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ARTICLE

A NEW PELICAN (AVES: PELECANIDAE) FROM THE UPPER MIOCENE OF ARGENTINA: NEW CLUES ABOUT THE ORIGIN OF THE NEW WORLD LINEAGES

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ABSTRACT—*Pelecanus paranensis* sp. nov., a new pelican (Aves, Pelecanidae) from the marine Upper Miocene Paraná Formation, which crops out in the Province of Entre Ríos, Argentina, is described. This record constitutes the first report of a fossil pelican from Argentina and the southernmost from South America. The holotypical specimen consists of a very large and nearly complete pelvis, which is characterized by having the cristae iliacae dorsales continuous throughout its entire length and a large foramen acetabuli. The U-shaped morphology of the postacetabular section of the pelvis of the new species as well as the wide incisura sutura iliosynsacralis, allow to infer its phylogenetic position within the New World pelican species clade, showing a close relationship with the clade (*P. occidentalis* + *P. thagus*). A probable trans-Atlantic dispersal route for the ancestor of the New World pelicans is thus inferred. The inland Paranaense Sea, which flooded the South American Chaco-Paraná basin during the mid-Neogene, is proposed as a south-north pathway for ancestral forms of the clade (*P. occidentalis* + *P. thagus*). These regressive marine paleoenvironments of the Late Miocene may have acted as the evolutionary driver for the transition of pelican species from brackish or freshwater habitats to those inhabiting strictly marine coastlines.

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INTRODUCTION

Pelicans are very large waterbirds with a long bill and a distensible pouch. They have a worldwide distribution, except for Antarctica and inland South America, from tropical to warm temperate regions, inhabiting coastal and open brackish and freshwater environments (Elliott, 1992). Pelecanidae comprises eight living species in the single genus *Pelecanus* Linnaeus, 1758 (Elliott, 1992; Gill et al., 2022). Recent studies based on DNA sequences taken from both mitochondrial and nuclear genes allowed to separate these eight species into two well-supported clades: an Old World clade including the Great White (*Pelecanus onocrotalus* Linnaeus, 1758), the Dalmatian (*Pelecanus crispus* Bruch, 1832), the Spot-billed (*Pelecanus philippensis* Gmelin, 1789), the Pink-backed (*Pelecanus rufescens* Gmelin, 1789), and the Australian (*Pelecanus conspicillatus* Temminck, 1824) pelicans; as well as a New World clade grouping the American White (*Pelecanus erythrorhynchos* Gmelin, 1789), the Brown (*Pelecanus occidentalis* Linnaeus, 1766), and the Peruvian (*Pelecanus thagus* Molina, 1782) pelicans (Kennedy et al., 2013) (Fig. S1). The latter has been treated as a subspecies of the Brown Pelican (i.e., *P. occidentalis thagus*; e.g., Nelson, 2005), but genetic distances, differences in body size, color of plumage and other soft parts, hypotarsal morphology, as well as absence of interbreeding between their sympatric populations, support the species status of *P. thagus* (e.g., Gill et al., 2022; Harrison and Walker, 1976; Kennedy et al., 2013; Sibley and Monroe, 1990).

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The paleontological record of pelicans is relatively poor (for a summary see Table S1), dating back to the late Eocene of Egypt with *Eopelecanus aegyptiacus* El Adli, Wilson Mantilla, Antar, and Gingerich, 2021. Other Old World fossil pelicans assigned to *Pelecanus* sp. are known from the early Oligocene of France (Louchart et al., 2011) and the Middle Miocene of Germany (Göhlich, 2017). *Pelecanus tirarensis* Miller, 1966, and *Pelecanus fraasi* Lydekker, 1891, were described from the late Oligocene of Australia and Middle Miocene of Germany, respectively (Olson, 1985; Rich and Van Tets, 1981; Worthy and Nguyen, 2020), and *Pelecanus odessanus* Widhalm, 1886, from the Upper Miocene of Ukraine (Olson, 1999; Zelenkov and Kurochkin, 2015). Two extinct taxa found in Pakistan and/or India, *Pelecanus cautleyi* Davies, 1880, and *Pelecanus sivalensis* Davies, 1880, are of an uncertain Late Miocene to Late Pliocene age (see Harrison and Walker, 1982; Lydekker, 1891; Stidham et al., 2014). *Pelecanus aethiopicus* Harrison and Walker, 1976, was described from the Upper Pliocene of Tanzania, although may be synonymous with the extant *P. onocrotalus* or *P. crispus* (see Louchart, 2008). Apart from *Eopelecanus*, the only fossil pelicans considered different from *Pelecanus* were placed in *Miopelecanus* Cheneval, 1984, including *Miopelecanus gracilis* (Milne-Edwards, 1867 from the Early Miocene of France, *Miopelecanus intermedius* (Fraas, 1870) from the Middle Miocene of Germany (Cheneval, 1984; Heizmann and Hesse, 1995), and putative specimens from the Middle Miocene of Kenya (Mayr, 2014).

The records of the New World include *Pelecanus* sp. from the Upper Miocene of Costa Rica (Valerio and Laurito, 2013; but see Discussion), Peru (Altamirano-Sierra, 2013), and Mexico (González Barba et al., 2021). *Pelecanus schreiberi* Olson, 1999, is the only undoubted fossil species described from the Lower Pliocene of Florida and North Carolina (U.S.A.; Olson, 1999; Olson and Rasmussen, 2001), whereas *Pelecanus halieus* Wetmore, 1933, from the Pliocene of Idaho, is probably a synonym of the living *P. erythrorhynchos* (see Becker, 1986; González Barba et al., 2021). Specimens tentatively attributed to *Pelecanus erythrorhynchos* were also recorded in the Upper Miocene of Oregon (Miller, 1944) and the Late Pliocene of California (Cassiliano, 1999) of Oregon and California (see González Barba et al., 2021). Fossil representatives of *P. occidentalis* are only known since the Late Pleistocene of North America (see Guthrie, 2009, 2010) (Table S1), but a fossilized egg from the Middle Pleistocene of Bermuda has also been referred to this species (Olson and Hearty, 2013). *Pelecanus thagus* has only been recorded in deposits from the latest Pleistocene–Holocene of Chile and Peru (see Dillehay et al., 2012; Peña-Villalobos et al. 2013) (Table S1).

Almost all Quaternary fossil specimens worldwide were assigned to extant species (e.g., Emslie, 1995; Louchart, 2008; Mead et al., 2006; Rich and Van Tets, 1981) (Table S1), except for *Pelecanus cadimurka* Rich and Van Tets, 1981 from Australia. The supposedly paleoendemic *Pelecanus novaezealandiae* described by Scarlett (1966) from the Holocene of New Zealand is now considered a synonym of *P. conspicillatus* (e.g., Gill et al., 2010).

During the Middle–Late Miocene of South America, the record of the Chaco-Paraná basin shows a large seawater ingression (Paranaense or Entrerriense Sea) which, in northeastern Argentina, consists of shallow marginal marine and littoral sedimentary sequences of the Paraná Formation (see Aceñolaza, 2000; Iriondo, 1973; Orfeo, 2005; Orfeo et al., 2011). In Entre Ríos Province, the Paraná Formation has provided many records of fossil invertebrates (Pérez, 2013a, 2013b), but relatively few continental vertebrates (Brandoni et al., 2019). Among birds, the fossil record is very scarce and consists of fragmentary remains of a flamingo (cf. *Phoenicopterus* sp.; Candela et al., 2012) and a large darter (*Macranhinga paranensis* Noriega, 1992; see Diederle et al., 2012). The discovery of a fossil pelican in the upper levels of the Paraná Formation in northeastern Argentina allows us to analyze for the first time the presence of pelecanids in high latitudes of the southwestern Atlantic Ocean and to discuss paleobiogeographic hypotheses about the origin and dispersal of this cosmopolitan family.

GEOLOGICAL SETTING

In the Province of Entre Ríos, Argentina, the marine Paraná Formation is mostly known from surface studies in different outcrops (e.g., Aceñolaza, 2000; Brandoni et al., 2019; del Río et al., 2018; Frenguelli, 1920; Pérez et al., 2013), with thicknesses between 5 and 40 m, and consist mainly of siliciclastic sandstone and mudstone layers that show high concentration of cemented bioclastic beds toward the top of the unit. The skeletal concentration described (see Brandoni et al., 2019; Pérez et al., 2013) is part of a diverse faunal association mostly marine in nature, with few recorded continental terrestrial vertebrates (Candela et al., 2012).

The specimen herein described comes from the sandstone marine beds of the Paraná Formation exposed near Victoria City at Cerro La Matanza locality, Entre Ríos Province, Argentina (Fig. 1A). It is associated, as is most of the characteristic fossil content of the unit including rich vertebrate and macroinvertebrate assemblages, with the upper section of the Paraná Formation (see Brandoni et al., 2019; Pérez et al., 2013). Local deposits of the Paraná Formation (Fig. 1B) are characterized mainly by white to yellowish cross-bedded sandstone with quartz clasts composition, and less commonly, by bioclastic sandstone and heterolithic levels. They form tabular bodies, 1.5 m thick and tens of meters long, bounded by sharp to slightly erosive surfaces at the base, and compose sets of 0.3–5 m thick. These deposits can be interpreted as sedimentary facies accumulated in shoreface to foreshore environments (Clifton, 2006; Collinson and Thompson, 1989).

The Paraná Formation has been mostly assigned to the Miocene (Aceñolaza, 1976; Aceñolaza and Sprechmann, 2002; Camacho, 1967; Cione et al., 2000; del Río, 1990, 1991; Frenguelli, 1920; Martínez and del Río, 2005). Recent analyses of strontium isotopes (87Sr/86Sr) from bivalves yielded ages of ~9.47 Ma (Pérez, 2013a, 2013b) and 7.55–6.67 Ma (del Río et al., 2018), which indicate a Late Miocene age at least for the western Entre Ríos Province.

MATERIAL AND METHODS

The osteological nomenclature follows Baumel and Witmer (1993) and Livezey and Zusi (2006) for pelvis, and Elzanowski et al. (2000) for quadrate bones. The following comparative specimens were used: *Chauna torquata*, *Phoenicopterus ruber*, *Vultur gryphus*, *Pygoscelis adeliae*, *Diomedea nigripes*, *Macronectes giganteus*, *Morus bassanus*, *Sula leucogaster*, *Fregata magnificens*, *Anhinga anhinga*, *Nannopterum auritum*, *Ardea herodias*, *Jabiru mycteria*, *Ciconia maguari*, *Scopus umbretta*, *Balaeniceps rex*, *Pelecanus occidentalis* (6), *P. thagus* (7), *P. conspicillatus* (2), *P. philippensis*, *P. rufescens*, *P. crispus* (2), *P. onocrotalus* (3), and *P. erythrorhynchos*.

Measurements were made with digital calipers with an accuracy of 0.1 mm.

Institutional Abbreviations—**CICYTTP**, Centro de Investigación Científica y de Transferencia de Tecnológica a la Producción, Diamante, Argentina; **FUR**, Flinders University, Adelaide, Australia; **IMNH**, Idaho Museum of Natural History, Pocatello, U.S.A.; **MNHT**, Museu de História Natural de Taubaté, Taubaté, Brazil; **MUSM**, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; **SMF**, Senckenberg Research Institute, Frankfurt, Germany; **UF**, Florida Museum of Natural History, Gainesville, U.S.A.;
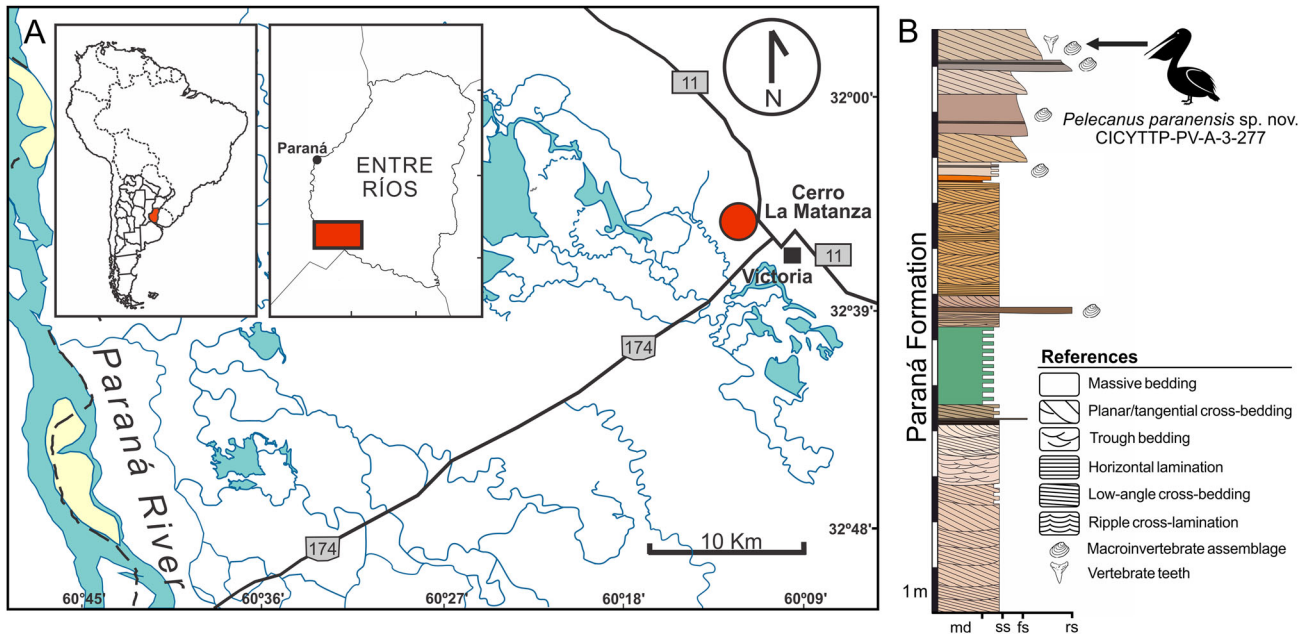
FIGURE 1. **A**, map of the study area, showing Cerro La Matanza locality (32°35′51″S, 60°11′22″W) in Victoria City (Entre Ríos Province, Argentina), where the holotype of *Pelecanus paranensis* comes from; **B**, stratigraphic local profile of the Paraná Formation.

USNM, National Museum of Natural History, Washington, U.S.A.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Clade AEQUORNITHES Mayr, 2011
Order PELECANIFORMES Sharpe, 1891
Family PELECANIDAE Rafinesque, 1815
Genus *PELECANUS* Linnaeus, 1758
PELECANUS PARANENSIS, sp. nov.
(Figs. 2, 3B, E, H, K, Q)

Holotype—A nearly complete pelvis, CICYTTP-PV-A-3-277 (Figs. 2, 3B, E, H, K, Q).

Etymology—*paranensis*, from the Paraná Formation, i.e., the stratigraphic provenance of the holotype.

Diagnosis—(1) large-sized species; (2) facies articularis cranialis of first fused vertebra thoracica compressed dorsoventrally; (3) processus transversales of three most cranial fused vertebrae thoracicae wide; (4) gap present between ala preacetabularis ilii and processus transversalis of third fused vertebra thoracica; (5) alae preacetabulares ilii strongly curved laterally; (6) planum transversalium and surface between cristae iliacae dorsales wide; (7) crista spinosa synsacralis robust, emerging cranially to alae preacetabulares ilii; (8) processus antitrochantericus not prominent; (9) cristae iliacae dorsales continuous throughout entire length (i.e., without flat notch for attachment of musculus iliotrochantericus caudalis); (10) postacetabular dorsocaudal section of pelvis U-shaped (i.e., crista iliaca dorsolateralis weak, blunt, and medially curved, caudally abbreviated and reduced to ridge; see below); (11) incisura sutura iliosynsacralis wide and shallow; (12) bulla intumescentia lumbosacralis slender; (13) processus costalis of last synostotic vertebra thoracica (i.e., eighth vertebra thoracica) stout and wide; (14) pila ilioischiadica short; (15) pars ischiadica of fossae renales quadrangular, narrow, and elongated craniocaudally; (16) caudal

section of postacetabular synsacrum robust, lacking longitudinal crista; (17) foramen acetabuli large; (18) lamina infracristalis ilii expanded dorsoventrally; (19) foramen ilioischiadicum subelliptical.

Differential Diagnosis—Differs from *P. occidentalis* in characters (1), (2), (8), (12), (13), (14), and (15); from *P. thagus* in (2), (4), (8), (12), (13), (14), (15), and (16); from *P. erythrorhynchos* in (3), (6), (7), (10), (11), (15), (16), and (18); from *P. onocrotalus* in (4), (5), (6), (8), (10), (11), (15), and (16); from *P. conspicillatus* in (4), (5), (6), (8), (10), (11), (15), (16), and (18); from *P. rufescens* in (1), (4), (5), (6), (8), (10), (11), (16), and (18); from *P. philippensis* in (1), (3), (4), (5), (6), (8), (10), (11), (15), (16), (18), and (19); and from *P. crispus* in (1), (4), (5), (6), (8), (10), (11), (16), (18), and (19). The characters (9) and (17) are putative autapomorphies of the new species.

Locality and Horizon—The material comes from Cerro La Matanza locality (32°35′51″S, 60°11′22″W) in Victoria City, Entre Ríos Province, Argentina, from the upper sandstone marine beds of the Paraná Formation (Fig. 1). Radiometric and biochronological data indicate that the age of the Paraná Formation corresponds to the Late Miocene (Tortonian–Messinian stage).

Measurements—See Table 1.

Description and Comparisons—The pelvis CICYTTP-PV-A-3-277 is referable to Pelecanidae and differs from other Aequornithes, as well as from other large extinct or living South American birds (e.g., Rheidae, Pelagornithidae, Anhimidae, Anatidae, Phoenicopteridae, Palaelodidae, Phorusrhacidae, Cathartidae, Teratornithidae), in the following combination of characters (see also Pycraft, 1898:96): (1) three additional vertebrae thoracicae fused cranially to corpora vertebrarum synsacri through well-developed aponeurosis ossificans along their processus transversales (Fig. 2A, B); (2) pila preacetabularis synsacri sturdy, cylindrical and, in lateral view, ventrally aligned in a horizontal plane, lacking any ventral expansion or cristae ventrales (Fig. 2B–D); (3) alae preacetabulares ilii not extended or fused dorsocranially over these two or three most cranial vertebrae (Fig. 2A); (4) relatively wide pelvis (not laterally compressed)
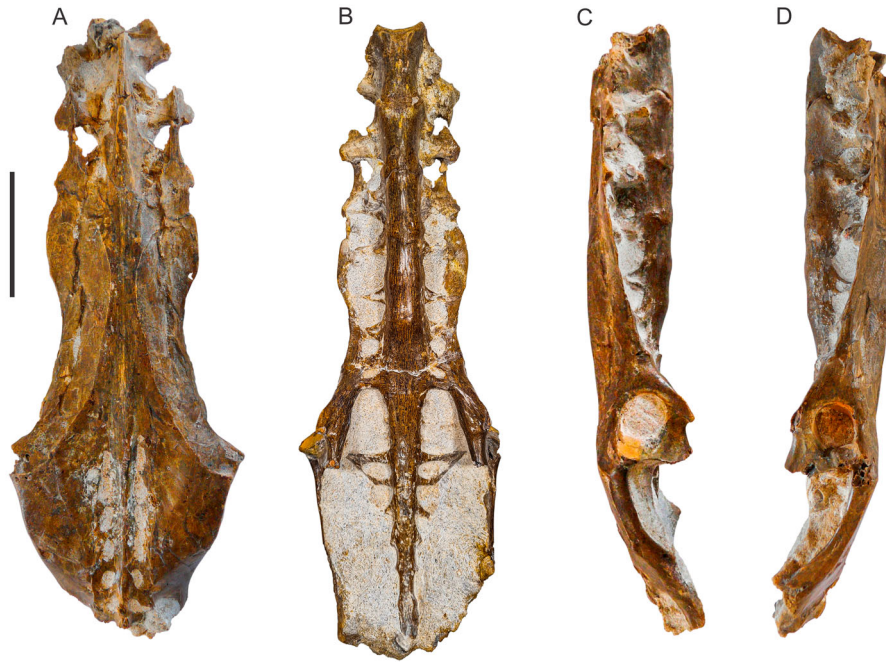
FIGURE 2. Nearly complete pelvis of *Pelecanus paranensis* (CICYTTP-PV-A-3-277) from Upper Miocene marine strata of Paraná Formation in Cerro La Matanza locality (Entre Ríos Province, Argentina). Holotype in dorsal (**A**), ventral (**B**), right (**C**), and left (**D**) views. Scale bar equals 50 mm.

TABLE 1. Comparative measurements (mm) of the pelvis plus synsacra, distal femora and quadrate bones in living *Pelecanus* spp., *Pelecanus paranensis* sp. nov. (holotype CICYTTP-PV-A-3-277), and other selected New World fossil taxa. Combined data from own measurements and those taken from (a) Rich and Van Tets (1981), (b) Olson (1999), and (c) Altamirano-Sierra (2013). **Abbreviations**: **D-cap**, depth of caput femoris; **L-dv**, dorsoventral length; **L-mand**, length of mandibular articulation; **TL**, total length; **W-II**, width of the second vertebra thoracica at the level of its processus transversales; **W-acet**, width of the foramen acetabuli; **W-dist**, distal width; **W-pa**, width between processes antitrochantericarum; **W-va**, width of the fossa renalis at the level of the processus costales of the vertebra acetabularis.

	Pelvis and synsacrum					Femur		Quadrate	
	TL	W-pa	W-II	W-va	W-acet	D-cap	W-dist	L-dv	L-mand
P. crispus	315	112–122 (2)	69	55–59(2)	21	15–16(2)[a]	35–37.4(4)[a,b]	32–37(3)[a,b]	23.9–27.3(3)[a,b]
P. conspicilliatus	269	79–112(22)[a]	59	61	20	13–16(14)[a]	30–37(15)[a]	28–36(11)[a]	22–27(11)[a]
P. onocrotalus	230–262(2)	94–99(4)[a]	50–54(2)	48	19	15[a]	33–37.6(9)[a,b]	30.4–40(3)[a,b]	25–30(5)[a,b]
P. thagus	210–234(4)	91–109(5)	44–63(4)	53–62(5)	15.5–20(5)	11.6–12.3(2)	26.7–29(2)	34.4–42.8(6)[c]	23–28.4(6)[c]
P. erythrorhynchos	227	84–97(3)[a]	42	50	15	13–14(5)[a]	28–33.2(17)[a,b]	28.7–29.8(8)[a,b]	23–23.9(8)[a,b]
P. rufescens	209	82–89(2)[a]	47	43	15	12–14(2)[a]	26–32(2)[a]	29–33(2)[a]	20–25(2)[a]
P. philippensis	–	–	–	–	–	15[a]	35[a]	33[a]	24[a]
P. occidentalis	180–181(2)	69–76(3)[a]	37–38(2)	46–48(2)	13(2)	9–12(10)[a]	20–26(6)[a]	32–35.2(2)[a,c]	20–22.8(2)[a,c]
P. paranensis†	242	96	56	53	22	–	–	–	–
P. schreiberi †	–	–	–	–	–	–	37.2–38.2(2)[b]	33[b]	25[b]
Pelecanus sp.† (Pisco Fm., Peru)	–	–	–	–	–	–	–	36.5[c]	23.8[c]

with a preacetabular section noticeably longer than the postacetabular section (Fig. 2A–D); (5) in lateral view, alae preacetabulares ilii oriented in a markedly horizontal plane (Fig. 2C, D); (6) reduced foramina intertransversaria and present only on the postacetabular section (Fig. 2A).

The size of the specimen representing the new taxon falls within the range of the large extant species *P. onocrotalus*, *P. conspicillatus*, *P. erythrorhynchos*, and *P. thagus*, being larger than *P. rufescens*, *P. philippensis*, and *P. occidentalis*, but smaller than *P. crispus* (Table 1).

In lateral and cranial view, unlike in *P. occidentalis* and *P. thagus*, the dorsoventrally compressed facies articularis

cranialis of the first fused vertebra thoracica is a character shared by *P. paranensis*, all the Old World species and *P. erythrorhynchos* (Figs. 2C, D, 3E, H). The great width of the cranial section of the dorsal synsacrum (i.e., the three most cranial fused vertebrae thoracicae) in *P. paranensis* constitutes a generalized condition which is observed in almost all pelicans (Figs. 2A, B, 3B, E), except in *P. erythrorhynchos* and *P. philippensis* where it is relatively narrower. In *P. paranensis* there is a gap between the cranial rim of the ala preacetabularis ilii and the processus transversales of the third vertebra thoracica (Figs. 2B, 3E), a character shared by *P. erythrorhynchos* and *P. occidentalis*, but absent or reduced in
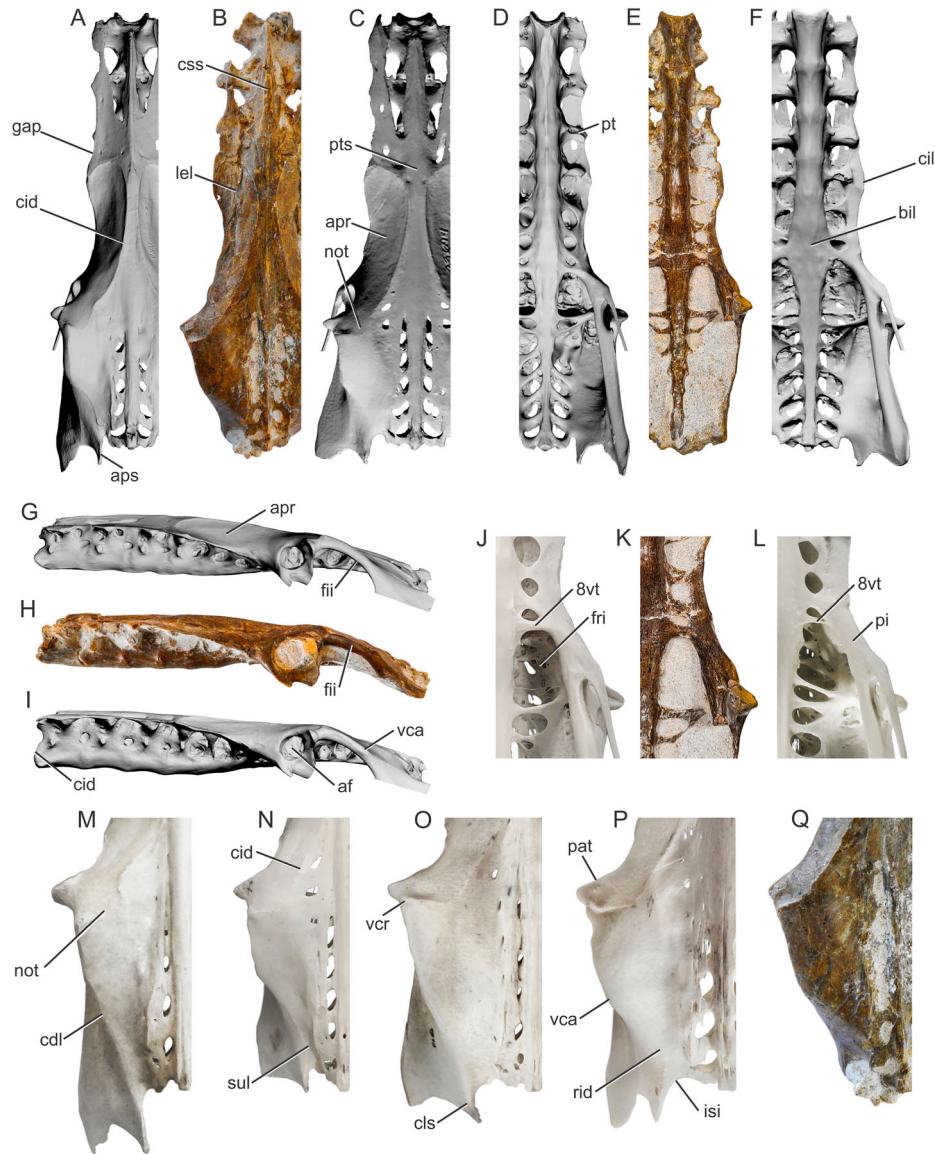
FIGURE 3. Comparisons of *Pelecanus paranensis* (holotype CICYTTP-PV-A-3-277) with the pelvic girdle of other *Pelecanus* spp. **A**, **D**, and **G**, *Pelecanus erythrorhynchos* (IMNH R-1901) in dorsal (**A**), ventral (**D**), and lateral (**G**) views; **B**, **E**, and **H**, *Pelecanus paranensis* (inverted) in dorsal (**B**), ventral (**E**), and lateral (**H**) views; **C**, **F**, and **I**, *Pelecanus occidentalis* (IMNH R-1605) in dorsal (**C**), ventral (**F**), and lateral (**I**) views; **J–L**, ventral detail of the synostotic vertebrae thoracicae and the fossae renales in *Pelecanus crispus* (SMF 21580, **J**), *Pelecanus paranensis* (inverted, **K**), and *Pelecanus thagus* (USNM 489428, **L**); **M–Q**, detail of postacetabular dorsocaudal section in *Pelecanus conspicillatus* (FUR 323, **M**), *Pelecanus crispus* (SMF, **N**), *Pelecanus onocrotalus* (MNHT 1979, **O**), *Pelecanus thagus* (USNM 489428, **P**), and *Pelecanus paranensis* (inverted, **Q**). Unscaled images for comparison, measurements in Table 1. **Abbreviations**: **af**, foramen acetabuli; **apr**, ala preacetabularis ilii; **aps**, ala postacetabularis ilii; **bil**, bulla intumescentia lumbosacralis; **cdl**, crista iliaca dorsolateralis; **cid**, crista iliaca dorsalis; **cil**, crista iliaca lateralis; **cls**, cristula lateralis spinae ilii; **css**, crista spinosa synsacralis; **fii**, foramen ilioischiadicum; **fri**, fossae renalis, pars ischiadica; **gap**, space between the ala preacetabularis ilii and the processus transversalis of the 3th vertebra thoracica; **isi**, incisura sutura iliosynsacralis; **lel**, lamina ellipsoidalis lateralis; **not**, notch for attachment of m. iliotrochantericus caudalis; **pat**, processus antitrochantericus; **pi**, pila ilioischiadica; **pt**, processus transversalis; **pts**, planum transversalium synsacralis; **rid**, ridge, reduced caudal crista iliaca dorsolateralis; **sul**, sulcus; **vca**, vertex caudolateralis ilii; **vcr**, vertex craniolateralis ilii; **8vt**, synostotic vertebra thoracica (i.e., 8th).

the other pelicans where the ala preacetabularis ilii rests directly on the processus.

In dorsal and, more evident, ventral views, the cranial section of the ala preacetabularis ilii of *P. paranensis* exhibits the crista iliaca lateralis laterally flared forming a rounded and prominent lamina ellipsoidalis lateralis (Figs. 2A, 3B). As a consequence of this cranial enlargement, the midsections of the alae preacetabulares ilii show strongly curved or laterally concave contours like in *P. erythrorhynchos*, *P. thagus*, and

P. occidentalis (Fig. 3A, C, D, F, K, L); whereas in *P. crispus* this is even more accentuated, but in the remaining species the cristae iliacae laterales are straighter and near parallel, giving the appearance that the alae preacetabulares ilii have similar transverse widths along the entire length.

In dorsal view, like in *P. occipitalis* and *P. thagus*, both the planum transversalium and the space between the cristae iliacae dorsales are wider than in other compared species. The crista spinosa synsacralis has a development similar to that of

P. onocrotalus, more robust than those of other *Pelecanus* spp. and, unlike in *P. erythrorhynchos*, it originates and rises more cranially (Figs. 2A, 3A–C).

The processus antitrochantericus of *P. paranensis* presents a moderate development as in *P. erythrorhynchos*, not as prominent as in the other compared species. The relative dorsal width between these processes is also similar to that observed in *P. erythrorhynchos*, being markedly wider in *P. onocrotalus*, *P. occidentalis*, and *P. thagus* (Fig. 3A–C, M–Q). At this level, the most caudal section of the cristae iliacae dorsales of *P. paranensis* are strongly developed and extend continuously to the vertex craniolateralis ilii (Figs. 2A, 3B, Q). This condition is unique and contrasts with that displayed by other pelicans, where these cristae are interrupted by a caudal extension of the area for attachment of musculus iliotrochantericus caudalis that define a shallow and flat notch with a variable inter- and intraspecific development (Fig. 3A–C, M–Q). This latter notch is missing or unapparent in the new taxon.

Although narrower, the relatively shorter and U-shaped post-acetabular dorsocaudal section of the pelvis of *P. paranensis* resembles those observed in *P. occipitalis* and *P. thagus* (Figs. 2A, 3B, C, P, Q). In dorsal view, this more rounded or globose configuration of the postacetabular pelvis is due to the laminae infracristales ilii being inflated laterally and the crista iliaca dorsolateralis being weak, blunt, and curved toward the sagittal plane, shrinking caudally to a short sigmoid ridge that extends to the cristula lateralis spinae ilii. On the caudodorsal surface of the ala postacetabularis ilii, this ridge laterally outlines a short and shallow sulcus which ends caudally in a wide incisura sutura iliosynsacralis (Figs. 2A, 3Q). In the remaining compared extant species, the postacetabular section is relatively longer and V-shaped because the crista iliaca dorsolateralis shows an acute and rather straight development to the cristula lateralis spinae ilii (Fig. 3A, M–O). In these species, caudal to the vertex caudolateralis ilii, unlike in *P. occipitalis*, *P. thagus*, and *P. paranensis*, the crista iliaca dorsolateralis is longer, more conspicuous, sharper, and outlines a deeper sulcus that ends in a narrower incisura sutura iliosynsacralis (Fig. 3A, M–O).

In ventral view, the proportions of the preacetabular corpora vertebrarum synsacri of *P. paranensis* are similar to those of *P. erythrorhynchos*, *P. onocrotalus*, and *P. rufescens*, being stouter than in *P. crispus*, and thinner than in *P. conspicillatus* and *P. philippensis* (mainly at the level of the third and fourth most cranial vertebrae thoracicae). The preacetabular corpora vertebrarum of *P. paranensis* is also slenderer than in *P. occipitalis* and *P. thagus*, where the last vertebrae thoracicae and first lumbares (bulla intumescentia lumbosacralis) are more laterally expanded than in the remaining pelicans. In this section, the processus costalis that joins the last synostotic vertebra thoracica (i.e., the eighth) with the pila ilioischiadica is stout and wide in *P. paranensis* (Fig. 3E, K), a character shared with the Old World species and *P. erythrorhynchos* (Fig. 3D, J). Instead, this process is strongly reduced or absent in *P. occipitalis* and *P. thagus* and in these species the main synostosis between the synsacrum and the pila ilioischiadica is the processus costalis of the penultimate vertebra thoracica (i.e., the seventh) (Fig. 3F, L). Related to this configuration, the pilae ilioischiadicae in the latter two species show a more elongated and divergent aspect, delimiting much wider and subtriangular fossae renales (pars ischiadica fossae) than in the remaining pelicans, including *P. paranensis* (Fig. 3F, L). These fossae are near quadrangular in *P. paranensis* (Fig. 3K), but narrower than in *P. onocrotalus* and *P. conspicillatus*, and more craniodorsally elongated than in *P. erythrorhynchos* and *P. philippensis*, close to the condition observed in *P. crispus* and *P. rufescens*. Ventrally, the caudal section of the postacetabular synsacrum in the new species is robust like in *P. occidentalis*, and lacks a longitudinal crista just as in some individuals of this species.

In lateral view, the foramen acetabuli of *P. paranensis* is relatively larger than in other pelicans, and the lamina infracristalis ilii is dorsoventrally expanded like in *P. onocrotalus*, *P. occidentalis*, and *P. thagus* (Figs. 2C, D, 3H). Unlike in *P. crispus* and *P. philippensis*, the foramen ilioischiadicum does not appear to have been subquadrangular in shape, but subelliptical.

DISCUSSION

Systematic and Phylogenetic Remarks

The striking similarities between the beak anatomy of fossil and living pelicans have been hypothesized to be indicative of long-term stasis in feeding morphology (Louchart et al., 2011). Other explanations for such conservatism consider the influence of flying ability as a constraint on the whole skeletal morphology (Louchart et al., 2011; Tyrberg, 2002). In a similar sense, Rich and Van Tets (1981; see also Olson, 1999) noted a wide uniformity in the general skeletal morphology among extant pelican species, except for that of the New World *P. occidentalis* (including *P. "occidentalis" thagus*, currently with full species status).

As evidenced in the comparative description, the pelvis of *P. paranensis* is no exception from this remarkable morphological uniformity detected from the oldest Paleogene pelicans to the extant taxa (Louchart et al., 2011). However, the unique combination of 19 characters provided in the diagnosis of *P. paranensis*, which includes two exclusive features (cristae iliacae dorsales continuous throughout the entire length without a flat notch for attachment of musculus iliotrochantericus caudalis and large foramen acetabuli), justifies the erection of the new species.

Pelecanus paranensis clearly shows closer affinities to the New World than to the Old World Pelican clade. Potential synapomorphies identified in the pelvis of the American species, including *P. paranensis*, are the presence of a gap between the cranial rim of the ala preacetabularis ilii and the processus transversalis of the third vertebra thoracica (probably secondarily reduced in *P. thagus*), and the strongly laterally curved alae preacetabulares ilii. This latter character is also observed, albeit better developed, in the large Dalmatian Pelican *P. crispus*. Other possible osteological synapomorphies of New World pelicans have been directly or indirectly suggested by previous authors, i.e., trochlea metatarsi II of the tarsometatarsus extending only slightly distal to the trochlea metatarsi IV (see Rich and Van Tets, 1981), the presence in the tarsometatarsus of a shallow and ridgeless surface proximal of the crista medialis hypotarsi and a square midplantar projection at the proximal end (see Stidham et al., 2014).

The general configuration of the pelvis of *P. paranensis* is more similar to those of the Brown and Peruvian pelicans, *P. occidentalis* and *P. thagus*. These three species exhibit a more derived morphology than the presumed ancestral condition observed in the American White Pelican, *P. erythrorhynchos*, which resembles the Old World taxa. *Pelecanus paranensis* shares some putative synapomorphic features with the clade (*P. occidentalis* + *P. thagus*), mainly the U-shaped postacetabular section and, related to this condition, the presence of a wide incisura sutura iliosynsacralis, but also a wide planum transversalium and space between the cristae iliacae dorsales.

Otherwise, like in *P. erythrorhynchos* and the Old World pelicans, *P. paranensis* lacks other possibly derived characters exclusive of the clade (*P. occipitalis* + *P. thagus*) such as: a high (not dorsoventrally compressed) facies articularis cranialis of the first fused vertebra thoracica, a well-developed bulla intumescentia lumbosacralis, a reduced or absent processus costalis of the last synostotic vertebra thoracica (i.e., the eighth), and the elongated and divergent pilae ilioischiadica delimiting wider and subtriangular fossae renales.
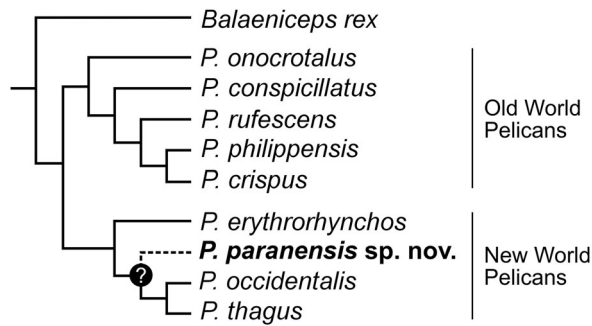
FIGURE 4. Hypothesized phylogenetic relationships of *Pelecanus paranensis* based on the morphological features of the pelvis observed in this study. The tree is based on the molecular phylogeny of extant pelicans of Kennedy et al. (2013).

In sum, the morphology of *P. paranensis* not only exhibits possible derived characters only shared with *P. occidentalis* and *P. thagus*, but it also shows putative plesiomorphic features widespread in the Old World pelicans and *P. erythrorhynchos*. The mapping of the distribution of all these characters on the topology resulting from the molecular phylogeny of Kennedy et al. (2013) suggests that *P. paranensis* is close to the clade including the New World species *P. occipitalis* and *P. thagus*, with *P. erythrorhynchos* being outside the clade including these three species (Fig. 4).

Comments on the Taxonomy and Phylogenetic Affinities of some New World Fossil Pelicans

Although the absence of homologous elements between *P. paranensis* and other New World fossil pelicans precludes direct comparisons, the review of the available paleontological record provides new clues to understand, at least preliminarily, the possible phylogenetic relationships among them.

Pelecanus schreiberi from the Lower Pliocene marine beds of Yorktown Formation, North Carolina (U.S.A.) was based on a distal femur and additional referred specimens (i.e., another distal femur and pedal phalanges from the type locality, but also an axis and two quadrate bones from coeval Bone Valley Formation, Florida; see Olson, 1999; Fig. S2). The femur of *P. schreiberi* is larger than those of the living New World species (Table 1), only comparable in size to the largest individuals of the largest living Old World species (*P. crispus* and *P. onocrotalus*), but the referred quadrates are smaller than those of South American *P. thagus* (not explicitly included in the comparisons by Olson, 1999; see below and Table 1). In any case, the holotype of *P. schreiberi* shows a very divergent femoral morphology with respect to all living or extinct species of *Pelecanus*, "so great that it almost suggests a generic distinction" (Olson, 1999:504). Furthermore, *P. schreiberi* also differs in size and morphology from smaller Early–Late Miocene species of *Miopelecanus* (Olson, 1999).

The assignment of a fragmentary specimen from the Upper Miocene of Costa Rica to *Pelecanus* sp. by Valerio and Laurito (2013) is controversial. The morphology and ossification pattern observed in the figured specimens (i.e., both *Pelecanus* sp. and Pelagornithidae indet.; see Valerio and Laurito, 2013: fig. 2) do not agree with any avian bone, but with autopodial mammal elements.

Prior to this contribution, the only known record of pelicans in the Neogene of South America was represented by an isolated quadrate bone from the Upper Miocene Pisco Formation of Peru (Altamirano-Sierra, 2013; Fig. S2), very close in age to *P. paranensis* (Montemar locality, ~7.15–6.3 Ma; see Ochoa et al., 2022) and referred to *Pelecanus* sp. Among New World

pelicans, the size of the Peruvian fossil specimen (MUSM 583, see Table 1) resembles that of *P. thagus*, being larger than that of *P. occidentalis* and *P. erythrorhynchos*, as well as than those quadrates assigned to *P. schreiberi* (UF 125031 and UF 125030; Fig. S2) from the Bone Valley Formation (Florida, U.S.A.). Olson (1999:504) did not provide any morphological evidence for an assignment of these latter specimens to *P. schreiberi* (based on a distal femur from a different locality and stratotype) and relied only on their larger sizes than the respective bones of *P. occidentalis* and *P. erythrorhynchos*. Similarly, the Peruvian specimen (MUSM 583) was compared in its original description with *P. schreiberi*, *P. occidentalis*, and *P. thagus*, whereas comparisons with *P. erythrorhynchos* were excluded (Altamirano-Sierra, 2013).

The overall robustness of the quadrates MUSM 583 and UF 125030 is close to that exhibited by *P. erythrorhynchos* rather than the slender configuration of *P. occipitalis* and *P. thagus* (Fig. S2). However, these specimens from Peru and Florida (especially UF 125030) exhibit a combination of unique traits among New World pelicans (e.g., large facies pterygoidea), as well as a mosaic of characters, some of them shared with *P. erythrorhynchos* (e.g., stoutness of corpus and processes; position and shape of cristae supraorbitalis, medialis, and infraorbitalis; location of condylus caudalis) and others with *P. occidentalis* and *P. thagus* (e.g., development and position of capitulum oticum; size of condyli medialis, caudalis, lateralis, and pterygoideus) (Fig. S2).

Thus, the congruence in sharing many characters with the "Brown" pelicans (*P. occidentalis* and *P. thagus*), their large sizes, as well as their nearly coeval ages and provenances from marine deposits, seem to suggest a possible close affinity between the specimens referred to *P. schreiberi* (but not with the holotype), the Peruvian *Pelecanus* sp., and *P. paranensis*.

Paleobiogeography of Pelecanidae and Implications of the New Record

The endemic African wading birds included in the families Scopidae and Balaenicipitidae, containing the extant hamerkop (*Scopus umbretta* Gmelin, 1789) and shoebill (*Balaeniceps rex* Gould, 1850), are recovered in molecular phylogenetic analyses together with *Pelecanus* as a clade different from other pelecaniforms (Cracraft et al., 2004; Ericson et al., 2006; Hackett et al., 2008; Prum et al., 2015). These phylogenetic hypotheses, coupled with the restriction of the fossil scopids and balaenicipitids to Africa (Rasmussen et al., 1987; Rich, 1972; Olson, 1984; Smith, 2013) and the recent finding of the late Eocene (early Priabonian) oldest known pelican (*E. aegyptiacus*) in Egypt (see El Adli et al., 2021), encouraged some authors to state that pelecanids emerged from Africa or southern Asia before dispersing to Europe, northern Asia, Australia, North America, and finally South America (El Adli et al., 2021; Johnsgard, 1993; Kennedy et al., 2013; Mayr, 2009).

Although the putative succession of events of allopatric speciation and dispersal of ancestral populations from Africa to Europe and from there to Asia, Australasia, and the eventual colonization of North America in a steady eastward direction is possible, it appears to constitute a fairly intricate evolutionary scenario. Alternative to this traditional view, the close relationship of *P. paranensis* to the New World clade, along with both its stratigraphic and geographic provenances, i.e., the Late Miocene (Tortonian/Messinian age) of southern South America, could be indicative of a different route of arrival of the ancestor of pelicans to the Americas. A trans-Atlantic dispersal route from Africa to the Americas could also explain the single colonization of this continent by a common ancestor of the New World clade after its basal divergence from the Old World clade.
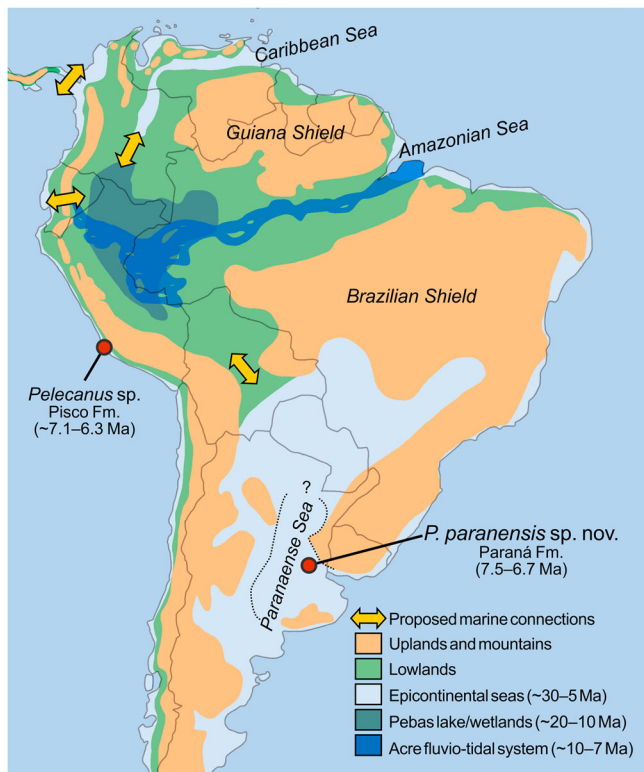
FIGURE 5. Tentative late Oligocene–Late Miocene paleogeography and pelican fossil records of South America. Probable extent of the Paranaense Sea indicated in dashed line. Modified from Hoorn et al. (2010), Gross et al. (2015) and references therein.

South American Miocene Wetlands/Inland Seas' Transitions: An Ecological Driver for the Radiation of "Brown" Pelicans?

The alleged phylogenetic position of the new taxon would give some clues about the split that gave rise to the strictly marine coastal "Brown" pelicans. *Pelecanus paranensis* comes from sediments representing the littoral to marginal marine facies of the shallow inland Paranaense Sea, which covered central and northern Argentina during the mid–Late Miocene (Aceñolaza, 2000; Alonso, 2000; Malumián and Náñez, 2011; Marengo et al., 2019) (Fig. 5).

From the late Oligocene to the Early Pliocene, as the uplift of the Andes progressed and basins rearranged under tectonic loading, rainfall increased in the eastern lowlands (Amazonas/Solimões basins) and the epicontinental seas invaded coastal and inland areas of the northern and southern regions (e.g., Bicudo et al. 2020; Hernández et al., 2005; Hoorn et al., 2010; Jaramillo et al., 2017) (Fig. 5). In western Amazonia, a megawetland with episodic marine influence from the Caribbean Sea (see, e.g., Wesselingh and Salo, 2006), known as the Pebas system, reached its climax phase during the Middle Miocene Climatic Optimum (Hoorn et al., 2010, 2022). With global cooling and sea-level drop in the Late Miocene, the Pebas wetland transitioned from a lacustrine to a fluvial or fluvio-tidal system (Acre system), starting its Atlantic drainage through the transcontinental Amazon River (Fig. 5).

Multiple proxies demonstrated that these highly dynamic, heterogeneous and extensive freshwater/marine environments (including lakes, swamps, marshes, tidal channels, estuaries, deltas, and large marine embayments with periods of variable salinity and vast flood-regressive plains) have played a particularly important role in the diversification of the South American biota as selective barriers for terrestrial taxa and speciation hotspots

for aquatic taxa during the Early–Late Miocene (e.g., Candela et al., 2012; Hoorn et al., 2010, 2022; Noriega et al., 2017; Ortiz Jaureguizar and Cladera, 2006).

The impact that the Early–Late Miocene marine ingressions would have had in the cladogenesis of different groups of South American birds has already been discussed, focusing on the idea of the imposition of dividing barriers of terrestrial avian populations (e.g., Cariamidae, Rheidae, and probably Tinamidae) on one or the other side of the marine flooding (Noriega et al., 2017). The radiation, dispersal, and extinction of large aquatic birds (i.e., Anhingidae) was even conditioned by the presence of extensive and highly productive marine/freshwater landscapes (Cenizo and Agnolín, 2010). Hoorn et al. (2022) proposed that repeatedly altered environmental conditions in the Pebas system by switching from brackish to freshwater due to marine incursions primarily favored the speciation of taxa living along niche gradients.

Although possibly with greater marine influence, this general appreciation can be extrapolated to the transgressive-regressive cycles of the Paranaense Sea. Indeed, the latter has been considered as a shallow seaway, with temperate-warm and brackish waters, not strictly salty, but with a great contribution of fresh water (Marengo et al., 2019; Pérez et al., 2010).

Considering the habitat preferences of living pelicans from a phylogenetic point of view, it is clear that the truly coastal marine species (*P. occidentalis* and *P. thagus*) have a derived ecology compared with *P. erythrorhynchos* within the New Word clade, as well as the remaining species of the Old World cluster, which are mainly inhabitants of freshwater and/or brackish mudflats (e.g., lakes, lagoons, rivers, wetlands). Likewise, the genetic distances between *P. erythrorhynchos* and *P. occidentalis* + *P. thagus* suggest that the separation of these two clades is evolutionarily long-standing (see Kennedy et al., 2013:219), and this is supported by the Late Miocene occurrence of representatives of both lineages (Fig. 4). Kennedy et al. (2013) hypothesized that the split between both habitats may have resulted in the appearance of the brown plumage as an adaptation to the wear and tear of salt water on feathers. In this context, the dynamic freshwater/brackish paleoenvironments associated with the Pebas megawetland and/or the Paranaense Sea seems to be the ideal scenario for such an evolutionary transition from ancestral freshwater-adapted forms to more derived, strictly coastal, marine forms. Only future findings of more complete fossil specimens can help evaluate with greater depth and accuracy the past diversity and biogeographic history of pelicans.

AUTHOR CONTRIBUTIONS

JIN and MC drafted the manuscript, LMP and DET gathered the geological data, MC and DB made the figures, JIN, MC, DB, JMD, and PB analyzed the paleontological data. All authors edited the manuscript.

LIST OF SUPPLEMENTARY FILES

Supplementary File 1: Figure S1.tif., full geographic ranges of living *Pelecanus* spp. with their superimposed phylogenetic affinities.

Supplementary File 2: Figure S2.tif, comparisons of the quadrate bone in fossil and living New World species of *Pelecanus*.

Supplementary File 3: Table S1.docx, summary of the global fossil record of Pelecanidae and main references.

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