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A PATAGONIAN SWAN (ANATIDAE: ANSERINAE) FROM THE UPPER PLEISTOCENE OF AUSTRAL CHACO (ARGENTINA)

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ABSTRACT – A new material of a Quaternary waterfowl is described here. The implications of this finding, in the context of the dispersal of Anatidae in the past, are discussed. The specimen consists in a partial humerus coming from the Upper Pleistocene of austral Chaco from Santiago del Estero Province, Argentina. The specimen here described belongs to the tribe Cygnini, being larger than most members of the clade. The humerus shows different size than with other members of the tribe Cygnini, being larger than the humeri referred to the Andean goose (*Oressochen melanopterus*), the Sheldgeese of the genus *Chloephaga*, the Comb Duck (*Sarkidiornis sylvicola*), and larger than the Ruddy Shelduck (*Tadorna ferruginea*). However, the humerus have several anatomical characters indicating that it belongs to a basal anserine duck. These combinations of features allow us to assign this fossil to a species of waterfowl: *Coscoroba coscoroba*. This finding, in context with the history of the South American Cygnini, provides new environmental interpretations associated with wetlands, which will be tested in the austral Chaco and Northern Pampa through future multi-proxy studies.

Keywords: Anseriformes bird, goose, *Coscoroba coscoroba*, Quaternary, South America, Santiago del Estero.

RESUMO – Um novo material de uma anátide, uma ave aquática do Quaternário, é descrito aqui. As implicações desta descoberta são discutidas, no contexto da dispersão de Anatidae no passado. O espécime consiste em um úmero parcial proveniente do Pleistoceno Superior do Chaco Austral da Província de Santiago del Estero, Argentina. A morfologia umeral examinada apresenta um tamanho diferente em relação aos de outros membros da tribo Cygnini, embora seja maior do que o úmero referido ao ganso andino (*Oressochen melanopterus*), “sheldgeese” do gênero *Chloephaga*, o pato-pente (*Sarkidiornis sylvicola*), e maior do que o pato-ferrugíneo (*Tadorna ferruginea*). No entanto, o úmero compartilha vários caracteres anatômicos indicando que ele pertence a um pato anserino basal. Essas combinações de características nos permitem atribuir esse registro fóssil a uma espécie de ave aquática, o cisne *Coscoroba coscoroba*. Esta descoberta, em contexto com a história dos Cygnini da América do Sul, fornecerá novas interpretações ambientais associadas às áreas úmidas, que serão testadas no Chaco Austral e no Pampa Norte por meio de futuros estudos multi-proxy.

Palavras-chaves: aves Anseriformes, ganso, *Coscoroba coscoroba*, Quaternário, América do Sul, Santiago del Estero.

INTRODUCTION

Anseriformes is a large and well-known order comprising more than 150 species (approximately 43 genera) of waterfowls. This group is now widely regarded as the sister group to Galliformes, which together form Galloanserae, as the sister group to the rest of Neornithes (Mayr, 2017). The systematic classification of the Anseriformes has been disputed and revised since the recognition of this group (Carboneras, 1992; Livezey, 1996, 1997; Worthy, 2008; Liu *et al.*, 2012). Currently, the order is divided into three extant families: Anatidae (ducks, geese, and swans), Anhimidae (screamers) and Anseranatidae (the magpie geese from Australia) (Worthy *et al.*, 2017). However, some researchers suggest that species of the genus *Dendrocygna* Swainson, 1837 should be considered as an independent true family (Sun *et al.*, 2017).

The fossil record of anatids in South America has expanded notably, although it is still relatively patchy compared to the waterfowl fauna in other regions as Europe and Australia (Mayr, 2017). Several Cenozoic anseriform ducks have been reported in different deposits from Ecuador (Cambell, 1976), Talara in Peru (Campbell, 1979), Argentina (*e.g.* Ameghino, 1895; Tambussi, 1998; Noriega *et al.*, 2008, Cenizo & Agnolin, 2010; Agnolin & Tomassini, 2012) and Uruguay (Tambussi *et al.*, 2005; Acosta Hospitaleche *et al.*, 2021). Nowadays, the Middle–Late Pleistocene fossil taxa are restricted to two subfamilies of Anatidae from Argentina: Tadorninae and Anatinae (Ameghino, 1891; Tonni, 1969; Agnolin, 2006). However, the mention of an Anserinae as *Coscoroba*, together with the Tadornian *Sarkidiornis sylvicola* Ihering & Ihering, 1907, is reported by Ameghino (1891) from post-Pampean deposits of the Holocene (Platean Stage *sensu* Ameghino, 1891) of Lujan in Buenos Aires, still needs to be confirmed.

Recently, a supposed Anserinae was mentioned from the Toropí/Yupoí Formation (Upper Pleistocene) from northern Mesopotamia of Argentina (Corrientes Province, Cuaranta *et al.*, 2019).

For the Upper Pleistocene of the austral Chaco region, several lithostratigraphic units from both principal fluvial basins are recognized, the Dulce and Northern Salado Rivers (Battaglia, 1982; Iriondo, 2010; Vezzosi *et al.*, 2019). Some of these sequences are fossiliferous with aquatic and continental vertebrates (Frenguelli, 1920; 1932; Castellanos, 1924; Vezzosi, 2016; Vallone *et al.*, 2017; Gaudioso *et al.*, 2017; Vezzosi *et al.*, 2017; Albino & Gaudioso, 2018; Brandoni & Vezzosi, 2019; Gaudioso *et al.*, 2019). Along the cut banks of the Dulce River the Tasigasta, Atamisqui and Dos de Mayo geological formations crop out, as well as other fluvial lithostratigraphic units such as the Capellanía Formation (Battaglia, 1982; Iriondo, 2010), that have reported continental Pleistocene vertebrate. Several fossil remains of continental mammals, as well as few reptiles, were recovered from the upper Dulce River catchment, where the Upper Pleistocene units crop out (Chimento & Agnolin, 2011;

Gaudioso *et al.*, 2017; Albino & Gaudioso, 2018); however, bird remains from these two important river basins have not yet been reported.

The aim of this contribution is to report and describe a partial humerus of a waterfowl duck-like bird from the Upper Pleistocene of the austral Chaco (Santiago del Estero Province, Argentina), and to discuss the implications of this finding in the context of dispersal of Neotropical swans during the Pleistocene.

Geographic and geological setting

The fossil comes from 10 km east of Las Termas de Río Hondo city, between Cañada de la Costa and Sotelo localities (27°28'42"S; 64°45'16"W), Río Hondo Department, Santiago del Estero Province, Argentina (Figure 1). The sediments of this area correspond to a Pleistocene–Holocene sequence of units that have been mentioned under different names in the literature, but without an appropriate stratigraphic systematization (Beder, 1928; Battaglia, 1982; Gramajo, 1992; Iriondo, 2010). However, Battaglia (1982) defines at the top of the Salí-Dulce Basin sand levels and in part conglomeratic, with sections with sandy silts, as part of the Capellanía Formation with a Pleistocene age. Recently Iriondo (2010) defined three lithostratigraphic units in the middle-down basin of the Dulce River, the former is referred to the Upper Pleistocene (Tasigasta Formation), while the others are referred to the Middle–Upper Holocene (Atamisqui and Dos de Mayo formations). Although for these latter formations no fossil remains of vertebrate Pleistocene megafauna have reported.

A general section where the fossil comes from, between the Río Hondo dam and the Sotelillos area and around 20 km long, shows the following sequence: from the regular level of the river, upwards, Las Cañas Formation appears first. This unit is constituted by red and brown silty sandstones, with variable thickness between 6 and 10 m, covered in several places by one or two levels of hardened tuff (Battaglia, 1982). This is followed by about 10 m of coarse to medium and fine sands, in part conglomeratic, and grey and beige fine or sandy silts. At the top of this sequence, 2 m of loess covers the whole region. The studied material comes from fluvial levels of coarse to medium and fine sands (Figure 1). These deposits are considered as being part of the Capellanía Formation (Battaglia, 1982), which is Upper Pleistocene (Cohen *et al.*, 2013; ICC, 2020). Moreover, the lithological descriptions of the three Quaternary formations defined by Iriondo (2010) do not coincide with the observed lithology in the area of the finding. On the contrary, this matches with the lithology of the lower member described by Battaglia (1982) for the Capellanía Formation.

MATERIAL AND METHODS

The material under study is housed in the repository collection of the Centro de Interpretación y Conservación del Patrimonio Cultural de Santiago del Estero (Argentina) under the identification CICPSGE 20/21.

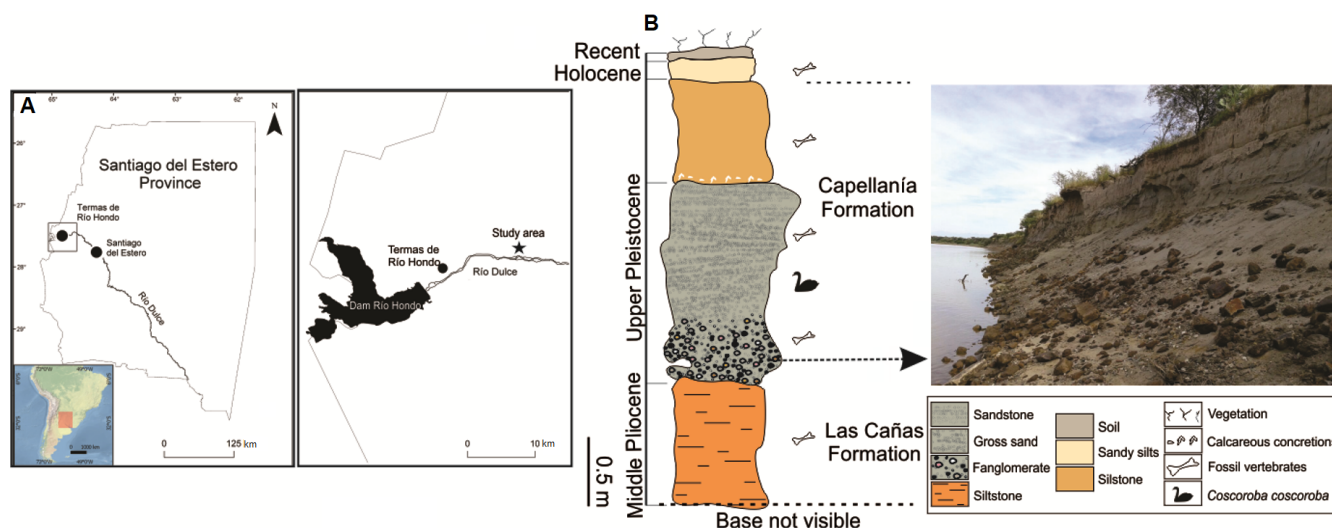


Figure 1. Location map of the fossil record of *Coscoroba coscoroba* from Santiago del Estero Province. **A**, Black star indicates the location of CICPSGE 20/21; **B**, lithostratigraphical sequence of Upper Pleistocene–Holocene deposits in the cliffs of Dulce river from which *Coscoroba* swan (CICPSGE 20/21) was recovered.

A direct comparison of the fossil specimen with the humerus of extant and extinct waterfowls Anatidae of the tribes Cygnini, Tadornini and Anatini was made. We follow the recent systematic revision done by Remsen *et al.* (2020) for the Anatidae *Oressochen melanopterus* (Eyton, 1838) (= *Chloephaga melanoptera* [Eyton, 1838]). Comparative osteological material of extant taxa, deposited in the ornithological collections of the Vertebrate Paleontology Laboratory, Centro de Investigación Científica y de Transferencia Tecnológica a la Producción (CICYTTP, Entre Ríos Argentina), Museo Nacional de Historia Natural de Montevideo (MNHN, Uruguay), the ornithological collection of the Fundación de Historia Natural ‘Félix de Azara’ (CFA-OR, Buenos Aires, Argentina) and the ornithological collection of the Smithsonian Natural History Museum (USNM, USA) were also used to aid in fossil identification.

The list of anatids specimens examined and their institutional collections is as follows: *Oressochen melanopterus* (CICYTTP-AAN 064), *Chloephaga picta* Gmelin, 1789 (CFA-OR 194, MNHN 6306), *Coscoroba coscoroba* (Molina, 1782) (CFA-OR 917, MNHN 7011), *Sarkidiornis sylvicola* (MNHN 7087), *Cygnus atratus* (Latham, 1790) (MNHN 6299), *C. melancoryphus* (Molina, 1782) (MNHN 5482), *C. olor* Gmelin, 1789 (MNHN 7010), *Branta canadensis* (Linnaeus, 1758) (USNM 343185) and *Anas flavirostris* Vieillot, 1816 (MNHN 6154). Comparisons with some fossil anatids taxa were based on Agnolin & Tomassini (2012). The anatomical nomenclature of the humerus follows Baumel & Witmer (1993) and Livezey & Zusi (2006). Measurements were taken with a digital caliper to the nearest 0.01 mm.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Order ANSERIFORMES (Wagler, 1831)

Family ANATIDAE Leach, 1820
Subfamily ANSERINAE Vigors, 1825
Tribe Cygnini Vigors, 1825

Coscoroba Reichenbach, 1852

Coscoroba coscoroba (Molina, 1782)
(Figures 2–3A, 4A)

Referred material. CICPSGE 20/21, distal portion of the humerus of an adult anatid swan (Figures 2–3A, 4A).

Locality and chronostratigraphy. Upper Pleistocene, levels of the lower member of Capellanía Formation (Dulce River between Cañada de la Costa and Sotelo localities, 27°28'42"S; 64°45'16"W), Santiago del Estero Province, Argentina.

Description and comparison. CICPSGE 20/21 does not resemble any another species of the tribes Tadornini or Anatini, and its general morphology is clearly different from that of any of the diving Anatidae. In fact, it has some characters of the tribe Cygnini, clearly recognized in the distal epiphysis of this humerus (Figures 2, 3), including a tuberculum supracondylare dorsale, not forming a process as in *Coscoroba coscoroba*, *Cygnus olor* and *C. melancoryphus*. Moreover, this tuberculum is more conspicuous than in *Sarkidiornis melanotos*, *Oresschen melanopterus*, *Chloephaga picta* and in some diving ducks as *Anas*. Such as in *Coscoroba coscoroba* (CFA-OR 917, MNHN 7011), the tuberculum supracondylare dorsal is present as a shallow facet as in *Cygnus* spp. (Figures 2, 3). Nevertheless, this facet is elongate and shows a prominent tubercle in *S. melanotos*, *O. melanopterus*, and *Ch. picta*. Dorsally, it shows a shallow fovea for the attachment of the m. pronator superficialis, with a subcircular shape as in the extant *C. coscoroba*. Although this fovea is also shallow in the species of *Cygnus*, it shows an enlarged shape. Whereas in *O. melanopterus*, *S. melanotos* it presents a comparatively large and deeper oval shape with a conspicuous rim, even more than in *Ch. picta*.



Figure 2. Humerus of CICPSGE 20/21 assigned to *Coscoroba coscoroba*. **A**, cranial view; **B**, caudal view; **C**, distal view; **D**, lateral view; **E**, medial view. Scale bar = 10 mm.

In cranial view (Figure 2A), CICPSGE 20/21 has an oval fossa for the m. brachialis with conspicuous rims as occurs in adult individuals of *Coscoroba* swan. Although all extant *Cygnus* spp., *Oressochen melanopterus* and *Chloephaga picta* bear a similar morphology for this fossa, but it is deeper in *C. coscoroba*. However, the last two taxa show a much smaller shape as observed in the majority of the Anatidae ducks as in *Anas*. Both condyles are similar in development and shape as in the living *Coscoroba* swan. Although the CICPSGE 20/21 has a more preserved ventral condyle with a subcircular shape (oval in *O. melanopterus* and *Sarkidiornis melanotus*), the preserved area of the dorsal condyle is still very similar to that of *C. coscoroba* (Figures 2A, 3). Between both condyles, there is a large and deep incisura intercondylaris, being shallow in *O. melanopterus* to not clearly distinguishable in *Ch. picta*. On the other hand, *S. melanotus* shows a larger but shallower incisura than that of the taxa compared here.

In caudal view (Figures 2B, 3A), the sulcus m. humerotricipitalis is deep and has conspicuous rims. Although the area for the sulcus m. scapulothoracalis is slightly fragmented, it is distally insinuated. The fossa olecrani is clearly deeper and well-developed as in all Cygnini birds, and much more than in all extant Anserinae and Dedrocygninae ducks. In distal view (Figure 4), the sulcus scapulothoracalis is large, deep and does not extend around the tuberculum supracondylare dorsale as in *Coscoroba coscoroba* and *Branta canadensis*, while in all species of *Cygnus* this groove distally surrounds the dorsal condyle. Moreover, the dimensions of the humerus analyzed here are congruent with those observed in *Coscoroba* swan and differing from other humeral dimensions of the tribes Cygnini, Anatini and Tadornini; and being bigger than the humerus of the Andean goose *O. melanopterus*, the sheldgeese *Chloephaga* spp., the American comb duck *Sarkidiornis sylvicola*, and bigger than that of the shelduck *Tadorna ferruginea* (Table 1).

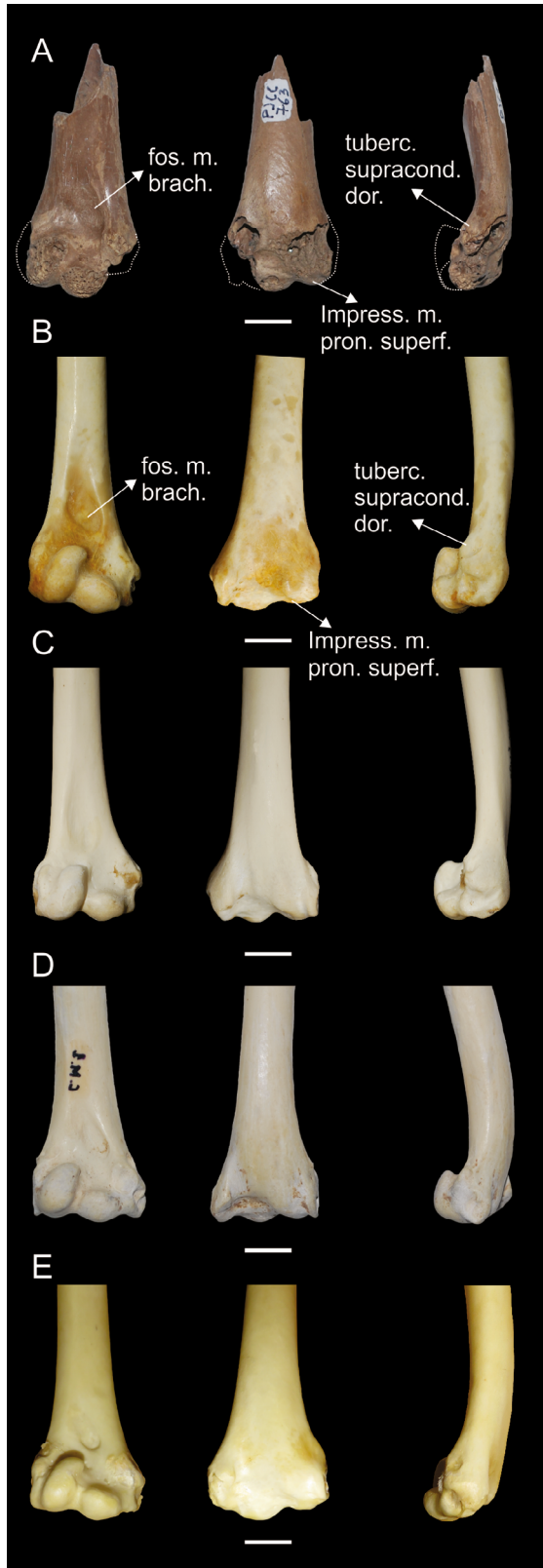


Figure 3. Humerus of the fossil *Coscoroba* swan compared with the humeri of living Anatidae in cranial, caudal and medial views. **A**, CICPSGE 20/21; **B**, *Coscoroba coscoroba* (MNHN 7011); **C**, *Cygnus melancoryphus* (MNHN 5482); **D**, *Oressochen melanopterus* (CICYTTP-AAN 064); **E**, *Chloephaga picta* (CFA 194). **Abbreviations:** **fos. m. brach.**, fossa m. brachialis; **Impress. m. pron. superf.**, Impressio m. pronator superficialis; **tuberc. supracond. dor.**, tuberculum supracondylare dorsale. Scale bars = 10 mm.

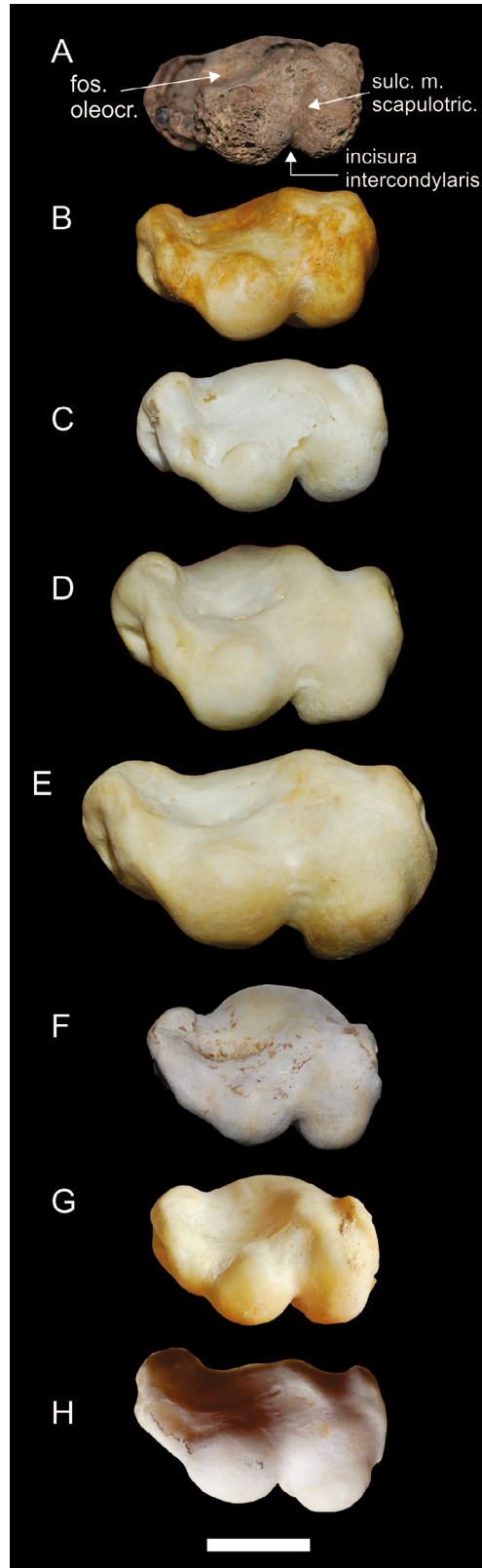


Figure 4. Distal view of the left humeri of living Anatidae compared with CICPSGE 20/21. **A**, CICPSGE 20/21. **B**, *Coscoroba coscoroba* (MNHN 7011). **C**, *Cygnus melancoryphus* (MNHN 5482). **D**, *C. atratus* (MNHN 6299). **E**, *C. olor* (MNHN 7010). **F**, *Oressochen melanopterus* (CI). **G**, *Chloephaga picta* (MNHN 6309). **H**, *Branta Canadensis* (USNM 343185). **Abbreviations:** **fos. oleocr.**, fossa oleocranialis; **sulc. m. scapulotric.**, sulcus scapulotricitalis. Scale bar = 10 mm.

Taphonomic approach. Although not common as other vertebrates, bird remains are relatively frequent in the fossil record of the Pleistocene, with taxa with different guilds such as aquatic, raptor or scavenger birds being represented (Campbell, 1979; Tambussi *et al.*, 2005; Cenizo & Agnolin, 2007; Cenizo & Tassara, 2013; Tambussi & Degrange, 2013; Jones *et al.*, 2021). However, most of the ecological and environmental information from avian fossil remains is lost, because of the unavoidable post-mortem destruction of the bones, or because detailed descriptions of its precise stratigraphic context are not known (Behrensmeyer *et al.*, 2003). In addition, it's possible that the abundance of wing elements, as in this case, is a characteristic of the natural context of deposition (Erickson, 1987). According to this, Livingston (1989) and Cruz (2005) have suggested that the bone structure and functional anatomy of birds are important factors affecting the representation of the skeletal parts in an environment of preservation. Thus, the presence of an aquatic bird from fluvial levels of coarse to medium and fine sands, with known ecological requirements preserved within stratigraphic settings, also allows obtaining information from the taphonomic features on the fossil and from the sedimentological aspects of the fossil bearing deposit. Thus, the new finding provide tools for a better understanding of the paleoenvironment at the time of its deposition.

The potential preservation of bird bones is related to the type of environment they live in, and their burial mainly depends on the substrate where the bones are deposited (Bickart, 1984; Lyman, 1994; Cruz, 2008; Lopes *et al.*, 2019). Fluvial environments, such as continental wetlands, exhibit an important potential for the preservation of fossil birds; in fact, aquatic birds are better represented in the fossil record than the ground-terrestrial species (Mitchell, 2015). The preservation of the specimen CICPSGE 20/21 was probably favored by its association with a depositional environment (*i.e.* fluvial deposits) and the sedimentological features of the deposits where the fossil comes from (Battaglia, 1982) that improved its preservation, suggesting a likely rapid burial due to increased deposition of sediment by the environment. Considering the prevailing fluvial origin of the sediments, and the evidence of fluvial transport, it is possible that there was a short distance fluvial transport for this remain.

On the other hand, fossil remains of vertebrates that come from the Dulce River Basin; represent a mixture of diverse taxa, mostly Pleistocene mammals, with different ages and states of preservation (Gramajo, 1992; Powell & Deraco, 2003; Alberdi *et al.*, 2008; Chimento & Agnolin, 2011; Gaudioso *et al.*, 2017; Albino & Gaudioso, 2018). These records suggest that the depositional environment is composed of remains from different sources with varying taphonomic histories and probably subject to several episodes of exhumation-transport-burial (Behrensmeyer, 1982; Montalvo *et al.*, 2008). Some of these remains (*e.g.* Chimento & Agnolin, 2011; Gaudioso *et al.*, 2017), as the *Coscoroba* swan, show several signs of abrasion (*e.g.* sharp broken edges in the shaft and abraded irregular surfaces in its distal end). The abrasion, present in the distal end of this fossil, in general suggests fluvial transport

(Aslan & Behrensmeyer, 1996; Montalvo *et al.*, 2013). Then the mixture of abraded and non-abraded bones could indicate that CICPSGE 20/21 was subjected to different flow regimes (*e.g.* velocity of the water current).

Shape is also a major factor influencing the transport of bone remains. Bones with irregular shapes have larger surfaces, which increases the potential for transport (Coard & Dennell, 1995). The fragmented areas of CICPSGE 20/21 are located in structures around its shaft, which suggest that it was transported in a manner similar to forelimbs of some terrestrial vertebrates (Hanson, 1980; Behrensmeyer *et al.*, 2003). The distal end exhibits a more extensive abrasion, which is eroded on the edges of its condylae and only is broken in the epicondyle area (Figure 2). This implies that as the current moved the humerus, it probably rolled uniformly as a cylindrical body, which would have distributed evenly the breaking and abrasion (Lopes & Ferigolo, 2015). The large form and dimension of this bone probably facilitated its entrainment by flow and its fragmentation would have been the result of several impacts with the bottom of the fluvial environment during its transport (Trapani, 1998; Fernández-Jalvo & Andrews, 2003; Montalvo *et al.*, 2013; Tomassini & Montalvo, 2013).

This novel taphonomic approach, together with the environmental interpretations reported here where the fossil come from, allow us to refer a paleoenvironment associated to wetlands. However, this claim would need to be tested in the austral Chaco and Northern Pampa regions through future multi-proxy studies. On the other hand, this record suggests here a broader geographic distribution during the Late Pleistocene as observed nowadays.

DISCUSSION

Woolfenden (1961) proposed that *Coscoroba* is closely related to other swans (*Cygnus*) than to any other waterfowl, despite some unusual behavioral and morphological characters (Worthy *et al.*, 2017). Based in our results, the general morphology of CICPSGE 20/21 closely resembles the humeri of the living South American forms of the Tribe Cygnini than any other known anatid tribes of ducks. In turn, it is apparent that this fossil is clearly distinguished from large swans, middle geese and small ducks, resembling the osteological morphology of the humerus that Cygnini species possess, which resembles a basal Anserinae duck.

Additionally, living *Coscoroba coscoroba* have several other features in the humerus that are different from all other geese (*i.e.* conspicuous tuberculum supracondylare dorsale, shallow tuberculum supracondylare ventrale; deep fossa m. brachialis). Anatomical combination of characters recognized here (Figures 2A–D, 3), together with the linear measurements employed (Table 1), reveal an affinity with the size and shape of the humerus of a basal *Coscoroba* swan, as follows: (i) fossa m. brachialis large and deeper; (ii) fossa olecrani deep and developed; (iii) condyles ventralis humeri distally developed; (iv) condyles dorsalis humeri with oval shape and separated by a deep incisura intercondylaris; and (v) conspicuous

Table 1. Humeral measurements (in mm) of CICPSGE 20/21 and living Anatidae. **Abbreviations:** **w-dist**, distal width; **w-hc**, medial humeral condyle width; **w-shaft-fb**, latero-medial width of the shaft at level of the Fossa m. brachialis; **d-shaft-fb**, craneo-caudal width of the shaft at level of the Fossa m. brachialis; **p**, preserved.

| taxon / measurements | w-dist | w-hc | w-shaft-fb | d-shaft-fb |
|---|----------------|---------------|------------|------------|
| CICPSGE 20/21 | 21.33 <i>p</i> | 8.25 <i>p</i> | 14.15 | 8.28 |
| <i>Coscoroba coscoroba</i> (MNHN 7011) | 23.98 | 11.19 | 13.41 | 8.14 |
| <i>Oressochen melanopterus</i> (AAN 064) | 22.13 | 8.53 | 13.10 | 8.91 |
| <i>Chloephaga picta</i> (MNHN 6306) | 19.75 | 7.45 | 12.40 | 7.14 |
| <i>Sarkidiornis melanotos</i> (MNHN 7087) | 19.43 | 6.69 | 11.37 | 7.47 |
| <i>Cygnus melancoryphus</i> (MNHN 5482) | 23.40 | 8.54 | 12.67 | 7.32 |
| <i>Branta canadensis</i> (USNM 343185) | 26.25 | 9.47 | 20.37 | 17.94 |

tuberculum supracondylare dorsale. As mentioned, it shares several characters that indicate that it belongs to a swan and more specifically related to *Coscoroba coscoroba*.

In an overall context for the Quaternary, no anatid swans remains are known for the Middle–Upper Pleistocene in South America. Remains attributed to a *Coscoroba* were reported by Ameghino (1891) from sediments regarded as Holocene (Platan South American Stage/Age, Cione *et al.*, 2015) in the Pampean plains from Argentina, but without detailed descriptions and precise stratigraphic context, that clearly needs to be confirmed. Currently, another possible record of a basal anserine has recently been reported from Upper Pleistocene deposits from northern Mesopotamia, although a taxonomic assignment other than that of being an Anserinae has not yet been proposed (Cuaranta *et al.*, 2019).

Amongst the Patagonian anatids, only *Coscoroba* swan has a greater distribution range than the *Chloephaga* and *Oressochen* species of sheldgeese described in northward areas (Bulgarella *et al.*, 2014). Its distribution includes a wide range (Figure 5) from Tierra del Fuego to central Chile and northern Argentina, including winters in northern Paraguay, Uruguay, southeastern Brazil, and the Bolivian Chaco (Carboneras & Kirwan, 2020). It is a common species in all austral open lowlands from Patagonia, even in the Malvinas Islands as a frequent visitor where it occasionally breeds (Madge & Burn, 1988; Woods & Woods, 1997; Carboneras & Kirwan, 2020), living in wetland areas including swamps, shallow lagoons, freshwater marshes, and lakes with abundant vegetation (Fjelds  & Krabbe, 1990; Denaly & Scott, 2006).

Fossil bird data have been valued in paleoenvironmental reconstructions (S nchez-Marco, 1999; Tambussi *et al.*, 2005; Prassack *et al.*, 2017). However, several factors as autoecology, behavior, phylogenetic constrains and anthropogenic impacts in living species distribution must be taken into account and the reliability of studies based on actualist principles have methodological constraints (Nieto & Rodr guez, 2003).

In this sense, the presence of the extant *Coscoroba* swan as a fossil record from the Upper Pleistocene in the northwestern of Argentina could be important from a paleoenvironmental standpoint. This taxon could be regarded as an indicator of wetland environments, if its fossils are usually found together

with aquatic taxa such as other anatids, ardeids and even associated with other vertebrates such as fish (*e.g.* Olson & Rasmussen, 1986; Rasmussen *et al.*, 1987; Diederle & Noriega, 2013). Although the *Coscoroba* swan is a permanent austral breeder in the cold Patagonian steppe environments, some individuals migrate to lower latitudes (*c.* 25° S) in winter (Carboneras & Kirwan, 2020). Extant reports of background of this swan outside of its austral range must be considered for a paleoecological interpretation of the record presented in this contribution. Even, this swan was reported in different environments, and there are extant records as a regular visitor to wetlands at the northernmost of its natural range of distribution (around 15°–17°S, Figure 5), between the Pantanal/Cerrado of Brazil (National Park of Chapada dos Guimar es, State of Mato Grosso do Sul, Sick, 1997; Silva, 2018) and the Bolivian Chaco (Camatindi lagoon, Santa Cruz de la Sierra, Tobias & Seddon, 2007). All this information suggests that some species of swans, as *C. coscoroba* here, could not have a restricted ecological tolerance, and therefore should not be considered as a reliable paleoclimatic fossil indicator as it was properly applied for some Quaternary geese remains (Tambussi *et al.*, 2005).

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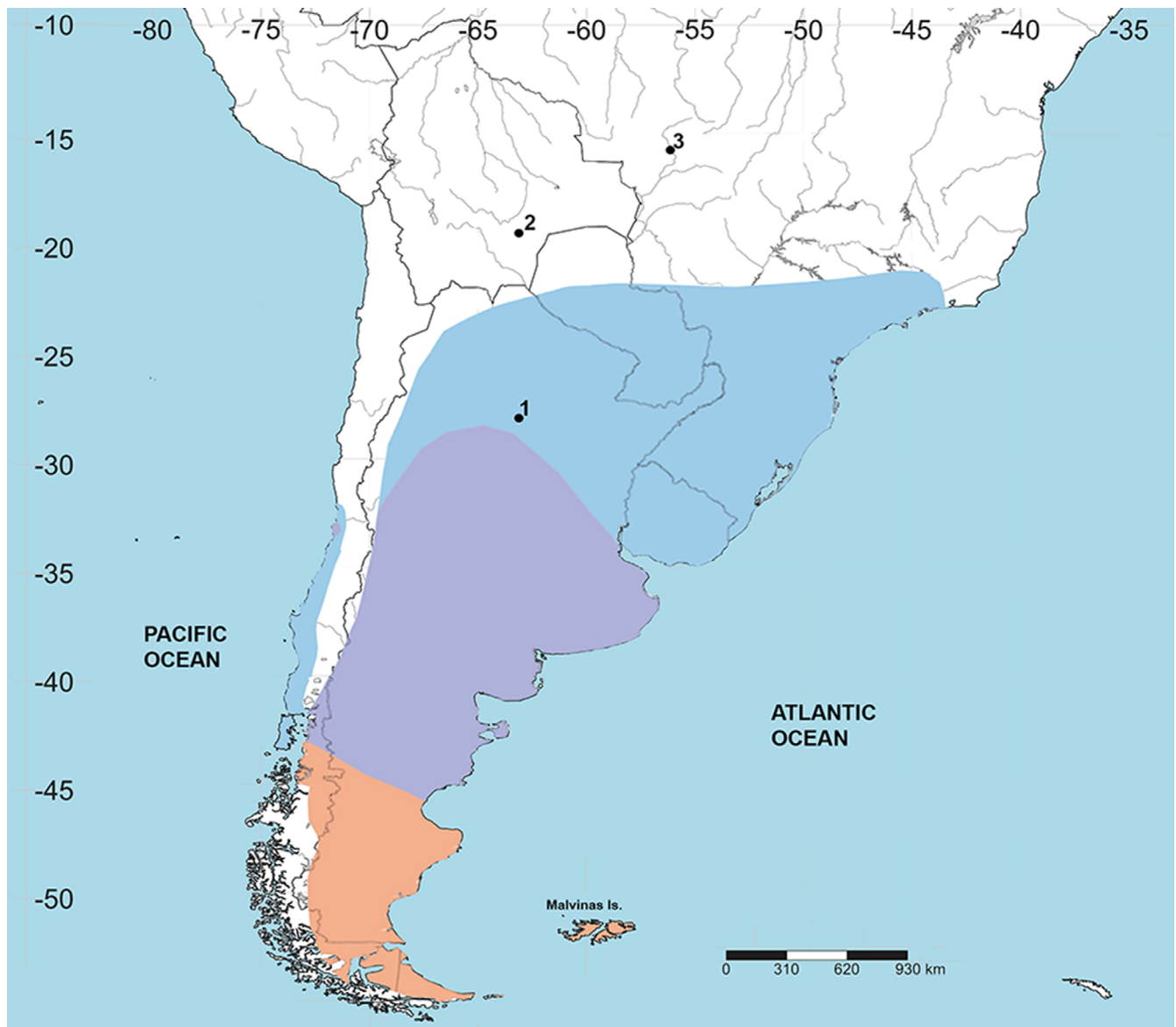


Figure 5. Map showing of the distribution of *Coscoroba* swan. Lotation of CICPSGE 20/21 (1), living northernmost records as a regular visitor from Bolivian Chaco (2) and a regular vistor of Pantanal/Cerrado of Brazil (3). Orange shading represents the natural range of breeding distribution, purple shading indicates its distribution as a resident all year round, while blue shading indicates its occasional breeding distribution.

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