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THEIR PHYLOGENETIC POSITION

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EARLIEST TINAMOUS (AVES: PALAEOGNATHAE) FROM THE MIOCENE OF ARGENTINA AND THEIR PHYLOGENETIC POSITION

SARA BERTELLI¹ AND LUIS M. CHIAPPE²

ABSTRACT. Several isolated bones of tinamous from Miocene deposits of Santa Cruz Province (southern Patagonia, Argentina) are the oldest known remains of this paleognath lineage. The specimens include an incomplete coracoid, proximal end of four coracoids, distal ends of two tibiotarsi, and distal ends of two humeri. They represent at least two species but cannot be assigned to any known taxon. A detailed description and phylogenetic interpretation of this material is provided here. Morphological data of the fossils are included in a matrix of 63 osteological characters and 34 terminal taxa incorporating 24 living species of Tinamidae in addition to the fossils under study. The cladistic analysis produced 81 optimal trees, in which the fossils are more closely related to the open-area tinamous (Nothurinae). Placement of the Santa Cruz fossil tinamous between the open-area (Nothurinae) and the forest-dwelling ("Tinaminae") tinamous is consistent with the paleoenvironmental conditions inferred from the associated fossil fauna.

RESUMEN. Varios fragmentos de huesos de tinámidos de depósitos del Mioceno de la Provincia de Santa Cruz (sur de Patagonia, Argentina), son los restos más antiguos que se conocen de este linaje de paleognatas. Los especímenes incluyen un coracoides incompleto, extremos proximales de cuatro coracoides, extremos distales de dos tibiotarsos y extremos distales de dos húmeros, cuya descripción e interpretación filogenética son provistas aquí. Estos especímenes representan al menos dos especies, las que no pueden ser asignadas a ningún taxón conocido. Los datos morfológicos de los fósiles aquí descriptos son incluidos en una matriz de 63 caracteres osteológicos y 34 taxones terminales que incluyen 24 especies de tinámidos vivientes además de los fósiles. El análisis cladístico produjo 81 árboles óptimos en los cuales los fósiles están más relacionados con los tinámidos de áreas abiertas (Nothurinae). La ubicación de los fósiles de Santa Cruz entre los tinámidos de áreas abiertas (Nothurinae) y los de selva ("Tinaminae") es consistente con las condiciones paleoambientales inferidas a partir de la fauna fósil asociada.

INTRODUCTION

A large collection of vertebrate remains from the continental Lower to Middle Miocene deposits of southern Patagonia, Argentina (The Fleagle Collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"), was recovered during a series of expeditions in the 1980s and early 1990s. Among these remains is a diverse collection of birds (Chiappe, 1991; Noriega and Chiappe, 1993) that includes several isolated bones of tinamous, for which we provide a detailed description and phylogenetic interpretation.

The Tertiary, and oldest, fossil record of Tinamidae is restricted to Argentina (Tonni, 1977; Tambussi and Tonni, 1985; Tambussi, 1987, 1989; Tambussi et al., 1993; Tambussi and Noriega, 1996). A Late Miocene tinamou was described as an indeterminate species of *Eudromia* Geoffroy,

1832, from La Pampa Province (Tambussi, 1987). Two extinct species, *Eudromia olsoni* Tambussi and Tonni, 1985, and *Nothura parvula* Tambussi, 1989, have been found in sediments from the Upper Pliocene of Buenos Aires Province. Reports of Quaternary tinamous include several extant species from Brazil (Brodkorb, 1963), the Pleistocene *Crypturellus* cf. *C. transfaciatus* (Campbell, 1979) from northwestern Peru, and the extinct *Nothura paludosa* Mercerat, 1897, from the Pleistocene of Argentina. Thus, the Early Miocene tinamous of the Fleagle Collection are the oldest known remains of this Neotropical group of paleognaths (Chiappe, 1991).

The specimens reported here include a partial coracoid, proximal ends of four coracoids, distal ends of two tibiotarsi, and distal ends of two humeri (Table 1). Most of this material comes from the Santa Cruz Formation in the Argentine province of Santa Cruz, from the fossil localities of Monte Observación, Monte León, and Cañadón de las Vacas (Fig. 1). The distal end of one tibiotarsus comes from beds of the middle part of the Pinturas Formation, from the locality of Portezuelo Sumich, also in the province of Santa Cruz (Fig. 1).

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Table 1 Taxonomy, stratigraphic horizon, and locality of the specimens described herein. All specimens come from the Lower to Middle Miocene of Santa Cruz Province, Argentina.

Specimen	Material	Taxonomy	Horizon	Locality
Coracoid				
MACN-SC-3610	Proximal end	Morphotype C1	Santa Cruz Formation	Monte Observación
MACN-SC-3613	Proximal end + shaft	Morphotype C2	Santa Cruz Formation	Monte Observación
MACN-SC-3609	Nearly complete	Morphotype C1 or C2	Santa Cruz Formation	Monte Observación
MACN-SC-3611	Proximal end + shaft	Morphotype C1 or C2	Santa Cruz Formation	Monte Observación
MACN-SC-3612	Proximal end	Morphotype C1 or C2	Santa Cruz Formation	Monte Observación
Humerus				
MACN-SC-1449	Distal end	Morphotype H1	Santa Cruz Formation	Monte Observación
MACN-SC-360	Distal end	Morphotype H2	Santa Cruz Formation	Cañadon de las Vacas
Tibiotarsus				
MACN-SC-1399	Distal end	Morphotype T1	Pinturas Formation	Portezuelo Sumich
MACN-SC-1440	Distal end	Morphotype T1	Santa Cruz Formation	Monte León

ABBREVIATIONS

AMNH	American Museum of Natural History, New York, New York, USA
BMNH	Natural History Museum, London, United Kingdom
COL	Colección Ornitológica Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Tucumán, Argentina
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
KU	Museum of Natural History, University of Kansas, Lawrence, Kansas, USA

LACM	Natural History Museum of Los Angeles County, Los Angeles, California, USA
LSUMNS	Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana, USA
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MGUH DK	Geologisk Museum, University of Copenhagen, Copenhagen, Denmark
MLP	Facultad de Ciencias Naturales y Museo de La Plata, División Paleontología de Vertebrados, La Plata, Argentina
PVL	Paleontología de Vertebrados, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Tucumán, Argentina
UCMVZ	Museum of Vertebrate Zoology, University of California, Berkeley, California, USA
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA
USNM	National Museum of Natural History, Washington, D.C., USA
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

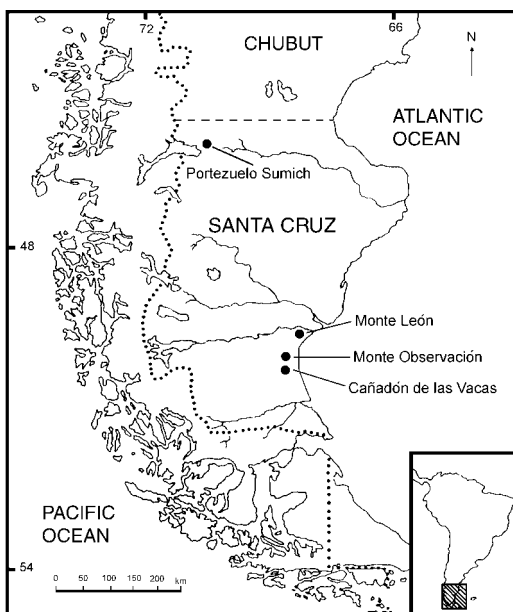


Figure 1 Lower to Middle Miocene localities where the studied specimens come from (modified from Marshall, 1976).

GEOLOGICAL SETTINGS

The material described here was found in sediments of the Pinturas and Santa Cruz formations in southern Argentina. The Pinturas Formation (Bown et al., 1988; Bown and Larriestra, 1990) is a pyroclastic and epiclastic aeolian deposit exposed in the upper valley of the Río Pinturas in southern Patagonia (Fig. 1). The Santa Cruz Formation is ex-

posed over much of southern Patagonia (Ameghino, 1906; Feruglio, 1938). This formation differs from the Pinturas Formation in having less unrecycled pyroclastic sediment, more fluvially deposited epiclastic sand bodies, significant marine intercalations, less paleodune sand, and relatively immature paleosols (Fleagle et al., 1995).

The sites in the Pinturas and Santa Cruz formations have yielded an important collection of Miocene fossil mammals, in particular primates, marsupials, and rodents (Ameghino, 1906; Marshall, 1976, 1990; Barrio et al., 1984; Bown and Fleagle, 1993). Among birds, representatives of Rheidae, Ciconiiformes, Galliformes, Anseriformes, and Cruiiformes are present in the Santa Cruz Formation (Ameghino, 1891, 1895); whereas members of the Falconiformes are known from both the Santa Cruz and Pinturas formations (Ameghino, 1895, 1899; Chiappe, 1991). The Pinturas Formation has also yielded the oldest known tinamou, a specimen included in this study, and indeterminate remains of members of the Passeriformes (Noriega and Chiappe, 1993) and Strigiformes (Chiappe, 1991).

The environmental conditions prevailing during deposition of the Pinturas Formation varied. Paleoenvironmental studies indicate that the lower sequence accumulated under warm, subtropical conditions and that the subsequent depositional sequences may have been characterized by periodically drier conditions and more open areas (Bown and Larriestra, 1990; Genise and Bown, 1994). The deposition of the Santa Cruz Formation appears to have occurred under warm, humid conditions, as indicated by calcareous steinkerns of trees. The presence of nests of scarabaeid beetles and burrows of solitary bees suggests the existence of open areas (Genise and Bown, 1994). Thus, the Pinturas and Santa Cruz formations appear to have been deposited at a time when open areas were expanding.

Ameghino (1906) and later workers regarded the Pinturas Formation as slightly older than the Santa Cruz Formation (Frenguelli, 1931; Barrio et al., 1984). However, others have questioned the distinctiveness of the Pinturas fauna and attributed it to the Santa Cruz Formation (Pascual and Odrerman-Rivas, 1971; Marshall, 1976). Bown and Larriestra (1990) described the Pinturas deposits as a separate formation, distinct from the Santa Cruz Formation. Biostratigraphic evidence, mainly derived from the record of paleothentid marsupials, supports an Early to Middle Miocene age for the Pinturas beds (Bown et al., 1988; Bown and Larriestra, 1990; MacFadden, 1990; Fleagle et al., 1995). Radioisotopic analysis supports an age between 17.5 and 16.5 Ma for the mammal-bearing beds of the Pinturas Formation and an age younger than 16.5 Ma for the localities of Monte Observación and Monte León from the Santa Cruz Formation (Fleagle et al., 1995).

SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758

Palaeognathae Pycraft, 1900

Tinamidae Gray, 1840

DIAGNOSIS. Paleognathous birds with supra-orbital bones (i.e., superorbital ossicles of Parker [1866]) roofing the orbit, lacrimal and ectethmoid partially fused into a lacrimal–ectethmoid complex (Cracraft, 1968), fossae piercing the interorbital septum (Bertelli, 2002), a sternum lacking a rostral external spine (Parker, 1866; Baumel et al., 1993) and bearing elongated lateral trabeculae (Bledsoe, 1988), a coracoid with a proximodorsal foramen (Parker, 1866) and lacking dorsodistal foramina (Bertelli, 2002), a humerus with a shallow transverse ligamental groove (Lee et al., 1997) and a ventral condyle longer than the dorsal condyle (Clarke and Chiappe, 2001), and a strong, rounded depression between tibiotarsal condyles (Bertelli, 2002).

REFERENCED SPECIMENS AND TAXONOMY. All studied specimens constitute isolated, right elements (Figs. 2–4): MACN-SC-3609, a nearly complete coracoid; MACN-SC-3610 and MACN-SC-3612, two proximal ends of coracoids; MACN-SC-3611 and MACN-SC-3613, two proximal ends and shafts of coracoids; MACN-SC-1449 and MACN-SC-360, two distal ends of humeri; and MACN-SC-1399 and MACN-SC-1440, two distal ends of tibiotarsi. The size of all these elements agrees well with that expected for tinamous slightly smaller than the Spotted Nothura, *Nothura maculosa* Temmink, 1815. There are two morphotypes of coracoids, two morphotypes of humeri, and a single morphotype of tibiotarsus (Table 1). Although none of these morphotypes can be associated to one another on the basis of anatomical evidence, differences between the two coracoids and the two humeri (see Anatomical Description section) indicate that the referred specimens represent at least two species. Because these specimens cannot be assigned to any known living or extinct species, we believe that they represent new species. However, given the fragmentary nature of the material, we refrain from naming them.

LOCALITY AND HORIZON. See Table 1 for details on the locality and horizon for each specimen.

ANATOMICAL DESCRIPTION. Anatomical nomenclature mainly follows Baumel et al. (1993); certain structures not cited herein follow Howard (1929). The Latin terminology used by Baumel et al. (1993) is retained for muscles and ligaments, whereas osteological structures are described with the English equivalents of the Latin terms.

Coracoid. All studied specimens (MACN-SC-3609, MACN-SC-3610, MACN-SC-3611, MACN-SC-3612, and MACN-SC-3613) exhibit a foramen on the dorsal surface, just distal to the triangular-shaped scapular facet (Figs. 2A, B, E, F). This feature is here interpreted as a synapomorphy of Tin-

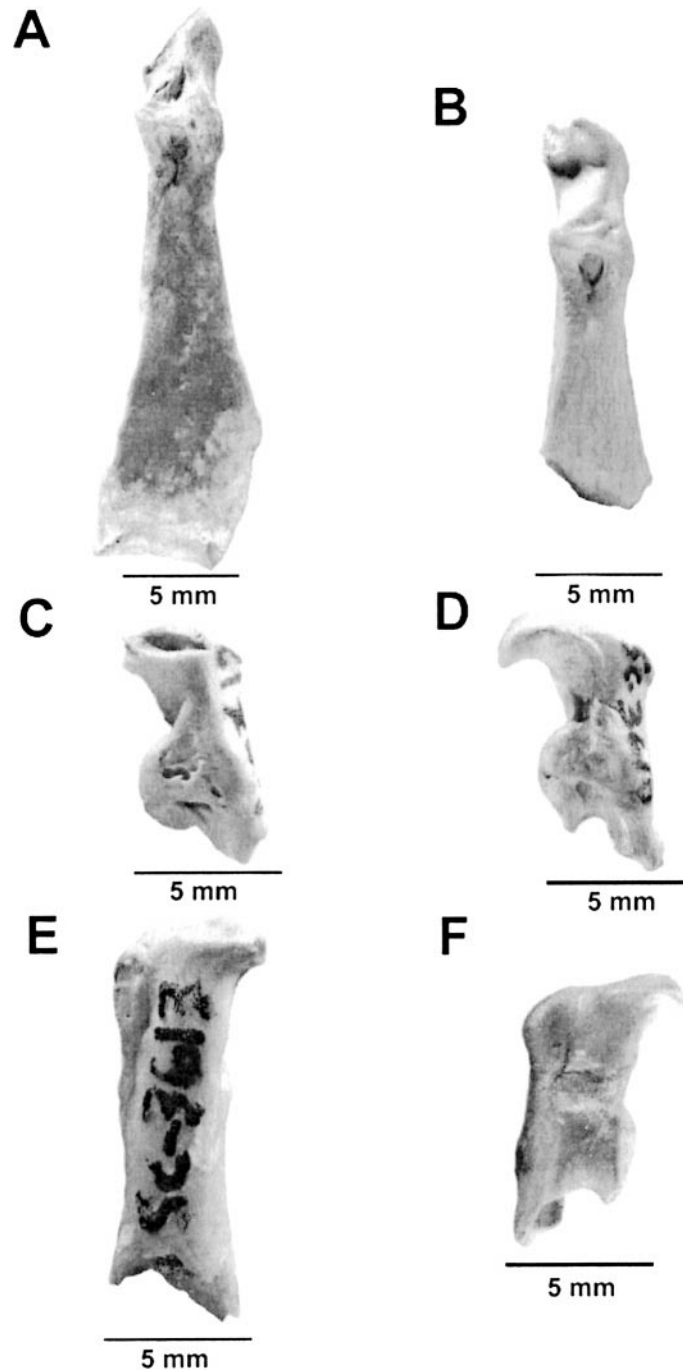


Figure 2 Coracoids. A, MACN-SC-3609, dorsal view; B, MACN-SC-3611, dorsal view; C, MACN-SC-3613, ventral view; D, MACN-SC-3610, ventral view; E, MACN-SC-3612, dorsal view; F, MACN-SC-3610, dorsal view. Anatomical abbreviations: ap, acrocoracoid process; bt, brachial tubercle; f, foramen; gl, groove for ligamentum acrocoracohumerale; hf, humeral articular facet; il, impression for insertion of musculus biceps brachii; im, impression for the origin of ligamentum sternoprocoracoideum of membrana sternocoracoclavicularis; pp, procoracoid process; sf, scapular articular facet; sg, supracoracoidal groove; st, sternal articular facet.

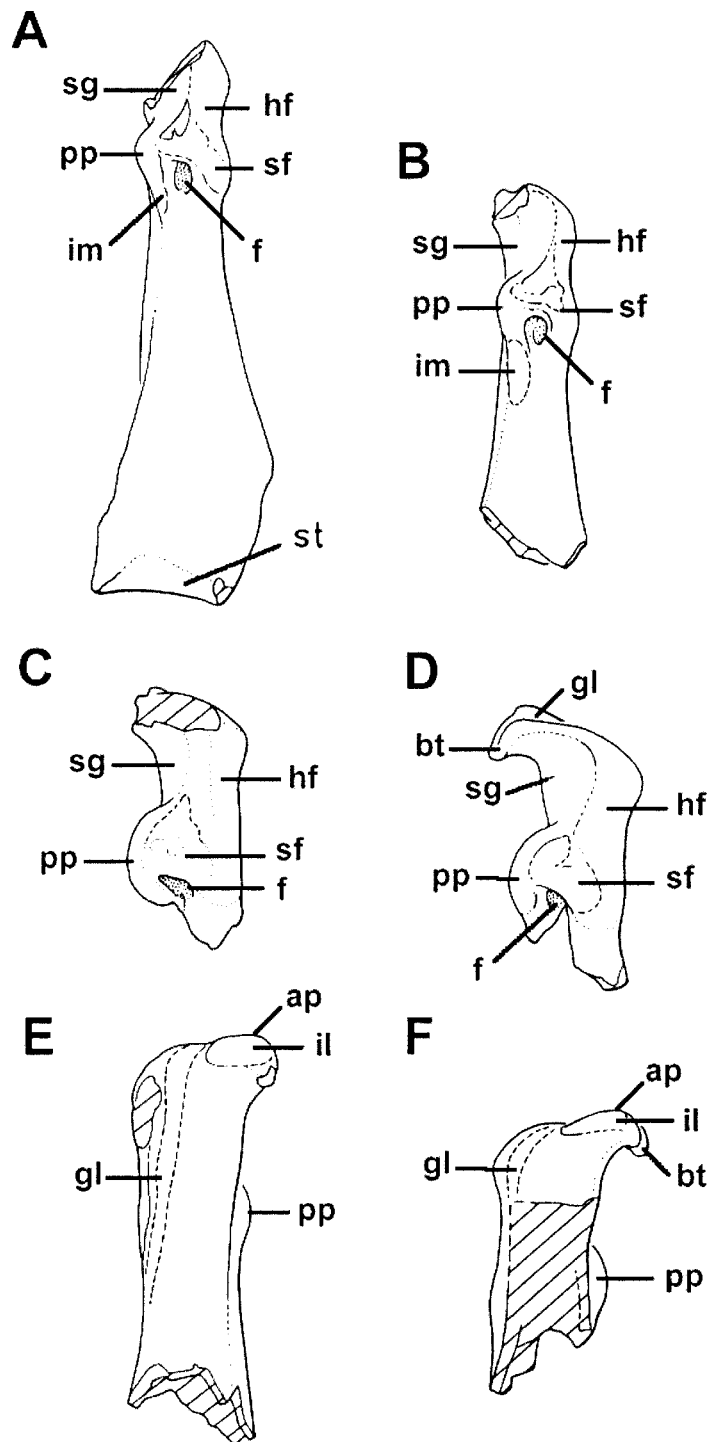


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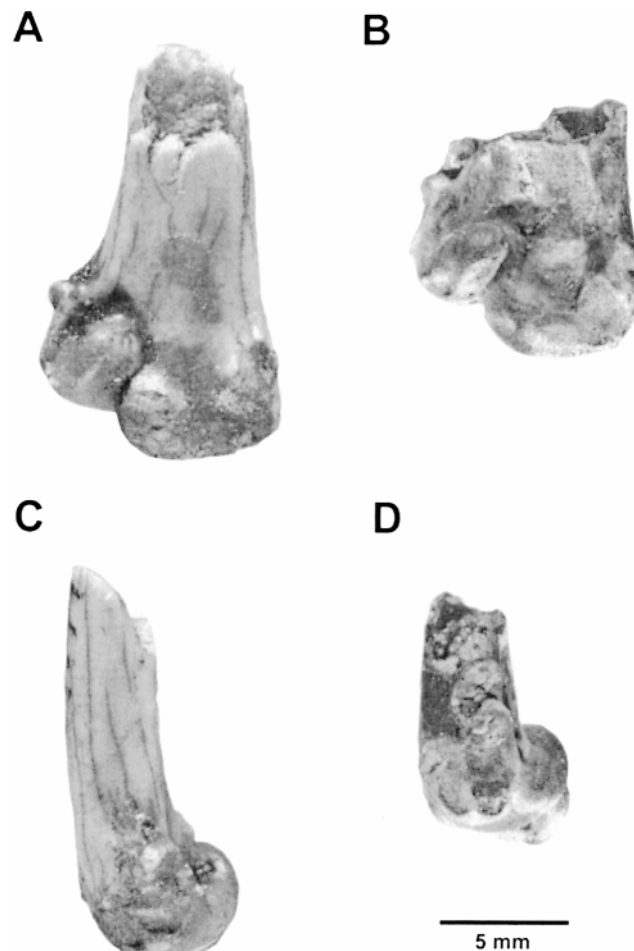


Figure 3 Humeri. A, MACN-SC-1449, cranial view; B, MACN-SC-360, cranial view; C, MACN-SC-1449, dorsal view; D, MACN-SC-360, dorsal view. Anatomical abbreviations: al, attachment of musculus pronator brevis (Howard, 1929); am, attachment of ligamentum articulare craniale (i.e., anterior articular ligament of Howard [1929]); dc, dorsal condyle; df, distal fossae; dp, dorsal supracondylar process; mb, impression for insertion of musculus brachialis; vc, ventral condyle.

amidae. Although a similar condition has been described for Opisthocomidae (Ericson, 1997), the presence of other tinamid synapomorphies in the acrocoracoid process of the Santa Cruz fossils (see below) supports our interpretation. Immediately above the scapular facet, on the dorsal surface of these coracoids, there is a deep fossa excavated on the upper edge of the procoracoid process. Distal to the base of this process, there is a distinct impression for the ligamentum sternoprocoracoideum of the membrana sternocoracoclavicularis (Baumel et al., 1993). Unlike the tinamous *Crypturellus* Bourne and Chubb, 1914, *Nothura* Wagler, 1827, *Nothoprocta* Sclater and Salvin, 1873, *Eudromia*, *Tinamotis* Vigors, 1837, *Rhynchotus* Spix, 1825, and *Taoniscus* Gloger, 1842, the base of the procoracoid process of the Santa Cruz coracoids does not project distally into a ridge (Figs. 2A, B). This

distal ridge of the procoracoid process is tentatively identified as a surface for the origin of the memb. sternocoracoclavicularis (Baumel et al., 1993). Like in many other birds (including the outgroups used in this study), the surface of the humeral facet of all of these coracoids is slightly convex and oriented laterally (Figs. 2A, B, E, F).

On the proximal end of MACN-SC-3610 and MACN-SC-3613, the acrocoracoid process is slender and it projects beyond the proximal edge of the humeral articular facet (Figs. 2E, F). The poorly developed acrocoracoid process of these specimens approaches the condition present in most tinamous, differing from the stronger development seen in *Eudromia*, *Tinamotis*, and *Nothocercus* Bonaparte, 1856, in which the acrocoracoid process reaches the development seen in galliforms. Immediately distal to the acrocoracoid process, there is a distinct

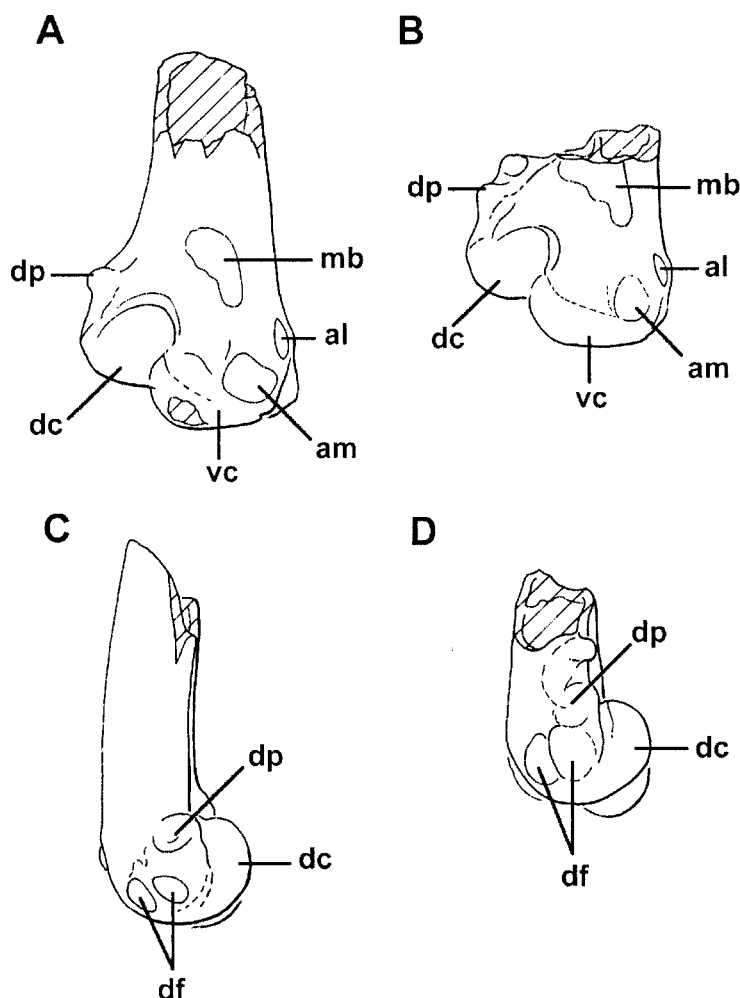


Figure 3 Continued.

impression for the insertion of the musculus biceps brachii (Figs. 2E, F). On the ventral border of this impression, a distinctive linear scar projects distally.

In MACN-SC-3610, the brachial tubercle projects strongly on the medial side of the acrocoracoid process as well as projecting ventrally, toward the triossial canal (Figs. 2D, F). In medial aspect, this projection gives a concave appearance to the distal margin of the clavicular articular facet. Only in *Tinamus* Hermann, 1783, *Eudromia*, and *Crypturellus* does the brachial tubercle project toward the triossial canal.

On the ventral surface of MACN-SC-3610, a shallow groove for the origin of the ligamentum acrocoracohumerale extends from the apex and lateral surface of the acrocoracoid process; this groove contacts the margin of the clavicular facet (Figs. 2D, F). In MACN-SC-3610, this groove does not converge with the dorsal margin of the supracoracoidal groove. Such a condition differs from that of

MACN-SC-3613 as well as from that of the tinamous *Nothocercus*, *Taoniscus*, *Nothura*, *Nothoprocta*, and *Rhynchotus*, and the condition in galliforms, in which the supracoracoidal groove and that for the lig. acrocoracohumerale are confluent.

The only specimen preserving the coracoidal shaft, MACN-SC-3609, is narrow and elongated in dorsal aspect (Fig. 2A). As in most other tinamous, its distal end shows no evidence of pneumatization (among tinamous, the presence of distal coracoidal pneumatization near to the scar of the musculus sternocoracoidei is only present in *Nothura* and *Nothoprocta*).

The lateral angle of the distal end of MACN-SC-3609 is broken and the morphology of the lateral process cannot be determined. As in most tinamous, the angular margin of this coracoid is truncated. However, this condition contrasts with the pointed aspect of the angular margin of the coracoids of the tinamous *Eudromia* and *Tinamotis*. A



Figure 4 Tibiotarsi. **A**, MACN-SC-1339, cranial view; **B**, MACN-SC-1440, cranial view; **C**, MACN-SC-1339, medial view; **D**, MACN-SC-1440, medial view. Anatomical abbreviations: ct, carpal trochlea; dt, depression for the intercotylar prominence; ec, extensor canal; lc, lateral condyle; mc, medial condyle; md, medial epicondyle depression; me, medial epicondyle; st, supratendinal bridge.

truncated aspect of the angular margin of the distal coracoid is also typical of galliforms. In the medial aspect of MACN-SC-3609, the areas occupied by the ventral and dorsal sternal facets are comparable in size, and the distal margin of this facet is straight, as observed in the examined tinamous (Fig. 2A).

Humerus. On the cranial surface of both humeri, MACN-SC-1449 and MACN-SC-360, the main axis of the ventral condyle is longer than that of the dorsal condyle (Figs. 3A, B). This condition is present in all examined tinamous except *Tinamotis*, where the main axis of both condyles is subequal in length. A shallow and wide intercondylar furrow

separates these condyles. The distal margin of the dorsal condyle is flat.

As in most tinamous, the flexor process projects distally as far as the ventral condyle. Only in *Nothocercus*, *Nothoprocta*, and *Taoniscus* does this process project farther distally than the ventral condyle.

The origin for the musculus brachialis, on the cranial surface of the humerus, is developed as a flat scar (Figs. 3A, B) instead of as the fossa of other basal neornithine birds. This faint scar is crescent-shaped in MACN-SC-1449 and MACN-SC-360, as it is in *Crypturellus*. However, its shape is less an-

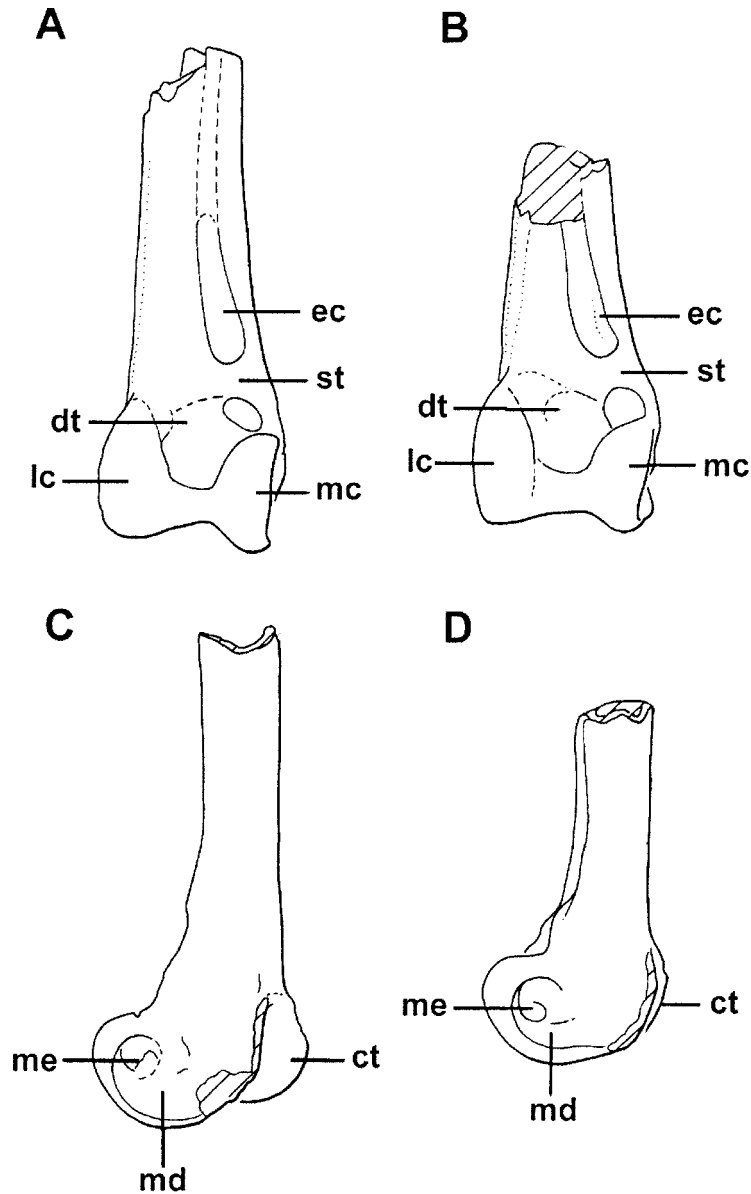


Figure 4 Continued.

gular and broader than in *Nothura* and *Nothoprocta*.

In MACN-SC-1449 and MACN-SC-360, the ventral supracondylar tubercle for the attachment of the musculus pronator brevis (Howard, 1929) is located on the cranioventral margin (Figs. 3A, B). This is generally the condition of species of Tinamidae, although it is also present in many other neornithine birds. Only in the tinamous *Tinamotis* and *Eudromia* is this pit directly on the cranial surface. Just distal to this pit, on the cranial surface of both humeri, the attachment of the ligamentum ar-

ticulare craniale (i.e., anterior articular ligament of Howard [1929]) forms a circular and distinctive depression (Figs. 3A, B). This depression differs from that of all other tinamous in that it is very strongly developed.

On the dorsal border of MACN-SC-1449 and MACN-SC-360, the dorsal supracondylar process is developed as a round, conspicuous tubercle (Figs. 3A–D). This condition is typical of most tinamous except *Nothocercus bonapartei* Gray, 1867, *Taoniscus*, *Tinamotis*, and *Eudromia*, which lack such a tubercle. Specimen MACN-SC-360 differs from

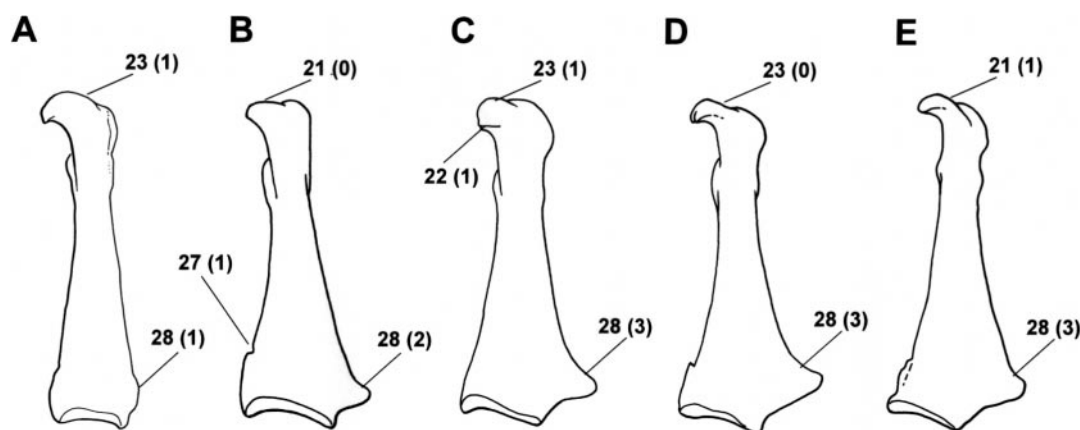


Figure 5 Coracoids of extant tinamous (see characters 21–23, 27–28 of Appendix 2). **A**, *Nothocercus nigrocapillus* Gray, 1867, ventral view; **B**, *Crypturellus soui* Hermann, 1783, ventral view; **C**, *Tinamotis pentlandi* Vigors, 1837, ventral view; **D**, *Nothoprocta cinerascens* Burmeister, 1860, ventral view; **E**, *Nothura darwini* Gray, 1867, ventral view.

most other tinamous examined in that another dorsally projected tubercle is developed proximal to the dorsal supracondylar process (Figs. 3B, D)—a vaguely similar condition has been observed in *Tinamus*, *Crypturellus tataupa* Temminck, 1815, and *Crypturellus parvirostris* Wagler, 1827. Thus, we regard this condition as an autapomorphy of MACN-SC-360.

Two fossae can be observed in dorsal view on the most distal end of both specimens (Figs. 3C, D). While two comparable fossae are present in *Taoniscus*, *Nothura*, *Nothoprocta*, *Rhynchotus*, *Eudromia*, and *Tinamotis*, three are present in the forest-dwelling tinamous and in galliforms. In contrast, only one fossa appears to be present in the humeri of ratites. On the caudal surface of MACN-SC-1449 and MACN-SC-360, the olecranon fossa is weakly defined.

Tibiotarsus. On the cranial surface of the two preserved tibiotarsi, MACN-SC-1399 and MACN-SC-1440, the extensor canal is medially placed, opening adjacent to the medial condyle (Figs. 4A, B). Both specimens exhibit an ossified supratendinal bridge proximal to the latter condyle.

In MACN-SC-1399 and MACN-SC-1440, the lateral condyle extends slightly more proximally than the medial condyle, although not as far proximally as the proximal extension of the supratendinal bridge (Figs. 4A, B). The tibiotarsi of these fossil tinamous share with those of most tinamous the presence of a medial condyle that is narrower transversely than the lateral condyle. Only in the Andean species of *Nothoprocta* (i.e., *Nothoprocta ornata* Gray, 1867, and *Nothoprocta perdicaria* Kittlitz, 1830) are both condyles of subequal width. The fossil tibiotarsi also resemble the general condition of those of extant tinamous in the elongation of the condyles. The medial condyle of MACN-SC-1399 and MACN-SC-1440 projects farther crani-

ally than the lateral condyle and its proximal extension is shorter than of the latter (Figs. 4A, B). In cranial view, the outline of the lateral condyle is straight and of subequal width along its extension. This character state is present in most tinamous except for *Tinamus*, *Nothocercus*, and *Eudromia*, in which the distal end of the lateral condyle is broader than its proximal end, with an acuminate proximal margin. The proximal edge of the medial condyle of MACN-SC-1440 is well defined and slightly more deflected medially than in MACN-SC-1399 (Figs. 4A, B). This deflection may be associated with the relative deepening and medial displacement of the impression of the ligamentum intercondylaris (Livezey, 1997).

As in all tinamous examined, MACN-SC-1440 and MACN-SC-1399 present a strong, rounded cranial depression between the condyles that at maximal flexion accommodates the intercylar prominence of the tarsometatarsus. In contrast to some tinamous, such as *Nothocercus*, *Tinamus*, and *Crypturellus*, the depression of the Patagonian fossils is not bordered proximally by a distinctive ridge.

In medial view, the medial epicondyle forms a small and pointed projection enclosed by a deep excavation (Figs. 4C, D). Only in *Crypturellus* and *Nothocercus* is this depression more excavated on the cranial margin and developed as a fossa.

On the caudal surface of MACN-SC-1440 and MACN-SC-1399, the carpal trochlea is wide; the margins on either side of it are broken (Figs. 4C, D).

CLADISTIC ANALYSIS

Morphological data of the fossils here described were included in a matrix of 63 osteological characters (Figs. 5–7; Appendices 2, 3). The 34 terminal

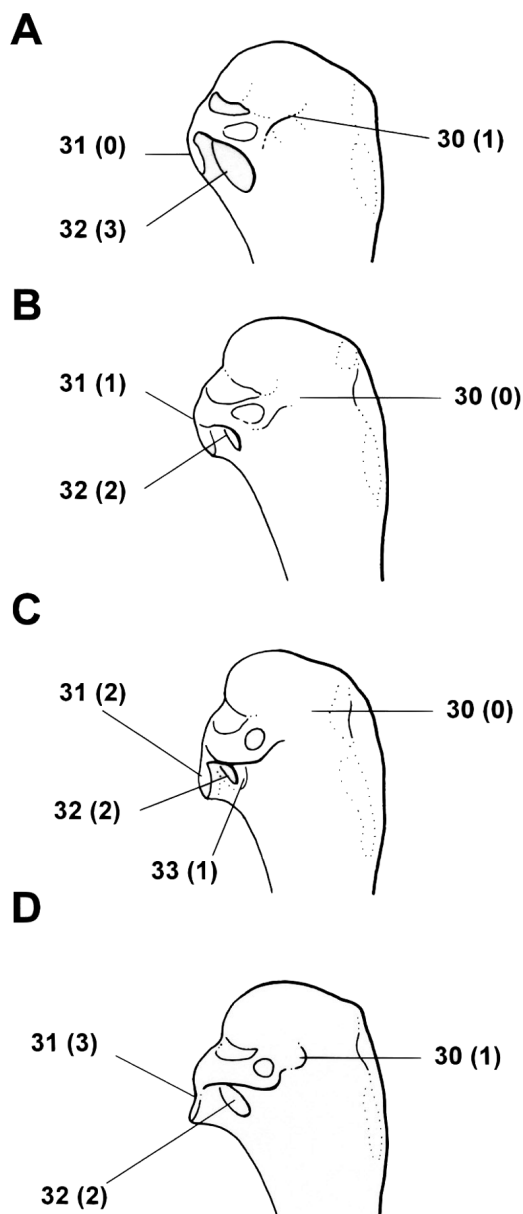


Figure 6 Humeri of extant tinamous (see characters 30–32 of Appendix 2). A, *Megapodius freycinet*, caudal view (proximal end); B, *Tinamus major* Gmelin, 1789, caudal view; C, *Rhynchotus rufescens* Temminck, 1815, caudal view; D, *Crypturellus soui* Hermann, 1783, caudal view.

taxa included 24 living species of Tinamidae plus the fossil specimens—with a single exception (*Lithornis*), all terminals were scored by using museum specimens (Appendix 1). Because no differences between the character-states scored for MACN-SC-1440 and MACN-SC-1399 (the tibiotarsi) were found, these two specimens were treated as one terminal unit and scored as MACN-SC-T in the data

matrix. Coracoids MACN-SC-3610 and MACN-SC-3613 scored differently and, as such, they were treated as separate terminals. Because the other coracoids (MACN-SC-3609, MACN-SC-3611, and MACN-SC-3612) could not be differentiated from either MACN-SC-3610 or MACN-SC-3613, they were not treated as separate terminal units. The two humeri, MACN-SC-360 and MACN-SC-1449, also differed from each other—and were scored as different terminals. Consequently, although it is impossible to ascertain the number of tinamous species represented in the collection of studied fossils, these were scored as five different terminals in the cladistic analysis (a tibiotarsus, two coracoids, and two humeri).

The cladistic analysis was conducted by using 20 replications of random addition sequences of the taxa, creating Wagner trees, each followed by tree bisection–reconnection (TBR) branch swapping and 25 iterations of jackknife ratchet (Nixon, 1999), collapsing the trees on TBR rearrangements. This search strategy—implemented by using Goloboff's (1993) program NONA—produced 81 optimal trees, each with a length of 184 steps. Given the size of the present data, this strategy is almost certain to produce an entirely accurate consensus tree (see Goloboff and Farris, 2001). Extensive data support the placement of tinamous within paleognathous birds (see Parker, 1866; Salvadori, 1895; Pycraft, 1900; Cracraft, 1974, 1981, 1988; Houde, 1988; Saiff, 1988; Bock and Bühler, 1990; Sibley and Ahlquist, 1990; Kurochkin, 1995; Lee et al., 1997; Groth and Barrowclough, 1999; Dyke, 2003). Consequently, the paleognaths *Pterocnemia pennata* d'Orbigny, 1834, *Apteryx australis* Shaw and Nodder, 1813, *Dinornis* Owen, 1843, and *Lithornis* Owen, 1840, were used as outgroups. Because galliforms are also widely considered to be basal neornithine birds (e.g., Cracraft, 1981, 1988; Houde, 1988; Ericson, 1997; Lee et al. 1997; Livezey, 1997; Groth and Barrowclough, 1999), we included the galliform *Megapodius freycinet* Gaimard, 1823, in the outgroup. The paleognath *Lithornis*, which cladistic analyses have placed closer to ratites than to tinamous (Houde, 1988; Dyke, 2003), was primarily scored from the description provided by Houde (1988), although material from the London Clay Formation and photographs of an as yet undescribed specimen (MGUH DK 330) from the Fur Formation of Denmark (G.J. Dyke, personal communication) were also used.

PHYLOGENETIC RESULTS

The present cladistic analysis resulted in a strict consensus tree (Fig. 8) supporting the monophyly of all open-area tinamous, the Nothurinae (*Taoniscus* + *Nothura* + *Nothoprocta* + *Eudromia* + *Tinamotis* + *Rhynchotus*), a conclusion previously supported by studies of immature and adult plumage (Miranda-Ribeiro, 1937; Jehl, 1971; Bertelli et al., 2002). The resultant consensus tree, however,

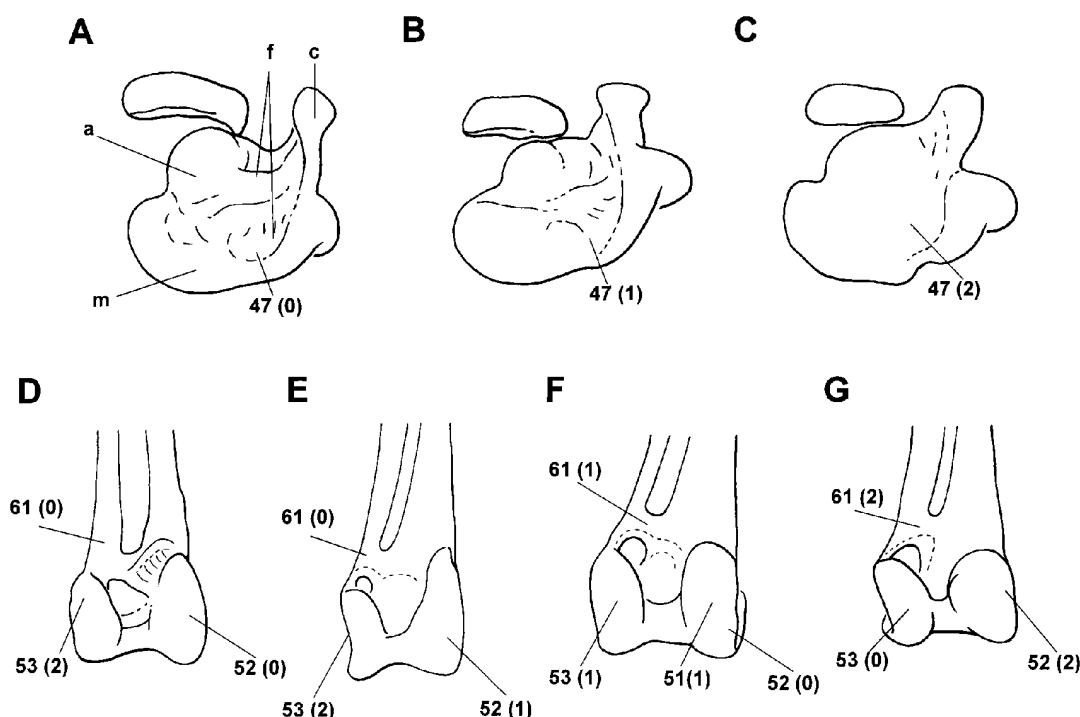


Figure 7 Tibiotarsi of extant tinamous (see characters 47, 51–53, 61 of Appendix 2). A, *Megapodius freycinet*, proximal view (proximal end); B, *Tinamotis pentlandi*, proximal view (proximal end); C, *Nothura darwini*, proximal view (proximal end); D, *Megapodius freycinet*, cranial view (distal end); E, *Tinamus tao* Temmink, 1815, cranial view (distal end); F, *Nothoprocta perdicaria*, cranial view (distal end); G, *Tinamotis pentlandi*, cranial view (distal end). Anatomical abbreviations: a, lateral articular facet; c, patellar crest; f, retropatellar fossa; m, medial articular facet.

did not support the monophyly of the forest-dwelling tinamous, “Tinaminae,” that some of these studies (with exception of Bertelli et al. [2002]) had also proposed. In the phylogenetic hypothesis here presented, “Tinaminae” (*Crypturellus* + *Tinamus* + *Nothocercus*) is paraphyletic and the forest-dwelling ecological niche is regarded as plesiomorphic.

Several synapomorphies support the identification of the fossils studied here as tinamous. The coracoids (MACN-SC-3609, MACN-SC-3610, MACN-SC-3611, MACN-SC-3612, and MACN-SC-3613) share with those of living tinamous the apomorphic presence of a large foramen on the dorsal surface of the coracoid (character 18 of node 3 in Fig. 8), distal to the articular facet for the scapula. The coracoids also possess a slender acrocoracoid process (character 23 of node 6 in Fig. 8; Fig. 5), a distinct impression for the coracoidal head of the musculus biceps brachii on the ventral surface of the acrocoracoid process (character 22 of node 13 in Fig. 8; Fig. 5), and a foramen perforating the upper margin of the scapular facet (character 24 of node 9 in Fig. 8).

The presence of a ventral condyle of the humerus with its main axis longer than that of the dorsal

condyle (character 36 of node 3 in Fig. 8) confirms the inclusion of the Santa Cruz fossil humeri (MACN-SC-1449 and MACN-SC-360) within Tinamidae. In other neornithine birds examined, the ventral condyle is significantly shorter than the dorsal one (see also Clarke and Chiappe, 2001). Another tinamid synapomorphy of the Santa Cruz humeri is the presence of a round and prominent dorsal supracondylar process (character 40 of node 3 in Fig. 8). Although this apomorphic character-state is not shared by all extant tinamous (it is lacking in *Tinamotis*, *Eudromia*, and *Taoniscus*), our cladistic analysis optimizes it as synapomorphy of Tinamidae. The Santa Cruz fossil humeri also display synapomorphies that support internal branches within Tinamidae. These include the presence of a crescent-shaped impression for the insertion of the musculus brachialis (character 37 of node 9 in Fig. 8), two distal fossae on the dorsal surface (character 41 of node 13 in Fig. 8), and a strongly developed depression on the ventrodiscal corner of the cranial surface (presumably for the attachment of the ligamentum articulare craniale; the anterior articular ligament of Howard [1929]; character 42 of node 13 in Fig. 8).

The presence of a medially placed extensor canal

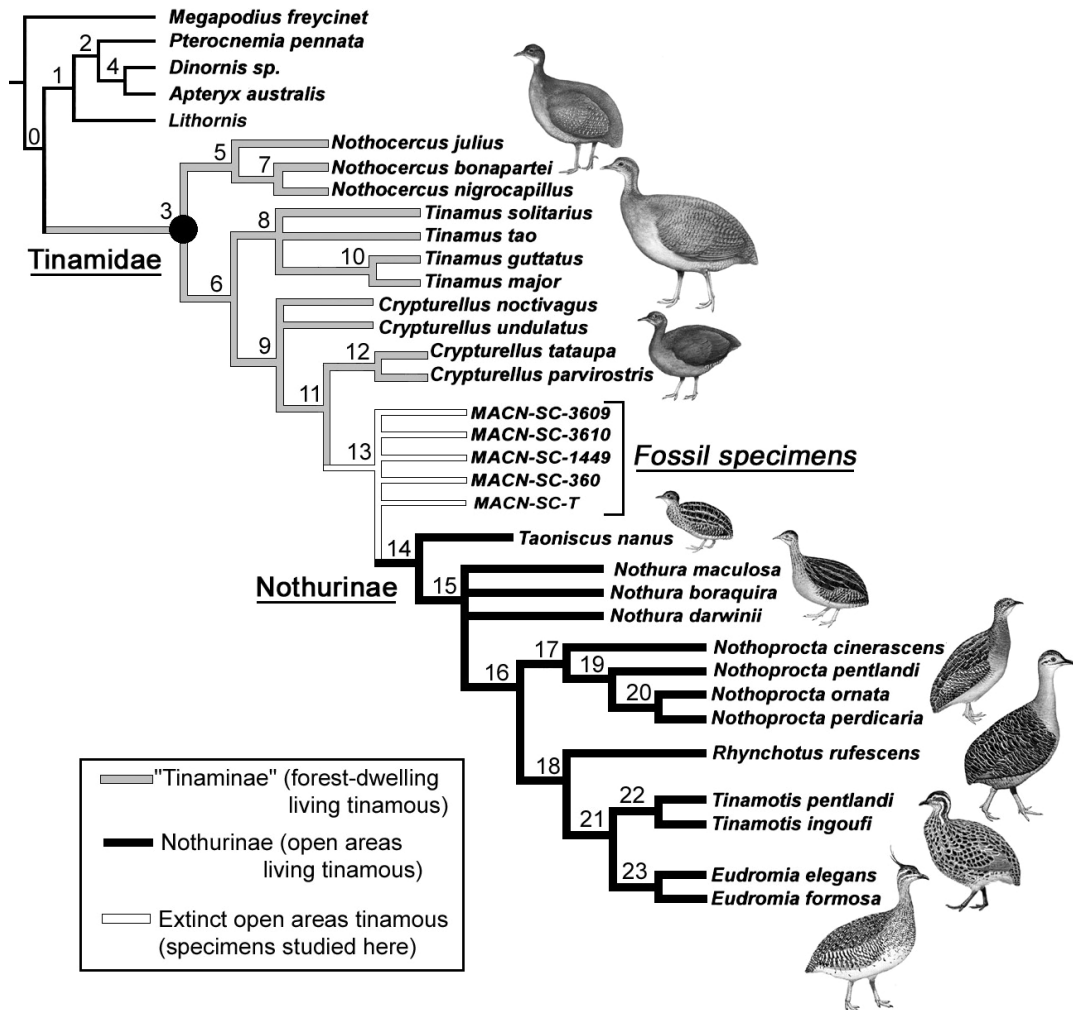


Figure 8 Strict consensus tree of 81 optimal trees (each 184 steps long), based on 63 osteological characters (Appendix 2). Unambiguous synapomorphies common to all optimal trees include (character-state in parentheses): **Node 0:** characters 10 (2), 27 (1), 30 (1), 31 (1), 42 (0), 44 (2), 47 (1), 59 (1); **Node 1:** characters 11 (0), 45 (1), 53 (1), 60 (0), 62 (1); **Node 2:** characters 14 (1), 15 (1), 17 (1), 28 (0), 32 (0), 46 (1), 48 (1), 52 (3); **Node 3:** characters 5 (1), 10 (1), 18 (2), 36 (2), 40 (1), 41 (2), 57 (1), 58 (1); **Node 4:** characters 3 (2), 4 (1), 5 (2), 9 (1), 13 (1), 50 (1); **Node 5:** characters 28 (1), 39 (0), 58 (2); **Node 6:** characters 7 (2), 20 (1), 23 (0), 34 (0), 43 (1), 63 (1); **Node 7:** character 11 (1); **Node 8:** characters 10 (0), 40 (2), 44 (1), 54 (0); **Node 9:** characters 24 (1), 30 (0), 31 (2), 37 (1), 61 (1); **Node 10:** character 11 (1); **Node 11:** characters 24 (1), 31 (3), 44 (3), 47 (2), 49 (0), 53 (1); **Node 12:** character 40 (2); **Node 14:** characters 18 (1), 19 (0), 24 (0), 26 (2), 37 (0), 54 (2); **Node 15:** characters 6 (1), 30 (1), 33 (1), 35 (1); **Node 16:** characters 3 (1), 31 (2), 47 (1); **Node 17:** characters 10 (3), 39 (0); **Node 18:** characters 49 (1), 56 (1); **Node 19:** character 11 (3); **Node 20:** character 51 (1); **Node 21:** characters 1 (0), 6 (2), 16 (0), 20 (1), 21 (0), 23 (1), 33 (0), 38 (2), 40 (0), 48 (1); **Node 22:** characters 36 (1), 42 (0), 52 (2), 53 (0), 54 (0), 61 (2); **Node 23:** characters 3 (0), 7 (1). Synapomorphies of **Node 13** include characters 21 (1), 22 (1), 41 (1), 42 (1), and 58 (0) (see Phylogenetic Results section).

in the Santa Cruz tibiotarsi (MACN-SC-1399 and MACN-SC-1440) supports the paleognath nature of these bones. Most important for our taxonomic identification of these elements is the presence of a strong, rounded depression between the distal condyles (character 57 of node 3 in Fig. 8), a character-state synapomorphic of Tinamidae. These two fos-

sil tibiotarsi also display synapomorphies that support internal branches of the tinamou tree: a medial condyle that is slightly shorter in cranial view than the lateral condyle (character 53 of node 11 in Fig. 8; Fig. 7) and an intercondylar depression that is not proximally delimited by a ridge (character 58 of node 13 in Fig. 8). Furthermore, that the exten-

sor canal is covered by an ossified supratendinal bridge, a condition that among paleognathous birds is known only for the extinct moas and the tinamous, is consistent with our taxonomic interpretation of the Santa Cruz fossil tibiotarsi, given the numerous other differences that distant them from the tibiotarsus of a moa.

Thus, our taxonomic identification of the Santa Cruz fossil coracoids, humeri, and tibiotarsi is based on both the presence of synapomorphies diagnostic of Tinamidae and the presence of derived character-states that support branches within this group. All these fossils fall between the open-area (Nothurinae) and the forest-dwelling ("Tinaminae") extant tinamous in all the shortest cladograms resulting from this analysis. However, because these fossils display many missing entries, derived character-states indicated as synapomorphic of node 13 of the consensus cladogram (21, 22, 41, 42, and 58; Fig. 8) are not unambiguously optimized in all shortest trees. This effect is not caused by homoplasy but by the ambiguity resultant from the limited evidence provided by these incomplete fossils.

CONCLUSIONS

The monophyletic recovery of Nothurinae supports a single event for the radiation of tinamous into open areas. The Santa Cruz fossils, the oldest known tinamous, are the closest relatives to Nothurinae. This phylogenetic inference combined with evidence indicating an environmental shift during the depositional time of the Río Pinturas and Santa Cruz formations (Bown and Larriestra, 1990; Genise and Bown, 1994) places these fossils at the base of this important ecological divergence and raises the possibility that they represent the earliest known examples of tinamous inhabiting open areas.

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APPENDICES

Appendix 1 Comparative material used in the construction of the data matrix.

Apteryx australis (AMNH11315, AMNH3739, LACM102334, USNM500629); *Crypturellus noctivagus* (AMNH2896, AMNH5871, AMNH10444, AMNH10445, YPM2120, YPM2121), *Crypturellus parvirostris* (AMNH2715, AMNH4095, USNM321587, USNM560073, USNM612015), *Crypturellus tataupa* (AMNH604, AMNH1260, AMNH2838, LACM18645, LACM35338, USNM319428, USNM345742, USNM345743), *Crypturellus undulatus* (AMNH2751, AMNH6479, AMNH6482, AMNH6484, USNM345740, USNM345741, USNM431553, USNM553127, YPM11564); *Dinornis* sp. (PVL5700); *Eudromia elegans* (AMNH8565, AMNH11395, AMNH11435, AMNH11436, AMNH17605, COL8, LACM88832, LACM90192, LACM91826, LACM101628, LACM107113, MACN1689a, MLP4, MLP12, MLP247, USNM227489, USNM344966, USNM344991, USNM345014, USNM345015, USNM345016, USNM345018, USNM345019, USNM345052, USNM345063, USNM345064, USNM345093, USNM345094, USNM346848, USNM347009, USNM345095, USNM345096, USNM345097, USNM345472, USNM553666, YPM6706), *Eudromia formosa* (COL9, COL39, COL57); *Lithornis hookeri* (BMNHA3679, BMNHA5202), *Lithornis nasi* (BMNHA5200, BMNHA5201, BMNHA5279); *Lithornis plebius* (BMNH5303), *Lithornis vulturinus* (BMNHA5204, BMNH33138, BMNH38934, BMNH38935); *Megapodius freycinet* (AMNH1389, USNM560650); *Nothocercus bonapartei* (UMMZ155485, USNM428790), *Nothocercus julius* (LSUMNS120893), *Nothocercus nigrocapillus* (LSUMNS99310); *Nothoprocta cinerascens* (AMNH6505, AMNH6507, AMNH6508, AMNH6509, COL6, COL7, COL9, COL10, COL11, COL13, COL15, USNM227806), *Nothoprocta ornata* (AMNH6498, AMNH6500, AMNH12375, UMMZ156780, UMMZ156781, UMMZ209964, UMMZ209965, USNM609491, USNM620750, USNM6207510, *Nothoprocta pentlandi* (AMNH6493, AMNH6494, AMNH6495, AMNH6496, LACM110083, LSUMNS79742, LSUMNS86442, MACN1027a, UMMZ156779, UMMZ156777, UMMZ158778, USNM555676), *Nothoprocta perdicaria* (LSUMNS164593, USNM227767, USNM321770, USNM491384, YPM2040, YPM6696); *Nothura boraquira* (AMNH5803, USNM490025), *Nothura darwini* (KU77981, KU78003, LSUMNS95354, UCMVZ125142, UCMVZ125143, UCMVZ125144, UCMVZ126349, UCMVZ127166, UCMVZ142291, YPM6697), *Nothura maculosa* (AMNH2325, AMNH2408, AMNH2864, AMNH3540, AMNH8341, AMNH24049, LACM93089, LACM93090, LACM93091, LACM93092, LACM93093, LACM93141, LACM93162, LACM93284, LACM93285, LACM93286, LACM93287, LACM93318, LACM101692, LACM104662, MACN1035a, MACN34760, MLP11, MLP48, MLP289, MLP290, MLP295, USNM227342, USNM343627, USNM343628, USNM343629, USNM343630, USNM343631, USNM343632, USNM345020, USNM345021, USNM345022, USNM347605, USNM347606, USNM347608, USNM347613, USNM347614, USNM347615, USNM347616, USNM347617, USNM347618, USNM560069, USNM612016, USNM6122021, USNM614499, USNM614500, USNM614501, USNM614502, USNM614503, USNM614504, USNM614505, USNM614506, USNM614507, USNM6620763, YPM2086); *Pterocnemia pennata* (AMNH4624, AMNH4367, AMNH12890, AMNH12891, AMNH12892); *Rhynchotus rufescens* (AMNH3533, FMNH105631, FMNH105649, LACM93346, LACM93347, LACM101691, MLP9, MLP10, MLP26, MLP30, USNM560065, USNM612017, USNM612018, USNM612019, USNM612020); *Taoniscus nanus* (MCZ341637, USNM310543); *Tinamotis ingoufi* (MACN52296, MLP332, MLP333), *Tinamotis pentlandi* (FMNH105919, MLP28, UCMVZ125148, UCMVZ125150, UCMVZ125151, UCMVZ125152, UCMVZ125153, UCMVZ127167, UCMVZ127168, UCMVZ127169, UCMVZ127170, UCMVZ142292, UCMVZ162355, UCMVZ162356, UCMVZ175958, YPM3673); *Tinamus guttatus* (LSUMNS13101, LSUMNS114567, LSUMNS121484, LSUMNS131402, USNM559457), *Tinamus major* (AMNH3675, AMNH5283, KU34972, KU84122, KU720506, LSUMNS13508, LSUMNS27851, LSUMNS64920, LSUMNS86441, UCMCZ342774, USNM15985, USNM288663, USNM347794, USNM347796, USNM498648, USNM562520, YPM374), *Tinamus solitarius* (AMNH21983, LACM101689, YPM2085), *Tinamus tao* (FMNH315145, FMNH330220, LSUMNS118167, USNM345738, USNM345739, USNM431551).

Appendix 2 List of characters and character-states used in the cladistic analysis. Note that *Apteryx australis*, *Pteronemia pennata*, and *Dinornis* sp. are not comparable for characters 19–26, in which the scapula and coracoid are fused. *Dinornis* sp. was scored as not comparable for characters 30–43 because of the complete reduction of the humerus and the carpometacarpus in this taxon. Because the states of several multistate characters (i.e., 3, 7, 10, 11, 18, 28, 31, 32, 36, 38, 40–42, 44, 53, 58, and 61) can be arranged as a morphological series, these characters were treated as ordered.

- 1 Cranium, interorbital septum, interorbital fossae of Baumel et al. (1993): absent (0); present (1).
- 2 Cranium, dorsal contact of interorbital septum with orbital roof: ossified (0); not ossified (1).
- 3 Cranium, basal tubercles, development on caudolateral regions of basitemporal plate (Lee et al., 1997: character 56 modified): absent (0); slightly developed (1); well developed (2). (Ordered).
- 4 Cranium, olfactory chamber/tubercle, degree of chamber ossification (Lee et al., 1997: character 58): poorly ossified (0); well ossified (1).
- 5 Cranium, ectethmoid: does not contact lacrimal (0); contacts lacrimal (1); fused extensively with lacrimal (2).
- 6 Cranium, ectethmoid, relative size lateral to the orbitonasal foramen: narrow plate (wide foramen), occupying the ventromedial part of the antorbital wall only (0); (Ordered). Similar development (1); wide plate (narrow foramen), occupying almost the entire surface of the antorbital wall (2). A not-comparable state was assigned to *Megapodius freycinet* and ratites, in which the lateral orbitonasal foramen delimited by the lacrimal–ectethmoid complex is absent.
- 7 Cranium, superorbital ossicles of Parker (1866): absent (0); incomplete row of superorbital ossicles (1); complete row of superorbital ossicles (2). (Ordered).
- 8 Cranium, squamosal, projection of zygomatic process over quadrate articulation (Lee et al., 1997: character 53): projects only slightly (0); projects for at least two thirds of the body of the quadrate (1).
- 9 Quadratum, intercondylar fossa (Lee et al., 1997: character 55): shallow (0); deep, rounded pit (1).
- 10 Mandible, dorsal view, medial mandibular process and development of caudal cotyla: broad process of triangular outline and a well-developed caudal cotyla that connects to lateral cotyla (0); triangular process and a caudal cotyla separated from lateral cotyla (1); elongated process and poorly developed caudal cotyla (2); narrow and very elongated process and reduced or absent caudal cotyla (3). (Ordered).
- 11 Notarium, degree of fused thoracic vertebrae: all unfused (0); three vertebrae fused (1); four vertebrae fused (2); five vertebrae fused (3). (Ordered).
- 12 Costae, uncinated process, shape: wide, broader than body of rib (0); elongated, narrower than body of rib (1).
- 13 Sternum, lateral view, sternal plate (Lee et al., 1997: character 5): moderately to highly curved (0); flattened (1).
- 14 Sternum carina (Cracraft, 1974: 503, 506): present (0); absent (1).
- 15 Sternum, rostrum (manubrium) (Lee et al., 1997: character 7): present (0); absent (1).
- 16 Scapula, caudal half of blade: expanding distally and with a blunt end (0); broadest at the midline and tapering distally (1).
- 17 Scapula and coracoid (Cracraft 1974: 503, 506): not fused (0); fused (1).
- 18 Coracoid, proximal end, large foramen located on dorsal surface, just distal to the articular surface for the scapula, development (Ericson, 1997: character 39 modified): not excavated (0); poorly developed, small opening (1); well developed, large opening (2). (Ordered).
- 19 Coracoid, shape of clavicular facet in medial view and development of brachial tubercle: circular to ovate facet lacking tubercle, (0); crescent facet with overhanging, well-developed tubercle (1).
- 20 Coracoid, groove for the origin of ligamentum acrocoracohumerales, confluence with clavicular facet: separated, contacts dorsal margin of the supracoracoidal groove (0); confluent (1).
- 21 Coracoid, acrocoracoid process, projecting proximally more than humeral articular facet (Fig. 5): absent (0); present (1).
- 22 Coracoid, distinctive scar on ventral surface of acrocoracoid process (impression for insertion of *Musculus biceps brachii*) (Fig. 5): absent (0); present (1).
- 23 Coracoid, acrocoracoid process, development (see Fig. 5): slender (0); broad (1).
- 24 Coracoid fossa on upper (proximal) margin of scapular facet, perforation: imperforated, foramen absent (0); perforated, with a foramen (1).
- 25 Coracoid, acrocoracoid process medial expansion: absent (0); present (1).
- 26 Coracoid, base of procoracoid process, medial edge, distal projection: not projected (0); projected as a short and stout crest (1); projected as a long and slender crest (2). (Ordered).
- 27 Coracoid, coracoidal fenestra (Howard, 1929), position (Fig. 5): level with lateral process (0); proximal to the position of lateral process (1).
- 28 Coracoid, lateral process, development (Fig. 5): not developed (0); poorly developed (1); well developed, but shorter than the sternal facet (2); prominent, equal or longer than the sternal facet (3). (Ordered).
- 29 Coracoid, pneumatic foramina on dorsal surface of distal end (impression for *musculus sternocoracoidei*): absent (0); present (1).
- 30 Humerus, capital groove, distal end obstructed by a prominent tubercle projecting from the distal border of humeral head (Fig. 6): present (0); absent (1).
- 31 Humerus, bicapital crest, aspect in caudal view (Fig. 6): rounded, continuously curving (0); intermediate between squared off and rounded (1); squared off (2); with a hook-shaped extension (3). (Ordered). (Because state assignment requires the presence of a bicapital crest, ratites were scored as not comparable.)
- 32 Humerus, ventral pneumatic fossa, development of pneumatic opening (Fig. 6): not excavated (0); poorly developed, small foramen (1); well-developed, moderate opening (2); conspicuously developed (3). (Ordered).

Appendix 2 Continued.

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- 33 Humerus, ventral pneumatic fossa, pneumatic foramen, osseous ring: absent (0); present (1). (A not-comparable state was scored for the ratites *Apteryx australis* and *Pterocnemeia pennata*, which lack a pneumatic foramen in the ventral pneumatic fossa.)
- 34 Humerus, transversal groove, position on the proximal end: ventral (0); cranial (1).
- 35 Humerus, ventral condyle, weakly defined proximally as opposed to a more sharply defined edge: present (0); absent (1).
- 36 Humerus, ventral condyle, length of main axis relative to that of dorsal condyle, cranial aspect (Clarke and Chiappe, 2001: character 17 modified): shorter (0); subequal (1); longer (2). (Ordered).
- 37 Humerus, impression for insertion of musculus brachialis, shape: circular to ovate (0); crescentlike (1); narrow (2).
- 38 Humerus, ventral supracondylar process (attachment of musculus pronator brevis sensu Howard, 1929), position: on ventral surface (0); on cranioventral margin (1); more cranially located (2). (Ordered).
- 39 Humerus, flexor process, distal prolongation viewed cranially: well projected, flexor process projects beyond the ventral condyle (0); moderate, as far as the ventral condyle (1).
- 40 Humerus, dorsal supracondylar process, development: poorly developed, blunt (0); rounded and compact tubercle on dorsal border (1); tubercle with a poorly developed second tubercle on the proximal margin (2); well-projected proximal and distal tubercles (3). (Ordered).
- 41 Humerus, fossae on distalmost end viewed dorsally, number: one (0); two (1); three (2). (Ordered).
- 42 Humerus, area of attachment for ligamentum articulare craniale (i.e., anterior articular ligament of Howard [1929]), depth of excavation: very shallow to not apparent (0); moderate, forming a circular and distinctive depression (1); deep and well-developed impression (2). (Ordered).
- 43 Carpometacarpus, fossa located on the ventral surface of proximal end, caudal to pisciform process, depth of excavation: virtually absent (0); deep and well defined (1). (The ratite *Apteryx australis* was scored as not comparable because of the complete reduction of the carpometacarpus in this taxon.)
- 44 Ilium, dorsal surface, relative length of portions (cranial and caudal) separated by dorsal iliac crest: cranial portion shorter than caudal portion (0); portions subequal (1); cranial portion longer than caudal portion but shorter than twice the length of the later (2); cranial portion more than twice the length of the caudal portion (3). (Ordered).
- 45 Femur, caudal margin of the proximal antitrochanteric articular surface (Lee et al., 197: character 43): curved sharply to form a lip that faces medially, surface highly concave (0); rounded edge, no lip present, surface flattened to slightly convex (1).
- 46 Femur, medial condyle, shape of caudal facet (Lee et al., 1997: character 49): ovoid (0); triangular (1).
- 47 Tibiotarsus, ridge subdividing retropatellar fossa development: complete and distinctive ridge, delimiting two deep depressions (0); incomplete, just prominent on caudal margin (1); not apparent (2). (Ordered). (Figs. 7A–C).
- 48 Tibiotarsus, cranial cnemial crest, distal projection relative to lateral cnemial crest: longer (0); similar (1).
- 49 Tibiotarsus, proximal extension of cranial cnemial crest (Bledsoe, 1988: character 53; Lee et al., 1997: character 34): greatly extended beyond articular surface (0); slightly beyond articular surface (1).
- 50 Tibiotarsus, medial condyle, cranial projection relative to lateral condyle in distal view (Cracraft, 1974: 501, 507–508): essentially leveled or slightly projected (0); strongly projected (1).
- 51 Tibiotarsus, medial and lateral condyles, relative width (Figs. 7D–G): lateral condyle broader (0); subequal (1). (Because state assignment requires the presence of condyles with well-defined outlines, ratites were scored as not comparable; see character 52 (3).)
- 52 Tibiotarsus, lateral condyle, shape in cranial view (Figs. 7D–G): elongated, subequal width proximally and distally (0); proximal margin angular and narrower than distal margin (1); rounded (2); poorly defined medial margin, smoothly grading into intercondylar surface (3).
- 53 Tibiotarsus, medial condyle, length relative to lateral condyle in cranial view (Figs. 7D–G): subequal (0); slightly shorter (1); much shorter (2). (Ordered).
- 54 Tibiotarsus, medial epicondylar depression, shape: reduced to poorly developed (0); deep pit on cranial margin (1); groove along caudal margin, bordered by a crest (2).
- 55 Tibiotarsus, lateral epicondylar depression (Bledsoe, 1988: character 63): shallow (0); deep (1).
- 56 Tibiotarsus, medial condyle, medial deflection of proximal edge in cranial view: slightly deflected proximal edge adjacent to distal opening of extensor canal (0); strongly deflected, proximal edge separated from distal opening of extensor canal by a conspicuous depression (1).
- 57 Tibiotarsus, intercondylar area, round depression proximally: absent (0); present (1).
- 58 Tibiotarsus, ridge along the proximal borer of the intercondylar area, development: not developed (0); incomplete, not continuous medially (1); complete and continuous across supratendinal bridge (2). (Ordered).
- 59 Tibiotarsus, groove for the tendon of musculus extensor digitorum longus, distinct medial location: absent (0); present (1).
- 60 Tibiotarsus, supratendinal bridge (Cracraft, 1974: 501; Bledsoe, 1988: character 57): absent (0); present (1).
- 61 Tibiotarsus, relative position of distal margin of supratendinal bridge to proximal end of lateral condyle: distal (0); level (1); proximal (2). (Ordered). (Because state assignment requires the presence of a supratendinal bridge, the ratites *Pterocnemeia pennata* and *Apteryx australis* were scored as not comparable.) (Figs. 7D–G).
- 62 Tarsometatarsus, intercotylar prominence, proximal extension relative to hypotarsus (Cracraft, 1974): extended beyond hypotarsus (0); level with hypotarsus (1).
- 63 Tarsometatarsus, hypotarsal ridges, shape and distal extension relative to proximal vascular foramina: truncated and squared off, ending proximal to foramina (0); acuminate, ending distal to foramina (1).
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Appendix 3 Data matrix used in the cladistic analysis.¹

	1 1234567890	1111111112 1234567890	222222223 1234567890	333333334 1234567890	444444445 1234567890	555555556 1234567890	666 123
<i>M. freycinet</i>	01000—0003	2?00010010	1010000210	0201100110	1101000010	0021000001	000
<i>Lithornis</i>	1?00?0?0??	0000010000	1110001201	120?100110	?0?[23]10?0?0	001??10?10	—10
<i>P. pennata</i>	00000—0102	01011?10—	———?011	—0—?0100?0	0000111110	—311110010	—11
<i>Dinornis</i> sp.	00212—011?	00111010—	———?0?—	———	——2112111	—311110011	210
<i>A. australis</i>	?0212—0112	01111?10—	———?01?	—0—???0?1?	?0—3111111	—311110010	—10
<i>Tm. solitarius</i>	1100102000	2000000211	1000001201	1100020112	2011001010	0120001111	001
<i>Tm. tao</i>	1100102000	2000000211	1000001201	1100020112	2011001010	0120001111	001
<i>Tm. guttatus</i>	1100102000	1000000211	1000001201	110002?112	2010001010	0120001111	001
<i>Tm. major</i>	1100102000	1000000211	1000001201	1100020112	2011001010	0120001111	001
<i>Nc. bonapartei</i>	110010?001	1100010200	1010001101	1101020100	2002001010	0121011211	000
<i>Nc. julius</i>	110010?001	2100010200	1010001101	1101021101	2002000010	0121011211	000
<i>Nc. nigrocapillus</i>	1100100001	1100010200	1010001101	1101020101	2003001010	0121011211	000
<i>C. noctivagus</i>	1100102001	2000000211	0001011200	2100021111	2012001010	0021001111	101
<i>C. undulatus</i>	1100102001	2000000211	0001011200	2100021111	2012001010	0021001111	101
<i>C. tataupa</i>	1100102001	20000[01]0211	0001111300	3100021112	2013002000	0011001111	101
<i>C. parvirostris</i>	1100102001	20000[01]0211	0001111300	3100021112	2013002000	0011001111	101
<i>Tn. nanus</i>	100010000?	2100010100	1100120200	3100020100	1?130020?0	0012001011	101
<i>Nt. maculosa</i>	1000110002	[23]100010100	1100121311	311012[12]111	1113002000	0012001011	101
<i>Nt. boraquira</i>	1000110002	[23]100010100	11001213?1	3110120111	1113002000	0012001011	101
<i>Nt. darwinii</i>	1000110002	2100010100	1100121311	3110122111	1113002000	0012001011	101
<i>Np. ornata</i>	1010110003	3100010200	110[01]121311	211012[012]101	1113001000	1012001011	101
<i>Np. cinerascens</i>	1010111003	2100010200	1100121311	2110122101	1113001000	0012001011	101
<i>Np. pentlandi</i>	1010110003	3100010200	110[01]121311	211012[12]101	1113001000	0012001011	101
<i>Np. perdicaria</i>	1010110003	3100010200	1101120311	211012?101	1113001000	1012001011	101
<i>R. rufescens</i>	1010100002	2100010200	1101120301	211012[01]111	1113001010	0022011011	101
<i>E. elegans</i>	0000121002	21000002[01]1	0111121301	210012[01]21[01]	1[01]13001110	00[12]2011011	101
<i>E. formosa</i>	0000121002	[12]100000211	0111121301	210012[01]210	1113001110	0122011011	101
<i>Tt. pentlandi</i>	0010120002	2100000201	0110121301	2100110210	1013001110	0200011011	201
<i>Tt. ingoufi</i>	0010120002	2100000201	0111121301	2100110210	1013001110	0200011011	201
MACN-SC-3610	??????????	????????211	110110?0?	??????????	??????????	??????????	???
MACN-SC-3613	??????????	????????210	110110?0?	??????????	??????????	??????????	???
MACN-SC-1449	??????????	??????????	??????????	???021111	12????????	??????????	???
MACN-SC-360	??????????	??????????	??????????	???021113	12????????	??????????	???
MACN-SC-T	??????????	??????????	??????????	??????????	?????????0	0011001011	1??

¹ M., *Megapodius*; P., *Pterocnemia*; A., *Apteryx*; Tm., *Tinamus*; Nc., *Nothocerus*; C., *Crypturellus*; Tn., *Taoniscus*; Nt., *Nothura*; Np., *Nothoprocta*; R., *Rhynchotus*; E., *Eudromia*; Tt., *Tinamotis*.

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