

Quantifying cranial morphological disparity in tenrecs (Afrosoricida, Tenrecidae) with implications for their designation as an adaptive radiation

Supplementary Material

Sive Finlay and Natalie Cooper

1 Photographing specimens

One of us (SF) photographed the specimens with a Canon EOS 650D camera fitted with an EF 100mm f/2.8 Macro USM lens. We used a remote control (hähnel Combi TF) to take the photos to avoid shaking the camera and distorting the images

We used photographic copy stands consisting of a camera attachment with an adjustable height bar, a flat stage on which to place the specimen and an adjustable light source to either side of the stage. We used the copy stands that were available at each museum which differed in how the camera height was adjusted and in the light sources available. To take the light variability into account, on each day we took a picture of a white sheet of paper and used the custom white balance function on the camera to set the image as the baseline white measurement for those particular light conditions.

We photographed the specimens on a black material background with the light source in the top left-hand corner of the picture. We positioned a piece of white card on the bottom right side of the specimen to reflect the light back onto the specimen and therefore minimise any shadows (figure 1 below). We made small bean bags (12 x 5cm) from the same black material as the background and filled them with plastic beads. We used these bags as necessary to hold the specimens in position while being photographed. For

example, when taking pictures of the lateral view of skulls, we placed one bean bag under the nose of the skull and another bag lying along the top (cranial) side of the skull to ensure that the side being photographed lay in a flat plane relative to the camera and did not tilt in any direction. We used the grid-line function on the live-view display screen of the camera to position the specimens in the centre of each image.

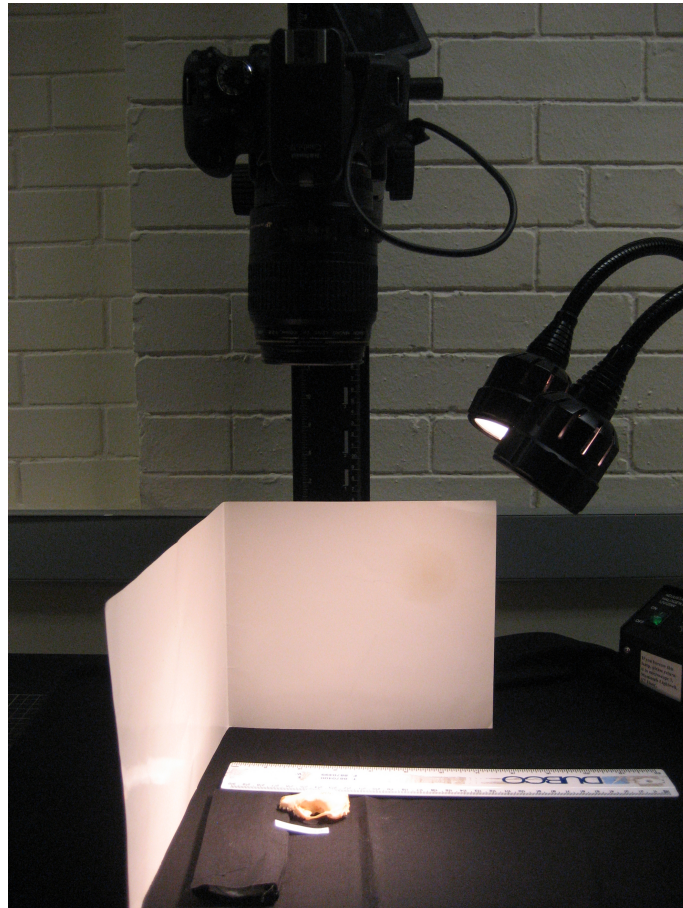


Figure 1: Photographic set up for taking pictures of skulls. The camera (above centre) is fitted to a copy stand, the light source is directed from the top-left corner of the image and the white card reflects the light back onto the skull.

Photographs were captured and saved in a raw file format. Before using the pictures for morphometric analyses, we converted the raw files to binary (grey scale) images and re-saved them as TIFF files. The black and white pictures were more useful for later analyses since we were not interested in including any colour comparisons and it is easier to see some biological features in binary images. TIFF files were the most appropriate to use for my morphometric analyses as they are uncompressed (in comparison to JPEG) images and therefore there is less chance of any picture distortions which may affect later

analyses (HERC, 2013).

2 Determining the number of semilandmarks to use for curves

When combining landmark and semi-landmark approaches, there is a potential problem of over-sampling the curves (REFS). To determine the number of semilandmark points required to adequately summarise the curves in our data sets, we followed the method outlined by MacLeod (2012). For each data set we chose a random selection of pictures of specimens which represented the breadth of the morphological data (i.e. specimens from each sub-group of species). We drew the appropriate curves on the each specimen and over-sampled the number of points on the curves (i.e. resampled the curves so that points were very close together). We measured the length of the line and regarded that as the 100%, true length of that outline. We then re-sampled the curves with decreasing numbers of points and measured the length of the outlines. We calculated the length of the curves resampled with fewer points as a percentage of the total length of the curve. We repeated these calculations for each specimen and then found the average percentage length for each resampled curve across all of the specimens in the test file. We continued this process until we found the minimum number of points that, on average, gave a curve length which was at least a 96% accurate representatio of the true (over-sampled) curve length. We repeated these curve-sampling tests for each analysis (skulls in dorsal/ventral/lateral views and mandibles in lateral view) to determine the minimum number of semilandmark points which would give accurate representations of morphological shape.

3 Additional skull analyses

3.1 Landmark placement

3.1.1 Skulls: lateral view

I placed nine landmarks on the lateral pictures (see figure 2) and also drew two semilandmark curves between landmarks 7 and 8 to represent the shape of the back of the

skull (resampled to 20 semilandmark points) and landmarks 8 and 1 (resampled to 15 semilandmark points) down the midline of the nose to represent the shape of the top of the skull. Table 1 describes the definitions for each of the landmark points. For specimens that were damaged on their right side we reflected photographs of the left lateral side of the skull so that all pictures would be in the same orientation.

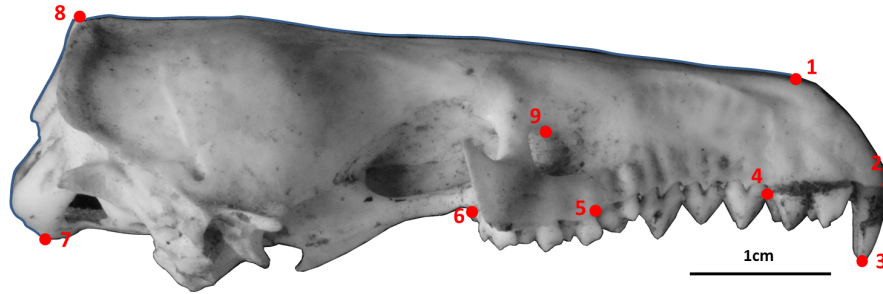


Figure 2: Landmarks (red) and curve (blue) for the lateral skull pictures, further descriptions in table 1. The specimen is a giant otter shrew tenrec, *Potamogale velox*, NHML 1934.6.16.2

Table 1: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in lateral view (see Figure 2.

Landmark	Description
1	Anterior, upper tip of the nasal bone
2	Anterior of the alveolus of the first incisor
3	Lowest point of the first incisor
4	Posterior of the alveolus of the last incisor
5	Anterior tip of the alveolus of the first molar
6	Posterior tip of the alveolus of the last molar
7	Lowest point of the basi-occipital (base of the back of the skull)
8	Highest point of the braincase
9	Highest point of the infraorbital foramen
Curve A	Between points 7 and 8
(20 points)	Back of the skull from the lowest to highest points
Curve B	Between points 8 and 1
(15 points)	From the highest point of the braincase to the front of the nasal

3.1.2 Skulls: ventral view

Most of the landmarks in this view are concentrated around the dentition and palate of the animals. We placed 13 landmarks and drew one outline curve (resampled to 60

semilandmark points) around the back of the skulls between landmarks 12 and 13 (figure 3). The high variability of the species basi-cranial region and difficulties associated with identifying developmentally or functionally homologous points precluded designation of additional landmarks towards the back of the skulls. Table 2 outlines the descriptions of the landmarks we placed on the ventral pictures.

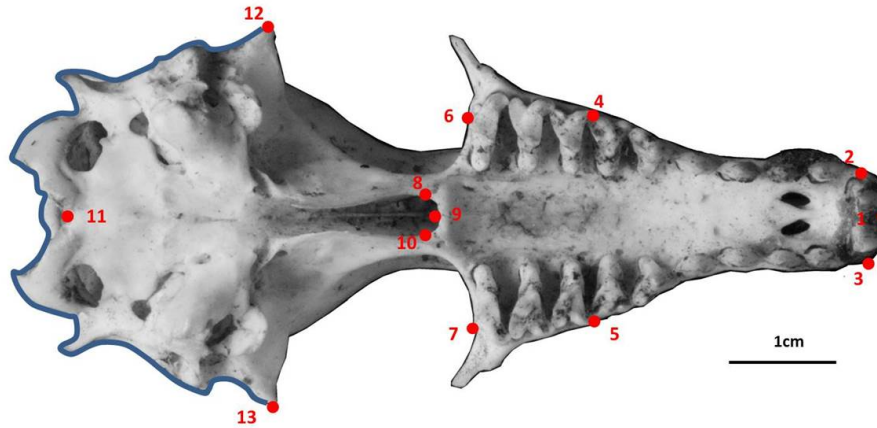


Figure 3: Landmarks (red) and curve (blue) for the ventral skull pictures, further descriptions in table 2. The specimen is a giant otter shrew tenrec, *Potamogale velox*, NHML 1934.6.16.2

Table 2: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in ventral view (see Figure 3).

Landmark	Description
1	Anterior point of the palate
2 + 3	Posterior, lateral extremity of the right (2) and left(3) incisor
4 + 5	Anterior, outer point of the first molar on the right (4) and left (5)
6 + 7	Posterior, outermost point of the molar surface on the right (6) and left (7)
8	Widest point of the curve of the palatine on the right side
9	Posterior point of the palatine in the midline
10	Widest point of the curve of the palatine on the left side
11	Anterior of the occipital foramen in the midline
12 + 13	Widest (extreme lateral) point of the braincase on the right (12) and left (13)
Curve*	Outline of the back of the skull (between landmarks 12 and 13), 60 points
*NB: This curve doesn't necessarily trace homologous features because of the variation in the position of the foramen magnum.	

Figures 4 and 5 depict the morphospace plots derived from our principal components analyses of average Procrustes-superimposed shape coordinates for each species in our lateral and ventral skull data respectively. We used the principal components axes which

accounted for 95% of the cumulative variation ($n = X$ axes for the lateral skulls analysis and $n = X$ axes for the ventral skulls analysis) to calculate the disparity of each family. In the analysis of skulls in lateral view, tenrecs had higher disparity than golden moles for all of the five metrics and they occupy a significantly different area of morphospace (npMANOVA, $F=75.07$, $R^2 = 0.65$, $p = 0.001$, figure 4).

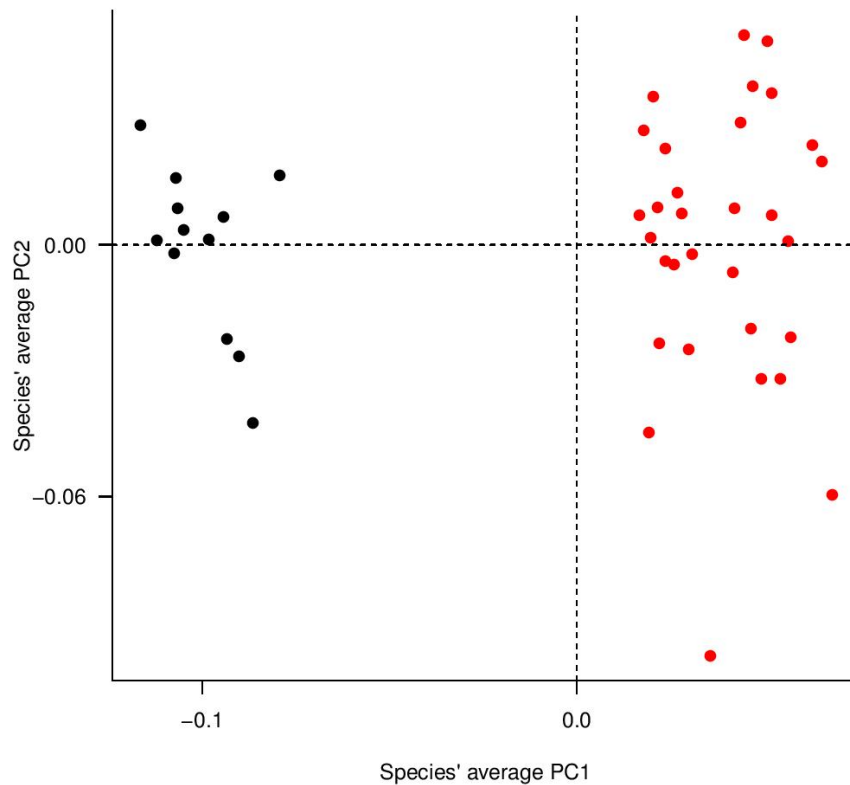


Figure 4: Principal components plot of the lateral skulls' morphospace occupied by tenrecs (red, $n=31$) and golden moles (black, $n=12$). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

In contrast, in the analysis of skulls in ventral view, tenrecs had higher disparity than golden moles in four of the five metrics but not when we calculated disparity as the sum of ranges. The two families occupy significantly different areas of morphospace (npMANOVA, $F=100.74$, $r^2 = 0.71$, $p=0.001$).

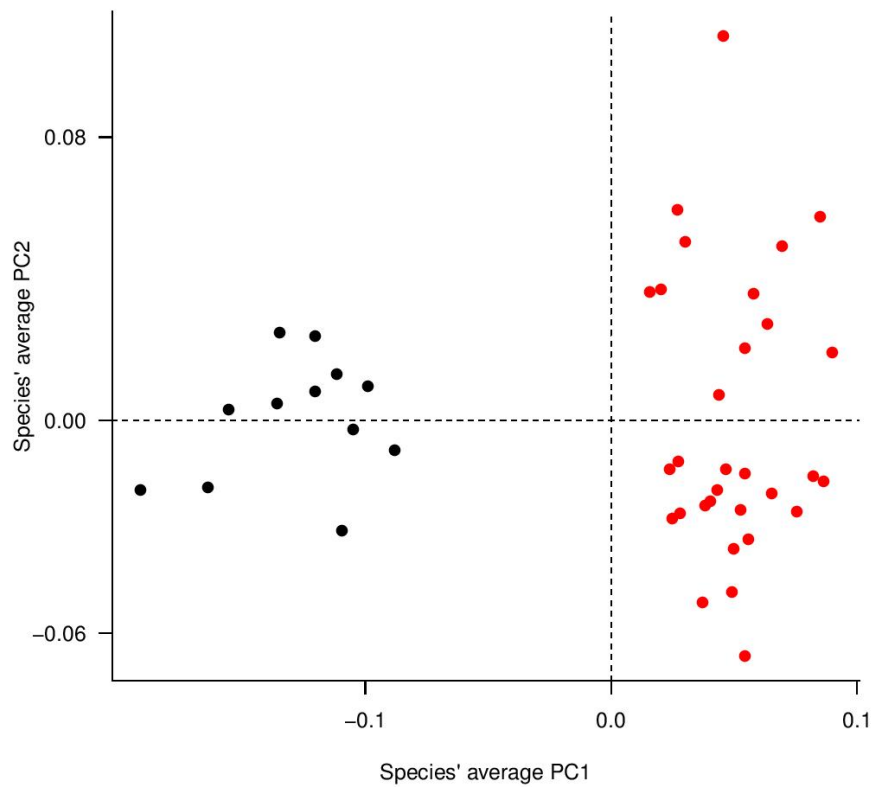


Figure 5: Principal components plot of the ventral skulls' morphospace occupied by tenrecs (red, n=31) and golden moles (black, n=12). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

3.2 Comparison of non-*Microgale* tenrecs

4 Additional mandible analyses

5 Museum specimens

Table 3: Museum accession numbers and taxonomic identification for all skull specimens. AMNH (American Museum of Natural History), FMNH (Field Museum of Natural History), MCZ (Museum of Comparative Zoology, Harvard), NHML (Natural History Museum London), SI (Smithsonian Institute)

1

Specimen ID	Order	Family	Genus	Species
AMNH_161526	Afrosoricida	Chrysochloridae	Chlorotalpa	duthieae
AMNH_161527	Afrosoricida	Chrysochloridae	Chlorotalpa	duthieae
AMNH_161559	Afrosoricida	Chrysochloridae	Eremitalpa	granti
AMNH_161571	Afrosoricida	Chrysochloridae	Eremitalpa	granti
AMNH_167961	Afrosoricida	Chrysochloridae	Chrysochloris	asiatica
AMNH_180911	Afrosoricida	Chrysochloridae	Chrysochloris	stuhlmanni
AMNH_180912	Afrosoricida	Chrysochloridae	Chrysochloris	stuhlmanni
AMNH_212938	Afrosoricida	Tenrecidae	Hemicentetes	semispinosus
AMNH_274982	Afrosoricida	Tenrecidae	Microgale	jobihely
AMNH_274986	Afrosoricida	Tenrecidae	Microgale	jobihely
AMNH_274987	Afrosoricida	Tenrecidae	Microgale	jobihely
AMNH_274988	Afrosoricida	Tenrecidae	Microgale	jobihely
AMNH_274989	Afrosoricida	Tenrecidae	Microgale	jobihely
AMNH_275041	Afrosoricida	Tenrecidae	Microgale	soricoides
AMNH_275088	Afrosoricida	Tenrecidae	Microgale	drouhardi
AMNH_275089	Afrosoricida	Tenrecidae	Microgale	drouhardi
AMNH_275090	Afrosoricida	Tenrecidae	Microgale	drouhardi
AMNH_275092	Afrosoricida	Tenrecidae	Microgale	drouhardi
AMNH_275095	Afrosoricida	Tenrecidae	Microgale	drouhardi
AMNH_275133	Afrosoricida	Tenrecidae	Microgale	fotsifotsy
AMNH_275134	Afrosoricida	Tenrecidae	Microgale	gymnorhyncha
AMNH_275135	Afrosoricida	Tenrecidae	Microgale	gymnorhyncha
<i>Continued on next page</i>				

Table 3 –Continues from previous page

SpecID	Order	Family	Genus	Species
AMNH_275136	Afrosoricida	Tenrecidae	Microgale	gymnorhyncha
AMNH_275137	Afrosoricida	Tenrecidae	Microgale	gymnorhyncha
AMNH_275138	Afrosoricida	Tenrecidae	Microgale	gymnorhyncha
AMNH_275141	Afrosoricida	Tenrecidae	Microgale	longicaudata
AMNH_275142	Afrosoricida	Tenrecidae	Microgale	longicaudata
AMNH_275143	Afrosoricida	Tenrecidae	Microgale	longicaudata
AMNH_275148	Afrosoricida	Tenrecidae	Microgale	longicaudata
AMNH_275149	Afrosoricida	Tenrecidae	Microgale	longicaudata
AMNH_275157	Afrosoricida	Tenrecidae	Microgale	parvula
AMNH_275158	Afrosoricida	Tenrecidae	Microgale	soricoides
AMNH_275160	Afrosoricida	Tenrecidae	Microgale	soricoides
AMNH_275162	Afrosoricida	Tenrecidae	Microgale	soricoides
AMNH_275163	Afrosoricida	Tenrecidae	Microgale	soricoides
AMNH_275189	Afrosoricida	Tenrecidae	Oryzorictes	hova
AMNH_275190	Afrosoricida	Tenrecidae	Oryzorictes	hova
AMNH_275191	Afrosoricida	Tenrecidae	Oryzorictes	hova
AMNH_275250	Afrosoricida	Tenrecidae	Microgale	brevicaudata
AMNH_275251	Afrosoricida	Tenrecidae	Microgale	brevicaudata
AMNH_275253	Afrosoricida	Tenrecidae	Microgale	brevicaudata
AMNH_275254	Afrosoricida	Tenrecidae	Microgale	brevicaudata
AMNH_275255	Afrosoricida	Tenrecidae	Microgale	brevicaudata
AMNH_275281	Afrosoricida	Tenrecidae	Microgale	fotsifotsy
AMNH_275282	Afrosoricida	Tenrecidae	Microgale	fotsifotsy
AMNH_275283	Afrosoricida	Tenrecidae	Microgale	fotsifotsy
AMNH_275298	Afrosoricida	Tenrecidae	Microgale	taiva
AMNH_275299	Afrosoricida	Tenrecidae	Microgale	taiva
AMNH_275300	Afrosoricida	Tenrecidae	Microgale	taiva
AMNH_275301	Afrosoricida	Tenrecidae	Microgale	taiva
<i>Continued on next page</i>				

Table 3 –Continues from previous page

SpecID	Order	Family	Genus	Species
AMNH_275360	Afrosoricida	Tenrecidae	Oryzorictes	hova
AMNH_275364	Afrosoricida	Tenrecidae	Microgale	parvula
AMNH_275365	Afrosoricida	Tenrecidae	Microgale	parvula
AMNH_275368	Afrosoricida	Tenrecidae	Microgale	parvula
AMNH_31243	Afrosoricida	Tenrecidae	Oryzorictes	tetradactylus
AMNH_31257	Afrosoricida	Tenrecidae	Oryzorictes	tetradactylus
AMNH_31270	Afrosoricida	Tenrecidae	Echinops	telfairi
AMNH_34647	Afrosoricida	Chrysochloridae	Chrysospalax	trevelyani
AMNH_51324	Afrosoricida	Tenrecidae	Potamogale	velox
AMNH_51327	Afrosoricida	Tenrecidae	Potamogale	velox
AMNH_54365	Afrosoricida	Chrysochloridae	Chrysospalax	trevelyani
AMNH_82399	Afrosoricida	Chrysochloridae	Chrysochloris	stuhlmanni
AMNH_89040	Afrosoricida	Chrysochloridae	Chrysospalax	trevelyani
AMNH_89046	Afrosoricida	Chrysochloridae	Cryptochloris	wintoni
FMNH_156226	Afrosoricida	Tenrecidae	Oryzorictes	tetradactylus
FMNH_159672	Afrosoricida	Tenrecidae	Microgale	monticola
FMNH_159673	Afrosoricida	Tenrecidae	Microgale	monticola
FMNH_159674	Afrosoricida	Tenrecidae	Microgale	monticola
FMNH_159675	Afrosoricida	Tenrecidae	Microgale	monticola
FMNH_159676	Afrosoricida	Tenrecidae	Microgale	monticola
FMNH_162893	Afrosoricida	Tenrecidae	Micropotamogale	lamottei
FMNH_166040	Afrosoricida	Tenrecidae	Microgale	pusilla
FMNH_166111	Afrosoricida	Tenrecidae	Microgale	gracilis
FMNH_166112	Afrosoricida	Tenrecidae	Microgale	gracilis
FMNH_166113	Afrosoricida	Tenrecidae	Microgale	gracilis
FMNH_166145	Afrosoricida	Tenrecidae	Microgale	gracilis
FMNH_167427	Afrosoricida	Tenrecidae	Microgale	dryas
FMNH_167621	Afrosoricida	Tenrecidae	Microgale	pusilla
<i>Continued on next page</i>				

Table 3 –Continues from previous page

SpecID	Order	Family	Genus	Species
FMNH_176203	Afrosoricida	Tenrecidae	Geogale	aurita
FMNH_176204	Afrosoricida	Tenrecidae	Geogale	aurita
FMNH_176211	Afrosoricida	Tenrecidae	Geogale	aurita
FMNH_176385	Afrosoricida	Tenrecidae	Microgale	dryas
FMNH_176387	Afrosoricida	Tenrecidae	Microgale	dryas
FMNH_176389	Afrosoricida	Tenrecidae	Microgale	dryas
FMNH_176395	Afrosoricida	Tenrecidae	Microgale	dryas
FMNH_209199	Afrosoricida	Tenrecidae	Microgale	grandidieri
FMNH_209200	Afrosoricida	Tenrecidae	Microgale	grandidieri
FMNH_209201	Afrosoricida	Tenrecidae	Microgale	grandidieri
FMNH_209202	Afrosoricida	Tenrecidae	Microgale	grandidieri
FMNH_209203	Afrosoricida	Tenrecidae	Microgale	grandidieri
FMNH_53073	Afrosoricida	Chrysochloridae	Amblysomus	corriae
FMNH_72831	Afrosoricida	Tenrecidae	Potamogale	velox
FMNH_81731	Afrosoricida	Chrysochloridae	Calcochloris	leucorhinus
FMNH_83540	Afrosoricida	Chrysochloridae	Calcochloris	leucorhinus
MCZ_23373	Afrosoricida	Chrysochloridae	Chrysochloris	stuhlmanni
MCZ_45021	Afrosoricida	Tenrecidae	Oryzorictes	tetradactylus
MCZ_45022	Afrosoricida	Tenrecidae	Oryzorictes	tetradactylus
MCZ_45033	Afrosoricida	Tenrecidae	Microgale	pusilla
MCZ_45050	Afrosoricida	Tenrecidae	Limnogale	mergulus
MCZ_45450	Afrosoricida	Tenrecidae	Geogale	aurita
MCZ_46274	Afrosoricida	Tenrecidae	Geogale	aurita
NHML_1870.3.10.15_1527.a	Afrosoricida	Tenrecidae	Setifer	setosus
NHML_1934.6.16.2	Afrosoricida	Tenrecidae	Potamogale	velox
NHML_1961.6.2.3	Afrosoricida	Chrysochloridae	Chrysospalax	trevelyani
NHML_3.1.1.1	Afrosoricida	Tenrecidae	Geogale	aurita
NHML_3.6.2.10	Afrosoricida	Chrysochloridae	Amblysomus	hottentotus
<i>Continued on next page</i>				

Table 3 –Continues from previous page

SpecID	Order	Family	Genus	Species
NHML_3509	Afrosoricida	Tenrecidae	Tenrec	ecaudatus
NHML_67.213	Afrosoricida	Tenrecidae	Micropotamogale	ruwenzorii
NHML_73.170	Afrosoricida	Tenrecidae	Micropotamogale	lamottei
NHML_74.668	Afrosoricida	Chrysochloridae	Chrysochloris	sp.
NHML_75.2223	Afrosoricida	Tenrecidae	Microgale	cowani
NHML_82.3.1.11	Afrosoricida	Tenrecidae	Hemicentetes	nigriceps
SI_083658	Afrosoricida	Tenrecidae	Hemicentetes	semispinosus
SI_154988	Afrosoricida	Tenrecidae	Microgale	dobsoni
SI_154989	Afrosoricida	Tenrecidae	Oryzorictes	tetradactylus
SI_221420	Afrosoricida	Chrysochloridae	Chlorotalpa	duthieae
SI_266897	Afrosoricida	Tenrecidae	Potamogale	velox
SI_294497	Afrosoricida	Tenrecidae	Setifer	setosus
SI_294504	Afrosoricida	Tenrecidae	Hemicentetes	semispinosus
SI_294507	Afrosoricida	Tenrecidae	Hemicentetes	nigriceps
SI_294508	Afrosoricida	Tenrecidae	Hemicentetes	nigriceps
SI_294510	Afrosoricida	Tenrecidae	Hemicentetes	nigriceps
SI_294511	Afrosoricida	Tenrecidae	Hemicentetes	nigriceps
SI_294520	Afrosoricida	Tenrecidae	Microgale	dobsoni
SI_328604	Afrosoricida	Tenrecidae	Setifer	setosus
SI_328605	Afrosoricida	Tenrecidae	Setifer	setosus
SI_328614	Afrosoricida	Tenrecidae	Setifer	setosus
SI_328616	Afrosoricida	Tenrecidae	Echinops	telfairi
SI_328619	Afrosoricida	Tenrecidae	Echinops	telfairi
SI_328622	Afrosoricida	Tenrecidae	Echinops	telfairi
SI_328624	Afrosoricida	Tenrecidae	Echinops	telfairi
SI_328653	Afrosoricida	Tenrecidae	Microgale	cowani
SI_328662	Afrosoricida	Tenrecidae	Microgale	cowani
SI_328667	Afrosoricida	Tenrecidae	Microgale	cowani
<i>Continued on next page</i>				

Table 3 –Continues from previous page

SpecID	Order	Family	Genus	Species
SI_328669	Afrosoricida	Tenrecidae	Microgale	cowani
SI_328670	Afrosoricida	Tenrecidae	Microgale	cowani
SI_328688	Afrosoricida	Tenrecidae	Microgale	pusilla
SI_328689	Afrosoricida	Tenrecidae	Microgale	pusilla
SI_328690	Afrosoricida	Tenrecidae	Microgale	pusilla
SI_328695	Afrosoricida	Tenrecidae	Microgale	dobsoni
SI_341621	Afrosoricida	Tenrecidae	Tenrec	ecaudatus
SI_341624	Afrosoricida	Tenrecidae	Tenrec	ecaudatus
SI_341661	Afrosoricida	Tenrecidae	Hemicentetes	semispinosus
SI_341688	Afrosoricida	Tenrecidae	Hemicentetes	semispinosus
SI_341689	Afrosoricida	Tenrecidae	Hemicentetes	semispinosus
SI_351334	Afrosoricida	Chrysochloridae	Calcochloris	obtusirostris
SI_351335	Afrosoricida	Chrysochloridae	Calcochloris	obtusirostris
SI_351336	Afrosoricida	Chrysochloridae	Chrysospalax	villosus
SI_351955	Afrosoricida	Chrysochloridae	Calcochloris	obtusirostris
SI_361482	Afrosoricida	Tenrecidae	Tenrec	ecaudatus
SI_365001	Afrosoricida	Chrysochloridae	Carpitalpa	arendsi
SI_380484	Afrosoricida	Chrysochloridae	Amblysomus	hottentotus
SI_380485	Afrosoricida	Chrysochloridae	Amblysomus	hottentotus
SI_381488	Afrosoricida	Chrysochloridae	Amblysomus	hottentotus
SI_395676	Afrosoricida	Tenrecidae	Geogale	aurita
SI_449177	Afrosoricida	Tenrecidae	Microgale	taiva
SI_449179	Afrosoricida	Tenrecidae	Microgale	gracilis
SI_449192	Afrosoricida	Tenrecidae	Microgale	dobsoni
SI_468315	Afrosoricida	Chrysochloridae	Chrysochloris	asiatica
SI_468316	Afrosoricida	Chrysochloridae	Chrysochloris	asiatica
SI_468317	Afrosoricida	Chrysochloridae	Chrysochloris	asiatica
SI_468318	Afrosoricida	Chrysochloridae	Eremitalpa	granti
<i>Continued on next page</i>				

Table 3 –Continues from previous page

SpecID	Order	Family	Genus	Species
SI_468319	Afrosoricida	Chrysochloridae	Cryptochloris	wintoni
SI_470211	Afrosoricida	Chrysochloridae	Calcochloris	obtusirostris
SI_537651	Afrosoricida	Tenrecidae	Potamogale	velox
SI_577052	Afrosoricida	Tenrecidae	Oryzorictes	hova
SI_577055	Afrosoricida	Tenrecidae	Microgale	talazaci
SI_578746	Afrosoricida	Tenrecidae	Microgale	talazaci
SI_578747	Afrosoricida	Tenrecidae	Microgale	talazaci
SI_578749	Afrosoricida	Tenrecidae	Microgale	dobsoni
SI_578753	Afrosoricida	Tenrecidae	Microgale	principula
SI_578756	Afrosoricida	Tenrecidae	Microgale	principula
SI_578759	Afrosoricida	Tenrecidae	Microgale	principula
SI_578760	Afrosoricida	Tenrecidae	Microgale	principula
SI_578762	Afrosoricida	Tenrecidae	Microgale	principula
SI_578768	Afrosoricida	Tenrecidae	Microgale	talazaci
SI_578769	Afrosoricida	Tenrecidae	Microgale	talazaci
SI_578772	Afrosoricida	Tenrecidae	Microgale	thomasi
SI_578773	Afrosoricida	Tenrecidae	Microgale	thomasi
SI_578774	Afrosoricida	Tenrecidae	Microgale	thomasi
SI_578775	Afrosoricida	Tenrecidae	Microgale	thomasi
SI_578776	Afrosoricida	Tenrecidae	Microgale	thomasi
SI_578784	Afrosoricida	Tenrecidae	Microgale	parvula
SI_578787	Afrosoricida	Tenrecidae	Microgale	fotsifotsy
SI_578789	Afrosoricida	Tenrecidae	Oryzorictes	sp.
SI_578791	Afrosoricida	Tenrecidae	Tenrec	ecaudatus
SI_578792	Afrosoricida	Tenrecidae	Tenrec	ecaudatus
SI_584649	Afrosoricida	Chrysochloridae	Calcochloris	leucorhinus

References

HERC, U.B. 2013. RHOI Fossil Photography Protocol.

MacLeod, N. 2012. Going Round the Bend ii: Extended Eigenshape Analysis.