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A NEW SPECIES OF *OPISTHODACTYLUS* AMEGHINO, 1891 (AVES, RHEIDAE), FROM THE LATE MIOCENE OF NORTHWESTERN ARGENTINA, WITH IMPLICATIONS FOR THE PALEOBIOGEOGRAPHY AND PHYLOGENY OF RHEAS

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ABSTRACT—A new species of rheid, *Opisthodactylus kirchneri*, sp. nov., is erected on the basis of associated elements of both hind limbs from the late Miocene in northwestern Argentina. The new species extends the biochron of *Opisthodactylus* from early Miocene to late Miocene and its distribution from Patagonia to northwest Argentina. Cladistic analysis recovered an *Opisthodactylus-Pterocnemia* clade as sister to a *Rhea americana* clade. The *Opisthodactylus-Pterocnemia* clade would have inhabited the most southern, central, and western regions of southern South America throughout the early-middle Neogene, whereas the *Rhea* stock would have had a north-northeastern or Brazilian ancestral distribution in the lowlands of the continent. The similar biogeographic patterns of living and fossil rheids, caramids, and tinamids seem to roughly reflect the environmental shift from closed to open habitats that took place at the southern end of South America during the Neogene and Pleistocene, and at least in the former two families the effects of isolation produced by the ‘Paranaense’ sea. Closed-habitat taxa of these three families are recorded at early Miocene localities in Patagonia (*O. horacioperezi*, *O. patagonicus*, *Noriegavis santacrucensis*, and *Crypturellus reai*), whereas open-habitat taxa come from late Miocene–early Pliocene sites at central (*Pterocnemia* sp. and *Euadromia* sp.), northwestern (*O. kirchneri* and *Pterocnemia* cf. *mesopotamica*), and northeastern (*Pterocnemia mesopotamica*) regions in Argentina.

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INTRODUCTION

The rheas, or ñandúes, are large, flightless birds restricted to South America. Typically, they include two living genera and species, *Rhea americana* (Linnaeus, 1758) and *Pterocnemia pennata* (d’Orbigny, 1834). However, some authors merge the two species in the genus *Rhea* Brisson (Sibley and Ahlquist, 1990; del Hoyo et al., 2014; Remsen et al., 2016), and others recognize the montane *Rhea tarapacensis* (Chubb, 1863) from the central Andean region as a separate species from Patagonian lowland *R. pennata* (e.g., del Hoyo et al., 2014).

The fossil record of rheas is relatively abundant in comparison with other cursorial birds. The earliest known fossil undoubtedly belonging to Rheidae corresponds to pedal phalanges of a robust indeterminate rheid reported from the middle Paleocene of Chubut Province, Argentina (Tambussi, 1995). *Diogenornis fragilis* Alvarenga, 1983, from the middle Paleocene of Brazil, was originally considered to be the oldest representative of the family. However, its phylogenetic position is in need of further clarification, because preliminary studies without definitive evidence seem to suggest that this taxon is more closely related to the Casuariidae than to Rheidae (Alvarenga, 2010).

Neogene records of rheids are known since the early Miocene where two species of *Opisthodactylus* have been described. The oldest species is *Opisthodactylus horacioperezi* Agnolin and Chafrat, 2015, from the lower Miocene (Colhuehuapian SALMA [South American Land Mammal Age]) Chichinales Formation at Rio Negro Province in Patagonia (Agnolin and Chafrat, 2015). The type species of the genus is *Opisthodactylus patagonicus* Ameghino, 1891, a younger Patagonian paleospecies coming from the lower Miocene (Santacrucian SALMA) Santa Cruz Formation at Cerro Observatorio locality (= Monte Observación; Vizcaíno et al., 2012). This taxon was based on very fragmentary and poorly described materials, including three incomplete distal ends of tarsometatarsi and a distal tibiotarsus among other bones (Ameghino, 1891). Recently, new Patagonian localities preserving *O. patagonicus* have been reported, which extend its geographic distribution (Buffetaut, 2014; Agnolin and Chafrat, 2015).

*Pterocnemia* appears later in the fossil record. Fragmentary fossil remains from the late Miocene (Huayquerian SALMA) of La Pampa Province (Argentina) referred to *Pterocnemia* sp. were recently reported (Cenizo et al., 2012). A new species of *Pterocnemia, P. mesopotamica* Agnolin and Noriega, 2012, was described from different middle–upper (Colloncuran–Huayquerian SALMAs) and upper (Huayquerian) Miocene geological units in Mendoza and Entre Ríos provinces of Argentina.

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respectively (Noriega and Agnolin, 2008; Agnolin and Noriega, 2012). Two extinct genera of uncertain affinities were described based on fragmentary bones from the late Miocene–early Pliocene (Montehermosan SALMA) of Buenos Aires Province: *Heterorhea dabbenei* Rovereto, 1914, and *Hinasuri nehuensis* Tambussi, 1995.

The last appearing genus in the fossil record is *Rhea*. Quaternary records comprise the extinct *Rhea anchorensis* (Ameghino and Rusconi, 1932) from the early Pleistocene of Buenos Aires (Tambussi, 1995), whereas *Rhea fossilis* Ameghino, 1882, and *Rhea pampeana* Moreno and Mercerat, 1890, were synonymized with the living *R. americana* by Picasso (2016). Finally, many fossil specimens have been attributed to *R. americana* from localities of Brazil, Argentina, and Uruguay and to *P. pennata* from Argentina and Chile (Brodtkorb, 1963; Tonni and Laza, 1980; Tambussi and Tonni, 1985; Cuello, 1988; Tambussi and Acosta Hospitaleche, 2002; Picasso et al., 2010).

In this contribution, we describe a new species of *Opisthodactylus* based on a well-preserved specimen from the late Miocene of northwestern Argentina. This find provides important phylogenetic information, allows emendation of the diagnosis of the genus *Opisthodactylus*, and contributes to the understanding of the paleobiogeography and evolutionary history of rheids, caramids, and tinamids.

**Institutional Abbreviations**—CICYTP, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MFA, Museo Provincial de Ciencias Naturales Florentino Ameghino; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Muséum National d’Histoire Naturelle, Paris, France; MPCN-PV, Museo Patagónico de Ciencias Naturales, General Roca, Argentina; MUFYCA, Museo Florentino y Carlos Ameghino (Instituto de Fisiografía y Geología), Rosario, Argentina.

**FIGURE 1.** *Opisthodactylus patagonicus* Ameghino, 1891. NHMUK A-586, tarsometatarsus, and NHMUK A-587, tibiotarsus. A, original drawings and B, photographs of the type materials. *Opisthodactylus kirchneri*, sp. nov. MUFYCA-647, holotype. C, right femur in posterior view; D, right tibiotarsus in anterior view; E, left tibiotarsus in posterior view; F, left tarsometatarsus in dorsal view; G, right tarsometatarsus in dorsal view; H, pedal phalanges of left foot in dorsal and lateral views: first phalanx of digit III and proximal end of first phalanx of digit IV; pedal phalanges of right foot in dorsal and lateral views: first phalanx of digit III and first, second, and third phalanges of digit IV; I, life restoration. Scale bars equal 5 cm.
We performed a cladistic phylogenetic analysis including seven taxa: three living species (*R. americana*, *P. pennata*, and *Eudromia elegans*) and four extinct species, *P. mesopotamica*, *O. patagonicus*, *O. horacioperezi*, and the new species of *Opisthodactylus* described herein (Appendix 1). Regrettably, the affinities of *Heterorhea dabbenei* and *Hinuasi nehuensis* could not be assessed because the holotype of the former is lost and material of the latter is too fragmentary.

We obtained 21 characters from the available bony elements of specimen MUFYCA-647 (see Appendix 2 for character definitions and states). The osteological nomenclature follows Howard (1929) and Baumel and Witmer (1993). Character polarity and rooting were established using outgroup comparisons (Nixon and Carpenter, 1993). A member of Timamidae, *Eudromia elegans*, was selected as the outgroup. Analysis of our data matrix (Appendix 3) was performed with TNT version 1.1 (Goloboff et al., 2003). Searches of the most parsimonious tree were made by implicit enumeration. Characters were equally weighted and coded as non-additive. Branch support was measured using two different methods: jackknifing (removal probability 36%) and symmetric resampling (change probability 33%).

Chronostratigraphic and geochronological schemes of the Neogene of Argentina were taken from Brandoni (2013).

**SYSTEMATIC PALEONTOLOGY**

**Order RHEIFORMES** (Forbes, 1884)

**Family RHEIDAE** Bonaparte, 1849

Genus *OPISTHODACTYLUS* Ameghino, 1891

*OPISTHODACTYLUS KIRCHNERI*, sp. nov. (Figs. 1–4)

**Diagnosis**—Lateral border of shaft of tarsometatarsus at level of fossa infracotylaris low (not elevated dorsally) and widened transversely, forming a large and convex ridge in lateral view. In lateral view, attachment of perforans brevis on proximal end of tarsometatarsus strong and located dorsally. Fossa parahypotarsalis lateralis large. Cross-sections of middle and distal portions of tarsometatarsal shaft of triangular form, with smooth anterior grooving. Sulcus extensorius of tibiotarsus deep and ending proximally. Ratio between tibiotarsal and tarsometatarsal length low (1.0), showing that *O. kirchneri* had relatively the longest tarsometatarsus among known rheiform taxa.

**Etymology**—In honor of the late Néstor Kirchner (1950–2010), past president of Argentina, for his achievements in promoting human rights and freedom of speech and his long-lasting contributions to the development of science in his home country. The walking habits of *O. kirchneri* undertook of putting Argentina forward on the world scene at the time he was in office. He had relatively the longest tarsometatarsus among known rheiform taxa.

**Holotype**—MUFYCA-647 is housed at the Museo Florentino Ameghino and includes the following associated elements of both hind limbs: the right femur, both tibiotarsi and tarsometatarsi, and six pedal phalanges (first phalanx of left digit II; first and second phalanges of left digit III; and first, second, and third phalanges of left digit IV).

**Locality and Horizon**—The original label of its collector (A. Castellanos) states that the specimen came from the ‘Aracanense medio’ levels of a locality situated north-northwest of Agua del Chañar in the Santa María (or Yocavil) valley, Tafi del Valle Department, Tucumán Province, Argentina (Fig. 5). Although the ‘Aracanense medio’ is not recognized in current stratigraphic nomenclature, the fossil-bearing horizon can be correlated with the lower levels of the Andahuila Formation (Castellanos, 1946; Marshall and Patterson, 1981; Bossi and Muruaga, 2009). Radiometric and biochronological analyses based on fossil mammals indicate that the age of the Andaluíala Formation ranges from the late Miocene (lower levels) to early Pliocene (upper levels) (Marshall and Patterson, 1981; Bossi and Muruaga, 2009; Reguero and Candela, 2011). Thus, the fossil horizon is assigned to the Huayquerian SALMA or Torontian (Global Stage/Age) (Fig. 5).

**DESCRIPTION**

The holotype, MUFYCA-647 (Fig. 1), is assigned to *Opisthodactylus* based on the following characters: prominence for attachment of the internal ligament of the tibiotarsus continuous with the insertion for the transverse ligament and not separated by the distal end of sulcus extensorius; distal end of the tarsometatarsus broadened, with marked medial and lateral spread of trochleae metatarsi II and IV, respectively; articular facets of trochleae metatarsi III and IV transversally widened and markedly grooved; and shaft dorsoventrally depressed above the level of trochleae. Dimensions and robustness resemble the holotype of *O. patagonicus* (Table 1).

**Femur**—The overall configuration of the femur of *O. kirchneri* is more robust than in living rheids (Fig. 4). The shaft is more curved than in *R. americana* and *P. pennata*, with the medial border of the shaft forming a greater angle between its proximal third and the base of the femoral head in anterior view. The facies articularis antitrochanterica is also larger. The distal end is also broader than in extant rheids. The sulcus patellaris is wider and deeper than in *R. americana* and *P. pennata*, but less excavated distally. The condylus lateralis is more protruding laterally. The posteroproximal border of the condylus medialis is well developed and very prominent proximally. The articular surface of the condylus medialis is larger than in living forms. The popliteal fossa is also larger, extending more proximally on the shaft and slightly shallower than in *R. americana*, resembling the condition in *P. pennata*.

**Tibiotarsus**—At the proximal end of the shaft, the lateral edge of the crista enemi lateralis is bulged, rounded, and with a short lateral projection (Fig. 3). The crista enemi medialis is short and with a broadened base, slightly more projected anteriorly than in *P. mesopotamica* and *P. pennata*, but less than in *R. americana*. The medial edge of the crista conemi medialis forms a sharp ridge that is less extended distally on the shaft than in *R. americana* and *P. pennata*, similar to *P. mesopotamica*.
Noriega et al.—New Opisthodactylus from Argentina (e1278005-5)
The facies gastrocnemialis is less excavated than in *P. mesopotamica* and *P. pennata*, similar to that of *R. americana*. The sulcus intercnemialis is wide. At the distal end, the attachment of the internal ligament is not completely separated from that of the transverse ligament (*ligamentum transversum*) by the distal portion of the sulcus extensorius, like in *O. patagonicus*, *P. pennata*, and *P. mesopotamica*; however, the portion of shaft just distal to the sulcus extensorius is broken, giving the appearance that both attachments are really not connected, as observed in *R. americana*. The sulcus extensorius is markedly excavated, well delimited, and ending proximally, similar to those of *O. patagonicus*, *O. horacioperezi*, *P. pennata*, and *P. mesopotamica*, and different from that of *R. americana*, which is shallower and ends farther distally. The trochlea cartilaginis tibialis is larger than in *O. horacioperezi* and more proximodistally developed where it joins the medial margin of the condylus lateralis in anterior view; although damaged in posterior aspect, the position of the ridge that delimits this trochlea proximally can easily be inferred, indicating that it was higher or more proximally extended than in *O. horacioperezi*. The medial ligamentary ridge is similar to that of *O. patagonicus* but sharper than in *O. horacioperezi*, ending distally in a more robust bump (*internal ligamental prominence*) on the medial view of condylus medialis. The external ligamentum prominens is more marked and more proximally placed than in *O. horacioperezi*. The cross-section of the distal shaft is more markedly compressed anteroposteriorly than in extant species, similar to the condition observed in *P. mesopotamica* and all other species of *Opisthodactylus*.

**Tarsometatarsus**—In dorsal view, the concavity located on the dorsal shaft proximal to the notch between trochlea metatarsi II and III is deeper and more clearly marked than in *P. mesopotamica* and living forms, similar to that of *O. patagonicus* (Fig. 3). In comparison with other trochlea, the trochlea metatarsi II is more distally and medially extended than in *P. mesopotamica* and living rheas, with a great posterior protrusion of its medial trocholear rim. The medial rim of trochlea metatarsi III is more prominent dorsally than the lateral rim compared with those of *O. patagonicus*, *P. mesopotamica*, and living rheas (which are subequal, with the medial one hardly more prominent); therefore, the median trocholear groove in *O. kirchneri* is deeper than in related taxa. The trocholear rims of trochlea metatarsi III are more divergent distally than in *P. mesopotamica*. The trochlea metatarsi IV is similar to that of *O. patagonicus*. The transversal facets of the tarsometatarsal of trochlea metatarsi IV are more divergent distally than in *R. americana*, *O. patagonicus*, *P. mesopotamica*, and *P. pennata*. The lateral rim of this trochlea is somewhat more prominent plantarily than the medial rim compared with the condition observed in *P. mesopotamica*, but less prominent than in extant species. In plantar view, the groove (*fossa parahypotarsalis medialis*) that parallels the calcaneal ridge (*crista medialis hypotarsi* and *crista medianoplarantis*) medially is shallower and wider than in *P. mesopotamica*, *P. pennata*, and *R. americana*. In lateral view of the proximal end of the shaft, the attachment of perforans brevis is more conspicuous than in *P. mesopotamica* and living rheas. This insertion of perforans brevis and the large distal fossa parahypotarsalis lateralis are located relatively more dorsally than in the compared taxa. The lateral border of the sulcus extensorius is broadened transversally and less prominent dorsally at the level of the fossa infracotylaris, forming a large concave surface that is clearly observed in lateral view, whereas in *P. mesopotamica* and living rheas this ridge is sharp, prominent, and rather straight when observed laterally, extending proximally to reach the anterior rim of the cotyla lateralis.

The cross-section of the distal shaft is triangular, with its anterior surface nearly flat. The dorsoplantar flattening of the shaft affects both sides of the bone just above the level of trochlea, giving it an elliptical cross-section.

**Digits**—The preserved first pedal phalanx of left digit III, the first and second pedal phalanges of left digit IV, and the first, second, and third phalanges of the right digit IV do not exhibit striking differences from those of living taxa, but they have their proximal articular facets slightly more broadened, in accordance with the transversally widened facets of the tarsometatarsal trochlea (Fig. 1).

**CLADISTIC ANALYSIS**

Parsimony analysis of our data set (Appendix 3) resulted in a single most parsimonious tree (Fig. 6; 27 steps in length, consistency index of 0.963, and retention index of 0.923). *Rhea americana* was found as sister to a clade including all other fossil and extant rheids studied. This clade comprises two groups: one including both *Pterocnemia* species and the other including all *Opisthodactylus* species, with *O. horacioperezi* as sister to the clade of *O. patagonicus* + *O. kirchneri*. Branch support was satisfactory (64–100) for all groups, except for the *Pterocnemia* clade (<50) (Fig. 6). Derived characters defining nodes and taxa are indicated on the cladogram (Fig. 6).

**DISCUSSION**

**Systematic Remarks**

Our data supports the traditional two-genus taxonomy of living Rheidae (Folch, 1992), because many osteological characters of the tibiotarsus and tarsometatarsus clearly support the distinction of *Rhea* and *Pterocnemia*. Moreover, our phylogenetic results indicate that *Pterocnemia + Opisthodactylus* constitute the sister group to *Rhea* (Fig. 6). Thus, the inclusion of *Pterocnemia in Rhea* is only possible if the distinctive genus *Opisthodactylus* is also included in *Rhea*.

**Cladogenesis and Paleobiogeography**

Until now, the fossil record of *Opisthodactylus* has consisted of fragmentary specimens that are widely distributed at different late-early Miocene (Santacrucian SALMA) localities of southern Patagonia from the Andean slopes to the Atlantic coast (*Amechino*, 1891; Sinclair and Farr, 1932; Buffetaut, 2014), and at a single earliest early Miocene (*Colhuehuapian SALMA*) site in northern Patagonia (*Agnonin* and *Chafrat*, 2015). The newly described *O. kirchneri* extends the biochron of *Opisthodactylus* by at least 10 Ma to the late Miocene (*Huayquerian SALMA*) and expands the geographic range of the genus by more than 2500 km northwest of the locality of the holotype of *O. patagonicus* and more than 1000 km from that of *O. horacioperezi* (Fig. 7). These data suggest that *Opisthodactylus* or another closely related taxon could have occupied a large ancestral area in the southern tip of South America at least during the early-middle Cenozoic (Fig. 7). Unfortunately, the Paleogene record of fossil rheids is restricted to an indeterminate species from the middle

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[FIGURE 3. *Opisthodactylus kirchneri*, sp. nov. MUFYCA-647, holotype, right tibiotarsus. A, proximal end in anterior view; B, proximal end in posterior view; C, proximal end in lateral view; D, proximal end in medial view; E, distal end in anterior view; F, distal end in posterior view; G, distal end in lateral view; H, distal end in medial view; I, proximal end of both tibiotarsi in anterior view. Abbreviations: ail, attachment of internal ligament; alt, attachment of ligamentum transversum; cf, crista fibularis; cm, crista cnemialis lateralis; cnel, crista cnemialis medialis; col, condylus lateralis; com, condylus medialis; del, depressio epicondylaris lateralis; dem, depressio epicondylaris medialis; elp, external ligamental prominence; fl, fibula; fa, facies articularis lateralis; fam, facies articularis medialis; fg, facies gastrocnemialis; ic, incisura intercondylaris; lp, internal ligamental prominence; mr, medial ligamentary ridge; se, sulcus extensorius; sm, sulcus internecialis; tc, trochlea cartilaginis tibialis; tnf, tubercle for musculus femorotibialis medialis. Scale bars equal 5 cm.]
Figure 4. *Opisthodactylus kirchneri*, sp. nov. MUFYCA-647, holotype, right femur. A, anterior view; B, posterior view; C, medial view; D, lateral view; E, detail of proximal end in posterior view; F, detail of distal end in posterior view; G, detail of proximal end in proximal view; H, detail of distal end in distal view. abbreviations: **cf**, collum femoris; **col**, condylus lateralis; **com**, condylus medialis; **faa**, facies articularis antitrochanterica; **fh**, femoral head; **flc**, fovea ligamentus capitis; **fp**, fossa poplitea; **fv**, foramen vasculare; **mol**, musculus obturatorius lateralis; **mom**, musculus obturatorius medialis; **sp**, sulcus patellaris; **tf**, trochlea fibularis. Scale bars equal 5 cm.
Paleocene of Patagonia (Tambussi, 1995), providing only inconclusive data on the geographic distribution of the oldest rheid.

Cladogenetic processes among vertebrates of South America during the Neogene were strongly linked to tectonism and climatic changes, as well as to cyclicity of ice ages during the Pleistocene (Marshall and Semper, 1993; Ortiz-Jaureguizar and Cladera, 2006; Hoorn et al., 2010). The influence of marine ingressions should also be evaluated as an important factor shaping the evolution of poor fliers and ground birds. We shall discuss these factors below.

Paleobotanical reconstructions of Patagonia during the Paleogene and early Neogene have proposed the progressive replacement of the original forested megathermal communities by meso- and microthermal forests due to both tectonic and climatic factors (Barreda and Palazzesi, 2007). The full opening of the Drake Passage during the Oligocene–Miocene, the global climatic deterioration of the Miocene, and the uplift of the Andes would have acted in concert to produce a fragmentation of habitats, leading to the development of aridity and extreme seasonality since the beginning of the Neogene (Blisniuk et al., 2005; Nullo and Combina, 2011). In particular, the late early Miocene vegetation inhabited by *O. patagonicus* in Patagonia was characterized by a mixture of open temperate semi-arid forests and humid warm-temperate forests (Brea et al., 2012), alternating with shrubby-herbaceous elements more typical of Chacoan floras. Later, during the middle late Miocene, the diversity and abundance of xerophytic-adapted taxa increased in Patagonia (Barreda and Palazzesi, 2007), leading to a more open ‘Proto-Espinal/Steppe Province’ in extra-Andean Patagonia (Iglesias et al., 2011). On the basis of these paleoenvironmental reconstructions, we hypothesize that ancestral populations of the *Opisthodactylus* + *Pterocnemia* lineage would have primarily occupied these more Chacoan environments during the late Paleogene–early Neogene. The successive paleoecological changes occurring from about the middle Miocene onwards would have led to the split of the first species of *Pterocnemia*, *P. mesopotamica* from the middle–late Miocene (Colloncuran?–Huayquerian?–Pliocene) (Fig. 7) can be interpreted in two different ways: (a) populations of *Pterocnemia* were isolated by the ‘Paranaense’ sea thus became an impassable and long-term geographic barrier would have isolated the ancestral population in the NW-C-SW region (NW-C-SW) for at least 5 Ma. The ‘Paranaense’ sea thus became an impassable and long-term water barrier for flightless or poorly flying birds (Fig. 7). This geographic barrier would have isolated the *Opisthodactylus* plus *Pterocnemia* stock in the NW-C-SW region from the *Rhea* stock in the E-NE Mesopotamia region, either directly splitting or accentuating previous differences among these clades (Fig. 7). In this context, the late Miocene records of *P. mesopotamica*, *P. cf. mesopotamica*, and *Pterocnemia* sp. from Entre Ríos, Mendoza, and La Pampa provinces (Agno lin and Noriega, 2012; Cenizo et al., 2012) (Fig. 7) can be interpreted in two different ways: (a) populations of *Pterocnemia* were isolated by the marine engulfment in both the Mesopotamian and NW-C-SW regions, and whereas the Mesopotamian populations became extinct, those of the NW-C-SW region survived and gave rise to the lineage leading to the living lesser rhea (*P. pennata*); or, alternatively, (b) the ancestral *Pterocnemia* clade was fully confined to the NW-C-SW side of the marine barrier and the presence of *P. mesopotamica* in Mesopotamia represents dispersal after the
disappearance of the ‘Paranaense’ sea. The possibility of a zoogeographic connection between the two sides of the marine barrier after the sea withdrawal was recently discussed by Brandoni (2013).

The Monte scrub and Patagonian shrub-steppe inhabited by *P. pennata* and the Puna grasslands of *P. tarapacensis* appeared in a stepwise fashion (Ortiz Jaureguizar and Cladera, 2006), first by the definitive continentalization of southern South America after the marine regression in the late Miocene (ca. 9.5 Ma; Pérez, 2013) and later by the severe rain shadow climatic consequences in the eastern lowlands caused by the last orogenic Andean phases during the Pliocene.

Birds with restricted flight capabilities and those strictly cursorial can be supposed to have been isolated geographically in similar regions by the same physical barriers. Extant and extinct seriemas (Cariamidae) exhibit rather coincident biogeographic patterns, ecological requirements, and locomotive constraints with rheas, suggesting a similar paleobiographical history. *Noria-gavis santacrucensis* (Noriega et al., 2009) is a ‘basal’ seriema from late-early Miocene levels of the Santa Cruz Formation, coming from the same horizon and in locations relatively close to those of *O. patagonicus* (Noriega et al., 2009; Mayr and Noriega, 2015) (Fig. 7). This ancestral cariamid has an old Patagonian history prior to the appearance of the ‘Paranaense’ sea during the middle-late Miocene. The living *Cariama cristata* and *Chunga burmeisteri* diverged ca. 7.5 Ma (Prum et al., 2015), suggesting that the ‘Paranaense’ sea could have split the Chacoan *Chunga* in the NW-C-SW region from the open grassland *Cariama* in the E-NE region. The latter might then have spread westwards, reaching its present-day wide distribution.

**Tinamous (Tinamidae)** are cursorial birds with shorter tarsi and smaller bodies in comparison with those of the long-legged and large rheids and cariamids. Two phylogenetic and ecological groups have been recognized: the open-area (Nothurinae) and forest-dwelling (Tinaminae) clades (Bertelli, 2016). The oldest known tinamous belong to the forest-dwelling clade and come from the early Miocene Santa Cruz and Pinturas formations (Bertelli and Chiappe, 2005; Chandler, 2012; Bertelli, 2016). The oldest record of the open-area clade belongs to an *Eudromia* sp. from the Cerro Azul Formation (Cenizo et al., 2012), where **FIGURE 6.** Cladogram showing the phylogenetic relationships of *Opisthodactylus kirchneri*, sp. nov., within Rheidae. The tree of 27 steps was built using parsimony analysis of non-additive, equally weighted characters, using TNT version 1.1. Synapomorphies are indicated above each branch (see Appendix 2). Node support values of symmetric resampling and jackknifing are indicated below each branch.
CONCLUSIONS

We propose the existence of two main clades of rheids based on our phylogenetic analysis: (1) an *Opisthodactylus* plus *Pterocnemia* stock that would have inhabited the most southern, central, and western regions of South America throughout the late Paleocene–early Neogene; and (2) the *Rhea* stock that would have had a north-northeastern or Brazilian distribution in the continent. The evolution of the former during the Miocene led to the emergence of at least five species grouped in two genera, the extinct *O. horacioperezi*, *O. patagonicus*, *O. kirchneri*, and *P. mesopotamica*, and the living *P. pennata*. The clade represented by the genus *Rhea* would have either split off or accentuated its prior distinctness from the *Opisthodactylus* plus *Pterocnemia* stock due to the barrier imposed by the ‘Paranaense’ sea.

Parallelisms found among the present and past histories of three South American avian groups (Rheidae, Cariamidae, and Tinamidae) may be explained by their shared life-history traits (reduced to absent flight capabilities and cursorial habits), which would have led to similar influences of biogeographic barriers and habitat changes in their evolution. Closed-forest taxa of these families are recorded at early Miocene localities in Patagonia (*O. horacioperezi*, *O. patagonicus*, *Noriegavis santacrucensis*, and *Crypturellus reai*), whereas more open-habitat taxa come from late Miocene–early Pliocene sites at central (*Pterocnemia* sp. and *Eudromia* sp.), northwestern (*O. kirchneri*, *Pterocnemia* cf. *mesopotamica*), and northeastern (*Pterocnemia mesopotamica*) regions in Argentina (Bertelli and Chiappe, 2005; Chandler, 2012; Mayr and Noriega, 2015; and that herein presented). Spatiotemporal patterns of living and fossil rheids, cariamids, and tinamids seem to roughly reflect the purported environmental shift from closed to open habitats that would have taken place at the southern end of South America during the Neogene and Pleistocene, and at least in the former two families the effects of isolation produced by the ‘Paranaense’ sea.

The role played by the southeastern Pampean region in the evolution of rheas will remain obscure until the systematic status of its fossil representatives can be established. Nevertheless, it seems possible that this small area had been biogeographically linked with the more extensive NW-C-SW region rather than with the geographically closer Mesopotamia.

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LITERATURE CITED


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APPENDIX 1. Comparative fossil and living specimens used in the study.

*Opisthodactylus horacioperezi* (MPCN-PV-376, 378, and 380)

*O. patagonicus* (NHMUK A-586, A-587, and A-588; MNHN 1900-18-1; PUM 15.804)

*Pterocnemia mesopotamica* (MACN 12743, 12735; MLP 41-XII-13-928, FMNH-PA-36)

*Pterocnemia pennata* (MLP 411, 671, 670, 676, 673, 791, and 833; MACN 4, 68028)

*Rhea americana* (MLP 650, 876–881, and 897; MFA-Zv 339, 341, and 571)

*Eudromia elegans* (MACN 1034, 1680, 68055, 68729)

APPENDIX 2. Description of characters used for phylogenetic analysis. Characters 0 to 11 correspond to the tarsometatarsus, 12 to 19 to the tibiotarsus, and 21 to the femur.

(0) Lateral border of shaft at the level of fossa infracotylaris: low, not elevated anteriorly, and widened transversally (0); high, forming a ridge (1).

(1) Muscular attachment of perforans brevis: strong and anteriorly located (0); moderate and posteriorly located (1).

(2) Fossa parahypotarsalis lateralis: large (0); small (1).

(3) Cross-sections of middle shaft of tarsometatarsus: with smooth anterior grooving and external posterior metatarsal border very prominent (0); with smooth anterior grooving and external posterior metatarsal border prominent (1); with deep anterior grooving, and external and mesial posterior metatarsal borders equally developed (2).

(4) Cross-sections of distal shaft of tarsometatarsus: triangular, without anterior grooving (0); subtriangular, with deep anterior grooving (1); quadrangular, with smooth anterior grooving (2).

(5) Spread of trochlea II and IV: strongly marked (0); marked (1); faintly marked (2).

(6) Facets of trochlea III and IV: transversally widened and markedly grooved (0); narrower and slightly grooved (1).

(7) Dorsoventral depression of shaft above level of trochlea: marked (0); moderate (1).

(8) Trochlea I: long in distal projection and well directed medi ally (0); distally shorter and less medially directed (1).

(9) Trochlea IV: short in distal projection (0); long in distal projection (1).

(10) Medial (of trochlea II) and lateral (of trochlea IV) rims of trochlea: not prominent posteriorly (0); prominent posteriorly (1).

(11) Groove (fossa parahypotarsalis medialis) th mediales parallels the calcaneal ridge in posterior view: wide and shallow (0); narrow and deep (1).

(12) Sulcus extensorius: deep and ending proximally (0); shallow and ending distally (1); shallow and well directed medially beneath the suprafemoral condus (2).

(13) Lateral edge of crista enemialis lateralis: bulged, rounded, and with short lateral projection (0); sharp, with enlarged lateral projection (1).

(14) Crista enemialis medialis in proximal view: short, with broadened base (0); long, with slender base (1).

(15) Medial edge of crista enemialis medialis: forming a rather short ridge extending distally on shaft (0); forming a large and sharp plate well projected distally on shaft (1).

(16) Facies gastrocnemialis: notably concave, well defined proximally on medial edge of inner enemial crest (0); shallow, largely extended distally on medial edge of inner enemial crest (1).

(17) Sulcus interenemialis: wide (0); narrow (1).

(18) Prominence for attachment of internal ligament: continuous with attachment of transverse ligament (0); separated from attachment of transverse ligament by distal tendinal groove (1).

(19) Cross-section of distal shaft: strongly compressed anteroposteriorly (0); slightly compressed anteroposteriorly (1).

(20) Tibiotarsus/tarsometatarsus length ratio: higher than 1.0 (0); equal or lower than 1.0 (1).

(21) Popliteal fossa: large, extending more proximally on shaft, and shallower (0); small surface, more distally located, and deeper (1).

APPENDIX 3. Character-taxon matrix used for phylogenetic analysis. Characters are equally weighted and coded as non-additive. Unknown character states were coded as ‘-’.

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<thead>
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<td>10000000001</td>
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<tr>
<td></td>
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