Convergence and disparity in the evolution of tenrecs (Afrosoricida, Tenrecidae)

by

Sive Finlay

B.A. (mod), Trinity College Dublin 2008

A thesis submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

School of Natural Sciences
(Zoology)

Trinity College Dublin

SOMETIME 2014

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

DATA COLLECTION

1.1 INTRODUCTION

The analyses in chapters use morphological and ecological data sets which I compiled for xx specimens representing xx species of small mammals. This chapter describes how the data were collected and checked for errors. First I outline how I compiled my morphological data set from museum specimens and secondly I describe the sources which contributed to my ecological dataset. Subsequent chapters will refer to both of these data sources but I will only describe the methods I used for their creation in detail here. Other methods I used which have specific relevance to subsequent chapters are described in those chapters.

1.2 STUDY SPECIES

I collected morphological measurements of xxx species from four mammalian orders; Afrosoricida, Erinaceomorpha, Soricomorpha and Notoryctemorphia comprising seven families of mammals; tenrecs (Tenrecidae), golden moles (Chrysochloridae), hedgehogs and gymnures(Erinaceidae), shrews (Soricidae), solenodons (Solenodontidae), moles and desmans(Talpidae) and marsupial moles (Notoryctidae). My aim was to include measurements of all tenrecs and their sister taxa, golden moles. For my comparative species from other mammalian orders, I chose a random sample of xx taxa which have been previously identi-

fied as convergent with tenrecs (e.g. Gould and Eisenberg, 1966; Symonds, 2005; Poux *et al.*, 2008; Olson, 2013). I followed the taxonomy in Wilson and Reeder's Mammal Species of the World (MSW) (2005). I used phylogenies for each order to select, at random, species representing the main sub-branches of each order which also represented the morphological diversity of that order. For example, within the Soricomorpha, I included both species of *Solenodon* but only xx (out of a total of xx) species of *Crocidura* as the former genus represents a separate subgroup to the rest of the order.

1.3 TAXONOMY

Although MSW is a comprehensive mammalian taxonomic reference, it does not include some known species. For example, Wilson and Reader (2005) record 30 species of tenrec but more recent studies indicate that there are now 34 recognised species of tenrec (Olson, 2013). The additional species belong to the shrew tenrec (*Microgale*) genus and represent either recognition of cryptic species boundaries (Olson *et al.*, 2004) or discovery of new species (Goodman *et al.*, 2006; Olson *et al.*, 2009). Only one of these four recent additions to the *Microgale* genus, *M. jobihely*, was present in museum collections and therefore I could not include the three other newly recognised species in my analyses.

As MSW does not include all known species, I used the International Union for the Conservation of Nature (IUCN, 2012) as an additional reference for the taxonomy and species diversity of each group. Table 1.1 outlines the number of species I measured from each family and how this sample relates to the overall number of species in that group as recorded by both MSW and the IUCN.

TABLE 1.1: The number of species I measured in each family compared to the total number of species in that family according to two sources; (Wilson and Reeder, 2005) and (IUCN, 2012)

Order	Family	Species measured	Species in MSW	Species in IUCN
Afrosoricida	Tenrecidae	X	30	34
Afrosoricida	Chrysochloridae	X	21	21
Erinaceomorpha	Erinaceidae	X	24	X
Soricomorpha	Soricidae	X	376	X
Soricomorpha	Solenodontidae	X	4	X
Soricomorpha	Talpidae	X	39	X
Notoryctemorphia	Notoryctidae	X	2	X

1.4 MORPHOLOGICAL DATA SET

To construct my morphological data set, I used museum specimens of my study species housed at five different institutions. I compiled morphological data using two complementary approaches; linear measurements using calipers and 2D landmark-based geometric morphometrics.

1.4.1 Museums visited

I measured and photographed the skulls, limbs and skins of tenrecs and the species they convergently resemble using the collections of five different museums; the Natural History Museum London (NHML), the Smithsonian Institute Natural History Museum (SI), the American Museum of Natural History (AMNH), Harvardâ ĂŹs Museum of Comparative Zoology (MCZ) and the Field Museum of Natural History (FMNH), Chicago. Between January and September 2013, I spent 9 weeks working in these collections and collected data from xxx skulls, xxx limbs and xxx skins of xxx species.
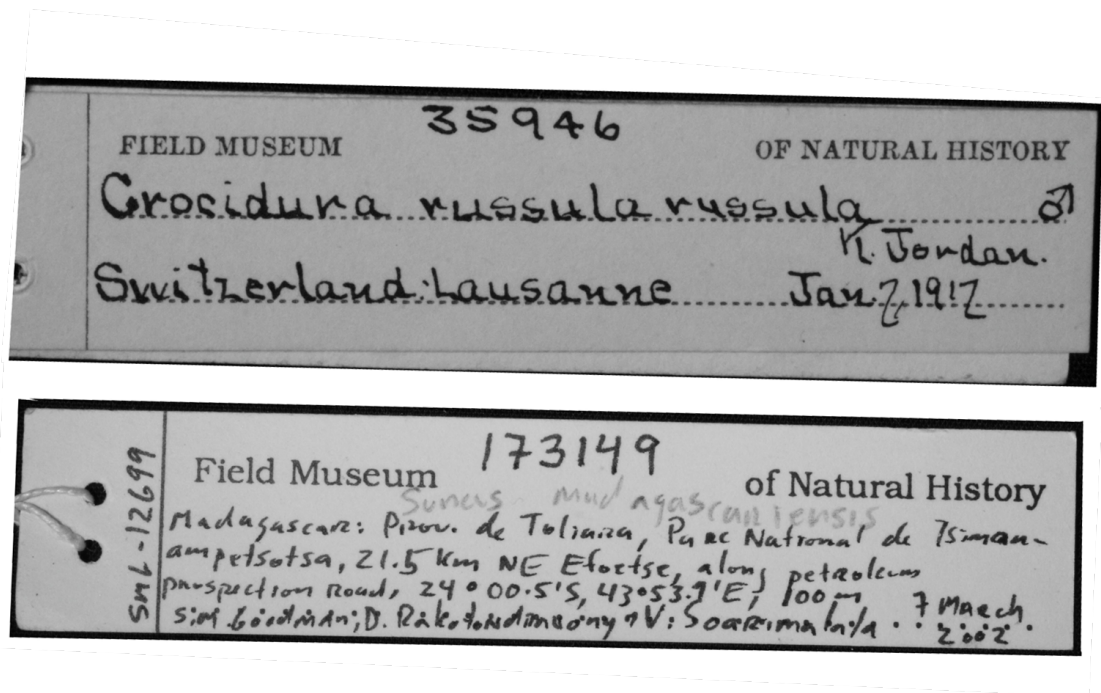
FIGURE 1.1: Examples of the variation in the detail of information which is available from museum labels

1.4.2 Museums label data

I recorded all the data on the specimen labels including any handwritten or printed notes which had been added by other users of the collection. The label data included the museum specimen ID number, genus, species, sex, collectorâĂŹs name, the date and location of where the specimen was collected. Some of the labels attached to skins had additional information such as the body, tail, hind foot and ear lengths as well as the body mass of the live individual. The level of detail recorded on the labels varied considerably (figure 1.1). For example recently collected specimens were more likely to have detailed information about the collection location, and some specimens did not have even basic information such as the sex recorded.

1.5 LINEAR MEASUREMENTS

Using a 15mm digital calipers (Mitutoyo Absolute digimatic calipers), I took 20 measurements of the skulls and mandibles (table 1.2) and 19 measurements of the limbs (table 1.3). My choice of which measurements to include was based on three main criteria; 1) their relevance to biological and ecological traits such as diet specialisation and locomotory adaptation, 2) their usefulness for assessing the overall shape and size of the specimen and 3) the ease with which they could be repeated both within and among specimens from different species. Figures x-x depict the linear measurements of skulls and figures xx show the limb measurements.

TABLE 1.2: Skull and mandible measurements

Abbreviation	Measurement	Description

TABLE 1.3: Limb measurements

Abbreviation	Measurement	Description

I took each linear measurement three times, cycling through all 20 skull or 19 limb measurements then repeating the cycle to avoid measuring the same variable twice in a row. Small measurements (<2 mm) are particularly prone to high error rates (Cardini and Elton, 2008). Therefore, I took five separate replicates of some of the variables which were most prone to errors (marked with PUT IN SYMBOL in tables 1.2 and 1.3). These included four of the skull measurements (PWa, IncisorH, IFD and IFcanal) and five of the limb measurements (FemD, TibD, HumD, UlnD, RadD). Five replicates should give a more reliable median value because even if there are one or two outlying measurements there should be at least three replicates which are in close agreement.

1.6 LANDMARK MORPHOMETRICS

1.6.1 Photographic setup

In order to get 2D landmarks for my specimens, I first had to photograph them. I 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. I 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 I 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 âĂIJwhiteâĂİ measurement for those particular light conditions.

1.6.2 Photographing specimens

I photographed the specimens with a Canon EOS 650D camera fitted with either an EF 100mm f/2.8 Macro USM lens (skulls and limbs) or EFS 18-55mm lens (skins). I used a remote control (hähnel Combi TF) to take the photos to avoid shaking the camera and distorting the images. I photographed the specimens on a black material background. I placed the light source from the top left-hand corner of the picture and positioned a piece of white card on the bottom right side of the specimen which reflected the light back onto the specimen and minimised any shadows (figure 1.2 below).

I made small bean bags (12 x 5cm) from the same black material as the background and filled them with plastic beads. I 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, I 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 I was photographing lay in a flat plane relative to
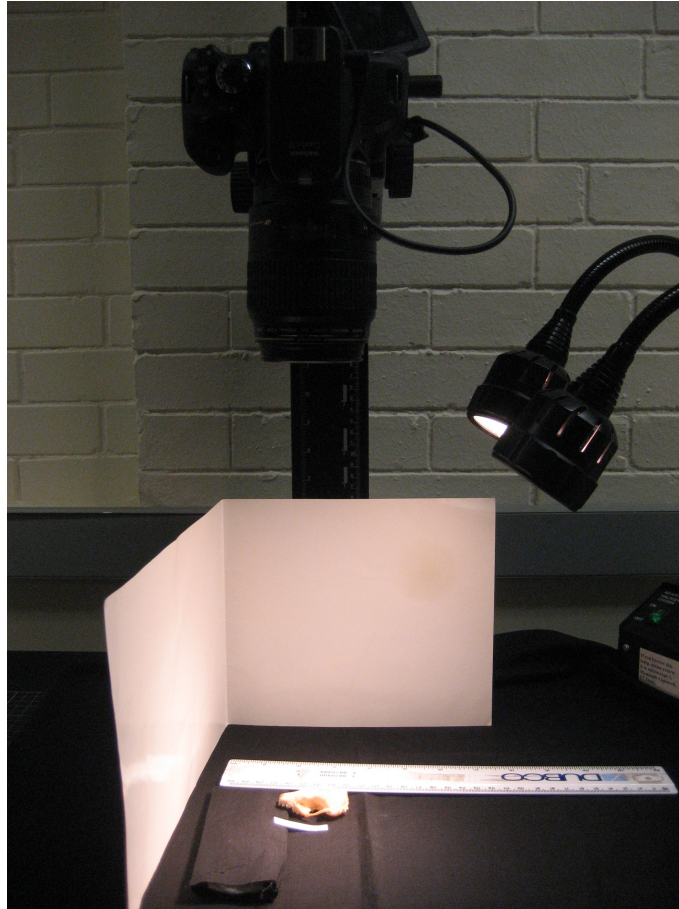
FIGURE 1.2: Photographic set up for taking images of my skulls. The camera (above centre) is fitted to a copy stand, the light source is directed from the top-left corner of the image and the white card reflects the light back onto the skull.

the camera and did not tilt in any direction. I used the grid-line function on the live-view display screen of the camera to position the specimens in the centre of each image.

1.6.3 Skulls

I photographed the skulls in three views; dorsal (top of the cranium), ventral (underside of the skull with the palate roof facing uppermost) and lateral (right side of the skull). I also photographed the outer (buccal) side of the right

mandible. When the right side of either the skull or mandibles were damaged or incomplete, I photographed the left sides and later reflected the images so that they could be compared to pictures of the right sides (e.g. Barrow and MacLeod, 2008).

1.6.4   Limbs

Initially, I tried to take pictures of the limbs in similar orientations to the skulls (dorsal, ventral and lateral). However, there was considerable variation in how the limbs were preserved. For example, some limbs were still articulated while others had fragmented bones. It therefore proved impossible to place the limb bones in consistent orientations that would be comparable across species. Similarly, the small size of some limbs, combined with the frequently incomplete nature of postcranial museum collections, made landmark-based morphometric analyses of any limb pictures impractical. Therefore, I photographed the fore- and hind-limb bones in outer (the side facing away from the rest of the body) and inner (the side facing in towards the centre of the body) views for reference purposes only.

1.6.5   Skins

As I was limited by the maximum camera height available on the copy stands, most skins were too large to be photographed with the 100mm macro lens. Therefore, I used an EFS 18-55mm lens to take pictures of the skins. I photographed skins in the same three orientations as the skulls; dorsal (the upper surface of the animal), ventral (the belly side of the skin) and lateral (right flank of the animal with the skin held in position using bean bags). The dorsal and ventral views give very approximate estimates of the overall body shape of the animal. The lateral views are less biologically relevant since the taxidermic

process is unlikely to produce specimens which represent the true body height of the animal.

1.6.6   Saving and processing images

Photographs were captured and saved in a raw file format. Before using the pictures for morphometric analyses, I 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 I was 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).

1.6.7   Landmark placement on images

I conducted geometric morphometric analyses of my skull and mandible photographs. I used a combination of landmark and semilandmark analysis approaches to assess the shape variability of the specimens. In contrast to detailed morphometric studies of single taxa (e.g. Refs), the interspecific and comparative nature of my work limited the number of points which could be reliably identified as landmarks in all speciesâĂę. I used the TPS software suite (Rohlf, 2013) to digitise landmarks and curves on my pictures. I set the scale on each pictures individually to standardise for the different camera heights I used when photographing my specimens. I created separate data files for each of my morphometric analyses (three views of skulls and lateral view of mandibles). I digitised landmarks and semilandmark points on each picture individually.

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 my data sets, I followed the method outlined by MacLeod (2012). For each data set I 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). I drew the appropriate curves on the each specimen and over-sampled the number of points on the curves. I measured the length of the line and regarded that as the 100%, true length of that outline. I then re-sampled the curves with decreasing numbers of points and measured the length of the outlines. I calculated the length of each re-sampled curve as a percentage of the total length of the curve and then found the average percentage length for across all of the specimens in my test file. I continued this process until I found the minimum number of points that gave a curve length which was at least 96% accurate. I repeated these curve-sampling tests for each analysis to determine the minimum number of semilandmark points which would give accurate representations of morphological shape. After creating my files with the landmarks and semilandmarks placed on each picture, I built sliders files (Zelditch *et al.*, 2012) to specify which points should be treated as semiland-marks in further analyses. After landmarking and building sliders files, I used R v3.02 (R Development Core Team, 2013) for all subsequent statistical analyses.

Here I summarise the landmarks and curves which I used on each of my different sets of pictures. For landmarks which are defined by dental structures, I used published dental formulae (Nowak, 1983; MacPhee, 1987; Knox Jones and Manning, 1992; Marshall and Eisenberg, 1996; Nagorsen, 2002; Goodman *et al.*, 2006; Asher and Lehmann, 2008; ADW, 2013) where available to identify the number and type of teeth in each species.

1.6.8 Skulls: ventral view

Most of the landmarks in this view are concentrated around the dentition and palate of the animals. I placed 13 landmarks and drew one outline curve (resampled to 60 semilandmark points) around the back of the skull between landmarks 12 and 13 (figure X). The high variability of my speciesâĂŹ 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 1.4 outlines the descriptions of the landmarks I placed in the ventral pictures.

TABLE 1.4: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in ventral view (see Figure X.

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.

1.6.9 Skulls: lateral view

I reflected photographs of the left lateral side of the skull so that all pictures would be in the same orientation. I placed nine landmarks on the lateral pictures (see figure X below) 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 semi-

landmark points) down the midline of the nose to represent the shape of the top of the skull. Table 1.5 describes my definitions for each of the landmark points. I originally tried to include more landmarks around the infraorbital foramina (IF) as a crude measure of facial sensitivity and because the IF area is correlated with ecotypes (Crumpton and Thompson, 2012). However, it proved impossible to see the boundaries of the IF in many species and single landmark points could not represent the shape of the full foramina.

TABLE 1.5: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in lateral view (see Figure X.

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

1.6.10 Skulls: dorsal view

There were even fewer identifiable landmarks in this view because none of the dental characteristics are visible. Therefore, most of my landmarks are relative (type 3) points which represent overall morphological shape but not necessarily homologous biological features (Zelditch *et al.*, 2012). I placed ten landmarks and drew four semilandmark curves to represent the shape of both the brain-

case (posterior) and nasal (anterior) area of the skulls. Table 1.6 describes how I
placed the landmarks and drew the outline curves for my dorsal skull pictures

TABLE 1.6: Descriptions of the landmarks (points) and curves (semilandmarks)
for the skulls in dorsal view (see Figure X.

Landmark	Description
1 + 2	Left (1) and right (2) anterior points of the premaxilla
3	Anterior of the nasal bones in the midline
4 + 5	Maximum width of the palate (maxillary) on the left (4) and right (5)
6	Midline intersection between nasal and frontal bones
7 + 8	Widest point of the skull on the left (7) and right (8)
9	Posterior of the skull in the midline
10	Posterior intersection between saggital and parietal sutures
Curve A	Outline of the braincase on the left side, between landmarks 9 and 7
(12 points)	(does not include visible features from the lower (ventral) side of the skull)
Curve B	Outline of the palate on the left side, between landamarks 4 and 1
(10 points)	(outline of the rostrum only, not the shape of the teeth)
Curve C	Outline of the braincase on the right side, between landmarks 9 and 8
(12 points)	(does not include visible features from the lower (ventral) side of the skull)
Curve D	Outline of the palate on the right side, between landamarks 5 and 2
(10 points)	(outline of the rostrum only, not the shape of the teeth)

1.6.11   Mandibles

I placed seven landmarks and drew four curves on each mandible picture (again,
reflecting any pictures of the left mandible so they could be compared to pic-
tures of the right side). I drew separate curves around each of the three pro-
cesses of the ascending ramus; coronoid, condyloid and angular and along the
base of the horizontal ramus of the jaw. While obviously part of an integrated
jaw unit, the development of the mandibular processes are also, in some as-
pects, independent since they attach different muscles which exert different
masticatory forces on the jaw (Barrow and MacLeod, 2008). Therefore, by
drawing separate curves around each of these elements, my ensuing analyses

could assess the relative shape changes of different components of the jaw with relevance to variation in feeding strategies and capabilities.

TABLE 1.7: Descriptions of the landmarks (points) and curves (semilandmarks) for the mandibles in lateral (buccal) view (see figure X

Landmark	Description
1	Anterior of the alveolus of the first incisor
2	Posterior of the alveolus of the first incisor
3	Anterior of the alveolus of the first molar
4	Posterior of the alveolus of the last molar
5	Maximum curvature between the coronoid and condylar processes
6	Maximum curvature between the condylar and angular processes
7	Maximum curvature between the angular process and the horizontal ramus
Curve A	Condyloid process (between landmarks 4 and 5, 15 points)
Curve B	Condylar process (between landmarks 5 and 6, 15 points)
Curve C	Angular process (between landmarks 6 and 7, 15 points)
Curve D	Base of the jaw (between landmarks 7 and 1, 12 points)

1.6.12   Skins

1.7   ERROR CHECKING

My data are prone to a number of different error sources. These include 1) taxonomic identification which has not been updated to currently accepted terms, 2) specimen ID errors, 3) possible variation associated with sex and age class of individuals, 4) the accuracy and repeatability with which species traits are measured, 5) morphometric errors associated with photographing specimens and the placement of landmarks. I address each of these possible sources of error below.

1.7.1   Taxonomic

I recorded species names as they were written on museum specimen labels and then corrected them to match the taxonomy Wilson and Reader'âĂŹs Mammal

Species of the World (2005). For recently identified species, such as *Microgale jobihely* (Goodman *et al.*, 2006), which are not included in Wilson and Reader (2005), I used the taxonomy recorded on the labels.

1.7.2 Specimen ID

There were four specimens from the Smithsonian Institute which had species labels which did not match between skulls and skins with the same specimen ID numbers. The four skulls were labelled as *Hemicentetes semispinosus*. The corresponding skins were originally labelled as *H. semispinosus* but this was crossed out and changed to *H. nigriceps*. The re-labelled skins looked clearly different to the undisputed *H. semispinosus* skins and also look more similar to other pictures of *H. nigriceps*. Therefore, I made the assumption that the re-labelling of the skins as *H. nigriceps* represents the true taxonomy and I treated the corresponding skulls as *H. nigriceps*.

1.7.3 Specimen sex and age

I included both male and female specimens in my data as significant sexual dimorphism in skull or body size has not been identified in any of my species (NEED MORE REFERENCES Olson *et al.*, 2004).

Information about the sex and/or age of an individual is often missing from museum records. Mammalian species can often be identified as juveniles by looking for incomplete fusion of the crania and non-fully erupted dentition (REFS) However, age classification in tenrecs is difficult using these criteria; in some species, the last molar does not erupt fully until the first molar has been shed so the full dentition is never present at any one time (Nowak, 1983). It is also difficult to distinguish deciduous from permanent teeth in *Microgale* tenrecs (Asher and Lehmann, 2008) which has led to confusion and misidentification of juvenile forms as separate species (Olson *et al.*, 2004). I excluded any

obvious juvenile specimens from my data set. Where specimens could not be obviously identified as juveniles I treated them all as equivalent adult forms.

1.7.4   Linear measurements

As mentioned above, I took three replicate measurements of most of my variables and five replicates of other variables. Some morphometric studies take replicate measurements of a trait and use the average value for further analyses. Rather than taking the mean of each of three (or five) measures, I used the median as it is less likely to be skewed by outliers and gives a more accurate representation of the true value of the trait. Before extracting the median values I followed the protocol for assessing measurement error outlined by (Cooper and Purvis, 2009). This method assesses whether there is a reasonable correlation among the replicate measurements of the same variable. The error checking criteria are based on two calculations; the coefficient of variation and the percentage spread. I calculated the coefficient of variation (standard deviation/mean*100) for each measurement. This value estimates the extent to which replicate measurements deviate from the mean. When the coefficient of variation was less than 5%, I accepted the median value as an accurate measurement of the size of the structure. If the coefficient of variation was greater than 5%, indicative of a low agreement between replicate measurements, I measured the percentage spread of the data. For variables measured three times, I calculated percentage spread as [(minimum difference between neighbouring measurements)/ (range of measured values)*100]. For variables that were measured five times, the differences between neighbouring values were calculated and labelled from smallest to largest as a, b, c, and d with the range of the measured values designated as e (Cooper and Purvis, 2009). For these variables, I calculated percentage spread as [(a/e + b/e + c/e)*100]. Small percentage spread values indicate close agreement between repeated

measurements. When percentage spread approaches 50% the data are evenly spread out and therefore there is no way of knowing whether the median value is an accurate measurement of the trait (Cooper and Purvis, 2009). I chose to use to use 25% as a cut off point for accepting the accuracy of measured traits.

I used these error checking criteria to assess the accuracy of my repeated measurements of both skulls and limbs. Of the 20 measurements for xxx skulls, there were xx variables belonging to xx skulls which had coefficient of variation > 5% and percentage spread >25 %. My final skull data set included xx replicates of xx variables from xx specimens comprising xx species.

Of the 19 measurements for xxx limbs, there were xx variables belonging to xx specimens which had coefficient of variation > 5% and percentage spread >25 %. My final limb data set included xx replicates of xx variables from xx specimens comprising xx species.

1.7.5 Landmark morphometrics

I used 2D morphometrics to compare the morphologies of the skulls. The small size of my specimens, combined with the number of specimens involved in my study made 3D imaging impractical. It takes roughly 1.5 hours for a good quality scan of each specimen so it would take XX hours to compile a useful data set. While 2D methods are an accepted means of comparing morphological shape (e.g. Adams *et al.*, 2004; Mitteroecker and Gunz, 2009), particularly for comparing skull morphologies of small mammals (e.g. Cardini, 2003; Panchetti *et al.*, 2008; White and Searle, 2008; Barrow and MacLeod, 2008; Scalici and Panchetti, 2011), the inherent discrepancies associated with comparing three dimensional objects using two dimensional pictures do introduce some difficulties of possible distortion of the image (Arnqvist and Mårtensson, 1998). Similarly, human error with how landmarks are positioned on specimens could also introduce noise into further analyses. In contrast to de-

tailed intraspecific work (REFS) photographic or landmark placement errors are unlikely to be significant in interspecific studies since one would expect that the morphological variation among species is large enough to be detected as a signal above any background noise associated with methodological error (REFS). Nevertheless, it is still important to assess measurement error in a morphometric data set to increase confidence in the outcome of final analyses. I identify two main sources of morphometric measurement error; specimen orientation and placement of landmarks.

1.7.6 Specimen orientation

Variation in the orientation of specimens for photography is one of the main sources of error in 2D morphometric studies (Adriaens, 2007). If specimens are not placed on a flat plane or in a consistent position relative to the camera, areas of the object which are tilted towards the camera will appear to be larger than reality, distorting any subsequent morphometric analyses of the shape. I used a random subset of skulls comprised of one representative from each of my 89 species

to estimate the overall specimen orientation error in my photographic dataset. This subset included representatives from each tenrec and golden mole species along with samples from my comparative species (total of xx moles, xx shrews, xx hedgehogsâĂę) I took three sets of pictures of each view of the skulls and mandibles, cycling through the pictures so that the specimen was removed and re-positioned before every shot (Viscosi and Cortini, 2011).

1.7.7 Landmark placement

I placed the landmarks on each set of pictures so inter-observer variation is not an issue for my study. However, repeatability and reliability of my choice of landmarks could affect the final results of my analyses (Arnqvist and Mårtens-

son, 1998). I used a combined, nested approach to test for both orientation and landmark placement error (Arnqvist and Mårtensson, 1998; Barrow and MacLeod, 2008). For each of the 89 specimens in my random subset of species, I photographed their skulls (dorsal, ventral and lateral views) and mandibles three times. I then copied these images and placed landmarks on 3 copies of each image. I used a nested mixed mode ANOVA to assess the measurement error of the Procrustes-superimposed coordinates. There were three factors in my ANOVA; specimen, photo (3 pictures of each specimen) and landmark trial (placed landmarks on 3 copies of each of my photos).

1.8 SUMMARY OF THE MORPHOLOGICAL DATA SET

1.9 ECOLOGICAL DATA

Bibliography

Adams D.C., Rohlf F.J., and Slice D. 2004. Geometric morphometrics: Ten years of progress following the "revolution". Italian Journal of Zoology 71:5–16.

Adriaens D. 2007. Protocol for error testing in landmark based geometric morphometrics.

ADW. 2013. Animal diversity web.

Arnqvist G. and Mårtensson T. 1998. Measurement error in geometric morphometrics; empirical strategies to assess and reduce its impact on measures of shape. Acta Zoologica Academiae Scientiarum Hungaricae 44:73–96.

Asher R.J. and Lehmann T. 2008. Dental eruption in Afrotherian mammals. BMC Biology 6, iSI Document Delivery No.: 286WD Times Cited: 31 Cited Reference Count: 46 Asher, Robert J. Lehmann, Thomas Biomed central ltd London.

Barrow E. and MacLeod N. 2008. Shape variation in the mole dentary (Talpidae: Mammalia). Zoological Journal of the Linnean Society 153:187–211, 10.1111/j.1096-3642.2008.00376.x.

Cardini A. 2003. The geometry of the marmot (Rodentia: Sciuridae) mandible: phylogeny and patterns of morphological evolution. Systematic Biology 52:186–205.

Cardini A. and Elton S. 2008. Does the skull carry a phylogenetic signal? Evolution and modularity in the guenons. Biological Journal of the Linnean Society 93:813–834.

Cooper N. and Purvis A. 2009. What factors shape rates of phenotypic evolution? A comparative study of cranial morphology of four mammalian clades. Journal of Evolutionary Biology 22:1024–1035.

Crumpton N. and Thompson R. 2012. The holes of moles: Osteological correlates of the trigeminal nerve in Talpidae. Journal of Mammalian Evolution .

Goodman S.M., Raxworthy C.J., Maminirina C.P., and Olson L.E. 2006. A new species of shrew tenrec (*Microgale jobihely*) from northern Madagascar. Journal of Zoology 270:384–398.

Gould E. and Eisenberg J.F. 1966. Notes on the biology of the Tenrecidae. Journal of Mammalogy 47:660–686.

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

IUCN. 2012. International Union for Conservation of Nature.

Knox Jones J. and Manning R. 1992. Insectivores.

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

MacPhee R. 1987. The shrew tenrecs of Madagascar: Systematic revision and holocene distribution of *Microgale* (Tenrecidae, Insectivora). American Museum Novitates Number 2889:1–45.

Marshall C. and Eisenberg J.F. 1996. *Hemicentetes semispinosus*.

Mitteroecker P. and Gunz P. 2009. Advances in geometric morphometrics. Evolutionary Biology 36:235–247, cited By (since 1996): 66 Export Date: 11 October 2012 Source: Scopus.

Nagorsen D. 2002. An identification manual to the small mammals of British Columbia.

Nowak R. 1983. Walker's Mammals of the World, 4th edition, vol. 1. Johns Hopkins University Press, Baltimore.

Olson L., Goodman S., and Yoder A. 2004. Illumination of cryptic species boundaries in long-tailed shrew tenrecs (Mammalia: Tenrecidae; *Microgale*), with new insights into geographic variation and distributional constraints. Biological Journal of the Linnean Society 83, 10.1111/j.1095-8312.2004.00366.x.

Olson L., Rakotomalala Z., Hildebrandt K., Lanier H., Raxworthy C., and Goodman S. 2009. Phylogeography of *Microgale brevicaudata* (Tenrecidae) and description of a new species from western Madagascar. Journal of Mammalogy 90:1095–1110.

Olson L.E. 2013. Tenrecs. Current Biology 23:R5–R8.

Panchetti F., Scalici M., Carpaneto G., and Gibertini G. 2008. Shape and size variations in the cranium of elephant-shrews: a morphometric contribution to a phylogenetic debate. Zoomorphology 127:69–82.

Poux C., Madsen O., Glos J., de Jong W.W., and Vences M. 2008. Molecular phylogeny and divergence times of Malagasy tenrecs: Influence of data partitioning and taxon sampling on dating analyses. BMC Evolutionary Biology 8.

Rohlf F. 2013. Tpsdig2 ver 2.17.

Scalici M. and Panchetti F. 2011. Morphological cranial diversity contributes to phylogeny in soft-furred sengis (Afrotheria, Macroscelidea). Zoology 114:85–94.

Symonds M.R.E. 2005. Phylogeny and life histories of the "Insectivora": controversies and consequences. Biological Reviews 80:93–128.

Team R.D.C. 2013. R: A language and environment for statistical computing.

Viscosi V. and Cortini A. 2011. Leaf morphology, taxonomy and geometric morphometrics: a simplified protocol for beginners. PLOS One 6:e25630.

White T. and Searle J. 2008. Mandible asymmetry and genetic diversity in island populations of the common shrew, *Sorex araneus*. Journal of Evolutionary Biology 21:636–641.

Wilson D. and Reeder D. 2005. Mammal species of the world. A taxonomic and geographic reference (3rd ed). Johns Hopkins University Press.

Zelditch M., Swiderski D., and Sheets D. 2012. Geometric Morphometrics for Biologists, second edition. Academic Press, Elsevier, United States of America.