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The Shrew Tenrecs of Madagascar: Systematic Revision and Holocene Distribution of *Microgale* (Tenrecidae, Insectivora)

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ABSTRACT

The shrew tenrecs of Madagascar—*Microgale* and the allied nominal genera *Leptogale*, *Paramicrogale*, and *Nesogale*—have never been formally revised. Examination of all relevant type material reveals that only 10 of the 22 nominal species-group names of shrew tenrecs deserve recognition. The large number of synonyms is principally due to authors' repeated commission of two substantial errors: (1) failing to recognize the juvenile status of many "adult" specimens used as holotypes, and (2) failing to appreciate the marked degree of within-group variation in these insectivores. Analysis of a range of metric and nonmetric traits further reveals that there are only three or four distinctively different morphological clusters of shrew tenrecs in the modern fauna, and that all species clusters can be comfortably accommodated in one genus, *Microgale*. Illustrations of deciduous and adult dentitions and a key to recognized and reorganized species are provided.

Revision permits, for the first time, an approximate idea of the true ranges and habitat preferences of shrew tenrec species. Although the majority of species appear to be restricted to the comparatively moist and equable conditions of the eastern rain forest, several species occur in forest islands and other favorable habitat in the eastern part of the highlands, and two (*M. pusilla* and *brevicaudata*) have occupied the dry, highly seasonal western side of the island in recent times. Despite its morphological primitiveness, *Microgale* can be aptly described as adaptively resilient. Colonization of the highlands and the far west presumably occurred by pioneering groups moving out from the eastern forest belt during times of climatic amelioration and forest expansion; isolation of these groups would have occurred when conditions deteriorated in the center. Emigration events could have occurred repeatedly, although the nature of Malagasy environmental dynamics

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is not known in detail before about 10,000 BP, and not at all before 35,000 BP. In any event, it is no longer necessary to believe that all known

disjunctions in the species ranges of Malagasy vertebrates occurred simultaneously about 2000 years ago, when the island was first settled by humans.

INTRODUCTION

PRELIMINARIES TO THE REVISION OF *MICROGALE*

Shrew tenrecs are sometimes considered to be the most primitive members of Tenrecidae (Eisenberg and Gould, 1970). They outwardly resemble other unspecialized soricomorph insectivores (e.g., *Crocidura*) in possessing dense, rather velvety fur, abundant vibrissae, tiny eyes, short pentadactyl limbs slung under a long, fusiform body, and an elongated skull tapering into a narrow rostrum. Notably, like other tenrecs they retain ancient plesiomorphies that have been lost in virtually all other eutherian lineages (including true shrews), such as variable and rather low body temperature and cloacae in both sexes (Nichol, 1984).

According to current species lists (Corbet and Hill, 1980; Honacki et al., 1982) and the relevant systematic literature, unrevised *Microgale* (21 nominal species, as grouped here) is the third most speciose genus in Insectivora, exceeded in this regard only by *Sorex* (50+ spp.) and *Crocidura* (100+ spp.). This is a remarkably large number of forms for a primitive island-bound insectivore genus, and implies that *Microgale* has undergone an impressive degree of adaptive radiation in Madagascar. Appearances are somewhat misleading, however, because at least half of the species of shrew tenrecs do not deserve recognition, and even the good taxa corporately represent no more than three or four adaptive types or lines.

Why have so many species of shrew tenrecs been distinguished? Apart from the ubiquitous problem of authors employing narrow criteria to distinguish species that later prove to be within the range of variation of taxa already long known, there are two other reasons for nomenclatural surplusage in *Microgale*. Since these reasons profoundly affect analysis of species limits within the genus, it is important to set them out here.

The first concerns the ontogeny of tooth replacement in *Microgale*. Dobson (1882), Forsyth Major (1897), and Leche (1907) pointed out long ago that some tenrecids erupt their molars before shedding any deciduous teeth other than the third milk incisors. Unfortunately, this fact was frequently ignored by later authors, who unwittingly distinguished juvenile and adult morphs of the same species according to supposed differentia of their "permanent" teeth.² More than a third of the nominal species in the genus are based on holotypes having part or all of their milk dentitions still in place—a record, of sorts, in insectivore systematics. The initial step in satisfactorily revising *Microgale* therefore involves matching older and younger ontogenetic stages of the same species.

The second reason for species splitting is related to the first, but is less amenable to ready solution unless large samples are available. Leche (1907) noted that, in *Microgale* and some other Tenrecidae, juveniles may attain the body size of many adults before replacing any deciduous teeth. However, the problem is actually more complicated than that, because unquestionably subadult animals frequently exceed average adult values for such measurements as head-and-body length and greatest skull length. These observations could be explained in either of two ways. One possibility is that cryptic species exist within *Microgale*, differing from one another only in size (and, of course, in whatever mechanisms are responsible for maintaining species integrity and reproductive isolation). But since "larger" and "smaller"

² The same error has also been committed in tenrecine systematics: the holotype of *Dasogale fontoynonti* (Grandidier, 1929) is actually a juvenile of *Setifer setosus*. This fact was first recognized by Poduschka and Poduschka (1982), and I deeply regret that I did not see their paper on the systematic status of *Dasogale* prior to the publication of mine on the same subject (MacPhee, 1987).

morphs have been collected in exactly the same places, on the same days, by the same collectors, one would also have to infer that the ranges of these species entirely overlap—an ecological improbability if reproductive isolation is really present, and reason enough for decisively rejecting this argument. The alternative would be to infer that the growth curve in some species of *Microgale* is not as tightly controlled, genetically or hormonally, as it is in most eutherians. Instead, there seems to be an almost reptilian propensity for individual size to vary significantly within and across age classes, perhaps in relation to nutrition or some other limiting factor. No longitudinal studies of growth in *Microgale* have been published, although the regulation of size in Tenrecidae should be an attractive problem in comparative physiology (see, however, Eisenberg and Maliniak [1974] for ontogenetic changes in single individuals of *M. dobsoni* and *talazaci*). For this study, high variance in metric traits complicates the definition of species boundaries.

ABBREVIATIONS AND MEASUREMENTS

Institutional abbreviations

AMNH	Department of Mammalogy, American Museum of Natural History, New York
BMNH	Department of Zoology (Mammals), British Museum of Natural History, London
FMNH	Department of Zoology, Field Museum of Natural History, Chicago
MNHN	Laboratoire de Zoologie (Oiseaux et Mammifères), Muséum National d'Histoire Naturelle, Paris
MCZ	Department of Mammals, Museum of Comparative Zoology, Harvard University
UM	Service de Paléontologie, Université de Madagascar, Antananarivo
USNM	Division of Mammals, United States National Museum

Anatomical abbreviations

aac	anterior accessory cusp (= paraconid)
abc	anterior buccal cleft
abci	anterobuccal cingulum
ae	anterior ectostyle

C or c	adult or deciduous canine
cbc	centrobuccal cleft
ds	distostyle
hld	hypoconulid
I or i	adult or deciduous incisor
iof	infraorbital foramen
L	lower (any tooth)
lf	lacrimal foramen
M	molar (followed by number of molar according to conventional primitive eutherian formula)
mf	mental foramen
ms	mesistyle
P or p	adult or deciduous premolar (followed by number of premolar, according to conventional primitive eutherian formula and assuming loss of P/p1)
pa	paracone
pac	posterior accessory cusp (= hypoconulid)
pad	paraconid (= anterior accessory cusp)
pbc	posterior buccal cleft
pe	posterior ectostyle
prd	protoconid
tpm	zygomatic process of maxilla
U	upper (any tooth)

Measurements and abbreviations used in tables and graphs

EL	ear length
GSkL	greatest skull length
H	holotype
HBL	head and body length
HFL	hind foot length, from calx (heel process) of calcaneus to claw tip of longest digit
ICW	width of anterior portion of rostrum, above canines
IMW	distance between buccal surfaces of upper third molars
L	lectotype
MdL	length of mandible, from angular process to alveolus of lower first incisor
MUTL	maximum upper tooththrow length, distal aspect of upper third molar to labial aspect of upper first incisor
P	paratype
TL	tail length
TotL	total length (HBL + TL)

Statistical symbols

CV	coefficient of variation (in %)
N	number in sample

SD standard deviation
 \bar{X} arithmetic mean

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SYSTEMATIC BACKGROUND AND PROPOSED REVISION OF *MICROGALE*

The genus *Microgale* was found in 1882 by Oldfield Thomas, who named *M. longicaudata* (type species of genus) and *M. cowani*. During the next half-century, some 20 additional nominal taxa were added to Thomas' initial pair, often on the basis of single, poorly described specimens. Although questions have been raised about the status of many of these named forms (e.g., by Thomas, 1918; Grandidier, 1934; Morrison-Scott, 1948; Eisenberg and Gould, 1970; Heim de Balsac, 1972), much type material has never been reexamined, and the genus has never been formally revised. Species distinctions are largely based on sketchily defined characters of the teeth, pelage, and body segments (especially tail length), and a minor miscellany of other traits.

Because of the large number of superfluous names, my proposed revision and synonymy are presented immediately after the list of validly published and available nomina, so that the descriptions which follow do not have

to be encumbered with numerous comparisons among exactly the same things. A key to retained and reorganized species is presented in the last section.

SYSTEMATIC HISTORY

All true shrew tenrecs are here regarded as members of genus *Microgale*, including taxa sometimes allocated to the following subsumed genera: (1) *Leptogale* (Thomas, 1918), for the species originally named "*Oryzorictes*" [sic] *gracilis* by Forsyth Major (1896a); (2) *Nesogale* (Thomas, 1918), for the species originally named *Microgale dobsoni* (Thomas, 1884) and *M. talazaci* (Forsyth Major, 1896a); and (3) *Paramicrogale* (Grandidier and Petit, 1931), for *P. occidentalis* (Grandidier and Petit, 1931) and the species originally named *Microgale decaryi* (Grandidier, 1928). Generic distinctions exaggerate the variety actually encountered among shrew tenrecs and have been essentially abandoned in most recent systematic compilations (e.g., Corbet and Hill, 1980; Honacki et al., 1982). The remaining members of Oryzorictinae, *Oryzorictes* (rice tenrecs) and *Limnogale* (water tenrecs), are not considered in this review.

The list which follows includes all validly published and available names that have been proposed for nominal species and subspecies of *Microgale* as defined above. Invalid names, validly published but unavailable names, and lapsi calami are presented in a second list at the end of this section.

Paraphrased type locality information (in quotes) presented in the original sources has been amplified by additional data, in this order: approximate elevation above sea level of cited locality and its position with respect to large population centers and major floral formations; province and prefecture in which locality is found; longitudinal and latitudinal coordinates; and a map sheet reference number (to 1:100,000 series published by Foiben-Taosaritanin'i Madagasikara [National Institute of Geodesy and Cartography], Antananarivo, Madagascar). Currently accepted toponyms, if different from locality names used in original sources, are set off by brackets (see also table 5). Quotes from French and German publications have been translated into English.

1. *longicaudata* Thomas 1882. Holotype: BMNH 82.3.1.15 (specimen a of original report), adult, female, skull and skin (in alcohol). Additional specimens in type series: BMNH 82.3.1.16, skull and skin (specimen b of original report; specimens c–f were later transferred to *majori* [Thomas, 1918]. Type locality: “Ankafina [not Ankafana] forest, eastern Betsileo.” Ankafina is a hill (1600 m) 10 km S of Ambohimahasoa and 3 km W of Tsarafidy town, on extreme western margin of eastern rain forest; Fianarantsoa, Fianarantsoa; 21°12'S, 47°13'E; sheet O-53. Collector: Rev. W. Deans Cowan between mid-February and mid-March, 1880. Derivation: ref. to long tail.

2. *cowani* Thomas 1882. Holotype: BMNH 82.3.1.25 (specimen a of original report), adult, female, skull and skin (in alcohol). Additional specimens in type series: BMNH 82.3.1.26 and 27 (skulls and skins in alcohol) and 82.3.1.28 (intact specimen in alcohol), corresponding to specimens b, c, and d of original report. Type locality: as for *longicaudata* (q.v.). Collector: Rev. W. Deans Cowan between mid-February and mid-March, 1880. Derivation: for collector.

3. *dobsoni* Thomas 1884. Holotype: BMNH 84.10.20.1, immature male, skull and skin (in alcohol). Additional specimens in type series: none. Type locality: “Nandesen forest, central Betsileo.” Uncertain location (see below), but perhaps the isolated patch of eastern rain forest situated east of Nandihizana village (1340 m), south of Ambositra; Fianarantsoa, Fianarantsoa; 20°27'S, 47°09'E; O-51. Collector: W. Waters in February or March, 1884. Derivation: for G. E. Dobson.

“Nandesen” is not Malagasy orthography and undoubtedly represents a quasiphonetic transcription. Morrison-Scott (1948: 819) noted that there “is a manuscript note in Thomas’s private copy of his paper which reads ‘Nandihizana, 10 miles south of Ambositra.’” This tiny village, which Morrison-Scott was apparently unable to find on maps available to him, is situated about 20 mi (30 km) SSW of Ambositra. Remnant patches of eastern forest exist nearby (forest of Ankazomivady; Tattersall, 1986).

4. *crassipes* Milne-Edwards 1893. Holotype: MNHN 1892-1560, adult, ?sex, skull and skin. Additional specimens in type series: none. Type locality: “in the environs of Tana-

narive.” Uncertain location (see below), but possibly as stated; 18°55'S, 47°32'E (coordinates of Antananarivo; 1310 m); Antananarivo, Antananarivo; Q-47. Collector: F. Sikora. Derivation: ref. to purportedly large foot.

Heim de Balsac (1972: 654) argues that the near environs of Antananarivo could not have yielded *Microgale crassipes*, and that Sikora probably collected his specimens farther east—perhaps around the mission at Andrangoloaka, about 70 km E of Antananarivo and 25 km SW of Moramanga, near the margin of the eastern rain forest. Ankeramadinika, a forest remnant only 25 km E of the capital, is another possibility.

5. *thomasi* Forsyth Major 1896a. Holotype: BMNH 97.9.1.108, adult, male, skull and skin. Additional specimens in type series: BMNH 97.9.1.109, skull and skin. Type locality: “Ampitambe forest (N. E. Betsileo).” Uncertain location. Tattersall (1986, personal commun.) believes that Forsyth Major’s Ampitambe (or Ampitabe) is located 150 km E of Antsirabe, within 40 km of the coastal town of Mahanoro. However, in another passage, Forsyth Major (1896a: 323) stated that Ampitambe was in “Betsimisarakana country (on the border of N.E. Betsileo), 6 hours S.E. of Fandriana.” That would seem to place this locality somewhere immediately to the east of Ambositra or Ambohimombo (see type locality information for *gracilis*). There is, in fact, an Ampitabe about 70 km SE of Fandriana, off the major (and presumably long-existing) road to Maroharatra, but this seems a bit far to do in a six-hour trip on foot. Tattersall’s candidate for this locality is more than 120 km NE of Fandriana—and there is no connecting road or path. Without identifying his source, Morrison-Scott (1948) claims that Ampitambe lies at 20°20'S, 47°30'E, which is only about 20 km due SE of Fandriana. However, there is no place with that name on the modern reference map (P-50). It is possible that Forsyth Major was mistaken about the locality’s distance from Fandriana, or that he collected at more than one Ampitambe (although this latter interpretation seems unlikely given Forsyth Major’s [1986c] account of his activities). The village of Ampitabe (600 m) SE of Fandriana is located deep within eastern rain forest; Fianarantsoa, Mananjary; 20°44'S, 47°38'E;

P-51. Collector: C. I. Forsyth Major, July 19, 1895. Derivation: for Oldfield Thomas.

6. *talazaci* Forsyth Major 1896a. Holotype: BMNH 97.9.1.107, adult, female, skull, axial skeleton, and skin. Additional specimens in type series: none. Type locality: "neighbourhood of Vinanitelo." Vinanitelo is a ridge (1290 m) 50 km SE of Fianarantsoa town and 10 km SSE of Vohitrafeno town, western margin of eastern forest; Fianarantsoa, Fianarantsoa; 21°45'S, 47°17'E; O-54. Collector: C. I. Forsyth Major, May 22, 1896. Derivation: for Rev. Père Talazac.

7. *longirostris* Forsyth Major 1896a. Holotype: BMNH 97.9.1.111, adult, female, skull, axial skeleton, and skin. Additional specimens in type series: none. Type locality: as for *thomasi* (q.v.). Collector: C. I. Forsyth Major, July 4, 1895. Derivation: ref. to long rostrum.

8. *gracilis* (Forsyth Major 1896a). Holotype: BMNH 97.9.1.78, adult, ?sex, skull and skin (in alcohol). Additional specimens in type series: a second specimen (skeleton only) is mentioned in the original report as having come from "Ankeramadinika forest," one day's journey E of Antananarivo (Forsyth Major, 1896c) in the southernmost part of the Hantsambaton' Angavo, the long escarpment covered by a great peninsula of eastern rain forest. Type locality: "Ambohimitombo forest." Ambohimitombo town (1300 m) is situated 43 km (by road) SE of Ambositra, 10 km into eastern forest; Fianarantsoa, Fianarantsoa; 20°43'S, 47°26'E; P-51. Collector: C. I. Forsyth Major, November 1894. Derivation: ref. to gracile skull, teeth.

9. *taiva* Forsyth Major 1896b. Holotype: BMNH 97.9.1.112, immature, female, skull and skin. Additional specimens in type series: none. Type locality: as for *gracilis* (q.v.). Collector: C. I. Forsyth Major, January 19, 1895. Derivation: ref. to Tanala form of tribal self-address.

10. *pusilla* Forsyth Major 1896b. Holotype: BMNH 97.9.1.93, adult, male, skull and skin. Additional specimens in type series: none mentioned, but there are many other skulls/skins of *pusilla* in BMNH collection having the same date of accession. Type locality: as for *talazaci* (q.v.). Collector: C. I. Forsyth Major, May 26, 1896. Derivation: ref. to small size.

11. *brevicaudata* Grandidier 1899. Lec-

totype: MNHN 1886-387, adult, male, skull and postcranial skeleton, no skin. Additional specimens in type series: 2 intact female specimens in alcohol (MNHN 1886-389 and 390), 1 immature female with skull removed and preserved and body in alcohol (MNHN 1886-388). Type locality: "in forest, along streams, environs of Mahanara, NE coast of Madagascar." The Mahanara River is situated 78 km S of Iharana [Vohimarina], and originates within the eastern part of the eastern rain forest; Antsiranana, Antalaha; 13°58'S, 49°58'E (coordinates of Antsirabe Avaratra, where Mahanara crosses Route Nationale 5A; 100 m); XY-34. Collector: not named. Derivation: ref. to short tail.

Grandidier did not name or illustrate a holotype. The lectotype designated here is the skeletonized specimen whose measurements were presented in the original report. Rode (1942) stated that the skull now numbered MNHN 1886-388 could be regarded as the holotype of the species because he incorrectly believed that it belonged to Grandidier's measured specimen (which could not then be found). Since then the measured specimen, now numbered MNHN 1886-387, has been relocated. Because Rode's intent was clear, MNHN 1886-387, not MNHN 1886-388, is properly regarded as the lectotype; the other specimens are paralectotypes.

12. *nigrescens* Elliot 1905 [proposed as subspecies of *M. cowani*]. Holotype: FMNH 1349 (skull) and 5644 (skin), female, possibly immature judging from reported hindfoot length. Additional specimens in type series: none. Type locality: "Ambohimananana, Bet-sileo." Ambohimananana village (1200 m) is located 9 km WNW of Ambohimitombo; Fianarantsoa, Fianarantsoa; 20°42'S, 47°21'E; O-51. Collector: C. I. Forsyth Major, May 26, 1896. Derivation: ref. to dark color of pelt.

13. *breviceps* Kaudern 1918. Holotype: two mandibular rami, one of which is clearly from an immature animal; present location not known, but illustrated by Kaudern (1918: pl. 9, figs. a-c). Additional specimens in type series: none. Type locality: "cave near Majunga [Mahajanga]." On accompanying map, cave is shown as ca. 12 km W of Mahajanga, in outcropping karsted Paleogene limestone, probably in or near patchy dry-mesic forest of Marohogo (100 m); Mahajanga, Mahajan-

ga; 15°45'S, 46°20'E; L-39. Collector: W. Kaudern in 1911 or 1912. Derivation: ref. to assumed shortness of head.

Name was offered conditionally, since Kaudern suspected that his specimens might represent *brevicaudata* (q.v.). However, for present purposes his name can be treated as available (ICZN, art. 11[d][i]).

Specimens found as "subfossils" in cave deposit, probably in owl pellet detritus (cf. MacPhee, 1986).

14. *majori* Thomas 1918. Holotype: BMNH 82.3.1.17, ?adult, female, skull and skin. Additional specimens in the series: 37 originally (Thomas, 1918), of which the following have been retained—BMNH 82.3.1.22 (skull and partial skin), 82.3.1.16, 18, and 21 (skulls only). Type locality: as for *longicaudata* (q.v.). Collector: Rev. W. Deans Cowan, February 1881. Derivation: for C. I. Forsyth Major.

15. *principula* Thomas 1918. Holotype: BMNH 25.8.3.15, adult female, skull and skin (in alcohol). Additional specimens in type series: none. Type locality: "Midongy du Sud [Midongy Atsimo], SE Madagascar." Midongy Atsimo town (500 m) is located deep within eastern rain forest; Fianarantsoa, Farafangana; 23°35'S, 47°01'E; N-59. Collector: C. Lamberton. Derivation: ref. to large size within genus *Microgale*, as restricted by Thomas.

16. *sorella* Thomas 1918. Holotype: BMNH 25.8.3.14, adult, male, skull and skin (in alcohol). Additional specimens in type series: none. Type locality: "Beforona forest, inland of Andevorante, E Madagascar." Beforona town (500 m) is located near margin between true eastern rain forest and "savoka" belt of humid secondary forest, 57 km W of Andevorante; Toamasina, Toamasina; 18°58'S, 48°35'E; S-47. Collector: C. Lamberton. Derivation: feminine diminutive of *sorex*?

17. *decaryi* Grandidier 1928. Holotype: MCZ 45049, adult, ?sex, broken skull with some teeth. Additional specimens in type series: 3 partial skulls and 5 mandibular rami, with few teeth, all apparently adult and bearing accession number MCZ 45048; plus 1 partial skull, apparently adult, in collections of Institut de Paléontologie, MNHN, bearing accession number MAD-1649 and labeled "co-type." Type locality: "Andrahomana

Cave, near Fort-Dauphin [Tôlaïaro]." Andrahomana (30 m) is a well-known subfossil cave site situated in a seacliff on Cape Andavaka, 50 km WSW of Tôlaïaro; within extreme eastern limit of xerophilous bushland thicket; Toliary, Tôlaïaro; 25°12'S, 46°38'E; M-62. Collector: R. Decary in 1926. Derivation: for collector.

18. *occidentalis* (Grandidier and Petit 1931). Holotype: MCZ 45047, immature (contra Grandidier and Petit, 1931) male, skull and skin (in alcohol). Additional specimens in type series: none stated (but see below). Type locality: "near Andriafavelo village, 42 km NE of Maintirano, 20 km from sea." Andriafavelo (80 m) is situated in open grasslands, and only small patches of western dry-mesic forest exist in its vicinity; Mahajanga, Maintirano; 17°47'S, 44°12'E; E-44. Collector: M. Aubert de la Rüe in 1930. Derivation: ref. to species' presence on western side of island.

The skeleton has not been extracted from the body bearing the accession number MCZ 45047, yet Grandidier and Petit (1931) provide extensive descriptions of a skeleton attributed to *occidentalis*. This is puzzling, for they state that they had only one specimen attributable to their new species. I cannot resolve the discrepancy.

19. *drouhardi* Grandidier 1934. Holotype: MCZ 45034 (specimen A of original report), immature (contra Grandidier, 1934) female, skull and skin (in alcohol). Additional specimens in type series: MCZ 46007–46011 (specimens B–F of original report) and MCZ 46012 (undesigned juvenile mentioned in text of original report). Type locality: "environs of Diego-Suarez [Antsiranana]." Uncertain location; there is considerable ecological variety within this area, including humid forest on Ambohitra [Montagne d'Ambre] and dry forest on Tendrombohitra Antsingy [Montagne des Français]; Antsiranana, Antsiranana; 12°16'S, 49°18'E (coordinates of Antsiranana); UV-30. Collector: M. E. Drouhard. Derivation: for collector.

MCZ 46017, a skeleton with skull, is not mentioned as part of the type series in the original report, but it was collected at the same time and place.

20. *parvula* Grandidier 1934. Holotype: MCZ 45465, immature (contra Grandidier, 1934), male, skull and skin (in alcohol). Ad-

ditional specimens in type series: none. Type locality: as for *drouhardi* (q.v.). Collector: M. Drouhard. Derivation: ref. to very small size.

21. *prolixacaudata* Grandidier 1937. Holotype: MCZ 45035, immature (contra Grandidier, 1937), ?sex, skull and skin (in alcohol). Additional specimens in type series: MCZ 46020, intact specimen in alcohol. Type locality: "zoological province of Diego-Suarez [Antsiranana]." See remarks for *drouhardi*. Collector: not named. Derivation: ref. to extremely long tail.

22. *melanorrhachis* Morrison-Scott 1948. Holotype: BMNH 48.88, immature (contra Morrison-Scott, 1948), female, partial skull and skin (in alcohol). Additional specimens in type series: BMNH 48.87, female, body in alcohol (head eaten off in trap). Type locality: "Perinet [Andasibe], near Moramanga, E Madagascar, 3000 ft [980 m], 19°00'S, 48°30'E [Toamasina, Ambatondrazaka; S-47]." Andasibe is an important wildlife collecting area in the central part of the eastern rain forest. Collector: C. S. Webb, November 22, 1939. Derivation: ref. to dark middorsal stripe.

OTHER NAMES

1. "*forimenjy*". In short note evidently written while he was still in the field in Madagascar, Forsyth Major (1895) listed a series of 11 "new species discovered by myself." The first entry reads as follows:

"*Microgale forimenjy*, sp. nov.; nat. names *Forimènjy*; loc. Antsirabè, Ampitambè."

The only additional reference to this species is a parenthetical note to reflect that it was "first discovered in a small cave near Antsirabè." This is undoubtedly a reference to Lavajaza, a small unlocated cave in the environs of Antsirabe (Forsyth Major, 1896c). The unworked "subfossil" faunal collection from Lavajaza, housed in the Department of Palaeontology of the BMNH, includes several specimens denoted as "*M. forimenjy*" in Forsyth Major's handwriting. One skull and jaw (unregistered) in the collection of the Department of Zoology is similarly identified, but judging from its fresh appearance the specimen must have been trapped.

For unknown reasons, Forsyth Major (1896a, 1896b) did not employ the name

"*forimenjy*" in either of his later official publications on new Malagasy insectivores. It is possible but not certain that his concept of "*forimenjy*" became the validly published and available nomen *longirostris* Forsyth Major 1896a (for which "*forimenjy*" is listed as a common name). According to ICZN art. 11d, "*forimenjy*" was validly proposed within the terms of art. 8. However, it is unavailable because it was not "indicated" in an acceptable manner (art. 12a-c). Nomen nudum.

2. "*parva*". This name appears on labels in Forsyth Major's handwriting in the BMNH faunal collection from Lavajaza. He may have believed that he had another small species of *Microgale*, or may have ultimately rejected this name in favor of the validly proposed and available *pusilla* Forsyth Major 1896a. Excluded name.

3. "*nigra*". This name appears as a subspecific ("var.") designation on certain labels in the *cowani* series of both the BMNH and MNHN, and is also noted in Leche's (1907) specimen list. The relevant specimens, which have melanistic pelts, were all collected by Forsyth Major and I assume that the name is his. In the late 1890s, the BMNH donated synoptic collections of *Microgale* to a number of major museums. That some *cowani* specimens were labeled "*nigra*" at the time of distribution must imply that Forsyth Major had a serious intent to publish the latter name, but I have not been able to find any record of his actually having done so. Excluded name.

4. *Lapsi calami*. Small spelling errors are of no interest, but these lapsi seem more substantial:

M. prolixacaudata: not "*amplexicaudata*" of Heim de Balsac (1972); not "*prolixicaudata*" of Eisenberg and Gould (1970); Honacki et al. (1982).

M. brevicaudata: not "*brevicauda*" of Kaudern (1918).

PROPOSED REVISION

After consideration of the evidence, presented and analyzed in succeeding sections, I conclude that fewer than half of the 21 nominal species just listed are good, and that the following synonymy, at a minimum, must prevail:

FAMILY TENRECIDAE

Subfamily Oryzorictinae

Genus *Microgale* (including "*Oryzorictes*"

Forsyth Major 1896a, *Nesogale* Thomas 1918, *Leptogale* Thomas 1918, *Paramicrogale* Grandidier and Petit 1931). Shrew tenrecs.

longicaudata Thomas 1882 (including *M. majori* Thomas 1918; *M. prolixacaudata* Grandidier 1937). Lesser long-tailed shrew tenrec.

cowani Thomas 1882 (including *M. crassipes* Milne-Edwards 1892; *M. longirostris* Forsyth Major 1896a; *M. taiva* Forsyth Major 1896b; *M. cowani nigrescens* Elliot 1905; *M. drouhardi* Grandidier 1934; *M. melanorrhachis* Morrison-Scott 1948). Cowan's shrew tenrec or forimenjy.

dobsoni Thomas 1884 (including *Nesogale dobsoni* Thomas 1918). Dobson's shrew tenrec.

thomasi Forsyth Major 1896a. Thomas' shrew tenrec.

talazaci Forsyth Major 1896a (including *Nesogale talazaci* Thomas 1918). Talazac's shrew tenrec.

gracilis Forsyth Major 1896a (including "*Oryzorictes*" *gracilis* Forsyth Major 1896a [subsequently *Leptogale gracilis* Thomas 1918]). Long-nosed shrew tenrec.

pusilla Forsyth Major 1896b. Lesser shrew tenrec.

brevicaudata Grandidier 1899 (including *M. breviceps* Kaudern 1918; *Paramicrogale occidentalis* Grandidier and Petit 1931). Short-tailed shrew tenrec.

principula Thomas 1926 (including *M. sorella* Thomas 1926; *M. decaryi* Grandidier 1928 [subsequently *Paramicrogale decaryi* Grandidier and Petit 1931]). Greater long-tailed shrew tenrec.

parvula Grandidier 1934. Pygmy shrew tenrec.

Strictly from a phenetic standpoint, these 10 species and their contained synonyms can be grouped into six "clusters" on the basis of dental traits, body segment proportions, and certain special features of individual taxa. These clusters are useful devices for reducing

the amount of description needed and enhancing the efficiency of comparison-making. They have no formal status and are not to be interpreted as implying the existence of any particular supraspecific groupings. Their significance for understanding the phylogeny of lineages within *Microgale* will be addressed in another paper. Clusters are named as follows:

cowani cluster: *M. cowani*, *M. thomasi*, *M. parvula*

gracilis cluster: *M. gracilis*

longicaudata cluster: *M. longicaudata*, *M. principula*

pusilla cluster: *M. pusilla*

brevicaudata cluster: *M. brevicaudata*

dobsoni cluster: *M. dobsoni*, *M. talazaci*

The number of separate clusters could be reduced still further (e.g., by including *M. gracilis* within the *cowani* group), but this would be unwieldy in some ways, and the present arrangement is satisfactory for its intended informal purpose.

DENTAL TRAITS

Three-quarters of the holotypes in *Microgale* have never been illustrated and there are no detailed, inclusive descriptions of either the morphology or the ontogeny of the dental apparatus. The closest approach to such a description is Leche's (1907) difficult-to-obtain monograph, which covers only a few species. Since the teeth are of fundamental importance for solving problems in the systematics of *Microgale*, I have attempted to redress the lack of comparative data by providing analyses of the permanent and deciduous dentitions (if known) of species in each cluster. These descriptions are complemented by a large number of line drawings (figs. 1-8).

Dental evidence establishes that several nominal taxa are simply the young stages of adults of other species (e.g., *M. prolixacaudata*, juvenile of *M. longicaudata*; *M. taiva* and *melanorrhachis*, juveniles of *M. cowani*; *M. occidentalis*, juvenile of *M. brevicaudata*). Dental criteria are also useful for determining the validity of taxa based on inadequate or biased samples (e.g., *M. sorella*, indistinguishable from *M. principula*; *M. crassipes*

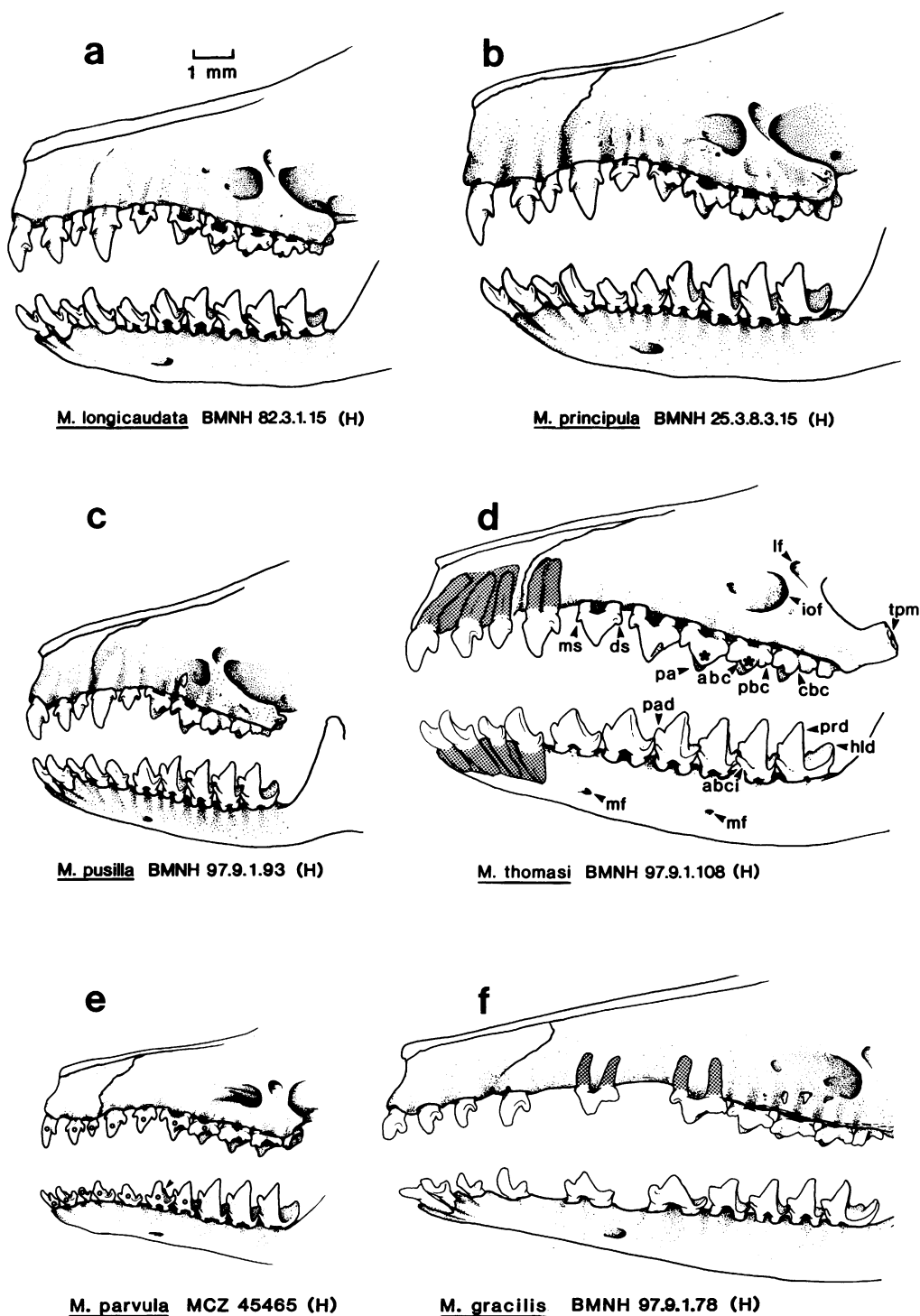
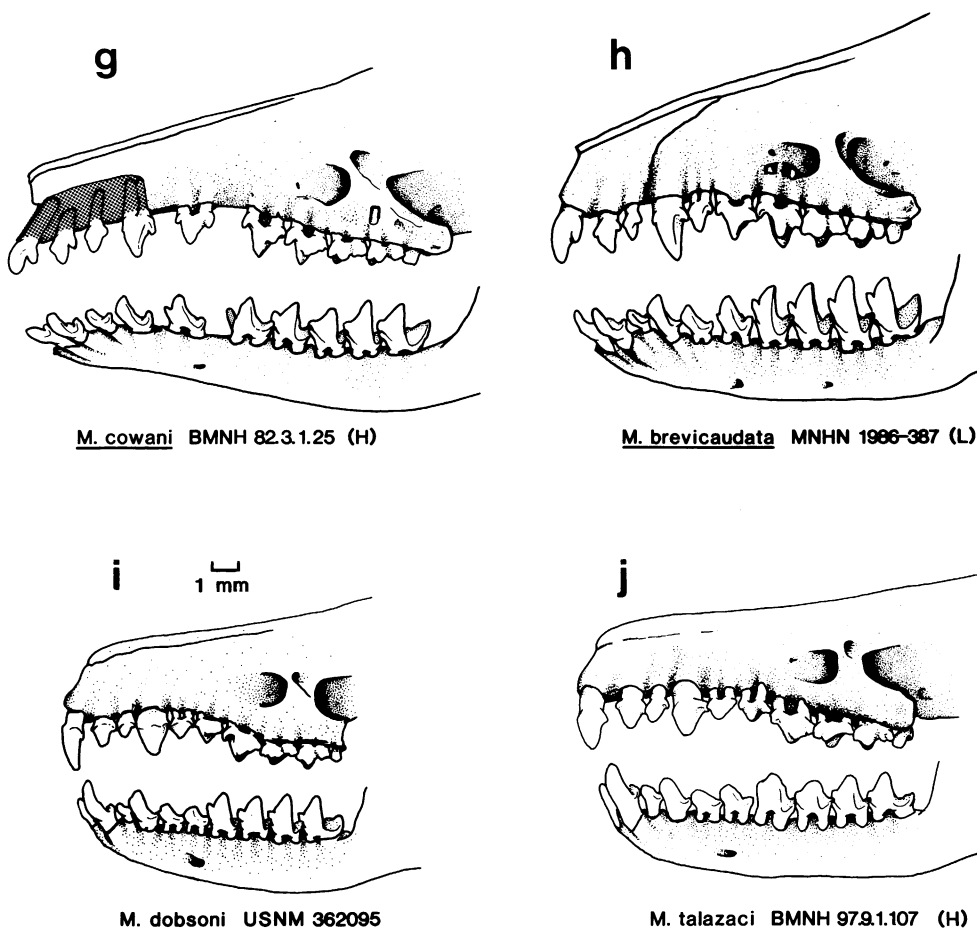


Fig. 1. *Microgale*, dentitions of holotypes of accepted species, left lateral aspect. The following shading conventions are used in this and succeeding figures: open circles, deciduous teeth; coarse stipple, damaged or dissected areas on skulls; and light stipple, reconstructed portions of damaged tooth crowns. Asterisks



in figure 1d identify anterior ectostyles on UP4 and UM1. Pointer in figure 1e indicates partly visible metaconid on an unworn Lp3. Holotype of *M. dobsoni* is too damaged to warrant illustration, and another specimen (fig. 1i) was chosen to represent this species. Figures 1a–h are drawn to same scale (millimeter bar above fig. 1a); figures 1i and 1j are at a different scale (bar above fig. 1i).

and *M. longirostris*, dentally identical to *M. cowani*).

DENTAL FORMULA

All members of *Microgale* possess the same number of teeth, with loci distributed as indicated in these conventional dental formulae:

$$\text{Deciduous: } \frac{3}{3} \frac{1}{1} \frac{3}{3} \quad \text{Adult: } \frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{3}{3}$$

Microgale apparently has no tendency to produce the UM4, occasionally seen in individual *Tenrec ecaudatus* that live long

enough to erupt it (Thomas, 1892; Butler, 1937).

Other than impactions and rotations, the only significant dental anomaly seen while I was collecting data for this investigation was a “second” Up2, on one side only, in a very young specimen (MNHN 1961-205) here allocated to *M. cowani*. Interestingly, the two teeth behind the Uc are not exactly alike, and it is the first rather than the second which more closely resembles the Up2 characteristic of other juvenile members of the *cowani* cluster. Prima facie, this might be considered as evidence that *Microgale* develops, but very rapidly sheds, its true Up2 (which then would

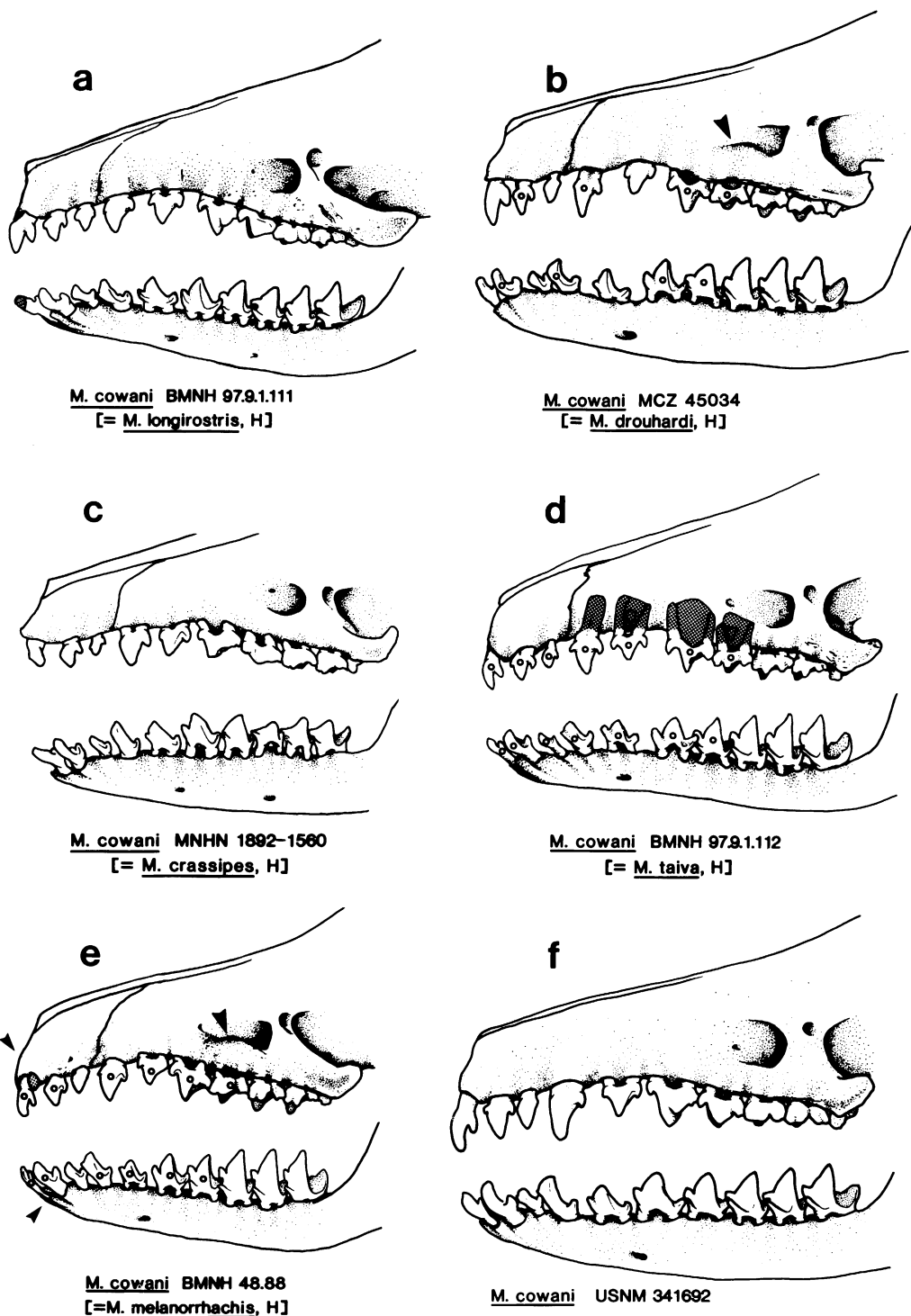


Fig. 2. *Microgale cowani*, dentitions of holotypes of synonymous species and referred specimens, left lateral aspect (except fig. 1c, which depicts reversed right lateral aspect). Large pointers (fig. 1b, e) identify swollen floor of infraorbital foramen, under which is UP4 crypt; small pointers (fig. 1e) indicate

have no successor), and that the tooth generally regarded as Up2 is actually Up1. However, since extra teeth were not encountered in any other young specimens, either duplication or "double initiation" (Phillips, 1971) is a better explanation.

ONTOGENY

ERUPTION PATTERN. As already mentioned, all molars are erupted and functional prior to the loss of any deciduous antemolar teeth except U/Li3 (Forsyth Major, 1897; Leche, 1907).³ Even when one is aware of this fact, however, it is often difficult to assess dental age in *Microgale*, for two good reasons. First, replacement at individual loci apparently occurs very rapidly, so that young specimens rarely betray their status by exhibiting a number of adult teeth in various stages of eruption. Secondly, milk and replacement teeth at most loci are so similar that considerable experience is needed before one can distinguish deciduous from adult antemolar teeth with some confidence (Leche, 1907).

Antemolar eruption sequences were investigated by Forsyth Major (1897) in a small series of *M. dobsoni*, *cowani*, and *thomasi*.⁴ He did not note any important individual variations. I make only one change in his interpretation of the eruption sequence (in upper premolar order), based on examination of a good series of *M. pusilla* and *M. cowani* collected by me from owl pellets at Antsifotrakely (a small rock shelter within Antsifotra volcano, 5 km E of Betafo, southwestern Antananarivo prov.). I assume that the fol-

lowing permanent-tooth eruption sequence is the same throughout *Microgale*, although information is obviously incomplete for several species:

Stage									
1	2			3			4		
UI3	UP2	UP4	UI1	UI2	UP3	UC			
LI3	LP2	LP4	LI1	LI2	LP3	LC			

Stage 1. In this stage, the only teeth being replaced are the third incisors (figs. 6a, 2d). (Eruption order of the deciduous teeth is not known, there being no specimens of sufficiently young age in any of the museum collections examined.) It is rare to see U/Li3s in the process of erupting (fig. 7a); either these teeth push into place very quickly, or young animals in which the act of replacement might be seen are rarely caught. Although the crowns of UI2, LP4, and LP2 are still only partly formed within their crypts, in some individuals the tips of their longest cusps may already be in evidence at the gum line, at the side of, or beneath their deciduous predecessors (e.g., fig. 5, bottom, in which Up2 is lost and UP2 slightly exposed although Ui3 has not been shed). The floor of the infraorbital fossa may appear slightly puffy, as a result of the enlargement of the crypt containing UP4 (fig. 5, bottom).

Stage 2. Forsyth Major (1897) states that UP4 is erupted before UP2, and implies that there is a significant time lag between these replacement events (UP4 is erupted in his stage 2, UP2 not until his stage 4). In young specimens examined by me, UP4 and UP2 display about the same degree of crown development within their crypts (in contrast to UP3, which is much less developed at this stage). However, when they begin to erupt (fig. 2b), LP2 loses the "cap" of its deciduous predecessor before LP4 does (but see Slaughter et al., 1974), probably because Lp2 is less firmly moored by its roots. The floor of the infraorbital foramen displays maximum puffiness at this stage (fig. 2e), as UP4 pushes to the gumline and begins to erupt. U/Li1 com-

³ This is an uncommon eruption sequence in living eutherians, although it unquestionably occurs in some extinct erinaceomorphs such as *Pholidocercus hassiacus* (Middle Eocene, Grube Messel; Koenigswald and Storch, 1983) and may therefore represent a eutherian sympleiomorphy.

⁴ Forsyth Major (1897) chose to number the premolar loci in a direction opposite to the conventionally accepted one; thus his "p/P1" = p/P4 of this report, "p/P2" = p/P3, and "p/P3" = p/P2. His designations have been altered to accepted ones in the eruption sequence diagram and accompanying text.

←
erupting tips of first permanent incisors. Although permanent first incisors are erupted in MCZ 45034 (fig. 2b), U/Lp4s have not yet been shed. For scale, see figure 1a.

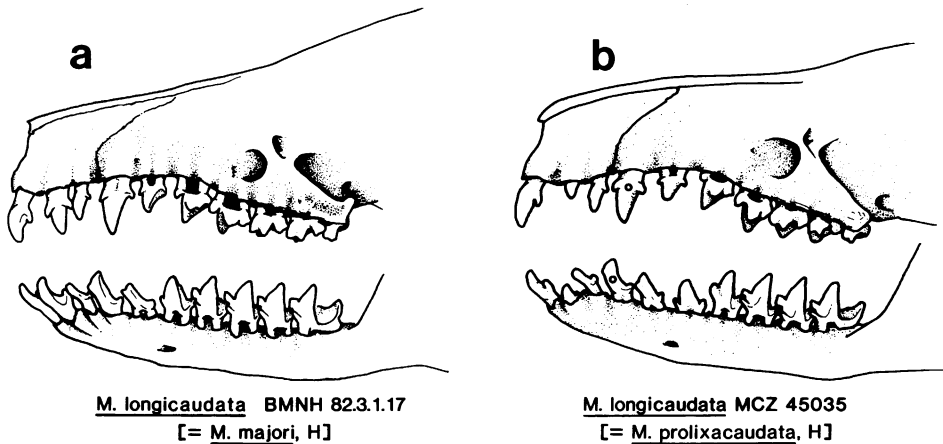


Fig. 3. *Microgale longicaudata*, dentitions of holotypes of synonymous species, left lateral aspect. Canines in BMNH 82.3.1.17 (fig. 3a) may be deciduous (cf. fig. 3b). In MCZ 45035, LP3 is not yet fully erupted. For scale, see figure 1a.

mences eruption at the end of this stage (fig. 2e).

Stage 3. At the start of this stage, U/LI2s begin to erupt and U/LP3s become visible between the roots of their predecessors (fig. 6b). By the end of this stage the U/Lp3s have been shed and the U/LP3s are pushing into their final positions (fig. 3b). The floor of the infraorbital foramen very rapidly loses its puffy appearance following eruption of UP4, and assumes its adult profile. The area immedi-

ately above the Uc may be slightly swollen as a result of UC development.

Stage 4. The last event in the eruption sequence is the appearance of the adult canines. U/LCs breach the gumline at about the same time, but LC is a little slower in completing eruption. Judging from the very small size of its canines, BMNH 82.3.1.17 (fig. 3a) is possibly at this stage of development, although there is no external sign that the U/LCs are still in their crypts.

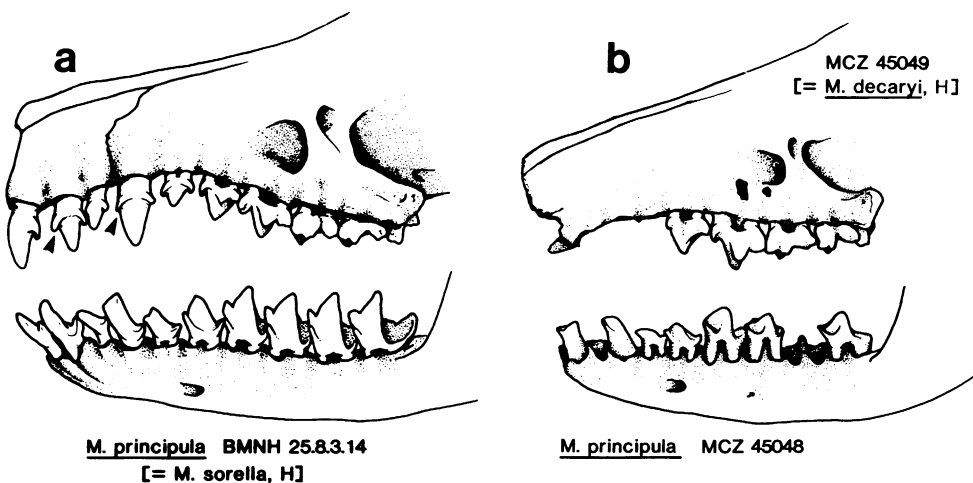


Fig. 4. *Microgale principula*, dentitions of holotypes of synonymous species and a referred specimen, left lateral aspect. Right UP2 of MCZ 45049, illustrated by Grandidier (1928), has since been lost. Mandible from MCZ 45048 series is reversed. Pointers in 4a identify prominent buccal ledges on UI2 and UC. For scale, see figure 1a.

FIELDS

Clusters of nominal species of *Microgale* differ not only in the detailed anatomy of individual teeth, but also in the relative proportions of the dental "fields" affecting the morphological differentiation of those teeth. ("Field" as used here is simply meant to encompass observed regularities and correlations in morphology among teeth occupying different positions in the jaws; no acceptance of any specific theory that seeks to explain these phenomena is implied.)

Two groupings can be discriminated on the basis of the relative size of the incisor/canine and premolar/molar fields in the adult dentition. In the first group (*dobsoni*, *brevicaudata*, *pusilla*, and, to a lesser degree, *longicaudata*), the incisor/canine field can be thought of as having shifted backward, so that the LP2 and LP3 express some traits characteristic of the incisors and canines (diminution or loss of paraconid, swelling of anterior slope of protoconid, obliquity of tooth in jaw). This is especially well seen in *M. pusilla*, in which LP2 is single-rooted and the crown is fully caniniform.

By contrast, in the second group (*cowani* and *gracilis* clusters) the opposite shift has occurred. LP3 is only slightly less molariform than LP4, LP2 always bears prominent accessory cusps, and the canine usually carries a small paraconid (especially noticeable in unworn canines).

The deciduous dentitions are much less distinctive, both groups expressing a pattern that is more like that of the adults of the first group than the second.

DENTAL ANATOMY AND VARIATION

Butler (1937) and Hershkovitz (1977) should be consulted for additional information on the molars, which vary little among clusters and hence receive only superficial treatment here. Figures 1–8 illustrate most of the features described below.

MANDIBULAR TEETH

MOLARS: Except in size, the lower molars do not vary appreciably among nominal species of *Microgale*. The buccal aspect of

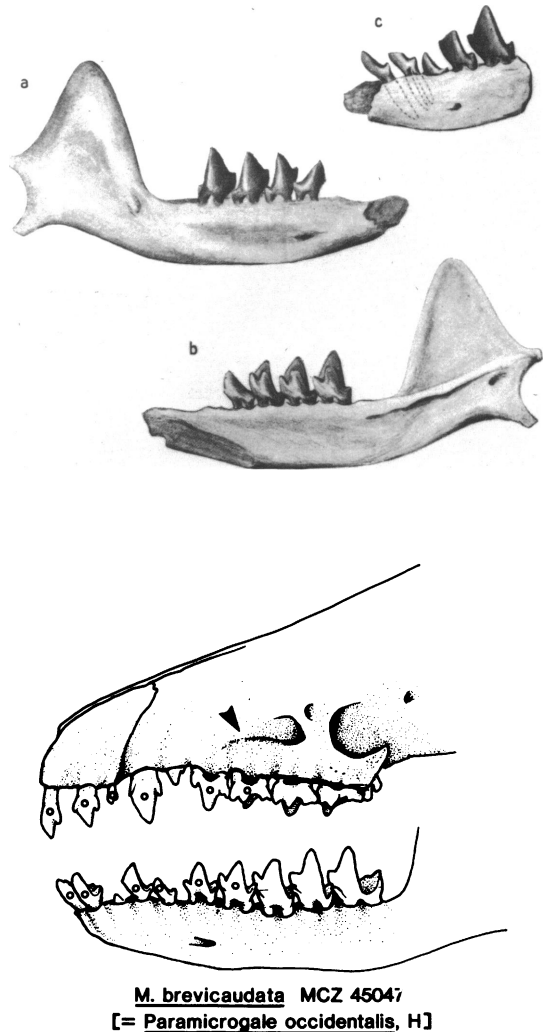


Fig. 5. *Microgale breviceps*, dentitions of holotypes of synonymous species, left lateral aspect. Figure 5, top, reproduction of original plate accompanying description of *M. breviceps* (Kaudern, 1918: pl. 8, enlargement $\times 4.3$). LM3 is missing in plate-figures a and b; in plate-figure c, LI3 and erupting LP2 are permanent teeth, but the rest appear to be deciduous. Lc has lost part of its crown (cf. fig. 2h). In figure 5, bottom, note erupting LI3 and UP2; large pointer identifies swollen floor of infraorbital foramen. For scale of figure 5, bottom, see figure 1a.

each lower molar (fig. 1d) is dominated by a large, tapering protoconid, a smaller paraconid, and a ridgelike hypoconulid bounding the talonid basin (basin insignificant in LM1 and LM2 but large in LM3). The metaconid

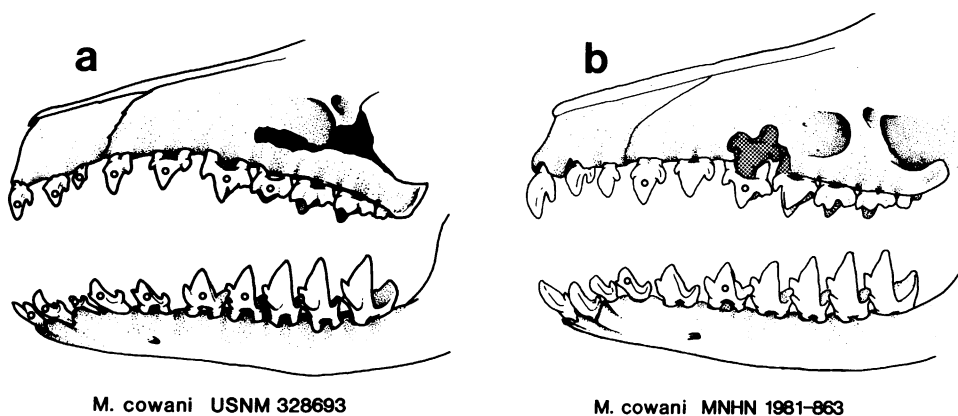


Fig. 6. Dental ontogeny in *Microgale cowani*. a. Specimen with a completely deciduous antemolar dentition at the beginning of stage 1 of the eruption sequence (see text). b. Specimen in late stage 3, in which U/LP3s are beginning to erupt and U/LI2s are nearly in place. For scale, see figure 1a.

is constantly present, but it is hidden by the larger protoconid in the buccal aspect (fig. 5a). These structures or their serial homologs can be traced from the last molar through the anteriormost premolar. In cases of advanced wear, the protoconid is considerably reduced in height (e.g., fig. 2c). Wear also opens the angle formed by the mesial margins (= protolophid) of the paraconid and protoconid.

The anterobuccal cingulum is another structure that can be traced at least as far as the fourth premolar in most nominal species of *Microgale* (fig. 1d). The anterobuccal cingulum terminates in a large prong, the tip of which is mortised into a complementary surface formed by the talonid basin of the tooth in front. Mortising is highly characteristic of *Microgale*; Grandidier's (1937: fig. 6) illustration of MCZ 45035 (holotype of *M. prolixicaudata*) implies that this feature is sometimes absent, but this is not correct (fig. 3b). Mortising is also seen in Mesozoic forms such as *Gypsonictops* and *Purgatorius* (Clemens, 1974) and is undoubtedly primitive.

In older animals the anterobuccal cingulum may show signs of wear (i.e., loss of definition, reduction of prong) as a consequence of being contacted by the distal aspect of upper molar paracones.

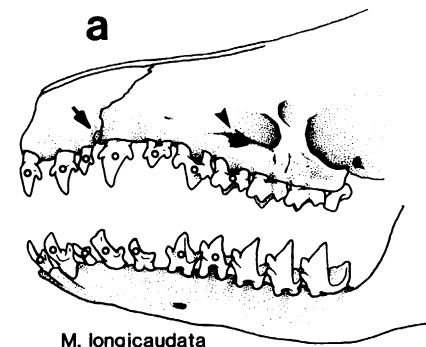
PREMOLARS: In contrast to the molars, the nonhomomorphic premolars are of considerable importance in diagnosing both age and cluster affiliation in *Microgale*.

Distinctively large diastemata occur on

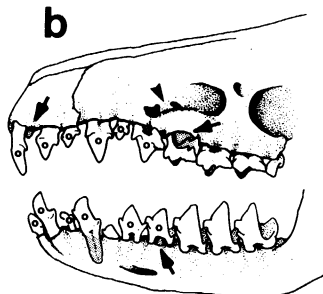
either side of the lower second premolar in *M. gracilis* (fig. 1f). Smaller gaps occur in most members of the *cowani* and *longicaudata* groups. In *M. brevicaudata* (fig. 1h), LP2 is slightly separated from LP3 but it contacts the LC. Diastemata do not occur in *M. dobsoni* and *M. talazaci* (fig. 1i, j).

Fourth Premolar. The conspicuously molariform Lp4 and LP4 vary little within *Microgale*. Although they seem nearly identical to LM1 in buccal aspect, compared to the first molar they are buccolingually compressed (especially in *M. brevicaudata*), with a smaller metaconid situated closer to the protoconid, a mesiobuccally rotated paraconid emplaced higher on the tooth, and a less distinct anterobuccal cingulum. On the other hand, the talonid area is normally larger than in LM1.

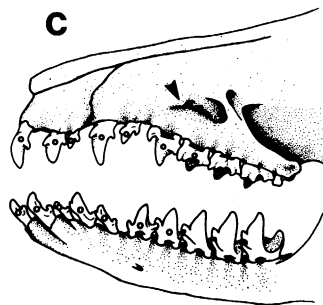
Lp4 is smaller than LP4 in all clusters, but it otherwise differs very little from its successor. In the deciduous tooth, the protoconid has a lower profile, with more evenly curved mesial and buccal slopes, and the paraconid and hypoconulid frequently have a more gracile appearance than their equivalents do on the adult tooth. In LP4, the anterior slope of the protoconid is usually convex or even sigmoidal while the posterior slope is slightly concave. As a result, in the worn condition the tip of the protoconid appears to be leaning backward or "retroflexed" (cf. *M. pusilla* [fig. 1c], in which this trait is especially noticeable). This appearance is



M. longicaudata
BMNH unreg. (Winton Coll.)



M. dobsoni USNM 154988



M. pusilla USNM 328688

Fig. 7. Dental ontogeny in other *Microgale*. Large pointers indicate swollen floor of infraorbital foramen; arrows point to tips of erupting permanent teeth. For scale of figures 7a and 7c, see figure 1a; for figure 7b, see figure 1i.

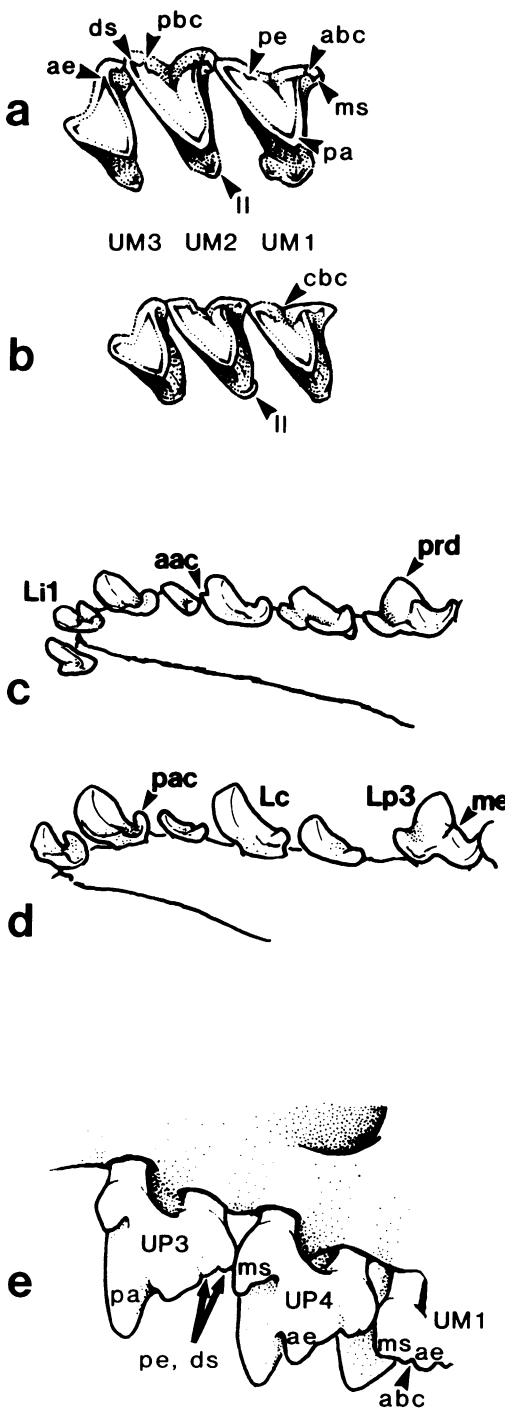


Fig. 8. Aspects of dental anatomy of *Microgale*. a, b. Compared occlusal surfaces of upper molars of *M. thomasi* (a) and *M. gracilis* (b); draw-

ings are based on several specimens of each species (9×). c, d. Lower anterior deciduous teeth of *M. parvula* MCZ 45465 (c) and *M. pusilla* USNM 328688 (d) in right oblique occlusal aspect (10×). e. Buccal aspect of left posterior premolars of *M. pusilla* USNM 328687 (18×).

rapidly altered by wear, so that in mature animals there is usually little difference between slopes.

Third Premolar. Compared to Lp/P4, teeth produced at the third premolar locus are narrower and less complex. The main cusp is the serial homolog of the protoconid (fig. 8b), while the anterior and posterior accessory cusps are equivalent to the paraconid and hypoconulid, respectively—now rotated into the same fore-aft plane as the main cusp. The area roughly equivalent to the talonid basin of the molars is set off by an indistinct post-cristid.

Lp3 anatomy is similar in most *Microgale* species, despite differences in the width of the molar field in the adult dentition. The tip of the conical protoconid tends to be centered over the middle of the tooth, and the anterior protoconid slope is only slightly shorter than the posterior (fig. 2c). The hypoconulid is large in relation to the size of the paraconid, and is joined to the latter by a crest. *M. parvula* exhibits a definite but tiny Lp3 metaconid (fig. 8b), a cusp which is usually absent in the homolog of this tooth in other species.

LP3s are more divergent, in line with the size of the premolar/molar field in different clusters. In the *cowani* cluster, the large paraconid is situated high on the mesial face of the tooth, the anterobuccal cingulum is often present, and the unworn protoconid is nearly as tall as that of the LP4 (fig. 2a, f). *M. thomasi* (fig. 1d) resembles *M. gracilis* (fig. 1f) in having a very large LP3 with remarkably prominent paraconids. By contrast, in the *dobsoni* cluster, the main cusp of LP3 is much lower than the protoconid of LP4, the paraconid is tiny or even absent, and the anterobuccal cingulum is never more than a wrinkle (fig. 1i, j). Additionally, the notably swollen anterior slope of the paraconid in this last cluster gives the tooth a strong resemblance to the LP2 and LC (see below). *M. brevicaudata* is similar in having a poorly defined LP3 paraconid, although the protoconid is comparatively taller.

Second Premolar. The adult deciduous and permanent second premolars are the smallest and simplest in their series. The accessory cusps of Lp/P2 are large in members of the *cowani* group and in *M. gracilis*, and small in the *dobsoni* cluster, *M. brevicaudata*, and *M. pusilla*. The anterobuccal cingulum is

never distinct, although there is normally a weak lingual cingulum (well marked in *M. parvula*, fig. 8b).

With the exception of *M. gracilis*, and to a lesser degree, *M. thomasi*, in *Microgale* the convex anterior slope of the LP2 protoconid is usually much shorter than the posterior slope, which is slightly to markedly concave. In most species the tip of the main cusp of LP3 is situated over, or even in front of, the anterior root. The effect of this is to make the crown of the LP2 appear forward-leaning or “anteroflexed,” like that of the LC.

M. pusilla (figs. 1c, 7c) has the most caniniform Lp/P2 in the genus. The deciduous and the adult tooth each bears a procumbent, narrow crown, perched on a single root. In *M. brevicaudata*, the homologous teeth possess two distinct, albeit tightly compressed, roots (figs. 1h, 5b). A tiny paraconid is variably present on the unworn LP/p2s of both species. The Lp/P2s of the *dobsoni* cluster are also markedly caniniform, but possess two roots (figs. 1i, 7b). The tiny paraconid is normally present but is quickly reduced through wear. The *longicaudata* cluster can be described as intermediate (figs. 3b, 7a): a small paraconid is sometimes present, but the protoconid is short and very gracile, and the roots are placed close together.

INCISORS AND CANINE: In all nominal species of *Microgale*, the canine is morphologically similar to the incisors and may be considered with them.

The lower incisors and canines are trenchant and single-rooted teeth in all clusters. *M. gracilis* has the most procumbent anterior teeth, while *M. dobsoni* and *talazaci* have the least.

Deciduous incisors and canines are approximately two-thirds to three-quarters the size of their permanent successors, although the degree of individual variation is large.

The deciduous and permanent second incisors are always the largest mandibular incisors within their respective dentitions, and LI2 is especially prominent in the *dobsoni* cluster (fig. 1i, j). LI3 is always the smallest, sometimes markedly so. *M. gracilis* differs from other *Microgale* in possessing incisors of roughly equal size (as seen from the buccal aspect) in each jaw, with the third being only slightly smaller than the first two (fig. 1f).

The Lc/C frequently has a distinct, if tiny,

anterior accessory cusp, giving it a slightly premolariform appearance (fig. 2a, e). This cusp does not occur on the incisors. Gaps between teeth in the lower incisor series are narrow or nonexistent, except in *M. gracilis* and some *M. cowani*.

MAXILLARY DENTITION

MOLARS: The zalambdodont molars of *Microgale* are dominated by a massive, pyramidal paracone (or zalambdocone). The portion of the tooth external to the paracone is considered to be homologous to the buccal styler shelf, and the small eminences that adorn its margin are regarded as the equivalent of the buccal styler cusps of nonzalambdodonts (Butler, 1937). As in most tenrecids, four of these cusps are more or less constant in *Microgale* (fig. 8a): the anteriormost and posteriormost may be usefully discriminated as the mesiostyle (= parastyle, anterior cusp) and distostyle (= metastyle, posterior cusp), while the two intermediate cusps can be simply identified as the anterior and posterior ectostyles (= anterobuccal and posterobuccal cusps). The two anteriorly situated cusps are separated from each other by a shallow notch (anterior buccal cleft) and from the two posteriorly situated cusps by a much deeper embrasure (centrobuccal cleft). Usually, there is also a very shallow posterior buccal cleft. A crest (buccal styler crest), truncated at the clefts, connects these cusps. Although the buccal styler cusps do not occlude with any part of the lower molars, their points are rather quickly worn down, perhaps by the transport of food boluses between the dentition and the cheeks. The third molar is reduced, specifically in the distal part of its crown and the wing supporting the posterior buccal styler cusps.

In describing the type of *M. gracilis*, Forsyth Major (1896a) stated that "the outer margins of the upper molars are more deeply notched than in all other known Centetidae," but wider comparisons demonstrate that this distinction is insubstantial. Furthermore, Thomas (1918) has stated also that the lingual shelf of *M. gracilis* is "suppressed." However, since it is obviously present (fig. 8a), it would be more accurate to describe it as "small" compared to its equivalent in other *Microgale*.

PREMOLARS: As in the case of the mandibular dentition, the largest premolar diastemata occur in *M. gracilis* (fig. 1f). Smaller gaps are seen on both sides of the second premolar in most but not all members of the *cowani* cluster (e.g., figs. 1d, 2a) and in the *longicaudata* group. By contrast, diastemata do not occur in *M. dobsoni* and *talazaci*, and are very narrow or absent in *M. brevicaudata*.

Fourth Premolar. The upper fourth premolar locus is the only one in either jaw at which markedly heteromorphic teeth are produced. In all species, the deciduous tooth is highly molariform, being almost indistinguishable from the true molars. The replacement tooth, however, is much less molariform and has a completely different buccal aspect.

The Up4 and UP4 resemble each other, as well as the molars, in the conformation of their lingual and distobuccal portions (the paracone, its attendant crests and lingual shelf, and the posterior ectostyle and distostyle cusps). By contrast, the organization of the anterobuccal portion is quite different. In the milk tooth, as in the true molars, the mesiostyle and anterior ectostyle are small and approximately equal in size to the distostyle and posterior ectostyle. In the adult tooth (fig. 8c), the anterior ectostyle is comparatively massive, and is separated from the mesiostyle by a greatly widened anterior buccal notch. The distance between these styler cusps is emphasized by the fact that the mesiostyle is situated very low on the crown (as seen from the occlusal aspect), appearing to emerge directly from the anterior root.

As in the case of the LP4, differences in UP4 construction among clusters are minor. The anterior ectostyle is broader and larger in members of the *cowani* cluster than in the *dobsoni* group, in which it is usually set off by a small secondary cleft and is more obviously merged with the main cusp. Both these conditions are frequently encountered in the other clusters. The mesiostyle is especially prominent in *M. pusilla* and *M. principula* (figs. 1c, 4).

Third Premolar. Up3 is rather constant in morphology throughout *Microgale*, but UP3 varies among clusters. The mesiostyle and distostyle of Up3 are well developed and distinctly set off from the paracone. The buccal styler crest can be traced from the distostyle

onto the buccal surface of the paracone, where it becomes indistinct. Ectostyles are usually distinguishable in the *cowani* group (e.g., figs. 1e, 2d), but they tend to be tiny or absent in other clusters.

In *M. brevicaudata*, *pusilla*, *dobsoni*, and *talazaci*, the replacing UP3s are no larger than their predecessors. The mesiostyle is small, and the anterior ectostyle is essentially absent except in *M. pusilla* (fig. 8c).

By contrast, in the *cowani* group the UP3 is slightly larger than the Up3, with a large mesiostyle and distostyle, and it nearly always bears a well-defined anterior ectostyle (fig. 1d). These features can be confirmed by examining the illustration of MNHN 1981-863 (fig. 6b), in which the UP3 crypt has been dissected above Up3 (latter still in situ).

An interesting contrast in third premolar morphology exists in the *longicaudata* group. In *M. longicaudata* (fig. 1a; 3a, b), the buccal aspects of UP3 and UP4 are very similar in size and shape. In *M. principula* (fig. 1b; 4a, b), on the other hand, UP3 is conspicuously smaller than UP4, and it has a much less distinct anterior ectostyle.

Second Premolar. Up/P2s are two-rooted and very simple in construction, invariably consisting of three cusps set in tandem, with no trace of an anterior ectostyle in any species.

The deciduous tooth is remarkably small in the *dobsoni* cluster (fig. 7b); in the *cowani* group the milk and adult teeth appear to be about the same size (fig. 2).

INCISORS AND CANINES: The upper incisors are more vertically implanted than the lower incisors. Posterior basal cusps (= distostyles) are found on all incisors and canines (cf. mandibular dentition). An anterior accessory cusp is always present on Ui/I2, often present on Uc/C, rare on Ui/I3, and absent on Ui/I1. A mesiolingual cusp, not visible from the buccal aspect, is consistently present in UI2 (fig. 8b).

The greatest development of accessory cusps occurs in the *longicaudata* cluster, although they are also well represented in the *cowani* cluster. In certain members of the *longicaudata* group, these cusps form a nearly continuous buccal ledge on the external aspect of the UI2 and UC (e.g., fig. 1a, b). The Uc/Cs vary within *M. cowani* in the degree of expression of the anterior basal cusp (fig. 2).

In all clusters, Ui2 is at least the equal of Ui1 in crown length, but in the adult dentition the crown of UI1 is always longer than that of UI2. UI1 is notably long in comparison to the UC in *M. principula*, *dobsoni*, and *talazaci*.

In the *dobsoni*, *brevicaudata*, *longicaudata*, and *pusilla* clusters, UI2 and UI3 are closely appressed, but are separated from adjacent teeth by diastemata. In the *cowani* group and *M. gracilis* all the incisors are separated by interproximal gaps.

The canine is comparatively short in the *cowani* group; in *M. parvula* the Uc is scarcely longer than the Up2 (figs. 1e, 8b).

PREMOLAR PROPORTIONS

Differences in the proportions of permanent premolars within and between clusters are significant and can be adequately characterized with simple metrics. I measured crown height (cervix to paracone/protoconid tip, minimum distance) and crown width (mesiostyle/paraconid to distostyle/hypoconulid, minimum distance), using 12× tracings of holotypes (including those of synonymous species, adults only). Modules (crown height × crown width) were then computed and used to rank premolars in order of proportions (*not* absolute size) in a premolar module formula (or PMF). Upper and lower premolars are not distinguished as such in PMFs because, within any one cluster, rank order of premolars was always found to be the same in both jaws. However, comparative proportions (expressed as percentages) do vary within clusters, and ranges, rounded to the nearest 5 percent, are briefly noted here.

1. *longicaudata* cluster, PMF = $P4 \geq P3 > P2$. *M. longicaudata*: LP4, 20–30% larger than LP3; UP4, 0–10% larger than UP3. *M. principula*: LP4, 40–50% larger than LP3; UP4, 40–50% larger than UP3.

2. *brevicaudata* cluster, PMF = $P4 > P3 > P2$. *M. brevicaudata*: LP4, 60% larger than LP3; UP4, 10% larger than UP3.

3. *pusilla* cluster, PMF = $P4 > P3 > P2$. *M. pusilla*: LP4, 60% larger than LP3; UP4, 20% larger than UP3.

4. *dobsoni* cluster, PMF = $P4 \gg P3 > P2$. *M. talazaci*: LP4, 70% larger than LP3; UP4, 100% larger than UP3. *M. dobsoni* (USNM

TABLE 1
Measurements of Holotype and Lectotype Specimens of Nominal Species of *Microgale*^a

Species	Accession no.	GSkL	MUTL	IMW	ICW	MdL	TotL	HBL	TL	HFL	EL
<i>M. cowani</i>	BMNH 82.3.1.125	23.1	10.9	6.0	2.4	15.6	140	76	64	16.3	12.7
<i>M. longirostris</i>	BMNH 97.9.1.111	22.3	10.3	6.1	2.5	14.8	135*	81*	54	17.5*	14.5
<i>M. crassipes</i> ^b	MNH 1892-1560	21.9	10.0	6.2	2.7	14.4	127	71*	56*	16.0*	7.0
<i>M. melanorrachis</i>	BMNH 48.88	—	9.7	6.3	3.0	14.5	149	74	75	16.0	13.0
<i>M. taiva</i>	BMNH 97.9.1.112	23.1	10.5	6.1	2.5	15.3	167	80	87	18.5	12.5
<i>M. drouhardi</i>	MCZ 45034	24.5	11.5	6.4	3.2	16.7	146	71	75	18.0	12.0
<i>M. thomasi</i>	BMNH 97.9.1.108	27.0*	13.0	7.5	3.1	19.5	173*	103*	70*	21.0*	19.5
<i>M. parvula</i>	MCZ 45465	15.5*	7.1	4.4	1.9	10.5	93	42	51	10.0	5.0
<i>M. gracilis</i>	BMNH 97.9.1.78	30.4	14.5	—	—	—	174	93	81	18.0	16.0
<i>M. longicaudata</i>	BMNH 82.3.1.15	21.5	9.6	6.6	3.1	13.5	225	67	158	18.2	15.2
<i>M. majori</i>	BMNH 82.3.1.17	20.1	9.0	5.8	2.5	12.5	172	62	110	16.1	13.0
<i>M. proluxacaudata</i>	MCZ 45035	20.9	9.6	5.9	2.8	13.0	181	51	130	15.0	10.0
<i>M. principula</i>	BMNH 25.8.3.15	24.5	11.0	6.6	3.1	15.7	230	73	157	20.0	15.0
<i>M. sorella</i>	BMNH 25.8.3.14	23.5	10.4	6.8	3.2	15.4	227	71	156	19.5	14.5
<i>M. decaryi</i> ^c	MCZ 45049	—	—	7.1	—	14.0	—	—	—	—	—
<i>M. pusilla</i>	BMNH 97.9.1.93	16.5*	7.2	4.9	2.3	10.4	124	52	72	12.0	11.0
<i>M. brevicaudata</i>	MNH 1986-387	21.7	9.5	6.5	3.5	15.0	99	66	33	13.0	13.0
<i>M. occidentalis</i>	MCZ 45047	20.2	9.4	6.5	3.3	14.0	92	55	37	13.0	12.0
<i>M. dobsoni</i> ^d	BMNH 84.10.20.1	30.0	15.1	9.8	—	—	194	92	102	—	—
<i>M. talazaci</i>	BMNH 97.9.1.107	36.1*	17.9	11.2	—	—	243	124	119	23.0	16.5

^a Nominal species organized by cluster (see text). List does not include holotype of subspecies *M. cowani nigrescens* (some measurements of which were published by Elliot [1905]). Asterisks denote cases where these measurements differ by more than 5% from those of describers. All measurements in mm.

^b EL as given by Genest and Petter (1971).

^c MdL based on most complete jaw in MCZ 45048 series.

^d Skull measurements as given by Morrison-Scott (1948).

362095): LP4, 90% larger than LP3; UP4, 90% larger than UP3.

5. *cowani* cluster, PMF = $P3 \geq P4 > P2$. *M. cowani*: LP3, 5–10% larger than LP4; UP3, 15–30% larger than UP4. *M. thomasi*: LP3, 0% larger than LP4; UP3, 5% larger than UP4.

6. *gracilis* cluster: PMF = $P3 > P4 > P2$. *M. gracilis*: LP3, 30% larger than LP4, UP3, 20% larger than UP4.

METRIC TRAITS

Measurements for holotype and lectotype specimens are listed in table 1. Descriptive statistics for each recognized species (adult samples only) are provided in table 2.

Shrinkage and distortion of study skins make it difficult to verify measurements taken when the material was fresh. I have usually accepted the original measurements listed in publications or on museum tickets, except where egregious error has obviously been committed (e.g., HBL and TL do not equal totL). Shrinkage can be discounted for osteological measurements, and I have corrected original measurements (to the nearest tenth of a millimeter) wherever necessary. Note that “skull length” is always greatest length, not condylobasal length.

Of the listed skull measurements, greatest skull length (GSKL) has most often been used to define or distinguish nominal species of *Microgale*. When arrayed against tail length, another important variable, reasonably good separation of clusters is achieved (fig. 9). As would be expected, within clusters separation is poorer, especially in the groups with the most nominal species. Ratios based on certain body measurements (fig. 11; tables 3, 4) are of potential importance for discriminating adaptive types within *Microgale* (Eisenberg and Gould, 1970).

SKULL MEASUREMENTS

1. The *cowani* cluster. The remarkably low CV (2.9%) for GSKL in *M. cowani* is at least partly artificial, because the stated range (20.9–23.5 mm) does not include values for the holotype and paratype of *M. drouhardi*, both of which are dental juveniles. Including these specimens in the sample raises both the mean and the standard deviation ($\bar{X} = 22.0$

mm, SD = 0.92 mm), and yields a CV of 4.2 percent. This is still a comparatively low figure, and the spread in raw values is about the same as in *M. dobsoni* and *M. talazaci* (both unquestionably “good” species). The rounded best estimate for adult *M. cowani* (as here delimited) is 21–25 mm, a range which easily encompasses the holotypes of *M. crassipes* and *longirostris* and is not too distant from that of *M. thomasi*. But is this range the natural one for *M. cowani*, or have two or more reproductively isolated morphs been inappropriately lumped?

Figure 10 graphs GSKL against maximum upper tooththrow length (MUTL) in all measurable specimens allocated to the *cowani* cluster. The isolated pair of points representing the holotype and paratype of *M. thomasi* are separated by an appreciable interval from all other adult specimens.⁵ Dental juveniles are also depicted, with their eruption stage indicated if known. Only three juveniles (other than the holotype of *M. parvula*) are actually smaller than the smallest adult *M. cowani* in this sample; the remainder are liberally distributed throughout the cluster, and two—the holotype and paratype of *M. drouhardi*—are beyond the range of the adult sample. Notably, eruption stage seems to have no correlation with skull length.

Since no juvenile specimens have been allocated to *M. thomasi* in this survey, it could be argued that its young have been misidentified as “large” juveniles of *M. cowani*. Some support for this position can be garnered by interpreting the apparently random spread of juveniles at different eruption stages in figure 10 as actually representing two separate but superimposed sequences. This solution is attractive: the holotypes of *M. taiva* and *M. drouhardi*, both of which are larger than average adult *M. cowani*, could now be viewed as representing the missing juveniles of *M. thomasi*. Unfortunately, this approach creates more problems than it solves. One obvious difficulty is that *M. thomasi* (fig. 1d) has massive U/LP2s, but the freshly erupted homologous teeth of the *drouhardi* holotype (fig. 2b)

⁵ Most of the published measurements (Forsyth Major, 1896a) for the holotype of *M. thomasi* (BMNH 97.9.1.108) are incorrect; corrected values are listed in tables 1 and 2.

TABLE 2
Descriptive Statistics of *Microgale*^{a,b}

Species	Measurement	Statistics				
		N	\bar{X}	Range	SD	CV
<i>M. dobsoni</i>	GSkL	20	31.2	29.4–33.0	1.06	3.4
	MUTL	20	15.4	14.7–16.0	0.45	2.9
	MdL	7	21.4	20.3–21.9	0.64	3.0
	TotL	9	209.5	192–221	9.94	4.7
	TL	8	103.8	102–108	2.92	2.8
	HBL	7	110.3	103–114	3.90	3.6
	HFL	3	23.3	23.0–24.0	0.47	2.0
<i>M. talazaci</i>	GSkL	33	35.8	34.0–38.7	1.32	3.7
	MUTL	37	17.8	16.8–18.9	0.54	3.0
	MdL	8	25.2	24.6–25.9	0.54	2.1
	TotL	18	266.2	243–295	14.79	5.6
	TL	18	142.4	119–155	9.75	6.8
	HBL	18	123.8	115–130	6.51	5.3
	HFL	9	26.1	23.0–28.0	1.62	6.2
<i>M. brevicaudata</i>	GSkL	3	21.0	20.6–21.7	0.61	2.9
	MUTL	3	9.5	9.2–9.8	0.25	2.7
	MdL	3	14.2	13.8–15.0	0.67	4.7
	TotL	2	100.8	(99.0, 102.5)	—	—
	TL	5	36.0	33–38	2.92	8.1
	HBL	2	67.0	(66, 68)	—	—
	HFL	5	12.5	12.2–12.9	0.38	3.0
<i>M. pusilla</i>	GSkL	9	17.1	16.3–18.0	0.57	3.3
	MUTL	8	7.7	7.2–8.3	0.40	5.2
	MdL	9	10.7	9.5–11.4	0.53	4.9
	TotL	10	131.2	121–146	7.76	5.9
	TL	10	74.7	61–85	7.12	9.5
	HBL	10	56.6	51–62	4.33	7.7
	HFL	8	12.6	12.0–14.0	0.74	5.9
<i>M. longicaudata</i>	GSkL	10	20.3	18.8–22.3	1.30	6.4
	MUTL	10	9.1	8.2–10.0	0.69	7.5
	MdL	10	12.6	11.0–13.5	0.73	5.8
	TotL	5	211.0	172–226	23.20	11.0
	TL	9	130.2	109–158	19.80	15.2
	HBL	5	68.6	62–76	6.12	9.0
	HFL	4	17.0	15.0–18.2	1.12	6.6
<i>M. principula</i>	GSkL	3	24.0	23.5–24.5	0.50	2.1
	MUTL	3	10.6	10.4–11.0	0.32	3.0
	MdL	3	15.3	14.7–15.7	0.51	3.4
	TotL	3	219.0	197–230	16.52	7.5
	TL	3	149.0	134–157	13.01	8.7
	HBL	3	70.0	66–73	3.61	5.4
	HFL	3	19.2	18.0–20.0	1.04	5.4
<i>M. parvula</i>	GSkL	1	(15.5)	—	—	—
	MUTL	1	(7.1)	—	—	—
	MdL	1	(10.5)	—	—	—
	TotL	1	(93.0)	—	—	—
	TL	1	(51.0)	—	—	—
	HBL	1	(42.0)	—	—	—
	HFL	1	(10.0)	—	—	—
<i>M. cowani</i>	GSkL	25	21.7	20.9–23.5	0.62	2.9
	MUTL	26	10.2	9.5–10.9	0.38	3.8

TABLE 2—(Continued)

Species	Measurement	Statistics				
		N	\bar{X}	Range	SD	CV
<i>M. thomasi</i>	MdL	23	14.7	14.1–16.0	0.55	3.8
	TotL	21	131.3	113–165	12.53	9.5
	TL	21	57.2	43–82	9.54	16.7
	HBL	19	75.1	66–83	6.78	9.0
	HFL	24	15.6	14.0–19.0	1.48	9.5
	GSKL	2	26.9	(27.0, 26.7)	—	—
	MUTL	2	12.7	(12.4, 13.0)	—	—
	MdL	2	18.9	(18.2, 19.5)	—	—
	TotL	3	163.7	143–175	17.93	11.0
	TL	3	67.2	62–70	4.91	7.3
<i>M. gracilis</i>	HBL	3	96.7	82–105	13.2	13.6
	HFL	3	20.3	19.8–21.0	0.64	3.2
	GSKL	1	(30.4)	—	—	—
	MUTL	1	(14.5)	—	—	—
	MdL	3	21.1	21.0–21.2	0.12	0.5
	TotL	4	170.3	164–174	4.50	2.6
	TL	4	78.0	73–81	3.46	4.4
	HBL	4	94.8	91–100	3.86	4.1
	HFL	4	20.5	18.0–22.0	1.91	9.3

^a All figures are in millimeters, except CVs which are in percentages. Reallocations of specimens having existing museum designations (e.g., *M. brevicaudata* MNHN 1981-1864) are indicated only for species recognized here.

^b Holotypes and referred specimens: (1) *M. dobsoni*, adult specimens (sample used for computations): BMNH 97.9.1.100 to 105; 1939.1631 to 1634; 35.1.8.260 to 262—AMNH 100695, 100705, 100798, 31261, 31244—USNM 362095, 328695, 294520, 49673. Confirmed immature specimens: BMNH 82.10.20.1 (*dobsoni* holotype); BMNH 97.9.1.106—USNM 154988. Other specimens: BMNH 35.1.8.263 to 277—USNM 154988—MNHN 1932-3484; 1967-1624 and 1629; 1972-610; 1973-531 and 532—AMNH 100693, 100694; 100696 to 100704; 100706 to 100708; 100945.

(2) *M. talazaci*, adult specimens (sample): BMNH 97.9.1.107 (*talazaci* holotype); BMNH 48.92 to 94, 96 to 99, 101, 103 to 106, 108, 110 to 119; 35.1.8.278 to 281, and 283—AMNH 100710, 100714, 100799, 207003—USNM 341696, 341697, 294621, 328694—MNHN 1967-1615 and 1616, 1620 to 1623. Confirmed immature specimens: BMNH 48.100, 102, and 107; 35.1.8.282—AMNH 100708, 100806. Other specimens: BMNH 48.109—AMNH 100709—USNM 341699—MNHN 1932-3488, 3489, 3492, and 3493; 1967-1617 and 1618; 1972-608 and 612; 1973-524, 525, and 529.

(3) *M. brevicaudata*, adult specimens (sample): MNHN 1986-387 (*brevicaudata* holotype); MNHN 1986-388; 1981-864 (originally referred to *M. longirostris*). MNHN 1986-389 and 390, assumed to be adult, could only be measured for TL and HFL. Confirmed immature specimen: MCZ 45047 (*occidentalis* holotype). Other specimen: holotype of *M. breviceps* (whereabouts not known).

(4) *M. pusilla*, adult specimens (sample): BMNH 97.9.1.93 (*pusilla* holotype); BMNH 97.9.1.94, 95, and 98—USNM 328689, 328690—MCZ 45033 (plus specimens believed to be adult, BMNH 1939.1621 and 1622—MNHN 1897-527; MNHN unreg. from Grandidier Coll., no location—MCZ 45032—USNM 327687, 328691). Confirmed immature specimen: USNM 328688.

(5) *M. longicaudata*, adult specimens (sample): BMNH 82.3.1.15 (*longicaudata* holotype); BMNH 82.3.1.17 (*majori* holotype, here assumed to be adult); BMNH 82.3.1.16, 18, 21, and 22; 97.9.1.110; 1939.1620—MNHN 1962-2464. Confirmed immature specimen: MCZ 45035 (*prolixicaudata* holotype)—BMNH unreg. from Winton Coll.; BMNH 25.8.3.16. Other specimens: BMNH 25.8.3.16; BMNH unreg. from Ambohimitombo—MCZ 46020. Total sample for tail length includes values reported by Thomas (1882) for his specimens c, d, e, f, later referred to *majori* (Thomas, 1918). Since the specimen eventually accessioned as the holotype of *majori* (BMNH 82.3.1.17) has a shorter tail than any of specimens c–f, I take this as evidence that these four individuals were among the large number of long-tailed shrew tenrecs given away to other museums by the BMNH.

(6) *M. principula*, adult specimens (sample): BMNH 25.8.3.15 (*principula* holotype); BMNH 25.8.3.14 (*sorella* holotype)—MNHN 1981-859, 860, and 861 (originally referred to *M. longicaudata*). Other specimens (skulls and jaws only): MCZ 45049 (*decaryi* holotype), MCZ 48048; MNHN (Inst. de Paléontologie) MAD-1649.

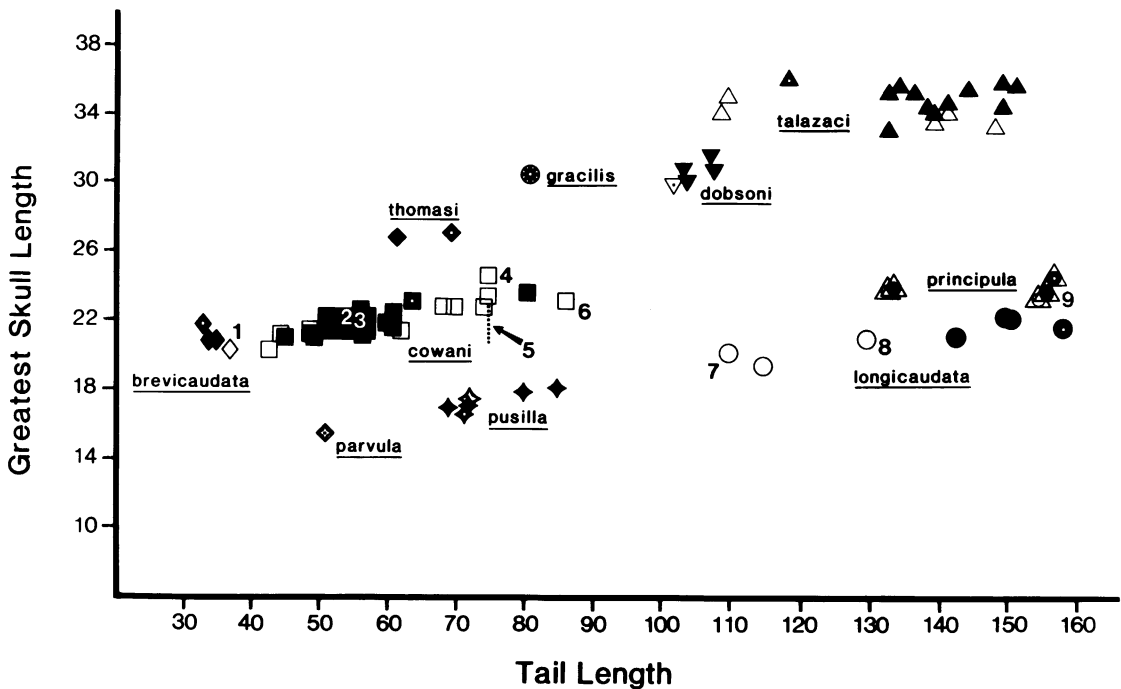


Fig. 9. Greatest skull length compared to tail length (both measurements in mm) in species of *Microgale*. Each species sample is represented by a different symbol: within samples, filled symbols indicate dentally mature specimens, while open ones represent immature specimens. Holotypes of recognized species are identified by a dot in center of symbol. Holotypes of synonymous species identified by numbers, as follows: 1, *Paramicrogale occidentalis* MCZ 45047; 2, *M. longirostris* BMNH 97.9.1.111; 3, *M. crassipes* MNHN 1892-1560; 4, *M. drouhardi* MCZ 45034; 5, *M. melanorrhachis* BMNH 48.88 (dashed line represents mean GSKL + 2 SD for *M. cowani*); 6, *M. taiva* BMNH 97.9.1.112; 7, *M. majori* BMNH 82.3.1.17; 8, *M. proluxacaudata* MCZ 45035; and 9, *M. sorella* BMNH 25.8.3.14.

are identical in size to those of typical *M. cowani*. The holotype of *M. taiva* (fig. 2d) cannot be compared because its antemolar dentition is entirely deciduous. However, its

molars, like those of the *drouhardi* holotype, are notably smaller than their homologs in *M. thomasi*, and are even somewhat smaller than those of USNM 341692 (fig. 2f) and

(7) *M. parvula*, holotype and only specimen (immature): MCZ 45465.

(8) *M. cowani*, adult specimens (sample): BMNH 82.3.1.25 (*cowani* holotype); BMNH 97.9.1.111 (*longirostris* holotype); MNHN 1852-1560 (*crassipes* holotype); BMNH 82.3.1.26; 97.9.1.81 to 87; 98.3.8.5 and 6; unreg. from Lavajaza; 1939.1628 and 1629—MNHN 1897-525 and 528; 1962-2473; 1967-1631; 1973-533—USNM 49675, 328692, 341693, and 341694 originally referred to *M. breviceaudata*—AMNH 31245. Confirmed immature specimen: MCZ 45034 (*drouhardi* holotype); BMNH 48.88 (*melanorrhachis* holotype); BMNH 97.9.1.112 (*taiva* holotype); BMNH 82.3.1.27; 97.9.1.80 and 92; 1939.1627—USNM 328693—MCZ 45028—MNHN 1961-205; 1981-862 and 863; 1972-611—MCZ 46012, 46017. Other specimens: BMNH 35.1.8.257 to 259; 1939.1623 and 1624; 48.87—MNHN 1932-3470; 1962-2476—USNM 49674; 328647 to 328649; 328653, 328654, 328656, 328657, 328659 to 328662, 328665, 328667 to 328672, 328674, 328675, 328677, 328678, 328680, 328683, 328686; 341692, 341693—MCZ 45023, 45024, 45028, 46007 to 11—FMNH 1349/5644 (*cowani nigrescens* holotype).

(9) *M. thomasi*, adult specimens (sample): BMNH 97.9.1.108 (*thomasi* holotype); BMNH 97.9.1.109; MNHN 1932-3469 (skin only).

(10) *M. gracilis*, adult specimens (sample): BMNH 97.9.1.78 (*gracilis* holotype)—MNHN 1961-204 (originally referred to *M. thomasi*); 1972-606 and 607. The ticket for AMNH 100717, cataloged as *M. gracilis*, is attached to the skin and skull of an example of *M. cowani*.

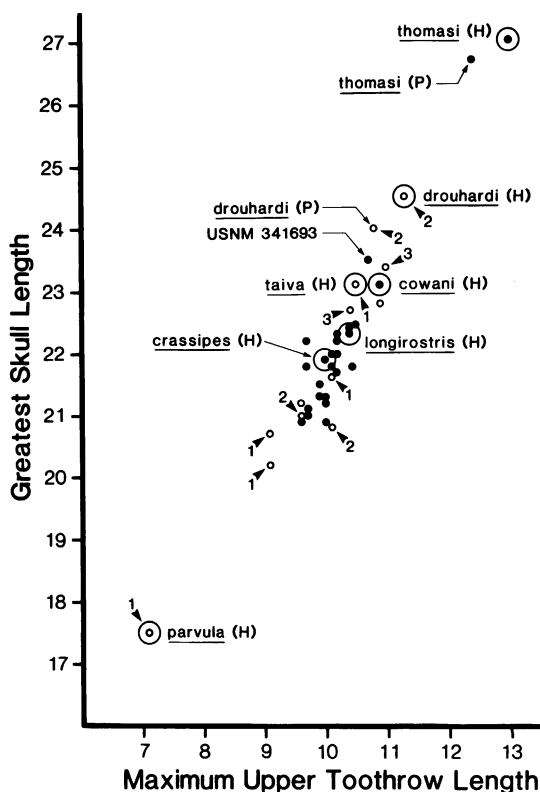


Fig. 10. Greatest skull length compared to maximum upper toothrow length (both measurements in mm) in members of *cowani* cluster. Dots represent dentally mature specimens; circles indicate immature specimens. Holotypes (H) and some paratypes (P) are named and ringed. The numbers 1, 2, and 3 next to symbols for immature specimens signify dental eruption stage (see text).

341693, both of which I place in *M. cowani*. The skull of USNM 341692 is broken, but that of similar-size USNM 341693 is 23.5 mm, only one millimeter smaller than the *drouhardi* holotype (fig. 10).

Another potential solution to the problem of correct species discrimination would be to leave *M. thomasi* as constituted, but to subdivide the large number of forms assigned to *M. cowani*. Although there is no obvious way to do this, an argument might be made for placing the lower limit for adult GSkL in *M. cowani* at about 22.5 mm, in order to take advantage of the apparent break in the distribution of adult data points at that position (fig. 10). The *cowani* holotype and USNM 341693 would be members of the larger-size

group, with the *drouhardi* and *taiva* holotypes representing juvenile stages of development. However, inspection of the relevant illustrations in figures 1 and 2 indicates that the "smaller" and "larger" morphs thus delimited would not be distinguishable dentally (cf. holotypes of *cowani* and *longirostris*).

2. The *longicaudata* cluster. A parallel set of allocation problems occurs within the *longicaudata* cluster, but the difficulty of resolution is exacerbated in this case by the small sample size (a total of 19 specimens, including juveniles). Morrison-Scott (1948) and Grandidier (1934) suggest that *majori*, the nominal species *M. sorella*, and *principula* could be synonyms of *M. longicaudata*, and Eisenberg (attrib. comment in Honacki et al. [1982]) notes that *M. prolixicaudata* may be a subspecies of the latter. This raises the possibility that all five nominal species (plus *M. decaryi*, which must be added to the group on dental grounds) may constitute a single polytypic species, *M. longicaudata*.

Setting aside all dental juveniles and broken specimens, average greatest skull length for the remaining combined sample of long-tailed shrew tenrecs is 21.2 mm ($N = 13$; $SD = 1.96$ mm). The accompanying CV (9.2%) of this small sample is rather large, although that by itself does not establish that the one-species argument is wrong. However, a two-species arrangement, consisting of *M. longicaudata* (including *M. majori* and *M. prolixicaudata*) and the larger *M. principula* (including *M. sorella* and *M. decaryi*) reflects some evident contrasts in tooth and skull morphology which are on par with those which divide *M. cowani* from *M. thomasi*. Although *M. longicaudata* and *M. principula* completely overlap in tail length, they are slightly separated in skull length (fig. 9). Larger sample sizes may reveal that these contrasts are merely the opposite ends of clines, but for the present I am forced to accept them as evidence for the existence of two independent species.

3. Other clusters and species. The other clusters are either monotypic or are composed of species whose metric traits are quite distinctive. Although *M. brevicaudata* overlaps completely with *M. cowani*, the two are easily distinguished by discrete traits of the dentition (q.v.).

BODY MEASUREMENTS

VARIATION IN THE *COWANI* AND *LONGICAUDATA* CLUSTERS

Hindfoot length. Considering the frequent recourse made to small differences in hindfoot length as species discriminators in shrew tenrec systematics, it is worth noting at the outset that all species display moderate to large ranges of variation in this variable. This is obviously true of *M. cowani*, which has a CV of 9.5 percent, but variation is marked even in some of the better-circumscribed species such as *M. talazaci* (6.2%) and *M. pusilla* (5.9%).

Among the traits used by Forsyth Major (1896a) to distinguish his concept of *M. longirostris* was hindfoot length, which he gave as 18.5 mm for the holotype. The foot of this specimen (BMNH 97.9.1.111) measures no more than 17.5 mm today. Even if shrinkage of the foot has occurred (which is doubtful, since total body length is actually 10 mm longer than the published value), Forsyth Major's measurement is equalled or even exceeded by other specimens allocated to this taxon. The same applies to the holotype of *M. crassipes*, whose allegedly broad foot is no longer than that of the average member of *M. cowani* (table 1). The hindfoot measurement (10 mm) reported for *M. cowani nigrescens* (Elliot, 1905) is as small as that of *M. parvula*, although greatest skull length is much longer (20.5 mm). If not a misprint, then the short foot length implies that Elliot's specimen is probably a young juvenile.

Tail length. Tail length is variable in all clusters except *M. dobsoni*, but it attains conspicuously high levels of variation in *M. cowani* (CV, 16.7%) and *M. longicaudata* (CV, 19.8%). It is particularly important to arrive at a reasonable explanation for the degree of variability encountered in *M. longicaudata*, since it was primarily the shorter length of the tail (and smaller body generally) that persuaded Thomas (1918) to divide his original concept of *M. longicaudata* into the latter and *M. majori*. Although the tail of the *majori* holotype is unquestionably short (110 mm), the now-dispersed series of specimens referred to *M. majori* by Thomas (1918) included some with longer tails (approx. 120, 117, 112, and 113 mm, converted from

Thomas' [1882] original measurements in inches). As mentioned earlier, the holotype of *M. majori* may not be fully adult, and it is therefore noteworthy that the holotype of *M. prolixicaudata* has a much shorter tail (130 mm) than does the holotype of *M. longicaudata* (158 mm). Since I am unable to detect any dental differences among the *longicaudata*, *majori*, and *prolixicaudata* morphs, I must infer that tail length is significantly variable in long-tailed shrew tenrecs, and that the value of this feature for delimiting natural populations within the *longicaudata* cluster is consequently nil.

An equivalent conclusion—high variability—is suggested for morphs here placed in *M. cowani*. For example, in Forsyth Major's Ambohimananana sample (see Pelage), tail length varies between 52 (BMNH 97.9.1.81) and 88 percent (BMNH 97.9.1.84) of head-and-body length. Similarly, although the holotype of *M. taiva* (fig. 2d) has a remarkably long tail (87 mm), in all important dental traits it matches USNM 328693 (fig. 6a)—which has a tail length of only 49 mm. In the case of *M. drouhardi*, tail length and other measurements as given by Grandidier (1934) appear to be dramatically greater than those of the single *M. cowani* to which they are compared. This appearance is deceiving, however, because the *cowani* specimen (undoubtedly a juvenile) is extremely small, being almost three SDs from the mean for GSKL and at the bottom of the observed range of variation for other measurements in my sample. As much additional evidence shows, the *drouhardi* morph is not fundamentally distinguishable from other *M. cowani*.

RATIOS OF BODY SEGMENT MEASUREMENTS AND ADAPTIVE TYPES

Eisenberg and Gould (1970) attempted to show that some general features of locomotor ability in nonaquatic oryzorictines can be inferred from ratios of certain body segments (TL/HBL, HFL/HBL). Their computations are based, for the most part, on published data and include heretofore unrecognized juveniles. Since their interpretations of these ratios, if substantiated, could have systematic importance, a new set of computations is in order. This has been done, and the results are presented in table 3 for the 10 species rec-

TABLE 3
Ratios of Tail and Hindfoot Lengths to Head-and-Body Length^a

	TL/HBL			HFL/HBL		
	N	\bar{X}	Range	N	\bar{X}	Range
<i>M. dobsoni</i>	5	0.96	0.89–1.05	3	0.21	0.20–0.23
<i>M. talazaci</i>	19	1.15	0.96–1.23	11	0.21	0.19–0.22
<i>M. brevicaudata</i>	2	0.51	0.50, 0.52	2	0.19	0.18, 0.20
<i>M. pusilla</i>	10	1.33	1.03–1.61	8	0.23	0.20–0.25
<i>M. longicaudata</i>	5	2.07	1.77–2.36	4	0.26	0.23–0.27
<i>M. principula</i>	3	2.13	2.03–2.20	3	0.27	0.27–0.28
<i>M. parvula</i>	1	(1.21)	—	1	(0.24)	—
<i>M. cowani</i>	21	0.76	0.52–0.99	21	0.21	0.17–0.23
<i>M. thomasi</i>	3	0.69	0.66–0.75	3	0.21	0.19–0.24
<i>M. gracilis</i>	4	0.83	0.73–0.87	4	0.21	0.19–0.23

^a Adults only, except in case of *M. parvula*.

ognized by me. Samples comprised dental adults only, except in the case of *M. parvula* where only one specimen (the juvenile holotype) was available. Table 4 is a reworking (for *Microgale* only) of Eisenberg and Gould's table 3, "Morphological Correlations Among the Terrestrial Oryzorictinae," and figure 11 is a graphic presentation of observed ranges of variation in the ratios, with juveniles included for comparative purposes.

The members of the *longicaudata* cluster are sharply distinguishable from other *Microgale* in having both very long tails and long hindfeet relative to head-and-body length.

The remaining species are much less distinctive: HFL/HBL values are little varied, and the TL/HBL range of *M. cowani* either significantly impinges on or completely overlaps the ranges of *M. brevicaudata*, *thomasi*, *gracilis*, and *dobsoni*. *M. talazaci*, *pusilla*, and juvenile *parvula* are somewhat distinguishable from the foregoing, and may be thought of as comprising an intermediate group with relatively longer tails and somewhat larger hindfeet. Eisenberg and Gould's (1970) reported range of 20–21 mm for HFL in *M. talazaci* is both too low and too narrow to be representative. As shown in figure 11, the

TABLE 4
Morphological Correlations Among Species of *Microgale*

HFL/HBL (mean)	Head-and-body length (in mm)			TL/HBL (mean)
	Small (<60)	Medium (>60 to <85)	Large (>85)	
<0.20		<i>M. brevicaudata</i>		0.51
		TL \approx 0.5 \times HBL:		
>0.20 to <0.21			<i>M. thomasi</i>	0.69
		<i>M. cowani</i>		0.76
			<i>M. gracilis</i>	0.83
			<i>M. dobsoni</i>	0.96
		TL \approx 1 \times HBL:		
>0.21 to <0.24			<i>M. talazaci</i>	1.15
	(<i>M. parvula</i>)			(1.21)
	<i>M. pusilla</i>			1.33
		TL \approx 2 \times HBL:		
>0.25		<i>M. longicaudata</i>		2.07
		<i>M. principula</i>		2.13

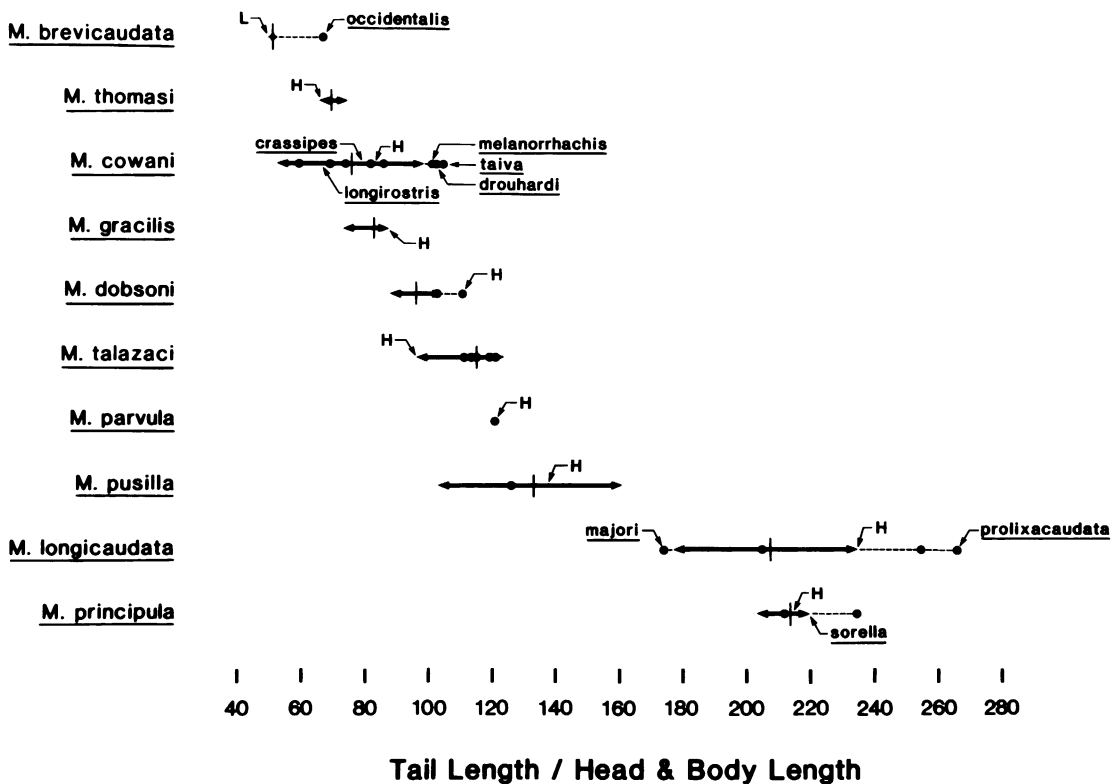


Fig. 11. Ratio of tail length to head-and-body length in species of *Microgale*. Ranges (solid horizontal lines) and averages (narrow vertical lines) are based on adult samples only; data points for immature specimens are indicated by dots (connected by dashed line to adult ranges in case of extralimitals). *M. parvula* is based on a unique, immature specimen. Positions of holotypes (H) and lectotypes (L) of accepted species are indicated by letters; of holotypes of subsumed species, by nomen of synonym.

inclusion of juvenile specimens within samples increases the range of variation, especially in the longest- and shortest-tailed taxa.

In view of these substantial overlaps, making locomotor or adaptive distinctions between species or species clusters seems dangerous. Thus while Eisenberg and Gould (1970) distinguish between taxa having semifossorial, surface foraging, and surface-foraging-and-climbing strategies, the benchmark values which they use to separate these behavioral types are entirely within the ontogenetic range of variation of a single species, *M. cowani* (as here defined).

It would be much easier to know how to interpret the differences that do seem to exist among species if there were adequate field studies of locomotor behavior in *Microgale* (cf. Nichol, 1984). Unfortunately, other than anecdotal information the only good observational data on any species are contained in

Eisenberg and Gould's (1970) classic work on *M. dobsoni* and *M. talazaci*. The authors note few important differences between these two species, although they place them in different categories (surface forager/moderate climber and surface forager/climber). Both are best described as scansorial (cf. Jenkins, 1974), having essentially equivalent abilities to scamper over horizontal or angled surfaces, climb over obstacles, and jump for short distances on the ground or between twigs and small branches. Interestingly, although *M. talazaci* has higher values for the ratios in question, it displays a burrowing proclivity not recorded for *M. dobsoni* (Eisenberg and Gould, 1970). Having said this, I do not doubt that the total adaptive strategies of *M. dobsoni* and *M. talazaci* are indeed different, or else they would not have differentiated as species. However, their divergence may have been accomplished without any important

modifications in locomotor behavior, and this should be borne in mind when contemplating the strong physical similarities of certain other dyads (e.g., *M. gracilis* and *M. thomasi*, *M. longicaudata* and *M. principula*). Conversely, if future fieldwork establishes that substantial variety exists in the locomotor behaviors of species of *Microgale*, it is clear that morphological correlates other than these ratios will have to be found to express them.

NONMETRIC TRAITS

SKELETON

Some clusters have distinctive suites of nondental cranial traits that help to distinguish them from other groups, but, generally speaking, differences are minor (cf. Heim de Balsac, 1972).

1. The *brevicaudata* cluster. *M. brevicaudata* is characterized by a robust skull and short rostrum (fig. 1h). From the lateral aspect, the nasal region has a swollen, slightly convex outline and appears to ascend more sharply toward the top of the skull than in other species (cf. Grandidier and Petit's [1931] description of *M. occidentalis* and fig. 5b). Due to the comparatively large size of the braincase and nuchal crest, the dorsal outline of the skull is sinuous rather than straight, a trait sometimes regarded as diagnostic of the *dobsoni* cluster (e.g., by Thomas, 1918). The corpus of the mandible is also thicker, for its length, than in *Microgale* species other than *M. dobsoni* and *talazaci*.

2. The *longicaudata* and *pusilla* clusters. Overall, the *longicaudata* cluster is more similar to *M. brevicaudata* than to *M. cowani*. The snout is almost as abbreviated, and its rostral end has a "squared-off" (or even slightly upturned) appearance, especially noticeable in *M. principula* (figs. 1b, 4a).

M. pusilla has the abbreviated snout of *M. brevicaudata*, but in other respects is more gracile and *longicaudata*-like (fig. 1c).

3. The *cowani* and *gracilis* clusters. The species in this grouping have gracile skulls, with long, narrow muzzles and small anterior nasal apertures. This lengthening and attenuation of the rostrum reaches its extreme in *M. gracilis* (fig. 1f). In both clusters, the anterior portion of the mandible frequently dis-

plays a constriction beneath the anteriormost teeth, giving it a sinuous rather than a convex profile (fig. 1f, g).

M. thomasi (fig. 1d) has a more robust skull and jaw than do other members of the *cowani* group, but the rostrum is still proportionately long and narrow compared to other clusters.

Contra Forsyth Major (1896a), the holotype of *M. longirostris* does not have a more "pyriform" skull or narrower rostrum than typical *M. cowani*. He may have been led to this view from his examination of the pelt rather than the skull; the muzzle of the study skin is decidedly elongated, but only because a metal wire (introduced into the body cavity in order to prevent contraction) caused the nose to stretch.

4. The *dobsoni* cluster. A distinguishing trait of the *dobsoni* cluster is the virtually horizontal setting of the anterior portion of the alveolar process of the maxilla. This feature is also seen, to a lesser degree, in *M. brevicaudata*, but in other species there is a more emphatic "inflection" of the maxilla above UP3.

The only nonmetric trait of the appendicular skeleton which has played a role in systematic discussions is the degree of fusion of the distal tibia and fibula. Grandidier and Petit (1931) claimed that fusion is absent in the form they named *Paramicrogale occidentalis*, unlike other known *Microgale* (cf. Thomas, 1882), and emphasized this fact in their generic and specific diagnoses. Uncertainty surrounds the identity of this skeleton (see Valid Nomina), but the simplest explanation for the reported observation is that the skeleton examined was that of a juvenile, in which tibia-fibula fusion was incomplete.

PELAGE

In all *Microgale*, the rather mousy-looking pelage consists of short, dense, velvety fur, from which projects a sparse array of guard hairs. Coloration is dominated by somber browns and russets on the dorsum, head, and flanks; the ventrum is usually a leaden gray, with yellowish tinges in some species. The color differences that do exist essentially depend on whether granules of one or both melanin types (eumelanin and pheomelanin) are represented in the hair shaft. Most hairs, for

most of their lengths, are a slaty gray; the distal one-third to one-quarter are differently colored, as follows: type I hairs, distal part brown to chocolate; type II hairs, distal part light brown to yellow; type III hairs, distal part russet, but extreme tip black. Unmelanized or "white" hairs also occur in low numbers in many individuals.

In most individuals of most nominal species, types I and III are both present and impart a characteristic agouti aspect to the pelt. The slaty gray hair bases are not conspicuous until the hair is parted. Type II hairs frequently predominate toward the midline, where they may produce a more or less definite dark stripe. Type III hairs are most common around the lips, on the underside of the neck, and on the ventrum, where they may be dense enough to produce an indistinct midline stripe. They thin out along the lateral aspect of the body and are rare on the dorsum in most individuals. Pelage differences between species are minor, and there is considerable within-group variation in some groups (especially the *cowani* cluster).

1. The *cowani* and *gracilis* clusters. The holotype of *M. cowani*, an adult female, has a dark brown dorsum which gradually darkens to chocolate toward the rump. No definite midline stripe can be identified on the back. There is some, but not much, russet flecking produced by scattered type III hairs. On the ventrum, type II hairs become progressively commoner toward the midline, although the dominant aspect is gray.

To illustrate just how unrepresentative the holotype pelt of *cowani* is, it is instructive to consider the skins of a dozen BMNH specimens from the vicinity of Ambohimananana, collected according to their tickets by Forsyth Major during the course of a few days in May 1896. All were assigned to *M. cowani* by their collector. Pelages within this series vary from chocolate brown over the entire dorsum, with few reddish highlights (e.g., BMNH 74.555), to a mousy brown, recalling the holotype but with a noticeably greater amount of red (e.g., BMNH 97.9.1.85, adult female). On the ventrum, darker individuals have predominantly gray bellies with little suggestion of type II hairs. Lighter individuals have a correspondingly greater density of type II hairs on their undersides, and some additionally show an

ill-defined chocolate middorsal stripe, which becomes identifiable at the level of the ears and runs to the rump (e.g., BMNH 97.9.1.87, adult female). Significantly, none of these traits can be definitely linked with either sex or dental age. The dental age of BMNH 74.555 could not be assessed since no skull accompanies the skin. However, the same very dark coloration occurs in other animals of different sexes and ages, also collected by Forsyth Major but originally in the Tring Museum collection (e.g., BMNH 1939.1628, adult male; 1939.1627, juvenile male; 1939.1629, adult female).

The dark-rumped holotype of *M. longirostris* is very similar to that of *M. cowani*, while the holotypes of *M. crassipes*, *M. drouhardi*, and *M. cowani nigrescens* as described by Elliot (1905) display pelt characters similar to those of the darker individuals previously mentioned. The dorsal stripe of the two specimens in the type series of *M. melanorrhachis* is better defined than in other material of *M. cowani*, although a close approach is seen in a few cases (e.g., BMNH 97.9.1.83, adult male). The sharpness of the stripe in the *melanorrhachis* holotype was regarded as a diagnostic character by Morrison-Scott (1948), who, however, misidentified this specimen as an adult. Although striping is allegedly a juvenile characteristic (cf. Grandidier, 1934), loss or diminution of this trait (? after molting) is evidently not in phase with the replacement of the deciduous dentition.

The holotype of *M. thomasi* has a coloration similar to the holotype of *M. cowani*, but a greater density of type III hairs on the shoulders and top of the head gives the forepart of the back a russet tone ("lighter tinge" of Forsyth Major, 1896a). There is a noticeable sprinkle of white hairs on the dorsum, but there is no middorsal stripe and the hindquarters are not darker than the rest of the back. The red highlights are even more obvious in the type of *M. taiva*, which otherwise agrees with *M. thomasi* save that its ventrum is entirely gray. Grandidier (1934) claimed that the skin of the holotype of *M. parvula* was "*complètement et intégralement noir*," but the preserved skin has a definite reddish-brown tinge which may or may not be due to the effects of preservation in alcohol (see below).

The holotype of *M. gracilis* is very similar to that of *M. cowani*.

2. The *longicaudata* and *pusilla* clusters. The skins of the holotypes of *M. longicaudata*, *prolixacaudata*, *majori*, *principula*, and *sorella* are quite similar. Their general aspect is agouti brown, like the holotype of *M. cowani*, but with a substantially greater sprinkling of russet over the back. This reddish cast was not noted by Thomas (1882, 1926) in his descriptions, but in his diagnosis of *M. majori* (Thomas, 1918) he stated that "Colour, of a specimen skinned from spirit and therefore probably too rufous, reddish brown above and near 'sayal-brown' below—but without specimens skinned fresh, these colours cannot be trusted." Fresh-skinned pelts of *M. longicaudata* in the BMNH and MNHN collections demonstrate that the russet hue is not an artifact in this cluster (cf. Grandidier's [1937] description of *M. prolixacaudata*). No stripes were seen, above or below, on any specimen.

In *M. pusilla*, as in *M. longicaudata*, there is a noticeable reddishness ("light brown" of Forsyth Major, 1896b) to the back and flanks, although the general effect is perhaps slightly darker. Pelts in the USNM collections, collected at Didy in north-central Madagascar during October and November, 1962, had relatively long individual hairs compared with skins from other locales.

3. The *brevicaudata* cluster. *M. brevicaudata* is very similar to *M. pusilla*. Grandidier and Petit (1931) describe *M. occidentalis* as having "beige" nuances, but in their microscopic description of hair shafts they note that these hairs are black-tipped (i.e., type III rather than type II). Reddish highlights were noticeable on the alcoholic skin of the type (MCZ 45047). They are noticeable as well in the type series of *M. brevicaudata* (cf. original description by Grandidier, 1899).

4. The *dobsoni* cluster. Specimens of *M. talazaci* vary much like specimens of *M. cowani*. Dark individuals seem to be common in this species, although I have not seen any as dark as the most melanistic *M. cowani*. Lighter individuals (e.g., USNM 328694) display russet tones ("dark coppery brown" of Forsyth Major, 1896a) over the back, with light yellow lower face and ventrum. The dorsal stripe is vaguely hinted at in USNM 341699,

a juvenile female. Most *dobsoni* agree with lighter *talazaci*.

In *M. dobsoni*, a molt to adult pelage is complete at 110 days after birth, according to Eisenberg and Maliniak (1970: 43). Unfortunately, they do not provide any details of color change in the pelt and it is not known at what dental stage the molt takes place.

TAIL

Although the length of the tail varies substantially within the genus, in other respects its morphology varies little from cluster to cluster. In most species the tail is evenly but very sparsely covered by short, spiky hairs. In members of the *longicaudata* cluster, however, its terminal portion bears a specialized, naked area on its dorsal surface. This feature was first recognized by Thomas (1918: 306), who observed that: "... long-tailed species of *Microgale* have the end of the tail for from half an inch to an inch naked and transversely wrinkled on its upper surface, just as in certain prehensile-tailed Muridae. This character, and also the more lengthened fifth hind toe of the same species, indicates that these forms are arboreal, being the only Insectivora—other than the Tupaiidae—which are so. Nor is any other truly prehensile tail known in the order."

Thomas (1918, 1926) confirmed the presence of this specialized area in type series of *M. longicaudata*, *majori*, *sorella*, and *principula*, but Grandidier (1937) claimed that the naked zone could not be made out in *prolixacaudata* and that there was no evidence that the tail was used in a prehensile fashion.

In the absence of any field observations pertaining to members of the *longicaudata* cluster, there is no direct evidence that the tail is used in a prehensile fashion in the manner of (for example) the murid *Pogonomys*. "Prehensile" is, of course, a word with rather strong connotations, and should only be applied to cases where the tail is actively used for support or purchase. The only record which I have seen of actual use of the tail during locomotion is Eisenberg and Gould's (1970: 46) note that *M. talazaci* may coil or drape its tail around twigs or projections of bark. They believe that this activity dem-

onstrates "some latent prehensility" of the tail, but take pains to point out that true prehensility is not present.

I confirm that the naked area at the tail tip exists in all members of the *longicaudata* cluster for which appropriate material exists, including the holotype and paratype of *M. prolixacaudata*. The length of the hairless area in the paratype of *M. longicaudata* (BMNH 82.3.1.16) is 11 mm (fig. 12A), while it is approximately 15 mm long in the alcohol-preserved holotypes of *M. sorella* and *principula*. The *sorella* holotype is exceptionally well preserved, and it is therefore noteworthy that in this specimen the glabrous area is smooth rather than wrinkled, as though the imbricating annulations seen along the rest of its tail had been worn down in life. In the holotype of *M. majori*, the glabrous area is about 9 mm long, but in a second specimen (BMNH 82.3.1.22) it is only 3 mm in length and appears to be crumpled or aberrant (fig. 12B). The naked area is also very small in the holotype and paratype of *M. prolixacaudata* (MCZ 45035, 46020), which presumably explains why Grandidier (1937) missed it. This specialization was not identifiable in *M. parvula* or *M. pusilla*.

The other important tail specialization seen in *Microgale* is dry-season incrustation, seen only in *M. dobsoni*. *M. talazaci* displays no tendency to store fat or to enter semitorpor, neither of which is a necessary adaptation (in the view of Eisenberg and Gould [1970]) in animals essentially confined to the "stable environment" of true rain forest. In light of this argument, it is odd that neither *M. brevicaudata* nor *M. pusilla*—both of which have populations on the western, highly seasonal side of the island (this paper; MacPhee, 1986)—is known to store fat.

KEY TO SPECIES AND REVISION SUMMARY

Although *Microgale*, even after revision, still remains the most speciose genus in Tenrecidae, it is now clear that there are only a few distinct lineages within the taxon. From this perspective it matters little whether I have lumped too many species under *M. cowani*, or *M. principula* has been wrongly kept separate from *M. longicaudata*, because no



Fig. 12. Tail morphology in *M. longicaudata*, illustrating terminal portions in BMNH 82.3.1.16 (A) and BMNH 82.3.1.22 (B), dorsal aspect (6×). In BMNH 82.3.1.22, unusually small and aberrant hairless area on dorsum of tail is bracketed.

further fine adjustments to taxonomic boundaries are likely to uncover convincing examples of heretofore unknown adaptive types.

In each of the three species represented by museum material sufficient for adequate analysis (*M. dobsoni*, *talazaci*, and *cowani*), within-deme variation in pelage and other obvious external features easily matches between-deme variation. Subspecies are therefore not distinguishable on present evidence and none is listed in the key below. Since some species occur or have recently occurred on both sides of the island, perhaps subspecies designations will turn out to be necessary in a few cases. However, there are no morphological grounds that would justify coining any new names at present. Karyological information is very limited for shrew tenrecs (see next section) and is not used in species definitions here.

The following key emphasizes the strongest available contrasts among species (cf. preliminary key assembled by Genest and Petter [1971]).

KEY TO SPECIES OF *MICROGALE*

1. TL 1.7 to 2.4 times HBL 2
TL <1.7 times HBL 3
2. UP3 and UP4 subequal in size; GSkL 18.8–22.3 mm *longicaudata*
UP4 up to 50% larger than UP3; GSkL 23.3–24.5 mm *principula*
3. LP2 single-rooted; TL 1.0 to 1.6 times HBL; GSkL 16.3–18.0 mm *pusilla*
LP2 double-rooted 4

4. Upper molars with very small lingual shelf;
GSKL large (≈ 30 mm) *gracilis*
Upper molars with large lingual shelf 5
5. LI2 much larger than LC, TotL > 190 mm
..... 6
LI2 slightly larger than or subequal to LC
..... 7
6. TotL 192–221 mm; GSKL 29.4–33.0 mm
..... *dobsoni*
TotL 243–295 mm; GSKL 34.0–38.7 mm
..... *talazaci*
7. TL 33–38 mm; GSKL 20.6–21.7 mm
..... *brevicaudata*
TL > 40 mm 8
8. Very robust LP2; HFL 19.8–21 mm; GSKL ≥ 26
mm *thomasi*
Less robust LP2, HFL 14.0–19.0 mm; GSKL
 ≤ 25 mm *cowani*

SUMMARY OF JUSTIFICATIONS FOR SPECIES REVISIONS

1. *M. longicaudata* and *principula*. Heim de Balsac (1972) concluded that *M. principula* and *M. sorella* were merely subspecies of *M. longicaudata*, but that *M. majori* could be validly separated from the latter. This conclusion, essentially the reverse of the one proposed here, was evidently based on the literature and not on a personal examination of type material. He noted, however, that the difference in skull length between the holotypes of *M. principula* and *M. longicaudata* was rather large for mere subspecies.

The nominal species *P. decaryi* is known from very incomplete material. Its distinctive features—marked brachycephaly, short dental arcade, wide anterior maxilla, and broad interorbital area (Grandidier, 1928)—are also characteristic of *M. principula*, and this is where I believe *decaryi* belongs. *M. prolixicaudata*, on the other hand, cannot be differentiated from juvenile *M. longicaudata*.

2. *M. pusilla*. The lesser shrew tenrec is dentally quite different from all members of the *cowani* group, although externally *M. parvula* and *pusilla* are somewhat similar—hence the suggestion of Eisenberg and Gould (1970) that they might be synonyms. Its comparatively long tail suggests an approach to the *longicaudata* cluster (cf. Heim de Balsac, 1972), although it is dentally distinct from *M. longicaudata* and *principula* and even shows a number of similarities to *M. brevicaudata*.

3. *M. gracilis*. Because of the rarity of *M. gracilis* in museum collections, its within-group variation cannot be adequately assessed at this moment (although ca. 30 mm for GSKL is probably a good estimate). For the measurements collected here, *M. gracilis* usually places between *M. dobsoni* and *M. thomasi*, although in skull shape and tooth structure it is much closer to the latter than the former. The only dental trait which sharply distinguishes this species from all other *Microgale* is the small size of the lingual shelves on the upper molars. Heim de Balsac (1972: 643) thought this was significant enough to warrant retention of the name *Lep togale*, but only as a subgeneric designation (but see p. 656). *M. gracilis* has much longer claws than do other species in its size range (e.g., *M. dobsoni*, *M. talazaci*), although whether this feature is correlated with arboreal or subterranean activity is not known.

4. *M. dobsoni* and *talazaci*. Although the distinctiveness of *M. dobsoni* and *M. talazaci* has not been in question since Morrison-Scott's (1948) study, their corporate differences from other shrew tenrecs do not, in my mind, justify their removal to a separate genus (cf. Heim de Balsac, 1972). According to Borgaonkar (1967, 1968), both species in this cluster have the same diploid chromosome number, $2n = 30$ (female NF = 52).

It is regrettable that the holotypes of these two species are rather unrepresentative, being near the limits of the ranges of variation for their respective species. Nevertheless, except in hindfoot length there is no observed overlap in sample ranges, and means are always well separated for the measurements considered here (almost 3 SDs in the case of GSKL, for example). Discrete traits of the teeth are much the same in these two taxa, although *M. talazaci* has a more robust dentition as befits its larger size.

5. *M. brevicaudata*. The short tail and abbreviated face of *Paramicrogale occidentalis* establishes that this taxon belongs in the *brevicaudata* cluster. Although immature, the holotype and only specimen (MCZ 45047) of *occidentalis* is within or near the known range of variation of *M. brevicaudata* for every metric trait listed in table 2. The jaws conditionally named *M. "breviceps"* by Kaudern (1918) contain teeth which are either iden-

tical or very similar to those at homologous loci in MCZ 45047. Kaudern (1918) provided no measurements of his material, but judging from his figures the two jaws are within the size range of *M. brevicaudata*.

The genus *Paramicrogale* was rendered polyphyletic at its inception by Grandidier and Petit's (1931) insertion of *M. decaryi* therein. That short- and long-tailed shrew tenrecs could be so easily muddled affirms the point that dental similarity among species clusters is very great.

6. *M. cowani*, *thomasi*, and *parvula*. *M. parvula* is not diagnosed in the key because the only known specimen is immature. However, juveniles of the pygmy shrew tenrec can be easily recognized on the basis of their very small skull size (<16 mm) and two-rooted, premolariform Lp2. This is the only good species of *Microgale* whose adult stage is still unknown (or unrecognized).

Other boundaries within the cluster are less clear. Heim de Balsac (1972) cites favorably, but does not expand on, Thomas' (1918) uncharacteristically vague statement that Forsyth Major's concept of *M. cowani* differs "in certain details of dentition" from the *cowani* holotype. In my opinion, all differences among nominal morphs in *M. cowani* appear to be clinal. I have no hesitancy in ascribing not only Forsyth Major's collection but also the type material of *M. crassipes*, *M. longirostris*, and *M. melanorrhachis* to the same species, which by virtue of priority is *M. cowani*. Although they appear to be rather distinct when viewed in isolation, the holotypes of *M. drouhardi* and *M. taiva* are best regarded as remarkably large juveniles of this same species. All of these forms except *longirostris* are retained as separate species by Heim de Balsac (1972), although he allows that *crassipes* may be distinguishable only at the subspecies level. He lists "small ear" as the sole distinguishing trait of *M. crassipes*, but all that is claimed in Milne-Edwards' (1893) original diagnosis is that the ear is (unsurprisingly) smaller than that of *M. dobsoni*. Genest and Petter (1971) list ear length for the *crassipes* holotype as 7 mm.

As Forsyth Major (1896a) noted in his original description, the holotype of *M. thomasi* is "very like *M. Cowani*, but much larger." Although I retain lingering doubts about

the validity of *M. thomasi* as distinct from *M. cowani*, it seems better to leave *thomasi* out of *cowani* than to try to fit it in. Combining these taxa would mean that fully adult common shrew tenrecs differ in measurements such as greatest skull length by as much as 33 percent. Such a range actually occurs in *Tenrec ecaudatus* (Dobson, 1882), but in that taxon there are important sexual differences in size that do not occur in *Microgale* (Butler, 1937; Nichol, 1984).

Another reason for keeping *cowani* and *thomasi* separate is karyological. According to Borgaonkar and Gould (1969), in *M. cowani* $2n = 54$ (female NF = 55 or 56; Reumer and Meylan, 1986). By contrast, in *M. thomasi* $2n = 30$, as in *M. dobsoni* and *talazaci* (Borgaonkar, 1967, 1968). Additional karyotypes, preferably G-banded, would be highly desirable for these as well as the uninvestigated species of *Microgale*.

SHREW TENRECS IN SPACE AND TIME

CLIMATE AND GEOGRAPHY

Now that the systematic status of constituent species of *Microgale* has been clarified, it is possible to make a few inferences about their ranges and habitat preferences within Madagascar. A physical description of the island will not be attempted here, but some understanding of its plants, precipitation, and physiognomy is necessary for an accurate evaluation of collecting records (for additional background, see Humbert and Cours Darne [1965], Battistini [1964], Martin [1972], and the volume edited by Battistini and Richard-Vindard [1972]).

Although an island, in several respects Madagascar has the attributes of a small continent (fig. 13). One of the most obvious expressions of its diversity is the character and distinctiveness of its major floral formations (Koechlin et al., 1974). Tropical rain forest and related formations (including secondary "savoka" and moist montane forest) are found in a comparatively thin strip along much of the eastern side of the island and in circumscribed parts of the far northwest (Sambirano) and extreme north (Ambohitra). The south is renowned for the unusual xerophilous bushland thicket that predomi-

 DRY-MESIC FOREST (WEST REGION)

 XEROPHILOUS BUSH & THICKETS

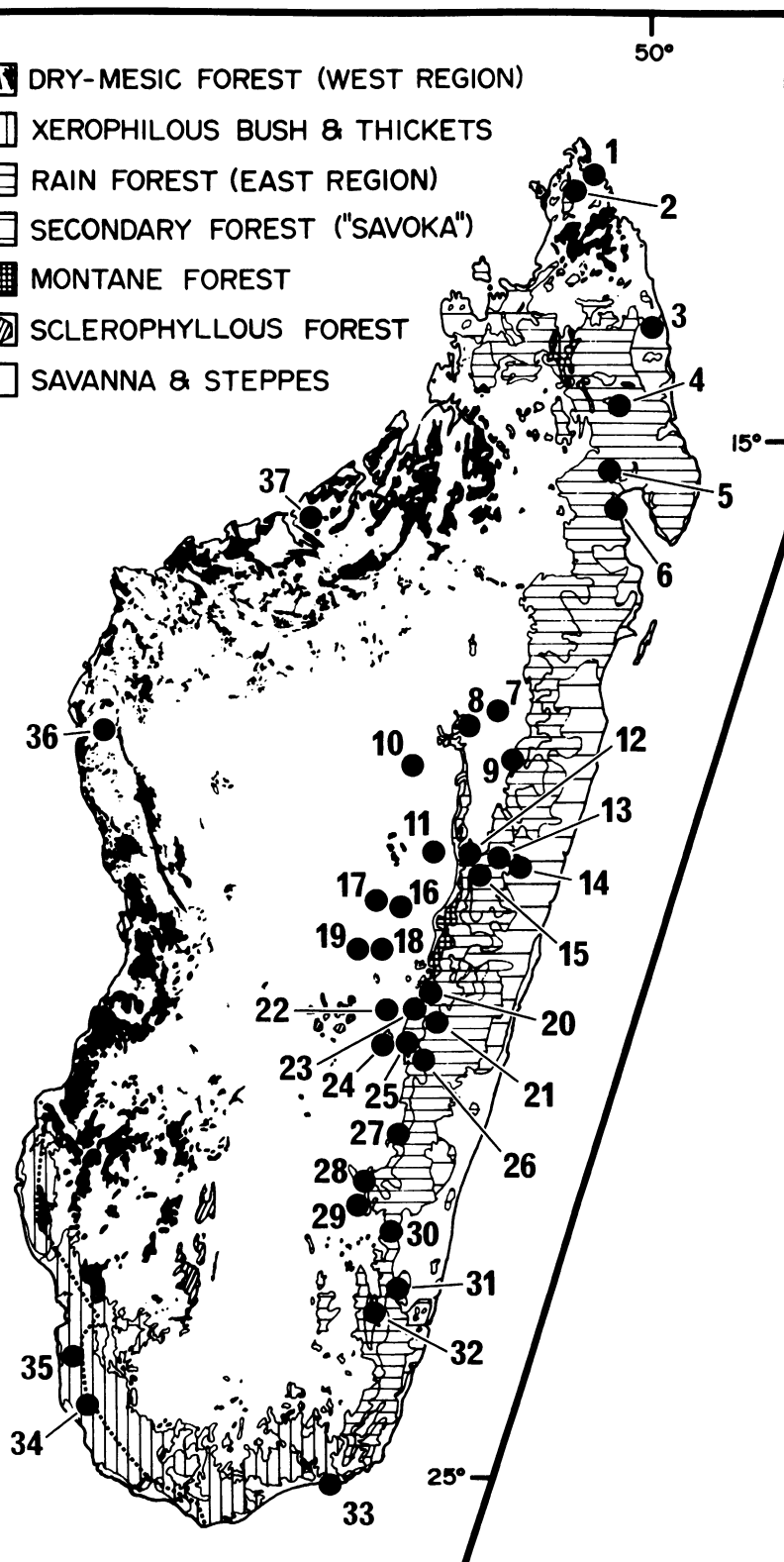
 RAIN FOREST (EAST REGION)

 SECONDARY FOREST ("SAVOKA")

 MONTANE FOREST

 SCLEROPHYLLOUS FOREST

 SAVANNA & STEPPES



nates on most soils from Morombe to Ambovombe. North of Morombe, conditions are more mesic, and southern bushlands are replaced by patchy dry deciduous forests that cover much of western and northernmost Madagascar. The core of the island is occupied not by forest but by grasslands, punctuated here and there by species-poor woodlands (e.g., sclerophyllous "forest," fig. 13) and thin gallery forests. The area of the grasslands is immense, occupying virtually three-quarters of the island (Guichon, 1960).

As might be predicted from the differing aspects of the various floral communities, precipitation varies markedly in both amount and delivery across the island (Donque, 1975). The tropical wet evergreen forests of the east receive 3600–1800 mm/year, and experience high humidity, even temperatures, and no annual dry period. The dry-mesic forests of the west and the grasslands of the center receive 1800–600 mm/year, but much of it (80–97%) falls in the October–April wet season. The extreme south is actually semiarid, receiving only 600–300 mm/year; what little rain falls does so unpredictably and dry "seasons" may last for years. The extreme north varies greatly over small distances: Ambohitra supports dense forest and is comparatively wet (2177 mm/year), but nearby Antsiranana and Cap d'Ambre [Tanjona Bobaomby] receive less than 1000 mm/year and are mostly vegetated by dry forest mosaics with many xerophiles.

There are no true mountain ranges in Madagascar, although the net elevation is high (ca. 1000 m elevation) on the cratonic block of crystalline rocks forming most of the island's east and center. For present purposes the most important heights-of-land are, from north to south, Ambohitra (1474 m), Ankaratra (2642 m), and Andringitra (2658 m). Unlike Ambohitra the other peaks are much higher than the net elevation, and support a characteristically different montane vegetation dominated by ericoid bush at high elevations (Koechlin et al., 1974). The highest parts of these isolated massifs may occasionally experience temperatures of 0°C during the aus-

tral winter (Donque, 1975). Even at lower elevations in the central highlands, frosts occasionally occur (e.g., at Antananarivo at 1300 m). However, winter diurnal variation in temperature in the center is also great (e.g., 5–12°C in July in Ambositra: av. minimum, 8.7°C; av. maximum, 19.4°C), and no part of the island can be described as having an unremittingly cold winter (Donque, 1975).

RANGE AND HABITAT

Specific collecting localities on record for *Microgale*, together with a listing of the shrew tenrec taxa recovered at each site or combination of nearby sites, are presented in figure 13. As far as I am aware, no tenrecid has been the subject of an organized census or collecting effort designed to fix its distributional limits. Most collecting expeditions have concentrated on the island's biotically diverse eastern side, and only a few areas (e.g., E of Antananarivo, SE of Ambositra, NE and SE of Fianarantsoa) can be regarded as having been adequately sampled for tenrecids. The rest of the island has barely been touched, although confident assertions are sometimes made that this or that species is "forest adapted" or "restricted to the wetter parts of the island." Yet it is clear from table 5 that several "eastern forest" shrew tenrecs range into the center, and some even have representatives on the western and southern sides of the island. Additional discoveries of "extralimital" populations can be anticipated for the future, and the following notes on range and habitat must therefore be taken as preliminary. They represent gleanings from the published literature, museum tickets, and the results of my own limited efforts while engaged in paleontological work in Madagascar during 1983–1985. In the absence of extended field observations for most species, brief collectors' comments may give the flavor (but probably little of the substance) of the range of microenvironments in which shrew tenrecs flourish.

In the range descriptions, vegetation types are coded by the following letters:

←

Fig. 13. Existing vegetation of Madagascar (modified from Humbert and Cours Darné, 1965) and collecting localities yielding *Microgale*. Locality names and taxa collected are listed in table 5.

TABLE 5
Microgale: collecting localities^a

Northern Madagascar^{b,c}

- (1) Antsiranana [Diego-Suarez] (10 m); Lakoton'i Akanga, ?carnivore den (30 m): *cowani* MCZ 45034, *talazaci* (UM unregistered), *longicaudata* MCZ 45035, *parvula* MCZ 45465, *brevicaudata* (UM unregistered)
- (2) Ambohitra [Joffreville, Montagne d'Ambre] (1000 m): *cowani* USNM 341692

Eastern Madagascar

- (3) Mahanara (100 m): *brevicaudata* MNHN 1986-387
- (4) Andapa, 1 day W (1000 m): *talazaci* AMNH 100709
- (5) Hiaraka; Maroantsetra, 40 km NW (700 m): *cowani* MNHN 1981-863, *talazaci* AMNH 100710
- (6) Rantabe (10 m): *talazaci* BMNH 48.92
- (7) Lac Alaotra; Amparafaravola ["Amparafara"] (800 m): *talazaci* BMNH 48.115
- (8) Manohilahy (1000 m): *dobsoni* (cf. Eisenberg and Gould, 1970: 127)
- (9) Didy; Ambohijanahary, 7 km N of Didy (1000 m): *cowani* USNM 328647, *pusilla* USNM 327687
- (10) Ambohitantely (1500 m): *cowani* (cf. Heim de Balzac, 1972: 658)
- (11) Ankeramadinika, 25 km E of Antananarivo (1400 m): *gracilis* (cf. Forsyth Major, 1896c)
- (12) Hantsambaton' Angavo, 69 km E of Antananarivo; Toamasina Road (1000 m): *talazaci* AMNH 294621, *dobsoni* AMNH 294520
- (13) Andasibe [Perinet], Ambodivoangy, Rogez (900 m): *cowani* BMNH 48.88, *talazaci* USNM 341698, *dobsoni* MNHN 1973-532, *pusilla* USNM 328688
- (14) Beforona; Fanovana (500 m): *principula* BMNH 25.8.3.14, *gracilis* MNHN 1961-204
- (15) Moramanga; Andrangoloaka ["Antrangolonka"] (950 m): *cowani* MNHN 1892-1560(?), *talazaci* (cf. Eisenberg and Gould, 1970)
- (16) Manjakatempo ["Monjakatempo"], at 1700–1950 m: *cowani* BMNH 35.1.8.257, *dobsoni* AMNH 100705
- (17) Ankaratra, on slopes cleared of forest (2600 m): *talazaci* MNHN 1973-525
- (18) Antsirabe ["Tsirabe"] (1500 m); Lavajaza: *cowani* BMNH 97.9.1.80, *pusilla* (cf. Forsyth Major, 1986b)
- (19) Antsifotrakely, owl pellets (1600 m): *cowani*, *dobsoni*, *pusilla* (all UM unregistered)
- (20) Ambohimitombo (1200 m): *cowani* BMNH 97.9.1.112, *dobsoni* AMNH 154988, *longicaudata* (BMNH unregistered), *gracilis* BMNH 97.9.1.78
- (21) Ivohimanitra (700 m): *thomasi* BMNH 97.9.1.109
- (22) Nandihizana ["Nandesen"] (1300 m): *dobsoni* BMNH 84.10.20.1
- (23) Ambohimanana ["Ambohimanara," "Ambonimanana"] (1200 m): *cowani* FMNH 1349/5644, *pusilla* BMNH 97.9.1.95
- (24) Ankafina ["Ankafana"] (1600 m): *cowani* BMNH 82.3.1.25, *longicaudata* BMNH 82.3.1.15
- (25) Andraina; Manandroy, 4–11 km E (1000 m): *dobsoni* AMNH 328695
- (26) Ranomafana; Ambatolahy ["Ambitolah"] (500 m): *talazaci* (cf. Eisenberg and Gould, 1970: 127)
- (27) Vinanitelo ["Vinanintelo"] (1300 m): *cowani* BMNH 97.9.1.85, *talazaci* BMNH 97.9.1.107, *pusilla* BMNH 97.9.1.93
- (28) Andringitra; Ibory camp; Anjavidilava; forêt d'Agauria (2600 m): *cowani* MNHN 1972-611, *talazaci* MNHN 1972-612, *dobsoni* MNHN 1972-610, *gracilis* MNHN 1972-606
- (29) Ivohibe, at 1600 m: *cowani* BMNH 48.87, *talazaci* MNHN 1973-524, *dobsoni* MNHN 1973-531
- (30) Vondrozo, 20 km W (500 m): *cowani* MNHN 1932-3470, *talazaci* MNHN 1932-3492, *thomasi* MNHN 1932-3469
- (31) Antampona, Ranomena (100 m): *cowani* MNHN 1967-1631, *dobsoni* MNHN 1967-1629, *principula* MNHN 1981-860
- (32) Midongy Atsimo [Midongy du Sud] (500 m): *principula* BMNH 25.8.3.15

Southern Madagascar

- (33) Andrahomana, owl pellets (30 m): *principula* MCZ 45049
- (34) Lelia, owl pellets (200 m): *pusilla* UM 3102, ?*brevicaudata* UM 3063
- (35) Anjohimpaty, owl pellets (100 m): *pusilla* UM 3033

Western Madagascar

- (36) Andriafavelo (80 m): *brevicaudata* MCZ 45047
 - (37) Marohogo, owl pellets (100 m): *brevicaudata* (unlocated specimen described by Kaudern [1918])
-

^a The specimens referred to by museum accession number (e.g., *cowani* MCZ 45034) are not necessarily the only members of their species found at the localities in question. They are meant to be "voucher" specimens, serving to justify the author's preliminary determination of species' ranges.

- E = lowland rain and moist montane forests of the eastern region
 EC = eastern part of the central highlands (not or only very patchily forested)
 W = dry-mesic forest and forest mosaic of the western region
 N = northernmost Madagascar (undifferentiated mosaics of forest and grassland of western and eastern aspect, cloud forest of Ambohitra)
 S = xerophilous bushland-thickets of southern Madagascar

M. cowani. Known range: E, EC, N. Cowan's shrew tenrec has a wide distribution. It has been collected throughout the central part of the eastern forests, from Andapa to Vondrozo, and populations also exist in the extreme north of Antsiranana province. Recovery of *cowani* specimens from Ambohitantely, Manjakatampo, and the region of Antsirabe implies that populations may persist in forest islands or other favorable places (e.g., riverain bush) throughout the eastern interior. Such records give credibility to Milne-Edwards (1893) statement that the holotype of *M. crassipes* was found in "the environs of Antananarivo," although admittedly there are no other records which could be quoted in support of this contention. Like *M. dobsoni* and *talazaci*, *cowani* appears to be able to flourish at both high and low elevations in eastern Madagascar, under widely differing conditions of temperature and precipitation. There is no evidence that this species presently occupies any part of the western side of the island, implying that it is not well adapted to the most seasonal environments on the island. Very common in collections.

Representative collectors' comments:

"grass by paddy field" (Manjakatampo); "grassy area near rain forest" (Andasibe); "ferns and grass of wooded area" (Andasibe); "wooded area, on bare forest floor, near marsh" (Didy); "deep grass 4 ft [1.3 m] high" (Didy); "high rain forest, 5000 ft [1635 m]" (Ivohibe); "grass tussock, on badly grazed-over land near second growth scrub" (Am-parafaravola).

M. thomasi. Known range: E. This species is known only from the southern part of the eastern rain forest (Ivohimanitra, Ampitambe, Vondrozo). A specimen from Fanovana, cited by Heim de Balsac (1972) as an example of *thomasi*, proves to be *gracilis* (MNHN 1961-204). Very rare in collections.

Representative collectors' comments: "ridge in forest" (Vondrozo).

M. gracilis. Known range: E. Like *thomasi*, *gracilis* is also restricted to eastern forest, but ranges at least as far north as the Beforona-Fanovana area and as high as the slopes of Andringitra. Very rare in collections.

Representative collectors' comments: "forest, in a dead tree trunk, near stream" (Fanovana); "Agauria forest" (Andringitra).

M. parvula. Known range: N? It would be premature to conclude that *M. parvula* is restricted to the extreme north of Madagascar, although this is obviously a possibility. Extremely rare (known from holotype only).

Representative collectors' comments: none; however, species presumably inhabits forested flanks of Ambohitra rather than the drier areas immediately adjacent to or north of Antsiranana town.

M. talazaci. Known range: E, EC, N. This species appears to be distributed throughout eastern Madagascar, including the extremely wet parts of northern Toamasina and southern Antsiranana provinces around the Bay of

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^b Not located:

Amboanara (near Fandriana/Ampitambe?): *longicaudata* BMNH 1939.1620

Ambolimanona (near Vinanitelo?): *cowani* MCZ 12431

Ampitambe ["Ampitabe," "Anysitame," "Amyristan"]: *cowani* BMNH 97.9.1.111, *dobsoni* AMNH 31261, *thomasi* BMNH 97.9.1.108

Ranobe (near Frandriana/Ampitambe?): *cowani* BMNH 97.9.1.81

Sihanaka (forest east of Lac Alaotra, but not more definitely fixed; Tattersall, personal commun.): *longicaudata* BMNH 1939.1620

Indefinitely large localities (e.g., "Betsileo," "NE Madagascar") are omitted from this listing.

^c All elevations above sea level. Except where made part of the locality name (e.g., "Manjakatampo, at 1700–1950 m"), elevations are for reference purposes and do not imply that specimens were recovered at indicated heights. Unless otherwise denoted (e.g., "owl pellets"), specimens were wild caught.

Antongil [Helodrano Antongila]. I have found material of this species in a subfossil faunal collection from Lakoton'i Akanga, a rock shelter near Antsiranana which appears to have been a *Cryptoprocta* den (R. E. Dewar, personal commun.). Whether *talazaci* is still extant in the N is not known. Over a large part of its apparent range it is sympatric with its close relative and probable sister-taxon, *M. dobsoni*. Sympatry occurs not only in the main eastern forest, but also in at least some parts of the eastern margin of the central plateau (e.g., Lac Alaotra area) and at high elevations (e.g., Ankaratra-Manjakatampo area, Andringitra). This is an unexpected finding, in view of Eisenberg and Gould's (1970) argument that *talazaci* is adapted to the equable conditions of the rain forest, and for this reason lacks the specializations for torpor seen in the wider-ranging *dobsoni*. Despite its apparent inability to store fat, *talazaci* is seemingly able to survive in places having fairly severe winters by Malagasy standards. However, on the whole it seems to prefer less exposed and moister conditions than does *dobsoni*, and is no doubt less common than the latter in the EC. Captive observations and some collection records referring to capture in trees suggests arboreal ability, according to Eisenberg and Gould (1970). Common in collections.

Representative collectors' comments: "forest, moss" (Andringitra); "rain forest, fairly open growth, ground cover not dense" (Andasibe); "rain forest in area of fallen trees and considerable ground cover" (Andasibe); "very moist, located in multistratal tropical evergreen forest habitat" (Ambatolahy); "banks of streams" (Andasibe); "mature second growth, multistratal tropical evergreen forest" (Andasibe); "in gaps on slopes where forest has disappeared" (Ankaratra).

M. dobsoni. Known range: E, EC. Judging from museum tickets only, this species is more common in "edge" environments, such as forest-swamp and forest-grassland ecotones, than is *talazaci*. According to the scanty existing records for northern Madagascar, it does not extend into the upper, wetter part of the range of *talazaci*. The most westerly record for *dobsoni* consists of jaws found in fresh owl pellets at Antsifotrakely. There is no forest of any consequence in this region,

although marshy conditions exist around nearby crater lakes (e.g., Lacs Tritriva, Andraikiba)—the kind of habitat in which *dobsoni* seems to flourish elsewhere. Common in collections, but less so than *talazaci*.

Representative collectors' comments: "hillside with considerable ground cover, moss, small trees, bamboo" (Andraina); "in deep woods, 5600 ft [1831 m]" (Manjakatampo); "grass, edge of swamp forest, 6000 ft [1962 m]" (Manjakatampo); "abundant in forested regions" (Manohilahy); "interface between marshy bog and second-growth scrub" (Manandroy); "at 1600 m" (Ivohibe).

M. longicaudata. Known range: E, N. This species has not been recorded outside the confines of the main eastern forest belt, save for one record from the N (*M. prolixicaudata* holotype and paratype, probably collected in forest of Ambohitra). In the main belt, confirmable records do not extend north of Ambohitombo, although the record for the unlocated "forest of Sihanaka" near Lac Alaotra suggests that this species ranges at least as far as the latitude of Andasibe. Arboreal ability inferred on morphological grounds, but not yet confirmed by observations. Rare in collections.

Representative collectors' comments: "forest" (Ankafina, Sihanaka).

M. principula. Known range: E, extreme eastern part of S. This species extends as far north as Beforona, and therefore must broadly overlap with its close relative, *longicaudata*, in the south-central part of the eastern forest belt. *M. longicaudata* has not been found south of Ankafina, but *principula* occurs in rain forest as far south as Midongy Atsimo. It also occurs outside of the existing rain forest (or did until recently) at the famous subfossil site of Andrahomana Cave. Although this locality lies only 50 km west of the southern boundary of the rain forest, there is a remarkably steep precipitation gradient (the "pluviometric fault" of Battistini [1964]) in this region. The area of Andrahomana, in the tail of the gradient, receives less than 600 mm of rain per year and is covered by xerophilous bush. However, Andrahomana itself—which more closely resembles a large sinkhole than a cave—supports a diverse flora of basically eastern aspect on its protected and moist floor (Walker,

1967; personal observ.). There are other, smaller caves and sinkholes in the area of Andrahomana, and it may be that *M. principula* still survives in these unusual microhabitats. Alternatively, if this area were more mesic in the recent past, perhaps forest of eastern type existed in near proximity. This interpretation is supported by the fact that the bones of large extinct lemurs (*Archaeolemur*, *Hadropithecus*, *Megaladapis*) have also been found at Andrahomana (Walker, 1967). The bones of *principula* from this site may or may not be as old as those of the extinct lemurs. Rare in collections.

Representative collectors' comments: "forest" (Midongy Atsimo).

M. pusilla. Known range: E, EC, S. This is another species with a distribution that seems peculiar in view of the present vegetation and climate of Madagascar. It was first recovered as a subfossil at Lavajaza (near Antsirabe, 70 km from the present boundary of the eastern forest), before it was discovered in the wild at Vinanitelo (Forsyth Major, 1896c). Virtually all other records for this species are from the eastern forest belt, although ticket records indicate that most captures took place in grassy areas or forest margins. Two new records, both based on bones recovered from owl pellets, indicate that *M. pusilla* has enjoyed a much wider distribution within recent times. Bones of *pusilla* recovered from fresh pellets at Antsifotrakely establish that populations of *pusilla* can survive in the EC at great distances from the eastern forest. Far more perplexing, however, is the presence of *pusilla* specimens in disintegrated pellets of indeterminate age from Anjohimpaty and Lelia on the Mahafaly Plateau (MacPhee, 1986). The closest "forest" site (Vinanitelo) is more than 400 km away from these caves, and the closest "center" site (Antsifotrakely) is almost twice that far away. How *M. pusilla* reached or managed to survive in this area of marked aridity is simply not known (but see next section). There are no permanent rivers or swamps on the plateau, and the only reliable sources of water are karst pools in the floors of huge, amphitheaterlike sinkholes (avens). It is possible but undemonstrated that these sinkholes offer microenvironments suitable for lesser shrew tenrecs (MacPhee, 1986). Moderately rare in collections.

Representative collectors' comments: "dense grass 4' [1.3 m] high" (Didy); "grass near sedge marsh" (Didy); "forest" (Vinanitelo).

M. brevicaudata. Known range: W, E, N. This species is very rare in museum collections and evidently has never been seen in the wild. This could be circumstantial evidence for fossorial behavior, although there is no evidence on point. *M. brevicaudata* occurs in both very humid evergreen (Mahanara) and dry deciduous forest (Marohogo, Andriafavelo), and appears to be yet another example of a shrew tenrec with wide environmental tolerances. It is worth noting here that Eisenberg and Gould's (1970: 28) assertion that the forested area near Mahajanga "climatically is very similar to the eastern rainforest" is not correct. The Mahajamba peninsula, on which Marohogo and Mahajanga are situated, receives about the same precipitation as does Didy (about 1600 mm/yr)—but only 3 percent of that total falls in the dry season lasting from May through September (Donque, 1975). In floral aspect the Mahajamba peninsula is nearly as xeric as Andriafavelo, which receives less than 1000 mm/year. The short-tailed shrew tenrec's range may extend even farther south: an edentulous mandible from Lelia (MacPhee, 1986), too large to belong to *pusilla*, may instead belong to *brevicaudata*.

I recently found a mandible of this species, this time with teeth, in a faunal collection from Lakoton'i Anja, another Holocene cave site near Antsiranana (R. E. Dewar, personal commun.). This discovery makes the far north of Madagascar as faunally diverse, in terms of the number of species of *Microgale* recently present, as the much better sampled eastern forest around Andasibe (table 5).

Representative collectors' comments: "in forest, by stream banks on broken ground" (Mahanara).

BIOGEOGRAPHY AND ADAPTATION

Four species of shrew tenrecs display disjunct or otherwise "anomalous" distributions: *brevicaudata*, *pusilla*, *cowani*, and *principula*. The first two have populations on opposite sides of the island, separated by hundreds of kilometers of grassland in which

these species apparently do not occur. The others are restricted to the eastern half of the island, but isolated populations of them occur far outside of their core rainforest habitat, without known linking populations in intermediate areas. *Microgale* is not unique among Malagasy mammals in these regards. *Geogale aurita*, for example, occurs in the far northeast (Fenoarivo) as well as in the south and southwest (Eisenberg and Gould, 1970), but apparently never in the center. Several extant primates and rodents (e.g., *Hapalemur simus*, *Avahi laniger*, *Phaner furcifer*, *Nesomys rufus*, *Eliurus myoxinus*) are also found on both sides of the island, although in some cases western and eastern populations are linked by intermediate demes in the far north (cf. *M. brevicaudata*). Several of these species, and a wide variety of others now confined to one or the other side of the island, have been found in Holocene subfossil localities in the center, where they do not, of course, exist today (MacPhee et al., 1985). Evidently, range truncations and subdivisions have affected many forms. What caused these disjunctions? How were island-spanning distributions originally achieved? What is their significance for understanding the historical biogeography and adaptational history of *Microgale*?

At one time it would have been simply assumed that all of the disjunctions in question occurred at about the same time, and that all could be tied to a single efficient agency, the loss of forest habitat during the last 2000 years. This inference derives from the heretofore widely accepted view that Madagascar was covered by dense forest formations throughout the Cenozoic, and that the enormous grasslands of the center are entirely an artifact of such destructive practices as purposeful burning (see, for example, Humbert, 1927; Tattersall, 1982). In this scenario, creation of the grasslands either led to the outright extinction of many taxa, or forced their more fortunate relatives to withdraw to the remnant primary forests along the coastal rim. Recent paleoenvironmental research by Burney (1986, 1987) demonstrates that this view is fundamentally unsound: grasslands have existed in Madagascar for at least the last 35,000 years, and the forests have waxed and waned in response to natural as well as

anthropogenic factors during this period. Thus there is no need to conclude that all disjunctions happened essentially simultaneously and in the very recent past; separation of eastern and western populations of *pusilla* and *brevicaudata*, for example, may have antedated the start of the Pleistocene. Indeed, earlier rather than later disjunction is plausible in the case of *pusilla* in the southwest: this area may have been wet enough for overland colonization several million years ago, but it has probably been dry to very dry for most of the Pleistocene (but see MacPhee, 1986, for alternative scenarios).

Shrew tenrecs probably originally evolved in forest environments, and are no doubt among the most ancient mammalian residents of the eastern side of the island (Eisenberg and Gould, 1970). Range extensions into the center and west could have occurred during relatively benign periods, when temperature, rainfall, and perhaps reduced seasonality would have favored forest expansion (cf. similar inferred cycle of events in northern South America during Quaternary; Eisenberg and Redford, 1979). Conversely, range contraction must have occurred in less favorable times—such as during pleniglacial periods, when much of the center seems to have been covered by the sorts of ericoid bush now found primarily at high elevations (Burney, 1986). But even under the harshest probable environmental regimes, small islands of forest presumably survived away from the coasts, in places where edaphic or other circumstances were favorable—much as they do today. Multiple fluxes in forest coverage may lie behind the patchwork distribution of *cowani* in the center, extreme north, and east, and the subrecent presence of *principula* at Andrahomana.

Finally, one of the broader conclusions that can be rendered from this survey is that, despite their thoroughgoing primitiveness, shrew tenrecs are adaptively resilient. They cannot be simply dismissed as early Tertiary holdovers that were saved from extinction only because they happened to occupy an island refugium. Species that are able to go, in both a historical and distributional sense, from wet forest to arid bushland are not “living fossils” ready for the phylogenetic boneyard, but have clearly devised successful and

continuing adaptive strategies that serve them in a wide variety of environmental contexts (Eisenberg, 1975). While continuing environmental degradation places many Malagasy vertebrates at great risk of extinction, one must wonder whether groups as successful as tenrecs and common shrews should be considered part of the risk group.

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