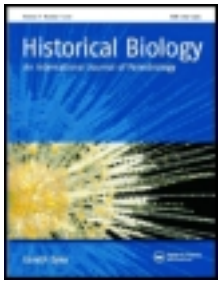

Historical Biology: An International Journal of Paleobiology

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ghbi20

A new species of Dasypodidae (Xenarthra: Cingulata) from the late Miocene of northwestern South America: implications in the Dasypodini phylogeny and diversity

Alfredo A. Carlini [a b], Mariela C. Castro [a c], Richard H. Madden [d] & Gustavo J. Scillato-Yané [a b]

[a] División Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900WFA, La Plata, Argentina

[b] CONICET, Argentina

[c] CAPES, Brazil

[d] Department of Organismal Biology and Anatomy, Chicago University, 1027 E. 57th St., Chicago, IL, 60637, USA

Published online: 29 Sep 2013.

To cite this article: Alfredo A. Carlini, Mariela C. Castro, Richard H. Madden & Gustavo J. Scillato-Yané, Historical Biology (2013): A new species of Dasypodidae (Xenarthra: Cingulata) from the late Miocene of northwestern South America: implications in the Dasypodini phylogeny and diversity, Historical Biology: An International Journal of Paleobiology, DOI: 10.1080/08912963.2013.840832

To link to this article: http://dx.doi.org/10.1080/08912963.2013.840832

Historical Biology, 2013
http://dx.doi.org/10.1080/08912963.2013.840832

Taylor & Francis
Taylor & Francis Group

A new species of Dasypodidae (Xenarthra: Cingulata) from the late Miocene of northwestern South America: implications in the Dasypodini phylogeny and diversity

Alfredo A. Carlini[a,b]*, Mariela C. Castro[a,c], Richard H. Madden[d] and Gustavo J. Scillato-Yané[a,b]

[a]*División Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900WFA La Plata, Argentina;* [b]*CONICET, Argentina;* [c]*CAPES, Brazil;* [d]*Department of Organismal Biology and Anatomy, Chicago University, 1027 E. 57th St., Chicago, IL 60637, USA*

(*Received 3 July 2013; final version received 1 September 2013*)

A new species of dasypodid armadillo (Xenarthra, Cingulata), *Anadasypus aequatorianus*, from the late Miocene of Ecuador is described. The remains were collected in sediments of the Letrero Formation, Nabón Basin, which is part of several intermontane basins related to Andean uplift. The genus represents the oldest record of Dasypodini, which also encompasses *Propraopus* (Pleistocene–early Holocene) and *Dasypus* (?Miocene–Recent). The new species is based on several osteoderms, which show more derived features than *Anadasypus hondanus*, from the middle Miocene of Colombia. In order to test the affinities of *A. aequatorianus* within Dasypodini, we conducted a cladistic analysis of 24 morphological characters for 10 taxa. The most parsimonious tree supports the generic attribution of the new species and places *Anadasypus* basal to *Propraopus* and *Dasypus*, agreeing with the stratigraphic evidence. The faunas from tropical Andean areas differ noticeably from the better-known assemblages of the classic South American sequences. In the case of dasypodines, their geochronological distribution shows that they were historically restricted to tropical and subtropical environments and the main cladogenetic events of the group probably occurred at lower latitudes. In this context, the taxon described herein fills important temporal and geographic gaps of early Neogene armadillos from intertropical areas.

http://www.zoobank.org/urn:lsid:zoobank.org:pub:9DC76603-D831-4E68-BE55-90113228E0F4

Keywords: Xenarthra; Dasypodidae; *Anadasypus*; Miocene; Ecuador; Nabón Basin

1. Introduction

The Dasypodinae armadillos (Cingulata, Dasypodidae) are the oldest known xenarthrans, dating back to the early Paleogene of Brazil (Scillato-Yané 1976; Oliveira and Bergqvist 1998; Bergqvist et al. 2004) and Argentina (Ameghino 1902; Simpson 1948; Tejedor et al. 2009; Carlini et al. 2010). They are subdivided into Astegotheriini (Itaboraian–Laventan South American Land Mammal Ages – SALMAs), Stegotheriini (Casamayoran–Friasian sensu lato SALMAs) and Dasypodini (Laventan SALMA–recent). The latter group corresponds to one of the most basal lineages (Gaudin and Wible 2006; Delsuc et al. 2012), and includes *Dasypus* Linnaeus, 1758, *Propraopus* Ameghino, 1881 and *Anadasypus* Carlini, Vizcaíno and Scillato-Yané, 1997 (Carlini et al. 1997). McKenna and Bell (1997) also included *Dasypodon* Castellanos 1925 (Pleistocene of Bolivia) within Dasypodini, but it actually corresponds to an Euphractinae, as pointed out by Marshall and Sempere (1991) and Carlini and Scillato-Yané (1999). The osteoderms of Dasypodini are characterised by the morphology of the peripheral figures of movable osteoderms (which suggests the presence of triangular epidermal scales with a posteriorly directed apex partially covering two adjacent osteoderms), and double line of osteoderms composing each ring of the caudal tube (Vizcaíno 1990; Carlini et al. 2008).

Nowadays, the long-nosed armadillo *Dasypus* is the most diverse extant xenarthran, with seven species (Wilson and Reeder 2005), and the most widespread species, ranging from 40°N to 40°S in the American continent (Wetzel 1985; Aguiar and da Fonseca 2008). The genus is recorded in the late Miocene of Argentina (*Dasypus neogaeus*, Mesopotamian, Huayquerian SALMA; Scillato-Yané 1982; Scillato-Yané et al. in press), but it is based on a single movable osteoderm that shows derived features, probably coming from upper (Pleistocene) deposits of the profile. Besides that, the oldest records of *Dasypus* are from the late Pliocene in North America (*D. bellus*, Blancan NALMA; Webb 2006) and from the late Pleistocene in South America (*D. punctatus* and *D. novemcinctus*, Lujanian SALMA; Scillato-Yané 1982; Castro et al. 2013). Fossils attributed to *Propraopus* are known from the Pleistocene–early Holocene of South America (Ensenadan–Lujanian SALMAs), but its specific composition has long been debated (Hoffstetter 1952, 1958; Paula-Couto 1979, 1982; Scillato-Yané 1982; Rincón et al. 2008; Oliveira and Pereira 2009; Castro et al. 2013). Presently, *Anadasypus* has a single nominal species, *A.*

*Corresponding author. Email: acarlini@fcnym.unlp.edu.ar

hondanus, and is the oldest known member of the tribe, dating back to the middle Miocene of Colombia (Carlini et al. 1997).

Living dasypodids show greater diversity in the forests and savannas of the equatorial tropics (Wetzel 1985), leading to the hypothesis that their major cladistic events, including the origin of Dasypodini, took place within tropical environments of South America (Scillato-Yané 1986; Vizcaíno 1990; Carlini et al. 2010; Ciancio et al. 2013). Also, the environmental conditions in the tropics would have been less affected by climatical zonation, evident in southern South America during the Miocene (Tauber 1997; Ortiz-Jaureguizar and Cladera 2006 and references therein).

In the comparative description of *A. hondanus*, Carlini et al. (1997) mentioned another species from Ecuador, which was first cited by Carlini et al. (1989). Here, we formally name and describe this new species of *Anadasypus* from the late Miocene of Ecuador and compare it with other Dasypodini. The new species is based on osteoderms, elements more frequently preserved as fossils and that historically underlie the systematics of cingulates (e.g. Ameghino 1902; Simpson 1948; Hoffstetter 1958; Scillato-Yané 1982; Vizcaíno 1994; Carlini et al. 1997, 2010). In addition, osteoderms are being recently included in phylogenetic studies, proving in many cases to be essential to investigate relationships among taxa (Abrantes and Bergqvist 2006; Croft et al. 2007; Ciancio 2010; Castro et al. 2013).

The material assigned to the new species was collected in sediments of Letrero Formation, in the south of Nabón Basin (Figures 1 and 2), which is part of several Miocene intermontane basins related to Andean uplift in southern

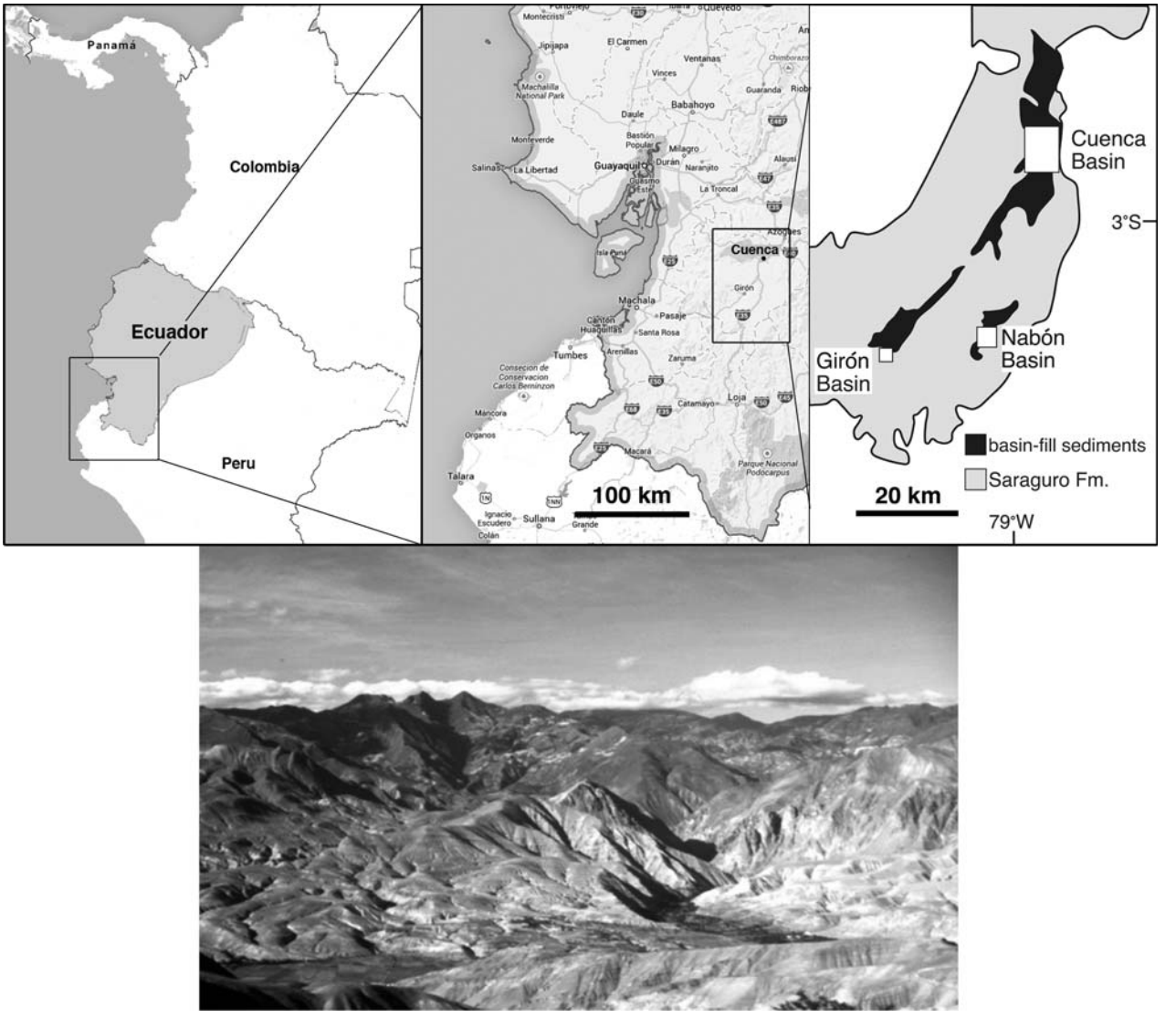

Figure 1. Nabón Basin, Ecuador. Upper, map showing location; lower, general photo of the fossil locality (facing South). Sediments of Saraguro Formation surround the Miocene basins Girón, Nabón and Cuenca.

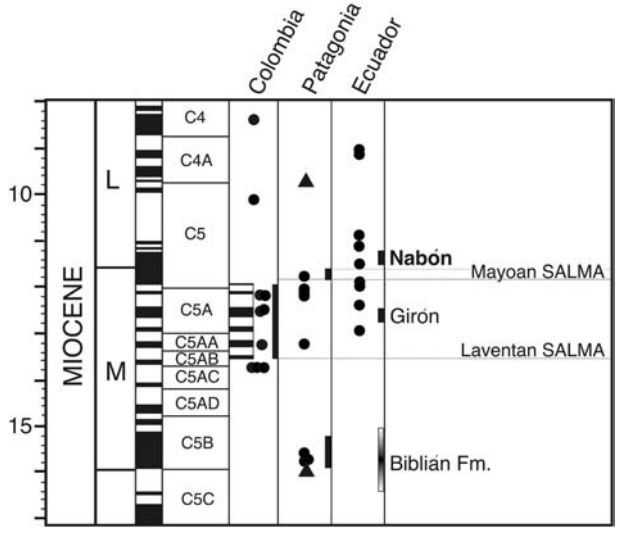

Figure 2. Geochronology of Nabón Basin compared with other Miocene sequences of South America. Black dots, Ar/Ar dates; black triangles, K/Ar dates (modified from Madden et al. in preparation).

Ecuador (see Hungerbühler et al. 2002 and references therein for a revision). The basin-fill series consist both of primary and reworked material derived from coeval volcanoes and adjacent metamorphic basement rocks (Hungerbühler et al. 1995). The Letrero Formation is composed of lacustrine sediments with strong fluvial clastic input and contains siltstones and fine-grained sandstones, probably indicating a period of decreased tectonic and volcanic activity (Hungerbühler et al. 1995, 2002). Combined zircon fission-track (ZFT) and paleomagnetic data suggest that most of it was formed in a relatively short time period in the late Miocene, and specifically for the Letrero Formation, ZFT yielded 9.0 ± 1.4 Ma (Hungerbühler et al. 1995). With respect to the fossil fauna, in contrast to the better-known Quaternary (Wolf 1892; Spillman 1931; Hoffstetter 1952; Edmund 1965), the records of mammals in the Tertiary of Ecuador are scarce: a toxodontid from the Biblián Formation (Repetto 1977) and a caviomorph rodent from in the vicinity of Nabón (Anthony 1922; Candela and Nasif 2006).

2. Materials and methods

The remains of the new species were collected approximately 2 km south-east of Nabón in the uppermost part of the Letrero Formation (Nabón Basin, Azuay Province) in 1987, during an expedition of researchers from Duke University and Escuela Politécnica Nacional. The terminology to describe the morphology and ornamentation of osteoderms follows recent works on closely related taxa (Hill 2006; Krmpotic et al. 2009; Castro et al. 2013). With respect to the taxonomy of Dasypodini, we primarily assume that *Propraopus grandis* and *P sulcatus* are valid, although a study by some of the authors favours the synonymisation of both species (Castro et al. in press).

Comparisons were based mostly on direct observations, but also on published accounts. Material deposited in the following institutions was analysed: AMNH, American Museum of Natural History; MEPN, Museo de Historia Natural 'Gustavo Orcés'; Escuela Politécnica Nacional, Quito, Ecuador; IGM, INGEOMINAS, Bogotá, Colombia; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MNRJ, Museu Nacional, Rio de Janeiro, Brazil. The examined material that provided the main basis for comparison is as follows: *Nanoastegotherium prostatum*, IGM 183912 (holotype); *A. hondanus*, IGM 183499 (holotype), 183320, 183448, 183722, 183862; *D. punctatus*: MN 552-V, MCN-PV 009, 014; *D. hybridus*: MLP 1-I-03-65, 1-I-03-67, 1-I-03-69, 1-I-03-70, 3-X-94-3, 3-X-96-1; *D. kappleri*: MZUSP 8950, 24798, AMNH 136251, 136253, 267011, 76573; *D. novemcinctus*: MCN-MA 99, 986, 2788, 2836, 3021, MZUSP 7996, 10431, 13800, 13801, 20189; *D. septemcinctus*: MZUSP 5111, 8111, 19983, 19984; *P. grandis*: MACN 1610, 1630, 7027, 17989, MACN-A 1170, 10989, 11108, MLP 58-IX-3-26, 69-IX-9-9, 90-V-1-4; *P. sulcatus*: photos in Winge (1915: pl. V.3, 4).

3. Systematic paleontology

Xenarthra Cope, 1889

Cingulata Illiger, 1811

Dasypodidae Gray, 1821

Dasypodinae Gray, 1821

Dasypodini Gray, 1821

Anadasypus Carlini, Vizcaíno and Scillato-Yané, 1997

Type species. *Anadasypus hondanus* Carlini, Vizcaíno and Scillato-Yané, 1997.

Included species. The type species and the species described herein.

Diagnosis (emended from Carlini et al. 1997). Size similar to *D. novemcinctus*. At least six movable bands (7 in *Propraopus*, 6–11 in *Dasypus*). Quadrangular to hexagonal buckler osteoderms (commonly hexagonal in *Propraopus* and *Dasypus*); 6.5–9.5 mm long and 6–7.5 mm wide, with an approximately lageniform (bottle shaped) main figure; two to five foramina in the principal sulcus, which is restricted to the anterior half of the osteoderm (sub-circular principal sulcus in *Propraopus* and *Dasypus*, never reaching the posterior margin); three anterolateral peripheral figures (three to six anterior, lateral and posterior peripheral figures in *Propraopus* and

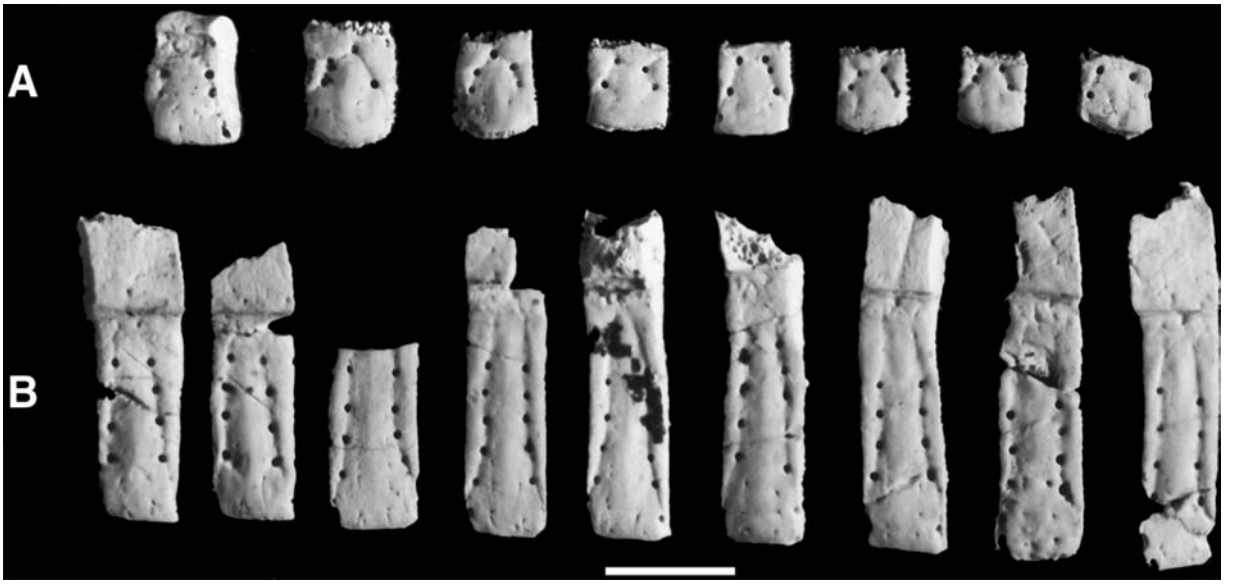

Figure 3. Osteoderms of *A. aequatorianus*. (A) Buckler osteoderms; (B) movable osteoderms.

Dasypus). Movable osteoderms 25–33 mm long and 6–9 mm wide with sub-rectangular main figure; three to five foramina in each sulcus delimiting the main figure (two to four in *Propraopus*, three to nine in *Dasypus*), and one or two foramina in the posterior margin (generally three in *Propraopus* and four in *Dasypus*). Caudal tube composed of rings with two rows of osteoderms without peripheral figures (peripheral figures present in the anterior row of each caudal ring in *Propraopus* and *Dasypus*).

***Anadasypus aequatorianus* sp. nov.** (Figure 3)

Differential diagnosis. Movable and buckler osteoderms with smooth main figures, lacking a longitudinal keel (present in *A. hondanus*); four or five foramina in the principal sulci of movable osteoderms (three or four in *A. hondanus*); buckler osteoderms with main figure less lageniform than in *A. hondanus* (Figure 4).

Derivation of name. Derived from the country of origin, Ecuador.

Holotype. MEPN 4363, 12 movable, 1 semi-movable and 10 buckler osteoderms of the carapace of a single individual.

Referred material. The holotype and MEPN 4361, three fragmentary movable osteoderms, also from RHM Locality 4.

Occurrence. RHM Locality 4, Tambo Viejo, Letrero Formation, Nabón Basin, about 2 km south-east of Nabón, Azuay Province, Ecuador (approximately 3°20′S and 79°03′W) (Figure 1).

3.1 Comparative description

Size comparable to *A. hondanus* and *D. novemcinctus*. As in other cingulates, the buckler osteoderms have variable

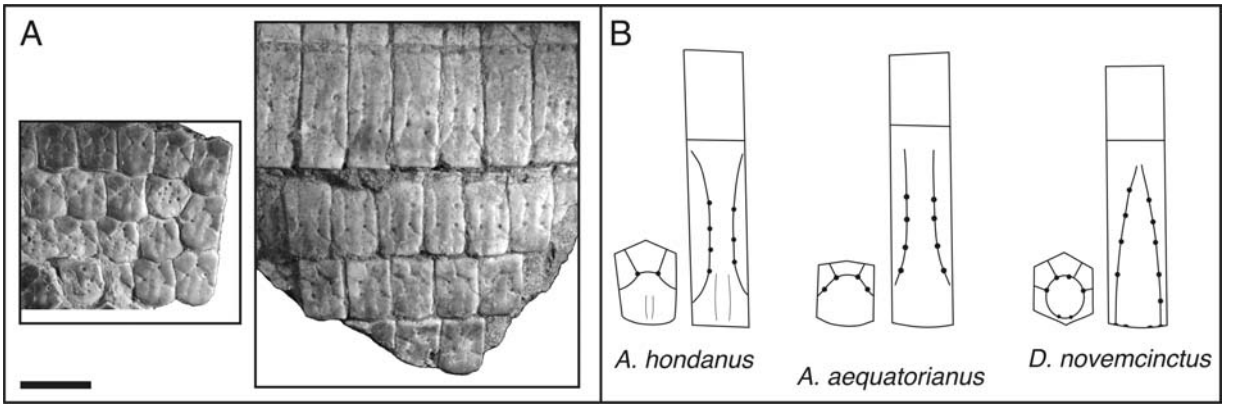

Figure 4. (A) Carapace fragments of *A. hondanus*; (B) schematic line drawings of buckler and movable osteoderms of *A. hondanus*, *A. aequatorianus* and *D. novemcinctus*.

morphology, depending upon their position on the carapace. Their surface is smooth and the borders are dentate and somewhat concave, except for the posterior border, which is convex and rounded. Although some are clearly hexagonal, most are quadrangular; in this matter, *Anadasypus* differs from both *Dasypus* and *Propraopus*, which have mostly hexagonal and clearly isodiametrical buckler osteoderms. The main figure is delimited by a shallow principal sulcus and pierced by several small foramina. Four to six (generally four) foramina occur on the principal sulcus, inclusive at the intersection with the radial sulci. These separate three anterior peripheral figures, which laterally occupy only the anterior half of the osteoderm. On the posterior margin, there are up to 11 foramina, much smaller than those of *Dasypus* (probably neurovascular). The buckler osteoderms of *A. aequatorianus* have a less lageniform (i.e. the neck of the bottle-shaped figure is wider), resulting in a more isodiametrical main figure than *A. hondanus* and lack the longitudinal keel on the main figure. Their size is approximately 6.5–9.5 mm long, 6.0–7.5 mm wide and 2.9–4.1 mm thick.

The exposed part of movable osteoderms is smooth and presents a triangular to lageniform main figure, with a very elongated neck. On the posterior third of the main figure, there are two parallel longitudinal lines of small foramina, as in *Dasypus* and *Propraopus*. Two shallow sulci separate the main figure from the two thin lateral peripheral figures. Approximately at the posterior fourth of the main figure, these sulci reach the lateral margin of the osteoderm and run contiguous with it until the posterior margin of the osteoderm. In each sulcus, there are four to five foramina, as large as those of the buckler osteoderms, and the most posterior one occurs by the lateral margin of the osteoderm. Along the posterior margin of the osteoderms, there is a non-aligned series of small neurovascular foramina; one or two larger foramina may occur at the intersection of the principal sulci with the posterior border. This pattern differs from that of the species of *Dasypus*, which have approximately four large foramina, two of which at the intersection with each principal sulcus, and also differs from the pattern of *Propraopus*, which usually displays three foramina, one central and two laterals, at the intersection with each sulcus. The surface of the peripheral figures is wrinkled. The lateral margins are dentate, except for the anterior overlapping articulation. The depression between the anterior articulation and the ornamented portion shows some delicate grooves and commonly a central foramen. The movable osteoderms are approximately 27.5–33.0 mm long, 6.3–9.0 mm wide and 3.7–4.2 mm thick at the overlapping anterior articulation.

The semimovable osteoderm, from the nuchal region, is 12.0 mm long, 8.2 mm wide and 4.2 mm thick. This osteoderm is most probably from the right side of the carapace, the left margin being bevelled towards the inside, and the right towards the outside. It displays six large foramina in the sulci surrounding the main figure (four in the right and two in the left sulcus). The posterior margin is concave, in the form of a trough or groove. The anterior overlapping articulation is very short and rounded.

3.2 *Phylogenetic affinities of* A. aequatorianus

To test the affinities of *A. aequatorianus* within the tribe, we conducted a phylogenetic study presented below (Appendices 1 and 2). The outgroup taxon is *Nanoastegotherium*, a derived Astegotheriini from the middle Miocene of La Venta, whereas ingroup taxa represent Dasypodini. Most characters are based on a previous analysis (Castro et al. 2013), and six new characters (19–24) were added. Ten are related to the cranial anatomy and 14 are related to the osteoderms; five characters were defined as multistate. With the maximum parsimony criterion, an exact analysis was conducted using TNT 1.1 (Goloboff et al. 2008). With multistate characters treated as non-additive, one most parsimonious tree (MPT) was found (tree length = 34; Figure 5). Considering these characters as additive, we found two MPTs that preserve the positions of the genera, differing on the relationship among *D. punctatus*, *D. kappleri* and *D. novemcinctus*. This analysis implies that: (1) the three known genera of Dasypodini (*Anadasypus*, *Propraopus* and *Dasypus*) are supported by apomorphic characters; (2) *Anadasypus* is more basal than *Propraopus* and *Dasypus*, in concordance with the stratigraphic evidence and (3) the sister–taxon relationship of *A. hondanus* and *A. aequatorianus* indicates that the attribution of the former to genus *Anadasypus* is correct.

4. Discussion and conclusion

Although the fact that the material from Ecuador is not abundant, it clearly represents a distinct species, using the same criteria that demarcate living species of *Dasypus* with respect to the morphology of the osteoderms. The genus *Anadasypus* was recognised as the potential structural ancestor of *Propraopus* and *Dasypus* (Vizcaíno 1990; Carlini et al. 1997). *Anadasypus* also shares similarities with the Astegotheriini: the buckler osteoderms lack posterolateral and posterior peripheral figures, which are present in *Dasypus* and *Propraopus* (Carlini et al. 1997). In *A. hondanus*, the main figure of buckler osteoderms is somewhat lageniform and displays a longitudinal keel, as in some Astegotheriini. On the other hand, the few osteoderms available for *A. aequatorianus* are more isodiametrical and lack that keel, as in the species of *Dasypus* and *Propraopus*.

Other undescribed cingulates recovered in the same locality are a new Lomaphorini glyptodont, based on poorly preserved portions of the carapace, and a new basal Hoplophorini glyptodont, which preserves osteoderms and

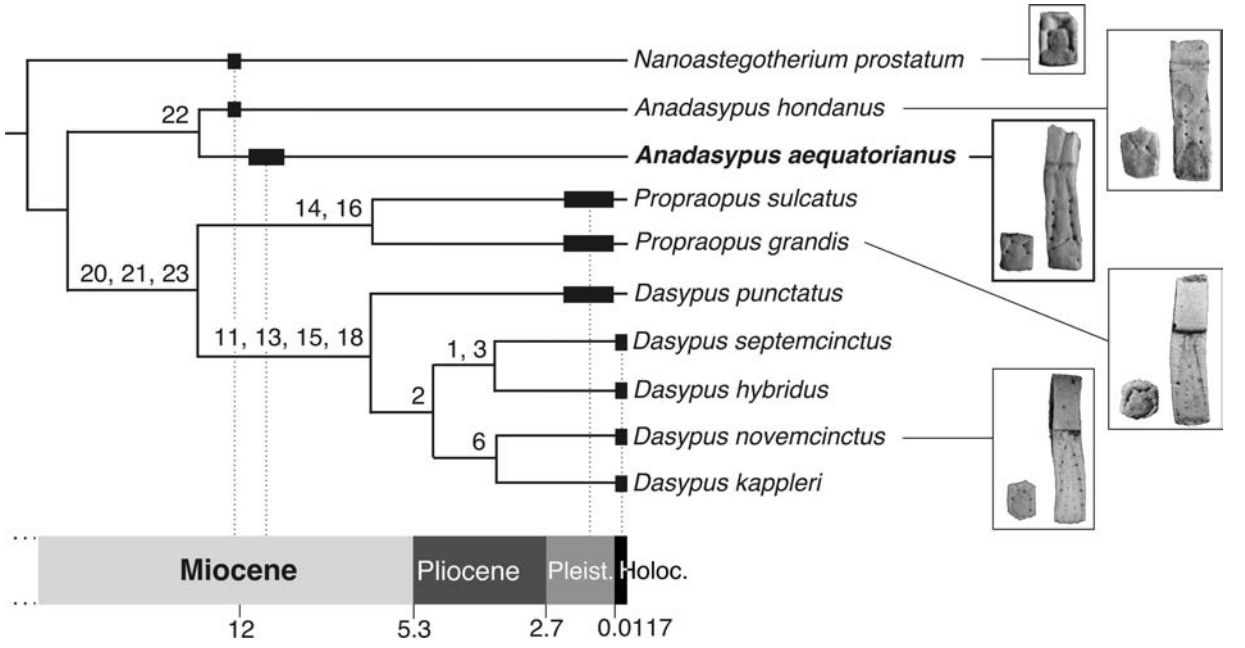

Figure 5. MPT resulting from the cladistic analysis of Dasypodini. The most relevant morphology for each genus in the comparisons is shown on the right side. Apomorphic characters are found in each node according to the numbers assigned in Appendix 2. Chronological distribution of taxa is represented by black rectangles.

cranial remains. Material assigned to a new caviomorph, a new toxodont, and a litoptern were also collected in this locality (AAC and RHM, personal observation).

Comparisons among the cingulates of Letrero Formation (see Carlini et al. 1989) and the known temporal span of their sister-taxa elsewhere in South America support a late Miocene correlation. It indicates that Letrero Formation postdates the middle Miocene fauna of La Venta, with possible correlations with the late Miocene 'Mayoan' and Chasicoan SALMAs (Zárate et al. 2007; De Iuliis et al. 2008). Also, the age estimations for the Letrero Formation predominantly confirm that the mammals from this stratum are younger than those of the Laventan SALMA.

The faunas from tropical Andean areas are very different from others in South America, sharing no species and few genera with well-known assemblages from classic sequences in Patagonia and elsewhere (Kay et al. 1997; Flynn and Wyss 1998; Croft 2007). It suggests that the biogeographical provinciality of modern South America was present at least as early as 13 Mya (Madden et al. 1997; Croft et al. 2007). Despite some recent work (Carlini and Scillato-Yané 1999; Carlini et al. 2008; Ciancio et al. 2013), Paleogene and Miocene dasypodids from tropical and subtropical areas are still scarce, as most remains come from the Argentinean Patagonia. Consequently, the taxon described herein helps to fill a void. In the Miocene of Patagonia, Euphractini and Eutatini occur along with Peltephilidae and Stegotheriini during the mid Miocene; those taxa are absent in Colombia and Ecuador (Carlini et al. 1997). On the other hand, Astegotheriini, Tolypeutinae and Dasypodini are exclusively recorded in low latitudes during that time (Carlini et al. 1997). It is also interesting to note that *Nanoastegotherium*, the latest record of Astegotheriini, is present in the same locality where Dasypodini is first recorded.

Anadasypus hondanus and *A. aequatorianus* occur in a geographically distant region from that of the oldest records of *Dasypus* and *Propraopus*. Despite that range, an analysis of the geochronological distribution of Dasypodinae shows that the group was restricted to tropical and subtropical environments. At present, *Dasypus* occupies distinct biomes in a wide range of latitudes in the American continent (Wetzel 1985; Aguiar and da Fonseca 2008), suggesting that its distribution is more limited by temperature and humidity than vegetal matrix. Also, the diversity and the size of the taxon increase at lower latitudes (Wetzel 1985).

Acknowledgements

We are grateful to N.B. Simmons and J. Meng (AMNH), A. Kramarz (MACN), J. Ferigolo and M. Jardim (MCN), A. I. Olivares, D. Verzi and M. Reguero (MLP), S.A.K. de Azevedo and D. Henriques (MNRJ) for allowing the study of material under their care.

Funding

UNLP N-593 (to AAC) and CAPES BEX 0840/10-6 (to MCC) supported this research.

References

Abrantes ÉAL, Bergqvist LP. 2006. Proposta filogenética para os Dasypodidae (Mammalia: Cingulata). In: Gallo V, Brito PM, Silva HMA, Figueiredo FJ, editors. Paleontologia de vertebrados: grandes temas e contribuições científicas. Rio de Janeiro, Brazil: Interciências. p. 261–274.

Aguiar JM, da Fonseca GAB. 2008. Conservation status of the Xenarthra. In: Vizcaíno SF, Loughry WJ, editors. The biology of the Xenarthra. Gainesville, FL: University Press of Florida. p. 215–231.

Ameghino F. 1881. La antiguedad del hombre en el Plata. Vol 2. Paris: Masson-Igon Hermanos.

Ameghino F. 1902. Notices préliminaires sur des mammiféres nouveaux des terrains crétacés de Patagonie. Bol Acad Nac Cienc Córdoba. 17:5–73.

Anthony HE. 1922. A new fossil rodent from Ecuador. Am Mus Novit. 35:1–4.

Bergqvist LP, Abrantes ÉAL, Avilla LS. 2004. The Xenarthra (Mammalia) of São José de Itaboraí Basin (upper Paleocene, Itaboraian), Rio de Janeiro, Brazil. Geodiversitas. 26:323–337.

Candela A, Nasif NL. 2006. Systematics and biogeographic significance of Drytomomys typicus (SCALABRINI in AMEGHINO, 1889) nov. comb., a Miocene Dinomyidae (Rodentia, Hystricognathi) from Northeast of Argentina. N Jb Geol Paläontol Abh. 3:165–181.

Carlini AA, Ciancio MR, Scillato-Yané GJ. 2010. Middle Eocene-Early Miocene Dasypodidae (Xenarthra) of southern South America: faunal succession at Gran Barranca-biostratigraphy and paleoecology. In: Madden RH, Carlini AA, Vucetich MG, Kay RF, editors. The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia. Cambridge: Cambridge University Press. p. 106–129.

Carlini AA, Scillato-Yané GJ. 1999. Evolution of Quaternary Xenarthrans (Mammalia) of Argentina. Quat S Am Antarct Penins. 12:149–175.

Carlini AA, Vizcaíno SF, Scillato-Yané GJ. 1989. Novedosos Cingulata (Mammalia, Xenarthra) del Mioceno de Ecuador. Actas del VI Jornadas Argentinas de Paleontología de Vertebrados; San Juan, Argentina.

Carlini AA, Vizcaíno SF, Scillato-Yané GJ. 1997. Armored xenarthrans: a unique taxonomic and ecologic assemblage. In: Kay RF, Madden RH, Cifelli R, Flynn JJ, editors. Vertebrate paleontology in the neotropics: the Miocene fauna of La Venta, Colombia. Washington, DC: Smithsonian Institution Press. p. 213–226.

Carlini AA, Zurita AE, Scillato-Yané GJ, Sanchez R, Aguilera OA. 2008. New Glyptodont from the Codore Formation (Pliocene), Falcón State, Venezuela, its relationship with the Asterostemma problem, and the paleobiogeography of the Glyptodontinae. Palaeontol Z. 82:139–152.

Castellanos A. 1925. Un nuevo dasipodino extinguido en la parte meridional de Bolívia, *Dasypodon atavus* n. g. et n. sp. Ann Mus Nac Hist Nat B Aires 'Bernardino Rivadavia'. 33:255–285.

Castro MC, Avilla LS, Freitas ML, Carlini AA. in press. The armadillo *Propraopus sulcatus* (Mammalia: Xenarthra) from the late Quaternary of northern Brazil and a revised synonymy with *Propraopus grandis*. Quat Int.

Castro MC, Ribeiro AM, Ferigolo J, Langer MC. 2013. Redescription of *Dasypus punctatus* Lund, 1840 and considerations on the genus *Propraopus* Ameghino, 1881 (Xenarthra, Cingulata). J Vert Paleontol. 33:434–447.

Ciancio MR. 2010. Los Dasypodoidea (Mammalia, Xenarthra) del Deseadense (Oligoceno) de América del Sur. Su importancia filogenética y bioestratigráfica [PhD thesis]. La Plata, Argentina: Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Ciancio MR, Carlini AA, Campbell KE, Scillato-Yané GJ. 2013. New paleogene cingulates (Mammalia, Xenarthra) from Santa Rosa, Perú and their importance in the context of South American faunas. J Syst Palaentol. 11:727–741.

Cope ED. 1889. The Edentata of North America. Am Nat. 23:657–664.

Croft DA. 2007. The middle Miocene (Laventan) Quebrada Honda Fauna, southern Bolivia, and a description of its notoungulates. Paleontology. 50:277–303.

Croft DA, Flynn JJ, Wyss AR. 2007. A new basal glyptodontid and other Xenarthra of the early Miocene Chucal fauna, Northern Chile. J Vert Paleontol. 27:781–797.

De Iuliis G, Brandoni D, Scillato-Yané GJ. 2008. New remains of *Megathericulus patagonicus* Ameghino, 1904 (Xenarthra, Megatheriidae): information on primitive features of megatheriines. J Vert Paleontol. 28:181–196.

Delsuc F, Superina M, Tilak MK, Douzery EJP, Hassanin A. 2012. Molecular phylogenetics unveils the ancient evolutionary origins of the enigmatic fairy armadillos. Mol Phylogenet Evol. 62:673–680.

Edmund AG. 1965. A late Pleistocene fauna from the Santa Elena Peninsula, Ecuador. R Ont Mus Life Sci Contrib. 63:1–21.

Flynn JJ, Wyss AR. 1998. Recent advances in South American mammalian paleontology. Trends Ecol Evol. 13:449–454.

Gaudin TJ, Wible JR. 2006. The phylogeny of living and extinct armadillos (Mammalia, Xenarthra, Cingulata): a craniodental analysis. In: Carrano MT, Gaudin TJ, Blob RW, Wible JR, editors. Amniote paleobiology: perspectives on the evolution of mammals, birds and reptiles. Chicago, IL: University of Chicago Press. p. 153–198.

Goloboff P, Farris J, Nixon K. 2008. TNT: a free program for phylogenetic analysis. Cladistics. 24:774–786.

Gray JE. 1821. On the natural arrangement of vertebrose animals. Lond Med Repos. 15:296–310.

Hill RV. 2006. Comparative anatomy and histology of xenarthran osteoderms. J Morphol. 267:1441–1460.

Hoffstetter R. 1952. Les Mammifères pléistocènes de la Republique de l'Equateur. Mem Soc Geol Fr, Nouv Ser. 31:1–391.

Hoffstetter R. 1958. Xenarthra. In: Piveteau J, editor. Traité de paléontologie. Paris, France: Masson. p. 535–636.

Hungerbühler D, Steinmann M, Winkler W, Seward D, Egüez A, Heller F, Ford M. 1995. An integrated study of fill and deformation in the Andean intermontane basin of Nabón (Late Miocene), southern Ecuador. Sediment Geol. 96:257–279.

Hungerbühler D, Steinmann M, Winkler W, Seward D, Egüez A, Peterson DE, Helg U, Hammer C. 2002. Neogene stratigraphy and Andean geodynamics of southern Ecuador. Earth-Sci Rev. 57:75–124.

Illiger C. 1811. Prodromus Systematis Mammalium et Avium additis terminis zoographicis utriudque classis. Berlin, Germany: C Salfeld.

Kay RF, Madden RH, Cifelli RL, Flynn JJ. 1997. Vertebrate paleontology in the neotropics: the Miocene fauna of La Venta, Colombia. Washington, DC: Smithsonian Institution Press.

Krmpotic CM, Ciancio MR, Barbeito C, Mario RC, Carlini AA. 2009. Osteoderm morphology in recent and fossil euphractine xenarthrans. Acta Zool-Stockholm. 90:339–351.

Linnaeus C. 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Vol. 1 10th ed. Stockholm, Sweden: Laurentii Salvii.

Madden RH, Guerrero J, Kay RF, Flynn JJ, Swisher CCIII, Walton AH. 1997. The Laventan Stage and Age. In: Kay RF, Madden RH, Cifelli R, Flynn JJ, editors. Vertebrate paleontology in the neotropics: the Miocene fauna of La Venta, Colombia. Washington, DC: Smithsonian Institution Press. p. 499–519.

Marshall LG, Sempere T. 1991. The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: a review. In: Suárez-Soruco R, editor. Fósiles y facies de Bolivia – Vol. I. Vertebrados. Santa Cruz, Bolivia: Yacimentos Petrolíferos Fiscales Bolivianos. p. 631–652.

McKenna MC, Bell SK. 1997. Classification of mammals above the species level. New York, NY: Columbia University Press.

Oliveira ÉV, Bergqvist LP. 1998. A new Paleocene armadillo (Mammalia, Dasypodoidea) from the Itaboraí Basin, Brazil. In: Paleógeno de América del Sur y de la Península Antártica. Asoc Paleontol Argent Publ Espec. 5:35–40.

Oliveira ÉV, Pereira JC. 2009. IIntertropical cingulates (Mammalia, Xenarthra) from the Quaternary of Southern Brazil: systematic and paleobiogeographical aspects. Rev Bras Paleontol. 12:167–178.

Ortiz-Jaureguizar E, Cladera GA. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. J Arid Environ. 66:498–532.

Paula-Couto C. 1979. Tratado de Paleomastozoologia. Rio de Janeiro, Brazil: Academia Brasileira de Ciências.

Paula-Couto C. 1982. Pleistocene armadillo from Cantagalo, State of Rio de Janeiro. Iheringia Ser Geol. 7:65–68.

Repetto F. 1977. Un mamífero fósil nuevo en el Terciario del Ecuador (Azuay, Cañar). Tecnológica, Escuela Politécnica del Litoral, Guayaquil. 1:33–38.
Rincón AD, White RS, McDonald HG. 2008. Late Pleistocene cingulates (Mammalia: Xenarthra) from Mene de Inciarte tar pits, Sierra de Perijá, western Venezuela. J Vert Paleontol. 28:197–207.
Scillato-Yané GJ. 1976. Dasypodidae from Riochican of Itaboraí (Brazil). An Acad Bras Cienc. 48:527–530.
Scillato-Yané GJ. 1982. Los Dasypodidae (Mammalia, Edentata) del Plioceno y Pleistoceno de Argentina [PhD thesis]. La Plata, Argentina: Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.
Scillato-Yané GJ. 1986. Los Xenarthra fósiles de Argentina (Mammalia, Edentata). Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía; Mendoza, Argentina.
Scillato-Yané GJ, Góis F, Zurita AE, Carlini AA, González Ruiz LR, Krmpotic CM, Oliva C, Zamorano M. in press. Los Cingulata (Mammalia, Xenarthra) del 'Conglomerado Osífero' (Mioceno tardío) de la Formación Ituzaingó, Entre Ríos, Argentina. Asociación Paleontológica Argentina. Publicación Especial.
Simpson GG. 1948. The beginning of the age of mammals in South America. Part I. Introduction, Edentata, Condylarthra, Litopterna, and Notioprotogonia. Bull Am Mus Nat Hist. 91:1–232.
Spillman F. 1931. Die Säugetiere Ecuadors im Wandel der Zeit (I. Teil). Quito, Ecuador: Universidad Central.
Tauber AA. 1997. Paleoecología de la Formación Santa Cruz (Mioceno Inferior) en el extremo sudeste de la Patagonia. Ameghiniana. 34:517–529.
Tejedor MF, Goin FJ, Gelfo JN, Lopez G, Bond M, Carlini AA, Scillato-Yané GJ, Woodburne MO, Chornogubsky L, Aragon E, et al., 2009. New Early Eocene mammalian fauna from western Patagonia, Argentina. Am Mus Novit. 3638:1–43.
Vizcaíno SF. 1990. Sistemática y evolución de los Dasypodinae Bonaparte, 1838 (Mammalia, Dasypodidae) [PhD thesis]. La Plata, Argentina: Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.
Vizcaíno SF. 1994. Systematics and anatomy of the Astegotheriini Ameghino 1906 (new rank) (Xenarthra, Dasypodidae, Dasypodinae). Ameghiniana. 31:3–13.
Webb S. 2006. The Great American biotic interchange: patterns and processes. Ann Mo Bot Gard. 93:245–257.
Wetzel RM. 1985. Taxonomy and distribution of armadillos. In: Montgomery GG, editor. The evolution and ecology of Armadillos, Sloths, and Vermilinguas. Washington, DC: Smithsonian Institution. p. 23–46.
Wilson DE, Reeder DM. 2005. Mammals species of the world: a taxonomic and geographic reference. 3rd ed. Baltimore, MD: Johns Hopkins University Press.
Wolf T. 1892. Geografía y geología del Ecuador. Leipzig, Germany: FA Brockhaus.
Zárate MA, Schultz PH, Blasi A, Heil C, King J, Hames W. 2007. Geology and geochronology of type Chasicoan (late Miocene) mammal-bearing deposits of Buenos Aires (Argentina). J S Am Earth Sci. 23:81–90.

Appendix 1

List of character and character states used in the cladistic analysis. Characters 1–18 are reproduced or modified from Castro et al. (2013).

(1) Condylobasal length (mm): <78 [0]; 78–111 [1]; 111–160 [2]; over 160 [3].
(2) Relative position of infraorbital foramen versus anterior border of the lacrimal: infraorbital foramen anterior [0]; both at same position or infraorbital foramen posterior [1].
(3) Dorsal contour of the rostrum in lateral view: nearly straight [0]; sigmoid [1].
(4) Length of upper tooth row (with all molariforms erupted) in relation to the maxillary length at ventral midsagittal line: $<60\%$ [0]; 60–70% [1]; over 70% [2].
(5) Posterior palatal border: long and narrow [0]; long and broad [1]; short and broad to straight [2].
(6) Posterior palatal angle (measured between the posterior-most point of the interpalatine suture and the posterior-most medial free border of the palate): $<80°$ [0]; over 80° [1].
(7) Posterolateral border of palate strongly keeled: absent [0]; present [1].
(8) Condition of palatine: with longitudinal wrinkle and lateral narrowing [0]; completely flat [1].
(9) Length of infraorbital canal in relation to antero-posterior dimension of lacrimal: $<40\%$ [0]; 40–60% [1]; over 60% [2].
(10) Width of temporal fossa in relation to cranial width at the level of the frontoparietal suture: $<9\%$ [0]; 9% and over [1].
(11) Foramina in principal sulcus of buckler osteoderms: restricted to cranial half [0]; all over the sulcus [1].
(12) Remarkably large foramina in principal sulcus of buckler osteoderms: absent [0]; present at least in some [1].
(13) Number of foramina in the principal sulcus of buckler osteoderms: never >5 [0]; at least some osteoderms with >5 [1].
(14) Foramina in the principal sulcus of buckler osteoderms: never in the intersection with the radial sulcus [0]; at least some osteoderms with one or more foramina in the intersection with the radial sulcus [1].
(15) Principal sulci in ornamented portion of movable osteoderms: anteriorly free in all osteoderms [0]; anteriorly connected in some osteoderms [1].
(16) Foramina anterior to principal sulcus/sulci in ornamented portion of movable osteoderms: absent [0]; present in at least some osteoderms [1].
(17) Total number of foramina in the principal sulcus/sulci of movable osteoderms: never >7 [0]; at least some osteoderms with >7 and <13 [1]; at least some osteoderms with >13 [2].
(18) Number of piliferous foramina in the posterior border of movable osteoderms: never >3 [0]; at least some osteoderms with 4 or more [1].
(19) Longitudinal keel in the main figure of osteoderms: absent [0]; present [1].
(20) Contour of main figure of buckler osteoderms: approximately lageniform [0]; subcircular [1].
(21) Outer contour of buckler osteoderms commonly: quadrangular [0]; hexagonal [1].
(22) Rounded posterior border of buckler osteoderms: absent [0]; present [1].

(23) Distribution of peripheral figures in buckler osteoderms: only anterior and lateral [0]; anterior, lateral and posterior [1].
(24) Sulci in the movable osteoderms: diverging and becoming confluent with the lateral margin [0]; reaching the posterior border of the osteoderm [1].

Appendix 2

Character–taxon matrix used in the cladistic analysis. (?), missing data.

N. prostatum	??????????	0101???00	000?
A. hondanus	??????????	0001010010	0101
A. aequatorianus	??????????	0001010000	0101
P. grandis	30??100000	0100001001	1010
P. sulcatus	??????????	0100001001	1210
D. punctatus	2012101 1??	1011112101	1010
D. hybridus	0101000011	1011111101	1010
D. kappleri	2110211111	10111?1101	1010
D. novemcinctus	1111210011	1011111101	1010
D. septemcinctus	0101??0021	?0?1??0101	1010