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## Solenodon paradoxus (Soricomorpha: Solenodontidae)

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Abstract: Solenodon paradoxus Brandt, 1833, is a large lipotyphlan insectivore commonly called the Hispaniolan solenodon. S. paradoxus is 1 of 2 extant species in the genus Solenodon, and 2 subspecies are recognized. The species is one of few venomous mammals with venom delivery through a channel in a modified lower incisor. Current distribution is limited to the Dominican Republic and southern Haiti. S. paradoxus is listed as "Endangered" by the International Union for Conservation of Nature and Natural Resources; threats to conservation include habitat loss, fragmentation, and degradation, predation by exotic carnivores, and persecution from farmers.

Key words: endangered species, Hispaniola, Hispaniolan solenodon, insectivore, lipotyphlan insectivore, venomous mammal

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## Solenodon paradoxus BRANDT, 1833 Hispaniolan Solenodon

Solenodon paradoxus Brandt, 1833. Type locality "Hispaniola"; restricted to Port-au-Prince, Haiti by Baranova et al. (1981:4; see "Nomenclatural Notes").

AND CONTENT. Order Soricomorpha, Context Solenodontidae. Solenodon paradoxus is 1 of 4 species in the genus Solenodon with S. cubanus, S. marcanoi (recently extinct), and S. arredondoi (recently extinct). Two subspecies of S. paradoxus are recognized (Ottenwalder 2001):

S. p. paradoxus (Brandt, 1833:459). See above.

S. p. woodi Ottenwalder, 2001:299. Type locality "Bucan de Tui, S. Oviedo, Peninsula de Barahona, Provincia Pedernales, Dominican Republic."

Nomenclatural Notes. Our taxonomy followed Hutterer (2005); however, much doubt remains about the original type locality of the type species. Baranova et al. (1981) restricted the type locality to Port-au-Prince although Solenodon paradoxus likely never occurred there (J. A. Ottenwalder, pers. comm.). The name Haiti was used in reference to the entire island of Hispaniola in some earlier works (Peters 1863; Allen 1908), possibly explaining the later restriction to Port-au-Prince. Although most authors maintain Solenodon as the sole genus, a separate genus for the Cuban solenodons, Atopogale, originally proposed by Cabrera (1925), is supported by genetic evidence of divergence between Hispaniolan and Cuban solenodons 25 million years ago (Roca et al. 2004). Nomenclatural uncertainties surround this species that has historically been placed in the unresolved Insectivora. Members of this order have been provisionally divided into 6 orders, but currently no consistent phylogeny exists at this taxonomic level (Hutterer 2005). The name Solenodon comes from the Greek solenos meaning channel or pipe, and odontos meaning tooth, referring to the deeply grooved 2nd lower incisor. The specific name is derived from the Greek paradoxos meaning contrary to all expectation (Woods and Ottenwalder 1992). The species is often locally known



Fig. 1.—An adult male Solenodon paradoxus at Mencia, Pedernales Region, southwest Dominican Republic. Used with permission of the photographer J. Nuñez-Miño.

as jutia or zagouti (Woods 1981; Turvey et al. 2014); these names are also used in Haiti and the Dominican Republic to refer to the native capromyid rodent, *Plagiodontia aedium* (*Hispaniola hutia*), and the rhinoceros iguana, *Cyclura cornuta*, in Haiti (Woods and Ottenwalder 1992). Many other local names have historically been recorded for *S. paradoxus* in the Dominican Republic, including orso, milqui, homigero, juron, and ground hog (Verrill 1907). In the Departemente of Grande-Anse in Haiti, the name pointe nez is used (Woods 1976), and *S. paradoxus* is known to local people in the Duchity region of the Massif de la Hotte by a variety of names including nez longe, nen long, bouche long, zagouti bouche long, cochon dinjue nen long, all referring to *S. paradoxus*' elongated snout (Turvey et al. 2008).

#### **DIAGNOSIS**

Solenodon paradoxus (Fig. 1) is the only extant member of the genus found on Hispaniola (i.e., Haiti and Dominican Republic) and can be distinguished from the only other extant member of the genus, the Cuban solenodon *S. cubanus* (endemic to Cuba) by the presence of a diastema between I3 and C1, smaller diastemas between I2–3 and C1–P1, absence of accessory cusps on C1, P1, and P2 (Fig. 2), and presence of an os proboscis (Ottenwalder 2001). A bony subquadrate plate that supports the proboscis in *S. paradoxus* is absent in *S. cubanus* (Allen 1908). *S. paradoxus* has 1 more thoracic vertebra, 1 less sacral, and 1 less caudal vertebra than in *S. cubanus* (Allen 1910).

Solenodon paradoxus (mean total length =  $539 \,\mathrm{mm}$ , n = 49) is larger than *S. cubanus* (mean total length =  $444 \,\mathrm{mm}$ , n = 10—Ottenwalder 2001). Solenodon cubanus has short and less robust foreclaws, and its pelage is shorter, less dense, and less wooly; nose, face, and feet are sparsely furred (Allen 1908). In both species, the head is lighter colored than the dorsal pelage, but the distinction is pronounced in *S. cubanus* where the head, neck, shoulders, and throat are an abruptly contrasting yellowish-white (Allen 1908).

The subspecies, S. p. woodi, is smaller overall than S. p. paradoxus. Ranges (mm) of select cranial characters and bones of S. p. paradoxus specimens from central, northeastern, and eastern Dominican Republic and S. p. woodi specimens from southwestern Dominican Republic and southwestern Haiti were: greatest length of skull, 80.9-91.5 (n = 75) versus 72.3-82.5 (n = 37); condylobasal length, 75.5-86.6 (n = 73) versus 67.1-79.4 (n = 37); palatal length, 34.8-40.4 (n = 75) versus 30.8-37.0 (n = 41); length of maxillary toothrow, 23.6–27.6 (n = 74) versus 21.6–25.7 (n = 43); maximum width of M3, 5.2–7.7 (n = 75) versus 4.4–7.2 (n = 41); greatest mandible length,  $50.9-58.1 \ (n = 78) \ \text{versus} \ 45.2-52.6$ (n = 43); length of mandibular toothrow, 23.3–28.9 (n = 78) versus 23.5–27.4 (n = 44); alveolar length of p4-m3, 14.9–18.5 (n = 76) versus 14.6-17.3 (n = 44); angular condylar height, 12.2-17.1(n = 78) versus 11.9–15.1 (n = 44); maximum length of p4, 3.7– 4.9 (n = 75) versus 3.5–4.9 (n = 43); maximum width of femur, 12.3-14.6 (n = 44) versus 11.4-13.4 (n = 42); and total length of humerus, 43.9-50.7 (n = 43) versus 40.6-46.8 (n = 37).



**Fig. 2.**—Dorsal, ventral, and lateral views of skull and lateral views of right and left mandible, respectively, of an adult female *Solenodon paradoxus* (Smithsonian Institution United States National Museum 217255) from near La Vega, Dominican Republic. The channel for the transport of venom is evident in i2 in the lower panel. Greatest length of skull is 86.6 mm.

## **GENERAL CHARACTERS**

Solenodon paradoxus is a large lipotyphlan insectivore (ca.  $800 \, \mathrm{g}$ , n=10—Ottenwalder 1999) with a body form suggesting a large shrew (Ottenwalder 2001). S. paradoxus shows no sexual dimorphism (Ottenwalder 2001). Means (mm; parenthetical ranges and sample sizes) for external measurements of S. paradoxus from central Dominican Republic were: total length, 539 (485–715, n=49); tail length, 225.5 (196–254, n=48); hind foot length, 64.1 (56–72, n=37); and ear length, 28.7 (21–38, n=37—Ottenwalder 2001). Cranial measurements and select measurements of major bones (mm; ranges) from these and specimens from northeastern, eastern, southwestern Dominican Republic, and southwestern Haiti were: greatest length of skull, 72.3–91.9 (n=112); condylobasal length, 67.1–86.6 (n=110); palatal length, 30.8–40.4

The Bahamas

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(n = 116); interorbital constriction, 13.6–16.5 (n = 118); zygomatic breadth, 30.1-39.0 (n = 100); mastoid breadth, 22.6-28.4 (n = 112); greatest mandible length, 45.2–58.1 (n = 121); length of mandibular toothrow, 23.3–28.9 (n = 122); length of maxillary toothrow, 21.6-27.6 (n = 117); and depth through coronoid process, 20.6-26.2 (n = 119); total length of femur, 41.0-50.4 (n = 84); maximum width of femur 11.4-14.6(n = 86); minimum shaft width of femur, 4.3–6.4 (n = 87); total length of humerus, 40.6-50.7 (n = 80); maximum width of humerus, 15.8-18.8 (n = 84); minimum shaft width of humerus, 4.3-5.8 (n = 83); total length of ulna, 40.6-58.0(n = 60); maximum width of ulna, 5.9–7.6 (n = 60); minimum shaft width of ulna, 1.5-2.5 (n = 60—Ottenwalder 2001).

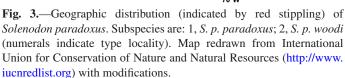
The long, bare-tipped snout extends beyond the nasal bones, with nostrils opening laterally and a dozen large vibrissae measuring up to 70 mm, as well as shorter, coarser hair on the sides of the snout serving a tactile purpose (Allen 1908; Ottenwalder 2001). An additional 1–3 vibrissae are located between the eye and mouth and on the midline of the chin below the angle of the mouth (Woods and Ottenwalder 1992). The ears are bluish gray with light edges, thin and rounded (Verrill 1907), but visible within pelage (Ottenwalder 2001). The eyes are small (Ottenwalder 2001). The eyelids, snout, and legs are hairless, as is the tail, which is also large, rat-like, and brown (Verrill 1907). The horn-colored claws and front feet are large and heavy, adapted for digging (Verrill 1907; Woods and Ottenwalder 1992). Females have a single pair of mammae positioned inguinally (Allen 1908; Nicoll 1984). Males have a retractable penis and testes are abdominal (Woods and Ottenwalder 1992).

Although a great degree of variation in color exists, pelage from the eye to the shoulder is generally ferruginous, with black or dark brown on the dorsal surface of the head, frequently with a whitish spot at the nape of the neck (Allen 1908; Allen 1910; Woods and Ottenwalder 1992). Dorsal pelage is dusky brown for the rest of the body (Verrill 1907), transitioning from dark near the median line to buff on the sides of the body and forearms (Woods and Ottenwalder 1992). Dorsal body hair consists of abundant short fine hairs and single rows of scattered long and coarse hairs, black-tipped hairs interspersed with pale, buffcolored hairs (Woods and Ottenwalder 1992). Hindquarters are sparsely haired (Verrill 1907). The ventral surface of the throat, upper chest, base of forelimbs, and lower abdominal area are deep ferruginous (Allen 1910; Woods and Ottenwalder 1992).

Juveniles can be distinguished from adults by cheek teeth that are not fully erupted, absence of sagittal crest formed by joined temporal ridges, lamboidal crest that is not well defined, and basioccipital and basisphenoid that are not fused (Ottenwalder 2001).

#### DISTRIBUTION

Solenodon paradoxus occurs on the island of Hispaniola. Distribution is now likely limited to the Dominican Republic and southern Haiti (Fig. 3; Ottenwalder 2001; Hutterer 2005).



Within the Macaya Biosphere Reserve Area on the Massif de la Hotte region of the Peninsula de Tiburon in Haiti, S. paradoxus is most abundant in mid-elevation mesic forest of 500-1,000 m east of Pic Macaya and west of Catiche and Duchity (Woods and Ottenwalder 1992). Fewer than 20 individuals were located northwest of Les Cayes and in the Duchity region in the 1970s (Woods 1976, 1981). Three specimens were collected in the Duchity region from 2006 to 2007, in areas with more anthropogenically degraded habitat at 831, 829, and 747 m, elevations lower than expected from previous surveys (Turvey et al. 2008). Within the Dominican Republic, 150 total specimens were collected in San Jose de las Matas and a wet, subtropical region northwest of Jarabacoa (Woods 1981). S. paradoxus was relatively widespread in the Dominican Republic during the 20th century, with credible evidence suggesting recent presence at over 50 sites (Ottenwalder 1999). The subspecies are allopatric: S. p. paradoxus is found in the Dominican Republic north of the Neiba Valley (Ottenwalder 2001); S. p. woodi occurs in south Hispaniola including the Sierra de Baoruco and the Peninsula de Barahona in the Dominican Republic and Peninsula de Tiburon in the Departement du Sud and Departement de l'Ouest in Haiti (Ottenwalder 2001).

## FOSSIL RECORD

Pre-Quaternary terrestrial vertebrate fossil sites are rare in the insular Caribbean, and no Solenodon paradoxus fossils are known from this period. In Haiti, Quaternary fossil remains are most abundant from the Massif de la Hotte area (Woods and Ottenwalder 1992). A single molar was collected at a cave deposit on Ile de la Gonave off the west coast of Haiti (Woods and Ottenwalder 1992). Fossil, subfossil, and post-Columbian remains have been discovered in a number of caves in Massif de La Hotte and Massif de La Selle (Woods and Ottenwalder 1992). Presence of S. paradoxus is known in northern Haiti only from fossils found in late Pleistocene deposits of the San Francisco Caves at St. Michel de L'Atalaye (Woods and Ottenwalder 1992). Fossil remains of a left horizontal ramus of a young S. paradoxus from a cave in Sierra de Neiba near Rancho la Guardia in San Rafael Province, Dominican Republic, are at least pre-Columbian (Patterson 1962). Solenodons most likely originated from a North American Tertiary (Paleogene-Neogene) form that colonized the Greater Antilles either by overwater dispersal or vicariance (Whidden and Asher 2001; Roca et al. 2004). The taxon diverged from other placental mammals an estimated 76 million years ago, which is consistent with the time of separation of proto-Antilles from North America (Roca et al. 2004). No near relatives exist on the mainland (Ottenwalder 2001). Two recently extinct species, Marcano's solenodon, S. marcanoi, from Hispaniola and the giant solenodon, S. arrendondoi, from Cuba (reviewed by Ottenwalder 2001) are known; S. marcanoi is the smallest of the 4 recent members of the genus, whereas S. arrendondoi is the largest (Ottenwalder 1991, 2001).

#### FORM AND FUNCTION

*Form.*—Dental formula is i 3/3, c 1/1, p 3/3, m 3/3, total 40 (Fig. 2). I1 and i2 are greatly enlarged (Pournelle 1968), and a deep groove runs along the lingual surface of i2 (Allen 1910; McDowell 1958). Upper molars are zalambodont and tritubercular (Dobson 1882–1890; Pournelle 1968; Ottenwalder 2001).

Vertebral formula is 7 C, 16 T, 4 L, 4 S, 24 Ca, total 55 (Allen 1910), although Gregory (1910) lists 2 true sacrals followed by 2 caudo-sacrals. The atlas has a ventral median hypapophysis that extends posteriorly from the anterior lip. The axis is large, with a high crest, and long transverse processes extend posteriorly at the ventral margin. An anterior projection is present on the transverse process of C4, increasing in C5 and C6. Spines of the T1–9 point sharply backwards, increasing in height for the first 3 vertebrae, decreasing in height from T4–9. A distinct diapophysis develops increasingly from T12–16 and continues along the lumbar vertebrae and the solidly fused sacral vertebrae. Dorsal spines are only well developed on the first 3 caudal vertebrae, and the neural canal is greatly diminished by C9 (Allen 1910).

There are 6 pieces to the sternum of of *Solenodon paradoxus*, with the 5th comprised of 3 fused elements. This differs from *Solenodon cubanus*, which has 7 pieces (Allen 1910). The tibia and fibula may be fused distally for 18 mm in adults, but not in juveniles (Allen 1910; Gregory 1910), unlike in *S. cubanus*, where they are described as distinct (Peters 1863; Dobson 1882–1890). The skull is unusual, with numerous uncommon features. A small (5 by 4 mm—Allen 1908), oval ossification, known as the os proboscidis, extends anteriorly from the ventral rim of the external nasal aperture to support the proboscis (Wible 2008).

The zygoma are incomplete, and the jugal is absent (Wible 2008). The mandible has a peculiar shape with angles that result from the true angular process and a process for the attachment of the digastric muscle (Wible 2008). A prootic canal for the lateral head vein in the petrosal bone is otherwise unknown among placental mammals but common among Mesozoic mammals (Wible 2008). The skull also lacks auditory bullae, the tympanics instead forming rings of bone (Dobson 1882–1890). An epiglotic prominence on the rostrodorsal margin of the hyoid and a mediolaterally oriented ceratohyal distinguish the larynx and hyoid from those described for other Soricomorpha (Wible 2010).

As the walls of the esophagus enter the stomach they form 8 corrugations. The stomach is subglobular and about 37 mm long and 25 mm wide. The small and large intestines merge imperceptibly, but thicker walls likely indicate the large intestine. Total intestine length is about 1,390 mm. Three main lobes form the liver. The pyriform gall bladder is about 30 mm long and opens into the small intestine. There are 2 main lobes of the pancreas. One is 55 mm long and 15 mm wide, the other is subtriangular and more robust. The pleural cavity of the lungs reaches to the 15th rib. The 3 lobes of the left lung are smaller than those of the right, which also has an azygos forming from the base of the 3rd lobe and a 2nd lobe that is divided into anterior and posterior sections. The heart is about 25 mm long, with the right auricle larger and thicker-walled than the left (Allen 1910). The testes are oval and 9 by 6 mm. The retractable penis lies 20 mm along the abdominal wall from the anus. The dark brown ovaries are 3 mm long. The uterus is narrow and 40 mm long (Allen 1910) and terminates in 2 short blunt horns (Wislocki 1940).

A ventral gland field located on each thigh is bare and darkened in coloration with a dense assemblage of apocrine glands but with no increase in sebaceous glands in males (Allen 1908; Starck and Poduschka 1982) with a reduced gland field located cranially in females (Starck and Poduschka 1982). Glands are tubule with adipose tissue septa; secretions are colorless and weak with seasonal production from January to March and May to November; glands are used during contact and communication behavior (Starck and Poduschka 1982).

Function.—Solenodon paradoxus and S. cubanus are the only extant mammals with a venom delivery system that uses an enlarged and modified i2 with an significant channel on the anteromesial tooth surface (Folinsbee et al. 2007). The channel is wrapped by enamel and a duct carries venom from glands at the base of these teeth (McDowell 1958). The submaxillary glands are relatively large (3-4g) and divided into 2 portions (Rabb 1959; Dufton 1992). A duct runs from the deep region of the gland, forward along the ramus to the root of the tongue, and opens into the groove at the base of i2 (Allen 1910; Pournelle 1968). The submaxillary glands contain large cells with coarse acidophilic granules and small nuclei that produce toxins (Rabb 1959; Pournelle 1968). Despite debate (Folinsbee et al. 2007), a maxillary fossa does not appear to be present (Fox and Scott 2005; Turvey 2010). Toxic saliva is thought to be drawn up by capillary action from the glands, through the grooves in i2, and into the wounds of prey bitten by S. paradoxus (Pournelle 1968). Experiments on the effect of envenomation showed intravenous injections of 0.38-0.55 mg/g of body mass and intraperitoneal injections of 1.0 mg/g of body mass were fatal for white mice (Mus musculus) in 2-6 and 13 min, respectively (Rabb 1959). A thorough pharmacological assessment has not been completed (Dufton 1992); the endangered status has hindered extensive laboratory assessments of the components (Dufton 1992) and effects of venom (Ligabue-Braun et al. 2012).

A female S. paradoxus demonstrated a diel pattern in rectal temperature that ranged from 30.5 to 33.7°C. Furthermore, this animal maintained a rectal temperature 6.4°C above ambient across a range of temperatures from 21.0 to 27.3°C, suggesting a well-refined ability to thermoregulate (Eisenberg and Gould 1966).

#### ONTOGENY AND REPRODUCTION

Newborns weigh 40-55 g and are naked, dark pink, with closed eyes. A complete coat of hair grows in 14 days. Young remain with their mother for several months, apparently learning foraging skills. During the first 2 months they are transported by their mother by hanging onto her inguinally placed pair of teats (Nicoll 1984). Weaning and sexual maturity are unknown, and life span is known only from captive animals that may live > 11 years (Fons 1990; Ottenwalder 1999).

Solenodon paradoxus has a low reproductive rate, and based on observations in captivity, females are receptive for < 1 day at 10-day intervals (Nicoll 1984), whereas males are continuously capable of mating (Fons 1990). Breeding can occur throughout the year but may peak during the dry season (Ottenwalder 1999). Gestation period is unknown but thought to be > 84 days (Ottenwalder 1979). The placenta is well-developed, complex, and labyrinthine with significant integration with the uterine walls; a placental scar remains evident after implantation (Wislocki 1940). Litter size is 1–3 (Verrill 1907; Wislocki 1940; Nicoll 1984). Infanticide occurred by a captive mother (Verrill 1907).

#### **ECOLOGY**

Solenodon paradoxus feeds mainly on arthropods including some species with chemical defense such as scorpions, centipedes, and millipedes but will also eat leaf litter, earthworms, land snails, grubs, rice, fruits, crabs, and small terrestrial vertebrates (lizards, snakes, frogs, and birds) and their eggs (Verrill 1907; Woods and Ottenwalder 1992; Ottenwalder 1999). In captivity, mice are actively pursued, killed, and eaten (Ottenwalder 1999). S. paradoxus can be found from sea level to 2,000 m, but most records are from < 1,000 m (Ottenwalder 1999). S. paradoxus tends to be associated with old, undisturbed mid-elevation broadleaf moist and wet forests (Woods and Ottenwalder 1992; Ottenwalder 1999; Pozo Rodríguez 2011), although the species has been reported at lower elevations and in more humandegraded habitat (Ottenwalder 1999; Turvey et al. 2008). In the Dominican Republic, it occurs across a gradient of dry to wet subtropical forest types, which may indicate a wider historical distribution in the island (Woods 1976; Ottenwalder 1999). S. paradoxus typically inhabits areas of limestone rock and thin, fine-textured, moderately permeable soil on steep topography (Woods and Ottenwalder 1992; Ottenwalder 1999; Pozo Rodríguez 2011). Native predators of S. paradoxus include Hispaniolan boa (Epicrates striatus), stygian owl (Asio stygius), and barn owl (Tyto alba). Introduced carnivores, particularly dogs (Canis lupus familiaris), but also cats (Felis sylvestris catus) and mongoose (Herpestes javanicus), have had a large detrimental impact on S. paradoxus (Woods and Ottenwalder 1992; Turvey et al. 2008, 2014).

#### **BEHAVIOR**

Solenodon paradoxus is nocturnal; however, individuals are sometimes seen sunning in the early morning, especially after rain (Ottenwalder 1999). Daylight hours are spent in caves, holes in limestone rocks, and hollow trees and logs; animals occasionally emerge to defecate, urinate, or groom (Verrill 1907; Woods and Ottenwalder 1992). Burrows may be complex systems of nest chambers and tunnels built under limestone boulders, large trees or dead stumps, or directly into the ground (Woods and Ottenwalder 1992; Ottenwalder 1999). Social organization usually consists of the adult pair and family groups of  $\leq 6$  individuals in the same hollow (Fons 1990; Woods and Ottenwalder 1992). Nests are built during the breeding season (Eisenberg and Gould 1966).

Solenodon paradoxus moves with zigzag, sideways, plantigrade motion and the tail is held straight back (Verrill 1907; Fons 1990). It digs with forepaws in soil and rotten logs, while moving its snout from side to side, sniffing in holes and crevices to locate prey (Eisenberg and Gould 1966). Foraging sign is most common in small depressions and ravines where soil and litter accumulate (Ottenwalder 1999). Aboveground activity appears to decrease from December to March (dry season), perhaps due to reduced abundance of invertebrate prey (Ottenwalder 1999). S. paradoxus captures victims by quickly extending its forepaws on either side of the target animal while sliding its head forward and engulfing the prey with its mouth (Woods and Ottenwalder 1992). When catching large prey such as mice in captivity, S. paradoxus uses its forepaws to tear carcasses into small pieces (Eisenberg and Gould 1966). The tail is sometimes used for additional rear support when feeding (Allen 1910; Fons 1990). No caching behavior has been observed (Eisenberg and Gould 1966). S. paradoxus uses feces and urine for scent marking. The function of glandular areas on the body (Allen 1908; Starck and Poduschka 1982) in chemical communication is not understood (Woods and Ottenwalder 1992). S. paradoxus urinates and defecates simultaneously and does not cover feces

with dirt (Eisenberg and Gould 1966). *S. paradoxus* cleans hind-quarters with tongue and teeth and uses the hind feet to scratch the body (Woods and Ottenwalder 1992).

Vocalizations in *S. paradoxus* tend to be associated with social behavior. The "chirp," described as a single, forceful note, is given when the animal is defensive, and a long, high-pitched "squeal" is produced during fights. A "soft squeak" is repeated in bursts of 2 or 3 notes when encountering familiar individuals. The "click" is a sharp, high-pitched sound produced when encountering strangers and when exploring novel areas. The "twitter," a longer, repeated version of the "soft squeak," with uncertain significance, is produced in situations of excitement such as feeding time in a cavity (Eisenberg and Gould 1966). *S. paradoxus* appears to relate digging sounds and chewing sounds to food, which may have influenced development of social organization (Eisenberg and Gould 1966). *S. paradoxus* uses echolocation for orientation by making clicking sounds with frequencies of 9–31 kHz and durations of 0.1–3.6 ms (Eisenberg and Gould 1966; Fons 1990).

#### **GENETICS**

The diploid number (2n) of chromosomes for *Solenodon* paradoxus (a single female individual) is 34, with a fundamental number (FN) of 64. The system of sex determination is assumed to be chromosomal with heterogametic sex chromosomes as in other members of the order (O'Brien et al. 2005).

Analysis of 16 nuclear and 3 mitochondrial genes and a separate analysis of *S. cubanus* supported a Mesozoic divergence from other placental mammals. The 76-million-year-old split, which places the genus *Solenodon* as the most basal among lipotyphlan insectivores, is older than the basal split of most mammalian orders (Roca et al. 2004). Mitochondrial DNA sequence data provide weak support for Solenodontidae as a sister taxon to Soricidae and Talpidae but not to Erinaceidae (Stanhope et al. 1998).

The subspecies split proposed by Ottenwalder (2001) has not been assessed by molecular genetic methods. An analysis of noncoding mitochondrial DNA from 3 *S. paradoxus* specimens indicated 3 haplotypes were defined by 6 variable positions, with a nucleotide diversity of 0.953% (Allard et al. 2001; Ottenwalder 2001). This is high relative to other endangered species, although the specimens may have come from reproductively isolated populations (Allard et al. 2001). Range-wide habitat fragmentation makes reproductive isolation a certainty for some populations, and the disappearance of this ancient lineage that evolved while dinosaurs existed may be increasingly likely (Roca et al. 2004).

## **CONSERVATION**

Solenodon paradoxus has long been considered highly threatened (Allen 1942) and was first listed as "Endangered" on the International Union for Conservation of Nature and Natural Resources Red List of Threatened Species (Turvey

and Incháustegui 2008) in 1986 due to a decreasing population and shrinking distribution. Habitat fragmentation and degradation, and range restriction have continued, and the declining population of this species is currently listed for these reasons as Endangered B2ab (iii, v—Turvey and Incháustegui 2008). S. paradoxus occupies < 500 km² and the proportion of sexually mature individuals in the population is declining (Turvey and Incháustegui 2008). S. paradoxus is viewed as a high priority for global mammal conservation (Isaac et al. 2007) due in part to its evolutionary distinctiveness among extant mammals (Roca et al. 2004).

In Haiti, S. paradoxus persists only in a single isolated population, occupying < 100 km<sup>2</sup>, and the species may warrant "Critically Endangered" status there. In addition to habitat loss and fragmentation, S. paradoxus is impacted by persecution from farmers and predation from exotic carnivores (Eisenberg and Gould 1966; Woods and Ottenwalder 1992; Turvey et al. 2008), with free-roaming village dogs reported as the leading anthropogenic mortality cause (Turvey et al. 2014). In 1983, a 5,500-ha national park was established in the Massif de la Hotte region of southwestern Haiti to protect the country's remaining S. paradoxus population. Recommendations were subsequently made that the park be expanded to 7,500 ha to include more S. paradoxus habitat west of Catiche and Duchity (Woods and Ottenwalder 1992). However, inadequate enforcement and poor infrastructure have apparently precluded conservation benefits from legal protection of the species, and the park remains confined to its 1983 boundaries (Turvey et al. 2008).

In the Dominican Republic, protected areas such as Sierra de Bahoruco National Park and Jaragua National Park maintain *S. paradoxus* populations, but buffer zones and corridors between these parks and the border with Haiti may be needed. Large areas of protected habitat free of human settlements and exotic carnivores may be necessary to protect this species, and conservation planning that involves local communities may be a prerequisite for success (Woods 1981; Pozo Rodríguez 2011).

Especially in the southern border areas of Hispaniola, Dominicans are more likely than Haitians to correctly identify solenodons, perhaps reflecting the species wider distribution in that country. In the same study solenodons were reported in far more localities in both countries than another endangered native mammal, the hutia (*Plagiodontia aedium*), indicating solenodon populations may be more resilient to habitat degradation (Turvey et al. 2014).

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- ALLARD, M. W., S. D. BAKER, G. L. EMERSON, J. A. OTTENWALDER, AND C. W. KILPATRICK. 2001. Characterization of the mitochondrial control region in *Solenodon paradoxus* from Hispaniola and the implications for biogeography, systematic, and conservation management. Pp. 331–334 in Biogeography of the West Indies: patterns and perspectives (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, Florida.
- ALLEN, G. M. 1910. *Solenodon paradoxus*. Memoirs of the Museum of Comparative Zoology at Harvard College 40:1–54.
- ALLEN, G. M. 1942. Extinct and vanishing mammals of the Western Hemisphere, with the marine species of all the oceans. American Committee on International Wild Life Protection, Special Publication 11:1–620.
- ALLEN, J. A. 1908. Notes on Solenodon paradoxus Brandt. Bulletin of the American Museum of Natural History 24:505–579.
- BARANOVA, G. I., A. A. GUREEV, AND P. P. STRELKOV. 1981. Catalog of type specimens in the collection of the Zoological Institute of the USSR, mammals (Mammalia). Part 1. shrews (Insectivora), bats (Chiroptera), hares (Lagomorpha). Nauka, Leningrad, Russia.
- Brandt, J. F. 1833. De solenodonte, novo mammalium insectivorum genere. Memoires de l'Académie Impériale des Sciences de St. Pétersbourg sciences mathématiques, physiques et naturelles, series 6 2:459–478.
- CABRERA, A. 1925. Genera mammalium—Insectivora, Galeopithecia. Museo Nacional de Ciencias Naturales, Madrid, Spain.
- Dobson, G. E. 1882–1890. A monograph of the Insectivora, systematic and anatomical. John Van Hoorst, London, United Kingdom.
- DUFTON, M. J. 1992. Venomous mammals. Pharmacology and Therapeutics 53:199–215.
- EISENBERG, J. F., AND E. GOULD. 1966. Behavior of *Solenodon paradoxus* in captivity with comments on behavior of other insectivora. Zoologica 51:49–57.
- Folinsbee, K. A., J. Müller, and R. R. Reisz. 2007. Canine grooves: morphology, function, and relevance to venom. Journal of Vertebrate Paleontology 27:547–551.
- Fons, R. 1990. Living Insectivores. Pp. 425–519 in Grzimek's encyclopedia of mammals (S. P. Parker, ed.). McGraw Hill Publishing Company, New York
- Fox, R. C., AND C. S. Scott. 2005. First evidence of a venom delivery apparatus in extinct mammals. Nature 435:1091–1093.
- Gregory, W. K. 1910. The orders of mammals. Bulletin of the American Museum of Natural History 27:1–524.
- HUTTERER, R. 2005. Order Soricomorpha. Pp. 220–311 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.), 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- ISAAC, N. J. B., S. T. TURVEY, B. COLLEN, C. WATERMAN, AND J. E. M. BAILLIE. 2007. Mammals on the EDGE: conservation priorities based on threat and phylogeny. PLoS One 2:e296.
- LIGABUE-BRAUN, R., H. VERLI, AND C. R. CARLINI. 2012. Venomous mammals: a review. Toxicon 59:680–695.
- McDowell, S. B., Jr. 1958. The Greater Antillean insectivores. Bulletin of the American Museum of Natural History 115:117–214.
- NICOLL, M. E. 1984. Solenodons. Pp. 748–749 in The encyclopedia of mammals (D. W. MacDonald, ed.). Facts on File, New York.
- O'Brien, S. J., J. C. Menninger, AND W. G. Nash (eds.). 2005. Laurasiatheria, in atlas of mammalian chromosomes. John Wiley & Sons, Hoboken, New Jersey.
- Ottenwalder, J. A. 1979. Hispaniolan solenodon born at Santo Domingo Zoo. International Zoo News 26:46–47.
- OTTENWALDER, J. A. 1991. The systematics, biology, and conservation of *Solenodon*. Ph.D. dissertation, University of Florida, Gainesville.
- Ottenwalder, J. A. 1999. Observations on the habitat and ecology of the Hispaniolan solenodon (*Solenodon paradoxus*) in the Dominican Republic. Pp. 123–168 in Ecologia de les Illes. Monografies de la Societat d'Historia Natural de les Balears No. 6, and Monografia de l'Institut d'Estudis Balearics No. 66 (J. A. Alcover, ed.). Institut d'Estudis Baleàrics, Palma, Mallorca, Spain.

- Ottenwalder, J. A. 2001. Systematics and biogeography of the West Indian genus Solenodon. Pp. 253–329 in Biogeography of the West Indies: patterns and perspectives (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, Florida.
- Patterson, B. 1962. An extinct solenodontid insectivore from Hispaniola. Breviora 165:1–11.
- Peters, W. 1863. Die säugethier-gattung *Solenodon*. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1863:1–22.
- POURNELLE, G. H. 1968. Classification, biology, and description of the venom apparatus of insectivores of the genera *Solenodon*, *Neomys*, and *Blarina*. Pp. 31–42 in Venomous animals and their venoms (W. Bucherl, E. E. Buckley, and V. Deulofeu, eds.). Academic Press, New York.
- Pozo Rodríguez, R. 2011. Habitat-species association in the Hispaniolan solenodon (*Solenodon paradoxus*); a quantitative study of an endangered Caribbean mammal. Masters thesis, Imperial College, London, United Kingdom.
- RABB, G. B. 1959. Toxic salivary glands in the primitive insectivore *Solenodon*. Natural History Miscellanea 170:1–3.
- Roca, A. L., ET AL. 2004. Mesozoic origin for West Indian insectivores. Nature 429:649–651.
- STANHOPE, M. J., ET AL. 1998. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. Proceedings of the National Academy of Sciences 95:9967–9972.
- STARCK, D., AND W. PODUSCHKA. 1982. On the ventral gland field of Solenodon paradoxus Brandt, 1833 (Mammalia, Insectivora). Zeitschrift fur Saugetierkunde 47:1–12.
- Turvey, S. T. 2010. Evolution of non-homologous venom delivery systems in West Indian insectivores? Journal of Vertebrate Paleontology 30:1294–1299.
- Turvey, S. T., C. Fernández-Secades, J. M. Nuñez-Miño, T. Hart, P. Martinez, J. L. Brocca, and R. P. Young. 2014. Is local ecological knowledge a useful conservation tool for small mammals in a Caribbean multicultural landscape? Biological Conservation 169:189–197.
- Turvey, S. T., and S. Incháustegui. 2008. *Solenodon paradoxus*. In: International Union for the Conservation of Nature and Natural Resources 2008. International Union for Conservation of Nature and Natural Resources Red list of threatened species. Version 2015.3. www.iucnredlist.org. Accessed 24 September 2015.
- Turvey, S. T., H. M. R. Meredith, and R. P. Scoffeld. 2008. Continued survival of Hispaniolan solenodon *Solenodon paradoxus* in Haiti. Oryx 42:611–614.
- VERRILL, A. H. 1907. Notes on the habits and external characters of the Solenodon of San Domingo (Solenodon paradoxus). American Journal of Science 24:55–57.
- WHIDDEN, H. P., AND R. J. ASHER. 2001. The origin of the greater Antillean insectivorans. Pp. 237–252 in Biogeography of the West Indies: patterns and perspectives (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, Florida.
- WIBLE, J. R. 2008. On the cranial osteology of the Hispaniolan solenodon, *Solenodon paradoxus* Brandt, 1833 (Mammalia, Lipotyphla, Solenodontidae). Annals of Carnegie Museum 77:321–402.
- Wible, J. R. 2010. On the hyoid and larynx of the Hispaniolan solenodon, *Solenodon paradoxus* Brandt, 1833 (Mammalia, Lipotyphla, Solenodontidae). Annals of Carnegie Museum 79:29–38.
- WISLOCKI, G. B. 1940. The placentation of *Solenodon paradoxus*. American Journal of Anatomy 66: 497–531.
- Woods, C. A. 1976. Solenodon paradoxus in Southern Haiti. Journal of Mammalogy 57:591–592.
- Woods, C. A. 1981. Last endemic mammals in Hispaniola. Oryx 16:146–152
- Woods, C. A., and J. A. Ottenwalder. 1992. The natural history of Southern Haiti. Florida Museum of Natural History, Gainesville.
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