# A NEW MESEMBRIORNITHINAE (AVES, PHORUSRHACIDAE) PROVIDES NEW INSIGHTS INTO THE PHYLOGENY AND SENSORY CAPABILITIES OF TERROR BIRDS

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## QUERY SHEET

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**Q4.** Au: Figure 7. Only one scale bar, correct?
**Q5.** Au: Which matches your meaning: "In all three vertebrae, . . . vertically oriented, and the processus spinosus is reduced and, as in the sixth vertebra, possesses…" or "In all three vertebrae, . . . vertically oriented, and the processus spinosus is reduced, and, as in the sixth vertebra, all three vertebrae possess…"?
**Q6.** Au: Cione and Tonni, 2005. Dates of the congress? Publisher (and location) of the proceedings?
**Q7.** Au: Fürbringer, 1888. Please confirm the number of pages.

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ARTICLE

# A NEW MESEMBRIORNITHINAE (AVES, PHORUSRHACIDAE) PROVIDES NEW INSIGHTS INTO THE PHYLOGENY AND SENSORY CAPABILITIES OF TERROR BIRDS

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ABSTRACT—Terror birds constitute the most outstanding group of the South American Cenozoic avifauna. Considered as apex predators, their hunting skills have recently been examined, but their diversity is still unresolved. Here we report a new terror bird from the late Pliocene of Argentina, represented by the most complete articulated skeleton of one yet found. Our phylogenetic analysis places this taxon among derived phorusrhacids (Mesembriornithinae). One of the most striking cranial features of the new species is the suppression of intracranial kinesis due to the presence of an independent ossified bone that increases the structural link between the lacrimal and jugal bars, and the absence of both palatal hinges. The new species possesses ossified tracheal rings and a tracheobronchial syrinx, as well as sclerotic ossicles to adjust the shape of the cornea during its diurnal vision, and reveals a mean hearing sensitivity (~2300 Hz) below the average for living species. The discovery of this new species provides new insights for studying the anatomy and phylogeny of phorusrhacids and a better understanding of this group's diversification.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

## INTRODUCTION

Terror birds (Phorusrhacidae) are extinct Cariamiformes with long hind limbs, a narrow pelvis, reduced forelimbs, and huge akinetic skulls endowed with a high, long, and compressed hooked beak (Ameghino, 1895; Blanco and Jones, 2005; Bertelli et al., 2007; Degrange et al., 2010; Degrange and Tambussi, 2011; Degrange, 2012; Tambussi et al., 2012). These birds were the predominant predators during the Cenozoic in South America (Tambussi and Degrange, 2013) and certainly one of the most striking groups that lived during that period. Although their hunting skills have recently been assessed, their diversity is still unresolved.

Here we report a new species of Mesembriornithinae represented by a nearly complete skeleton and an additional fragmentary neurocranium collected at the Atlantic cliff of the Pampean Region, Argentina (Fig. 1). The new species belongs to Mesembriornithinae, the shortest-lived and most diverse phorusrhacid subgroup, with a fossil record extending from the late Miocene to the late Pliocene. Basal phorusrhacids are relatively small, but very large body mass (up to 70 kg) was acquired at least twice in different lineages. Members of Mesembriornithinae are small to very large birds, and the new species falls within the middle of this size range. The discovery of this new species provides new insights for studying the anatomy and phylogeny of phorusrhacids and a better understanding of this group's diversification.

If not indicated otherwise, osteological terminology follows Baumel and Witmer (1993).

**Institutional Abbreviations—AMNH,** American Museum of Natural History, New York, New York, U.S.A.; **BAR**, Museo Asociación Paleontológica Bariloche, Río Negro, Argentina; **CORD-PZ**, Museo de Paleontología de la Universidad de Córdoba, Córdoba, Argentina; **FM**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **MACN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciudad Autónoma de Buenos Aires, Buenos Aires, Argentina; **MLP**, Museo de La Plata, Buenos Aires, Argentina; **MMP**, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Buenos Aires, Argentina; **MNHN**, Museo Nacional de Historia Natural de Montevideo, Montevideo, Uruguay; **MPM-PV**, Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina; **NHMUK**, Natural History Museum, London, U.K.; **YPM-PU**, Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

## METHODS

### Phylogenetic Analysis

We analyzed the intrafamiliar relationships among phorusrhacids using a data matrix of 84 characters and 19 taxa (Supplementary Data, Appendix S1). The problematic phorusrhacid *Lavocatavis africana* was excluded from the analysis because it is represented by a single fragmentary femur. In our matrix, 69 characters are binary, 15 are multistate, and seven are polymorphic (encoded in brackets). All missing data were scored as '?'. All characters were treated as unordered, and Cariamidae was selected as the outgroup.

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*Corresponding author.

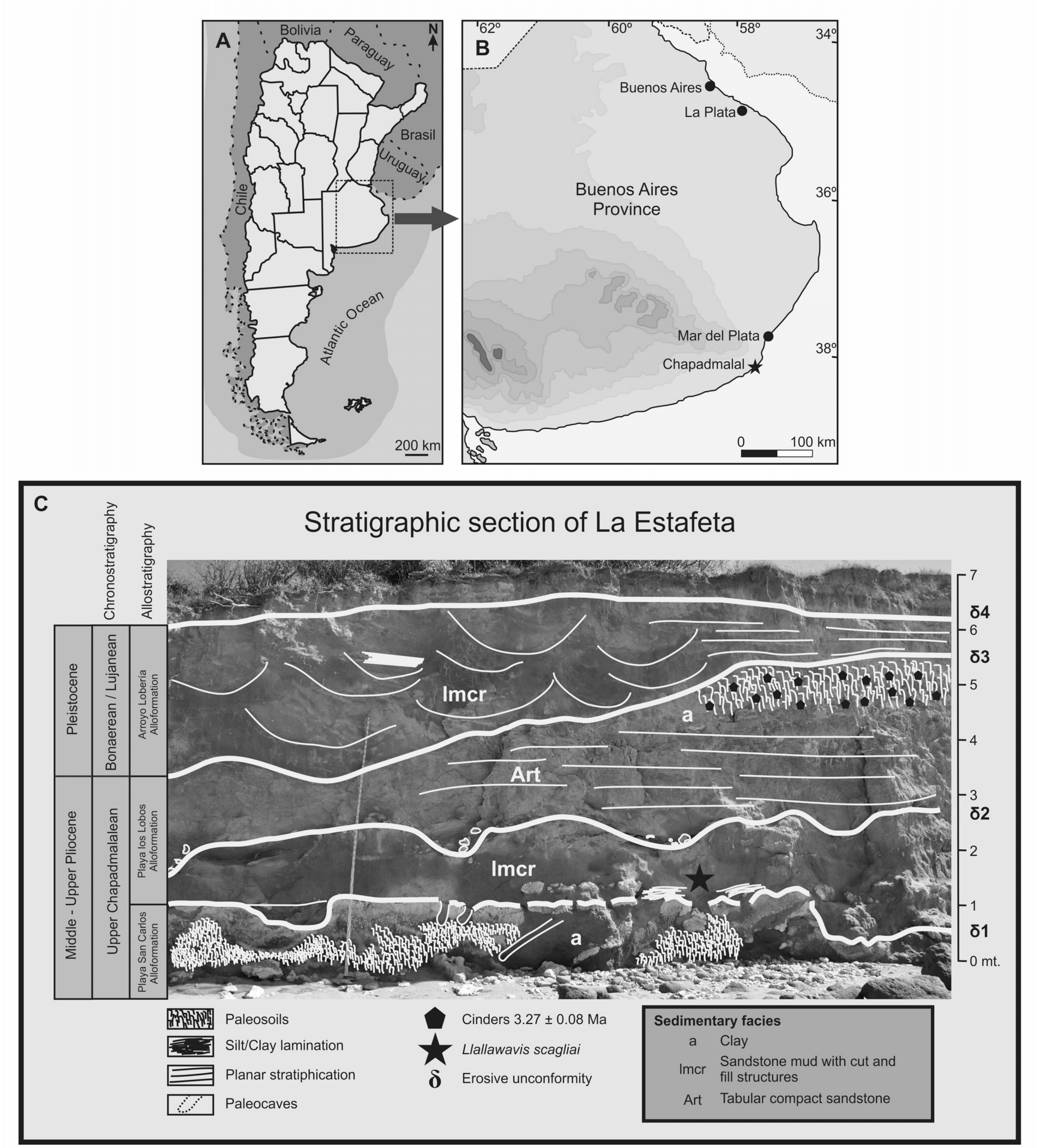

FIGURE 1. Geographic and stratigraphic provenance of *Llallawavis scagliai*, gen. et sp. nov. Maps of **A**, Argentina and **B**, Buenos Aires Province showing location of fossil locality (S38°9′59.47″, W57°38′1.90″); **C**, stratigraphy of the locality. Chronostratigraphy after Cione and Tonni (2005), allostratigraphy and sedimentary facies from Zárate and Fasano (1989), and cinders according to Schultz et al. (1998).

A parsimony analysis was performed using TNT (Tree analysis using New Technology) version 1.1 (Goloboff et al., 2008). For the analysis, no implied weighting was used because its use is not exempt of criticism (Farris, 1969, 1989; Goloboff, 1993; Kluge, 1997).

Random 100 Wagner trees were generated with 100 additional replicates, using the TBR algorithm and saving 100 trees per replicate, collapsing the trees after the search. From the trees obtained, the strict consensus tree was generated.

### Inner Ear Reconstruction

Computed tomography (CT) scans in the transverse plane of skull material referred to the new species MLP 89-III-20-1 and *Patagornis marshi* CORD-PZ 1341 were obtained using spiral CT performed at Hospital San Juan de Dios, La Plata, Argentina (General Electric Bright Speed; HiSpeed CT scanner, 140 kV, 300 mA, 0.62 mm slice thickness). The DICOM images were processed, and the reconstruction of the three-dimensional (3D) models of the inner ear were made using Materialise Mimics software 10.01 (Materialise, Leuven, Belgium) trial version.

## SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Subclass NEOGNATHAE Pycraft, 1900
Order CARIAMIFORMES Verheyen, 1957
Suborder CARIAMAE Fürbringer, 1888
Family PHORUSRHACIDAE (Ameghino, 1889)
Subfamily MESEMBRIORNITHINAE (Moreno, 1889)
*LLALLAWAVIS*, gen. nov.

**Type and Only Known Species**—*Llallawavis scagliai*, gen. et sp. nov.

**Diagnosis**—As for the type species.

Q3 **Etymology**—The name '*Llallawa*' means 'magnificent' in Quechua in reference to the nature of the remains, and 'avis' means 'bird.'

*LLALLAWAVIS SCAGLIAI*, gen. et sp. nov.
(Figs. 2–8)

**Etymology**—The species name is after Galileo Juan Scaglia (1915–1989), naturalist and director of the MMP during 1940–1980.

**Holotype**—MMP 5050 (Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina), a nearly complete articulated skeleton (Fig. 2); the right ulna, both radii and carpometacarpi, the pygostyle, and a few phalanges are missing.

**Referred Material**—MLP 89-III-20-1 (Museo de La Plata), fragmentary braincase.

**Occurrence**—La Estafeta Beach, Mar del Plata, Buenos Aires Province, Argentina (Fig. 1). Lowest part of Playa Los Lobos Allo Formation (Zárate and Fasano, 1989), older than 3.3 million years (Orgeira, 1987; Schultz et al., 1998), middle Pliocene.

**Diagnosis**—A phorusrhacid diagnosed by the following combination of characters (autapomorphies are noted by an asterisk here and in Figs. 6–8): high, long, and narrow beak with narial knob; wide sagittal nuchal crest; fonticuli occipitalis present*; parasphenoidal wings absent*; caudally long supraorbital process (lacrimal bone) not leaned toward the frontals; os lacrimale communicans present as an independent bone; palatal fenestra obliterated*; craniofacial hinge present; palatal and jugal bar hinges absent; caudal pneumatic foramen of the os quadratum absent*; coracoid and scapula fused medially*; supratrochanteric crest more extended laterally than the antitrochanter*; caudal margin of the ischium forming a marked obtuse angle*; tarsometatarsus shaft distally tapered*; and an asymmetric hypotarsus in caudal view.

## DESCRIPTION

*Llallawavis scagliai* is a medium-sized phorusrhacid with an estimated body mass of 18 kg and estimated height of 1.2 m (Degrange, 2012).

### Skull

A striking feature of the skull (Fig. 3) is that its structure does not allow the palate and beak to be bent upward (akinesis; Degrange et al., 2010) due to the absence of the zona flexoria palatina and the zona flexoria arcus jugalis, although the zona flexoria craniofascialis (the craniofacial hinge) is present.

The neurocranium of *Llallawavis* is globose, a feature it shares with *Psilopterus* and *Procariama*. The occiput is vertical and wide. The prominentia cerebellaris is prominent and acute. The crista nuchalis sagittalis is wide, as in *Procariama* (narrow in *Psilopterus*). The condylus occipitalis is oval and not pedicelated, with a poorly marked incisura medialis condylaris. The fonticuli occipitalis are present. The processus paroccipitali are remarkably developed and are parallel to the occiput in orientation. As in all phorusrhacids, the fossae temporalis are wide and triangular in shape. The processus suprameaticus is stout. The robust processus zygomaticus is ventrocranially directed. The processus postorbitalis is quadrangular in shape. The fossa subtemporalis has a non-inverted-trianglar shape. The lamina parasphenoidalis is strongly expanded. The alae parasphenoidalis are absent. The processus medialis parasphenoidalis and the processus basipterygoideus are very well developed, as in all phorusrhacids.

The septum interorbitale is complete and thin, with a large fonticuli orbitocranialis. The ossa ectethmoidalis are represented by two small projections that do not contact the descending branch (processus orbitalis) of the os lacrimale.

The sutura lacrimofrontalis is straight, contacts the ossa frontalis caudally, but is mainly located on the ossa nasalis. The supraorbital process of the os lacrimale is remarkably developed caudally and not directed toward the orbital margin. The processus orbitalis of the os lacrimale is stout, widened ventrally, and endowed with two pneumatic foramina. As in cariamids, the os lacrimale communicans is an independent bone. It is compressed and short, dorsally expanded, with a large medial foramen pneumaticum, which is dorsally located. This bone corresponds to the ossification of the ligamentum lacrimojugale and connects the processus orbitalis of the os lacrimale with the arcus jugalis.

Both annulus ossicularis sclerae were recovered. The ossiculae sclerae are rectangular in shape. The right annulus has 13 ossiculae (in order: one overplate, one interlocking plate, one underplate, four interlocking plates, one overplate, three interlocking plates, one underplate, and one interlocking plate; two overplates, two underplates, and nine interlocking plates in total); meanwhile, the left annulus possesses 14 ossiculae (one overplate, six interlocking plates, one overplate, four interlocking plates, one underplate, and one interlocking plate; two overplates, one underplate, and 11 interlocking plates in total).

The palate of *Llallawavis* is complete and beautifully preserved, the only complete one known for any phorusrhacid. Broken or deformed palates are also known for *Psilopterus, Patagornis*, and *Andalgalornis*. The processus rostralis of the ossa palatina are notably developed. The pars lateralis is narrow and long, with a deep fossa ventralis, limited by two remarkably developed and sharp cristae: the crista medialis is poorly extended ventrally, contrary to the crista lateralis, and markedly extended ventrally. The fossa choanalis is long and narrow. The ossa pterygoidei present a stout corpus and a sturdy process that contacts the processus basipterygoideus. The fenestra palatalis is obliterated. A thin vomer is present (a feature previously unknown for any phorusrhacid). The arci jugalis are gracile, forming a thin compressed bar.

The beak is tall and narrow, as in all phorusrhacids (Ameghino, 1895; Alvarenga and Höfling, 2003), although it has a narial knob and is proportionally longer than in Patagornithinae. It is endowed with a small distal hook. The nares are large and triangular and have a cranial prenarial fossa.

The os quadratum has two pneumatic foramina on its medial surface and three very well marked condyli for the articulation with the mandible. The caudal pneumatic foramen is absent. The processus orbitalis is long, thin, and rectangular. The incisura intercapitularis is wide. The condylus pterygoideus is very well

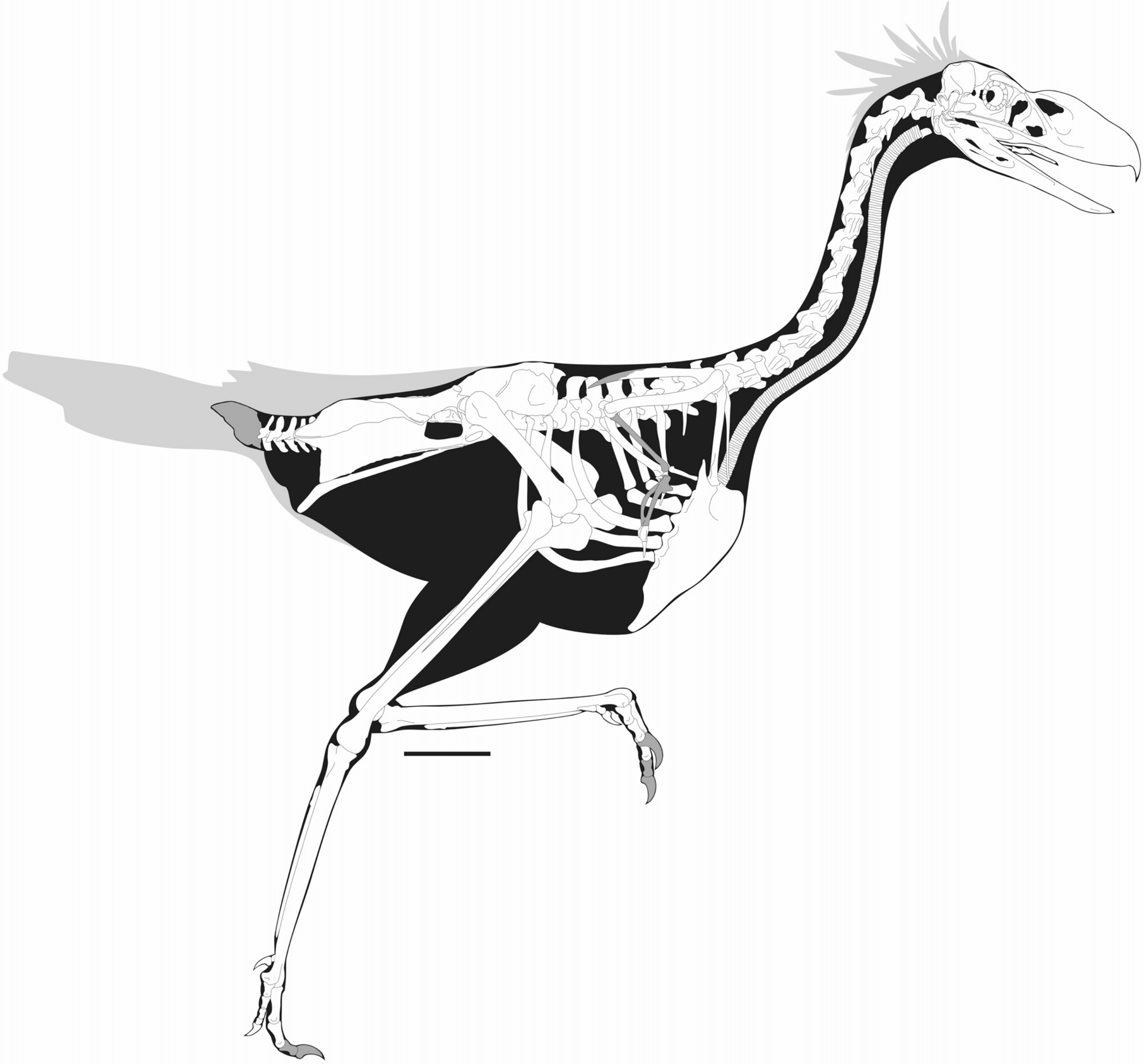

FIGURE 2. Skeletal anatomy of *Llallawavis scagliai*, gen. et sp. nov. MMP 5050. Bones colored in gray are missing. Scale bar equals 0.10 m.

developed and oval. The cotyla quadratojugalis is rounded and deep. The caudal pneumatic foramen of the corpus is absent, an exclusive feature of this taxon.

### Mandible

The mandible (Fig. 3A) is long and narrow, showing three fenestrae, a short and straight symphysis, a very pronounced processus coronoideus, and a short (shorter than in *Psilopterus*), high, and caudally directed processus retroarticularis. The cotyla medialis is wide and deep, whereas the cotyla caudalis is convex and confluent with the subcircular cotyla lateralis. Both processus lateralis mandibulae and medialis mandibulae are remarkably developed, especially the latter, as is typical of Phorusrhacidae (Degrange, 2012). The foramen pneumaticum articulare is large and located on the processus medialis mandibulae.

### Hyoideus Apparatus

The hyoideus apparatus is complete and well ossified, with two long paraglossum (fused in *Patagornis*; Andrews, 1899), one long basihyale, and two double-piece hyoid rami (cornu branchiale; Figs. 3D, 4A). The urohyal is absent, a derived condition in Neornithes (Baumel and Witmer, 1993) as in *Patagornis* (Andrews, 1899). The paraglosum are long, flattened, and caudally expanded to form stout cornua for contact with the basihyale. The latter is a stout bone, endowed with a cranioventrally

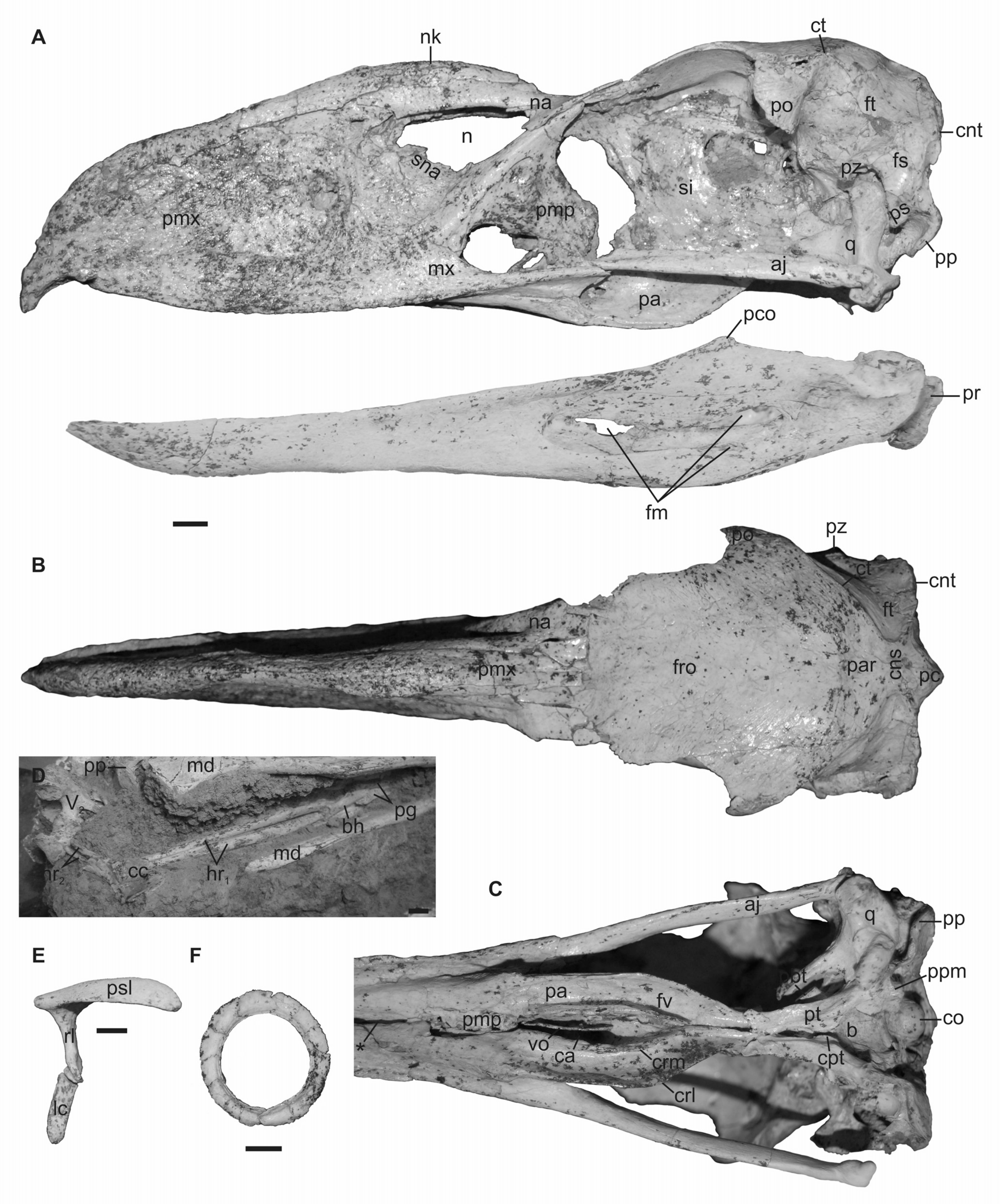

FIGURE 3. The skull of *Llallawavis scagliai*, gen. et sp. nov. Autapomorphies are noted by an asterisk. **A**, **B**, skull and mandible in **A**, lateral view and **B**, dorsal view; **C**, detail of the palate (ventral view); **D**, hyoid apparatus (during preparation); **E**, os lacrimale and os lacrimale communicans; **F**, scleral ring of the left eye. Note that the beak is high and narrow, as in all phorusrhacids, although it is proportionally longer. **Abbreviations**: **aj**, arcus jugalis; **b**, lamina basitemporalis (= lamina parasphenoidalis); **bh**, basihyale; **ca**, choanes; **cc**, cricoid cartilage; **cns**, crista nuchalis sagittalis; **cnt**, crista nuchalis transversa; **co**, condylus occipitalis; **crl**, crista lateralis (os palatinum); **crm**, crista medialis (os palatinum); **cpt**, pterygoid process; **ct**, crista temporalis; **fm**, mandible fenestra; **fro**, os frontale; **fs**, fossa subtemporalis; **ft**, fossa temporalis; **fv**, fossa ventralis (os palatinum); **hr**, hyoid ramus; **lc**, os lacrimale communicans; **md**, mandible; **mx**, os maxillare; **n**, nares; **na**, os nasale; **nk**, narial knob; **pa**, os palatinum; **par**, os parietale; **pbt**, processus basipterygoideus; **pc**, prominentia cerebellaris; **pco**, processus coronoideus; **pg**, paraglosum; **pmp**, processus maxillopalatinus; **pmx**, os premaxillare; **po**, processus postorbitalis; **pp**, processus paraoccipitalis; **ppm**, processus medialis parasphenoidalis; **pr**, processus retroarticularis; **ps**, processus suprameaticus; **psl**, processus supraorbitalis (os lacrimale); **pt**, os pterygoideus; **pz**, processus zygomaticus; **q**, os quadratum; **rl**, processus orbitalis (os lacrimale); **si**, septum interorbitale; **sna**, septum nasi osseum; **V$_2$**, second cervical vertebra (axis); **vo**, vomer. Scale bars equal 1 cm.

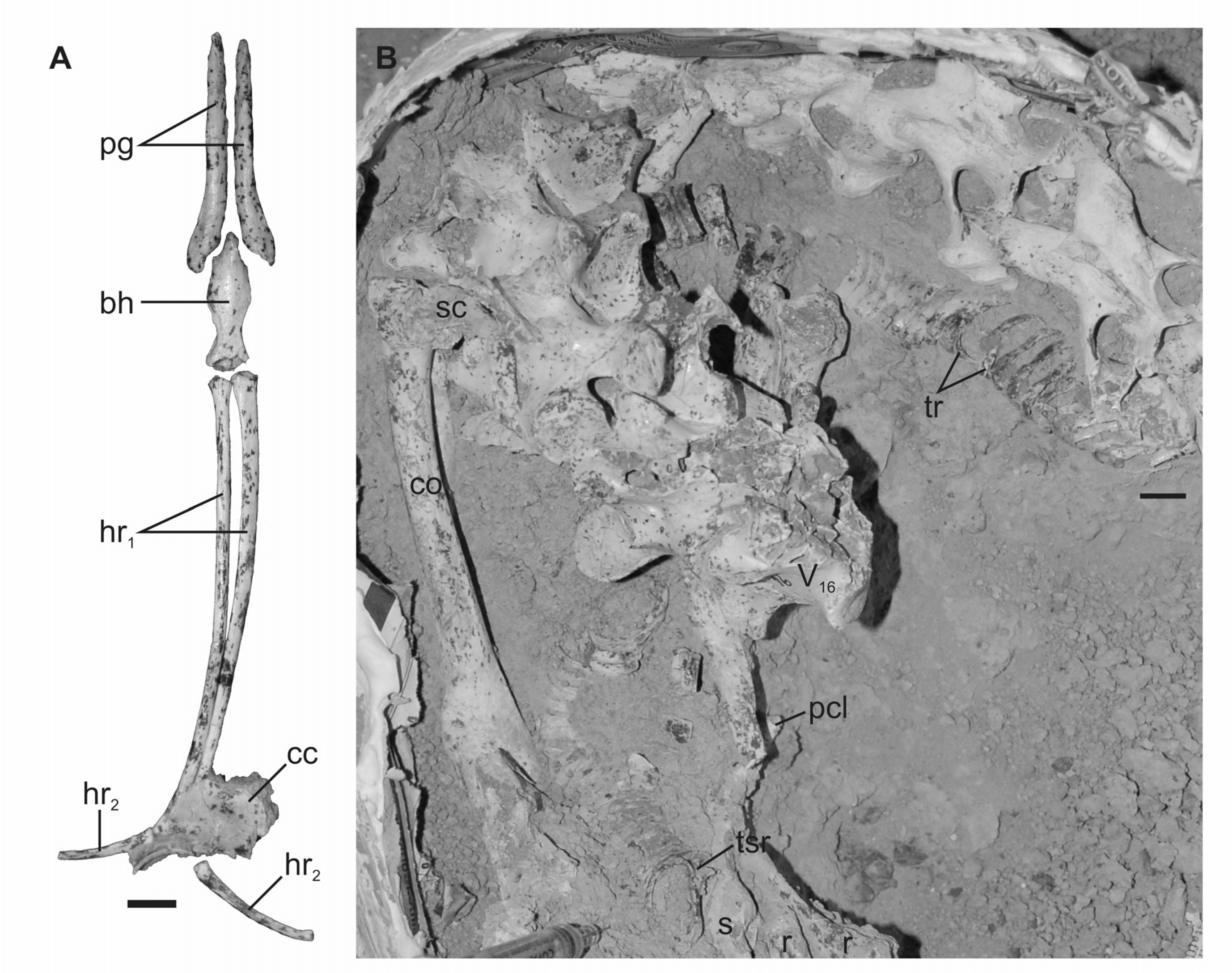

FIGURE 4. **A**, hyoid apparatus of *Llallawavis scagliai*, gen. et sp. nov., in ventral view (after preparation); **B**, trachea of *Llallawavis*, gen. et sp. nov., during preparation. **Abbreviations**: **bh**, basihyale; **cc**, cricoid cartilage; **co**, coracoid; **hr**, hyoid ramus; **pcl**, processus craniolateralis; **pg**, paraglossum; **r**, rib; **s**, sternum; **sc**, scapula; **tr**, tracheal ring; **tsr**, tracheosyringeal ring; $\mathbf{V_{16}}$, 16th vertebra. Scale bars equal 1 cm.

directed spine, and it is caudally expanded for contact with the cornu branchiale. Each cornus is composed of two segments: the most cranial is also the longer. It is curved and circular in section, with both articular facets expanded and convex. The caudal segment (not preserved in *Patagornis*; see Andrews, 1899) is shorter that the cranial and oval in section. Meanwhile, the cranial articular facet is subcircular and convex; the caudal facet is small and concave.

## Trachea

The trachea of *Llallawavis* (Fig. 4B) is the only complete trachea known for a terror bird. It is long with its caudal end opening at the cranial margin of the sternum. The cricoideus cartilage is preserved, although crushed. Its corpus is wide, with a medium spine that is caudally directed. The trachea is composed of ossified rings until the first probable tracheosyringeal (syrinx) ring, which is also ossified. It seems that *Llallawavis* has a mainly cartilaginous tracheobronchial syrinx, so it is not possible to determine the complexity of their sound producing structures.

## Vertebral Column

The presacral vertebral column has 19 heterocoelous vertebrae (Fig. 5). In *Llallawavis*, these presacral vertebrae are divided into 12 true cervical vertebrae, one cervicodorsal vertebra, and six dorsal vertebrae. Some cervical vertebrae show bifid neural spines, a peculiar character that has also been observed in *Andalgalornis* (Tambussi et al., 2012).

The morphology of the atlas is quite similar to that of *M. milneedwardsi*. It is a small vertebra that has a deep and subcircular fossa condyloidea, a stout processus costalis that is caudally directed, and very well marked incisura fossae. The arcus atlantis is broken but was clearly wide. The ventral crest is small and stout. The incisura arcus caudalis is dorsoventrally wide, although it is not strongly expanded craniocaudally. The processus spinalis is absent. The zygapophyses caudalis are located on well-developed, caudally projecting shelves. The facies articularis axialis is bordered ventrally by a distinct lip.

The axis has a stout corpus, endowed with large pneumatic foramina. The dens is short and robust, and the facies articularis

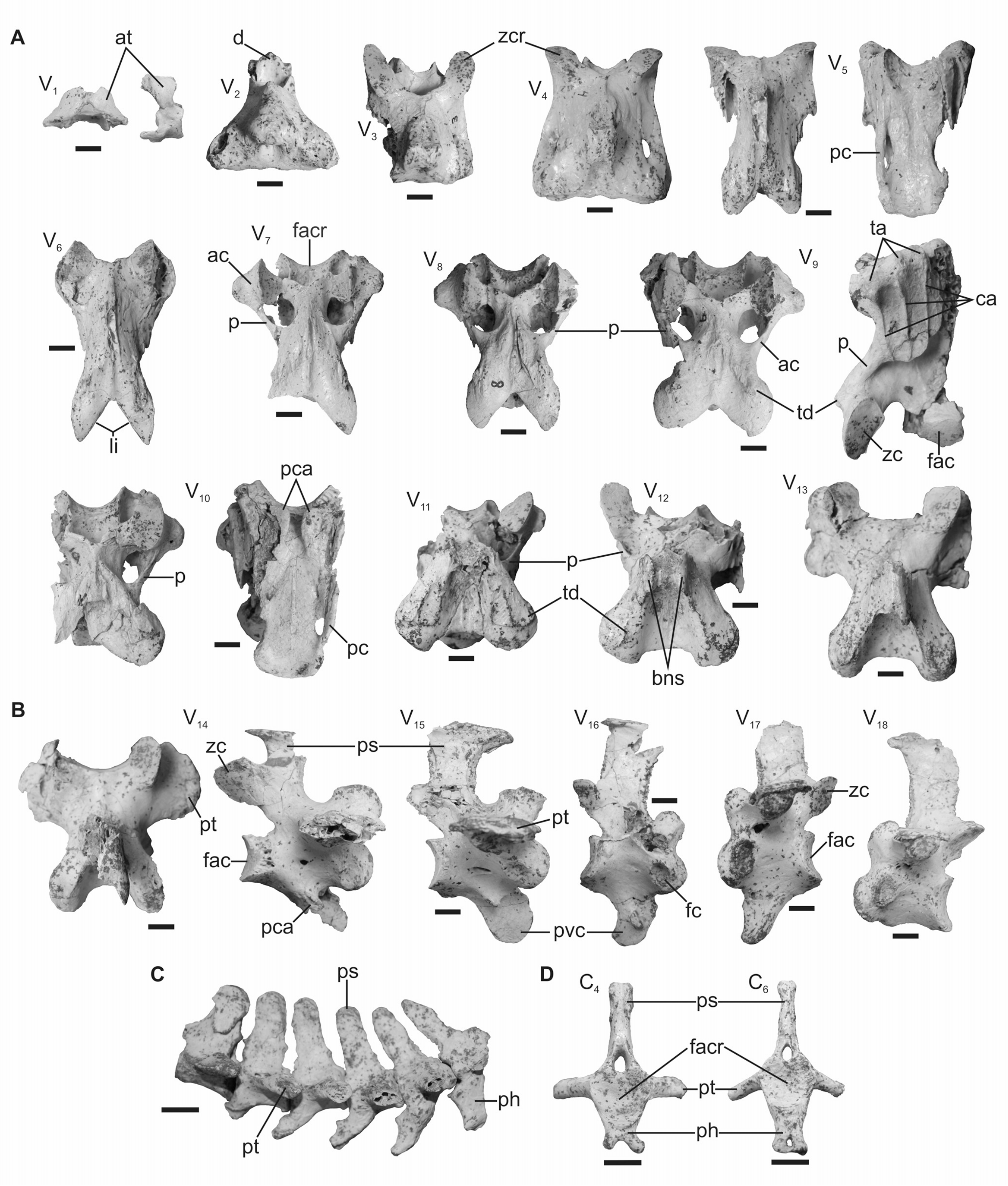

FIGURE 5. Vertebrae of *Llallawavis scagliai*, gen. et sp. nov. **A**, cervical vertebrae. Vertebrae 5 and 10 are in dorsal and ventral views, vertebrae 1 and 9 are in dorsal and lateral views, all other vertebrae are in dorsal view; **B**, thoracic vertebrae. Vertebra 14 is in dorsal and right views, vertebrae 15–16 are in right view, whereas vertebrae 17–18 are in left view; **C**, caudal vertebrae 2–7 in lateral view; **D**, caudal vertebrae 4 and 6 in cranial view. **Abbreviations**: **ac**, ansa costotransversaria; **at**, arcus atlantis; **bns**, bifid neural spine; **C**, caudal vertebra; **ca**, crista ansae; **d**, dens; **fac**, facies articularis caudalis; **facr**, facies articularis cranialis; **fc**, fossa costalis; **li**, lacuna interzygapophysaria; **p**, process that unites the ansa costotransversaria with the torus dorsalis; **pc**, processus costalis; **pca**, processus caroticus; **ph**, processus haemalis; **ps**, processus spinosus; **pt**, processus transversus; **pvc**, processus ventralis corporis; **ta**, tuberculum ansae; **td**, torus dorsalis; **V**, presacral vertebra; **zc**, zygapophysis caudalis; **zcr**, zygapophysis cranialis. Scale bars equal 1 cm.

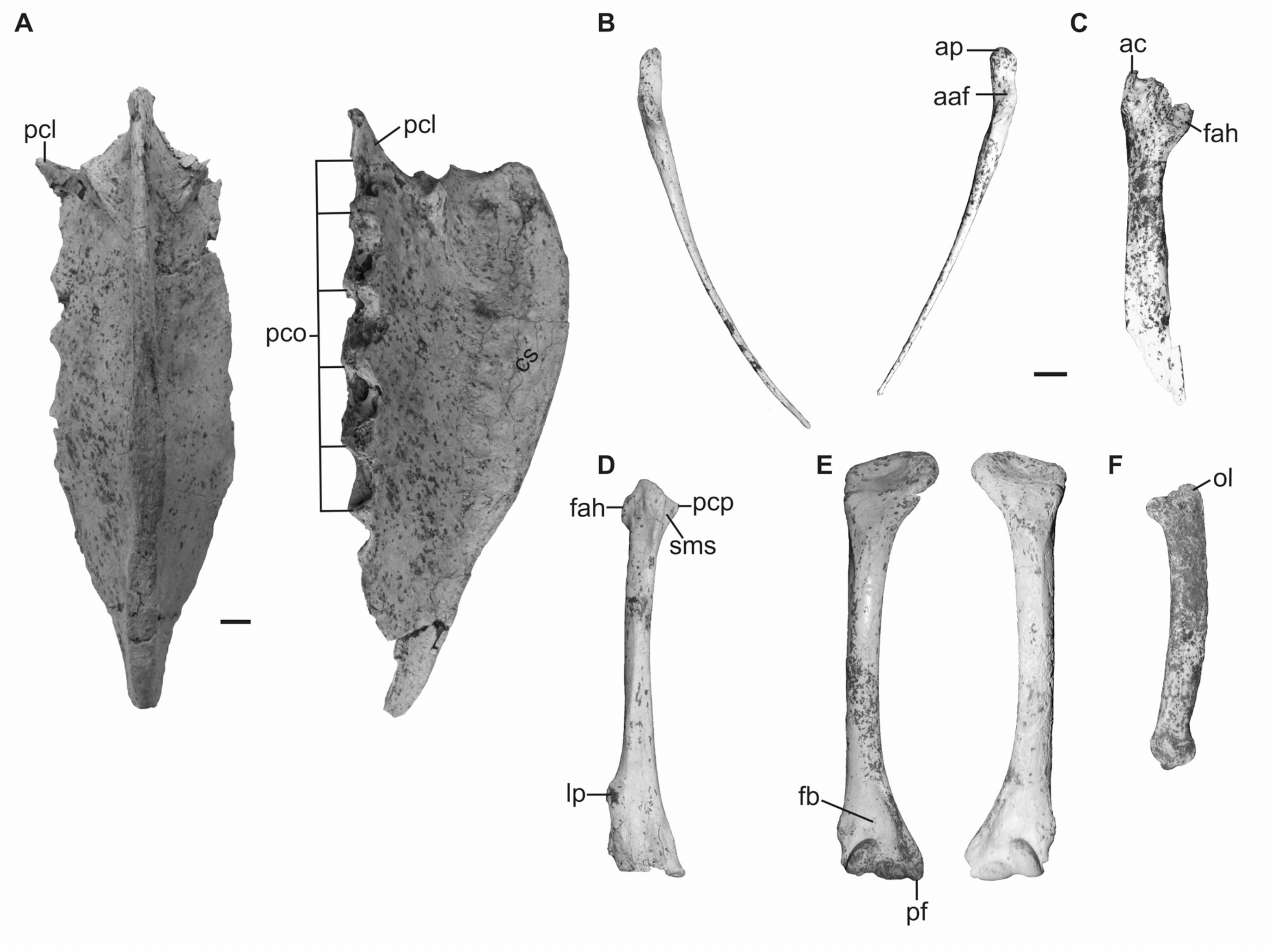

FIGURE 6. Pectoral girdle and forelimbs of *Llallawavis scagliai*, gen. et sp. nov. **A**, sternum in cranial and lateral views; **B**, furcula in cranial view; **C**, right scapula in dorsal view; **D**, right coracoid in cranial view; **E**, both humeri in cranial view; **F**, left ulna in lateral view. **Abbreviations**: **aaf**, facies articularis acrocoracoidea; **ac**, acromium; **ap**, processus acromialis claviculae; **fah**, facies articularis humeralis; **fb**, fossa m. brachialis; **lp**, processus lateralis; **ol**, olecranon; **pcl**, processus craniolateralis; **pco**, processus costalis; **pcp**, processus procoracoideus; **pf**, processus flexorius; **sms**, sulcus m. supracoracoideus. Scale bars equal 1 cm.

atlantica is shallow. The zygapophyses cranialis are small, and the ansae costotransversaria are absent (as in *Procariama* and *M. milneedwardsi*). The arcus axis is tall and stout. The processus costales are absent. The processus ventralis is stout. The zygapophyses caudalis are rounded, concave, and located on very robust processus articularis caudalis. The facies articularis caudalis is ventrocaudally slanted.

The corpus of the third cervical vertebra is wide, with a trapezoidal shape (it is longer than wide), and has pneumatic foramina. The zygapophyses cranialis are strongly extended craniocaudally. The ansae costotransversaria are well developed and endowed with two cristae laterales ansae. The processus costales are also very well developed. The arcus vertebrae is stout and caudally located. The tori dorsalis are elevated, located at the same level that the zygapophyses caudalis. The latter are concave and facing ventrally.

The fourth vertebra has a trapezoidal corpus, without concavitas lateralis, but with a pair of conspicuous oval foramina. The facies articularis cranialis is very narrow dorsoventrally, but strongly extended caudally. The processus carotici are stout and well developed. The facies articularis caudalis is obliquely oriented. The tori dorsalis are more cranially located than in the third vertebra.

The fifth vertebra is very similar in morphology to that of *M. milneedwardsi*, although more slender and proportionally longer. Viewed laterally, the ventral margin of the corpus describes a very marked curved (whereas it is straight in *M. milneedwardsi*). The processus transversi are prominent and caudally extended. The ansae costotransversaria are stout and endowed with two cristae laterales ansae (as in *M. milneedwardsi*, but these are absent in *Procariama*). The facies articularis caudalis is vertical. The concavitas lateralis are present, and a small foramen is located cranially to them on the processus transversus. The processus spinosus is centrally located on the corpus. The lacuna interzygapophysialis shows a marked 'V'-shape. The zygapophyses cranialis are slanted cranially and are circular and convex, whereas the zygapophyses caudalis are oval and concave. The processus costales are very well developed and fused caudally with the corpus, as in *Psilopterus lemoinei, M. milneedwardsi*, and *Procariama*. This is a transitional vertebra between regions 2 and 3 of the neck according to the subdivisions of Boas (1929). The same condition occurs in the patagornithine *Andalgalornis*.

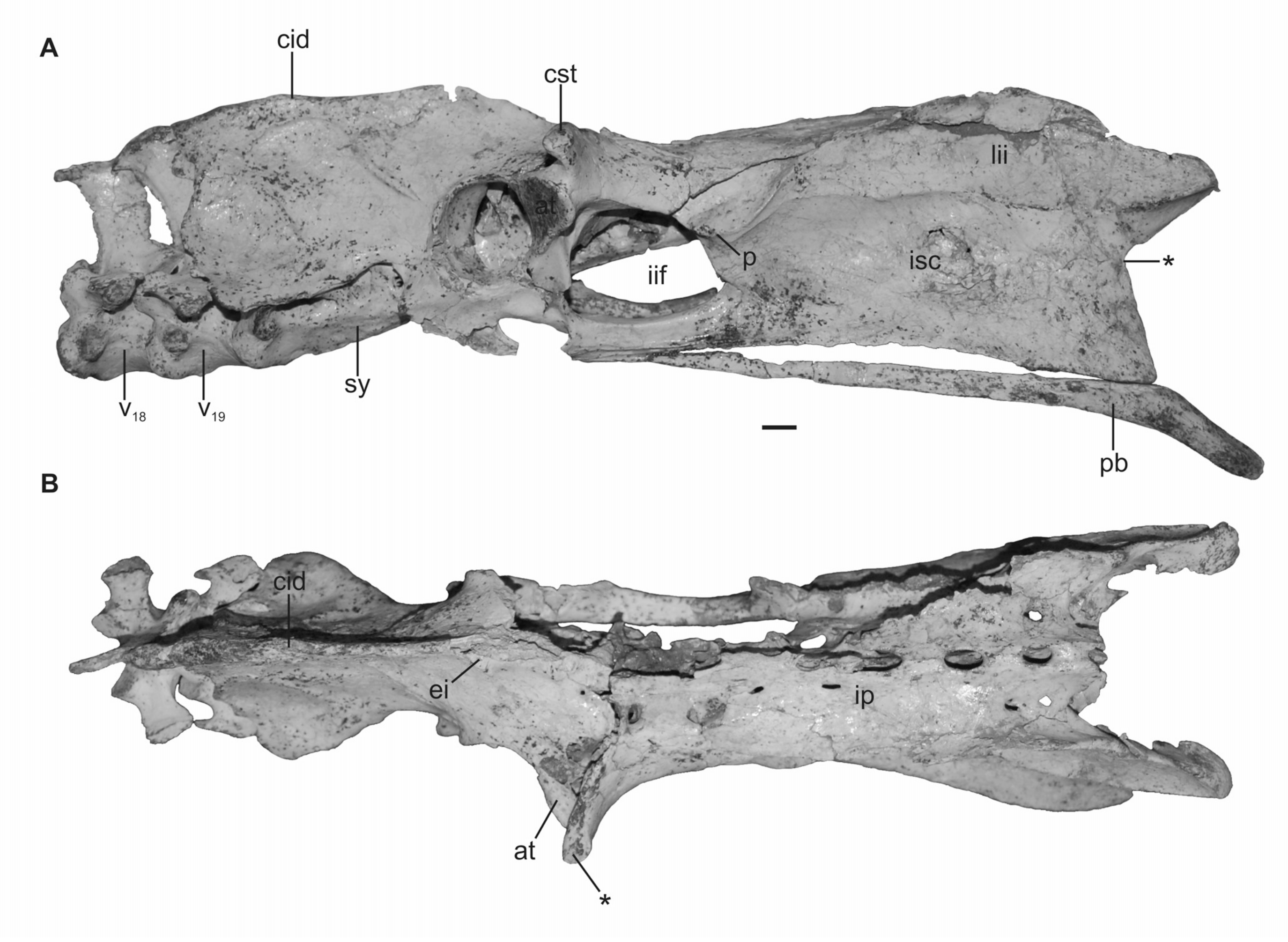

FIGURE 7. Pelvis of *Llallawavis scagliai*, gen. et sp. nov., in **A**, lateral and **B**, dorsal views. Autapomorphies are noted by an asterisk. **Abbreviations**: **at**, antitrochanter; **cid**, crista iliaca dorsalis; **cst**, crista supratrochanterica; **ei**, iliac shield; **iif**, foramen ilioischiadicum; **ip**, iliac platform; **isc**, ischium; **lii**, lamina infracristalis ilii; **p**, caudal process of the ilioischiadic foramen; **pb**, pubis; **sy**, synsacrum; $\mathbf{V_{18}}$, vertebra 18; $\mathbf{V_{19}}$, vertebra 19. Scale bar equals 1 cm. Q4

The sixth vertebra possesses an intermediate morphology between the fifth and seventh vertebrae. It is proportionally longer than that of *M. milneedwardsi*, but similar to that of *Procariama*. The zygapophyses cranialis are large. The processus transversi are obliquely oriented, a condition shared with *Procariama*, but in contrast to *Andalgalornis* (Tambussi et al., 2012). These processus are caudally connected to the base of the tori dorsalis by thin projections. These projections are characteristic of all phorusrhacids, but the degree of development is variable among species (see Tambussi et al., 2012): they are present in cervical vertebrae 6–9 of *A. steulleti*; barely present in vertebra 6 and highly developed in vertebrae 8–11 in *Procariama* (it is not possible to establish the presence of this feature in vertebra 7 due to breakage); and well developed in vertebrae 6–9 in *M. milneedwardsi*. *Llallawavis* shows this feature from the sixth to the 12th vertebra, although in the first and last vertebrae this feature is poorly developed. The ansae costotransversaria, the tuberculi, and the cristae ansae are well developed. The processus carotici are stout. The processus spinosus is medially located (whereas it is caudally located in *Andalgalornis*). The lacuna interzygapophysiaria is remarkably deep.

The seventh, eighth, and ninth vertebrae are quite similar (Fig. 5). However, the latter is shorter, the tori are more strongly developed, and it possesses rounded caudal margins for the zygapophyses caudalis. In all three vertebrae, the processus carotici are stout, the ansae costotransversaria are very robust and endowed with stout tuberculi and cristae ansae, the zygapophysis cranialis are vertically oriented, the processus spinosus is reduced, and, as in the sixth vertebra, possess an attachment area for the ligamentum elasticum interlaminare subdivided by a medial crest. Q5 The facies articularis caudalis is laterally expanded in ventral view. These lateral expansions are also curved ventrally. This is the result of lateral fusion with the caudal portion of the processus costalis (Fig. 5), an evident feature in vertebrae 5 (see above) and 10 (in *Procariama* it is evident in the ninth). As in vertebra 9, the tori and ansae costotransversaria of vertebra 10 are very well developed and the cristae and tuberculi ansae are very robust. However, this vertebra is shorter and sturdier than the ninth and has robust and medioventrally directed processus carotici, a low processus spinosus (lower than in *Procariama*), and a wide lacuna interzygapophysiaria but lacks a processus ventralis corporis (which is present in *Andalgalornis*; Tambussi et al., 2012).

The 11th vertebra is shorter, taller, and wider than the 10th. The processus carotici are robust. The processus spinosus is more cranially located than in the 10th vertebra. The lacuna

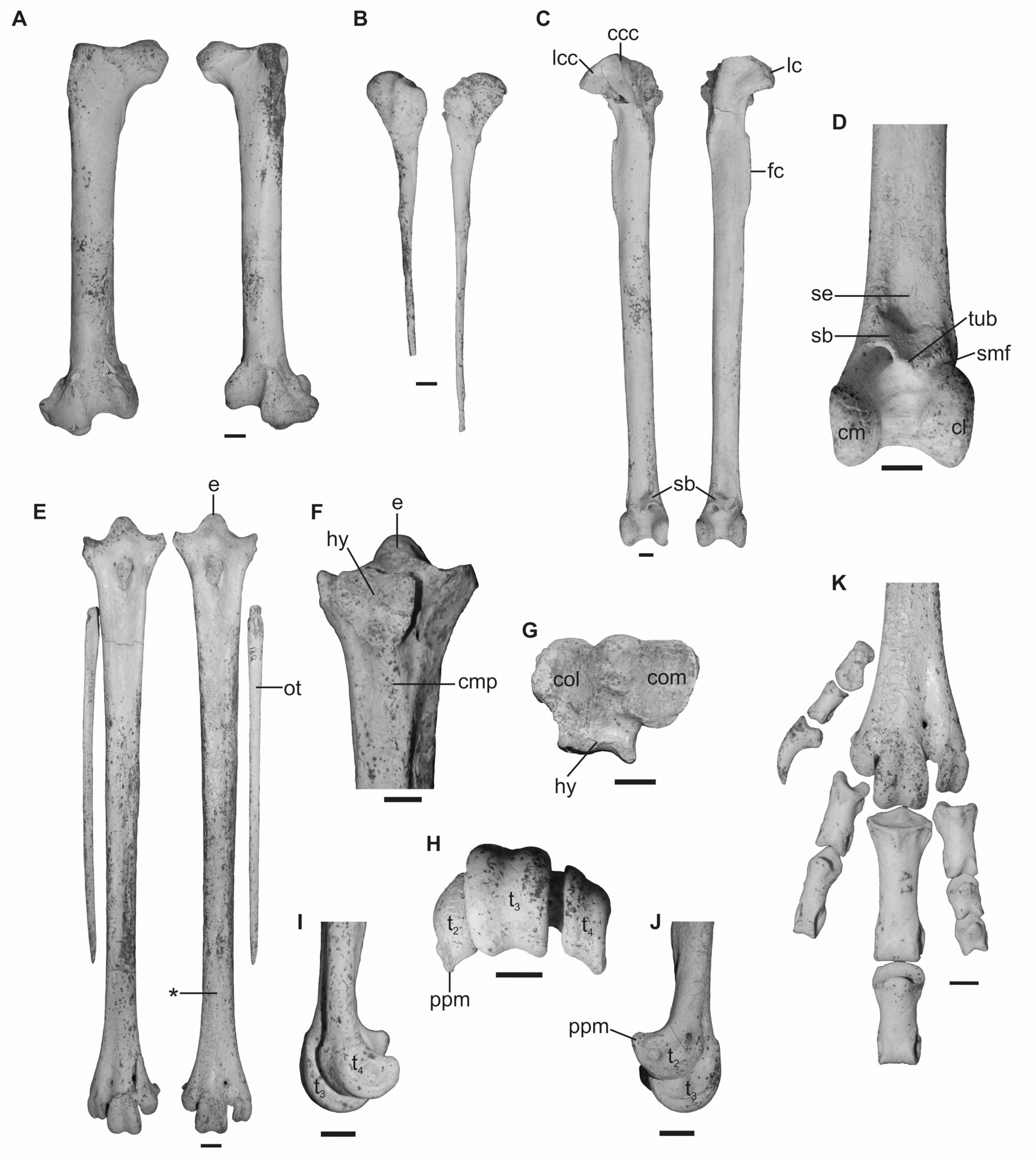

FIGURE 8. Hind limbs of *Llallawavis scagliai*, gen. et sp. nov. Autapomorphies are noted by an asterisk. **A**, both femora in cranial view; **B**, tibiotarsi in cranial view; **C**, both fibulae in lateral view; **D**, detail of the distal portion of the left tibiotarsus in cranial view; **E**, tarsometatarsi and ossified tendons in cranial view; **F**, detail of the left hypotarsus; **G**, proximal view of the left tarsometatarsus; **H**, distal view of the left tarsometatarsus; **I**, detail of the left fourth trochlea; **J**, detail of the left second trochlea; **K**, left foot. Note that in **F** the lateral flange of the hypotarsus is more strongly projected laterally than the medial flange is medially, which produces an asymmetrical shape. **Abbreviations**: **ccc**, crista cnemialis cranialis; **cl**, condylus lateralis; **cm**, condylus medialis; **cmp**, crista medianoplantaris; **col**, cotyla lateralis; **com**, cotyla medialis; **e**, eminentia intercotylaris; **fc**, crista fibularis; **hy**, hypotarsus; **lc**, tibiotarsus lateral corbet; **lcc**, crista cnemialis lateralis; **ot**, ossified tendon; **ppm**, posteromedial crest of the trochlea metatarsi II; **sb**, pons supratendineus; **se**, sulcus extensorius; **smf**, sulcus m. fibularis; **$t_2$**, trochlea metatarsi II; **$t_3$**, trochlea metatarsi III; **$t_4$**, trochlea metatarsi IV; **tub**, tubercle. Scale bars equal 1 cm.

interzygapophysiaria is wide, with an open ‘U’-shape. The processus costales are present, although poorly extended caudally. They are united to the corpus through a flat medial process, delimiting an oval foramen. The presence of rough areas at the extremities of these processes and in the ventrocranial part of the lateral expansions of the facies articularis caudalis may indicate that the processus costales were connected via soft tissue with the facies.

The 12th vertebra is the transitional vertebra between regions 2 and 3. This is a marked difference from *Andalgalornis*, whose transitional vertebra between these regions is the ninth (Tambussi et al., 2012). It possesses a high processus spinosus, which is centrally located, the lacuna interzygapophysiaria has a trapezoidal shape, the processus costales are poorly developed, united medially to the corpus through a small flat process, the processus ventralis corporis is present and cranially directed, and the facies articularis caudalis is enlarged. As in *Andalgalornis*, vertebrae 7–12 are endowed with bifurcated neural spines (metapophyses), a feature absent in cariamids (Tambussi et al., 2012).

The 13th vertebra is the only cervicodorsal vertebra of *Llallawavis*. The corpus is short and wide, the ansae costotransversaria are slender with well-developed tuberculi ansae (the cristae are poorly developed), and the processus costales are poorly developed. The processus ventralis corporis is notably developed and possesses an incisure on its dorsal aspect. The tori are conspicuous. Both facies articularis cranialis and caudalis are wide, but shallow.

The trunk (or thoracic) vertebrae (14–19) have short and robust corpus and very high processus spinosus that are expanded dorsally; the processus transversi are stout, the fossa costalis are shallow and rounded, and the facies articularis cranialis are wide, whereas the facies caudalis is narrower and the processus ventralis corporis is notably developed (broken in vertebra 14 and not developed in vertebrae 18 and 19). In vertebrae 14 and 15, the processus carotici are developed and craniolaterally directed.

Similar to *Psilopterus*, the synsacrum has 13 vertebrae. It also possesses tall cristae spinosa synsacri, a long corpus synsacri, and a wide sulcus ventralis synsacri, and the lamina transversa synsacri is not developed.

Seven caudal vertebrae are preserved (Fig. 5C, D). The corpus vertebrale is small and flattened dorsoventrally. The processus transversi are stout, caudally directed from the second to the fifth vertebrae (broken in the first), and possess pneumatic foramina from vertebrae 1–6. The processus spinosus is also robust, except in vertebra 1 where it is broken and in the seventh where it is slender. From vertebrae 3–7 there is a prominently developed processus haemalis (which is bifurcated distally in vertebrae 4 and 5 and endowed with a distal foramen in vertebrae 6 and 7). The facies articularis cranialis is slightly concave, whereas the facies caudalis is slightly convex. The foramina vertebrale diminish in size caudally. On vertebrae 2 and 3, a pair of oval and markedly developed shelves are located above the processus spinosi.

## Ribs

Seven pairs of ribs were present in *Llallawavis*: one pair of floating ribs in association with the first thoracic vertebra (vertebra 14), five pairs articulating with vertebrae 15–19, and one pair with the cranial-most synsacral vertebra. The ribs lack uncinate processes, as in all phorusrhacids (Alvarenga and Höfling, 2003), and present a medial pneumatic foramen. The first rib is conspicuously shorter than the following elements and has a straight corpus, as does the second rib. However, the third to seventh ribs possess an open ‘S’-shape (accentuated caudally) and a cranial ridge on the lateral surface of the extremitas dorsalis costae. The incisura capitulotubercularis is wide in the cranial ribs, but its width decreases caudally. The corpus costae has a convex facies medialis and a flat facies lateralis (in the first rib the situation is the inverse). The shape of the facies articularis intercostalis also changes caudally, being oval in ribs 2, 3, and 7, subcircular in ribs 4 and 5, and triangular in rib 6. The length of the six costae sternalis increases caudally: the first one being short, straight, and rod-like, and the sixth very long, curved, compressed, and expanded ventrally.

## Pectoral Girdle

**Sternum**—The sternum (Fig. 6A) is long and narrow. It is endowed with a robust carina sterni that is not expanded ventrally, except caudoventrally. The pila carinae is short but stout, and the apex carinae is poorly projected cranially. The processus craniolaterales are strongly developed, forming a flat spine. The pila coracoidea is narrow. The sulcus articularis coracoideus is deep, narrow, and dorsoventrally extended. The labrum externum is sharp, with a lateral tuberculum labri externum; the labrum internum is robust. Both spina interna and externa rostri are absent. The facies muscularis sterni is wide. The six processus costales have a subquadrangular shape and are slightly flat. The incisura costales are deep and endowed with pneumatic foramina. The pars cardiaca is long and narrow and has several pneumatic foramina on its surface. The pars hepatica has a smooth surface and strongly concave surface. The lateral incisures of the caudal margin are absent (in contrast to cariamids), but the sternum continues caudally via a robust spine. The margo caudalis are strongly convergent.

**Scapula**—The scapula (Fig. 6C) is wide, with a poorly developed acromium. The corpus is straight. The extremitas caudalis is not preserved. The margo dorsalis is sharp, as in *Psilopterus* (Degrange and Tambussi, 2011). The facies costalis is slightly concave. Although broken, it is apparent that the facies articularis coracoidea was wide. The facies articularis clavicularis is wide and very well marked (contrary to *Psilopterus*). The facies articularis humeralis is slightly concave. The labrum glenoidale is stout, although poorly projected.

**Coracoid**—As in all phorusrhacids, the coracoid (Fig. 6D) is robust, with the extremitas omalis coracoidei reduced, lacking the processus acrocoracoideus, but presenting a poorly developed processus procoracoideus. The facies articularis clavicularis is long and located cranial to the sulcus m. supracoracoidei, which is deep. The facies articularis humeralis is oval in shape, concave, and bordered ventrally by a labrum glenoidale. The facies articularis scapularis is expanded. The corpus has a suboval section, and it is slightly curved medially. There is no incisura nor a foramen n. supracoracoidei. The extremitas sternalis coracoidei have well-defined facies interna and externa, separated by a robust crista intermedia. The processus lateralis is well developed and more extended proximally than in *Psilopterus*. Dorsally, it possesses small pneumatic foramina. The margo supra-angularis is strongly slanted proximomedially. In contrast to *Mesembriornis*, the furcula and coracoid are not fused (Fig. 6B, D). However, although some breakage has occurred in the area, it is evident that the scapula is fused to the coracoid.

**Furcula**—The furcula (Fig. 6B) is slender and curved with a wide, robust facies articularis acrocoracoidea and a short, robust processus acromialis. Its synostosis interclavicularis is not ossified, in contrast to *Psilopterus bachmanni* (Degrange et al., 2011). The canalis triosseus is small and oval in shape.

## Forelimb

**Humerus**—The humerus (Fig. 6E) has the general morphology of the smaller phorusrhacids (Psilopterinae) and is quite similar to that of *Mesembriornis incertus*. The shaft is straight (as in *Mesembriornis incertus* and *Psilopterus colzecus* [Tonni and Tambussi, 1988] but in contrast to *Psilopterus lemoinei*

[Degrange and Tambussi, 2011] and hollow, unlike the condition in larger phorusrhacids, such as *Titanis*, which have a reduced pneumatic network of bone (Chandler, 1994:176). The caput humeri is elongated and oriented obliquely with respect to the shaft, as in *Psilopterus* (Degrange and Tambussi, 2011). The sulcus ligamentum transversus is circular and shallow. The tuberculum dorsalis is absent, whereas the tuberculum ventralis is very prominent, as in all phorusrhacids (Alvarenga and Höfling, 2003). The crista deltopectoralis is absent, as in *Psilopterus* (Degrange and Tambussi, 2011). The fossa pneumotricipitalis is subrounded and deep. The incisura capitis is discernible and widened caudally. The cruci dorsale and ventrale are not distinguishable. The sulci scapulotricipitalis and humerotricipitalis are shallow. The fossa olecrani is deep. The processus flexorius is very well developed, as in all phorusrhacids (Alvarenga and Höfling, 2003). Both epicondylus dorsalis and ventralis are inconspicuous. The incisura intercondylaris is narrow and deep. The condylus ventralis is horizontal, whereas the condylus dorsalis is obliquely inclined. As in *M. incertus*, the fossa m. brachialis is deeper than in psilopterines, and limited medially by a ridge.

**Ulna**—The ulna (Fig. 6F) is shorter than the humerus, with a reduced olecranon (more so than in *Psilopterus*), and eight caudal and six ventral remigial papillae that are poorly developed. Both cotylae ventralis and dorsalis are shallow, and the crista intercotylaris is not salient. The processus cotylaris dorsalis is well developed. The cotyla flexoria is deep. The impressio m. scapulotricipitalis is absent. The incisura radialis is long. In general, all of the distal features of the ulna (i.e., the trochlea carpalis) are not pronounced. The incisura tendinosa is deep. The tuberculum carpale is remarkable and located caudal to both condyli. The depressio radialis is shallow. The sulcus intercondylaris, the tuberculum lig. collateralis ventralis, and the incisura tuberculi carpalis are absent.

**Manus**—The manus is incomplete. The os carpi radiale is small, short, and wide. The os carpi ulnare has a wide, but poorly excavated, incisura metacarpalis. The crus breve and the crus longum are short, although the former is stout. The processus muscularis is not marked. The facies articularis metacarpalis is convex and oval in shape. The carpometacarpus is missing. The phalanx proximalis digiti majoris has a stout pila cranialis, a shallow concave facies articularis metacarpalis, a long and shallow fossa dorsalis and ventralis, and a facies articularis phalangealis that is slightly convex. The phalanx distalis digiti majoris is a short bone (shorter than the preceding bone), with a subtriangular section and a deep facies articularis.

## Pelvis

The pelvis (Fig. 7) is long and widened caudally, as in Psilopterinae and in contrast to the pelves of *Patagornis* and *Andalgalornis*. The crista iliacae dorsalis are fused to each other along the midline, dorsal to the crista spinosa synsacri (to which the crista iliacae are also fused), describing a conspicuous arc in lateral view, as in *Psilopterus, Procariama*, and *Mesembriornis*; the cristae are unfused in the postacetabular region, forming a wide and long iliac platform (contrary to the condition in *Patagornis* and *Andalgalornis*). The alae preacetabularis ilii are vertically inclined, with a shallow fossa iliaca dorsalis. The acetabulum is subcircular. The foramen ilioischiadicum is relatively small compared with the total length of the pelvis, presenting a curved cranial margin (whereas this is straight in *Psilopterus* and *Andalgalornis*). The antitrochanters are extended laterally, and the robust cristae supratrochanterica are more extended laterally than the antitrochanter. The extended laterally crista supratrochanterica is a feature that *Llallawavis* shares with *Mesembriornis*. However, in the latter, the crista does not extend beyond the lateral margin of the antitrochanter. The sulcus antitrochantericus is deep. At the caudal end of the foramen ilioischiadicum, a small, blunt process is present (in *Psilopterus*, this process is more prominent with a lateroventral orientation). The foramen obturatum is oval in shape and closed caudally. The sulcus obturatorius is long and deep. The tuberculum preacetabulare is fragmentary, and its development cannot be established. Few foramina intertransversaria are present. The postacetabular region is two times longer than the preacetabular part. The spina dorsolateralis ilii is caudally projected, but not dorsally curved as in *Psilopterus*. The caudal border of the ischium forms a marked obtuse angle, contrary to the condition in *Psilopterus* and *Andalgalornis* where it forms an arc. The crista dorsolateralis ilii is developed from the caudal tip of the spina dorsolateralis ilii, describing a dorsal and conspicuous arc, which contacts the caudal margin of the foramen ilioischiadicum cranially. Rising from the spina, the synchondrosis ilioischiadica is marked by a subhorizontal line that converges cranially with the crista dorsolateralis ilii. The wide lentiform lamina infracristalis ilii is placed between the crista and the synchondrosis. The processus terminalis ischii is shorter than the spina dorsolateralis ilii. The fossa renalis is deep and extended caudally. The pubis is complete. The corpus is slender, with the cranial portion fused widely to the pelvis, contacting the processus terminalis ischii caudally. It delimits a long and narrow fenestra ischiopubica ventrally. The apex of the pubis is very stout and medioventrally directed. This contrasts with the hypothesis of Sinclair and Farr (1932) who stated that for *Psilopterus*, there was no pubic posterior projection beyond the foramen obturatum. Also, it is not consistent with Patterson and Kraglievich's (1960) or Alvarenga and Höfling's (2003) arguments that the pubis would be atrophied in all phorusrhacids.

## Hind Limb

**Femur**—The femur (Fig. 8A) has the general morphology seen in all phorusrhacids. The facies articularis antitrochanterica is notable and lacks cranial and caudal projections (as in *Mesembriornis*). The caput femoris is more proximally located than the crista trochanteris, which is prominent and expanded craniad. The fovea ligamentum capitis is not marked. The collum femoris is 'constricted' (not so in *P. lemoinei*). Laterally, the shaft describes a weak arc (as in *M. milneedwardsi*; Kraglievich, 1946; Tambussi, 1989), and the linea intermuscularis cranialis is weak (as in *M. milneedwardsi*). Both the sulcus patellaris and sulcus intercondylaris are deep and wide. The fossa poplitea is oval and deep and has few pneumatic foramina. The crista tibiofibularis is narrow, with a medial projection in distal view. The lateral margin of the incisura fibularis is a narrow flange.

**Fibula**—The fibula (Fig. 8B) is quite similar to that of cariamids and has the general morphology seen in all phorusrhacids (see Degrange, 2012). The tuberculum m. iliofibularis is oval and shorter than in *Psilopterus*. The spina fibulae has a triangular section proximally and is oval distally.

**Tibiotarsus**—The tibiotarsus (Fig. 8C) is longer and more slender than in *Mesembriornis*. The facies articularis medialis is flat, whereas the facies articularis lateralis is globose and prominent. The fossa retropatellaris is deep. The incisura tibialis is craniocaudally wide. The crista patellaris is weak. The fossa flexoria is deep. Both cristae cnemialis are very well developed. The crista cnemialis lateralis is expanded laterally and possesses a shelf on its lateral surface. The sulcus intercnemialis is deep. The facies gastrocnemialis is deep and greatly expanded. The crista fibularis is short and stout. The tuberositas poplitea comprises two tubercles. The shaft is slightly curved when viewed laterally, describing a very smooth distal sigmoid curve. The linea extensoria is conspicuous. The sulcus extensorius is deep, medially located, with a short proximal extension. The pons supratendineus is wide and oblique, and, as in *Procariama simplex*, it lacks the distal lip. Laterodistally to the bridge, a prominent tubercle is present (Fig. 8D), as in *Mesembriornis* and *Psilopterus* *lemoinei*. The condylus lateralis is rounded when viewed laterally, whereas the condylus medialis is tall and proximodistally longer than its lateral opposite. The incisura intercondylaris is deep. The depressio epicondylaris lateralis is shallow. The epicondylus medialis is not prominent, and the epicondylus lateralis is absent (as in cariamids). The trochlea cartilaginalis tibialis is poorly extended proximally (as in *Mesembriornis* and contrary to *Psilopterus*), and both cristae lateralis and medialis are sharp (stout in *Mesembriornis*) and proximally confluent.

**Tarsometatarsus**—The tarsometatarsus (Fig. 8E) is very long, reaching 91% of tibiotarsus length. As in *Mesembriornis* and *Procariama*, the hypotarsus is subtriangular and asymmetrical in outline (with one of its flanges projecting further laterally) (Fig. 8F). It has two shelves located at different levels: the medial shelf is less extended plantarly and exhibits a deep, conspicuous furrow, whereas the lateral shelf is slightly convex. Viewed proximally, it is evident that the medial shelf is extended plantarmedially as a sharp flange (in a similar manner to that in *Procariama*, but different from that in *Psilopterus*). The hypotarsus continues distally via a stout and unique crista medianoplantaris. The margins of the hypotarsus do not protrude proximally (as in *Procariama*; Alvarenga and Höfling, 2003). Viewed caudally, the foramina vascularia proximalia are visible and located at the same proximodistal level. The cotyla medialis is oval, and the ventral margin of the cotyla lateralis is subquadrangular. There is a lateral tubercle on the corpus, which is located distal to the cotyla lateralis (which is absent in *Psilopterus*). The eminentia intercotylaris is prominent and projects proximally, with a distinctive furrow on its base. The fossa infracotylaris dorsalis is oval, deep, and restricted to the most proximal portion of the shaft. The tuberositas m. tibialis cranialis is located in the most distal portion of the fossa infracotylaris dorsalis. The impressio retinaculi extensorii is medial and forms a unique tubercle located on the margin of the shaft. Medial to the impressio, there is a notable impressio lig. collateralis lateralis. Contrary to other phorusrhacids, the shaft narrows distally. Both the sulcus extensorius and the flexorius have an extension minor to the half of the shaft. The former is shallow and delimited by stout, low ridges, whereas the latter is deep, with the crista plantaris lateralis projected. The fossa supratrochlearis plantaris is shallow. The fossa metatarsi I is oval and laterally delimited by a plantar crest (absent in *Psilopterus*). The foramen vasculare distale is slightly oval and conspicuous. The trochlea metatarsi II is not turned medially (as in Psilopterinae; Alvarenga et al., 2010). As in *Procariama*, this trochlea has a caudomedial triangular crest, which is almost equally developed in the trochlea metatarsi IV (Figs. 8H–J). The trochlea metatarsi III has proximally directed margins.

A significant feature is the presence of a long, unique, stout ossified tendon, which is located caudomedially to the tarsometatarsus (Fig. 8E). This tendon has an acicular shape and reaches 60% of the length of the tarsometatarsus. It has been hypothesized that ossified tendons in birds may serve to reinforce muscle action, as well as to accurately control the positions of the digits (Bock and von Wahlert, 1965; Bennett and Stafford, 1988; Bledsoe et al., 1993), which is essential for running in cursorial birds.

**Foot**—The foot of *Llallawavis* (Fig. 8K) is incomplete (only the right fourth digit is complete), but it shows the morphology typical of phorusrhacids. The first digit is very reduced and elevated and would not have been in contact with the ground. The os metatarsale I is as short as the first phalanx of digit I. The latter is quadrangular in shape. The ungual phalanx possesses a prominent tuberculum flexorium and a medial longitudinal furrow, which is closed distally. In digit II, the proximal phalanx is excavated ventrally, has a flange extending lateroventrally, and a trochlea articularis that is deeply excavated. The second phalanx is more slender and longer. The first phalanx of digit III is the longest of the foot (it is twice the length of the second phalanx of digit III). The cotyla articularis of both phalanges is pentagonal, whereas the trochlea articularis are not excavated as in digit II but presents their margins converging caudally. Regarding digit IV, the first phalanx is the longest and presents a cotyla articularis similar to that of the first phalanx of digit II and the edges of the trochlea articularis are totally converging caudally. The trochlea articularis of the second, third, and fourth phalanges are deeply excavated. The ungual phalanx exhibits lateral furrows and a conspicuous tuberculum flexorium, with an oval wide scar on its ventral surface.

## INNER EAR MORPHOLOGY AND HEARING CAPABILITIES

For the first time, the endosseous labyrinth of the inner ear of a terror bird can be reconstructed in a comparative context. The otic capsules of *Llallawavis, Patagornis*, and living seriemas were CT scanned, and the vestibular and cochlear structures were reconstructed and measured from digitally prepared volumes.

In the endocast of the bony labyrinth of *Llallawavis*, all three canals are intact on the right side, and each corresponding ampulla, vestibular fenestra, and cochlea are also observable (Fig. 9). The ratio between labyrinth system and basicranial length is smaller in *Llallawavis* than in *Patagornis*, and its craniocaudal extension is lower than in the extant seriemas. Compared with living birds regarded as flyers (Sipla, 2007), the semicircular canals of *Llallawavis* are identically well expanded.

The canals are aligned in approximately orthogonal planes in three-dimensional (3D) space. This is true for both phorusrhacids, but not for seriemas where the rostral and caudal canals are medially curved. The lateral, rostral, and caudal canals are thin, long, and circular in cross-section in *Llallawavis*. The canals of *Patagornis* are grossly enlarged, whereas in the extant seriemas they are relatively shorter and elliptical in cross-section. Strongly elliptical canals were also observed in some anseriform birds, *Struthio*, and in the extinct Paleogene *Halcyornis* (Walsh and Milner, 2010), and their functional meaning is still unknown.

The longest of the three canals, the rostral, is strongly tilted caudally, whereas the shortest, the caudal, is ventrally extended below the lateral, as is normal for living species of birds and some non-avian theropods (Turkewitsch, 1934; Witmer and Ridgely, 2009). However, in extant seriemas, the rostral canal is straight in its cranial section, less tilted caudally, and its lumen is wider. In *Llallawavis*, the rostral canal enters its ampulla cranially (Fig. 9), but in seriemas the canal slopes markedly downwards and enters the ampulla from the lateral side.

The lateral canal is tilted upwards from the basicranial plane (generally ~15°; Erichsen et al., 1989). Positions of the head at rest and the orientation of the lateral canal are related: the head is positioned with this canal parallel to the substrate. The origin of the lateral canal lies on the lateral surface of the common crus, which is long and stylized in *Llallawavis*. Interestingly, in extant seriemas, the three canals leave the vestibular system together.

The cochlear duct is a long, straight, finger-like tube (which is longer and slightly curved in extant seriemas), with a distal tip that is strongly directed mediad. This represents a dramatic difference from *Patagornis*, in which the cochlea is shorter and its longitudinal axis is almost perpendicular to the base of the skull. The vestibular fenestra is conspicuously marked and located at the same level as the dorsal margin of the cochlear fenestra (whereas in seriemas the vestibular fenestra is located well above this margin). The latter is wide, oval, and more elongate than in *Llallawavis*, and especially large in *Patagornis*.

## PHYLOGENETIC ANALYSIS

Initial analysis of the character matrix (Appendix S1, Supplementary Data) resulted in five most parsimonious trees of length

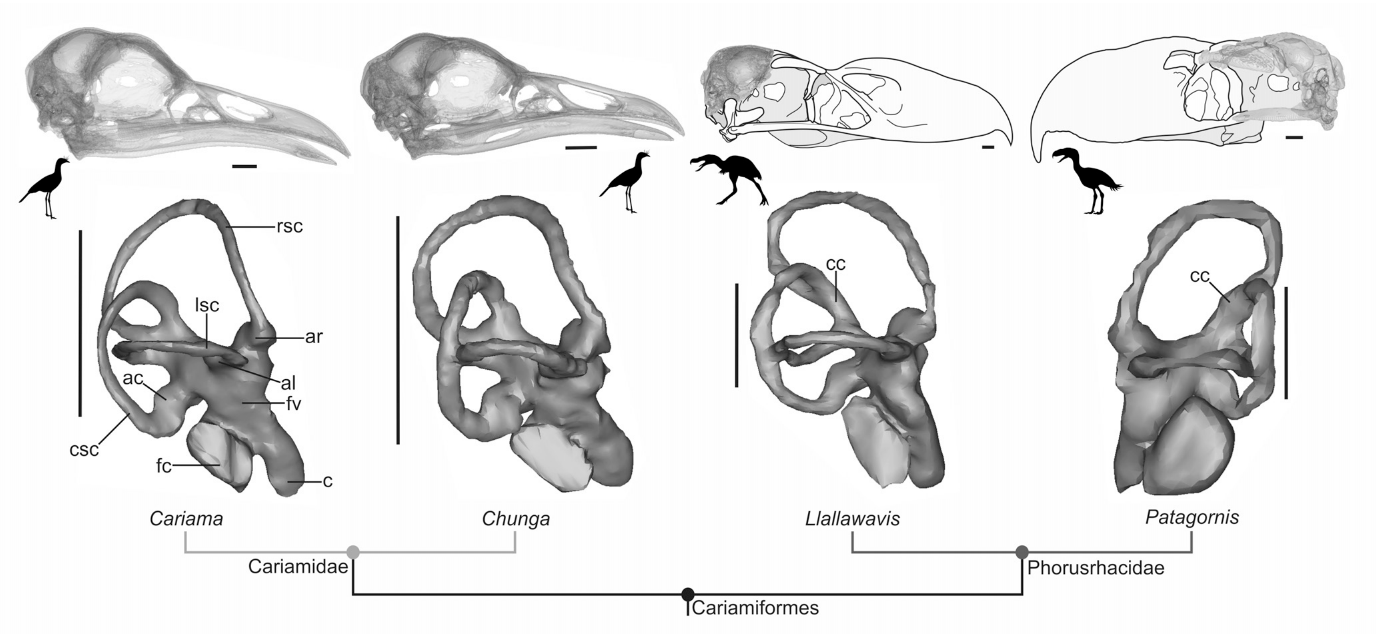

FIGURE 9. Endosseous labyrinths (lateral view) of Cariamiformes displayed in a simplified phylogenetic context. From left to right, *Cariama cristata* and *Chunga burmeisteri* (Cariamidae), *Llallawavis scagliai* and *Patagornis marshi* (Phorusrhacidae). **Abbreviations**: **ac**, caudal ampulla; **al**, lateral ampulla; **ar**, rostral ampulla; **c**, cochlea; **cc**, common crus; **csc**, caudal semicircular canal; **fc**, cochlear fenestra; **fv**, vestibular fenestra; **lsc**, lateral semicircular canal; **rsc**, rostral semicircular canal. Scale bars equal 1 cm.

314 steps (consistency index [CI] = 0.716; retention index [RI] = 0.68), the consensus tree of which is shown in Fig. 10. The consensus tree has a length of 135 steps and a CI of 0.711 and a RI of 0.672. This analysis supported the monophyly of Phorusrhacidae.

Our comprehensive phylogenetic analysis places *Llallawavis* as a derived member of Mesembriornithinae (Fig. 10) and sister taxa of *Procariama*, a genus previously considered part of Psilopterinae (Alvarenga and Höfling, 2003; Agnolín, 2009, 2013; Alvarenga et al., 2011; Vezzosi, 2012a). Characters supporting the inclusion of *Llallawavis* within Mesembriornithinae include the presence of a triangular asymmetric hypotarsus and a third metatarsal trochlea that is widened distally. Psilopterinae is the sister clade of Mesembriornithinae within Phorusrhacidae. The phylogenetic relationships of Phorusrhacidae in the context of neornithine relationships are discussed in Appendix S2.

## DISCUSSION

### Phylogenetic Relationships of *Llallawavis scagliai*

Previous attempts have been made to analyze the relationships among terror birds. Agnolín (2009) made the first effort, but the characters he chose are hard to interpret (characters 7, 18, and 21 of the skull and character 83 of the tarsometatarsus), and in several cases he scored characters in elements unknown for any phorusrhacid at that time (e.g., he coded characters 7, 21, and 25 for the skull of *Mesembriornis incertus*, which is still unknown; characters 1–5, 7–10, 12–14, 16–18, 20, 21, and 26–31 in *Mesembriornis milneedwardsi*; characters 1, 4–7, 27, and 28 in *Procariama simplex*; and characters 5, 7, and 8 in *Devincenzia pozzi*; all of these not preserved in the original specimens). The later analysis of Alvarenga et al. (2011) could not resolve the relationships among several taxa. More recently, Agnolín (2013) presented a new phylogenetic hypothesis, adding 10 characters to his initial analysis. The beautifully preserved and almost complete skeleton of *Llallawavis* represents a superb opportunity to present a new and more comprehensive phylogenetic analysis.

Comparing our character list with those previous published, of the 84 characters selected here only three could not be scored in *Llallawavis*: one character of the scapula and two of the carpometacarpus. This means that only 3.6% of the data are missing. With reference to the matrix of Agnolín (2009), of his 100 characters 40 could not be scored for the new taxon because they were inapplicable or difficult to interpret (see above). Thus, 40% of the data are missing. Similarly, 45 of the 110 characters provided in Agnolín (2013) could not be scored, with 40.9% missing data. Alvarenga et al. (2011) provided 61 characters, and only two of these were not scored for *Llallawavis*, meaning that there are only 3.3% missing data. However, as stated previously, the cladogram presented by the latter authors does not resolve several relationships among phorusrhacids.

Our phylogenetic analysis nests *Procariama* within Mesembriornithinae, a relationship that had been proposed by Rovereto (1914) but rejected by Agnolín (2009, 2013) and Alvarenga et al. (2011). This inclusion is supported by presence of a long tarsometatarsus (almost 80% of tibiotarsus length); the dorsal iliac crest describing a very pronounced arc (more so than in *Psilopterus*); and the presence of an asymmetric hypotarsus, with caudally projecting crests (Alvarenga and Höfling, 2003; Vezzosi, 2012a).

Mesembriornithinae (three genera and four species) includes basal species with larger body sizes (~70 kg); more derived species tend to diminish in body size, as in *Procariama* (11 kg; but see Vezzosi, 2012b) and *Llallawavis* (20 kg). Notably, basal phorusrhacids are relatively small and very large sizes (adult body mass up to 70 kg) were acquired at least twice in different lineages (Fig. 10). This conclusion contrasts with that of Agnolín (2013) who located *Mesembriornis* (*Hermosiornis* sec.) as the sister group of the remaining Neorhaci in the sense of Agnolín (2013), with gigantism occurring only in the latter lineage. We believe that the conflict between our results and those of Agnolín

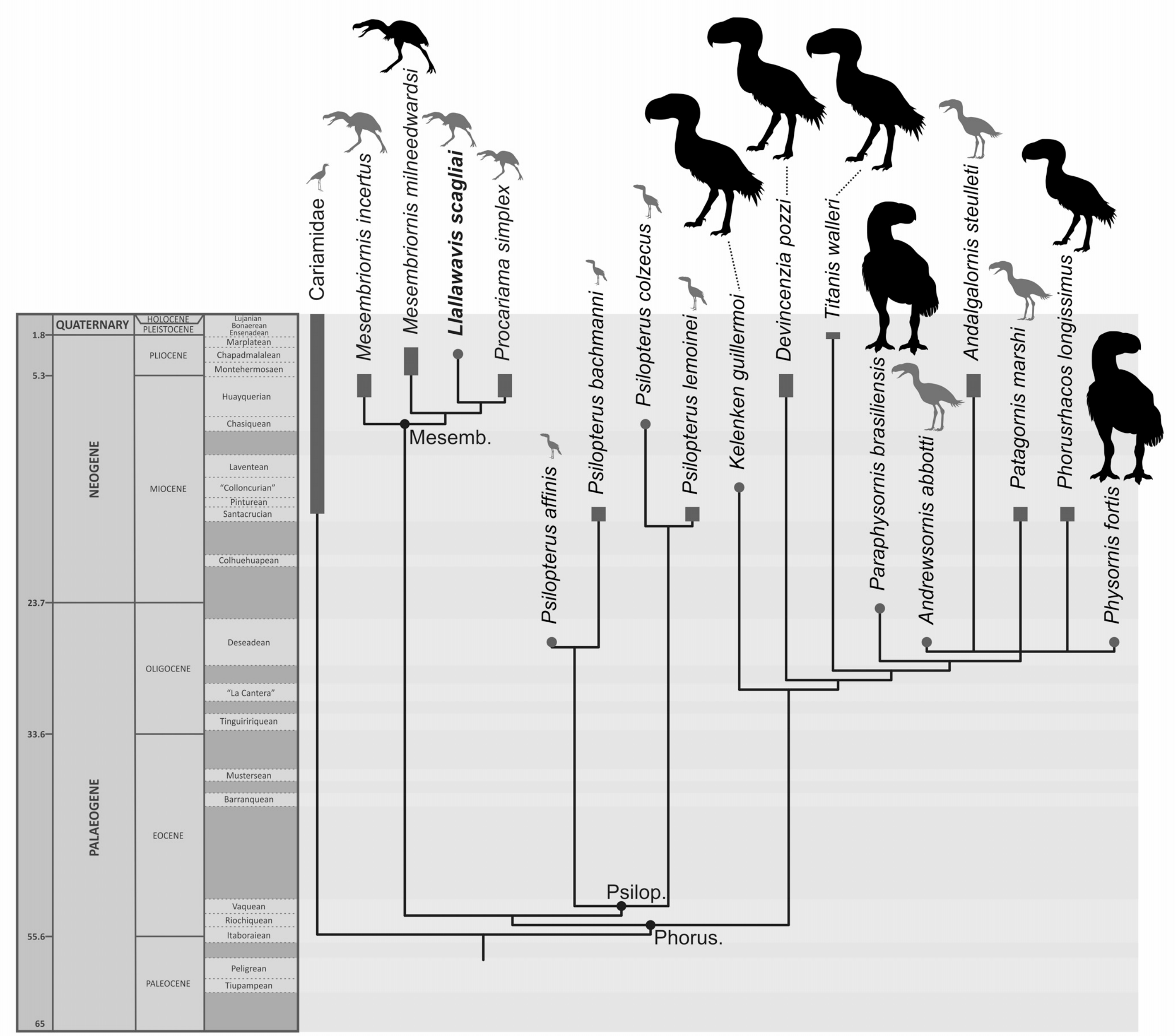

FIGURE 10. Phylogenetic relationships of *L. scagliai* among phorusrhacids. Silhouettes indicate body size according to Degrange (2012). Black silhouettes indicate birds of more than ~70 kg. Different phorusrhacids seem to have attained gigantic body size independently in the early Miocene and Pliocene. **Abbreviations**: **Mesemb**., Mesembriornithinae; **Phorus**., Phorusrhacidae; **Psilop**., Psilopterinae.

(2009, 2013) are a consequence of his erroneous scores for many characters. To give one example, his character 14 (craniocaudal extension of the fossa temporalis) is scored in different ways in different phorusrhacids, whereas it should be coded identically according to our criterion. We are critical of the results obtained by Agnolín (2009, 2013) because his evaluation includes characters of elements still unknown or traits of specimens of questionable reconstruction, as previously mentioned.

According to our phylogenetic analysis, the monophyly of Phorusrhacidae is supported (Figs. 10, S1) and the group includes two main clades: one represented by the small- and medium-sized Psilopterinae and Mesembriornithinae that we call here 'psilopterines' and a second that includes the giant phorusrhacids Physornithinae, Phorusrhacinae (both polyphyletic), and Patagornithinae (paraphyletic) that we call the true 'terror birds.' *Llallawavis scagliai* belongs to the first clade (Fig. 10). A task that is beyond the scope of the present article is to discuss in depth the relationships of *Brontornis* (for this topic, see Agnolín, 2007, 2009, 2013), but our analysis indicates a relationship with anseriforms (see Supplementary Data) (contra Alvarenga et al., 2011).

## Inner Ear Morphology and Hearing Sensitivity

It is known that the vestibular organs provide information on gravity, motion, and vibration (Rabbitt et al., 2010). Signals from the semicircular canals are combined with other cues (visual and somatosensorial) that are used to generate a wide range of automatic behaviors necessary for positioning the head and eyes, stabilizing posture, and coordinating body actions. The

TABLE 1. Mean hearing and hearing range estimations (Hz) for phorusrhacids.

| | | | | Sensu Walsh et al. (2009) | | | |
|---|---|---|---|---|---|---|---|
| | | | | | | Range | |
| Taxa | Family | Order | Sensu Gleich et al. (2005)[a] | Mean hearing | Hearing range | Lower | Upper |
| *Cariama* | Cariamidae | Cariamiformes | 2100 | 2231.99 | 3714.45 | 374.76 | 4089.21 |
| *Chunga* | Cariamidae | Cariamiformes | 2100 | 2458.66 | 4132.3 | 392.51 | 4524.81 |
| *Llallawavis* | Phorusrhacidae | Cariamiformes | 1600 | 2305.08 | 3849.1 | 380.53 | 4229.63 |
| *Patagornis* | Phorusrhacidae | Cariamiformes | 1500 | 2047.8 | 3374.8 | 360.40 | 3735.20 |
| *Apteryx* | Apterygidae | Apterygiformes | ~2100 | 1972.85 | 3236.73 | 354.48 | 3591.21 |
| *Struthio* | Struthionidae | Struthioniformes | 1399.4 | 2036.8 | 3354.62 | 359.49 | 3714.11 |
| *Dromaius** | Casuariidae | Casuariiformes | 1565.1 | 1680.53 | 2697.85 | 331.6 | 3029.45 |
| *Rhea* | Rheidae | Rheiformes | 1642.1 | 1816.15 | 2947.86 | 342.22 | 3290.08 |
| *Crypturellus* | Tinamidae | Tinamiformes | 2465.07 | 2307.7 | 3854.02 | 380.69 | 4234.71 |
| *Tyto* | Tytonidae | Strigiformes | — | 5000 | 9000 | 500 | 9500 |
| *Melopsittacus* | Psittacidae | Psittaciformes | — | 3650 | 6700 | 300 | 7000 |
| *Dromaius*** | Casuariidae | Casuariiformes | — | 1790 | 3420 | 80 | 3500 |
| *Spheniscus* | Spheniscidae | Sphenisciformes | — | 2300 | 3400 | 600 | 4000 |
| *Corvus* | Corvidae | Passeriformes | — | 2550 | 4900 | 100 | 5000 |
| *Taeniopygia* | Estrildidae | Passeriformes | — | 3350 | 4700 | 1000 | 5700 |

[a] Body masses from Degrange (2012) and Dunning (2008).

*Based on a different specimen (MLP 681) than, **from Walsh et al. (2009).

canals sense angular accelerations produced by the head and body during movement (Spoor et al., 2002; Sipla, 2007). The vertical canals produce a unilateral effect on the response of the body muscles, whereas the lateral canals produce a symmetrical effect on the muscles of both sides of the body to enable avoidance of falling to one side as might occur if the muscles were subjected to unilateral stimulation (Hullar, 2006). Also, the development of a long lateral canal is associated with increased sensitivity to twisting movements, for example, during running; meanwhile, vertical canals control reflex adjustments (Cox and Jeffrey, 2010). Intriguingly, the lateral canal of *Patagornis* is not as strongly developed as in *Llallawavis*.

If *Llallawavis* predatory behavior involved rapid head movements in the sagittal plane, as assumed for *Andalgalornis* (Degrange et al., 2010), the length of its semicircular canals should enable the appropriate response to such high angular movements. Conversely, the canals of *Patagornis* are shorter, its body mass is greater, and it therefore seems valid to assume more sluggish head movements in this taxon, with enhanced sensitivity to low-amplitude motions (Jones and Spells, 1963).

To estimate mean hearing range (range of audibility) and sensitivity of *Llallawavis*, we applied the method of Walsh et al. (2009) using scaled and transformed cochlear duct lengths. We calculate that *Llallawavis* would have had a mean hearing range of approximately 3800 Hz and a mean hearing sensitivity of approximately 2300 Hz. *Patagornis* displays the smallest hearing range among the Cariamiformes studied (with similar values to the ostrich; see Table 1) (Walsh et al., 2009; Walsh and Milner, 2010).

Our estimations of hearing sensitivity in Cariamiformes places *Llallawavis* below the average for living species. Because the vocalization range of most birds falls within the lower half of their hearing sensitivity range (Konishi, 1970), *Llallawavis* may have had a narrow, low vocalization frequency range. Frequency estimations in Cariamiformes and Palaeognathae are around 350 Hz, representing low values in comparison with other birds (Table 1). At the lower frequency end of the range of hearing, the ear becomes less sensitive to soft sounds. It seems plausible to hypothesize that *Llallawavis* had enhanced acoustic abilities at lower frequency registers, presumably used for intraspecific acoustic communication or prey detection. This phenomenon deserves further study with these results as benchmark for understanding phorusrhacid sensibility.

## CONCLUSION

Features of the posterior limb and pelvis, such as the long tarsometatarsus (surpassing 80% of tibiotarsus length), the dorsal iliac crest describing a very pronounced arc, and the asymmetric hypotarsus with caudally projecting crests, identify *Llallawavis scagliai* as a member of Mesembriornithinae, an extinct clade of medium- to large-sized predatory birds. Our phylogenetic proposal also shows that *Procariama* is a member of Mesembriornithinae, whereas in previous studies it was considered a Psilopterinae.

Suppression of intracranial kinesis due to the presence of an independent bone increasing the structural link between the lacrimal and jugal bars and the absence of both palatal hinges also characterized *Llallawavis*. Before the discovery of *Llalawavis*, knowledge of Mesembriornithinae cranial morphology was limited to that observed in the mostly incomplete and poorly reconstructed *Mesembriornis milneedwardsi*.

The processus rostrales of the ossa palatinum, ossa ectethmoidalis, vomer, annulus ossicularis sclera, tracheal rings, tracheobronchial syrinx, furcula, sternum, pubis, and ossified tendons are features that are described for the first time in Mesembriornithinae or in phorusrhacids more generally (e.g., syrinx, ossified tendons).

From the study of the complete skeleton of this new taxon, it is possible to corroborate or discard critical anatomical information that was previously proposed for Phorusrhacidae and allow the building of stronger phylogenetic hypotheses.

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