*Anhangueridae indet.*) and YPM 2692 (*Pteranodon longiceps*) are representatives of this stage. In NHMUK PVR 3867, it can be observed that all neural spines are firmly united, with the exception of the last cervical vertebra, which strongly resembles a dorsal vertebra, and was slightly shifted anteriorly during preservation. Ossified tendons can be seen covering the top of the spines in all notariums (Figure 8) (Personal Observation).

In AMNH 22571 (Figure 9a–c), all the vertebrae are united by the apical region of the spines (between the second and third, the specimen is fractured, due to breaking during the preparation). Fusion occurs between more than half of the neural spine height in the five true dorsal vertebrae and beginning at the apices between these. The last dorsal cervical (C9 or first notarial vertebra), indicates a late fusion with this element. Attached ossified tendons are evident in the apical region, especially on the latter, and the facet for articulation with the scapula occupies the side of the fifth and part of the sixth notarial vertebra (Personal Observation).

NS 7—Complete notarium. Finally, in the mature stage, all neural spines are fused into a single structure, including C9 as the

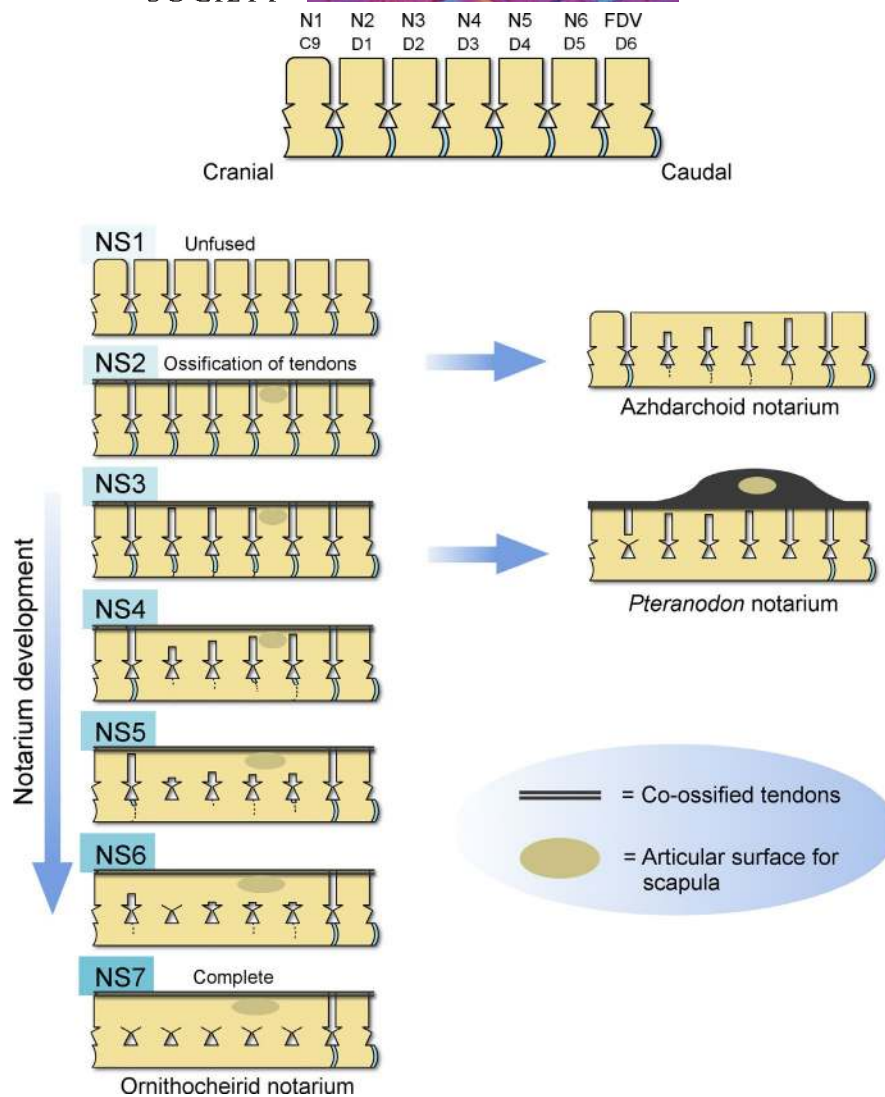
first notarial, and completely ossified tendons join the apical extremities of the spinous processes, as observed in all spines and vertebral centra are completely fused, including the last cervical, forming a continuous structure. The specimen RGM 401880 (*Anhanguera spielbergi*) is the most complete, and the best specimen that represents this final stage (Figure 9d–f) and NHMUK R 3299 (*Pteranodon* sp.) is possibly close to the equivalent final stage. Also, NHMUK R 3299 preserves only five fused vertebrae in ventral view, with all centra completely attached, mainly between the third, fourth, and fifth notariums, without any suture marks (Personal Observation).

4 | DISCUSSION

4.1 | The earliest notarium

Overall, in *Ardeadactylus*, several instances of fusion can be recognized along the axial series. Moreover, whenever fusion cannot be confirmed, poor preservation hinders a proper evaluation of vertebral structure. Unambiguous central fusion is evident in D1–D3 and D5–D7. Fusion between D3–D4 and D4–D5 centra cannot be confirmed (or discarded) because of the damage sustained by centrum

FIGURE 6 Scheme showing how occurs the notarial fusion in Pterosauria based in stages reported in literature, analyzed specimens and comparative with birds. C9, last cervical vertebra; D, dorsal vertebra; FDV, free dorsal vertebra; N, notarial vertebra; NS, "Notarium Stage" (see text)



of D4, which extends to the articulation surfaces of D3 and D5. Poor preservation is clearly the cause of disconnection seen at D4, but even in this case the shaft created by the ossified tendons can be recognized. Conversely, the displaced position of the neural spine of D4 can also be easily recognized. A continuous D1–D8 beam of supraneural tendons (which sustained damage on D4) is doubtlessly present, and supports the interpretation of continuous vertebral fusion from D1 to D7. This is more reasonable than to assume that in *Ardeadactylus*, the notarial series was divided into two series of fused vertebrae, separated by one unfused element (D4).

The fusion process can be partially determined in *Ardeadactylus*. The full fusion from D1 to D6, and the partial fusion between D6 and D7 suggest that the fusion process has a main anterior–posterior progression sequence. On the other hand, the putative incorporation of cervical vertebrae to the notarium, seen in other taxa, was not observed in specimen. It may be that cervical vertebrae are never incorporated into the notarium of *Ardeadactylus*, or it may be that this particular specimen just does not display this feature because cervicals were to be incorporated at a later developmental stage. In this last case, ossification sequence would also have progressed

anteriorly later in ontogeny, after the initial wave of anterior–posterior fusion.

The connection between neural spines occurs on two fronts. The tendons ossify as a beam. This fusion is easily identifiable as the tendons are preserved as a solid, continuous structure. When the beam of tendons is broken (e.g., D4), it retains its shape and position. A broken, unossified section of the beam would easily deform, then mineralize, resulting in a rather different arrangement. The beam section on top of the D4 of *Ardeadactylus*, although displaced, retains its form as expected for an *in vivo* ossification (Figure 3).

The ossification of tendons may progress to the spine table through ankylosis (Figure 3). The ankylosing process in some pterosaurs may obliterate the contact of shelves of adjacent vertebrae, fusing the apical parts of the neural spines and forming a neural plate. This, however, is not observed in this particular specimen. What can be observed is that the beam of tendons is a separate structure on top of some of the neural spines (D4–D7), whereas in others (D1–D3 and D8) it is not. It can be speculated that fusion begins at D1 and D8 separately, then progresses to the median region of the notarium;

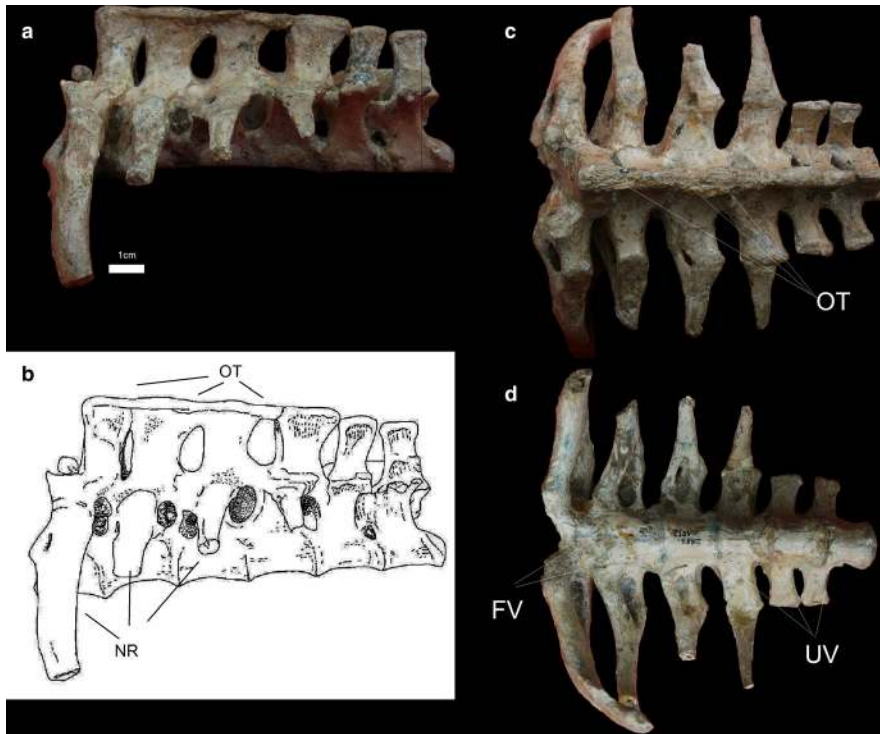


FIGURE 7 Notarium of the *Tupuxuara leonardii* IMCF 1052 in following views: left side (a and b), dorsal (c) and ventral (d). FV, fused vertebral centra; NR, notarial ribs; OT, ossified tendons; UV, unfused vertebrae. Drawing by Luciano Vidal; photo courtesy of André J. Veldmeijer. Scale bar = 10 mm

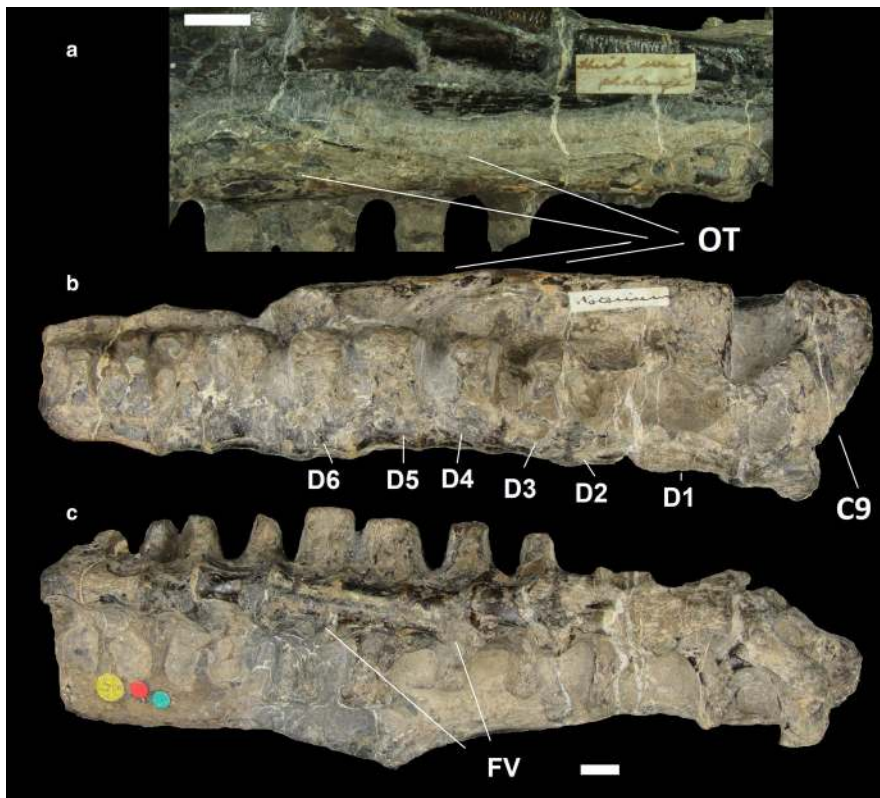
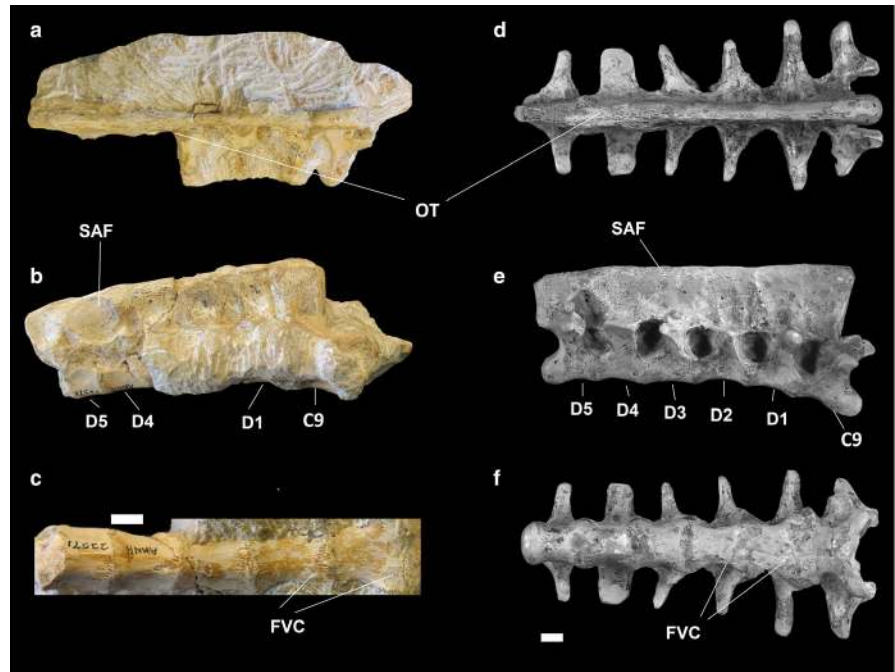


FIGURE 8 Notarium of *Istiodactylus latidens* NHMUK PVR 3867 in following views: dorsal (a), right side (b) and ventral (c). C9, last cervical vertebra; D, dorsal vertebrae; FV, fused vertebral centra; OT, ossified tendons. Scale bar = 10

or that the distinction between tendons and shelf may be biased by preservation. In any case, as fusion progress, it seems clear that ossification begins in the beam of tendons, and then proceeds to the neural spines via an ankylosing process. It remains inconclusive if the shelves form synchronously.

Other structures commonly referred to as part of the notarium are not found in *Ardeadactylus* SMNS 56603. The neural plate, supraneural plate, and the articular surface for the scapular blade, common in Pteranodontia, are absent. These absences may reflect the developmental stage or true absence of the character in the evolutionary

FIGURE 9 Notaria of the anhanguerid pterosaurs in different ontogenetic stages: AMNH 22571 in dorsal view (a), right view (b) and ventral view (c); RGM 401 880 in dorsal view (d), right view (e) and ventral view (f) (RGM 401 880 photo courtesy of André J. Veldmeijer and 'A.'t Hooft, Naturalis, Leiden). C9, last cervical vertebra; D, dorsal vertebrae; FVC, fused vertebral centra; OT, ossified tendons; SAF, scapular articulation facet. Scale bar = 10 mm



lineage of *Ardeadactylus*, but not poor preservation. Bennett (2013) points out that the specimen SMNS 56603 represents a skeletally mature individual, due to the greater relative proportions of the skull, neck, metacarpal IV, and proximal phalanx, as well as the presence of complete ossification of the sternal plate. We can infer that the notarium is at least close to its final stage of development. On the other hand, the putative sister taxon—*Germanodactylus*—also does not show a neural or supraneural plate nor an articular surface for the scapular blade. Currently, we agree with Bennett (2013) that these absences are not reflecting the developmental stage, and thus interpret their absence a true feature of *Ardeadactylus*.

Vidovic and Martill (2017) reported the presence of three fused dorsal vertebrae forming a notarium in *Germanodactylus cristatus* (BSP 1892 IV1), making this taxon together with *Ardeadactylus*, the earlier record of the presence of this structure in the phylogeny of Pterosauria. However, the notarium of *Ardeadactylus* is thus far the oldest in the fossil record, as this taxon comes from the Nusplingen Limestone (Upper Kimmeridgian), about 0.5 million years older than *Germanodactylus* and from the Solnhofen Limestone (Lower Tithonian; Schmid *et al.*, 2005) (Figure 4). In addition, the notarium of *Ardeadactylus* differs from that of *Germanodactylus* in the inclusion of more vertebrae. The acquisition of the notarium in pterosaurs appears to have occurred during Middle to Late Jurassic, when the Rhamphorhynchoidea–Pterodactyloidea transition caused changes in the center of mass due to decreased size of tail and increased size of neck and body (Lü *et al.*, 2009b).

4.2 | The process of fusion in the pterosaur notarium

From these analyses and following Bennett (2001), an anterior–posterior sequence can be envisioned for the fusion of the vertebral

centra, generally starting from the second notarial vertebrae (first true dorsal or D1). In the vast majority of cases, especially in *Pteranodon* and anhanguerids, the first three dorsal vertebrae (D1, D2, and D3) always fuse prior to the remaining vertebrae, the only exception being BSP 1991 I27 (*Brasileodactylus* sp.) (Veldmeijer, 2003), in which vertebral fusion begins with the second and third dorsal vertebrae. The vertebral centra apparently began to fuse shortly after the spines, but obeying the same principal pattern; fusion begins between the first two dorsal vertebrae, proceeds posteriorly until the last notarial, and finishes with the fusion of the last cervical. Considering each instance of fusion between two vertebral bodies, the process would begin in the ventral portion of the intervertebral cartilage and proceed dorsally and from the center to the periphery. This condition can be seen in birds, like Galliformes, Suliformes, Podicipediformes, and some Passeriformes. A suture line is formed first, and then a complete ossification occurs, leaving all the centra of the notarial vertebrae as a single and continuous tubular or flattened structure.

The immature or unfused notarium presents vertebrae that do not show any signs of co-ossification, but are very close to each other, joined by tendons, especially between the neural spines and on their sides. The beginning of co-ossification of tendons occurs, with anchoring and serving as the basis for a posterior fusion of the spinal processes. This can also occur on the sides of the spinal processes and on the transverse processes in some species of birds, such as several Anseriiformes and gruiformes (Storer, 1982). As seen in birds, the ossification of the epineural tendons always precedes the notarial fusion of the vertebrae. In pteranodontid pterosaurs, these tendons are in larger numbers.

The next step, is the beginning of the fusion between the vertebral bodies and at the top of the neural spines. Fusion is more advanced between the first and second dorsal and less between the third and

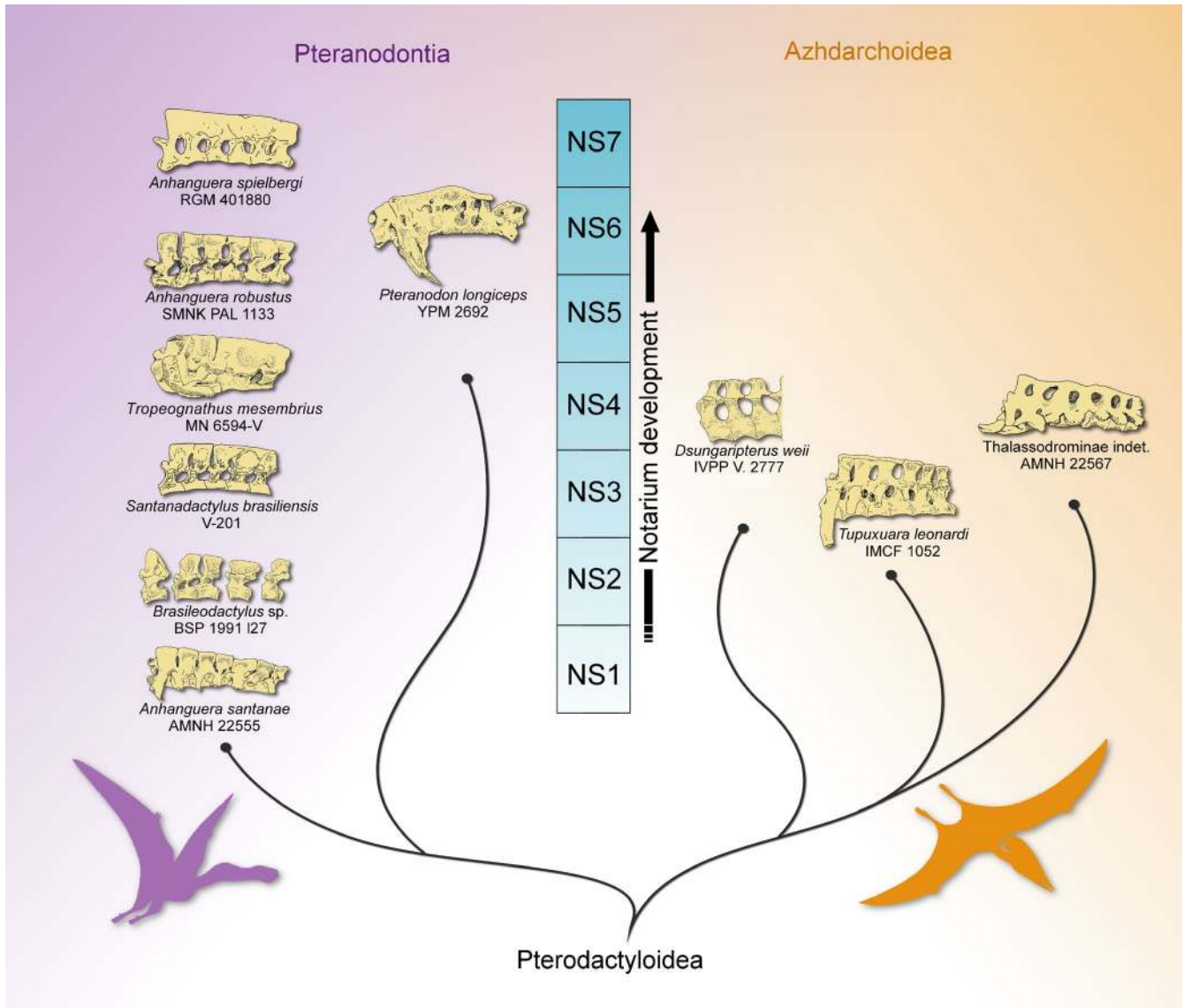


FIGURE 10 Schematic cladogram showing the different pterosaur notaria verified in the literature and corresponding stage. NS, Notarium Stage. (silhouettes created by Rodrigo T. Muller based on the artwork by Raúl Martín)

fourth dorsal vertebra. It can occur at different rates, in some species more quickly in spinous processes than in other vertebral bodies.

In sequence, the ossification advances in the neural spines in all the dorsal vertebrae that form the notarium (total number is variable in the species). In Ornithocheiroidea, advanced ossification is observed between the first two and between the third, fourth, and fifth notarial elements, exactly in the zone of the facet for scapular articulation and less between the second and third dorsal ones. First dorsal vertebrae are completely fused before the last. The ossification between the last cervical vertebra (C9) and the other notarial vertebrae advances more slowly, consisting of the last step for the formation of the notarium.

The fusion of the spines can occur independently of the vertebral body, as shown by the second and third notariales and the region of articulation with the scapula, which may involve the third, fourth, and fifth, or the fourth, fifth, and sixth, according to

the species. The union of the neural spines usually occurs starting from the apical region after the ossification of the ligaments, which are compacted in a continuous band joining the notarium apex. However, in some species of birds, the process begins more diffusely at several spots along the spinal process, inside the interspinous cartilage.

Finally, in the mature stage, all neural spines are fused into a single structure, including C9 as the first notarial, and completely ossified tendons join the apical extremities of the spinous processes, as observed all spines and vertebral bodies are completely fused, forming a continuous structure.

The development of the *Pteranodon* notaria follows a different path from the common sequence observed in other pterosaurs, as there is little fusion between the middle region of the neural spines, which is probably a divergent form in the early stages; the emphasis is on the ossified tendons that condense forming the large

supraneural plate that will later include the scapular facet, rather than on the sides of the spines (Figures 6 and 10).

The notarium of the tapejarids diverges in the fusion in neural spines, was in lesser degree than in other pterosaurs. This model, however, can be altered with the discovery of new specimens with a preserved notarium. Azhdarchoids apparently follow the stages until the SN3 or SN4 (Figure 6) without suffering a greater densification in the ossified tendons, however, the specimens that we have in the collections do not allow a greater evaluation as to the more mature development of the notarium.

What differentiates them is the absence of a supraneural plate, as well as of an articulation facet with the scapula, and thickened notarium ribs. On the other hand, some birds display a ventral plate or conjoined ventral processes, which were thus far not reported for pterosaurs. Although they do not condense as in Pterosauria, ossified ligaments are frequent in birds, in some species in larger, in others in smaller numbers, but they are equally important in the stiffening of the spine and in the initial formation process of the notarium.

The identification of developmental stages of the notarium allowed us to observe how the dorsal portion of the vertebral column becomes a rigid structure in some groups of pterosaurs, their similarities and differences, as well as the import role of ossified tendons.

In birds, there is a big difference in the notarium morphology in the different taxonomic groups, possibly related to evolutionary factors and the type of flight (Storer, 1982; Samejima and Otsuka, 1984). The differences between the notarium in azhdarchoids, ornithocheiroids, and pteranodontids are probably the same way. For example, according Martin-Silverstone *et al.* (2019), the sizes of the sacral and notarial neural canals provide interpretations of paleoecology and locomotion. The relatively large sacral neural canal of azhdarchids implies a sacral enlargement for innervation of the legs and lumbosacral plexus. When compared with anhanguerids, the authors claim that these supports indicate that azhdarchoids were more hindlimb-proficient than ornithocheiroids. Neural canal size in the ornithocheirid notarium suggests that ornithocheirids spent less time on the ground, their brachial enlargement, and small sacral region indicating enhanced innervation of the wings and poor innervation of the sacrum and legs. Propably, pteranodontians should use their wings more than azhdarchoids, which can be a factor in the possession of a more developed notarium (Figure 10).

The notarium of azhdarchoids is more similar to the notarium of *Ardeadactylus*, with less degree of fusion in neural spines, which may indicate less derivation when compared to the notarium of pteranodontians.

5 | CONCLUSIONS

Ardeadactylus longicollum is the oldest record of a notarium to date, demonstrating that this structure evolved in the Archaeopteroedactyloidea, being likely a synapomorphy not only of the large Ornithocheiroidea, but of a wider group. The fusion of the

anterior dorsal vertebrae in the Pterosauria arose sometime in the Middle–Upper Jurassic, reaching relative success and remaining in later taxa, with considerable representation and diversity during the Early Cretaceous (Barremian to Albian) and remaining the last pterosaur taxa in the Upper Cretaceous.

Notarium formation usually follows anterior–posterior sequence through the dorsal vertebrae, both in pterosaurs and birds, and the union with the last dorsalized cervical occurs later. Ossified tendons are present in various groups and are important for joining the neural spines before fusion, which usually occurs from the top to the base of spines. The vertebral bodies fuse in ventro-dorsal direction, as seen in some birds.

Tracing notarial development in Pterosauria may be useful in answering phylogenetic and morphofunctional questions, and compare and add to other studies in the identification of ontogenetic stages in pterosaurs. This work intends to initiate and motivate new studies involving embryology, histology, biomechanics, and other tools which can better elucidate questions related to the evolution and development of the notarium.

ACKNOWLEDGEMENTS

Access to specimens and data in scientific collections were provided by Dr. Oliver Rauhut (BSP, München), Dr. Rainer Schoch (SMNS, Stuttgart), Dr. Lorna Steel (NHMUK, London), Dr. Mark A. Norell, and Carl Mehling (AMNH, New York), Dr. Carla Suertegaray Fontana (MCT/PUCRS, Porto Alegre), Dr. Glayson Bencke (FZB-RS, Porto Alegre), Dr. Herculano Alvarenga (MHNT, Taubaté), and Dr. Alexandre Aleixo (MPEG, Belém). The authors are indebted to Dr. Satoru Nabana (Iwaki Coal and Fossil Museum, Japan) for an image of *Tupuxuara leonardi* IMCF 1052 used in Figure 7, and to Dr. Yukimitsu Tomida (National Museum of Nature and Science, Tokyo) for his assistance in obtaining the original photograph and the permission to use it; and also Dr. André J. Veldmeijer (PalArch Foundation) for the photograph of *Tupuxuara leonardi* IMCF 1052 and *Anhanguera spielbergi* RGM 401880, used to produce Figures 2, 7 and 9. We are grateful to the reviewers, who contributed immensely with their comments, criticisms and suggestions for this work. Conselho Nacional de Desenvolvimento Científico e Tecnológico provided financial support to ASSA (CNPq process141041/2015-3).

AUTHOR CONTRIBUTIONS

ASSA: concept/design, acquisition of data, data analysis/interpretation, drafting of manuscript, and revision. LMMR: acquisition of data, data analysis/interpretation. RTM: data analysis/interpretation, drafting of manuscript, and revision. FLP: data analysis/interpretation, drafting of manuscript, and revision. MBA: drafting of manuscript, revision, and approval of the article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Aires AS, Reichert LM, Müller RT, Pinheiro FL, Andrade MB. Development and evolution of the notarium in Pterosauria. *J. Anat.* 2021;238:400–415. <https://doi.org/10.1111/joa.13319>