

“The present state of knowledge of the Cenozoic birds of Argentina” by Tonni 1980: four decades after

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Recibido: 09 de marzo 2022 - Aceptado: 13 de agosto 2022 - Publicado: 15 de mayo 2023

Para citar este artículo: Claudia P. Tambussi, Federico J. Degrange, & Ricardo S. De Mendoza (2023). “The present state of knowledge of the Cenozoic birds of Argentina” by Tonni 1980: four decades after. *Publicación Electrónica de la Asociación Paleontológica Argentina* 23(1): 255–295.

Link a este artículo: <http://dx.doi.org/10.5710/PEAPA.13.08.2022.418>

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ISSN 2469-0228

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“THE PRESENT STATE OF KNOWLEDGE OF THE CENOZOIC BIRDS OF ARGENTINA” BY TONNI 1980: FOUR DECADES AFTER

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Abstract. “The present state of knowledge of the Cenozoic birds of Argentina” published in *Contribution in Sciences* in the year 1980, written by the Argentine paleontologist Eduardo Pedro Tonni, became a must-read for those interested in the record of fossil birds. In that work, all the records known up to that time are compiled and some comments are made. Since then, there have been crucial advances in unraveling the diversity of Cenozoic birds in Argentina. Based on that work, here is a detailed updated, and annotated list of all known avian records in Argentina that includes representatives of Palaeognathae (Tinamiformes and Rheiformes), Galloanseres (Anseriformes), and Neoaves (Sphenisciformes, Procellariiformes, Suliformes, Charadriiformes, Phoenicopteriformes, Ciconiiformes, Pelecaniformes, Coraciiformes, Cathartiformes, Accipitriformes, Falconiformes, Cariamiformes, Psittaciformes and Passeriformes). Besides, a substantial contribution is that here are photographs of the holotypes of all the new species that were nominated after Tonni’s paper.

Key words. Cenozoic. Argentina. Avian Fossil record. 66 Mega-anna–Recent.

Resumen. “EL ESTADO ACTUAL DEL CONOCIMIENTO DE LAS AVES CENOZOICAS DE ARGENTINA” DE TONNI 1980: CUATRO DÉCADAS DESPUÉS. “The present state of knowledge of the Cenozoic birds of Argentina” publicado en *Contribution in Sciences* en el año 1980, escrito por el paleontólogo argentino Eduardo Pedro Tonni, se convirtió por varias décadas en una lectura obligada para quienes estuvieran interesados en el registro de aves fósiles. Dicha contribución recopila todas las especies conocidas en Argentina hasta aquel momento, con comentarios sobre algunas de estas. Desde entonces, ha habido avances cruciales para desentrañar la diversidad de las aves cenozoicas de la Argentina. Basados en dicho trabajo, aquí se realiza un listado actualizado y comentado de todas las especies descritas hasta el momento en la Argentina que incluye representantes de Palaeognathae (Tinamiformes y Rheiformes), Galloanseres (Anseriformes) y Neoaves (Sphenisciformes, Procellariiformes, Suliformes, Charadriiformes, Phoenicopteriformes, Ciconiiformes, Pelecaniformes, Coraciiformes, Cathartiformes, Accipitriformes, Falconiformes, Cariamiformes, Psittaciformes y Passeriformes). Además, una contribución sustancial de este trabajo es que aquí se reúnen fotografías de los holotipos de todas las especies que fueron nominadas después del trabajo de Tonni.

Palabras clave. Cenozoico. Argentina. Registro fósil de aves. 66 Mega-anna–actualidad.

IN THE 80s, Eduardo Pedro Tonni summarized the then known avian fossil record in Argentina, a reference point for scholars in bird systematics, biogeography, and evolution (Tonni, 1980). He was preceded by a small number of researchers interested in fossil birds (e.g., Ameghino, 1891, 1895, 1899; Moreno & Mercerat, 1891; Rovereto, 1914; Kraglievich, 1931, 1932), but the knowledge regarding fossil birds was very uneven between families. Tonni’s work gathered all the available information in an ordered list following the Mammal Ages proposed by Pascual *et al.* (1965; Casamayoran, Divisaderan, Deseadan, Patagonian, Santacrucian, Friasan, Chasican, Huayquerian, Montehermosan,

Mesopotamian, Ensenadan, Lujanian), ending with the Recent with discussions towards the end of some cases that he considered most relevant. Numerous bird taxa were described after the publication of Tonni (1980), many of them collected in later compilation works (Tonni & Tambussi, 1986; Tambussi & Noriega, 1996; Tambussi, 2011; Tambussi & Degrange, 2013; Agnolín, 2016a). Together, these fossils provide valuable information on the ecology, biogeography, evolution, and past diversity of birds.

Keeping up with scientific advances is a core activity of the academic researcher and scientists must locate relevant information within a body of literature that is growing by

millions of new articles per year. In this sense, this work aims to be an aid by gathering all the fossil bird records of the Cenozoic of Argentina. All known bony records are included here, except some remains of uncertain affinities. Footprints, feathers, and eggshells are excluded. We order this work by gathering the records by systematics and secondly by lithostratigraphic units and their suggested geochronology from the oldest to youngest, and not by Land Mammal Ages. A substantial contribution to this updated list of records is that photographs of the holotypes of all the species that were nominated after the work of Tonni (1980) are gathered here. Photographs of some taxa are even published for the first time (*Pseudoseisura cursor* Tonni & Noriega, 2001 and *Lophiornis obliquus* Ameghino, 1891). After the section in which the records are listed according to the most recent knowledge, some general considerations are made.

MATERIALS AND METHODS

Author's names are only given for fossil species at first mention. When necessary, the terminology of Baumel & Witmer (2003) is used to refer to a bone accident. The terms "crown group" and "stem group" specify the position of fossil taxa relative to their existing relatives. Systematic paleontology includes cenozoic bird records, their current status, and pertinent references, which are organized following the order proposed by the IOC World Bird List (Gill *et al.*, 2022). For species primarily registered outside Argentina, both the holotype and the Argentinean specimens are listed.

Institutional acronyms. **AMNH**, American Museum of Natural History, New York, EEUU. **BAR**, Museo Asociación Paleontológica Bariloche, San Carlos de Bariloche, Río Negro, Argentina. **CADIC P**, Centro Austral de Investigaciones Científicas, Ushuaia, Tierra del Fuego, Antártida e Islas del Atlántico Sur, Argentina. **CCM**, Casa de la Cultura de Médanos, Médanos, Buenos Aires, Argentina. **CM**, Carnegie Museum of Natural History, Vertebrate Paleontology, Pittsburgh, Pensilvania, USA. **FM-P**, Field Museum of Natural History, Chicago, Illinois, USA. **GHUNLPam**, Cátedra de Geología Histórica, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina. **MACN-A/MACN-Pv**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Buenos Aires, Argentina. **MCNAM-PV**, Colección de Paleontología de

Vertebrados del Museo de Ciencias Naturales y Antropológicas Juan Cornelio Moyano, Mendoza, Mendoza, Argentina. **MEF-PV/MPEF**, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina. **MFJM**, Museo Francisco Javier Muñiz, Moreno, Buenos Aires, Argentina. **MLP**, Museo de La Plata, La Plata, Buenos Aires, Argentina. **MMP**, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Buenos Aires, Argentina. **MPCN-PV**, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina. **MPLK**, Museo de Ciencias Naturales Lucas Kraglievich, Marcos Paz, Buenos Aires, Argentina. **MPM-PV**, Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina. **MUFYCA**, Museo Florentino y Carlos Ameghino, Instituto de Fisiografía y Geología, Rosario, Santa Fé, Argentina. **NHMUK**, Natural History Museum, London, United Kingdom. **NRM**, Swedish Museum of Natural History (Naturhistoriska Riksmuseet of Stockholm), Stockholm, Sweden. **PULR-V**, Museo de Ciencias Antropológicas y Naturales de la Universidad de La Rioja, La Rioja, La Rioja, Argentina. **PVL**, Colección de Paleontología de Vertebrados del Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina. **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada. **UFAC**, Paleontological Research Laboratory of the Federal University of Acre, Río Branco, Acre, Brazil. **YPM-PVU**, Peabody Museum of Natural History, New Haven, Connecticut, USA.

SUCCINCT COMMENTS ON THE AVIAN CENOZOIC RECORD OF ARGENTINA

Palaeognathae

Rheiformes. Palaeognaths include both the flying tinamous (Tinamiformes) and the different flightless ratite lineages, the latter are represented in South America by rheids (Rheiformes). Rheiformes are endemic to the Neotropical Region; they are the largest birds in South America, runners unable to fly, omnivorous, and inhabitants of open grasslands throughout the southern part of the continent (Folch, 1992; Winkler *et al.*, 2020a).

The oldest records of supposed rheiforms correspond to a badly eroded tibiotarsus (Agnolín, 2016b) from the middle Eocene (Río Chico Group, Koluel Kaike Formation, Chubut Province) and a set of pedal phalanges of an unidentified species (Tambussi, 1995a) from the early Eocene (Raigemborn

et al., 2010, 2018; Krause *et al.*, 2017) of yacimiento Las Flores locality (Las Flores Formation, Río Chico Group, Chubut Province).

Agnolín (2016b) doubtfully assigns to *Diogenornis* Alvarenga, 1983 material exhumed in Río Chico Formation from Chubut Province, which he mistakenly considers to be the middle Paleocene (Picasso *et al.*, 2022). Regardless of the taxonomic position of the material, the Río Chico Group is late Paleocene–middle Eocene in age according to the most recent stratigraphic studies (Raingemborn *et al.*, 2010; Krause *et al.*, 2017), in such a way that these remains would be somewhat more modern. *Diogenornis fragilis* Alvarenga, 1983 is a taxon from the early Eocene of Brazil described by Alvarenga (1983) whose affinities with Rheiformes are still controversial (Mayr, 2009; Alvarenga, 2010). In the same work, Agnolín (2016b) describes two other very fragmentary remains that he assigns to possible rheids. One of them consists of a highly eroded portion of tibiotarsus exhumed in the Gauchito locality (early Eocene, Koluel Kaike Formation, Chubut Province); and the second is a pedal phalanx whose stratigraphic provenance is uncertain (Picasso *et al.*, 2022). The assignment of both remains is doubtful.

To the best of our knowledge, no Oligocene Rheiformes remains have been reported to date. From the Early Miocene, greater diversity and frequency of representatives of this clade begins to be documented, which are no longer restricted to the Patagonian provinces. During this epoch, the Rheiformes are represented by species belonging to *Opisthodactylus* (until the Pliocene) and *Rhea* that reach to the present. The extinct *Opisthodactylus horacioperezi* Agnolín & Chafrat, 2015, *O. kirchneri* Noriega *et al.*, 2017, *O. patagonicus* Ameghino, 1895, *Rhea mesopotamica* (Agnolín & Noriega, 2012), and possibly another unnamed species of *Rhea* (Cenizo *et al.*, 2012) are strong evidence of the rooting of this clade in southern South America. It should be clarified that we follow here the most recent systematic proposals that consider *Pterocnemia* to be synonymous with *Rhea* (Winkler *et al.*, 2020a; IOC World Bird List, Gill *et al.*, 2022).

Two extinct species have been described for the Early Pliocene of Monte Hermoso Formation at the Pampean Region: *Heterorhea dabbenei* Rovereto, 1914 whose revision has not been possible because its holotype is lost, and *Hinasuri nehuensis* Tambussi, 1995a undoubtedly the largest of all

known rheiforms (Picasso & Mosto, 2016).

The modern species *Rhea americana* and *Rhea pennata* have their first records in the Early–Middle Pleistocene, not only from the Pampean Region but also from other fossiliferous localities of the country. Various species of extinct rheas (*R. anchorenensis*, *R. pampeana*, *R. fossilis*, and *R. subpampeana*) recovered from Quaternary sediments were described at the end of the 19th or early 20th centuries, all of them are considered synonyms of the living *Rhea americana* (Picasso *et al.*, 2022).

Tinamiformes. Inambues, tinamous, and allies are emblematic Neotropical birds, capable of flight even though flight is not their preferred mode of locomotion (Winkler *et al.*, 2020b). Tinamids are gathered in two phylogenetic and ecologically different groups (Noriega *et al.*, 2017), the Nothurinae of open areas and the Tinaminae inhabitants of closed forest-type environments. The earliest tinamid fossil record comes from the Early Miocene and corresponds to both ecological/phylogenetical groups (Bertelli, 2017; Almeida *et al.*, 2022). The oldest record of Tinaminae comes from the Early Miocene of the Santa Cruz and Pinturas formations (Bertelli & Chiappe, 2005; Chandler, 2012; Diederle & Noriega, 2019). From the Early–Middle Miocene, Chandler (2012) described a humerus from the old Patagonia collections that Barnum Brown collected far from the current range of the genus. He identified it as the Tinaminae *Crypturellus reai* Chandler, 2012. The proper taxonomic position of the material is still up for debate (Tambussi & Degrange, 2013). *Crypturellus* is the most specious genus of the family including land-dwelling birds with current distribution from north-central Argentina to central America (Winkler *et al.*, 2020b). The oldest record of a Nothurinae assignable to an extant genus corresponds to an undetermined species of *Eudromia* exhumed in sediments of the Cerro Azul Formation (Cenizo *et al.*, 2012).

Two extinct tinamids for the Early to Late Pliocene, *Nothura parvula* (Rovereto, 1914) and *Eudromia olsoni* (Rovereto, 1914) are included as valid taxa. Remains assigned to an indeterminate species of *Nothura* and *Eudromia* have been recovered from the Late Miocene of Cerro Azul Formation in the Pampean Region (Cenizo *et al.*, 2012) and from the Middle to Late Pleistocene localities, as for example Punta Indio, Paso Otero, Chacra Santo Domingo or Bajo

San José at southern Pampean Region (Picasso & Degrange, 2009; Cenizo *et al.*, 2015; Deschamps & Tomassini, 2016).

Galloanserae

The Galloanserae (Anseriformes and Galliformes) comprise one of the major lineages of birds, generally considered to be a monophyletic group of early divergence, nearly worldwide in distribution, and of lower diversity compared with its sister group, the Neoaves.

Galliformes. There are no undisputed records of fossil Galliformes (landfowl) for Argentina throughout the Cenozoic.

Anseriformes. Anseriformes is a well-known clade of mostly medium-sized birds, most inhabitants of aquatic environments that feed on plants or small invertebrates. Living Anseriformes included three families: Anhimidae (screamers of South America), Anseranatidae (magpie geese from Australia), and Anatidae (ducks and allies, with worldwide distribution), although some authors (Sun *et al.*, 2017; Zelenkov, 2020) separates the whistling ducks from Anatidae by placing it in its own family Dendrocygnidae. The extinct families Presbyornithidae (America, Europe, Mongolia), the giant flightless Dromornithidae (Australia), Gastornithidae (Eurasia), and Diatrymidae (North America) have been referred to Anseriformes, in addition to various extinct taxa, many of them with uncertain affinities.

Anhimidae (late Oligocene or Early Miocene–Recent) are medium-large, almost entirely herbivorous birds that differ from the duck morphotype in that they have non-palmated feet and a short, straight beak. Its three extant species have an exclusively South American distribution but putative anhimids have been reported in the early Eocene of North America and Europe (Ericson, 1997; Feduccia, 1999). The fossil record of Argentinian screamers included *Loxornis clivus* Ameghino, 1895 that was exhumed in sediments from the late Oligocene of Santa Cruz Province, and considered to be of an uncertain family by Tonni (1980), but later relocated to Anhimidae (Alvarenga, 1999).

Among anseriforms, the globally distributed Anatidae is the family most represented from the Cenozoic of Argentina. The earliest records are *Aminornis excavatus* Ameghino, 1899 and *Teleornis impressus* Ameghino, 1899 from the late Oligocene of Santa Cruz. Subsequent studies (*e.g.*, Agnolín, 2004) assign *Aminornis* to the Anserinae based

on osteological characters (such as a highly excavated *cotyla scapularis*, very well developed and caudally directed *processus procoracoidei*, and excavated *sulcus m. supracoracoidei*) that are shared with other Anatidae non-Anserinae, which is why it is preferred here to keep the assignment of this taxon only at the family level. *Teleornis impressus* is here considered a Tadorninae, a criterion suggested by Agnolín (2004) and Tambussi & Degrange (2013).

Ameghino (1891) funded the species *Eoneornis australis* based on a fragment of the distal portion of the radius exhumed in the Santa Cruz Formation (Early–Middle Miocene). He assigns it to the Anatidae but this family assignment has subsequently been challenged (see Tambussi & Degrange, 2013 for more details on its systematic position).

Anatids are also represented during the Miocene. *Ankonetta larriestrai* Cenizo & Agnolín, 2010 a presumed basal anatid; *Eutelornis patagonicus* Ameghino, 1891 whose affinities are still debated (see a compendium of the hypotheses raised in Worthy, 2008) and Degrange *et al.*, 2012 and *Cayaoa bruneti* Tonni, 1979. *Cayaoa bruneti* from the Early Miocene of Gaiman Formation, Chubut Province, was a foot-propelled diver, with greatly reduced wings, and flightless. De Mendoza (2019) states that it has intermediate characters between basal and derived anatid taxa. He finds that *Cayaoa bruneti* is “to be the sister taxon to the extant Erismaturinae (synonymous “Oxyurinae”), being part of the Erismaturinae global radiation of the Oligocene–Miocene” (De Mendoza, 2019, p. 8).

Dendrocygninae fossils have been known from the Late Miocene of Chubut (Dozo *et al.*, 2010) and Entre Ríos provinces (Tambussi & Degrange, 2013; Diederle, 2015). A putative Dendrocygninae has been recorded in the Santa Cruz Formation (Noriega *et al.*, 2021). There is a distal end of humerus referable to Dendrocygninae recovered from the Early Pliocene of Monte Hermoso Formation (Agnolín & Tomassini, 2012). Abundant remains assigned to the subfamily have been also recovered from various Early Pliocene or Pleistocene localities such as Farola de Monte Hermoso, Bajo San José, and Paso Otero from the Pampean Region, (Cenizo *et al.*, 2015; Deschamps & Tomassini, 2016).

The record of modern species of Anatidae goes back no further than the Middle Pleistocene and is restricted to specimens assigned to the cosmopolitan genus *Anas*, such

as *Anas bahamensis* Linnaeus, 1758 and *Anas platalea* Vieillot, 1816, a fact that had already been noted by Tambussi *et al.* (1993) and has not changed, even with the most recent discoveries of fossil birds. All other fossils assigned to the family have no living representatives.

Undoubtedly, amongst the most unusual anseriforms are the Presbyornithidae, characterized by having long legs and a skull similar to that of ducks but a different postcranial skeleton, resembling that of a flamingo. Remains of presbyornithids are abundant in Paleogene localities in both Americas, particularly in North America. The oldest Argentinian fossil record dates back to the early Eocene of El Fresco Formation of La Pampa Province (Tambussi & Noriega, 1998). Two species have also been described: *Telmabates howardae* Cracraft, 1970 and *Telmabates antiquus* Howard, 1955 both from the Early Eocene of Cañadón Hondo locality at Chubut Province.

Additionally, *Telmabates howardae* Cracraft, 1970 from the Eocene deposits of Cañadón Hondo of Chubut Province, was formally described and originally attributed to Presbyornithidae. It was considered synonymous with *Presbyornis pervetus* by Feduccia & McGrew (1974) but Ericson (2000) later recognized it as a valid species of an uncertain order (see Systematic Paleontology section). Discarded if belonging to *Telmabates*, a re-assignment is required.

Neoaves

Gruiformes. Gruiformes is a diverse and monophyletic group of Neoaves (the clade that comprises all Neornithes or modern birds with the exclusion of Palaeognathae and Galloanserae) which include many extant families, although the two more speciose and well-known are Gruidae (cranes) and Rallidae (rails and coots). The affinities of *Anisolornis excavatus* Ameghino, 1891, from the Early–Middle Miocene of Santa Cruz Formation, have been debated by different authors. It was considered as a Phorusrhacidae (Ameghino, 1891), a phasianid galliform (Ameghino, 1895), a cracid or a Tinamidae (Brodkorb, 1964), and later removed to the Aramidae (Cracraft, 1973) or the Psophiidae (Olson, 1985). Here we follow this last criterium (see below). The last revision of the taxon with the material in hand locates it as a Gruiformes, without any further assignment to an extant family (Degrange *et al.*, 2012).

Fragmentary remains from the Ituzaingó Formation (Late Miocene) have been identified as related to the extant genus *Grus* (Noriega & Agnolín, 2008). There are some fossil remains identified as different species of the genus *Fulica* (all belonging to the extant species *F. leucoptera*, *F. rufifrons* and *F. armillata*) coming from the Late Pleistocene of Luján Formation, Buenos Aires Province (Cenizo *et al.*, 2015) and also an indeterminate species of *Porphyrio* Brisson, 1760 recovered from Middle Pleistocene of Bajo San José at upstream of the Río Sauce Grande (Deschamps & Tomassini, 2016).

Ciconiiformes. Storks and marabous (Ciconiidae) are heavy, long-legged scavengers or carnivorous waders that live in aquatic or semi-aquatic environments. In the Cenozoic of Argentina, three extinct species have been recovered. The oldest species, of Lower–Middle Miocene strata of the Santa Cruz Formation, is *Lophiornis obliquus* Ameghino, 1891 which was placed within the Psilopteridae by Tonni (1980), removed from the Phorusrhacidae by Alvarenga & Höfling (2003) and provisionally placed among Ciconiiformes by Agnolín (2009a) and Anseriformes by Tambussi & Degrange (2013). At the time of this publication, the systematic status of this taxon with the holotype is being carried out.

An unambiguous representative of Ciconiiformes is *Leptoptilos patagonicus* Noriega & Cladera, 2008 from the Late Miocene Puerto Madryn Formation. Living marabous are distributed in Africa and Asia, but in the past, they had a greater geographic range (Mayr, 2017) including the extinct species from Argentina.

On the other hand, possible Ciconiini cf. *Ciconia* and Mycteriinae cf. *Mycteria* have been reported from the Late Miocene (“Mesopotamian”) Ituzaingó Formation outcropping at Entre Ríos Province (Diederle & Noriega, 2013; Noriega & Agnolín, 2008). Finally, *Ciconia lydekkeri* (Ameghino, 1891) from the Late Pleistocene of Buenos Aires is an extinct species of stork that belongs to the most diverse genus of living storks worldwide (Agnolín, 2009b).

Suliformes. Most of the species of shags and cormorants (Phalacrocoracidae) live on the worldwide sea coasts and reproduce in large coastal colonies, although some species are primarily freshwater dwellers. The fossil record is scarce in Cenozoic rocks of Argentina, and is limited to the living Neotropic Cormorant *Nannopterum brasilianum* (Gmelin, 1789)

for the Late Pleistocene of the Luján Formation in Buenos Aires and remains of many living species from Middle to Late Holocene archaeological sites in Tierra del Fuego (Causey & Lefèvre, 2007).

The extant darters or snakebirds (Anhingidae) are morphologically conservative (Kennedy *et al.*, 2019). They are foot-propelled divers that primarily inhabit freshwater habitats in the tropics and subtropics of the southern hemisphere. Anhingids feed mainly on small fish, crustaceans, mollusks, insects, and amphibians that they hunt by swimming underwater (Winkler *et al.*, 2020c). At least six extinct species are known for the Miocene, evidencing a very marked diversity that includes very large species.

The Argentinian fossil record of darters starts in the Miocene of Patagonia and includes: a nondescript species of *Macranhinga* from the Early–Middle Miocene Santa Cruz Formation from Santa Cruz Province (Cenizo & Agnolín, 2010); *Macranhinga ameghinoi* Diederle & Agnolín, 2017 exhumed 2 km southwestern to Puesto Marileo, near Ingeniero Jacobacci at Río Negro Province; *Macranhinga paranaensis* Noriega, 1992, *M. ranzii* Alvarenga & Guilherme, 2003 and a putative *Giganhinga* sp. exhumed from the Late Miocene Ituzaingó Formation of Entre Ríos Province (Areta *et al.*, 2007; Noriega & Agnolín, 2008). *M. paranaensis* was also exhumed (Diederle *et al.*, 2012) from the Paraná Formation (Middle–Late Miocene) at La Ensenada Stream (Diamante, Entre Ríos Province).

Liptornis hesternus (Ameghino, 1895) is an Anhingidae from the Early–Middle Miocene of Santa Cruz, originally described by Ameghino (1895) and reassigned to the darters Degrange *et al.* (2012). Based on this, Diederle (2015) proposed the new combination *Anhinga hesterna*.

Tonni (1980) places the species *Pseudolarus eoacenus* Ameghino, 1895 from the Early–Middle Miocene of Santa Cruz among Psilopteridae, but more recently Agnolín (2016a) moved it to Anhingidae.

Small species of darters coexisted with the large forms during the Miocene of Argentina, one of which was smaller than all extant Anhingidae and was assigned to the taxon *Anhinga minuta* Alvarenga & Guilherme, 2003. Remains potentially belonging to this species originally recognized for the Late Miocene of Brazil were exhumed in the Miocene of the Ituzaingó Formation (Noriega & Agnolín, 2008) in the

Argentine Mesopotamia. As Mayr (2009) points out, although flightlessness and giant size evolved in other aquatic birds, giant darters (as the species of *Macranhinga* were) illustrate an infrequent case of these traits occurring in freshwater taxa.

Pelecaniiformes. Ibises and spoonbills (Threskiornithidae) are typical but not exclusive to the southern hemisphere and are particularly characterized by their long and decurved or wide and flat bills. They are recorded from the Early–Middle Miocene, Santa Cruz Formation. This record consists of a distal end of the right tibiotarsus that Ameghino (1891) assigned to the extinct species *Protibis cnemialis* Ameghino, 1891.

Based on some material exhumed from the Late Pleistocene of Buenos Aires, Cenizo *et al.* (2015) recognize the presence of a species probably similar to the white-faced ibis (*Plegadis chihh*) that inhabits primarily freshwater wetlands.

Charadriiformes. Charadriiformes (shorebirds, gulls, plovers, and allies) are a highly diverse group, distributed throughout the world in a wide variety of aquatic habitats, both marine and freshwater. Representatives of Charadriiformes were identified since the Early Miocene in the Chichinales Formation of Río Negro (Agnolín & Chafrat, 2015) and Late Miocene Loma de las Tapias Formation in San Juan Province (Agnolín *et al.*, 2016). The latter remain belongs to Thinocoridae (seedsnipes).

Isolated remains of Scolopacidae (sandpipers) and Charadriidae (plovers) were recorded in the Pliocene and Pleistocene (Tambussi, 1995b), including modern species (*Vanellus chilensis*) and extinct taxa (*Vanellus lilloi* [formerly *Belonopterus lilloi*] described by Cenizo & Agnolín, 2017). Additional indeterminate species belonging to these families have been recorded in the Late Pleistocene of Paso Otero locality, Buenos Aires Province (Cenizo *et al.*, 2015). More modern records of *Vanellus chilensis* correspond to that of the Holocene from Cañada de Rocha, Buenos Aires Province (Ameghino, 1891).

Supposed Laridae (gulls) of Late Pleistocene age were described at the end of the 19th century by Mercerat (1897): *Pseudosterna degener* and *P. pampeana* but were never illustrated and were subsequently lost (Olson, 1985), thus their status cannot be revalidated.

The living species *Thinocorus rumicivorus* Eschscholtz, 1829 and *T. orbignyanus* Saint-Hilaire & Lesson, 1831, have their earliest records in the Early Pleistocene of southeast Buenos Aires Province (Tonni *et al.*, 1998; Picasso *et al.*, 2019).

In short, the record of Charadriiformes is uneven and, consequently, provides little information about the history of the group in South America.

Sphenisciformes. Penguins (Sphenisciformes) live in highly productive oceanic environments in the Southern Hemisphere. The only recognized family Spheniscidae is part of the larger Aequornithes clade of “waterbirds” that also includes Gaviiformes, Procellariiformes, Ciconiiformes, Suliformes, and Pelecaniformes.

The fossil record of penguins on the Patagonian Atlantic coast is characterized by the abundance of isolated elements and is restricted to sediments from the middle Eocene (Clarke *et al.*, 2003; Acosta Hospitaleche & Olivero, 2016), late Oligocene (Simpson, 1946, 1972), and early Late Miocene (Simpson, 1981; Acosta Hospitaleche *et al.*, 2007). At least nine extinct species have been recognized, the majority assigned to *Palaeospheniscus* Moreno & Mercerat, 1891 (three species) and *Parapterodytes* Ameghino, 1891 (two species) in addition to *Eretiscus tonnii* (Simpson, 1981), *Arthrodytes andrewsi* (Ameghino, 1901), *Palaeodyptes gunnari* (Wiman, 1905) and *Madrynornis mirandus* Acosta Hospitaleche *et al.*, 2007.

Interestingly, Chávez Hoffmeister *et al.* (2014) point out that the record of South American penguins shows the co-existence of stem and crown taxa until the end of the Miocene. We refer to the literature cited there to see a synthesis of the record of South American penguins and also the following list (Acosta Hospitaleche, 2003, 2004, 2007, 2009, 2010; Acosta Hospitaleche & Tambussi, 2008; Acosta Hospitaleche *et al.*, 2008; Bertelli *et al.*, 2006).

Procellariiformes. Within this clade Procellariiformes (albatrosses, shearwaters, and petrels), are the birds with the longest wings of all birds. It is an exclusively marine, flying group well adapted to a pelagic way of life and also capable divers. Analysis of nuclear gene sequences supported close relationships with the Sphenisciformes (Hackett *et al.*, 2008; Prum *et al.*, 2015). In Argentina, the fossil record is practically non-existent.

Initially considered as Sphenisciformes, *Argyrodyptes microtarsus* Ameghino, 1905 comes from late Eocene–early Oligocene, San Julián Formation at Chubut Province, and was later placed within the Procellariidae (see Agnolín, 2007a). Other remains include a right carpometacarpus coming from Gaiman Formation (Early Miocene), which belongs to a new and still non-described species (Piro & Acosta Hospitaleche, 2022), and a putative albatross (Procellariidae) from the Early–Late Miocene of Península Valdés at Chubut Province mentioned but not described by Olson (1984).

Phoenicopteriformes. Flamingos (Phoenicopteriformes) are large birds with long legs, currently distributed in preferably brackish aquatic environments on all continents except Antarctica. Its fossil record is scarce and discontinuous. The oldest record for Argentina is *Tiliornis senex* Ameghino, 1899 from the Oligocene of Patagonia, but its inclusion in this order is still questioned (Olson & Feduccia, 1980; Tambussi & Degrange, 2013).

The two extinct species that are unambiguously assigned to this group come from the Late Miocene Ituzaingó Formation (*Palaeolodus* cf. *Palaeolodus ambiguous* and *Megapalaeolodus* sp.; Noriega & Agnolín, 2008; Diederle & Noriega, 2013) and Andalhuala Formation (*Megapalaeolodus peiranoi* Agnolín, 2009c). Palaeolodidae (the family to which they belong) is considered to be the sister of Phoenicopteridae. They are known from Australia, North and South America (Noriega, 1995), and Africa, usually recovered from lacustrine deposits (Worthy *et al.*, 2010). The Argentinean fossil record of Phoenicopteridae is scarce. It is represented by a poorly preserved ulna assigned to Phoenicopterinae (Noriega & Agnolín, 2008) recovered from the basal sediments of the Late Miocene Ituzaingó Formation, outcropping in Entre Ríos Province and also, by a distal fragment of a tarsometatarsus recovered from the Late Pleistocene levels of the Luján Formation, Paso Otero locality at Buenos Aires Province (Cenizo *et al.*, 2015).

Podicipediformes. Grebes are widely distributed freshwater diving birds with few species inhabiting marine environments, all grouped in a single family Podicipedidae. Only fossil remains referable to extant species such as *Rollandia rolland* (Quoy & Gaimard, 1824) from the Late Pleistocene Luján Formation, at Paso Otero Locality of Buenos Aires

Province have been reported (Cenizo *et al.*, 2015).

Cathartiformes. New World vultures (Cathartidae) are characterized by their carrion feeding habits and soaring flight mode. The oldest record in Argentina is *Dryornis hatcheri* Degrange, 2022 coming from the Early–Middle Miocene of the Santa Cruz Formation (Degrange, 2022). *Dryornis pampeanus* Moreno & Mercerat, 1891 was originally described from Early Pliocene sediments of Buenos Aires Province. Additional materials recently recovered from Upper Pliocene sediments of Chapadmalal Formation, Buenos Aires Province, allow to know characters from other elements of the skeleton and to infer its enormous size (Degrange *et al.*, 2021a). Materials supposedly assigned to the same genus were exhumed from the Late Miocene of La Rioja Province (Rodríguez Brizuela, 2004). Taken together, these findings show a very wide distribution of the genus both temporally and geographically. Cathartiformes like condors were highly diversified during the Pleistocene of the Pampean region (Tambussi & Noriega, 1996, 1999; Tonni & Noriega, 1998; Agnolín, 2016a; Agnolín *et al.*, 2017) and Uruguay (Jones *et al.*, 2021). Findings in Argentina include extinct species like *Pampagyps imperator* Agnolín *et al.*, 2017, recovered from the Late Pleistocene outcrops of Luján Formation, in Buenos Aires Province, and *Geranogyps reliquus* Campbell, 1979, found in the Late Pleistocene Salto Ander Egg Formation (Noriega & Tonni, 2007), of Entre Ríos Province. Also from the Pleistocene, there are several remains belonging to living species such as *Vultur gryphus* (but see Agnolín *et al.*, 2017), and *Sarcoramphus papa* (Noriega & Areta, 2005). It has been hypothesized that this diversity would have been related to the high abundance of carcasses of giant South American mammals.

Accipitriformes. Accipitridae is the clade that includes eagles and hawks, and also kites and Old-World vultures. It is a diverse clade of zoophagous birds, but their fossil record in Argentina is scarce, besides having new recently described species. The oldest Argentinian remain of Accipitridae is a fragmentary ungual phalanx from the Oligocene of Río Chico locality in Patagonia (Degrange *et al.*, 2021b). *Geranoaetus* cf. *ales* from the Late Miocene of Andalhuala Formation is also known (Agnolín, 2006b). *Vinchinavis paka* Tambussi *et al.*, 2021 from the Late Miocene of Toro Negro Formation in La Rioja, described on the basis of a left ulna and radius adds

to the high taxonomic diversity of the clade (Tambussi *et al.*, 2021). From the Late Pliocene of Chapadmalal Formation, there is a partial left hindlimb nominated as *Buteo dondasi* (Degrange *et al.*, 2021b). Finally, from the Late Pleistocene there are remains identified as *Buteo*, from the Luján Formation (Cenizo *et al.*, 2015), and remains assigned to the living species *Geranoaetus melanoleucus* from the Miramar Formation (Agnolín, 2006b).

Strigiformes. The fossil record of owls in Argentina is extremely scarce. The oldest remains are from the Early Miocene reported by Chiappe (1991) of Pinturas Formation, and Tambussi & Noriega (1996) from Middle Miocene Collón Curá Formation. The extant genera *Athene* (including an un-nominated fossil species), *Asio*, and *Tyto* have records in the Late Pleistocene of Buenos Aires Province (Cenizo & de los Reyes, 2008; Cenizo *et al.*, 2015).

Coraciiformes. Coraciiformes is a highly diverse clade that contains rollers, motmots, bee-eaters, and kingfishers among others. Unlike in the Old World, in the New World, its diversity is low, both living and fossil species. The single representative of the Coraciiformes in Argentina is *Ueekenkcoracias tambussiae* Degrange *et al.*, 2021c, from the early Eocene Huitrera Formation of Patagonia, and considered the most basal member of the Coracii. However, its affinities with Coracii have been recently disputed (Mayr, 2021).

Piciformes. Recent Piciformes (woodpeckers and allies) are an order of mostly arboreal and insectivorous birds. The fossil record of modern type Piciformes is very sparse in Argentina. A new species in the modern genus *Colaptes* was described from the Late Pleistocene near Merlo city in Buenos Aires Province. This extinct species *Colaptes naroskyi* named by Agnolín & Jofré (2017), is also known from additional Pleistocene localities in southern Buenos Aires Province and Uruguay. Tonni & Fidalgo (1982) report the presence of the extant species *Colaptes campestris* in the Pleistocene of Punta Hermengo locality, Buenos Aires Province.

Cariamiformes. One of the most speciose clades of the Argentinean fossil avifauna is the Cariamiformes. Although, it is still a subject of debate, this clade comprises at least six families: Salmilidae, Bathornithidae, Ameghinornithidae, Idiornithidae, Cariamidae, and Phorusrhacidae, being only

the last three represented in the fossil record of Argentina. Putative Idiornithidae are recorded based on fragmentary remains from the middle Eocene of Gran Hondonada locality, Chubut Province (Acosta Hospitaleche & Tambussi, 2005; Agnolín, 2009a; Tambussi & Degrange, 2013), and from Santa Cruz (Agnolín, 2016a). The oldest records of Cariamidae are those from the Early Miocene Pinturas Formation (Chiappe, 1991), and from the Early–Middle Santa Cruz Formation. The latter corresponds to an extinct taxon known as *Miocariama patagonica* Mayr & Noriega, 2017, represented by a fairly complete skeleton. Extant genera of Cariamidae find their oldest record in *Chunga incerta* Tonni, 1974 from the Early Pliocene of Buenos Aires Province, and represented by fragmentary hind limb bones.

Phorusrhacidae is a group of cursorial predatory birds that originated in South America and posteriorly dispersed to Africa in the Paleocene or early Eocene, and to North America in the Plio–Pleistocene (Mourer-Chauviré *et al.*, 2011; MacFadden *et al.*, 2007). Nevertheless, its highest diversity and the most abundant fossil record are that of Argentina. The oldest record of phorusrhacids is that from the middle Eocene of Cañadón Vaca (Tonni & Tambussi, 1986). It is only from the Oligocene and on that the Phorusrhacidae are represented by at least three species: *Andrewsornis abbotti* Patterson, 1941 and *Psilopterus affinis* (Ameghino, 1899) from Chubut, and *Physornis fortis* Ameghino, 1895 from Santa Cruz, being this last one enormous. Additionally, Ameghino erected the species *Ciconiopsis antarctica* Ameghino, 1899 based on a fragmentary carpometacarpus that shows some phorusrhacid features. Because further studies are needed to confidently assign it to this group, the taxon is considered as a *nomen inquirendum* (Tambussi & Degrange, 2013). Phorusrhacidae reached their maximum diversity in the Early–Middle Miocene where up to four species are recorded coexisting in one locality (Degrange *et al.*, 2012): *Phorusrhacos longissimus* Ameghino, 1887; *Patagonis marshi* Moreno & Mercerat, 1891; *Psilopterus lemoinei* (Moreno & Mercerat, 1891); and *Ps. bachamni* (Moreno & Mercerat, 1891). By the Middle–Late Miocene, phorusrhacids have a more disperse record with one species coming from Patagonia, *Kelenken guillermoi* Bertelli *et al.*, 2007; one from Buenos Aires, *Psilopterus colzecus* Tonni & Tambussi, 1988; and one from La Pampa, *Procarriama*

simplex Rovereto, 1914, where an indeterminate species of larger size has also been recorded (Cenizo *et al.*, 2012). *Procarriama simplex* is also reported in the Late Miocene of Andalhuala Formation in Catamarca Province together with *Mesembriornis incertus* (Rovereto, 1914), and *Andalgalornis steulleti* (Kraglievich, 1932) (about other positions on the valid name of this taxon, we refer to the work of Agnolín, 2013). *Andalgalornis steulleti* finds additional records in the Ituzaingó Formation (Noriega & Agnolín, 2008), together with *Devincenzia pozzi* (Kraglievich, 1931), a gigantic phorusracid that also comes from the Late Miocene, Cerro Azul Formation of Adolfo Alsina locality at La Pampa Province. Although there are some Early to Late Pleistocene remains recorded in Uruguay (Jones *et al.*, 2018), the latest record of phorusrhacids in Argentina comes from the Late Pliocene of the marine cliffs of Buenos Aires Province. *Llallawavis scagliai* Degrange *et al.*, 2015 comes from the Chapadmalal Formation, together with *Mesembriornis milneedwardsi* Moreno, 1889 that also has unambiguous records coming from Early Pliocene Monte Hermoso Formation.

Falconiformes. The fossil record of Falconiformes in Argentina is meagre, mostly fragmentary but with some evolutionarily significant remains. *Badiostes patagonicus* Ameghino, 1895, *Thegornis debilis* Ameghino, 1895 and *T. musculosus* Ameghino, 1895 were recovered from Early–Middle Miocene sediments of the Santa Cruz Formation. Additional remains of *Thegornis* from Miocene of Ingeniero Jacobacci, Neuquén Province (Tonni, 1980), and from the Late Miocene of Puerto Madryn Formation (Dozo *et al.*, 2010) are also recognized (Agnolín, 2016a). *Thegornis musculosus*, that was also found in the Sarmiento Formation (middle Eocene–Early Miocene) of Chubut Province (Tambussi & Degrange, 2013), is related to the extant laughing falcon *Herpetotheres cachinnans* as Noriega *et al.* (2011) point out when studying a magnificent skeleton recently found. Coincidentally, Agnolín (2016a) indicated that *Badiostes patagonicus* belongs also the Herpetotherinae radiation. Fragmentary remains of Falconids have been reported in the Miocene Pinturas Formation (Chiappe, 1991). *Asthenopterus* [formerly *Lagopterus*] *minutus* (Moreno & Mercerat, 1891) is a falconid related to caracaras (Tonni, 1980) that comes from the Late Pleistocene of Buenos Aires Province. Some few remains referable to extant taxa such as *Milvago* sp. coming from the Late Miocene

Cerro Azul Formation (Cenizo *et al.*, 2012), and *Falco femoralis* and *Caracara* sp. from the Late Pleistocene of Buenos Aires have also been reported (Cenizo & Tassara, 2013; Cenizo *et al.*, 2015). A large species belonging to the genus *Caracara* has also been reported in the Late Pleistocene of Río Quequén Grande locality, Buenos Aires Province (Jones *et al.*, 2015).

Psittaciformes. Fossil parrots are known since the Late Pliocene but the most abundant records are Pleistocene and all from the Pampean Region (Tambussi *et al.*, 2007). The oldest record is *Aratinga* [formerly *Nandayus*] *vorohuensis* Tonni & Noriega, 1996 whose skull was recovered from the Late Pliocene “Vorohué Formation” exposed in southeastern Buenos Aires Province. All Pleistocene records are represented by postcranial, non-articulated remains assigned to the extant *Cyanoliseus patagonus* recorded in Punta Hermengo and in the outcrops of the Luján Formation in Arroyo Chelforó, Buenos Aires Province, and in Centinela del Mar locality, the extinct *Cyanoliseus ensenadensis* (Cattoi, 1957) from Ensenada Formation, and *Cyanoliseus patagonopsis* Acosta Hospitaleche & Tambussi, 2006 from “Miramar Formation”.

Passeriformes. Passeriformes (perching birds) are nowadays the most diverse and widespread bird order with more than half of the total species of Neornithes (Barker *et al.*, 2004; Barker, 2014) and the most diverse among the tetrapods. They exhibit high diversity both taxonomically and in terms of body sizes, feeding adaptations (from nectarivory to carnivory), social systems (from lekking to coloniality), locomotion (terrestrial to hyperaerial), and plumages (from modest monochromatic to spectacular multicolors). Despite this, its fossil record is particularly scarce in Argentina. The oldest record is an unnamed species from the Miocene Pinturas Formation (Noriega & Chiappe, 1993). Undeterminate Tyrannidae (tyrants or flycatchers) was reported from the Late Miocene Cerro Azul Formation (Cenizo *et al.*, 2012). Undeterminate Furnariidae (ovenbirds) have been reported for the Late Pliocene of Chapadmalal Formation (Tambussi, 2011). Most significant remains of Passeriformes are Suboscines (Tyrannides) exhumed from the Early–Middle Pleistocene of the Buenos Aires Province (*Pseudoseisuropsis nehuén* Noriega, 1991; *Pseudoseisuropsis wintu* Stefanini *et al.*, 2016; *Pseudoseisura*

cursor Tonni & Noriega, 2001, and *Cinclodes major* Tonni, 1977). Oscines (Passeri) are represented only in the Middle Pleistocene of Buenos Aires Province (*Zonotrichia robusta* Tonni, 1970; *Pampaemberiza olrogii* Agnolín, 2007b and *Sicalis* sp., Tonni 1980). Fragments assigned to Passeriformes without further details have also been reported for other localities in the same province (Agnolín & Chimento, 2014; Cenizo *et al.*, 2015).

SYSTEMATIC PALEONTOLOGY

RHEIFORMES (Forbes, 1884)

RHEIDAE Bonaparte, 1849

Genus *Opisthodactylus* Ameghino, 1895

Type species. *Opisthodactylus patagonicus* Ameghino, 1895. Early–Middle Miocene, Santa Cruz Formation, Cerro Observatorio locality, Santa Cruz Province.

Opisthodactylus patagonicus Ameghino, 1895

Holotype. NHMUK A586, pedal phalanges and distal fragments of tarsometatarsus.

Geographic and stratigraphic occurrence. The holotype proceeds from Cerro Observatorio locality, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation. Additional specimens have been recovered on the outcrops of Santa Cruz Formation in the course of the Río Santa Cruz, at Estancia (Ea.) Santa Lucía and Ea. El Refugio localities (Diederle & Noriega, 2019), and from Lago Ecker and Lago Pueyrredón in the Andean region of Santa Cruz Province (Sinclair & Farr, 1932).

Opisthodactylus kirchneri Noriega, Jordan,

Vezzosi & Areta, 2017

Figure 1.1

Holotype. MUFYCA-647, right femur, both tibiotarsi and tarsometatarsi, six pedal phalanges.

Geographic and stratigraphic occurrence. Agua del Chañar locality, Santa María valley, Tucumán Province, Late Miocene, Andalhuala Formation.

Comments. A specimen assigned to *O. cf. kirchneri* has been

recorded in the lower levels of the Toro Negro Formation (Late Miocene), at the Quebrada de la Troya, La Rioja Province (Tambussi *et al.*, 2021).

Opisthodactylus horacioperezi Agnolín & Chafrat, 2015

Figure 1.2

Holotype. MPCN-PV-380, distal end of left tibiotarsus.

Geographic and stratigraphic occurrence. Paso Córdoba, southwestern of General Roca city, Río Negro Province, Early Miocene, Chichinales Formation.

Genus *Rhea* Brisson, 1760

Type species. *Rhea americana* (Linnaeus, 1758). Recent, southern and eastern South America.

Rhea mesopotamica (Agnolín & Noriega, 2012) comb. nov.

Figure 1.4

Holotype. MACN-Pv 12743, distal end of right tarsometatarsus.

Geographic and stratigraphic occurrence. Besides the holotype locality, *Rhea mesopotamica* also has records in the Aisol Formation (Middle–Late Miocene), Mendoza Province (Noriega & Agnolín, 2008).

Comments. The South American Classification Committee SACC proposes to include *Pterocnemia* within *Rhea* (Proposal 348, SACC updated 31 January 2022). The current nomenclature code recommends not using a generic name if it has been replaced by a subjective synonym (recommendation 6A of the current Code, ICZN 1999: 5).

Genus *Heterorhea* Rovereto, 1914

Type species. *Heterorhea dabbenei* Rovereto, 1914. Early Pliocene, Monte Hermoso Formation, cliffs along the coast at Monte Hermoso, 17 km WSW of Pehuen-Có locality, Buenos Aires Province.

Heterorhea dabbenei Rovereto, 1914

Holotype. Lost, left tarsometatarsus.

Geographic and stratigraphic occurrence. Cliffs along the coast at Monte Hermoso, 17 km WSW of Pehuen-Có locality,

Buenos Aires Province, Early Pliocene, Monte Hermoso Formation.

Genus *Hinasuri* Tambussi, 1995a

Type species. *Hinasuri nehuensis* Tambussi, 1995a. Early Pliocene, Monte Hermoso Formation, cliffs along the coast at Monte Hermoso, Coronel de Marina L. Rosales district, Buenos Aires Province.

Hinasuri nehuensis Tambussi, 1995a

Figure 1.3

Holotype. MLP 86-VI-21-1, femur lacking the distal end.

Geographic and stratigraphic occurrence. Cliffs along the coast at Monte Hermoso, Coronel de Marina L. Rosales district, Buenos Aires Province, Early Pliocene, Monte Hermoso Formation.

TINAMIFORMES Huxley, 1872

TINAMIDAE Gray, 1840

Genus *Crypturellus* Brabourne & Chubb, 1914

Type species. *Crypturellus tataupa* (Temminck, 1815). Recent, east central of South America, and parts of Peru and Bolivia.

Crypturellus reai Chandler, 2012

Figure 1.5

Holotype. AMNH-FAM 9151, left humerus.

Geographic and stratigraphic occurrence. Cañadón de las Vacas, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Genus *Eudromia* Saint-Hilaire, 1832

Type species. *Eudromia elegans* Saint-Hilaire, 1832. Recent, western Argentina and windswept Patagonia.

Eudromia olsoni (Rovereto, 1914)

Figure 1.6

Holotype. MACN-Pv 16597A, left humerus.

Geographic and stratigraphic occurrence. Cliffs along the coast at Monte Hermoso, 17 km WSW of Pehuen-Có locality,

Buenos Aires Province, Early Pliocene, Monte Hermoso Formation.

Nothura parvula (Rovereto, 1914)

Genus *Nothura* Wagler, 1827

Type species. *Nothura boraquira* (Spix, 1825). Recent, northern Chaco region in central southern South America, in eastern Bolivia, Paraguay, and southwest Brazil.

Holotype. MACN-Pv 16596, right humerus, carpometacarpus, left coracoid, and tarsometatarsus.

Geographic and stratigraphic occurrence. Cliffs along the coast at Monte Hermoso, 17 km WSW of Pehuen-Có locality, Buenos Aires Province, Early Pliocene, Monte Hermoso Formation.



Figure 1. Palaeognathae. 1–4, Rheiformes. 1, *Opisthodactylus kirchneri*, MUFYCA-647, right femur and tibiotarsus, tarsometatarsi and toes; 2, *Opisthodactylus horacioperezi*, MPCN-PV-380, fragmentary tibiotarsus; 3, *Hinasuri nehuensis*, MLP 86-VI-21-I, left femur; 4, *Rhea mesopotamica*, MACN-Pv 12743, right tarsometatarsus. 5–6, Tinamiformes. 5, *Crypturellus reai*, AMNH 9151, left humerus; 6, *Eudromia olsoni*, MACN-Pv 16597A, left humerus. Scale=1 cm.

ANSERIFORMES Wagler, 1831
PRESBYORNITHIDAE Wetmore, 1926

Genus *Telmabates* Howard, 1955

Type species. *Telmabates antiquus* Howard, 1955. Early Eocene, Las Flores Formation, south of Río Chico in Cañadón Hondo locality, near Paso Niemann, Chubut Province.

Telmabates antiquus Howard, 1955

Holotype. AMNH 3170, a partial skeleton (associated elements of most of the postcranial skeleton).

Geographic and stratigraphic occurrence. South of Río Chico in Cañadón Hondo locality, near Paso Niemann, Chubut Province, early Eocene, Las Flores Formation.

Comments. Associated with the holotype, several individuals (at least, nine) have been found (Howard, 1955).

ANATIDAE Vigors, 1825

Genus *Aminornis* Ameghino, 1899

Type species. *Aminornis excavatus* Ameghino, 1899. Late Oligocene, Deseado Formation, locality not specified by the author, Santa Cruz Province.

Aminornis excavatus Ameghino, 1899

Holotype. MACN-A 10305, dorsal end of right coracoid.

Geographic and stratigraphic occurrence. Locality not specified by the author (see Agnolín, 2004), Santa Cruz Province, late Oligocene, Deseado Formation.

Genus *Teleornis* Ameghino, 1899

Type species. *Teleornis impressus* Ameghino, 1899. Late Oligocene, Deseado Formation, locality not specified by the author, Santa Cruz Province.

Teleornis impressus Ameghino, 1899

Holotype. MACN-A 10899, distal half of right humerus.

Geographic and stratigraphic occurrence. Locality not specified by the author (see Agnolín, 2004), Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. A review of the material in hand carried out by Agnolín (2004) suggests that this taxon may belong to the Anatidae Tadorninae.

Genus *Loxornis* Ameghino, 1895

Type species. *Loxornis clivus* Ameghino, 1895. Late Oligocene, Deseado Formation, Río Deseado, Cabeza Blanca locality, Santa Cruz Province.

Loxornis clivus Ameghino, 1895

Holotype. NHMUK A597, distal end of left tibiotarsus.

Geographic and stratigraphic occurrence. Río Deseado, Cabeza Blanca locality, Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. Tonni (1980) states that this species is recorded in two localities (Río Deseado and Río Chico) from two different provinces, Santa Cruz and Chubut. Nevertheless, the only record known is the holotype coming from Santa Cruz Province. At the present state, it is not possible to corroborate Tonni's statement of this larger distribution.

Genus *Cayaoa* Tonni, 1979

Type species. *Cayaoa bruneti* Tonni, 1979. Early Miocene, Gaiman Formation, south margin of Chubut River, between Gaiman and Trelew cities, Santiago Rodríguez's small farm, Chubut Province.

Cayaoa bruneti Tonni, 1979

Holotype. MLP 77-XII-22-1, right tarsometatarsus without the trochlea IV.

Geographic and stratigraphic occurrence. South margin of Chubut River, between Gaiman and Trelew cities, Santiago Rodríguez's small farm, Chubut Province, Early Miocene, Gaiman Formation.

Genus *Eoneornis* Ameghino, 1891

Type species. *Eoneornis australis* Ameghino, 1891. Early–Middle Miocene, Santa Cruz Formation, Monte Observación locality, Santa Cruz Province.

Eoneornis australis Ameghino, 1891

Holotype. NHMUK-A595, distal end of radius.

Geographic and stratigraphic occurrence. Monte Observación locality, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Genus *Eutelornis* Ameghino, 1891

Type species. *Eutelornis patagonicus* Ameghino, 1891. Early–Middle Miocene, Santa Cruz Formation, Monte Observación locality, Santa Cruz Province.

Eutelornis patagonicus Ameghino, 1891

Holotype. NHMUK-A596, distal end of humerus, and proximal end of tibiotarsus.

Geographic and stratigraphic occurrence. Monte Observación locality, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Genus *Ankonetta* Cenizo & Agnolín, 2010

Type species. *Ankonetta larriestrai* Cenizo & Agnolín, 2010. Early–Middle Miocene, Santa Cruz Formation, Upper Bandurrias River, 12 km south of Calafate, Santa Cruz Province.

Ankonetta larriestrai Cenizo & Agnolín, 2010

Figure 2.2

Holotype. GHUNLPam, 14935.8–14933.4, incomplete tarsometatarsus.

Geographic and stratigraphic occurrence. Upper Bandurrias River, 12 km south of Calafate, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Genus *Chloephaga* Eyton, 1838

Type species. *Chloephaga picta* Gmelin, 1789. Recent, southern South America.

Chloephaga robusta Tambussi, 1998

Figure 2.3

Holotype. MLP 57-VII-23-47, distal fragment of right ulna.

Geographic and stratigraphic occurrence. Cascada Grande, cliffs of Quequén Salado river, Buenos Aires Province, Early Pliocene, "Irene Formation".

Genus *Pleistoanser* Agnolín, 2006a

Type species. *Pleistoanser bravardi* Agnolín, 2006a. Early–Middle Pleistocene, Miramar Formation, Malacara locality, Centinela del Mar, Buenos Aires Province.

Pleistoanser bravardi Agnolín, 2006a

Figure 2.4

Holotype. MACN-Pv 6399, fragments of left coracoid, humerus, ulna, radius, and both carpometacarpus.

Geographic and stratigraphic occurrence. Malacara locality, Centinela del Mar, Buenos Aires Province, Early–Middle Pleistocene, Miramar Formation.

Genus *Anas* Linnaeus, 1758

Type species. *Anas platyrhynchos* Linnaeus, 1758. Recent, widely distributed in the Northern Hemisphere.

Anas cheuen Agnolín, 2006a

Figure 2.1

Holotype. MACN-Pv 12475, proximal end of left carpometacarpus.

Geographic and stratigraphic occurrence. Marine cliffs of La Chata, Lobería locality, Buenos Aires Province, Early–Middle Pleistocene, Miramar Formation.

Genus *Callonetta* Delacour, 1936

Type species. *Callonetta leucophrys* (Vieillot, 1816). Recent, central South America.

Callonetta talarae (Campbell, 1979)

Holotype. ROM12904, left humerus.

Geographic and stratigraphic occurrence. The holotype comes from the Talara Tar Seeps in Peru, from the Late Pleistocene, Mancora Tablazo terrace. The Argentinean record of this species consists of three elements. MLP 64-VIII-31-2 is a left humerus, MLP 76-VII-2-13 consists on a proximal end right humerus, and MLP 76-VI-2-21 is represented by a left carpometacarpus. These remains are Early–Middle Pleistocene in age (Miramar Formation), and comes

from Centinela del Mar locality, Buenos Aires Province (Agnolín, 2006a).

Genus *Oressochen* Bannister, 1870

Type species. *Oressochen jubatus* (Spix, 1825). Recent, eastern South America.

Oressochen debilis (Ameghino, 1891) comb. nov.

Holotype. Lost (Mones, 1986; Agnolín, 2006a), tarsometatarsus.

Geographic and stratigraphic occurrence. La Plata City, Buenos Aires Province, Late Pleistocene, Belgrano Formation.

Comments. This species was previously included in *Neochen* Oberholser, 1918. However, the South American Classification Committee SACC proposed that *Neochen* be replaced by *Oressochen* (Proposal 637).

GRUIFORMES Bonaparte, 1854

INCERTAE FAMILIAE

Genus *Anisolornis* Ameghino, 1891

Type species. *Anisolornis excavatus* Ameghino, 1891. Early–Middle Miocene, Santa Cruz Formation, Karaiken locality, upstream of the Río Santa Cruz near Lago Argentino, Santa Cruz Province.

Anisolornis excavatus Ameghino, 1891

Holotype. NHMUK-A594, distal portion of left tarsometatarsus.

Geographic and stratigraphic occurrence. Karaiken locality, upstream of the Río Santa Cruz near Lago Argentino, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

CICONIIFORMES Bonaparte, 1854

INCERTAE FAMILIAE

Genus *Lophiornis* Ameghino, 1891

Type species. *Lophiornis obliquus* Ameghino, 1891. Early–Middle Miocene, Santa Cruz Formation, Monte Observación, Santa Cruz Province.

Lophiornis obliquus Ameghino, 1891

Figure 2.8

Holotype. NHMUK A584, distal end of left tibiotarsus.

Geographic and stratigraphic occurrence. Monte Observación, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

CICONIIDAE Gray, 1831

Genus *Leptoptilos* Lesson, 1831

Type species. *Leptoptilos dubius* (Gmelin, 1789). Recent, east Nepal, northern India and Bangladesh, and Indochina.

Leptoptilos patagonicus

Noriega & Cladera, 2008

Figure 2.9

Holotype. MEF1363, associated partial skeleton including skull fragments, wing and leg bones.

Geographic and stratigraphic occurrence. Punta Buenos Aires, Península Valdés, Chubut Province, Late Miocene, Puerto Madryn Formation.

Genus *Ciconia* Brisson, 1760

Type species. *Ciconia ciconia* (Linnaeus, 1758). Recent, north and southern Africa, west Asia, and Europe.

Ciconia lydekkeri (Ameghino, 1891)

Holotype. NHMUK 18879, distal end of right tarsometatarsus.

Geographic and stratigraphic occurrence. The holotype comes from the Late Pleistocene of Lagoa Santa, Minas Gerais, Brazil. The record from Argentina consists on a distal fragment of right humerus coming from the Late Pleistocene of the Luján Formation, outcropping in Monte Hermoso, Buenos Aires Province (see Tonni, 1984). The taxon is also known from Bolivia.

Comments. This taxon was formerly named as *Prociconia lydekkeri*. Nevertheless, Agnolín (2009b) proposed the new combination *Ciconia lydekkeri*.



SULIFORMES Reichenbach, 1849

ANHINGIDAE Reichenbach, 1849

Genus *Anhinga* Brisson, 1760

Type species. *Anhinga anhinga* (Linnaeus, 1766). Recent, southern North America to eastern South America.

Anhinga hesterna (Ameghino, 1895)

Holotype. NHMUK-A599, eleventh cervical vertebra.

Geographic and stratigraphic occurrence. La Cueva locality, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Comments. Initially referred to the monotypic genus *Liptornis* Ameghino, 1895, this taxon has been recently included in the extant genus *Anhinga* by Diederle (2015).

Genus *Pseudolarus* Ameghino, 1891

Type species. *Pseudolarus eocaenus* Ameghino, 1891. Early–Middle Miocene, Santa Cruz Formation, Monte Observación, Santa Cruz Province.

Pseudolarus eocaenus Ameghino, 1891

Holotype. NHMUK A585, fragmentary proximal end of humerus.

Geographic and stratigraphic occurrence. Monte Observación, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Comments. This taxon was considered as a Phorusrhacidae Psilopterinae by several authors (Agnolín, 2006b; Tambussi & Degrange, 2013), but recently included among Anhingidae by Agnolín (2016a), a criterion followed by Diederle & Agnolín (2017).

Genus *Macranhinga* Noriega, 1992

Type species. *Macranhinga paranensis* Noriega, 1992. Late Miocene, Ituzaingó Formation, cliffs of Paraná River, Paraná city, Entre Ríos Province.

Macranhinga ameghinoi Diederle & Agnolín, 2017

Figure 2.6

Holotype. MLP 10-X-15-1, proximal end of right tarsometatarsus.

Geographic and stratigraphic occurrence. Southwestern to Puesto Marileo, near Ingeniero Jacobacci City, Río Negro Province, early Middle Miocene.

Macranhinga paranensis Noriega, 1992

Figure 2.5

Holotype. MACN-Pv 13507, right tarsometatarsus.

Geographic and stratigraphic occurrence. The holotype comes from the cliffs of Paraná River, Paraná city, Entre Ríos Province, Late Miocene, Ituzaingó Formation. Older specimens have been recovered from the Middle–Late Miocene of Paraná Formation, in the outcrops of the cliffs of Paraná River in Entre Ríos Province (Diederle *et al.*, 2012).

Macranhinga ranzii Alvarenga & Guilherme, 2003

Holotype. UFAC-3640, left femur lacking distal end.

Geographic and stratigraphic occurrence. The holotype comes from the Sitio Niteroi, 20 km south to the city of Rio Branco, Brazil, Late Miocene–Early Pliocene, Solimões Formation. The material MACN-Pv 14371 recovered in the cliffs of Paraná River, in Argentina corresponds to a femur coming from the Late Miocene, Ituzaingó Formation, Entre Ríos.

Figure 2. 1–4, Anseriformes. **1,** *Anas cheuen*, MACN-Pv 12475, fragmentary left carpometacarpus; **2,** *Ankonetta larriestrai*, GHUNLPam 14935.8–14933.4, fragmentary right tarsometatarsus; **3,** *Chloephaga robusta*, MLP 57-VII-23-47, left ulna; **4,** *Pleistoanser bravardi*, MACN-Pv 6399, left fragmentary coracoid, humerus, ulna, radius, and carpometacarpus. **5–10,** Aequorlithornithes. **5,** *Macranhinga paranensis*, MACN-Pv 13507, right tarsometatarsus; **6,** *Macranhinga ameghinoi*, MLP 10-X-15-1, proximal end of right tarsometatarsus; **7,** *Vanellus lilloi*, MACN-Pv 12475e, distal end of right humerus; **8,** *Lophiornis obliquus*, NHMUK A584, distal end of left tibiotarsus; **9,** *Leptoptilos patagonicus*, MPEF-1363, right humerus, left ulna, radii, left carpometacarpus, pelvis, fragmentary symphysis, detail of the distal portion of left tibiotarsus, and sternum; **10,** *Megapaloelodus peiranoi*, PVL 3327, cervical vertebra, right coracoid, right humerus, proximal extremity of right radius, phalanx, and fragmentary synsacrum; **11,** *Madrynornis mirandus*, MEF-PV 100, selected skeletal elements of the complete skeleton found. Scale= 1 cm.

PELECANIFORMES Sharpe, 1891
THRESKIORNITHIDAE Richmond, 1917

Genus *Protibis* Ameghino, 1891

Type species. *Protibis cnemialis* Ameghino, 1891. Early–Middle Miocene, Santa Cruz Formation, Monte Observación, Santa Cruz Province.

Protibis cnemialis Ameghino, 1891

Holotype. NHMUK-A598 distal end of right tibiotarsus.

Geographic and stratigraphic occurrence. Monte Observación, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

CHARADRIIFORMES (Huxley, 1867)
CHARADRIIDAE (Vigors, 1825)

Genus *Vanellus* Brisson, 1760

Type species. *Vanellus vanellus* (Linnaeus, 1758). Recent, Europe, Turkey and northwestern Iran through western Russia and Kazakhstan to southern and eastern Siberia, Mongolia, and northern China.

Vanellus lilloi (Cenizo & Agnolín, 2017) comb. nov.
Figure 2.7

Holotype. MACN Pv 12475e, distal end of right humerus.

Geographic and stratigraphic occurrence. Coastal cliffs of La Chata, Buenos Aires Province, Early–Middle Pleistocene, Miramar Formation.

Genus *Pseudosterna* Mercerat, 1897

Type species. *Pseudosterna degener* Mercerat, 1897. Late Pleistocene, Luján Formation, Luján, Buenos Aires Province.

Pseudosterna degener Mercerat, 1897

Holotype. Lost, supposedly from the MLP collections, distal portion of left humerus.

Geographic and stratigraphic occurrence. Luján, Buenos Aires Province, Late Pleistocene, Luján Formation.

Pseudosterna pampeana Mercerat, 1897

Holotype. Lost, supposedly from the MLP collections, distal end of left ulna.

Geographic and stratigraphic occurrence. Arrecifes City, Buenos Aires Province, Late Pleistocene, Luján Formation.

SPHENISCIFORMES Sharpe, 1891
SPHENISCIDAE Bonaparte, 1831

Genus *Palaeudyptes* Huxley, 1859

Type species. *Palaeudyptes antarcticus* Huxley, 1859. Late Oligocene, Otekaike Limestone, Kakanui, New Zealand.

Palaeudyptes gunnari (Wiman, 1905)

Holotype. NRM A.7, Incomplete tarsometatarsus.

Geographic and stratigraphic occurrence. The holotype has been found in Seymour Island, Antarctica, in the Eocene of La Meseta Formation. This species is also recorded in the late middle Eocene of La Leticia Formation, in the outcrops of Punta Torcida locality, Tierra del Fuego Province. The specimens consist of a pelvis, right femur, and right tibiotarsus (CADIC P 21), and a coracoid (CADIC P 22).

Genus *Arthrodytes* Ameghino, 1905

Type species. *Arthrodytes andrewsi* (Ameghino, 1905). Late Eocene–early Oligocene, San Julián Formation, Bajo de San Julián, Santa Cruz Province.

Arthrodytes andrewsi (Ameghino, 1905)

Holotype. MLP-606, right humerus.

Geographic and stratigraphic occurrence. Bajo de San Julián, Santa Cruz Province, late Eocene–early Oligocene, San Julián Formation.

Comments. Originally described as *Parapterodytes* by Ameghino (1905), its assignment was reconsidered by Simpson (1946) and Acosta Hospitaleche (2005).

Genus *Eretiscus* Olson, 1986

Type species. *Eretiscus tonnii* (Simpson, 1981). Early Miocene, Gaiman Formation, south Chubut River, Bryn Gwyn locality, Chubut Province.

Eretiscus tonnii (Simpson, 1981)

Holotype. MLP 81-VI-26-1, right tarsometatarsus lacking trochleae II and IV.

Geographic and stratigraphic occurrence. South Chubut River, Bryn Gwyn locality, Chubut Province, Early Miocene, Gaiman Formation.

Comments. The genus was proposed by Olson (1986) to replace *Microdytes* Simpson, 1981 which had already been used as the name of a beetle (Acosta Hospitaleche *et al.*, 2004).

Genus *Palaeospheniscus* Moreno & Mercerat, 1891

Type species. *Palaeospheniscus patagonicus* Moreno & Mercerat, 1891. Early Miocene, Gaiman Formation, Bryn Gwyn locality, Chubut Province.

Palaeospheniscus bergi Moreno & Mercerat, 1891

Holotype. MLP 20-81, left tarsometatarsus.

Geographic and stratigraphic occurrence. Bryn Gwyn locality, Chubut Province, Early Miocene, Gaiman Formation.

Palaeospheniscus patagonicus Moreno & Mercerat, 1891

Lectotype. MLP 20-34, left tarsometatarsus.

Geographic and stratigraphic occurrence. Bryn Gwyn locality, Chubut Province, Early Miocene, Gaiman Formation.

Palaeospheniscus biloculata (Simpson, 1970)

Holotype. AMNH 3346, fragment of right humerus.

Geographic and stratigraphic occurrence. Bryn Gwyn locality, Chubut Province, Early Miocene, Gaiman Formation.

Genus *Parapterodytes* Ameghino, 1891

Type species. *Parapterodytes antarcticus* (Moreno & Mercerat, 1891). Early Miocene, Monte León Formation, "Santa Cruz River mouth" (locality not well specified by the authors), Santa Cruz Province.

Parapterodytes antarcticus (Moreno & Mercerat, 1891)

Syntype. MLP 20-1, right ulna (lost); MLP 20-2, complete right femur; MLP 20-3, fragmentary right femur (lost); MLP

20-4, incomplete right tibiotarsus; MLP 20-5, left tibiotarsus (lost); MLP 20-6, incomplete right tarsometatarsus.

Geographic and stratigraphic occurrence. The holotype comes from "Santa Cruz River mouth" (locality not well specified by the authors), Santa Cruz Province, Early Miocene, Monte León Formation. Additional specimens have been recovered from the early Late Miocene of Puerto Madryn Formation (Acosta Hospitaleche, 2003). An almost complete skeleton has been found in the Early Miocene of Gaiman Formation (Bertelli *et al.*, 2006).

Comments. According to Moreno & Mercerat (1891), the specimens MLP 20-1, 20-3, and 20-5 come from Chubut Province.

Parapterodytes robustus (Ameghino, 1895)

Holotype. NHMUK A/591, humerus.

Geographic and stratigraphic occurrence. Locality not specified by the author, Santa Cruz Province, late Eocene–early Oligocene, San Julián Formation.

Genus *Madrynornis* Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007

Type species. *Madrynornis mirandus* Acosta Hospitaleche *et al.*, 2007. Early Late Miocene, Puerto Madryn Formation, Playa Larralde, Península Valdés, Chubut Province.

Madrynornis mirandus Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007

Figure 2.11

Holotype. MEF-PV 100, a nearly complete skeleton.

Geographic and stratigraphic occurrence. Playa Larralde, Península Valdés, Chubut Province, early Late Miocene, Puerto Madryn Formation.

PROCELLARIIFORMES Fürbringer, 1888

PROCELLARIIDAE (Boie, 1826)

Genus *Argyrodyptes* Ameghino, 1905

Type species. *Argyrodyptes microtarsus* Ameghino, 1905. Late Eocene–early Oligocene, San Julián Formation, Río Seco locality, Chubut Province.

Argyrodypetes microtarsus Ameghino, 1905

Holotype. MACN-A 11037, left femur without *extremitas distalis*, and left tibiotarsus without *extremitas proximalis*.

Geographic and stratigraphic occurrence. Río Seco locality, Chubut Province, late Eocene–early Oligocene, San Julián Formation.

PHOENICOPTERIFORMES Fürbringer, 1888
INCERTAE FAMILIAEGenus *Tiliornis* Ameghino, 1899

Type species. *Tiliornis senex* Ameghino, 1899. Late Oligocene, Deseado Formation, locality not specified by the author, Santa Cruz Province.

Tiliornis senex Ameghino, 1899

Holotype. Lost, collection number is unknown, coracoid.

Geographic and stratigraphic occurrence. Locality not specified by the author, Santa Cruz Province, late Oligocene, Deseado Formation.

PALAEOLODIDAE Stejneger, 1885

Genus *Megapaloelodus* Miller, 1944

Type species. *Megapaloelodus connectens* Miller, 1944. Early Miocene, Rosebud Formation, Flint Hill, South Dakota, USA.

Megapaloelodus peiranoi Agnolín, 2009c

Figure 2.10

Holotype. PVL 3327, right coracoid, distal and proximal ends of right humerus, proximal end of right radius, phalanx digit majoris II, and fragment of notarium and synsacrum.

Geographic and stratigraphic occurrence. El Molle Grande locality, valle del Cajón, Catamarca Province, Late Miocene, Andalhuala Formation.

CATHARTIFORMES Coues, 1884

CATHARTIDAE Lafresnaye, 1839

Genus *Dryornis* Moreno & Mercerat, 1891

Type species. *Dryornis pampeanus* Moreno & Mercerat, 1891. Early Pliocene, Monte Hermoso Formation, cliffs along the coast at Monte Hermoso, 17 km WSW of Pehuen-Có locality, Buenos Aires Province.

Dryornis pampeanus Moreno & Mercerat, 1891

Lectotype. MLP 20-169, distal portion of a right humerus.

Geographic and stratigraphic occurrence. The holotype comes from the Farola de Monte Hermoso locality, in the coast of Buenos Aires Province, in the outcrops of Monte Hermoso Formation (Early Pliocene). Additional and more complete material (MMP 5731) coming from the Chapadmalal Formation (Late Pliocene), in Playa La Estafeta locality in Mar del Plata city, Buenos Aires Province was recently described by Degrange *et al.* (2021a).

Dryornis hatcheri Degrange, 2022

Figure 3.4

Holotype. YMP-PVVU 15866, left fragmentary humerus.

Geographic and stratigraphic occurrence. Lago Pueyrredón locality, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Genus *Geronogyps* Campbell, 1979

Type species. *Geronogyps reliquus* Campbell, 1979. Late Pleistocene, Mancora Tablazo terrace, Talara Tar Seeps, Peru.

Geronogyps reliquus Campbell, 1979

Holotype. ROM 12986, complete right tarsometatarsus.

Geographic and stratigraphic occurrence. The holotype comes from the Talara Tar Seeps in Peru, from the Late Pleistocene, Mancora Tablazo terrace. Records of this taxon from Argentina correspond to those coming from the Late Pleistocene–Early Holocene, Salto Ander Egg Formation (following Brunetto *et al.*, 2015) outcropping in Ensenada and Barrenechea rivers in Entre Ríos Province (Noriega & Areta, 2005); and also, from the left margin of Arroyo Chasicó, Pleistocene *sensu lato*, Buenos Aires Province (Tambussi & Noriega, 1999).

Genus *Pampagyps* Agnolín, Brissón, Soibelzon, Rodríguez, Soibelzon, Iacona, & Piazza, 2017

Type species. *Pampagyps imperator* Agnolín *et al.*, 2017. Late Pleistocene–Early Holocene, Cantera Nicolás Vignogna III, Marcos Paz, Buenos Aires Province.

Pampagyps imperator Agnolín, Brissón, Soibelzon, Rodríguez, Soibelzon, Iacona, & Piazza, 2017
Figure 3.3

Holotype. MPLK-00001, right tarsometatarsus.

Geographic and stratigraphic occurrence. Cantera Nicolás Vignogna III, Marcos Paz, Buenos Aires Province, Late Pleistocene–Early Holocene.

ACCIPITRIFORMES Voous, 1973
ACCIPITRIDAE Vieillot, 1816

Genus *Vinchinavis* Tambussi, Degrange, Ciccioi & Prevosti, 2021

Type species. *Vinchinavis paka* Tambussi *et al.*, 2021. Late Miocene, lower levels of Toro Negro Formation, Quebrada de la Troya, between Vinchina and Jagüé localities, La Rioja Province.

Vinchinavis paka Tambussi, Degrange, Ciccioi, & Prevosti, 2021
Figure 3.1

Holotype. PULR-V 130, left ulna and radius lacking the proximal ends.

Geographic and stratigraphic occurrence. Quebrada de la Troya, between Vinchina and Jagüé localities, La Rioja Province, Late Miocene, lower levels of Toro Negro Formation.

Genus *Buteo* Lacépède, 1799

Type species. *Buteo buteo* (Linnaeus, 1758). Recent, Europe, central Asia, northwestern, and southern Africa.

Buteo dondasi Degrange, Tambussi, Taglioretti, & Scaglia, 2021
Figure 3.2

Holotype. MMP 5730, incomplete left hind limb with distal

fragments of tibiotarsus, tarsometatarsus, os metatarsal I and toes I and II.

Geographic and stratigraphic occurrence. Playa La Estafeta, Mar del Plata, Buenos Aires Province, lowest part of Playa Los Lobos Alloformation, Late Pliocene, Chapadmalal Formation.

CORACIIFORMES Forbes, 1884
INCERTAE FAMILIAE

Genus *Ueekenkoracias* Degrange, Pol, Puerta & Wilf, 2021

Type species. *Ueekenkoracias tambussiae* Degrange *et al.*, 2021c. Early Eocene, Huitrera Formation, Laguna del Hunco locality, Chubut Province.

Ueekenkoracias tambussiae Degrange, Pol, Puerta, & Wilf, 2021c
Figure 3.5

Holotype. MPEF-PV 10991, incomplete right hind limb.

Geographic and stratigraphic occurrence. Laguna del Hunco locality, Chubut Province, early Eocene, Huitrera Formation.

PICIFORMES Meyer & Wolf, 1810
PICIDAE Vigors, 1825

Genus *Colaptes* Swainson, 1825

Type species. *Colaptes auratus* (Linnaeus, 1758). Recent, North America to north-central Nicaragua, Cuba, and Grand Cayman Island.

Colaptes naroskyi Agnolín & Jofré, 2017
Figure 3.6

Holotype. MFJM 00639, incomplete skeleton.

Geographic and stratigraphic occurrence. The holotype comes from De la Reconquista River, in Agustín Ferrari locality, near Merlo city, Buenos Aires Province, from the outcrops of the Jáuregui Member of Luján Formation (Late Pleistocene). Additional material recovered from the Early–Middle Pleistocene of Punta Hermengo locality, Buenos Aires Province is housed in La Plata Museum.

CARIAMIFORMES Verheyen, 1957
PHORUSRHACIDAE Ameghino, 1889

Genus *Physornis* Ameghino, 1895

Type species. *Physornis fortis* Ameghino, 1895. Late Oligocene, Deseado Formation, Río Deseado, Santa Cruz Province.

Physornis fortis Ameghino, 1895

Holotype. NHMUK-A583, mandible fragment including the ventral portion of the mandibular symphysis and part of the right mandibular branch.

Geographic and stratigraphic occurrence. Río Deseado, Santa Cruz Province, late Oligocene, Deseado Formation.

Genus *Andrewsornis* Patterson, 1941

Type species. *Andrewsornis abbotti* Patterson, 1941. Late Oligocene, Deseado Formation, Cabeza Blanca locality, Chubut Province.

Andrewsornis abbotti Patterson, 1941

Holotype. FM-P13417, partial cranium, fragments of the mandible. Also, coracoid and pedal phalanges but lost.

Geographic and stratigraphic occurrence. Cabeza Blanca locality, Chubut Province, late Oligocene, Deseado Formation.

Comments. Putative *Andrewsornis* has been recovered from the Oligocene outcrops of the Deseado Formation, at Pico Truncado locality in Santa Cruz Province.

Genus *Psilopterus* Moreno & Mercerat, 1891

Type species. *Psilopterus bachmanni* (Moreno & Mercerat, 1891). Early–Middle Miocene, Santa Cruz Formation, specific locality not specified by the author, Santa Cruz Province.

Psilopterus affinis (Ameghino, 1899)

Holotype. MACN-A 52-184, right tarsometatarsus lacking a portion of the diaphysis.

Geographic and stratigraphic occurrence. Locality not specified by the author, Chubut Province, late Oligocene, Deseado Formation.

Comments. Although Alvarenga & Höfling (2003) indicates

that this taxon is recorded in Cabeza Blanca locality, the locality of the single specimen known (the holotype) is unknown as pointed out by Agnolín (2006b). A fragmentary right femur coming from the Deseado River area, and considered *Psilopterus* cf. *affinis* have been reported by Buffetaut (2014).

Psilopterus lemoinei (Moreno & Mercerat, 1891)

Lectotype. MLP 20-162, distal end of right tibiotarsus.

Geographic and stratigraphic occurrence. The lectotype comes from a locality not specified by the authors in Santa Cruz Province, corresponding to the Early–Middle Miocene of Santa Cruz Formation. *Psilopterus lemoinei* is one of the best documented species of phorusrhacids, including several skull remains (Sinclair & Farr, 1932; Degrange & Tambussi, 2011). This species is recorded mainly in the eastern outcrops of the Santa Cruz Formation: Killik Aike Norte, Ea. Halliday, Puesto Ea. La Costa, Anfiteatro, Coyle River, Cañadón de Las Vacas, Jack Harvey, Yegua Quemada, La Cueva, Monte Observación, and Monte León. Additional specimens have been recovered on the central outcrops of Santa Cruz Formation in the course of the Río Santa Cruz, in Santa Cruz Province, at Ea. Santa Lucía (Diederle & Noriega, 2019), and in the Karaiken locality on the west.

Psilopterus bachmanni (Moreno & Mercerat, 1891)

Lectotype. MLP 20-168, proximal end of left tarsometatarsus.

Geographic and stratigraphic occurrence. The lectotype comes from a locality not specified by the author, in Santa Cruz Province, corresponding to the Early–Middle Miocene of Santa Cruz Formation. Additional remains have been recovered from several localities of Santa Cruz Province: Puesto Ea. La Costa, La Cueva, Monte Observación, Río Chaliá, and a fairly complete skeleton coming from Lake Pueyrredón.

Psilopterus colzecus Tonni & Tambussi, 1988

Figure 4.2

Holotype. MLP-76-VI-12-2, incomplete skeleton.

Geographic and stratigraphic occurrence. Chasicó stream,

Villarino Department, Buenos Aires Province, Late Miocene, Arroyo Chasicó Formation.

Genus *Phorusrhacos* Ameghino, 1887

Type species. *Phorusrhacos longissimus* Ameghino, 1887. Early–Middle Miocene, Santa Cruz Formation, specific locality not specified by the author, Santa Cruz Province.

Phorusrhacos longissimus Ameghino, 1887

Holotype. MLP 20-118, mandibular symphysis.

Geographic and stratigraphic occurrence. The holotype comes from a locality not specified by the author in Santa Cruz Province, from the Early–Middle Miocene of Santa Cruz Formation. This species has been registered in several

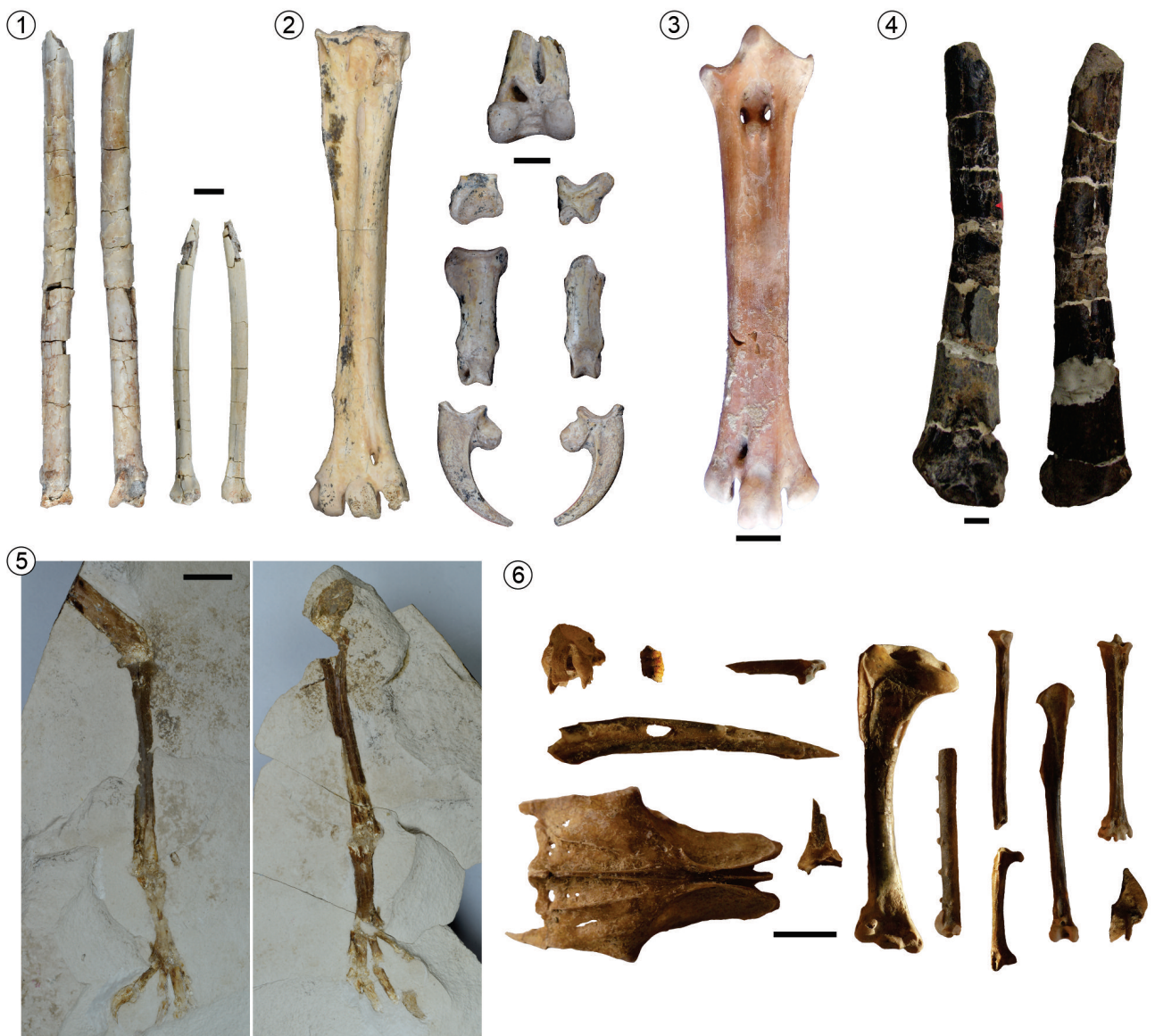


Figure 3. 1–2, Accipitriformes. 1, *Vinchinavis paka*, PULR-V 13–1998, left ulna and radius; 2, *Buteo dondasi*, MMP 5730, incomplete left hind limb. 3–4, Cathartiformes. 3, *Pampagyps imperator*, MPLK-0001, right tarsometatarsus; 4, *Dryornis hatcheri*, YMP-PVVU 15866, left fragmentary humerus. 5, Coraciiformes: *Ueekenkoracias tambussiae*, MPEF-PV 10991, incomplete right hind limb. 6, Piciformes: *Colaptes naroskyi*, MFJM 00639, fragmentary neurocranium tracheal rings, left scapula, jaw, pelvis, left coracoid, right humerus, and ulna, left radius, left femur, right tibiotarsus and tarsometatarsus, pygostyle. Scale=1 cm.

places from Santa Cruz Province, indicating a widespread distribution from southeast to the northwest: Ea. La Costa, Campo Barranca, Yegua Quemada, La Cueva, Monte Observación, Monte León, Río Chalía, and Lago Belgrano localities (Alvarenga & Höfling, 2003; Degrange *et al.*, 2012, 2019).

Genus *Patagonis* Moreno & Mercerat, 1891

Type species. *Patagonis marshi* Moreno & Mercerat, 1891. Early–Middle Miocene, Santa Cruz Formation, specific locality not specified by the author, Santa Cruz Province.

Patagonis marshi Moreno & Mercerat, 1891

Lectotype. MLP 20-143, mandibular symphysis.

Geographic and stratigraphic occurrence. The lectotype comes from a locality not specified by the author in Santa Cruz Province, from the Early–Middle Miocene of Santa Cruz Formation. *Patagonis marshi* is very well documented by several specimens, including a fairly complete skeleton described by Andrews (1899) that comes from Monte Observación. This species has been registered only in the southeast outcrops of the Santa Cruz Formation in Santa Cruz Province, in several localities: Cabo Buen Tiempo, Ea. La Angelina, Ea. La Costa, Cañadón de Las Vacas, Yegua Quemada, La Cueva, Monte Observación, Ea. La Ensenada.

Genus *Kelenken* Bertelli, Chiappe & Tambussi, 2007

Type species. *Kelenken guillermoi* Bertelli *et al.*, 2007. Middle Miocene, Collón Curá Formation, Comallo, Río Negro Province.

Kelenken guillermoi Bertelli, Chiappe & Tambussi, 2007

Figure 4.4

Holotype. BAR 3877-11, a nearly complete skull, left tarsometatarsus, proximal pedal phalanx.

Geographic and stratigraphic occurrence. Comallo, Río Negro Province, Middle Miocene, Collón Curá Formation.

Genus *Devincenzia* Kraglievich, 1932

Type species. *Devincenzia pozzi* (Kraglievich, 1931). Late Miocene, Ituzaingó Formation, El Brete locality, Río Paraná, Entre Ríos Province.

Devincenzia pozzi (Kraglievich, 1931)

Holotype. MACN-Pv 6554 and 6681, distal portion of right tarsometatarsus and ungual phalanx II.

Geographic and stratigraphic occurrence. The holotype comes from El Brete locality, Río Paraná, Entre Ríos Province, corresponding to the Late Miocene of the Ituzaingó Formation. Additional specimens have been recovered from the same formation (Noriega & Agnolín, 2008). A deformed and restored fragmentary skull of this species has been recovered from the Epecuén lagoon, Adolfo Alsina locality, Buenos Aires Province, in sediments corresponding to the lower Pliocene of Cerro Azul Formation.

Genus *Andalgalornis* Patterson & Kraglievich, 1960

Type species. *Andalgalornis steulleti* (Kraglievich, 1931). Late Miocene, Ituzaingó Formation, cliffs of the Paraná River, Entre Ríos Province.

Andalgalornis steulleti (Kraglievich, 1931)

Holotype. MACN-Pv 4244, left phalanx 1 of digit IV.

Geographic and stratigraphic occurrence. The holotype comes from the Late Miocene of the Ituzaingó Formation, outcropping in the cliffs of Paraná River, at Entre Ríos Province. Additional specimens have been recovered from the same formation (Noriega & Agnolín, 2008), and from the Late Miocene of Andalhuala Formation, Catamarca Province (Patterson & Kraglievich, 1960).

Genus *Procarriama* Rovereto, 1914

Type species. *Procarriama simplex* Rovereto, 1914. Late Miocene, Andalhuala Formation, specific locality not specified by the author, Catamarca Province.

Procarriama simplex Rovereto, 1914

Lectotype. MACN-Pv 8225, incomplete skeleton.

Geographic and stratigraphic occurrence. The lectotype comes from a locality not specified by the author in Catamarca Province, but from the outcrops of the Late Miocene of Andalhuala Formation. More specimens have

been recorded coming from Chiquimil and Puerta de Corral Quemado (Marshall & Patterson, 1981; Vezzosi, 2012). Additional records are known from the Late Miocene Cerro Azul Formation, outcropping in Salinas Grandes de Hidalgo, La Pampa Province (Vezzosi, 2012).

Genus *Mesembriornis* Moreno, 1889

Type species. *Mesembriornis milneedwardsi* Moreno, 1889. Late Pliocene, Monte Hermoso Formation, coastal cliffs of Monte Hermoso, Buenos Aires Province.

Mesembriornis incertus (Rovereto, 1914)

Holotype. MACN-Pv 6934, incomplete skeleton.

Geographic and stratigraphic occurrence. The holotype comes from an unknown locality not specified by the author in Catamarca Province (although Patterson & Kraglievich, 1960 states that may be from Santa María Valley), from the Late Miocene–Early Pliocene of Andalhuala Formation. Additional remains have been recorded in the level 17 of Marshall & Patterson (1981) in Puerta de Corral Quemado, corresponding to the Andalhuala Formation.

Mesembriornis milneedwardsi Moreno, 1889

Syntype. MLP 20-140, cervical vertebra; MLP 20-141, proximal portion of right tibiotarsus; MLP 20-142, proximal portion of right fibula.

Geographic and stratigraphic occurrence. The holotype has been found in the coastal cliffs of Monte Hermoso in Buenos Aires Province, coming from the Late Pliocene of Monte Hermoso Formation. An incomplete skeleton also proceeds from this locality (Rovereto, 1914; Kraglievich, 1940). Additional records are known from the Late Pliocene of Chapadmalal Formation, coming from Punta Lobería, in Buenos Aires Province (Kraglievich, 1946).

Comments. A *Mesembriornis* cf. *milneedwardsi* specimen has been recovered from the late Miocene of Andalhuala Formation, outcropping in Yocavil Valley, east of Loma Rica locality, Catamarca Province (Vezzosi & Noriega, 2018).

Genus *Llallawavis* Degrange, Tambussi, Taglioretti, Dondas, & Scaglia, 2015

Type species. *Llallawavis scagliai* Degrange *et al.*, 2015. Late Pliocene, Chapadmalal Formation, lowest part of Playa Los Lobos Alloformation, Playa La Estafeta, Mar del Plata, Buenos Aires Province.

Llallawavis scagliai Degrange, Tambussi, Taglioretti, Dondas, & Scaglia, 2015

Figure 4.3

Holotype. MMP 5050, a nearly complete articulated skeleton.

Geographic and stratigraphic occurrence. La Estafeta Beach, Mar del Plata, Buenos Aires Province, lowest part of Playa Los Lobos Alloformation, Late Pliocene, Chapadmalal Formation.

CARIAMIDAE Bonaparte, 1853

Genus *Miocariama* Noriega & Mayr, 2017

Type species. *Miocariama patagonica* Noriega & Mayr, 2017. Early–Middle Miocene, Santa Cruz Formation, Monte Tigre locality, Santa Cruz Province.

Miocariama patagonica Noriega & Mayr, 2017

Figure 4.1

Holotype. MPM-PV 15049, incomplete skeleton.

Geographic and stratigraphic occurrence. Monte Tigre locality, between Coyle and Gallegos rivers, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Comments. Based on a fragmentary skull, Noriega *et al.* (2009) proposed the taxon *Cariama santacrucensis*, lately transferred to *Noriegavis santacrucensis* by Agnolín (2009a). The finding of the holotype of *Miocariama patagonica*, initially considered as *Noriegavis santacrucensis*, allowed to determine that the holotype of *Noriegavis santacrucensis* was actually a Falconiformes referable to *Thegornis* Ameghino, 1895.

Genus *Chunga* Hartlaub, 1860

Type species. *Chunga burmeisteri* Hartlaub, 1860. Recent, Chaco region of central southern South America, in Bolivia, Argentina, and Paraguay.

Chunga incerta Tonni, 1974

Holotype. MLP 71-VII-5-1, distal end of right tibiotarsus.

Geographic and stratigraphic occurrence. 17 km SW to Pehuen-Có, Buenos Aires Province, Early Pliocene, Monte Hermoso Formation.

FALCONIFORMES Sharpe, 1874

FALCONIDAE Vigors, 1824

Genus *Thegornis* Ameghino, 1895

Type species. *Thegornis musculosus* Ameghino, 1895. Early–Middle Miocene, Santa Cruz Formation, Yegua Quemada, Monte León National Park, Santa Cruz Province.

Thegornis musculosus Ameghino, 1895

Holotype. NHMUK-A600, distal fragment of right tarsometatarsus.

Geographic and stratigraphic occurrence. Yegua Quemada, Monte León National Park, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation. Additional records are known from the Early Miocene of Sarmiento Formation, in Chubut Province (Tambussi & Degrange, 2013).

Thegornis debilis Ameghino, 1895

Holotype. NHMUK-A601, distal portion of right tarsometatarsus.

Geographic and stratigraphic occurrence. Corriguen Aike locality, Santa Cruz Province, Early–Middle Miocene, Santa Cruz Formation.

Genus *Badiostes* Ameghino, 1895

Type species. *Badiostes patagonicus* Ameghino, 1895. Early–Middle Miocene, Santa Cruz Formation, La Cueva locality, Santa Cruz Province.

Badiostes patagonicus Ameghino, 1895

Holotype. NHMUK-A602, fragmentary ulna, femur, and tarsometatarsus.

Geographic and stratigraphic occurrence. La Cueva locality, Santa Cruz Province. Early–Middle Miocene, Santa Cruz Formation.

Genus *Asthenopterus* Ameghino, 1891

Type species. *Asthenopterus minutus* (Moreno & Mercerat, 1891). Late Pleistocene, Buenos Aires Formation, specific locality not specified by the author, Buenos Aires Province.

Asthenopterus minutus (Moreno & Mercerat, 1891)

Holotype. Lost, MLP 20-183, right humerus.

Geographic and stratigraphic occurrence. Specific locality not specified by the author, Buenos Aires Province, Late Pleistocene, Buenos Aires Formation.

PSITTACIFORMES Wagler, 1830

PSITTACIDAE Illiger, 1811

Genus *Aratinga* Spix, 1824

Type species. *Aratinga solstitialis* (Linnaeus, 1758). Recent, north Brazil and west Guyana.

Aratinga vorohuensis (Tonni & Noriega, 1996)

Figure 5.1

Holotype. MLP 94-IV-1-1, incomplete skull and an almost complete mandible.

Geographic and stratigraphic occurrence. Balneario Terrazas del Marquesado, General Pueyrredón locality, Buenos Aires Province, Late Pliocene, "Vorohué Formation".

Comments. The South American Classification Committee SACC proposed that *Nandayus* should be included in *Aratinga* (Proposal 578).

Genus *Cyanoliseus* Bonaparte, 1854

Type species. *Cyanoliseus patagonus* (Vieillot, 1818). Recent, Chaco of northern Argentina south to southeast Argentina, and central Chilean coast.

Cyanoliseus patagonopsis Acosta Hospitaleche

& Tambussi, 2006

Figure 5.2

Holotype. MLP 81-VII-20-20, right humerus.

Geographic and stratigraphic occurrence. Punta Hermengo



Figure 4. Cariamiformes. 1, *Miocariama patagonica*, MPM-PV-15049, skull, jaw, pelvis and tarsometatarsi; 2, *Psilopterus colzecus*, MLP 76-VI-12-2, jaw, right forelimb, right femur, tibiotarsi, tarsometatarsi, left foot; 3, *Llawawavis scagliai*, MMP 5050, selected skeletal elements of the complete skeleton found. Scale=1 cm. 4, *Kelenken guillermoi*, BAR 3877-11, skull. Scale= 10 cm.

locality, Buenos Aires Province, early Middle Pleistocene, Miramar Formation.

Cyanoliseus ensenadensis (Cattoi, 1957)

Holotype. MACN-Pv 17716, left humerus.

Geographic and stratigraphic occurrence. Olivos locality, Buenos Aires Province, Middle–Late Pleistocene, Ensenada Formation.

PASSERIFORMES Linnaeus, 1758

FURNARIIDAE Gray, 1840

Genus *Pseudoseisuropsis* Noriega, 1991

Type species. *Pseudoseisuropsis nehuén* Noriega, 1991. Early Middle Pleistocene, Miramar Formation, southwestern cliffs of Punta Hermengo locality, Miramar, Buenos Aires Province.

Pseudoseisuropsis nehuén Noriega, 1991

Figure 5.4

Holotype. MLP 69-XII-3-1, skull.

Geographic and stratigraphic occurrence. Southwestern cliffs of Punta Hermengo locality, Miramar, Buenos Aires Province, early Middle Pleistocene, Miramar Formation.

Pseudoseisuropsis wintu Stefanini, Gómez,
& Tambussi, 2016

Figure 5.5

Holotype. MMP 570-M, fragmentary skull.

Geographic and stratigraphic occurrence. Near Camet Norte, north of Mar del Plata, Buenos Aires Province, early Middle Pleistocene, Miramar Formation.

Genus *Pseudoseisura* Reichenbach, 1853

Type species. *Pseudoseisura gutturalis* (D'Orbigny & Lafresnaye, 1838). Recent, west and central Argentina.

Pseudoseisura cursor Tonni & Noriega, 2001

Figure 5.6

Holotype. MLP 69-XI-14-1, incomplete skeleton.

Geographic and stratigraphic occurrence. Río de La Plata coast, in front of the Anchorena Station of the Tren de la Costa train, Vicente López Department, Buenos Aires Province, early Middle Pleistocene, Ensenada Formation.

Genus *Cinclodes* Gray, 1840

Type species. *Cinclodes patagonicus* (Gmelin, 1789). Recent, southwestern Chile and Argentina.

Cinclodes major Tonni, 1977

Holotype. MMP 161S, incomplete skeleton.

Geographic and stratigraphic occurrence. Coastal cliffs at the NNE of Mar del Plata, in front of Cobo field, Buenos Aires Province, early Middle Pleistocene, Miramar Formation.

PASSERELLIDAE Cabanis, 1851

Genus *Zonotrichia* Swainson, 1832

Type species. *Zonotrichia albicollis* (Gmelin, 1789). Recent, North America.

Zonotrichia robusta Tonni, 1970

Holotype. MLP 63-VI-30-6, upper beak and lower jaw.

Geographic and stratigraphic occurrence. SW of Punta Hermengo, Miramar, Buenos Aires Province, early Middle Pleistocene, Miramar Formation.

EMBERIZIDAE Vigors, 1831

Genus *Pampaemberiza* Agnolín, 2007b

Type species. *Pampaemberiza olrogi* Agnolín, 2007b. Middle Pleistocene, LG4 layer of Bidegain *et al.* (2005), coastal cliffs of Necochea city, Buenos Aires Province.

Pampaemberiza olrogi Agnolín, 2007b

Figure 5.3

Holotype. MLP 04-XIII-1-1, fragmentary rostrum.

Geographic and stratigraphic occurrence. Coastal cliffs of Necochea, Buenos Aires Province, Middle Pleistocene, LG4 layer of Bidegain *et al.* (2005).

INCERTAE ORDINIS

Genus *Onychopteryx* Cracraft, 1971

Type species. *Onychopteryx simpsoni* Cracraft, 1971. Early Eocene, Las Flores Formation, Cañadón Hondo locality, Chubut Province.

Onychopteryx simpsoni Cracraft, 1971

Holotype. AMNH 3188, proximal end of tarsometatarsus.

Geographic and stratigraphic occurrence. Cañadón Hondo locality, Chubut Province, early Eocene, Las Flores Formation.

Comments. Cracraft (1971) reported the presence of an Opisthocomiformes in the Eocene of Patagonia, *Onychopteryx simpsoni* including it in the monotypic family Onychopteridae. Nevertheless, Brodkorb (1978) pointed out that this taxon is based on a fragmentary proximal end of a tarsometatarsus that should be considered of indeterminate affinities, a criterion followed by several authors (Mayr *et al.*, 2011; Tambussi & Degrange, 2013; Agnolín, 2016a).

Genus *Riacama* Ameghino, 1899

Type species. *Riacama caliginea* Ameghino, 1899. Late Oligocene, Deseado Formation, specific locality not specified by the author, Santa Cruz Province.

Riacama caliginea Ameghino, 1899

Holotype. MACN-A 52-189, fragmentary right coracoid.

Geographic and stratigraphic occurrence. Specific locality not specified by the author, Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. *Riacama caliginea* from the Oligocene of Santa Cruz was originally assigned to Cariamidae by Ameghino, to Phorusrhacidae by Brodkorb (1967), again to Cariamidae by Tonni (1980) and Agnolín (2004), and to Idiornithidae by Agnolín (2009a). However, the fragmentary nature of the holotype does not allow a precise assignation of this taxon (Alvarenga & Höfling, 2003; Tambussi & Degrange, 2013).

Genus *Smiliornis* Ameghino, 1899

Type species. *Smiliornis penetrans* Ameghino, 1899. Late Oligocene, Deseado Formation, specific locality not specified by the author, Santa Cruz Province.

Smiliornis penetrans Ameghino, 1899

Holotype. MACN-A 183, proximal end of left coracoid.

Geographic and stratigraphic occurrence. Specific locality not specified by the author, Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. Also, from the Oligocene of Santa Cruz and originally assigned as a Phorusrhacidae Psilopterinae, a criterion followed by Patterson (1941), and Tonni (1980), comes *Smiliornis penetrans* based on a very fragmentary coracoid. Alvarenga & Höfling (2003) consider to be a synonym of *Psilopterus affinis*. Later, Agnolín (2009a) assigned this taxon to the family Idiornithidae. Nevertheless, the peculiar morphology precludes its assignation and led Tambussi & Degrange (2013) to consider it as *incerti ordinis*.

Genus *Cruschedula* Ameghino, 1899

Type species. *Cruschedula revola* Ameghino, 1899. Late Oligocene, Deseado Formation, specific locality not specified by the author, Santa Cruz Province.

Cruschedula revola Ameghino, 1899

Holotype. MACN-A 11039, proximal end of right scapula.

Geographic and stratigraphic occurrence. Specific locality not specified by the author, Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. Although it was considered as belonging to Accipitridae (Brodkorb, 1964; Tonni, 1980; Agnolín, 2006c), the morphology of the holotypic fragmentary scapula does not allow to infer reliable phylogenetic analysis (Mayr, 2009; Tambussi & Degrange, 2013).

Genus *Cladornis* Ameghino, 1895

Type species. *Cladornis pachypus* Ameghino, 1895. Late Oligocene, Deseado Formation, Río Deseado, Santa Cruz Province.

Cladornis pachypus Ameghino, 1895

Holotype. NHMUK A 589, right tarsometatarsus.

Geographic and stratigraphic occurrence. Río Deseado, Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. Included here is the late Oligocene taxon *Cladornis*



Figure 5. 1-2, Psittaciformes. 1, *Aratinga vorohuensis*, MLP 94-IV-1-1, skull and mandible; 2, *Cyanoliseus patagonopsis*, MLP 81-VII-20-20, right humerus. 3-7, Passeriformes. 3, *Pampaemberiza ologi*, MLP 04-XIII-1-1, fragmentary upper beak (Scale= 5 mm); 4, *Pseudoseiuropsis nehuen*, MLP 69-XII-3-1, skull; 5, *Pseudoseiuropsis wintu*, MMP 570S, fragmentary skull; 6, *Pseudoseisura cursor*, MLP 69-XI-14-1, incomplete skeleton. Scale= 1 cm.

pachypus from the Deseado Formation of Patagonia, which is based on a very peculiar tarsometatarsus whose affinities are still uncertain. Olson (1985) proposes its probable zygodactyly, which gives it possible arboreal habits, an idea followed by Mayr (2009) who places it in its own family, Cladornithidae.

Genus *Patagorhacos* Agnolín & Chafrat, 2015

Type species. *Patagorhacos terrificus* Agnolín & Chafrat, 2015. Early Miocene, Chichinales Formation, Paso Córdoba, southwestern of General Roca, Río Negro Province.

Patagorhacos terrificus Agnolín & Chafrat, 2015

Figure 6.2

Holotype. MPCM-PV-377, distal end of right quadrate.

Geographic and stratigraphic occurrence. Paso Córdoba, southwestern of General Roca, Río Negro Province, Early Miocene, Chichinales Formation.

Comments. *Patagorhacos terrificus* was described based on a fragmentary *pars articularis* of a right quadrate, and placed within Phorusrhacidae. Degrange (2021) criticizes this assignment due to the complete absence of typical features

of known quadrates of the group. The material is too fragmentary to allow a more precise assignment.

Genus *Querandiornis* Rusconi, 1958

Type species. *Querandiornis romani* Rusconi, 1958. Early Middle Pleistocene, Ensenada Formation, Río de La Plata coast, near Anchorena Station of the Tren de la Costa train, Vicente López Department, Buenos Aires Province.

Querandiornis romani Rusconi, 1958

Holotype. Lost, fragmentary skull without institutional number.

Geographic and stratigraphic occurrence. Río de La Plata coast, near Anchorena Station of the Tren de la Costa train, Vicente López Department, Buenos Aires Province, early Middle Pleistocene, Ensenada Formation.

Comments. On its original description, Rusconi (1958) named *Querandiornis romani* based on a skull from the Pleistocene that he placed, although not with total confidence, within Tinamiformes. Tonni (1980) questioned the assignment, but posteriorly Houde (1988) followed the original criterion of Rusconi. More recently, this species has



Figure 6. *Aves incerti ordinis*. 1, *Argentavis magnificens*, MLP 65-VII-29-49, fragmentary neurocranium, facial skull fragments, right quadrate, fragmentary right tarsometatarsus, distal portion of right coracoid, shaft of right tibiotarsus and left humerus; 2, *Patagorhacos terrificus*, MPCN-PV-377, distal end of right quadrate. Scale= 1 cm.

been included among Passeriformes (Agnolín & Chimento, 2014; Agnolín, 2016a). Unfortunately, this material seems lost before Tonni's publication and could not be located for reevaluation.

Genus Euryonotus Mercerat, 1897

Type species. *Euryonotus brachypterus* Mercerat, 1897. Late Pleistocene, Buenos Aires Formation, locality not specified by the author, Buenos Aires Province.

Euryonotus argentinus Mercerat, 1897

Holotype. Lost, collection number and repository unknown, proximal portion of humerus.

Geographic and stratigraphic occurrence. Locality not specified by the author, Buenos Aires Province, Late Pleistocene, Buenos Aires Formation.

Euryonotus brachypterus Mercerat, 1897

Holotype. Lost, collection number is unknown, supposedly it would belong to the MACN collections, right humerus lacking the proximal end.

Geographic and stratigraphic occurrence. Specific locality not specified by the author, Buenos Aires Province, Late Pleistocene, Buenos Aires Formation.

Comments. Based on remains coming from the Late Pleistocene of Buenos Aires Formation, Mercerat (1897) creates the species *Euryonotus brachypterus* and *E. argentinus*, which he includes in Rallidae (a criterion followed by Tonni, 1980). However, based on the ambiguous description and the absence of illustrations, Olson (1977) questioned this assignment. Unfortunately, both type materials are lost.

"Telmabates" howardae Cracraft, 1970

Holotype. AMNH 3189, distal end of right tibiotarsus.

Geographic and stratigraphic occurrence. Cañadón Hondo, Chubut Province, early Eocene, Las Flores Formation.

Comments. Feduccia & McGrew (1974) considered "*Telmabates" howardae*, originally attributed to Presbyornithidae, as a senior synonym of *Presbyornis pervetus*. However, Ericson

(2000) recognized it as a valid species with uncertain affinities. At the time of this publication, the authors are currently reviewing the systematic status of this taxon.

BRONTORNITHIDAE Moreno & Mercerat, 1891

Genus Brontornis Moreno & Mercerat, 1891

Type species. *Brontornis burmeisteri* Moreno & Mercerat, 1891. Early–Middle Miocene, Santa Cruz Formation, Lago Argentino, Santa Cruz Province.

Brontornis burmeisteri Moreno
& Mercerat, 1891

Lectotype. MLP 20-88, left femur and tibiotarsus; MLP 20-90, left fibula, and MLP 20-91, left tarsometatarsus.

Geographic and stratigraphic occurrence. The lectotype comes from the Lago Argentino locality in Santa Cruz Province, being Early–Middle Miocene in age (Santa Cruz Formation). Other remains, all Early–Middle Miocene in age, have been recovered from Karaiken, La Cueva, Rincón del Buque, Río Coyle, Killik Aike, but most of the specimens come from Monte Observación and Monte León localities.

Comments. The striking characteristics of this taxon are its size and robustness. Its supposed trophic habit is still discussed: scavenger, herbivorous (Agnolín, 2007c; Angst & Buffetaut, 2018), or omnivorous/zoophagous (Worthy *et al.*, 2017). It has been related to extremely diverse groups and its affinities are still debated. The most exhaustive phylogenetic analysis that includes this taxon is that of Worthy *et al.* (2017) who maintain that *Brontornis* is not a Galloanserae, but a member of Neoaves related to Cariamiformes, while Agnolín (2021) found it to be nested within Galloanserae as a sister group of the Australian Mihirungs, large flightless and extinct birds classified as Dromornithidae.

TERATORNITHIDAE Miller, 1909

Genus Argentavis Campbell & Tonni, 1980

Type species. *Argentavis magnificens* Campbell & Tonni, 1980. Late Miocene, Cerro Azul Formation, Salinas Grandes de Hidalgo, La Pampa Province.

Argentavis magnificens

Campbell & Tonni, 1980

Figure 6.1

Holotype. MLP 65-VII-29-49, incomplete humerus, fragments of ulna, coracoid, skull, and leg bones.

Geographic and stratigraphic occurrence. The holotype is registered in the Late Miocene Cerro Azul Formation, outcropping in Salinas Grandes de Hidalgo in La Pampa Province. An additional specimen comes from the same age but from a locality near Carhué, in Buenos Aires Province. Additional records are known from the Late Miocene of Andalhuala Formation, in San José and Cuenca del Río de los Añacos localities, in Valle de Santa María, Catamarca Province (Campbell, 1995).

Comments. The Teratornithidae is an extinct family known only for the Americas. They are among the largest known flying carnivorous birds, probably sister group of Cathartidae (Mayr, 2017). The greatest abundance of remains comes from Rancho la Brea, a very rich fossil site from the Late Pleistocene of the United States. Its oldest records are from the Oligocene or Early Miocene of Brazil (Olson & Alvarenga, 2002) which supports an apparent origin in South America. In Argentina, the oldest remain is an incomplete ulna and fragmentary radius coming from the early Late Miocene Arroyo Chasicó Formation (De Mendoza & Picasso, 2019), and a fragment of the left coracoid and a distal end of left tibiotarsus assigned to *A. magnificens* from the Late Miocene Andalhuala Formation (Campbell, 1995). Undoubtedly the most eloquent of its fossil remains is *Argentavis magnificens* Campbell & Tonni, 1980 whose wingspan was estimated at 6–8 meters (Campbell & Tonni, 1980; Vizcaíno & Fariña, 1999) and close to 70 kilograms of body mass (Chatterjee *et al.*, 2007). Other remains assigned to this extinct family have been reported for the Pleistocene of the Pampean Region (Cenizo *et al.*, 2021).

NOMEN DUBIUM

Genus *Aucornis* Ameghino, 1898

Type species. *Aucornis euryrhynchus* Ameghino, 1898. Late Oligocene, Deseado Formation, Mazaredo locality, Santa Cruz Province.

Aucornis solidus Ameghino, 1899

Holotype. MACN-A 11052, proximal half of phalanx I of the left digit 2.

Geographic and stratigraphic occurrence. Locality not specified by the author, Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. This taxon has been considered as a synonym of *Physornis fortis* (Brdokorb, 1967), and a senior synonym of *Andrewsornis abbotti* (Alvarenga & Höfling, 2003). Nevertheless, the incompleteness of the material does not allow comparisons between homologous elements, so it was considered as a *nomen dubium* by Agnolín (2006c) and Tambussi & Degrange (2013).

Genus *Climacarthrus* Ameghino, 1895

Type species. *Climacarthrus incompletus* Ameghino, 1895. Late Oligocene, Deseado Formation, specific locality not specified by the author, Santa Cruz Province.

Climacarthrus incompletus Ameghino, 1895

Holotype. MACN-A 11667, fragmentary distal end of right tarsometatarsus, lacking trochlea metatarsi IV.

Geographic and stratigraphic occurrence. Specific locality not specified by the author, Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. Although Brodkorb (1964) and Agnolín (2006b) considered *Climacarthrus* as an Accipitrinae, this taxon was considered as a *nomen dubium* by Tambussi & Degrange (2013) based on the poorly preserved material.

Genus *Pseudolarus* Ameghino, 1891

Type species. *Pseudolarus eocaenus* Ameghino, 1891. Early–Middle Miocene, Santa Cruz Formation, Monte Observación, Santa Cruz Province.

Pseudolarus guaraniticus Ameghino, 1899

Holotype. MACN-A 52-190/12190, fragmentary right proximal end of humerus.

Geographic and stratigraphic occurrence. Specific locality not specified by the author, Santa Cruz Province, late Oligocene, Deseado Formation.

Comments. This taxon has been considered as a phorusrhacid belonging to the genus *Psilopterus* by Agnolín (2006c), even recognizing that this may be *Psilopterus affinis* (although he points out that there are considerable size differences between the materials known for both species). However, the fragmentary nature of this material does not allow a reliable assignation and is considered as *nomen dubium* (Tambussi & Degrange, 2013).

Genus *Nothura* Wagler, 1827

Type species. *Nothura boraquira* (Spix, 1825). Recent, central southern South America, eastern Bolivia, Paraguay, and southwest Brazil.

Nothura paludosa Mercerat, 1897

Holotype. Lost, collection number unknown, repository supposed to be the MLP, right femur.

Geographic and stratigraphic occurrence. Arrecifes locality, Buenos Aires Province, Late Pleistocene, Buenos Aires Formation.

Comments. The femur, on which the species was based and is currently lost, was described very briefly and never illustrated, a fact previously noted by Cenizo *et al.* (2012) who questioned the validity of the species, a criterion that we follow here. In this sense *Nothura paludosa* is considered here as *nomen dubium*.

CONCLUDING REMARKS

Since the contribution of Tonni (1980), there have been crucial breakthroughs in unraveling the diversity of the South American Cenozoic birds, mainly due to two reasons: an increased number of researchers dedicated to these topics, and a growth, although not always constant, in founding for scientific research granted by the Argentine State. Deep reviews on fossil birds such as Sphenisciformes (Acosta Hospitaleche, 2004), Phorusrhacidae (Jones, 2010; Degrange, 2012), Anseriformes (De Mendoza, 2017), Anhingidae (Diederle, 2015) or the avian record from classic paleontological sites such as those of the Pampean (Tambussi, 1989) or Mesopotamian (Noriega, 1994) regions, were reasons for academic theses in many of which Eduardo Tonni was related.

Many extinct taxa are only known from a few fragments of bones. Unfortunately, some holotypes, especially those on which the Ameghino's species were based, are lost. For this reason, some subsequent reviews of the materials have had to be based on images that are not always detailed, which resulted in diverse and conflicting opinions among different reviewers and complex synonymous lists. A list of the 81 fossil birds named by Ameghino between the years 1882 and 1905, their status, and the relevant bibliographical references can be consulted in Tambussi & Degrange (2013, table 5.1).

Tonni (1980) listed 70 extinct species, most of which were named by Florentino Ameghino, Francisco Moreno, and Alcides Mercerat to the end of the 19th century. Four decades later, the list that is included here has 86 species of which 12 have not been assigned to any order or are of doubtful assignment, one (*Ciconiopsis antarctica*) is considered as *nomen inquirendum*, and four (*Nothura paludosa*, *Aucornis solidus*; *Climacarthrus incompletus*; and *Pseudolarus guaraniticus* see Agnolín, 2008) are considered *nomen dubium* or *vanum* (see Mones, 1989) for a proper definition of terms). Two of the taxa on Tonni's list were removed for not being birds (*Cunampaia simplex* and *Loncornis erectus*). Six of the recorded families are extinct (Presbyornithidae, Phorusrhacidae, Brontornithidae, Teratornithidae, Cladornithidae, and Onychopteridae) with the higher ordinal rank placement of three of them still discussed (Brontornithidae, Teratornithidae, and Cladornithidae).

Representatives of the three major subclades of Neornithes or modern birds (Palaeognathae, Galloanseres, and Neoaves) have records during the Argentine Cenozoic. Even so, the record is highly skewed towards medium to large size specimens. Nonetheless, from the point of view of ecological and morphological diversity, it shows representatives of diverse trophic and environmental guilds: terrestrial palaeognathous tinamids and rheids; terrestrial and aquatic Galloanserae, particularly Anseriformes; freshwater and marine Aequorlithornithes such as Sphenisciformes, Suliformes, Charadriiformes, Phoenicopteriformes, Ciconiiformes, Pelecaniiformes; arboreal stem Coraciiformes, Passeriformes and Psittaciformes; flying and flightless land predators Cathartiformes, Accipitriformes, Falconiformes, and Cariamiformes.

ACKNOWLEDGEMENTS

To Eduardo Tonni, for accompanying the first stages of her career of one of the authors (C.P.T). Thanks to two anonymous reviewers and editors for their valuable comments. For providing us with photographs of fossil specimens we especially thank Jorge Noriega, Federico Agnolín, Alejo Scarano, Raúl Vezzosi, Juan Diederle, and Martín Ezcurra. Thanks to ANPCyT and CONICET from Argentina for their support. This is a contribution to PICT 2019-771 and PUE 2016 – CONICET – CICTERRA.

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LSID urn:lsid:zoobank.org:pub:3A2DC716-154F-47D0-80E1-173B04065E98

doi: 10.5710/PEAPA.13.08.2022.418

Recibido: 09 de marzo 2022

Aceptado: 13 de agosto 2022

Publicado: 15 de mayo 2023



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