

Hemicentetes semispinosus.

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Hemicentetes Mivart, 1871

Hemicentetes Mivart, 1871:58. Generic type *Erinaceus madagascariensis* Shaw.

CONTEXT AND CONTENT. Order Insectivora, Family Tenrecidae, Subfamily Tenrecinae. Genest and Petter (1975) and Hutterer (1993) consider the genus to be monotypic with two subspecies (*semispinosus* and *nigriceps*); however, some authors, such as Eisenberg and Gould (1970), Nicoll and Rathbun (1990), and Stephenson and Racey (1994) consider each to be a separate species on the basis of morphological characteristics and distribution. Given the similarities, the two forms of *Hemicentetes* will be treated as subspecies of a single species in a monotypic genus for convenience in order that contrasts and comparisons between the two may be made.

Hemicentetes semispinosus Mivart, 1871

Streaked Tenrec

Ericulus semispinosus G. Cuvier, 1797:108. Madagascar.

Erinaceus madagascariensis Shaw, 1800:548 (not Zimmermann). Madagascar.

Hemicentetes nigriceps Günther, 1875:125. Fienrentova. Madagascar.

CONTEXT AND CONTENT. Context noted in generic summary above. We have chosen to follow Hutterer (1993) which lists two subspecies:

H. s. semispinosus (Cuvier), 1797. See above. Includes variegatus E. Geoffroy as a synonym.

H. s. nigriceps Günther. 1875. See above. Includes *buffoni* Ventinck as a synonym.

DIAGNOSIS. *Hemicentetes semispinosus semispinosus* is covered with black and yellow quills (Fig. 1). The animal is black with a median yellow stripe down the rostrum and three yellow stripes (one dorsally and two laterally) which run along the length of the body. Quills are more numerous on the head and nuchal area and are longer in this region. The ventral region usually contains no or only a few quills (Eisenberg and Gould, 1970; Gould and Eisenberg, 1966).

In contrast, the stripes of *H. s. nigriceps* are white (Fig. 2). The rostrum lacks a median stripe present in *H. s. semispinosus*, but two bold white stripes are present along the length of the body. The density of quills is less than in *H. s. semispinosus* and the woolly undercoat is more prominent. The modal number of quills within the stridulation organ is 11 in *H. s. nigriceps* and 14 in *H. s. semispinosus* (Eisenberg and Gould, 1970; Gould and Eisenberg, 1966). The juvenile *Tenrec ecaudatus* superficially resembles *Hemicentetes*, possessing two rows of moveable quills in the midline and cream to yellow horizontal stripes, one on the dorsal midline and two on each side. For a discussion, see Eisenberg and Gould (1970:116).

GENERAL CHARACTERS. The skull has an elongate rostrum and dentition is reduced in size. The zygomatic arch is reduced (Mivart, 1871). The upper molars are zalambdodont (Fig. 3). *H. s. semispinosus* possesses a black spiny pelage that is marked with three yellow stripes along the length of the body. *H. s. nigriceps* also possesses a blackspiny pelage, but is not as spinescent compared to *H. s. semispinosus*. The underfur takes on a woolly appearance. Two white stripes run along the length of the body in a similar manner to *H. s. semispinosus*. Barbed quills of both subspecies are easily detached and act as an antipredation device. The

bright coloration of the yellow or white stripes may serve as a warning to predators (Eisenberg and Gould, 1970). Average body length of both *H. s. semispinosus* and *H. s. nigriceps* is approximately 140 mm. Maximum adult body length found for *H. s. semispinosus* is 172 mm and body weights of adults range from 125 to 280 g. Maximum adult body length found for *H. s. nigriceps* is 180 mm and adult body weight ranges from 80 to 150 g (Eisenberg and Gould, 1970; Gould and Eisenberg, 1966). Other than genital tracts, morphological differences are not apparent when the sexes are compared. Sensory hairs similar to vibrissae are scattered over the dorsum of both subspecies. A tail is reduced or absent (Eisenberg and Gould, 1970).

DISTRIBUTION. The distribution of the two subspecies is allopatric. *H. s. semispinosus* is restricted to the rainforests of Madagascar. Specifically, this form is found in the eastern sub-plateau rainforests from Ivohibé to Maroantsetra. In contrast, *H. s. nigriceps* is found in the central, upland region of Madagascar from Manandoy south to Fianarantsoa, within the transitional area between the rainforests and the plateau savanna (Fig. 4). Information from the fossil record is lacking for both subspecies (Eisenberg and Gould, 1970).

FORM AND FUNCTION. A group of seven to 16 specialized spines arranged in three rows on the medio-posterior dorsum, together with the underlying dermal musculature, form the stridulation organ that is found in both *H. s. semispinosus* and *H. s. nigriceps* (Gould, 1965). The stridulation organ of *H. s. nigriceps* contains a lower number of specialized spines (mode 12) compared to *H. s. semispinosus* (13 to 18). Vigorous movement of these spines causes the tips to rub together and produce high-frequency sounds (Gould, 1965). The stridulation organ is thought to be used for communication between members of foraging groups and/or as a warning signal to predators (Eisenberg and Gould, 1970). Petter and Petter-Rousseaux (1963) provide the first report of the stridulating organ, which consists of specialized quills on the medio-posterior dorsum. Quills of the stridulation organ are arranged in parallel rows and move independent of other quills.

The skull is elongated (Fig. 3), tapering anteriorly, and lacks a prominent sagittal crest. The dental formula is $i\ 3/3, c\ 1/1, p\ 3/3, m\ 3/3$, total 40. Teeth show a reduction in size compared to other genera of Tenrecidae (Eisenberg and Gould, 1970; Mivart, 1871). There are 20-21 lumbar vertebrae and the pubic symphysis is widely open in some individuals, presumably females (Mivart,



FIG. 1. Photograph of captive *H. s. semispinosus* at National Zoological Park (JFE).



FIG. 2. Photograph of wild *H. s. nigriceps* in Madagascar (JFE).

1871). The urogenital and excretory systems exit the body through a common cloaca (Gould and Eisenberg, 1966).

Both subspecies have the ability to enter torpor. Torpor in *H. s. semispinosus* is usually seasonal and dependent upon altitude, ambient temperature, age, and fat reserves (Gould and Eisenberg, 1966). Captive animals have a greater tendency to go into torpor than wild animals (Eisenberg and Gould, 1970; Herter, 1963). Torpor generally occurs during the months of June and July. Torpid animals exhibited a drop in body temperature to ambient levels, decreased activity, and they ceased activity (Eisenberg and Gould, 1970).

Resting metabolic rate (RMR) and body temperature of both subspecies were reduced between mid-April and mid-September and reported to be annually cyclic and unrelated to body mass (Stephenson and Racey, 1994). Mean RMR between mid-September and mid-April was 49% and 69% lower than expected from body mass from the Kleiber (1961) curve for *H. s. semispinosus* and *H. s. nigriceps*, respectively. *H. s. semispinosus* and *H. s. nigriceps* are less active during the austral winter; however, activity levels of *H. s. nigriceps* were much lower than *H. s. semispinosus*. *H. s. semispinosus* is reported to come out of torpor and forage during the winter months. Differences in torpor might reflect different winter strategies in streaked tenrecs; *H. s. nigriceps* appears to be an obligate hibernator in nature, whereas *H. s. semispinosus* appears to be a facultative hibernator (Stephenson and Racey, 1994). Resting metabolic rate was elevated in both forms of pregnant females. A prolonged torpid period may prolong gestation and result in differences in reproductive output. The reduced torpid time of *H. s. semispinosus* may allow a greater annual productivity *H. s. nigriceps* (Stephenson and Racey, 1994).

ONTOGENY AND REPRODUCTION. Reproduction is varied but occurs most often during the rainy season (Gould and Eisenberg, 1966). Eisenberg (1975) speculated that tenrecs in general may be induced ovulators, and conception may not always occur during the first copulation. Gestation ranges from 55 to 58 days in both subspecies (Eisenberg, 1975; Eisenberg and Gould, 1967, 1970). The average litter size of *H. s. semispinosus* in the wild (6.3) is greater than that of *H. s. nigriceps* (1.3). Litter size for both subspecies was greater in captivity. *H. s. semispinosus* produced as many as 11 altricial young in captivity (Eisenberg and Muckenhirn, 1968). The development of young in *H. s. semispinosus* and *H. s. nigriceps* is very similar. Young are born without spines, weigh approximately 11 g, and range from 55 to 67 mm in length (Eisenberg and Gould, 1970; Gould and Eisenberg, 1966). Development occurs quickly. Hair and spines begin to develop within 24 hours. At day 4, young are able to explore the burrow. Quills appear on the head and nuchal area and teeth erupt at day 5. The ears and eyes open between 8 and 10 days, and the stridulation organ begins to vibrate, although no sound is produced until day 16. Fully coordinated locomotion, as well as complete development of pelage and spines, occurs at day 20; by day 25, young are completely weaned (Gould and Eisenberg, 1966). Females are

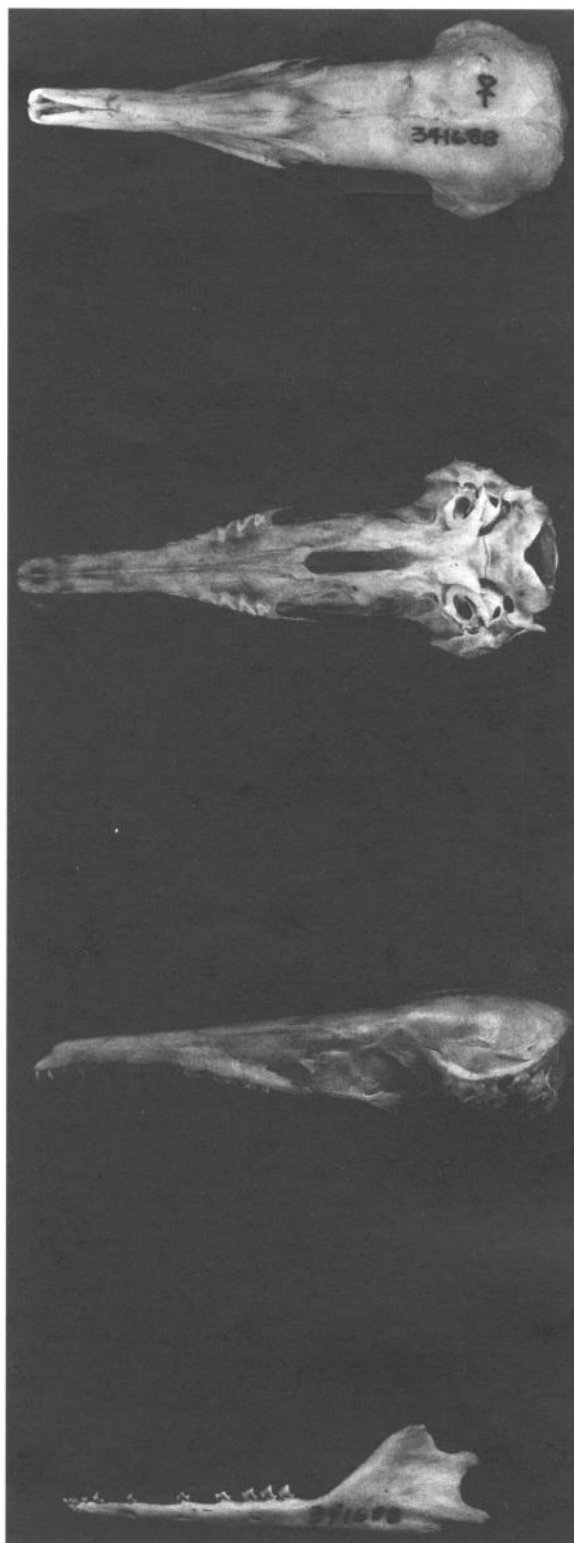


FIG. 3. Dorsal, ventral, and lateral views of the skull, and lateral view of the mandible of *H. s. semispinosus* (United States National Museum 341688). Greatest length of cranium is 41.6 mm.

able to conceive at 35 days of age (Eisenberg and Gould, 1970). *H. s. semispinosus* appears to be the only tenrec that can breed in the same season in which it was born (Eisenberg and Muckenhirn, 1968).

Growth curves of *H. s. semispinosus* and *H. s. nigriceps* also are similar. Individuals of both subspecies grow steadily until ap-

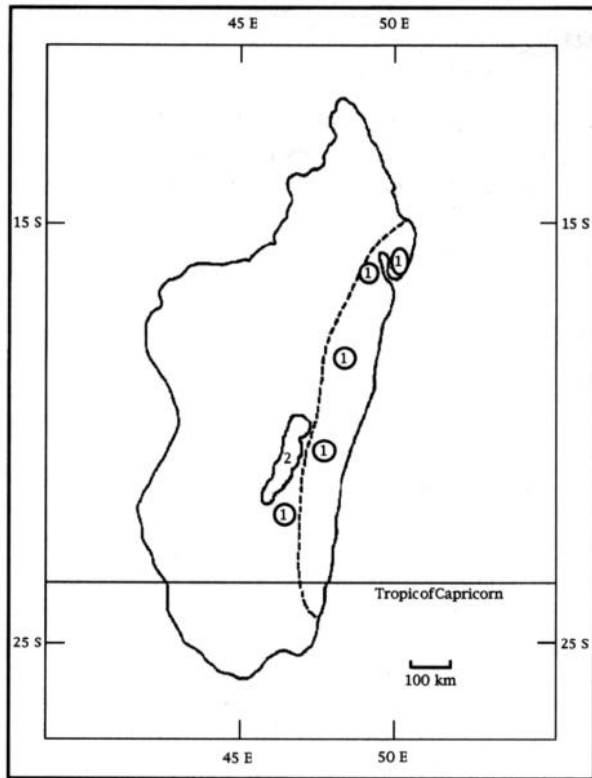


FIG. 4. Historic range of *H. semispinosus* is probably coincident with the eastern tropical rainforest region. 1 = Known recent locations for *H. s. semispinosus*. 2 = Known recent location for *H. s. nigriceps*.

proximately day 40. After day 40, growth curves for both subspecies plateau. At this time, the average individual length for both subspecies is approximately 140 mm. The growth curve for *H. s. semispinosus* is slightly lower initially, which is most likely due to the larger litter size and initial limitations on the lactation of the mother (Eisenberg and Gould, 1970).

ECOLOGY. A general description of habits indicates that *H. semispinosus* can be collected near brush lands and forest edges (Rand, 1935). Streaked tenrecs erect the crest of spines located on the head and moved the head upwards repeatedly when disturbed. Individuals also uttered chattering or squeaking sounds when disturbed. The animals observed were active the entire year, but less so from May to October. Individuals from Ivohibé between August and September were sluggish after cold nights, but usually had fine ground material in the intestinal tract indicating that they had not been long inactive.

Streaked tenrecs are likely to be preyed upon by any relatively large carnivore capable of penetrating their antipredator mechanisms. The boa, *Acrantophis dumerilli*, is especially effective. Individuals have been reported to display defensive behavior when exposed to the scents of *Galidia elegans* (Malagasy ring-tailed mongoose) or *Fossa fossa* (Malagasy civet). Both genera kill *Hemicentetes* (Eisenberg and Gould, 1970).

Dens and burrows of *H. s. semispinosus* are found in primary and secondary forests. Dens in more mature forests are usually found near water such as a stream. Burrows tend to be shallow (5 to 8 cm in depth), contain a single entrance, and located near fallen logs or tree roots. Entrances to burrow systems are typically plugged with leaves. Total length of burrows may be 2 to 3 m. Burrows are of two types, a small burrow inhabited by an individual or small group, or a larger system that is occupied by large family groups. During the breeding season, family groups as large as 23 individuals may use the same burrow system and forage together (Eisenberg and Gould, 1970).

Dens and burrows of *H. s. nigriceps* are typically found along forest fringes on the plateau edge and also near cultivated fields.

These tenrecs will even den in forests of introduced *Eucalyptus* sp. There is usually only one entrance, which is plugged with leaves. The burrows tend to be relatively shallow and short (approximately 75 mm deep and 450 mm long) compared to those of *H. s. semispinosus*. Generally, burrows of *H. s. nigriceps* lack the complexities of burrows created by *H. s. semispinosus*. *H. s. nigriceps* does not form large family groups or colonies. Temperatures of burrows sampled in the Manandroy area ranged from 20.4° to 26.5°C. Burrow temperatures were consistently equal to or cooler than the ambient temperature at the time of sampling (20.4° to 30.5°C). *H. s. nigriceps* is most active at night; peak activity occurs in the early evening. Body temperature in *H. s. nigriceps* appears to fluctuate in a diel pattern; body temperature rises in the late afternoon just before the peak activity level in the early evening and drops to low levels in morning hours. Burrows are most likely used not only to avoid predation but also to thermoregulate behaviorally against extremes of ambient temperatures (Eisenberg and Gould, 1970).

The principal food of *H. s. semispinosus* and *H. s. nigriceps* is earthworms, but other small invertebrates are eaten as well. Eisenberg and Gould (1970) reported that individuals exhibited foraging behavior in areas impregnated with earthworm scent; however, determination of the extent to which olfaction is used to detect prey is difficult. Foraging occurred in natural clearings where the soil was soft, damp, and shaded. Other areas are sometimes utilized if sufficient leaf litter for invertebrates is available. It is noteworthy that while pulling an earthworm from the ground a "stamp" with their forepaws may stimulate earthworm activity.

H. s. semispinosus has been bred in captivity but with mixed success. Breeding was accomplished by holding pairs in cages with a floor area of 2,000 square cm. All tenrecids were maintained in captivity by feeding raw, chopped horsemeat mixed with condensed milk and baby cereal to form a paste; however, *Hemicentetes* required supplements of earthworms (Eisenberg, 1967). Captive breeding of *H. s. semispinosus* did not persist past the third generation, deriving in part from a failure to initiate breeding in the year following the birth of the next generation. Maximum longevity in captivity was 30 months. The short fertility period of *H. s. semispinosus* must be taken into consideration when trying to maintain a captive colony. In order to maintain a captive population, females must be allowed to breed in the year of their birth or the year after birth; after this time females become senescent (Eisenberg, 1975).

BEHAVIOR. When aggravated or disturbed, both *H. s. semispinosus* and *H. s. nigriceps* respond by erecting the quills on the head and nuchal region. Quills that normally lie flat are erected laterally and forward. Quills along the dorsum will also be erected when the animal is highly disturbed. A vocalization or buzz is sometimes associated with erection of quills. Highly disturbed individuals will erect quills, vocalize, and stamp several times with both their forefeet. Continued aggravation results in flight, or bobbing of the head laterally and forward in an effort to impale the source of disturbance with the detachable quills. This defense posture can be elicited also by sudden exposure to bright light; individuals will spread the quills of the head and nuchal areas but rarely vocalize, buck, or jump under these circumstances (Gould and Eisenberg, 1966). The odor alone of potential predators (*Fossa fossa* and *Galidia elegans*) will elicit a complete antipredator display (Eisenberg and Gould, 1970).

Offensive behavior toward conspecifics is less aggressive; encounters among individuals may result in head butting and striking with the nose, pivoting on forelegs to push the body or rump into another animal, or biting at the facial region. Fighting males often bite each other in the flank or shoulder and may grapple with each other, resulting in tumbling of both individuals. In some instances, quills may become erect in an effort to impale the offending animal. Unfamiliar males will often fight with each other, especially if females are present (Eisenberg and Gould, 1970).

Female-female encounters usually begin with tactile contact, followed by an increase in distance and general avoidance behavior. Non-aggressive interaction between conspecifics involves tactile communication such as naso-anal, naso-nasal, nose to ear, nose to body, nose to nape contact, and crawling over another. Male-female encounters depend upon female sexual receptivity. If the female is not receptive she will move away and the quills will become erect if the male persists. If the female is receptive, a series of contact behaviors (naso-nose, naso-anal, nose to ear, etc.) is followed by

mounting by the male and lordosis by the female (Eisenberg and Gould, 1970).

Gould (1965) and Eisenberg and Gould (1970) determined experimentally that the stridulation organ produced sound with frequencies between 2 and 200 KHz, but could not determine if this sound was used for echolocation. Maximum amplitude lies between 50 and 150 KHz. Wever and Herman (1968) reported that maximum cochlear sensitivity ranged from 10 to 15 KHz when potentials were recorded from anesthetized animals. The range of greatest cochlear sensitivity was not correlated with the range of sound produced by the stridulation organ; however, some cochlear sensitivity occurred within the lower range of the stridulation frequencies (18 to 20 KHz). Therefore it is possible that individuals can hear sounds produced by the stridulation organ at distances <10 m (Wever and Herman, 1968). The range of greatest cochlear sensitivity did correspond to the range of sounds (11 to 16 KHz) produced by tongue clicks (as recorded by Gould, 1965). In a series of experiments, Gould (1965) determined that *Hemicentetes* used tongue clicks as an echolocating device when exploring an unfamiliar environment.

Observations and recordings of stridulation rates and intensity of stridulation seem to correlate with the activity levels of an individual. However, state of arousal, such as quill erection is not necessarily correlated with stridulation rates and intensity levels. Changes in rates and intensity of stridulation may relay certain information to surrounding individuals such as the motivational state of the stridulating animal or the position of the sender, or to allow females to maintain contact with young during foraging episodes. When the stridulation organ was rendered inoperative in foraging females with young, approximate mother-young distances were significantly closer than when the stridulation organ was operative. Young presumably use sound and/or odor of the mother for recognition, which requires closer contact with the female. Playback of stridulation to solitary young in an experimental arena demonstrated the ability of young animals to "home" in the direction of a speaker producing stridulation as opposed to a control sound of "white noise" of equal amplitude (Eisenberg and Gould, 1970).

When placed into an unfamiliar environment, such as observation pens, individuals explored slowly, alternately testing the air and substrate with their noses. A change in background noise elicited a defensive response and individuals would erect their spines. After sufficient exploration of an area, individuals chose a location for defecation and repeatedly used this area as a latrine. However, burrow entrances occasionally were marked with feces, often an alternate area was selected for a burrow site, and a nest was constructed using grass and leaves. Burrows were excavated with alternate movement of the forelimbs: accumulated soil was kicked out of the burrow with the hind feet. Eisenberg and Gould (1970) reported that burrow sites may be abandoned and new burrows constructed in a nearby vicinity on a 10 to 15 day cycle.

When foraging, animals prod the leaf litter and soil with the tip of the nose. When a worm is detected, an individual will bite and pull at the worm while simultaneously digging at the soil on either side of the worm. Once the worm is pulled from the ground, it is shaken, seized and bitten again, and then forepaws stroke down on either side of the worm in a patting motion. This sequence is observed when individuals first encounter any foodstuff.

GENETICS. The chromosome number for both *H. s. semispinosus* and *H. s. nigriceps* is thirty-eight (Borgaonkar, 1966, 1967).

REMARKS. Although the two forms of *H. semispinosus* have been treated as subspecies for convenience in this account, the taxonomy of the genus *Hemicentetes* is still unclear. Although Genest and Peter (1975) and Hutterer (1993) refer to the two forms (*semispinosus* and *nigriceps*) as subspecies, the authors contend that these two forms are separate species. Clearly, the evidence for classifying these two forms as distinct species warrants further investigation.

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