

MORPHOLOGICAL DIVERSITY IN THE
EVOLUTION OF TENRECS
(AFROSORICIDA, TENRECIDAE)

by

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ABSTRACT

Here is the abstract of my thesis.

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CHAPTER 1

INTRODUCTION

1.1 PATTERNS OF MORPHOLOGICAL DIVERSITY

Patterns of morphological diversity are one of the most interesting aspects of evolutionary biology. Understanding why and how some groups of species are more morphologically diverse than others remains a central challenge.

Morphological diversity has important implications for a variety of ecological traits. For example, morphological characteristics of limbs inform us about the evolution of locomotory style (e.g. Bou *et al.*, 1987) and the trophic niches associated with particular dental morphologies affect speciation and diversification rates through time (Price *et al.*, 2012).

Apart from a few examples (e.g. Brusatte *et al.*, 2008; Goswami *et al.*, 2011; Ruta *et al.*, 2013), it is still common to study morphological diversity from a qualitative rather than quantitative perspective. However, it is important to quantify morphological diversity because it has implications for studies of adaptive radiations (Losos, 2010), convergent evolution (e.g. Muschick *et al.*, 2012; Harmon *et al.*, 2005) and our understanding of biodiversity (Roy and Foote, 1997).

Yet morphological diversity is difficult to quantify. Studies are inevitably constrained to measure the diversity of specific traits rather than overall morphologies (Roy and Foote, 1997). Different trait axes (such as cranial compared to limb morphologies) may yield different patterns of morphological diversity

(Foth *et al.*, 2012). Furthermore, linear measurements of morphological traits can restrict our understanding of overall morphological variation (Rohlf and Marcus, 1993).

Geometric morphometric approaches help to overcome some of the limitations of traditional morphological studies (Adams *et al.*, 2004). Morphometric studies based on caliper measurements of particular features can only describe a limited set of distances, ratios and angles which often fail to capture the overall shape of a particular structure (Slice, 2007). Geometric morphometrics circumvents these issues by using a system of Cartesian landmark coordinates to defined anatomical points. This method captures more of the true, overall anatomical shape of particular structures (Mitteroecker and Gunz, 2009).

Quantifying morphological diversity through geometric morphometric approaches reveals insights into evolutionary patterns and processes through time. These methods are particularly applicable for investigations of two major evolutionary patterns: adaptive radiations and convergent evolution.

1.2 MORPHOLOGICAL DIVERSITY AND ADAPTIVE RADIATIONS

Studies of morphological diversity have important implications for our understanding of adaptive radiations: 'evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms' (Futuyama 1998, cited by Losos, 2010). There are many famous examples of adaptive radiations including Darwin's finches, Caribbean *Anolis* lizards and cichlid fish (Gavrilets and Losos, 2009). Each of these cases are characterised by striking morphological diversity.

Of course adaptive radiations are not defined by morphological diversity alone. Some authors argue that speciation rates and patterns of taxonomic diversity are equally if not more important than morphological variety for

identifying adaptively radiated groups (Glor, 2010; Losos and Mahler, 2010). Furthermore, it is difficult to identify a clade as an adaptive radiation or not because any classification will necessarily be based on arbitrary statistical cut-offs of particular measures of diversity, be they taxonomic, morphological or functional (Olson and Arroyo-Santos, 2009). Identifying and defining specific characteristics of adaptive radiations remains a challenge.

However, despite the controversies, there is a consensus that high morphological diversity is a unifying characteristic of adaptive radiations (Losos and Mahler, 2010; Olson and Arroyo-Santos, 2009). In particular, identifying high levels of morphological diversity in 'adaptive' (i.e. functionally significant) traits is an important aspect of identifying adaptively radiated clades (Losos and Mahler, 2010). For example, the morphological traits which define ecomorph classes in the adaptive radiation of Caribbean *Anole* lizards are closely linked to habitat use (Losos *et al.*, 1998).

Even if the adaptive significance of traits is known, we need to quantify morphological diversity to be able to identify exceptionally diverse groups. One approach is through sister taxa comparisons. This has the advantage of comparing the morphological diversity of clades that have been evolving for the same amount of time since diverging from a common ancestor (Losos and Miles, 2002). Of course, this is a relatively limited measure of whether a group shows exceptional morphological diversity but it is a start. Studies of morphological diversity can be an important first step towards characterising an adaptive radiation.

1.3 MORPHOLOGICAL CONVERGENT EVOLUTION

Studying morphological diversity is also important for our understanding of convergent evolution: the "evolution of similar features independently through-

out the tree of life" (Futuyma 1998, cited in Losos, 2011). There are many famous examples of morphologically convergent groups including freshwater cichlid fish (Muschick *et al.*, 2012), Caribbean *Anole* lizards (Mahler *et al.*, 2013) and convergence between placental and marsupial mammals (Wroe and Milne, 2007). Characterising convergence within these groups is interesting because it gives an insight into the relative repeatability of evolution (Losos, 2011).

Theoretical studies have demonstrated that the evolution of convergent phenotypes is not as surprising as it might appear (Stayton, 2008). Given this information, there has been increasing interest in developing quantitative approaches towards measuring convergence. These methods allow us to measure the degree of convergence among particular groups so that we can assess whether observed similarities are greater than what we would expect to have evolved by chance (e.g. Muschick *et al.*, 2012).

There are many different methods for quantifying morphological convergence. These include methods for measuring convergence across a phylogenetic tree (Stayton, 2008), between *a priori*-identified species pairs (Arbuckle *et al.*, 2014; Muschick *et al.*, 2012; Stayton, 2006) and combining morphological data with measures of ecological similarity to determine community or faunal convergence (Ingram *et al.*, 2013; Mahler *et al.*, 2013; Moen *et al.*, 2013; Melville *et al.*, 2006). Each method has strengths and weaknesses depending on the type of data used and the exact questions asked. However, they all require researchers to collect detailed morphological trait data before the methods can be applied. Unfortunately, this data is missing for many groups so the methods have been developed using very few convergent clades (predominantly cichlids and *Anoles*). Therefore it is important to collect detailed morphological trait data for other convergent groups, both to analyse their convergence and to test whether existing methods of measuring convergence can be applied to non-traditional case studies.

1.4 TENRECS

Tenrecs (Afrosoricida, Tenrecidae) are a morphologically diverse group which is commonly cited as an example of both convergent evolution and an adaptive radiation (Soarimalala and Goodman, 2011; Eisenberg and Gould, 1969). The Family is comprised of 34 species, 31 of which are endemic to Madagascar (Olson, 2013). Body sizes of tenrecs span three orders of magnitude (2.5 to > 2,000g) which is a greater range than all other Families, and most Orders, of living mammals (Olson and Goodman, 2003).

Within this vast size range there are tenrecs which convergently resemble shrews (*Microgale* tenrecs), moles (*Oryzorictes* tenrecs) and hedgehogs (*Echinops* and *Setifer* tenrecs) (Eisenberg and Gould, 1969). Their similarities include examples of morphological, behavioural and ecological convergence (Soarimalala and Goodman, 2011). Tenrecs are one of only four endemic mammalian clades in Madagascar and the small mammal species which they resemble are absent from the island (Garbutt, 1999). Therefore, it appears that the tenrecs evolved as an adaptive radiation of species which filled otherwise vacant ecological niches (Soarimalala and Goodman, 2011).

The similarities among tenrecs and other small mammals are even more remarkable when you consider tenrecs' phylogenetic history. Tenrecs used to be classified within the general "insectivore" clade and only molecular studies revealed their true phylogenetic affinities within the Afrotherian mammals (Stanhope *et al.*, 1998). Therefore, despite initial appearances, tenrecs are more closely related to elephants, manatees and aardvarks than they are to shrews, moles or hedgehogs.

Although tenrecs are often cited as an example of an adaptively radiated Family which exhibits exceptional convergent evolution, these claims have not been investigated quantitatively. There are qualitative similarities between the hind limb morphologies of tenrecs and several other unrelated species with

similar locomotory styles (Salton and Sargis, 2009) but the degree of morphological similarity has not been established. Morphological diversity is an important feature of adaptive radiations (Losos and Mahler, 2010) and it also informs our understanding of convergent phenotypes (Muschick *et al.*, 2012). Therefore, understanding and quantifying patterns of morphological diversity in tenrecs is of vital importance. My thesis is the first study to address this issue.

1.5 STRUCTURE & CONTENTS OF THIS THESIS

In this thesis I present the first quantitative study of patterns of morphological diversity in tenrecs. I compiled an extensive data set of morphological characteristics in tenrecs, their closest relatives (golden moles) and the mammals that they convergently resemble. Chapter 2 includes details about my data collection and the general morphometrics analyses which form the basis for my study. I collected morphological data on the skulls, limbs and skins from 366 specimens representing 99 species of small mammals.

I used a subset of this data in chapter 3 to quantify the morphological diversity of tenrec skulls compared to their closest relatives, the golden mole. The rest of the data represents a significant resource for future studies of morphological diversity and convergence.

Finally, in chapter 4, I discuss the implications of my findings within the context of our understanding of tenrec evolution. My results reveal new insights into our understanding of morphological variety in tenrecs and prompt many new questions and possible avenues for further research.

CHAPTER 2

DATA COLLECTION AND PROCESSING

2.1 INTRODUCTION

I compiled a morphological data set of both photographs and linear measurements from 366 specimens representing 99 species of small mammals. I collected morphological data from skulls, limbs and skins. However, for this thesis, I have only analysed a subset of the skull data (chapter 3). Therefore my linear measurements of skulls and limbs along with photographic record of skins represent significant data sources for future work.

I have divided my description of how the data were collected and analysed into three sections:

i Data collection (section 2.2):

Summary of the species measured, information recorded from the museum labels, linear measurements and photographic set up.

ii Geometric morphometric analyses (section 2.3):

Landmark and semilandmark placement on different views of skulls and mandibles.

iii Error checking (section 2.4):

How I dealt with errors in taxonomic and specimen identification, possible variation associated with sex and age class, accuracy and repeatability of linear measurements and morphometric errors associated with photographing specimens and the placement of landmarks.

2.2 DATA COLLECTION

2.2.1 Species measured and taxonomy

Between January and September 2013, I spent a total of 9 weeks working in the collections of five museums: the Natural History Museum London (BMNH), the Smithsonian Institute Natural History Museum (SI), the American Museum of Natural History (AMNH), Harvard's Museum of Comparative Zoology (MCZ) and the Field Museum of Natural History (FMNH), Chicago. I measured and photographed 366 skulls, 248 post-cranial skeletons and 277 skins from 101 species belonging to four mammalian Orders; Afrosoricida, Erinaceomorpha, Soricomorpha and Notoryctemorphia. These belonged to 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).

I measured all of the tenrecs and their sister taxa the golden moles that were available in the collections (31 species of tenrec, 12 species of golden moles, table 2.1).

For my comparative species of non-Afrosoricida species, I chose a random sample of 56 taxa which have been previously identified as convergent with tenrecs (e.g. Gould and Eisenberg, 1966; Symonds, 2005; Poux *et al.*, 2008; Olson, 2013). Following the taxonomy in Wilson and Reeder's Mammal Species of the World (MSW) (2005), I used phylogenies for each Order to select species at random which represented the main sub-branches and morphological diversity of each Order. For example, within the Soricomorpha, I only included 3 species of *Crocidura* (out of a total of 230, Wilson and Reeder 2005) but both species of the *Solenodon* Genus because it represents a separate subgroup to the rest of the Order.

I used the taxonomy of Wilson and Reeder's Mammal Species of the World (MSW, 2005) supplemented with more recent sources (e.g. Olson, 2013; Soari-

malala and Goodman, 2011) to identify the specimens. Table 2.1 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 MSW (2005).

TABLE 2.1: The number of species I measured in each Family compared to the total number of species in that Family according to Wilson and Reeder's Mammal Species of the World 2005 (MSW).

Order	Family	Species measured	Species in MSW
Afrosoricida	Tenrecidae	31	30
Afrosoricida	Chrysochloridae	12	21
Erinaceomorpha	Erinaceidae	16	24
Soricomorpha	Soricidae	22	376
Soricomorpha	Solenodontidae	2	4
Soricomorpha	Talpidae	15	39
Notoryctemorphia	Notoryctidae	1	2

Wilson and Reader (2005) record 30 species of tenrec but more recent studies indicate that there are now 34 species(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 and Arroyo-Santos, 2009). Only one of these four recent additions, *M. jobihely*, was present in the museum collections and therefore I could not include the three other newly recognised species in my analyses.

2.2.2 Museum 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, collector's name, the date and location of collection. 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 2.1). For example recently collected specimens were more likely to have detailed information about the collection location whereas some specimens did not have even basic information such as the sex recorded.

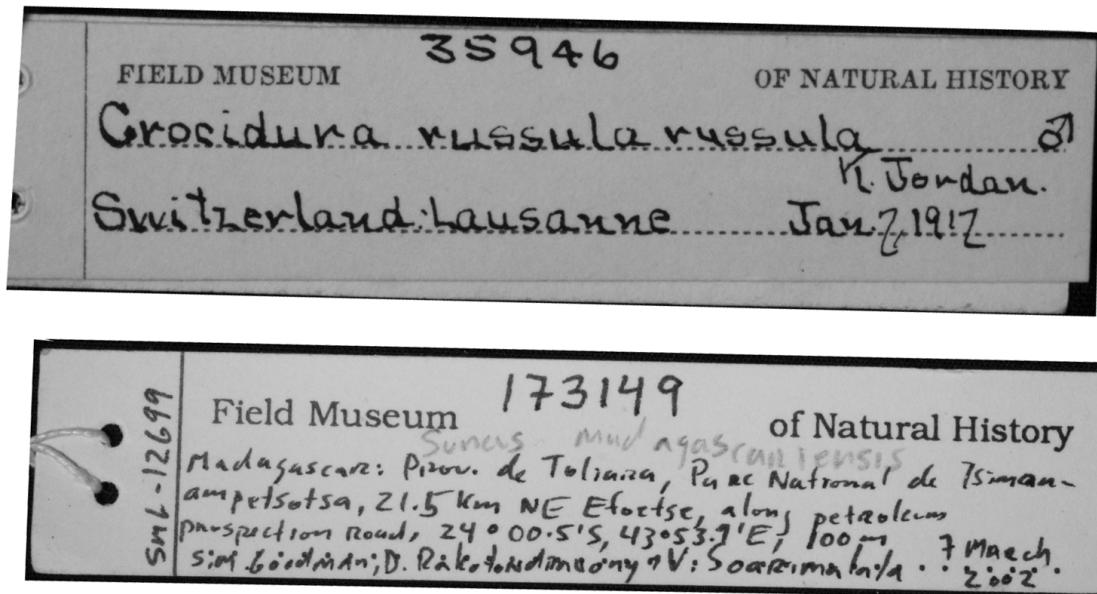


FIGURE 2.1: Examples of the variation in the detail of information which is available from museum labels.

2.2.3 Linear measurements

Using a 15mm digital calipers (Mitutoyo Absolute digimatic calipers), I took 5 measurements of the mandibles (table 2.2), 15 of the skulls (table 2.3) and 19 of the limbs (table 2.4). 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.

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 measurements which were often less than 2mm and consequently most prone to errors (marked with * in tables 2.3 and 2.4). These included four of the skull measurements (PWa, IncisorH, IFD and IFcanal, table 2.2) and five of the limb measurements (FemD, TibD, HumD, UlnD, RadD, table 2.4). 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 (Cooper and Purvis, 2009).

TABLE 2.2: Measurement abbreviations and descriptions for the mandibles, all taken from the labial (outer) side of the right jaw unless that side was broken or missing. All measurements were repeated three times except for those marked with * which were measured five times.

Abbreviation	Measurement	Description
ML	Mandible length	Maximum jaw length measured from the symphysis to the end of the jaw in a straight line to the condyloid crest/posterior notch
MTR	Mandible tooth row length	Anterior edge of the alveolus of the first tooth to the posterior edge of the alveolus of the last tooth on the same side
CorP	Coronoid process height	Perpendicular height from the top of the coronoid process to the base of the jaw bone
ConY	Condylloid height	Perpendicular height from the top of the mandibular condyle to the base of the jaw
CorCon	Coronoid-condyloid length	Diagonal distance from the coronoid tip to the condyloid crest/ posterior notch (Carraway <i>et al.</i> , 1996)

TABLE 2.3: Measurement abbreviations and descriptions for the skulls. All measurements were repeated three times except for those marked with * which were measured five times.

Abbreviation	Measurement	Description
CB	Condyllobasal length	Total skull length from the front of the premaxillary bones to the rear of the occipital condyles, measured from below
PL	Palate length	Maximum length of the palate from the anterior of the pre-maxilla to the posterior of the hard palate
TR	Tooth row length	From the front of the alveolus of the first incisor to the rear of the alveolus of the last molar on the same side
PWa*	Palate width anterior	Width across the palate measured between the posterior, outer-most points of the alveoli of the first pair of teeth
maxPW	Maximum palate width	Measured at the widest point of the palate
IncisorH*	Incisor height	Maximum height of the first incisor on the right
ZW	Zygomatic width	Maximum width between the zygomatic arches (measured within the arches from below the skull)
MX	Maxilla width	Width between the maxillary bones, measured from above the skull. Species with zygomatic arches; width from the innermost connection between the anterior of the arch and the skull. No arches; width between the anterior skull constrictions.
SQ	Squamosal width	Width between the squamosal bones, measured from above the skull. Species with zygomatic arches; width from the innermost connection between the posterior of the arch and the skull. No arches; width between the posterior skull constrictions
OL	Orbit length	Longitudinal length of the orbit opening measured along the edge of the skull from the maxilla to the squamosal.
IFD*	Interorbital foramen width	The maximum (vertical) diameter of the right interorbital foramen
IFW	Interorbital foramen width	Maximum width across the skull between the two interorbital foramina, measured from above
IFcanal*	Interorbital foramen canal	Length of the right IF canal measured between the anterior and posterior openings from above
BW	Braincase width	Width across the braincase at the widest point of the skull
SkH	Skull height	Perpendicular height from the highest point on the braincase to the base of the skull

TABLE 2.4: Measurement abbreviations and descriptions for the limbs. All measurements were repeated three times except for those marked with * which were measured five times.

Abbreviation	Measurement	Description
Inn	Innominate length	Maximum longitudinal length of the pelvic bone measured in a straight line from the anterior tip to the posterior curve
Obt	Obturator foramen	Maximum diameter of the opening in the pelvic bone
FemL	Femur length	Length of the bone excluding the femoral head (i.e. length of the bone without the joint area)
FemD*	Femur diameter	Minimum width across the shaft of the bone
TibL	Tibia length	Maximum longitudinal length of the tibia
TibU	Tibia unfused length	Length of the tibia which is not fused with the fibula
TibD*	Tibia diameter	Minimum diameter across the shaft of the tibia bone
Foot	Foot length	Maximum length of the entire foot (heel to longest toe)
Toe	Toe length	Length of the longest toe bone (just the phalange bone up to the metatarsal joint)
ScapL	Scapula length	Perpendicular length of the scapula from the curved end to the anterior point
ScapW	Scapula width	Maximum perpendicular width across the bone
HumL	Humerus length	Maximum length of the bone. In golden moles (L-shaped humerus): diagonal distance between the two ends of the bone
HumLvert	Humerus length vertical	Only for golden moles with L-shaped humerus: length of the vertical (longer) side of the bone
HumLhori	Humerus length horizontal	Only for golden moles with L-shaped humerus: length of the horizontal (shorter) side of the bone
HumD*	Humerus diameter	Minimum diameter across the shaft of the humerus
UlnL	Ulna length	Length of the bone from the posterior tip to the wrist joint
RadL	Radius length	Length of the bone from the posterior tip to the wrist
UlnD*	Ulna diameter	Minimum diameter across the ulna
RadD*	Radius diameter	Minimum diameter across the radius
Hand	Hand length	Maximum length of the entire hand (wrist to longest finger)
Finger	Finger length	Length of the longest finger bone (to the metatarsal joint)

2.2.4 Photographic set up

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 "white" measurement for those particular light conditions.

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 2.2).

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 (dorsal) side of the skull to ensure that the side I was photographing lay in a flat plane relative to 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.

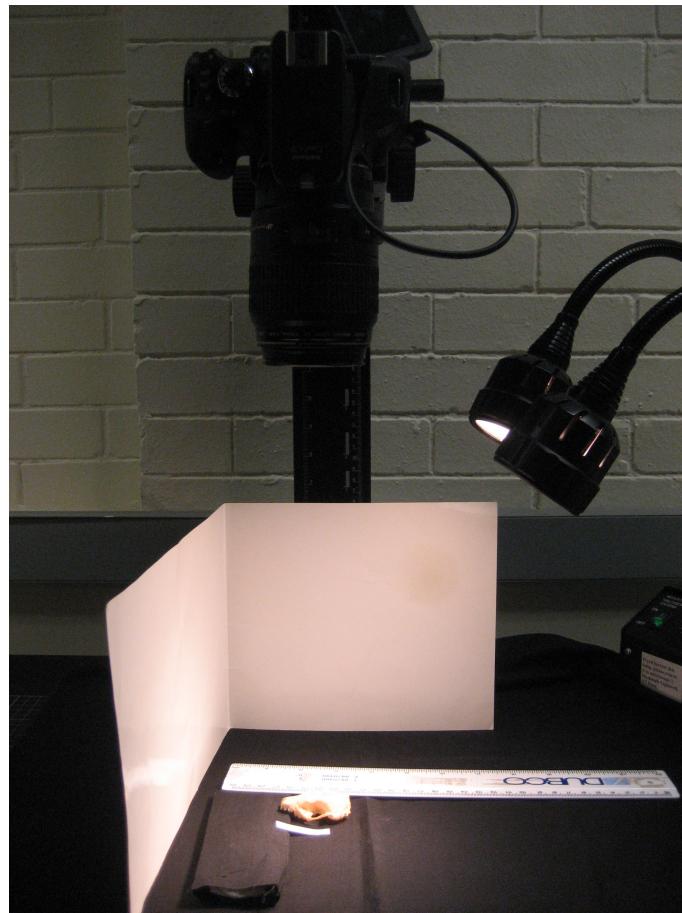


FIGURE 2.2: Photographic set up for taking pictures of my skulls. The camera (above centre) is fitted to a copy stand, the light source is directed from the top-left corner of the image and the white card reflects the light back onto the skull.

2.2.5 Photographing specimens

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 sides 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).

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.

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.

2.2.6 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 also appropriate because 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). Photographs of the specimens from the American Museum of Natural History and the Smithsonian Institute are available on figshare in separate file sets for the dorsal (Finlay and Cooper, 2013b), ventral (Finlay and Cooper, 2013d) and lateral (Finlay and Cooper, 2013c) skull pictures along with the mandibles (Finlay and Cooper, 2013a). Copyright restrictions from the other museums prevent public sharing of their images however they are available on request and I will save copies within the Department.

2.3 GEOMETRIC MORPHOMETRIC ANALYSES

2.3.1 Landmark placement on images

I used a combination of landmark and semilandmark analysis approaches to assess the shape variability in my skull and mandible specimens specimens.

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 four morphometric analyses (skulls in dorsal, ventral and lateral views and mandibles in lateral view). I digitised landmarks and semilandmark points on every picture individually. Some specimens were too damaged to use so I had a slightly different total number of images for each analysis: skulls dorsal (356), ventral (346), lateral (336) and mandibles (356).

When combining landmark and semi-landmark approaches, there is a potential problem of over-sampling the curves (MacLeod, 2012). 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 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 that reduced number of semilandmark points 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 95% 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.

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 sources (Repenning, 1967; Eisenberg and Gould, 1969; Nowak, 1983; MacPhee, 1987; Knox Jones and Manning, 1992; Davis and Schmidly, 1997; Quérouil *et al.*, 2001; Nagorsen, 2002; Wilson and Reeder, 2005; Goodman *et al.*, 2006; Karataş *et al.*, 2007; Hoffmann and Lunde, 2008; Asher and Lehmann, 2008; Lin and Motokawa, 2010; Muldoon *et al.*, 2009) where available to identify the number and type of teeth in each species.

2.3.2 Skulls: dorsal view

Most of my landmarks in this view 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 braincase (posterior) and nasal (anterior) area of the skulls (figure 2.3). Table 2.5 describes how I placed the landmarks and drew the outline curves for my dorsal skull pictures

2.3.3 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 2.3). The high variability of my 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 2.6 outlines the descriptions of the landmarks I placed on the ventral pictures.

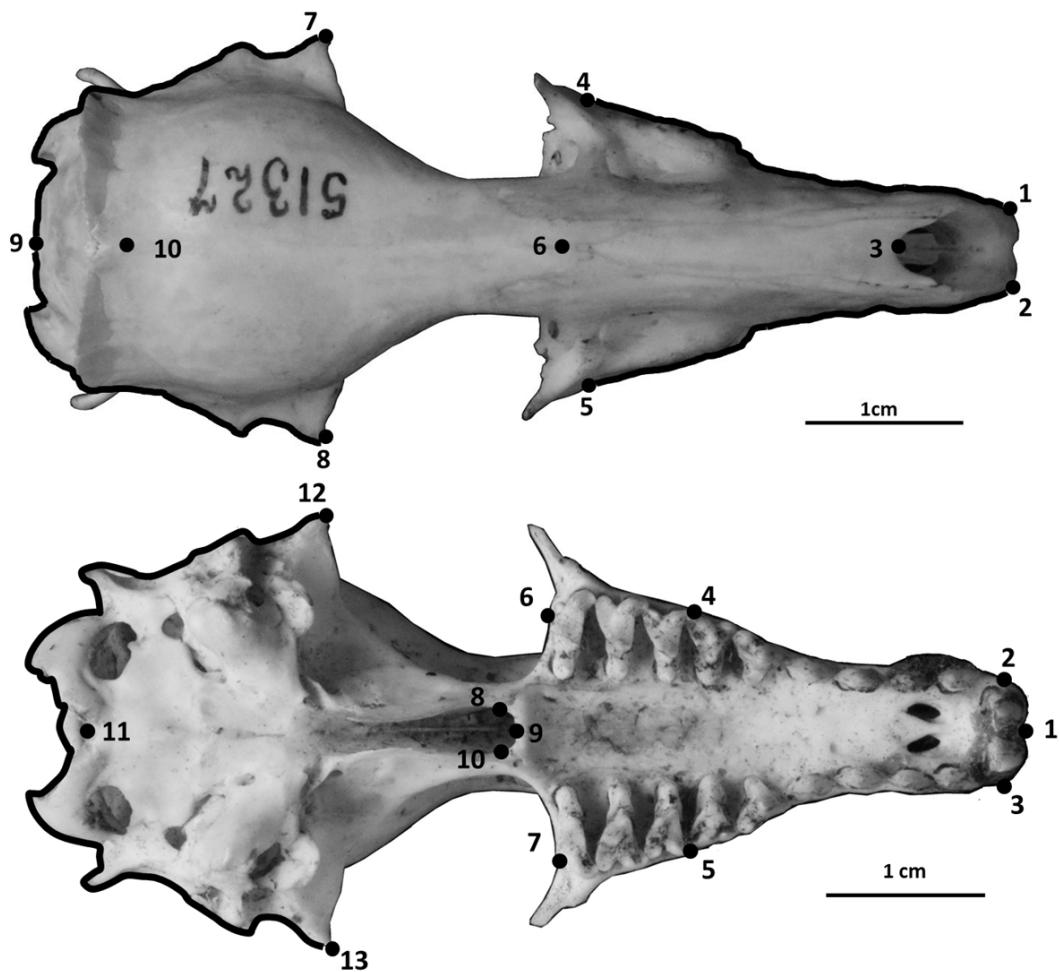


FIGURE 2.3: Landmarks (numbered points) and curves(outlines) for the skulls in dorsal and ventral view. See tables 2.5 and 2.6 for landmark descriptions. The skulls are two different specimens of *Potamogale velox* (otter shrew tenrec), museum accession numbers AMNH 51327 and BMNH 1934.6.16.2.

TABLE 2.5: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in dorsal view (figure 2.3)

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 sagittal and parietal sutures
Curve A (12 points)	Outline of the braincase on the left side, between landmarks 9 and 7 (does not include visible features from the lower (ventral) side of the skull)
Curve B (10 points)	Outline of the palate on the left side, between landmarks 4 and 1 (outline of the rostrum only, not the shape of the teeth)
Curve C (12 points)	Outline of the braincase on the right side, between landmarks 9 and 8 (does not include visible features from the lower (ventral) side of the skull)
Curve D (10 points)	Outline of the palate on the right side, between landmarks 5 and 2 (outline of the rostrum only, not the shape of the teeth)

TABLE 2.6: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in ventral view (figure 2.3).

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 last 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.

2.3.4 Skulls: lateral view

I placed nine landmarks on the lateral pictures (figure 2.4) 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 2.7 describes my definitions for each of the landmark points. If specimens were damaged on their right side I reflected photographs of the left lateral side of the skull so that all pictures would be in the same orientation. 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.

2.3.5 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 pictures of the right side, figure 2.4). I drew separate curves around each of the three processes 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 aspects, 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.

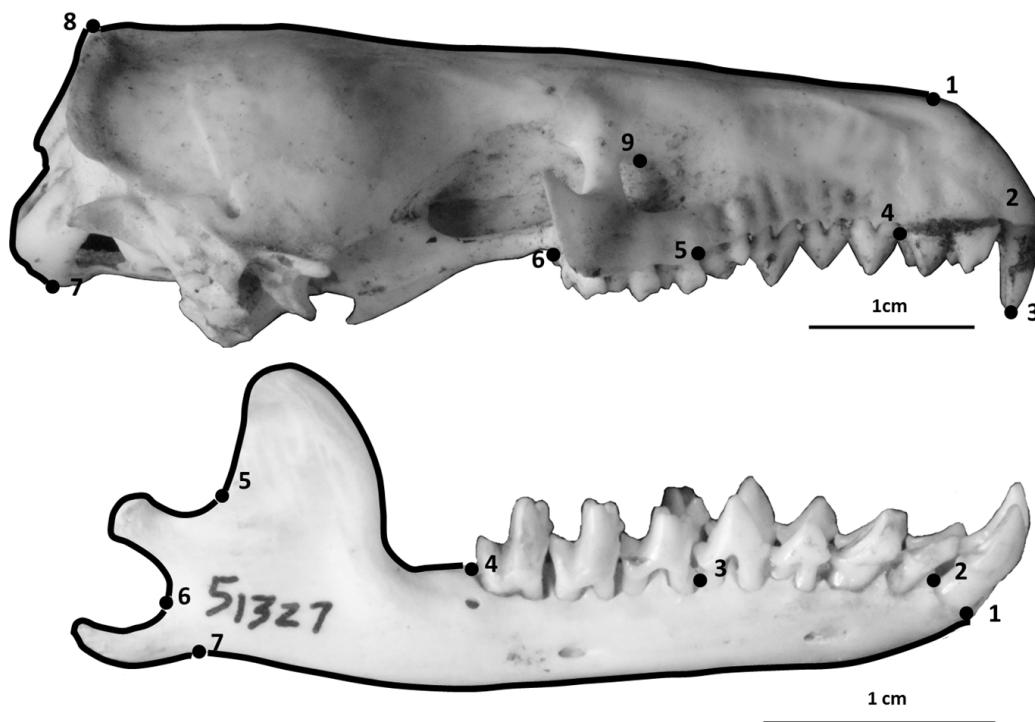


FIGURE 2.4: Landmarks (numbered points) and curves(outlines) for the skulls and mandibles in lateral view. See tables 2.7 and 2.8 for landmark descriptions. The skull (BMNH 1934.6.16.2.) and mandible (AMNH 51327) belong to two different specimens of *Potamogale velox* (otter shrew tenrec).

TABLE 2.7: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in lateral view (figure 2.4).

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 (20 points)	Between points 7 and 8 Back of the skull from the lowest to highest points
Curve B (15 points)	Between points 8 and 1 From the highest point of the braincase to the front of the nasal

TABLE 2.8: Descriptions of the landmarks (points) and curves (semilandmarks) for the mandibles in lateral (buccal) view (figure 2.4).

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	Condylloid 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)

2.3.6 Procrustes superimposition

After creating my files with the landmarks and semilandmarks placed on each picture, I used TPSUtil (Rohlf, 2012) to create "sliders" files that defined which points in the TPS files should be treated as semilandmarks (Zelditch *et al.*, 2012).

I conducted all further morphometric analyses in R version 3.0.2 (R Core Team, 2014) within the geomorph package (Adams *et al.*, 2013).

I placed landmarks and semilandmarks on all the pictures from every specimen. However, for the purposes of comparing morphological diversity in tenrecs to their closest relatives (chapter 3 I only used the tenrec and golden mole subset of the data. However, the TPS files containing landmark coordinates for all remaining species could be used for future analyses of morphological convergence (see discussion in chapter 4).

I used the gpagen function in the geomorph package (Adams *et al.*, 2013) to run a general Procrustes alignment (Rohlf and Marcus, 1993) of the landmark coordinates while sliding the semilandmarks by minimising Procrustes distance (Bookstein, 1997). I used these Procrustes-aligned coordinates of all specimens to calculate average shape values for each species which I then used for a principal components (PC) analysis with the plotTangentSpace function (Adams *et al.*, 2013).

2.4 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.

2.4.1 Taxonomic

I recorded species names as they were written on museum specimen labels and then corrected them to match the taxonomy in Wilson and Reeder's 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 Reeder (2005), I used the taxonomy recorded on the labels.

2.4.2 Specimen ID

There were four specimens from the Smithsonian Institute that 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*.

2.4.3 Specimen sex and age

Age classification of mammal skulls is usually based on dental characteristics and cranial fusion. However, it is difficult to age-classify tenrecs in this way. 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). Furthermore, it is 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 identified and excluded any obviously juvenile specimens based on incomplete

cranial fusion. When specimens could not be obviously identified as juveniles I treated them all as equivalent adult forms. I included both male and female specimens in my data as I am interested in cranial shape of the species as a whole regardless of whether or not there are differences due to sexual size dimorphism.

2.4.4 Linear measurements

As mentioned above (section 2.2.3), I took three replicate measurements of most of my variables and five replicates of other, smaller variables. Some morphometric studies take replicate measurements of a trait and use the average value for further analyses (REFS). 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 (REFS?).

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 $[(\text{minimum difference between neighbouring measurements}) / (\text{range of measured values}) * 100]$. For variables that I 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.

2.4.5 Potential morphometrics errors

I used 2D morphometrics to compare the morphologies of the skulls (section 2.3). 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 have taken me at least 550 hours to scan the 366 specimens that I photographed.

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 can introduce some potential problems of possible image distortion (Arnqvist and Mårtensson, 1998). Similarly, human error with how landmarks are positioned on specimens could also introduce noise into further analyses.

In contrast to detailed intraspecific work (e.g. Bornholdt *et al.*, 2008; Blagojević and Milošević-Zlatanović, 2011) photographic or landmark placement er-

rors are unlikely to be significant in my interspecific study 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 (Arnqvist and Mårtensson, 1998). 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.

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 placed the landmarks on each set of pictures so inter-observer variation in landmark placement 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 Mårtensson, 1998).

To measure potential orientation error, I photographed the skulls (dorsal, ventral and lateral views) and mandibles of each specimen three times, cycling through the pictures so that the specimen was removed and re-positioned before every shot (Viscosi and Cortini, 2011). I used a subset of my ventral skull pictures to test for two sources of error: specimen orientation and landmark placement error (Arnqvist and Mårtensson, 1998; Barrow and Macleod, 2008). Of the specimens which I photographed three times, I chose a random subset of seven skulls from four different Families: 3 tenrecs and single representatives of shrews, moles, hedgehogs and golden moles. I copied these images and placed landmarks on three copies of each image to compare variation in landmark placement within each orientation (three copies of the one image). This gave 9 replicates of each skull: 3 separate pictures, and 3 copies of each

of those pictures. As before, I ran a general Procrustes alignment (Rohlf and Marcus, 1993) of the specimens, calculated the average shape values for each skull (average of all 9 pictures) and used these values for a PC analysis.

I used a nested, linear mixed effects model to model the shape variation (first PC axis) associated with specimen(fixed effect) and two nested random effects: picture identity and picture replicate. I ran the test using the lmer function in the lme4 package (Bates *et al.*, 2014). The model formula was:
lmer(PC1 ~ specimen + (specimen | picture) + (picture | replicate)).

Specimen orientation and landmark placement had negligible effects on the overall shape variation between different skulls ($2.76 \times 10^{-16} \pm 1.66 \times 10^{-8}$ and $7.4 \times 10^{-14} \pm 2.72 \times 10^{-7}$ respectively).

Therefore, I was confident that shape variation between the specimens in the rest of my analyses reflected true morphological differences rather than methodological error.

CHAPTER 3

MORPHOLOGICAL DIVERSITY IN TENRECS COMPARED TO THEIR CLOSEST RELATIVES

3.1 INTRODUCTION

3.2 METHODS

3.3 RESULTS

3.4 DISCUSSION

CHAPTER 4

DISCUSSION

Overall summary of points and implications of findings

4.1 GENERAL DISCUSSION

4.2 POSSIBLE ISSUES

4.3 FUTURE DIRECTIONS

4.3.1 Measuring the adaptiveness of phenotypic traits

4.3.2 Evolutionary predictions of divergence and convergence

4.3.3 Ecological convergence

4.3.4 Studies of behavioural convergence

I have focused on morphological (phenotypic) similarities among tenrecs and other small mammals. These studies could be extended to tests of functional or behavioural convergences among tenrecs and other distantly related species. One particularly interesting extension would be to study echolocatory capabilities in tenrecs.

Gould 1965 demonstrated echolocatory abilities in three species of tenrec; *Echinops telfairi*, *Hemicentetes semispinosus* and *Microgale dobsoni*, indicating that they share behavioural similarities with some shrews (Gould *et al.*, 1964; Tomasi, 1979; Siemers *et al.*, 2009). Subsequent work demonstrated that the auditory range of *Echinops telfairi* includes ultrasonic frequencies (Drexel *et al.*, 2003) and

there have also been physiological investigations of stridulation behaviour in *Hemicentetes* tenrecs (Eisenberg and Gould, 1969; Endo *et al.*, 2010). However, aside from these studies echolocatory capabilities in tenrecs have not been investigated further. Recent studies have found evidence for sequence-level genomic convergence underlying independent origins of echolocation in multiple mammalian lineages (Parker *et al.*, 2013). Therefore, re-assessing and expanding behavioural echolocatory capabilities within tenrecs could be an important first step towards looking for further convergence at the genetic level.

I went to Madagascar in March/April 2014 as part of a research trip led by Dr. Steve Goodman to conduct behavioural tests of echolocation in *Microgale*. My aim was to record the sounds made by the animals as they moved through a wooden maze towards a food reward to determine whether there was evidence that they were using sounds to navigate through their environment. I tried multiple variations of our protocol but unfortunately none of the animals we tested produced any noise (17 individuals from 5 different species). However, it is clear that this negative result is a failure of the experimental design rather than an indication that *Microgale* don't navigate using sounds. My sample included *Microgale dobsoni* which is one of the few species that is known to echolocate from previous experiments (Gould, 1965). Similarly, other more experienced researchers in the group had heard the *Microgale* making sounds while foraging.

Previous studies of echolocation in small mammals (Gould *et al.*, 1964; Gould, 1965; Tomasi, 1979; Siemers *et al.*, 2009) all used captive individuals which were trained to perform specific tasks. Unfortunately such a prolonged procedure was not possible for me within constraints of time and facilities. However similar, more prolonged studies could reveal very interesting insights into echolocatory behaviour and capabilities within tenrecs. This work would also fit in with a more holistic view of understanding convergence among tenrecs and other

CHAPTER 4

small mammals within morphological, ecological, behavioural and potentially genetic contexts.

4.4 CONCLUSIONS

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