



FIRST RECORD OF *TETRASTYLUS* AMEGHINO, 1886 (RODENTIA; DINOMYIDAE) FROM THE UPPER MIOCENE OF URUGUAY

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ABSTRACT – The first record for Uruguay of the dinomyid rodent *Tetrastylus* Ameghino, an almost complete right mandible from the upper Miocene Camacho Formation, is described. According to the p4 and m3 morphology it is inferred a juvenile-subadult ontogenetic stage for this specimen.

Keywords: Rodentia, Dinomyidae, upper Miocene, Uruguay.

RESUMO – O primeiro registro para o Uruguai do roedor dinomiídeo *Tetrastylus* Ameghino, baseado em uma mandíbula direita quase completa do Mioceno superior da Formação Camacho, é descrito. O material provém de sedimentos do Mioceno superior do Uruguai (Formação Camacho). Tendo em conta a morfologia do p4 e m3 é inferido um estágio ontogenético juvenil-subadulto para este espécime.

Palavras-chave: Rodentia, Dinomyidae, Mioceno superior, Uruguai.

INTRODUCTION

Dinomyidae is one of the three families of ‘giant’ rodents known from South America (Bondesio, 1978 and references therein). Nowadays the family includes only the “pacarana” (*Dinomys branickii* Peters, 1873), which is a peculiar “long headed” cursorial Amazonian caviomorph considered among the largest living rodents, with a body mass of approximately 15 kg (Collins & Eisenberg, 1972; Peters, 1873; Pocock, 1926; Sanborn, 1931; White & Alberico, 1992). Contrary to this impoverished current record, the past diversity of the group was notable, with a large number of fossil genera and species reaching body sizes even larger than that of the pacarana. The most extreme example is the giant *Josephoartigasia monesi* Rinderknecht & Blanco, 2008, the largest rodent ever recorded with an estimated mean body mass close to a ton (Rinderknecht & Blanco, 2008; but see Blanco, 2008; Millien, 2008). The fossil record of the Dinomyidae undoubtedly begins during the middle Miocene (Friasian?/Laventan SALMA), but the genus *Branisamys* Hoffstetter & Lavocat, 1970 from the Salla beds in Bolivia (Deseadan SALMA, late Oligocene) has been placed in the family by some authors (see Vucetich *et al.*, 1999; Nasif, 2009; Nasif & Abdala, 2015). Fossil members of the Dinomyidae have been described from almost every South American country (Figure 1), being the

collections from Argentina, Colombia, Venezuela, Brazil and Uruguay the most important.

While the first described fossils of the family date back to the late 19th century (Ameghino, 1883, 1885, 1886, 1891a, 1981b, 1889; Burmeister, 1885), only in recent years the phylogeny of Dinomyidae has been addressed using a modern cladistic approach (see Nasif, 2009; Kramarz, 2013; Kerber *et al.*, 2016a,b; 2018). The revision made by Kraglievich (1926, 1932) remains as the current systematic arrangement for the entire family (but see Rinderknecht *et al.*, 2018). Following Kraglievich’s main framework complemented and corrected by Fields (1957), Pascual (1967), and Mones (1981), the family is subdivided into four to five subfamilies: Potamarchinae (including the oldest known representatives of the family, extending from the late Oligocene? to the early? Pliocene); Gyriabrininae (late Miocene–late? Pliocene); Dinomyinae (including only the extant *Dinomys branickii*); Eumegamyinae (late Miocene–late Pliocene? including the largest representatives of the family), and Tetrastylinae (late Miocene–Pleistocene), considered by many authors as a subgroup of the Eumegamyinae or Dinomyinae (see Fields, 1957; Mones, 1981). According to the latest systematic revisions (Rinderknecht *et al.*, 2011; 2018; Rinderknecht & Blanco, 2015; Kerber *et al.*, 2018), the family is composed only by the subfamilies Eumegamyinae, Tetrastylinae and



Figure 1. Map of South America showing the approximate current distribution of *Dinomys branickii* (black) and the locations (points) with a fossil record of the Dinomyidae. Modified from Rinderknecht *et al.* (2011, fig. 1).

Potamarchinae. Although this systematic scheme gives some stability to the more than 60 fossil species described (Kraglievich, 1926, 1930; Mones, 1986), knowledge of the morphology of these animals is far from been satisfactory due to the lack of associated cranial and postcranial remains. In fact, most specimens are known only by isolated teeth and/or small fragments of skulls or mandibles (Mones, 1986), preventing any possibility of developing a comprehensive comparative analysis of the different lineages in Dinomyidae.

In Uruguay, in comparison with other groups of mammals, the fossil record of the family is poor and restricted to the southwest portion of the country (Figure 1). The study of these animals began during the first half of the 20th century with the discovery and description of a partial palate without clear stratigraphic provenance assigned to one new species: *Gyriabrus teisseirei* Kraglievich (1930). Later, Francis & Mones (1966) described *Artigasias magna* (see Mones, 2007) based on a reworked jaw fragment bearing part of the dental series and an isolated incisor of presumed late Pliocene age, and tentatively ascribed to the San José Formation (currently Raigón Formation, see Tofalo *et al.*, 2009, or San José Member of Raigón Formation, Bossi *et al.*, 2009). Calcaterra (1972) proposed the presence of *Eumegamys* sp. based on a reworked incisor fragment recovered from the coast of El Real de San Carlos, Colonia Department. The new species *Isostylomys intermedius* Mones & Castiglioni, 1979 was based on a single premolar collected in the upper Miocene sediments of the

Camacho Formation, San José Department. This last taxon was synonymized with *Isostylomys laurillardi* by Rinderknecht *et al.* (2018). Recent revisions of the materials deposited in the collection of the Museo Nacional de Historia Natural de Montevideo, Uruguay (MNHN), have contributed to the knowledge of the morphology of the group. Rinderknecht (2007) reported the first known articulated postcranial remains of an eumegamyine; Rinderknecht and Blanco (2008) described the well preserved skull of *Josephoartigasia monesi*; Rinderknecht *et al.* (2011) described a new genus (*Arazamys*) based on remains coming from Miocene deposits of the Camacho Formation. Finally, Rinderknecht *et al.* (2018) presented the first associated craniomandibular remains of the genus *Isostylomys* Kraglievich, 1926 and the first juvenile remains known for the subfamily Eumegamyinae, addressing some aspects of dental development in eumegamyines.

In this work we reported for first time in Uruguay the presence of the dinomyid rodent *Tetrastylus* Ameghino, 1886, based on an almost complete right mandible ramus. The material comes from sediments of the upper Miocene.

MATERIAL AND METHODS

The studied specimen is housed in the Vertebrate Paleontological Collection of the Facultad de Ciencias, Departamento de Paleontología, Uruguay (FC-DPV). As a comparative framework oriented towards analysing the ontogenetic development of the Tetrastylinae, we studied specimens in different ontogenetic stages of the genus *Dinomys*, and followed the recent study of Nasif & Abdala (2015) about the craniodental ontogeny of this genus. The present study considers four stages of ontogenetic development: the neonate, juvenile (specimens with some unerupted tooth, or some tooth with minimal worn, including the stages juvenile II-V in Nasif & Abdala, 2015), subadult (specimens with all erupted and functional tooth, but less worn than in full-growth adult, subadult VI in Nasif & Abdala, 2015) and adult stage (adult VII in Nasif & Abdala, 2015).

The morphological terminology used in this paper follows Nasif & Abdala (2015), Rinderknecht *et al.* (2018), and Patterson & Wood (1982). The examined specimens that were used as comparison and their institutional abbreviations are listed in the Appendix 1. The fossil material was measured with a digital Vernier caliper (0.1mm accuracy).

GEOLOGICAL SETTING

The fossil-bearing strata are located in southwestern Uruguay (San José Department; 34°34'S, 56°58'W) in exposures located on the coastal cliffs and littoral platform of the Río de La Plata (Figure 2). There, the lithostratigraphic units recognized from base to top are the Camacho (upper Miocene), Raigón (Pliocene and Pleistocene) and Libertad (Pleistocene) formations (Bossi & Navarro, 1991; Tófaló *et al.*, 2009). The first two units yield many vertebrate fossils, including a variety of cingulates, ground sloths, rodents and notoungulates (Vizcaíno *et al.*, 2003; Rinderknecht *et al.*,

2011; 2018; Perea *et al.*, 2013). The remains described here were found in sediments of the Camacho Formation. This Formation is the representation in Uruguay of an extended, late Miocene, eustatic event regionally known as the *Paranean transgression* or *Paranean Sea* (Sprechmann *et al.*, 2000). In the San José Department, the facies are related to the regressive phase characterized as estuarine and/or paralic environments. Terrestrial and marine vertebrates in association with marine invertebrates and ichnofossils comprise the fossil assemblage of the unit (Ubilla *et al.*, 1990; Perea *et al.*, 1996; Sprechmann *et al.*, 2000; Perea, 2005; Perea *et al.*, 2013). The sediments of the Camacho Formation are composed by greenish-grey friable and medium compacted pelite that becomes greenish-brownish towards the top of the formation. The mammalian fossil assemblage includes marsupial carnivores, xenarthrans, notoungulates, litopterns, hystricognath rodents, and cetaceans, showing affinities with the upper Miocene Chasicuan and Huayquerian Ages/Stages of Argentina, especially with the one informally known as the “*Mesopotamiense*” (formerly considered as a Huayquerian local fossil fauna), of the Entre Ríos Province (Bostelmann & Rinderknecht, 2010; Brandoni, 2013; Mones & Rinderknecht, 2004; Perea *et al.*, 1994; Perea, 2005; Perea *et al.*, 2013; Rinderknecht *et al.*, 2011; Vizcaíno *et al.*, 2003). $^{40}\text{Sr}/^{87}\text{Sr}$ dated levels of the Paraná Formation and its southern correlative, the Puerto Madryn Formation

(Scasso *et al.*, 2001), renders a late Miocene 9.5 Ma–10 Ma (Tortonian) age for the top of the *Paranean Sea* in Argentina. Recently, the Camacho Formation was dated in 7.5–6 Ma. using Sr-isotope stratigraphy (del Río *et al.*, 2018) or 11–9 Ma. (Soibelzon *et al.*, 2019).

SYSTEMATIC PALEONTOLOGY

Family DINOMYIDAE Alston, 1876
Subfamily TETRASTYLINAE Kraglievich, 1931

Tetrastylus Ameghino, 1886

Tetrastylus sp.
(Figures 3–5; Table 1)

Material. FC-DPV 2891: An almost complete right mandible with incisor and p4–m3 (Figures 3–5 and Table 1).

Geographic and Stratigraphic provenance. Uruguay, Departamento de San José. Puerto Arazatí, Camacho Formation (upper Miocene, Huayquerian SALMA).

DESCRIPTION

The mandible is almost complete, lacking most of the angular process, the ascending ramus, and the extralveolar portion of the incisive. The masseteric fossa is not well defined and is located below the m1. Like all Dinomyidae (especially Eumegamyinae and Tetrastylinae) the coronoid process is reduced, forming a small uneven surface on the posterolabial side at the m3 level. The incisor is robust and the enamel surface does not have the tiny longitudinal ridges commonly observed in Eumegamyinae (see Rinderknecht *et al.*, 2018). The alveolar portion of the incisor shows a slight curvature starting below the m3. The grinding teeth are constituted by four lophids of dentine recovered by enamel, which is thicker in the posterior face than in the anterior one (Figures 3–4). A thin layer of cementum separates the lophids. The two-anterior lophids are labially joined in m1–m2 and completely free in p4 and m3. Three poorly defined columns of enamel form the anterior lophid of the p4. The cheek teeth of Dinomyidae usually have these columns before complete the ontogenetic process (see Kraglievich, 1932; Mones, 1997; Nasif & Abdala, 2015; Rinderknecht *et al.*, 2018). In fact, these are cusps that meanwhile the specimen is growing become fused to form a complete lophid (see Marivaux *et al.*, 2004; Nasif & Abdala, 2015). Similar structures can be seen in the M3 of many giant dinomyids, but these structures can remain in the adult stage (Rinderknecht *et al.*, 2018). The specimen FC-DPV 2891 present the last two lophids of the p4 free and a small enamel column located between the lingual borders of both lophids can be identified. This structure is also considered characterizing juvenile and subadult stages and probably disappears in the adult stage (see Figure 5, and Nasif & Abdala, 2015, fig. 11a). The m1 and m2 are similar in morphology with the two first lophids joined in the labial face and free in the lingual ones. The two posterior most lophids of m1 and m2 are completely

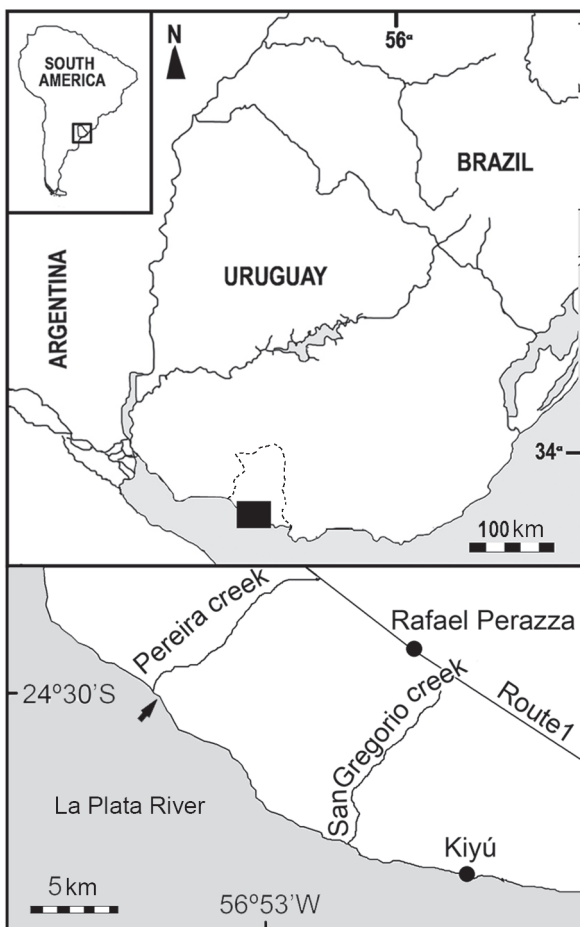


Figure 2. Geographic location of *Tetrastylus* sp. (FC-DPV 2891) in Department of San José (dotted line). The arrow shows the approximate site of collection.

free and only are connected each other by a thin layer of interprismatic cementum. The m3 has the four lophids free and is the smallest tooth of the cheek teeth due it is in phase of eruption; it has a cone configuration observed in juvenile and subadult hypselodont mammals (Kraglievich, 1930). The first lophid is the smallest and has a mesial projection in the

medial portion of the anterior border (see Figures 3–4). This structure is the remnant of an enamel column recently fused to the lophid. The last lophid of m3 is the smallest and lacks the projections or columns of enamel. All the aforementioned features indicate that FC-DPV 2891 was a juvenile (state V *sensu* Nasif & Abdala, 2015) - subadult specimen.



Figure 3. Right mandible of *Tetrastylus* sp. (FC-DPV 2891) in occlusal (A), external (B), and internal (C) views. Scale bar = 50 mm.

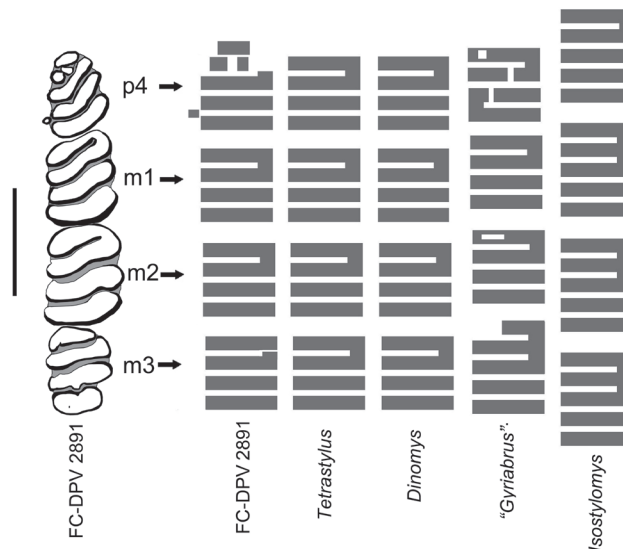


Figure 4. Right p4-m3 of *Tetrastylus* sp. (FC-DPV 2891), in occlusal view, and schemes (not at scale) of lower cheek-tooth in different Dinomyidae genera. Scale bar = 10 mm.

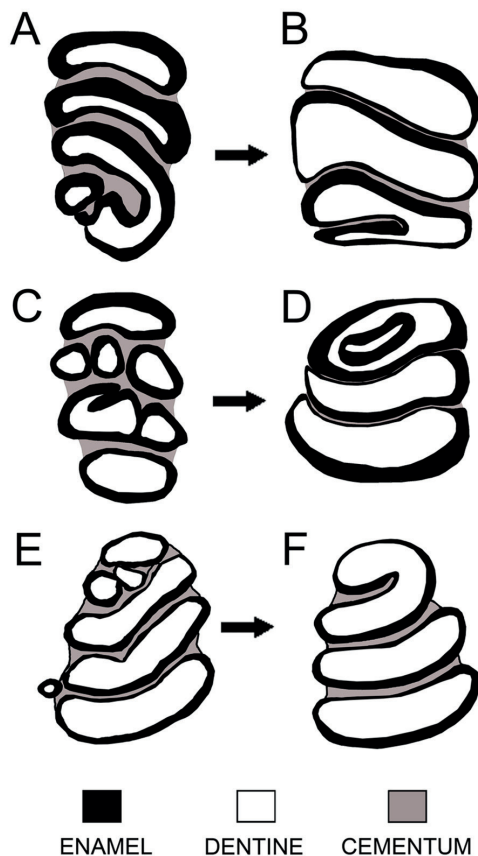


Figure 5. Occlusal view of Dinomyidae adult and juvenile teeth (not to scale). **A**, right upper first molar of *Dinomys branickii* juvenile (NHMUK 12.1.15.14). **B**, right upper first molar of *D. branickii* adult (NHMUK 3796). **C**, left first lower molar of *D. branickii* juvenile (MACN 12962). **D**, left first lower molar of *D. branickii* subadult (NHMUK 34.9.10.191). **E**, lower premolar of *Tetrastylus* sp. (FC-DPV 2891). **F**, lower premolar of *Tetrastylus laevigatus* (Ameghino, 1885) adult (MLP52-X-1-59). Modified from Rinderknecht *et al.* (2018, fig. 11), and Kraglievich (1932, fig. 5).

Table 1. Dental measurements (in mm) of *Tetrastylus* sp. (FC-DPV 2891).

	Mesiodistal length	Buccolingual width
Right p4	7.9	6.2
Right m1	8.7	6.9
Right m2	10.0	7.5
Right m3	8.2	6.1
Right i	6.5	7.0

DISCUSSION AND CONCLUSIONS

Tetrastylus is the best-represented dinomyid in the fossil record. This genus has at least eight species described (see Mones, 1986), ranging from Miocene to late Pliocene (or even Late Pleistocene, see Paula Couto, 1951), and mainly recovered in the fossil record of Argentina, Venezuela, Brazil and Peru. Some of these species were described based on well-preserved specimens (like *T. intermedius* Rovereto, 1914) but others on scarce and fragmentary materials. Nasif *et al.* (2013) indicate a non-monophyletic condition for this group of species mainly based on an unpublished work (Nasif, 2009).

Due to the high overall similarity among the species described and included into the subfamily Tetrastylinae, is extremely difficult to identify species based on mandibles not associated to skulls. Nevertheless, the material here described yields useful characters, enough to confidently assign it to this genus according to the present state of knowledge.

FC-DPV 2891 is assigned to the subfamily Tetrastylinae based on hypselodont teeth and tetralophodont grinding teeth condition, differing from Eumegamyinae because this last subfamily has lower grinding teeth (except the m1 of some taxa) with five lophids. The teeth of FC-DPV 2891 has all the lophids free in the lingual face, differing from the members of the subfamily Gyriabrininae that exhibit joined lophids in this face. However, it should be highlighted that the validity of Gyriabrininae was questioned because its included taxa could be in fact juvenile specimens of other subfamilies of Dinomyidae (Rinderknecht *et al.*, 2018). The possession in FC-DPV 2891 of joined lophids only in the labial face of lower teeth, and rudimentary coronoid process, also allows to dismiss the subfamily Potamarchinae (see Kerber *et al.*, 2016a,b). The differentiation of the studied material of Uruguay with regard to the giant tetrastylines *Telicomys* and *Carlesia* (this last genus sometimes equivocally assigned to Eumegamyinae, see Bondesio, 1978), is based on the relation between the incisor size and grinding teeth. *Telicomys* and *Carlesia* yield extremely large incisors even for the entire family, meanwhile the material here studied follow the pattern showed by *Dinomys* and *Tetrastylus*. The smaller size of our material (Table 1) compared with *Telicomys* and *Carlesia* could be an additional difference. However, caution should be taken with size when having only mandibular remains, since some members of fossil Dinomyidae could reach the complete configuration of the mandible early in the ontogeny, still being smaller compared with adults (see Nasif & Abdala, 2015; Rinderknecht *et al.*, 2018).

The genus *Tetrastylopsis* Kraglievich, 1931 has lower teeth with lophids lingually joined (p4); lophids joined in the labial face (last two lophids of m1) and in the lingual face (two anterior lophids of m1). This pattern clearly differentiates it from the Uruguayan specimen.

Tetrastylomys Kraglievich, 1926 was described on an isolated tooth with four free lophids. Even though there is no assignment to a specific tooth (grinding teeth, premolar, lower or upper) it could belong to the subfamily Tetrastylinae based on the morphology of the lophids and because its small size. Nevertheless, Kraglievich (1926) hesitantly refer it to some antillean giant rodents and not to Dinomyidae. Unfortunately, the fragmentary information available precludes any comparison with the Uruguayan material. In addition, due to the fragmentary condition of *Tetrastylomys* it should be considered as a “nomen inquirendum”.

The FC-DPV 2891 specimen differs from *Dinomys* in having a larger size, relatively larger teeth and by a lesser curvature radius of the incisor. This last feature turn the FC-DPV 2891 incisor more proodont than *Dinomys*. In addition, the masseteric mandibular fossa is more anteriorly located in *Dinomys* than in the Uruguayan specimen. It is important to note that this last characteristic changes during the ontogenetic

development in *Dinomys*, since the juvenile individuals present the masseteric mandibular fossa in a more anterior position than the adults (see Nasif & Abdala, 2015). However, in FC-DPV 2891 this structure is in a more posterior location even than the adults of *Dinomys*.

Despite having a characteristic morphology, in particular the p4 and m3, FC-DPV 2891 is interpreted as having a juvenile-subadult condition. Juvenile specimens of *Dinomys* show similar morphology in the erupting teeth, maintaining enamel column not yet joined forming a lophid (NHMUK 12.1.15.4, UDCA-UIFS 032, UDCA-UIFS 098, UDCA-UIFS 136, and see Nasif & Abdala, p.11, 13). This last condition also can see in the p4 of subadult specimens (NHMUK 34.9.10.191) but with a somewhat higher degree of fusion of columns than in the FC-DPV 2891. Our studies on ontogeny of *Dinomys* and previous works (Ray, 1964; Mones, 1997; Nasif & Abdala, 2015; Rinderknecht *et al.*, 2018) show that the last two teeth in eruption are the p4 and m3. This is the reason of the peculiar morphology of these teeth of FC-DPV 2891. Due to the late eruption stage of the p4 and m3, it is expected to have less wear than the remaining teeth, and reach later the definitive configuration than the m1 and m2. Far from considering this morphology as having taxonomic value, we conclude that caution should be taken about any specific taxonomic decision about this material.

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Appendix 1. Examined specimens that were used as comparison and their institutional abbreviations.

Specimens of *Dinomys branickii* utilized in our analysis belong to the following institutions: **MACN**, Colección Mastozoológica del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN**, Museo Nacional de Historia Natural, Montevideo, Uruguay; **NHMUK**, The Natural History Museum, London, United Kingdom; **UDCA-UIFS**, Unidad de Investigación en Fauna Silvestre de la Universidad de Ciencias Aplicadas y Ambientales, Bogotá, Colombia; **UNMSM-MUSM**, Colección de Mastozoológica del Museo de Historia Natural de la Universidad Nacional de San Marcos, Lima, Perú.

List of specimens (*Dinomys branickii*): nearly complete skeleton (MNHN 3795, adult); skull and mandibles: (MNHN 3796, adult); (NHMUK 34.9.10.191, subadult); (NHMUK 12.1.15.4, juvenile); (MACN 12961, adult); (MACN-M 12962, neonate); (UNMSM-MUSM 2217); (UNMSM-MUSM 5048); (UNMSM-MUSM 7887); (UNMSM-MUSM 11231); (UNMSM-MUSM 19855); (UNMSM-MUSM 23153); (UNMSM-MUSM 25759); (UDCA – UIFS 032, juvenile); (UDCA-UIFS 098, juvenile); (UDCA – UIFS 094, neonate); (UDCA – UIFS 136, juvenile).