

New material of *Cayaoa bruneti* TONNI, an Early Miocene anseriform (Aves) from Patagonia, Argentina

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With 7 figures and 1 table

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Abstract: *Cayaoa bruneti* TONNI, 1979 is an early Neogene anseriform exhumed from marine sediments of the lower levels of the Gaiman Formation (“Patagoniano”, Leonian Marine Stage, Chubut, Argentina). It was originally based on a partial tarsometatarsus that was not assigned to subfamily or tribe. We re-examine the holotype and study new tarsometatarsi, and previously undescribed skeletal elements including partial femora, tibiotarsi, partial humeri and carpometacarpus. *Cayaoa bruneti* was a strictly foot-propelled diving bird that exhibited an extreme reduction of the fore-limb, being probably the earliest recorded flightless duck. Similarly reduced wings are found in the distantly related anseriform *Cnemiornis* OWEN, 1866 of subrecent deposits of New Zealand, *Chendytes* MILLER, 1925 of the Pleistocene of California, and the moa-nalos of the Late Quaternary of Hawaii.

Key words: Anatidae, *Cayaoa bruneti*, flightlessness, Miocene, South America.

1. Introduction

Cayaoa bruneti TONNI, 1979 is an early Neogene duck from Patagonia, originally described from a partial tarsometatarsus. The holotype and all the material previously and here referred to the species, comes from the marine sediments of the lower levels of the Gaiman Formation (Marine Leonian Stage, “Patagoniano”) at Chubut Province, Argentina. *Cayaoa bruneti* is the second most numerous component of the avifauna at these levels and locality whereas the penguins (Sphenisciformes) represent the first in abundance (TONNI 1980; ACOSTA HOSPITALECHE 2005; ACOSTA HOSPITALECHE et al. 2007). TONNI (1979) assigned *C. bruneti* to the Anatidae

(Anseriformes) and suggested its close phylogenetic affinities with the species of *Tachyeres* OWEN, 1875, the steamer-ducks of southern South America. However, this hypothesis of relationship was never checked by cladistic methods.

Our contribution includes valuable new data on this poorly known species of Tertiary diving duck, with descriptions and figures of previously unreported skeletal bones.

2. Geographic and stratigraphic location

All the material assigned to *C. bruneti* was recovered from the southern margin of the Chubut River, between Gaiman and Rawson cities, Chubut Province,



Fig. 1. Map location of the lower Chubut River Valley (Chubut Province, Argentina, South America), showing the extension of the fossiliferous area at the river basin as a shaded surface.

Argentina (Fig. 1) from rocks of Early Miocene age (MALUMIÁN 1999) possibly Aquitanian. The fossil bearing sediments were deposited in a shallow marine environment of temperate waters of relatively high productivity (MENDÍA & BAYARSKY 1981). The lower levels of the Gaimán Formation (Leonian Marine Stage, "Patagoniano"), from which *C. bruneti* comes, are dominated by a conglomerate or transgressive phosphatic coquina. They gradually turn into a tuff containing abundant teeth of sharks and rays, together with other marine vertebrates (CIONE 1986, 1988; CIONE & PANDOLFI 1984; CIONE & COZZUOL 1990; ARRATIA & CIONE 1996; SCASSO & CASTRO 1999).

3. Material and methods

This work is based on the original material studied by TONNI (1979) and a new set of undescribed skeletal elements. The previously unknown bones consist of twelve distal fragments of femora, nine tibiotarsi, two carpometacarpi, and four incomplete humeri.

The holotype of *C. bruneti* is an isolated tarso-metatarsus and, consequently, the only positively identifiable elements are the homologous bones. TONNI (1979:13) refrained from assigning all the

material then available to the same species due mainly to variation in size. As it is common with fossil bird remains coming from the Gaimán Formation sediments at the Chubut valley, the skeletal parts were not found in direct association. Nevertheless, a relatively large number of specimens of each element are available; for each element no more than a single species is represented. The size disproportion between the pectoral and pelvic bones may suggest that two different ducks inhabited the same area at that time. However, we consider it very implausible that in the relatively large sample of post-cranial bones that one species is represented exclusively by pectoral elements and the other only by pelvic bones. Taking into account the above observations, we propose here the hypothesis that all the materials belong to a single taxon. Consequently, we assume that the pectoral limb of *C. bruneti* was greatly reduced and that the variability in size among different specimens may be related to sexual dimorphism or intraspecific variation.

Comparative osteology is performed by using the following Recent species from the collections of Museo de La Plata (MLP), Centro Nacional Patagónico (CENPAT) and National Museum of Natural History (NMNH): Anhimidae: *Chauna torquata*

Table 1. Measurements (in mm) for specimens of *Cayaoa bruneti*. The abbreviation c. indicates estimation in incomplete specimens. When more than one bone is available, the average is given with the range in parentheses.

	Humerus	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
Total length	71.60 [82.00c.]	32.50	48.50 [75.00c.]	161.00	72.00 (71.30-72.70)
Distal width	11.85	6.20	19.82 (18.30-21.00)	19.70 (19.40-20.00)	17.60 (17.20-18.00)
Distal depth	8.50	4.70	15.20 (14.90-15.70)	17.40 (16.70-18.20)	
Width of midshaft	7.00	3.20	7.50 [8.50c.]	10.00	8.27 (8.00-8.80)
Length of deltoid crest	[25.00c.]				
Proximal depth		4.70	17.00		15.40 (14.20-16.30)
Proximal width		10.00	17.20		16.92 (16.20-18.20)
Length of metacarpal I		5.90 (5.50-6.30)			
Depth of midshaft		4.70	9.00	7.65 (7.30-8.00)	7.00 (6.50-7.70)

(OKEN, 1816), *Chauna chavaria* GRAY, 1846; Anatidae: *Dendrocygna viduata* (LINNAEUS, 1766), *Thalassornis leuconotus* EYTON, 1838; *Coscoroba coscoroba* (MOLINA, 1782), *Cygnus melanocoryphus* (MOLINA, 1782); *Chloephaga rubidiceps* SCLATER, 1860, *Chloephaga picta* (GMELIN, 1789), *Tachyeres brachypterus* (LATHAM, 1790), *Tachyeres leucocephalus* HUMPHREY AND THOMPSON, 1981, *Tachyeres patachonicus* (KING, 1831); *Anas platalea* VIEILLLOT, 1816, *Biziura lobata* (SHAW, 1796); *Oxyura dominica* (LINNAEUS, 1776); *Oxyura vittata* (PHILIPPI, 1860). We also include data obtained from the literature (WOOLFENDEN 1961; LIVEZEY 1986, 1989, 1996) of other Recent taxa, and of the Miocene duck *Mionetta* (see LIVEZEY & MARTIN 1988) and *Cnemiornis* OWEN, 1866 (from LIVEZEY 1989, 1996; WORTHY et al. 1997).

Osteological terminology with English equivalents of the Latin names follows BAUMEL & WITMER (1993) and, where necessary, HOWARD (1929) and WOOLFENDEN (1961).

The measurements (Table 1), given in millimeters, were as used by BECKER (1986, 1987). When the fossil is incomplete, the measurement was estimated and indicated by the abbreviation c. (circa).

Institutional abbreviations: MLP, Museo de La Plata, La Plata, Argentina; CENPAT, Centro Nacional Patagónico, Consejo Nacional de Investigaciones Científicas y Técnicas, Puerto Madryn, Argentina; MEF-PV, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; NMNH, National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.

4. Systematic paleontology

Class Aves LINNAEUS, 1758
Order Anseriformes WAGLER, 1831
Suborder Anseres WAGLER, 1831
Family Anatidae LEACH, 1820

Cayaoa bruneti TONNI, 1979
Figs. 2-7

Holotype: Right tarsometatarsus without trochlea for digit IV, MLP 77-XII-22-1.

Referred material: Two carpometacarpi MPEF-PV-3104 and 3105; four partial humeri MPEF-PV-3100 to 3103; twelve partial femora MPEF-PV-3106 to 3114, MLP 71-VII-14-7, MLP 69-III-29-13, and MLP 69-III-29-15; nearly complete left tibiotarsus MPEF-PV-3115; nearly complete juvenile right tibiotarsus MPEF-PV-3121, six partial tibiotarsi MLP 69-III-29-10, MPEF-PV-3116 to 3120, complete left tarsometatarsus MPEF-PV-3122; a nearly complete left tarsometatarsi without trochlea for digit IV MPEF-PV-3123; distal ends of right tarsometatarsus, MLP 77-XII-22-3 (paratype), MPEF-PV-3124 to 3126; proximal fragments of right tarsometatarsus MPEF-PV-3127, and left tarsometatarsus MLP 77-XII-22-2 (paratype).

Emended diagnosis of genus: A flightless anatid with a fairly robust hindlimb, but with the wing extremely reduced; the carpometacarpus being relatively smaller than in most species of Anatidae, excepting the flightless *Moa-nalos* of Hawaii (OLSON & JAMES 1991) and *Anas marecula* OLSON & JOUVENTIN, 1996. The characters exhibited by the tarsometatarsus of *Cayaoa* are the following: outer margin of shaft markedly concave in anterior



Fig. 2. Humerus of *Cayaoa bruneti*. Proximal end in anconal (A) and palmar (B) views, MPEF-PV-3103 specimen. Palmar (C) and anconal (D) views, MPEF-PV-3100 specimen. Scale bar equals 1 cm.

aspect; extensor sulcus wide and deeply excavated; internal and, specially external, ridges of shaft prominent in anterior extent, associated with moderate twisting of shaft about its long axis; outer proximal foramen opens plantarly immediately distad to the groove between the first and second calcaneal ridges of hypotarsus; lateral side of intercotylar prominence with a shallow groove anteriorly; trochlea for digits II and III divergent; trochlea for digit II lies more postero-proximally than the other two, not projecting beyond the proximal extent of the trochlea for digit III and lacking a complete median groove; trochlea for digits III and IV distinctly oblique in distal view.

Species diagnosis: As for the genus (monotypy).

5. Description and comparisons

Humerus: The most striking peculiarity of the humerus is the relatively small size and stoutness (Fig. 2). The capital shaft ridge (margo caudalis) is directed towards the external tuberosity (tuberculum dorsale), as in *Mionetta*, *Stictonetta*, and the Tadorninae. The capital groove (incisura capitis) deeply undercuts the head, ending at the external tuberosity, a character separating *C. bruneti* from the more primitive Anserinae and Dendrocygninae. In anconal view, the proximal region of the shaft is depressed transversely by a continuous trench. The deltoid crest (crista deltopectoralis) flares laterally, with its external margin rounded and its surface concave anconally; this is a primitive feature for Anatidae which is shared, e.g. by *Thalassornis*, *Biziura*, *Malacorhynchus*, the Anserinae, Dendrocygninae, and some Tadorninae. The internal tuberosity (tuberculum ventrale) is produced distally, partially obscuring the pneumatic fossa (fossa pneumotricipitalis). This fossa is completely closed, as in *Thalassornis* and other diving ducks. However, this fossa is also closed in non-divers (e.g. *Malacorhynchus*), and open in some divers (e.g. *Mergus*). The external tuberosity is prominent and buttressed. The impression of *M. brachialis anticus* (fossa *m. brachialis*) is a deep subelliptical scar whose medial border constitutes a sharp ridge on the internal margin of shaft. In distal view, *C. bruneti* has the same relative anconal heights of the ectepicondyle (epicondylus dorsalis) and the entepicondyle (epicondylus ventralis). The external tricipital groove (sulcus scapulotricipitalis) is obsolete because the ectepicondyle, which constitutes its outer margin, is reduced. The entepicondyle is more distally projected than the ectepicondyle. There is a prominent pit for the attachment of *M. flexor carpi ulnaris* (processus flexorius). The attachment for the anterior articular ligament (tuberculum supracondylare ventrale) is elevated and angled medially as in some diving ducks.

Carpometacarpus: The carpometacarpus is the most modified known element of the skeleton. It is a very short and robust bone (Fig. 3). Consequently, the wing of *C. bruneti* is reduced in size compared with the leg (Table 1). The fossil shares few characters with the more primitive genera of Anserinae. The lower portion of the external rim of the carpal trochlea is unnotched, a character present in the Anhimidae, some Dendrocygninae, Thalassornithinae, and Anseranatinae, having a uniform thickness along its whole

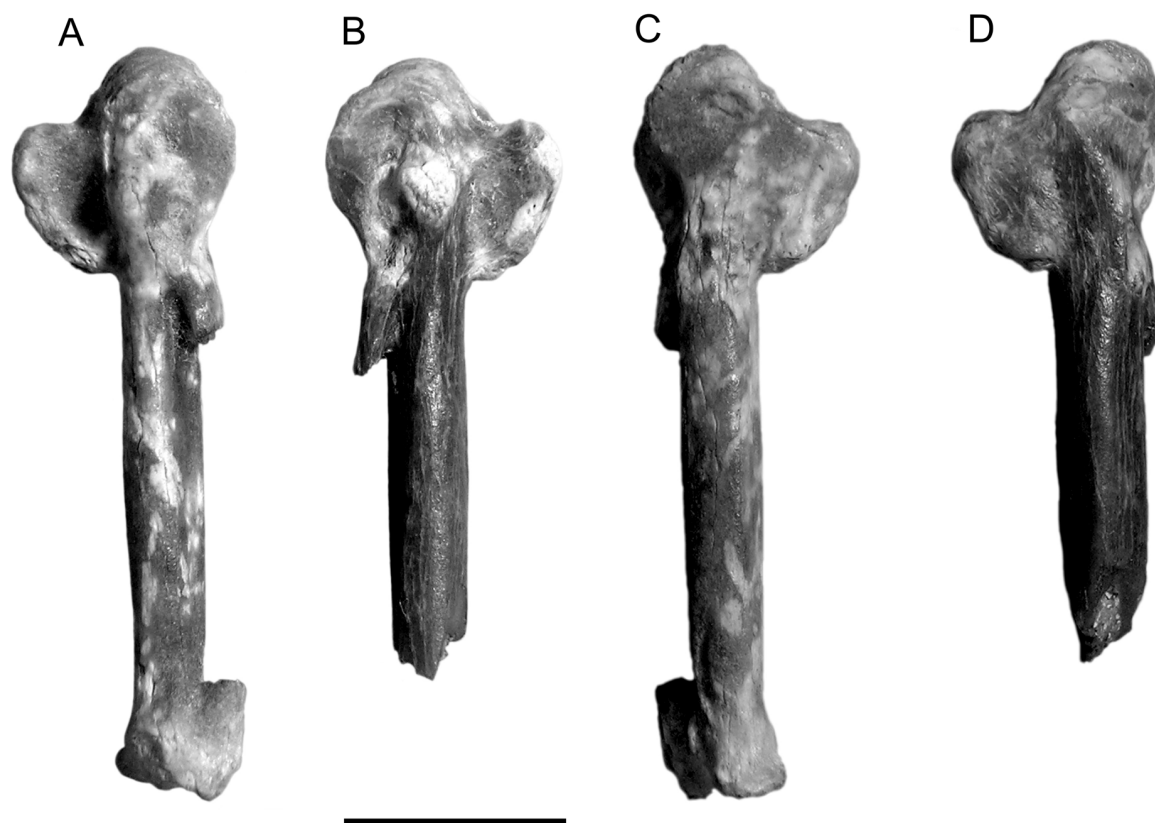


Fig. 3. Carpometacarpus of *Cayaoa bruneti*. Internal (A, B) and external (C, D) views, MPEF-PV-3104 and MPEF-PV-3105 specimens, respectively. Scale bar equals 1 cm.

extent. On the posterior face, the external edge of the carpal trochlea is much shorter than the internal edge. The distal portion of the upper surface of metacarpal II (os metacarpale majus) is flat and forms a sharp angle with the external face. The process of metacarpal I (os metacarpale alulare) is broad and not protrudent, its extension being less than the width of the trochlea. The external attachment of the cunifur ligament is a prominent elliptical scar well proximad. The scapholunar attachment lies on the ridge that extends from the insertion of the cunifur ligament and the proximal fornix. Other characteristics present in *C. bruneti* are: pisiform process (processus pisiformis) blunt; cunifur fossa (fovea carpalis caudalis) shallow; attachment site of *M. extensor metacarpi ulnaris* (processus intermetacarpalis) proximal to proximal fornix of metacarpal II and III. At the distal end, the articular facets for digits II and III (facies articularis digitalis major and minor) are situated almost in the same plane.

Femur: In general appearance, the femora attributed to *C. bruneti* resembles that of *Thalassornis* and all other genera of diving ducks because of the curved shaft and reduced anterior extent of the trochanter (Fig. 4). The outer surfaces of the condyles diverge posteriorly. The anterior edge of the external condyle forms a straight line with the shaft, whereas it is elevated from the latter in the whistling ducks and swans. The popliteal area (fossa poplitea) is deep. The rotular groove is wide and deep. The lobe on the posterior intermuscular line (linea intermuscularis caudalis), near the midpoint of shaft, is not prominent. The fibular groove (trochlea fibularis) is notably wide, a feature related to diving habits. The tuberculum *M. gastrocnemialis lateralis* is strong and proximolaterally placed. Another feature that characterizes *C. bruneti* is the presence of a conspicuous ridge extending up the posterior surface of shaft from the internal condyle (crista supracondylaris medialis). In distal view, the femur of *C. bruneti* shows a strong

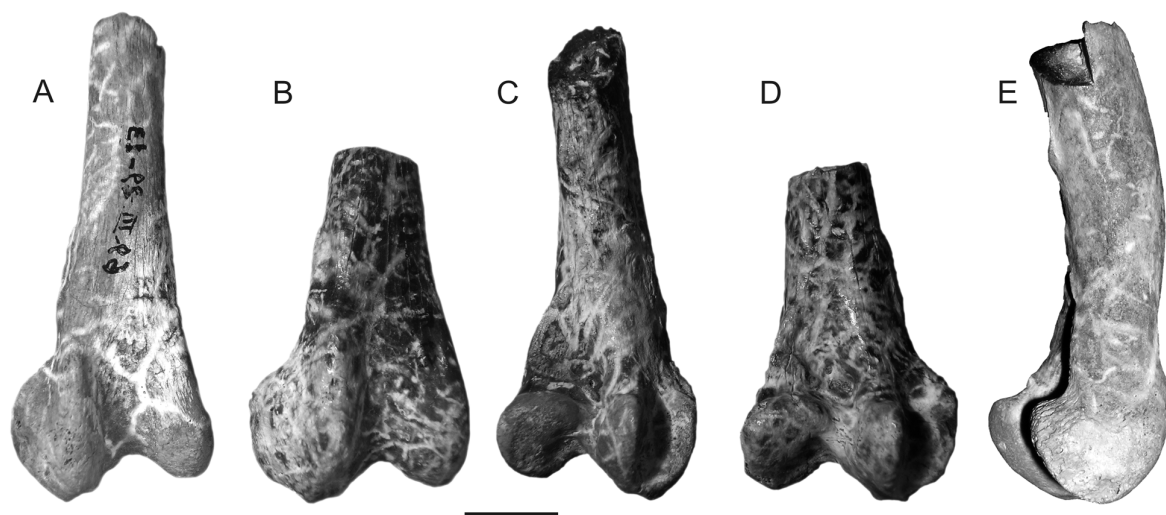


Figure 4: Femur of *Cayaoa bruneti*. Anterior (A, B), posterior (C, D), and medial (E) views, MLP 69-II-29-15 and MLP 69-II-29-13. Scale bar equals 1 cm.



Fig. 5. Tibiotarsus of *Cayaoa bruneti*. Anterior (A, B) and posterior (C, D) views, MPEF-PV-3115 and MPEF-PV-3116 specimens. Scale bar equals 1 cm.

impression of the ligamentum cruciati cranialis. All of these features are related to diving behaviour and, consequently, shared with all divers.

Tibiotarsus: The tibiotarsus is similar in size to that of *Coscoroba*, but it is more robust and the shaft is flattened anteroposteriorly (Fig. 5). The proximal articular surface is in line with the shaft, squaring with distal condyles (condylus medialis and condylus lateralis). The cross-section of the shaft through the fibular crest (crista fibularis) has a flattened anterior surface and a rounded posterior one. The inner cnemial crest (crista cnemialis cranialis) is deflected laterally and extends distally to about the proximal end of the fibular crest. The fibular crest extends distally occupying 24.4 % of the total length of bone, one of the higher values for the species we measured. It is only surpassed by *Thalassornis* (25.6 %) and is very close to *Tachyeres leucocephalus* (23.8 %), suggesting a relation between foot-propelled diving and the length of the fibular crest. The outer cnemial crest (crista cnemialis lateralis) is not continued by a distinct ridge distally along anterior surface of shaft to a point well beyond proximal terminus of fibular crest, as in *Tachyeres* and *Dendrocygna*, but becomes flush with the fibular crest (Fig. 5). The condyles exhibit a pronounced medial deflection with broad anterior articular surfaces. The internal condyle (condylus medialis) extends distally than the external condyle (condylus lateralis), but the former is still more deflected. The anterior extent of condyles is essentially equal, like in *Thalassornis* and other diving ducks. The posterior end of the rim of the internal condyle is well extended posteromedially and squares with shaft. The distal rim of the internal condyle is weakly notched. The tendinal groove (sulcus extensorius) is extremely wide and deep. The anterior intercondylar fossa (incisura intercondylaris) is a broadened, quadrangular-shaped surface. The groove for M. peroneus profundus (sulcus M. fibularis) is deep and lies in line with the outer border of shaft. The external ligamental prominence (epicondylus lateralis) is essentially continuous with the curvature of shaft. The internal ligamental prominence (epicondylus medialis) is strong and lies quite distal.

Tarsometatarsus: There are four calcaneal ridges on the hypotarsus (crista hypotarsi); the internal ridge (crista medialis hypotarsi) is the most distoposteriorly extended. The outer proximal foramen (foramen

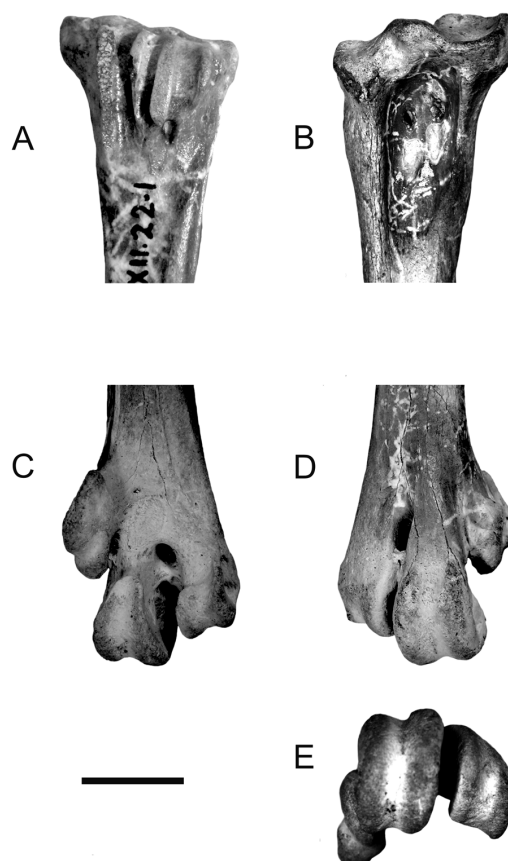


Fig. 6. Tarsometatarsus of *Cayaoa bruneti*. Details of posterior (A) and anterior (B) views, holotype MLP 77-XII-22-1. Posterior (C), anterior (D), and distal (E) views, MPEF-PV-3122 specimen. Scale bar equals 1 cm.

vasculare proximale) opens plantarly distad to the groove between the first and second calcaneal ridges. The internal cotyla (cotyla medialis) is deeply cupped as in *Tachyeres* and *Thalassornis*. The intercotylar depression (sulcus ligamentosus) is large. Laterally the base of the intercotylar prominence (eminentia intercondylaris) has a shallow groove anteriorly (Figs. 6-7).

The shaft is robust, its width ranging in three specimens from 11.18 % to 12.5 % of the length. The anterior metatarsal groove (sulcus extensorius) is wider and more excavated than all the species compared but less than in *Stictonetta* (Figs. 6-7). The internal and specially the external ridges of the shaft are prominent in anterior extent. The shaft is moderately twisted about its long axis as in *Tachyeres*, but less than in *Thalassornis* and other diving ducks. Viewed medially, the anterior surface of shaft displays



Fig. 7. Tarsometatarsus of *Cayaoa bruneti*, holotype MLP 77-XII-22-1. Posterior (A) and anterior (B) views. Scale bar equals 1 cm.

a prominent curve out onto the trochlea for digit III (Figs. 6-7).

The tarsometatarsus of *C. bruneti* resembles those of the swans (*Coscoroba* REICHENBACH, 1852; *Cygnus* BECHSTEIN, 1803) and sheldrakes (*Chloephaga* EYTON, 1838; *Tachyeres*) in that the trochleae for digits II and IV (trochlea metatarsi) are divergent. However, it differs markedly from anserines and tadornines in that the trochlea for digit II projects strongly plantad, and does not extend farther than the base of the middle trochlea (trochlea metatarsi III). This condition is similar to that observed in diving taxa. The trochlea for digit II has a well marked articular groove on the distal surface; the anterior and posterior surfaces are faintly grooved. Viewed distally, the trochleae for digits III and IV form a pronounced angle with the shaft, so that they are more inclined medially than all other waterfowl compared. In posterior view, the distal foramen (foramen vasculare distale) appears, like sheldrakes, less transverse to the shaft than in swans.

6. Discussion

The most outstanding aspect to discuss is that related to the locomotory mode of *C. bruneti*, taking into account the skeletal elements herein described for the first time, i.e. femora, tibiotarsi, humeri, and carpometacarpi.

Cayaoa bruneti seems to have been a strictly foot-propelled diving bird as indicated by several osteological characters of the hind-limb: short femur with a deep popliteal area, and strong curvature of the femoral shaft; long tibiotarsus with very well developed inner cnemial and fibular crests; internal condyle extending anteriorly more than the external; laterally compressed tarsometatarsus with a conspicuous hypotarsus; large and grooved intercotylar depression related with the presence of a strong cartilago tibialis; unequal anterior extent of the lateral and medial ridges of the shaft; and moderate twisting of the diaphysis. These characters, present in *C. bruneti*, have been previously reported as avian adaptive specializations for diving or swimming (STORER 1971; LIVEZEY 1993; RAIKOW 1971).

On the other hand, the severe reduction of the fore-limb of *C. bruneti* has not counterpart among the species compared. The extreme degeneration of the wing bones of *C. bruneti*, that is undoubtedly associated with a flightlessness condition, is also found in the subfossil anseriforms of the genus *Cnemiornis* from New Zealand (LIVEZEY 1989), the North American Pleistocene Diving-geese *Chendytes* (LIVEZEY 1993), and the terrestrial Moa-nalos from the Holocene of Hawaii (OLSON & JAMES 1991). It is also clear that the wings of *Cayaoa* were not functional for underwater propulsion. As noted earlier, the deep subelliptical and relatively large scar for the insertion of *M. brachialis anticus* (fossa m. brachialis) indicates the probable adduction of the wing to the body during dives, as in *Chendytes* (LIVEZEY 1993). Thus, we conclude that *Cayaoa bruneti* becomes the earliest fossil record of a flightless duck.

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