

**EVOLUTIONARY MORPHOLOGY OF THE POSTCRANIAL SKELETON IN
AFRO-MALAGASY TENRECOIDEA (MAMMALIA)**

by

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Abstract

EVOLUTIONARY MORPHOLOGY OF THE POSTCRANIAL SKELETON IN
AFRO-MALAGASY TENRECOIDEA

by

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The 26+/- extant species of small mammals in Tenrecoidea live in a diverse range of microhabitats, primarily in Madagascar, and provide an excellent model for exploring the adaptive and phylogenetic significance of skeletal form. This study is a descriptive and quantitative morphological assessment of the tenrecoid skeleton with a focus on postcranial elements and identification of habitus- and heritage-related characters. 273 specimens from ten genera of Tenrecoidea and three outgroups (Macroscelididae, Erinaceidae, and Solenodontidae) were studied and digitally imaged for acquisition of two-dimensional landmark data. Results were evaluated in an ecological and evolutionary framework; features were assessed in the context of known positional behaviors and tested against current phylogenetic hypotheses.

Comparisons of the Tenrecinae and Oryzorictinae postcranium indicated a basic difference in postural behavior between the two major subfamilies, which was confirmed by observations of live animals during field study in Madagascar. The tenrecine hindlimb is more habitually laterally abducted, and more multiaxially mobile than that of the oryzorictines, as reflected at the hip, knee, and upper ankle joints. Despite their superficial similarities, *Echinops* and *Setifer* exhibit a series of differences based on arboreal locomotor behavior in the former and more terrestrial behavior in the latter. *Oryzorictes*

has a suite of postcranial adaptations related to its subterranean microhabitat, but these are distinct from those of *Hemicentetes*, illustrating their different digging-styles and independent acquisition of digging-related traits. Although *Microgale cowani* is not known to be a digger, it shares a series of characters with *Oryzorictes*, and most likely has a more fossorial lifestyle than previously recorded. Although *Limnogale* and *Potamogale* share postcranial adaptations for swimming behaviors, few characteristics are similar between the two. *Limnogale* is most likely part of the oryzorictine clade, leaving the Malagasy Tenrecidae as an intact monophyletic taxon. A family-level potamogalid status is supported. Solenodontids, macroscelidids, and erinaceids are considered as tenrecoid outgroups and higher-level eutherian phylogeny is discussed. Finally, I present a preliminary overview of the tenrecoid skull, axial skeleton, and cross-sectional geometry of the humerus and femur with recommendations for future work.

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TABLE OF CONTENTS

CHAPTER I: Introduction	p.1
Tenrecoid ecology and locomotor behavior	
Tenrecoid phylogeny	
The postcranial skeleton as phylogenetic and functional indicator	
References cited	
CHAPTER II: Tarsal Complex	p.42
Introduction	
Materials and methods	
Results and discussion	
Upper ankle joint, distal crus	
Upper ankle joint, dorsal astragalus	
Lower ankle joint, dorsal calcaneus	
Transverse tarsal joint, astragalar head and neck	
Transverse tarsal joint, distal calcaneus	
Distal tarsals and metatarsals	
Summary and conclusions	
References cited	
Appendix 2.1. Linear measurements	
Appendix 2.2. Linear measurement means/SDs	
Appendix 2.3. Raw index scores	
Appendix 2.4. Index summary statistics and Tukey post-hoc results	
CHAPTER III: Carpal Complex	p.117
Introduction	
Primary carpal joints	
Materials and methods	
Results and discussion	
Proximal carpal joint	
Mid-carpal joint	
Distal carpal joint	
Summary and conclusions	
References cited	
Appendix 3.1. Linear measurements	
Appendix 3.2. Linear measurement means/SDs	
Appendix 3.3. Raw index scores	
Appendix 3.4. Index summary statistics and Tukey post-hoc results	
CHAPTER IV: Hindlimb	p.201
Introduction	

Pelvis and hip joint	
Femur, tibia and knee joint	
Tibia and fibula	
Materials and methods	
Results and discussion	
Pelvis	
Proximal femur	
Distal femur	
Tibia/fibula	
Summary and conclusions	
References cited	
Appendix 4.1. Linear measurements	
Appendix 4.2. Linear measurement means/SDs	
Appendix 4.3. Raw index scores	
Appendix 4.4. Index summary statistics and Tukey post-hoc results	

CHAPTER V: Forelimb p.313

Introduction	
General form and variation of the scapula and forelimb	
Materials and methods	
Results and discussion	
Scapula	
Humerus	
Ulna	
Radius	
Summary and conclusions	
References cited	
Appendix 5.1. Linear measurements	
Appendix 5.2. Linear measurement means/SDs	
Appendix 5.3. Raw index scores	
Appendix 5.4. Index summary statistics and Tukey post-hoc results	

CHAPTER VI: Axial Skeleton, Skull, and Cross-Sectional Geometry p.411

Functional morphology of the axial skeleton: a preliminary qualitative analysis	
Material and methods	
Results and discussion	
Summary and conclusions	
Functional morphology of the skull: a preliminary qualitative analysis	
Material and methods	
Results and discussion	
Summary and conclusions	
Long bone cross-sectional geometry	
Material and methods	
Results and discussion	

Summary and conclusions	
References cited	
Appendix 6.1. Cross-sectional geometry data	
Appendix 6.2. Tukey post-hoc results for cortical area/body mass	

<u>SUMMARY</u>	<u>p.464</u>
<u>APPENDIX I.: Specimen list</u>	<u>p.471</u>
<u>COMPLETE REFERENCES CITED</u>	<u>p.475</u>

Tables

Table 1.1. Taxonomy of studied tenrecoid taxa	p. 4
Table 1.2. Tenrecoid taxonomy from Simpson, 1945	p. 22
Table 2.1. Sample taxonomy and primary locomotor behavior	p. 50
Table 2.2. Measurements	p. 50
Table 2.3. Indices	p. 51
Table 3.1. Aspects of the mammalian carpus with proposed functional significance	p. 123
Table 3.2. Condition of the proximal carpal row in mammalian taxa	p. 125
Table 3.3. Taxonomy and primary locomotor behavior	p. 130
Table 3.4. Measurements	p. 130
Table 3.5 Indices	p. 131
Table 4.1. Aspects of the mammalian hindlimb with proposed functional significance	p. 208
Table 4.2. Taxonomy and primary locomotor behavior	p. 212
Table 4.3. Measurements	p. 212
Table 4.4. Indices	p. 214
Table 5.1. Aspects of the mammalian forelimb with proposed functional significance	p. 321
Table 5.2. Taxonomy and primary locomotor behavior	p. 324
Table 5.3. Measurements	p. 324
Table 5.4. Indices	p. 325
Table 6.1. Taxonomy and primary locomotor behavior	p. 414
Table 6.2. Taxonomy and primary locomotor behavior	p. 430
Table 6.3. Sample for cross-sectional geometric analyses	p. 446

Figures

Figure 1.1. Representative tenrecoids	p. 7
Figure 1.2. Tenrecoid phylogeny – Asher	p. 23
Figure 1.3. Ordinal-level mammalian relationships	p. 25
Figure 2.1. Left foot of <i>Hemicentetes</i>	p. 45
Figure 2.2. Anterior view of distal crus	p. 45
Figure 2.3. Two astragalar views of <i>Tenrec</i>	p. 46
Figure 2.4. Three calcaneal views of <i>Tenrec</i>	p. 46
Figure 2.5. Distal tarsal and metatarsal complex of <i>Echinops</i>	p. 47
Figure 2.6. Distal crus measurements	p. 52
Figure 2.7. Astragalus measurements	p. 52
Figure 2.8. Calcaneus measurements	p. 53
Figure 2.9. Distal tarsal/metatarsal measurements	p. 53
Figure 2.10. Distal crus comparisons	p. 55
Figure 2.11. Medial/lateral malleolus index	p. 56
Figure 2.12. Malleolus Depth Index- tenrecines	p. 57
Figure 2.13. Medial/Lateral Malleolus Index- tenrecines vs. oryzorictines	p. 57
Figure 2.14. Medial/Lateral Malleolus Index- oryzorictines	p. 58
Figure 2.15. Medial/Lateral Malleolus Index by subfamily	p. 58
Figure 2.16. Malleolus Depth Index by subfamily	p. 59
Figure 2.17. Anterior Tibial Tubercle Index – tenrecines	p. 61
Figure 2.18. Anterior Tibial Tubercle Index by subfamily	p. 61
Figure 2.19. Tenrecine vs. oryzorictine foot position – live animals	p. 62
Figure 2.20. Dorsal astragalus comparison	p. 65
Figure 2.21. Trochlear Crest Height Index - tenrecines	p. 66
Figure 2.22. Medial/Lateral Trochlear Crest Height Index - tenrecines	p. 67
Figure 2.23. Trochlear Crest Midpoint Index by subfamily	p. 68
Figure 2.24. Distal astragalus comparisons	p. 68
Figure 2.25. Calcaneal Length Index by subfamily	p. 70
Figure 2.26. Dorsal calcaneus comparisons	p. 70
Figure 2.27. Calcaneal Astragalocalcaneal Facet Index by subfamily	p. 71
Figure 2.28. Calcaneal Tuber Length Index by subfamily	p. 72
Figure 2.29. Calcaneal Tuber Length Index – tenrecines vs. oryzorictines	p. 73

Figure 2.30. Astragalar Neck Width Index - oryzorictines	p. 76
Figure 2.31. Distal articular surface of the astragalar head - comparisons	p. 77
Figure 2.32. Peroneal Process Position Index by subfamily	p. 80
Figure 2.33. Right foot comparisons	p. 81
Figure 2.34. Navicular Proximomedial Shelf Index - tenrecines	p. 82
Figure 2.35. Navicular Proximomedial Shelf Index – <i>Microgale spp.</i>	p. 82
Figure 2.36. Metatarsal III Shape Index by subfamily	p. 83
Figure 2.37. Metatarsal III Shape Index - oryzorictines	p. 83
Figure 3.1. Dorsal aspect of the carpus	p. 120
Figure 3.2. Linear measurements taken from the carpals and metacarpals	p. 127
Figure 3.3. Linear measurements taken from the distal ulna/radius	p. 128
Figure 3.4. Linear measurements taken from the lateral and medial sides of carpus	p. 128
Figure 3.5. Distal articular surfaces of the left radius and ulna in <i>Echinops</i>	p. 133
Figure 3.6. Distal articular surfaces of the radius and ulna - comparisons	p. 134
Figure 3.7. Radial Width Index – tenrecines and oryzorictines	p. 136
Figure 3.8. Ulnar Width Index	p. 139
Figure 3.9. Distal antebrachium comparisons	p. 139
Figure 3.10. Lateral side of the distal ulna, carpus and the first metacarpal - comparisons	p. 141
Figure 3.11. Pisiform Length Index - tenrecines	p. 142
Figure 3.12. Pisiform Shape Index	p. 143
Figure 3.13. Proximal articular surfaces of the first carpal row - comparisons	p. 146
Figure 3.14. Scaphoid-lunate Cuneiform Width Index - tenrecines	p. 147
Figure 3.15. Carpal complex, dorsal view - comparisons	p. 150
Figure 3.16. Unciform-Magnum Size Index - tenrecines	p. 151
Figure 3.17. Unciform Shape Index - tenrecines	p. 152
Figure 3.18. Centrale Shape Index - tenrecines	p. 153
Figure 3.19. Radial side of the carpus - comparisons	p. 156
Figure 3.20. Prepollex Shape Index - tenrecines	p. 156
Figure 3.21. Dorsal view of the hand - comparisons	p. 159
Figure 3.22. Indices related to length and shape of the metacarpals and phalanges in Tenrecinae	p. 161
Figure 3.23. Indices related to length and shape of the metacarpals and phalanges in Oryzorictinae	p. 162
Figure 3.24. Metacarpal Robusticity Index – tenrecines vs. oryzorictines	p. 164
Figure 3.25. Dorsal view of carpals and metacarpals of the oryzorictine digger <i>Oryzorictes</i>	p. 164
Figure 3.26. Claws of the second digit - comparisons	p. 165
Figure 4.1. <i>Hemicentetes</i> pelvis	p. 203
Figure 4.2. <i>Microgale cowani</i> femur	p. 205
Figure 4.3. <i>Tenrec ecaudatus</i> tibia and fibula	p. 206
Figure 4.4. Linear measurements taken from the pelvis, femur, and tibia	p. 213
Figure 4.5. Lateral pelvis – comparisons	p. 215
Figure 4.6. Acetabulum Size Index – tenrecines	p. 215
Figure 4.7. Acetabulum shape index – tenrecines	p. 217
Figure 4.8. Obturator Foramen Shape Index	p. 218
Figure 4.9. Ischium Dorsal Shape Index - tenrecines	p. 220
Figure 4.10. Pelvis/Femur Length Index	p. 221
Figure 4.11. Pelvis length relative to femur length	p. 221
Figure 4.12. Anterior views of femora - comparisons	p. 223
Figure 4.13. Proximal articular surfaces of femora – comparisons	p. 224
Figure 4.14. Femoral Head Size Index– tenrecines	p. 224
Figure 4.15. Anterior views of proximal femora - comparisons	p. 226
Figure 4.16. Femoral Head Width Index - tenrecines	p. 227
Figure 4.17. Femoral Head Depth Index – tenrecines vs. oryzorictines	p. 227
Figure 4.18. Femoral Neck Width Index – tenrecines vs. oryzorictines	p. 228
Figure 4.19. Greater Trochanter Height Index	p. 229
Figure 4.20. Lesser Trochanter Size Index - tenrecines	p. 231
Figure 4.21. Lesser Trochanter Position Index	p. 231
Figure 4.22. Third Trochanter Shape Index – tenrecines vs. oryzorictines	p. 233

Figure 4.23. Third Trochanter Position Index	p. 234
Figure 4.24. Anterior views of distal femora - comparisons	p. 236
Figure 4.25. Patellar Groove Width Index	p. 236
Figure 4.26. Distal Femur Width Index – tenrecines	p. 237
Figure 4.27. Patellar Groove Shape Index	p. 237
Figure 4.28. Posterior views of distal femora - comparisons	p. 238
Figure 4.29. Distal views of femora - comparisons	p. 239
Figure 4.30. Femoral Condyle Shape Index	p. 240
Figure 4.31. Femoral Condyle Depth Index	p. 241
Figure 4.32. Medial/Lateral Femoral Condyle Index	p. 241
Figure 4.33. Proximal articular surfaces of tibiae/fibulae – comparisons	p. 243
Figure 4.34. Tibial Tuberosity Shape Index	p. 243
Figure 4.35. Medial/Lateral Tibial Condyle Index	p. 244
Figure 4.36. Posterior views of proximal tibiae and fibulae - comparisons	p. 244
Figure 4.37. Anterior views of crura - comparisons	p. 248
Figure 4.38. Tibia Shape Index - tenrecines	p. 249
Figure 4.39. Tibia Shape Index	p. 250
Figure 4.40. Femur/Tibia Length Index	p. 251
Figure 5.1. <i>Potamogale</i> and <i>Echinops</i> scapulae	p. 316
Figure 5.2. <i>Solenodon</i> and <i>Microgale</i> humeri	p. 319
Figure 5.3. <i>Setifer</i> , <i>Limnogale</i> , and <i>Tenrec</i> radii and ulnae	p. 320
Figure 5.4. Linear measurements of forelimb elements used for indices	p. 326
Figure 5.5. Lateral views of scapulae – comparisons	p. 328
Figure 5.6. Scapula Shape Index – tenrecines and oryzorictines	p. 329
Figure 5.7. Dorsal view of scapulae – comparisons	p. 331
Figure 5.8. Acromion Process Length Index - tenrecines and oryzorictines	p. 332
Figure 5.9. Articular surface of scapulae - comparisons	p. 333
Figure 5.10. Glenoid Fossa Shape Index – tenrecines and oryzorictines	p. 335
Figure 5.11. Anterior view of humeri – comparisons	p. 337
Figure 5.12. Humerus Shape Index	p. 338
Figure 5.13. Humerus/Radius Length Index (brachial index)	p. 338
Figure 5.14. Proximal articular surfaces of humeri - comparisons	p. 339
Figure 5.15. Humeral Head Shape Index - tenrecines	p. 340
Figure 5.16. Humeral Head Shape Index	p. 341
Figure 5.17. Proximal articular surfaces of humeri in two digging tenrecoids	p. 341
Figure 5.18. Posterior surfaces of humeri - comparisons	p. 343
Figure 5.19. Greater Tuberosity Size Index and Lesser Tuberosity Size Index - tenrecines	p. 345
Figure 5.20. Distal surfaces of humeri - comparisons	p. 347
Figure 5.21. Distal Humerus Width Index	p. 348
Figure 5.22. Medial Epicondyle Width Index - oryzorictines	p. 348
Figure 5.23. Medial Epicondyle Width Index	p. 349
Figure 5.24. Lateral Epicondyle Width Index	p. 349
Figure 5.25. Anterior views of distal humeri - comparisons	p. 353
Figure 5.26. Trochlear Height Index – tenrecines	p. 353
Figure 5.27. Anterior surfaces of ulnae and radii - comparisons	p. 355
Figure 5.28. Medial views of ulnae and radii – comparisons	p. 356
Figure 5.29. Ulnar Width Index	p. 357
Figure 5.30. Olecranon Process Length Index	p. 357
Figure 5.31. Olecranon Process Length Index - oryzorictines	p. 358
Figure 5.32. Radius Width Index	p. 359
Figure 5.33. Proximal surfaces of radii - comparisons	p. 360
Figure 6.1. Lateral view of cervical and thoracic vertebrae and ribs – comparisons	p. 417
Figure 6.2. Right lateral view of ribs in an arboreal tenrecine and a terrestrial digging tenrecine	p. 418
Figure 6.3. Right lateral view of thoracic spines in <i>Oryzorictes</i> and <i>Microgale</i>	p. 418
Figure 6.4. Lateral view of the axis - comparisons	p. 421
Figure 6.5. Lateral view of axis in two tenrecines	p. 421

Figure 6.6. Anterior view of the atlas – comparisons	p. 423
Figure 6.7. Anterior view of the atlas in <i>Echinops</i> and <i>Hemicentetes</i>	p. 424
Figure 6.8. Dorsal view of the skull – comparisons	p. 433
Figure 6.9. Lateral view of the cranium – comparisons	p. 435
Figure 6.10. . Lateral view of the cranium in <i>Oryzomys</i>	p. 435
Figure 6.11. Ventral view of the skull – comparisons	p. 437
Figure 6.12. Lateral view of the right mandible	p. 439
Figure 6.13. Cross-sectional comparisons of the humerus and femur	p. 449
Figure 6.14. Cortical area in six tenrecid species, shown as a function of body size	p. 451
Figure 6.15. Cortical area of the humerus/cortical area of the femur	p. 451
Figure 6.16. Cross-section of the femur midshaft	p. 453
Figure 6.17. Cross-section of the humerus midshaft	p. 454
Figure 6.18. Cross-sections and anterior views of the humerus	p. 454

CHAPTER I

AN INTRODUCTION TO TENRECOIDEA ECOLOGY, PHYLOGENY, AND FUNCTIONAL MORPHOLOGY

“Living matter is forever dealing with a future by means of a present which has grown out of a past... the past is irrevocable and cumulative and thus progressively limits the ‘freedom’ of the future”

W.K. Gregory, 1924.

Introduction

Tenrecoidea includes ten genera represented by twenty-six extant species, twenty-three of which have been isolated on Madagascar since at least the mid-Miocene (Tenrecinae and Oryzorictinae), and three of which are still found on mainland Africa (Potamogalidae^{*}). From the hedgehog-like *Setifer*, to the otter-like aquatic *Limnogale* to the mole-like fossorial *Oryzorictes*, tenrecids show an extensive range of morphologies and correlated biological roles. This diversity coupled with the long-standing isolation of tenrecids on Madagascar has made the tenrecids a textbook example of adaptive radiation. In the sense that adaptive radiation is an “ecological divergence (of a taxon) accompanied by morphological and physiological changes that elevate the capacity to utilize those environments” (Schluter, 2000, p19), the tenrecoids, and the Malagasy tenrecids in particular, seem to fit the mold. Alternatively, tenrecids have been cited as models of primitive, underived eutherians due to their retention of mammalian plesiomorphies such as a cloaca, heterothermic regulation, altricial young, and undescended testes (e.g., Crompton, 1978; Helglund, 1979). Aside from cursory

^{*} The familial name Potamogalidae (Allman, 1865) is used here as opposed to including potamogalines in Tenrecidae (for discussion, see Salton and Szalay, 2004)

acknowledgements that tenrecoids are superficially diverse, convergent with other mainland mammalian taxa, and yet retain a number of primitive eutherian traits, relationships between tenrecoid morphology and ecology remain virtually unexplored.

In addition to functional morphology, there are many questions regarding Tenrecoidea* phylogeny, both within the two tenrecoid families and between tenrecoids and other eutherians, that remain unresolved. There have been a few recent attempts to clarify relationships within and between the two families Tenrecidae and Potamogalidae (Asher, 1999, 2001; Olson and Goodman, 2003), yet their resulting taxonomies and biogeographic hypotheses are not in agreement and several key issues are not addressed. Furthermore, tenrecoid phylogeny has received a great deal of recent attention in the literature because of its important role for understanding ordinal and superordinal-level mammalian phylogeny (Asher et al., 2002; Springer et al., 2004). Although Tenrecoidea monophyly is not disputed, the taxon plays a key position in determining the monophyletic status of the proposed groups Lipotyphla and Afrotheria, and the alternate biogeographic scenarios associated with each. Although other lipotyphlans (classic “insectivorans”), such as shrews and moles, share several primitive characteristics with tenrecoids, molecular studies suggest that tenrecoids, along with golden moles, may be more closely related to other African mammals such as elephants and hyraxes (Springer et al., 1997; Stanhope et al., 1998a,b; Emerson, 1999; Madsen et al., 2001; Murphy et al., 2001; van Dijk et al. 2001). Paleontological data does not support the hypothesis of a monophyletic Afrotheria (Zack et al., 2005), leaving tenrecoid ordinal relationships

* As used in this paper “Tenrecoidea” includes only the Malagasy tenrecids and the African potamogalids, and does not include solenodontids unless otherwise stated.

unresolved. The relationship between tenrecids and the enigmatic West Indian zambododont *Solenodon* is also unclear, with its attendant biogeographic implications.

This study is the first broad-scale comparison of tenrecoid skeletal morphology concerned with the adaptive aspects of the skeleton and focused on the postcranium. Morphology of selected areas of the skeleton in tenrecoids and several outgroups (*Solenodon*, *Petrodromus*, and *Echinosorex*) are descriptively and quantitatively analyzed in relation to known ecological factors and the known positional (locomotor and postural) behaviors of the selected species. The adaptive significance of various skeletal traits, and differences between species, are assessed in the context of their differential substrate use. Once defined attributes of the skeleton are analyzed in terms of their functional-adaptive and historical significance (e.g., *fide* Bock, 1981; Szalay, 2000) I attempt to improve the phylogenetic estimation within Tenrecoidea and between Tenrecoidea and several proposed outgroup taxa. Within each chapter I address:

- 1) To what degree do aspects of the tenrecoid postcranial skeleton exhibit convergence with other mammalian locomotor specialists? Which regions of the skeleton demonstrate considerable plasticity of form in response to known positional behaviors, and in what way do the details of convergent form differ?
- 2) Are there postcranial homologies between tenrecoid subfamilies and/or genera that are useful for resolving intra-tenrecoid phylogenetic relationships?
- 3) Do any shared traits between tenrecoids and solenodons (*Solenodon*), elephant shrews (*Petrodromus*), and/or gymnures (*Echinosorex*) indicate meaningful phylogenetic affiliation(s) between taxa?

Tenrecoid Ecology and Locomotor Behavior

Four tenrecoid subfamilies are currently recognized, including Potamogalinae, Tenrecinae, Oryzorictinae, and Geogalinae (Olson and Goodman, 2003; Salton and Szalay, 2004; see Table 1.1). Tenrecoidea here refers to the two families Potamogalidae and Tenrecidae, whereas some earlier texts include the West Indian solenodontids (e.g., Butler, 1956; Simpson, 1945; Van Valen, 1967), and some consider *Potamogale* and *Micropotamogale* as part of a tenrecid subfamily (e.g., McKenna and Bell, 1997; Asher, 2000; Olson and Goodman, 2003). Although an estimate of the number of Malagasy founder species is still under contention (e.g., Asher, 1999; Olson and Goodman, 2003), one or possibly two species most likely rafted to the island across the 400km Mozambique Channel between 45-26 Ma (Martin, 2000). Tenrecids may have been the first mammals to arrive to Madagascar, and therefore would not have encountered competition from other mammals for at least several million years (Krause 1997). Furthermore, Madagascar offers a great variety of habitat types within its delimited geography of 590,000km², including lowland and montane rainforests, dry deciduous forests, xerophytic forests, palm savannas, and rapidly expanding regions of anthropogenic grassland. On the bases of habitat availability and range, the assertion that tenrecid interspecific variation is the result of “one of the more spectacular adaptive radiations of mammals in the world” (Jenkins et al., 1996) seems reasonable. Early Malagasy tenrecids lacked the major ecological constraints imposed by the presence of other mammals that might restrict mammalian immigrants when entering new geographical arenas. These

circumstances allowed for their expansion into a variety of habitat types, and their subsequent adaptations.

Tenrecids are also a common textbook example of morphological evolutionary convergence, the Malagasy species being somewhat of a caricature of the other insectivorans, including forms with superficial similarities to hedgehogs (*Echinops* and *Setifer*), shrews (*Microgale*), gymnures (*Tenrec*) and moles (*Oryzorictes*). These multiple cases of convergence and the wide range of ecological roles of tenrecoids provide an ideal foundation for testing the specifics of their radiation, and exploring a variety of form-function and birole related questions. To what degree are aspects of tenrecoid skeletons correlated with their locomotor behavioral repertoires? Do superficial convergences with other mammals translate to skeletal features as well, and, if so, where and how? A first step to addressing these questions is an exploration of tenrecoid habitat and locomotor behavior.

The few available empirical studies that mention tenrecoid locomotion are based on animals in captivity and these cannot account for a complete repertoire of habitual positional behaviors. Nonetheless, there are generalizations about the locomotor modes of several tenrecoids based primarily on the works of Eisenberg and Gould (1966, 1970), Rand (1935), Honegger (1965), and Stephenson (1994). In addition to these reports, I was able to observe several tenrec species in Madagascar during two field trips in Winter 2002-2003, and Summer 2003. Live-captured animals (*Echinops telfairi*, *Setifer setosus*, *Hemicentetes semispinosus*, *Microgale cowani*, *M. dobsoni*, *Oryzorictes tetradactylus*, *Geogale aurita*) were kept in a large plastic enclosure and I observed and videotaped locomotor and postural behavior on a variety of substrates. Several species (*E. telfairi*, *M.*

cowani, *M. dobsoni*, *O. tetradactylus*, *G. aurita*) were run on a portable treadmill and their locomotor behavior was videotaped at incremental speeds.

The following brief overview of tenrecoid general ecology and positional behavior is based on published accounts with some personal comment on observed locomotor behavior. *Solenodon*, *Petrodromus*, and *Echinosorex* were used as outgroups in this study and are therefore also discussed.

TABLE 1.1. Taxonomy of studied tenrecoid taxa
(based on Salton and Szalay, 2004)

Tenrecoidea
Potamogalidae
Potamogalinae
<i>Micropotamogale</i> (sp=2)
<i>Potamogale</i> (sp=1)
Tenrecidae
Geogalinae
<i>Geogale</i> (sp=1)
Tenrecinae
<i>Echinops</i> (sp=1)
<i>Hemicentetes</i> (spp=2)
<i>Setifer</i> (sp=1)
<i>Tenrec</i> (sp=1)
Oryzorictinae
<i>Limnogale</i> (sp=1)
<i>Microgale</i> (sp=15)
<i>Oryzorictes</i> (spp=2-3)

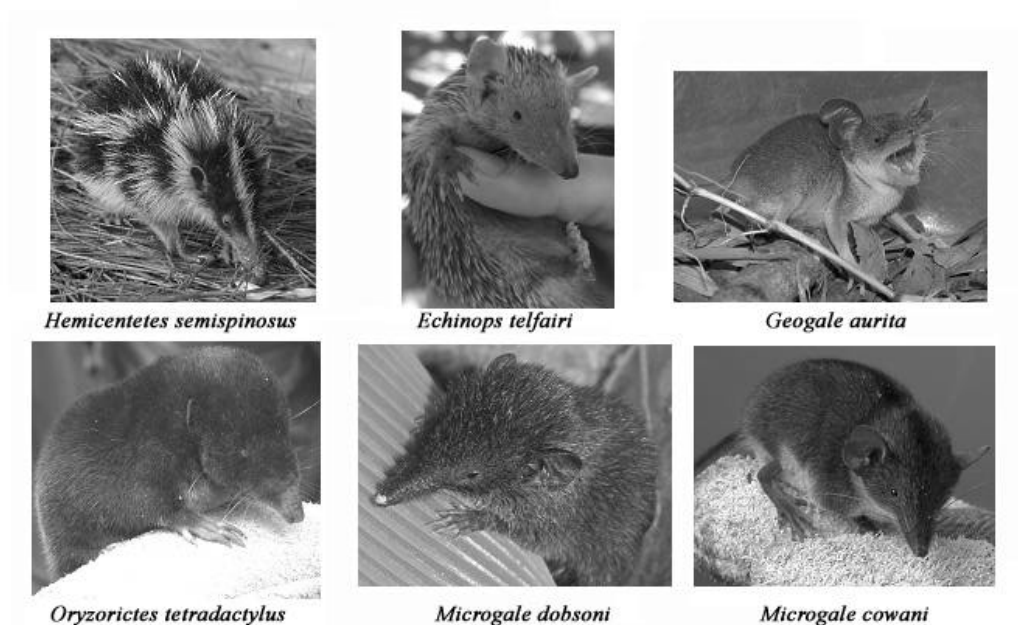


Figure 1.1. Representative tenrecoids (images from Madagascar fieldwork, 2003)

Tenrecinae: This group includes four genera endemic to Madagascar: *Echinops*, *Hemicentetes*, *Setifer*, and *Tenrec*. All four genera are relatively tailless with some form of spines emerging from the dorsal pelage. Of these, all but *Hemicentetes* have been kept in zoos worldwide, and *Echinops* is currently bred for neurological research at the University of Munich. There is, therefore, a small body of literature that describes tenrecine locomotor behavior (Hoenegger and Noth, 1965; Eisenberg and Gould, 1970; Helglund, 1979).

Echinops and *Setifer*, the lesser and greater hedgehog tenrec respectively, are both characterized by a very densely-spined, thick pelage which is remarkably similar to that of the European hedgehog, *Erinaceus europaeus* (see Zherebtsova et al., 2001). The two genera are difficult to distinguish from superficial characteristics, except that *Setifer* tends to be slightly larger than *Echinops* (~225g vs. ~180g). *Echinops* has four fewer molars than *Setifer* (32 vs. 36), but otherwise, skeletal differences between the two have not been described.

Echinops (1 sp) is found in the more arid habitats of southwestern Madagascar, including dry forest, scrub, cultivated land, dry coastal regions, and semi-deserts. Rather than burrowing in subterranean dens, as do *Tenrec* and *Hemicentetes*, they rest in trees and under logs. All of the 44 animals studied in our 2003 Madagascar field season were found in trees, from approximately one-two meters off of the ground, which led us to believe that *Echinops* is indeed a habitual climber. In a captive environment, if a stick or small log is introduced, *Echinops* will almost immediately climb to reach the highest point of the enclosure (pers. obs.). Although the tail is not well developed, a caudal overhang of spinous skin is used as a brace against the branch as it climbs (Eisenberg and Gould, 1970, pers. obs.). While this animal seems an unlikely climber given its thick, rounded body and stocky limbs it moves skillfully from branch to branch, slowly grasping with its hands and feet. When walking and climbing, its hands and feet are plantigrade, and when running, the heel is lifted off the ground. It climbs down trees with hands and head first (Hoenegger and Noth, 1965; pers. obs.) and laterally reverses the hind feet on descent, similar to a squirrel or kinkajou. Hoenegger and Noth (1965) provide a detailed account of *Echinops*' climbing behavior that suggests *Echinops* will climb to explore for prey in addition to nesting. When branches were introduced to *Echinops*' captive environment, the animals spent "stundenlang" (hours) climbing; but after the branches were thoroughly explored the animals returned to the ground. When a live grasshopper was introduced to an individual's cage, the animal climbed and balanced amongst the branches to capture it.

Hoenegger and Noth (1965) also observed several juveniles and adults perform the same peculiar locomotor behavior, which seems related to predator escape: while

climbing, the animal released the branch with its forepaws and hung with its head and hands stretched towards the ground, grasping the branch with laterally turned, flexed and abducted hind feet. It then released its hold, dropped to the ground, and landed full-force on extended hands. Juveniles showed a particular affinity for this behavior, occasionally doing it several times serially, and sometimes curling into a defensive, hedgehog-like position following the fall. Eisenberg and Gould (1970) commented that newborns have difficulty coordinating hind limb movement, but are already able to curl their bodies into a protective ball. By two weeks of age, individuals walk using a crossed extension pattern.

A diagnosis of *Echinops*' locomotor behavior would therefore be semi-arboreal, most likely climbing for shelter and prey capture, as well as foraging on the ground. Although other tenrecids *can* climb (Eisenberg and Gould, 1970; pers. obs.), *Echinops* is most likely the only species that habitually does so. It is therefore expected that postcranial skeletal characteristics related to *Echinops*' mode of arboreal behavior are present.

There is less known about the locomotor behavior of *Setifer* (1 sp.). This species is found in a variety of Malagasy habitats, including dryforests of southern Madagascar and rainforests of northern and eastern Madagascar. *Echinops* and *Setifer* are found in overlapping regions in the southwest (Garbutt, 1999; pers. obs.) This suggests that there may be a microhabitat overlap between these two species. Unlike *Echinops*, *Setifer* nests in underground burrows that are either formed naturally (e.g., tree root hollows) or formed by the individual (Eisenberg and Gould, 1970). Individuals are found foraging on the forest floor, probing soil and leaf litter for invertebrates. Like *Echinops*, *Setifer*

newborns have a difficult time coordinating hindlimb movement. Adults are plantigrade when walking and digitigrade when running, and Eisenberg and Gould (1970) recorded an individual running at 3ft per second, but movement on the ground is generally slow and deliberate (pers. obs.). *Setifer* will climb when prodded up a branch and climbs well, but it is most likely not a habitual climber (Eisenberg and Gould, 1970, pers. obs.). The locomotor behavior of *Setifer* can be generalized as primarily terrestrial, with climbing and digging abilities.

The other tenrecine genera, *Hemicentetes* and *Tenrec*, are divergent in overall size (145g vs. 2000g), yet *Hemicentetes* adults and *Tenrec* juveniles share external similarities such as a pelage with well-defined longitudinal stripes, and a specialized “stridulating organ”^{*} (Eisenberg and Gould, 1970) in the mid-dorsum. As *Tenrec* grows, these characteristics are lost, and the spines are reduced and become comparably soft. *Hemicentetes* (2 spp.), streaked tenrecs, are the smallest of the Tenrecinae, weighing from 130-160g. They inhabit eastern Malagasy rainforests and higher elevation plateau savannas. Individuals are spined, like *Echinops* and *Setifer*, but the spines are sharper and detachable. A densely spined area in the mid-dorsum can vibrate independently, which is most likely a means for some sort of communication. Longitudinal white stripes span the otherwise black- or brownish colored animal.

The skull of *Hemicentetes* is elongated, and the dental formula is 3/3,1/1,3/3,3/3 compared to *Echinops* (3/3,1/1,2/2,2/2), *Setifer*, (3/3,1/1,2/2,3/3), and *Tenrec*, (2/3,1/1,3/3,4-3/3). Fragile small teeth, and elongation of skull may relate to a primary diet of earthworms, and *Hemicentetes* may be the most specialized feeder among

^{*} The stridulating organ is a region of the mid-dorsal pelage where spines are elongated. Young *Tenrec* and *Hemicentetes* can produce a scraping sound by rubbing the spines together, a possible means for intraspecific communication (Eisenberg and Gould, 1970).

tenrecids (Eisenberg and Gould, 1970). Deep nest burrows are made by forelimb digging with its well-developed claws. Burrows are significantly longer than those of *Setifer*, measuring one to three meters in length, and sometimes have more than one enlarged hollow within a nest (Eisenberg and Gould, 1970). Up to nineteen individuals (2 males, 2 females, and 15 juveniles) have been found in a single burrow “system” (Eisenberg and Gould, 1975). *Hemicentetes* is not an adept climber, and will slide off a steep incline or narrow substrate (pers. obs.). When startled, *H. semispinosus* is capable of running for short bursts at fairly high speeds, up to 2.7 feet per second (Eisenberg and Gould, 1970). Like *Echinops* and *Setifer*, *Hemicentetes* is generally plantigrade, and the heel is lifted when running at high speeds. For the first 10 days of life neonates exhibit a lateral spread of the limbs (abducted limbs) and drag their bellies on the ground, and by 10-20 days, the limbs are more adducted (Eisenberg and Gould, 1970). This species is terrestrial with an aptitude for digging deep burrows and an ability to run at moderate speeds.

Tenrec ecaudatus, the common tenrec, is the largest of the Tenrecidae and one of the largest living insectivorans (or afrosoricidans), weighing up to 2.4kg. They are found throughout Madagascar, but less so in arid regions of the southwest. Its spiny pelage, though stiff, is softer than that of the other tenrecines, with interspersed hairs and very long facial vibrissae. The snout is elongated and is midway in relative length between *Hemicentetes* and *Setifer*. *Tenrec*’s adult body is superficially similar to *Echinosorex* (the erinaceid Malasian moonrat) in some respects, but *Tenrec* has smaller eyes, a uniform coat color, and no tail.

Tenrec juveniles have notably different external morphology than the adults. Their coats have five longitudinal bands of white spines, and the spines at the mid-

dorsum are most likely rubbed together as a means for communicating with the mother (Eisenberg and Gould, 1970). The striped coat may be cryptic coloration, as *Tenrec* mothers have been seen to feed with their young during daylight hours, and *Hemicentetes*, also striped, is the only other tenrec to habitually feed during the day (Eisenberg and Gould, 1970). They are almost entirely terrestrial, with some time spent in burrowed nests. Burrows, dug with the manus, reach up to two meters in length and one meter in depth. It is plantigrade and walks by diagonal limb extension. As with other tenrecines, the young are born with relatively abducted limbs, and around two weeks, the limbs assume a more parasagittal posture. *T. ecaudatus* forages by rooting about with its longish snout, and will occasionally rush at prey, piercing it with its sharp, long canines (Eisenberg and Gould, 1970). Overall, the genus is terrestrial, with strong digging ability and little to no recorded arboreal activity.

Oryzoricinae: This group includes the three genera *Microgale*, *Oryzorictes*, and *Limnogale*. *Microgale* is the most speciose of all tenrecoids with 10-21 species (18 species are recognized by Jenkins (2003), 20 species by Yoder et al. (2005)), and are most commonly found in the eastern and northern rainforests. All species are small (approximately 40-60g), tailed (30-150mm), and generally shrew-like in appearance. Although at least 10 species are morphologically distinct, MacPhee (1987) notes that *Microgale* of the same species have a remarkable range of adult body size and may have “an almost reptilian propensity for individual size to vary significantly within and across age classes, perhaps in relation to nutrition or some other limiting factor.” This marked degree of intraspecific variation may account for exaggerated species number reports,

though recent molecular study has revealed cryptic *Microgale* species (Yoder et al., 2005).

Based on external morphology, Eisenberg and Gould (1970) proposed four behavioral types for *Microgale*: 1. semi-fossorial, 2. surface forager, 3. surface forager/climber, and 4. climber/springer. These distinctions were based on superficial form-function attributes (e.g., long foot and tail suggesting a climber), without behavioral data. According to Eisenberg and Gould (1970), *M. dobsoni* and *M. talazaci* will climb for at least a short distance, especially when trying to reach prey, and *M. dobsoni* and several other species have been trapped in tree branches (Jenkins, 2003). *M. talazaci* can spring for short distances, using a quadrupedal ricochet (Eisenberg and Gould, 1970). *M. cowani* has relatively small pinnae and a short tail, adaptations associated with a subterranean microhabitat, yet no fossorial behavior has been explicitly observed. Unlike the other two observed species, *M. cowani* does not climb. Although some species may exhibit more or less climbing and/or digging behavior, *Microgale*'s general locomotor behavior can be described as terrestrial, yet most likely including soft-soil burrowing and some climbing.

Surface attributes of *Oryzorictes* and *Limnogale* suggest that they are well adapted for their respective subterranean and semi-aquatic microhabitats respectively, yet there are few published descriptions of their locomotor behaviors. *Oryzorictes* (2 spp.) is mole-like in appearance, with small pinnae and eyes, short tail, large, clawed manus, short velvety fur, and a blunt, hairless nose (Goodman, 2003). Body mass averages 28-40g and dental formula is the same as that of *Limnogale* and *Microgale* ($3/3, 1/1, 3/3, 3/3$). According to Eisenberg and Gould (1970), *O. tetradactylus* is found in burrows near

lakes and streams, and is commonly found burrowing in soil that has been cultivated for rice. Stephenson (1993) captured two *O. hova* specimens in the eastern rainforest and observed them foraging above ground upon release, suggesting that they are not entirely subterranean. We captured five *Oryzorictes* individuals in bucket traps in the eastern rainforest Analamazaotra in June 2003, which also suggests that they forage above ground at night. Trapping *Oryzorictes* was particularly successful following wet nights when insects are found closer to the soil surface (Goodman, 2003; pers. obs.). Although we gave *Oryzorictes* the opportunity to dig in soil, it only occasionally scratched with its forelimbs when exploring for prey. Its feet were most often in plantigrade position as it moved slowly over the ground, though it lifted its heels to a plantigrade posture when running on the treadmill.

Limnogale (1 sp) is found on the banks of streams in the central eastern highlands. Due to its rarity and the human degradation of potentially suitable habitats, *Limnogale* is considered to be the most endangered of Malagasy tenrecoids (Benstead and Olson, 2003). It is the largest oryzorictine, weighing approximately 75g, and has webbed fingers and toes, reduced pinnae, small eyes, and soft, short, dense fur with a fringe of stiff hairs along the foot (Benstead and Olson, 2003). Eisenberg and Gould (1970) note that it builds burrows on the banks of streams and swims as a means for catching its primary diet of shrimp, frogs, aquatic insects, and fish. More recent fecal analyses indicate a diet of larval and adult aquatic insects, larval anurans, and crayfish (Benstead et al., 2001). Both the tail and hind feet are most likely used to propel *Limnogale* through streams, with hindfoot propulsion and the tail used as a rudder (Benstead and Olson, 2003). Radio-

tracking suggests that *Limnogale* is strictly nocturnal and spends most of the day in streamside burrows (Benstead et al., 2001).

Geogalinae: *Geogale* (1 sp.) is the smallest tenrecoid, weighing an average of 7g (6.3g from Beza Mahafaly in July 2003, n=25). Although similar in external morphology to *Microgale*, this genus has particularly large ears, short feet, and a distinguishable dental formula of 2/2,1/1,3/2,3/3 (*Microgale*'s is 3/3,1/1,3/3,3/3). *Geogale* is generally found in the southwest and southernmost regions of Madagascar and despite a reported affinity for termites (Stephenson, 2003), the captured *Geogale* specimens of Beza Mahafaly preferred Malagasy giant hissing cockroaches, and animals routinely killed and consumed cockroaches up to their own body lengths (pers. obs.). Although aspects of its reproductive physiology have been studied (Stephenson, 1993,1994; Stephenson and Racey, 1993), its locomotor behavior has not been described. Our observations of 25 captured animals indicate that *Geogale* rests on its heel, and transitions to a digitigrade posture when moving even slowly. It is able to climb (though not vertically), and laterally abducts the foot approximately 90 degrees when climbing on uneven substrates. All of our specimens were captured under fallen logs, either resting on the ground or in small shallow burrows.

Potamogalinae: includes the two African genera *Potamogale* (1 sp.) and *Micropotamogale* (2 spp.). These three species share a similar semi-aquatic lifestyle with *Limnogale*; they burrow on the banks of streams and dive and swim for aquatic prey. Individuals from all three species are rare and most likely endangered (IUCN). The giant otter shrew, *Potamogale*, is found along streams in central African rainforests, including those of Nigeria, Kenya, Zambia, and Angola. *Potamogale* is larger than most tenrecoids,

weighing approximately 370g and most likely spends more time in the water than *Micropotamogale* and *Limnogale* (a judgment based only on external adaptations for an aquatic habitus). As their common name implies, the giant otter shrews' heads and bodies somewhat resemble those of otters, having dorsoventrally flattened muzzles, small, rounded pinnae, short appendages and long vibrissae. Unlike the dorsoventrally flattened tail of the carnivoran otter, the tail of *Potamogale* is laterally flattened (as is that of *Limnogale*), suggesting that it swims by lateral undulation of the body and tail. The feet are not webbed. On land, *Potamogale* is plantigrade, and burrows are formed from either above or below water level along stream banks. As the name implies, *Micropotamogale* is smaller than *Potamogale*, weighing an average 135g. Their tails are long and round, and only one of the two species has webbed feet (*M. ruwenzorii*). The tail of *M. ruwenzorii* also has a slight dorsoventral keel. Both species spend considerably less time in the water than *Potamogale* and either dive for aquatic prey, or hunt on land (Nowak, 1999). The dorsoventral keel of *M. ruwenzorii* suggests that it swims with lateral undulations of the tail, but details of how *Micropotamogale* moves in water and/or on land have not been published.

Solenodontidae: The sole genus *Solenodon* includes two confirmed living species, *S. paradoxus* and *S. cubanus*, the former of which is endemic to Cuba, and the latter to the island of Hispanola (Haiti and the Dominican Republic). Both are now endangered due to habitat loss and introduced predators. Solenodons have been included in a tenrecoid clade based on their shared zalambdodont dentition (e.g., van Valen, 1967), yet molecular work and biogeographic evidence suggests that *Solenodon* does not form a monophyletic clade with tenrecoids, and is an early placentalian taxon most likely at the

root of the lipotyphlan (eulipotyphlan) tree (Waddell and Shelley, 2003; Roca et al., 2004).

They are similar in size to smaller *Tenrec ecaudatus*, weighing approximately 1kg, and have long, naked tails, extremely long and narrow snouts, small eyes, and fairly large pinnae. The forelimbs have pronounced, sharp claws, which are used to dig extensive burrows in soft soils and to pin down insect and small vertebrate prey. They are reportedly digitigrade (Nowak, 1999), yet photos suggest that they rest on their hind feet. In captivity solenodons will climb on logs, but they are not arboreal. They probably root in, on, and amongst fallen logs in search for prey. They walk with a cross-extension limb pattern, will quadrupedally ricochet when disturbed and can reportedly run at surprisingly high speeds (Eisenberg and Gould, 1966). Yet Nowak (1999) describes solenodons as having a “stiff waddling gait” (p. 201), and they are apparently easily captured by humans and predators, including introduced mongooses and cats. Overall, the genus is most likely terrestrial with frequent digging behavior.

Macroscelididae: The 15 living species of macroscelidids are distributed throughout Africa, primarily south of the Sahara (see Douady et al., 2003 for discussion of macroscelidid vicariance and speciation). Several recent molecular studies suggest that Macroscelidea is the sister taxon to Afrosoricida (see Springer et al., 2004). *Petrodromus* is the genus used for comparisons in this study, primarily due to specimen availability. *Rhynchocyon* might have been a more appropriate taxon, given its basal status in the macroscelidid clade (Douady et al., 2003).

Despite their proposed phylogenetic affinity to tenrecoids, elephant shrews are morphologically (superficially at least) and behaviorally distinct. They are diurnal and

use high-speed saltatory locomotion for predator escape, and forage for small, soft-bodied invertebrates (Nowak, 1999). Zack et al. (2005) have noted several postcranial adaptations for cursorial locomotion, and propose that the derived similarities between macroselidids and Paleocene apheliscines from North America, contesting a monophyletic Afrotheria (see discussion below). *Petrodromus* therefore serves as a good comparison with tenrecoids in terms of its locomotor specialization as well as its proposed sister taxon status.

Erinaceidae: The single species of *Echinosorex*, the Southeast Asian *E. gymnurus*, is superficially similar to *Tenrec*, with a body weight of two kilograms, a long, pointy snout, and rough, thick fur. It is also a terrestrial, nocturnal insectivore, though it prefers wet areas and most likely eats aquatic invertebrates as well as earthworms and terrestrial arthropods (Nowak, 1999). The locomotor behavior of *E. gymnurus* has not been documented and its postcranium has not been previously studied. It is a proposed basal lipotyphlan (or eulipotyphlan) clade (Douady and Douzery, 2003; Grenyer and Purvis, 2003) and therefore an interesting outgroup for exploring the Afrotheria hypothesis.

Tenrecoid Phylogeny

Functional-adaptive analysis of representative tenrecoid genera has potential for identification of generic and higher level synapomorphies between taxa. Results from functional adaptive studies, character analyses in a biologically meaningful sense, can also serve as explicit tests of phylogenetic hypotheses drawn from other types of analyses (e.g., molecular, morphology-based parsimony, etc.). In the Darwinian sense, phylogeny

is largely the adaptive history of lineages; function-based studies build a framework of organismal biological role within which significant markers of phylogenetic history can be established and interpreted (see Bock, 1981; Szalay and Bock, 1991; Szalay, 2000). This study aims to investigate tenrecoid phylogenetic affinities at several taxonomic levels, in addition to its major questions related to the evolution of aspects of form with functional significance.

There is a profusion of academic arguments concerned with “Insectivora” phylogeny and taxonomy, due largely to the few synapomorphies that bind traditional insectivorans in a single clade. Until recently, tenrecoids have received little attention in this literature, but developments in molecular systematics have highlighted Tenrecoidea phylogeny as important for understanding mammalian ordinal and supraordinal relationships. The following is a brief review of the relevant literature on the history of tenrecoid systematics and an update on the current status of tenrecoid taxonomy at the genus to supraordinal rank.

Almost all taxonomic works until the 1990s considered tenrecids (and solenodontids) as close affiliates of moles and shrews. Lacépède (1799) classified *Tenrec* as part of a ‘Plantigrades’ subdivision of quadrupedal mammals, and grouped it with an assortment of other insectivores and carnivores. *Solenodon* was first written about in Pomel (1849), where it was placed in the Talpiens tribe, based on the modification of the forelimb for digging. In 1864, Wilhelm Peters divided insectivores into two groups, based on the presence or absence of a caecum, later termed Menotyphla and Lipotyphla respectively by Haeckel in 1866 (Gill, 1875). Peters’ Centetinae (including *Solenodon*), included within Lipotyphla, is affiliated with Erinacei, Talpina, and Sorices on the basis

of the lack of a caecum and a simple gut. Cetetinae is further demarcated by the lack of a zygomatic arch and ossified bullae, a simple, ring-shaped tympanic, and separate “unterschenkelknochen” (=tibia/fibula). This marks the first consideration of an exclusive relationship between tenrecids and solenodontids.

Tenrecids, solenodontids and chrysochlorids (golden moles) are all characterized by zalambdodont molars, which bear a superficial resemblance to metatherian and fossil tribosphenic molars. Mivart (1871) concluded that the zalambdodont condition in tenrecids and solenodontids, and the tribosphenic condition in fossil mammals are not homologous. Rather, the apparent protocone of zalambdodonts is homologous to a fused paracone and metacone. This concept was later revised by Winge (1882 – see translation 1941) and Woodward (1896), who suggested that the prominent lingual cusp is the paracone, and the metacone and protocone are reduced or absent^{*}. Gill (1875) assigned Malagasy tenrecids and solenodontids to Centetidae, and placed potamogales in a separate family, Potamogalidae, on the basis of several skeletal characteristics. In 1885 he suggested common usage of the term Zalambdodonta to suggest the significant affiliation between potamogales, Malagasy tenrecids, solenodontids, and chrysochlorids. Dobson (1883) removed *Solenodon* from Centetidae and devised the new family name, Solenodontidae.

Leche (1907) offered one of the few in-depth anatomy-based interpretations of intergeneric relationships. He suggested that *Microgale* is most likely the most primitive Malagasy tenrecid, implicated by its lack of habitat-related specializations, retention of

^{*} Contra Leche’s (1907etc) and Gregory’s (1910) reinterpretations, which again regard the prominent cusp as protocone, Woodward’s is most likely an accurate interpretation (as confirmed by Patterson, 1956). *Solenodon* (and possibly *Microgale*) retains a small protocone and hypocone, and *Potamogale* retains a relatively prominent protocone. All other tenrecs have no protocone, suggesting to many that *Potamogale* represents a basal tenrec form (first formally suggested by Huxley, 1880).

an episternum, few lumbar vertebrae, retention of milk dentition into adulthood, and its overall resemblance to an embryonic *Tenrec*. He suggested that, based on the shape of incisors and canines, the aquatic *Limnogale* may also be primitive, representing a link between *Potamogale* and *Microgale*. Finally, he proposed several morphological links between solenodontids and tenrecids: possession of a fibula that articulates solely with the astragalus, a non-articulated tibia and fibula, and molars with an internal ledge having two small cusps (based on *Microgale* and *Solenodon*). Gregory (1910) built on Leche's interpretation, outlining a scenario for tenrecid evolution. He suggested that the continental genus, *Potamogale*, is most like the ancestral type, sharing a common ancestor with a *Microgale*-like form that found its way to Madagascar. He added that *Echinops* and *Microgale* share a more recent ancestor, and that *Hemicentetes* and *Tenrec* arose from the ancestral *Echinops*. Allen (1910) in his monograph on *Solenodon* observed that solenodonts are "undoubtedly near Centetidae", yet some considerable differences, such as position of the penis, molar shape, development of the rostrum and the ankylosis of the tibia and fibula, suggest a very ancient common ancestor with *Potamogale*.

Simpson's classification of 1945 is similar to the classification used in this study except that he included *Solenodon* in Tenrecoidea, he placed *Geogale* in the oryzorictine subfamily, and *Dasogale* and *Cryptogale* are now considered to be synonymous with *Setifer* and *Microgale* respectively (Table 1.2).

TABLE 1.2. Tenrecoid taxonomy from Simpson, 1945

Tenrecoidea
Solenodontidae
<i>Solenodon</i>
Tenrecidae
Tenrecinae
<i>Tenrec, Setifer, Hemicentetes, Dasogale, Echinops</i>
Oryzorictinae
<i>Oryzorictes, Microgale, Cryptogale, Limnogale, Geogale</i>
Potamogalidae
<i>Potamogale</i>

Based on behavioral/ecological characteristics, Eisenberg and Gould (1970, 1975) suggested that the “soft” tenrecids (i.e. oryzorictines and *Geogale*) are ancestral to the “spiny” ones (i.e. tenrecines). *Limnogale* is most basal of all Malagasy tenrecids (evolving from a *Potamogale*-like ancestor), branching into two clades, one with *Geogale*, giving rise to *Oryzorictes* and then *Microgale*. The other branch leads to *Echinops* and *Setifer*, which then split to *Tenrec* and *Hemicentetes*.

Several recent studies have attempted to resolve relationships within Tenrecoidea using morphological and/or molecular data, yet results from these are not in agreement (Asher, 1999, 2000; Olson, 2003). Asher’s (1999) cladistic analysis was based on 71 morphological characters (35 cranial, 17 dental, and 19 postcranial), resulting in a large number of most parsimonious trees, many of which indicated a non-monophyletic Malagasy Tenrecidae, as well as a non-monophyletic Tenrecidae (Tenrecoidea). Though Asher admitted to the tenuousness of tenrecid paraphyly (also discussed in Asher, 2002), he was more confident about a potamogaline-*Limnogale* clade, supported by such characters as an absent lacrimal foramina and a fenestrate basioccipital (Fig. 1.2). Oryzorictinae is not consistently recovered, and he leaves oryzorictine monophyly open

to question. Asher's dissertation work (2000) combined additional morphological and published molecular data, and confirmed a paraphyletic Malagasy Tenrecidae, with *Limnogale* included in a potamogaline clade. Because Asher (1999, 2000) does not find unambiguous support for a *Geogale*-Oryzorictine clade, he leaves the monotypic *Geogale* in its own subfamily, Geogalinae.

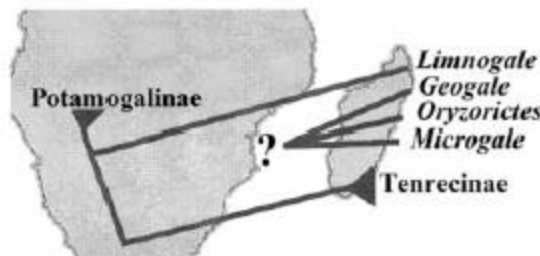


Figure 1. 2. Tenrecoid phylogeny as inferred from morphological data in Asher (1999)

Olson (1999) disputed Asher's paraphyletic Malagasy Tenrecidae, based on molecular, and combined morphological and molecular data (see review in Olson and Goodman, 2003). A *Limnogale*-potamogalinid clade is consistently rejected in his analyses, yet *Limnogale* appears to be nested in *Microgale*, rendering *Microgale* polyphyletic. Molecular and combined analyses also place *Geogale* as a basal taxon to the oryzorictines and tenrecines, and agree with maintaining the subfamily status of Geogalinae (as opposed to grouping *Geogale* with the oryzorictines as in Eisenberg, 1981).

Tenrecinae (including *Echinops*, *Setifer*, *Hemicentetes*, and *Tenrec*) forms the only uncontested monophyletic group in Asher (1999, 2000) as well as Olson (1999), and it seems clear that *Echinops* and *Setifer* are sister taxa, as are *Tenrec* and *Hemicentetes*. Yet the evolution of morphology between these taxa is unexplored and several questions persist: for example, do *Echinops* and *Setifer* most likely share a terrestrial or arboreal

common ancestor, and might be features of *Hemicentetes* suggestive of paedomorphism from a *Tenrec*-like form?

Recent interest investigations into tenrecoid relationships stem largely from new (1997-present) studies in molecular phylogenetics that radically reassemble mammalian ordinal-level relationships and suggest that tenrecoids and chrysochlorids form an order (Afrosoricida) within a larger afrotherian superorder (Springer et al., 1997; Stanhope et al. 1998b, Mouchaty, 2000; etc.). Tenrecoids have historically been considered as part of an insectivoran order, later split by Haeckel (1866) into a lipotyphlan suborder along with hedgehogs, shrews, moles, golden moles, and solenodons. Morphological studies of Lipotyphla have determined that few synapomorphic characters (six in Butler, 1988; three in MacPhee and Novacek, 1993) bind the taxon. Soon thereafter, molecular phylogenetic studies by Stanhope et al. (1998a,b) resulted in the disassembly of Lipotyphla, with chrysochlorids and tenrecs (the proposed afrosoricidans) as part of, or at the root of a larger endemic African mammalian tree (the proposed Afrotheria), including elephants, hyraxes, manatees, elephant shrews, and armadillos (Fig. 1.3). Molecular clock estimates for the separation of xenarthrans and afrotherians are congruent with plate-tectonic dates for the separation of South America and Africa, which both strengthens the Afrotheria hypothesis, and suggests a Gondwanan placentalian origin.

Members of the same research team and others have since published a series of molecular phylogenetic work that disbands Lipotyphla into two or more clades, with tenrecoids (not including *Solenodon*) consistently nesting with the chrysochlorids in an afrotherian superorder (e.g., van Dijk et al., 2001; Madsen et al., 2001; Murphy et al., 2001; Scally et al., 2001; Douady et al., 2002; Murata et al., 2003; Douady et al., 2004).

Several of these suggest that macroscelidids are the closest extant relative to the afrosoricidans, yet relationships within afrotheria are not yet resolved (Fig. 1.3, see Springer et al., 2004 for review).

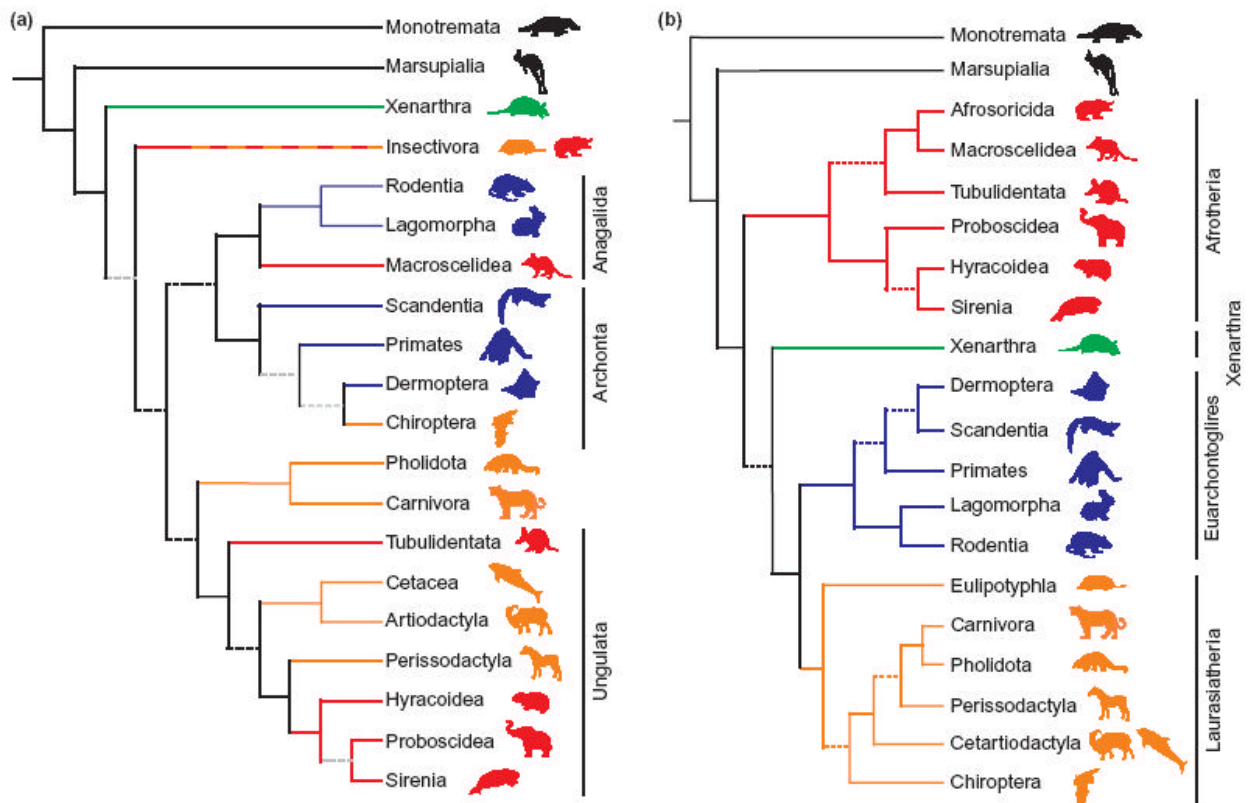


Figure 1.3. (a) Traditional morphological view of ordinal-level mammalian relationships, with tenrecoids and chrysochlorids nested in Insectivora. **(b)** current molecular view, with tenrecoids and chrysochlorids forming the order Afrosoricida, nested within an afrotherian superorder (images from Springer et al., 2004).

Despite increased robusticity and replication of molecular studies consistently resulting in an Afrotheria hypothesis (including an afrosoricidan order), there is still no corroborating morphological evidence. In his comparative study of mammalian soft-tissue cranial anatomy Asher (2001) found two characters (internal carotid artery entering braincase lateral to anterior pole of cochlea, and small blood vessels dispersed throughout vomeronasal organ) that “could be consistent with monophyly of the Afrotheria” (p47), yet neither of these characters is synapomorphic in a broader sense; they are found in non-afrotherian taxa and not found in all afrotherians. Asher et al.’s (2003) study of

combined morphological (including fossil taxa) and molecular data supports an afrotherian clade including afrosoricidans. Contrary to other molecular studies, which generally contend a basally positioned Afrotheria, they find that Afrotheria is well nested within other placentalian clades. Yet the morphological data from this study do not support an afrotherian clade, and trees with a monophyletic Afrotheria are only generated when molecular data are included.

A recent description of postcrania from the North American fossil taxa *Apheliscus* and *Haplomylus* (early Eocene) also contradict a monophyletic Afrotheria that originated in Gondwana (Zack et al. 2005). A series of features in common between apheliscine and macroscelidean postcrania suggest a close relationship, and therefore a North American origin for macroscelideans and possibly other afrotherians (excluding afrosoricidans). Most of the characters described are adaptive features of high-speed cursors that are found in other cursorial mammals (e.g., reduced medial condyle, posteromedially directed lesser trochanter and prominent third trochanter, narrow and deep patellar groove, fused distal tibia/fibula, etc.), and may therefore be convergent. The authors argue that despite the presence of these characters in other mammalian cursors, “the combination in apheliscines occurs only in macroscelideans” (p500), which they take to be indicative of close common ancestry, but might alternatively be the result of ecological convergence from an early placentalian bauplan (if macroscelideans are considered as basal afrotherians). Several features in common between apheliscines and macroscelideans are less common in other mammals and more strongly support phylogenetic affiliation, such as an enlarged medial malleolus and anterior tubercle of the distal tibia, large cuboid facet, a sharp angle between the proximal and distal portions of

the calcaneal ectal (astragalocalcaneal) facet, and an elongate cuboid. Although the authors again maintain that this combination of features is only found in apheliscines and macroscelideans, these are all characters related to stabilization of the hindlimb, and are furthermore found in the tenrecoid *Potamogale* (Salton and Szalay, 2004; see Chapter II). The large number of features in common between apheliscines and macroscelideans is suggestive of their close common ancestry and a North American origin for macroscelideans; Yet the combination of shared characteristics due to a common locomotor repertoire, lack of synapomorphic characters, and similarities between other locomotor specialists (e.g., *Potamogale*) and macroscelidids leave the apheliscine-macroscelidean relationship, as well as the Afrotheria hypothesis, open to question.

The Postcranial Skeleton as Phylogenetic and Functional Indicator

This study of tenrecoid postcrania is specifically concerned with interpretation of “shapes” of skeletal attributes, and an investigation of a connection between shape, phylogeny, and function (see Szalay, 2000; Szalay and Sargis, 2001 for an exploration of these connections). Analysis of skeletal form from an evolutionary perspective requires subdivision of bones into constituent regions that might reflect functional and/or historical factors. Although such selected “characters” cannot realistically be considered as separate entities from the rest of a bone, they nonetheless are identifiable regions that may potentially reflect specific bioroles within the framework of the whole habitus of an animal. Functional features of long bones have been described for many mammalian taxa, including those specialized for different degrees and types of arboreal, terrestrial and fossorial locomotor behaviors. Although many of these investigations are based on skeletal characteristics of either thoroughly-researched primate species (e.g., Rose, 1989;

Gebo and Sargis, 1994), marsupials (Szalay, 1994; Argot, 2001, 2002; Szalay and Sargis, 2001), or particular ecological specialists (e.g., Smith and Savage, 1956; Reed, 1951; Yalden, 1966; Taylor, 1989; Casinos et al. 1993; Stein, 2000), such adaptive complexes are undoubtedly found to some degree in a host of other yet unstudied mammals that exhibit similar functional solutions, given the limitations of their heritage. Analysis of skeletal convergence based on specific function-based hypotheses can also identify important phylogenetic-based similarities and differences between taxa. Convergent features associated with habitus coexist with distinctive heritage-based attributes which are the sought after apomorphies and synapomorphies of phylogeny estimation (Szalay, 2000).

What is a postcranial “character”?

Although the primary goal of this study is to better understand the ecological significance of tenrecoid form-function relationships, a potential fall-out from such research is a better understanding of tenrecoid phylogeny via the identification of skeletal homologies. “Strictly functional and adaptational (ecological utilitarian) assessment of traits in both extant and extinct organisms is necessary (whenever possible) in order to reliably establish polarities of homologous features. Such practice enables students of phylogeny to cull convergent attributes from a body of characteristic features” (Szalay & Sargis, 2001, p. 288). There are potential issues regarding the use of skeletal features for systematic analysis (Lieberman et al., 1996; Sanchez-Villagra et al., 1998; Lovejoy et al., 1999; Lovejoy et al. 2000; Collard and Wood., 2001). Due to the malleability of skeletal tissue in response to direct biomechanical stimuli, fine details of bone morphology can be attributed to ontogenetically acquired “environmental” effects. This is especially so for

the postcranium and aspects of the masticatory skeleton as opposed to the basicranium and teeth (Lieberman et al., 1996; Sanchez-Villagra and Williams, 1998; Collard and Wood, 2001). As a result, whole skeletal regions (e.g., “postcrania”) are not considered to be of systematic value by some because details of form are environmentally induced, more so than other features that are potentially specifically genomically “determined”. This does not seem to be the case assumed for vertebrates other than mammals, highlighting a theoretical schism within the field of vertebrate biology. Furthermore, there is a related, underlying assumption that postcrania are rife with homoplasies due to a limited number of solutions to a limited number of locomotor regimens (see Sanchez-Villagra and Williams, 1998).

Is the response of the developing (or remodeling) skeleton to environmental stimuli fundamentally different from any epigenetic response to a changing developmental environment? Manifestation of even the most stringently genomically-controlled traits is still highly dependent on an environment, be it an external or internal one (Pigliucci, 2001). Wagner (2001) introduced the obvious, yet often overlooked concept that an organism develops via ordinary, albeit remarkable, physico-chemical processes. Development is the physical expression of the interaction between molecules and their surroundings, be they organic or inorganic. Bone is experimentally plastic under varying external environmental conditions, yet so are “hard-wired” features of an organism when *internal* environmental conditions are altered. The role of environmental effects cannot be limited to those outside the developing organism, nor can epigenetic effects only derive from internal, developmental environments (Newman et al., 2001). So can we assert that external and internal environments are so different? If not, and if

postcranial attributes sampled from natural populations are consistently present then these features of the postcranium may be safely considered to be no more developmentally “labile” than any other aspect of the developing organism.

West-Eberhard (2005) argues along these lines in her defense of phenotypic natural selection and the concepts of developmental recombination and genetic accommodation. She maintains that the phenotype of the developing organism responds to any and all “new input,” and the phenotypic response to such input, whether it is the result of a genomic mutation or a temperature change, determines the differential survival of the individual and the eventual population-level evolution of taxa. In this framework, developmental plasticity plays an essential role in phenotypic evolution because plasticity itself and phenotypic responses to particular environments are heritable. The concept of developmental recombination means that genetic mutations are not necessary for phenotypic evolution: “a set of ancestral genes are now coexpressed, or their products used, in a new combination or a new context and the ancestral regulatory mechanisms are now triggered by a new inducer or an old one in some new sequence or environmental context” (p.6546). In theory then, the environment can not be separated from the individual, or more pragmatically put, the individual cannot be considered without environmental context.

Lovejoy et al. (1999, 2000) argue that environmentally-“produced”, i.e. biomechanically-induced skeletal features can not be selected for, and therefore cannot be useful taxonomic characters. Lieberman et al. (1996) raise a similar issue in regards to the skeleton, arguing that:

“...characters used in any analysis must be heritable, with as clear a link to the genome as possible. Morphological features that are highly influenced by

exogenetic stimuli are unreliable indicators of phylogeny because they are not shaped by evolutionary events and, thus, may appear in distantly related taxa...” (p.110).

Aside from raising the obvious point that all features of an organism are one way or another products of epigenetic effects (as defined above), if an osteological feature is unequivocally present in a given taxon, even with various degrees of variation, it is a heritable feature, and phylogeny estimation is based on such heritable characters. Even if the principal “cause” of a feature is an environmental factor (e.g., a specific habitus and the consequent causal biomechanical forces) more so than the internal developmental mechanisms that also played a role in its manifestation, the feature’s reliable presence under natural conditions renders it heritable, in a broader, but no less significant sense from a systematic perspective. To ascertain whether all taxonomically diagnostic features would or would not be present in an abstract developmental environment is not possible.

Almost no skeletal characteristic would develop normally under altered environmental (i.e. internal and/or external) conditions. Subsequently if a feature is consistently present in the natural environment, such a feature is a dependable, developmental manifestation of a given developmental “program” reflecting a specific habitus. West-Eberhard (2005) considers the dependability of the environment and its developmental/phenotypic effects:

“it takes only a little reflection on the nature of development to appreciate the dependability of environmental factors. All organisms depend on the cross-generational presence of large numbers of highly specific environmental inputs: particular foods, vitamins,...and specific regimes of temperature, humidity, oxygen... Such environmental

elements are as essential and as dependably present as are particular genes” (p. 6547).

The potential absence or alteration of a skeletal feature under experimentally controlled conditions (such as those that an organism does not routinely experience) is not a meaningful pretext for rejecting its phylogenetic significance. If it is reliably manifested via epigenetic interactions with a developmental “program” (as all organismal characters are), it is heritable.

In defense against arguments that specific skeletal regions are unreliable for phylogeny estimation, one may ask if there are in general more homoplasies to be found in postcranial and masticatory-related traits than in those from skulls and/or teeth. In their study of dental vs. cranial vs. postcranial characters, Sanchez-Villagra and Williams (1998) found that there is an equal level of homoplasy found between the three types of characters. Collard and Wood (2001) found equal levels of homoplasy between masticatory characters (palate, dentition and mandible) and those from the basicranium and neurocranium. The postcranial skeleton, considered as a whole, is subject to a greater and more complex variety of loads than the skull, yet there are, in general, probably as many functional demands and phylogenetic constraints on details of the skeleton as there are on the skull. This is decidedly the case for the carpus and the tarsus in the Mammalia (Szalay, 1977, 1984, 1994.)

Specific patterns of postcranial skeletal form exist that can be correlated with specific substrate use or bioroles, and the major focus of this study is to identify such patterns to understand the degree to which adaptation has played a role in the evolution and diversification of tenrecoid postcranial form in the sundry known lineages. Yet there

are evident differences in the means and modes by which different mammalian taxa have achieved similar morphological ends. Because mammals have a limited number of locomotor solutions open to them on different substrates (e.g., running, climbing, digging) which involve approximately predictable biomechanics, and because bone is directly responsive to biomechanical stimuli, it does not follow that general convergences and parallelisms in mechanical solutions are anywhere near identical in mammalian postcranial evolution (see extensive demonstration of this in Szalay and Sargis, 2001; in spite of the manifest general mechanical similarities due to convergence, between metatherian and eutherian solutions, all of which are highly taxon specific). Thus careful identification and analysis of postcranial adaptations of tenrecoids, solenodontids and macroscelidids reveal fine-scale similarities and differences that are valuable for testing a number of phylogenetic hypotheses.

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CHAPTER II

EVOLUTIONARY MORPHOLOGY OF THE TENRECOID TARSAL COMPLEX

Introduction

The crus (shin) and tarsus present a challenging and highly informative region of the mammalian postcranium for both adaptational and phyletic assessments (Szalay and Decker, 1974; Szalay, 1994). The functional significance of the various joint articulations of the tarsus is difficult to interpret due to a) its composite structure and multi-axial actions, b) the relative scarcity of research on the relationship between tarsal morphology and substrate use, and c) the influence of phylogenetic history.

The many complex articulations in the tarsus sustain some of the most complex loads in the body and are particularly sensitive to relatively small changes in loading regime. Consequently, small modifications in form-function can reflect significant changes in loading, all within the phylogenetic constraints of a lineage (Szalay, 1994; Szalay and Sargis, 2001). Tarsals and carpals (and their contact with the distal long bones), perhaps more than the rest of the postcranial skeleton, therefore, retain both functional and systematic information that is best understood by through ecological and functional (functional-adaptive) analyses (Decker and Szalay, 1974; Szalay and Decker, 1974; Bock, 1981; Cifelli, 1983, 1997; Dagosto, 1986; Gebo and Dagosto, 1988; Gebo, 1993; Szalay, 1994; Muizon et al., 1998).

This study addresses the following questions with regards to the tenrecoïd tarsal complex:

- 1) To what degree are differences in tenrecoïd tarsal form attributable to differences in known positional (locomotor, feeding, resting, etc.)

behaviors? To what degree do tarsal features parallel those found in other mammalian groups?

- 2) Given the functional-adaptive nature of traits, are there skeletal features that also suggest homologies shared between species, and/or within and between subfamilies? How do trait patterns conform to proposed tenrecid relationships and to the broader questions of tenrecoid affinities among placentarians?
- 3) In particular, how do features of tenrecoid tarsals compare to those of solenodontids and macroscelidids?

The primary mobile regions of the tarsus include the cruroastragalar joint (i.e. upper ankle), the astragalocalcaneal joint (i.e. lower ankle) and the transverse tarsal joint (between the astragalus/calcaneus and navicular/cuboid) (Fig. 2.1). All three allow for slight to extreme extension/flexion, inversion/eversion and adduction/abduction of the foot. In Late Cretaceous-modern placentals, the upper ankle joint is relatively restricted to the plane of dorsiflexion (Szalay 1984, 1994; Szalay and Sargis, 2001; Sargis 2002); deep tibial and fibular malleoli tightly brace the astragalar trochlea along its medial and lateral sides, allowing for fore-and aft motion along the sagittal plane. Nonetheless, there are variations in the depth and shape of the malleoli that allow for different ranges of motion. Depending on substrate use, morphology of the placental lower ankle joint is usually indicative of degrees of inversion and eversion of the foot along its long axis. The transverse tarsal joint does not accommodate a great range of movement, yet its detailed morphology is also representative of the degree to which an individual is able to invert

and/or evert the more distal portion of the foot. Flexion and extension, and abduction and adduction may also be reflected in this four-bone intersection. Although the relationship between the proximal metatarsals and distal tarsals is also informative about function and intertaxon relationships, this study focuses primarily on the upper ankle joint (UAJ), lower ankle joint (LAJ), and transverse tarsal joint (TTJ), including their characteristic features and functional and phyletic attributes.

A large portion of the literature on mammalian tarsal bone morphology is concerned with primates. Of the non-primate papers, several offer comparative functional-adaptive approaches to osteology and musculo-skeletal analysis (e.g., Lewis, 1962, 1989; Szalay, 1966, 1994; Jenkins and McClearn, 1984; Strasser, 1988; Prasad and Godinot, 1994; Martinez and Sudre, 1995; Szalay and Lucas, 1996; Muizon et al., 1998; Rose, 1999; Gebu et al., 2001; Szalay and Sargis, 2001; Argot, 2002). It is clear that although different taxa have various, phyletically constrained adaptive solutions to similar problems (e.g., lengthening different bones of the foot to achieve the common goal of increased propulsive ability), there are many elements of the tarsus that seem to have parallels across taxa and can therefore strongly predict similar functional-adaptive solutions. A taxon specific example for therians is the dorsoventral vs. mediolateral extension of the astragalar head as indicative of plantar/dorsiflexion vs. greater degrees of inversion/eversion respectively (Szalay and Decker, 1974). The relative scarcity of an adequate body of research for comparisons on the tarsal morphology of eutherian mammals stipulates that interpreting the adaptive and/or phyletic meaning of homologous regions should be approached with caution.



Figure 2. 1. Left foot of *Hemicentetes* outlining general articulations of the three major ankle joints: upper (UAJ), lower (LAJ), and transverse tarsal (TTJ).



Figure 2. 2. Anterior view of the distal crus of *Tenrec* (left side), outlining characters for functional and/or phylogenetic assessment. Fibula can be distally fused, unfused, or bound by a fibrous sheath; relative depth of the tibial and fibular malleoli can be assessed and compared with one another; a tibial distal anterior tubercle is either present or absent and if present, its depth and shape can be assessed.

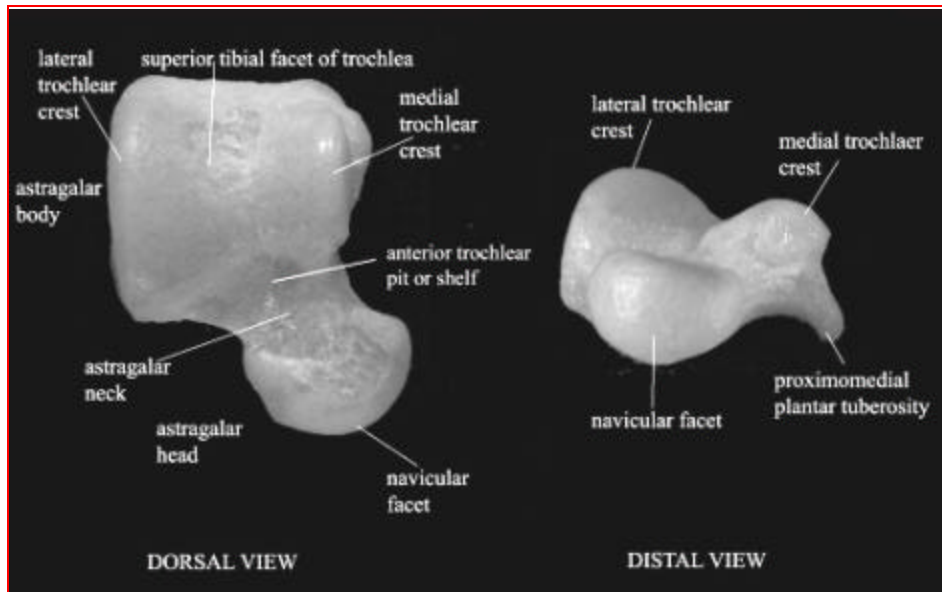


Figure 2. 3. Two astragalar views of *Tenrec* (right side), indicating potentially significant characters for assessing functional-adaptive and/or phylogenetically relevant attributes. Characters include: length and width of the astragalar neck; mediolateral width of the navicular facet; presence/absence of a pit or shelf at the dorsal junction between the trochlea and astragalar neck (anterior trochlear pit or shelf); if present, depth and shape of the anterior trochlear pit or shelf; trochlear crest height; medial vs. lateral trochlear crest height; slope of the trochlear crests.

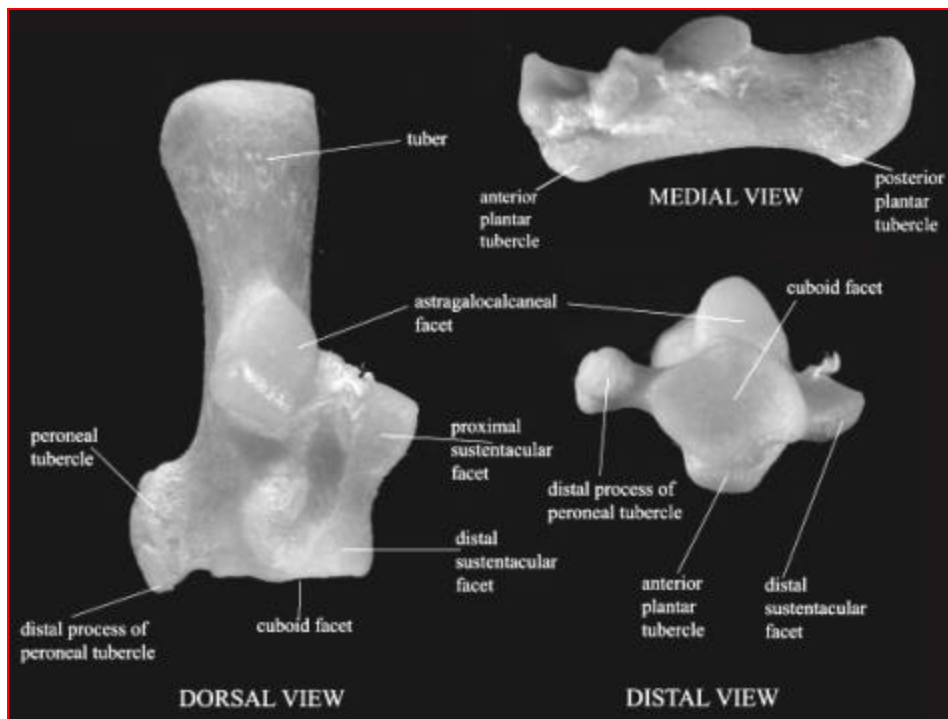


Figure 2. 4. Three calcaneal views of *Tenrec* (right side) illustrating regions of potential interest. Characters include: relative tuber length; tuber robusticity; astragalocalcaneal facet position and shape; peroneal tubercle lateral and distal extension; presence/absence and robusticity of anterior and posterior plantar tubercles; concavity of calcaneal plantar surface.

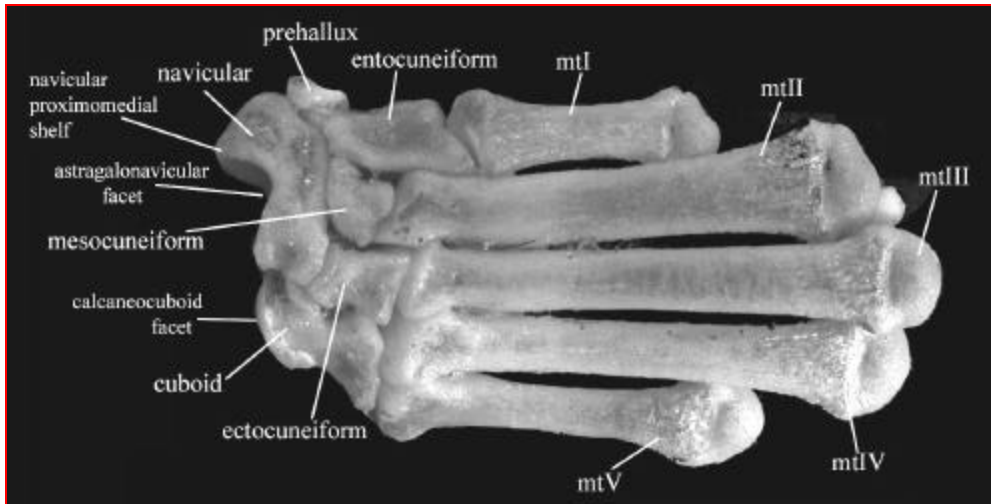


Figure 2. 5. Distal tarsal and metatarsal complex of *Echinops* (right side), illustrating characters of potential interest, including: astragalonavicular facet width; navicular proximomedial shelf extension; calcaneocuboid facet width; cuneiform lengths; metatarsal lengths.

Materials and Methods

The tarsal complex (distal crus; astragalus; calcaneus; proximal articular navicular and cuboid surfaces; articulated navicular, cuboid, distal tarsals and metatarsals) from 130 specimens was studied and photographed (Nikon Coolpix 995) from several standardized perspectives. The sample included one species from each of the tenrecid genera (see Table 2.1), excluding *Micropotamogale* due to unavailability of postcranial material. *Microgale* is the most speciose of tenrecids, with anywhere from 10-19 (MacPhee, 1987; Stephenson, 1995) species depending on the source whereas the other tenrecid genera include only 1-2 species each. Although *Microgale* are all primarily terrestrial, Eisenberg and Gould (1970) note that there is variation in foot and tail length, and different species may be more or less semi-fossorial or semi-arboreal. Three species of *Microgale* were studied for this project, including two (*M. cowani* and *M. dobsoni*) from Eisenberg and Gould's "terrestrial" group, and one (*M. talazaci*) from the "terrestrial with some climbing ability" group.

Specimens were photographed from the mammals collections at the American Museum of Natural History, Field Museum of Natural History, Harvard Museum of Comparative Zoology, and National Museum of Natural History. Two *Echinops* specimens were from H. Kuenzle's laboratory at the University of Munich, Germany (see Appendix I for specimen list).

Digital image files were written into TPSdig (Version 1.31, 2001 F.J. Rohlf), which allows for superimposition of landmarks (x,y coordinates) onto images, and calibration of image scale from a mm ruler. Twenty-eight linear measurements were then calculated from desired coordinates (Table 2.2; Microsoft Excel). Measurements included

those that have been used in previous studies of the tarsus (e.g., Carrano, 1997; Hooker, 2001; Argot, 2002; Sargis 2002) and those that incorporated features with proposed functional and/or phylogenetic significance (e.g., Szalay and Decker, 1974; Jenkins and McClearn, 1984; Gebo, 1993; Szalay, 1994). Precision of measurements was tested on several larger-scale measurements from three complete specimens using a fine-point caliper, and there were no significant differences between caliper and digital measurements ($p < 0.05$). In order to control for size differences, linear measurements were transformed to index measurements (Table 2.3). All statistical analyses (one-way ANOVAs, correlation matrices) were performed using STATISTICA (Version 6.0, StatSoft Inc). Significance values reported in the text for two-group comparisons refer to Tukey post-hoc results; those for more than two groups refer to ANOVAs (see Appendix 2.4 for index means and standard deviations).

TABLE 2.1. Sample Taxonomy and Primary Locomotor Behavior

Family/subfamily	Genus	Species	n	Locomotor Behavior
Tenrecidae/Tenrecinae	<i>Echinops</i>	<i>telfairi</i>	18	Arboreal/terrestrial
Tenrecidae/Tenrecinae	<i>Hemicentetes</i>	<i>semispinosus</i>	15	Terrestrial/fossorial
Tenrecidae/Tenrecinae	<i>Hemicentetes</i>	<i>nigriceps</i>	3	Terrestrial/fossorial
Tenrecidae/Tenrecinae	<i>Setifer</i>	<i>setosus</i>	14	Terrestrial
Tenrecidae/Tenrecinae	<i>Tenrec</i>	<i>ecaudatus</i>	12	Terrestrial
Tenrecidae/Oryzorictinae	<i>Limnogale</i>	<i>mergulus</i>	2	Aquatic/terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>cowani</i>	15	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>dobsoni</i>	10	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>talazaci</i>	7	Terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>hova</i>	7	Fossorial/terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>tetradactylus</i>	3	Fossorial/terrestrial
Tenrecidae/Geogalinae	<i>Geogale</i>	<i>aurita</i>	2	Terrestrial
Potamogalidae	<i>Potamogale</i>	<i>velox</i>	7	Aquatic/terrestrial
Macroscelididae	<i>Nasilio</i>	<i>brachyrhyncha</i>	3	Terrestrial
Macroscelididae	<i>Petrodromus</i>	<i>tetradactylus</i>	3	Terrestrial/saltatory
Solenodontidae	<i>Solenodon</i>	<i>paradoxus</i>	9	Terrestrial/fossorial

TABLE 2.2. Measurements (see Appendix 2.1 and 2.2)

Asthead1	<i>Astragalar head dorsoplantar depth:</i> from distal (articular) view of astragalar head, distance from dorsalmost point of head to plantar point of head, at midline
Asthead2	<i>Astragalar head medial dorsoplantar depth:</i> from distal (articular) view of astragalar head, point from dorsalmost point of head to plantar point of head, halfway between midpoint and the medial side of the head.
Asthead3	<i>Astragalar head lateral dorsoplantar depth:</i> from distal (articular) view of astragalar head, point from dorsalmost point of head to plantar point of head, halfway between midpoint and the lateral side of the head.
Asthead4	<i>Astragalar head mediolateral width:</i> from distal view of astragalus, maximum mediolateral width of the head of the astragalus, perpendicular to astragalar head dorsoplantar height.
Astneck1	<i>Astragalus body length:</i> from dorsal view of astragalus, anteroposterior length of the astragalus at midline.
Astneck2	<i>Astragalus body width:</i> from dorsal view of astragalus, mediolateral width of the astragalus at midline.
Astneck3	<i>Astragalar neck length:</i> from dorsal view of astragalus, length from base of astragalar neck to distal end of astragalar head, running through midline of neck and head.
Astneck4	<i>Astragalar neck width:</i> from dorsal view of astragalus, width of astragalar neck at narrowest point, perpendicular to long axis of neck and head.
Astroch1	<i>Astragalar lateral trochlear crest height:</i> from distal view of the astragalus, proximalmost point of the lateral trochlear crest to distal point of the crest, even with the lowest point of the trochlear trough.
Astroch2	<i>Astragalar medial trochlear crest height:</i> from distal view of the astragalus, proximalmost point of the medial trochlear crest to distal point of the crest, even with the lowest point of the trochlear trough.
Astroch3	<i>Average trochlea crest height:</i> from anterior view of astragalus, distance from lowest point of trochlear trough, to point of midline height between medial and lateral trochlear crests.
Calc1	<i>Anterior border of astragalocalcaneal facet to distalmost calcaneus:</i> from dorsal view of calcaneus, distance from anterior (distal) border of calcaneus to anterior (distal) border of astragalocalcaneal facet, along midline of calcaneus.

- Calc2** *Calcaneal tuber length*: from dorsal view of calcaneus, length from posterior (proximal) border of astragalocalcaneal facet to posterior (proximal) border of calcaneus, along midline of calcaneus.
- Calc3** *Calcaneus length*: from dorsal view of calcaneus, maximum length of calcaneus from proximal (posteriormost) border, to distal (anteriormost) border, along midline of calcaneus.
- Calc4** *Minimum calcaneal tuber width*: from dorsal view of calcaneus, minimum mediolateral width of calcaneal tuber, perpendicular to calcaneal tuber length.
- Calc5** *Peroneal process distal extension*: from dorsal view of calcaneus, distance from distalmost point of calcaneus to distalmost point of peroneal process, along midline axis of calcaneus.
- Calc6** *Peroneal process length*: from dorsal view of calcaneus, distance from proximalmost (posterior) point of peroneal process, to distalmost (anterior) point of peroneal process.
- Foot1** *Cuboid length*: from dorsal view of cuboid, proximodistal (anteroposterior) length of cuboid along midline, from articular surface with calcaneus to articular surface with metacarpals.
- Foot2** *Cuboid width*: from dorsal view of cuboid, mediolateral width of cuboid at midpoint, perpendicular to cuboid length.
- Foot3** *Metatarsal III mediolateral width*: from dorsal view of mtIII, from medial to lateral side of mtIII, at midpoint of bone, perpendicular to mtIII length.
- Foot4** *Metatarsal III proximodistal (anteroposterior) length*: from dorsal view of mtIII, from proximal midpoint of mtIII to distal midpoint of mtIII.
- Foot5** *Navicular mediolateral width*: from dorsal view of navicular, mediolateral width along widest axis of navicular, perpendicular to proximodistal length.
- Foot6** *Navicular proximodistal (anteroposterior) length*: from dorsal view of navicular, proximodistal length of navicular along midpoint, perpendicular to navicular mediolateral width.
- Foot7** *Navicular shelf depth*: from dorsal view of navicular, from proximal articular surface of navicular at midpoint, to proximalmost point of navicular at medial side.
- Malleoli1** *Anterior tibial tubercle depth*: from anterior view of tibia, from proximal point of distal epiphysis to distalmost point of distal epiphysis at midline of tibia, or where anterior tubercle reaches distalmost point.
- Malleoli2** *Fibular malleolus depth*: from anterior view of fibula, proximodistal length from proximal point of distal epiphysis to distalmost point of fibular malleolus.
- Malleoli3** *Tibia distal epiphysis minimum depth*: from anterior view of tibia, minimum depth, from proximal point of distal epiphysis to distalmost point of distal epiphysis.
- Malleoli4** *Tibial malleolus depth*: from anterior view of tibia, proximodistal length from proximal point of distal epiphysis to distalmost point of tibial malleolus.

TABLE 2.3. Indices (see Appendix 2.3 and 2.4)

- AHSI** astragalar head shape index: astragalar head articular surface mediolateral width/dorsoplantar height (see Fig. 2.7C).
- ANLI** astragalar neck length index: astragalar neck length/(astragalus body mediolateral width+body anteroposterior length) (see Fig. 2.7A).
- ANWI** astragalar neck width index: astragalar neck width/(astragalus body mediolateral width+body anteroposterior length) (see Fig. 2.7A).
- ATDI** anterior tibial tubercle depth index: anterior tubercle depth/minimum distal epiphyseal depth (see Fig. 2.6).
- CAFPI** calcaneal astragalocalcaneal facet position index: distance between anterior astragalocalcaneal facet border and anterior calcaneus/tuber length (see Fig. 2.8).
- CLI** calcaneal length index: calcaneal length/minimum calcaneal tuber width (see Fig. 2.8).
- CTLI** calcaneal tuber length index: calcaneus length/tuber length (see Fig. 2.8).

CUSI cuboid shape index: cuboid anteroposterior length/mediolateral width (see Fig. 2.9).

MDI malleolus depth index: minimum epiphyseal depth/(tibial+fibular malleolus depth) (see Fig. 2.6).

MLAHI medial/lateral astragalar head index: astragalar head articular surface dorsoplantar depth of medial side/dorsoplantar depth of lateral side (see Fig. 2.7C).

MLCHI medial/lateral astragalar trochlear crest height index: medial trochlear crest height/lateral trochlear crest height (see Fig. 2.7B).

MLMI medial malleolus/lateral malleolus depth index: tibial malleolus depth/fibular malleolus depth (see Fig. 2.6).

MT3I metatarsal III shape index: mtIII midshaft width/mtIII maximum length.

NPDI navicular proximomedial shelf depth index: navicular proximomedial shelf depth/(navicular anteroposterior length+mediolateral width) (see Fig. 2.9).

PPPI peroneal process position index: distance between the distal end of the peroneal process and distal end of the calcaneus/ peroneal process length (see Fig. 2.8).

TCHI trochlear crest height index: trochlear height/astragalar body mediolateral width (see fig 7B).

TCMI trochlear crest midpoint index: medial trochlear crest width/lateral trochlear crest width (see Fig. 2.7B).



Figure 2. 6. Distal crus measurements (right side).

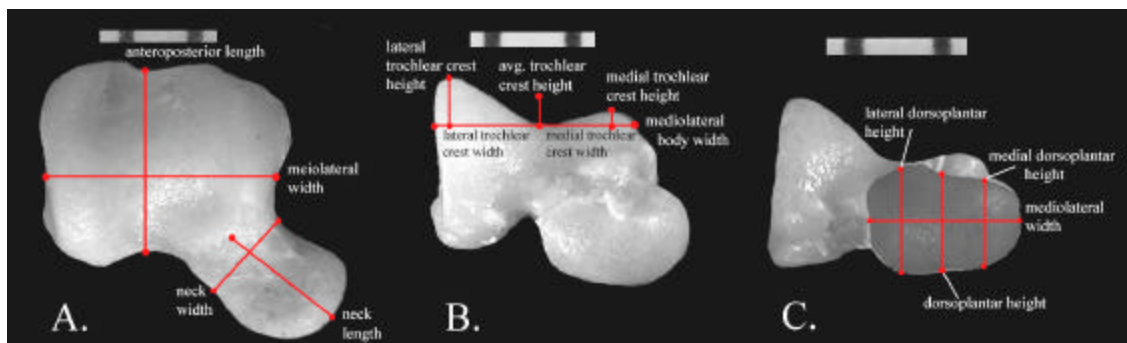


Figure 2. 7. Astragalus Measurements (right side). A. Dorsal view, showing measurements related to the astragalar body and neck; B. Anterior (distal) view, showing measurements related to the astragalar trochlea; C. Distal view of astragalar head articular surface.

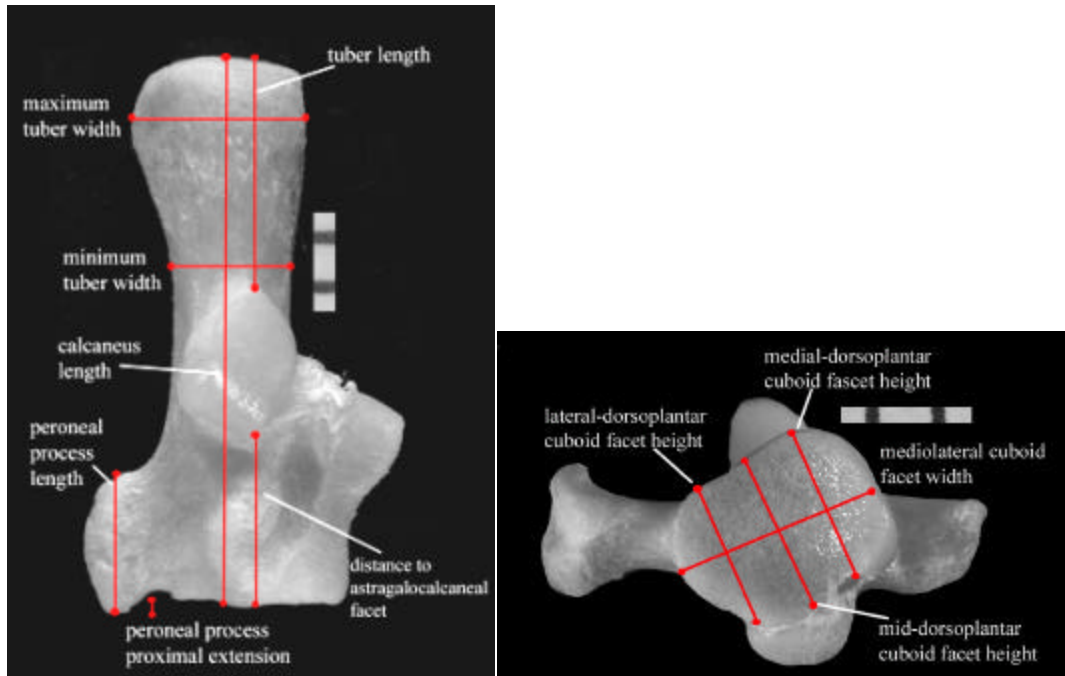


Figure 2. 8. Calcaneus measurements (right side). Dorsal and distal views.

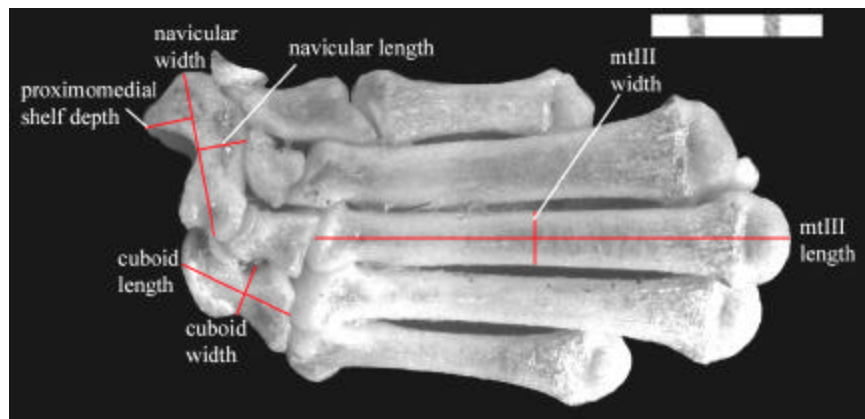


Figure 2. 9. Distal tarsal/metatarsal measurements (right side).

Results and Discussion

Upper ankle joint (UAJ), distal crus

The upper ankle joint consists of articulations between the distal crus (tibia and fibula) and dorsal astragalus. In the upper ankle joint of modern therians major loads are transmitted along the long axis of the tibia to the astragalus, as opposed to the primitive synapsid condition, where loads were transmitted primarily both from the fibula and tibia

to the astragalus and calcaneus that were adjacent to one another, probably similar to that seen in extant monotremes. In contrast to extant monotremes, most metatherians, and early and some extant eutherians (Szalay, 1994), there is no calcaneofibular contact in tenrecoids (the latter assessment is based on the 113 specimens examined).

Fusion of the distal fibula to the tibia is a well-noted, functionally significant trait in many placental specialists that has evolved numerous times (Hildebrand, 1995). For example many subterranean rodents, such as bathyergids, have a distally fused crus (Stein, 2000). Fusion in this case (and in general) stabilizes movement in flexion-extension, and reduces the likelihood of lateral dislocation. This also applies to many cursors, which have extensively fused crura (Hildebrand, 1995). As stated above, an unfused distal crus, with the fibula playing a significant to prominent supportive role in the upper ankle joint, is a primitive therian, metatherian, and eutherian feature. Retention of this ancestral condition facilitates greater freedom of adjustment in the UAJ. An unfused crus with a relatively wide distal fibula may be functionally indicative of high lateral loads, while allowing for rotational movement at the UAJ.

Despite distinct differences in locomotor behavior and loading, the distal crura of all four tenrecine species and *Solenodon* are unfused, except for a light to dense fibrous sheath between the distal approximate one-fifth of the two bones (Fig. 2.10). *Geogale* is similar to the tenrecines, but the sheath extends slightly more proximally on the crus, approximately one-quarter from the distal end. *Potamogale* and the macroscelidid *Petrodromus* have regions of complete fusion between the tibia and fibula. This is consistent with other features like the elongated malleoli of these species, suggesting that movement of the lower limb is highly restricted to the parasagittal plane (Fig. 2.10). The

fibulae of oryzorictine tenrecoids are 50 to 75% fused from the distal end, although fusion in *Limnogale* is less complete. Fusion of the distal crus is functionally consistent with fossorial behavior in *Oryzorictes*, and the stabilization necessary for bracing the body with the hindlimbs, and may be consistent with hindfoot-dominated swimming in *Limnogale*. It does not, however, correspond with what one would expect in *Microgale*, suggesting that a fused distal crus is a primitive feature for the oryzorictine subfamily.

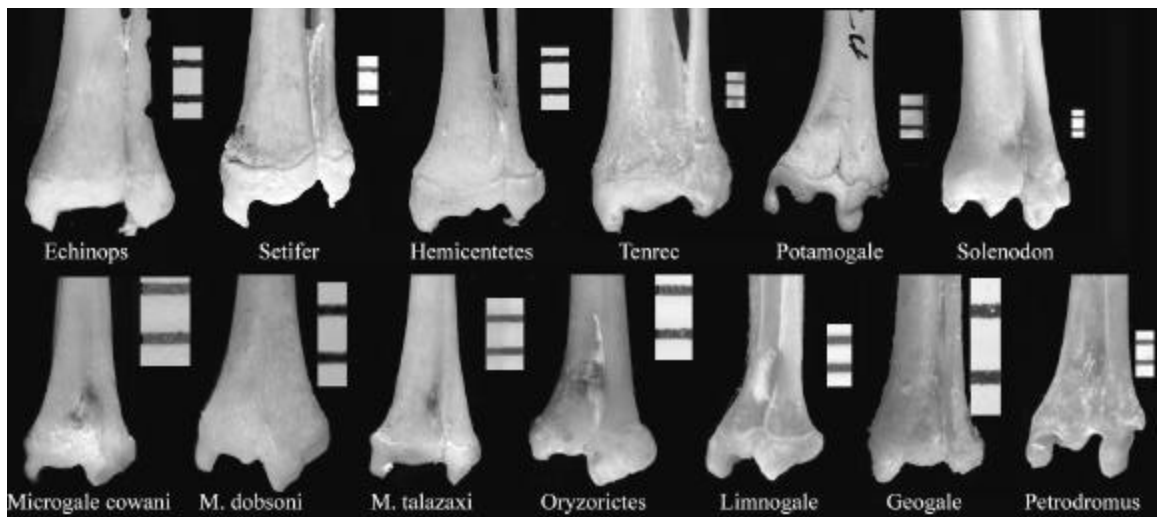


Figure 2. 10. The distal crus of four tenrecines (*Echinops*, *Setifer*, *Hemicentetes* and *Tenrec*), five Oryzorictines (*Microgale cowani*, *M. dobsoni*, *M. talazaci*, *Oryzorictes*, and *Limnogale*), a potamogalinid (*Potamogale*), geogalinid (*Geogale*), solenodontid (*Solenodon*) and macroscelidid (*Petrodromus*). Note especially differences and similarities in malleolar orientation (anteriorly vs. medially directed) malleolar depth, medial vs. lateral malleolar depth, and anterior tubercle presence and depth. *Potamogale* and *Petrodromus* have convergently long and similar malleoli, which stabilize the UAJ in dorsiflexion. Within the tenrecine subfamily, the relatively short, evenly elongated malleoli of *Echinops* are associated with climbing. The long lateral malleolus in *Oryzorictes* is associated with lateral bracing while digging.

The tibial malleolus of the tibia articulates with the medial trochlear crest of the astragalus, and therefore its depth is a general indicator of the restriction of the astragalus to the parasagittal plane. Although the distal elongation of the medial malleolus is probably primitive for eutherians (Szalay, 1984, 1994), its conformation and dimension clearly have a functional correspondence with the UAJ restriction of mobility. An extended tibial malleolus such as that seen in leaping rodents and lagomorphs (Szalay, 1977), and leaping primates (Dagosto, 1985), and in eutherians in general, is shared with

the more terrestrial metatherians where the UAJ evolved from a mediolaterally mobile one to a more restricted one (Szalay, 1994). The distally projecting lateral fibular malleolus of eutherians completes their tenon-mortise configuration. (for a contrast, see the plesiomorphic metatherian condition; Szalay, 1994).

There is significant variation, within and between subfamilies, in the degree to which the tibial and fibular malleoli are distally extended, indicating differences in ankle stability and mobility. The tenrecines have tibial malleoli that are generally deeper than the fibular malleoli, suggesting a limited mobility in the UAJ, but facilitating dorsi- and plantarflexion. Unlike the other tenrecines, the malleoli of *Echinops* are almost equally extended distally (Figs. 2.10, 2.11; MLMI, $p=0.004$); the fibular malleolus is relatively deep (though still less deep than the tibial one), serving as a lateral brace for some degree of mobility to adjust the foot during climbing. Both *Setifer* and *Echinops* have shallower malleoli than *Tenrec* and *Hemicentetes*, indicating a less restricted UAJ (Fig. 2.12; MDI, $p=0.009$). This is one of several traits that suggest a shared arboreal ancestor for both *Setifer* and *Echinops*, rather than independent adaptations.

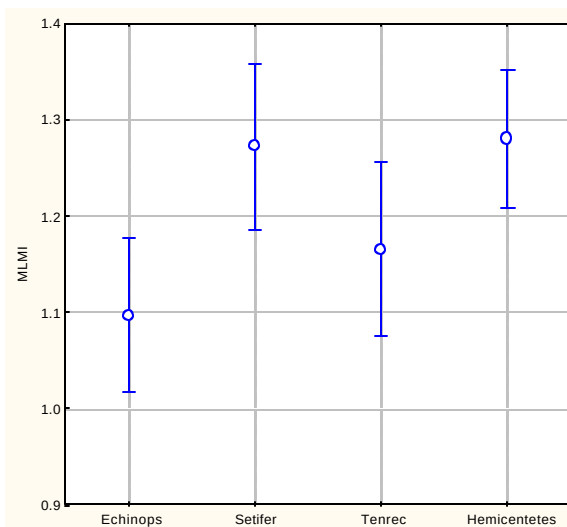


Figure 2. 11. Medial/Lateral Malleolus Index for tenrecines ($p=0.009$). Note that the fibular (lateral) malleolus of *Echinops* is longer than those of the other tenrecines, providing a lateral brace for an inverted foot during climbing.

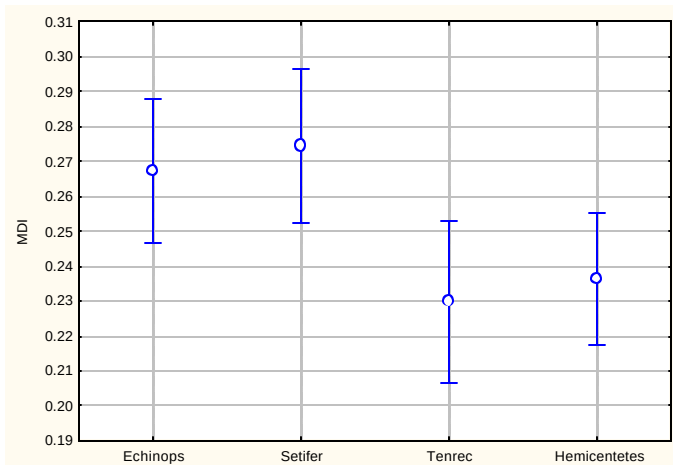


Figure 2. 12. Malleolus depth index for tenrecines ($p=0.004$). Lower value=longer malleoli. Note that *Echinops* and *Setifer* have relatively shorter malleoli than the other tenrecines, indicating greater restriction in the latter.

In contrast to tenrecines, oryzorictines have malleoli that are either equally extended, or else the fibular malleolus is deeper than the tibial (Figs. 2.10, 2.13; MLMI, $p=0.000$). *Oryzorictes* has a deeply extended fibular malleolus and a relatively shallow tibial malleolus, suggesting lateral stabilization. This is consistent with digging behavior, which involves the resolution of potentially heavy loads by the lateral side of the foot during eversion and flexion (Figs. 2.10, 2.14; MLMI, $p=0.033$).

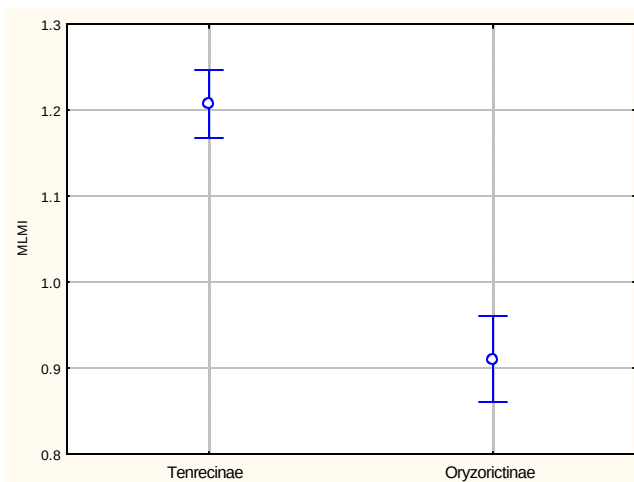


Figure 2. 13. Medial/Lateral Malleolus Index between tenrecine and oryzorictine subfamilies ($p=0.000$). Tenrecines have significantly longer medial malleoli than oryzorictines, representing a historically relevant

trait.

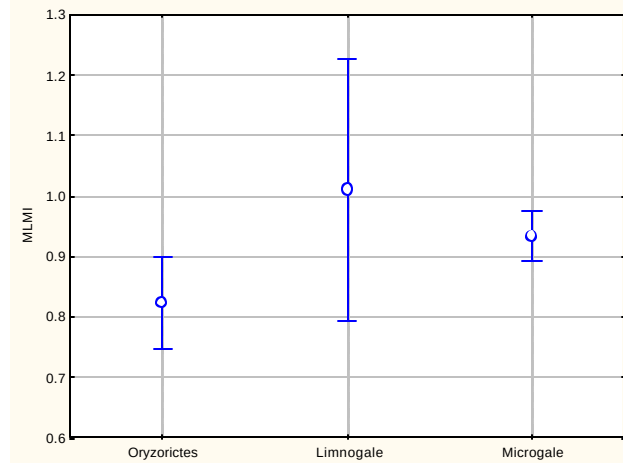


Figure 2. 14. Medial/Lateral Malleolus Index between oryzorictine genera. *Oryzorictes* has a significantly longer lateral malleolus than the other oryzorictines ($p=0.033$; see Fig. 2.10), most likely an adaptation for lateral stabilization of the tarsus while digging with the forelimbs.

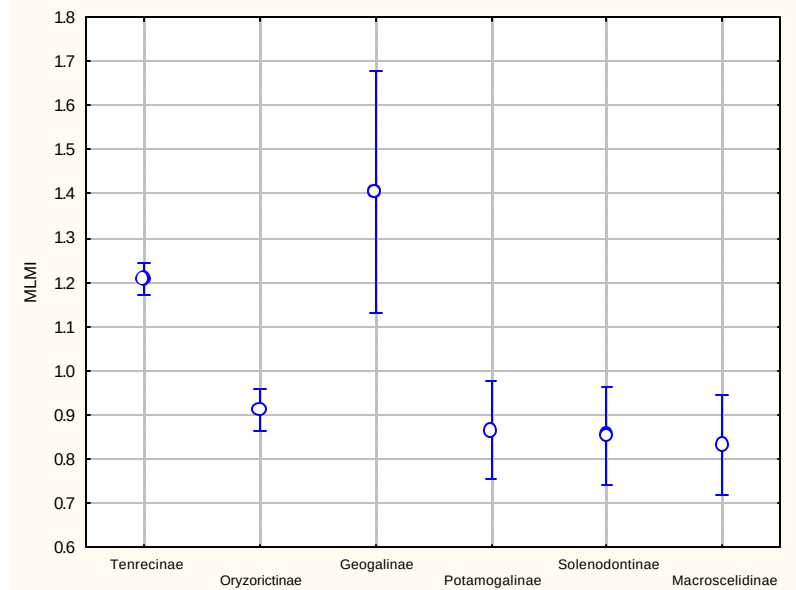


Figure 2. 15. Medial/Lateral Malleolus Index by subfamily. *Geogale* has a longer medial malleolus than lateral, similar to the tenrecines ($p=0.000$). The oryzorictines, potamogalines, solenodontids and macroscelidids all have slightly longer lateral malleoli.

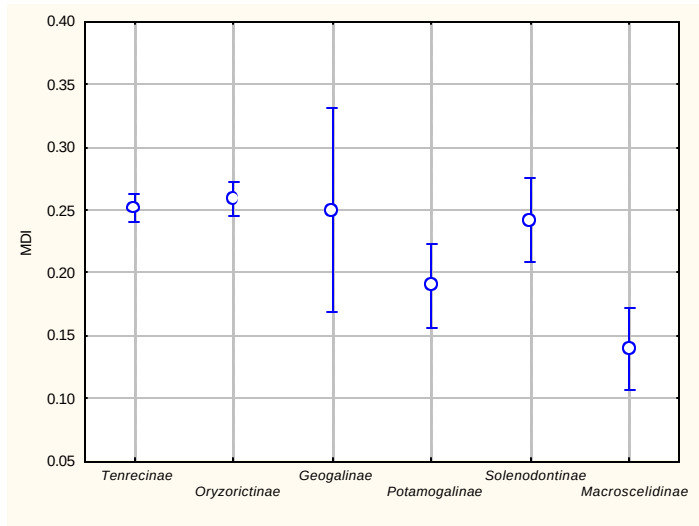


Figure 2. 16. Malleolus Depth Index by subfamily. There is no significant difference between tenrecines, oryzorictines, *Geogale*, and *Solenodon* ($p=0.764$). *Potamogale* and macroscelidids have longer malleoli ($p=0.000$), which is most likely a functional correlate with extreme UAJ stabilization.

Geogale is again dissimilar from the oryzorictines in that its tibial malleolus is longer than the fibular one, similar in form to those in tenrecines (Figs. 2.10, 2.15; MLMI, $p=0.000$). *Limnogale*, *Potamogale*, and especially the macroscelidids have very deep tibial and fibular malleoli, suggesting enhanced stability for flexion-extension. The crural malleoli of *Potamogale* and macroscelidids are equal in length (Fig. 2.16; MDI, $p=0.28$), and are both positioned at the anteriormost ends of the crus. Their exaggerated length and narrowness, and their anterior positioning suggest that there is habitual heavy loading in the anterior upper ankle joint, and UAJ stabilization plays an important role both in the terrestrial propulsion of macroscelidids and aquatic propulsion of *Potamogale*. The crural malleoli of *Solenodon* are morphologically distinct from those of *Potamogale* and macroscelidids (Fig. 2.10). The malleoli of the former are both deep and, unlike *Potamogale* and macroscelidids, anteroposteriorly wide, indicating a more stable UAJ.

A projection on the anteriormost aspect of the distal tibia (Fig. 2.2) may be present as part of a “lock”, which fits into an astragalo-tibial pit (Fig. 2.3) at the dorsal

base of the astragalar neck, at the limit of the dorsiflexed foot (Conroy and Rose, 1993; Szalay, 1994; Davis, 1996; Seiffert and Simons, 2001). Its presence and function during the close packed position indicates high loads as the foot is forced into extreme dorsiflexion when these loads are the greatest, e.g., during digging or galloping. A distinct tubercle is seen in *Hemicentetes*, *Microgale*, *Oryzorictes*, *Limnogale*, *Potamogale*, macroscelidids and *Solenodon*.

The anterior distal tibia is mediolaterally blunter in *Echinops* than in any other tenrecoid (Figs. 2.10, 2.17; ATDI, $p=0.007$), i.e. there is no trace of a tubercle or shelf. This most likely indicates a trade-off of stability for some mobility. The anterior distal tibia of both *Setifer* and *Tenrec* lacks this tubercle, yet there is a shallow protruding shelf. This edge fits into a broad gully on the astragalus (at the junction between the astragalar trochlea neck) to prevent extreme dorsiflexion beyond mechanically permissible limits. *Microgale cowani* and *M. talazaci*, as well as *Geogale* have a very slight overhang at the anterior distal tibia (Fig. 2.10). The tubercle in *M. dobsoni*, *Oryzorictes* and *Limnogale* is small but distinct, while *Hemicentetes* has two small overhanging tubercles, perhaps representing two loading positions – a dorsiflexed vs. everted position (Fig. 2.10). The tibial tubercle of *Potamogale* and macroscelidids are most prominent, and again indicate the importance of plantar push-off of the foot while swimming and jumping respectively. The tibial tubercle of *Solenodon* is different from that of the tenrecoids. It is narrow, almost as deep as the tibial malleolus, and sharply pointed (Figs. 2.10, 2.18)

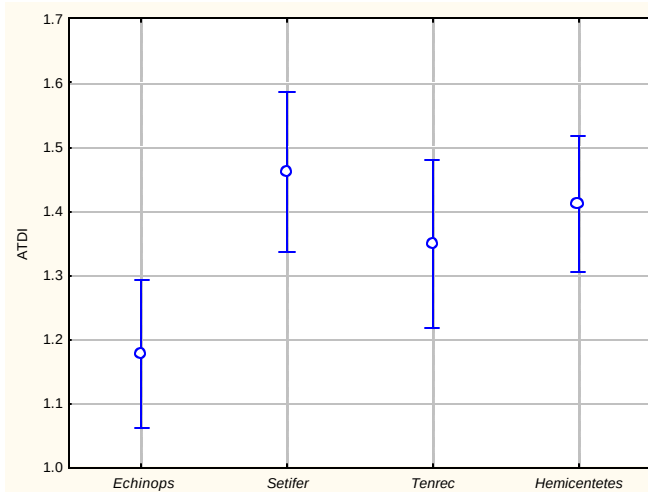


Figure 2. 17. Anterior Tibial Tubercle Index comparing tenrecine genera. Note *Setifer*, *Tenrec*, and *Hemicentetes* have deeper tubercles or shelves at the anterior distal tibia relative to *Echinops* ($p=0.007$).

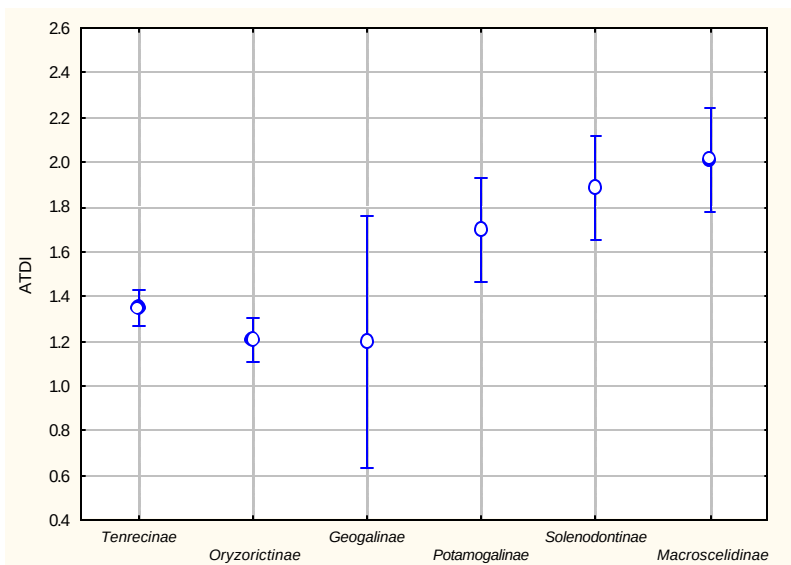


Figure 2. 18. Anterior Tibial Tubercle Index by subfamily. Note the pronounced tubercles in *Potamogale*, *Solenodon* and macroscelidids, indicating high loads on the anterior UAJ as the foot transits from dorsi- to plantarflexion (Fig. 2.10; $p=0.000$).

Orientation of the tibial and fibular malleoli may be a historically relevant signal, although this is difficult to measure quantitatively. When the tibia and fibula are aligned such that the long axis of the anterior tibial spine is oriented vertically, there are apparent interspecific differences in the orientation of the tibial and fibular malleoli (Fig. 2.10). This condition most likely indicates some deep-rooted differences in the mechanics of the crus and foot. The malleoli of the four tenrecines (*Echinops*, *Setifer*, *Tenrec*, and

Hemicentetes) are parallel to the sagittal plane of the tibia, aligned with the long axis of the tibial spine. The oryzorictine (*Microgale*, *Oryzorictes*, and *Limnogale*) malleoli are directed slightly medially, suggesting that 1) their feet are habitually directed medially with respect to the femur and proximal tibia, or 2) their femora are laterally rotated and the malleoli are medially directed in order to keep the feet axially aligned with the body. Observation of live *Echinops*, *Setifer*, and *Hemicentetes*, vs. *Microgale dobsoni*, *M. cowani* and *Oryzorictes* suggests that the latter explanation is probable. The oryzorictine foot is axially aligned and the tenrecine foot is more laterally rotated in its habitual position (see Fig. 2.19). Malleolar orientation in *Geogale* is similar to the tenrecines. The malleoli are directed anteroposteriorly, keeping the foot in line with the proximal tibia. The tibial and fibular malleoli of *Potamogale* are medially directed to the extreme, most similar in form to *Limnogale* (Fig. 2.10).



Figure 2. 19. From left to right, *Oryzorictes*, *Microgale*, *Hemicentetes*, *Echinops*. Note foot position in the oryzorictines (first two) is more axially aligned than the more laterally splayed foot in tenrecines (latter two). This difference in foot posture correlates with the orientation of the tibial and fibular malleoli (see Fig 10).

Upper ankle joint (UAJ), dorsal astragalus

During dorsiflexion, the anterior extensor musculature pulls on the pes, resulting in the distal tibia and fibula to be positioned on the anteriormost aspect of the astragalar trochlea, at the base of the astragalar neck. As a consequence, in some cases there is an astragalo-tibial pit at the dorsal base of the neck, preventing more extreme dorsiflexion of

the astragalus. Presence of a deep astragalo-tibial pit, often correlated with the above-mentioned anterior tibial tubercle, indicates relatively extreme contact during dorsiflexion, e.g., during leaping (Godinot and Dagosto, 1983; Dagosto, 1988). The slow moving, scansorial/arboreal *Echinops* has no trace of a hollowing at the junction between the astragalar trochlea and neck (Fig. 2.20). The transition from the dorsal surface of the astragalar trochlea to that of the neck is smooth, indicating no tibial stop, a feature consistent with somewhat facilitated rotational ability of the astragalus within the crural mortise. The distal astragalar trochleae of terrestrial *Setifer* and *Hemicentetes*, however, have a slight shelf at the inner border of the medial side. Though both are broader than in *Echinops*, the shelf is much broader in *Hemicentetes* than in *Setifer* and emerges directly from the anterior-most surface of the medial trochlea (Fig. 2.20). In *Hemicentetes*, there is a deep pit lateral to this shelf. Each of these two regions (the shelf and pit) in *Hemicentetes*, most likely represents a tibial brace, and might be of use depending upon the direction of loading. Alternatively, they may function together, in that the shelf may provide a broad, stable surface for high loads, while the inner pit prevents rotational movement. The double tubercles at the anterior distal tibia of *Hemicentetes* are consistent with either of these interpretations. *Tenrec* also has a distal trochlear shelf, which hollows slightly, located on the inner border of the lateral trochlea.

None of the oryzorictines has a discernable tibioastragalar pit or distinct shelf, despite the presence of small tubercles on the anterior distal tibia in *Oryzorictes*, *Limnogale*, and *Microgale dobsoni* (Fig. 2.20), which may simply mean that there is a cartilaginous receptacle for the tubercles that does not manifest itself on the bone. One would predict presence of such a pit, especially in *Oryzorictes*, but none is found in the

species examined. There appears to be a slight hollowing in the *Geogale aurita* astragalus, but it is difficult to discern in the available specimens due to covering fibrous material.

Unlike the smooth dorsal transition from the trochlea to neck in *Limnogale*, *Potamogale* presents the most distinct distal astragalar pit of all the tenrecoids surveyed (Fig. 2.20). The deep hollow is located directly at the midline of the astragalus, and is most likely used as a buttress, preventing tibial dislocation during the inception of heavy foot thrusts from a dorsiflexed position involved in swimming.

Solenodon is distinct from all of the above in having a shallow, wide hollowing at the anterior base of the trochlea (Fig. 2.20). There is no distinct pit, but the transition between the trochlea and astragalar neck is sharp, resulting in the formation of a shelf. The broad hollowing may serve as a tibial buttress in a wide range of mediolateral astragalar positions. The macroscelidids are also distinct from the tenrecoids in having a deep hollowing at the base of the trochlea, which is intermediate in form between *Potamogale* and *Solenodon*; rather than forming a distinct rounded pit, the hollowing is ovoid, allowing distal movement of the astragalus on the tibia which sharply restricts movement on the proximal, lateral and medial sides (Fig. 2.20).

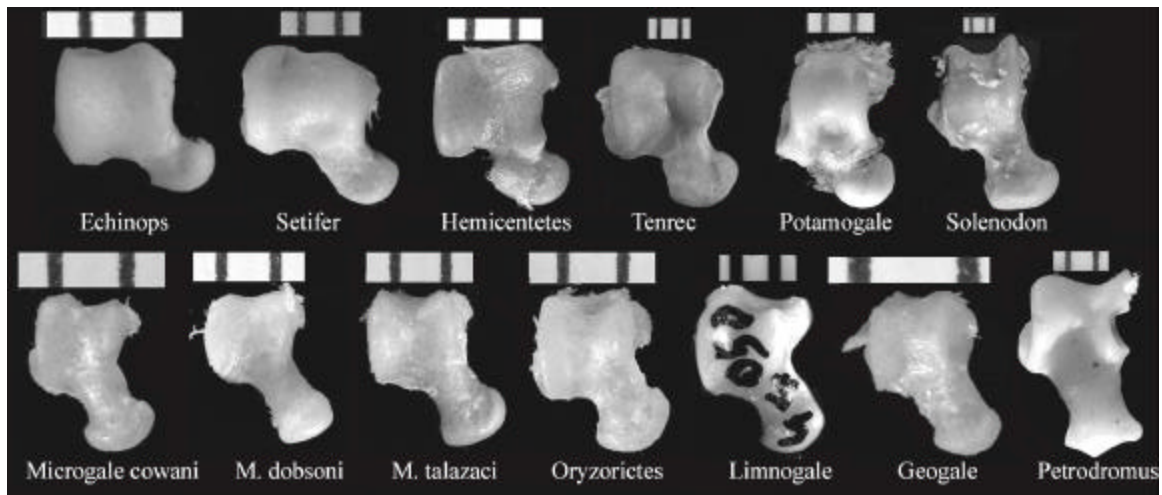


Figure 2.20. Dorsal astragalus (right side) of four tenrecines (*Echinops*, *Setifer*, *Hemicentetes* and *Tenrec*), five Oryzorictines (*Microgale cowani*, *M. dobsoni*, *M. talazaci*, *Oryzorictes*, and *Limnogale*), a potamogalinid (*Potamogale*), geogalinid (*Geogale*), solenodontid (*Solenodon*) and macroselidid (*Petrodromus*). Note especially differences in astragalar neck length, angle and robusticity, and presence/absence/shape of a pit or shelf at the proximal base of the neck.

The shape of the astragalar body and the configuration of the trochlea and its crests closely track the direction and distribution of incurred loads from the crus (Szalay, 1994). High, prominent lateral and medial crests and a deep trochlear groove indicate restriction of mediolateral UAJ mobility and facilitation of rapid flexion-extension (Szalay and Drawhorn, 1980; Godinot and Dagosto, 1983; Szalay, 1984; Dagosto, 1985, 1988).

There are apparent differences in tenrecoid astragalar trochlear crest morphology, with clear functional significance. *Echinops* has significantly lower crests than the other tenrecines (Fig. 2.21; TCHI, $p=0.000$) with a broad and higher lateral side (Fig. 2.22; MLCHI, $p=0.037$) that shifts the midpoint of the trochlea towards the medial edge (Fig. 2.24). In contrast, *Setifer* has high, narrow, even-sided crests. Arboreal marsupials tend to have an astragalar body with a shallow trochlea, whereas more terrestrial species (such as macropodids) tend to have a deeper trochlea with an increasingly well-defined lateral crest, which delineates a more angled astragalofibular contact (Argot, 2002; Szalay,

1994). In arboreal primates, kinkajous, and squirrels, the lateral crest is generally higher than the medial crest, which reflects a well-stabilized upper ankle joint that facilitates speed in flexion-extension coupled with habitual inversion. More terrestrial mammals have trochlear crests of even height and a body with nearly vertical medial and lateral sides (Jenkins and McClearn, 1984; Fleagle, 1988; Rose, 1999; Seiffert and Simons, 2001; Argot, 2002). Although the degree to which *Echinops* is arboreal has been disputed (and live *Setifer* and *Echinops* are extremely difficult to distinguish without skeletal material), the low medial and high lateral crests in *Echinops* strongly suggest its arboreality in contrast to *Setifer*.

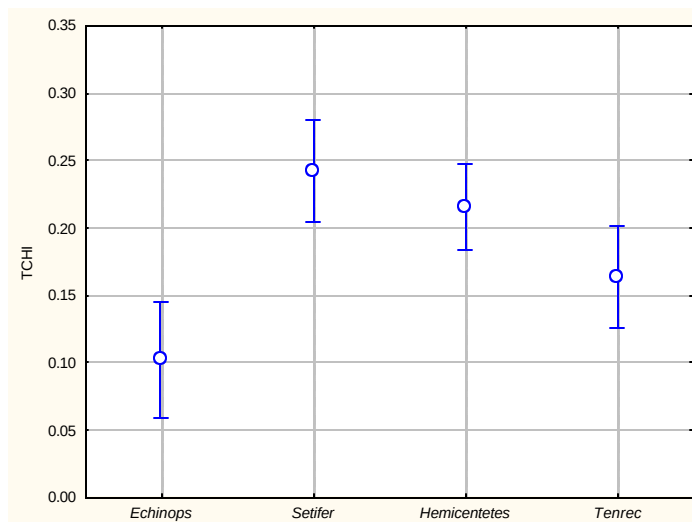


Figure 2. 21. Trochlear Crest Height Index comparing tenrecines. Note that *Echinops* has significantly lower trochlear crests than the other tenrecines (0.000), which corresponds with arboreal foot mobility.

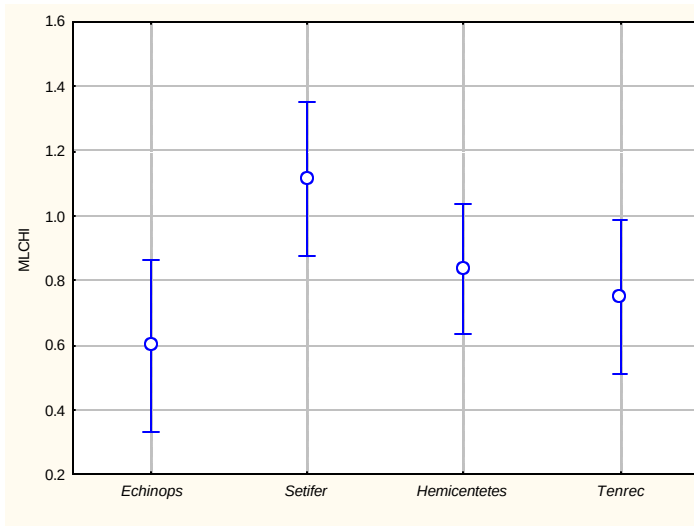


Figure 2. 22. Medial/Lateral Trochlear Crest Height Index comparing tenrecines. Note that *Echinops* has a significantly higher lateral than medial trochlear crest (0.037), which corresponds with arboreality in other placentals.

Tenrecines have mediolaterally long, sloping astragalar lateral crests with the midline shifted towards the medial trochlea. In contrast, oryzorictines have a laterally shifted trochlear midline, with a more sharply sloped lateral crest (Figs 2.23, 2.24; $p=0.001$). *Limnogale* resembles the other oryzorictines in this respect, and is unlike *Potamogale*, despite a shared swimming habitus. Most likely this difference between tenrecines and oryzorictines, like the difference in malleolar orientation, reflects different approaches to locomotion and hence foot postures between the two groups. *Oryzorictes* has especially narrow and sharp lateral trochlear crests, most likely related to stabilization of the UAJ while digging. *Geogale*'s trochlear crests are shallow and smooth, with a slightly sharper lateral side, as found in the oryzorictines, but a medially shifted trochlear midpoint, as in the tenrecines. Similar to the oryzorictines, *Potamogale* has a slightly laterally shifted trochlear midpoint. *Solenodon* is markedly different from all of the above, in having a long and almost flat lateral trochlear crest and a narrow, high and

sharp medial crest. This is typical of a plantigrade and mediolaterally stabilized foot posture (Carrano, 1997; Argot, 2002).

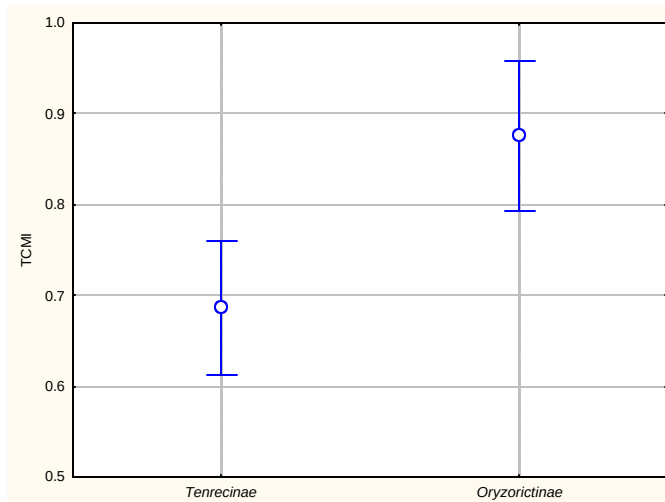


Figure 2. 23. Trochlear Crest Midpoint Index showing subfamily differences between tenrecines and oryzorictines ($p=0.001$). Tenrecines have a medially shifted trochlear midpoint, whereas oryzorictines' is closer to midpoint.

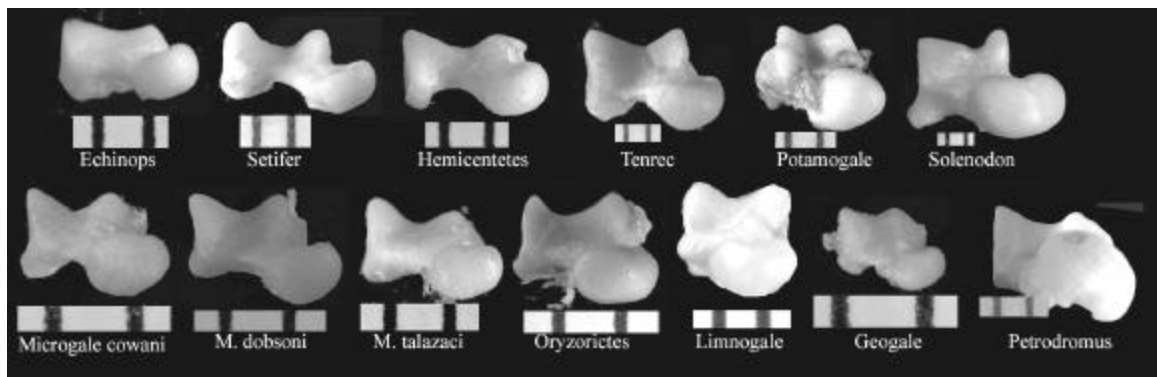


Figure 2. 24. Distal astragalus (right side) of four tenrecines (Echinops, Setifer, Hemicentetes and Tenrec), five Oryzorictines (Microgale cowani, M. dobsoni, M. talazaci, Oryzorictes, and Limnogale), a potamogalinid (Potamogale), geogalinid (Geogale), solenodontid (Solenodon) and macroselidid (Petrodromus). Note especially differences in trochlear crest height, medial/lateral crest height, and trochlear midpoint. The astragalar trochlea of *Geogale* is more similar to the tenrecines. *Limnogale* is more similar to the other oryzorictines than to *Potamogale*, despite its shared aquatic habitus with the latter.

Lower ankle joint (LAJ), dorsal calcaneus

Superposition of the astragalus upon the calcaneus is a derived placental tarsal feature, in contrast to the primitive therian condition in which the astragalus is positioned

medial to the calcaneus (Kemp, 1982; Szalay, 1984, 1994; Lewis, 1989). In the primitive mammalian condition, articulations between the tibia, fibula, astragalus and calcaneus were, therefore, more interdependent than those in many placentalian eutherians. Astragalar superposition on the calcaneus allowed for the two joints (UAJ and LAJ) to act far more independently than before, the UAJ allowing for extended dorsi- and plantarflexion, and the LAJ primarily allowing for subtle to extreme inversion and eversion of the foot, as well as adduction and abduction, and slight dorsi- and plantarflexion.

The tenrecoid calcanea appear to retain more phylogenetically useful attributes than other regions of the tarsus (Fig. 2.26). This conclusion is based on the fact that fewer characters correlate closely with function- and adaptation-based hypotheses. Although several arboreal mammals have posteriorly raised and rotated calcaneal astragalocalcaneal facets (Jenkins and McClearn, 1984; Szalay, 1984; Szalay and Decker, 1974), this feature is not apparent in *Echinops*. Nor is it evident in any of the tenrecoids that LAJ stabilization is achieved by flattening and locking (e.g., as in perissodactyls or macropodids) of the astragalocalcaneal facets, as noted for terrestrial mammals (Argot, 2002; Barnett, 1970; Szalay, 1994). Tenrecines have relatively shorter and wider calcanea vs. those of the longer, narrower oryzorictines (Figs. 2.25, 2.26; CLI, $p=0.000$)

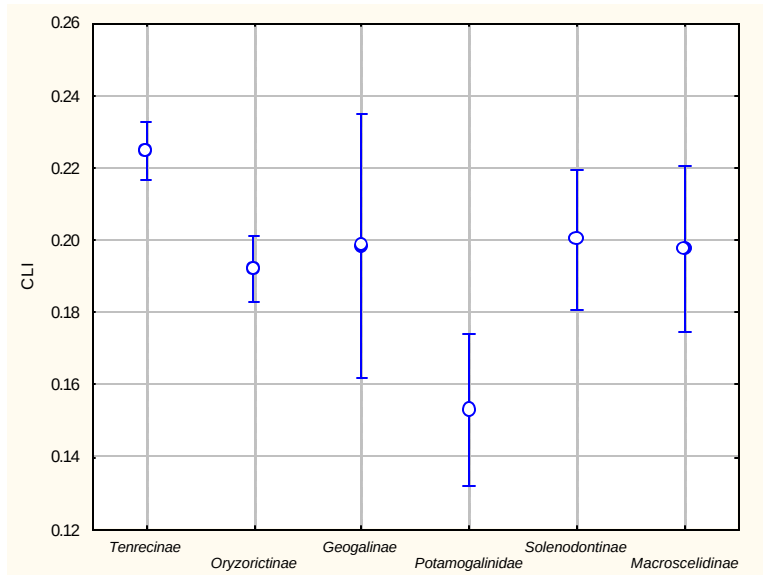


Figure 2. 25. Calcaneal Length Index by subfamily. Tenrecines have a relatively short, wide calcaneus, whereas that of *Potamogale* is extremely long and narrow. *Geogale* is similar to the oryzorictines in this respect. The tenrecine, as well as potamogaline condition are most likely derived tenrecoid traits.

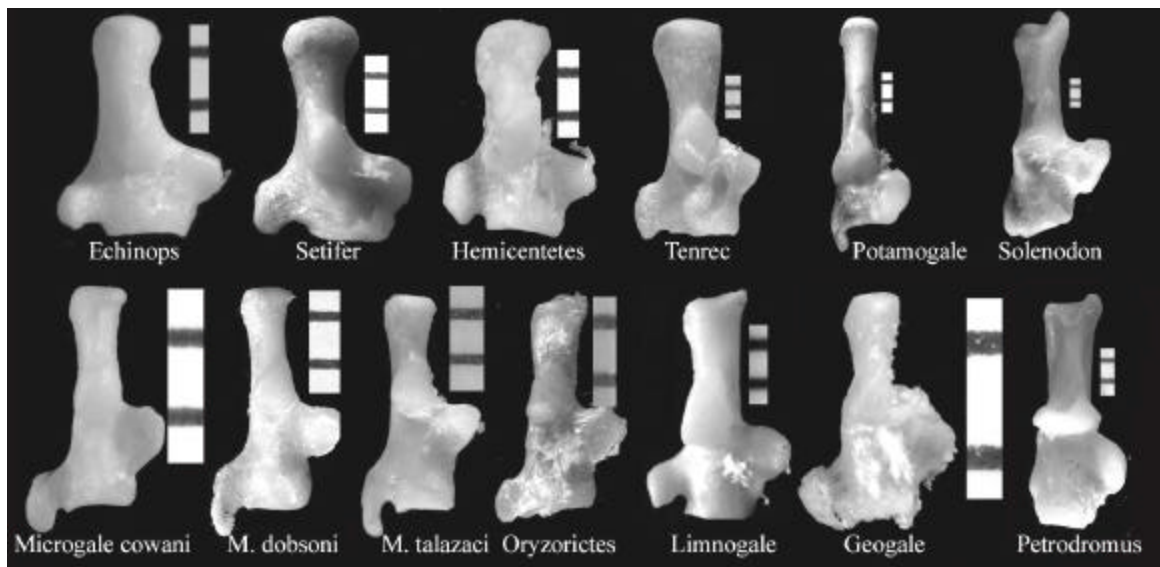


Figure 2. 26. Dorsal calcaneus (right side) of four tenrecines (*Echinops*, *Setifer*, *Hemicentetes* and *Tenrec*), five Oryzorictines (*Microgale cowani*, *M. dobsoni*, *M. talazaci*, *Oryzorictes*, and *Limnogale*), a potamogalinid (*Potamogale*), geogalinid (*Geogale*), solenodontid (*Solenodon*) and macroscelidid (*Petrodromus*). Note differences in tuber length and width, astragalocalcaneal facet position, and peroneal process shape. The tenrecine calcaneus is relatively shorter and wider than that of the oryzorictines'; *Potamogale* has an extremely long and narrow calcaneus with a long tuber, appropriate for strong, dorsolateral aquatic propulsion. Calcaneal features in *Limnogale* are more similar to the other oryzorictines than to *Potamogale*.

There are significant family group level differences (i.e., both subfamilial and familial) between tenrecoids in the position of the astragalocalcaneal facet on the calcaneus relative to the shaft of the tuber and cuboid facet (Figs. 2.26, 2.27; ACFI, $p=0.000$). The calcaneal astragalocalcaneal facet in oryzorictines is located substantially closer to the posterior border of the calcaneus compared to that of tenrecines, in which it is located near the center of the bone (Figs. 2.26, 2.28; ACFI, $p=0.000$). *Geogale*'s facet position is similar to the oryzorictines'. Unlike that of *Limnogale* or any other tenrecid, the astragalocalcaneal facet of *Potamogale* is distinctive in being positioned at the distal end of the calcaneus.

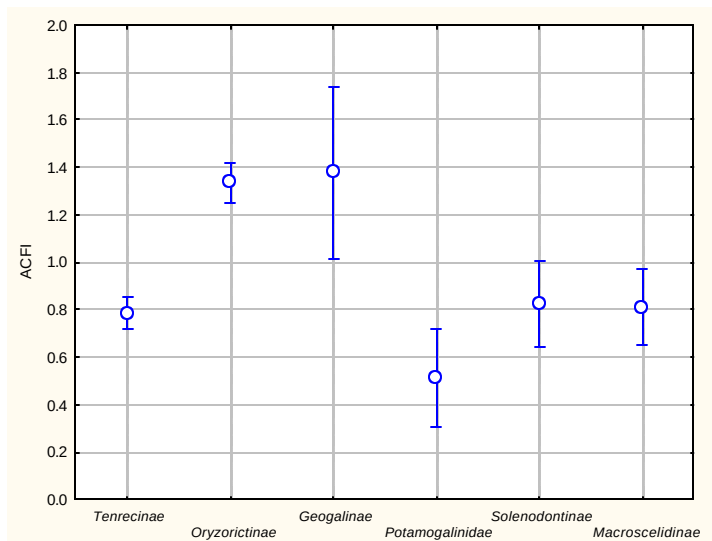


Figure 2. 27. Calcaneal Astragalocalcaneal Facet Index by subfamily. Lower values indicate relatively anteriorly positioned facets, vs. higher values, which indicate posteriorly positioned facets (see Fig. 2.14).

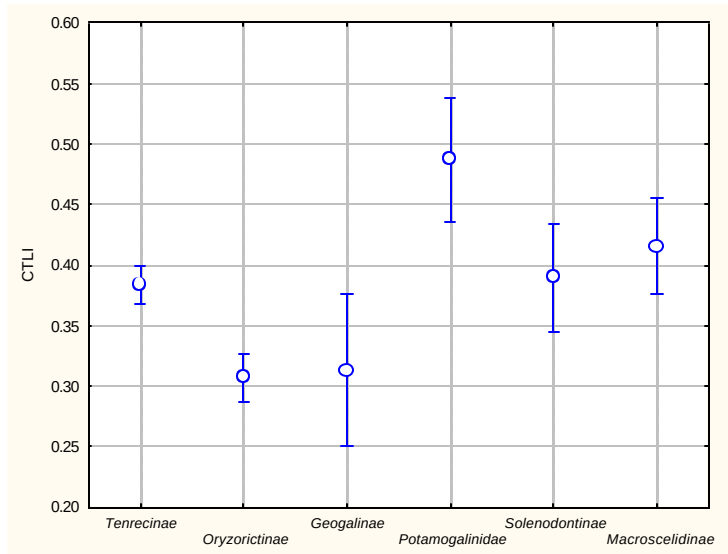


Figure 2. 28. Calcaneal Tuber Length Index by subfamily. Higher values indicate a longer calcaneal tuber. Note that the relative position of the astragalocalcaneal facet (graph 12) is directly related to tuber length. Except in *Potamogale*, which has a long tuber, most likely correlated with aquatic foot propulsion, tenrecid tuber lengths do not correspond to function-based hypotheses.

Differential positioning of the astragalocalcaneal facet is directly (and negatively) correlated with differences in the length of the calcaneal tuber (correlations matrix value=-0.89). A more distally positioned facet results in a relatively longer tuber, whereas a more proximally positioned facet results in a relatively shorter tuber (Fig. 2.26). Differences in tuber length can be suggestive of locomotor mechanics (Szalay and Decker, 1974). A shorter shaft of the calcaneal tuber results in greater speed for flexion-extension. Conversely, a longer tuber shaft provides greater torque for more powerful, deliberate foot movements, e.g., in hindlimb digging or slow climbing (Szalay and Langdon, 1986; Muizon et al., 1998).

The relatively proximal position of the astragalocalcaneal facet in the oryzoricines results in a relatively shorter calcaneal tuber (in relation to total calcaneus length) when compared to the tenrecines, whereas the tuber in *Potamogale* is exceptionally long, due both to the distal position of the astragalocalcaneal facet, and the

excessive elongation of the tuber even without the distal displacement of the LAJ (Figs. 2.26, 2.29). Although relatively longer tubers (i.e., which increase the torque of the M. gastrocnemius) were expected in the slow climbing and digging tenrecines *Echinops* and *Hemicentetes*, but these two species have relatively *shorter* tubers than those of other subfamily members (Fig. 2.26). The oryzorictine digger, *Oryzorictes*, also does not have a significantly longer tuber than its other subfamily members.

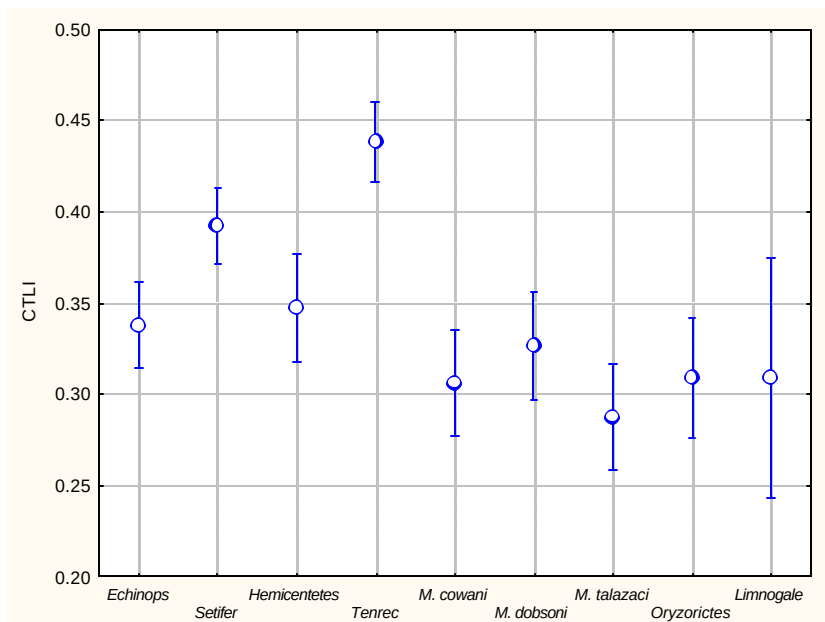


Figure 2. 29. Calcaneal Tuber Length Index showing tenrecine and oryzorictine species. *Echinops* and *Hemicentetes* have relatively short tubers compared to the other tenrecines *Setifer* and *Tenrec*, and there is no significant difference between *Oryzorictes* and the other oryzorictines. Within the tenrecines, there is an apparent size-based allometry for tuber length, yet this is not the case for oryzorictines.

The position of the sustentacular facet is also correlated with astragalocalcaneal facet position (correlations matrix value=0.81). The sustentacular facet of tenrecines is located near the distal side of the calcaneus, whereas in oryzorictines (excluding *M. cowani*), it is more proximal at approximately 1/3 of the length of the calcaneus from the distal end.

In tenrecines the posterior border of the sustentacular facets slope distally from the calcaneus at a 45° angle. In contrast, in all observed oryzorictines the facet protrudes at a near 90° (Fig. 2.26). This feature may have phylogenetic significance at the subfamily level, although its functional significance (if any) is unexplored. In *Potamogale*, the sustentacular facet is unlike that in either of the tenrecid subfamilies in having a proximodistally long sustentaculum that is adjacent to the distalmost border of the calcaneus.

Transverse tarsal joint (TTJ), astragalar head and neck

The transverse tarsal joint facilitates dorsiflexion and plantarflexion, and to a lesser degree pronation (eversion of the pes) and supination (inversion of the pes), and can be an important indicator of certain postural behaviors. There are diagnostic differences between tenrecoids in the length and orientation of the astragalar neck. Of the tenrecines, *Echinops* and *Setifer* have a more medially directed neck than *Hemicentetes* and *Tenrec* (Fig. 2.20). This would suggest medial loading during inversion (Szalay, 1994, 1985), expected in the arboreal *Echinops*, but not necessarily in the ground-living *Setifer*. Of these two species, *Echinops* has a shorter neck (ANWI, $p=0.029$), which would better withstand loads incurred during climbing (Szalay, 1985, 1994; Conroy and Rose, 1993). The more distally extended robust necks of *Hemicentetes* and *Tenrec* (Fig. 2.20; ANWI, $p=0.046$) reflect their terrestrial lifestyles (Szalay, 1985, 1994; Conroy and Rose, 1993; Muizon et al., 1998), which include multi-axial loading related to some digging behavior. *Potamogale* has an unusually short and robust neck, directed along the axis of the medial malleolus, whereas that of *Solenodon* is long and relatively narrow, also facing along the axis of the medial malleolus (Fig. 2.20). The astragalus of

Potamogale is most likely resisting significant multiaxial loads at its navicular contact, whereas *Solenodon* is loading more regularly during dorsi- and plantarflexion.

Petrodromus' astragalar neck is distally directed and both long and robust, reflecting high loads in the plane of dorsiflexion, and resistance against mediolateral shifting (Szalay and Decker, 1974; Muizon et al., 1998). *Microgale*, *Limnogale*, and *Geogale* have consistently long astragalar necks that are directed medially 45° away from the astragalar trochlea. Seiffert and Simons (2001) suggested that the length of the astragalar neck is particularly subject to allometric influences: smaller forms tend to have relatively longer astragalar necks. Although oryzorictines have longer astragalar necks than tenrecines, there is no significant correlation between neck length and body mass within Oryzorictinae, or between the other species examined for this study. A somewhat elongated astragalar neck (compared to a more primitive rounded distal end of the astragalus that is present even in extant didelphids among therians) is a derived condition, probably of the stem placentarians (of the Eutheria) (Szalay and Decker, 1974).

Within the oryzorictines the astragalar neck of *Oryzorictes* is more robust (Figs. 2.20, 2.30; ANWI, $p=0.002$), an apparent adaptive response to relatively high multiaxial loading presumably incurred when digging (Szalay, 1985, 1994; Conroy and Rose, 1993).

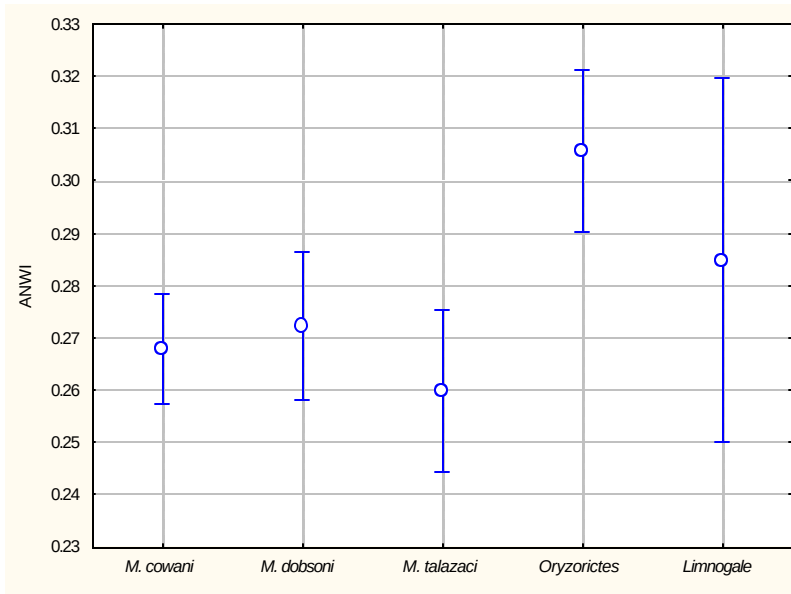


Figure 2. 30. Astragalar Neck Width Index, comparing oryzorictines. Note the significantly more robust neck in the digging tenrecoid, *Oryzorictes*. *Limnogale* also appears to have a wider neck than the *Microgale* species, which is indicative of multiaxial loading.

Astragalar head shape varies considerably between species, yet functional hypotheses were not consistently supported (Fig. 2.31). Amongst the tenrecines, *Tenrec* and *Hemicentetes* have mediolaterally extended heads compared to those of *Echinops* and *Setifer* ($p=0.001$). This may reflect transverse shifting, as occurs with considerable medial and lateral loads from inversion and eversion (Szalay and Decker, 1974; Szalay, 1994; Argot, 2002). Despite its arboreal activity, *Echinops* does not exhibit a wide articular surface of the astragalar head, as is found in arboreal primates (Szalay and Langdon, 1986; Szalay and Decker, 1974); nor did *Echinops* exhibit a widened medial side of the astragalar head. A mediolaterally wide astragalar head may be more indicative of digging behavior, as suggested by the significantly wider heads in *Hemicentetes*, *Tenrec*, *Oryzorictes* and *Solenodon* (Fig. 2.31; $p=0.000$). *Limnogale* also has a wide articular surface of the astragalar head, which correlates with its wide astragalar neck; this may be related to some mediolateral shifting of the foot while swimming, and is, in any case,

significantly different ($p=0.001$) from the dorsoplantarly deep astragalar head of *Potamogale* (Fig. 2.31). The elephant shrews *Petrodromus* and *Nasilio* have a distinct half-moon shaped notch at the plantar surface of the astragalar head, which indicates a highly immobile articulation at the macroscelidid TTJ.

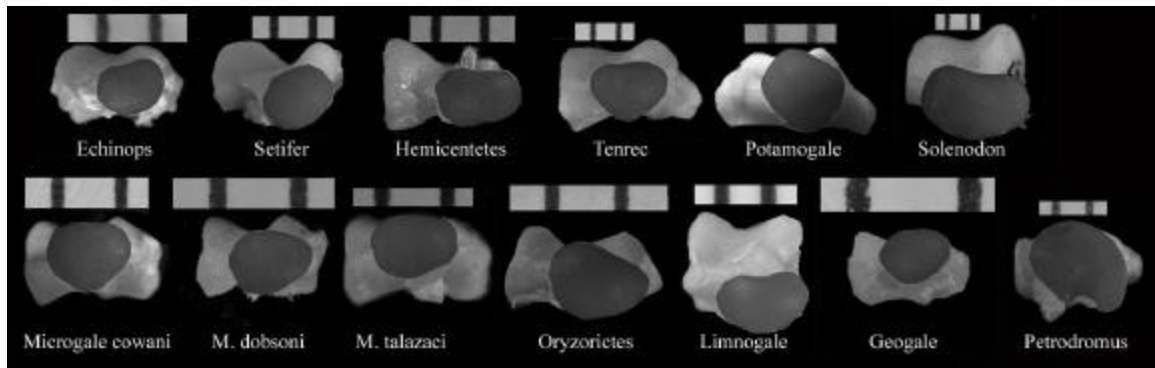


Figure 2. 31. Distal articular surface of the astragalar head (right side). Species that dig (*Hemicentetes*, *Tenrec*, *Oryzorictes* and *Solenodon*) have significantly wider articular surfaces, as does *Limnogale*. Macroscelidids have a characteristic gap on the plantar lateral side of the astragalar head, where the astragalus tightly articulates with a proximally extended navicular.

Transverse tarsal joint (TTJ), distal calcaneus

During inversion, the calcaneus rotates laterally until the cuboid facet is entirely plantar to the astragalar head. The cuboid shifts towards the lateral edge of the calcaneus, while the greatest loads are sustained on the medial surface. A laterally expanded calcaneal cuboid facet that is considerably larger than its conarticular counterpart should therefore correlate with a more extensive range of inversion (Szalay and Decker, 1974; Solomon et al., 1990; Neveu and Gasc, 2002;). Nonetheless, no significant differences in calcaneal cuboid facet shape were found between (or within) tenrecoid subfamilies ($p=0.883$). Tenrecoids have more ovoid vs. rounded calcaneal cuboid facets than *Solenodon* and the macroscelidids ($p=0.000$), which may indicate some relative degree of TTJ mobility in the tenrecoid common ancestor.

Although not directly involved with the transverse tarsal joint, the mammalian peroneal tubercle of the calcaneus is taxonomically variable both in its position along the lateral border of the calcaneus and in its conformation (Romankowowa, 1963; Stains, 1973, 1975; Szalay and Decker, 1974; Jenkins and McClearn, 1984; Szalay, 1985; Rose, 1999;). It serves as a brace and a lever for the lateral passage of the peroneal muscles (Decker and Szalay, 1974), but the significance of its taxonomic diversity in therians is clearly tied to its functional role rather than to some phylogenetic issue. The peroneal shelf of the earliest mammals was originally wide in the earliest mammals, and has been reduced to differing extents in the numerous clades derived from the plesiomorphic mammalian condition. Its phyletic value as a character is that its large dimensions indicate an early stage of functional configuration from which various departures probably originated. In addition, its extremely reduced state was unlikely to have been ancestral to taxa with large peroneal processes. This issue has not been extensively explored. The peroneal process is extremely variable between tenrecoid species, and there is a significant difference in shape and distal extension between tenrecine and oryzorictine subfamilies (Figs. 2.26, 2.32; PPPI, $p=0.000$). In the extant hindfoot reversers *Potos* and *Sciurus*, (as well as in their respective Paleocene ancestries) the peroneal tubercle is greatly reduced as in other carnivorans and rodents, and shifted proximally, farther than, for example, in archaic primates, dermopterans, or a variety of early condylarths (see figures in Szalay and Drawhorn, 1980; Jenkins and McClearn, 1984; Szalay, 1985). Among the tenrecines *Echinops* has the most proximally positioned peroneal process, which may be functionally related to hindfoot reversal.

The peroneal process in *Microgale* and *Oryzorictes* is mediolaterally narrow and, especially in *Microgale*, projects far beyond the distal border of the calcaneal body. The tenrecine peroneal process is mediolaterally wider and does not reach far beyond the calcaneal cuboid facet, if at all. *Geogale* is intermediate in form between the tenrecines, *Microgale*, and *Oryzorictes*, and may represent the tenrecoid ancestral form (based on the peroneal tubercle of known early, and therefore probably primitive, placentalian eutherians, which is a wide lateral shelf, projecting off the anteriormost lateral side of the calcaneus (Szalay and Decker, 1974; see a limited survey of early Mammalia in Szalay, 1994). *Limnogale* is different from the other oryzorictines in having a wide, relatively distally displaced process. It is, however, unlike *Potamogale*, in which the process is thin and elongated (as in *Microgale*), but unique in jutting directly from the distalmost border of the calcaneus and abutting the articulating lateral side of the cuboid. The way in which the peroneal process closely aligns with the cuboid in *Potamogale* suggests that it stabilizes and prevents lateral dislocation of the cuboid. This is consistent with other regions of the tarsus that maximize stability for flexion-extension based foot paddling while swimming.

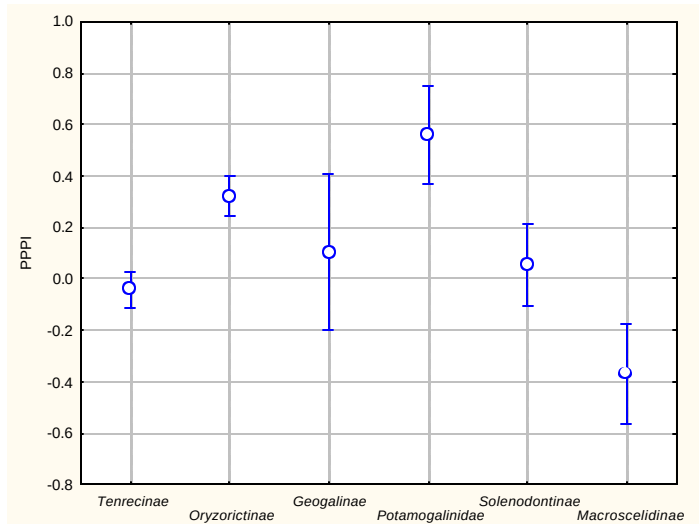


Figure 2.32. Peroneal Process Position Index. Higher values indicate a peroneal process that extends beyond the distal end of the calcaneus, whereas lower values indicate more posteriorly positioned processes. Note the long, anteriorly positioned process in *Potamogale* in contrast to the posteriorly positioned process in macroselidids. There are significant differences between tenrecines and oryzictines, with *Geogale* falling in between.

Distal tarsals and metatarsals

Direction of curvature of the proximal articular surface of the navicular reflects components of various axes of foot mobility, and in particular rotation of the astragalar head (Szalay and Decker, 1974). All tenrecids have a medial shelf of the proximal navicular (Fig. 2.33) that resists medial loading of the astragalar head. There are significant differences between tenrecines in navicular shelf length. The climber *Echinops*, and the digger *Hemicentetes* have longer shelves than the other tenrecines (Figs. 2.33, 2.34; NPDI, $p=0.001$), reflecting a more stabilized LAJ. The long medial border of the navicular facet in *Echinops* projects proximally at a sharp 90-degree angle (Fig. 2.33), buffering forces from the medially loading astragalar head during inversion. *Setifer* has a shorter medially projecting navicular border, but it projects proximomedially at a 50° slope, as in the other tenrecines. The navicular of the three *Microgale* species examined is distinct from the other tenrecoids in being proximally elongated in a way that

the lateral side has a broad articulation with the calcaneus. In all other examined tenrecoids there is minimal naviculocalcaneal articulation. The navicular facet in *Limnogale* is unlike that in *Potamogale* and resembles that of the other oryzorictines in overall shape (Figs. 2.33, 2.34).

Stability of the astragalonavicular joint in *Solenodon paradoxus* is accomplished in a significantly different way from that in the tenrecoids. The articulating navicular does not have the projecting borders seen in the latter (Fig. 2.33). In contrast, the entocuneiform is long, and extends proximally beyond the proximal border of the navicular. It narrows at its proximal end and twists laterally, forming a large, concave underlying shelf for the plantar support of the distal astragalus (Fig. 2.33).

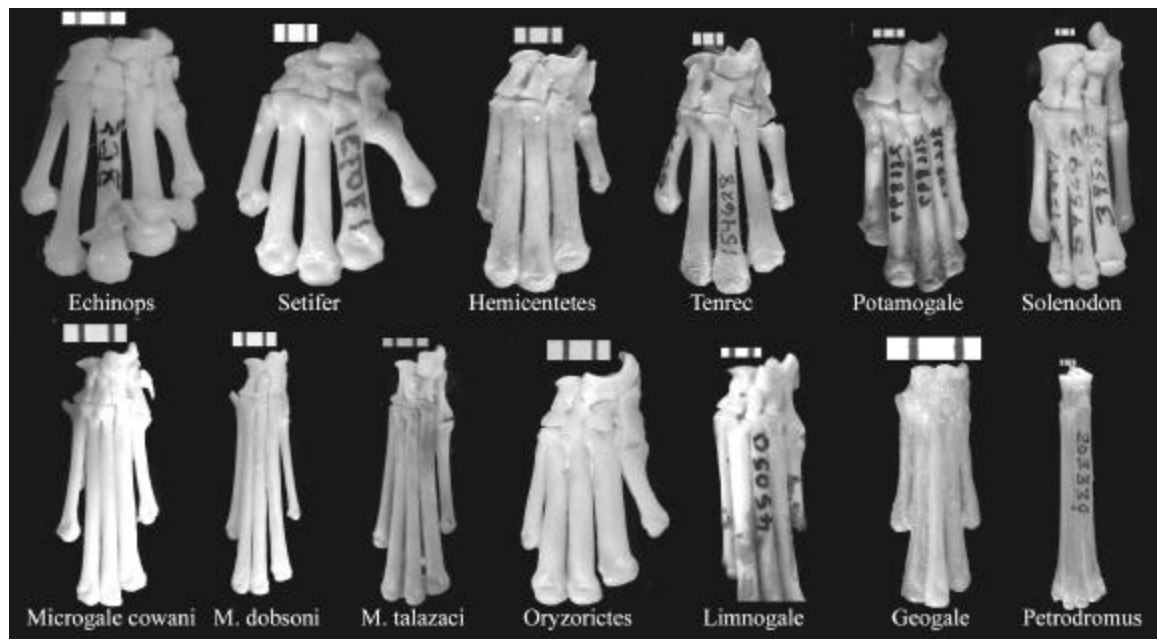


Figure 2.33. Right foot, dorsal view. Differences in the navicular proximomedial shelf reflect functional demands; that of *Echinops* projects at a sharp 90deg. angle, resisting medial loading.

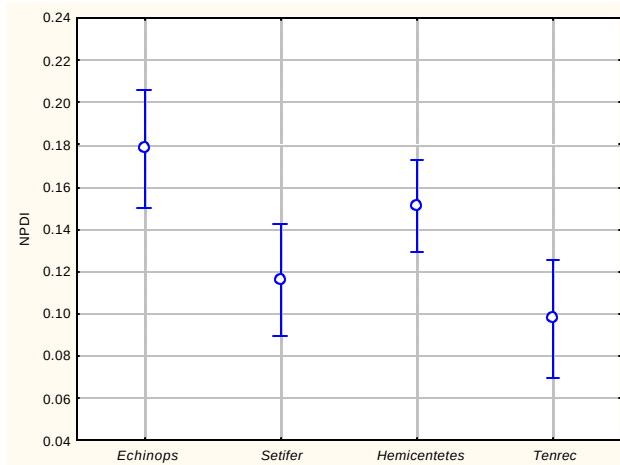


Figure 2. 34. Navicular Proximomedial Shelf Index, comparing tenrecines. Note the relatively longer shelves in the arboreal *Echinops* and semi-fossorial *Hemicentetes* indicating heightened buffering against loads from the medial astragalar head.

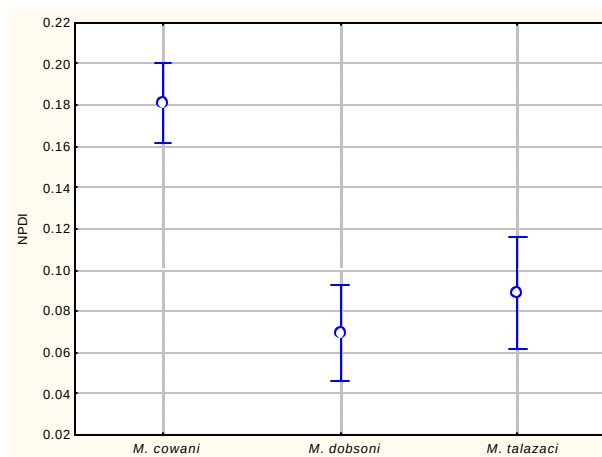


Figure 2. 35. Navicular Proximomedial Shelf Index, comparing *Microgale* species. *M. cowani* has a markedly longer shelf than the other two *Microgale* species, indicating increased buffering against loads from the medial astragalar head. The other oryzorictines, *Limnogale* and *Oryzorictes*, as well as *Geogale* have values similar to *M. cowani*, suggesting that the shelves in *M. dobsoni* and *M. talazaci* are reduced relative to the primitive oryzorictine condition.

The proportions of the tarsometatarsal complex show a fairly consistent correlation between length of the distal tarsals and metatarsal length (Fig. 2.16). Tenrecines have relatively shorter metatarsals than oryzorictines (Figs. 2.33, 2.36; MT3I, $p=0.000$). Among the tenrecines *Echinops* has the shortest metatarsals, followed by *Hemicentetes*, but the differences are not significant ($p=0.522$). Within the oryzorictines however, *Oryzorictes* has significantly shorter metatarsals than the other oryzorictines (Figs. 2.33, 2.37; MT3I, $p=0.000$), reflecting a more powerful and deliberate dorsiflexion

(Hildebrand, 1995; Stein, 2000). The mtIII proportions of *Limnogale* are similar to the other oryzorictines, as are those of *Geogale*. *Potamogale* has a distinct distal tarsal/metatarsal complex in having relatively long first and fifth metatarsals (as in *Solenodon*), elongated distal tarsals (as in *Tenrec*), and robust, long metatarsals (as in *Hemicentetes*). The studied macroselidid species have the longest mtIII index values, reflecting their saltatory habitus (Fig. 2.33).

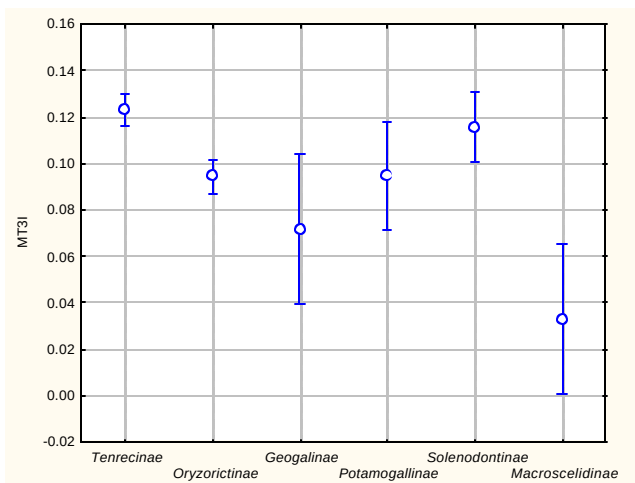


Figure 2. 36. Metatarsal III Shape Index comparing subfamilies. Higher values indicate shorter mtIIIs. Tenrecines have significantly shorter metatarsals than the other tenrecoids, indicating a more powerful foot grasp. Solenodontids also have short, stout metatarsals, most likely correlated with its digging behavior, whereas the saltatorial macroselidids have the relatively longest metatarsals for swift terrestrial movement.

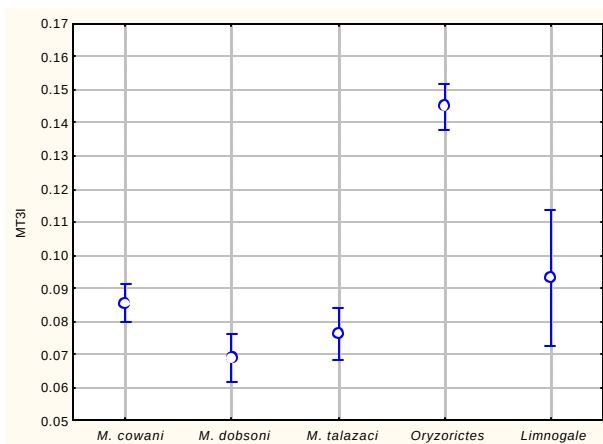


Figure 2. 37. Metatarsal III Shape Index comparing oryzorictines. The digger, *Oryzorictes*, has a significantly shorter mtIII than the other oryzorictines, indicating a shorter out-lever for more powerful load resistance.

Summary and Conclusions

Subfamily Tenrecinae. *Echinops* and *Setifer* are classified as separate genera based on differing dental formulae, but they are otherwise extremely difficult to distinguish from external morphology. *Echinops* is more often found nesting in trees, while *Setifer* is found in low trunk hollows or underground burrows (Eisenberg and Gould, 1970; pers. obs.). There are a series of significant function-based differences in tarsal morphology between the two genera; several features of the *Echinops* tarsal complex suggest arboreal positional behavior, including significantly greater degrees of freedom at the UAJ and LAJ, with stabilization of the medial TTJ. The few similarities in tarsal form between *Setifer* and *Echinops*, suggest that *Setifer* may have evolved from a smaller, arboreal, *Echinops*-like ancestor, and has since modified several characteristics to accommodate a more terrestrial lifestyle. The tarsus of *Hemicentetes* has several features that suggest moderate hindlimb use for digging. *Tenrec* tarsal morphology shows that it is most stabilized for movement involved with dorsi- and plantarflexion. There are a few indications of strong hindlimb loading, probably indicative of some digging.

Despite suspected locomotor convergence across the subfamilies (such as those found between *Hemicentetes* and *Oryzorictes*, and between *Limnogale* and *Potamogale*), tenrecines have a number of tarsal characteristics that are significantly different from those of oryzorictines. Tenrecines have anterior as opposed to medially directed malleoli, a deeper tibial than fibular malleolus, a medially shifted trochlear midpoint, a distally positioned sustentacular facet that slopes forward at a 45° angle, and a mediolaterally wide peroneal process. The first of these listed differences is based on foot posture. Tenrecines have a more laterally pointing hindfoot than the oryzorictines, which is a

taxonomic and phylogenetically important feature. Such fundamental constructional difference results in the distinctive structure and function of the UAJ. Tenrecine features such as a short astragalar neck, wide calcaneus, and short metatarsals suggest that the tarsal complex of the common tenrecine ancestor was more mobile and resistant to multiaxial loads than that of oryzorictines.

Subfamily Oryzorictinae. Differences in tarsal morphology support the distinctiveness of the Geogalinae, leaving *Microgale*, *Oryzorictes* and *Limnogale* in Oryzorictinae. The *Limnogale* tarsal complex is considerably different from *Potamogale* in almost every aspect of morphology, suggesting that these two swimmers use different modes of aquatic propulsion. Furthermore, there are many similarities between *Limnogale* and the other oryzorictines, suggesting that *Limnogale* should remain in Oryzorictinae (as in Douady, 2002; Olson, 2003), as opposed to its recommended inclusion in Potamogalinae (contra Asher, 2000). Although relatively little is documented about the aquatic locomotor behavior of *Limnogale*, the tarsal complex indicates that its hind limbs are less important for propulsion than those of *Potamogale*. Several features may serve to stabilize the foot during swimming, but most are similar to those in other oryzorictines, and are probably indicative of relationship in a foot relatively unmodified for aquatic function. The tarsal complex of *Oryzorictes* reflects many digging-related traits (e.g., a deeply extended fibular malleolus, a narrow and sharp lateral trochlea, a laterally wide astragalar head, and short, wide metatarsals). Some general features are convergent with those of *Hemicentetes*, but this oryzorictine evidently loads and everts the foot to a greater degree than the tenrecine. Several shared oryzorictine features, that are distinct from those of the tenrecines (e.g., evenly extended tibial and fibular malleoli,

fused tibia-fibula, even-sided astragalar trochlea, long and narrow distal tarsals and metatarsals), indicate a UAJ, LAJ and TTJ that are relatively restricted to movement in the sagittal plane, and are not extensively buffered against mediolateral shifting.

Subfamily Geogalinae. *Geogale aurita* is most often recognized as a member of Oryzorictinae, although its suite of unusual cranial characteristics has prompted suggestions of an independent Geogalinae (Dobson, 1882; Asher 2000). On phenotypic grounds alone *Geogale* tarsal morphology indicates that a subfamily status is warranted. *Geogale* shares several features with the oryzorictines (e.g., a relatively long astragalar neck and calcaneus and long metatarsals), as well as with the tenrecines (e.g., its distal tibia is directed parasagittally and the tibial malleolus is longer than the fibular), although its morphology is distinctive in most details. The geogaline characteristics that are shared with *Microgale* indicate a closer affiliation with oryzorictines than with tenrecines.

Subfamily Potamogalinae. Tarsal morphology of *Potamogale velox* is substantially different from that of the other tenrecoids, including the semi-aquatic *Limnogale*. It is characterized by a suite of highly derived, diagnostic characteristics related to stabilizing the foot while swimming.

Family Solenodontidae. *Solenodon*'s dissimilarity from the tenrecoids in detail, general shape and overall proportions of the individual tarsals supports evidence that despite shared zalambdodonty, the relationship between *Solenodon* and tenrecids is remote; there is no indication of shared tarsal form aside from proportional similarities based on digging behavior. Comparison of *Solenodon* tarsal features with those in the subfossil *Nesophontes* is important for establishing possible homologies between the two.

Family Macroscelididae. *Petrodromus* and *Nasilio* share some distinct features with *Potamogale*, especially in the UAJ, which are most likely convergences based on stabilizing the foot during extreme plantarflexion. Although the macroscelidid tarsal complex shares more features with tenrecoids than does *Solenodon*'s, this is most likely due to *Solenodon*'s highly modified tarsus and not necessarily an indicator of phylogenetic alliance between tenrecoids and macroscelidids. A more complete ecomorphological analysis of the afrotherian and soricoid tarsus will be more decisive for addressing questions of afrotherian skeletal evolution.

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APPENDIX 2.1 Linear Measurements (mm)

Taxon	ID	Asthead1	Asthead2	Asthead3	Asthead4	Taxon	ID	Asthead1	Asthead2	Asthead3	Asthead4
E. telfairi	101	1.1162	0.9226	0.9873	1.4851	M. cowani	165673	0.6945	0.5625	0.6575	1.0223
E. telfairi	127274	1.1207	0.8809	1.0231	1.3771	M. cowani	165680	0.7282	0.5776	0.6688	1.0117
E. telfairi	159729	1.0180	0.7656	0.8557	1.4796	M. cowani	165689	0.7188	0.5981	0.7113	1.0537
E. telfairi	170605	0.9916	0.8544	0.8461	1.3232	M. dobsoni	161940	0.9408	0.7135	0.7789	1.0860
E. telfairi	207717	0.8870	0.6971	0.7939	1.0873	M. dobsoni	165774	1.0775	0.8958	0.8801	1.3076
E. telfairi	207718	0.9138	0.0090		1.2104	M. dobsoni	165775	0.9013	0.7002	0.7231	1.2315
E. telfairi	212918	1.0229	0.8923	0.8779	1.2826	M. dobsoni	166198	0.7932	0.6526	0.7533	1.0722
E. telfairi	212919	0.9883	0.8673	0.9020	1.3881	M. dobsoni	578749	1.0225	0.6773	0.8579	1.2821
E. telfairi	328620	0.9470	0.8098	0.9217	1.3169	M. dobsoni	582730	0.9636	0.7217	0.9246	1.1396
E. telfairi	328637	0.8801	0.7870	0.8147	1.2300	M. dobsoni	166200	0.7800	0.6385	0.6756	1.0180
S. setosus	124554	1.4007	1.1664	1.1237	1.8104	M. talazaci	154581	1.2187	1.0021	0.9859	1.3692
S. setosus	154033	1.3335	1.0924	1.2081	1.7402	M. talazaci	154585	1.1986	0.8806	0.9449	1.3230
S. setosus	165494	1.3232	1.1511	1.0788	1.5528	M. talazaci	162040	1.0445	0.9110	0.9596	1.3996
S. setosus	170532	1.1652	1.0777	0.9676	1.6513	M. talazaci	167501	1.1266	0.8233	0.9388	1.3056
S. setosus	328612	1.5271	1.0679	1.1940	1.6894	Oryzorictes	161746	0.6959	0.6351	0.7652	1.3369
S. setosus	395513	1.4652	1.2360	1.2302	1.9093	Oryzorictes	162053	1.1408	0.8583	0.9841	1.5766
S. setosus	541443	1.4452	1.1153	1.2508	1.7718	Oryzorictes	166240	0.9314	0.7808	0.9293	1.4728
S. setosus	578790	1.4342	1.1009	1.1376	1.6939	Oryzorictes	167480	0.8397			1.3870
S. setosus	85170	1.4003	1.2559	1.1626	1.7454	Oryzorictes	45018	0.8900	0.7382	0.8997	1.3929
S. setosus	85513	1.1550	1.0470	1.0188	1.6639	Oryzorictes	5639	0.9900	0.7551	0.9618	1.3687
H. semispinosus	10001	1.3336	1.1033	1.1403	1.6070	Oryzorictes	31257	0.7676	0.6985	0.6849	1.2611
H. semispinosus	161757	1.4268	1.3241	1.3559	1.7207	L. mergulus	45050	1.1795	0.9481	1.0976	1.8799
H. semispinosus	162062	1.0450	0.9951	1.1625	1.7484	G. aurita	161594	0.4584	0.3812	0.3997	0.6042
H. semispinosus	207712	1.2313	0.9813	1.0678	1.9480	P. velox	266897	2.2756	1.7579	1.6335	2.1693
H. semispinosus	207715	0.8937	0.8106	0.8871	1.3802	P. velox	51324	2.0620	1.6503	1.5918	2.1471
H. semispinosus	212922	1.2872	0.9395	0.9873	1.8635	P. velox	51333	2.3313	1.6295	1.6556	2.3128
H. semispinosus	339992	1.3136	0.9838	1.2126	1.8190	P. velox	55204	1.7489	1.2225	1.1605	1.7959
H. semispinosus	354998	1.0787	0.8481	0.8164	1.5779	Solenodon	57320	2.9441	2.5430	3.0916	5.2347

Appendix 2.1 (con't)

Taxon	ID	Asthead1	Asthead2	Asthead3	Asthead4	Taxon	ID	Asthead1	Asthead2	Asthead3	Asthead4
T. ecaudatus	154628	1.8158	1.5858	1.8199	3.0133	Solenodon	238263	3.1671	2.7296	2.9437	4.8389
T. ecaudatus	166047	2.1133	1.7177	1.7239	3.6727	Solenodon	290520	3.6018	2.9815	3.1636	5.8954
T. ecaudatus	170511	2.4389	1.9013	2.2432	3.7238	Solenodon	395697	2.9732	2.6539	3.1234	5.2611
T. ecaudatus	361485	1.8623	1.8079	1.8541	3.0919	Solenodon	395819	3.1186	2.7355	2.9609	5.1053
T. ecaudatus	577051	2.4518	1.7791	2.1163	3.2747	Petrodomus	150415	2.1148	1.8030	1.8545	3.0672
T. ecaudatus	578792	2.0844	1.6756	1.9280	3.1278	Petrodomus	203336	1.8359	1.7527	1.6302	3.0773
T. ecaudatus	59011	2.2000	1.8869	2.0538	3.2666	Petrodomus	203339	2.2761	1.8941	1.8036	3.1498
T. ecaudatus	60587	2.2242	1.6614	1.8211	2.9966	Nasilio	86568	1.1744	1.0688	0.8346	1.4564
M. cowani	156221	0.8559	0.6356	0.8006	1.0990	Nasilio	86585	1.4935	1.1990	1.0133	1.6675
M. cowani	156222	0.7697	0.5486	0.6920	0.9903	Nasilio	86587	1.4163	1.1805	0.9366	1.5337
M. cowani	156223	0.6998	0.5588	0.7700	1.0344						

Taxon	ID	Astneck1	Astneck2	Astneck3	Astneck4	Taxon	ID	Astneck1	Astneck2	Astneck3	Astneck4
Echinops	101	2.0573	2.2508	1.3965	1.0684	M. cowani	165676	1.2432	1.2179	1.2064	0.6440
Echinops	153785	1.7725	2.0215	1.0525	0.9235	M. cowani	165689	1.2304	1.1853	1.2056	0.6348
Echinops	159730		1.8532	1.2254		M. cowani	328658	0.7885	1.0935	1.1663	0.5461
Echinops	170605	1.6369	1.9587	1.1203	0.8873	M. cowani	449184	1.1246	1.1538	0.9775	0.6134
Echinops	207717	1.7001	1.9708	1.0462	0.8028	M. cowani	449186	1.0709	1.0301	0.9517	0.5699
Echinops	207718	1.7928	1.7657	0.9469	0.8053	M. cowani	449187	1.1964	1.0967	1.0515	0.6471
Echinops	212918	1.6987	1.7760	0.9242	0.8720	M. dobsoni	161935	1.5691	1.6231	1.2438	0.8645
Echinops	212919	1.6216	1.9274	1.3096	0.9463	M. dobsoni	161940	1.5777	1.7465	1.4954	0.8456
Echinops	328637	1.9032	2.0904	1.1035	0.8842	M. dobsoni	165467	1.6915	1.7785	1.6059	0.9905
Echinops	588220	1.9245	1.9164	1.1943		M. dobsoni	165774	1.7970	1.6011	1.5357	0.9500
Setifer	165494	2.4729	3.1274	1.8229	1.3401	M. dobsoni	165775	1.5710	1.5318	1.3466	0.8736
Setifer	170532	2.5310	3.0505	2.1381	1.2574	M. dobsoni	166198	1.3470	1.5689	1.5204	0.7631
Setifer	328612	2.3502	3.0022	1.7281	1.2547	M. dobsoni	578749		1.7647	1.5506	0.7732
Setifer	395513	2.8483	3.4223	1.9617	1.6329	M. dobsoni	582730		1.5593	1.4009	0.9244
Setifer	395719	2.3415	3.1172	1.7928	1.2843	M. talazaci	154581	1.7310	1.7268	1.4326	0.8981
Setifer	578790	2.7580	3.4636	1.9743	1.4333	M. talazaci	154585	1.7030	2.0505	1.4727	0.9108
Setifer	85170	2.7537	3.4481	2.2686	1.2875	M. talazaci	162040	1.7857	1.8757	1.4428	0.9582

Appendix 2.1 (con't)

Taxon	ID	Astneck1	Astneck2	Astneck3	Astneck4	Taxon	ID	Astneck1	Astneck2	Astneck3	Astneck4
Hemicentetes	10001	2.1852	2.3782	1.6567	1.2064	M. talazaci	167502	1.8227	1.8009	1.7946	0.9451
Hemicentetes	161757	2.2494	2.7180	1.6570	1.5357	M. talazaci	167503			1.5164	0.9547
Hemicentetes	162062	2.3069	2.5021	1.5494	1.0998	M. talazaci	577056	1.7542	1.6947	1.5588	0.9466
Hemicentetes	166132	2.5603	2.5018	1.7373	1.2333	Oryzorictes	161746	1.6748	1.6487	1.3224	0.9591
Hemicentetes	170593	1.9684	2.2619	1.3757	0.9578	Oryzorictes	162058		1.6653	1.2079	1.0864
Hemicentetes	207712	2.3304	2.6313	1.5019	1.5167	Oryzorictes	166240	1.9182	1.8415	1.5075	1.1790
Hemicentetes	207715	2.3337	1.9978	1.7209	1.0449	Oryzorictes	45018	1.7595	1.7441	1.4171	1.0141
Hemicentetes	212920	2.6070	2.1862	1.7194	1.1353	Oryzorictes	5639	2.0347	1.7824	1.5018	1.1177
Hemicentetes	212922	2.6069	2.3040	1.9910	1.1946	Oryzorictes	31257	1.5402	1.5654	1.1314	1.0690
Hemicentetes	212924	2.5494	2.4060	1.8991	1.3003	Limnogale	45050	2.6346	2.4120	1.7524	1.4372
Hemicentetes	354998	2.1341	2.3751	1.4924	1.0051	Geogale	161594	0.8559	0.9243	0.7236	0.5382
Hemicentetes	50911		2.5447	1.7656	1.3801	Potamogale	266897	3.5715	2.6395	2.0317	1.7753
Tenrec	63313	4.7054	4.8558	2.8463	2.5167	Potamogale	51324	3.5305	3.1368	2.2904	1.9342
Tenrec	154628	4.3184	4.8483	2.8464	2.3682	Potamogale	51333	3.8207	2.6083	2.2529	1.7669
Tenrec	166047	4.8066	5.1071	2.5673	2.6006	Potamogale	55204	3.1359	2.4135	2.1400	1.5284
Tenrec	170511	4.6781	4.8187	2.7033	2.5128	Solenodon	238263	6.2052	5.2960	5.2302	3.1441
Tenrec	30398	5.0184	4.7038			Solenodon	290520	7.0952	5.7481	6.2879	3.6206
Tenrec	361485	4.8363	5.4639	3.2636	2.8520	Solenodon	395697	6.4128	5.4937	5.9401	3.3523
Tenrec	364955	4.6594	5.1513	3.0880	2.9100	Solenodon	395819	6.9371	5.7187	6.1024	3.4131
Tenrec	50911	3.0388	3.0716	2.2654	1.5242	Solenodon	51068	6.5675	5.5677	6.0284	3.4167
Tenrec	577051	4.9328	4.7694	3.1375	2.3582	Solenodon	57320	5.7921	5.3535	6.8980	3.3025
Tenrec	578792	4.6161	4.7083	3.2781	2.3420	Petrodomus	150415	2.9148	2.9747	2.7694	1.9039
Tenrec	60587	4.8673	4.3819	2.3197	2.3005	Petrodomus	203336	3.1494	2.8463	2.8884	2.1168
M. cowani	156221	1.1764	1.2746	1.1524	0.6787	Petrodomus	203339	3.1174	2.6821	2.8286	2.0275
M. cowani	156222	1.2275	1.1496	1.1169	0.6662	Nasilio	86568	1.6379	1.5490	1.2907	1.0192
M. cowani	156223	1.1596	1.1474	1.2737	0.5328	Nasilio	86585	1.6913	1.7240	1.5844	1.0151
M. cowani	165672	1.0741	1.2189	0.9285	0.5624	Nasilio	86587	1.4676	2.0391	1.3670	0.9325
M. cowani	165673	1.1792	1.1698	1.0181	0.6500						

Taxon	ID	Astroch2	Astroch1	Astroch3	Taxon	ID	Astroch2	Astroch1	Astroch3
Echinops	207717	0.1111	0.2983	0.1571	M. cowani	165676	0.2874	0.3977	0.3038

Appendix 2.1 (con't)

Taxon	ID	Astroch2	Astroch1	Astroch3	Taxon	ID	Astroch2	Astroch1	Astroch3
Echinops	212918	0.1143	0.3429	0.1333	M. cowani	165680	0.3571	0.3486	0.3508
Echinops	212919	0.1708	0.3652	0.2053	M. cowani	165689	0.2576	0.4083	0.3334
Echinops	153785	0.3002	0.2203	0.1986	M. cowani	449186	0.2612	0.3771	0.3022
Echinops	328620	0.1602	0.1891	0.1781	M. cowani	449187	0.3241	0.3898	0.3572
Echinops	328637	0.2245	0.3265	0.2516	M. dobsoni	161935	0.2258	0.3934	0.2938
Echinops	464980	0.0907	0.5074	0.2272	M. dobsoni	161940	0.3431	0.3226	0.3033
Echinops	588220	0.1100	0.2014	0.1212	M. dobsoni	165467	0.1259	0.5581	0.2896
Setifer	85170	0.6155	0.6457	0.6782	M. dobsoni	165774	0.3304	0.5119	0.3904
Setifer	85513	0.7296	0.9686	0.6971	M. dobsoni	165775	0.1818	0.2302	0.1838
Setifer	124554	1.0258	0.6501	1.0853	M. dobsoni	166107	0.1982	0.2665	0.2369
Setifer	154033	1.1831	0.4863	0.9747	M. dobsoni	166198	0.2316	0.2022	0.2012
Setifer	165494	0.8866	0.5520	0.8312	M. dobsoni	166200	0.1662	0.2817	0.2330
Setifer	170532	0.5911	0.6553	0.4626	M. dobsoni	578749	0.2226	0.2033	0.2067
Setifer	170731	0.4389	0.5370	0.5143	M. talazaci	154581	0.1969	0.1873	0.2168
Setifer	328612	0.7617	1.4280	0.9747	M. talazaci	154585	0.2297	0.2295	0.2497
Setifer	541443	0.6003	0.7217	0.6563	M. talazaci	162040	0.1975	0.2741	0.2248
Setifer	578790	0.4872	0.6669	0.5662	M. talazaci	167501	0.1277	0.2268	0.1696
Hemicentetes	161757	0.2401	0.3263	0.2299	M. talazaci	167503	0.1744	0.2325	0.2123
Hemicentetes	161758	0.2604	0.3327	0.2964	M. talazaci	577056	0.3539	0.3952	0.3308
Hemicentetes	162059	0.2621	0.2686	0.2788	Oryzorictes	161746	0.2587	0.3611	0.2503
Hemicentetes	162062	0.2846	0.2738	0.9281	Oryzorictes	162053	0.2811	0.3390	0.3205
Hemicentetes	166132	0.4953	0.7218	0.5756	Oryzorictes	162054	0.3400	0.3350	0.3239
Hemicentetes	170593	0.3663	0.6867	0.5384	Oryzorictes	162058	0.4025	0.4214	0.3695
Hemicentetes	207714	0.6309	0.5491	0.5808	Oryzorictes	166240	0.3156	0.4249	0.3359
Hemicentetes	212920	0.2822	0.7104	0.4498	Oryzorictes	167480	0.3049	0.4064	0.3207
Hemicentetes	212921	0.5911	0.9436	0.6515	Oryzorictes	5639	0.3119	0.2874	0.3343
Hemicentetes	212922	0.5692	0.3904	0.4111	Oryzorictes	31257	0.2522	0.3940	0.3302
Hemicentetes	212924	0.5959	0.6043	0.5673	Limnogale	45050	0.3082	0.4113	0.3559
Hemicentetes	339992	0.4088	0.3909	0.4454	Geogale	159733	0.1111	0.2983	0.2187
Hemicentetes	83658	0.4690	0.6344	0.5504	Geogale	161594	0.1143	0.3429	0.1526
Hemicentetes	354998	0.4837	0.9147	0.5797	Potamogale	266897	0.3060	0.4074	0.3241
Tenrec	59011	0.5911	0.6553	0.4626	Potamogale	34881	0.2924	0.4040	0.2718
Tenrec	60587	0.4389	0.5370	0.5460	Potamogale	51324	0.3452	0.3541	0.3871
Tenrec	63313	0.7617	1.4280	0.9747	Potamogale	51333	0.3137	0.3527	0.3107

Appendix 2.1 (con't)

Taxon	ID	Astroch2	Astroch1	Astroch3	Taxon	ID	Astroch2	Astroch1	Astroch3
Tenrec	154628	0.6003	0.7217	0.6563	Potamogale	55204	0.2845	0.4220	0.3432
Tenrec	166047	0.4872	0.6669	0.5662	Potamogale	51322	0.2801	0.3494	0.2895
Tenrec	170511	0.6155	0.6457	0.6782	Solenodon	395697	0.2715	0.4333	0.3393
Tenrec	361485	0.7296	0.9686	0.8232	Solenodon	51068	0.1843	0.2072	0.2570
Tenrec	364955	0.6564	1.0013	0.7652	Solenodon	57320	0.4227	0.4151	0.4284
Tenrec	577051	0.6386	1.0744	0.7944	Petrodomus	150415	0.1708	0.3652	0.2303
Tenrec	578792	0.3927	0.5294	0.3680	Petrodomus	203336	0.3002	0.2203	0.2185
M. cowani	156221	0.1391	0.4071	0.3035	Petrodomus	203339	0.1602	0.1891	0.1891
M. cowani	156222	0.2011	0.4807	0.2920	Nasilio	86568	0.2245	0.3265	0.2516
M. cowani	165672	0.3184	0.3958	0.2947	Nasilio	86581	0.0907	0.5074	0.2881
M. cowani	165673	0.1953	0.5632	0.3376	Nasilio	86585	0.0904	0.1102	0.1234
M. cowani	165674	0.1239	0.2596	0.1758	Nasilio	86587	0.0975	0.0780	0.1018

Taxon	ID	Calc1	Calc2	Calc3	Calc4	Calc5	Calc6	Taxon	ID	Calc1	Calc2	Calc3	Calc4	Calc5	Calc6
Echinops	127274	1.1246	1.4300	3.9055	0.8511	-0.1825	0.9850	M. cowani	449186	0.9261	0.8951	2.7019	0.5010	0.2930	0.7317
Echinops	153785			4.0264	0.8361	-0.0983	0.9611	M. cowani	449187	1.1866	0.8670	2.9667	0.5620	0.3538	0.8961
Echinops	159730	1.0139	1.1973	3.8479	1.0097	-0.1660	0.9830	M. cowani	449188			2.9900	0.5531	0.4201	0.9575
Echinops	170605	1.1295	1.6214	4.0509	0.7413	-0.3780	0.7736	M. dobsoni	161935			4.4608	0.8725	0.6840	1.4134
Echinops	207718	0.9441	0.9221	3.3147	0.9359	-0.1006	0.8202	M. dobsoni	161940			4.3803	0.7573	0.6119	1.3656
Echinops	212918	0.9456		3.4945	0.8298	-0.0883	0.9369	M. dobsoni	165467	1.7296	1.9800	5.0892	0.7724	0.7236	1.5783
Echinops	212919	1.1220	1.2090	3.6950	0.9125	0.1559	0.9762	M. dobsoni	165774	1.9477	1.4443	4.5944	0.7492	0.5738	1.4536
Echinops	328637	1.1156	1.3453	4.0428	1.0067	-0.1450	0.7565	M. dobsoni	165775	2.0630	1.3281	4.4315	0.8649	0.5308	1.4799
Echinops	588220	1.1900	1.4080	4.0519	0.9194			M. dobsoni	166107	0.0097		4.5347	0.8924	0.3998	1.4153
Echinops	207717	0.9598	1.1900	3.5165	0.6370	-0.1937	0.7659	M. dobsoni	166198	1.7896	1.2275	4.1699	0.7428	0.5148	1.2852
Setifer	124554		2.7448	5.5453	1.4902	0.5846	1.6174	M. dobsoni	166200			4.1499	0.7076	0.6978	1.3786
Setifer	154033	1.9773	2.1201	6.0554	1.3512	-0.4442	1.3511	M. dobsoni	578749			4.4196	0.7391	0.4302	1.4465
Setifer	165494	1.6077	2.4271	5.9377	1.2261	0.1975	1.7949	M. dobsoni	582730	1.9513	1.5159	4.5318	0.8701	0.6313	1.5812
Setifer	170532	1.6568	2.0361	5.8409	1.2710	-0.5446	1.4872	M. talazaci	154585	2.1763	1.4655	4.9229	0.9207	0.5411	1.7544
Setifer	170731	1.8018	2.3621	6.2368	1.3728	-0.4886	1.6772	M. talazaci	162040	2.1105	1.2654	4.5775	0.8188	0.4888	1.7412
Setifer	317872			6.2286	1.2825	-0.6734	1.2005	M. talazaci	167501	2.2374	1.4330	4.8745	0.7331	0.5552	1.4386
Setifer	328612			5.7025	1.0259	-0.3090	1.2057	M. talazaci	167502			4.8509	0.8498	0.5877	1.7271
Setifer	395513	1.9763	2.3459	6.4933	1.3183	0.7173	1.4427	M. talazaci	167503	2.3342	1.3313	4.9393	0.9454	0.5747	1.7737
Setifer	541443		2.3578	6.0022	1.2637	0.2643	1.4630	M. talazaci	577056	2.2101	1.4501	4.8323	0.8302	0.5689	1.5808
Setifer	578790	1.8355	2.3610	6.2981	1.2635	-0.7168	1.3832	Oryzorictes	161746	1.3816	1.1037	3.7494	0.8809	0.0677	0.8077

Appendix 2.1 (con't)

Taxon	ID	Calc1	Calc2	Calc3	Calc4	Calc5	Calc6
Setifer	85170		2.6001	6.8870	1.2780	-0.4367	1.7303
Setifer	85513	1.8704	2.7914	6.4518	1.3664	0.2182	1.5103
Hemicentetes	161757	1.9373	1.5850	5.2661	1.3514	-0.1451	1.9800
Hemicentetes	161758			5.4402	1.1873	0.1989	1.8475
Hemicentetes	162062	1.3935	1.8665	4.9327	1.0832	-0.1165	1.5088
Hemicentetes	207712	2.2695	1.9052	5.6326	1.4999	0.0821	1.9490
Hemicentetes	207715			4.6577	1.0127	0.1350	1.4587
Hemicentetes	212922	1.5474	1.8856	5.1738	1.2675	0.1094	1.8995
Hemicentetes	354998	1.3474	1.6842	4.7686	1.1530	-0.3016	1.4007
Hemicentetes	364954			5.2499	1.4480	-0.3068	1.7755
Tenrec	154628	3.1938	4.5357	10.9402	1.9303	0.3840	2.7959
Tenrec	166047	2.9882	4.2685	10.4060	2.3154	0.2722	2.3450
Tenrec	170511	2.9320	4.7802	10.6034	2.1331	0.7000	3.1389
Tenrec	30398	3.0973	4.8270	10.9855	2.7178	0.1396	2.9841
Tenrec	361485	3.0600	4.8440	10.9649	2.1970	0.3636	2.9612
Tenrec	364955			10.8200	2.8903	0.2756	2.8039
Tenrec	577051	2.7211	4.0905	10.0764	2.5480	0.4009	2.5929
Tenrec	578792	3.3277	4.7122	11.0030	2.3738	0.2416	2.6563
Tenrec	59011	3.0878	5.2187	11.5234	2.7698	0.5536	3.3827
Tenrec	60587	2.6712	5.7988	11.6104	2.2336	0.6090	3.2913
M. cowani	156223			3.1998	0.6939	0.3163	1.1013
M. cowani	165673	1.1435	0.9485	3.1932	0.7437	0.3813	0.9082
M. cowani	165674			3.4486	0.7131	0.3578	1.0168
M. cowani	165680		0.8668	3.0165	0.5832	0.3205	0.9790
M. cowani	165689	1.2742	1.0920	3.3817	0.6444	0.3833	1.0452
M. cowani	168017			3.1059	0.5552	0.3108	0.8920

Taxon	ID	Foot1	Foot 2	Foot3	Foot4	Foot5	Foot6	Foot7
Echinops	134550	1.6378	0.9459	0.9262	6.0429	2.2850	0.7890	0.5649
Echinops	153785	1.4129	0.7181	0.7158	5.6258	1.7117	0.4509	0.2959
Echinops	159730	1.5302	0.9515	0.6251	6.1166	1.7332	0.7641	0.5256
Echinops	207718	1.4472	0.8745	0.7132	5.6505	1.6194	0.5859	0.5114
Echinops	212918	1.2603	0.4562	0.7187	5.3780	1.5912	0.6406	0.3214
Echinops	31270			0.7058	5.6644			

Taxon	ID	Calc1	Calc2	Calc3	Calc4	Calc5	Calc6
Oryzorictes	162054			4.3257	0.9032	0.1516	0.9437
Oryzorictes	45018	1.6446	1.2396	4.0839	0.8280	0.1301	0.9527
Oryzorictes	578789	1.3906	1.2341	3.9051	1.0512	0.2062	0.8543
Oryzorictes	31257	1.5773	1.1789	3.6585	0.7386	0.1858	0.7246
Limnogale	45050	1.6081	1.5052	4.8793	1.0808	-0.2752	0.9003
Geogale	159733		0.6200	1.9301	0.4145	0.0305	0.5533
Geogale	161594	0.8309	0.6026	1.9742	0.3597	0.0879	0.5731
Potamogale	266897	2.5242	6.0931	11.3291	1.7529	1.4768	1.4888
Potamogale	34881			9.7570	1.7079	0.6456	0.9101
Potamogale	51324			10.4162	1.5783	1.2157	1.4836
Potamogale	51333	2.5858	5.0106	10.2024	1.4206	0.5615	2.3015
Potamogale	55204	2.4260	3.9729	9.1826	1.4015	0.0544	1.5834
Potamogale	51322			10.3198	1.4978		
Solenodon	172745			14.0049	3.2410	0.3499	2.3500
Solenodon	238263	4.6015	5.1298	16.2462	2.7805	0.2216	3.3387
Solenodon	290520	5.4749	7.9302	18.3528	3.9173	0.2330	4.5800
Solenodon	395697			17.8302	3.5855	0.2553	4.1733
Solenodon	395819	6.0059	7.6389	17.9107	3.4952	0.0809	4.1745
Solenodon	51068	6.2442		18.4730	2.9018	0.0716	3.7881
Solenodon	57320	5.7580	6.2902	16.3293	3.7789	0.0449	2.7136
Petrodomus	150415	3.2999	4.4198	10.3211	1.8164	-0.6123	2.6142
Petrodomus	203336	3.6116	4.1774	10.4367	2.0541	-1.0929	1.6278
Petrodomus	203339	3.3982	4.4368	10.5907	1.9987	-1.2235	1.8241
Nasilio	86585	2.3308	2.3621	6.1953	1.3183	-0.3318	1.4330
Nasilio	86587	1.6118	2.3534	5.2532	1.1221	-0.0400	1.0369
Nasilio	86581				1.1400		

Taxon	ID	Foot1	Foot 2	Foot3	Foot4	Foot5	Foot6	Foot7
M. cowani	165676	1.5052	0.5435	0.5711	6.6046			
M. cowani	165680	1.4725	0.3590	0.5530	6.7042	1.3669	0.7373	0.3905
M. cowani	165689	0.2896	1.5412	0.6176	6.7169	1.5503	0.7570	0.4113
M. cowani	168017	1.5736	0.3945	0.4829	6.6414	0.9879	0.7796	0.4521
M. cowani	328658	1.3909	0.4903	0.5372	6.2294	1.0224	0.6771	0.2618
M. cowani	449184	1.0710	0.3688	0.4401	5.7501	0.9419	0.5357	0.2176

Appendix 2.1 (con't)

Taxon	ID	Foot1	Foot 2	Foot3	Foot4	Foot5	Foot6	Foot7
Echinops	328636			0.8033	5.9893			
Echinops	328637	1.4784	0.8649	0.7373	6.3154	1.9757	0.7635	0.3785
Echinops	464980	1.3638	0.8977	0.7058	5.8236	1.9689	0.5817	0.2904
Echinops	588220	1.0498	1.3416	0.9319	5.4050	1.8108	0.4484	0.4037
Echinops	207717	1.4484	0.5903	0.7003	6.1140	2.0106	0.6303	0.7101
Setifer	154033	2.4248	1.5500	1.1043	9.5897	2.4541	0.9748	0.3551
Setifer	154034	2.3615	1.1703	0.9944	8.4107	2.2407	0.9600	0.4910
Setifer	165494	2.4241	1.1149	1.0370	9.7596	2.6675	1.1362	0.5694
Setifer	170532	2.4947	1.1391	1.2130	8.2624	2.9444	1.2022	0.4501
Setifer	170731	2.0258	1.0399	1.2770	9.4744	2.7803	1.2286	0.4128
Setifer	328612	2.5034	1.0031	0.9715	9.4226	2.6288	1.0238	0.4516
Setifer	395513	2.7211	1.3958	1.1420	9.5971	2.8922	1.3052	0.5004
Setifer	395719	2.6709	0.9899	0.8665	9.1843	2.6875	1.0141	0.3695
Setifer	541443	1.9582	1.2631	1.0662	9.0789	2.8305	0.9245	0.4590
Setifer	578790	1.3603	0.8119	0.7186	5.7522	1.4823	0.6712	0.1724
Hemicentetes	10001	2.2146	0.7003	1.2583	6.9176	2.0380	0.7224	0.4642
Hemicentetes	161757	2.4835	1.1339	1.0758	8.7433	2.3330	1.0834	0.4577
Hemicentetes	161758	2.3053	0.9014	1.1593	8.5062	2.0900	0.9999	0.4208
Hemicentetes	162059	2.1641	1.0616	0.9947	8.3575	2.1120	0.7377	0.5252
Hemicentetes	162062	2.1310	1.0153	0.9436	8.2283	1.8297	0.6705	0.3559
Hemicentetes	166132	2.3997	0.7748	1.0505	8.6576	2.1119	0.8301	0.5114
Hemicentetes	207712	2.3443	1.1902	0.9082	9.2769	2.0843	1.1274	0.3552
Hemicentetes	207714	2.3004	0.9972	1.2924	8.6856	1.9825	0.7144	0.3848
Hemicentetes	207715	1.7369	0.8078	1.0576	8.3503	1.9824	0.9117	0.1410
Hemicentetes	212920	2.2096	0.8498	0.9180	8.4547	2.1737	0.8878	0.4542
Hemicentetes	212921	2.1704	1.1171	1.2477	9.1464	1.9836	1.0011	0.3937
Hemicentetes	212922	2.1845	0.7905	0.9913	8.2944	2.4283	0.8958	0.2995
Hemicentetes	212924	2.1986	1.0128	0.9785	9.0130	2.0950	0.6827	
Hemicentetes	339992	2.3775	1.1868	0.9809	9.1714	2.1564	0.7086	0.6524
Hemicentetes	354998	2.3144	1.0078			2.1929	0.6618	0.6454
Hemicentetes	364954	2.1406	0.8876	0.7971	8.5032	1.8190	0.5397	0.4678
Tenrec	63313	4.2998	2.3910	1.8553	14.4886	4.1857	1.6798	0.3839
Tenrec	154628	4.3251	1.3839	1.4627	13.9489	3.6860	1.8332	0.5554
Tenrec	166047	4.2761	1.8359	1.9093	14.5364	4.1515	1.6822	0.4061
Tenrec	170511	3.9226	1.9272	1.7300	14.8971	4.3447	1.2998	0.2657

Taxon	ID	Foot1	Foot 2	Foot3	Foot4	Foot5	Foot6	Foot7
M. cowani	449186	1.2395	0.3936	0.4960	6.2013	1.0236	0.5551	0.1879
M. cowani	449187	1.5551	0.5823	0.5205	5.2788	0.8745	0.7353	0.2551
M. dobsoni	161935	2.0897	0.5604	0.7094	9.1583	1.2611	1.4022	0.2614
M. dobsoni	161940	2.0274	0.5303	0.5950	9.2036	1.3085	1.3243	0.2090
M. dobsoni	165467	2.2373	0.6012	0.6528	10.2736	1.2547	1.4264	0.1401
M. dobsoni	165774	2.0828	0.5907	0.7061	9.8421	1.5195	1.4303	0.2183
M. dobsoni	165775	2.0562	0.7012	0.6059	8.8407	1.2349	1.4176	0.2121
M. dobsoni	166107	2.0278	0.5804	0.6466	9.6666	1.4132	1.3430	0.0790
M. dobsoni	166198	1.9641	0.5806	0.6584	9.5941	0.9937	1.2602	0.2197
M. dobsoni	166200	1.8472	0.6057	0.6537	9.4753	1.1781	1.2122	0.1055
M. talazaci	154581	2.2522	0.5909	0.7899	9.1563	1.3670	1.4480	0.2456
M. talazaci	154585	2.1808	0.6499	0.8274	9.3003	1.0011	1.3515	0.1795
M. talazaci	162040	2.0056	0.6258	0.6578	9.5060	1.1563	1.4280	0.2278
M. talazaci	167501	2.2327	0.5163	0.6907	9.7596	1.3013	1.4090	0.2359
M. talazaci	167502	2.0397	0.6416	0.8032	10.2052	1.3002	1.1898	0.1653
M. talazaci	167503	2.2681	0.5182	0.7076	9.8042	1.1277	1.4569	
M. talazaci	577056	2.2096	0.3634	0.6596	9.6649	1.2483	1.3050	0.3328
Oryzorictes	161746	2.0028	0.6887	0.7887	5.0432	1.8043	0.7228	0.3535
Oryzorictes	162053	1.8028	0.9114	0.9233	5.8464	1.9313	0.6986	0.4061
Oryzorictes	162054	1.7714	0.7719	0.7982	5.5862	2.0021	0.6972	0.2836
Oryzorictes	162058	1.7933	0.6798	0.7699	5.1870	2.0235	0.7279	0.3288
Oryzorictes	167480	1.7871	0.6141	0.8819	5.6456	2.1125	0.7269	0.4518
Oryzorictes	45018	1.7525	0.6104	0.7178	5.4829	1.8660	0.8679	0.3217
Oryzorictes	5639	1.6015	0.8559	0.6487	5.6796	1.7260	0.8888	0.4429
Oryzorictes	578789	1.7778	0.7768	0.8996	5.4355	1.6931	0.8151	0.5120
Oryzorictes	31257	1.7368	0.5614	0.6963	5.2957	1.6133	0.7043	0.5932
Limnogale	45050	2.4264	0.9004	0.8945	9.5997	2.3267	1.0628	0.6319
Geogale	159733	0.6117	0.3596	0.2676	4.2712	0.6400	0.2021	0.1278
Geogale	161594	0.7444	0.4174	0.3527	4.3854	0.7128	0.4111	
Potamogale	266897	4.3499	1.8277	1.3612	13.7678	2.9854	2.0777	0.3764
Potamogale	34881	0.7291	0.3580			0.5894	0.2955	0.0830
Potamogale	51324			1.3523	14.3222			
Potamogale	51333	3.6791	1.5636	1.1581	12.6624	3.3334	1.4319	0.1878
Potamogale	51322	3.9668	1.5888	1.2266	13.0348	3.0724	1.2395	0.4349
Soleondon	49508			2.1364	19.7669			

Appendix 2.1 (con't)

Taxon	ID	Foot1	Foot 2	Foot3	Foot4	Foot5	Foot6	Foot7
Tenrec	30398	4.2532	1.9070	1.7603	14.7191	4.0265	1.6246	0.6241
Tenrec	361485	4.5137	1.9593	1.6591	16.3060	4.9419	1.7011	1.0390
Tenrec	364955	4.4060	2.4911	2.0180	15.6224	4.6137	1.0826	0.6959
Tenrec	577051	4.7155	2.0944	1.9204	14.8341	3.9008	1.7768	0.5268
Tenrec	578792	4.6739	2.4038	1.9309	14.1643	4.3103	2.0951	0.7457
Tenrec	60587	4.4142	1.9921	1.8567	15.1461	3.3741	1.7511	0.4555
M. cowani	156222	1.4252	0.5618	0.6238	6.8706	0.9568	0.8563	0.4415
M. cowani	156223	1.4463	0.4111	0.5789	6.4985	1.2419	0.7757	0.3367
M. cowani	165672	1.3042	0.5633	0.5315	6.1756	0.8021	0.7156	0.3217
M. cowani	165673	1.4098	0.3633	0.6150	6.7553	1.3085	0.6869	0.3404
M. cowani	165674	1.4187	0.4197	0.5435	6.9465	1.3083	0.7099	0.3556

Taxon	ID	Foot1	Foot 2	Foot3	Foot4	Foot5	Foot6	Foot7
Soleondon	172680	7.2346	3.4308	2.3311	18.0353	3.2436	2.0899	0.1114
Soleondon	172745	6.7031	2.4256	1.9546	16.7736	3.1661	2.3553	0.3125
Soleondon	238263	6.1141	1.7181	2.1729	19.7149	3.1579	2.5428	0.1622
Soleondon	290520	7.6380	3.5306	2.2014	21.5400	3.4868	2.8339	0.0993
Soleondon	395697	7.1728	2.6654	2.0421	19.5248	3.5753	2.6112	0.1374
Soleondon	395819	7.5900	2.8607	2.4778	20.5378	3.2372	2.1903	0.1268
Soleondon	51068	7.4173	2.5402	2.2541	19.8433	3.6925	2.4806	0.1611
Soleondon	57320	7.1388	1.5861	2.4854	18.4534	3.5782	2.1396	0.0958
Petrodromus	203336	4.9012	1.0424	0.9420	28.0214	2.5539	1.9475	0.7390
Petrodromus	203339	4.8444	1.0875	0.8568	26.4742	2.6650	1.7451	0.9226
Elephantulus	86585	3.1847	1.0174	0.7411	12.2457	1.1425	1.0210	0.1768

Taxon	ID	Malleoli1	Malleoli2	Malleoli3	Malleoli4	Taxon	ID	Malleoli1	Malleoli2	Malleoli3	Malleoli4
Echinops	127274	0.9007	1.4471	0.7406	1.4311	M. cowani	156221	0.6074	1.0081	0.5676	0.8691
Echinops	159728	0.9301	1.4574	0.7645	1.6247	M. cowani	156222	0.5140	0.8787	0.4112	0.7229
Echinops	159729	1.3334	1.6090	1.1109	1.8750	M. cowani	156223	0.5411	0.9357	0.4681	0.8777
Echinops	159730	0.8915	1.4022	0.8636	1.5372	M. cowani	165672	0.6343	0.9147	0.5855	0.9025
Echinops	170605	0.6206	0.9479	0.4956	1.1049	M. cowani	165673	0.6142	0.9829	0.5321	0.8746
Echinops	207717	0.8261	1.2227	0.7652	1.1980	M. cowani	165674	0.5587	0.9406	0.5083	0.8520
Echinops	207718	0.8641	1.3226	0.8522	1.1213	M. cowani	165676	0.5495	0.9224	0.4637	0.8146
Echinops	212918	0.8537	1.2394	0.6378	1.3350	M. cowani	165680	0.6466	0.9055	0.5346	0.9770
Echinops	212919	0.7863	1.2775	0.6216	1.4616	M. cowani	165689	0.6664	0.7654	0.5801	0.9998
Echinops	328620	0.7531	1.2426	0.7006	1.5825	M. cowani	168017	0.6410	0.9347	0.5406	0.8840
Echinops	328637	0.8256	1.4901	0.6874	1.6136	M. cowani	328658	0.5157	0.8640	0.4678	0.7677
Echinops	395835	1.1044	1.4870	0.8335	1.6003	M. cowani	449184	0.5023	0.9064	0.4161	0.7654
Echinops	464980	0.6849	1.0368	0.5114	1.2195	M. cowani	449186	0.5142	0.8415	0.4550	0.7345
Echinops	588220	0.6382	1.1634	0.6980	1.3600	M. dobsoni	161935	0.7975	1.3303	0.7670	1.1172
Setifer	85170	1.7386	1.8428	0.8684	2.6159	M. dobsoni	161940	0.7753	1.2567	0.6582	1.0468
Setifer	124554	1.6935	1.9482	0.9118	2.4749	M. dobsoni	165467	0.6420	1.1264	0.5716	1.1703
Setifer	154033	1.8805	1.9779	1.3380	2.6544	M. dobsoni	165774	0.7156	1.2500	0.4216	1.1912
Setifer	154034	2.0421	2.3986	1.7231	2.6612	M. dobsoni	165775	0.5236	0.9043	0.4068	0.8842
Setifer	170532	1.7767	2.3061	1.4925	2.4606	M. dobsoni	166107	0.4505	1.0750	0.3576	0.7847
Setifer	170548	1.6306	1.7205	1.1417	2.3976	M. dobsoni	166198	0.6524	1.0469	0.4616	1.0015
Setifer	170731	2.0190	2.3180	1.3306	2.8540	M. talazaci	154581	0.9978	1.5305	0.7126	1.5682

Appendix 2.1 (con't)

Taxon	ID	Malleoli1	Malleoli2	Malleoli3	Malleoli4	Taxon	ID	Malleoli1	Malleoli2	Malleoli3	Malleoli4
Setifer	207076	1.4903	1.9227	1.1418	1.9599	M. talazaci	162040	0.9271	1.4618	0.8184	1.2672
Setifer	317872	1.8064	1.9877	1.4252	2.6749	M. talazaci	167501	0.9500	1.3471	0.7202	1.4324
Setifer	395513	2.0453	2.2675	1.5316	2.8703	M. talazaci	167502	0.8112	1.3315	0.6456	1.1600
Setifer	395719	1.9239	2.0757	1.2708	2.7411	M. talazaci	167503	0.7863	1.2923	0.7417	1.2121
Setifer	578790	2.0123	2.0991	1.3197	3.1269	M. talazaci	577056	0.8639	1.3852	0.6392	1.3434
Tenrec	154628	1.9574	2.9684	1.3962	3.5112	Oryzorictes	31257	0.4038	0.8518	0.3612	0.8143
Tenrec	156337	1.7993	3.2298	1.5859	2.8794	Oryzorictes	161746	0.5956	1.1356	0.4232	0.9116
Tenrec	166047	1.7799	2.8348	1.1667	3.1694	Oryzorictes	162053	0.6640	1.3551	0.5366	1.1098
Tenrec	170511	2.1090	2.9578	1.3236	3.5680	Oryzorictes	162054	0.6328	1.3563	0.6104	1.0116
Tenrec	30398	2.4042	3.0760	1.8675	3.7267	Oryzorictes	162058	0.5964	1.1338	0.5076	0.9737
Tenrec	361485	1.9974	3.3013	1.9170	3.7546	Oryzorictes	166240	0.6734	1.2393	0.5768	1.1568
Tenrec	364955	2.0267	3.1903	2.0846	4.1778	Oryzorictes	167480	0.6804	1.4673	0.5771	1.0801
Tenrec	50911	1.7792	3.3088	1.8876	3.8162	Oryzorictes	578789	0.6426	1.2368	0.5797	0.9110
Tenrec	577051	2.1461	3.0229	1.2013	3.8624	Limnogale	45050	0.9629	1.7064	0.7436	1.7244
Tenrec	578792	2.0611	3.1306	1.2733	3.7349	Geogale	161594	0.3483	0.4844	0.2908	0.6803
Tenrec	85514	1.9414	2.9220	1.2674	3.3395	Potamogale	34881	1.9471	3.0531	1.4312	2.5730
Hemicentetes	33951	1.0294	1.6177	0.8747	2.1863	Potamogale	51324	1.6302	2.7286	0.9980	2.5514
Hemicentetes	161757	1.0165	1.5439	0.7946	2.1541	Potamogale	266897	1.9266	3.1180	1.3040	2.5029
Hemicentetes	161758	0.9558	1.6057	0.6323	1.1082	Potamogale	51333	1.4658	2.7692	0.8803	2.5898
Hemicentetes	162059	1.0741	1.4402	0.8673	2.0480	Potamogale	55204	1.1094	2.1915	0.7944	1.8216
Hemicentetes	162062	1.1023	1.4954	0.8500	1.8704	Potamogale	51322	1.1574	2.2957	0.4364	1.9416
Hemicentetes	166132	1.0501	1.2917	0.6928	1.6130	Solenodon	49508	2.3014	3.9811	1.8430	3.2397
Hemicentetes	170593	1.3394	1.2377	0.7674	1.6952	Solenodon	72809	4.0677	4.1625	1.7856	3.6765
Hemicentetes	206755	1.0046	1.3087	0.6841	1.7289	Solenodon	217256	4.2029	5.1612	2.4463	4.0210
Hemicentetes	207712	1.2160	1.6964	0.7116	1.9293	Solenodon	238263	3.5002	5.1589	2.5410	4.3256
Hemicentetes	207715	0.9787	1.4110	0.6829	1.6305	Solenodon	395697	2.8546	3.6166	2.1451	3.5651
Hemicentetes	212920	1.2307	1.6373	0.8579	2.1389	Solenodon	395819	3.7580	4.6011	1.1174	3.7903
Hemicentetes	212922	1.1051	1.5106	0.7427	2.2319	Elephantulus	86566	0.9447	1.7165	0.5179	1.4840
Hemicentetes	212924	1.2549	1.4023	0.8005	1.9695	Elephantulus	86568	0.6888	1.5855	0.4187	1.1049
Hemicentetes	339992	1.2739	1.3823	0.8615	2.2189	Elephantulus	86581	0.7580	1.4047	0.3632	1.1997
Hemicentetes	354998	0.9943	1.4276	0.8512	1.7004	Elephantulus	86585	0.8408	1.6176	0.3879	1.4876
Hemicentetes	364954	1.2171	1.5589	1.1501	1.9238	Petrodromus	203336	1.4173	2.8296	0.6579	2.2875
Hemicentetes	395510	1.0534	1.7841	0.7436	2.1611	Petrodromus	203339	1.3951	2.7234	0.6331	2.3138

Appendix 2.2. Linear Measurement Means/SDs (mm)

Taxon		Asthead1	Asthead2	Asthead3	Asthead4	Astneck1	Astneck2	Astne ck3	Astneck 4	Astroch 2	Astroch1	Astroch 3	Calc1
E. telfairi	Mean	0.9886	0.7486	0.8914	1.3180	1.7897	1.9531	1.1319	0.8987	0.1602	0.3064	0.1841	1.0606
	SD	0.0851	0.2685	0.0762	0.1231	0.1462	0.1457	0.1513	0.0851	0.0714	0.1054	0.0453	0.0945
	n	10	10	9	10	9	10	10	8	8	8	8	9
S. setosus	Mean	1.3650	1.1311	1.1372	1.7228	2.5794	3.2330	1.9552	1.3557	0.7320	0.7312	0.7440	1.8180
	SD	0.1233	0.0706	0.0924	0.0972	0.2071	0.2027	0.1947	0.1371	0.2383	0.2780	0.2130	0.1437
	n	10	10	10	10	7	7	7	7	10	10	10	7
H. semispinosus	Mean	1.2012	0.9982	1.0787	1.7081	2.3483	2.4006	1.6722	1.2175	0.4243	0.5534	0.5059	1.6990
	SD	0.1786	0.1599	0.1771	0.1814	0.2117	0.1984	0.1746	0.1878	0.1419	0.2279	0.1775	0.3944
	n	8	8	8	8	12	12	12	12	14	14	14	5
T. ecaudatus	Mean	2.1488	1.7520	1.9450	3.2709	4.5889	4.7164	2.8316	2.4285	0.5912	0.8228	0.6635	3.0088
	SD	0.2338	0.1116	0.1767	0.2830	0.5470	0.6138	0.3674	0.3809	0.1196	0.2876	0.1829	0.2109
	n	8	8	8	8	11	11	10	10	10	10	10	9
M. cowani	Mean	0.7445	0.5802	0.7167	1.0352	1.1337	1.1580	1.0953	0.6132	0.2465	0.4028	0.3051	1.1326
	SD	0.0608	0.0321	0.0571	0.0378	0.1286	0.0680	0.1163	0.0514	0.0794	0.0790	0.0513	0.1480
	n	6	6	6	6	11	11	11	11	10	10	10	4
M. dobsoni	Mean	0.9256	0.7142	0.7991	1.1624	1.5922	1.6467	1.4624	0.8731	0.2251	0.3300	0.2599	1.5818
	SD	0.1107	0.0858	0.0907	0.1122	0.1504	0.1006	0.1214	0.0804	0.0716	0.1313	0.0654	0.7795
	n	7	7	7	7	6	8	8	8	9	9	9	5
M. talazaci	Mean	1.1471	0.9042	0.9573	1.3493	1.7593	1.8297	1.5363	0.9356	0.2133	0.2576	0.2340	2.2137
	SD	0.0790	0.0746	0.0210	0.0430	0.0467	0.1419	0.1350	0.0249	0.0767	0.0728	0.0541	0.0824
	n	4	4	4	4	5	5	6	6	6	6	6	5
Oryzorictes	Mean	0.8936	0.7443	0.8708	1.3994	1.7855	1.7079	1.3480	1.0709	0.3084	0.3712	0.3232	1.4985
	SD	0.1471	0.0755	0.1192	0.1008	0.1955	0.1003	0.1556	0.0772	0.0483	0.0487	0.0334	0.1327
	n	7	6	6	7	5	6	6	6	8	8	8	4
L. mergulus	Mean	1.1795	0.9481	1.0976	1.8799	2.6346	2.4120	1.7524	1.4372	0.3082	0.4113	0.3559	1.6081
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	n	1	1	1	1	1	1	1	1	1	1	1	1
G. aurita	Mean	0.4584	0.3812	0.3997	0.6042	0.8559	0.9243	0.7236	0.5382	0.1127	0.3206	0.1856	0.8309

Appendix 2.2 (con't)

Taxon		Asthead1	Asthead2	Asthead3	Asthead4	Astneck1	Astneck2	Astneck3	Astneck4	Astroch2	Astroch1	Astroch3	Calc1
P. velox	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	0.0022	0.0315	0.0467	
	n	1	1	1	1	1	1	1	1	1	1	1	1
	Mean	2.1044	1.5650	1.5103	2.1063	3.5146	2.6995	2.1787	1.7512	0.3037	0.3816	0.3211	1.9187
	SD	0.2639	0.2352	0.2347	0.2196	0.2832	0.3082	0.1170	0.1673	0.0240	0.0329	0.0410	0.8352
	n	4	4	4	4	4	4	4	4	6	6	6	3
Solenodon	Mean	3.1609	2.7287	3.0567	5.2671	6.5017	5.5296	6.0812	3.3749	0.2928	0.3519	0.3416	5.6169
	SD	0.2638	0.1613	0.0988	0.3891	0.4786	0.1854	0.5399	0.1566	0.1206	0.1256	0.0857	0.6356
	n	5	5	5	5	6	6	6	6	3	3	3	5
Petrodomus	Mean	2.0756	1.8166	1.7628	3.0981	3.0606	2.8343	2.8288	2.0161	0.2104	0.2582	0.2126	3.4366
	SD	0.2227	0.0717	0.1176	0.0451	0.1272	0.1467	0.0595	0.1069	0.0780	0.0939	0.0212	0.1593
	n	3	3	3	3	3	3	3	3	3	3	3	3
Nasilio	Mean	1.3614	1.1494	0.9282	1.5525	1.5990	1.7707	1.4141	0.9890	0.1257	0.2555	0.1912	1.9713
	SD	0.1664	0.0705	0.0897	0.1068	0.1168	0.2484	0.1524	0.0489	0.0659	0.2009	0.0924	0.5084
	n	3	3	3	3	3	3	3	3	3	3	3	2
Taxon		Calc2	Calc3	Calc4	Calc5	Calc6	Foot1	Foot 2	Foot3	Foot4	Foot5	Foot6	Foot7
E. telfairi	Mean	1.2904	3.7946	0.8680	-0.1329	0.8843	1.4032	0.8490	0.7530	5.8296	1.8563	0.6283	0.4446
	SD	0.2094	0.2729	0.1158	0.1392	0.1023	0.1687	0.2510	0.0962	0.3091	0.2233	0.1277	0.1428
	n	8	10	10	9	9	9	9	11	11	9	9	9
S. setosus	Mean	2.4146	6.1400	1.2925	-0.1360	1.4886	2.2945	1.1478	1.0390	8.8532	2.5608	1.0441	0.4231
	SD	0.2425	0.3722	0.1100	0.5025	0.1909	0.4088	0.2131	0.1638	1.1995	0.4330	0.1832	0.1081
	n	10	12	12	12	12	10	10	10	10	10	10	10
H. semispinosus	Mean	1.7853	5.1402	1.2504	-0.0431	1.7275	2.2297	0.9647	1.0436	8.5538	2.0883	0.8234	0.4353
	SD	0.1426	0.3328	0.1731	0.2005	0.2348	0.1670	0.1535	0.1420	0.5654	0.1581	0.1698	0.1282
	n	5	8	8	8	8	16	16	15	15	16	16	15
T. ecaudatus	Mean	4.7862	10.8933	2.4109	0.3940	2.8952	4.3800	2.0386	1.8103	14.8663	4.1535	1.6526	0.5698
	SD	0.5047	0.4635	0.3104	0.1774	0.3224	0.2271	0.3288	0.1621	0.6938	0.4474	0.2804	0.2208
	n	9	10	10	10	10	10	10	10	10	10	10	10
M. cowani	Mean	0.9339	3.1116	0.6166	0.3485	0.9475	1.3155	0.5379	0.5470	6.4133	1.1154	0.7101	0.3310
	SD	0.0945	0.2274	0.0848	0.0416	0.1078	0.3363	0.3129	0.0550	0.4783	0.2311	0.0905	0.0861
	n	5	9	9	9	9	13	13	13	13	12	12	12

Appendix 2.2 (con't)

Taxon		Calc2	Calc3	Calc4	Calc5	Calc6	Foot1	Foot 2	Foot3	Foot4	Foot5	Foot6	Foot7
M. dobsoni	Mean	1.4992	4.4762	0.7968	0.5798	1.4397	2.0416	0.5938	0.6535	9.5068	1.2705	1.3520	0.1806
	SD	0.2905	0.2606	0.0695	0.1108	0.0916	0.1113	0.0496	0.0408	0.4459	0.1561	0.0822	0.0642
	n	4	10	10	10	10	8	8	8	8	8	8	8
M. talazaci	Mean	1.3891	4.8329	0.8497	0.5527	1.6693	2.1698	0.5580	0.7337	9.6281	1.2146	1.3697	0.2311
	SD	0.0868	0.1317	0.0763	0.0352	0.1324	0.1049	0.1019	0.0714	0.3483	0.1263	0.0962	0.0593
	n	5	6	6	6	6	7	7	7	7	7	7	6
Oryzorictes	Mean	1.1891	3.9445	0.8804	0.1483	0.8566	1.7807	0.7189	0.7916	5.4669	1.8635	0.7611	0.4104
	SD	0.0632	0.2675	0.1146	0.0538	0.0957	0.1031	0.1183	0.0953	0.2559	0.1679	0.0755	0.1002
	n	4	5	5	5	5	9	9	9	9	9	9	9
L. mergulus	Mean	1.5052	4.8793	1.0808	-0.2752	0.9003	2.4264	0.9004	0.8945	9.5997	2.3267	1.0628	0.6319
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	n	1	1	1	1	1	1	1	1	1	1	1	1
G. aurita	Mean	0.6113	1.9521	0.3871	0.0592	0.5632	0.6780	0.3885	0.3101	4.3283	0.6764	0.3066	0.1278
	SD	0.0123	0.0312	0.0388	0.0406	0.0140	0.0938	0.0409	0.0602	0.0808	0.0515	0.1478	
	n	1	1	1	1	1	2	2	2	2	2	2	1
P. velox	Mean	5.0255	10.2012	1.5598	0.7908	1.5535	3.1812	1.3345	1.2746	13.4468	2.4951	1.2612	0.2705
	SD	1.0602	0.7166	0.1469	0.5628	0.4958	1.6577	0.6618	0.0990	0.7426	1.2791	0.7368	0.1635
	n	3	6	6	5	5	4	4	4	4	4	4	4
Solenodon	Mean	6.7473	17.0210	3.3858	0.1796	3.5883	7.1261	2.5947	2.2284	19.3544	3.3922	2.4055	0.1508
	SD	1.2935	1.6075	0.4302	0.1146	0.8236	0.5042	0.7039	0.1808	1.4123	0.2136	0.2590	0.0701
	n	4	7	7	7	7	8	8	9	9	8	8	8
Petrodomus	Mean	4.3447	10.4495	1.9564	-0.9762	2.0220	4.8728	1.0650	0.8994	27.2478	2.6094	1.8463	0.8308
	SD	0.1451	0.1352	0.1243	0.3219	0.5222	0.0401	0.0319	0.0603	1.0940	0.0786	0.1431	0.1298
	n	3	3	3	3	3	2	2	2	2	2	2	2
Nasilio	Mean	2.3578	5.7243	1.1935	-0.1859	1.2349	3.1847	1.0174	0.7411	12.2457	1.1425	1.0210	0.1768
	SD	0.0061	0.6662	0.1085	0.2063	0.2801	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	n	2	2	3	2	2	1	1	1	1	1	1	1
Taxon		Malleoli1	Malleoli2	Malleoli3	Malleoli4	Taxon		Malleoli1	Malleoli2	Malleoli3	Malleoli4		
E. telfairi	Mean	0.8581	1.3104	0.7345	1.4332	Petrodomus Mean		0.808	1.5811	0.4219	1.3191		
	SD	0.1856	0.1856	0.1563	0.2231	SD		0.1103	0.1301	0.0679	0.1964		

Appendix 2.2 (con't)

Taxon		Malleoli1	Malleoli2	Malleoli3	Malleoli4
	n	14	14	14	14
S. setosus	Mean	1.8383	2.0721	1.2913	2.6243
	SD	0.18	0.2112	0.2478	0.2902
	n	12	12	12	12
H. semispinosus	Mean	2.0002	3.0857	1.5428	3.5946
	SD	0.1854	0.1593	0.337	0.359
	n	11	11	11	11
T. ecaudatus	Mean	1.1115	1.4913	0.798	1.9005
	SD	0.119	0.1492	0.1191	0.2964
	n	17	17	17	17
M. cowani	Mean	0.5773	0.9077	0.5024	0.8494
	SD	0.0593	0.0619	0.0595	0.0861
	n	13	13	13	13
M. dobsoni	Mean	0.651	1.1414	0.5207	1.028
	SD	0.1276	0.1475	0.15	0.1504
	n	7	7	7	7
M. talazaci	Mean	0.8894	1.3914	0.713	1.3306
	SD	0.0827	0.0891	0.0663	0.1511
	n	6	6	6	6
Oryzorictes	Mean	0.6111	1.222	0.5216	0.9961
	SD	0.0897	0.1885	0.0872	0.1159
	n	8	8	8	8
L. mergulus	Mean	0.9629	1.7064	0.7436	1.7244
	SD	n/a	n/a	n/a	n/a
	n	1	1	1	1
G. aurita	Mean	0.3483	0.4844	0.2908	0.6803
	SD	n/a	n/a	n/a	n/a
	n	1	1	1	1

Taxon		Malleoli1	Malleoli2	Malleoli3	Malleoli4
	n	4	4	4	4
Nasilio	Mean	1.4062	2.7765	0.6455	2.3006
	SD	0.0157	0.0751	0.0176	0.0186
	n	2	2	2	2
P. velox	Mean	1.5394	2.6927	0.974	2.33
	SD	0.3635	0.3812	0.3601	0.3507
	n	6	6	6	6
Solenodon	Mean	3.4475	4.4469	1.9797	3.7697
	SD	0.7375	0.6369	0.5215	0.3753
	n	6	6	6	6

Appendix 2.3. Raw Index Scores

Taxon	ID	MLAHI	AHSI	Taxon	ID	ANLI	ANWI	Taxon	ID	MDI	ATDI	MLMI
E. telfairi	101	0.9345	1.3305	Echinops	101	0.3242	0.2480	Echinops	127274	0.2573	1.2162	0.9889
E. telfairi	127274	0.8610	1.2288	Echinops	153785	0.2774	0.2434	Echinops	159728	0.2480	1.2166	1.1148
E. telfairi	159729	0.8947	1.4534	Echinops	159730			Echinops	159729	0.3188	1.2003	1.1653
E. telfairi	170605	1.0098	1.3344	Echinops	170605	0.3116	0.2468	Echinops	159730	0.2938	1.0323	1.0962
E. telfairi	207717	0.8781	1.2257	Echinops	207717	0.2850	0.2187	Echinops	170605	0.2414	1.2523	1.1656
E. telfairi	207718			Echinops	207718	0.2661	0.2263	Echinops	207717	0.3161	1.0797	0.9798
E. telfairi	212918	1.0163	1.2539	Echinops	212918	0.2660	0.2510	Echinops	207718	0.3487	1.0139	0.8478
E. telfairi	212919	0.9615	1.4045	Echinops	212919	0.3690	0.2666	Echinops	212918	0.2478	1.3384	1.0771
E. telfairi	328620	0.8785	1.3906	Echinops	328637	0.2763	0.2214	Echinops	212919	0.2269	1.2648	1.1441
E. telfairi	328637	0.9661	1.3976	Echinops	588220	0.3109		Echinops	328620	0.2480	1.0750	1.2736
S. setosus	124554	1.0380	1.2925	Setifer	165494	0.3255	0.2393	Echinops	328637	0.2215	1.2011	1.0829
S. setosus	154033	0.9042	1.3050	Setifer	170532	0.3831	0.2253	Echinops	395835	0.2700	1.3249	1.0762
S. setosus	165494	1.0671	1.1736	Setifer	328612	0.3229	0.2344	Echinops	464980	0.2266	1.3395	1.1762
S. setosus	170532	1.1138	1.4172	Setifer	395513	0.3128	0.2604	Echinops	588220	0.2766	0.9143	1.1690
S. setosus	328612	0.8944	1.1063	Setifer	395719	0.3284	0.2353	Setifer	85170	0.1948	2.0021	1.4195
S. setosus	395513	1.0047	1.3031	Setifer	578790	0.3173	0.2304	Setifer	124554	0.2061	1.8573	1.2703
S. setosus	541443	0.8916	1.2260	Setifer	85170	0.3658	0.2076	Setifer	154033	0.2888	1.4054	1.3420
S. setosus	578790	0.9678	1.1811	Hemicentetes	10001	0.3630	0.2644	Setifer	154034	0.3406	1.1851	1.1094
S. setosus	85170	1.0803	1.2464	Hemicentetes	161757	0.3336	0.3092	Setifer	170532	0.3131	1.1904	1.0670
S. setosus	85513	1.0277	1.4406	Hemicentetes	162062	0.3222	0.2287	Setifer	170548	0.2772	1.4282	1.3936
H. semispinosus	10001	0.9676	1.2049	Hemicentetes	166132	0.3432	0.2436	Setifer	170731	0.2573	1.5173	1.2313
H. semispinosus	161757	0.9766	1.2060	Hemicentetes	170593	0.3252	0.2264	Setifer	207076	0.2941	1.3053	1.0193
H. semispinosus	162062	0.8560	1.6731	Hemicentetes	207712	0.3027	0.3057	Setifer	317872	0.3057	1.2675	1.3457
H. semispinosus	207712	0.9190	1.5821	Hemicentetes	207715	0.3973	0.2412	Setifer	395513	0.2981	1.3354	1.2658
H. semispinosus	207715	0.9138	1.5444	Hemicentetes	212920	0.3587	0.2369	Setifer	395719	0.2638	1.5139	1.3206
H. semispinosus	212922	0.9516	1.4477	Hemicentetes	212922	0.4054	0.2433	Setifer	578790	0.2525	1.5249	1.4896
H. semispinosus	339992	0.8113	1.3848	Hemicentetes	212924	0.3832	0.2624	Tenrec	154628	0.2155	1.4019	1.1829
H. semispinosus	354998	1.0389	1.4628	Hemicentetes	354998	0.3310	0.2229	Tenrec	156337	0.2596	1.1346	0.8915
T. ecaudatus	154628	0.8714	1.6595	Hemicentetes	50911			Tenrec	166047	0.1943	1.5256	1.1180
T. ecaudatus	166047	0.9964	1.7379	Tenrec	63313	0.2977	0.2632	Tenrec	170511	0.2028	1.5934	1.2063
T. ecaudatus	170511	0.8476	1.5268	Tenrec	154628	0.3105	0.2583	Tenrec	30398	0.2745	1.2874	1.2116
T. ecaudatus	361485	0.9751	1.6602	Tenrec	166047	0.2590	0.2623	Tenrec	361485	0.2717	1.0420	1.1373
T. ecaudatus	577051	0.8407	1.3356	Tenrec	170511	0.2847	0.2646	Tenrec	364955	0.2829	0.9722	1.3095
T. ecaudatus	578792	0.8690	1.5006	Tenrec	30398			Tenrec	50911	0.2649	0.9425	1.1533

Appendix 2.3 (con't)

Taxon	ID	MLAHI	AHSI	Taxon	ID	ANLI	ANWI	Taxon	ID	MDI	ATDI
T. ecaudatus	59011	0.9187	1.4848	Tenrec	361485	0.3168	0.2769	Tenrec	577051	0.1745	1.7864
T. ecaudatus	60587	0.9123	1.3473	Tenrec	364955	0.3148	0.2966	Tenrec	578792	0.1855	1.6188
M. cowani	156221	0.7938	1.2840	Tenrec	50911	0.3707	0.2494	Tenrec	85514	0.2024	1.5317
M. cowani	156222	0.7928	1.2866	Tenrec	577051	0.3234	0.2431	Hemicentetes	33951	0.2299	1.1769
M. cowani	156223	0.7257	1.4780	Tenrec	578792	0.3516	0.2512	Hemicentetes	161757	0.2149	1.2793
M. cowani	165673	0.8556	1.4720	Tenrec	60587	0.2508	0.2487	Hemicentetes	161758	0.2330	1.5116
M. cowani	165680	0.8636	1.3893	M. cowani	156221	0.4702	0.2769	Hemicentetes	162059	0.2487	1.2383
M. cowani	165689	0.8408	1.4659	M. cowani	156222	0.4699	0.2803	Hemicentetes	162062	0.2525	1.2968
M. dobsoni	161940	0.9160	1.1542	M. cowani	156223	0.5521	0.2309	Hemicentetes	166132	0.2385	1.5157
M. dobsoni	165774	1.0178	1.2135	M. cowani	165672	0.4049	0.2453	Hemicentetes	170593	0.2616	1.7454
M. dobsoni	165775	0.9682	1.3663	M. cowani	165673	0.4334	0.2767	Hemicentetes	206755	0.2252	1.4685
M. dobsoni	166198	0.8664	1.3518	M. cowani	165676	0.4902	0.2617	Hemicentetes	207712	0.1963	1.7089
M. dobsoni	578749	0.7895	1.2539	M. cowani	165689	0.4991	0.2628	Hemicentetes	207715	0.2245	1.4331
M. dobsoni	582730	0.7806	1.1826	M. cowani	328658	0.6197	0.2902	Hemicentetes	212920	0.2272	1.4345
M. dobsoni	166200	0.9451	1.3052	M. cowani	449184	0.4290	0.2692	Hemicentetes	212922	0.1985	1.4879
M. talazaci	154581	1.0164	1.1235	M. cowani	449186	0.4530	0.2713	Hemicentetes	212924	0.2374	1.5677
M. talazaci	154585	0.9320	1.1038	M. cowani	449187	0.4586	0.2822	Hemicentetes	339992	0.2392	1.4787
M. talazaci	162040	0.9494	1.3400	M. dobsoni	161935	0.3896	0.2708	Hemicentetes	354998	0.2721	1.1681
M. talazaci	167501	0.8771	1.1589	M. dobsoni	161940	0.4499	0.2544	Hemicentetes	364954	0.3302	1.0583
Oryzorictes	161746	0.8300	1.9212	M. dobsoni	165467	0.4628	0.2854	Hemicentetes	395510	0.1885	1.4167
Oryzorictes	162053	0.8722	1.3820	M. dobsoni	165774	0.4519	0.2796	M. cowani	156221	0.3024	1.0701
Oryzorictes	166240	0.8403	1.5813	M. dobsoni	165775	0.4340	0.2815	M. cowani	156222	0.2567	1.2501
Oryzorictes	167480		1.6518	M. dobsoni	166198	0.5214	0.2617	M. cowani	156223	0.2581	1.1561
Oryzorictes	45018	0.8204	1.5651	M. dobsoni	578749			M. cowani	165672	0.3222	1.0833
Oryzorictes	5639	0.7851	1.3825	M. dobsoni	582730			M. cowani	165673	0.2865	1.1542
Oryzorictes	31257	1.0198	1.6429	M. talazaci	154581	0.4143	0.2597	M. cowani	165674	0.2836	1.0992
L. mergulus	45050	0.8637	1.5938	M. talazaci	154585	0.3924	0.2427	M. cowani	165676	0.2670	1.1850
G. aurita	161594	0.9537	1.3180	M. talazaci	162040	0.3940	0.2617	M. cowani	165680	0.2840	1.2095
P. velox	266897	1.0761	0.9533	M. talazaci	167502	0.4953	0.2608	M. cowani	165689	0.3286	1.1489
P. velox	51324	1.0368	1.0413	M. talazaci	167503			M. cowani	168017	0.2972	1.1856
P. velox	51333	0.9842	0.9921	M. talazaci	577056	0.4520	0.2745	M. cowani	328658	0.2867	1.1025
P. velox	55204	1.0534	1.0269	Oryzorictes	161746	0.3979	0.2886	M. cowani	449184	0.2489	1.2071
Solenodon	57320	0.8225	1.7781	Oryzorictes	162058			M. cowani	449186	0.2887	1.1302
Solenodon	238263	0.9273	1.5279	Oryzorictes	166240	0.4010	0.3136	M. dobsoni	161935	0.3134	1.0398
Solenodon	290520	0.9424	1.6368	Oryzorictes	45018	0.4045	0.2895	M. dobsoni	161940	0.2857	1.1779
Solenodon	395697	0.8497	1.7695	Oryzorictes	5639	0.3934	0.2928	M. dobsoni	165467	0.2489	1.1230

Appendix 2.3 (con't)

Taxon	ID	ANLI	ANWI	Taxon	ID	MDI	ATDI	MLM I
Solenodon	395819	0.9239	1.6370	Oryzorictes	31257	0.3643	0.3442	
Petrodomus	150415	0.9722	1.4503	Limnogale	45050	0.3472	0.2848	
Petrodomus	203336	1.0751	1.6762	Geogale	161594	0.4065	0.3023	
Petrodomus	203339	1.0502	1.3839	Potamogale	266897	0.3271	0.2858	
Nasilio	86568	1.2806	1.2401	Potamogale	51324	0.3435	0.2901	
Nasilio	86585	1.1832	1.1165	Potamogale	51333	0.3504	0.2748	
Nasilio	86587	1.2604	1.0829	Potamogale	55204	0.3856	0.2754	
Solenodon	290520	0.4896	0.2819	M. talazaci	167503	0.2962	1.0602	0.9379
Solenodon	395697	0.4989	0.2816	M. talazaci	577056	0.2343	1.3514	0.9698
Solenodon	395819	0.4822	0.2697	Oryzorictes	31257	0.2168	1.1180	0.9559
Solenodon	51068	0.4968	0.2816	Oryzorictes	161746	0.2067	1.4075	0.8027
Solenodon	57320	0.6189	0.2963	Oryzorictes	162053	0.2177	1.2375	0.8189
Petrodomus	150415	0.4702	0.3233	Oryzorictes	162054	0.2578	1.0367	0.7458
Petrodomus	203336	0.4817	0.3531	Oryzorictes	162058	0.2409	1.1749	0.8589
Petrodomus	203339	0.4877	0.3496	Oryzorictes	166240	0.2407	1.1674	0.9334
Nasilio	86568	0.4050	0.3198	Oryzorictes	167480	0.2265	1.1790	0.7361
Nasilio	86585	0.4639	0.2972	Oryzorictes	578789	0.2699	1.1085	0.7366
Nasilio	86587	0.3898	0.2659	Limnogale	45050	0.2168	1.2948	1.0106
				Geogale	161594	0.2496	1.1978	1.4045
				Potamogale	34881	0.2544	1.3605	0.8427
				Potamogale	51324	0.1890	1.6336	0.9351
				Potamogale	266897	0.2320	1.4775	0.8027
				Potamogale	51333	0.1643	1.6651	0.9352
				Potamogale	55204	0.1979	1.3966	0.8312
				Potamogale	51322	0.1030	2.6522	0.8457
				Solenodon	49508	0.2552	1.2487	0.8138
				Solenodon	72809	0.2278	2.2781	0.8833
				Solenodon	217256	0.2664	1.7180	0.7791
				Solenodon	238263	0.2679	1.3775	0.8385
				Solenodon	395697	0.2987	1.3308	0.9857
				Solenodon	395819	0.1332	3.3631	0.8238
				Nasilio	86566	0.1618	1.8240	0.8645
				Nasilio	86568	0.1556	1.6448	0.6969
				Nasilio	86581	0.1395	2.0870	0.8541
				Nasilio	86585	0.1249	2.1674	0.9197
				Petrodromus	203336	0.1286	2.1543	0.8084
Taxon	ID	MDI	ATDI	MLMI				
M. dobsoni	165774	0.1727	1.6975	0.9530				
M. dobsoni	165775	0.2275	1.2869	0.9778				
M. dobsoni	166107	0.1923	1.2596	0.7300				
M. dobsoni	166198	0.2254	1.4132	0.9566				
M. talazaci	154581	0.2300	1.4003	1.0246				
M. talazaci	162040	0.2999	1.1328	0.8669				
M. talazaci	167501	0.2591	1.3191	1.0634				
Petrodromus	203339	0.1257	2.2037	0.8496				

Appendix 2.3 (con't)

Taxon	ID	CLI	CAFP	PPPI	CTLI	Taxon	ID	MT3I	CUSI	NPDI	Taxon	ID	TCHI	MLCHI	TCMI
Echinops	127274	0.2179	0.7864	-0.1852	0.3661	Echinops	134550	0.1533	1.7314	0.1838	Echinops	207717	0.0963	0.3725	0.8218
Echinops	153785	0.2076		-0.1023		Echinops	153785	0.1272	1.9677	0.1368	Echinops	212918	0.0703	0.3332	0.4387
Echinops	159730	0.2624	0.8469	-0.1689	0.3111	Echinops	159730	0.1022	1.6082	0.2105	Echinops	212919	0.1060	0.4678	0.6158
Echinops	170605	0.1830	0.6966	-0.4886	0.4003	Echinops	207718	0.1262	1.6549	0.2319	Echinops	153785	0.1032	1.3631	1.2019
Echinops	207718	0.2824	1.0239	-0.1226	0.2782	Echinops	212918	0.1336	2.7626	0.1440	Echinops	328620	0.0959	0.8471	0.7849
Echinops	212918	0.2375		-0.0942		Echinops	31270	0.1246			Echinops	328637	0.1414	0.6875	0.7512
Echinops	212919	0.2470	0.9281	0.1597	0.3272	Echinops	328636	0.1341			Echinops	464980	0.1218	0.1788	0.7214
Echinops	328637	0.2490	0.8292	-0.1917	0.3328	Echinops	328637	0.1167	1.7094	0.1382	Echinops	588220	0.0818	0.5462	0.8220
Echinops	588220	0.2269	0.8452		0.3475	Echinops	464980	0.1212	1.5192	0.1138	Setifer	85170	0.2474	0.9532	0.7310
Echinops	207717	0.1811	0.8066	-0.2529	0.3384	Echinops	588220	0.1724	0.7825	0.1787	Setifer	85513	0.2361	0.7533	0.6691
Setifer	124554	0.2687		0.3615	0.4950	Echinops	207717	0.1145	2.4536	0.2689	Setifer	124554	0.3607	1.5779	0.5963
Setifer	154033	0.2231	0.9326	-0.3287	0.3501	Setifer	154033	0.1152	1.5643	0.1036	Setifer	154033	0.3054	2.4328	0.7318
Setifer	165494	0.2065	0.6624	0.1100	0.4088	Setifer	154034	0.1182	2.0179	0.1534	Setifer	165494	0.2660	1.6061	0.5690
Setifer	170532	0.2176	0.8137	-0.3662	0.3486	Setifer	165494	0.1063	2.1743	0.1497	Setifer	170532	0.1525	0.9019	0.6608
Setifer	170731	0.2201	0.7628	-0.2913	0.3787	Setifer	170532	0.1468	2.1900	0.1086	Setifer	170731	0.1870	0.8174	0.6447
Setifer	317872	0.2059		-0.5610		Setifer	170731	0.1348	1.9481	0.1030	Setifer	328612	0.2883	0.5334	0.6651
Setifer	328612	0.1799		-0.2563		Setifer	328612	0.1031	2.4956	0.1236	Setifer	541443	0.1966	0.8317	0.5726
Setifer	395513	0.2030	0.8424	0.4972	0.3613	Setifer	395513	0.1190	1.9495	0.1192	Setifer	578790	0.1829	0.7305	0.5102
Setifer	541443	0.2105		0.1806	0.3928	Setifer	395719	0.0943	2.6982	0.0998	Hemicentetes	161757	0.0887	0.7358	0.8566
Setifer	578790	0.2006	0.7774	-0.5182	0.3749	Setifer	541443	0.1174	1.5504	0.1222	Hemicentetes	161758	0.1187	0.7825	1.0363
Setifer	85170	0.1856		-0.2524	0.3775	Setifer	578790	0.1249	1.6754	0.0801	Hemicentetes	162059	0.1237	0.9760	0.9995
Setifer	85513	0.2118	0.6700	0.1445	0.4327	Hemicentetes	10001	0.1819	3.1623	0.1682	Hemicentetes	162062	0.3946	1.0397	0.4205
Hemicentetes	161757	0.2566	1.2223	-0.0733	0.3010	Hemicentetes	161757	0.1230	2.1901	0.1340	Hemicentetes	166132	0.2480	0.6863	0.5680
Hemicentetes	161758	0.2182		0.1076		Hemicentetes	161758	0.1363	2.5575	0.1362	Hemicentetes	170593	0.2541	0.5334	0.6364
Hemicentetes	162062	0.2196	0.7466	-0.0772	0.3784	Hemicentetes	162059	0.1190	2.0385	0.1843	Hemicentetes	207714	0.2418	1.1489	0.7771
Hemicentetes	207712	0.2663	1.1912	0.0421	0.3382	Hemicentetes	162062	0.1147	2.0989	0.1424	Hemicentetes	212920	0.1644	0.3973	0.9006
Hemicentetes	207715	0.2174		0.0925		Hemicentetes	166132	0.1213	3.0971	0.1738	Hemicentetes	212921	0.2715	0.6264	0.5271
Hemicentetes	212922	0.2450	0.8206	0.0576	0.3645	Hemicentetes	207712	0.0979	1.9697	0.1106	Hemicentetes	212922	0.1810	1.4581	1.0134
Hemicentetes	354998	0.2418	0.8001	-0.2153	0.3532	Hemicentetes	207714	0.1488	2.3068	0.1427	Hemicentetes	212924	0.2684	0.9859	0.7189
Hemicentetes	364954	0.2758		-0.1728		Hemicentetes	207715	0.1266	2.1503	0.0487	Hemicentetes	339992	0.2069	1.0456	0.5117
Tenrec	154628	0.1764	0.7042	0.1373	0.4146	Hemicentetes	212920	0.1086	2.6001	0.1483	Hemicentetes	83658	0.2646	0.7392	0.6252
Tenrec	166047	0.2225	0.7001	0.1161	0.4102	Hemicentetes	212921	0.1364	1.9428	0.1319	Hemicentetes	354998	0.1929	0.5289	0.4777
Tenrec	170511	0.2012	0.6134	0.2230	0.4508	Hemicentetes	212922	0.1195	2.7633	0.0901	Tenrec	59011	0.1205	0.9019	0.6608
Tenrec	30398	0.2474	0.6417	0.0468	0.4394	Hemicentetes	212924	0.1086	2.1709		Tenrec	60587	0.1372	0.8174	0.6688

Appendix 2.3 (con't)

Taxon	ID	CLI	CAFPI	PPPI	CTLI	Taxon	ID	MT3I	CUSI	NPDI	Taxon	ID	TCHI	MLCHI	TCMI
Tenrec	361485	0.2004	0.6317	0.1228	0.4418	Hemicentetes	339992	0.1070	2.0033	0.2277	Tenrec	63313	0.2169	0.5334	0.6651
Tenrec	364955	0.2671		0.0983		Hemicentetes	354998		2.2965	0.2261	Tenrec	154628	0.1641	0.8317	0.5726
Tenrec	577051	0.2529	0.6652	0.1546	0.4059	Hemicentetes	364954	0.0937	2.4119	0.1983	Tenrec	166047	0.1532	0.7305	0.5102
Tenrec	578792	0.2157	0.7062	0.0910	0.4283	Tenrec	63313	0.1281	1.7983	0.0655	Tenrec	170511	0.1723	0.9532	0.7310
Tenrec	59011	0.2404	0.5917	0.1636	0.4529	Tenrec	154628	0.1049	3.1252	0.1006	Tenrec	361485	0.1802	0.7533	0.6691
Tenrec	60587	0.1924	0.4606	0.1850	0.4995	Tenrec	166047	0.1313	2.3291	0.0696	Tenrec	364955	0.2065	0.6556	0.6005
M. cowani	156223	0.2169		0.2872		Tenrec	170511	0.1161	2.0353	0.0471	Tenrec	577051	0.1849	0.5944	0.6372
M. cowani	165673	0.2329	1.2057	0.4199	0.2970	Tenrec	30398	0.1196	2.2303	0.1104	Tenrec	578792	0.1048	0.7418	0.5162
M. cowani	165674	0.2068		0.3519		Tenrec	361485	0.1017	2.3037	0.1564	M. cowani	156221	0.2761	0.3416	0.6965
M. cowani	165680	0.1933		0.3274	0.2873	Tenrec	364955	0.1292	1.7687	0.1222	M. cowani	156222	0.2847	0.4183	1.6706
M. cowani	165689	0.1905	1.1668	0.3667	0.3229	Tenrec	577051	0.1295	2.2515	0.0928	M. cowani	165672	0.2763	0.8045	0.6541
M. cowani	168017	0.1788		0.3484		Tenrec	578792	0.1363	1.9444	0.1164	M. cowani	165673	0.3047	0.3468	0.6928
M. cowani	449186	0.1854	1.0346	0.4004	0.3313	Tenrec	60587	0.1226	2.2158	0.0889	M. cowani	165674	0.1475	0.4772	0.6101
M. cowani	449187	0.1894	1.3685	0.3948	0.2923	M. cowani	156222	0.0908	2.5369	0.2435	M. cowani	165676	0.2488	0.7227	0.7239
M. cowani	449188	0.1850		0.4387		M. cowani	156223	0.0891	3.5181	0.1669	M. cowani	165680	0.2834	1.0242	0.5717
M. dobsoni	161935	0.1956		0.4839		M. cowani	165672	0.0861	2.3154	0.2119	M. cowani	165689	0.2840	0.6310	0.8819
M. dobsoni	161940	0.1729		0.4481		M. cowani	165673	0.0910	3.8803	0.1706	M. cowani	449186	0.3302	0.6928	0.5535
M. dobsoni	165467	0.1518	0.8736	0.4585	0.3891	M. cowani	165674	0.0782	3.3801	0.1762	M. cowani	449187	0.3360	0.8316	0.9161
M. dobsoni	165774	0.1631	1.3485	0.3947	0.3144	M. cowani	165676	0.0865	2.7696		M. dobsoni	161935	0.2029	0.5739	0.6453
M. dobsoni	165775	0.1952	1.5534	0.3587	0.2997	M. cowani	165680	0.0825	4.1019	0.1856	M. dobsoni	161940	0.2087	1.0636	0.8758
M. dobsoni	166107	0.1968		0.2825		M. cowani	165689	0.0920	0.1879	0.1783	M. dobsoni	165467	0.2170	0.2256	0.4318
M. dobsoni	166198	0.1781	1.4579	0.4005	0.2944	M. cowani	168017	0.0727	3.9893	0.2558	M. dobsoni	165774	0.2908	0.6455	0.4780
M. dobsoni	166200	0.1705		0.5062		M. cowani	328658	0.0862	2.8370	0.1541	M. dobsoni	165775	0.1415	0.7900	1.4266
M. dobsoni	578749	0.1672		0.2974		M. cowani	449184	0.0765	2.9038	0.1472	M. dobsoni	166107	0.1804	0.7439	0.7834
M. dobsoni	582730	0.1920	1.2872	0.3993	0.3345	M. cowani	449186	0.0800	3.1494	0.1190	M. dobsoni	166198	0.1405	1.1454	0.9471
M. talazaci	154585	0.1870	1.4850	0.3084	0.2977	M. cowani	449187	0.0986	2.6704	0.1585	M. dobsoni	166200	0.1587	0.5899	0.7552
M. talazaci	162040	0.1789	1.6678	0.2807	0.2764	M. dobsoni	161935	0.0775	3.7289	0.0981	M. dobsoni	578749	0.1486	1.0950	1.2999
M. talazaci	167501	0.1504	1.5614	0.3859	0.2940	M. dobsoni	161940	0.0647	3.8234	0.0794	M. talazaci	154581	0.1323	1.0512	1.0717
M. talazaci	167502	0.1752		0.3403		M. dobsoni	165467	0.0635	3.7215	0.0523	M. talazaci	154585	0.1451	1.0009	0.9260
M. talazaci	167503	0.1914	1.7534	0.3240	0.2695	M. dobsoni	165774	0.0717	3.5260	0.0740	M. talazaci	162040	0.1367	0.7204	0.6794
M. talazaci	577056	0.1718	1.5241	0.3599	0.3001	M. dobsoni	165775	0.0685	2.9326	0.0800	M. talazaci	167501	0.1072	0.5631	1.5831
Oryzorictes	161746	0.2349	1.2518	0.0838	0.2944	M. dobsoni	166107	0.0669	3.4938	0.0287	M. talazaci	167503	0.1376	0.7498	0.8175
Oryzorictes	162054	0.2088		0.1606		M. dobsoni	166198	0.0686	3.3828	0.0975	M. talazaci	577056	0.2245	0.8954	0.8344
Oryzorictes	45018	0.2027	1.3267	0.1366	0.3035	M. dobsoni	166200	0.0690	3.0496	0.0442	Oryzorictes	161746	0.1741	0.7164	0.6922

Appendix 2.3 (con't)

Taxon	ID	CLI	CAFPI	PPPI	CTLI
Oryzorictes	578789	0.2692	1.1268	0.2413	0.3160
Oryzorictes	31257	0.2019	1.3380	0.2564	0.3222
Limnogale	45050	0.2215	1.0683	-0.3057	0.3085
Geogale	159733	0.2148		0.0551	0.3212
Geogale	161594	0.1822	1.3788	0.1534	0.3052
Potamogale	266897	0.1547	0.4143	0.9919	0.5378
Potamogale	34881	0.1750		0.7094	
Potamogale	51324	0.1515		0.8194	
Potamogale	51333	0.1392	0.5161	0.2440	0.4911
Potamogale	55204	0.1526	0.6106	0.0344	0.4327
Potamogale	51322	0.1451			
Solenodon	172745	0.2314		0.1489	
Solenodon	238263	0.1711	0.8970	0.0664	0.3158
Solenodon	290520	0.2134	0.6904	0.0509	0.4321
Solenodon	395697	0.2011		0.0612	
Solenodon	395819	0.1951	0.7862	0.0194	0.4265
Solenodon	51068	0.1571		0.0189	
Solenodon	57320	0.2314	0.9154	0.0166	0.3852
Petrodomus	150415	0.1760	0.7466	-0.2342	0.4282
Petrodomus	203336	0.1968	0.8645	-0.6714	0.4003
Petrodomus	203339	0.1887	0.7659	-0.6707	0.4189
Nasilio	86585	0.2128	0.9867	-0.2315	0.3813
Nasilio	86587	0.2136	0.6849	-0.0386	0.4480
Nasilio	86581				

Taxon	ID	MT3I	CUSI	NPDI
M. talazaci	154581	0.0863	3.8115	0.0873
M. talazaci	154585	0.0890	3.3554	0.0763
M. talazaci	162040	0.0692	3.2051	0.0881
M. talazaci	167501	0.0708	4.3242	0.0870
M. talazaci	167502	0.0787	3.1789	0.0664
M. talazaci	167503	0.0722	4.3773	
M. talazaci	577056	0.0682	6.0796	0.1303
Oryzorictes	161746	0.1564	2.9083	0.1399
Oryzorictes	162053	0.1579	1.9781	0.1544
Oryzorictes	162054	0.1429	2.2949	0.1051
Oryzorictes	162058	0.1484	2.6380	0.1195
Oryzorictes	167480	0.1562	2.9099	0.1591
Oryzorictes	45018	0.1309	2.8712	0.1177
Oryzorictes	5639	0.1142	1.8712	0.1694
Oryzorictes	578789	0.1655	2.2886	0.2041
Oryzorictes	31257	0.1315	3.0935	0.2560
Limnogale	45050	0.0932	2.6950	0.1864
Geogale	159733	0.0627	1.7013	0.1518
Geogale	161594	0.0804	1.7832	
Potamogale	266897	0.0989	2.3800	0.0743
Potamogale	34881		2.0366	0.0938
Potamogale	51324	0.0944		
Potamogale	51333	0.0915	2.3530	0.0394
Potamogale	51322	0.0941	2.4967	0.1009
Soleondon	49508	0.1081		
Soleondon	172680	0.1293	2.1087	0.0209
Soleondon	172745	0.1165	2.7635	0.0566
Soleondon	238263	0.1102	3.5587	0.0284
Soleondon	290520	0.1022	2.1634	0.0157
Soleondon	395697	0.1046	2.6910	0.0222
Soleondon	395819	0.1206	2.6532	0.0234
Soleondon	51068	0.1136	2.9200	0.0261
Soleondon	57320	0.1347	4.5008	0.0168
Petrodromus	203336	0.0336	4.7017	0.1642

Taxon	ID	TCHI	MLCHI	TCMI
Oryzorictes	162053	0.2266	0.8292	0.8304
Oryzorictes	162054	0.2265	1.0148	1.0361
Oryzorictes	162058	0.2736	0.9552	0.9789
Oryzorictes	166240	0.2138	0.7429	0.6430
Oryzorictes	167480	0.1577	0.7502	1.5399
Oryzorictes	5639	0.2248	1.0853	0.7249
Oryzorictes	31257	0.2437	0.6400	0.7590
Limnogale	45050	0.1663	0.7494	1.0279
Geogale	159733	0.3039	0.3725	0.5962
Geogale	161594	0.2270	0.3332	0.4387
Potamogale	266897	0.1557	0.7512	0.7999
Potamogale	34881	0.1600	0.7238	0.7030
Potamogale	51324	0.1698	0.9749	0.7999
Potamogale	51333	0.1359	0.8894	0.7727
Potamogale	55204	0.1636	0.6741	0.9444
Potamogale	51322	0.1479	0.8017	0.7357
Solenodon	395697	0.0692	0.6266	0.7047
Solenodon	51068	0.0488	0.8893	0.6768
Solenodon	57320	0.0822	1.0183	0.6950
Petrodomus	150415	0.0882	0.4678	0.6158
Petrodomus	203336	0.0816	1.3631	1.2019
Petrodomus	203339	0.0684	0.8471	0.7849
Nasilio	86568	0.1939	0.6875	0.7512
Nasilio	86581	0.1986	0.1788	0.7214
Nasilio	86585	0.0853	0.8198	1.3294
Nasilio	86587	0.0742	1.2500	0.6640

Taxon	ID	MT3I	CUSI	NPDI
Petrodromus	203339	0.0324	4.4545	0.2092
Elephantulus	86585	0.0605	3.1301	

APPENDIX 2.4 Index Summary Statistics and Tukey Post-Hoc Results

Genus	MLMI	MLMI	MLMI
	Means	N	Std.Dev.
Echinops	1.096977	14	0.104916
Setifer	1.272847	12	0.144786
Tenrec	1.165827	11	0.108142
Hemicentetes	1.280708	17	0.195182
All Grps	1.207926	54	0.164410
	{1}	{2}	{3}
	M=1.0970	M=1.2728	M=1.1658
Echinops {1}		0.020513	0.659518
Setifer {2}	0.020513		0.320170
Tenrec {3}	0.659518	0.320170	
Hemicentetes {4}	0.006551	0.999059	0.201273

Subfamily	MLMI	MLMI	MLMI
	Means	N	Std.Dev.
Tenrecinae	1.207926	54	0.164410
Oryzorictinae	0.911055	35	0.114527
All Grps	1.091179	89	0.206435
	{1}	{2}	
	M=1.2079	M=.91105	
Tenrecinae {1}		0.000114	
Oryzorictinae {2}	0.000114		

Genus	MLMI	MLMI	MLMI		
	Means	N	Std.Dev.		
M. cowani	0.940382	13	0.128662		
M. dobsoni	0.904166	7	0.106674		
M. talazaci	0.955632	6	0.079853		
Oryzorictes	0.823550	8	0.086647		
Limnogale	1.010595	1	0.000000		
All Grps	0.911055	35	0.114527		
	{1}	{2}	{3}	{4}	{5}
	M=.94038	M=.90417	M=.95563	M=.82355	M=1.0106
M. cowani {1}		0.951741	0.998527	0.142476	0.969895
M. dobsoni {2}	0.951741		0.910961	0.608148	0.887012
M. talazaci {3}	0.998527	0.910961		0.186239	0.989543
Oryzorictes {4}	0.142476	0.608148	0.186239		0.491091
Limnogale {5}	0.969895	0.887012	0.989543	0.491091	

Genus	MDI	MDI	MDI
	Means	N	Std.Dev.
Echinops	0.267257	14	0.038967
Setifer	0.274344	12	0.042536
Tenrec	0.229875	11	0.040825
Hemicentetes	0.236369	17	0.032937
All Grps	0.251493	54	0.041763

{1}	{2}	{3}	{4}
M=.26726	M=.27434	M=.22988	M=.23637
Echinops {1}		0.965494	0.086923 0.129333
Setifer {2}	0.965494		0.037659 0.054249
Tenrec {3}	0.086923	0.037659	0.971797
Hemicentetes {4}	0.129333	0.054249	0.971797

Subfamily	MDI	MDI	MDI
	Means	N	Std.Dev.
Tenrecinae	0.251493	54	0.041763
Oryzorientinae	0.258535	35	0.037622
Geogalinae	0.249642	1	0.000000
Potamogalinae	0.190095	6	0.053301
Solenodontinae	0.241533	6	0.057797
Macroscelidinae	0.139349	6	0.016013
All Grps	0.243563	108	0.049895

	{1}	{2}	{3}	{4}	{5}	{6}
	M=.25149	M=.25853	M=.24964	M=.19009	M=.24153	M=.13935
Tenrecinae {1}		0.968957	1.000000	0.009885	0.993245	0.000121
Oryzorientinae {2}	0.968957		0.999945	0.003800	0.936569	0.000121
Geogalinae {3}	1.000000	0.999945		0.762343	0.999974	0.139523
Potamogalinae {4}	0.009885	0.003800	0.762343		0.263429	0.277622
Solenodontinae {5}	0.993245	0.936569	0.999974	0.263429		0.000656
Macroscelidinae {6}	0.000121	0.000121	0.139523	0.277622	0.000656	

Genus	ATDI	ATDI	ATDI
	Means	N	Std.Dev.
Echinops	1.176384	14	0.132542
Setifer	1.461058	12	0.250602
Tenrec	1.348775	11	0.290253
Hemicentetes	1.410957	17	0.187004
All Grps	1.348609	54	0.236095

	{1}	{2}	{3}	{4}
	M=1.1764	M=1.4611	M=1.3488	M=1.4110
Echinops {1}		0.008055	0.207105	0.020364
Setifer {2}	0.008055		0.599575	0.926346
Tenrec {3}	0.207105	0.599575		0.878093
Hemicentetes {4}	0.020364	0.926346	0.878093	

Genus	TCHI	TCHI	TCHI
	Means	N	Std.Dev.
Echinops	0.102117	8	0.022180
Setifer	0.242291	10	0.064536
Hemicentetes	0.215658	14	0.079389
Tenrec	0.164074	10	0.035901
All Grps	0.188090	42	0.076410

	{1}	{2}	{3}	{4}
	M=.10212	M=.24229	M=.21566	M=.16407
Echinops {1}		0.000236	0.000756	0.142863
Setifer {2}	0.000236		0.702943	0.027373
Hemicentetes {3}	0.000756	0.702943		0.173400
Tenrec {4}	0.142863	0.027373	0.173400	

Genus	MLCHI	MLCHI	MLCHI	
	Means	N	Std.Dev.	
Echinops	0.599529	8	0.372586	
Setifer	1.113827	10	0.582073	
Hemicentetes	0.834572	14	0.288145	
Tenrec	0.751319	10	0.131693	
All Grps	0.836469	42	0.399616	
	{1}	{2}	{3}	{4}
	M=.59953	M=1.1138	M=.83457	M=.75132
Echinops {1}		0.029098	0.491538	0.825103
Setifer {2}	0.029098		0.283020	0.147474
Hemicentetes {3}	0.491538	0.283020		0.948566
Tenrec {4}	0.825103	0.147474	0.948566	

Subfamily	TCMI	TCMI	TCMI	
	Means	N	Std.Dev.	
Tenrecinae	0.685917	42	0.167144	
Oryzorictinae	0.875250	34	0.309924	
All Grps	0.770619	76	0.257907	
	{1}	{2}		
	M=.68592	M=.87525		
Tenrecinae {1}		0.001217		
Oryzorictinae {2}	0.001217			

Subfamily	CLI	CLI	CLI	
	Means	N	Std.Dev.	
Tenrecinae	0.224635	40	0.028541	
Oryzorictinae	0.192126	31	0.024972	
All Grps	0.210441	71	0.031381	
	{1}	{2}		
	M=.22463	M=.19213		
Tenrecinae {1}		0.000115		
Oryzorictinae {2}	0.000115			

Subfamily	ACFI	ACFI	ACFI	
	Means	N	Std.Dev.	
Tenrecinae	0.783436	29	0.164695	
Oryzorictinae	1.336811	19	0.227456	
Geogalinae	1.378810	1	0.000000	
Potamogalinidae	0.513659	3	0.098199	
Solenodontinae	0.822253	4	0.104803	
Macroscelidinae	0.809740	5	0.118143	
All Grps	0.956992	61	0.325626	

	{1}	{2}	{3}	{4}	{5}	{6}
	M=.78344	M=1.3368	M=1.3788	M=.51366	M=.82225	M=.80974
Tenrecinae {1}		0.000137	0.023914	0.154426	0.998628	0.999684
Oryzorictinae {2}	0.000137		0.999921	0.000137	0.000177	0.000141
Geogalinae {3}	0.023914	0.999921		0.001693	0.081173	0.061034
Potamogalinidae {4}	0.154426	0.000137	0.001693		0.239294	0.235979
Solenodontinae {5}	0.998628	0.000177	0.081173	0.239294		0.999998
Macroscelidinae {6}	0.999684	0.000141	0.061034	0.235979	0.999998	

Genus	ANWI	ANWI	ANWI
	Means	N	Std.Dev.
Echinops	0.240276	8	0.016641
Setifer	0.233234	7	0.015857
Hemicentetes	0.253144	11	0.029885
Tenrec	0.261438	10	0.015806
All Grps	0.248717	36	0.023120

	{1}	{2}	{3}	{4}
	M=.24028	M=.23323	M=.25314	M=.26144
Echinops {1}		0.919523	0.572557	0.179233
Setifer {2}	0.919523		0.237628	0.053891
Hemicentetes {3}	0.572557	0.237628		0.811240
Tenrec {4}	0.179233	0.053891	0.811240	

Genus	ANWI	ANWI	ANWI
	Means	N	Std.Dev.
M. cow ani	0.267944	11	0.017231
M. dobsoni	0.272242	6	0.012220
M. talazaci	0.259872	5	0.011331
Oryzorictes	0.305734	5	0.023822
Limnogale	0.284783	1	0.000000
All Grps	0.274773	28	0.021988

	{1}	{2}	{3}	{4}	{5}
	M=.26794	M=.27224	M=.25987	M=.30573	M=.28478
M. cowani {1}		0.986225	0.897635	0.003187	0.870454
M. dobsoni {2}	0.986225		0.742878	0.024173	0.956535
M. talazaci {3}	0.897635	0.742878		0.002279	0.662413
Oryzorictes {4}	0.003187	0.024173	0.002279		0.785200
Limnogale {5}	0.870454	0.956535	0.662413	0.785200	

Subfamily	CACUI	CACUI	CACUI
	Means	N	Std.Dev.
Tenrecinae	1.364748	30	0.141852
Oryzorictinae	1.396046	14	0.192363
Geogalinae	1.295411	1	0.000000
Potamogalinidae	1.378686	4	0.043017
Solenodontinae	1.009544	5	0.117019
Macroscelidinae	0.985284	4	0.043475
All Grps	1.315278	58	0.197118

	{1}	{2}	{3}	{4}	{5}	{6}
	M=1.3647	M=1.3960	M=1.2954	M=1.3787	M=1.0095	M=.98528
Tenrecinae {1}		0.985961	0.997246	0.999976	0.000228	0.000294
Oryzorictinae {2}	0.985961		0.985599	0.999948	0.000215	0.000256
Geogalinae {3}	0.997246	0.985599		0.995828	0.493694	0.425055
Potamogalinae {4}	0.999976	0.999948	0.995828		0.006072	0.005364
Solenodontinae {5}	0.000228	0.000215	0.493694	0.006072		0.999883
Macroscelidinae {6}	0.000294	0.000256	0.425055	0.005364	0.999883	

Subfamily	PPPI Means	PPPI N	PPPI Std.Dev.
Tenrecinae	-0.041724	39	0.240201
Oryzorictinae	0.320557	31	0.151081
All Grps	0.118715	70	0.273041

	{1}	{2}
	M=-.0417	M=.32056
Tenrecinae {1}		0.000112
Oryzorictinae {2}	0.000112	

Genus	NPDI Means	NPDI N	NPDI Std.Dev.
Echinops	0.178504	9	0.050992
Setifer	0.116315	10	0.022541
Hemicentetes	0.150889	15	0.048188
Tenrec	0.096983	10	0.031718
All Grps	0.136429	44	0.049559

	{1}	{2}	{3}	{4}
	M=.17850	M=.11632	M=.15089	M=.09698
Echinops {1}		0.010407	0.389681	0.000661
Setifer {2}	0.010407		0.180470	0.717463
Hemicentetes {3}	0.389681	0.180470		0.012877
Tenrec {4}	0.000661	0.717463	0.012877	

Genus	MT3I Means	MT3I N	MT3I Std.Dev.
Echinops	0.129652	11	0.019197
Setifer	0.118004	10	0.015231
Hemicentetes	0.122892	15	0.021982
Tenrec	0.121927	10	0.011453
All Grps	0.123236	46	0.017928

	{1}	{2}	{3}	{4}
	M=.12965	M=.11800	M=.12289	M=.12193
Echinops {1}		0.461343	0.782433	0.762547
Setifer {2}	0.461343		0.910592	0.962003
Hemicentetes {3}	0.782433	0.910592		0.999249
Tenrec {4}	0.762547	0.962003	0.999249	

Genus	MT3I Means	MT3I N	MT3I Std.Dev.		
M. cowani	0.085401	13	0.007204		
M. dobsoni	0.068805	8	0.004347		
M. talazaci	0.076332	7	0.008452		
Oryzorictes	0.144886	9	0.016538		
Limnogale	0.093181	1	0.000000		
All Grps	0.094530	38	0.030708		
	{1}	{2}	{3}	{4}	{5}
	M=.08540	M=.06880	M=.07633	M=.14489	M=.09318
M. cowani {1}		0.007514	0.330232	0.000129	0.945048
M. dobsoni {2}	0.007514		0.607941	0.000129	0.179173
M. talazaci {3}	0.330232	0.607941		0.000129	0.533000
Oryzorictes {4}	0.000129	0.000129	0.000129		0.000381
Limnogale {5}	0.945048	0.179173	0.533000	0.000381	

Subfamily	MT3I Means	MT3I N	MT3I Std.Dev.		
Tenrecinae	0.123236	46	0.017928		
Oryzorictinae	0.094530	38	0.030708		
All Grps	0.110250	84	0.028306		
	{1}	{2}			
	M=.12324	M=.09453			
Tenrecinae {1}		0.000116			
Oryzorictinae {2}	0.000116				

CHAPTER III

EVOLUTIONARY MORPHOLOGY OF THE TENRECOIDEA CARPAL COMPLEX

Introduction

The carpal region of the mammalian postcranium can be difficult to interpret both functionally and phylogenetically. Like all areas of the skeleton, it is evolutionarily constrained to some degree, and there is considerable variation within and between many studied eutherian and metatherian lower and higher level taxa that reflects a mix of both functional and phyletic attributes (e.g., Hopwood, 1945; Jenkins, 1981; Szalay, 1994; Hamrick, 1997; Stafford and Thorington, 1998; Thorington and Darrow, 2000; Argot, 2001; Sargis, 2002). The functional significance of carpal features and the presence, absence and/or fusion of carpal elements has been proposed, yet consistent convergences of form in relation to ecological differences between taxa are not as apparent as they are in other general regions of the postcranial skeleton such as the shoulder and elbow (Lehman, 1963; Jouffroy, Godinot, and Nakano, 1993; Rose, 1993; Argot, 2001; Sargis, 2002), or the tarsus (Gebo, 1993; Szalay, 1994; Salton and Szalay, 2004).

Difficulties in functional interpretation of carpal form have been attributed to several fundamental properties of the mammalian wrist. First, like the tarsus, the carpus is a weight-bearing region made up of small bones with multiple complex joint articulations and loading relationships. Unlike joint regions that involve fewer skeletal articular relationships such as the knee or hip, a slight change in shape of a single carpal (or tarsal) bone has potential impact on a number of interdependent skeletal elements with a

potential consequent impairment of locomotor function. Phyletic shape change may therefore be more conservative in the carpus (and tarsus) due to the constraints imposed on a multifaceted performing system. Consequently, carpal variation with notable behavioral correlation may be less prevalent (Swiderski, 1991; Szalay, 1994). Because of this functional constraint, bones of the wrist, as well as those of the ankle, are regarded as potentially important for resolving phylogenetic relationships of higher and lower level mammalian taxa (Court, 1994; Szalay, 1994; Luo et al., 2003; Salton and Szalay, 2004). As stated by Szalay (1994:89): “The more complex the articular relationships, the more they are going to be constrained by, and therefore reflect, phylogeny.”

Second, and unlike the tarsus, the carpus is employed for a range of positional behaviors, such as those involved with feeding, grooming, and habitat exploration, in addition to those primarily concerned with locomotion. Specific elements of carpal, as well as general forelimb form are therefore less directly attributable to particular locomotor regimes such as climbing, digging or swimming (Jenkins, 1981; Szalay, 1994; Argot, 2001).

The primary focus of this chapter is to explore the functional significance of variable elements in the tenrecoid wrist. Previous works have explained aspects of carpal form based on the specific positional behavior of a taxon, and these have served as solid foundations for this analysis (Hopwood, 1945; Yalden, 1966, 1970, 1971, 1972; Taylor, 1974; Gonyea, 1978; Jenkins, 1981; Hamrick, 1997; Stafford and Thorington, 1998; Godinot and Beard, 1993; Court, 1994; Szalay, 1994; Thorington, Darrow, and Betts, 1997; Hamrick, Simons, and Jungers, 2000; Argot, 2001; Sargis, 2002; Thorington and Darrow, 2000;). Such functional analyses of the tenrecoid and other mammalian carpal

elements are likely to prove valuable not only for a general understanding of the evolution of skeletal form, but also for interpreting positional behaviors of fossil taxa and the phylogenetic relationships of tenrecoids to other clades. A second focus of the study is to identify features of the tenrecoid carpus that may be of phylogenetic significance, which will be useful for resolving questions of intertenrecoid relationships.

Primary Carpal Joints

The primitive placentalian wrist includes an arrangement of eight carpal bones, and two carpal accessory bones (Fig. 3.1; see figure legend for differences in terminology). Three primary joint regions are recognized as sites of major wrist movement, although varying degrees of movement occur between all articulating carpal bones. The proximal carpal joint (PCJ) refers to the articulations between the radius and ulna proximally, and the scaphoid, lunate and cuneiform distally. The pisiform, generally considered as a carpal accessory (sesamoid) bone as opposed to a carpal bone, is also part of the PCJ, articulating between the ulna and the cuneiform on the ulnar side. Most flexion of the wrist occurs at the PCJ (Yalden, 1966). The greatest degree of movement at the PCJ in most mammals is in the plane of dorsiflexion, followed by supination/pronation, and radial and ulnar deviation. Those with relatively mobile wrists, e.g., most squirrels and primates, are able to circumduct the wrist to varying degrees (Thorington and Darrow, 2000). The midcarpal joint (MCJ) refers to the articulations between the scaphoid, centrale, lunate and cuneiform proximally, and the trapezium, trapezoid, magnum, and unciform distally. The prepollex is part of the MCJ and hangs radially and palmarly between the scaphoid and trapezium. In tree squirrels and ground

squirrels, there appear to be equal degrees of movement at the PCJ and MCJ, as well as slight movement between the scapholunate and cuneiform during pronation and supination (Thorington and Darrow, 2000). In brachiating primates, most movement occurs at the MCJ during arm swinging (Jenkins, 1981). The carpometacarpal joint (CMJ) refers to the trapezium, trapezoid, magnum and unciform proximally, and the metacarpals I-V distally. There is relatively less movement at the CMJ, and Thorington and Darrow (2000) found less variation in articular morphology at the CMJ than the other two major joints.

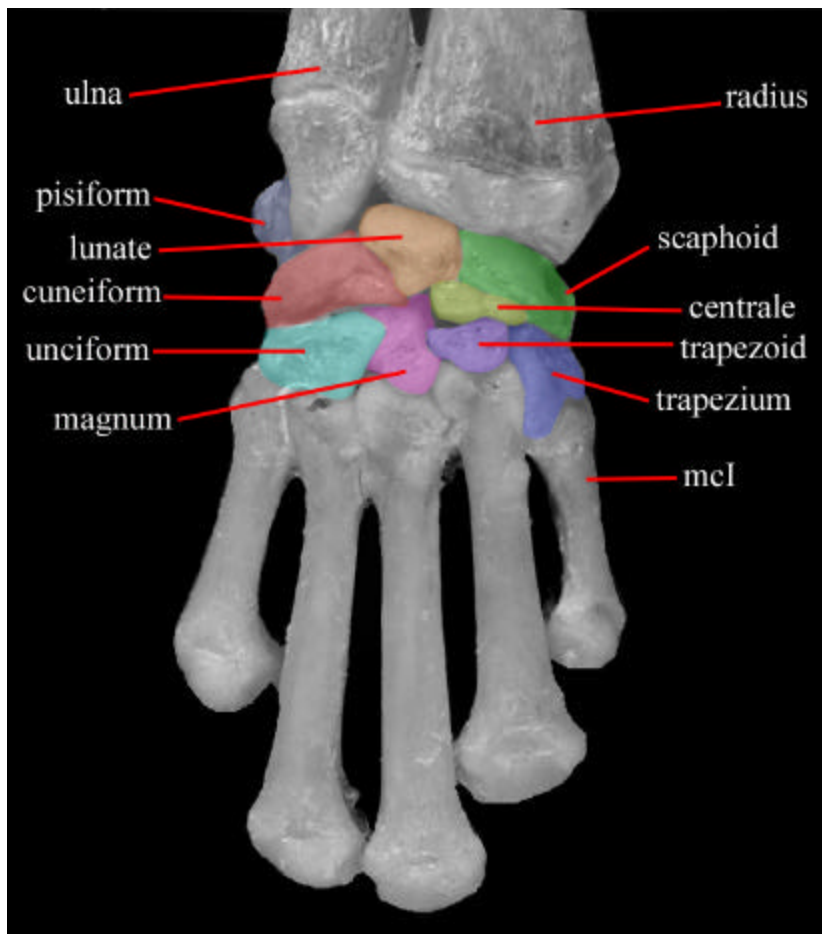


Figure 3.1. Dorsal aspect of the right carpus, *Setifer setosus* (FMNH 169731), illustrating the general placentalian arrangement of carpal bones. **Cuneiform**=Triquetrum, Pyramidal, Triangular; **Trapezium**=Greater Multangular; **Trapezoid**=Lesser Multangular; **Magnum**=Capitate; **Unciform**=Hamate; **Pisiform**=Accessory Carpal; **Prepollex** (not shown, on the lateral palmar surface between the scaphoid and trapezium)=Falciform.

Much of the described variation in mammalian carpal bones does not have obvious functional or phylogenetic significance. It might therefore be concluded that the wrist is not a particularly informative region for functional and/or phylogenetic interpretation. There is a small compilation of carpal characteristics with proposed functional significance that has been relatively well tested within at least a single taxon, and for which there is little conflicting evidence within or between taxa (see Table 3.1); for example, tree-climbing mammals (i.e., felids, primates, and sciurids) tend to have greater curvature of the proximal carpal articular surfaces as opposed to the flatter PCJ surfaces of terrestrial species (Gonyea, 1978; Hamrick et al., 2000; Thorington and Darrow, 2000), and the centrale tends to expand ulnarly in some arboreal tupaiids capable of grasping (Stafford and Thorington, 1998; Sargis, 2002).

There are two major recurring, unresolved issues regarding the functional significance of carpal features. First: what is the significance of fusion between the scaphoid, centrale, and lunate? These three bones are often fused, forming the scaphocentralunate (as in chiropterans), or else the scaphoid and lunate are fused, forming the scapholunate, and the centrale is present (as in scandentians) or lost. Alternatively, the scaphoid and centrale are fused to form the scaphocentrale (as in *Dromiciops*, see Szalay and Trofimov, 1996) and the lunate remains free. (see Table 3.2). (As noted by Thorington and Darrow, the terms “fused” and “lost” are often used in association with the scapholunate and scaphocentralunate, but these terms are usually assumptions, not based on developmental data that demonstrate whether specific elements are actually fused or lost). The question of whether these fusions and/or losses are of functional and/or phylogenetic significance is often raised, but has not been well

tested. Second: is the size and shape of the pisiform and/or prepollex indicative of function? These accessory bones are a consistent presence in the carpus of most mammalian taxa, and there is obvious variation in the size and shape of these bones within and between taxa. The functional significance of pisiform and prepollex morphology has often been proposed, but specific hypotheses have not been well tested.

This study addresses the following specific questions:

- 1) Are aspects of carpal morphology with proposed locomotor functional significance in other mammals found in tenrecoid locomotor specialists? Specifically, do the arboreal *Echinops*, the semi-fossorial *Hemicentetes*, the fossorial *Oryzorictes*, the swimming *Limnogale* and *Potamogale* and the generalized (in an ecological sense) terrestrial tenrecoids show carpal features that can be correlated with their primary locomotor behaviors?
- 2) Do carpal characteristics with unresolved significance such as an elongate pisiform or fused scaphoid and lunate vary within Tenrecoidea and are there patterns of morphology that corroborate previous functional hypotheses?
- 3) Do characteristics of tenrecoid carpal form appear to be distinctly “tenrecoid” when compared to non-tenrecoid taxa with proposed phylogenetic affinity to Tenrecoidea?
- 4) Within Tenrecoidea, are there carpal features that support subfamilial associations that comply with or contradict proposed evolutionary relationships?

Table 3.1. Aspects of the Mammalian Carpus with Proposed Functional Significance

	arboreal	fossorial	terrestrial
General Features ^{1,2,16}	short carpals long hand	short carpals short hand	long carpals short hand
Proximal Carpal Joint			
General ³	curved articular surfaces		less curved articular surfaces
Radius/Ulna ⁴	unfused		distally fused
Radial dorsal distal surface ⁵	less grooved		deeply grooved
Radius distal surface ^{5,6}	deep	cylindrical	broad and shallow
Radius distal dorsal surface ⁷	no pseudostyloid process	pseudostyloid process	no pseudostyloid process
Radial facet (art w. ulna) ⁵	well-defined		not well-defined
Radioulnar distal surface ²	mediolaterally wide	mediolaterally wide	less wide
Ulnar distal surface ^{5,8}	stout, well developed articular surface		slender, not well developed articular surface
Ulnar distal surface ⁹	rounded	mediolateral elongation	mediolateral elongation
Ulnocarpal articulation ^{6, 10}	mortar pestle	cylindrical	less convex/concave
Ulnar head ^{9,10}	distally short		distally elongated
Distal lateral ulna ¹¹	well-developed groove for extensor carpi ulnaris tendon		less well-developed groove
Styliiform process of ulna ³	spherical		convex, columnar
Joint curvature ³	curved		flat
Pisiform ^{1,2}	long	long	short
Pisiform ^{8,10,11,12}	short, less robust	long	long, robust
Pisiform ³	articulated with either ulna or cuneiform	articulated with both ulna and cuneiform	articulated with both ulna and cuneiform
Pisiform ^{3,10}	short articulation with cuneiform	elongate articulation with cuneiform	elongate articulation with cuneiform
Pisiform ¹²	interposed between cuneiform/ulna		less interposed bet. cuneiform/ulna
Pisiform ¹²	ulnarly directed		
Lunate-Scaphoid transition ⁵	hemispherical to flat		lunate forms a transverse ridge
Scaphoid-Lunate fusion ^{13,15,18}	unfused		fused
Scaphoid-Lunate fusion ¹⁴	fused		fused
Scaphoid proximal facet ^{2,11}	radioulnarly wide		dorsopalmarly high

	arboreal	fossorial	terrestrial
Mid-Carpal Joint			
Unciform ⁸	large		small
Unciform ²	radial expansion to centrale		no radial expansion
Unciform ¹⁰	ulnarly directed cuneiform facet		distally directed cuneiform facet
Unciform ¹⁰	dorsal extension of the cuneiform facet		no dorsal extension
Centrale (when present) ^{13,14}	ulnar expansion		no ulnar expansion
Centrale-Unciform ⁸	contact		no contact
Scaphoid tubercle ⁸	elongate		not as elongated
Unciform hamulus ⁸	elongate		not as elongated
Carpal arch ⁸	deep	shallow	shallow
Magnum ¹³	does not contact proximal carpal row		contacts proximal carpals
Magnum head ²	dorsopalmar extension		dorsopalmar reduction
Trapezium ¹⁴	large		not as large
Carpometacarpal Joint			
Proximal mCI surface ¹²	large		not as large
Metacarpals	² dorsal extension of distal articular facet		less dorsal extension
	^{2,19} short relative to phalanges		longer relative to climbing taxa
	² increasing robusticity from mcII to mcV		no increasing robusticity
	² relatively long mcIV		mcIV not relatively long
	² large heads and bases		less pronounced heads/bases
	¹¹ robust mCI		less robust mCI
	¹¹ mCI dorsoventral compression		
	¹² “waisted” and spaced apart		not waisted and narrowly spaced
Phalanges		¹ bony stops preventing	
	^{2,11,16} curved	curved	hyperextension
	^{2,10,12} long, narrow		straight
Claws/Unguals ^{12,14,15,17}	short, deep	long, shallow	short, stout
			long, shallow

¹ Hildebrand, 1995; ² Godinot and Beard, 1993; ³ Thorington and Darrow, 2000; ⁴ Court, 1994; ⁵ Hopwood, 1945; ⁶ Yalden, 1966; ⁷ Lehman, 1963; ⁸ Hamrick, 1997; ⁹ Swiderski, 1991; ¹⁰ Hamrick et al., 2000; ¹¹ Argot, 2001; ¹² Taylor, 1974; ¹³ Stafford and Thorington, 1998; ¹⁴ Sargis, 2002; ¹⁵ Forster, 1932; ¹⁶ Luo et al., 2003; ¹⁷ Martin, 1984; ¹⁸ Yalden, 1970; ¹⁹ Hamrick, 2001.

Table 3.2. Condition of the Proximal Carpal Row in Mammalian Taxa

	<u>separate scaphoid, lunate, centrale</u>	<u>no centrale</u>	<u>scapholunate</u>	<u>scaphocentralunate</u>	<u>scaphocentrale</u>
stem eutherian ¹	stem metatherian ¹			<i>Dromiciops</i> ⁸	
bathyergids and ctenodactylid rodents ²		most Recent rodents ²			
Eocene squirrel ²		Recent squirrels ²			
		carnivorans ⁵			
most shrews ³		<i>Sorex</i> ⁵	<i>Blarina</i> and <i>Cryptotis</i> ³		
<i>Talpa</i> ⁷			chiropterans ^{4,6}		
			dermopterans ^{4,6}		
<i>Dendrogale</i> and <i>Ptilocercus</i> ⁴		most scandentians ⁴			
		all scandentians ⁶			

¹ Szalay, 1994; ² Thorington and Darrow, 2000; ³ Swiderski, 1991; ⁴ Stafford and Thorington, 1998; ⁵ Yalden, 1970; ⁶ Sargis, 2002; ⁷ Yalden, 1966; ⁸ Szalay and Trofimov, 1996.

Materials and Methods

The antebrachium, carpals, metacarpals and phalanges from 131 specimens were studied and digitally photographed (Nikon Coolpix 995) from several standardized perspectives. Skeletal specimens were photographed from collections at the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Harvard Museum of Comparative Zoology (MCZ), and United States National Museum of Natural History (USNM) (see Appendix I for specimen list). Two *Echinops* specimens were borrowed from H. Kuenzle's laboratory at the University of Munich (UMUN), Germany, and a *Hemicentetes* and *Tenrec* specimen were borrowed from the University of Darmstadt, Germany (DARM) (Table 3.2). Digital image files were written into TPSdig (Version 1.31, 2001 F.J. Rohlf), which allows for superimposition of landmarks (x,y coordinates) onto images, and calibration of image scale from a mm ruler. Twenty-five linear measurements were then calculated from desired coordinates (Figs. 3.2-3.4). Measurements included those that incorporate features with proposed functional and/or phylogenetic significance (see Tables 3.1, 3.4). Precision of digital measurements was tested against fine-point caliper measurements from 3 complete specimens, and there were no significant differences between caliper and digital values ($p < 0.05$). In order to control for size differences between species, linear measurements were transformed to 31 index variables (Table 3.5). Statistical analyses (one-way ANOVAs and Tukey honest significance (HSD) post-hoc tests) were performed using STATISTICA (Version 6.0, StatSoft Inc). Significance values reported in the text for two-group comparisons refer to Tukey post-hoc results; those for more than two groups refer to ANOVAs.

It is particularly difficult to accrue large sample sizes for studies on the carpal skeleton. Many museum specimens with postcranial material are missing hands and feet, usually because they are left inside the prepared skin. In many cases it is difficult or impossible to discern boundaries of individual carpals because of overlapping dried tendon and ligament. Sample sizes in this study are therefore small. For *Geogale*, only a single decent specimen was available for complete study, and for others, a few specimens were available for examination, but only one or two were well-enough exposed for accurate measurement. The following tenrecoid species were studied: *Echinops telfairi*, *Setifer setosus*, *Hemicentetes semispinosus*, *Tenrec ecaudatus*, *Microgale cowani*, *M. dobsoni*, *M. talazaci*, *Oryzorictes tetradactylus* (or *O. hova*), *Limnogale mergulus*, *Geogale aurita*, and *Potamogale velox* (see Table 3.3).

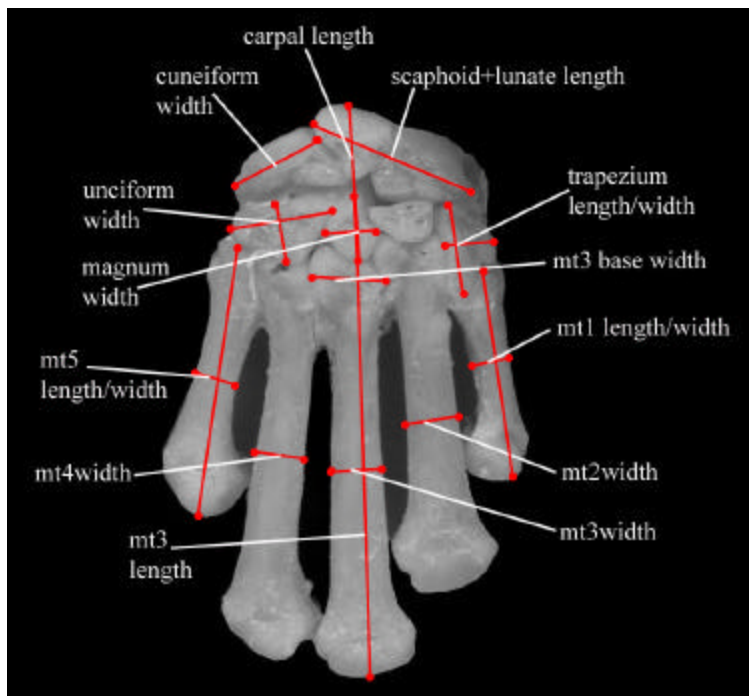


Figure 3.2. Linear measurements taken from the carpals and metacarpals (right hand, dorsal view). (Not shown: width and length measurements from the proximal, middle and distal phalanx of digit III).

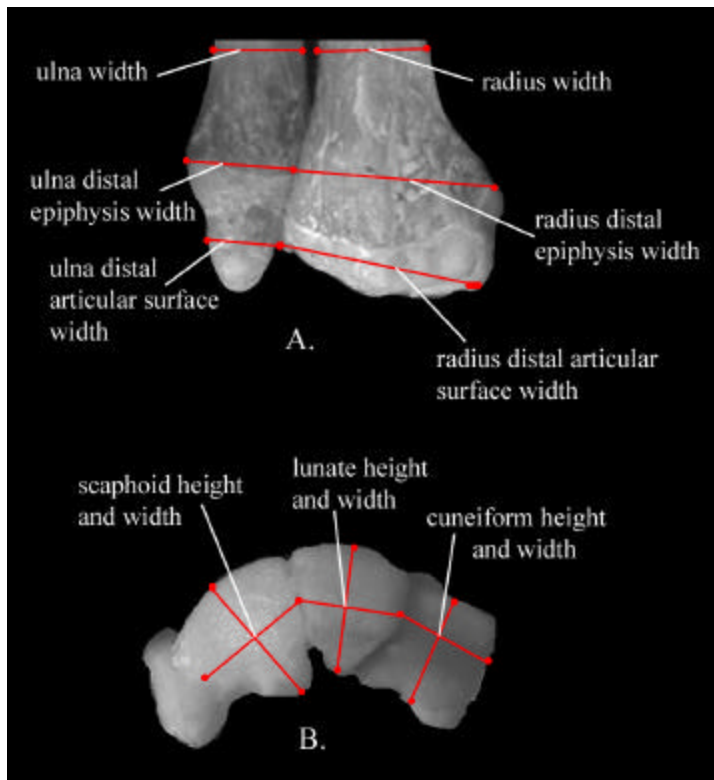


Figure 3.3. Linear measurements taken from the distal ulna/radius (A) and proximal articular surface of the first carpal row (B) (right side).

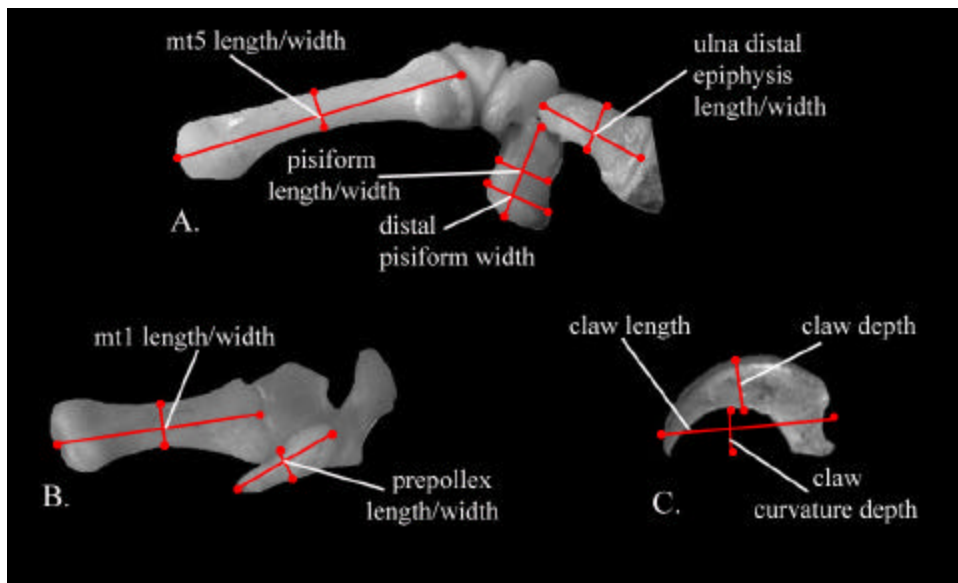


Figure 3.4. Linear measurements taken from the lateral (A) and medial (B) sides of the carpus, and the claw from the third digit (C).

There is no obvious outgroup for comparison with tenrecoids. Their closest relative is most likely Chrysochloridae (Stanhope et al., 1998), whose skeletal form is

highly derived, reflecting a subterranean lifestyle. Homology assessment between tenrecoids and chrysochlorids, therefore, is extremely difficult. Beyond chrysochlorids, it is still unclear whether tenrecoids are part of a lipotyphlan (Butler, 1988) or afrotherian (Springer et al., 1997) and/or zambododontoid (Van Valen, 1967) assemblage, though there is compelling molecular evidence for an afrotherian superorder, including tenrecoids (Springer et al., 2004). I have therefore included the following species for comparison (orders according to Springer et al., 2004): *Solenodon paradoxus* (Eulipotyphla), *Petrodromus tetradactylus* (Macroscelidea), and *Hemiechinus auritus* (Eulipotyphla). *Solenodon* was included as a representative “zambododontoid”, *Petrodromus* and *Elephantulus* as “afrosoricoids” and *Hemiechinus* as a “eulipotyphlan” (see Table 3.3).

Most hypotheses regarding carpal functional morphology refer to differences between climbing and non-climbing mammals, and several refer to diggers vs. non-diggers. I therefore focus primarily on the tenrecine subfamily, which includes the climbing species *Echinops telfairi*, the primarily terrestrial *Setifer setosus*, which is *Echinops*’ closest relative (Olson and Goodman, 2003), the digging *Hemicentetes*, and the primarily terrestrial *Tenrec*. When testing functional hypotheses about digging behavior, I also refer to the fossorial genus *Oryzorictes* in contrast to the other oryzorictines, *Microgale cowani*, *M. dobsoni*, *M. talazaci*, and *Limnogale*. Unfortunately, there is very little *Limnogale* postcranial material. When *Limnogale* is omitted from analyses/discussions on oryzorictine morphology, it is because there was no material available for study. The phylogenetic relationship between *Geogale* and the other tenrecoids is uncertain (Asher, 1999; Olson and Goodman, 2003); many carpal characters

may be too variable *within* subfamilies to use as indicators for resolving geogalinid phylogenetic affiliations. When there are substantial differences between the tenrecines and oryzorictines that appear to have some phylogenetic basis (i.e. traits that are shared amongst members of the same subfamily, different between subfamilies, and independent of substrate-specific locomotor behavior), I use *Geogale* as well as *Potamogale* as tenrecoid comparisons, and *Solenodon*, *Hemiechinus* and *Petrodromus* as tenrecoid outgroups in an attempt to better understand evolutionary relationships among the study taxa.

TABLE 3.3. Taxonomy and Primary Locomotor Behavior of study taxa

Subfamily	Genus	Species	n	Locomotor Behavior
Tenrecidae/Tenrecinae	<i>Echinops</i>	<i>telfairi</i>	17	Arboreal/terrestrial
Tenrecidae/Tenrecinae	<i>Hemicentetes</i>	<i>semispinosus</i>	15	Terrestrial/fossorial
Tenrecidae/Tenrecinae	<i>Hemicentetes</i>	<i>nigriceps</i>	2	Terrestrial/fossorial
Tenrecidae/Tenrecinae	<i>Setifer</i>	<i>setosus</i>	16	Terrestrial
Tenrecidae/Tenrecinae	<i>Tenrec</i>	<i>ecaudatus</i>	12	Terrestrial
Tenrecidae/Oryzorictinae	<i>Limnogale</i>	<i>mergulus</i>	1	Aquatic/terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>cowani</i>	15	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>dobsoni</i>	10	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>talazaci</i>	5	Terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>hova</i>	6	Fossorial/terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>tetradactylus</i>	2	Fossorial/terrestrial
Tenrecidae/Geogalinae	<i>Geogale</i>	<i>aurita</i>	2	Terrestrial
Potamogalidae	<i>Potamogale</i>	<i>velox</i>	10	Aquatic/terrestrial
Macroscelididae	<i>Petrodromus</i>	<i>tetradactylus</i>	4	Terrestrial/saltatory
Solenodontidae	<i>Solenodon</i>	<i>paradoxus</i>	10	Terrestrial/fossorial
Erinaceidae	<i>Hemiechinus</i>	<i>auritus</i>	4	Terrestrial/some digging

Table 3.4. Measurements (see Appendix 3.1 and 3.2)

- Dorsal1** *Cuneiform mediolateral width*: from dorsal view of carpals, mediolateral width at articular surface.
- Dorsal2** *Magnum mediolateral width*: from dorsal view of carpals, mediolateral width of magnum, along midpoint of bone, perpendicular to magnum length.
- Dorsal3** *Magnum proximodistal length*: from dorsal view of carpals, distance from proximal magnum to distal magnum, along midpoint of bone, perpendicular to magnum width.
- Dorsal4** *Metacarpal II mediolateral width*: from dorsal view of mcII, mediolateral width at midpoint, perpendicular to long axis of bone.
- Dorsal5** *Metacarpal III length*: from dorsal view of mcIII, distance from proximalmost mcIII to distalmost mcIII along midline of bone.
- Dorsal6** *Metacarpal III mediolateral width*: from dorsal view of mcIII, mediolateral width at midpoint, perpendicular to long axis of bone.

- Dorsal7** Metacarpal IV mediolateral width: from dorsal view of mcIV, mediolateral width at midpoint, perpendicular to long axis of bone.
- Dorsal8** Metacarpal V mediolateral width: from dorsal view of mcV, mediolateral width at midpoint, perpendicular to long axis of bone.
- Dorsal9** Mid-phalanx III length: from dorsal view of mid-phalanx III, distance from proximalmost to distalmost mid-phalanx III along midline of bone.
- Dorsal10** Proximodistal (anteroposterior) length of carpals: from dorsal view of carpals, distance from proximal articular surface of carpals to proximal surface of mcIII, along axis of mcIII.
- Dorsal11** Proximal phalanx III length: from dorsal view of proximal phalanx III, distance from proximalmost to distalmost proximal phalanx III along midline of bone.
- Dorsal12** Scaphoid+Lunate width: from dorsal view of carpals, distance from medial point of scaphoid to lateral point of lunate (or scapholunate), along approximate midpoint of bones.
- Dorsal13** Unciform mediolateral width: from dorsal view of carpals, mediolateral width of unciform, along midpoint of bone, perpendicular to unciform length.
- Dorsal14** Unciform proximodistal length: from dorsal view of carpals, distance from proximal unciform to distal unciform, along midpoint of bone, perpendicular to unciform width.
- Lateral1** Distal ulna epiphysis anteroposterior width: from lateral view of ulna and hand, from anterior to posterior surface at midpoint of ulnar distal epiphysis.
- Lateral2** Pisiform dorsopalmar (proximodistal) length: from lateral view of hand, distance from proximal midpoint of pisiform to distal midpoint of pisiform.
- Lateral3** Pisiform anteroposterior width: from lateral view of hand, distance from anterior to posterior pisiform at midpoint, perpendicular to long pisiform length.
- Medial1** Metacarpal I mediolateral width: from dorsal view of mCI or medial view of hand, mediolateral width at midpoint, perpendicular to long axis of bone.
- Medial2** Metacarpal I proximodistal length: from dorsal view of mCI or medial view of hand, distance from proximal mCI to distal mCI along midline of bone.
- Medial3** **Prepollux dorsopalmar length: from medial view of hand, distance from dorsal (proximal) to palmar (distal) points of prepollux along midline of bone.**
- Medial4** Prepollux anteroposterior width: from medial view of hand, anteroposterior width of prepollux at midpoint of bone, perpendicular to prepollux length.
- Forearm1** Radius distal epiphysis mediolateral width: from anterior view of radius, mediolateral width at widest point of distal epiphysis, perpendicular to long axis of bone.
- Forearm2** Radius distal shaft width: from anterior view of radius, mediolateral width at narrowest point of distal third of radius.
- Forearm3** Ulna distal epiphysis mediolateral width: from anterior view of ulna, maximum mediolateral width of ulna distal epiphysis.
- Forearm4** Ulna distal shaft mediolateral width: from anterior view of ulna, mediolateral width of ulnar shaft at minimum width of ulna distal 1/3^d.

Table 3.5. Indices (see Appendix 3.3 and 3.4)

CMI	Carpals -Metacarpals Index = Anteroposterior carpal length/metacarpal III length
CSI	Centrale Shape Index = Centrale mediolateral width/centrale anteroposterior length
HLI	Hand Length Index = Carpal anteroposterior length/metacarpal III length + proximal phalanx III length + mid-phalanx III length
MRI	Metacarpal Robusticity Index = Metacarpal II+III mediolateral width/metacarpal IV+V mediolateral width
M1SI	Metacarpal I Shape Index = Metacarpal I length/metacarpal I width
M3SI	Metacarpal III Shape Index = Metacarpal III length/metacarpal III width
PSHI	Pisiform Shape Index = Pisiform dorsopalmar length/pisiform anteroposterior width
PPSI	Prepollux Shape Index = Prepollux dorsopalmar length/prepollux anteroposterior width
PSI	Pisiform Size Index = Pisiform dorsopalmar length/distal ulna anteroposterior width
RWI	Radius Width Index = distalmost radial mediolateral width/radial distal epiphysis width
SLCI	Scaphoid-lunate Cuneiform Width Index = mediolateral width of the cuneiform/mediolateral width of the scaphoid + lunate

- UMSI** Unciform-Magnum Size Index = $\frac{\text{Unciform mediolateral length} + \text{anteroposterior width}}{\text{magnum mediolateral length} + \text{anteroposterior width}}$
- USI** Unciform Shape Index = $\frac{\text{Unciform mediolateral width}}{\text{unciform anteroposterior length}}$
- UWI** Ulna Width Index = $\frac{\text{distalmost ulna mediolateral width}}{\text{ulna distal epiphysis width}}$

Results and Discussion

Proximal Carpal Joint (PCJ)

The proximal carpal joint consists of articulations between the ulna and radius proximally, and the scaphoid, lunate, and cuneiform distally. Most dorsi- and palmar flexion occurs at the PCJ, as do most movements that deviate from the dorsopalmar plane. The distal arm and the proximal articular surfaces of the carpus are therefore particularly important indicators of positional behavior.

Distal fusion of the ulna and radius is an indicator of cursorial locomotion, e.g., in ungulates (Court, 1994; Hildebrand, 1995). Functionally, distal fusion of the ulna and radius restricts movement to flexion and extension in the parasagittal plane in runners, while decreasing the range of mobility. Of the species studied here, the elephant shrews, *Petrodromus* and *Elephantulus*, have a distally fused radius and ulna. In both, the distalmost lateral (ulnar) side of the ulna (the ulnar styloid process) is still present as a separate small piece of bone and serves to laterally brace the carpus, further stabilizing the PCJ and restricting movement to the dorsopalmar plane.

Hopwood (1945) found that the dorsal surface of the distal radius in the cheetah is more grooved (referring to grooves for passage of the extensor musculature; see Fig. 3.5) than in the less cursorial lion and tiger. Extensor musculature may be particularly well developed in cursors, which require rapid and complete hand recovery after the propulsive phase of running, where the hand is flexed. There are qualitative differences between the species studied in the general morphology of the dorsal surface of the distal

radius (see Figs. 3.6,3.9). There is, however, no measurable statistical difference in terms of the prominence of these grooves and their relation to locomotion.

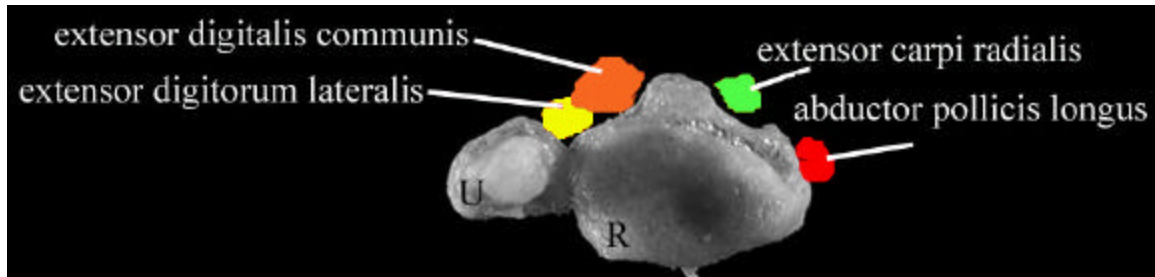


Figure 3.5. Distal articular surfaces of the left radius (R) and ulna (U) in *Echinops*. Colored areas are estimated positions of the tendons of the extensor musculature.

Within the Tenrecoidea, there is a difference between tenrecines and oryzorictines in the positioning of the radial dorsal ridges that define the positioning of the grooves for the extensor musculature. In tenrecines, the major ridge that divides the passage of the extensor carpi radialis radially and the extensor digitalis communis and digitorum lateralis ulnarly (Fig. 3.5) is positioned sagittally, at the dorsal midpoint of the radius. In contrast, the same ridge in oryzorictines is positioned at the ulnar edge of the radius. This subfamilial difference is most likely related to the position of the hand, which is more laterally splayed in tenrecines than in oryzorictines. Similar differences exist between tenrecine and oryzorictine foot morphology based on differential positioning of the foot relative to the crus (Salton and Szalay, 2004); like the hand, tenrecines have a more laterally splayed foot than oryzorictines (Salton and Szalay, 2004). *Geogale* is similar to the oryzorictines in having ulnarly-shifted grooves for the extensor musculature. Its resting hand posture is most likely similar to that of the oryzorictines despite its resting foot posture, which is more similar to the tenrecines (Salton and Szalay, 2004). Specialized locomotor behavior does not appear to affect the position of the extensor grooves, which suggests that hand posture is conservative, perhaps a phylogenetic

indicator. This would further suggest that the shared morphology of oryzorictine, geogaline and potamogalid hand posture is primitive for Tenrecoidea, as opposed to the more derived, laterally positioned hand of tenrecines.

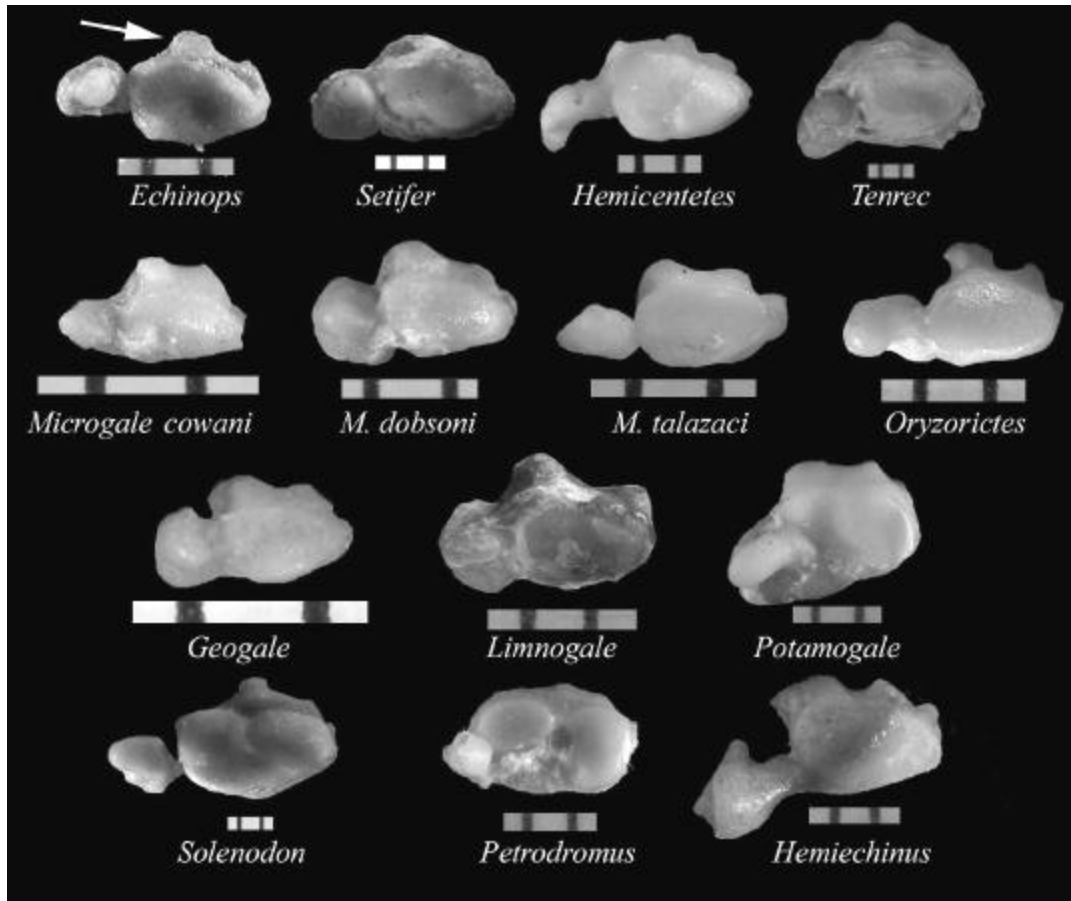


Figure 3.6. Distal articular surfaces of the left radius (right) and ulna (left) in tenrecines (top row), oryzorictines (second row + *Limnogale*), other tenrecoids (third row) and non-tenrecoids (bottom row). In tenrecines, the major radial dorsal ridge (arrow), which forms the main medial and lateral grooves for the extensor musculature, is at the dorsal midpoint of the radius. In oryzorictines, the ridge is shifted laterally. Both *Potamogale* and *Geogale* are similar to oryzorictines in this respect. See text for functional correlates. Differential radial and ulnar widths likely indicate differences in loading regimes.

Relative mediolateral width of the distal articular surface of the radius and ulna is indicative of locomotor behavior in some primates (Godinot and Beard, 1993), insectivorans (Yalden, 1966), and carnivorans (Hopwood, 1945). Climbers and diggers have a mediolaterally expanded distal antebrachium, which bears shifting ulnar and radial loads associated with climbing and digging (Godinot and Beard, 1993; Swiderski, 1991).

Cursors and ecologically generalized quadrupeds have a dorsopalmarly wider distal antebrachium (Hopwood, 1945), which bears the loads associated with movement along the axes of dorso- and palmarflexion. Within Tenrecoidea, the climber *Echinops* and the diggers *Hemicentetes* and *Oryzorictes* should therefore have mediolaterally wider distal forearms than the other species of their subfamilies. Yet, there are no statistically significant differences between any of the studied taxa in distal radius mediolateral width/dorsoplantar height (ANOVA for DARI, $p=0.56$) despite differences in scaphoid and lunate width and height (see below). Sample sizes for this index were extremely small because specimens with disarticulated and clear distal antebrachium articular surfaces are rare.

Another measurement of the distal antebrachium (RWI) with a larger sample size illustrates significant differences between tenrecine species (Fig. 3.7A, $p=0.00$). *Echinops* and *Hemicentetes* have mediolaterally expanded distal radii. This is consistent with mediolateral loading in these genera and movement that is more restricted to the dorsopalmar plane in *Setifer* and *Tenrec*. *Oryzorictes* has a mediolaterally expanded distal articular radial surface relative to other oryzorictines, though the difference is not significant (Fig. 3.7B, $p=0.12$).

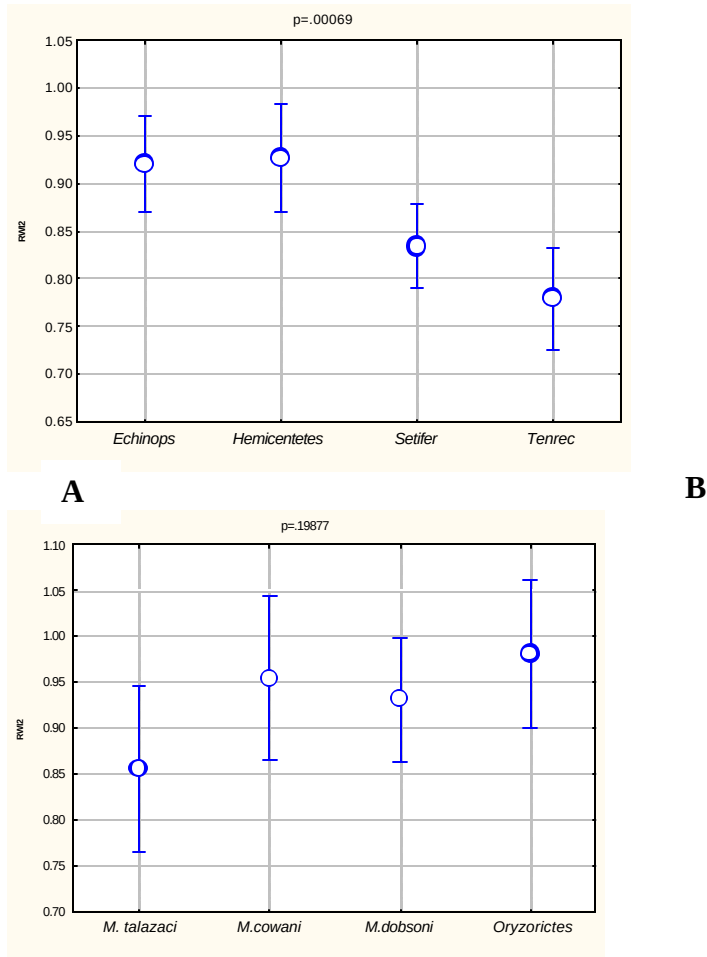


Figure 3.7. Means of Radial Width Index (RWI) in tenrecines (A) and oryzorictines (B).

In several eutherian taxa, the shape of the distal ulna correlates strongly with positional behavior (Hopwood, 1945; Yalden, 1966; Swiderski, 1991; Hamrick, 1997; Hamrick et al., 2000; Thorington and Darrow, 2000;). This is also the case for tenrecoids (Figs. 3.6, 3.9). The subterranean *Oryzorictes* has a wider distalmost surface of the ulna than any of the other tenrecoids (Fig. 3.8; ANOVA, $p=0.000$; Tukey HSD, $p<0.03$ for *Echinops*, *Hemicentetes* and *Setifer*, but not significant for others). Mediolateral extension of the ulnar head prevents carpal rotation and abduction (Swiderski, 1991), and most likely serves to withstand heavy loads from digging. There is considerable variation

in distal ulnar morphology within the tenrecines. Despite expectations that *Hemicentetes* would have a wider distal ulna than other tenrecines, *Hemicentetes* and *Echinops* have narrower articular surfaces of the ulna than *Setifer* and *Tenrec*. A closer look at the shape of the tenrecine distal ulna reveals that in the former two genera the distal ulna is pestle-like in form, vs. in the latter two genera, where the articular surface of the ulna is flatter. Mortar/pestle articular morphology is conducive to multiaxial movement, which is expected in the climbing *Echinops*, but not necessarily in *Hemicentetes*. *Hemicentetes* uses its hands for prey-capture, feeding and extensive grooming, in addition to digging (pers obs). Morphology of the distal antebrachium related to multiaxial movement may be related to these behaviors (which I did not see as much of in *Echinops* and *Setifer*, but I have not observed *Tenrec*). *Echinops* has a shorter (more spherical) articular surface of the ulna than *Setifer* (though the difference is not statistically significant at $p=0.25$), which is consistent with arboreal behavior.

There appears to be a subfamilial difference between tenrecines and oryzorictines in the distal elongation of the ulnar styloid process (Fig. 3.9). In tenrecines, the styloid process barely, if even, reaches beyond the distalmost surface of the radius. A short styloid process leaves the ulnar side of the wrist free, allowing for a greater degree of ulnar movement and eversion (Hamrick et al., 2000; Swiderski, 1991). In the oryzorictines, the ulnar styloid process is long (except in *Limnogale*), limiting ulnar movement and restricting the plane of movement to the dorsopalmar plane. This finding is consistent with a suite of other features that suggest a greater degree of manipulation (manifest in the carpus) in tenrecines than in oryzorictines. The single specimen of *Limnogale* has a short ulnar styloid process unlike the other oryzorictines, as well as an

expanded medial articular surface of the radius. Its distal antebrachium morphology indicates that this genus loads its wrist radially (perhaps it uses its hands as rudders while swimming), and has more mobile wrists than other oryzorictines, perhaps also for food capture and manipulation in an aquatic environment

Close to the distal end of the radius, on the ulnar side just above the epiphysis, there is a projection or tubercle (see *Oryzorictes*, Fig. 3.9) that represents the origin of attachment for the short radial collateral ligament. The ligament inserts on the radial and palmar surface of the scaphoid (Evans, 1993). In *Oryzorictes*, the tubercle is proximally positioned and enlarged, suggesting a very well stabilized articulation of the radial antebrachium and wrist that is resistant to radial forces from digging. The forelimb digger *Hemicentetes* also has a prominent medial expansion. The three *Microgale* species, *Potamogale* and *Petrodromus* have smooth medial surfaces of the distal radius vs. the broader medial sides of all other species studied.

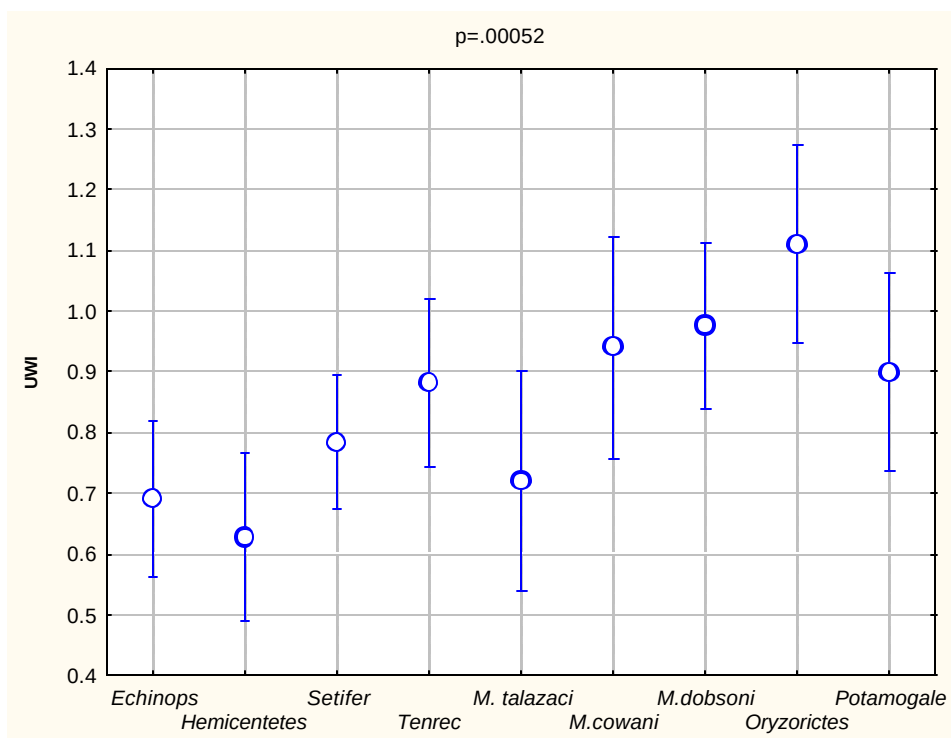


Figure 3.8. Means of Ulnar Width Index (UWI) in Tenrecoidea.

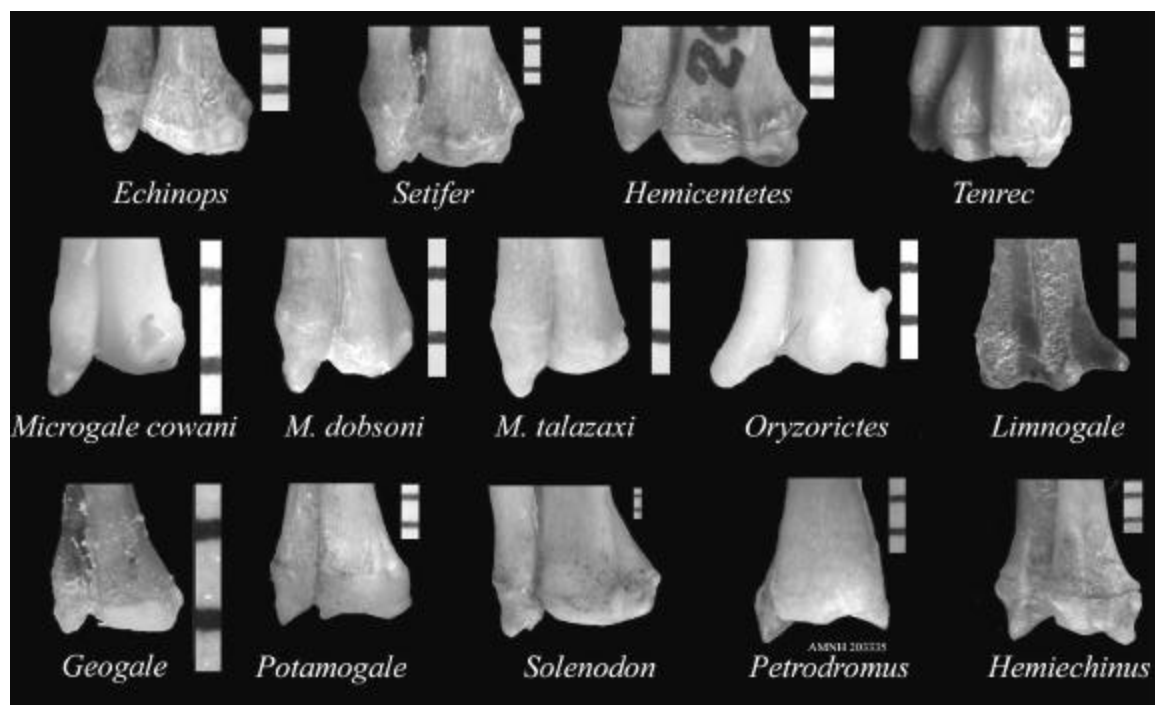


Figure 3.9. Distal antebrachium, dorsal surface, right side in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, two left) and non-tenrecoids (bottom row, three right). Note relatively wide distal forearms in the diggers *Hemidentetes* (of the tenrecines) and *Oryzorictes* (of the oryzorictines). The leaper *Petrodromus* has a fused distal ulna and radius, with the ulnar styloid process remaining for stabilization of movement in the dorsopalmar plane and lateral resistance. See text for further comparison.

The functional significance of the size and shape of the pisiform is unclear. The pisiform is the major insertion site for the *M. flexor carpi ulnaris*, which originates from the distal humerus (medial epicondyle) and proximal ulna and serves to flex the wrist with some abduction (Evans, 1993; Thorington and Stafford, 2001; Neveu and Gasc, 2002). The pisiform is also the origin for the *M. abductor digiti minimi*, which unites with the *M. flexor digiti minimi* and inserts on the ulnar sesamoid of metacarpal V and the proximal palmar surface of proximal phalanx V (Evans, 1993; Thorington and Stafford, 2001). Finally, the pisiform is an attachment site for the palmar ligaments (flexor retinaculum), which extend from the pisiform ulnarly to the styloid process of the radius and the radial palmar surface of the scaphoid and trapezium. Short ligaments may also extend from the distalmost aspect of the pisiform to the proximoulnar surfaces of metacarpals IV and V (Evans, 1993; Thorington and Stafford, 2001). A long pisiform may increase the torque of the carpal flexors, as these are particularly long in some eutherian diggers (Taylor, 1974; Hildebrand, 1995;). Yet a long pisiform would only directly impact the lever length of the inserting *M. flexor carpi ulnaris*. The tendons of the other major carpal flexors (*M. flexor digitorum superficialis* and *profundus*) do not pass over the pisiform, but run radial to it, passing under (*profundus*) and over (*superficialis*) the flexor retinaculum. A long pisiform may therefore indicate a deeper space for the passage of *M. flexor digitorum profundus*, increased torque for *M. flexor carpi ulnaris*, and/or a large attachment area for the flexor retinaculum for stabilization of the major carpal and digital flexors.

Diggers from several mammalian taxa have relatively long pisiform bones, most likely to accommodate powerful flexion for digging (Taylor, 1974; Godinot and Beard,

1993; Hildebrand, 1995; Hamrick, 1997; Hamrick et al., 2000; Argot, 2001). There is, however, disagreement as to whether climbers have long pisiform bones relative to a shorter pisiform in terrestrial cursors because of their reliance on strong carpal flexors for climbing (Hopwood, 1945; Godinot and Beard, 1993). Alternatively, the pisiform is relatively short in climbers, and longer in cursors, who rely on a powerful *M. flexor carpi ulnaris* for flexing the hand from an extended, fully loaded position while walking, running and/or bounding (Argot, 2001). It is also proposed that a relatively long pisiform is a primitive mammalian feature, and has been secondarily reduced in climbers (Godinot and Beard, 1993; Hamrick, 1997).

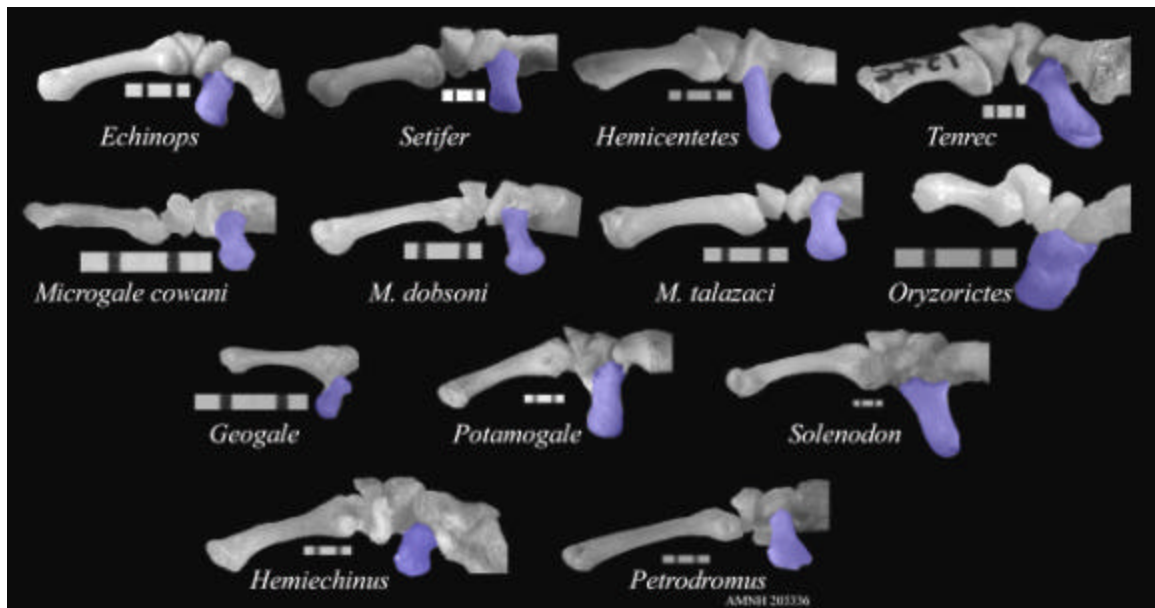


Figure 3.10. The left lateral side of the distal ulna, carpus and the first metacarpal, with the pisiform highlighted in blue. Top row: tenrecines; second row from top: oryzorictines; third row: other tenrecoids and *Solenodon*; bottom row: erinaceid (left) and macroselidid (right). Note the robust and squared pisiform and short mCI in *Oryzorictes* and the relatively short pisiforms in *Echinops* and *Setifer* compared to the other tenrecines.

There is no significant difference between tenrecoid subfamilies in pisiform length (as determined by the two pisiform shape indices). There is, however, a significant difference within the tenrecine subfamily (Fig. 3.10, top row). *Hemicentetes* has a

significantly longer pisiform than the other three tenrecines (Figs. 3.10, 3.11; $p=0.02$). For this taxon at least, a long pisiform appears to be functionally related to digging, whereas the climbing *Echinops* does not have a longer pisiform than the other three tenrecines (although the *Echinops* specimen in Fig. 3.10 has a relatively short pisiform compared to the other tenrecines, the difference is not significant when a larger sample size is included in comparisons). Although we would therefore expect *Oryzorictes* to have a lengthened pisiform relative to the other oryzorictines, it is not longer relative to the width of the distal ulna. Relative to the length of the rest of the hand, which is extremely short in *Oryzorictes*, the pisiform is effectively lengthened in terms of its function as an in-lever for the M. flexor carpi ulnaris when compared to the other oryzorictines. The pisiform of *Oryzorictes* is also much more massive, in terms of added length and width, than that of any other species examined (Fig. 3.10), providing a broad area of muscular attachment and longer lever arm for the M. flexor carpi ulnaris.

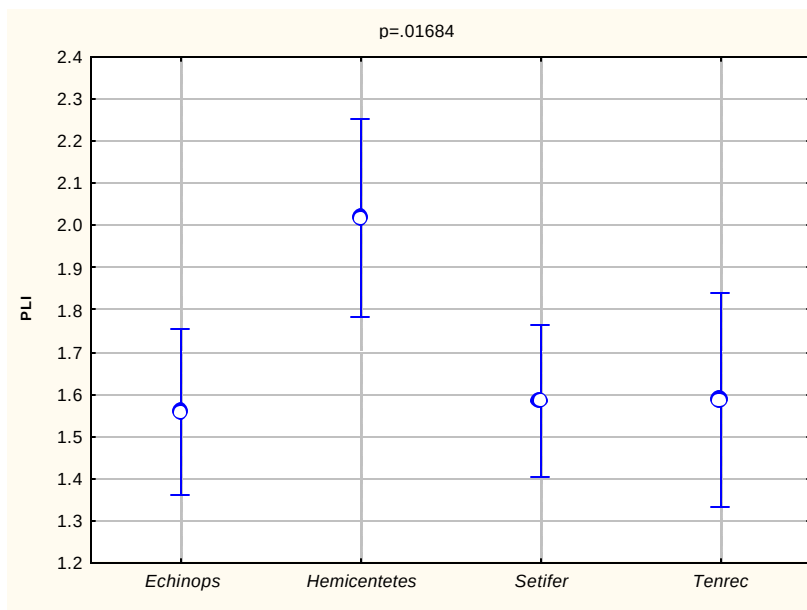


Figure 3.11. Means of Pisiform Length Index (PLI) in the Tenrecinae. The semi-fossorial *Hemicentetes* has a relatively long pisiform relative to ulnar width (see also Fig. 3.9).

The Pisiform Shape index (PSHI) demonstrates significant differences between tenrecoids in pisiform shape (Fig. 3.12), as well as discrepancies in predicted functional morphology. The oryzorictine digger *Oryzorictes* has the relatively stoutest pisiform, whereas the tenrecine digger *Hemicentetes* has the thinnest. Both are long relative to the rest of the hand, and therefore effectively lengthen the in-lever for the M. flexor carpi ulnaris, as predicted. The thickness of the pisiform in *Oryzorictes* vs. *Hemicentetes* may therefore be indicative of relatively hypertrophied muscles in the former requiring a larger area for attachment.

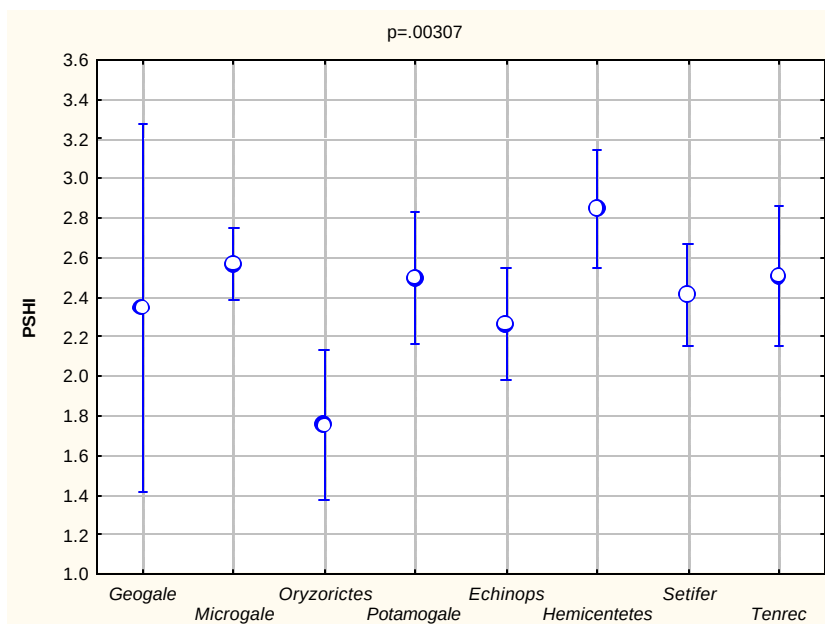


Figure 3.12. Means of Pisiform Shape Index (PSHI) in tenrecoids. Note extreme intergeneric variability in pisiform shape. *Hemicentetes* has the highest index value, indicating a long and narrow pisiform. *Oryzorictes*' pisiform shape values are the lowest; this is a product of its extreme width (see Fig. 3.9). The pisiform in *Oryzorictes* is actually long relative to its extremely short carpals and metacarpals.

The pisiform is posteriorly positioned against the ulna in climbers, allowing for more wrist mobility, as opposed to stabilized articulation with the ulna and cuneiform (Hamrick et al., 2000; Thorington and Darrow, 2000). Despite such hypothesized

difference in relative position of the pisiform between climbers and non-climbers, there appears to be no difference in the position of the pisiform relative to the ulna and cuneiform between *Echinops* and the non-climbing tenrecines, or between tenrecines and oryzorictines.

In primates and marsupials, a relatively wide proximal articular surface of the scaphoid may be indicative of a wider range of multiaxial motion, indicating some degree of arboreality (Godinot and Beard, 1993; Argot, 2001). Within the Tenrecinae, *Tenrec* appears to have the widest combined scaphoid/lunate width relative to dorsopalmar height (though not statistically significant and sample for each species is 2), whereas this measure of *Echinops* is in the same range as those of *Hemicentetes* and *Setifer* (Fig. 3.13, top row). The digger, *Oryzorictes*, has a deeper articular scapholunate surface (dorsopalmarly deep as opposed to mediolaterally wide) than any of the other tenrecoids, which is most likely related to the high loads of dorsopalmar extension and flexion during digging (Fig. 3.13; although, again, not significant; N=1 for *Oryzorictes*). This is a trait shared with *Potamogale* and macroscelidids, which also employ locomotor behaviors that incur high loads on the wrist from dorsopalmar extension and flexion. When the two diggers *Oryzorictes* and *Hemicentetes* are compared, there is again a trend showing more forelimb multiaxial mobility in *Hemicentetes* as compared with the more fossorial *Oryzorictes*.

The width of the proximal articular scaphoid-lunate relative to that of the cuneiform (Fig. 3.13) appears to be a functional indicator in tenrecoids. Within the Tenrecinae, *Echinops* has the greatest cuneiform proximal articular area relative to the scaphoid and lunate articular area (Fig. 3.14), which suggests lateral excursion of the

hand. This expansion provides a wide range of articular area for the cylindrical surface of the ulnar styloid process. The most terrestrial of the tenrecines, *Tenrec*, has the smallest cuneiform articular area, and relatively greatest scaphoid and lunate articular area. This makes sense in functional terms; *Tenrec* and *Setifer* are more terrestrial and therefore have a decreased reliance on ulnar expansion and potential mobility of the wrist, as opposed to *Echinops*. *Hemicentetes*' morphology is again inconsistent with that of *Oryzorictes*, showing a potentially greater degree of multiaxial movement. Relative to the other oryzorictines, *Oryzorictes* does not have a particularly widened or reduced articular surface of the cuneiform.

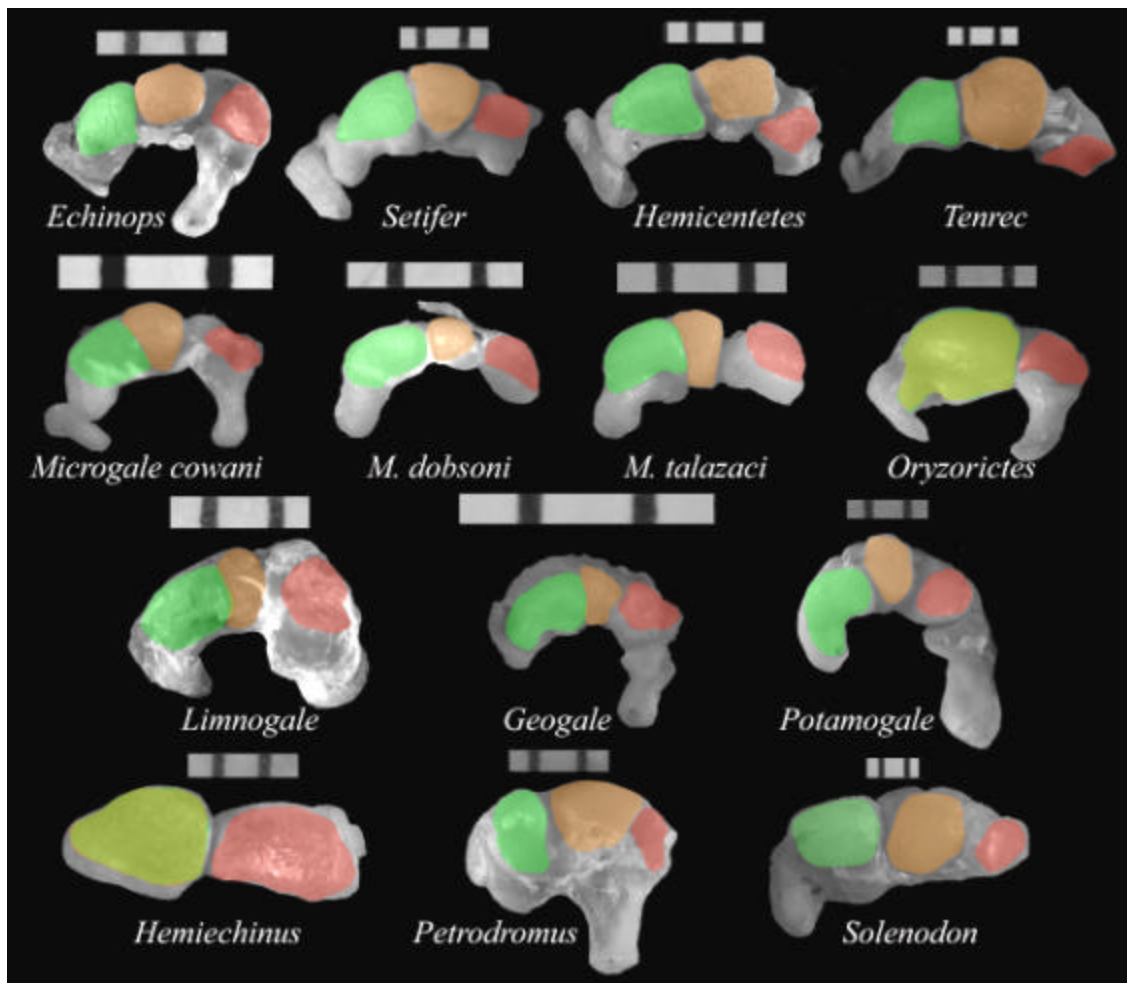


Figure 3.13. Proximal articular surfaces of the first carpal row, right side. Some specimens have an articulating pisiform and/or prepollex, whereas some have been disassociated. Note the particularly close articulation between the scaphoid and lunate in tenrecoids (top three rows) vs. non-tenrecoids (bottom row). The scaphoid and lunate are fused in *Oryzorictes* and *Hemiechinus*. The scaphoid is mediopalmarly curved in *Potamogale*, taking the place of its reduced prepollex. (green=scaphoid; orange=lunate; red=cuneiform; yellow=scapholunate).

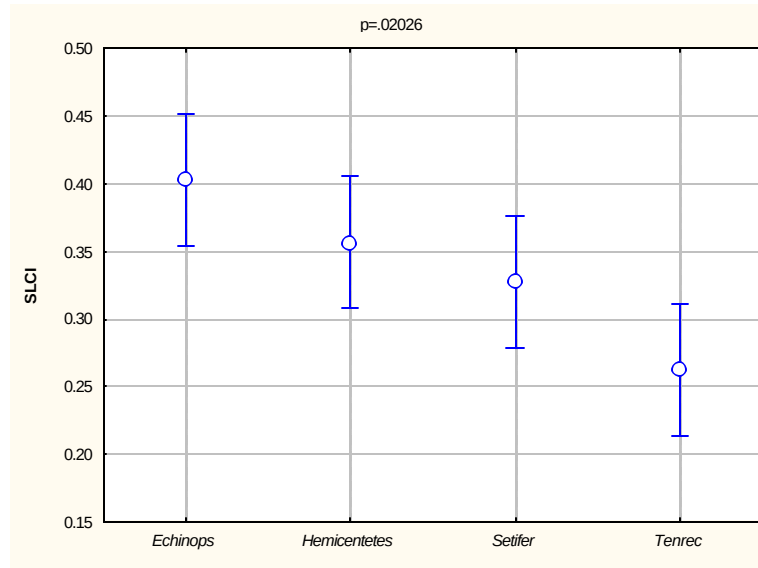


Figure 3.14. Scaphoid-lunate Cuneiform Width Index value means (SLCI) in the Tenrecinae. *Tenrec* has a mediolaterally narrow cuneiform articular surface relative to the others (Tukey HSD, $p < 0.02$), indicative of movement restricted to the sagittal plane. *Echinops* has an expanded cuneiform relative to the others (though not significantly different from *Hemicentetes* and *Setifer*).

The functional and/or phylogenetic significance of fusion between the scaphoid, lunate and centrale in mammals is unresolved. Within orders at least, there seems to be some consistency as to whether these bones are separate or fused, e.g., dermopterans and chiropterans all have a scaphocentralunate, scandentians have a scapholunate, as do most recent rodents (except for bathyergid and ctenodactylid rodents; see Table 3.2). The microbiotheriid marsupial *Dromiciops* has a fused scaphoid and centrale (scaphocentrale) (Szalay and Trofimov, 1996). Early eutherians had a separate scaphoid, lunate and centrale (Szalay 1994), and it remains unclear whether fusion of these elements in more recent taxa is indicative of restricted carpal mobility and/or increased stability for carpal loading. Yalden (1970), citing Forster (1932), suggested that the unfused condition in carnivorans allows for a greater degree of joint movement, and climbers would therefore be expected to retain the unfused condition for maximizing rotational hand movement. Within Scandentia, there is disagreement as to whether the scaphoid and lunate in

Ptilocercus, an arboreal scandentian, are fused into a single scapholunate. Stafford and Thorington (1998) report that they remain separate in *Ptilocercus*, which allows for increased manual mobility. Sargis (2002) noted that the scaphoid and lunate are fused in *Ptilocercus*, which may be related to incurring greater loads on the radial side of the wrist when the pollex is abducted

Patterns of fusion of the scaphoid, lunate and centrale in Tenrecoidea suggest that fusion is most likely functionally related to increased carpal loading. Of the tenrecoids studied, the two diggers, *Hemicentetes* and *Oryzorictes* both exhibit carpal fusion, as does *M. cowani* and *Potamogale* (Fig. 3.15). In *Hemicentetes*, the scaphoid and lunate remain separate, but the centrale is fused with the scaphoid; it is still possible to discern a slight groove between the scaphoid and centrale, but in all observed cases (N=14), fusion was complete. *Oryzorictes* has a single scaphocentralunate; fusion between the three bones is complete. Given the suite of other modifications found in *Oryzorictes* related to digging behavior, fusion of the scaphoid, centrale and lunate in this genus is most likely related to reduced mobility in the carpals, which incur heavy loads during forelimb scratch digging. Fusion of only the centrale in *Hemicentetes* is concordant with greater mobility of the proximal carpal joint relative to *Oryzorictes*. Within *Microgale*, one of the three examined species (*M. cowani*) has a fused centrale. In seven of the nine *M. cowani* specimens examined, fusion was complete, whereas in two specimens, fusion was incomplete. In all other *M. dobsoni* (N=10 with discernable scaphoid/centrale/lunate region) and *M. talazaci* (N=6) examined, the centrale remained distinct. According to previous studies, and as far as I have observed in live individuals, *M. cowani* does not exhibit specialized locomotor behavior that would account for fusion of the centrale, but

other characters (see below) suggest that *M. cowani* may incorporate digging into its locomotor repertoire more so than the other *Microgale* species examined.

Potamogale (N=9) also lacks a separate centrale, although it is most likely fused to the scaphoid. It is also possible that the centrale in *Potamogale* does not develop at all (see Fig. 3.15). In one *Potamogale* specimen, the scaphoid and lunate are partially fused. *Potamogale*'s swimming behavior may involve palmar push-off from the wrist that incurs high loads, similar to those of the diggers.

A shared characteristic within all of the Tenrecoidea, which is different from both *Solenodon* and the macroscelidids, is the close articulation between the scaphoid and lunate in the former, as opposed to the closer association between the lunate and cuneiform in the latter (Fig. 3.13). In tenrecoids, the scaphoid and lunate generally form a continuous articular surface at the proximal carpal joint, with a break between the lunate and cuneiform. The disjoint between the proximal articular edges of the lunate and cuneiform is particularly evident in tenrecines and *Potamogale* (Fig. 3.13). *Solenodon* and *Petrodromus* have a smooth proximal transition between the lunate and cuneiform, with a break between the lunate and scaphoid. In the erinaceid *Hemiechinus*, the massive scaphocentralunate is continuous with the cuneiform and shows no separation. This difference between tenrecoids and non-tenrecoids is also apparent at the distal articular surface of the radius; in the former, the division on the radius between the articular surfaces for the scaphoid and lunate is unclear, whereas the division in *Solenodon* and *Petrodromus* is marked (Fig. 3.6).

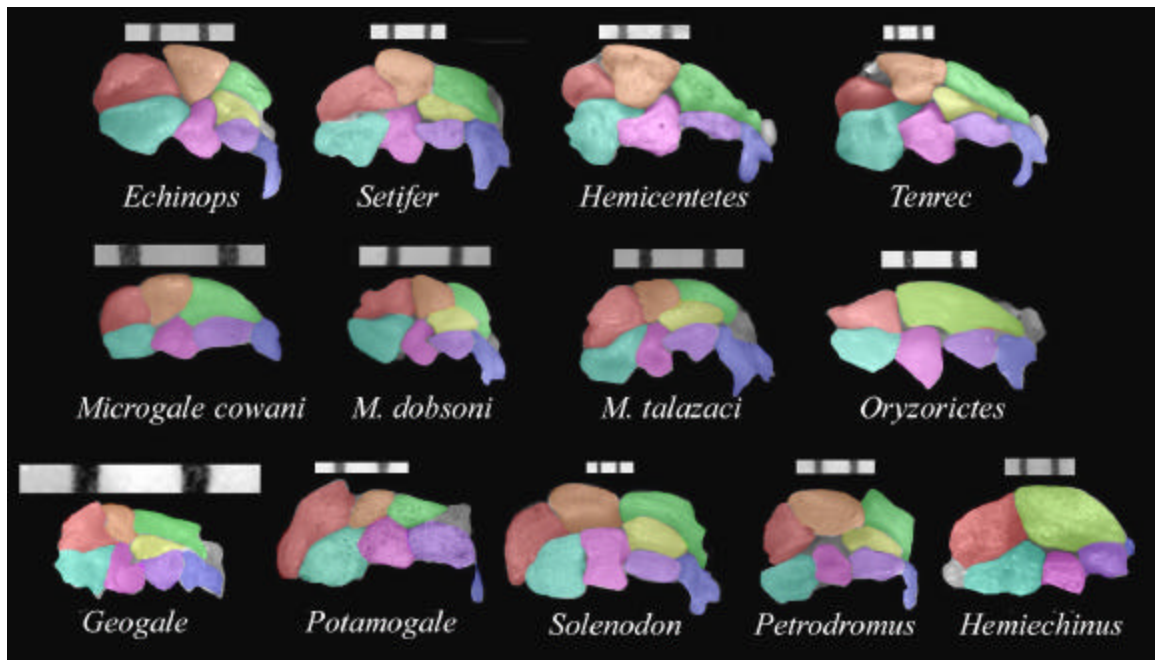


Figure 3.15. The carpal complex, right side, dorsal view, top is proximal, bottom is distal. Red: cuneiform; orange: lunate; green: scaphoid; yellow: centrale; blue: trapezium; purple: trapezoid; pink: magnum; turquoise: unciform. In *Oryzorictes* and *Hemiechinus*, the scaphoid, lunate and centrale are fused into a single bone. In *Hemicentetes*, *Microgale cowani*, and *Potamogale*, the centrale is most likely fused with the scaphoid. See text for comparisons.

Mid-Carpal Joint (MCJ)

An enlarged and mediolaterally wide unciform is found in more arboreal vs. terrestrial primates, and may be indicative of frequent ulnar deviation at the mid-carpal joint (Godinot and Beard, 1993; Hamrick, 1997; Hamrick, et al., 2000). Within the tenrecines, the climbing *Echinops* has a larger and mediolaterally wider unciform than the other tenrecines, which suggests that ulnar deviation associated with climbing in *Echinops* is more a function of the MCJ than the PCJ (Fig. 3.15, top row; Figs. 3.16, 3.17, $p=0.000$). Unciform size in *Echinops* is significantly different from that of *Hemicentetes* ($p=0.00$) and *Tenrec* ($p=0.03$), but not that of *Setifer* ($p=0.34$). Unciform mediolateral width in *Echinops* is significantly different from *Hemicentetes* and *Tenrec* ($p<0.00$ for both), but not from *Setifer* ($p=0.81$). *Setifer*'s relatively large unciform may

have been retained from an arboreal *Echinops/Setifer* common ancestor. An analysis of oryzorictine unciform size complicates the picture. *M. cowani* and *Oryzorictes* have significantly smaller unciforms than *M. dobsoni* and *M. talazaci* ($p=0.00$), and *Geogale* falls within the range of *M. cowani* and *Oryzorictes*. There is no obvious functional interpretation for these differences, but it is consistent with recurring differences in form between *M. cowani* and the other two *Microgale* species, and some similarities between *M. cowani* and *Oryzorictes* (e.g., missing centrale, pisiform shape, unciform size, distal ulna shape, claw shape). These similarities might be explained by a better understanding of *M. cowani* locomotor behavior. There is no significant difference among oryzorictines in unciform mediolateral width ($p=0.31$), though *Oryzorictes* has a wider unciform than the other oryzorictines.

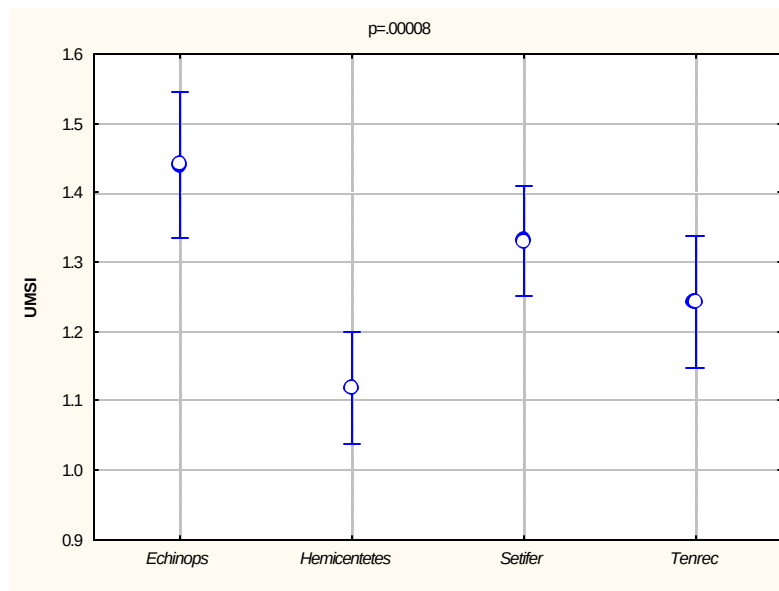


Figure 3.16. Means of Unciform-Magnum Size Index (UMSI). *Echinops* has a relatively large unciform relative to other tenrecines, a character associated with arboreal locomotor behavior. *Setifer* also has a relatively large unciform, which may be retained from an arboreal *Echinops/Setifer* common ancestor.

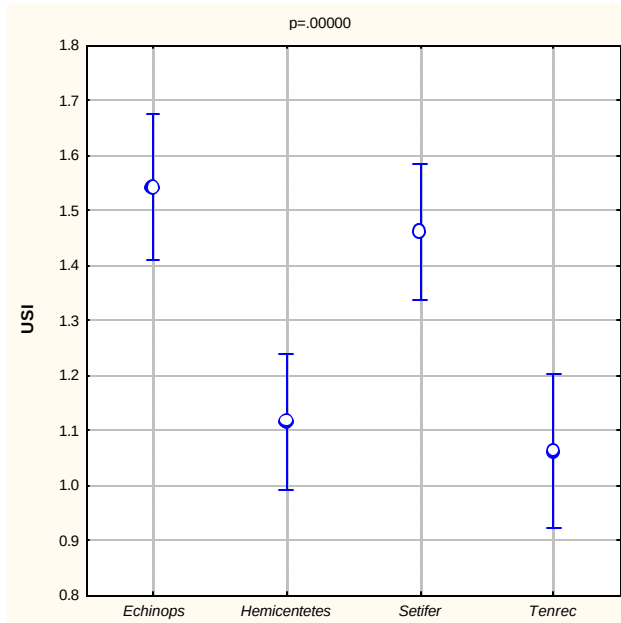


Figure 3.17. Means of Unciform Shape Index for tenrecines (USI). The unciform in *Echinops* and *Setifer* are radially expanded, a character associated with arboreal behavior.

The centrale is mediolaterally expanded in the arboreal scandentian *Ptilocercus*, which may be related to intense radial loading on the carpus relative to non-arboreal scandentians (Stafford and Thorington, 1998; Sargis, 2002). The centrale in *Echinops* is also mediolaterally expanded relative to *Tenrec* (ANOVA, $p < 0.04$), which may be indicative of its climbing behavior (Figs. 3.15, 3.18). Mean Centrale Shape Index values for *Setifer* fall between *Echinops* and *Tenrec* and are not significantly different from either (Fig. 3.18).

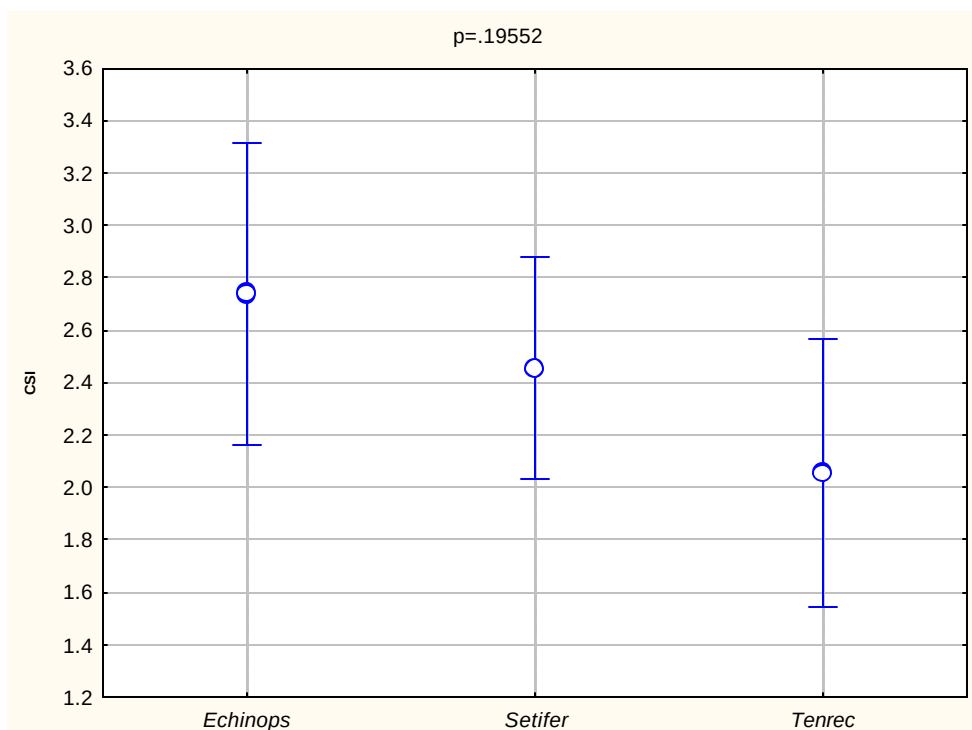


Figure 3.18. Means of Centrale Shape Index in tenrecines (CSI); *Hemicentetes* is omitted because it has no separate centrale). The centrale in *Echinops* is mediolaterally expanded relative to *Tenrec*, a character associated with arboreal behavior (ANOVA, $p=0.04$). *Setifer* is not significantly different from either *Echinops* or *Tenrec*.

The relative size of the trapezoid compared to the other carpals seems to be relatively invariant amongst all of the studied taxa except for *Potamogale* ($p=0.83$ with *Potamogale* removed from analysis). *Potamogale* has an unusually robust trapezoid relative to the other carpals (Fig 15; $p<0.02$ for comparison to all but macroscelidids where $p=0.11$). The trapezium in *Potamogale* is shifted radially, such that the palmar surface of the articulating mCI faces ulnarly in the resting position. The trapezoid most likely expanded radially as the trapezium shifted, maintaining carpal support for loading involved with palmar push-off during swimming.

The prepollex, or falciform (named for its scythe or sickle-like shape in some mammals) was almost certainly present in stem eutherians (Szalay, 1994), and is found in most placentalian mammals (although reduced or fused with the trapezium in some). It

extends palmarly on the radial side of the MCJ, and articulates with the distal scaphoid and proximal trapezium (Fig. 3.19). I have not encountered any discussions in the literature that refer to the functional relevance of the prepollex in relation to positional behavior. In tree and ground squirrels, the prepollex is a partial attachment site for the flexor retinaculum, which extends ulnarly to the palmar surface of the pisiform (Thorington and Darrow, 2000). In guinea pigs, the proximal end of the prepollex is the site of origin for the M. flexor digitorum brevis (which flexes digits I and IV), and the mid-dorsal side is the origin for the M. abductor digiti I (abductor pollicis brevis as well as longus in primates, as illustrated in Lewis, 1989; Cooper and Schiller, 1975). The major carpal flexors pass along the palmar ulnar surface of the prepollex. Lewis (1989) suggested that the prepollex has little influence on the mechanics of the MCJ, but did not discuss any particular function-based differences in prepollex form.

All of the studied tenrecids have a prominent prepollex, as does *Solenodon*. In one specimen of *Potamogale*, I noted a very small round bone where the prepollex is normally found; this may be a vestigial prepollex (Fig. 3.19), but no other *Potamogale* specimens had a prepollex. *Potamogale* has a palmar process of the radial scaphoid (Fig. 3.13) that most likely receives the tendinous and ligamentous attachments that are received by the prepollex in other taxa. *Gorilla* has a similar palmar process of the scaphoid that Lewis (1989) suggested is a fused prepollex. In the case of *Potamogale*, the vestigial prepollex in one specimen suggests that the scaphoid process is not homologous with the prepollex and is an extension of the original scaphoid developmental anlage. The macroscelidid *Petrodromus* had a small circular prepollex (Fig. 3.19) in two of three specimens. None of the studied *Hemiechinus* specimens had a prepollex. Of the taxa

studied (other than *Potamogale*, *Petrodromus* and *Hemiechinus*), there is a strong correlation between pisiform and prepollex length ($r=0.86$), yet there is little correlation between the pisiform and prepollex shape ($r=0.24$). The prepollex is less variable in shape than the pisiform (intergenerically that is), which may be a result of its absolute size relative to the pisiform; the prepollex is a smaller bone with more overlapping tendinous and ligamentous attachments than the pisiform, which is longer and has more independent sites of attachment (and therefore may be more susceptible to variation in shape).

There are no subfamily-based differences in prepollex shape between tenrecines and oryzorictines. Within the tenrecines, there are significant differences in shape; *Tenrec* has a significantly longer and narrower prepollex than *Setifer*, in which the prepollex is relatively small and short (Figs. 3.19, 3.20; $p=0.01$). *Tenrec*'s prepollex is also longer than that of *Echinops* ($p=0.06$) and slightly longer than in *Hemicentetes* ($p=0.80$). There is little consistent intergeneric variation in oryzorictine prepollex size and shape ($p=0.78$); all species/genus means are within the range of *Hemicentetes*, and demonstrate that *Echinops* and *Setifer* have a particularly short prepollex for tenrecids. Presence or absence of the prepollex in a taxon seems to be a higher taxon-specific trait. Between family, and subfamily members, and probably between species, length of the prepollex and pisiform is most likely some indicator of the size of the major carpal flexors. For example, within tenrecines, *Tenrec* and *Hemicentetes* have the longest prepollex and pisiform, and these species rely on the major carpal flexors for terrestrial ground push-off and digging, respectively. *Echinops*, a climbing species, relies less on musculature for palmar push-off than on the muscles responsible for grasping (i.e., digital flexors).

Setifer's similarity to *Echinops* in prepollex size, as well as other traits of the carpus and tarsus, is related to their close common ancestry and indicates that *Setifer* may have evolved from a semi-arboreal *Echinops*-like ancestor.

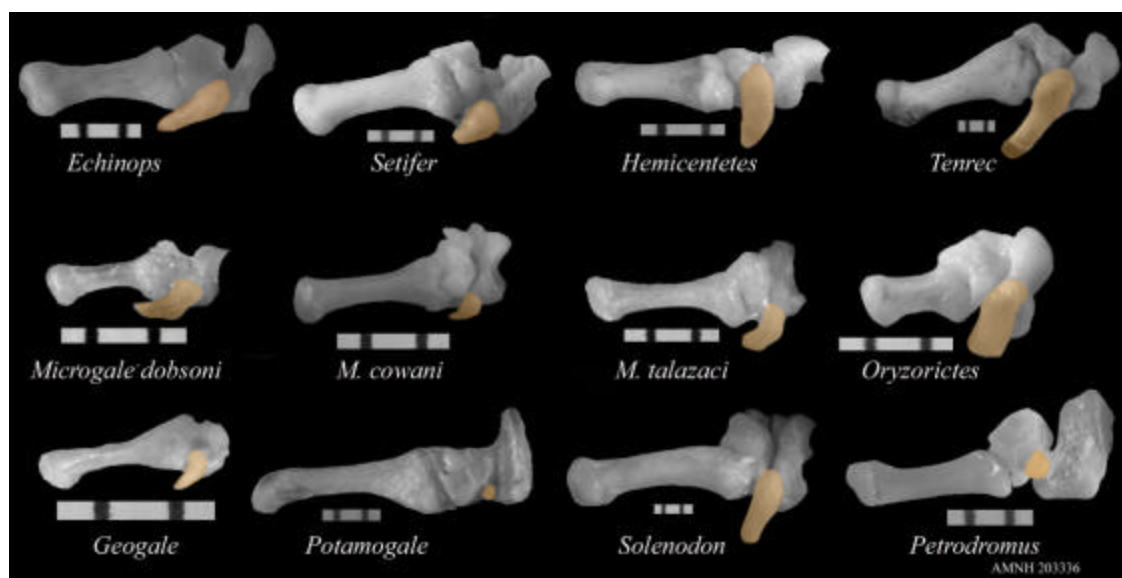


Figure 3.19. Radial side of the carpus (scaphoid and trapezium) and first metacarpal, with prepollex shaded in orange. Top row: tenrecines; middle row: oryzorictines. Note intergeneric variation in relative size and shape of prepollex. When present, length of the prepollex correlates positively with length of the pisiform ($r=0.86$), and may be functionally related to carpal flexion (see text).

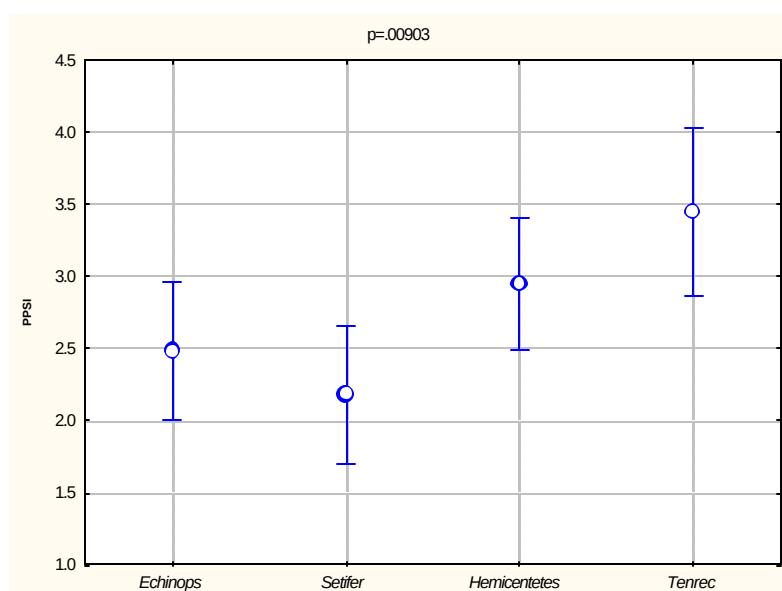


Figure 3.20. Means of Prepollex Shape Index (PPSI). *Hemicentetes* and *Tenrec* have the highest values, indicating a long and narrow prepollex in these genera.

Other MCJ features that might indicate arboreal behavior include ulnar expansion of the centrale, such that it contacts the unciform; a magnum that does not contact the proximal carpal row (related to centrale-unciform contact); an elongate unciform hamulus and scaphoid tubercle; and a dorsopalmarly expanded articular surface of the magnum (Table 3.1). The centrale does not contact the unciform in any of the specimens studied, although it is closest in the terrestrial *Tenrec* (Fig. 3.15). None of these other characters could be observed or measured because bones of the MCJ were generally articulated in museum specimens, and articular surfaces obscured.

Distal Carpal Joint (DCJ), Metacarpals and Phalanges

Carpal, metacarpal and phalanx proportions are often used as indicators of specialized locomotor behavior (Godinot and Beard, 1993; Hildebrand, 1995; Luo et al., 2003 etc.). Arboreal climbers and quadrupeds tend to have a relatively short carpal region and long metacarpals and phalanges, providing increased multiaxial mobility at the carpal joints combined with increased surface area for grasping (Table 3.1).

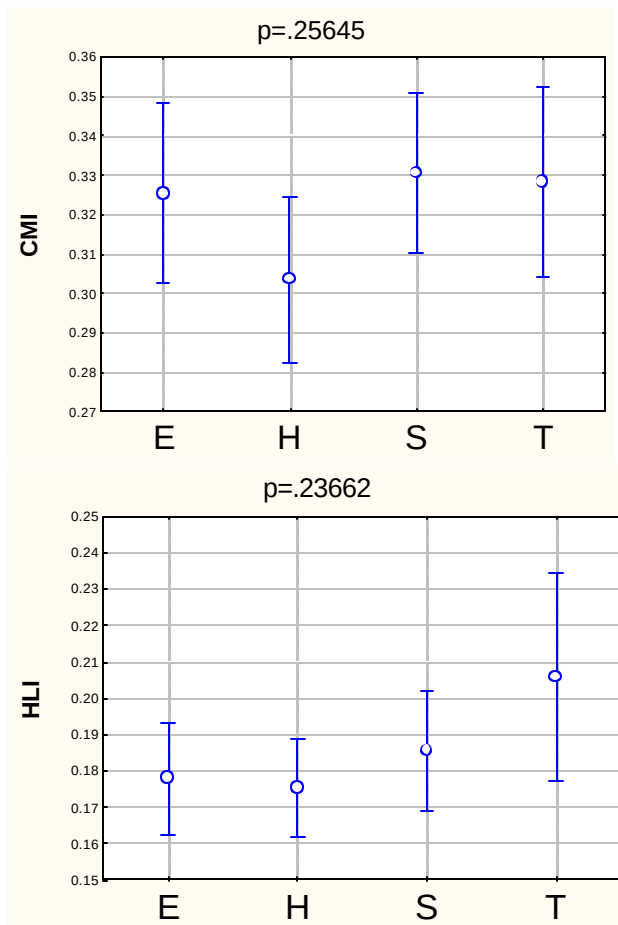
The skeletal components of arboreal species tend to elongate towards the distal end, such that there is an increased length (compared to relative lengths in other non-arboreal species) from metacarpals to proximal- to mid- to distal phalanges (Godinot and Beard, 1993; Hamrick, 2001; Luo et al., 2003). Diggers have relatively short carpals, as well as short metacarpals and phalanges, which provides greater outforce for digging. Terrestrial cursors tend to have long carpals and metacarpals and short phalanges, a combination that stabilizes and maximizes speed at the carpal-metacarpal joints and provides a short, powerful surface for cursorial (usually digitigrade) push-off (Table 3.1).

There is no significant difference in carpal length relative to metacarpal length in the tenrecines (CMI, $p=0.26$), despite expectations that *Echinops* should have a relatively short carpal region (Figs. 3.21, 3.22). Of the four tenrecines, the digger *Hemicentetes* has a low CMI (Fig. 3.22), which reflects its relatively short and wide carpal region (though the difference is still not significant); this is consistent with expectations based on other diggers. The Hand Length Index (HLI) describes the length of the metacarpals + phalanges relative to the carpal region. There are no significant differences among tenrecines ($p=0.24$), though *Tenrec* tends to have relatively shorter digits and longer carpals than the other species (Fig. 3.21). *Echinops* has the shortest carpals and longest digits, but the difference between *Echinops* and *Hemicentetes* is minimal. Differences between the Carpals-Metacarpals Index and the HLI (Fig. 3.22) demonstrate that in *Echinops* and *Setifer*, the phalanges are relatively long; *Echinops* and *Setifer*'s index values move from relatively high in CMI to relatively low in HLI, meaning that phalanx lengths are high relative to *Hemicentetes* and *Tenrec*. This meets functional expectations in the climber, *Echinops*, and I would again attribute the similarity of *Setifer* to a possible shared arboreal ancestor with its closest tenrecine relative *Echinops*. The HLI of *Hemicentetes* is also low, suggesting that it has long fingers relative to the carpal region. However, the value was also low for CMI, suggesting that the phalanges do not contribute disproportionately to hand length, as in *Echinops* and *Setifer*. There are no differences in the phalanx length index among tenrecines ($p=0.63$). The phalanges of *Echinops* do not appear to increase proportionately towards the distal end as in some other climbers (Hamrick, 2001; Luo et al., 2003).

Metacarpal shape seems to be a highly significant indicator of function in tenrecines (Fig. 3.22; M3SI, $p=0.00$; M1SI, $p=0.00$). The third metacarpal of *Hemicentetes* is relatively shorter/wider than that of any other tenrecine ($p<0.01$), whereas there is no significant difference found among the others. The first metacarpal of

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Hemicentetes is similarly shorter/wider than that of the other tenrecines (though $p=0.2$ for comparisons with *Setifer* and *Tenrec*, $p=0.00$ compared to *Echinops*), which is consistent with mcIII shape. The mcI of *Echinops* is significantly longer than that of the other tenrecines (Fig. 3.21, 22; $p<0.02$ for all). A relatively longer mcI, resulting in a longer pollex, would be functionally advantageous for small-branch grasping, which is part of its regular behavioral repertoire (Honegger and Noth, 1965; pers. obs.). In climbing/arboreal walking viverrids, the proximal articular surface of mcI is wider than in non-climbing viverrids and “permits a variety of movements” (Taylor, 1974: 328), but this does not appear to be the case in *Echinops* relative to other tenrecines.



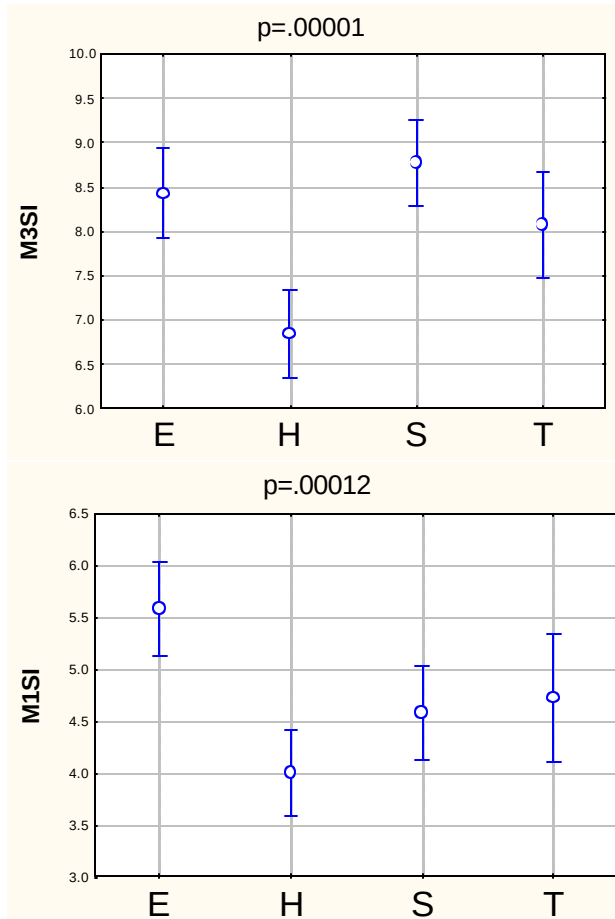


Figure 3.22. Indices related to the length and shape of the metacarpals and phalanges in Tenrecinae. Carpal-Metacarpal Index (CMI); Hand Length Index (HLI); Metacarpal III Shape Index (M3SI); Metacarpal I Shape Index (M1SI). See text for comparisons. (E=*Echinops*; H=*Hemicentetes*; S=*Setifer*; T=*Tenrec*).

There is a significant difference between *Oryzorictes* and the three species of *Microgale* in both the Carpals-Metacarpals Index and Hand Length Index (Fig. 3.23, $p=0.00$); *Oryzorictes* has a relatively short carpal region coupled with extremely short metacarpals, which is expected in a subterranean digger (Figs. 3.21, 3.23). There are no significant differences among the three species of *Microgale*, which all have relatively long and narrow hands. Both M3SI and M1SI illustrate that *Oryzorictes* has a shorter and wider mcIII and mcI than *Microgale* (Fig. 3.23, $p=0.00$). Note in Figure 3.23 that

although *M. cowani* is always within the range of other species of *Microgale*, its mean is consistently slightly skewed towards that of *Oryzorictes*.

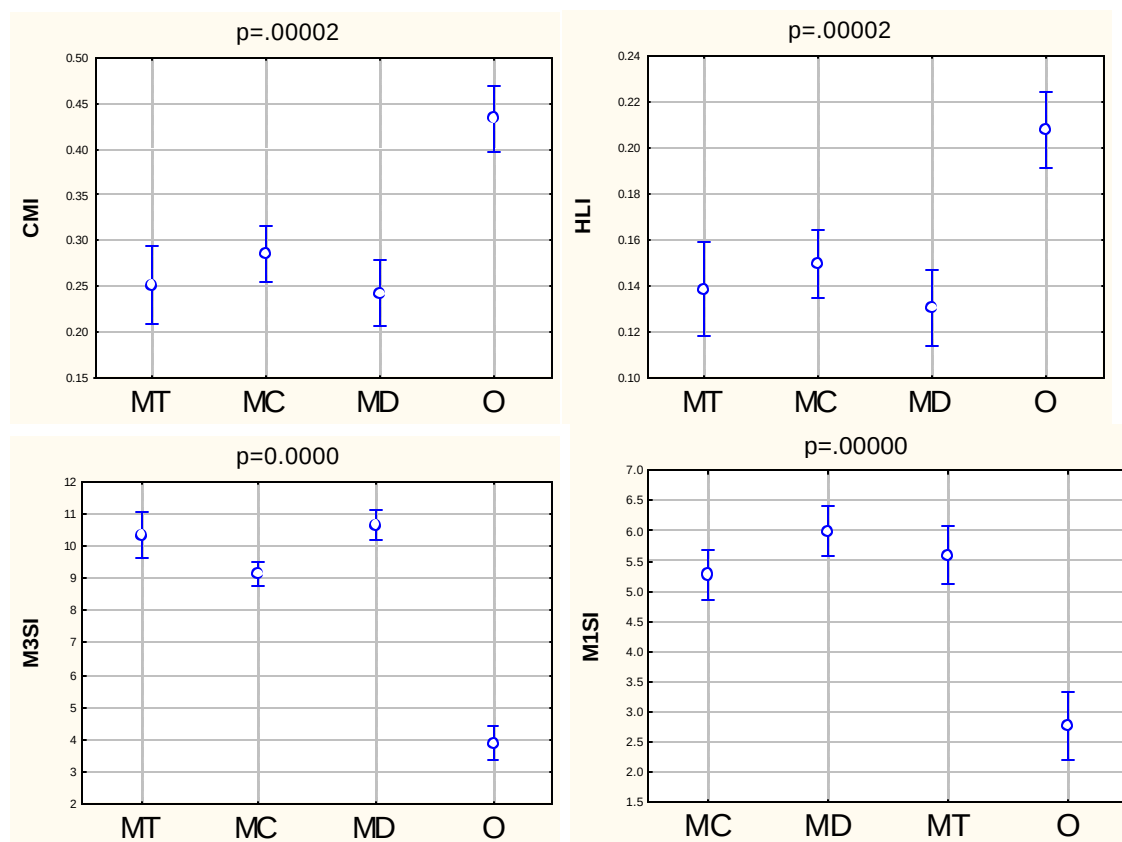


Figure 3.23. Indices related to the length and shape of the metacarpals and phalanges in Oryzorictinae. Carpals-Metacarpals Index (CMI); Hand Length Index (HLI); Metacarpal III Shape Index (M3SI); Metacarpal I Shape Index (M1SI). Note significant differences between the fossorial *Oryzorictes* (O) and the three terrestrial *Microgale* species. See text for comparisons. (MT=*Microgale talazaci*; MC=*M. cowani*; MD=*M. dobsoni*; O=*Oryzorictes*).

Subfamily-based trends are not evident with respect to overall proportions of the hand. Nonetheless, *Geogale*, *Potamogale* and macroscelidids all have relatively long metacarpals compared to carpals (Fig 21). They are all in the general range of *Microgale*, whereas tenrecines tend to have shorter, more robust metacarpals relative to carpals than the other taxa (though subfamilial differences between tenrecines and oryzorictines are not significant in any of the above variables because of the influence of the outlier

Oryzorictes). *Hemiechinus* and *Solenodon*, which both exhibit semi-fossorial behavior, have short metacarpals relative to carpals, as well as robust metacarpals and phalanges.

Godinot and Beard (1993) suggested that increasing robusticity from the second to fifth metacarpal is indicative of greater degrees of ulnar loading in vertical clingers among primates, a condition associated with high degrees of ulnar loading relative to radial loading. There are significant differences among tenrecoids in relative metacarpal robusticity. Compared with other tenrecines, the mcII and III of *Hemicentetes* are robust relative to mcIV and V, suggesting relatively greater radial loading. *Oryzorictes* also has a more robust mcII and mcIII relative to the species of *Microgale* (Fig. 3.24; $p=0.00$). Both *Hemicentetes* and *Oryzorictes* have enlarged digit II and III claws compared to those of IV and V, which also suggests that digging in these species involves a greater degree of loading on the radial rather than ulnar side of the wrist. An unusual autapomorphy of mcIII in *Oryzorictes* supports the view that digging in this species is directed by the second digit, followed by the third, fourth and fifth. At the proximal dorsal surface of the third metacarpal, there is a radial protuberance, an extension of the already expanded proximal metacarpal that rests on top of the second metacarpal, providing dorsal support for a region that clearly incurs high loads from the ventral side (see Fig. 3.25).

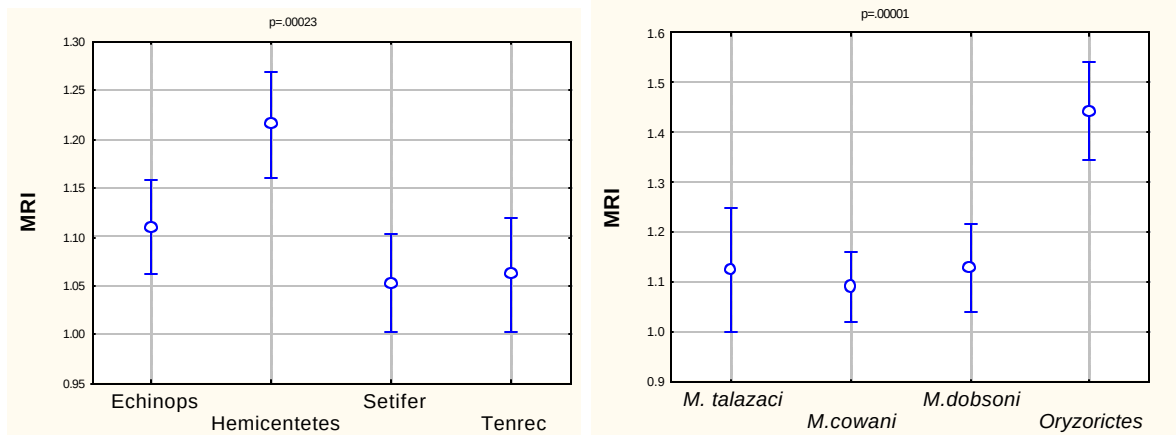


Figure 3.24. Means of Metacarpal Robusticity Index (MRI) in tenrecines (left) and oryzorictines (right). In both subfamilies, the radial metacarpals are more robust than the ulnar ones, but in the diggers *Hemicentetes* and *Oryzorictes*, mcII and mcIII are significantly more robust.



Figure 3.25. Dorsal view of right carpals and metacarpals of the oryzorictine digger *Oryzorictes*. Pink ellipse highlights an unusual autapomorphy of this genus, a dorsal protuberance on the proximal radial side of mcIII that supports the dorsal surface of mcII.

Claw and ungual shape is highly indicative of hand function. Habitual climbers tend to have short, deep and highly curved claws while those of diggers are long and shallow (e.g., Taylor, 1974; Martin, 1984; Hildebrand, 1995; Sargis, 2002). Among the tenrecines, *Echinops* and *Setifer* have extremely short and curved claws, typical of climbers (Fig. 3.26), but the claws of *Echinops* are deeper and shorter than those of *Setifer*. Claws of *Hemicentetes* and *Tenrec* are long and shallow in comparison, with

those of *Hemicentetes* being enormously long in comparison with all other tenrecines. Among the oryzorictines, the claws of *Oryzorictes* are also extremely long, and deeper and more sharply pointed than those of *Hemicentetes*. Within *Microgale*, *M. cowani* has conspicuously longer claws than *M. dobsoni* and *M. talazaci* (Fig. 3.26), which further supports some degree of convergence between *M. cowani* and *Oryzorictes*. *Geogale* and *Petrodromus* have claws fairly typical of terrestrial non-specialists, whereas those of *Solenodon* are long, and similar in morphology to those of *Oryzorictes* (though relatively smaller), indicative of its semi-fossorial locomotor behavior.

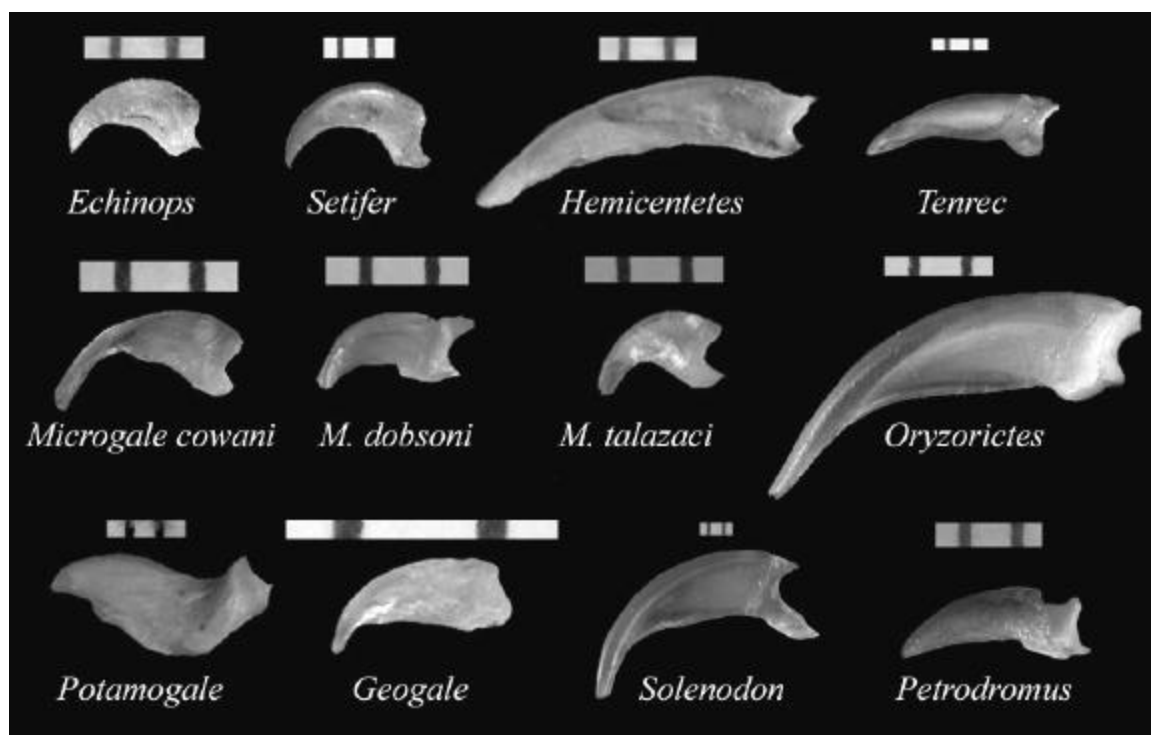


Figure 3.26. Claws of the second digit in tenrecines (top row), oryzorictines (second row from top), other tenrecoids (two bottom left) and non-tenrecoids (two bottom right). All claws are scaled to same height of the proximal articular surface. The claw is an approximate indicator of habitus. The tenrecoid diggers *Hemicentetes* and *Oryzorictes* and the non-tenrecoid burrower *Solenodon* have relatively long and shallow claws, whereas those of the climber *Echinops* are short, curved and deep. Of the three *Microgale* species, *M. cowani*'s claws are relatively long, indicative of more burrowing than in the other two species.

Summary and Conclusions

Subfamily Tenrecinae

In the tenrecines, as in the other tenrecoid taxa, the more distal elements of the hand appear to have a stronger correlation with genus-specific locomotor function. There are few characteristics that distinguish tenrecines from oryzorictines as a subfamily. The difference in the position of the major dorsal ridge of the distal radius is most likely a product of different hand positions in tenrecines and oryzorictines (Fig 6). Like the tenrecine foot (see Salton and Szalay, 2004), the tenrecine hand is more laterally splayed than in oryzorictines, which have a forward (parallel to the axial plane) to medially positioned resting hand. This aspect of the distal forearm, as well as characters of the distal hindlimb, suggests that the primary posture of the hand and foot was conserved in the evolution of tenrecoid taxa, and associated characters are useful indicators of subfamilial phylogenetic associations. Compared to oryzorictines, the tenrecine carpals are more multiaxially mobile. This is especially true for *Echinops* and *Setifer*, which have a number of characteristics related to climbing (though *Setifer* is not a habitual climber). Comparisons between the tenrecine digger *Hemicentetes* and the oryzorictine digger *Oryzorictes* also support the proposal of relatively increased carpal mobility in tenrecines. Although I expected to find a highly stabilized wrist in *Hemicentetes*, as found in *Oryzorictes*, several carpal characteristics (e.g., pestle-shaped distal ulna, no scaphoid-lunate fusion, wide scaphoid) suggest that the wrist of *Hemicentetes* is capable of flexible multiaxial movement.

Though several carpal and distal hand characteristics in *Echinops* are consistent with expected morphology for a climber (e.g., mortar/pestle ulnar/cuneiform joint,

mediolateral expansion of the distal radius, relatively large and mediolaterally wide unciform), many function-based traits in other arboreal climbers are not convergently shared by *Echinops* (e.g., longer pisiform in some, mediolaterally wide and shallow scaphoid, wide proximal articular surface of mCI). *Echinops* and *Setifer* share a suite of characteristics that correlate with climbing behavior despite the primarily terrestrial behavior of *Setifer*, which is also the case for several tarsal characters (Salton and Szalay, 2004). This again suggests that their common ancestor may have been an *Echinops*-like climber, rather than terrestrial.

Compared with other tenrecines, *Hemicentetes*' carpal morphology is a combination of several characters indicative of digging behavior (e.g., mediolaterally expanded distal radius, scaphoid-centrale fusion, generally short and wide carpals) and some indicative of carpal mobility, especially at the proximal carpal joint (see above). The distal elements of the hand are more directly indicative of digging behavior; e.g., short and wide mcIII and mCI, robust mcII and III relative to IV and V, and extremely long claws.

Subfamily Oryzoricinae

Comparisons of *Oryzorictes*' morphology with the three species of *Microgale*, the available material for *Limnogale* and the other studied taxa demonstrate that most aspects of the unusual carpal morphology of *Oryzorictes* are attributable to its subterranean ecology. Many of the traits expected in a fossorial, forelimb-digging mammal are found in the carpus and distal hand of *Oryzorictes*, and are apparent from qualitative as well as quantitative examination. The distal radius and ulna are mediolaterally expanded relative to all other species studied, and the articular surface is cylindrical (Figs. 3.6, 3.9). The

styloid process of the ulna is laterally sprawled and shallow (Fig 9). The pisiform is not elongated, but it is stouter and relatively wider than in any other species (Fig. 3.10). There is complete fusion between the scaphoid, lunate and centrale (Fig. 3.15). The carpals, metacarpals and phalanges are relatively short (Fig. 3.21), and the claws are shallow and long (Fig. 3.26). There is an unusual protuberance on the proximal radial side of mcIII that dorsally overhangs mcII and stabilizes the second digit for digging (Fig. 3.25).

Significant differences between the three studied species of *Microgale* were unexpected. In several species of *Microgale*, secondary locomotor behaviors have been inferred based on external morphology (e.g., *Microgale longicaudatus* has a long tail with a prehensile tip and *M. gymnorhyncha* has small eyes and enlarged forefeet, associated with climbing and digging, respectively; Eisenberg and Gould, 1970; Jenkins, 2003). But the three *Microgale* species used in this study are thought to be generally terrestrial with some limited climbing ability in *M. dobsoni* (Jenkins, 2003). The consistent similarity between *M. cowani* and *Oryzorictes* (though measurements for *M. cowani* did not reach the extremes of *Oryzorictes*) was surprising. This similarity suggests that several traits in *M. cowani* are either related to digging, or a close phylogenetic affinity with *Oryzorictes*. If Olson and Goodman's (2003) oryzorictine phylogeny is accurate, then *M. cowani* is morphologically far removed from the common ancestor of *Microgale* and *Oryzorictes*. Shared traits between these two taxa are therefore most likely not homologous, and are probably related to digging behavior in *M. cowani* that has not yet been documented.

The two *Limnogale* specimens with available carpal joints consisted only of the distal ulna and radius in one (Figs. 3.6, 3.9), and a proximal carpal row in poor condition in another (Fig. 3.13). Characteristics of the distal antebrachium of *Limnogale* most resemble *M. dobsoni* (see Fig. 3.9), yet the ulna is mediolaterally wider, relatively large and blunt, and the radius has an extensive and shallow ulnar projection, suggesting some radial carpal mobility at the PCJ. The grooves for the passage of the major extensor musculature are very large. *Limnogale*'s prepollex appears to be medium-size (Fig. 3.13), similar to other oryzorictines, and unlike *Potamogale*'s rudimentary prepollex. The scaphoid in *Limnogale* is not as radially and palmarly expanded as in *Potamogale*. On the other hand, *Limnogale* shares with *Potamogale* a greatly enlarged base of the pisiform with a wide distal end (see Fig. 3.13). On the basis of carpal morphology alone, I would affiliate *Limnogale* with the other oryzorictines (Olson and Goodman, 2003; Salton and Szalay, 2004) as opposed to *Potamogale* (Asher, 1999). When carpal and tarsal evidence is combined, there is a strong case for *Limnogale*'s affiliation with other oryzorictines rather than potamogalids. The modifications of the distal antebrachium suggest that *Limnogale*'s hands are active in swimming, as well as multiaxially mobile, perhaps playing an important role in changing direction underwater and/or feeding.

Potamogale* and *Geogale

The *Potamogale* tarsus (as opposed to carpus) reveals a number of characteristics that emphasize importance of stability in the plane of dorsoplantar flexion and extension, most likely for foot propulsion involved in swimming (Salton and Szalay, 2004). The carpus also appears to be stabilized for dorsoplantar flexion, but function-based traits are not as apparent as in the tarsus, suggesting that *Potamogale*'s hand does not incur the

same propulsive loads from swimming behavior as does its foot. A notable feature of the carpus is the radial palmar curvature of the scaphoid (Fig. 3.13), which most likely accommodates the attachments found on the prepollex in other tenrecoids. The prepollex in *Potamogale* is a rudimentary sesamoid (Fig. 3.19) as opposed to the well-formed crescent-shaped palmarly extending bone in many other mammals (and all other tenrecoids studied). Palmar curvature of the scaphoid results in a relatively narrowed dorsal surface of the hand, with the pollex and second digit tucked palmarly. Functional interpretation of this cupping of the hand is not entirely clear (but see Taylor, 1989). *Potamogale* also has a fused scaphoid-centrale or absent centrale (Fig. 3.15), which is suggestive of considerable carpal loading on the radial side.

Geogale's carpal morphology is not as informative as the tarsus for understanding its intrafamilial relationships within Tenrecoidea. The positioning of the grooves of the dorsodistal radius, which appears to be a subfamily-level specific trait, is more similar to oryzorictines than tenrecines, but there are few other characteristics that support phylogenetic affiliations. Its carpal morphology also does not exhibit any remarkable traits that are suggestive of locomotor behaviors other than those of a generalized terrestrial mammal.

Solenodon, Petrodromus, and Hemiechinus

Although I have found few taxon-specific traits in the tenrecoid carpal complex and distal hand, comparisons with *Solenodon*, *Petrodromus*, and *Hemiechinus* served as useful morphological contrasts. Comparisons of the proximal articular surface of the first carpal row (Figs. 3.13, 3.15) show a consistent close association between the scaphoid and lunate in tenrecoids vs. a closer association of the lunate and cuneiform in

Petrodromus and *Solenodon* (*Hemiechinus* has a fused scaphoid-lunate and a massive cuneiform, unlike any of the other taxa). The macroscelidid *Petrodromus* has a suite of carpal characteristics that is typical of a terrestrial cursor (though macroscelidids use saltatory locomotion, function-based morphology would be similar to cursors in many respects). The PCJ and MCJ of *Hemiechinus* seem to be typical of a subterranean mammal, yet features of the DCJ and distal hand are more typical of a general terrestrial one. Little is known about the locomotor behavior of *Hemiechinus*, but this initial examination of its carpal morphology suggests that it may have evolved from a “digging” ancestor and has subsequently become a more generalized terrestrial form. The carpal morphology of *Solenodon* indicates locomotor behavior similar to that indicated by its tarsus (see Salton and Szalay, 2004). Much of its carpal morphology is typical of the ancestral eutherian form, but several aspects (e.g., a cylindrical radial articular facet, wide distal radius, relatively short metacarpals and long, shallow claws) demonstrate that it uses its hands for digging.

The carpus is perhaps the most complex region of the postcranial skeleton for interpreting locomotor function. This study demonstrates the importance of considering ecomorphology within the context of closely related genera before meaningful functional or phylogenetic interpretations can be made. There appear to be many functional correlates with skeletal form, yet these are extremely variable between the sub-families and families studied here. Unusual aspects of carpal form, e.g., the protuberance found on the proximal mcIII in *Oryzorictes*, are indicative of positional behaviors, but similar characteristics are not consistently present in genera with the same general locomotor

behaviors. In this respect, the carpus does seem to be a relatively conserved region of the postcranial skeleton. Yet, this study has also confirmed that the carpus is not an easy indicator for testing phylogenetic relationships. There is considerable intraspecific variation in carpal morphology, as well as differences between closely related species that do not corroborate functional expectations. These interspecific differences may be suggestive of hand positions that are not directly related to locomotor function, and are therefore difficult to interpret. It is also very possible that there are subtle differences in form that have not been identified in this study due to the extremely small sample sizes available for analysis (due to the rarity of museum specimens with available and/or visible carpal regions). This comparative study of the tenrecoid carpus has highlighted the need for similar work in other mammals in order to make sense of variation, homology, and convergence in this morphologically complex postcranial region.

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Appendix 3.1. Linear Measurements (mm)

Taxon	ID	Dorsal1	Dorsal2	Dorsal3	Dorsal4	Dorsal5	Dorsal6	Dorsal7	Dorsal8	Dorsal9	Dorsal10	Dorsal11	Dorsal12	Dorsal13	Dorsal14
Echinops	134550	1.6015	0.8403	1.0987	0.8502	6.5500	0.8603	0.8073	0.6850		2.2272		2.3899	1.7321	1.0978
Echinops	153785	1.5351			0.6500	5.7530	0.6511	0.6124	0.5726	1.5819	2.0366	3.5619	2.3437	1.4703	0.9152
Echinops	159730	1.5720			0.6942	6.4157	0.6018	0.5726	0.4865	1.5269		3.4213	2.4300	1.1969	0.9098
Echinops	170605				0.6432		0.6587	0.7845	0.5921		5.7637	3.2703			
Echinops	170607				0.6475		0.6366	0.6958	0.5048		6.5371	2.4444			
Echinops	207717				0.6941	6.1573	0.6488	0.6027	0.6022			2.7465			
Echinops	207718	1.3461	0.6226	0.7559	0.7040	6.1333	0.7253	0.7359	0.6785	1.6161	1.7576	3.3366	2.2016	1.6583	0.9378
Echinops	212918	1.1446	0.8422	0.7017	0.7681	5.2416	0.7981	0.6503			1.7166		2.4479	1.3343	0.7342
Echinops	212919	0.0119				6.3382				1.6753	1.6593	3.6038			
Echinops	31270	1.2590	0.9414	0.6963	0.7668	5.8263	0.7083	0.6585	0.6194	0.0120	1.9477	3.1167	2.0859	1.2355	0.8938
Echinops	328636	1.1901			0.7625	6.3502	0.7876	0.6206	0.6096		1.9385	3.5300	2.3282	1.3029	0.9501
Echinops	328637	1.4089	1.0041	0.9606	0.8463	6.5046	0.8469	0.7583	0.5908		2.2883	3.7600	2.7771	1.5770	1.0513
Echinops	464980	1.1477	0.7932	0.9032	0.8107	6.2725	0.6903	0.7549	0.6512	1.2788	1.9477	3.9578	3.0064	1.4259	0.8894
Echinops	57579				0.7267	5.8290	0.7305	0.5578	0.5673	2.3785		3.8942		1.5489	1.2400
Echinops	57580		0.8710	0.8017	0.7226	6.6828	0.7246	0.7275	0.6331	1.9050	2.2199	3.3734		1.8307	0.8968
Echinops	57581				0.6773	5.4140	0.5779	0.7031	0.7150	2.0869	2.0358	3.5086			0.0119
Echinops	588220		0.8509	0.9578	0.9642	5.6054	0.8401	0.8908	0.8233	2.1809	2.4314	3.5896	3.2462	1.2224	0.9713
Hemicentetes	83658				1.6089	9.3626	1.2286	1.2368			2.5190	4.3283			
Hemicentetes	10001	1.3831	1.2748	0.8891	1.1376	6.8703	1.2280	1.1376	0.8500	1.1722	1.7182	3.0647	3.8427	1.4505	0.9610
Hemicentetes	161757	1.3571	1.5688	1.4684	1.4109	7.4108	1.2106	1.1276	0.9746		2.9983	3.3818	4.0683	1.4211	1.6574
Hemicentetes	162059	1.4509	1.4524	0.9328	1.1394	7.7481	1.1403	1.0870	0.9905	1.2847	1.9223	3.6787	3.1885	1.4500	1.1387
Hemicentetes	162062	1.4108	1.3394	0.7738	1.1878	7.5731	1.0980	0.9621	0.9013	1.6270	2.2713	3.4034	3.7942	1.2026	1.2211
Hemicentetes	166132	1.0289	1.3269	0.8369	1.2515	8.1578	1.1372	1.0525	0.8415	1.5179	2.1613	3.6247	3.8668	1.0118	1.2728
Hemicentetes	170593		1.1361	1.0049	1.1716	7.0217	1.1060	0.8242				3.8567		1.1719	0.9692
Hemicentetes	207712	1.5889	1.4379	1.1577	1.1139	8.3184	1.0921	1.0068	0.7055	1.8233	2.3625	4.1092	4.2569	1.6182	1.2898
Hemicentetes	207714		1.2286	0.8870	1.2055	7.8369	1.1150	1.0269	0.7612				3.7962	1.0388	1.3094
Hemicentetes	207715	1.3410	1.4048	0.9776	1.2083	7.9258	1.1414	0.9844	0.8603	1.5234	2.2163	3.5655	3.9691	1.2100	1.4574
Hemicentetes	212920	1.4993	1.4296	0.8194	1.2261	7.9450	1.3212	1.1557	0.7886	0.9834	2.3885	3.3832	3.3482	1.4073	1.2400
Hemicentetes	212922				1.2782	7.4092	1.1994	1.3351		1.9402	2.4001	3.5521			
Hemicentetes	212924	2.0087	1.3733	1.5504	1.2773	8.8226	1.2435	1.2157	0.9185		3.1639		4.6131	1.8382	1.4139
Hemicentetes	212940	1.3051	1.2535	0.9019	1.3403	7.6587	1.3132	0.9325			2.4527	3.6410	3.7661	1.2128	1.2798
Hemicentetes	339992	1.4111	1.6612	1.0540	1.2599		1.0928	1.0418	1.0164		2.9270		4.1902	1.8701	1.1446

Appendix 3.1 (con't)

Taxon	ID	Dorsal1	Dorsal2	Dorsal3	Dorsal4	Dorsal5	Dorsal6	Dorsal7	Dorsal8	Dorsal9	Dorsal10	Dorsal11	Dorsal12	Dorsal13	Dorsal14
Hemicentetes	364954	0.4623	0.4623	0.3088	0.3380	2.7437	0.2904	0.2684	0.3202	0.4849	0.9433	1.2177	1.5009	0.5409	0.4925
Hemicentetes	5299				1.1053		1.2186	1.2690				4.6390			
Setifer	124554	2.0114	1.1889	1.1254	0.9804	9.6620	0.9750	1.0399	0.6716			5.4041	3.9035	1.8932	1.2275
Setifer	154033	2.5684	1.9982	0.7620	1.1042	9.5417	1.0794	1.0572	1.0620	3.5206	3.6302	5.3480	2.9280	2.5222	1.4724
Setifer	154034	2.3746	0.8168	2.1790									3.9837	2.7678	2.1028
Setifer	159731	1.9283	1.4065	1.0629	1.0346	8.5306	1.0114	0.9748	0.9254	2.3930	3.0896	4.8515	3.4628	1.8900	1.1168
Setifer	165494	1.4500	0.7998	1.7137	1.0501	10.0226	1.0518	1.0227	0.9600	2.7154	2.9778	4.9755	3.4651	1.7290	1.3782
Setifer	170532	1.6241	1.3316	1.0261	1.1438	8.8035	1.0581	1.0326			3.0061	4.6873	4.0426	1.4633	1.1136
Setifer	170581	1.8012	0.9861	1.4761	1.3179	8.8709	1.1469	1.2760	1.0156		3.3153		4.0017	2.1908	1.5266
Setifer	170731	2.5615	1.0181	1.5094	1.3132	9.8831	1.2691	1.2979	1.3335		3.5340	5.6662	3.7487	2.3364	1.1934
Setifer	395513				1.0505	10.1200	0.9804	1.0206	1.2087	2.9449	3.3264	5.0670			
Setifer	395719	2.3501	1.2215	1.2835	1.0077	10.3611	1.0525	0.9344	0.8846		3.2036	5.4693	3.7926	1.5993	1.2531
Setifer	42957	1.9743	1.1735	1.0930	1.1279	9.0120	1.0425	1.0549	1.1998		2.5800		3.8954	1.7061	1.0686
Setifer	42959	1.5610	1.0850	0.8890	1.0386	9.3325	1.0896	0.9330	0.8880		2.5723		3.9113	1.6290	1.2157
Setifer	5112	2.5792	1.2453	1.4570	1.3895	9.4975	1.3599	1.2998	1.1945		3.7172	5.3779	3.9722	1.9520	1.5556
Setifer	541443	1.7278	1.3553	1.0785	1.1212	10.4035	1.1042	1.0434	1.1446		2.7275		4.0108	1.6622	1.2058
Setifer	578790	2.3162	1.4156	0.9269	1.1171	9.4877	1.1155	1.0337	1.1528	2.9831	3.0133	5.1648	3.8938	1.9977	1.4502
Setifer	85170	2.3387			1.1258	9.8379	1.1309	1.0527	1.0932	2.3229	3.4021	5.0213	3.9782		
Tenrec	1001		1.4763	1.5772	1.1538	9.7578	1.2591	1.2055	0.7955		3.5446	4.1421		1.7237	1.9216
Tenrec	154628	1.9365	2.1335	1.9279	1.6492	12.6590	1.6348	1.4849	1.6485	3.2838	4.2733	5.3220	5.8257	3.0195	2.1714
Tenrec	170511	2.1870	1.8367	2.0100	1.6651	13.8315	1.6512	1.5233	1.3258		4.2655	6.1994	6.8814	1.8301	2.4145
Tenrec	174727	2.9350	1.8360	1.7038							3.9175		6.0004	2.1202	2.0616
Tenrec	30398	2.3805	2.0874	2.1010	1.5177	14.0708	1.6355	1.6248	1.6643		4.3444	5.6885	6.0177	2.6024	2.4243
Tenrec	361485	1.8492			1.4385	14.1492	1.4920	1.4790	1.5592		3.9674		5.3060	2.3319	1.9935
Tenrec	364955	2.1461	2.1941	1.5542	1.7126	15.0180	1.8511	1.7669	1.9285	3.5156	5.1529	5.9027	6.7395	2.4660	2.6365
Tenrec	44967	3.8159	2.4011	2.4703	2.1001	15.0161	2.1450	2.1136	1.8642		5.0639		5.3307	3.3646	2.7702
Tenrec	577051	1.5879	2.1516	2.0880	1.6528	13.9861	1.6669	1.6028	1.3779		4.5672	5.1538	6.5270	2.5411	2.3578
Tenrec	578792	2.7744	1.9027	1.9064	1.6951	13.6312	1.7794	1.7631	1.7473		4.4489		5.5415	3.3002	2.7419
Tenrec	59011	2.5502	2.4432	1.9296	1.9605	15.5119	2.0208	1.9457	1.5594		5.4575	6.9993	7.0402	2.3381	2.5299
Tenrec	60587		1.9510	1.8681	1.8793	15.1360	1.8671	1.7707	1.5722		4.5354		7.0170	2.2893	1.8468
M. talazaci	154581	1.4414	0.6665	0.5797	0.6684	6.4604	0.6524	0.5999	0.4775		1.7291	3.5822	1.6401	1.0240	0.6854
M. talazaci	154585	1.1116	0.6675	0.6284	0.6577	6.5313	0.6498	0.6208	0.5853	2.3637	1.8545	3.6501	1.6024	0.9840	0.7923
M. talazaci	167502	0.9113	0.5109	0.5502	0.6318	6.3922	0.5841	0.5385	0.4404	1.3592	1.5727	3.7499	1.7285	0.8529	0.6079
M. talazaci	167503	0.9083	0.6483	0.7699	0.6050	6.4701	0.5984	0.6093	0.6353	2.6157	1.7511	3.5894	1.4588	1.1132	0.9051

Appendix 3.1 (con't)

Taxon	ID	Dorsal1	Dorsal2	Dorsal3	Dorsal4	Dorsal5	Dorsal6	Dorsal7	Dorsal8	Dorsal9	Dorsal10	Dorsal11	Dorsal12	Dorsal13	Dorsal14
M. talazaci	577056	1.3264	0.6778	0.5573	0.6331	6.7106	0.6709	0.5950	0.5876	1.4937	1.3786	2.2860	1.5378	1.0123	0.6641
M.cowani	156221				0.4088	3.8725	0.3770	0.3780	0.4199	1.2068	1.2763	2.4308			
M.cowani	156222	0.6389			0.4813	3.8838	0.4283	0.4505	0.4322		0.5858	1.8723	1.2604		
M.cowani	156223	0.6607			0.5619	3.5079	0.4650	0.4380	0.4168		1.1297	1.8512	1.2826		
M.cowani	165672		0.4563	0.4000	0.3985	3.6576	0.3878	0.3810	0.3939	0.9008	0.8673	2.1045		0.6570	0.3781
M.cowani	165673		0.4649	0.2720	0.4287	3.8627	0.4261	0.4353	0.4822		0.9851	2.0481		0.6778	0.3167
M.cowani	165674	0.6076	0.4290	0.4203	0.4360	3.7487	0.4176	0.3684	0.3625	1.1333	1.0951	2.2915	1.2729	0.5341	0.4370
M.cowani	165676				0.4365	3.4040	0.4098	0.4023	0.3749	1.0772	0.9287	2.1913	0.0099		
M.cowani	165680	0.5187	0.4161	0.3530	0.4508	3.7567	0.4145	0.3851	0.3568	1.2461	1.0313	2.0630	1.3800	0.3922	0.3736
M.cowani	165689	0.6441	0.4563	0.3663	0.4890	3.9868	0.4251	0.4173	0.3890		0.9820	2.1260	1.3068	0.6732	0.3916
M.cowani	168017	0.5856			0.4383	3.9709	0.4073	0.3675	0.3249	1.1569	1.1451	2.1860	1.2664	0.0102	
M.cowani	328658	0.6231			0.3606	3.5465	0.3570	0.3656	0.4094		0.7326			0.5875	0.3044
M.cowani	449184	0.5870	0.3743	0.3523	0.4137	3.3397	0.3686	0.3707	0.3304	1.4875	0.8912	1.7441	1.1314	0.5519	0.3039
M.cowani	449186	0.5703	0.3791	0.3275	0.3889	3.5329	0.3577	0.3671	0.2960		0.8336		1.1916	0.3988	0.2498
M.cowani	449187	0.6652	0.4120	0.4247	0.4471	3.5274	0.4101	0.3649	0.3839		1.0987		1.1273	0.4950	0.3579
M.cowani	449188		0.4085	0.5113	0.4820	3.4165	0.3922	0.4007	0.3889	1.4595	1.0961	1.7441		0.5206	0.3773
M.dobsoni	161935				0.5899	5.7859	0.5360	0.5467	0.5170	1.1421	1.2810	3.3869			
M.dobsoni	161940		0.5289	0.4201	0.5815	5.4867	0.5605	0.5946	0.4843	2.3433	1.3998	3.0592		0.7913	0.4017
M.dobsoni	165467	1.1447			0.5709	6.8430	0.5581	0.5626	0.5832	1.9174	1.5563	3.4919	1.6920		
M.dobsoni	165774	1.2378	0.5699	0.3870	0.5656	6.2139	0.5468	0.5268	0.5082		1.5253		1.5779	1.0127	0.5927
M.dobsoni	165775	0.8557			0.6338	6.0980	0.6473	0.5564	0.5180		1.2495		1.3530		
M.dobsoni	166107	1.2310			0.5825	5.9824	0.5851	0.5486	0.4652		1.5296	2.8816	1.3018		
M.dobsoni	166198	0.8654	0.6032	0.4238	0.5750	5.9796	0.5106	0.5001	0.4254	1.8995	1.4323	3.3648	1.2920	0.8203	0.7012
M.dobsoni	166200	1.3747	0.5278	0.3562	0.5612	5.7103	0.4996	0.5089	0.5210		1.2854	2.6805	1.2938	0.9435	0.4620
M.dobsoni	578749	0.6537	0.5243	0.4791	0.6334	6.0377	0.6860	0.5534	0.3981	1.4312	1.4227	3.3875	1.4909	0.7431	0.5966
M.dobsoni	582730	0.8726	0.4238	0.5211	0.5175	5.6284	0.5226	0.4524	0.4327	2.1329	1.5535	3.0226	1.4537	0.4108	0.7123
Oryzorictes	161746	0.7986	0.9009	0.6467	0.9646	3.7571	1.0094	0.7352	0.4523	0.9249	1.3519	2.5770	2.4256	0.7332	0.6389
Oryzorictes	162053		0.8379	0.7285	1.3576	3.8160	1.0383	0.8082	0.9287	2.1083	1.5514	2.3945		1.1525	0.7522
Oryzorictes	162054	0.8887	0.8331	0.6161	1.1380	4.0327	0.9458	0.7983	0.6212	1.7994	1.6477	2.7979	2.4754	1.0429	0.6484
Oryzorictes	162058	1.0884	0.8721	0.6371	1.1499	3.7901	1.0126	0.7271	0.4879		1.4732		2.2983	1.0526	0.5658
Oryzorictes	166240	1.3774	1.1748	0.9446	1.2312	4.7148	1.1227	0.9584	0.8187	1.8146	2.2093	3.0498	2.9336	1.4873	0.9064
Oryzorictes	167480	1.4328	0.8180	1.1891	1.2741	3.9790	1.1470	0.8626	0.6973	1.6895	2.2004	2.5566	2.6878	1.4975	0.8192
Oryzorictes	31257	1.0671	0.8513	0.5022	0.8353	3.7241	0.8239	0.7679	0.5333		1.0594	2.4172	1.6300	0.9969	0.3866
Oryzorictes	578789	0.9475	0.8522	0.5965	1.0637	3.5118	1.0104	1.0214	0.8763	1.2341	1.4131	2.9187	2.1685	0.9727	0.5062

Appendix 3.1 (con't)

Taxon	ID	Dorsal1	Dorsal2	Dorsal3	Dorsal4	Dorsal5	Dorsal6	Dorsal7	Dorsal8	Dorsal9	Dorsal10	Dorsal11	Dorsal12	Dorsal13	Dorsal14
Geogale	159733				0.2831	3.3563	0.2714	0.2544	0.2941	1.1589		2.0724			
Geogale	161594	0.4083	0.3333	0.3720	0.3282	3.3721	0.3145	0.2844	0.2740		0.6950	1.6393	1.1054	0.4013	0.2742
Potamogale	266897		1.1243	1.5649	1.1011	13.2151	1.3917	1.2704	1.3325		2.6768			2.1425	1.6841
Potamogale	34881	2.3069	1.2917	1.0769	1.0654	11.6606	1.2481	1.1882			2.2590		3.1229	1.5419	1.4354
Potamogale	34881											6.0707			
Potamogale	51322	2.4941	1.0336	1.3745	1.0459	11.8032	1.3193	1.1859	1.0914		1.9285		3.0025	2.0606	1.4051
Potamogale	51324	0.0167			1.2225	13.5515	1.4093	1.2364	0.9881		1.9111				
Potamogale	51324	2.9724	1.3959	1.3188									3.2584	2.1989	1.5328
Potamogale	51327	1.6612	1.4969	1.1226	1.1022	10.7484	1.3063	1.1888			2.8166	5.3134	3.1496	1.2999	1.3359
Potamogale	51339		1.6885	1.1854	1.2904	12.8827	1.4131	1.4446	1.0948		2.3596	9.1670		2.0829	1.9303
Potamogale	51344	1.7433	0.9834	1.6616	1.1285	13.7552	1.3528	1.2605	1.1743	1.4197	2.4027	7.6908	4.3149	2.3389	1.5388
Potamogale	55204	1.5970	1.0234	1.6863	0.0112		0.0159	0.0159	0.0159				3.7788	1.8068	1.6593
Macroscelidid	203335	1.1966	0.8681	1.2843	0.9606	9.8335	1.0645	1.0549	0.9713		2.2592	4.0057	3.3465	1.5449	1.0712
Macroscelidid	203336	1.2358	1.0528	1.0348	1.1082	10.5545	1.2257	1.1060	1.0836		2.5889	4.3061	3.6583	1.5690	1.0869
Macroscelidid	203337	1.5424	0.9813	1.0624	0.9388	9.7753	1.0610	0.9677	1.0176		2.1426	4.0889	3.1029	1.6737	1.0290
Macroscelidid	203339				1.3623	13.5111	1.4060	1.4040	1.4520		2.6385				
Solenodon	172680	3.0726	1.5348	3.2062	2.0838	17.4347	1.9666	1.9241	1.9290	4.6529	5.7334	8.7729	8.0536	2.7866	2.9048
Solenodon	172745	4.2842	3.5710	1.7518	2.2159	16.3462	1.9462	1.9176	2.7251	5.2998	6.7557	9.1386	6.5256	2.8883	2.9591
Solenodon	217256	3.7376	3.8504	2.0410									8.9443	3.8121	2.9071
Solenodon	238263				2.2702	17.7380	2.2648	2.2551	1.7435		5.5596				
Solenodon	290520	3.7432	3.5427	1.7146	2.2725	18.8152	2.3344	2.1470	2.1255		5.9391	9.9658	8.5888	3.3329	2.7702
Solenodon	34859		4.0766	2.1477	1.7853	15.3865	2.3979				5.5500			2.5854	4.1017
Solenodon	395697	3.4337	1.6561	2.9816	2.0054	15.6375	1.9878	1.8847	1.6678		5.6559		7.2090	2.8549	3.0346
Solenodon	395819	4.5308	3.1265	1.7011	2.1200	18.7386	2.0947	2.1468	2.2116		5.2663	8.8941	8.2789	3.0603	2.8585
Solenodon	51068	2.3573	2.9091	1.5013	2.3568	18.1653	2.1022	2.0134	1.6933		5.5670	9.3560	7.3732	2.9681	2.4367
Solenodon	57320	3.5425	3.2261	1.7147	2.2727	16.6534	2.1084	2.0522	2.1374		6.0186	8.3291	7.1706	2.9055	2.7658
Hemiechinus	185374	2.1945	1.3961	1.1131	1.2532	9.2707	1.4687	1.1244	1.0592	2.4314	3.3961	3.3771	3.5239	2.2421	1.1187
Hemiechinus	185374									3.7386					
Hemiechinus	51530	1.9797	1.2154	1.0978	1.0265	7.6656	1.2116	1.0938	1.1957		3.9118	3.7366	2.8976	2.3107	1.0331
Hemiechinus	6021	2.4949	1.9132	1.3648	1.6796	12.5755	1.9124	1.6473	1.7313		3.9817		4.3736	2.7514	1.4588

Taxon	ID	Lateral1	Lateral2	Lateral3	Taxon	ID	Medial1	Medial2	Medial3	Medial4
Echinops	134550	1.9831	1.5900	0.8853	Echinops	134550	0.8109	3.6287	1.1783	0.3618

Appendix 3.1 (con't)

Taxon	ID	Lateral1	Lateral2	Lateral3	Taxon	ID	Medial1	Medial2	Medial3	Medial4
Echinops	153785	1.0444	2.1355	0.7596	Echinops	153785	0.6130	3.5913	1.9089	0.4702
Echinops	159730	1.7186	1.8704	0.8081	Echinops	159730	0.6121	3.7060	1.0169	0.5604
Echinops	170607	1.7617	2.0630	0.7759	Echinops	170607	0.4026	3.1443	1.4762	0.7573
Echinops	207718		1.6408	0.8616	Echinops	207718	0.6373	3.1262	1.0534	0.7745
Echinops	31270	1.6354	1.8504	0.8983	Echinops	212918	0.6845	3.4108		
Echinops	328636	2.0515	1.7292	1.0688	Echinops	31270	0.7098	3.2171	1.2418	0.6834
Echinops	42958	1.7133	1.7819	0.5325	Echinops	328636	0.7403	3.6376		
Echinops	57579	1.5781	1.9610	0.8690	Echinops	464980	0.8657	3.8746	2.0652	0.6021
Echinops	57580	1.5202	1.7824	0.8856	Echinops	57580	0.6874	4.1776		
Echinops	57581	1.5722	2.0742	0.9814	Echinops	57581	0.6078	3.7456	1.7320	0.7982
Hemicentetes	161757	1.9135	2.3759		Echinops	588220	0.8253	4.5985	1.9753	0.7970
Hemicentetes	162059	1.8068			Hemicentetes	161757	0.9107	2.9816	2.4883	0.6551
Hemicentetes	162062	1.7304		0.0154	Hemicentetes	161758	0.9040	3.3317	1.8759	0.7451
Hemicentetes	166132	1.6719	2.2094	0.8001	Hemicentetes	162059	0.6740	3.8018		
Hemicentetes	170593	1.3898			Hemicentetes	162062	0.8743	3.4173	1.5509	0.6743
Hemicentetes	207715		2.1915	0.8739	Hemicentetes	166132	0.7158	3.2499	1.7873	0.6643
Hemicentetes	212920	1.4444	2.4733	0.9728	Hemicentetes	170593	0.8396	3.3623		
Hemicentetes	212922		2.5940	0.7136	Hemicentetes	207714	0.8635	3.3491	2.2517	0.7003
Hemicentetes	212924	0.0115	3.2736	1.1887	Hemicentetes	207715	0.9371	3.3297	1.6551	0.4654
Hemicentetes	212940	1.4017	2.9971	0.8445	Hemicentetes	212920	0.8506	3.4869	1.8675	0.5387
Hemicentetes	29245	1.2550	2.3841	1.0612	Hemicentetes	212940	0.9902	3.3110	0.0102	
Hemicentetes	339992	1.1832			Hemicentetes	339992	1.0113	3.8960	1.5098	0.5300
Hemicentetes	354998	1.6705	2.5782	0.9363	Hemicentetes	354998			1.9614	0.8620
Hemicentetes	364954	1.8638	2.9192	0.8517	Hemicentetes	364954	0.8012	4.1642	2.0259	0.7140
Hemicentetes	5299		2.2877	1.0074	Hemicentetes	5299	2.6141			
Setifer	124554	2.6767	2.5920	1.1390	Hemicentetes	10001	0.8368	2.5091		
Setifer	154033	2.9218	2.7798	1.2733	Setifer	124554	1.0368	4.9080		
Setifer	154034	3.1321	3.7038	1.3502	Setifer	154033	1.0838	5.4711		
Setifer	159731	2.2298	2.8634	1.0183	Setifer	159731	1.1008	4.1457		
Setifer	165494	2.4306	1.3506	0.6906	Setifer	165494	0.9587	5.2243	1.6975	0.7892

Appendix 3.1 (con't)

Taxon	ID	Lateral1	Lateral2	Lateral3	Taxon	ID	Medial1	Medial2	Medial3	Medial4
Setifer	170532	0.0151	2.8415	1.3099	Setifer	170532	1.1294	4.5084	1.4302	1.0935
Setifer	170581	2.3394	2.9171	1.2507	Setifer	170581			1.5396	0.7681
Setifer	170731	2.8378	3.0204	1.3331	Setifer	170731	1.2174	5.7557		
Setifer	395513	2.4136	3.5122	1.4383	Setifer	395513	1.3376	5.1899	1.8961	0.5739
Setifer	42957	2.2009	2.8592	1.0996	Setifer	42957			2.0563	0.9541
Setifer	42959	2.3893	2.4882	1.1381	Setifer	42959	0.8817	4.8498	1.7015	0.9825
Setifer	5112	2.3087	3.1559	1.2548	Setifer	5112	1.1514	4.7648	1.5137	0.9125
Setifer	85170	2.5105	3.0521	1.0596	Setifer	541443	1.1253	5.0559	2.5402	0.9800
Tenrec	1001	3.0013	4.9736	2.1803	Setifer	85170	1.1101	5.1163	2.0476	0.7477
Tenrec	154628	3.1028	5.1147	1.6769	Tenrec	1001	1.5002	7.4188	4.8823	1.4494
Tenrec	174727	3.4917	4.4153	2.5977	Tenrec	30398	1.4586	7.2912	3.0023	1.4185
Tenrec	30398		5.9099	2.3575	Tenrec	361485	1.6729	8.2734	5.6110	1.2963
Tenrec	361485	4.0302	5.9064	1.9519	Tenrec	364955	1.8829	7.9499	5.1574	1.4142
Tenrec	364955	3.1136	5.0354	2.3129	Tenrec	44967	1.9066	8.5360	5.0765	1.4423
Tenrec	44967	3.5869	5.9635	2.1319	Tenrec	59011	1.7079	8.1575	5.5644	1.5009
Tenrec	59011	3.9543			M. cowani	156221	0.3868	2.0334	0.0000	0.0000
M. cowani	156221		0.6526	0.4968	M. cowani	156222	0.3769	2.0195	0.0000	0.0000
M. cowani	156222	0.5124	0.9821	0.4468	M. cowani	156223	0.4518	2.0406	1.1455	0.4100
M. cowani	156223	0.5527	0.9911	0.4058	M. cowani	165672	0.3607	1.6971	0.8118	0.2602
M. cowani	165672	0.6029	0.9908	0.5245	M. cowani	165673	0.3355	1.7675	1.0604	0.3568
M. cowani	165673		0.8527	0.4026	M. cowani	165674	0.3691	2.1305	0.9904	0.2768
M. cowani	165674	0.6182	0.9593	0.4617	M. cowani	165689	0.3350	2.1261	1.1591	0.3687
M. cowani	165676	0.3870	0.8359	0.3417	M. cowani	168017	0.3703	1.7807	0.0000	0.0000
M. cowani	165689		1.0514	0.4011	M. cowani	449186	0.3018	1.8682	0.7326	0.2263
M. cowani	168017	0.1795	0.1877	0.0868	M. cowani	449187	0.4080	1.8079	0.8178	0.3594
M. cowani	449186		0.8870	0.3889	M. dobsoni	161935	0.5189	2.9224		
M. cowani	449187	0.7605	1.0233	0.4682	M. dobsoni	161940	0.3997	2.8192	1.1360	0.3638
M. dobsoni	161935	0.8676	1.5625	0.5603	M. dobsoni	165467	0.5245	3.0763		0.0101
M. dobsoni	161940	0.8811	1.4428	0.4937	M. dobsoni	165774	0.5771	2.9693	0.8265	0.3422
M. dobsoni	165467	1.1281	1.5880	0.5303	M. dobsoni	165775	0.4175	2.8567	1.1487	0.4062

Appendix 3.1 (con't)

Taxon	ID	Lateral1	Lateral2	Lateral3	Taxon	ID	Medial1	Medial2	Medial3	Medial4
M. dobsoni	165774	0.9421	1.6073	0.4277	M. dobsoni	166107	0.5004	2.7499	0.7842	0.3207
M. dobsoni	165775		1.6452	0.4591	M. dobsoni	166198	0.4678	2.7954	0.6078	0.2480
M. dobsoni	166107	0.9487	1.5446	0.4704	M. dobsoni	578749	0.4699	3.1799	1.0094	0.2872
M. dobsoni	166198	1.0948	1.3207	0.4583	M. dobsoni	582730	0.5323	2.7515	0.0100	
M. dobsoni	578749	1.1452	1.3956	0.5286	M. talazaci	154581	0.6743	3.2694	0.0097	
M. dobsoni	582730	1.3912	1.4228	0.5433	M. talazaci	154585	0.5946	3.0259		
M. talazaci	154581	1.1234	1.6669	0.6434	M. talazaci	167500	0.5321	3.1938	1.0314	0.4839
M. talazaci	154585	1.1766	1.3590	0.6439	M. talazaci	167501	0.5861	3.3631	1.4594	0.5032
M. talazaci	167500	1.0869	1.6736	0.6455	M. talazaci	167502	0.5598	3.2668		
M. talazaci	167501	0.9960			M. talazaci	167503	0.5211	3.3344	1.3716	0.4420
M. talazaci	167502	1.0770	1.6592	0.6202	M. talazaci	577056	0.5733	2.9729	1.3206	
M. talazaci	167503	1.1299	1.7957	0.6167	Oryzorictes	161746	0.5778	1.8076	1.5073	0.5741
M. talazaci	577056	1.3316	1.4790	0.5575	Oryzorictes	162053	0.5476	1.5103		
Oryzorictes	161746	0.8393	1.0965	0.8319	Oryzorictes	162058	0.5979	1.6508	1.6820	0.5552
Oryzorictes	162053	0.9098	1.6694	0.8260	Oryzorictes	166240	0.6141	1.7256	1.3742	0.6169
Oryzorictes	162054	1.3599	1.7638	0.8234	Oryzorictes	167480	0.7113	1.7055	1.4172	0.3631
Oryzorictes	162058	0.8599	1.4059	0.9392	Geogale	161594	0.2879	2.0748	0.5794	0.1942
Oryzorictes	166240	1.1724	1.3618	0.9810	Potamogale	34881	1.0369	5.5722		
Oryzorictes	167480	0.0193	1.4724	0.6864	Potamogale	51322	1.1938	5.9108		
Potamogale	34881	1.9742	3.6680	1.4567	Potamogale	51324		0.0096		
Potamogale	51322	2.3996	4.6809	1.8542	Potamogale	51327	0.9813	6.4054		
Potamogale	51324		4.5141	1.6595	Potamogale	51333	1.0369	10.0870		
Potamogale	51327	2.3509	4.0125	1.3813	Potamogale	51339	1.0230	6.4431	0.5750	0.3741
Potamogale	51333	2.0907	4.3263	1.4345	Potamogale	51344	1.1751	6.4194		
Potamogale	51339	2.4711	4.5913	1.7997	Potamogale	55204	0.8406	4.6308		
Potamogale	51344	2.8047	3.7897	2.2447	Solenodon	172680			2.7482	1.6854
Potamogale	55204	1.8115	2.8586	1.3979	Solenodon	172745	1.9962	8.8520		
Geogale	161594		0.8115	0.3458	Solenodon	290520	2.7234	12.3353	3.7590	1.6110
Petrodromus	203335	1.7742	2.1194	1.1594	Solenodon	395697	1.8611	9.9507	3.9859	1.3589
Petrodromus	203336	2.4578	2.9959	1.2865	Solenodon	395819	1.6215	10.6891		

Appendix 3.1 (con't)

Taxon	ID	Lateral1	Lateral2	Lateral3
Petrodromus	203337	2.0363	2.6104	1.2216
Petrodromus	203339		3.1689	1.3067
Solenodon	172680	5.5207		
Solenodon	290520	4.6418	7.6756	3.1442
Solenodon	395697		4.7452	3.2624
Solenodon	51068	3.9392	6.1802	2.3702
Solenodon	57320		4.9404	2.8912
Hemiechinus	185374	2.4037	2.5078	1.2671
Hemiechinus	51530	2.3026	2.1236	1.5853

Taxon	ID	Medial1	Medial2	Medial3	Medial4
Solenodon	51068	1.8956	9.7287	4.4799	2.0479
Solenodon	57320	1.9585	9.9016	2.5164	1.2406
Petrodromus	203335	0.9132		1.2050	0.5453
Petrodromus	203336	0.8091	8.8120	0.7219	0.4885
Petrodromus	203337	0.8617	7.7719		

Taxon	ID	Forearm1	Forearm2	Forearm3	Forearm4
Echinops	170605	2.3232	1.0216	0.6183	1.0916
Echinops	170607	2.3107	1.2557	0.8132	0.9624
Echinops	207717	2.3608	1.0452	1.0452	1.3358
Echinops	207718	2.3336	1.1376	0.8376	1.2910
Echinops	212918	2.1544	1.1102		
Echinops	31270	2.3547	1.0746	0.7959	0.0155
Echinops	328636		1.0326		
Echinops	328637	2.4404	1.1601		
Echinops	42958	2.4310	1.1068	0.9855	1.4190
Echinops	464980		1.0804		
Echinops	588220		1.3522		
Geogale	161594	0.9420	0.4613	0.2886	0.4110
Hemiechinus	185374	3.8422	1.6226	1.8926	2.2978
Hemicentetes	83658	3.5116	1.8534	1.1326	0.9554
Hemicentetes	10001	3.6077	1.2808	0.5697	1.1017
Hemicentetes	166132	2.5985	1.3738	0.4626	0.9968
Hemicentetes	170593	3.2652	1.0847		
Hemicentetes	206755		1.6219		
Hemicentetes	207714	2.4475	1.6767	1.0027	1.1917
Hemicentetes	207715		1.3176		
Hemicentetes	212920		1.4052		
Hemicentetes	212922		1.4709		

Taxon	ID	Forearm1	Forearm2	Forearm3	Forearm4
macroscelidid	203335	5.9770	3.1679	1.3369	0.8952
macroscelidid	203336	1.7649	0.9581	0.1305	
macroscelidid	203337	2.2520	1.0875		
Oryzorictes	161746		0.9986		
Oryzorictes	162053		1.0694		
Oryzorictes	162054		0.9964		
Oryzorictes	162058		1.0732	0.0112	
Oryzorictes	167480		1.1310		
Oryzorictes	578789		1.1150		
Potamogale	266897	3.6063	2.0090		1.0742
Potamogale	34881	3.2195	1.7362	1.4242	1.5651
Potamogale	35321	3.0816	1.8121	1.2619	2.4906
Potamogale	51322	3.6690	1.9973	1.5944	1.8689
Potamogale	51324	3.4322		1.5609	2.3245
Potamogale	51324		2.2027		
Potamogale	51333	2.8924		1.5903	2.6917
Potamogale	55204	2.9703	1.4779	1.4856	2.1933
Setifer	154033		1.9627		
Setifer	154034		1.9564		
Setifer	159731	3.4123	1.5858	0.6363	0.9005
Setifer	165494		1.5822		
Setifer	170532		1.6342		

Appendix 3.1 (con't)

Taxon	ID	Forearm1	Forearm2	Forearm3	Forearm4	Taxon	ID	Forearm1	Forearm2	Forearm3	Forearm4
Hemicentetes	212924		1.5516			Setifer	170548		2.1065		
Hemicentetes	29245	3.7761	1.2148	0.5683	1.3710	Setifer	170731		1.8957		
Hemicentetes	364954	3.5219	1.2346			Setifer	207076		1.6968		
Limngale	45050	2.0602	1.1125	1.0839	1.3006	Setifer	317872	3.8577	1.6887		
M cowani	156221		0.5340			Setifer	33948		1.6271		
M cowani	156222		0.5935			Setifer	395513		1.7229		
M cowani	156223		0.5913			Setifer	395719		1.2469		
M cowani	165672		0.5067			Setifer	42957	3.9153	2.1371	1.1663	1.5867
M cowani	165673		0.5918			Setifer	42959	3.3935	1.5953	1.7218	1.7735
M cowani	165674		0.5307			Setifer	541443		1.8734		
M cowani	165676		0.5581			Setifer	578790		1.7662		
M cowani	165680		0.5392			Setifer	85170		1.7636		
M cowani	165689		0.5186			Setifer	85513		1.7078		
M cowani	168017		0.6583			Solenodon	172680		3.1222		
M cowani	328658		0.5947			Solenodon	238263		2.7519		
M cowani	449184		0.5071			Solenodon	290520		2.5185		
M cowani	449186		0.5490			Solenodon	34859	9.2409	4.5674	2.5853	2.3200
M cowani	449187		0.5941			Solenodon	395697		3.9787		
M cowani	449188	1.1354	0.5197	0.3753	0.2941	Solenodon	395819		4.1472		
M. dobsoni	151624		0.7149			Solenodon	51068		3.3739		
M. dobsoni	161935	1.6568	0.7772			Solenodon	72809		3.7991		
M. dobsoni	161940		0.7828			Solenodon	290520		2.5571		
M. dobsoni	165467		0.7370			Tenrec	1001		3.1163		
M. dobsoni	165774		0.7788			Tenrec	1001	6.9346	2.7645	1.1561	1.7520
M. dobsoni	165775		0.6900			Tenrec	154628		2.3971		
M. dobsoni	166107		0.8070			Tenrec	156337	6.2138	2.4253		
M. dobsoni	166198	1.3670	0.6529	0.4508	0.6239	Tenrec	170511		2.6714		
M. dobsoni	166200		0.7864			Tenrec	174727		3.4116		
M. dobsoni	578749		0.7741			Tenrec	30398		2.5631	0.0350	
M. talazaci	154581		1.0408			Tenrec	364955		3.6557		
M. talazaci	154585		1.0690			Tenrec	577051		3.1933		
M. talazaci	577056		0.8203		0.0162	Tenrec	578792	7.4549	2.3805		0.0311

Appendix 3.2. Linear Measurement Means/SDs

Taxon		Forearm1	Forearm2	Forearm3	Forearm4	Dorsal1	Dorsal2	Dorsal3	Dorsal4	Dorsal5	Dorsal6	Dorsal7	Dorsal8	Dorsal9
Echinops	Mean	2.3386	1.1252	0.8493	1.0192	1.2217	0.8457	0.8595	0.7455	6.0716	0.7179	0.6958	0.6221	1.6242
	SD	0.0884	0.1004	0.1514	0.5196	0.4351	0.1046	0.1345	0.0852	0.4217	0.0854	0.0892	0.0805	0.6249
	n	8	11	6	6	10	8	8	16	15	16	16	15	10
Setifer	Mean	3.6447	1.7527	1.1748	1.4202	2.0778	1.2173	1.2559	1.1282	9.5578	1.0978	1.0716	1.0524	2.8133
	SD	0.2803	0.2130	0.5428	0.4597	0.3756	0.2886	0.3652	0.1168	0.5502	0.0991	0.1163	0.1673	0.4027
	n	4	18	3	3	15	14	14	15	15	15	15	14	6
Hemicentetes	Mean	3.2469	1.4238	0.7472	1.1233	1.3539	1.3107	0.9688	1.1918	7.5203	1.1280	1.0391	0.8274	1.3730
	SD	0.5411	0.2265	0.3260	0.1916	0.3446	0.2693	0.2884	0.2446	1.4181	0.2211	0.2308	0.1774	0.4244
	n	7	12	5	5	12	14	14	17	15	17	17	12	9
Tenrec	Mean	6.8678	2.8579	0.5955	0.8915	2.4163	2.0376	1.9215	1.6750	13.8879	1.7275	1.6618	1.5493	3.3997
	SD	0.6232	0.4571	0.7928	1.2169	0.6115	0.2641	0.2473	0.2448	1.5224	0.2334	0.2364	0.2944	0.1159
	n	3	10	2	2	10	11	11	11	11	11	11	11	2
M. cowani	Mean	1.1354	0.5591	0.3753	0.2941	0.6101	0.4218	0.3808	0.4415	3.6676	0.4029	0.3928	0.3841	1.2085
	SD	n/a	0.0433	n/a	n/a	0.0434	0.0311	0.0644	0.0471	0.2087	0.0287	0.0286	0.0451	0.1811
	n	1	15	1	1	10	9	9	15	15	15	15	15	8
M. dobsoni	Mean	1.5119	0.7501	0.4508	0.6239	1.0294	0.5296	0.4312	0.5811	5.9766	0.5653	0.5351	0.4853	1.8111
	SD	0.2050	0.0497	n/a	n/a	0.2344	0.0552	0.0550	0.0323	0.3597	0.0566	0.0377	0.0527	0.4078
	n	2	10	1	1	8	6	6	10	10	10	10	10	6
M. talazaci	Mean	n/a	0.9767	n/a	0.0162	1.1398	0.6342	0.6171	0.6392	6.5129	0.6311	0.5927	0.5452	1.9581
	SD	n/a	0.1362	n/a	n/a	0.2156	0.0624	0.0811	0.0221	0.1083	0.0336	0.0285	0.0736	0.5411
	n		3		1	5	5	5	5	5	5	5	5	4
Oryzorictes	Mean	n/a	1.0639	0.0112	n/a	1.0858	0.8925	0.7326	1.1268	3.9157	1.0138	0.8349	0.6770	1.5951
	SD	n/a	0.0567	n/a	n/a	0.2224	0.1093	0.2107	0.1588	0.3367	0.0942	0.0993	0.1709	0.3961
	n		6	1	0	7	8	8	8	8	8	8	8	6
Limngale	Mean	2.0602	1.1125	1.0839	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	n	1	1	1	1									
Geogale	Mean	0.9420	0.4613	0.2886	0.4110	0.4083	0.3333	0.3720	0.3056	3.3642	0.2930	0.2694	0.2840	1.1589
	SD	n/a	n/a	n/a	n/a	0.0000	0.0000	0.0000	0.0226	0.0079	0.0215	0.0150	0.0100	0.0000
	n	1	1	1	1	1	1	1	2	2	2	2	2	1

Appendix 3.2 (con't)

Taxon		Forearm1	Forearm2	Forearm3	Forearm4	Dorsal1	Dorsal2	Dorsal3	Dorsal4	Dorsal5	Dorsal6	Dorsal7	Dorsal8	Dorsal9
Potamogale	Mean	3.2673	1.8725	1.4862	2.0298	1.8274	1.2547	1.3739	0.9959	12.5167	1.1821	1.0988	0.9495	1.4197
	SD	0.3080	0.2535	0.1283	0.5656	0.8744	0.2401	0.2255	0.3799	1.0417	0.4439	0.4169	0.4304	0.0000
	n	7	7	6	7	7	8	8	8	7	8	8	6	1
Solenodon	Mean	9.2409	3.4240	2.5853	2.3200	3.5877	3.0548	2.0844	2.1536	17.2128	2.1337	2.0426	2.0292	4.9764
	SD	n/a	0.7412	n/a	n/a	0.6351	0.8501	0.5716	0.1669	1.2023	0.1545	0.1237	0.3305	0.3235
	n	1	9	1	1	8	9	9	9	9	9	8	8	2
Petrodromus	Mean	3.3313	1.7378	0.7337	0.8952	1.3249	0.9674	1.1272	1.0925	10.9186	1.1893	1.1332	1.1311	n/a
	SD	2.3042	1.2402	0.8531	n/a	0.1546	0.0760	0.1117	0.1688	1.5279	0.1417	0.1640	0.1895	n/a
	n	3	3	2	1	3	3	3	4	4	4	4	4	0
Hemiechinus	Mean	3.8422	1.6226	1.8926	2.2978	2.2230	1.5082	1.1919	1.3198	9.8373	1.5309	1.2885	1.3287	3.0850
	SD	n/a	n/a	n/a	n/a	0.2113	0.2957	0.1224	0.2707	2.0441	0.2895	0.2540	0.2901	0.6536
	n	1	1	1	1	3	3	3	3	3	3	3	3	3

Taxon		Dorsal10	Dorsal11	Dorsal12	Dorsal13	Dorsal14	Lateral1	Lateral2	Lateral3	Medial1	Medial2	Medial3	Medial4
Echinops	Mean	2.6077	3.4077	2.5257	1.4613	0.8846	1.6579	1.8617	0.8478	0.6831	3.6549	1.5164	0.6450
	SD	1.4691	0.3881	0.3489	0.2021	0.2774	0.2764	0.1799	0.1366	0.1244	0.4284	0.4134	0.1570
	n	14	15	10	12	13	10	11	11	12	12	9	9
Setifer	Mean	3.1497	5.1848	3.7994	1.9528	1.3486	2.3389	2.8566	1.1812	1.1030	4.9991	1.8247	0.8668
	SD	0.3520	0.2809	0.2909	0.3651	0.2595	0.7533	0.5617	0.1926	0.1209	0.4420	0.3510	0.1593
	n	14	11	15	14	14	13	13	13	11	11	9	9
Hemicentetes	Mean	2.3175	3.5319	3.7078	1.3174	1.2034	1.4452	2.5713	0.8423	0.9874	3.3993	1.7258	0.6549
	SD	0.5388	0.7548	0.7277	0.3330	0.2636	0.5111	0.3514	0.3040	0.4772	0.4095	0.6384	0.1164
	n	14	14	13	14	14	12	11	11	14	13	11	11
Tenrec	Mean	4.4615	5.6297	6.2025	2.4939	2.3225	3.4687	5.3312	2.1727	1.6882	7.9378	4.8823	1.4203
	SD	0.5258	0.8292	0.6351	0.4971	0.3061	0.4171	0.6009	0.2974	0.1867	0.4912	0.9637	0.0682
	n	12	7	11	12	12	7	7	7	6	6	6	6
M. cowani	Mean	0.9786	2.0544	1.1229	0.4998	0.3490	0.5162	0.8558	0.4023	0.3696	1.9272	0.6718	0.2258
	SD	0.1717	0.2059	0.3783	0.1809	0.0518	0.1866	0.2487	0.1171	0.0416	0.1603	0.4845	0.1654
	n	15	12	10	11	10	7	11	11	10	10	10	10
M. dobsoni	Mean	1.4236	3.1594	1.4319	0.7870	0.5777	1.0498	1.5033	0.4969	0.4898	2.9023	0.7889	0.2826
	SD	0.1125	0.2720	0.1391	0.1915	0.1143	0.1762	0.1109	0.0457	0.0568	0.1494	0.3957	0.1306
	n	10	8	8	6	6	8	9	9	9	9	7	7
M. talazaci	Mean	1.6572	3.3715	1.5935	0.9973	0.7310	1.1316	1.6055	0.6212	0.5773	3.2038	1.0385	0.4764
	SD	0.1659	0.5461	0.0914	0.0842	0.1056	0.1045	0.1576	0.0337	0.0505	0.1504	0.5971	0.0313

Appendix 3.2 (con't)

Taxon		Dorsal10	Dorsal11	Dorsal12	Dorsal13	Dorsal14	Lateral1	Lateral2	Lateral3	Medial1	Medial2	Medial3	Medial4
	n	5	5	5	5	5	7	6	6	7	7	5	3
Oryzorictes	Mean	1.6133	2.6731	2.3742	1.1169	0.6530	0.8601	1.4616	0.8480	0.6097	1.6800	1.4952	0.5273
	SD	0.3774	0.2341	0.3829	0.2438	0.1589	0.4598	0.2371	0.1034	0.0620	0.1103	0.1363	0.1125
	n	8	7	7	8	8	6	6	6	5	5	4	4
Limngale	Mean	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SD	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Geogale	Mean	0.6950	1.8558	1.1054	0.4013	0.2742	n/a	0.8115	0.3458	0.2879	2.0748	0.5794	0.1942
	SD	0.0000	0.2166	0.0000	0.0000	0.0000	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	n	1	2	1	1	1		1	1	1	1	1	1
Potamogale	Mean	2.3363	7.0604	3.4379	1.9340	1.5652	2.2718	4.0552	1.6536	1.0411	5.6848	0.5750	0.3741
	SD	0.3173	1.4888	0.4636	0.3331	0.1779	0.3365	0.6115	0.3017	0.1193	2.7876	n/a	n/a
	n	7	4	6	8	8				7	8	1	1
Solenodon	Mean	5.7828	9.0761	7.7680	3.0216	2.9709	4.7006	5.8853	2.9170	2.0094	10.2429	3.4979	1.5887
	SD	0.4031	0.5094	0.7721	0.3384	0.4310	0.7924	1.3522	0.3961	0.3736	1.1814	0.8361	0.3141
	n	9	6	8	9	9	3	4	4	6	6	5	5
Petrodromus	Mean	2.4073	4.1335	3.3692	1.5958	1.0623	2.0894	2.7237	1.2436	0.8613	8.2920	0.9635	0.5169
	SD	0.2112	0.1267	0.2273	0.0559	0.0245	0.3449	0.4656	0.0668	0.0521	0.7355	0.3416	0.0402
	n	4	3	3	3	3	3	4	4	3	2	2	2
Hemiechinus	Mean	3.7632	3.5568	3.5984	2.4347	1.2035	2.3532	2.3157	1.4262	n/a	n/a	n/a	n/a
	SD	0.2612	0.1798	0.6049	0.2257	0.1838	0.0715	0.2717	0.2250	n/a	n/a	n/a	n/a

Appendix 3.3. Raw Index Scores

ID	Genus	CMI	CSI	HLI	MRI	M3SI	RWI	UMSI	USI	UWI	Genus	ID	SLCI
134550	Echinops	0.3400	2.3387		1.1463	7.6133	0.8829	1.4595	1.5778	0.7183	erinaceid	185374	1.5837
153785	Echinops	0.3540	2.8617	0.1869	1.0980	8.8357	1.0485		1.6065	0.6980	Geogale	161594	1.7282
159730	Echinops				1.2237	10.6611	0.8618		1.3155	0.8345	macroscelidids	203336	1.8228
170605	Echinops				0.9457						macroscelidids	203337	2.1846
170607	Echinops				1.0695		0.9515			0.8887	macroscelidids	203339	2.5309
207717	Echinops				1.1145	9.4907					Limnogale	45050	1.5408
207718	Echinops	0.2866	3.4603	0.1585	1.0104	8.4568		1.8832	1.7683		M. cowani	156221	1.8794
212918	Echinops	0.3275	2.7389			6.5675		1.3398	1.8175		M. cowani	165672	1.5665
212919	Echinops	0.2618		0.1428							M. cowani	165673	1.7898
31270	Echinops	0.3343		0.2175	1.1543	8.2254	0.9491	1.3001	1.3823		M. cowani	165680	1.6953
328636	Echinops	0.3053			1.2601	8.0627			1.3714		M. cowani	165689	1.4971
328637	Echinops	0.3518	2.5017		1.2551	7.6807	0.7914	1.3377	1.5000	0.6002	M. cowani	449186	1.7691
464980	Echinops	0.3105	2.4244	0.1692	1.0674	9.0872		1.3648	1.6032		M. dobsoni	161935	1.4863
57579	Echinops				1.2950	7.9797	0.8793		1.2491	0.5333	M. dobsoni	161940	1.6829
57580	Echinops	0.3322		0.1856	1.0636	9.2229	0.9938	1.6306	2.0414	0.5479	M. dobsoni	165467	1.9294
57581	Echinops	0.3760		0.1849	0.8852	9.3683	0.9203			0.7104	M. dobsoni	165774	1.8218
588220	Echinops		2.8509		1.0526	6.6727		1.2128	1.2585		M. dobsoni	165775	1.6589
83658	Hemicentetes	0.2691		0.1840		7.6203					M. dobsoni	166107	1.7081
10001	Hemicentetes	0.2501		0.1547	1.1902	5.5947		1.1144	1.5093		M. dobsoni	578749	1.7498
161757	Hemicentetes	0.4046			1.2471	6.1215		1.0136	0.8574		M. talazaci	154581	1.6238
162059	Hemicentetes	0.2481		0.1512	1.0973	6.7946		1.0853	1.2734		Oryzorictes	162058	1.6924
162062	Hemicentetes	0.2999		0.1802	1.2267	6.8970	0.9558	1.1469	0.9849	0.4922	Potamogale	34881	1.9712
166132	Hemicentetes	0.2649		0.1625	1.2612	7.1737		1.0558	0.7949		Potamogale	35321	1.8222
170593	Hemicentetes					6.3485		1.0000	1.2091		Potamogale	51322	1.6052
207712	Hemicentetes	0.2840		0.1658	1.2883	7.6172		1.1204	1.2547		Potamogale	51324	2.1169
207714	Hemicentetes				1.2977	7.0289	0.9377	1.1099	0.7933	0.5527	Potamogale	51327	1.8848
207715	Hemicentetes	0.2796		0.1703	1.2737	6.9439		1.1197	0.8303		Potamogale	51333	1.7454
212920	Hemicentetes	0.3006		0.1940	1.3101	6.0133	0.9247	1.1771	1.1349	0.8135	Potamogale	51334	1.9381
212922	Hemicentetes	0.3239		0.1860		6.1776	1.0134			0.5781	Solenodon	34859	1.9277
212924	Hemicentetes	0.3586			1.1812	7.0948		1.1123	1.3001		Solenodon	72809	1.9599
212940	Hemicentetes	0.3203				5.8319	0.8503	1.1564	0.9476	0.4005	Echinops	42958	1.6922
339992	Hemicentetes				1.1431		0.8983	1.1103	1.6339	0.8153	Echinops	207717	1.5870

Appendix 3.3 (con't)

ID	Genus	CMI	CSI	HLI	MRI	M3SI	RWI	UMSI	USI	UWI	Genus	ID	SLCI
364954	Hemicentetes	0.3438		0.2122	1.0674	9.4475	0.9065	1.3401	1.0982	0.7380	Echinops	207718	1.5931
124554	Setifer		2.5179		1.1425	9.9095	0.8335	1.3484	1.5424	0.5166	Hemicentetes	364954	1.5361
154033	Setifer	0.3805	1.6894	0.1972	1.0304	8.8400	0.9290	1.4472	1.7130	0.6790	Setifer	5112	1.6854
154034	Setifer		2.1624				0.7629	1.6258	1.3162	0.5177	Setifer	33948	1.8105
159731	Setifer	0.3622	2.8466	0.1958	1.0767	8.4343	0.8081	1.2176	1.6924	0.8099	Setifer	42959	1.9437
165494	Setifer	0.2971	1.6668	0.1681	1.0601	9.5294	0.8451	1.2362	1.2545	0.8925	Setifer	85513	1.4425
170532	Setifer	0.3415	2.5248			8.3199	0.7704	1.0930	1.3141		Setifer	165494	1.9413
170581	Setifer	0.3737	2.1838		1.0756	7.7345	0.8993	1.5097	1.4351	1.1326	Tenrec	156337	1.6284
170731	Setifer	0.3576	1.6971		0.9813	7.7876	0.8026	1.3966	1.9578	0.7877			
395513	Setifer	0.3287		0.1835	0.9110	10.3225	0.8729			0.6483			
395719	Setifer	0.3092	2.4718		1.1326	9.8442		1.1387	1.2763				
42957	Setifer	0.2863	2.6231		0.9626	8.6447	0.7429	1.2242	1.5966	0.9797			
42959	Setifer	0.2756	5.0254		1.1687	8.5654		1.4411	1.3400				
5112	Setifer	0.3914	1.6307		1.1023	6.9841		1.2980	1.2548				
541443	Setifer	0.2622			1.0171	9.4221		1.1784	1.3785				
578790	Setifer	0.3176	2.8667	0.1709	1.0211	8.5051	0.8016	1.4719	1.3775	0.8582			
85170	Setifer	0.3458		0.1980	1.0516	8.6989	0.9342			0.7987			
1001	Tenrec	0.3633			1.2058	7.7496	0.8557	1.1938	0.8970				
154628	Tenrec	0.3376	1.3259	0.2010	1.0481	7.7435	0.7294	1.2781	1.3906	0.9115			
170511	Tenrec	0.3084	2.5006		1.1640	8.3768		1.1034	0.7580				
174727	Tenrec		3.5103					1.1813	1.0284				
30398	Tenrec	0.3088	2.4023		0.9587	8.6035		1.2001	1.0735				
361485	Tenrec	0.2804			0.9646	9.4831	0.7239		1.1698	0.9896			
364955	Tenrec	0.3431	1.4984	0.2109	0.9643	8.1129	0.7134	1.3613	0.9353	1.0654			
44967	Tenrec	0.3372	1.3383		1.0672	7.0006	0.9865	1.2593	1.2146	0.4830			
577051	Tenrec	0.3266	1.8469		1.1137	8.3907	0.8121	1.1555	1.0778	1.0921			
578792	Tenrec	0.3264	1.7898		0.9898	7.6606	0.6767	1.5862	1.2036	0.7905			
59011	Tenrec	0.3518	2.2678		1.1359	7.6762	0.7344	1.1132	0.9242	0.8424			
154581	M. talazaci	0.2676	2.2161		1.2259	9.9031	0.8588	1.3717	1.4942	0.6621			
154585	M. talazaci	0.2839	2.1616	0.1478	1.0840	10.0513	0.8618	1.3708	1.2419	0.7860			
167502	M. talazaci	0.2460	3.3945	0.1367	1.2421	10.9437	0.7774	1.3766	1.4029	0.8248			
167503	M. talazaci	0.2706		0.1382	0.9669	10.8114	0.9246	1.4231	1.2299	0.6059			
577056	M. talazaci	0.2054	2.6038	0.1314	1.1027	10.0026		1.3573	1.5244				
156221	M.cowani	0.3296		0.1699	0.9850	10.2709							
156222	M.cowani	0.1508			1.0303	9.0686							

Appendix 3.3 (con't)

ID	Genus	CMI	CSI	HLI	MRI	M3SI	RWI	UMSI	USI	UWI	Genus	ID	SLCI
156223	M.cowani	0.3220			1.2012	7.5445							
165672	M.cowani	0.2371		0.1302	1.0147	9.4330		1.2086	1.7375				
165673	M.cowani	0.2550			0.9316	9.0652		1.3495	2.1399				
165674	M.cowani	0.2921		0.1527	1.1679	8.9768		1.1435	1.2221				
165676	M.cowani	0.2728		0.1392	1.0890	8.3059	0.9896			0.9106			

Appendix 3.3 (con't)

ID	Genus	CMI	CSI	HLI	MRI	M3SI	RWI	UMSI	USI	UWI
165680	M.cowani	0.2745		0.1460	1.1665	9.0620		0.9958	1.0497	
165689	M.cowani	0.2463			1.1337	9.3789		1.2945	1.7191	
168017	M.cowani	0.2884		0.1566	1.2212	9.7500	0.9086			1.2195
328658	M.cowani	0.2066			0.9260	9.9329			1.9303	
449184	M.cowani	0.2668		0.1356	1.1157	9.0610		1.1778	1.8157	
449186	M.cowani	0.2360			1.1261	9.8765		0.9179	1.5965	
449187	M.cowani	0.3115			1.1449	8.6006	0.9659	1.0194	1.3829	0.8372
449188	M.cowani	0.3208		0.1656	1.1071	8.7105	0.9530	0.9761	1.3798	0.7930
161935	M.dobsoni	0.2214		0.1242	1.0586	10.7937				
161940	M.dobsoni	0.2551	1.7484	0.1286	1.0585	9.7882	0.8174	1.2571	1.9700	1.5327
165467	M.dobsoni	0.2274		0.1270	0.9854	12.2603	0.9469			1.0580
165774	M.dobsoni	0.2455	2.0352		1.0747	11.3644		1.6776	1.7086	
165775	M.dobsoni	0.2049	2.0751		1.1923	9.4211	1.1214			0.8585
166107	M.dobsoni	0.2557			1.1517	10.2247	0.9389			0.9870
166198	M.dobsoni	0.2395	2.4226	0.1274	1.1731	11.7101	0.9010	1.4815	1.1698	0.6718
166200	M.dobsoni	0.2251	1.7732		1.0300	11.4306		1.5900	2.0424	
578749	M.dobsoni	0.2356	2.6824	0.1310	1.3866	8.8011	0.9211	1.3352	1.2455	0.7825
582730	M.dobsoni	0.2760	1.6433	0.1441	1.1751	10.7705	0.8757	1.1886	0.5768	0.9345
161746	Oryzorictes	0.3598		0.1862	1.6624	3.7222	0.8291	0.8866	1.1476	1.1755
162053	Oryzorictes	0.4065		0.1865	1.3794	3.6752	0.9505	1.2160	1.5321	1.0420
162054	Oryzorictes	0.4086		0.1909	1.4681	4.2638	1.1187	1.1670	1.6083	0.9676
162058	Oryzorictes	0.3887			1.7798	3.7430		1.0724	1.8603	
166240	Oryzorictes	0.4686		0.2306	1.3246	4.1995	0.9687	1.1294	1.6408	1.0903
167480	Oryzorictes	0.5530		0.2675	1.5520	3.4691	1.0386	1.1543	1.8281	1.2733
31257	Oryzorictes	0.2845			1.2750	4.5204		1.0221	2.5787	
578789	Oryzorictes	0.4024		0.1844	1.0930	3.4756		1.0208	1.9214	
159733	Geogale				1.0110	12.3655				
161594	Geogale	0.2061	2.0166		1.1509	10.7225		0.9578	1.4638	
266897	Potamogale	0.2026			0.9577	9.4955	1.0772	1.4229	1.2722	1.0529
34881	Potamogale	0.1937				9.3430	1.0053	1.2570	1.0742	0.9192
34881	Potamogale							1.4392		
51322	Potamogale	0.1634			1.0385	8.9466			1.4666	
51324	Potamogale	0.1410			1.1831	9.6156				
51324	Potamogale							1.3746	1.4346	
51327	Potamogale	0.2620				8.2283	1.0283	1.0062	0.9730	0.6942
51339	Potamogale	0.1832			1.0646	9.1166	0.9799	1.3964	1.0791	0.9185
51344	Potamogale	0.1747		0.1051	1.0191	10.1677	0.8919	1.4660	1.5199	0.9096
55204	Potamogale				0.8536			1.2791	1.0889	
203335	Macroscelidid	0.2297	3.4405		0.9994	9.2379	0.8470	1.2154	1.4422	1.6232
203336	Macroscelidid	0.2453	2.8104		1.0659	8.6112	0.8526	1.2722	1.4435	1.6023
203337	Macroscelidid	0.2192	2.7009		1.0073	9.2133	0.8139	1.3224	1.6266	1.5700
203339	Macroscelidid	0.1953			0.9693	9.6096				
49508	Solenodon							1.2005	0.9593	
172680	Solenodon	0.3288	2.2884	0.1858	1.0512	8.8652	0.8907	1.0986	0.9761	0.8783
172745	Solenodon	0.4133	1.7662	0.2195	0.8965	8.3989		1.1405	1.3113	
217256	Solenodon		2.4395				0.8743			
238263	Solenodon	0.3134			1.1342	7.8321		1.1609	1.2031	
290520	Solenodon	0.3157	3.0461		1.0783	8.0600	0.8614	1.0744	0.6303	0.8769
34859	Solenodon	0.3607	2.1010			6.4166		1.2699	0.9408	
395697	Solenodon	0.3617	2.4639		1.1240	7.8669		1.2260	1.0706	
395819	Solenodon	0.2810	1.8739		0.9670	8.9458		1.2255	1.2180	
51068	Solenodon	0.3065	2.6431		1.2030	8.6412	0.9139	1.1478	1.0505	1.2355
57320	Solenodon	0.3614	2.7818		1.0457	7.8987		1.3394	2.0043	

Appendix 3.3 (con't)

ID	Genus	CMI	CSI	HLI	MRI	M3SI	RWI	UMSI	USI	UWI
185374	Erinaceid	0.3663		0.2252	1.2465	6.3121	0.9002			0.7824
51530	Erinaceid	0.5103			0.9776	6.3270	1.1189	1.4455	2.2366	0.7703
6021	Erinaceid	0.3166			1.0632	6.5759	0.8854	1.2844	1.8861	0.8062

ID	Taxon	PPSI	M1SI	ID	Taxon	Genus	PSI	PSHI
134550	Echinops	3.2571		134550	Echinops	Echinops	1.7961	1.6775
153785	Echinops	4.0600	5.8586	153785	Echinops	Echinops	2.8113	2.5421
159730	Echinops	1.8146	6.0541	159730	Echinops	Echinops	2.3146	2.5380
170607	Echinops	1.9493	7.8102	170607	Echinops	Echinops	2.6589	2.2465
207718	Echinops	1.3601	4.9053	207718	Echinops	Echinops	1.9043	
212918	Echinops		4.9826	31270	Echinops	Echinops	2.0599	2.2568
31270	Echinops	1.8172	4.5325	328636	Echinops	Echinops	1.6178	2.0965
328636	Echinops		4.9138	42958	Echinops	Echinops	3.3460	2.1588
464980	Echinops	3.4299	4.4757	57579	Echinops	Echinops	2.2567	2.4086
57580	Echinops		6.0771	57580	Echinops	Echinops	2.0126	2.0039
57581	Echinops	2.1698	6.1622	57581	Echinops	Echinops	2.1135	2.5452
588220	Echinops	2.4784	5.5719	161757	Hemicentetes	Hemicentetes		1.6328
161757	Hemicentetes	3.7982	3.2740	162059	Hemicentetes	Hemicentetes		
161758	Hemicentetes	2.5177	3.6855	162062	Hemicentetes	Hemicentetes		0.0133
162059	Hemicentetes		5.6402	166132	Hemicentetes	Hemicentetes	2.7613	2.4544
162062	Hemicentetes	2.2999	3.9084	170593	Hemicentetes	Hemicentetes		
166132	Hemicentetes	2.6907	4.5402	207715	Hemicentetes	Hemicentetes	2.5078	
170593	Hemicentetes		4.0044	212920	Hemicentetes	Hemicentetes	2.5426	2.9991
207714	Hemicentetes	3.2153	3.8784	212922	Hemicentetes	Hemicentetes	3.6350	
207715	Hemicentetes	3.5567	3.5534	212924	Hemicentetes	Hemicentetes	2.7541	
212920	Hemicentetes	3.4663	4.0994	212940	Hemicentetes	Hemicentetes	3.5490	2.9907
212940	Hemicentetes		3.3437	29245	Hemicentetes	Hemicentetes	2.2466	2.2360
339992	Hemicentetes	2.8485	3.8525	339992	Hemicentetes	Hemicentetes		
354998	Hemicentetes	2.2755		354998	Hemicentetes	Hemicentetes	2.7535	3.1336
364954	Hemicentetes	2.8376	5.1975	364954	Hemicentetes	Hemicentetes	3.4274	3.0423
5299	Hemicentetes			5299	Hemicentetes	Hemicentetes	2.2709	
10001	Hemicentetes		2.9986	124554	Setifer	Setifer	2.2756	2.0843
124554	Setifer		4.7340	154033	Setifer	Setifer	2.1832	2.7256
154033	Setifer		5.0481	154034	Setifer	Setifer	2.7431	2.8665
159731	Setifer		3.7660	159731	Setifer	Setifer	2.8120	2.2423
165494	Setifer	2.1508	5.4494	165494	Setifer	Setifer	1.9556	1.0423
170532	Setifer	1.3079	3.9919	170532	Setifer	Setifer	2.1693	
170581	Setifer	2.0045		170581	Setifer	Setifer	2.3324	2.1641
170731	Setifer		4.7279	170731	Setifer	Setifer	2.2658	2.8295
395513	Setifer	3.3037	3.8801	395513	Setifer	Setifer	2.4419	2.4383
42957	Setifer	2.1552		42957	Setifer	Setifer	2.6002	2.2587
42959	Setifer	1.7318	5.5007	42959	Setifer	Setifer	2.1863	1.9484
5112	Setifer	1.6587	4.1382	5112	Setifer	Setifer	2.5150	2.2357
541443	Setifer	2.5921	4.4929	85170	Setifer	Setifer	2.8806	1.9881
85170	Setifer	2.7387	4.6090	1001	Tenrec	Tenrec	2.2812	2.6729
1001	Tenrec	3.3685	4.9452	154628	Tenrec	Tenrec	3.0500	2.0899
174727	Tenrec			174727	Tenrec	Tenrec	1.6997	2.0233
30398	Tenrec	2.1165	4.9988	30398	Tenrec	Tenrec	2.5068	
361485	Tenrec	4.3283	4.9456	361485	Tenrec	Tenrec	3.0260	2.1428
364955	Tenrec	3.6469	4.2222	364955	Tenrec	Tenrec	2.1771	2.2476
44967	Tenrec	3.5196	4.4772	44967	Tenrec	Tenrec	2.7973	2.2451
59011	Tenrec	3.7074	4.7765	59011	Tenrec	Tenrec		

Appendix 3.3 (con't)

ID	Taxon	PPSI	M1SI	ID	Taxon	Genus	PSI	PSHI
156221	M. cowani		5.2574	156221	M. cowani	Microgale	1.3137	
156222	M. cowani		5.3576	156222	M. cowani	Microgale	2.1981	2.0321
156223	M. cowani	2.7935	4.5171	156223	M. cowani	Microgale	2.4424	1.9815
165672	M. cowani	3.1205	4.7054	165672	M. cowani	Microgale	1.8891	4.2429
165673	M. cowani	2.9716	5.2683	165673	M. cowani	Microgale	2.1179	
165674	M. cowani	3.5783	5.7730	165674	M. cowani	Microgale	2.0775	1.9541
165689	M. cow ani	3.1441	6.3458	165676	M. cowani	Microgale	2.4461	1.7981
168017	M. cowani		4.8084	165689	M. cowani	Microgale	2.6211	
449186	M. cowani	3.2374	6.1895	168017	M. cowani	Microgale	2.1625	2.3070
449187	M. cowani	2.2754	4.4313	449186	M. cowani	Microgale	2.2804	
161935	M. dobsoni		5.6317	449187	M. cowani	Microgale	2.1858	2.5167
161940	M. dobsoni	3.1225	7.0530	161935	M. dobsoni	Microgale	2.7888	2.1850
165467	M. dobsoni		5.8647	161940	M. dobsoni	Microgale	2.9223	2.2383
165774	M. dobsoni	2.4150	5.1455	165467	M. dobsoni	Microgale	2.9945	1.8861
165775	M. dobsoni	2.8281	6.8423	165774	M. dobsoni	Microgale	3.7579	1.9123
166107	M. dobsoni	2.4454	5.4955	165775	M. dobsoni	Microgale	3.5837	
166198	M. dobsoni	2.4507	5.9763	166107	M. dobsoni	Microgale	3.2833	1.7089
578749	M. dobsoni	3.5153	6.7667	166198	M. dobsoni	Microgale	2.8816	1.8673
582730	M. dobsoni		5.1694	578749	M. dobsoni	Microgale	2.6401	1.8535
154581	M. talazaci		4.8486	582730	M. dobsoni	Microgale	2.6186	2.1456
154585	M. talazaci		5.0892	154581	M. talazaci	Microgale	2.5908	2.1737
167500	M. talazaci	2.1313	6.0024	154585	M. talazaci	Microgale	2.1107	1.7140
167501	M. talazaci	2.9003	5.7379	167500	M. talazaci	Microgale	2.5926	2.2400
167502	M. talazaci		5.8362	167501	M. talazaci	Microgale		
167503	M. talazaci	3.1034	6.3990	167502	M. talazaci	Microgale	2.6753	2.4456
577056	M. talazaci		5.1854	167503	M. talazaci	Microgale	2.9119	2.2084
161746	Oryzorictes	2.6257	3.1283	577056	M. talazaci	Microgale	2.6531	2.1622
162053	Oryzorictes		2.7582	161746	Oryzorictes	Oryzorictes	1.3180	2.8502
162058	Oryzorictes	3.0295	2.7609	162053	Oryzorictes	Oryzorictes	2.0210	2.1089
166240	Oryzorictes	2.2276	2.8101	162054	Oryzorictes	Oryzorictes	2.1421	2.0782
167480	Oryzorictes	3.9034	2.3977	162058	Oryzorictes	Oryzorictes	1.4970	3.8808
161594	Geogale	2.9840	7.2061	166240	Oryzorictes	Oryzorictes	1.3882	2.1678
34881	Potamogale		5.3741	167480	Oryzorictes	Oryzorictes	2.1450	
51322	Potamogale		4.9512	34881	Potamogale	Potamogale	2.5180	3.1003
51324	Potamogale			51322	Potamogale	Potamogale	2.5244	2.6826
51327	Potamogale		6.5276	51324	Potamogale	Potamogale	2.7202	
51333	Potamogale		9.7285	51327	Potamogale	Potamogale	2.9049	2.2468
51339	Potamogale	1.5369	6.2981	51333	Potamogale	Potamogale	3.0158	
51344	Potamogale		5.4628	51339	Potamogale	Potamogale	2.5512	2.2679
55204	Potamogale		5.5089	51344	Potamogale	Potamogale	1.6883	2.7666
172680	Solenodon	1.6306		55204	Potamogale	Potamogale	2.0448	2.3244
172745	Solenodon		4.4345	161594	Geogale	Geogale	2.3465	
290520	Solenodon	2.3333	4.5294	203335	Macroscelidids	Macroscelidids	1.8280	3.4805
395697	Solenodon	2.9332	5.3468	203336	Macroscelidids	Macroscelidids	2.3288	4.7536
395819	Solenodon		6.5920	203337	Macroscelidids	Macroscelidids	2.1369	5.2992
51068	Solenodon	2.1876	5.1322	203339	Macroscelidids	Macroscelidids	2.4251	
57320	Solenodon	2.0283	5.0557	172680	Solenodon	Solenodon		
203335	Macroscelidid	2.2098		290520	Solenodon	Solenodon	2.4412	2.8096
203336	Macroscelidid	1.4779	10.8912	395697	Solenodon	Solenodon	1.4545	
203337	Macroscelidid		9.0188	51068	Solenodon	Solenodon	2.6075	2.7960
				57320	Solenodon	Solenodon	1.7088	
				185374	Erinaceid	Erinaceid	1.9792	1.6040
				51530	Erinaceid	Erinaceid	1.3395	1.8075

Appendix 3.4. Index Summary Statistics and Tukey Post-Hoc Results

Taxon	RWI		RWI				
	Means	N	Std.Dev.				
Tenrecinae	1.846680	24	0.368896				
Oryzorictinae	1.913605	17	0.199597				
Potamogalinae	1.802780	2	0.069760				
Macroscelidinae	2.488952	3	1.325683				
Solenodontinae	2.665685	3	0.374436				
Erinaceinae	2.312304	3	0.438644				
All Grps	1.978038	52	0.465165				
	{1}	{2}	{3}	{4}	{5}	{6}	{7}
	M=1.8467	M=1.9136	M=0.0000	M=1.8028	M=2.4890	M=2.6657	M=2.3123
Tenrecinae {1}		0.995691		0.999992	0.138832	0.027113	0.458170
Oryzorictinae {2}	0.995691			0.999246	0.253285	0.061433	0.646446
Geogalinae {3}							
Potamogalinae {4}	0.999992	0.999246			0.471044	0.225865	0.760091
Macroscelidinae {5}	0.138832	0.253285		0.471044		0.995157	0.995168
Solenodontinae {6}	0.027113	0.061433		0.225865	0.995157		0.901532
Erinaceinae {7}	0.458170	0.646446		0.760091	0.995168	0.901532	

Taxon	UWI		UWI				
	Means	N	Std.Dev.				
Tenrecinae	0.748990	33	0.189674				
Oryzorictinae	0.950627	20	0.230093				
Geogalinae		0					
Potamogalinae	0.898884	5	0.128953				
Macroscelidinae	1.598508	3	0.026793				
Solenodontinae	0.996888	3	0.206640				
Erinaceinae	0.786324	3	0.018279				
All Grps	0.871176	67	0.263714				
	{1}	{2}	{3}	{4}	{5}	{6}	{7}
	M=.74899	M=.95063	M=0.0000	M=.89888	M=1.5985	M=.99689	M=.78632
Tenrecinae {1}		0.006908		0.598780	0.000132	0.295076	0.999587
Oryzorictinae {2}	0.006908			0.994718	0.000147	0.998915	0.748389
Geogalinae {3}							
Potamogalinae {4}	0.598780	0.994718			0.000218	0.982540	0.967938
Macroscelidinae {5}	0.000132	0.000147		0.000218		0.004642	0.000173
Solenodontinae {6}	0.295076	0.998915		0.982540	0.004642		0.770232
Erinaceinae {7}	0.999587	0.748389		0.967938	0.000173	0.770232	

Taxon	PLI		PLI	
	Means	N	Std.Dev.	
Echinops	1.556991	10	0.247936	
Hemicentetes	2.017375	7	0.348006	
Setifer	1.584427	12	0.358873	
Tenrec	1.585087	6	0.189202	
All Grps	1.663291	35	0.342032	

	{1}	{2}	{3}	{4}
	M=1.5570	M=2.0174	M=1.5844	M=1.5851
Echinops {1}		0.022031	0.996706	0.998003
Hemicentetes {2}	0.022031		0.026566	0.071556
Setifer {3}	0.996706	0.026566		1.000000
Tenrec {4}	0.998003	0.071556	1.000000	

Taxon	PSI	PSI	PSI
	Means	N	Std.Dev.
Echinops	2.262880	11	0.502214
Hemicentetes	2.844809	10	0.513747
Setifer	2.412380	13	0.281786
Tenrec	2.505439	7	0.493300
Microgale	2.566919	26	0.521892
Oryzorictes	1.751898	6	0.391093
Potamogale	2.495958	8	0.438822
All Grps	2.462441	81	0.518413

	{1}	{2}	{3}	{4}	{5}	{6}	{7}
	M=2.2629	M=2.8448	M=2.4124	M=2.5054	M=2.5669	M=1.7519	M=2.4960
Echinops {1}		0.080336	0.986352	0.934604	0.549196	0.335465	0.934645
Hemicentetes {2}	0.080336		0.310834	0.761230	0.686206	0.000563	0.701381
Setifer {3}	0.986352	0.310834		0.999568	0.958646	0.077714	0.999703
Tenrec {4}	0.934604	0.761230	0.999568		0.999932	0.071368	1.000000
Microgale {5}	0.549196	0.686206	0.958646	0.999932		0.004671	0.999788
Oryzorictes {6}	0.335465	0.000563	0.077714	0.071368	0.004671		0.062991
Potamogale {7}	0.934645	0.701381	0.999703	1.000000	0.999788	0.062991	

Taxon	SLCI	SLCI	SLCI
Echinops	0.402421	2	0.037948
Hemicentetes	0.356253	2	0.000703
Setifer	0.327280	2	0.030020
Tenrec	0.262057	2	0.010582
All Grps	0.337003	8	0.057541

	{1}	{2}	{3}	{4}
	M=.40242	M=.35625	M=.32728	M=.26206
Echinops {1}		0.366814	0.120736	0.016386
Hemicentetes {2}	0.366814		0.673458	0.062104
Setifer {3}	0.120736	0.673458		0.175138
Tenrec {4}	0.016386	0.062104	0.175138	

Taxon	UMSI	UMSI	UMSI
	Means	N	Std.Dev.
Echinops	1.441067	8	0.217277
Hemicentetes	1.118738	14	0.080888
Setifer	1.330497	14	0.156942
Tenrec	1.243242	10	0.143502

All Grps	1.266310	46	0.184587	
	{1}	{2}	{3}	{4}
	M=1.4411	M=1.1187	M=1.3305	M=1.2432
Echinops {1}		0.000240	0.344462	0.035786
Hemicentetes {2}	0.000240		0.002751	0.193317
Setifer {3}	0.344462	0.002751		0.492467
Tenrec {4}	0.035786	0.193317	0.492467	

Taxon	USI	USI	USI	
	Means	N	Std.Dev.	
Echinops	1.540962	12	0.244846	
Hemicentetes	1.115853	14	0.264783	
Setifer	1.460655	14	0.211177	
Tenrec	1.061145	11	0.178632	
All Grps	1.298730	51	0.304304	
	{1}	{2}	{3}	{4}
	M=1.5410	M=1.1159	M=1.4607	M=1.0611
Echinops {1}		0.000280	0.809837	0.000207
Hemicentetes {2}	0.000280		0.001440	0.933985
Setifer {3}	0.809837	0.001440		0.000585
Tenrec {4}	0.000207	0.933985	0.000585	

Taxon	CSI	CSI	CSI	
	Means	N	Std.Dev.	
Echinops	2.739503	7	0.379339	
Hemicentetes		0		
Setifer	2.454349	13	0.893853	
Tenrec	2.053376	9	0.702758	
All Grps	2.398740	29	0.763651	
	{1}	{2}	{3}	{4}
	M=2.7395	M=0.0000	M=2.4543	M=2.0534
Echinops {1}			0.695939	0.180077
Hemicentetes {2}				
Setifer {3}	0.695939			0.439734
Tenrec {4}	0.180077		0.439734	

Taxon	PPPI	PPPI	PPPI	
	Means	N	Std.Dev.	
Echinops	5.432910	8	0.605081	
Hemicentetes	3.281640	10	0.653731	
Setifer	5.491367	4	0.613113	
Tenrec	3.477874	2	0.738398	
All Grps	4.383371	24	1.243818	
	{1}	{2}	{3}	{4}
	M=5.4329	M=3.2816	M=5.4914	M=3.4779
Echinops {1}		0.000177	0.998814	0.004753
Hemicentetes {2}	0.000177		0.000215	0.978042
Setifer {3}	0.998814	0.000215		0.007945
Tenrec {4}	0.004753	0.978042	0.007945	

Taxon	M1SI Means	M1SI N	M1SI Std.Dev.	
Echinops	5.576740	11	0.971347	
Hemicentetes	3.998164	13	0.748877	
Setifer	4.576202	11	0.597497	
Tenrec	4.727557	6	0.312717	
All Grps	4.683508	41	0.938680	
	{1}	{2}	{3}	{4}
	M=5.5767	M=3.9982	M=4.5762	M=4.7276
Echinops {1}		0.000200	0.015427	0.125502
Hemicentetes {2}	0.000200		0.242162	0.206897
Setifer {3}	0.015427	0.242162		0.977546
Tenrec {4}	0.125502	0.206897	0.977546	

Taxon	M1SI Means	M1SI N	M1SI Std.Dev.	
M. cowani	5.265379	10	0.672100	
M. dobsoni	5.993890	9	0.727575	
M. talazaci	5.585512	7	0.558439	
Oryzorictes	2.771029	5	0.259222	
All Grps	5.146856	31	1.246431	
	{1}	{2}	{3}	{4}
	M=5.2654	M=5.9939	M=5.5855	M=2.7710
M. cowani {1}		0.074603	0.725180	0.000167
M. dobsoni {2}	0.074603		0.568997	0.000167
M. talazaci {3}	0.725180	0.568997		0.000167
Oryzorictes {4}	0.000167	0.000167	0.000167	

Taxon	M3SI Means	M3SI N	M3SI Std.Dev.	
Echinops	8.423182	14	1.122278	
Hemicentetes	6.847034	15	0.951923	
Setifer	8.769469	15	0.908066	
Tenrec	8.079751	10	0.679463	
All Grps	8.017956	54	1.198533	
	{1}	{2}	{3}	{4}
	M=8.4232	M=6.8470	M=8.7695	M=8.0798
Echinops {1}		0.000389	0.758718	0.816933
Hemicentetes {2}	0.000389		0.000169	0.012762
Setifer {3}	0.758718	0.000169		0.292266
Tenrec {4}	0.816933	0.012762	0.292266	

Taxon	M3SI Means	M3SI N	M3SI Std.Dev.
M. talazaci	10.34241	5	0.493655
M. cowani	9.13581	15	0.693397
M. dobsoni	10.65648	10	1.091563

Oryzorictes	3.88359	8	0.392317	
All Grps	8.58902	38	2.646957	
	{1}	{2}	{3}	{4}
	M=10.342	M=9.1358	M=10.656	M=3.8836
M. talazaci {1}		0.020138	0.873104	0.000162
M.cowani {2}	0.020138		0.000274	0.000162
M.dobsoni {3}	0.873104	0.000274		0.000162
Oryzorictes {4}	0.000162	0.000162	0.000162	

Taxon	CMI	CMI	CMI	
	Means	N	Std.Dev.	
Echinops	0.325452	11	0.032559	
Hemicentetes	0.303658	13	0.045775	
Setifer	0.330664	14	0.040701	
Tenrec	0.328347	10	0.024130	
All Grps	0.321673	48	0.038169	
	{1}	{2}	{3}	{4}
	M=.32545	M=.30366	M=.33066	M=.32835
Echinops {1}		0.499291	0.985992	0.998104
Hemicentetes {2}	0.499291		0.260014	0.413239
Setifer {3}	0.985992	0.260014		0.998889
Tenrec {4}	0.998104	0.413239	0.998889	

Taxon	HLI	HLI	HLI	
	Means	N	Std.Dev.	
Echinops	0.177929	7	0.023934	
Hemicentetes	0.176088	10	0.018858	
Setifer	0.185577	6	0.013570	
Tenrec	0.205912	2	0.007012	
All Grps	0.181267	25	0.019664	
	{1}	{2}	{3}	{4}
	M=.17793	M=.17609	M=.18558	M=.20591
Echinops {1}		0.997295	0.887187	0.286240
Hemicentetes {2}	0.997295		0.770245	0.211602
Setifer {3}	0.887187	0.770245		0.567956
Tenrec {4}	0.286240	0.211602	0.567956	

Taxon	CMI	CMI	CMI	
	Means	N	Std.Dev.	
M. talazaci	0.254741	5	0.030735	
M.cowani	0.267361	15	0.048236	
M.dobsoni	0.238632	10	0.020439	
Oryzorictes	0.409013	8	0.078079	
All Grps	0.287962	38	0.079904	

	{1}	{2}	{3}	{4}
	M=.25474	M=.26736	M=.23863	M=.40901
M. talazaci {1}		0.959669	0.932654	0.000178
M.cowani {2}	0.959669		0.492340	0.000162
M.dobsoni {3}	0.932654	0.492340		0.000162
Oryzorientes {4}	0.000178	0.000162	0.000162	

CHAPTER IV

EVOLUTIONARY MORPHOLOGY OF THE TENRECOIDEA HINDLIMB

Introduction

A diversity of taxon-specific locomotor and postural behaviors in the Tenrecoidea provides the groundwork for testing function-based hypotheses of hindlimb morphology. Study of the tenrecoid tarsal complex has demonstrated that in addition to similarities between taxa, which appear to be convergences based on microhabitat-specific positional behaviors, differences in morphology due to phylogeny are also evident, especially at the upper ankle joint (Chapter 2). Although the skeleton of the mammalian hindlimb exhibits extensive function-based homoplasy (e.g., Reed, 1951; Smith and Savage, 1956; Taylor, 1989; Gebo and Sargis, 1994; Hildebrand, 1995; Stein, 2000; Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002), the taxon-based postural differences found in the tenrecoid tarsus most likely extend to differences in the knee and hip joints, despite locomotor diversity and the relative simplicity of the joints themselves (in terms of the number of bones involved at each joint). Identification of taxon-specific traits related to general phylogenetically constrained posture (vs. specific locomotion), have the potential for better understanding unresolved relationships within Tenrecoidea. This study will examine specific features of the tenrecoid pelvis, femur, tibia, and fibula, as well as details of the hip and knee joint in the context of taxon locomotor behavior. I will specifically address the questions:

- 1) To what extent do tenrecoids share convergences of the hindlimb skeleton with other mammalian locomotor specialists? Do hypotheses of function-based form in other mammals correspond with tenrecoid skeletal features?
- 2) Are there posture-related subfamily level traits in the hindlimb (i.e., those that are phylogenetically constrained from the ancestral condition) that correspond to those found in the tarsus? Do these support hypotheses of unresolved phylogenetic relationships within Tenrecoidea (e.g., the relationship of Geogale and Limnogale to other taxa)?

Pelvis and Hip Joint

The ilium, ischium and pubis of the innominate incur the shifting loads of the hindlimbs during locomotion. Overall shape and relative size, as well as rugosities and tubercles on the surface of the three innominate components, are useful indicators for functional interpretation (e.g., Camp and Borell, 1937; Fleagle and Anapol, 1992; Gebo and Sargis, 1994; Heinrich and Rose, 1997; Anemone and Covert, 2000; Stein, 2000; Argot, 2002; Sargis, 2002). Of the two pelvic joints (femoral and vertebral), acetabular position, relative size and shape are particularly informative for interpretation of both postural and locomotor behavior. At least 15 muscles have attachment sites on the body of the pelvis, and innominate morphology is perhaps best understood through study of attachment sites and the effects of associated muscles on positional behavior (Fig. 4.1). The ilium serves as the attachment site for various muscles, including the gluteals (attach dorsolaterally; act as rapid-movement extensors at end of stroke and abductors of the thigh), M. iliacus (iliac fossa; acts as thigh flexor), tensor fasciae latae (anterior border; acts as thigh

flexor), rectus femoris (immediately anterior to acetabulum; acts as thigh flexor/knee extensor), and oblique abdominal muscles. The major ischial muscles include the gemelli (attach at ischial spine; abductors and lateral rotators of thigh), and the ischiopubic complex (biceps femoris, semitendinosus, semimembranosus, gracilis, adductor magnus, and quadratus femoris – originate from posterior ischium and pubis; act as thigh extensors at beginning of stroke). In addition, the pubic ramus is the attachment site for *M. gracilis* (hip adductor), *pectinaeus* (hip flexor and thigh abductor), and the adductors.

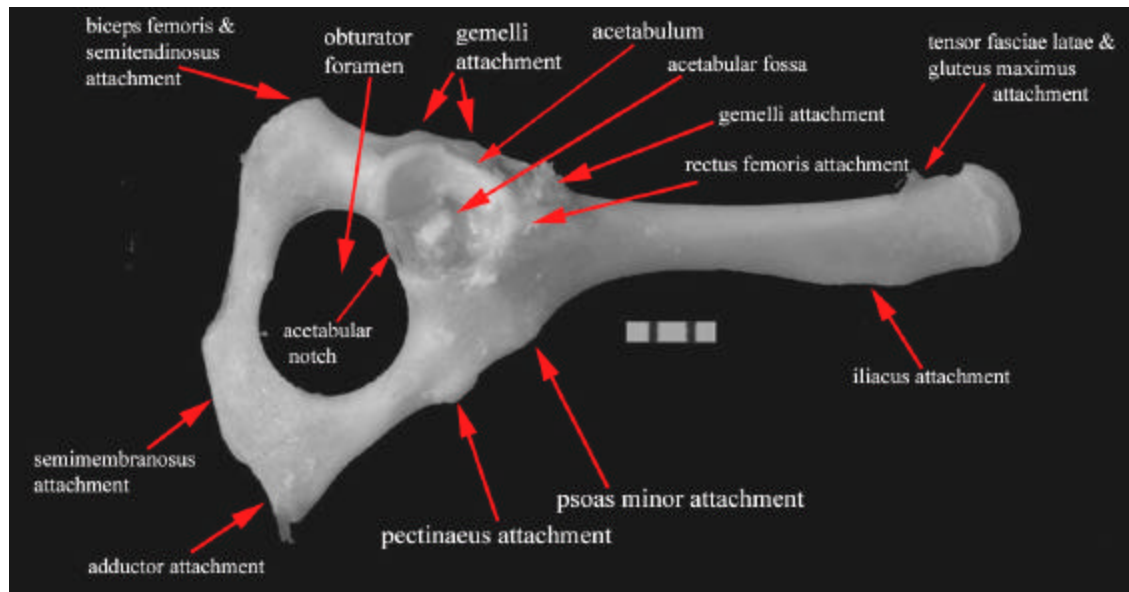


Figure 4.1. *Hemicentetes* pelvis, right side, indicating variable characters and their muscular associations.

Femur, Tibia, and Knee Joint

Shape and relative size of the femoral head, and the angle of the femoral neck indicate resting posture of the hindlimb as well as specialized locomotor behavior (e.g., Camp and Borell, 1937; Kappelman, 1988; Gebo and Sargis, 1994; Rose, 1999; Anemone and Covert, 2000; Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002). The greater trochanter is the attachment site of *Mm. gluteus medius* and *minimus*, *gemelli*, *piriformis*, *vastus lateralis* and *medialis*, and its proximal and anterior projection are

indicative of aspects of hip joint mobility Taylor, 1976; (Gebo and Sargis, 1994; Heinrich and Rose, 1997; Anemone and Covert, 2000; Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002). Lesser trochanter (attachment site of *M. iliopsoas*) size and position correlates with hip flexion and adduction, whereas form and position of the third trochanter (attachment site of *Mm. gluteus superficialis (maximus)*, *tensor fasciae femoris*, *vastus intermedius*, *quadratus femoris*; trochanter not present in australidelphian marsupials or didelphids; anthropoids, and viverrids; Sargis, 2002) correlate with movement related to hindlimb flexion and medial rotation, and/or thigh extension and abduction (Verma, 1963; Szalay and Schrenk, 1998; Anemone and Covert, 2000; Sargis, 2002).

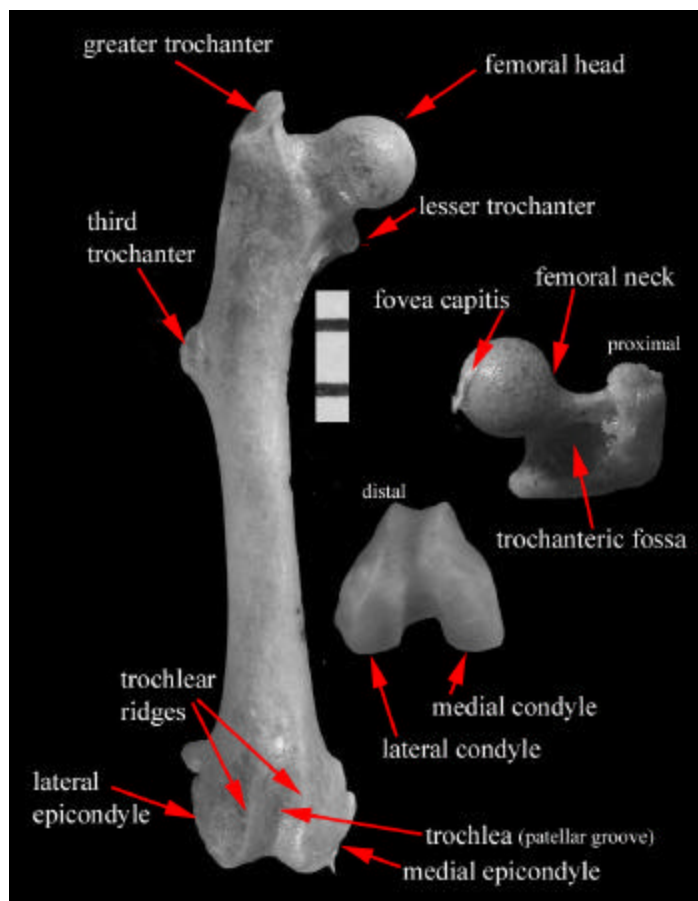


Figure 4.2. *Microgale cowani* femur, right side, indicating characters with documented functional significance.

Condylar morphology at the distal femur is suggestive of rotational facilitation and/or constraint at the knee joint. The width or narrowness of the patellar groove (intercondylar trochlea) and the height of the trochlear ridges reflect the degree to which joint movement is constrained to the parasagittal plane vs. a more substantial range of mediolateral motion (Verma, 1963; Taylor, 1976; Gebo and Sargis, 1994; Carrano, 1997; Anemone and Covert, 2000; Argot, 2002). Shape and relative size of the medial and lateral femoral condyles is correlated with both locomotor and postural behaviors (Verma, 1963; Taylor, 1989; Gebo and Sargis, 1994; Godfrey et al., 1997; Heinrich and Rose, 1997; Szalay and Sargis, 2001; Sargis, 2002), and may also be constrained to some degree by individual body mass (Kappelman, 1988; Ruff, 1990).

Tibia and Fibula

The tibial tuberosity on the proximal anterior surface of the tibia, representing the insertion site of the patellar ligament (an extension of the M. quadratus femoris tendon), is highly variable in shape between mammalian taxa. A sharp-edged and anteriorly prominent tuberosity generally represents movement at the knee that is restricted to the parasagittal plane vs. a shallower, rounded tuberosity which allows for a greater degree of multiaxial rotation (e.g., Taylor, 1976; Heinrich and Rose, 1997; Argot, 2002; Szalay and Sargis, 2001; Sargis, 2002). The medial and lateral tibial condyles, which receive loads directly from the corresponding distal femoral condyles, are variable between taxa in terms of the spacing between the condyles, the height of their interior spines, their

concavity/convexity, relative size, and anteroposterior vs. mediolateral width (Fleagle and Simons, 1995; White and Gebo, 2004).

Though primitive therians had an unfused crus, with the fibula playing a more significant load-bearing role at both the knee and upper ankle joints (Kemp, 1982), fusion of the distal fibula to the tibia is a well-noted, functionally significant trait that has evolved numerous times in many placental specialists (Hildebrand, 1995; Stein, 2000). Fusion of the two bones at their distal ends stabilizes movement in flexion-extension, and limits rotation at the upper ankle joint, whereas retention of the unfused crus facilitates greater freedom of adjustment in the UAJ.

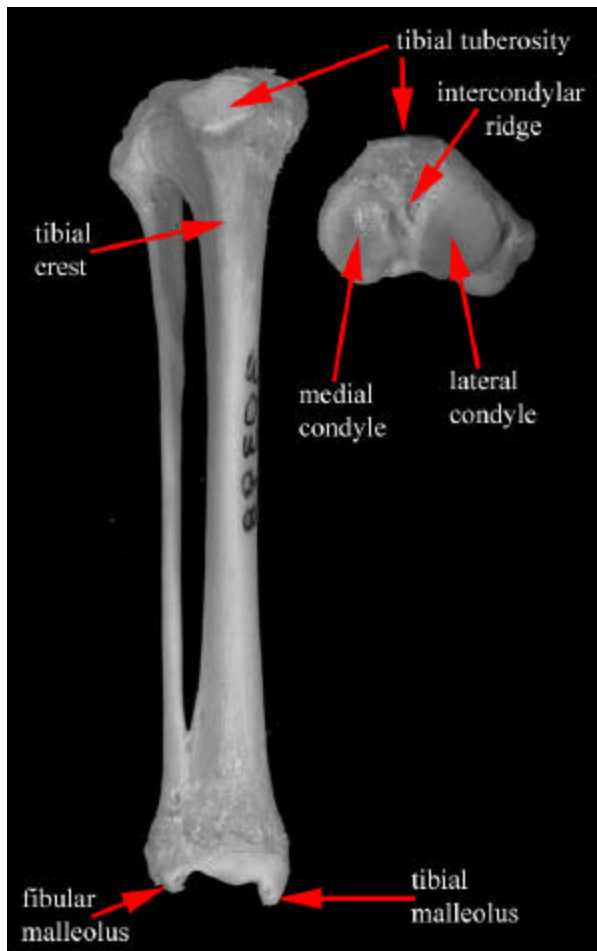


Figure 4.3. *Tenrec ecaudatus* tibia and fibula, right side, indicating characters with documented functional significance.

TABLE 4.1. ASPECTS OF THE MAMMALIAN HINDLIMB WITH PROPOSED RELATIONSHIP TO LOCOMOTOR BEHAVIOR

	Climber	Digger	Terrestrial/Runner	Leaper
PELVIS:				
Pelvis ⁵			longer than femur	shorter than femur
Pelvis ⁷		relatively anteroposteriorly short		
Ischium ^{1,2,3}	long with moderate dorsal projection (in general climbers) short ischia, long dorsal projection (in climbing leapers)		long ischia, short ilia	short ischia and long ilia
Ischium ⁸	greater distance between ischial spine and acetabulum		less distance	
Ischium ²⁷		long		
Ilium ^{1,3}	narrow		wide	wide
Ilium ²⁶			long	
Acetabulum ^{4,12}	shallow, open, oval, faces laterally			deep, less open, more round, faces ventrolaterally
Acetabulum ⁵				more anteriorly positioned
Acetabulum ³	elliptical with cranial expansion of articular surface		circular	
Acetabulum ¹¹		facing ventrally		
FEMUR:				
Femur length ^{14,22,23,24}	long	short	short	
Fovea capitis	medial, proximal			
Femoral head ¹				cylindrical, posterior expansion
Femoral head ^{4,6,12}	cylindrical, medially expanded towards trochanteric fossa		spherical, small	spherical, small
Femoral head ⁸	spherical		forms less complete sphere	
Femoral head ⁹			rectangular, medially extended	
Femoral head ¹⁰	dorsolaterally extended	dorsolaterally extended		
Femoral head ^{3,6,12}	relatively large		relatively small	
Femoral head angle ⁶	head (and neck) less perpendicular to shaft		head (and neck) more perpendicular to shaft	
Femoral head angle ⁹			head more perpendicular to shaft (in open vs. closed environment)	
Femoral head angle ¹				head more perpendicular to shaft
Femoral head angle ¹¹		head more perpendicular to shaft		
Femoral neck ⁸	short, less distinct from femoral head		long, distinct from head	
Proximal shaft ⁹			mediolaterally wider (in open-environment vs. AP wider in closed)	

	Climber	Digger	Terrestrial/Runner	Leaper
Greater trochanter ¹				projects anterior (ventral) to femoral shaft
Greater troch ^{3,4,6,8,12-14}	does not project above femoral head		projects above femoral head	projects above femoral head
Lesser troch ^{1,12}	relatively large		small	large
Lesser troch ^{1,4,6,8,10,14}	medially oriented, distal from femoral head		posteriorly oriented, close to femoral head	
Third troch ^{1,3,16}	smaller	laterally expanded (large)	laterally expanded (large)	short (small)
Third troch ¹⁵		distally positioned		
Patellar groove ^{14,16,17}	shallow, low	shallow, low	deep, high	deep, high
Trochlear ridges ^{1,4,6}	low (proximodistally and anteroposteriorly)		high	high
Condyles ¹⁶				deeper than wide
Condyles ^{3,6,8,18}	anteroposteriorly compressed (mediolaterally wide)		mediolaterally compressed (anteroposteriorly long)	
Condyles ⁶	small diameter		larger diameter	
Condyles ¹⁹			posteriorly expanded	
Medial condyle ^{13,18}	slightly broader than lateral		much broader than lateral	
TIBIA:				
Relative crus length ^{6,11,23,26}		short	long (short in terrestrial guenons)	long
Tibial tuberosity ^{3,4,8,12,14}	wide, shallow		narrow, sharp-edged	narrow, sharp-edged
Tibial condyle spines ²⁰	single spine or reduced medial spine		double spine eminence	
Intercondylar groove ²⁰	small, if present		larger	
Tibial condyles ²¹				large, convex lateral w/small concave
medial				
Tibial condyles ⁴	project less posteriorly		project more posteriorly	
Tibial crest	long		not as long	
Tib/fibula fusion ^{1,7,19,27}	unfused	fused	fused	fused

1. Anemone & Covert, 2000; 2. Fleagle & Anapol, 1992; 3. Sargis, 2002; 4. Argot, 2002; 5. Camp & Borell, 1937; 6. Gebo & Sargis, 1994; 7. Stein, 2000; 8. Heinrich & Rose, 1997; 9. Kappelman, 1988; 10. Rose, 1999; 11. Reed, 1951; 12. Szalay & Sargis, 2001; 13. Godfrey et al., 1997; 14. Taylor, 1976; 15. Szalay & Schrenk, 1998; 16. Verma, 1963; 17. Carrano, 1997; 18. Elton, 2001; 19. Taylor, 1989; 20. White & Gebo, 2004; 21. Fleagle & Simons, 1995; 22. VanValkenburgh, 1987; 23. Casinos et al., 1993; 24. Shimer, 1903; 25. Berman, 1985; 26. Smith & Savage, 1956; 27. Hildebrand, 1995.

Methods and Materials

The pelvis, femur, tibia, and fibula from 170 specimens were studied and digitally photographed (Nikon Coolpix 995) from several standardized perspectives. Skeletal specimens were photographed from collections at the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Harvard Museum of Comparative Zoology (MCZ), and United States National Museum of Natural History (USNM) (see Appendix I for specimen list). Two *Echinops* specimens were borrowed from H. Kuenzle's laboratory at the University of Munich (UMUN), Germany, and a *Hemicentetes* and *Tenrec* specimen were borrowed from the University of Darmstadt, Germany (DARM). Digital image files were written into TPSdig (Version 1.31, 2001 F.J. Rohlf), which allows for superimposition of landmarks (x,y coordinates) onto images, and calibration of image scale from a mm ruler. Thirty-six linear measurements were then calculated from desired coordinates (Fig. 4.3). Measurements included those that incorporate features with proposed functional and/or phylogenetic significance (see Table 4.1). Precision of digital measurements was tested against fine-point caliper measurements from 3 complete specimens, and there were no significant differences between caliper and digital values ($p < 0.05$). In order to control for size differences between species, linear measurements were transformed to 31 index variables (Table 4.4). Statistical analyses (one-way ANOVAs & Tukey honest significance (HSD) post-hoc tests) were performed using STATISTICA (Version 6.0, StatSoft Inc). Significance values reported in the text for two-group comparisons refer to Tukey post-hoc results; those for more than two groups refer to ANOVAs.

The following tenrecoid species were studied: *Echinops telfairi*, *Setifer setosus*, *Hemicentetes semispinosus*, *Tenrec ecaudatus*, *Microgale cowani*, *M. dobsoni*, *M. talazaci*, *Oryzorictes tetradactylus* (or *O. hova*), *Limnogale mergulus*, *Geogale aurita*, and *Potamogale velox* (see Table 4.2). I included the following non-tenrecoids as outgroups: *Solenodon paradoxus*, *Nesophontes edithae* and sp. unknown (not included in quantitative analyses), *Petrodromus*, and *Echinosorex*. I took 56 linear measurements (see Fig. 4.4) and used some of these to construct 26 index variables (Table 4.4).

TABLE 4.2. Taxonomy and Primary Locomotor Behavior of study taxa

Family/subfamily	Genus	Species	n	Locomotor Behavior
Tenrecidae/Tenrecinae	<i>Echinops</i>	<i>telfairi</i>	12	Arboreal/terrestrial
Tenrecidae/Tenrecinae	<i>Hemicentetes</i>	<i>semispinosus</i>	18	Terrestrial/fossorial
Tenrecidae/Tenrecinae	<i>Setifer</i>	<i>setosus</i>	20	Terrestrial
Tenrecidae/Tenrecinae	<i>Tenrec</i>	<i>ecaudatus</i>	8	Terrestrial
Tenrecidae/Oryzorictinae	<i>Limnogale</i>	<i>mergulus</i>	5	Aquatic/terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>cowani</i>	22	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>dobsoni</i>	20	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>talazaci</i>	3	Terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>hova</i>	22	Fossorial/terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>tetradactylus</i>	10	Fossorial/terrestrial
Tenrecidae/Geogalinae	<i>Geogale</i>	<i>aurita</i>	5	Terrestrial
Potamogalidae	<i>Potamogale</i>	<i>velox</i>	3	Aquatic/terrestrial
Macroscelididae	<i>Petrodromus</i>	<i>tetradactylus</i>	3	Terrestrial/saltatory
Solenodontidae	<i>Solenodon</i>	<i>paradoxus</i>	11	Terrestrial/fossorial
Erinaceidae	<i>Echinosorex</i>	<i>gymnurus</i>	1	Terrestrial/some digging
Nesophontidae	<i>Nesophontes</i>	<i>edithae</i> & sp.?	7	?

Table 4.3. Measurements (see Appendix 4.1 and 4.2)

PELVIS	
Pelvis1	<i>Acetabulum height</i> : from lateral view of the pelvis, dorsoventral height of the acetabulum through midline, perpendicular to acetabulum width.
Pelvis2	<i>Acetabulum width</i> : from lateral view of pelvis, anteroposterior (caudocranial) width of acetabulum through midline, perpendicular to acetabulum height.
Pelvis3	<i>Dorsal ischium height</i> : from lateral view of pelvis, distance between dorsalmost point of ischium and dorsalmost point of obturator foramen, perpendicular to dorsal ischium width.
Pelvis4	<i>Dorsal ischium width</i> : from lateral view of pelvis, anteroposterior width of dorsal projection of ischium, measured between the midline of dorsal ischium height and the dorsalmost projection of the ischium, perpendicular to dorsal ischium height.
Pelvis5	<i>Ilium length</i> : from lateral view of pelvis, distance from midpoint of acetabulum to anteriormost point of ilium along long central axis of ilium.
Pelvis6	<i>Ilium width</i> : from lateral view of pelvis, minimum dorsoventral width of ilium, perpendicular to ilium length.

- Pelvis7** *Obturator foramen length*: from lateral view of pelvis, dorsoventral length (height) of obturator foramen, through midpoint of foramen, perpendicular to foramen width.
- Pelvis8** *Obturator foramen width*: from lateral view of pelvis, craniocaudal width of obturator foramen, through midpoint of foramen, perpendicular to obturator foramen length.

FEMUR

- Afem1 Femur1,7-8** *Femoral head mediolateral width II*: from anterior view of femur, width of femoral head perpendicular to femoral head proximodistal length.
- Afem2 Femur1,5-6** *Femoral head proximodistal length*: from anterior view of femur, length of femoral head along axis of femoral neck, perpendicular to femoral head mediolateral width II.
- Afem3 Femur1,33-34** *Femur distal epiphysis width*: from anterior view of femur, mediolaterally widest length of distal femoral epiphysis, perpendicular to long axis of femoral shaft.
- Afem4 Femur1,1-2** *Femur length*: from anterior view of femur, distance from distalmost point of femoral neck to proximalmost point of femoral trochlea.
- Afem5 Femur1,3-4** *Femoral midshaft mediolateral width*: from anterior view of femur, midshaft mediolateral width, as determined by midpoint of femur length, perpendicular to the long axis of the femoral shaft.
- Afem6 Femur1,19-20** *Lesser trochanter distance from distal femur*: from anterior view of femur, distance from widest point of lesser trochanter to proximalmost point of femoral trochlea, measured parallel to long axis of femoral shaft.
- Afem7 Femur1,17-18** *Lesser trochanter distance from proximal femur*: from anterior view of femur, distance from widest point of lesser trochanter to distalmost point of femoral neck, measured parallel to long axis of femoral shaft.
- Afem8 Femur1,13-14** *Lesser trochanter mediolateral width*: from anterior view of femur, mediolaterally widest point of lesser trochanter, perpendicular to long axis of femur. Measured from most medially projecting point to midpoint between base of lesser trochanter to distal/medial base of femoral head.
- Afem9 Femur1,9-10** *Greater trochanter height*: from anterior view of femur, distance from distalmost point of femoral neck to proximalmost point of greater trochanter, parallel to long axis of the femur.
- Afem10 Femur1,27-28** *Patellar groove anteroposterior height*: from anterior view of femur, distance from proximalmost (determined by approximate or evident epiphyseal line) to distalmost point of patellar groove, parallel with long axis of femoral shaft.
- Afem11 Femur1,31-32** *Patellar groove mediolateral width*: mediolateral width of patellar groove measured at anterior midpoint of groove, perpendicular to groove anteroposterior height.
- Afem12 Femur1,25-26** *Third trochanter distance from distal femur*: from anterior view of femur, distance from widest point of third trochanter to proximalmost point of femoral trochlea, measured parallel to long axis of femur.
- Afem13 Femur1,23-24** *Third trochanter distance from proximal femur*: from anterior view of femur, distance from widest point of third trochanter to distalmost point of femoral neck, measured parallel to long axis of femoral shaft.
- Afem14 Femur1,21-22** *Third trochanter mediolateral width*: from anterior view of femur, from lateralmost point of third trochanter to point aligned with lateral side of femoral shaft.
- Mfem1** *Medial femoral condyle mediolateral width*: from distal view of femur, distance from medial to lateral side of medial femoral condyle, measured at midpoint of condyle.
- Mfem2** *Lateral femoral condyle mediolateral width*: from distal view of femur, distance from medial to lateral side of lateral femoral condyle, measured at midpoint of condyle.
- Lfem1** *Femoral midshaft anteroposterior width*: from medial view of femur, midshaft anteroposterior width, as determined by midpoint of femur length, perpendicular to long axis of femoral shaft.
- Lfem2** *Medial femoral condyle anteroposterior depth*: from medial view of femur, anteroposteriorly widest length of medial femoral condyle.
- Pfem1** *Femoral head anteroposterior width*: from proximal view of femoral head, anteroposterior width, perpendicular to mediolateral width.
- Pfem2** *Femoral head mediolateral width*: from proximal view of femoral head, mediolateral width, perpendicular to anteroposterior width.
- Pfem3** *Femoral neck anteroposterior width*: from proximal view of femur, anteroposterior width of neck.

Pfem4 *Femoral neck mediolateral width*: from proximal view of femur, narrowest width of femoral neck, perpendicular to long axis of neck.

TIBIA/FIBULA

Atibfib1 *Tibia length*: from anterior view of tibia, proximodistal length of tibial diaphysis, measured along longest axis of tibial shaft.

Atibfib2 *Tibia midshaft width*: from anterior view of tibia, mediolateral width of tibial diaphysis at midshaft, as determined by tibia length.

Ptibfib1 *Lateral tibial condyle width*: from proximal view of tibia, mediolateral width of lateral tibial condyle, running through midpoint of lateral condyle, perpendicular to anteroposterior length of tibial tuberosity.

Ptibfib2 *Medial tibial condyle width*: from proximal view of tibia, mediolateral width of medial tibial condyle, running through midpoint of medial condyle, perpendicular to anteroposterior length of tibial tuberosity.

Ptibfib3 *Proximal tibia anteroposterior length*: from proximal view of tibia, distance from anteriormost point of tibial tuberosity to posteriormost point of tibia proximal articular surface, measured along midpoint of tibial tuberosity, perpendicular to mediolateral width of condyles.

Ptibfib4 *Tibial tuberosity anteroposterior length*: from proximal view of tibia, distance from anteriormost point of tibial tuberosity to midpoint between the anteriormost points of tibial condyles.

Table 4.4. Indices (see Appendix 4.3 and 4.4)

PELVIS	
ASHI	Acetabulum Shape Index = Acetabulum height/acetabulum width
ASZI	Acetabulum Size Index = (Ilium length + ilium width)/(Acetabulum height + acetabulum width)
IDSH	Ischium Dorsal Shape Index = Dorsal ischium height/dorsal ischium width
OFSI	Obturator Foramen Shape Index = Obturator foramen length/foramen width
FEMUR	
PFLI	Pelvis/Femur Length Index = Pelvis length/femur length
FHSZI	Femoral Head Size Index = (Femoral head mediolateral width/head anteroposterior width)/femoral midshaft mediolateral width
FHDI	Femoral Head Depth Index = Femoral head proximodistal length (along axis of neck)/head mediolateral width (perpendicular to neck axis)
FHWI	Femoral Head Width Index = Femoral head mediolateral width (from proximal view)/head anteroposterior width
FNWI	Femoral Neck Width Index = Femoral neck mediolateral width/femoral neck anteroposterior width
GTRHI	Greater Trochanter Height Index = Greater trochanter height/femur midshaft width
LTRSI	Lesser Trochanter Size Index = Lesser trochanter mediolateral width/diaphysis width
LTRPI	Lesser Trochanter Position Index = Lesser trochanter distance from proximal femur/distance from distal femur
TTRSI	Third Trochanter Size Index = Third trochanter mediolateral width/diaphysis width
TTRPI	Third Trochanter Position Index = Third trochanter distance from proximal femur/distance from distal femur
PGSI	Patellar Groove Shape Index = Anteroposterior height of patellar groove/mediolateral width of groove
PGWI	Patellar Groove Width Index = Width of patellar groove/distal femoral epiphysis width
DFWI	Distal Femur Width Index = Width of distal femur/femoral diaphysis width
FCDI	Femoral Condyle Depth Index = Anteroposterior depth of medial femoral condyle/diaphysis anteroposterior depth
FCSI	Femoral Condyle Shape Index = Proximodistal length of medial + lateral condyles/mediolateral width of medial + lateral condyles
MLFCI	Medial/Lateral Femoral Condyle Index = Medial condyle mediolateral width/lateral condyle width

TIBIA/FIBULA

TTSI Tibial Tuberosity Shape Index = Tibial tuberosity anteroposterior length/anteroposterior length of proximal tibia

MLTCI Medial/Lateral Tibial Condyle Index = Medial tibial condyle width/Lateral condyle width

TSI Tibia Shape Index = Tibia length/tibia width at midshaft



Figure 4.4. Linear measurements taken from the right side pelvis, femur (anterior, proximal and distal posterior), and tibia (anterior and proximal). Not to scale.

Results and Discussion

Pelvis

Even a cursory examination of the tenrecoid pelvis reveals several straightforward differences in form between the tenrecines and oryzorictines (Fig. 4.5). The acetabulum is relatively large in all four tenrecine genera compared to the oryzorictine acetabulum, which is small and has a steep shelf across the dorsal posterior border (Fig. 4.6; $p < 0.00$). This marked difference in size between subfamilies suggests that for tenrecoids at least,

acetabulum diameter is not a good general indicator of body mass (as opposed to primates; see Fleagle and Anapol, 1992). A relatively large elliptical acetabulum is shared by plesiadapids, dermopterans, euprimates (Szalay et al. 1975), and *Ptilocercus* (Sargis, 2002), and Gebo and Sargis (1994), Szalay and Sargis (2001), and Sargis (2002) found a relatively large femoral head in arboreal guenons, arboreal marsupials, and *Ptilocercus*. Given the traits of the tenrecine upper ankle joint (UAJ) that suggest a greater degree of joint rotation vs. those of the more restricted oryzorictine UAJ (Salton and Szalay, 2004), a relatively large acetabulum in tenrecoids is most likely related to increased hip mobility. As is the case with arboreal marsupials (Argot, 2002), *Echinops* has a shallower acetabulum than the other tenrecines, suggesting less restriction at the hip joint for increased multiaxial mobility. Within Oryzorictinae, the fossorial *Oryzorictes* has a relatively large acetabulum (Fig. 4.6), which is consistent with its requirement for an abducted femoral position while digging and rotational movement for maneuvering within a burrow. Of all the taxa sampled, the saltatory *Petrodromus* has the relatively smallest acetabulum, which is indicative of its need for restricting femoral movement to a single plane during leaping.

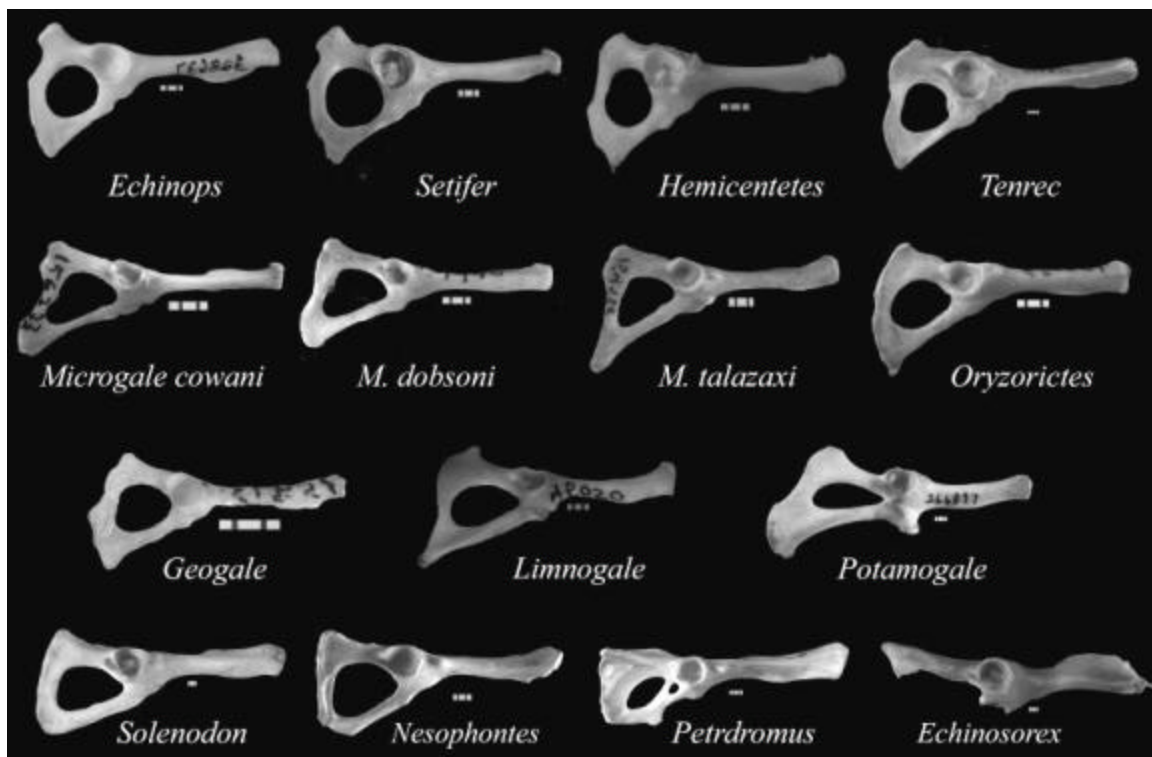


FIGURE 4.5. Pelvis (right side, lateral view). Note in particular: taxon-based difference in relative acetabulum size and pubis shape between tenrecines (top row) and oryzorictines (second row), indicating a wider range of hip mobility in the former; the shallow acetabulum of *Echinops*, indicative of its climbing behavior; the dorsal process of the ischium in *Echinops* and *Setifer*, also indicative of climbing behavior; the marked difference in pelvis shape between *Potamogale* and the elephant shrew *Petrodromus*, despite remarkable convergence at the distal crus (see Fig. 4.6).

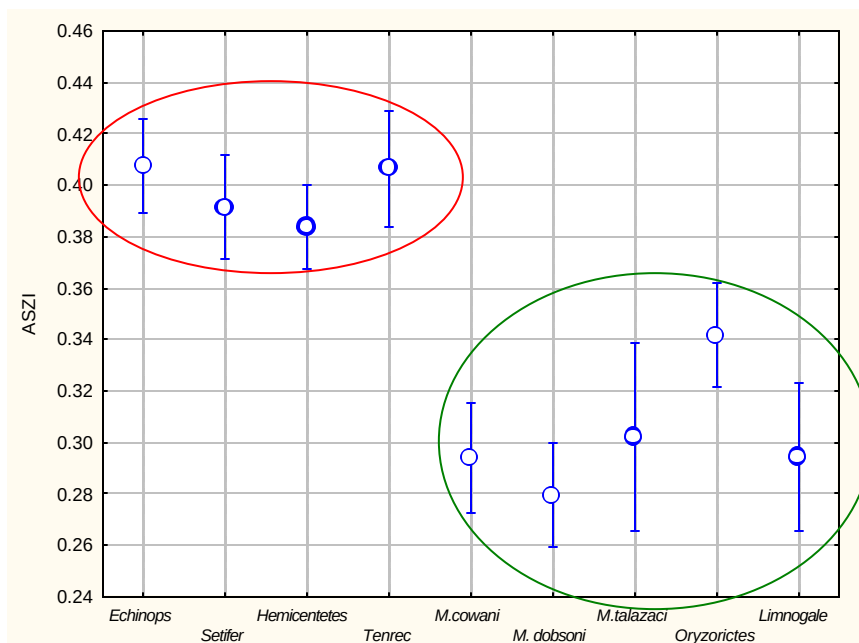


Figure 4.6. Acetabulum Size Index in tenrecines (red circle) vs. oryzorictines (green), illustrating the considerably larger acetabulum in tenrecines despite overlapping locomotor behaviors between the two groups.

Although the acetabulum of some mammalian climbers is elliptical, cranially expanded and/or laterally (vs. ventrolaterally) oriented (Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002), *Echinops* does not exhibit these features. Tenrecines in general have a rounder acetabulum vs. a dorsoventrally flattened (craniocaudally expanded) acetabulum in oryzorictines (Fig 7; $p < 0.00$). This does not correspond with function-based hypotheses gleaned from scandentians and marsupials, yet the circular acetabulum in tenrecines paired with a relatively larger, open form may contribute to a wider range of motion compared with a smaller, tightly articulating, anteroposterior-oriented acetabulum, which may play a role in restricting femoral movement to the parasagittal plane. *Limnogale* has an especially low acetabulum shape index (ASHI) score, indicating a particularly oblate shaped acetabulum (Fig. 4.7). The swimmer *Potamogale* does not share this feature with *Limnogale*, and has a rounded acetabulum. Yet to the exclusion of all other taxa, both *Potamogale* and *Limnogale* have dorsally-oriented acetabula, located high on the pelvis (Fig. 4.5). Acetabulum shape index (ASHI) and size index (ASZI) values in *Geogale* both fall within the range of Oryzorictinae.

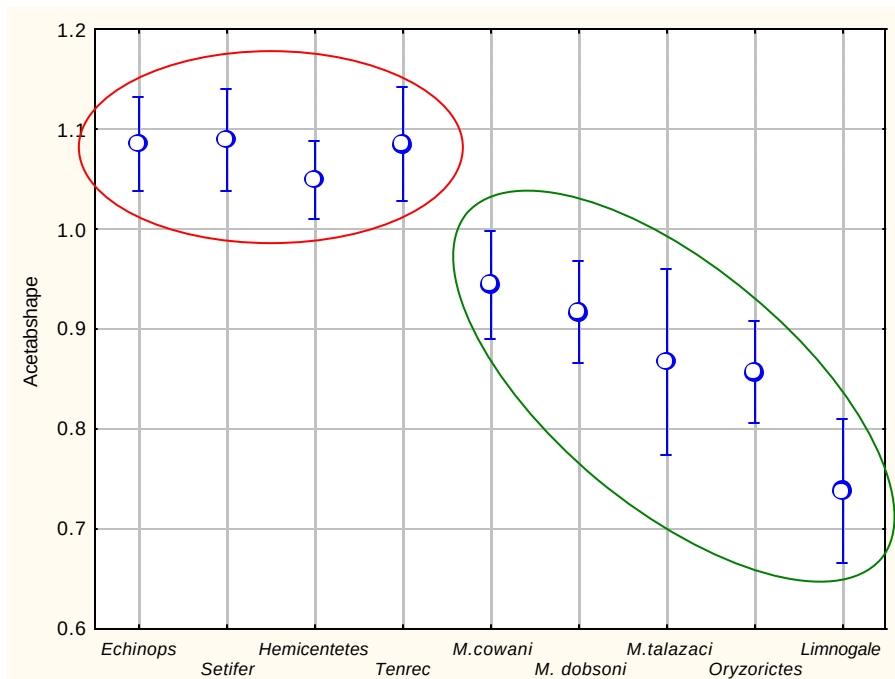


Figure 4.7. Acetabulum shape index (ASI) in tenrecines (left four – red circle) vs. oryzorictines (right four – green). Note that the four tenrecines have a relative rounded to dorsoventrally expanded acetabulum (high values), whereas that in oryzorictines is craniocaudally expanded.

The shape of the obturator foramen is uniquely large and rounded in Tenrecinae as opposed to a more anteroposteriorly-elongate foramen in all other studied taxa (Fig. 4.8). This characteristic is an artifact of the surrounding innominate architecture and its direct functional significance is difficult to interpret. The rounded shape in tenrecines is most likely a result of the ventrally reaching caudal ramus of the pubis, vs. a ventral and posteriorly (caudally) reaching pubis in other taxa (Fig. 4.5). The muscles most influencing the posterior pubis are *M. semimembranosus* and the adductors. *M. semimembranosus* is a femoral extensor, part of the ischiopubic muscle complex that is responsible for slow, powerful movement at the beginning of the leg stroke (Smith and Savage, 1956). The adductors, as well as *M. semimembranosus*, play a role in adducting the thigh, and assist with extension of the femur (Argot, 2002). A more caudally positioned posterior ramus, i.e. a more posteriorly displaced origin of the adductor

muscles and *M. semimembranosus* may promote more of an extensor role for these muscles, as opposed to an origin that is closer to the point of rotation (the acetabulum), in which case the adductors and *semimembranosus* would serve to more forcefully adduct the thigh.

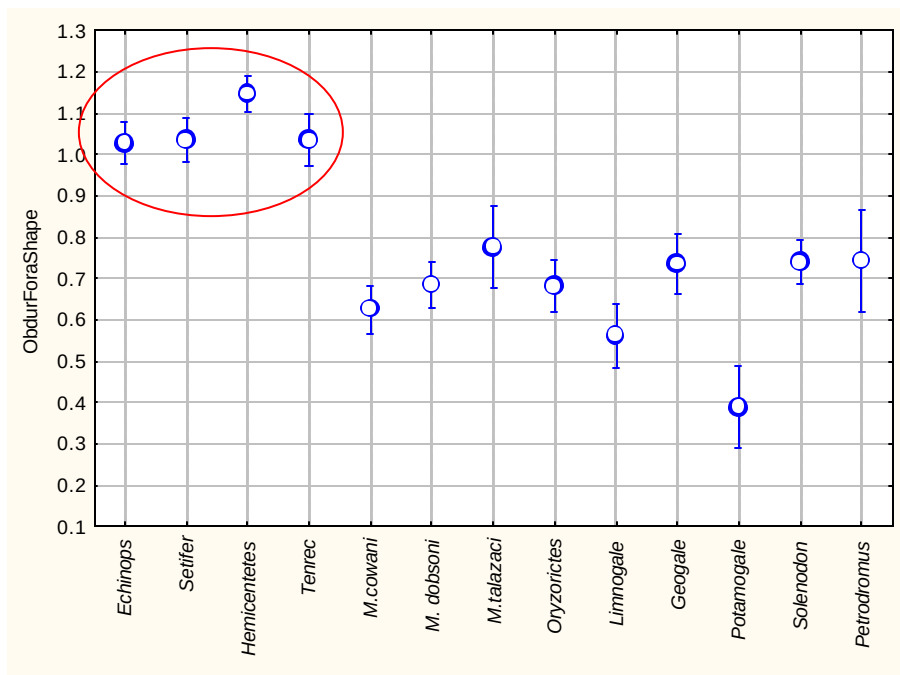


Figure 4.8. Obturator Foramen Shape Index (OFSI). Note the particularly rounded obturator foramen in the four tenrecine genera as opposed to the anteroposteriorly elongate obturator foramen in other studied taxa.

The ilium of some mammalian climbers and leapers is long compared to that of terrestrial mammals (Anemone and Covert, 2000). Nonetheless, neither the arboreal *Echinops* nor the saltatory *Petrodromus* has a particularly long ilium. *Echinops* has the lowest Ilium/Ischium Length Index (IILI) of all tenrecines (though not significantly lower than *Tenrec*, $p=0.28$, or *Setifer*, $p=0.61$), and *Petrodromus*' mean value is not significantly higher than *Solenodon*, *Echinosorex*, *Geogale*, *Microgale* or *Oryzorictes* ($p>0.05$). Of the tenrecines, *Hemicentetes* has a significantly long ilium ($p<0.05$), but this is not functionally consistent with the average-length ilium of the other fossorial tenrecid *Oryzorictes*. Smith and Savage (1956) correlate ilium/ischium length with degrees of

power vs. speed in hindlimb propulsion. The ischiopubic muscle complex (including the Mm. biceps femoris, semitendinosus, semimembranosus, gracilis and adductor magnus) is responsible for the beginning of the propulsive phase in extension, when there is considerable resistance and greater force is necessary for push-off. The gluteal complex, which originates on the ilium, is primarily responsible for the end-stroke in hindlimb propulsion, where there is less resistance and greater potential for speed. Smith and Savage (1956) find that highly cursorial mammals, e.g., *Equus*, have a long ilium vs. ischium, emphasizing a robust gluteal muscle group, whereas aquatic mammals, which rely on high-power hindlimb propulsion at the expense of speed, have shorter ilia and longer ischia. In light of this generalization, it is logical that *Echinops* has the relatively shortest ilium of the tenrecines; yet the long ilium of *Hemicentetes* is still puzzling. Nonetheless, IILI values for *Limnogale* and *Potamogale* fit the Smith and Savage (1956) model; *Limnogale* has the shortest ilium of all oryzorictines ($p < 0.00$), and *Potamogale* has a shorter ilium than any other studied taxon ($p < 0.03$).

The dorsal aspect of the ischium is the attachment site for the thigh extensors Mm. biceps femoris, semitendinosus, and semimembranosus (hamstrings). Anemone and Covert (2000) argued that specialized clingers and leapers have relatively short ischia with large dorsal projections, which allows for femoral push-off from a beginning vertical posture. Mammals that leap from a horizontal posture have a more posterior insertion of the hamstring musculature and a longer ischium with no dorsal projection (Anemone and Covert, 2000). Interestingly, *Echinops* has a conspicuous dorsal projection of the ischium (Figs. 4.5, 4.9), also shared by *Setifer*. Although *Echinops* is not a specialized leaper, it is the only arboreal species, and spends much of its active time

extending the hindlimb from a vertical position. Although *Setifer* is more, if not exclusively terrestrial, it shares a number of traits with *Echinops*, which most likely arose from an arboreal common ancestor (see Salton and Szalay, 2004).

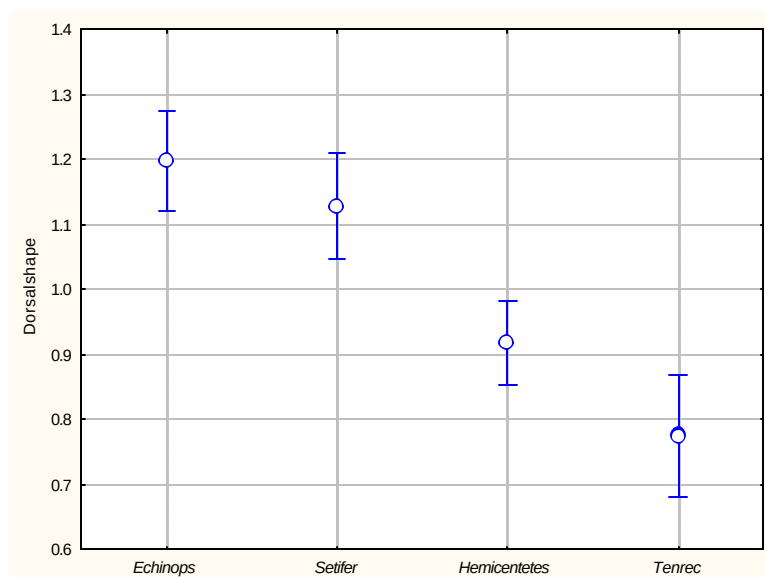


Figure 4.9. Ischium Dorsal Shape Index (IDSI), illustrating the more prominent dorsal projection of the ischium in *Echinops* and *Setifer* ($p < 0.00$).

Of all studied tenrecoids, the tenrecines and *Geogale* have a pelvis length that approximates the length of the femur, whereas the oryzorictines and *Potamogale* have a short femur relative to the pelvis (Fig. 4.10). A scatterplot of femur length to pelvis length illustrates the relatively short femur and long pelvis of the semiaquatic genera *Potamogale* and *Limnogale* (Fig. 4.11). The combined features of a relatively long pelvis, short femur, posteriorly extended ischium, and dorsally positioned acetabulum in these two genera results in a more powerful lever system for strong propulsive and recovery hindlimb phases at the expense of longer out-levers for speed.

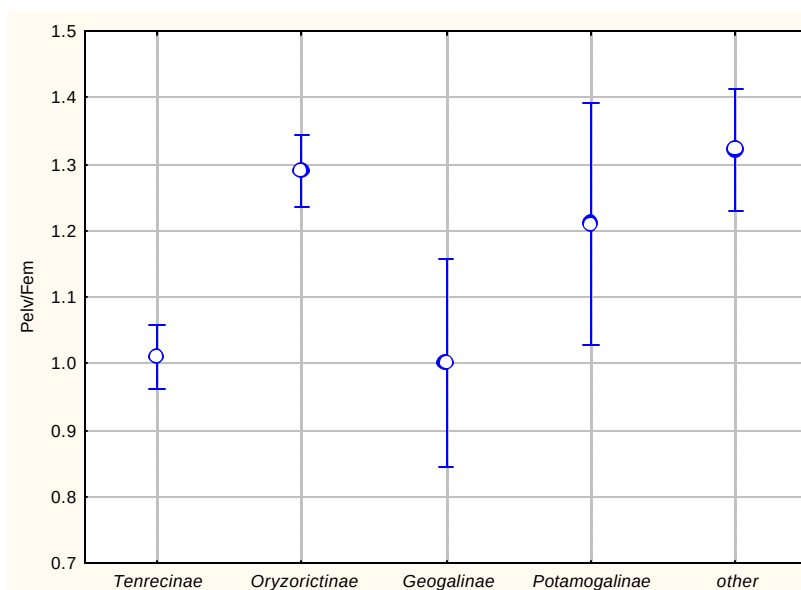


Figure 4.10. Pelvis/Femur Length Index (PFLI), illustrating the relatively long pelvis/short femur in oryzoricines and *Potamogale*.

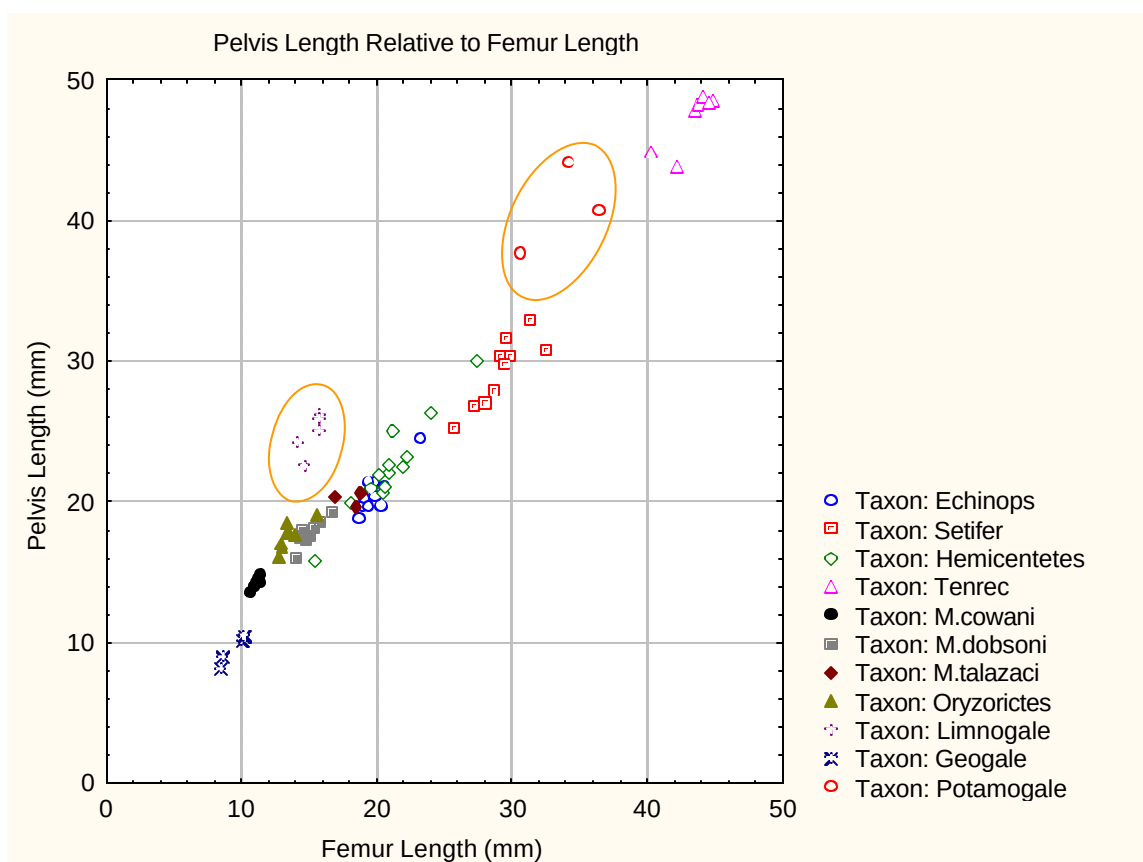


Figure 4.11. Pelvis length relative to femur length. Note the relatively long pelvis (short femur) in the swimmers *Limnogale* and *Potamogale*.

Proximal Femur

There are various functional interpretations of mammalian femoral head shape and relative size (Camp and Borell, 1937; Kappelman, 1988; Heinrich and Rose, 1997; Gebo and Sargis, 1994; Rose, 1999; Anemone and Covert, 2000; Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002). The arboreal *Echinops* has a relatively larger femoral head than any of the studied taxa (Figs. 4.12-4.14; $p < 0.02$), which agrees with data from arboreal primates, treeshrews, and marsupials (Gebo and Sargis, 1994; Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002), and implies a less constrained hip joint and broader surface for multiaxial femoral movement. Tenrecines tend to have larger femoral heads than oryzorictines, though the difference is not significant among all taxa (due to *M. cowani*'s relatively large femoral head). *Geogale*'s Femoral Head Size Index (FHSZI) value is high and within the range of the tenrecines. *Potamogale* and *Limnogale* have the lowest index values of the tenrecoids, suggesting a more restricted hip joint in these swimmers, whereas *Petrodromus* and *Echinosorex* have the smallest femoral heads of all the studied taxa (see Figs. 4.12, 4.13, 4.15).

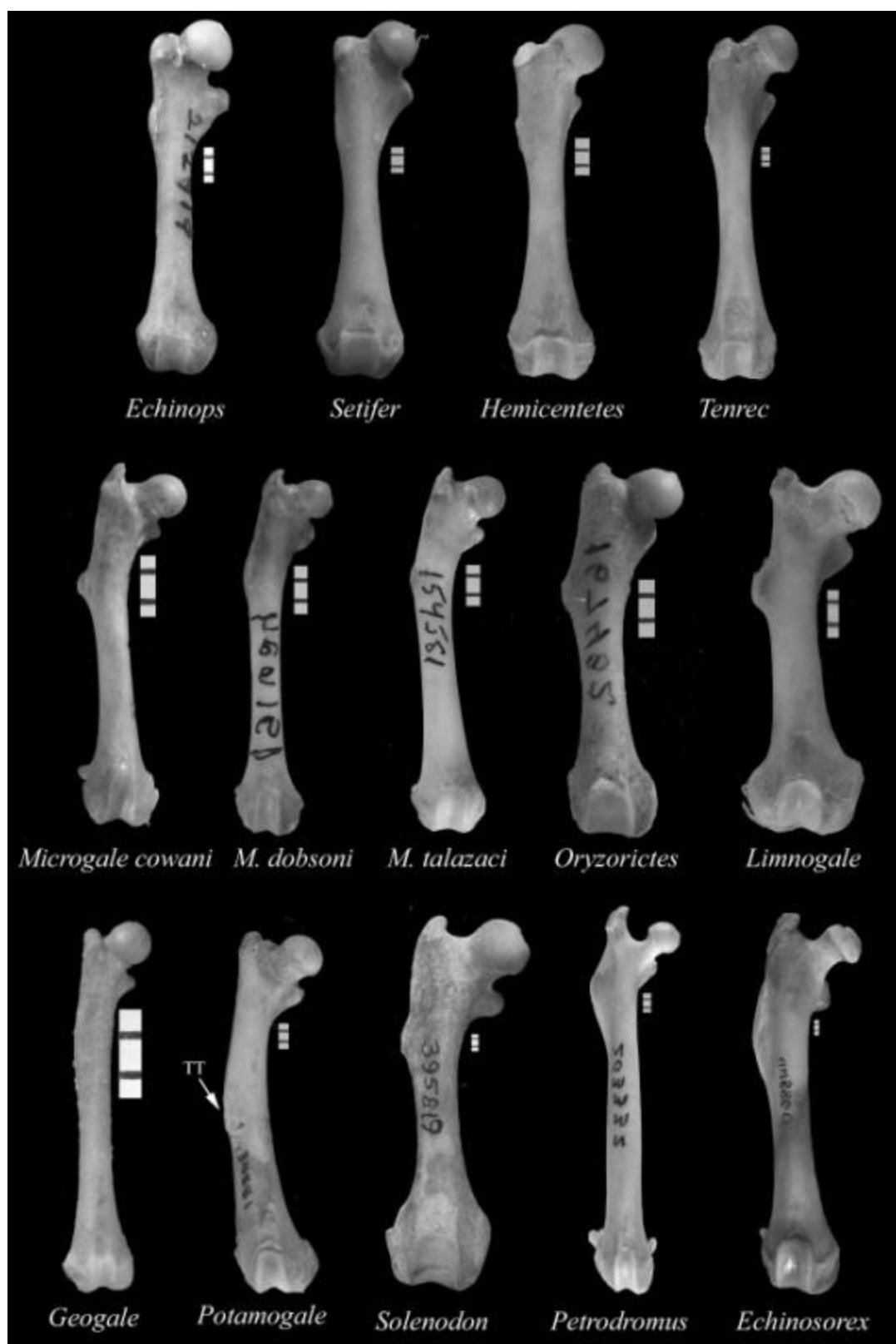


FIGURE 4.12. Anterior views of femora, right side, in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, first two from the left), and selected outgroups (bottom row, three right). TT=third trochanter in *Potamogale*.

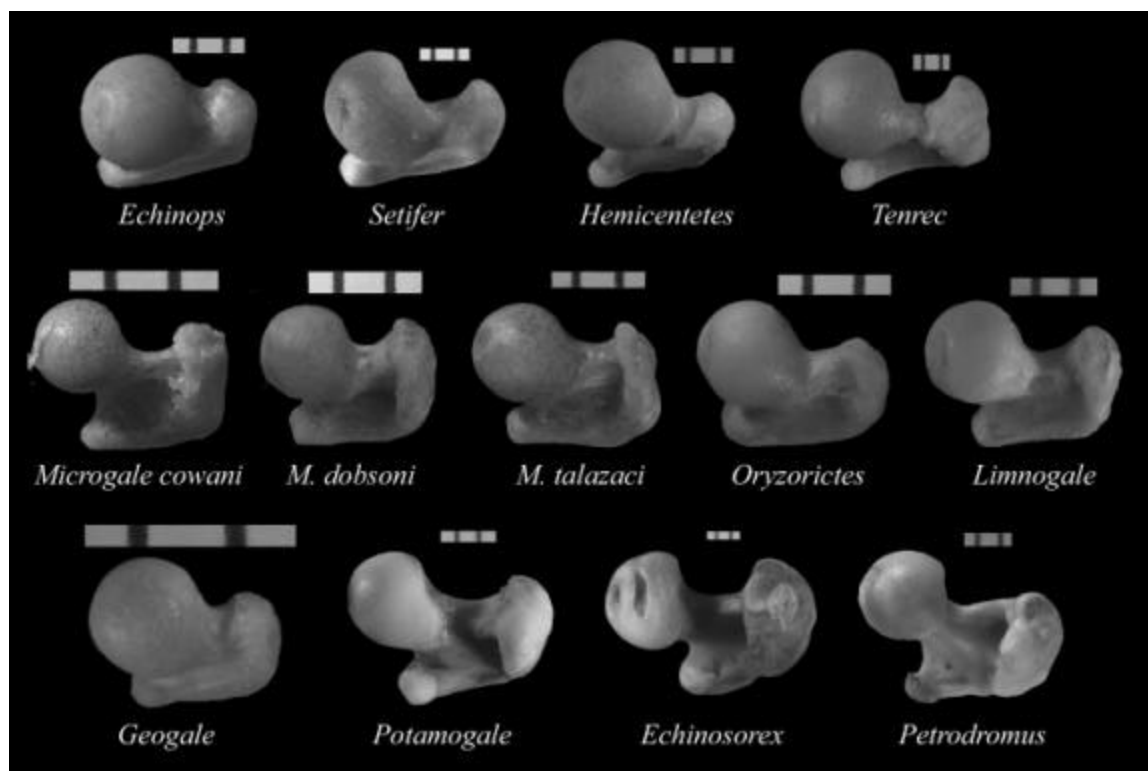


FIGURE 4.13. Proximal articular surfaces of femora (right side) in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, first two from the left), and selected outgroups (bottom row, three right).

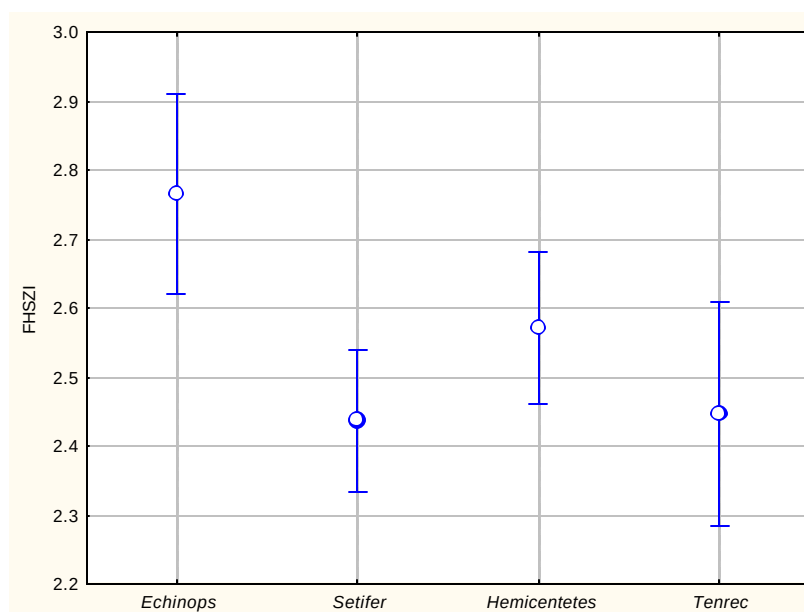


Figure 4.14. Femoral Head Size Index in four tenrecine taxa. The climber *Echinops* has a relatively larger femoral head than any of the other tenrecines, as well as any of the other taxa studied.

Unlike femoral head size, the functional significance of femoral head *shape* is not consistent across mammalian taxa. In primate vertical clingers and leapers, the femoral head is semi-cylindrical with posterior expansion of the articular surface (Anemone and Covert, 2000). Arboreal marsupials tend to have a cylindrical femoral head, but with lateral expansion, vs. the more spherical femoral head of terrestrial taxa (Szalay and Sargis, 2001; Argot, 2002;), whereas the arboreal *Ptilocercus* does not have a more or less spherical femoral head than non-arboreal scandentians, despite a suite of other postcranial traits associated with arboreal locomotor behavior (Sargis, 2002). In a comparison of forest vs. open-terrain bovids, Kappelman (1988) found that forest species have more rounded femoral heads, related to greater degrees of abduction and femoral rotation, versus open-terrain bovids, which have more cylindrical heads. Arboreal and scansorial carnivorans have rounded femoral heads as opposed to the less complete sphere (more hemi-spherical) femoral head in terrestrial species (Heinrich and Rose, 1997).

In all the taxa studied, the femoral head is generally spherical (proximally) as opposed to cylindrical, although *Setifer* has a slightly mediolaterally flattened head, different from the rounder head of its closest relative *Echinops* and the other tenrecines (Figs. 4.13, 4.16). Femoral Head Depth Index (FHDI) values represent the proximodistal depth of the head along the axis of the femoral neck. Higher FHDI values indicate a more complete sphere, whereas lower values indicate a proximodistally-shallower head. These values appear to have more functional relevance in tenrecoids than femoral width. *Echinops* has a particularly deep femoral head (see Figs. 4.13, 4.15, 4.17; $p < 0.00$). *Limnogale* has a shallow, more hemispherical femoral head relative to the other tenrecids,

providing a more limited joint surface area at the hip. These findings are consistent with Heinrich and Rose's (1997) model for a less-restricted, rounder and deeper femoral head in arboreal vs. terrestrial carnivorans.

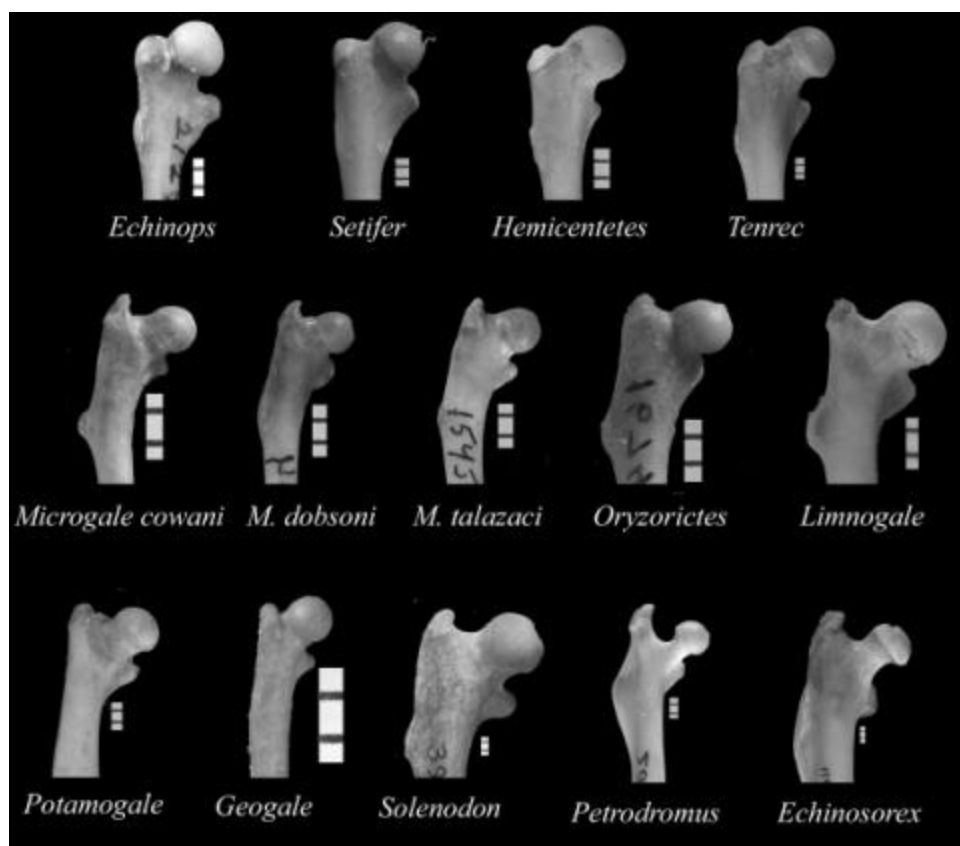


FIGURE 4.15. Anterior views of proximal ends of femora, in tenrecines (top row), oryziroctines (middle row), other tenrecoids (bottom row, first two from the left), and selected outgroups (bottom row, three right), highlighting differences between femoral head shape and the greater, lesser, and third trochanters.

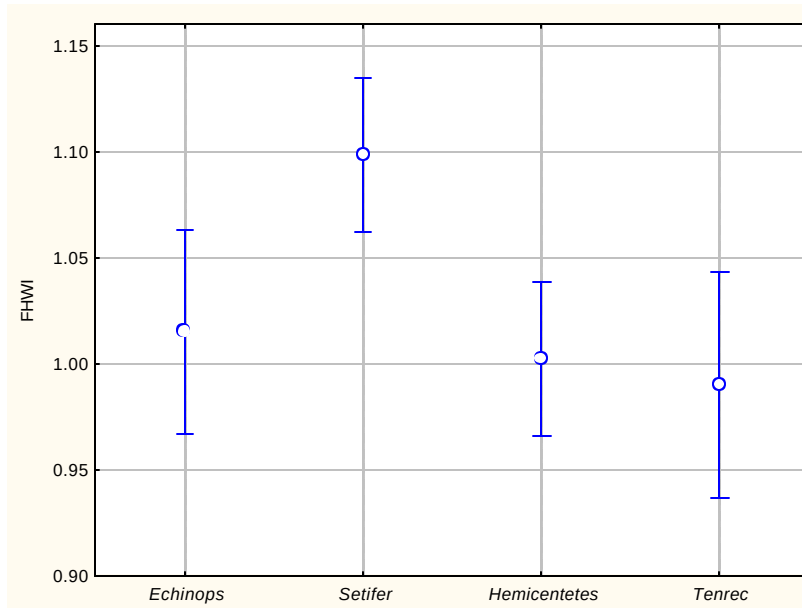


Figure 4.16. Femoral Head Width Index.

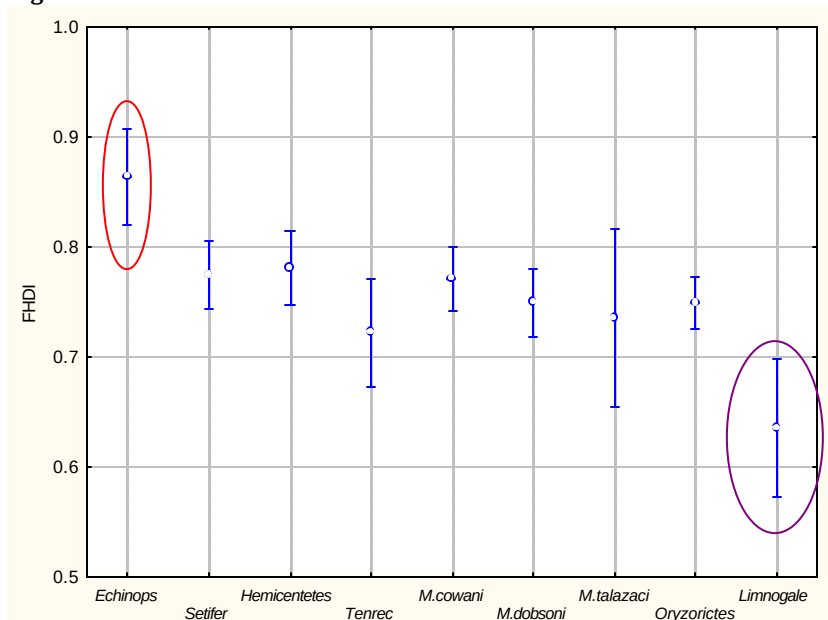


Figure 4.17. Femoral Head Depth Index values in tenrecines (left four) and oryzorientines (right five). Note the particularly deep femoral head in *Echinops*, representative of its more fully spherical head, versus that of *Limnogale*, which has an proximodistally flattened, hemispherical head with less articular surface area.

The length and angle of the femoral neck and the angle of the femoral head most likely correspond with the degree to which the femur is restricted to limited planes of motion. In more terrestrial forms, including runners and leapers, the femoral neck is longer, and the head is less parallel and more perpendicular to the long axis of the femur; in more arboreal forms, the femoral neck is short, and the head is more in line with the

femoral shaft (Reed, 1951; Kappelman, 1988; Gebo and Sargis, 1994; Heinrich and Rose, 1997; Anemone and Covert, 2000).

Relative to the long, narrow, and distinct femoral necks of *Echinosorex* and *Petrodromus*, the tenrecoid and *Solenodon* femoral neck is short and thick. Tenrecines have significantly shorter femoral necks than oryzorictines, with a femoral head that is more in line with the long axis of the diaphysis (Figs. 4.15, 4.18; $p < 0.00$). *Echinops*' in particular extends almost directly out from the base of the greater trochanter, whereas oryzorictines have a longer, perpendicularly (medially) oriented neck and head. *Geogale*'s femoral head and neck angle, as well as neck width, are similar to the tenrecines in being short, wide, and proximally oriented (Fig. 4.15).

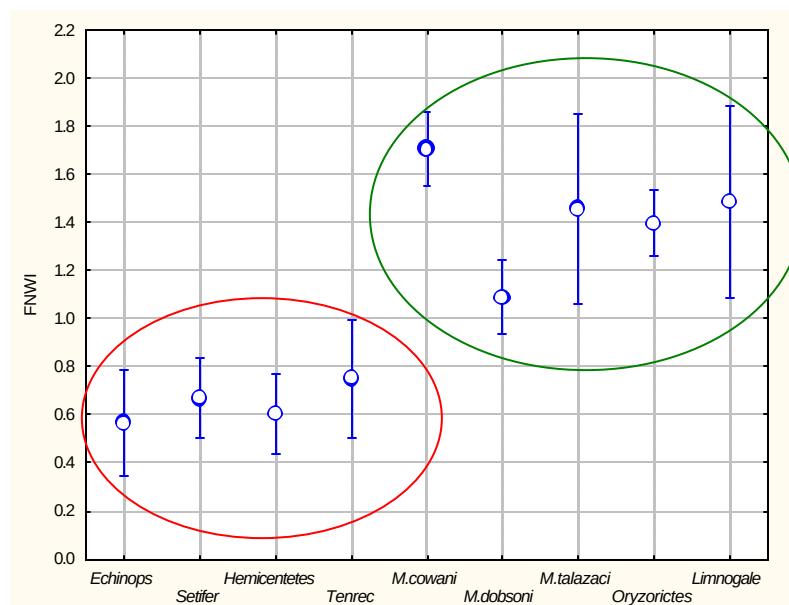


Figure 4.18. Femoral Neck Width Index (FNWI). Tenrecines (red circle) have mediolaterally shorter femoral necks than oryzorictines (green circle).

The greater trochanter of the proximal femur is the attachment site of the gluteus medius and minimus, piriformis, and vastus lateralis, and its height is generally positively correlated with powerful thigh extension associated with terrestrial running and leaping (Taylor, 1976; Godfrey et al., 1997; Heinrich and Rose, 1997; Gebo and Sargis, 1994;

Anemone and Covert, 2000; Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002).

Tenrecines have a short greater trochanter compared to all other taxa studied (Figs. 4.15, 4.19; $p < 0.00$), whereas the saltatory *Petrodromus* has an extremely long greater trochanter. Differences in the Greater Trochanter Height Index (GTRHI) within the tenrecines do not fit function-based hypotheses: *Setifer* and *Hemicentetes* have lower index values than the climber *Echinops*; yet within Oryzorictinae, the height of the greater trochanter in the terrestrial *Microgale* species is greater than that of the digger *Oryzorictes* and swimmer *Limnogale*. *Geogale* has a notable greater trochanter, but it does not project above the proximal end of the femoral head (due primarily to the relatively large size and proximal projection of the head).

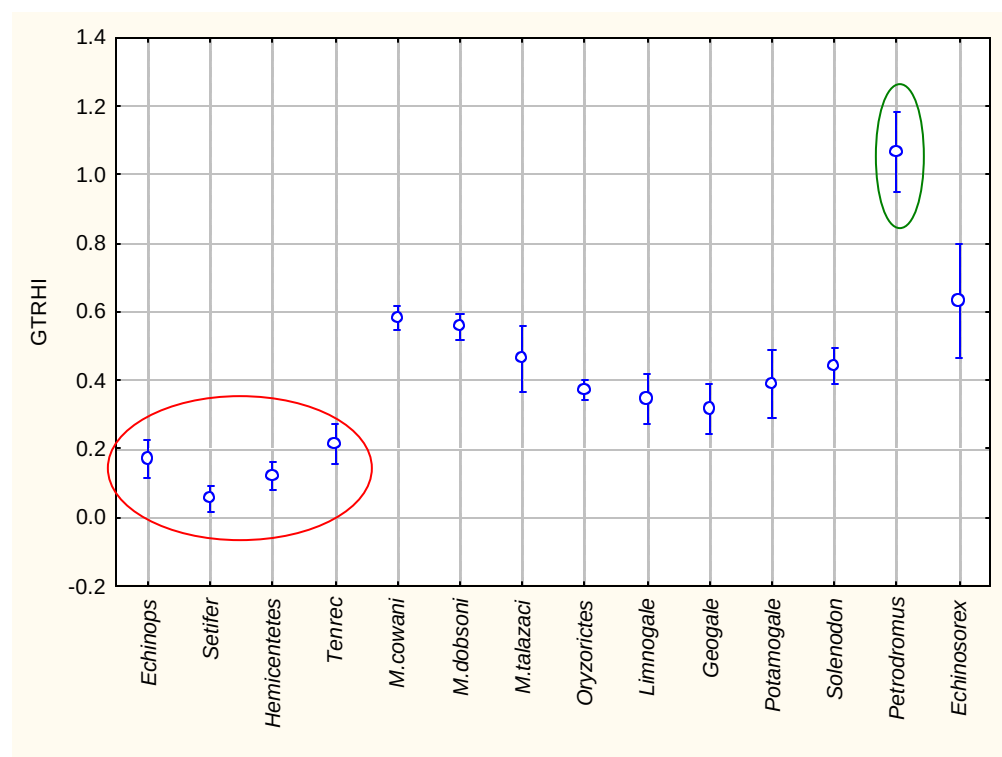


Figure 4.19. Greater Trochanter Height Index values, showing the relatively low greater trochanter height in tenrecines (red circle) vs. other taxa ($p < 0.00$). The terrestrial leaper *Petrodromus* has a particularly high greater trochanter (green circle).

Size and position of the lesser trochanter, the attachment site of flexors M. iliopsoas, and M. quadratus femoris, are correlated with direction of movement of the thigh. Arboreal mammals tend to have a medially projecting and large lesser trochanter, which is distally positioned relative to the femoral head, whereas in terrestrial taxa, the trochanter is posteriorly and proximally positioned (Taylor, 1976; Gebo and Sargis, 1994; Heinrich and Rose, 1997; Rose, 1999; Anemone and Covert, 2000; Szalay and Sargis, 2001; Argot, 2002).

The climber *Echinops* has a particularly large and medially directed lesser trochanter (Figs 15, 20; $p < 0.00$ within Tenrecinae) relative to the other tenrecines and most other taxa studied, though the trochanter is of comparable size in both *Geogale* and *Solenodon* ($p > 0.05$). *Oryzorictes* has a posteriorly oriented lesser trochanter, similar to *Petrodromus* and *Echinosorex*, that is not a shared trait with the other diggers *Hemicentetes* and *Solenodon*, but is notably different than the trochanter orientation of the other oryzorictines (Fig 15; $p < 0.00$ except in *M. talazaci*, $p = 0.16$). The lesser trochanter tends to be more proximally positioned in oryzorictines and distally positioned in tenrecines, with the exception of *Limnogale*, which has a low Lesser Trochanter Position Index value (see Fig. 4.21; yet this value is also indicative of total femur length, which is markedly short in *Limnogale* resulting in a lower LTRPI value). Within Tenrecinae, *Echinops* does not have a significantly more distally positioned lesser trochanter, and the digging taxa (*Oryzorictes*, *Hemicentetes*, and *Solenodon*) do not have LTRPI values that are functionally correlated (Figs. 4.15, 4.21). Despite its other shared traits of the proximal femur with tenrecines, *Geogale*'s lesser trochanter is not as distally positioned, and shares high LTRPI values with the *Microgale* species and *Oryzorictes*

(Fig. 4.21). Of the non-tenrecoid taxa, the saltatory genus *Petrodromus* has a notably high LTRPI value, indicating a lesser trochanter that is placed directly under the femoral head (Figs. 4.15, 4.21).

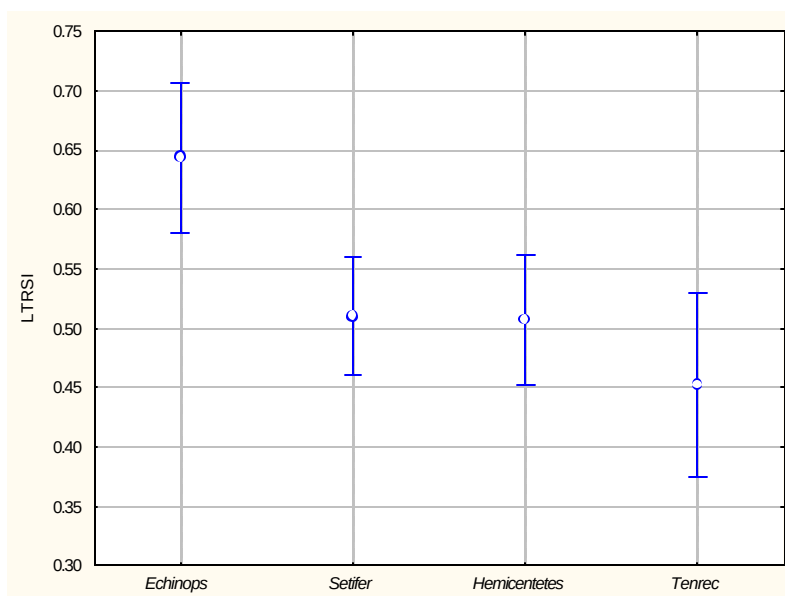


Figure 4.20. Lesser Trochanter Size Index values, demonstrating a relatively large lesser trochanter in the climber *Echinops* ($p=0.01$).

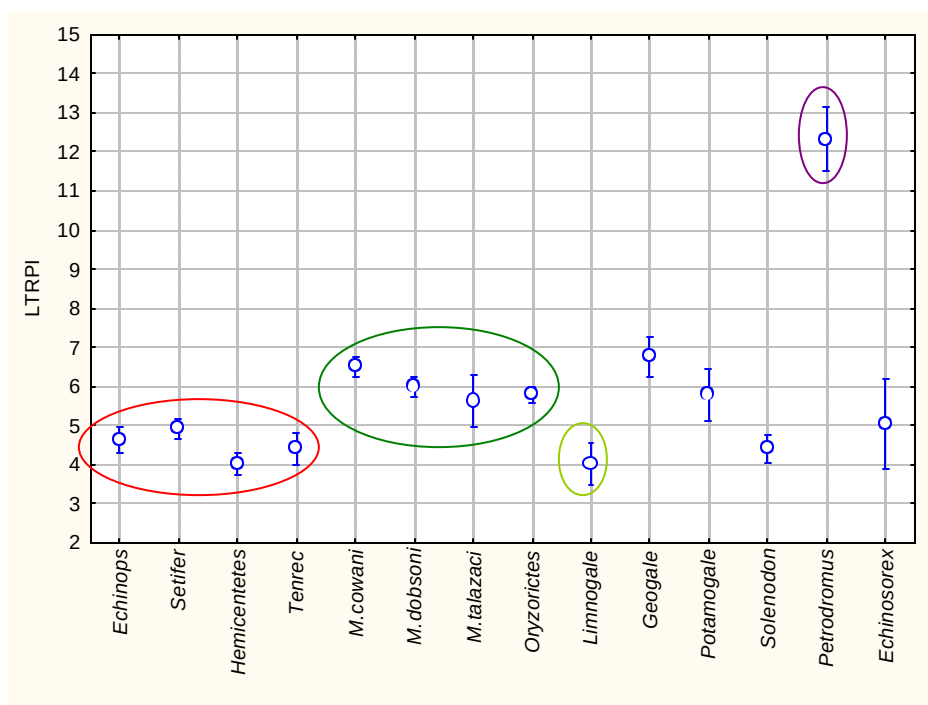


Figure 4.21. Lesser Trochanter Position Index. Tenrecines (red circle) have low LTRPI values relative to oryzictines (dark green), with the exception of *Limnogale* (though *Limnogale*'s low score is most likely

related to its short femur - see text). Note the high value of *Petrodromus* (purple) indicating a proximally positioned lesser trochanter.

The third trochanter is a highly variable mammalian trait, in terms of presense/absence, lateral expansion, and proximodistal length. Didelphids, australidelphians, anthropoids, and viverrids lack a third trochanter (Sargis, 2002). When present, it can mark the attachment sites of Mm. gluteus superficialis (maximus), quadratus femoris, vastus intermedius, and/or tensor fasciae; in most mammals, M. gluteus superficialis is most likely the major influential muscle on third trochanter size, position and shape (Hermanson and MacFadden, 1996; Heinrich and Rose, 1997; Szalay and Schrenk, 1998; Animone and Covert, 2000; Sargis, 2002). Primate leapers tend to have small and proximally positioned third trochanters (Anemone and Covert, 2000). Arboreal mammals also tend to have a relatively small third trochanter compared to a larger and laterally expanded trochanter in terrestrial mammals (Verma, 1963; Sargis, 2002). Its distal placement on the femur suggests an increased power of the M. gluteus superficialis and is a derived characteristic in edentates, pholidotans, and erinaceids (Verma, 1963; Szalay and Schrenk, 1998).

There are significant differences between taxa in third trochanter shape and position, but they do not correspond with intergeneric functional expectations. The third trochanter of the arboreal *Echinops* is not significantly smaller than those of the other tenrecines, nor is the digging *Hemicentetes* any larger (Fig. 4.12). *Setifer* and *Geogale* have the smallest (least laterally protruding) trochanters, whereas that of the leaping *Petrodromus* is at least twice the width of that of the average tenrecoid (Fig. 4.12). Within the studied oryzorictines there is marked variation in third trochanter form. All have evident third trochanters, which are on average larger than the tenrecine trochanter

(Fig. 4.22, $p=0.00$). This is consistent with the series of traits suggestive of a greater degree of facilitated multiaxial movement in the tenrecine hindlimb. *Oryzorictes*, *Limnogale*, and *Microgale cowani* have particularly large and distinct third trochanters relative to other tenrecoids, similar in overall morphology to *Solenodon* (Fig. 4.12) and the subterranean naked mole rat *Heterocephalus* (pers. obs.). This may be indicative of powerful thigh extension with some degree of abduction, related to bracing against a tunnel or pushing back soil while digging (in *Oryzorictes*, *Solenodon*, *Heterocephalus*, and most likely *M. cowani*), and an abducted extension while swimming (in *Limnogale*). *Potamogale*'s third trochanter is unlike *Limnogale*'s; it is extremely small and located farther distally on the diaphysis than any other studied taxon (Fig. 4.12).

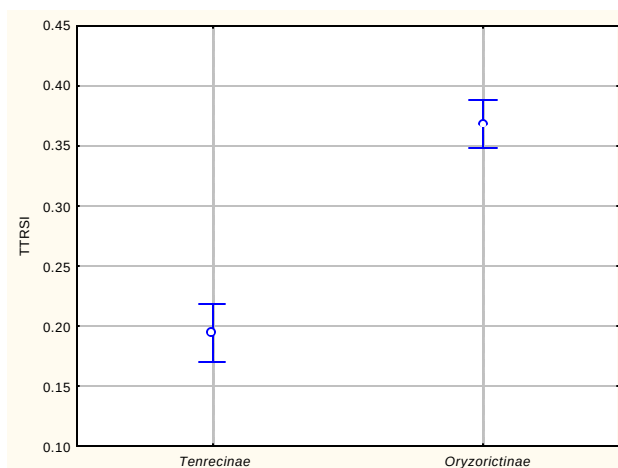


Figure 4.22. Third Trochanter Shape Index, demonstrating the larger (mediolaterally expanded) third trochanter in oryzorictines (see Fig. 4.12).

The position of the third trochanter along the femoral diaphysis does not vary greatly between any of the studied taxa, with the exceptions of *Potamogale* and *Petrodromus* (Figs. 4.12, 4.23). *Potamogale*' third trochanter is located below the midpoint of the diaphysis, most likely indicating powerful gluteal lever mechanics. Its

difference in morphology from *Limnogale*, which has a larger and more proximally positioned third trochanter, suggests a different style of hindlimb extension while swimming. *Petrodromus*' large and proximally situated trochanter provides a small moment arm for rapid extension, similar to primate vertical clingers and leapers (Anemone and Covert, 2000).

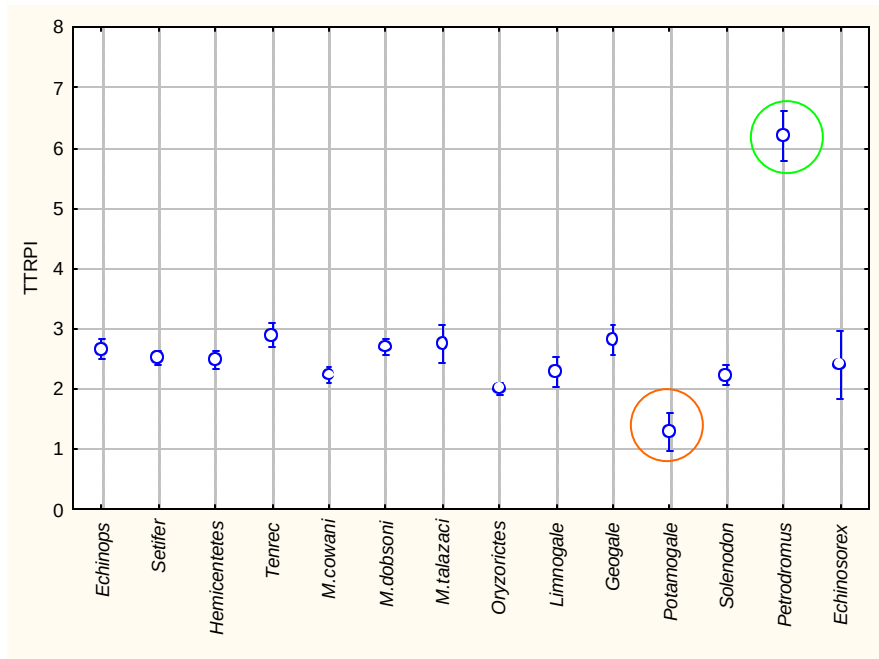


Figure 4.23. Third Trochanter Position Index, illustrating a relatively uniformly positioned third trochanter across taxa, with the exceptions of *Potamogale* (orange circle), which has a more distally placed third trochanter, and that of *Petrodromus* (green circle), which is at the proximal-most end of the femur.

Distal Femur

The trochlea of the distal femur with its patellar groove demarcates the placement and range of motion of the patella, and its form is most likely related to restriction and facilitation of movement at the knee joint. Taylor (1976; 1989) found a wider and shallow patella in arboreal carnivores vs. a deep and high-crested groove in more terrestrial and cursorial species, and Verma (1963) noted a shallow and wide patellar groove in the fossorial Indian hedgehog. Digitigrade mammals, which tend to be

cursorial, have a more restricted knee joint with a deep and narrow trochlea (Carrano, 1997).

The patellar groove in tenrecines is generally wider than in oryzorictines (Figs. 4.24, 4.25; $p < 0.05$ except for *Oryzorictes*), which is concordant with data from innominate and proximal femur, as well as the tarsals, suggesting a more multiaxially mobile hindlimb in Tenrecinae. Though all tenrecine patellar grooves are wide, that of the arboreal *Echinops* is not significantly wider than the others. *Oryzorictes* and *Solenodon* also have wide patellar grooves, most likely indicative of lateral abduction and rotation of the crus while digging and bracing against a subterranean habitat. This specialization is not found in *Hemicentetes* when patellar groove width is compared with the width of the distal epiphysis. Yet the entire width of the distal femur is wider in *Hemicentetes* than in the other tenrecines (Fig. 4.26; $p = 0.00$), as well as wider than in most other studied taxa, reflecting its wide patellar groove and femoral epicondyles. Patellar Groove Shape Index (PGSI) values are also representative of relative trochlear width, and demonstrate a relatively long (AP) and narrow (ML) trochlea in the three *Microgale* species and *Petrodromus*, and a particularly short and wide trochlea in *Hemicentetes* and *Solenodon* (Fig. 4.27)

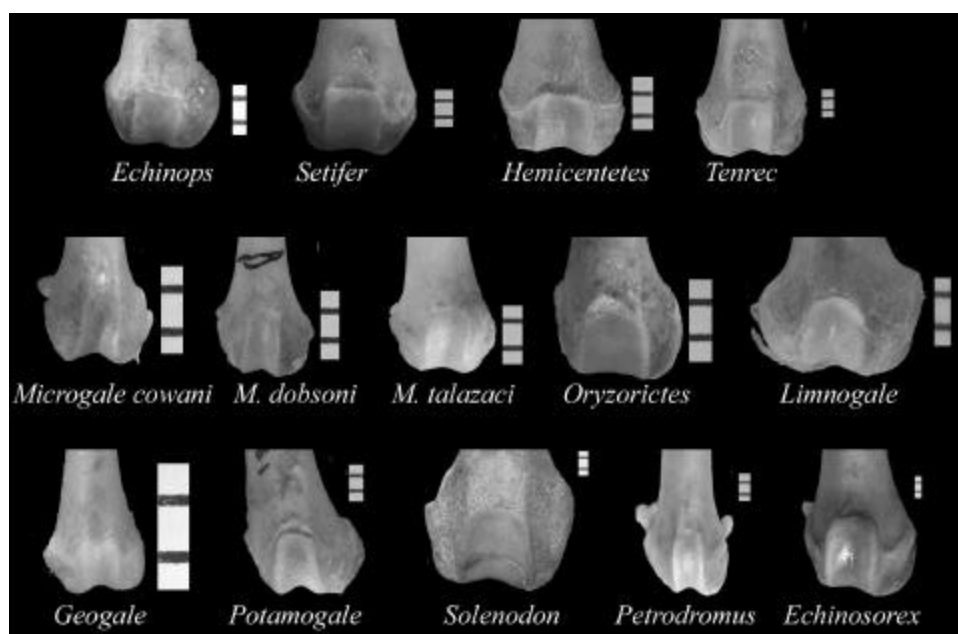


Figure 4.24. Anterior views of distal femora, right side, in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, first two from the left), and selected outgroups (bottom row, three right), illustrating relative widths of the femoral trochlea with its patellar groove.

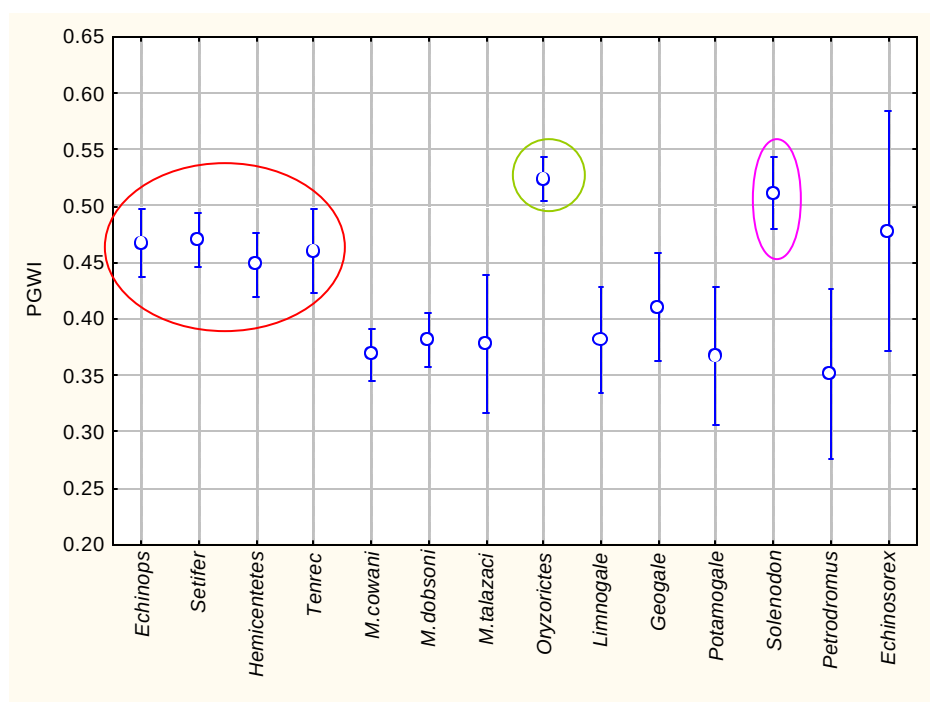


Figure 4.25. Patellar Groove Width Index, illustrating a generally deep (AP) patellar groove in tenrecines (red circle), as well as the subterranean oryzorictine *Oryzorictes* (green circle) and the digging *Solenodon* (pink circle).

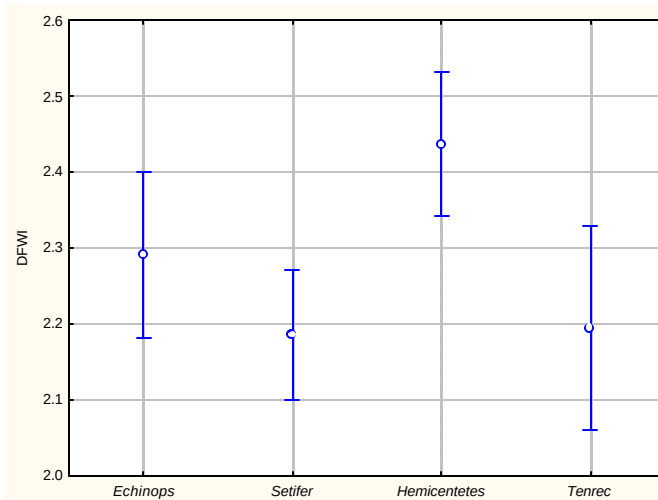


Figure 4.26. Distal Femur Width Index, demonstrating a relatively wide distal femur in the digging tenrecine *Hemicentetes* ($p < 0.02$ for *Tenrec* and *Setifer* and $p = 0.19$ for *Echinops*).

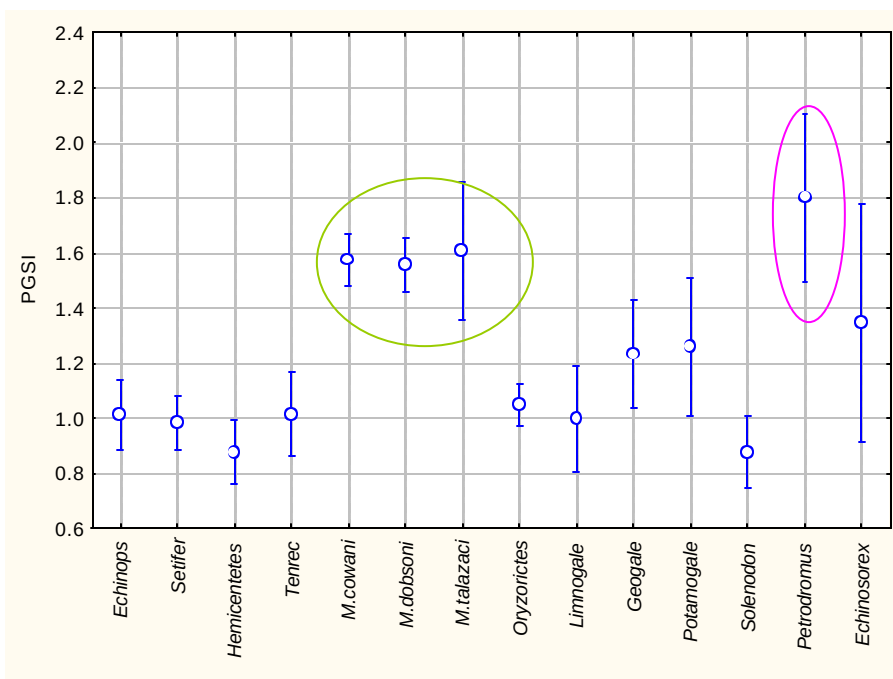


Figure 4.27. Patellar Groove Shape Index, demonstrating a particularly high and narrow patellar groove in the three *Microgale* species (green circle) and *Petrodromus* (pink circle).

As with the femoral trochlea, the condyles of the distal femur tend to be mediolaterally wide and anteroposteriorly compressed in arboreal vs. terrestrial mammals. Primate leapers have relatively anteroposteriorly deep and proximodistally

long condyles (Gebo and Sargis, 1994; Anemone and Covert, 2000), whereas those in a range of mammalian climbers tend to be mediolaterally wide, proximodistally short, and anteroposteriorly shallow (Heinrich and Rose, 1997; Elton, 2001; Argot, 2002; Sargis, 2002). Mammals with a somewhat more laterally abducted femur, as in arboreal marsupials, have a mediolaterally expanded lateral femoral condyle (Szalay and Sargis, 2000; Argot, 2002). In eutherian climbers, the medial condyle tends to be only slightly broader than the lateral condyle, whereas in terrestrial forms, the medial condyle is much expanded (Godfrey, 1997; Elton, 2001).

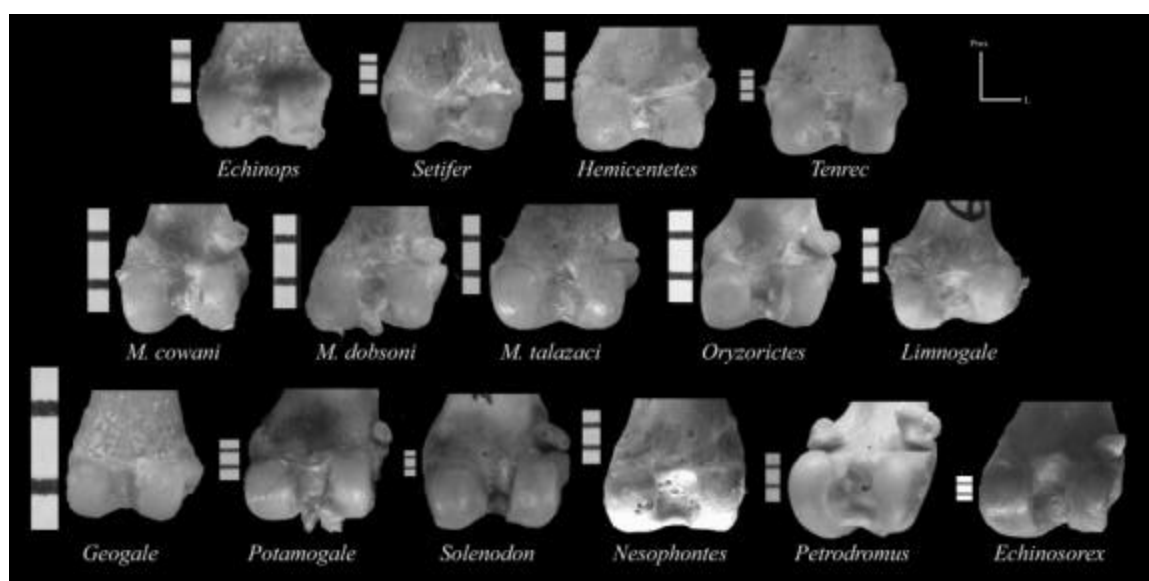


FIGURE 4.28. Posterior views of distal femora, right side, in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, first two from the left), and selected outgroups (bottom row, third to fifth from the left).

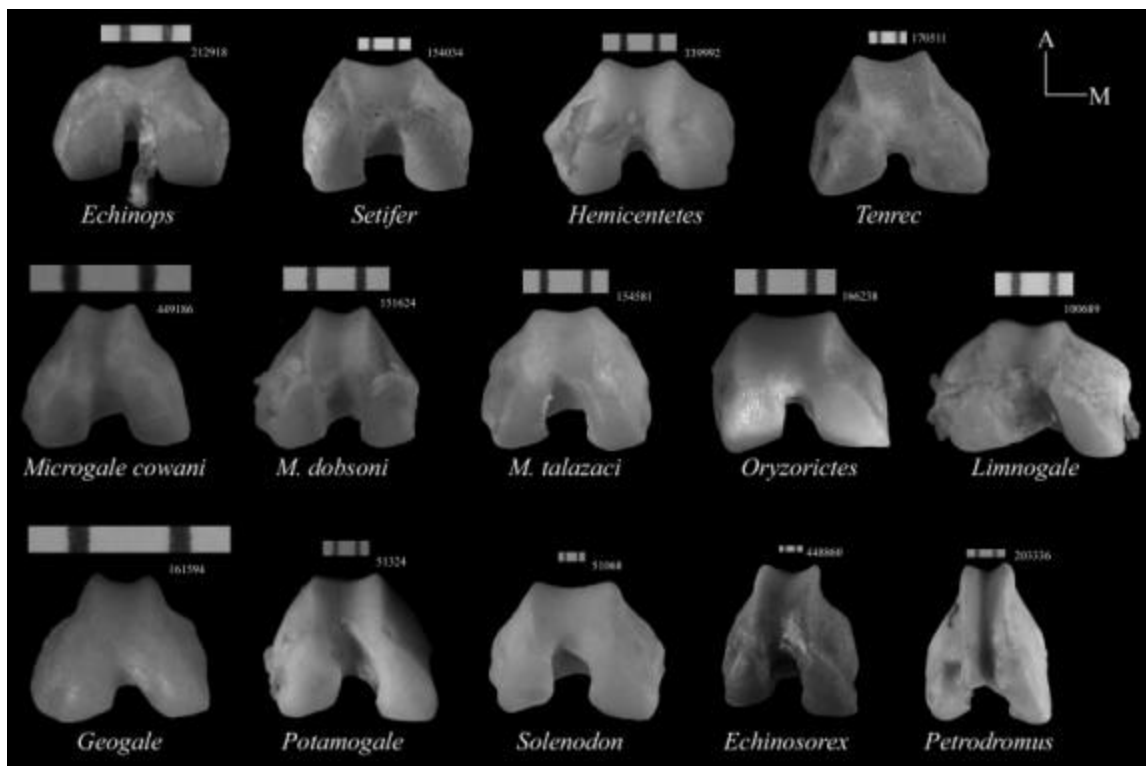


FIGURE 4.29. Distal views of right femora in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, first two from the left), and outgroups (bottom row, third to sixth from the left).

Tenrecines tend to have mediolaterally wider femoral condyles than oryzorictines (Figs. 4.28, 4.30, $p=0.00$), with the exception of the subterranean *Oryzorictes*, which has the same condylar width as *Hemicentetes* and has the greatest mean width of all studied taxa. There are no significant differences within Tenrecinae; *Echinops* does not have wider femoral condyles than the terrestrial non-climbers. Both *Echinops* and *Oryzorictes* have anteroposteriorly shallow femoral condyles, whereas those of *Potamogale* and *Petrodromus* are deep (see Fig. 4.29, 4.31, though sample size for this variable is small, except for *Oryzorictes*, $p>0.05$). Relative femoral condyle widths (medial/lateral) are surprisingly uniform across Tenrecoidea, with the exceptions of *Limnogale* and *Geogale*. The mean value for most tenrecoids is 1.1-1.2, demonstrating a medial condyle that is slightly wider than the lateral with relatively little interspecific variation (Figs. 4.28, 4.29,

4.32). This condition is reversed in *Limnogale* and *Geogale*, which both have slightly wider lateral condyles (Figs. 4.29, 4.32). This trait may be correlated with a relatively high femoral neck angle in these two taxa relative to the other oryzorictines, and a consequently more laterally splayed femur, as in marsupials and primitive therians (although the width of the lateral condyle in these taxa does not approach that in marsupials). Tenrecines have a laterally splayed femur, but the crus, ankle, and foot are also laterally splayed, so the lateral condyle does not compensate by widening. In *Limnogale* and *Geogale*, the crus is more anteriorly directed, so the lateral condyle would need to widen to maintain its full load bearing joint contact.

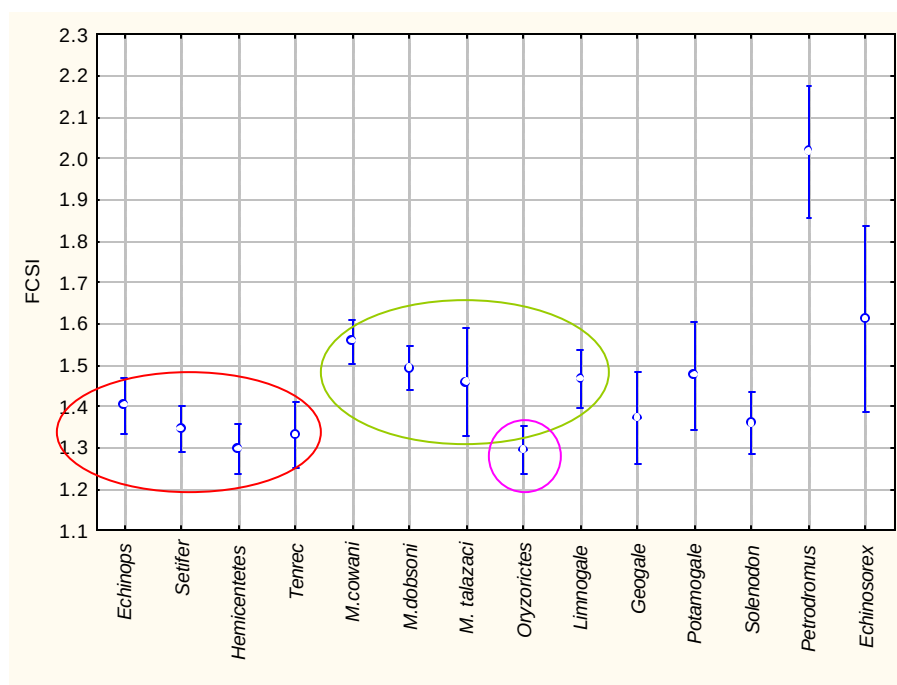


Figure 4.30. Femoral Condyle Shape Index. Tenrecines (red circle) tend to have mediolaterally wider femoral condyles than oryzorictines (green circle), with the exception of the digging *Oryzorictes* (pink). The elephant shrew *Petrodromus* has narrow and proximodistally long condyles.

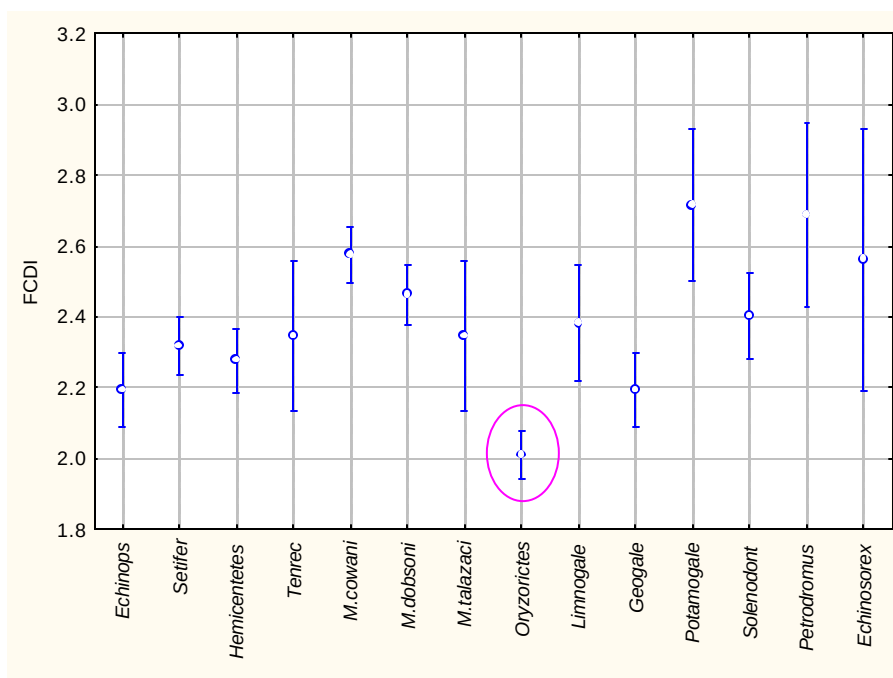


Figure 4.31. Femoral Condyle Depth Index. *Oryzorictes* has particularly shallow (anteroposteriorly) femoral condyles, whereas those in *Potamogale*, *Petrodromus* and *Echinorex* are deeper. Sample sizes are small; significant differences only found in *Oryzorictes*.

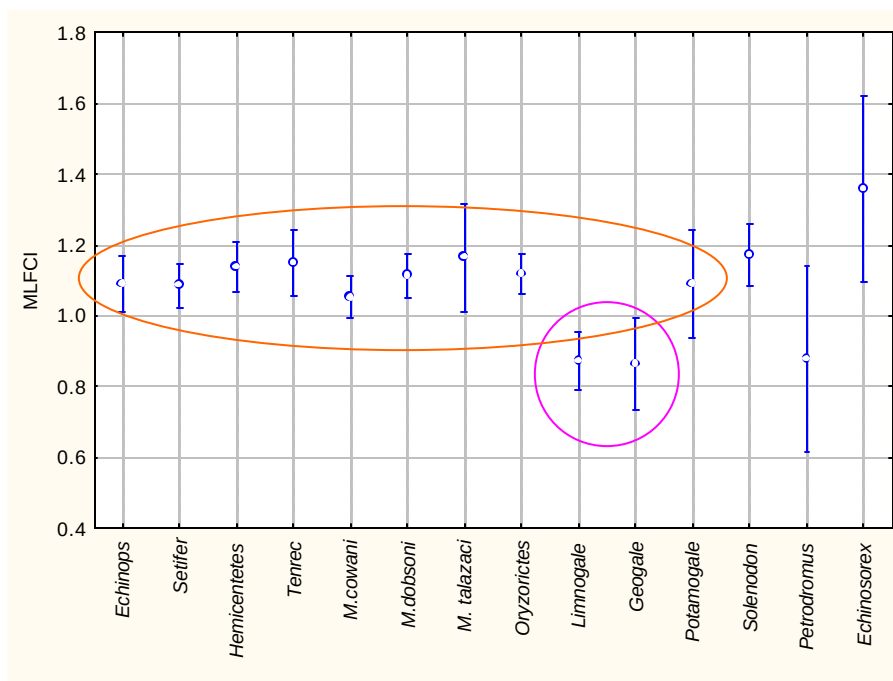


Figure 4.32. Medial/Lateral Femoral Condyle Index, demonstrating a slightly wider medial condyle in most tenrecoids (orange circle), with the exceptions of *Limnogale* and *Geogale* (pink circle), which have slightly wider lateral condyles.

Tibia/Fibula

The tibial tuberosity of the proximal tibia is the major insertion site of M. quadriceps femoris. A sharp and anteriorly projecting tuberosity is generally correlated with speed and agility (rapid knee extension), whereas a flat, rounded tuberosity is more often found in slow climbers (Gebo and Sargis, 1994; Heinrich and Rose, 1997; Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002). *Echinops* has the flattest and widest tibial tuberosity of all studied taxa, though the difference is not significant from its sister taxon *Setifer* (most likely due to small sample size; see Figs. 4.33, 4.34). Oryzorictines tend to have a narrower and anteriorly projecting tuberosity (Figs. 4.33, 4.44), yet relative to the other oryzorictines, *Limnogale* has a mediolaterally wide and rounded tibial tuberosity, suitable for a more powerful extension of the knee in an aquatic environment. *Geogale* has a rounded and anteroposteriorly short tuberosity, similar in form to that of the tenrecines (Fig. 4.33).

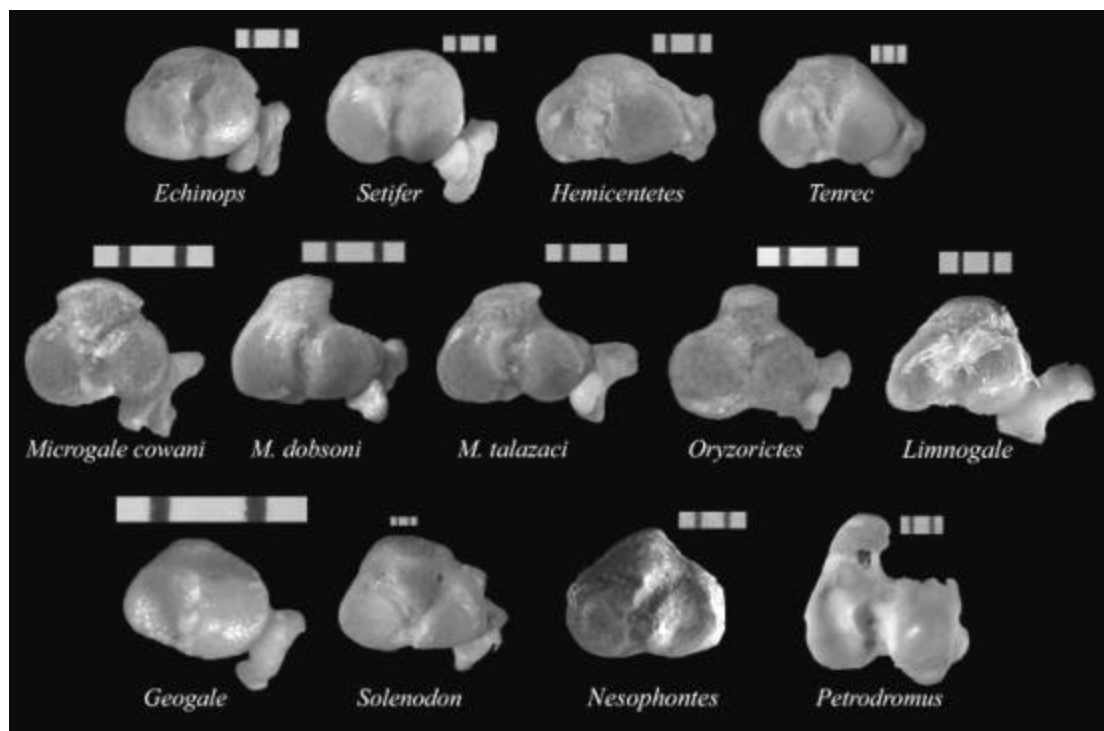


FIGURE 4.33. Proximal Articular Surfaces of Tibiae/Fibulae, right side, in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, first two from the left), and selected outgroups (bottom row, three right). Note: the relatively larger tibial tuberosities in oryzorictines (middle row) than in tenrecines (top row); the wide knee joint in the digging *Hemicentetes* relative to the other tenrecines (top row); the enormous tibial tuberosity in the elephant shrew (*Petrodromus*), associated with rapid knee extension.

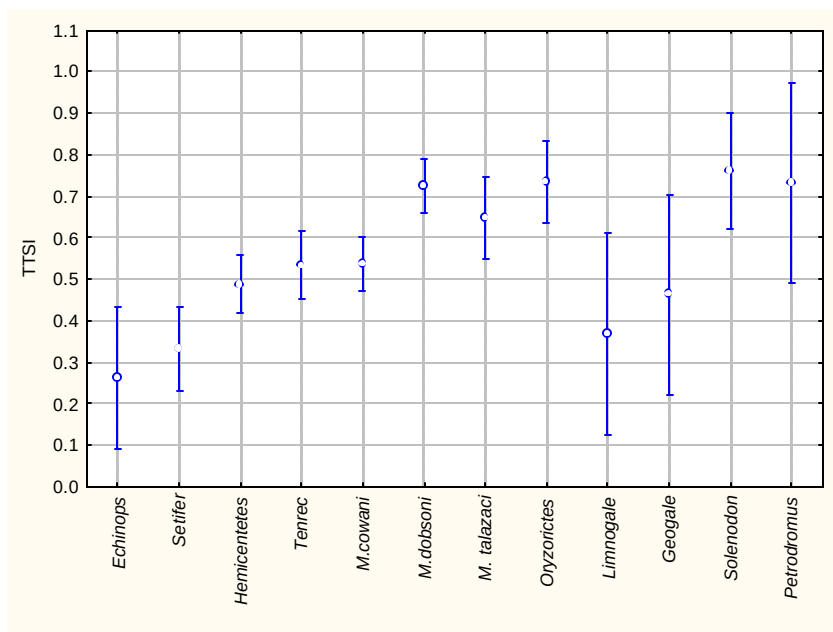


Figure 4.34. Tibial Tuberosity Shape Index, illustrating a particularly small tibial tuberosity in the climber *Echinops* compared with the more terrestrial taxa. The diggers *Oryzorictes* and *Solenodon*, and the saltatory *Petrodromus* have particularly long tuberosities.

Relative size of the medial and lateral tibial condyles would logically correlate with the size of the articulating femoral condyles. Nonetheless, mean values for this index (medial/lateral tibial condyle index, MLTCI) demonstrate a relatively wider lateral than medial condyle in most tenrecoid taxa, as opposed to a wider medial than lateral femoral condylar surface. This is an artifact of the rounded, concave surface of the medial tibial condylar surface, as opposed to the flatter and more open lateral condyle (Figs. 4.35, 4.36). *Echinops* has a high MLTCI mean value, which is representative of a slightly wider and flatter medial condyle in *Echinops* relative to other taxa (Fig. 4.35). Although *Limnogale* falls into the range of the other tenrecoids for this index variable, *Geogale*'s

medial condyle, like the medial condyle of the femur, highlights a particularly expanded lateral side of the knee joint (Figs. 4.35, 4.36).

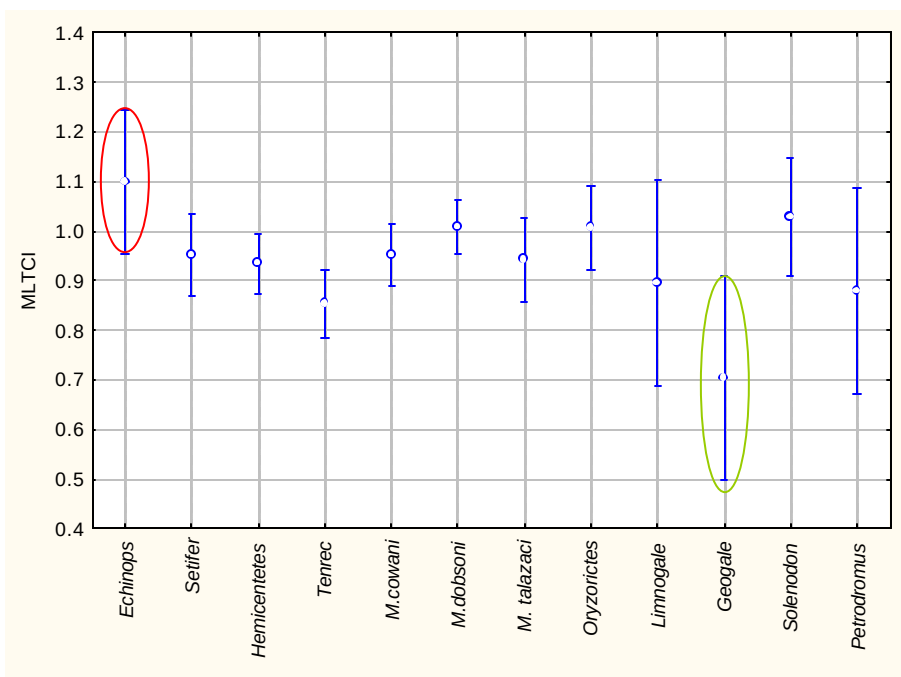


Figure 4.35. Medial/Lateral Tibial Condyle Index, illustrating a particularly wide medial condyle in *Echinops* (red), and a wide lateral condyle in *Geogale* (green).

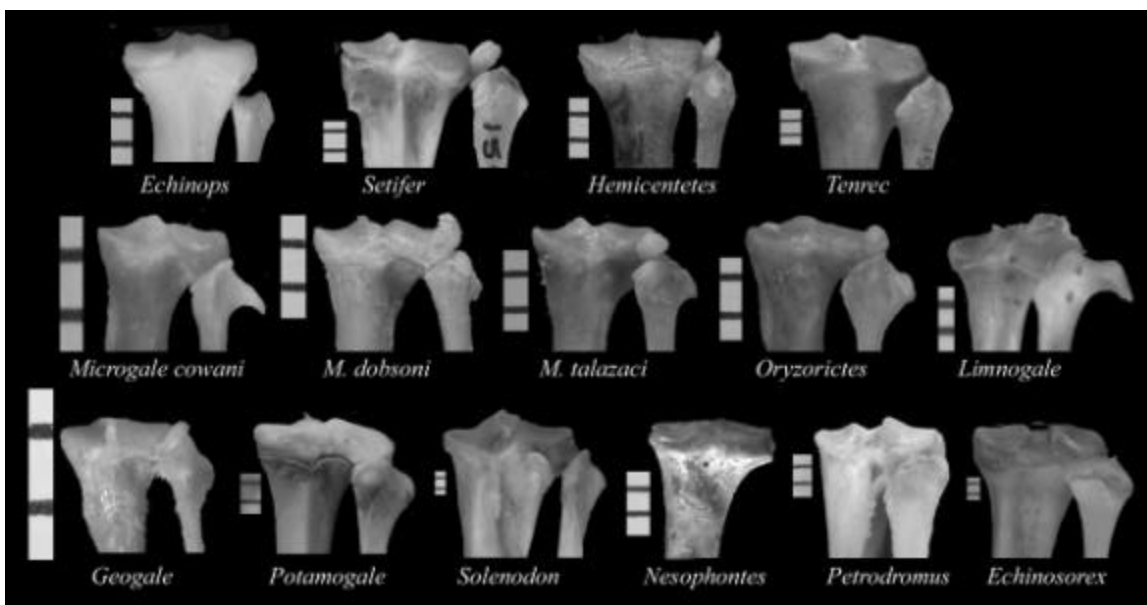


FIGURE 4.36. Posterior views of proximal tibiae and fibulae right side, in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, first two from the left), and selected outgroups (bottom row, three right), demonstrating the convex medial surface of the medial tibial condyle vs. a flattened lateral condyle.

The relative length of the tibia and the extent of tibial/fibular fusion/apposition are highly indicative of locomotor behavior in a wide range of eutherian mammals (Reed, 1951; Smith and Savage, 1956; Taylor, 1989; Casinos et al., 1993; Hildebrand, 1995; Gebo and Sargis, 1994; Rose, 1999; Anemone and Covert, 2000; Stein, 2000). Fusion of the distal half of the tibia and fibula is common in most erinaceids, soricids, talpids, and leporids. Leaping primates tend to have a closely positioned tibia and fibula relative to the more widely spaced tibia/fibula in non-leaping primates (Anemone and Covert, 2000), and the distal half of the tibia and fibula in the vertical clinger and leaper *Tarsius* is completely fused. The tibia is relatively short in terrestrial vs. arboreal guenons, despite a trend of lengthened distal limb elements in cursorial mammals (Gebo and Sargis, 1994). Fossorial and graviportal mammals tend to have relatively short tibiae (Reed, 1951; Smith and Savage, 1956; Casinos et al., 1993), whereas those in leaping mammals are long and usually combined with a lengthened foot and well-developed gastrocnemius muscle (Smith and Savage, 1956).

There are several apparent differences in form between the tenrecine and oryzorictine crus. The tenrecine tibia and fibula are proximodistally straight compared to the more sigmoid form seen in the oryzorictines, and especially in *Limnogale*, which has an extreme medial bowing of the proximal tibia relative to all other studied taxa (Fig. 4.37). *Geogale* and *Potamogale* are more similar to tenrecines in this respect, and have relatively axially aligned tibiae. Sigmoid curvature of the crus is also found in didelphids, and may represent a primitive therian or pretherian feature related to an abducted femoral stroke (Argot, 2002; Szalay and Sargis, 2001). Foot position in oryzorictines is aligned with the axial skeleton, as opposed to a more laterally splayed foot in tenrecines (see

Salton and Szalay, 2004). The tibial bowing in oryzorictines might be related to their medially shifted foot and the need to compensate for medially oriented loading. In *Limnogale*, the extreme medial bowing of the tibia is most likely correlated with the enlarged lateral condyles of the femur and tibia, similar to the combined sigmoid tibia and extremely enlarged lateral condyles seen in didelphids (though perhaps with different functional implications).

The oryzorictines and *Potamogale* have distally fused crura, as does *Petrodromus* and *Echinosorex*, though fusion in *Limnogale* is not complete. Fusion of the distal crus is consistent with function-based hypotheses in the heavily loaded hindlimbs of *Petrodromus*, *Potamogale*, *Limnogale* and *Oryzorictes*, and non-fusion is consistent with the more multiaxially mobile hindlimbs of the tenrecines; yet it does not necessarily follow that the crus in *Microgale* would be fused as well. And why is the distal crus unfused in the digger *Solenodon*? Fusion of the distal crus is a derived condition relative to metatherians and prototherians, which have separate and well-spaced tibiae and fibulae, and a greater dependence on the fibula for load-bearing relative to eutherian mammals (Kemp, 1982). Fusion of the tibia and fibula is a derived condition, perhaps initially based on a heavy load-impacted crus, and retained in descendant taxa with less severely loaded limbs (see Winge, 1941; Reed, 1951). This would suggest a fossorial *Oryzorictes*- or *M. cowani*-like ancestor for Oryzorictinae, which is not supported by molecular phylogenetic studies (Olson and Goodman, 2003). Another possibility is that the fused crus was a response to the shifting loads involved with a medially rotated, axially aligned foot. Yet this shift in foot posture was also most likely related to a more stabilized hindlimb in oryzorictines (relative to tenrecines), which leaves open the

question: what were oryzorictines doing that required a more stabilized foot relative to tenrecines?

Both *Limnogale* and *Microgale cowani* (though not the other two *Microgale* species) have a lateral process of the proximal fibula (Fig. 4.39), most likely indicating an enlarged attachment area for the peroneal musculature, responsible for eversion and flexion of the foot. Though *Oryzorictes* does not have a similar process, the entire head of the fibula is especially large relative to that of the other oryzorictines (Fig. 4.37). The consistent presence of this trait in *M. cowani* (in addition to a suite of other traits in common with *Oryzorictes*, see Salton and Szalay, 2004) may be indicative of fossorial behavior, though it is not a documented digger. Its difference from *Oryzorictes* in this respect suggests a convergence of digging related traits as opposed to particularly close common ancestry.

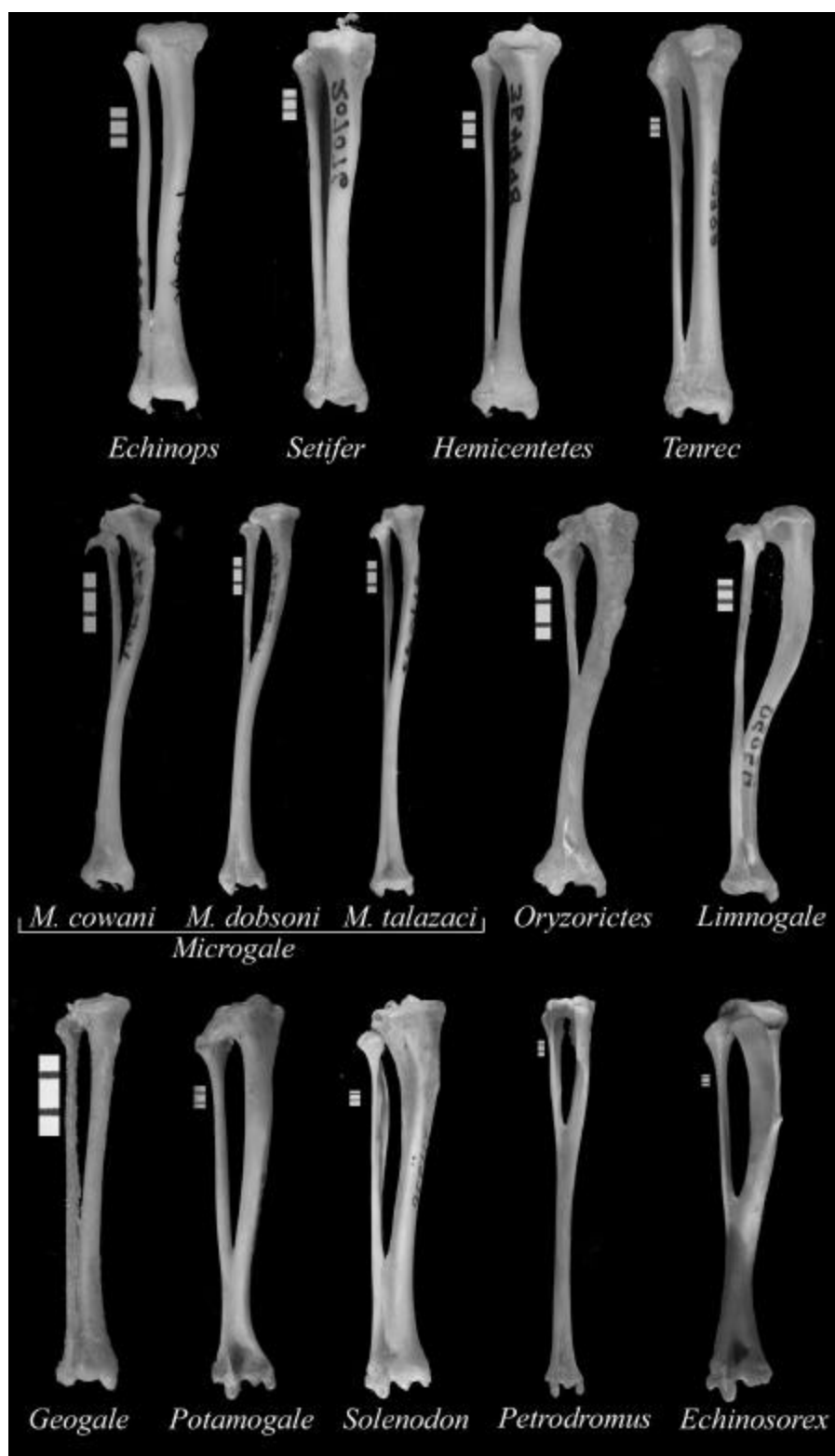


FIGURE 4.37. Anterior views of crura, right side, in tenrecines (top row), oryzorictines (middle row), other tenrecoids (bottom row, first two from the left), and selected outgroups (bottom row, three right). Note the straight and unfused crus of tenrecines (top row), whereas the tibia of oryzorictines is medially bowed on the proximal end and fused to the fibula on the distal end.

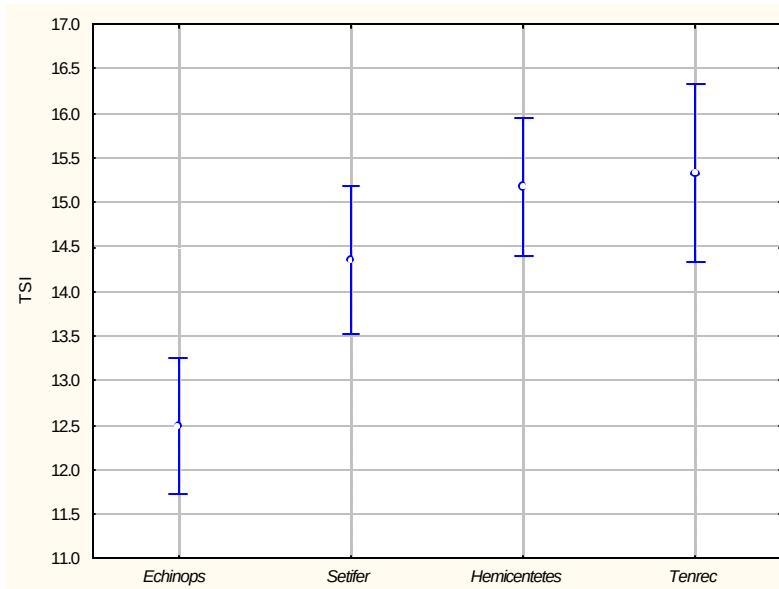


Figure 4.38. Tibia Shape Index in tenrecines. The climber *Echinops* has a significantly shorter/wider tibia than the other three tenrecine species.

Although the bones of the hindlimb tend to lengthen distally (i.e. femur vs. crus) in high-speed cursors such as *Equus* (Smith and Savage, 1956), the functional significance of lengthened hindlimb elements in other locomotor specialists is not straightforward. The phrase “lengthening of the distal hindlimb elements” is used to describe adaptations of cursorial and leaping mammals (e.g., Smith and Savage, 1956; Gebo and Sargis, 1994; Hermanson and MacFadden, 1996), but it is not always clear *which* distal hindlimb bones are lengthened, if any (Lammers and German, 2002). In digging mammals, the crus is expectedly short and wide (Reed 1951; Casinos et al., 1993), as are all of the bones of the appendicular skeleton.

Tenrecoid tibia shape (as measured by length/width) is highly variable across taxa. *Echinops* has the relatively shortest and broadest tibia of all tenrecoids (Fig. 4.38; $p < 0.00$), as well as the highest crural index ($p < 0.00$; Figs. 4.37, 4.39, 4.40). *Hemicentetes* does not have a particularly stout tibia, though all of the tenrecine tibiae are shorter and wider than in most other studied taxa (Fig. 4.39). *Oryzorictes* has a particularly

short/wide tibia relative to the other oryzorictines, as well as a high crural index, which is indicative of powerful thigh extension for digging (Figs. 4.39, 4.40; though for TSI $p > 0.05$ for *Limnogale*, most likely due to small sample size for *Limnogale* tibia measurements). Although *Limnogale*'s tibia is not particularly robust (as is the femur; see Fig. 4.12), it has a long tibia relative to the femur, which is unexpected for a swimmer (Figs. 4.37, 4.40); this morphology is indicative of high-speed thigh extension at the expense of power, not necessarily of the strength needed to propel the foot through water. As expected, the elephant shrew *Petrodromus* has a very long and narrow tibia (Figs. 4.37, 4.39) that is considerably longer than the femur (Fig. 4.40), which, combined with its relatively long pes, is suggestive of its high-speed leaping behavior.

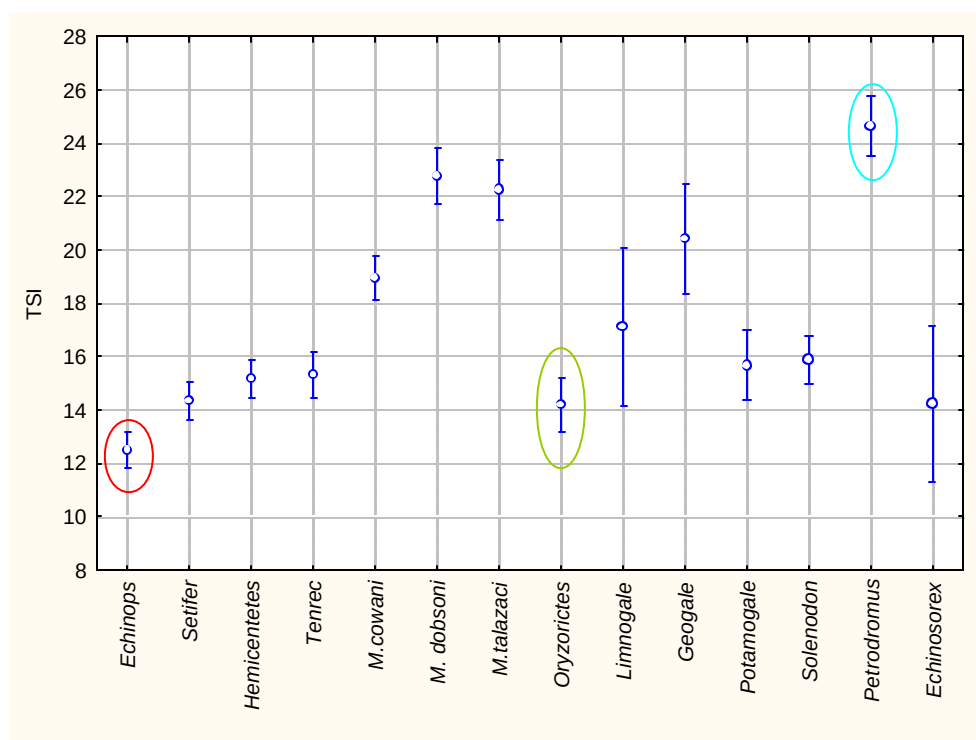


Figure 4.39. Tibia Shape Index, illustrating the relatively short/wide tibia in the climber *Echinops* (red). *Oryzorictes* (green) has a low TSI index relative to the other tenrecines, and *Petrodromus* (blue) has a high index, representative of its long and narrow tibia.

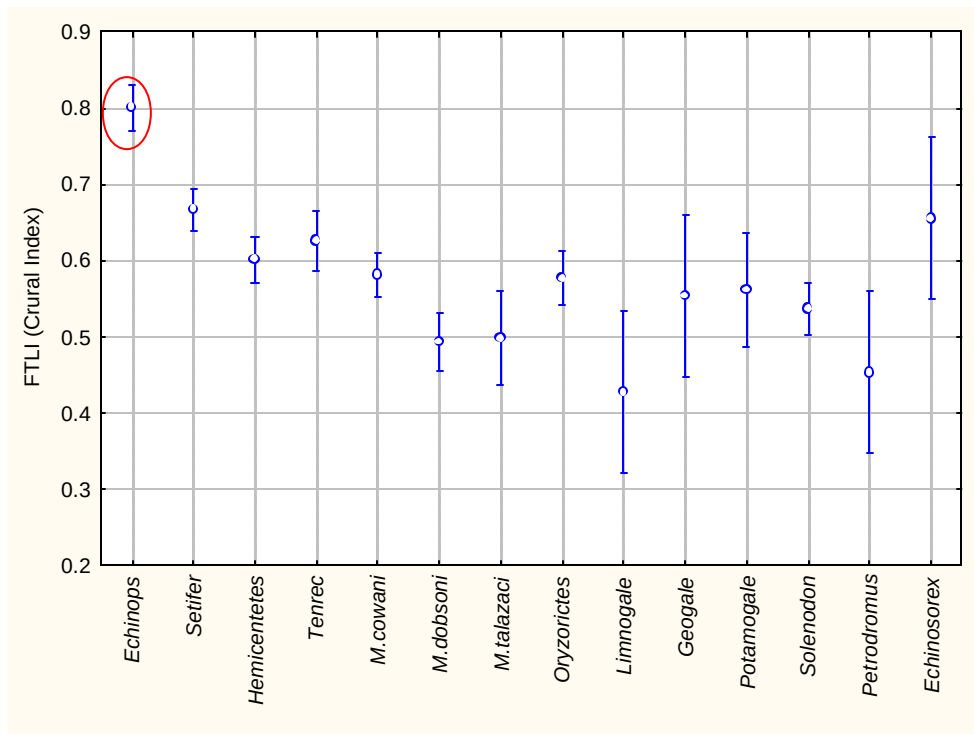


Figure 4.40. Femur/Tibia Length Index (Crural Index), demonstrating the relatively long femur/short tibia in the climber *Echinops* (red).

Summary and Conclusions

As with the skeleton of the tenrecoid hand and foot, the pelvis and hindlimb demonstrate complex and graded levels of functional and phylogenetic significance. Several characteristics correspond with expected form related to function-based convergences in other mammalian taxa. For example, *Echinops* has several traits that correlate with behavior in an arboreal microhabitat, such as a relatively shallow acetabulum, large and deep femoral head, and short tibia. The digger *Oryzomys* has a particularly wide acetabulum, wide patellar groove, shallow femoral condyles, and stout tibia. The swimmers *Potamogale* and *Limnogale* have long innomates relative to a short femur. Hindlimb morphology of the outgroup taxon *Petrodromus* fit almost every model of form/function correlation for a highly specialized terrestrial leaper.

Yet an assemblage of characters is strongly correlated with subfamily-level taxonomy. Some of these appear to be related to general hindlimb mobility and constraint, especially in tenrecines vs. oryzorictines. Tenrecines have a much more multiaxially mobile hindlimb than tenrecines, as evidenced by features such as a large acetabulum and femoral head, a short femoral neck, a wide patellar groove, and wide femoral condyles. Yet some may represent features that are primitive for a particular taxon (e.g., a fused distal crus inherited from a hypothetical fossorial ancestor of Oryzorictinae), or primitive therian traits (e.g., *Geogale*'s expanded lateral femoral and tibial condyle).

Geogale shares a number of features with both tenrecines and oryzorictines. It has a relatively long pelvis, large femoral head, short femoral neck, small third trochanter, and small, rounded tibial tuberosity, all traits shared with tenrecines. Yet it also has a narrow and projecting femoral trochlea, proximally positioned lesser trochanter, and a long, narrow tibia, more similar to those of oryzorictines. Morphology of the *Geogale* wrist and ankle are supported by these hindlimb data, which suggest that *Geogale* is not oryzorictine, and Geogalinae most likely represents an early split from the other Malagasy tenrecoids. Relative to the other taxa studied, its hindlimb skeleton is unremarkable in terms of locomotor specialization, and *Geogale* may represent an appropriate model of primitive tenrecoid postcranial form.

The tenrecoid swimmers *Potamogale* and *Limnogale* share more characters of the hindlimb than at the wrist or ankle, especially at the hip joint. For example, both have small femora relative to the pelvis, high acetabula, and short, hemispherical femoral heads. Yet morphology of the more distal hindlimb demonstrates that *Limnogale* has a

much more mobile knee joint, as well as upper ankle joint, than *Potamogale*. The general form of the femur is quite different; that of *Potamogale* is laterally bowed with a small, distally positioned third trochanter and a narrow, restricted trochlea. In *Limnogale*, the femur is short and wide, with a large, projecting third trochanter and very broad patellar groove. The crus exhibits more differences between these two taxa, and that of *Limnogale* has a proximal sigmoid curvature, typical of the other oryzorictines. Morphology of the hindlimb in *Limnogale* and *Potamogale* corroborates the analyses of the hand and foot, as well as recent molecular data (Olson and Goodman, 2003; but see Asher 1999) suggesting that *Limnogale* is oryzorictine, and has convergently evolved a number of traits related to its semi-aquatic behavior.

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Appendix 4.1. Linear Measurements (mm)

Taxon	ID	Pelvis1	Pelvis2	Pelvis3	Pelvis4	Pelvis5	Pelvis6	Pelvis7	Pelvis8
Echinops	31270	3.0302	2.4036	3.1318	2.5206	13.5805	1.6036	4.6098	4.0340
Echinops	207717	3.3579	3.2945	3.3772	2.0918	12.1943	1.7921	4.0937	3.8319
Echinops	207718	2.6462	2.7488	3.1950	2.6855	12.2678	1.4995	4.3647	4.0857
Echinops	212918	3.2524	3.1957	3.4716	3.2125	12.5968	1.4441	4.4068	4.5553
Echinops	212919	3.1244	2.8895	3.5342	2.8442	13.9095	1.7447	4.9362	4.9043
Echinops	31270	2.9949	2.5829	3.1865	2.4915	13.7482	1.5397	4.6346	4.0013
Echinops	328620	3.3303	3.0427	3.3490	3.1372	12.7876	1.7915	4.4918	4.6729
Echinops	328636	3.1180	2.5948	3.0288	3.0276	13.8032	1.6989	3.9796	4.1604
Echinops	328637	3.4512	3.2632	4.3280	3.0507	16.2972	1.7456	4.9373	5.0554
Echinops	395835	3.2018	3.0008	3.6154	3.3134	13.5881	1.8719	5.0399	5.1433
Echinops	464980	3.2007	3.0219	3.4298	2.9033	12.6657	1.5758	4.6164	4.1565
Echinops	588220	3.3834	3.2183	3.0696	3.1318	13.3134	1.7542	4.8702	5.2209
Setifer	154033	0.0000	0.0000	5.0169	4.0121	0.0000	2.2388	5.9587	5.7367
Setifer	154034	5.0252	4.3139	5.4406	4.5782	22.5610	2.8423	7.2960	6.9046
Setifer	159731	4.1221	3.6724	4.7311	4.0738	17.2835	1.9547	5.4792	5.2684
Setifer	165494	4.5290	4.2796	4.2187	3.8886	21.2179	2.1559	6.9687	6.4050
Setifer	166159	4.3840	4.5567	3.7736	4.1754	17.3058	2.1107	6.4792	6.1138
Setifer	170532	4.4823	4.0263	4.1802	3.4276	17.8567	2.0022	5.7717	5.9188
Setifer	170548	4.4135	4.4297	4.9971	4.1463	20.4650	2.2523	6.8197	5.9732
Setifer	170581	4.1484	3.3838	4.5529	3.8969	20.1529	2.5891	6.0868	6.5426
Setifer	170730	4.4885	4.2109	4.4579	4.5085	21.4400	2.7838	7.0630	6.8420
Setifer	170731	4.5918	4.2258	4.6925	4.4049	19.9390	2.2468	7.1930	7.0853
Setifer	207076	4.1843	3.7955	4.3394	3.6850	18.2090	1.9102	6.1885	6.1622
Hemicentetes	83658	4.1330	4.0536	3.7308	4.5355	21.3325	2.1970	6.1295	5.8264
Hemicentetes	162062	3.3463	3.1601	3.2338	3.5344	15.6653	1.7019	5.5010	4.3659
Hemicentetes	166132	3.1569	3.3005	3.5727	4.0932	17.2369	1.9227	4.4177	5.4991
Hemicentetes	170593	2.6199	2.1269	2.5580	2.9405	10.8340	1.4384	2.9772	3.2626
Hemicentetes	206755	3.1251	3.2283	2.8731	3.0499	13.5730	1.5351	4.3803	3.6993
Hemicentetes	207712	3.9097	3.8663	3.2025	3.8514		1.7075	5.1533	4.4230
Hemicentetes	207714	4.0874	3.5611	3.7019	3.1949	16.6449	1.6473	4.8700	4.2569
Hemicentetes	207715	3.1783	2.8173	2.7845	2.3531		1.4361	3.8905	3.4738
Hemicentetes	212920	3.2029	2.8790	3.1932	3.0874	14.2663	1.5335	4.1253	3.8883
Hemicentetes	212921	3.7602	3.4326	3.3987	3.5993	17.1880	1.8777	5.8578	4.6223
Hemicentetes	212922	3.5782	3.3503	3.1203	3.0053	14.7854	1.8121	5.5771	4.1853
Hemicentetes	212924	3.5746	3.3081	3.1541	3.8077	17.8173	1.8573	4.6522	4.3497
Hemicentetes	212940	3.5936	3.4024	2.9224	3.5248	16.3508	1.7181	4.9639	3.7370
Hemicentetes	339992	3.4816	3.4300	2.8628	3.4831	14.4011	1.7505	5.0809	3.8291
Hemicentetes	354998	3.4330	3.3770	3.2888	3.4711	16.1222	1.4518	4.7029	4.8708
Hemicentetes	364954	3.0053	3.1724	2.9012	3.3223	14.7536	1.6452	4.5959	3.7520
Hemicentetes	395510	3.6470	3.9120	3.1195	4.4376	19.0098	1.7935	6.1232	4.7726
Tenrec	154628	6.8461	6.8785	5.7660	7.8998	32.0895	2.6307	10.5878	10.2649
Tenrec	156337	7.0236	6.0582	5.8175	6.5629	30.7618	2.7687	10.1091	9.3174
Tenrec	170511	7.2939	7.0429	5.6305	9.2827	32.9595	2.8319	9.0315	9.7961
Tenrec	30398	8.7141	7.5524	6.1588	8.1553	33.0332	3.4031	10.1526	9.7325
Tenrec	361485	7.1796	6.6421	6.6089	8.5753	33.4685	2.9739	10.6363	9.7235
Tenrec	364955	7.9411	6.7957	7.0814	8.5756	32.7212	3.5667	9.2609	9.8079
Tenrec	577051	7.2594	7.2615	6.5742	8.1057	29.5931	3.1311	9.2713	8.3775
Tenrec	578792	7.3516	6.7498	6.9392	8.5132	32.7105	3.4346	10.8349	10.2381
M.cowani	151654	1.3421	1.4262	2.2949	2.0912	8.8606	0.9368	2.3317	4.0021
M.cowani	151656	1.3896	1.6438	2.0841	1.9114	9.1061	0.9649	2.3090	3.6985

Taxon	ID	Pelvis1	Pelvis2	Pelvis3	Pelvis4	Pelvis5	Pelvis 6	Pelvis7	Pelvis8
M.cowani	154020	1.4725	1.5704	2.1895	1.8492	8.8542	0.8148	2.4749	4.2488
M.cowani	154026	1.5340	1.3928	2.3526	1.9403	9.4171	0.9291	2.4611	3.9085
M.cowani	156195	1.3091	1.3379	2.2491	2.0232	8.6929	0.7738	2.0839	3.4924
M.cowani	156196	1.2962	1.4304	2.2733	2.2709	9.1622	0.7225	2.2242	3.7524
M.cowani	156197	1.3804	1.4419	1.9401	2.1689	8.9702	0.8289	2.2575	3.5126
M.cowani	156221	1.5722	1.5927	2.2226	2.3230	9.3773	0.8492	2.6776	3.6002
M.cowani	156222	1.4209	1.6704	2.4030	2.2936	9.1188	0.8263	2.4826	3.8850
M. dobsoni	151624	1.6392	1.9126	2.5890	2.8901	12.1763	1.1516	3.1639	4.7698
M. dobsoni	151625	1.4561	1.6369	1.9815	2.3248	11.5061	0.9988	3.2270	4.8459
M. dobsoni	156224	1.6902	1.7941	2.6900	3.1113	11.8016	1.1305	2.9312	4.9100
M. dobsoni	156225	1.7403	1.7417	2.4602	2.3210	11.1798	1.1319	2.9010	4.3861
M. dobsoni	159497	2.0132	1.9901	2.2787	2.7126	11.3280	1.0127	3.2114	4.7417
M. dobsoni	159498	1.5627	1.7533	1.8679	2.5900	10.8394	1.0457	3.4545	4.6579
M. dobsoni	159499	1.5610	1.7131	2.1940	2.4076	10.8273	1.0298	3.2340	4.1440
M. dobsoni	161678	1.5420	1.9412	2.0005	2.3254	10.3890	0.9986	2.3545	3.7758
M. dobsoni	161935	1.6844	1.9796	2.4282	3.0412	12.0219	1.2549	3.0011	4.2397
M. dobsoni	161940	1.7197	1.6796	2.5294	2.4862	11.5578	1.1406	3.2085	4.4305
M.talazaci	154581	2.0321	2.3820	2.8262	3.3077	13.1178	1.3086	3.7654	4.4475
M.talazaci	154585	2.0746	2.4924	2.9492	3.5156	12.7201	1.5019	3.6771	4.3897
M.talazaci	577056	1.8926	2.0637	2.3282	3.0714	12.9652	1.1919	3.3560	5.2217
Oryzorictes	12430	1.8697	1.8383	2.8663	2.5160	12.2077	1.5973	2.8667	4.3410
Oryzorictes	156226	2.1805	2.2353	2.7321	2.7925	12.0518	1.4945	3.3419	5.0789
Oryzorictes	156601	2.2320	2.4018	2.4166	3.4325	11.4608	1.3837	3.0921	4.4839
Oryzorictes	156602	1.9861	2.2053	2.4222	3.4593	11.5135	1.4669	2.7173	4.0955
Oryzorictes	159466	1.9549	2.8135	3.3555	3.9528	10.8201	1.4922	2.4787	3.8483
Oryzorictes	161744	1.8768	2.3156	3.1953	2.8754	11.2601	1.5524	0.0000	0.0000
Oryzorictes	161745	1.7231	2.5882	2.9144	3.1462	11.4683	1.4801	2.4603	3.9610
Oryzorictes	161746	1.9667	2.2067	3.0280	3.4995	10.4384	1.5137	0.0000	0.0000
Oryzorictes	162052	2.0541	2.4260	2.7698	3.3422	10.1180	1.3661	2.6330	3.5237
Oryzorictes	162055	1.9226	2.3107	2.5574	2.7216	10.7672	1.3368	2.8775	3.7039
Limnogale	100688	1.3678	1.9605	3.2995	2.1063	14.6960	1.6262	3.1403	5.6935
Limnogale	100689	2.4039	2.9531	4.2304	3.9401	14.6199	1.6400	3.6025	6.6260
Limnogale	100801	2.5300	3.2572	4.1912	4.4237	15.2065	1.6684	4.1005	6.9922
Limnogale	45050	2.0886	2.8621	4.4089	4.8641	15.1845	1.6378	4.1828	7.5176
Limnogale	45056	1.8617	2.7787	3.0826	3.7950	13.9283	1.4821	3.3122	5.7393
Geogale	151947	0.9789	1.0313	0.9980	1.2429	5.2592	0.6110	1.5385	1.8902
Geogale	156552	1.0998	1.1151	1.2374	1.3679	6.2360	0.6858	1.8046	2.4506
Geogale	156553	0.9528	1.0266	1.3937	1.8709	6.8371	0.7622	1.7533	2.3974
Geogale	159732	1.0324	1.1466	1.1113	1.0791	5.6608	0.6964	1.6532	2.1445
Geogale	159733	0.8990	1.0381	1.0622	1.2077	5.4728	0.5764	1.5923	2.0724
Geogale	161594	0.0000	0.0000	1.3468	1.2756	5.7458	0.6263	1.0877	1.8309
Potamogale	266897	3.9867	4.5321	6.7864	8.3996	23.9369	4.5319	4.4376	12.7541
Potamogale	34881	3.9532	4.4826	5.1098	6.7455	20.3660	2.8744	4.2105	10.9673
Potamogale	51324	4.5764	5.4445	6.2074	7.0193	23.1621	3.4074	5.9037	13.6204
Solenodon	49508	7.9906	6.7715	9.1772	8.0970	42.6708	4.6059	11.0576	17.3667
Solenodon	172680	6.3566	6.4675	9.2597	8.3739	37.2151	3.8604	11.8610	14.9759
Solenodon	217256	8.1967	7.9684	9.5038	10.1499	41.8105	4.4945	12.5260	15.1165
Solenodon	238263	6.3670	6.6908	9.5153	9.9513	37.2724	4.8579	10.0635	15.0787
Solenodon	290520	8.3487	8.4093	10.4847	8.8739	40.7999	5.1552	11.5952	15.8638
Solenodon	395819	7.2831	8.9652	9.9117	8.3507	37.5684	4.7736	12.2818	15.5402
Solenodon	51068	7.6424	8.6702	11.0130	10.5904	43.2714	5.0569	11.4344	16.1574
Solenodon	57320	6.9583	6.7902	9.3536	10.6799	39.9322	4.4043	11.7407	17.9530
Solenodon	72809	6.3969	7.3260	9.3102	11.0790	36.3161	4.1934	13.2727	16.1911

Taxon	ID	Pelvis1	Pelvis2	Pelvis3	Pelvis4	Pelvis5	Pelvis6	Pelvis7	Pelvis8
Solenodon	89448	7.7029	7.6614	9.6284	10.5917	40.5413	5.1611	11.9440	15.4968
Petrodromus	203332	3.9790	4.1572	8.4426	10.1456	26.7637	3.8833	3.9368	5.9677
Petrodromus	203336	4.1047	4.2237	8.4011	7.1581	26.3203	3.4239	5.2204	6.3154
Echinosorex	448860	7.4405	7.6611	6.7918	9.0160	38.2825	6.1057	0.0000	0.0000

Taxon	ID	Atibfib1	Atibfib2	Taxon	ID	Ptibfib1	Ptibfib2	Ptibfib3	Ptibfib4
Echinops	127274	19.5898	1.3262	Echinops	127274	2.0356	2.0291	3.4795	0.9202
Echinops	134550	17.0117	1.5825	Echinops	134550	1.5960	1.9161	3.6030	0.9391
Echinops	153785	17.2778	1.9208	Setifer	124554	2.4974	2.2302	3.4422	1.1392
Echinops	159728	19.1561	1.2464	Setifer	154034	2.8156	2.9057	3.9698	1.5749
Echinops	159729	18.9376	1.4436	Setifer	159731	2.6828	2.3156	3.6808	0.9512
Echinops	159730	17.2975	1.2056	Setifer	170731	2.5012	2.5864	4.1179	1.0891
Echinops	170605	18.4662	1.4638	Setifer	85170	2.6411	2.5988	3.3608	1.1766
Echinops	170607	17.1796	1.2761	Setifer	85513	2.6495	2.3891	3.6057	1.4195
Echinops	207717	16.8922	1.2280	Hemicentetes	161757	2.3402	2.1645	2.7830	1.0798
Echinops	207718	16.1427	1.3620	Hemicentetes	161758	2.4000	2.1461	2.4238	1.3061
Echinops	212918	15.9812	1.5051	Hemicentetes	162059	2.1875	2.0412	2.5624	0.8824
Echinops	212919	17.2270	1.5180	Hemicentetes	162062	1.8565	1.7029	2.4311	0.9455
Echinops	31270	17.3613	1.2143	Hemicentetes	166132	2.6339	1.9574	2.6117	1.1096
Echinops	328620	17.8715	1.3415	Hemicentetes	170593	1.6360	1.4985	1.8278	1.0211
Echinops	328636	18.3748	1.5476	Hemicentetes	206755	1.8658	1.5771	1.9425	1.2390
Echinops	328637	21.2127	1.4458	Hemicentetes	212920	2.1246	2.1615	2.3326	1.3318
Echinops	395835	17.3515	1.5153	Hemicentetes	212922	1.8946	1.9328	2.2161	1.3337
Echinops	464980	17.7568	1.4594	Hemicentetes	339992	2.4140	2.2449	2.5936	0.8308
Echinops	588220	18.6211	2.1900	Hemicentetes	354998	2.0381	2.1087	2.3565	1.2322
Setifer	124554	29.3252	2.0095	Hemicentetes	395510	2.2978	2.3887	2.6592	1.4382
Setifer	154033	27.2812	2.0649	Tenrec	154628	4.1517	3.4023	4.9862	2.2728
Setifer	154034	31.7181	2.1925	Tenrec	154629	4.0415	3.4907	4.4995	2.3262
Setifer	165494	29.7234	1.8811	Tenrec	156337	4.1718	3.5242	4.4758	2.5464
Setifer	170532	27.7883	2.1495	Tenrec	166047	4.0874	3.2592	5.1845	1.8493
Setifer	170548	32.1478	2.1499	Tenrec	30398	3.9405	3.3808	4.7832	2.8229
Setifer	170581	30.4380	2.2827	Tenrec	364955	4.6331	3.4025	3.6700	3.8571
Setifer	170731	30.2833	2.2748	Tenrec	50911	4.5523	4.3302	5.6851	2.4205
Setifer	207076	28.8661	1.7956	Tenrec	60587	4.1873	3.9115	5.4200	2.2324
Setifer	317872	30.7609	1.9587	Tenrec	85514	4.5072	3.9585	5.5886	2.3901
Setifer	328612	0.0000	0.0000	M.cowani	151654	0.0000	0.0000	1.3095	0.6517
Setifer	395513	27.9070	2.2175	M.cowani	154020	1.2796	1.1113	1.4239	0.7106
Setifer	395719	27.5149	1.8021	M.cowani	154026	1.1209	1.1803	1.4012	0.6142
Setifer	541443	31.0104	2.1222	M.cowani	156196	1.1359	0.9845	1.2826	0.6964
Setifer	578790	27.0063	1.9443	M.cowani	156221	1.1270	0.9641	1.2859	0.6934
Setifer	85170	30.0545	2.2633	M.cowani	156222	1.0646	0.9901	1.2954	0.7104
Setifer	85513	29.8928	1.9194	M.cowani	156223	1.1384	1.1437	1.3965	0.7542
Hemicentetes	83658	25.0787	2.1442	M.cowani	165673	1.0316	1.1620	1.3371	0.6796
Hemicentetes	161757	20.2000	1.3214	M.cowani	165676	1.0191	1.0538	1.2097	0.7903
Hemicentetes	161758	22.1638	1.3814	M.cowani	165680	1.1980	0.9081	1.2700	0.7608
Hemicentetes	162059	20.1441	1.4610	M.cowani	165689	0.0000	0.0000	1.4662	0.7105
Hemicentetes	162062	20.4477	1.5893	M.cowani	449186	0.8220	0.7234	1.0533	0.6241
Hemicentetes	166132	21.1756	1.3332	M.cowani	449187	0.8777	0.9620	1.1884	0.6436
Hemicentetes	170593	15.7183	1.1001	M.dobsoni	151624	1.1772	1.2442	1.6110	0.9220
Hemicentetes	206755	18.7623	1.2264	M.dobsoni	151625	1.1622	1.0988	1.5337	0.9474
Hemicentetes	207712	24.2514	1.3831	M.dobsoni	156225	1.2184	1.2881	1.3752	0.9915
Hemicentetes	207715	18.5381	1.1484	M.dobsoni	159497	1.3890	1.3011	1.6721	1.0275

Taxon	ID	Atibfib1	Atibfib2	Taxon	ID	Ptibfib1	Ptibfib2	Ptibfib3	Ptibfib4
Hemicentetes	212920	21.3469	1.5456	M.dobsoni	159498	1.2148	1.1522	1.3586	1.0264
Hemicentetes	212922	19.8384	1.4641	M.dobsoni	161679	1.3339	1.3135	1.5782	0.9099
Hemicentetes	212924	23.3827	1.4493	M.dobsoni	161935	1.1792	1.2982	1.4724	1.0466
Hemicentetes	33951	23.0607	1.6292	M.dobsoni	161940	1.1518	1.5000	1.4987	1.0021
Hemicentetes	339992	21.5531	1.4948	M.dobsoni	165467	1.3949	1.2248	1.7644	1.1316
Hemicentetes	354998	22.9043	1.2331	M.dobsoni	165774	1.3843	1.1850	1.5809	1.0391
Hemicentetes	364954	20.6900	1.1578	M.dobsoni	165775	1.1942	1.2330	1.4803	1.1466
Hemicentetes	395510	24.5129	1.5583	M.dobsoni	166107	1.2945	1.3075	1.4424	1.1548
Tenrec	154628	41.8463	2.5649	M.dobsoni	166198	1.0530	1.0078	1.1759	1.1419
Tenrec	156337	38.6118	2.2231	M.dobsoni	166200	1.1638	1.2241	1.2490	1.3208
Tenrec	166047	41.4656	2.6046	M. talazaci	154581	1.4348	1.3876	1.9399	1.1239
Tenrec	170511	43.3613	2.3757	M. talazaci	154585	1.6268	1.3619	1.8049	1.1670
Tenrec	30398	43.8187	3.1446	M. talazaci	167501	1.5335	1.3562	1.7421	1.2000
Tenrec	361485	43.0270	2.8877	M. talazaci	167502	1.3327	1.2606	1.7392	1.3009
Tenrec	364955	45.1875	3.4765	M. talazaci	167503	1.4260	1.3195	1.6749	1.2041
Tenrec	50911	45.3571	3.1246	M. talazaci	577056	1.4341	1.5703	1.7311	0.8686
Tenrec	577051	41.3339	2.7342	Oryzorictes	162058	1.3005	1.4500	1.6945	1.0362
Tenrec	578792	41.6338	2.7138	Oryzorictes	166157	1.2177	1.3906	1.5683	1.1736
Tenrec	85514	41.8602	3.0072	Oryzorictes	166239	1.3604	1.3405	1.5263	1.3272
M.cowani	156221	16.2187	0.8538	Oryzorictes	166240	1.4342	1.4355	1.6511	1.1890
M.cowani	156222	16.1643	0.7861	Oryzorictes	167481	1.5443	1.2155	1.7158	1.2451
M.cowani	156223	16.2920	0.9202	Oryzorictes	167482	1.3164	1.3350	1.5996	1.1745
M.cowani	165672	12.5599	0.6131	Limnogale	45050	2.1139	1.8916	3.6088	1.3280
M.cowani	165673	15.7154	0.9279	Geogale	161594	0.6884	0.4843	0.7625	0.3535
M.cowani	165674	16.0489	0.8976	Solenodon	51068	4.1026	4.7514	5.0687	4.3574
M.cowani	165676	3.0232	0.1589	Solenodon	57320	4.3076	3.5937	4.8982	4.0176
M.cowani	165680	16.0509	0.8348	Solenodon	72809	4.1771	4.5560	5.1281	3.0976
M.cowani	165689	16.3983	0.8540	Petrodromus	203336	2.7968	2.4597	4.4679	3.2686
M.cowani	168017	15.8693	0.8452						
M.cowani	328658	14.6791	0.8117						
M.cowani	449184	15.1814	0.7042						
M.cowani	449186	14.2353	0.7972						
M.cowani	449187	0.0000	0.1597						
M.cowani	449188	0.0000	0.7876						
M. dobsoni	151624	0.0000	1.0564						
M. dobsoni	161935	22.9097	1.0753						
M. dobsoni	161940	23.6194	0.9991						
M. dobsoni	165467	24.3001	1.0705						
M. dobsoni	165774	23.5415	1.1025						
M. dobsoni	165775	21.8699	0.9538						
M. dobsoni	166107	24.2294	0.9922						
M. dobsoni	166198	23.0721	0.9611						
M. dobsoni	166200	24.2324	1.1136						
M. talazaci	154581	24.9775	1.2385						
M. talazaci	154585	25.4724	1.1928						
M. talazaci	162040	24.9560	1.0522						
M. talazaci	167501	25.7182	1.1680						
M. talazaci	167502	25.7136	1.1254						
M. talazaci	167503	25.4812	1.1402						
M. talazaci	577056	25.3032	1.0769						
Oryzorictes	161746	15.2939	1.0808						
Oryzorictes	162053	15.6781	1.2258						
Oryzorictes	162054	14.5882	1.0418						

Taxon	ID	Atibfib1	Atibfib2
Oryzorictes	162058	15.6894	1.1005
Oryzorictes	166239	0.0000	1.1071
Oryzorictes	166240	16.9533	1.0424
Oryzorictes	167480	16.1345	1.1603
Oryzorictes	31257	16.4859	1.1486
Oryzorictes	45018	18.6250	1.1644
Oryzorictes	578789	15.5338	1.2932
Limnogale	45050	25.9360	1.5139
Geogale	161594	9.8136	0.5088
Geogale	45043	12.1179	0.5617
Potamogale	266897	36.0622	2.2047
Potamogale	34881	31.4669	0.0000
Potamogale	51322	37.0184	2.2088
Potamogale	51324	39.1768	3.0043
Potamogale	51333	32.2446	2.0593
Potamogale	55204	29.2365	1.7651
Solenodon	49508	58.1753	3.0465
Solenodon	172680	50.2912	3.3050
Solenodon	217256	54.4549	3.5850
Solenodon	238263	56.1860	3.8601
Solenodon	290520	58.7437	3.8643
Solenodon	395697	57.9161	3.5690
Solenodon	395819	58.5257	3.7005
Solenodon	51068	60.1004	3.6792
Solenodon	57320	56.4909	3.5492
Solenodon	72809	54.3441	3.5471
Petrodromus	150415	56.7658	2.1959
Petrodromus	203336	56.3054	2.3272
Petrodromus	203339	55.8321	2.3177
Petrodromus	86566	27.7655	1.1376
Petrodromus	86568	28.3373	1.1964
Petrodromus	86581	29.4075	1.1730
Petrodromus	86585	30.6528	1.2134
Echinosorex	448860	64.1058	4.5039

Appendix 4.1 (con't)

TaxonID		Afem1	Afem2	Afem3	Afem4	Afem5	Afem6	Afem7	Afem8	Afem9	Afem10	Afem11	Afem12	Afem13	Afem14
Echinops	170605	3.0228	2.7139	4.3609	20.6890	1.8313	17.1962	3.5385	1.3673	0.5884	2.0332	1.9509	15.2252	5.4505	0.1961
Echinops	170607	3.2286	2.6773	4.2167	19.5377	1.8454	16.6668	2.8186	1.3119	0.1477	2.3520	2.1812	13.5065	6.0570	0.4462
Echinops	207717	3.0947	2.2238	5.1007	18.7555	1.7806	15.5191	3.2504	0.9406	0.3137	1.8243	2.1225	12.6871	6.0997	0.4567
Echinops	212918	2.7409	2.6541	4.3677	18.9675	2.0568	15.6809	3.3773	1.0865	0.3024	1.9348	2.1315	14.1197	4.8896	0.2416
Echinops	212919	3.2582	2.5937	4.7869	19.8332	2.1365	15.9574	3.9194	1.3606	0.3893	2.1471	2.2767	14.9300	4.9340	0.4952
Echinops	31270	2.9127	2.3366	4.4163	20.3847	1.8593	16.8345	3.5587	1.3650	0.3492	2.2130	1.9660	14.6876	5.7122	0.3294
Echinops	328620			4.2772	19.1825	1.8782	15.8385	3.3809	1.2867		1.9708	1.9691	14.0243	5.1680	0.4617
Echinops	328636			4.4830	19.9357	1.7897	16.2662	3.6971	1.1929		2.0699	2.0825	14.1653	5.8049	0.2411
Echinops	328637	2.7754	3.3501	4.8957	23.3360	2.2051	19.1779	4.1366	1.9455	0.4137	2.9768	1.9932	18.1054	5.2155	0.5197
Echinops	395835	3.3012	2.5460	4.8467	20.5732	2.3266	16.2516	4.3388	1.2445	0.2881	2.1524	2.2579	15.3082	5.3224	0.3538
Echinops	464980	2.9220	2.7843	4.6106	19.3758	2.0389	15.9005	3.4911	1.4857	0.4014	2.2177	2.4811	13.9586	5.4177	0.4447
Echinops	588220	3.3761	2.3364	5.1945	19.4041	2.7779	15.8597	3.5861	0.9461	0.2809	2.1393	2.4908	13.4834	5.9314	0.5141
Setifer	154033	4.0649	3.4602	6.1571	27.9385	3.1487	23.2535	4.6920	1.4233	0.2272	3.2095	2.9026	20.0253	8.0042	0.3914
Setifer	154034	4.2755	2.7534	7.0401	31.4630	3.4807	26.4849	4.9619	1.1457	0.2434	3.0985	3.3849	22.9686	8.4517	0.7165
Setifer	159731	3.8035	2.8808	6.3889	25.7568	2.8235	21.4245	4.3488	1.4654	0.0182	2.6536	2.8294	18.4041	7.3962	0.4927
Setifer	165494	4.2414	3.2713	7.1030	29.1687	2.6540	23.5136	5.7062	1.6004	0.5386	3.1018	2.7573	20.7658	8.3421	0.2972
Setifer	166159	3.9169	2.9134	6.3365	27.2491	2.9818	22.8978	4.3722	1.5631	0.3592	3.3860	3.2810	18.6322	8.6646	0.2567
Setifer	170532	4.1813	3.3253	6.4798	28.0918	2.9776	23.6221	4.4686	1.6929	0.0190	3.4056	3.2272	20.5066	7.6623	0.5896
Setifer	170548	4.2663	3.7719	6.6524	32.5701	3.0765	26.9071	5.6911	1.9272	0.0917	3.0046	3.1563	23.5326	9.0671	0.5581
Setifer	170581	4.3230	2.9956	6.9214	29.9356	3.2459	25.3286	4.6297	1.7686	0.2194	0.0000	0.0000	20.9512	8.9408	0.6332
Setifer	170730	4.1965	3.2943	6.9672	29.6132	3.4502	24.4817	5.1435	1.9425	0.2380	2.9602	2.8155	20.6084	9.0547	0.4443
Setifer	170731	4.1506	3.0787	7.6718	29.5532	3.1956	24.5833	5.0152	1.2915	0.1625	3.6306	3.3924	21.1044	8.5369	0.2628
Setifer	207076	4.3226	3.4737	6.5290	28.7190	2.9667	23.9367	4.8958	2.1670	0.1679	2.8719	2.6524	20.7503	8.0439	0.4075
Setifer	317872	4.0313	3.0841	6.0899	29.9465	3.0173	24.9873	5.0010	1.6343	0.1818	3.0552	3.2817	22.3085	7.6507	0.3636
Setifer	328612	3.8839	3.1820	6.1968	27.8557	2.7938	23.0257	4.8315	1.4316	0.0266	2.8404	3.0750	19.5858	8.1611	0.3201
Setifer	33948	4.5571	3.4209	7.1306	29.3253	2.8759	24.0315	5.3148	1.4932	0.2005	3.0428	3.4369	20.6475	8.6898	0.6969
Setifer	395513	4.3647	3.4333	6.4520	28.7396	3.3489	23.7709	5.0073	0.9340	0.1210	2.8025	3.0883	19.9144	8.8712	0.4239
Setifer	395719	3.9722	3.2797	6.4813	27.2955	2.8273	22.5838	4.7847	1.4717	0.0778	2.9463	3.3438	18.9250	8.3277	0.2264
Setifer	541443	4.4193	2.9933	6.9526	29.1549	3.0325	24.4243	4.7752	1.3374	0.0833	2.7754	2.9386	21.5668	7.6409	0.3366
Setifer	578790	4.2255	3.3842	6.5891	26.3734	2.9943	22.1843	4.2377	1.2557	0.2571	2.6366	2.9885	18.8720	7.5291	0.1286
Setifer	85170	4.1192	3.3133	6.5345	30.5776	2.9501	25.4401	5.1226	1.7602	0.0821	3.0145	3.2051	22.2920	8.3300	0.1195
Setifer	85513	4.3471	3.4032	6.3752	29.6867	3.3229	24.5853	5.0863	1.6976	0.0466	3.3776	3.2872	22.1200	7.6519	0.4587
Hemicentetes	83658	4.3516	3.5415	7.5676	27.3647	3.1488	22.2163	5.1735	1.7043	0.3304	2.6068	3.1731	19.6244	7.7823	0.8357
Hemicentetes	162062	2.9219	2.2748	5.3680	20.9414	2.2790	16.6081	4.3519	1.4414	0.2094	2.1994	2.1658	14.8069	6.2190	0.5630

Appendix 4.1 (con't)

Hemicentetes	166132	3.3550	2.5177	5.3323	21.1538	2.3442	17.2757	3.8864	0.5451	0.2083	2.3113	2.5499	15.3670	5.8201	0.7400
Taxon	ID	Afem1	Afem2	Afem3	Afem4	Afem5	Afem6	Afem7	Afem8	Afem9	Afem10	Afem11	Afem12	Afem13	Afem14
Hemicentetes	170593	2.4931	1.8994	4.7464	15.4049	1.9732	12.3955	3.0318	0.9439	0.2909	1.7610	2.0648	11.0491	4.3863	0.1975
Hemicentetes	206755	2.9557	2.4403	5.1006	18.0399	1.9520	14.5109	3.5668	0.9489	0.1388	1.6628	2.3871	13.4603	4.6339	0.2136
Hemicentetes	207712	3.8195	3.1699	6.0679	24.5874	2.3512	20.2402	4.3667	1.1500	0.2505	2.6032	2.5666	17.9193	6.7292	0.7070
Hemicentetes	207714	3.6736	2.6347	5.6855	20.9417	2.3914	13.5998	7.3960	1.0879	0.5805	2.1480	3.0018	15.1788	5.8185	0.7293
Hemicentetes	207715	3.0037	2.1364	5.1461	17.4136	1.9156	13.9278	3.5009	1.1782	0.2281	1.9929	2.6378	12.4301	4.9937	0.1642
Hemicentetes	212920	3.2830	2.5658	5.0507	20.4411	2.3006	17.0862	3.4383	0.9588	0.3868	0.0000	0.0000	15.1651	5.2924	0.5239
Hemicentetes	212922	3.4563	2.7534	5.4291	20.1805	2.5012	16.5946	3.5933	1.2029	0.3671	0.0000	0.0000	13.4450	6.8417	0.5754
Hemicentetes	212924	3.1896	3.0152	0.0000	0.0000	2.6134	0.0000	0.0000	1.4865	0.0000	0.0000	0.0000	0.0000	0.0000	0.6995
Hemicentetes	212940	3.4746	2.7327	5.4380	21.9734	2.2705	17.6469	4.3709	0.8790	0.1667	1.9909	2.1675	16.2286	5.8313	0.7461
Hemicentetes	29245	3.4423	2.7943	5.6452	19.7379	2.1648	15.9293	3.8138	1.5370	0.1613	2.5253	2.3207	13.7247	6.0509	0.4843
Hemicentetes	339992	3.2618	2.6175	6.1250	20.6386	2.3195	16.4884	4.1741	1.2113	0.4658	2.1730	2.8040	14.8038	5.8519	0.5731
Hemicentetes	354998	3.4496	2.4091	5.1508	22.2658	2.1644	17.7397	4.5521	1.1029	0.2207	2.3659	2.3439	14.6991	7.5962	0.7734
Hemicentetes	364954	3.1139	2.1552	5.5814	19.5377	2.2490	15.4743	4.4780	0.0000	0.3269	1.9511	2.2352	14.2112	5.7270	0.7903
Hemicentetes	395510	3.7725	2.8905	6.3310	24.0406	2.6205	19.1584	4.9495	1.5455	0.1286	2.6011	3.0659	16.4749	7.6710	1.0848
Tenrec	154628	6.3636	4.4089	9.8593	43.5772	4.2389	36.0333	7.5736	1.7169	1.3101	3.9008	4.4770	32.8300	10.7328	0.9508
Tenrec	156337	5.8903	4.2402	9.0529	40.3161	4.0450	33.2530	7.0300	1.7274	0.8031	4.1657	3.5199	29.4035	10.9911	1.1493
Tenrec	16364	5.6852	4.3923	9.0429	42.1778	4.5616	34.4884	7.6638	2.5173	0.5002	4.8338	4.1612	31.9347	10.4174	1.0220
Tenrec	170511	6.2014	4.3857	9.5396	43.7918	4.2946	35.5310	8.2297	1.7095	1.3715	4.5707	4.3442	32.8814	10.9444	0.7542
Tenrec	361485	6.5591	5.0372	10.6337	44.0931	4.7444	34.9949	8.0410	2.0815	1.0846	4.9996	6.0379	32.3477	11.9437	1.3883
Tenrec	364955	6.6436	4.9075	10.3455	44.9071	5.4483	36.3088	8.6432	2.4573	0.8118	4.4454	4.5672	34.2971	10.6532	1.7965
Tenrec	577051	6.4396	4.4708	9.4169	42.2552	4.0100	33.8965	8.4567	1.8035	0.8285	4.4614	4.4490	30.8889	11.4789	0.6000
Tenrec	578792	6.6786	4.5683	10.0632	44.5275	4.3808	36.3238	8.1818	2.1892	0.8710	4.6253	4.4299	32.6325	11.9615	0.4706
M.cowani	151654	1.4900	1.0912	2.3663	11.1144	1.0951	9.5712	1.5796	0.4968	0.6160	1.2770	0.8455	7.7345	3.5131	0.4636
M.cowani	151656	1.4069	1.1312	2.5605	11.3333	1.1536	9.7446	1.5996	0.4712	0.5861	1.3730	0.9008	7.6286	3.7516	0.5711
M.cowani	154020	1.5777	1.1047	2.5410	11.2446	1.1067	9.7529	1.4926	0.4648	0.5739	1.6304	1.0761	7.4821	3.8330	0.3766
M.cowani	154026	1.4636	1.1900	2.4504	11.3731	1.0469	9.8332	1.5923	0.3447	0.5269	1.2997	0.9606	7.8687	3.6425	0.5189
M.cowani	156195	1.3002	1.1737	2.1506	10.6326	0.9367	9.2891	1.3621	0.4890	0.5080	1.1279	0.7287	7.5809	3.1191	0.3453
M.cowani	156196	1.2279	1.0748	2.2114	10.9627	1.0078	9.5684	1.4130	0.4080	0.6181	1.2381	0.8450	7.8504	3.1594	0.4317
M.cowani	156197	1.2715	1.0001	0.0000	0.0000	0.9876	0.0000	1.1345	0.4584	0.5691	0.0000	0.0000	0.0000	0.0000	0.3950
M.cowani	156221	1.4315	1.1376	2.3710	11.4643	1.0587	9.8906	1.6926	0.5631	0.6967	1.3910	0.8801	8.2890	3.3545	0.3858
M.cowani	156222	1.3503	0.9271	2.3537	11.0051	1.0651	9.6522	1.3924	0.3855	0.5658	1.4759	0.7650	7.7504	3.4136	0.3044
M.cowani	156223	1.4255	1.0156	2.3376	11.4595	1.1336	9.8353	1.6497	0.4993	0.5398	1.3650	0.7887	8.1231	3.4597	0.2718
M.cowani	165672	1.2627	0.9109	2.3634	10.5872	0.8319	9.2602	1.3715	0.4279	0.8042	1.5784	0.9735	7.3131	3.3906	0.4540
M.cowani	165673	1.5377	1.1032	2.5354	11.4232	1.0340	9.9113	1.5527	0.4384	0.5652	1.2986	0.9561	7.5540	3.9807	0.4871

Appendix 4.1 (con't)

M.cowani	165674	1.5992	1.1378	2.4694	11.4702	1.0616	9.9920	1.5200	0.4822	0.6306	1.4265	0.8653	7.7505	3.8661	0.4228
Taxon	ID	Afem1	Afem2	Afem3	Afem4	Afem5	Afem6	Afem7	Afem8	Afem9	Afem10	Afem11	Afem12	Afem13	Afem14
M.cowani	165676	1.3563	1.1518	2.3755	10.8066	0.9964	9.2507	1.5636	0.4834	0.5840	1.4190	0.9390	7.5395	3.3479	0.4555
M.cowani	165680	1.4107	1.0566	2.5152	11.1501	0.9983	9.7817	1.3932	0.4597	0.8174	1.1915	1.2442	7.5177	3.7211	0.4450
M.cowani	165689	1.4366	1.0189	2.5458	11.2112	0.9152	9.8318	1.4525	0.3908	0.5735	1.5709	0.7828	7.8522	3.5207	0.4413
M.cowani	168017	1.3470	1.0237	2.2002	11.2227	1.0069	9.8395	1.4057	0.5020	0.6238	1.4608	0.7199	7.7568	3.5260	0.1818
M.cowani	328658	1.2619	0.9583	2.1543	10.4031	1.0291	8.8382	1.5684	0.5334	0.4326	1.4046	0.8266	7.5517	2.9674	0.3132
M.cowani	449184	1.2125	1.1306	2.0766	10.1246	0.9142	8.8717	1.2529	0.2730	0.5604	1.1061	0.7340	7.1678	3.0282	0.4289
M.cowani	449186	1.3061	0.9972	2.0619	10.2363	0.9901	8.9242	1.3820	0.3341	0.4020	1.2269	0.7373	7.3016	3.0681	0.4681
M.cowani	449187	1.3390	1.0208	2.5208	10.7635	1.1117	9.2897	1.4444	0.4418	0.5414	1.3155	0.8405	7.7774	3.0934	0.4142
M.cowani	449188	1.2626	0.9041	2.2698	10.5693	1.0200	9.3251	1.2481	0.2289	0.6043	1.1119	0.8174	7.2134	3.4828	0.5318
M.dobsoni	151624	1.8522	1.3847	3.2494	16.7139	1.4347	14.4212	2.3246	0.7489	0.7390	2.1343	1.1304	12.3846	4.4203	0.4353
M.dobsoni	151625	1.5670	1.1824	2.8104	14.6244	1.2584	12.7339	1.9051	0.5065	0.7993	1.7787	1.0841	10.5651	4.1219	0.2893
M.dobsoni	156225	1.6742	1.3227	3.0271	14.3716	1.4439	12.1654	2.2268	0.8514	0.6092	1.7857	0.9764	10.5488	3.9082	0.2025
M.dobsoni	159497	1.8610	1.2388	2.6148	14.5509	1.3753	12.3271	2.2270	0.6113	0.6797	1.7523	1.5124	10.5656	4.0857	0.5384
M.dobsoni	159498	1.6397	1.2473	2.9898	15.1488	1.5302	12.8486	2.3256	0.7995	0.4410	1.8440	1.1027	10.6682	4.5786	0.4714
M.dobsoni	159499	1.6733	1.3529	2.8767	14.7727	1.2593	12.5347	2.2770	0.9634	0.9106	1.9268	1.1397	10.6540	4.2336	0.2472
M.dobsoni	161678	1.6860	1.2226	2.9865	14.1015	1.2948	11.9656	2.1659	0.7515	0.7329	1.6344	1.0059	10.1435	4.1053	0.4313
M.dobsoni	161679	1.6362	1.2925	2.9805	15.3537	1.5596	13.0440	2.3552	0.8867	0.8250	1.5973	1.2588	11.2970	4.1247	0.4078
M.dobsoni	161718	1.9125	1.3927	3.3260	15.8858	1.5276	14.0764	1.8512	0.5289	0.8649	1.8750	1.2107	11.9072	4.1648	0.4243
M.dobsoni	161935	1.9224	1.6379	3.2235	15.9034	1.5108	13.7092	2.2430	0.8095	0.6968	1.8240	1.1134	11.8564	4.1656	0.3140
M.dobsoni	161940	1.7045	1.2054	2.9388	15.3685	1.3935	12.9031	2.5055	0.6831	0.6818	1.7066	1.0909	11.4242	4.0484	0.4940
M.dobsoni	165467	2.0254	1.4851	3.4811	17.6573	1.5940	15.0735	2.6460	0.8439	0.9988	1.8691	1.1760	12.8973	4.9362	0.2774
M.dobsoni	165774	1.7554	1.2290	3.1324	15.3214	1.4722	13.1210	2.2367	0.6012	0.8927	1.9335	1.2792	11.2114	4.2359	0.4632
M.dobsoni	165775	1.7450	1.1516	3.0884	14.5849	1.3700	12.5046	2.0721	0.7427	0.6477	1.5733	1.0632	10.5908	4.0647	0.4838
M.dobsoni	166107	1.7923	1.4131	2.9952	15.8935	1.3257	13.8997	2.0974	0.6442	0.8631	1.8846	1.1237	11.8785	4.1473	0.5708
M.dobsoni	166108	1.7380	1.3816	3.1684	15.8531	1.4493	13.6884	2.2032	0.8295	0.9131	2.0222	1.1361	11.4717	4.4679	0.4790
M.dobsoni	166198	1.6636	1.2490	2.8009	14.4497	1.2393	12.4536	2.0363	0.7121	0.7630	1.8171	1.1390	11.1137	3.3936	0.3474
M.dobsoni	166200	1.6636	1.2252	3.0034	15.0370	1.2202	13.1814	1.8644	0.5984	0.7350	1.8214	1.1012	11.2896	3.8023	0.4439
M.dobsoni	578749	1.5817	1.1483	3.3254	14.8898	1.3395	12.8733	2.0237	0.7622	0.7902	1.5120	1.3748	10.7883	4.2061	0.2865
M.dobsoni	582730	1.8344	1.4087	3.1969	15.1576	1.3770	12.6602	2.5871	0.7999	0.9264	1.5325	1.2169	11.1391	4.1894	0.4913
M.talazaci	154581	2.1831	1.6324	3.8509	18.7741	1.8794	15.8893	2.9476	0.7755	0.6934	2.2346	1.5812	13.6632	5.2913	0.5615
M.talazaci	154585	2.2962	1.6324	3.9643	18.4744	1.7656	15.9223	2.6186	0.8576	0.6557	2.4648	1.4405	13.6456	5.0990	0.4718
M.talazaci	577056	1.7732	1.3243	3.4134	16.9611	1.4231	14.3866	2.6693	0.8216	0.9280	2.1014	1.2333	12.8874	4.3020	0.3872
Oryzorictes	156226	1.9712	1.4771	3.5421	15.6242	1.7534	13.7539	1.9079	0.6910	0.5602	2.0106	1.4807	10.7314	5.1045	0.5987
Oryzorictes	156601	2.1060	1.6045	4.6693	13.3986	1.4720	11.7661	1.6953	0.5028	0.5652	1.9302	0.6970	0.0165	4.4823	0.4802

Appendix 4.1 (con't)

Oryzorictes	156602	2.1399	1.6154	3.2441	13.3966	1.6522	11.6202	1.7774	0.7726	0.5601	1.6951	1.8074	9.0003	4.5225	0.4005
Taxon	ID	Afem1	Afem2	Afem3	Afem4	Afem5	Afem6	Afem7	Afem8	Afem9	Afem10	Afem11	Afem12	Afem13	Afem14
Oryzorictes	156603	2.0676	1.4025	3.1859	13.2192	1.6326	11.4444	1.8381	0.4485	0.3757	1.3080	1.6336	9.1990	4.2976	0.5429
Oryzorictes	159695	1.9555	1.3289	3.3869	13.5705	1.5903	11.6320	1.8810	0.6653	0.6847	1.8300	1.7732	9.3060	4.3580	0.7399
Oryzorictes	161744	2.0512	1.6786	3.5583	13.9957	1.7116	11.5780	2.4793	0.7208	0.7628	2.1946	1.6822	9.5783	4.5296	0.6606
Oryzorictes	161745	2.0919	1.2280	3.3246	13.4905	1.7536	11.3972	2.1144	0.6536	0.5579	1.8362	1.7082	8.9437	4.6411	0.6592
Oryzorictes	161746	1.9687	1.3737	3.4494	12.9755	1.6531	10.9743	2.0714	0.7960	0.7307	1.5554	1.7434	8.6759	4.4326	0.6624
Oryzorictes	162052	1.8217	1.6858	3.2677	12.8500	1.7155	11.0590	2.7457	0.5120	0.5056	1.7809	1.7539	8.1419	4.8569	0.4981
Oryzorictes	162053	1.9891	1.4855	3.4269	13.7255	1.8360	11.7206	2.0735	0.7068	0.6342	1.4309	0.0000	9.9660	3.8951	0.5346
Oryzorictes	162054	2.0833	1.5254	3.2923	13.4847	1.9054	11.5795	1.9526	0.5190	0.5439	1.6416	1.8173	9.1379	4.3623	0.5158
Oryzorictes	162055	1.9939	1.6179	3.2660	12.9990	1.6167	10.8817	2.1627	0.6374	0.9225	1.7459	1.6701	9.1942	3.8978	0.5902
Oryzorictes	162057	2.0060	1.6153	3.0925	13.6620	1.7283	12.0948	1.6148	0.5842	0.4768	1.7394	1.5811	9.2048	4.6270	0.6386
Oryzorictes	162058	2.0122	1.3898	3.2480	13.3710	1.5678	11.3313	2.0707	0.3341	0.7564	1.7091	1.6955	9.1459	4.3532	0.8599
Oryzorictes	165490	2.0320	1.7747	3.3498	13.9634	1.7085	11.9032	2.0919	0.4610	0.5131	2.1682	1.9358	9.1527	4.8926	0.6826
Oryzorictes	165491	1.8953	1.4424	3.6114	13.7489	1.8113	11.5832	2.1951	0.5563	0.5876	1.7980	1.6667	8.6934	5.1528	1.0408
Oryzorictes	165492	1.8023	1.4432	3.3329	13.7112	1.6342	11.6662	2.0972	0.5204	0.4877	2.0741	2.0537	9.1892	4.5989	0.5792
Oryzorictes	165705	2.0545	1.4904	3.5100	13.2842	1.6619	11.1932	2.1275	0.6987	0.7817	1.8160	1.9747	9.3230	4.0815	0.5993
Oryzorictes	166157	2.0630	1.4735	3.3627	13.4809	1.6624	11.4442	2.1071	0.5357	0.7061	1.8120	1.8934	9.2686	4.3479	0.7895
Oryzorictes	166208	2.1552	1.7214	3.7606	14.2224	1.9056	12.3984	1.8349	0.5762	0.4777	1.9911	2.0771	9.7504	4.6528	0.6195
Oryzorictes	166237	2.0006	1.3589	3.5209	14.1749	1.7152	12.2496	1.9569	0.6598	0.6749	2.0833	1.9880	9.2967	4.9593	0.7791
Oryzorictes	166238	1.9683	1.4020	3.4023	14.2861	1.6769	12.1621	2.1591	0.3519	0.6145	1.7598	1.9382	10.0423	4.3940	0.8253
Oryzorictes	166239	2.1988	1.5833	3.5487	14.1994	1.7286	11.8144	2.5088	0.6773	0.6692	1.7289	1.9710	9.7401	4.5776	0.6139
Oryzorictes	166240	2.0365	1.5731	3.5930	14.3137	1.7231	12.0770	2.2701	0.6128	0.7121	2.2351	2.1421	9.8528	4.6063	0.7003
Oryzorictes	167480	2.2455	1.7963	4.0600	13.9540	2.0303	11.8225	2.1309	0.4542	0.7382	1.8306	2.1309	9.2019	4.7779	1.0407
Oryzorictes	167481	2.2574	1.6507	3.5171	14.4120	1.6230	12.4542	1.9086	0.6031	0.6044	1.5738	1.8239	9.8735	4.5855	0.6568
Oryzorictes	167482	2.0888	1.5266	3.4669	14.1433	1.7669	12.0940	2.0265	0.5969	0.4841	2.0594	1.9094	9.7715	4.4741	0.6094
Oryzorictes	169239	1.8961	1.3927	3.3956	12.9342	1.7798	11.0464	1.8851	0.5781	0.6802	1.8640	1.8378	8.8351	4.1998	0.6793
Oryzorictes	169240	1.9712	1.5331	3.3054	13.0269	1.6000	11.1867	1.8597	0.5099	0.6097	1.6146	1.9238	8.6552	4.4646	0.5288
Oryzorictes	31257	1.8009	1.2674	2.9244	13.5201	1.5403	11.5473	1.9767	0.4110	0.7399	1.5007	1.3838	9.3327	4.3001	0.4930
Oryzorictes	45018	2.1801	1.8321	3.4583	16.1737	1.5721	13.9037	2.3026	0.5832	0.8336	1.5461	1.9369	10.9667	5.3137	0.7613
Oryzorictes	577052	2.0726	1.2908	3.5456	0.0000	1.5560	0.0141	0.0000	0.0000	0.0000	1.9227	2.1335	0.0000	0.0000	0.0000
Oryzorictes	578789	1.9495	1.5178	3.4025	13.4507	1.6315	11.3924	2.0722	0.6202	0.6022	1.6998	1.7247	9.2534	4.3122	0.4594
Limnogale	100688	2.4363	1.6395	4.5334	14.1905	1.8752	11.4497	2.7475	0.9735	0.2705	1.8331	1.8438	9.9842	4.2775	0.8914
Limnogale	100689	2.7414	1.6191	5.3820	15.7948	2.3013	12.5338	3.2791	1.2857	0.7871	2.1950	2.0439	11.0359	4.8986	0.8487
Limnogale	100801	2.7972	1.7116	5.4378	15.8658	2.4175	12.7220	3.1774	1.4057	0.7981	1.9049	1.7254	10.9515	5.0218	1.0813
Limnogale	45050	2.6144	1.8291	5.2249	15.7870	2.1575	12.6482	3.1389	1.5011	0.8522	1.8374	2.0520	11.0746	4.7632	1.0803

Appendix 4.1 (con't)

Limnogale	45056	2.4155	1.4564	4.6527	14.7015	1.9909	11.7476	2.9007	0.6571	1.0278	1.7657	1.9095	10.3377	4.4463	1.0476
Taxon	ID	Afem1	Afem2	Afem3	Afem4	Afem5	Afem6	Afem7	Afem8	Afem9	Afem10	Afem11	Afem12	Afem13	Afem14
Geogale	151947	1.0139	0.8514	1.6433	8.5123	0.7903	7.4024	1.1036	0.4868	0.2740	0.7905	0.8220	6.1745	2.3617	0.1417
Geogale	156551	1.0476	0.7382	1.7935	7.2142	0.7296	6.1718	1.0488	0.5464	0.2290	0.7942	0.6772	5.1203	2.1229	0.0595
Geogale	156552	1.2074	1.1465	1.8003	10.0750	0.8806	8.7565	1.3308	0.5878	0.2783	1.0784	0.7099	7.5827	2.5142	0.1174
Geogale	156553	1.0714	1.0019	1.7674	10.2260	0.9446	9.1070	1.1191	0.3935	0.2977	0.9754	0.6880	7.8451	2.4039	0.1543
Geogale	161594	1.0787	0.8880	1.7211	8.6597	0.8103	7.5121	1.1577	0.4320	0.2337	0.7394	0.6715	6.3830	2.2950	0.1488
Potamogale	266897	4.3869	2.7183	8.0456	34.2813	4.3625	28.4505	5.8896	1.3881	1.9014	3.3701	2.6902	19.7696	14.8789	0.7638
Potamogale	34881	3.9612	2.7010	7.1341	30.6803	3.8271	26.2209	4.5875	2.1781	1.4401	3.3515	2.5383	16.9688	14.2314	0.5803
Potamogale	51324	4.1675	2.1999	8.0005	36.5066	4.3501	31.9694	4.7070	1.1992	1.5424	3.9197	3.2718	21.2931	15.5971	1.0666
Solenodon	49508	6.7479	4.9970	11.5343	46.3624	4.7552	37.2029	9.2799	3.4313	2.3619	5.5348	6.4543	33.2567	13.3742	1.7789
Solenodon	172680	6.7942	5.4477	13.3431	41.6650	4.8686	33.7689	7.8451	3.1458	2.2122	5.5655	6.2265	28.3896	13.5653	1.9505
Solenodon	172745	6.3367	4.9091	12.1736	37.4448	4.7943	30.5415	6.9856	2.3640	2.2147	4.6326	6.3185	25.8456	11.9449	2.0584
Solenodon	217256	7.2640	5.3171	13.4953	45.8959	5.2572	38.1106	7.8528	3.1729	2.6672	5.8654	6.4807	32.6342	13.4950	2.2900
Solenodon	238263	6.5522	4.5027	12.1163	44.0905	5.6884	35.6207	8.4117	3.5348	1.9517	4.9993	6.3563	30.7760	13.5505	1.4265
Solenodon	290520	7.7869	6.0040	13.0144	47.7451	5.6245	38.7598	9.0812	4.2809	2.1613	6.7375	6.6677	34.0923	13.8501	2.4657
Solenodon	395697	6.8052	5.7010	12.7749	44.2855	5.6213	36.2786	8.1532	3.1711	2.8102	5.0681	6.1314	30.3955	14.2848	1.7685
Solenodon	395819	7.5493	5.2620	12.9287	44.2814	5.5049	35.8339	8.5202	3.4645	2.3304	6.3617	6.5216	30.3326	14.0420	1.6196
Solenodon	51068	7.4723	4.9768	13.6364	48.0347	5.1307	40.2497	8.1128	3.2764	2.3860	6.3512	7.2698	34.1214	14.4676	1.6116
Solenodon	57320	6.6475	5.2214	12.2044	44.3021	5.2582	35.9557	8.3811	3.5111	2.2469	5.7415	6.4323	29.8578	14.7849	0.8829
Solenodon	72809	6.5555	4.7834	11.8616	43.0552	5.2838	35.4657	7.6924	3.2351	2.1127	5.4368	6.1492	28.6314	14.5968	1.3678
Petrodromus	203332	3.8357	3.0482	7.0781	41.8101	4.1321	38.8689	2.8578	1.4842	4.0970	4.8045	2.3340	35.9280	6.0351	3.1288
Petrodromus	203336	3.7829	3.1863	6.9344	40.1302	3.6645	36.7988	3.3342	1.3694	4.1748	3.9786	2.5774	34.8105	5.3998	2.6083
Echinosorex	448860	6.6723	3.6357	12.1073	54.3298	5.8281	45.3952	9.0087	1.7361	3.6764	7.7991	5.7817	38.6174	16.0397	2.7505
Taxon	ID	Mfem1	Mfem2		Taxon	ID	Lfem1	Lfem2		Taxon	ID	Pfem1	Pfem2	Pfem3	Pfem4
Echinops	170605	1.4825	1.3092		Echinops	170605	1.6176	3.6069		Echinops	170605	3.2427	3.5292	1.2273	0.4644
Echinops	170607	1.6166	1.4493		Echinops	170607	1.4832	3.7569		Echinops	170607	3.1930	3.2088	1.2440	0.6410
Echinops	207717	1.6383	1.6162		Echinops	207717	1.5817	3.8144		Echinops	207717	3.5108	3.2533	1.0925	0.8456
Echinops	212918	1.8357	1.6399		Echinops	212918	1.8035	4.2079		Echinops	212918	2.8720	2.8343	1.3578	0.9520
Echinops	212919	1.6410	1.5298		Echinops	212919	1.6908	3.6928		Echinops	212919	3.1487	3.2135	1.0760	0.6111
Echinops	31270	1.4734	1.1196		Echinops	31270	1.5738	3.4872		Echinops	31270	2.6975	2.7446	1.0834	0.7427
Echinops	328620	1.2677	1.3225		Echinops	328620	1.5330	3.4033		Echinops	328637	3.4194	3.6155	1.3573	0.8236
Echinops	328636	1.5264	1.2094		Echinops	328636	1.5571	3.9307		Echinops	395835	3.2027	3.5034	1.4371	0.8642
Echinops	395835	1.8733	1.7007		Echinops	328637	1.7865	3.6254		Echinops	464980	3.1611	3.1702	1.2062	0.5221

Appendix 4.1 (con't)

Echinops	464980	1.7514	1.9711	Echinops	395835	2.0370	3.9395	Echinops	588220	3.4799	3.3126	1.7163	0.6684
Taxon	ID	Mfem1	Mfem2	Taxon	ID	Lfem1	Lfem2	Taxon	ID	Pfem1	Pfem2	Pfem3	Pfem4
Echinops	588220	1.8332	1.7873	Echinops	464980	1.9616	3.8941	Setifer	154033	4.1634	4.6281	2.0754	1.1125
Setifer	154033	2.0783	1.9269	Echinops	588220	2.3925	4.1250	Setifer	154034	4.3707	5.2293	1.4418	1.1666
Setifer	154034	2.5245	2.2059	Setifer	154033	2.3925	5.2896	Setifer	159731	3.9976	3.6320	1.5653	1.0674
Setifer	159731	2.3007	2.0109	Setifer	154034	2.7878	5.9977	Setifer	165494	4.3456	4.3782	1.3847	0.9143
Setifer	166159	2.3158	2.1986	Setifer	159731	2.1750	4.8524	Setifer	166159	3.9103	4.7709	1.4250	0.9338
Setifer	170532	2.2267	2.2602	Setifer	165494	2.0490	5.4441	Setifer	170532	4.1632	4.9865	1.7250	0.9887
Setifer	170548	2.1739	2.3632	Setifer	166159	2.2060	5.5919	Setifer	170548	4.5237	4.8840	1.8027	0.8512
Setifer	170581	2.1614	2.0190	Setifer	170532	2.6051	5.1578	Setifer	170730	4.4519	5.1442	1.4468	0.9352
Setifer	170730	2.3892	2.1727	Setifer	170548	2.6957	6.1814	Setifer	170731	4.4465	5.0254	1.6319	1.3364
Setifer	170731	2.6117	2.4028	Setifer	170581	2.5793	5.8535	Setifer	207076	4.0232	4.4423	1.3856	0.9332
Setifer	207076	2.2352	2.1494	Setifer	170730	2.4808	5.6407	Setifer	317872	4.1179	4.3679	2.0184	1.4234
Setifer	317872	2.2603	2.2670	Setifer	170731	2.4597	5.6195	Setifer	33948	4.2365	4.5285	1.9212	1.6219
Setifer	328612	2.2176	1.8972	Setifer	207076	2.0388	5.1271	Setifer	395513	4.6086	4.9026	2.0987	1.2729
Setifer	33948	2.3066	0.0000	Setifer	317872	2.4021	5.1207	Setifer	395719	4.0191	4.5836	1.8123	0.8077
Setifer	395513	2.4201	2.1615	Setifer	328612	1.9487	4.8445	Setifer	578790	4.5015	4.8107	1.6967	0.9409
Taxon	ID	Mfem1	Mfem2	Taxon	ID	Lfem1	Lfem2	Taxon	ID	Pfem1	Pfem2	Pfem3	Pfem4
Setifer	395719	2.5081	2.1329	Setifer	33948	2.3685	6.2871	Setifer	85170	4.6124	4.8740	2.0023	1.3514
Setifer	541443	2.6441	2.0501	Setifer	395513	2.3328	5.5123	Setifer	85513	4.3728	4.8148	1.5483	1.5571
Setifer	578790	2.2490	2.1172	Setifer	395719	2.0115	5.2441	Hemicentetes	83658	4.2729	4.5452	2.0808	1.0320
Setifer	85170	2.2640	2.0247	Setifer	541443	2.6253	4.7824	Hemicentetes	162062	3.1146	3.3512	1.2148	0.6036
Setifer	85513	2.1244	2.1280	Setifer	578790	2.2879	5.4045	Hemicentetes	166132	3.6061	3.8784	1.4655	0.6496
Hemicentetes	83658	2.3302	2.2310	Setifer	85170	2.4303	5.6265	Hemicentetes	170593	2.4475	2.6301	1.0413	0.6449
Hemicentetes	162062	1.9785	1.6860	Setifer	85513	2.4468	5.4296	Hemicentetes	206755	3.0957	3.0986	1.3745	0.7154
Hemicentetes	166132	2.1347	1.7984	Hemicentetes	83658	2.3001	4.9427	Hemicentetes	207712	3.5859	3.2839	1.2191	0.9511
Hemicentetes	170593	1.6139	1.3768	Hemicentetes	162062	1.7850	3.7274	Hemicentetes	207714	3.4876	3.6187	1.2747	0.6577
Hemicentetes	206755	1.7304	1.5042	Hemicentetes	166132	2.0692	3.8145	Hemicentetes	207715	2.9151	3.0454	1.0957	0.8332
Hemicentetes	207712	2.1410	1.8960	Hemicentetes	170593	1.5617	3.7413	Hemicentetes	212920	3.2903	3.2816	1.2217	0.7286
Hemicentetes	207714	2.0067	1.8166	Hemicentetes	206755	1.5417	3.9746	Hemicentetes	212922	3.3398	3.2468	1.4341	0.8483
Hemicentetes	207715	1.6756	1.8365	Hemicentetes	207712	1.9784	4.5586	Hemicentetes	212924	3.8432	3.8349	1.4492	0.8790
Hemicentetes	212920	1.8693	1.7652	Hemicentetes	207714	1.7617	4.0245	Hemicentetes	212940	3.2844	3.3280	1.5179	0.8823
Hemicentetes	212922	1.8441	1.7114	Hemicentetes	207715	1.7943	3.6499	Hemicentetes	29245	3.4617	3.0580	1.1676	0.8845
Hemicentetes	212924	1.9850	1.9050	Hemicentetes	212920	1.9336	4.3916	Hemicentetes	339992	3.3196	3.5231	1.2876	0.6362
Hemicentetes	212940	2.0296	1.5840	Hemicentetes	212922	1.5984	3.9528	Hemicentetes	354998	3.2353	3.3632	1.4346	0.8944
Hemicentetes	29245	2.1172	1.6939	Hemicentetes	212924	1.9692	4.3946	Hemicentetes	364954	3.2185	3.0848	1.3705	0.6533

Appendix 4.1 (con't)

Hemicentetes	339992	2.2158	1.6696	Hemicentetes	212940	1.8357	4.2117	Hemicentetes	395510	3.8411	3.1804	1.6834	1.5044
Taxon	ID	Mfem1	Mfem2	Taxon	ID	Lfem1	Lfem2	Taxon	ID	Pfem1	Pfem2	Pfem3	Pfem4
Hemicentetes	354998	1.8691	1.6035	Hemicentetes	29245	1.7601	4.2846	Tenrec	154628	6.7388	6.7463	1.2729	2.8228
Tenrec	154628	3.7421	3.2349	Hemicentetes	339992	1.8843	4.2786	Tenrec	156337	6.2283	6.6375	2.0566	1.4728
Tenrec	156337	3.4617	2.7272	Hemicentetes	354998	1.6075	3.8490	Tenrec	16364	5.8644	4.6750	2.7092	1.5890
Tenrec	16364	3.4416	2.8436	Hemicentetes	364954	1.5843	3.9225	Tenrec	170511	6.3097	6.4779	2.3508	1.5743
Tenrec	170511	3.9241	3.4909	Hemicentetes	395510	1.9677	4.3402	Tenrec	361485	6.7125	7.0394	3.1421	1.3898
Tenrec	361485	3.7165	3.5413	Tenrec	154581	1.6168	3.7519	Tenrec	364955	6.6384	5.8031	3.2140	1.3745
Tenrec	364955	4.3439	3.6975	Tenrec	154585	1.6655	3.6805	Tenrec	577051	6.1738	6.4630	2.3721	1.1851
Tenrec	577051	3.2306	3.0633	Tenrec	577056	1.3096	3.2884	Tenrec	578792	6.4926	6.8956	2.2320	0.9811
Tenrec	578792	3.9890	3.4271	M.cowani	151654	1.0819	2.4418	M.cowani	151654	1.3594	1.2180	0.5454	0.6952
M.cowani	151654	0.9214	0.7529	M.cowani	151656	1.0243	2.7012	M.cowani	151656	1.4001	1.2585	0.4700	0.7199
M.cowani	151656	0.9388	0.8023	M.cowani	154020	1.0638	2.8608	M.cowani	154020	1.4740	1.4349	0.4150	0.6317
M.cowani	154020	0.9115	0.8466	M.cowani	154026	0.9809	2.5339	M.cowani	154026	1.4892	1.3306	0.4718	0.5321
M.cowani	154026	0.8632	0.8393	M.cowani	156195	0.9918	2.3662	M.cowani	156195	1.2579	1.1748	0.2652	0.6130
M.cowani	156195	0.8343	0.7989	M.cowani	156196	0.9556	2.4517	M.cowani	156196	1.2429	1.0042	0.3548	0.4384
M.cowani	156196	0.7821	0.8112	M.cowani	156221	0.8948	2.6235	M.cowani	156197	1.0463	1.0964	0.2587	0.6161
M.cowani	156221	0.9293	0.9155	M.cowani	156222	0.8786	2.2369	M.cowani	156221	1.3293	1.0105	0.3550	0.5119
M.cowani	156222	0.8901	0.7923	M.cowani	156223	1.0665	2.5811	M.cowani	156222	1.2884	1.0794	0.3482	0.5788
M.cowani	156223	0.8812	0.8722	M.cowani	165672	0.9387	2.5258	M.cowani	156223	1.4110	1.4394	0.2986	0.4671
M.cowani	165672	0.8995	0.7257	M.cowani	165673	1.0504	2.6257	M.cowani	165672	1.2366	1.1237	0.3343	0.4184
M.cowani	165673	0.9481	0.8730	M.cowani	165674	1.0483	2.7137	M.cowani	165673	1.4524	1.3088	0.2528	0.6540
M.cowani	165674	0.9463	0.8892	M.cowani	165676	0.9355	2.5774	M.cowani	165674	1.4273	1.2391	0.2944	0.6597
M.cowani	165676	0.8615	0.8935	M.cowani	165680	0.9470	2.7003	M.cowani	165676	1.3028	1.1450	0.3054	0.6675
M.cowani	165680	0.8480	0.8506	M.cowani	165689	1.0444	2.6105	M.cowani	165680	1.3446	1.2902	0.3469	0.6798
M.cowani	165689	0.9217	0.8830	M.cowani	168017	0.9168	2.4949	M.cowani	165689	1.4018	1.4025	0.3168	0.6543
M.cowani	168017	0.7359	0.7973	M.cowani	328658	0.9388	2.2370	M.cowani	168017	1.2761	1.0928	0.3123	0.3662
M.cowani	449184	0.7110	0.6770	M.cowani	449184	0.8020	2.1123	M.cowani	328658	1.1859	0.9766	0.4207	0.5184
M.cowani	449186	0.7005	0.7304	M.cowani	449186	0.8852	2.0279	M.cowani	449186	1.2257	1.1469	0.1875	0.2948
M.cowani	449187	0.7940	0.8047	M.cowani	449187	0.9680	2.6113	M.cowani	449187	1.3452	1.2454	0.3547	0.5305
M.cowani	449188	0.7917	0.7306	M.cowani	449188	0.9763	2.4040	M.cowani	449188	1.1964	1.0604	0.2625	0.5220
M.dobsoni	151624	1.0537	1.0253	M.dobsoni	151624	1.3070	3.3490	M.dobsoni	151624	1.7969	1.7455	0.6408	0.5948
M.dobsoni	151625	0.8731	0.9311	M.dobsoni	151625	1.0706	2.9722	M.dobsoni	151625	1.5271	1.4145	0.6748	0.6152
M.dobsoni	156225	1.1097	1.0967	M.dobsoni	156225	1.3390	2.9492	M.dobsoni	156225	1.5876	1.5508	0.5714	0.7170
M.dobsoni	159497	1.1211	1.1393	M.dobsoni	159497	1.1830	3.1502	M.dobsoni	159497	1.7105	1.6621	0.7433	0.6705
M.dobsoni	159498	1.0827	1.0522	M.dobsoni	159498	1.3516	2.9277	M.dobsoni	159498	1.4583	1.5435	0.3905	0.5869

Appendix 4.1 (con't)

M.dobsoni	159499	1.5173	0.6897	M.dobsoni	159499	1.1338	2.8209	M.dobsoni	159499	1.6181	1.2653	0.6217	0.5009
Taxon	ID	Mfem1	Mfem2	Taxon	ID	Lfem1	Lfem2	Taxon	ID	Pfem1	Pfem2	Pfem3	Pfem4
M.dobsoni	161679	1.0398	1.0271	M.dobsoni	161678	1.1898	2.8296	M.dobsoni	161678	1.6003	1.6225	0.3384	0.4632
M.dobsoni	161718	1.1548	1.0905	M.dobsoni	161679	1.3660	2.8008	M.dobsoni	161679	1.6199	1.6964	0.5413	0.8544
M.dobsoni	161935	1.1216	0.9003	M.dobsoni	161718	1.4182	3.2815	M.dobsoni	161718	1.6973	1.9424	0.5148	0.5054
M.dobsoni	161940	0.9520	1.0361	M.dobsoni	161935	1.3318	3.4967	M.dobsoni	161935	1.7335	1.7710	0.5797	0.5814
M.dobsoni	165467	1.3340	1.1455	M.dobsoni	161940	1.2867	3.1541	M.dobsoni	161940	1.6566	1.5875	0.5413	0.5459
M.dobsoni	165774	1.0585	1.1149	M.dobsoni	165467	1.5471	3.5185	M.dobsoni	165467	1.9024	1.7807	0.7317	0.7593
M.dobsoni	165775	1.1112	1.0435	M.dobsoni	165774	1.3525	3.4785	M.dobsoni	165774	1.5780	1.4849	0.6803	0.6002
M.dobsoni	166107	1.1287	1.0682	M.dobsoni	165775	1.1924	3.3518	M.dobsoni	165775	1.7258	1.6808	0.6363	0.7919
M.dobsoni	166108	1.0810	0.9097	M.dobsoni	166107	1.3530	3.2281	M.dobsoni	166107	1.7456	1.5774	0.5996	0.7109
M.dobsoni	166198	0.9935	0.9884	M.dobsoni	166108	1.4092	3.2588	M.dobsoni	166108	1.7753	1.6778	0.6563	0.7078
M.dobsoni	166200	1.0802	1.0017	M.dobsoni	166198	1.2553	3.1124	M.dobsoni	166198	1.5707	1.4424	0.4254	0.5995
M.dobsoni	578749	1.0452	0.9246	M.dobsoni	166200	1.2520	3.1516	M.dobsoni	166200	1.5528	1.5797	0.8527	0.5177
M. talazaci	154581	1.3972	1.2446	M.dobsoni	578749	1.2189	3.2499	M.dobsoni	578749	1.4740	1.3330	0.5906	0.5639
M. talazaci	154585	1.4449	1.3054	M.dobsoni	582730	1.2368	3.1723	M.dobsoni	582730	1.6903	1.4614	0.5699	0.6331
M. talazaci	577056	1.2552	0.9900	M.talazaci	154581	1.6168	3.7519	M.talazaci	154581	2.0689	2.0855	0.4747	0.6059
Oryzorictes	156226	1.3237	1.1741	M.talazaci	154585	1.6655	3.6805	M.talazaci	154585	2.2407	1.9453	0.5828	0.9964
Oryzorictes	156601	1.2506	1.0958	M.talazaci	577056	1.3096	3.2884	M.talazaci	577056	1.7960	1.5623	0.5006	0.6917
Oryzorictes	156602	1.2288	1.0841	Oryzorictes	156226	1.4364	3.1828	Oryzorictes	156226	2.0472	2.0133	0.4272	0.7482
Oryzorictes	156603	1.2379	1.1430	Oryzorictes	156601	1.2993	2.9877	Oryzorictes	156601	1.9507	2.1240	0.6859	0.7057
Oryzorictes	159695	1.3513	1.0928	Oryzorictes	156602	1.4352	3.1378	Oryzorictes	156602	1.9691	2.0910	0.8327	0.6883
Oryzorictes	161745	1.3388	1.1309	Oryzorictes	156603	1.3883	2.6890	Oryzorictes	161744	2.0815	2.0799	0.7623	1.0626
Oryzorictes	162053	1.2867	1.1860	Oryzorictes	159695	1.4837	2.6656	Oryzorictes	161745	2.0298	2.0523	0.6015	0.8560
Oryzorictes	162054	1.2582	1.3844	Oryzorictes	161744	1.4214	2.9878	Oryzorictes	161746	1.8132	1.7746	0.5908	0.7337
Oryzorictes	162058	1.3806	1.1306	Oryzorictes	161745	1.4110	3.0929	Oryzorictes	162052	2.0032	2.0628	0.4601	0.6877
Oryzorictes	166157	1.3536	1.1708	Oryzorictes	161746	1.3668	2.7065	Oryzorictes	162053	1.9534	1.9153	0.5298	0.7253
Oryzorictes	166239	1.3823	1.1954	Oryzorictes	162052	1.3009		Oryzorictes	162054	2.0184	2.0218	0.5856	0.8768
Oryzorictes	166240	1.4934	1.2592	Oryzorictes	162053	1.4479	2.6605	Oryzorictes	162055	1.9985	1.8508	0.6242	0.8235
Oryzorictes	167481	1.3812	1.1539	Oryzorictes	162054	1.3108	2.6651	Oryzorictes	162057	1.9201	1.7115	0.5239	0.6582
Oryzorictes	167482	1.2865	1.1774	Oryzorictes	162055	1.3982	2.5889	Oryzorictes	162058	1.9774	1.8252	0.5452	0.7784
Oryzorictes	169239	1.2877	1.2644	Oryzorictes	162057	1.3654	2.5867	Oryzorictes	165490	1.9643	1.9643	0.6181	0.7139
Oryzorictes	169240	1.3262	1.1461	Oryzorictes	162058	1.3394	2.9147	Oryzorictes	165491	1.8515	1.8338	0.5544	0.7340
Oryzorictes	31257	1.0523	1.0459	Oryzorictes	165490	1.5313	2.9229	Oryzorictes	165492	1.7938	1.7930	0.6780	0.8556
Oryzorictes	45018	1.4498	1.2457	Oryzorictes	165491	1.4195	2.9681	Oryzorictes	166157	1.8778	1.7806	0.4949	0.6411
Oryzorictes	577052	1.4214	1.2559	Oryzorictes	165492	1.4165	3.0560	Oryzorictes	166208	2.1019	1.9982	0.4069	0.7403

Appendix 4.1 (con't)

Oryzorictes	578789	1.1328	1.1395
Taxon	ID	Mfem1	Mfem2
Limnogale	100688	1.1908	1.3286
Limnogale	100689	1.5033	1.7631
Limnogale	100801	1.6164	1.7257
Limnogale	45050	1.5796	1.7697
Limnogale	45056	1.2983	1.6508
Limnogale	100688	1.1908	1.3286
Limnogale	100689	1.5033	1.7631
Limnogale	100801	1.6164	1.7257
Limnogale	45050	1.5796	1.7697
Limnogale	45056	1.2983	1.6508
Geogale	151947	0.5600	0.6103
Geogale	156551	0.5428	0.6216
Geogale	156552	0.5295	0.6350
Geogale	161594	0.5015	0.6009
Potamogale	266897	3.1042	2.4436
Potamogale	34881	2.3866	2.5052
Potamogale	51324	2.8624	2.7312
Solenodon	49508	4.5620	3.8028
Solenodon	172680	4.6591	4.0106
Solenodon	217256	4.8215	4.3068
Solenodon	238263	4.3626	3.9833
Solenodon	290520	4.9597	4.1620
Solenodon	395697	4.5202	3.7406
Solenodon	395819	4.9245	4.1177
Solenodon	57320	3.7424	3.5317
Solenodon	72809	4.9390	3.7433
Petrodromus	203332	2.4137	
Petrodromus	203336	2.0195	2.3014
Echinosorex	448860	4.9731	3.6622

Oryzorictes	165705	1.3827	2.9383
Taxon	ID	Lfem1	Lfem2
Oryzorictes	166157	1.3805	2.6178
Oryzorictes	166208	1.6747	2.8573
Oryzorictes	166237	1.5246	2.7748
Oryzorictes	166238	1.5406	2.9123
Oryzorictes	166239	1.5125	2.8649
Oryzorictes	166240	1.4595	2.9852
Oryzorictes	167481	1.4594	3.0376
Oryzorictes	167482	1.6014	3.0960
Oryzorictes	169239	1.4715	2.9392
Oryzorictes	169240	1.3971	2.6535
Oryzorictes	31257	1.3416	2.9324
Oryzorictes	45018	1.4799	2.9486
Oryzorictes	577052	1.4022	3.1872
Oryzorictes	578789	1.4520	2.7794
Limnogale	100688	1.5946	3.6472
Limnogale	100689	1.7412	3.9834
Limnogale	100801	1.7934	4.6077
Limnogale	45050	1.6786	3.7920
Limnogale	45056	1.4474	3.6324
Geogale	170605	1.6176	3.6069
Geogale	170607	1.4832	3.7569
Geogale	207717	1.5817	3.8144
Geogale	212918	1.8035	4.2079
Geogale	212919	1.6908	3.6928
Geogale	31270	1.5738	3.4872
Geogale	328620	1.5330	3.4033
Geogale	328636	1.5571	3.9307
Geogale	328637	1.7865	3.6254
Geogale	395835	2.0370	3.9395
Geogale	464980	1.9616	3.8941
Geogale	588220	2.3925	4.1250
Potamogale	266897	2.9149	8.0051
Potamogale	34881	2.7935	7.3897
Potamogale	51324	3.0247	8.3299

Oryzorictes	166237	1.9673	1.9582	0.5416	0.6570
Taxon	ID	Pfem1	Pfem2	Pfem3	Pfem4
Oryzorictes	166238	2.0278	1.9446	0.6463	0.6094
Oryzorictes	166239	2.0050	1.8379	0.5455	0.6822
Oryzorictes	166240	2.0335	2.0521	0.5497	0.5410
Oryzorictes	167481	2.0409	1.7037	0.6793	1.0207
Oryzorictes	167482	2.0780	2.0170	0.5666	0.7451
Oryzorictes	169239	1.9212	1.7601	0.5013	0.7327
Oryzorictes	577052	2.1107	1.9948	0.0000	0.0000
Oryzorictes	578789	1.8943	1.5889	0.2512	0.8403
Limnogale	100688	2.2614	2.2762	0.6806	0.9495
Limnogale	100689	2.5553	2.7581	1.0639	1.3160
Limnogale	100801	2.6623	2.4901	0.8605	1.5732
Geogale	151947	1.0316	1.0820	0.3910	0.3430
Geogale	156551	1.0052	1.0518	0.3134	0.2428
Geogale	156552	1.1207	1.2106	0.4645	0.2579
Geogale	156553	1.0964	1.1369	0.4196	0.3996
Geogale	161594	1.0668	1.0462	0.4467	0.2423
Potamogale	266897	4.3207	5.0109	1.6906	2.5101
Potamogale	34881	3.9177	3.7587	1.3279	1.7508
Potamogale	51324	4.3542	3.9092	1.3417	2.1215
Solenodon	49508	6.3871	6.3191	0.7010	2.1962
Solenodon	172680	6.4275	6.0164	1.5328	2.1730
Solenodon	172745	6.2969	5.6727	1.8023	3.1355
Solenodon	217256	7.0885	6.7820	1.0723	2.1333
Solenodon	238263	6.4279	5.9297	1.3822	2.8375
Solenodon	290520	7.2054	7.5313	1.4257	2.1350
Solenodon	395697	6.6807	6.8652	0.7446	2.1004
Solenodon	395819	7.3164	7.1740	1.1506	3.2922
Solenodon	51068	7.5875	6.1164	1.3159	2.7518
Solenodon	57320	6.5762	7.1113	1.6108	2.4868
Solenodon	72809	6.6581	6.3322	1.1893	1.6819
Petrodromus	203332	3.9076	4.0608	0.3751	2.9200
Petrodromus	203336	3.8930	3.8328	0.7666	2.3962
Echinosorex	448860	6.8100	6.0065	1.5628	3.9526

Appendix 4.1 (con't)

Solenodon	49508	4.3035	10.4027
Taxon	ID	Lfem1	Lfem2
Solenodon	172680	4.9191	11.2990
Solenodon	217256	4.2280	10.8801
Solenodon	290520	4.9992	11.6981
Solenodon	395697	4.3397	10.9659
Solenodon	395819	4.7697	11.2694
Solenodon	51068	5.0620	11.7350
Solenodon	57320	4.4929	10.8871
Solenodon	72809	4.4023	10.4071
Petrodromus	203332	3.7060	9.8373
Petrodromus	203336	3.4387	9.3542
Echinosorex	448860	5.4974	14.0908

Appendix 4.2. Linear Measurement Means/SDs (mm)

Taxon	Afem1	Afem1	Afem1	Afem2	Afem2	Afem2	Afem3	Afem3	Afem3	Afem4	Afem4	Afem4
	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>
Echinops	3.0633	10	0.2240	2.6216	10	0.3157	4.6297	12	0.3284	19.9979	12	1.2193
Setifer	4.1831	20	0.1928	3.2356	20	0.2479	6.6525	20	0.3994	28.9507	20	1.6405
Hemicentetes	3.3540	17	0.4212	2.6205	17	0.4047	5.2803	17	1.5083	19.6860	17	5.7805
Tenrec	6.3077	8	0.3600	4.5514	8	0.2776	9.7442	8	0.5839	43.2058	8	1.5223
M.cowani	1.3762	22	0.1114	1.0573	22	0.0856	2.2469	22	0.5259	10.4799	22	2.3765
M.dobsoni	1.7464	20	0.1221	1.3086	20	0.1237	3.0608	20	0.2076	15.2820	20	0.8594
M.talazaci	2.0841	3	0.2752	1.5297	3	0.1778	3.7429	3	0.2909	18.0699	3	0.9719
Oryzorictes	2.0281	33	0.1136	1.5181	33	0.1536	3.4552	33	0.2949	13.3565	33	2.4984
Limnogale	2.6009	5	0.1731	1.6511	5	0.1364	5.0462	5	0.4230	15.2679	5	0.7724
Geogale	1.0838	5	0.0736	0.9252	5	0.1555	1.7451	5	0.0649	8.9374	5	1.2432
Potamogale	4.1719	3	0.2129	2.5398	3	0.2944	7.7267	3	0.5138	33.8228	3	2.9401
Solenodon	6.9556	11	0.4794	5.1929	11	0.4256	12.6439	11	0.7050	44.2875	11	2.9689
Petrodromus	3.8093	2	0.0374	3.1172	2	0.0977	7.0062	2	0.1016	40.9702	2	1.1879
Echinosorex	6.6723	1	0.0000	3.6357	1	0.0000	12.1073	1	0.0000	54.3298	1	0.0000
Taxon	Afem5	Afem5	Afem5	Afem6	Afem6	Afem6	Afem7	Afem7	Afem7	Afem8	Afem8	Afem8
	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>
Echinops	2.0439	12	0.2913	16.4291	12	0.9994	3.5911	12	0.4036	1.2944	12	0.2660
Setifer	3.0582	20	0.2251	24.0733	20	1.3673	4.9043	20	0.3965	1.5502	20	0.2910
Hemicentetes	2.3270	17	0.2936	15.6995	17	4.7178	4.0379	17	1.4285	1.1132	17	0.4095
Tenrec	4.4654	8	0.4668	35.1037	8	1.1502	7.9775	8	0.5267	2.0253	8	0.3363
M.cowani	1.0228	22	0.0775	9.1024	22	2.0636	1.4574	22	0.1395	0.4353	22	0.0821
M.dobsoni	1.3988	20	0.1123	13.1092	20	0.8042	2.2087	20	0.2193	0.7337	20	0.1220
M.talazaci	1.6894	3	0.2375	15.3994	3	0.8772	2.7452	3	0.1772	0.8182	3	0.0411
Oryzorictes	1.6944	33	0.1161	11.4178	33	2.1520	1.9968	33	0.4261	0.5621	33	0.1501
Limnogale	2.1485	5	0.2210	12.2202	5	0.5810	3.0487	5	0.2182	1.1646	5	0.3464
Geogale	0.8311	5	0.0832	7.7900	5	1.1742	1.1520	5	0.1073	0.4893	5	0.0797
Potamogale	4.1799	3	0.3056	28.8803	3	2.8982	5.0614	3	0.7198	1.5884	3	0.5193
Solenodon	5.2534	11	0.3389	36.1626	11	2.5806	8.2105	11	0.6411	3.3262	11	0.4512
Petrodromus	3.8983	2	0.3306	37.8339	2	1.4638	3.0960	2	0.3369	1.4268	2	0.0811
Echinosorex	5.8281	1	0.0000	45.3952	1	0.0000	9.0087	1	0.0000	1.7361	1	0.0000

Appendix 4.2 (con't)

Taxon	Afem9	Afem9	Afem9	Afem10	Afem10	Afem10	Afem11	Afem11	Afem11	Afem12	Afem12	Afem12
	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>
Echinops	0.3475	10	0.1146	2.1693	12	0.2913	2.1586	12	0.1883	14.5168	12	1.3644
Setifer	0.1681	20	0.1277	2.8907	20	0.7281	2.9522	20	0.7325	20.7241	20	1.4452
Hemicentetes	0.2624	17	0.1389	1.8172	17	0.9116	2.0873	17	1.0473	14.0346	17	4.1258
Tenrec	0.9476	8	0.2902	4.5003	8	0.3499	4.4983	8	0.7048	32.1520	8	1.4667
M.cowani	0.5882	22	0.0957	1.2859	22	0.3226	0.8285	22	0.2230	7.3002	22	1.6531
M.dobsoni	0.7755	20	0.1313	1.7912	20	0.1623	1.1618	20	0.1236	11.2197	20	0.6992
M.talazaci	0.7590	3	0.1476	2.2669	3	0.1838	1.4183	3	0.1750	13.3987	3	0.4429
Oryzorictes	0.6107	33	0.1617	1.8026	33	0.2215	1.7421	33	0.4125	8.8012	33	2.3365
Limnogale	0.7471	5	0.2833	1.9072	5	0.1682	1.9149	5	0.1382	10.6768	5	0.4892
Geogale	0.2625	5	0.0299	0.8756	5	0.1445	0.7137	5	0.0623	6.6211	5	1.1103
Potamogale	1.6280	3	0.2423	3.5471	3	0.3228	2.8334	3	0.3871	19.3438	3	2.1934
Solenodon	2.3141	11	0.2446	5.6631	11	0.6400	6.4553	11	0.3152	30.7576	11	2.5996
Petrodromus	4.1359	2	0.0550	4.3916	2	0.5839	2.4557	2	0.1721	35.3693	2	0.7902
Echinosorex	3.6764	1	0.0000	7.7991	1	0.0000	5.7817	1	0.0000	38.6174	1	0.0000

Taxon	Afem13	Afem13	Afem13	Afem14	Afem14	Afem14	Lfem1	Lfem1	Lfem1	Lfem2	Lfem2	Lfem2
	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>
Echinops	5.5002	12	0.4177	0.3917	12	0.1151	1.751542	12	0.266285	3.79034	12	0.243627
Setifer	8.2508	20	0.5371	0.4062	20	0.1719	2.366179	20	0.237064	5.45036	20	0.420334
Hemicentetes	5.7203	17	1.7792	0.6118	17	0.2445	1.819594	17	0.206452	4.12112	17	0.345501
Tenrec	11.1404	8	0.5881	1.0164	8	0.4324	1.530629	3	0.192954	3.57361	3	0.249555
M.cowani	3.2836	22	0.7872	0.4140	22	0.0898	0.970922	21	0.073645	2.49705	21	0.208662
M.dobsoni	4.1700	20	0.3047	0.4049	20	0.1038	1.289731	20	0.110670	3.16268	20	0.222717
M.talazaci	4.8975	3	0.5246	0.4735	3	0.0872	1.530629	3	0.192954	3.57361	3	0.249555
Oryzorictes	4.3955	33	0.8518	0.6315	33	0.1857	1.432880	32	0.084075	2.88185	31	0.180772
Limnogale	4.6815	5	0.3115	0.9899	5	0.1112	1.651052	5	0.135859	3.93252	5	0.403004
Geogale	2.3395	5	0.1450	0.1244	5	0.0389	1.751542	12	0.266285	3.79034	12	0.243627
Potamogale	14.9025	3	0.6832	0.8036	3	0.2456	2.911044	3	0.115673	7.90822	3	0.477536
Solenodon	13.8142	11	0.7860	1.7473	11	0.4449	4.612942	9	0.325304	11.06048	9	0.486471
Petrodromus	5.7175	2	0.4492	2.8685	2	0.3680	3.572351	2	0.188966	9.59578	2	0.341626
Echinosorex	16.0397	1	0.0000	2.7505	1	0.0000	5.497377	1	0.000000	14.09078	1	0.000000

Appendix 4.2 (con't)

Taxon	Mfem1	Mfem1	Mfem1	Mfem2	Mfem2	Mfem2	Pfem1	Pfem1	Pfem1	Pfem2	Pfem2	Pfem2	Pfem3	Pfem3	Pfem3
	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.
Echinops	1.6309	11	0.1861	1.5141	11	0.2600	3.1928	10	0.2558	3.2385	10	0.2821	1.2798	10	0.1978
Setifer	2.3164	19	0.1605	2.0257	19	0.5082	4.2862	17	0.2251	4.7060	17	0.3766	1.7048	17	0.2519
Hemicentetes	1.9694	15	0.2036	1.7385	15	0.1988	3.3741	17	0.4064	3.3737	17	0.4268	1.3725	17	0.2447
Tenrec	3.7312	8	0.3559	3.2532	8	0.3480	6.3948	8	0.3055	6.3422	8	0.7696	2.4187	8	0.6240
M.cowani	0.8555	20	0.0788	0.8143	20	0.0659	1.3187	21	0.1101	1.1942	21	0.1396	0.3415	21	0.0851
M.dobsoni	1.1032	18	0.1393	1.0103	18	0.1102	1.6510	20	0.1130	1.5910	20	0.1633	0.5950	20	0.1212
M. talazaci	1.3658	3	0.0987	1.1800	3	0.1673	2.0352	3	0.2243	1.8644	3	0.2708	0.5194	3	0.0565
Oryzorictes	1.3112	20	0.1034	1.1738	20	0.0783	1.9781	26	0.0840	1.9135	26	0.1421	0.5463	26	0.1604
Limnogale	1.4377	10	0.1743	1.6476	10	0.1739	2.4930	3	0.2076	2.5081	3	0.2415	0.8683	3	0.1918
Geogale	0.5334	4	0.0247	0.6169	4	0.0147	1.0641	5	0.0468	1.1055	5	0.0689	0.4070	5	0.0593
Potamogale	2.7844	3	0.3651	2.5600	3	0.1514	4.1975	3	0.2429	4.2263	3	0.6837	1.4534	3	0.2055
Solenodon	4.6101	9	0.3874	3.9332	9	0.2464	6.7866	11	0.4379	6.5319	11	0.5954	1.2661	11	0.3416
Petrodromus	2.2166	2	0.2788	2.3014	1	0.0000	3.9003	2	0.0104	3.9468	2	0.1612	0.5709	2	0.2768
Echinosorex	4.9731	1	0.0000	3.6622	1	0.0000	6.8100	1	0.0000	6.0065	1	0.0000	1.5628	1	0.0000

Taxon	Pfem4	Pfem4	Pfem4	Pelvis1	Pelvis1	Pelvis1	Pelvis2	Pelvis2	Pelvis2	Pelvis3	Pelvis3	Pelvis3	Pelvis4	Pelvis4	Pelvis4
	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.
Echinops	0.7135	10	0.1586	3.1743	12	0.2182	2.9381	12	0.2966	3.3931	12	0.3491	2.8675	12	0.3590
Setifer	1.1303	17	0.2534	4.0336	11	1.3612	3.7177	11	1.2814	4.5819	11	0.4642	4.0725	11	0.3474
Hemicentetes	0.8234	17	0.2183	3.4608	17	0.3949	3.3164	17	0.4477	3.1540	17	0.3232	3.4877	17	0.5535
Tenrec	1.5487	8	0.5531	7.4512	8	0.6011	6.8726	8	0.4440	6.3221	8	0.5570	8.2088	8	0.7867
M.cowani	0.5605	21	0.1156	1.4130	9	0.0966	1.5007	9	0.1197	2.2232	9	0.1406	2.0968	9	0.1771
M. dobsoni	0.6260	20	0.1042	1.6609	10	0.1533	1.8142	10	0.1305	2.3019	10	0.2828	2.6210	10	0.3032
M.talazaci	0.7647	3	0.2053	1.9997	3	0.0952	2.3127	3	0.2226	2.7012	3	0.3288	3.2982	3	0.2222
Oryzorictes	0.7253	26	0.1876	1.9767	10	0.1498	2.3342	10	0.2575	2.8258	10	0.3130	3.1738	10	0.4425
Limnogale	1.2796	3	0.3135	2.0504	5	0.4631	2.7623	5	0.4833	3.8425	5	0.6052	3.8258	5	1.0496
Geogale	0.2971	5	0.0709	0.8271	6	0.4110	0.8930	6	0.4403	1.1916	6	0.1598	1.3407	6	0.2763
Potamogale	2.1275	3	0.3797	4.1721	3	0.3505	4.8197	3	0.5416	6.0345	3	0.8516	7.3882	3	0.8866
Solenodon	2.4476	11	0.4974	7.3243	10	0.7708	7.5720	10	0.9020	9.7158	10	0.5962	9.6738	10	1.1323
Petrodromus	2.6581	2	0.3704	4.0419	2	0.0889	4.1904	2	0.0470	8.4219	2	0.0293	8.6518	2	2.1125
Echinosorex	3.9526	1	0.0000	7.4405	1	0.0000	7.6611	1	0.0000	6.7918	1	0.0000	9.0160	1	0.0000

Appendix 4.2 (con't)

Taxon	Pelvis5	Pelvis5	Pelvis5	Pelvis6	Pelvis6	Pelvis6	Pelvis7	Pelvis7	Pelvis7	Pelvis8	Pelvis8	Pelvis8	Atibfib1	Atibfib1	Atibfib1
	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.
Echinops	13.3960	12	1.0999	1.6718	12	0.1348	4.5818	12	0.3353	4.4852	12	0.5003	17.8794	19	1.2572
Setifer	17.8573	11	6.1830	2.2806	11	0.3214	6.4822	11	0.6231	6.2684	11	0.5498	27.7481	17	7.3181
Hemicentetes	15.9987	15	2.4723	1.7074	17	0.1995	4.8823	17	0.8236	4.2832	17	0.6883	21.3205	18	2.3658
Tenrec	32.1672	8	1.3245	3.0926	8	0.3464	9.9855	8	0.7067	9.6572	8	0.5990	42.5003	11	1.9308
M.cowani	9.0622	9	0.2422	0.8496	9	0.0801	2.3670	9	0.1759	3.7889	9	0.2474	12.5624	15	6.0999
M. dobsoni	11.3627	10	0.5668	1.0895	10	0.0851	3.0687	10	0.3004	4.4901	10	0.3620	20.8638	9	7.8630
M.talazaci	12.9344	3	0.2007	1.3341	3	0.1565	3.5995	3	0.2154	4.6863	3	0.4646	25.3746	7	0.3141
Oryzorictes	11.2106	10	0.6720	1.4684	10	0.0830	2.2468	10	1.2139	3.3036	10	1.7955	14.4982	10	5.2112
Limnogale	14.7271	5	0.5219	1.6109	5	0.0737	3.6676	5	0.4641	6.5137	5	0.7940	25.9360	1	0.0000
Geogale	5.8686	6	0.5761	0.6597	6	0.0678	1.5716	6	0.2567	2.1310	6	0.2549	10.9657	2	1.6294
Potamogale	22.4883	3	1.8784	3.6046	3	0.8462	4.8506	3	0.9191	12.4473	3	1.3529	34.2009	6	3.7976
Solenodon	39.7398	10	2.4956	4.6563	10	0.4293	11.7777	10	0.8624	15.9740	10	0.9943	56.5228	10	2.8749
Petrodromus	26.5420	2	0.3135	3.6536	2	0.3249	4.5786	2	0.9076	6.1415	2	0.2459	40.7238	7	14.6015
Echinosorex	38.2825	1	0.0000	6.1057	1	0.0000	0.0000	1	0.0000	0.0000	1	0.0000	64.1058	1	0.0000

Taxon	Atibfib2	Atibfib2	Atibfib2	Ptibfib1	Ptibfib1	Ptibfib1	Ptibfib2	Ptibfib2	Ptibfib2	Ptibfib3	Ptibfib3	Ptibfib3	Ptibfib4	Ptibfib4	Ptibfib4
	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.
Echinops	1.4627	19	0.2446	1.8158	2	0.3109	1.9726	2	0.0799	3.5413	2	0.0874	0.9297	2	0.0134
Setifer	1.9428	17	0.5258	2.6313	6	0.1199	2.5043	6	0.2453	3.6962	6	0.2960	1.2251	6	0.2295
Hemicentetes	1.4234	18	0.2400	2.1408	12	0.2914	1.9937	12	0.2736	2.3950	12	0.2862	1.1459	12	0.1971
Tenrec	2.8052	11	0.3674	4.2525	9	0.2474	3.6289	9	0.3555	4.9214	9	0.6435	2.5242	9	0.5633
M.cowani	0.7301	15	0.2452	0.9088	13	0.4213	0.8603	13	0.4009	1.3015	13	0.1106	0.6954	13	0.0532
M. dobsoni	1.0360	9	0.0605	1.2365	14	0.1053	1.2413	14	0.1151	1.4852	14	0.1595	1.0577	14	0.1114
M.talazaci	1.1420	7	0.0647	1.4647	6	0.1018	1.3760	6	0.1049	1.7720	6	0.0920	1.1441	6	0.1471
Oryzorictes	1.1365	10	0.0796	1.3623	6	0.1141	1.3612	6	0.0856	1.6260	6	0.0739	1.1909	6	0.0959
Limnogale	1.5139	1	0.0000	2.1139	1	0.0000	1.8916	1	0.0000	3.6088	1	0.0000	1.3280	1	0.0000
Geogale	0.5353	2	0.0375	0.6884	1	0.0000	0.4843	1	0.0000	0.7625	1	0.0000	0.3535	1	0.0000
Potamogale	1.8737	6	1.0057												
Solenodon	3.5706	10	0.2461	4.1958	3	0.1037	4.3003	3	0.6197	5.0317	3	0.1193	3.8242	3	0.6518
Petrodromus	1.6516	7	0.5900	2.7968	1	0.0000	2.4597	1	0.0000	4.4679	1	0.0000	3.2686	1	0.0000

Appendix 4.3. Raw Index Scores

Taxon	ID	ASHI	ASZI	IDSH	OFSI
Echinops	31270	1.2607	0.3579	1.2425	1.1427
Echinops	207717	1.0192	0.4756	1.6145	1.0683
Echinops	207718	0.9627	0.3919	1.1897	1.0683
Echinops	212918	1.0177	0.4592	1.0807	0.9674
Echinops	212919	1.0813	0.3842	1.2426	1.0065
Echinops	31270	1.1595	0.3648	1.2789	1.1583
Echinops	328620	1.0945	0.4371	1.0675	0.9613
Echinops	328636	1.2016	0.3685	1.0004	0.9566
Echinops	328637	1.0576	0.3721	1.4187	0.9766
Echinops	395835	1.0670	0.4012	1.0911	0.9799
Echinops	464980	1.0592	0.4369	1.1814	1.1106
Echinops	588220	1.0513	0.4381	0.9802	0.9328
Setifer	154033			1.2504	1.0387
Setifer	154034	1.1649	0.3676	1.1884	1.0567
Setifer	159731	1.1224	0.4052	1.1614	1.0400
Setifer	165494	1.0583	0.3769	1.0849	1.0880
Setifer	166159	0.9621	0.4605	0.9038	1.0598
Setifer	170532	1.1132	0.4285	1.2196	0.9752
Setifer	170548	0.9963	0.3893	1.2052	1.1417
Setifer	170581	1.2260	0.3312	1.1683	0.9303
Setifer	170730	1.0659	0.3591	0.9888	1.0323
Setifer	170731	1.0866	0.3974	1.0653	1.0152
Setifer	207076	1.1025	0.3966	1.1776	1.0043
Hemicentetes	83658	1.0196	0.3479	0.8226	1.0520
Hemicentetes	162062	1.0589	0.3746	0.9150	1.2600
Hemicentetes	166132	0.9565	0.3370	0.8728	0.8033
Hemicentetes	170593	1.2318	0.3868	0.8699	0.9125
Hemicentetes	206755	0.9680	0.4205	0.9420	1.1841
Hemicentetes	207712	1.0112		0.8315	1.1651
Hemicentetes	207714	1.1478	0.4181	1.1587	1.1440
Hemicentetes	207715	1.1281		1.1833	1.1200
Hemicentetes	212920	1.1125	0.3849	1.0343	1.0609

Taxon	ID	PFLI
Echinops	31270	0.9663
Echinops	207717	1.0031
Echinops	212918	1.0344
Echinops	212919	1.0786
Echinops	328620	1.0549
Echinops	328636	1.0178
Echinops	328637	1.0491
Echinops	395835	1.0254
Echinops	464980	1.0141
Echinops	588220	1.1039
Setifer	154034	1.0433
Setifer	159731	0.9781
Setifer	165494	1.0394
Setifer	166159	0.9805
Setifer	170532	0.9601
Setifer	170548	0.9425
Setifer	170581	1.0136
Setifer	170730	1.0651
Setifer	170731	1.0064
Setifer	207076	0.9693
Hemicentetes	83658	1.0965
Hemicentetes	162062	1.0510
Hemicentetes	166132	1.1843
Hemicentetes	170593	1.0252
Hemicentetes	206755	1.1026
Hemicentetes	207714	1.0782
Hemicentetes	212920	1.0080
Hemicentetes	212922	1.0867
Hemicentetes	212940	1.0234
Hemicentetes	339992	1.0220
Hemicentetes	354998	1.0397
Hemicentetes	364954	1.0742

Taxon	ID	FNWI	FHWI
Echinops	170605	0.3784	1.0884
Echinops	170607	0.5153	1.0050
Echinops	207717	0.7739	0.9267
Echinops	212918	0.7011	0.9869
Echinops	212919	0.5679	1.0206
Echinops	31270	0.6855	1.0174
Echinops	328637	0.6068	1.0573
Echinops	395835	0.6013	1.0939
Echinops	464980	0.4329	1.0029
Echinops	588220	0.3894	0.9519
Setifer	154033	0.5360	1.1116
Setifer	154034	0.8091	1.1964
Setifer	159731	0.6819	0.9085
Setifer	165494	0.6603	1.0075
Setifer	166159	0.6553	1.2201
Setifer	170532	0.5731	1.1978
Setifer	170548	0.4722	1.0797
Setifer	170730	0.6464	1.1555
Setifer	170731	0.8189	1.1302
Setifer	207076	0.6735	1.1042
Setifer	317872	0.7052	1.0607
Setifer	33948	0.8442	1.0689
Setifer	395513	0.6065	1.0638
Setifer	395719	0.4457	1.1404
Setifer	578790	0.5546	1.0687
Setifer	85170	0.6749	1.0567
Setifer	85513	1.0057	1.1011
Hemicentetes	83658	0.4960	1.0637
Hemicentetes	162062	0.4969	1.0760
Hemicentetes	166132	0.4433	1.0755
Hemicentetes	170593	0.6193	1.0746
Hemicentetes	206755	0.5205	1.0009

Appendix 4.3 (con't)

Taxon	ID	ASHI	ASZI	IDSH	OFSI
Hemicentetes	212921	1.0954	0.3773	0.9442	1.2673
Hemicentetes	212922	1.0680	0.4174	1.0383	1.3325
Hemicentetes	212924	1.0806	0.3498	0.8283	1.0695
Hemicentetes	212940	1.0562	0.3872	0.8291	1.3283
Hemicentetes	339992	1.0150	0.4279	0.8219	1.3269
Hemicentetes	354998	1.0166	0.3875	0.9475	0.9655
Hemicentetes	364954	0.9473	0.3767	0.8733	1.2249
Hemicentetes	395510	0.9323	0.3634	0.7030	1.2830
Tenrec	154628	0.9953	0.3953	0.7299	1.0315
Tenrec	156337	1.1594	0.3901	0.8864	1.0850
Tenrec	170511	1.0357	0.4006	0.6066	0.9220
Tenrec	30398	1.1538	0.4464	0.7552	1.0432
Tenrec	361485	1.0809	0.3793	0.7707	1.0939
Tenrec	364955	1.1685	0.4061	0.8258	0.9442
Tenrec	577051	0.9997	0.4437	0.8111	1.1067
Tenrec	578792	1.0892	0.3901	0.8151	1.0583
M.cowani	151654	0.9411	0.2826	1.0974	0.5826
M.cowani	151656	0.8454	0.3012	1.0904	0.6243
M.cowani	154020	0.9377	0.3147	1.1840	0.5825
M.cowani	154026	1.1014	0.2829	1.2125	0.6297
M.cowani	156195	0.9784	0.2796	1.1116	0.5967
M.cowani	156196	0.9062	0.2758	1.0010	0.5928
M.cowani	156197	0.9574	0.2880	0.8945	0.6427
M.cowani	156221	0.9871	0.3095	0.9568	0.7437
M.cowani	156222	0.8506	0.3108	1.0477	0.6390
M. dobsoni	151624	0.8571	0.2665	0.8958	0.6633
M. dobsoni	151625	0.8895	0.2473	0.8523	0.6659
M. dobsoni	156224	0.9420	0.2694	0.8646	0.5970
M. dobsoni	156225	0.9992	0.2828	1.0600	0.6614
M. dobsoni	159497	1.0116	0.3244	0.8400	0.6773
M. dobsoni	159498	0.8913	0.2790	0.7212	0.7416
M. dobsoni	159499	0.9112	0.2761	0.9113	0.7804
M. dobsoni	161678	0.7943	0.3059	0.8603	0.6236
M. dobsoni	161935	0.8509	0.2760	0.7984	0.7078

Taxon	ID	PFLI
Hemicentetes	395510	1.0931
Tenrec	154628	1.0962
Tenrec	156337	1.1127
Tenrec	170511	1.1008
Tenrec	361485	1.1056
Tenrec	364955	1.0806
Tenrec	577051	1.0353
Tenrec	578792	1.0855
M.cowani	151654	1.2763
M.cowani	151656	1.2748
M.cowani	154020	1.2802
M.cowani	154026	1.2555
M.cowani	156195	1.2668
M.cowani	156196	1.2698
M.cowani	156221	1.2877
M.cowani	156222	1.2724
M.dobsoni	151624	1.1528
M.dobsoni	151625	1.1966
M.dobsoni	156225	1.2064
M.dobsoni	159497	1.2337
M.dobsoni	159498	1.1554
M.dobsoni	159499	1.1654
M.dobsoni	161678	1.1322
M.dobsoni	161935	1.1647
M.dobsoni	161940	1.1728
M.talazaci	154581	1.0988
M.talazaci	154585	1.0630
M.talazaci	577056	1.1990
Oryzorictes	156226	1.2227
Oryzorictes	156601	1.3802
Oryzorictes	156602	1.3298
Oryzorictes	161744	1.2627
Oryzorictes	161745	1.3174
Oryzorictes	161746	1.3097

Taxon	ID	FNWI	FHWI
Hemicentetes	207712	0.7801	0.9158
Hemicentetes	207714	0.5160	1.0376
Hemicentetes	207715	0.7604	1.0447
Hemicentetes	212920	0.5964	0.9974
Hemicentetes	212922	0.5915	0.9722
Hemicentetes	212924	0.6065	0.9978
Hemicentetes	212940	0.5813	1.0133
Hemicentetes	29245	0.7575	0.8834
Hemicentetes	339992	0.4941	1.0613
Hemicentetes	354998	0.6234	1.0396
Hemicentetes	364954	0.4767	0.9585
Hemicentetes	395510	0.8937	0.8280
Tenrec	154628	2.2176	1.0011
Tenrec	156337	0.7162	1.0657
Tenrec	16364	0.5865	0.7972
Tenrec	170511	0.6697	1.0267
Tenrec	361485	0.4423	1.0487
Tenrec	364955	0.4277	0.8742
Tenrec	577051	0.4996	1.0468
Tenrec	578792	0.4396	1.0621
M.cowani	151654	1.2747	0.8960
M.cowani	151656	1.5317	0.8989
M.cowani	154020	1.5221	0.9735
M.cowani	154026	1.1278	0.8936
M.cowani	156195	2.3115	0.9340
M.cowani	156196	1.2357	0.8079
M.cowani	156197	2.3820	1.0479
M.cowani	156221	1.4422	0.7602
M.cowani	156222	1.6626	0.8378
M.cowani	156223	1.5643	1.0201
M.cowani	165672	1.2516	0.9087
M.cowani	165673	2.5871	0.9011
M.cowani	165674	2.2408	0.8681
M.cowani	165676	2.1860	0.8789

Appendix 4.3 (con't)

Taxon	ID	ASHI	ASZI	IDSH	OFSI
M. dobsoni	161940	1.0239	0.2677	1.0174	0.7242
M.talazaci	154581	0.8531	0.3060	0.8544	0.8466
M.talazaci	154585	0.8323	0.3211	0.8389	0.8377
M.talazaci	577056	0.9171	0.2795	0.7580	0.6427
Oryzorictes	12430	1.0171	0.2686	1.1392	0.6604
Oryzorictes	156226	0.9755	0.3260	0.9784	0.6580
Oryzorictes	156601	0.9293	0.3608	0.7040	0.6896
Oryzorictes	156602	0.9006	0.3229	0.7002	0.6635
Oryzorictes	159466	0.6948	0.3873	0.8489	0.6441
Oryzorictes	161744	0.8105	0.3272	1.1113	
Oryzorictes	161745	0.6657	0.3330	0.9263	0.6211
Oryzorictes	161746	0.8912	0.3492	0.8653	
Oryzorictes	162052	0.8467	0.3901	0.8287	0.7472
Oryzorictes	162055	0.8321	0.3497	0.9397	0.7769
Limnogale	100688	0.6977	0.2039	1.5665	0.5516
Limnogale	100689	0.8140	0.3295	1.0737	0.5437
Limnogale	100801	0.7767	0.3429	0.9474	0.5864
Limnogale	45050	0.7297	0.2943	0.9064	0.5564
Limnogale	45056	0.6700	0.3011	0.8123	0.5771
Geogale	151947	0.9491	0.3424	0.8030	0.8139
Geogale	156552	0.9863	0.3200	0.9046	0.7364
Geogale	156553	0.9281	0.2605	0.7449	0.7313
Geogale	159732	0.9003	0.3428	1.0299	0.7709
Geogale	159733	0.8660	0.3202	0.8795	0.7683
Geogale	161594			1.0558	0.5941
Potamogale	266897	0.8797	0.2992	0.8079	0.3479
Potamogale	34881	0.8819	0.3630	0.7575	0.3839
Potamogale	51324	0.8406	0.3772	0.8843	0.4334
Solenodon	49508	1.1800	0.3122	1.1334	0.6367
Solenodon	172680	0.9829	0.3122	1.1058	0.7920
Solenodon	217256	1.0286	0.3491	0.9363	0.8286
Solenodon	238263	0.9516	0.3099	0.9562	0.6674
Solenodon	290520	0.9928	0.3647	1.1815	0.7309
Solenodon	395819	0.8124	0.3837	1.1869	0.7903

Taxon	ID	PFLI
Oryzorictes	162052	1.2521
Oryzorictes	162055	1.2866
Limnogale	100688	1.7048
Limnogale	100689	1.5830
Limnogale	100801	1.6470
Limnogale	45050	1.6384
Limnogale	45056	1.5312
Geogale	151947	0.9513
Geogale	156552	1.0025
Geogale	156553	1.0208
Geogale	161594	1.0307
Potamogale	266897	1.2878
Potamogale	34881	1.2267
Potamogale	51324	1.1144
Solenodon	49508	1.4467
Solenodon	172680	1.4345
Solenodon	217256	1.4148
Solenodon	238263	1.3591
Solenodon	290520	1.3952
Solenodon	395819	1.3626
Solenodon	51068	1.4066
Solenodon	57320	1.4186
Solenodon	72809	1.3835
Petrodromus	203332	1.0178
Petrodromus	203336	1.0565
Echinosorex	448860	1.1664

Taxon	ID	FNWI	FHWI
M.cowani	165680	1.9596	0.9595
M.cowani	165689	2.0655	1.0005
M.cowani	168017	1.1724	0.8564
M.cowani	328658	1.2323	0.8235
M.cowani	449186	1.5722	0.9357
M.cowani	449187	1.4958	0.9258
M.cowani	449188	1.9887	0.8863
M.dobsoni	151624	0.9283	0.9714
M.dobsoni	151625	0.9118	0.9263
M.dobsoni	156225	1.2548	0.9768
M.dobsoni	159497	0.9021	0.9717
M.dobsoni	159498	1.5030	1.0585
M.dobsoni	159499	0.8057	0.7820
M.dobsoni	161678	1.3690	1.0139
M.dobsoni	161679	1.5784	1.0472
M.dobsoni	161718	0.9817	1.1444
M.dobsoni	161935	1.0028	1.0216
M.dobsoni	161940	1.0085	0.9583
M.dobsoni	165467	1.0377	0.9360
M.dobsoni	165774	0.8822	0.9410
M.dobsoni	165775	1.2447	0.9739
M.dobsoni	166107	1.1857	0.9036
M.dobsoni	166108	1.0785	0.9450
M.dobsoni	166198	1.4092	0.9183
M.dobsoni	166200	0.6071	1.0173
M.dobsoni	578749	0.9548	0.9043
M.dobsoni	582730	1.1108	0.8646
M.talazaci	154581	1.2763	1.0080
M.talazaci	154585	1.7096	0.8681
M.talazaci	577056	1.3818	0.8699
Oryzorictes	156226	1.7515	0.9834
Oryzorictes	156601	1.0289	1.0888
Oryzorictes	156602	0.8265	1.0619
Oryzorictes	161744	1.3940	0.9992

Appendix 4.3 (con't)

Solenodon	51068	0.8815	0.3375	1.0399	0.7077
Solenodon	57320	1.0248	0.3101	0.8758	0.6540
Solenodon	72809	0.8732	0.3388	0.8403	0.8198
Solenodon	89448	1.0054	0.3362	0.9091	0.7707
Petrodromus	203332	0.9571	0.2655	0.8321	0.6597
Petrodromus	203336	0.9718	0.2800	1.1737	0.8266
Echinosorex	448860	0.9712	0.3402	0.7533	

Oryzorictes	161745	1.4230	1.0111
Oryzorictes	161746	1.2418	0.9787
Oryzorictes	162052	1.4948	1.0298
Oryzorictes	162053	1.3691	0.9805
Oryzorictes	162054	1.4971	1.0017
Oryzorictes	162055	1.3192	0.9261
Oryzorictes	162057	1.2563	0.8913
Oryzorictes	162058	1.4279	0.9231

Taxon	ID	FNWI	FHWI	Taxon	ID	FNWI	FHWI
Oryzorictes	165490	1.1549	1.0000	Geogale	156553	0.9523	1.0370
Oryzorictes	165491	1.3239	0.9905	Geogale	161594	0.5423	0.9807
Oryzorictes	165492	1.2619	0.9995	Potamogale	266897	1.4848	1.1597
Oryzorictes	166157	1.2954	0.9482	Potamogale	34881	1.3184	0.9594
Oryzorictes	166208	1.8194	0.9506	Potamogale	51324	1.5812	0.8978
Oryzorictes	166237	1.2131	0.9954	Solenodon	49508	3.1327	0.9894
Oryzorictes	166238	0.9431	0.9590	Solenodon	172680	1.4176	0.9360
Oryzorictes	166239	1.2505	0.9167	Solenodon	172745	1.7397	0.9009
Oryzorictes	166240	0.9841	1.0091	Solenodon	217256	1.9895	0.9568
Oryzorictes	167481	1.5026	0.8348	Solenodon	238263	2.0528	0.9225
Oryzorictes	167482	1.3151	0.9707	Solenodon	290520	1.4975	1.0452
Oryzorictes	169239	1.4615	0.9162	Solenodon	395697	2.8210	1.0276
Oryzorictes	577052		0.9451	Solenodon	395819	2.8614	0.9805
Oryzorictes	578789	3.3456	0.8388	Solenodon	51068	2.0912	0.8061
Limnogale	100688	1.3952	1.0065	Solenodon	57320	1.5438	1.0814
Limnogale	100689	1.2370	1.0794	Solenodon	72809	1.4142	0.9511
Limnogale	100801	1.8283	0.9353	Petrodromus	203332		1.0392
Geogale	151947	0.8773	1.0488	Petrodromus	203336	3.1258	0.9845
Geogale	156551	0.7749	1.0464	Echinosorex	448860	2.5292	0.8820
Geogale	156552	0.5551	1.0803				

Taxon	ID	FHSZI	FHDI	GTRHI	LTRSI	LTRPI	TTRSI	TTRPI	PGSI	PGWI	DFWI	Taxon	ID	FCSI	MLFCI
Echinops	170605	3.1326	0.8978	0.3213	0.7466	0.1710	0.1071	2.7933	1.0422	0.4474	2.3813	Echinops	170605	1.5542	1.1324
Echinops	170607	3.2004	0.8293	0.0800	0.7109	0.1443	0.2418	2.2299	1.0783	0.5173	2.2850	Echinops	170607	1.3849	1.1155
Echinops	207717	2.9869	0.7186	0.1762	0.5282	0.1733	0.2565	2.0800	0.8595	0.4161	2.8645	Echinops	207717	1.3666	1.0137

Appendix 4.3 (con't)

Taxon	ID	FHSZI	FHDI	GTRHI	LTRSI	LTRPI	TTRSI	TTRPI	PGSI	PGWI	DFWI	Taxon	ID	FCSI	MLFCI
Echinops	212918	2.6231	0.9683	0.1470	0.5282	0.1781	0.1175	2.8877	0.9077	0.4880	2.1236	Echinops	212918	1.3115	1.1194
Echinops	212919	2.7390	0.7961	0.1822	0.6369	0.1976	0.2318	3.0260	0.9431	0.4756	2.2406	Echinops	212919	1.4335	1.0727
Echinops	31270	2.8233	0.8022	0.1878	0.7341	0.1746	0.1772	2.5713	1.1256	0.4452	2.3752	Echinops	31270	1.4106	1.3161
Echinops	328620				0.6850	0.1762	0.2458	2.7137	1.0009	0.4604	2.2773	Echinops	328620	1.6309	0.9586
Echinops	328636				0.6666	0.1854	0.1347	2.4402	0.9939	0.4645	2.5049	Echinops	328636	1.5148	1.2621
Echinops	328637	2.7779	1.2071	0.1876	0.8823	0.1773	0.2357	3.4715	1.4935	0.4071	2.2202	Echinops	395835	1.1940	1.1015
Echinops	395835	2.5132	0.7712	0.1238	0.5349	0.2109	0.1521	2.8762	0.9533	0.4659	2.0832	Echinops	464980	1.3252	0.8885
Echinops	464980	2.7987	0.9529	0.1969	0.7287	0.1802	0.2181	2.5765	0.8938	0.5381	2.2613	Echinops	588220	1.3084	1.0257
Echinops	588220	2.0564	0.6920	0.1011	0.3406	0.1848	0.1851	2.2732	0.8589	0.4795	1.8699	Setifer	154033	1.4299	1.0786
Setifer	154033	2.3899	0.8512	0.0722	0.4520	0.1679	0.1243	2.5018	1.1057	0.4714	1.9554	Setifer	154034	1.3359	1.1444
Setifer	154034	2.0194	0.6440	0.0699	0.3292	0.1577	0.2059	2.7176	0.9154	0.4808	2.0226	Setifer	159731	1.2067	1.1441
Setifer	159731	2.3674	0.7574	0.0065	0.5190	0.1688	0.1745	2.4883	0.9379	0.4429	2.2628	Setifer	166159		1.0533
Setifer	165494	2.8307	0.7713	0.2029	0.6030	0.1956	0.1120	2.4893	1.1249	0.3882	2.6764	Setifer	170532	1.2856	0.9852
Setifer	166159	2.2907	0.7438	0.1205	0.5242	0.1605	0.0861	2.1504	1.0320	0.5178	2.1251	Setifer	170548	1.4232	0.9199
Setifer	170532	2.5210	0.7953	0.0064	0.5686	0.1591	0.1980	2.6763	1.0553	0.4980	2.1762	Setifer	170581	1.3693	1.0705
Setifer	170548	2.6128	0.8841	0.0298	0.6264	0.1747	0.1814	2.5954	0.9519	0.4745	2.1623	Setifer	170730		1.0997
Setifer	170581	2.2548	0.6929	0.0676	0.5449	0.1547	0.1951	2.3433			2.1324	Setifer	170731	1.3100	1.0869
Setifer	170730	2.1712	0.7850	0.0690	0.5630	0.1737	0.1288	2.2760	1.0514	0.4041	2.0194	Setifer	207076	1.3363	1.0399
Setifer	170731	2.2623	0.7417	0.0509	0.4041	0.1697	0.0822	2.4721	1.0702	0.4422	2.4008	Setifer	317872	1.3143	0.9970
Setifer	207076	2.6279	0.8036	0.0566	0.7304	0.1705	0.1373	2.5796	1.0828	0.4062	2.2007	Setifer	328612	1.4548	1.1688
Setifer	317872	2.3582	0.7651	0.0603	0.5417	0.1670	0.1205	2.9159	0.9310	0.5389	2.0183	Setifer	33948	1.4041	
Setifer	328612	2.5291	0.8193	0.0095	0.5124	0.1734	0.1146	2.3999	0.9237	0.4962	2.2181	Setifer	395513	1.3256	1.1196
Setifer	33948	2.7741	0.7507	0.0697	0.5192	0.1812	0.2423	2.3761	0.8853	0.4820	2.4794	Setifer	395719	1.3400	1.1760
Setifer	395513	2.3285	0.7866	0.0361	0.2789	0.1742	0.1266	2.2448	0.9074	0.4787	1.9266	Setifer	541443	1.2388	1.2898
Setifer	395719	2.5649	0.8257	0.0275	0.5205	0.1753	0.0801	2.2725	0.8811	0.5159	2.2924	Setifer	578790	1.3329	1.0622
Setifer	541443	2.4444	0.6773	0.0275	0.4410	0.1638	0.1110	2.8225	0.9445	0.4227	2.2927	Setifer	85170	1.4045	1.1182
Setifer	578790	2.5414	0.8009	0.0859	0.4194	0.1607	0.0429	2.5065	0.8822	0.4536	2.2006	Setifer	85513	1.3778	0.9983
Setifer	85170	2.5194	0.8044	0.0278	0.5967	0.1675	0.0405	2.6761	0.9405	0.4905	2.2150	Hemicentetes	83658	1.2166	1.0445
Setifer	85513	2.3324	0.7829	0.0140	0.5109	0.1713	0.1381	2.8908	1.0275	0.5156	1.9186	Hemicentetes	162062	1.2778	1.1735
Hemicentetes	83658	2.5066	0.8138	0.1049	0.5413	0.1891	0.2654	2.5217	0.8215	0.4193	2.4033	Hemicentetes	166132	1.1297	1.1870

Appendix 4.3 (con't)

Taxon	ID	FHSZI	FHDI	GTRHI	LTRSI	LTRPI	TTRSI	TTRPI	PGSI	PGWI	DFWI	Taxon	ID	FCSI	MLFCI
Hemicentetes	162062	2.2803	0.7785	0.0919	0.6325	0.2078	0.2470	2.3809	1.0156	0.4035	2.3554	Hemicentetes	170593	1.3790	1.1722
Hemicentetes	166132	2.5051	0.7504	0.0889	0.2325	0.1837	0.3157	2.6403	0.9064	0.4782	2.2746	Hemicentetes	206755	1.3464	1.1504
Hemicentetes	170593	2.2261	0.7618	0.1474	0.4784	0.1968	0.1001	2.5190	0.8528	0.4350	2.4055	Hemicentetes	207712	1.1355	1.1292
Hemicentetes	206755	2.7643	0.8256	0.0711	0.4861	0.1977	0.1094	2.9048	0.6966	0.4680	2.6130	Hemicentetes	207714	1.2750	1.1047
Hemicentetes	207712	2.9726	0.8299	0.1066	0.4891	0.1776	0.3007	2.6629	1.0142	0.4230	2.5807	Hemicentetes	207715	1.2412	0.9124
Hemicentetes	207714	2.6379	0.7172	0.2428	0.4549	0.3532	0.3050	2.6087	0.7156	0.5280	2.3775	Hemicentetes	212920		1.0589
Hemicentetes	207715	2.6833	0.7113	0.1191	0.6150	0.2010	0.0857	2.4891	0.7555	0.5126	2.6864	Hemicentetes	212922	1.3898	1.0775
Hemicentetes	212920	2.5423	0.7815	0.1681	0.4168	0.1682	0.2277	2.8654			2.1954	Hemicentetes	212924	1.3991	1.0420
Hemicentetes	212922	2.4827	0.7966	0.1468	0.4809	0.1781	0.2300	1.9652			2.1706	Hemicentetes	212940	1.2596	1.2813
Hemicentetes	212924	2.3742	0.9453		0.5688		0.2677					Hemicentetes	29245	1.4250	1.2499
Hemicentetes	212940	2.7339	0.7865	0.0734	0.3872	0.1989	0.3286	2.7830	0.9185	0.3986	2.3951	Hemicentetes	339992	1.3056	1.3272
Hemicentetes	29245	2.8809	0.8117	0.0745	0.7100	0.1932	0.2237	2.2682	1.0882	0.4111	2.6077	Hemicentetes	354998	1.3787	1.1657
Hemicentetes	339992	2.5347	0.8025	0.2008	0.5222	0.2022	0.2471	2.5297	0.7750	0.4578	2.6406	Tenrec	154628	1.3342	1.1568
Hemicentetes	354998	2.7068	0.6984	0.1020	0.5096	0.2044	0.3573	1.9351	1.0094	0.4551	2.3798	Tenrec	156337	1.3163	1.2693
Hemicentetes	364954	2.3428	0.6921	0.1453		0.2292	0.3514	2.4814	0.8729	0.4005	2.4817	Tenrec	16364	1.4710	1.2103
Hemicentetes	395510	2.5426	0.7662	0.0491	0.5898	0.2059	0.4140	2.1477	0.8484	0.4843	2.4160	Tenrec	170511	1.2696	1.1241
Tenrec	154628	2.5414	0.6928	0.3091	0.4050	0.1738	0.2243	3.0588	0.8713	0.4541	2.3259	Tenrec	361485	1.4153	1.0495
Tenrec	156337	2.5044	0.7199	0.1985	0.4270	0.1744	0.2841	2.6752	1.1835	0.3888	2.2380	Tenrec	364955	1.0870	1.1748
Tenrec	16364	2.2092	0.7726	0.1097	0.5519	0.1817	0.2240	3.0655	1.1616	0.4602	1.9824	Tenrec	577051	1.4235	1.0546
Tenrec	170511	2.4652	0.7072	0.3194	0.3981	0.1879	0.1756	3.0044	1.0522	0.4554	2.2213	Tenrec	578792	1.3331	1.1640
Tenrec	361485	2.4442	0.7680	0.2286	0.4387	0.1824	0.2926	2.7083	0.8280	0.5678	2.2413	M.cowani	151654	1.6499	1.2238
Tenrec	364955	2.1201	0.7387	0.1490	0.4510	0.1925	0.3297	3.2194	0.9733	0.4415	1.8988	M.cowani	151656	1.5666	1.1702
Tenrec	577051	2.7208	0.6943	0.2066	0.4498	0.2001	0.1496	2.6909	1.0028	0.4725	2.3484	M.cowani	154020	1.3857	1.0767
Tenrec	578792	2.5673	0.6840	0.1988	0.4997	0.1837	0.1074	2.7281	1.0441	0.4402	2.2971	M.cowani	154026	1.6828	1.0284
M.cowani	151654	2.3571	0.7324	0.5625	0.4536	0.1421	0.4233	2.2016	1.5104	0.3573	2.1608	M.cowani	156195	1.5054	1.0443
M.cowani	151656	2.2002	0.8040	0.5081	0.4085	0.1411	0.4950	2.0334	1.5243	0.3518	2.2196	M.cowani	156196	1.6252	0.9642
M.cowani	154020	2.4237	0.7002	0.5185	0.4200	0.1327	0.3403	1.9520	1.5151	0.4235	2.2960	M.cowani	156221	1.5491	1.0150
M.cowani	154026	2.5346	0.8131	0.5033	0.3292	0.1400	0.4957	2.1602	1.3529	0.3920	2.3405	M.cowani	156222	1.4801	1.1235
M.cowani	156195	2.6410	0.9027	0.5423	0.5220	0.1281	0.3686	2.4305	1.5479	0.3388	2.2959	M.cowani	156223	1.5506	1.0103
M.cowani	156196	2.2849	0.8754	0.6133	0.4049	0.1289	0.4284	2.4848	1.4651	0.3821	2.1943	M.cowani	165672	1.5430	1.2396

Appendix 4.3 (con't)

Taxon	ID	FHSZI	FHDI	GTRHI	LTRSI	LTRPI	TTRSI	TTRPI	PGSI	PGWI	DFWI	Taxon	ID	FCSI	MLFCI
M.cowani	156197	2.3002	0.7865	0.5762	0.4642		0.4000					M.cowani	165673	1.4589	1.0860
M.cowani	156221	2.4266	0.7947	0.6580	0.5319	0.1476	0.3644	2.4710	1.5804	0.3712	2.2395	M.cowani	165674		1.0642
M.cowani	156222	2.1382	0.6866	0.5312	0.3620	0.1265	0.2858	2.2704	1.9294	0.3250	2.2099	M.cowani	165676	1.4896	0.9641
M.cowani	156223	2.1533	0.7125	0.4762	0.4405	0.1440	0.2398	2.3479	1.7308	0.3374	2.0620	M.cowani	165680	1.5800	0.9970
M.cowani	165672	2.6128	0.7214	0.9667	0.5144	0.1295	0.5458	2.1569	1.6215	0.4119	2.8410	M.cowani	165689	1.5095	1.0438
M.cowani	165673	2.5541	0.7174	0.5466	0.4240	0.1359	0.4711	1.8976	1.3583	0.3771	2.4521	M.cowani	168017		0.9230
M.cowani	165674	2.5782	0.7115	0.5940	0.4542	0.1325	0.3983	2.0048	1.6485	0.3504	2.3261	M.cowani	449184	1.5488	1.0501
M.cowani	165676	2.5172	0.8492	0.5861	0.4852	0.1447	0.4571	2.2520	1.5112	0.3953	2.3841	M.cowani	449186	1.5824	0.9591
M.cowani	165680	2.4714	0.7490	0.8188	0.4605	0.1250	0.4458	2.0203	0.9577	0.4947	2.5195	M.cowani	449187	1.6838	0.9866
M.cowani	165689	2.6832	0.7093	0.6266	0.4270	0.1296	0.4822	2.2303	2.0067	0.3075	2.7818	M.cowani	449188	1.6519	1.0837
M.cowani	168017	2.3546	0.7600	0.6195	0.4986	0.1253	0.1806	2.1998	2.0292	0.3272	2.1852	M.dobsoni	151624	1.4529	1.0277
M.cowani	328658	2.1574	0.7594	0.4204	0.5183	0.1508	0.3043	2.5449	1.6992	0.3837	2.0934	M.dobsoni	151625	1.6043	0.9376
M.cowani	449184	2.5629	0.9325	0.6129	0.2986	0.1237	0.4691	2.3671	1.5070	0.3535	2.2714	M.dobsoni	156225	1.3914	1.0119
M.cowani	449186	2.3264	0.7635	0.4060	0.3374	0.1350	0.4728	2.3799	1.6640	0.3576	2.0825	M.dobsoni	159497	1.2520	0.9840
M.cowani	449187	2.1227	0.7624	0.4870	0.3974	0.1342	0.3726	2.5142	1.5652	0.3334	2.2674	M.dobsoni	159498	1.4360	1.0290
M.cowani	449188	2.1242	0.7161	0.5925	0.2244	0.1181	0.5213	2.0712	1.3602	0.3601	2.2252	M.dobsoni	159499	1.1194	2.1999
M.dobsoni	151624	2.2562	0.7476	0.5151	0.5220	0.1391	0.3034	2.8017	1.8881	0.3479	2.2649	M.dobsoni	161679	1.6292	1.0123
M.dobsoni	151625	2.1849	0.7546	0.6352	0.4025	0.1303	0.2299	2.5632	1.6408	0.3857	2.2333	M.dobsoni	161718	1.5159	1.0590
M.dobsoni	156225	2.0755	0.7900	0.4219	0.5896	0.1549	0.1403	2.6991	1.8289	0.3225	2.0965	M.dobsoni	161935	1.5815	1.2458
M.dobsoni	159497	2.2539	0.6656	0.4942	0.4445	0.1530	0.3914	2.5860	1.1586	0.5784	1.9013	M.dobsoni	161940	1.5244	0.9188
M.dobsoni	159498	1.8867	0.7607	0.2882	0.5225	0.1535	0.3080	2.3300	1.6723	0.3688	1.9539	M.dobsoni	165467	1.3913	1.1645
M.dobsoni	159499	2.4031	0.8085	0.7231	0.7650	0.1541	0.1963	2.5166	1.6907	0.3962	2.2843	M.dobsoni	165774	1.6497	0.9495
M.dobsoni	161678	2.2464	0.7252	0.5660	0.5804	0.1536	0.3331	2.4708	1.6248	0.3368	2.3066	M.dobsoni	165775	1.5249	1.0648
M.dobsoni	161679	1.8778	0.7899	0.5289	0.5685	0.1534	0.2615	2.7388	1.2689	0.4223	1.9110	M.dobsoni	166107	1.4537	1.0566
M.dobsoni	161718	2.1636	0.7282	0.5661	0.3462	0.1165	0.2778	2.8590	1.5486	0.3640	2.1772	M.dobsoni	166108	1.7131	1.1883
M.dobsoni	161935	2.3565	0.8520	0.4612	0.5358	0.1410	0.2078	2.8463	1.6381	0.3454	2.1336	M.dobsoni	166198	1.6109	1.0052
M.dobsoni	161940	2.0882	0.7072	0.4893	0.4902	0.1630	0.3545	2.8219	1.5644	0.3712	2.1089	M.dobsoni	166200	1.5327	1.0784
M.dobsoni	165467	2.2023	0.7333	0.6266	0.5294	0.1499	0.1740	2.6128	1.5893	0.3378	2.1838	M.dobsoni	578749	1.4794	1.1304
M.dobsoni	165774	2.0271	0.7001	0.6064	0.4083	0.1460	0.3146	2.6467	1.5115	0.4084	2.1277	M. talazaci	154581	1.4441	1.1226
M.dobsoni	165775	2.1144	0.6600	0.4728	0.5421	0.1421	0.3532	2.6056	1.4798	0.3442	2.2544	M. talazaci	154585	1.3813	1.1069

Appendix 4.3 (con't)

Taxon	ID	FHSZI	FHDI	GTRHI	LTRSI	LTRPI	TTRSI	TTRPI	PGSI	PGWI	DFWI	Taxon	ID	FCSI	MLFCI
M.dobsoni	166107	2.4178	0.7884	0.6511	0.4859	0.1320	0.4306	2.8642	1.6771	0.3752	2.2593	M. talazaci	577056	1.5497	1.2679
M.dobsoni	166108	2.1524	0.7950	0.6300	0.5723	0.1390	0.3305	2.5676	1.7799	0.3586	2.1861	Oryzorictes	156226	1.3915	1.1274
M.dobsoni	166198	2.3502	0.7508	0.6157	0.5746	0.1409	0.2803	3.2749	1.5953	0.4067	2.2601	Oryzorictes	156601	1.3930	1.1412
M.dobsoni	166200	2.3674	0.7365	0.6023	0.4904	0.1240	0.3638	2.9691	1.6541	0.3666	2.4613	Oryzorictes	156602	1.4213	1.1335
M.dobsoni	578749	2.0382	0.7260	0.5899	0.5690	0.1359	0.2139	2.5649	1.0998	0.4134	2.4826	Oryzorictes	156603	1.3483	1.0830
M.dobsoni	582730	2.3552	0.7679	0.6728	0.5809	0.1707	0.3568	2.6589	1.2593	0.3807	2.3216	Oryzorictes	159695		1.2365
M.talazaci	154581	2.0302	0.7477	0.3689	0.4126	0.1570	0.2988	2.5822	1.4133	0.4106	2.0490	Oryzorictes	161745		1.1839
M.talazaci	154585	2.2251	0.7109	0.3714	0.4857	0.1417	0.2672	2.6761	1.7111	0.3634	2.2453	Oryzorictes	162053		1.0849
M.talazaci	577056	2.1766	0.7469	0.6521	0.5773	0.1574	0.2721	2.9957	1.7039	0.3613	2.3986	Oryzorictes	162054	0.6696	0.9088
Oryzorictes	156226	1.9667	0.7493	0.3195	0.3941	0.1221	0.3414	2.1023	1.3579	0.4180	2.0202	Oryzorictes	162058	1.3840	1.2211
Oryzorictes	156601	2.5208	0.7619	0.3840	0.3416	0.1265	0.3262	0.0037	2.7695	0.1493	3.1721	Oryzorictes	166157	1.3003	1.1562
Oryzorictes	156602	2.2729	0.7549	0.3390	0.4676	0.1327	0.2424	1.9901	0.9379	0.5571	1.9636	Oryzorictes	166239	1.3182	1.1564
Oryzorictes	156603	2.1254	0.6783	0.2301	0.2747	0.1390	0.3325	2.1405	0.8007	0.5128	1.9514	Oryzorictes	166240	1.2778	1.1860
Oryzorictes	159695	2.0653	0.6796	0.4305	0.4184	0.1386	0.4653	2.1354	1.0320	0.5236	2.1297	Oryzorictes	167481	1.4023	1.1970
Oryzorictes	161744	2.1791	0.8184	0.4456	0.4211	0.1771	0.3860	2.1146	1.3046	0.4727	2.0790	Oryzorictes	167482	1.4342	1.0927
Oryzorictes	161745	1.8932	0.5870	0.3181	0.3727	0.1567	0.3759	1.9270	1.0750	0.5138	1.8959	Oryzorictes	169239	1.2728	1.0185
Oryzorictes	161746	2.0219	0.6978	0.4420	0.4815	0.1596	0.4007	1.9573	0.8922	0.5054	2.0866	Oryzorictes	169240	1.2338	1.1572
Oryzorictes	162052	2.0447	0.9254	0.2947	0.2985	0.2137	0.2903	1.6764	1.0154	0.5368	1.9048	Oryzorictes	31257		1.0061
Oryzorictes	162053	1.8924	0.7468	0.3454	0.3849	0.1511	0.2912	2.5586			1.8664	Oryzorictes	45018	1.3230	1.1639
Oryzorictes	162054	1.8939	0.7322	0.2854	0.2724	0.1448	0.2707	2.0948	0.9033	0.5520	1.7278	Oryzorictes	577052	1.3019	1.1318
Oryzorictes	162055	2.2341	0.8115	0.5706	0.3942	0.1664	0.3651	2.3588	1.0454	0.5114	2.0202	Oryzorictes	578789	1.2467	0.9941
Oryzorictes	162057	2.0953	0.8052	0.2759	0.3380	0.1182	0.3695	1.9893	1.1002	0.5113	1.7893	Limnogale	100688	1.5681	0.8962
Oryzorictes	162058	2.1699	0.6907	0.4825	0.2131	0.1549	0.5485	2.1010	1.0080	0.5220	2.0717	Limnogale	100689	1.4471	0.8527
Oryzorictes	165490	2.2281	0.8734	0.3003	0.2698	0.1498	0.3995	1.8707	1.1201	0.5779	1.9606	Limnogale	100801	1.4723	0.9366
Oryzorictes	165491	1.8426	0.7610	0.3244	0.3071	0.1597	0.5746	1.6871	1.0788	0.4615	1.9938	Limnogale	45050	1.4720	0.8926
Oryzorictes	165492	1.9860	0.8008	0.2984	0.3184	0.1530	0.3544	1.9982	1.0100	0.6162	2.0395	Limnogale	45056	1.3721	0.7865
Oryzorictes	165705	2.1331	0.7254	0.4704	0.4204	0.1602	0.3606	2.2842	0.9196	0.5626	2.1121	Limnogale	100688	1.5681	0.8962
Oryzorictes	166157	2.1274	0.7142	0.4247	0.3222	0.1563	0.4750	2.1318	0.9570	0.5631	2.0228	Limnogale	100689	1.4471	0.8527
Oryzorictes	166208	2.0343	0.7987	0.2507	0.3024	0.1290	0.3251	2.0956	0.9586	0.5523	1.9734	Limnogale	100801	1.4723	0.9366
Oryzorictes	166237	1.9586	0.6792	0.3935	0.3847	0.1381	0.4542	1.8746	1.0479	0.5646	2.0527	Limnogale	45050	1.4720	0.8926

Appendix 4.3 (con't)

Taxon	ID	FHSZI	FHDI	GTRHI	LTRSI	LTRPI	TTRSI	TTRPI	PGSI	PGWI	DFWI	Taxon	ID	FCSI	MLFCI
Oryzorictes	166238	2.0098	0.7123	0.3665	0.2099	0.1511	0.4922	2.2854	0.9079	0.5697	2.0289	Limnogale	45056	1.3721	0.7865
Oryzorictes	166239	2.1880	0.7201	0.3872	0.3918	0.1767	0.3552	2.1278	0.8772	0.5554	2.0530	Geogale	151947	1.4291	0.9175
Oryzorictes	166240	2.0948	0.7725	0.4133	0.3556	0.1586	0.4064	2.1390	1.0434	0.5962	2.0852	Geogale	156551	1.2145	0.8732
Oryzorictes	167480	1.9907	0.8000	0.3636	0.2237	0.1527	0.5126	1.9259	0.8591	0.5249	1.9997	Geogale	156552	1.4896	0.8339
Oryzorictes	167481	2.4079	0.7312	0.3724	0.3716	0.1324	0.4047	2.1532	0.8628	0.5186	2.1670	Geogale	161594	1.3582	0.8346
Oryzorictes	167482	2.0462	0.7308	0.2740	0.3378	0.1433	0.3449	2.1840	1.0785	0.5508	1.9621	Potamogale	266897	1.4425	1.2703
Oryzorictes	169239	1.8478	0.7345	0.3822	0.3248	0.1457	0.3816	2.1037	1.0142	0.5412	1.9079	Potamogale	34881	1.5859	0.9527
Oryzorictes	169240	2.1902	0.7778	0.3810	0.3187	0.1428	0.3305	1.9386	0.8393	0.5820	2.0659	Potamogale	51324	1.3996	1.0480
Oryzorictes	31257	1.9920	0.7038	0.4804	0.2669	0.1462	0.3201	2.1703	1.0845	0.4732	1.8986	Solenodon	49508	1.3835	1.1997
Oryzorictes	45018	2.5521	0.8404	0.5303	0.3710	0.1424	0.4842	2.0638	0.7982	0.5601	2.1998	Solenodon	172680	1.3829	1.1617
Oryzorictes	577052	2.1615	0.6228						0.9012	0.6017	2.2786	Solenodon	217256	1.2681	1.1195
Oryzorictes	578789	2.1253	0.7786	0.3691	0.3801	0.1541	0.2816	2.1459	0.9856	0.5069	2.0855	Solenodon	238263	1.2600	1.0952
Limnogale	100688	2.1735	0.6729	0.1443	0.5192	0.1936	0.4754	2.3341	0.9942	0.4067	2.4175	Solenodon	290520	1.4115	1.1917
Limnogale	100689	1.8948	0.5906	0.3420	0.5587	0.2076	0.3688	2.2529	1.0739	0.3798	2.3387	Solenodon	395697	1.3510	1.2084
Limnogale	100801	1.8651	0.6119	0.3302	0.5815	0.2003	0.4473	2.1808	1.1040	0.3173	2.2493	Solenodon	395819	1.2945	1.1959
Limnogale	45050	2.0596	0.6996	0.3950	0.6958	0.1988	0.5007	2.3250	0.8954	0.3927	2.4218	Solenodon	57320	1.5047	1.0597
Limnogale	45056	1.9448	0.6030	0.5162	0.3301	0.1973	0.5262	2.3250	0.9247	0.4104	2.3370	Solenodon	72809	1.3686	1.3194
Geogale	151947	2.3601	0.8397	0.3467	0.6159	0.1296	0.1793	2.6144	0.9617	0.5002	2.0792	Petrodromus	203332	1.9528	
Geogale	156551	2.4474	0.7046	0.3139	0.7489	0.1454	0.0816	2.4119	1.1727	0.3776	2.4581	Petrodromus	203336	2.0814	0.8775
Geogale	156552	2.6731	0.9496	0.3160	0.6675	0.1321	0.1333	3.0159	1.5190	0.3943	2.0443	Echinosorex	448860	1.6124	1.3580
Geogale	156553	2.1949	0.9351	0.3152	0.4166	0.1094	0.1634	3.2635	1.4178	0.3893	1.8711				
Geogale	161594	2.4272	0.8232	0.2884	0.5331	0.1337	0.1836	2.7813	1.1011	0.3902	2.1240				
Potamogale	266897	1.6287	0.6196	0.4358	0.3182	0.1718	0.1751	1.3287	1.2527	0.3344	1.8443				
Potamogale	34881	1.7408	0.6819	0.3763	0.5691	0.1495	0.1516	1.1923	1.3204	0.3558	1.8641				
Potamogale	51324	1.4637	0.5279	0.3546	0.2757	0.1289	0.2452	1.3652	1.1980	0.4089	1.8392				
Solenodon	49508	2.4699	0.7405	0.4967	0.7216	0.2002	0.3741	2.4866	0.8575	0.5596	2.4256				
Solenodon	172680	2.5145	0.8018	0.4544	0.6461	0.1883	0.4006	2.0928	0.8938	0.4666	2.7407				
Solenodon	172745	2.3457	0.7747	0.4619	0.4931	0.1866	0.4293	2.1637	0.7332	0.5190	2.5392				
Solenodon	217256	2.3931	0.7320	0.5073	0.6035	0.1711	0.4356	2.4182	0.9051	0.4802	2.5670				
Solenodon	238263	1.9434	0.6872	0.3431	0.6214	0.1908	0.2508	2.2712	0.7865	0.5246	2.1300				

Appendix 4.3 (con't)

Taxon	ID	FHSZI	FHDI	GTRHI	LTRSI	LTRPI	TTRS	TTRPI	PGSI	PGWI	DFWI
Solenodon	290520	2.4519	0.7710	0.3843	0.7611	0.1902	0.4384	2.4615	1.0105	0.5123	2.3139
Solenodon	395697	2.2248	0.8377	0.4999	0.5641	0.1841	0.3146	2.1278	0.8266	0.4800	2.2726
Solenodon	395819	2.3272	0.6970	0.4233	0.6293	0.1924	0.2942	2.1601	0.9755	0.5044	2.3486
Solenodon	51068	2.4264	0.6660	0.4650	0.6386	0.1689	0.3141	2.3585	0.8736	0.5331	2.6578
Solenodon	57320	2.2572	0.7855	0.4273	0.6677	0.1892	0.1679	2.0195	0.8926	0.5270	2.3210
Solenodon	72809	2.1460	0.7297	0.3998	0.6123	0.1787	0.2589	1.9615	0.8842	0.5184	2.2449
Petrodromus	203332	1.6660	0.7947	0.9915	0.3592	0.0684	0.7572	5.9531	2.0585	0.3297	1.7130
Petrodromus	203336	1.9018	0.8423	1.1392	0.3737	0.0831	0.7118	6.4466	1.5437	0.3717	1.8923
Echinosorex	448860	1.7687	0.5449	0.6308	0.2979	0.1658	0.4719	2.4076	1.3489	0.4775	2.0774

Taxon	ID	FCDI	Taxon	ID	TSI	Taxon	ID	TTSI	MLTCI
Echinops	170605	2.2298	Echinops	127274	14.7713	Echinops	127274	0.3789	0.9968
Echinops	170607	2.5330	Echinops	134550	10.7500	Echinops	134550	0.3720	1.2006
Echinops	207717	2.4116	Echinops	153785	8.9953	Setifer	124554	0.3014	0.8930
Echinops	212918	2.3331	Echinops	159728	15.3688	Setifer	154034	0.3747	1.0320
Echinops	212919	2.1840	Echinops	159729	13.1184	Setifer	159731	0.2692	0.8631
Echinops	31270	2.2157	Echinops	159730	14.3479	Setifer	170731	0.2538	1.0341
Echinops	328620	2.2200	Echinops	170605	12.6155	Setifer	85170	0.2896	0.9840
Echinops	328636	2.5243	Echinops	170607	13.4629	Setifer	85513	0.3688	0.9017
Echinops	328637	2.0293	Echinops	207717	13.7556	Hemicentetes	161757	0.4247	0.9249
Echinops	395835	1.9340	Echinops	207718	11.8526	Hemicentetes	161758	0.4808	0.8942
Echinops	464980	1.9852	Echinops	212918	10.6182	Hemicentetes	162059	0.3843	0.9331
Echinops	588220	1.7241	Echinops	212919	11.3486	Hemicentetes	162062	0.4428	0.9173
Setifer	154033	2.2109	Echinops	31270	14.2969	Hemicentetes	166132	0.3997	0.7432
Setifer	154034	2.1514	Echinops	328620	13.3221	Hemicentetes	170593	0.5302	0.9159
Setifer	159731	2.2310	Echinops	328636	11.8734	Hemicentetes	206755	0.4977	0.8452
Setifer	165494	2.6570	Echinops	328637	14.6717	Hemicentetes	212920	0.5413	1.0174
Setifer	166159	2.5349	Echinops	395835	11.4506	Hemicentetes	212922	0.5187	1.0202
Setifer	170532	1.9799	Echinops	464980	12.1669	Hemicentetes	339992	0.3302	0.9300
Setifer	170548	2.2930	Echinops	588220	8.5029	Hemicentetes	354998	0.4972	1.0347

Appendix 4.3 (con't)

Taxon	ID	FCDI	Taxon	ID	TSI	Taxon	ID	TTSI	MLTCI
Setifer	170581	2.2694	Setifer	124554	14.5936	Hemicentetes	395510	0.5103	1.0395
Setifer	170730	2.2738	Setifer	154033	13.2121	Tenrec	154628	0.4416	0.8195
Setifer	170731	2.2846	Setifer	154034	14.4664	Tenrec	154629	0.4624	0.8637
Setifer	207076	2.5147	Setifer	165494	15.8014	Tenrec	156337	0.5093	0.8448
Setifer	317872	2.1317	Setifer	170532	12.9276	Tenrec	166047	0.3557	0.7974
Setifer	328612	2.4860	Setifer	170548	14.9531	Tenrec	30398	0.4482	0.8580
Setifer	33948	2.6545	Setifer	170581	13.3340	Tenrec	364955	0.6412	0.7344
Setifer	395513	2.3630	Setifer	170731	13.3128	Tenrec	50911	0.3907	0.9512
Setifer	395719	2.6070	Setifer	207076	16.0762	Tenrec	60587	0.5153	0.9341
Setifer	541443	1.8217	Setifer	317872	15.7050	Tenrec	85514	0.4591	0.8783
Setifer	578790	2.3622	Setifer	328612		M.cowani	151654	0.4438	
Setifer	85170	2.3151	Setifer	395513	12.5847	M.cowani	154020	0.4874	0.8685
Setifer	85513	2.2191	Setifer	395719	15.2684	M.cowani	154026		1.0530
Hemicentetes	83658	2.1489	Setifer	541443	14.6122	M.cowani	156196	0.6084	0.8668
Hemicentetes	162062	2.0881	Setifer	578790	13.8902	M.cowani	156221	0.4730	0.8555
Hemicentetes	166132	1.8434	Setifer	85170	13.2789	M.cowani	156222	0.5809	0.9300
Hemicentetes	170593	2.3957	Setifer	85513	15.5742	M.cowani	156223	0.5106	1.0046
Hemicentetes	206755	2.5781	Hemicentetes	83658	11.6958	M.cowani	165673	0.3967	1.1264
Hemicentetes	207712	2.3042	Hemicentetes	161757	15.2873	M.cowani	165676	0.4922	1.0340
Hemicentetes	207714	2.2845	Hemicentetes	161758	16.0449	M.cowani	165680	0.5077	0.7580
Hemicentetes	207715	2.0342	Hemicentetes	162059	13.7884	M.cowani	165689	0.4722	
Hemicentetes	212920	2.2712	Hemicentetes	162062	12.8663	M.cowani	449186	0.6240	0.8800
Hemicentetes	212922	2.4729	Hemicentetes	166132	15.8833	M.cowani	449187	0.5219	1.0961
Hemicentetes	212924	2.2316	Hemicentetes	170593	14.2874	M.dobsoni	151624	0.8047	1.0569
Hemicentetes	212940	2.2943	Hemicentetes	206755	15.2990	M.dobsoni	151625	0.7100	0.9454
Hemicentetes	29245	2.4342	Hemicentetes	207712	17.5344	M.dobsoni	156225	0.7332	1.0572
Hemicentetes	339992	2.2706	Hemicentetes	207715	16.1428	M.dobsoni	159497	0.8419	0.9368
Hemicentetes	354998	2.3944	Hemicentetes	212920	13.8114	M.dobsoni	159498	0.8773	0.9485
Hemicentetes	364954	2.4759	Hemicentetes	212922	13.5503	M.dobsoni	161679	0.6415	0.9847
Hemicentetes	395510	2.2057	Hemicentetes	212924	16.1341	M.dobsoni	161935	0.7877	1.1010

Appendix 4.3 (con't)

Taxon	ID	FCDI	Taxon	ID	TSI	Taxon	ID	TTSI	MLTCI
Tenrec	154581	2.3206	Hemicentetes	33951	14.1547	M.dobsoni	161940	0.7315	1.3023
Tenrec	154585	2.2099	Hemicentetes	339992	14.4187	M.dobsoni	165467	0.7606	0.8781
Tenrec	577056	2.5110	Hemicentetes	354998	18.5745	M.dobsoni	165774	0.7579	0.8560
M.cowani	151654	2.2570	Hemicentetes	364954	17.8700	M.dobsoni	165775	0.7951	1.0325
M.cowani	151656	2.6372	Hemicentetes	395510	15.7309	M.dobsoni	166107	0.8293	1.0100
M.cowani	154020	2.6892	Tenrec	154628	16.3151	M.dobsoni	166198	0.8730	0.9570
M.cowani	154026	2.5833	Tenrec	156337	17.3684	M.dobsoni	166200	1.1237	1.0518
M.cowani	156195	2.3859	Tenrec	166047	15.9204	M. talazaci	154581	0.6305	0.9671
M.cowani	156196	2.5656	Tenrec	170511	18.2517	M. talazaci	154585	0.7073	0.8371
M.cowani	156221	2.9321	Tenrec	30398	13.9348	M. talazaci	167501	0.7695	0.8844
M.cowani	156222	2.5461	Tenrec	361485	14.9003	M. talazaci	167502	0.7968	0.9459
M.cowani	156223	2.4203	Tenrec	364955	12.9981	M. talazaci	167503	0.7366	0.9253
M.cowani	165672	2.6908	Tenrec	50911	14.5159	M. talazaci	577056	0.5952	1.0950
M.cowani	165673	2.4998	Tenrec	577051	15.1175	Oryzorictes	162058	0.8355	1.1149
M.cowani	165674	2.5888	Tenrec	578792	15.3417	Oryzorictes	166157	0.8500	1.1420
M.cowani	165676	2.7552	Tenrec	85514	13.9200	Oryzorictes	166239	1.0533	0.9854
M.cowani	165680	2.8513	M.cowani	156221	18.9963	Oryzorictes	166240	0.9170	1.0009
M.cowani	165689	2.4995	M.cowani	156222	20.5623	Oryzorictes	167481	0.8963	0.7871
M.cowani	168017	2.7212	M.cowani	156223	17.7044	Oryzorictes	167482	0.8397	1.0141
M.cowani	328658	2.3828	M.cowani	165672	20.4862	Limnogale	45050	0.5445	0.8948
M.cowani	449184	2.6340	M.cowani	165673	16.9364	Geogale	161594	0.5386	0.7036
M.cowani	449186	2.2909	M.cowani	165674	17.8805	Solenodon	51068	0.5655	1.1581
M.cowani	449187	2.6977	M.cowani	165676	19.0259	Solenodon	57320	0.5837	0.8343
M.cowani	449188	2.4623	M.cowani	165680	19.2274	Solenodon	72809	0.4743	1.0907
M.dobsoni	151624	2.5623	M.cowani	165689	19.2014	Petrodromus	203336	1.2832	0.8795
M.dobsoni	151625	2.7761	M.cowani	168017	18.7749				
M.dobsoni	156225	2.2025	M.cowani	328658	18.0838				
M.dobsoni	159497	2.6630	M.cowani	449184	21.5595				
M.dobsoni	159498	2.1661	M.cowani	449186	17.8570				
M.dobsoni	159499	2.4880	M.cowani	449187					

Appendix 4.3 (con't)

Taxon	ID	FCDI	Taxon	ID	TSI	Taxon	ID	TSI	Taxon	ID	TSI
M.dobsoni	161678	2.3782	M.cowani	449188		Oryzorictes	162058	2.1761	Potamogale	266897	16.3569
M.dobsoni	161679	2.0504	M. dobsoni	151624		Oryzorictes	165490	1.9087	Potamogale	34881	
M.dobsoni	161718	2.3138	M. dobsoni	161935	21.3054	Oryzorictes	165491	2.0910	Potamogale	51322	16.7594
M.dobsoni	161935	2.6256	M. dobsoni	161940	23.6415	Oryzorictes	165492	2.1575	Potamogale	51324	13.0403
M.dobsoni	161940	2.4512	M. dobsoni	165467	22.7001	Oryzorictes	165705	2.1250	Potamogale	51333	15.6577
M.dobsoni	165467	2.2743	M. dobsoni	165774	21.3533	Oryzorictes	166157	1.8963	Potamogale	55204	16.5639
M.dobsoni	165774	2.5718	M. dobsoni	165775	22.9296	Oryzorictes	166208	1.7061	Solenodon	49508	19.0956
M.dobsoni	165775	2.8109	M. dobsoni	166107	24.4211	Oryzorictes	166237	1.8200	Solenodon	172680	15.2169
M.dobsoni	166107	2.3860	M. dobsoni	166198	24.0051	Oryzorictes	166238	1.8903	Solenodon	217256	15.1895
M.dobsoni	166108	2.3125	M. dobsoni	166200	21.7610	Oryzorictes	166239	1.8942	Solenodon	238263	14.5557
M.dobsoni	166198	2.4795	M.talazaci	154581	20.1674	Oryzorictes	166240	2.0453	Solenodon	290520	15.2016
M.dobsoni	166200	2.5174	M.talazaci	154585	21.3548	Oryzorictes	167481	2.0814	Solenodon	395697	16.2276
M.dobsoni	578749	2.6663	M.talazaci	162040	23.7175	Oryzorictes	167482	1.9333	Solenodon	395819	15.8157
M.dobsoni	582730	2.5649	M.talazaci	167501	22.0196	Oryzorictes	169239	1.9975	Solenodon	51068	16.3351
M.talazaci	154581	2.3206	M.talazaci	167502	22.8487	Oryzorictes	169240	1.8993	Solenodon	57320	15.9167
M.talazaci	154585	2.2099	M.talazaci	167503	22.3474	Oryzorictes	31257	2.1857	Solenodon	72809	15.3207
M.talazaci	577056	2.5110	M.talazaci	577056	23.4955	Oryzorictes	45018	1.9924	Petrodromus	150415	25.8504
Oryzorictes	156226	2.2159	Oryzorictes	161746	14.1502	Oryzorictes	577052	2.2730	Petrodromus	203336	24.1944
Oryzorictes	156601	2.2994	Oryzorictes	162053	12.7906	Oryzorictes	578789	1.9142	Petrodromus	203339	24.0893
Oryzorictes	156602	2.1864	Oryzorictes	162054	14.0032	Limnogale	100688	2.2873	Petrodromus	86566	24.4061
Oryzorictes	156603	1.9369	Oryzorictes	162058	14.2570	Limnogale	100689	2.2877	Petrodromus	86568	23.6854
Oryzorictes	159695	1.7966	Oryzorictes	166239		Limnogale	100801	2.5692	Petrodromus	86581	25.0702
Oryzorictes	161744	2.1020	Oryzorictes	166240	16.2632	Limnogale	45050	2.2590	Petrodromus	86585	25.2620
Oryzorictes	161745	2.1920	Oryzorictes	167480	13.9051	Limnogale	45056	2.5096	Echinosorex	448860	14.2335
Oryzorictes	161746	1.9803	Oryzorictes	31257	14.3536	Geogale	170605	2.2298			
Oryzorictes	162052		Oryzorictes	45018	15.9949	Geogale	170607	2.5330			
Oryzorictes	162053	1.8374	Oryzorictes	578789	12.0120	Geogale	207717	2.4116			
Oryzorictes	162054	2.0332	Limnogale	45050	17.1320	Geogale	212918	2.3331			
Oryzorictes	162055	1.8516	Geogale	161594	19.2889	Geogale	212919	2.1840			
Oryzorictes	162057	1.8945	Geogale	45043	21.5718	Geogale	31270	2.2157			

Appendix 4.4. Index Summary Statistics and Tukey Post-Hoc Results (see Table 4.4 for index abbreviations)

Taxon	ASZI Means	ASZI N	ASZI Std.Dev.						
Echinops	0.407	12	0.040						
Setifer	0.391	10	0.036						
Hemicentetes	0.384	15	0.028						
Tenrec	0.406	8	0.025						
M.cowani	0.294	9	0.015						
M. dobsoni	0.280	10	0.022						
M.talazaci	0.302	3	0.021						
Oryzorictes	0.341	10	0.035						
Limnogale	0.294	5	0.054						
All Grps	0.354	82	0.058						
	{1} M=.40731	{2} M=.39123	{3} M=.38381	{4} M=.40646	{5} M=.29391	{6} M=.27951	{7} M=.30218	{8} M=.34147	{9} M=.29435
Echinops {1}		0.960	0.620	1.000	0.000	0.000	0.000	0.000	0.000
Setifer {2}	0.960		1.000	0.985	0.000	0.000	0.002	0.023	0.000
Hemicentetes {3}	0.620	1.000		0.793	0.000	0.000	0.004	0.045	0.000
Tenrec {4}	1.000	0.985	0.793		0.000	0.000	0.000	0.002	0.000
M.cowani {5}	0.000	0.000	0.000	0.000		0.987	1.000	0.045	1.000
M. dobsoni {6}	0.000	0.000	0.000	0.000	0.987		0.976	0.002	0.995
M.talazaci {7}	0.000	0.002	0.004	0.000	1.000	0.976		0.640	1.000
Oryzorictes {8}	0.000	0.023	0.045	0.002	0.045	0.002	0.640		0.171
Limnogale {9}	0.000	0.000	0.000	0.000	1.000	0.995	1.000	0.171	

Appendix 4.4 (con't)

Taxon	ASI Means	ASI N	ASI Std.Dev.
Echinops	1.086	12	0.084
Setifer	1.090	10	0.076
Hemicentetes	1.050	17	0.079
Tenrec	1.085	8	0.071
M.cowani	0.945	9	0.077
M. dobsoni	0.917	10	0.076
M.talazaci	0.868	3	0.044
Oryzorictes	0.856	10	0.112
Limnogale	0.738	5	0.058
All Grps	0.988	84	0.132

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}
	M=1.0860	M=1.0898	M=1.0498	M=1.0853	M=.94501	M=.91710	M=.86751	M=.85635	M=.73764
Echinops {1}		1.000	0.958	1.000	0.006	0.000	0.003	0.000	0.000
Setifer {2}	1.000		0.946	1.000	0.007	0.000	0.003	0.000	0.000
Hemicentetes {3}	0.958	0.946		0.983	0.060	0.003	0.017	0.000	0.000
Tenrec {4}	1.000	1.000	0.983		0.018	0.001	0.005	0.000	0.000
M.cow ani {5}	0.006	0.007	0.060	0.018		0.998	0.883	0.315	0.001
M. dobsoni {6}	0.000	0.000	0.003	0.001	0.998		0.991	0.763	0.004
M.talazaci {7}	0.003	0.003	0.017	0.005	0.883	0.991		1.000	0.425
Oryzorictes {8}	0.000	0.000	0.000	0.000	0.315	0.763	1.000		0.179
Limnogale {9}	0.000	0.000	0.000	0.000	0.001	0.004	0.425	0.179	

Taxon	OFSI Means	OFSI N	OFSI Std.Dev.
Echinops	1.027	12	0.079
Setifer	1.035	11	0.056
Hemicentetes	1.147	17	0.155

Appendix 4.4 (con't)

Tenrec	1.036	8	0.068
M.cowani	0.626	9	0.050
M. dobsoni	0.684	10	0.055
M.talazaci	0.776	3	0.115
Oryzorictes	0.683	8	0.053
Limnogale	0.563	5	0.018
Geogale	0.736	6	0.075
Potamogale	0.388	3	0.043
Solenodon	0.740	10	0.071
Petrodromus	0.743	2	0.118
All Grps	0.856	104	0.230

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}
	M=1.0274	M=1.0347	M=1.1471	M=1.0356	M=.62600	M=.68426	M=.77567	M=.68260	M=.56304	M=.73582	M=.38843	M=.73981	M=.74315
Echinops {1}		1.000	0.027	1.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.004
Setifer {2}	1.000		0.065	1.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.003
Hemicentetes {3}	0.027	0.065		0.154	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tenrec {4}	1.000	1.000	0.154		0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.004
M.cowani {5}	0.000	0.000	0.000	0.000		0.964	0.350	0.981	0.986	0.471	0.006	0.210	0.886
M. dobsoni {6}	0.000	0.000	0.000	0.000	0.964		0.931	1.000	0.373	0.995	0.000	0.969	1.000
M.talazaci {7}	0.002	0.001	0.000	0.002	0.350	0.931		0.935	0.063	1.000	0.000	1.000	1.000
Oryzorictes {8}	0.000	0.000	0.000	0.000	0.981	1.000	0.935		0.460	0.996	0.000	0.975	1.000
Limnogale {9}	0.000	0.000	0.000	0.000	0.986	0.373	0.063	0.460		0.075	0.257	0.022	0.417
Geogale {10}	0.000	0.000	0.000	0.000	0.471	0.995	1.000	0.996	0.075		0.000	1.000	1.000
Potamogale {11}	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.257	0.000		0.000	0.002
Solenodon {12}	0.000	0.000	0.000	0.000	0.210	0.969	1.000	0.975	0.022	1.000	0.000		1.000
Petrodromus {13}	0.004	0.003	0.000	0.004	0.886	1.000	1.000	1.000	0.417	1.000	0.002	1.000	

Taxon	IDSL	IDSL	IDSL
	Means	N	Std.Dev.

Appendix 4.4 (con't)

Echinops	1.199	12	0.181
Setifer	1.129	11	0.107
Hemicentetes	0.919	17	0.126
Tenrec	0.775	8	0.083
All Grps	1.013	48	0.203

	{1}	{2}	{3}	{4}
	M=1.1990	M=1.1285	M=.91857	M=.77508
Echinops {1}		0.586	0.000	0.000
Setifer {2}	0.586		0.001	0.000
Hemicentetes {3}	0.000	0.001		0.071
Tenrec {4}	0.000	0.000	0.071	

Taxon	PFLI Means	PFLI N	PFLI Std.Dev.
Tenrecinae	1.046	40	0.051
Oryzorictinae	1.291	33	0.159
Geogalinae	1.001	4	0.035
Potamogalinae	1.210	3	0.088
other	1.322	12	0.152
All Grps	1.173	92	0.171

	{1}	{2}	{3}	{4}	{5}
	M=1.0462	M=1.2906	M=1.0013	M=1.2096	M=1.3218
Tenrecinae {1}		0.000	0.948	0.141	0.000
Oryzorictinae {2}	0.000		0.000	0.778	0.931
Geogalinae {3}	0.948	0.000		0.142	0.000
Potamogalinae {4}	0.141	0.778	0.142		0.570
other {5}	0.000	0.931	0.000	0.570	
Geogalinae {3}					

Appendix 4.4 (con't)

Taxon	FHSZI Means	FHSZI N	FHSZI Std.Dev.	
Echinops	2.765	10	0.327	
Setifer	2.437	20	0.199	
Hemicentetes	2.572	17	0.205	
Tenrec	2.447	8	0.195	
All Grps	2.540	55	0.253	
	{1}	{2}	{3}	{4}
	M=2.7651	M=2.4370	M=2.5716	M=2.4466
Echinops {1}		0.003	0.158	0.024
Setifer {2}	0.003		0.291	1.000
Hemicentetes {3}	0.158	0.291		0.581
Tenrec {4}	0.024	1.000	0.581	

Taxon	FHWI Means	FHWI N	FHWI Std.Dev.	
Echinops	1.015	10	0.054	
Setifer	1.098	17	0.076	
Hemicentetes	1.002	17	0.072	
Tenrec	0.990	8	0.100	
All Grps	1.034	52	0.086	
	{1}	{2}	{3}	{4}
	M=1.0151	M=1.0983	M=1.0024	M=.99031
Echinops {1}		0.037	0.974	0.898
Setifer {2}	0.037		0.003	0.008
Hemicentetes {3}	0.974	0.003		0.982
Tenrec {4}	0.898	0.008	0.982	

Appendix 4.4 (con't)

Taxon	FHDI Means	FHDI N	FHDI Std.Dev.
Echinops	0.864	10	0.152
Setifer	0.774	20	0.057
Hemicentetes	0.781	17	0.061
Tenrec	0.722	8	0.034
M.cowani	0.771	22	0.068
M.dobsoni	0.749	20	0.047
M.talazaci	0.735	3	0.021
Oryzorictes	0.749	33	0.068
Limnogale	0.636	5	0.048
All Grps	0.762	138	0.079

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}
	M=.86355	M=.77416	M=.78056	M=.72218	M=.77090	M=.74937	M=.73518	M=.74898	M=.63560
Echinops {1}		0.028	0.073	0.001	0.015	0.001	0.120	0.000	0.000
Setifer {2}	0.028		1.000	0.700	1.000	0.972	0.993	0.941	0.003
Hemicentetes {3}	0.073	1.000		0.584	1.000	0.916	0.983	0.851	0.002
Tenrec {4}	0.001	0.700	0.584		0.757	0.991	1.000	0.988	0.427
M.cowani {5}	0.015	1.000	1.000	0.757		0.986	0.996	0.969	0.003
M.dobsoni {6}	0.001	0.972	0.916	0.991	0.986		1.000	1.000	0.032
M.talazaci {7}	0.120	0.993	0.983	1.000	0.996	1.000		1.000	0.582
Oryzorictes {8}	0.000	0.941	0.851	0.988	0.969	1.000	1.000		0.021
Limnogale {9}	0.000	0.003	0.002	0.427	0.003	0.032	0.582	0.021	

Taxon	FNWI Means	FNWI N	FNWI Std.Dev.
Echinops	0.565	10	0.136
Setifer	0.668	17	0.142
Hemicentetes	0.603	17	0.127

Appendix 4.4 (con't)

Tenrec	0.750	8	0.603
M.cowani	1.705	21	0.451
M.dobsoni	1.088	20	0.246
M.talazaci	1.456	3	0.226
Oryzoricted	1.396	25	0.465
Limnogale	1.487	3	0.306
All Grps	1.085	124	0.540

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}
	M=.56526	M=.66845	M=.60315	M=.74988	M=1.7051	M=1.0878	M=1.4559	M=1.3960	M=1.4868
Echinops {1}		0.998	1.000	0.971	0.000	0.006	0.005	0.000	0.003
Setifer {2}	0.998		1.000	1.000	0.000	0.012	0.013	0.000	0.008
Hemicentetes {3}	1.000	1.000		0.987	0.000	0.002	0.005	0.000	0.003
Tenrec {4}	0.971	1.000	0.987		0.000	0.340	0.079	0.001	0.056
M.cowani {5}	0.000	0.000	0.000	0.000		0.000	0.963	0.078	0.984
M.dobsoni {6}	0.006	0.012	0.002	0.340	0.000		0.742	0.088	0.650
M.talazaci {7}	0.005	0.013	0.005	0.079	0.963	0.742		1.000	1.000
Oryzoricted {8}	0.000	0.000	0.000	0.001	0.078	0.088	1.000		1.000
Limnogale {9}	0.003	0.008	0.003	0.056	0.984	0.650	1.000	1.000	

Taxon	GTRHI Means	GTRHI N	GTRHI Std.Dev.
Echinops	0.170	10	0.067
Setifer	0.056	20	0.046
Hemicentetes	0.121	16	0.052
Tenrec	0.215	8	0.072

Appendix 4.4 (con't)

M.cowani	0.580	22	0.122
M.dobsoni	0.558	20	0.101
M.talazaci	0.464	3	0.163
Oryzorictes	0.373	32	0.081
Limnogale	0.346	5	0.134
Geogale	0.316	5	0.021
Potamogale	0.389	3	0.042
Solenodon	0.442	11	0.052
Petrodromus	1.065	2	0.104
Echinosorex	0.631	1	0.000
All Grps	0.353	158	0.217

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=.17040	M=.05553	M=.12078	M=.21496	M=.58031	M=.55784	M=.46415	M=.37330	M=.34553	M=.31604	M=.38890	M=.44211	M=1.0654	M=.63079
Echinops {1}		0.032	0.976	0.998	0.000	0.000	0.000	0.000	0.012	0.096	0.007	0.000	0.000	0.000
Setifer {2}	0.032		0.560	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Hemicentetes {3}	0.976	0.560		0.365	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000
Tenrec {4}	0.998	0.001	0.365		0.000	0.000	0.001	0.000	0.279	0.709	0.128	0.000	0.000	0.000
M.cowani {5}	0.000	0.000	0.000	0.000		1.000	0.612	0.000	0.000	0.000	0.018	0.001	0.000	1.000
M.dobsoni {6}	0.000	0.000	0.000	0.000	1.000		0.884	0.000	0.000	0.000	0.076	0.020	0.000	1.000
M.talazaci {7}	0.000	0.000	0.000	0.001	0.612	0.884		0.888	0.819	0.488	0.998	1.000	0.000	0.916
Oryzorictes {8}	0.000	0.000	0.000	0.000	0.000	0.000	0.888		1.000	0.982	1.000	0.540	0.000	0.142
Limnogale {9}	0.012	0.000	0.000	0.279	0.000	0.000	0.819	1.000		1.000	1.000	0.695	0.000	0.115
Geogale {10}	0.096	0.000	0.001	0.709	0.000	0.000	0.488	0.982	1.000		0.996	0.248	0.000	0.045
Potamogale {11}	0.007	0.000	0.000	0.128	0.018	0.076	0.998	1.000	1.000	0.996		1.000	0.000	0.430
Solenodon {12}	0.000	0.000	0.000	0.000	0.001	0.020	1.000	0.540	0.695	0.248	1.000		0.000	0.681
Petrodromus {13}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.002
Echinosorex {14}	0.000	0.000	0.000	0.000	1.000	1.000	0.916	0.142	0.115	0.045	0.430	0.681	0.002	

Appendix 4.4 (con't)

Taxon	LTRSI	LTRSI	LTRSI
	Means	N	Std.Dev.
Echinops	0.644	12	0.141
Setifer	0.510	20	0.103
Hemicentetes	0.507	16	0.111
Tenrec	0.453	8	0.051
All Grps	0.530	56	0.124

	{1}	{2}	{3}	{4}
	M=.64358	M=.51027	M=.50719	M=.45265
Echinops {1}		0.008	0.010	0.002
Setifer {2}	0.008		1.000	0.593
Hemicentetes {3}	0.010	1.000		0.660
Tenrec {4}	0.002	0.593	0.660	

Taxon	LTRPI	LTRPI	LTRPI
	Means	N	Std.Dev.
Echinops	0.179	12	0.016
Setifer	0.169	20	0.009
Hemicentetes	0.205	16	0.042
Tenrec	0.185	8	0.009
M.cowani	0.134	21	0.009
M.dobsoni	0.145	20	0.013
M.talazaci	0.152	3	0.009
Oryzorictes	0.150	32	0.018
Limnogale	0.200	5	0.005
Geogale	0.130	5	0.013
Potamogale	0.150	3	0.021
Solenodon	0.185	11	0.009
Petrodromus	0.076	2	0.010

Appendix 4.4 (con't)

Echinosorex	0.166	1	0.000
All Grps	0.162	159	0.031

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=.17947	M=.16937	M=.20544	M=.18456	M=.13407	M=.14465	M=.15204	M=.14979	M=.19952	M=.13005	M=.15009	M=.18549	M=.07572	M=.16581
Echinops {1}		0.968	0.016	1.000	0.000	0.000	0.551	0.000	0.740	0.000	0.429	1.000	0.000	1.000
Setifer {2}	0.968		0.000	0.787	0.000	0.002	0.965	0.014	0.064	0.002	0.920	0.533	0.000	1.000
Hemicentetes {3}	0.016	0.000		0.330	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.243	0.000	0.711
Tenrec {4}	1.000	0.787	0.330		0.000	0.000	0.336	0.000	0.979	0.000	0.244	1.000	0.000	1.000
M.cowani {5}	0.000	0.000	0.000	0.000		0.859	0.952	0.125	0.000	1.000	0.981	0.000	0.002	0.922
M.dobsoni {6}	0.000	0.002	0.000	0.000	0.859		1.000	0.999	0.000	0.951	1.000	0.000	0.000	0.998
M.talazaci {7}	0.551	0.965	0.000	0.336	0.952	1.000		1.000	0.028	0.937	1.000	0.232	0.000	1.000
Oryzorictes {8}	0.000	0.014	0.000	0.000	0.125	0.999	1.000		0.000	0.609	1.000	0.000	0.000	1.000
Limnogale {9}	0.740	0.064	1.000	0.979	0.000	0.000	0.028	0.000		0.000	0.017	0.981	0.000	0.927
Geogale {10}	0.000	0.002	0.000	0.000	1.000	0.951	0.937	0.609	0.000		0.970	0.000	0.029	0.889
Potamogale {11}	0.429	0.920	0.000	0.244	0.981	1.000	1.000	1.000	0.017	0.970		0.157	0.001	1.000
Solenodon {12}	1.000	0.533	0.243	1.000	0.000	0.000	0.232	0.000	0.981	0.000	0.157		0.000	0.999
Petrodromus {13}	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.029	0.001	0.000		0.005
Echinosorex {14}	1.000	1.000	0.711	1.000	0.922	0.998	1.000	1.000	0.927	0.889	1.000	0.999	0.005	

Taxon	TTRSI Means	TTRSI N	TTRSI Std.Dev.
Tenrecine	0.195	57	0.086
Oryzorictine	0.368	82	0.096
All Grps	0.297	139	0.126

	{1}	{2}
	M=.19490	M=.36834
Tenrecine {1}		0.000
Oryzorictine {2}	0.000	

Appendix 4.4 (con't)

Taxon	TTRPI Means	TTRPI N	TTRPI Std.Dev.											
Echinops	2.662	12	0.387											
Setifer	2.520	20	0.216											
Hemicentetes	2.481	16	0.286											
Tenrec	2.894	8	0.216											
M.cowani	2.238	21	0.195											
M.dobsoni	2.700	20	0.207											
M.talazaci	2.751	3	0.217											
Oryzorictes	2.010	32	0.406											
Limnogale	2.284	5	0.066											
Geogale	2.817	5	0.334											
Potamogale	1.295	3	0.091											
Solenodon	2.229	11	0.181											
Petrodromus	6.200	2	0.349											
Echinosorex	2.408	1	0.000											
All Grps	2.437	159	0.596											
	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=2.6616	M=2.5198	M=2.4814	M=2.8939	M=2.2377	M=2.6999	M=2.7513	M=2.0103	M=2.2836	M=2.8174	M=1.2954	M=2.2292	M=6.1999	M=2.4076
Echinops {1}		0.986	0.931	0.883	0.003	1.000	1.000	0.000	0.414	0.999	0.000	0.020	0.000	1.000
Setifer {2}	0.986		1.000	0.095	0.087	0.769	0.990	0.000	0.931	0.710	0.000	0.270	0.000	1.000
Hemicentetes {3}	0.931	1.000		0.052	0.355	0.566	0.967	0.000	0.987	0.555	0.000	0.586	0.000	1.000
Tenrec {4}	0.883	0.095	0.052		0.000	0.940	1.000	0.000	0.013	1.000	0.000	0.000	0.000	0.945
M.cowani {5}	0.003	0.087	0.355	0.000		0.000	0.169	0.205	1.000	0.003	0.000	1.000	0.000	1.000
M.dobsoni {6}	1.000	0.769	0.566	0.940	0.000		1.000	0.000	0.169	1.000	0.000	0.001	0.000	0.999
M.talazaci {7}	1.000	0.990	0.967	1.000	0.169	1.000		0.001	0.595	1.000	0.000	0.218	0.000	0.999
Oryzorictes {8}	0.000	0.000	0.000	0.000	0.205	0.000	0.001		0.772	0.000	0.003	0.632	0.000	0.985
Limnogale {9}	0.414	0.931	0.987	0.013	1.000	0.169	0.595	0.772		0.153	0.000	1.000	0.000	1.000
Geogale {10}	0.999	0.710	0.555	1.000	0.003	1.000	1.000	0.000	0.153		0.000	0.010	0.000	0.990
Potamogale {11}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000		0.000	0.000	0.046
Solenodon {12}	0.020	0.270	0.586	0.000	1.000	0.001	0.218	0.632	1.000	0.010	0.000		0.000	1.000

Appendix 4.4 (con't)

Petrodromus {13}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Echinosorex {14}	1.000	1.000	1.000	0.945	1.000	0.999	0.999	0.985	1.000	0.990	0.046	1.000	0.000

Taxon	PGWI Means	PGWI N	PGWI Std.Dev.
Echinops	0.467	12	0.037
Setifer	0.469	19	0.043
Hemicentetes	0.448	14	0.042
Tenrec	0.460	8	0.050
M.cowani	0.368	21	0.041
M.dobsoni	0.382	20	0.054
M.talazaci	0.378	3	0.028
Oryzorictes	0.524	32	0.081
Limnogale	0.381	5	0.038
Geogale	0.410	5	0.051
Potamogale	0.366	3	0.038
Solenodon	0.511	11	0.027
Petrodromus	0.351	2	0.030
Echinosorex	0.478	1	0.000
All Grps	0.446	156	0.079

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=.46709	M=.46948	M=.44820	M=.46005	M=.36817	M=.38155	M=.37843	M=.52390	M=.38138	M=.41031	M=.36637	M=.51140	M=.35072	M=.47754
Echinops {1}		1.000	1.000	1.000	0.000	0.001	0.365	0.097	0.136	0.774	0.173	0.780	0.203	1.000
Setifer {2}	1.000		0.998	1.000	0.000	0.000	0.259	0.031	0.065	0.632	0.107	0.726	0.145	1.000
Hemicentetes {3}	1.000	0.998		1.000	0.001	0.025	0.738	0.001	0.485	0.986	0.480	0.166	0.476	1.000
Tenrec {4}	1.000	1.000	1.000		0.003	0.031	0.593	0.133	0.357	0.939	0.352	0.728	0.353	1.000
M.cowani {5}	0.000	0.000	0.001	0.003		1.000	1.000	0.000	1.000	0.951	1.000	0.000	1.000	0.772
M.dobsoni {6}	0.001	0.000	0.025	0.031	1.000		1.000	0.000	1.000	0.999	1.000	0.000	1.000	0.899
M.talazaci {7}	0.365	0.259	0.738	0.593	1.000	1.000		0.001	1.000	1.000	1.000	0.010	1.000	0.946
Oryzorictes {8}	0.097	0.031	0.001	0.133	0.000	0.000	0.001		0.000	0.001	0.000	1.000	0.001	1.000

Appendix 4.4 (con't)

Limnogale {9}	0.136	0.065	0.485	0.357	1.000	1.000	1.000	0.000		1.000	1.000	0.001	1.000	0.936
Geogale {10}	0.774	0.632	0.986	0.939	0.951	0.999	1.000	0.001	1.000		0.998	0.031	0.989	0.997
Potamogale {11}	0.173	0.107	0.480	0.352	1.000	1.000	1.000	0.000	1.000	0.998		0.003	1.000	0.878
Solenodon {12}	0.780	0.726	0.166	0.728	0.000	0.000	0.010	1.000	0.001	0.031	0.003		0.007	1.000
Petrodromus {13}	0.203	0.145	0.476	0.353	1.000	1.000	1.000	0.001	1.000	0.989	1.000	0.007		0.809
Echinosorex {14}	1.000	1.000	1.000	1.000	0.772	0.899	0.946	1.000	0.936	0.997	0.878	1.000	0.809	

Taxon	DFWI	DFWI	DFWI
Echinops	2.291	12	0.243
Setifer	2.185	20	0.190
Hemicentetes	2.436	16	0.155
Tenrec	2.194	8	0.164
All Grps	2.281	56	0.214

	{1}	{2}	{3}	{4}
	M=2.2906	M=2.1848	M=2.4364	M=2.1942
Echinops {1}		0.431	0.198	0.685
Setifer {2}	0.431		0.001	0.999
Hemicentetes {3}	0.198	0.001		0.024
Tenrec {4}	0.685	0.999	0.024	

Taxon	PGSI	PGSI	PGSI
	Means	N	Std.Dev.
Echinops	1.013	12	0.173
Setifer	0.982	19	0.082
Hemicentetes	0.878	14	0.121
Tenrec	1.015	8	0.125
M.cowani	1.575	21	0.238
M.dobsoni	1.559	20	0.212

Appendix 4.4 (con't)

M.talazaci	1.609	3	0.170
Oryzorictes	1.050	32	0.338
Limnogale	0.998	5	0.091
Geogale	1.234	5	0.229
Potamogale	1.257	3	0.061
Solenodon	0.876	11	0.078
Petrodromus	1.801	2	0.364
Echinosorex	1.349	1	0.000
All Grps	1.176	156	0.347

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=1.0126	M=.98162	M=.87790	M=1.0146	M=1.5755	M=1.5585	M=1.6094	M=1.0496	M=.99844	M=1.2345	M=1.2570	M=.87628	M=1.8011	M=1.3489
Echinops {1}		1.000	0.955	1.000	0.000	0.000	0.002	1.000	1.000	0.823	0.904	0.969	0.000	0.972
Setifer {2}	1.000		0.987	1.000	0.000	0.000	0.000	0.999	1.000	0.554	0.750	0.993	0.000	0.936
Hemicentetes {3}	0.955	0.987		0.981	0.000	0.000	0.000	0.443	0.999	0.097	0.263	1.000	0.000	0.714
Tenrec {4}	1.000	1.000	0.981		0.000	0.000	0.005	1.000	1.000	0.892	0.936	0.986	0.000	0.977
M.cowani {5}	0.000	0.000	0.000	0.000		1.000	1.000	0.000	0.000	0.096	0.509	0.000	0.983	0.999
M.dobsoni {6}	0.000	0.000	0.000	0.000	1.000		1.000	0.000	0.000	0.151	0.609	0.000	0.969	1.000
M.talazaci {7}	0.002	0.000	0.000	0.005	1.000	1.000		0.002	0.010	0.518	0.784	0.000	1.000	0.999
Oryzorictes {8}	1.000	0.999	0.443	1.000	0.000	0.000	0.002		1.000	0.894	0.953	0.579	0.000	0.987
Limnogale {9}	1.000	1.000	0.999	1.000	0.000	0.000	0.010	1.000		0.914	0.941	0.999	0.001	0.974
Geogale {10}	0.823	0.554	0.097	0.892	0.096	0.151	0.518	0.894	0.914		1.000	0.125	0.106	1.000
Potamogale {11}	0.904	0.750	0.263	0.936	0.509	0.609	0.784	0.953	0.941	1.000		0.293	0.263	1.000
Solenodon {12}	0.969	0.993	1.000	0.986	0.000	0.000	0.000	0.579	0.999	0.125	0.293		0.000	0.722
Petrodromus {13}	0.000	0.000	0.000	0.000	0.983	0.969	1.000	0.000	0.001	0.106	0.263	0.000		0.920
Echinosorex {14}	0.972	0.936	0.714	0.977	0.999	1.000	0.999	0.987	0.974	1.000	1.000	0.722	0.920	

Taxon	FCSI	FCSI	FCSI
	Means	N	Std.Dev.
Echinops	1.403	11	0.125
Setifer	1.346	17	0.067
Hemicentetes	1.297	14	0.095

Appendix 4.4 (con't)

Tenrec	1.331	8	0.119
M.cowani	1.558	18	0.081
M.dobsoni	1.492	18	0.144
M. talazaci	1.458	3	0.085
Oryzorictes	1.295	16	0.178
Limnogale	1.466	10	0.066
Geogale	1.373	4	0.118
Potamogale	1.476	3	0.098
Solenodon	1.358	9	0.077
Petrodromus	2.017	2	0.091
Echinosorex	1.612	1	0.000
All Grps	1.415	134	0.161

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=1.4031	M=1.3465	M=1.2971	M=1.3313	M=1.5580	M=1.4924	M=1.4583	M=1.2949	M=1.4663	M=1.3729	M=1.4760	M=1.3583	M=2.0171	M=1.6124
Echinops {1}		0.991	0.549	0.985	0.034	0.734	1.000	0.468	0.992	1.000	0.999	1.000	0.000	0.889
Setifer {2}	0.991		0.995	1.000	0.000	0.016	0.951	0.990	0.326	1.000	0.864	1.000	0.000	0.580
Hemicentetes {3}	0.549	0.995		1.000	0.000	0.000	0.611	1.000	0.031	0.996	0.438	0.992	0.000	0.306
Tenrec {4}	0.985	1.000	1.000		0.001	0.065	0.929	1.000	0.417	1.000	0.834	1.000	0.000	0.538
M.cowani {5}	0.034	0.000	0.000	0.001		0.902	0.980	0.000	0.739	0.176	0.997	0.003	0.000	1.000
M.dobsoni {6}	0.734	0.016	0.000	0.065	0.902		1.000	0.000	1.000	0.823	1.000	0.199	0.000	0.999
M. talazaci {7}	1.000	0.951	0.611	0.929	0.980	1.000		0.572	1.000	0.999	1.000	0.988	0.000	0.996
Oryzorictes {8}	0.468	0.990	1.000	1.000	0.000	0.000	0.572		0.019	0.994	0.399	0.987	0.000	0.289
Limnogale {9}	0.992	0.326	0.031	0.417	0.739	1.000	1.000	0.019		0.982	1.000	0.723	0.000	0.994
Geogale {10}	1.000	1.000	0.996	1.000	0.176	0.823	0.999	0.994	0.982		0.996	1.000	0.000	0.832
Potamogale {11}	0.999	0.864	0.438	0.834	0.997	1.000	1.000	0.399	1.000	0.996		0.955	0.000	0.999
Solenodon {12}	1.000	1.000	0.992	1.000	0.003	0.199	0.988	0.987	0.723	1.000	0.955		0.000	0.688
Petrodromus {13}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.192
Echinosorex {14}	0.889	0.580	0.306	0.538	1.000	0.999	0.996	0.289	0.994	0.832	0.999	0.688	0.192	

Appendix 4.4 (con't)

Taxon	FCDI Means	FCDI N	FCDI Std.Dev.
Echinops	2.194	12	0.244
Setifer	2.318	20	0.216
Hemicentetes	2.278	17	0.182
Tenrec	2.347	3	0.152
M.cowani	2.576	21	0.175
M.dobsoni	2.463	20	0.203
M.talazaci	2.347	3	0.152
Oryzorictes	2.010	31	0.153
Limnogale	2.383	5	0.145
Geogale	2.194	12	0.244
Potamogale	2.715	3	0.061
Solenodon	2.403	9	0.094
Petrodromus	2.687	2	0.047
Echinosorex	2.563	1	0.000
All Grps	2.309	159	0.265

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=2.1937	M=2.3180	M=2.2781	M=2.3471	M=2.5757	M=2.4630	M=2.3471	M=2.0101	M=2.3825	M=2.1937	M=2.7152	M=2.4025	M=2.6874	M=2.5632
Echinops {1}		0.867	0.996	0.993	0.000	0.006	0.993	0.183	0.829	1.000	0.001	0.386	0.036	0.828
Setifer {2}	0.867		1.000	1.000	0.001	0.443	1.000	0.000	1.000	0.867	0.039	0.998	0.301	0.992
Hemicentetes {3}	0.996	1.000		1.000	0.000	0.139	1.000	0.000	0.998	0.996	0.014	0.943	0.166	0.971
Tenrec {4}	0.993	1.000	1.000		0.781	0.999	1.000	0.145	1.000	0.993	0.473	1.000	0.773	0.999
M.cowani {5}	0.000	0.001	0.000	0.781		0.811	0.781	0.000	0.718	0.000	0.995	0.536	1.000	1.000
M.dobsoni {6}	0.006	0.443	0.139	0.999	0.811		0.999	0.000	1.000	0.006	0.646	1.000	0.942	1.000
M.talazaci {7}	0.993	1.000	1.000	1.000	0.781	0.999		0.145	1.000	0.993	0.473	1.000	0.773	0.999
Oryzorictes {8}	0.183	0.000	0.000	0.145	0.000	0.000	0.145		0.003	0.183	0.000	0.000	0.000	0.173
Limnogale {9}	0.829	1.000	0.998	1.000	0.718	1.000	1.000	0.003		0.829	0.454	1.000	0.800	1.000
Geogale {10}	1.000	0.867	0.996	0.993	0.000	0.006	0.993	0.183	0.829		0.001	0.386	0.036	0.828

Appendix 4.4 (con't)

Potamogale {11}	0.001	0.039	0.014	0.473	0.995	0.646	0.473	0.000	0.454	0.001		0.403	1.000	1.000
Solenodon {12}	0.386	0.998	0.943	1.000	0.536	1.000	1.000	0.000	1.000	0.386	0.403		0.800	1.000
Petrodromus {13}	0.036	0.301	0.166	0.773	1.000	0.942	0.773	0.000	0.800	0.036	1.000	0.800		1.000
Echinosorex {14}	0.828	0.992	0.971	0.999	1.000	1.000	0.999	0.173	1.000	0.828	1.000	1.000	1.000	

Taxon	MLFCI	MLFCI	MLFCI
	Means	N	Std.Dev.
Echinops	1.091	11	0.123
Setifer	1.086	18	0.085
Hemicentetes	1.138	15	0.105
Tenrec	1.150	8	0.074
M.cowani	1.053	20	0.085
M.dobsoni	1.115	18	0.284
M. talazaci	1.166	3	0.089
Oryzorictes	1.119	20	0.083
Limnogale	0.873	10	0.053
Geogale	0.865	4	0.040
Potamogale	1.090	3	0.163
Solenodon	1.172	9	0.076
Petrodromus	0.878	1	0.000
Echinosorex	1.358	1	0.000
All Grps	1.086	141	0.152

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=1.0915	M=1.0863	M=1.1384	M=1.1504	M=1.0527	M=1.1146	M=1.1658	M=1.1190	M=.87292	M=.86480	M=1.0904	M=1.1724	M=.87751	M=1.3580
Echinops {1}		1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.013	0.173	1.000	0.987	0.961	0.820
Setifer {2}	1.000		0.998	0.998	1.000	1.000	1.000	1.000	0.004	0.137	1.000	0.951	0.964	0.779
Hemicentetes {3}	1.000	0.998		1.000	0.837	1.000	1.000	1.000	0.000	0.019	1.000	1.000	0.830	0.948
Tenrec {4}	1.000	0.998	1.000		0.897	1.000	1.000	1.000	0.001	0.031	1.000	1.000	0.811	0.973
M.cowani {5}	1.000	1.000	0.837	0.897		0.979	0.985	0.953	0.033	0.359	1.000	0.604	0.992	0.605
M.dobsoni {6}	1.000	1.000	1.000	1.000	0.979		1.000	1.000	0.000	0.045	1.000	0.999	0.905	0.887
M. talazaci {7}	1.000	1.000	1.000	1.000	0.985	1.000		1.000	0.053	0.155	1.000	1.000	0.842	0.994

Appendix 4.4 (con't)

Oryzorictes {8}	1.000	1.000	1.000	1.000	0.953	1.000	1.000		0.000	0.033	1.000	0.999	0.891	0.899
Limnogale {9}	0.013	0.004	0.000	0.001	0.033	0.000	0.053	0.000		1.000	0.425	0.000	1.000	0.035
Geogale {10}	0.173	0.137	0.019	0.031	0.359	0.045	0.155	0.033	1.000		0.619	0.009	1.000	0.058
Potamogale {11}	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.425	0.619		1.000	0.984	0.903
Solenodon {12}	0.987	0.951	1.000	1.000	0.604	0.999	1.000	0.999	0.000	0.009	1.000		0.704	0.989
Petrodromus {13}	0.961	0.964	0.830	0.811	0.992	0.905	0.842	0.891	1.000	1.000	0.984	0.704		0.375
Echinosorex {14}	0.820	0.779	0.948	0.973	0.605	0.887	0.994	0.899	0.035	0.058	0.903	0.989	0.375	

Taxon	TTSI2 Means	TTSI2 N	TTSI2 Std.Dev.
Echinops	0.263	2	0.003
Setifer	0.332	6	0.060
Hemicentetes	0.487	12	0.107
Tenrec	0.534	9	0.208
M.cowani	0.537	13	0.055
M.dobsoni	0.724	14	0.143
M. talazaci	0.647	6	0.092
Oryzorictes	0.735	6	0.082
Limnogale	0.368	1	0.000
Geogale	0.464	1	0.000
Solenodon	0.761	3	0.138
Petrodromus	0.732	1	0.000
All Grps	0.573	74	0.176

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}
	M=.26256	M=.33240	M=.48653	M=.53388	M=.53731	M=.72425	M=.64724	M=.73490	M=.36798	M=.46356	M=.76131	M=.73158
Echinops {1}		1.000	0.407	0.178	0.137	0.000	0.012	0.001	1.000	0.967	0.002	0.090
Setifer {2}	1.000		0.332	0.092	0.046	0.000	0.002	0.000	1.000	0.997	0.000	0.118
Hemicentetes {3}	0.407	0.332		0.999	0.996	0.000	0.273	0.006	0.998	1.000	0.036	0.726
Tenrec {4}	0.178	0.092	0.999		1.000	0.023	0.824	0.093	0.976	1.000	0.198	0.920

Appendix 4.4 (con't)

M.cowani {5}	0.137	0.046	0.996	1.000		0.008	0.789	0.063	0.969	1.000	0.170	0.921
M.dobsoni {6}	0.000	0.000	0.000	0.023	0.008		0.976	1.000	0.188	0.637	1.000	1.000
M. talazaci {7}	0.012	0.002	0.273	0.824	0.789	0.976		0.982	0.600	0.958	0.971	1.000
Oryzorictes {8}	0.001	0.000	0.006	0.093	0.063	1.000	0.982		0.203	0.641	1.000	1.000
Limnogale {9}	1.000	1.000	0.998	0.976	0.969	0.188	0.600	0.203		1.000	0.199	0.608
Geogale {10}	0.967	0.997	1.000	1.000	1.000	0.637	0.958	0.641	1.000		0.604	0.915
Solenodon {11}	0.002	0.000	0.036	0.198	0.170	1.000	0.971	1.000	0.199	0.604		1.000
Petrodromus {12}	0.090	0.118	0.726	0.920	0.921	1.000	1.000	1.000	0.608	0.915	1.000	

Taxon	MLTCI Means	MLTCI N	MLTCI Std.Dev.
Echinops	1.099	2	0.144
Setifer	0.951	6	0.075
Hemicentetes	0.935	12	0.086
Tenrec	0.853	9	0.066
M.cowani	0.952	11	0.117
M.dobsoni	1.008	14	0.110
M. talazaci	0.942	6	0.088
Oryzorictes	1.007	6	0.126
Limnogale	0.895	1	0.000
Geogale	0.704	1	0.000
Solenodon	1.028	3	0.171
Petrodromus	0.879	1	0.000
All Grps	0.954	72	0.114

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}
	M=1.0987	M=.95132	M=.93463	M=.85348	M=.95208	M=1.0084	M=.94248	M=1.0074	M=.89483	M=.70360	M=1.0277	M=.87948
Echinops {1}		0.837	0.636	0.122	0.784	0.990	0.781	0.994	0.897	0.100	1.000	0.844
Setifer {2}	0.837		1.000	0.812	1.000	0.992	1.000	0.998	1.000	0.540	0.996	1.000
Hemicentetes {3}	0.636	1.000		0.820	1.000	0.801	1.000	0.957	1.000	0.589	0.960	1.000

Appendix 4.4 (con't)

Tenrec {4}	0.122	0.812	0.820		0.606	0.037	0.888	0.194	1.000	0.963	0.340	1.000
M.cowani {5}	0.784	1.000	1.000	0.606		0.967	1.000	0.995	1.000	0.484	0.992	1.000
M.dobsoni {6}	0.990	0.992	0.801	0.037	0.967		0.975	1.000	0.995	0.184	1.000	0.986
M. talazaci {7}	0.781	1.000	1.000	0.888	1.000	0.975		0.994	1.000	0.594	0.990	1.000
Oryzorictes {8}	0.994	0.998	0.957	0.194	0.995	1.000	0.994		0.997	0.239	1.000	0.991
Limnogale {9}	0.897	1.000	1.000	1.000	1.000	0.995	1.000	0.997		0.974	0.993	1.000
Geogale {10}	0.100	0.540	0.589	0.963	0.484	0.184	0.594	0.239	0.974		0.242	0.987
Solenodon {11}	1.000	0.996	0.960	0.340	0.992	1.000	0.990	1.000	0.993	0.242		0.983
Petrodromus {12}	0.844	1.000	1.000	1.000	1.000	0.986	1.000	0.991	1.000	0.987	0.983	

Taxon	TSI	TSI	TSI
	Means	N	Std.Dev.
Echinops	12.489	19	1.923
Setifer	14.349	16	1.145
Hemicentetes	15.171	18	1.784
Tenrec	15.326	11	1.558
M.cowani	18.946	13	1.312
M. dobsoni	22.765	8	1.208
M.talazaci	22.279	7	1.242
Oryzorictes	14.192	9	1.342
Limnogale	17.132	1	0.000
Geogale	20.430	2	1.614
Potamogale	15.676	5	1.531
Solenodon	15.888	10	1.252
Petrodromus	24.651	7	0.764
Echinosorex	14.234	1	0.000
All Grps	16.556	127	3.839

Appendix 4.4 (con't)

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=12.489	M=14.349	M=15.171	M=15.326	M=18.946	M=22.765	M=22.279	M=14.192	M=17.132	M=20.430	M=15.676	M=15.888	M=24.651	M=14.234
Echinops {1}		0.022	0.000	0.000	0.000	0.000	0.000	0.222	0.136	0.000	0.003	0.000	0.000	0.997
Setifer {2}	0.022		0.940	0.919	0.000	0.000	0.000	1.000	0.863	0.000	0.895	0.370	0.000	1.000
Hemicentetes {3}	0.000	0.940		1.000	0.000	0.000	0.000	0.938	0.991	0.001	1.000	0.994	0.000	1.000
Tenrec {4}	0.000	0.919	1.000		0.000	0.000	0.000	0.912	0.996	0.002	1.000	1.000	0.000	1.000
M.cowani {5}	0.000	0.000	0.000	0.000		0.000	0.001	0.000	0.996	0.988	0.004	0.000	0.000	0.133
M. dobsoni {6}	0.000	0.000	0.000	0.000	0.000		1.000	0.000	0.032	0.770	0.000	0.000	0.447	0.000
M.talazaci {7}	0.000	0.000	0.000	0.000	0.001	1.000		0.000	0.083	0.954	0.000	0.000	0.157	0.000
Oryzorictes {8}	0.222	1.000	0.938	0.912	0.000	0.000	0.000		0.833	0.000	0.875	0.426	0.000	1.000
Limnogale {9}	0.136	0.863	0.991	0.996	0.996	0.032	0.083	0.833		0.865	1.000	1.000	0.001	0.982
Geogale {10}	0.000	0.000	0.001	0.002	0.988	0.770	0.954	0.000	0.865		0.014	0.010	0.035	0.053
Potamogale {11}	0.003	0.895	1.000	1.000	0.004	0.000	0.000	0.875	1.000	0.014		1.000	0.000	1.000
Solenodon {12}	0.000	0.370	0.994	1.000	0.000	0.000	0.000	0.426	1.000	0.010	1.000		0.000	0.999
Petrodromus {13}	0.000	0.000	0.000	0.000	0.000	0.447	0.157	0.000	0.001	0.035	0.000	0.000		0.000
Echinosorex {14}	0.997	1.000	1.000	1.000	0.133	0.000	0.000	1.000	0.982	0.053	1.000	0.999	0.000	
Taxon	FTLI	FTLI	FTLI											
	Means	N	Std.Dev.											
Echinops	0.801	12	0.061											
Setifer	0.667	15	0.053											
Hemicentetes	0.601	13	0.069											
Tenrec	0.626	7	0.048											
M.cowani	0.581	13	0.043											
M.dobsoni	0.493	8	0.032											
M.talazaci	0.498	3	0.009											
Oryzorictes	0.577	9	0.066											
Limnogale	0.427	1	0.000											
Geogale	0.554	1	0.000											
Potamogale	0.562	2	0.115											
Solenodon	0.537	10	0.030											
Petrodromus	0.453	1	0.000											

Appendix 4.4 (con't)

Echinosorex	0.655	1	0.000
All Grps	0.610	96	0.103

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=.80096	M=.66738	M=.60110	M=.62572	M=.58120	M=.49289	M=.49753	M=.57654	M=.42711	M=.55406	M=.56198	M=.53671	M=.45262	M=.65493
Echinops {1}		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.345
Setifer {2}	0.000		0.084	0.910	0.004	0.000	0.000	0.009	0.003	0.733	0.348	0.000	0.014	1.000
Hemicentetes {3}	0.000	0.084		0.999	1.000	0.002	0.153	0.999	0.118	1.000	0.999	0.218	0.314	0.999
Tenrec {4}	0.000	0.910	0.999		0.882	0.001	0.049	0.860	0.048	0.992	0.967	0.063	0.152	1.000
M.cowani {5}	0.000	0.004	1.000	0.882		0.027	0.463	1.000	0.260	1.000	1.000	0.778	0.551	0.987
M.dobsoni {6}	0.000	0.000	0.002	0.001	0.027		1.000	0.096	0.996	0.998	0.932	0.901	1.000	0.221
M.talazaci {7}	0.000	0.000	0.153	0.049	0.463	1.000		0.622	0.997	1.000	0.988	0.998	1.000	0.392
Oryzorictes {8}	0.000	0.009	0.999	0.860	1.000	0.096	0.622		0.329	1.000	1.000	0.936	0.634	0.981
Limnogale {9}	0.000	0.003	0.118	0.048	0.260	0.996	0.997	0.329		0.918	0.728	0.792	1.000	0.157
Geogale {10}	0.002	0.733	1.000	0.992	1.000	0.998	1.000	1.000	0.918		1.000	1.000	0.986	0.987
Potamogale {11}	0.000	0.348	0.999	0.967	1.000	0.932	0.988	1.000	0.728	1.000		1.000	0.921	0.977
Solenodon {12}	0.000	0.000	0.218	0.063	0.778	0.901	0.998	0.936	0.792	1.000	1.000		0.965	0.696
Petrodromus {13}	0.000	0.014	0.314	0.152	0.551	1.000	1.000	0.634	1.000	0.986	0.921	0.965		0.315
Echinosorex {14}	0.345	1.000	0.999	1.000	0.987	0.221	0.392	0.981	0.157	0.987	0.977	0.696	0.315	

CHAPTER V

EVOLUTIONARY MORPHOLOGY OF THE TENRECOIDEA FORELIMB

Introduction

Functional morphology of the mammalian forelimb skeleton and the details of its joints have been explored and discussed in great depth relative to other postcranial regions, despite potential difficulties with interpretative morphology of this region. The mammalian forelimb performs a variety of biological roles, including postural, locomotor, feeding, exploratory, grooming, and defense related behaviors. Detailed morphology might therefore reflect several overlapping functions and compromises between various demands. Much work has focused on primates, with a particular interest in climbing and rotational mechanics of the shoulder and elbow (e.g., Roberts, 1974; Roberts and Davidson, 1975; Fleagle and Simons, 1982; Rose, 1988; Rose, 1989; Harrison, 1989; Ciochon, 1993; Gebo and Sargis, 1994;). Function-based analyses of mammalian diggers such as geomyids and vermilinguans focus on aspects of the shoulder, elbow, and wrist that correlate with digging and movement of soil (e.g., Campbell, 1939; Reed, 1951; Yalden, 1966; Taylor, 1978, 1985; Rose and Emry, 1983; Szalay and Schrenk, 1998; Stein, 2000). Study of proportional differences and details of the shoulder and elbow joints in cursorial mammals has identified a suite of characteristics associated with lengthening the stride and securing joints along the parasagittal plane for high-speed locomotion (e.g., Hopwood, 1945; Smith and Savage, 1956; Taylor, 1974; Hildebrand, 1995). There has been less published work on functional

morphology in aquatic mammals (though see Osburn 1903; Howell, 1970; Smith and Savage, 1956; Kerbis Peterhans and Patterson, 1995). This chapter is a comparative morphological study of the tenrecoid scapula, humerus, ulna, and radius, with particular emphasis on the shoulder and elbow joints. I address the following questions:

- 1) Do aspects of the tenrecoid forelimb exhibit intergeneric variation that correlate with expected differences based on positional behavior in other mammalian locomotor specialists?
- 2) Do taxon-specific features of the tenrecoid forelimb suggest phylogenetic affiliation between tenrecoid subfamilies, such as those found in the hindlimb?
- 3) Do *Solenodon*, *Petrodromus*, and/or *Echinosorex* share characteristics of the forelimb with tenrecoids that might be phylogenetically meaningful?

General Form and Variation of the Mammalian Scapula and Forelimb

Studies on mammalian forelimb form and function focus on a series of general skeletal characteristics that demonstrate considerable variability among taxa. The study of highly variable aspects of form can result in differences in interpretations of what a particular aspect of form is, i.e. where it begins and ends, in addition to how it is defined. I therefore briefly define and discuss the particular characters of form that are often identified and described in the literature discussed here, and illustrate some aspects of their variability (for this section, refer to Table 5.1 for proposed locomotor correlates of form). In the Results/Discussion section I further address functional and phylogenetic interpretation of these characters and their finer aspects in relation to taxon differences.

Overall scapular shape varies considerably. At one end of the spectrum of form there is a triangular scapula, as in humans, with a expanded vertebral (medial) border, and the humeral articular surface at the apex. This is generally an effect of a relatively

small supraspinous fossa and expanded infraspinous fossa. At the other end of the spectrum is a more rectangular form, usually the correlate of a more moderate vertebral border, a broader axillary (lateral) border towards the glenoid fossa, and a broader supraspinous fossa with a steeply inclined cranial (superior) border towards the glenoid fossa (Fig. 5.1; see Argot, 2001, for scapular morphotypes in metatherians). Differences in form are attributed to various muscular attachments that protract, retract and rotate the scapula and humerus, stabilize the shoulder joint, and anchor the scapula itself, yet there are also differences in the position of the scapula against the lateral ribcage resulting in various muscle mass distributions. Scapular position is difficult to determine on a disarticulated skeleton, although it is undoubtedly strongly correlated with differences in scapular shape.

The scapular spine denotes the border between the supraspinous fossa and infraspinous fossa and the Mm. supraspinatus and infraspinatus. Some taxa develop a secondary spine, posterior and ventral to the primary spine, which is associated with an expanded teres major and scapular head of the triceps (Taylor, 1978, Rose and Emry, 1983). A secondary spine located superior to the primary scapular spine, within the space of the supraspinous fossa might be associated with an expanded M. rhomboideus or a laterally expanding M. subscapularis.

The acromion process of the scapular spine, when present as a process, is highly variable and can reach well beyond the humeral articulation (Fig. 5.1). A metacromion process may or may not be present, hanging caudally from the acromion and extending back along the scapular spine. Development, presence, and absence of the acromion and metacromion are associated with protraction and lateral rotation of the humerus, as well

as scapular stabilization. The coracoid is another highly variable feature of the scapula, and, when present, can extend proximally/ventrally and laterally to differing degrees. Its relative length is correlated with the M. coracobrachialis and associated with humeral adduction (Stein, 2000; Argot, 2001; Sargis, 2002). Finally, the shape and size of the glenoid fossa varies amongst mammalian locomotor specialists, presumably in correlation with a shoulder joint that facilitates multiaxial rotation vs. one that restricts movement to a particular plane (Fig 1).

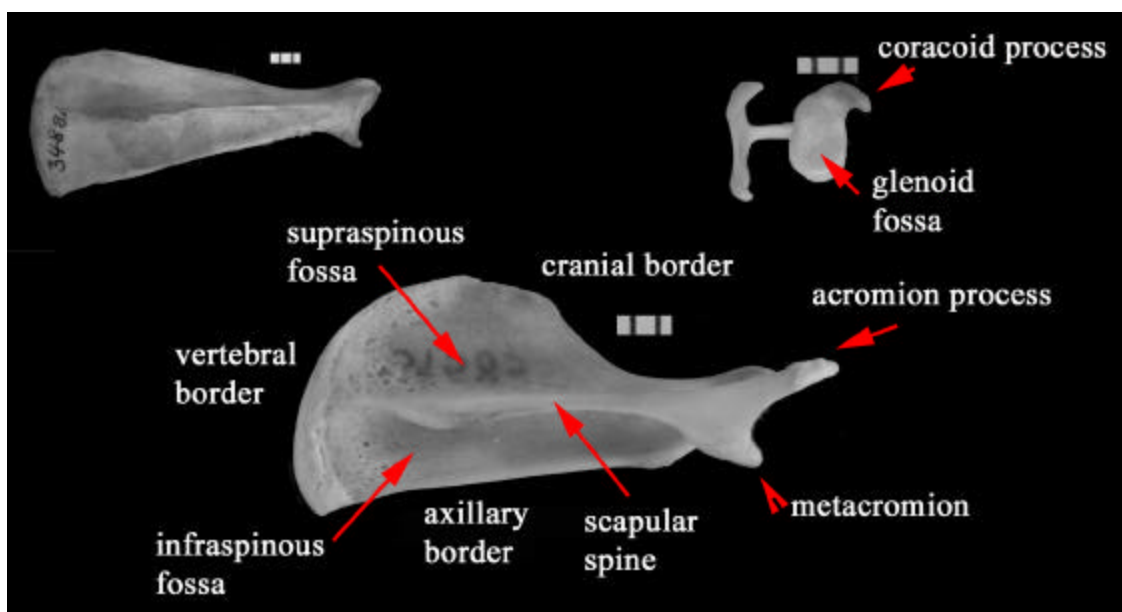


Figure 5.1. Right scapulae of *Potamogale* and *Echinops*. Top left is lateral view of *Potamogale*, demonstrating a greatly attenuated triangular form and no articular processes. Middle is lateral view of *Echinops*, which is more rectangular, somewhat circular cranially, with distinct acromion, metacromion, and coracoid processes. Top right is articular surface of scapula of same *Echinops* specimen.

Relative length and width of the humerus vary dramatically, from the relatively slender, elongated humerus of a brachiating primate (e.g., *Hylobates*) to a short and robust block-like humerus of a chrysochlorid mole (Fig. 5.2). Relative differences in length and width are generally ascribed to differences in functional mechanics of the musculoskeletal lever system; a relatively short humerus provides increased force of the muscles originating on the scapula, and a longer humerus provides a longer stride for

high-speed motion (at the expense of power). Yet the more distal forelimb bones also need to be considered relative to the humerus to interpret mechanical output. For example in high-speed cursors, lengthened and narrow limbs are expected for long-strides with minimal resistance. Yet the humerus is often short and somewhat robust and the distal elements of the limb are long and thin because muscle mass of the limb is concentrated at the shoulder and proximal arm with long elastic tendons extending to the distal elements (see Hildebrand, 1995).

Shape and relative size of the humeral head varies with differences in rotational facilitation of the glenohumeral joint, yet characteristics of the head do not reliably or necessarily intuitively correlate with features of the glenoid fossa (see Taylor, 1974). The greater tuberosity, attachment site for the humeral retractor *M. infraspinatus* and protractor *M. supraspinatus*, is generally interpreted in terms of its robusticity and proximodistal height above or below the humeral head. The lesser tuberosity is the primary attachment site for *M. subscapularis*, a humeral rotator and adductor, and is also discussed in terms of its length and robusticity. The position of the greater and lesser tubercles might also be of functional relevance; more anteriorly positioned tubercles result in increased, uninterrupted surface area along the proximal surface of the humeral head, and may be related to rotational facilitation (Fig. 5.2). The bicipital groove (or tunnel in some cases), positioned anteriorly between the two tubercles, carries the tendon for the *M. biceps brachii* and its development might be correlated with powerful forelimb flexion (Fig. 5.2).

Muscles associated with the deltoids and pectorals attach at several sites along the anterior and lateral humerus, and are usually associated with characters designated as the

deltopectoral crest (ridge, process or eminence), deltoid tubercle (tuberosity), and/or pectoral process (Fig. 5.2). Many mammalian taxa have a deltopectoral crest running down the anterior third of the humerus with a deltoid tubercle towards the distal end of the crest, as in *Didelphis* (Taylor, 1978). In some forms, the deltoid musculature inserts on the lateral edge of the humerus where a deltoid tubercle is formed and the pectorals attach on the anterior surface, in which case the ridge is referred to as a pectoral ridge (e.g., in tamanduas, Taylor, 1978; Szalay and Schrenk, 1998). The deltoids often act as lateral rotators and abductors of the humerus whereas the pectorals adduct and retract the humerus (Larson, 1993; Argot, 2001).

At the distal end of the humerus, the coronoid (ulnar) fossa marks the point at which the coronoid process of the ulna (ulnar distal trochlear crest of the semilunar or trochlear notch) rests when the forearm is completely flexed. When the forearm is extended, the ulnar proximal trochlear crest (olecranon beak) inserts into the olecranon fossa of the humerus. A deep and/or perforated coronoid/olecranon fossa is generally attributed to more extreme degrees of forearm flexion and extension, respectively.

The trochlea and capitulum of the distal humerus mark the articular surfaces with the ulna and radius respectively (Fig. 5.2). Differences in mediolateral widths of each suggest how much body weight is distributed to one side of the humerus relative to the other. Capitulum shape is correlated with movement of the radius against the humerus, and a more rounded shape is generally indicative of multiaxial movement, whereas a trochleated capitulum is correlated to varying degrees with fast flexion/extension of the ulna that require lateral bracing.

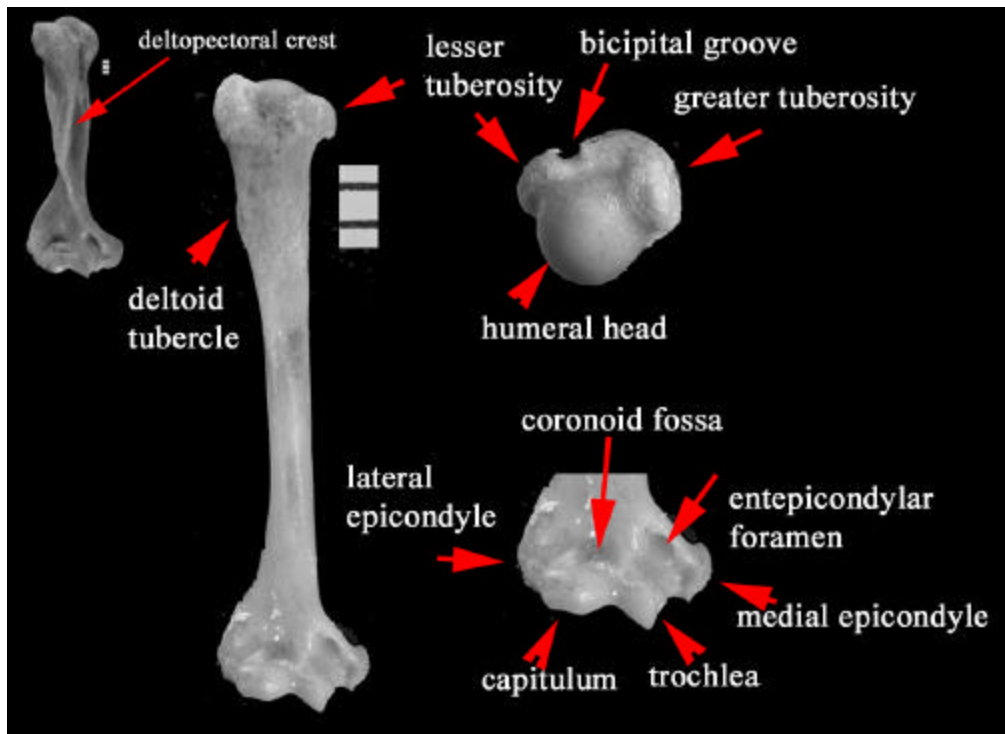


Figure 5.2. Right humeri of *Solenodon* and *Microgale*. Upper left is anterior view of *Solenodon*, demonstrating a humerus with pronounced crests and processes, including a deltopectoral crest, and wider shaft. Anterior view of whole humerus (center left) and views of proximal humerus (upper right) and distal humerus (lower right) of *Microgale dobsoni*.

The olecranon process of the ulna is the attachment site for the *M. biceps brachii*, which is the primary forearm extensor (Fig. 5.3). The olecranon process is generally considered in terms of its robusticity and length relative to the rest of the ulna. Overall ulnar and radial proportions are commonly compared to humeral lengths to determine mechanical compromises between speed (a relatively longer forearm) and power (a relatively shortened forearm).

Lastly, the articular surface of the radial head ranges from completely rounded to a mediolaterally-expanded ellipse, indicating greater degrees of mobility in the former and a more restricted lateral elbow joint in the latter (Fig 5.3).

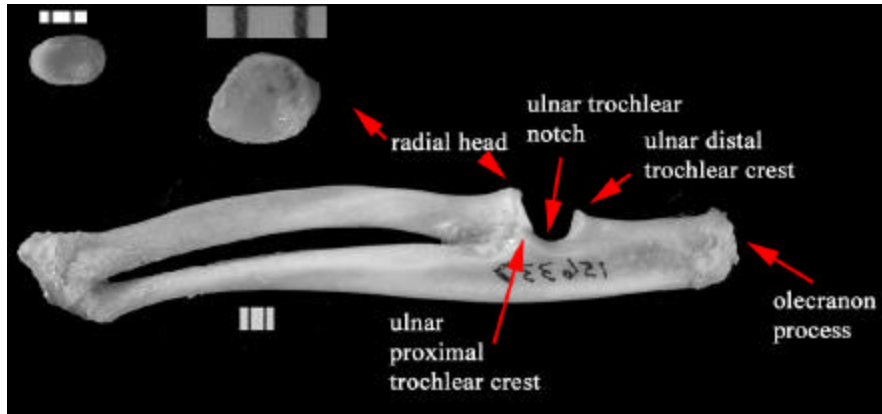


Figure 5.3. Right radius and ulna of *Setifer*, *Limnogale*, and *Tenrec*. Proximal view of *Setifer* radius (top left), illustrating mediolaterally elliptical radial head, proximal view of *Limnogale* radius (middle top), demonstrating a rounded head, and medial view of *Tenrec* antebrachium (bottom).

TABLE 5.1. ASPECTS OF THE MAMMALIAN FORELIMB WITH PROPOSED FUNCTIONAL SIGNIFICANCE

	Climber	Digger	Terrestrial/Runner	Leaper	Swimmer
SCAPULA					
Scapula shape ^{3,8,13}	short and broad	elongated	long and narrow		
Scapular shape ⁶		short	long, narrow		short
Scapular spine ⁶		high and long	present, not enlarged		low
Supraspinous fossa ¹	large		less well-developed		
Supraspinous fossa ¹⁰	cranially expanded			large	
Infraspinous fossa ^{1,10,11,22}	broad		narrow and deep		
Vertebral border ^{10,13,22}	extended relative to length				
Acromion ^{3,6,8,10,13}	large, angled cranially	long, flaring	not as large		
Coracoid process ^{8,10,13}	long, caudally oriented	stout, prominent	short, medially oriented		
Glenoid fossa ^{3,8,15}	wide	elliptical	tall and narrow		
HUMERUS					
Humerus shape ^{6,7,12,14,23}	long, narrow	robust, short, wide			
Humerus/radius length ¹⁶	long, narrow	short	long	long	
Humeral head ^{3,8,10}	hemispherical	elliptical	anteroposteriorly elongated		
Humeral head ¹⁷	large		smaller		
Bicipital groove ^{3,11}	clearly defined	well-formed into tunnel	not as well-formed		
Lesser tuberosity ^{8,10,13,17,22}	low, small (but bigger than greater tuberosity)	pronounced	higher, larger		
Greater tuberosity ^{8,10,13,17,18,23}	lower than head	pronounced	prominent, high		
Deltopectoral crest ^{8,10,19,22}	large, high, distal extend.	prominent, distally extend.	small, short		
Midshaft ²		wide			
Distal end of humerus ¹³	wide		narrow		
Entepicondylar foramen ³		elongated			
Medial epicondyle ^{8,9,10,13,14,20,22}	well-developed, long	enlarged	short		
Lateral epicondyle ^{8,9,10,14,22}	well-extended	enlarged			
Capitulum ^{4,13}	spherical		spindle-shaped		
Trochlea ¹⁰	developed anteriorly more than posteriorly		more concave posteriorly		
Trochlea ¹⁰	well separated from capitulum				
Trochlea ^{13,19,20}	mediolaterally longer, shallow		mediolaterally short, deep		
Coronoid fossa ¹⁰			deep		
Olecranon fossa ^{10,21}	shallow		deep		

	<u>Climber</u>	<u>Digger</u>	<u>Terrestrial/Runner</u>
ULNA			
Ulnar length ^{2,8,11,12,14,16}	long	short, wide	long
Olecranon process ^{2,5,8,9,10,13,14,21,22}	less prominent	large	prominent
Olecranon process ^{5,13}	cranially bent		caudally bent
Semilunar notch (proximal lip) ³		long	shorter
Trochlear notch ¹⁰			deep
RADIUS			
Radius shape ^{2,10,12,13,14,23}	long, bowed	short, wide	
Radial head ^{3,4,8,10,13}	circular	elliptical	elliptical

1. Roberts and Davidson, 1975; 2. Verma, 1963; 3. Reed, 1951; 4. Szalay and Dagosto, 1980; 5. Van Valkenburgh, 1987; 6. Smith and Savage, 1956; 7. Yalden, 1966; 8. Stein, 2000; 9. Biknevicius, 1993; 10. Argot, 2001; 11. Taylor, 1974; 12. Casinos et al., 1993; 13. Sargis, 2002; 14. Grand and Barboza, 2001; 15. Larson, 1993; 16. Hildebrand, 1995; 17. Rose, 1989; 18. Heinrich and Rose, 1997; 19. Gebo and Sargis, 1994; 20. Szalay and Sargis, 2001; 21. Ciochon, 1993; 22. Rose and Emry, 1983; 23. Hopwood, 1945.

Materials and Methods

The scapula, humerus, radius, and ulna from 174 specimens were studied and digitally photographed (Nikon Coolpix 995) from several standardized perspectives. Skeletal specimens were photographed from collections at the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Harvard Museum of Comparative Zoology (MCZ), and United States National Museum of Natural History (USNM). Two *Echinops* specimens were borrowed from H. Kuenzle's laboratory at the University of Munich (UMUN), Germany, and a *Hemicentetes* and *Tenrec* specimen were borrowed from the University of Darmstadt, Germany (DARM) (see Appendix I for specimen list). Digital image files were written into TPSdig (Version 1.31, 2001 F.J. Rohlf), which allows for superimposition of landmarks (x,y coordinates) onto images, and calibration of image scale from a mm ruler. Twenty-two linear measurements were then calculated from desired coordinates (Fig. 5.3, 5.5). Measurements included those that incorporate features with proposed functional and/or phylogenetic significance (see Table 5.1). Precision of digital measurements was tested against fine-point caliper measurements from 3 complete specimens, and there were no significant differences between caliper and digital values ($p < 0.05$). In order to control for size differences between species, linear measurements were transformed to 31 index variables (Table 5.4). Statistical analyses (one-way ANOVAs & Tukey honest significance (HSD) post-hoc tests) were performed using STATISTICA (Version 6.0, StatSoft Inc). Significance values reported in the text for two-group comparisons refer to Tukey post-hoc results; those for more than two groups refer to ANOVAs.

Thirty linear measurements from 64 landmark points were taken and transformed to 15 indices (Tables 5.3, 5.4). The following tenrecoid species were studied: *Echinops telfairi*, *Setifer setosus*, *Hemicentetes semispinosus*, *Tenrec ecaudatus*, *Microgale cowani*, *M. dobsoni*, *M. talazaci*, *Oryzorictes tetradactylus* (or *O. hova*), *Limnogale mergulus*, *Geogale aurita*, and *Potamogale velox* (see Table 5.2). The following non-tenrecoids were included as outgroups, based on discussion in Chapter I: *Solenodon paradoxus*, *Petrodromus tetradactylus*, and *Echinosorex gymnurus*.

TABLE 5.2. Taxonomy and Primary Locomotor Behavior of study taxa

Family/subfamily	Genus	Species	n	Locomotor Behavior
Tenrecidae/Tenrecinae	<i>Echinops</i>	<i>telfairi</i>	13	Arboreal/terrestrial
Tenrecidae/Tenrecinae	<i>Hemicentetes</i>	<i>semispinosus</i>	18	Terrestrial/fossorial
Tenrecidae/Tenrecinae	<i>Setifer</i>	<i>setosus</i>	19	Terrestrial
Tenrecidae/Tenrecinae	<i>Tenrec</i>	<i>ecaudatus</i>	12	Terrestrial
Tenrecidae/Oryzorictinae	<i>Limnogale</i>	<i>mergulus</i>	5	Aquatic/terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>cowani</i>	22	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>dobsoni</i>	21	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>talazaci</i>	12	Terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>hova</i>	22	Fossorial/terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>tetradactylus</i>	10	Fossorial/terrestrial
Tenrecidae/Geogalinae	<i>Geogale</i>	<i>aurita</i>	4	Terrestrial
Potamogalidae	<i>Potamogale</i>	<i>velox</i>	3	Aquatic/terrestrial
Macroscelididae	<i>Petrodromus</i>	<i>tetradactylus</i>	2	Terrestrial/saltatory
Solenodontidae	<i>Solenodon</i>	<i>paradoxus</i>	10	Terrestrial/fossorial
Erinaceidae	<i>Echinosorex</i>	<i>gymnurus</i>	1	Terrestrial

Table 5.3. Measurements (see Appendix 5.1 and 5.2)

Lscap1	<i>Scapula length</i> : from lateral view of scapula, from end of vertebral border (furthest distance from glenoid fossa) to edge of glenoid fossa, along axis of scapular spine, perpendicular to scapula width.
Lscap2	<i>Scapula width</i> : from lateral view of scapula, from highest point of cranial border (furthest from scapular spine), to edge of axillary border, perpendicular to axis of scapular spine, perpendicular to scapula length.
Dscap1	<i>Scapula + acromion process length</i> : from dorsal view of scapula, distance from distal end of scapula to proximalmost (cranioventral) point of acromion process, parallel to long axis of scapula.
Pscap3	<i>Glenoid fossa dorsoventral height</i> : from proximal view of scapula, dorsoventral/anteroposterior height of glenoid fossa, perpendicular to glenoid fossa width.
Pscap3	<i>Glenoid fossa mediolateral width</i> : from proximal view of scapula, mediolateral width of glenoid fossa, perpendicular to fossa dorsoventral height.
Hum1	<i>Distal humerus width</i> : from posterior view of humerus, widest line across mediolateral width of the distal humerus, perpendicular to long axis of humeral shaft.

- Hum2** *Humeral head proximodistal depth*: from posterior view of humerus, proximodistal depth of humeral head, through midpoint of head, perpendicular to humeral head width.
- Hum3** *Humeral head width*: from posterior view of humerus, mediolateral width of humeral head, through midpoint of head, perpendicular to humeral head length.
- Hum4** *Humerus length*: from posterior view of humerus, from proximalmost point of humeral head to proximalmost point of trochlea, parallel to long axis of shaft.
- Hum5** *Humerus midshaft width*: from posterior view of humerus, mediolateral width of humeral midshaft, as determined by humerus length.
- Hum6** *Humeral trochlea width*: from distal view of humerus, mediolateral width of trochlea, from distalmost points of trochlear crests.
- Hum7** *Lateral epicondyle width*: from posterior view of humerus, from lateralmost point of lateral epicondyle to point even with lateral crest of trochlea, perpendicular to long axis of humeral shaft.
- Hum8** *Medial epicondyle width*: from posterior view of humerus, from medialmost point of medial epicondyle to point even with medial crest of trochlea, perpendicular to long axis of humeral shaft.
- Phum1** *Greater tuberosity mediolateral width*: from proximal view of humerus, mediolateral width of greater tuberosity, along midline of long axis of tuberosity, perpendicular to greater tuberosity proximodistal length.
- Phum2** *Greater tuberosity proximodistal length*: from proximal view of humerus, anteroposterior length (depth) of greater tuberosity, along middle of short axis of tuberosity, at angle perpendicular to mediolateral width.
- Phum3** *Lesser tuberosity mediolateral width*: from proximal view of humerus, mediolateral width of lesser tuberosity, along midline of long axis of tuberosity, perpendicular to lesser tuberosity proximodistal length.
- Phum4** *Lesser tuberosity proximodistal length*: from proximal view of humerus, anteroposterior length (depth) of lesser tuberosity, along middle of short axis of tuberosity, at angle perpendicular to lesser tuberosity mediolateral width.
- Ulnarad3** *Olecranon process length*: from medial view of ulna, from lowest point of ulnar trochlear notch to end of olecranon process, parallel to long axis of ulna.
- Ulnarad2** *Radius length*: from medial view of radius, from midpoint of radial head to midpoint of distalmost diaphysis, parallel to long axis of radial shaft.
- Ulnarad3** *Ulna length*: from medial view of ulna, from distalmost point of ulna diaphysis to end of olecranon process, parallel to long axis of ulna.

Table 5.4. Indices (see Appendix 5.3 and 5.4)

APLI	Acromion Process Length Index = length of scapula from distal end to tip of acromion process/length of scapula to base of glenoid fossa
DHWI	Distal Humerus Width Index = Distal humerus width/trochlear width (distal view)
GFSI	Glenoid Fossa Shape Index = dorsoventral height of the glenoid fossa/mediolateral width of the fossa
GTSI	Greater Tuberosity Size Index = (Greater tuberosity proximal length + width)/(humeral head proximal length + width)
HHZI	Humeral Head Size Index = (Humeral head width+length)/midshaft width
HRLI	Humerus/Radius Length Index (Brachial Index) = Humerus length/radius length
HSI	Humerus Shape Index = Humerus width/humerus length
LEPW	Lateral Epicondyle Width Index = Lateral epicondyle width/trochlear width (distal view)
LTSI	Lesser Tuberosity Size Index = (Lesser tuberosity proximal length + width)/(humeral head proximal length + width)
MEPW	Medial Epicondyle Width Index = Medial epicondyle width/trochlear width (distal view)
OPLI	Olecranon Process Length Index = Olecranon process length/ulnar length
SCSI	Scapula Shape Index = Scapula width/scapula length (longest line of scapula)
TRHI	Trochlear Height Index = Proximodistal trochlear height (posterior)/mediolateral width of proximal trochlea (posterior)

- TSI** Tuberosity Size Index = $((\text{Greater tuberosity proximal length} + \text{width}) + (\text{lesser tuberosity length} + \text{width})) / (\text{humeral head proximal length} + \text{width})$
- UWI** Ulnar Width Index = $\text{Ulnar width} / \text{ulnar length}$



Fig. 5.4. Linear measurements of forelimb elements used for indices.

Results and Discussion

Scapula

Within the Tenrecinae, there is a significant difference in the Scapular Shape Index (SHSI) between *Hemicentetes* and *Tenrec* (Figs. 5.5, 5.6; $p=0.00$). *Hemicentetes* has a significantly longer and thinner scapula than the wide, relatively shorter scapula of *Tenrec*. The other two tenrecines, *Echinops* and *Setifer*, are intermediate in shape and their SHSI values are not significantly different from each other or the other tenrecines. Unlike the other two, they have a relatively flat (vs. angled) axillary border and steeply rising cranial border, resulting in an enlarged broad supraspinous fossa. The supraspinous fossa is large and cranially expanded in arboreal scandentians, primates, and xenarthrans

(Roberts and Davidson, 1975; Gebo and Sargis, 1994; Monteiro and Abe, 1999; Sargis, 2002), related to an enlarged attachment area for the *M. supraspinatus* and its function as a scapular suspensor and forelimb protractor (Taylor, 1974, 1978; Roberts and Davidson, 1975; Argot, 2001; Vasquez-Molinero et al., 2001). Both *Echinops* and *Setifer* have a rectangular infraspinous fossa vs. a more triangular fossa (flared at the vertebral border) in *Tenrec* and *Hemicentetes*. This results in a larger anterior/ventral surface area for the *M. subscapularis*, a medial rotator of the humerus.

A narrow, elongated scapula is characteristic of some fossorial rodents and soricids (Reed, 1951; Stein, 2000), and this might be expected in *Hemicentetes*. Lengthening of the scapula is presumably correlated with a large and posteriorly displaced origin of the *M. teres major* and *M. triceps brachii caput longum*, which retract and rotate the shoulder and extend the forearm, respectively (Yalden, 1966; Taylor, 1978; Neveu and Gasc, 2002).

There are no subfamily-level differences in scapular shape between the tenrecines and oryzorictines due to the considerable variation within Oryzorictinae and their overlapping ranges with Tenrecinae (Fig. 5.6; $p=0.00$). There are significant differences between the three *Microgale* species; *M. cowani* has a significantly longer and narrower scapula than *M. dobsoni* and *M. talazaci*. This is consistent with a series of other postcranial traits that suggests *M. cowani* is more of a habitual digger than previously recorded. *Oryzorictes* has a narrow and elongate scapula, substantially more so than in any of the other studied taxa, and similar in form to subterranean talpids. The swimmers *Limnogale* and *Potamogale* do not have similar scapular morphology, yet they both have long and narrow scapulae relative to the other tenrecoids (except *Oryzorictes*), which

suggests considerable retraction-based loading during aquatic propulsion (Fig. 5.5).

Although the supraspinous fossa is well developed in leaping marsupials (Argot, 2001), the supraspinous fossa in the elephant shrew *Petrodromus* is not remarkable. Rather, its infraspinous fossa is deep and expanded at the caudal vertebral border, highlighting the importance of the teres major in powerful forelimb retraction.

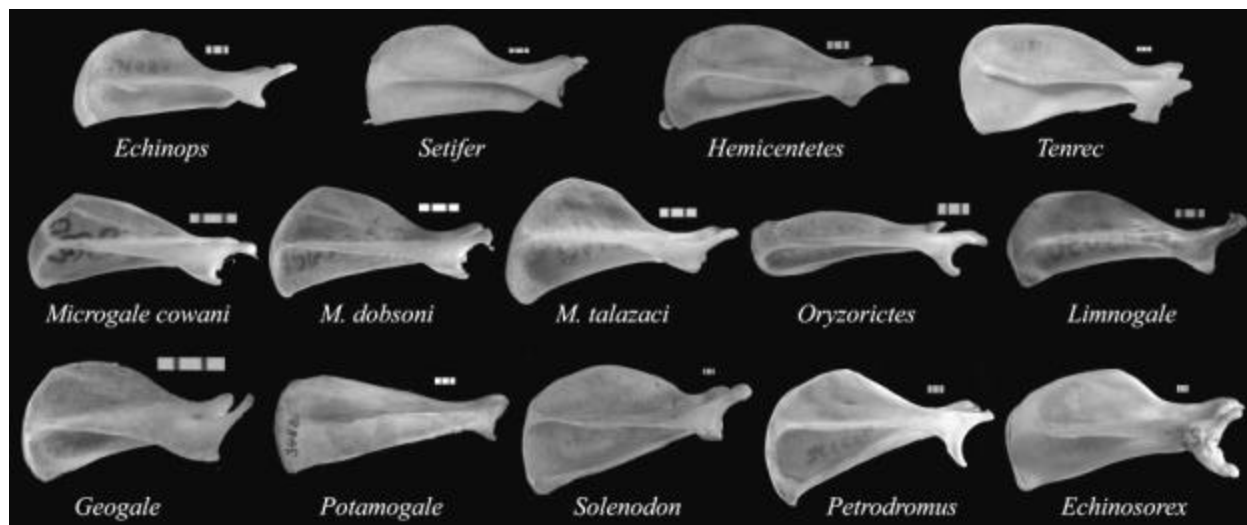


Figure 5.5. Lateral views of right scapulae scaled to length in tenrecines (top row), oryzorictines (middle row), two other tenrecoids (bottom left), and outgroups (bottom right). Note differences in the relative length and width of the whole scapula, angle of the axillary border, breadth of the vertebral border, depth of the supraspinous and infraspinous fossae, and shape of the acromion and metacromion processes.

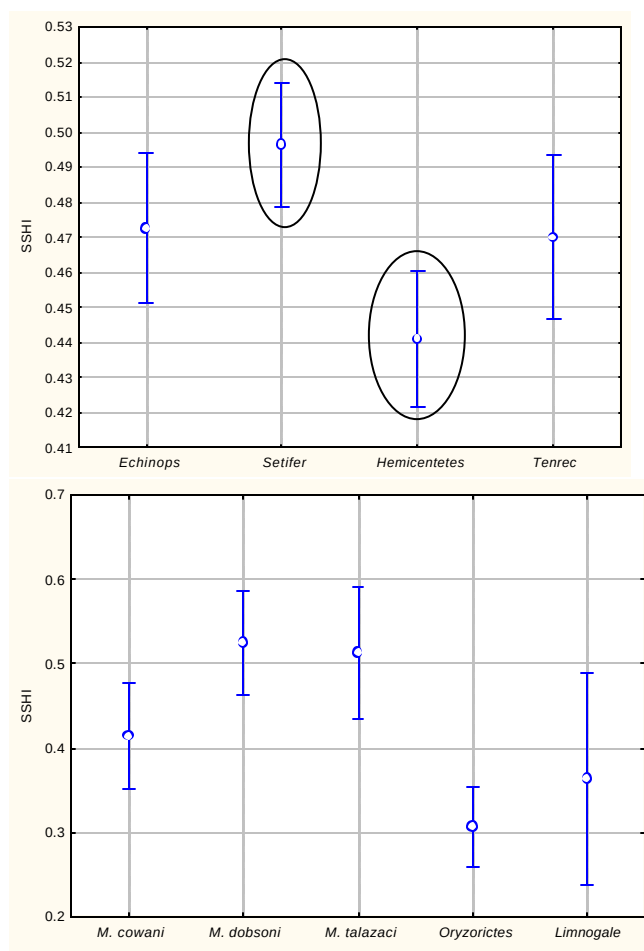


Figure 5.6. Scapula Shape Index in tenrecines (top) and oryzorictines (bottom). Within the Tenrecinae note the relatively broader scapula in *Setifer* and a narrower one in *Hemicentetes* ($p=0.00$). In Oryzorictinae, the digger *Oryzorictes* and swimmer *Limnogale* have narrower scapulae than the others. *Microgale cowani* has a narrower scapula than the other two *Microgale* species which may be indicative of some digging behavior.

Within the Tenrecinae, the acromion process reaches proximally well beyond the glenoid fossa in *Echinops* and *Hemicentetes*, whereas that in *Tenrec* and *Setifer* is less proximally extended (though $p>0.05$ between all tenrecines, see Figs. 5.5, 5.7, 5.8).

Though there is considerable intraspecific variation for this variable, the trend of a longer acromion in a digger and climber is consistent with data from rodents and marsupials (Stein, 2000; Argot, 2001). *Oryzorictes* has a significantly longer acromion process than all other studied taxa, including the other oryzorictines (Figs. 5.7, 5.8; $p<0.00$).

Limnogale also has a relatively long process relative to *Microgale* ($p=0.00$), and is unlike

Potamogale, which is lacking an acromion process almost altogether (of the three available *Potamogale* scapulae, two had broken scapular spines, so $n=1$ for this variable). The acromion process is the site of origin for *M. deltoideus* pars acromialis (Neveu and Gasc, 2002), which acts as a protractor and lateral rotator of the humerus. Although some forelimb diggers have large acromion processes, they are reduced in some, e.g., talpids and erinaceids (Reed, 1951; Verma, 1963). Length of the acromion in a digger might therefore be indicative of whether the animal is generating force from the shoulder musculature, as in *Oryzomys* and xenarthrans (Smith and Savage, 1956), or more from the forearm, as in *Talpa* and erinaceids.

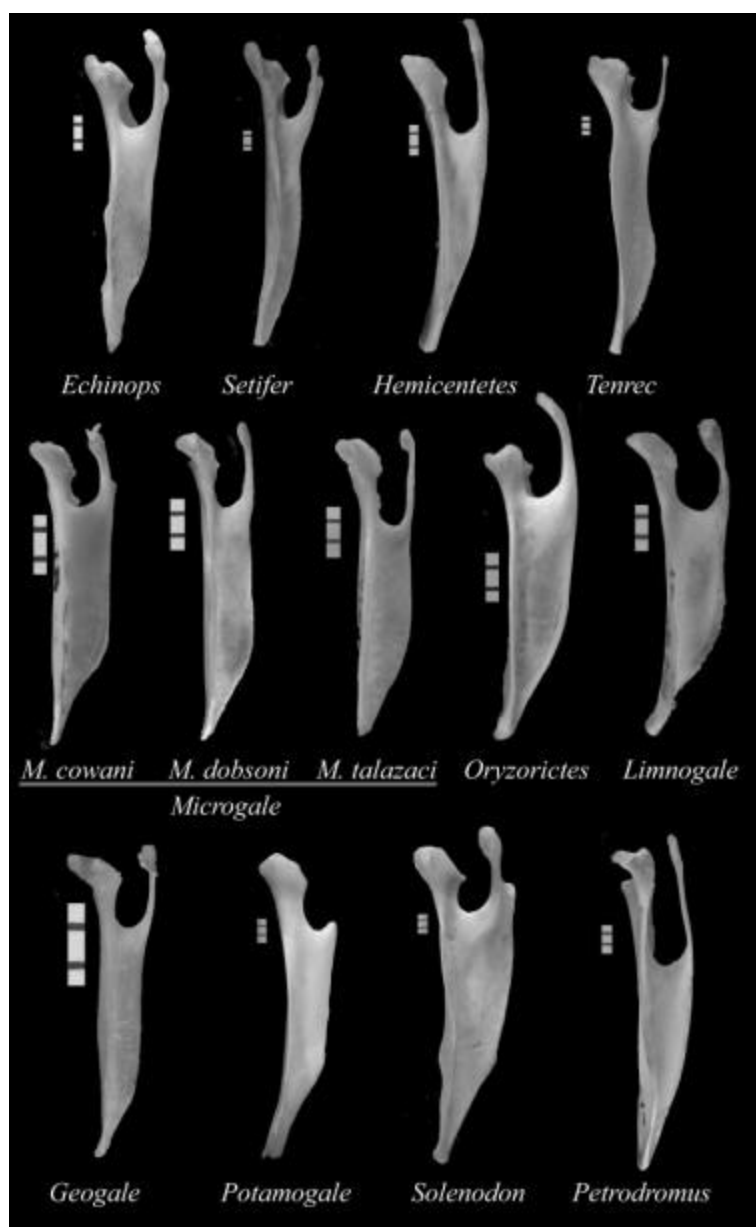


Figure 5.7. Dorsal view of right scapulae scaled to length in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left) and two outgroups (bottom right). Note lengths of the acromion process, which is longer in the climber *Echinops* (though not statistically when the whole sample is considered) and the diggers.

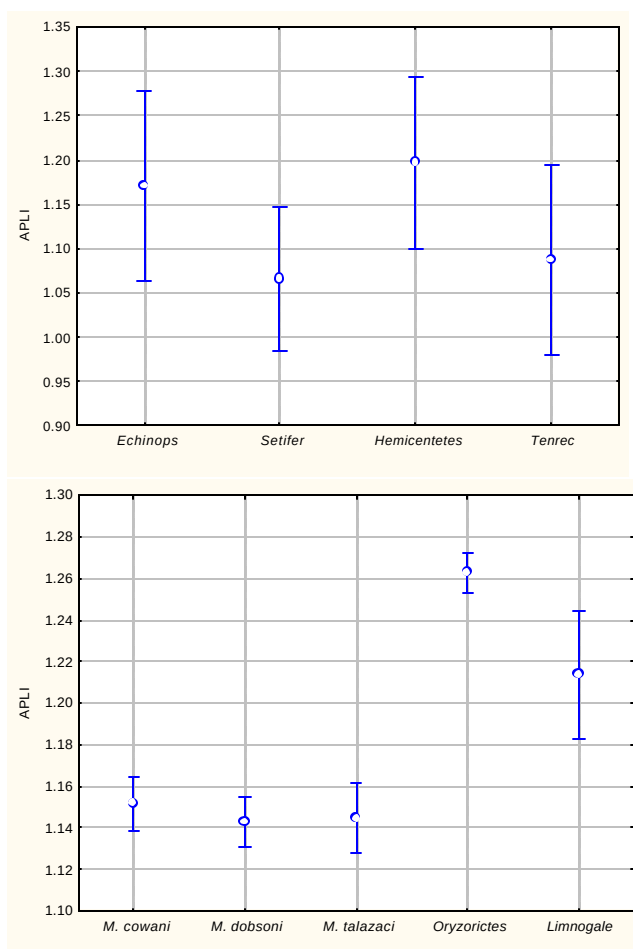


Figure 5.8. Acromion Process Length Index in tenrecines (top) and oryzorictines (bottom). *Echinops* and *Hemicentetes* tend to have a long acromion process relative to the other tenrecines, but the difference is not significant. *Oryzorictes* and *Limnogale* have considerably longer processes than the other oryzorictines ($p=0.00$).

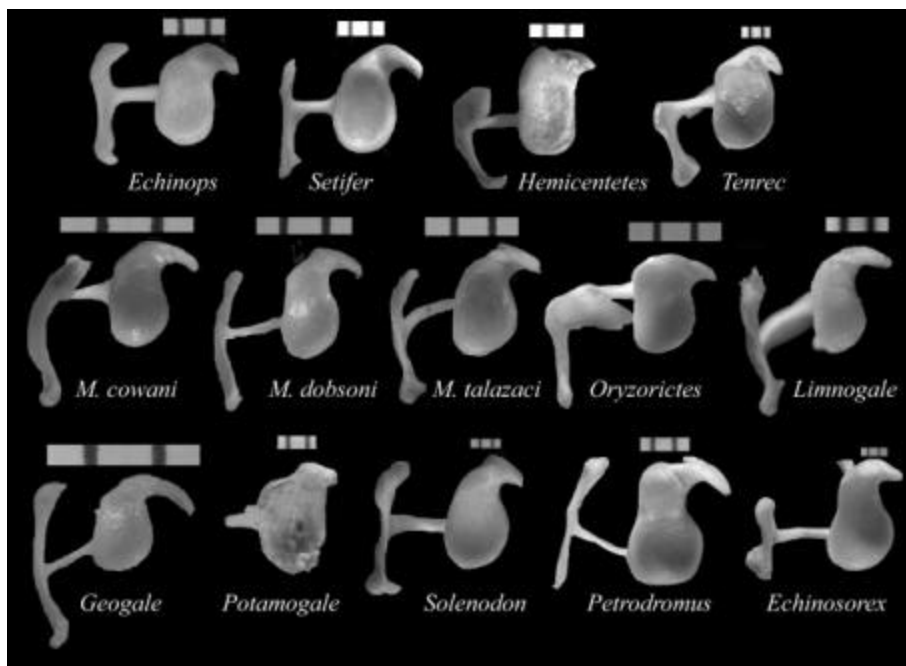


Figure 5.9. Articular surface of right scapulae scaled to height in four tenrecines (top), four oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa. Note the shape of the glenoid fossa, ranging from rectangular in *Hemicentetes* to spherical in *Petrodromus*.

The metacromion is an attachment site for Mm. trapezius, atlantoscapularis, omotransversarius anterior and for the extension of the deltoideus pars acromialis (Campbell, 1939; Neveu and Gasc, 2002), muscles involved with scapular stabilization and humeral rotation. A conspicuous arc of the metacromion is only present in the two most extreme locomotor specialists, *Oryzorictes* and *Petrodromus*, suggesting that the metacromion, when present, is a good indicator of heavy loading at the shoulder. *Geogale* has an unusual metacromion process, which does not project anteriorly in a characteristic “c” shape, but reaches back (posteriorly along the long axis of the scapula) and forms a wide, thin sheet of bone confluent with the scapular spine (Fig. 5.5). It is unclear which of the attached muscles is most influencing this form, but given the lack of rotational arm movement in *Geogale* (pers. obs.), it is most likely a reflection of a strongly anchored scapula.

Although there are apparent differences in the shape of the glenoid fossa between taxa, the Glenoid Fossa Shape Index (GFSI) may not be a reliable variable because it is difficult to discern the limits of humeral head rotation against the fossa (see Taylor, 1974). Nonetheless, the glenoid fossa of tenrecoids appears to be generally dorsoventrally (anteroposteriorly, if facing ventrally) narrow with some variation between taxa. Within tenrecines, the shape of the glenoid fossa in *Hemicentetes* is distinctive in its high, narrow, almost rectangular shape (Figs. 5.9, 5.10), which is consistent with glenoid fossa shape in other mammalian diggers (Reed, 1951; Stein, 2000). The glenoid fossa in *Echinops* is wider than in other tenrecoids, but not significantly wider than in other taxa (Fig. 5.9). *Limnogale* has a narrower glenoid fossa than in any other studied taxon, yet the functional interpretation of this trait is unclear. Though it seems as if a narrow glenoid fossa would restrict motion to a single plane, the highly restricted shoulder joints of *Potamogale* and *Petrodromus* (based on their humeral morphology) have rounded glenoid fossae.

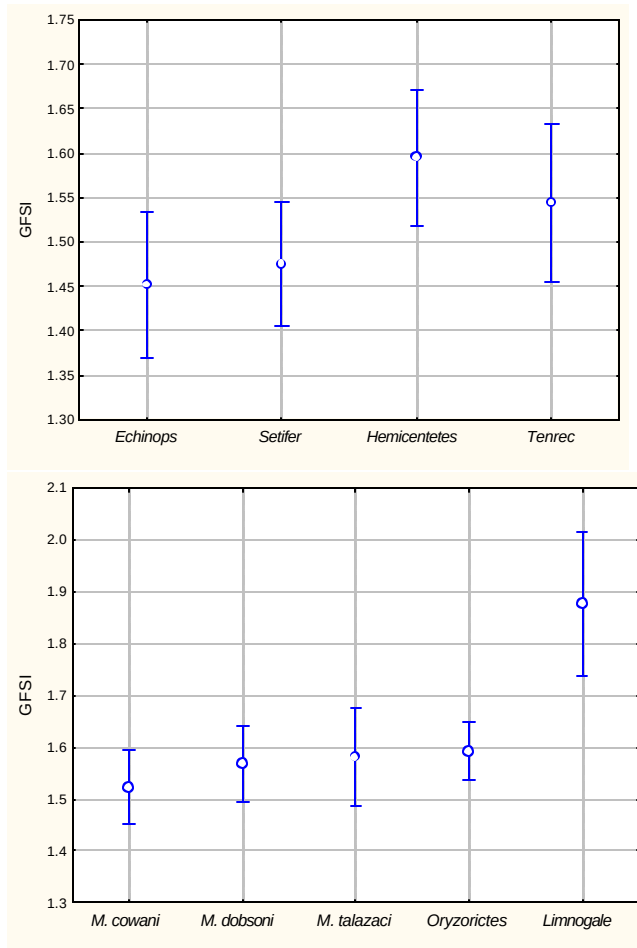


Figure 5.10. Glenoid Fossa Shape Index in tenrecines (top) and oryzorictines (bottom). Note high values in *Hemicentetes* and *Limnogale* indicating an elliptical vs. more rounded fossa.

Humerus

Overall shape of the humerus in terms of its length relative to width does not appear to be reliably correlated with positional behavior, except for the consistent finding of a relatively short, wide humerus correlated with digging (Smith and Savage, 1956; Yalden, 1966; Casinos et al., 1993; Hildebrand, 1995; Grand and Barboza, 2001; Luo and Wible, 2005). This is also the case with the taxa studied here; the humerus of *Hemicentetes*, *Oryzorictes*, and *Solenodon* is significantly wider at its midshaft than that of any other taxon (Figs. 5.11, 5.12). With the exception of *Oryzorictes*, the oryzorictines have longer, thinner humeri than the tenrecines. Despite other traits that correlate with

digging in the *M. cowani* postcranium, its humeral shape as defined by the Humeral Shape Index is within the range of the other *Microgale* species (Fig. 5.12).

There are no significant differences between tenrecines in humerus length relative to the radius (HRLI, or brachial index); all have a humerus that is slightly longer than the radius, although *Tenrec* has a slightly higher value than the others (Fig. 5.13). In oryzorictines, the humerus tends to be shorter than the radius, except in the digging *Oryzorictes*, in which the humerus is just longer than the radius, as in tenrecines (Fig. 5.13). The swimmer *Potamogale* and the saltatory *Petrodromus* represent two ends of a spectrum; *Potamogale* has an extremely long humerus relative to radius, whereas *Petrodromus* has a short brachial index (Fig. 5.13). Lengthening of the distal limb elements has been well correlated with the mechanics of higher-speed locomotion, whereas shortened distal limbs, and short limbs in general are correlated with more powerful forelimb (and hindlimb) thrust. *Petrodromus* most likely concentrates muscle mass at the proximal end of the limb, as in other mammalian cursors, and effectively lengthens its stride with a long distal limb and long tendinous insertions (Hildebrand, 1995). Smith and Savage (1956) noted similarities in scapular form between aquatic mammals and fossorial mammals. The extreme shortening of the distal limb in *Potamogale* suggests that it uses its arms for some aquatic paddling, which, in terms of movement and direction of reactive force, is similar to digging in *Oryzorictes* (though differences in humeral shape reflect the lighter resistance of water vs. soil, and considerably less powerful elbow flexion/extension in *Potamogale*).

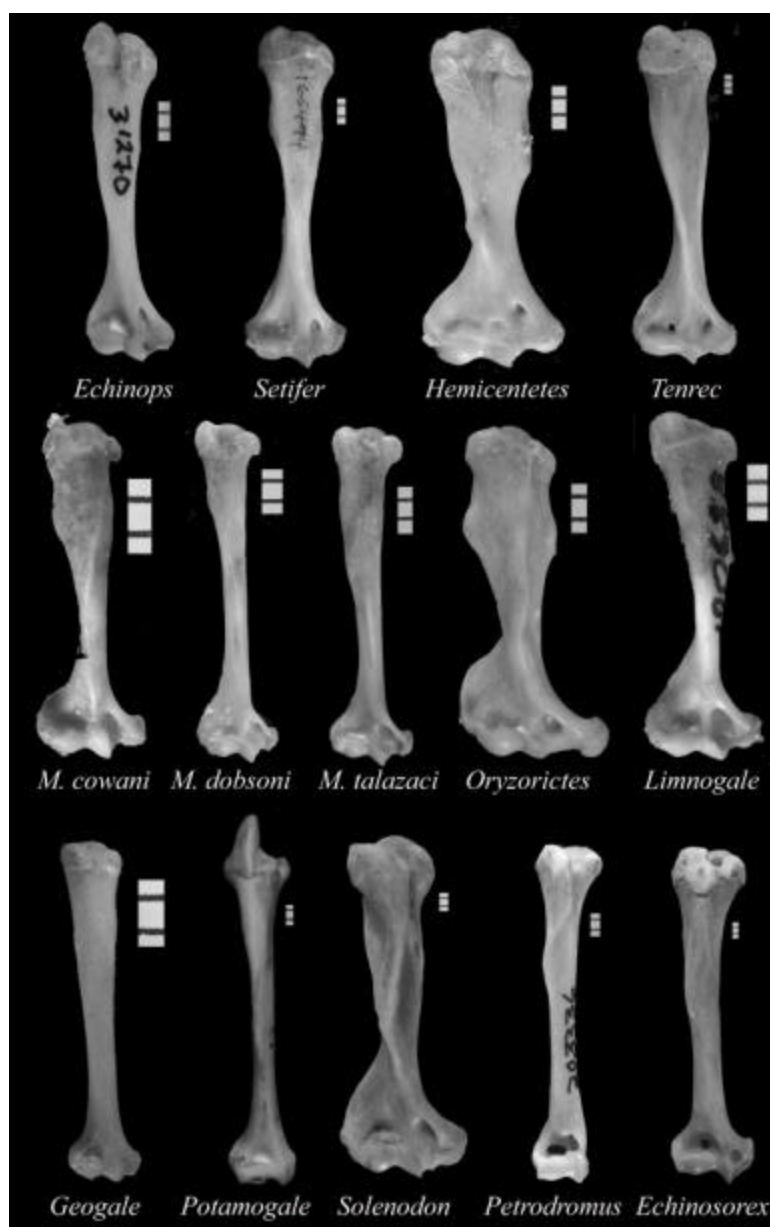


Figure 5.11. Anterior view of right humeri scaled to height in four tenrecines (top), four oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa. Note differences in relative midshaft width, greater and lesser trochanter height, distal humerus width, epicondyle widths, trochlea and capitulum shape, presence/absence of entepicondylar foramen and coronoid fossa, and deltoid tuberosity/deltpectoral crest shape.

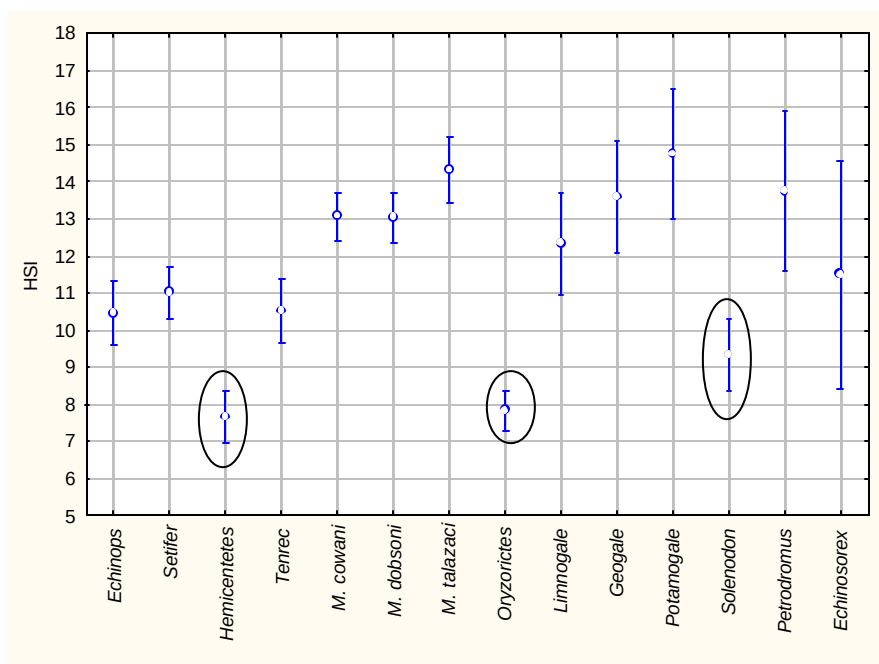


Figure 5.12. Humerus Shape Index in all studied taxa. The diggers *Hemicientetes*, *Oryzorictes*, and *Solenodon* have particularly low values, representative of short and wide humeri relative to the others.

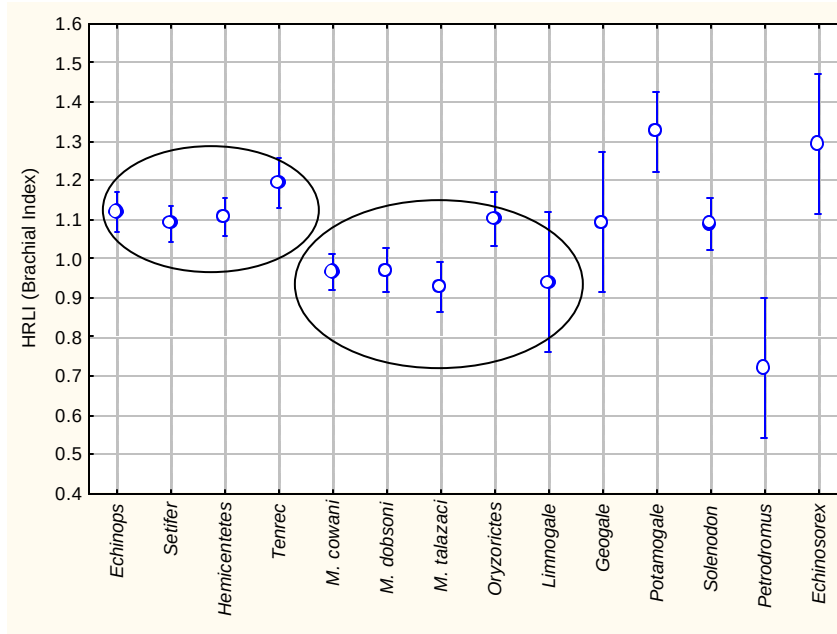


Figure 5.13. Humerus/Radius Length Index (brachial index) in all studied taxa. Note the relatively longer humerus/radius length in tenrecines (left circle) relative to oryzorictines (right circle), and the particularly long humerus/short radius in the swimmer *Potamogale*.

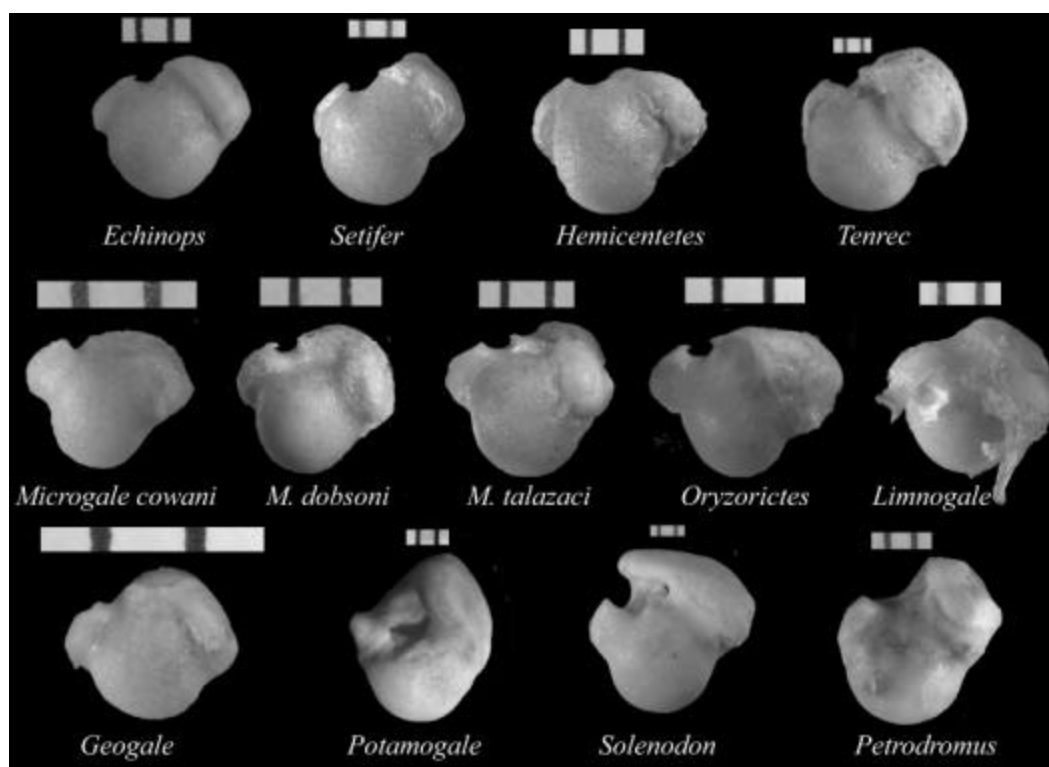


Figure 5.14. Proximal articular surfaces of right humeri of four tenrecines (top), four oryzorictines (middle), two other tenrecoids (bottom left), and two outgroup taxa. Note differences in greater and lesser tuberosity size and presence/absence of a bicipital groove.

Humeral head shape varies significantly with locomotor behavior in the Tenrecinae (Figs. 5.14, 5.15). The digging tenrecine *Hemicentetes* has a proximodistally/anteroposteriorly lengthened head, whereas the climber *Echinops* has a more rounded humeral head, even more so than its sister taxon *Setifer* ($p=0.01$). This is consistent with data from arboreal primates and several small digging mammals, and reflects multiaxial rotational movement in the climbers and more restricted shoulder motion in the diggers (Reed, 1951; Stein, 2000; Argot, 2001). A comparison across all taxa demonstrates that the diggers *Hemicentetes*, *Oryzorictes*, and *Solenodon* share an elliptical articular surface of the humeral head vs. a more rounded head in the others (Fig. 5.16).

A well-formed bicipital groove is most likely correlated with the size of the tendon of the *M. biceps brachii* which passes through it, and may be indicative of powerful flexion associated with climbing (Taylor, 1976; Argot, 2001) or digging (Campbell, 1939; Reed, 1951). There is tremendous intraspecific variation in the formation of the bicipital groove. In several *Hemicentetes* and *Oryzorictes* specimens, the groove is completely closed to form a bicipital tunnel (Fig. 5.17), characteristic of talpids (Barnosky, 1982), but this is not the norm for either tenrecoid genus. The presence of a well formed bicipital groove or tunnel may be indicative of digging, yet the absence of this trait is not clear in terms of positional behavior.

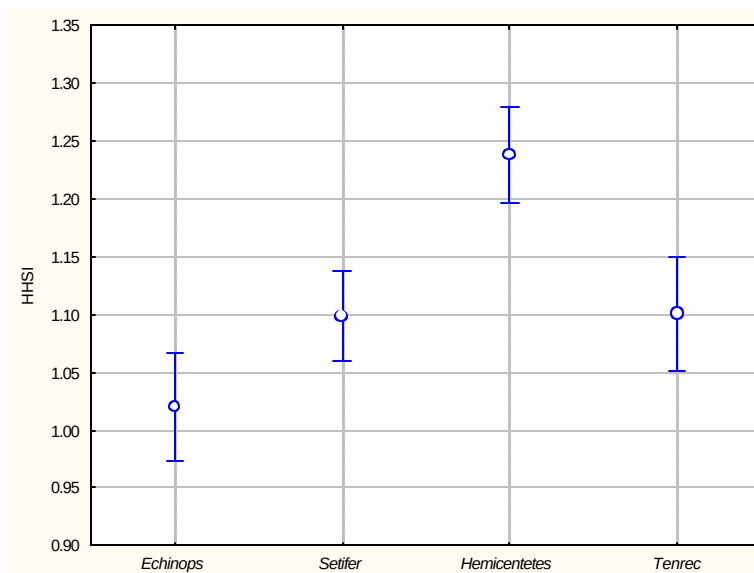


Figure 5.15. Humeral Head Shape Index in tenrecines. *Hemicentetes* has a significantly higher value than the other tenrecines, indicating a more elliptical humeral head.

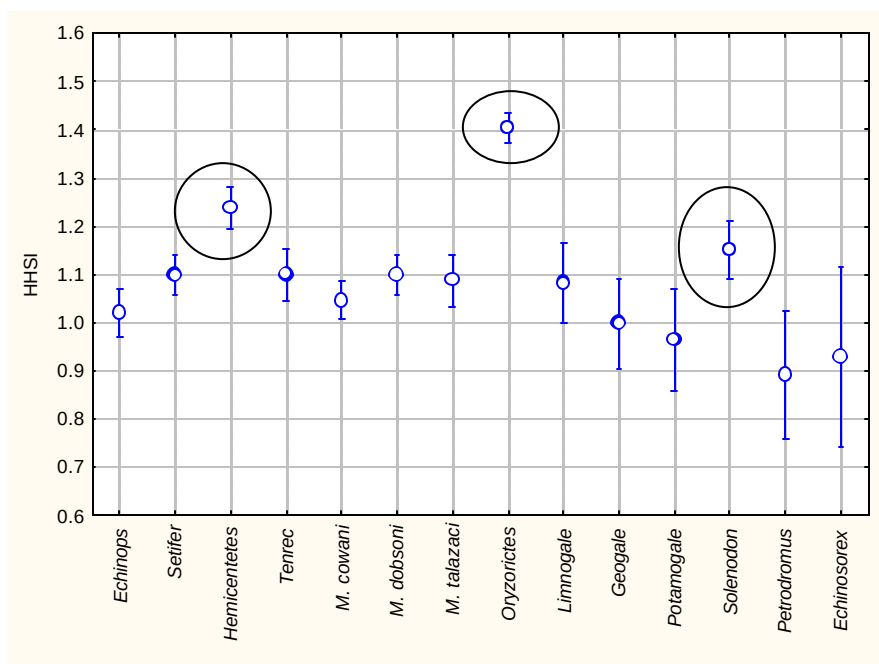


Figure 5.16. Humeral Head Shape Index in all studied taxa. The three diggers *Hemicentetes*, *Oryzorictes*, and *Solenodon*, have more elliptical humeral heads.

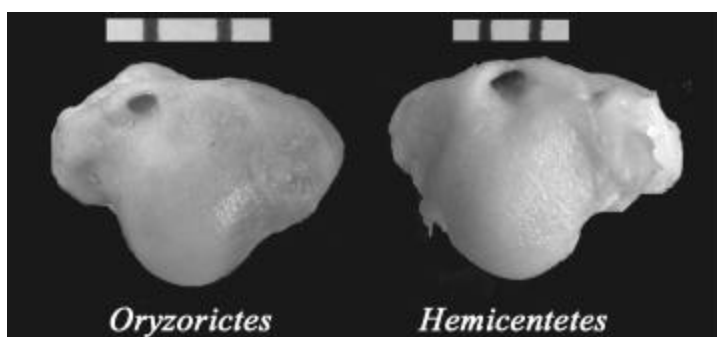


Figure 5.17. Proximal articular surfaces of right humeri in two digging tenrecoids, illustrating the formation of a complete bicapital tunnel. Most specimens from each of these two genera have a bicapital groove and only a few have a completely formed tunnel.

Rose (1989) discussed several features of arboreal vs. more terrestrial primates, and suggested that climbers have an enlarged humeral head relative to shaft size. Humeral head size index (HHSZI) in tenrecoids demonstrates a slightly larger humeral head in *Echinops*, and significantly smaller heads in *Hemicentetes* and *Oryzorictes*; yet this index is highly sensitive to variation in midshaft width, which is especially inflated in the diggers.

Tenrec has a significantly larger greater tuberosity (in terms of mediolateral and anteroposterior width) than the other tenrecines (Fig. 5.19; $p=0.00$), which might indicate a more restricted shoulder joint with powerful parasagittal forelimb movement.

Hemicentetes does not have a more pronounced greater tuberosity despite predictions based on other mammalian diggers, nor does *Echinops* have a smaller one relative to the others (see Table 5.1.). The greater tuberosity of the humerus serves as an attachment site for *M. infraspinatus*, which retracts the humerus, and *M. supraspinatus*, which protracts the humerus. Both muscles serve to stabilize the shoulder joint, and the relative size of the greater tuberosity may therefore correlate with restriction of shoulder mobility (Roberts and Davidson, 1975; Argot, 2001; Sargis, 2002). Amongst the oryzorictines, *Oryzorictes* has a significantly larger greater tuberosity, suggesting a more powerful and restricted fore and aft stroke, and perhaps implying that *Oryzorictes* and *Hemicentetes* utilize different types of arm strokes when digging (Figs. 5.14, 5.18, 5.19). The greater tuberosity in *Potamogale* is remarkable relative to the tenrecids and highly unusual for any mammal (Fig. 5.11). Interestingly, it is somewhat convergent with the greater tuberosity in microchiropteran bats. It extends proximally and anteriorly as a sharp process that is claw-like in shape. It reaches high beyond the proximal surface of the humeral head. Although different from bats in its shape and anterior position on the humerus, the greater tuberosity projection in *Potamogale* most likely serves as a protective lock against the scapula and helps to prevent overextension of the forearm when swimming.

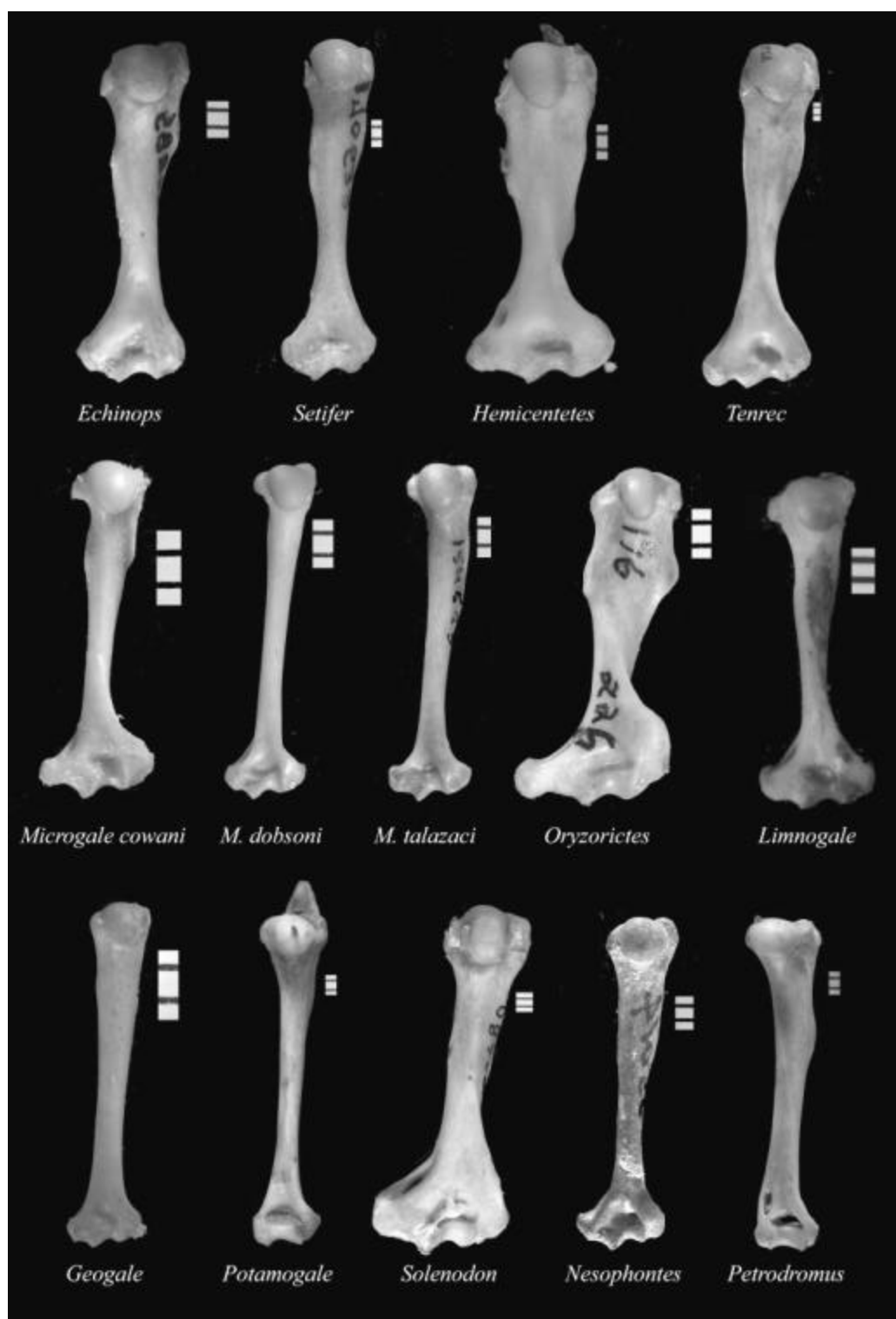


Figure 5.18. Posterior surfaces of right humeri in four tenrecines (top), four oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa. Note differences in proximodistal length of the humeral head and tuberosities, and shape of the trochlea.

The tenrecine digger *Hemicentetes* has a broad lesser tuberosity relative to other subfamily members, and *Tenrec* has a significantly smaller lesser tuberosity (Figs. 5.18, 5.19; $p=0.00$). The lesser tuberosity is the primary attachment site for *M. subscapularis*, a medial rotator and adductor of the arm (Taylor, 1978; Argot, 2001). One might therefore expect a larger lesser tuberosity in diggers (Rose and Emry, 1983; Stein, 2000), and perhaps a larger tuberosity (relative to the greater tuberosity) in climbers (Argot, 2001; Sargis, 2002). The small lesser tuberosity in *Tenrec* is consistent with its large greater tuberosity, suggesting a forearm with very limited rotational mobility. There is a strong negative correlation between the size of the greater tuberosity and lesser tuberosity in tenrecines, as well as all taxa studied (-0.87 for tenrecines, -0.70 for all). Like *Tenrec*, *Potamogale* has a diminutive lesser tuberosity which, when coupled with the large greater tuberosity, suggests an armstroke that is limited to one major directional plane (as in forward and backwards paddling). The other semi-aquatic taxon, *Limnogale*, has a relatively large lesser tuberosity, as in *Oryzomys*, suggesting more rotational arm movement while swimming (Fig. 5.18). This is consistent with tarsal and hindlimb morphology, which suggests more varied limb movements in *Limnogale* compared to the more restricted and powerful swimming strokes in *Potamogale* (Salton and Szalay, 2004; Salton, in review).

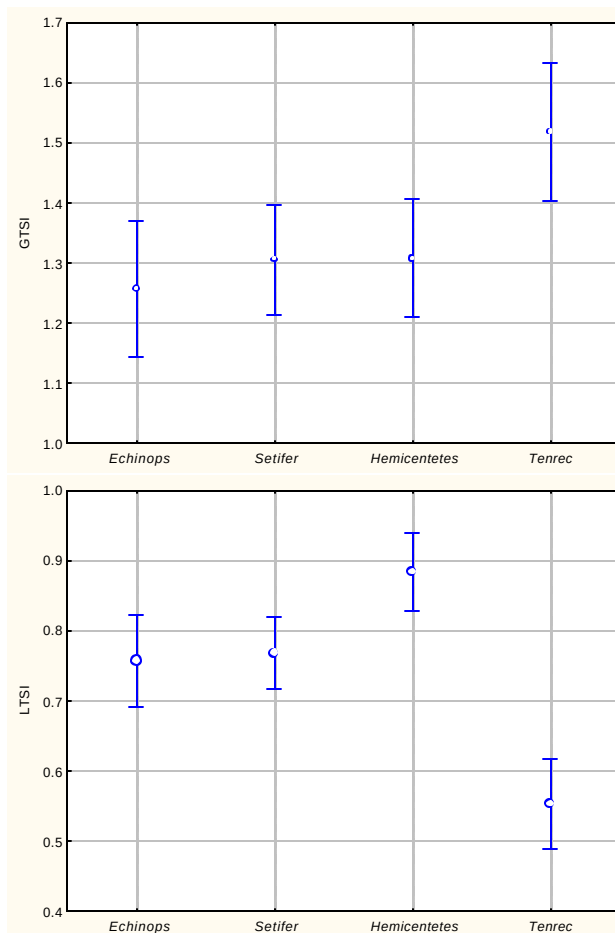


Figure 5.19. Greater Tuberosity Size Index (top) and Lesser Tuberosity Size Index (bottom) in tenrecines. *Tenrec* has a particularly large greater tuberosity paired with a small lesser tuberosity. *Hemicentetes* has a significantly larger lesser tuberosity than the other tenrecines ($p=0.00$).

Interpretation of the deltopectoral region of the humerus is difficult, due to an interplay of the attachment of the Mm. deltoideus and pectoralis musculature, which results in their varying functions as lateral rotators and abductors (deltoids), and adductors and retractors (pectorals). A large and/or expanded deltopectoral crest is found in arboreal marsupials (Argot 2001), arboreal primates (Gebo and Sargis, 1994) and fossorial rodents (Rose and Emry, 1983; Stein, 2000). In tenrecines, there is little development of the deltopectoral crest or deltoid tubercle. There is a small deltoid tubercle on the proximal quarter of most *Echinops* and *Setifer* specimens, a moderate crest in *Hemicentetes* and *Tenrec*, and a moderate tubercle at the distal third of the

Hemicentetes humerus (Fig 10). Of the oryzorictines, *Microgale cowani* and *Oryzorictes* have noticeable anterior pectoral crests and lateral deltoid tubercles, whereas *M. dobsoni*, *M. talazaci*, and *Limnogale* do not. The similarity between *M. cowani* and *Oryzorictes* is another indication (in addition to a lengthened scapula and other postcranial traits – see below) that *M. cowani* utilizes digging behavior more than the other two *Microgale* species.

Most of the variation in the width of the distal humerus is accounted for by the medial and lateral epicondyles. The medial and lateral epicondyles and the supracondylar ridge of the lateral epicondyle serve as origins for the wrist and digital flexor musculature (medially) and the extensors (laterally). These areas are therefore reliable indicators of flexion and extension of the hand, and are particularly well developed in a taxonomic range of climbers and diggers (e.g., Rose and Emry, 1983; Biknevicius, 1993; Stein, 2000; Argot, 2001; Grand and Barboza, 2001; Sargis, 2002). Relative to the width of the distal trochlea, overall width of the distal humerus is particularly great in the diggers *Hemicentetes*, *Oryzorictes*, and *Solenodon* (Figs. 5.11, 5.20, 5.21). *Potamogale* and *Petrodromus* have the narrowest distal humeri, reflecting less powerful wrist and hand flexion/extension.

There are significant differences between all tenrecines in medial epicondyle width (Figs. 5.11, 5.20, 5.23; $p < 0.02$ for all), indicating varying power of the flexors. *Echinops* has a significantly mediolaterally wider medial epicondyle than its sister taxon *Setifer*. *Hemicentetes* has the widest medial epicondyle, which is consistent with data from other mammalian diggers (Biknevicius, 1993; Stein, 2000; Grand and Barboza, 2001), and the relatively wide medial epicondyle in *Tenrec* suggests that it utilizes some

hand scratch digging that is not reflected at the shoulder joint. Of the oryzorictines, *Oryzorictes* has a significantly wider medial epicondyle than the others (Figs. 5.22, 5.23; $p=0.00$), and *Microgale cowani* has a significantly wider medial epicondyle than the other *Microgale* species. The medial epicondyle in *Solenodon* is wide, reflecting its digging behavior, and that of *Echinosorex* is low, within the range of *Potamogale* and *Petrodromus*. *Hemicentetes* has a wider lateral epicondyle than the other tenrecines or any other studied taxon (Fig. 5.24; $p<0.00$), but there are no significant differences between the other tenrecines or oryzorictines.

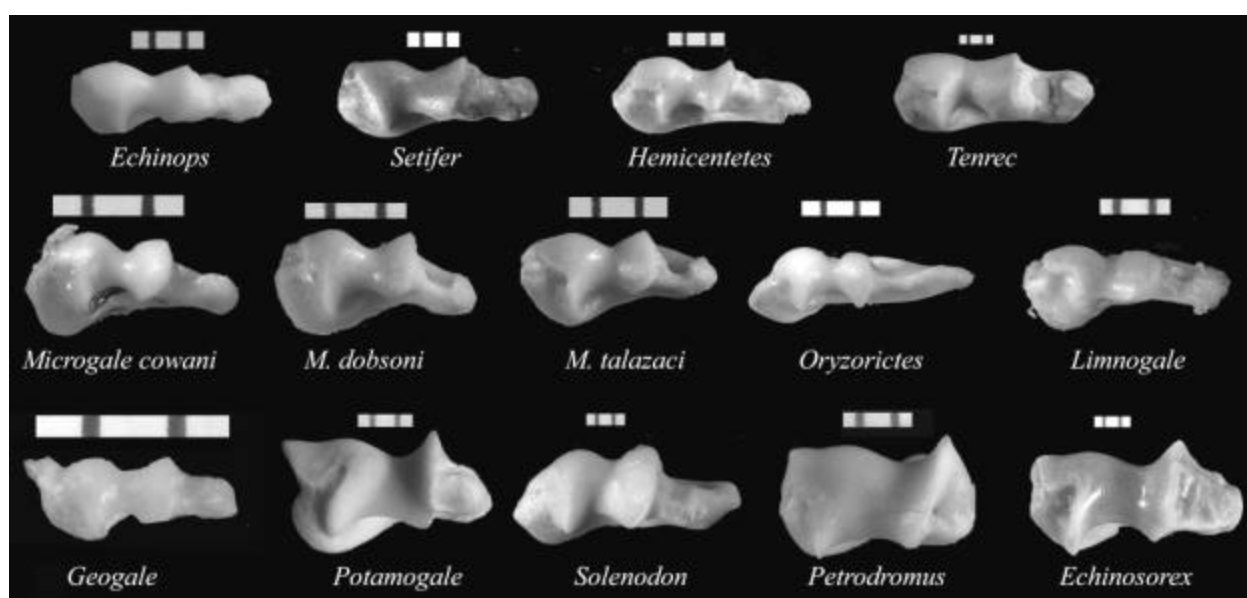


Figure 5.20. Distal surfaces of right humeri in four tenrecines (top), four oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa. Note differences in medial epicondyle mediolateral length, and sharpness of trochlear and capitulum edges.

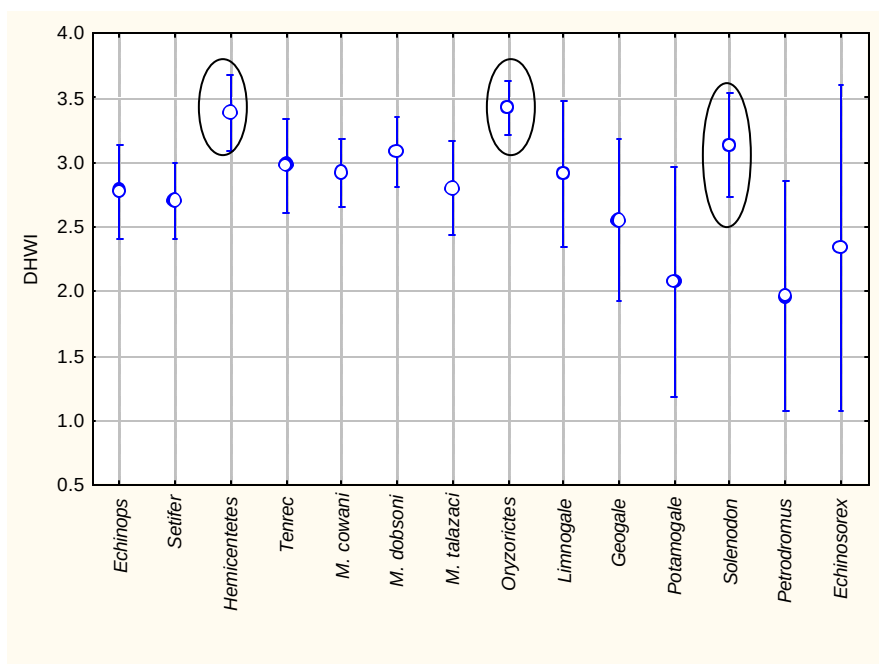


Figure 5.21. Distal Humerus Width Index in all studied taxa. The diggers *Hemicentetes*, *Oryzorictes* and *Solenodon* have particularly wide distal humeri.

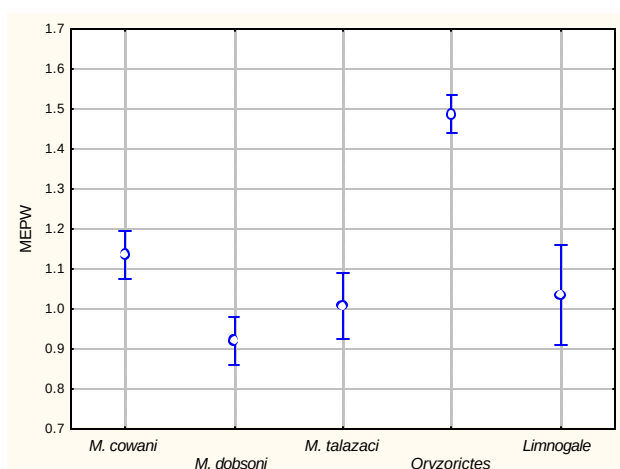


Figure 5.22. Medial Epicondyle Width Index in oryzorictines. The medial epicondyle in *Oryzorictes* is significantly wider than that of the others ($p=0.00$). *Microgale cowani* has a wider medial epicondyle than the other two *Microgale* species.

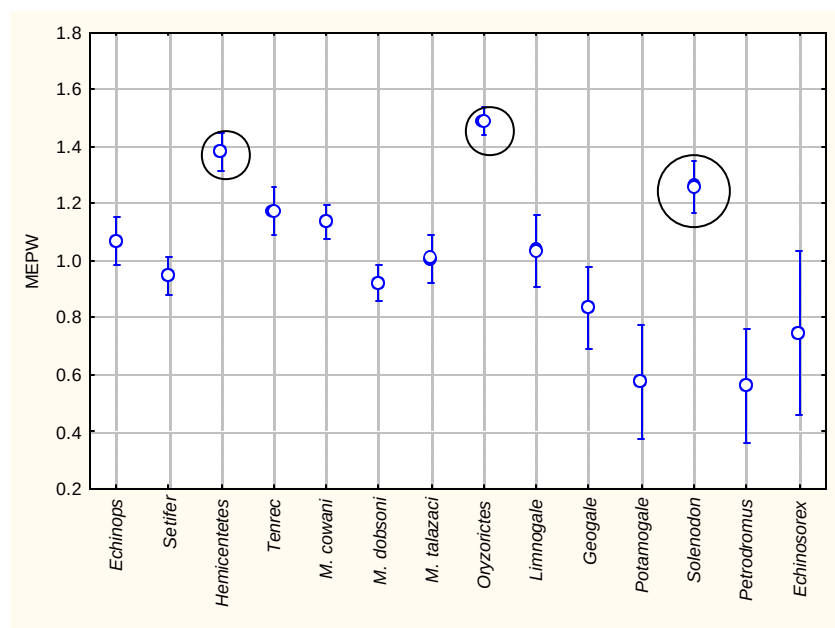


Figure 5.23. Medial Epicondyle Width Index in all studied taxa. The medial epicondyle is particularly wide in the three diggers (circled).

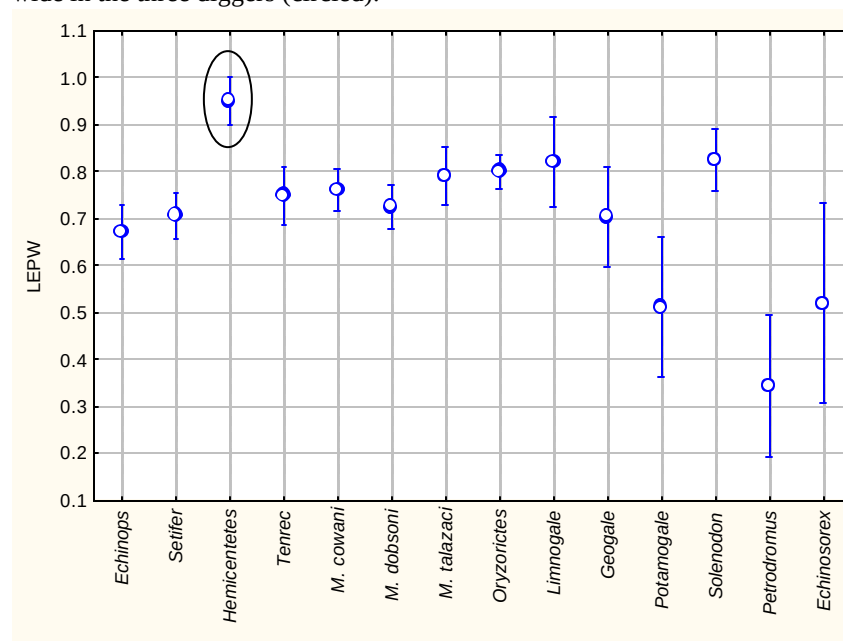


Figure 5.24. Lateral Epicondyle Width Index in all studied taxa. The tenrecine digger *Hemicentetes* has a particularly wide lateral epicondyle.

The entepicondylar foramen, which transmits the median nerve (Reed, 1951), is considered to be a primitive therian trait that has been lost in several mammalian taxa such as bats and catarrhine primates (e.g., Szalay and Dagosto, 1980; Ciochon, 1993; Simmons, 1994; Sargis, 2002). Interestingly, the presumably more basal of the tenrecoid

taxa, *Geogale* and *Potamogale* do not have an entepicondylar foramen, whereas there is a moderate entepicondylar foramen in all of the other tenrecoids (Fig. 5.11). Sargis (2002) suggested that its absence in the tupaiid *Urogale* might be related to digging, yet the tenrecine diggers (and *Solenodon*) have large entepicondylar foramina. In the Tenrecoidea there is little intraspecific variability (i.e. a foramen is always present or absent in adults of a given species), and the entepicondylar foramen is retained in all of the Malagasy tenrecoids, aside from *Geogale*. The loss of an entepicondylar foramen in *Potamogale* might have functional significance given the narrowing and specialization of its distal humerus, yet it does not follow for *Geogale*, which has few specializations of the forelimb. Additionally, macroscelidids retain an entepicondylar foramen, despite a similar narrowing and specialization of the distal humerus. This is most likely a trait that is easily lost in any particular taxon, and was perhaps lost later (relative to the branching off of Malagasy tenrecids) in the *Potamogale* and *Geogale* lineages.

Another highly variable, simple (and therefore taxonomically useless) feature on the mammalian humerus is the perforation of the coronoid fossa, through to the olecranon fossa. In tenrecoids, occasional perforation of the fossa occurs in the more terrestrial taxa, but, when present, this is an intraspecifically variable characteristic. None of the *Echinops* and *Hemicentetes* specimens have a perforated coronoid fossa, whereas 11% of *Setifer* specimens and 61% of *Tenrec* specimens have a complete perforation. Perforations were present in 10% of *Microgale cowani* and *M. dobsoni* humeri and 25% of *M. talazaci* specimens, but none were present in the humeri of *Oryzorictes*, *Geogale*, *Limnogale*, or *Potamogale*. The complete absence of this trait in a taxon is correlated with generally shallow coronoid and olecranon fossae, and its presence indicates deeper

fossae. Similar to the bicipital groove, the absence of a perforated coronoid fossa is not particularly meaningful functionally, as all taxa include specimens with a non-perforated fossa. Yet the presence of this trait is most likely correlated with a greatly extended forearm, indicative of terrestrial locomotion (see Szalay and Sargis, 2001).

All Malagasy tenrecoids have a well-defined, slightly rounded capitulum, whereas *Potamogale* has a mediolaterally lengthened and rectangular one with sharply defined medial and lateral borders (Fig. 5.11, 5.25). A distally flattened (as opposed to rounded) capitulum with well-defined borders is characteristic of more terrestrial vs. arboreal carnivores, primates, and scandentians (Szalay and Dagosto, 1980; Harrison, 1989; Rose, 1989; Gebo and Sargis, 1994; Sargis, 2002), and represents a restriction of radial rotation against the humerus. Aside from the flattened capitulum in *Potamogale*, the other tenrecids have a rather uniformly rounded capitulum that does not seem to vary with locomotor behavior. The capitulum in all tenrecoids remains relatively large and plays a significant role in load-bearing at the elbow, as opposed to a more derived mammalian condition where the trochlea takes over more direct loads at the elbow and the capitulum is reduced playing a more important role in movement associated with radial rotation (Szalay and Dagosto, 1980). *Potamogale*'s distal humerus suggests a highly stabilized forearm that does not allow for mediolateral excursion at the elbow. Its trochlea is mediolaterally short, medially bound by a steep incline and laterally bound by the sharp rectangular edge of the capitulum (Fig. 5.20). *Potamogale* and the elephant shrew *Petrodromus* share similar capitulum/trochlea articular form, yet other aspects of the distal humerus are distinct: *Petrodromus* has a wide entepicondylar foramen, complete perforation of the coronoid fossa, and a less extended medial epicondyle.

Setifer has a significantly deeper (proximodistally) trochlea than the other tenrecines (Figs. 5.18, 5.25, 5.26; $p=0.00$), which is typical of a more terrestrial animal (Szalay and Dagosto, 1980; Gebo and Sargis, 1994; Szalay and Sargis, 2001; Sargis, 2002) and represents extended surface area for ulnar articulation and medial restriction of ulnar articulation. *Microgale talazaci* has a significantly deeper trochlea than the other oryzorictines ($p=0.00$), yet other postcranial traits do not suggest that this species is more or less terrestrial than the others. There are no significant differences between any other taxa, reaffirming that such a highly function related trait as trochlear depth is not a particularly informative trait by itself, and certainly not of use for phylogenetic assessment in tenrecoids.

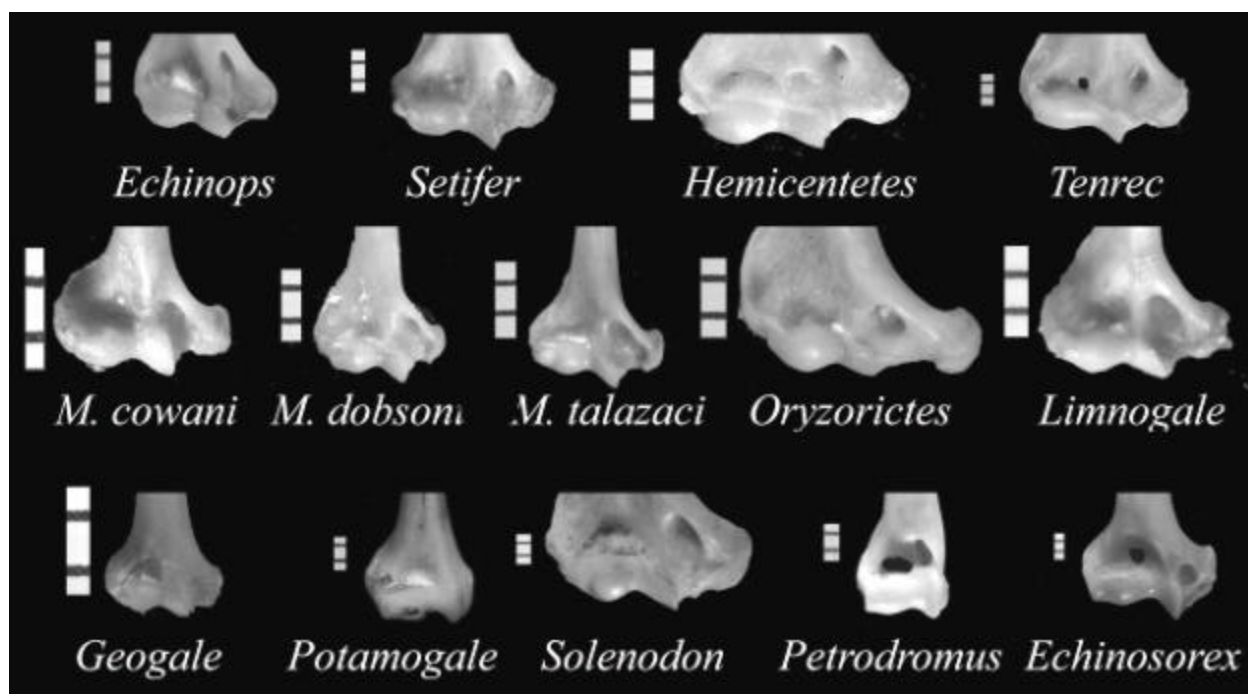


Figure 5.25. Anterior views of right distal humeri in four tenrecines (top), four oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa. Note differences in the shape of the trochlea and capitulum, especially the convergence in form between *Potamogale* and *Petrodromus*.

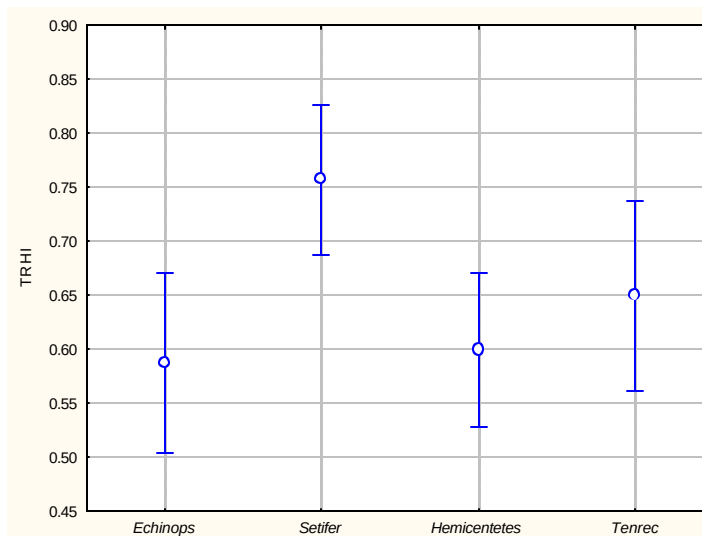


Figure 5.26. Trochlear Height Index in Tenrecinae. *Setifer* has a significantly higher trochlea than that in the other tenrecines.

Ulna

The overall shape of the ulna, as measured by width/height (UWI), is extremely variable between tenrecoid taxa, and highly correlated with locomotor behavior (Figs. 5.27, 5.28, 5.29). Other mammalian diggers exhibit relatively short, curved, and wide ulnae, while those of climbers tend to be relatively lengthened and narrow (Verma, 1963; Taylor, 1974; Casinos et al., 1993; Hildebrand, 1995; Stein, 2000; Grand and Barboza, 2001). Of the tenrecines, *Hemicentetes* has the widest ulna, and *Echinops* has the narrowest (Figs. 5.27, 5.29). *Setifer*'s UWI values are not significantly different from its sister taxon *Echinops*, and *Tenrec* is not significantly different from *Hemicentetes*, perhaps reflecting some climbing and digging, respectively, in these taxa. All three *Microgale* species have relatively long ulnae, though *M. cowani* has a significantly wider ulna than the other two (Fig. 5.29; $p=0.05$). *Oryzorictes*, *Potamogale*, and *Solenodon* have the shortest ulnae, with similar UWI values as *Hemicentetes*, reflecting a decreased out-lever of the forearm for increased out-force against a resistant substrate (i.e., soil/water). Despite some other shared traits with *Potamogale* that are related to

stabilizing articulations at potentially vulnerable joints, *Petrodromus* has an extremely long and narrow ulna which denotes its high-speed terrestrial mode of locomotion.

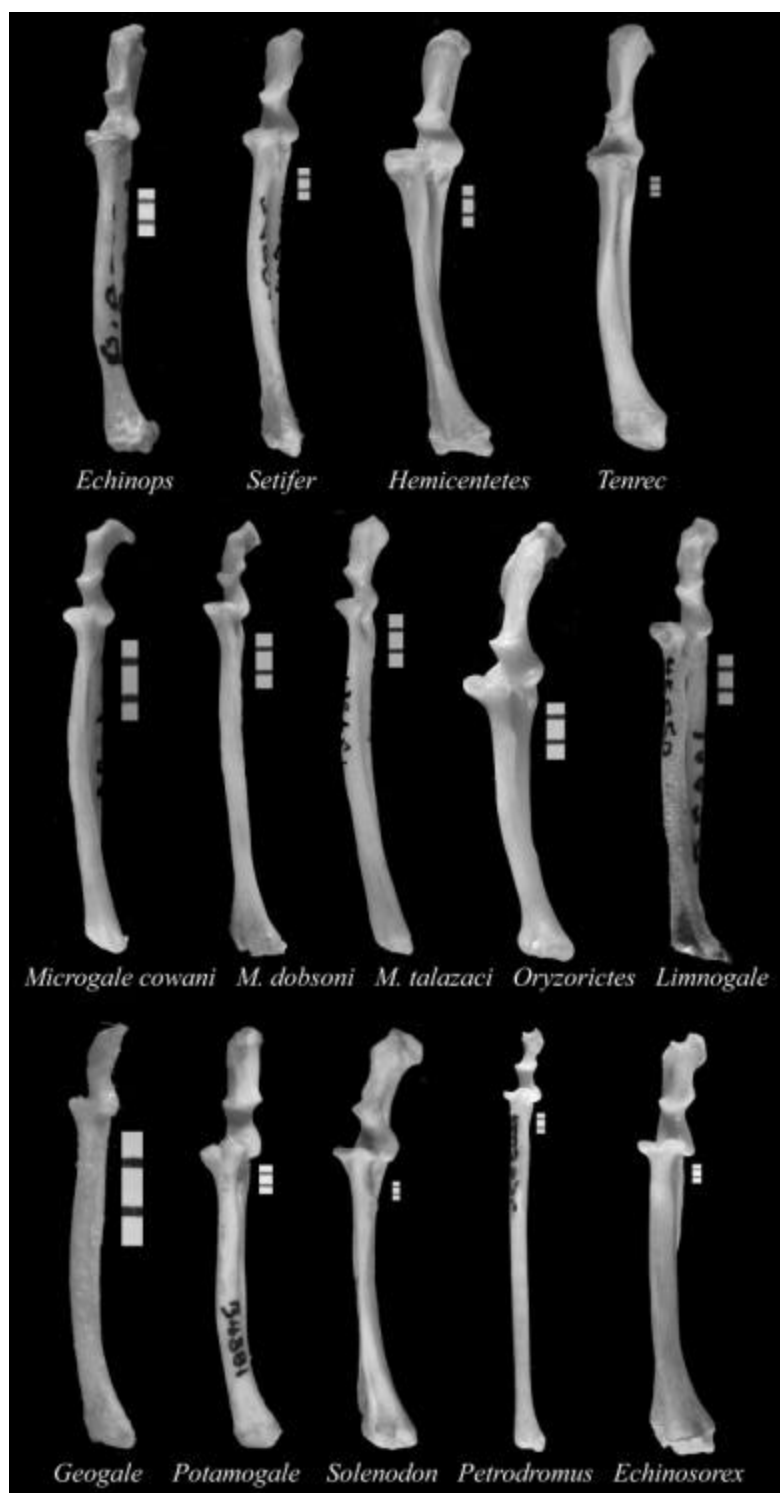


Figure 5.27. Anterior surfaces of right ulnae and radii in four tenrecines (top), four oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa. Note differences in ulna and radius shape, and relative length of the olecranon process.

The olecranon process, the attachment site for the long and lateral heads of the triceps brachii, has been well correlated with locomotor behavior in arboreal, terrestrial, and fossorial mammals (Verma, 1963; Rose and Emry, 1983; Van Valkenburgh, 1987; Biknevicius, 1993; Ciochon, 1993; Stein, 2000; Argot, 2001; Sargis, 2002; Grand and Barboza, 2001). As the olecranon process increases, the Mm. triceps gain leverage for powerful ulnar extension against the humeral trochlea. Fossorial mammals have a particularly elongated olecranon process for digging, whereas those of climbers are less elongated, which allows for maximal elbow extension (Hildebrand, 1995).

As with ulnar shape, there are significant function-based differences between tenrecoids in the length of the olecranon process. Within Tenrecinae, both *Hemicentetes* and *Tenrec* have high Olecranon Process Length Index (OPLI) values, whereas *Echinops* and *Setifer* have low values, indicating a shorter process (Figs. 5.28, 5.30). All three *Microgale* species have relatively small olecranon processes, yet that of *M. cowani* is significantly longer than the others (Figs. 5.28, 5.31, $p=0.00$), suggestive of some digging. *Oryzorictes* has a much longer olecranon process than any of the studied taxa (Figs. 5.28, 5.30; $p=0.00$). *Limnogale* and *Potamogale* both have long processes, with similar average OPLI values as *M. cowani*. Surprisingly, *Solenodon* has a shorter olecranon process than the other diggers, as well as *Tenrec*, although it is still of moderate size, in the range of *Potamogale* and *Echinosorex*.

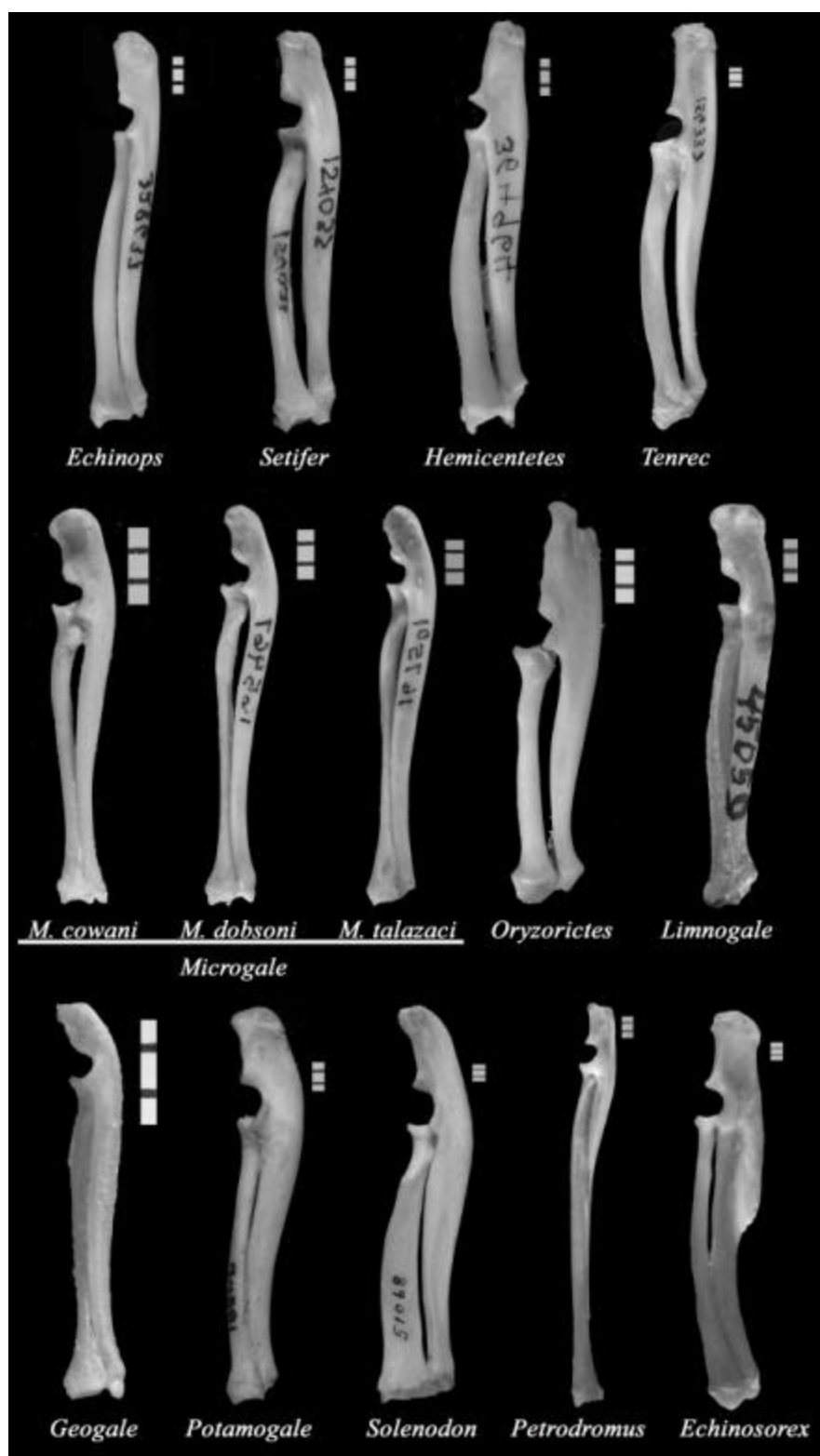


Figure 5.28. Medial views of right ulnae and radii in tenrecines (top row), oryzorictines (middle row), two other tenrecoids (bottom left), and three outgroup taxa (bottom right). Note differences in olecranon process length and shape, trochlear notch shape, and widening of the radius along the shaft.

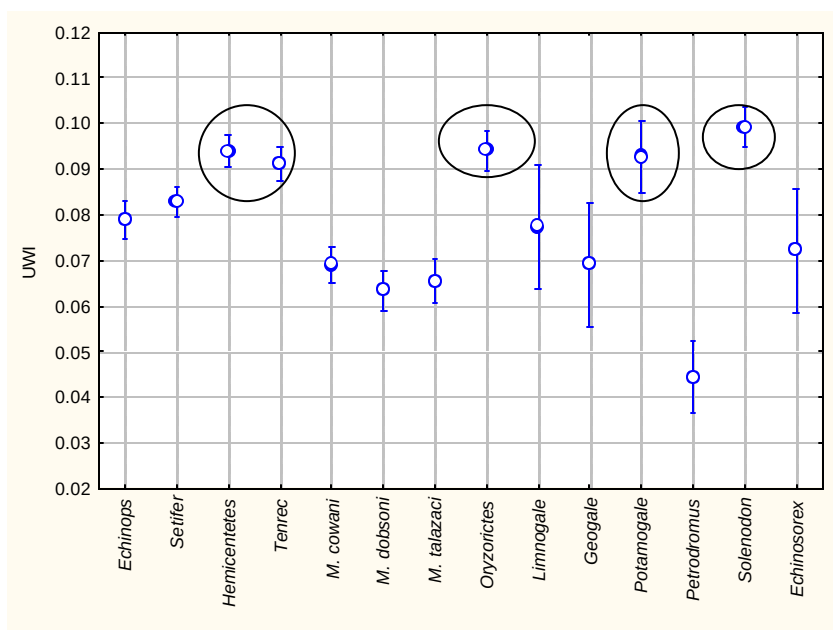


Figure 5.29. Ulnar Width Index in all studied taxa. Digging taxa and *Potamogale* have a particularly wide and short ulna.

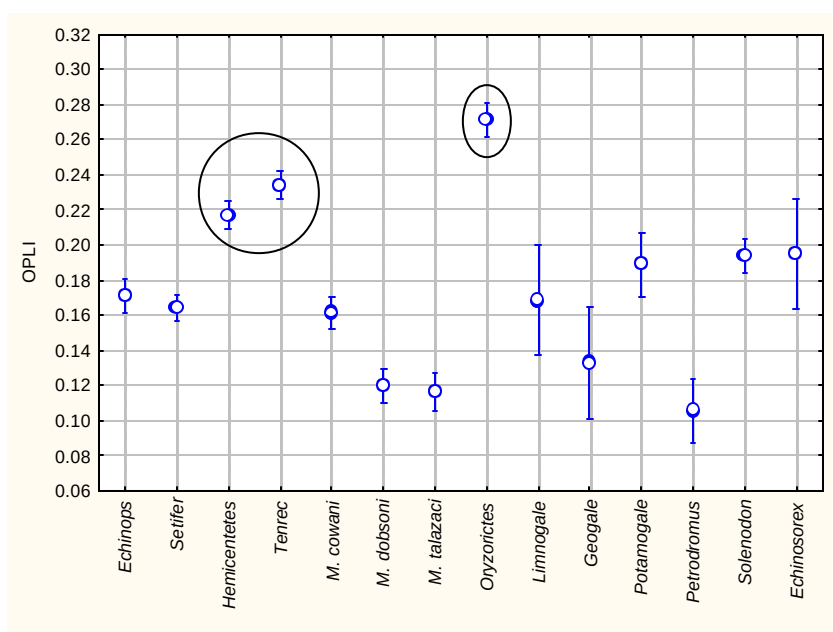


Figure 5.30. Olecranon Process Length Index in all studied taxa. The digging tenrecines and *Oryzomys* have relatively long olecranon processes.

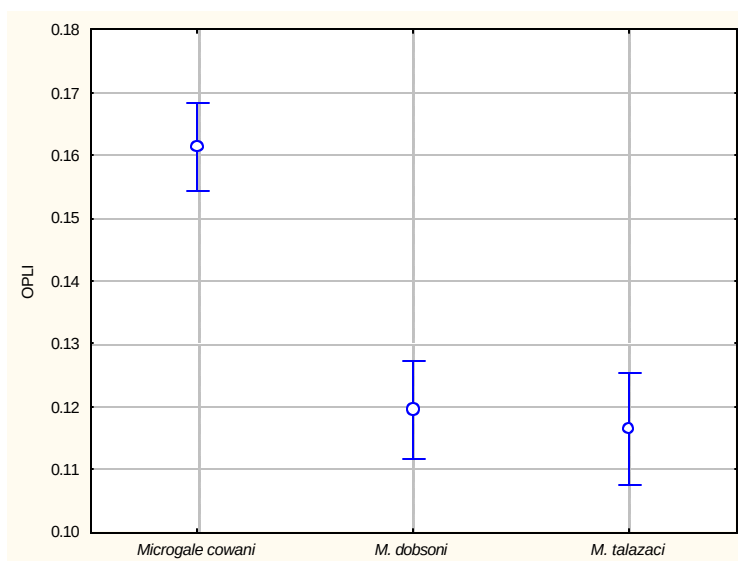


Figure 5.31. Olecranon Process Length Index in the three *Microgale* species. *M. cowani* has a significantly longer olecranon process than the other two species ($p=0.00$).

Radius

Results from the Radial Width Index are almost identical to the ulnar width index: digging tenrecoids, *Potamogale*, and *Solenodon* all have relatively wide radii, whereas the climber and more terrestrial genera have a longer, narrower radius (Fig. 5.32). This makes sense from the same general function-based perspective for the ulna. Radial form in the diggers *Hemicentetes*, *Oryzorictes*, and *Solenodon* is also distinct in its transition from being relatively narrow at its proximal shaft to up to twice its proximal thickness at the distal shaft. In contrast, the ulna, with its long and thick olecranon process, narrows at its distal end to the same degree as in the other taxa (Fig. 5.28). Clearly the radius plays an important load-bearing role at the proximal wrist joint, and limits rotational movement of the wrist, whereas the proximal ulna plays more of a load-bearing role at the elbow joint, and the relatively small radial head does little to facilitate rotation. Although other studies have found a more elliptical radial head in diggers (Reed, 1951; Stein, 2000), the shape of the radial head is not more elliptical in *Oryzorictes* than in the other taxa, yet it

is distinct in form. Two processes of the anterior radial head surface (which are present but small in some other taxa) serve to fold over and cup the capitulum, stabilizing the elbow joint along its anteroposterior axis (Fig. 5.33). *Potamogale* and *Solenodon* have similar outgrowths of the proximal radial head, and *Potamogale* has an additional posterior notch that fits into a distinct groove at the distalmost aspect of the capitulum (see *Potamogale* distal humerus, Fig. 5.20). The radial head in the arboreal *Echinops* is more rounded than in the other three tenrecines, but not more so than in *Limnogale* or *Geogale*, which also have rounded radial head surfaces. *Petrodromus* represents the extreme in having an enormously mediolaterally elongated capitulum, which offers a large surface area for humeral articulation and restricts rotation.

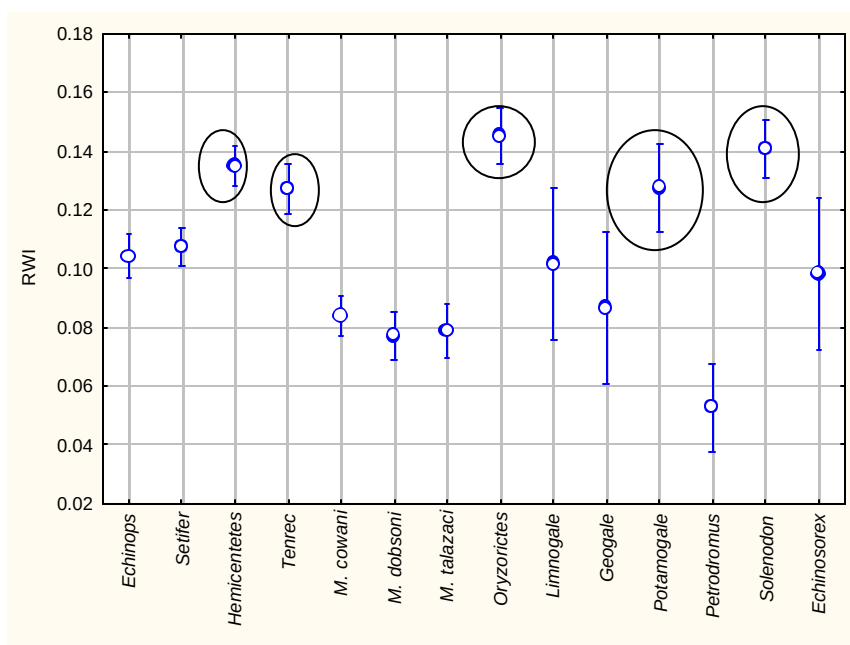


Figure 5.32. Radius Width Index in all studied taxa. The radius is relatively wide and short in digging taxa and *Potamogale*.

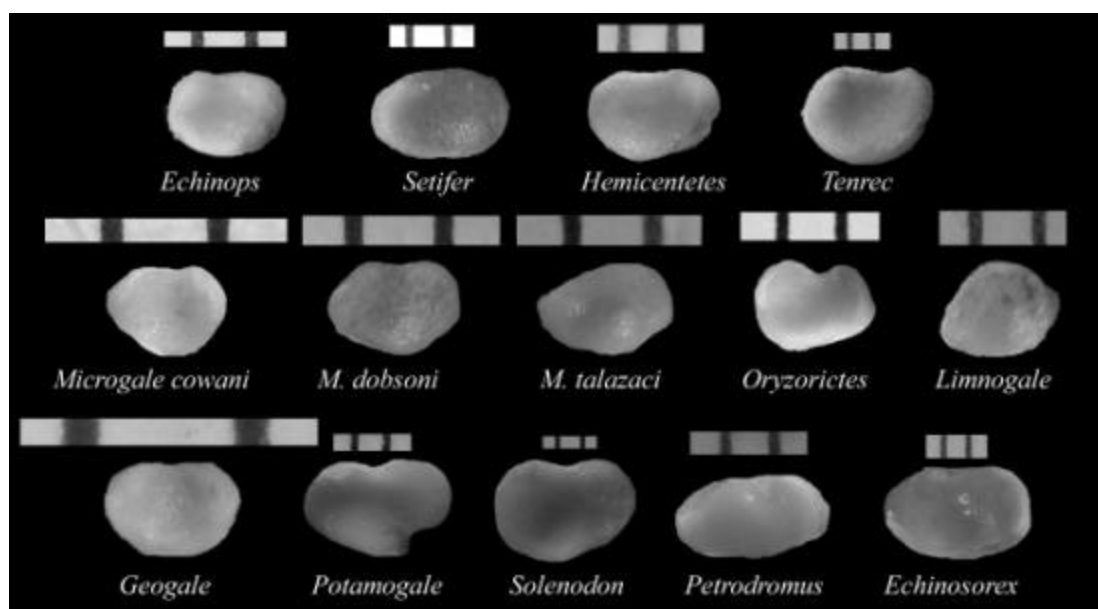


Figure 5.33. Proximal surfaces of right radii, top is anterior, bottom is posterior. Note differences in radial head shape, ranging from rounded, as in *Limnogale*, to elliptical, as in *Petrodromus*.

Summary and Conclusions

In the previous chapters on the tenrecoid tarsals, carpals, and hindlimb, the conclusions were presented separately under the various subfamily headings, and variation in skeletal form, in addition to features with clear function-based correlates were included within. Unlike other regions of the postcranial skeleton in this study, the forelimb offered little in terms of understanding phylogenetic relationships between taxa. Features of the shoulder and elbow joints, and the associated bones, are highly variable between particular genera and species and show few consistent subfamily-level differences. Forelimb (and scapular) form is highly dependent on species-specific behavior, and is not as constrained as, for example, aspects of the hindlimb.

As discussed in Chapter IV, tenrecines and oryzorictines have a series of differences in the hindlimb skeleton that are correlated with differences in basic posture. The tenrecine hindlimb is more laterally rotated, and allows for much more general rotational movement than the oryzorictine hindlimb. Oryzorictines have a parasagittally

directed knee and foot and show much more constraint against mediolateral leg movement. Both *Geogale* and *Potamogale* vary from the tenrecine and oryzorictine hindlimb patterns, exhibiting some novel aspects of form, as well as some combination of tenrecine and oryzorictine traits. The forelimb, however, does not exhibit subfamily-level differences between tenrecines and oryzorictines that can be attributed to any basic differences in known positional behavior, or which may be attributed to phylogenetic inertia. Analysis of variance does not show tenrecine and oryzorictine indices to cluster as they did in analyses from other postcranial regions. Aside from some similarities between the sister taxa *Echinops* and *Setifer* that appear to be phylogenetically significant and unrelated to locomotor specialization, each genus demonstrates function-based variation that often corresponds with hypotheses based on other mammalian locomotor specialists.

***Echinops* and *Setifer*: arboreal vs. terrestrial tenrecines**

The tenrecines *Echinops* and *Setifer* offer a good model for investigating skeletal differences that have been strongly influenced by an arboreal habitat. These sister taxa are extremely difficult to distinguish with superficial characteristics, though *Setifer* has four extra molars, and tends to have a greater average body mass. Postcranial regions other than the forelimb show several similarities between the two taxa that seem to be based on climbing behavior (see previous chapters and Salton and Szalay, 2004), and might indicate an arboreal common ancestor between the two. Postcranial differences, especially in the tarsus, demonstrate convergences between *Echinops* and other mammalian climbers, and between *Setifer* and more terrestrial taxa.

The forelimb of *Echinops* exhibits several differences from *Setifer* that are indicative of arboreal, as opposed to more terrestrial, behavior in the latter, including a longer acromion process, a slightly wider glenoid fossa, a rounder and larger humeral head, a mediolaterally wider medial epicondyle, a narrow, relatively long ulna, and a round articular surface of the radial head. Several features in common between the two taxa and not shared by *Hemicentetes* or *Tenrec* include a large, rounded scapular surface area for the supraspinatus with a steep cranial border, rectangular infraspinous fossa, deltoid tubercle on the lateral edge of the humerus, wide distal humerus, short olecranon process, and long, narrow radius. These shared traits have been associated with climbing in other mammals (see Table 4.1), and other shared postcranial characteristics also tend to be characteristic of arboreal behavior (see Chapters II-IV). It is possible that *Setifer* climbs more than reports would suggest. My experience with *Setifer* in the field led me to believe that *Setifer* nests on the ground, but is able to climb when prodded to do so (as can *Tenrec*, see Eisenberg and Gould, 1970). As I suggested in earlier chapters, the shared traits between *Setifer* and *Echinops* more likely reflect a shared common ancestor that was arboreal rather than the proposed model of a *Setifer*-like ancestor.

***Hemicentetes*, *Oryzorictes*, and *Solenodon*: fossorial/semi-fossorial**

As already established by many other studies on fossorial mammals, digging behavior is strongly indicated in scapular and forelimb morphology. The semi-fossorial *Hemicentetes* and *Solenodon*, as well as the fossorial *Oryzorictes*, have a suite of characteristics that demonstrate extremely high loads incurred by the elbow and shoulder during digging. The *Tenrec* postcranium has some characteristics that suggest digging

behavior as well, though not to the extent of the other three genera. Particularly evident traits include: an elongated, narrow scapula, short and wide humerus with flared medial epicondyles, pronounced attachment sites for the deltoid and pectoral musculature, well-developed bicipital grooves (sometimes forming a complete tunnel), proximodistally and anteroposteriorly elliptical humeral heads, long olecranon processes, and short and wide ulnae and radii.

***Limnogale* and *Potamogale*: semi-aquatic**

Other regions of the postcranium demonstrate some similarities between *Limnogale* and *Potamogale*, which are most likely based on a shared semi-aquatic habitus. In previous chapters I proposed that differences in the details of postcranial form do not point to a close common ancestry between *Limnogale* and *Potamogale*, and rather suggest that *Limnogale* is an oryzorictine, as supported by recent molecular data (Olson and Goodman, 2003). Morphology of the forelimb demonstrates very little similarity at all between *Limnogale* and *Potamogale*, despite their shared swimming behavior, and suggests that they use their arms in very different ways. *Limnogale* has a large acromion process (*Potamogale* has almost none), large lesser tuberosity, small greater tuberosity, relatively short humerus, wide distal humerus and medial epicondyle with entepicondylar foramen, and rounded capitulum. *Limnogale* shares several of these features with the other oryzorictines, and it seems apparent that its similarities to *Potamogale* are function-based convergences rather than phylogenetically meaningful attributes. The differences between them emphasize the importance for forelimb stability and unilateral motion in the *Potamogale* limb, whereas *Limnogale* most likely uses its arms for steering and

changing direction (and perhaps more grooming and digging while on land), in addition to aquatic paddling. Unlike the other tenrecoids, *Potamogale* and *Geogale* have no entepicondylar foramen, which is an interesting observation given that *Potamogale* and *Geogale* are hypothesized basal tenrecoid taxa. This is demonstrative of the argument made by Szalay and Bock (1991); character states, e.g., the presence of an entepicondylar foramen, might be primitive for a particular taxon, but a more basal taxon does not necessarily provide a suite of primitive taxon-specific traits. This presents a potential problem for cladistic analyses that are weighted by outgroups which are assumed to have a compilation of primitive characters, but may exhibit a number of derived traits based on taxon-specific habitus.

***Microgale* spp.: terrestrial/fossorial?**

The three *Microgale* species examined for this study are usually referred to as terrestrial, with some possible climbing in *M. talazaci* (based on foot and tail length, Eisenberg and Gould, 1970). This study, as well those of the preceding chapters, confirms a series of characteristics correlated with terrestrial running, and does not find any traits in *M. talazaci* that suggest climbing behavior. Rather, the forelimb (and other regions) of the *M. cowani* skeleton exhibits several features characteristic of a digger, such as a long and narrow scapula, large pectoral crest and deltoid tubercle, wide medial epicondyle, and short and wide ulna with a long olecranon process. Olson and Goodman's (2003) molecular phylogeny of *Microgale* does not place *M. cowani* anywhere near the root of the *Microgale* tree. This suggests that *M. cowani*, rather than

being a close relative of *Oryzorictes*, may have convergently evolved a series of similar traits based on more frequent digging behavior than is recognized in the literature.

***Petrodromus*: cursorial**

The elephant shrew *Petrodromus* is the fastest running animal of all the taxa examined in this study, and the forelimb exhibits many traits (as does the hindlimb) that reflect the importance of joint stabilization and restriction of movement to the parasagittal plane. Though its overall scapular shape is unremarkable, the metacromion process is long and narrow, and the glenoid fossa is spherical with a long overhanging coracoid process. The humerus is narrow and long with an enormous coronoid/olecranon fossa and a flat, spindle-shaped capitulum. The greater tuberosity is very robust and rises above the humeral head, and the medial and lateral epicondyles are almost nonexistent. The ulna has a very short olecranon process, and is completely straight, long and thin. The radius is also long and thin, and the radial head is mediolaterally elliptical to an extreme.

Petrodromus and *Potamogale* share similar form at the distal articular surface of the humerus. But small-scale differences, such as the angle of the trochlea and the shape of the capitular tail, strongly suggest that the similarities are convergent and based on the need for joint stabilization.

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Appendix 5.1. Linear Measurements (mm)

Taxon	ID	Lscap1	Lscap2	Taxon	ID	Dscap1	Taxon	ID	Pscap	Pscap
Echinops	170605	17.1326	7.4992	Echinops	207717	17.1349	Echinops	170605	1.9190	1.7035
Echinops	170607	14.6771	7.4417	Echinops	207718	19.1147	Echinops	170607	2.5417	1.8647
Echinops	207717	14.3799	6.1508	Echinops	212918	17.8261	Echinops	207717	2.7345	1.8650
Echinops	207718	12.8442	7.2245	Echinops	212919	19.7240	Echinops	207718	2.7564	1.8843
Echinops	212918	14.3277	7.7974	Echinops	328620	17.7911	Echinops	212918	2.7596	1.7973
Echinops	212919	15.1419	7.4090	Echinops	328636	17.3481	Echinops	212919	2.7863	1.6010
Echinops	31270	17.7356	6.9525	Echinops	328637	22.6406	Echinops	31270	2.6045	1.9282
Echinops	328620	15.8020	7.9744	Echinops	395835	20.4044	Echinops	328620	2.7430	1.6649
Echinops	328636	16.0933	6.2541	Echinops	464980	18.4318	Echinops	328636	2.4734	1.6711
Echinops	328637	19.3287	8.3509	Echinops	588220	21.7152	Echinops	328637	2.5206	1.9257
Echinops	395835	16.4752	8.1596	Setifer	154034	30.1199	Echinops	395835	2.6184	1.8397
Echinops	464980	17.0609	7.8924	Setifer	159731	24.1428	Echinops	464980	2.6285	1.8783
Echinops	588220	16.9681	8.4542	Setifer	165494	27.3623	Echinops	588220	2.8978	1.8464
Setifer	154033	22.5001	10.5082	Setifer	166159	23.5834	Setifer	154033	4.1178	2.7288
Setifer	154034	27.3940	13.3422	Setifer	170532	27.5493	Setifer	154034	3.8778	2.9919
Setifer	159731	20.7090	9.9562	Setifer	170548	29.5086	Setifer	159731	3.4026	2.2211
Setifer	165494	24.7156	12.0198	Setifer	170581	27.4053	Setifer	165494	4.0333	2.7071
Setifer	166159	19.9589	11.7614	Setifer	170731	27.5149	Setifer	166159	3.8285	2.3686
Setifer	170532	22.4492	11.0661	Setifer	207076	27.9086	Setifer	170532	3.3638	2.5083
Setifer	170548	23.7724	11.9812	Setifer	328612	23.6821	Setifer	170548	4.2751	2.6094
Setifer	170581	24.3725	10.8359	Setifer	33948	26.1968	Setifer	170581	3.3498	2.6448
Setifer	170730	24.7499	12.3742	Setifer	395719	23.6713	Setifer	170730	4.2941	2.7152
Setifer	170731	22.1868	12.3282	Setifer	541443	27.8349	Setifer	170731	3.7391	2.7812
Setifer	207076	22.3740	9.4244	Setifer	578790	25.5752	Setifer	207076	3.6984	2.4444
Setifer	328612	21.9677	10.3284	Setifer	85170	27.5185	Setifer	328612	3.5341	2.4741
Setifer	33948	23.7890	11.1966	Setifer	85513	26.1373	Setifer	33948	4.2536	2.9515
Setifer	395513	22.7878	12.0036	Hemicentetes	83658	35.9552	Setifer	395513	3.9784	2.7627
Setifer	395719	20.8662	9.6021	Hemicentetes	166132	24.5798	Setifer	395719	4.0077	2.5129
Setifer	541443	24.0981	13.2091	Hemicentetes	206755	21.2149	Setifer	541443	4.2464	2.7337
Setifer	578790	19.5393	9.5269	Hemicentetes	207712	29.0047	Setifer	85170	4.4513	2.8448
Setifer	85170	24.1201	13.0129	Hemicentetes	207714	23.1654	Setifer	85513	4.0952	2.9257
Setifer	85513	24.7283	12.3996	Hemicentetes	212920	22.1824	Hemicentetes	83658	4.5344	2.7530

Appendix 5.1 (con't)

Taxon	ID	Lscap1	Lscap2	Taxon	ID	Dscap1	Taxon	ID	Pscap	Pscap
Hemicentetes	83658	29.1609	12.6810	Hemicentetes	212921	26.7902	Hemicentetes	162062	3.8531	1.9902
Hemicentetes	162062	20.2495	9.0431	Hemicentetes	212922	0.0236	Hemicentetes	166132	3.7613	2.2866
Hemicentetes	166132	20.9389	9.1227	Hemicentetes	212924	26.7265	Hemicentetes	170593	2.6019	1.7750
Hemicentetes	170593	13.6264	5.8692	Hemicentetes	212940	23.1480	Hemicentetes	206755	2.3149	1.6388
Hemicentetes	206755	17.4092	7.6259	Hemicentetes	339992	22.2429	Hemicentetes	207712	3.8501	2.5887
Hemicentetes	207712	22.5474	9.4756	Hemicentetes	354998	22.2988	Hemicentetes	207714	3.8579	2.1402
Hemicentetes	207714	20.1286	9.5475	Hemicentetes	364954	21.7626	Hemicentetes	207715	3.0270	1.9558
Hemicentetes	207715	17.3510	7.8112	Tenrec	154628	39.6039	Hemicentetes	212920	3.3514	2.2319
Hemicentetes	212920	19.4936	7.8052	Tenrec	156337	36.2999	Hemicentetes	212921	3.3786	2.4868
Hemicentetes	212921	22.2206	9.4536	Tenrec	170511	41.0950	Hemicentetes	212922		
Hemicentetes	212922	18.6792	8.9987	Tenrec	361485	42.0785	Hemicentetes	212924	3.9465	2.2628
Hemicentetes	212924	22.2433	9.0809	Tenrec	364955	44.3734	Hemicentetes	212940	3.6477	2.2716
Hemicentetes	212940	19.5960	8.8721	Tenrec	577051	36.9040	Hemicentetes	339992	3.5765	2.2600
Hemicentetes	339992	18.7130	8.3769	Tenrec	578792	40.7505	Hemicentetes	354998	3.3424	2.0947
Hemicentetes	354998	20.2483	9.3355	Tenrec	154629	39.4003	Hemicentetes	364954	3.3330	2.0915
Hemicentetes	364954	18.5729	8.3060	Tenrec	59011	48.4559	Tenrec	154628	6.4703	4.0076
Tenrec	154628	36.6893	16.4227	Tenrec	60587	45.9011	Tenrec	156337	6.5308	3.9328
Tenrec	156337	35.6462	18.0560	M. cowani	151654	9.9627	Tenrec	170511	7.0511	4.3216
Tenrec	170511	37.8881	17.4162	M. cowani	151656	0.5711	Tenrec	30398	7.2669	5.2234
Tenrec	30398	39.7064	17.7555	M. cowani	154020	9.2439	Tenrec	361485	6.4061	3.7158
Tenrec	361485	39.2795	20.6014	M. cowani	154026	10.5099	Tenrec	364955	6.5127	4.0410
Tenrec	364955	41.8090	19.6467	M. cowani	156195	9.3730	Tenrec	577051	7.0207	4.1873
Tenrec	577051	35.2218	15.3755	M. cowani	156196	9.7286	Tenrec	578792	4.2240	3.9074
Tenrec	578792	37.9039	16.5736	M. cowani	156197	10.7061	Tenrec	154629	5.9731	3.6923
Tenrec	154629	35.0538	17.4231	M. cowani	156221	10.4063	Tenrec	59011	7.8716	5.3123
Tenrec	59011	46.9683	21.1853	M. cowani	156222	10.2593	Tenrec	60587	5.7331	3.8331
Tenrec	60587	40.8872	20.1204	M. cowani	156223	10.8699	M. cowani	151654	1.2204	0.8769
M. cowani	151654	8.9399	3.2898	M. cowani	165672	9.9906	M. cowani	151656	1.2113	0.8574
M. cowani	151656	9.5307	3.5730	M. cowani	165674	10.5017	M. cowani	154020	1.4642	0.9094
M. cowani	154020	8.8152	3.2773	M. cowani	165676	10.1758	M. cowani	154026	1.3976	0.9166
M. cowani	154026	8.4878	3.1819	M. cowani	165689	10.5896	M. cowani	156195	1.2215	0.8025
M. cowani	156195	8.8427	3.3531	M. cowani	168017	9.8851	M. cowani	156197	1.2998	0.9236
M. cowani	156196	9.2060	4.2490	M. cowani	328658	10.1879	M. cowani	156221	1.4216	0.9918
M. cowani	156197	9.2614	3.4839	M. cowani	449186	9.4828	M. cowani	156222	1.4368	0.9328
M. cowani	156221	8.9383	4.1710	M. cowani	449187	9.5975	M. cowani	156223	1.5688	0.9980

Appendix 5.1 (con't)

Taxon	ID	Lscap1	Lscap2	Taxon	ID	Dscap1	Taxon	ID	Pscap	Pscap
M. cowani	156222	9.1212	4.1086	M. cowani	449188	10.1890	M. cowani	165672	1.3190	0.8820
M. cowani	156223	9.1914	4.2517	M. dobsoni	151624	13.8712	M. cowani	165674	1.6000	1.0313
M. cowani	165672	8.8422	3.5999	M. dobsoni	151625	12.9660	M. cowani	165676	1.3972	0.9355
M. cowani	165674	9.0829	4.0134	M. dobsoni	156224	13.0850	M. cowani	165689	1.5009	0.9775
M. cowani	165676	8.7706	3.8112	M. dobsoni	156225	12.7985	M. cowani	168017	1.4364	0.8576
M. cowani	165689	9.3441	3.7259	M. dobsoni	159497	12.5384	M. cowani	328658	1.4423	0.7688
M. cowani	168017	8.9928	4.3337	M. dobsoni	159498	12.7468	M. cowani	449184	1.2529	1.0222
M. cowani	328658	8.4289	3.3724	M. dobsoni	159499	13.0564	M. cowani	449186	1.2746	0.8413
M. cowani	449184	8.9237	3.7889	M. dobsoni	161678	12.6229	M. cowani	449187	1.3213	0.9002
M. cowani	449186	8.6215	3.6190	M. dobsoni	161679	12.3655	M. cowani	449188	1.3426	0.7996
M. cowani	449187	8.9108	3.7608	M. dobsoni	161718	14.0121	M. dobsoni	151624	2.0659	1.3320
M. cowani	449188	8.6929	3.2935	M. dobsoni	161935	13.6998	M. dobsoni	151625	1.8999	1.0821
M. dobsoni	151624	5.2064	9.3305	M. dobsoni	161940	13.5025	M. dobsoni	156224	1.8213	1.2527
M. dobsoni	151625	11.8896	5.1628	M. dobsoni	165467	14.9906	M. dobsoni	156225	1.8908	1.2781
M. dobsoni	156224	11.9238	5.5215	M. dobsoni	165774	13.2180	M. dobsoni	159497	1.8405	1.1851
M. dobsoni	156225	11.6930	5.7355	M. dobsoni	165775	2.5132	M. dobsoni	159498	1.8224	1.1454
M. dobsoni	159497	11.6624	5.2381	M. dobsoni	166107	14.2422	M. dobsoni	159499	1.9590	1.1503
M. dobsoni	159498	11.5669	5.2302	M. dobsoni	166198	12.4022	M. dobsoni	161718	2.2316	1.2720
M. dobsoni	159499	11.1548	5.0343	M. dobsoni	166200	12.9510	M. dobsoni	161935	2.1395	1.2750
M. dobsoni	161678	12.2459	5.0434	M. dobsoni	578749	12.3514	M. dobsoni	161940	1.9484	1.2525
M. dobsoni	161679	11.9172	4.9867	M. dobsoni	582730	13.1628	M. dobsoni	165467	1.9189	1.2140
M. dobsoni	161718	12.2191	6.0039	M. dobsoni	578749	12.1702	M. dobsoni	165774	1.7686	1.2717
M. dobsoni	161935	12.7232	5.5926	M. talazaci	154581	14.4679	M. dobsoni	165775	1.7106	1.2396
M. dobsoni	161940	11.7247	6.0271	M. talazaci	154585	14.9704	M. dobsoni	166107	2.0601	1.3345
M. dobsoni	165467	13.1015	6.5349	M. talazaci	577056	14.1012	M. dobsoni	166198	1.8175	1.0820
M. dobsoni	165774	11.7725	5.5470	M. talazaci	159692	15.7318	M. dobsoni	166200	1.7912	1.1360
M. dobsoni	165775	10.6687	5.0689	M. talazaci	162038	14.1791	M. dobsoni	578749	1.6179	1.0677
M. dobsoni	166107	13.3253	6.0421	M. talazaci	162039	0.0839	M. dobsoni	582730	1.7613	1.2011
M. dobsoni	166198	11.0406	4.4584	M. talazaci	162040	14.8631	M. talazaci	154581	2.2587	1.3547
M. dobsoni	166200	11.3391	5.1506	M. talazaci	167500	15.5288	M. talazaci	154585	2.1041	1.4371
M. dobsoni	578749	11.0818	5.5784	M. talazaci	167501	15.4580	M. talazaci	577056	2.0851	1.2448
M. dobsoni	582730	12.0898	5.5811	M. talazaci	167502	15.2050	M. talazaci	159692	2.4121	1.4527
M. dobsoni	578749	11.0867	5.5709	M. talazaci	167503	15.5637	M. talazaci	162039	2.1212	1.4156
M. talazaci	154581	12.4695	6.9169	Oryzorientes	156226	16.6716	M. talazaci	162040	1.9727	1.2215
M. talazaci	154585	13.2948	7.6402	Oryzorientes	156601	16.4372	M. talazaci	166234	2.2151	1.4305

Appendix 5.1 (con't)

Taxon	ID	Lscap1	Lscap2	Taxon	ID	Dscap1	Taxon	ID	Pscap	Pscap
M. talazaci	577056	13.3162	6.6101	Oryzorictes	156602	16.3029	M. talazaci	167500	1.9145	1.1679
M. talazaci	159692	13.7853	7.4038	Oryzorictes	156603	15.5378	M. talazaci	167501	1.7499	1.2081
M. talazaci	162037	12.8547	7.9651	Oryzorictes	159466	0.0216	M. talazaci	167502	2.2767	1.3253
M. talazaci	162038	12.7470	5.9796	Oryzorictes	159695	16.4839	M. talazaci	167503	2.0320	1.3901
M. talazaci	162039	13.7187	6.1663	Oryzorictes	161744	17.1350	Oryzorictes	156226	2.3830	1.2794
M. talazaci	162040	13.1386	6.5657	Oryzorictes	161745	17.1780	Oryzorictes	156601	2.1123	1.5933
M. talazaci	166234	14.2301	6.9531	Oryzorictes	161746	0.9730	Oryzorictes	156602	2.2903	1.4307
M. talazaci	167500	13.6693	7.1548	Oryzorictes	162052	15.7763	Oryzorictes	156603	2.1233	1.5460
M. talazaci	167501	13.6012	6.8656	Oryzorictes	162053	15.7792	Oryzorictes	159466	2.0561	1.2638
M. talazaci	167502	13.5043	6.7679	Oryzorictes	162054	16.3803	Oryzorictes	161744	1.9809	1.3444
M. talazaci	167503	14.0255	6.2094	Oryzorictes	162055	15.9233	Oryzorictes	162052	2.0551	1.3312
Oryzorictes	156226	13.4661	4.9632	Oryzorictes	162056	15.5001	Oryzorictes	162053	2.2846	1.4270
Oryzorictes	156601	13.8150	4.0334	Oryzorictes	162057	16.1846	Oryzorictes	162055	2.1804	1.3712
Oryzorictes	156602	13.2239	3.7646	Oryzorictes	162058	17.1426	Oryzorictes	162056	2.3508	1.1269
Oryzorictes	156603	12.6922	3.9109	Oryzorictes	165490	17.3361	Oryzorictes	162057	2.0715	1.4277
Oryzorictes	159466	13.1933	4.1539	Oryzorictes	165491	16.3221	Oryzorictes	162058	1.8715	1.4513
Oryzorictes	159695	13.9138	4.2191	Oryzorictes	165705	16.7883	Oryzorictes	165490	2.1144	1.3299
Oryzorictes	161744	14.0584	4.0221	Oryzorictes	166157	16.6955	Oryzorictes	165491	2.3748	1.3883
Oryzorictes	161745	13.8070	3.9676	Oryzorictes	166208	16.7766	Oryzorictes	165705	2.1563	1.5091
Oryzorictes	161746	13.3989	4.0349	Oryzorictes	166237	16.9814	Oryzorictes	166157	2.1003	1.4238
Oryzorictes	162052	12.6595	3.5270	Oryzorictes	166238	17.5023	Oryzorictes	166208	2.4377	1.5376
Oryzorictes	162053	13.9921	3.9135	Oryzorictes	166239	16.6982	Oryzorictes	166237	2.2189	1.3113
Oryzorictes	162054	13.0668	3.7692	Oryzorictes	166240	16.8692	Oryzorictes	166238	3.0121	1.7452
Oryzorictes	162055	12.6570	3.6786	Oryzorictes	167480	17.5355	Oryzorictes	166239	2.2005	1.3474
Oryzorictes	162056	12.5103	3.9320	Oryzorictes	167481	17.7329	Oryzorictes	166240	2.1313	1.5159
Oryzorictes	162057	13.0337	4.2073	Oryzorictes	167482	16.9163	Oryzorictes	167480	2.5741	1.5976
Oryzorictes	162058	14.1572	4.4623	Oryzorictes	169239	15.6746	Oryzorictes	167481	2.5100	1.6593
Oryzorictes	165490	13.9774	4.2845	Oryzorictes	169240	15.3848	Oryzorictes	167482	2.2189	1.4315
Oryzorictes	165491	13.4984	4.4605	Oryzorictes	31257	16.1505	Oryzorictes	169239	2.1139	1.3709
Oryzorictes	165705	13.4870	3.8166	Oryzorictes	577052	18.9952	Oryzorictes	169240	2.1648	1.1919
Oryzorictes	166157	13.3659	4.1469	Oryzorictes	578789	15.9403	Oryzorictes	31257	2.2527	1.4344
Oryzorictes	166208	13.7568	3.8562	Limnogale	100688	16.4243	Oryzorictes	45018	2.3211	1.2843
Oryzorictes	166237	13.6993	3.6924	Limnogale	100689	17.4106	Oryzorictes	577052	2.3765	1.4263
Oryzorictes	166238	14.0132	4.3202	Limnogale	100801	17.5595	Oryzorictes	578789	2.1391	1.3119
Oryzorictes	166239	13.9339	4.0090	Geogale	151947	6.8696	Limnogale	100688	2.1449	1.3445

Appendix 5.1 (con't)

Taxon	ID	Lscap1	Lscap2	Taxon	ID	Dscap1	Taxon	ID	Pscap	Pscap
Oryzorictes	166240	13.3727	4.2868	Geogale	156552	7.9836	Limnogale	100689	2.3352	1.5407
Oryzorictes	167480	14.1036	5.5649	Geogale	156553	8.3193	Limnogale	100801	2.6297	1.4189
Oryzorictes	167481	14.6681	4.7426	Potamogale	266897	24.6608	Limnogale	45050	3.0746	1.3846
Oryzorictes	167482	13.7869	4.4378	Potamogale	51324	26.3925	Limnogale	45056	3.0425	1.3837
Oryzorictes	169239	13.0409	3.8683	Solenodon	49508	43.5033	Geogale	156552	1.0825	0.7300
Oryzorictes	169240	12.8259	3.2427	Solenodon	172680	37.8129	Geogale	156553	1.1211	0.7370
Oryzorictes	31257	13.3344	4.7365	Solenodon	217256	45.5834	Potamogale	266897	5.1165	3.8674
Oryzorictes	45018	14.7684	4.9624	Solenodon	238263	40.5737	Potamogale	34881	4.3706	3.1041
Oryzorictes	5639	11.9349	4.0997	Solenodon	290520	42.2745	Potamogale	51324	5.2044	3.7954
Oryzorictes	577052	16.0301	3.9876	Solenodon	395697	41.1546	Solenodon	49508	6.7289	4.7581
Oryzorictes	578789	12.3036	3.7018	Solenodon	395819	36.7262	Solenodon	172680	6.1424	4.5525
Limnogale	100688	13.5430	5.0105	Solenodon	51068	48.1690	Solenodon	217256	6.4570	5.0158
Limnogale	100689	13.5990	5.1157	Solenodon	57320	42.5350	Solenodon	238263	5.8613	4.6356
Limnogale	100801	13.9394	5.1702	Solenodon	72809	44.3595	Solenodon	290520	6.4357	4.8535
Limnogale	45050	14.9510	5.4322	Solenodon	89448	44.8384	Solenodon	395697	6.4133	4.8027
Limnogale	45056	12.2159	4.0959	Petrodromus	203332	32.7377	Solenodon	395819	7.1668	4.9949
Geogale	151947	6.5935	2.6845	Petrodromus	203336	30.8648	Solenodon	51068	6.6700	5.4128
Geogale	156552	7.3293	3.0338	Echinosorex	448860	48.0582	Solenodon	57320	5.7535	4.3222
Geogale	156553	8.1181	3.4067				Solenodon	72809	6.1192	4.3009
Potamogale	266897	28.1556	13.6907				Solenodon	89448	5.7629	5.1099
Potamogale	34881	27.5530	10.7347				Petrodromus	203332	3.2782	2.9486
Potamogale	51324	29.9771	12.7248				Petrodromus	203336	3.3819	3.1846
Solenodon	49508	35.6730	19.4557				Echinosorex	448860	7.7071	5.3039
Solenodon	172680	34.9393	19.0020							
Solenodon	217256	39.1190	22.8602							
Solenodon	238263	36.6183	21.6146							
Solenodon	290520	41.0553	22.2362							
Solenodon	395697	37.7733	20.7584							
Solenodon	395819	36.5439	21.4020							
Solenodon	51068	41.9731	23.7464							
Solenodon	57320	37.4729	19.7653							
Solenodon	72809	38.4878	19.6632							
Solenodon	89448	40.4263	22.7245							
Petrodromus	203332	31.8522	15.1370							
Petrodromus	203336	28.0418	14.8017							
Echinosorex	448860	44.1272	20.2313							

Appendix 5.1 (con't)

Taxon	ID	Hum1	Hum2	Hum3	Hum4	Hum5	Hum6	Hum7	Hum8
Echinops	170605	5.4466	3.0731	3.0197	20.1936	1.8572	2.0634	1.3768	1.8990
Echinops	170607	5.6405	2.9842	2.7117	18.6507	1.6248	1.9872	1.4644	2.1490
Echinops	207717	5.7233	3.3376	3.3502	17.4357	1.6022	1.9180	1.5411	2.2499
Echinops	207718	5.1577	2.9681	2.9121	17.2326	1.7767	1.7623	1.1294	2.2833
Echinops	212918	5.2341	3.0587	3.1326	17.8182	1.8930	1.9594	1.4400	1.9309
Echinops	212919	5.9041	3.2870	3.1744	18.7855	1.8010	2.1539	1.6148	2.3274
Echinops	31270	5.2244	2.9895	2.9709	19.0456	1.5712	2.1742	1.2270	1.8346
Echinops	328620		2.8475	2.8447	18.5513	1.8025	2.0360	1.0645	
Echinops	328636	5.7018	3.0515	3.2776	18.6096	1.6914	1.8041	1.3780	2.3690
Echinops	328637	6.4075	3.3905	3.4746	21.5732	1.9012	2.0652	1.6428	2.6038
Echinops	395835	6.3759	3.7650	3.8034	19.6030	2.1000	2.5180	1.2059	2.4490
Echinops	464980	5.8236	3.5131	2.9463	19.1709	1.8845	2.2986	1.3189	2.0945
Echinops	588220	6.4309	3.3975	3.3251	19.3823	2.1856	2.2951	1.6072	2.2410
Setifer	154033	8.4091	4.5328	3.8318	28.3458	2.7820	3.1033	2.0937	2.9696
Setifer	154034	9.3452	4.2426	4.3000	31.0029	3.0877	3.2205	2.6956	3.4934
Setifer	159731	7.5696	4.0298	4.1242	25.0374	2.3409	2.5995	2.0436	2.7974
Setifer	165494	8.8840	4.4530	3.6978	29.1024	2.2336	3.3762	1.9365	3.3908
Setifer	166159	8.6402	4.3505	3.9303	27.0445	2.6554	3.2350	2.2739	2.5546
Setifer	170532	7.9933	4.2866	4.0212	27.3735	2.3236	3.1981	2.0644	2.7373
Setifer	170581	8.0896	4.1622	4.0435	30.1709	2.7011	2.8254	2.3753	2.7218
Setifer	170730	8.5349	4.8744	4.1289	29.8953	2.5003	2.9726	2.5504	3.0191
Setifer	170731	8.0255	4.6114	4.2939	29.0139	2.7870	3.1459	2.5283	2.0339
Setifer	207076	7.6939	3.9914	3.8595	28.0468	2.3633	3.1006	1.8493	2.4297
Setifer	317872	8.2668	4.9333	3.9446	29.8241	2.7959	2.8989	2.1714	2.9777
Setifer	328612	7.4066	4.0653	3.6425	26.6019	2.3802	2.7259	2.0855	2.6228
Setifer	33948	8.5272	4.5007	3.9656	28.7699	2.6669	3.4479	1.7520	3.1690
Setifer	395513	8.2389	4.6493	4.6648	29.1273	2.7846	3.0398	2.1756	3.0369
Setifer	395719	7.7826	4.6349	4.3696	25.7966	2.1126	2.6190	1.8505	3.0949
Setifer	541443	9.0505	4.5298	4.2926	28.5119	2.6382	3.3828	2.1158	3.3015
Setifer	578790	7.8749	4.5445	3.9160	26.8906	2.6149	2.8632	2.2089	2.7292
Setifer	85170	8.1713	4.4428	4.0358	29.4459	2.6266	2.9983	2.2122	2.8118
Setifer	85513	7.7279	4.5176	3.9273	29.0238	2.8113	3.2324	1.7735	2.7479
Hemicentetes	162062	8.6597	3.4420	3.0562	19.4358	2.7276	2.4438	2.3891	3.6594
Hemicentetes	166132	8.5362	3.7100	3.2463	19.4343	2.6693	2.8271	2.0380	3.5195
Hemicentetes	170593	6.8491	3.1541	2.4381	15.0917	2.1451	2.4354	1.8361	2.3625
Hemicentetes	206755	7.9417	3.3968	2.6714	17.5676	2.2212	2.0307	2.3945	3.4083
Hemicentetes	207712	9.1488	3.6048	3.4916	21.3486	2.6994	2.4489	2.5503	3.7509

Appendix 5.1 (con't)

Taxon	ID	Hum1	Hum2	Hum3	Hum4	Hum5	Hum6	Hum7	Hum8
Hemicentetes	207714	9.4328	3.9269	2.9331	19.0700	2.5351	2.4995	2.7769	3.9187
Hemicentetes	207715	7.9808	3.2814	2.4582	16.8353	2.2133	2.0916	2.2766	3.5697
Hemicentetes	212920	8.4266	4.0696	3.1321	18.7495	2.6095	2.3456	2.2151	3.8005
Hemicentetes	212921	8.9737	3.7384	3.2123	21.7737	2.8242	2.7989	2.5327	3.4547
Hemicentetes	212922	7.8345			17.9242	2.4481	2.3801	2.3124	3.1100
Hemicentetes	212924	8.7311	3.8858	2.8463	21.1531	3.0036	2.6335	2.4733	3.6574
Hemicentetes	212940	8.9405	3.8144	3.1652	20.7472	2.5139	2.7571	2.3528	3.5517
Hemicentetes	29245	8.3247	4.0124	3.5420	18.1872	2.4278	2.4753	2.2538	3.5530
Hemicentetes	339992	9.2062	4.0734	3.2569	20.2900	2.6525	2.7679	2.6262	3.7580
Hemicentetes	354998	8.0215	3.8698	2.9632	20.7719	2.6179	2.4385	2.3608	3.0967
Hemicentetes	364954	8.0979	4.0751	2.9050	19.0574	2.3389	2.6091	2.3949	2.8737
Hemicentetes	83658	11.4461	4.5342	3.7972	25.9241	3.0826	3.2262	3.1238	5.0200
Hemicentetes	395510	9.2154	3.7523	3.1471	22.9300	2.7343	3.0454	2.8041	3.3802
Tenrec	154628	13.8678	7.6117	6.4265	42.2931	3.7131	4.7587	3.4117	5.6284
Tenrec	156337	13.3950	6.7566	6.2589	41.1443	3.4483	4.4254	3.3690	5.3542
Tenrec	16364	13.7520	6.6454	5.1652	41.7470	4.2389	4.5851	3.2923	5.8230
Tenrec	170511	13.8989	7.4074	6.8527	42.1740	4.1404	4.7231	3.6099	5.5289
Tenrec	30398	14.9159	7.1071	7.3954	44.8135	4.0765	4.4446	4.0477	6.1794
Tenrec	361485	15.3766	7.2833	6.7860	44.2619	4.0563	4.9083	4.3061	5.9864
Tenrec	364955	15.1156	7.7267	6.3811	45.7392	4.6978	5.4535	3.9069	5.3706
Tenrec	577051	13.1707	7.4489	7.1047	41.4031	4.1482	4.7047	3.0658	4.6299
Tenrec	578792	14.6001	7.3859	6.9218	44.6612	3.8160	5.0935	3.0832	6.2879
Tenrec	154629	14.3776	6.4887	6.4740	43.5400	4.1984	4.7530	4.2482	5.1403
Tenrec	59011	16.6826	8.4729	7.7549	51.9553	5.4747	5.4290	4.3688	6.1132
Tenrec	60587	14.5073	7.4990	6.7113	44.8192	4.6502	5.1058	2.9352	6.2174
M. cowani	151654	3.2546	1.4967	1.4554	9.5328	0.8760	1.1181	0.9154	1.1543
M. cowani	151656	3.6637	1.5295	1.5840	10.0651	0.8265	1.1912	0.9962	1.4816
M. cowani	154020	3.7555	1.6497	1.5789	10.0512	0.7463	1.1218	1.0116	1.4926
M. cowani	154026	3.5809	1.7030	1.4640	9.9589	0.6966	1.1953	0.9194	1.4827
M. cowani	156195	3.2142	1.5968	1.5949	9.7383	0.7695	1.1300	0.8712	1.2385
M. cowani	156196	3.2757	1.4438	1.3954	9.9519	0.7515	1.1413	0.8844	1.1570
M. cowani	156197	3.2107	1.5377	1.5117	9.7401	0.7556	0.9862	0.7640	1.4082
M. cowani	156221	3.4876	1.5568	1.5609	10.6234	0.7485	1.3761	0.8693	1.3011
M. cowani	156222	3.4448	1.4504	1.4754	10.2410	0.7963	1.2163	0.8223	1.2977
M. cowani	156223	3.5714	1.6087	1.5571	10.4300	0.8314	1.3526	0.8411	1.3343
M. cowani	165672	3.4149	1.4586	1.4065	9.7366	0.6924	1.1723	0.8780	1.3564
M. cowani	165673	3.6683	1.5844	1.4678	10.3779	0.7868	1.1899	0.9386	1.5635

Appendix 5.1 (con't)

Taxon	ID	Hum1	Hum2	Hum3	Hum4	Hum5	Hum6	Hum7	Hum8
M. cowani	165674	3.5747	1.6617	1.6130	10.1086	0.7520	1.1634	1.0439	1.3599
M. cowani	165676	3.4611	1.4312	1.3644	9.5661	0.7739	1.1578	0.9191	1.3865
M. cowani	165680	3.6950	1.5625	1.5744	10.2469	0.7590	1.1560	1.0147	1.3600
M. cowani	165689	3.5187	1.4766	1.4555	10.0020	0.7128	1.1623	0.9700	1.3722
M. cowani	168017	3.3696	1.5228	1.5144	10.1379	0.7905	1.2162	0.9807	1.3155
M. cowani	328658	3.2567	1.5703	1.1866	9.4339	0.6902	1.0678	0.8146	1.3837
M. cowani	449184	3.1491	1.2559	1.3785	9.5365	0.7464	1.1524	0.7963	1.1108
M. cowani	449186	3.0358	1.4228	1.4722	9.4630	0.7179	1.0879	0.8267	1.1151
M. cowani	449187	3.3849	1.5841	1.5033	9.7945	0.7776	1.2303	0.7569	1.3268
M. cowani	449188	3.3027	1.6654	1.2993	9.6761	0.7723	1.2923	0.7397	1.2334
M. dobsoni	151624	3.9293	2.2155	2.1318	16.0740	1.1264	1.6479	0.9009	1.3542
M. dobsoni	151625	3.7054	1.9351	1.6785	14.8284	0.9679	1.3531	1.0988	1.1655
M. dobsoni	156224	3.8561	2.1617	2.0445	15.5642	1.0358	1.4930	0.9689	1.3580
M. dobsoni	156225	14.8486	2.0948	1.8697	3.7469	1.0918	1.4126	0.9734	1.2934
M. dobsoni	159497	3.7553	2.1508	2.0104	15.2508	1.0068	1.4599	0.8414	1.4883
M. dobsoni	159498	3.7350	2.0681	1.8141	15.2041	1.1383	1.3838	0.8989	1.4128
M. dobsoni	159499	3.7364	2.0545	1.8790	14.9524	0.9521	1.2976	0.8873	1.2065
M. dobsoni	161678	3.8582			0.0267	1.0026	1.3660	0.9377	1.4792
M. dobsoni	161679	3.9013	2.1405	1.9543	15.1418	1.2224	1.4617	1.1933	1.2294
M. dobsoni	161718	3.8960	2.1133	1.8980	15.7631	1.1567	1.4743	1.0587	1.2234
M. dobsoni	161935	3.9386	2.3170	2.2785	15.9832	1.0641	1.5443	1.1470	1.1965
M. dobsoni	161940	3.6989	2.0187	1.8004	15.8665	1.0669	1.3556	1.1413	1.1610
M. dobsoni	165467	4.2501	2.2691	2.1231	16.8196	1.2014	1.4413	1.2096	1.5486
M. dobsoni	165774	3.9510	2.1984	1.8712	15.5926	1.1395	1.5010	0.9335	1.2672
M. dobsoni	165775	4.7792	2.8765	2.3939	19.1698	1.3673	1.7161	1.2533	1.3812
M. dobsoni	166107	4.0421	2.2420	2.0238	16.0485	1.1470	1.6313	0.9350	1.4423
M. dobsoni	166198	3.6543	2.0332	1.8643	14.6571	1.0366	1.2883	0.9115	1.4311
M. dobsoni	166200	3.6445	1.9551	1.9072	15.1912	1.0393	1.3332	1.0007	1.2596
M. dobsoni	45736	4.4241	2.5236	2.1687	17.8772	1.4474	1.4585	1.6023	1.3411
M. dobsoni	578749	3.9328	2.0705	1.9092	15.0945	1.0316	1.3382	1.1030	1.3911
M. dobsoni	582730	3.7602	2.1508	2.0300	14.8806	1.0468	1.4528	0.9828	1.2040
M. talazaci	154581	4.4681	2.5554	2.2917	17.6291	1.1943	1.5717	1.3107	1.5377
M. talazaci	154585	4.5736	2.5884	2.3960	17.9841	1.3127	1.5972	1.4460	1.5926
M. talazaci	577056	4.3205	2.1653	1.9841	16.8281	1.1123	1.4277	1.1721	1.6396
M. talazaci	159692	4.4577	2.5808	2.3297	17.3847	1.2957	1.5186	1.3064	1.6931
M. talazaci	162038	4.0610	1.9508	1.9011	15.4057	1.0884	1.4204	1.1561	1.4560
M. talazaci	162039	4.2403	2.6493	2.3933	17.7990	1.2401	1.6334	1.0952	1.5356

Appendix 5.1 (con't)

Taxon	ID	Hum1	Hum2	Hum3	Hum4	Hum5	Hum6	Hum7	Hum8
M. talazaci	162040	4.4266	2.1781	2.2204	17.7412	1.2787	1.4538	1.2259	1.6819
M. talazaci	166234	4.5947	2.6185	2.4021	18.3831	1.1563	1.7745	1.2345	1.6298
M. talazaci	167500	4.3659	2.3800	2.1503	17.6420	1.1734	1.4341	1.2989	1.6400
M. talazaci	167501	4.3231	2.5018	2.3321	17.4388	1.3252	1.5371	1.3230	1.5035
M. talazaci	167502	4.4553	2.6000	2.0778	17.5952	1.2531	1.7961	1.1693	1.5448
M. talazaci	167503	4.2424	2.3675	2.2962	17.2683	1.1979	1.7259	1.0728	1.4104
Oryzorictes	156601	6.5704	2.4961	1.9571	13.2862	1.7647	2.1055	1.4510	2.6844
Oryzorictes	156602	7.2289	2.5153	1.6701	12.8436	1.5936	2.0637	1.5440	3.1708
Oryzorictes	156603	6.6317	2.2518	1.7381	12.5080	1.4692	2.2619	1.4639	2.6582
Oryzorictes	159695	7.1278	2.3436	1.6798	13.1688	1.6027	2.1947	1.8732	3.0243
Oryzorictes	161744	7.0783	2.2750	1.5557	12.9542	1.7358	2.0435	1.7497	3.0925
Oryzorictes	161745	7.2303	2.4540	1.8558	13.6477	1.9790	2.4494	1.8335	3.0380
Oryzorictes	161746	6.8562	2.4155	1.5310	13.0449	1.5465	2.2547	1.4549	2.7377
Oryzorictes	162052	6.9802	2.3602	1.5491	12.7988	1.6674	2.2020	1.5324	2.8695
Oryzorictes	162053	7.4040	2.4640	1.8946	13.7561	1.8094	2.1427	1.9541	3.1100
Oryzorictes	162054	7.9446	2.5597	1.6457	13.7362	1.8358	2.1587	2.2450	3.5051
Oryzorictes	162055	8.1414	2.8551	2.0270	15.0843	1.8127	2.1306	1.8802	3.4441
Oryzorictes	162056	6.6346	2.2968	1.6781	12.8600	1.7575	2.2347	1.6817	2.5893
Oryzorictes	162057	6.9034	2.1883	1.7904	12.7935	1.7554	2.1309	2.1686	2.5911
Oryzorictes	162058	7.2547	2.2776	1.4563	13.4342	1.5613	2.1130	1.7463	3.0247
Oryzorictes	165490	7.1440	2.6659	1.8228	13.7354	1.7038	2.0070	1.2657	3.1890
Oryzorictes	165491	6.6998	2.3941	1.7730	13.7566	1.9619	1.9923	1.5394	2.9766
Oryzorictes	165492	6.9726	2.4134	1.5801	13.2771	1.6472	2.0878	1.6251	3.0800
Oryzorictes	165705	6.7635	2.2782	1.8477	12.8248	1.6113	1.8548	1.4708	3.0965
Oryzorictes	166157	7.0943	2.5205	1.7816	13.0099	1.7823	2.1121	1.7461	3.0297
Oryzorictes	166208	7.1875	2.5164	1.7945	13.7014	1.8140	2.2206	1.5293	3.1520
Oryzorictes	166237	6.8931	2.5189	1.8115	13.7895	1.5958	2.0365	1.3937	3.0324
Oryzorictes	166238	7.3311	2.6088	1.6686	13.7835	1.6203	1.9438	1.5459	3.4750
Oryzorictes	166239	7.2607	2.4337	1.9306	13.5801	1.8594	2.1913	1.7174	3.0811
Oryzorictes	166240	7.3412	2.7219	1.7337	13.6277	1.6591	2.0684	1.5753	3.4230
Oryzorictes	167480	7.3805	2.5715	2.2477	14.0499	1.8821	2.0953	1.4348	3.5969
Oryzorictes	167481	7.2804	2.6411	1.7812	14.0469	1.7571	2.0099	1.4847	3.4020
Oryzorictes	167482	7.1388	2.6595	1.8662	14.0370	1.7714	1.8245	1.8173	3.2717
Oryzorictes	169239	6.7332	2.4421	1.9799	12.6589	1.6751	2.0160	1.3405	2.8282
Oryzorictes	169240	6.8511	2.3794	1.6312	12.5427	1.5079	1.9326	1.6835	2.9406
Oryzorictes	31257	6.1574	1.9182	1.6967	12.5826	1.5896	1.7759	1.7872	2.6449
Oryzorictes	45018	6.8785	2.1699	1.5775	13.1965	1.8138	1.8027	1.7945	2.9982

Appendix 5.1 (con't)

Taxon	ID	Hum1	Hum2	Hum3	Hum4	Hum5	Hum6	Hum7	Hum8
Oryzorictes	577052	6.9612	2.2073	1.6624	13.4929	1.6158	2.0288	1.7559	2.8800
Oryzorictes	578789	6.8328	2.4968	1.4930	12.8943	1.7540	1.9641	1.3605	3.0572
Oryzorictes	156226	6.6820	2.2587	1.4883	14.1773	1.7347	1.8235	1.6175	3.1279
Limnogale	100688	5.0911	2.6112	2.1255	14.5076	1.1167	1.7956	1.2994	1.9154
Limnogale	100689	5.7540	2.8850	2.8484	15.9950	1.3788	1.9554	1.7155	1.8842
Limnogale	100801	5.8670	3.1162	2.7881	16.6739	1.3908	2.0692	1.6627	2.0711
Limnogale	45050	5.8705	2.8382	3.0586	16.6508	1.3539	1.8954	1.7767	2.0818
Limnogale	45056	5.4737	2.5656	2.2863	15.3664	1.1985	1.9349	1.4648	2.0105
Geogale	156551	1.9559	1.1295	1.1578	7.3968	0.6032	0.8149	0.4738	0.6839
Geogale	156552	2.1271	1.1834	1.1711	9.8532	0.6621	0.8097	0.5774	0.6953
Geogale	156553	2.2865	1.3197	1.1976	10.1803	0.8692	0.8303	0.6407	0.7502
Geogale	161594	1.8110	1.0046	1.1069	8.6473	0.5577	0.7473	0.5607	0.5423
Potamogale	266897		5.0273	5.1958	36.4142	2.2886			
Potamogale	34881	7.5247	4.7572	5.1010	35.4816	2.3530	3.7597	1.9867	1.7159
Potamogale	51324	8.4405	5.6542	5.6881	38.5044	2.9036	3.9139	1.9362	2.7155
Solenodon	49508	14.1620	6.3055	5.3929	41.9595	3.8219	4.7058	3.4916	5.7786
Solenodon	172680	17.6227	7.6442	5.8405	43.5664	4.8180	4.9319	4.8446	7.2751
Solenodon	217256	18.6226	6.7928	6.0471	48.2856	4.8442	5.7048	5.0658	7.5723
Solenodon	238263	16.5255	6.1509	5.2122	44.6756	5.9158	5.6848	3.6904	6.8823
Solenodon	290520	18.8599	6.8216	6.2020	48.3485	4.9782	5.7087	5.2266	7.6372
Solenodon	395697	18.8184	7.1931	5.9373	47.4093	4.9853	6.2581	4.8574	7.4566
Solenodon	395819	18.2198	7.1819	6.1534	46.7732	5.2319	6.1235	4.4277	7.4258
Solenodon	51068	19.7282	7.6626	6.6668	49.5524	4.9433	6.4370	5.0704	7.2963
Solenodon	57320	16.8670	5.9962	5.6941	44.1900	4.8324	5.5470	4.8348	6.5660
Solenodon	72809	16.4179	5.9187	5.6363	43.8305	5.2060	5.1411	4.6624	6.5556
Petrodromus	203332	5.3929	4.1603	4.5164	33.5257	2.3416	2.7344	0.7353	1.5373
Petrodromus	203336	5.4021	3.6662	4.2498	32.0685	2.4367	2.7679	1.1607	1.5416
Echinosorex	448860	13.1601	8.0353	8.6416	51.5039	4.4811	5.6275	2.9263	4.1993

Taxon	ID	Phum1	Phum2	Phum3	Phum4	Taxon	ID	Phum1	Phum2	Phum3	Phum4
Echinops	170605	2.7925	1.3811	1.7151	0.6051	M. dobsoni	156224	1.9914	0.8710	1.0100	0.6805
Echinops	170607	2.2542	1.1780	1.6754	0.3594	M. dobsoni	156225	1.6489	0.7860	1.1827	0.5298
Echinops	207717	2.7795	1.0271	1.8041	0.9586	M. dobsoni	159497	1.9167	0.8864	1.0807	0.7006
Echinops	212918	2.4403	1.3037	1.9063	0.5716	M. dobsoni	159498	2.0365	0.9250	1.0591	0.6280
Echinops	212919	2.5375	1.0820	1.8053	0.5060	M. dobsoni	159499	2.2462	0.9855	1.4719	0.6432
Echinops	31270	2.4498	1.2705	1.5315	0.3176	M. dobsoni	161679	1.9447	0.9514	1.1420	0.7068

Appendix 5.1 (con't)

Taxon	ID	Phum1	Phum2	Phum3	Phum4	Taxon	ID	Phum1	Phum2	Phum3	Phum4
Echinops	328620	2.5246	1.1006	1.6589	0.5072	M. dobsoni	161718	2.0483	0.8953	1.1743	0.6707
Echinops	328636	2.6898	1.3117	1.6425	0.6117	M. dobsoni	161935	2.0928	0.9815	1.2324	0.8950
Echinops	328637	2.4525	1.4042	1.9208	0.9962	M. dobsoni	161940	1.4807	0.9972	1.1034	0.7266
Echinops	395835	2.8876	1.3872	1.9455	0.5335	M. dobsoni	165467	1.4517	0.8981	1.0861	0.7780
Echinops	464980	2.8425	1.0921	1.7289	0.6038	M. dobsoni	165774	1.7149	0.9530	1.0851	0.6115
Echinops	588220	3.0775	1.3009	1.9044	0.7477	M. dobsoni	165775	1.9586	0.7744	1.1356	0.6628
Setifer	154034	4.0002	1.8209	2.7501	1.0624	M. dobsoni	166107	1.7063	1.1316	1.2443	0.6332
Setifer	159731	3.4352	1.6885	2.4010	0.7144	M. dobsoni	166198	1.3793	1.0980	0.9267	0.5607
Setifer	165494	3.9290	1.8161	2.2780	1.0103	M. dobsoni	166200	1.9664	0.7511	1.0021	0.7105
Setifer	166159	3.6921	1.4839	2.4346	1.0499	M. dobsoni	578749	1.9372	1.2493	1.2771	0.6474
Setifer	170532	3.5225	1.5094	1.8721	0.4114	M. dobsoni	582730	1.9052	1.0457	1.2457	0.7561
Setifer	170548	4.4348	1.8771	2.7912	1.1433	M. talazaci	154581	2.1556	0.9500	1.3808	0.8474
Setifer	170581	3.9004	1.8002	2.5316	1.1620	M. talazaci	154585	1.8525	1.0368	1.3459	0.7117
Setifer	170730	3.8484	1.9182	2.0313	0.7164	M. talazaci	577056	1.6267	1.1088	1.2652	0.6375
Setifer	170731	3.9061	1.6362	2.4492	0.8402	M. talazaci	159692	2.0567	1.1515	1.1248	0.7830
Setifer	207076	3.5349	1.3279	2.5058	0.7754	M. talazaci	162039	1.7784	1.1683	1.2745	0.7487
Setifer	317872	4.2219	2.4056	2.3926	0.7372	M. talazaci	162040	2.3499	1.2995	1.2085	0.7187
Setifer	33948	3.5686	1.5500	2.5952	1.4318	M. talazaci	166234	2.0081	1.0050	1.2835	0.9181
Setifer	395513	4.3546	1.9613	2.3193	1.0284	M. talazaci	167500	1.8740	1.1333	1.2920	0.7184
Setifer	395719	3.9258	1.8123	2.3695	1.1464	M. talazaci	167501	1.7641	0.9769	1.2697	0.6854
Setifer	541443	4.1580	2.2122	2.2365	0.6282	M. talazaci	167502	1.7448	0.9859	1.3081	0.8193
Setifer	578790	4.2554	3.0729	2.4599	1.1046	M. talazaci	167503	1.6304	0.9503	1.1890	0.6225
Setifer	85170	3.9479	1.7394	2.7636	0.9623	Oryzorictes	156226	1.6107	1.1424	1.2762	0.9102
Setifer	85513	3.6133	1.4795	2.7114	0.6271	Oryzorictes	156601	1.8507	1.1856	1.3220	1.0373
Setifer	154033	3.7068	1.8634	2.4328	0.9903	Oryzorictes	156602	1.9426	1.1691	1.4482	0.9343
Hemicentetes	83658	4.0505	2.0001	3.1304	0.8744	Oryzorictes	156603	1.7976	1.0991	1.1434	0.7892
Hemicentetes	162062	2.5415	1.3261	2.2195	0.5442	Oryzorictes	159695	1.6100	1.3363	1.2943	0.8934
Hemicentetes	166132	3.2157	1.2643	2.4055	1.1012	Oryzorictes	161744	1.6171	1.1909	1.1377	0.8083
Hemicentetes	170593	2.8228	1.5281	1.4722	1.0213	Oryzorictes	161745	1.8000	1.3110	1.4237	1.0118
Hemicentetes	206755	2.2073	1.4016	1.5019	0.6798	Oryzorictes	161746	1.8381	1.4693	1.2522	0.7969
Hemicentetes	207712	3.1258	1.5448	3.0904	1.2483	Oryzorictes	162052	1.7157	0.9967	1.3180	0.7715
Hemicentetes	207714	2.8479	1.5762	2.3871	1.0474	Oryzorictes	162053	2.0759	1.4602	1.1697	1.1221
Hemicentetes	212921	3.2218	1.6574	2.8759	0.6437	Oryzorictes	162055	1.7069	1.2142	1.0724	0.8241
Hemicentetes	212922	2.9217	1.2411	2.2277	0.7237	Oryzorictes	162057	1.8330	1.1648	1.2007	0.9344

Appendix 5.1 (con't)

Taxon	ID	Phum1	Phum2	Phum3	Phum4	Taxon	ID	Phum1	Phum2	Phum3	Phum4
Hemicentetes	212924	3.4836	1.5821	2.0801	0.4906	Oryzorictes	162058	2.0239	1.3509	1.2845	0.6840
Hemicentetes	212940	2.7388	1.3530	2.3941	0.6325	Oryzorictes	165490	1.8532	1.2915	1.2766	0.7196
Hemicentetes	29245	2.4595	1.6743	2.3139	0.7713	Oryzorictes	165491	1.7582	1.3730	1.0898	0.8009
Hemicentetes	339992	3.1009	1.8472	2.0883	1.0786	Oryzorictes	165705	1.8542	1.1693	1.2639	0.6682
Hemicentetes	354998	3.2206	1.6873	2.2969	0.9689	Oryzorictes	166157	1.8524	1.2372	1.2328	1.0423
Hemicentetes	364954	2.6004	1.6777	2.3672	1.1583	Oryzorictes	166208	1.8873	1.3399	1.4346	0.8439
Hemicentetes	395510	3.1953	2.3456	2.6635	1.1125	Oryzorictes	166237	2.0258	1.3293	1.0749	0.7871
Tenrec	154628	7.0609	2.3347	4.0417	0.3066	Oryzorictes	166238	1.8005	1.5168	1.2310	0.9536
Tenrec	156337	6.2423	2.7216	2.9664	0.6592	Oryzorictes	166239	1.8961	1.4970	1.2607	0.7967
Tenrec	16364	5.8277	3.6613	2.0840	0.7790	Oryzorictes	167480	1.8531	1.2295	1.2770	0.7680
Tenrec	170511	5.5501	2.6760	3.2067	0.9477	Oryzorictes	167481	1.9034	1.5408	1.3056	0.6756
Tenrec	30398	7.2907	3.4904	3.0160	1.4480	Oryzorictes	167482	1.9468	1.0555	1.3199	1.0467
Tenrec	361485	7.5373	3.6505	2.6512	0.7151	Oryzorictes	169239	1.9541	1.2176	1.0836	0.7686
Tenrec	364955	7.8414	4.8171	3.3540	1.3431	Oryzorictes	169240	1.8171	1.2161	1.1145	0.9996
Tenrec	577051	6.6767	3.1979	3.1345	1.4798	Oryzorictes	577052	2.0946	1.4053	1.3027	0.9669
Tenrec	578792	6.4173	3.7633	2.8659	1.0645	Oryzorictes	578789	2.0525	1.3326	1.0283	0.6607
Tenrec	154629	6.4367	3.1223	3.8604	0.5992	Limnogale	100688	2.1264	1.1494	1.2743	0.9438
Tenrec	59011	8.5375	3.7753	3.3879	1.0206	Limnogale	100689	3.0574	1.4685	1.7724	1.0153
Tenrec	60587	8.1457	3.7320	3.7981	0.6205	Limnogale	100801	2.3860	1.6887	1.5323	1.0462
M. cowani	151654	1.4669	0.7172	0.9207	0.4284	Geogale	156551	1.0023	0.4119	0.6836	0.3010
M. cowani	151656	1.2157	0.7454	0.8679	0.5274	Geogale	156552	0.9129	0.3784	0.7480	0.3156
M. cowani	154020	1.0705	0.8088	0.9279	0.4324	Geogale	156553	1.1095	0.3865	0.7482	0.3621
M. cowani	154026	1.0666	0.6043	0.8920	0.3438	Geogale	161594	1.0170	0.2904	0.5911	0.3373
M. cowani	156195	1.1617	0.7132	0.7262	0.4265	Potamogale	266897	3.9009	3.4862	2.5863	1.4249
M. cowani	156196	1.0309	0.5964	0.7482	0.4596	Potamogale	34881	4.9899	4.5637	1.7825	1.1131
M. cowani	156221	1.1522	0.5665	0.8163	0.5283	Potamogale	51324	5.3007	3.9655	1.4916	1.7141
M. cowani	156222	1.0939	0.5988	0.8422	0.4589	Solenodon	49508	8.9843	4.2823	2.8778	2.1781
M. cowani	156223	1.2819	0.6297	0.9398	0.5657	Solenodon	172680	7.8368	3.8007	2.9473	2.1259
M. cowani	165672	1.1439	0.9036	0.8169	0.4423	Solenodon	217256	8.0508	3.8205	3.9296	2.4408
M. cowani	165673	1.1057	0.5696	0.9863	0.5226	Solenodon	238263	7.8207	3.1312	3.1418	2.1571
M. cowani	165676	0.9839	0.6748	0.8009	0.4652	Solenodon	290520	8.5049	3.5031	4.0396	3.3213
M. cowani	165689	1.0730	0.5428	0.8623	0.4877	Solenodon	395697	8.1763	3.4753	3.2636	2.5528
M. cowani	168017	1.0867	0.7647	0.7331	0.4242	Solenodon	395819	9.0452	3.6765	3.6205	2.9040
M. cowani	328658	1.0480	0.6224	0.7550	0.4730	Solenodon	51068	9.3752	3.7291	3.8527	1.9804

Appendix 5.1 (con't)

Taxon	ID	Phum1	Phum2	Phum3	Phum4	Taxon	ID	Phum1	Phum2	Phum3	Phum4
M. cowani	449186	1.3108	0.5165	0.6730	0.3810	Solenodon	57320	7.8984	3.0986	3.7006	2.8945
M. cowani	449187	1.2679	0.6659	0.7862	0.4168	Petrodromus	203332	3.9208	2.4175	2.4403	1.0692
M. cowani	449188	1.4214	0.6512	0.8102	0.5277	Petrodromus	203336	3.5665	2.6687	1.8885	0.9810
M. dobsoni	151624	1.4854	0.7730	1.1035	0.6408	Echinosorex	448860	8.3396	4.6586	5.4449	2.1491
M. dobsoni	151625	1.7485	0.8435	1.1335	0.7005						

Taxon	ID	Ulrad1	Ulrad2	Ulrad3	Taxon	ID	Ulrad1	Ulrad2	Ulrad3	Taxon	ID	Ulrad1	Ulrad2	Ulrad3
Echinops	170605	2.4698	15.8217	21.0037	Tenrec	30398	11.1567	31.0719	43.7527	M. talazaci	166234	2.4403		
Echinops	170607	3.2861	14.6130	19.7316	Tenrec	361485	10.9775	31.7430	46.0421	M. talazaci	167500	2.3184	16.1942	19.7645
Echinops	207717	3.2850	14.2263	18.3143	Tenrec	364955	10.8666	32.3232	46.1018	M. talazaci	167501	2.3264	16.7946	20.0182
Echinops	207718	2.6828	13.0244	17.6792	Tenrec	577051	8.7438	30.1337	41.6127	M. talazaci	167502	2.2595	16.7360	20.3986
Echinops	212918	3.4141	14.1204	18.3646	Tenrec	578792	10.0757	30.7000	43.3409	M. talazaci	167503	1.9387	16.4726	19.4550
Echinops	212919	3.6900	14.5060	19.0688	Tenrec	59011	11.9835		50.9991	Oryzorictes	161746	4.2852	9.8536	15.8536
Echinops	31270	3.3945	15.5370	19.6332	Tenrec	60587	10.9082		51.7386	Oryzorictes	162052	4.3398		
Echinops	328620	4.0233	14.6812		Tenrec	85514	9.8632		42.5954	Oryzorictes	162053	4.3643	10.5742	15.5610
Echinops	328636	3.8315	15.5021	20.2157	M. cowani	151654	1.6954			Oryzorictes	162054	4.4740	10.0524	15.9165
Echinops	328637	4.3239	17.4094	23.1795	M. cowani	151656	1.8609			Oryzorictes	162055	4.4988		
Echinops	464980	3.1084	15.3139	19.8006	M. cowani	154020	1.8319			Oryzorictes	162057	4.1924		
Echinops	588220	3.9133	15.4707	21.6230	M. cowani	154026	2.0457			Oryzorictes	162058	4.9414	10.6303	16.6177
Setifer	154033	4.7975	21.2328	27.7652	M. cowani	156195	1.6190			Oryzorictes	165491	4.2432		
Setifer	154034	5.6375	24.1804	31.4269	M. cowani	156196	1.5519			Oryzorictes	165492	4.4661		0.0122
Setifer	159731	4.5323	19.0555	25.8857	M. cowani	156197	1.6104			Oryzorictes	165705	4.3985		0.0210
Setifer	165494	4.5241	23.2642	30.2473	M. cowani	156221	2.0178	9.3646	12.2537	Oryzorictes	166157	4.5833		
Setifer	166159	5.5072			M. cowani	156222		9.5924		Oryzorictes	166208	4.1080		
Setifer	170532	5.0107	22.0660	28.5405	M. cowani	156223	1.9443	9.6577	12.5821	Oryzorictes	166237	3.8289		
Setifer	170548	5.3198	24.9582	32.0089	M. cowani	165672	1.9211	8.9067	11.7828	Oryzorictes	166238	4.3398		
Setifer	170730	4.8093			M. cowani	165673	2.2078	9.6106	12.4530	Oryzorictes	166239	4.2848		
Setifer	170731	4.8270	22.9072	29.1763	M. cowani	165674	1.7932	9.5679	12.1188	Oryzorictes	166240	4.4323		15.5414
Setifer	207076	4.3195	22.6240	29.0987	M. cowani	165676	1.9465	8.9771	11.7329	Oryzorictes	167480	4.9158	10.8883	17.1232
Setifer	317872	5.5185	22.9520	30.3448	M. cowani	165689	2.0354	9.5963	12.2811	Oryzorictes	167481	4.6139		
Setifer	328612	4.0723		26.6029	M. cowani	168017	1.8032	9.7071	12.9244	Oryzorictes	167482	4.6410		
Setifer	33948	4.7440	22.8596	29.3571	M. cowani	328658	2.1068	9.0284	11.8316	Oryzorictes	169239	4.2552		
Setifer	395513	4.6514	22.0009	27.7829	M. cowani	449184	1.5328	8.4989	10.9763	Oryzorictes	31257	3.4014	10.1612	14.8272
Setifer	395719	4.4957	19.8147	25.6636	M. cowani	449186	1.6850	8.8668	11.3611	Oryzorictes	45018	3.3573		15.6231

Appendix 5.1 (con't)

Setifer	541443	4.6330	23.0056	28.5965	M. cowani	449187	1.9654	8.8670	11.7041	Oryzorictes	577052	4.5439		16.7688
Setifer	578790	4.7492	21.0907	27.3474	M. cowani	449188	2.0926	8.5809	11.2669	Oryzorictes	578789	4.3495	9.9553	14.6746
Setifer	85170	4.1830	23.0901	29.0906	M. dobsoni	151624	2.0630			Limnogale	45050	3.2551	14.7406	19.3350
Setifer	85513	4.0545	23.1187	29.6960	M. dobsoni	151625	2.0269			Geogale	156551	0.9638		
Hemicentetes	83658	6.0492	19.2910	27.9340	M. dobsoni	156224	1.9783			Geogale	156552	1.2321		
Hemicentetes	10001	3.7471	11.4543	16.6116	M. dobsoni	156225	1.8519			Geogale	156553	1.2461		
Hemicentetes	162062	4.8960	15.9384	22.5338	M. dobsoni	159497	2.0297			Geogale	161594	1.0933	6.5825	8.2265
Hemicentetes	166132	4.9968	15.1777	22.4930	M. dobsoni	159498	1.9394			Potamogale	266897	6.4981	24.3992	32.2700
Hemicentetes	170593	3.8930	11.2245	17.2222	M. dobsoni	159499	2.1088			Potamogale	34881	5.7734	22.1502	30.8466
Hemicentetes	206755	4.3519		0.0130	M. dobsoni	161679	2.0857			Potamogale	51324	6.3995	25.2547	35.7950
Hemicentetes	207712	5.5404	18.7048	25.3278	M. dobsoni	161718	1.9515			Petrodromus	203335	5.1888	40.5556	47.9358
Hemicentetes	207714	5.7876	14.9590	22.3680	M. dobsoni	161935	2.1695	14.6230	17.6929	Petrodromus	203336	4.5201	39.5152	46.9192
Hemicentetes	207715	4.3657	13.3860	20.1431	M. dobsoni	161940	1.8189	14.6046	17.7901	Petrodromus	203337	5.0809	37.6440	45.2458
Hemicentetes	212920	4.5311	15.4824	22.9807	M. dobsoni	165467	2.4351	15.1458	18.5557	Solenodon	49508	8.4739		47.6615
Hemicentetes	212922	4.5114	14.4017	21.9312	M. dobsoni	165774	2.0685	14.9586	18.1939	Solenodon	172680	10.0333	33.8001	46.9573
Hemicentetes	212924	5.2211	16.9247	25.1257	M. dobsoni	165775	1.8944	13.0399	16.0382	Solenodon	217256	9.3142		48.6525
Hemicentetes	212940	4.7306	16.7922	21.8845	M. dobsoni	166107	2.2485	15.0155	18.1580	Solenodon	238263	10.2761	36.7879	50.5890
Hemicentetes	339992	4.9131	15.8455	22.4714	M. dobsoni	166198	1.8884	14.0705	17.0727	Solenodon	290520	10.3693	36.6002	52.4538
Hemicentetes	354998	4.7620	16.4216	23.0227	M. dobsoni	166200	2.0154	14.2989	17.2701	Solenodon	395697	10.8517	36.0668	50.6409
Hemicentetes	364954	4.6265	16.6557	22.3049	M. dobsoni	578749	2.3920	14.3102	17.4287	Solenodon	395819	10.2753	37.6600	53.5668
Hemicentetes	395510	5.5554		26.4535	M. dobsoni	582730	2.0415	14.2214	17.1899	Solenodon	51068	10.5267	37.5403	52.6673
Tenrec	1001	11.7005	35.6464	49.6325	M. talazaci	154581	2.2199	16.0227	19.4947	Solenodon	57320	7.5542		46.2383
Tenrec	154628	10.0483	30.4721	43.7390	M. talazaci	154585	2.3849	16.0417	19.5139	Solenodon	72809	9.1997	36.1180	49.4987
Tenrec	154629	9.6837		40.7918	M. talazaci	577056	2.5790	15.8795	19.2718	Echinosorex	448860	10.5576	39.8234	54.1515
Tenrec	156337	9.8579	30.3299	42.6630	M. talazaci	162037	2.1716							
Tenrec	170511	10.7127	31.4712	44.3185	M. talazaci	162039	2.3400							
Tenrec	174727	11.4707	31.9415	45.3412	M. talazaci	162040	2.2994	16.5009	19.4926					

Appendix 5.2. Linear Measurement Means/SDs (mm)

Taxon	Hum1	Hum1	Hum1	Hum2	Hum2	Hum2	Hum3	Hum3	Hum3	Hum4	Hum4	Hum4	Hum5	Hum5	Hum5
	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>
Echinops	5.7559	12	0.4589	3.2049	13	0.2655	3.1495	13	0.2962	18.9271	13	1.1549	1.8224	13	0.1816
Setifer	8.2227	19	0.5179	4.4396	19	0.2623	4.0521	19	0.2487	28.3698	19	1.5600	2.5898	19	0.2439
Hemicentetes	8.6537	18	0.9465	3.7848	17	0.3411	3.0743	17	0.3601	19.7940	18	2.4498	2.5813	18	0.2572
Tenrec	14.4717	12	0.9727	7.3195	12	0.5352	6.6860	12	0.6477	44.0460	12	2.9319	4.2216	12	0.5277
M. cowani	3.4223	22	0.1949	1.5350	22	0.1020	1.4733	22	0.1049	9.9279	22	0.3342	0.7623	22	0.0461
M. dobsoni	4.4427	21	2.3998	2.1795	20	0.2114	1.9825	20	0.1724	14.4635	21	4.3550	1.1090	21	0.1233
M. talazaci	4.3774	12	0.1515	2.4280	12	0.2238	2.2313	12	0.1680	17.4249	12	0.7415	1.2190	12	0.0778
Oryzorictes	7.0462	34	0.3762	2.4285	34	0.1853	1.7411	34	0.1728	13.3730	34	0.5761	1.7132	34	0.1235
Limnogale	5.6113	5	0.3326	2.8032	5	0.2232	2.6214	5	0.3964	15.8388	5	0.9188	1.2877	5	0.1230
Geogale	2.0451	4	0.2064	1.1593	4	0.1305	1.1584	4	0.0381	9.0194	4	1.2668	0.6730	4	0.1376
Potamogale	7.9826	2	0.6476	5.1462	3	0.4602	5.3283	3	0.3152	36.8001	3	1.5479	2.5151	3	0.3380
Solenodon	17.5844	10	1.6309	6.7667	10	0.6528	5.8783	10	0.4226	45.8591	10	2.5327	4.9577	10	0.5158
Petrodromus	5.3975	2	0.0065	3.9132	2	0.3494	4.3831	2	0.1885	32.7971	2	1.0304	2.3891	2	0.0672
Echinosorex	13.1601	1	0.0000	8.0353	1	0.0000	8.6416	1	0.0000	51.5039	1	0.0000	4.4811	1	0.0000

Taxon	Hum6	Hum6	Hum6	Hum7	Hum7	Hum7	Hum8	Hum8	Hum8	Phum1	Phum1	Phum1	Phum2	Phum2	Phum2
	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>	<i>Means</i>	<i>N</i>	<i>Std.Dev.</i>
Echinops	2.0796	13	0.2100	1.3854	13	0.1897	2.2026	12	0.2318	2.6440	12	0.2379	1.2366	12	0.1341
Setifer	3.0519	19	0.2494	2.1451	19	0.2612	2.8758	19	0.3491	3.8924	19	0.2953	1.8408	19	0.3938
Hemicentetes	2.5697	18	0.3011	2.4284	18	0.2913	3.5247	18	0.5303	2.9846	16	0.4443	1.6067	16	0.2858
Tenrec	4.8654	12	0.3430	3.6371	12	0.5193	5.6883	12	0.5072	6.9637	12	0.9321	3.4119	12	0.6582
M. cowani	1.1763	22	0.0869	0.8897	22	0.0892	1.3287	22	0.1232	1.1657	18	0.1354	0.6607	18	0.1002
M. dobsoni	1.4481	21	0.1148	1.0466	21	0.1744	1.3254	21	0.1159	1.8242	19	0.2456	0.9367	19	0.1315
M. talazaci	1.5742	12	0.1349	1.2342	12	0.1077	1.5721	12	0.0890	1.8947	11	0.2261	1.0697	11	0.1115
Oryzorictes	2.0669	34	0.1487	1.6489	34	0.2234	3.0536	34	0.2650	1.8561	28	0.1323	1.2801	28	0.1408
Limnogale	1.9301	5	0.0991	1.5838	5	0.1974	1.9926	5	0.0896	2.5233	3	0.4804	1.4355	3	0.2711

Appendix 5.2 (con't)

Taxon	Hum6	Hum6	Hum6	Hum7	Hum7	Hum7	Hum8	Hum8	Hum8	Phum1	Phum1	Phum1	Phum2	Phum2	Phum2
Geogale	0.8006	4	0.0365	0.5631	4	0.0688	0.6679	4	0.0886	1.0104	4	0.0805	0.3668	4	0.0529
Potamogale	3.8368	2	0.1091	1.9614	2	0.0357	2.2157	2	0.7069	4.7305	3	0.7351	4.0051	3	0.5398
Solenodon	5.6243	10	0.5668	4.6172	10	0.5868	7.0446	10	0.5924	8.4103	9	0.5911	3.6130	9	0.3660
Echinosorex	5.6275	1	0.0000	2.9263	1	0.0000	4.1993	1	0.0000	8.3396	1	0.0000	4.6586	1	0.0000

Taxon	Phum3	Phum3	Phum3	Phum4	Phum4	Phum4	Lscap1	Lscap1	Lscap1	Lscap2	Lscap2	Lscap2	Dscap1	Dscap1	Dscap1
	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.
Echinops	1.7699	12	0.1320	0.6099	12	0.2060	15.9975	13	1.7219	7.5047	13	0.7244	19.2131	10	1.8871
Setifer	2.4382	19	0.2375	0.9233	19	0.2465	23.0042	19	1.9380	11.4146	19	1.2652	26.6069	16	2.0257
Hemicentetes	2.3447	16	0.4623	0.8810	16	0.2407	20.0737	16	3.2815	8.8378	16	1.4003	23.0073	13	8.0055
Tenrec	3.1972	12	0.5487	0.9153	12	0.3695	38.8230	11	3.5221	18.2342	11	1.8885	41.4862	10	3.8476
M. cowani	0.8281	18	0.0845	0.4617	18	0.0573	8.9472	20	0.2807	3.7129	20	0.3702	9.5911	19	2.2318
M. dobsoni	1.1419	19	0.1208	0.6780	19	0.0806	11.4968	21	1.5892	5.6399	21	0.9638	12.6317	21	2.4246
M. talazaci	1.2674	11	0.0718	0.7464	11	0.0895	13.4119	13	0.5106	6.8614	13	0.5818	13.6503	11	4.5345
Oryzorictes	1.2371	28	0.1125	0.8577	28	0.1302	13.5299	35	0.7702	4.1365	35	0.4558	15.6281	33	3.9765
Limnogale	1.5263	3	0.2491	1.0018	3	0.0525	13.6497	5	0.9807	4.9649	5	0.5100	17.1315	3	0.6169
Geogale	0.6927	4	0.0742	0.3290	4	0.0266	7.3470	3	0.7625	3.0417	3	0.3611	7.7242	3	0.7589
Potamogale	1.9534	3	0.5670	1.4174	3	0.3006	28.5619	3	1.2621	12.3834	3	1.5073	25.5266	2	1.2245
Solenodon	3.4859	9	0.4373	2.5061	9	0.4515	38.1893	11	2.2637	21.2026	11	1.5918	42.5028	11	3.3534
Petrodromus	2.1644	2	0.3902	1.0251	2	0.0623	29.9470	2	2.6943	14.9693	2	0.2371	31.8013	2	1.3243
Echinosorex	5.4449	1	0.0000	2.1491	1	0.0000	44.1272	1	0.0000	20.2313	1	0.0000	48.0582	1	0.0000

Taxon	Pscap1	Pscap2	Pscap3	Pscap2	Pscap3	Pscap4	Ulradi1	Ulradi1	Ulradi1	Ulradi2	Ulradi2	Ulradi2	Ulradi3	Ulradi3	Ulradi3
	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.	Means	N	Std.Dev.
Echinops	2.6141	13	0.2415	1.8054	13	0.1084	3.4519	12	0.5423	15.0188	12	1.0916	19.8740	11	1.6012
Setifer	3.9193	18	0.3433	2.6626	18	0.2095	4.7572	19	0.4709	22.3888	16	1.5024	28.7430	17	1.7772
Hemicentetes	3.4918	15	0.5519	2.1885	15	0.2908	4.8517	17	0.6305	15.5106	15	2.2608	21.2248	17	6.1615
Tenrec	6.4600	11	0.9531	4.1977	11	0.5608	10.5749	14	0.8972	31.5833	10	1.6046	45.1907	14	3.4144
M. cowani	1.3752	19	0.1153	0.9066	19	0.0758	1.8634	20	0.1979	9.2016	14	0.4270	11.9437	13	0.5585

Appendix 5.2 (con't)

Taxon	Pscap1	Pscap2	Pscap3	Pscap2	Pscap3	Pscap4	Ulr1	Ulr1	Ulr1	Ulr2	Ulr2	Ulr2	Ulr3	Ulr3	Ulr3
M. dobsoni	1.8925	18	0.1557	1.2096	18	0.0834	2.0530	19	0.1660	14.4288	10	0.6091	17.5390	10	0.7156
M. talazaci	2.1038	11	0.1858	1.3317	11	0.1041	2.2980	11	0.1620	16.3303	8	0.3442	19.6762	8	0.3688
Oryzorictes	2.2392	30	0.2135	1.4137	30	0.1350	4.3274	24	0.3750	10.3022	7	0.3935	13.2117	12	6.2054
Limnogale	2.6454	5	0.4150	1.4145	5	0.0753	3.2551	1	0.0000	14.7406	1	0.0000	19.3350	1	0.0000
Geogale	1.1018	2	0.0273	0.7335	2	0.0050	1.1338	4	0.1326	6.5825	1	0.0000	8.2265	1	0.0000
Potamogale	4.8972	3	0.4581	3.5890	3	0.4214	6.2237	3	0.3931	23.9347	3	1.6035	32.9705	3	2.5475
Solenodon	6.3192	11	0.4429	4.7963	11	0.3356	4.9299	3	0.3590	39.2383	3	1.4754	46.7003	3	1.3583
Petrodromus	3.3301	2	0.0734	3.0666	2	0.1669	9.6874	10	1.0402	36.3676	7	1.2924	49.8926	10	2.5264
Echinosorex	7.7071	1	0.0000	5.3039	1	0.0000	10.5576	1	0.0000	39.8234	1	0.0000	54.1515	1	0.0000

Appendix 5.3. Raw Index Scores

Taxon	ID	APLI	Taxon	ID	DHWI	HHSZI	HSI	MEPW	LEPW	TRHI	Taxon	ID	SCSI
Echinops	170605		Echinops	170605	2.6396	3.2806	10.8730	0.9203	0.6672	0.5754	Echinops	170605	0.4377
Echinops	170607		Echinops	170607	2.8385	3.5056	11.4786	1.0814	0.7369	0.6707	Echinops	170607	0.5070
Echinops	207717	1.1780	Echinops	207717	2.9839	4.1741	10.8822	1.1730	0.8035	0.6107	Echinops	207717	0.4277
Echinops	207718	1.1388	Echinops	207718	2.9266	3.3096	9.6993	1.2956	0.6409	0.6793	Echinops	207718	0.5625
Echinops	212918	1.1478	Echinops	212918	2.6712	3.2706	9.4126	0.9855	0.7349	0.5017	Echinops	212918	0.5442
Echinops	212919	1.2015	Echinops	212919	2.7411	3.5876	10.4303	1.0806	0.7497	0.5201	Echinops	212919	0.4893
Echinops	328620	1.1577	Echinops	31270	2.4029	3.7936	12.1219	0.8438	0.5643	0.4239	Echinops	31270	0.3920
Echinops	328636	1.1373	Echinops	328620		3.1579	10.2920		0.5228	0.5094	Echinops	328620	0.5046
Echinops	328637	1.1858	Echinops	328636	3.1606	3.7419	11.0022	1.3132	0.7638	0.9420	Echinops	328636	0.3886
Echinops	395835	1.2097	Echinops	328637	3.1027	3.6110	11.3473	1.2608	0.7955	0.4894	Echinops	328637	0.4320
Echinops	464980	1.1039	Echinops	395835	2.5321	3.6040	9.3347	0.9726	0.4789	0.5160	Echinops	395835	0.4953
Echinops	588220	1.2462	Echinops	464980	2.5336	3.4277	10.1730	0.9112	0.5738	0.4597	Echinops	464980	0.4626
Setifer	154033	0.0000	Echinops	588220	2.8021	3.0759	8.8683	0.9765	0.7003	0.7383	Echinops	588220	0.4982
Setifer	154034	1.1370	Setifer	154033	2.7097	3.0067	10.1890	0.9569	0.6747	0.5811	Setifer	154033	0.4670
Setifer	159731	1.2197	Setifer	154034	2.9018	2.7667	10.0409	1.0847	0.8370	1.4045	Setifer	154034	0.4870
Setifer	165494	1.0928	Setifer	159731	2.9120	3.4833	10.6955	1.0761	0.7862	0.6608	Setifer	159731	0.4808
Setifer	166159	1.1064	Setifer	165494	2.6313	3.6492	13.0296	1.0043	0.5736	0.5362	Setifer	165494	0.4863
Setifer	170532	1.1742	Setifer	166159	2.6708	3.1185	10.1849	0.7897	0.7029	0.5398	Setifer	166159	0.5893
Setifer	170548	1.0966	Setifer	170532	2.4994	3.5753	11.7805	0.8559	0.6455	0.7233	Setifer	170532	0.4929
Setifer	170581	1.1000	Setifer	170581	2.8632	3.0380	11.1700	0.9634	0.8407	0.5811	Setifer	170548	0.5040
Setifer	170731	1.1938	Setifer	170730	2.8712	3.6009	11.9568	1.0156	0.8580	0.9383	Setifer	170581	0.4446
Setifer	207076	1.1632	Setifer	170731	2.5511	3.1953	10.4105	0.6465	0.8037	0.6999	Setifer	170730	0.5000
Setifer	328612	1.0571	Setifer	207076	2.4814	3.3220	11.8678	0.7836	0.5964	0.6956	Setifer	170731	0.5557
Setifer	33948	1.1214	Setifer	317872	2.8517	3.1753	10.6671	1.0272	0.7490	0.9559	Setifer	207076	0.4212
Setifer	395719	1.1018	Setifer	328612	2.7171	3.2383	11.1764	0.9622	0.7651	0.5925	Setifer	328612	0.4702
Setifer	541443	1.1532	Setifer	33948	2.4732	3.1746	10.7877	0.9191	0.5081	0.9431	Setifer	33948	0.4707
Setifer	578790	1.1771	Setifer	395513	2.7104	3.3449	10.4601	0.9990	0.7157	0.8239	Setifer	395513	0.5268
Setifer	85170	1.1455	Setifer	395719	2.9716	4.2623	12.2110	1.1817	0.7066	0.9356	Setifer	395719	0.4602
Setifer	85513	1.0822	Setifer	541443	2.6755	3.3441	10.8073	0.9760	0.6255	0.6997	Setifer	541443	0.5481
Hemicentetes	83658	1.2151	Setifer	578790	2.7504	3.2355	10.2836	0.9532	0.7715	0.7632	Setifer	578790	0.4876
Hemicentetes	162062		Setifer	85170	2.7253	3.2280	11.2107	0.9378	0.7378	0.5707	Setifer	85170	0.5395
Hemicentetes	166132	1.2260	Setifer	85513	2.3907	3.0039	10.3240	0.8501	0.5487	0.7400	Setifer	85513	0.5014

Appendix 5.3 (con't)

Taxon	ID	APLI	Taxon	ID	DHWI	HHSZI	HSI	MEPW	LEPW	TRHI	Taxon	ID	SCSI
Hemicentetes	170593		Hemicentetes	162062	3.5435	2.3824	7.1257	1.4974	0.9776	0.6133	Hemicentetes	83658	0.4349
Hemicentetes	206755	1.2140	Hemicentetes	166132	3.0194	2.6060	7.2807	1.2449	0.7209	0.4687	Hemicentetes	162062	0.4466
Hemicentetes	207712	1.2030	Hemicentetes	170593	2.8123	2.6070	7.0354	0.9701	0.7539	0.4202	Hemicentetes	166132	0.4357
Hemicentetes	207714	1.2034	Hemicentetes	206755	3.9108	2.7319	7.9090	1.6784	1.1791	0.5742	Hemicentetes	170593	0.4307
Hemicentetes	207715		Hemicentetes	207712	3.7359	2.6289	7.9088	1.5316	1.0414	0.4856	Hemicentetes	206755	0.4380
Hemicentetes	212920	1.1948	Hemicentetes	207714	3.7738	2.7061	7.5225	1.5678	1.1110	0.5039	Hemicentetes	207712	0.4203
Hemicentetes	212921	1.1652	Hemicentetes	207715	3.8157	2.5932	7.6064	1.7067	1.0885	0.5946	Hemicentetes	207714	0.4743
Hemicentetes	212922		Hemicentetes	212920	3.5925	2.7598	7.1852	1.6203	0.9444	0.5178	Hemicentetes	207715	0.4502
Hemicentetes	212924	1.1964	Hemicentetes	212921	3.2062	2.4611	7.7096	1.2343	0.9049	0.6292	Hemicentetes	212920	0.4004
Hemicentetes	212940	1.1654	Hemicentetes	212922	3.2916		7.3217	1.3066	0.9715	0.6998	Hemicentetes	212921	0.4254
Hemicentetes	339992	1.2191	Hemicentetes	212924	3.3154	2.2413	7.0426	1.3888	0.9392	0.7730	Hemicentetes	212922	0.4818
Hemicentetes	354998	1.1782	Hemicentetes	212940	3.2427	2.7764	8.2531	1.2882	0.8533	0.6672	Hemicentetes	212924	0.4083
Hemicentetes	364954	1.1876	Hemicentetes	29245	3.3631	3.1116	7.4912	1.4354	0.9105	0.5537	Hemicentetes	212940	0.4528
Tenrec	154628	1.0862	Hemicentetes	339992	3.3260	2.7636	7.6495	1.3577	0.9488	0.6409	Hemicentetes	339992	0.4477
Tenrec	156337	1.0735	Hemicentetes	354998	3.2896	2.6101	7.9345	1.2699	0.9681	0.7614	Hemicentetes	354998	0.4611
Tenrec	170511	1.0887	Hemicentetes	364954	3.1037	2.9844	8.1482	1.1014	0.9179	0.5535	Hemicentetes	364954	0.4472
Tenrec	361485	1.1030	Hemicentetes	83658	3.5479	2.7027	8.4098	1.5560	0.9683	0.5886	Tenrec	154628	0.4476
Tenrec	364955	1.0978	Hemicentetes	395510	3.0260	2.5233	8.3862	1.1099	0.9208	0.7471	Tenrec	156337	0.5065
Tenrec	577051	1.0808	Tenrec	154628	2.9142	3.7807	11.3902	1.1828	0.7169	0.7746	Tenrec	170511	0.4597
Tenrec	578792	1.0947	Tenrec	156337	3.0268	3.7745	11.9317	1.2099	0.7613	0.6553	Tenrec	30398	0.4472
Tenrec	154629	1.0888	Tenrec	16364	2.9993	2.7862	9.8486	1.2700	0.7180	0.8054	Tenrec	361485	0.5245
Tenrec	59011	1.0754	Tenrec	170511	2.9427	3.4442	10.1860	1.1706	0.7643	0.6197	Tenrec	364955	0.4699
Tenrec	60587	1.0869	Tenrec	30398	3.3560	3.5575	10.9930	1.3903	0.9107	0.6515	Tenrec	577051	0.4365
M. cowani	151654	1.1600	Tenrec	361485	3.1328	3.4685	10.9118	1.2197	0.8773	0.5209	Tenrec	578792	0.4373
M. cowani	151656		Tenrec	364955	2.7717	3.0030	9.7362	0.9848	0.7164	0.5418	Tenrec	154629	0.4970
M. cowani	154020	1.0864	Tenrec	577051	2.7995	3.5084	9.9809	0.9841	0.6516	0.5899	Tenrec	59011	0.4511
M. cowani	154026	1.1635	Tenrec	578792	2.8664	3.7493	11.7035	1.2345	0.6053	0.6625	Tenrec	60587	0.4921
M. cowani	156195	1.1296	Tenrec	154629	3.0249	3.0875	10.3705	1.0815	0.8938	0.7969	M. cowani	151654	0.3680
M. cowani	156196	1.1325	Tenrec	59011	3.0729	2.9641	9.4901	1.1260	0.8047	0.5821	M. cowani	151656	0.3749
M. cowani	156197	1.1515	Tenrec	60587	2.8413	3.0559	9.6382	1.2177	0.5749	0.5939	M. cowani	154020	0.3718
M. cowani	156221	1.1711	M. cowani	151654	2.9108	3.3698	10.8817	1.0323	0.8186	0.4827	M. cowani	154026	0.3749
M. cowani	156222	1.1523	M. cowani	151656	3.0756	3.7672	12.1784	1.2438	0.8363	0.6419	M. cowani	156195	0.3792
M. cowani	156223	1.1539	M. cowani	154020	3.3476	4.3260	13.4678	1.3305	0.9018	0.5820	M. cowani	156196	0.4615
M. cowani	165672	1.1899	M. cowani	154026	2.9957	4.5461	14.2961	1.2404	0.7692	0.8569	M. cowani	156197	0.3762

Appendix 5.3 (con't)

Taxon	ID	APLI	Taxon	ID	DHWI	HHSZI	HSI	MEPW	LEPW	TRHI	Taxon	ID	SCSI
M. cowani	165674	1.1661	M. cowani	156195	2.8444	4.1478	12.6555	1.0961	0.7710	1.0954	M. cowani	156221	0.4666
M. cowani	165676	1.1468	M. cowani	156196	2.8701	3.7780	13.2426	1.0138	0.7749	0.6669	M. cowani	156222	0.4505
M. cowani	165689	1.1718	M. cowani	156197	3.2556	4.0358	12.8909	1.4279	0.7747	1.0246	M. cowani	156223	0.4626
M. cowani	168017	1.1486	M. cowani	156221	2.5344	4.1651	14.1923	0.9455	0.6317	0.6674	M. cowani	165672	0.4071
M. cowani	328658	1.1504	M. cowani	156222	2.8321	3.6740	12.8603	1.0669	0.6761	0.7283	M. cowani	165674	0.4419
M. cowani	449186	1.1512	M. cowani	156223	2.6404	3.8077	12.5448	0.9865	0.6218	0.6308	M. cowani	165676	0.4345
M. cowani	449187	1.1662	M. cowani	165672	2.9131	4.1379	14.0621	1.1571	0.7490	0.6489	M. cowani	165689	0.3987
M. cowani	449188	1.1356	M. cowani	165673	3.0828	3.8796	13.1908	1.3139	0.7888	1.1100	M. cowani	168017	0.4819
M. dobsoni	151624	1.1430	M. cowani	165674	3.0727	4.3549	13.4430	1.1689	0.8973	0.7466	M. cowani	328658	0.4001
M. dobsoni	151625	1.1584	M. cowani	165676	2.9893	3.6126	12.3616	1.1975	0.7938	1.0031	M. cowani	449184	0.4246
M. dobsoni	156224	1.1296	M. cowani	165680	3.1962	4.1331	13.5012	1.1765	0.8778	0.7054	M. cowani	449186	0.4198
M. dobsoni	156225	1.1049	M. cowani	165689	3.0273	4.1137	14.0325	1.1806	0.8345	0.6065	M. cowani	449187	0.4221
M. dobsoni	159497	1.1485	M. cowani	168017	2.7706	3.8423	12.8251	1.0817	0.8064	0.7340	M. cowani	449188	0.3789
M. dobsoni	159498	1.1453	M. cowani	328658	3.0499	3.9943	13.6681	1.2958	0.7629	0.5434	M. dobsoni	151624	1.7921
M. dobsoni	159499	1.1533	M. cowani	449184	2.7326	3.5293	12.7760	0.9639	0.6910	0.9026	M. dobsoni	151625	0.4342
M. dobsoni	161678	1.1736	M. cowani	449186	2.7905	4.0327	13.1817	1.0250	0.7599	0.3007	M. dobsoni	156224	0.4631
M. dobsoni	161679	1.1389	M. cowani	449187	2.7514	3.9705	12.5961	1.0785	0.6152	0.4619	M. dobsoni	156225	0.4905
M. dobsoni	161718	1.1539	M. cowani	449188	2.5556	3.8386	12.5285	0.9544	0.5723	0.5348	M. dobsoni	159497	0.4491
M. dobsoni	161935	1.1029	M. dobsoni	151624	2.3843	3.8596	14.2706	0.8217	0.5467	0.9087	M. dobsoni	159498	0.4522
M. dobsoni	161940	1.1389	M. dobsoni	151625	2.7384	3.7334	15.3204	0.8613	0.8121	0.5403	M. dobsoni	159499	0.4513
M. dobsoni	165467	1.1667	M. dobsoni	156224	2.5828	4.0608	15.0263	0.9096	0.6490	0.8641	M. dobsoni	161678	0.4118
M. dobsoni	165774	1.1530	M. dobsoni	156225	10.5115	3.6313	3.4320	0.9156	0.6891	0.7046	M. dobsoni	161679	0.4184
M. dobsoni	165775	1.1513	M. dobsoni	159497	2.5723	4.1331	15.1480	1.0195	0.5764	1.4010	M. dobsoni	161718	0.4913
M. dobsoni	166107	1.1071	M. dobsoni	159498	2.6991	3.4106	13.3572	1.0210	0.6496	0.7555	M. dobsoni	161935	0.4396
M. dobsoni	166198	1.1341	M. dobsoni	159499	2.8795	4.1313	15.7041	0.9298	0.6838	0.4897	M. dobsoni	161940	0.5141
M. dobsoni	166200	1.1471	M. dobsoni	161678	2.8245		0.0266	1.0829	0.6865	0.8326	M. dobsoni	165467	0.4988
M. dobsoni	578749	1.1476	M. dobsoni	161679	2.6691	3.3497	12.3865	0.8411	0.8164	0.5256	M. dobsoni	165774	0.4712
M. dobsoni	582730	1.1824	M. dobsoni	161718	2.6426	3.4679	13.6277	0.8298	0.7181	0.6646	M. dobsoni	165775	0.4751
M. dobsoni	578749	1.1202	M. dobsoni	161935	2.5504	4.3187	15.0206	0.7748	0.7427	0.5073	M. dobsoni	166107	0.4534
M. talazaci	154581	1.1713	M. dobsoni	161940	2.7286	3.5796	14.8717	0.8564	0.8419	0.7142	M. dobsoni	166198	0.4038
M. talazaci	154585	1.1379	M. dobsoni	165467	2.9489	3.6558	13.9999	1.0745	0.8393	0.8699	M. dobsoni	166200	0.4542
M. talazaci	577056	1.1085	M. dobsoni	165774	2.6323	3.5714	13.6836	0.8442	0.6219	0.7065	M. dobsoni	578749	0.5034
M. talazaci	159692	1.1613	M. dobsoni	165775	2.7849	3.8547	14.0205	0.8049	0.7303	0.4502	M. dobsoni	582730	0.4616
M. talazaci	162038	1.1418	M. dobsoni	166107	2.4778	3.7190	13.9914	0.8841	0.5731	0.9219	M. dobsoni	578749	0.5025

Appendix 5.3 (con't)

Taxon	ID	APLI	Taxon	ID	DHWI	HHSZI	HSI	MEPW	LEPW	TRHI	Taxon	ID	SCSI
M. talazaci	162039		M. dobsoni	166198	2.8365	3.7601	14.1402	1.1108	0.7075	1.0788	M. talazaci	154581	0.5547
M. talazaci	162040	1.1193	M. dobsoni	166200	2.7337	3.7162	14.6169	0.9448	0.7506	0.8276	M. talazaci	154585	0.5747
M. talazaci	166234		M. dobsoni	45736	3.0333	3.2420	12.3513	0.9195	1.0986	0.6015	M. talazaci	577056	0.4964
M. talazaci	167500	1.1660	M. dobsoni	578749	2.9389	3.8577	14.6319	1.0395	0.8243	0.7520	M. talazaci	159692	0.5371
M. talazaci	167501	1.1498	M. dobsoni	582730	2.5882	3.9938	14.2150	0.8287	0.6765	0.7108	M. talazaci	162037	0.6196
M. talazaci	167502	1.1406	M. talazaci	154581	2.8428	4.0586	14.7612	0.9784	0.8339	1.3088	M. talazaci	162038	0.4691
M. talazaci	167503	1.1494	M. talazaci	154585	2.8635	3.7971	13.7002	0.9971	0.9053	1.5566	M. talazaci	162039	0.4495
Oryzorictes	156226	1.2499	M. talazaci	577056	3.0263	3.7303	15.1285	1.1485	0.8210	0.7902	M. talazaci	162040	0.4997
Oryzorictes	156601	1.2690	M. talazaci	159692	2.9354	3.7897	13.4168	1.1149	0.8603	1.2789	M. talazaci	166234	0.4886
Oryzorictes	156602	1.2639	M. talazaci	162038	2.8591	3.5392	14.1546	1.0250	0.8139	0.8484	M. talazaci	167500	0.5234
Oryzorictes	156603	1.2624	M. talazaci	162039	2.5959	4.0664	14.3532	0.9401	0.6705	0.6446	M. talazaci	167501	0.5048
Oryzorictes	159466		M. talazaci	162040	3.0448	3.4399	13.8748	1.1569	0.8432	1.3404	M. talazaci	167502	0.5012
Oryzorictes	159695	1.2133	M. talazaci	166234	2.5894	4.3422	15.8989	0.9185	0.6957	0.6262	M. talazaci	167503	0.4427
Oryzorictes	161744	1.2570	M. talazaci	167500	3.0443	3.8609	15.0352	1.1435	0.9057	1.0708	Oryzorictes	156226	0.3686
Oryzorictes	161745	1.2650	M. talazaci	167501	2.8124	3.6478	13.1597	0.9781	0.8607	0.7387	Oryzorictes	156601	0.2920
Oryzorictes	161746		M. talazaci	167502	2.4805	3.7330	14.0410	0.8601	0.6510	0.9605	Oryzorictes	156602	0.2847
Oryzorictes	162052	1.2535	M. talazaci	167503	2.4581	3.8934	14.4161	0.8172	0.6216	0.8605	Oryzorictes	156603	0.3081
Oryzorictes	162053	1.2080	Oryzorictes	156601	3.1205	2.5235	7.5289	1.2749	0.6891	0.7201	Oryzorictes	159466	0.3148
Oryzorictes	162054	1.2739	Oryzorictes	156602	3.5029	2.6264	8.0594	1.5365	0.7482	0.9843	Oryzorictes	159695	0.3032
Oryzorictes	162055	1.2641	Oryzorictes	156603	2.9320	2.7157	8.5138	1.1752	0.6472	0.6913	Oryzorictes	161744	0.2861
Oryzorictes	162056	1.3023	Oryzorictes	159695	3.2477	2.5105	8.2168	1.3780	0.8535	0.7935	Oryzorictes	161745	0.2874
Oryzorictes	162057	1.2632	Oryzorictes	161744	3.4639	2.2069	7.4631	1.5134	0.8562	0.9121	Oryzorictes	161746	0.3011
Oryzorictes	162058	1.2735	Oryzorictes	161745	2.9519	2.1778	6.8962	1.2403	0.7486	0.8529	Oryzorictes	162052	0.2786
Oryzorictes	165490	1.2670	Oryzorictes	161746	3.0409	2.5519	8.4352	1.2143	0.6453	0.6644	Oryzorictes	162053	0.2797
Oryzorictes	165491	1.2671	Oryzorictes	162052	3.1699	2.3445	7.6757	1.3031	0.6959	0.5843	Oryzorictes	162054	0.2885
Oryzorictes	165705	1.2854	Oryzorictes	162053	3.4554	2.4089	7.6028	1.4514	0.9120	0.6776	Oryzorictes	162055	0.2906
Oryzorictes	166157	1.2834	Oryzorictes	162054	3.6803	2.2907	7.4823	1.6237	1.0400	0.9333	Oryzorictes	162056	0.3143
Oryzorictes	166208	1.2894	Oryzorictes	162055	3.8211	2.6932	8.3213	1.6165	0.8824	0.7070	Oryzorictes	162057	0.3228
Oryzorictes	166237	1.2812	Oryzorictes	162056	2.9688	2.2617	7.3172	1.1587	0.7525	0.8281	Oryzorictes	162058	0.3152
Oryzorictes	166238	1.2786	Oryzorictes	162057	3.2397	2.2666	7.2882	1.2160	1.0177	0.4534	Oryzorictes	165490	0.3065
Oryzorictes	166239	1.2620	Oryzorictes	162058	3.4334	2.3915	8.6043	1.4315	0.8265	0.7679	Oryzorictes	165491	0.3304
Oryzorictes	166240	1.2626	Oryzorictes	165490	3.5595	2.6346	8.0617	1.5889	0.6306	0.6523	Oryzorictes	165705	0.2830
Oryzorictes	167480	1.2829	Oryzorictes	165491	3.3628	2.1240	7.0117	1.4940	0.7727	0.7927	Oryzorictes	166157	0.3103
Oryzorictes	167481	1.2488	Oryzorictes	165492	3.3397	2.4244	8.0603	1.4753	0.7784	0.6709	Oryzorictes	166208	0.2803

Appendix 5.3 (con't)

Taxon	ID	APLI	Taxon	ID	DHWI	HHSZI	HSI	MEPW	LEPW	TRHI	Taxon	ID	SCSI
Oryzorictes	167482	1.2813	Oryzorictes	165705	3.6465	2.5607	7.9595	1.6695	0.7930	0.6811	Oryzorictes	166237	0.2695
Oryzorictes	169239	1.2723	Oryzorictes	166157	3.3589	2.4138	7.2996	1.4345	0.8267	0.6283	Oryzorictes	166238	0.3083
Oryzorictes	169240	1.2981	Oryzorictes	166208	3.2367	2.3764	7.5530	1.4194	0.6887	0.6804	Oryzorictes	166239	0.2877
Oryzorictes	31257	1.1751	Oryzorictes	166237	3.3847	2.7137	8.6412	1.4890	0.6843	0.7534	Oryzorictes	166240	0.3206
Oryzorictes	577052	1.2684	Oryzorictes	166238	3.7715	2.6398	8.5066	1.7877	0.7953	0.6969	Oryzorictes	167480	0.3946
Oryzorictes	578789	1.2250	Oryzorictes	166239	3.3134	2.3472	7.3037	1.4061	0.7837	0.5379	Oryzorictes	167481	0.3233
Limnogale	100688	1.1707	Oryzorictes	166240	3.5492	2.6855	8.2139	1.6549	0.7616	0.6059	Oryzorictes	167482	0.3219
Limnogale	100689	1.3116	Oryzorictes	167480	3.5224	2.5605	7.4650	1.7166	0.6848	1.0831	Oryzorictes	169239	0.2966
Limnogale	100801	1.1590	Oryzorictes	167481	3.6222	2.5169	7.9945	1.6926	0.7387	0.6171	Oryzorictes	169240	0.2528
Geogale	151947	1.1003	Oryzorictes	167482	3.9127	2.5549	7.9244	1.7932	0.9960	0.6483	Oryzorictes	31257	0.3552
Geogale	156552	1.1253	Oryzorictes	169239	3.3399	2.6399	7.5572	1.4029	0.6649	0.9131	Oryzorictes	45018	0.3360
Geogale	156553	1.1796	Oryzorictes	169240	3.5449	2.6596	8.3178	1.5215	0.8711	0.6966	Oryzorictes	5639	0.3435
Potamogale	266897	0.8449	Oryzorictes	31257	3.4673	2.2741	7.9156	1.4893	1.0064	0.6293	Oryzorictes	577052	0.2488
Potamogale	34881		Oryzorictes	45018	3.8156	2.0660	7.2756	1.6631	0.9954	0.9534	Oryzorictes	578789	0.3009
Potamogale	51324	0.8658	Oryzorictes	577052	3.4311	2.3950	8.3508	1.4195	0.8655	0.5734	Limnogale	100688	0.3700
Solenodon	49508	1.1661	Oryzorictes	578789	3.4789	2.2746	7.3512	1.5566	0.6927	0.8681	Limnogale	100689	0.3762
Solenodon	172680	1.1553	Oryzorictes	156226	3.6644	2.1600	8.1726	1.7153	0.8870	0.6540	Limnogale	100801	0.3709
Solenodon	217256	1.1271	Limnogale	100688	2.8353	4.2419	12.9920	1.0667	0.7237	0.8735	Limnogale	45050	0.3633
Solenodon	238263	1.1476	Limnogale	100689	2.9427	4.1582	11.6005	0.9636	0.8773	0.6778	Limnogale	45056	0.3353
Solenodon	290520	1.1505	Limnogale	100801	2.8354	4.2454	11.9891	1.0009	0.8035	0.4797	Geogale	151947	0.4071
Solenodon	395697	1.2133	Limnogale	45050	3.0973	4.3554	12.2983	1.0984	0.9374	0.8511	Geogale	156552	0.4139
Solenodon	395819	1.1065	Limnogale	45056	2.8289	4.0481	12.8210	1.0390	0.7570	0.7738	Geogale	156553	0.4196
Solenodon	51068	1.1531	Geogale	156551	2.4002	3.7923	12.2633	0.8392	0.5814	0.7327	Potamogale	266897	0.4863
Solenodon	57320	1.1849	Geogale	156552	2.6271	3.5561	14.8818	0.8587	0.7132	0.6369	Potamogale	34881	0.3896
Solenodon	72809	1.1899	Geogale	156553	2.7537	2.8962	11.7126	0.9035	0.7716	0.6073	Potamogale	51324	0.4245
Solenodon	89448	1.1919	Geogale	161594	2.4232	3.7865	15.5064	0.7257	0.7502	0.9149	Solenodon	49508	0.5454
Petrodromus	203332	1.1781	Potamogale	266897		4.4668	15.9108				Solenodon	172680	0.5439
Petrodromus	203336	1.1618	Potamogale	34881	2.0014	4.1897	15.0796	0.4564	0.5284	0.5768	Solenodon	217256	0.5844
Echinosorex	448860	1.1037	Potamogale	51324	2.1565	3.9062	13.2607	0.6938	0.4947	0.7540	Solenodon	238263	0.5903
			Solenodon	49508	3.0095	3.0609	10.9786	1.2280	0.7420	0.8580	Solenodon	290520	0.5416
			Solenodon	172680	3.5732	2.7988	9.0424	1.4751	0.9823	0.6178	Solenodon	395697	0.5496
			Solenodon	217256	3.2643	2.6506	9.9678	1.3273	0.8880	0.7147	Solenodon	395819	0.5857
			Solenodon	238263	2.9070	1.9208	7.5519	1.2107	0.6492	0.4654	Solenodon	51068	0.5658
			Solenodon	290520	3.3037	2.6161	9.7120	1.3378	0.9155	0.6787	Solenodon	57320	0.5275

Appendix 5.3 (con't)

Taxon	ID	DHWI	HHSZI	HSI	MEPW	LEPW	TRHI
Solenodon	395697	3.0070	2.6338	9.5099	1.1915	0.7762	0.5918
Solenodon	395819	2.9754	2.5488	8.9400	1.2127	0.7231	0.5864
Solenodon	51068	3.0648	2.8988	10.0242	1.1335	0.7877	0.6924
Solenodon	57320	3.0407	2.4192	9.1445	1.1837	0.8716	0.8290
Solenodon	72809	3.1935	2.2195	8.4192	1.2751	0.9069	0.6065
Petrodromus	203332	1.9722	3.7055	14.3177	0.5622	0.2689	0.7868
Petrodromus	203336	1.9517	3.2487	13.1608	0.5570	0.4193	0.7978
Echinosorex	448860	2.3385	3.7216	11.4936	0.7462	0.5200	0.5860

Taxon	ID	SCSI
Solenodon	72809	0.5109
Solenodon	89448	0.5621
Petrodromus	203332	0.4752
Petrodromus	203336	0.5278
Echinosorex	448860	0.4585

Taxon	ID	GFSI	Taxon	ID	TSI	GTSI	LTSI	Taxon	ID	UWI	OPLI	Taxon	ID	HRLI
Echinops	170605	1.1266	Echinops	170605	1.1260	1.4913	0.7816	Echinops	170605	0.0808	0.1176	Echinops	170605	1.2772
Echinops	170607	1.3631	Echinops	170607	0.9230	1.1989	0.6649	Echinops	170607	0.0826	0.1665	Echinops	170607	1.2781
Echinops	207717	1.4663	Echinops	207717	1.0526	1.1516	0.9410	Echinops	207717	0.0722	0.1794	Echinops	207717	1.2273
Echinops	207718	1.4628	Echinops	212918	1.0452	1.2962	0.8086	Echinops	207718	0.0770	0.1517	Echinops	207718	1.3231
Echinops	212918	1.5355	Echinops	212919	0.9482	1.1745	0.7283	Echinops	212918	0.0882	0.1859	Echinops	212918	1.0455
Echinops	212919	1.7403	Echinops	31270	0.9350	1.3311	0.5849	Echinops	212919	0.0798	0.1935	Echinops	212919	1.0667
Echinops	31270	1.3507	Echinops	328620	0.9145	1.1510	0.6806	Echinops	31270	0.0763	0.1729	Echinops	31270	1.0329
Echinops	328620	1.6476	Echinops	328636	1.1178	1.4591	0.7898	Echinops	328620			Echinops	328620	1.0726
Echinops	328636	1.4801	Echinops	328637	1.0647	1.1455	0.9738	Echinops	328636	0.0643	0.1895	Echinops	328636	1.0045
Echinops	328637	1.3089	Echinops	395835	0.9549	1.2701	0.6687	Echinops	328637	0.0710	0.1865	Echinops	328637	1.0472
Echinops	395835	1.4233	Echinops	464980	0.9646	1.1761	0.7402	Echinops	464980	0.0833	0.1570	Echinops	464980	1.0240
Echinops	464980	1.3994	Echinops	588220	0.9831	1.2477	0.7282	Echinops	588220	0.0925	0.1810	Echinops	588220	1.0335
Echinops	588220	1.5694	Setifer	154034	0.9683	1.1326	0.7927	Setifer	154033	0.0883	0.1728	Setifer	154033	1.1209
Setifer	154033	1.5090	Setifer	159731	1.0759	1.3583	0.8018	Setifer	154034	0.0833	0.1794	Setifer	154034	1.1090
Setifer	154034	1.2961	Setifer	165494	1.0497	1.3305	0.7669	Setifer	159731	0.0886	0.1751	Setifer	159731	1.1034
Setifer	159731	1.5319	Setifer	166159	0.9809	1.0984	0.8464	Setifer	165494	0.0812	0.1496	Setifer	165494	1.0605
Setifer	165494	1.4899	Setifer	170532	0.8454	1.1465	0.5355	Setifer	166159			Setifer	170532	1.0498
Setifer	166159	1.6164	Setifer	170548	1.0748	1.3085	0.8355	Setifer	170532	0.0770	0.1756	Setifer	170731	1.0649
Setifer	170532	1.3410	Setifer	170581	1.1098	1.3255	0.8870	Setifer	170548	0.0843	0.1662	Setifer	207076	1.0645
Setifer	170548	1.6383	Setifer	170730	0.9346	1.3075	0.5846	Setifer	170730			Setifer	317872	1.0843
Setifer	170581	1.2666	Setifer	170731	0.9512	1.1845	0.7141	Setifer	170731	0.0923	0.1654	Setifer	33948	1.0600

Appendix 5.3 (con't)

Taxon	ID	GFSI	Taxon	ID	TSI	GTSI	LTSI	Taxon	ID	UWI	OPLI	Taxon	ID	HRLI
Setifer	170730	1.5815	Setifer	207076	0.9121	1.0609	0.7551	Setifer	207076	0.0836	0.1484	Setifer	395513	1.1122
Setifer	170731	1.3444	Setifer	317872	1.1204	1.6233	0.6766	Setifer	317872	0.0690	0.1819	Setifer	395719	1.0700
Setifer	207076	1.5130	Setifer	33948	0.9894	1.0114	0.9627	Setifer	328612	0.0783	0.1531	Setifer	541443	1.0460
Setifer	328612	1.4284	Setifer	395513	1.1062	1.4388	0.7703	Setifer	33948	0.0802	0.1616	Setifer	578790	1.0611
Setifer	33948	1.4412	Setifer	395719	1.1107	1.4009	0.8301	Setifer	395513	0.0924	0.1674	Setifer	85170	1.0843
Setifer	395513	1.4401	Setifer	541443	1.0275	1.5383	0.5911	Setifer	395719	0.0783	0.1752	Setifer	85513	1.2555
Setifer	395719	1.5948	Setifer	578790	1.3007	1.8858	0.7942	Setifer	541443	0.0870	0.1620	Hemicentetes	83658	1.1124
Setifer	541443	1.5533	Setifer	85170	1.0797	1.2943	0.8616	Setifer	578790	0.0752	0.1737	Hemicentetes	162062	1.2176
Setifer	85170	1.5647	Setifer	85513	0.9084	1.0913	0.7235	Setifer	85170	0.0870	0.1438	Hemicentetes	166132	1.2806
Setifer	85513	1.3997	Setifer	154033	1.0876	1.2851	0.8700	Setifer	85513	0.0840	0.1365	Hemicentetes	170593	1.0655
Hemicentetes	83658	1.6470	Hemicentetes	83658	1.1079	1.3451	0.8748	Hemicentetes	83658	0.0884	0.2166	Hemicentetes	207712	1.1406
Hemicentetes	162062	1.9361	Hemicentetes	162062	0.9590	1.1490	0.7788	Hemicentetes	10001	0.0878	0.2256	Hemicentetes	207714	1.0130
Hemicentetes	166132	1.6449	Hemicentetes	166132	1.0694	1.1502	0.9813	Hemicentetes	162062	0.1131	0.2173	Hemicentetes	207715	1.0115
Hemicentetes	170593	1.4659	Hemicentetes	170593	1.3015	1.7161	0.9156	Hemicentetes	166132	0.0934	0.2221	Hemicentetes	212920	0.9551
Hemicentetes	206755	1.4126	Hemicentetes	206755	0.9094	1.1494	0.6760	Hemicentetes	170593	0.0797	0.2260	Hemicentetes	212922	1.2534
Hemicentetes	207712	1.4873	Hemicentetes	207712	1.1695	1.2150	1.1242	Hemicentetes	206755			Hemicentetes	212924	1.0219
Hemicentetes	207714	1.8025	Hemicentetes	207714	1.1337	1.2997	0.9735	Hemicentetes	207712	0.0948	0.2187	Hemicentetes	212940	1.0122
Hemicentetes	207715	1.5477	Hemicentetes	212921	1.0973	1.3529	0.8695	Hemicentetes	207714	0.0852	0.2587	Hemicentetes	339992	1.0225
Hemicentetes	212920	1.5016	Hemicentetes	212922	0.9611	1.1154	0.8041	Hemicentetes	207715	0.0896	0.2167	Hemicentetes	354998	1.2651
Hemicentetes	212921	1.3586	Hemicentetes	212924	1.0424	1.4327	0.6783	Hemicentetes	212920	0.0858	0.1972	Hemicentetes	364954	1.1422
Hemicentetes	212922		Hemicentetes	212940	0.9994	1.1225	0.8702	Hemicentetes	212922	0.1106	0.2057	Tenrec	154628	1.1465
Hemicentetes	212924	1.7441	Hemicentetes	29245	0.9981	1.1952	0.8175	Hemicentetes	212924	0.0969	0.2078	Tenrec	156337	1.1344
Hemicentetes	212940	1.6058	Hemicentetes	339992	1.1541	1.4210	0.8923	Hemicentetes	212940	0.1022	0.2162	Tenrec	170511	1.1076
Hemicentetes	339992	1.5825	Hemicentetes	354998	1.2166	1.5048	0.9447	Hemicentetes	339992	0.0881	0.2186	Tenrec	30398	1.4418
Hemicentetes	354998	1.5957	Hemicentetes	364954	1.1847	1.3125	1.0595	Hemicentetes	354998	0.0908	0.2068	Tenrec	361485	1.1751
Hemicentetes	364954	1.5936	Hemicentetes	395510	1.1589	1.4481	0.8963	Hemicentetes	364954	0.0985	0.2074	Tenrec	364955	1.1906
Tenrec	154628	1.6145	Tenrec	154628	0.9326	1.3128	0.5737	Hemicentetes	395510	0.0991	0.2100	Tenrec	577051	1.1351
Tenrec	156337	1.6606	Tenrec	156337	0.8999	1.2447	0.5341	Tenrec	1001	0.0836	0.2357	Tenrec	578792	1.2160
Tenrec	170511	1.6316	Tenrec	16364	0.9158	1.4559	0.4107	Tenrec	154628	0.0866	0.2297	M. cowani	156221	0.9679
Tenrec	30398	1.3912	Tenrec	170511	0.9222	1.2963	0.5868	Tenrec	154629	0.0953	0.2374	M. cowani	156222	0.9176

Appendix 5.3 (con't)

Taxon	ID	GFSI	Taxon	ID	TSI	GTSI	LTSI	Taxon	ID	UWI	OPLI	Taxon	ID	HRLI
Tenrec	361485	1.7240	Tenrec	30398	0.9915	1.3773	0.5914	Tenrec	156337	0.0799	0.2311	M. cowani	156223	0.9187
Tenrec	364955	1.6116	Tenrec	361485	0.9484	1.6858	0.3865	Tenrec	170511	0.0896	0.2417	M. cowani	165672	1.0922
Tenrec	577051	1.6767	Tenrec	364955	1.2928	2.1726	0.6182	Tenrec	174727		0.2530	M. cowani	165673	0.9212
Tenrec	578792	1.0810	Tenrec	577051	1.1706	1.5835	0.7514	Tenrec	30398	0.0878	0.2550	M. cowani	165674	0.8867
Tenrec	154629	1.6177	Tenrec	578792	1.0725	1.6959	0.5494	Tenrec	361485	0.0940	0.2384	M. cowani	165676	0.9069
Tenrec	59011	1.4818	Tenrec	154629	0.9821	1.3676	0.6121	Tenrec	364955	0.0987	0.2357	M. cowani	165689	0.8873
Tenrec	60587	1.4957	Tenrec	59011	0.9368	1.4140	0.4822	Tenrec	577051	0.1010	0.2101	M. cowani	168017	1.0434
M. cowani	151654	1.3916	Tenrec	60587	1.0599	1.6227	0.5485	Tenrec	578792	0.0874	0.2325	M. cowani	328658	1.0460
M. cowani	151656	1.4128	M. cowani	151654	1.1641	1.5156	0.8463	Tenrec	59011	0.1006	0.2350	M. cowani	449184	0.9744
M. cowani	154020	1.6100	M. cowani	151656	1.1378	1.3547	0.9287	Tenrec	60587	0.0875	0.2108	M. cowani	449186	0.9041
M. cowani	154026	1.5249	M. cowani	154020	1.0412	1.3550	0.7888	Tenrec	85514	0.0921	0.2316	M. cowani	449187	0.9276
M. cowani	156195	1.5221	M. cowani	154026	0.9120	1.1197	0.7291	M. cowani	151654			M. cowani	449188	1.1302
M. cowani	156197	1.4073	M. cowani	156195	1.1218	1.4871	0.8016	M. cowani	151656			M. dobsoni	161935	0.9363
M. cowani	156221	1.4334	M. cowani	156196	0.9512	1.1290	0.7847	M. cowani	154020			M. dobsoni	161940	0.9519
M. cowani	156222	1.5403	M. cowani	156221	1.0237	1.1475	0.8997	M. cowani	154026			M. dobsoni	165467	0.9625
M. cowani	156223	1.5719	M. cowani	156222	1.0123	1.1781	0.8557	M. cowani	156195			M. dobsoni	165774	1.0433
M. cowani	165672	1.4955	M. cowani	156223	1.0914	1.2072	0.9730	M. cowani	156196			M. dobsoni	165775	1.2516
M. cowani	165674	1.5514	M. cowani	165672	1.2864	1.7811	0.8861	M. cowani	156197			M. dobsoni	166107	0.9212
M. cowani	165676	1.4936	M. cowani	165673	1.0498	1.0818	1.0166	M. cowani	156221	0.0705	0.1647	M. dobsoni	166198	0.8974
M. cowani	165689	1.5355	M. cowani	165676	1.0389	1.1918	0.8893	M. cowani	156222			M. dobsoni	166200	0.9251
M. cowani	168017	1.6750	M. cowani	165689	0.9278	0.9845	0.8679	M. cowani	156223	0.0760	0.1545	M. dobsoni	578749	0.9117
M. cowani	328658	1.8760	M. cowani	168017	1.1809	1.5460	0.8571	M. cowani	165672	0.0770	0.1630	M. dobsoni	582730	0.8927
M. cowani	449184	1.2257	M. cowani	328658	1.1608	1.3299	0.9897	M. cowani	165673	0.0705	0.1773	M. talazaci	154581	0.9440
M. cowani	449186	1.5151	M. cowani	449186	1.1050	1.4351	0.7900	M. cowani	165674	0.0720	0.1480	M. talazaci	154585	0.9608
M. cowani	449187	1.4678	M. cowani	449187	1.1331	1.4343	0.8471	M. cowani	165676	0.0665	0.1659	M. talazaci	577056	0.9290
M. cowani	449188	1.6790	M. cowani	449188	1.2920	1.5914	1.0004	M. cowani	165680			M. talazaci	162040	0.9427
M. dobsoni	151624	1.5510	M. dobsoni	151624	0.9595	1.0804	0.8382	M. cowani	165689	0.0674	0.1657	M. talazaci	167500	0.9449
M. dobsoni	151625	1.7558	M. dobsoni	151625	1.2569	1.4467	1.0603	M. cowani	168017		0.1395	M. talazaci	167501	0.8934
M. dobsoni	156224	1.4539	M. dobsoni	156224	1.1532	1.4360	0.8649	M. cowani	328658	0.0630	0.1781	M. talazaci	167502	0.9046
M. dobsoni	156225	1.4793	M. dobsoni	156225	1.0486	1.2498	0.8532	M. cowani	449184	0.0698	0.1397	M. talazaci	167503	0.9072

Appendix 5.3 (con't)

Taxon	ID	GFSI	Taxon	ID	TSI	GTSI	LTSI	Taxon	ID	UWI	OPLI	Taxon	ID	HRLI
M. dobsoni	159497	1.5530	M. dobsoni	159497	1.1982	1.4077	0.9708	M. cowani	449186	0.0708	0.1483	Oryzorictes	161746	1.0819
M. dobsoni	159498	1.5910	M. dobsoni	159498	1.3324	1.7837	0.9226	M. cowani	449187	0.0654	0.1679	Oryzorictes	162053	1.0678
M. dobsoni	159499	1.7030	M. dobsoni	159499	1.3846	1.7563	1.0462	M. cowani	449188	0.0601	0.1857	Oryzorictes	162054	1.3631
M. dobsoni	161718	1.7543	M. dobsoni	161679	1.1854	1.5006	0.8918	M. dobsoni	151624			Oryzorictes	162058	1.0505
M. dobsoni	161935	1.6781	M. dobsoni	161718	1.1409	1.3773	0.8956	M. dobsoni	151625			Oryzorictes	167480	1.0509
M. dobsoni	161940	1.5556	M. dobsoni	161935	1.4103	1.5942	1.2088	M. dobsoni	156224			Oryzorictes	31257	1.0523
M. dobsoni	165467	1.5806	M. dobsoni	161940	1.2260	1.4773	0.9965	M. dobsoni	156225			Oryzorictes	578789	1.0420
M. dobsoni	165774	1.3908	M. dobsoni	165467	0.9685	1.0567	0.8762	M. dobsoni	159497			Limnogale	45050	0.9383
M. dobsoni	165775	1.3800	M. dobsoni	165774	1.1126	1.4317	0.8238	M. dobsoni	159498			Geogale	161594	1.0919
M. dobsoni	166107	1.5437	M. dobsoni	165775	1.0951	1.3139	0.8739	M. dobsoni	159499			Potamogale	266897	1.2853
M. dobsoni	166198	1.6798	M. dobsoni	166107	1.1027	1.3884	0.8411	M. dobsoni	161679			Potamogale	34881	1.3865
M. dobsoni	166200	1.5768	M. dobsoni	166198	1.0366	1.3112	0.7685	M. dobsoni	161718			Potamogale	51324	1.3020
M. dobsoni	578749	1.5153	M. dobsoni	166200	1.1241	1.3977	0.8577	M. dobsoni	161935	0.0597	0.1226	Solenodon	172680	1.0640
M. dobsoni	582730	1.4664	M. dobsoni	578749	1.4008	1.9460	0.9569	M. dobsoni	161940	0.0681	0.1022	Solenodon	238263	1.0865
M. talazaci	154581	1.6673	M. dobsoni	582730	1.3808	1.7047	1.0787	M. dobsoni	165467	0.0644	0.1312	Solenodon	290520	1.1372
M. talazaci	154585	1.4642	M. talazaci	154581	1.1478	1.4272	0.9018	M. dobsoni	165774	0.0653	0.1137	Solenodon	395697	1.1151
M. talazaci	577056	1.6750	M. talazaci	154585	0.9783	1.2482	0.7504	M. dobsoni	165775	0.0713	0.1181	Solenodon	395819	1.0522
M. talazaci	159692	1.6604	M. talazaci	577056	1.0971	1.4351	0.8196	M. dobsoni	166107	0.0610	0.1238	Solenodon	51068	1.1166
M. talazaci	162039	1.4984	M. talazaci	159692	1.0389	1.4560	0.7011	M. dobsoni	166198	0.0584	0.1106	Solenodon	72809	1.0502
M. talazaci	162040	1.6150	M. talazaci	162039	1.0548	1.3443	0.8030	M. dobsoni	166200	0.0577	0.1167	Petrodromus	203336	0.7206
M. talazaci	166234	1.5485	M. talazaci	162040	1.2817	1.8472	0.8113	M. dobsoni	578749	0.0533	0.1372	Echinosorex	448860	1.2929
Taxon	ID	GFSI	Taxon	ID	TSI	GTSI	LTSI	Taxon	ID	UWI	OPLI			
M. talazaci	167500	1.6393	M. talazaci	166234	1.0640	1.2624	0.8756	M. dobsoni	582730	0.0754	0.1188			
M. talazaci	167501	1.4485	M. talazaci	167500	1.1658	1.5325	0.8586	M. talazaci	154581	0.0650	0.1139			
M. talazaci	167502	1.7178	M. talazaci	167501	1.0091	1.2555	0.7914	M. talazaci	154585	0.0679	0.1222			
M. talazaci	167503	1.4617	M. talazaci	167502	1.0387	1.2587	0.8484	M. talazaci	577056	0.0623	0.1338			
Oryzorictes	156226	1.8625	M. talazaci	167503	0.9685	1.2047	0.7571	M. talazaci	162037					
Oryzorictes	156601	1.3258	Oryzorictes	156226	1.1922	1.4350	0.9828	M. talazaci	162039					
Oryzorictes	156602	1.6009	Oryzorictes	156601	1.2461	1.4060	1.0870	M. talazaci	162040	0.0612	0.1180			
Oryzorictes	156603	1.3734	Oryzorictes	156602	1.2992	1.5467	1.0746	M. talazaci	166234					

Appendix 5.3 (con't)

Taxon	ID	GFSI	Taxon	ID	TSI	GTSI	LTSI	Taxon	ID	UWI	OPLI
Oryzorictes	159466	1.6269	Oryzorictes	156603	1.0647	1.3406	0.8137	M. talazaci	167500	0.0672	0.1173
Oryzorictes	161744	1.4734	Oryzorictes	159695	1.1732	1.4039	0.9606	M. talazaci	167501	0.0701	0.1162
Oryzorictes	162052	1.5438	Oryzorictes	161744	1.1865	1.4882	0.9180	M. talazaci	167502	0.0644	0.1108
Oryzorictes	162053	1.6010	Oryzorictes	161745	1.2951	1.4622	1.1301	M. talazaci	167503	0.0655	0.0997
Oryzorictes	162055	1.5901	Oryzorictes	161746	1.3934	1.9813	0.9422	Oryzorictes	161746	0.0947	0.2703
Oryzorictes	162056	2.0861	Oryzorictes	162052	1.2008	1.3780	1.0290	Oryzorictes	162052		
Oryzorictes	162057	1.4509	Oryzorictes	162053	1.5008	1.9506	1.1070	Oryzorictes	162053	0.1048	0.2805
Oryzorictes	162058	1.2895	Oryzorictes	162055	1.0993	1.3693	0.8432	Oryzorictes	162054	0.0949	0.2811
Oryzorictes	165490	1.5899	Oryzorictes	162057	1.2353	1.4530	1.0206	Oryzorictes	162055		
Oryzorictes	165491	1.7105	Oryzorictes	162058	1.4082	1.9236	0.9649	Oryzorictes	162057		
Oryzorictes	165705	1.4289	Oryzorictes	165490	1.2082	1.5943	0.8746	Oryzorictes	162058	0.0995	0.2974
Oryzorictes	166157	1.4752	Oryzorictes	165491	1.2983	1.7648	0.9031	Oryzorictes	165491		
Oryzorictes	166208	1.5854	Oryzorictes	165705	1.0948	1.4092	0.8114	Oryzorictes	165492		
Oryzorictes	166237	1.6921	Oryzorictes	166157	1.2819	1.4726	1.0901	Oryzorictes	165705		
Oryzorictes	166238	1.7259	Oryzorictes	166208	1.2055	1.4489	0.9737	Oryzorictes	166157		
Oryzorictes	166239	1.6331	Oryzorictes	166237	1.4044	2.0582	0.8931	Oryzorictes	166208		
Oryzorictes	166240	1.4059	Oryzorictes	166238	1.4669	1.9703	1.0569	Oryzorictes	166237		
Oryzorictes	167480	1.6112	Oryzorictes	166239	1.2903	1.7598	0.8960	Oryzorictes	166238		
Oryzorictes	167481	1.5127	Oryzorictes	167480	1.1525	1.4902	0.8590	Oryzorictes	166239		
Oryzorictes	167482	1.5501	Oryzorictes	167481	1.1978	1.7291	0.7808	Oryzorictes	166240	0.0988	0.2852
Oryzorictes	169239	1.5419	Oryzorictes	167482	1.2365	1.3921	1.0830	Oryzorictes	167480	0.0929	0.2871
Oryzorictes	169240	1.8162	Oryzorictes	169239	1.2143	1.6061	0.8566	Oryzorictes	167481		
Oryzorictes	31257	1.5705	Oryzorictes	169240	1.2516	1.4413	1.0528	Oryzorictes	167482		
Oryzorictes	45018	1.8073	Oryzorictes	577052	1.5081	1.9687	1.1083	Oryzorictes	169239		
Oryzorictes	577052	1.6662	Oryzorictes	578789	1.2636	1.9628	0.7372	Oryzorictes	31257	0.0898	0.2294
Oryzorictes	578789	1.6305	Limnogale	100688	1.1054	1.2967	0.9076	Oryzorictes	45018	0.0929	0.2149
Limnogale	100688	1.5953	Limnogale	100689	1.3565	1.7793	0.9788	Oryzorictes	577052	0.0869	0.2710
Limnogale	100689	1.5157	Limnogale	100801	1.2479	1.6535	0.8993	Oryzorictes	578789	0.0859	0.2964
Limnogale	100801	1.8533	Geogale	156551	1.0155	1.2514	0.7992	Limnogale	45050	0.0774	0.1684
Limnogale	45050	2.2206	Geogale	156552	0.9697	1.0629	0.8765	Geogale	156551		

Appendix 5.3 (con't)

Taxon	ID	GFSI	Taxon	ID	TSI	GTSI	LTSI	Taxon	ID	UWI	OPLI
Limnogale	45056	2.1989	Geogale	156553	0.9886	1.0986	0.8711	Geogale	156552		
Geogale	156552	1.4830	Geogale	161594	1.0138	1.1472	0.8712	Geogale	156553		
Geogale	156553	1.5211	Potamogale	266897	1.0649	1.3881	0.7453	Geogale	161594	0.0692	0.1329
Potamogale	266897	1.3230	Potamogale	34881	1.4210	2.5700	0.5741	Potamogale	266897	0.0936	0.2014
Potamogale	34881	1.4080	Potamogale	51324	1.2127	1.9066	0.5909	Potamogale	34881	0.0979	0.1872
Potamogale	51324	1.3712	Solenodon	49508	1.5638	2.2555	0.8665	Potamogale	51324	0.0866	0.1788
Solenodon	49508	1.4142	Solenodon	172680	1.2936	1.8210	0.7772	Petrodromus	203335	0.0436	0.1082
Solenodon	172680	1.3492	Solenodon	217256	1.2967	1.6335	0.9368	Petrodromus	203336	0.0470	0.0963
Solenodon	217256	1.2873	Solenodon	238263	1.3187	1.6500	0.9319	Petrodromus	203337	0.0427	0.1123
Solenodon	238263	1.2644	Solenodon	290520	1.4082	1.5892	1.1876	Solenodon	49508	0.0817	0.1778
Solenodon	290520	1.3260	Solenodon	395697	1.3402	1.6812	0.9530	Solenodon	172680	0.1036	0.2137
Solenodon	395697	1.3354	Solenodon	395819	1.3931	1.7256	1.0127	Solenodon	217256	0.1086	0.1914
Solenodon	395819	1.4348	Solenodon	51068	1.2331	1.7317	0.7487	Solenodon	238263	0.0916	0.2031
Solenodon	51068	1.2323	Solenodon	57320	1.3044	1.5143	1.0594	Solenodon	290520	0.1036	0.1977
Solenodon	57320	1.3312	Petrodromus	203332	1.1791	1.5632	0.8167	Solenodon	395697	0.1032	0.2143
Solenodon	72809	1.4228	Petrodromus	203336	1.1397	1.6461	0.6831	Solenodon	395819	0.0936	0.1918
Solenodon	89448	1.1278	Echinosorex	448860	1.4093	1.8315	1.0106	Solenodon	51068	0.1090	0.1999
Petrodromu	203332	1.1118						Solenodon	57320	0.0974	0.1634
Petrodromu	203336	1.0620						Solenodon	72809	0.0995	0.1859
Echinosorex	448860	1.4531						Echinosorex	448860	0.0722	0.1950

Appendix 5.4. Index Summary Statistics and Tukey Post-Hoc Results

Taxon	SSH Means	SSH N	SSH Std.Dev.						
Echinops	0.472454	13	0.054308						
Setifer	0.496486	19	0.040875						
Hemicentetes	0.440948	16	0.021731						
Tenrec	0.469942	11	0.030336						
M. cowani	0.414784	20	0.037018						
M. dobsoni	0.525326	21	0.291882						
M. talazaci	0.512423	13	0.049792						
Oryzorictes	0.305884	35	0.030136						
Limnogale	0.363136	5	0.016224						
All Grps	0.433401	153	0.136781						

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}
	M=.47245	M=.49649	M=.44095	M=.46994	M=.41478	M=.52533	M=.51242	M=.30588	M=.36314
Echinops {1}		0.999678	0.998218	1.000000	0.890826	0.927672	0.993367	0.000265	0.668000
Setifer {2}	0.999678		0.884463	0.999540	0.382119	0.996937	0.999986	0.000010	0.326209
Hemicentetes {3}	0.998218	0.884463		0.999309	0.998988	0.386385	0.760099	0.002823	0.922087
Tenrec {4}	1.000000	0.999540	0.999309		0.935049	0.930336	0.992539	0.001072	0.724109
M. cowani {5}	0.890826	0.382119	0.998988	0.935049		0.049975	0.282166	0.019018	0.992729
M. dobsoni {6}	0.927672	0.996937	0.386385	0.930336	0.049975		0.999997	0.000010	0.099218
M. talazaci {7}	0.993367	0.999986	0.760099	0.992539	0.282166	0.999997		0.000011	0.238024
Oryzorictes {8}	0.000265	0.000010	0.002823	0.001072	0.019018	0.000010	0.000011		0.980879
Limnogale {9}	0.668000	0.326209	0.922087	0.724109	0.992729	0.099218	0.238024	0.980879	

Taxon	APLI Means	APLI N	APLI Std.Dev.
Echinops	1.170659	10	0.041816
Setifer	1.066010	17	0.278156
Hemicentetes	1.197352	12	0.020166

Appendix 5.4. (con't)

Tenrec	1.087572	10	0.009381
M. cowani	1.151515	18	0.022081
M. dobsoni	1.142893	21	0.021113
M. talazaci	1.144589	10	0.019765
Oryzorictes	1.262824	31	0.026638
Limnogale	1.213763	3	0.084904
All Grps	1.166935	132	0.119661

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}
	M=1.1707	M=1.0660	M=1.1974	M=1.0876	M=1.1515	M=1.1429	M=1.1446	M=1.2628	M=1.2138
Echinops {1}		0.213119	0.999599	0.684609	0.999939	0.998816	0.999757	0.256568	0.999424
Setifer {2}	0.213119		0.021566	0.999861	0.259615	0.355000	0.609081	0.000010	0.353256
Hemicentetes {3}	0.999599	0.021566		0.241956	0.958959	0.875999	0.958497	0.640021	1.000000
Tenrec {4}	0.684609	0.999861	0.241956		0.822494	0.901124	0.949386	0.000141	0.645856
M. cowani {5}	0.999939	0.259615	0.958959	0.822494		0.999999	1.000000	0.008591	0.988886
M. dobsoni {6}	0.998816	0.355000	0.875999	0.901124	0.999999		1.000000	0.001362	0.972883
M. talazaci {7}	0.999757	0.609081	0.958497	0.949386	1.000000	1.000000		0.044057	0.984477
Oryzorictes {8}	0.256568	0.000010	0.640021	0.000141	0.008591	0.001362	0.044057		0.997294
Limnogale {9}	0.999424	0.353256	1.000000	0.645856	0.988886	0.972883	0.984477	0.997294	

Taxon	GFSI Means	GFSI N	GFSI Std.Dev.
Echinops	1.451838	13	0.155828
Setifer	1.475021	18	0.112001
Hemicentetes	1.595055	15	0.150113
Tenrec	1.544224	11	0.181694
M. cowani	1.522579	19	0.134830
M. dobsoni	1.567135	18	0.112609
M. talazaci	1.581472	11	0.099578
Oryzorictes	1.592597	30	0.165959
Limnogale	1.876760	5	0.328683
All Grps	1.557371	140	0.167321

Appendix 5.4. (con't)

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}
	M=1.4518	M=1.4750	M=1.5951	M=1.5442	M=1.5226	M=1.5671	M=1.5815	M=1.5926	M=1.8768
Echinops {1}		0.999975	0.237639	0.863136	0.933492	0.483449	0.485002	0.118014	0.000014
Setifer {2}	0.999975		0.366651	0.958757	0.989868	0.669467	0.661387	0.188037	0.000016
Hemicentetes {3}	0.237639	0.366651		0.995541	0.905164	0.999856	1.000000	1.000000	0.009976
Tenrec {4}	0.863136	0.958757	0.995541		0.999989	0.999984	0.999718	0.992848	0.001639
M. cowani {5}	0.933492	0.989868	0.905164	0.999989		0.993450	0.983767	0.820234	0.000153
M. dobsoni {6}	0.483449	0.669467	0.999856	0.999984	0.993450		1.000000	0.999762	0.001828
M. talazaci {7}	0.485002	0.661387	1.000000	0.999718	0.983767	1.000000		1.000000	0.009522
Oryzorictes {8}	0.118014	0.188037	1.000000	0.992848	0.820234	0.999762	1.000000		0.003458
Limnogale {9}	0.000014	0.000016	0.009976	0.001639	0.000153	0.001828	0.009522	0.003458	

Taxon	HSI Means	HSI N	HSI Std.Dev.
Echinops	10.45504	13	0.949398
Setifer	11.01333	19	0.819924
Hemicentetes	7.66223	18	0.451943
Tenrec	10.51506	12	0.845084
M. cowani	13.06258	22	0.782063
M. dobsoni	13.04012	21	3.894240
M. talazaci	14.32834	12	0.781142
Oryzorictes	7.83356	34	0.487173
Limnogale	12.34017	5	0.576259
Geogale	13.59099	4	1.882020
Potamogale	14.75036	3	1.355363
Solenodon	9.32905	10	0.945467
Petrodromus	13.73922	2	0.818030
Echinosorex	11.49365	1	0.000000
All Grps	10.80312	176	2.793566

Appendix 5.4. (con't)

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=10.455	M=11.013	M=7.6622	M=10.515	M=13.063	M=13.040	M=14.328	M=7.8336	M=12.340	M=13.591	M=14.750	M=9.3291	M=13.739	M=11.494
Echinops {1}		0.999334	0.000084	1.000000	0.000149	0.000213	0.000023	0.000040	0.546665	0.027356	0.001262	0.906769	0.229667	0.999996
Setifer {2}	0.999334		0.000023	0.999853	0.001983	0.002930	0.000024	0.000023	0.915468	0.130030	0.007901	0.233900	0.505766	1.000000
Hemicentetes {3}	0.000084	0.000023		0.000088	0.000023	0.000023	0.000023	1.000000	0.000023	0.000023	0.000023	0.263561	0.000035	0.475868
Tenrec {4}	1.000000	0.999853	0.000088		0.000410	0.000581	0.000023	0.000044	0.620824	0.038314	0.001887	0.882497	0.265290	0.999998
M. cowani {5}	0.000149	0.001983	0.000023	0.000410		1.000000	0.573452	0.000023	0.999658	0.999997	0.890077	0.000023	0.999998	0.999406
M. dobsoni {6}	0.000213	0.002930	0.000023	0.000581	1.000000		0.557542	0.000023	0.999770	0.999995	0.882217	0.000023	0.999998	0.999497
M. talazaci {7}	0.000023	0.000024	0.000023	0.000023	0.573452	0.557542		0.000023	0.473063	0.999922	1.000000	0.000023	1.000000	0.895069
Oryzorictes {8}	0.000040	0.000023	1.000000	0.000044	0.000023	0.000023	0.000023		0.000023	0.000023	0.000023	0.289279	0.000036	0.534482
Limnogale {9}	0.546665	0.915468	0.000023	0.620824	0.999658	0.999770	0.473063	0.000023		0.995618	0.681155	0.026592	0.998532	1.000000
Geogale {10}	0.027356	0.130030	0.000023	0.038314	0.999997	0.999995	0.999922	0.000023	0.995618		0.999471	0.000302	1.000000	0.995353
Potamogale {11}	0.001262	0.007901	0.000023	0.001887	0.890077	0.882217	1.000000	0.000023	0.681155	0.999471		0.000032	0.999985	0.867812
Solenodon {12}	0.906769	0.233900	0.263561	0.882497	0.000023	0.000023	0.000023	0.289279	0.026592	0.000302	0.000032		0.017085	0.988593
Petrodromus {13}	0.229667	0.505766	0.000035	0.265290	0.999998	0.999998	1.000000	0.000036	0.998532	1.000000	0.999985	0.017085		0.996284
Echinosorex {14}	0.999996	1.000000	0.475868	0.999998	0.999406	0.999497	0.895069	0.534482	1.000000	0.995353	0.867812	0.988593	0.996284	

Taxon	HRLI Means	HRLI N	HRLI Std.Dev.
Echinops	1.119381	12	0.119093
Setifer	1.089769	15	0.051607
Hemicentetes	1.108110	14	0.109989
Tenrec	1.193387	8	0.106236
M. cowani	0.966006	14	0.080015
M. dobsoni	0.969381	10	0.108136
M. talazaci	0.928316	8	0.023911
Oryzorictes	1.101197	7	0.116233
Limnogale	0.938331	1	0.000000
Geogale	1.091922	1	0.000000
Potamogale	1.324609	3	0.054231
Solenodon	1.088838	7	0.034783
Petrodromus	0.720560	1	0.000000
Echinosorex	1.292873	1	0.000000

Appendix 5.4. (con't)

All Grps 1.066980 102 0.129706

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=1.1194	M=1.0898	M=1.1081	M=1.1934	M=.96601	M=.96938	M=.92832	M=1.1012	M=.93833	M=1.0919	M=1.3246	M=1.0888	M=.72056	M=1.2929
Echinops {1}		0.999866	1.000000	0.871484	0.003163	0.013578	0.001066	1.000000	0.805519	1.000000	0.040503	0.999982	0.004096	0.847864
Setifer {2}	0.999866		0.999999	0.341420	0.024655	0.081778	0.006970	1.000000	0.934566	1.000000	0.006351	1.000000	0.010515	0.644608
Hemicentetes {3}	1.000000	0.999999		0.677082	0.005349	0.023031	0.001724	1.000000	0.861986	1.000000	0.019260	1.000000	0.005667	0.776352
Tenrec {4}	0.871484	0.341420	0.677082		0.000148	0.000222	0.000141	0.778782	0.316503	0.998510	0.666320	0.602833	0.000416	0.998781
M. cowani {5}	0.003163	0.024655	0.005349	0.000148		1.000000	0.999572	0.088753	1.000000	0.985196	0.000138	0.180767	0.338464	0.043373
M. dobsoni {6}	0.013578	0.081778	0.023031	0.000222	1.000000		0.999483	0.171466	1.000000	0.989641	0.000140	0.304194	0.337679	0.054548
M. talazaci {7}	0.001066	0.006970	0.001724	0.000141	0.999572	0.999483		0.023843	1.000000	0.906964	0.000137	0.051728	0.650640	0.017115
Oryzorictes {8}	1.000000	1.000000	1.000000	0.778782	0.088753	0.171466	0.023843		0.914462	1.000000	0.033555	1.000000	0.011069	0.771040
Limnogale {9}	0.805519	0.934566	0.861986	0.316503	1.000000	1.000000	1.000000	0.914462		0.994726	0.023452	0.951471	0.908023	0.254668
Geogale {10}	1.000000	1.000000	1.000000	0.998510	0.985196	0.989641	0.906964	1.000000	0.994726		0.606726	1.000000	0.193311	0.947995
Potamogale {11}	0.040503	0.006351	0.019260	0.666320	0.000138	0.000140	0.000137	0.033555	0.023452	0.606726		0.018369	0.000143	1.000000
Solenodon {12}	0.999982	1.000000	1.000000	0.602833	0.180767	0.304194	0.051728	1.000000	0.951471	1.000000	0.018369		0.016655	0.688771
Petrodromus {13}	0.004096	0.010515	0.005667	0.000416	0.338464	0.337679	0.650640	0.011069	0.908023	0.193311	0.000143	0.016655		0.001789
Echinosorex {14}	0.847864	0.644608	0.776352	0.998781	0.043373	0.054548	0.017115	0.771040	0.254668	0.947995	1.000000	0.688771	0.001789	

Taxon	HHSI Means	HHSI N	HHSI Std.Dev.
Echinops	1.020269	13	0.064702
Setifer	1.098308	19	0.077428
Hemicentetes	1.238378	17	0.100350
Tenrec	1.100361	12	0.089791
M. cowani	1.046060	22	0.096132
M. dobsoni	1.099822	20	0.049970
M. talazaci	1.088372	12	0.065606
Oryzorictes	1.403545	34	0.133052
Limnogale	1.081809	5	0.114950
Geogale	0.998896	4	0.080869
Potamogale	0.964742	3	0.030813
Solenodon	1.151252	10	0.076857

Appendix 5.4. (con't)

Petrodromus	0.891918	2	0.041368
Echinosorex	0.929845	1	0.000000
All Grps	1.153471	174	0.165850

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=1.0203	M=1.0983	M=1.2384	M=1.1004	M=1.0461	M=1.0998	M=1.0884	M=1.4035	M=1.0818	M=.99890	M=.96474	M=1.1513	M=.89192	M=.92984
Echinops {1}		0.547847	0.000023	0.679732	0.999955	0.496091	0.871248	0.000023	0.993865	1.000000	0.999721	0.056052	0.876739	0.999705
Setifer {2}	0.547847		0.000672	1.000000	0.886761	1.000000	1.000000	0.000023	1.000000	0.813214	0.562420	0.976768	0.153934	0.898263
Hemicentetes {3}	0.000023	0.000672		0.007354	0.000023	0.000657	0.001846	0.000023	0.063118	0.000390	0.000293	0.533373	0.000088	0.081028
Tenrec {4}	0.679732	1.000000	0.007354		0.943560	1.000000	1.000000	0.000023	1.000000	0.841952	0.601499	0.992845	0.174382	0.899824
M. cowani {5}	0.999955	0.886761	0.000023	0.943560		0.851346	0.993370	0.000023	0.999965	0.999718	0.981316	0.161589	0.612534	0.995334
M. dobsoni {6}	0.496091	1.000000	0.000657	1.000000	0.851346		1.000000	0.000023	1.000000	0.791100	0.536937	0.980483	0.143044	0.890989
M. talazaci {7}	0.871248	1.000000	0.001846	1.000000	0.993370	1.000000		0.000023	1.000000	0.932498	0.742290	0.955177	0.256070	0.940686
Oryzorictes {8}	0.000023	0.000023	0.000023	0.000023	0.000023	0.000023	0.000023		0.000023	0.000023	0.000023	0.000023	0.000023	0.000077
Limnogale {9}	0.993865	1.000000	0.063118	1.000000	0.999965	1.000000	1.000000	0.000023		0.989706	0.913877	0.987029	0.467196	0.971719
Geogale {10}	1.000000	0.813214	0.000390	0.841952	0.999718	0.791100	0.932498	0.000023	0.989706		1.000000	0.254256	0.989759	0.999994
Potamogale {11}	0.999721	0.562420	0.000293	0.601499	0.981316	0.536937	0.742290	0.000023	0.913877	1.000000		0.131686	0.999890	1.000000
Solenodon {12}	0.056052	0.976768	0.533373	0.992845	0.161589	0.980483	0.955177	0.000023	0.987029	0.254256	0.131686		0.024862	0.593506
Petrodromus {13}	0.876739	0.153934	0.000088	0.174382	0.612534	0.143044	0.256070	0.000023	0.467196	0.989759	0.999890	0.024862		1.000000
Echinosorex {14}	0.999705	0.898263	0.081028	0.899824	0.995334	0.890989	0.940686	0.000077	0.971719	0.999994	1.000000	0.593506	1.000000	

Taxon	GTSI Means	GTSI N	GTSI Std.Dev.
Echinops	1.257755	12	0.118518
Setifer	1.306442	19	0.214477
Hemicentetes	1.308115	16	0.168308
Tenrec	1.519090	12	0.257016
All Grps	1.340243	59	0.213258

	{1}	{2}	{3}	{4}
	M=1.2578	M=1.3064	M=1.3081	M=1.5191
Echinops {1}		0.907915	0.908220	0.010433
Setifer {2}	0.907915		0.999995	0.024925
Hemicentetes {3}	0.908220	0.999995		0.034191
Tenrec {4}	0.010433	0.024925	0.034191	

Appendix 5.4. (con't)

Taxon	LTSI Means	LTSI N	LTSI Std.Dev.
Echinops	0.757553	12	0.112379
Setifer	0.768406	19	0.110719
Hemicentetes	0.884777	16	0.120772
Tenrec	0.553753	12	0.097008
All Grps	0.754099	59	0.157612

	{1}	{2}	{3}	{4}
	M=.75755	M=.76841	M=.88478	M=.55375
Echinops {1}		0.993533	0.021055	0.000357
Setifer {2}	0.993533		0.016633	0.000173
Hemicentetes {3}	0.021055	0.016633		0.000161
Tenrec {4}	0.000357	0.000173	0.000161	

Taxon	DHWI Means	DHWI N	DHWI Std.Dev.
Echinops	2.777906	12	0.236131
Setifer	2.703044	19	0.167558
Hemicentetes	3.384228	18	0.304813
Tenrec	2.979047	12	0.162850
M. cowani	2.919944	22	0.214157
M. dobsoni	3.083678	21	1.709645
M. talazaci	2.796034	12	0.213932
Oryzorictes	3.422075	34	0.250250
Limnogale	2.907920	5	0.116025
Geogale	2.551055	4	0.169285
Potamogale	2.078976	2	0.109691
Solenodon	3.133917	10	0.201114
Petrodromus	1.961969	2	0.014524
Echinosorex	2.338531	1	0.000000
All Grps	3.027355	174	0.690389

Appendix 5.4. (con't)

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=2.7779	M=2.7030	M=3.3842	M=2.9790	M=2.9199	M=3.0837	M=2.7960	M=3.4221	M=2.9079	M=2.5511	M=2.0790	M=3.1339	M=1.9620	M=2.3385
Echinops {1}		1.000000	0.378131	0.999964	0.999997	0.989405	1.000000	0.138520	1.000000	0.999998	0.978517	0.990865	0.926601	0.999994
Setifer {2}	1.000000		0.071408	0.996664	0.998479	0.838284	1.000000	0.006688	0.999996	1.000000	0.990019	0.907944	0.956544	0.999999
Hemicentetes {3}	0.378131	0.071408		0.916751	0.567500	0.974057	0.431375	1.000000	0.972504	0.512994	0.257581	0.999393	0.144384	0.948913
Tenrec {4}	0.999964	0.996664	0.916751		1.000000	1.000000	0.999988	0.727513	1.000000	0.996970	0.857068	0.999999	0.714488	0.999565
M. cowani {5}	0.999997	0.998479	0.567500	1.000000		0.999905	0.999999	0.191398	1.000000	0.998767	0.885585	0.999843	0.750624	0.999817
M. dobsoni {6}	0.989405	0.838284	0.974057	1.000000	0.999905		0.994016	0.823927	0.999999	0.963195	0.686131	1.000000	0.503027	0.997472
M. talazaci {7}	1.000000	1.000000	0.431375	0.999988	0.999999	0.994016		0.171370	1.000000	0.999994	0.973312	0.994418	0.914097	0.999991
Oryzorictes {8}	0.138520	0.006688	1.000000	0.727513	0.191398	0.823927	0.171370		0.924001	0.356198	0.183864	0.993561	0.095427	0.926781
Limnogale {9}	1.000000	0.999996	0.972504	1.000000	1.000000	0.999999	1.000000	0.924001		0.999914	0.958604	0.999996	0.890885	0.999934
Geogale {10}	0.999998	1.000000	0.512994	0.996970	0.998767	0.963195	0.999994	0.356198	0.999914		0.999886	0.960417	0.998738	1.000000
Potamogale {11}	0.978517	0.990019	0.257581	0.857068	0.885585	0.686131	0.973312	0.183864	0.958604	0.999886		0.681427	1.000000	1.000000
Solenodon {12}	0.990865	0.907944	0.999393	0.999999	0.999843	1.000000	0.994418	0.993561	0.999996	0.960417	0.681427		0.506315	0.996205
Petrodromus {13}	0.926601	0.956544	0.144384	0.714488	0.750624	0.503027	0.914097	0.095427	0.890885	0.998738	1.000000	0.506315		1.000000
Echinosorex {14}	0.999994	0.999999	0.948913	0.999565	0.999817	0.997472	0.999991	0.926781	0.999934	1.000000	1.000000	0.996205	1.000000	

Taxon	MEPW Means	MEPW N	MEPW Std.Dev.
Echinops	1.067869	12	0.159955
Setifer	0.946482	19	0.122389
Hemicentetes	1.381416	18	0.209215
Tenrec	1.172653	12	0.115888
M. cowani	1.135332	22	0.135149
M. dobsoni	0.919736	21	0.100806
M. talazaci	1.006524	12	0.114706
Oryzorictes	1.485979	34	0.175224
Limnogale	1.033737	5	0.053119
Geogale	0.831764	4	0.075654
Potamogale	0.575096	2	0.167883
Solenodon	1.257541	10	0.099584
Petrodromus	0.559591	2	0.003722
Echinosorex	0.746214	1	0.000000
All Grps	1.153534	174	0.268610

Appendix 5.4. (con't)

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=1.0679	M=.94648	M=1.3814	M=1.1727	M=1.1353	M=.91974	M=1.0065	M=1.4860	M=1.0337	M=.83176	M=.57510	M=1.2575	M=.55959	M=.74621
Echinops {1}		0.569427	0.000024	0.886236	0.990681	0.206484	0.998987	0.000023	1.000000	0.207828	0.000669	0.114948	0.000356	0.672609
Setifer {2}	0.569427		0.000023	0.001757	0.002403	0.999999	0.997682	0.000023	0.995625	0.976596	0.035394	0.000026	0.021687	0.986867
Hemicentetes {3}	0.000024	0.000023		0.007889	0.000029	0.000023	0.000023	0.418274	0.000180	0.000023	0.000023	0.647304	0.000023	0.001519
Tenrec {4}	0.886236	0.001757	0.007889		0.999984	0.000129	0.214616	0.000023	0.873071	0.003436	0.000028	0.984913	0.000025	0.205296
M. cowani {5}	0.990681	0.002403	0.000029	0.999984		0.000104	0.417245	0.000023	0.979729	0.008251	0.000035	0.614844	0.000028	0.316850
M. dobsoni {6}	0.206484	0.999999	0.000023	0.000129	0.000104		0.929188	0.000023	0.949804	0.997899	0.073632	0.000023	0.047240	0.996532
M. talazaci {7}	0.998987	0.997682	0.000023	0.214616	0.417245	0.929188		0.000023	1.000000	0.703646	0.006956	0.003865	0.003984	0.904594
Oryzorictes {8}	0.000023	0.000023	0.418274	0.000023	0.000023	0.000023	0.000023		0.000023	0.000023	0.000023	0.000915	0.000023	0.000059
Limnogale {9}	1.000000	0.995625	0.000180	0.873071	0.979729	0.949804	1.000000	0.000023		0.711359	0.010812	0.208960	0.006619	0.868302
Geogale {10}	0.207828	0.976596	0.000023	0.003436	0.008251	0.997899	0.703646	0.000023	0.711359		0.733511	0.000073	0.646309	1.000000
Potamogale {11}	0.000669	0.035394	0.000023	0.000028	0.000035	0.073632	0.006956	0.000023	0.010812	0.733511		0.000023	1.000000	0.999534
Solenodon {12}	0.114948	0.000026	0.647304	0.984913	0.614844	0.000023	0.003865	0.000915	0.208960	0.000073	0.000023		0.000023	0.046359
Petrodromus {13}	0.000356	0.021687	0.000023	0.000025	0.000028	0.047240	0.003984	0.000023	0.006619	0.646309	1.000000	0.000023		0.998827
Echinosorex {14}	0.672609	0.986867	0.001519	0.205296	0.316850	0.996532	0.904594	0.000059	0.868302	1.000000	0.999534	0.046359	0.998827	

Taxon	LEPW Means	LEPW N	LEPW Std.Dev.
Echinops	0.671738	13	0.107137
Setifer	0.707714	19	0.102648
Hemicentetes	0.951115	18	0.112124
Tenrec	0.749611	12	0.108944
M. cowani	0.760229	22	0.091565
M. dobsoni	0.725437	21	0.122329
M. talazaci	0.790233	12	0.101702
Oryzorictes	0.800963	34	0.116792
Limnogale	0.819797	5	0.087444
Geogale	0.704099	4	0.085260
Potamogale	0.511550	2	0.023845
Solenodon	0.824238	10	0.104218
Petrodromus	0.344133	2	0.106360
Echinosorex	0.520000	1	0.000000
All Grps	0.767763	175	0.139087

Appendix 5.4. (con't)

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=.67174	M=.70771	M=.95112	M=.74961	M=.76023	M=.72544	M=.79023	M=.80096	M=.81980	M=.70410	M=.51155	M=.82424	M=.34413	M=.52000
Echinops {1}		0.999710	0.000023	0.875111	0.520852	0.980918	0.253537	0.017006	0.334565	1.000000	0.795496	0.048785	0.004970	0.986574
Setifer {2}	0.999710		0.000023	0.998853	0.957300	1.000000	0.718930	0.131526	0.723937	1.000000	0.446004	0.242238	0.000501	0.917775
Hemicentetes {3}	0.000023	0.000023		0.000067	0.000025	0.000023	0.004901	0.000171	0.473893	0.002770	0.000027	0.144320	0.000023	0.007602
Tenrec {4}	0.875111	0.998853	0.000067		1.000000	0.999997	0.999724	0.980060	0.994873	0.999981	0.181766	0.942419	0.000093	0.738810
M. cowani {5}	0.520852	0.957300	0.000025	1.000000		0.998807	0.999961	0.984243	0.997945	0.999586	0.099409	0.956993	0.000037	0.645563
M. dobsoni {6}	0.980918	1.000000	0.000023	0.999997	0.998807		0.929620	0.391759	0.894585	1.000000	0.290494	0.491821	0.000170	0.847598
M. talazaci {7}	0.253537	0.718930	0.004901	0.999724	0.999961	0.929620		1.000000	1.000000	0.983943	0.045571	0.999979	0.000028	0.474806
Oryzorictes {8}	0.017006	0.131526	0.000171	0.980060	0.984243	0.391759	1.000000		1.000000	0.916853	0.016192	0.999998	0.000024	0.361523
Limnogale {9}	0.334565	0.723937	0.473893	0.994873	0.997945	0.894585	1.000000	1.000000		0.946836	0.041018	1.000000	0.000034	0.381860
Geogale {10}	1.000000	1.000000	0.002770	0.999981	0.999586	1.000000	0.983943	0.916853	0.946836		0.728063	0.836265	0.008753	0.963054
Potamogale {11}	0.795496	0.446004	0.000027	0.181766	0.099409	0.290494	0.045571	0.016192	0.041018	0.728063		0.013263	0.957826	1.000000
Solenodon {12}	0.048785	0.242238	0.144320	0.942419	0.956993	0.491821	0.999979	0.999998	1.000000	0.836265	0.013263		0.000024	0.284743
Petrodromus {13}	0.004970	0.000501	0.000023	0.000093	0.000037	0.000170	0.000028	0.000024	0.000034	0.008753	0.957826	0.000024		0.988598
Echinosorex {14}	0.986574	0.917775	0.007602	0.738810	0.645563	0.847598	0.474806	0.361523	0.381860	0.963054	1.000000	0.284743	0.988598	

Taxon	TRHI Means	TRHI N	TRHI Std.Dev.
Echinops	0.587427	13	0.141508
Setifer	0.757125	19	0.211256
Hemicentetes	0.599606	18	0.102491
Tenrec	0.649542	12	0.096350
All Grps	0.654989	62	0.163838

	{1}	{2}	{3}	{4}
	M=.58743	M=.75712	M=.59961	M=.64954
Echinops {1}		0.014645	0.996192	0.734555
Setifer {2}			0.012789	0.226741
Hemicentetes {3}		0.012789		0.811790
Tenrec {4}		0.226741	0.811790	

Appendix 5.4. (con't)

Taxon	UWI Means	UWI N	UWI Std.Dev.											
Echinops	0.078913	11	0.008000											
Setifer	0.082944	17	0.006207											
Hemicentetes	0.093996	16	0.009111											
Tenrec	0.091078	13	0.006544											
M. cowani	0.069087	12	0.004923											
M. dobsoni	0.063458	10	0.006766											
M. talazaci	0.065442	8	0.002932											
Oryzorictes	0.094108	10	0.005820											
Limnogale	0.077428	1	0.000000											
Geogale	0.069222	1	0.000000											
Potamogale	0.092693	3	0.005680											
Petrodromus	0.044422	3	0.002282											
Solenodon	0.099194	10	0.008406											
Echinosorex	0.072223	1	0.000000											
All Grps	0.082038	116	0.014796											
	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=.07891	M=.08294	M=.09400	M=.09108	M=.06909	M=.06346	M=.06544	M=.09411	M=.07743	M=.06922	M=.09269	M=.04442	M=.09919	M=.07222
Echinops {1}		0.960121	0.000148	0.002635	0.049207	0.000222	0.003826	0.000261	1.000000	0.984667	0.124319	0.000138	0.000138	0.999615
Setifer {2}	0.960121		0.000942	0.088429	0.000171	0.000138	0.000140	0.006236	0.999946	0.793680	0.575786	0.000138	0.000140	0.960126
Hemicentetes {3}	0.000148	0.000942		0.996888	0.000138	0.000138	0.000138	1.000000	0.522715	0.039912	1.000000	0.000138	0.829331	0.125837
Tenrec {4}	0.002635	0.088429	0.996888		0.000138	0.000138	0.000138	0.998647	0.808845	0.128652	1.000000	0.000138	0.230807	0.319230
M. cowani {5}	0.049207	0.000171	0.000138	0.000138		0.809518	0.996170	0.000138	0.996028	1.000000	0.000176	0.000150	0.000138	1.000000
M. dobsoni {6}	0.000222	0.000138	0.000138	0.000138	0.809518		0.999997	0.000138	0.795065	0.999929	0.000138	0.003964	0.000138	0.994067
M. talazaci {7}	0.003826	0.000140	0.000138	0.000138	0.996170	0.999997		0.000138	0.927134	1.000000	0.000140	0.001320	0.000138	0.999623
Oryzorictes {8}	0.000261	0.006236	1.000000	0.998647	0.000138	0.000138	0.000138		0.540448	0.045457	1.000000	0.000138	0.923777	0.137784
Limnogale {9}	1.000000	0.999946	0.522715	0.808845	0.996028	0.795065	0.927134	0.540448		0.999869	0.803386	0.004692	0.143348	0.999999
Geogale {10}	0.984667	0.793680	0.039912	0.128652	1.000000	0.999929	1.000000	0.045457	0.999869		0.165831	0.110683	0.004707	1.000000
Potamogale {11}	0.124319	0.575786	1.000000	1.000000	0.000176	0.000138	0.000140	1.000000	0.803386	0.165831		0.000138	0.974021	0.358507
Petrodromus {12}	0.000138	0.000138	0.000138	0.000138	0.000150	0.003964	0.001320	0.000138	0.004692	0.110683	0.000138		0.000138	0.039203
Solenodon {13}	0.000138	0.000140	0.829331	0.230807	0.000138	0.000138	0.000138	0.923777	0.143348	0.004707	0.974021	0.000138		0.018833
Echinosorex {14}	0.999615	0.960126	0.125837	0.319230	1.000000	0.994067	0.999623	0.137784	0.999999	1.000000	0.358507	0.039203	0.018833	

Appendix 5.4. (con't)

Taxon	OPLI Means	OPLI N	OPLI Std.Dev.
Echinops	0.171054	11	0.022197
Setifer	0.163977	17	0.013389
Hemicentetes	0.216972	16	0.013615
Tenrec	0.234124	14	0.012529
M. cowani	0.161411	13	0.014628
M. dobsoni	0.119505	10	0.010009
M. talazaci	0.116476	8	0.009704
Oryzorictes	0.271315	10	0.027626
Limnogale	0.168352	1	0.000000
Geogale	0.132896	1	0.000000
Potamogale	0.189105	3	0.011416
Petrodromus	0.105626	3	0.008295
Solenodon	0.193893	10	0.015663
Echinosorex	0.194965	1	0.000000
All Grps	0.183696	118	0.048113

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=.17105	M=.16398	M=.21697	M=.23412	M=.16141	M=.11950	M=.11648	M=.27131	M=.16835	M=.13290	M=.18911	M=.10563	M=.19389	M=.19496
Echinops {1}		0.996658	0.000137	0.000137	0.967971	0.000137	0.000137	0.000137	1.000000	0.558273	0.894295	0.000138	0.074378	0.974433
Setifer {2}	0.996658		0.000137	0.000137	1.000000	0.000137	0.000137	0.000137	1.000000	0.820578	0.400387	0.000140	0.000683	0.823627
Hemicentetes {3}	0.000137	0.000137		0.173583	0.000137	0.000137	0.000137	0.000137	0.166233	0.000233	0.246406	0.000137	0.030273	0.985868
Tenrec {4}	0.000137	0.000137	0.173583		0.000137	0.000137	0.000137	0.000146	0.008504	0.000138	0.001743	0.000137	0.000138	0.499821
M. cowani {5}	0.967971	1.000000	0.000137	0.000137		0.000138	0.000138	0.000137	1.000000	0.900118	0.281349	0.000157	0.000449	0.741330
M. dobsoni {6}	0.000137	0.000137	0.000137	0.000137	0.000138		1.000000	0.000137	0.180966	0.999929	0.000137	0.987345	0.000137	0.001344
M. talazaci {7}	0.000137	0.000137	0.000137	0.000137	0.000138	1.000000		0.000137	0.128214	0.999413	0.000137	0.999144	0.000137	0.000868
Oryzorictes {8}	0.000137	0.000137	0.000137	0.000146	0.000137	0.000137	0.000137		0.000138	0.000137	0.000137	0.000137	0.000137	0.001118
Limnogale {9}	1.000000	1.000000	0.166233	0.008504	1.000000	0.180966	0.128214	0.000138		0.947739	0.997186	0.052030	0.958119	0.995586
Geogale {10}	0.558273	0.820578	0.000233	0.000138	0.900118	0.999929	0.999413	0.000137	0.947739		0.132830	0.967089	0.025407	0.259420
Potamogale {11}	0.894295	0.400387	0.246406	0.001743	0.281349	0.000137	0.000137	0.000137	0.997186	0.132830		0.000137	1.000000	1.000000
Petrodromus {12}	0.000138	0.000140	0.000137	0.000137	0.000157	0.987345	0.999144	0.000137	0.052030	0.967089	0.000137		0.000137	0.000437
Solenodon {13}	0.074378	0.000683	0.030273	0.000138	0.000449	0.000137	0.000137	0.000137	0.958119	0.025407	1.000000	0.000137		1.000000
Echinosorex {14}	0.974433	0.823627	0.985868	0.499821	0.741330	0.001344	0.000868	0.001118	0.995586	0.259420	1.000000	0.000437	1.000000	

Appendix 5.4. (con't)

Taxon	RWI Means	RWI N	RWI Std.Dev.
Echinops	0.104180	12	0.011733
Setifer	0.107378	16	0.007769
Hemicentetes	0.134896	15	0.013162
Tenrec	0.126984	9	0.009940
M. cowani	0.083882	14	0.024912
M. dobsoni	0.077155	10	0.008363
M. talazaci	0.078867	8	0.003827
Oryzorictes	0.145150	7	0.011603
Limnogale	0.101561	1	0.000000
Geogale	0.086510	1	0.000000
Potamogale	0.127615	3	0.007536
Petrodromus	0.052874	3	0.002541
Solenodon	0.140815	7	0.009388
Echinosorex	0.098208	1	0.000000
All Grps	0.107858	107	0.027930

	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}
	M=.10418	M=.10738	M=.13490	M=.12698	M=.08388	M=.07716	M=.07887	M=.14515	M=.10156	M=.08651	M=.12761	M=.05287	M=.14081	M=.09821
Echinops {1}		0.999995	0.000136	0.010471	0.010780	0.000548	0.004018	0.000135	1.000000	0.989478	0.254759	0.000136	0.000138	1.000000
Setifer {2}	0.999995		0.000138	0.031976	0.000430	0.000142	0.000311	0.000135	1.000000	0.954484	0.446604	0.000134	0.000146	0.999989
Hemicentetes {3}	0.000136	0.000138		0.975069	0.000134	0.000134	0.000134	0.905954	0.440821	0.033493	0.999798	0.000134	0.999299	0.286474
Tenrec {4}	0.010471	0.031976	0.975069		0.000134	0.000134	0.000134	0.264910	0.849658	0.181519	1.000000	0.000134	0.699914	0.707376
M. cowani {5}	0.010780	0.000430	0.000134	0.000134		0.992962	0.999833	0.000134	0.988897	1.000000	0.000205	0.021605	0.000134	0.998554
M. dobsoni {6}	0.000548	0.000142	0.000134	0.000134	0.992962		1.000000	0.000134	0.879444	0.999989	0.000138	0.232693	0.000134	0.957366
M. talazaci {7}	0.004018	0.000311	0.000134	0.000134	0.999833	1.000000		0.000134	0.931563	0.999999	0.000161	0.181568	0.000134	0.980370
Oryzorictes {8}	0.000135	0.000135	0.905954	0.264910	0.000134	0.000134	0.000134		0.118573	0.004705	0.797081	0.000134	0.999996	0.063559
Limnogale {9}	1.000000	1.000000	0.440821	0.849658	0.988897	0.879444	0.931563	0.118573		0.999916	0.901346	0.090646	0.238930	1.000000
Geogale {10}	0.989478	0.954484	0.033493	0.181519	1.000000	0.999989	0.999999	0.004705	0.999916		0.283337	0.610637	0.013147	0.999995
Potamogale {11}	0.254759	0.446604	0.999798	1.000000	0.000205	0.000138	0.000161	0.797081	0.901346	0.283337		0.000134	0.970854	0.794626
Petrodromus {12}	0.000136	0.000134	0.000134	0.000134	0.021605	0.232693	0.181568	0.000134	0.090646	0.610637	0.000134		0.000134	0.156240
Solenodon {13}	0.000138	0.000146	0.999299	0.699914	0.000134	0.000134	0.000134	0.999996	0.238930	0.013147	0.970854	0.000134		0.140477
Echinosorex {14}	1.000000	0.999989	0.286474	0.707376	0.998554	0.957366	0.980370	0.063559	1.000000	0.999995	0.794626	0.156240	0.140477	

CHAPTER VI

OVERVIEW OF THE AXIAL SKELETON, SKULL, AND LONG BONE CROSS-SECTIONAL GEOMETRY

Functional Morphology of the Tenrecoidea Axial Skeleton: A Preliminary Qualitative Analysis

Relative to the extensive body of research on functional morphology of the limbs, few studies have focused on function-based differences in bony features of the vertebrae and ribs in mammals. Most of the literature concerned with functional aspects of the mammalian axial skeleton is centered on primates and adaptations of the lumbar vertebrae to arboreal and bipedal locomotion (e.g., Ankel, 1972; Rose, 1975; Shapiro, 1993; Johnson and Shapiro, 1998; Shapiro et al., 2001), although other mammalian groups have not been ignored (e.g., xenarthrans, pholidotans, etc.). Several important works have identified details of the axial skeleton with specific locomotor- and dietary-based differences in other mammalian locomotor specialists including aspects of the cervical vertebrae (craniocaudal width, atlas and axis shape), ribs (craniocaudal width and depth), spinous processes of the cervical and thoracic vertebrae (length), and number of vertebrae (thoracic vs. lumbar vs. caudal) (Hatt, 1932; Howell, 1944; Grasse, 1955; Shapiro, 1993; Sargis, 2001; Argot, 2003).

In a qualitative comparative study of the scandentian axial skeleton, Sargis (2001) found a series of differences between *Ptilocercus* and terrestrial scandentians that are indicative of arboreal locomotor behavior in the former. Most of these are likely related to stabilizing the thorax for facilitation of bridging from branch to branch, whereas the more terrestrial tupaiids exhibit axial skeletal form consistent with dorsoventral mobility for increasing stride length. For example, relative to terrestrial tupaiids, *Ptilocercus* has craniocaudally-expanded ribs (as do chiropterans and dermopterans), more thoracic and

fewer lumbar vertebrae, a craniocaudally-expanded atlas, a more cranially oriented spine of the axis, and short and wide cervical and thoracic spinous processes.

In her comprehensive functional-adaptive study of the axial skeleton in the two Early Paleocene marsupials *Mayulestes* and *Pucadelphys*, Argot (2003) included nine extant marsupial species that could be contrasted by diet (carnivorous vs. insectivorous) and substrate preference (arboreal vs. terrestrial). She conceded that many aspects of the axial skeleton are difficult to interpret in a functional context, yet also found a series of interspecific skeletal differences that are suggestive of various functional roles. For example, arboreal marsupial taxa such as *Caluromys* have a series of traits at the cervical vertebrae that indicate facilitated mobility at the atlas-axis joint, and more stability at the posterior cervical articulations, and compared to arboreal marsupials, terrestrial taxa have longer neural spines of the cervical vertebrae.

Relative length and shape of the cervical and thoracic vertebral spines have been discussed in the context of locomotor and feeding behaviors in several mammals (Evans, 1939; Howell, 1944; Schultz, 1961; Shapiro, 1993). The spines of the cervical vertebrae are particularly elongated and caudally directed in mammals with heavy heads, such as male great apes (Gregory, 1936; Howell, 1944; Schultz, 1961; Shapiro, 1993). The thoracic spines are also long in mammals with large, heavy heads, and are particularly long in ungulate grazers that keep the head low to the ground while feeding vs. ungulate browsers that feed from head-level or higher branches (Howell, 1944). Evans (1939) noted particularly short cervical spines and transverse processes in the cat vs. the opossum and suggested that these features facilitate neck mobility in the former. Sargis (2001) suggested that the width of the spinous process, and not the length, is more

significantly related to spinal stability and mobility; wider spinous processes that limit the space between processes restrict mobility, as opposed to longer, thinner vertebrae with intervertebral space that allow for a wider range of flexion/extension.

The following section is a qualitative comparison of several aspects of the tenrecoid axial skeleton focused on the more cranial elements, including morphology of the ribs, cervical and thoracic spines, and detailed form of the atlas and axis. Unlike other regions of the postcranial skeleton, there are few well-tested function-based hypotheses of mammalian vertebral and/or rib form. I will therefore focus on the three questions:

- 1) Does the arboreal taxon *Echinops* exhibit features such as those found other arboreal (vs. terrestrial) mammals (as modeled in Sargis (2001) and Argot (2003))?
- 2) Do the locomotor specialists *Hemicentetes* and *Oryzorictes* (diggers), and *Potamogale* and *Limnogale* (swimmers) demonstrate notable differences in vertebral or rib form that might represent function-based specialization?
- 3) Are there taxon-based similarities that might be phylogenetically meaningful?

Materials and Methods

Specimens were examined and photographed from the following collections: American Museum of Natural History, New York, NY; Field Museum of Natural History, Chicago, IL; Harvard Museum of Comparative Zoology, Cambridge, MA; and National Museum of Natural History, Washington, D.C.. Two *Echinops* specimens were borrowed from H. Kuenzle's laboratory at the University of Munich, Germany, and a *Hemicentetes* and *Tenrec* specimen were borrowed from the University of Darmstadt, Germany. Digital images were captured with a Nikon Coolpix 995 and edited for figures

in Adobe Photoshop CS. Tenrecoid taxa included *Echinops telfairi*, *Setifer setosus*, *Hemicentetes semispinosus*, *Tenrec ecaudatus*, *Microgale cowani*, *M. dobsoni*, *M. talazaci*, *Oryzorictes hova*, *O. tetradactylus*, *Limnogale mergulus*, *Geogale aurita*, and *Potamogale velox*. For comparison I included *Solenodon paradoxus*, *Petrodromus tetradactylus*, and *Echinosorex gymnurus* (see Table 6.1.).

TABLE 6.1. Taxonomy and Primary Locomotor Behavior of study taxa

Family/subfamily	Genus	Species	n	Locomotor Behavior
Tenrecidae/Tenrecinae	<i>Echinops</i>	<i>telfairi</i>	12	Arboreal/terrestrial
Tenrecidae/Tenrecinae	<i>Hemicentetes</i>	<i>semispinosus</i>	17	Terrestrial/fossorial
Tenrecidae/Tenrecinae	<i>Setifer</i>	<i>setosus</i>	20	Terrestrial
Tenrecidae/Tenrecinae	<i>Tenrec</i>	<i>ecaudatus</i>	8	Terrestrial
Tenrecidae/Oryzorictinae	<i>Limnogale</i>	<i>mergulus</i>	4	Aquatic/terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>cowani</i>	22	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>dobsoni</i>	21	Terrestrial
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>talazaci</i>	12	Terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>hova</i>	22	Fossorial/terrestrial
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>tetradactylus</i>	10	Fossorial/terrestrial
Tenrecidae/Geogalinae	<i>Geogale</i>	<i>aurita</i>	7	Terrestrial
Potamogalidae	<i>Potamogale</i>	<i>velox</i>	3	Aquatic/terrestrial
Macroscelididae	<i>Petrodromus</i>	<i>tetradactylus</i>	2	Terrestrial/saltatory
Solenodontidae	<i>Solenodon</i>	<i>paradoxus</i>	12	Terrestrial/fossorial
Erinaceidae	<i>Echinosorex</i>	<i>gymnurus</i>	1	Terrestrial

Results and Discussion

Although there is notable variation in rib form between tenrecoid species, *Echinops* does not have craniocaudally-expanded ribs, as expected based on rib morphology of arboreal treeshrews, lorissine primates, colugos, and bats (Jenkins, 1970; Sargis, 2001). *Echinops* has particularly thin ribs with large intercostal spaces. While thick ribs may be useful for bridging behavior in some other arboreal mammals, the thin, widely spaced ribs in *Echinops* may be more useful for maximizing lateral bending in

tight arboreal nesting spaces. *Echinops* are often found in extremely small tree hollows (pers. obs.), and their thick rounded bodies and spinous skin make movement in a tight space extremely difficult. *Echinops* also tightly flexes the entire body when taking on its defense posture of rolling into a tight ball, similar to the European hedgehog. Thick ribs would not allow sufficient space for curling the thoracic region. *Setifer* employs a similar defense posture and its thin, widely spaced ribs may also facilitate a deeply flexed spine.

When the four tenrecine genera are compared, the digger *Hemicentetes* has notably wider ribs with less intercostal space than the other three (Figs. 1 and 2). In contrast, the digging oryzorictine *Oryzorictes* does not have wider ribs than the other oryzorictines, and *Microgale cowani*, which exhibits digging-related traits at other postcranial regions, has the craniocaudally narrowest ribs of all studied taxa. This suggests that the widening of the ribs in *Hemicentetes* may not be broadly correlated with its semi-fossorial habitus, but may rather be related to some other behavior such as feeding. *Hemicentetes* has a greatly elongated rostrum and smaller teeth than the other tenrecoids, most likely for feeding on a specialized diet of earthworms. Wide ribs are suggestive of a stabilized thoracic region (Jenkins, 1970; Sargis, 2001), which, in the case of *Hemicentetes*, might be useful for resisting forces of rostral probing. *Solenodon* is the only other taxon with noticeably wide ribs (Fig. 1). *Solenodon*, like *Hemicentetes*, is a forelimb digger, but has an elongated snout for rostral probing for insects, similar to *Hemicentetes* (though *Hemicentetes* does not have an extra bone for support of the snout like *Solenodon* does). A comparison of rib shape in tooth-diggers, such as bathyergid rodents vs. forelimb-digging rodents might shed more light on correlations between direct rostral loading and thoracic stabilization in diggers.

The spinous processes of the thoracic vertebrae in *Hemicentetes* are also suggestive of a well-stabilized thorax. The spinous processes of the more anterior thorax serve as insertion points for the semi-spinalis and multifidus dorsi of the epaxial musculature (Argot, 2003). Long, widely spaced spines most likely indicate a strong and more flexible thoracic region (though see Gebo, 1989), whereas shorter, robust spines increase thoracic rigidity and stability (Sargis, 2001; Argot, 2003). Relative to the other tenrecoids the thoracic spinous processes in *Hemicentetes* are short, robust, closely-packed, and caudally oriented (Figs. 1 and 2). Tenrecines have craniocaudally wider thoracic spines than oryzorictines, in which the thoracic spines are equally long, but thin and delicate. The first thoracic spine in *Oryzorictes* is considerably longer than any of the other vertebral spines, and longer and craniocaudally wider than the vertebral spines in any other taxon (Figs. 1 and 3). The major muscular attachments of the T1 spinous process include the M. splenius and Mm. rhomboid major and minor (Cooper and Schiller, 1975; Argot, 2003; Martini et al., 2005). Given the set of unique derived traits related to digging that characterize other postcranial regions of the *Oryzorictes* skeleton, the elongated T1 spine is most likely due to an enlarged origin site of the rhomboids, which adduct and rotate the scapula. The spinous process of T1 is also particularly enlarged in highly terrestrial vs. arboreal marsupials, but the functional significance of this difference is unclear and, in this case, most likely related to enlarged nuchal musculature for a more carnivorous diet in the terrestrial species (Argot, 2003).

The thoracic spines of *Geogale* are short and caudally bent, barely visible above the dorsal edge of the vertebrae (Fig. 1). The thoracic spinous processes of both *Potamogale*, and the elephant shrew *Petrodromus* are both long and craniocaudally wide,

indicating the combination of a well-stabilized thorax with powerful neck musculature. Thoracic vertebra form in the swimmer *Potamogale* contrasts with that of the oryzorictine swimmer *Limnogale*, which has dorsoventrally short thoracic spines with tapered ends similar to the other oryzorictines (though more robust than those of *Microgale*).

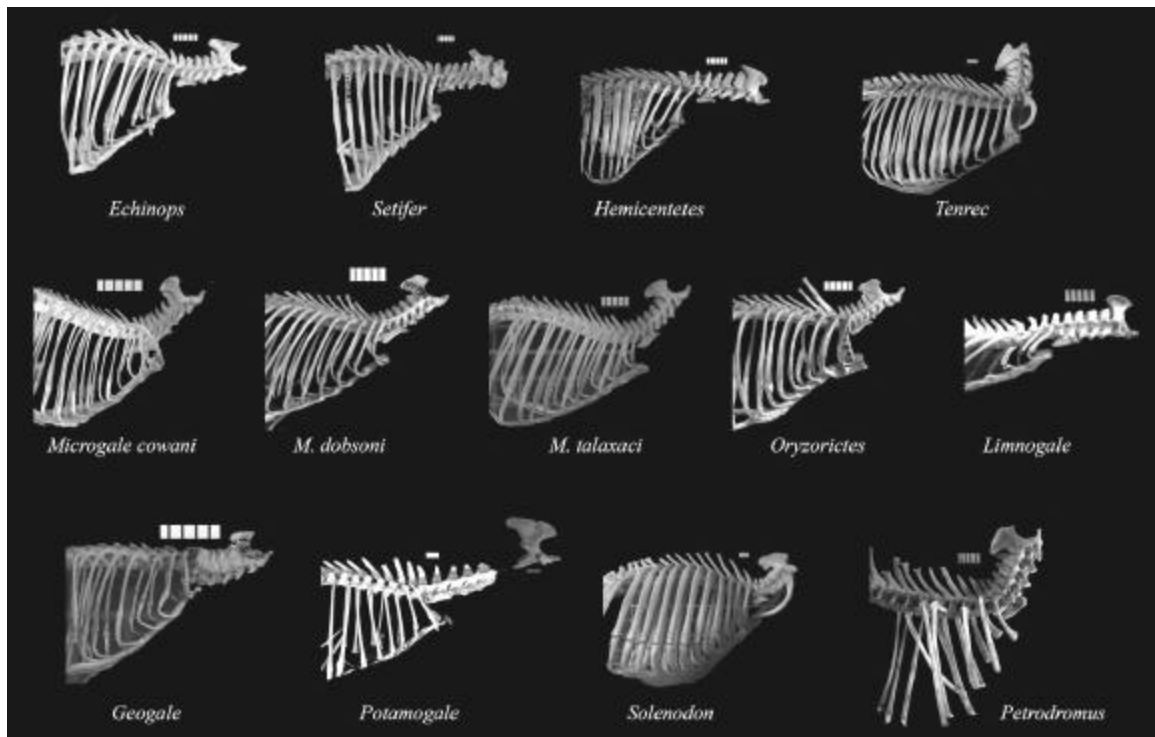


Figure 6.1. Right lateral view of cervical and thoracic vertebrae and ribs in tenrecines (top row), oryzorictines (middle row), two other tenrecoids (bottom left) and two non-tenrecoid taxa. Note differences in craniocaudal rib width and cervical and thoracic spine shape and height. Scale units=mm.

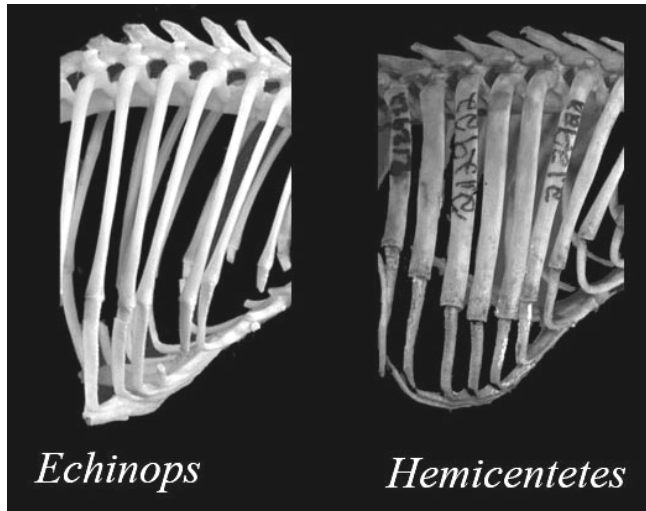


Figure 6.2. Right lateral view of ribs in an arboreal tenrecine (left) and a terrestrial digging tenrecine (right). Note the craniocaudally wider ribs and caudally-facing thoracic spines in *Hemicentetes*.

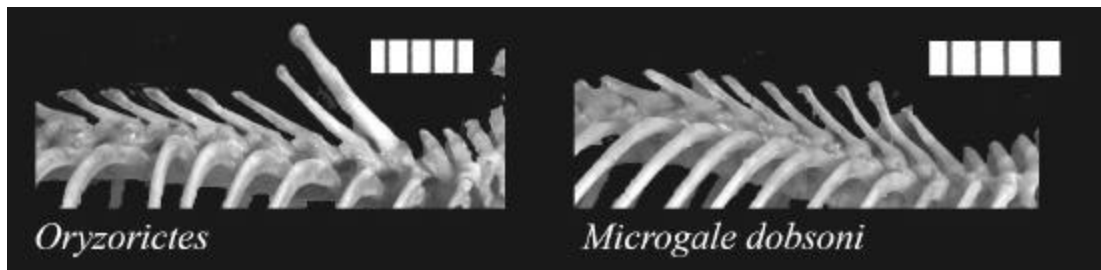


Figure 6.3. Right lateral view of thoracic spines in the forelimb digger *Oryzorictes*, and the terrestrial *Microgale*. Note the conspicuously elongated first thoracic spine in *Oryzorictes*. Scale units=mm.

The spinous process of the axis, which is broadened into a laterally flattened plate, is the origin for *M. rectus capitus dorsalis major*, which inserts on the occipital region of the skull, dorsally extending the head, and *M. obliquus capitus caudalis*, which provides rotational movement of the skull (Evans, 1939; Cooper and Schiller, 1975; Argot, 2003). There is considerable interspecific variation between tenrecoids in the shape of the axial spinous process, yet the functional significance of these differences is not straightforward. Within Tenrecinae, *Setifer* has a longer axial spinous process than *Echinops*, and *Echinops* has a wider base of the spine (Fig. 4). *Echinops* does not have a more cranially directed process than the other tenrecoids, as one might have expected based on the study of the arboreal *Ptilocercus* (Sargis, 2001). The spinous process of the

axis in *Tenrec* is long and projects more dorsally (vs. dorsocaudally) than that of the other tenrecines (Fig. 4). *Microgale* and *Limnogale* have anvil-shaped axial spinous processes with short cranial and caudal projections, while the other taxa have longer dorsocaudal projections (Fig. 4). *Oryzorictes* is unlike the other oryzorictines in this respect, having a caudodorsally projecting process, similar to the tenrecines and *Geogale*. Although a more cranially oriented spinous process of the axis may be a primitive therian trait (Sargis, 2001), and *Geogale* may represent a basal Malagasy tenrecoid taxon with a series of generalized placentalian traits (see previous chapters), *Geogale* has a dorsocaudally deflected axial spine as well, unlike *Microgale*, similar in form to the tenrecines, and in marked contrast to *Potamogale*, which has a spine that is more cranially and caudally expanded than in any other taxon (Fig. 4).

Echinosorex and *Solenodon* demonstrate two extremes of axis morphology. Although both are dorsally expanded, the spinous process of *Solenodon* is cranially and caudally filled in, forming a rounded plate, whereas *Echinosorex* has dorsally expanded and craniocaudally thinner spine with no cranial or caudal expansion (Fig. 4). The craniocaudal thickness of both of these spines is indicative of well stabilized and strong neck. The widened plate in *Solenodon* most likely offers more stabilization for rostral rooting, whereas the dorsal expansion in *Echinosorex*, similar to *Tenrec* in terms of dorsal projection, probably serves to more forcefully lift the head.

Caudal expansion of the axial spinous process may serve to increase the lever advantage for the rectus capitus dorsalis musculature, and may indicate an overall stronger neck. A caudally expanded process may also indicate a “triangular shaped” M. obliquus capitis caudalis that would increase the rotational range of head movement

(Argot, 2003: 292). A long, dorsocaudally-facing spine of the axis is therefore difficult to interpret in terms of neck mobility. Is it indicative of strong musculature attachment for support of multiaxial movement or limited movement and increased stability? Taxa with caudally expanded spines tend to have a more restricted anterior space for articulation with the dorsal aspect of the atlas; that is, there is a narrower space between the anteriormost and ventral aspect of the axial spine and the dorsal base of the dens (Fig. 5). A comparison of *Echinops* and *Setifer* demonstrates a shorter neural spine and a wide and shallow space for atlas articulation in the climber, and a long, caudally expanded spine and more restricted atlas-axis articulation in *Setifer* (Fig. 5). This suggests that there is more of a functional correlation between neck strength and close-packed stability of the atlas-axis articulation, as opposed to strength and multiaxial rotation.

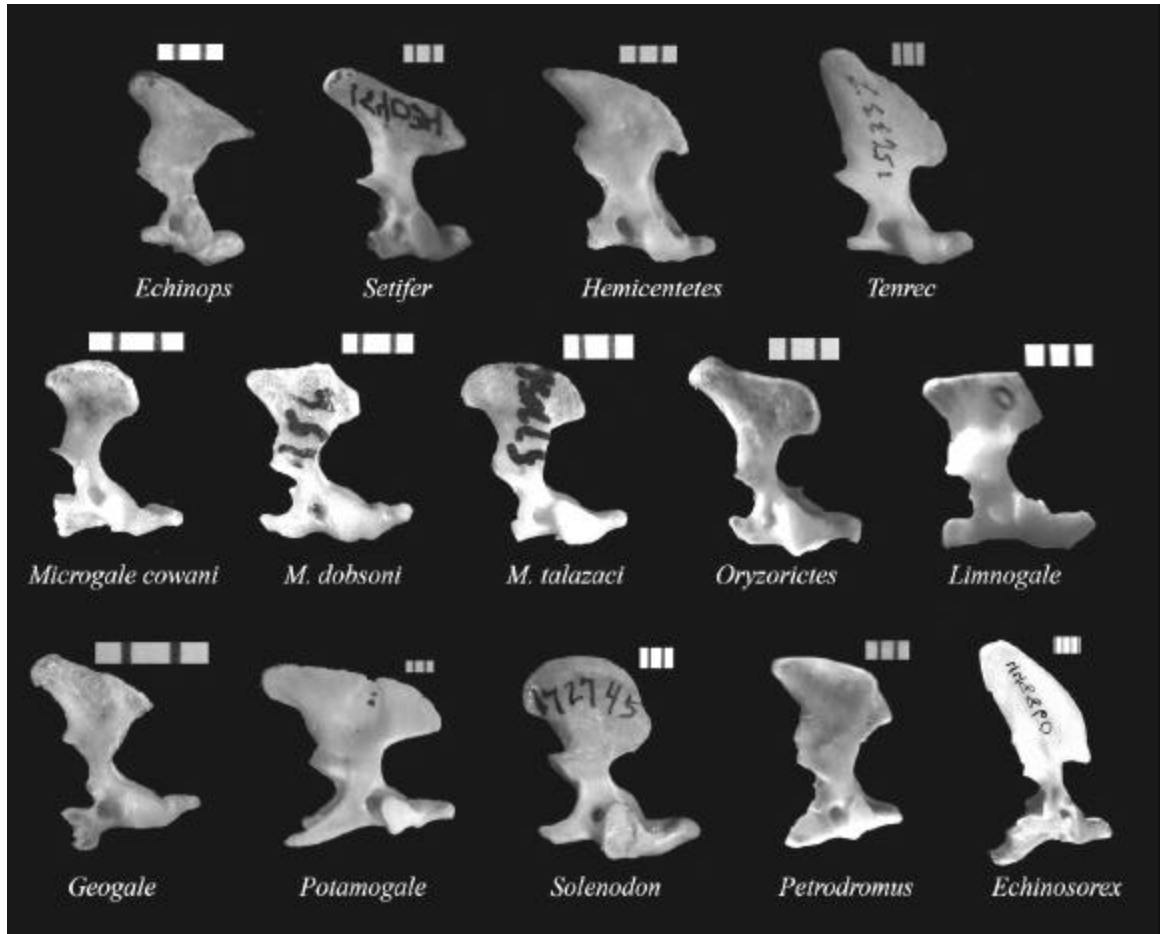


Figure 6.4. Right lateral view of the axis in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroups (bottom right). Scale units=mm.

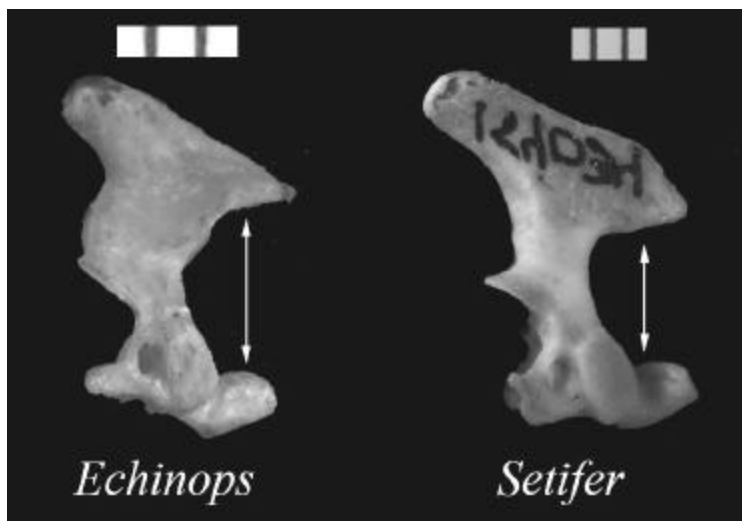


Figure 6.5. Right lateral view of axis in two tenrecines. A larger space for articulation of the atlas (white arrow) correlates with a relatively longer axial spinous process. Scale units=mm.

Overall shape of the atlas is rather uniform between tenrecoids, with the exception of *Potamogale*. Several interspecific small-scale differences include the extension of the ventral and dorsal tubercles, and the extent of the dorsal shelf of the anterior articular facets. When present, the ventral tubercle of the atlas marks an attachment site for *M. longus colli*, which is a major neck flexor. All of the oryzorictines have notable ventral tubercles, whereas the tenrecines either have a small tubercle or none at all (Fig. 6). *Echinops* and *Setifer* have slight ventral tubercles, whereas *Hemicentetes* and *Tenrec* do not. Perhaps the presence of this trait in *Echinops* and *Setifer* is related to an expanded *M. longus colli*, which is involved in curling their bodies into a completely flexed, spiny ball when threatened. The functional implication of the absence of a ventral tubercle in *Hemicentetes* and *Tenrec* is unclear.

The dorsal tubercle, an attachment site for *M. semispinalis cervicis* and *M. rectus capitis posterior minor*, as well as ligamentous attachments to the occipital, shows variation between genera with possible functional significance. It is dorsally expanded and thicker in *Hemicentetes* and *Tenrec* than in *Echinops* and *Setifer*, and also expanded and thick in *Oryzorictes* and *Limnogale* compared to *Microgale*. *Geogale* and *Potamogale* have no dorsal tubercles. The presence of a broad and conspicuous tubercle is most likely indicative of powerful neck muscles and large stabilizing ligaments, yet the absence of this trait is most likely primitive, as it is absent in *Potamogale* which has other indicators of a powerful and well-stabilized neck.

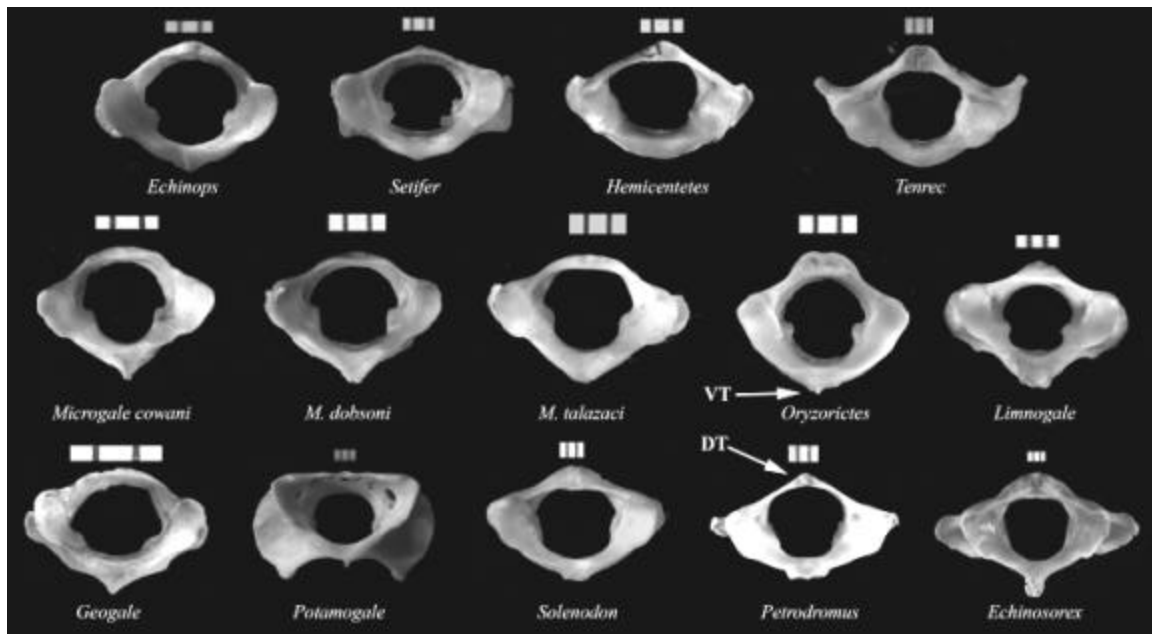


Figure 6.6. Anterior view of the atlas in four tenrecines (top), five oryzorictines (middle), two other tenrecoids (bottom left), and three outgroups (bottom right). Note differences in the dorsal and ventral tubercles and extent of anterior articular facets. VT=ventral tubercle; DT=dorsal tubercle. Scale units=mm.

An anterodorsally overhanging process of the anterior articular facets would act to stabilize the facets against the occipital condyles of the skull (Fig. 7). Both *Tenrec* and *Hemicentetes* have curved, anteriorly projecting dorsal processes, whereas those in *Echinops* and *Setifer* are shallower and indicate a less stabilized atlas-occipital condyle joint (Fig. 6). There are no significant differences in this trait between oryzorictines and *Geogale*, as all have a moderate dorsal projecting shelf. *Potamogale* is unique in that the entire dorsal surface of the atlas is widened and anteriorly flared, providing a deep space for articulation with the occipital condyles (Fig. 6). The anterior articular facet anterodorsal processes in the three outgroups are all similar and exhibit a dorsally well-stabilized articulation of the atlas-occipital condyles (Fig. 6).

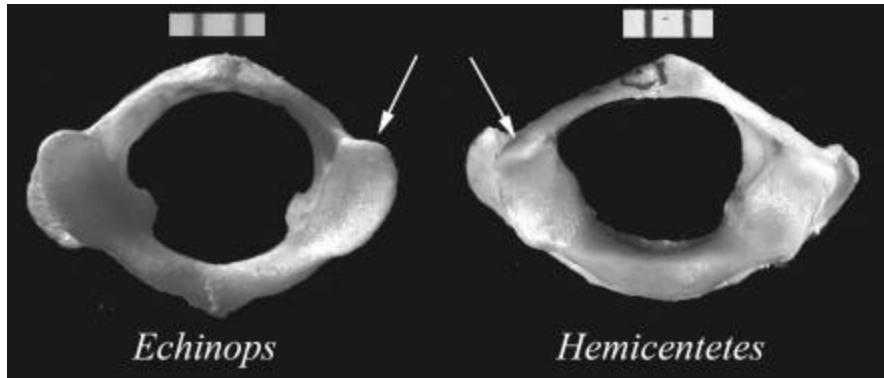


Figure 6.7. Anterior view of the atlas in the climber *Echinops* and the digger *Hemicentetes*. Arrows demonstrate the dorsally overhanging process of the anterior articular facet, which is shallow in *Echinops* and deep in *Hemicentetes*.

Summary

The arboreal species *Echinops telfairi* appears to have a far more flexible thoracic and cervical region than the arboreal scandentians discussed in Sargis (2001) and Argot (2003). A stable thorax for bridging behavior such as that described for *Ptilocercus*, is most likely not as important for *Echinops* relative to the flexibility needed for moving in tight arboreal nests and rolling into a defensive posture. Unlike *Ptilocercus*, the ribs are thin, the atlas is not craniocaudally expanded, the spine of the axis is not more cranially oriented, and the cervical and thoracic processes are longer than those of other taxa, e.g., *Hemicentetes*. Arboreal marsupials tend to have more mobile cervical and more restricted thoracic regions (see Gaudin and Biewener, 1992). While *Echinops* did not demonstrate stability at the thorax, it does have several traits that indicate more mobility/less stability at the neck than in more terrestrial taxa, e.g., a more loosely articulating atlas-axis, absent dorsal tubercles of the atlas, and shallow anterodorsal processes of the anterior articular facets of the atlas.

Of the studied skeletal characters, I found no ubiquitous characteristics related to “digging” in *Oryzorictes* and *Hemicentetes* or “swimming” in *Limnogale* or *Potamogale*,

although several taxon-specific aspects of form are most likely habitus-specific adaptations. For example, the conspicuously wide ribs and short, wide thoracic vertebrae in *Hemicentetes* serve to stabilize the thorax, whether for feeding or digging or both. *Oryzorictes* has an usually elongated T1, not found in any other of the studied taxa, most likely serving as a site of origin for the rhomboid musculature. *Potamogale* demonstrates a series of vertebral traits that suggest the combination of a very well stabilized thorax and neck with facilitated multiaxial head movement.

Unlike other regions of the postcranial skeleton, there are few characteristics of the axial skeleton that serve as useful indicators of phylogenetic significance. This is most likely a function of two principal factors: 1) the vital and highly sensitive role of the vertebrae in protecting the spinal cord while supporting the weight of the trunk, and, therefore, a resistance to overall shape change of the vertebral bodies, and 2) the considerable degree of variation in the vertebral processes that vary significantly both within and between taxa depending on small-scale internal and external environmental loads, and phylogenetic inertia (as in non-digging xenarthrans; Szalay and Schrenk, 1998).

Functional Morphology of the Tenrecoidea Skull: A Preliminary Quantitative Analysis

Although the skull and its dentition have been studied and written about more than any other region of the mammalian skeleton, most of the literature is focused on ontogenetic and functional studies, the mechanics of one or two taxa, or comparative character-based and morphometric accounts, and not on function-based variation. Despite extensive use of cranial and dental characters for systematic research, few studies considered function-based hypotheses of cranial and/or dental characters from a wide range of mammalian taxa (Radinsky, 1985). Many aspects of the postcranial skeleton can be directly correlated with taxon-specific positional behaviors, whereas the bones of the skull are associated with several potential biological roles, including those involved with food capture and processing, olfaction, sight, hearing, tactile reception, and even some aspects of locomotion. I here focus on a few major features of the tenrecoidean skull with hypothesized functional significance that have been comparatively well studied in other mammals.

The relationship between mandibular form and mechanical function has been well explored from ecological perspectives, primarily because of the jaw's obvious role in feeding behaviors (e.g., Smith and Savage, 1959; Crompton and Hiiemae, 1970; Demes et al., 1984; Hildebrand, 1995; Ravosa, 1996; Satoh, 1997; Taylor, 2002, 2005). Height of the mandibular condyles relative to the height of the bottom cheek teeth row varies significantly between mammals that process their foods with more direct, temporalis-driven dorsoventral occlusal bits, and those that mediolaterally, anteroposteriorly, and obliquely grind harder, tougher foods (Hildebrand, 1995; Taylor, 2002, 2005). A higher mandibular condyle increases the lever arm of the masseter, and allows more jaw

mobility for multiaxial grinding of the jaw, whereas a lower condyle provides a more stable jaw joint that allows less mediolateral and anteroposterior mandibular displacement (Hildebrand, 1995; Taylor, 2002, 2005). Condylar shape varies significantly amongst mammals with different food processing requirements, e.g., more stabilized temporomandibular joints are characterized by a small, mediolaterally cylindrical condyle, as opposed to the more circular or anteroposteriorly lengthened condyle of more mobile jaw joints (Hildebrand, 1995; Taylor, 2002, 2005).

Endo et al. (2003) compared several cranial characteristics of 14 species of scandentians and analyzed their results in terms of habitat groups ranging from fully arboreal to fully terrestrial. They found a graded series of differences in skull metrics correlated with primary locomotor behavior, including more rostrocaudally elongated elements of the skull in terrestrial species vs. shortening and mediolateral widening of the skull in more arboreal species. They focus on locomotor behavior, presumably because this variable is fairly reliable for scandentians, whereas other ecological variables, such as diet, have not been well studied. The longer skull components of the terrestrial species is most likely related to rostral probing for soil invertebrates, whereas the more arboreal species are likely eating more leaf-dwelling insects.

Aquatic and semi-aquatic mammals exhibit an array of skull modifications that have been correlated various modes of swimming, but consistent morphological convergences between distantly related taxa are rare (Osburn, 1903; Howell, 1930). Many aquatic mammals have mediolaterally wide and short rostrums, which has been correlated with locomotor efficiency in water (presumably by allowing for head movements while swimming with minimal drag), as well as an increase in the surface

area for mystacial vibrissae (Voss, 1988; Kerbis Peterhans and Patterson, 1995) and the associated supporting pads that additionally “crowd” the nares and allow for narial closure with minimal muscular effort (Howell, 1930:89). Many aquatic mammals also have shortened nasal bones for dorsally and posteriorly shifted nares; large infraorbital foramen for passage of the trigeminal nerves to the vibrissae; large occipital condyles for a well-stabilized neck; and an enlarged cranial capacity, which has uncertain functional significance, but is most likely related to an enlarged medulla oblongata for enhanced tactile sensory capacity (Osburn, 1903; Howell, 1930; Voss, 1988; Kerbis Peterhans and Patterson, 1995). An enlarged foramen magnum in some aquatic rodents may also be associated with a large medulla oblongata (Stephan and Dieterlen, 1982; Voss, 1988; Kerbis Peterhans and Patterson, 1995)

Fossorial mammals have a series of more ubiquitous skull characteristics with functional relationships to digging, including features that involve stabilization of the neck for direct loading against soil. These are particularly pronounced in mammals that dig with their teeth, e.g., chrysochlorids and bathyergids (Stein, 2000). Yet despite differences in modes of digging and microhabitat (e.g., forelimb diggers vs. tooth chiseling; hard soil vs. looser sand; laterally splayed forelimb digging vs. more sagittally aligned forelimb digging, etc.) many diggers exhibit features in common that are associated with a strong head and neck. These include a) a dorsally flattened, broad and deep skull, for increased muscle attachment surface area; b) an enlarged and cranially-domed occipital region for insertion of enlarged neck musculature (Mm. trapezius anticus, rhomboideus anticus, splenius capitis and biceps cervicis); c) a triangular shape of the skull, with the broad base at the occipital related to the enlargement of the

muscles attaching at the occipital; d) a downward (ventrally) sloping dorsal surface of the skull from posterior to anterior resulting from a high occipital; e) posteriorly wide zygoma (in mammals with zygomatic arches); inflated tympanic bullae; f) a long and deep mandible to accommodate large jaw muscles, lateral expansion of the squamosals; g) a prominent masseteric crest marking the insertion of an enlarged masseter; and h) a large nuchal crest marking the insertion of enlarged neck musculature (Rose and Emry, 1983; Stein, 2000).

The following section is a preliminary qualitative survey of the tenrecoid skull, focused on several of the variables noted above with proposed functional significance. There has been relatively little published on the feeding behaviors of tenrecoids (though see Eisenberg and Gould, 1970; Nicoll, 1985; Garbutt, 1999; Benstead et al., 2001 for some specifics; Table 6.2), so it is difficult to develop connections between orphology and dietary preference. The diet of *Limnogale* has been comparatively well studied (Benstead et al., 2001), and consists primarily of mixed hard and soft foods including larval and adult aquatic insects, larval anurans, and crayfish. The other aquatic tenrecoid *Potamogale* consumes smaller insect prey and larger animals, such as mollusks, crabs, prawns, frogs, and small fish (Nicoll, 1985). Captive *Hemicentetes* and *Oryzorictes* exhibit a preference for worms (Eisenberg and Gould, 1970; Garbutt, 1999; pers. obs.). Despite its reported preference for small, soft-bodied invertebrates (Garbutt, 1999; Peveling et al., 2003), field-captured *Geogale* always preferred large, hard-bodied cockroaches to termites, and were able to kill and consume cockroaches up to their own size (pers. obs.). *Echinops* and *Setifer* eat a variety of invertebrates, including grasshoppers and cockroaches, and would not eat fruit, despite reports of a mixed

invertebrate/fruit diet (Garbutt, 1999). Because *Echinops* is a climber, it most likely eats fewer ground-dwelling invertebrates than *Setifer* and other terrestrial taxa, which might be reflected in overall cranial dimensions (as in Endo et al., 2003). Owing to its large body size, *Tenrec* consumes small vertebrates, including anurans and small mammals, and it also probes for smaller insects with its snout. The other tenrecoid taxa studied here are all reported “insectivores,” with diets consisting of various invertebrates and, in the case of *Tenrec*, small vertebrates, although explicit dietary variation within these groups has not been explored (Table 6.2). With respect to functional aspects of the skull, I therefore focus on known differences in locomotor behavior and feeding strategies.

Materials and Methods

Materials and methods concerning aspects of the skull were the same as above for the axial skeleton, yet the sample sizes for the skull vary from those of the axial skeleton (see Table 6.2).

TABLE 6.2. Taxonomy and Primary Locomotor Behavior of taxa examined.

Family/subfamily	Genus	Species	n	Locomotor Behavior	Primary Diet
Tenrecidae/Tenrecinae	<i>Echinops</i>	<i>telfairi</i>	7	Arboreal/terrestrial	Non-soil inverts
Tenrecidae/Tenrecinae	<i>Hemicentetes</i>	<i>semispinosus</i>	17	Terrestrial/fossorial	Earthworms
Tenrecidae/Tenrecinae	<i>Setifer</i>	<i>setosus</i>	20	Terrestrial	Mixed soil inverts
Tenrecidae/Tenrecinae	<i>Tenrec</i>	<i>ecaudatus</i>	5	Terrestrial	Inverts/small verts
Tenrecidae/Oryzorictinae	<i>Limnogale</i>	<i>mergulus</i>	4	Aquatic/terrestrial	Aquatic larvae, crayfish
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>cowani</i>	22	Terrestrial	Mixed soil inverts
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>dobsoni</i>	21	Terrestrial	Mixed soil inverts
Tenrecidae/Oryzorictinae	<i>Microgale</i>	<i>talazaci</i>	6	Terrestrial	Mixed soil inverts
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>hova</i>	22	Fossorial/terrestrial	Soil inverts/worms
Tenrecidae/Oryzorictinae	<i>Oryzorictes</i>	<i>tetradactylus</i>	15	Fossorial/terrestrial	Soil inverts/worms
Tenrecidae/Geogalinae	<i>Geogale</i>	<i>aurita</i>	12	Terrestrial	Hard-bodied inverts
Potamogalidae	<i>Potamogale</i>	<i>velox</i>	3	Aquatic/terrestrial	Aquatic inverts
Macroscelididae	<i>Petrodromus</i>	<i>tetradactylus</i>	2	Terrestrial/saltatory	Termites, ants ¹
Solenodontidae	<i>Solenodon</i>	<i>paradoxus</i>	4	Terrestrial/fossorial	Mixed soil inverts ²
Erinaceidae	<i>Echinorex</i>	<i>gymnurus</i>	1	Terrestrial	Soil & aquatic inverts ³

1. Rathburn, 1979; 2. Fons, 1990; 3. Nowak, 1991.

Results and Discussion

Comparisons of overall cranial proportions between the four tenrecine genera demonstrate clear function-based differences in form. *Hemicentetes* and *Tenrec* both have anteroposteriorly-elongated skulls with wide occipital regions and extremely tapered rostrums. A dorsal view of the skull (Fig.8) shows similarities in elongation of the rostrum in *Hemicentetes* and *Tenrec*, with more flaring anterior zygomatic processes in *Tenrec*, and a more streamlined and anteriorly delicate skull in *Hemicentetes*. From a lateral perspective (Fig. 9), the occipital is dorsally raised in both genera, but in *Hemicentetes*, the occipital and parietals are expanded, whereas in *Tenrec*, the dorsal expansion is a product of relatively enormous sagittal and nuchal crests. Both *Hemicentetes* and *Tenrec* use their snouts for probing for soil invertebrates, and occipital expansion (for strengthened neck musculature) and rostral lengthening and tapering (for probing small spaces in soil) are therefore expected. The differences between taxa at the occipital region make sense in terms of what we know about their diets. *Hemicentetes* prefers earthworms, and does not require strong masseter or temporalis musculature for food processing. The occipital is therefore expanded primarily as a function of stabilization of neck musculature for digging and soil probing, and the anterior rostrum is relatively thin and most likely does not incur strong occlusal forces. *Tenrec* is the only Malagasy tenrecoid to eat larger prey, including small anurans and mammals, and exhibits a high sagittal crest, which supports a large temporalis for a more forceful bite. These differences are also clearly reflected in their dental morphology; *Hemicentetes* has small, relatively peg-like teeth that would not be efficient for grinding hard foods, whereas those of *Tenrec* are much more robust (Fig. 9).

Relative to *Hemicentetes* and *Tenrec*, both *Echinops* and *Setifer* have short and wide skulls, but there are differences between the latter two that might be indicative of habitat/diet preferences. *Setifer* has a relatively longer palate and tooth row, and longer nasals than *Echinops* (Figs. 8, 9, and 11), and *Echinops* has a shorter, wider rostrum. These findings are in agreement with microhabitat-based differences found in Scandentia, and which also correlate with terrestrial substrate preference and a longer rostrum, vs. an arboreal substrate preference and a shorter rostrum (Endo et al., 2003). In scandentians as well as tenrecoids, these differences most likely represent differences in available invertebrate prey on the ground and in and around trees. Soft-bodied invertebrates such as earthworms, termites, ants, and insect larvae are more commonly found at or under the ground surface, whereas harder-bodied invertebrates, e.g., cockroaches and crickets, are commonly found above ground.

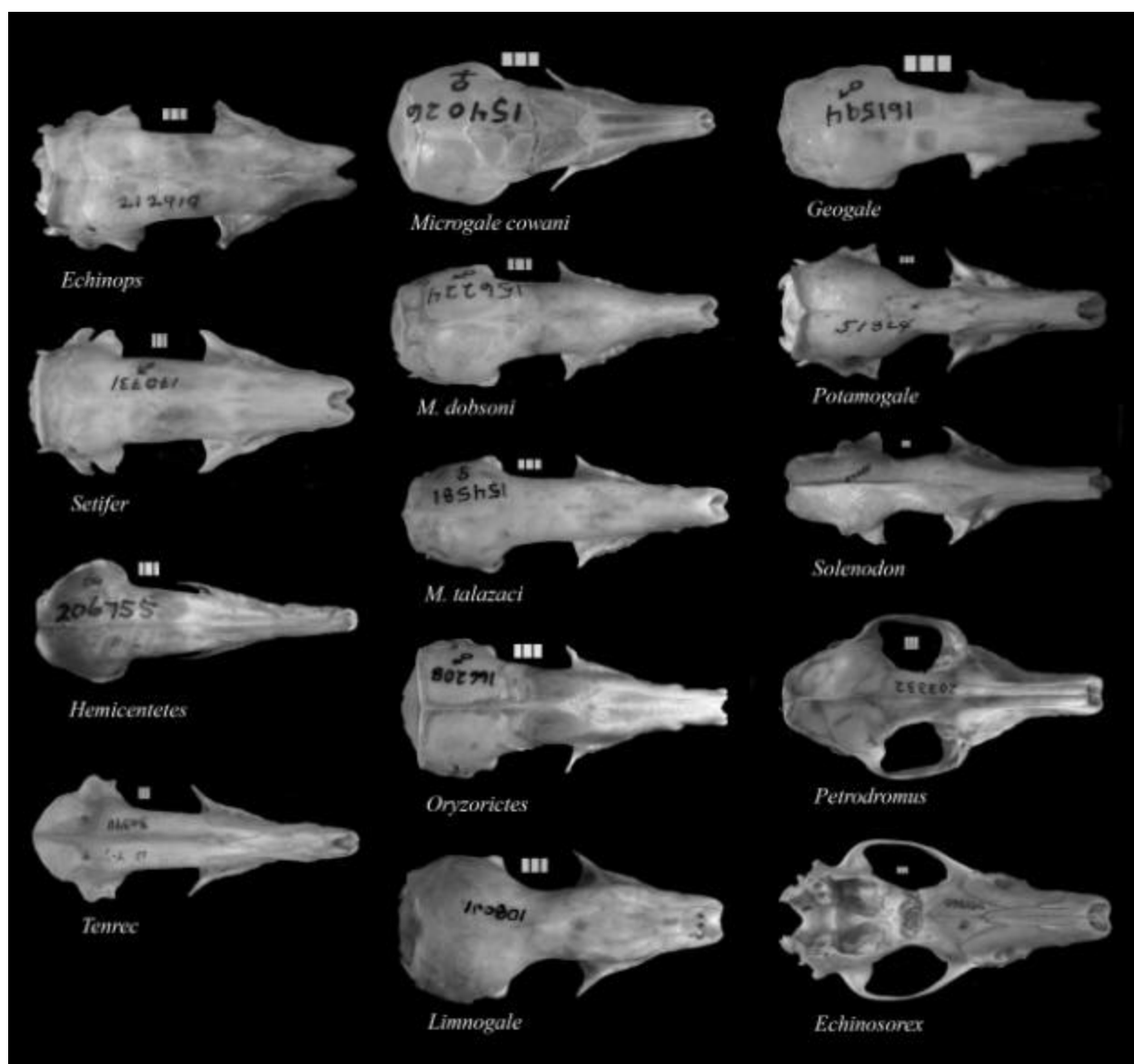


Figure 6.8. Dorsal view of the skull in four tenrecines (left row), four oryzorictines (middle row), two other tenrecoids (right row, two top), and three outgroups (right row, bottom three). Scale units=mm.

Within Oryzorictinae, *Oryzorictes* shows some general dimensions of the skull that are convergent with other fossorial mammals. The occipital region is expanded and cranially domed relative to other oryzorictines, although *M. cowani* also exhibits these features to some degree (Fig. 9). Features throughout the postcranial skeleton suggest that *M. cowani* may practice more fossorial behavior than previously suggested in the literature (see Chapters II-V). When the skull is viewed from a dorsal perspective,

Oryzorictes and *M. cowani* have more triangular shaped skulls than other oryzorictines, owing to the mediolateral expansion of the occipital and squamosal regions. The nuchal crest is anteriorly expanded in both taxa, allowing for greater attachment area of the neck musculature, but the crest itself is not particularly enlarged. *Oryzorictes* and *M. cowani* share relatively large tympanic rings relative to the three other oryzorictine taxa, a convergence with other subterranean mammals based on reliance of low-frequency hearing (in addition to tactile sensory reception) as a substitute for sight. The teeth of these two taxa are also small relative to the others, which may reflect a reliance on more soft-bodied invertebrates, and agrees with a preferred diet of earthworms in *Oryzorictes* (see above).

An obvious and unusual feature on the dorsolateral aspect of the *Oryzorictes* cranium is the presence of two greatly enlarged sinus canals (Novacek, 1993, p.459), which are consistently much larger than those (when present) in the other tenrecoids (Figs. 9,10). Although I am unsure of the functional significance of this feature, the superior ramus of the stapedia artery passes through the sinus canal (Asher, 2001), and a large canal may be correlated with a larger superior ramus, which may in turn be related to a large or unusually-shaped stapes.

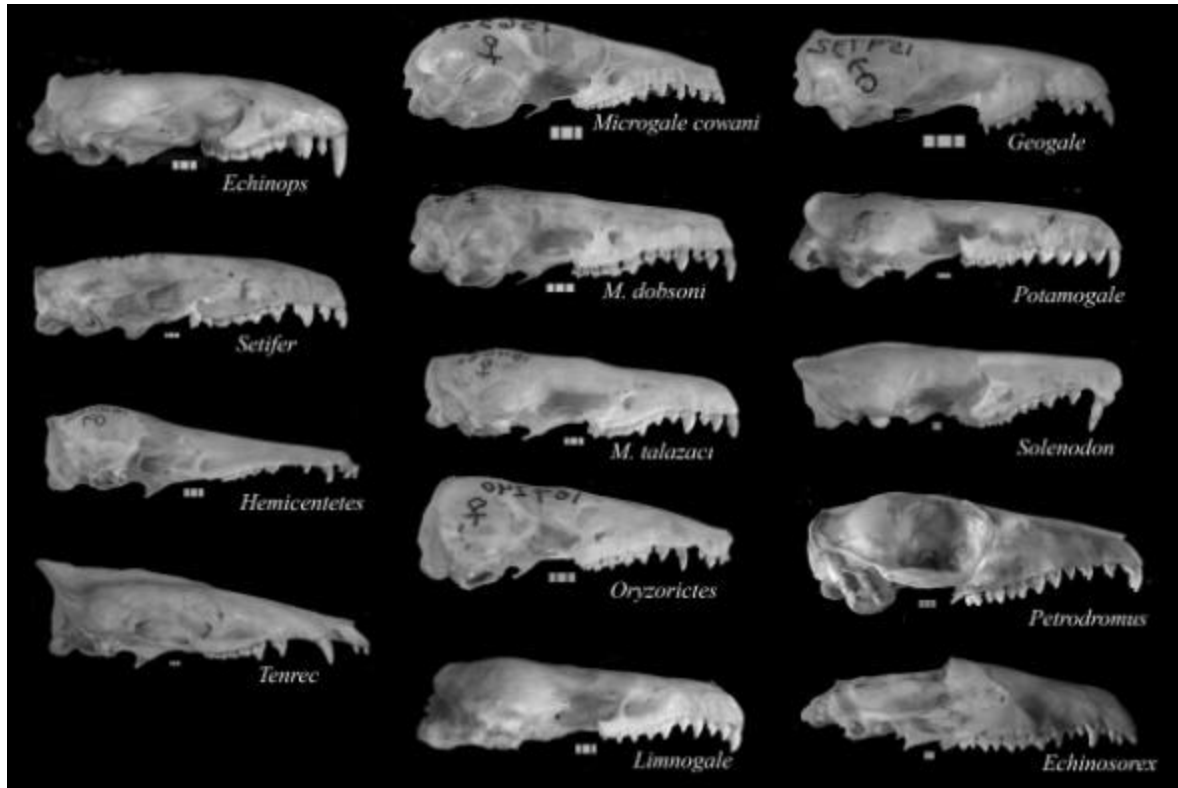


Figure 6.9. Lateral view of the cranium, right side, in four tenrecines (left row), four oryzorictines (middle row), two other tenrecoids (right row, two top), and three outgroups (right row, bottom three). Scale units=mm.



Figure 6.10. Lateral view of the cranium, right side, in the tenrecine digger *Oryzorictes*. Arrows show the two greatly enlarged sinus canals. Scale units=mm.

The semi-aquatic oryzorictine *Limnogale* demonstrates several characteristics that are common in other aquatic mammals. Relative to the other oryzorictines, the anterior rostrum is relatively wide, including wider nasals and premaxillae, and dorsolaterally flared anterior squamosals (Fig. 8). The nasals are also considerably shorter due to the

dorsoposteriorly rescinded nasal apertures. Similar to other semi-aquatic rodents, *Limnogale* also has very large infraorbital foramen for passage of the trigeminal nerves, and a large foramen magnum (except for *M. cowani*) (Figs. 9,11). Relative cranial capacity of *Limnogale* may also be greater than that of other oryzorictines and appears to be large relative to all of the studied taxa (see Fig. 8), but this is difficult to assess qualitatively.

The skull of the other semi-aquatic tenrecoid, *Potmogale*, has fewer features that are characteristic of aquatic mammals. The rostrum is not broad, and is more similar to *Microgale talazaci* in form than to *Limnogale*. The nares are shifted dorsoposteriorly and the infraorbital canal is large, but not as enlarged as in *Limnogale*. Also similar to *Limnogale*, the foramen magnum is mediolaterally wide and the basicranium has a relatively large surface area (Fig. 11).

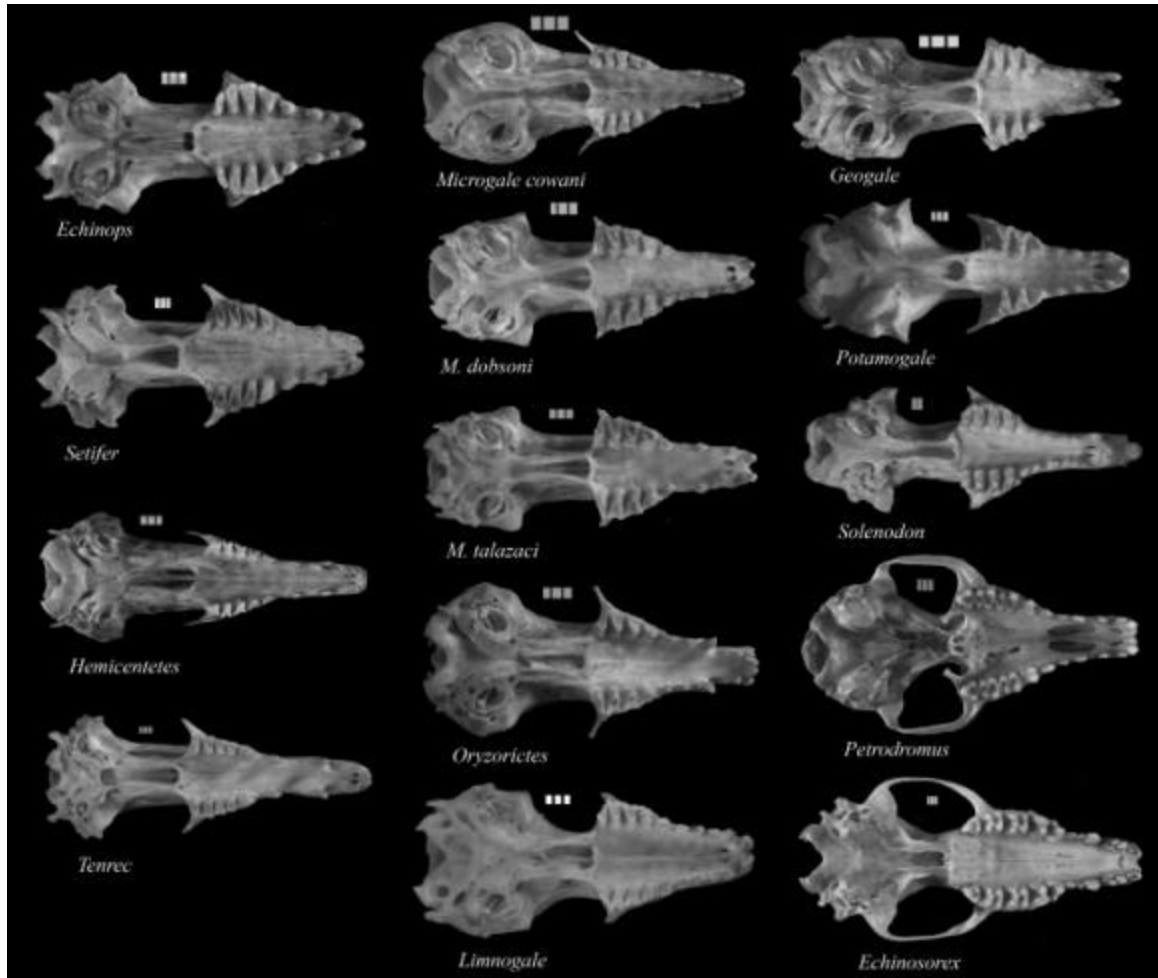


Figure 6.11. Ventral view of the skull in four tenrecines (left row), four oryzorictines (middle row), two other tenrecoids (right row, two top), and three outgroups (right row, bottom three). Scale units=mm.

Although I am not aware of specific differences in diet between *Echinops* and *Setifer*, differences in mandibular morphology, in addition to the cranial differences noted above, suggest a diet of tougher foods in *Echinops* than in *Setifer*. This may be related to the availability of more soft-bodied invertebrates to *Setifer* on the ground, and fewer available to *Echinops* in its primarily arboreal habitat. *Echinops* has a higher mandibular condyle relative to the height of the tooth row (Fig. 12), increasing the lever arm of the masseter and allowing more oblique jaw movement for the grinding of food. There do not appear to be significant differences in condylar shape between the two. *Echinops* has a

higher coronoid process and a larger surface area for the temporalis, indicative of a powerful occlusal bite (Fig. 12).

In contrast to both *Echinops* and *Setifer*, *Hemicentetes* and *Tenrec* have long, narrow mandibles with mandibular condyles almost in line with the chewing surface of the molars (Fig. 12). The condyles are particularly low in *Hemicentetes*, suggesting that its food is not thoroughly processed by chewing, which would make sense for a diet consisting largely of earthworms. The mandible in *Hemicentetes* is also extremely thin (dorsolaterally), with little space for attachment of masseter musculature. *Tenrec* has a broad coronoid process and a deeper mandible, suggestive of greater chewing forces than *Hemicentetes*, and in agreement with its more varied diet of soft and hard insects and small vertebrates.

Within the oryzorictines, *Microgale cowani* has a markedly dorsoventrally narrow mandible and small teeth relative to the other two *Microgale* species. Its coronoid process, mandibular condyle, and angular process project as thin processes, leaving little space for muscle attachments (Fig. 12). The other two *Microgale* species, *Oryzorictes*, and especially *Limnogale*, have more robust mandibles with broader masseteric attachment surface area and anteroposteriorly wider coronoid processes. The mandibular condyle in *Oryzorictes* is thin and not well defined, similar to *M. cowani*, which may be related to a weaker articulation associated with a diet of soft-bodied invertebrates. The mandible of *Potamogale* is unlike *Limnogale* in that the mandibular condyle is almost directly in line with the tooth row in the former, similar to carnivores with a powerful bite driven by the temporalis. The coronoid process is also anteroposteriorly broad in *Potamogale* as opposed to a more dorsally projecting and narrow process in *Limnogale*.

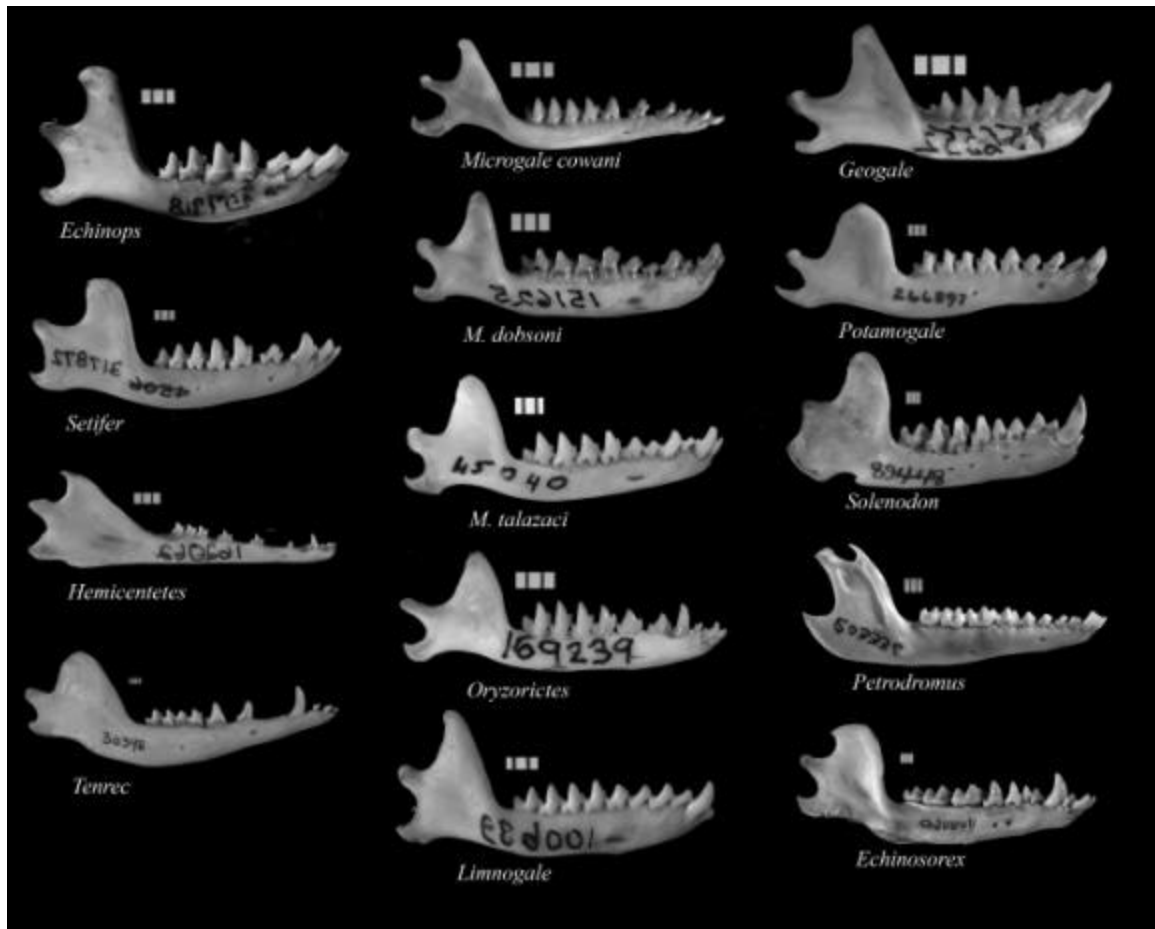


Figure 6.12. Lateral view of the right mandible in four tenrecines (left row), four oryzorictines (middle row), two other tenrecoids (right row, two top), and three outgroups (right row, bottom three). Scale units=mm.

Summary and Conclusions

Several observations in this study require future quantitative verification, yet there is clear and considerable function-based variation in some general features of the tenrecoid cranium and mandible. Despite their shared “insectivorous” diet, taxon-specific dietary preferences have driven the evolution of particular features of the tenrecoid skull, which are convergent with those of other mammals with similar dietary regimes. Taxon-specific postural behavior directly influences aspects of the occipital region, owing to

attachments of the neck musculature, and habitat preference more indirectly influences skull morphology by determining an animal's available diet.

Despite their superficial similarities, *Echinops* and *Setifer* have a series of distinctions that correlate with arboreal locomotor behavior in the former and a more terrestrial habitat in the latter, which is in turn correlated with a diet of more hard-bodied invertebrates in *Echinops* and more soft-bodied invertebrates in *Setifer*. Both *Hemicentetes* and *Tenrec* use their snouts to root for soil invertebrates, and this is clear from their overall rostral morphology. Yet *Hemicentetes* most likely largely subsists on earthworms, and this soft-bodied invertebrate diet is reflected in a weak mandibular symphysis and diminutive muscle attachment areas.

Many regions of the postcranial skeleton suggest that *Microgale cowani* exhibits more digging behavior than *M. dobsoni* and *M. talazaci*, and this is supported by several features of the skull, including those of the occipital region that indicate strong neck musculature, and those of the snout and mandible that suggest a specialized soft-bodied invertebrate diet. The semi-aquatic tenrecid *Limnogale* is dissimilar from the other oryzorictines and *Potamogale*, and has a series of features convergent with other semi-aquatic mammals, including adaptations involved with sensory perception from the mystacial vibrissae and a strong mandible for a diet including hard-bodied invertebrates such as crayfish. Aside from having an enlarged basicranium and foramen magnum, *Potamogale* is unlike *Limnogale* in most aspects of the skull, suggesting that traits associated with a semi-aquatic habitus were likely independently acquired in each. This is supported by morphology throughout the postcranial skeleton.

Although I have not focused on the tenrecoid dentition here, there are apparent differences in dental form associated with taxon-specific feeding behaviors (e.g., reduced dentition in *Hemicentetes*, *Oryzorictes*, and *M. cowani* associated with feeding on subterranean invertebrates) that warrant further exploration and quantitative study. Due to the large body of systematic work on the mammalian skull, and the myriad cranial, mandibular, and dental characters used for taxonomic and phylogenetic assessments, a complete study of the tenrecoid skull and features with phylogenetic significance is an extensive endeavor and a topic for future work. Although studies have discussed the phylogenetic significance of features of the tenrecoid skull and its dentition (e.g., Van Valen, 1967; Butler, 1988; MacPhee, 1993; Asher, 1999, 2001, 2003; Olson and Goodman, 2003), these do not account for the many function-based features (some of which are briefly identified here) that are part of a tightly integrated system of parts. These factors should be contextually considered in any process of tenrecoid phylogenetic assessment that considers “characters” of the skull.

Long Bone Cross-Sectional Geometry in Tenrecidae

Although habitus-specific mechanical environments undoubtedly influence bone form (see Chapter I for discussion), the extent to which the specific geometry of a given bone is developmentally optimized to withstand particular loading regimes (variable tensile, compressive, torsional, and/or bending magnitudes, frequencies, etc.) is less clear (Thomason, 1995; Polk, et al., 2000; Lieberman et al., 2004). Long bone cross-sectional shape varies considerably depending on the particular bone and taxon under consideration. Cortical area is used as a measure of bone strength, and is important for the consideration of axial loading and tension. Overall cortical thickness can vary, as can cortical thickness at different regions of a single section. Body size plays an important role in understanding cortical thickness variation across taxa. For instance, cortical thickness scales nearly isometrically with body mass in smaller mammals (less than 100kg), and allometrically in larger mammals (Bertram and Biewner, 1990). But cortical thickness is also highly variable in animals with similar body masses, which is presumably correlated to taxon-specific axial loading and tension. Cross-sectional shape of the cortex might be a better measure of torsional and bending resistance, because calculation of total cortical area does not take into account that bone is differentially distributed around its centroid. The shape of the outer cortex can be circular, elliptical, rectangular, triangular, etc., and cortical thickness can vary at any given point. A rounded cortex with constant cortical thickness would theoretically optimize torsional resistance because the polar moment area (or polar moment of inertia, J) is maximized; i.e. there is an equal distribution of bone around the centroid and vulnerability to torsion is therefore minimized. Irregularly shaped bones generally favor resistance to bending in the plane of

the longest axis (represented by an increased second moment of area, or moment of inertia, I) (Alexander, 1968).

Most determinations of cross-sectional moment areas depend on calculation of the geometric centroid, assuming that the cortical center of mass is representative of the neutral axis (axis of transition from tensile to compressive loads in bending). Lieberman et al. (2004) raise several problems with the interpretation of cross-sectional geometric (CSG) data, based on the principal that the neutral axis is most often not represented by the centroid (due to interaction between bending and compression). The neutral axis for any given loading regime can only be determined experimentally, and most CSG data are therefore not particularly reliable. Furthermore, experimental work with strain gauges on sheep demonstrated that $I_{\max}$ (the maximum second moment of area) does not correspond to the plane of maximum bending, even when the neutral axis is corrected. They recommend that CSG data are valuable for identifying general patterns between closely related taxa, but are less meaningful for comparisons of distantly related taxa with differing musculoskeletal anatomies, and absolute values of most variables (J , I , and especially Z), even within a species, are not accurate.

Despite potential theoretical and practical problems with interpretation of CSG variables, several studies have found correlations between locomotor behavior and cross-sectional dimensions, suggesting that, in proper phylogenetic context, CSG analysis is useful for understanding relationships between loading patterns and form, and may be valuable for paleobiological interpretations of locomotor behavior. Many of these studies focus on primates (e.g., Burr et al., 1982; Schaffler et al., 1985; Burr et al., 1989; Demes and Jungers, 1993; Runestad, 1997), and several focus on a wider range of taxa (Currey

and Alexander, 1985; Demes et al., 1991; Cubo and Casinos, 1998; Polk et al., 2000; De Margerie, 2005).

Comparisons of cross-sectional moments of inertia in the AP and ML planes (CSMI) in macaques with different locomotor behaviors demonstrated higher CSMI values in terrestrial vs. arboreal species, suggesting increased structural rigidity for higher speed animals (Burr et al., 1989). Schaffler et al. (1985) compared four non-human primates, focusing on cross-sectional moments of inertia (CSMI) of the humerus vs. femur, and the relationship between locomotor behavior and CSMI values. They found the greatest forelimb/hindlimb CSMI values in forelimb brachiators (gibbons), whereas hindlimb leapers (leaf monkeys) had the lowest values, and macaques had a mid-range value. In all primates studied, values were below 1.0, indicating more hindlimb strength regardless of behavioral forelimb dominance.

Demes and Jungers (1993) studied cross-sectional geometric properties of the humerus and femur in prosimians with various locomotor behaviors and found that leapers have more robust and anteroposteriorly elongated femora, whereas no significant habitus-related differences were found in the humerus. They emphasize the importance of considering body size in CSG analyses; all variables scaled allometrically with body mass, and function-based differences between taxa were most robust when body size was taken into account. In a comparison of several CSG variables in the lesser bushbaby, macaque, and human, including cross-sectional area (CA), polar moment (J) and principal moments (I_{min} and I_{max}), Burr et al. (1982) similarly found that the femur of the lesser bushbaby seems well-adapted for leaping. Their data indicate that the bushbaby

femoral midshaft is resistant to large compressive axial loads in the anteroposterior plane, whereas human and macaque femora are more resistant to bending.

Runestad (1997) studied CSG differences in a wider range of primates and found that the humerus and femur of slow-climbing lorids have greater resistance to axial compression and torsion than those of other primates (as determined by comparisons of cortical area (CA) and polar moment (J) values). These parameters were correlated with overall humeral and femoral head size, and, furthermore, body mass was not a critical factor in variation of cross-sectional shape. Polk et al. (2000) compared CSG properties in primates, rodents and carnivorans in order to test the hypothesis that the long bones of arboreal mammals have greater cross-sectional strength than terrestrial mammals, and that primates in general have higher CSG values. Their analyses demonstrated several significant differences between terrestrial and arboreal taxa: values of compression resistance were greater in arboreal vs. terrestrial rodent humeri, carnivoran femora, and carnivoran humeri. Similar to the argument made by Lieberman et al. (2004), the authors caution against generalizing optimal CSG values across taxa, although taxon-specific values might indicate functionally meaningful patterns.

Questions

Although it is beyond the scope of this dissertation to undertake a comprehensive study of cross-sectional geometric properties here, several prepared specimens allow me to explore several questions at a preliminary level. Are there cross-sectional geometric differences between tenrecoids with different taxon-specific positional behaviors? For example, do CSG analyses indicate a greater resistance to axial loading in the subterranean species *Oryzomys* and/or *Hemicentetes*? Are there differences between

them that might correlate with subfamily-level status? Do the digging species exhibit greater cross-sectional area (CA) in the forearm than the hindlimb? Are there significant differences with respect to bending resistance in the femoral midshaft between tenrecines and oryzorictines based on a laterally abducted resting position in the former and a more parasagittal position in the latter?

Materials/Methods

12 humeri and 12 femora from eight species (six genera) were borrowed from the Field Museum of Natural History (FMNH), Museum of Comparative Zoology at Harvard (MCZ), and the Smithsonian Museum of Natural History (USNM) (see Table 6.3).

TABLE 6.3. Sample for Cross-Sectional Geometric Analyses (see text for abbreviations)

ID	Species	Bone Right/Left	Source
161577	<i>Echinops telfairi</i>	Femur (R)	FMNH
161577	<i>Echinops telfairi</i>	Humerus (R)	FMNH
29245	<i>Hemicentetes semispinosus</i>	Femur (L)	MCZ
29245	<i>Hemicentetes semispinosus</i>	Humerus (L)	MCZ
33951	<i>Hemicentetes semispinosus</i>	Femur (L)	FMNH
33952	<i>Hemicentetes semispinosus</i>	Femur (R)	FMNH
33952	<i>Hemicentetes semispinosus</i>	Humerus (R)	FMNH
169241	<i>Hemicentetes semispinosus</i>	Femur (L)	FMNH
169241	<i>Hemicentetes semispinosus</i>	Humerus (L)	FMNH
1001	<i>Hemicentetes semispinosus</i>	Femur (L)	DARM
449184	<i>Microgale cowani</i>	Humerus (R)	USNM
449184	<i>Microgale cowani</i>	Femur (R)	USNM
165468	<i>Microgale dobsoni</i>	Humerus (R)	FMNH
162052	<i>Oryzorictes hova</i>	Femur (L)	FMNH
45018	<i>Oryzorictes tetradactylus</i>	Femur (R)	MCZ
45018	<i>Oryzorictes tetradactylus</i>	Humerus (R)	MCZ
151936	<i>Setifer setosus</i>	Femur (L)	FMNH
151936	<i>Setifer setosus</i>	Humerus (L)	FMNH
16364	<i>Tenrec ecaudatus</i>	Humerus (L)	MCZ
16364	<i>Tenrec ecaudatus</i>	Humerus (L)	MCZ
16798	<i>Tenrec ecaudatus</i>	Femur (L)	FMNH
16798	<i>Tenrec ecaudatus</i>	Humerus (L)	USNM
DARM	<i>Tenrec ecaudatus</i>	Humerus (R)	DARM
DARM	<i>Tenrec ecaudatus</i>	Femur (R)	DARM

Specimens were prepared based on methods from Goldman et al. (1999) with the intention of future microstructural analyses. Humeri and femora were cleaned with a proteolytic enzyme (2% Terg-a-zyme). Midsection of each shaft (humerus and femur) was determined as $\frac{1}{2}$ the distance from proximal to distal diaphysis and cut with an 180 μ -thick diamond blade saw. The specimen was soaked with occasional ultrasonication and vacuuming in a graded series of ethanol solutions (for dehydration), 50:50 isopropanol/heptane (for defatting), and a graded series of acetone/methyl methacrylate solutions (for final dehydration and preparation for polymerization), and were then left in methyl methacrylate solution with asobisisobutyronitrile for final polymerization. After approximately four weeks, the specimens were embedded in a block of poly(methyl methacrylate). The block with embedded specimen was cut and ground to expose the midshaft surface and then adhered to a glass slide with dental adhesives. Sections were cut to approximately 200 μ , as determined with a digital micrometer and 3D stereoscopic microscope. Sections were polished to approximately 100 μ with a graded series of polishing papers.

Images were acquired from the slides with a Leica-Leitz DMRX/E Universal Microscope, JVC KY-F55BE color video camera, and Syncroscopy Montage Explorer software (Synoptics, Ltd.). TIF files were transferred to Adobe Photoshop CS (8.0) for binary color assignment. Images are then imported into Scion Image (Scion Corporation, 4.0.3.2) where the following parameters were calculated: CA=cortical area; Xbar= x coordinate of centroid; Ybar=y coordinate of centroid; Ix=second moment of area about x axis; Iy=second moment of area about y axis; Imax=maximum second moment of area; Imin=minimum second moment of area; Theta=angle from M-L axis counterclockwise to

major axis; Z_x =section modulus about x axis ($I_x/\text{max y radius}$); Z_y =section modulus about y axis ($I_y/\text{max x radius}$); Max x radius=x distance from centroid to outermost fiber (used in calculating Z_y); Max y radius=y distance from centroid to outermost fiber (used in calculating Z_x). Data were transferred to STATISTICA (6.0) for statistical analyses (ANOVAs and Tukey HSD post hoc tests).

Results and Discussion

Despite a small sample size with unknown ages and body masses, there are several developmental and function-based patterns here that warrant discussion and future study with larger samples. Figure 6.13 illustrates cross-sectional size differences between taxa in the humerus and femur, and it is evident that the bones of tenrecines are relatively thicker with increasing bone diameter. Particularly within Tenrecinae, cortical thickness (CA) is positively correlated with average species body mass ($r = 0.95$, $p < 0.05$; see Appendix 6.1. for values). Note, though, that *Hemicentetes* has similar cross-sectional areas to that of *Setifer* despite *Setifer*'s substantially larger body mass (225g vs. 145g) (Fig. 6.13; $CA = 2.0 \text{ mm}^2$ femur, 3.2 mm^2 humerus in *Hemicentetes* and 2.1 mm^2 , 2.3 mm^2 in *Setifer*). *Hemicentetes* has a relatively short and wide humerus and femur (see Chapters IV and V), similar to other digging tenrecoids and digging mammals in general, whereas *Setifer* has a longer, more gracile humerus and femur. The relatively thicker cortex in *Hemicentetes* corresponds with greater axial loading of the limbs related to digging, whereas *Setifer* is a non-digger with a series of traits suggestive of a common arboreal ancestor with *Echinops*.

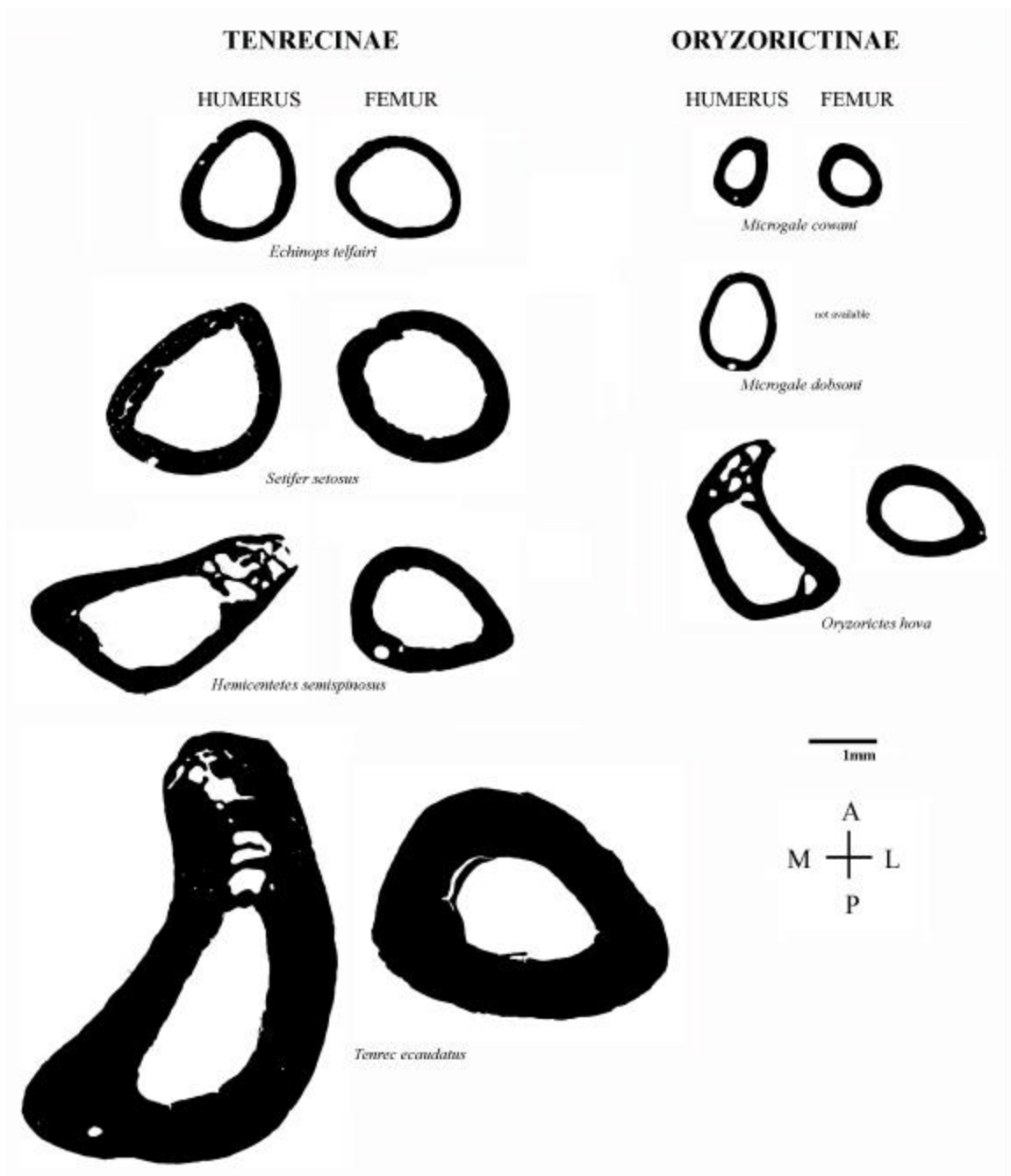


Figure 6.13. Comparisons of the humerus and femur in each of the studied tenrecoid species, illustrating size differences within and between taxa.

Increased cortical thickness and total area related to digging behavior is also evident in the three species of Oryzomys (Fig. 6.14). *Microgale cowani* is the smallest of the three, with an average body mass (BM) of 11g; yet the cortex of its humerus is

considerably thicker than that of *M. dobsoni* (0.80mm^2 vs. 0.49mm^2), which has an average BM of 38g (Fig. 6.13, top right). *Oryzorictes* has a thick cortex relative to the *Microgale* species, which would appear to be a scaling effect, related to *Oryzorictes*' larger size (Fig. 6.13). Yet average *Oryzorictes* BM is 40g, while *M. dobsoni* average BM is almost the same at 38g. Relative to *M. dobsoni*, *Oryzorictes* has a massive humerus cross sectional diameter as well as area (*M. dobsoni* CA= 0.49 mm^2 ; *Oryzorictes* CA= 1.8 mm^2).

Figure 6.13 also illustrates relative differences in forelimb and hindlimb cross-sectional area. Unlike primates (Schaffler et al., 1985), all of the studied tenrecids have greater CA values for the forelimb than for the hindlimb. The difference is most significant in the digger *Oryzorictes*, which has a CA(hum)/CA(fem) score over 1.8 (Figure 6.15). There is a significant subfamily-level difference between tenrecine and oryzorictine cross-sectional area when CA is corrected for size ($p < 0.00$). Oryzorictines have relatively greater bone cortical area than tenrecines, which I would attribute to one of two factors: 1) one, and probably two of the three oryzorictine species studied here are diggers, which correlates with greater CA values; and/or 2) the postural behavior of oryzorictines is such that the humerus and femur is positioned underneath the body experiencing regularly high axial loads, whereas tenrecines have more laterally abducted limbs (see previous chapters), more subject to bending. More non-digging oryzorictine species need to be sampled to explore the effects of taxon-specific postural (as opposed to locomotor) behavior in the two subfamilies.

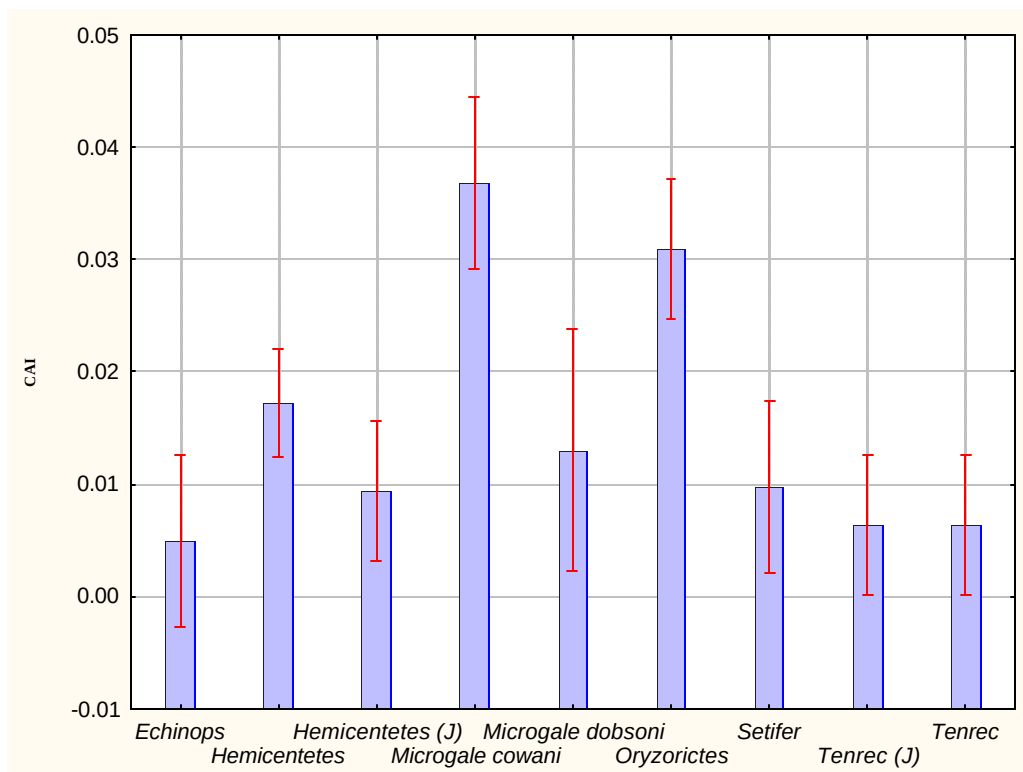


Figure 6.14. Cortical area in six tenrecid species, shown as a function of body size (mm^2/BM). The more fossorial species have relatively greater cortical areas, including *Hemicentetes*, *Microgale cowani*, and *Oryzorictes*. ($p < 0.00$ for *M. cowani* and *Oryzorictes*, but sample sizes are only 1-4n per species (see Appendix 6.1, 6.2). J=Juvenile.

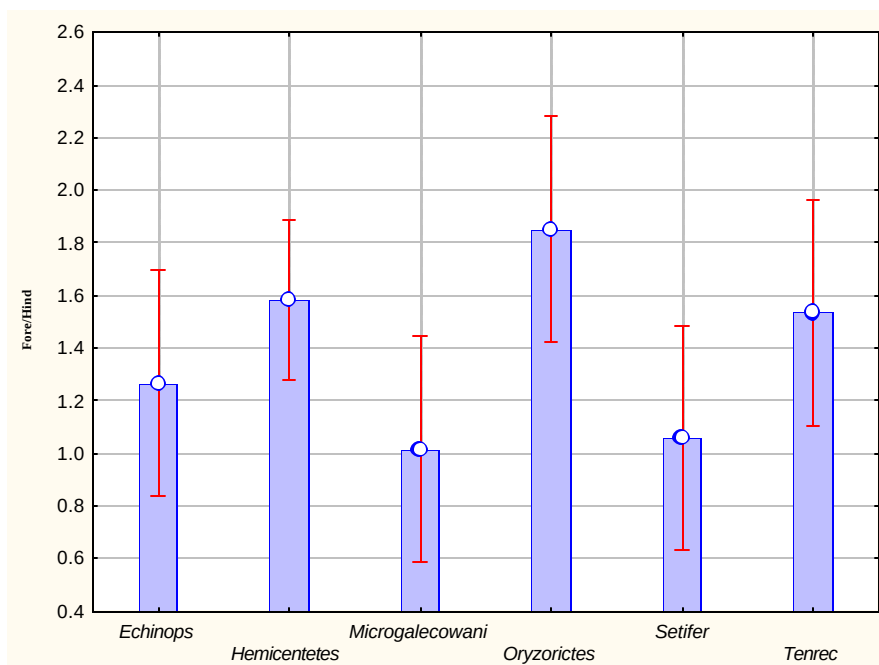


Figure 6.15. Cortical area of the humerus/cortical area of the femur, illustrating “forelimb dominance” in all the studied tenrecids, with particularly high values in *Oryzorictes*.

Despite some straightforward differences in tenrecoid long bone cross-sectional area that correspond with function-based hypotheses, cortical area does not account for differences in bone shape that can significantly alter the resistance of bone to bending and torsion. Figures 6.16 and 6.17 illustrate cross-sections from the humerus and femur of six tenrecoid species that have been scaled to the same approximate anteroposterior diameters, allowing for visual comparisons of overall shape. The femur (Fig. 6.16) shows much less overall variation in shape than the humerus (Fig. 6.17), which varies considerably between taxa. There are no significant subfamily-level differences in femoral or humeral shape in any of the other tested CSG parameters (I_x/I_y , I_{max}/I_{min} , J/BM ; $p > 0.05$; Appendix 6.1), despite expectations that tenrecines would have higher polar moment scores due to more laterally positioned limbs and greater bending loads. This is most likely due to the relatively similarly shaped femoral cross-section in the studied taxa, and the considerable variation of the humerus cross-sections within subfamilies (Fig. 6.17).

Although cross-sectional variation is subtler at the femur than at the humerus, both digging taxa *Hemicentetes* and *Oryzorictes* have a slight posterolateral elongation which is the distal aspect of a long and distally reaching third trochanter. The other taxa have rounder femoral cross-sections, which may represent resistance to more varied tensile loads vs. bending stresses (presumably resisting forelimb digging) in a single plane. Within Tenrecinae, *Echinops* and *Setifer* have similarly shaped cross-sections of the humerus, with a slight lateral keel and slightly thicker anteromedial side. *Hemicentetes* and *Tenrec* are both irregularly shaped and somewhat triangular, but the axes of orientation are different in each; *Hemicentetes* has a mediolaterally-elongated

cross-section, whereas that of *Tenrec* is anteroposteriorly elongated. *Oryzorictes* is also anteroposteriorly elongated, but the long axis of orientation is slightly medially tilted as opposed to a lateral tilt in the others (Fig. 6.17). In all three of these (*Hemicentetes*, *Tenrec*, and *Oryzorictes*), the deltopectoral crest and its attaching muscles plays a major role in warping the circularity of the section. In *Hemicentetes* and *Tenrec*, the lateral elongation and associated trabecular strutting of the humerus cross-section is the site of an enlarged deltopectoral crest, whereas *Oryzorictes* has a prominent anterior pectoral crests (Fig. 6.18).

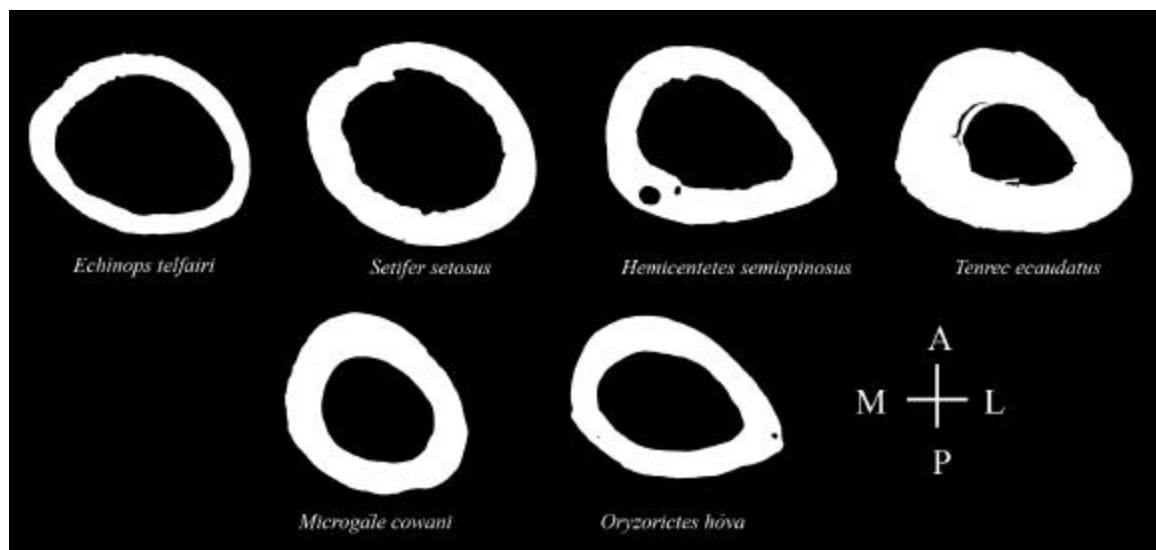


Figure 6.16. Cross-section of the femur midshaft in four tenrecines (top row), and two oryzorictines (bottom two). Images are scaled to same approximate AP diameter (see Fig. 6.13 for relative size differences between taxa).

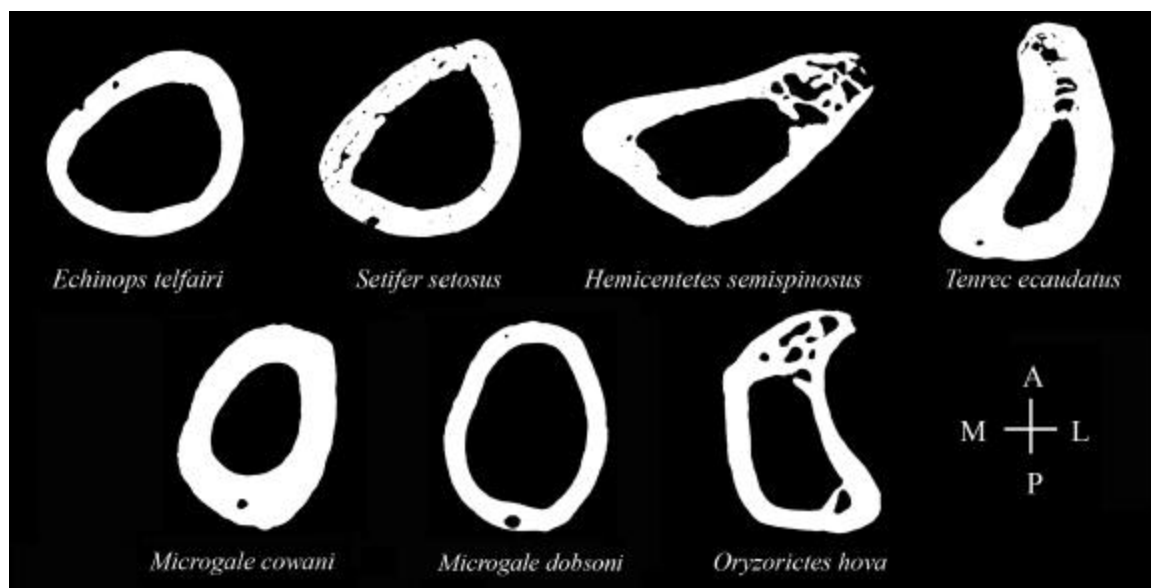


Figure 6.17. Cross-section of the humerus midshaft in four tenrecines (top row), and two oryzorictines (bottom two). Images are scaled to same approximate AP diameter (see Fig. 6.13 for relative size differences between taxa).

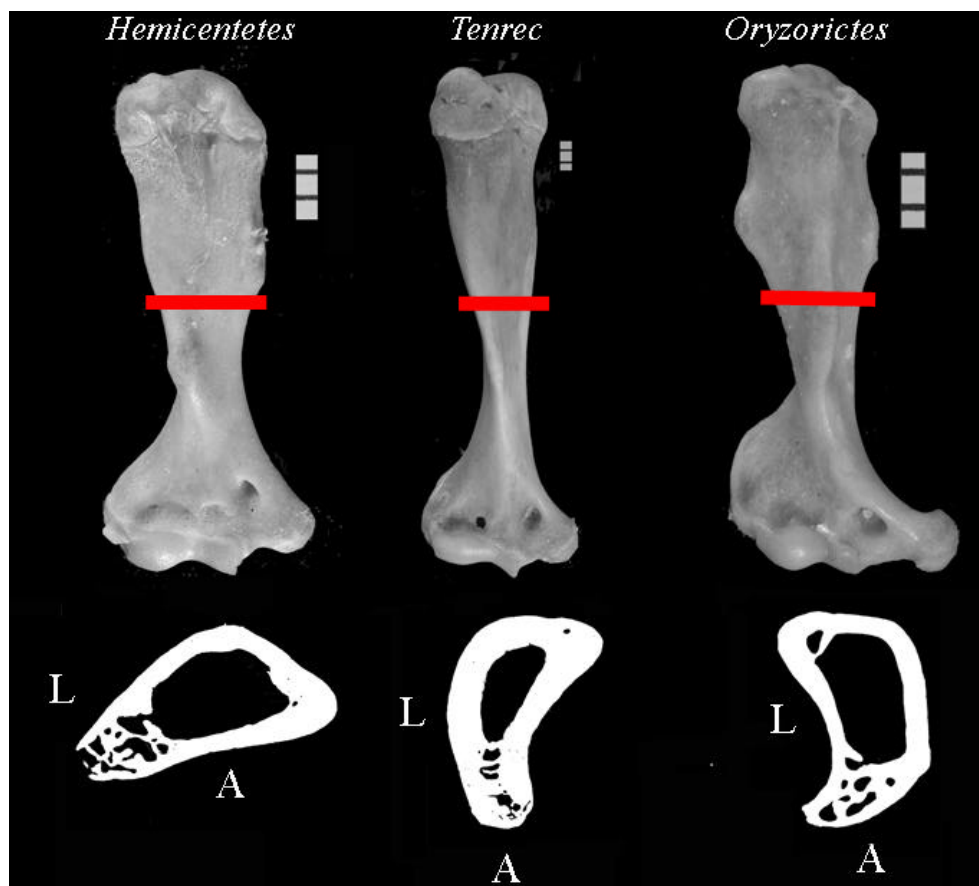


Figure 6.18. Anterior view of right humerus in three tenrecids (top), and midshaft cross-sections of each humerus below. All three have irregularly shaped sections due to prominent deltopectoral crests in *Hemicentetes* and *Tenrec*, and pectoral crest in *Oryzorictes*.

Conclusion and Summary

Despite a small sample size, preliminary cross-sectional geometric studies of the midshaft humerus and femur in six tenrecid species illustrate several morphological trends worth further exploration. Cross-sectional area of the cortex varied significantly between genera as well as subfamilies, and although CA is positively correlated with body size, there is variation that is not accounted for by size alone, such as the thick cortex of the smallest of the studied species, *Microgale cowani* (11g). These preliminary data support the hypotheses of 1) increased midshaft CA in diggers due to increased axial loading of the limbs, as well as 2) increased CA in oryzorictines vs. tenrecines due to more directly axially-loaded limbs.

All of the tenrecoids have greater CA values for the forelimb than for the hindlimb, which might be due to greater direct axial loads on the forelimb than on the hindlimb for all tenrecoids. The tenrecine, and to some extent oryzorictine, forelimb tends to be less multiaxially mobile than the hindlimb, and plays less of a role in grooming and changing direction in locomotion (pers. obs.; see Chapters II and III). Greater CA in the forelimb midshaft relative to the hindlimb might be characteristic of Tenrecoidea.

Although I did not find significant differences in moment area parameters, there are evident differences in cross-sectional shape that are strongly influenced by the attaching musculature: those attaching to a distally extended third trochanter of the femur in some taxa (Mm. gluteus superficialis, tensor fasciae femoris, vastus intermedius, quadratus femoris) and to the deltopectoral crest of the humerus (Mm. deltoideus and pectoralis). Although subtle differences in moment area parameters, e.g., between *Setifer*

and *Echinops*, and *Microgale cowani* and *dobsoni*, were not detected here, function-, development-, and size-based hypotheses would be worth testing on a larger and more diverse sample of Tenrecoidea with known body mass and age.

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Appendix 6.1. Cross-sectional geometry data

ID	Taxon	Bone	BM (g)	CA (mm ³)	CA/BM	Ix	Iy	Ix/y	J/BM	Imax	Imin	Imax/min
161577	Echinops	femur	180	0.7864	0.00437	0.1768	0.2467	0.71666	0.00235	0.254	0.1695	1.49853
161577	Echinops	humerus	180	0.995	0.00553	0.2692	0.2797	0.96246	0.00305	0.327	0.2218	1.4743
29245	Hemicentetes	femur	145	2.0193	0.01393	0.5181	0.9561	0.54189	0.01017	1.0055	0.4687	2.1453
29245	Hemicentetes	humerus	145	3.2479	0.0224	1.817	3.7743	0.48141	0.03856	4.2091	1.3822	3.04522
33952	Hemicentetes	femur	145	1.7822	0.01229	0.5225	0.8404	0.62173	0.0094	0.8757	0.4873	1.79704
33952	Hemicentetes	humerus	145	2.7814	0.01918	1.0012	3.1818	0.31466	0.02885	3.3255	0.8574	3.87859
169241	Hemicentetes	humerus	145	2.657	0.01832	1.469	2.486	0.59091	0.02728	2.93	1.025	2.85854
Darm	Hemicentetes (J)	femur	145	1.1547	0.00796	0.4383	0.5201	0.84272	0.00661	0.5208	0.4376	1.19013
Darm	Hemicentetes (J)	femur	145	1.0406	0.00718	0.3988	0.4326	0.92187	0.00573	0.4378	0.3936	1.1123
Darm	Hemicentetes (J)	humerus	145	1.8694	0.01289	0.8218	1.6554	0.49644	0.01708	1.6838	0.7935	2.12199
449184	Microgalecowani	femur	11	0.4019	0.03654	0.029	0.0284	1.02113	0.00522	0.0342	0.0232	1.47414
449184	Microgalecowani	humerus	11	0.4079	0.03708	0.0343	0.0202	1.69802	0.00495	0.0361	0.0184	1.96196
165468	Microgale dobsoni	humerus	38	0.4947	0.01302	0.0972	0.0608	1.59868	0.00416	0.0979	0.0601	1.62895
45018	Oryzorictes	humerus	40	1.7912	0.04478	0.9613	0.6231	1.54277	0.03961	1.1534	0.4311	2.67548
45018	Oryzorictes	femur	40	0.9678	0.0242	0.1895	0.2829	0.66985	0.01181	0.3082	0.1642	1.87698
162052	Oryzorictes	femur	40	0.9505	0.02376	0.1526	0.2365	0.64524	0.00973	0.2588	0.1303	1.98619
151936	Setifer	femur	225	2.1289	0.00946	0.936	1.1888	0.78735	0.00944	1.2554	0.8695	1.44382
151936	Setifer	humerus	225	2.2534	0.01002	1.1977	1.2865	0.93098	0.01104	1.5293	0.955	1.60136
16364	Tenrec (J)	humerus	1500	9.978	0.00665	34.5016	12.9671	2.6607	0.03165	37.4063	10.0624	3.71743
16798	Tenrec (J)	femur	200	0.9328	0.00466	0.2476	0.3363	0.73625	0.00292	0.3573	0.2266	1.57679
16798	Tenrec (J)	humerus	200	1.5383	0.00769	0.9179	0.5725	1.60332	0.00745	0.9342	0.5562	1.67961
Darm	Tenrec	femur	1500	8.2253	0.00548	6.909	10.7827	0.64075	0.01179	11.2652	6.4265	1.75293
Darm	Tenrec	humerus	1500	12.6308	0.00842	39.0781	16.1116	2.42546	0.03679	43.0906	12.0991	3.56147
16564	Tenrec	femur	1500	7.9054	0.00527	7.1215	13.008	0.54747	0.01342	13.9316	6.1979	2.24779

BM=body mass; CA=cortical area; Ix=second moment of area about x axis; Iy=second moment of area about y axis; Imax=maximum second moment of area; Imin=minimum second moment of area; J=Ix+Iy

Appendix 6.2. Probability scores for Cortical Area/Body Mass from Tukey Honest Significant Difference post hoc test

Taxon	Tukey HSD test; Variable: ^{CAI} Marked differences are significant at $p < .05000$								
	{1} M=.00495	{2} M=.01722	{3} M=.00934	{4} M=.03681	{5} M=.01302	{6} M=.03091	{7} M=.00974	{8} M=.00634	{9} M=.00639
Echinops {1}		0.167767	0.985524	0.000521	0.917249	0.001352	0.985983	0.999996	0.999995
Hemicentetes {2}	0.167767		0.492858	0.007666	0.996651	0.041654	0.703643	0.155496	0.159350
Hemicentetes (J) {3}	0.985524	0.492858		0.000823	0.999098	0.002648	1.000000	0.997477	0.997779
Microgalecowani {4}	0.000521	0.007666	0.000823		0.032587	0.925031	0.002117	0.000382	0.000386
Microgale dobsoni {5}	0.917249	0.996651	0.999098	0.032587		0.128400	0.999740	0.957860	0.959746
Oryzorictes {6}	0.001352	0.041654	0.002648	0.925031	0.128400		0.008279	0.000820	0.000836
Setifer {7}	0.985983	0.703643	1.000000	0.002117	0.999740	0.008279		0.997267	0.997559
Tenrec (J) {8}	0.999996	0.155496	0.997477	0.000382	0.957860	0.000820	0.997267		1.000000
Tenrec {9}	0.999995	0.159350	0.997779	0.000386	0.959746	0.000836	0.997559	1.000000	

SUMMARY

The 26^{+/-} species of Tenrecoidea from Central Africa and Madagascar are most likely derived from an early branch of Placentalia, and are, in this sense, an ancient placentalian taxon. Yet they exhibit a remarkable degree of species-specific variation of the postcranium and skull, much of which corresponds with known locomotor behaviors. Many derived characteristics of the tenrecoidean skeleton are convergent with other mammalian locomotor specialists, including those associated with terrestrial running, climbing, swimming, and forelimb digging. Detailed study of these characters, as well as those without apparent functional significance, also reveal sets of phylogenetically constrained traits, which are useful for resolving tenrecoidean evolutionary relationships. The primary focus of this study was to illustrate, describe, and compare postcranial elements of the tenrecoidean skeleton in order to better understand the evolution of mammalian form within taxon-specific ecological/behavioral contexts. Several of these results, as well as the consequentially derived phylogenetic hypotheses are summarized below.

***Echinops*, *Setifer*, and an Arboreal History**

Although *Echinops* and *Setifer* are difficult to distinguish from superficial characteristics, the semi-arboreal *Echinops* exhibits many postcranial features that distinguish it as a habitual climber vs. the more terrestrial *Setifer*. For example *Echinops* has a relatively long fibular malleolus, shallow astragalar trochlea with low crest, large femoral head, and rounded articular surface of the radial head. Yet *Setifer* shares several

characters with *Echinops* that are correlated with climbing, and might indicate an arboreal common ancestor between the two. This is particularly relevant to the hypothesis that *Echinops* retains several pedomorphic traits relative to *Setifer*, e.g., a reduced dentition and heterothermic thermoregulation (Harris et al., 2004). Rather than a pedomorphic *Echinops*, a series of traits in *Setifer* may be peramorphic relative to *Echinops*. The acquisition of four extra molars and homeothermy in *Setifer* may have been associated with a larger body size, transition to more terrestrial prey (see Chapter VI), and, subsequently, a wider distribution across Madagascar. Heterothermy in *Echinops* may be a retained primitive trait, as in *Geogale*, which is adaptive in the context of its dry-forest habitat in southeastern Madagascar.

Tenrecines and Oryzorictines: Posture vs. Locomotion

Details of the tenrecoid hindlimb and its tarsal complex indicate a fundamental difference in posture between the two major subfamilies Tenrecinae and Oryzorictinae, which was confirmed by observations of live animals during field study in Madagascar. The tenrecine femur and foot are more habitually laterally abducted than those of oryzorictines. The laterally displaced hindlimb in tenrecines is also more multiaxially mobile, which is reflected by features of the hip, knee, and upper ankle joints that are common in other mammalian climbers. In contrast, the oryzorictine hindlimb is positioned under the body, and more restricted to movement in the parasagittal plane. The femur is more restricted to fore-and-aft motion at the hip joint, and, as evidenced by features of the upper ankle joint, the foot is directed forward and more constrained to dorsoplantar movement.

Tenrecid Diggers: *Hemicentetes*, *Oryzorictes*, and *Microgale cowani*

The fossorial taxa *Hemicentetes* and *Oryzorictes* share many traits that correspond with those found in other mammalian diggers. For example, both have relatively mediolaterally wide distal forearms, short and wide metacarpals, elongated and narrow scapulae, and variably well-developed bicipital tunnels. However, detailed, as well as large-scale differences in form illustrate 1) more pronounced adaptations for subterranean life in *Oryzorictes*, and 2) lineage-based constraints in each, resulting in different adaptive solutions to a subterranean habitat. For example: though both genera have wide distal forearms, the distal ulna is widened in *Oryzorictes*, whereas the distal radius is wide in *Hemicentetes*; both have fused centrale bones of the wrist, but *Oryzorictes* has a fused and small lunate region, whereas the lunate in *Hemicentetes* remains unfused and very large; both have proximodistally lengthened humeral heads, but that of *Oryzorictes* is small and tightly articulating with the scapula, whereas that of *Hemicentetes* is large. *Hemicentetes* has a much more multiaxially mobile hindlimb than *Oryzorictes* or the other oryzorictines, which is particularly evident at the hip and upper ankle joints. This was confirmed by the observation of live animals in Madagascar: captive *Hemicentetes* will use its hindfoot to groom and scratch its face, upper arms, and sides, whereas the hindlimb of *Oryzorictes* is less flexible, and plays less of a role in grooming and grasping.

Although *Microgale cowani* is not recognized in the literature as a digger, it shares a series of characters with *Oryzorictes* (e.g., a long olecranon process, wide

humeral epicondyles, centrale fusion, short and wide mcIII, long and sharp claws, large cortical area of the humerus, expanded and rounded occipital region of the skull), and most likely has a more fossorial habitus than previously recorded. Alternatively, *M. cowani* may have some retained traits from an *Oryzorictes*-like ancestor, but there are no detailed non-functionally related aspects of the skeleton that support this hypothesis, nor does recent molecular phylogenetic work (Olson and Goodman, 2003).

Geogalinae

Although Dobson's (1882) Oryzorictinae included the monotypic *Geogale aurita*, most authors assign *G. aurita* to its own subfamily clade, Geogalinae. Differences between *G. aurita* and the oryzorictines have been demonstrated by dental and brain morphology, and chromosomal and nucleotide data (e.g., Butler, 1985; Rehkamper et al., 1986; Olson, 1997; Olson and Goodman, 2003). This study agrees with the subfamily status of *Geogale*, and suggests that it represents an early branching from the Malagasy tenrecid lineage. *G. aurita* has few distinctive, unique postcranial features; rather, it has characteristics that are similar to *either* the tenrecine or oryzorictine clade. It shares no distinctive features with the potamogalids, which most likely diverged from the tenrecid lineage long before geogalinids branched from the tenrecines and oryzorictines.

Tenrecoid Swimmers: *Limnogale* and *Potamogale*

Limnogale mergulus and *Potamogale velox* share a semi-aquatic habitus, yet the details of their postcrania unambiguously demonstrate that 1) they utilize different modes of aquatic locomotor behavior, and 2) *Limnogale* shares a considerable number of

characters with the other oryzorictines. *Potamogale* reportedly swims with side-to-side propulsions of its mediolaterally-flattened tail (Howell, 1970). However, the joints of the forelimb and hindlimb are highly resistant to mediolateral excursions and constrained to parasagittal motion, which suggests that *Potamogale* incurs significant loads on the hands and feet. Several features (e.g., palmar curvature of the scaphoid, deep femoral condyles, fused distal tibia and fibula, deep medial and lateral tibial malleoli, large anterior tubercle of the distal tibia,) are similar to those in high-speed cursors, which also rely on parasagittally restricted limb movement. Morphology of the limb joints indicates that *P. velox* swims with its arms and legs, in addition to mediolateral tail propulsion. A recent sighting of *Potamogale* in a branch of the Korup River at the Cameroon/Nigeria border confirmed that when swimming on the surface, *Potamogale* splashes “dog paddle fashion” with its hands and feet (Gartshore, pers. com.). *Limnogale* also most likely uses its hands and feet for aquatic propulsion, yet postcranial characters of the hip and elbow in particular indicate that its swimming style involves considerably more rotational movement of the limbs.

Tenrecidae Monophyly in Madagascar

If *Limnogale* is part of a potamogalid clade, as suggested by Asher (1999, 2000), and its semi-aquatic habitus is parsimoniously derived from a shared common ancestry, one would expect a significant overlap of postcranial characters, with both adaptive and non-adaptive significance. Yet I have found no unique features in common between *Limnogale* and *Potamogale*, and a large number of characters in common between *Limnogale* and *Microgale*, which have no clear common functional role. *Limnogale* is

most likely part of the oryzorictine clade, leaving the Malagasy Tenrecidae as an intact monophyletic taxon.

The Open Afrotherian Question

Outgroups included in this project (*Solenodon*, *Petrodromus*, and *Echinosorex*) served as useful taxa for comparison with tenrecoids, primarily as contrasts that illustrated adaptations for particular locomotor regimes. *Petrodromus* and *Potamogale* share several postcranial characters, particularly at the upper ankle joint, yet these features most likely represent responses to similar mechanical demands rather than shared close common ancestry. Several of the same features (e.g., long, anterodistally expanded medial and lateral malleoli, a large and distinctly rounded anterior tubercle of the distal tibia) are used as support for a close phylogenetic relationship between North American fossil apheliscines and macroscelidids, weakening arguments for an African origin of the afrotherian clade. Yet the striking similarity between the distal crus of the tenrecoid, *Potamogale*, and the macroscelidid, *Petrodromus*, suggests that these features are not a combination uniquely shared by apheliscines and macroscelidids. Further investigation of afrotherian monophyly and origins from a morphological perspective will depend on comparisons from a larger sample of afrotherian and eulipotyphlan taxa. Furthermore, resolution of the afrotherian question, as well as further investigation into Malagasy tenrecid origins is highly dependent upon the collection and analysis of new African and Malagasy tenrecoid fossils. This study will provide a solid foundation for phylogenetic, as well as functional interpretation of this future work.

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APPENDIX I: Specimen List (see Methods, Chapters II-VI for abbreviations)

101	<i>Echinops</i>	<i>telfairi</i>	KUNZ		156552	<i>Geogale</i>	<i>aurita</i>	FMNH
31270	<i>Echinops</i>	<i>telfairi</i>	AMNH		156553	<i>Geogale</i>	<i>aurita</i>	FMNH
42958	<i>Echinops</i>	<i>telfairi</i>	MCZ		159732	<i>Geogale</i>	<i>aurita</i>	FMNH
57579	<i>Echinops</i>	<i>telfairi</i>	MCZ		159733	<i>Geogale</i>	<i>aurita</i>	FMNH
57580	<i>Echinops</i>	<i>telfairi</i>	MCZ		161594	<i>Geogale</i>	<i>aurita</i>	FMNH
57581	<i>Echinops</i>	<i>telfairi</i>	MCZ		159495	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
124574	<i>Echinops</i>	<i>telfairi</i>	FMNH		159496	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
127274	<i>Echinops</i>	<i>telfairi</i>	FMNH		161748	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
134550	<i>Echinops</i>	<i>telfairi</i>	FMNH		161751	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
153785	<i>Echinops</i>	<i>telfairi</i>	FMNH		161755	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
156189	<i>Echinops</i>	<i>telfairi</i>	FMNH		161756	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
159728	<i>Echinops</i>	<i>telfairi</i>	FMNH		161757	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
159729	<i>Echinops</i>	<i>telfairi</i>	FMNH		161758	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
159730	<i>Echinops</i>	<i>telfairi</i>	FMNH		166131	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
161577	<i>Echinops</i>	<i>telfairi</i>	FMNH		166132	<i>Hemicentetes</i>	<i>nigriceps</i>	FMNH
170605	<i>Echinops</i>	<i>telfairi</i>	AMNH		5299	<i>Hemicentetes</i>	<i>semispinosus</i>	MCZ
170607	<i>Echinops</i>	<i>telfairi</i>	AMNH		10001	<i>Hemicentetes</i>	<i>semispinosus</i>	DARM
207717	<i>Echinops</i>	<i>telfairi</i>	AMNH		29245	<i>Hemicentetes</i>	<i>semispinosus</i>	MCZ
207718	<i>Echinops</i>	<i>telfairi</i>	AMNH		33951	<i>Hemicentetes</i>	<i>semispinosus</i>	FMNH
212918	<i>Echinops</i>	<i>telfairi</i>	AMNH		33952	<i>Hemicentetes</i>	<i>semispinosus</i>	FMNH
212919	<i>Echinops</i>	<i>telfairi</i>	AMNH		83658	<i>Hemicentetes</i>	<i>semispinosus</i>	NMNH
328620	<i>Echinops</i>	<i>telfairi</i>	NMNH		83661	<i>Hemicentetes</i>	<i>semispinosus</i>	NMNH
328636	<i>Echinops</i>	<i>telfairi</i>	NMNH		162059	<i>Hemicentetes</i>	<i>semispinosus</i>	FMNH
328637	<i>Echinops</i>	<i>telfairi</i>	NMNH		162062	<i>Hemicentetes</i>	<i>semispinosus</i>	FMNH
382620	<i>Echinops</i>	<i>telfairi</i>	NMNH		169241	<i>Hemicentetes</i>	<i>semispinosus</i>	FMNH
395835	<i>Echinops</i>	<i>telfairi</i>	NMNH		170593	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
464980	<i>Echinops</i>	<i>telfairi</i>	NMNH		206755	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
588220	<i>Echinops</i>	<i>telfairi</i>	NMNH		207712	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
145583	<i>Echinosorex</i>	<i>gymnura alba</i>	NMNH		207714	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
448860	<i>Echinosorex</i>	<i>gymnura alba</i>	NMNH		207715	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
6021	<i>Erinaceus</i>	<i>europaeus</i>	MCZ		212920	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
37807	<i>Geogale</i>	<i>aurita</i>	MCZ		212921	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
45043	<i>Geogale</i>	<i>aurita</i>	MCZ		212922	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
45450	<i>Geogale</i>	<i>aurita</i>	MCZ		212924	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
45496	<i>Geogale</i>	<i>aurita</i>	MCZ		212940	<i>Hemicentetes</i>	<i>semispinosus</i>	AMNH
46274	<i>Geogale</i>	<i>aurita</i>	MCZ		339992	<i>Hemicentetes</i>	<i>semispinosus</i>	NMNH
46286	<i>Geogale</i>	<i>aurita</i>	MCZ		354998	<i>Hemicentetes</i>	<i>semispinosus</i>	NMNH
46286	<i>Geogale</i>	<i>aurita</i>	MCZ		364954	<i>Hemicentetes</i>	<i>semispinosus</i>	NMNH

151947	<i>Geogale</i>	<i>aurita</i>	FMNH		395510	<i>Hemicentetes</i>	<i>semispinosus</i>	NMNH
156551	<i>Geogale</i>	<i>aurita</i>	FMNH		51530	<i>Hemiechinus</i>	<i>auritus</i>	MCZ
185374	<i>Hemiechinus</i>	<i>auritus</i>	AMNH		161679	<i>Microgale</i>	<i>dobsoni</i>	FMNH
45050	<i>Limnogale</i>	<i>mergulus</i>	MCZ		161718	<i>Microgale</i>	<i>dobsoni</i>	FMNH
45056	<i>Limnogale</i>	<i>mergulus</i>	MCZ		161935	<i>Microgale</i>	<i>dobsoni</i>	FMNH
100688	<i>Limnogale</i>	<i>mergulus</i>	AMNH		161940	<i>Microgale</i>	<i>dobsoni</i>	FMNH
100689	<i>Limnogale</i>	<i>mergulus</i>	AMNH		165467	<i>Microgale</i>	<i>dobsoni</i>	FMNH
100801	<i>Limnogale</i>	<i>mergulus</i>	AMNH		165468	<i>Microgale</i>	<i>dobsoni</i>	FMNH
151654	<i>Microgale</i>	<i>cowani</i>	FMNH		165774	<i>Microgale</i>	<i>dobsoni</i>	FMNH
151656	<i>Microgale</i>	<i>cowani</i>	FMNH		165775	<i>Microgale</i>	<i>dobsoni</i>	FMNH
154020	<i>Microgale</i>	<i>cowani</i>	FMNH		166107	<i>Microgale</i>	<i>dobsoni</i>	FMNH
154026	<i>Microgale</i>	<i>cowani</i>	FMNH		166108	<i>Microgale</i>	<i>dobsoni</i>	FMNH
156195	<i>Microgale</i>	<i>cowani</i>	FMNH		166198	<i>Microgale</i>	<i>dobsoni</i>	FMNH
156196	<i>Microgale</i>	<i>cowani</i>	FMNH		166200	<i>Microgale</i>	<i>dobsoni</i>	FMNH
156197	<i>Microgale</i>	<i>cowani</i>	FMNH		578749	<i>Microgale</i>	<i>dobsoni</i>	NMNH
156221	<i>Microgale</i>	<i>cowani</i>	FMNH		582730	<i>Microgale</i>	<i>dobsoni</i>	NMNH
156222	<i>Microgale</i>	<i>cowani</i>	FMNH		46017	<i>Microgale</i>	<i>drouhardi</i>	MCZ
156223	<i>Microgale</i>	<i>cowani</i>	FMNH		45040	<i>Microgale</i>	<i>talazaci</i>	MCZ
165672	<i>Microgale</i>	<i>cowani</i>	FMNH		45475	<i>Microgale</i>	<i>talazaci</i>	MCZ
165673	<i>Microgale</i>	<i>cowani</i>	FMNH		154581	<i>Microgale</i>	<i>talazaci</i>	FMNH
165674	<i>Microgale</i>	<i>cowani</i>	FMNH		154585	<i>Microgale</i>	<i>talazaci</i>	FMNH
165676	<i>Microgale</i>	<i>cowani</i>	FMNH		159692	<i>Microgale</i>	<i>talazaci</i>	FMNH
165680	<i>Microgale</i>	<i>cowani</i>	FMNH		162037	<i>Microgale</i>	<i>talazaci</i>	FMNH
165689	<i>Microgale</i>	<i>cowani</i>	FMNH		162038	<i>Microgale</i>	<i>talazaci</i>	FMNH
168017	<i>Microgale</i>	<i>cowani</i>	FMNH		162039	<i>Microgale</i>	<i>talazaci</i>	FMNH
328658	<i>Microgale</i>	<i>cowani</i>	NMNH		162040	<i>Microgale</i>	<i>talazaci</i>	FMNH
449184	<i>Microgale</i>	<i>cowani</i>	NMNH		166234	<i>Microgale</i>	<i>talazaci</i>	FMNH
449186	<i>Microgale</i>	<i>cowani</i>	NMNH		167500	<i>Microgale</i>	<i>talazaci</i>	FMNH
449187	<i>Microgale</i>	<i>cowani</i>	NMNH		167501	<i>Microgale</i>	<i>talazaci</i>	FMNH
449188	<i>Microgale</i>	<i>cowani</i>	NMNH		167502	<i>Microgale</i>	<i>talazaci</i>	FMNH
45037	<i>Microgale</i>	<i>dobsoni</i>	MCZ		167503	<i>Microgale</i>	<i>talazaci</i>	FMNH
45038	<i>Microgale</i>	<i>dobsoni</i>	MCZ		577056	<i>Microgale</i>	<i>talazaci</i>	NMNH
45661	<i>Microgale</i>	<i>dobsoni</i>	MCZ		86566	<i>Nasilio</i>	<i>brachymylncha</i>	AMNH
45736	<i>Microgale</i>	<i>dobsoni</i>	MCZ		86568	<i>Nasilio</i>	<i>brachymylncha</i>	AMNH
151624	<i>Microgale</i>	<i>dobsoni</i>	FMNH		86581	<i>Nasilio</i>	<i>brachymylncha</i>	AMNH
151625	<i>Microgale</i>	<i>dobsoni</i>	FMNH		86585	<i>Nasilio</i>	<i>brachymylncha</i>	AMNH
156224	<i>Microgale</i>	<i>dobsoni</i>	FMNH		86587	<i>Nasilio</i>	<i>brachymylncha</i>	AMNH
156225	<i>Microgale</i>	<i>dobsoni</i>	FMNH		159466	<i>Oryzomys</i>	<i>hova</i>	FMNH

159497	<i>Microgale</i>	<i>dobsoni</i>	FMNH		159695	<i>Oryzorictes</i>	<i>hova</i>	FMNH
159498	<i>Microgale</i>	<i>dobsoni</i>	FMNH		161744	<i>Oryzorictes</i>	<i>hova</i>	FMNH
159499	<i>Microgale</i>	<i>dobsoni</i>	FMNH		161745	<i>Oryzorictes</i>	<i>hova</i>	FMNH
161678	<i>Microgale</i>	<i>dobsoni</i>	FMNH		161746	<i>Oryzorictes</i>	<i>hova</i>	FMNH
162052	<i>Oryzorictes</i>	<i>hova</i>	FMNH		203337	<i>Petrodromus</i>	<i>tetradactylus</i>	AMNH
162053	<i>Oryzorictes</i>	<i>hova</i>	FMNH		203339	<i>Petrodromus</i>	<i>tetradactylus</i>	AMNH
162054	<i>Oryzorictes</i>	<i>hova</i>	FMNH		34881	<i>Potamogale</i>	<i>velox</i>	AMNH
162055	<i>Oryzorictes</i>	<i>hova</i>	FMNH		51322	<i>Potamogale</i>	<i>velox</i>	AMNH
162056	<i>Oryzorictes</i>	<i>hova</i>	FMNH		51324	<i>Potamogale</i>	<i>velox</i>	AMNH
162057	<i>Oryzorictes</i>	<i>hova</i>	FMNH		51327	<i>Potamogale</i>	<i>velox</i>	AMNH
162058	<i>Oryzorictes</i>	<i>hova</i>	FMNH		51333	<i>Potamogale</i>	<i>velox</i>	AMNH
165490	<i>Oryzorictes</i>	<i>hova</i>	FMNH		51334	<i>Potamogale</i>	<i>velox</i>	AMNH
165491	<i>Oryzorictes</i>	<i>hova</i>	FMNH		51339	<i>Potamogale</i>	<i>velox</i>	AMNH
165492	<i>Oryzorictes</i>	<i>hova</i>	FMNH		51344	<i>Potamogale</i>	<i>velox</i>	AMNH
165705	<i>Oryzorictes</i>	<i>hova</i>	FMNH		55204	<i>Potamogale</i>	<i>velox</i>	AMNH
166157	<i>Oryzorictes</i>	<i>hova</i>	FMNH		124327	<i>Potamogale</i>	<i>velox</i>	NMNH
166208	<i>Oryzorictes</i>	<i>hova</i>	FMNH		266897	<i>Potamogale</i>	<i>velox</i>	NMNH
166237	<i>Oryzorictes</i>	<i>hova</i>	FMNH		537651	<i>Potamogale</i>	<i>velox</i>	NMNH
166238	<i>Oryzorictes</i>	<i>hova</i>	FMNH		35321	<i>Potamogale</i>	<i>velox</i>	MCZ
166239	<i>Oryzorictes</i>	<i>hova</i>	FMNH		5112	<i>Setifer</i>	<i>setosus</i>	MCZ
166240	<i>Oryzorictes</i>	<i>hova</i>	FMNH		33948	<i>Setifer</i>	<i>setosus</i>	FMNH
167480	<i>Oryzorictes</i>	<i>hova</i>	FMNH		42957	<i>Setifer</i>	<i>setosus</i>	MCZ
167481	<i>Oryzorictes</i>	<i>hova</i>	FMNH		42959	<i>Setifer</i>	<i>setosus</i>	MCZ
167482	<i>Oryzorictes</i>	<i>hova</i>	FMNH		85170	<i>Setifer</i>	<i>setosus</i>	FMNH
169240	<i>Oryzorictes</i>	<i>hova</i>	FMNH		85513	<i>Setifer</i>	<i>setosus</i>	FMNH
577052	<i>Oryzorictes</i>	<i>hova</i>	NMNH		124554	<i>Setifer</i>	<i>setosus</i>	FMNH
578789	<i>Oryzorictes</i>	<i>sp?</i>	NMNH		151936	<i>Setifer</i>	<i>setosus</i>	FMNH
156601	<i>Oryzorictes</i>	<i>talpoides</i>	FMNH		154033	<i>Setifer</i>	<i>setosus</i>	FMNH
156602	<i>Oryzorictes</i>	<i>talpoides</i>	FMNH		154034	<i>Setifer</i>	<i>setosus</i>	FMNH
156603	<i>Oryzorictes</i>	<i>talpoides</i>	FMNH		159731	<i>Setifer</i>	<i>setosus</i>	FMNH
5639	<i>Oryzorictes</i>	<i>tetradactylus</i>	FMNH		165494	<i>Setifer</i>	<i>setosus</i>	FMNH
12430	<i>Oryzorictes</i>	<i>tetradactylus</i>	MCZ		166159	<i>Setifer</i>	<i>setosus</i>	FMNH
31243	<i>Oryzorictes</i>	<i>tetradactylus</i>	AMNH		169242	<i>Setifer</i>	<i>setosus</i>	FMNH
31257	<i>Oryzorictes</i>	<i>tetradactylus</i>	AMNH		170532	<i>Setifer</i>	<i>setosus</i>	AMNH
45018	<i>Oryzorictes</i>	<i>tetradactylus</i>	MCZ		170548	<i>Setifer</i>	<i>setosus</i>	AMNH
45018	<i>Oryzorictes</i>	<i>tetradactylus</i>	MCZ		170581	<i>Setifer</i>	<i>setosus</i>	AMNH
45021	<i>Oryzorictes</i>	<i>tetradactylus</i>	MCZ		170730	<i>Setifer</i>	<i>setosus</i>	FMNH
45022	<i>Oryzorictes</i>	<i>tetradactylus</i>	MCZ		170731	<i>Setifer</i>	<i>setosus</i>	FMNH

156226	<i>Oryzorictes</i>	<i>tetradactylus</i>	FMNH		578792	<i>Tenrec</i>	<i>ecaudatus</i>	NMNH
169239	<i>Oryzorictes</i>	<i>tetradactylus</i>	FMNH		207076	<i>Setifer</i>	<i>setosus</i>	AMNH
150415	<i>Petrodromus</i>	<i>tetradactylus</i>	AMNH		317872	<i>Setifer</i>	<i>setosus</i>	NMNH
203332	<i>Petrodromus</i>	<i>tetradactylus</i>	AMNH		328612	<i>Setifer</i>	<i>setosus</i>	NMNH
203335	<i>Petrodromus</i>	<i>tetradactylus</i>	AMNH		395513	<i>Setifer</i>	<i>setosus</i>	NMNH
203336	<i>Petrodromus</i>	<i>tetradactylus</i>	AMNH		395719	<i>Setifer</i>	<i>setosus</i>	NMNH
578790	<i>Setifer</i>	<i>setosus</i>	NMNH		541443	<i>Setifer</i>	<i>setosus</i>	NMNH
49508	<i>Solenodon</i>	<i>cubanus</i>	NMNH					
34859	<i>Solenodon</i>	<i>paradoxus</i>	MCZ					
51068	<i>Solenodon</i>	<i>paradoxus</i>	FMNH					
57320	<i>Solenodon</i>	<i>paradoxus</i>	FMNH					
72809	<i>Solenodon</i>	<i>paradoxus</i>	FMNH					
89448	<i>Solenodon</i>	<i>paradoxus</i>	FMNH					
172680	<i>Solenodon</i>	<i>paradoxus</i>	NMNH					
172745	<i>Solenodon</i>	<i>paradoxus</i>	NMNH					
217256	<i>Solenodon</i>	<i>paradoxus</i>	NMNH					
238263	<i>Solenodon</i>	<i>paradoxus</i>	NMNH					
290520	<i>Solenodon</i>	<i>paradoxus</i>	NMNH					
395697	<i>Solenodon</i>	<i>paradoxus</i>	NMNH					
395819	<i>Solenodon</i>	<i>paradoxus</i>	NMNH					
396963	<i>Solenodon</i>	<i>paradoxus</i>	NMNH					
3301	<i>Tenrec</i>	<i>ecaudatus</i>	NMNH					
16364	<i>Tenrec</i>	<i>ecaudatus</i>	MCZ					
30398	<i>Tenrec</i>	<i>ecaudatus</i>	AMNH					
44967	<i>Tenrec</i>	<i>ecaudatus</i>	MCZ					
59011	<i>Tenrec</i>	<i>ecaudatus</i>	FMNH					
60587	<i>Tenrec</i>	<i>ecaudatus</i>	FMNH					
63313	<i>Tenrec</i>	<i>ecaudatus</i>	NMNH					
154628	<i>Tenrec</i>	<i>ecaudatus</i>	FMNH					
154629	<i>Tenrec</i>	<i>ecaudatus</i>	FMNH					
156337	<i>Tenrec</i>	<i>ecaudatus</i>	FMNH					
166047	<i>Tenrec</i>	<i>ecaudatus</i>	FMNH					
167980	<i>Tenrec</i>	<i>ecaudatus</i>	FMNH					
170511	<i>Tenrec</i>	<i>ecaudatus</i>	AMNH					
174727	<i>Tenrec</i>	<i>ecaudatus</i>	NMNH					
361485	<i>Tenrec</i>	<i>ecaudatus</i>	NMNH					
364955	<i>Tenrec</i>	<i>ecaudatus</i>	NMNH					
577051	<i>Tenrec</i>	<i>ecaudatus</i>	NMNH					

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