Condylura (Mammalia, Talpidae) reloaded: New insights about the fossil representatives of the genus

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ABSTRACT

The star nosed mole, *Condylura cristata,* due to its morphological and behavioural peculiarities, has been deeply investigated by different authors. By contrast, very little is known about the phylogenetic relationships, evolution and diversity of the fossil members of this genus. In the present study we provide new insights about the fossil specimens ascribed to *Condylura* taking into account systematic, palaeobiogeographical and palaeoecological aspects. Further, we provide a re-description of a fossil *Condylura* from the middle Miocene of Kazakhstan. We confirm that the Kazakh fossil belongs to the genus *Condylura*, based on humeral morphological features, and we discuss its implications and impact on the phylogenetic scenario and ecology of this peculiar talpid genus. This specimen represents the earliest record of the genus, thus suggesting an Eurasiatic origin instead of the most commonly accepted scenario of a North American one. The presence of both plesiomorphic and apomorphic characters in *Condylura* strongly supports the hypothesis that this genus could be considered as sister clade of Talpinae.

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INTRODUCTION

The extant star nosed mole, *Condylura cristata* Illiger, 1811, shows a series of unique features among mammals. It is an accomplished diver and frequents tunnel systems excavated along the edges of streambeds and lakes relying on aquatic insects and annelids for a substantial proportion of its diet (Hamilton, 1931; Rust, 1966; McIntyre et al., 2002). *Condylura cristata* is the sole extant representative of the genus and of the tribe Condylurini (Hutterer, 2005). This species possesses 22 fleshy and mobile appendages that surround the nose (Figure 1). These appendages are unique not only in their star-like appearance but also in their function. The star functions much like a tactile eye (Eimer, 1871), with a small but high-resolution pair of central appendages and a number of larger, low-resolution peripheral appendages (Catania, 1995; Catania and Kaas, 1996; Catania et al., 1999). *Condylura cristata* is an endemic North-American species, it occurs throughout much of North-Eastern United States and Eastern Canada (Petersen and Yates, 1980). In the northern part of its recent distribution it is found from extreme Eastern Manitoba and Minnesota to as far northeast as Labrador and Nova Scotia. The species ranges south-eastward through Wisconsin, Ohio and northern Indiana. Along the Atlantic coast as far as south-eastern Georgia and in the Appalachian mountains, to eastern Tennessee and western North Carolina (Petersen and Yates 1980). Despite the presence of an abundant literature about life history of the extant *C. cristata* (Hamilton, 1931; Hickman, 1984; Gould et al., 1993; Catania et al., 1999; Campbell et al., 2000; McIntyre et al., 2002; Catania, 2012a; Signore et al., 2012; Marzban et al., 2014; among others), the past diversity of this genus is poorly known. *Condylura* fossils were found at the New Paris sinkholes near Bedford, Pennsylvania. These remains trace back to the late Pleistocene (~11 ky; Guilday et al., 1964). Other *Condylura* fossils were recovered from Virginia, West Virginia, Maryland, Tennessee, and Missouri localities and trace back to the middle Pleistocene (~700 ky; Parmalee et al., 1969; Guilday, 1979; Gunnell et al., 2008). All these specimens were referred to the extant species *C. cristata* (Gunnell et al., 2008). Skoczeń (1976) described two additional species belonging to the genus: *Condylura kowalskii* Skoczeń, 1976 and *Condylura izabellae* Skoczeń, 1976 from the Polish Pliocene localities of Węże 1 and Rębielice Królewskie 1A and 2. Skoczeń (1976) reported these species as the first records of condylurine moles in the Old World, hypothesizing that the North-American *Condylura* are descendants of European immigrants. Hutchinson (1984) reported the presence of cf. *Condylura* sp. from the locality of Malheur River, Oregon (USA). Two formations, Mascall and Rattlesnake,
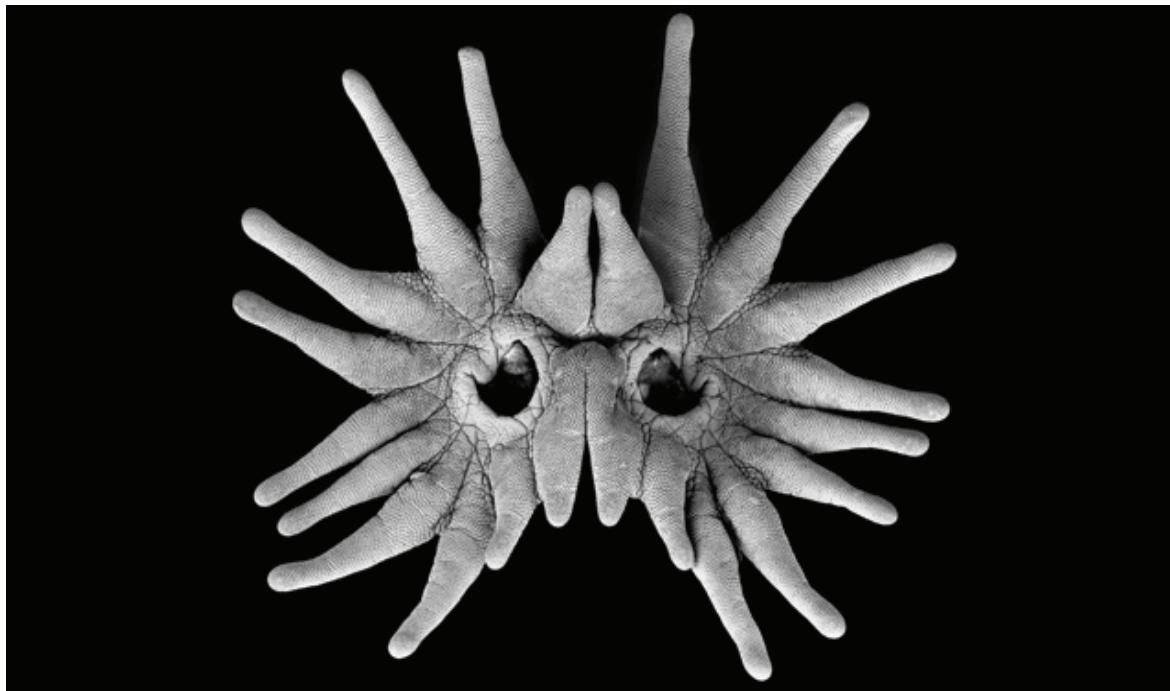
FIGURE 1. A detail of the star-like appendages from a preserved specimen. Image modified from Catania (2012b).

are exposed in that area. Mascall formation is dated to middle Miocene (14-15 m.y.a., Barstovian), while Rattlesnake formation is dated to the late Miocene (Hemphillian, ~7.5 m.y.a). Hutchinson (1984), basing on the lesser degree of mineralization of the bone, on its lighter coloration and on the museum label, suggested this specimen to be from the Rattlesnake formation. Further, Gunnell et al. (2008) accepted the original stratigraphical attribution by Hutchinson (1984).

He described a humerus that resembles in all of its features to that of the extant *C. cristata*. Hutchinson (1984) considered it as the earliest record for the genus and indicates a broader distribution for this taxon in the past. However, Lychev (1963) ascribed a humeral fragment from Kalkaman Lake, Pavlodar Priirtysch locality (Kazakhstan) to *Condylura* sp. Lychev (1963) attributed the Kalkaman Lake fauna to the late Miocene or early Pliocene, but different authors reported an older stratigraphic placement (middle Miocene; Tleuberdina, 1989; Tleuberdina et al., 1993; Tleuberdina and Forsten, 2001; Mirzaie Ataabadi et al., 2013). In particular, Tleuberdina and Forsten (2001) dated the fauna from Kalkaman Lake to the early Sarmatian or Late Astaracian mammal age equivalent (MN8; 11.9-11.1 m.y.a.). Hence, the specimen described by Lychev (1963) should be considered as the earliest record of *Condylura*. However, this record has been apparently unnoticed since the vast majority of the authors that discussed the problem of *Condylura* origin did not consider this finding (Skoczeń, 1976, 1993; Hutchinson, 1984; Sánchez-Villagra et al., 2006; Rzebik-Kowalska, 2014), while this record has been cited in fossil mammalian lists (McKenna and Bell, 1997; Gunnell et al., 2008).

The biogeography of *Condylura* is still debated. *Achlyoscapter longirostris* Hutchinson, 1968 (middle Miocene of Oregon and late Miocene of Nebraska, Bown, 1980) is the sole extinct genus tentatively ascribed to the tribe Condylurini. Hutchinson (1968, 1984) suggested this genus as the possible ancestor of *Condylura* basing on its brachyodont, non specialized and complete dental series. However, Hutchinson (1984) pointed out that the specialization present in the incisors and premolars of *Condylura* is not visible in *Achlyoscapter* remains. Rzebik-Kowalska (2014) highlighted that it is still uncertain whether *Condylura* originated in North America and then spread to Europe or vice versa. Possibly, it colonized North America from Europe via Asia.

The phylogenetic position of the genus represents another enigma; *Condylura* has been considered as a basal clade in Talpidae phylogeny, being placed as sister clade of uropsilines, desmans and shrew-moles (Hutchinson, 1976; Yates and Moore, 1990; Whidden, 2000; Shinohara et al., 2003; Motokawa, 2004; Cabria et al., 2006; Piras et al., 2012; Crumpton and Thompson, 2013). However, in the last decade, different authors, basing on morphological cladistic approaches, revealed closer affinities between *Condylura* and the highly fossorial moles (Sánchez-Villagra et al., 2006; Schwermann and Thompson, 2015). Here, we re-examine, from literature, the fossil material described by Lychev (1963), and we provide new evidences helping to unravel the debated phylogenetic relationships of *Condylura*. We also contribute to better understand the origin of the fossorial lifestyle. Finally, we provide new insights about the paleobiogeography and paleoecology of the genus.

MATERIAL AND METHODS

Material

Unfortunately, we did not have the ability to directly access the fossil material and to report the accession number and the exact location of the fossil material described by Lychev (1963). The material reported by Lychev (1963) has not been inventoried, and there is no possibility to contact the personnel that curated the material in past years (Tleuberdina, personal commun., 2015). Further, the *Condylura* sp. material was not housed in the Institute of Zoology, Laboratory of Paleozoology, National Academy of Sciences, Almaty, Kazakhstan, since it was not included in successive studies performed on vertebrate fossil material from Kalkaman locality (Tleuberdina, 1988, 1989; Tleuberdina et al., 1993; Tleuberdina and Forsten, 2001). See Figure 2 for the anatomical terminology. See Appendix for the complete list of the specimens used for comparisons.

Institutional Abbreviations

ISEZ-PAN: Institute of Systematics and Evolution of Animals, Krakow, Poland; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NHMA: Natural History Museum Augsburg, Augsburg, Germany; NHMW: Natural History Museum Wien, Wien, Austria; UO: University of Oregon, Oregon, USA; YPM: Yale Peabody Museum, New Haven, Connecticut, USA.
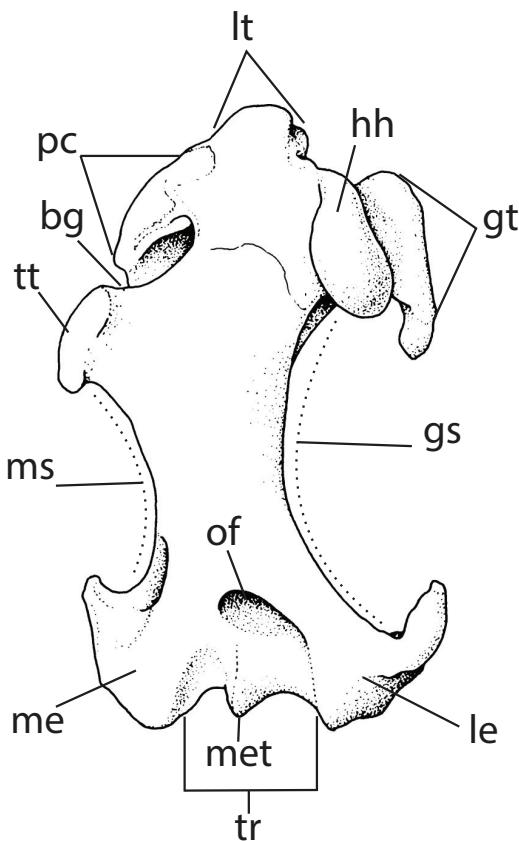
FIGURE 2. Drawing of a left humerus of *Condylura cristata* showing the anatomical terms used in this study (modified from Hutchinson, 1984). Abbreviations: bg, bicipital groove; gt, greater tuberosity; gs, greater sulcus; hh, humeral head; le, lateral epicondyle; lt, lesser tuberosity; me, medial epicondyle; met, medial edge of the trochlea; ms, minor sulcus; of, olecranon fossa; pc, pectoral crest; tr, trochlea; tt, teres tubercle.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order EULIPOTYPHLA Waddel, Okada,
Hasegawa, 1999
Family TALPIDAE Fischer von Waldheim, 1814
Subfamily TALPINAE Fischer von Waldheim, 1814
Tribe CONDYLURINI Gill, 1875
Genus CONDYLURA Illiger, 1811
Condylura sp.

1963   *Condylura* sp.; Lychev, p. 13, figs 1A, 1a.
1997   *Condylura* sp.; McKenna and Bell, p.282.
2008   *Condylura* sp.; Gunnel, Bown, Hutchinson, and Bloch, p. 103.

Material

Sample. 1 left humeral fragment
Locality. Kalkaman Lake, Kazakhstan

Age. mammal age equivalent MN8; 11.9-11.1 m.y.a.
Horizon. Early Sarmatian or Late Astaracian mammal age equivalent (MN8; 11.9-11.1 m.y.a.).

Description

Humeral fragment (Figure 3.1-2). Maximal width of distal region: 8.5 mm; width of the humeral shaft: 3.6 mm. The proximal part is lost and the humeral head is not preserved. The capitulum is also broken. The fossa for flexor digitorum profundus is round and deep. The supracondylar foramen is wide and triangular in shape. The humerus shows a torsion of the shaft as occurs in fossorial moles. The distal part of the pectoral crest is slightly pronounced. Enlarged distal region of the humerus with the medial edge of the trochlea placed in the middle of the trochlear area. The greater sulcus is wide.

New Diagnostic Feature

Position of the medial edge of the trochlea and humeral shaft width. The medial edge of the trochlea is positioned in the middle of the trochlea in the shrew-moles (Urotrichini, Neurotrichini and *Scaptonyx*) while all highly fossorial moles (Talpini and Scalopini) have it medially displaced. Nevertheless, the humeral shaft of the highly fossorial talpids is more robust than that of the shrew-moles.

This genus-diagnostic character was detected among humeral material from both shrew-moles and true-moles (Hutchinson, 1968; Hutchinson, 1974; Ziegler, 2003; Sánchez-Villagra et al., 2004; Piras et al., 2012; Piras et al., 2015; Schwerman and Thompson, 2015; Sansalone et al., 2016).

Comparisons

We excluded from the comparisons all the robust highly fossorial moles (i.e., Talpini and the more robust Scalopini) due to the evident difference in the overall robustness of the humeral shaft. Furthermore, the Kazakh specimen is more robust than all the shrew-moles (Urotrichini and Neurotrichini); therefore we did not include these taxa in the comparisons. We compared the mole from Kalkaman Lake with all the Neogene less robust Scalopini and with the other described *Condylura* species.

cf. *Condylura* sp. The specimen from Kalkaman Lake differs from the cf. *Condylura* sp. from Hemphillian of Oregon (Hutchinson, 1984) in having a reduced minor sulcus. The two specimens are identical in the humeral distal region morphology. They share the triangular supracondylar fora-
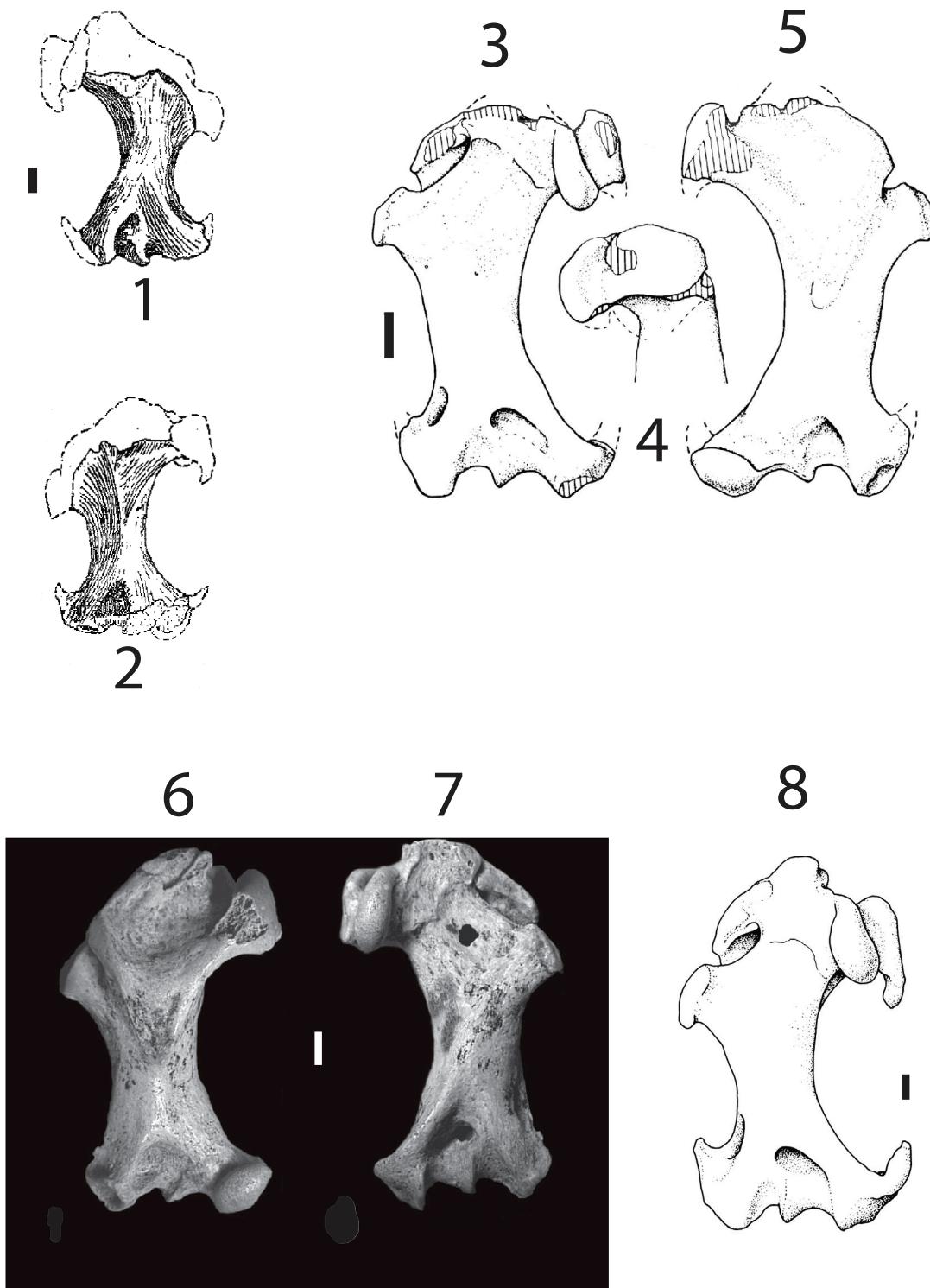
FIGURE 3. Drawings (**1-5, 8**) and photographs (**6 and 7**) showing fossil and extant representatives of genus *Condylura*. **1 and 2,** *Condylura* sp., left humerus in caudal (**1**) and frontal (**2**) views, modified from Lychev (1963). **3-5,** cf. *Condylura* sp., right humerus (YPM 20699, YPM) in caudal (**3**) and lateral (**4**) views and close-up of the greater tuberosity in medial view (**5**), modified from Hutchinson (1984, figure 1B). **6 and 7,** *Condylura kowalskii*, left humerus (MF/1006/16, ISEZ-PAN) in frontal (**6**) and caudal (**7**) views, modified from Rzebik-Kowalska (2014, figure 2.1, 2.2). **8,** *Condylura cristata*, right humerus in caudal view, modified from Hutchinson (1984, figure 1A). Scale bars represent 1 mm.
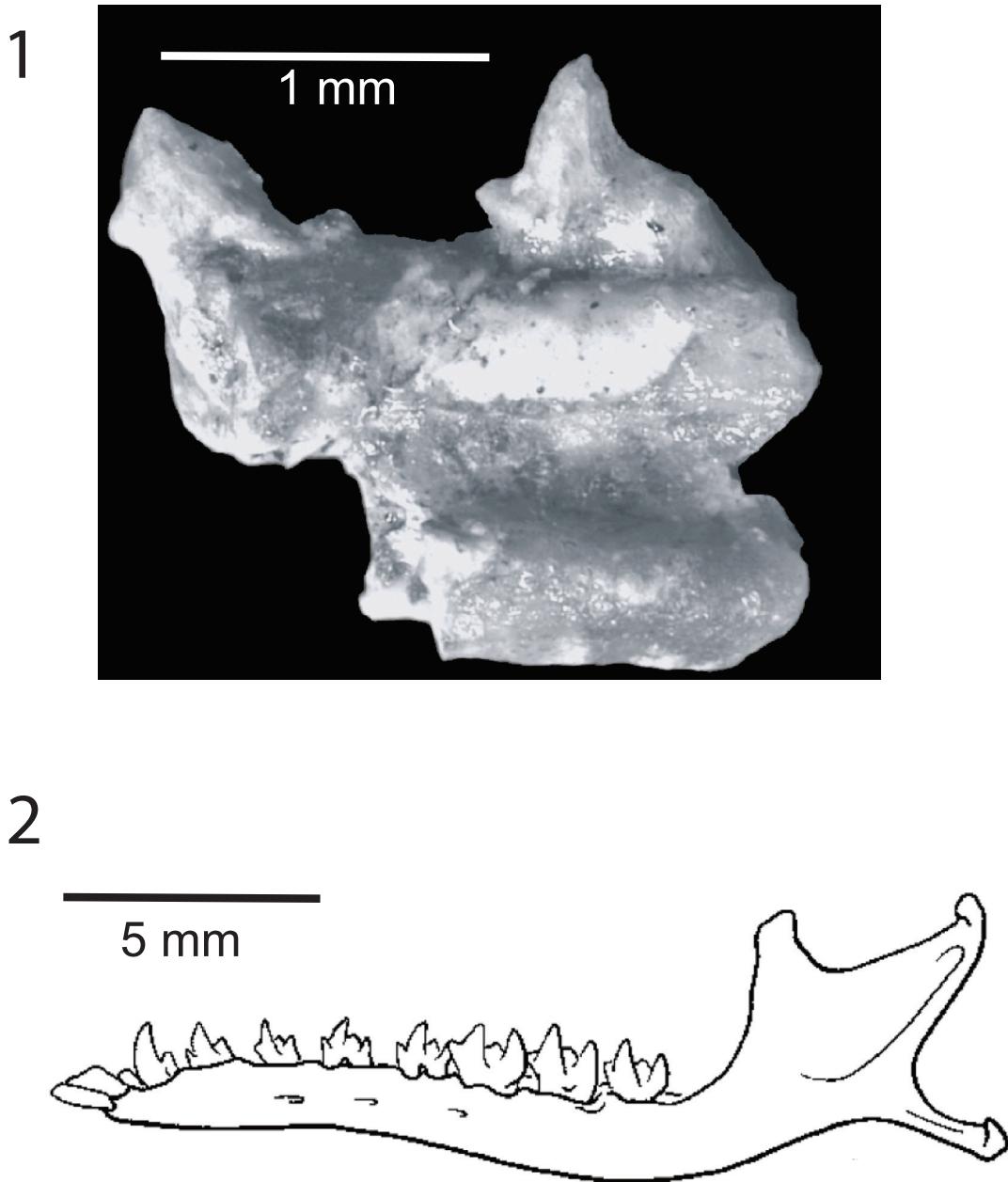
FIGURE 4. 1, *Condylura kowalskii*, mandible fragment bearing p1 and p2 in lingual view (MF/1006/4, ISEZ-PAN); from Rzebik-Kowalska (2014, figure 1.3). **2,** Line drawing of a left mandible of *Condylura cristata* in labial view, modified from Laerm et al. (2007).

men and the central position of the trochlear medial edge (Figure 3.3-5).

***Condylura kowalskii* Skoczeń, 1976.** The Kazakh specimen is very similar to the Polish species in the overall shape of the humeral shaft (Figures 3.6-7, 4.1). It is almost identical in the trochlear morphology sharing the central position of trochlear medial edge. However, *C. kowalskii* possesses a minor sulcus wider than the Kazakh condylurine mole (Skoczeń, 1976; Rzebik-Kowalska, 2014).

***Condylura izabellae* Skoczeń, 1976.** The Kazakh specimen differs from the Polish smaller *Condylura* (Skoczeń, 1976; Rzebik-Kowalska, 2014) for the same features of *C. kowalskii*.
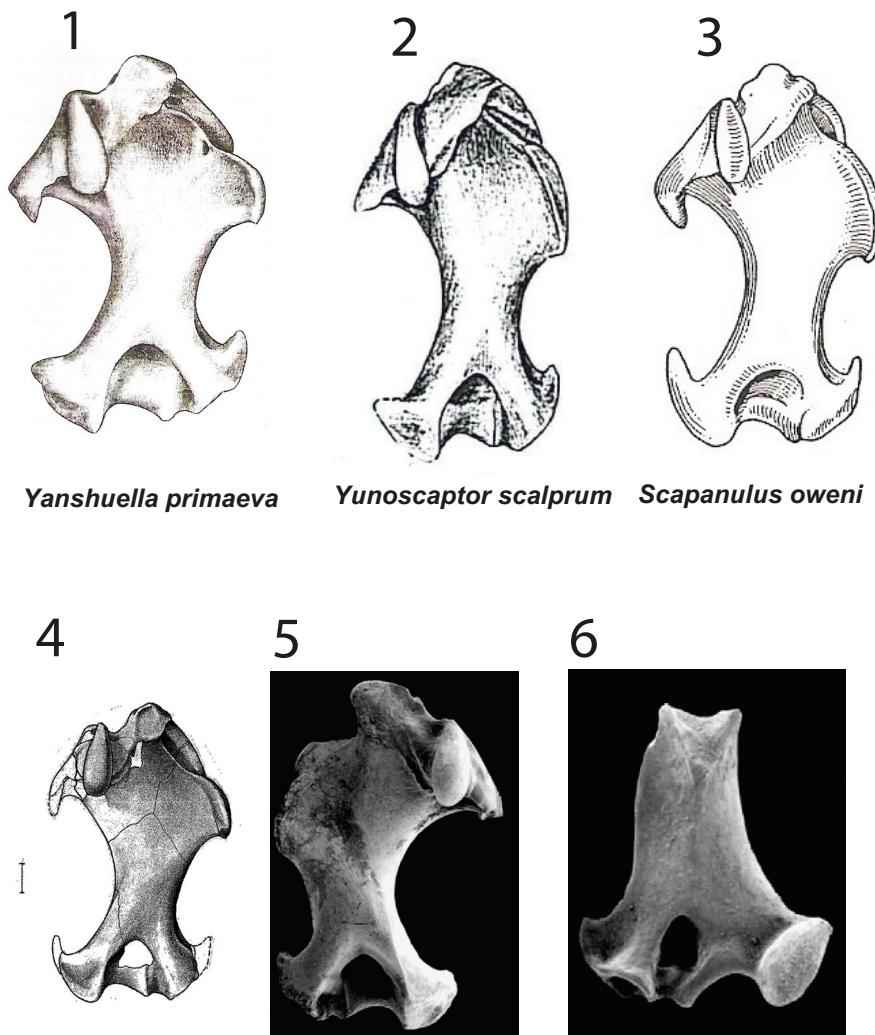
FIGURE 5. Drawings (**1-4**) and photographs (**5-6**) of talpid species humeri in caudal view. **1,** *Yanshuella primaeva*, left humerus (IVPP-6455, IVPP), from Storch and Qiu (1983, figure 39b). **2,** *Yunoscaptor scalprum*, left humerus (IVPP-V-9741.38, IVPP), from Storch and Qiu (1991, figure 48b). **3,** *Scapanulus oweni*, left humerus, from Hutchinson (1968). **4,** *Wilsonius ripafodiator*, left humerus (UO-22366, UO), from Hutchinson (1968, figure 55). **5,** *Leptoscaptor robustior,* right humerus (P35-58.6, NHMA), from Ziegler (2003, figure 3B2). **6,** *Leptoscaptor bavaricum*, left humerus (P10-610.2, NHMA), from Ziegler (2003, figure 2I).

***Condylura cristata* Illiger, 1811.** The specimen from Kalkaman closely resembles *C. cristata* in the width of both sulci (Hutchinson, 1984). The distal part of the pectoral crest is slightly pronounced, as in *C. cristata*. The similarities in the trochlea are even more striking, both taxa share the medial edge positioned in the middle of the trochlea. However, the Kazakh specimen possesses the spine of the medial edge of the trochlea medially bended while it is straight in *C. cristata* (Figures 3.8, 4.2).

***Yanshuella primaeava* Storch and Qiu, 1983.** *Condylura* sp. possesses a wider greater sulcus and a wider minor sulcus. Further, the distal end of the pectoral crest is less pronounced. Finally, in *Yanshuella*, the medial edge of the trochlea is medially displaced (as in all other highly fossorial talpids; Storch and Qiu. 1983), while in *Condylura* sp. is placed in the middle of the trochlea (Figure 5.1).

***Yunoscaptor scalprum* Storch and Qiu, 1991.** The same considerations made for the comparison with *Yanshuella* hold for *Yunoscaptor* (Storch and Qiu, 1991). They differ for the trochlea medial edge and, further, for the shape of the supratrochlear fossa (frontal view) (Figure 5.2).

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***Scapanulus oweni* Thomas, 1912**. The differences in the width of both minor and greater sulci are less evident, though *S. oweni* possesses the medially displaced medial edge of the trochlea (Figure 5.3). The last evidence leaves no doubt in excluding close relationships with *Scapanulus* (Hutchinson, 1968; Storch and Qiu, 1983).

***Wilsonius ripafodiator* Hutchinson, 1968.** The two taxa are almost indistinguishable for the width of both sulci, evidencing the plesiomorphic state of these characters (Hutchinson, 1968). However, the shape of the trochlea is, again, highly different. The Kazakh specimen clearly shows the plesiomorphic features of the humeral distal region, while *Mioscalops*, possessing the medially displaced medial edge of the trochlea, shows apomorphic characters that reflect a better adaptation to digging (Hutchinson, 1968) (Figure 5.4).

***Leptoscaptor robustior* Ziegler, 2003.** *Condylura* sp. clearly differs from *L. robustior* in the width of the humeral shaft. In *L. robustior* the minor and greater sulci are narrower, and the medial edge of trochlea is medially displaced as in other highly fossorial moles (Ziegler, 2003) (Figure 5.5).

***Leptoscaptor bavaricum* Ziegler, 2003.** *Condylura* sp. resembles *L. bavaricum* in the overall slenderness of the humeral shaft and in the width of minor and greater sulci. On the other hand, *L. bavaricum* shows an elliptic supracondylar foramen and the medial edge of the trochlea medially displaced (Ziegler, 2003) (Figure 5.6). These features clearly separate the two taxa.

Remarks

The humeral fragment from Kalkaman Lake shows close affinities with the other condylurine moles. In particular, the morphology of the trochlear area appears to be distinctive for the genus *Condylura*. This feature unambiguously separates *Condylura* from all highly fossorial moles. However, Urotrichini, Neurotrichini and *Scaptonyx* also show a trochlear medial edge placed in the middle of the trochlea (Hutchinson, 1968; Sánchez-Villagra et al., 2004; Schwerman and Thompson, 2015; Sansalone et al., in press). Despite this evidence, the more robust and wide humeral shaft leaves no doubt about the attribution of the Kazakh specimen to the genus *Condylura*. Unfortunately, the poor conditions of the proximal region of the humerus do not allow any specific attribution.

DISCUSSION

Phylogenetic Scenario

We suggest excluding *Achlyoscapter* as a stem lineage of Condylurini. *Achlyoscapter* is known from the middle Miocene of Oregon and late Miocene of Nebraska (Bown, 1980), but only mandibles and teeth have been ascribed to this genus (Hutchinson, 1968; 1984). The unspecialized brachyodont teeth and the absence of humeri do not allow inferring the lifestyle of this genus. Further, the dentition of *Achlyoscapter* does not bear any of the specializations present in *C. cristata*. *Achlyoscapter* lacks molariform lower premolars separated by diastemata. In *Achlyoscapter* the crista obliqua joins the posterior wall of the trigonid while in *Condylura* it joins directly the metastylid. Further, *C. cristata* shows greatly reduced incisors modified into a tweezer-like form used to rapidly and precisely grasp small food items (Catania and Remple, 2005). Catania and Remple (2005) suggested that the unusual dentition of *C. cristata* provide evidences for a long history of selective pressures for feeding on small preys, and that the possible ancestor of *Condylura* should have characteristics of exaptation for a feeding apparatus capable of increasing the prey detecting and catching speed. Unfortunately none of these features are recognized in *A. longirostris*. Therefore, we suggest to consider *Achlyoscapter* as Talpidae *incertae sedis* and as a lineage evolved independently of the Condylurini (Hutchinson, 1968; Klietmann et al., 2014).

The *Condylura* humerus shows a unique combination of derived and plesiomorphic features. It possesses an enlarged proximal region, where the main digging muscles insert (Gambaryan et al., 2003; Piras et al., 2012; Piras et al., 2015). However, the greater tuberosity and the trochlea resemble that of shrew-moles in their overall shape. Among the fossorial moles *Condylura* is the sole taxon presenting the trochlear medial edge placed in the middle of the trochlea. This feature is also shared by Urotrichini and, more evidently, by Neurotrichini and *Scaptonyx*. Modifications of this trait probably influence the articulation of the humerus with the ulna and, hence, the relative position of the forearm (Dobson, 1883; Edwards, 1937; Hutchinson, 1968; Gambaryan et al., 2003). On the other hand, highly fossorial moles (Talpini and Scalopini) all possess the trochlear medial edge medially displaced. *Condylura cristata* shows a large bicipital notch between the teres tubercle and the lesser tuberosity, where the pectoral ridge
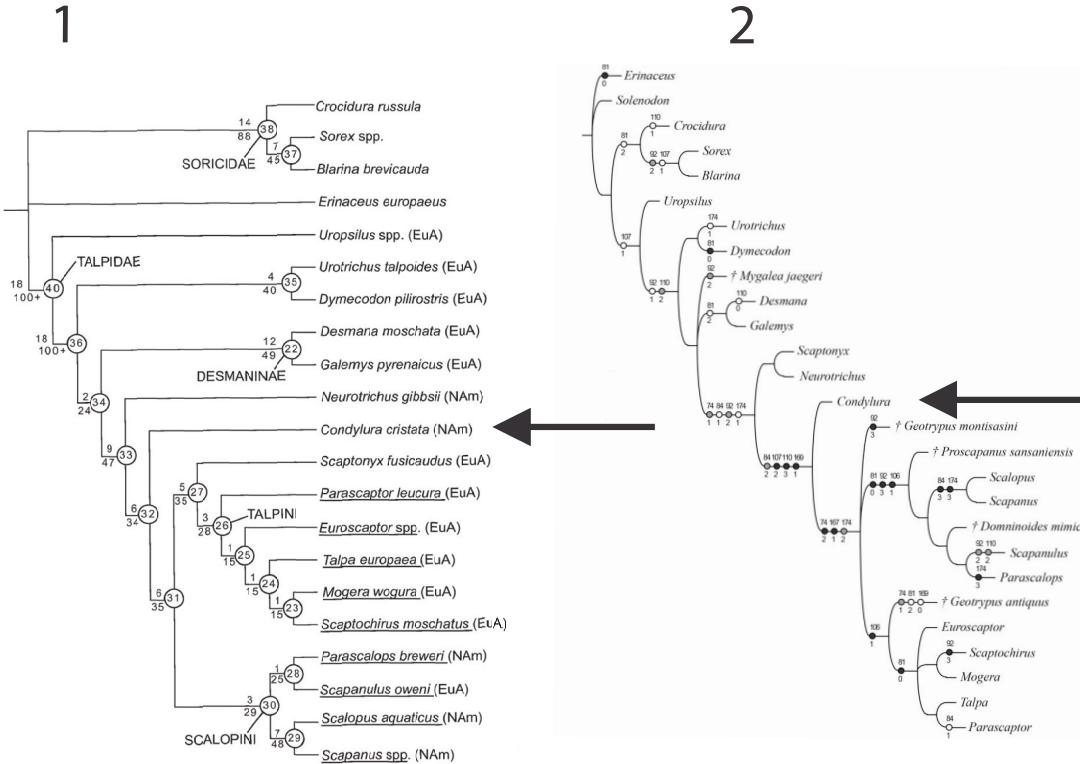
FIGURE 6. 1, Talpidae phylogeny resulting from a parsimony analysis based on 157 discrete morphological characters, modified from Sánchez-Villagra et al. (2006, figure 1). **2**, Unconstrained Talpidae phylogeny based on a parsimony analysis (DELTRAN optimization) based on 176 discrete morphological characters, modified from Schwermann and Thompson (2015, figure 16A).

arises. This character is also well evident in *Geotrypus antiquus* de Blainville, 1840. Schwermann and Martin (2012) evidenced several plesiomorphic features present in *G. antiquus* such as elongate clavicle, distinct metacromion process on the scapula, lack of the terminal process of the ulna and very weak capitular process of the radius. Based on these traits Schwermann and Thompson (2015) interpreted *G. antiquus* as the least fossorial species among Talpini and suggested that a number of plesiomorphic, shrew-mole-like characters might have been present in the last common ancestor of the highly fossorial moles. In this framework, we provided a stronger support to the hypothesis that *Condylura* and highly fossorial moles share a shrew-mole-like ancestor. We agree with the phylogenetic hypothesis proposed by Sánchez-Villagra et al. (2006) and Schwermann and Thompson (2015). These authors proposed *Condylura* as sister clade of Talpinae basing on discrete morphological characters (Figure 6).

Lifestyle

Some authors suggested that moles adopted the fossorial lifestyle following an aquatic adaptation (Campbell, 1939; Whidden, 1999; Schwerman and Thompson, 2015), while other researchers rejected this view, concluding instead that fossorial and semi-fossorial forms evolved from a cursorial ancestor and that the adaptation to aquatic environment is actually an exaptation (Hickman, 1984; Sánchez-Villagra et al., 2006; Piras et al., 2012; Hooker, 2015). We hypothesize that the shrew-mole-like ancestor of *Condylura* and true moles probably were showing a lifestyle and feeding habit similar to that of extant Urotrichini. Sansalone (2015) reported the Japanese shrew-moles showing two different feeding strategies: 'back-with-grip' and 'bite-and-retreat', depending on whether the prey is either underground or on the ground, respectively. The 'back-with-grip' feeding is faster and probably safer (startled shrew-moles usually abandon prey; Imaizumi, 1979), therefore underground feeding could have contributed to promote, together with the other advantages of the subterra-

nean ecotope (Nevo, 1979), the evolution of the specialized fossorial lifestyle observed in true moles. According to these evidences we prefer to consider the semi-aquatic lifestyle of *Condylura* as an autapomorphy and as a case of exaptation (Sánchez-Villagra et al., 2006; Piras et al., 2012; Hooker, 2015).

Palaeoecology

Condylura cristata shows a unique mixed lifestyle. This species is adapted to burrowing but also has a good performance as a diver (McIntyre et al., 2002). The 22 fleshy appendages surrounding the nostrils can be compared to a visual organ as the tendrils intensively touch substrate or food items (Catania et al., 1999; see Figure 1). The star-like appendages also allow *Condylura* to "smell underwater": although the star-like structure is not a chemoreceptor itself, it helps the star-nosed mole to blow small air bubbles onto objects or scent trails. These bubbles are then drawn back into the nostrils so that odorant molecules in the air bubbles are wafted over the olfactory receptors (Catania, 2006). According to Skoczeń (1976), we hypothesize that the lifestyle of the extinct *C. kowalskii* and *C. izabellae* was very similar to that of the extant North American species. The mandible of *C. cristata* is more elongated and slender than that of other talpids (Barrow and MacLeod, 2008). It appears that development of a unique nasomaxillary articulation and nasolabial musculature associated with the starry-nose relates to the evolution of the star-like tendrils. This has shifted the plane of the anterior teeth, creating the unique diastemas between the premolars and lengthened the horizontal ramus (Barrow and MacLeod, 2008; see Figure 4.2). In this context, the presence of a mandibular fragment, bearing p1 and p2 with an evident diastema (Figure 4.1), from Węże 1 locality, strongly supports the hypothesis that both *C. kowalskii* and *C. izabellae* possessed the star-like appendages. The p1 and p2 of *C. kowalskii* are almost identical in shape to those of *C. cristata*, probably reflecting a similar adaptation to a fast feeding.

This should be considered as the first, albeit indirect, evidence of the presence of this highly specialized organ in the fossil record. Unfortunately, the lack of dental remains attributed to the cf. *Condylura* sp. from Oregon and to *Condylura* sp. from Kazakhstan does not allow inferring the presence of the star-like appendages. However, basing on the palaeobiogeographical hypothesis exposed in the following paragraph, we suggest

the possibility that this organ was already developed in the ancestors of Condylurini.

Skoczeń (1976) hypothesized that the Polish fossil *Condylura* spp. lived in an environment with conditions similar to that of the extant species. In particular, species associated to aquatic environments (amphibians, water turtles and mammals) are well represented in Węże 1 and Rębielice Królewskie 1A and 2 localities (Rzebik-Kowalska, 1971). Among these semi-aquatic forms, the presence of *Desmana* and *Galemys* is of particular interest. Skoczeń (1976) hypothesized that the Polish species were outcompeted by desmans (Desmaninae), which were larger, had stronger dentition and already lived in Europe at that time, and likely occupied the same ecological niche (Rzebik-Kowalska, 2014). In this framework, we hypothesize that the cf. *Condylura* sp. from Oregon experienced a similar fate. In the Hemphillian of Oregon the presence of *Gaillardia thomsoni* Matthew, 1932, a talpid species well adapted to aquatic environment (Hutchinson, 1968), is reported. The cf. *Condylura* sp. might have been outcompeted by *G. thomsoni* due to its larger size and stronger dentition. By contrast, *C. cristata*, colonizing the East Coast, probably did not experience the competitive pressure exerted by other semi-aquatic lipotyphlans and was able to survive until today.

The presence of two Polish *Condylura* species, highly different in size (*C. kowalskii*: larger; *C. izabellae*: smaller), suggests that a speciation process could have occurred in response to eco-evolutionary constraints, such as inter-specific competition and the ability to exploit low productive habitats. Size differences between sympatric sister species is a very common pattern in Talpidae and has been extensively documented for several highly fossorial and shrew-mole taxa (Loy et al., 1996; Loy and Capanna, 1998; van Cleef-Roders and van den Hoek Ostende, 2001; van den Hoek Ostende, 2001; Yokohata, 2005; Bego et al., 2008; Klietmann et al., 2014; Sansalone, 2015; Sansalone et al., 2016).

Palaeobiogeography

The presence of a *Condylura* in the middle Miocene of Asia opens new scenarios about the origin of this genus. The specimen from Kalkaman Lake represents the earliest record for the genus, thus supporting the hypothesis of a Eurasian origin for *Condylura* (Skoczeń, 1976). Further, the fossil from Kazakhstan would bridge the geographical gap between the Polish Pliocene *Condylura* spp.

FIGURE 7. Map showing *Condylura* fossil bearing localities and a possible palaeobiogeographical scenario. The orange striped area represents the present distribution of the extant *C. cristata*. The orange star represents *Condylura* sp. (middle Miocene locality of Kalkaman Lake, Kazakhstan). The red square represents cf. *Condylura* sp. (late Miocene locality of Malheur River, Oregon, USA). The green triangles represent *C. kowalskii* and *C. izabellae* (Pliocene Polish localities). The blue circles represent the late Pleistocene-Holocene localities of *C. cristata*.

and the North American ones (Figure 7). Sansalone et al. (2016), reviewing the neurotrichine fauna from the same Polish localities, revealed the link between the European and Asiatic shrew-moles. They showed as Neurotrichini originated in Asia and then followed two colonization routes: one toward Eastern Europe and the other leading to North America. In this framework, we hypothesize that *Condylura* spread following a similar pattern. *Condylura* members could have colonized North America during the early middle Hemphillian. In fact, during the Hemphillian different dispersal waves occurred between Asia and North America. Mammals migrating from Eurasia to North America included Mustelids (*Eomellivora* and *Plesiogulo*), Felids (*Machairodus*), Procyonids (*Simocyon*), Arvicolids (several genera) and Bovids (*Neotragoceros*) (Webb, 1985, 1998; Baskin, 1998a, 1998b; Martin, 2008). In particular, during the early middle Hemphillian, the migration of forms linked to the aquatic environment such as *Castor* is reported (Flynn and Jacobs, 2008). In North America, *Condylura* members could have followed two colonization routes: one toward the West Coast and the other toward the East Coast (Figure 7). This view is supported by the presence of cf. *Condylura* sp. in the late Miocene of Oregon and by the presence of *Condylura* fossil remains in several Pleistocene localities within or just south of the present range of *C. cristata* (Petersen and Yates, 1980; Hutchinson, 1984; Gunnell et al., 2008).

On the European side, *Condylura* members could have spread from Asia through Eastern Europe during the early Pliocene. At that time several talpid genera colonized Poland from Asia (*Rzebikia*, *Quyania*, *Parascalops*; Rzebik-Kowalska, 2014; Sansalone et al., 2016).

However, in the very unlikely case that cf. *Condylura* sp. from Oregon could belong to the Mascall formation (middle Miocene 14-15 m.y.a., Barsovian) a different scenario would open to us. The specimen described by Hutchinson (1984) should be considered as the earliest record of the genus. In this case we could hypothesize that *Condylura* originated in the West Coast of North American and subsequently colonized Asia during the middle Miocene and, then, spread through Eastern Europe during the early Pliocene. It is well accepted that faunal inter-changes between Asia and North America are often asymmetrical. In fact, a large number of immigrants from Old World constituted a significant component of local communities in North America. On the contrary, few mammals of New World origin did the same in Asia (Wang et al., 2013). Despite the evident unbalance in the faunal exchange between the two continents, we recognize two possible colonization events during which *Condylura* members could have spread through Asia. The first one could have occurred during the middle Miocene (end of MN6 ~13 m.y.a.). At that time the migration into Asia, from North America, of the mustelids *Leptarctus* and *Sthenictis* is recorded (Qiu, 2003; Tseng et al., 2009). Another possible migration event could correspond with the arrival in the Old World of "*Hipparion*" (early late Miocene MN7-8, ~11.5 m.y.a.) that

could have crossed the Bering Land Bridge during the TB3.1 sea level lowstand (Garcés et al., 1997; Tseng et al., 2009).

CONCLUSIONS

The re-appraisal of the *Condylura* sp. in the middle Miocene of Kazakhstan gives a stronger support to the hypothesis of a Eurasiatic origin of the genus *Condylura*. Further, this fossil contributes to bridging the geographic gap between the Eastern Europe *Condylura* spp. and the North American ones. We provided a stronger support to the hypothesis that see *Condylura* as sister clade of Talpinae and that both clades originated from a semi-fossorial shrew-mole like ancestor.

ACKNOWLEDGEMENTS

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APPENDIX

List of material used for comparisons.

Condylura cristata. NHM-3.11.5, humerus and mandible. NHM-3.11.6, humerus and mandible. NHM-1.7.4, mandible. NHM-12.12.1, mandible. NHM-1.25.2, mandible. NHM-7.7.2659, mandible. NHM-7.7.132, mandible. NHM-7.7.2792, mandible. NHM-12.5.3, mandible. NHM-1.7.2, mandible. NHM-1.7.3, mandible. Natural History Museum NHM, London, UK. 62567, mandible. NHMW.

Condylura izabellae. MF/1007/01, humerus. ISEZ-PAN.

Condylura kowalskii. MF/1006/4, mandibular fragment bearing p1-p2. MF/1006/16, humerus. MF/1006/18, humerus. MF/1006/21, humerus. MF/1006/22, humerus. MF/1006/23, humerus. ISEZ-PAN.

Leptoscaptor bavaricum. P10-610.2, humerus. Ptb68_1962, humerus. Ptb68_1962b, humerus. Ptb68_1962c, humerus. NHMA.

Leptoscaptor robustior. P35-58.6, humerus. NHMA.

Scapanulus oweni. Drawings from Hutchinson, 1968; Storch and Qiu, 1983.

Mioscalops ripafodiator. UCMP-70140b, humerus. UCMP-V70140a, humerus. UCMP-V70140d, humerus. University of California Museum of Palaeontology, UCMP, Berkeley, California, USA.

Yanshuella primaeva. IVPP-6455, humerus. IVPP-6456, humerus. IVPP.

Yunoscaptor scalprum. IVPP-V-9741.38, humerus. IVPP.