A new species of shrew tenrec (*Microgale jobihely*) from northern Madagascar

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Abstract

A new species of shrew tenrec in the genus *Microgale* is described from a series of 12 specimens taken on the south-western slopes of the Tsaratanana Massif in northern Madagascar and is named *Microgale jobihely*. This new species is distinguished from other named members of this endemic genus by a variety of mensural and discrete morphological characters. Phylogenetic analysis of the mitochondrial ND2 gene supports its recognition as a distinct species and suggests a sister relationship with the much more widespread *Microgale cowani*. *Microgale jobihely* appears to be the only member of this genus that is a very localized endemic, and a biogeographic scenario is presented to explain this observation. It is currently known from a small area of forest, outside of the protected areas system, that is faced with considerable anthropogenic pressure.

Introduction

Over the past two decades, the Tenrecidae, a family of small mammals largely endemic to Madagascar, has been the subject of a broad range of studies focusing on their physiology, ecology, reproductive anatomy, phylogeny and taxonomy (e.g. Racey & Stephenson, 1996; Jenkins, 2003; Olson & Goodman, 2003; Bedford, 2004; Bedford, Mock & Goodman, 2004; Olson, Goodman & Yoder, 2004). This group, representing one of the most remarkable adaptive radiations found in living mammals, includes the genus *Microgale* or shrew tenrecs. Members of this genus, which are placed in the subfamily Oryzorictinae, are broadly distributed in natural forest formations. As is currently understood, the genus includes 21 species (Jenkins, 2003; Goodman & Soarimalala, 2004; Olson *et al*., 2004), and certain sites in the montane portions of the island's humid forests can have up to 11 species occurring in sympatry (Goodman *et al*., 2000).

Since 1988, eight new species of *Microgale* have been described (one of which has been subsequently considered invalid) and three have been resurrected from synonymy (details summarized in Jenkins, 2003; Goodman & Soarimalala, 2004; Olson *et al*., 2004). These discoveries have been based largely on specimens obtained during biological inventories of poorly known areas of forest, including elevational transects of the major mountain systems of the east. The utilization of pitfall traps, with associated plastic drift fences, during these surveys has considerably augmented the capture rates of shrew tenrecs and has resulted in a substantial growth of information on this reclusive group of animals. The continued exploration of the montane humid forest regions of the island, a zone *c*. 1300 km in length spanning 12° in latitude, has revealed that most of these recently described taxa have relatively broad latitudinal distributions in this forest formation, although many appear to be altitudinally restricted. One of the last vast zoologically unexplored areas of montane forest on the island is the Tsaratanana Massif in the north. This mountain system, which is the highest on the island and rises to 2876 m, has been the subject of recent detailed vertebrate inventories directed by C. J. R. During the course of these explorations, a species of *Microgale* was captured on the south-western slope of this massif, which is sufficiently distinct from all other recognized members of the genus to warrant recognition as a new species.

Collections

Although the Tsaratanana Massif (Fig. 1) is one of the last continuous tracts of humid forest on Madagascar, very little has been published on its small mammal fauna (MacPhee, 1987; Carleton & Schmidt, 1990). In November 1966, a small collection of rodents and tenrecs was made on the slopes of the mountain (Albignac, 1970; Andriamialisoa & Langrand, 2003). During the course of three field seasons between 2001 and 2003, faunal inventories by field biologists from the American Museum of Natural History and Département de
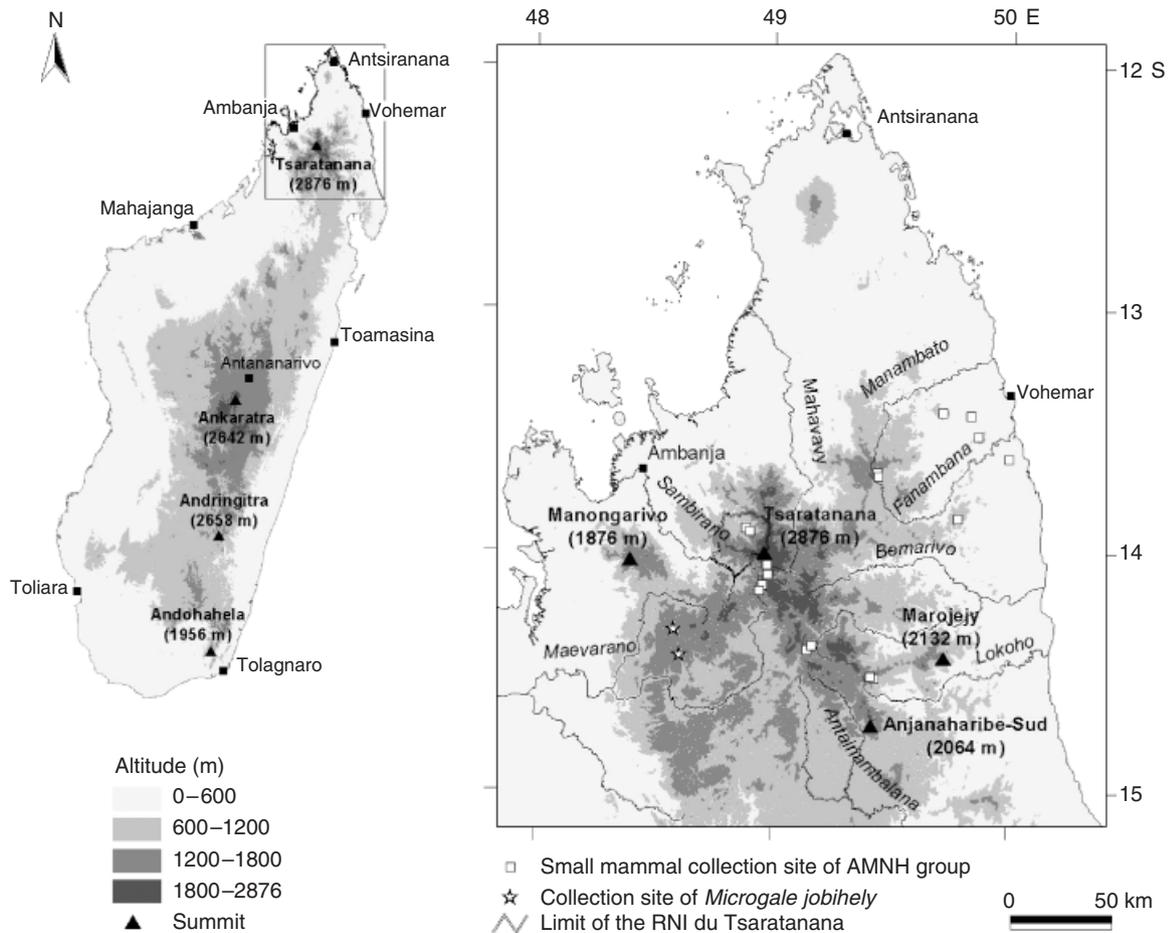
Figure 1 Map of Madagascar showing some topographic features of the highland areas of the island and the principal peaks. The inset is a map of the Tsaratanana Massif, river systems originating from this mountain and surrounding areas. The sites surveyed for small mammals between 2001 and 2003 by C. P. M. and C. J. R. regions are indicated, which include the two sites where the new taxon described herein was captured.

Biologie Animale at the Université d'Antananarivo were conducted on the Tsaratanana Massif and surrounding areas. In total, 18 different sites were visited and sampled (Fig. 1). The principal objectives of these surveys were both herpetological and mammalogical, and one of the field researchers (C. P. M.) concentrated her efforts on terrestrial small mammals (shrews, tenrecs and rodents). These collections, which are housed in the two institutions named above, are currently under study by the field collector, and a review of this material will be published elsewhere. Here we describe a new taxon from this collection.

Methods

Field methods

All field techniques (e.g. pitfall trapping protocols, field measurements, preparation of specimens) follow those described by Raxworthy & Nussbaum (1994) and Goodman & Jenkins (1998, 2000).

Morphological analyses

To help resolve the taxonomic status of the 12 specimens of the unknown species of *Microgale*, we have consulted material housed in several natural history museums, which include AMNH – American Museum of Natural History, New York; BMNH – The Natural History Museum, London (formerly British Museum of Natural History); FMNH – Field Museum of Natural History, Chicago; MNHN – Muséum national d'Histoire naturelle, Paris; PBZT – Parc Botanique et Zoologique de Tsimbazaza, Antananarivo; UADBA – Université d'Antananarivo, Département de Biologie Animale, Antananarivo; UMMZ – The University of Michigan Museum of Zoology, Ann Arbor; and USNM – The National Museum of Natural History (formerly The United States National Museum), Washington, DC.

Five standard external measurements (in millimetres) were taken from specimens before preparation and included total length, head and body length, tail length, hind foot length (not including claw) and ear length. All the material reported on herein from Tsaratanana was measured for

these five external variables by C. P. M. and much of the balance by S. M. G. Mass was taken with the use of a spring balance and recorded in grams. Unless otherwise specified, measurements and weights are reported for dental adults only (defined by the presence of a fully erupted permanent dentition). Tooth abbreviations include: I, incisor; d, deciduous; C, canine; P, premolar; M, molar. Uppercase abbreviations are used for upper teeth and lowercase abbreviations for lower teeth. Cranial and dental nomenclature follows Hershkovitz (1977) and MacPhee (1987).

A series of 17 craniodental measurements was recorded to the nearest 0.01 mm by L. E. O. using digital calipers. These measurements include: condylopremaxillary length (CPM) – posteriormost (caudal) surface of occipital condyle to anteriormost (rostral) surface of the premaxilla; condylo-I2 length (CI2) – posteriormost (caudal) surface of occipital condyle to anteriormost (rostral) surface of I2; condylo-C1 length (CC) – posteriormost (caudal) surface of occipital condyle to anteriormost (rostral) surface of C1; condylo-P3 length (CP3) – posteriormost (caudal) surface of occipital condyle to anteriormost (rostral) surface of P3; condylo-entoglenoid length (CEG) – posteriormost (caudal) surface of occipital condyle to anteriormost (rostral) surface of the entoglenoid process of the squamosal; premaxillary to zygomatic length (PZ) – rostral surface of premaxilla to caudal surface of zygomatic process of maxilla; paroccipital process to entoglenoid length (PEG) – rostral surface of entoglenoid process of squamosal to caudal surface of paroccipital process of basioccipital; braincase breadth (BB) – greatest cranial breadth, as measured across squamosals; greatest breadth across M3 (M3B) – greatest breadth across M3, as measured from lateral surface of distostyle; greatest breadth across M2 (M2B) – greatest breadth across M2, as measured from lateral surface of distostyle; greatest posterior width across M1 (M1WP) – greatest breadth across M1 as measured from lateral surface of distostyle; greatest anterior width across M1 (M1WA) – greatest breadth across M1 as measured from lateral surface of anterior ectostyle and/or mesiostyle; greatest width across P4 (P4W) – greatest breadth across P4; greatest width across P3 (P3W) – greatest breadth across P3; upper toothrow length (UTR) – rostral surface of I1 to caudal surface of M3; height of mandible (MH) – greatest distance between coronoid and angular processes of mandible; and mandibular condyle width (MCW) – greatest breadth across buccal and labial surfaces of mandibular condyle. With the exception of condylo-C1 length, these represent a subset of the 21 craniodental measurements defined and used in Olson *et al.* (2004).

Only dental adult specimens were measured. As in Olson *et al.* (2004), linear measurements were taken between explicitly defined landmarks without reference to any particular axis (e.g. the midline of the skull), thereby facilitating repeatability. Univariate and bivariate analyses were conducted using Microsoft Excel and StatView version 4.5. Principal components were extracted from a variance–covariance matrix using log-transformed (base 10) measurements with the program JMP version 3.1.6. Given that all 12 specimens of the new species described herein are readily distinguishable from most other similarly sized species of shrew tenrecs (see below), we limited our sample of specimens included in morphometric analyses to representatives of *Microgale taiva* ($n = 37$) and *Microgale cowani* ($n = 100$) from throughout much of their respective known ranges. Our final sample included multiple representatives of all three species from the Tsaratanana region. Voucher information for all specimens is provided in Supplementary Material Appendix S1.

Molecular analysis

In order to further explore the taxonomic status of this presumed new species, we conducted phylogenetic analysis of the 5′ half of the mitochondrial NADH dehydrogenase subunit 2 gene (ND2). This gene has proven useful in elucidating species boundaries among other morphologically similar species of shrew tenrecs (Olson *et al.*, 2004). In this current study, we sequenced seven of the 12 specimens discussed above for which fresh tissues were available (including the holotype). As with the morphometric analyses, we limited our sample of sequenced specimens to available representatives of *M. cowani* (20 specimens representing 18 localities) and *M. taiva* (11 specimens from eight localities; see Fig. 2). We also included representatives of the major mitochondrial haplotype clades reported by Olson *et al.* (2004) for *M. longicaudata*, *M. principula*, *M. pusilla* and the recently re-elevated species *M. majori*. A single representative of *Oryzorictes hova* was used as an outgroup for rooting purposes. Voucher information for sequenced specimens is included in Supplementary Material Appendix S1.

Extraction, amplification and sequencing of all new ND2 sequences reported here followed Olson *et al.* (2004). Briefly, genomic DNA was extracted from frozen or buffered tissue using the PureGene kit (Gentra Systems Inc., Minneapolis, MN, USA). Initial amplifications were performed using the forward and reverse primers Met-1 and Trp-2, respectively, which amplify the entire ND2 gene and portions of the flanking tRNA genes. Aliquots of the initial amplification reaction were electrophoresed and visualized on 1.5% TBE agarose gels, and bands of the appropriate size were excised and melted in $200\,\mu$L sdH$_2$O. Resuspended PCR products (1–$3\,\mu$L) were used as template DNA in a second, nested amplification with Met-1 and an internal reverse primer (LOR2). Reamplification products were purified using either GeneClean (Bio101) or Exo-SAP It (USB Corp., Cleveland, OH, USA) kits following the manufacturer's instructions. Purified reamplification products (1–$5\,\mu$L) were cycle sequenced for both strands using BigDye Terminator 3.0 and 3.1 (Perkin-Elmer, Boston, MA, USA) according to the manufacturer's directions. Sequencing reactions were purified using ethanol/sodium acetate precipitation and electrophoresed on an ABI 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). Resulting output was imported and edited using Sequencher 4.2.2 (Genecodes, Ann Arbor, MI, USA). All new sequences have been deposited in GenBank (accession numbers DQ324740–DQ324778).
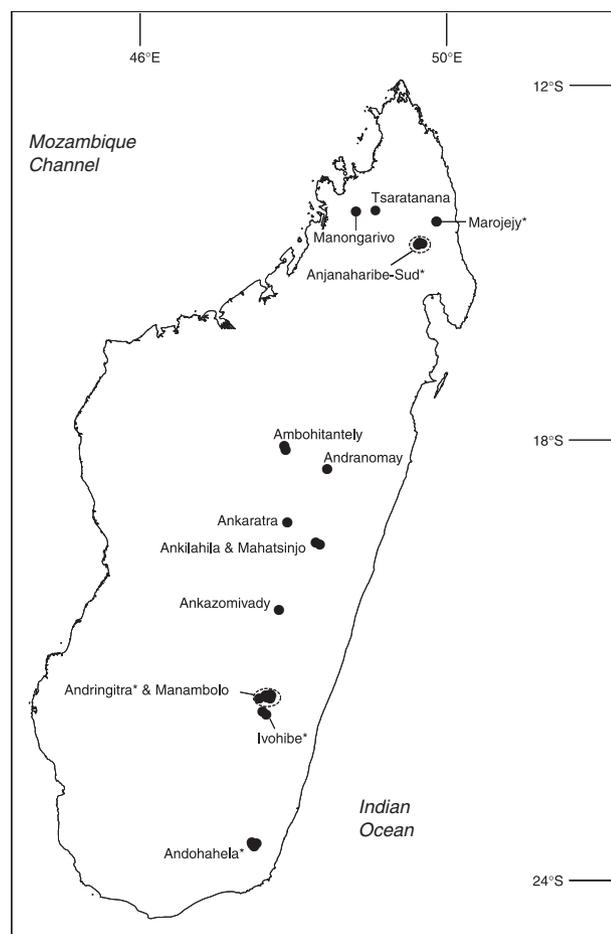
Figure 2 Collecting localities for all *Microgale jobihely, M. cowani* and *M. taiva* sequenced for the ND2 gene in this study. Asterisks indicate localities from which specimens from multiple elevations of one or more species were included (see Supplementary Material Appendix S1 for detailed locality and voucher information).

Inspection of the resulting 523 nucleotides of the ND2 gene with reference to the translated amino acid sequence was conducted using MacClade 4.0 (Maddison & Maddison, 2000) and revealed no evidence of insertions or deletions. The complete, annotated alignment has been submitted to TreeBASE (www.treebase.org). Phylogenetic analysis was performed under the maximum parsimony (MP) and maximum likelihood (ML) criteria using PAUP* 4.0 (Swofford, 2002). Heuristic MP tree searches were conducted using stepwise addition (100 random addition sequences) with the tree bisection-reconnection (TBR) branch swapping algorithm. All characters were treated as equally weighted and unordered. Nodal support was estimated by bootstrap re-sampling using 1000 pseudoreplicates, TBR branch swapping and 10 replicates per pseudoreplicate. For ML analyses, a best-fit model of nucleotide substitution was estimated using the program Modeltest 3.6 (Posada & Crandall, 1998) under the Akaike Information Criterion. The resulting model (GTR+I+G; additional parameters are included in the matrix submitted to TreeBASE) was specified in heuristic tree searches (20 random addition sequences, TBR branch swapping) and bootstrap resampling (1000 pseudoreplicates, NNI branch swapping and one random addition replicate per pseudoreplicate).

Description of the new species

Microgale jobihely sp. nov.

Holotype

AMNH 274984, adult female, collected on 14 March 2003 by Claudette Patricia Maminirina, field number RAX (Christopher J. Raxworthy) 6235. The specimen was preserved in formalhyde and subsequently transferred to ethanol. The skull was removed and cleaned; it is in fine condition. Muscle samples were frozen in liquid nitrogen and also preserved in lysis buffer. The fluid-preserved specimen has a thoracic incision and the skin surrounding the head is partially torn associated with the extraction of the cranium. The dental age of the specimen is adult (*sensu* MacPhee, 1987), with all of the permanent teeth in place and the basisphenoid–basioccipital sutures completely fused. External measurements are total length 121 mm, head and body length 62 mm, tail length 45 mm, hind foot length (without claw) 12 mm and ear length 13 mm. The animal weighed 10.0 g (Table 1).

Type locality

Madagascar: Province de Mahajanga (Massif de Tsaratanana), forêt du lac Matsaborimena, 4 km N de Bemanevika village, 14°19.859′S, 48°35.240′E, 1600–1680 m.

Paratypes

AMNH 274983 (RAX 6486), adult female, collected 22 March 2003, full skeleton with associated skull; AMNH 274981 (RAX 6266), adult male, collected 17 March 2003, fluid specimen with extracted and cleaned skull, and preserved tissues; AMNH 274987 (RAX 6366), male, dental eruption pattern fits MacPhee's (1987) stage 3–4, collected 18 March 2003, fluid specimen with extracted and cleaned skull, and preserved tissues; AMNH 274985 (RAX 6278), female, dental eruption pattern fits MacPhee's (1987) stage 3–4, collected 17 March 2003, fluid specimen with extracted and cleaned skull, and preserved tissues; AMNH 274982 (RAX 6270), female, dental eruption pattern fits MacPhee's (1987) stage 2–3, 17 March 2003, fluid specimen with extracted and cleaned skull, and preserved tissues; AMNH 274989 (RAX 6436), male, dental eruption pattern fits MacPhee's (1987) stage 2–3, 20 March 2003, fluid specimen with extracted and cleaned skull; AMNH 274986 (RAX 6282), female, dental eruption pattern fits MacPhee's (1987) stage 1, 17 March 2003, fluid specimen with extracted and cleaned skull, and preserved tissues; AMNH 274988 (RAX

Table 1 External measurements (in mm) and weight (in g) of *Microgale jobihely* and other species of small to medium *Microgale*

Species	Total length	Head–body length	Tail length	Hind foot length	Ear length	Weight
Microgale jobihely						
(Holotype AMNH 274984)	121	62	45	12	13	10.0
Adult[a]	121.0 ± 0.00	56.7 ± 4.73	52.3 ± 6.43	12.7 ± 0.58	13.7 ± 0.58	9.0 ± 1.00
	121–121, *n*=3	53–62, *n*=3	45–57, *n*=3	12–13, *n*=3	13–14, *n*=3	8.0–10.0, *n*=3
Stage 3/4	114–123, *n*=2	54–57, *n*=2	51–55, *n*=2	13–13, *n*=2	13–13, *n*=2	7.0–9.0, *n*=2
Stage 2/3	116–117, *n*=2	52–54, *n*=2	51–53, *n*=2	13–13, *n*=2	12–14, *n*=2	7.0–9.0, *n*=2
Stage 1	113–114, *n*=2	42–55, *n*=2	51–55, *n*=2	12–14, *n*=2	12–12, *n*=2	5.3–8.0, *n*=2
Subadults[b]	116.2 ± 3.66	52.3 ± 5.32	52.7 ± 1.97	13.0 ± 0.63	12.7 ± 0.82	7.6 ± 1.42
	113–123, *n*=6	42–57, *n*=6	51–55, *n*=6	12–14, *n*=6	12–14, *n*=6	5.3–9.0, *n*=6
Microgale cowani[c]						
Adult	141.2 ± 5.50	68.6 ± 5.18	65.8 ± 3.52	16.1 ± 1.10	15.1 ± 0.91	13.8 ± 0.87
	130–151, *n*=18	60–78, *n*=25	60–72, *n*=19	12–17, *n*=19	13–17, *n*=19	12.0–15.0, *n*=19
Subadult	139.4 ± 11.8	65.9 ± 6.86	64.4 ± 3.50	15.8 ± 1.42	14.5 ± 0.67	12.2 ± 1.30
	126–151, *n*=12	52–77, *n*=17	61–70, *n*=11	12–18, *n*=13	14–16, *n*=12	11.0–15.0, *n*=13
Microgale taiva[c]						
Adult	153.4 ± 5.83	67.1 ± 5.19	77.3 ± 5.00	16.4 ± 0.50	15.3 ± 1.19	11.8 ± 1.89
	142–163, *n*=21	58–76, *n*=21	70–88, *n*=21	16–17, *n*=22	14–19, *n*=21	9.0–16.0, *n*=21
Subadult	148.9 ± 7.56	66.4 ± 5.55	76.4 ± 5.18	16.2 ± 1.04	14.7 ± 1.06	9.9 ± 1.59
	140–166, *n*=21	56–78, *n*=21	66–85, *n*=21	13–17, *n*=20	13–17, *n*=21	7.8–15.0, *n*=20
Microgale pusilla						
Adult	127.4 ± 6.16	51.4 ± 2.70	69.9 ± 4.18	11.4 ± 0.53	11.4 ± 0.98	3.5 ± 0.40
	119–136, *n*=7	47–56, *n*=7	65–77, *n*=7	11–12, *n*=7	10–13, *n*=7	3.1–4.2, *n*=7
Microgale parvula						
Adult	117.7 ± 5.83	57.2 ± 4.17	58.4 ± 4.39	9.6 ± 0.50	8.6 ± 0.45	3.2 ± 0.56
	110–128, *n*=11	51–64, *n*=11	53–66, *n*=11	9–10, *n*=11	8–9, *n*=11	2.1–4.1, *n*=11
Microgale brevicaudata						
Adult	115.7 ± 6.68	68.9 ± 0.35	41.9 ± 5.92	12.4 ± 0.96	13.7 ± 1.32	8.9 ± 1.59
	107–129, *n*=13	63–74, *n*=13	35–41, *n*=13	11–14, *n*=13	12–16, *n*=13	6.3–12, *n*=11
Microgale fotsifotsy						
Adult	159.3 ± 6.34	70.8 ± 6.71	85.8 ± 3.98	15.9 ± 0.90	16.1 ± 0.67	9.4 ± 2.97
	150–169, *n*=11	64–85, *n*=10	80–93, *n*=12	15–17, *n*=12	15–17, *n*=12	6.8–15, *n*=10

Measurements presented as mean ± SD (minimum–maximum, *n*). For samples of two or fewer specimens, only the measurements are presented.
[a]Includes holotype.
[b]Includes all non-adult age classes.
[c]Includes specimens collected by C. P. M. in the general Tsaratanana region.

6431), male, dental eruption pattern fits MacPhee's (1987) stage 1, 19 March 2003, fluid specimen with extracted and cleaned skull, and preserved tissues; AMNH 274992 (RAX 6489), female, undetermined age, 22 March 2003, fluid-preserved specimen; AMNH 274990 (RAX 6487), male, undetermined age, 22 March 2003, fluid-preserved specimen; and AMNH 274991 (RAX 6488), male, undetermined age, 22 March 2003, fluid-preserved specimen. All of the paratype specimens were collected at Madagascar: Province de Mahajanga (Massif de Tsaratanana), forêt d'Analapaki-la, 4.5 km NNO d'Amberivery, 14°26.233′S, 48°36.696′E, 1420–1480 m.

Diagnosis

A small species of the medium-sized members of the genus *Microgale*. In adults (*n* = 3 unless otherwise noted), the average total length is 121.0 mm, tail length is 52.3 mm, hind foot length is 12.7 mm and condyloincisive length ranges

from 17.3 to 17.8 (*n* = 2). The average ear length of 13.7 mm is short for a shrew tenrec of this size.

Description

A small medium-sized *Microgale* having a tail notably shorter than the head and body (Table 1). The dorsal fur is dense and soft. Pelage from the level of the ears to the base of the tail (including the flanks) is a mixture of completely black or dark reddish-brown hairs, or black-tipped dark reddish-brown hair giving an agouti appearance. Individual guard hairs along the dorsum measure 5–6 mm and the guard hairs are dark grey. Ventral pelage has a finer texture than dorsal pelage and is notably lighter in coloration; the agouti fur has a mixed tannish-brown and greyish-brown coloration, with distinctly medium grey bases. The distinction between the ventral and dorsal colour pattern is pronounced, but these grade into each other laterally instead of forming a well-demarcated line.

Upper surfaces of fore feet and hind feet are covered with dark brown fur, which on the hind feet extends slightly beyond the claws as ungual tufts. The mystacial and rhinarial vibrissae are generally black and measure *c.* 15 and 5 mm, respectively. Pinnae are short (13–14 mm) for a *Microgale* of this body size, dark brown in colour, and covered internally and externally with fine dark brown or black hairs. All individuals of this species available for study were conserved in formaldehyde and subsequently transferred to alcohol. Our colour assessments of these animals were made from air-dried specimens within 2 years of their collection and there is no evidence of any pelage fading.

The hind foot is relatively short (average 12.7 mm) for a *Microgale* of this size, particularly with respect to *M. cowani* (average 16.1 mm) and *M. taiva* (average 16.4 mm; Table 1). The first digit of the hind foot is less than one-third the length of the second digit. The second to fourth digits are largely equal in length and the fifth digit is about two-thirds the length of the fourth. On both the forelimbs and hindlimbs there are four interdigital pads located at the base of digits 1 and 5, in intermediate positions between the base of digits 2 and 3 and digits 3 and 4, and notably reduced as distal hypothenar and proximal thenar pads.

In dentally adult individuals, the tail skin is dark brown dorsally and dark tannish-brown ventrally. There is not a well-demarcated lateral line separating these two surfaces, but rather the two colours diffuse into one another. On closer examination under a binocular scope of the tail, there is little difference in skin coloration between the two surfaces, but rather the dorsal surface has fine black fur and the ventral surface reddish-grey fur. In subadults the tail is in general dark brownish-black with little differentiation between the dorsal and ventral surfaces.

The skull is relatively short as compared with *Microgale* species of comparable body size (Table 2), slightly flattened dorsolaterally, with a slightly constricted interorbital region (Fig. 3). In dorsal view the rostrum is moderately short and narrow and nasals elongated anteriorly as parallel-sided structures. The anterior portion of the frontals consists of two slightly concave plates divided at the mid-dorsal line and forming a sulcus, whereas the posterior portion is slightly domed. The braincase has a slightly bulbous parietal and interparietal, a slightly rounded supraoccipital and occipital, and a weakly developed occipital crest. Dentally the holotype is adult with all of the teeth, including the canines, representing the adult dentition (MacPhee, 1987). The upper tooth rows from I1 to P2 slightly converge anteriorly, although the portions between I2 and C are largely in parallel, as are the lingual margins of P3 to M3. Palatal foramina are present. Pterygoids are short and broad, and the pterygoid processes are wing shaped and curved mid-ventrally. The glenoid fossa is shallow and narrowly curved. The mandibles are slender, the coronoid processes are pointed dorsally, the superior mandibular notch is arc-shaped and the angular processes are short and narrow, with no marked expansion of the dorsal surface.

Table 2 Cranial and mixed cranial–dental measurements (in mm) of *Microgale jobihely* and other similarly sized species of *Microgale*

Species	BB	CIL	CEG	CI2	CP3	CPM	MH	PZ	ZYGO
Microgale jobihely (Holotype AMNH 274984)	9.2	17.3	6.8	19.0	15.1	20.0	5.6	10.7	8.0
Adult	9.2–9.2, *n*=2	17.3–17.8, *n*=2	6.8–6.9, *n*=2	19.0–19.5, *n*=2	15.1–15.5 *n*=2	20.0–20.6, *n*=2	5.5–5.8, *n*=3	10.4–10.8, *n*=3	7.3–8.0, *n*=3
Microgale cowani[a] Adult	10.4±0.17 9.9–10.7, *n*=24	20.0±0.63 18.9–21.2, *n*=25	7.5±0.21 7.1–7.8, *n*=25	21.9±0.73 20.7–23.3, *n*=25	17.3±0.61 16.0–18.4, *n*=25	22.9±0.79 21.7–24.5, *n*=25	6.0±0.32 5.5–6.5, *n*=24	12.5±0.42 11.9–13.4, *n*=25	9.2±0.38 8.4–9.7, *n*=17
Microgale taiva[a] Adult	10.2±0.21 9.7–10.7, *n*=21	20.3±0.51 19.3–21.2, *n*=21	7.6±0.20 7.2–8.1, *n*=21	22.2±0.55 21.1–23.1, *n*=21	17.5±0.48 16.4–18.2, *n*=21	23.2±0.59 22.0–24.2, *n*=21	6.1±0.19 5.7–6.5, *n*=20	12.4±0.39 11.6–13.4, *n*=21	8.7±0.43 8.2–9.8, *n*=15

Measurements presented as mean±SD (minimum–maximum, *n*). For samples of two or fewer specimens, only the measurements are presented.
[a]Includes specimens collected by C. P. M. in the general Tsaratanana region.
BB, braincase breadth; CIL, condyle incisor length; CEG, condylo-entoglenoid length; CI2, condylo-I2 length; CP3, condylo-P3 length; CPM, condylopremaxillary length; MH, height of mandible; PZ, premaxillary to zygomatic length.

Figure 3 Views of the cranium and mandible of the holotype of *Microgale jobihely* (AMNH 274984): upper left, dorsal view; upper right, ventral view; lower centre, lateral view of cranium and mandible. (Photograph taken by J. Weinstein, FMNH image number Z94432_05d.)

Habitat

The holotype was collected in montane forest habitat near Matsaborimena Lake. The largest trees at the site are about 15 m tall, the canopy is partially open, the sub-canopy contains few lianas, sparse herbaceous ground cover, and on slopes and in valleys a considerable number of downed and rotten tree trunks. The site is relatively close to the village of Bemanevika and is partially disturbed, with numerous trails associated with different minor types of forest exploitation, including cattle grazing. The single individual of *M. jobihely* collected at this site was captured in a pitfall trap placed in a valley bottom close to Matsaborimena Lake.

The second locality this species is known from is the Analapakila Forest, which shows considerable signs of anthropogenic disturbance. At this site the canopy is open, the remaining trees are notably separated from one another, the sub-canopy has a dense growth of small lianas, and the forest floor has considerable fallen and decomposing tree trunks and branches. The site is located next to an extensive marsh, which has been partially converted to rice paddy. Within the forest there are numerous signs of human disturbance, including cattle grazing, wood cutting, hunting of forest animals and coffee cultivation. This second site is 12 km linear distance from the holotype locality.

Etymology

The species epithet is derived from northern dialects of Malagasy, with *joby* meaning dark or black and *hely* small. When configured as a compound word in Malagasy the '*y*' in *joby* becomes an '*i*'. The combination of these two words alludes to the observation that this species is a small and dark animal.

Distribution

Microgale jobihely is known only from two sites on the south-western slopes of the Tsaratanana Massif and across an elevational gradient from 1420 to 1680 m (Fig. 1).

Adult dentition

The dentition is not markedly robust (Fig. 3). There are gaps between I1 and I2, C and P1, and no prominent gap in the lower dentition. I1 is moderate in size, bicuspid (bidentate) and with a well-developed distostyle; I2 is about one-half the crown height of I1, the tricuspid (tridentate) shows approximately the same level of development between the anterior accessory cusp and the distostyle; unicuspid I3 is three-quarters the crown height of I2 and reaches considerably beyond the level of the distostyle of I2; C is relatively robust with crown height reaching that of I2, with a rudimentary accessory anterior cusp and small distostyle; P2 is large, three-quarters the crown height of C, and with moderately well-developed anterior and posterior cuspids; P3 is large, slightly greater in crown height than C, with a slightly elongated paracone, a lingual ledge with a well-developed protocone, and mesiostyle, anterior ectostyle and distostyle present; P4 is large, slightly longer in crown length than M1–M3, with an elongated paracone, a lingual ledge with a protocone similarly developed to P3, but more robust than in M1–M3, anterior ectostyle less than one-half the length as paracone, and mesiostyle and distostyle present; M1 and M2 large, mesiostyle, anterior ectostyle and distostyle present, and the centro-buccal cleft is more prominent in M2 than in M1; M3 is reduced in size and compressed anterioposteriorly, but retains a developed lingual ledge with a protocone and mesiostyle.

The first lower incisor (i1) is large, slightly shorter in crown length to i2, the hypoconule is well developed; i2 is large, the hypoconule is well developed; i3 is small, about three-quarters the crown length of the lower canine and with a slightly developed hypoconule; c is large, hypoconulid present, no paraconid; p2 (double rooted) is moderate in size, slightly shorter in crown height to p3, and moderately

developed paraconid and hypoconulid; p3 is moderate in size, moderately developed paraconid and hypoconulid; p4 is large, equal in crown height (formed by a prominent protoconid) to m1, paraconid and hypoconulid present, and slightly developed anterobuccal cingulum; m1 and m2 are large, m1 slightly subequal in crown height to m2, both with well-developed protoconid, paraconid and hypoconulid, and slightly elongated anterobuccal cingulum; m3 is large and equal to m2 in crown height, and with a well-developed protoconid, paraconid and prominent hypoconulid, and slightly elongated anterobuccal cingulum.

Deciduous dentition

Certain portions of the deciduous anterior teeth are reduced in size as compared with the same teeth in the permanent dentition; most notable in this regard are dI3, dC, di3 and dc. dI1 is bicuspid, with the principal cusp being slender and the distostyle notably reduced in size. The shape and morphology of dI2 is similar to I2. In dI3 there is a slightly developed distostyle and in dC the mesiostyle and distostyle are more developed than in the homologous permanent dentition. dI3 is approximately one-half the crown height of dC, whereas the latter is about three-quarters the length of dP2. In dP2 the anterior and posterior cuspids are present, but not well developed. dP3 is large, considerably greater in crown height than C, with a notably elongated paracone, a lingual ledge with a protocone, and the mesiostyle is distinctly hook shaped. dP4 is moderately large, equal in crown height to dP3 and shorter than M1, with an elongated paracone, although less than in dP3, and the anterior ectostyle is smaller than in P3.

The first deciduous lower incisor (di1) is subequal in length to the second deciduous lower incisor (di2). In di1 and di1 the hypoconule is more developed than in the permanent tooth counterparts, particularly di1, where it is recurved and hook shaped. The third deciduous lower incisor (di3) is notably small, with a peg-like shape and reduced cusp surfaces. The dc is notably smaller than c, although it has a paraconid. The first lower deciduous premolar (dp2) is double rooted and notably smaller than dc and the second lower deciduous premolar (dp3). The general tooth structure of dp2, dp3 and dp4 is similar to the permanent equivalents, but paraconids and hypoconulids are more hook shaped, particularly in dp2 and dp3; this difference might be related to wear in the adult individuals available for comparison.

Comparisons

Microgale jobihely is readily distinguished from an assortment of medium to small-sized species of shrew tenrecs known to occur in humid forest formations based on external measurements and pelage coloration (Table 1). It is notably larger than *M. pusilla* and *M. parvula* in hind foot and ear lengths. Furthermore, *M. parvula* has a dark brown dorsum and a dark greyish-brown ventrum, and *M. pusilla*

has a distinctly light to medium brown dorsum and a lighter coloured ventrum. *Microgale brevicaudata* is more stockily built than *M. jobihely* and has a proportionately shorter tail, medium brown dorsum and dull greyish-brown ventrum. *Microgale jobihely* is distinctly smaller in all external measurements than *M. fotsifotsy*, which has a white-tipped tail, upper surfaces of the feet clothed with short silver-white fur and a greyish dorsal pelage coloration. Several other small shrew tenrecs (*M. principula*, *M. longicaudata* and *M. majori*) are all readily distinguished from *M. jobihely*, with tails two or nearly three times the head–body length; the measurements of these species are not presented in Table 1 (see Olson *et al.*, 2004).

The pelage coloration of *M. jobihely* closely resembles that of *M. cowani* and *M. taiva*, but these latter two species are notably larger in external measurements. For example, based on adult specimens taken in the Tsaratanana region by C. P. M., there is no overlap in the total length measurement between *M. jobihely* and these other two taxa: in *M. jobihely* the mean measurement is 121.0 mm (range 121–121 mm, $n = 3$), in *M. cowani* 141.2 mm (range 130–151 mm, $n = 18$) and in *M. taiva* 153.4 mm (142–163 mm, $n = 21$). On the Andringitra Massif in central eastern Madagascar, the ratio of tail length to condyloincisive length readily separated *M. taiva* and *M. cowani* (Jenkins, Goodman & Raxworthy, 1996). The same is true for specimens from the Tsaratanana region (here the ratio of tail length to condylo-canine length), where the mean of this ratio for *M. cowani* is 3.3 ± 0.22 (2.8–3.6, $n = 24$) and for *M. taiva* 4.0 ± 0.19 (3.7–4.3, $n = 19$), whereas the range for *M. jobihely* is 2.6–3.2 ($n = 2$). Even though there is overlap in this ratio between *M. jobihely* and *M. cowani*, these two species can be easily differentiated by a wide variety of external, cranial and dental characters (Tables 1–3; Fig. 4). In adults of *M. taiva* the tail coloration is a uniform black on the dorsal and ventral surfaces, whereas in *M. jobihely* and *M. cowani* it is bicolored, with the dorsal surface being black and the ventral surface a dark tannish-brown.

Certain dental characters clearly separate *M. jobihely* and *M. cowani*. In adult specimens, for example, I3 of *M. jobihely* is distinctly peg shaped, as compared with *M. cowani*, and lacks the distostyle found in the latter species. C in *M. jobihely* lacks a mesiostyle and a well-formed distostyle, whereas P2 has reduced mesiostyle and distostyle – in *M. cowani* these styles are prominent on C and P2. The gap between C and P1 is proportionately and absolutely greater in *M. cowani* than in *M. jobihely*.

Both *M. taiva* and *M. cowani* have notably broad distributions across the humid forest formations of the island. The holotype of *M. taiva* was taken in the Ankeramadinka forest, about 1 day's journey east of Antananarivo (Major, 1896), and that of *M. cowani* at Ankafina in the eastern Betsileo portion of the island (Thomas, 1882). Both these sites are well to the south of the Tsaratanana Massif and in the Central Highlands. Given that cryptic species have been detected in other broadly distributed taxa in the genus *Microgale* (Olson *et al.*, 2004; Yoder *et al.*, 2005), a multivariate analysis was conducted to further examine the

Table 3 Dental measurements (in mm) of *Microgale jobihely* and other similarly sized species of *Microgale*

Species	M1WP	M2B	M3B	P3W	P4W	UTR
Microgale jobihely						
(Holotype AMNH 274984)	5.1	5.4	5.5	3.8	4.6	9.6
Adult	5.0 ± 0.14	5.3 ± 0.17	5.4 ± 0.22	3.7 ± 0.08	4.5 ± 0.09	9.5 ± 0.21
	4.9–5.1, *n*=3	5.1–5.4, *n*=3	5.2–5.6, *n*=3	3.7–3.8, *n*=3	4.4–4.6, *n*=3	9.2–9.6, *n*=3
Microgale cowani[a]						
Adult	6.0 ± 0.32	6.3 ± 0.31	6.4 ± 0.29	4.5 ± 0.22	5.4 ± 0.26	11.2 ± 0.42
	5.5–6.4, *n*=25	5.8–6.8, *n*=25	6.0–6.8, *n*=25	4.2–4.9, *n*=25	5.0–5.7, *n*=25	10.5–11.9, *n*=25
Microgale taiva[a]						
Adult	5.9 ± 0.24	6.4 ± 0.25	6.5 ± 0.23	4.4 ± 0.18	5.3 ± 0.20	11.4 ± 0.29
	5.5–6.5, *n*=20	5.8–6.9, *n*=20	5.9–7.0, *n*=20	4.2–4.9, *n*=21	5.0–5.8, *n*=20	10.7–12.0, *n*=21

Measurements presented as mean ± sᴅ (minimum–maximum, *n*). For samples of two or fewer specimens, only the measurements are presented.
[a]Includes specimens collected by C. P. M. in the general Tsaratanana region.
MIWP, greatest posterior width across M1; M2B, greatest breadth across M2; M3B, greatest breadth across M3; P3W, greatest width across P3; P4W, greatest width across P4; UTR, upper tooth row length.
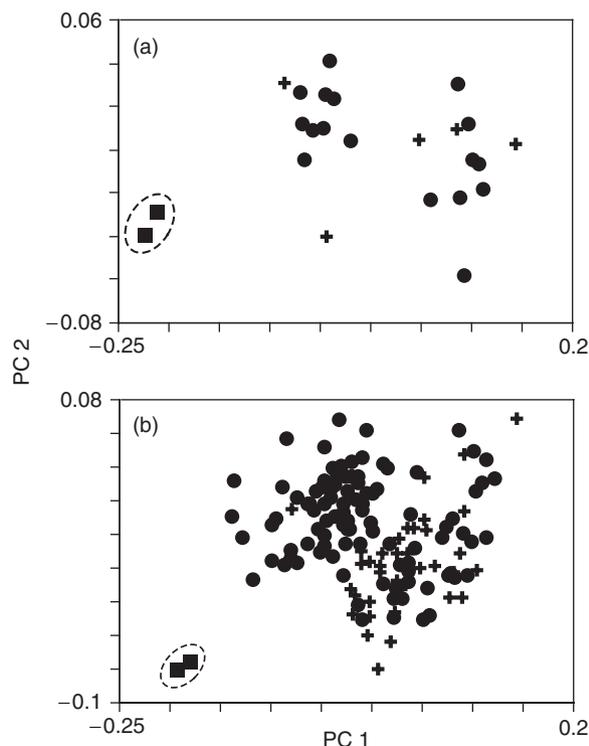

Figure 4 Bivariate plot of the first two principal components from an analysis of 17 log-transformed craniodental measurements recorded for specimens of *Microgale jobihely* (squares), *M. cowani* (circles) and *M. taiva* (crosses). Analysis (a) was limited to specimens collected from the Tsaratanana Massif region, whereas (b) included additional specimens of *M. cowani* and *M. taiva* from throughout much of their known distributions. The dashed line encircling the two *M. jobihely* specimens is added for visualization purposes only.

morphological distinctiveness of *M. jobihely* with respect to both *M. cowani* and *M. taiva*. A bivariate plot of the first two principal components clearly separates *M. jobihely* from both the other species, whether the sample of the latter two is restricted to the Tsaratanana region (Fig. 4a) or expanded to include representatives from throughout each species' known distribution (Fig. 4b). Interestingly, *M. cowani* and *M. taiva* broadly overlap in multivariate space, despite their phylogenetic distinctiveness (see below) and the relative ease with which they can be distinguished based on the relative length and bicoloration of their tails (Jenkins, 2003).

Molecular phylogenetics

Three unique ND2 haplotypes were found among the seven sequenced specimens of *M. jobihely* and no two sequences differed at more than three positions in the 523 nucleotides sequenced. This is not surprising given that all but one of the specimens were collected from a single locality, and the second (type) locality is only 12 km away. However, these three variable positions include one replacement substitution at nucleotide position 178. The type specimen, which was the only specimen collected from the type locality, represents a unique haplotype. Although our total sample for *M. jobihely* is not extensive, this nonetheless suggests some geographic structuring of genetic diversity within this species.

Phylogenetic analysis of the ND2 gene in select shrew tenrecs corroborates the morphological evidence supporting the recognition of *M. jobihely* as a distinct species. The heuristic MP search resulted in four equally parsimonious trees 810 steps long (not shown; see below), with a consistency index of 0.5. The single optimal tree recovered in the heuristic ML search ($-\ln L = 4138.5719$) with bootstrap support values for select nodes is shown in Fig. 5. As can be seen from the topology in Fig. 5, all sequenced specimens of *M. jobihely*, *M. cowani* and *M. taiva* form reciprocally monophyletic haplotype clades under the likelihood criterion. However, all four MP trees recovered a sister relationship between *M. jobihely* and the two *M. cowani* haplotypes shown in bold text in Fig. 5, but this grouping was only recovered in 56% of the MP bootstrap pseudoreplicates. Although the optimal ML tree did recover a monophyletic
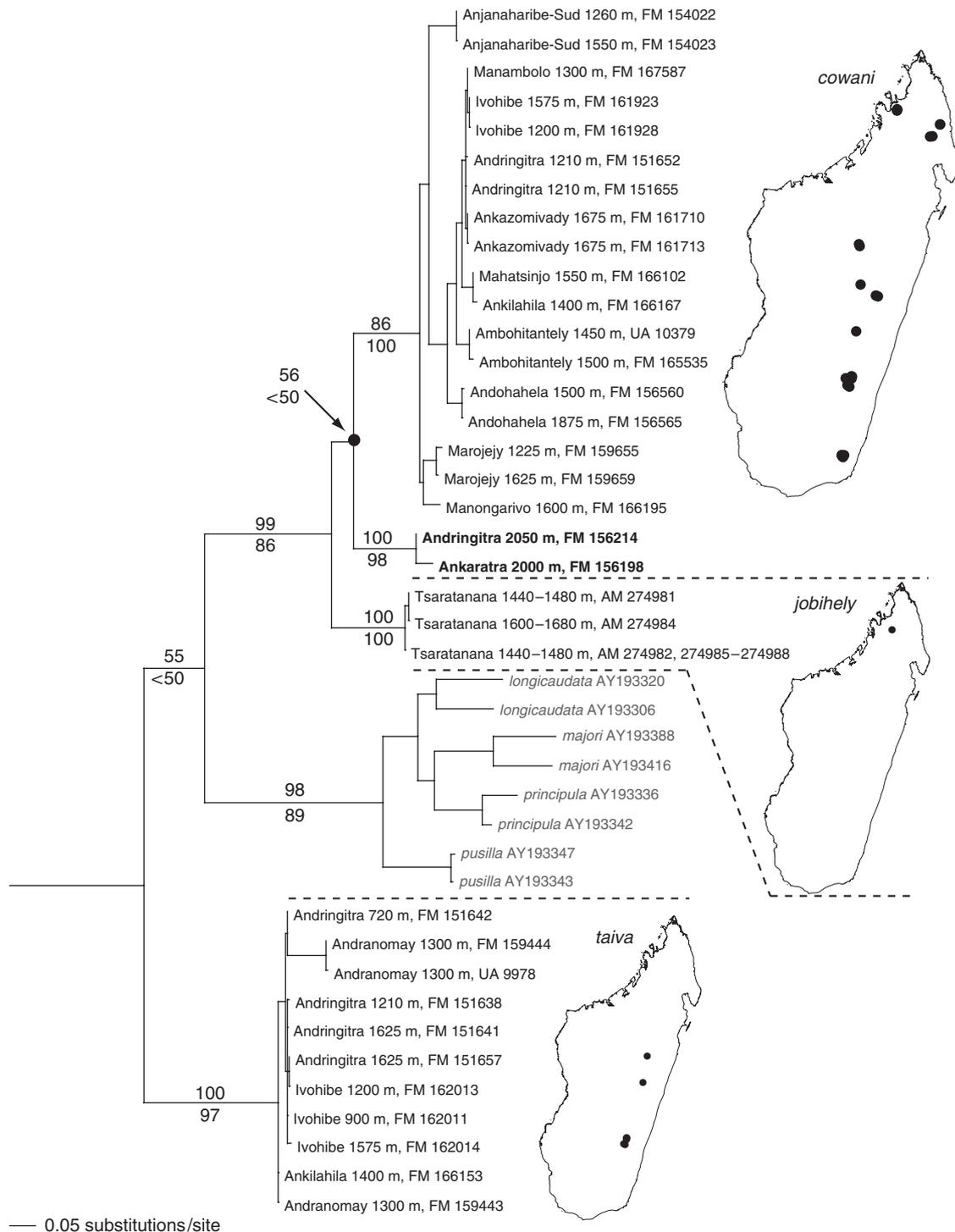
Figure 5 Phylogenetic position of *Microgale jobihely* with respect to *M. cowani*, *M. taiva* and several other species of shrew tenrec based on the mitochondrial ND2 gene. The tree shown is the single optimal tree recovered in the maximum likelihood tree search and was rooted with *Oryzorictes hova* (not shown). Numbers at select nodes represent bootstrap support values under the maximum parsimony (top) and maximum likelihood (bottom) criteria; support values for more terminal nodes are not shown. Collecting localities for sequenced samples of *M. jobihely*, *M. cowani* and *M. taiva* are shown to the right of each species' mitochondrial haplotype clade. Tip labels indicate (in order) the collecting locality (see Fig. 2), elevation in metres and museum catalogue number (FM, Field Museum of Natural History; AM, American Museum of Natural History; UA, Université d'Antananarivo). GenBank accession numbers are provided for *M. longicaudata, M. majori, M. principula* and *M. pusilla* (see Olson *et al.*, 2004). Identical haplotypes for *M. jobihely* are indicated by their catalogue numbers. The two specimens of *M. cowani* shown in bold type are discussed in the text and may represent an undescribed species.

M. cowani, inclusion of the two aforementioned *M. cowani* haplotypes in this clade was not strongly supported by bootstrap analysis. Furthermore, a heuristic ML search constrained to recover a monophyletic grouping of these two haplotypes with all *M. jobihely* haplotypes (but otherwise unconstrained and identical to the unconstrained analysis) resulted in a single tree whose log-likelihood value was not significantly different from that of the tree shown in Fig. 5 (as evaluated by a one-tailed Shimodaira–Hasegawa test with 1000 RELL replicates; $P = 0.476$). Interestingly, these two putative *M. cowani* specimens were both collected at much higher elevations (2000–2050 m) than the remaining *M. cowani* specimens sampled (1210–1875 m) and may represent an undescribed species. This is supported by the fact that specimens collected from multiple elevations in Andringitra (see Fig. 2) are recovered in distinct haplotype clades, as well as relatively high levels of uncorrected sequence divergence separating these clades (13.2–15.1%). Further investigation of these observations will be featured in a future study (L. E. Olson & S. M. Goodman, unpubl. data). Uncorrected pairwise sequence divergence between *M. jobihely* and all *M. cowani* specimens ranges from 14.7 to 16.8%, which is on par with similar comparisons among morphologically distinct species of long-tailed shrew tenrecs (Olson *et al.*, 2004).

Discussion

Taxonomic status of *Microgale jobihely*

Comparative qualitative and quantitative morphology readily distinguishes *M. jobihely* from all other currently recognized shrew tenrec species of similar size (Tables 1–3, Fig. 4). Phylogenetic analysis of sequence variation in the mitochondrial ND2 gene likewise supports the recognition of *M. jobihely* as a distinct species. It could be argued, based solely on the topological results shown in Fig. 5, that the sequenced specimens of *M. jobihely* merely represent the basalmost (and northernmost) haplotype clade within *M. cowani*. Indeed, latitudinally structured variation in mitochondrial DNA has previously been reported in other shrew tenrec species (Olson *et al.*, 2004). However, when considered together with the fact that *M. jobihely* can be differentiated from sympatric specimens of both *M. taiva* and *M. cowani* based on its diminutive size alone (Table 1), as well as multivariate analysis (Fig. 4a), there is virtually no evidence of conspecificity with *M. cowani*. Even when a much larger geographic sample of *M. cowani* and *M. taiva* is included in multivariate analysis, *M. jobihely* is still markedly distinct (Fig. 4b). These results collectively suggest that *M. jobihely* has been reproductively isolated from other shrew tenrec species for some time. As such, this raises the total number of accepted shrew tenrec species to 21, slightly twice the number recognized by MacPhee (1987) less than two decades ago. *Microgale* therefore remains the most speciose genus of terrestrial mammal on Madagascar today.

Ecology

Microgale jobihely is currently known from 12 specimens taken at two sites on the south-western slopes of the Tsaratanana Massif: the forêt du lac Matsiborimena between 1600 and 1680 m (one specimen) and the forêt d'Analapakila between 1420 and 1480 m (11 specimens). All of these animals were captured during a brief period between 14 and 22 March 2003. Even given the narrowness of this temporal window, a few inferences can be made about certain aspects of the natural history of this new species.

Eleven of the 12 animals were captured in pitfall buckets dug into the soil and with the rim even with ground level. The 12th individual was obtained in a Sherman trap set on the ground. Thus, these records confirm that the species is terrestrial, which is also supported by certain aspects of its foot structure, specifically that the three central toes are largely the same length and the outer toes are notably reduced in length.

Within the sample, there is a gamut of age classes and reproductive states, ranging from subadults of dental stage 1 (MacPhee, 1987) to an adult female that was lactating at the time of capture. No male was noted as having a developed epididymis. Given that all of these specimens were collected during a period slightly over 1 week, it would appear that this species does not have a temporally limited breeding period.

The other species of small mammals collected at the same time from the forêt d'Analapakila, where the majority of the *M. jobihely* specimens were collected, include the tenrecids *Tenrec ecaudatus*, *Setifer setosus* and *Hemicentetes semispinosus*, the introduced soricid shrew *Suncus murinus*, and the introduced murid rodent *Rattus rattus* that was in very high local abundance (specimens in the AMNH and UADBA). At the forêt de Lac Matsaborimena site, where the holotype of *M. jobihely* was obtained, the following species of small mammals were also collected on the same survey: *H. semispinosus*, *M. dobsoni*, *M. gymnorhyncha*, *M. parvula*, *M. soricoides* and the nesomyine rodents *Eliurus majori* and *E. tanala* and *R. rattus* (specimens in the AMNH and UADBA). To the best of our knowledge, no other small mammal collections have ever been made at these two sites.

Biogeography

On the basis of the distribution of small mammals, Carleton & Goodman (1998) distinguished the massifs of the northern portion of Madagascar as faunistically different from montane zones in the Central Highlands, and coined the term 'Northern Highlands' for this region, which includes the mountains surrounding the Andapa basin (Anjanaharibe-Sud and Marojejy) as well as the prominent Tsaratanana Massif and the Manongarivo Massif. In the majority of cases, even after extensive small mammal inventories of other montane zones of the island, several of the unique faunal elements originally used to define the Northern Highlands have not been found outside of this zone, although there are some exceptions (see Goodman *et al.*, 2005).

Over the course of the past two decades, a number of new species of *Microgale* have been discovered during surveys of montane regions in the humid forests of the island. In virtually all cases, these animals have subsequently been found at sites considerable distances from the type locality, and have turned out to be widely distributed across the nearly 1300 km length of this forest formation. For example, *M. gymnorhyncha* was described from the montane forest of the Andringitra Massif in central-eastern Madagascar (Jenkins *et al.*, 1996) and is now known from numerous localities in the same habitat from Andohahela in the south to Marojejy in the north, and then north-west to the Tsaratanana Massif (Goodman, Jenkins & Pidgeon, 1999; Goodman & Jenkins, 2000; herein). One of the interesting exceptions to this rule is *M. monticola*, originally described from the Anjanaharibe-Sud Massif. This species has been subsequently trapped at numerous sites in the appropriate elevational zones on nearby massifs (Goodman & Jenkins, 1998; Soarimalala & Goodman, 2003). However, it is unknown from the other well-surveyed Northern Highland massifs of Tsaratanana and Manongarivo (Goodman & Soarimalala, 2002; C. P. Maminirina, unpubl. data). Thus, *M. monticola* is not restricted to a single massif *per se*, but appears to be more of a regional endemic to the mountains surrounding the Andapa basin.

The case with *M. jobihely* appears to be different. Eighteen different sites were sampled during the 2001–2003 inventories of the Tsaratanana Massif by C. P. M. and C. J. R., of which the majority were within montane forests, the zone *M. jobihely* is known from. Further, numerous massifs in the Northern Highlands have been surveyed at the appropriate elevation, and no evidence of this species has been found. These sites include the massifs of Manongarivo, Anjanaharibe-Sud and Marojejy (Goodman & Jenkins, 1998; Goodman & Soarimalala, 2002; Soarimalala & Goodman, 2003; Fig. 1). At all of these sites intensive pitfall trapping was conducted, a technique that is very effective in capturing *Microgale* spp. Given these results, it would appear that *M. jobihely* has a very limited distribution, known from one zone along the south-western slopes of the Tsaratanana Massif. Here we present a biogeographic scenario, based on the topographic configuration of Tsaratanana and other large massifs on the island, in an attempt to explain this observation.

Madagascar has a north–south orientation, being notably longer than it is wide, and the majority of rivers drain to the east or west (Chaperon, Danloux & Ferry, 1993). Given the geological history of the island associated with the break-up of IndoMadagascar and that the India portion was attached to the eastern side (Wells, 2003), the island now shows considerable topographic asymmetry (Goodman & Ganzhorn, 2004). Numerous peaks along the north–south oriented chain of mountains represent important divides between different watersheds. The three highest peaks (from north to south) are Maromokotro (2876 m) on the Tsaratanana Massif, Tsiafajavona (2642 m) on the Ankaratra Massif and Boby (2658 m) on the Andringitra Massif (Fig. 6). The first of these three mountains, as compared with the other two, shows considerable difference in its shape and associated topo-

graphic structure within a 150 km radius of the summit, and this gives rise to asymmetric differences in the distribution of the surface area in different elevational zones.

The Tsaratanana Massif complex is a steep cone-shaped mountain with considerable west–east symmetry and a greater proportion of its surface area in the foothills below 500 m. Several rivers have their origin on the massif, radiating in various directions, bisecting the landscape, and represent the major water drainages of northern Madagascar (Fig. 1). Proportionately little of this mountain's total surface area is within the montane zone between 1000 and 2000 m. It is important to note that the other important massifs of the Northern Highlands, such as Manongarivo, Anjanaharibe-Sud and Marojejy, fall within the interior of the 150 km radius drawn around Tsaratanana.

In contrast, the other two massifs, Ankaratra and Andringitra, have notably less steep topographic profiles, their major drainages descend to the east or the west, and the largest proportion of their surface area is in the mid-elevational zone between 1000 and 2000 m and 1000 and 1500 m, respectively. Further, for both of these massifs, the montane zone is contiguous with vast areas of the Central Highlands at similar elevations, whereas that of Tsaratanana, or the Northern Highlands at large, is distinctly more isolated. These factors overlaid on the waning and waxing of different climatic regimes during the Quaternary, giving rise to periods when montane vegetation descended notable distances along the flanks of mountains during warmer and wetter periods or was isolated in the summital zones during cooler and drier periods (Burney, 1987, 1997; Straka, 1996; Gasse & Van Campo, 1998). These vegetation shifts might have created opportunities for allopatric speciation on Tsaratanana for montane-restricted organisms. The herpetological endemism found at Tsaratanana is striking (Raxworthy & Nussbaum, 1996) and no montane-restricted species of amphibian or reptile is shared with any Central Highland massif (Raxworthy, 2003). The continuity of montane elevations in the Central Highlands might also explain why small mammals of this zone have broad distributions and show no microendemism as in the Northern Highlands. There is good evidence of glaciation on the Andringitra Massif, a mountain notably further south than the Ankaratra and Tsaratanana Massifs, during the Pleistocene–Holocene boundary (Vidal Romani, Mosquera & Campos, 2002).

There are a series of ridges radiating off Tsaratanana that fall within the elevational range of 1200–1800 m that are in direct contact with other massifs, such as Anjanaharibe-Sud, or that form close stepping-stones to massifs, such as Marojejy. Thus, the observation that certain endemic species of small mammals, such as *M. jobihely*, are not distributed across these nearly continuous montane areas of the Northern Highlands is incongruous with this analysis. For potentially fossorial animals, such as *Microgale* spp. that are difficult to capture and notably seasonal, long-term inventory work is obligatory to draw definitive conclusions on their distribution. Based on current data and many years of fieldwork in the montane areas of Madagascar, there appears to be a repetitive pattern of more local endemism in
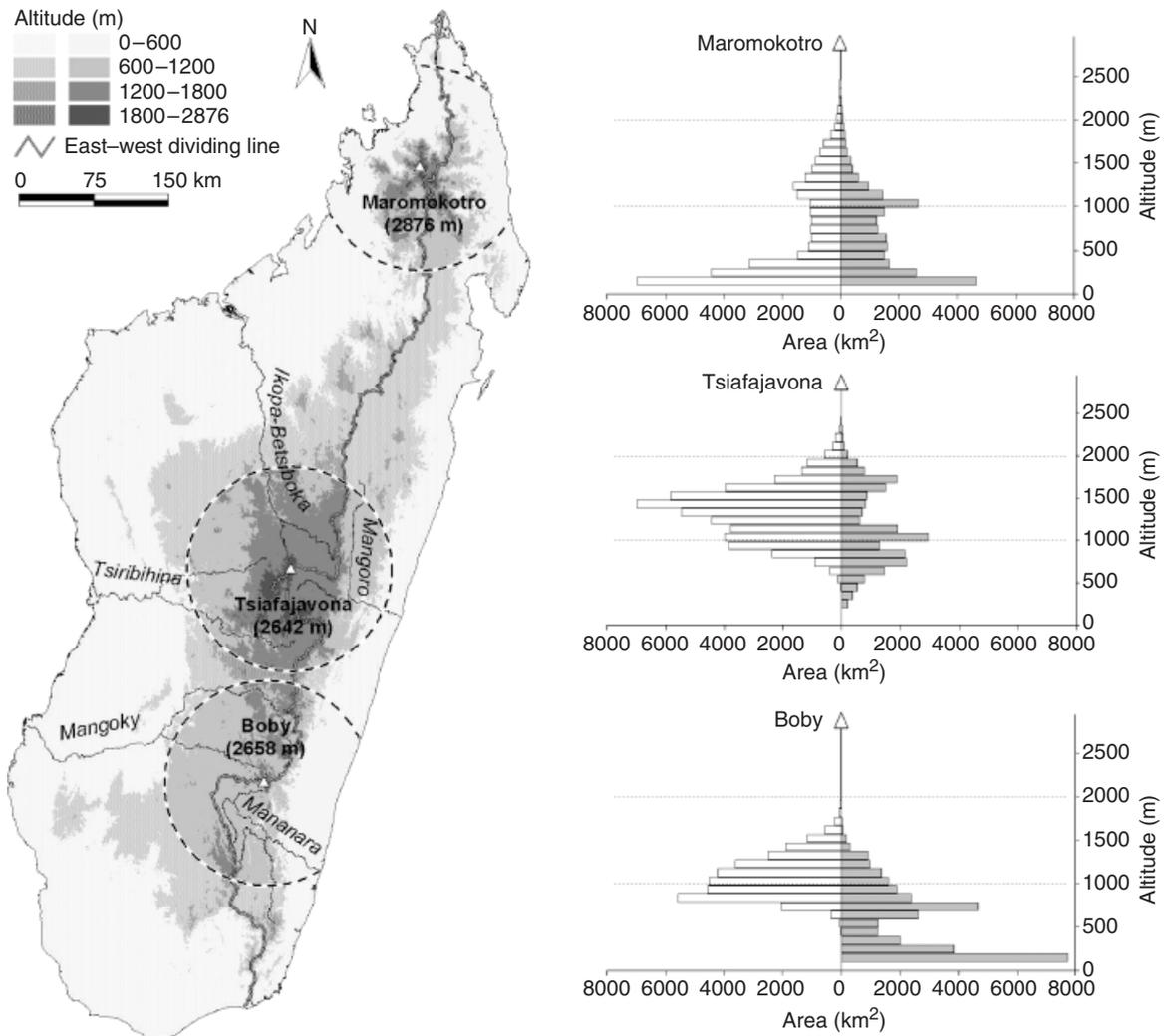
Figure 6 A map of the river basins surrounding the three highest peaks of Madagascar and the topographic distribution of these mountains. Left: The three principal mountains of Madagascar and their associated peaks (from north to south): Tsaratanana Massif with its summit of Maromokotro (2876 m); Ankaratra Massif with its summit of Tsiafajavona (2642 m); and Andringitra Massif with its summit of Boby (2658 m). The principal rivers of each of the two southern peaks are noted. For the Tsaratanana Massif these are presented in Fig. 1. The circle represents a 150 km radius from the principal summit of each massif. Right: Bar diagrams of the proportion of surface area within the 150 km radius, as measured by km², presented in different elevational zones on the three principal peaks of Madagascar and divided into the east and west slopes of each massif. Oceanic surface area is not included in the histograms.

the Northern Highlands than in the Central Highlands, which are correlated with notable differences in the topographic structure of these two regions. With continued survey work in these regions, it will be possible to refine some of these conclusions, particularly with respect to the distribution of the endemics of the Northern Highlands.

Conservation status

The two sites from which *M. jobihely* has been recorded are in a relatively remote forested region extending off the south-western flank of the Tsaratanana Massif (Fig. 1). This is a zone outside the protected area of the Réserve Naturelle Intégrale du Tsaratanana. In both the forêt du lac Matsiborimena and the forêt d'Analapakila, there is local human pressure on the forest, mostly in the form of slash and burn agriculture (*tavy*), as well as non-commercial timber extraction. Further, the marshlands close to the sites from which this species was obtained are being converted to rice paddies. On the basis of current information, *M. jobihely* has a notably restricted distribution and can be considered as one of the few endemic small mammals of the island that show microendemism. The future of the ecosystem where this species is known from, as well as a plethora of other local organisms (including other microendemics; C. J.

Raxworthy, pers. obs.), depends on the rational long-term management of forest and marshland habitat, which may invoke considerable socioeconomic change for the local human population to allow them other means of existence than current techniques of subsistence agriculture.

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Supplementary material

The following material is available for this article online:

Appendix S1 Voucher information on the specimens used in this study.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-7998.2006.00146.x

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