4. Evolutionary Morphology of the Tenrecoidea (Mammalia) Forelimb Skeleton

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4.1 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 interpreting the 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, 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). Studies of proportional differences and details of the shoulder and elbow joints in cursorial mammals have identified a suite of characteristics associated with lengthening the stride and stabilizing joints in the parasagittal plane for high-speed locomotion (e.g., Hopwood, 1947; Smith and Savage, 1956; Taylor, 1974; Hildebrand, 1995). There has been less published work on the functional morphology of aquatic mammals (but 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. The following questions are addressed:

(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 among members of the 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?

4.1.1 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

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E.J. Sargis and M. Dagosto (eds.), *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay,* 51–71.

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. Particular characters of form are, therefore, briefly defined and discussed, especially those that are often identified and described in the literature discussed here. Some aspects of their variability are also illustrated (for this section, refer to Table 4.1 for proposed locomotor correlates of form). Functional and phylogenetic interpretation of these characters in relation to taxon differences are addressed further in the Results/Discussion section.

Overall scapular shape varies considerably among mammals. At one end of the spectrum of form there is a triangular scapula, as in humans, with an 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 (Figure 4.1; see Argot, 2001, for scapular morphotypes in metatherians). Differences in form are attributed to various attachments of muscles that protract, retract, and rotate the scapula and humerus, stabilize the shoulder joint, and anchor the scapula, yet there

TABLE 4.1. Aspects of the mammalian forelimb with proposed relationship to locomotor behavior.

	Climber	Digger	Terrestrial/runner	Leaper	Swimmer
SCAPULA					
Scapula shape[3,8, 13]	Short and broad	Elongated	Long and narrow		
Scapula 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, distally extended	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[10,13]	Well-separated from capitulum		Continuous with capitulum		
Trochlea [13,19,20]	Mediolaterally wide, shallow		Mediolaterally narrow, deep		
Coronoid fossa [10]			Deep		
Olecranon fossa[10,21]	Shallow		Deep		
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]	Curved anteriorly		Straight or curved posteriorly		
Trochlear 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 (1947)

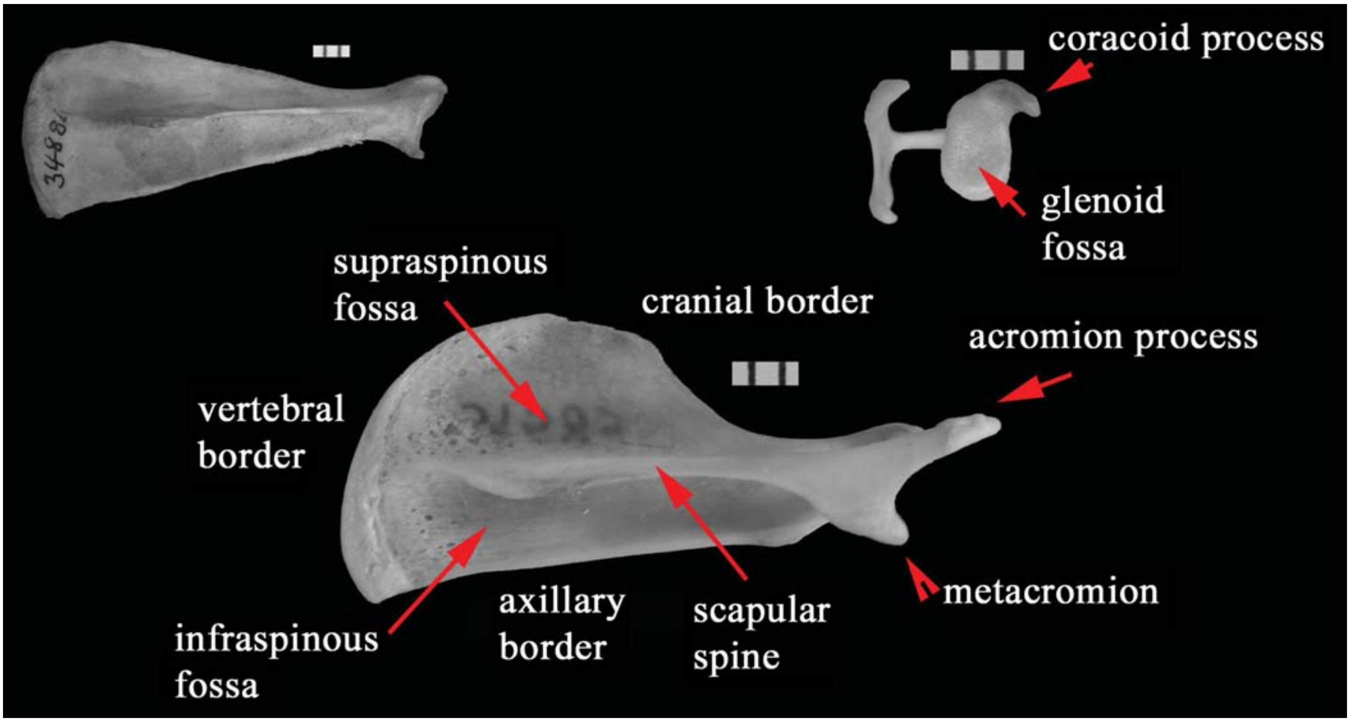

FIGURE 4.1. Right scapulae of *Potamogale* and *Echinops*. Lateral view of *Potamogale* (top left), demonstrating a greatly attenuated triangular form and no articular processes. Lateral view of *Echinops* (center), which is more rectangular, somewhat circular cranially, with distinct acromion, metacromion, and coracoid processes. Articular surface of scapula of same *Echinops* specimen (top right). Subdivisions on scale are 1.0 mm.

are also differences in the position of the scapula against the lateral ribcage resulting in a variety of 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 M. teres major and scapular head of the M. triceps brachii (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 (Figure 4.1). 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 (Figure 4.1).

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 golden mole (Figure 4.2). Relative differences in length and width are generally ascribed to differences in functional mechanics of the musculoskeletal lever system; a relatively short humerus is related to increased force of the muscles originating on the scapula, and a longer humerus contributes to 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 medial rotator and adductor of the humerus, and is also discussed in terms of its length and robusticity. The position of the greater and lesser tuberosities might also be of functional relevance; more anteriorly positioned tuberosities result in increased, uninterrupted surface area along the proximal surface of the humeral head, and may be related to rotational facilitation (Figure 4.2). The bicipital groove (or tunnel in some cases), positioned anteriorly between the two tuberosities, transmits a tendon of the M. biceps brachii, and its development might be correlated with powerful forelimb flexion (Figure 4.2).

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 (Figure 4.2). 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. Deep or perforated coronoid and/or olecranon fossae are 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 (Figure 4.2). Differences in mediolateral widths of each sug-

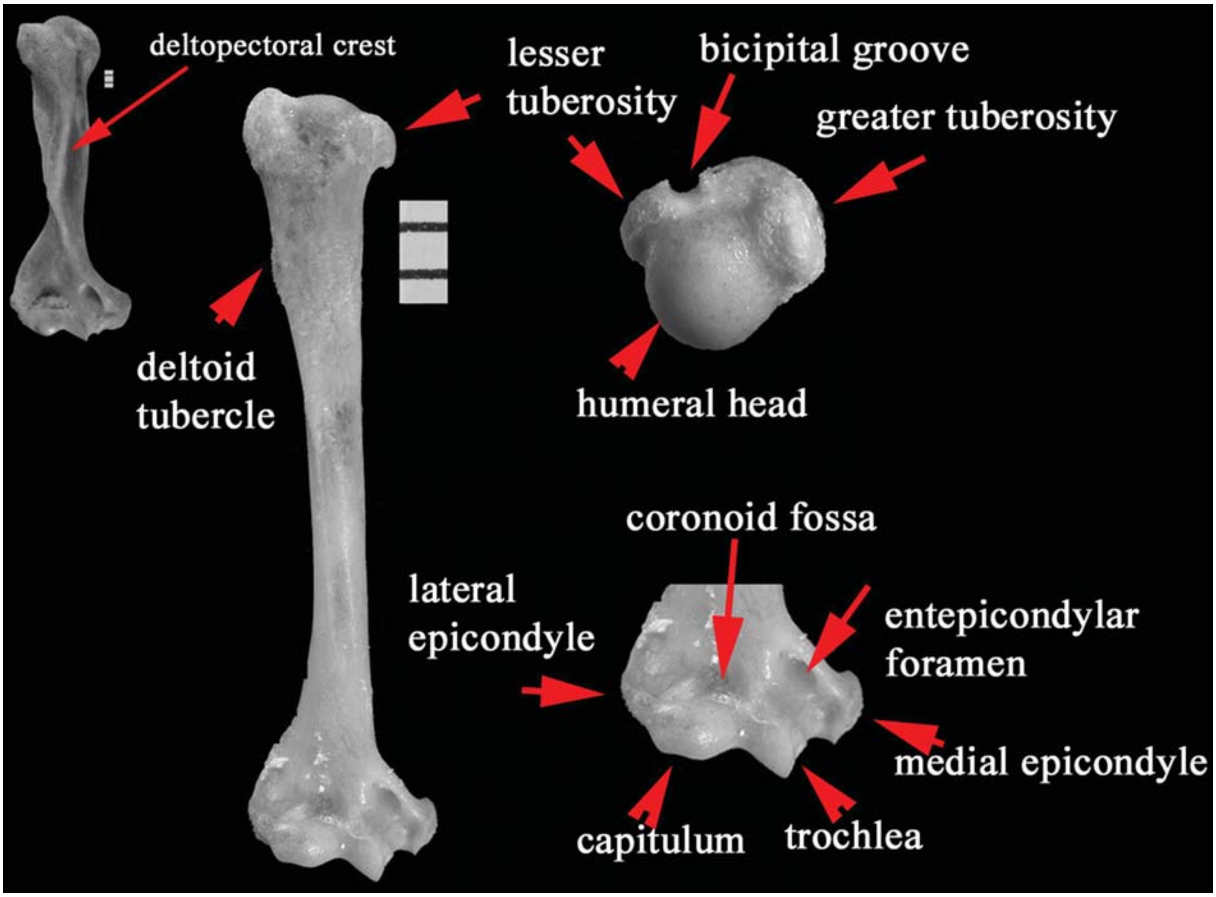

FIGURE 4.2. Right humeri of *Solenodon* and *Microgale*. Anterior view of *Solenodon* (top left), demonstrating a humerus with pronounced crests and processes, including a deltopectoral crest, and wider shaft. Anterior view of whole humerus (center left) and views of proximal humerus (upper right) and distal humerus (lower right) of *Microgale dobsoni*. Subdivisions on scale are 1.0 mm.

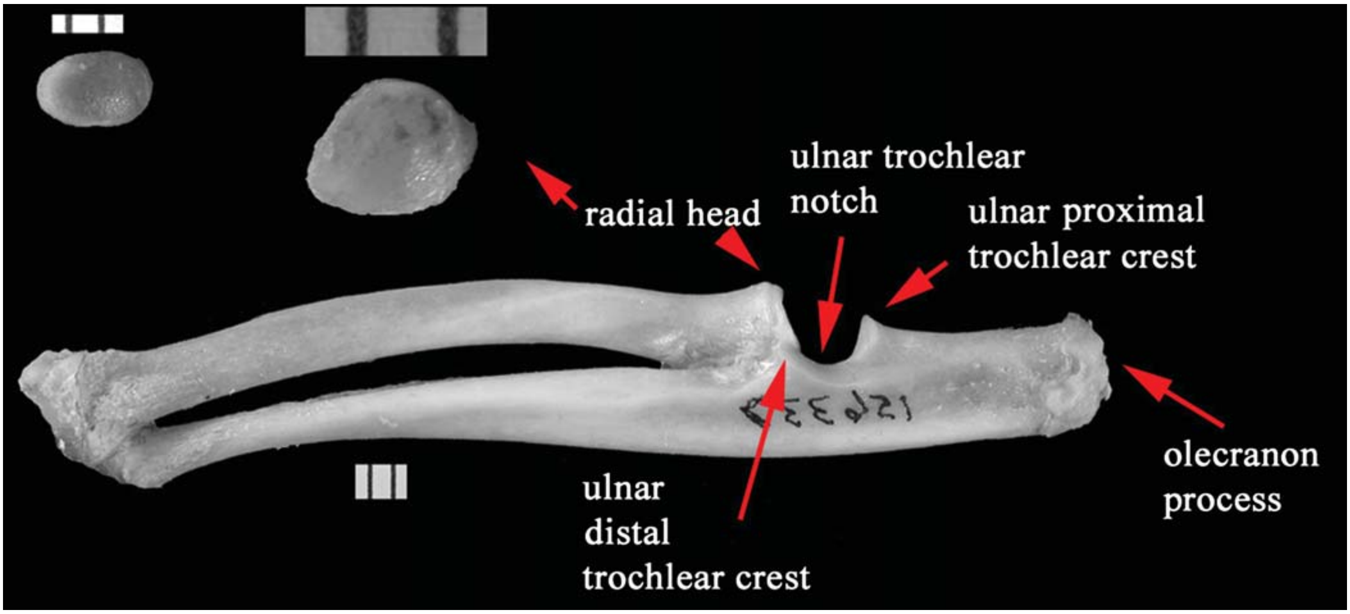

FIGURE 4.3. Right radii and ulna of *Setifer, Limnogale*, and *Tenrec*. Proximal view of *Setifer* radius (top left), illustrating mediolaterally elliptical radial head, proximal view of *Limnogale* radius (middle top), demonstrating a rounded head, and medial view of *Tenrec* antebrachium (bottom). Subdivisions on scale are 1.0 mm.

gest how much body weight is distributed on one side of the humerus relative to the other. Capitulum shape is correlated with movement of the radius on the humerus, and a more spherical shape is generally indicative of multiaxial movement, whereas a trochleated capitulum is correlated to varying degrees with fast flexion/extension of the ulna that requires lateral bracing.

The olecranon process of the ulna is the attachment site for the M. triceps brachii, which is the primary forearm extensor (Figure 4.3). 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 humerus length 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 (Figure 4.3). All of these characteristics are considered in tenrecoids below.

4.2 Materials and Methods

The scapula, humerus, radius, and ulna of 12 tenrecoids and 3 outgroups were studied and digitally photographed (Nikon Coolpix 995) in several standardized views. Skeletal specimens were examined at the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Harvard University 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 (DARM), Germany (see Salton, 2005, 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 millimeter ruler. Linear measurements were then calculated from specific coordinates (Salton, 2005). 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 three complete specimens, and there were no significant differences ($P < 0.05$) between caliper and digital values.

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* (Table 4.2). The following species were included as outgroups for comparison with tenrecoids (orders according to Springer et al., 2004): *Solenodon paradoxus* (Eulipotyphla), *Petrodromus tetradactylus* (Macroscelidea), and *Echinosorex gymnurus* (Eulipotyphla). These taxa were chosen because tenrecoids have traditionally been included in Lipotyphla, but have more recently been allied with other African mammals in Afrotheria (Springer et al., 2004; for further discussion of outgroup choices see Salton and Szalay, 2004; Salton, 2005; Salton and Sargis, 2008).

TABLE 4.2. Taxonomy and primary locomotor behavior of study taxa.

Family/subfamily	Genus	Species	n	Locomotor Behavior
Tenrecidae/Tenrecinae	*Echinops*	*telfairi*	13	Arboreal/terrestrial
Tenrecidae/Tenrecinae	*Hemicentetes*	*semispinosus*	18	Terrestrial/fossorial
Tenrecidae/Tenrecinae	*Setifer*	*setosus*	19	Terrestrial
Tenrecidae/Tenrecinae	*Tenrec*	*ecaudatus*	14	Terrestrial
Tenrecidae/Oryzorictinae	*Limnogale*	*mergulus*	5	Aquatic/terrestrial
Tenrecidae/Oryzorictinae	*Microgale*	*cowani*	22	Terrestrial
Tenrecidae/Oryzorictinae	*Microgale*	*dobsoni*	21	Terrestrial
Tenrecidae/Oryzorictinae	*Microgale*	*talazaci*	13	Terrestrial
Tenrecidae/Oryzorictinae	*Oryzorictes*	*tetradactylus/hova*	35	Fossorial/terrestrial
Tenrecidae/Geogalinae	*Geogale*	*aurita*	4	Terrestrial
Potamogalidae	*Potamogale*	*velox*	3	Aquatic/terrestrial
Macroscelididae	*Petrodromus*	*tetradactylus*	3	Terrestrial/saltatory
Solenodontidae	*Solenodon*	*paradoxus*	10	Terrestrial/fossorial
Erinaceidae	*Echinosorex*	*gymnurus*	1	Terrestrial

TABLE 4.3. Indices.

APLI	Acromion Process Length Index = length of scapula from distal end to tip of acromion process/length of scapula to base of glenoid fossa
GFSI	Glenoid Fossa Shape Index = Glenoid fossa dorsoventral length/mediolateral width
HHSI	Humeral Head Shape Index = Humeral head length/width
HRLI	Humerus/Radius Length Index (Brachial Index) = Humerus length/radius length
HSI	Humerus Shape Index = Humerus width/length
MEWI	Medial Epicondyle Width Index = Medial epicondyle width/trochlear width (distal view)
OPLI	Olecranon Process Length Index = Olecranon process length/ulna length
RSI	Radius Shape Index = Radius depth/length
SSI	Scapula Shape Index = Scapula width/length
USI	Ulna Shape Index = Ulna depth/length

In order to control for size differences between species, linear measurements (see Salton, 2005) were transformed into ten indices (Table 4.3). Statistical analyses were performed using STATISTICA (Version 6.0, StatSoft Inc., Tulsa, OK). Indices were each compared between species using one-way ANOVA and the Tukey honest significant difference (HSD) post hoc test ($P < 0.05$). All ANOVA tables are in Salton (2005).

4.3 Results and Discussion

4.3.1 Scapula

There are no subfamily-level differences in the Scapular Shape Index (SSI) between the tenrecines and oryzorictines due to the considerable variation within Oryzorictinae and their overlapping ranges with Tenrecinae (Table 4.4). 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). *Microgale cowani* has a significantly longer and narrower scapula than *M. dobsoni* (Figure 4.4, Table 4.4; $P < 0.05$). 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 (Figure 4.4), significantly more so than in any of the other study taxa (Table 4.4; $P < 0.05$), and similar in form to subterranean talpids.

The swimmers *Limnogale* and *Potamogale* do not have similar scapular morphology (Figure 4.4), yet they both have long and narrow scapulae relative to the other tenrecoids (except *Oryzorictes*), which suggests considerable retraction-based loading during aquatic propulsion. Although the supraspinous fossa is well-developed in leaping marsupials (Argot, 2001), the supraspinous fossa in the elephant shrew *Petrodromus* is not remarkable (Figure 4.4). Rather, its infraspinous fossa is deep and expanded at the caudal vertebral border, highlighting the importance of the M. teres major in powerful forelimb retraction. Unlike *Hemicentetes* and *Tenrec, Echinops* and *Setifer* have a relatively flat (vs. angled) axillary border and steeply rising cranial border, resulting in an enlarged, broad supraspinous fossa (Figure 4.4). 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; Taylor, 1978; Roberts and Davidson, 1975; Argot, 2001; Vasquez-Molinero et al., 2001).

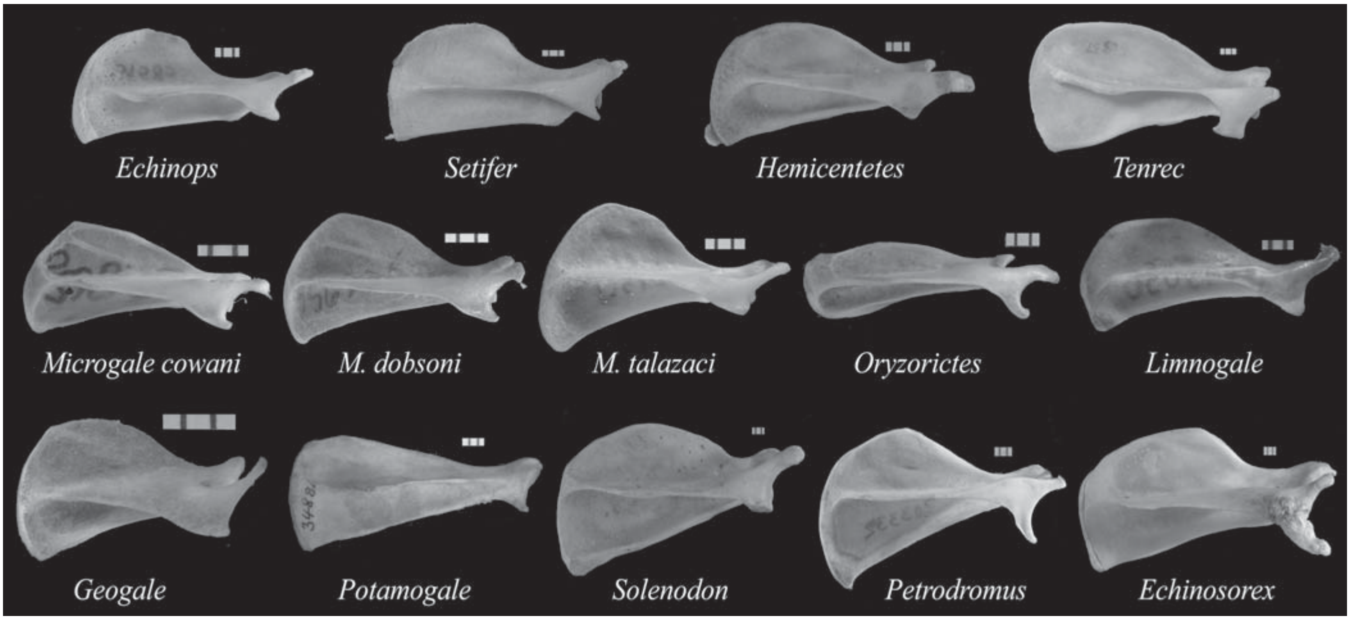

FIGURE 4.4. Lateral view of right scapulae scaled to length in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa (bottom right). Note differences in the relative length and width of the whole scapula, angle of the axillary border, breadth of the vertebral border, depth of the supraspinous and infraspinous fossae, and shape of the acromion and metacromion processes. Subdivisions on scale are 1.0 mm.

Within the Tenrecinae, the acromion process reaches ventrally well beyond the glenoid fossa in *Echinops* and *Hemicentetes*, whereas that in *Tenrec* and *Setifer* is less ventrally extended (Figures 4.4, 4.5). Though there is considerable intraspecific variation for the Acromion Process Length Index (APLI), the trend of a longer acromion in a climber and a digger is consistent with data from rodents and marsupials (Stein, 2000; Argot, 2001). *Oryzorictes* has a significantly longer acromion process than *Setifer, Tenrec*, and *Microgale* (Figures 4.4, 4.5, Table 4.4; $P < 0.05$). *Limnogale* is unlike *Potamogale*, which lacks an acromion process almost altogether (Figures 4.4, 4.5; 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 *Oryzorictes* and xenarthrans (Smith and Savage, 1956), or more from the forearm, as in *Talpa* and erinaceids.

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* (Figure 4.4), 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 extends back (posteriorly along the long axis of the scapula) and forms a wide, thin sheet of bone confluent with the scapular spine (Figure 4.4). It is unclear which of the attached muscles is most influencing this form, but given the lack of rotational arm movement in *Geogale* (JAS 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 Tenrecinae, the shape of the glenoid fossa in *Hemicentetes* is distinctive in its high, narrow, almost rectangular shape (Figure 4.6), which is consistent with glenoid fossa shape in other mammalian diggers (Reed, 1951; Stein, 2000). *Limnogale* has a significantly narrower glenoid fossa than in any other tenrecoid (Figure 4.6, Table 4.4; $P < 0.05$), 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 4.6).

TABLE 4.4. Index summary statistics*

Taxon		SSI	APLI	GFSI	HSI	HRLI	HHSI	MEWI	USI	OPLI	RSI
Echinops telfairi	Mean	0.47	1.17	1.45	10.46	1.12	1.02	1.07	0.079	0.17	0.10
	SD	0.05	0.04	0.16	0.95	0.12	0.06	0.16	0.008	0.02	0.01
	n	13	10	13	13	12	13	12	11	11	12
Setifer setosus	Mean	0.50	1.07	1.48	11.01	1.09	1.10	0.95	0.083	0.16	0.11
	SD	0.04	0.28	0.11	0.82	0.05	0.08	0.12	0.006	0.01	0.01
	n	19	17	18	19	15	19	19	17	17	16
Hemicentetes semispinosus	Mean	0.44	1.20	1.60	**7.66**	1.11	**1.24**	**1.38**	**0.094**	**0.22**	**0.13**
	SD	0.02	0.02	0.15	0.45	0.11	0.10	0.21	0.009	0.01	0.01
	n	16	12	15	18	14	17	18	16	16	15
Tenrec ecaudatus	Mean	0.47	1.09	1.54	10.52	1.19	1.10	1.17	**0.091**	**0.23**	**0.13**
	SD	0.03	0.01	0.18	0.85	0.11	0.09	0.12	0.007	0.01	0.01
	n	11	10	11	12	8	12	12	13	14	9
Microgale cowani	Mean	0.41	1.15	1.52	13.06	0.97	1.05	1.14	0.069	0.16	0.08
	SD	0.04	0.02	0.13	0.78	0.08	0.10	0.14	0.005	0.01	0.02
	n	20	18	19	22	14	22	22	12	13	14
Microgale dobsoni	Mean	0.53	1.14	1.57	13.04	0.97	1.10	0.92	0.063	0.12	0.08
	SD	0.29	0.02	0.11	3.89	0.11	0.05	0.10	0.007	0.01	0.01
	n	21	21	18	21	10	20	21	10	10	10
Microgale talazaci	Mean	0.51	1.14	1.58	14.33	0.93	1.09	1.01	0.065	0.12	0.08
	SD	0.05	0.02	0.10	0.78	0.02	0.07	0.11	0.003	0.01	0.004
	n	13	10	11	12	8	12	12	8	8	8
Oryzorictes sp.	Mean	**0.31**	**1.26**	1.59	**7.83**	1.10	**1.40**	**1.49**	**0.094**	**0.27**	**0.15**
	SD	0.03	0.03	0.17	0.49	0.12	0.13	0.18	0.006	0.03	0.01
	n	35	31	30	34	7	34	34	10	10	7
Limnogale mergulus	Mean	0.36	1.21	**1.88**	12.34	0.94	1.08	1.03	0.077	0.17	0.10
	SD	0.02	0.08	0.33	0.58		0.11	0.05			
	n	5	3	5	5	1	5	5	1	1	1
Geogale aurita	Mean				13.59	1.09	1.00	0.83	0.069	0.13	0.09
	SD				1.88		0.08	0.08			
	n				4	1	4	4	1	1	1
Potamogale velox	Mean				14.75	**1.32**	0.96	**0.58**	**0.093**	0.19	**0.13**
	SD				1.36	0.05	0.03	0.17	0.006	0.01	0.01
	n				3	3	3	2	3	3	3
Solenodon paradoxus	Mean				**9.33**	1.09	**1.15**	**1.26**	**0.099**	0.19	**0.14**
	SD				0.95	0.03	0.08	0.10	0.008	0.02	0.01
	n				10	7	10	10	10	10	7
Petrodromus tetradactylus	Mean				13.74	**0.72**	0.89	**0.56**	**0.044**	0.11	0.05
	SD				0.82		0.04	0.004	0.002	0.01	0.003
	n				2	1	2	2	3	3	3
Echinosorex gymnurus					11.49	1.29	0.93	0.75	0.072	0.19	0.10
	n				1	1	1	1	1	1	1

*See Table 4.3 for index descriptions; values in bold are discussed in the text

4.3.2 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 humeri of *Hemicentetes, Oryzorictes*, and *Solenodon* are significantly wider at midshaft than those of the other study taxa (Figure 4.7, Table 4.4; $P < 0.05$). With the exception of *Oryzorictes*, the oryzorictines have longer, thinner humeri than the tenrecines (Figure 4.7). Despite other traits that correlate with digging in the *M. cowani* postcranium, its humeral shape as defined by the Humeral Shape Index (HSI) is within the range of the other *Microgale* species (Table 4.4).

There are no significant differences among 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 (Table 4.4). 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 (Table 4.4). The swimmer *Potamogale* and the saltatory *Petrodromus* represent two ends of a spectrum; *Potamogale* has an extremely long humerus relative to the radius, whereas *Petrodromus* has a low brachial index (Table 4.4). 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 hind limb) thrust. *Petrodromus* most likely concentrates muscle mass at the proximal end

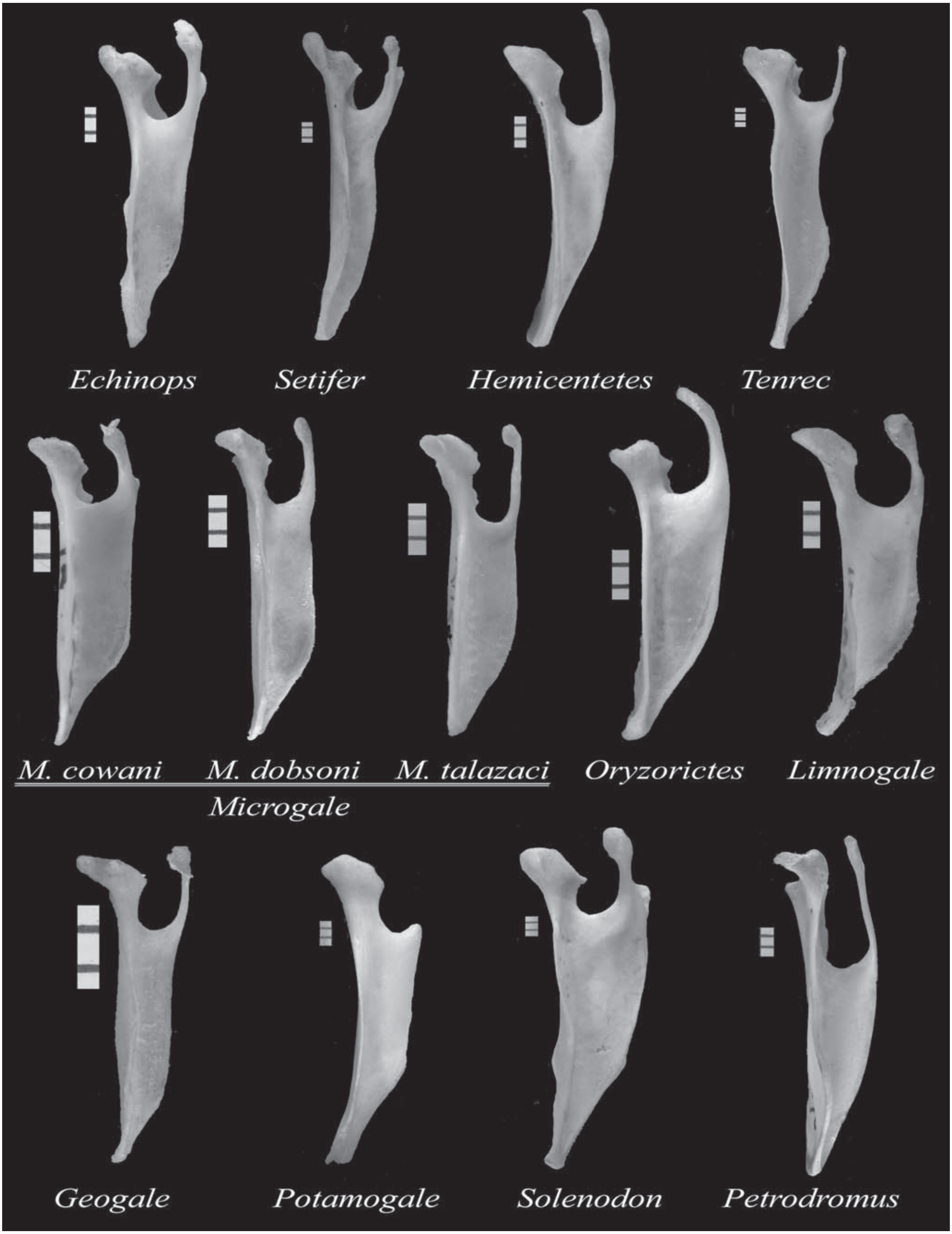

FIGURE 4.5. Dorsal view of right scapulae scaled to length in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and two outgroup taxa (bottom right). Note length of the acromion process, which is longer in the diggers. Subdivisions on scale are 1.0 mm.

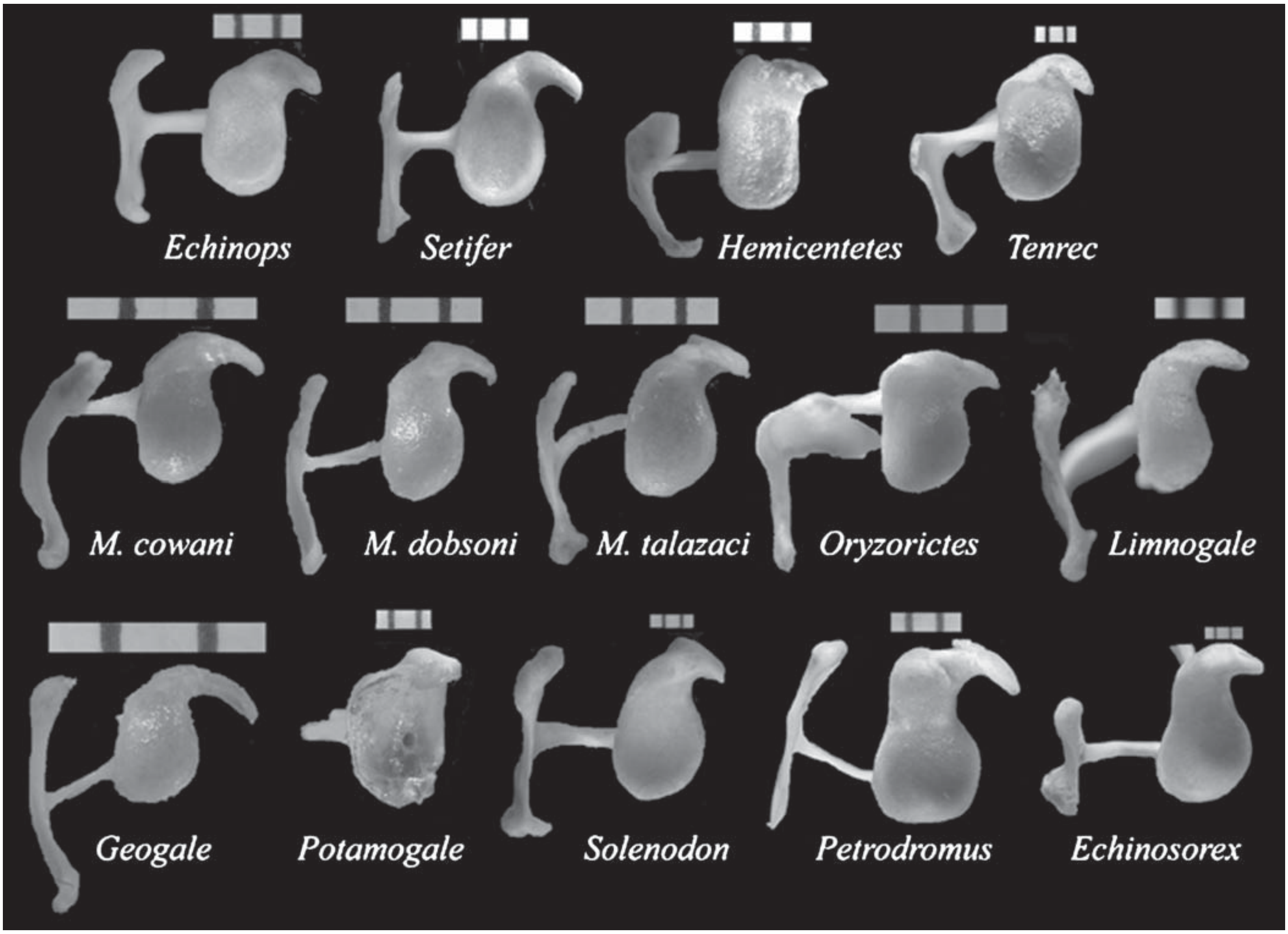

FIGURE 4.6. Articular surface of right scapulae scaled to height in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa (bottom right). Note the shape of the glenoid fossa, ranging from rectangular in *Hemicentetes* to spherical in *Petrodromus*. Subdivisions on scale are 1.0 mm.

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*).

Humeral head shape (HHSI) varies with locomotor behavior in the Tenrecinae. The digging *Hemicentetes* has a significantly (anteroposteriorly) longer head than the other tenrecines (Table 4.4; $P < 0.05$), whereas the climber *Echinops* has a more rounded humeral head (Figure 4.8). 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 (Figure 4.8, Table 4.4), and *Oryzorictes*, like *Hemicentetes*, has a significantly higher HHSI than the other tenrecoids (Table 4.4; $P < 0.05$).

A well-formed bicipital groove is likely correlated with the size of the tendon of the M. biceps brachii that passes through it, and may be indicative of powerful flexion associated with climbing (Taylor, 1974; 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 (Figure 4.9), 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.

Tenrec has a larger greater tuberosity (in terms of mediolateral width and anteroposterior length) than the other tenrecines (Figure 4.8; Salton, 2005), which might indicate

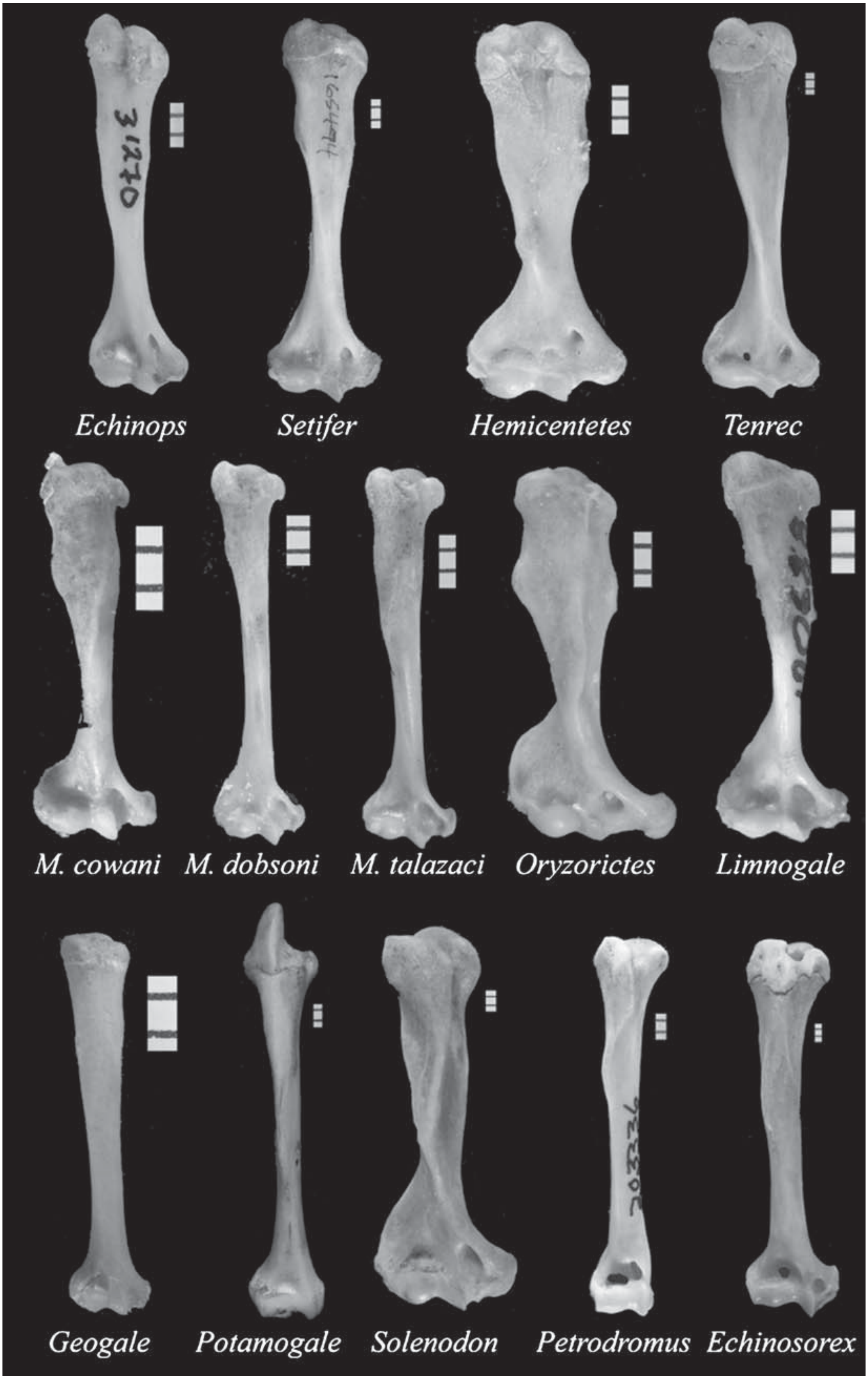

FIGURE 4.7. Anterior view of right humeri scaled to height in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa (bottom right). Note differences in relative midshaft width, greater and lesser tuberosity height, distal humerus width, epicondyle widths, trochlea and capitulum shape, presence/absence of entepicondylar foramen and coronoid fossa, and deltoid tuberosity/deltopectoral crest shape. Subdivisions on scale are 1.0 mm.

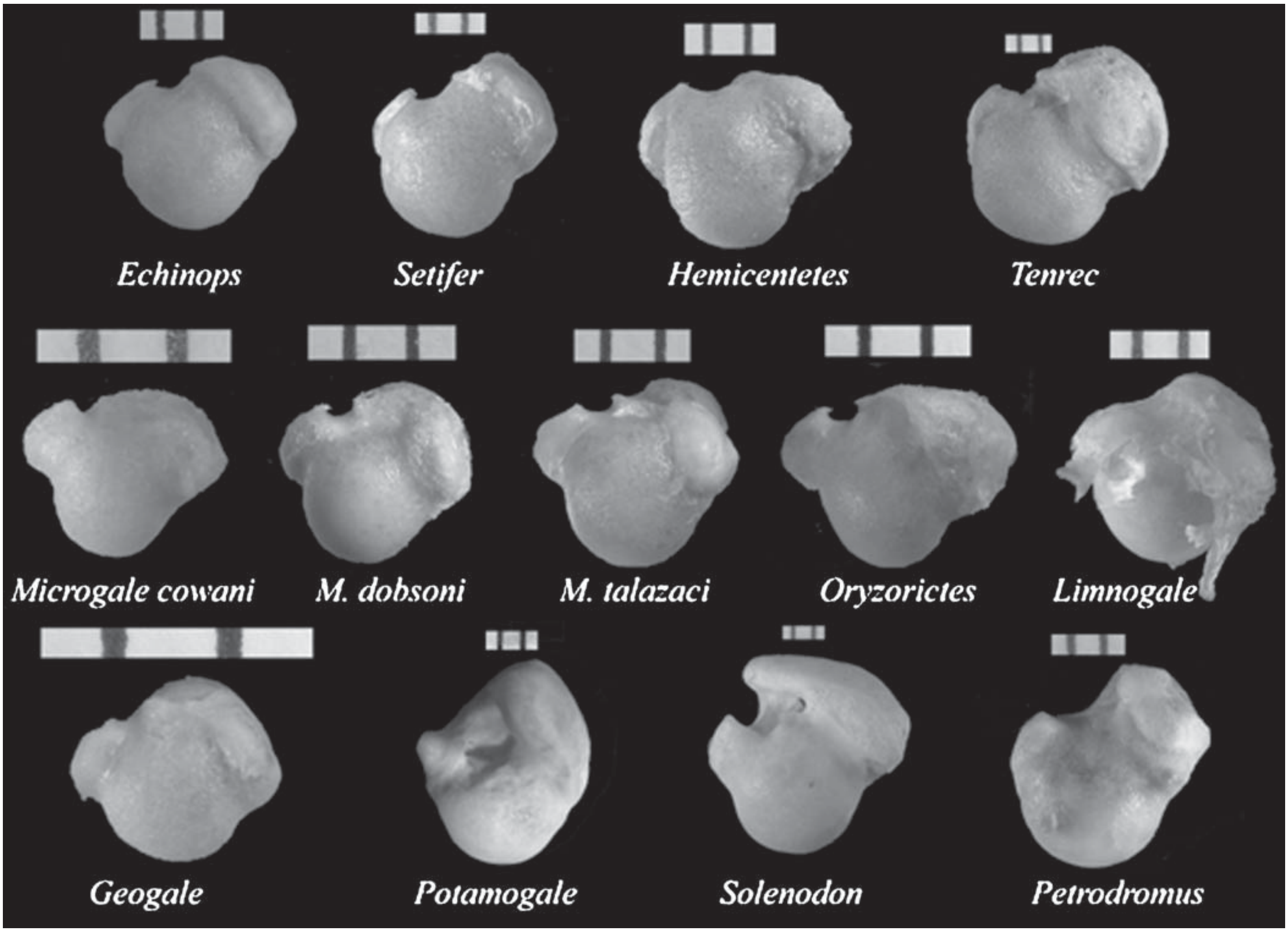

FIGURE 4.8. Proximal articular surfaces of the right humeri of tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and two outgroup taxa (bottom right). Note differences in greater and lesser tuberosity size and presence/absence of a bicipital groove. Subdivisions on scale are 1.0 mm.

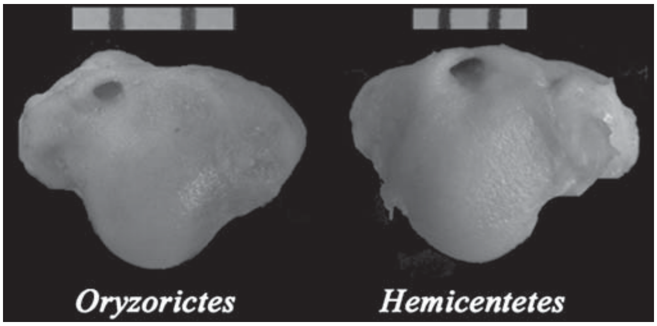

FIGURE 4.9. Proximal articular surfaces of right humeri in two digging tenrecoids, illustrating the formation of a complete bicipital tunnel. Most specimens from each of these two genera have a bicipital groove; only a few have a completely formed tunnel. Subdivisions on scale are 1.0 mm.

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 4.1). 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, so the relative size of the greater tuberosity may correlate with restriction of shoulder mobility (Roberts and Davidson, 1975; Argot, 2001; Sargis, 2002). Among the oryzorictines, *Oryzorictes* has a larger greater tuberosity (Figure 4.8; Salton, 2005), 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 (Figure 4.8). The greater tuberosity in *Potamogale* is remarkable compared to that of the tenrecids and highly unusual for any mammal (Figures 4.7, 4.8), although it is somewhat similar to the condition found 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* may serve as a protective lock against the scapula and help to prevent overextension of the forelimb during swimming.

The digger *Hemicentetes* has a broad lesser tuberosity relative to other tenrecines, and *Tenrec* has a smaller lesser tuberosity (Figure 4.8; Salton, 2005). 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 forelimb 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 the other study taxa (−0.87 for tenrecines, −0.70 for all study taxa; Salton, 2005). Like *Tenrec, Potamogale* has a diminutive lesser tuberosity (Figure 4.8), which, when coupled with the large greater tuberosity, suggests an armstroke that is limited to one major directional plane (as in forward and backward paddling). The other semiaquatic taxon, *Limnogale*, has a relatively large lesser tuberosity (Figure 4.7), as in *Oryzorictes*, suggesting more rotational arm movement during swimming. This is consistent with tarsal and hind limb morphology, which suggests more varied limb movements in *Limnogale* compared to more restricted and powerful swimming strokes in *Potamogale* (Salton and Szalay, 2004; Salton, 2005).

Interpretation of the deltopectoral region of the humerus is difficult, due to the interplay between 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 (Figure 4.7). Among the oryzorictines, *Microgale cowani* and *Oryzorictes* have noticeable anterior pectoral crests and lateral deltoid tubercles, whereas *M. dobsoni, M. talazaci*, and *Limnogale* do not (Figure 4.7). 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. These structures serve as areas of origin for the wrist and digital flexors (medially) and extensors (laterally). They 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). Overall width of the distal humerus is particularly great in the diggers *Hemicentetes, Oryzorictes*, and *Solenodon* (Figure 4.7). *Potamogale* and *Petrodromus* have the narrowest distal humeri, reflecting less powerful wrist and digital flexion/extension.

There are significant differences among the tenrecines in medial epicondyle width (MEWI; Figures 4.7, 4.10, Table 4.4; $P < 0.05$), indicating varying development of the wrist and digital flexors. *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 of *Tenrec* suggests that it utilizes some manual scratch digging that is not reflected at the shoulder joint. Of the oryzorictines, *Oryzorictes* has a significantly wider medial epicondyle than the others (Figures 4.7, 4.10, Table 4.4; $P < 0.05$), and *Microgale cowani* has a wider medial epicondyle than the other *Microgale* species (Figures 4.7, 4.10, Table 4.4). The medial epicondyle of *Solenodon* is wide, reflecting its digging behavior, whereas that of *Potamogale* and *Petrodromus* is narrow (Figures 4.7, 4.10, Table 4.4).

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, catarrhine primates, and some treeshrews (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 (Figure 4.7). Sargis (2002) suggested that its absence in the tupaiid *Urogale* might be related to digging, yet the tenrecid 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 the Malagasy tenrecoids except for *Geogale*. The loss of the entepicondylar foramen in *Potamogale* might have functional significance given the narrowing and specialization of its distal humerus, but this does not apply to *Geogale*, which has few specializations of the forelimb. Additionally, macroscelidids retain an entepicondylar foramen, despite the narrowing and specialization of their distal humeri. This is likely a trait that is easily lost in any particular taxon, and was perhaps lost relatively late in both the *Potamogale* and *Geogale* lineages.

Another highly variable, simple feature of 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* or *Hemicentetes* specimens had a perforated coronoid fossa, whereas 11% of *Setifer* specimens and 61% of *Tenrec* specimens had 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*.

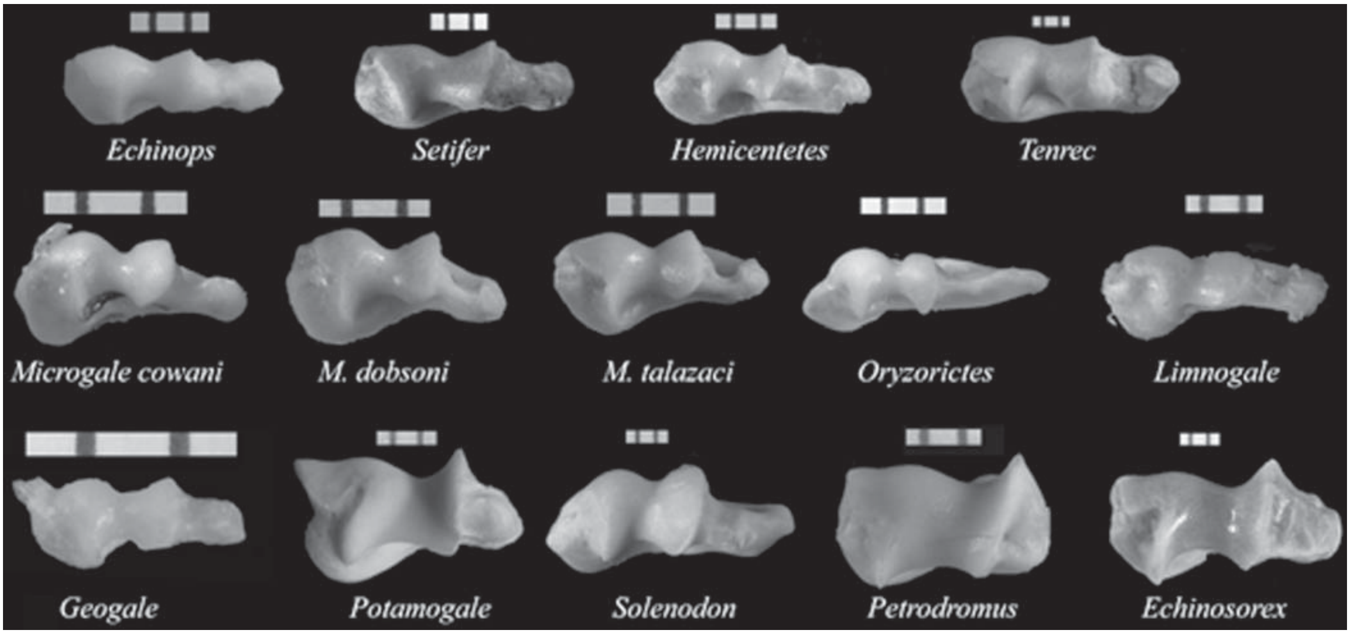

FIGURE 4.10. Distal surfaces of the right humeri in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa (bottom right). Note differences in medial epicondyle mediolateral length and sharpness of trochlear and capitular edges. Subdivisions on scale are 1.0 mm.

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 likely correlated with great extension of the forearm during terrestrial locomotion (see Szalay and Sargis, 2001).

All Malagasy tenrecoids have a well-defined, slightly rounded capitulum, whereas that of *Potamogale* is mediolaterally lengthened and rectangular, with sharply defined medial and lateral borders (Figures 4.7, 4.11). A distally flattened (as opposed to rounded) capitulum with well-defined borders is characteristic of more terrestrial vs. arboreal carnivorans, 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 tenrecoids 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 narrow, medially bound by a steep incline, and laterally bound by the sharp rectangular edge of the capitulum (Figure 4.10). *Potamogale* and the elephant shrew *Petrodromus* share similar capitulum/trochlea articular form, yet other aspects of their distal humeri are distinct: *Petrodromus* has a wide entepicondylar foramen, complete perforation of the coronoid fossa, and a less extended medial epicondyle (Figures 4.7, 4.11).

Setifer has a deeper (proximodistally) trochlea than the other tenrecines (Figure 4.11; Salton, 2005), which is typical of a more terrestrial mammal (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 that articulation. *Microgale talazaci* has a deeper trochlea than the other oryzorictines (Figure 4.11; Salton, 2005), yet other postcranial traits do not suggest that this species is more or less terrestrial than the others.

4.3.3 Ulna

The Ulna Shape Index (USI) is extremely variable among tenrecoid taxa and highly correlated with locomotor behavior (Figures 4.12, 4.13, Table 4.4). Other mammalian diggers exhibit relatively short, curved, and deep ulnae, whereas those of climbers tend to be relatively long and shallow (Verma, 1963; Taylor, 1974; Casinos et al., 1993; Hildebrand, 1995; Stein, 2000; Grand and Barboza, 2001). Of the tenrecines, *Hemicentetes* has the highest USI, and *Echinops* has the lowest (Figure 4.13, Table 4.4). The USI in *Setifer* is not significantly different from its sister taxon *Echinops*, and that of *Tenrec* is not significantly different from *Hemicentetes* (Table 4.4; $P < 0.05$), perhaps reflecting some climbing and digging, respectively, in these taxa. All

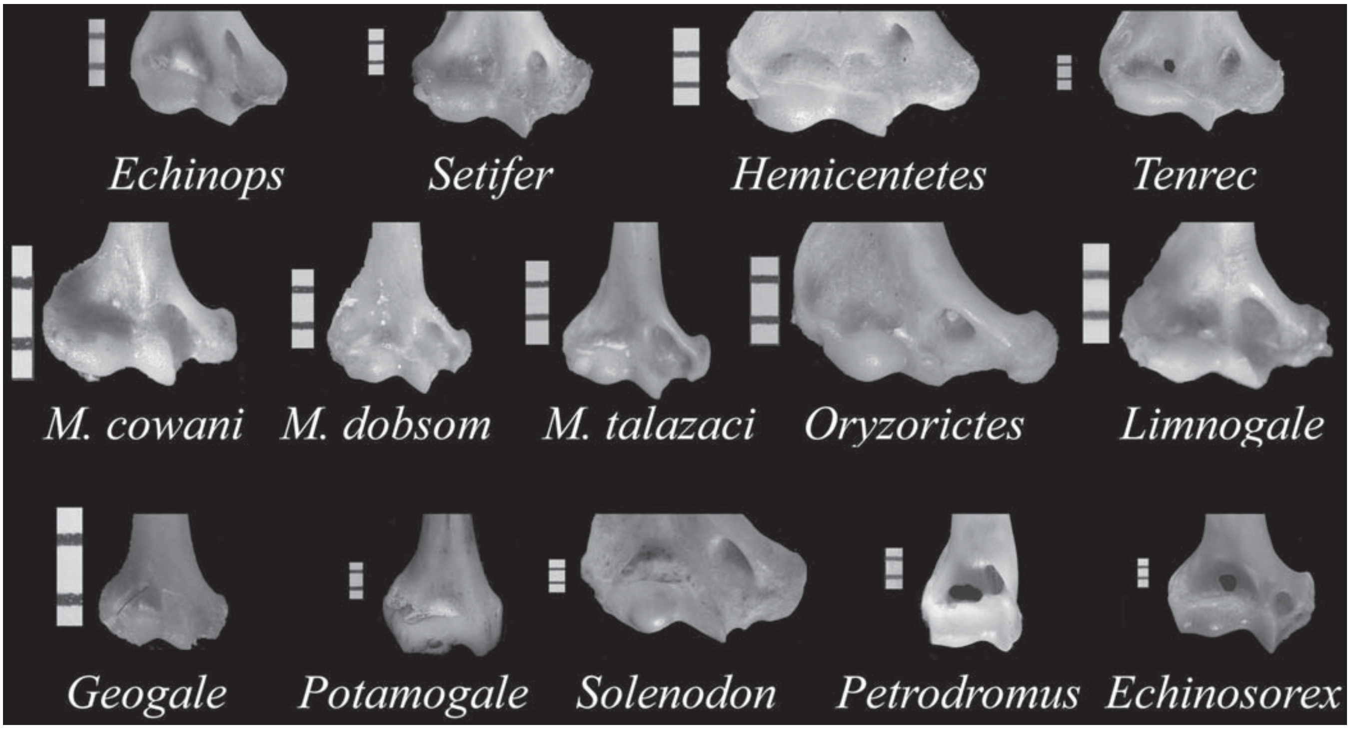

FIGURE 4.11. Anterior view of right distal humerus in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa (bottom right). Note differences in the shape of the trochlea and capitulum, especially the convergence in form between *Potamogale* and *Petrodromus*. Subdivisions on scale are 1.0 mm.

three *Microgale* species have relatively long ulnae, though *M. cowani* has a slightly deeper ulna than the other two (Figure 4.13, Table 4.4). *Oryzorictes, Potamogale*, and *Solenodon* have the shortest, deepest ulnae (Figure 4.13), with similar USI values as *Hemicentetes* (Table 4.4), 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 shallow ulna (Figure 4.13, Table 4.4), which denotes its high-speed terrestrial mode of locomotion.

The olecranon process, the attachment site for the M. 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; Grand and Barboza, 2001; Sargis, 2002). As the olecranon process length increases, triceps gains leverage for powerful ulnar extension against the humeral trochlea. Fossorial mammals have a particularly elongated olecranon process for digging, whereas that of climbers is less elongated, which allows for maximal elbow extension (Hildebrand, 1995).

As with ulnar shape, there are significant function-based differences among 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 (Figure 4.13, Table 4.4). All three *Microgale* species have relatively short olecranon processes, yet that of *M. cowani* is significantly longer than the others (Figure 4.13, Table 4.4; $P < 0.05$), suggestive of some digging. The fossorial *Oryzorictes* has a significantly longer olecranon process than any of the other study taxa (Figures 4.12, 4.13, Table 4.4; $P < 0.05$). *Limnogale* and *Potamogale* both have long processes, with similar OPLI values as *M. cowani*. Surprisingly, *Solenodon* has a shorter olecranon process than the other diggers and *Tenrec*, although it is still of moderate size, in the range of *Potamogale* and *Echinosorex*. However, *Solenodon* is similar to *Oryzorictes* in the medial curvature of its olecranon process (Figure 4.12), which, like the wide medial epicondyle, is related to the origin of powerful wrist and digital flexors necessary for scratch digging (Hildebrand, 1985).

4.3.4 Radius

Results from the Radial Shape Index (RSI) are almost identical to those from the Ulna Shape Index: digging tenrecoids, *Potamogale*, and *Solenodon* all have relatively deep radii, whereas the climber and more terrestrial genera have longer, shallower radii (Figure 4.13, Table 4.4). This makes sense from the same general function-based perspective for the ulna; the deep forearm bones are related to powerful displacement of dirt and water during digging and swimming, respectively (see above). Radial form in the diggers *Hemicentetes, Oryzorictes*, and *Solenodon* is also distinct in its transition

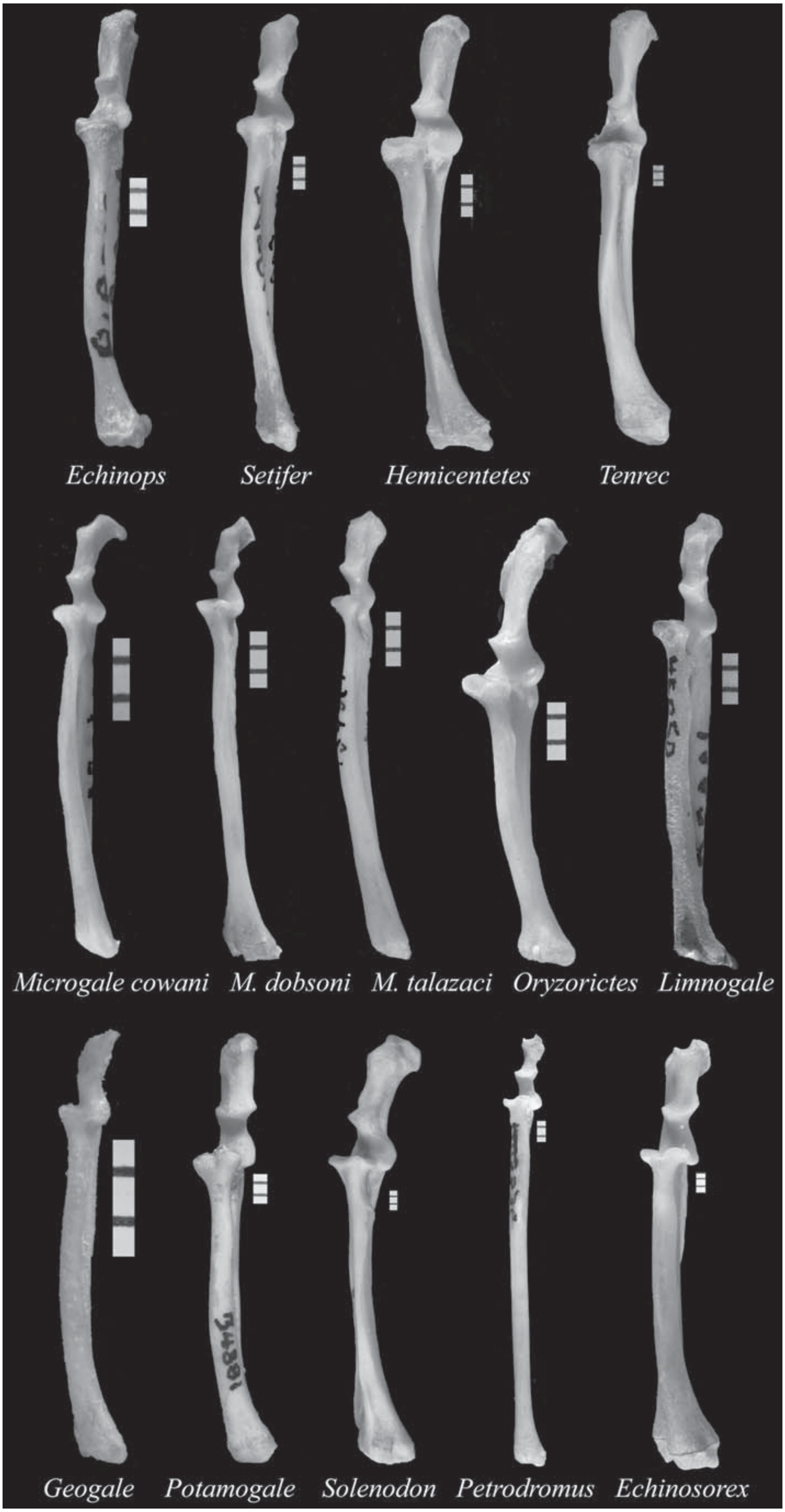

FIGURE 4.12. Anterior surfaces of right ulnae and radii in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa (bottom right). Note differences in ulna and radius shape, and relative length of the olecranon process. Subdivisions on scale are 1.0 mm.

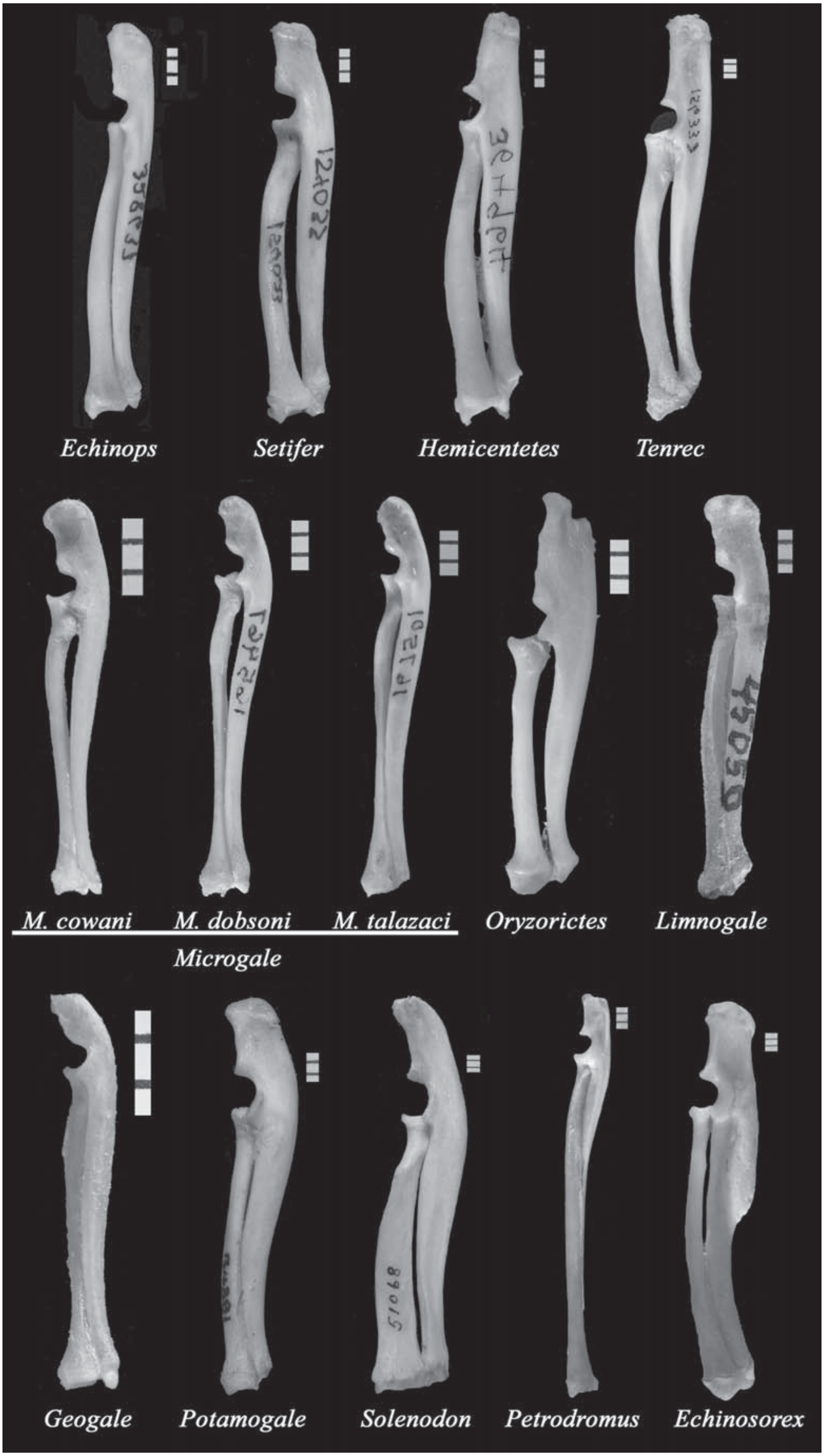

FIGURE 4.13. Medial view of right ulnae and radii in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa (bottom right). Note differences in olecranon process length and shape, trochlear notch shape, and widening of the radius along the shaft. Subdivisions on scale are 1.0 mm.

from being relatively shallow at the proximal shaft to up to twice its proximal depth 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 (Figure 4.13). The radius plays an important load-bearing role at the proximal wrist joint and limits rotational movement of the carpus, 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 (Figure 4.14). 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 (Figure 4.14). *Potamogale* and *Solenodon* have similar outgrowths of the proximal radial head, and *Potamogale* has an additional posterior notch capitulum (see *Potamogale* distal humerus, Figure 4.10). 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 widened radial head, which offers a large surface area for humeral articulation and restricts rotation.

4.4 Summary and Conclusions

4.4.1 *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 an additional molar in its dental formula 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 related to climbing behavior (see Salton and Szalay, 2004; Salton, 2005), which may indicate that their common ancestor was arboreal. Postcranial differences, especially in the tarsus, demonstrate convergences between *Echinops* and other mammalian climbers, and between *Setifer* and more terrestrial taxa (Salton and Szalay, 2004).

The forelimb of *Echinops* exhibits several differences from *Setifer* that are indicative of arboreal behavior in the former, including a longer acromion process; a slightly wider glenoid fossa; a rounder, larger humeral head; a mediolaterally wider medial epicondyle; a shallower, longer ulna; and a rounder articular surface of the radial head. Several features in common between the two taxa and not shared by *Hemicentetes* or

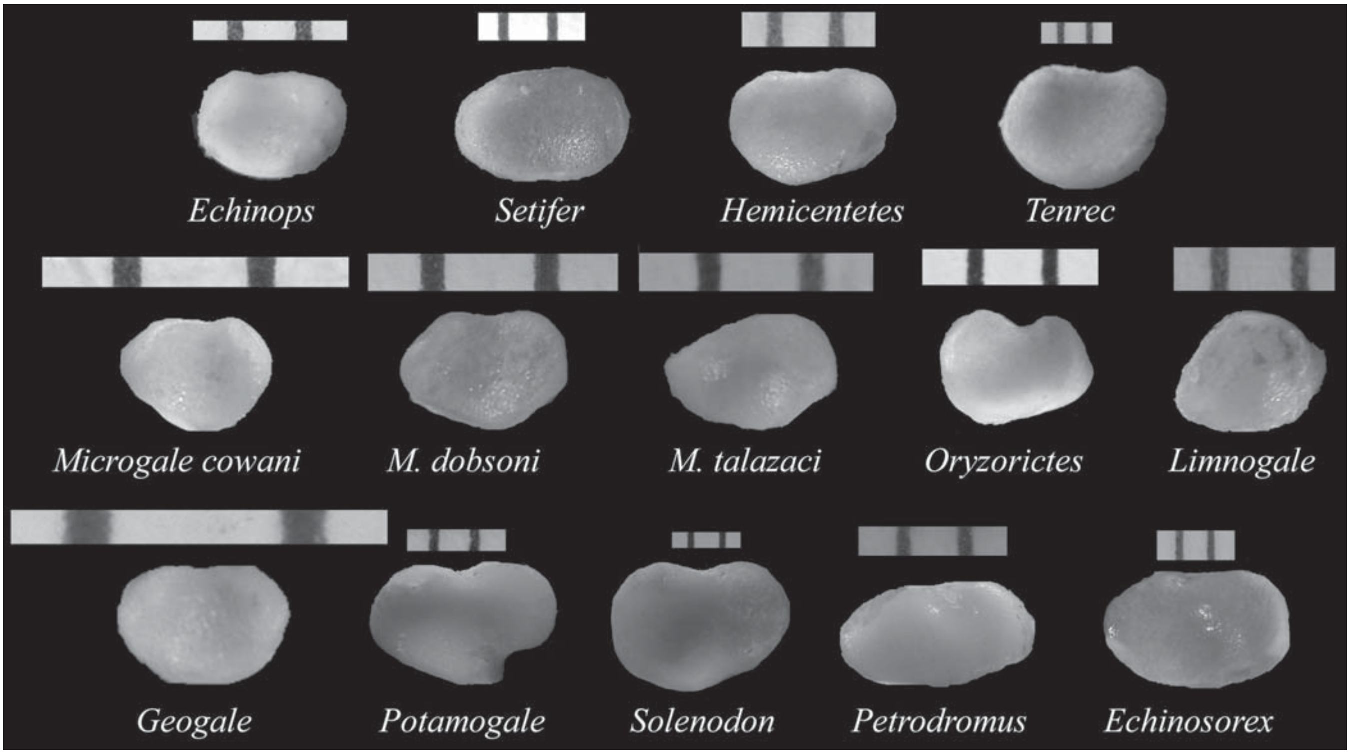

FIGURE 4.14. Proximal surfaces of right radii in tenrecines (top), oryzorictines (middle), two other tenrecoids (bottom left), and three outgroup taxa (bottom right); top is anterior, bottom is posterior. Note differences in radial head shape, ranging from rounded in *Limnogale* to elliptical in *Petrodromus*. Subdivisions on scale are 1.0 mm.

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; short olecranon process; and long, shallow 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 Salton and Szalay, 2004; Salton, 2005; Salton and Sargis, 2008). It is possible that *Setifer* climbs more than reports would suggest. JAS observed *Setifer* in the field and found that although *Setifer* nests on the ground, it is able to climb when prodded to do so (as can *Tenrec*; see Eisenberg and Gould, 1970). The traits shared by *Setifer* and *Echinops* more likely reflect a common ancestor that was arboreal rather than being *Setifer*-like.

4.4.2 *Hemicentetes, Oryzorictes*, and *Solenodon*: Fossorial/Semi-fossorial

As already established by many other studies on fossorial mammals, digging behavior is strongly indicated in 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. Traits related to digging in these taxa include: an elongated, narrow scapula; short, wide humerus with a widened medial epicondyle; pronounced attachment sites for the deltoid and pectoral musculature; well-developed bicipital groove (sometimes forming a complete tunnel); proximodistally and anteroposteriorly elliptical humeral head; long (and sometimes medially curved) olecranon process; and short, deep ulna and radius.

4.4.3 *Limnogale* and *Potamogale*: Semi-aquatic

Other regions of the postcranium demonstrate some similarities between *Limnogale* and *Potamogale*, which are likely based on a shared semi-aquatic habitus. However, 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 oryzoríctine, 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 an entepicondylar foramen, and rounded capitulum. *Limnogale* shares several of these features with the other oryzorictines, and it seems that its similarities to *Potamogale* are function-based convergences rather than synapomorphies. The differences between them emphasize the importance of forelimb stability and unilateral motion in the *Potamogale* forelimb, whereas *Limnogale* probably 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 to be basally divergent tenrecoid taxa (see Olson and Goodman, 2003).

4.4.4 *Microgale* spp.: Terrestrial/Fossorial?

The three *Microgale* species examined in 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 confirmed a series of characteristics correlated with terrestrial running, and did not reveal 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, narrow scapula; large pectoral crest and deltoid tubercle; wide medial epicondyle; and short, deep 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.

4.4.5 *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 hind limb) 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, perforated 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 is completely straight, long, and shallow, and has a very short olecranon process. The radius is also long and shallow, and the radial head is mediolaterally elliptical to an extreme. *Petrodromus* and *Potamogale* share a similar form of the humeral distal articular surface. But small-scale differences, such as the angle of the trochlea and shape of the capitular tail, strongly suggest that the similarities are convergent and based on the need for joint stabilization.

Unlike other regions of the postcranial skeleton (Salton and Szalay, 2004; Salton, 2005; Salton and Sargis, 2008), 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 form is highly dependent on species-specific behavior, and is not as constrained as, for example, aspects of the hind limb (Salton and Szalay, 2004; Salton, 2005).

As discussed in Salton and Szalay (2004) and Salton (2005), tenrecines and oryzorictines have a series of differences in the hind limb skeleton that are correlated with differences in basic posture. The tenrecine hind limb is more laterally rotated, and allows for much more general rotational movement than the oryzorictine hind limb. Oryzorictines have a parasagitally directed knee and foot and show much more constraint against mediolateral leg movement (Salton and Szalay, 2004). Both *Geogale* and *Potamogale* vary from the tenrecine and oryzorictine hind limb 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 that may be attributed to phylogenetic inertia. Analysis of forelimb indices did not differentiate tenrecines from oryzorictines, unlike analyses of other postcranial regions. Aside from some similarities between the sister taxa *Echinops* and *Setifer* that appear to be phylogenetically important and unrelated to locomotor specialization, each tenrecoid genus exhibits function-based variation that often corresponds with hypotheses based on other mammalian locomotor specialists.

Acknowledgments. Thanks to Raphael Allison, Rochelle Buffenstein, John Wahlert, Johanna Warshaw, Link Olson, Lawrence Heaney, William Stanley, Judy Chupasko, Linda Gordon, Heinz Künzle, Angelos Tianarifidy Stila, Carl Terranova, Marian Dagosto, Stephen Chester, and the mammal collection staff at MCZ, FMNH, AMNH, and USNM. We especially thank our graduate advisor, Fred Szalay, for all his guidance, encouragement, and friendship over the years. This project was funded in part by the National Science Foundation, National Geographic Society, Association for Women in Science, Field Museum of Natural History, CUNY GC Mario Cappeloni Fellowship, and Scholarships Foundation.

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