Patterns of evolutionary transformation in the humerus of moles (Talpidae, Mammalia): a character analysis

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Abstract. Twenty-eight humeral characters were coded based on examination of osteological specimens representing 11 extant talpid genera (13 spp.) as well as two shrews and a hedgehog as outgroups. The characters were mapped onto four alternative talpid phylogenies, resulting in tree lengths ranging from 66 to 74 steps. The humerus provides a complex of characteristics that in many cases are congruent with characters from other data sets. Seven character transformations characterize the base of the talpid tree, resulting in the humerus showing the following conditions in that node: lateral edge to center of head is positioned in line with lateral edge of shaft, long axis of head at oblique angle to long axis of shaft, floor of bicipital groove is displaced medially by pectoral crest near proximal end of humerus, teres tubercle is separate from medial epicondyle, lesser tuberosity is in line with proximal edge of head or superior to head, pectoral crest forms single curved process and entepicondylar foramen is absent. When the monophyly of Neurotrichus with Urotrichus is assumed, the following derived conditions support that clade: lateral end of the lateral epicondyle has a proximally directed hook and there is a deep groove between head of humerus and greater tuberosity. A high scalopine ridge supports a clade of Scalopus and Scapanus. Several other transformations support clades that had been proposed based by previous morphological and/or molecular studies.

Key words: humerus, phylogeny, Talpa, Talpidae.

The mammalian clade Talpidae contains the fossorial moles, the shrew moles, and the desmans. The group is distributed widely throughout the temperate areas of the Holarctic. There is a great diversity of life styles among taxa, including strictly subterranean, semifossorial and semiaquatic species. Recent revisions of talpid taxonomy recognized 16 genera and 42 species (Hutterer 1993; Motokawa et al. 2001). Relationships among these taxa are controversial (Yates and Moore 1990; Grenyer and Purvis 2003), as demonstrated by the disparate results achieved by recent cladistic analyses of talpids based on characters of the musculature (Whidden 2000), on sequence data of the cytochrome b mitochondrial gene (Shinohara et al. 2003), and on cranio-dental characters (Motokawa 2004). Although Talpidae is holarctic, each genus is restricted to a single continent or Eurasia, thus alternative phylogenetic hypotheses of this group have differing implications for their biogeographic history (Hutchison 1968, 1974; Yates and Moore 1990; Whidden 2000).

As discussed by Reed (1951), in no other group of mammals has the humerus undergone as remarkable a transformation as in talpids. The most specialized species have a highly-derived humeral form, in which the main function is its rotation (Campbell 1939). Associated changes are related to the development of areas of muscle attachment, as analyzed by Gambaryan (2000, p. 1), who stated: ‘The expansion of the humerus proximal end increases the abduction moment and it is necessary for the sprawling soil by hands in moles. The dilation in the region of medial epicondylus of the mole humerus increases the tension of the M. flex. digitorum

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own observations. Our 28 characters were also coded for some of the characters, character coding was based on Hutchison 1968, 1974) were consulted in developing our works (Campbell 1939; Reed and Turnbull 1965; 1971) were not treated in the analysis. Although previous studies of mammalian phylogeny (Gregory 1949) and lower levels of tetrapod phylogeny (Woodman et al. 2003) that are of taxonomic and systematic value. Since the humerus of talpids has become a uniquely specialized in a step-wise fashion, then it likely contains phylogenetically useful information. The highly autapomorphic nature of talpid humerus has allowed many fossil taxa (McKenna and Bell 1997) to be recognized on humeri alone.

There are detailed studies on aspects of forelimb anatomy and functional morphology for some species (Campbell 1939; Reed 1951; Yalden 1966; Castiella et al. 1992; Sánchez-Villagra and Menke 2005); however, the morphology of several talpid taxa that are critical to understand the phylogeny of the group have not been adequately studied. The goal of the present study is to characterize the morphological diversity of talpid humeri in a character/taxon matrix and then to measure the phylogenetic utility of these characters by optimizing them on alternative talpid phylogenies. This study is part of a large ongoing project (M. R. Sánchez-Villagra et al. unpublished) that aims to resolve talpid phylogeny using the total evidence approach.

Materials and methods

Osteological specimens representing 13 species and 11 currently recognized recent talpid genera were examined (Hutterer 1993) and scored for 70 character states distributed among 28 discrete morphological characters. Two species of shrews (Blarina brevicauda, Sorex arcticus) and a hedgehog (Erinaceus europaeus) were used as outgroups because soricids and erinaceids are the most likely sister-groups of talpids according to recent comprehensive studies of mammalian phylogeny (e.g. Murphy et al. 2001; Asher et al. 2003). Features that show intraspecific variation in Talpa caeca (Grulich 1971) were not treated in the analysis. Although previous works (Campbell 1939; Reed and Turnbull 1965; Hutchison 1968, 1974) were consulted in developing some of the characters, character coding was based on own observations. Our 28 characters were also coded for 16 fossil Eurasian species for use in ongoing studies in talpid systematics, but these taxa were not considered in the present analyses because their relationships to extant talpids are unclear (Appendix 1).

The specimens examined are listed in Appendix 2 and are housed in the following institutions: American Museum of Natural History, New York (AMNH); Bayerische Staatssammlung für Paläontologie, München (BSP); Los Angeles County Museum, Los Angeles (LACM); Rosensteinmuseum, Stuttgart (RMS); Senckenberg Museum, Frankfurt (SMF); Staatliches Museum für Naturkunde, Stuttgart (SMNH); Zoologische Staatssammlung, München (ZSM) and the Zoologische Schausammlung Universität Tübingen (ZST).

Using the computer program MacClade (Maddison and Maddison 1992), we mapped our 28 humeral characters onto four phylogenetic hypotheses: Whidden (2000), Shinohara et al. (2003, maximum likelihood tree based on cytochrome b gene sequences with a selected model), Motokawa (2004), and Grenyer and Purvis (2003). While we report tree lengths for all four hypotheses, we investigated possible synapomorphies of talpid clades on the phylogenies of Whidden (2000) and Shinohara et al. (2003). Since some talpid genera were not sampled in these two studies, those missing taxa that we studied were placed in their phylogenies following either current classification (Hutterer 1993) and/or the topology resulting from the supertree analysis of Grenyer and Purvis (2003). In three out of four studies, the base of the tree is depicted as a trichotomy because the relationships among the three groups of Eulipotyphla examined remain unresolved (as summarized by Springer et al. 2004). In the fourth study, Grenyer and Purvis (2003), soricids are depicted as the sister-group of talpids.

A critical point in understanding the humeral anatomy of fossorial Talpidae is the orientation of the humerus. We follow Reed (1951, p. 542) who stated: ‘The anterior and posterior surfaces remain theoretically the same as in the shrew, but the medial and lateral surfaces, which in the shrew are normal for mammals, change to ventral to dorsal, and to lateral and medial, respectively, in shrew-mole and mole, as the distal end of the humerus becomes more and more elevated’. Taking this into consideration, and for the sake of consistency, we follow Reed in retaining the terms ‘lateral’ and ‘medial’ in the sense in which they apply to the shrew, so that the greater tuberosity and the lateral epicondyle, for instance, are always on the ‘lateral’ side of the humerus, no matter what position they may assume in the body.
Characters

All characters were treated as non-additive or unordered, with the exception of character 4. The character matrix is presented in Appendix 1. Figure 1 shows drawings of humeri from one outgroup and five talpid specimens in anterior and posterior views, illustrating several of the character states described below. Readers are also referred to Storch and Dahlmann (2000), who illustrated the humerus of a specimen of *Uropsilus gracilis*, which is a member of a critical genus to understanding talpid phylogeny because of its basal phylogenetic position.

1. Deltoid process
   (0) absent, (1) present as flange distal to the greater tuberosity or (2) present as elongate hook on lateral edge of greater tuberosity.

Comment: The deltoid process has often been the source of terminological confusion (Edwards 1937; Campbell 1939). In the shrew the deltoid process can be homologised with a short ridge on the lateral shaft of the humerus that lies distal to the greater tuberosity — a typically mammalian position. The hypertrophy of the greater tuberosity has caused in some talpids (e.g. *Neurotrichus*) the reduction of the deltoid process and in others (e.g. *Scapanus*) we can find it as an even larger element in the same relative position. Some authors have chosen instead to refer to the process at the distal

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Fig. 1. Anterior (left) and posterior (right) views in specimens of one outgroup and five talpid species, indicating several of the character states described in the text. Specimen numbers are as follows: *Sorex arcticus* (ZSM 676); *Condylura cristata* (ZST 32943); *Desmana moschata* (ZST 160); *Scapanus latimanus* (LACM 88352); *Talpa europaea* (ZST 3843); *Urotrichus talpoides* (G-0029).
end of the pectoral crest as the deltoid process (see character 5) (e.g. Barnosky 1981; Geisler 2004).

2. Position of humeral head
   - (0) on posterior to posteromedial side of proximal end,
   - (1) lateral edge to center of head in line with lateral edge of shaft, (2) medial edge of head in line with lateral edge of shaft or (3) entire head lateral to lateral edge of shaft.

3. Orientation of humeral head
   - (0) long axis of head parallel or subparallel to long axis of shaft or (1) long axis of head at oblique angle to long axis of shaft.

4. Minimum width of humerus
   - (0) approximately 1/9–1/10th of the maximum length of humerus, (1) approximately 1/7th, (2) approximately 1/4–1/5th or (3) approximately 1/3rd or less (ordered).

Comment: The broadening and thickening of the humeral shaft reflects the physical stresses upon it and occurs in the more fossorial forms.

5. Distal end of pectoral crest
   - (0) does not form pronounced and distinct process, (1) forms pronounced and distinct process oriented proximally.

6. Proximity of pectoral crest to lesser tuberosity
   - (0) clear gap with a low proximal end of pectoral process, (1) narrow gap or fused to form a bicipital tunnel.

Comments: The tendon of origin of the M. biceps brachii passes through the bicipital groove. The plesiomorphic condition can be seen in Uropsilus, which is, according to Reed (1951, p. 543), the same as in Sorex: ‘In these forms the groove lies on the anterior face of the humerus between the pectoral ridge and the teres tubercle, as Campbell stated, but more important to its future development, the proximal part of it lies between the lesser tuberosity and the proximal end of the pectoral ridge’.

Where are the beginnings of the typical talpid bicipital tunnel? According to Reed (1951, p. 543), Neurotrichus gibbsii is a good example to show this transition: ‘The widening of the proximal end of the humerus of Neurotrichus is caused by a transverse growth of the lesser tuberosity, while the greater tuberosity and the head have moved more onto the lateral and posterior surfaces, respectively. This transverse growth of the lesser tuberosity would, in itself, merely displace the biceps tendon laterally, were it not that the proximal part of the pectoral process has increased to such size that the biceps tendon cannot ride over it, but must pass medially to it; indeed the proximal part of the pectoral ridge and the lesser tuberosity meet above the tendon and form the bicipital tunnel. Neurotrichus has already begun the process of transverse growth of the pectoral crest which is completed in the talmipes to form a longer bicipital tunnel across the proximal end of the humerus’.

The Talpinini (sensu Hutchison 1968) clearly show the bicipital tunnel. The bicipital groove lies partly on the posterior surface of the humerus. The medial surface of the pectoral ridge is occupied by the bicipital groove. The original medial surface of the pectoral ridge is located parallel with and proximal to the teres tubercle. The biceps tendon traverses the bicipital notch between the teres tubercle and the pectoral crest to get to the orthodox position on the anterior surface of the humerus (Reed 1951).

7. Floor of bicipital groove
   - (0) straight and parallel to long axis of humerus, (1) displaced medially by pectoral crest near proximal end of humerus.

8. Open portion of proximal half of bicipital groove
   - (0) visible in anterior view, (1) visible in posterior view or (2) not visible.

9. Teres tubercle
   - (0) absent, (1) separate from medial epicondyle, (2) fused to shaft proximally.

10. Pit for M. flexor digitorum profundus
    - (0) absent or (1) present.

11. Medial edge of trochea
    - (0) sharp, ventrally projecting ridge or (1) straight or low ridge.

12. Lateral epicondyle
    - (0) present as rounded protuberance, (1) distal end forms laterally extended flange, (2) lateral end has proximally directed hook, (3) lateral end has spine-like proximally pointed hook.

13. Brachial fossa
    - (0) small pit or (1) cavernous excavation underlying greater tuberosity.

14. Crest between greater tuberosity and distal end of pectoral ridge
    - (0) present or (1) absent.

15. Trough between head of humerus and greater tuberosity
    - (0) no groove/very shallow or (1) deep groove.

16. Lesser tuberosity
    - (0) in posterior view, inferior to proximal edge of head of humerus, (1) in line with proximal edge of head or superior to head of humerus.

17. Head of humerus
    - (0) round or (1) elliptical.
Comment: Talpids except *Uropsilus* show elliptical humeral heads, a condition associated with differences in the angles between the main axis of the humerus and the main axis of the humeral head (Reed 1951).

18. **Medial epicondyle builds proximally elongated flange or process**
   (0) absent or (1) present.

19. **Greatest length of greater tuberosity and deltoid process**
   (0) relatively short, approximately <1/4 length of humerus or (1) relatively long.

20. **Pectoral crest**
   (0) single straight process parallel to long axis of humerus, (1) forms single curved process or (2) long axis of humerus and pectoral crest having a perpendicular orientation (approximately 90°).

21. **Scalopine ridge**
   (0) absent, (1) connects entirely but low, (2) medial half present or (3) connects to head of humerus.

Comment: As defined by Campbell (1939, p. 16), the scalopine ridge ‘is a sharp ridge running from the medial side of the scapular facet to the distal end of the lesser tuberosity. This divides the flattened area at the base of the lesser tuberosity from the nearly perpendicular proximal wall of the large medial triceps fossa’.

22. **Distinct notch (seen in distal view) separates capitulum and trochlea**
   (0) absent or (1) present.

23. **Articulation of clavicle and humerus**
   (0) absent or (1) present.

24. **Lateral edge of trochlea**
   (0) medial edge of capitulum forms obtuse angle with lateral edge of trochlea or (1) distinct notch separates capitulum and trochlea.

25. **Supracondylar foramen (= entepicondylar foramen)**
   (0) absent or (1) present.

26. **Clavicular facet**
   (0) absent, (1) in lateral view wedge-shaped, (2) rectangular, (3) sharp ending.

27. **Capitulum**
   (0) in anterior view, capitulum has a rounded distal edge or (1) capitulum has a distal ridge or medial edge.

28. **Lateral side of capitulum**
   (0) not noticeably elongated or (1) laterally elongated so that capitulum has ‘football’ shape.

**Results**

When the 28 characters of the present study are optimized onto previous phylogenetic hypotheses, Whidden’s (2000) hypothesis presents the best fitting one with 66 steps, followed by Grenyer and Purvis (2003) with 67 steps, Motokawa (2004) with 71 steps and finally Shinohara et al. (2003) with 74. In addition, Figure 2 shows reconstructions of the evolutionary histories of the characters on two hypotheses: Whidden (2000) and Shinohara et al. (2003).

**Discussion**

As demonstrated here, the humerus provides a complex of characteristics that in many cases are congruent with characters from other data sets. For example, a high scalopine ridge supports a clade of *Scalopus* and *Scapanus* whose monophyly is supported by myological and DNA sequence data (Whidden 2000; Shinohara et al. 2003). However, we did not conduct a phylogenetic analysis based just on humeral characters because it encompasses such a small portion of the organism’s anatomy. Nevertheless the mapping of such characters allowed us to test previous phylogenies, and we found that Whidden’s (2000) hypothesis presents the best fitting one (66 steps) while Motokawa’s (2004) needs 71 steps and Shinohara’s et al. (2003) phylogeny suggests 74 steps. Since Whidden’s (2000) hypothesis is based on myological features, it is evident that our humeral characters correlate with Whidden’s characters or may not be entirely independent of them.

Seven character transformations characterize talpids, resulting in the humerus showing the following conditions at the base of the talpid tree: lateral edge to center of head is positioned in line with lateral edge of shaft, long axis of head at oblique angle to long axis of shaft, floor of bicipital groove is displaced medially by pectoral crest near proximal end of humerus, teres tubercle is separate from medial epicondyle, lesser tuberosity is in line with proximal edge of head or superior to head, pectoral crest forms single curved process and entepicondylar foramen is absent. When the monophyly of *Neurotrichus* with *Urotrichus* is assumed (Fig. 2a), the following derived conditions support that clade: lateral end of the lateral epicondyle has a proximally directed hook and there is a deep groove between head of humerus and greater tuberosity. As depicted in Figure 2, several other transformations support clades that have been proposed based by previous morphological and/or molecular studies.

The goal of this study was to examine humeral evo-
Fig. 2. Transformations of humeral characters across Talpidae and three outgroup species reconstructed using parsimony on the phylogenies (with modifications, see text) postulated by (A) Whidden (2000) and (B) Shinohara et al. (2003, maximum likelihood tree based on cytochrome *b* gene sequences with a selected model). In cases of uncertainty, the DELTRAN (Maddison and Maddison 1992) option was used. In case of ambiguity at the base of the tree, the condition in *Erinaceus* was taken as basal. See Appendix 1 for data matrix and text for details. Character states hypothesized for the base of the tree are as follows: 1 (1), 2 (0), 3 (0), 4 (0), 5 (0), 6 (0), 7 (0), 8 (0), 9 (0), 10 (0), 11 (0), 12 (0), 13 (0), 14 (0), 15 (0), 16 (0), 17 (0), 18 (0), 19 (0), 20 (0), 21 (0), 22 (0), 23 (0), 24 (0), 25 (2), 26 (0), 27 (1), 28 (0).

In talpids in the context of a character analysis. These characters will be used in the near future in a more comprehensive analysis of talpid relationships (M. R. Sánchez-Villagra et al. unpublished).

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‘51st Symposium of Vertebrate Paleontology and Comparative Anatomy’ in Oxford/England, where preliminary results of this work were presented. JHG’s contribution to this project was completed while he was in graduate school, where he was supported by a National Science Foundation Graduate Fellowship, a Faculty Fellowship in the Department of Earth and Environmental Sciences at Columbia University, and the Office of Grants and Fellowships at the American Museum of Natural History. MRSV thanks the support of the European Community — Access to Research Infrastructure Action of the Improving Human Potential Programme (High Lat at the Swedish Museum of Natural History).

References


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## Appendix 1.

Character matrix. Please refer to text for description of characters and character states.

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## Appendix 2.

List of specimens examined. Species names follow Hutterer (1993).

Recent talpids: *Condylura cristata* (ZST 32943–32942); *Desmana moschata* (ZST 160); *Galemys pyrenaicus* (ZSM AM 867); *Mogera wogura* (G-0064); *Neurotrichus gibbsii* (LACM 95926); *Parascalops brevari* (AMNH 140405); *Scalopus aquaticus* (AMNH 235615); *Scapanus latimanus* (LACM 88352); *Talpa caeca* (ZSM AM 869); *Talpa europaea* (ZST 3843, RMS 32981); *Uropsilus gracilis* (SMF II 94/687); *Dymecodon pilirostris* (G-0548); *Urotrichus talpoides* (G-0029).

Fossil talpids: *Asthenoscapter* sp. (SMNH-unnumbered); *Desmanella engesseri* (BSP 1937II20448); *Geotrypus aff. montisasini* (SMNH 45103); *Geotrypus montisasini* (SMNH 43499); *Geotrypus tomerdingensis* (SMNH 43496); *Mygalea sp.* (SMF 2000/697–700); *Mygatalpa aff. arvernensis* (SMNH 45170); *Paratalpa meyeri* (SMNH 44810, 45159); *Proscapanus primitivus* (BSP 1881IX524); *Proscapanus sansaniensis* (BSP 1970XVIII, 7244); *Quyania chowi* (BSP 1986I IVPP6453.15); *Talpa fossiis* (BSP 1951XXVI); *Talpa gracilis episcopalis* (BSP 1956XII310); *Talpa minor* (BSP 1963XIV, 10–17); *Talpa minuta* (BSP 1937II20559); *Talpa tenuidentata* (SMNH 45152); *Yanshuella primaeva* (SMF 82/3–4).

Outgroups: *Blarina brevicauda* (ZST-unnumbered); *Erinaceus europaeus* (RMS SM 23600); *Sorex arcticus* (ZSM 676).