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Original article

New fossil records of *Tapirus* (Mammalia, Perissodactyla) from Brazil, with a critical analysis of intra-generic diversity assessments based on lower molar size variability☆

Nouveaux fossiles de Tapirus *(Mammalia, Perissodactyla) du Brésil, avec une analyse critique des estimations de diversité intra-génériques basées sur la variabilité de taille des molaires inférieures*

Fernando A. Perini, João A. Oliveira, Leandro O. Salles *, Carlos R. Moraes Neto, Patrícia G. Guedes, Luiz Flamarion B. Oliveira, Marcelo Weksler

Museu Nacional/UFRJ, Departamento de Vertebrados, Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brazil

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Abstract

A large set of South American fossils belonging to the genus *Tapirus* has been described on the basis of differences in size and proportions of lower molariform teeth. Nevertheless, the reliability of dental proportions for the diagnosis of fossil tapir species is controversial. In this paper, we describe new fossil material of *Tapirus* from the Quaternary of Serra da Bodoquena, Southwestern Brazil, comparing it to other fossil and extant specimens of the genus by means of multivariate morphometric analyses of lower molariform teeth linear dimensions. The results of Principal Component Analyses indicate that some of the extant and extinct material attributed to *Tapirus* fall within the range of variation in size and proportions of lower molariform teeth exhibited by recent species of the genus. Therefore, part of the fossil material attributed to new species or to *Tapirus* sp. may be referable to the extant species *Tapirus terrestris*. We conclude that the sole use of lower molariform teeth size and proportions to erect new species of *Tapirus* may not be reliable, and therefore we advocate caution when describing fossil tapirs exclusively based on these criteria.

Keywords: South America; Quaternary; Dentition; *Tapirus*; Taxonomy; Multivariate analysis

Résumé

De nombreux fossiles sud-américains du genre *Tapirus* ont été décrits à partir de la différence des tailles et des proportions des dents molariformes inférieures. Néanmoins, la fiabilité des proportions dentaires pour la diagnose des espèces de tapirs fossiles est controversée. Dans cet article, de nouveaux fossiles attribués au genre *Tapirus* sont décrits du Quaternaire de la Serra da Bodoquena, sud-ouest brésilien. L'analyse morphométrique multivariée du dentaire nous permet de constater une large part de variation individuelle non imputable à l'origine géographique des échantillons. En outre, une série d'analyses en composante principale indique que la taille et les proportions des dents molariformes inférieures chez quelques espèces actuelles et éteintes de *Tapirus* s'insèrent dans la variation observée pour l'espèce actuelle *Tapirus terrestris*. En conséquence, de nombreux échantillons attribués à de nouvelles espèces, ou simplement à *Tapirus* sp., pourraient, en réalité, appartenir à *T. terrestris*. Nous invitons à plus de prudence à l'égard des descriptions de nouvelles espèces de *Tapirus* basées sur les seules dents jugales.

Mots clés : Amérique du Sud ; Quaternaire ; Dentition ; *Tapirus* ; Taxonomie ; Analyse multivariée

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* Corresponding author.
E-mail address: losalles@mn.ufrj.br (L.O. Salles).

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1. Introduction

The genus *Tapirus* Brisson, 1762 is currently the only representative of the family Tapiridae and includes four extant species (Grubb, 2005): *T. terrestris* (Linnaeus, 1758), *T. indicus* Desmarest, 1819, *T. bairdii* (Gill, 1865) and *T. pinchaque* (Roulin, 1829). Several additional fossil species are recognized for the genus, with the earlier records dating from the Miocene of Europe and North America (Guérin and Eisenmann, 1994; Colbert and Schoch, 1998). In South America, the first records of tapirs appear at the onset of the Great American Biotic Interchange, with remains dating from the early Pleistocene of Argentina (Tonni, 1992; Ferrero and Noriega, 2007). Although currently represented by three extant species in this continent (*T. bairdii*, *T. pinchaque*, *T. terrestris*), the genus seems to have harbored a considerably higher diversity in the South American Pleistocene (Holanda and Cozzuol, 2006; Ferrero and Noriega, 2007). Seven extinct species have been described so far: *T. tarijensis* Ameghino, 1902, *T. cristatellus* Winge, 1906, *T. dupuyi* Ameghino, 1916, *T. australis* Rusconi, 1928, *T. rioplatensis* Cattoi, 1957, *T. oliverasi* Ubilla, 1983 and *T. mesopotamicus* Ferrero and Noriega, 2007. In addition, unnamed forms identified only as "*Tapirus* sp." are frequently mentioned in the literature (Ubilla, 1983; Sedor et al., 2004; Holanda and Cozzuol, 2006).

On the course of the exploration of a rich Holo-Pleistocene mammal fauna associated to the Bodoquena Karst, Mato Grosso do Sul State (Brazil) (Salles et al., 2006), new *Tapirus* remains were unveiled. As usual for the genus, most of the fossils consisted of dental and mandibular fragments, but some upper dentition and postcranial material were also recovered. During the identification process, the difficulties and inconsistencies of the use of dental variability as diagnostic characters for South American tapirs became evident.

Although skull characters are clearly diagnostic for different tapir species, with some authors even suggesting that they might indicate generic differentiation in modern species (Hershkovitz, 1954), the genus *Tapirus* is known to have uniform dental morphology (Colbert and Schoch, 1998). This problematic issue has not prevented the description of new fossil species based exclusively on dental attributes, mainly because detached mandibles and lower teeth comprise the majority of the fossil remains of *Tapirus* (Ray, 1964; Ubilla, 1983; Agenbroad and Downs, 1984; Tonni, 1992; Tong, 2005; Holanda and Cozzuol, 2006). In fact, most of the fossil forms were described solely on the basis of mandibular fragments and lower molariform teeth: of the seven extinct South American species, only two were based on material other than lower dentition and mandible fragments, namely *T. cristatellus* and *T. mesopotamicus*. In addition, most comparisons with fossil material are undertaken with limited sample sizes. The shortcomings of such sample limitations are evident when the extant *T. terrestris* is taken as a reference for comparisons, since this species shows a highly variable body size and a wide geographic distribution (Hershkovitz, 1954). Discussing the taxonomy of fossils tapirs, Simpson (1945) had already warned that most size-based dental differences might not be a reliable character information for diagnostic purposes.

Thereby, the present study is undertaken with two aims:

- to provide descriptions of the new fossil material of *Tapirus* recovered from Southwestern Brazil;
- to critically analyze the dental morphometric criteria frequently employed to distinguish and diagnose new fossil species attributed to this genus in South America.

2. Material and methods

2.1. Geological setting and associated fauna

The Serra da Bodoquena (19° 48′–22° 16′ S, 56° 32′–57° 24′ W) is located at the southeastern part of the Mato Grosso do Sul State, harboring the municipalities of Jardim, Bonito, Bela Vista, Porto Murtinho, and Bodoquena (Fig. 1). A more detailed description of its geological and phytogeographic settings can be found in Boggiani and Coimbra (1995) and Salles et al. (2006). Few studies concerning the Quaternary period have been conducted in the region, namely the restricted studies of Almeida (1965) and the chartered speleological studies of Mendes (1957), Gnaspini et al. (1994), and Ayub et al. (1996). There are hundreds of caves in the Serra da Bodoquena Karst, but no more than 50 have been formally described and mapped (Gnaspini et al., 1994; Ayub et al., 1996).

The fossil tapirs were recovered from two underwater caves, namely "Caverna do Japonês" (21° 35′ 63″ S, 56° 39′ 59″ W) and "Nascente do Formoso" (21° 15′ 35″ S, 56° 38′ 26″ W). Age of specimens presumably ranges from latest Pleistocene to mid-Holocene. Dating of the collagen extracted from a ground sloth from a dry cave of the Bodoquena Karst resulted in an age estimate of 9960 ± 60 BP (unpublished result), but the material from the submerged caves likely represent a mixed assemblage from different horizons. Numerous fossil mammals typical of the South American Quaternary have been found in the clayey sedimentary layers associated to the tapir fragments here described; these include xenarthrans (*Dasypus*, *Euphractus*, *Propaopus*, *Pampatherium*, *Glossotherium*, *Mylodonopsis*, *Eremotherium* and *Glyptodon*), carnivores (*Smilodon*, *Panthera*, *Leopardus*, *Chrysocyon*, *Protocyon* and *Pteronura*), mastodons (*Haplomastodon*), horses (*Equus*), deer (*Mazama* and *Ozotoceros*), peccaries (*Tayassu*), llamas (*Palaeolama*), and members of South American endemic ungulate orders (*Macrauchenia* and *Toxodon*) (Salles et al., 2006; Perini et al., 2009). All collected material is housed at the Mammal collection of the Museu Nacional (MN) at Rio de Janeiro, Brazil.

2.2. Taxonomic sampling and measurements

A set of 17 measurements typically employed in the characterization of fossil tapir species (Simpson, 1945; Cattoi, 1951; Ubilla, 1983; Tonni, 1992) was taken from the lower cheek teeth of fossil and recent tapir specimens (Fig. 2). All measurements were obtained with 150 mm digital calipers with 0.02 mm accuracy.