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NOTES ON THE BIOLOGY OF THE TENRECIDAE

EDWIN GOULD AND JOHN F. EISENBERG

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By Edwin Gould and John F. Eisenberg

Abstract: Laboratory and field observations provide data on the life history and growth of *Hemicentetes, Centetes, Echinops* and *Setifer.* Comments on *Geogale, Microgale* (*Nesogale*) and *Limnogale* are also included. Similarities in courtship and agonistic behavior are noted. Some data on torpor indicate the irregularity of its occurrence, particularly in *Hemicentetes semispinosus.* A comparison of age at which the eyes open in four insectivore families indicates that tenrecs mature earliest, about 14 to 22 days in Talpidae, Soricidae and Erinaceidae, 7 to 13 days in Tenrecidae. *Hemicentetes semispinosus* and *Echinops telfairi* attain adult size at 6 to 8 weeks of age under laboratory conditions.

INTRODUCTION

This is a report of field and laboratory observations on species of tenrecs, recorded while Gould was in Madagascar in 1963 and while he and Eisenberg kept specimens in their respective laboratories from 1961 to 1962 and from 1963 to 1965. Study areas visited by Gould included the following: Perinet, 18° 54′ S, 48° 24′ E, 18–22 January and 10–17 March; Ampansandrano (between Faratsiho and Ambatolampy), 19° 37′ S, 47° 04′ E, 14–18 June; Morondava, 20° 18′ S, 44° 18′ E, 24 June–2 July; Manandroy, about 35 km NW of Ranomafana, 21° 9′ S, 47° 15′ E, 7–10 July; Ambodivoangy, about 12 km N of Rogez, just north of Maromitety, 18° 46′ S, 48° 45′ E, 27 July–5 August.

Approximately 100 tenrecs were brought back from Madagascar, including: Tenrecinae—53 *Hemicentetes semispinosus* G. Cuvier, three *Hemicentetes nigriceps* Gunther, six *Setifer setosus* Schreb, 12 *Centetes ecaudatus* Schreb, 22 *Echinops telfairi* O. Thomas; and Oryzorictinae—two *Microgale* (*Nesogale*) *dobsoni* O. Thomas. In addition two specimens of *Setifer setosus* were donated to Eisenberg by Dr. F. Bouliere. For comparative purposes Eisenberg studied the following specimens of the Erinaceidae: three *Erinaceus europaeus* and two *Paraechinus micropus. Erinaceus* was collected by Eisenberg in Germany, whereas the specimens of *Paraechinus* were purchased from a commercial dealer who designated Pakistan as the capture locality. Specimens of *Centetes,*

Hemicentetes and *Echinops* are still living at the New York and the National Zoological Parks.

METHODS

At Johns Hopkins University all tenrecs, except *Centetes*, were kept in plastic tubs 60 × 34 × 26 (deep) cm. Each tub held from one to eight tenrecs. Individuals of *Centetes* were kept in the same room, but in a round watering trough 2 × 0.7 m. Temperature ranged from 18° to 23° C. The cage floors were lined with wood shavings and newspaper, and all of the cage interiors were dark because of opaque sides; holes were drilled in the metal covers. To minimize disturbances, cages were cleaned weekly rather than daily. At the University of Maryland, the smaller tenrecs were held as pairs or family groups in screen-topped cages with floors measuring 122 × 61 cm. Specimens of *Centetes* were held in larger cages with floor areas of 122 × 122 cm. Aside from the changes in holding cages, the animals were maintained as noted above.

A diet of condensed milk, raw horsemeat, powdered Pablum, egg noodles and vitamin supplement served as the staple food ration. *Hemicentetes* was also fed supplementary earthworms and crickets or grasshoppers. In most cases, when a female gave birth, other males and females were removed from the cage, and earthworms or mealworms ad lib. were supplied to *Hemicentetes* and *Echinops*, respectively.

Observations of maintenance behavior were made in either the holding cages or in special cages provided with earth, rotten logs and small tree branches for climbing. Mating behavior was studied in detail by allowing a male and a female to interact in a neutral cage. Pair tolerance throughout pregnancy and parturition was investigated only with *Hemicentetes*. Developing young were weighed, measured and photographed. Initially the young were studied at widely spaced intervals to avoid possible desertion by the mother; however, as the reproductive success of the captive colonies continued, more regular measurements were made. Body temperatures were recorded in the laboratory with a telethermometer (Yellow Springs Instrument Co.), whereas in the field a rapid recording rectal thermometer was employed.

RESULTS

Hemicentetes semispinosus

Hemicentetes is one of the most specialized members of the Tenrecidae. Its distribution is restricted to the eastern belt of rain forest, and its primary food is earthworms. Adults are about 135 mm long and weigh about 130 g. Its relationship to *Centetes* is supported by morphological (Butler, 1937) and cytological evidence; both species have a diploid chromosome number of 38 (Borgaonkar and Gould, 1965).

The animal is black with a nuchal crown of yellow spines and three yellow dorsal stripes, one median and two lateral (Fig. 1). On the center of its back is a group of 14–16 specialized quills that cover an area about 1 cm^2. By twitching the subdermal musculature the animal can cause the quills to rub against each other, producing a sound composed of frequencies ranging from about 2 kc to 80 kc. This "stridulating organ" produces sounds in different repetitive patterns depending on the coincident behavior of the tenrec (Gould, 1965; also see Rand, 1935). The organ and its sounds are believed to be associated with intragroup communication.

In the course of experiments on echolocation (Gould, 1965), several *Hemicentetes* were shaved of all their fur. Quills on the nape and head of adults were

FIG. 1.—A torpid *Hemicentetes semispinosus* in the laboratory. The hindfeet swelled after several weeks in hibernation. This animal was captured about 3 months previously.

replaced more rapidly than on other areas; adults failed to replace stridulating organ quills that had been cut. However, young tenrecs did replace the stridulating quills. Four days after these quills were cut in 11-day-old animals, they had regrown enough to produce sounds. Some subadults replaced stridulating quills with yellow and black quills that failed to produce sounds, though they were observed to vibrate. Recently captured tenrecs, at least 1 yr old, often lacked 7–10 of the stridulating quills.

Presumably the quills are effective deterrents to enemies. They also function to ward off others of the same species. A large male that tried to copulate with an unreceptive female had a number of quills sticking into his genital area after the attempt. While eating earthworms, *Hemicentetes* often pivots rapidly from one side to the other and thrusts a quill into a passing tenrec that attempts to take the prey.

Offensive and defensive behavior—A sudden disturbance elicits a highly stereotyped pattern of defense from *Hemicentetes*. Erection of the body quills is the initial and most obvious response. Quills that lie flat on the nape in a relaxed animal can erect 180° forward and lateral. Thus, they are oriented posteriorly in the relaxed position and anteriorly and laterally in the fully erect position. Moderate disturbances often elicit simultaneous defecation and urination. The defense reaction includes the following components: (a) nape and head quills are spread laterally and forward, (b) all body quills are

erected, (c) a vocal buzz is emitted, and (d) the head is jerked back, or the tenrec jumps up and down several times in succession on its forefeet.

The extent of quill erection on the nape constitutes a continuously graded measure of the emotional state of an individual. For example, a particularly excitable tenrec raises its nape quills only slightly at a sharp but low-intensity sound. Successively louder sounds elicit anterior and lateral erection of more and more nape quills until the entire body is a virtual pin cushion and the jumping and buzzing components of the repertoire are included. Individuals differ with respect to the kind and intensity of disturbance that brings on the protective posture.

When *Hemicentetes* is alarmed and all quills are erect, it pivots so that its head is facing the disturbance. If the observer touches any part of the tenrec's head, it will suddenly jerk its head upward or upward and laterally, driving the detachable nape spines into the offending hand. Some docile *Hemicentetes* were never observed to display the defense posture unless a brilliant light was shone on them. The defense posture is particularly dramatic if an open cage of several *Hemicentetes* is carried from the shade into full sunlight. Most tenrecs spread and erect their nape and body quills. This response to bright light is rarely accompanied by the buzz or by bucking or jumping.

Feeding behavior.—Supplementary feeding of earthworms was essential to keeping *Hemicentetes* alive in the laboratory. Several lived as long as 2 years in captivity. They ate beef, lung, heart and dry baby cereal moistened with milk. They refused adult insects of numerous kinds but did accept large beetle grubs, from which they squeezed the body juice and entrails.

The tenrec eats a worm by grasping it between its jaws in whatever position it is initially encountered. With a pawing motion of the forefeet, it manipulates the worm sideways until an end is in the mouth. The worm is then swallowed whole. Occasionally it is broken during the manipulation and eaten in sections. A worm that is too large chokes a small tenrec; he regurgitates it and repeats the process of manipulation. After several unsuccessful tries, he often breaks it in two by stepping on it and pulling an end in his clamped jaws.

Since these animals appear to forage in family groups, it is interesting to note the influence a feeding animal has on its fellow group members. On one occasion an adult *Hemicentetes* was the first member of a group of three to discover a pan of earthworms that had been quietly placed in a cage. It immediately began eating. At the same time, two other cage mates, one adult and one juvenile, began rooting about in the wood shavings of the cage. They continued to root in the shavings in various parts of the cage for 15 min before coming upon the pan; they began eating at once in the presence of the adult that had nearly finished its meal. Perhaps the earthworms' odor or the sounds of the stridulating organ of the first adult or his chewing sounds elicited the rooting behavior.

A tenrec that was fed earthworms outside his cage was returned to its cage mates. When they smelled his snout at close quarters, they immediately began

to root in the shavings in an almost frantic manner. The same effect was produced by placing an object that smelled heavily of earthworms near a group of sleeping tenrecs.

While feeding they pivot and swing their rumps swiftly from side to side. This maneuver effectively wards off tenrecs that try to take earthworms from them. The sight of two tenrecs pulling on opposite ends of a worm was a common one. Larger individuals often succeeded in taking worms from smaller ones.

The preoccupation with which *Hemicentetes* feeds on an earthworm is remarkable. An animal that would erect its quills and buck under any other unusual circumstance seems undisturbed when picked up during feeding. Removing the worm does elicit quill erection.

Activity and torpor.—An animal was considered torpid when its respiratory rate was slow and irregular and when arousal from sleep was also slow. An active but torpid individual stumbled about its cage and drank, ate and cleaned itself very slowly.

The season of torpor is dependent on the age and geographical area. Fully active families of *Hemicentetes* occur only 25 km from a region of higher elevation where, at the same time, another population is solitary and hibernating. In the laboratory at the Institut de Recherches Scientifiques à Madagascar during April, *Hemicentetes* that were caught in March were in various states of activity. Several very fat adults were torpid and curled up, usually lying on the water-soaked newspaper at one corner of their cage. Others, probably young of the year, were giving birth or were pregnant. This varied activity suggests that torpor may extend over a prolonged period, particularly in the case of reproductively inactive adults.

During torpor *Hemicentetes* sleeps curled on its side or on its back with legs up (Fig. 1). Often the hindlegs seem swelled with fluid. Usually the forefeet are tucked in under and close to the chin, while the hindfeet are free from the body. From time to time torpid *Hemicentetes* wobble about their cages, drink, scratch themselves, bite the dirt from their toenails and even devour earthworms. The feces are composed of undigested earthworms. A sharp sound, a touch or a shake of their cage elicits an increase of respiration rate and erection of quills, and eventually the tenrec may walk about. When ambient temperature was 25° C, the respiration rate of a sleeping torpid *H. semispinosus* was 26 per min; the rate increased to 110 per min when it was disturbed. Respiration rates of sleeping torpid individuals were as low as 5–7 per min.

Probably depending on body temperateure, some torpid individuals can spread the nape spines and erect all body quills, as well as emit the vocal buzz associated with the defense repertoire. On 19 July 1963 a thermometer, accurate to 0.1° C, inserted 1 cm into the cloaca of adults that were walking in their cage, read 23.8° C, while the temperature of two others that were sleeping in the same cage was 22.0° C. Likewise, a torpid, unreceptive female with which an active male attempted to copulate responded by erecting her quills slightly and

TABLE 1.—*Group size and composition of four families of* Hemicentetes

Locality and date	Juvenile	Sub-adults	ADULTS ♂	ADULTS ♀	ADULTS undet.	No. of litters	Total no. in group	Comments
Perinet								
17 March 1963	20				3	2	23	Age of litters not determined. At least 2 litters.
Ambodivoangy								
(1) 29 July 1963 Near Ambodivoangy in cutover forest at Ambalatingy	7	2	1	2	1	2	13	Total length of 2 juveniles = 95 mm, 92 mm. About 3 weeks old: 1 ♀ pregnant (4+ young). 1 female nursing. 1 male courted and mounted a female while the entire group of 13 were contained in a small basket.
(2) 2 Aug 1963 These were dug from a burrow in a coffee grove.	7	3			2	4	12	3 young of litter Total length = 124 mm; about 4 to 10 weeks. All young buzzing and well furred. 2 young of litter Total length = 89 mm; about 2–3 weeks. 2 young of a third litter Total length = 106 mm; about 3–4 weeks.
(3) 6 Aug 1963 Found walking together in the forest about 10 km north of Ambodivoangy	2			1		1	3	Juvenile Total length = 65 mm; about 1–2 weeks. 1 adult female nursing.

bucking her head back; at the same time she emitted a squeak that was nearly identical to the sound emitted by active, unreceptive females. On this occasion, however, the sound was lower in frequency and somewhat distorted.

Social groupings.—During the breeding season *H. semispinosus* occurs in family groups which may number up to 23 individuals. These groups may live in the same burrow and forage as a unit. Table 1 contains a summary of group size and composition of four captures during 1963. M. Lepiso of Varifouna provided information he gained as a collector to further confirm the hypothesis that this animal forages and lives in groups.

When the animals become torpid, there may be a tendency for the groups to fractionate, for solitary animals may be excavated at this time. It would also appear that male-male antagonism is high at the onset of the breeding season, since each group appears to contain an adult male and one or two adult females with their subadult and juvenile offspring. Evidence for male-male antagonism is also provided by the following laboratory observations.

Between February and August in the Madagascar laboratory no fighting was observed. But later in the U.S., particularly during the beginning of the natural breeding season in November, several adult males were seen fighting. They erected their body quills, but the nuchal crest was only partly raised, if at all. Attacks were centered on the flanks just behind the forelegs. Each male took the flank of his opponent in his jaws and held so tightly that separation was nearly impossible for several minutes. In one case a tenrec died a day after such a battle. Severe subdermal bleeding occurred in the area of the bite.

Reproduction.—The reproductive season in Madagascar varies depending on local conditions; in general, it occurs throughout the rainy season, from November to May, plus or minus one month. During late July, *Hermicentetes* was solitary and hibernating in the region of Perinet (950 m above sea level), while only 25 km NE (411 m) near Rogez, they were active and reproducing. This difference is probably a reflection of the later initiation of the dry season at lower elevation; for example, guava fruits ripen two months apart: in Perinet during May and early June, at the onset of the dry season, and in Rogez during August.

In the Perinet region a native had trained his dog to find *Hermicentetes;* the native captured several dozen in March. During July, 2 days of searching yielded none, whereas in Ambodivoangy the natives brought several family groups, each of which was taken from a single burrow. The dates of six births occurring in the laboratory in 1964 are shown in Table 2. In all cases the parents were wild caught and had been in captivity for about 8–12 months.

During courtship the male approaches the female loudly hissing, with the end of the snout turned up in a characteristic manner. He thrusts his upturned snout into her ears and cheeks and into her body quills and nuchal crest, while continuing to emit a drawn-out hiss. This initial contact behavior resembles that of *Solenodon* (Eisenberg and Gould, 1966).

TABLE 2.—*Date of birth and litter size in captive* Hemicentetes semispinosus*

Date	Female no.	Litter size	Fate of young
24 January 1964	3	2	Young died
27 January 1964	4	3	Young died
11 February 1964	5	4	Young survived
22 March 1964	4	7	One young died
18 March 1963	1	5	Young stunted, did not survive
7 April 1963	2	6	One young died

* Male left with female throughout parturition and rearing except for 18 March 1963 and 7 April 1963 births.

An unreceptive female wards off a male by her frequent bucking of the head and partial erection of body spines. This rejection of the male is accompanied by her emission of a high pitched chirp resembling the sound emitted by a female *Echinops* when a male is courting her. With each chirp *Hemicentetes* bucks her head back as the mounted male thrusts his snout into her nuchal crest. In no instance on six occasions did an unreceptive female spread the quills of the nape.

A receptive female *Hemicentetes* relaxes all of her quills and hugs her belly close to the substrate. On one occasion a male appeared to bite gently at her nape spines in an effort to maintain his balance during copulation. When a male attempts copulation his quills are erect over most of the body with the exception of the nape; his stridulating organ is usually very active, while that of the female is still.

A female can conceive a second time in the same breeding season if she has recently lost a litter. In one example, a pair was left together through parturition. The male attempted courtship shortly after the birth, but the female was unreceptive. This particular female was unsuccessful in rearing her litter of three, and 55 days after the death of her litter she gave birth a second time.

Birth and parental care.—Several days before parturition a female slept on her back with her four legs up. Twenty–30 min prior to giving birth, the female thurst her snout down and forward and back in a very stereotyped manner. Her snout worked almost as a spade as she cleared away soil and debris in a circle several centimeters around her. She repeated this "spade" work before each birth. This may be an adaptation to giving birth in a burrow crowded with 10–15 other tenrecs as well as nesting material. During partus she panted deeply and rolled the fur and quills on her back and flank backward and forward in a snake-like motion. At least two young were born head first. Immediately after birth, the mother bit the umbilicus, then pulled the placenta from her cloaca, ate it and licked the blood from the faces of the babies. In one instance, the mother failed to remove the tissue surrounding the baby and it died.

FIG. 2.—*Hemicentetes semispinosus* on the day of birth. Note the expanded white patch mid-dorso-posteriorly, where specialized quills will grow and compose the stridulating organ. The white patch on the nape is the future site of the nuchal crest of protective yellow quills. The light nasal stripe will be covered with yellow fur.

When the male is left with the female and her litter (Table 2), the female does most of the nest building. The diameter of the nest is about 15 cm. As the mother tidies the nest from the outside, the young huddle about the male. Once, when the female was giving birth to the second member of a litter, the male carried shredded newspaper to the nest beneath a log and covered the baby with it. In a large 2-m diameter cage where green plants grew, the mother pulled a philodendron leaf from a plant and lined the bottom of the nest.

Both male and female lightly press the underside of their snout against the body of a baby that is wandering from the nest (as in *Echinops*). Twice when a baby, less than a day old, had crawled away from the nest, the female took it in her mouth and carried it back to the nest.

Growth and development.—On the day of birth *Hemicentetes* are nearly

naked, but distinctly pigmented (Fig. 2). There are three pink stripes down the back, one central and two lateral. The central stripe is the most prominent; at the nape it broadens into a triangle where the nuchal crest of protective yellow spines will develop. Lateral to the stripes the skin is black where black quills will erupt. The snout has a broad pink stripe down the center. The belly and feet are also pink. The central stripe broadens slightly where the stridulating organ will develop; the area is not yet mobile. Growth of quills is most rapid mid-dorsally and on the nuchal crest. Average weights and measurements for a new-born litter of four were: weight, 11.5 g (9.9–12.9); total length, 60.5 mm (60–62); hind foot, 11.2 mm (10–12); ear, 4.7 mm (4–5). At birth the eyes and ears are shut, but the pinnae are free from the head. The vibrissae about the snout are already 6 mm long. The animals walk shakily and easily fall off the edge of a table. They produce a low frequency sound resembling the frequently emitted sputter of adults. A yellow slime was defecated by one. On the second day they immediately freeze when a bright light is shined on them. The distance from the light to the animals (0.5 m) and the power of the light suggest a light rather than heat stimulus.

At 4 days they explore their cage and walk with much greater stability. The babies spread what few quills are on their nape, erect those of the body and emit a buzz, typical of adults on the defensive, when the male (their sire) sniffs at them. The male approaches in the manner it would adopt if courting an adult female, hissing with the end of his snout turned up.

At 5 days the longest spines (4 mm) are found on the nape. When alarmed the young display most of the defense repertoire. The brow is rolled forward and all head spines erect to the sides. All body spines are erect; the head is jerked back sharply and the buzz is emitted; the stridulating organ vibrates, though the quills are too short (½ mm) to produce sounds. There was no jumping up and down. One baby at this age performed the defense repertoire with the exception of the accompanying buzz, suggesting that the larynx may have been undeveloped. Teeth are not yet visible. Black and white belly spines have become prominent. The chin and throat are bare except for two long mental vibrissae.

At 8–10 days the longest nape spines are 10 mm. The eyes and ears are open. Opening of the ears slightly precedes the opening of the eyes.

At 12 days the defense repertoire, which is elicited by a sudden disturbance such as handling, includes jumping up and down on the forefeet. The longest stridulating spines are 2.5 mm; no sounds are yet produced from the organ. The animals walk cautiously at the edge of a table. If an animal is handled carelessly, it injects nape spines into the hand. The young rights itself when dropped a few inches above the ground from an upside-down position.

At 16 days the stridulating organ produces sounds.

At 21 days some animals still suckle and eat small worms.

At 25 days they eat full-size earthworms as well as raw beef. None is suckling.

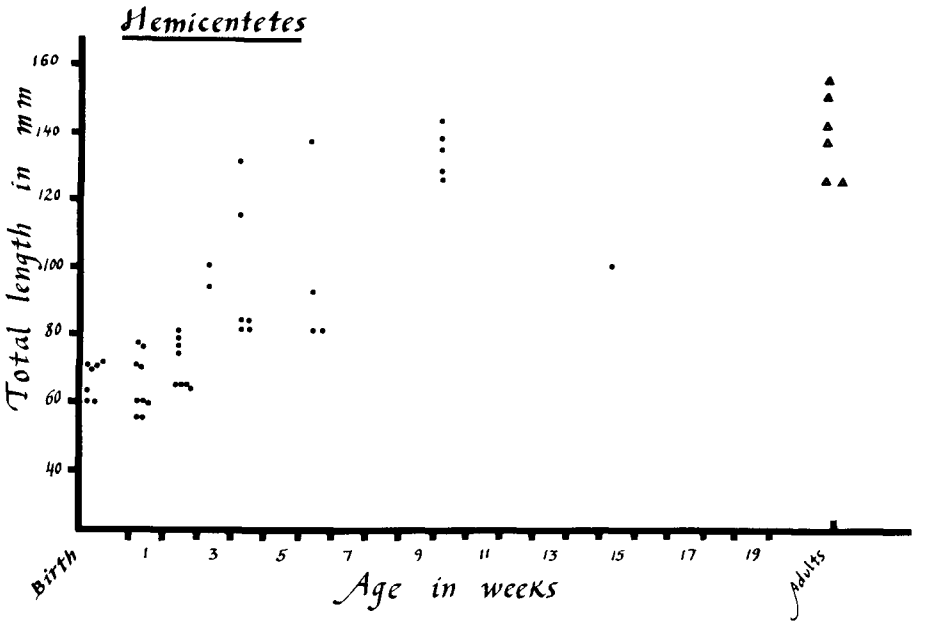

FIG. 3.—Growth in total length of *Hemicentetes semispinosus*. Measurements of adults shown by triangles were at least 12 months old. Weight data were too variable to use as an age criterion. The figure includes data from 16 known-age *Hemicentetes* from four litters.

At 8 weeks females are sexually mature. One male, apparently courting, approached a sibling female with upturned snout and sniffed her. A litter of six that had been separated from their parents contributed to the construction of a communal nest.

At 18 weeks a female that died during an experiment was pregnant with three embryos (36 mm crown-rump).

The growth data for *Hemicentetes* are summarized in Fig. 3.

Hemicentetes nigriceps

The pelage of *H. nigriceps* is much softer and has more fur than quills compared to that of *H. semispinosus,* which consists primarily of quills. The denser fur of *H. nigriceps* is probably an adaptation to the lower temperatures of higher elevation.

Where *H. semispinosus* is yellow, *H. nigriceps* is white. The snout of *H. nigriceps* is completely black, while *H. semispinosus* has a yellow line down the snout. Dense fur covers the belly of the former; the belly of the latter is scantily clad with soft spines. The belly marking of *H. nigriceps* consists of a black mid-line, rather than the two lateral lines of *H. semispinosus.*

Four specimens were collected on 8–9 July 1963 in the vicinity of Manandroy, 35 km NW of Ranomafana. Most of these tenrecs were in solitary hibernation, according to the local natives. A boy found one *Hemicentetes* at the end

of a small tunnel under the mat of needles beneath a pine grove located 100 yards above a rice paddy. The others were found walking along the edge of a *Eucalyptus* grove that bordered a rice paddy. On 17 July all four werc torpid in the laboratory.

The natives pointed out areas where large groups of *Hemicentetes* feed during the rainy season: on the soft, rich, black soil bordering the rice paddies. The habitats of *Hemicentetes nigriceps* are much drier than those of *H. semispinosus* and occur at higher elevation. The latter species also seems to prefer open arcas.

Centetes ecaudatus

Centetes ecaudatus is the largest living insectivore; it appears to feed on a variety of animal matter. Of all the tenrecs it has the greatest distribution, ranging from humid rain forest to nearly arid desert. It is swifter on foot than other tenrecs and is seemingly more alert because of its apparent visual acuity. Resembling the other tenrecs in its nocturnal activity rhythms, it also undergoes a seasonal period of torpidity (Herter, 1962a).

The adult pelage of *Centetes* is composed of soft hairs interspersed with spines on the dorsum. The spines are concentrated on the nape to form a nuchal crown similar to that of *Hemicentetes.* The adults vary in color from buff to light agouti-brown; however, the young are colored in a manner similar to *Hemicentetes.* The young further resemble *Hemicentetes* in their possession of a prominent row of specialized quills 40 mm long extending from the rump forward in the mid-dorsum. The young animal can vibrate these quills when it is aroused, producing a sound ranging from about 2 kc to 20 kc (Gould 1965). As the animal matures and body length increases, there is more space among the quills that eventually disappear during a molt. Some adult *Centetes* that are alarmed continue to vibrate that hind portion of their back, even though sound is not produced.

Study skins of *Centetes* taken in arid regions are far more spinescent than the furry pelage of those taken in the rain forest. Specimens for Diego Juarez are similar to those from Tananarive; both regions are moderately humid. Three spinescent specimens are from the arid south: MCZ 44971, 44969, 44970 from Ampandrandava near Ambovambe. One MCZ specimen having soft fur is from the humid Fito Forest northwest of Tamatave. *Centetes* taken from arid plains, such as one taken by a USNM expedition from south of Moramonga in 1963, is nearly all spinescent on the back; guard hairs compose the soft fur on the back; the stridulating organ is much more extensively developed than in rain forest specimens. Perhaps in arid regions adults as well as juveniles produce sounds. Considering the extensive development of spines on *Centetes* found in arid regions, we would expect the sounds of the juvenile stridulating organ to be louder. Food might be sparser in open, drier regions, favoring a more dispersed family group. A more efficient communication device would be highly adaptive, if, as we believe, these stridulating spines are employed in social communication.

Offensive and defensive behaviors.—As in *Hemicentetes* the defensive behavior of *Centetes* includes an active attempt to drive spines into an opponent. During arousal, *Centetes* erects its spines, particularly in the nuchal crest region. Extending a hand toward *Centetes* may cause it to back away or pivot while pointing its head toward the hand. Much nasal hissing accompanies the defensive posture. Some alarmed *Centetes* stamp their forefeet and hindfeet while raising their nuchal crests and bucking their heads. The stamping component resembles the jumping of *Hemicentetes* during its defense display. *Centetes* may also threaten by opening its mouth, a trait shared by *Setifer* and *Microgale*. This open-mouth threat was displayed by a lactating female *Centetes* when disturbed in the nest (J. A. Davis, Jr., pers. comm.). The gape is immense, about 13 cm (Attenborough, 1961).

In the field, young *Centetes* feeding or traveling in a group scatter and freeze if disturbed (Petter, 1963). Further observations in captivity indicate that not only do the young *Centetes* scramble away and freeze, but they also vibrate their stridulating quills. The defensive repertoire of juveniles also includes the emission of a vocal buzz similar to the sound emitted by *Hemicentetes* under comparable circumstances. Adult *Centetes* do not produce the vocal buzz and are incapable of stridulating, since the concentration of median spines is generally lost during the molt to adult pelage.

Reproduction.—Courtship behavior is quite similar to that described by Petter (1963). A male and female *Centetes* were caged side by side with an opaque door between them. They probably could smell and hear each other through the doors. An encounter was initiated by removing the door. Between November 1964 and January 1965, four paired encounters were observed between a total of three males and two females. The male first nosed about the female's neck and then her cloacal region. When approached face to face, the female opened her mouth and enclosed his snout between her jaws. This is a common pattern in *Solenodon* (Eisenberg and Gould, 1966). The male pressed his snout across her back and suddenly bit her on the flank. This biting of the female's flank around the hind quarter was observed in three paired encounters between three males and two females. Petter (1963) also noted this aggressive pattern during courtship. The female frequently avoided the male's hind quarter approach by quickly tossing her head to and fro and pivoting her body so as to block his advance. During the pivot she rested her weight on her forefeet while shifting the position of her hind end.

Successful breeding of *Centetes* did not occur in captivity. General observations on known-age juveniles indicate that 3- to 4-week-old *Centetes* are being weaned and are beginning to take solid food.

Social groupings.—During the breeding season *Centetes* can be found foraging in family groups. Each group appears to consist of an adult female and her litter. The native animal collector of Varifouna once saw 30 *Centetes* hunting together. Another native reported seeing 20 *Centetes* in a pack. Petter (1963) illustrated a family of 19 young and two adults hunting in the wild.

The members of the family group were apparently following one another. Embryo counts of 16 (Rand, 1935) and 32 (Goetz, 1937) substantiate the possibility of a single family group, rather than coalitions of unrelated families. In captivity, young followed other young as well as a strange adult in a 6-ft diameter cage. As they matured, following was no longer apparent. No data are available concerning the permanence of such family groups, but presumably they break up as the young mature.

Echinops and *Setifer*

The hedgehog tenrecs, *Echinops telfairi* and *Setifer setosus*, are similar in external appearance to the continental Old World hedgehogs of the family Erinaceidae. The Erinaceidae and the tenrecoid genera *Echinops* and *Setifer* represent a classical case of convergent evolution.

Setifer and *Echinops* are less than half the size of *Erinaceus europaeus*. Both of the former kinds are covered with spines over the dorsal side of the body, while the face, legs and ventrum are covered with hair. The spines of *Setifer* are short (about 15 mm) and fine, whereas *Erinaceus* has heavier and longer spines. All three species can erect the spines and roll into a ball because of the extreme development of the panniculus carnosus; however, *Setifer* has not developed the complex connections of this muscle to the cervical vetebrae as has *Erinaceus* (Dobson, 1882).

Setifer and *Echinops* have longer and more highly patterned vibrissae than does *Erinaceus*, but the eye of *Setifer* is very reduced when compared to the other two forms. It would seem that *Setifer* relies even less on vision and more on its tactile senses than do *Erinaceus* and *Echinops*. The tail of *Erinaceus* is naked and rudimentary; however, *Setifer* and *Echinops* have short but stout, muscular tails, covered with spines.

Echinops differs from *Setifer* in being smaller in size and probably more arboreal. *Echinops* occupies the drier regions of Madagascar, where it feeds on insects captured among the branches of trees and shrubbery as well as on the ground. They scratch insects out of the crevices of dead logs with the sharp toenails on their forefeet. In captivity they drink water, but much less frequently than *Hemicentetes* or *Centetes*. Feces of *Echinops* are much drier than those of other tenrecs. This tenrec may be adapted for long periods of drought.

Setifer is very common in and about Tananarive, where it is frequently found raiding garbage cans. Live trapping a 5-acre woodlot in Tananarive (Tsimbazaza region) yielded seven *Setifer*. Mr. Kenneth Lang of the 1963 Smithsonian Institution expedition reported that in one scrubby area far to the north of Tananarive, the natives brought in 53 animals in just a few days. Gould was told of other areas of local abundance near Fianarantsoa and near Morondava.

Setifer and *Echinops* are both active at night. The exhibit a diel variation in their body temperature and a seasonal torpidity (Kayser, 1960; Herter,

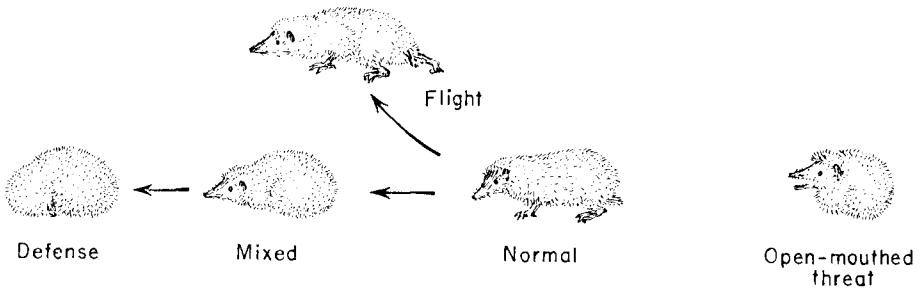

FIG. 4.—Postures and the degree of spinal erection during defensive behaviors by *Setifer*. The maximum spinal erection is exemplified by the defense posture in which the animal is rolled into a ball and by the open-mouthed threat posture.

1962b; 1963a). Data on thermoregulation and activity were included in the publications of Kayser (1960) and Herter (1962b; 1963a).

The climbing ability of *Echinops* is remarkable. Its movements are very slow and deliberate, but its sharp toenails rarely slip. *Echinops* can hang by a single foot from the rim of a flat surface and then regain its position with remarkable agility. This feat involves an undulating motion of the flanks and repeated reaching and grasping of the free feet. (Also see Herter, 1963a).

Offensive and defensive behaviors.—The hedgehog tenrecs have an ultimate form of defense behavior, not found in the other genera of spiny tenrecs, that involves the ability to roll into a ball while tucking the head and limbs ventrad. The sphincter muscles running around the body at the junction of the spiny dorsum and the hairy venter permit the spiny dorsal skin to be drawn together, thus enclosing the animal in an impregnable shield of spines. This defensive rolling behavior is also exhibited by the true hedgehogs of the family Erinaceidae. Fig. 4 indicates the alternative types of behavior shown by *Setifer* when it is disturbed. The variable degree of spinal erection is probably dependent on the degree of autonomic discharge, which in turn is a function of the stimulus strength. Maximal spinal erection is concomitant with rolling into a ball, while intermediate degrees of erection are manifest during exploratory, flight and attack behaviors.

Both *Erinaceus* and *Echinops* differ from *Setifer* in that the open-mouth threat is not a normal component of their threat behaviors. All three forms attack in the following manner: the quills are erected, the head is lowered, and the brow quills are raised and directed forward. The head may be switched from side to side or jerked sharply upwards toward an offending object. The animal may rush at an opponent and either bite or seek to drive its head spines into an opponent's body. While the animal is rolled into a ball, head jerking may also be shown. When attacking, the hedgehog utters an explosive hiss, while the tenrecs employ a slightly different sound, an expiration and a definite abrasive sound, perhaps caused by grinding the teeth. All three species produce a violent hissing sound while inspiring and expiring. This rapid hissing gen-

erally occurs during a bout of head "boxing" or when each is rolled into a ball.

Setifer and *Echinops* each produces a characteristic pulsed sound when rolled into a ball. This sound is barely audible, including frequencies above 20 kc. It is delivered as a chain of pulses at a rate of 8 per sec.

Setifer differs from *Echinops* and *Erinaceus* in that it will defecate and urinate if picked up suddenly.

Social groupings of Echinops.—*Echinops* does not appear to be as social as *Hemicentetes*. Although individuals in groups are tolerant in captivity, fighting occurs, especially between males at the onset of breeding. The newly maturing young follow the female during her foraging trips, and in captivity the following reaction was amply displayed. During torpor the animals are solitary or in groups of two or three.

In late June six *Echinops* hibernacula in cavities of tree branches were chopped open near the small village of Bekonazy, 25 km E of Morondava. Some animals were located in the hollows of tree branches near the ground and others high off the ground. To locate the animals, the natives struck a log or branch with an axe and then listened for the huffing and puffing response of an *Echinops* within. A brief description of the hibernacula follows. A branch 6 m from the ground contained three adults. The wood surrounding the *Echinops* ranged from 60 to 75 mm in thickness. A few fecal droppings were present. A tree hollow 4 m high contained two subadults. One *Echinops* occurred in each of three different stumps on the ground. No feces were present. One of the logs was lying in a ditch along the road; the others were in dense brush country beneath towering baobab trees. Two adults slept in the hollow branch of a fallen tree 3.5 m high. Wood thickness of the hibernaculum varied from 22 to 75 mm.

None of the *Echinops* was found in a balled-up posture; all were fully extended. In two cases the narrow passage in the hollow branch was too slight to permit rolling. When they were touched they immediately rolled. The temperatures of two just taken from a hollow were 21° and 22° C (41 mm insertion of the thermometer); air temperature in the shade was 30° C. The temperature inside one hollow branch was 23.5° C. The animals shivered for more than 1 hr after they were collected.

Reproduction and development in Setifer.—A female *Setifer* gave birth to a litter of four babies on 31 January 1963 (Fig. 5). At birth the babies were nearly naked; the skin was gray with very short white-to-tan bristles less than 0.5 mm long that were present only on the head and back. Short belly hairs were white to gray. The ears were folded but free from the head. Prominent vibrissae occurred on the chin, snout, below and in front of the ears, and below and in back of the eyes. There was a prominent fold of skin below and continuous with the ears, and a black mask circled the eyes. Teeth had not erupted. The neonate crawled slowly on its belly, and when it was picked up it rolled into a tight ball but emitted no sounds.

By the 7th day the longest spines on the forehead were 4 mm. Eyes and ears

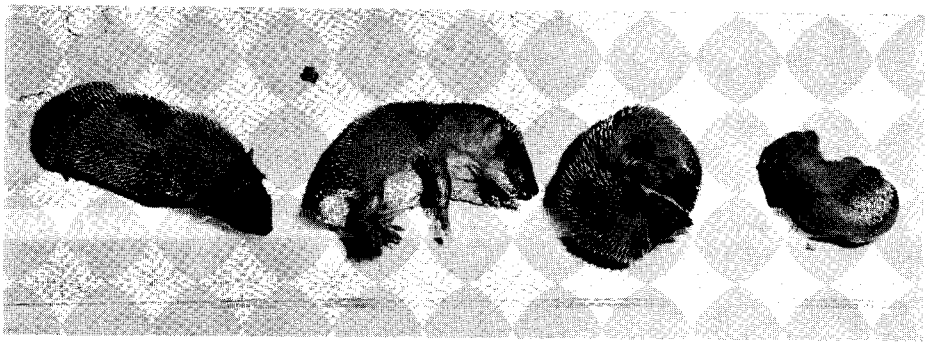

FIG. 5.—A litter of four *Setifer setosus* 1 day old. The prominent black mask of *Setifer* is absent in the young of *Echinops*. The baby second from the right had just been handled. Note the extreme difference in the size of these littermates. A similar phenomenon was noted with *Echinops*.

were still shut. Between the 11th and 13th days the eyes opened, but the ear canals were still closed. Quills were large; if an animal was handled carelessly, the quills were sharp enough to injure a bare hand. During the 3rd week a second set of quills was evident; these quills were oriented at a different angle from the first set of quills. Dispersed among the quills was soft fur, absent in the adults. Unfortunately, this litter of four did not mature. The mother apparently failed to supply sufficient milk for their survival; however, one lived 4 months and ate the prepared food mixture of meat and cereal.

Measurements of the single *Setifer* that survived 4 months in capitivity are included in Table 3.

Reproduction in Echinops.—In the field *Echinops* probably mates at the beginning of the austral summer in November and December. After 5–16 months in captivity, 12 females gave birth to 13 litters (Table 4). Females that littered in late 1965 were born in 1963 or 1964 in the laboratory. Animals born in captivity began courting in late August, about 2–3 months before this activity begins in Madagascar.

During initial courtship the male and female exhibit some head-butting with explosive hissing. If the female is receptive, the male mounts while biting the female on the nape or just behind the foreleg. While the male is mounted and throughout intromission, the female emits a repetitive, high-pitched chirp.

TABLE 3.—*Development of* Setifer

Age in days	Total length (mm)	Weight (g)
Birth	78	24.7
7	85	25.4
13	94	33.1
22	101	32.6
31	110	35.8

TABLE 4.—*Date of birth and young born to captive* Echinops

Date	Number per litter	Number reared
1963		
7 January	5	all survived
26 December	2	1 survived
9 December	10	all survived
1964		
23 November	4	all survived
27 November	6	all survived
7 December	7	all survived
16 December	7	4 survived
29 December	7	5 survived
1965		
11 January	6	all survived
29 October	5	all survived
4 November	6	all survived
5 November	3	all survived
9 November	8	all survived

At the time of parturition, the female constructs a nest from leaves or paper strips and fills the nest box with these materials, which she has carried in her mouth. If no nest box is provided, the female does not build an organized nest.

From the day of birth until the young are 8 days old, the mother is very aggressive toward any human disturbance. She turns quickly toward any sound or a baby returning to the nest. As she localizes the position of one's hand, she pivots her body in place so that her head faces the disturbance and her body protects the babies beneath her. In this position her quills are erect, her forehead is rolled forward, she emits a grinding sound, her snout turns up, thus baring the incisors, and produces an explosive huffing. She turns, attacks and bites only when she hears or feels something foreign. A silently waving hand elicits no response.

During the first week after birth, the mother picks up the babies in her mouth when they have crawled away from her. One pattern of maternal care is identical in *Hemicentetes* and *Echinops*: the mother often presses her chin and throat against the baby as it crawls the slightest distance from her. This motion probably renders information about the mother's position to the baby. Chin-pressing of a baby by the mother is very gentle; the contact seems to be a tactile guide rather than a device to press the animal nearer the litter or the mother. Chin-pressing is generally followed by the baby's crawling back to the nursing site.

On one occasion the mother mouthed a baby three times, first by the back, then by the flanks and neck, and finally by a hindleg, seeming to settle on the last and most gentle grip. She picked up an unidentified baby that was displaced and brought it back to the nursing site. No sounds were heard. A preg-

nant female in the same cage as one that had just littered picked up one of the babies in her mouth during the excitement of the observer's opening the cage top. On another occasion a runt, 17 days old, was picked up and placed near its nursing mother. She pushed it away from her snout; it died a few days afterwards.

Growth and development of Echinops.—Two peculiar features characterize the development and birth of young *Echinops* in captivity. First, at birth the young may range from 3.8 to 9.6 g; generally the smaller young fail to develop, and die within the first week. Second, the first and last young may be born as much as 30 hr apart. This difference in time of birth enables a first-born young to nurse and add to its weight and strength almost a day before the complete litter is born. Birth weights do not necessarily correspond to an order in size, since a large neonate may be born last. Our one record for *Setifer* suggests a similar disparity in birth weights.

On the day of birth young *Echinops* are nearly naked. Their eyes and ear canals are closed, but the pinnae are free from the head. They wobble on their four legs and drag themselves short distances on their belly. The longest vibrissae, on the snout, are 6 mm; the longest spines are around the forelegs and are about 1 mm. The rest of the body is either naked or just becoming rough with short bristles. Babies in the same litter are spinescent to varying degrees. The toenails are sharp, and the animals cling with such tenacity that one can pick them up as they encircle a small finger. This grasping ability is probably an adaptation to aboreal life.

Two sets of quills are evident. The directional orientation of these quills differs so that they form an effective defense when erected. A second set is not visible on *Setifer* until the 3rd week. The two sets of quills are quite distinct, the longer set being gray to black and the shorter set white. The white set is absent dorsally but prominent laterally. The long, black set is present dorsally and laterally.

The animals right themselves very slowly when turned on their backs. They are very cautious about exploring and falling off the edge of a table; this behavior is probably an adaptation to arboreal life. Crawling is accomplished by all four legs moving with nearly equal strength.

When a baby is disturbed or picked up, it rolls its brow forward in the protective manner of adults (see Fig. 6). Some of the one-day-old babies rolled in a tight ball that was difficult to unfold. In the rolled position some babies grasped their hind legs with their forepaws in the manner of adults; others did not. In a litter of ten, two out of eight did not roll. A disturbance elicits a musky odor that elosely resembles the odor of the vespertilionid bat *Eptesicus fucus* as well as that of the poisonous house plant, *Dieffenbachia*. While nursing, the babies emit a high-pitched peep.

Eyes are open or beginning to open between 7 and 9 days of age. Quills are predominantly white on the sides and gray on the back. Soft fur is present between the eyes. A disturbed juvenile now shows defensive behavior similar

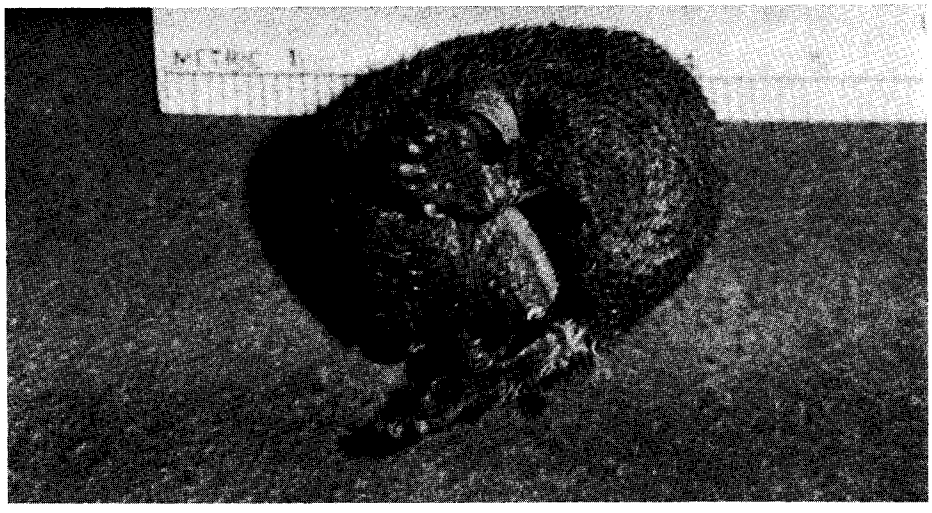

FIG. 6.—*Echinops telfairi* on the day of birth. It had just been disturbed; note the characteristic clasping of the hind and forefeet.

to that of adults, erecting its quills, huffing and puffing, and raising and lowering its snout. The crunching sound is not heard. When a finger was rubbed over the head of some babies, they rolled; but when rubbed on the rump, they unfolded. The manner of rolling was variable; some young rolled tightly with all legs pulled in; others rolled with the feet exposed.

At 10 days they begin to follow the female when she leaves the nest.

At 15 days the ears are open or partly so. Young walk with their bellies high off the ground; formerly the venters tended to drag on the substrate.

At 18 days weaning has begun. All young still nursed, but one ate a baby mouse. Teeth are just exposed. The babies still emit a high-pitched peep whenever the mother shifts her position during nursing. Self-annointing is first observed; a baby scratches at sparse shavings on the slick floor of the plastic cage and then scratches its flank. They drink from the water dish, and bite the handler with its sharp incisors.

At 19 days they wander about the cage more freely. They right themselves quickly when placed on their backs. The spines are pearly white at the base and gray on the distal three quarters. Perhaps because of the amount of handling several of the young failed to ball up when disturbed; however, touching the snout elicited the forward roll of the brow and down-turning of the ears.

At 20–22 days the fastest-growing quills (1 cm) are on the back. The criss-crossing of two sets of dark gray spines is quite prominent dorsally from head to rump. Laterally they are white. The musk odor is no longer evident when a baby is handled. The defensive sequence now includes grinding of the teeth.

At 28 days some still did not roll. One, of a litter of eight that had been

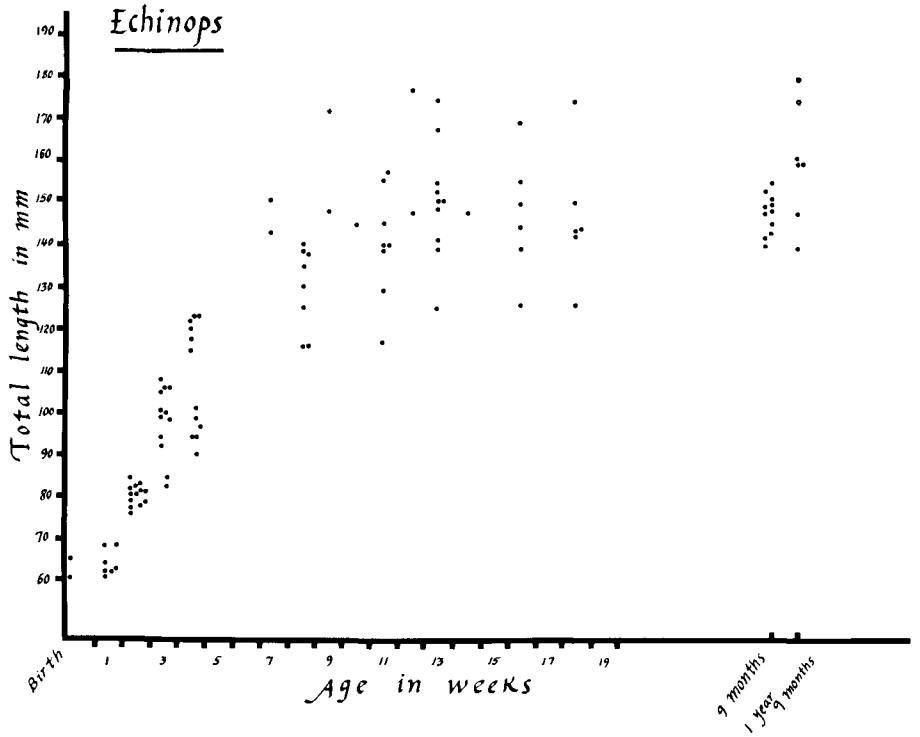

FIG. 7.—Growth of *Echinops telfairi* by total length. The regular increase of total length provides a dependable measure of age under laboratory conditions. Thirty-one known-age animals from six litters were used.

separated from their mother, carried shredded newspaper in its mouth, after the observer removed a sheet of paper covering the group.

At 32 days a few still nursed, though all were eating solid food. They emitted the same peep when the nursing mother shifted her position or when several crowded about a small dish to eat mealworms.

In captivity *Echinops* does not become sexually mature until the second year. Growth data for total length and weight are given in Fig. 7 and 8.

Self-annointing behavior.—Echinops exhibits a behavior pattern which bears a resemblance to self-annointing or *selbstbespuchen* as described for the true hedgehogs, *Erinaceus, Paraechinus* and *Hemiechinus* (Herter, 1957); Eisentraut, 1953). A variety of chemical stimuli release the self-annointing reaction in *Echinops,* but urine from another specimen frequently serves as a releaser. The animal sniffs the urine and begins to lick. At this point it begins to salivate excessively. The mixture of urine and saliva on the substrate is wiped with one forepaw. The forepaw, now impregnated with urine, is wiped on the animal's side. This wiping process is often repeated several times on opposite sides of the body. Frequently the animal begins to wash while sitting upright and wiping its muzzle with alternate strokes of its forepaw.

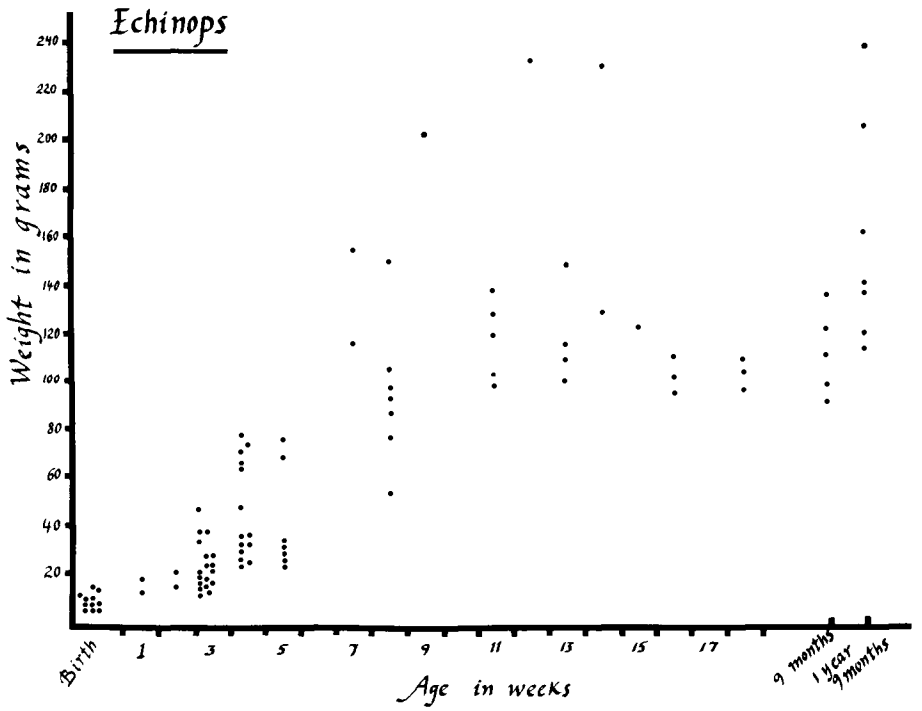

FIG. 8.—Growth of *Echinops telfairi* by weight. Thirty-one known-age animals from six litters were used.

Erinaceus exhibits self-annointing in the following fashion. The stimulus object eliciting the reaction is variable: dung, a new cage, a shoe, soap, crayon and mothballs have all proved effective stimuli. The hedgehog may sniff or lick the object and, while moving the tongue, accumulates a great quantity of white, foamy liquid in the mouth. The animal lifts its head, with nose high and teeth exposed, and turns to either the left or right. It then spreads the liquid on its spines by rapidly extending and retracting the tongue. During this phase the body is rigid and the movements are jerky. The animal then turns its head back to the stimulus object, which may be sniffed or licked following the initial response, and with sporadic, additional references to the stimulus, the animal repeats the above reaction by spreading the liquid alternately on each side of its body. In general, each subsequent pair of alternate "depositions" is anterior in position to the preceding pair. This reaction terminates after a rather variable number of acts.

These two stereotyped action patterns of *Echinops* and *Erinaceus* are similar in these respects: excessive salivation occurs on perceiving an unknown chemical releaser; after the animal licks the alien substance it spreads the substance on its body. The patterns are different in that *Erinaceus* completely lacks a face-washing movement pattern and thus does not combine self-

annointing with washing; *Erinaceus* spreads the substance and quantities of saliva with its tongue, whereas *Echinops* spreads the alien substance with a forepaw. Such differences suggest that ritualization through natural selection has proceeded independently to produce a generally similar behavior. The functional significance of self-annointing in *Erinaceus* and *Echinops* is unknown.

Microgale dobsoni

Ten specimens of *Microgale* (*Nesogale*) *dobsoni* were trapped at Ambodivoangy and Perinet. In Perinet, they were taken during March, along the rocky slopes of steep stream banks of dense rain forest, as well as from wet cut-over rain forest in the lowlands. At Ambodivoangy, trapping in rain forest yielded none; traps set beside a mountain stream along cut-over woods yielded several. One female trapped in August had two embryos (25 mm, crown to rump). The natives claimed that *Microgale dobsoni* ate rice in the paddies. In captivity *Microgale* ate dried rice sparingly, but preferred a variety of hard-bodied insects including beetles, dragon flies, walking sticks and mealworms.

Two female *Microgale dobsoni* were kept in the same cage for several months. Very often when they fed on a large beetle grub, one animal ate a small portion and then permitted the other *Microgale* to tug the food from its mouth. After this animal devoured a portion of the grub, it allowed the first *Microgale* to tug the remnants from its mouth. The exchange continued until the last morsel was eaten. These two females organized a small but sparsely constructed nest.

At least two sounds are emitted, though rarely is either one used. Once during three months of captivity a female *Microgale* emitted a loud, high-pitched, ear-splitting shriek with her mouth open at full gape when suddenly disturbed by another *Microgale* that ran up to her. During test runs in an apparatus that required *Microgale* to jump from a disc onto a platform, it occasionally emitted a high-pitched but very low intensity "chrrr" when it seemed apprehensive about jumping (Gould, 1965). When in a strange situation, *Microgale* shivers, yawns and sits in one place for several minutes to ½ hr without moving. Its gait is halting and the long tail often drags at the tip, the rest being held curved and free from the ground. There was no evidence of the tail being prehensile.

When a strange conspecific approaches a *Microgale,* the approached individual opens its mouth full gape and pivots its head, keeping the snout directed toward the other animal, undoubtedly localizing its position by hearing and smelling.

The temperature of one female on 30 January 1964, after 1 yr in captivity, was 35.0–35.2° C after 1.5 min of cloacal insertion (55 mm); room temperature was 26.2° C.

Limnogale mergulus

No *Limnogale mergulus* F. Major was taken. However, the natives of two

localities insisted that they were present and confirmed identification of *Limnogale* droppings. In the Ambodivoangy region, *Limnogale* is rare; only two droppings were found on the rocks. Grandidier (1932) collected the animal in this vicinity, but on the Antsampandrano River region their droppings were abundant on rocks in the stream. The feces were 5–15 mm, black and cylindrical. The odor resembled that of *Sorex palustris* or dried shrimp. The droppings contained the remains of insects and crawfish. The natives insisted that the mainstay of *Limnogale* was crawfish.

The forester at the Antsampandrano station had seen this aquatic tenrec swimming beneath the bridge near headquarters. On 14 June 1963 the water level at the bridge was 65 cm; but in January–February 1963 it had risen to 230 cm, and in March 1959 to 450 cm. Malzy (1965) recorded a nest very close to water level when this river was low. *Limnogale* must change its burrow sites seasonally in order to avoid flooding.

Apparently temperature is not an important factor in the distribution of *Limnogale*. It occurs near Rogez (411 m) and at Antsampandrano at 1,900 m, where ice and snow are present in July and August. On the night of 15 June 1963, the temperature dropped to 1° C at the station. Frost coated the grass and rocks along the stream, yet fresh *Limnogale* droppings were present in the morning. Grandidier and Petit (1932) believed that *Limnogale* fed on the riparian plant *Aponogenton*. More likely, the robust feet, sharp claws and leathery snout of this tenrec are adaptations to feeding on the abundant invertebrate life nestled within the protective foliage of *Aponogenton*, a plant that grows in very swift water.

At Ampansandrano 83 trap-nights along the stream yielded 18 *Rattus* and 13 *Suncus*. Droppings of *Rattus* usually occurred near shore and those of *Limnogale* nearer the center of the stream, but several times both types of droppings occurred on the same rock. By walking up the stream one could easily see and smell the abundance or scarcity of *Limnogale* droppings. They were more common below the nickpoint and below the station, where *Hydrostachys* was abundant and *Aponogenton* was rare to absent; droppings were scarce above the nickpoint, where the water was deeper and rocks in the stream were fewer. If the close association among *Aponogenton*, *Hydrostachys* and *Limnogale* does exist, one may expect to find the aquatic tenrec in several other localities, because *Aponogenton* occurs in eastern, western and central Madagascar (Jumelle, 1936).

Geogale aurita

A single specimen of *Geogale aurita* A. Milne-Edwards and A. Grandidier was taken from beneath a fallen tree where it was sleeping in a cavity of sand. It was apparently torpid and lived for 10 days in captivity without drinking or eating. It was found late in June in dry, open woods 3 km W of Lake Ihotry, Caton de Basy-Basy in the Prefecture de Morombe, Province of Tulear. This is the first record of torpor in the Oryzorictinae.

DISCUSSION

When the behavior patterns of the tenrecs are compared, the agonistic patterns of attack and defense show strong similarities among the closely related species of the subfamily Tenrecinae. All Tenrecinae roll their brows forward when disturbed; *Setifer*, *Echinops* and *Centetes* produce a great deal of hissing and other nasal sounds during defensive postures when quill erection is most apparent. However, loud nasal sniffing is not produced by *Hemicentetes* under similar circumstances. Further behavioral comparisons indicate a close affinity between *Echinops* and *Setifer* and a remarkable similarity in the behaviors of *Centetes* and *Hemicentetes*. The resemblance between stridulation in *Centetes* and *Hemicentetes* is most pronounced when the behavior of juvenile *Centetes* is considered, a factor which implies that *Hemicentetes* is in many ways a neotenic form of *Centetes*. Certain greeting ceremonies and contact-promoting behaviors of the tenrecoids resemble functionally similar patterns in *Solenodon*; these similarities attest to the phylogenetic age of these behavioral forms. A comparison of the hedgehog tenrecs (*Setifer* and *Echinops*) with the true hedgehogs (*Erinaceidae*) indicates striking behavioral convergences which parallel their morphological convergence. Especially informative is the occurrence of self-annointing patterns in both the Erinaceidae and *Echinops*. The behavorial differences in the performance of this functionally similar act imply a case of convergent behavioral evolution.

A comparison of development in the young of insectivore families (Table 5) indicates that tenrecs mature rapidly. The age at which the eyes open serves as a criterion suggesting that tenrecs are able to forage with the adult at about 1–2 weeks earlier than hedgehogs, shrews or moles. In addition, the rolling response occurs earlier in *Echinops* and *Setifer* than in the hedgehog, *Paraechinus* (Gupta and Sharma, 1961); both tenrecs roll into a ball on the day of birth; *Paraechinus* rolls at 1 week. Since all tenrecs are born in a rather altricial state, their rapid maturation can be attributed to a very efficient means of maternal nutrition. If precocity were important at birth, the litter size would of necessity be reduced; however, this has not occurrred in the family Tenrecidae. Furthermore, the Macroscelididae is the only family of insectivores including species that have evolved truly precocial young with a concomitant gross reduction in litter size (Walker, 1964).

Comparative data on temperature regulation in the tenrecs are still incomplete. Herter (1962b) reports that one *Echinops* studied in his laboratory was active during the night and torpid or lethargic during the day. Kayser (1960) found that both *Centetes* and *Setifer* hibernate, but that *Setifer* thermoregulates more than *Centetes;* i.e., *Centetes* behaves like a poikilotherm during the austral winter. The irregularity with which individual *Hemicentetes* were torpid for several days or weeks in the laboratory suggests that intrinsic mechanisms were the primary control, rather than any single environmental cue. Frequent periods of torpor may be an important adaptation to spermatogenesis. The testes of all Tenrecinae are adjacent to the kidneys,

TABLE 5.—*Eye-opening in selected insectivores*

Family	Genus	Eyes open	Age in weeks
Soricidae	*Sorex*	18–21 days, Crowcroft (1957)	2–3
Erinaceidae	*Erinaceus*	14–18 days, Herter (1957)	2
	Paraechinus	21 days, Gupta & Sharma (1961)	3
Talpidae	*Talpa*	22 days, Godfrey & Crowcroft (1960)	3
Tenrecidae	*Hemicentetes*	8–10 days, this report	1
	Echinops	7–9 days, this report	1
	Setifer	13 days, this report (possibly earlier)	1½

where body temperature is probably higher than in the pelvis. The testes of Oryzorictinae are pelvic, as are those of most mammals; *Microgale dobsoni* generally maintains a higher body temperature than at least three genera of the Tenrecinae.

Having found young *Hemicentetes* in June and December, Petter and Petter-Rousseaux (1963) suggested that there may be two hibernating periods, in June and in December. The age composition of family groups in March and July indicates that littering probably begins in November or December and continues until June. Hibernation in the adults of the previous year may begin as early as April or May, while breeding occurs quite late in the young from the first litter of the year. The size of young *Hemicentetes* from Ambodivoangy suggests that reproduction may occur throughout the year in that region. If not, the breeding season certainly lasts longer than in the Perinet region, where *Hemicentetes* had disappeared a month or two earlier.

Breeding success in captivity was variable from species to species. The restricted diet of *Hemicentetes* rendered its maintenance in captivity extremely difficult. On the other hand, *Echinops* was fed a variety of substitute preparations, and it bred readily. Of all the tenrec species thus far studied, *Echinops* appears to lend itself most readily to the techniques of captive maintenance. *Echinops* will undoubtedly prove to be the best experimental subject for future research on tenrec thermoregulation, reproduction and neurophysiology if breeding colonies are a necessary prerequisite.

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Department of Mental Hygiene, Laboratory of Comparative Behavior, Johns Hopkins University, Baltimore, Maryland, and Smithsonian Institution, National Zoological Park, Washington, D.C. *Accepted 2 August 1966.*