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A well-preserved partial skeleton of the poorly known early Miocene seriema *Noriegavis santacruzensis*

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Seriemas (Cariamidae) include two extant species, *Cariama cristata* and *Chunga burmeisteri*, which live in semi-open plains of South America and have a poorly documented evolutionary history. One of the earliest fossil representatives of Cariamidae is the recently described *Noriegavis santacruzensis* from the early Miocene Santa Cruz Formation (Argentina). So far, however, this species was only known from a cranium and tentatively referred distal tibiotarsi, and its phylogenetic assignment has been questioned. Here we describe a well-preserved partial skeleton from the Santa Cruz Formation, which substantiates the classification of *Noriegavis* in Cariamidae. Plesiomorphic features show *N. santacruzensis* to be outside crown group Cariamidae, but the species is nevertheless very similar to its modern relatives and documents that the osteology of seriemas underwent only few changes during the past 16 million years.

Key words: Aves, Cariamiformes, Cariamidae, Miocene, Santa Cruz Formation, Argentina.

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Introduction

The two extant species of seriemas (Cariamidae), the Red-legged Seriema, *Cariama cristata*, and the Black-legged Seriema, *Chunga burmeisteri*, are cursorial birds, which live in semi-open plains of South America (Gonzaga 1996). Seriemas were long assigned to “gruiform” birds (cranes and allies), but analyses of nuclear sequence and retroposon data indicate that they are part of a clade including diurnal birds of prey and the “higher land bird” assemblage (Ericson et al. 2006; Hackett et al. 2008; Suh et al. 2011; Kimball et al. 2013). Accordingly, recent authors classified seriemas in their own higher-level taxon Cariamiformes (e.g., Degrange and Tambussi 2011; Saiff 2011).

Stem group representatives of Cariamiformes diversified in the Cenozoic and also occurred outside South America. The earliest tentative records are from the Paleocene of Brazil and Germany, but classification of these fossils has not yet been unambiguously established (Mayr 2007; Agnolín 2009; Mayr et al. 2011a). Most taxa were characteristic of certain continents, with South America having long been considered the center of origin of the large, flightless and carnivorous Phorusrhacidae, a view that may now be challenged by a re-

cord of these birds from the Eocene of Africa (Mourer-Chauviré et al. 2011). Phorusrhacids were reported from the late Paleocene of Brazil (Alvarenga 1985), although their correct allocation was doubted by Agnolín (2009), who considered the earliest definite records to be of Eocene age. North America was home of the poorly known and probably non-monophyletic Bathornithidae, which occur in Eocene and Oligocene deposits (Olson 1985; Agnolín 2009; Mayr 2009). Fossil stem group Cariamiformes from the Eocene and Oligocene of Europe were assigned to the Idiornithidae (Mourer-Chauviré 1983), but the latter taxon is also not monophyletic, with *Elaphrocnemus* being outside a clade including *Dynamopterus* (formerly “*Idiornis*”, see Mourer-Chauviré 2013) and Cariamidae (Mayr 2002, 2009; Mayr and Mourer-Chauviré 2006). A putative record of Idiornithidae from Africa (Mourer-Chauviré 2003) has been revised, and the species is now assigned to Opisthocomiformes (Mayr et al. 2011b).

Despite this comprehensive fossil record of stem-group Cariamiformes, only very few fossils belong to the stem lineage of Cariamidae. The holotype of *Chunga incerta* from the early/middle Pliocene of Argentina is a distal end of a tibiotarsus (Tonni 1974), and *Riacama caliginea* from the late Oligocene Deseado Formation in Argentina is only known from a fragmentary coracoid, correct identification

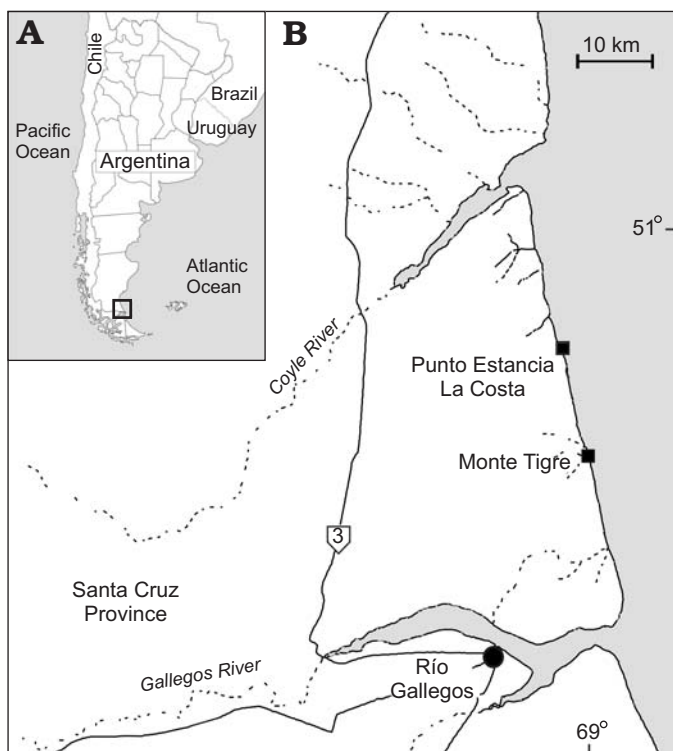


Fig. 1. Map of southeastern Patagonia (A) and detail map (B) showing the position of the Monte Tigre locality, from which the new *Noriegavis santacrucensis* fossil comes, and the holotype locality Punta Estancia La Costa.

of which is anything but certain (contra Agnolín 2004, 2009 the bone is quite different from the coracoid of extant Cariamidae; see also Alvarenga and Höfling 2003; Tambussi and Degrangé 2013).

Most recently, Noriega et al. (2009) described a cranium from the early Miocene of the Santa Cruz Formation as *Cariama santacrucensis*, and also referred two distal tibiotarsi from the type locality to Cariamidae (see also Degrangé et al. 2012). Agnolín (2009), however, classified *C. santacrucensis* in the new taxon *Noriegavis* and suggested its removal from Cariamidae, considering the species to be of indeterminate phylogenetic affinities within Cariamiformes.

Here we describe a partial skeleton of *N. santacrucensis*, recovered in 2012 by a joint expedition of the Museo de La Plata (Argentina) and Duke University (USA), which supports the original assignment of Noriega et al. (2009). The skeleton was found disarticulated but in close association of the bones at the Monte Tigre coastal locality, about 20 km south of the type locality in the Santa Cruz Province in Argentina (Fig. 1). It comes from the stratigraphic unit of the holotype, i.e. the early Miocene Estancia La Costa member of the Santa Cruz Formation (Tauber 1997; Tauber et al. 2004; Vizcaíno et al. 2012), which is exposed along the Atlantic coast and adjacent estuaries of southernmost continental Patagonia.

Institutional abbreviations.—MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MPM-PV, Museo Regional Provincial Padre

Manuel Jesús Molina; Río Gallegos, Santa Cruz Province, Argentina; SMF, Senckenberg Research Institute and Natural History Museum Frankfurt.

Material and methods

Osteological terminology follows Baumel and Witmer (1993). Measurements are in millimeters.

In order to establish the affinities of *Noriegavis* relative to the two extant species, we performed a phylogenetic analysis of 35 morphological characters (see SOM 1 and 2 in Supplementary Online Material available at http://app.pan.pl/SOM/app60-Mayr_Noriega_SOM.pdf) with the heuristic search modus of NONA 2.0 (Goloboff 1993) through the WINCLADA 1.00.08 interface (Nixon 2002), with the commands hold 10000, mult*1000, hold/10 and max*. Bootstrap support values were calculated with 1000 replicates, three searches holding one tree per replicate, and TBR branch swapping without max*. All characters were coded as non-additive, and consistency (CI) and retention (RI) indices are indicated. Character distribution was optimized with the “unambiguous changes only” mode of WINCLADA. Outgroup comparisons were made with *Eupodotis vigorsii* (Otidae, a taxon of the traditional “Gruiformes”) and *Micrastur semitorquatus* (an early diverging [Griffiths 1999] species of Falconidae, which resulted as close relatives of Cariamiformes in molecular analyses [e.g., Ericson et al. 2006; Hackett et al. 2008; Suh et al. 2011]).

Systematic palaeontology

Aves Linnaeus, 1758

Cariamiformes Verheyen, 1957

Cariamidae Bonaparte, 1853

Genus *Noriegavis* Agnolín, 2009

Type species: *Noriegavis santacrucensis* (Noriega, Vizcaíno, and Bargo, 2009); Santa Cruz Province, Argentina; early Miocene Estancia La Costa member of the Santa Cruz Formation.

Emended diagnosis.—Distinguished from the two extant taxa of Cariamidae, *Cariama* and *Chunga*, in the following features: (i) prominentia cerebellaris more conspicuous and globose (Noriega et al. 2009); (ii) foramen magnum dorsally bordered by well-developed crests (Noriega et al. 2009); (iii) dorsal surface of cranium forming two elevated areas that are each separated by a depression from the orbital rim (Fig. 2A₅); (iv) processus supraorbitalis proportionally larger; (v) carina sterni proportionally deeper (Fig. 3); pelvis with (vi) postacetabular region proportionally shorter (Fig. 4), and (vii) cristae iliacae dorsales not fused on level of crista spinosa (Fig. 4A₂); femur with (viii) narrower proximal end, and (ix) less medially inflected distal end (Fig. 5); (x) cristae cnemiales of tibiotarsus less proximally protruding (Fig. 5);

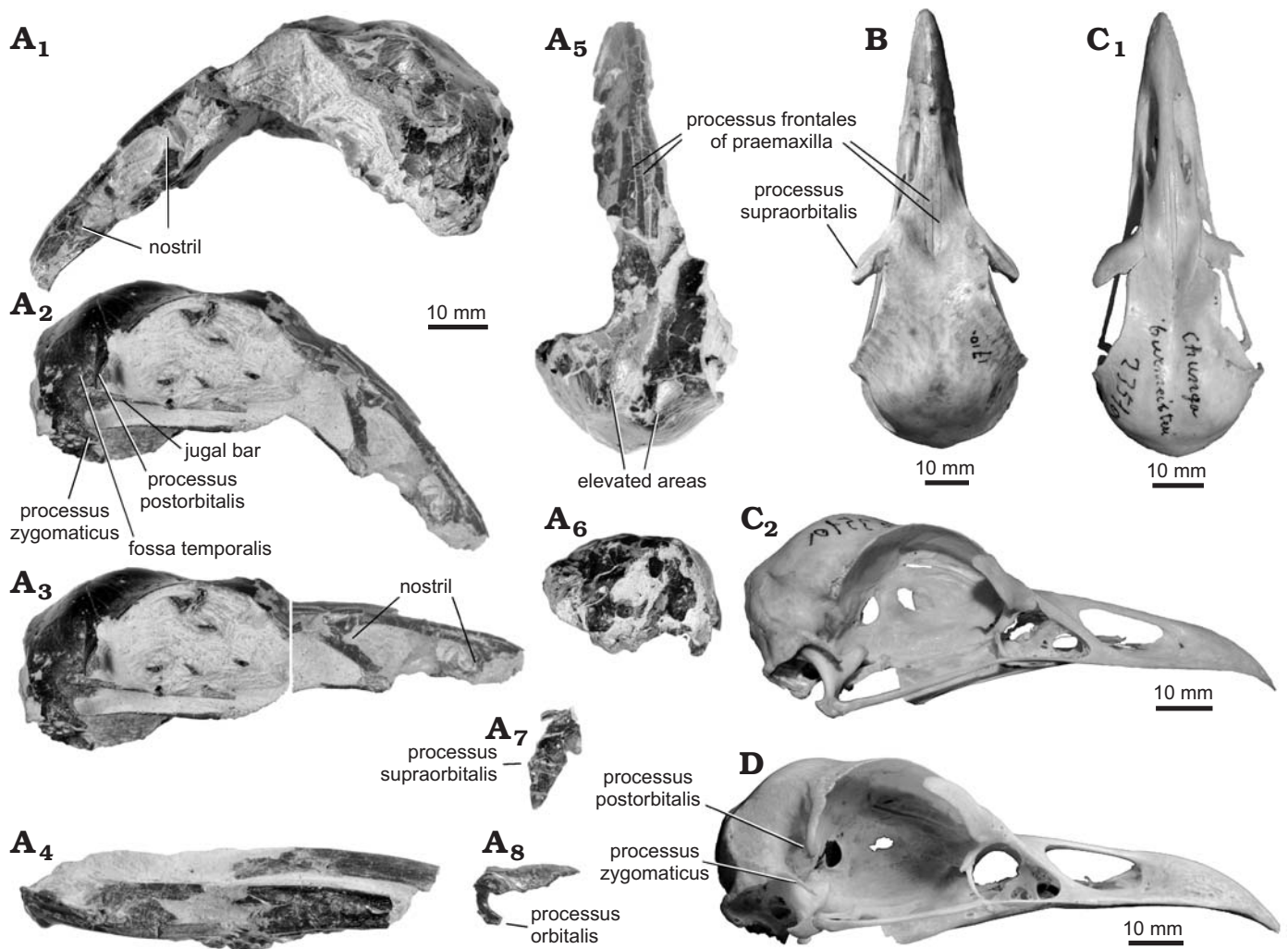


Fig. 2. Comparison of skulls and mandibles of the seriema (Cariamidae) *Noriegavis santacruzensis* (Noriega Vizcaino, and Bargo, 2009) from the early Miocene Santa Cruz Formation in Argentina (A) with extant *Chunga burmeisteri* (Hartlaub, 1860) (C) and extant *Cariama cristata* Bonaparte, 1853 (B, D). **A.** MPM-PV 15049, skull in left lateral (A₁), right lateral (A₂), dorsal (A₃), and caudal (A₄) views, skull with upper beak oriented in its natural position (A₅); partial mandible in right lateral view (A₆); left os lacrimale in dorsal (A₇) and lateral (A₈) views. **B.** SMF 1710, skull in dorsal view. **C.** MACN 2351, skull in dorsal (C₁) and lateral (C₂) views. **D.** SMF 1862, skull in lateral view.

(xi) medial flange of trochlea metatarsi II better developed plantarly (Fig. 5A₁₄). Three of the five characters listed in the original diagnosis of Noriega et al. (2009), i.e., the length and orientation of the postorbital and zygomaticus processes and the shape of the foramen magnum, are revised below and no longer considered to be diagnostic.

Stratigraphic and geographic range.—Early Miocene Estancia La Costa member of the Santa Cruz Formation; Santa Cruz Province, Argentina.

Noriegavis santacruzensis (Noriega, Vizcaino, and Bargo, 2009)

Figs. 2–5.

Material.—MPM-PV 15049, consisting of associated skeletal elements of a single individual including the skull, left os lacrimale, caudal portion of right ramus mandibulae, partial sternum and pelvis, fragmentary proximal half of left humerus, proximal end of right ulna, distal end of left ulna,

right phalanx proximalis digiti majoris, left femur, nearly complete right tibiotarsus (broken in two pieces), distal end of right tarsometatarsus, midsection of shaft and distal end of left tarsometatarsus, as well as four pedal phalanges. Specimen collected from Monte Tigre locality, between Coyle and Gallegos rivers (approximately at 51°20' S and 69°02' W), 20 km south of the type locality, Santa Cruz Province, Argentina (Fig. 1). Estancia La Costa Member of the Santa Cruz Formation, early Miocene, 16 million years ago (Vizcaino et al. 2012; Fleagle et al. 2012).

Dimensions (in mm).—Skull: length as preserved, ~95.6; width on level of processus postorbitales, ~36.1; length of beak as preserved, ~47.2; greatest width of beak, 14.0; length of nostril, 21.3; greatest depth of beak, 7.6. Humerus: width of shaft at distal end of crista deltopectoralis; 8.6. Ulna: proximal width, 13.3; distal width, 8.7. Femur: length, 78.6; proximal width, 16.5; distal width, 17.1. Tibiotarsus: length as preserved, ~175.0; proximal width of cranial portion, from facies

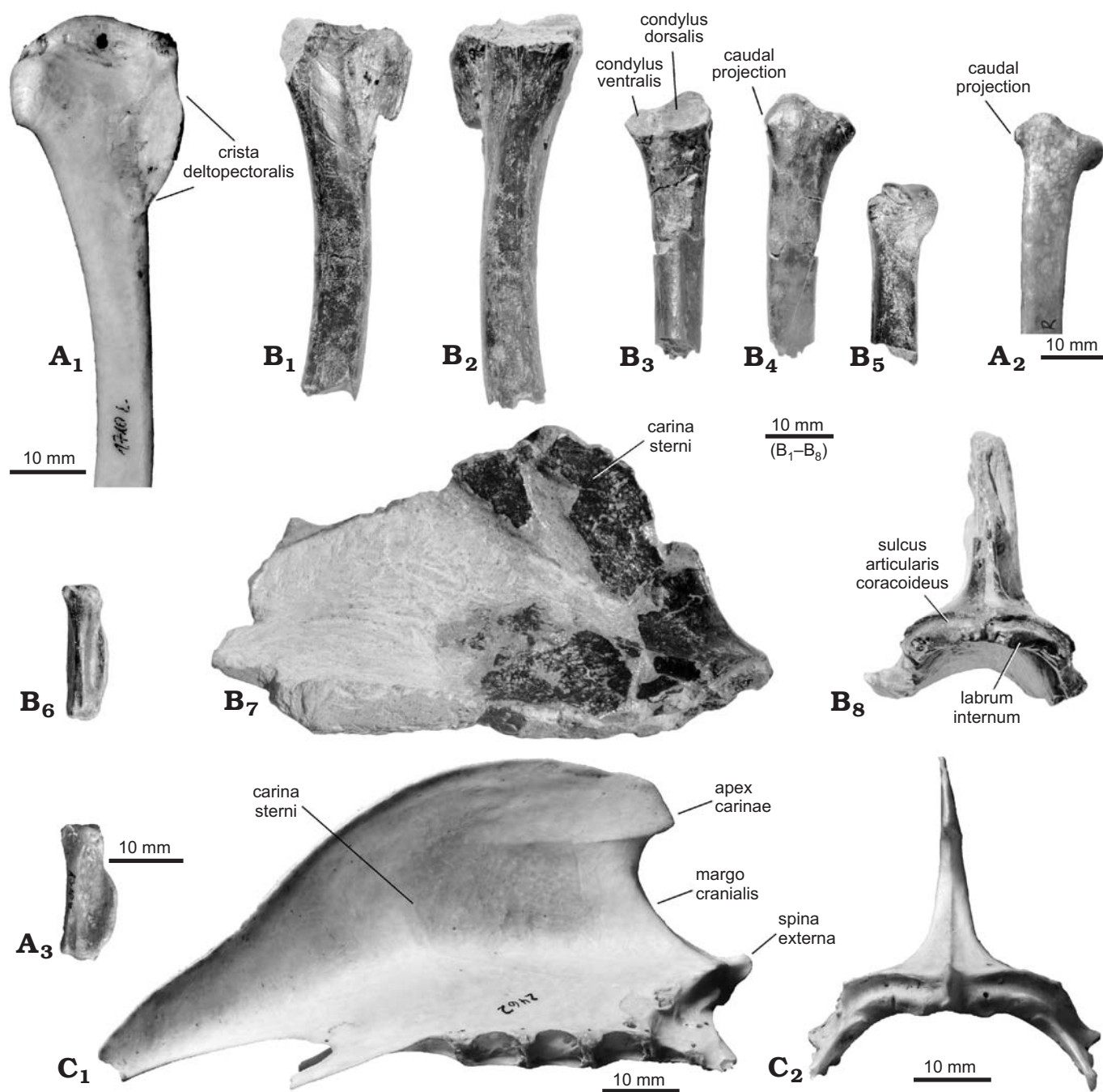


Fig. 3. Wing bones and sternum of the seriema (Cariamidae) *Noriegavis santacrucensis* (Noriega, Vizcaino, and Bargo, 2009) from the early Miocene Santa Cruz Formation in Argentina (B), in comparison with extant *Cariama cristata* Bonaparte, 1853 (A, C). **A.** SMF 1710, proximal left humerus in cranial view (A_1), proximal right ulna in caudal view (A_2), right phalanx proximalis digiti majoris in ventral view (A_3). **B.** MPM-PV 15049, proximal half of left humerus in cranial (B_1) and caudal (B_2) views, proximal portion of right ulna in cranial (B_3) and caudal (B_4) views, distal end of left ulna in ventral view (B_5), right phalanx proximalis digiti majoris in ventral view (B_6), sternum in right lateral (B_7) and cranial (B_8) views. **C.** SMF 2462, sternum in lateral (C_1) and cranial (C_2) views.

articularis medialis to crista cnemialis lateralis, 24.2; proximal width of caudal portion, from facies articularis medialis to facies articularis lateralis, 13.3; width of mid section of shaft, 8.5; depth of mid section of shaft, 6.6; depth of condylus lateralis, 12.2. Tarsometatarsus: width of mid section of shaft, 5.9; depth of mid section of shaft, 6.3 (medial portion), 6.6 (lateral portion); distal width, 13.4; width of trochlea metatarsi III, 5.6.

Description and comparisons.—The cranium of *Noriegavis santacrucensis* was described by Noriega et al. (2009), who noted the following differences to extant Cariamidae: (i) shorter and more vertically oriented processus postorbitalis, (ii) shorter and less cranially protruding processus zygomaticus, (iii) better developed prominentia cerebellaris, and (iv) elliptical foramen magnum, which is (v) dorsally bordered

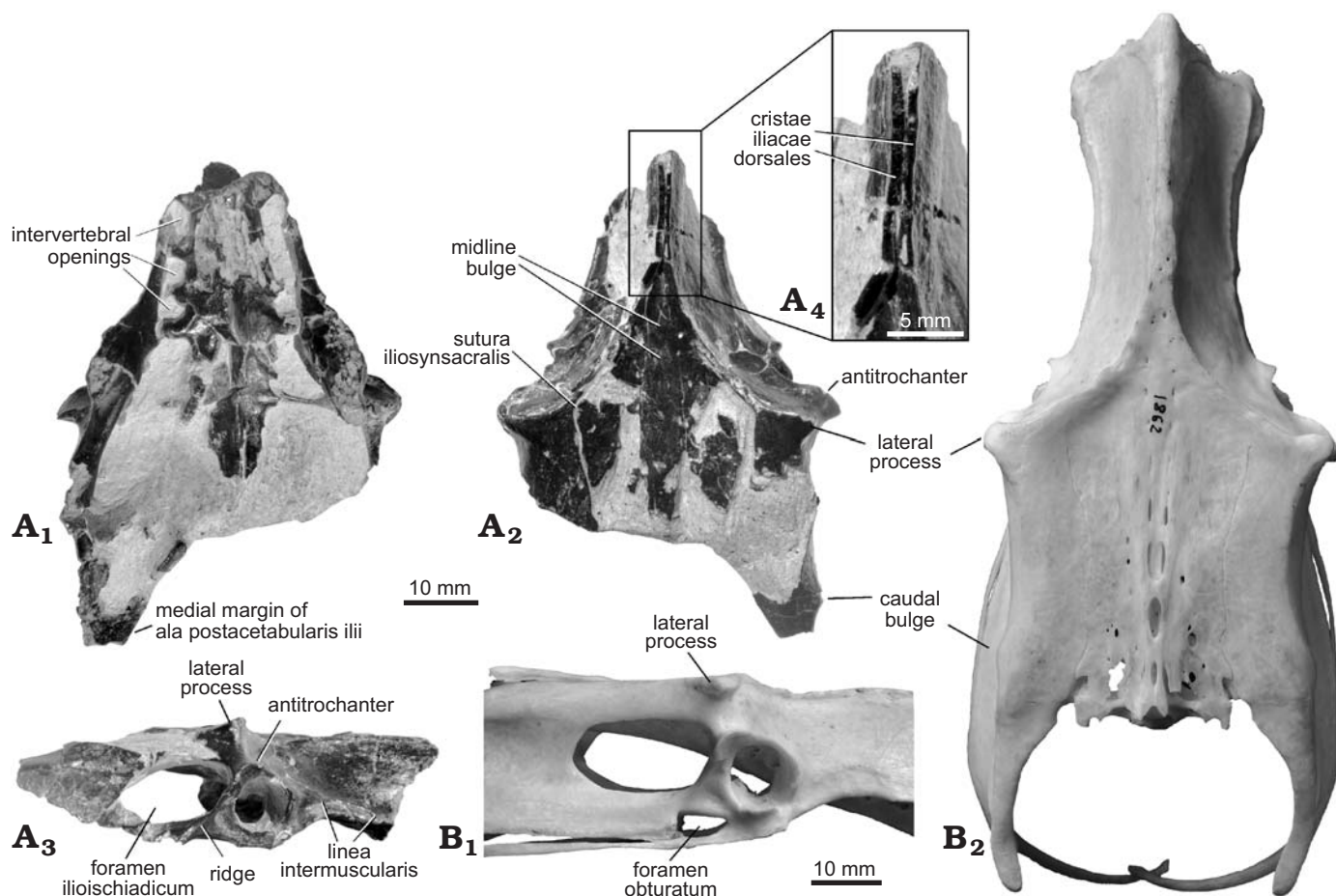


Fig. 4. Pelvis of the seriema (Cariamidae) *Noriegavis santacruzensis* (Noriega, Vizcaino, and Bargo, 2009) from the early Miocene Santa Cruz Formation in Argentina (A) in comparison with extant *Cariama cristata* Bonaparte, 1853 (B). A. MPM-PV 15049, in ventral (A₁), dorsal (A₂), and lateral (A₃) views, with detail of cristae iliacae dorsales (A₄). B. SMF 1862, pelvis in dorsal view (B₁) and detail in lateral view (B₂).

by well-developed crests. The comments on the orientation of the postorbital and zygomatic processes in the original diagnosis of *N. santacruzensis* (Noriega et al. 2009: 621) need to be revised, however, based on the information provided by specimen MPM-PV 15049, whose better preserved cranium allows a more accurate assessment of the relative inclinations of the postorbital and zygomatic processes. The correct orientation of these processes can be obtained if the holotype skull figured in lateral view by Noriega et al. (2009: fig. 3A, B) is slightly rotated counterclockwise towards its true horizontal position, in which case it becomes evident that the processus postorbitalis is not more vertically oriented and the processus zygomaticus is not less cranially protruding than in extant seriemas. In MPM-PV 15049 the tip of the processus postorbitalis is broken, but the remaining portion shows that it was mediolaterally thin as in *Chunga burmeisteri*, whereas it is somewhat broader in *Cariama cristata*. The processus zygomaticus is damaged in both, the holotype and the new specimen MPM-PV 15049, but appears to have had a similar length to that of modern Cariamidae. Both, the postorbital and zygomatic processes of *N. santacruzensis* exhibit similar angles to those of *C. cristata* and *Ch. burmeisteri*, with the tip of the processus

zygomaticus reaching the vertical level of the processus postorbitalis.

The prominentia cerebellaris is poorly preserved, but exhibits two lateral depressions on both sides, as in the holotype. Although the prominentia itself is badly crushed in the new specimen, its fragments overlie a “sedimentary cast” that allows to infer its prominent condition. As in *C. cristata*, the fossa temporalis is ventrally bordered by a faintly marked crista nuchalis transversa, whereas this crest forms a distinctly arched ridge in *Ch. burmeisteri*, which runs obliquely across the squamosum and joins the processus zygomaticus. The impression of the origin of musculus adductor mandibulae externus, pars rostralis, in the fossa temporalis is similar to that of *C. cristata*, i.e., is relatively wide and shallow with a rounded medial margin, whereas it forms a more elongated, more confined, and deeper mark in *Ch. burmeisteri*.

The right margin of the foramen magnum is damaged, but the remaining parts indicate that it was less dorsoventrally elongated than in the holotype and more closely corresponded in its shape with the foramen magnum of extant Cariamidae. We consider these differences to be due to distortion of the holotype, in which the foramen has an asymmetric shape,

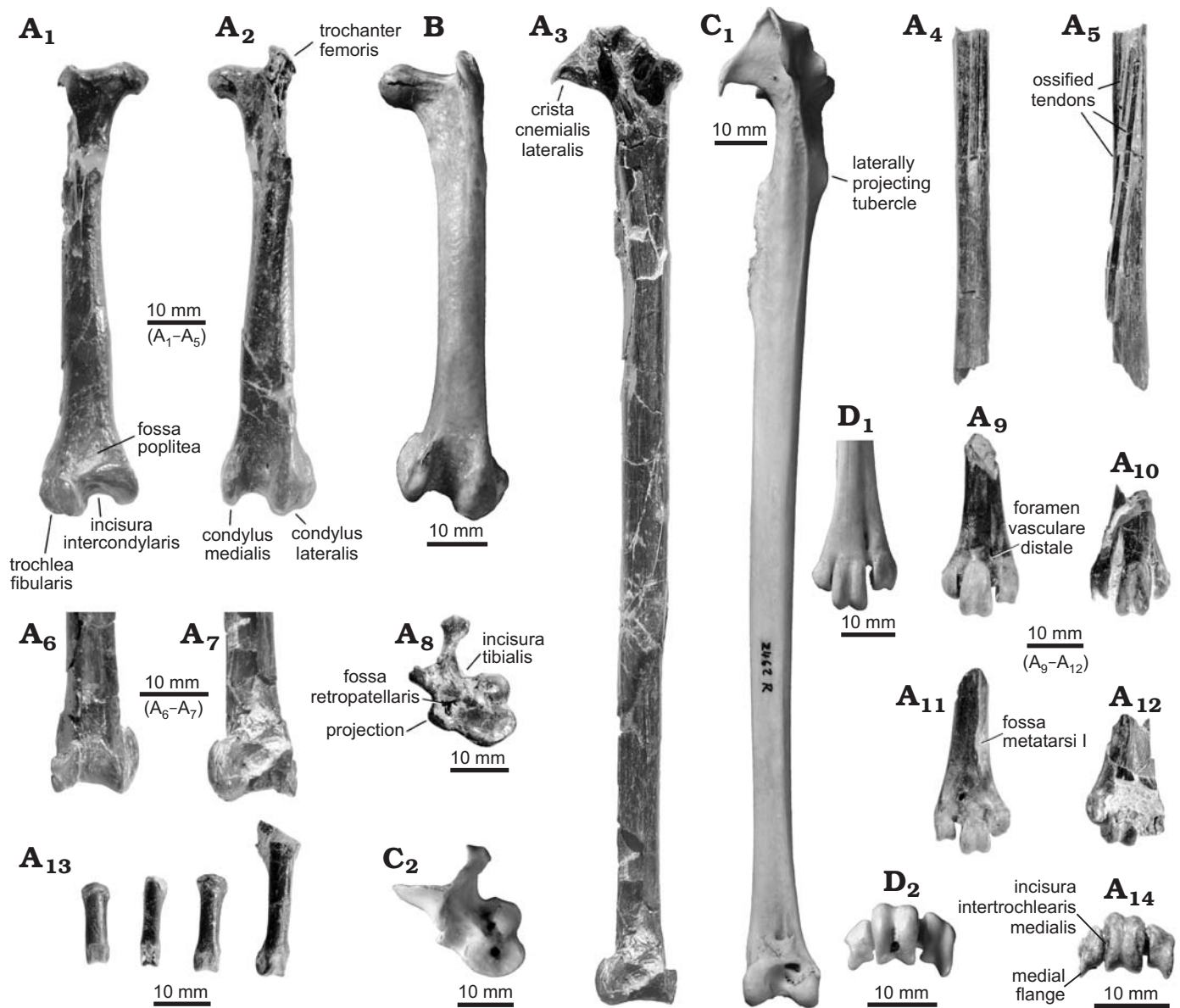


Fig. 5. Hindlimb bones of the seriema (Cariamidae) *Noriegavis santacrucensis* (Noriega, Vizcaino, and Bargo, 2009) from the early Miocene Santa Cruz Formation in Argentina (A) in comparison with extant *Cariama cristata* Bonaparte, 1853 (B–D). A. MPM-PV 15049. B. SMF 1710. C. SMF 2462. D. SMF 1862. Right femur in caudal (A₁, B) and cranial (A₂) views. Right tibiotarsus: cranial view (A₃, C₁), distal end in caudal (A₆) and cranial (A₇) views, proximal end in proximal view (A₈, C₂). Left tarsometatarsus: shaft in cranial (A₄) and caudal (A₅) views, distal end in dorsal (A₉, D₁), plantar (A₁₁), and distal (A₁₄, D₂) views. Right tarsometatarsus in dorsal (A₁₀) and plantar (A₁₂) views, pedal phalanges (A₁₃)

and the new specimen presumably better reflects the true morphology of the foramen magnum of *N. santacrucensis*.

The dorsal surface of the cranium forms two elevated areas, which are each separated by a depression from the orbital rim (Fig. 2A₅). This condition is approached by *Ch. burmeisteri* where those bulges and the depression are, however, less marked. As in modern seriemas, the skull roof bears numerous impressions of blood vessels, which are particularly pronounced along the orbital rims. The interorbital section of the skull roof is of similar width to *Chunga*, whereas it is wider in *Cariama* (Fig. 2). The processus supraorbitalis of the os lacrimale is proportionally larger than in both species of extant seriemas (Fig. 2). The processus orbitalis of the os lac-

rimale is thin and laterally notched, being more slender than in *Ch. burmeisteri* and much more so than in *C. cristata*. The preserved neurovascular foramina on the left os exoccipitale show the same pattern as in the holotype, but other details of the basicranial and palatal areas cannot be recognized.

The beak is broken from the cranium and angled in an unnatural position. In its overall proportions, with a straight culmen and a slightly deflected tip, it resembles that of modern Cariamidae, but the nostrils are proportionally larger than in the two extant species (Fig. 2). The processus frontales of the ossa praemaxillaria are unfused, of similar width to those of *C. cristata* and somewhat broader than in *Ch. burmeisteri*. Of the mandible only the caudal portion of the right

ramus is preserved, which has similar proportions to modern seriemas, but is not well enough preserved for meaningful comparisons (Fig. 2A₄).

The sternum preserves the cranial portion and much of the carina sterni, which, however, lacks the ventral rim and the apex carinae (the latter being cranially prominent in modern Cariamidae). The preserved part of the carina still shows that it was proportionally deeper dorsoventrally than in extant seriemas, and whereas the margo cranialis carinae, i.e., the cranial margin dorsal to the apex carinae, measures only slightly more than the distance across the sulci articulares coracoidei in extant Cariamidae, it is more than two-thirds of the width across the sulci articulares coracoidei in *Noriegavis* (Fig. 3). The preserved margo cranialis of the carina is further steeper, i.e., less curved, than in extant Cariamidae, which may indicate that the apex may did not form a marked overhang. The sulci articulares coracoidei are narrower than in extant Cariamidae, and the medial section of the labrum internum is dorsoventrally narrower (Fig. 3). The spina externa is broken.

Only the fragmentary proximal half of the left humerus is preserved, which, as far as comparisons are possible, resembles the corresponding part of the humerus of extant seriemas. The cranial surface of the distal section of the shaft is, however, more flattened than in extant Cariamidae, with the craniodorsal margin forming a sharp edge.

The preserved fragments of the proximal right ulna and the distal left ulna correspond with extant seriemas in shape and proportions, but the condylus dorsalis has a somewhat more rounded outline than in the modern species. On the caudal surface of the proximal end, there is a projection, just distal to the olecranon (Fig. 3A₂), which is also present in extant seriemas and *Elaphrocnemus* (Mourer-Chauviré 1983: pl. 1: 7). The phalanx proximalis digiti majoris resembles that of extant *Chunga* in its shape, whereas the caudal margin of this phalanx is more bulged in *Cariama* (Fig. 3).

The pelvis differs in its proportions and some morphological characters from that of modern seriemas. In particular, and as can be deduced from the proportions of the ala postacetabularis ilii, the medial margin of which is preserved (Fig. 4A₁), the caudal part is proportionally shorter. The cristae iliacae dorsales contact each other and the crista spinosa of the synsacrum, but unlike in extant Cariamidae these crests do not fuse and a suture is still visible (Fig. 4A₄). As in modern seriemas and Phorusrhacidae but unlike the bathornithid *Paracrax wetmorei* (Cracraft 1968: fig. 10), there is a well-defined, laterally prominent process dorsal of the antitrochanter (Fig. 4). The suturae iliosynsacrales are less obliterated than in extant *C. cristata* (Fig. 4A₂), and further unlike the latter the synsacrum forms a midline bulge on the dorsal surface of the caudal part of the pelvis; with regard to the degree of sutural obliteration and bulging of the synsacrum, *Noriegavis* is more similar to *Ch. burmeisteri*. As in extant Cariamidae there is a curved linea intermuscularis along the ventral section of the alae praeacetabularis ilii (Fig. 4A₃). The foramen ilioischadicum is of similar relative

size to that of modern seriemas, with a distinct ridge, which runs from its cranial margin ventrally across the ala ischii (Fig. 4A₃). Of the foramen obturatum only the dorsal rim is preserved, and it can thus not be said whether the processus obturatorius only contacted the pubis as in extant Cariamidae, or was fused with it as in *Paracrax* (Bathornithidae) and Phorusrhacidae (Cracraft 1968: fig. 10; Sinclair and Farr 1932: pl. 28). Unlike in *Paracrax*, there is no well-defined tuberculum praeacetabulare, and as in extant seriemas, the alae postacetabulares ilii form a laterally projecting bulge in their midsection (Fig. 4). The processus costales of the synsacral vertebra cranial to the vertebra acetabularis are narrower than in extant seriemas, the intervertebral openings are thus larger. Whether there was a marked recessus caudalis fossae as in extant Cariamidae cannot be ascertained.

The femur, the shaft of which is damaged in the lateral section of the proximal end, is also distinguished from that of extant seriemas in some features. Like in extant Cariamidae there is a marked trochanter with a well-developed crista trochanteris. The proximal and distal ends of the bone are, however, proportionally narrower than in extant seriemas (Fig. 5A₂, B). The distal end, and the condylus medialis in particular, is less medially inflected, and the trochlea fibularis is less strongly laterally projected. The sulcus intercondylaris is narrower than in modern seriemas and the fossa poplitea is less marked. The latter feature also distinguishes the bone from the femur of *Dynamopterus* (Idiornithidae), in which the fossa poplitea is more marked and in which the femur shaft is more slender.

The right tibiotarsus has similar overall proportions to that of the two living species of Cariamidae. In proximal view, the bone also corresponds well with extant seriemas. As in the latter and *Dynamopterus* (Mourer-Chauviré 1983: fig. 3), there is a marked incisura tibialis, which is somewhat wider in the fossil than in the two living species (Fig. 5A₈, C₂). In proximal view, and as in extant Cariamidae, there is further a prominent projection medial to the fossa retropatellaris, which is steeply sloping towards facies gastrocnemialis (Fig. 5A₈). The cristae cnemiales are better developed than in *Dynamopterus*. Although only the base of the crista cnemialis cranialis is preserved, the cristae appear to have been less strongly proximally protruding than the cristae cnemiales of extant seriemas (Fig. 5A₃, C₁). The distal end of the bone is damaged, but corresponds in size to specimen MPM-PV 3510, the larger of the two distal tibiotarsi figured by Noriega et al. (2009). These authors noted that in lateral view the condylus lateralis has a more rounded outline than in extant seriemas.

Of the tarsometatarsus only the distal ends and part of the left shaft are preserved. The proportions of the latter indicate that the bone was long and slender like in extant seriemas. On the plantar surface, three ossified tendons are preserved in situ (Fig. 5A₅). As in modern Cariamidae there is a sulcus for musculus extensor hallucis longus on the medial surface of the distal shaft, which terminates at the proximal end of the fossa metatarsi I. The fossa metatarsi I itself is a well-defined concavity as in the fossil species *Chunga incerta* and extant

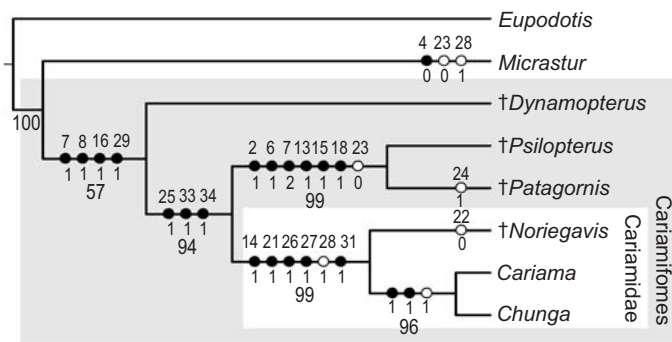


Fig. 6. Strict consensus tree of two most parsimonious tree resulting from analysis of the character matrix in SOM 1 (Supplementary Online Material available at http://app.pan.pl/SOM/app60-Mayr_Noriega_SOM.pdf) (length = 55, CI = 0.70, RI = 0.72). Characters (top) and character states (bottom) are listed, with filled circles representing unambiguous apomorphies. Bootstrap support values are indicated next to the internodes, fossil taxa are marked with a dagger.

seriemas. The foramen vasculare distale is proportionally larger and situated farther distally than in extant seriemas. The distal end closely resembles the distal tarsometatarsus of extant seriemas, but the trochleae metatarsorum III and IV are mediolaterally narrower, the medial flange on the plantar surface of the trochlea metatarsi II is better developed (Fig. 5A₁₄), and the incisura intertrochlearis medialis is wider (Fig. 5A₁₄). The lateral portion of the trochlea metatarsi IV reaches as far distally as the medial one, whereas it is shorter in extant seriemas. Compared to fossil Cariamiformes, the distal tarsometatarsus of *Noriegavis* more closely resembles that of Phorusrhacidae than that of *Dynamopterus* (Idiornithidae), and the trochleae metatarsorum II and IV of *Noriegavis* are less plantarly deflected and reach farther distally (beyond the middle of the trochlea metatarsi III) than in *Dynamopterus*. The distal end of the trochlea metatarsi IV is further oriented rectangular to the longitudinal axis of the shaft and not laterally tilted. The phalanges (Fig. 5A₁₃) correspond with those of extant Cariamidae.

Stratigraphic and geographic range.—Early Miocene Estancia La Costa member of the Santa Cruz Formation; Santa Cruz Province, Argentina.

Results of phylogenetic analysis and conclusions

Analysis of the character matrix in the SOM 2 resulted in two most parsimonious trees, the consensus tree of which is shown in Fig. 6. The analysis shows *Noriegavis* to be the sister taxon of the clade (*Chunga* + *Cariama*), and thus supports the original assignment of *Noriegavis santacrucensis* to Cariamidae (Noriega et al. 2009, contra Agnolín 2009). The following six characters were optimized as apomorphies of a clade including *Noriegavis*, *Chunga*, and *Cariama* (numbers refer to the character list in the SOM 1: (14) ulna, caudal surface of proximal end with marked projection, just distal

to olecranon (Fig. 3A₂₂, B₄); (21) pelvis with alae postacetabulares ilii forming a laterally projecting bulge in their midsection (Fig. 4A₂₂, B₁); (26) tibiotarsus with medial surface of proximal end bearing a prominent projection medial of fossa retropatellaris that is steeply sloping towards facies gastrocnemialis (Fig. 5A₈); (27) tibiotarsus, medial surface of proximal end bearing a marked laterally projecting tubercle next to the impressio ligamenti collateralis ventralis (Fig. 5C₁); (28) tarsometatarsus, shaft greatly elongated and very slender, with length of bone measuring more than ten times the width of the distal end (for *Noriegavis* a tarsometatarsus of similar proportions to that of extant Cariamidae can be assumed from the preserved portions of this bone); and (31) tarsometatarsus with marked sulcus for musculus extensor hallucis longus on medial surface of distal shaft.

Three characters support a clade (*Chunga* + *Cariama*) to the exclusion of *Noriegavis*: (1) processus supraorbitalis small, measuring less than half of the rostrocaudal diameter of the orbit; (10) sternum, medial section of labrum internum dorsoventrally wide; (24) femur stout and with wide proximal end, with ratio maximum length of bone: width of proximal end 4.5 or less. Agnolín (2009) erected the taxon *Noriegavis* based on two putatively autapomorphic characters (foramen magnum elliptical, very high, and dorsally delimited by two crests, as well as a conspicuous and globose cerebellar prominence). As detailed above, the shape of the foramen magnum is not a valid character due to distortion of the holotype, but we follow Agnolín's (2009) proposal to classify the fossil species in the taxon *Noriegavis*, and emend his diagnosis with information provided by the new specimen.

The overall morphology of all of the preserved bones of *N. santacrucensis* is very similar to extant seriemas, but there are some differences that indicate somewhat different life habits of the fossil species. The proportionally deeper carina sterni of *N. santacrucensis* indicates that the Santacrucian species had better developed flight capabilities than modern seriemas, which do not perform sustained flights over longer distances (Gonzaga 1996). The differences in the proportions of pelvis and femur (Fig. 4) and the less strongly proximally protruding cristae cnemiales further suggest that *N. santacrucensis* was less cursorial than its extant relatives.

The interrelationships of stem group Cariamiformes are still poorly understood, and no consensus exists on which of the various fossil stem group Cariamiformes is the closest relative of seriemas (Mayr 2002, 2009; Agnolín 2009; Alvarenga et al. 2011). In concordance with the phylogeny proposed by Mayr (2002), our analysis supports a sister group relationship between Phorusrhacidae and Cariamidae (Fig. 6), whereas the analysis of Agnolín (2009) resulted in the clades (*Dynamopterus* ["*Idiornis*"] + *Paracrax* + Cariamidae) and (*Bathornis* + Phorusrhacidae). Knowledge of the exact interrelationships of Cariamiformes is of significance, because the two hypotheses would lead to different conclusions concerning the biogeographic history of these birds. In the former case (sister group relationship between Cariami-

dae and Phorusrhacidae), Cariamidae probably evolved in South America, whereas they would more likely have dispersed into that continent from the Northern Hemisphere, if *Dynamopterus* and the North American “bathornithid” *Paracrax* were the closest relatives of Cariamidae.

Mayr (2002) listed the short second toe and its sharply curved claw as apomorphies of a clade (Cariamidae + Phorusrhacidae). Both features are absent in Idiornithidae (Peters 1995; Mayr 2000), but the second toe is likewise very short in Bathornithidae (Wetmore 1933, 1944), which were omitted from Mayr’s (2002) analysis (the ungual phalanx of the second toe of Bathornithidae is unknown). In addition to these two features, eight further characters were optimized as apomorphies of a clade (Cariamidae + Phorusrhacidae) in the present analysis (Fig. 6).

The two synapomorphies Agnolín (2009) identified for his Cariamoidea, i.e., a clade including *Dynamopterus* [“*Idiornis*”], *Paracrax*, and Cariamidae), concern the extremitas omalis of the coracoid and are a well developed processus procoracoideus, which closely approaches the hook-like tip of the processus acrocoracoideus (with which it fuses and forms a bony ring in some species of *Dynamopterus* [Mourer-Chauviré 1983: pl. 13: 15] and in extant Cariamidae), and a dorsoventrally compressed facies articularis scapularis of the coracoid. The extremitas omalis of the coracoid of Phorusrhacidae is, however, strongly reduced owing to their loss of flight capability, so that absence of these characters may be due to a secondary loss (features related to the extremitas omalis were therefore coded as unknown rather than absent for phorusrhacids by Mayr 2002).

Sister group relationship between *Bathornis* and phorusrhacids, as obtained by Agnolín (2009), is an intriguing novel hypothesis, but the three characters listed in support of it (robust jugal [Agnolín 2009: character 25], high and robust processus orbitalis of quadrate [Agnolín 2009: character 26], and reduced processus acrocoracoideus of coracoid [Agnolín 2009: character 41] do not constitute strong evidence, because they are either unknown from other stem group Cariamiformes (jugal and quadrate morphology) or characteristic for flightless birds in general (reduced acrocoracoid process). We further note that, according to the published figures (Wetmore 1944), *Bathornis grallator* does not have the caudally projecting processus supraorbitales, which are characteristic of cariamiform birds (contra Agnolín 2009, who coded these processes as present). The published figures of *B. grallator* are mainly graphic reconstructions and do not allow a critical assessment of some key features of this species. For this reason, bathornithids were not included in the present analysis, and an evaluation of their affinities has to await a revision of the original fossils.

Because of the great osteological resemblance of *Noriegavis santacrucensis* to modern seriemas and the fact that key skeletal elements—especially the coracoid—are still unknown, the Santacrucian species does not contribute to a resolution of the affinities of Cariamidae. However, *N. santacrucensis* shows that the osteology of seriemas underwent

few morphological changes since the early Miocene. Seriemas further have an isolated systematic position, exhibit a relictual distribution compared to Cariamiformes as a total group, and represent a taxon with only few extant species, and thus are among the few extant bird groups, which qualify as living fossils sensu Thenius (2000).

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