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New systematic insights about Plio-Pleistocene moles from Poland

GABRIELE SANSALONE, TASSOS KOTSAKIS, and PAOLO PIRAS



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The generic attribution of the Plio-Pleistocene Polish moles ?*Neurotrichus polonicus* and ?*Neurotrichus skoczeni* has been questioned several times in the past. The fossil material belonging to ?*Neurotrichus polonicus* and ?*Neurotrichus skoczeni* is re-evaluated here and a new diagnosis is provided on the basis of qualitative considerations. In addition, a Geometric Morphometric analysis of the humerus has been performed including both extant and extinct Neurotrichini and Urotrichini taxa for comparison. Our results proved the unique morphology of the Polish material suggesting a distinct taxonomic state. The morphological variations evidenced by the humeral shape analysis agree with the observed qualitative differences and support a new generic allocation. The new genus *Rzebikia* gen. nov. is proposed for all the material previoulsly ascribed to ?*Neurotrichus polonicus* and ?*Neurotrichus skoczeni*.

Key words: Mammalia, Talpidae, *Neurotrichus*, Geometric Morphometrics, humerus, systematics, taxonomy, Pliocene, Pleistocene, Poland.

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Introduction

The Polish Plio-Pleistocene mammal bearing localities provided a huge amount of fossil talpid remains (Rzebik-Kowalska 2005). Skoczeń (1976, 1980, 1993) described five new species belonging to extant genera currently endemic of North America: *Condylura kowalskii* Skoczeń, 1976, *Condylura izabellae* Skoczeń, 1976, *Parascalops fossilis* Skoczeń, 1993, ?*Neurotrichus polonicus* Skoczeń, 1980 and ?*Neurotrichus minor* Skoczeń, 1993. Storch and Qiu (1983) suggested the inclusion of ?*Neurotrichus polonicus* in the genus *Quyania*, but, due to the lack of the upper and lower antemolar rows they maintained the generic status given by Skoczeń (1980). They suggested that the Polish species is inserted in an ancestor-descendant lineage in relationship with *Quyania chowi* Storch and Qiu, 1983, hypothesizing a lineage characterized by a gradual reduction of the precingulid, the strenghtening of the upper molar protoconules and size increase. The description of the small species ?*Neurotrichus minor* raised the question by the large size as an advanced evolutionary character (Skoczeń 1993). Popov (2004), following the hypothesis of Storch and Qiu (1983), assigned the material from Varshets (Early Pleistocene, Bulgaria) to *Quyania* aff. *Q. polonica*. Popov (2004) considered the Polish species as more advanced than *Neurotrichus gibbsii* by having reduced precingulids and a humerus more adapted to a fossorial lifestyle. Rzebik-Kowalska (2005), maintained the original taxonomic identification provided by Skoczeń (1980). Dalquest and Burgner (1941) described the extant North-American subspecies *Neurotrichus gibbsii minor* which is still considered valid. Therefore Zijlstra (2010) proposed the new name *Neurotrichus skoczeni*. Rzebik-Kowalska (2014) pointed out that the generic attribution of ?*Neurotrichus polonicus* still represents an open question. Her revision showed that the Polish species displays characters shared by both genera *Neurotrichus* and *Quyania*. Rzebik-Kowalska (2014) left the generic attribution given by Skoczeń (1980) considering the attribution to the genus *Quyania* as still im-

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motivated. Although the generic attribution of these species has been questioned (Storch and Qiu 1983; Popov 2004; Rzebik-Kowalska 2014), no new analyses or diagnoses have been provided till now. Here we re-examined the material previously attributed to ?*Neurotrichus polonicus* and ?*Neurotrichus skoczeni* and provided a new generic diagnosis in the light of the most recent studies on talpid morphology and evolution (Gambaryan et al. 2003; Sánchez-Villagra et al. 2004, 2006; Piras et al. 2012). We also investigated the patterns of shape and size variation of the humerus by means of Geometric Morphometrics Analysis. The humerus experienced the most remarkable transformations during talpid evolution (Dobson 1882; Freeman 1886; Reed 1951; Yalden 1966; Sánchez-Villagra et al. 2004; Piras et al. 2012). This skeletal element is usually found well preserved and abundant in fossil assemblages. It is thus widely used in systematic studies of extinct Talpidae (Ziegler 2003) and, due to its abundance, allows the use of modern multivariate and univariate statistical methods.

Institutional abbreviations.—LACM, Los Angeles County Museum, Los Angeles, USA; MF, Institute of Systematic and Evolution of Animals, Kraków, Poland; NMNS, National Museum of Nature and Science, Tsukuba, Japan; V, Institute of Zoology, Bulgarian Academy of Sciences, Sofia, Bulgaria; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

Other abbreviations.—ANOVA, univariate analysis of variance; bgPCA, between group Principal Components Analysis; CS, Centroid Size; GM, Geometric Morphometrics; MANOVA, multivariate analysis of variance; UPGMA, Unweighted Pair Group Method with Arithmetic Mean.

Material and methods

Specimens collection.—We analyzed a total of 48 left humeri belonging to *Urotrichus talpoides* Temminck, 1841 (n = 12), *Dymecodon pilirostris* True, 1886 (n = 8), *Urotrichus dolichochir* Gaillard, 1889 (n = 5), *Quyania chowi* Storch and Qiu, 1983 (n = 2), *Neurotrichus gibbsii* Baird, 1856 (n = 16), *Rzebikia polonica* Skoczeń, 1980 (n = 6). We included in the analysis all the Late Neogene Neurotrichini and Urotrichini species for which complete humerus was available. For details about specimen codes, localities, and collection storage see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Sansalone_etal_SOM.pdf.

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 105mm lens. We digitized 21 landmarks and 15 semi-landmarks (Fig. 1) using the tpsDig2 software (Rohlf 2006). Semi-landmarks are a useful tool to capture the morphology of complex outlines due to the lack of homologous anatomical points. They assume that curves or contours are homologous among

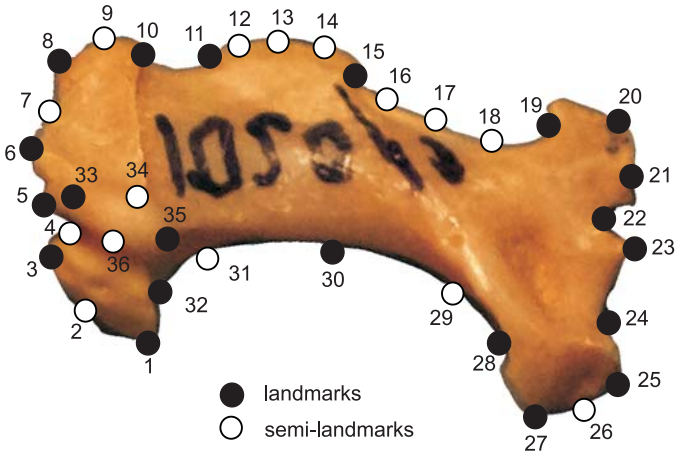


Fig. 1. Landmarks (black circles) and semilandmarks (white circles) digitized on the humerus in caudal norm: 1, lateral end of greater tuberosity; 2, articular facet for clavicula; 3, proximal edge of the articular facet for clavicula; 4, bicipital notch; 5, proximal end of lesser tuberosity; 6, medial 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; 20–22, 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.

specimens (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 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). This 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. In order to visualize the ordination of the aligned specimens we performed a between group PCA (bgPCA), using the function groupPCA() included in the R-package "Morpho". The bgPCA provides a projection of the data onto the principal components of the group means, leading to an ordination of the shape variables between the group means. The new axes are orthogonal and can be computed even when the data are not of full rank, such as for Procrustes shape coordinates (Mitteroecker and Bookstein 2011). This method offers a good performance when the number of observations is smaller than the number of variables (Boulesteix 2005), which is often the case for

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GM analyses. The significance of the observed shape differences among species was evaluated by performing a permutational multivariate analysis of variance (perMANOVA) on Procrustes coordinates using adonis() function included in the "vegan" R package (Oksanen 2013). The significance of shape differences between species was then evaluated performing a pairwise permuted MANOVA using the pwpermanovac() wrapper function, available in SOM 4. Size variation was visualized using a boxplot. The significance of size differences has been evaluated by performing a permutational univariate analysis of variance (perANOVA) on CS using the function adonis(). Between species size differences were evaluated performing a pairwise permuted ANOVA using the wrapper function pwperanovac(), available in SOM 4. All p-values were corrected using "Holm" correction. We excluded *Quyania chowi* from all the pairwise permuted comparisons due to its small sample size (n = 2). The phenetic relationships among the taxa included in this study have been visualized performing an UPGMA on the Euclidean distance matrix computed on per-species mean shape variables.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Eulipotyphla Waddel, Okada, and Hasegawa, 1999

Family Talpidae Fischer, 1814

Subfamily Talpinae Fischer, 1814

Tribe Neurotrichini Hutterer, 2005

Genus *Rzebikia* nov.

Type species: *Rzebikia polonica* (Skoczeń, 1980); see below.

Included species: Type species and *Rzebikia skoczeni* (Zijlstra, 2010).

Etymology: Dedicated to Barbara Rzebik-Kowalska for her extensive and fundamental contributions to the knowledge of Eulipotyphla.

Diagnosis.—Humerus with moderate digging adaptations having a large teres tubercle separated by a marked notch from the pectoral ridge, partially unfused bicipital tunnel (the suture between the proximity of the pectoral ridge and the lesser tuberosity is present but not complete; see Fig. 2A), large minor sulcus, lesser tuberosity poorly developed toward the proximal end of the shaft. p4 with straight metacristid and distinct entoconid separated from the protoconid by a furrow. The cingula are weakly developed with the M_1 having the precingulid extending only halfway its

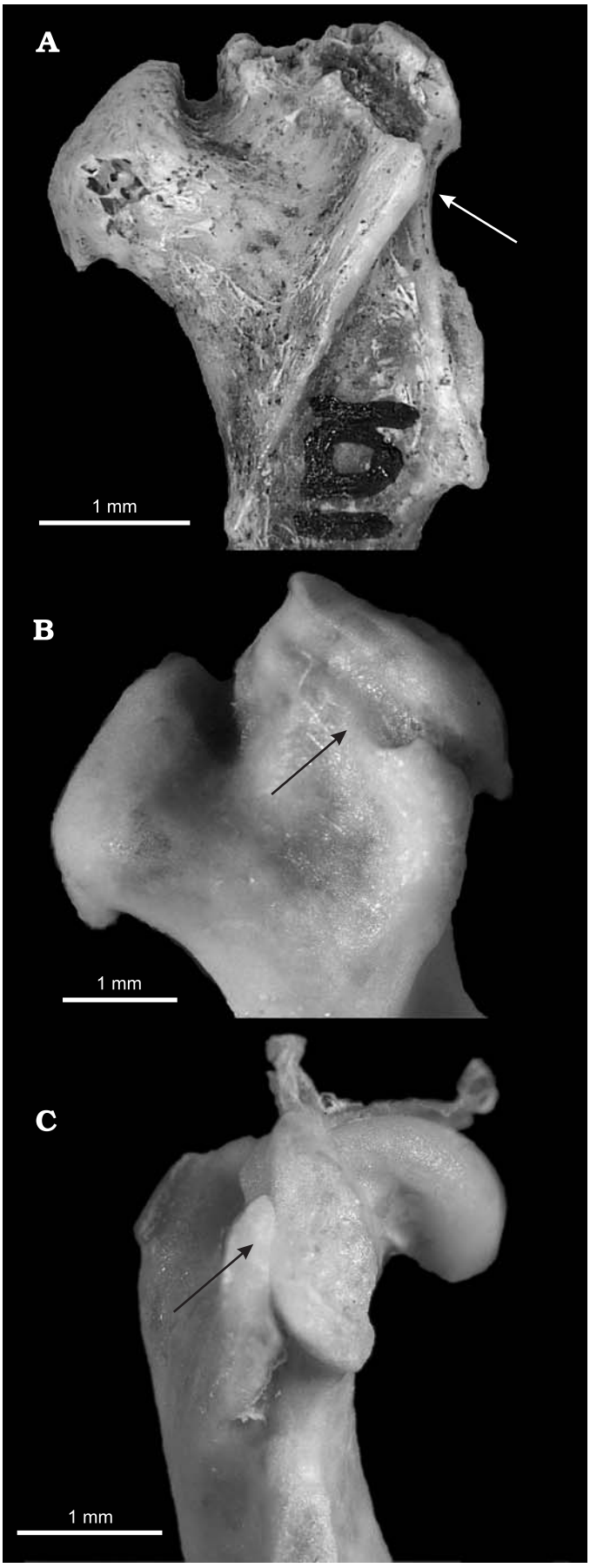


Fig. 2. Photographs showing the different conditions of the bicipital tunnel (arrowed) in talpid mammals. **A**. *Rzebikia polonica* (Skoczeń, 1980) gen. nov. (MF/1020/1), Early Villanyian (MN 16) of Poland, Rębielice Królewskie 1A, frontal view with partially unfused bicipital tunnel. **B**. *Urotrichus talpoides* Temminck, 1841 (NMNS 28207), Recent, frontal view with completely open bicipital tunnel. **C**. *Neurotrichus gibbsii* Baird, 1856 (LACM 93944), Recent, lateral view with completely fused bicipital tunnel.

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width. The entoconids of both M_1 and M_2 are robust and displaced lingually making the lingual side of the lower molars concave. The M1 and M2 bear a strong paraconule. The M2 lack precingulum and the parastyle is separated from the paracrista. The clavicle dorsal prominence of the manubrial articular facet is straight and the ventral process line is concave and possess two small spines.

Stratigraphic and geographic range.—Pliocene–Pleistocene boundary, Poland, Late Villanyian (MN17) localities: Kadzielnia, Zamkowa Dolna Cave A, Kielniki 3B; Ruscinian–Villanyian (MN15, MN16) boundary, locality Węże 2, Early Villanyian (MN16), locality Rębielice Królewskie 1A. Bulgaria, Villanyian (MN17), locality Varshets.

Rzebikia polonica (Skoczeń, 1980) comb. nov.

Fig. 2A.

1980 ?*Neurotrichus polonicus* Skoczeń; Skoczeń 1980: 427–440, pls. V–VI.
1983 ?*Neurotrichus polonicus* Skoczeń; Storch and Qiu 1983: 100–101, 105.
1993 *Neurotrichus polonicus* Skoczeń; Skoczeń 1993: 133–134, fig. 4.
1994 "?*Neurotrichus polonicus*" Skoczeń; Rzebik-Kowalska 1994: 80, 89–91.
1995 ?*Neurotrichus polonicus* Skoczeń; Doukas et al. 1995: 51.
2003 *Neurotrichus polonicus* Skoczeń; Ziegler 2003: 639.
2004 *Quyania polonica* (Skoczeń); Popov 2004: 71–75, fig. 6–8.
2005 *Neurotrichus? polonicus*; Rzebik-Kowalska 2005: 128–131.
2006 *Neurotrichus polonicus*; Ziegler 2006: 139, 141.
2009 *Neurotrichus polonicus* Skoczeń; Rzebik-Kowalska 2009: 9, 22, 24–26, 51.
2014 ?*Neurotrichus polonicus* Skoczeń; Rzebik-Kowalska 2014: 9–11, figs. 2, 3.

Etymology: In reference to its origin from Poland.

Holotype: Incomplete right mandible with p4–m2 (MF/1016/1) (Skoczeń 1980: pl. VI).

Type locality: Kadzielnia, Poland.

Type horizon: Late Villanyian (MN17) or Pliocene–Pleistocene boundary.

Material.—Rębielice Królewskie 1A, Poland: One right P4 (MF/1015/1); one right and two left M1 (MF/1015/2–4); right M3 (MF/1015/5); incomplete premolar portion of the right mandible with p3 (MF/1015/6); incomplete premolar portion of the right mandible with m1 and m2 (MF/1015/7); two middle fragments of left mandibles with m1 and m2 (MF/1015/8, 9); posterior part of left mandible with m2 and m3 (MF/1015/10); right m1 (MF/1015/11); three m2 (MF/1015/12–14); right and left m3 (MF/1015/15, 16); six clavicles (MF/1015/17–22); 13 humeri (MF/1015/23–35); ulna (MF/1015/36); radius (MF/1015/37). Zamkowa Dolna Cave near Częstochowa, layer C, Poland: three M1 (MF/1017/1–3); right M2 (MF/1017/4); right m1 (MF/1017/5); right m2 (MF/1017/6); right and left m3 (MF/1017/7, 8); right humerus (MF/1017/9). Kadzielnia, Poland: two right mandible (MF/1016/1, 2), one with p4–m2 and other with m1–m2, 2 humeri (MF/1016/3, 4). Kielniki 3B, Poland: 1 humerus (MF/1020/1). Varshets, North Bulgaria: 3 fragments of mandible with m1–m3 and one m2 (V23: 4–5, V339), 3 humeri (V23: 1–3). All from Villanyian (Pliocene–Pleistocene). See SOM 2 for linear measurements of the material.

Emended diagnosis.—Medium to large sized shrew-mole with moderate adaptation to digging. The humerus has an evident scalopine ridge and partially unfused bicipital tunnel (Fig. 2A). The protoconules are absent or vestigial. Lower molars have vestigial mesoconids.

Description.—See Skoczeń (1980, 1993), Popov (2004) and Rzebik-Kowalska (2014) for a complete and detailed description of the material.

Remarks.—The material from Varshets (Popov 2004) fit well in both size and morphological characters with that of *Rzebikia polonica* from Poland, so we ascribe the Bulgarian material to the Polish species.

Stratigraphic and geographic range.—Pliocene–Pleistocene boundary, Poland, Late Villanyian (MN17) localities: Kadzielnia, Zamkowa Dolna Cave A, Kielniki 3B; Early Villanyian (MN16), locality Rębielice Królewskie 1A. Bulgaria, Villanyian (MN17), locality Varshets.

Rzebikia skoczeni (Zijlstra, 2010) comb. nov.

1993 *Neurotrichus minor* Skoczeń; Skoczeń 1993: 130–133, fig. 4.
1994 *Neurotrichus minor* Skoczeń; Rzebik-Kowalska 1994: 80, 88.
2004 *Quyania minor* (Skoczeń); Popov 2004: 75.
2005 *Neurotrichus minor* Skoczeń; Rzebik-Kowalska 2005: 127.
2009 *Neurotrichus minor* Skoczeń; Rzebik-Kowalska 2009: 9, 21.
2010 *Neurotrichus skoczeni*; Zijlstra 2010: 1903.
2014 ?*Neurotrichus skoczeni* Zijlstra; Rzebik-Kowalska 2014: 11–12.

Etymology: In honor of Stanisław Skoczeń, who originally described this species.

Type material: Holotype: right humerus ZPAL/M-2/2 (Skoczeń 1993: fig. 4). Paratype: isolated left M1 (ZPAL/M-2/1).

Type locality: Węże 2, Poland.

Type horizon: Ruscinian–Villanyian boundary (MN 15, MN 16).

Emended diagnosis.—Small sized shrew-mole with moderate digging adaptation. The humerus have a well developed scalopine ridge and partially unfused bicipital tunnel, the pectoral tubercle is laterally displaced. The cingula of the M1 weaker and reduced.

Description.—See Skoczeń (1993) for a complete and detailed description of the material. See SOM 2 for linear measurements of the material.

Remarks.—The humerus is very similar to that of *Rzebikia polonica*, it differs only for its smaller size and the laterally displaced pectoral tubercle. The M1 is longer and narrower relative to that of *Rzebikia polonica* and differs for the shorter protoconus lacking a cingulum, the paraconus is narrower, the proto- and metaconuli are less prominent and the precingulum is markedly weak and short.

This species has been previously described as *Neurotrichus minor* by Skoczeń (1993). Although we changed the generic attribution for this species we maintained the specific attribution of *skoczeni* because the name *minor* is

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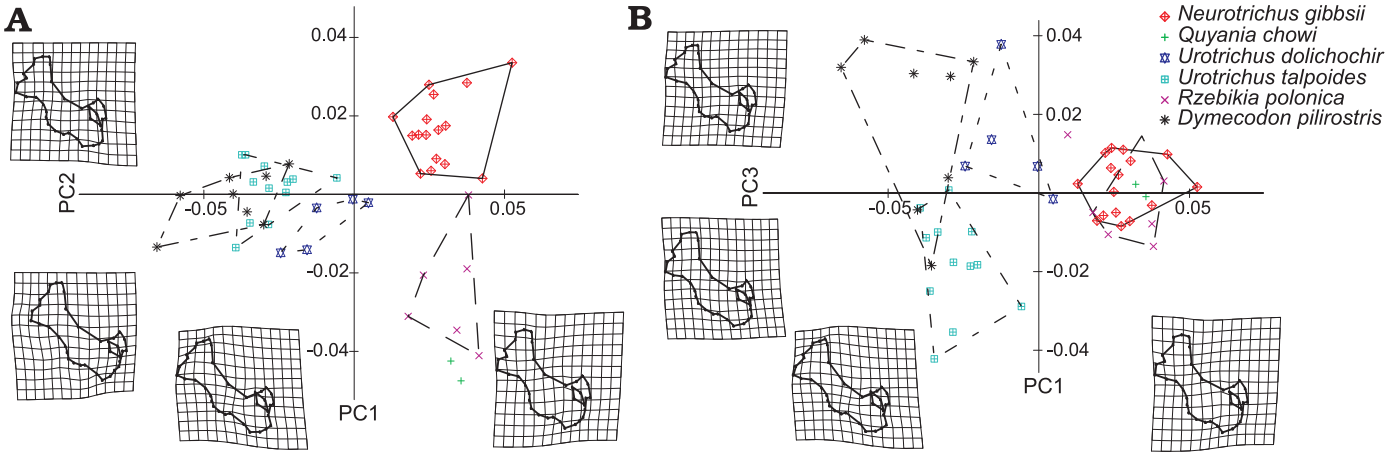


Fig. 3. **A**. Scatterplot of the first two axes of the bgPCA. Deformation grids refer to axes extremes (positive and negative values). **B**. Scatterplot of the first and third axes of bgPCA. Deformation grids refer to axes extremes (positive and negative values).

a primary homonym and permanently invalid (ICZN 1999: art. 57.2; Zijlstra 2010).

The following differential diagnoses are based on *Rzebikia polonica* because of the high similarity with the smaller species *Rzebikia skoczeni* and because of the most abundant material available for comparison.

Neurotrichus gibbsii: *Rzebikia polonica* shows many similarities in particular for the teeth (see Skoczeń 1980 for a detailed description) with the North American shrew mole, but differs by having reduced precingulids in m1. It is distinct from *Neurotrichus gibbsii* in the morphology of the humerus which is clearly less adapted to fossoriality by having: (i) a partially unfused bicipital tunnel, (ii) a more conspicuous scalopine ridge, (iii) a shorter teres tubercle, (iv) a longer greater sulcus, (v) the lesser tuberosity is less expanded in proximal direction.

Urotrichus talpoides: *Rzebikia polonica* is different in many features from the Japanese greater shrew mole in particular by having: (i) a partially unfused bicipital tunnel, (ii) a longer teres tubercle, (iii) a lesser distance between the teres tubercle and the lesser tuberosity, (iv) the presence of the scalopine ridge, (v) metacristid of the p4 in stright line, (vi) less robust mandible, (vii) presence of the p3, (viii) presence of the talonid notch.

Urotrichus dolichochir: This species presents clear Urotrichine affinity. It resembles the ex species *Urotrichus talpoides* in both size and shape of the humerus. *Urotrichus dolichochir* presents some primitive humeral features compared with extant Urotrichini such as an even small teres tubercle, open bicipital tunnel and a more slender shaft of the humerus. *Rzebikia polonica* differs from this species mainly for the same characters expressed for *U. talpoides*.

Dymecodon pilirostris: This species has been considered for long time as a congeneric member of *Urotrichus* because of the strong similarities in their morphology (Kawada and Obara 1999). *Rzebikia polonica* is different from the lesser Japanese shrew mole by the same features of *U. talpoides*.

Quyania chowi: *Rzebikia polonica* resembles *Q. chowi* in many features (see Storch and Qiu 1983 for a detailed description) whereas it is distinct from the Chinese species by having: (i) a more rounded and larger teres tubercle, (ii) a partially unfused bicipital tunnel, (iii) a shorter distance between the teres tubercle and the lesser tuberosity, (iv) a weaker development of the cingula, (v) unbent lingual side of the lower molars, (vi) more conspicous protoconules of the M1 and M2, (vii) parastyle of the M2 separated from the paracrista.

Quyania europaea Rzebik-Kowalska, 2014: *Rzebikia polonica* differs from the European species of *Quyania* by having: (i) more robust shaft of the humerus, (ii) larger teres tubercle, (iii) more evident and straight scalopine ridge, (vi) partially unfused bicipital tunnel, (v) the presence of vestigial mesoconids, (vi) mental foramen situated under the p3.

Neurotrichus columbianus Hutchinson, 1968: According with Storch and Qiu (1983) and Popov (2004), *Neurotrichus columbianus* should be related to the genus *Yanshuella* Storch and Qiu, 1983 and does not belong to Neurotrichini tribe at all.

Stratigraphic and geographic range.—Pliocene–Pleistocene boundary, Poland, Ruscinian–Villanyian (MN15, MN16) boundary, locality Węże 2.

Shape and size analyses

The bgPCA performed on the procrustes coordinates shows a neat separation between the urotrichine and neurotrichine shrew moles in particular across the PC1 (Fig. 3A). At positive values of the PC1 (62.80% of the total variance) the humeral shape shows an enlargement of the teres tubercle, an enlargement of the medial epicondyle and an expansion of the greater tuberosity, while at negative values the humerus shows a contraction of these regions. Along the PC2 (17.56% of the total variance) it is possible to observe a separation between *Neurotrichus gibbsii* and *Rzebikia polonica* At positive values the humeral morphology shows a reduction of the teres tubercle, a lengthening of the greater

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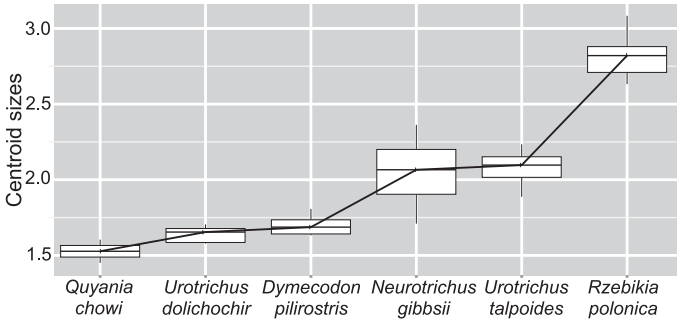


Fig. 4. Boxplot of the centroid sizes. Bottom and top of the boxes are the first and third quartiles, the horizontal black lines represent the median, the whiskers represent the minimum and maximum values.

sulcus and a contraction of the lesser tuberosity, while at negative values the humerus shows an enlargement of the teres tubercle and of the lesser tuberosity while the greater sulcus becomes shorter. Along the PC3 (10.84% of the total variance) it is possible to appreciate the separation between *Urotrichus talpoides* and *Dymecodon pilirostris* (Fig. 3B). At positive values the humeral shape shows an enlargement of the medial epicondyle and an increase of the greater tuberosity, while at negative values it is possible to observe a contraction of the regions previously described.

Permutational MANOVA returned an overall highly significant difference (p-value < 0.001) among species and pairwise permutation MANOVA returned significant values (Table 1) for all the comparisons.

The boxplot computed for the CS (Fig. 4) showed a significant size variation (permutational ANOVA p-value < 0.001) among species. *R. polonica* was significantly different from all other taxa by means of pairwise permuted ANOVA (Table 2).

The UPGMA computed on the Euclidean distance matrix calculated on the shape variables (Fig. 5A) evidenced a neat morphological difference between the Urotrichini, where *Urotrichus talpoides* and *Dymecodon pilirostris* showed close similarities, and Neurotrichini, where *Neurotrichus gibbsii* and *R. polonica* showed the closest morphological affinities.

Discussion and concluding remarks

The continuous humeral shape variation evidenced by the GM analysis was congruent with the qualitative morphological differences observed in the specimens included in this study. In particular, the neat separation between Urotrichini and Neurotrichini observed along the PC1 is due to major modifications of the regions mainly involved in the digging process (Gambaryan et al. 2003; Piras et al. 2012), such as the expansion of the teres tubercle. *Rzebikia polonica* has a partially unfused bicipital tunnel (Fig. 2A) while the Urotrichini have it open (Fig. 2B). Field observations on the extant *Neurotrichus gibbsii* (Campbell and Hochachka 2000: 578; Stone 1995: 57) and recent Finite Elements Analysis (Piras et al. 2012) suggest that Neurotrichini are more adapted to a fossorial lifestyle than Urotrichini. The UPGMA (Fig. 5A) confirmed the distinction between Neurotrichini and Urotrichini. Rzebik-Kowalska (2014) pointed out that *Quyania chowi* and *R. polonica* should be included in the Neurotrichini tribe. Our results support the inclusion of *R. polonica* in Neurotrichini tribe and exclude any Urotrichine affinity. Along the PC2 *R. polonica* sets apart from *N. gibbsii* and from *Q. chowi*. According to Storch and Qiu (1983) and Popov (2004), *R. polonica* descends from *Q. chowi*. In fact, the Polish genus has a more robust humerus, a bicipital tunnel showing a higher fusion degree between the pectoral crest and the lesser tuberosity, and a teres tubercle larger and more rounded. The phenetic relationships support *R. polonica* being more advanced than *Quyania chowi* and hence justify its different generic allocation. Storch and Qiu (1983) hypothesized a parallel evolution of *Neurotrichus gibbsii* and *Rzebikia polonica*, suggesting that the Polish species is more andvanced than *N. gibbsii* by having a relatively larger size. Popov (2004), following Storch and Qiu (1983), considered *R. polonica* as more advanced than *N. gibbsii*. Here we reject such hypothesis because *Rzebikia* gen. nov. shows many primitive features of the humerus when compared with the North American forms. The most striking features are the partially unfused bicipital tunnel (Fig. 2A), that is completely

Table 1. Pairwise permuted MANOVA results. All p-values are corrected using "Holm" correction.

	Urotrichus dolichochir	*Urotrichus talpoides*	*Rzebikia polonica*	*Dymecodon pilirostris*
Neurotrichus gibbsii	0.0009	0.0009	0.0009	0.0009
Urotrichus dolichochir		0.0019	0.0045	0.0134
Urotrichus talpoides			0.0009	0.0019
Rzebikia polonica				0.0019

Table 2. Pairwise permuted ANOVA results. All p-values are corrected using "Holm" correction.

	Urotrichus dolichochir	*Urotrichus talpoides*	*Rzebikia polonica*	*Dymecodon pilirostris*
Neurotrichus gibbsii	0.00159	0.76802	0.00099	0.00559
Urotrichus dolichochir		0.00239	0.00779	0.40215
Urotrichus talpoides			0.00099	0.00159
Rzebikia polonica				0.00449

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fused (Fig. 2C) in *N. gibbsii* (Reed 1951; Sánchez-Villagra et al. 2004), the reduced teres tubercle, and the widened minor sulcus. The enlargement of the teres tubercle is an important character of talpids evolution (Gambaryan et al. 2003; Piras et al. 2012). This humeral region allows the insertion of the muscles Teres major and Latissimus dorsi, two of the main muscles involved during burrowing (Gorman and Stone 1990; Gambaryan et al. 2003; Piras et al. 2012). A larger teres tubercle would allow the insertion of larger and more powerful digging muscles. *N. gibbsii* and *R. polonica* are separated along the PC2 and the humeral shape changes associated with this axis are in good agreement with our qualitative observations about the humeral morphological differences between these two taxa. Moreover, *N. gibbsii* and *R. polonica* are significantly different under pairwise permutational MANOVA. These evidences suggest that *N. gibbsii* is better adapted to digging than *R. polonica* and in a more derived evolutionary state. Nevertheless, *R. polonica* shows some derived features on teeth such as the reduced precingulid of m1 and more reduced protoconules (Storch and Qiu 1983; Popov 2004), not equally advanced in *N. gibbsii*. Rzebik-Kowalska (2014) noted that, in *R. polonica*, the protoconules are absent and vestigial only in one specimen. Moreover, the upper and lower teeth of *R. polonica* are wider than those of *N. gibbsii* and more similar to those of *Quyania* (Rzebik-Kowalska 2014). All of these evidences well support a new generic allocation. The UPGMA (Fig. 5A) shows close similarities with the phylogenetic hypothesis (Fig. 5B) proposed by Storch and Qiu (1983). We follow them in considering *Q. chowi* as the probable ancestor to *N. gibbsii, R. polonica*, and *R. skoczeni*. According to Storch and Qiu (1983) *Q. chowi* can be considered the ancestor of the neurotrichine lineage. *N. gibbsii* could represent a derived form that colonized North America during the Early Pliocene, while one or two colonization events towards Eastern Europe could have occurred. A colonization event could have involved the ancestor of *Quyania europaea* during the Early Pliocene. Another colonization wave from Asia, that involved the Urotrichini, during the Miocene–Pliocene boundary, is testified by the presence of *Urotrichus* sp. (Maramena locality; see Doukas et al. 1995). In this scenario it is possible to hypothesize *Rzebikia* gen. nov. being derived from the European *Q. europaea*. This represents the most parsimonious explanation, although we note that *Rzebikia* gen. nov. is more similar to *Quyania chowi* (Storch and Qiu 1983; Popov 2004). If we consider *Rzebikia* gen. nov. directly derived from *Q. chowi* we should hypothesize a subsequent colonization event during the late Early Pliocene. *Q. europaea* is clearly distinct from *Rzebikia* gen. nov. by its slender humerus and relative smaller size (Rzebik-Kowalska 2014), suggesting a different digging capability and ecological adaptation. *Rzebikia skoczeni* and *Rzebikia polonica* are both larger than *Q. europaea* (Skoczeń 1993; Rzebik-Kowalska 2014). *R. skoczeni* has been found in the MN15 locality of Węże 2 only (see SOM 3), where no

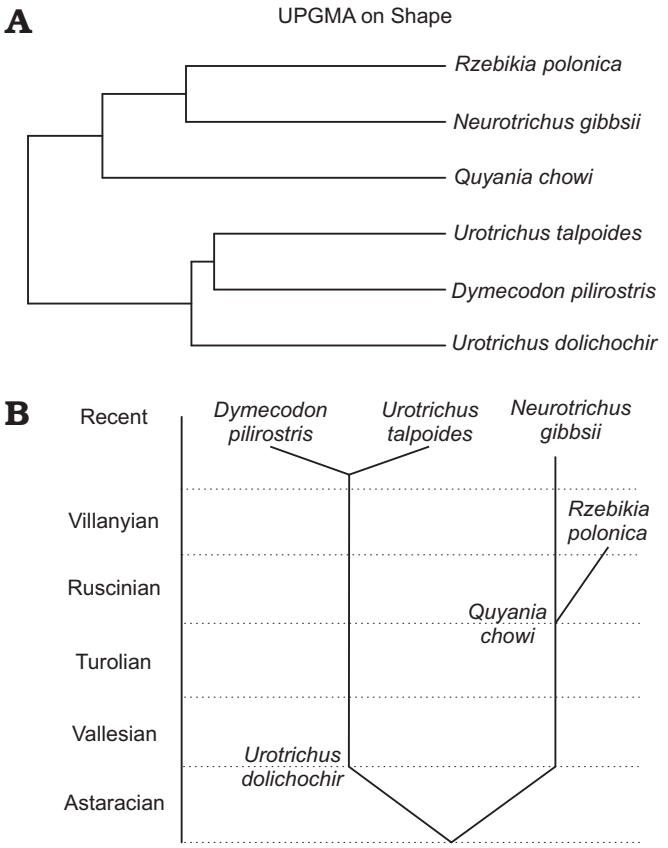


Fig. 5. **A**. UPGMA calculated on the Euclidean distance matrix computed on the shape variables. **B**. Phylogenetic hypothesis of Storch and Qiu (1983).

other neurotrichine moles are present. *R. polonica* first appearence is in the MN16 Rębielice Królewskie 1A locality (see SOM 3). This species could be descended from *R. skoczeni* anagenetically by an increase in size. However, due to the scarcity of the *R. skoczeni* fossil record it is not possible to test this hypothesis. *R. polonica* have been found in sympatry with *Q. europaea* (MN16, Rębielice Królewskie 1A and MN17, Kadzielnia localities). Size differences have been documented for sympatric species belonging to genera *Talpa* and *Mogera* (Abe 1996; Loy et al. 1996; Loy and Capanna 1998; Cleef-Roders and Hoek Ostende 2001; Yokohata 2005; Bego et al. 2008; Loy 2008), this phenomenon has been documented also in the extinct genus *Geotrypus* (Hoek Ostende 2001). Moreover, we found a significant size difference between *Urotrichus talpoides* and *Dymecodon pilirostris* which has been reported to live in sympatry in Honshu and Shikoku regions (Abe 1967). Following this evidence, the size displacement between the species of *Rzebikia* and *Quyania europaea* could have occurred in response to eco-evolutionary constraints, such as inter-specific competition and the ability to exploit low productive habitats. Size character displacement between pairs of ecologically close and geographically overlapping species is a common pattern in mammals (Simberloff and Boecklen 1981; Dayan and Simberloff 1998) and could represent a rapid response to strong inter-specific competition in talpids (Loy and Capanna 1998; Loy et al. 2001).

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Finally, recent contributions highlighted that humeral morphology possesses a taxonomic value at the genus level and in some cases at the species level as well (Hoek Ostende 1997; Ziegler 2003; Klietmann et al. 2014). In the present paper the highly significant values reported by pairwise permutational MANOVA confirm the chance to consider the humerus as a diagnostic element. Moreover, our results suggest that the landmark based shape analysis is useful in supporting systematics in palaeontological investigations where only skeletal elements are avilable.

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