EXTRAORDINARILY PRESERVED TALPIDS (MAMMALIA, LIPOTYPHLA) AND THE EVOLUTION OF FOSSORIALITY

ACHIM H. SCHWERMANN* and RICHARD S. THOMPSON

1Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Rheinische Friedrich-Wilhelms-Universität Bonn, Nussallee 8, 53115 Bonn, Germany, achim.schwermann@uni-bonn.de;
2University Museum of Zoology, The University of Cambridge, Downing Street, Cambridge, CB2 3EJ, U.K., rst32@cam.ac.uk

ABSTRACT—We describe four exceptionally preserved Miocene talpid specimens from Germany (representing Mygalea jaegeri, Proscapanus sansaniensis, and Geotrypus montisasini), expanding and amending the original descriptions based on micro-computed tomography (μ-CT) data. These specimens are scored into an enlarged version of the Sánchez-Villagra et al. (2006) character set, along with newly collected data for extant talpids and the fossil species Geotrypus antiquus, Domninoidea mimicus, Eotalpa belgica, and E. anglica. The extant genus Scaptonyx is here resolved as the sister taxon to the American shrew-mole, Neurotrichus, and not as a close relative of the Talpini. Of the fossil talpids, Mygalea jaegeri is recovered as the sister taxon of extant desmans only in the context of genetic constraints; morphological data alone suggest that it represents a shrew-mole/desman-grade animal. Proscapanus sansaniensis is placed at the base of the Scalopini, whereas Domninoidea mimicus is the sister taxon to Parascalops and Scapanus. Geotrypus represents an early fossorial form, with G. antiquus retaining its position at the base of the Talpini, although G. montisasini’s placement remains uncertain. Interestingly, the placement of these fossils causes character states more commonly associated with the semi-fossorial shrew-moles to be optimized to the root of the highly fossorial Talpini. Thus, despite the close relationship between Talpini and Scalopini based on morphological data, the fossil record provides evidence to support the independent evolution of extreme fossoriality in these groups. This finding is in agreement with genetic data sets, despite obvious topological differences.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The northern moles, or Talpidae Fischer von Waldheim, 1817, are a diverse family of small insectivorous mammals closely related to the hedgehogs (Erinaceidae Fischer von Waldheim, 1817) and shrews (Soricidae Fischer von Waldheim, 1817) in the order Lipotyphla Haeckel, 1866. There are 17 extant genera (Hutterer, 2005), nine of which almost exclusively occupy a subterranean habitat. Other taxa, including the desmans and star-nosed moles, exhibit semiaquatic adaptations, whereas more still live a generalized ambulatory or semi-fossorial life among the leaf litter. The group’s diversity has led to a number of hypotheses regarding the evolution of fossoriality. Some authors suggest that fossoriality developed gradually throughout the lineage, with highly fossorial taxa evolving from semiaquatic and semi-fossorial ancestors (Campbell, 1939; Reed, 1951; Whidden, 2000; Sánchez-Villagra et al., 2006). Such hypotheses are generally supported by morphological cladistic analyses and find a close relationship between the two clades of highly fossorial moles: the Eurasiatic tribe Talpini Fischer von Waldheim, 1814, and the predominantly American Scalopini Gill, 1875. Other studies suggest some level of convergence between these two strikingly similar groups (Hutchison, 1976; Yates and Moore, 1990; Motokawa, 2004; Piras et al., 2012). This view is also supported by the relatively small molecular systematic data sets available for the group (Shinohara et al., 2003, 2004; Cabria et al., 2006; Crumpton and Thompson, 2013); however, the low level of genetic coverage in current family-level molecular data sets makes this hypothesis far from conclusive. Despite our poor understanding of their evolution, there has been little recent focus on the fossil record of the Talpidae, and what this can reveal about the evolution of fossoriality.

The talpid fossil record, like that of most small mammals, consists primarily of isolated teeth and fragmented mandibles (e.g., Hugueney, 1972; Ziegler, 1990; Crochet, 1995). The oldest known talpids from the upper Eocene of both Eurasia (Eotalpa anglica Sige et al., 1977) and North America (Oreotalpa florissantensis Lloyd and Eberle, 2008) are represented by such material, which proves useful for both taxonomic and systematic purposes. However, the talpid fossil record also features a high frequency of isolated humeri. This is a consequence of the robust form of these humeri, as well as the family’s fossorial tendencies, both increasing their potential for fossilization. Furthermore, a highly derived humeral form makes talpid humeri highly diagnostic elements (Fig. 1), which are more readily identified.

As a result, the talpid fossil record includes a series of specimens that can potentially provide direct evidence of the diversity of locomotor habits in the Talpidae through geological time. Currently, moles from the early Oligocene of Europe (Geotrypus minor Ziegler, 2012) are thought to represent the oldest known highly fossorial forms. The extent of fossoriality is generally estimated only by the length-to-width ratio of the humerus. This methodology tends to classify specimens into discrete locomotor groups, but does not lend itself to the understanding of the initial evolution of fossoriality within Talpidae. The extent of such evolutionary and ecological problems can only be fully understood...
by the establishment of a robust talpid phylogeny, which fully encompasses both molecular and morphological data, while including both extinct and extant taxa.

The integration of multiple fragmentary fossil taxa into existing systematic data sets may hamper resolution through the addition of missing data. Of course, the placement of any taxon in a phylogeny depends upon the unique combination of characters it possesses, meaning that highly fragmentary fossil can be placed with some degree of confidence (e.g., Wiens, 2003). High levels of missing data simply increase the likelihood of multiple equally parsimonious (or likely) placements for a taxon on a tree. Given this, well-preserved, partially articulated fossil specimens have the potential to improve phylogenetic accuracy due to their character richness and sampling across morphological partitions (Patton et al., 2015). Such specimens also provide the only definitive association of the upper and lower dentitions and dental and postcranial elements (Hutchison, 1974; Schwermann and Martin, 2012). Furthermore, they provide an insight into the morphology of less commonly preserved or nondiagnostic postcranial elements; those associated with the forelimb are particularly important to understand talpid evolution. Such talpid specimens may prove crucial in furthering our understanding of the evolution of fossoriality, helping to unify previously disparate specimens, revealing new morphological conditions, and providing a larger number of characters for accurate placement in a phylogenetic analysis.

Because of its peculiar development, the forelimb of extant talpids has been the focus of much study (e.g., Edwards, 1937; Campbell, 1939; Reed, 1951; Sánchez-Villagra et al., 2004; Sánchez-Villagra and Menke, 2005). As well as an unusual humeral form, the extreme fossoriality of the Scalopini and Talpini necessitates a unique shoulder girdle anatomy: the scapula is elongated with a reduced acromion, the manubrium has a dorsoventrally deep keel (aligned in the sagittal plane), and the clavicle is remarkably stout, articulating distally with the greater tuberosity of the humerus rather than the scapula. As well as the typically massive and widened humerus, which bears a large teres tubercle, highly fossorial talpids exhibit a robust radius and a complex sigmoidal ulna with an elongated olecranon process. The hand is composed of stout carpals, metacarpals, and phalanges, which terminate in large claws. The broad hand is enlarged by an additional bone, the prepollex or os falciforme, which sits alongside the radius, carpals, and first metacarpal. This bone is present in most extant talpids (Sánchez-Villagra and Menke, 2005; Mitgutsch et al., 2012). The only fossil evidence of the prepollex is found in a partial skeleton of Geotrypus antiquus (de Blainville, 1840) from Ensper, Germany (Schwermann and Martin, 2012).

Here, we describe four partial skeletons of fossil talpids, representing three distinct genera, using micro-computed tomography (µ-CT). All have been described previously while partially embedded in matrix: Mygalea jaegeri and Proscapanus sansaniensis from Viehhausen by Seemann (1938) and Geotrypus montisasini from Ulm by Ziegler (1990) (Fig. 2). The µ-CT scans revealed new information about both tiny and embedded postcranial elements, as well as details of exposed regions. We document these four talpid fossils in detail, using the new insights gained through µ-CT analysis to supplement and enhance their original descriptions. These new descriptions are used to code these crucial talpid fossils into the morphological cladistic matrix of Sánchez-Villagra et al. (2006), which represents the most thorough morphological analysis of the extant Talpidae to date. We include 19 new characters in this analysis, focusing on the postcranial anatomy of the group and their fossorial adaptations. To these characters we added new data for the extant talpid radiation, including scores based on the first description of the hand skeleton of Scapanus oweni Thomas, 1912. This data set is further supplemented by the inclusion of the extinct taxa Domniodes mimicus Wilson, 1968, and both Eotalpa belgica and E. anglica. In addition, we apply two molecular phylogenetic hypotheses of the Talpidae that differ in their reconstructions of intertribal relationships (Shinohara et al., 2004; Crumpton and Thompson, 2013). Crumpton and Thompson (2012) contains the best sample of extant talpids yet published and enables us to investigate the impact of fossil data on the competing hypothesis of talpid evolution, and the evolution of a highly fossorial lifestyle.

MATERIALS AND METHODS

We follow Hutterer (2005) for higher taxonomic classification. Terminology for the dentition, skull, and postcranial skeleton (Fig. 3) follows Schaller (2007), with additions from Campbell (1939:figs. 15, 20) and Hutchison (1968:figs. 12, 14; 1974:figs. 1, 3). Teeth of the upper jaw are denoted by uppercase letters and those of the lower jaw by lowercase letters.

µ-CT Analysis

In order to enable a complete investigation that included the embedded skeletal fragments, several µ-CT scans were performed using the v(tome)x s 240 scanner (GE Sensing and Inspection Technologies Phoenix X-ray) at the Steinmann-
Phylogenetic Analysis

Taxon Sampling—Details of the four specimens investigated in this study are provided in the descriptions below. Throughout our descriptions, comparisons are made to a number of extant and extinct talpid taxa, observed by one of the authors (R.S.T.) during the course of his doctoral studies. A large number of characters missing from the Sánchez-Villagra et al. (2006) morphological cladistic data set have also been coded based on these observations. Specimens have been observed from a number of collections, including the University Museum of Zoology, Cambridge, U.K. (UMZC); the Natural History Museum, London, U.K. (NHMUK); the Naturhistorisches Museum Wien, Vienna, Austria (NHMW); the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS); the Smithsonian Institution, National Museum of Natural History, Washington, D.C., U.S.A. (USNM); and the American Museum of Natural History, New York, U.S.A. (AMNH). Of particular value to the cladistic data set are the postcranial specimens of Scaptonyx fusicaudus Milne-Edwards, 1872 (USNM 574303), Parascaptor leucura (Blyth, 1850; NHMUK 1951.11.12.9), Scapanulus oweni 1850; NHMUK 1951.11.12.9), Edwars, 1872 (USMN 574303), and Proscapanus sp. (UMZC M45350) from the NHMUK and specimens from RBINS (IRSNB M 1929-34), respectively. Details of all specimens observed are given in Supplementary Data (Section 2).

Character Sampling—The character sample of Sánchez-Villagra et al. (2006) was expanded by 19 new characters, derived from the literature and our own observations (see Supplementary Data: Section 1). Three existing characters were modified to account for the variation we observed. Character 21 was excluded from our analysis because we could not consistently reproduce the codings of Sánchez-Villagra et al. (2006) or provide any meaningful coding for our new taxa. The ordering of the 33 characters from the Sánchez-Villagra et al. (2006) analysis is maintained here (note that we follow the ordering instructions in their original character list, which produced the correct tree length, rather than those in their methodology that suggest the ordering of only 13 characters). Details of all modifications to the character sample can be found in Supplementary Data (Section 1).

Analysis—Analyses were carried out in PAUP* version 4.0 (Swofford, 2002) using the heuristic search algorithm with 1000 replications and a random addition sequence. Branch supports (Bremer, 1988, 1994) were calculated using the same tree searching strategy, coupled with reverse constraints to calculate support for each node. Bootstrap supports were calculated using 1000 random addition sequences per 1000 bootstrap pseudoreplicates. We used the topologies of Crompton and Thomson (2013:fig. 2) and Shinohara et al. (2004:fig. 1) as backbone constraints, allowing taxa not present in these topologies to join any clade in the model. The former was chosen because it represents the molecular study with the largest sample of extant talpid taxa; in the latter, we used the strict consensus of their cytochrome b analysis (Shinohara et al., 2004:fig. 1), which places the Talpini in a closer relationship with the shrew-moles than the Scalopini. Character optimizations for all analyses were performed in Winclada version 1 (Nixon, 1999–2002).

Descriptions

talpidae Fischer von Waldheim, 1817
Desmanini Thomas, 1912
Mygalea Schreuder, 1940
Mygalea jaegeri (Seemann, 1938)

Specimen: BSP 2008 LI280; formerly IPW 280—The genus Mygalea was erected by Schreuder in 1940 based on a collection of fragmentary remains of M. antiqua Pomel, 1848, found in the collections of the Muséum national d’Histoire naturelle, Paris. The material had been known since the early 19th century (de Blainville, 1840; Pomel, 1848; Pictet, 1853–1857; Schlosser, 1887; Filhol, 1891) and assigned to genera of varying validity, before being unified under a single novel generic classification in Schreuder’s (1940) review.

Schreuder (1940) considered Mygalea a relative of the extant Desmanini, primarily due to the presence of deeply divided molarostyles, prominent paraconules and metaconules on the upper molars, and a distinct humeral form. Rümke (1985) disagreed based on the lack of morphological continuity in the fossil record between Schreuder’s (1940) specimens and the extant Desmanini. However, most recent authors agree with the traditional placement of Mygalea (Ziegler, 1990; Van den Hoek Ostende and Fejfar, 2006; Engesser, 2009). As summarized by Ziegler (2003), there are three species of Mygalea known from the Miocene of Europe, namely, M. antiqua, M. magna Ziegler, 1990, and M. jaegeri.

Our specimen of Mygalea jaegeri (BSP 2008 LI280; Fig. 4) was excavated from the Miocene brown coal mine at Viehhausen near Regensburg, Germany (Fig. 2), by the Institut der Paläontologie der Universität Würzburg (IPW) in the 1930s.
This site was assigned to MN5/6 by Ziegler et al. (2005). The specimen was transferred from its lignite matrix to paraffin, in which it remains embedded. Although originally housed in Würzburg (Seemann, 1938; Hutchison, 1974; Ziegler, 1990), the Viehhausen specimens are now stored at the Bayerische Staats-sammlung für Paläontologie und Historische Geologie (BSP) in Munich.

*Mygalea jaegeri* (BSP 2008 LI280) was originally assigned to the genus *Scaptonyx* by Seemann (*Scaptonyx jaegeri* sp. nov. Seemann, 1938) before being reallocated to the desmanin genus *Mygalea* by Hutchison in 1974, based on Seemann’s description and figures. Hutchison designated this partial skeleton as a lectotype, but recommended its redescription based on first-hand observations in order to confirm his assignment and extract further information from this positively associated specimen. Hutchison’s (1974) reclassification was supported by Ziegler (1990), who also described some new material from Ulm that he assigned to this species. The Seemann specimen includes fragmentary remains of the skull and the left dentary, the right one (Seemann, 1938:fig. 15) having been lost subsequent to its original description. Postcranial remains include both scapulae and humeri, along with the left clavicle, right ulna, left radius, and a number of vertebrae and fragmented ribs, mostly described by Seemann (1938). The bones of the hands and feet, along with a number of unidentified elements, remain undescribed.

**Description**

**Upper Dentition**—The upper molars from both sides of the dentition are preserved, although their advanced wear makes it difficult to identify many diagnostic features (Fig. 5G–I). The teeth are distinctly dilambdodont, as in all talpids. Seemann (1938) described them as very similar to the molars of *Talpa europaea*, potentially due to perceived affinities with *Scaptonyx*. The molars of *M. jaegeri* decrease in size from anterior to posterior (*M1 > M2 > M3*), as seen in *Talpa*, but also in both modern desmans and shrew-moles such as *Uroticichus*. Due to heavy lingual wear, there is no evidence for the presence of paraconules or metaconules (contra Hutchison, 1974). The stylar shelf is less...
worn, with an anteriorly projecting parastyle identifiable in the left and right M1. The M1 shows an elongate postparacrista relative to the paracrista. The left M1 and both right and left M3 show evidence of a divided mesostyle, although its depth is uncertain due to wear. The form of the mesostyle varies widely in the Talpidae, with a deeply divided mesostyle seen in the Desmanini and Scalopini, and a much weaker division in the Talpini.

Both P4s are preserved, showing three distinct roots (Seemann, 1938; Hutchison, 1974), the third of which occupies a lingual position beneath a slight lingual shelf. This triple-rooted form differs from Ziegler’s (1990) description of *Mygalea jaegeri*, where he suggested a double-rooted P4 as a synapomorphy for this species. *Mygalea antiqua* and *M. magna* also have a triple-rooted P4 (Van den Hoek Ostende and Fejfar, 2006; Engesser, 2009). There is an anterior cingulum on the P4, which may have supported a small, anteriorly projecting parastyle. A posterobuccally directed crest projects from its primary cusp, as is common in the Talpidae. Seemann’s (1938) comparison of the molars with those of *Talpa* could be extended to include the P4, which lacks the enlarged lingual shelf and strong accessory cusps seen in modern desmanins. The left tooth row also preserves the double-rooted P3, which differs from the triple-rooted form seen in *M. antiqua* (Schreuder, 1940) and *M. magna* (Van den Hoek Ostende and Fejfar, 2006), although the premolar root number of recent desmanins is known to vary within species (Rümke, 1985).

Three antemolars were preserved anterior to the left molar row. Seemann’s (1938) suggestion that these represent the P2, P1, and C seems plausible based on the presence of two roots in the two most posterior teeth. To our knowledge, no extant talpid exhibits double-rooted incisors; hence, the canine must be represented by either the single-rooted tooth or the most anterior of the double-rooted teeth. Seemann’s (1938) hypothesis of dental homology leads to a dental phenotype only seen in a single extant talpid genus, *Condylura*: a single-rooted upper canine combined with four double-rooted premolars. Otherwise, single-rooted upper canines are only known in the Scalopini (excluding *Scapanus*) and the shrew-moles *Urotrichus*, *Uropsilus*, and *Dymecodon* (Sánchez-Villagra et al., 2006). The alternative hypothesis is to assume that the first of these three preserved teeth represents an incisor, with the second tooth a double-rooted canine, as seen in *M. antiqua* (Schreuder, 1940; Engesser, 2009), and a double-rooted first premolar. This hypothesis suggests that a single premolar is missing from the specimen, preventing the confirmation of a complete upper premolar row. The crowns of these antemolars are relatively worn but appear rather simple and conical, with slight anterior and posterior cingula, particularly in the second tooth.

**Lower Dentition**—The left mandible is damaged, containing only the p3–m3 (Fig. 5A–C). The lower dentition was completely preserved in the right dentary according to Seemann (1938:fig. 15). A fragment of a right dentary, labeled as the lectotype and including the anterior portion of the horizontal ramus, was also investigated (Fig. 5D–F). In spite of its label, this specimen does not seem to represent the missing right dentary of the lectotype, due to its preservation (Seemann, 1938:fig. 15) and the stage of dental wear. It includes the i1 to p4 and a damaged m1, helping to confirm the dental formula of 3.1.4.3 when combined with the left mandible (p4–m3) of the lectotype. The double-rooted molars decrease in size along the tooth row (Seemann, 1938), although the m1 and m2 are very similar in size. They are heavily

---

**FIGURE 4.** The partial skeleton of *Mygalea jaegeri* (BSP 2008 LI280) from the lower Miocene deposits at Viehhausen, including a photograph of the specimen and a labeled drawing. **Abbreviations:** C, remains of cranium; Cl, clavicle; H, humerus; M, mandible; Ma, manubrium; P 3, distal phalanx; R, radius; S, scapula; T, tibia; U, ulna; cV, caudal vertebra. Elements from the left (l) or right (r) side of the body are marked respectively. Note that the right mandible was removed from this specimen and damaged. The reconstruction and position of the missing dentary is based on the work of Seemann (1938:fig. 36).
worn and poorly preserved, but all exhibit a talonid basin of similar size to the trigonid. There is no suggestion of a metastylid in any of the teeth. The protoconid is taller than the hypoconid, despite wear, and a distinct ectocingulum is present in all three molars. Lingually, the paraconids are very heavily worn whereas the metaconid and entoconid remain distinct and of similar height. The entoconid is exceptionally long in the m2 and m3, with a distinct entocristid that appears to limit the depth of the talonid notch. This character was poorly figured by Seemann (1938) and led Hutchison to suspect anteroposterior compression of the talonid basin in this group, thus strengthening its affinity to Mygalea antiqua. Hutchison (1974) also described persistent pre- and postcingulids based on Seemann’s (1938) figures. Although there is a suggestion of a posterior accessory cusp on the m2, our reconstructions show no evidence of pre- or postcingulids on the lower molars.

The second, third, and fourth premolars are double-rooted, with anterior and posterior crests that end with small cuspsules. The p1 is single-rooted and similar in size to the single-rooted canine and i3 (Seemann, 1938). The teeth increase in size from the p1 to p4, whereas the procumbent i1 and i2 are slightly larger than the i3. The anterior two incisors are spatulate in form, with the i1 larger than the i2, a pattern reversed in modern desmanins. The canine is incisiform and very similar in shape to the i3 and p1. There are no interdental gaps, and all the antemolar tooth crowns overlap slightly.

**Mandible**—Our description of the coronoid and angular processes follow Seemann (1938), due to damage (Fig. 5A–C). The coronoid, articular, and angular processes are well differentiated, with a posteriorly hooked coronoid process and thick, rounded angular process. There are two mental foramina, the first of which lies below the boundary of the canine and p1. The second is beneath the anterior root of the m1.

**Pectoral Girdle**—Both scapulae are only represented by their midlength of the manubrium. This is somewhat intermediate in form to the 'T'-shaped manubria of Galemys and Desmana (Campbell, 1939; Schreuder, 1940; Sánchez-Villagra et al., 2006), and to a lesser extent in shrew-moles such as Neurotrichus (Campbell, 1939; Reed, 1951; Sánchez-Villagra et al., 2006) and Urotrichus (Sánchez-Villagra et al., 2006). Unlike desmans, the clavicles of shrew-moles exhibit posterovertically projecting processes. Mygalea jaegeri exhibits such processes along its length (see Fig. 6F), although they are less pronounced than in the reconstructions of Neurotrichus produced by Reed (1951). The clavicle is also longer than those exhibiting such processes in the reconstructions of Campbell (1939).

The manubrium (Fig. 6R, S) has a distinct ventral keel, although this is far less pronounced than in highly fossorial forms. There are also distinct lateral wings projecting from the midlength of the manubrium. This is somewhat intermediate in form to the 'T'-shaped manubria of Galemys and Desmana and the anteroposteriorly elongated wings that project from the midlength of the shrew-mole manubrium (e.g., Scaptonyx and Neurotrichus Campbell, 1939; Reed, 1951). The broad posterior margin of the manubrium and its roughly equal length-to-width ratio are also reminiscent of the desmanin condition.

**Forelimb**—The humerus (Fig. 6A–E) is narrow, with the distal end wider than the proximal. The humeral head is elliptical (Fig. 6E), with its long axis roughly in line with the humeral shaft, from which the entire head is offset laterally. The floor of the bicipital groove has been displaced medially by the pectoral crest. The lesser tuberosity and pectoral crest just contact one another, forming a very short bicipital tunnel proximally (Fig. 6D). This partially encloses the passage of the biceps...
FIGURE 6. Digital models of the postcranial elements of *Mygalea jaegeri* (BSP 2008 LI280). Right humerus in anterior (A) and posterior (B) views. Left humerus in anterior (C), medial (D), and posterior (E) views. Right ulna in lateral (F), anterior (G), and medial (H) views. Distal fragment of right tibia in anterior (I), distal (J), and posterior (K) views. Left radius in posterior (L), medial (M), and mediodistal (N) views. Left clavicle in anterior (O), ventral (P), and posterior (Q) views. Manubrium in ventral (R) and anterior (S) views. Right scapula in ventral (T), glenoid (U), and dorsal (V) views; the arrow indicates the canal of the suprascapular nerve.
tendon, producing a bicipital tunnel much shorter than seen in extant desmans. This is different to Engesser's (2009) description of *Mygalea antiqua*, in which the bicipital groove is said to remain open, although his figured humerus (fig. 22) does appear damaged in this region. An open bicipital tunnel is only known from *Uropsilus* within the extant talpid radiation. Seemann (1938) described a well-developed clavicular facet on the greater tuberosity, although this facet is missing according to our micro-CT data. There is a distinct trough between the greater tuberosity and humeral head, visible in proximal view. The shaft is much more slender than in highly fossorial talpids, with the impression of lateral curvature. Its shape is reminiscent of both desmans and shrew-moles. The teres tubercle is medially extended, and proximodistally more elongate than in extant desmans. The pectoral crest is a prominent straight process and runs approximately half the length of the humeral shaft. It lacks a distinct distal process and is not met distally by a crest running from the greater tuberosity. The distal end of the humerus features large lateral and medial epicondyles. The lateral epicondyloide has a laterally projecting flange, which has the slightest proximally directed hook. This is very similar to the shape of *Desmana*. The medial epicondyle is hooked proximally. The pit for the M. flexor digitorum profundus is visible distally on the medial epicondyle, close to the midline of the humerus. Just above this, the medial epicondyle is perforated by the entepicondyar foramen, which opens into the deep supratrochlear fossa. The capitulum is roughly spherical, whereas the trochea is low, without a sharp medial border visible in the posterior view of the right humerus (Fig. 6A–B).

The bones of the forearm were described by Seemann (1938): The radius is slender and straight; the ulna is curved and narrower distally than proximally; the total size and depth of the longitudinal groove (or adductor fossa) are smaller than in *Talpa europaea*; and the olecranon is proportionally shorter than in *T. europaea*. The distal end of the ulna (Fig. 6F–H) is certainly much narrower than in *Talpa*, primarily due to a shorter styloid process and the absence of a pronounced posteriorly expanded terminal process (sensu Hutchison, 1968). The left radius is preserved (Seemann, 1938), and is gracile, lacking a pronounced capitular facet seen in highly fossorial forms (Fig. 6L–N).

We found only one proximal part of a terminal phalanx in this specimen, which reveals little about the animal's fossorial capability. However, *M. juegeri* lacks the remarkable lateral extensions of the digital flexor tubercle, which are present in both the *Talpini* and *Scalopini* at the palmar rim of the distal phalanx.

**Other Elements**—Seemann (1938: fig. 35) identified two vertebrae, suspecting that they came from the neck, along with some rib fragments. We have identified four bones from the slab as caudal vertebrae, along with a series of rib fragments. The preserved caudal vertebrae are relatively large in size, which is also seen in the long tailed extant desmans.

Our analysis allowed the identification of one further bone: the distal part of the right tibia (Fig. 6I–K). Like all extant talpids, this lacks the distal tibial bridge; however, it does show a distinct medial malleolus, which braces the side of the astragalus in life.

**TALPIDAE** Fischer von Waldheim, 1817

**SCALOPINII** Gill, 1875

**PROSCAPANUS** Gaillard, 1899

**PROSCAPANUS SANSA aniensis** (Lartet, 1851)

**Specimen: BSP 2008 L1282; Formerly IPW 282**—The genus *Proscapanus* is well known from the Miocene of Western Europe, including the species *P. austriacus* Ziegler, 2006, *P. intercedens* Ziegler, 1985, *P. minor* Ziegler, 2006, *P. lehmani* (Gibert, 1974), and the relatively common *P. sansaniensis*. One study assigned this genus to the Urotrichini (Van Valen, 1967), but the majority of work on this highly fossorial taxon has noted its scalopine affinities (Gaillard, 1899; Hutchison, 1974; Ziegler, 2003; Engesser, 2009). The genus shows a strong scalopine ridge on the humerus, an enlarged I1, and small p1. The majority of the extant Scalopini are North American, although one genus, *Scapanulus oweni*, is found in China. This biogeographic disjunction between extant and extinct Scalopini was hypothesized to be a consequence of an origin for the group in the Oligocene of Asia (Hutchison, 1974), with *Proscapanus* representing an extinct western radiation and the extant lineage the descendants of an eastern migration. The discovery of a specimen of *Proscapanus* in the late Oligocene of Kazakhstan (Lucas et al., 1998) lends weight to this theory.

The *Proscapanus sansaniensis* specimen (BSP 2008 L1282) was excavated by the Institut der Paläontologie der Universität Würzburg (IPW) in the 1930s from the Miocene brown coal mine at Viehhausen near Regensburg, Germany (MNS/6; Ziegler et al., 2005; Fig. 2). The specimen was transferred from its ignitary matrix to paraffin and relocated from Würzburg (Seemann, 1938; Hutchison, 1974; Ziegler, 1990) to the Bayerische Staatsammlung für Paläontologie und Historische Geologie (BSP) in Munich. This specimen helped to clarify the taxonomic problems surrounding *Proscapanus sansaniensis* (Hutchison, 1974). It provides a definitive association of a humeral form named ‘*Talpa sansaniensis*’ by Lartet (1851) and a mandibular form named ‘*Mygale sansaniensis*’ by the same author (Lartet, 1851), thus confirming Galliard’s (1899) reallocation of Lartet’s early specimens to the genus *Proscapanus*.

Specimen (BSP 2008 L1282; Fig. 7), an exception preserved partial talpid skeleton, was identified as the remains of *Proscapanus sansaniensis* by Seemann (1938). The specimen preserves a fully articulated right forelimb, including the humerus, radius, and ulna, along with several carpals and phalanges. Crucially, this is associated with fragments of the upper and lower dentition, as well as the left humerus, left scapula, right clavicle, and sternum, all of which were described in detail by Seemann (1938). In a recent redescription of French material, Engesser (2009) presented an amended diagnosis for the species. This is in close agreement with our material, reaffirming Seemann’s (1938) allocation. Due to the similarity of the material, a number of characters missing from specimen BSP 2008 L1282 have been coded into our phylogenetic analysis based on Engesser’s (2009) descriptions.

**Description**

**Upper Dentition**—The distal part of the left upper dentition is preserved (Fig. 8G–I), identified as P4, M1, M2, and M3 by Seemann (1938). All four teeth are in occlusion with the left lower posteriorly expanded terminal process (sensu Hutchison, 1968). The left radius is preserved (Seemann, 1938), and is gracile, lacking a pronounced capitular facet seen in highly fossorial forms (Fig. 6L–N).

We found only one proximal part of a terminal phalanx in this specimen, which reveals little about the animal’s fossorial capability. However, *M. juegeri* lacks the remarkable lateral extensions of the digital flexor tubercle, which are present in both the *Talpini* and *Scalopini* at the palmar rim of the distal phalanx.

**Other Elements**—Seemann (1938:fig. 35) identified two vertebrae, suspecting that they came from the neck, along with some rib fragments. We have identified four bones from the slab as caudal vertebrae, along with a series of rib fragments. The preserved caudal vertebrae are relatively large in size, which is also seen in the long tailed extant desmans.

Our analysis allowed the identification of one further bone: the distal part of the right tibia (Fig. 6I–K). Like all extant talpids, this lacks the distal tibial bridge; however, it does show a distinct medial malleolus, which braces the side of the astragalus in life.

**PROSCAPANUS** Gaillard, 1899

**PROSCAPANUS SANSA aniensis** (Lartet, 1851)
labially. The large P4 is triple-rooted, in agreement with Engesser (2009), with a lingual root beneath a small lingual cus- pule. Seemann (1938) could not identify the root number for this tooth, but noted the distal curvature of the main cusp and its accompanying distal crest. Beneath this is a clear distal cingulum. There is also a slight mesial cingulum on the P4, but no distinct parastyle.

The molars are distinctly dilambdodont, with a deep stylar shelf (Seemann, 1938) and high crested paracones and meta- cones. The M1 is triple-rooted, with a single lingual root. As See- mann (1938) observed, the M1 has no parastyle, in contrast to the French specimens (Engesser, 2009); its absence is unlikely to be taphonomic, because the tooth’s mesial surface is not obvi- ously damaged, and the M1 and P4 are in contact at their buccal margin. The mesostyle is deeply divided, as in the Scalopini. The metastylar region of the tooth is missing due to damage. The form of the M1 is quite distinct. Most talpid M1s are mesiodis- tally elongate, with the Talpini exhibiting a relatively narrow and pointed lingual region. Extant scalopins generally have a much broader lingual region, although this is divided into distinct lobes in both Parascalops and Scalopus. Proscapanus sansaniensis has a mesiodistally short M1 (although this is confounded by the loss of the metastylar region), with a broad, lobe-free lingual region. This form is most similar to the M1 of the Asian scalopin Scapanulus. Despite the absence of distinct lobes at its lingual margin, the protocone is surrounded by a distinct metaconule and a pron- nounced postmetaconule crista (see also Engesser, 2009). The paraconule is indistinct, because the preprotocrista is very high. It may be present proximal to the protocone, but this is far from certain in our digital reconstructions.

The second molar is shorter than the first and possesses a flat and massive mesostyle (Seemann, 1938). We suspect that this has suffered significant wear, obliterating any signs of mesostylar division. The parastyle and metastyle are distinct, but do not project from the main body of the tooth. The M2 bears a distinct paraconule and metaconule. The third upper molar is similar in size to the other molars. It is the least well preserved of all the teeth, although all three major cusps are present. The buccal roots are obliterated; however, a single lingual root can be identified in the digital reconstructions.

Lower Dentition—Our µ-CT data have revealed a complete lower dentition, 3.1.4.3, based on both mandibles (Fig. 8A–F). Seemann (1938) identified six complete teeth and a single broken root in the left mandible. The posterior five teeth are clearly p3 to m3; however, our images revealed roots, and some damaged crowns, for all teeth in the left mandible. There are three roots anterior to a complete incisiform tooth (Fig. 8A–C), which was previously identified as the i2 by Seemann. This tooth must instead represent a procumbent, incisiform canine. The right lower jaw was prepared from the back side of the slab for Seemann’s (1938) investigation of the dentition, before being recovered by paraffin. The digital reconstruction con- firmed the presence of a complete tooth row from c to m3, with three more anterior alveoli. The mandible bearing these teeth is broken just anterior to the m1, and the damaged molars reveal little of P. sansaniensis’ molar form.

Only the roots of the three left incisors are preserved, showing that the incisors were procumbent. The canines share this simple, single-rooted form, and lack any distal crest. The first premolar (p1) is similar in size to the p3, although both are slightly larger than p2 (see also Engesser, 2009). The last premolar (p4) is sig- nificantly larger than the other premolars, and it is the only one supported by two roots (Seemann, 1938). This tooth shows the

FIGURE 7. The partial skeleton of Proscapanus sansaniensis (BSP 2008 LI282) from the Lower Miocene deposits at Viehhausen, including a photograph of the specimen and a labeled drawing. Abbreviations: C, remains of cranium; Ce, centrale; Cl, clavicle; H, humerus; Lu, lunate; M, mandible; Ma, manubrium; Mc, metacarpal; P 2, central phalanx; P 3, distal phalanx; Pi, pisiform; R, radius; S, scapula; Se, scaphoid; Se, sesamoid; Ti, triquetrum; Tr, trapezium; U, ulna.
most complex form, with a distinct distal crest and posterior accessory cusp.

The molars are all of a similar size, the m2 being marginally longer than the other molars (contra Seemann, 1938). All are double-rooted with a mesiodistally wide hypoflexid. In all teeth the metaconid is higher than the entoconid. The m2 has distinct anterior and posterior accessory cuspids, with a strong precingulid. Although the hypoflexid is wide, there is no definitive evidence of a metastylid in any of the left molars. This is somewhat surprising, because metastylids are visible in the lower molars of *P. austriacus* (NHMW 2004z0196/0003-0005; see also Ziegler, 2006) and *P. minor* (Ziegler, 2006). However, both the m2 and m3 possess distinct metacristids at which the oblique cristid terminates (Engesser, 2009). The m1 lacks this crest, with the oblique cristid reaching the base of the metaconid (Engesser, 2009). Like the m2, the m3 has a prominent mesial cingulum and anterior accessory cusp.

**Mandible**—Both dentaries are damaged. There are two distinct mental foramina beneath the tooth row of the left dentary, the anterior-most ventral to the p2, and the posterior-most just beneath the p4–m1 border.

**Pectoral Girdle**—Only the humeral end of the left scapula is well preserved, showing an ovoid glenoid facet and a short, triangular acromion process (Fig. 9N–Q). This form of acromion is seen in extant Scalopini and Talpini, although the perforation of this process by a suprascapular foramen (see arrow in Fig. 9O) is only seen in extant Desmanini and Scalopini (Campbell, 1939; Sánchez-Villagra et al., 2006). The scapula has neither a distinct coracoid process nor a metacromion process.

The clavicles (Fig. 9R–S) are very stout and nearly quadratic, a form characteristic of extant highly fossorial moles. Seemann (1938) compared it with the clavicles of *Talpa europaea*, which are slightly longer than wide, with a distinct ventrally projecting process at their midline. The clavicle of *Proscapanus sansaniensis* is wider than long, with processes at its proximal and distal ends rather than the midline (Fig. 9R). These characters bear a much greater similarity to *Scapanus latimanus* (Bachman, 1842) (Campbell, 1939; Reed, 1951), reaffirming the scalopin affinities of *Proscapanus*. Seemann (1938) described a posterior foramen in the right clavicle; a similar but much smaller foramen is revealed in the left clavicle of our digital reconstructions. This seems to be a trait that varies greatly, not only between, but also within taxa; in *T. europaea* this foramen can lack consistent expression in a single individual. The specimen StIPB M7089 (from the collection of the paleontological section at the Steinmann Institut in Bonn; see Supplementary Data: Section 5) has a well-developed foramen in the right clavicle, but no opening in the left one.

Seemann (1938) was unable to give a detailed description of the manubrium (Fig. 9J–M), because it is preserved beneath the left clavicle. There is a deep keel on the ventral surface of the
FIGURE 9. Digital models of postcranial elements of *Proscapanus sansaniensis* (BSP 2008 LI282). Right humerus in anterior (A) and posterior (B) views; note that the humeral head is missing. Left humerus in anterior (C) and posterior (D) views. Right ulna in lateral (E), anterior (F), and medial (G) views. Proximally damaged right radius in lateral (H) and medial (I) views. Manubrium in right (J), anterior (K), posterior (L), and dorsal (M) views. Left scapula from glenoid (N) and anteroglenoid (O), anterior (P), and ventral (Q) views; note that the arrow in O indicates the canal of the suprascapular nerve. Right clavicle in posterior (R) and anterior (S) views. Remains of the right hand in palmar (T) and dorsal (U) views. Abbreviations: Ce, centrale; Lu, lunate; Mc, metacarpal; P2, central phalanx; P3, distal phalanx; Pi, pisiform; R, radius; Sc, scaphoid; Se, sesamoid; Ti, triquetrum; Tr, trapezium.
sternum, and although damaged, the main body of the sternum is slender, unlike the manubrium of soricids or desmans. There is the cranial end of a single groove in its dorsal surface, a character known from extant Scalopus, Talpa, Scaptochirus, and Mogera (Campbell, 1939). The lateral wings are broken off, so the sternum’s width remains uncertain.

Forelimb—The right humerus (Fig. 9A–B) is well preserved, although both the humeral head and medial epicondyle are damaged. The left humerus (Fig. 9C–D) preserves the proximolateral portion of the bone, including the humeral head. The general form is typical for highly fossorial moles; the bone is massive with widened proximal and distal ends, and strongly hooked processes. The humerus of *Proscapanus sansaniensis* is wider proximally than distally. The anteroproximal area is dominated by a large pectoral crest, which is distinctly superior to the greater tuberosity, creating a distinct notch between the two processes. This same notch is seen posteriorly, between the humeral head and the lesser tuberosity, and is noted as a distinctive characteristic of the Scalopini (Campbell, 1939). The pectoral crest almost completely hides the lesser tuberosity from anterior view and forms a tunnel for the biceps tendon. The crest also exhibits a near 90° turn at the bicipital notch, where the pectoral ridge (sensu Hutchison, 1974) meets the pectoral crest. This is again characteristic of highly fossorial taxa.

The greater tuberosity bears a large articulation facet for the clavicle on its posterolateral face. The deltoid process is also present, forming a distinct distally projecting spine. The humeral head is positioned posterior to the greater tuberosity and has a characteristic elliptical form. It is separate from the greater tuberosity based on the left humerus (Fig. 9D), but damage to the greater tuberosity precludes the identification of a distinct trough running between them. The greater tuberosity overhangs a deeply excavated brachial fossa. Medial to the humeral head is a strong ridge that runs proximomedially to the distal edge of the lesser tuberosity. Hutchison (1968) referred to this as the ‘scapoline ridge,’ which Campbell (1939) again described as a character unique to the Scalopini.

The teres tubercle is large, as in most fossorial talpids. The humeral shaft is relatively short and broad. The distal end of the pectoral crest meets a short crest projecting spine. The humeral head is positioned posterior to the greater tuberosity and has a characteristic elliptical form. It is separate from the greater tuberosity based on the left humerus (Fig. 9D), but damage to the greater tuberosity precludes the identification of a distinct trough running between them. The greater tuberosity overhangs a deeply excavated brachial fossa. Medial to the humeral head is a strong ridge that runs proximomedially to the distal edge of the lesser tuberosity. Hutchison (1968) referred to this as the ‘scapoline ridge,’ which Campbell (1939) again described as a character unique to the Scalopini.

The teres tubercle is large, as in most fossorial talpids. The humeral head is positioned posterior to the greater tuberosity and has a characteristic elliptical form. It is separate from the greater tuberosity based on the left humerus (Fig. 9D), but damage to the greater tuberosity precludes the identification of a distinct trough running between them. The greater tuberosity overhangs a deeply excavated brachial fossa. Medial to the humeral head is a strong ridge that runs proximomedially to the distal edge of the lesser tuberosity. Hutchison (1968) referred to this as the ‘scapoline ridge,’ which Campbell (1939) again described as a character unique to the Scalopini.

Both the right radius (Fig. 9F, I) and ulna (Fig. 9E–H) are preserved, although the proximal part of the radius is heavily damaged. The stout radial shaft is similar to that of *Talpa europaea* and *Scapanus latimanus* (Reed, 1951). Its distal end is widened for a broad contact with the carpals; in fact, they remain in articulation with the radius (Fig. 9T, U). Despite damage to the lateral expansion of the olecranon, it was clearly transversely broad and lunate in form. The adductor fossa forms a thin and deep plate of bone. A styloid process is mentioned by Seemann (1938) for both radius and ulna, at their distal ends. The stylloid process of the ulna, or more specifically its terminal process (sensu Hutchison, 1968), is expanded posteriorly in *Proscapanus sansaniensis*, as in *T. europaea* and *S. latimanus*.

Six carpals are preserved in this specimen (Fig. 9T, U). Seemann (1938) mentioned the scaphoid, the lunate, the triquetrum, and a bone, which she thought to be a pisiform. There is distinct ulnar expansion of the triquetrum. This character is seen in all extant talpids excluding the desmans and *Urotrachelus* (Sánchez-Villagra and Menke, 2005). The pisiform is present between the ulna and triquetrum. It is relatively small, but appears damaged, making the extent of palmar expansion hard to assess. The digital reconstruction confirms Seemann’s (1938) other identifications and shows that the scaphoid and lunate are unfused. The trapezium is distal to the scaphoid and has a simple triangular shape, lacking the distinct arms seen in many taxa (Sánchez-Villagra and Menke, 2005). A metacarpal and the proximal phalanx are articulated with the trapezium. A sesamoid bone is located between and slightly beneath the metacarpal and the trapezium. Similar bones are known in extant moles. Two terminal phalanges are preserved in this conglomerate of hand bones. Furthermore, there is one bone, identified by Seemann (1938) as a metacarpal, which seems to be the centrale based on our digital analysis.

**TALPIDAE** Fischer von Waldheim, 1817

**TALPINI** Fischer von Waldheim, 1817

**GEOTRYPUS** Pomel, 1848

**GEOTRYPUS MONTISASINI** Ziegler, 1990

**Specimens: SMNS 44523 (Holotype) and SMNS 43499—**Geotrypus is known from throughout the middle Oligocene and early Miocene of Europe. It is one of the more species-rich genera, currently with at least nine valid and up to five unnamed species (e.g., Lavocat, 1951; Ziegler, 1990; Crochet, 1995; Van den Hoek Ostende, 2001; Schwermann and Martin, 2012; Ziegler, 2012). Most recent studies assign Geotrypus to the base of the Talpini (Ziegler, 1990; Van den Hoek Ostende, 2001; Schwermann and Martin, 2012) based on characters such as a talpin-like lower dentition, featuring an incisiform canine and caniniform p1. Crochet (1995) suggested a placement within the Scaptonychini Van Valen, 1967, a tribe containing a single extant genus Scaptonyx (Hutterer, 2005). There are a number of similarities in the postcrania of *G. antiquus* and *Scaptonyx*, notably the presence of an elongate metacromion process of the scapula, and a non-quadrat frame. However, a reappraisal of Sánchez-Villagra et al.’s (2006) data set including *G. antiquus* resolved it as a basal talpin, to the exclusion of *Scaptonyx* (Schwermann and Martin, 2012), supporting the hypotheses of Ziegler (1990) and Van den Hoek Ostende (2001).

The holotype of *Geotrypus montisasini* (SMNS 44523; Fig. 10) was found in the Miocene (MN2a) of Ulm-Westtangente (Fig. 2) and described in German by Ziegler (1990). The specimen includes a chalk block with components of the upper and lower dentitions in association with a disarticulated partial skeleton. Postcranial material includes both radii, a damaged right ulna, a collection of disarticulated bones of the manus, and a near-complete left humerus, lacking only the complete medial epicondyle but exhibiting imperfect surface preservation. The second specimen discussed herein (SMNS 43499; Fig. 11) is contained within a chalk block from the Lower Freshwater Molasse of Haslach (MN2a). Originally it was described and figured by Jäger (1850). Ziegler (1990) also used it for the description of *G. montisasini*. It contains four bones of the left forelimb (scapula, clavicle, humerus, and radius) and a single, unidentified bony fragment. The humerus is complete and well preserved, featuring the medial epicondyle missing from the holotype specimen. Neither the clavicle nor the scapula is known from the holotype. The description of *Geotrypus montisasini* by Ziegler (1990) is diagnostic and detailed. Elements of this original description are repeated here in English, supplemented by our digital investigation of the material.

**Description**

**Upper Dentition—**As Ziegler (1990) mentioned, the skull of SMNS 44523 is heavily damaged, with only P2–M3 of the left
maxilla preserved (Fig. 12D, H, I). Both the P2 and P3 are double-rooted, simple unicuspid teeth with a slight posterior heel (Ziegler, 1990). Small pre- and postcingula are only present in P3 (Ziegler, 1990). P4 has three roots, the third in a lingual position beneath a slight expansion at the tooth’s base. It has an elongate and straight metacrista, a weak precingulum that may have supported a small parastylar cusp, and a lingual trigon, which has no protocone, but a thin entocingulum (Ziegler, 1990).

Ziegler (1990) described the molars as similar to Talpa europaea, with a narrow, sharpened, and undifferentiated lingual region. Our data revealed damage between the lingual and buccal regions of the tooth that obliterated any sign of the conules in the M1, although a small paraconule does appear to be preserved in the M2. Following Ziegler (1990), M1 has a prominent anteriorly projecting parastyle and a wide and slightly divided mesostyle. The mesostylar form is similar in M2 and neither tooth exhibits any cingula. The M3 is a much smaller tooth, with a single mesostyle and small metacone.

**Lower Dentition**—The description of Ziegler (1990) recorded a dental formula of 2.1.3.3, assuming a procumbent, single-rooted incisiform canine. The large left mandible fragment in SMNS 44523 only retains the most posterior of these procumbent anterior teeth (Fig. 12C, G, J), along with the alveoli of the remaining two. This is consistent with Ziegler’s (1990) description. A second mandibular fragment (SMNS 44523; Ziegler, 1990:pl. 8, fig. 2) contains at least three anterior teeth from the right side of the jaw (Fig. 12B, F). These are all single-rooted and procumbent, forming a tightly packed row of spatulate teeth. There are two root fragments positioned posteriorly to this, which lie at a different angle to the more anterior teeth. These
roots converge, suggesting that they both belong to a double-rooted tooth. Given the form of the other dental fragment and the lack of space for additional teeth, we believe that these two roots are best interpreted as those of the anterior-most premolar seen in the left mandible fragment. We thus maintain Ziegler’s (1990) dental formula. This means that the canine has the form of an incisor, and is inclined anteriorly, overlapping the two incisors based on the alveolar form and the small antemolar-bearing tooth fragment (Ziegler, 1990). It is worth noting that this formula does not correspond with that seen in *Scaptochiro*rus, and incisor loss in *Mogera*. In order to maximize the similarity with the tooth formulae of extant talpids, we follow Ziegler (1971) in assuming the i3 is lost in *G. montisasini*, as in *Mogera*, rather than Ziegler (1990) who hypothesized the loss of the i1.

All three premolars visible in the left mandibular fragment are double-rooted (Ziegler, 1990). The anterior-most premolar is the largest. It is caniform, a morphology seen in the p1 of modern Talpini (Ziegler, 1971). It is lingually convex and buccally more flat, without any cutting crests (Ziegler, 1990). There is also a weak entocingulid and a distal basal cusp (Ziegler, 1990). The following two premolars overlap each other slightly and have sharp mesiodistally oriented ridges running across the primary cusp, accentuated by posterior cingulids (Ziegler, 1990).

The molars decrease in size from anterior to posterior (Ziegler, 1990). The trigonid is raised above the talonid in m1 and m2, but not in m3 (Ziegler, 1990). All molars have a low paraconid relative to the other cusps, with the tallest lingual cusp being the metaconid. There are no ecto- or entocingulids in any molar, nor any pronounced mesial or distal cingulid. There are anterior accessory cuspsids on the m2 and m3 and posterior accessory cuspsids on the m1 and m2. In all molars the oblique cristid slopes down mesially and ends in a position distal to the back wall of the trigonid, and more buccally in m1 and m2 than the m3 (Ziegler, 1990). Neither the entocristid nor metaenacristid is developed in the lower molars of *G. montisasini* (Ziegler, 1990). This results in a deep talonid notch, which opens at the base of the talonid basin in lingual view.

**Mandible**—The distal part of the left dentary is preserved in this specimen along with fragments of the ascending ramus (Fig. 12C, G). Ziegler (1990) noted the high anteroposterior length of the ascending ramus, which is more distinct in a second mandibular specimen (SMNS 44522; Ziegler, 1990:pl. 8, fig. 2), as well as the position of the articular process above the level of the dentition. The embedded buccal surface of the mandible is damaged, yielding no information about the mental foramina (Fig. 12G).

**Pectoral Girdle**—A fragment of the manubrium was the only element of the pectoral girdle identified by our μ-CT investigation of the holotype (Fig. 13P–S), although this was not previously known. The manubrium shows a deep ventral keel and distinct anteriorly positioned clavicular facets. The anterior base of the lateral wings is visible at the posterior margin of the fragment, but the processes are broken off. There is no indication of their width. The dorsal surface appears worn, although there is no direct evidence of the trough seen in the extant highly fossorial talpids.

Specimen SMNS 43499 preserves both a scapula fragment (Fig. 13N, O), which was also identified by Jäger (1850) and Ziegler (1990), and a left clavicle (identified by our μ-CT investigation; Fig. 13L–M). Ziegler (1990) noted the presence of a short, triangular (deltoid) metacromion process on the humeral end of the scapula. This process is considered lost in the extant Scalopini and Talpini (Campbell, 1939; Sánchez-Villagra et al., 2006), which simply possess a smaller deltoid acromion. The process in *Geotrypus montisasini* is distinct, appearing to develop from the distal edge of the acromion. It is, however, much shorter than that reported in *Geotrypus antiquus* by Schwermann and Martin (2012). The base of the acromion is not perforated by a foramen.

The clavicle is stout, almost quadrangular in form (Fig. 13L–M). This differs again from the more rectangular form seen in *Geotrypus antiquus* and suggests an increased level of fossorial adaptation in *G. montisasini*. There are no obvious ventral processes on the clavicle, although the posterior view (Fig. 13M) has the slightest suggestion of a process at the midline of the shaft. Such midline processes are common in extant Talpini, such as *Talpa europaea*, whereas scalopin moles tend to exhibit proximal and distal expansions of the ventral clavicular surface as seen in *Proscapamus* (Fig. 9R).

**Forelimb**—Both the holotype (SMNS 44523; Fig. 13C, D) and its accompanying specimen from Haslach (SMNS 43499; Fig. 13A, B) include information on humeral form. There is a very small gap between the teres tubercle and medial epicondyle in the Haslach specimen (Fig. 13A). This shape gives the humerus an unusual compressed appearance, with the elongated teres tubercle in a more distal position than expected for a highly fossorial talpid. However, the expansion of the pectoral crest over the lesser tuberosity to form an elongate bicipital tunnel at right angles to the humeral shaft (Ziegler, 1990), the hooked shape of the deltoid process and lateral epicondyle, and the wide, robust humeral habitus all suggest a highly fossorial animal.

Ziegler (1990) identified a ‘flat, bent scalopine ridge’ on the posterior surface of the humerus. In both specimens, the ridge...
FIGURE 13. Digital models of postcranial elements of *Geotrypus montisasini* (SMNS 43499: A, B, I–O; SMNS 44523: C–H, P–S). Left humerus in anterior (A) and posterior (B) views. Left humerus in anterior (C), posterior (D), and medial (E) views. Right ulna in lateral (F), anterior (G), and medial (H) views, along with a photo of the original specimen showing an impression of the distal part of the ulna in the matrix (I). Left radius in medial (J) and lateral (K) views. Left clavicle in anterior (L) and posterior (M) views. Left scapula in anterior (N) and posterior (O) views. Manubrium in anterior (P), dorsal (Q), lateral (R), and posterior (S) views.
and three terminal phalanges are preserved, some of them and a pisiform, and tentatively recognize the triquetrum and case in G. antiquus (Campbell, 1939), although the capitular process is more developed than that of (Campbell, 1939), although the capitular process is more similar to that of other Talpini, such as Ziegler (1990) noted the distinct capitular process of the humeral head. A deeply excavated branchial fossa is present posterior to the greater tuberosity, beneath the humeral head. The deltoid process is distinct and proximally elongate in the Haslach humerus (Fig. 13A, B). There is also a distinct crest running from the greater tuberosity to the distal end of the pectoral ridge; their convergence in this specimen forms the flat, triangular pectoral tubercle that is seen in most highly fossorial talpids.

Distally, the holotype humerus (SMNS 44523) has a damaged medial epicondyle, although Ziegler (1990) described the entepicondylar foramen, which passes from the supratrochlear fossa to open distal to the teres tubercle. The fossa for the ligament of the M. flexoris digitorum profundus was also described as being ‘strongly distocranially directed.’ Both characteristics are confirmed by the Haslach humerus, which also preserves an elongate proximally directed spine on the medial epicondyle. The lateral epicondyle retains a small proximally directed hook in the holotype, which is much stronger in the better-preserved Haslach humerus. Both specimens retain a large, ovoid capitulum, with a sharp medial border to the trochea. In addition to these two left humeri, a part of the right humerus of the holotype specimen was identified using the μ-CT images (Fig. 10). It includes the proximolateral part of the humerus, including the oval-shaped humeral head.

The bones of the forearm are preserved in the holotype. Ziegler (1990) noted the distinct capitular process of the radius along with its dorsally widened distal end. The form is very similar to that of other Talpini, such as Talpa europaea (Campbell, 1939), although the capitular process is more developed than that of Geotrypus antiquus (Schwermann and Martin, 2012). Only the right ulna is preserved. Its distal end is visible, both showing expansion at right angles to their long axis. There is an ovoid bulge at the distal end of the ulna. We interpret this as a small posteriorly projecting terminal process at the end of the styloid process, which correlates with the broadening of the hand. However, because the X-ray is unclear, this structure warrants further investigation. It could represent a separate element, either a part of the pisiform or an additional sesamoid bone. The latter is seen in Condylura, Urotichus, and Desmana (Sánchez-Villagra and Menke, 2005). Scapanulus is missing from their sample, and due to the lack of information on this taxon in the literature, we include a brief description of its manus here, based on X-ray images of the skull of Scapanulus oweni (NMNH 240757; Fig. 14) obtained on a recent visit to the Smithsonian Institution in Washington, D.C., by R.S.T.

The distal end of both the radius and ulna are visible, both showing expansion at right angles to their long axis. There is an ovoid bulge at the distal end of the ulna. We interpret this as a small posteriorly projecting terminal process at the end of the styloid process, which correlates with the broadening of the hand. However, because the X-ray is unclear, this structure warrants further investigation. It could represent a separate element, either a part of the pisiform or an additional sesamoid bone. The latter is seen in Condylura, Urotichus, and Desmana (Sánchez-Villagra and Menke, 2005), where it is smaller and located more laterally to the triquetrum than in our Scapanulus specimen. The width-to-length ratio of the manus (character 174; 1.68) is somewhat intermediate to semi-fossorial shrew-mole taxa (e.g., Neurotrichus gibbsii = 1.46; Urotichus talpoides = 1.2) and highly fossorial taxa (Scapanus townsendii = 2.71; Talpa europaea = 1.82). The proximal carpals are all easily identifiable. The scaphoid and lunate are not fused, because there is a distinct suture visible between them. Like the majority of talpids, the triquetrum is expanded with an elongate ulnopalmar process. There is no sesamoid lateral to the triquetrum. The centrale is present in the manus, intermediate to the two carpal rows. The hamate and capitare are both distinct beneath the metacarpal row. Unfortunately, the suture between the trapezium and trapezoid cannot be identified, and it is unclear whether the former shows the distal arms present in some taxa. The prepollex is distinct, contacting the scaphoid and radius. It is relatively short when compared with the highly fossorial forms, only just reaching the level of the first metacarpal: again intermediate to the shrew-moles and highly fossorial taxa. The form of the prepollex is also unusual; it has a distinct posteriorly directed angle, giving the bone a broader base. This form is very similar to Parascalops, a taxon with which Scapanulus shares a number of synapomorphies. This form is also similar to that seen in Geotrypus antiquus (Schwermann and Martin, 2012), although the prepollex of Scapanulus is smaller than that of both Geotrypus and Parascalops.

**CLADISTIC ANALYSIS**

The results of the cladistic analyses are summarized in Figure 15. The analysis including the exceptionally preserved
talpid specimens in combination with the extant radiation produced six most-parsimonious trees (MPTs) of 614 steps, resulting in a well-resolved strict consensus topology (Fig. 15A) that closely resembles that of Sánchez-Villagra et al. (2006). Only Parascaptor and Scaptonyx exhibit novel topological placements, both of which received additional character scores in our study. Parascaptor is here resolved as the sister taxon to Talpa, and Scaptonyx as the sister of Neurotrichus rather than the Talpini.

Both Mygalea jaegeri and Geotrypus montisasini are recovered in polytomies, the former with the Desmanini and more fossorial talpid forms (node X), the latter with the two highly fossorial tribes Talpini and Scalopini. Both Domninoides mimicus and Proscapanus sarsanienis are recovered as members of the Scalopini. The former is the sister taxon to Scapanulus and Parascalops, with which it shares a double-grooved dorsal surface of the manubrium and a lower molar metastylid. Finally, Geotrypus antiquus is recovered as the sister group to the extant Talpini, in agreement with the findings of Schwermann and Martin (2012). A number of clades are well supported (branch support [BS] > 5; bootstrap > 70%) by both bootstrap and branch support indices (e.g., Talpidae, all non-uropine talpids, and the Scalopini-Scapanus sister group), although the presence of fossil taxa at a node generally results in bootstrap support lower than 50% and a BS not higher than 2. The placement of Geotrypus montisasini in a trichotomy with Talpini and Scalopini is a notable exception, with a BS of 3 and bootstrap of 62%.

The addition of the two Eotalpa species to the analysis destabilized the phylogeny, producing 208 MPTs of 615 steps. This resulted in a poorly resolved strict consensus topology (Fig. 15B), in which the two Eotalpa species are resolved in a large polytomous clade with the more fossorial talpids (Talpini, Scalopini, Condylura, Scaptonyx, and Neurotrichus). The 50% majority rule consensus tree shows that the two Eotalpa species are most frequently attracted to the other extinct groups (excluding Domninoides and Mygalea), resulting in a polytomy of these taxa and the monophyletic Talpini and Scalopini. This suggests that Eotalpa is likely to represent a stem highly fossorial talpid.

The two constraint analyses (Fig. 15C, D) represent two molecular hypotheses of talpid systematics. Both constraint topologies are substantially longer than the most parsimonious tree (Fig. 15C, representing the Shinohara et al. [2004] constraint, is 39 steps longer and Fig. 15D, representing the Crump-ton and Thompson [2013] constraint, is 43 steps longer than Fig. 15A). Both constraint analyses improve the resolution of the fossil taxa, a phenomenon observed previously when applying molecular constraints to paleontological data (Asher et al., 2005). Geotrypus montisasini is resolved, somewhat surprisingly, as a basal scalopin, and Mygalea jaegeri as a desmanin. The relationships within Scalopini also vary substantially in these analyses, with the monophyletic clade of Domninoides, Scapanus, and Parascalops seen in the unconstrained topology (Fig. 15A) broken into a basal paraphyletic assemblage (Fig. 15C, D).

DISCUSSION

After completing their own morphological studies on the extant talpid radiation, both Whidden (2000) and Sánchez-Villagra et al. (2006) suggested incorporating fossil talpids into a phylogenetic framework. The phylogeny presented here is the first published analysis of multiple extinct talpids using a cladistic methodology. A recent paper by Meier et al. (2013) featured a composite phylogeny that positioned a number of extinct talpids in an extant phylogeny based on the taxonomic opinions expressed in the paleontological literature (e.g., Hutchison, 1974; Ziegler, 1999) rather than cladistics. Sánchez-Villagra et al. (2004) provided character codes for the humeri of 18 extinct talpid taxa, but never presented an analysis of these data. The only recent cladistic study to include fossil talpids is that of Schwermann and Martin (2012), which included a single taxon, Geotrypus antiquus, in the original Sánchez-Villagra et al. (2006) matrix.

The differences between our unconstrained topology (Fig. 15A) and that of Sánchez-Villagra et al. (2006) are primarily a consequence of scoring character data missing for some extant taxa in the original analysis. The addition of multiple...
Schwermann and Thompson—Fossil talpids and evolution of fossoriality (e934828-18)

Constraint: Shinohara et al. 2004

Constraint: Crumpton & Thompson 2013
extinct taxa has had little impact on the extant topology (Fig. 15A). The combination of dental and postcranial characters has allowed more decisive placement of these fossil groups, resulting in a well-resolved consensus topology. The poor resolution of the phylogeny incorporating the two Eotalpa species (Fig. 15B), based entirely on dental material, highlights the potential for fossils that sample few characters from limited partitions of the data set (in this case dentition) to reduce resolution (Pattinson et al., 2015). Our exceptionally preserved fossil talpid specimens represent a diverse subset of the family, including a member of the desmanin/shrew-mole grade, two scalopins, a talpin, and a basal highly fossorial form. This diversity, combined with good resolution, has allowed the extinct taxa to influence the pattern of character evolution across the tree. This is particularly interesting when we consider the distribution of characters linked to fossoriality. The presence of Geotrypus antiquus at the root of the Talpini (Fig. 15A) suggests the potential independent evolution of a number of these characters in the Scalopini and Talpini. Such changes make independent specialization into a highly fossorial niche in the Scalopini and Talpini plausible. This finding is interesting because when reconstructing talpid evolution using morphology alone, there is the potential for characters correlated with extreme fossoriality, found in both Scalopini and Talpini, to draw these taxa together. Such a similarity in fossorial adaptations may represent a true phylogenetic signal or be a consequence of ancestral constraints. Indeed, long-standing theories of an aquatic origin for the Talpidae (Campbell, 1939) were recently supported based on studies of their myoglobin (Mirzeta et al., 2013). If the earliest adaptations for fossoriality in the Talpidae evolved in a semiaquatic animal, the mode of digging in the whole clade could be constrained to allow their forelimb to also function as a paddle. This could explain the unusual tunneling technique seen in the Talpidae, as well as constraining the two highly fossorial tribes to adapt to a fully subterranean life in the same way. By including fossil specimens in our analyses, we have incorporated taxa, such as Geotrypus antiquus, G. montisatis, and Proscapanus sansaniensis, whose character complement includes a mixture of fossorial and semi-fossorial postcranial adaptations, coupled with either talpin or scalopin craniodental traits. Their placement towards the roots of both the Talpini and Scalopini is at least suggestive of convergence between the highly fossorial tribes, providing some level of consensus between talpid phylogenies with dramatic topological differences.

The Phylogeny of the Extant Talpidae

The topological differences between the Sánchez-Villagra et al. (2006) results and the unconstrained topology presented here (Fig. 15A) are small, with only Parascaptor and Scaptonyx exhibiting novel interrelationships. The Scaptonyx-Neurotrichus clade is maintained even in the absence of fossil taxa. In contrast, Parascaptor is recovered in a polytomy with Scaptochirus, Mogera, and Eurosaptor in an extant-only data set, rather than in a sister-group relationship with Talpa in the presence of the fossil taxa. This highlights the potential for improved resolution with the inclusion of fragmentary fossils. Regardless, it is clear that the morphological characters coded for the first time in this study are responsible for the topological differences between our analyses and those of Sánchez-Villagra et al. (2006).

Our Talpa-Parascaptor sister group receives little clade support, like the rest of the internal relationships of the Talpini (Fig. 15A). There is great uncertainty about the internal relationships of the extant Talpini in both our different topologies and in the literature. In contrast to Sánchez-Villagra et al. (2006), most molecular data sets suggest that Mogera and Eurosaptor are sister taxa, to the exclusion of Talpa (Yates and Moore, 1990; Tsuchiya et al., 2000; Shinhohara et al., 2003, 2004, 2005, 2008; Cabria et al., 2006; Colangelo et al., 2010). Furthermore, the genus Eurosaptor is often found to be paraphyletic in both molecular (Shinhohara et al., 2005, 2008; Colangelo et al., 2010; Crumpton and Thompson, 2013; He et al., 2014) and morphological (Motokawa, 2004) studies, whereas both Parascaptor and Scaptochirus are little studied; the former has only recently been included in a molecular phylogeny (He et al., 2014). In this study, the interrelationships of the Talpini are investigated using a relatively large molecular data set (~10 kb) that also supports the paraphyly of Eurosaptor and a sister-group relationship between Scaptochirus and Parascaptor, which themselves form nested sister clades with Eurosaptor (to the exclusion of E. mizura), Mogera, E. mizura, and finally Talpa. Although our new morphological characters do not resolve Scaptochiris and Parascaptor as sister groups, as in this most recent molecular hypothesis, they do help to recover a monophyletic clade of Parascaptor, Mogera, Scaptochirus, and Talpa. This group was not recovered by Sánchez-Villagra et al. (2006) but is a hypothesis consistent with He et al. (2014) and many other phylogenies (e.g., Cabria et al., 2006; Shinhohara et al., 2008; Crumpton and Thompson, 2013). The topology of He et al. (2014) is presently the standard for talpin systematics, due to its extensive character and taxon sampling. However, only with species level sampling of molecular, morphological, and paleontological data will a complete understanding of this clade of highly fossorial talpids be reached.

The placement of Scaptonyx in a clade with the American shrew-mole, Neurotrichus, as suggested by Whidden (2000), rather than the sister-group relationship with the Talpini seen in Sánchez-Villagra et al. (2006), is better supported. Since its first description in 1871 by Milne-Edwards, the monotypic genus Scaptonyx has been something of an enigma. Milne-Edwards noted that Scaptonyx “looks like a mole with the feet of Urotichus, or Urotrichus with the head of a mole” (Nowak, 1999:233). Its placement as the sister taxon to the Talpini in both the analyses of Motokawa (2004) and Sánchez-Villagra et al. (2006) is therefore likely due to the cranial bias of their sampled characters. The Scaptonyx dentition and skull are rather talpin-like in general form, with elongate upper canines (characters 10:1, 30:2, 31:1, 32:0) and relatively small and spatulate upper incisiform teeth positioned at the anterior edge of the rostrum. Inspection of the complete postcranial specimen from the Smithsonian Institution (USNM 574303) revealed a number of characters that it shares with less fossorial forms. The small but elongate metacromion process of the scapula (81:1), elongate humerus (92:2; 31:1, 32:0) and relatively small and spatulate upper incisiform teeth positioned at the anterior edge of the rostrum. Inspection of the complete postcranial specimen from the Smithsonian Institution (USNM 574303) revealed a number of characters that it shares with less fossorial forms. The small but elongate metacromion process of the scapula (81:1), elongate humerus (92:2; 31:1, 32:0) and relatively small and spatulate upper incisiform teeth positioned at the anterior edge of the rostrum.

—FIGURE 15. Phylogenies of the Talpidae based on our expanded version of the Sánchez-Villagra et al. (2006) matrix analyzed under a parsimony framework in PAUP*. Major taxonomic groups are labeled in all trees. A, unconstrained strict consensus topology excluding both Eotalpa species, derived from six most-parasimous trees (MPTs) of 64 steps. Node numbers represent clad numbers; those above nodes are branch supports (Bremer, 1988, 1994) and those below nodes are bootstrap percentages. Nodes lacking numbers have a branch support of 1 or bootstrap support lower than 50%; B, unconstrained strict consensus topology including both Eotalpa species, derived from 208 MPTs of 615 steps. C, strict consensus topology excluding both Eotalpa species and constrained to the topology of the molecular phylogeny of Shinhohara et al. (2004). The consensus tree is derived from four MPTs of 645 steps. D, strict consensus topology excluding both Eotalpa species and constrained to the topology of the molecular phylogeny of Crampton and Thompson (2013). The consensus tree is derived from six MPTs of 657 steps.
(125:2) are all plesiomorphic, based on our unconstrained analysis (Fig. 15A). However, the presence of broad lateral wings on a long manusbrum (84:1), a prominent process at the end of the pectoral crest (93:2), and a double-rooted P4 (11:1) all unambiguously optimize to the Scaptonyx-Neurotrichus clade. Those molecular studies that include Scaptonyx (Shinohara et al., 2004, 2005; Crompton and Thompson, 2013) also conflict with the placement of Scaptonyx in a sister-group relationship with the Talpini. Indeed, the most recent analysis (Crompton and Thompson, 2013) is in agreement with the placement recovered here. Regardless, it seems likely that either the dental or postcranial similarities to other talpid taxa are the product of convergent evolution in Scaptonyx. Although the postcranial similarities between Scaptonyx and other shrew-mole taxa seem to dominate its placement in this analysis, the biogeographic disjunction between the Asian Scaptonyx and North American Neurotrichus could still be viewed as an argument against the hypothesis of their close relatedness. More thorough character sampling is required to test this hypothesis of relatedness prior to any taxonomic revision.

The Phylogenetic Placement of the Extinct Talpids

Mygalea jaegeri—Mygalea is recovered in a polytomy with the Desmanini and more fossorial talpids (node X) in our strict consensus tree (Fig. 15A). In all of the MPTs, Mygalea groups with either the Desmanini, as in both constraint trees (Fig. 15C, D), or at the root of the more fossorial talpid clade (node X). The two shrew-mole clades, Urotrichini and Scaptonychini (Van Valen, 1967) (or Neurotrichini [Hutterer, 2005] depending on preference) surround this node, with Urotrichini one node basal and Scaptonychini one node more derived. Mygalea's placement therefore reflects its similarity to both desmans and shrew-moles, noted in our redescription. However, it is notable that Mygalea is recovered as a stem desman in both constraint analyses, where the distance between the Desmanini and Scaptonychini is increased.

In those MPTs that recover Mygalea as a stem desman, two characters unambiguously support the clade: the deep division of the mesostyle (19:3) and the presence of a supracapular canal through the base of the acromion process (78:1). Both of these characters are also known convergently in the Scalopini. The clavicular form of Mygalea, which differs dramatically from extant desmans due to its relatively shorted length and the presence of a small ventral process, is resolved as a plesiomorphic character. The same form is seen in both clades of shrew-moles and seems to have evolved early in the talpid lineage. When recovered as the sister group to the more fossorial taxa (node X), only a single character unambiguously unites the group: a humerus with a width between one-quarter and one-fifth of its length (92:2). In our unconstrained topology (Fig. 15A), in which we reconstruct a gradual increase in fossorial capability across the talpids. Those molecular studies that include Scaptonyx (Shinohara et al., 2004, 2005; Crompton and Thompson, 2013) also conflict with the placement of Scaptonyx in a sister-group relationship with the Talpini. Indeed, the most recent analysis (Crompton and Thompson, 2013) is in agreement with the placement recovered here. Regardless, it seems likely that either the dental or postcranial similarities to other talpid taxa are the product of convergent evolution in Scaptonyx. Although the postcranial similarities between Scaptonyx and other shrew-mole taxa seem to dominate its placement in this analysis, the biogeographic disjunction between the Asian Scaptonyx and North American Neurotrichus could still be viewed as an argument against the hypothesis of their close relatedness. More thorough character sampling is required to test this hypothesis of relatedness prior to any taxonomic revision.

The Phylogenetic Placement of the Extinct Talpids

Mygalea jaegeri—Mygalea is recovered in a polytomy with the Desmanini and more fossorial talpids (node X) in our strict consensus tree (Fig. 15A). In all of the MPTs, Mygalea groups with either the Desmanini, as in both constraint trees (Fig. 15C, D), or at the root of the more fossorial talpid clade (node X). The two shrew-mole clades, Urotrichini and Scaptonychini (Van Valen, 1967) (or Neurotrichini [Hutterer, 2005] depending on preference) surround this node, with Urotrichini one node basal and Scaptonychini one node more derived. Mygalea's placement therefore reflects its similarity to both desmans and shrew-moles, noted in our redescription. However, it is notable that Mygalea is recovered as a stem desman in both constraint analyses, where the distance between the Desmanini and Scaptonychini is increased.

In those MPTs that recover Mygalea as a stem desman, two characters unambiguously support the clade: the deep division of the mesostyle (19:3) and the presence of a supracapular canal through the base of the acromion process (78:1). Both of these characters are also known convergently in the Scalopini. The clavicular form of Mygalea, which differs dramatically from extant desmans due to its relatively shorted length and the presence of a small ventral process, is resolved as a plesiomorphic character. The same form is seen in both clades of shrew-moles and seems to have evolved early in the talpid lineage. When recovered as the sister group to the more fossorial taxa (node X), only a single character unambiguously unites the group: a humerus with a width between one-quarter and one-fifth of its length (92:2). In our unconstrained topology (Fig. 15A), in which we reconstruct a gradual increase in fossorial capability across the talpids, Mygalea seems to represent a transitional form in the evolution of semiaquatic taxa from a semifossorial stock.

Proscapanus sansaniensis—This species is recovered as a stem scapanus in our unconstrained and constrained topologies. This placement is in line with our expectations based on our redescription of this taxon, its geologic age in comparison with extant taxa and is in agreement with previous authors (Gaillard, 1899; Hutchison, 1974; Ziegler, 2003; Engesser, 2009). Proscapanus is united with the Scalopini based on three unambiguous synapomorphies in the unconstrained analysis: a supracapular canal perforating the base of the acromion process of the scapula (78:1), the absence of a metacromion process of the scapula (81:0), and the presence of a deep scalopine ridge (171:1). A further 18 characters optimize to this node ambiguously, five of which are related to the anatomy of the forelimb (ACCTRAN: no trough between the greater tuberosity and the humeral head [102:0], a wedge-shaped clavicular facet [108:2], a broad manus [174:3]; DELTRAN: a short broad humerus [92:3], a long greater tuberosity [106:1]), suggesting an increased level of fossorial specialization in the group. Four of these character states occur independently within Talpini (81:0, 92:3, 102:0, 106:1), suggesting some potential for convergence between the two highly fossorial clades even when they are recovered as sister groups.

The placement of Proscapanus at the base of our scalopine clade could be used to suggest a Eurasian origin for the Scalopini. The extant Scalopini are predominantly North American, although Scapanulus oweni is only found in China. The Neogene radiation of the Scalopini is believed to be much more cosmopolitan, with Scalopoides known from the Oligocene and Miocene of the U.S.A. (Hutchison, 1968) and Europe (Hutchison, 1974; Dahlmann, 2001), Yanshuella from the Neogene of Mongolia (Storch and Qui, 1983), and Leptoscaptor from the Miocene of Germany (Ziegler, 2003). The confirmation of scalopine affinities for the European Proscapanus sansaniensisis based on a cladistic analysis strengthens previous hypotheses of an Asian origin for the group (e.g., Hutchison, 1974; Whidden, 2000). Regardless, further extinct putative scalopine taxa should be sampled to provide a more robust test of their phylogenetic affinities, and thus the proposed models for their biogeographic radiation.

Domminoides mimicus—This species is here recovered as the sister group of Scapanulus and Parascalops, nested within the extant scalopine radiation (Fig. 15A). In her detailed description of the AMNH specimen, Freeman (1979) noted strong similarities between D. mimicus and both Scalopus and Parascalops. Although she did not go so far as to suggest its closest relative, its placement in the Scalopini was found to be unequivocal. The affinity with the Parascalops-Scapanulus clade recovered by our unconstrained analysis is driven by the shared presence of a metastyloid in the lower molars (48:1) as well as the presence of a ridge on the dorsum of the manusbrum (158:2) and a ventral process on the clavicle (164:1), all of which optimize as unambiguous synapomorphies of the clade. The latter two characters are based on material recovered from the same locality as that described by Freeman (1979), and recorded under the same specimen number, but with slightly differing preservation. This includes a damaged humerus, clavicle (with a very small medially directed ventral process), astragalus, and manusbrum.

The placement of Domminoides shows a degree of plasticity in the constraint analyses. Under the Crompton and Thompson (2013) constraint tree, Domminoides, Parascalops, Scapanulus, and the Scapanus-Scalopus clade are resolved in a polytomy (Fig. 15D). The Shinohara et al. (2004) constraint tree produces a better-resolved topology in which Scapanulus, Parascalops, and Domminoides form successively nested sister groups to the Scalopus-Scapanus clade. This latter topology (with which the former is consistent) is particularly interesting. The placement of Scapanulus (and Proscapanus) at the root of the clade is congruent with the biogeographic evidence that suggests an Asian origin for the group (Hutchison, 1974). Furthermore, this topology suggests an increase in fossoriality through the extant scalopine radiation: Scapanulus is clearly the least fossorial of the Scalopini, with relatively elongate humerus and manus and comparatively short propallex. Domminoides, Scalopus, and Scapanus thus form a clade of highly fossorial forms, to the exclusion of Parascalops, which Freeman (1979) and Campbell (1939) consider ‘a more generalized talpid.’ Of course, the placement of
Proscopanus as a stem Scalopin somewhat disturbs this smooth transition due to its robust humeral form, although it is possible that this specimen represents a second origin of extreme fossoriality within the now extinct Oligocene-Miocene Eurasian scalopin radiation.

One additional line of evidence in support of the topology produced by the Shinohara et al. (2004) constraint tree (Fig. 15C) is the striking similarity in clavicular form between the three highly fossorial groups. Both Scalopus and Scapanus lack a ventral process of the clavicle, but this appears to be caused by a massive increase in the size of the bone’s main body, which essentially closes the gap to the process. Remnants of a small process are visible as a fold of bone in posterior view (R. S. Thompson, pers. observ.). Although Domninoides retains a ventral process, it is very small, and almost completely obscured by the robust main body of the clavicle. This clavicular body is much more robust than seen in either Parascalops or Scapanus, and a level of continuity between the forms is certainly discernable. Domninoides could therefore represent a transitional form in the evolution of the more highly fossorial of American talpids.

Geotrypus antiquus—The placement of Geotrypus antiquus as the sister group to the extant Talpini (Fig. 15A) is consistent with the findings of Schwermann and Martin (2012), and is unaffected by either molecular constraint. Affinities with the Talpini were suggested previously by Ziegler (1990) and Van den Hoek Ostende (2001), and are unsurprising given both its dentition and robust forelimb skeleton. However, the specimen described by Schwermann and Martin (2012) does introduce a number of surprising characters to the root of the talpid clade. G. antiquus has a distinct metacromion process on the scapula, lacks the terminal process of the ulna, and has a very weak capitular process of the radius. Such traits are generally seen in the less fossorially specialized talpids, such as Condylura and Neurotrichus. Furthermore, its clavicle is quite different to other talpins, lacking a distinct ventral process and being somewhat more elongate. All of these traits allow us to interpret G. antiquus as the least fossorial of the Talpini and suggest that a number of plesiomorphic, shrew-mole-like characters may have been present in the last common ancestor of the Talpini and Scalopini. G. antiquus therefore provides a crucial line of morphological evidence to support the hypothesis of the independent specialization for extreme fossoriality in the Talpini and Scalopini. However, it is important to note that under the current topology, the majority of these characters are reconstructed as reversals within the G. antiquus lineage. Of the aforementioned characters, only the loss of the metacromion process is resolved as convergent between the Talpini and Scalopini as a consequence of G. antiquus’ placement.

Geotrypus montisasini—Of all the taxa added to our data set, the placement of Geotrypus montisasini is the most problematic. Its postcranial anatomy is indicative of a highly fossorial talpid, and its dentition appears talpin, yet in our unconstrained analysis it is resolved in a polytomy with both the Talpini and Scalopini. Furthermore, both constraint analyses recover G. montisasini as a highly fossorial stem scalopin.

Inspection of the characters that optimize to the Talpini and Scalopini when G. montisasini is resolved at the base of each clade, and in a polytomy with both (see Supplementary Data: Section 4) reveal that G. montisasini shares no unambiguous synapomorphies with either tribe. When using a delayed optimization (DELTRAN) to trace characters across the polytomy, G. montisasini shares two states with the Talpini (19:2 and 20:2—weakened divided M1 and M2 mesostyles, respectively) and two with the Scalopini (34:1—an inconspicuous P4 parastyle; and 92:3—humeral width over a third the humeral length). Indeed, arbitrarily resolving the strict consensus topology to produce a G. montisasini-Talpini clad yields only a single character scored for G. montisasini that supports the node, and only under accelerated transformation (ACCTRAN): namely, the connection of the oblique cristid to the talonid of the lower molars (26:1). All other characters uniting Talpini + G. montisasini are missing from G. montisasini. In contrast, resolving the strict consensus topology to produce a G. montisasini-Scalopini clad yields two unambiguous synapomorphies (34:1—an inconspicuous P4 parastyle; and 92:3—humeral width greater than one third humeral length). Furthermore, there are two scored characters shared between the groups under both ACCTRAN (40:1—no anterior cingulum cusp on the p4; and 161:0—a deltoid metacromion) and DELTRAN (74:2—a quadrangle clavicle; and 164:0—a smooth ventral surface of the clavicle) optimizations. Notably, those characteristics that promoted our interpretation of G. montisasini as a talpin, namely, the enlarged, caniniform p1 and the lack of a scalopine ridge, is not a character in the matrix and recovered as plesiomorphic for the Talpini, respectively.

The fact that G. montisasini shares scores for a greater number of characters that can define the scalopin node than the talpin node explains its affinity to the Scalopini in the constraint analyses. A number of these characters are linked to the extreme fossorial specialization. It seems that the last common ancestor of the Scalopini is reconstructed as more fossorially competent than that of the Talpini, and that this element of the optimization attracts Geotrypus montisasini to the root of the Scalopini. Further sampling of extinct taxa, particularly putative stem scalopins such as Scalopoids (Hutchinson, 1974), could help to more accurately capture the transition to extreme fossoriality within this clade and thus dramatically impact the placement of G. montisasini. Indeed, not only does G. montisasini share more scores with characters that can define the scalopin node than the talpin node, it also has more conflicting scores with characters that can define the scalopin node than the talpin node (see Supplementary Data: Section 4). This suggests that the placement of Geotrypus montisasini is quite labile, and that improved taxon sampling, character sampling, and preservation would greatly affect its placement. Given the current data set, it seems that this taxon’s available character sample could simply represent a potentially phylogenetically misleading subsample of characters. Artificial extinction experiments (Asher and Hofreiter, 2006; Pattinson et al., 2015) would be an ideal method to test these assumptions. Due to the relative uncertainty in the phylogenetic placement of G. montisasini in our current data set, we have refrained from taxonomic revision; however, if further material, or improved taxon sampling, corroborates its position as a stem scalopin, this taxon could not remain within the genus Geotrypus.

Eotalpa anglica and E. belgica—The addition of the two Eotalpa species to the analysis produces a poorly resolved phylogeny (Fig. 15B). This is in many ways unsurprising, given the high level of missing data for both taxa: E. anglica is known only from two upper molars (Sigé et al., 1977), whereas E. belgica is known from the upper and lower molar rows (Smith 2007). Hooker (2010) described a small ulna fragment also attributed to Eotalpa sp. Interestingly, inclusion of both taxa only produces trees one step longer than those lacking Eotalpa. This suggests that these taxa do little to affect the optimization of characters across the tree; their instability, and destabilizing effect upon the topology, is therefore likely due to either a lack of characters synapomorphic in a given clade, or similarity to other fossil groups, which are in turn destabilized by their presence. When the other extinct taxa are removed from the analysis (see Supplementary Data: Section 3 for details), the Desmanini are drawn into the tree’s large polytomy (Fig. 15B); this means that the other fossil taxa act to stabilize the placement of Eotalpa while their own position becomes unstable. Clearly, Eotalpa is attracted to one or more of the fossil taxa other than Mygalea, and this attraction removes an affinity to the desmans. Indeed, if both Eotalpa species are the only fossils present in both
constrained analyses. *E. anglica* is resolved as a talpin and *E. belgica* as the sister group to *Desmana*. The increased extinct taxon sample aids the placement of *E. belgica* by providing character combinations intermediate to those in the extant radiation and therefore a more plausible taxonomic position for it. Unfortunately, the presence of such poorly represented specimens destabilizes the other fossils, and we lose resolution in the wider topology.

Interestingly, the 50% majority rule consensus tree from an analysis lacking the other fossils resolves both *E. anglica* and *E. belgica* within the Talpini, more closely related to *Scaptochirus, Mogera, Parascaptor*, and *Euroscaptor* than to *Talpa* in 75% of the MPTs. The placement of *Eotalpa* is far from conclusive, but it is clear that this taxon shares a number of similarities with the Talpini, and the highly fossorial talpids in general. As the oldest known talpid from Eurasia, dated to the late Eocene and roughly contemporaneous with the North American talpid *Oreotalpa* (Lloyd and Eberle, 2008), *Eotalpa* represents a key snapshot of early talpid evolution. Its dental morphology suggests an affinity with the relatively derived highly fossorial clades, and regardless of the favored hypothesis for talpid evolution (Fig. 15), this placement suggests that a large proportion of talpid evolution predates the late Eocene and remains undiscovered. Furthermore, this placement suggests that *Eotalpa* may have been a semi-fossorial or early highly fossorial mole, or at least is descended from a fossorially competent form. Of course, extrapolating the locomotor lifestyle of an extinct organism from its dentition alone is exceptionally uncertain, and any such conclusions must be treated with skepticism. Regardless, it remains possible that much of the earliest evolution of talpid fossoriality may be missing from the known fossil record, and we should search for the origins of their unique mode of locomotion deeper in the Eocene.The Evolution of Fossoriality in Talpids—With the placement of *Scaptonyx* as the sister taxon of *Neurotrichus*, the morphological data now unambiguously support the presence of a monophyletic lineage of highly fossorial talpids. The strict consensus tree from our unconstrained analysis (Fig. 15A) unites the Talpini and Scalopini as sister groups. This topology suggests a single origin of extreme fossoriality, shared through common ancestry in these two clades. Although the optimization of characters that correlate strongly with extreme fossoriality tend to support this view (Fig. 16A), there are reasons to be cautious about this interpretation, other than the conflictive signal reported by molecular systematics (e.g., Shinohara et al., 2004; Cabrío et al., 2006; Crumpton and Thompson, 2013).

As already discussed, *Geotrypus antiquus* introduces a number of shrew-mole-like characters to the base of the Talpini. The presence of a distinct metacromion process on the scapula, the lack of a terminal process of the ulna, a weak capitular process of the radius, and an elongate clavicle without a distinct ventral process all suggest the potential for independent change in these characters within the talpin and scalopin lineages. However, due to the sister-group relationship between the Talpini and Scalopini recovered by the morphological data set, the majority of these character states are optimized on the branch leading to *G. antiquus* itself (Fig. 16A). Of the unusual forelimb characters in *G. antiquus*, only the presence of the metacromion leads to convergence between Talpini and Scalopini. Another character link to fossoriality, namely, the elongation of the deltoid process and greater tuberosity, is also seen to converge between the Talpini (106:1; Fig. 16A). This convergence is caused by the placement of *G. montisasinii*, rather than *G. antiquus*. Thus, the addition of the fossil taxon unambiguously suggests some level of independent evolution of highly fossorial adaptations between the groups, while introducing a number of traits that could readily be resolved as convergent between the clades with an improved representation of the extinct fauna.

The form of the clavicle differs significantly between the highly fossorial tribes: Talpines generally possess a large ventral process of the clavicle, in some cases with a slight lateral hook; Scalopins have a smaller, medially directed ventral process, which is reduced and covered by the ventral expansion of the clavicular body in *Scalopus, Scapanus*, and to a lesser extent *Domninoides* (see earlier discussion of *Domninoides mimicus*). Such differences provide further evidence of the independent specialization of forelimb anatomy and hint at parallel increases in robusticity, particularly when we consider the more elongate clavicle associated with *Geotrypus antiquus*. The form of the manus of the extant *Scapanus* also complicates character acquisition within the Scalopini. *Scapanus* introduces a short triangular prepollex to the clade, and a manus that is less broad than other forms. With the current topology, this indicates a reduction in fossoriality in this taxon (Fig. 16A); however, based on its Chinese origins, *Scapanus* could represent a relict member of the Asian scalopin radiation, suggesting that a less fossorially adapted forelimb was present in the ancestors of the American taxa.

Such lines of evidence serve to highlight the complexity of forelimb evolution, and therefore the evolution of fossoriality, within the Talpidae. The incorporation of fossil taxa into an extant phylogenetic framework has revealed character transitions otherwise absent from extant lineages, affecting our interpretation of the resultant topology, while revealing characters whose evolutionary patterns may be more complex than suggested by optimization across a phylogeny alone. Of course, such interpretations are far from clear-cut: *Geotrypus montisasinii* and *Proscapanus sansaniensis* place extremely robust forelimb morphologies towards the root of both tribes. Such taxa could represent early independent forays into the highly fossorial niche, misplaced members of more deeply nested clades, or point to the presence of a highly fossorial common ancestor for scalopins and talpins. Given the molecular evidence (Fig. 15C, D), the former explanations currently seem more favorable; however, further sampling is clearly needed to improve this assessment.

Both molecular constraint trees break the talpin-scalopin sister group relationship (Fig. 15C, D). They thus favor either independent origins of extreme fossoriality in the Talpini or Scalopini or the early evolution of fossoriality in the talpid lineage, with secondary loss of fossorial adaptations in the desman and shrew-mole clades. When character-state changes for 10 characters whose states correlate with extreme fossoriality are examined across the constraint topologies, an increase in the instance of convergence between the Talpini and Scalopini is observed for both constraints when compared with the unconstrained topology (Fig. 16). Similarly, a number of character states are seen to change from a highly fossorial to less fossorial state in the desman and shrew-mole clades. The main difference between the two models is that the Shinohara et al. (2004) topology predicts a slightly higher degree of fossorial competence in the ancestor of all non-uropsiline talpids than seen in the Crumpton and Thompson (2013) topology (compare Fig. 16B and C). Shinohara et al.'s (2004) hypothetical ancestor to this clade has a more elongate sternum (84:2 rather than 0), a pectoral crest of the humerus perpendicular to its shaft (107:2 rather than 1), and a stout, but non-quadrate, clavicle (74:1 rather than 0). This increased level of ancestral fossoriality, caused by the more derived placement of the Desmanini, results in a higher level of secondary loss under the Shinohara et al. (2004) model than Crumpton and Thompson (2013), which shows a correspondingly high level of convergence (Fig. 16). Regardless, the molecular models of talpid evolution seem to suggest that the ancestor of all non-uropsiline talpids had a reasonably derived, but nonspecialized
FIGURE 16. DELTRAN optimizations of 10 forelimb characters with states that show a strong correlation with extreme fossoriality across A, the unconstrained topology; B, the Shinohara et al. (2004) constraint topology; C, the Crumpton and Thompson (2013) constraint topology. Circles indicate a change of state along a branch. Character numbers are shown above the circles, state numbers below. Gray circles represent states generally associated with semi-fossorial taxa in our study, black circles states associated with highly fossorial taxa. Characters are as follows: (74) Clavicle: (0) elongated; (1) semi-rectangular, stout; (2) quadratic. (81) Scapula, metacromion: (0) absent; (1) present, small; (2) present, large. (84) Sternum, proportions of manubrium (x = length/width): (0) < 1.5; (1) 1.5 < x < 3; (2) 3 < x < 4.5; (3) > 4.5. (92) Minimum width of humerus compared with its maximum length: (0) ≈ 1/9–1/10; (1) ≈ 1/7; (2) ≈ 1/4–1/5; (3) ≈ 1/3 or less. (106) Greatest length of greater tuberosity and deltoide process: (0) short, less than ≈ 1/4 length of humerus; (1) long. (107) Pectoral crest: (0) single straight process parallel to long axis of humerus; (1) forms single curved process; (2) long axis of humerus and pectoral crest having a perpendicular orientation. (110) Prepollex: (0) absent; (1) just a knob; (2) elongated, but does not reach first metatarsal; (3) present, extends to proximal portion of first metatarsal or beyond. (167) Ratio of the length of the olecranon process of the ulna to the length of the shaft: olecranon/shaft (0) < 0.4; (1) > 0.4. (169) Terminal process of the distal ulna: (0) absent; (1) present. (174) Ratio of the maximum width across the metacarpals to the maximum length of the carpals and metacarpals (x = width/length): (0) < 1; (1) 1 ≤ x < 1.5; (2) 1.5 ≤ x < 2; (3) ≥ 2.
forelimb. This structure was likely competent in a semi-fosso-
rial, semiaquatic, and ambulatory niche, somewhat similar to
the extant *Condylura* (Nowak, 1999), and the various extinct
talpid tribes have specialized independently into one of these
locomotor habitats.

### CONCLUSIONS

In this study, we have focused almost exclusively on exception-
ally preserved talpid fossils, allowing a combination of dental,
cranial, and postcranial characters from fossil taxa to influence
our topology. This approach minimized the potential impact of
poor resolution on our study (a problem highlighted by the addi-
tion of the highly fragmented *Eotalpa* specimens). The inclusion
of such fossils has introduced more varied character combina-
tions to the analysis, effectively acting to break long branches of
morphological evolution, thereby revealing new patterns of char-
acter evolution in the talpid lineage. Of particular note are con-
vergences in the form of the scapula and humerus of the Talpini
and Scalopini, hinting at their independent specialization into
extreme fossoriality.

Our well-resolved morphological topology has also allowed
detailed comparisons with molecularly derived hypotheses of tal-
pid evolution, through the use of constraint trees. However, our
bias towards exceptional specimens has limited our taxon sam-
ples. Variation in taxon sample is known to have a large impact on
a phylogenetic hypothesis (Heath et al., 2008). The great
diversity of extinct talpid clades may well possess character states
that are crucial to the accurate resolution of the group’s true phy-
ology. Of course, due to their fragmentary nature, such fossils are
more likely to hamper resolution through the generation of a
vast number of MPTs. The addition of further taxa to this analy-
sis is certainly an area for further investigation. A potential
expansion is to incorporate these fossil taxa into a combined
morphological and molecular phylogeny, analyzed in a statistical
framework. In such a scenario, given enough data, a strongly sup-
ported extant topology may prove more resistant to the inclusion
of fragmentary fossil taxa and thus provide a more complete and
informative explanation of talpid evolution. Such an approach
would certainly expand upon our ideas of talpid character evolu-
tion, while providing more robust hypotheses for talpid inter-
tribal relationships and the affinities of the shrew-moles, both of
which remain contentious based on current data sets.

The topologies presented here highlight the benefits of the
inclusion of fossil taxa in cladistic analyses, while providing an
excellent framework for the taxonomic placement of fossil tal-
pids. The specimens central to our analysis have been known for
decades, but have received little study or attention. Character-
rich specimens with postcranial material, published in little
known papers, could provide key insights into the history of a
wide range of fossil groups and should be used to inform phylo-
genetics wherever possible.

### ACKNOWLEDGMENTS

We would like to give special thanks to both R. Ziegler (Staat-
lisches Museum für Naturkunde Stuttgart, Stuttgart) and G.
Rößner (Bayerische Staatssammlung für Paläontologie und
Geologie, Munich) for loaning the exceptionally preserved talpid specimens to A.H.S. for μ-CT investigation, thus making this
study possible. We also thank T. Smith (Royal Belgian Institute
of Natural Sciences, Brussels) for granting both authors access to
the collections at RBINS, particularly the holotype specimens of
*Eotalpa belgica*, and for facilitating our first meeting and there-
fore our collaboration.

R.S.T. would like to thank J. Hooker (Natural History Museum,
London) for access to casts of *Eotalpa anglica*, and the collections
staff in the Zoology Department of the Natural History
Museum (London), particularly R. Portela-Miguez, for

### LITERATURE CITED

Asher, R. J., and M. Hofreiter. 2006. Tenrec phylogeny and the noninva-
sive extraction of nuclear DNA. Systematic Biology 55:181–194.

Asher, R. J., R. J. Emry, and M. C. McKenna. 2005. New material of Cen-
tetodont (Mammalia, Lipotyphla) and the importance of (missing)
DNA sequences in systematic paleontology. Journal of Vertebrae
Paleontology 25:911–923.

Bachman, D. D. 1843. Observation on the genus Scallops, Shrew Moles,
with descriptions of the species found in North America. Boston
Journal of Natural History 4:26–34.

Blainville, H. M. D. de. 1840. Osteographie des mammifères insectivores
(*Talpa, Sorex et Erinaceus L.); pp. 115 in H. M. D. de Blainville
(ed.), Osteographie des Mammifères, Bailliure, Paris.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm
phylogenetic reconstruction. Evolution 42:795–803.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10:295–304.

Cabrera, M. T., J. Rubines, B. Gomez-Moliner, and R. Zardoya. 2006. On
the phylogenetic position of a rare Iberian endemic mammal, the
Pyrenean desman (*Galaxias pyrenaeicus*). Gene 375:1–13.

Campbell, B. 1939. The shoulder anatomy of the moles. A study in phylo-
geny and adaptation. The American Journal of Anatomy 64:1–39.

Colangelo, P., A. A. Bannikova, B. Krystufek, V. S. Lebedev, F. Annesi,
E. Capanna, and A. Loy. 2010. Molecular systematics and evolu-
tionary biogeography of the genus *Talpa* (*Soricomorpha: Talpidae*).
Molecular Phylogenetics and Evolution 55:372–380.

Crocqet, J.-Y. 1995. Le Garouillas et les sites contemporains (Oligocene,
MP 25) des phosphorites du Quercy (Lot, Tarn-et-Garonne,
France) et leurs faunes de vertébrés 4. Marsupiaux et Insectivores.
Palaontographica Abteilung A 236:39–75.

Crumpston, N., and R. S. Thompson. 2013. The holes of moles: osteologi-
cal correlates of the trigeminal nerve in Talpidae. Journal of Mamm-
alian Evolution 20:213–225.

Dahmann, T. 2001. Die Kleinsäuger der untertieflozänen Fundstelle
Wölfsheimer in der Wetterau (Mammalia: Lipotyphla, Chiroptera,
Rodentia). Courier Forschungsinstitut Senckenberg 227:1–129.

Edwards, L. F. 1937. Morphology of the fore-limb of the mole (*Scalops
aquaticus*, L.) in relation to its fossorial habits. Ohio Journal of Sci-
enary Biogeography of the genus *Talpa* (*Soricomorpha: Talpidae*).

Engesser, B. 2009. The insectivores (Mammalia) from Sansan (Middle
Miocene, south-western France). Schweizerische Paläontologische
Abhandlungen 128:1–95.

Filhol, M. H. 1891. Etudes sur les mammifères fossiles de Sansan.
Annales des Sciences Geologiques 21:1–319.

Fischer von Waldheim, J. G. 1817. Adversaria zoologica.

Fischer von Waldheim, J. G. 1841. Adversaria zoologica.

Fischer von Waldheim, J. G. 1849. Adversaria zoologica.

Fischer von Waldheim, J. G. 1891. Adversaria zoologica.

Filhol, M. H. 1891. Etudes sur les mammifères fossiles de Sansan.
Annales des Sciences Geologiques 21:1–319.

Fischer von Waldheim, J. G. 1817. Adversaria zoologica.

Fischer von Waldheim, J. G. 1841. Adversaria zoologica.

Fischer von Waldheim, J. G. 1849. Adversaria zoologica.

Fischer von Waldheim, J. G. 1891. Adversaria zoologica.
Gaillard, C. 1899. Mammifères Miocènes de La Grive-Saint-Alban (Isère). Archives du Muséum d’Histoire Naturelle de Lyon 7:1–79.

Gibert, J. 1974. Etude des insectivores du Miocène de Vallès-Pencès, Calatayud-Daroca et Rubielos de Mora. Ph.D. Thesis, University of Barcelona, Barcelona, Spain, 225 pp.

Gill, T. N. 1875. Synopsis of the insectivorous mammals. Bulletin of the United States Geological and Geographical Survey, second series 2:91–120.

Haeckel, E. 1866. Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie. G. Reimer, Berlin, 574 pp.

He, K., A. Shinohara, X. L. Jiang, and K. L. Campbell. 2014. Multilocus phylogeny of Talpini (Talpidae, Eulipotyphla) and its implications for systematics. Molecular Phylogenetics and Evolution 70:513–521.

He, K., J.-H. Wang, W.-T. Su, Q. Li, W.-H. Nie, and X.-L. Jiang. 2012. Karyotype of the Gansu mole (Scapanulias oweni): further evidence for karyotypic stability in talpid. Mammal Study 37:341–348.

Heath, T. A., S. M. Hedtke, and D. M. Hillies. 2008. Taxon sampling and the accuracy of phylogenetic analyses. Journal of Systematics and Evolution 46:239–257.

Hooker, J. J. 2010. The ‘Grande Coupure’ in the Hampshire Basin, UK: taxonomy and stratigraphy of the mammals on either side of this major Palaeogene faunal turnover; pp. 47–215 in J. E. Whittaker and M. B. Hart (eds.), Micropalaeontology, Sedimentary Environments and Stratigraphy: A Tribute to Dennis Curry (1912–2001). Geological Society Publishing House, Bath.

Hugueney, M. 1972. Les talpids (Mammalia, Insectivora) de Coderet-Bransat (Allier) et l’'extension de la faune des mammifères du Miocène inférieur de France. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon D 50:1–81.

Hutchison, J. H. 1968. Fossil Talpidae (Insectivora, Mammalia) from the late Tertiary of Oregon. Bulletin of the Museum of Natural History, University of Oregon 11:1–117.

Hutchison, J. H. 1974. Notes on type specimens of European Miocene Talpidae and a tentative classification of old world Tertiary Talpidae (Insectivora: Mammalia). Geobios 7:211–256.

Hutchison, J. H. 1976. The Talpidae (Insectivora, Mammalia): Evolution, Phylogeny, and Classification. University of California Press, Berkeley, California, 400 pp.

Hutterer, R. 2005. Order Soricomorpha in D. E. Wilson and D. Reeder (eds.), Mammal Species of the World. A Taxonomic and Geographic Reference. John Hopkins University Press, Baltimore, Maryland.

Jäger, G. F. 1850. Über die fossilen Säugethiere, welche in Württemberg in verschiedenen Formationen aufgefundenes sind, und nähere Beschreibungen und Abbildungen einzelner der selben. Nova Acta Academiae Naturalae Curiosorum 22:695–934.

Lartet, E. A. 1853. Notice sur la colline de Sansan, suivie d’une récapitulation des divers espèces d’animaux vertébrés fossiles, trouvés soit à Sansan, soit dans d’autres gisements du terrain tertiaire du miocène dans le bassin sous-pyrénéen, Annuaire du Département du Gers, Auch, 45 pp.

Lavocat, R. 1951. Révision de la Faune des Mammifères Oligocènes d’Anvergne et du Velay. Ed. Sciences et Avenir, Paris, 153.

Lloyd, K. J., and J. J. Eberle. 2008. A new talpid from the Late Eocene of Oregon. Bulletin of the Museum of Natural History 34:313–348.

Lucas, S. G., E. G. Kordikova, and R. J. Emry. 1998. Oligocene stratigraphy, sequence stratigraphy, and mammalian biochronology north of the Aral Sea, Western Kazakhstan. Bulletin of the Carnegie Museum of Natural History 34:313–348.

Meier, P. S., C. Bickelmann, T. Scheyer, D. Kotsakis, P. Colangelo, and A. Loy. 2012. Testing convergent and parallel adaptations in talpids humeral mechanical performance by means of geometric morphometrics and finite element analysis. Journal of Morphology 273:696–711.

Pomel, A. 1848. Etudes sur les carnassiers insectivores (Extrait) seconde partie, classification des insectivores; pp. 244–251 in Archives des Sciences physiques et naturelles. Bibliothèque Universelle, Genève.

Rabecker, G. 1998. Säugetiere (Mammalia) aus dem Karpat des Korneuburger Beckens. Beiträge zur Paläontologie 23:347–362.

Reed, C. A. 1951. Locomotion and appendicular anatomy in three soricid insectivores. The American Midland Naturalist 45: 513–671.

Rüschin, C. G. 1985. A review of fossil and recent Desmaninae (Talpidae, Insectivora); pp. 1–11 in P. Marks (ed.), Utrecht Micropalaeontological Bulletins: Special Publication. Department of Stratigraphy and Paleontology, State University of Utrecht, Utrecht, The Netherlands.

Sánchez-Villagra, M. R., and P. R. Menke. 2005. The mole’s thumb—evolution of the hand skeleton in talpids (Mammalia). Zoology 108:3–12.

Sánchez-Villagra, M. R., R. L. Horovitz, and M. Motokawa. 2006. A comprehensive morphological analysis of talpid moles (Mammalia) phylogenetic relationships. Cladistics 22:59–88.

Sánchez-Villagra, M. R., P. R. Menke, and J. H. Geisler. 2004. Patterns of evolutionary transformation in the humerus of moles (Talpidae, Mammalia): a character analysis. Mammal Study 29:163–170.

Schaller, O. 2007. Illustrated Veterinary Anatomical Nomenclature. Georg Thieme Verlag, Stuttgart, 615 pp.

Schlosser, M. 1887. Die Affen, Lemuren, Chiropeteren, Insectivoren, Marsupialier, Condonten und Carnivoren des Europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen australis europäischen Verwandten. Beiträge zur Paläontologie Österreich-Ungarns 6:125–134.

Schreuder, A. 1940. A revision of the fossil water-moles (Desmaninae). Archives Neerlandaises de Zoologie 4:201–333.

Schwermann, A. H., and T. Martin. 2012. A partial skeleton of Geotrypus antiquus (Talpidae, Mammalia) from the Late Oligocene of the Enspel fossillocality in Germany. Paläontologische Zeitschrift 86:409–439.

Seemann, I. 1938. Die Insektenfresser, Fledermäuse und Nager aus der obermiocänen Braunkohle von Viehhäusen bei Regensburg. Palaeontographica A 89:1–55.

Shinohara, A., K. L. Campbell, and H. Suzuki. 2003. Molecular phylogenetic relationships of moles, shrews, and desmans from the new and old worlds. Molecular Phylogenetics and Evolution 27:247–258.

Shinohara, A., K. L. Campbell, and H. Suzuki. 2005. An evolutionary view on the Japanese talpids based on nucleotide sequences. Mammal Study 30:19–24.

Shinohara, A., S.-i. Kawada, M. Harada, K. Koyasu, S.-i. Oda, and H. Suzuki. 2008. Phylogenetic relationships of the short-faced mole, Scaptochirus moschatus (Mammalia: Eulipotyphla), among Eurasian fossorial moles, as inferred from mitochondrial and nuclear gene sequences. Mammal Study 33:77–82.

Shinohara, A., H. Suzuki, K. Tsuchiya, Y.-P. Zhang, J. Luo, X.-L. Jiang, X.-X. Wang, and K. L. Campbell. 2004. Evolution and biogeography of talpid moles from continental East Asia and the Japanese islands inferred from mitochondrial and nuclear gene sequences. Zoological Science 21:1177–1185.

Sigé, B., J.-Y. Crochet, and A. Insole. 1977. Les plus vieilles Taupes. Géobiomériaux, Special Publication. Department of Stratigraphy and Paleontology, State University of Utrecht, Utrecht, The Netherlands.

Smith, R. 2007. Presence of the genus Eotalpa (Mammalia, Talpidae) in the Oligocene inferior of Belgique (Formation of Borgloon, MP 21).
Schwermann and Thompson—Fossil talpids and evolution of fossoriality (e934828-26)

Bulletin de l’Institut Royal des Sciences Naturelles de Belgique 77:159–165.

Storch, G., and Z. Qiu. 1983. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. 2. Moles—Insectivora: Talpidae. Senckenbergiana lethaea 64:89–127.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*And Other Methods), version 4. Sinauer Associates, Sunderland, Massachusetts.

Thomas, M. R. O. 1912. On a collection of small mammals from the Tsinling Mountains, central China. Annals and Magazine of Natural History, Including Zoology, Botany, and Geology; Series 8 10:395–403.

Tsuchiya, K., H. Suzuki, A. Shinohara, M. Harada, S. Wakana, M. Sakaizumi, S. H. Han, L. K. Lin, and A. P. Kryukov. 2000. Molecular phylogeny of East Asian moles inferred from the sequence variation of the mitochondrial cytochrome b gene. Genes and Genetic Systems 75:17–24.

Van den Hoek Ostende, L. W. 2001. Insectivore faunas from the Lower Miocene of Anatolia—part 5: Talpidae. Scripta Geologica 122:1–45.

Van den Hoek Ostende, L. W., and O. Fejfar. 2006. Erinaceidae and Talpidae (Erinaceomorpha, Sorcomorpha, Mammalia) from the Lower Miocene of Merkur-Nord (Czech Republic, MN 3). Beiträge zur Paläontologie 30:175–203.

Van Valen, L. 1967. New Paleocene insectivores and insectivore classification. Bulletin American Museum of Natural History 135:217–284.

Whidden, H. P. 2000. Comparative myology of moles and the phylogeny of the Talpidae (Mammalia, Lipotyphla). American Museum Novitates 3294:1–53.

Wiens, J. J. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. Systematic Biology 52:528–538.

Wilson, R. L. 1968. Systematics and faunal analysis of a Lower Pliocene vertebrate assemblage from Trego County, Kansas. Contributions from the Museum of Paleontology, University of Michigan 22:75–126.

Yates, T. L., and D. W. Moore. 1990. Specification and evolution in the family Talpidae (Mammalia, Insectivora); pp. 1–22 in E. Nevo and O. A. Reig (eds.), Evolution of Subterranean Mammals at the Organismal and Molecular Levels. Liss, New York.

Ziegler, A. C. 1971. Dental homologies and possible relationships of recent Talpidae. Journal of Mammalogy 52:50–68.

Ziegler, R. 1985. Talpiden (Mammalia, Insectivora) aus dem Orleanium und Astaracium Bayerns. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historischen Geologie 25:131–175.

Ziegler, R. 1990. Talpidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 167:1–81.

Ziegler, R. 1999. Order Insectivora: pp. 53–74 in G. E. Rössner and K. Heissig (eds.), The Miocene—Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich.

Ziegler, R. 2003. Moles (Talpidae) from the late Middle Miocene of South Germany. Acta Palaeontologica Polonica 48:617–648.

Ziegler, R. 2006. Insectivores (Lipotyphla) and bats (Chiroptera) from the Late Miocene of Austria. Annalen des Naturhistorischen Museums in Wien A 107:93–196.

Ziegler, R. 2012. Moles (Talpidae, Mammalia) from Early Oligocene karstic fissure fillings in South Germany. Geobios 45:501–513.

Ziegler, R., T. Dahlmann, J. W. F. Reumer, and G. Storch. 2005. Germany. Scripta Geologica 3:61–98.

Submitted March 2, 2014; revisions received June 3, 2014; accepted June 9, 2014.

Handling editor: Thomas Martin.

Citation for this article: Schwermann, A. H., and R. S. Thompson. 2015. Extraordinarily preserved talpids (Mammalia, Lipotyphla) and the evolution of fossoriality. Journal of Vertebrate Paleontology.DOI: 10.1080/02724634.2014.934828.