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Tapirus pinchaque (Perissodactyla: Tapiridae)

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Abstract: Tapirus pinchaque (Roulin, 1829), the mountain tapir, is considered the smallest and least specialized of the 4 species of *Tapirus*. It is restricted to parts of temperate areas from Colombia and Ecuador to extreme northwestern Peru. It is a foliage browser that generally inhabits moist habitats that facilitate bathing; however, they are frequently found in thick bush in the cold and humid zones of the Andes between 1,400 and 4,400 m. *T. pinchaque*, one of the rarest mammals in the world, is listed under Appendix I of the Convention on International Trade in Endangered Species of Fauna and Flora and is considered "Endangered" by the International Union for Conservation of Nature and Natural Resources. DOI: 10.1644/ 863.1.

Key words: Andes, endangered species, keystone species, mountain tapir, mutualism, proboscis, seed dispersal, tapir

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Tapirus Brisson, 1762

- Tapirus Brisson, 1762:81. Type species Hippopotamus terrestris Linnaeus, 1758, by plenary action (International Commission on Zoological Nomenclature 1998).
- *Tapirussa* Frisch, 1775:4. Unavailable name vide Grubb (2005).
- *Tapir* Blumenbach, 1779:129. Incorrect subsequent spelling of *Tapirus* Brisson, 1762.
- *Hydrochoerus* Gray, 1821:306. Nomen nudum vide Grubb (2005).
- Syspotamus Billberg, 1827:conspectus A, before page 1. Replacement name for *Tapir* Gmelin, 1788.
- Rhinochoerus Wagler 1830:17. Replacement name for Tapirus Brisson, 1762.
- *Elasmognathus* Gill, 1865:183. Type species *Elasmognathus bairdii* Gill, 1865, by original designation; preoccupied by *Elasmognathus* Fieber, 1844, a genus of Hemiptera.
- Tapyra Liais, 1872:397. Incorrect subsequent spelling of Tapirus Brisson, 1762.
- Cinchacus Gray, 1873:34. Type species Tapirus leucogenys Gray, 1873, by monotypy.
- Tapirella Palmer, 1903:873. Replacement name for *Elas-mognathus* Gill, 1865.
- Acrocodia Goldman, 1913:65. Type species Tapirus indicus Desmarest, 1819, by original designation.
- *Pinchacus* Hershkovitz, 1954:469. Replacement name for *Cinchacus* Gray, 1873, vide Cabrera (1961).

CONTEXT AND CONTENT. Order Perissodactyla, suborder Ceratomorpha, superfamily Tapiroidea, family Tapiridae. Two hypotheses have been proposed to explain tapir speciation in the Neotropics. Hershkovitz (1966, 1969) speculated that the distributional patterns of tapirs indicate 3 independent invasions of South America from Central America. The prototypes of *Tapirus pinchaque* and *T*.



Fig. 1.—Female *Tapirus pinchaque* with young. Photograph of captive animals by R. Garrison, used with permission of Zoological Society of San Diego.

terrestris are thought to have reached South America by an oversea route at widely different times when climate and topography were different, although which species was 1st is unknown. *T. bairdii* is thought to be a late overland arrival.

Haffer (1970) hypothesized that the 3 forms may have originated during the Pleistocene in the Neotropics from 1 Pliocene immigrant, with *T. pinchaque* arising in the Andes, *T. terrestris* in the lowlands east of the Andes, and *T. bairdii* west of the Andes. Downer (2001) suggested that with the rise of the Andes above the tree line at 2,000 m, an unoccupied, treeless habitat could have caused the speciation from the Pliocene immigrant that resulted in *T. terrestris* and *T. pinchaque*. Hatcher (1896) concluded that *T. bairdii* is the most specialized tapir and was probably derived from *T. pinchaque* through *T. terrestris*. Simpson (1945) also noted that *T. pinchaque* is commonly considered a close ally of *T. terrestris*.

The genus contains 4 species (Grubb 2005). A key to the species of *Tapirus* (modified from Hatcher 1896; Ray and Sanders 1984) follows:

- Premaxillo-maxillary suture bisects alveolus for canine; sagittal crest broad and low; nasals broad and long; p2 molariform; color pattern of contrasting black or dark brown (head, neck, shoulders, and fore- and hind legs) and white (remainder of body) T. indicus
- - Premaxilla scarcely embraced by superior branch of maxilla; sagittal crest low; nasals long and narrow; hair soft, woolly, and noticeably long *T. pinchaque*

Tapirus pinchaque (Roulin, 1829) Mountain Tapir

Tapir pinchaque Roulin, 1829:46. Type locality "une journée de cetta ville, dans le Parama de Suma-Paz," vide Grubb (2005); further defined as "Páramo of Sumapaz, Cordillera Oriental, south of Bogotá, extreme southern part of Department of Cundinamarca, Colombia" by Hershkovitz (1954:472).

- *T*[*apirus*]. *Roulinii* Fischer, 1830:604. Replacement name for *Tapir pinchaque* Roulin, 1829.
- *Rhinochoerus villosus* Wagler, 1830:17, footnote 2. Replacement name for "le Pinchaque" Cuvier = *Tapir pinchaque* Roulin, 1829 (Hershkovitz 1954).
- *T*[*apirus*]. *andicola* Gloger, 1841:124. Replacement name for *Tapir pinchaque* Roulin, 1829.
- *Tapirus roulini* de Blainville, 1846:22. Incorrect subsequent spelling of *Tapirus roulinii* Fischer, 1830.
- *Tapirus pinchacus* de Blainville, 1846:pls. i-v. Incorrect subsequent spelling of *Tapirus pinchaque* Roulin, 1829.
- *Tapirus leucogenys* Gray, 1872:488, pl. xxi. Type locality "Ecuador, on the Cordilleras at Sunia and Assuay;" further restricted to "Páramo of Asuay Cordillera Oriental, southern Ecuador" by Lydekker (1916:44).

CONTEXT AND CONTENT. Context as above. *Tapirus pinch-aque* is monotypic (Hershkovitz 1954).

NOMENCLATURAL NOTES. *Tapirus pinchaque* escaped scientific detection until the 19th century, when 2 specimens were taken on the páramos of Quindío and Sumapaz, Colombia (Roulin 1829), and the finding was reported (Cuvier 1829).

Hershkovitz (1954) rejected Brisson's *Tapirus*, citing Hopwood (1947). Hopwood (1947) rejected Brisson's *Regnum Animale* (Brisson 1762), wherein *Tapirus* was 1st offered, because it was not Linnaean, not consistently binomial, and because it was essentially a reprint of a pre-Linnaean book. However, Hopwood was a malacologist and had little experience in mammalogy. Merriam (1895) argued that Brisson's work is valid for genera, 11 of which (including *Tapirus*) were introduced by Brisson and are entitled to recognition. Gentry (1995) and others have disputed Hopwood and urged conservation of Brisson's generic names.

Hershkovitz (1954) revised the classification of the Neotropical tapirs, noting that cranial and external differences warranted full generic rank for each species. Although agreeing in principle, Simpson (1945) found this to be impractical and so simply grouped all tapirs under the same genus. Consequently, Hershkovitz (1954:466) adopted Simpson's system and modified it by adding subgeneric names in order to emphasize the "real separation between each of the species."

Citing Hershkovitz's (1954) subgeneric classification, Cabrera (1961) added that the taxonomy should be further emended along 1 of 2 possible lines. Either *T. terrestris* and *T. pinchaque* should be included in the same genus but different subgenera, with *T. bairdii* in a separate genus, or all 3 should be placed in the same genus with *T. terrestris* and *T. pinchaque* in 1 subgenus and *T. bairdii* in a separate subgenus. Cabrera (1961) adopted the latter approach, which is used herein. Eisenberg et al. (1990), Hall (1981), and Nowak (1999) also recognized this "1 genus/3 subgenera" scheme, placing *T. pinchaque* and *T. terrestris* in *Tapirus*, *T. bairdii* in *Tapirella*, and *T. indicus* in *Acrocodia*. *T. indicus* was relegated to a separate genus, *Acrocodia*, by Eisenberg et al. (1990), whereas Grubb (2005) listed this latter genus as a synonym of *Tapirus*.

The word tapir comes from the Brazilian Tupi language, and may refer to the thick hide (Cabrera and Yepes 1960). The common name danta is a corruption of the Spanish word for elk, alce or anta (Hershkovitz 1954). The word pinchaque is supposedly the name of a large mythical animal believed to occupy the range of *T. pinchaque* in the Colombian Andes (Allen 1942; Cabrera and Yepes 1960; Geroudet 1970); the mythical animal may have been the mastodon (Hershkovitz 1954).

Common names used in parts of the animal's range are: English, woolly tapir, Roulin's tapir, and páramo tapir; French, tapir pinchaque, tapir de Roulin, and tapir des Andes; German, Wolltapir and Bergtapir; Spanish, danta lanuda, danta cordillerana, danta conga, danta negra, danta del páramo, danta apizarrada, gran bestia, bestia negra, ante, and pizarra (Acosta et al. 1996; Grimwood 1969; Hershkovitz 1954; Rodríguez-Mahecha et al. 1995; Schauenberg 1969; Simpson 1945); and Quechua: sacha huagra (Schauenberg 1969). Huagra is another Quechua term for tapir, although it also is used for cattle (Hershkovitz 1954).

DIAGNOSIS

Body size of Tapirus pinchaque (Fig. 1) averages smaller than that of the South American tapir (T. terrestris-Hershkovitz 1954) and T. pinchaque is considered the smallest species of tapir (Hatcher 1896). The skull of T. pinchaque (Fig. 2) and that of T. terrestris have single sagittal crests whereas skulls of Baird's tapir (T. bairdii) and the Malayan tapir (T. indicus) have double crests (Simpson 1945). The sagittal crest of T. pinchaque splits anteriorly into a triangular table above occiput, in contrast with that of T. terrestris (Eisenberg et al. 1990). Temporal ridges form on each side of the skull that gradually migrate dorsally and medially to form the sagittal crest, in contrast with T. terrestris where the sagittal crest simply erupts from midline of skull (Holbrook 2002). Although the sagittal crest develops very early in T. terrestris, it may develop somewhat later in T. pinchaque (Ray and Sanders 1984).

Tapirus bairdii, T. indicus, and some *T. terrestris* have a maxillary flange that embraces the mesethmoid; none of the skulls of *T. pinchaque* examined displayed this structure. Ascending process of maxilla ascends posterodorsally and borders descending process of nasal (Ray and Sanders 1984), which is more delicate than that of other tapirs (Hershkovitz 1954). The ascending process is grooved and creased in *T. indicus* and *T. bairdii*, but not in *T. terrestris* and *T. pinchaque* (Ray and Sanders 1984). Morphology of nasal



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of female *Tapirus pinchaque* (American Museum of Natural History 149424). Total length of skull is 345 mm.

bones is much more complex in *T. bairdii* and *T. indicus* than in *T. pinchaque* and *T. terrestris* (Witmer et al. 1999).

Whereas interparietal bones were found in some skulls of *T. bairdii* (10 of 60), *T. indicus* (1 of 10) and *T. terrestris* (1

of 46), none were found in 6 skulls of adult *T. pinchaque* (Ray and Sanders 1984). A free interparietal has been reported in a young animal (Lundelius and Slaughter 1976). Base of orbit is shallow, but not as shallow as in *T. indicus* (Hatcher 1896). Foramen magnum in *T. pinchaque* is absolutely and relatively larger than that of other species (Hatcher 1896). *T. indicus* has a vestigial 1st metacarpal bone; *T. pinchaque* and other tapir species do not (Eisenberg et al. 1990).

Manes are found on *T. bairdii* and *T. terrestris*, but not on *T. indicus* and *T. pinchaque* (Eigener 1954). Skin of neck does not form a crest in *T. indicus* and *T. pinchaque* (Jorgenson 1988). Pelage of *T. pinchaque* is thick and curly whereas pelage of other species is short and smooth (Pournelle 1965); hair of *T. pinchaque* can be ≥ 3.5 cm long in places (Jorgenson 1988). Unlike other tapirs, *T. pinchaque* has a distinct white furry edge around lips (Eisenberg et al. 1990) and a near-bare patch on rump bisected by a line of hairs (Crandall 1964; Downer 1995; Eigener 1954; Gale and Sedgwick 1968). Juvenile markings in *T. pinchaque* are more distinct than in other tapir species (Bonney and Crotty 1979).

Proboscides of *T. pinchaque* and *T. bairdii* are intermediate in size to that of *T. indicus*, the longest, and *T. terrestris*, the shortest (Witmer et al. 1999). In G- and Cbanded preparations, the X chromosome of *T. pinchaque* differed from those of *T. bairdii*, *T. indicus*, and *T. terrestris* by a heterochromatic addition at terminal end of Xq (Houck et al. 2000).

GENERAL CHARACTERS

The head of *Tapirus pinchaque* has a flat appearance because of a relatively low sagittal crest (Gray 1867; Hershkovitz 1954), although anterior dorsum is convex (Gale and Sedgwick 1968). Nasal bone is elongate (Gray 1867), diastema is moderate, 2 or more molariform premolars are present (Hall 1981), and I3 is functionally a canine that occludes against front of lower canine (Radinsky 1965). Second upper premolar of *T. pinchaque* is not molarized (Eisenberg et al. 1990).

Nostrils are transverse (Nowak 1999); long upper lip and short proboscis are prehensile. Eyes are round with bright yellow tapetum lucidum. Rhinarium is highly glandular. Ears, legs, and tail are short, with only 11 coccygeal vertebrae in tail (Eisenberg et al. 1990). Rear of body is rounded. Body tapers toward front, facilitating movement through heavy underbrush (Nowak 1999).

External measurements (mm) of an adult male *T. pinchaque* with worn dentition were: total length of body, about 1,800; height at shoulder, about 900; length of manus, about 433; circumference of upper foreleg, > 400; and after evisceration, a body mass of between "240–250 French pounds" (Hershkovitz 1954:474). Measurements (mm) of an

adult female were: total length, 2,000; length of tail, 50; length of pes (from skeleton), 310; length of ear, 170; height at shoulder (from skeleton), 870; height at hips (from skeleton), 910; and body mass, 264.7 kg, including a 4.5-kg fetus (Hershkovitz 1954). Measurements (mm) of an adult female 3.5-4 years of age were: total body length, 1,829; length of tail, 51; height at shoulder, 800; height at hips, 851; and greatest circumference, 1,295 (Crandall 1951). Body measurements for other individuals also are available (Schauenberg 1969). Recorded masses of 2 adult females of unspecified age were 125 and 149 kg (Tapir Research Institute 1971), an adult male taken in Quito, Ecuador, had a mass of 243 kg (Schauenberg 1969), and a 2.5 year old of unspecified sex had a mass of 101.2 kg (Crandall 1964). Apart from genitalia, sexual dimorphism in T. pinchaque is not obvious (Kuehn 1986; Schauenberg 1969), although female mass was generally 25–100 kg more than male mass (Barongi 1986).

Body is usually blackish brown to black dorsally, becoming progressively lighter on sides, in anal region, and ventrally. Individuals have white or other pale hairs spread diffusely along back and laterally down one-third of sides (Crandall 1964; Gale and Sedgwick 1968; Hershkovitz 1954; Schauenberg 1969). Individual hairs on dorsum are black basally with brown tips, whereas hairs on sides may be brown or gray basally (Hershkovitz 1954). An area immediately behind the foreleg had a denser coating of white hairs in 1 individual (Gale and Sedgwick 1968). *T. pinchaque* living at higher elevations of the Sangay Mountains, Ecuador, were darker and had longer hair than those living at lower elevations (Schauenberg 1969).

Cheeks may be light colored (Eigener 1954; Gray 1872), even gray or ashy (Schauenberg 1969). Sides of head and anterior cervical region have mixed brown, ochraceous, and buffy coloration. In 1 individual, the white band extending along lip decreased in width from 2.5 cm at commissures to 1 cm at anterior aspect of mouth (Gale and Sedgwick 1968). Extent of white band can vary among individuals; in some it reaches all around mouth to base of trunk and in others it occurs only at commissures (Schauenberg 1969).

As with lip band, tops of ears also tend to be edged in white (Hershkovitz 1954; Schauenberg 1969), although this edging may be indistinct or even absent on otherwise black ears (Gale and Sedgwick 1968; Heran 1989). Edging on ears may vary from a mere blemish to a full border 10–15 cm wide. A clump of long gray or white hairs may occur at base of ear (Schauenberg 1969).

DISTRIBUTION

Tapirus pinchaque is restricted to parts of temperate areas from Colombia and Ecuador to extreme northwestern Peru (Fig. 3; Hershkovitz 1954; Lizcano et al. 2002; Lizcano and Sissa 2003; Nowak 1999; Thornback and Jenkins 1982). *T. pinchaque* is found in the Eastern and Central Cordilleras



Fig. 3.—Current known distribution of *Tapirus pinchaque*. Areas of former occurrence and possible occurrence are detailed in Downer (1996a).

of Colombia (Acosta et al. 1996; Lizcano et al. 2002; Velasco-Abad and Alberico 1984) and the Eastern Cordillera of Ecuador (Geroudet 1970; Schauenberg 1969). Geographical isolation may have kept T. pinchaque out of the Western Cordillera of Colombia (Lizcano et al. 2002). In Peru, T. pinchaque is found only in Ayabaca and Huancabamba provinces of the Department of Piura and Jaen Province of the Department of Cajamarca to about 6°S (Grimwood 1969), and along the Peru-Ecuador border in the Cordillera del Condor (Mittermeier et al. 1975). Although T. pinchaque may once have occurred in western Venezuela (Cabrera 1961; Hershkovitz 1954), it probably no longer occurs there (Acosta et al. 1996; Downer 1996a). Altitudinal range is from 1,400 to 4,700 m (Acosta et al. 1996; Downer 1996a; Goudot 1843; Roulin 1829); T. pinchaque is most commonly found between 2,000 and 4.300 m (Downer 1996a).

FOSSIL RECORD

In the New World, the geological range of the family Tapiridae is Oligocene to Recent in North America, and Pliocene to Recent in South America; geological range of the genus *Tapirus* is early Miocene to Recent (Schoch 1989). Earliest known record of *Tapirus* in South America is from the Uquian land mammal age $(2.5-1.5 \times 10^6$ years ago) in Argentina. *Tapirus* also is known from the Ensenadan land mammal age $(1.5-0.5 \times 10^6$ years ago) in Bolivia and Peru (Webb 1985). *T. tarijensis* was reported from Pleistocene deposits of the Eastern Cordillera of southern Bolivia (Hoffstetter 1986). Although fossil tapir remains are found in Pleistocene deposits throughout the rest of South America, Hoffstetter (1952) noted the absence of such remains in Ecuadorian deposits.

Tapirs are evolutionarily conservative animals with little structural change since their Oligocene origin (Radinsky 1965; Schoch 1989; Simpson 1945). The only features distinguishing extant from fossil tapirs are development of proboscis; relative enlargement and change in proportions of brain, especially rhinencephalon (Eisenberg et al. 1990; Radinsky 1965); and increased specialization of masticatory apparatus. The postcranial skeleton has remained basically unchanged with some modifications resulting from larger size of modern tapirs (Radinsky 1965). *T. pinchaque* is the least specialized tapir (Hershkovitz 1954) and its skull most closely resembles that of the early tapirid *Protapirus* (Hatcher 1896) and tapiroid *Heptodon* (Radinsky 1965).

FORM AND FUNCTION

Manus is tetradactyl and pes is tridactyl (Kuehn 1986). Each toe is covered by a large nail and supported by a padded sole. Outermost toe on manus does not reach ground (Eisenberg et al. 1990), except if ground is soft (Nowak 1999). *Tapirus pinchaque* is a good swimmer, runner, and climber, and usually walks with its snout close to ground (Nowak 1999). Eye color has been described as pale brown (Crandall 1951; Gale and Sedgwick 1968) or bluish (Allen 1942; Gale and Sedgwick 1968); this variation has been attributed to age, with older animals having darker eyes (Schauenberg 1969).

Described as dense and matted, adult pelage has hair from 1 to 3.5 cm in length along back (Crandall 1951; Gale and Sedgwick 1968; Hershkovitz 1954), and progressively longer hair along sides (Hershkovitz 1954). Longest hair occurs along belly, chest, and flank, whereas shortest occurs along back and limbs (Schauenberg 1969). Hairs have 1 or 2 kinks (Crandall 1951).

Dorsal cover hairs are very fine and crinkly, whereas lateral and ventral lanugo is long and crinkly. Guard hairs are stiffer than cover hairs (Hershkovitz 1954). The dark coat insulates and absorbs solar heat (Downer 1997). Although both sides of ears are hairy, outer side is more densely haired (Gale and Sedgwick 1968). Manus and pes are ringed with an area of bare skin just above digits, from 1 to 3 cm in width, and white, pink, or gray in color. *Tapirus pinchaque* has a bare patch of skin on rump, bisected by a line of hair (Eigener 1954; Hershkovitz 1954). The patches, which lie along the sagittal line, are paired, symmetrical, and vary in width from 12 to 60 cm. Patches have been attributed to rubbing to relieve itching or, according to native hunters, downhill sliding (Kuehn 1986). Such patches also may occur naturally in this species (Crandall 1964; Downer 1995; Eigener 1954; Gale and Sedgwick 1968). Bare patches appear even in animals that have lived their entire lives in captivity, and develop in most animals, regardless of sex, upon reaching 66% of adult size; thus, patches may relate to sexual maturity (Schauenberg 1969). Hide is relatively thin and scars easily; skins of wild *T. pinchaque* are covered with scars (Schauenberg 1969).

Tapirus pinchaque has long-persisting and well-developed deciduous dentition. Teeth are brachyodont, lack cement, and molars are bilophodont. First upper premolar is longer than it is broad; internal cone, located on the extreme postero-internal angle, is rudimentary. On P2, anterointernal cone is a tubercle with no anterior cross crest (Hatcher 1896). First upper premolar may or may not have a cinguloid shelf. Upper incisors are particularly opisthodont (Hershkovitz 1954). Adult dental formula is i 3/3, c 1/1, p 4/3, m 3/3, total 42 (Hall 1981).

A detailed description of the skeleton of *T. pinchaque* is available (Döderlein 1877), as is a partial description (Radinsky 1965). Dorsomedial border of maxilla, prior to termination of premaxilla, is rolled ventrally. Laterally adjacent body of maxilla is inflated, creating a semienclosed chamber on either side of the bony snout anterior to infraorbital foramen.

Facial osteology is greatly reduced to accommodate the fleshy proboscis (Witmer et al. 1999). Nasal bones are long, slender (Ray and Sanders 1984), co-ossified, and posteriorly lower than frontals (Hatcher 1896). Anterior nasal openings are enlarged and recessed (Hall 1981). Ossified septum does not extend in front of posterior border of nasal opening. Extending slightly upon base of nasals, cavity for lodgment of cartilaginous air sinus is deep (Hatcher 1896).

Facial exposure of lacrimal is high and narrow in *T. pinchaque* because of spicular preorbital process, rugose sculpturing, and a tendency to develop a 2nd anterior process. Often, there are 3 lacrimal foramina, 2 of which lie inside orbital margin (Ray and Sanders 1984). Lacrimal foramen is "double" because fossa is bridged posteriorly by a thin osseous lamina (Cave 1965). Facial nerve runs posteriorly along lateral face of petrosal in a ventrally open groove (Radinsky 1965).

Temporal lines of adults converge posteriorly at about midsagittal frontoparietal boundary and then move forward while diverging obliquely. The skull of a *T. pinchaque* showed evidence of an antorbital traction epiphysis (Cave 1965). Sagittal crest is formed across fused posterior one-half of parietals, whereas parasagittal crests are narrowly

separated by a longitudinal groove on anterior half (Ray and Sanders 1984) that obsolesces with age (Hershkovitz 1954). Low and relatively short sagittal crest gives skull a flattened dorsal cranial contour. Dorsal profile is almost parallel to basicranial profile; dorsal frontal region is broad (Radinsky 1965; Ray and Sanders 1984). Mean (n = 5) greatest length of skull, from gnathion to nuchal crest and measured on a horizontal plane, was 35 cm with a functional M1, 38.5 cm with a functional M2, and 37.5 cm with a functional M3 (Hershkovitz 1954).

Proboscis is a fleshy, tubular structure arising from tissues of upper lip and nose, and extending rostrally from a point caudodorsal to orbit beyond premaxillary rostrum to drape ventrally past lower lip. Key facial muscles, including caninus, lateralis nasi, levator labi superioris, and levator nasolabialis, have all been co-opted to function in movement of proboscis. Proboscis also has undergone such a radical transformation that it is essentially a muscular hydrostat. A relatively rigid, osseocartilaginous, narial support structure has been replaced by a flexible, prehensile structure composed of connective tissue and muscle (Witmer et al. 1999).

Nasal bones are reduced and retracted, and several cartilaginous components found in other perissodactyls have been apomorphically lost, including alar and medial accessory cartilages, rostral portion of nasal septum, and associated musculature (dilatator naris apicalis and lateralis nasi pars ventralis). Rostral one-half of proboscis lacks any significant internal osseocartilaginous support (Witmer et al. 1999).

Expansion of nasal vestibule compressed and simplified caudal components of nasal cavity, resulting in reduction of dorsal and middle nasal conchae, and loss of plica recta and plica basalis. In spite of large proboscis, length of nasal cavity relative to total length of head is comparable to that of other animals, including bison (*Bison*), deer (*Odocoileus*), horses (*Equus caballus*), and pigs (*Sus*), but nasal vestibule of the tapirs, including *T. pinchaque*, occupies a greater proportion (75%) of nasal cavity (Witmer et al. 1999).

Outpocketings of eustachian tubes of *T. pinchaque*, as in the other tapirs, form a pair of cartilaginous palatal cavities in upper pharynx; their function is unknown (Eisenberg et al. 1990). Guttural pouches are located in pharyngeal region, alongside hyoid bones (Kuehn 1986).

Tapirus pinchaque is a hindgut fermenter (Olmos 1997) with a simple stomach (Eisenberg et al. 1990), the squamous portion of which is small and located in the cardia (Janssen et al. 1996). Cecum is short and lumen large. Testes lie in a scrotum alongside penis, which is very long and slightly curved. Glans penis is surrounded by flaplike erectible structures (Eisenberg et al. 1990). *T. pinchaque* has a single pair of inguinal mammary glands (Hershkovitz 1954; Kuehn 1986).

The renal cortex of *T. pinchaque* is continuous, nonlobed, and constitutes about 80% of renal mass in adults and 71% in term neonates. Medulla is of the simple crest type, lacking pelvic extensions along the major intrarenal blood vessels and pelvic intravascular eminences. *T. pinchaque* may have about 3×10^6 glomeruli per kidney. Number of glomeruli per gram of cortex was 13,400 in *T. pinchaque*. Measurements (g or mm) of a single kidney in an adult female *T. pinchaque* were: mass, 262; length, 150; greatest width, 90; greatest thickness, 40 (Maluf 1991).

Two healthy adult male *T. pinchaque* had erythrocyte counts of $5,500,000/\text{mm}^3$ and $6,900,000/\text{mm}^3$, leukocyte counts of $8,600/\text{mm}^3$ and $11,000/\text{mm}^3$, 42% and 46% neutrophils, 58% and 34% lymphocytes, 11.5 g/dl and 12.0 g/dl hemoglobin, and 30% and 35% packed cell volume, respectively. The 1st of the 2 *T. pinchaque* had a 0.5-mm buffy coat of leukocytes above packed erythrocytes (Kuehn 1986). Hematologic and serum chemistry values fall within the following values: hematocrit, 31-47%; white blood count, 5,000-16,000 cells/µl; fibrinogen, 100-400 mg/dl; blood urea nitrogen, 3-20 mg/dl; creatinine, 0.5-1.9 mg/dl; glucose, 70-120 mg/dl; sodium, 128-145 meq/l; potassium, 3.1-4.5 meq/l; chloride, 85-110 meq/l; calcium, 8.5-12.5 meq/l; and phosphorus, 3.2-7.0 meq/l (Janssen et al. 1996).

Primary structure of pancreatic polypeptide was nearly identical to that of Przewalski's horse (*Equus caballus przewalskii*), and the mountain zebra (*Equus zebra*), with only 1 substitution of leucine for methionine 3 (Henry et al. 1991). The alpha chain insulin of *T. pinchaque* is the same as that of the white rhinoceros (*Ceratotherium simum*), but differs from that of Przewalski's horse and the mountain zebra by the substitution of a serine by a glycine residue. Otherwise, the overall structure of insulin is similar and composition of the beta chain of insulin is the same for all 4 species of perissodactyls (Henry et al. 1993).

ONTOGENY AND REPRODUCTION

Ontogeny.—A single young is the norm in Tapirus pinchaque (Schauenberg 1969). Three T. pinchaque calves, 1 dying shortly after birth from a congenital defect, 1 dead at birth, and 1 born alive, had masses of 4.1 (Tapir Research Institute 1971), 4.15, and 5.4 kg (Bonney and Crotty 1979), respectively. Measurements (cm) made on the 1st calf, of unidentified sex, were: height at shoulder, 27.5; total length, 57.8; length of tail, 4.4; length of ear (from notch), 5.6; and length of the dorsal hair, 2.5 (Tapir Research Institute 1971). The 2nd calf, a female, had a height at shoulder of 27.9 and a total length of 58.7. The last calf, a male, had a height of shoulder of 31 and total length of 62.2. At 11 months, this male had a mass of 91 kg with a height at shoulder of 78.7 and total length of 132 (Bonney and Crotty 1979). A calf born in 1968 in Quito, Ecuador, had a mass of 6.2 kg at birth (Schauenberg 1969).

Juveniles are usually brown with a variable pattern of yellow and white longitudinal stripes and spots (Hershkovitz 1954; Kuehn 1986). A thin white stripe and 3 rounded light spots occur at the margin of the incisura intertragica and at the caudal ear side, respectively (Heran 1989). Hair of newborn is soft and thick measuring from 2 to 5 cm in length (Bonney and Crotty 1979). Juvenile markings may last up to a year (Barongi 1993; Bonney and Crotty 1979). In 1 calf, premolars erupted on day 7, bottom incisors on day 8, top incisors on day 9, and molars on day 55 (Bonney and Crotty 1979). A female calf with all deciduous premolars and M1 in place had a fully formed sagittal crest (Lundelius and Slaughter 1976).

Weaning begins at 3 months (Kuehn 1986). Immunoglobulin transfer from mother can be tested using glutaraldehyde coagulation on serum from calf. Preferred site for venipuncture in a newborn is the jugular (Janssen et al. 1996). Wild mothers care for young for 18 months. Mothers keep young well hidden by vegetation and will defend young by biting (Downer 1996a).

Tapirus pinchaque reaches definitive adult size (in terms of skull length) by the time M2 appears (Hershkovitz 1954). There appears to be no significant relationship between age and size after 2nd upper molar becomes functional (Hershkovitz 1954). Longevity record for a captive *T. pinchaque* is 27 years, 8 months, and 21 days at the Wilhelma Zoo in Stuttgart (Holtkötter 1998).

Reproduction.—Captive Neotropical tapirs become sexually mature between 14 and 24 months of age (Barongi 1993). Mating behavior of 1 pair of captive *Tapirus pinchaque* indicated a 30-day estrous cycle (Bonney and Crotty 1979). Although postpartum estrus is possible, interbirth intervals are rarely 18 months. One exception involved a captive *T. pinchaque* that gave birth on 12 March 1992, reared the calf, and gave birth to a full-term calf on 20 May 1993, a 14-month interval (Barongi 1993).

Using 3 separate enzyme immunoassay methods on urinary steroids, it was determined that C-19 and C-21 nonspecific progesterone metabolites were best for detecting and monitoring pregnancies in *T. pinchaque* (Ramsay et al. 1994). Cage-side real-time ultrasound scanning was used to confirm a pregnancy in a captive animal (O'Grady et al. 1978).

Pregnancy in a captive female was signaled by a vaginal discharge. Ten days later, a clear fluid was extractable from udder and about 1 month later, pregnancy was confirmed by palpation. Five days after confirmation, vulva was slightly dilated with loss of muscle tone in posterior region. Waxing of nipples was 1st observed about 3 days after confirmation and 11 days later, when milk began to drip, birth occurred. Nursing was not observed until the day after birth and mating was observed about 1 month later. Gestation period was estimated to be 392 or 393 days (Bonney and Crotty 1979).

ECOLOGY

Population characteristics.—Population densities were estimated at 1 individual/587 ha in Sangay National Park, Ecuador (Downer 1996a); 1 individual/400 ha in Ucumari Regional Park, Colombia (Acosta et al. 1996); and 1 individual/551 ha in Los Nevados Natural National Park, Colombia (Lizcano and Cavelier 2000b). These figures (1 individual/400–587 ha) give *Tapirus pinchaque* the lowest population density of all American tapirs (Lizcano and Cavelier 2000a).

Space use.—Average home range in the Sangay National Park, Ecuador, was estimated at 880 ha. Adult females seem to have a larger home range and often are found in partial association with male territories. *Tapirus pinchaque* traverses these territories often using tunnel-like trails through heavy vegetation and on slopes of $\geq 45^{\circ}$ (Downer 1996a). Home range of a male wearing a global position system collar was estimated to be 3.5 km² using the minimum convex polygon and 2.5 km² using the fixed kernel method (Lizcano and Cavelier 2004b). That tapir moved 94.1 km over a 6-month period. In Colombia's Valle de los Venados, a family group used trails to cross a territory composed of 3 eating grounds, 5 sleeping places, 5 scratching places, and 3 latrine sites (Acosta et al. 1996).

Although *T. pinchaque* generally inhabits moist habitats that facilitate bathing (Downer 1996a), it also frequents thick bush in the cold and humid zones of Andean mountains between 1,400 and 4,400 m (Acosta et al. 1996; Downer 1996a; Geroudet 1970). These areas include stands of wind-dwarfed *Polylepis* and *Hypericum* trees in Peru (Grimwood 1969), up to snow-covered parts of the Ecuadorian cordilleras (Goudot 1843; Gray 1872). *T. pinchaque* has been classified as a characteristic species of Andean temperate rain forest, and a member of the "fringe fauna" of the páramos (Hershkovitz 1969).

Of 5 identified habitat types, average habitat use was 28.7% in Andean forest, 22.9% in riverine meadow, 22.3% in chaparral, 19.7% in páramo, and 6.4% in pampas. Andean forest may be the most important because it provides food, protection, and shelter (Downer 1996a). One group of *T. pinchaque* in Colombia primarily used the root systems of large trees for sleeping sites (Acosta et al. 1996). Sleeping sites, however, are usually limited to heavily forested thickets (Schauenberg 1969).

Elevational range spans 3 habitat types including wet cloud forest, intergrading chaparral, and páramo (Downer 1995). Over the course of a year, individuals may engage in an annual elevational migration up to the páramo during the dry season and down into forested areas during the wet season (Acosta et al. 1996; Downer 1996a, 1997; Stummer 1971). However, in a study of *T. pinchaque* in Colombia, no consistent data were found to support the hypothesis that *T. pinchaque* was more active at higher elevations during the dry season. Although no correlation was found between

monthly rainfall and seasonal activity (Lizcano and Cavelier 2000a), a correlation was found between temperature and activity (Lizcano and Cavelier 2004b).

Diet.-Tapirus pinchaque is a foliage browser that will eat a broad array of plant material, including bromeliads, ferns, grasses, herbs, shrubs, and trees (Downer 2001, 2006). Stomach content analysis of specimens of wild T. pinchaque indicated the presence of ferns and shoots of chusque (Chusquea-Hershkovitz 1954), including Chusquea scandens. In the páramo, T. pinchaque feeds on shoots of frailejon (Espeletia grandiflora) and rough grasses (Goudot 1843) and during the dry season of the Andean páramo, T. pinchaque eats berries of Vaccinium and Pernettya (Olmos 1997). T. pinchaque also will raid crops, including potatoes (Suárez and Lizcano 2002). In the Central Cordillera of Colombia, T. pinchaque browses sites located near water. Twenty-three species of food plants were identified, along with another 23 that also may be eaten. These plants were almost all characteristic of secondary succession, with the family Compositae having the most representatives (Acosta et al. 1996). In Sangay National Park, Ecuador, T. pinchaque consumed 205 of 264 identified vascular plant species, including 35 of 59 species of Asteraceae and 13 of 14 species of Rosaceae, showing clear preferences for certain plant taxa (Downer 1996a). Of 28 plant families, the Asteraceae had the greatest number of species eaten, followed by the Gramineae, Rosaceae, Cyperaceae, Fabaceae, Scrophulareaceae, and Valerianaceae (Downer 2001). Although Lupinus held the highest dietary preference ratio (indicating those food groups that are most sought relative to their presence in the studied habitat), the leaves of a Gynoxys accounted for 24% of the diet, and fern fronds 19%. The umbrella plant (Gunnera brephogea) is a dietary mainstay (leaves and trunk are consumed) and a source of shelter for T. pinchaque (Downer 1996a, 2006).

Tapirus pinchaque frequents mineral seeps and other salt accumulations (Acosta et al. 1996; Downer 1996b; Goudot 1843; Stummer 1971), which may either provide necessary trace elements or neutralize toxins contained in certain food plants, including *Gunnera manicata* and *Oxalis subintegra* (Acosta et al. 1996). The animals may also be seeking Na, N₂H₄, and N₂O₃, found in higher concentrations in the water at 1 salt lick; these substances may have been fixed by *Nostoc*, a cyanobacterium associated with *G. manicata* and *G. magnifolia*. *T. pinchaque* may have been supplementing a diet low in nitrogen, which is common in tropical montane forests (Lizcano and Cavelier 2004a). Preference for nitrogen fixers such as *Gunnera* and *Lupinus* also may result from the high nitrogen content of those plants (Downer 2001).

Diseases and parasites.—Tapirus pinchaque is host to large numbers of ticks (species unidentified—Hershkovitz 1954). During the dry season, tabanid flies may trigger the elevational migration of populations in the Central Cordillera of Colombia (Acosta et al. 1996) and in Ecuador (Stummer 1971).

Interspecific interactions.—Tapirus pinchaque and T. terrestris may occur sympatrically on the eastern half of the eastern Andes of Colombia (Hershkovitz 1954) and Ecuador (Downer 2001). T. pinchaque does not occur sympatrically with T. bairdii. It is believed that there are no environmental, morphological, or physiological barriers to preclude coexistence of all 3 species (Hershkovitz 1954). Interspecific competition is not thought to limit tapir dispersal (Hershkovitz 1969).

Consumption of minerals also may explain the high germination rate of seeds found in feces of *T. pinchaque* in Sangay National Park (Downer 1996a) and other areas (Olmos 1997). Of the 205 species of vascular plants consumed, 42% of their seeds were found to germinate in feces of *T. pinchaque* (Downer 1996a). Among other factors, greater inefficiency in seed digestion relative to other ruminants, a tendency to defecate in water, and selective feeding habits make tapirs important seed dispersers (Olmos 1997).

Considering their evolutionary history (Radinsky 1965; Schoch 1989; Simpson 1945), Neotropical tapirs may play a vital role as surrogate seed dispersers for existing largefruited plant species that were once dispersed by the Pleistocene megafauna (Janzen and Martin 1982). This role reaches its apex in *T. pinchaque*, which among other things, disperses seeds of grasses and sedges, plant species having no special adaptation for endozoochory (Downer 1996a; Olmos 1997). *T. pinchaque* may have coevolved and become coadapted with Andean plants as a result of mutualistic relationships (Downer 2001).

Tapirus pinchaque also disperses seeds for other plant species, including the endangered wax palm (*Ceroxylon quindiuense*), Colombia's national tree (Downer 1996a), whose decline further jeopardizes the nearly extinct yelloweared parrot (*Ognorhynchus icterotis*—Olmos 1997). *T. pinchaque* may be an obligate symbiont for *C. quindiuense*, which, like the highland lupine (*Lupinus caucensis*), has declined wherever *T. pinchaque* has been eliminated (Downer 1996a). The high Andean ecosystem is faunistically and botanically less complex than the lowland rain forests, so *T. pinchaque* may be a more crucial component of this ecosystem than similar seed dispersers in the lowland ecosystems (Downer 2001).

Tapirus pinchaque levels vegetation and topples trees, rendering this material accessible to other herbivores (Downer 1996a), including the pudu deer (*Pudu mephistophiles*) and cavy (*Cavia aperea*—Downer 1997). *T. pinchaque* also creates latrine sites (Acosta et al. 1996), which may significantly impact soil formation (Olmos 1997). Because of these and other traits, including seed dispersal, *T. pinchaque* has been called a keystone or flagship species for the Andean ecosystem (Downer 1997; Olmos 1997). Moreover, there may be a significant relationship between rise of the Andes, occupation of the mid- to high northern Andes by this seed disperser and its ancestors, and formation of montane forest and páramo ecosystems. It has been suggested that *T. pinchaque* played a role in the evolution (Downer 2001) and conservation of the mid- to high northern Andes ecosystem (Downer 1997).

Mountain lions (*Puma concolor*—Downer 1996a) and, possibly, spectacled bears (*Tremarctos ornatus*—Peyton 1980) prey on *T. pinchaque*. Jaguars (*Panthera onca*) also may kill *T. pinchaque* driven to higher elevations due to deforestation (Downer 1996a). Andean condors (*Vultur* gryphus) reportedly kill abandoned newborns and weakened individuals (Downer 1995).

HUSBANDRY

Spread thinly throughout its range, the remote habitat of *Tapirus pinchaque*, difficulty in adjusting to captive diets, and long acclimation period make it a rarity in captivity (Wilson and Wilson 1973). In 1979, there were only 7 *T. pinchaque* in captivity (Thornback and Jenkins 1982), and 24 years later, there were still only 9 animals in zoos, with 2 pairs at the Los Angeles Zoo, 2 males and a female at the San Diego Zoo, and 1 pair at the zoo in Stuttgart, Germany (Anonymous 1993). There were only 6 animals in North American zoos as of 2003 (Barongi 2003). The Los Angeles Zoo, where the 1st captive live birth took place (Bonney and Crotty 1979), has had the greatest success in breeding mountain tapirs and as of 1987, 12 had been born there (Eisenberg et al. 1990).

Captive *T. pinchaque* require a more specialized diet than other tapirs (Crandall 1964; Tapir Research Institute 1971). The main difficulty in maintaining captives is providing a nutritionally adequate diet that will be accepted by the animals. Reasonably successful zoos have used the following diets: 2 kg cooked rice, 1.5 kg diced carrots and apples, 0.3 kg bread, and 1 kg lucerne or alfalfa (Parc Zoologique de Paris, France); 1.82 kg Purina Dog Chow, 1.82 kg Purina Monkey Chow, 1.82 kg Purina Dairy Conditioner, 1 head of lettuce, 0.45 kg carrots, 4 slices of bread, alfalfa, and hay (Gladys Porter Zoo, Brownsville, Texas); and 5 heads of lettuce, 3.6 kg apples, 0.9 kg carrots, 2.7 kg bananas, 0.5 kg Purina Monkey Chow, and 1.8 kg yams (Los Angeles Zoo, California—Bonney and Crotty 1979).

Two animals at the Los Angeles Zoo were gradually weaned off an exclusive diet of romaine lettuce, ripe bananas, and apples, and on to a dampened alfalfa meal, rolled barley, green vegetables, commercial vitamin–mineral supplements, and a homogenized food concentrate in pellet form (Gale and Sedgwick 1968). Very young animals can be raised on evaporated or powdered bovine milk plus bone meal and vitamins. Cod liver oil is preferred and can be used to induce juveniles to try new foods (Kuehn 1986).

Tapirus pinchaque is known to frequent mineral accumulations in the wild (Downer 1996b; Stummer 1971),

and to feed on silica-rich horsetails (*Equisetum*—Olmos 1997) and clayish mud (Hershkovitz 1954). Clinically low values of serum copper may indicate a unique metabolic requirement for copper (Janssen et al. 1996). In captivity, salt blocks or other sources of minerals should be provided (Kuehn 1986).

Recommended total daily intake for a mature adult is 4– 5% of body weight, with pregnant or lactating females and calves requiring slightly more (Barongi 1993). Because overeating can cause problems in herbivores with hindgut fermentation, it is recommended that feeding occurs 2 or 3 times each day (Janssen et al. 1996).

Acclimation of wild animals requires health monitoring and frequent use of antibiotics. Individuals of T. pinchaque taken in the Ecuadorian Andes and being conditioned to captivity were fed a diet of carrots, alfalfa hay, and mineral salts for several weeks while still in Ecuador (Pournelle 1965). Given carefully controlled handling during capture and transport, breeding potential is reasonable (Mallinson 1969). The following guidelines for transfer of tapirs, including T. pinchaque, are available: fecal analysis for parasites; fecal culture for Campylobacter and Salmonella; tuberculin skin testing; bovine tuberculosis testing at time of tuberculin testing or reading; hemoanalysis for complete blood count and fibrinogen and serum chemistries; regionally dependent testing for tetanus, other clostridial diseases, or equine encephalitis; and a complete physical examination, including oral, ophthalmic, and footpad inspections (Janssen et al. 1996).

Indoor and outdoor components for exhibit and holding areas are necessary (Barongi 1993). A suggested minimum enclosure size is 10 by 20 m without corners (Kuehn 1986). Walls without footholds and heights of ≥ 2 m also are suggested because T. pinchaque is an adept climber and will stand on its hind legs and pull itself over (Barongi 1993; Crandall 1964; Kuehn 1986). A protected stall, heated quarters where severe cold occurs, and an exercise area with relatively soft materials for flooring are required (Kuehn 1986). Pools in enclosures are desirable, if not essential (Crandall 1964). The Los Angeles Zoo's exhibit of T. *pinchaque* included a 3 by 5 by 1-m pool, an adjoining 7 by 7-m yard to be used when necessary to house animals separately, and a barn with 2 stalls and 2.7 by 3.7-m wooden pallets for sleeping (Tapir Research Institute 1971). Other requirements for tapir housing have been provided by Barongi (1993) and Crandall (1964).

Two or more *T. pinchaque* of the same sex have been kept together in captivity (Tapir Research Institute 1971); *T. pinchaque* at the Los Angeles Zoo was kept with a group of Patagonian cavies (*Dolichotis patagonum*). At least 1 male *T. pinchaque* had to have the 2 lower canines and 3 lower incisors blunted as a result of aggressive behavior (Bonney and Crotty 1979).

Fecal analysis of *T. pinchaque* taken from the wild showed possible *Strongylus*, *Strongyloides*, and possible

contamination with *Paranoplocephala*. Captive *T. pinchaque* have been subject to balantidiasis (Bonney and Crotty 1979), infestation with *Paranoplocephala* (Reichel 1983), and possible giardiasis (Gale and Sedgwick 1968). The negative impact of livestock invasion into habitat occupied by wild *T. pinchaque* in Ecuador's Sangay National Park, including the transmission of parasites, has been discussed (Downer 2003a).

Deaths in captive *T. pinchaque* have been attributed to possible infectious pericarditis and pneumonia, acute hemorrhagic gastroenteritis, complicated by balantidiasis and chronic endometreitis in animals whose cecum and colon contained 2.25 kg of sand; enterotoxemia resulting from a cervical abscess (Bonney and Crotty 1979); herpes virus infections (Reichel and Mayer 1972); tuberculosis; and nonacceptance of food. Mortality factors for captive tapirs have been compiled (Janssen et al. 1996; Tapir Research Institute 1971).

Although the most common cause of death in captive adult *T. pinchaque* was tuberculosis, in juveniles the most frequent cause was drowning (Tapir Research Institute 1971). A released domesticated juvenile female *T. pinchaque*, about 3 years of age, died of rabies after having been bitten by a domestic cat in the mid-1990s, in the Pasochoa Nature Reserve several kilometers south of Quito, Ecuador (Castellanos-Peñafiel 1994).

Although no reports of tetanus have been found (Ramsay and Zainuddin 1993), tetanus toxoid vaccinations are recommended (Barongi 1993; Janssen et al. 1996; Kuehn 1986; Ramsay and Zainuddin 1993). Vaccinations for certain equine encephalomyelitides, if present in the area, also should be administered. Parasite treatment schedules are the same as for large livestock (Gale and Sedgwick 1968; Kuehn 1986; Ramsay and Zainuddin 1993). Using a *Microsporum bovis* antigen, inguinal region may be the best site for tuberculin skin testing, although skin around perineum also can be used. The bovine tuberculosis test can be useful during diagnosis (Janssen et al. 1996).

Periodic, watery, rust-colored diarrhea, containing *Balantidium*- and *Giardia*-like protozoans, was treated in a captive *T. pinchaque* with chlortetracycline in a carob flour base in food (Kuehn 1986). *Paranoplocephala* in another captive was treated with chlorsalicylamide (Reichel 1983). *Microsporum canis* caused lesions and alopecia of the body and proximal extremities of a captive, and was cured with griseofulvin (Schnurrbusch et al. 1972); *M. canis* found in an untreated animal resolved spontaneously (Saez et al. 1977).

Chemical tranquilization of an average captive adult can be achieved within 15–30 min by use of 1 mg etorphine and 1 mg atropine sulfate via intramuscular injection and maintained using supplemental doses of etorphine or halothane or methoxyflurane gas. Complications such as hypersalivation and pulmonary edema can be regulated using atropine; diprenorphine will reverse effects of etorphine (Kuehn 1986). An alternative to etorphine, butorphenol used in conjunction with an alpha-2 adrenergic, like xylazine ordetomidine, has cardiovascular advantages (Janssen et al. 1996). Tranquilization through a combination of carfentanil, ketamine, and xylazine also has been discussed (Miller-Edge and Amsel 1994).

Simple sedation can be achieved using azaperone (1.0 mg/kg intramuscular) or the less-reliable xylazine (1.0 mg/kg intramuscular—Janssen et al. 1996). In capturing a pair of wild animals with masses of 180 kg (male) and 200 kg (female), an anesthetic dart was used with a solution of detomidine, 100 mg of ketamine, 500 mg of tiletamine/ zolazepam, and 5 mg of atropine (Lizcano and Cavelier 2004b).

BEHAVIOR

Tapirus pinchaque is a solitary animal, found in the presence of others mainly while mating, rearing young (Eisenberg et al. 1990), and fighting rivals (Downer 1996a), which may be a function of human disturbance (Barongi 1993). Territories of an adult male and female will overlap, so that 1 area may host a family group composed of the adult pair, a subadult, and young (Acosta et al. 1996).

Although it is active both day and night (Lizcano and Cavelier 2000a), *T. pinchaque* tends to be crepuscular in nature (Barongi 1993; Downer 1995, 1996a). *T. pinchaque* has been found to be more diurnally active (about 50%—Downer 1996a) than was once thought to be the norm for all tapirs (Cabrera and Yepes 1960). In Sangay National Park, *T. pinchaque* 3–10 years of age slept mostly between midnight and dawn, and had peaks of activity between 1500 and 2100 h and between dawn and 0900 h. A resting period occurred between 1200 and 1500 h. Subadults were mainly inactive throughout the day (Downer 1996a).

Studies of a population living in mature and secondary montane forests of the Colombian Central Andes demonstrated a bimodal activity pattern, with a peak from 0500 through 0700 h, and then again from 1800 through 2000 h. At a salt lick, activity peaks occurred bimodally at midnight through 0200 h, and then again at 1100 through 1400 h. Within a belt of the Colombian Central Andes ranging from 3,100 to 3,600 m elevation, T. pinchaque was more active at lower than higher elevations, and in mature than secondary forests; nocturnal activity was greater during periods of full moon than during other lunar phases (Lizcano and Cavelier 2000a). A subsequent study of 2 T. pinchaque with global positioning system collars indicated a pattern with higher activity during 0700-0800 h, and then again between 1300 and 1400 h with a decrease in activity at 1200 h and late afternoon. A correlation between temperature and activity may exist because T. pinchaque rests during hottest parts of the day (Lizcano and Cavelier 2004b).

Bedding sites normally are hidden in heavy vegetation. However, in areas used by cattle or that are otherwise disturbed, bedding sites are located on steep, forested mountain slopes (Schauenberg 1969). Foraging occurs in a perambulating manner, possibly as much for predator avoidance as for foraging efficiency (Downer 1997). Using global positioning system collars, it was determined that 2 animals traveled 91.4 km over 6 months. Traveling an average distance of 326 m between fixed locations, their average speed was 0.6 km/h (Lizcano and Cavelier 2004b). A selective browser, T. pinchaque chooses certain food items over others using bristles on the end of its prehensile proboscis in addition to other sensory organs. T. pinchaque also will raise itself onto its hind legs and, using the proboscis, reach for food nearly 3 m off the ground (Downer 1997).

In captivity, courtship is characterized by nose-to-tail pursuit by the male, which uses playful, soft bites and grunts and squeals to attract the attention of the female. Attempted matings in the water have been observed. At 1 zoo, however, the male of a pair had to be separated from the female for long periods of time due to his very aggressive behavior. During courtship, this male chased the female and, although smaller, would corner the female and bite her. In response, the female would simply lie down, squeal, and allow herself to be bitten. Courtship involved frequent vocalization, mostly by the female. Six weeks after the male was allowed to join the female and his calf, the male had to be removed because of his aggressive behavior toward his mate and offspring. From that point on, the male was placed with his mate and offspring for only a few hours each day (Tapir Research Institute 1971).

Although generally nonaggressive, *T. pinchaque* has a dangerous bite and can be incited to charge humans. Several incidents involving charging *T. pinchaque* have been described (Goudot 1843; Schauenberg 1969). In a single incident in the Sangay National Park, 1 of us (C. C. Downer) observed an adult male *T. pinchaque* give a low guttural grunt before charging. *T. pinchaque* also will draw water into its trunk and spray it at potential predators (Downer 1996b). Males fight viciously among themselves, inflicting deep bites that damage the ears and rear limbs (Schauenberg 1969). Wild males may engage in violent fights over receptive females (Downer 1996a; Eisenberg et al. 1990).

In the Central Cordillera of Colombia, the local populace distinguishes *T. pinchaque* from *T. terrestris* and *T. bairdii* based on its color and behavior. *T. pinchaque* is called "pizarra" for its darker coloration and is known for its habit of confronting potential predators and standing its ground. In contrast, the other tapirs are called "revolcadoras" for their habit of moving back and forth and heading for the closest body of water when similarly confronted (Acosta et al. 1996). There is a report that *T. pinchaque* will

also head for water at the 1st hint of danger (Goudot 1843). *T. pinchaque* has been observed by 1 of us (C. C. Downer) rolling on its back ("revolcar" in Spanish) in muddy soils when pursued by natural predators or dogs and hunters, probably to disguise its scent.

Tapirus pinchaque has been maintained as a pet (Crandall 1964), becoming docile and "attached" to its captors after a relatively brief period of time (Cordier 1952; Gale and Sedgwick 1968). However, these animals are also known to go "berserk" and break out of formidable enclosures; during these episodes, they have been known to attack all around them with their teeth (Downer 2003b).

Ear movement in *T. pinchaque* may function as a visual signal to conspecifics. The contrasting white edging of the upper ear tips may facilitate this signal in the poorly lit habitats that these nearsighted animals occupy (Heran 1989). *T. pinchaque* maintains contact acoustically using high-pitched whistles and also emits a high-pitched squeal to warn others of danger (as observed in adults), and to solicit help when in danger or attacked (as observed in subadults and juveniles by C. C. Downer).

Tapirus pinchaque delineates individual territories through urine marking (Moehlman 1985; Schauenberg 1969) and dung piles (Downer 1995, 1996a; Moehlman 1985). Urine marking is commonly accompanied by a reflexive pawing of the pes (Downer 1997). Females can spray urine for 1 m and males for 4–5 m. *T. pinchaque* engages in flehmen (Schauenberg 1969).

GENETICS

Tapirus pinchaque has a diploid number (2n) of 76 chromosomes (Fig. 4). Autosomes consist of 6 metacentrics/ submetacentrics and 68 acrocentrics/telocentrics (Barongi 1993; Houck et al. 2000); number of autosomal arms is 80. The Y chromosome is a small acrocentric and the X is a large submetacentric. There are at least 13 conserved autosomes between *T. bairdii* and *T. terrestris*, and at least 15 between *T. bairdii* and *T. pinchaque* (Houck et al. 2000).

Recent phylogenetic analysis using sequences of the mitochondrial cytochrome-c oxidase subunit II gene indicates that 3 separate tapir mitochondrial lineages, including a South American (*T. pinchaque* and *T. terrestris*), a Central American (*T. bairdii*), and an Asian (*T. indicus*), may have diverged rapidly beginning $20{-}30 \times 10^6$ years ago. The estimates of divergence dates support the hypothesis of migration of a single tapir lineage into South America following the emergence of the Isthmus of Panama about 3×10^6 years ago. This event was followed by the existing speciation. Rate of evolution for the cytochrome-c oxidase subunit II gene in equids and tapirs was calibrated to be approximately 0.22% lineage⁻¹ million years⁻¹, a rate that is 3- to 4-fold lower than for hominoid primates (Ashley et al. 1996).



Fig. 4.—Karyotype of a male *Tapirus pinchaque* by M. L. Houck, Center for Reproduction of Endangered Species, Zoological Society of San Diego.

CONSERVATION

One of the largest indigenous terrestrial mammals in Latin America (Jorgenson 1988), *Tapirus pinchaque* also is one of the rarest mammals in the world (Barongi 1993). This critically endangered species was estimated to number 1,000–2,500 individuals (Barongi 1993; Downer 1997), spread over 20 remnant populations (Downer 1996a). The Peruvian population was estimated at up to a few hundred individuals (Downer 1997; Grimwood 1969) that live within an area of about 206,000 ha (Lizcano and Sissa 2003). Populations of Ecuador and Colombia have each been estimated at about 1,000 breeding adults (Downer 1997).

Although *T. pinchaque* in Colombia may once have been distributed over an area of 74,556 km², the present area is 14,385 km², or 19% of past distribution (Lizcano et al. 2002). In the northern Andes region (north of the Huancabamba Depression), there is suitable habitat for 5,349-5,699 animals, but only one-half these numbers (2,675–2,850) may actually survive because of extirpation by hunters, habitat invasion and disease transmission by livestock,

habitat fragmentation, and global warming, because *T. pinchaque* depends on cold, moist Andean forests and páramos (Cavelier et al., in press; Lizcano et al. 2005). Of the 35 patches of habitat, only 5 or 6 are large enough to maintain the minimal number of animals that can maintain a viable population in the short term. The status of *T. pinchaque* throughout its range and regional threats to individual populations have been discussed (Downer 1997). The number of animals in the Colombian Andes has been estimated at 2,500 animals in 35 forest patches (Lizcano et al. 2002).

Tapirus pinchaque is classified under Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (2009). It also is listed as "Endangered" by the International Union for Conservation of Nature and Natural Resources (2009), and under the United States Endangered Species Act (Grubb 2005). Tapir specialists for the International Union for Conservation of Nature and Natural Resources estimated that T. pinchague has a >20% probability of disappearing within the next 20 years (Downer 1996a; Mace and Lande 1991). More recent estimates suggest that its state of endangerment is even more critical due to meat and trophy hunting, illegal commerce in its parts, park and reserve colonization, mining claims and activities in habitat of T. pinchaque, and accelerating habitat destruction and fragmentation (Cavelier et al., in press; Downer 1997; International Union for Conservation of Nature and Natural Resources 2009; Lizcano et al. 2005). In 1980, the International Union for Conservation of Nature and Natural Resources' Species Survival Commission created the Tapir Specialist Group to develop conservation measures (Thornback and Jenkins 1982). Among other measures, the group is studying ecotourism, alternative markets, and agroforestry as a way of transforming human lifestyles; sympatric species, translocation, and captive breeding programs are also being examined (Downer 1997; Lizcano et al. 2005).

Tapirus pinchaque has a slow reproductive rate, large individual home range, and is a solitary animal (Downer 1997), making it highly sensitive to disturbance (Downer 1996a; Geroudet 1970; Grimwood 1969; International Union for Conservation of Nature and Natural Resources 2009). Unfortunately, even the severity of its habitat does not sufficiently protect the animal from human-induced fires, cattle and sheep ranching, hunting, mining, deforestation, and other forms of human encroachment (Allen 1942; Downer 1997, 2003a; Geroudet 1970; Lizcano et al. 2002; Lizcano and Sissa 2003; Suárez and Lizcano 2002). Although habitat alteration and human disturbance are the primary threats to existing populations (Lizcano et al. 2002; Thornback and Jenkins 1982), hunting is becoming an increasingly greater problem (Downer 1997), at least in Ecuador and Peru, and perhaps in Colombia (Lizcano et al. 2005).

In the past, *T. pinchaque* was hunted for its meat (Downer 1997; Eisenberg et al. 1990; Goudot 1843); its hides, which are used in rugs and blankets (Downer 1996a; Goudot 1843); and recreationally by trophy hunters. The hooves and snout are sought after in Ecuador, Peru, and Colombia for use in folk medicines as aphrodisiacs and for treatment of epilepsy and heart ailments (Downer 1996a, 1997). The hooves also are used as amulets (Allen 1942). The intestines are added to a soup that is consumed by those with intestinal parasites (Downer 1997). In Ecuador, indigenous people also kill *T. pinchaque* that raid crops (Naundorff 1953).

Although it is now illegal to hunt *T. pinchaque* in Colombia, Ecuador, and Peru (Downer 1997), where they are protected by law (Thornback and Jenkins 1982), people of European, indigenous, and mestizo descent regularly kill *T. pinchaque* due to ineffective law enforcement (Downer 1997). In Colombia's Los Nevadas National Park, potato farmers living within the park kill *T. pinchaque* that raids their crops (Suárez and Lizcano 2002). Even in Peru, where hunting pressure had abated, *T. pinchaque* continued to decline in areas where it was once common (Downer 2009; Grimwood 1969). Native hunting techniques in Ecuador have been described (Frädrich 1970).

Exploitation of wild populations for the zoo trade is another factor endangering *T. pinchaque*. In 1966, an American zoo spent 6 months attempting to obtain live specimens. Using hunting dogs and tranquilizer guns, they failed to acquire a live animal, but did manage to kill about 20 individuals during their efforts. During the period from 1967 until September of 1968, about 30 animals passed successfully through the hands of animal traders while 100 died in the process. Wounds and other injuries caused by the dogs and lassos used in the hunts, as well as by panictriggered falls from cliffs, contributed to the high losses. The monetary bounty for a pair of live *T. pinchaque*, \$5,000– \$8,000 during the 1960s, may continue to drive this trade (Geroudet 1970). Ecuador and Colombia now restrict the export of live animals (Thornback and Jenkins 1982).

It is estimated that each adult needs about 880 ha of Andean habitat to survive, and a minimum of 1,000 reproducing adults in order to have a viable population; such a population, in turn, would need at least 293,500 ha (Downer 1996a). With population numbers falling below these levels, genetic bottlenecking is an increasing concern (Downer 1995). While emphasizing the pivotal importance of protecting and interconnecting existing reserves, the urgent need for additional measures, including public education, development of alternative lifestyles for the local populace, population monitoring programs, additional reserves, and effective law enforcement, has been raised (Downer 1997, 2009). In an effort to raise ecological awareness of *T. pinchaque* and its habitat, a survey of 15 human settlements around Sangay National Park in Ecuador was conducted to gauge current attitudes and knowledge. A majority of local inhabitants indicated a willingness to change destructive lifestyles if provided the necessary support through government or privately supported programs, or both (Downer 2002, 2003c).

Tapirus pinchaque plays a crucial role in a rapidly disappearing ecosystem. Although a superb mountain climber, it now finds itself precariously balanced on the edge of extinction's precipice. Habitat alteration and destruction, hunting and commerce in its parts, and the potential coup de grâce of global warming drying highland habitat are pushing it over the brink. There exists an urgent need for immediate conservation measures ranging from the traditional (protection of parks, public education, and translocation) to innovative strategies that concretely modify and refine human values, attitudes, and their resultant lifestyles. The latter include novel forms of conservation-oriented and participative ecotourism and sustainably produced and ecologically harmonious crops and other products, and their markets. With sound knowledge and caring endeavor on the part of local populations and governments, T. pinchaque may avoid falling off the cliff of extinction as have so many of its Pleistocene tapir cousins.

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This account is dedicated to the memory of Michael Alberico, who contributed greatly to the field of mammalogy in Colombia. Michael served in the Peace Corps in Colombia and went on to earn his Ph.D. in the United States, later returning to Colombia where he became a professor at the University of Valle, Cali. He was a dedicated wildlife conservationist and took a courageous stand against the fumigation of forests in Colombia as part of the United States-backed drug eradication program called "Plan Colombia." His loss is much lamented in this nation, as it is worldwide.

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