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Dinomys branickii.

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Dinomys Peters, 1873

Dinomys Peters, 1873*a*:551. Type species *Dinomys branickii* Peters, 1873, by monotypy.

CONTEXT AND CONTENT. Order Rodentia, Suborder Hystricognathi, Infraorder Caviomorpha (Carleton, 1984), Superfamily Dinomyoidea (Reig, 1981; Wendt, 1968), Family Dinomyidae, Subfamily Dinomyinae, Tribe Dinomyini (Mones, 1981). The genus *Dinomys* contains one species.

Dinomys branickii Peters, 1873

Pacarana

Dinomys branickii Peters, 1873*a*:551. Type locality "der Colonia Amable Maria, in der Montaña de Vitoc, in den Hochgebirgen Perus erlegt," Department of Junín, Perú.

Dinomys pacarana de Miranda-Ribeiro, 1919:13. Type locality "procedente do Amazonas," Brazil. Reportedly "probably came from Río Purús region" of Brazil (Sanborn, 1931:151).

Dinomys branickii occidentalis Lönnberg, 1921:49. Type locality "road to Gualea, about 6,000 feet; . . . llambo near Gualea, about 5,000 feet," ca. 1,500–1,800 m, Provincia de Pichincha, Ecuador (0°07′N, 78°45′W).

Dinomys gigas Anthony, 1921:6. Type locality "La Candela, Huila, altitude, 6,500 ft.," 1,950 m, Colombia.

Dinomys sp. n.? Niceforo, 1923:317. From Santa Elena, 1,520 m, Antioquia, Colombia.

CONTEXT AND CONTENT. As in generic account. Sanborn (1931) synonymized all named forms with *D. branickii.*

DIAGNOSIS. Dorsal surface of skull relatively flat. Occiput semicircular, flattened, and nearly vertical; occipitals broadly expanded externally. Occipital condyles extend laterally nearly to postoccipital processes. Bony palate slightly concave, extending to or slightly beyond posterior margin of M3. Mandible with coronoid process reduced to a low medial projection behind last molar. Incisors extremely heavy and broad, width > transverse diameter of molariforms. Upper diastema > combined length of cheekteeth. Lower incisors rooted in prominent flattened curvature, extending to behind last molar. Cheekteeth evergrowing (=euhypsodont; Mones, 1982), and tetralophodont. Upper cheekteeth with anterior two lamina isolated and posterior two lamina united. Lower cheekteeth with anterior two lamina united and posterior two lamina isolated. Second and third cervical vertebrae fused (Mones, 1981; Woods, 1984).

GENERAL CHARACTERS. The pacarana is a large, heavily-built nocturnal rodent (Fig. 1; Goeldi, 1904; Mohr, 1937). The head is massive, ears are short and rounded, and the limbs are short. Feet are broad, each bearing four digits, all armed with a long, strongly curved claw. *Dinomys* is plantigrade, raising only the heel of the hind feet above the ground while it walks, which gives it a waddling gait (Goeldi, 1904; Pocock, 1926). The soles are hairless and have digital and plantar pads containing the remaining skeletal elements of pollex and hallux. Webbing extends about halfway between the plantar pad and the tips of the small digital pads (Grand and Eisenberg, 1982; Pocock, 1926). The incisors are long, broad and chisel-like (Pocock, 1926). The cheekteeth are multilaminar, have high crowns, are rootless, and continuously growing (Woods, 1984). The upper lip is deeply cleft (Pocock, 1926),

Length of head and body is 730–790 mm, length of tail is about 190 mm, and body mass is 10–15 kg (Allen, 1942; Sanborn, 1931; Wendt, 1968). The upper parts are black or brown, adult females possibly being brown, and adult males, black (Lönnberg, 1921). Two more or less continuous broad white stripes are located on each side of the midline of the back beginning from the shoulders, and two shorter rows of white spots are on the sides (Goeldi, 1904). In older individuals, the stripes seem to be broader and more conspicuously white. The underparts are paler than the upper parts and are not marked. The pelage is rather coarse, scant, and of varied length. The tail is stout, cylindrical, and fully haired. The whiskers are numerous and long, the longest reaching back as far as the neck (Pocock, 1926). Females have two lateral-thoracic and two lateral-abdominal pairs of mammae (Weir, 1974).

DISTRIBUTION. Pacaranas occur in all three cordilleras of the Colombian Andes (Allen, 1916; Niceforo, 1923; Velasco and Alberico, 1984), in Ecuador (Lönnberg, 1921), Peru (Grimwood, 1969), Brazil (de Miranda-Ribeiro, 1918; Sanborn, 1931), and Bolivia (Anderson, 1985; Cabrera, 1961). They also have been recently collected from the Cordillera de Mérida, states of Mérida and Táchira, northwestern Venezuela (Fig. 2; Boher and Marín, 1988; Boher et al., 1988). The altitudinal range of this species is 240-2,000 m in Peru (Grimwood, 1969) and to 2,400 m in Venezuela (Boher and Marín, 1988). The collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, houses a skull from the Páramo de Toquilla, Boyacá at 3,200 m (Hernández-Camacho, pers. comm.).

FOSSIL RECORD. *Dinomys branickii* is the only living survivor of a once diversified and highly successful group of rodents. It has no fossil record. However, *Tetrastylus atropheatus* is so much like *Dinomys* in tooth character that it may be a species of this genus (Fields, 1957).

The Dinomyidae are represented by a large number of fossils found in Argentina, Uruguay, Brazil, Venezuela, Colombia, and Bolivia. The geologic range is Deseadan Oligocene to Recent in South America except Chile, Paraguay, and the Guyanas (Woods, 1984). A spectacular dinomyid radiation occurred during the Miocene and Pliocene epochs, in the late Tertiary (Fields, 1957; Patterson and Wood, 1982). At that time the Dinomyidae had already differentiated into several size classes, species, and presumably, diverse ecological niches (Fields, 1957). The family produced the largest known rodents. *Telicomys gigantissimus*, in Argentina, was nearly as large as a rhinoceros (Simpson, 1980). *Eumegamys*, a highly specialized genus, possibly derived during Chasicoan time, was as large as a hippopotamus (Fields, 1957). *Artigasia magna* from Uruguay, whose upper dentition was reported by Mones (1988) was even larger (A. Mones, in litt.).

Mones (1981) placed the origin of the Dinomyidae in the Friasian Miocene, and recognized 4 subfamilies (Potamarchinae, Gyriabrinae, Phoberomyinae, and Dinomyinae, the latter composed

FIG. 1. Photograph of adult *Dinomys branickii* in the Pereira Zoo, Colombia.

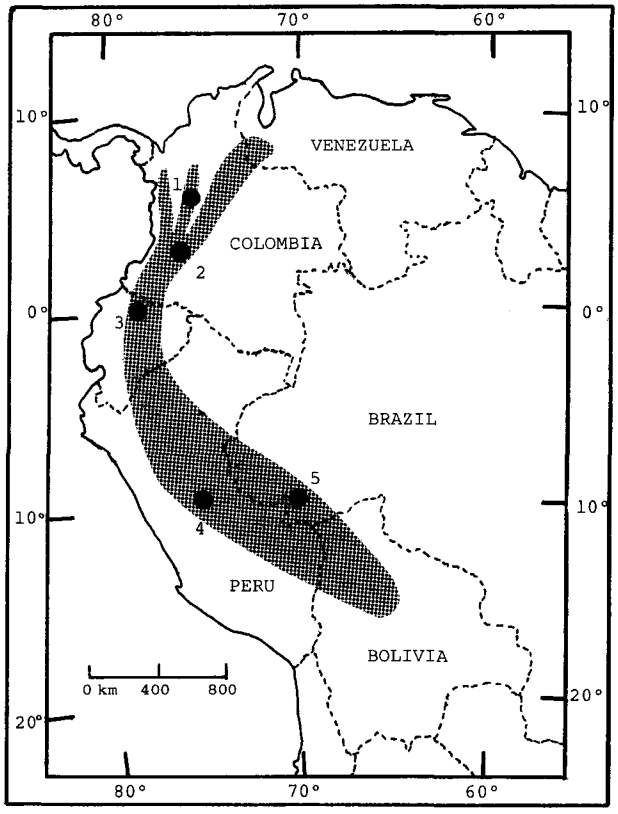

FIG. 2. Map of distribution of *Dinomys branickii* with type localities of synonyms indicated: 1, Santa Elena, Antioquia, Colombia; 2, La Candela, Huila, Colombia; 3, near Gualea, Provinicia de Pichincha, Ecuador; 4, Colonia Amable María, Montaña de Vitoc, Departamento de Junín, Peru; 5, rio Purus region, Amazonas, Brazil.

FIG. 3. Dorsal, ventral, and lateral views of the cranium, and lateral view of the mandible of an adult male *Dinomys branickii* (m-5,400, Instituto Nacional de los Recursos Naturales Renovables y del Ambiente) from the Pereira Zoo, Colombia (reportedly from near Santa Rosa del Cabal, Risaralda). Occipitonasal length is 148.0 mm.

of the tribes Dinomyini and Eumegamyini), 28 genera, and 58 species. Stirton (1953) reported what he thought was the oldest recognizable record of a dinomyid from the late Oligocene Coyaima fauna of Colombia. More recently, *Branisamys*, a fossil rodent from the Deseadan Oligocene of Bolivia (Lavocat, 1976), was included in the Dinomyidae by Patterson and Wood (1982), thus becoming the oldest known fossil member of the family.

FORM AND FUNCTION. The skull (Fig. 3; de Miranda-Ribeiro, 1918; Peters, 1873b) measures up to 153 mm in length in the adult male and 141 mm in females (Allen, 1942). The dental formula is i 1/1, c 0/0, p 1/1, 3/3, total 20, with flat-crowned molars each composed of a series of four transverse plates. The incisors are broad and powerful, auditory bullae are of medium size. The supraoccipital lacks a lateral process. The zygoma is heavy, without a jugal fossa and the jugal does not join the lacrimal. The lacrimal canal does not open on side of rostrum. The infraorbital foramen is large, without a ventral canal for nerve passage. The skull is massive, but only slightly ridged. The angular process of the dentary is strongly deflected and the coronoid process is vestigial (Woods, 1984).

The second and third cervical vertebrae are firmly fused together (Ray, 1958; Woods, 1984). In immature individuals, the neural spines are closely appressed and largely fused, while the mutual zygapophyseal articulations are already completely fused (Ray, 1958).

Dinomys, although terrestrial, has many characters of a semi-arboreal animal. It has about equal musculature to forelimbs and hind limbs, a low proportion of back extensor muscle, and limb muscles which are not aligned or developed for linear propulsive thrust. Its terrestrial walk is plantigrade, ungainly, and inefficient with a side-to-side waddle (Grand and Eisenberg, 1982).

ONTOGENY AND REPRODUCTION. Field data and information gathered from captive animals are scarce. The gestation period was first estimated as 223–283 days (Collins and Eisenberg, 1972), but Meritt (1984) reported that it could not exceed 252 days. Litter size is considered to be one or two (Collins and Eisenberg, 1972; Weir, 1974). Meritt (1984) reported two litters of twins, one of triplets, and one of quadruplets at Tokyo University. A cellular vaginal closure membrane, open at estrus and parturition, was present in two specimens (Weir, 1974).

Gravid females were captured at an un-named locality in February and May, and another female of unspecified origin gave birth to two young in January (Collins and Eisenberg, 1972). A pregnant female, apparently captured in the field in Brazil, delivered twins in May (Goeldi, 1904). In captivity, births have been reported in January (Meritt, 1984) and February (Collins and Eisenberg, 1972), and there have been births in the Cali Zoo in January, March, May, June, October, and November.

Body mass increases suddenly at 3 months of gestation, and the pregnant female has periodic bouts of irritability (Collins and Eisenberg, 1972; Meritt, 1984). No abdominal enlargement or fullness, and no nipple or breast development were noted by Meritt (1984), while Collins and Eisenberg (1972) reported gradual nipple elongation and dark pink pigmentation. Nest-building behavior by

pregnant females or females after parturition was not observed (Collins and Eisenberg, 1972).

Newborn animals are precocious. They are dry, clean, alert, and active. They stay close to the mother, almost touching her, and the mother is cautious while moving, taking care not to step on or walk over the newborn. The mass at birth is 570–660 g; nursing was observed within 10 h of the infant's discovery (Meritt, 1984). Weir (1974) gave the mass of newborns as 900 g. One baby began exploration of its environment during its second day of life. At this same age it began self-grooming including scratching, and ate its first solid food, a piece of spinach. Beginning at 2 weeks of age, the baby ate solid food daily, including raw peanuts in the shell, spinach, celery, green beans, apple, banana, lettuce, and bread. The mother allowed the baby to nurse whenever hungry and showed a preference for being in an upright position, either sitting erect, or leaning upright against a nest box or one of the habitat walls (Meritt, 1984).

ECOLOGY. *Dinomys* has always seemed rare, and there has been concern for its survival (Grimwood, 1969), so much so that at times it was feared extinct (Nowak and Paradiso, 1983; Wendt, 1968). However, Goeldi (1904) considered this apparent rarity a possible result of a lack of information about the real habitat of the species. Grimwood (1969) described the pacarana as an animal of the high selva (500–2,500 m) and upper parts of the low selva zone (below 500 m). de Miranda-Ribeiro (1918) suggested that *Dinomys* occurs along the Peruvian and Brazilian border, in the headwaters of the Acre, Purús, and Juruá rivers, and reported a specimen from the state of Amazonas, in Northwestern Brazil.

In the wild, pacaranas are thought to eat palm and other fruits, leaves, and tender stems (Wendt, 1968; Woods, 1984). Captive animals in Parque Zoológico Caricuao, Venezuela, were fed vegetables and fruits (Boher and Marín, 1988). Other institutions include in their diet boiled eggs, dried fish, rabbit chow, monkey chow, bread, seeds, nuts, grains, and a supplement of vitamins and minerals in addition to fresh fruit and vegetables (Meritt, 1984). An animal kept at the New York Zoological Park from 1915 to 1922 was fed crushed oats, greens, raw vegetables, bananas, apples, and bread (Crandall, 1964).

In nature, the slow-moving pacarana has few enemies except humans. Known predators include *Felis pardalis*, *Eira barbara*, and *Nasua nasua*; larger predators such as *Felis concolor* and *Panthera onca* should also be considered as potential threats (Meritt, 1984; Sanborn, 1931). There is one report of pacaranas in captivity killing a paca (*Agouti paca*) when they were placed in the same cage (de Miranda-Ribeiro, 1918).

Wellcomia branickii is a nematode parasite of *Dinomys* (McClure, 1932). Strongyles were found by staff of Lincoln Park Zoological Gardens in a wild-caught juvenile male from Colombian. A specimen from Bolivia contained ascarids and strongyles (Meritt, 1984). Nine genera of nematodes were found in three captive specimens held at the Parque Zoológico Caricuao, including *Ancylostoma*, *Ascaris*, *Capillaria*, *Oesophagostomum*, *Oxyurus*, *Strongyloides*, *Strongylus*, *Trichostrogylus*, and *Trichuris*. One cestode (*Hemynolepis nana*) and one protozoan (*Eimeria*) species were also found (Boher and Marín, 1988).

The pacarana is among the rarest of mammals in captivity. Approximately 36 are held worldwide (Meritt, 1984). There are published reports of captive reproduction in New York Zoological Gardens (Sanborn, 1931), Lincoln Park Zoological Gardens (Meritt, 1984), San Antonio Zoological Gardens (Collins and Eisenberg, 1972; Meritt, 1984), National Zoological Park (Collins and Eisenberg, 1972), and the Tokyo University (Meritt, 1984). We have reports of reproduction in the Cali and Pereira Zoos in Colombia.

Numerous cases of death in captivity due to unspecified causes, suggest that pacaranas do not adapt easily to captivity. Known causes of death in captivity include myodarditis (Collins and Eisenberg, 1972), heat exhaustion complicated by a heavy parasite load, and a hereditary nuclear anomaly (Meritt, 1984). One captive individual died at parturition (Goeldi, 1904). The longevity of individuals in captivity is about 8–9 years (Crandall, 1964; Jones, 1982; Meritt, 1984).

Use of the pacarana by man primarily is restricted to food. Additional and new threats to its survival include land reform and deforestation (Meritt, 1984; Nowak and Paradiso, 1983).

BEHAVIOR. There is little known about the behavior of free-living specimens, but some accounts have been published based on observations of pacaranas in captivity. They are slow moving and peaceful. Occasionally they manifest their displeasure by a low-guttural growl (Alho, 1982; Crandall, 1964; Goeldi, 1904; Mohr, 1937). They cannot turn about quickly, and have no rear protection from alert foes like ocelots (*Felis pardalis*), tayras (*Eira barbara*), and coatis (*Nasua nasua*). They live in rocky cliffs, or holes in the ground, where they can back up and secure rear protection (Sanborn, 1931). Wild animals are said to shelter in natural crevices, which they enlarge with their strong claws, but although captives are known to use log hollows and nest boxes, they do not seem to dig (Meritt, 1984). The family unit generally consists of male, female, and two young (Crandall, 1964). Woods (1984) mentioned that they are found either solitary or in pairs, while Boher and Marín (1988) stated that pacaranas are seen usually in groups of two to five individuals.

While eating, pacaranas usually sit on their hind feet and hold the food in their forefeet (Goeldi, 1904; Mohr, 1937). No caching behavior was detected in individuals at the National Zoological Park (Collins and Eisenberg, 1972). Pacaranas are contact animals and their behavior does not seem to include maintaining a certain distance between individual animals. Pacaranas are frequently described as gentle, but there have been reports of their viciousness (Collins and Eisenberg, 1972; de Miranda-Ribeiro, 1918). Many dogs are afraid to confront pacaranas in the wild because of the savage defense they put up (Grimwood, 1969).

Although most of their activities are terrestrial, pacaranas do climb (Woods, 1984). Their long claws aid them in ascending trunks, their climbing ability being similar to that of the porcupine in North America. With growth, however, these skills decline and climbing persists only in a restricted fashion (Collins and Eisenberg, 1972).

Captives usually sleep in elevated places (Collins nd Eisenberg, 1972), but apparently do not have well-defined paths or routes within their home range (Meritt, 1984). They can walk bipedally and very frequently do so during social encounters. Active primarily after dark, they will urinate and defecate in a communal area within the cage, which suggests a marking function. When moving in an enclosure, males rub their cheeks on branches or other surfaces. This apparently unique marking behavior involves whitish secretions from the glands surrounding the eye, which drain into the nasal cavity (Collins and Eisenberg, 1972). Gnawing at selected points also serves as a marking function.

There is an elaborate communication system that consists of foot stamping with forepaws, tooth chattering, and whimpers, whines, songs, and hisses. Seven vocalizations were defined in social interactions, the hiss, growl, and staccato whimper being the most common sounds heard in male-female encounters (Collins and Eisenberg, 1972). During courtship the male utters a series of whimpering notes that may be combined into an extended song lasting >2 min. Although this call might be an artifact of isolation in captivity, it may serve to attract sexual partners as seems to be the case in *Erethizon* (Eisenberg, 1974). In the initial phases of male-female encounters, contact-promoting behavior included marking, naso-naso contact, naso-genital investigations, upright confrontation and grappling, incisor coupling, head-over/head-under, head toss and pivot, ritualistic dance, and grooming. The receptive female tolerates naso-genital contact from the male, walking with her tail arched. Driving, lordosis, and mounting constitute the sexual response components. Intromissions are brief, lasting <20 s. Several intromissions may precede ejaculation (Collins and Eisenberg, 1972).

REMARKS. The Dinomyidae have been classified most frequently within the Superfamily Cavioidea (Fields, 1957; Patterson and Wood, 1982) or the Chinchilloidea (Mones, 1981; Reig, 1986). However, their resemblance to the Erethizontidae has repeatedly been noted (Fields, 1957; Grand and Eisenberg, 1982; Quentin, 1973; Ray, 1958; Woods, 1984; Woods and Hermanson, 1985) and Eisenberg (1981) placed them in the Superfamily Erethizontoidea. Characteristics of the musculature, genetics, blood components, and arterial patterns of *Dinomys* are still unknown. Until more data on the interfamilial relations of these rodents become available, we recommend leaving the dinomyids in a separate superfamily as suggested by Wendt (1968) and Reig (1981).

The generic name *Dinomys* means terrible mouse. Best known as *pacarana*, a Tupí indian name meaning false paca (Goeldi, 1904), this rodent is also called *machetero* because of its habit of cutting cleanly through the stems of corn plants as though with a knife

(Grimwood, 1969). Other names used are *rukupi* (Meritt, 1984), *piro, teconi, tecón, lapa rabuda, lapo, lapa cacique* (Boher and Marín, 1988), *guagua lanuda* (Velasco and Alberico, 1984), and *guagua loba*. The report of *Dinomys* from Pará, Brazil (Alho, 1982) is erroneous (A. Mones, in litt.).

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