



The youngest record of phorusrhacid birds (Aves, Phorusrhacidae) from the late Pleistocene of Uruguay

Herculano Alvarenga, Taubaté, Washington Jones, Montevideo
and Andrés Rinderknecht, Montevideo

With 2 figures

ALVARENGA, H., JONES, W. & RINDERKNECHT, A. (2010): The youngest record of phorusrhacid birds (Aves, Phorusrhacidae) from the late Pleistocene of Uruguay. – Neues Jahrbuch für Geologie and Paläont. Abh., 256: 229–234; Stuttgart.

Abstract: We report the youngest record of a phorusrhacid bird based on a distal portion of a right tarsometatarsus. This fossil comes from late Pleistocene sediments of Uruguay. The age determination was based on lithological features, biostratigraphical studies and absolute dating. The evidence indicates that these groundbirds co-occurred with the typical Pleistocene South American megafaunal mammals. The so far youngest fossils of phorusrhacids stem from the Pliocene or lower Pleistocene of South and North America.

Key words: Giant groundbird, Phorusrhacidae, late Pleistocene, youngest record, South America, Uruguay

1. Introduction

The phorusrhacids, also called “terror-birds”, were carnivorous groundbirds that lived mainly in Cenozoic environments of South America. Probably, evolved to giant sizes due the geographic isolation of South American continent. These birds are amongst the largest birds that have ever existed on the planet, ranging in height from approximately 1 to 3 meters (MARSHALL 1994; ALVARENGA & HÖFLING 2003). Phorusrhacid birds apparently shared with borhyaenid marsupials the predator niche of grassland ecosystems, and perhaps open areas in dry forest. Because its huge skull with a powerful hooked beak, large curved claws and considerable running abilities (BLANCO & JONES 2005), are generally considered as swift cursorial predators. About 13 genera, and 18 species are known for this family, and these are distributed over five subfamilies (ALVARENGA &

HÖFLING 2003; BERTELLI et al. 2007). The oldest record of this family is from the Paleocene of Brazil (ALVARENGA 1985), and the youngest to date may either be a large tibiotarsus assigned to Pliocene or lower Pleistocene of the Raigón Formation in Uruguay (TAMBUSSI et al. 1999) or the various remains of another gigantic species, *Titanis walleri*, from the Pliocene (late Hemphillian to late Blancan), of Texas and Florida, USA (BRODKORB 1963; CHANDLER 1994; BASKIN 1995; GOULD & QUITMEYR 2005; MACFADDEN et al. 2006). These latter discoveries show phorusrhacids to have been part of the Great American Biotic Interchange, and they were the only carnivorous group of South American animals to disperse northward (MARSHALL 1988, 1994). The present note documents the occurrence of a specimen of terror bird from the late Pleistocene of Uruguay that constitutes the latest geologic occurrence of the Phorusrhacidae.

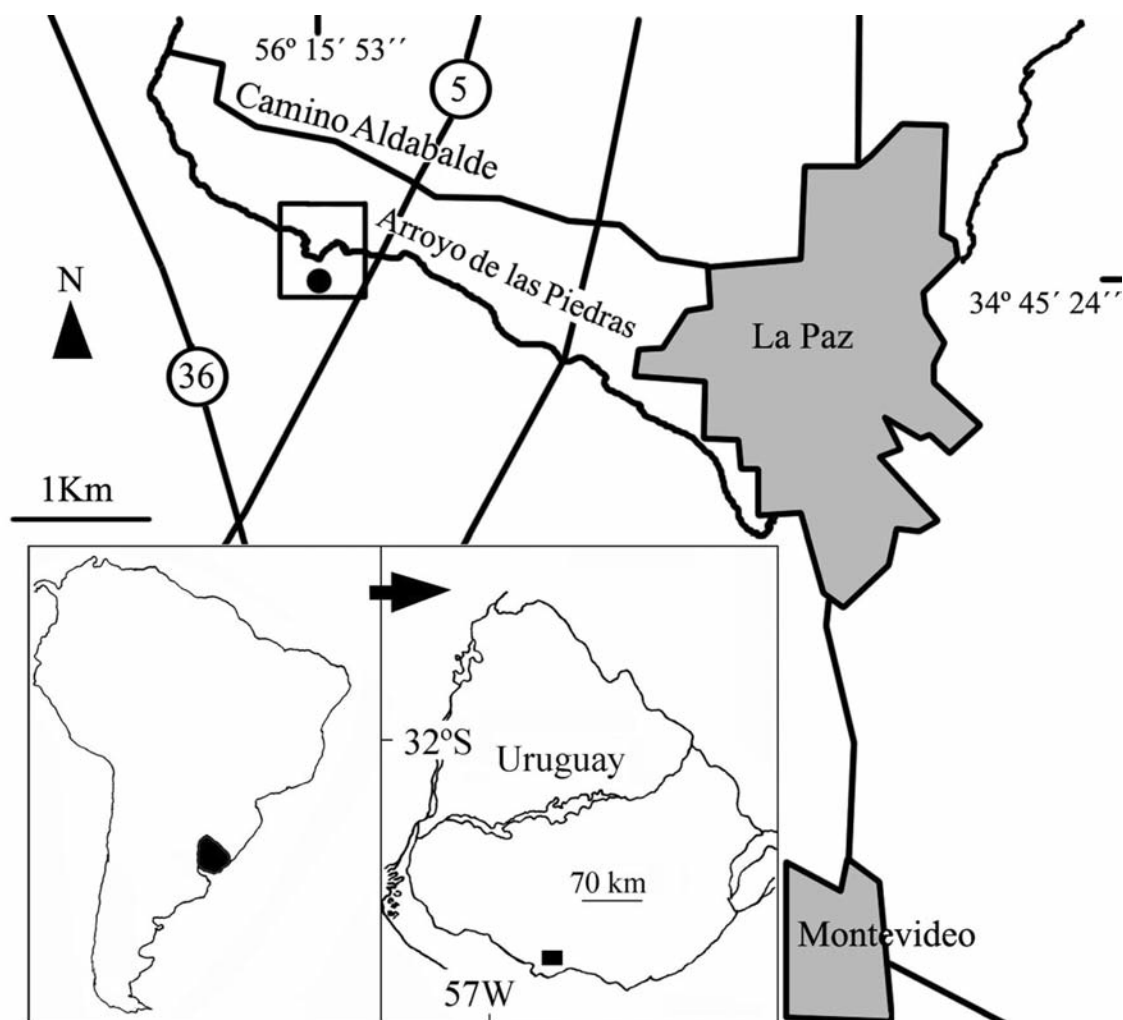


Fig. 1. Map of Uruguay with solid circle indicating the locality where the specimen. MNHN-1736 was collected.

2. Locality and geological setting

The material described in this study was collected by Luis Castiglioni in Casil Quarry, Department of Montevideo, about 2.4 km west from the town of La Paz ($34^{\circ}45'24\text{S}$, $56^{\circ}15'53\text{W}$), Uruguay (Fig. 1). It comes from sediment belonging to the Dolores Formation, usually considered to be of middle-late Pleistocene age (ANTÓN & GOSO 1974). This lithological unit is characterized by siltstones, pelites, sandy to gravely pelites, and sandstones with argillaceous matrix. Calcium carbonate is abundant in various forms (BOSSI & NAVARRO 1991; GUTIÉRREZ et al. 2005). The tarsometatarsus comes from a bone bed in greenish clayish siltstone with sand and gravel

clasts. Its color, texture, and degree of abrasion are consistent with those of other fossils from the same bone bed. Taphonomic information, sedimentological features, and mineralogical studies suggest that the depositional event was a high energy deposit such as a mud flow (CORONA et al. 2005, 2007). The associated fauna includes several genera of cingulates (*Glyptodon* sp., *Panochthus* sp., *Doedicurus* sp., *Neuryurus* sp., *Propaopus* sp.); ground sloths (*Lestodon armatus* and Megatheriinae gen. et. sp. indet.); several ungulates (*Macrauchenia patachonica*, *Toxodon* cf. *T. platensis*, *Hemiauchenia* sp., *Ozotocerus* cf. *bezoarticus*, *Hippidion* sp., and *Stegomastodon waringi*); a rodent (*Myocastor* sp.), and some indeterminate bird bones. This faunal association, especially the taxa

Macrauchenia patachonica, *Lestodon armatus* and *Stegomastodon waringi*, restricts the age of this fauna to middle or late Pleistocene (PEREA et al. 2001; MARCHESANO et al. 2002; CORONA et al. 2005). A sample of enamel from a proboscidean molar from the same stratigraphic level was dated to 17620 ± 100 years BP by AMS 14C (see GUTIÉRREZ et al. 2005). Thus, various lines of evidence confirm a late Pleistocene age for this quarry.

3. Material and methods

The specimen consists of the distal portion of a right tarsometatarsus (Fig. 2), lacking the trochlea metatarsi IV. The texture of the periosteum indicates an adult individual. The specimen was compared with the homologous bone of all orders and almost all families of extant non-passerine birds in the osteological collections of the Museu de Historia Natural de Taubaté, Brazil, and the Museo Nacional de Historia Natural y Antropología de Montevideo, Uruguay. Comparisons were also made with published illustrations of extinct families such as Teratornithidae, Diatrymidae, Plotopteridae, Odontopterygidae, and Pseudodontornithidae (MILLER 1909, 1910; MATTHEW & GRANGER 1917; OLSON & HASEGAWA 1979; HARRISON & WALKER 1976). Comparisons were also made with tarsometatarsi attributed to the Phorusrhacidae, using the original data from ALVARENGA & HÖFLING (2003). Anatomical terminology follows BAUMEL and WITMER (1993). The material described here is deposited in the Museo Nacional de Historia Natural y Antropología, Montevideo (MNHN-1736).

4. Description and comparisons

Compared with extant birds of South America, the specimen (MNHN-1736) is smaller than the tarsometatarsus of rheas (Rheidae) but larger than that of all other terrestrial birds, including storks. Among the phorusrhacids the specimen is smaller than *Mesembriornis incertus* (the smallest Mesembriornithinae) but is of similar size to that of *Procarriama simplex*, the largest of the Psilopterinae (the subfamily that includes the smallest species of Phorusrhacidae). The bone lacks the trochlea metatarsi IV, but the remainder is well preserved and shows some important features. On the lateral side, across the damaged area (Fig. 2D), it is possible to observe the longitudinal section of the canalis interosseus distalis and its ventral branch, which conducts the tendon of *Musculus extensor brevis digiti*

IV and blood vessels into the lateral intertrochlear incisure (BAUMEL & WITMER 1993). In dorsal view it is possible to see the foramen vasculare distale located more proximally than the proximal rim of the middle trochlea (Fig. 2A). We can conclude that the specimen came from a large, cursorial bird characterized by: (1) a large and distally expanded trochlea metatarsi III (middle trochlea); (2) a very narrow trochlea metatarsi II (inner trochlea,) with the articular surface transversally convex and without a longitudinal sulcus (in dorsal and distal view); (3) the trochlea metatarsi II in dorsal view is not turned mediad, being almost parallel and much shorter than the middle trochlea, and forming a narrow notch between trochleae II and III. It is important to note that in most extant birds, including some cursorial ones such as Rheidae, Tinamidae, Cariamididae, and Otididae, the trochlea metatarsi II is deflected medially; in Teratornithidae, Vulturidae and Ciconiidae, the trochlea II is much wider and reaches almost the same distal size as the trochlea III.

The three features outlined above identify the specimen as a phorusrhacid bird. In addition, the morphology of trochleae II and III in medial view, including the very deep *foveae ligamentum col-lateralium*, is very typical of the Phorusrhacidae.

Among the terror birds, MNHN-1736 differs from the Psilopterinae in most representatives of which the trochlea metatarsi II is wider and its inner edge is considerably expanded (SINCLAIR & FARR 1932). It also differs from the Brontornithinae, the largest of the Phorusrhacidae, in lacking the expansion of the dorso-medial extremity of the articular surface of trochleae III (ALVARENGA & HÖFLING 2003). Some features of this specimen are shared with *Titanis walleri* (see BRODKORB 1963 and Fig. 2) of North America, such as the distally expanded trochlea metatarsi III (dorsal view), which is unlike that in *Phorusrhacos* or *Devincenzia*. Likewise, the morphology of the plantar supratrochlear surface and of trochleae II and III in medial view resembles that of *Titanis*.

5. Discussion

Fossils of *Titanis* are from temporally mixed faunas associated with Hemphillian (5 Mya) and late Blancan (2.4 to 2.0 Mya) ages in North America (MACFADDEN et al. 2006). TAMBUSI et al. (1999) identified a large tibiotarsus of the Phorusrhacinae (MNHN-1563) from Uruguay, to the Pliocene or early Pleistocene of Raigón Formation (Uruguay). Thus the new fossil described here is the youngest occurrence

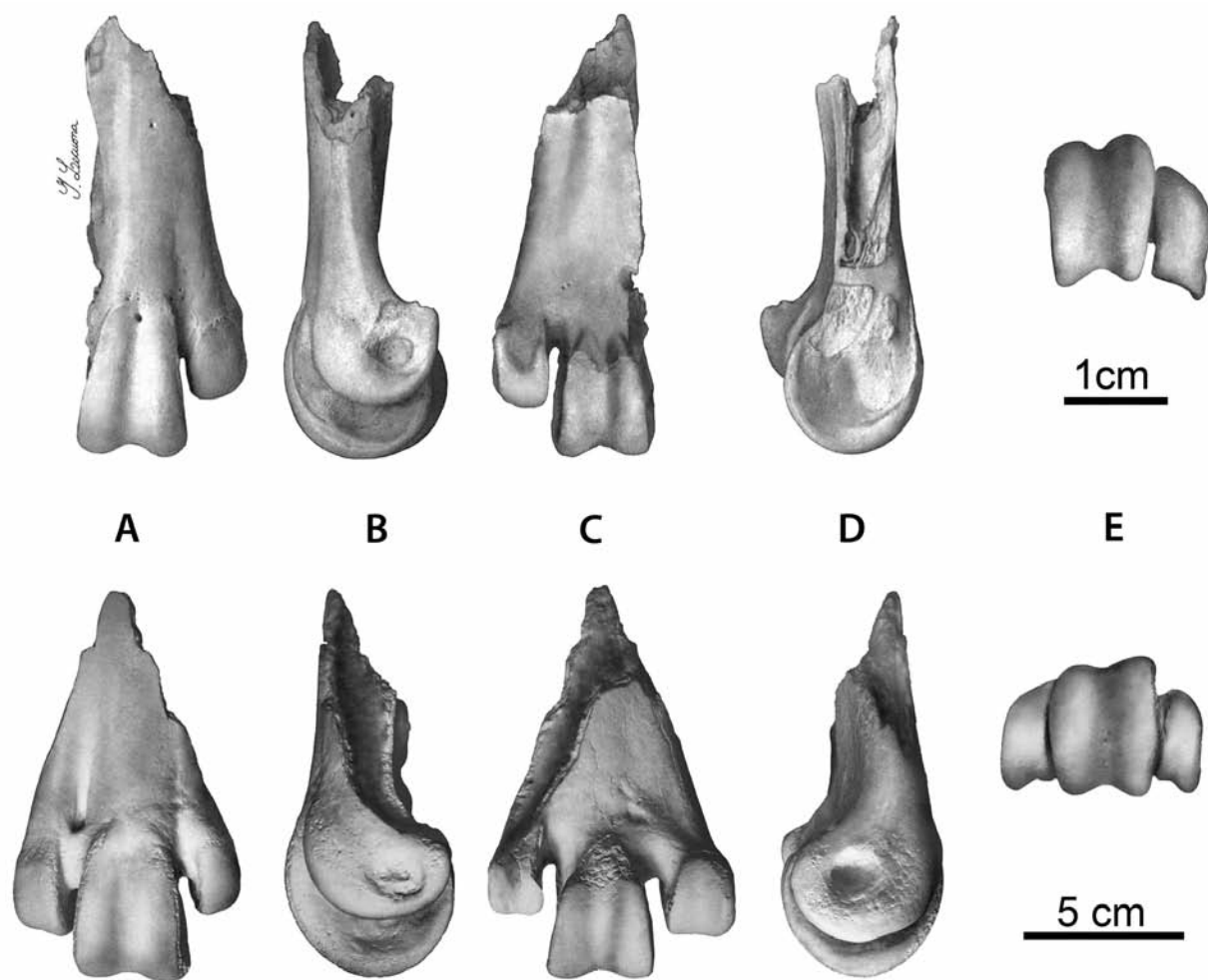


Fig. 2. Distal end of right tarsometatarsus of a Phorusrhacidae from the late Pleistocene of Uruguay (MNHN-1736) (top) and *Titanis walleri* (holotype, University of Florida, UF-4108) (below). A, dorsal, B, medial, C, planar, D, lateral and E, distal views.

of the Phorusrhacidae and extends the family into the late Pleistocene of South America.

The three other Phorusrhacidae specimens previously described from Uruguay – a tarsometatarsus MNHN-189 (type of *Devincenzia pozzi*), a distal portion of tarsometatarsus assigned to *Devincenzia* sp. (Museo Municipal “Bautista Rebuffo”, Uruguay, MR-1215) described by PEREA and ALFARO (2004), and a tibiotarsus MNHN-1563 (TAMBUSSI et al. 1999) – are all from the Pliocene or lower Pleistocene. All these fossils belong to very large species, different from the smaller and more recent fossil described here. Although the present specimen (MNHN-1736) is insufficient for generic determination, some features (the distally expanded trochlea metatarsi III and a

narrow trochlea metatarsi II) are shared with *Titanis walleri* from North America, and other features (as the trochlea metatarsi II not turned medially, and almost parallel to the middle trochlea and also the absence of a dorsomedial expansion of the trochlea III) preclude a close relationship with the subfamilies Brontornithinae and Psilopterninae suggesting that the last representative of the terror birds may belong to one of the subfamilies Phorusrhacinae, Patagornithinae, or Mesembriornithinae. The extinction of phorusrhacids was presumably due to the invasion into South America of North America flesh-eating placental mammals (see MARSHALL 1988, 1994; WOODBURN et al. 2006). This hypothesis could be precluded because the presence of at least one phorusrhacid

representative in the South American late Pleistocene, coexisting with many predators, even actual species. For these reasons, the extinction causes should be reevaluated in function of this fossil finding.

Acknowledgements

We thank LUIS CASTIGLIONI who collected the specimen described here, permitted our study of it, and provided additional information. GUSTAVO LECUONA prepared the map and figure. STORRS L. OLSON critically reviewed a preliminary version and greatly improved this paper. Also we thank CECILÉ MOURER-CHAUVIRÉ and GERALD MAYR for their final reviews that greatly improved this paper.

References

- ALVARENGA, H. (1985): Um novo Psilopteridae (Aves: Gruiformes) dos sedimentos Terciários de Itaboraí, Rio de Janeiro, Brasil. – Congresso Brasileiro de Paleontologia, 8. Rio de Janeiro, 1983, NME-DNPM sér. Geol. V, **27**: 17-20.
- ALVARENGA, H., & HÖFFLING, E. (2003): Systematic revision of the Phorusrhacidae (Aves: Ralliformes). – Papeis Avulsos de Zoologia. Museu de Zoologia da Universidade de São Paulo, **43**: 55-91.
- ANTÓN, D. & GOSO, H. (1974): Estado actual de los conocimientos sobre el Cuaternario en el Uruguay. Dirección de Suelos y fertilizantes. – 12 pp.; Montevideo.
- BASKIN, J. A. (1995): The giant flightless bird *Titanis walleri* (Aves: Phorusrhacidae) from the Pleistocene coastal plain of south Texas. – Journal of Vertebrate Paleontology, **15**: 842-844.
- BAUMEL, J. & WITMER, L. (1993): Osteologia. – In: BAUMEL, J. J., KING, A. S., BREAZILE, J. E., EVANS, H. E. & VANDEN BERGE, J. C. (Eds.): Handbook of Avian Anatomy: Nomina Anatomica Avium, 2nd ed., 45-132; Cambridge (Publications of the Nuttall Ornithological Club).
- BERTELLI, S., CHIAPPE, L. & TAMBUSI, C. (2007): A new phorusrhacid (Aves, Cariamidae) from the middle Miocene of Patagonia, Argentina. – Journal of Vertebrate Paleontology, **27**: 409-419.
- BLANCO, R. E. & JONES, W.W. (2005): Terror bird on the run: a mechanical model to estimate its maximum running speed. – Proceedings of the Royal Society, (B), **272**: 1769-1773.
- BOSSI, J. & NAVARRO, R. (1991): Geología del Uruguay, **2**: 970 pp.; Montevideo (Departamento de Publicaciones de la Universidad de la República).
- BRODKORB, P. (1963): A giant flightless bird from the Pleistocene of Florida. – Auk, **80**: 111-115.
- CHANDLER, R. M. (1994): The wing of *Titanis walleri* (Aves: Phorusrhacidae) from the late Blancan of Florida. – Bulletin of Florida Museum of Natural History, **36**: 175-180.
- CORONA, A., CAWEN, E., TORIÑO, P., PEREA, D. & GOSO, C. (2005): Nuevos aportes al conocimiento de un yacimiento fosilífero del Pleistoceno de Uruguay. – Publicación especial de la Sociedad zoológica del Uruguay Actas de las VIII Jornadas de Zoología del Uruguay. – 54 pp.; Montevideo.
- CORONA A., PEREA, D., GOSO, C., TORIÑO, P. & CASTIGLIONI, L. (2007): Tafonomía de la “Fauna Local La Paz” (Pleistoceno Tardío) y mineralogía de sedimentos continentales asociados, Montevideo, Uruguay. – Actas V Congreso Uruguayo de Geología. Versión Electrónica; Montevideo.
- GOULD, G. & QUITMYER, I. R. (2005): *Titanis walleri*: bones of contention. – Bulletin of the Florida Museum of Natural History, **45**: 201-229.
- GUTIÉRREZ, M., ALBERDI, M. T., PRADO, J. L. & PEREA, D. (2005): Late Pleistocene *Stegomastodon* (Mammalia, Proboscidea) from Uruguay. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **2005**: 641-662.
- HARRISON, C. J. O. & WALKER, C. A. (1976): A review of the bony-toothed birds (Odontopterygiformes): with descriptions of some new species. – Tertiary Research, Special Papers, **2**: 1-62.
- MACFADDEN, B., LABS-HOCHSTEIN, J., HULBERT, R. & BASKIN, J. (2006): Refined age of the late Neogene Terror Bird (*Titanis*) from Florida and Texas using rare earth elements. – Journal of Vertebrate Paleontology, **26** (Supplement 3): 92A.
- MARCHESANO, M., M. ROVIRA, L. CASTIGLIONI & PEREA, D. (2002): Lista taxonómica actualizada y comentarios sobre un yacimiento con mamíferos pleistocénicos del Depto. de Montevideo. – Actas II Jornadas Uruguayas del Cenozoico, 63-67; Montevideo.
- MARSHALL, L. (1988): Land Mammals and the Great American Interchange. – American Scientist, **76**: 380-388.
- (1994): The terror birds of South America. – Scientific American, **270**: 90-95.
- MATTHEW, W. D. & GRANGER, W. (1917): The skeleton of *Diatryma*, a gigantic bird from the Lower Eocene of Wyoming. – Bulletin of the American Museum of Natural History, **37**: 307-326.
- MILLER, L. H. (1909): *Teratornis*, a new avian genus from Rancho La Brea. – Bulletins of the University of California, Department of Geology, **5**: 305-317.
- (1910): The condor like-vultures of Rancho La Brea. – Bulletin of the University of California, Department of Geology, **6**: 1-19.
- OLSON, S. L. & HASEGAWA, Y. (1979): Fossil counterparts of giant penguins from the North Pacific. – Science, **206**: 688-689.
- PEREA, D. & ALFARO, M. (2004): Nuevos datos sobre la cronoestratigrafía de *Devincenzia* (Aves, Ralliformes, Cariamae) en Uruguay. – Actas IV Congreso Uruguayo de Geología; Montevideo.
- PEREA, D., LORENZO, N., MARCHESANO, M. & ROVIRA, M. (2001): Un nuevo yacimiento con mamíferos cuaternarios del Uruguay. – Revista Geológica Uruguaya, **1**: 38-42.
- SINCLAIR, W. J. & FARR, M. S. (1932): Aves of the Santa Cruz Beds. – In: SCOTT, W. B. (Ed.): Reports of The Princeton University Expeditions to Patagonia (1896-1899), **7**: 157-191; Princeton (Princeton University).

- TAMBUSSI, C., UBILLA, M. & PEREA, D. (1999): The youngest large carnassial bird (Phorusrhacidae, Phorusrhacinae) from South America (Pliocene-Early Pleistocene of Uruguay). – *Journal of Vertebrate Paleontology*, **19**: 404-406.
- WOODBURNE, M.O., CIONE, A. L. & TONNI, E. P. (2006): Central American provincialism and the Great American Biotic Interchange. – In: CARRANZA-CASTAÑEDA, O. & LINDSAY, E. H. (Eds.): *Advances in late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange*. – Universidad Nacional Autónoma de México, Instituto de Geología and Centro de Geociencias, *Publicación Especial*, **4**: 73-101.

Manuscript received: February 5th, 2009.

Revised version accepted by the Stuttgart editor: March 23rd, 2009.

Addresses of the authors:

H. ALVARENGA, Museu de História Natural de Taubaté. Rua Juvenal Dias de Carvalho, 111. Taubaté, SP, 12070-640 Brazil;

e-mail: halvarenga@uol.com.br

W. JONES, Museo Nacional de Historia Natural y Antropología. 25 de Mayo 582. Montevideo, 11300 Uruguay;

e-mail: wawijo@yahoo.com.ar

A. RINDERKNECHT, Museo Nacional de Historia Natural y Antropología. 25 de Mayo 582. Montevideo, 11300 Uruguay;

e-mail: rinderk@adinet.com.uy