

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. arrendonoi*, from Cuba (reviewed by Ottenwalder 2001) are known; *S. marcanoi* is the smallest of the 4 recent members of the genus, whereas *S. arrendonoi* 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 *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 epiglottic prominence on the rostradorsal 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 (3–4 g) 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 human-degraded 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 sylvestriscatus*) 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 ≤ 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 Inchaústegui 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 Inchaústegui 2008). *S. paradoxus* occupies < 500 km² and the proportion of sexually mature individuals in the population is declining (Turvey and Inchaústegui 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 km², 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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