

Pleistocene record of *Chloephaga* Eyton, 1838
(Anseriformes: Anatidae) in the Argentine Pampas,
with the description of a new species

Federico L. AGNOLÍN, Gerardo P. ÁLVAREZ HERRERA &
Rodrigo TOMASSINI



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ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

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Submitted on 6 March 2023 | Accepted on 11 March 2024 | Published on 21 June 2024

urn:lsid:zoobank.org:pub:DA010DA2-D34B-4ABD-AE36-DF1782751589

Agnolin F. L., Álvarez Herrera G. P. & Tomassini R. 2024. — Pleistocene record of *Chloephaga* Eyton, 1838 (Anseriformes: Anatidae) in the Argentine Pampas, with the description of a new species. *Comptes Rendus Palevol* 23 (18): 241-255. <https://doi.org/10.5852/cr-palevol2024v23a18>

ABSTRACT

The genus *Chloephaga* Eyton, 1838, consisting of four species that breed in Patagonia, encompasses anatids endemic to South America. Despite their prominence in the present-day avifauna, these species have left behind a limited fossil record. The aim of the present contribution is to describe *Chloephaga* fossils coming from Middle Pleistocene levels (San José Sequence) cropping out at Bajo San José site, southwestern Buenos Aires Province, Argentina. The specimens are referred to three different taxa, including a new species, *Chloephaga dabbenei* n. sp., a smaller but indeterminate taxon, which is also probably a new species, and the extant species *C. picta* (J.F.Gmelin, 1789). The newly described species is notably large, falling within the upper size range observed in males of *C. picta*. The tarsometatarsus is straight-shafted with poorly divergent distal trochleae, features that are correlated with cursorial habits, that are absent in other members of *Chloephaga*. The co-occurrence of three species of the genus *Chloephaga* is registered nowadays in the Argentine Patagonia and in the southeast of Buenos Aires Province, when they migrate during the winter season.

KEY WORDS

Sheldgoose,
Tadorninae,
fossil diversity,
Buenos Aires Province,
Quaternary,
new species.

RÉSUMÉ

Signalement pléistocène du genre *Chloephaga* Eyton, 1838 (Anseriformes: Anatidae) dans la Pampa argentine, avec la description d'une nouvelle espèce.

Le genre *Chloephaga* Eyton, 1838 comprend des anatidés endémiques d'Amérique du Sud. Le genre est composé de quatre espèces qui se reproduisent en Patagonie. Malgré leur importance dans l'avifaune existante, les archives fossiles de ce genre sont rares. L'objectif de la présente contribution est de décrire les fossiles de *Chloephaga* provenant des niveaux du Pléistocène moyen (séquence de San José) affleurant sur le site de Bajo San José, au sud-ouest de la province de Buenos Aires, en Argentine. Les spécimens sont référés à trois taxons différents, dont une nouvelle espèce, *Chloephaga dabbenei* n. sp., un taxon plus petit mais indéterminé, qui est aussi probablement une nouvelle espèce, et l'espèce existante *C. picta* (J.F.Gmelin, 1789). La nouvelle espèce décrite ici est très grande et se situe dans la fourchette supérieure de taille corporelle des membres mâles de *C. picta*. Le tarsométatarse est à tige droite avec des trochlées distales peu divergentes, caractéristiques corrélées à la course, qui sont absentes chez les autres membres de *Chloephaga*. La cooccurrence de trois espèces du genre *Chloephaga* est signalée de nos jours en Patagonie argentine et dans le sud-est de la province de Buenos Aires, lorsqu'elles migrent pendant la saison hivernale.

MOTS CLÉS
Tadorne,
Tadorninae,
diversité fossile,
province de
Buenos Aires,
Quaternaire,
espèce nouvelle.

INTRODUCTION

The genus *Chloephaga* Eyton, 1838 includes goose-like anatids characteristic of southern South America, represented by four living species, *C. picta* (J.F.Gmelin, 1789), *C. poliocephala* P.L.Sclater, 1857, *C. rubidiceps* P.L.Sclater, 1861, and *C. hybrida* (Molina, 1782). All of them are migratory, and the last two are restricted to near-shore environments (de la Peña 2020). The migration occurs between their breeding site in Patagonia to northern locations during the winter season, reaching the southern region of the Buenos Aires Province in Argentina (Narosky & Di Giacomo 1993), and the Maule Region in Chile, as is the case of *C. picta* and *C. poliocephala*. Anthropogenic activities, including consumption and agriculture, have strongly affected *Chloephaga* populations, which results in dramatic population decline, as occurs with the endangered species *Chloephaga rubidiceps* (Giusti *et al.* 2020).

The finding of extinct members of the genus *Chloephaga* in Quaternary beds of southern South America is common (Tonni & Deschamps 2001; Agnolín 2006; Álvarez Herrera *et al.* 2022). Degrange *et al.* (2006), based on a tibiotarsus, highlighted the presence of a very large representative of *Chloephaga* from the lower Upper Pleistocene of central Buenos Aires Province, in Argentine Pampas. Specimens closely related or belonging to the extant species *Chloephaga picta* have been reported from Pleistocene and Holocene paleontological and archeological sites from Argentina, Uruguay, and Chile (Tonni 1970; Tambussi 1989; Latorre *et al.* 1991; Deschamps & Borromei 1992; Tambussi & Noriega 1996; Tambussi *et al.* 2005; Agnolín 2006; Sallaberry *et al.* 2015). The pre-Quaternary record only includes the extinct species “*Chloephaga*” *robusta* Tambussi, 1995, coming from lower Pliocene levels of Buenos Aires Province (Tambussi 1998); however, this taxon is based on a distal ulna of uncertain generic position (Agnolín 2006).

The aim of the present contribution is to describe in detail and re-evaluate postcranial elements belonging to *Chloephaga*

coming from Middle Pleistocene levels of the San José Sequence, cropping out at Bajo San José site (southwestern Buenos Aires Province, Argentine Pampas) (Fig. 1). These specimens were previously mentioned in an abstract by Tonni & Deschamps (2001), who recognized two possible species, one of them larger than the largest extant species of the genus (*C. picta*). Deschamps (2003), in her unpublished PhD thesis, briefly described and figured part of these materials, which were referred to two different species. Here we identify a new species, as well as a smaller innominate *Chloephaga*, and the extant species *C. picta*. This study provides novel information on the diversity, distribution, and evolution of this genus during the Pleistocene.

MATERIAL AND METHODS

The specimens here described were recovered from the classical fossiliferous site Bajo San José (38°29'12.10”S, 61°46'59.60”W), located at southwestern Buenos Aires Province (Fig. 1). The bearing levels correspond to pencon-temporaneous fluvial facies included in Lower section of the San José Sequence (Borromei 1990; Zavala & Quattrocchio 2001). From an environmental viewpoint, the deposits of this site represent a system of braided rivers with representation of channels, bars, and floodplains (Borromei 1990; Deschamps & Borromei 1992). Based on the mammalian record, particularly the presence of the ctenomyid rodent *Ctenomys kraglievichi* Rusconi, 1930, these levels were assigned to the Middle Pleistocene (Verzi *et al.* 2004; Deschamps 2005; Deschamps & Tomassini 2016).

The avifauna from this site, including the remains of *Chloephaga* studied herein, was mentioned and partially described in previous works. There are representatives of the orders Anseriformes, Gruiformes, and Passeriformes (Tonni & Deschamps 2001; Deschamps 2003; Deschamps & Tomassini 2016).

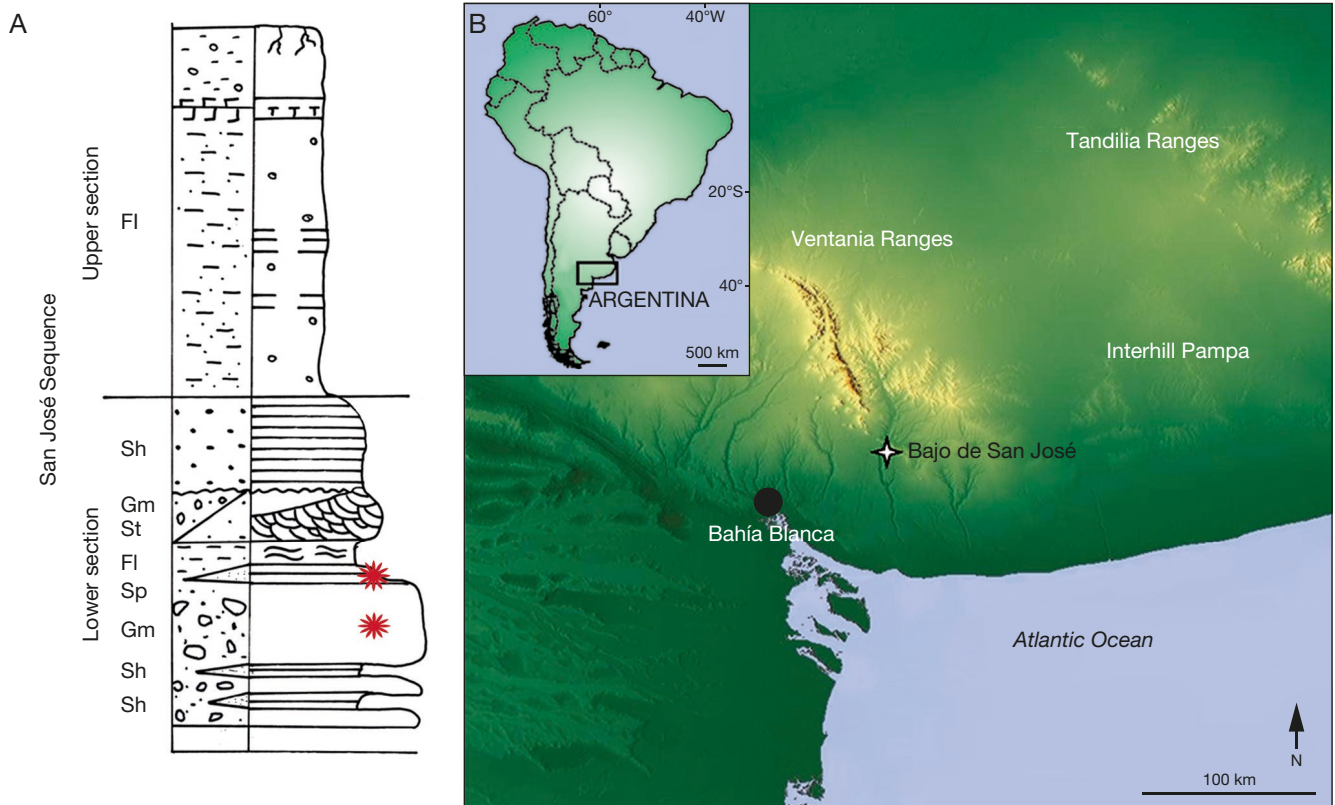


FIG. 1. — **A**, Geographic and stratigraphic setting. Stratigraphic profile of San José Sequence at this site, highlighting the facies distribution and the bearing levels of the studied specimens; modified from Deschamps 2003; **B**, map showing the location of Bajo San José site.

The taxonomic scheme follows Livezey (1997). We consider four valid species within *Chloephaga* following recent works (*C. picta*, *C. poliocephala*, *C. rubidiceps*, and *C. hybrida*). On the contrary, “*Chloephaga melanoptera* (Eyton, 1838), a very divergent species in anatomical traits and behaviour, is excluded (see Osinaga Acosta & Martin 2018); this species was referred to the monotypic genus *Oressochen* Bannister, 1870, which represents the sister taxon of *Neochen* Oberholser, 1918 (Bulgarella *et al.* 2014).

Most diagnostic traits for anatic clades are taken and modified from Woolfenden (1961). Anatomical terminology follows Baumel & Witmer (1993), but non-latinized, and with some modifications made by Livezey & Zusi (2006). Comparisons include the following extant and extinct species: *Chloephaga picta* (CFA-OR-194, CFA-OR-1480, CFA-OR-1597, MLP-PV-OR 14479; MLP-PV-OR 568; MACN-OR-68581, MACN-OR-68728, MACN-OR-68740), *Chloephaga rubidiceps* (MACN-OR 4978), *Chloephaga poliocephala* (MACN-OR 68401; MACN-OR 68575), *Oressochen melanopterus* (Eyton, 1838) (CICYTTP-AAN 064), and *Neochen pugil* (Winge, 1887) (ZMUC 12084, ZMUC 12115). Information from *C. hybrida* comes exclusively from the bibliography, which corresponds to the length of the tarsus taken from collection skins (Phillips 1916). Additional measurements were taken from the work of Blake (1977), Lefèvre (1989), and Watanabe (2017).

INSTITUTIONAL ABBREVIATIONS

CFA-OR	Ornithology collection, Félix de Azara Natural History Foundation, Buenos Aires;
CICYTTP-AAN	Vertebrate Paleontology Laboratory of the Center for Scientific Research and Technological Transference to Production, Diamante;
MACN-OR	Ornithology collection, Argentine Museum of Natural Sciences “Bernardino Rivadavia”, Buenos Aires;
MLP-PV-OR	Osteological collection of extant birds, La Plata Museum, La Plata;
PV-UNS	Vertebrate paleontological collection, National University of the South, Bahía Blanca;
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen.

SYSTEMATIC PALEONTOLOGY

Order ANSERIFORMES Wagler, 1831
 Family ANATIDAE Leach, 1820
 Subfamily TADORNINAE Reichenbach, 1850

Genus *Chloephaga* Eyton, 1838

REMARKS

The specimens here reported can be referred to the genus *Chloephaga* by having: 1) coracoid with a notch on the furcular facet and foramina behind the furcular facet (shared

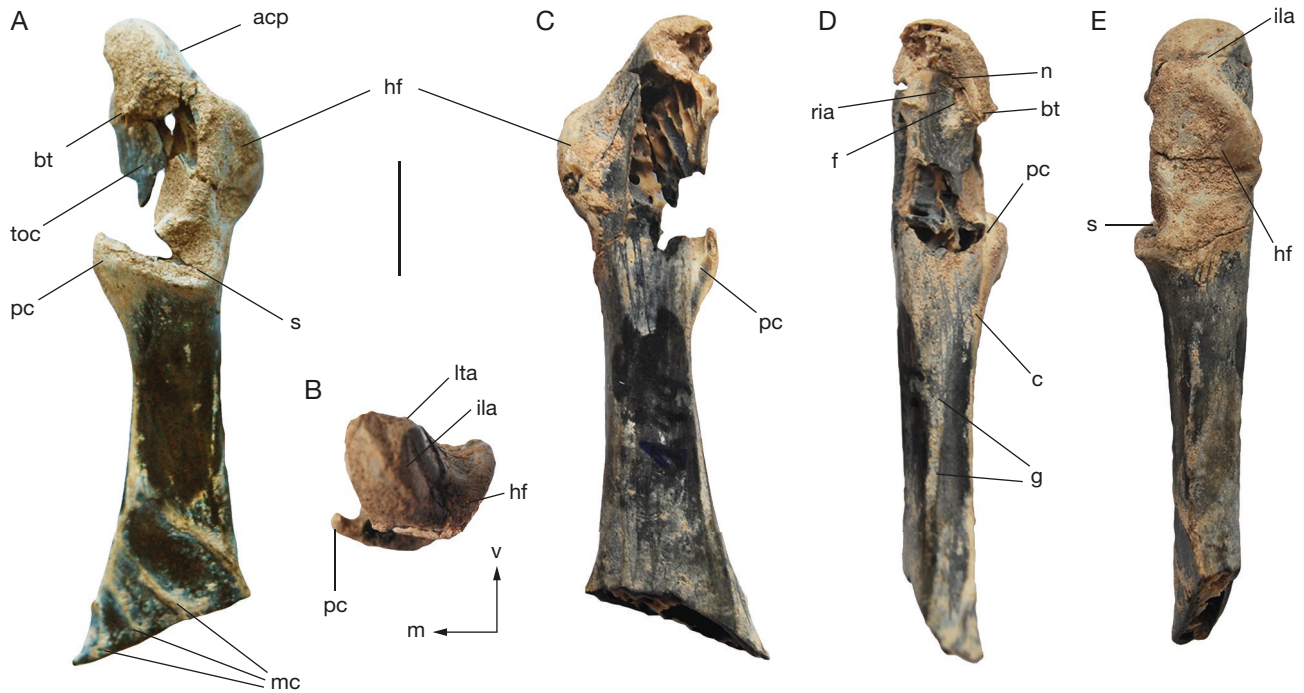


FIG. 2. — Omal half of the right coracoid of *Chloephaga dabbenei* n. sp. (PV-UNS-149), in: **A**, dorsal; **B**, distal; **C**, ventral; **D**, medial; **E**, lateral views. Abbreviations: **acp**, acrocoracoid process; **bt**, brachial tubercle; **c**, crest; **f**, foramina; **g**, groove of the coracoid neck; **hf**, humeral facet; **ila**, impressio ligament acrocoracohumeralis; **lta**, lateral tubercle of acrocoracoid; **m**, medial; **mc**, muscular crest; **n**, notch on the furcular facet; **pc**, procoracoid process; **ria**, recessus infra-acrocoracoides; **s**, scapular facet; **toc**, triosseal canal; **v**, ventral. Scale bar: 1 cm.

with *Neochen* and *Alopothen* Stejneger, 1885 [Woolfenden 1961; Álvarez-Herrera *et al.* 2022]), cranially divergent *impressio ligamentum acrocoracohumeralis* (Álvarez-Herrera *et al.* 2022), shallow triosseal canal (notably deep in other geese, such as *Oressochen* [Woolfenden 1961; Álvarez-Herrera *et al.* 2022]), prominent lateral tubercle of the acrocoracoid (modified from Woolfenden 1961; Álvarez-Herrera *et al.* 2022), humeral articular surface not laterally deflected (in contrast to *Oressochen*); 2) humerus with enlarged and globose humeral head (Miller 1937), elevated internal tuberosity (this tuberosity is even larger in *Oressochen* [Woolfenden 1961]), very weak capital ridge and the shaft compressed adjacent to the angle of the deltoid crest but well-rounded from there (Worthy 2009; modified from Miller 1937), depression for the m. triceps notably broad extends far laterally and proximally, so that it is overhung by the crest of the head (Miller 1937), distally curved humeral shaft (Miller 1937), high elevation and flat surface for the anterior articular ligament (Woolfenden 1961); 3) ulna with distal end having external cotyla projects farther distally than the others (Miller 1937); 4) femur with narrowing of the popliteal excavation due to inflation of the lateral margin, resulting in a deep and narrow trough, patellar groove transversely expanded (Miller 1937); and 5) tarsometatarsus with posterior surface proximal to the trochleae wide and flattened, trochlea II strongly medially deflected (Miller 1937), trochlea II lies farther distal and it extends beyond the base of the external intertrochlear notch, and relatively robust shaft (the shaft measures between 7.2-7.9% of the total length of the bone; *c.* 6.7% in *Neochen*

[Woolfenden 1961]). This combination of characters clearly distinguishes *Chloephaga* species from closely related taxa such as *Oressochen* and *Neochen*.

Chloephaga dabbenei n. sp.
(Figs 2-9)

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TYPE MATERIAL. — **Holotype**. Argentina • PV-UNS-54, left tarso-metatarsus with slightly abraded hypotarsus.

REFERRED MATERIAL. — **Argentina** • PV-UNS-149, right coracoid lacking sternal end; PV-UNS-364, left ulna lacking proximal end; PV-UNS-562, proximal end of left ulna; PV-UNS-428, left femur. The specimens are referred to *C. dabbenei* n. sp. because they came from the same site, are congruent in most characters and they are notably robust and large, falling among the largest specimens of *C. picta*.

STRATIGRAPHIC AND GEOGRAPHIC PROVENANCE. — Facies Gm (holotype) and Sp (referred materials), Lower Section of the San José Sequence. Middle Pleistocene. Argentina, Buenos Aires province, Bajo de San José.

DIAGNOSIS. — Large species of the genus diagnosable on the basis of the following unique combination of characters: 1) very elongate tarsometatarsus with proximal end showing a thick, prominent, and proximodistally extended (more than one third of the entire bone length) surface for the lateral collateral ligament; 2) distal trochleae subparallel to each other and trochlea II strongly posteriorly retracted; and 3) articular surfaces of distal trochleae proximodistally elon-

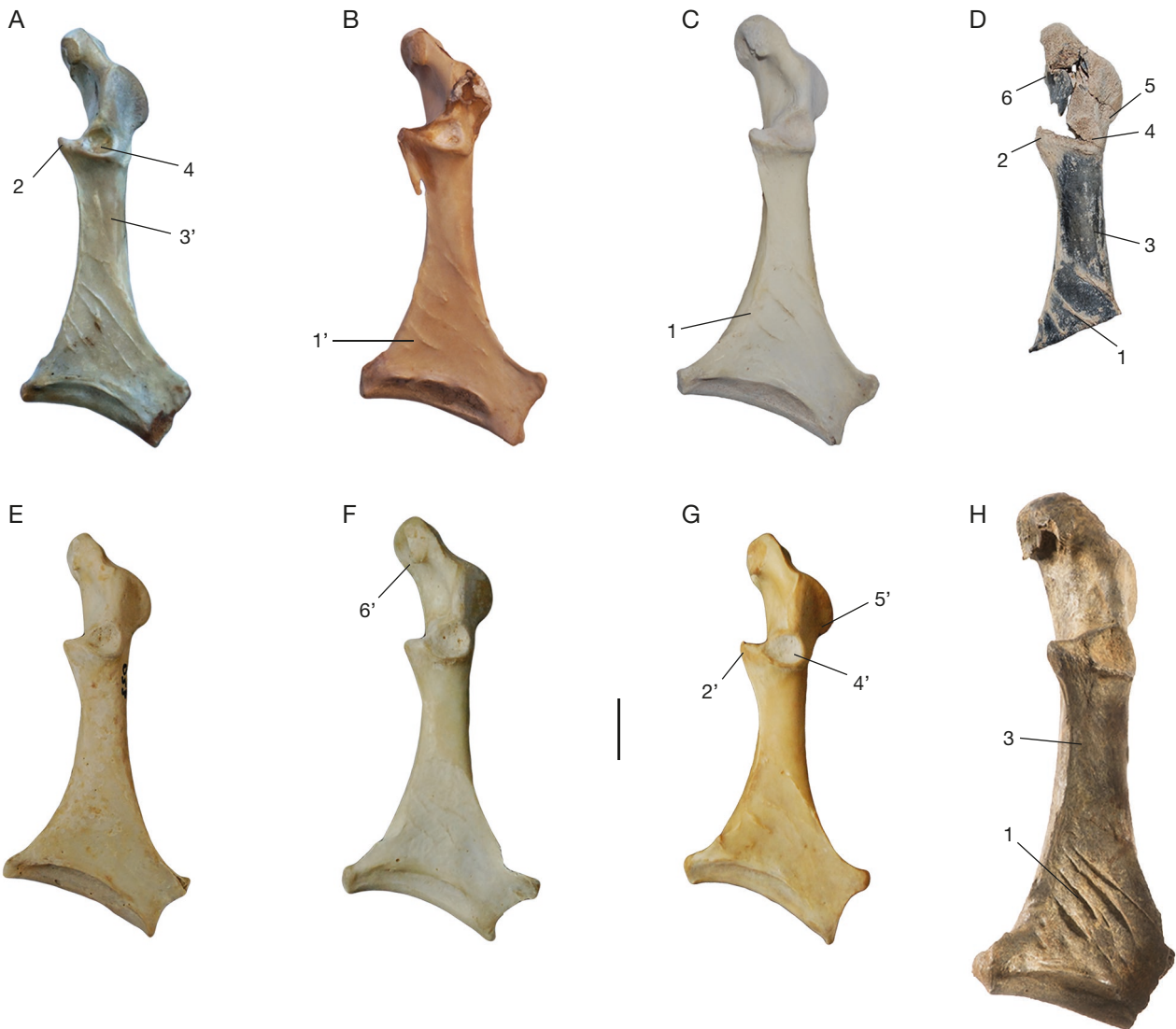


FIG. 3. — Comparison of coracoids between *Chloephaga* Eyton, 1838 species and other tadornine taxa: **A**, *Chloephaga poliocephala* P.L.Sclater, 1857; **B**, *C. rubidiceps* P.L.Sclater, 1861; **C**, *Oressochen melanopterus* (Eyton, 1838); **D**, *C. dabbenei* n. sp. (PV-UNS-149); **E-G**, *C. picta* (J.F.Gmelin, 1789): **E**, CFA-OR-1480; **F**, CFA-OR-194; **G**, CFA-OR-1597; **H**, *Neochen pugil* (Winge, 1887), in dorsal view. Distinctive traits are marked as follows: **1**, well marked muscular crests; **1'**, weakly developed muscular crests; **2**, long and distally deflected procoracoid process; **2'**, stout and straight procoracoid process; **3**, wide coracoidal neck; **3'**, narrow and elongated coracoidal neck; **4**, small and subtriangular scapular facet; **4'**, big and subcircular scapular facet; **5**, distal end of the humeral facet gradually merged with the coracoidal neck; **5'**, distal end of the humeral facet abruptly angled with the coracoidal neck; **6**, deep recessus infraacroracoides; **6'**, shallow recessus infraacroracoides. Scale bar: 1 cm.

gated (particularly evident on the elongate subrectangular contour of trochlea III in posterior view).

ETYMOLOGY. — The specific epithet honors the great ornithologist Roberto Dabbene (1864-1938).

LOCALITY. — Argentina, Buenos Aires province, Bajo de San José.

DESCRIPTION AND COMPARISONS

All the specimens assigned to *Chloephaga dabbenei* n. sp. are notably large and robust (Table 1).

The coracoid shows a notably thick neck (much thicker than any known species). *Chloephaga poliocephala* has the narrowest and more elongated neck among species of the genus. In medial view the coracoid neck is notably thick and

shows a proximodistally extended and obliquely oriented groove, a feature shared with *C. poliocephala* (see “groove of the coracoid neck” in Figure 2). Muscular crests are more marked than in other species (e.g. *C. poliocephala*, *C. picta*, *C. rubidiceps*), but similar to *Oressochen*. The triosseal canal is poorly excavated and non-pneumatic. The scapular facet is relatively small and subtriangular in contour, similar to other species, but different from the more excavated and rounded condition present in *C. picta*.

The humeral facet is very wide, as occurs in *C. picta*. In contrast to the latter, the distal end of the facet gradually merges with the coracoidal neck. The procoracoid process is long and distally deflected, as occurs in *C. poliocephala*, but not in *C. picta*. In *C. dabbenei* n. sp. the procoracoid is also



FIG. 4. — Left ulnae of *Chloephaga dabbenei* n. sp.: **A, B, E**, PV-UNS-562; **C, D, F**, PV-UNS-364. **A, D**, ventral; **B**, anterior; **C**, dorsal; **E**, proximal; **F**, distal views. Abbreviations: **bi**, brachial impression; **cs**, concave surface; **ct**, carpal tubercle; **dc**, dorsal cotyle; **duc**, dorsal ulnar condyle; **f**, nutritious foramen; **ras**, radial articular surface; **vc**, ventral cotyle; **vuc**, ventral ulnar condyle. Scale bar: 2 cm.

slightly medially oriented. The recessus infra-acrocoracoideus is deeply marked, as is present in *C. poliocephala*, but not in *C. picta* and *C. rubidiceps*.

The ulna is notably robust. The radial articular surface of the dorsal cotyle is relatively transversely wide, but does not extend distally, as occurs in *C. picta*, in which it is tongue-like. A relatively wide and concave surface (see Fig. 4) is located between the ventral cotyle, and proximal to the ventral collateral ligament tuberosity, similar to *C. picta*, whereas in other species it is relatively small, shallower and not well-defined. The brachial impression is also more defined, deeper, and more proximodistally elongated than in *C. picta*. The nutritious foramen of the shaft is located at the proximal half of the bone, whereas it is more distally positioned in *C. poliocephala*. The distal end of the bone distinguishes from other species in being more robustly built. The distal crest in *C. rubidiceps* is notably sharp and extensive, which differs from the condition observed in other species of the genus.

The femur shows the anterior and posterior muscular lines more marked than other species, with the possible exception of *C. poliocephala*. Proximal to the posterior intermuscular line exists a marked muscular surface, as occurs in *C. picta*, whereas it is absent in *C. rubidiceps* and *C. poliocephala*. Both *C. rubidiceps* and *C. poliocephala* show a narrower (especially towards the distal end of the bone) and more curved shaft; these features are especially evident in *C. rubidiceps*. In *C. dabbenei* n. sp. and *C. picta* the shaft is straighter and thicker than in other species. The surface for the gastrocnemius muscle is present but smooth, as occurs in *C. picta*, whereas in *C. rubidiceps* and *C. poliocephala* is much prominent and well-separated from the shaft.

The tarsometatarsus is elongated and shows non-divergent distal trochleae. The proximal end of the bone in anterior view shows a deeply excavated extensor groove with poorly defined tubercles of the muscle tibialis cranialis, as occurs in *C. picta*. In other species, the anterior surface of the bone is

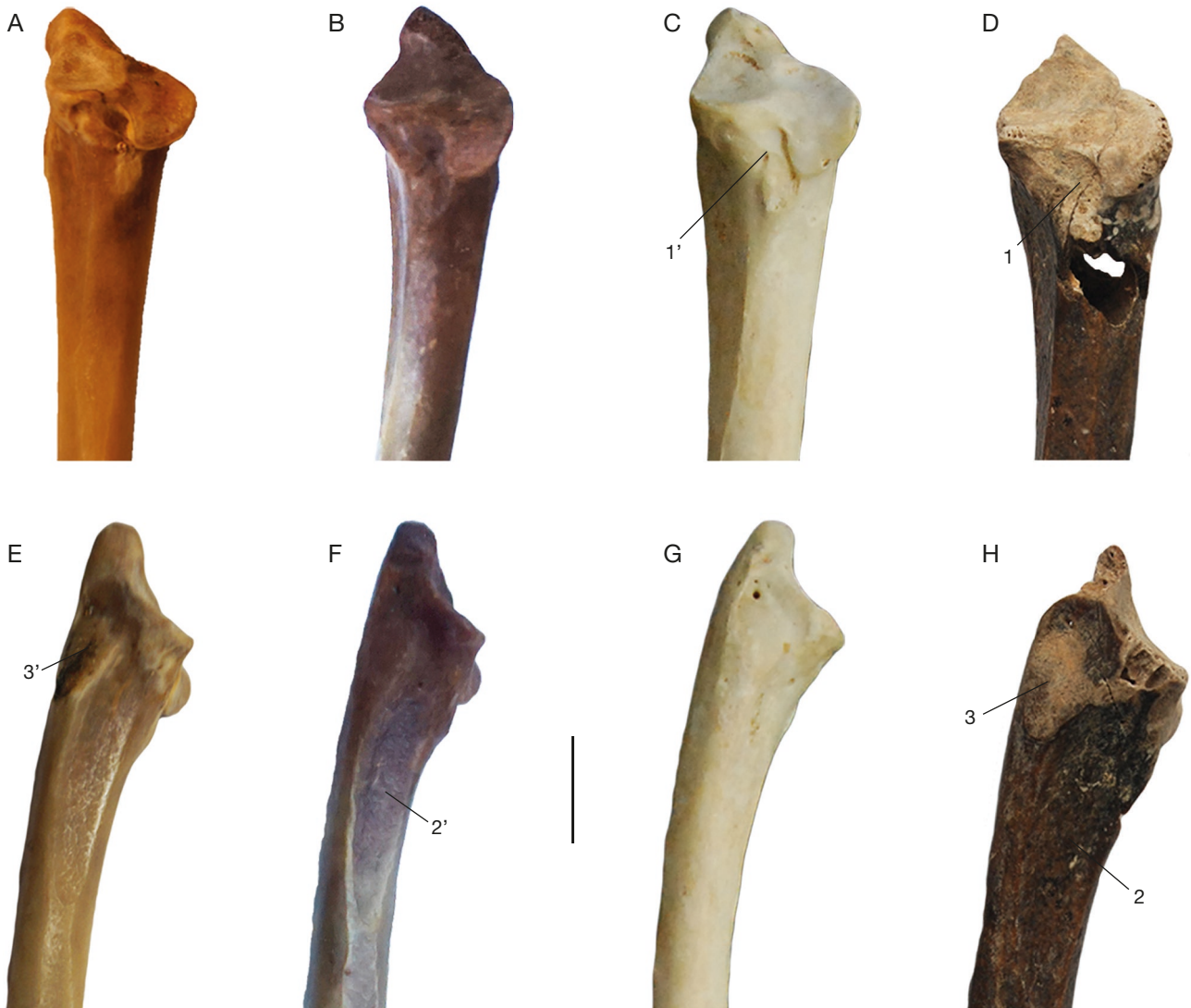


FIG. 5. — Comparison of ulnae between *Chloephaga* Eyton, 1838 species and other tadorphine taxa: **A, E**, *Chloephaga rubidiceps* P.L.Sclater, 1861; **B, F**, *C. poliocephala* P.L.Sclater, 1857; **C, G**, *C. picta* (J.F.Gmelin, 1789); **D, H**, *Chloephaga dabbenei* n. sp. (PV-UNS-562). **A-D**, anterior views; **E-H**, ventral views. Distinctive traits are marked as follows: **1**, transversely wide radial articular surface; **1'**, distally extended, tongue-like radial articular surface; **2**, deep and elongated brachial impression; **2'**, shallower and shorter brachial impression; **3**, well marked posterior concave surface; **3'**, shallow and poorly defined posterior surface. Scale bar: 1 cm.

TABLE 1. — Comparison between *Chloephaga dabbenei* n. sp., PV-UNS-104 (*Chloephaga picta* (J.F.Gmelin, 1789)), PV-UNS-394 (*Chloephaga* sp.), from Bajo San José site, and extant tadorphine taxa. Abbreviations: **FL**, femur length (the greatest length from the femoral trochanter to the lateral condyle); **HDW**, distal width of the humerus (the greatest width between epicondyles); **HPW**, humerus proximal width (the greatest distance between the dorsal and ventral tubercles); **L/W T**, tarsometatarsus ratio (the length of tarsometatarsus divided by the width between the most distal tip of the medial surface of trochlea II and the most distal tip of the lateral surface of trochlea IV); **TL**, tarsometatarsus length (the greatest length from the eminentia intercotylaris to trochlea III). Measurements of *Oressochen melanopterus* (Eyton, 1838) are taken from Watanabe (2017); and of *C. hybrida* (Molina, 1782) are taken from dry skins, based on Phillips (1916), Blake (1977), and Lefèvre (1989). *, Specimens of the subspecies *C. picta leucoptera* exclusive of the Malvinas Islands, and measured on dry skins by Blake (1977) yielded tarsus length values that range from 92 to 95 mm. Regrettably, no skeletal specimens of this form were available for present study; **, Lefèvre (1989) cited a putative specimen of *C. picta* having the exceptional size of 96.7 mm. of maximum metatarsal length. This specimen was housed in a private collection and is no longer available for further analysis, and thus, its measurements are not taken into consideration here.

Taxon	HPW	HDW	FL	TL	L/W T
<i>Chloephaga dabbenei</i> n. sp.	–	–	89.9	96.3	4.96
PV-UNS-104 (<i>Chloephaga picta</i> (J.F.Gmelin, 1789))	26.6	–	–	–	–
PV-UNS-394 (<i>Chloephaga</i> sp.)	–	16.8	–	–	–
<i>Chloephaga picta</i>	25.4-27	21.4-23.6	73-89.3	76.3-93**, **	4.38-4.77
<i>Chloephaga poliocephala</i> P.L.Sclater, 1857	25.0	20.0-20.1	69.3-71.6	69.6-71.1	4.42
<i>Chloephaga hybrida</i> (Molina, 1782)	–	–	–	58-76	–
<i>Chloephaga rubidiceps</i> P.L.Sclater, 1861	23.6-24.6	19.4-20.2	75.4-75.6	60-76.8	4.74
<i>Oressochen melanopterus</i> (Eyton, 1838)	–	–	75.2	80.6	–

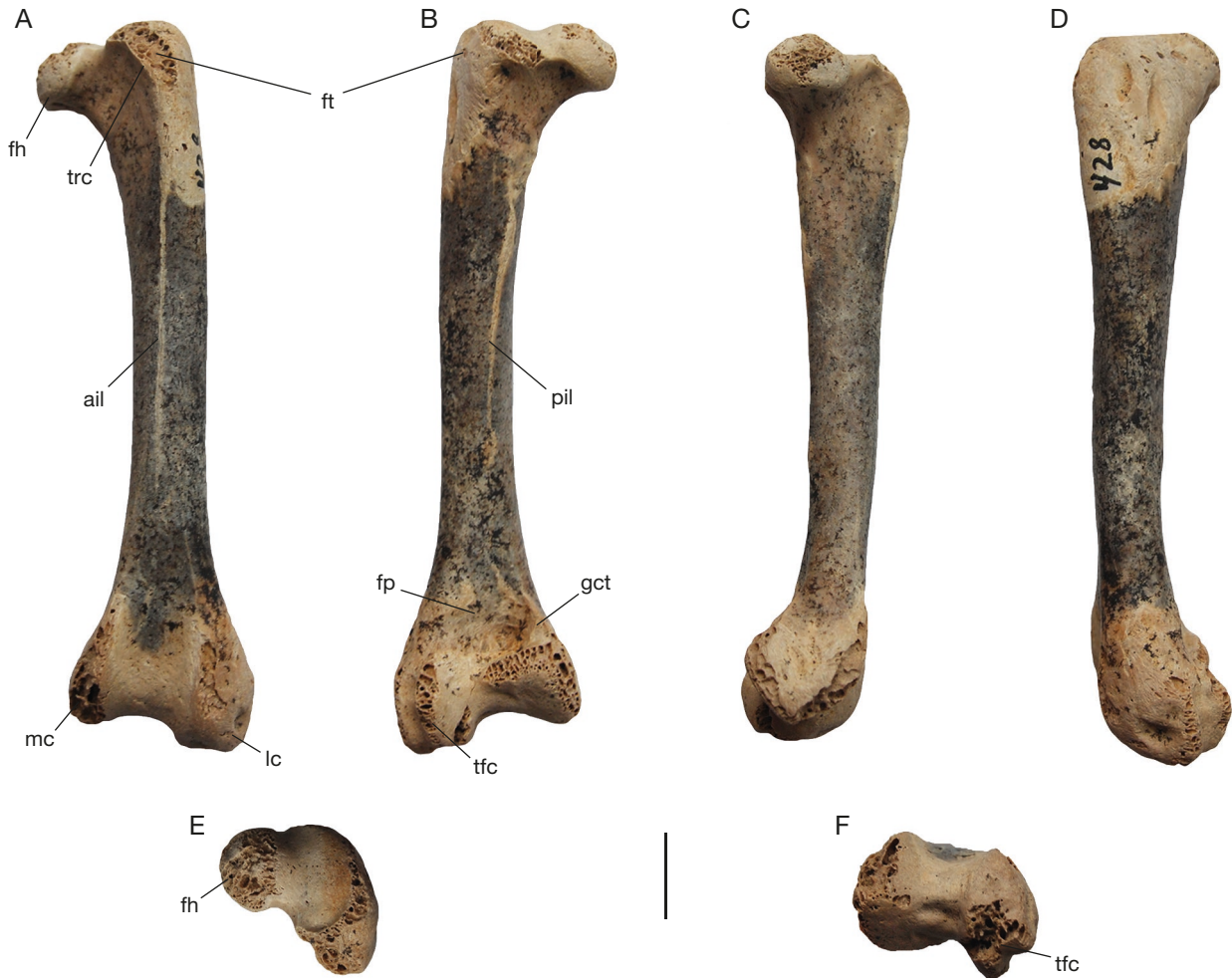


FIG. 6. — Left femur of *Chloephaga dabbenei* n. sp. (PV-UNS, 428): **A**, anterior; **B**, posterior; **C**, medial; **D**, lateral; **E**, proximal; **F**, distal views. Abbreviations: **ail**, anterior intermuscular line; **fh**, femoral head; **fp**, fossa poplitea; **ft**, femoral trochanter; **gct**, gastrocnemial tubercle; **lc**, lateral condyle; **mc**, medial condyle; **pil**, posterior intermuscular line; **tfc**, tibiofibular crest; **trc**, trochanteric crest. Scale bar: 1 cm.

poorly excavated and is nearly flat, with the tubercles of the muscle tibialis cranialis very well-developed and well-defined. Distal trochleae are notably proximodistally elongate. In posterior view the articular surface of the III trochlea is notably elongate and subrectangular in contour, a condition that resembles *C. poliocephala* and *C. rubidiceps*. Distal trochleae are much more robust and divergent in *C. picta*. The trochlea II is notably posteriorly retracted, in contrast to other *Chloephaga* species. Trochlea IV shows the posterolateral wing proximodistally extended and prominent, differing from the much shorter exhibited by *C. picta*. The tarsometatarsus clearly differs from that of *Oressochen*, which shows very short and divergent distal trochleae, and with posterior wings of II and IV trochleae reduced (Fig. 9). In *C. dabbenei* n. sp. the distal vascular foramen is very wide and ellipsoidal in contour, as occurs in *C. picta*, whereas in *C. rubidiceps* and *C. poliocephala* it is smaller and subcircular in contour.

REMARKS

Chloephaga dabbenei n. sp. is a very distinctive species of the genus. It is much larger than extant species (with exception

of *C. picta*) and has very elongated hindlimb, particularly the tarsometatarsus. In this sense, tarsometatarsus with straightness and uniformity of the shaft throughout its length, and with elongated trochleae that are in line with the shaft (poorly spreading), are features associated with cursorial habits (Miller 1937). This morphology differs from the much more robust and divergent distal trochleae present in other members of the genus *Chloephaga*, as well as the closely related taxa *Neochen jubata* (Spix, 1825) and *Oressochen melanopterus*.

In spite that *C. dabbenei* n. sp. may fall within the range of the largest specimens of *C. picta* (see Table 1), there are several features that clearly distinguish both taxa. The coracoid of *C. dabbenei* n. sp. shows a notably thick coracoidal neck that is medially excavated by a groove (the neck is very narrow and the groove is absent in *C. picta*), relatively small and subtriangular-shaped scapular cotyla (wide, deep and rounded cotyla in *C. picta*), distal end of humeral facet gradually merges with the coracoidal neck (forms a marked step in *C. picta*), procoracoid process long and distally deflected (much shorter and straight in *C. picta*), recessus infra-acrocoracoideus deeply marked (shallow in *C. picta*), ulna with radial articular surface

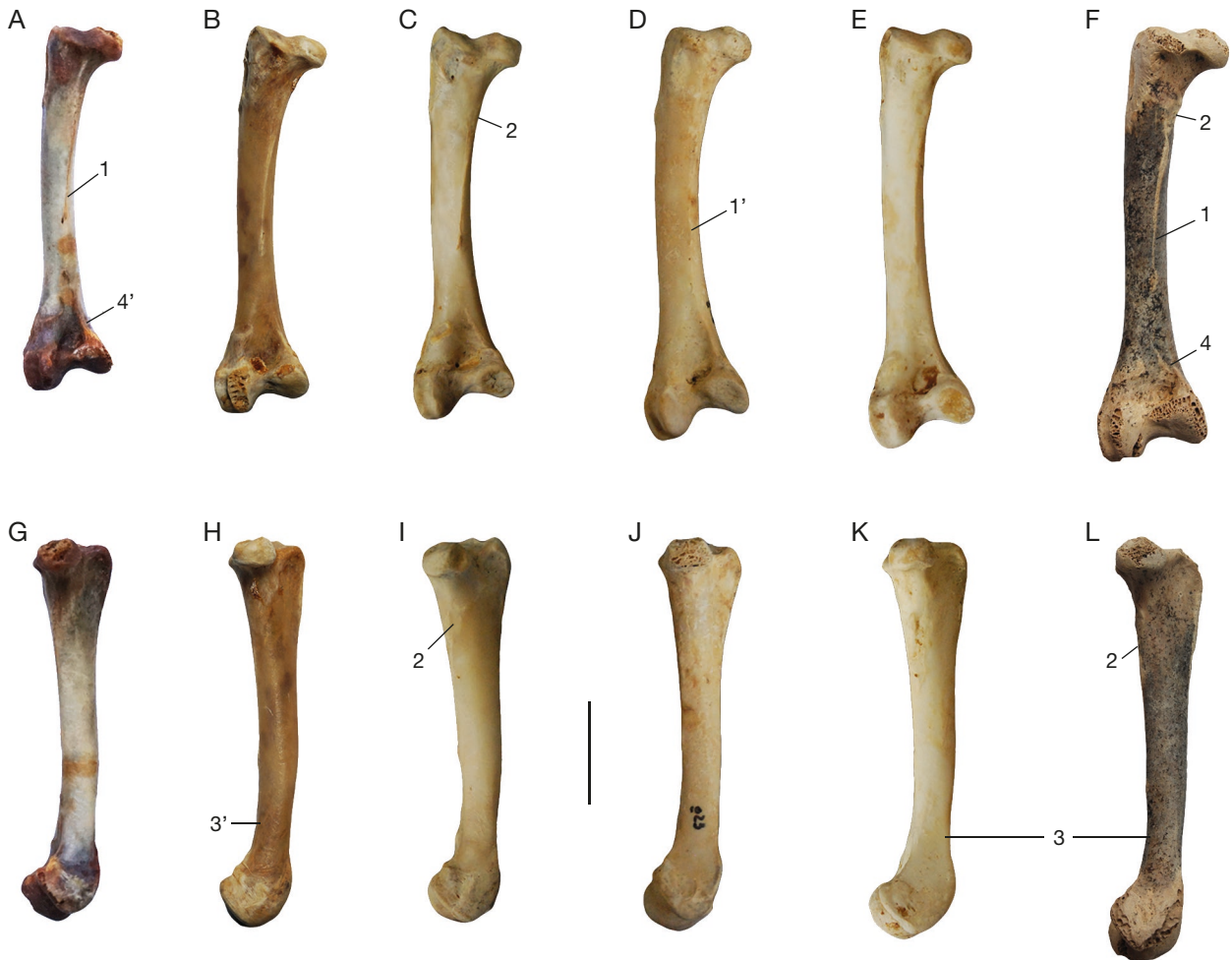


FIG. 7. — Comparison of femora between *Chloephaga* Eyton, 1838 species and other tadornine taxa: **A, G**, *Chloephaga poliocephala* P.L.Sclater, 1857; **B, H**, *C. rubidiceps* P.L.Sclater, 1861; **C-E, I-K**, *C. picta* (J.F.Gmelin, 1789): **C, I**, CFA-OR-1597; **D, J**, CFA-OR-1480; **E, K**, CFA-OR-194; **F, L**, *Chloephaga dabbenei* n. sp. (PV-UNS-428). **A-F**, posterior views; **G-L**, medial views. Distinctive traits are marked as follows: **1**, well marked intermuscular lines; **1'**, poorly marked intermuscular lines; **2**, marked proximal posterior muscular surface; **3**, thick and straight shaft; **3'**, curved and narrow shaft; **4**, smooth surface of the gastrocnemius muscle; **4'**, prominent surface of the gastrocnemius muscle. Scale bar: 2 cm.

of the dorsal cotyle distally straight (in *C. picta*, is distally extended and tongue-like), brachial impression is also more defined, deeper, and more proximodistally elongated than in *C. picta*, tarsometatarsus with distal trochleae notably proximodistally elongate, in particular the articular surface of the III trochlea in posterior view is notably elongate and subrectangular in contour (distal trochleae are much more robust and divergent in *C. picta*), the trochlea II is notably posteriorly retracted (in contrast to other *Chloephaga* species, including *C. picta*, in which the trochlea II is nearly in line with trochlea IV), and trochlea IV with posterolateral wing proximodistally extended and prominent (much shorter in *C. picta*). This combination of characters, and particularly distal tarsometatarsus shape, clearly distinguish *C. dabbenei* n. sp. from *C. picta* and any known species belonging to the genus.

The ulna of the extinct Pliocene species “*Chloephaga*” *robusta* is much larger than that of *C. dabbenei* n. sp. and shows a more extensive distal crest, separated by a very deep groove and that it smoothly contacts the ulnar shaft (Tambussi 1998). This combination of characters, that separates “*Chloephaga*”

robusta from *C. dabbenei* n. sp., are reminiscent to the genera *Neochen* and *Alopochen* (Agnolín 2006).

Neochen pugil is an extinct goose coming from Upper Pleistocene of Lagoa Santa, Minas Gerais State, Brazil (Winge 1887; Nascimento & Silveira 2020). In spite that it was referred to the genus *Neochen*, *N. pugil* is similar to *C. dabbenei* n. sp. in having relatively gracile tarsometatarsus, coracoid with strong transverse muscular lines, and thick coracoid neck with a medially located and obliquely oriented groove. However, it differs in having much larger size (tarsometatarsus total length is 13.5 cm, when compared with the 11 cm of *C. dabbenei* n. sp.), tarsometatarsus with proportionally short distal trochleae, a more strongly divergent II trochlea and coracoid with pneumaticity below brachial tuberosity and a more deeply excavated triosseal canal. Taking into account the similarities between *C. dabbenei* n. sp. and *Neochen pugil*, it is not improbable that, in fact, the latter belongs to the genus *Chloephaga*.

Neochen debilis (Ameghino, 1891) is a species described by Ameghino (1891) on the basis of an incomplete tarsometatarsus coming from the Pleistocene of Buenos Aires province. It

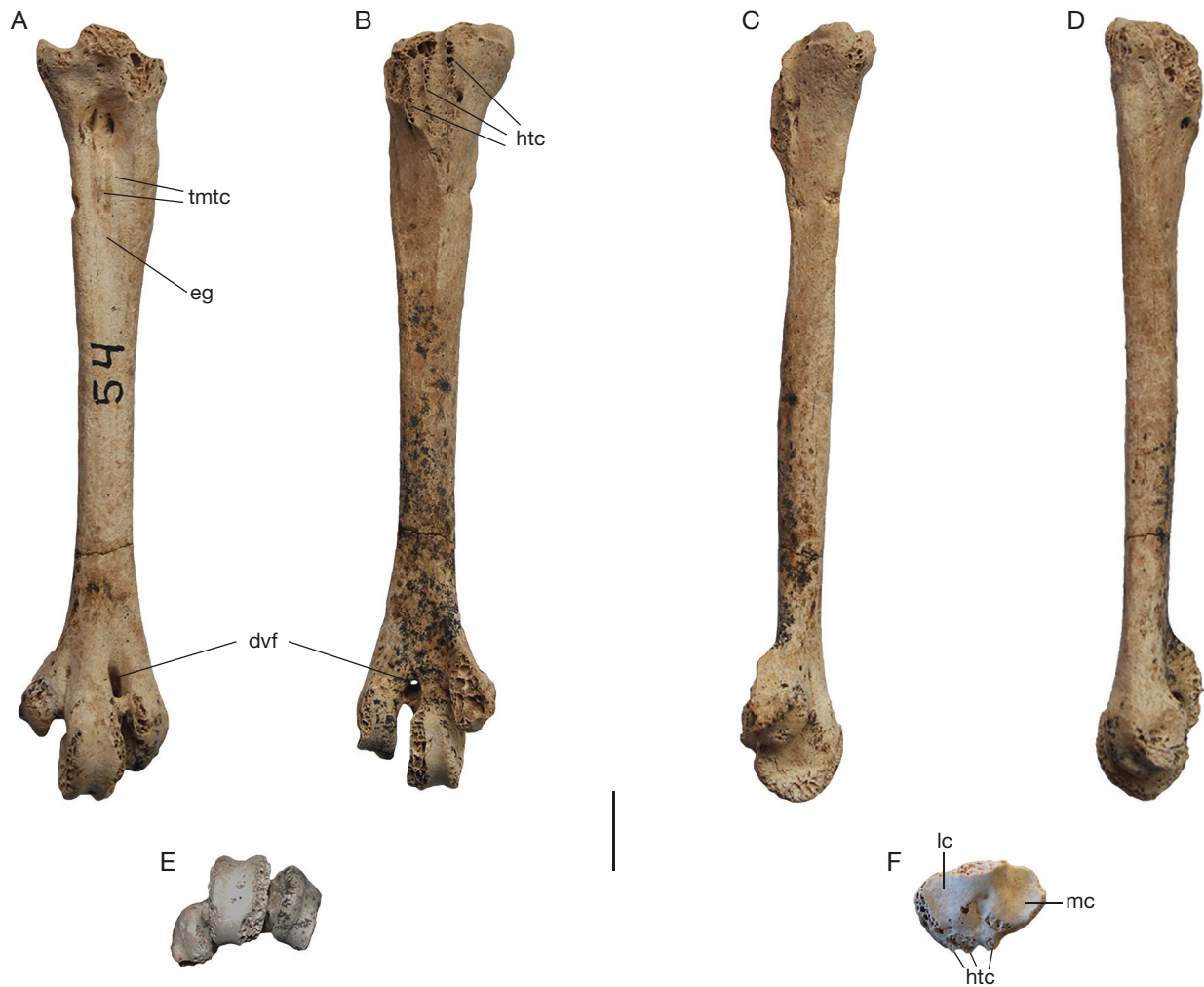


FIG. 8. — Left tarsometatarsus of *Chloephaga dabbenei* n. sp. (PV-UNS-54): **A**, anterior; **B**, posterior; **C**, medial; **D**, lateral; **E**, distal; **F**, proximal views. Abbreviations: **dvt**, distal vascular foramen; **eg**, extensor groove; **htc**, hipotarsal crests; **lc**, lateral cotyle; **mc**, medial cotyle; **tmtc**, tubercles of the muscle tibialis cranialis. Scale bar: 1 cm.

was originally included under the genus *Chenalopex* Stephens, 1824 and lately regarded as belonging to *Neochen* (Agnolín 2006). The description made by Ameghino is very brief and lacks figures, and the material in which the species is based is currently lost. However, Ameghino points that the maximum width between the distal trochleae of the tarsometatarsus is of 8 mm, being much smaller than the 18 mm of *C. dabbenei* n. sp.

Chloephaga picta (J.F.Gmelin, 1789)
(Figs 10F-J; 11)

Anas picta J.F.Gmelin, 1789: 504.

REFERRED MATERIAL. — PV-UNS-104, proximal end of left humerus.

STRATIGRAPHIC PROVENANCE AND AGE. — Facies Sp, Lower Section of the San José Sequence. Middle Pleistocene.

DESCRIPTION AND COMPARISONS

The proximal end of the humerus in the different species of *Chloephaga* is very difficult to distinguish. The only clear dif-

ference resides in the shape of the pneumotricipital fossa. In posterior view, PV-UNS-104 and specimens of *C. picta* show a wider and more widely exposed fossa respect to the other species of the genus. *Chloephaga poliocephala* shows a flat surface that distally surrounds the pneumatic foramen of the pneumotricipital fossa is very wide and is well proximally delimited by a nearly continuous crest (interrupted and poorly defined in the other species). The pneumotricipital fossa is much smaller in *Oressochen*. In PV-UNS-104 and *C. picta*, the bicipital crest is proximodistally expanded and mediolaterally extended, whereas in *C. rubidiceps* it is very wide, but shorter and it is distally delimited by a marked concavity. In summary, PV-UNS-104 is indistinguishable in size and anatomical features from the extant *C. picta*, and consequently is referred to this taxon.

Chloephaga sp.
(Fig. 10A-E)

REFERRED MATERIAL. — PV-UNS-394, right humerus lacking proximal end.



FIG. 9. — Comparison of tarsometatarsi between *Chloephaga* Eyton, 1838 species and other tadornine taxa: **A, H**, *Chloephaga poliocephala* P.L.Sclater, 1857; **B, I**, *C. rubidiceps* P.L.Sclater, 1861; **C, J**, *Oressochen melanopterus* (Eyton, 1838); **D, K**, *C. picta* (J.F.Gmelin, 1789): **D**, CFA-OR-194; **K**, CFA-OR-1480; **E, L**, *Chloephaga dabbenei* n. sp. (PV-UNS-54); **F, G**, *Neochen pugil* (Winge, 1887). **A-F**, anterior views; **G-L**, posterior views. Distinctive traits are marked as follows: **1**, deep extensor groove and well-marked tubercles of the muscle tibialis cranialis; **1'**, weakly developed extensor groove and tubercles of the muscle tibialis cranialis; **2**, elongated distal vascular foramen; **2'**, subcircular distal vascular foramen; **3**, elongated, subrectangular distal III trochlea; **3'**, short distal III trochlea; **4**, posterolateral wing of the trochlea IV proximodistally extended; **4'**, posterolateral wing of the trochlea IV short; **5**, proportionally long shaft; **5'**, proportionally short shaft. Scale bar: 1 cm.

STRATIGRAPHIC PROVENANCE AND AGE. — Facies Sp, Lower Section of the San José Sequence. Middle Pleistocene.

DESCRIPTION AND COMPARISONS

PV-UNS-394 belongs to a very small representative of *Chloephaga*, probably the smaller of the genus. It is similar in proportions and humeral curvature to other species of the genus. The distal end of the humerus shows lateral and medial margins subvertically oriented, whereas they are somewhat divergent in the other species. The ring surrounding the facet for the collateral dorsal ligament is poorly defined, as occurs in *C. rubidiceps* and *C. poliocephala*, whereas in *C. picta* this facet is delimited by a prominent subcircular bony rim. In

posterior view, such a rim is less evident in PV-UNS-394 than in other species. The anterior articular ligament is almost subvertically oriented, as occurs in *C. poliocephala*, whereas in *C. picta* and *C. rubidiceps* it is distally oriented.

REMARKS

PV-UNS-394 shows differences in size and anatomical features with respect to the extant species of the genus *Chloephaga*. Besides, although there are no comparable skeletal elements, the specimen shows a much smaller size than what could be inferred for the extinct *C. dabbenei* n. sp. Based on these points, it is considered that this specimen probably corresponds to a new species of *Chloephaga*.



FIG. 10. — **A-E**, Right humerus of *Chloephaga* sp. (PV-UNS-394); **F-J**, left humerus of *Chloephaga picta* (J.F.Gmelin, 1789) (PV-UNS-104), from Bajo San José site; **A, F**, anterior; **B, G**, posterior; **C**, distal; **D, I**, lateral; **E, J**, medial; **H**, proximal views. Abbreviations: **bc**, bicipital crest; **bf**, brachial fossa; **br**, bony rim; **cdl**, collateral dorsal ligament; **ch**, caput humeri; **dc**, dorsal condyle; **de**, dorsal epicondyle; **dpc**, deltopectoral crest; **dt**, dorsal tubercle; **f**, pneumotricipital foramen; **fp**, flexor process; **ic**, incisura capitis; **ig**, intercondylar groove; **ih**, intumescencia humeris; **of**, olecranal fossa; **pf**, pmumotricipital fossa; **sht**, sulcus humerotricipitalis; **sst**, sulcus ligamentum transversus; **vc**, ventral condyle; **ve**, ventral epicondyle. Scale bar: 2 cm.

DISCUSSION AND CONCLUSIONS

The studied sample includes different skeletal elements belonging to a new species, *Chloephaga dabbenei* n. sp., a humerus that is indistinguishable in size and anatomical features from the extant species *C. picta*, and a humerus that is clearly smaller than any of the former two, and probably represents a new *Chloephaga* species.

Fossil specimens here described belong to Tadorninae, a clade that is well-represented in the fossil record of South America by pre-Holocene times (Tambussi 2011), and rein-

forces the proposal that tadornines and other basal anatids were more abundant than Anatini Leach, 1820 previous to Holocene times (Agnolín & Tomassini 2012). Even though the oldest Anatini occur in the Miocene (Zelenkov 2012; Zelenkov & Kurochkin 2012; Boev 2020), they have their first fossil records in South America at the lower Pleistocene (Cenizo *et al.* 2015). Since then, they became the predominant anseriform group in the fossil record, being at present much more diverse than non-anatini anseriforms (Agnolín & Tomassini 2012). In this regard, there are several characteristics present in Anatini that are absent in more

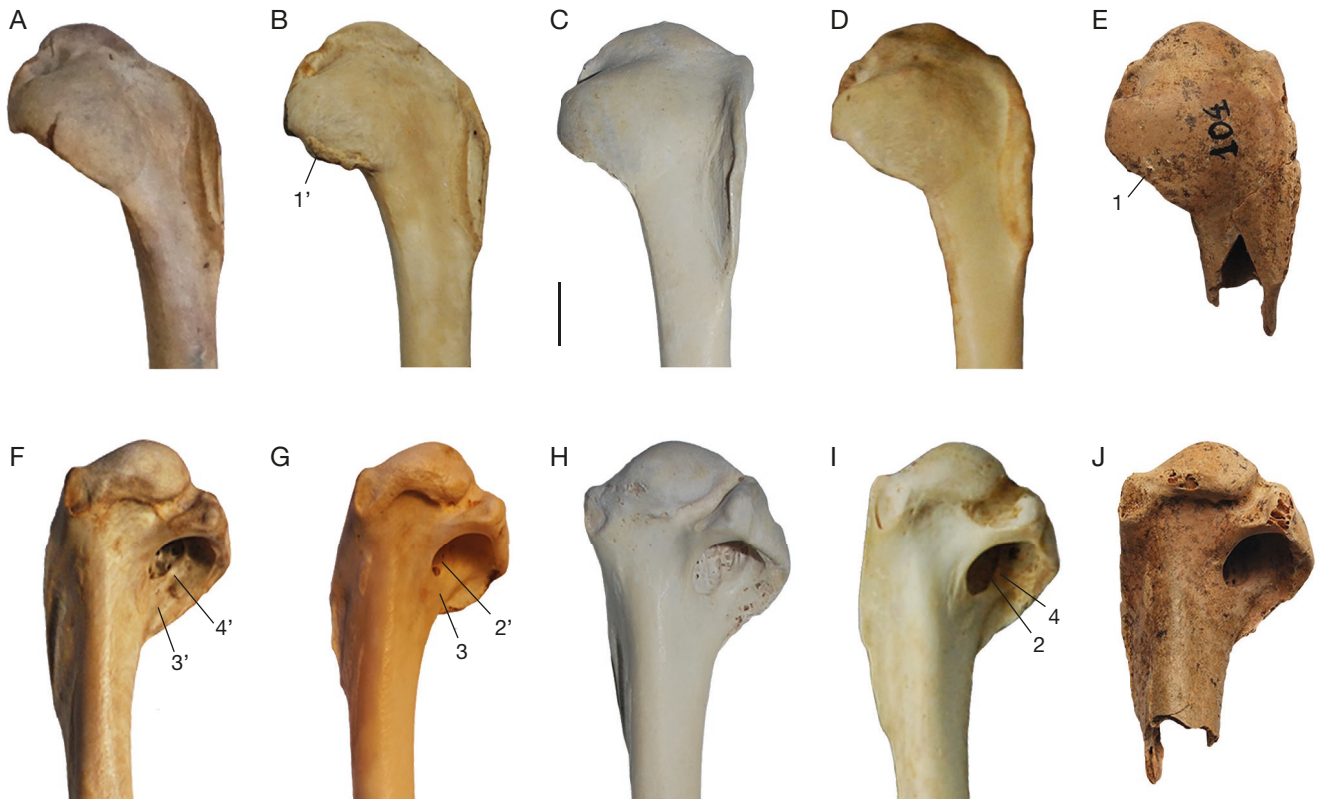


FIG. 11. — Comparison of humeri between *Chloephaga* Eyton, 1838 species and other tadornine taxa: **A, F**, *Chloephaga poliocephala* P.L.Sclater, 1857; **B, G**, *C. rubidiceps* P.L.Sclater, 1861; **C, H**, *Oressochen melanopterus* (Eyton, 1838); **D, I**, *C. picta* (J.F.Gmelin, 1789); **E, J**, PV-UNS-104, the *C. picta* from Bajo San José site. **A-E**, anterior; **F-J**, posterior views. Distinctive traits are marked as follows: **1**, bicipital crest expanded proximodistally and mediolaterally; **1'**, short bicipital crest; **2**, widely exposed pneumotricipital fossa; **2'**, narrow pneumotricipital fossa; **3**, wide area distal to the pneumotricipital fossa; **3'**, narrow area distal to the pneumotricipital fossa; **4**, low, interrupted crest delimiting distally the pneumotricipital foramen; **4'**, well defined, continuous crest separating the distal surrounding area of the pneumotricipital fossa. Scale bar: 1 cm.

basal anseriforms, such as Anserinae, Anhimidae Stejneger, 1885 or Tadornini (Reichenbach, 1850), that may explain the success of this waterfowl tribe. The most important of these differences are related to reproductive fitness, and were analyzed in detail by Delacour & Mayr (1945). Members of Anatinae rely more on an R reproductive strategy, which is further developed in the Anatini. For example, sexual dimorphism is notorious in Anatini, weak in tadornines, and almost absent in Anserinae; Anatini males abandon the female after copulation, while they form lifelong bonds in Tadorninae or Anserinae; parental care extends longer in time in Anserinae; and Anatinae males have more marked sexual displays, principally among Anatini (Delacour & Mayr 1945; Johnson *et al.* 2000). These traits could be the key characters that led Anatini to their explosive diversification.

The specimens from Bajo San José site constitute the most ancient record of *Chloephaga*, if “*Chloephaga*” *robusta* is not included within the genus (see above; Agnolín 2006). In this context, *Chloephaga dabbenei* n. sp. would also represent the extinct fossil species that unambiguously belong to *Chloephaga*. This new species bears a notably elongated and large tarsometatarsus with poorly spreading distal trochleae with respect to other species of the genus. These features are usually considered as being related to cursoriality (de Mendoza & Gómez 2022), which suggests that this new species was a walking sheldgoose.

Curiously, several previously described Pleistocene birds from the Argentine Pampas (i.e., *Pseudoseisuropsis nehuen* Noriega, 1991, *Pseudoseisuropsis cursor* Tonni & Noriega, 2001, *Colaptes naroskyi* Agnolín & Jofré, 2007) also show strong cursorial adaptations, particularly in their tarsometatarsus (Noriega 1991; Tonni & Noriega 2001; Agnolín & Jofré 2007). All of these cursorial birds went extinct by the Late Pleistocene, whilst their less-cursorial counterparts lived through the Pleistocene/Holocene boundary. This is the case of *Chloephaga*, which during the Late Pleistocene and early Holocene is represented by specimens assigned to the extant species *C. picta*. In this context, it is not improbable that the cursorial lifestyle inferred for *Chloephaga dabbenei* n. sp., has been a factor that influenced in their extinction. It is well-known that, in several cases, cursorial birds are more sensitive to environmental changes, and particularly predation (e.g. Olson & James 1991; Feduccia 1999). However, the fossil record of the Argentine Pampas is still very poor, and thus, this hypothesis should be tested further with new fossil findings and detailed analyses that are beyond the scope of present contribution.

The paleoenvironment interpreted for the Lower Section of the San José Sequence at Bajo San José site is congruent with the ecological requirements of the extant *Chloephaga* species. Sedimentological characteristics (see Borrromei 1990),

and taphonomic features of the bone remains (Tomassini, personal observation) suggest that the formation of the vertebrate assemblage from this site occurred over a short time; therefore, the recognition of three different taxa of *Chloephaga* may be considered as sympatric.

Nowadays different species of *Chloephaga* coexist in the same place, even forming mixed flocks and sharing the same foraging areas. Interestingly, three of these species (*C. picta*, *C. poliocephala*, and *C. rubidiceps*) migrate during the southern winter season from Patagonia to the south and east of Buenos Aires province, in points located very close to the Bajo San José site (de la Peña 2020). Therefore, it would not be surprising that the ancient representatives of the genus also had the gregarious behavior observed in the extant species.

The vertebrate assemblage from Bajo San José site is composed of taxa indicating different climatic and environmental conditions. This is evident among birds, with the presence of *Chloephaga*, which is adapted to arid and/ or cold conditions, together with the co-occurrence of the rallid *Porphyryula*, adapted to temperate/warm conditions. Deschamps (2003) interpreted that this may reflect a warm pulse during the MIS 11 (400 ky), in which northern faunas may have arrived to southern latitudes.

Acknowledgements

We thank K. Lykke Hansen and R. Vezzosi for the information on *Neochen pugil* and *Oressochen melanopterus*, respectively. S. Bogan helped with the photographs of fossil *Chloephaga* specimens. We deeply thank the help of Y. Davies and S. Bogan for granting us the access to the collections under their care. This work was partially supported by project PGI 24 H/154 (Universidad Nacional del Sur) to RLT, and PICT 2018-01390 PMO BID to FLA. Special thanks to two anonymous reviewers and the associated editor Eric Buffetaut for their comments that greatly improved the quality of the manuscript.

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Submitted on 6 March 2023;
accepted on 11 March 2024;
published on 21 June 2024.