Agouti pacu. By Elizabeth M. Pérez

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Agouti Lacèpède, 1799

*Mus* Linnaeus, 1766:79 (part).
*Cavia* Erxleben, 1777:348 (part, not *Cavia* Pallas, 1766).
*Coelogenys* Cuvier, 1807:203. Type species *Mus pacu* Linnaeus, 1766, by subsequent designation (Thomas, 1924).
*Coelogenys* Illiger, 1811:92. Emendation of *Coelogenys* Cuvier, 1807.

*Osteoperura* Harlan, 1825:126. Type species *Osteoperura platycephala* Harlan, 1825, by monotypy.
*Caniculus* Hollister, 1913:79. Based on *Paca* Brisson, 1762 (=*Mus pacu* Linnaeus, 1766). *Caniculus* Hollister, 1913, is a junior homonym of *Caniculus* Wagler, 1830:21 (a microtine rodent).
*Stictomys* Thomas, 1924:238. Type species *Stictomys taczanowski* (Stollman, 1885), by original designation. Valid as a subgenus; used at generic level by Cabrera (1961).

CONTEX AND CONTENT. Order Rodentia, Suborder Hysterognathi, Infraorder Caviomorpha, Superfamily Cavioidae, Family Agoutiidae. The family contains one genus with two extant species: *Agouti taczanowski* and *A. pacu*. A key to species follows:

Reddish-brown coat color, soft fur, shorter length of body and zygomatic region less rugose than the other species

Reddish-brown to dark chocolate or smoke-gray coat color, harsh fur, larger length of body and zygomatic region more rugose than the other species

*Agouti pacu* (Linnaeus, 1766)

Paca

[*Mus*] *paca* Linnaeus, 1766:81. Type locality "Brasilia, Guiana."
Restricted to Pernambuco, Brazil, by Lömberg (1921:43).
*Cavia* *paca* Erxleben, 1777:356 (=*Mus pacu* Linnaeus, 1766).
*Agouti* pacu Lacèpède, 1799:9 (=*Mus pacu* Linnaeus, 1766).
*Cavia* *paca* alba Kerr, 1792:216. Type locality "environs of the river St. Francis in South America (=Rio Sao Francisco, Minas Gerais, Brazil).
*Coelogenys* subniger Cuvier, 1807:206. Type locality "Toabgo." *Coelogenys fulvus* Cuvier, 1807:207. Based on Brisson (1762), Buffon (1763), and Geoffroy St.-Hilaire (1803); therefore, type locality is Cayenne, French Guiana.

*Paca* *maculata* Fisher, 1814:87. Type locality "Guiana, Brasilia."

*Coelogenys* brunnnea Von Olfers, 1818:213. Type locality "Sudamerica."
*Coelogenys* rufa Von Olfers, 1818:213. Type locality "Sudamerica."

*Coelogenys pacu*: Wind-Neuwied, 1821:254, name combination.
*Osteoperura* platycephala Harlan, 1825:126. Based on a skull of unknown origin found on "the shore of the river Delaware," U.S.A.

*Coelogenys* fulvus: Wind-Neuwied, 1826:247, name combination.
*Coelogenys* subniger: Wind-Neuwied, 1826:457, name combination.

*Coelogenys pacu*: Rengger, 1830:251, name combination.
*Coelogenys fuscus* Lesson, 1842:103. Type locality "Guyane; Brésil."
*Coelogenys sublaevis* Gervais, 1854:326. Type locality "Colombie."

*Paca americana* Linnaeus, 1782:538. Type locality "le Brésil, la Guyane et le Paraguay."

*Agouti pacu* virgatus Bangs, 1902:47. Type locality "Divala," Chiriqui, Panama.

*Coelogenys pacus mexicanae* Hagmann, 1908:25. Type locality "Insel Mexicana," Para, Brazil.

*Agouti pacus nelsoni* Goldman, 1913:9. Type locality "Catemaco, southern Vera Cruz, Mexico."

*Caniculus pacus nelsoni* Hollister, 1913:79, name combination.

*Caniculus pacus pacus* Hollister, 1913:79, name combination.

*Caniculus pacus virgatus* Hollister, 1913:79, name combination.

*Caniculus pacus sublaevis* Hollister, 1913:79, name combination.

*Coelogenys*, *paca*, *virgatus*: Lömberg, 1921:45, name combination.

*Coelogenys pacus guanta* Lömberg, 1921:45. Type locality "Gua- lea, 5,000 feet," Pichincha, Ecuador.

*Coelogenys* guanta: Thomas, 1924:239, name combination.

*Caniculus* *paca* alba: Tate, 1935:316, name combination.

*Caniculus* subniger: Tate, 1935:316, name combination.

*Caniculus* *paca* var. fulvus: Tate, 1935:316, name combination.

*Caniculus* sublaevis: Tate, 1935:316, name combination.

*Caniculus pacus mexicanae*: Tate, 1935:316, name combination.

*Agouti*, *paca*, *virgatus*: Lömberg, 1921:45, name combination.

*Agouti pacus venezuelica* Kuhnbigel, 1940:233. Type locality "Marayaca, Venezuela."

*Agouti pacus* guanta: Kuhnbigel, 1940:237, name combination.

CONTEX AND CONTENT. Context as in generic summary above. Five subspecies of *Agouti pacu* are recognized (Cabrera, 1961; Hall, 1981):

*P. pacus* guanta Lömberg, 1921:45. Type locality "Gualea, 5,000 feet," Province of Pichincha, Ecuador.

*P. pacus* mexicanae Hagmann, 1908:25. Type locality "Insel Mexicana," Para, Brazil.

*P. nelsoni* Goldman, 1913:9. Type locality "Catemaco, southern Vera Cruz, Mexico."

*P. pacus* Linnaeus, 1766:81. Type locality "Pernambuco, Brazil."

*P. pacus* virgatus Bangs, 1902:47. Type locality "Divala," Chiriqui, Panama.

DIAGNOSIS. *Agouti pacus* resembles *A. taczanowski* in most external features. *A. pacus* is distinguished by its relatively larger body size, thinner and harsher fur, shorter nasals, larger orbits, more posteriorly situated postorbital, thicker claws and less granulated soles. The zygomatic region generally is more rugose (Ellerman, 1940).

Fig. 1. Adult female pacu (*Agouti pacu*) in Venezuela. Photograph by E. Pérez.
DISTRIBUTION. Originally a South American species, *A. pacas* is presently distributed from southern Mexico to northern Argentina. This distribution includes Central America, the Lesser Antilles, Cuba (Varona, 1974), Colombia, Venezuela, Guiana, Ecuador, Peru, Bolivia, Paraguay and Argentina (Fig. 2). Actititudinally, its range extends from sea level to about 1,600 m (Mondolfi, 1972). *A. pacas* has been identified only from late Pleistocene cave deposits in Minas Gerais, Brazil (Winge, 1888).

FORM AND FUNCTION. The skin of the young is covered with large scales of varying polygonal shapes and sizes that average about 2 mm in diameter. Each scale is surrounded by a depression in which the cuticle is thinner and pliable. On the anterior border, the scale is perforated by a group of three bristle hairs. Skin of adult pacas shows little evidence of these horn scales (Allen, 1940).

The skulls of adult pacas have a zygomatic region exceptionally modified by outgrowths from the maxillary and jugal to form large bony cheekplates (Fig. 3). These plates, about two-thirds as long as the palate, extend downward and conceal a large part of the mandible. Anteriorly, these plates enclose the roots of the teeth. This zygomatic development is known only in one other rodent, the African maned rat (*Lophiomys*; Randial, 1972). The zygomatic region quickly changes from the slender and smooth condition of young pacas to the elaborate structure of adults (Nelson and Shump, 1978).

The infraorbital foramen is reduced to form a narrow canal almost entirely enclosed by bone. The nasals are broad and short, while the paroccipital processes are thick (Ellerman, 1940). The hind limbs are about 50% longer than the forelimbs (324 mm and 219 mm, respectively). The tibia (106 mm in length) is almost the same size as the femur (109 mm in length) and provides a huge lever which allows the animal to make big jumps when is disturbed (Quezada and Hanan, 1988).

The dental formula, as in other caviomorphs, is 1/1, c 0/0, p 1/1, m 3/3, total 20. The incisors are relatively thin and compressed. The cheekteeth are composed of four to five reentrant enamel folds in a crown pattern that varies as a result of wear (Friant, 1968). The fully-occupied M3 or the presence of a permanent P4 indicates that a paca is about 1 year of age (Collett, 1981).

The paca has a pair of external and a pair of internal cheek pouches. The external pouches are rather small and formed by the downward growth of the zygomatic arches, with no apparent primary use. The internal pouches extend over the metalconic surface of the maxillary root of the zygomatic arch (Howell, 1940). Hershkovic (1955) and Howell (1940) suggested that the function of the internal pouches is to amplify and reverberate sounds.

The transverse dimension of the brain is greater than the anteroposterior dimension and has prominent occipital lobes. The neocortex is slightly convoluted (Kraus et al., 1970). Fixed in formalin, the mass of the brain is 20.4–26 g. The ratio of brain mass to total mass varies from 1.78 to 1.157 (Pillert, 1959). The olfactory and tactile sensnses are well developed, while the visual sense is poorly developed (Kraus et al., 1970).

The basal metabolic rate has been calculated at 0.30 ml O₂ g⁻¹ h⁻¹ and represents 86% of the value expected from Kleiber’s allometric equation for body mass. Minimal thermal conductance is 0.028 cm² g⁻¹ h⁻¹ °C⁻¹. The ratio of percent basal metabolic rate to percent minimal conductance is 0.32, the lowest value obtained for 11 rodent species from South America. Body temperature is 37.2°C and the lower limit of thermoneutrality is 26°C (McNab, 1982).

External genitalia in both sexes are hidden in an anal sac. Adult males have two oval testes at least 38 mm in length and 15 to 25 mm in diameter (Lander, 1974). Size of testes remains constant after 1 year of age (Collett, 1981). There is no scrotum. Accessory reproductive glands of males consist of a pair of preputial glands and white and irregular vesicular glands (4.5 cm long by 1.7 cm wide). The seminiferous tubules of males contain A and B spermatogenias, young and old spermatocytes, secondary spermatocytes, spermatids, and spermatooza (Pushov and Matamoros, 1984; Ureña and Bolado, 1988).

The penis (50–70 mm in length) has a protatelic glans profusely armored with small spines and two horn spines 12–13 mm in length on the tips. The dorsal surface has short and proximally directed spicules, whereas the ventral face is smooth with the baculum relief visible medially. Cornified plates of 15–17 mm with serrat
borders occupy the sides of the penis (Matamoros, 1981; Mondolfi, 1972). Mondolfi (1972) suggested that this complex structure stimulates ovulation in the female, but Matamoros and Pashov (1984) found that the paca is a spontaneous ovulator.

Female reproductive organs consist of paired ovaries (8 by 5 mm), oviducts (50 mm in length), bicorunuate uterus formed by a pair of horns (each 120 mm in length), and a vagina (140 mm in length). The ovaries of pregnant females show a large corpus luteum and numerous small accessory corpora lutea. In early pregnancy, the corpus luteum is composed entirely of large glandular cells whereas in lactating parous females it is irregular and degenerating with a loss of the thecal layers (Collett, 1981). Matamoros and Pashov (1984) found five types of oestral cycles, the most common lasting 14.3 days.

The tongue of *A. paca* (88 mm in length) is fleshy and rounded at the tip (Martin, 1838). The stomach, 152 mm in length, is separated from the duodenum by a well-defined sphincter (Matamoros and Pashov, 1982). The small intestine is large and measures 6.6 m in length. The caecum, with a basal circumference about 178 mm and 711 mm in length, is irregularly sacculated (Martin, 1838). *A. paca* has paired eversible anal glands that open into the anus. These glands are formed by sebaceous cells and measure 25–30 by 17–20 mm (Mondolfi, 1972).

During the wet season, with more abundant food available, pacas accumulate fat in the inguinal and retroperitoneal regions; this energy reserve is quickly consumed in the dry season. Bourlière (1973) called attention to evolutionary convergence between paca and chinchilla (*Hylomyscus*), an ungulate that inhabits the African rain forest. Both species have similar size, body form, color pattern, diet and habitat.

**Ontogeny and Reproduction.** *Agouti paca* breeds all year. Based on cytological examination of vaginal epithelium, Matamoros and Pashov (1984) concluded that females are receptive throughout the year and that adult males produce spermatozoa throughout the year. There is no indication of seasonal clustering of births or significant age-specific variation in fecundity (Collett, 1981). Females become reproductively active at approximately 9 months of age, while males reach sexual maturity at 1 year (Collett, 1981; Matamoros, 1981).

Typically, *A. paca* bears one young once or twice annually (Mondolfi, 1972). In captivity, 38.5% of females reproduce once, 38.5% twice, and 23.1% three times/year; only one of 31 births bore two young (Matamoros, 1981). In captivity, the gestation period was from 114 days (Matamoros and Pashov, 1984) to 119 days (Lander, 1974). The average interval between births was 191 days for wild females (Collett, 1981). In captive pacas, estrus occurs shortly after birth and again toward the end of lactation (Matamoros, 1981). Collett (1981) found 12 wild females parous and pregnant, simultaneously.

Newborn are precocial, with adult appearance, open eyes, well-developed pelage, erupted incisors, and cheekteeth appearing through the gums. They are active and able to walk well. Neonates born in captivity measure 240–300 mm in total length and mass 550–800 g (Lander, 1974; Mondolfi, 1972).

Captive young are weaned when about 12 weeks old, but take solid food after 3 weeks of age (Matamoros, 1981). For wild animals, Collett (1981) suggested that the suckling period does not exceed 6 weeks.

**Ecology.** Pacas primarily inhabit tropical rain forest, although they occur in a wide variety of forest habitats, including mangrove swamps, deciduous and semi-deciduous forest, narrow riparian growth, and dense underbrush. They prefer areas near water (Collett, 1981; Pérez, 1983). *Agouti paca* is an opportunistic feeder. Mainly frugivorous, the diet of this species changes throughout its range and shows seasonal variation according to the availability of fruits (Collett, 1981; Gallina, 1980; Mondolfi, 1972). *A. paca* is unable to open some hard-shelled fruits, but eats the softer péricarps when the fruit has been opened by other animals; occasionally it feeds on leaves, buds, and flowers. Collett (1981) examined 116 stomachs and found that 112 contained exclusively fruit parts and four showed leaf or flower parts. Analysis of five *Agouti* feces by Gallina (1980) revealed only fruit fragments. In captivity, it consumes a great variety of food items, including cultivated fruits and vegetables, raw meat, lizards, and insects (Lander, 1974; Pérez, 1983). Coprophagy is rare (Matamoros, 1981; Mondolfi, 1972).

Population density of *A. paca* has been estimated in three localities. Using track frequency, Eisenberg et al. (1979) reported 25 pacas/km² for Fundo Agropecuarie Masaguaral in the llanos of Venezuela. On the basis of 7 years of live-trapping data, Smythe et al. (1983) estimated the density of adult pacas on Barro Colorado Island, Panama, at 70 adults/km². Also on Barro Colorado Island, Glanz (1983) conducted a census transect and found 40 pacas/km². Collett (1981) reported densities of 38, 56, and 51 adult pacas/km² for three intensively hunted sites in the llanos of Colombia and suggested that 40–70 adult pacas/km² of suitable forest habitat is a reasonable estimate for the abundance of pacas in the llanos. At Parque Nacional Guatopo, Venezuela, Eisenberg et al. (1979) found that pacas represented 16% of the biomass of the 35 species of nonvomant mammals comprising the community. Similar representation has been demonstrated for this species in Panama (Eisenberg and Thorington, 1973).

Based on numbers of cementum layers in the first molar of 205 pacas from the llanos of Colombia, Collett (1981) reported the
following age structure: <1 year, 87; 1–2 years, 25; 2–3 years, 17; 3–4 years, 16; 4–5 years, 12; 5–6 years, 11; 6–7 years, 11; 7–8 years, 9; 8–9 years, 7; 9–10 years, 5; and >10 years, 5. The age of the oldest individual was 12–13 years. The sex ratio was nearly 1:1.

Agouti paca has low fecundity and high survivorship of adults. Annual survivorship was estimated to be 0.8 for adult females, 0.97 for adult males, and 0.93 for young (Collett, 1981). Smythe et al. (1983) suggested that high disappearance rate of young pacas is trapped on Barro Colorado Island, Panama, indicated that the population was regulated by the availability of suitable territories.

Glaza (1983) and Smythe (1986) indicated varying diets of age and habitat overlap of A. pacas with Dasyprocta, Proechimys, Sciurus, Tayassu, Mazama, Eira, Nasua, Potos, Coendou, Cebus, Caluromys, Metachirus, Atelom, and Alouatta. Smythe (1986) supposed that interspecific competition for food during the dry season is the main factor of population regulation.

Agouti paca has a unique known occurrence of parasites in A. paca: Acanthocephalans, Ancylostoma, Anisakis, Lepidoptera, and Caenophthalmus. Other parasites are Echinococcus, Cestoda, Ancylostoma, and Heterocotylidae. The major parasites are trypanosomes (Gonzalez and Espino, 1974), and Histosoma spinulosum (Naiff et al., 1985).

The primary predators of A. paca are Felis onca, F. pardalis, F. concolor, F. weddelli, F. rufina, F. yaguarondi, and Canis latrans. Other predators are Crocodylus, Boa constrictor, and Speothos venaticus (Deutsch, 1983; Lander, 1974; Mondolfi, 1972;Ramidj, 1972).

Paca are rarely caught in live-traps, however, the use of trained dogs is an effective capture method. The procedure involves one or more hunters with dogs in the forest and the pacas to be tracked for scenting pacas until an occupied burrow is located. At night, pacas are hunted near a fruitfall by shining a carbine light into their eyes. This temporarily blinds and confuses them, allowing them to be shot by the hunter (Ferrer, 1983).

Bears are frequently kept in captivity. Because of their economic potential for meat production, intensive management has been proposed. Several studies provide information on the requirements to maintain this species in captivity, including characteristics of fences and burrows, enclosure size and amount of animals by enclosure (Aguirre and Fey, 1981; Matamoro, 1981; Pèrez, 1983; Smythe, 1987).

BEHAVIOR. Agouti paca is nocturnal, although sometimes it is active in the early morning and late afternoon (Smythe, 1970). The paca walks along fixed trails, but if any of these trails is altered, the animal immediately rejects it and uses another path. It restricts its activity during bright moonlight. A. paca is a good swimmer and, when pursued, tries to reach a river or pond where it may remain submerged for a long period (Alho, 1982).

During the day, the paca remains in burrows. Pacas may live in hollow trees or among rocks (Contreras and Zetina, 1979; Walker, 1974). Burrows have two or more entrances concealed with wads of leaf litter, and an average diameter of 0.2 m. Burrows may descend to depths of 0.3–0.8 m and can extend for 2.8–9 m. It is commonly believed that pacas adapt and modify the diggings of armadillos (Dasypus novemcinctus and D. kappleri) rather than excavating entire burrows by themselves (Lander, 1974).

Agouti paca is a solitary mammal. Of 108 encounters recorded by Collett (1981), 86 involved pacas that were alone, 21 involved two pacas (usually an adult and a young), and only once were three pacas seen together. In captivity, adults moderately tolerate the presence of conspecifics, but frequently attack recently introduced animals; they may kill new born (Lander, 1974; Matamoro, 1981).

Frequently, A. paca emits a low-pitched prairie dog chirp with a frequency of 1–4 kHz at intervals of 0.5–2.5 s, and at 1–2 kHz at intervals of 0.3–0.5 s, with 2.5 kHz at intervals of 0.3–0.5 s. This sound is repeated four times at intervals of 35–75 s (Eisenberg, 1974). When threatened, it exhibits pilo-erection and tooth-chattering with grunting; if provoked, it will growl loudly. Females call their young with a low grunt (Eisenberg, 1974).

Agouti paca exhibits the frisky-hop syndrome, common in other hystrixmorphs (Kleiman, 1974). The syndrome, apparently induced by olfactory stimulation, involves rapid locomotor and rotational body movement, approaches, and withdrawals, but little physical contact between conspecifics. It primarily occurs in males during courtship, although it is common in females that have been sprayed with urine during an encounter. It has not been reported in juveniles (Smythe, 1970).

When courtship begins, the female avoids the approaching male and occasionally attacks him. The male approaches her, at an angle, and then turns and attempts to urinate on her. Usually, the female reacts trying to avoid the spray. The male keeps repeating this behavior until he finally sprays her. After a number of sprayings, the female may crouch down at the approach of a male and make a low, muttering squeak. The copulation then takes place and is short in duration (Freibert, 1966).

After parturition, the male rears up and urinates extensively over the female. It also may urinate over the young if the infant attempts to muzzle him in the perineal region. During nursing, the female adopts a lying position while the infant rests between her feet (Smythe, 1979). In captivity, A. paca generally urinates and defecates in the periphery of their enclosures as a way of scent-marking (Kraus et al., 1970).

GENETICS. Agouti paca has a diploid number of 74 chromosomes and a fundamental number (FN) of 56. The karyotype consists of 12 pairs of metaconic, 2 pairs of submetaconic, 8 pairs of acrocentric, and 2 pairs of subacrocentric chromosomes (Fredj, 1966).

Agouti taczanowskii, the only other species in the genus, has a different karyotype with a diploid number of 42 and FN of 80. Most of the chromosomes of A. taczanowskii are larger in size than those of A. paca (Gardner, 1971).

REMARKS. Cuniculus Brisson, 1762, the oldest denomination generic name is rejected by many authorities. Despite Tate's (1935, 1939) interpretation that Opinion 90 (ICZN, 1925) validated the name Cuniculus Brisson, 1762, Cuniculus is unavailable from Brissius (1762) because it is a replacement of Brissius (1756—pre-Linnean) and his names are not consistently binomial (Hopwood, 1947). Tate (1935) believed, however, that because Brissius's generic bird names were accepted for nomenclatural purposes (ICZN, 1911), his generic names for mammals also should be accepted. On the contrary, Brissius's generic names for mammals are not used for nomenclatural purposes, except when validated under the plenary powers of the International Commission on Zoological Nomenclature (e.g., Odobenus Brisson, 1762, see Hemming, 1957).

In 1924, Thomas and other European authorities proposed to the International Commission on Zoological Nomenclature that priority rules be suspended to keep Coelogenys as the generic name of this species. The International Commission in Opinion 90 rejected this suspension (Tate, 1935).

There is no general agreement concerning the familial status of this taxon. Some authors place this genus in the family Dasyproctidae (Anderson and Jones, 1967; Corbett and Hill, 1980); however, chromosomal and serological evidence support a separate family (George and Weir, 1974; Woods, 1982).

Other vernacular names for the species are conejo pintado (Panama), tepecuncnte (Costa Rica), guardatapas (Mexico), tee (Suriname), and lamp (Venezuela). Paca is the common name in Brazil and Argentina.

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