



## ***Talpa fossilis* or *Talpa europaea*? Using geometric morphometrics and allometric trajectories of humeral moles remains from Hungary to answer a taxonomic debate**

**Gabriele Sansalone, Tassos Kotsakis, and Paolo Piras**

### **ABSTRACT**

The taxonomic validity of *Talpa fossilis* has been subject to a longstanding debate. *Talpa fossilis* has been considered as a chronospecies, stratigraphic species, and finally as junior synonym of *Talpa europaea*. In this study, the large humeral sample of *T. fossilis* and *T. europaea* from the Plio-Pleistocene of Hungary is re-investigated using a geometric morphometrics analysis. Furthermore, the differences in the static allometric slopes under the allometric constraint hypothesis were tested. The results indicate that *T. fossilis* and *T. europaea* have significant differences in both size and shape. The allometric slopes of *T. fossilis* and *T. europaea* were found to be different, revealing that the two taxa follow different patterns of shape modification according to size. In light of this evidence, *T. fossilis* and *T. europaea* are supported as two distinct species.

Gabriele Sansalone. Università di Roma Tre, Dipartimento di Scienze, L.S. Murialdo, 1 – 00146 Roma, Italy and Center of evolutionary ecology, Pesche, Italy. [gsansalone@uniroma3.it](mailto:gsansalone@uniroma3.it)

Tassos Kotsakis. Università di Roma Tre, Dipartimento di Scienze, L.S. Murialdo, 1 – 00146 Roma, Italy and Center of evolutionary ecology, Pesche, Italy. [kotsakis@uniroma3.it](mailto:kotsakis@uniroma3.it)

Paolo Piras. Università di Roma Tre, Dipartimento di Scienze, L.S. Murialdo, 1 – 00146 Roma, Italy and Center of evolutionary ecology, Pesche, Italy and Dipartimento di Scienze Cardiovascolari, Respiratorie, Nefrologiche, Anestesiologiche e Geriatriche, Sapienza-Università di Roma, Roma, Italy and Dipartimento di Ingegneria Strutturale e Geotecnica Sapienza, Università di Roma. [paolo.piras@uniroma3.it](mailto:paolo.piras@uniroma3.it)

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### **INTRODUCTION**

Ontogenetic, static, and evolutionary allometries are recognized depending on whether the relationship between shape and size is taken over the development of an individual, across individu-

als at a similar developmental stage within a population, or across separate evolutionary lineages (Cock, 1966; Gould, 1966; Cheverud, 1982). The allometric-constraint hypothesis states that the allometric slope remains stable at the above-spe-

cies level and is able to constrain the evolutionary divergence in the morphospace along its specific trajectories (Firmat et al., 2014; Pélabon et al., 2014; Voje et al., 2014). Many recent comparative studies have provided evidence of the constraining role of static allometry, revealing that intraspecific static allometric trajectories remain constant through time (Voje and Hansen, 2013; Firmat et al., 2014; Voje et al., 2014). On the basis of the allometric-constraint hypothesis, statistically significant differences in static allometric slopes are not expected within the same species. Firmat et al. (2014), analysing a time-ordered sample of *Miomys savini*, showed how the static allometric slopes remained constant through time. With the allometric-constraint as a background hypothesis, divergence in allometric slopes, in populations distributed across a time-ordered series, could indicate the presence of separate species. The humerus of highly fossorial moles is well suited for this kind of investigation, as this skeletal element is often abundant and well preserved in fossil assemblages.

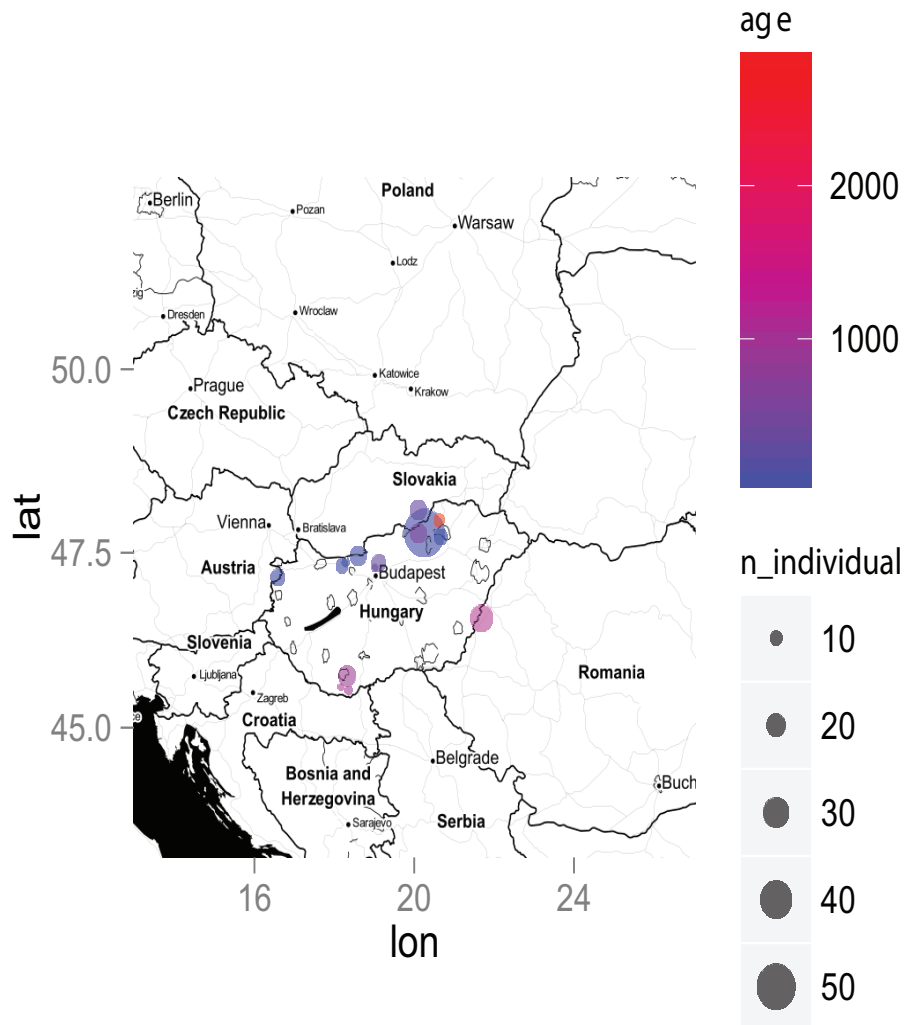
Diverse lifestyles have evolved among Talpidae, which includes species that are ambulatory (the shrew-like moles), semi-aquatic (desmans), semi-fossorial (shrew moles), and fully fossorial (Hutchison, 1976; Yates and Moore, 1990). The fully fossorial taxa evolved a unique humeral morphology (Gambaryan et al., 2003; Sánchez-Villagra et al., 2004; Piras et al., 2012). As a result of the adaptation to burrowing, the humerus is widened and flattened, and presents an elliptically shaped, ventrally directed head of humerus, a heavily expanded proximal end, an enlarged teres major tubercle, a deep brachialis fossa, a large, hemicylindrical clavicular facet, and an enlarged medial epicondyle bearing a deep fossa for the attachment of the Flexor digitorum profundus tendon-muscle (Edwards, 1937; Hutchinson, 1968). The complexity of the humerus makes this bone a potentially rich source of evolutionary characters (Sánchez-Villagra et al., 2004); this bone experienced transformations that are of taxonomic and systematic interest (van den Hoek Ostende, 1997; Ziegler, 2003; Klietmann et al., 2014; Sansalone et al., in press).

Systematics and taxonomy of fossil moles have often been based on humeri, in particular when teeth materials are morphologically indistinguishable or very scarce (Ziegler, 2003). Moreover, many fossil species have been described on humeral remains alone (Ziegler, 2006). In the present contribution the humeral fossil material of *Talpa*

*fossilis* and *T. europaea* from several Hungarian localities and from the German locality of Petersbuch 1 were re-investigated (Figure 1; Table 1). Hungarian localities provided a large amount of fossil material belonging to the genus *Talpa*. Classification of this material was based not only upon humeral remains, but also upon other skeletal elements, such as mandibles, teeth, and skull rostra (Petényi, 1864; Kormos, 1930; Kretzoi, 1938; Sulimski, 1959; Jánossy, 1979). The Late Pliocene-Middle Pleistocene *Talpa* material has been attributed to *T. fossilis*, whereas the Late-Pleistocene specimens to *T. europaea* (Jánossy, 1979). A geometric morphometric (GM) analysis of the humerus was used to quantitatively evaluate the differences (if any) in their shape and size as well as in their relationship. The static allometric trajectories of the two taxa were also investigated.

Pomel (1848), describing *Talpa fossilis*, suggested that the new species was somewhat larger and more robust and differed from other species in the shape of the carpals. However, the description made by Pomel (1848) has gone unnoticed since *T. fossilis* is attributed to Petényi (1864), who described *T. vulgaris fossilis* from the Hungarian fossil bearing locality of Beremend. The original description translated by van Cleef-Rodgers and van den Hoek Ostende (2001) states: “*Talpa vulgaris fossilis* Petényi. The fossil bone material of this animal totally agrees with the corresponding bones of the recent common mole, both in morphology and size; thus this fossil mole does not differ from the recent mole on the specific level, if one does not take into account the only difference noted by me, viz. that in the modern mole the labial side of the mandible has only two foramina mentale, one under the second premolar, the other under the first molar, whereas in the fossil mole three of such foramina are found, one under the first premolar, but two—be it one of them very shallow— under the first molar.”

Following the original description of Petényi (1864), *Talpa fossilis* could not be distinguished from *T. europaea* Linnaeus, 1758, and justified a distinction only at subspecific level. Despite this, the middle-sized *Talpa* specimens from Late Pliocene to Middle Pleistocene deposits are often attributed to *T. fossilis*, whereas in more recent deposits they are often classified as *T. europaea* (Jánossy, 1979). Kormos (1930) described *T. praeglacialis* from the Early Pleistocene locality Püspökfürdő (Betfia 2), accounting for a higher number of foramina mentale than in *T. europaea*. Kretzoi (1938) then placed *T. praeglacialis* in syn-



**FIGURE 1.** Geographical map showing the fossil bearing localities. Circles size is proportional to the number of individuals. Colour scale is proportional to relative age (ka).

onymy with *T. fossilis*. Von Koenigswald (1970), in his discussion about the *Talpa* specimens from the German locality Petersbuch 1, suggested that there were no differences in size and morphology between *T. fossilis* and *T. europaea*. Rabeder (1972), in his discussion about the *Talpa* material from Hundsheim, suggested the presence of some slight morphological differences between *T. fossilis* and *T. europaea* such as the width of the M3 talonid and the number of the mental foramina. However, such differences were thought to be distinctive at the subspecific level only. Robert (1983), investigating the moles remains from the Middle Pleistocene of Saint Saveur, France, proposed to retain the name *T. fossilis* as a chronospecies since she observed a gradual size increase during the Pleistocene. Niethammer

(1990), following von Koenigswald (1970), considered *T. fossilis* as a stratigraphic species. However, van Cleef-Roders and van den Hoek Ostende (2001) pointed out that the material from Saint Saveur could be referred to *T. caeca sensu lato* because of the division of the mesostyle and the lack of humeri in the sample in addition to questioning the evolutionary trend proposed by Robert (1983). Van Cleef-Roders and van den Hoek Ostende (2001), reviewing the literature concerning *T. fossilis*, suggested considering *T. fossilis* as a junior synonym of *T. europaea*. They pointed out, however, that including all the material belonging to *T. fossilis* into *T. europaea* would probably be misleading. Thus, they noted the need for a more thorough review of the fossil assemblages bearing both taxa.

**TABLE 1.** List of the fossil site localities, corresponding ages, and sample size of *Talpa fossilis* and *T. europaea* used in the analyses.

| Locality                  | Age                | <i>T. fossilis</i> | <i>T. europaea</i> |
|---------------------------|--------------------|--------------------|--------------------|
| Osztramos 7               | MN16 (2.8 ma)      | 1                  | /                  |
| Villany 3                 | MN17 (2.3 ma)      | 2                  | /                  |
| Betfia                    | Early Pleistocene  | 5                  | /                  |
| Puspokfurdo               | Early Pleistocene  | 4                  | /                  |
| Beremend 15-16            | Early Pleistocene  | 3                  | /                  |
| Somssich Hegy 2           | Middle Pleistocene | 3                  | /                  |
| Villany 8                 | Middle Pleistocene | 11                 | /                  |
| Koversvarad               | Middle Pleistocene | 9                  | /                  |
| Tarkò                     | Middle Pleistocene | 3                  | /                  |
| Brassò                    | Middle Pleistocene | 4                  | /                  |
| 25-Fortuna Utca, Budapest | Middle Pleistocene | 3                  | /                  |
| Petersbuch 1              | Middle Pleistocene | 3                  | /                  |
| Istalloskò                | Late Pleistocene   | /                  | 50                 |
| Bivak Barlang             | Late Pleistocene   | /                  | 6                  |
| Kofulke                   | Late Pleistocene   | /                  | 4                  |
| Szelim Barlang            | Late Pleistocene   | /                  | 4                  |
| Koszeg-Puskaporos         | Late Pleistocene   | /                  | 3                  |

From this brief summary of the major contributions to the debate, it is evident that most researchers tend to consider *Talpa fossilis* as a subspecies or as a synonym of *T. europaea*. By contrast, many authors (Martín-Suárez and Mein, 2004; Sánchez-Villagra et al., 2004; Crochet et al., 2009; Colangelo et al., 2010; Rzebik-Kowalska, 2014) still consider the specific distinction as valid. Moreover, many of the measurements and morphological differences reported in the literature remain statistically untested. This study contributes to the debate by introducing the study of static allometric trajectories via geometric morphometrics (GM) analysis in order to reveal (if any) the potential different shape-size relationship between *T. fossilis* and *T. europaea*. Statistically significant differences in static allometric trajectories could suggest, on the basis of the allometric-constraint hypothesis (Firmat et al., 2014; Voje et al., 2014), that a specific distinction could be justified upon an inherent underlying biological process.

## MATERIAL AND METHODS

### Material

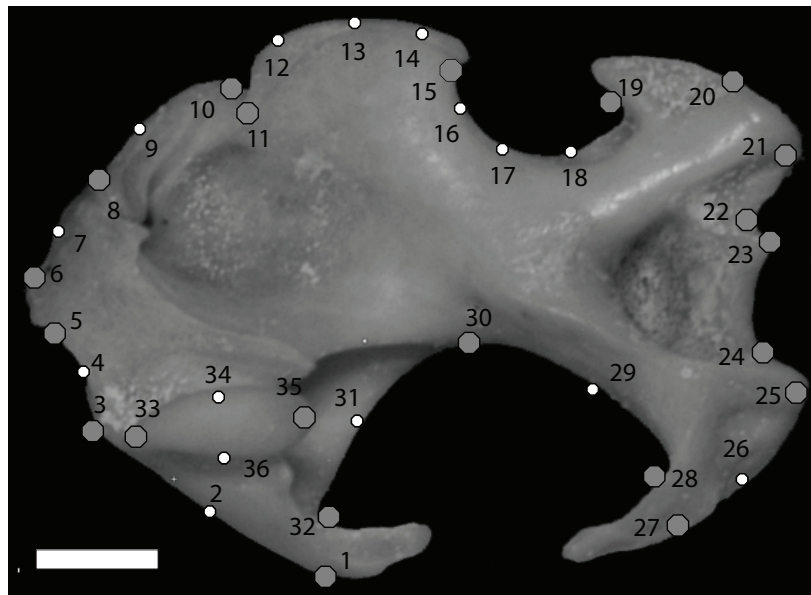
A total of 113 left humeri belonging to *Talpa europaea* Linnaeus, 1758 (n = 67) and *Talpa fossilis* Petényi, 1864 (n = 46) were analyzed. See

Table 1 and Figure 1 for specimen localities and corresponding ages. See Appendix 1 for specimen accession numbers and housing institutions.

### Geometric Morphometrics

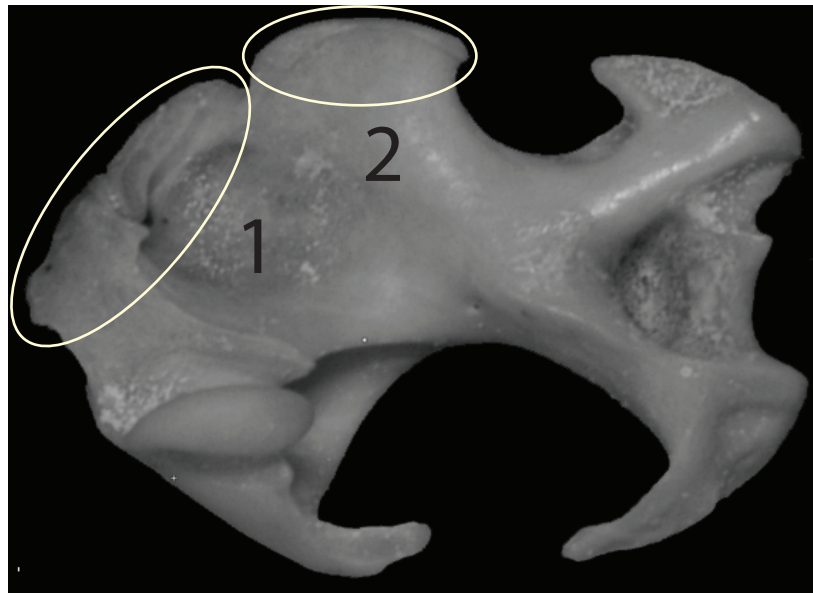
The humeri have been photographed in caudal view at a fixed distance of 50 cm with a Nikon D100 camera with a Micro-Nikkor 105 mm lens. We digitized 21 landmarks and 15 semi-landmarks (Figure 2.1) using the tpsDig2 software (Rohlf, 2006). Semi-landmarks are used to optimally translate, scale, and rotate landmarks, as well as to slide along the outline curve until they match as closely as possible the positions of the corresponding points along an outline in a reference configuration (Adams et al., 2004; Perez et al., 2006). Thus, semi-landmarks are useful to depict the shape of curved lines where landmarks cannot be detected. Successively a generalized procrustes analysis (GPA) (Bookstein, 1991; Goodall, 1991) implemented in the procSym() function from R-package “Morpho” (Schlager, 2014) was used to rotate, translate, and scale landmark configurations to the unit centroid size (CS = the square root of the sum of squared distances of a set of landmarks from their centroid) (Bookstein, 1986). Rotation of the scaled and translated landmark sets starts by comparison with a reference configuration, usually the

1



● Landmark  
○ Semi-Landmark

2



**FIGURE 2. 1**, Landmarks (large grey circles) and semilandmarks (small white circles) digitized on the humerus in caudal norm: 1) lateral end of greater tuberosity; 2) articular facet for clavícula; 3) proximal edge of the articular facet for clavícula; 4) bicipital notch; 5) proximal end of lesser tuberosity; 6) medial edge of the minor tuberosity; 7) lateral edge of the lesser tuberosity; 8) bicipital ridge; 9) middle point of the bicipital tunnel; 10) lateral end of the scalopine ridge; 11) proximal end of the teres tubercle; 12-14) surface of the teres tubercle; 15) distal end of the teres tubercle; 16-18) minor sulcus; 19) posterior margin of the lateral epicondyle; 21-22) lateral epicondyle; 22-24) trochlear area; 25-27) medial epicondyle; 28) posterior margin of the medial epicondyle; 29-32) greater sulcus; 33-36) humeral head. Scalebar equals 1 mm. **2**, Insertion areas of the main muscles involved in the digging movement. **1**. Pectoral ridge where muscle *Pectoralis pars sternalis* inserts. **2**. Teres tubercle where muscles *Teres major* and *Latissimus dorsi* inserts.

first specimen in the dataset. Once the first rotation is completed, a mean shape is calculated and the rotation process is repeated using the mean shape as the reference configuration for the sample (including the reference-specimen configuration). The mean shape/rotation procedure is iterated to minimize rotation differences between subsequent iterations through a least-square procedure (Rohlf and Slice, 1990). The residual differences correspond to real shape differences plus measurement error. A principal components analysis (PCA) was used to visualize the ordination of the aligned specimens. The significance of the observed shape differences among species was evaluated by performing a permutational multivariate analysis of variance (perMANOVA) on Procrustes coordinates using the `adonis()` function included in the “vegan” R package (Oksanen et al., 2013). Deformations associated to the extreme of PC axes have been visualized through deformation grids. The grids have been built using the thin-plate spline methodology (Bookstein, 1989).

The significance of size differences has been evaluated by performing a permutational univariate analysis of variance (perANOVA) on CS using the function `adonis()`. Size variation was visualized using a boxplot.

### Measurement Error

Measurement error associated with landmarks digitization was determined by first calculating the mean Procrustes distances between all combinations of two specimens in the dataset using TPSsmall software. The same values were then calculated for each cluster of replicas (three replicas were generated). The mean Procrustes distances were calculated for each set of replica's per specimen, including the same values for the total dataset. As an overall measure for digitisation error, the minimum and maximum values observed in all separate specimens were extracted, and the average of all mean values for those specimens was calculated. The amount of digitisation error with respect to the total variation in shape can be expressed as a percentage. Finally, the ratio of the mean value for total digitisation and the mean of the total dataset was calculated.

### Static Allometry

The relationship between size (independent variable) and shape (dependent variable) was tested performing a multivariate regression of shape on size values averaged by species. All individuals analyzed are adult or subadult based on

the ossification status of humeral epiphysis and diaphysis. Thus the allometric trajectories belong to the category of static allometry. A permutational multivariate analysis of covariance (perMANCOVA), using species as groups and size as covariate, was used to test for differences in slopes among species (Zelditch et al., 2004, 2012). This analysis was performed using the function `adonis()`. If slopes do not differ significantly (in this case the species and size interaction of the MANCOVA is not statistically significant), it is possible to control for the allometric effect and compute size-corrected shape variables (Viscosi and Cardini, 2011; Viscosi et al., 2012; Zelditch et al., 2012). For the sake of visualization a canonical correlation analysis (CCA) was performed, which determines a Y axis that represents the amount of Y (shape variables) that is best explained by the independent variable X (CS). In order to study interspecific shape differences, the intraspecific variation was removed by performing separate per-species multivariate regressions between shape and size. Then, for each species, the residuals were added to species specific shapes predicted at maximum and minimum, species-specific size values. This procedure ensures elimination of intraspecific allometry while maintaining the interspecific size-shape differences due to evolutionary allometry (Piras et al., 2011, 2014). The differences between the predicted shape variables have been evaluated performing a perMANOVA using the function `adonis()`. This strategy, common in GM studies, allows the standardization of shape variables at determined size values (Zelditch et al., 2004, 2012). Finally, the Euclidean distances between shapes predicted at 10 equal CS values for *Talpa fossilis* and *T. europaea* were plotted in order to visualize the course of interspecific morphological distances along the static allometry.

### Variation Partitioning Analysis

A variation partitioning analysis (VARPART) (Legendre and Legendre, 2012; Legendre et al., 2012) was performed to take into account the influence of space and climate on shape variables. The technique of variation partitioning is used when two or more complementary sets of hypotheses can be invoked to explain the variation of a response variable (Legendre, 2008). For this purpose, the latitude and longitude coordinates of each locality were transformed using the principal coordinates of neighbour matrices method (PCNM; Borcard and Legendre, 2002; Borcard et al., 2004). PCNM produces orthogonal (linearly independent) spatial

**TABLE 2.** Results of the VARPART analysis.

| <b>Humeral shape/entire sample</b>         | <b>df</b> | <b>R<sup>2</sup></b> | <b>Adjusted R<sup>2</sup></b> | <b>p</b> |
|--|-----------|----------------------|-------------------------------|----------|
| Full model                                 | 7         | 0.17                 | 0.12                          | 0.001    |
| individual fractions                       |           |                      |                               |          |
| pure time                                  | 1         | 0.048                | 0.041                         | 0.001    |
| pure geography                             | 3         | 0.05                 | 0.026                         | 0.001    |
| pure climate                               | 1         | 0.009                | -0.005                        | 0.858    |
| <b>Humeral shape/<i>Talpa europaea</i></b> |           |                      |                               |          |
| Full model                                 | 5         | 0.11                 | 0.04                          | 0.002    |
| individual fractions                       |           |                      |                               |          |
| pure time                                  | 1         | 0.01                 | -0.002                        | 0.678    |
| pure geography                             | 3         | 0.07                 | 0.02                          | 0.005    |
| pure climate                               | 1         | 0.009                | -0.005                        | 0.879    |
| <b>Humeral shape/<i>Talpa fossilis</i></b> |           |                      |                               |          |
| Full model                                 | 5         | 0.13                 | 0.032                         | 0.056    |
| individual fractions                       |           |                      |                               |          |
| pure time                                  | 1         | 0.04                 | 0.029                         | 0.128    |
| pure geography                             | 3         | 0.08                 | 0.02                          | 0.087    |
| pure climate                               | 1         | 0.035                | 0.014                         | 0.059    |

variables over a much wider range of spatial scales (Borcard and Legendre, 2002). The residuals of multivariate regression of the shape variables on the transformed geographical coordinates were calculated in order to remove the effect (if any) of spatial influence. Then, the residual scores to the mean shape value were summed. Once the spatial effect has been removed it is possible to run a per-MANOVA test to ascertain if significant shape differences still occur among populations. It was hypothesized that a spatial influence would only occur for *T. europaea* specimens.

The VARPART analysis was performed using the `varpart()` function in “vegan” R package (Oksanen et al., 2013). The significance of the model was tested with a redundancy analysis (RDA). Climatic data were taken from Zachos et al. (2001). The oxygen isotopic data have been already used as a proxy for climatic changes in several previous works (Raia et al., 2005; Meloro et al., 2008; Sansalone et al., 2015) and was included as the climatic data in the VARPART model. The VARPART analysis was performed on the whole sample as well as on the separate samples of *T. europaea* and *T. fossilis*.

## RESULTS

### Measurement Error

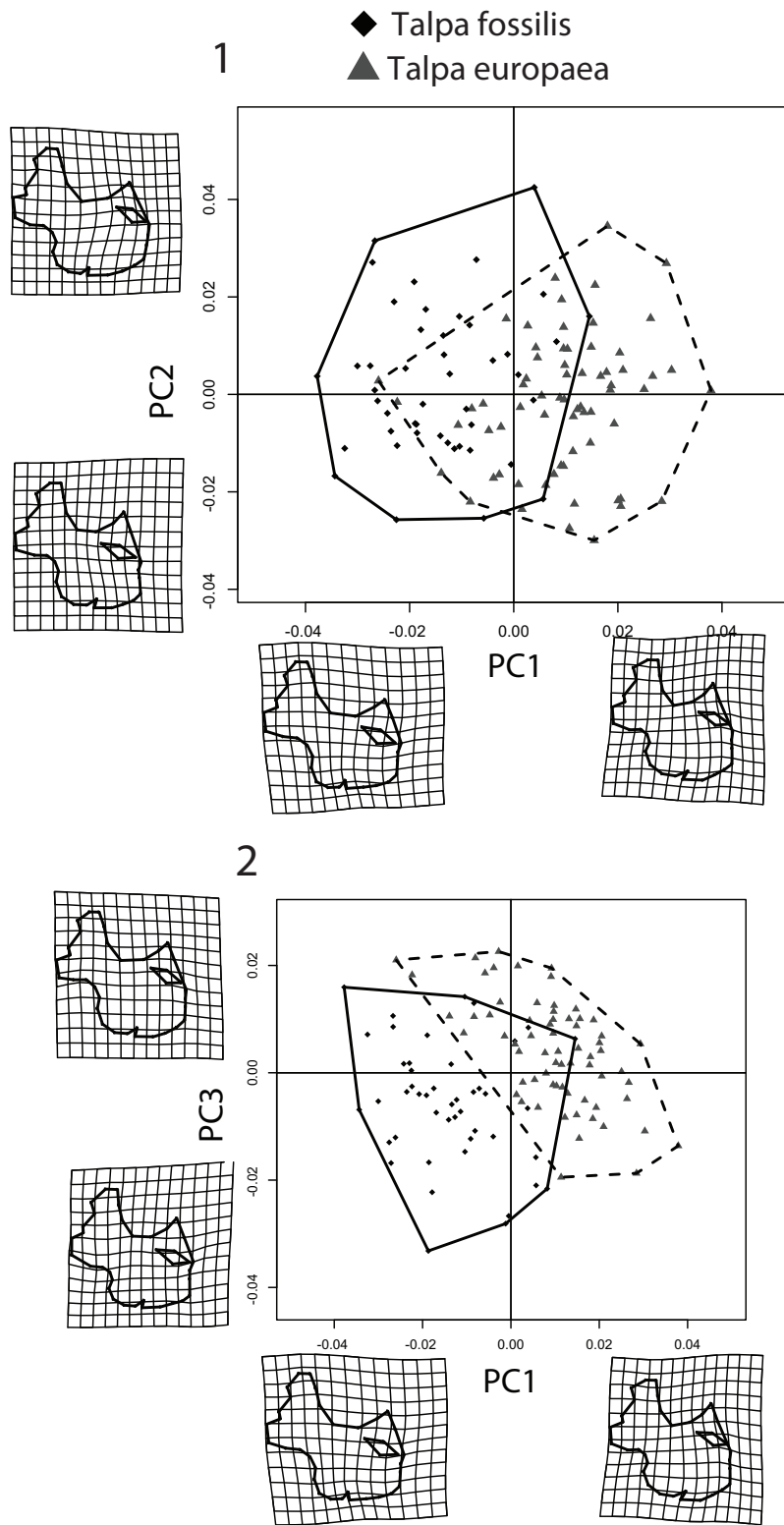
The measurement error analysis revealed that 2.9% of the total variation was due to digitisation error. Since the measurement error was smaller than 5%, it was judged as not significantly influencing further analysis.

### Variation Partitioning Analysis

The results of the VARPART analysis are summarized in Table 2. A significant geographic and temporal interaction in the whole sample was found, whereas there was no correlation with climate. However, temporal and climate interactions were found to be negligible in both the separate species. A significant geographic influence was found only for *Talpa europaea*.

### Shape and Size Analyses

The PCA performed on the aligned procrustes coordinates (Figure 3.1–2) show a good degree of separation between *Talpa fossilis* and *T. europaea* in particular along the PC1 (17.18% of the total variance). At positive values of the PC1 the humeral morphology shows an enlargement of the pectoral ridge and of the teres tubercle, an enlargement of the greater tuberosity and a medial shift of the humeral head. At negative values of the PC1 it



**FIGURE 3. 1**, Scatterplot of the first two axes of the PCA. Deformation grids refer to axes extremes (positive and negative values). **2**, Scatterplot of the first and third axes of PCA. Deformation grids refer to axes extremes (positive and negative values).



presents a contraction of the pectoral ridge and a reduction of the teres tubercle, a reduction of the greater tuberosity and a lateral shift of the humeral head. At positive values of the PC2 (13.6% of the total variance) the humeral morphology shows an elongation of the teres tubercle and a shortening of the pectoral ridge. At negative values of the PC2 it shows a shortening of the teres tubercle and an elongation of the pectoral ridge. At positive values of the PC3 (8.17% of the total variance) the humeral shape shows a contraction of the lateral epicondyle and an enlargement of the minor sulcus. At negative values of the PC3 it shows an enlargement of the lateral epicondyle and a contraction of the minor sulcus.

The perMANOVA test returned a statistically significant difference ( $p < 0.001$ ;  $F_{1,111} = 12.98$ ) between the two species. Even when using the space corrected values for *Talpa europaea* the perMANOVA test returned a statistically significant result ( $p < 0.001$ ;  $F_{1,111} = 13.48$ ). The boxplot computed for the CS (Figure 4) showed a statistically significant size variation (perANOVA,  $p < 0.001$ ;  $F_{1,111} = 46.041$ ) between *T. europaea* and *T. fossilis*, with the former being larger than the latter.

### Static Allometry

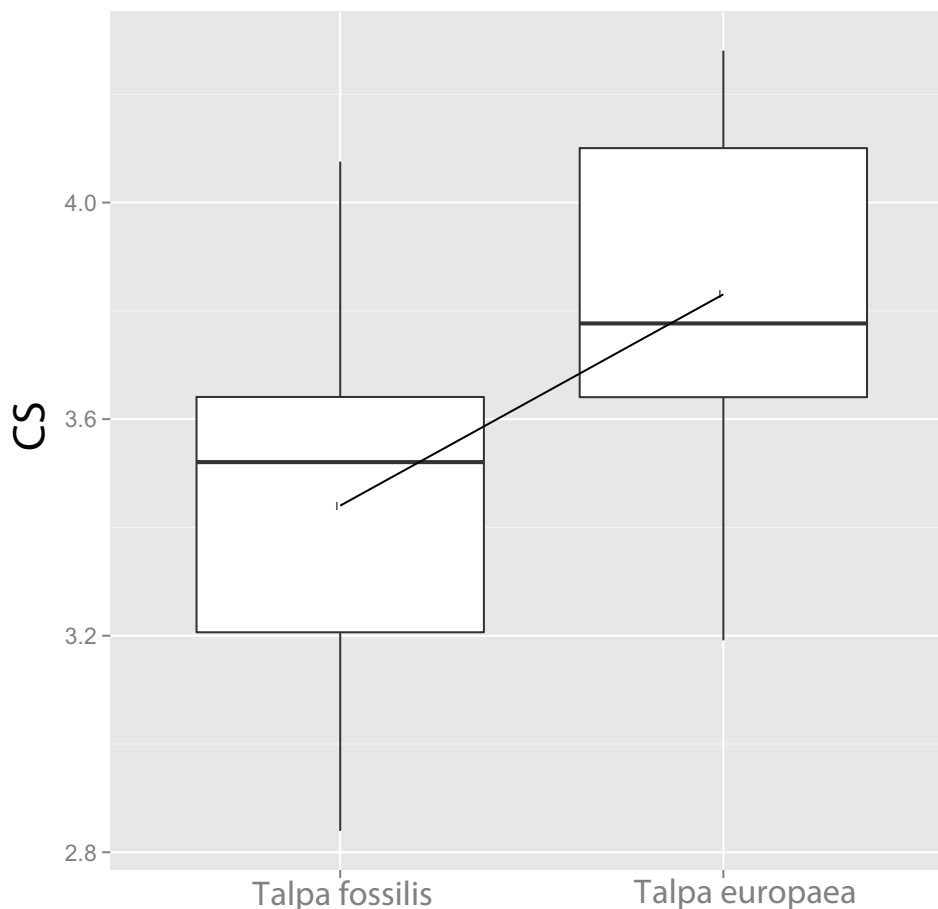
According to the significant interaction ( $p = 0.0199$ ;  $F_1 = 1.92$ ) between species and size effects in the perMANCOVA, specific allometric trajectories were proved to be non-parallel between the two species. Multivariate regression of shape data on size returned a statistically significant result ( $p < 0.001$ ;  $F_{1,109} = 7.86$ ;  $R^2 = 0.061$ ), with size accounting for 6% of the total shape variance (Figure 5.1). Separate multivariate regressions on *Talpa fossilis* and *T. europaea* returned statistically significant results ( $p = 0.003$ ,  $R^2 = 0.048$ ;  $p < 0.001$ ,  $R^2 = 0.034$ ; respectively). PerMANOVA returned statistically significant values for the shape variables standardized at maximum and minimum CS values ( $p < 0.001$ ,  $F_{1,111} = 26.51$  and  $p < 0.001$ ,  $F_{1,111} = 12.09$ ; respectively). Euclidean distances show a decrement toward the CS value of 3.3 (though not becoming zero) from that value they tend to augment (Figure 5.2).

### DISCUSSION AND CONCLUDING REMARKS

The separation between *Talpa fossilis* and *T. europaea*, observed along the PC1 (Figure 3.1–2), is due to changes in the teres tubercle and pectoral ridge. In particular, *T. europaea* has a larger teres tubercle and pectoral ridge than *T. fossilis*. In these

humeral regions two of the main muscles associated with the burrowing motion are inserted (Figure 2.2) (Gambaryan et al., 2003; Piras et al., 2012, 2015). On the teres tubercle the Teres major and Latissimus dorsi muscles are inserted, while on the pectoral ridge the Pectoralis Pars Sternalis muscle inserts (Dobson, 1882; Freeman, 1886; Gambaryan et al., 2003). These muscles account for the 42.5% of the total digging muscle weight (Gambaryan et al., 2003). Piras et al. (2012) showed that the enlargement of the teres tubercle and of the pectoral ridge was a key factor in the evolution of fossoriality, and that the development of these anatomical regions significantly reduced the mechanic stress on the humerus across Talpidae phylogeny. Sansalone et al. (in press) re-assessed the taxonomy of the Plio-Pleistocene Neurotrichine moles and applied GM techniques on humeral remains. Their analysis showed the primitive morphology of the teres tubercle, pectoral ridge, and bicipital tunnel in the extinct Polish *Rzebikia polonica* and *R. skoczni*, whereas the extant North American *Neurotrichus gibbsii* was in a more derived state (Sansalone et al., in press). Within this framework, we suggest that *T. europaea* was better adapted to burrowing, as this taxon had a larger area of insertion for the main digging muscles and is more specialized than *T. fossilis*.

This study showed that the allometric trajectories of *Talpa europaea* and *T. fossilis* were significantly different (they cross each other) by having different starting and ending points. This evidence excludes the possibility that *T. fossilis* should be considered as a stratigraphic species (Rabeder, 1972). In this case we would expect to find very similar static allometric trajectories, as predicted by the allometric-constraint theory (Voje and Hansen, 2013; Firmat et al., 2014; Voje et al., 2014). The humerus of highly fossorial moles experienced a strong phenotypical channeling in order to adapt to the underground environment (Nevo, 1979; Sánchez-Villagra et al., 2006; Piras et al., 2012, 2015). The absence of a climatic influence on humeral shape, related to the climatic stability of the subterranean ecotope (Nevo, 1979), supports the evidence that the different allometric slopes likely indicate the presence of two separate species. Furthermore, the hypothesis that *T. fossilis* be considered a chronospecies of *T. europaea* (Robert, 1983) has been proven to be false. The significant shape differences found between *T. europaea* and *T. fossilis*, even when the shape variables are predicted at the same CS values, indicate that the two taxa have different allometric patterns and humeral

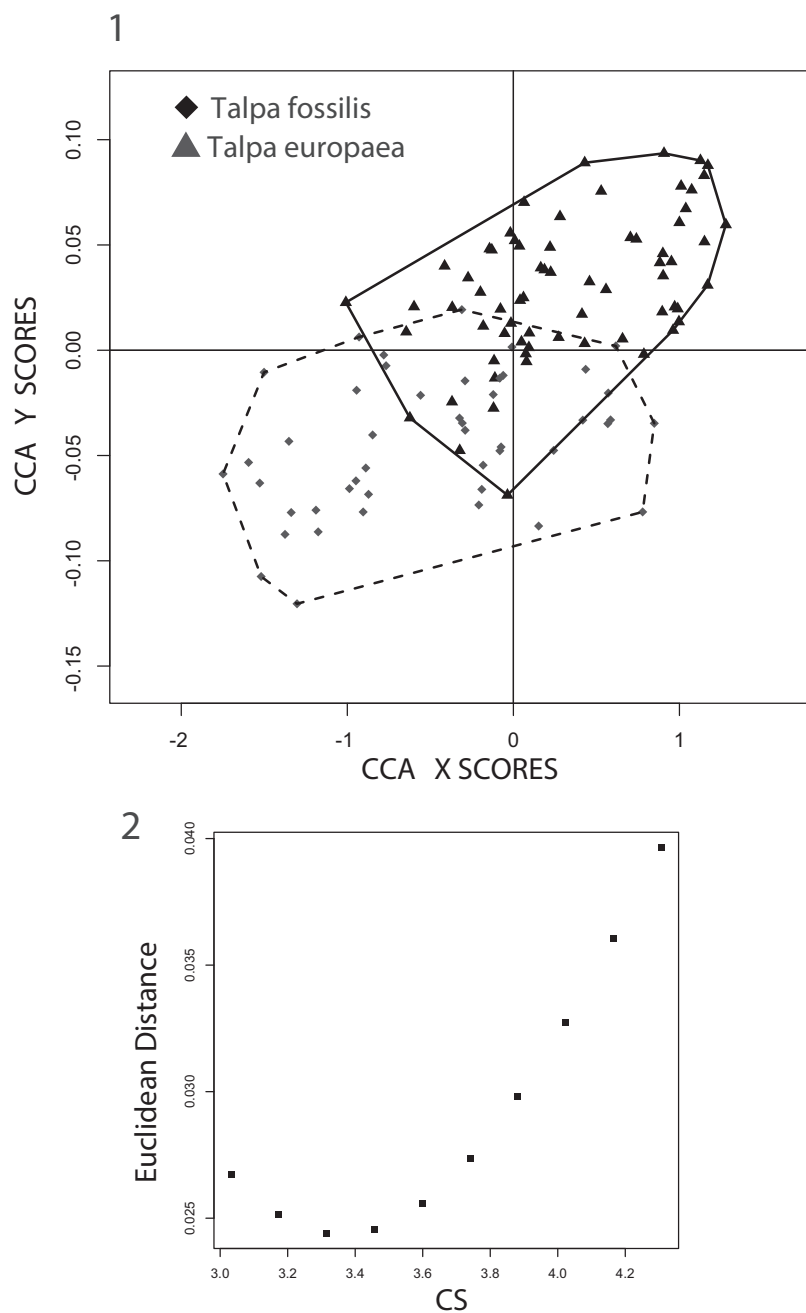


**FIGURE 4.** Boxplot of the centroid sizes. Bottom and top of the boxes are the first and third quartiles; horizontal solid black lines represent the median; whiskers represent the minimum and maximum values.

morphologies even under the same adaptive pressure.

Given these results *Talpa fossilis* is considered to be a distinct species from *T. europaea*. Separating these two taxa would also fit with molecular data. According to Colangelo et al. (2010) and Feuda et al. (2015) the *T. europaea* basal split has a mean divergence time estimate of 0.7 m.y. The time estimate would be in agreement with the fossil record and the species distinction usually presented in literature (Sulimski, 1959; Jánossy, 1979). From the results of this study, *T. fossilis*, which has a more primitive humeral morphology, is hypothesized to have originated from a different lineage than *T. europaea*. The fossil record (Ziegler, 1999; van den Hoek Ostende and Fejfar, 2006; Ziegler, 2006; Engesser, 2009) support the presence of four *Talpa* species since the early Miocene: *T. tenuidentata* Ziegler, 1990 (MN2-

3; 22-18 Ma), *T. minuta* de Blainville, 1840 (MN2-9; 22-10 Ma), *T. vallesensis* de Villalta Comella and Crusafont Pairó, 1944 (MN7-11; 12-8.5 Ma) and *T. gilothei* Storch, 1978 (MN9-11; 11.5-8.5 Ma). It is possible that the *T. fossilis* lineage originated from an offshoot of the Miocene mole lineages, which had a different allometric pattern and primitive humeral features, and spread across Europe during the Pliocene, surviving until the end of the Middle Pleistocene. In another possible scenario, *T. fossilis* could be derived from an eastern branch and may have colonized Europe during the Early Pliocene. According to Colangelo et al. (2010), *T. europaea* was derived from the eastern lineage of the genus *Talpa*. Therefore, it is hypothesized that *T. europaea*, during its colonization routes, could have come in contact with *T. fossilis* and out-competed it due to its larger size and superior digging capability. Competition in moles is a well-known



**FIGURE 5. 1**, CCA scatterplot of the shape and size variables. **2**, Plot of the Euclidean distances between the predicted shape values of *Talpa fossilis* and *T. europaea* against 10 discrete CS intervals.

phenomenon and is described in detail for the genera *Talpa* and *Mogera* (Abe, 1996; Loy et al., 1996; Loy and Capanna, 1998; van Cleef-Roders and van den Hoek Ostende, 2001; Yokohata, 2005; Bego et al., 2008; Loy, 2008). Furthermore, highly fossorial moles have been extensively reported to be solitary, territorial, and actively patrolling their tunnels, which they defend against intruders (Gorman and Stone, 1990; Loy et al., 1994).

The results of this study suggest that the landmark-based shape analysis is useful in supporting systematics in palaeontological investigations, in particular when morphological differences are elusive. In order to extend these findings on humeral static allometric trajectories to larger portions of the occurrence areas of these two species, the systematics of every assemblage bearing *Talpa fossilis* and *T. europaea* should be reviewed, based not

only on humeral morphologies, but also on other skeletal elements following the methodologies used in this study.

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## APPENDIX.

Specimen accession numbers and housing institutions.

| Species               | Accession number | Housing Institution             |
|-----------------------|------------------|---------------------------------|
| <i>Talpa fossilis</i> | 3701_01          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 3701_02          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 3701_03          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 3701_04          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4721             | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4741_01          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4741_02          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4741_03          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4750_01          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4750_02          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | B_01             | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | B_02             | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 3702             | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_01 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_02 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_03 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_04 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_05 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_06 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_07 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_08 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_09 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_10 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_10_11 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_11_01 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_11_02 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_11_03 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_11_04 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Villany_08_12a   | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | V_65482          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Somssichhegy_4_1 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Somssichhegy_4_2 | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Ostramos_7_01    | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | Ostramos_7_02    | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4743_01          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4743_02          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4743_03          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4743_04          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4743_05          | Budapest Natural History Museum |
| <i>Talpa fossilis</i> | 4743_06          | Budapest Natural History Museum |

| <b>Species</b>        | <b>Accession number</b> | <b>Housing Institution</b>         |
|-----------------------|-------------------------|------------------------------------|
| <i>Talpa fossilis</i> | 4743_07                 | Budapest Natural History Museum    |
| <i>Talpa fossilis</i> | 4743_08                 | Budapest Natural History Museum    |
| <i>Talpa fossilis</i> | 4743_09                 | Budapest Natural History Museum    |
| <i>Talpa fossilis</i> | 4743_10                 | Budapest Natural History Museum    |
| <i>Talpa fossilis</i> | HP18                    | BSPG Munich Natural History Museum |
| <i>Talpa fossilis</i> | 5.24                    | BSPG Munich Natural History Museum |
| <i>Talpa fossilis</i> | 5.24a                   | BSPG Munich Natural History Museum |
| <i>Talpa europaea</i> | V57760_01               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V57760_02               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V57760_03               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V57760_04               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V57760_05               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59143                 | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_01              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_02              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_03              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_04              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_05              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_06              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_07              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_08              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_59145_09              | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_01               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_02               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_03               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_04               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_05               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_06               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_07               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_08               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_09               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_10               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5915_11               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_01               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_02               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_03               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_04               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_05               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_06               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_07               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_08               | Budapest Natural History Museum    |
| <i>Talpa europaea</i> | V_5917_09               | Budapest Natural History Museum    |



| <b>Species</b>        | <b>Accession number</b> | <b>Housing Institution</b>      |
|-----------------------|-------------------------|---------------------------------|
| <i>Talpa europaea</i> | V_5917_10               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_11               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_12               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_13               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_14               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_15               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_16               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_17               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_18               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_19               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_20               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_21               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_22               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_23               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_24               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_25               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_26               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_27               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_28               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_29               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_30               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_31               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_32               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_5917_33               | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_621116                | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_621172_01             | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_621172_02             | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_621172_03             | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_621172_04             | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_621172_05             | Budapest Natural History Museum |
| <i>Talpa europaea</i> | V_631274                | Budapest Natural History Museum |