




Functional morphology and identity of the thenar pad in the subterranean genus *Ctenomys* (Rodentia, Caviomorpha)

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Abstract

As in many other fossorial tetrapods, the most obvious adaptations to scratch-digging in the subterranean tuco-tuco (Rodentia, Ctenomyidae, *Ctenomys*) are found in the hands, which among other adaptations, present the mesaxonic condition; i.e. the central digits are more developed, and also their claws, which are curved and elongated. The thumb is atrophied and aligned with the rest of the digits, showing a small and flat claw. This configuration of digits and claws seems to be in accordance with what it is expected for rodents: rudimentary movements when handling food items. However, on the palmar side of the hand, tuco-tucos have several pads, the thenar (located under the thumb) being the most developed. In this study, we investigated the functional morphology of the thenar pad through different approaches: musculoskeletal anatomy, histology and functionality. The analysis of radiographs and clarified and double-stained hand samples of *Ctenomys talarum* and *C. australis* showed that the thenar pad is supported by a paddle-shaped bone that articulates with a protrusion in the scapholunate bone. This bone, flat and long, continues in a flat cartilaginous structure, with a shape similar to a claw. Dissections showed that the thenar pad has several associated muscles: the m. palmaris longus, the m. abductor pollicis longus, and a massive muscular complex located between the thumb and the thenar pad. By topology it might be inferred that this complex is formed by the m. abductor pollicis brevis, the m. flexor pollicis brevis and the m. adductor pollicis brevis. Longitudinal histological sections of the thenar pad stained with hematoxylin-eosin showed a thick layer of keratin at the distal end, external face. The observation of live specimens of *C. talarum* foraging on two food items of different size and filmed at 300 fps showed that the thenar pad acts as an opposable thumb, with digit-like movements. Tuco-tucos are able to perform more precise movements than expected, and to grasp and manipulate the food with one hand. In previous studies, it was suggested that the thenar pad was supported by a 'palmar ossicle', or 'prepollex' (= radial sesamoid bone). Our results suggest that this sesamoid underwent a radical change on its morphology, making the thenar pad a part of the food handling system in *Ctenomys*, so the thenar pad might be considered a 'false thumb', rather than a palmar pad. It is suggested to advance on the description and functional analysis of the thenar pad, redefining the structure, since the terms used so far to define it would not be accurate.

Key words: adaptations; forelimb; palmar pads; pentadactily; prepollex; radial sesamoid; scratch-digging; skilled movements.

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Introduction

Mammals have evolved several distinct modes of burrow excavation. Particularly in rodents, the predominant mode used for burrowing is scratch-digging (see Stein, 2000), method in which the foreclaws are used to break up the soil (Hopkins, 2005). As in many other fossorial tetrapods, some of the most obvious adaptations for burrowing in scratch-diggers are found in the hand (Kley & Kearney,

2007), especially in the metacarpals and the digits, which consist of different numbers of phalanx bones. Unlike the limbs of cursors, the limbs of diggers have relatively short distal segments (Hildebrand & Goslow, 2001). The radius is almost always shorter than the humerus, and the hand is markedly shorter than the radius. In general, the hand is shorter in diggers than in closely related nondiggers, due largely to a relative reduction in the lengths of the carpals, metacarpals and all but the distalmost phalanges (Hildebrand, 1985). The distal phalanges are mostly long and robust, providing strong internal support for the enlarged claws, which in some species show markedly bifid tips, forming V-shaped notches that embrace internal vertical ridges within the keratinous claws (Kley & Kearney, 2007; and references therein).

Fossorial and subterranean habits have evolved independently in five extant rodent families (i.e. Geomyidae, Ctenomyidae, Octodontidae, Bathyergidae, and Muridae, including Spalacinae and Rhizomyinae), and at least, in two extinct ones (i.e. Mylagaulidae and Tsaganomyidae). All genera have five digits on the forefoot, although a reduction of the digits I and V occurs in some taxa (Stein, 2000). This is the case of the family Ctenomyidae, which includes the South American rodents mostly specialized for subterranean life, and nowadays represented by the sole living genus *Ctenomys* (i.e. tuco-tucos). Tuco-tucos has five digits (numbered digits DI–DV, medial to lateral), and according to Lessertisseur & Jouffroy's (1978) classification of autopodia, their hand exhibits the mesaxonic condition; i.e. the third longitudinal axis (DIII) is the longest, followed by the second (DII), the fourth (DIV), and the first (DI) and the fifth (DV) are more reduced, especially the former (Ubilla & Altuna, 1990; Reig & Quintana, 1992). The DI (also named *pollex* in Latin, or thumb) is aligned with the other digits, and features a short, flat and blunt claw. The three central digits show curved long claws that are used for digging and expelling soil out of tunnels. The ventral palm is characterized by five elevated pads that cover most of the palmar surface. Three interdigital pads are located directly beneath DII–DV. Palmar pad 1 lies beneath DII and part of DIII, pad 2 lies beneath DIII and DIV, and pad 3 lies beneath DIV and DV. A large thenar pad (TP) of digital form is located adjacent to DI and extends in a proximal direction beneath this digit, and a hypothenar pad is located proximally beneath DV. In previous studies the TP was considered to be proximally supported by a 'palmar ossicle', or 'prepollex' (also called 'os falciforme', a radial sesamoid; Woods, 1972; Ubilla & Altuna, 1990; Morgan & Verzi, 2011), and distally by a cartilaginous axis (Ubilla & Altuna, 1990). In mammals, footpads (found in the fore and hind limbs) act as a shock absorbers during locomotion and protect the skeleton of the manus – and pes – from mechanical pressure (König & Liebich, 2015); a cushion for the load-bearing limbs of the animal. However, Ubilla & Altuna (1990) and Altuna et al. (1998) suggested that the TP acts as a supernumerary finger

during prehension, replacing the atrophied thumb characteristic of this genus, although this has not yet been studied in detail. Further, it has been suggested that the well-developed prepollex and pisiform observed in *Ctenomys* and other fossorial rodents increase the mechanical advantage of carpal flexors by increasing the in-lever arm of these muscles (Morgan & Verzi, 2011).

All *Ctenomys* species are herbivorous and they are considered mainly generalists, due to the high costs of burrow-digging (Comparatore et al. 1995). They show a wide geographical distribution (Mares & Ojeda, 1982), which involves some remarkable range of underlying environmental physical properties, from soft and very friable sandy soils to hard-and-clayey or well compacted soils (see Table 1 in Echeverría et al. 2017). They construct their burrows primarily by scratch-digging using their strongly developed foreclaws, and secondarily by using their large and procumbent incisors to assist in loosening and breaking obstacles (e.g. rocks, nodules of CaCO₃ or hard soil, and fibrous roots; Ubilla & Altuna, 1990; De Santis et al. 1998; Vassallo, 1998; Stein, 2000). However, despite having large foreclaws, which would difficult to perform skilled movements of the digits, it has been observed that tuco-tucos show some ability to manipulate small food items such as grass stems (e.g. *Bromus unioloides*) and sunflower seeds (*Helianthus annuus* L.) (A. I. Echeverría, unpubl. data). Previously, it was proposed that rodents perform rudimentary movements because, for example, mammals with claws or nails, especially small ones, would be limited in their ability to grab the food between their two hands, since they would impose a mechanical obstruction that would eliminate any capacity of precision (Napier, 1980). For instance, Heffner & Master-ton (1975, 1983) used anatomical and behavioral evidence to classify movements of different groups of mammals and included rodents in the intermediate group between mammals specialized for locomotion and mammals specialized for manipulation. However, there are cases such as rats (*Rattus*) which show the ability to perform a more precise manipulation of the food, even with a single hand (see references in Whishaw et al. 1998). In the case of *Ctenomys*, Echeverría & Vassallo (2012) observed that, when foraging on the two preferred grasses, *C. talarum* (Los Talas' tuco-tuco) consumed both grasses through two different foraging techniques. When foraging on panicgrass (*Panicum racemosum*) individuals handled the culm using both hands at once and rotated it for peeling the cataphylls using their incisors. Conversely, bromegrass (*Bromus unioloides*), which contains more water than panicgrass, was consumed directly, without peeling or rotating, and the subjects handled it using one or both hands at once. Moreover, it was observed that, when foraging, *C. talarum* can hold stems and roots between the central digits flexed against the thenar and the hypothenar pads (A. I. Echeverría, pers. obs.). In this context, the well-developed palmar pads would appear to play a very important role during food manipulation.

Some mammals, such as the giant panda *Ailuropoda melanoleuca* (Carnivora, Ursidae), possess a 'false-thumb' (an enlarged radial sesamoid), contributing to gripping actions and compensating for the lack of prehensile abilities in a hand where the thumb is aligned with the other digits (Antón et al. 2006). Bridging the phylogenetic distance, the way in which the giant panda uses the radial sesamoid bone for grasping makes it one of the most extraordinary manipulation systems in mammalian evolution (Endo et al. 1999a, and references therein; see also Salesa et al. 2006). Recently, Abella et al. (2016) proposed the action of a radial sesamoid as a real false-thumb for the first time outside the mammalian carnivorans, specifically in the cotton rat *Sigmodon peruanus* (Rodentia, Sigmodontinae, Cricetidae). However, those authors did not present conclusive evidence on the functional capabilities of this structure or the anatomical description of the related muscles. In the case of *Ctenomys*, field observations and our video records have shown that adult specimens use their hands to grasp food with quite complex movements. It could be proposed that the TP acts as an opposable 'sixth digit', with a high versatility of movements, acting as a pincer-like apparatus. In this work, we evaluate the ability of tuco-tucos to make prehensile movements with their hands and the role and functional capabilities of the TP during food handling. We also analyze the gross morphology of the forepaw including bones, muscles and histology, expecting to find an anatomical framework similar to a digit, able to account for the TP movements. Finally, we consider the evidence of all these sources to discuss the identity of the thenar pad.

Materials and methods

Specimens

Forepaws of adult specimens of the Southern tuco-tuco (*C. australis*, $n = 10$) and Los Talas' tuco-tuco (*C. talarum*, $n = 7$) were dissected at the Instituto de Herpetología (CONICET - Fundación Miguel Lillo, San Miguel de Tucumán, Argentina), and at the Laboratorio de Morfología Funcional y Comportamiento [Instituto de Investigaciones Marinas y Costeras, IIMyC (UNMdP- CONICET), Mar del Plata, Argentina]. Specimens belonged to the collections of Grupo Morfología Funcional y Comportamiento and Grupo Ecología Fisiológica y del Comportamiento [Instituto de Investigaciones Marinas y Costeras, IIMyC (UNMdP- CONICET), Mar del Plata, Argentina]. They were kept frozen until just before dissection, thus the muscles were in excellent condition and all the structures and muscular attachments were visible.

Hand bones

We used radiographic images taken of the intact forelimbs of two adult males of *C. australis* as reference for the

anatomical position of the hand bones in articulation. Images were obtained through radiovisiography (i.e. digital radiology) using a digital sensor RVG 6200 (Carestream Dental).

Due to the small size of the analyzed material, hand bones (carpals, metacarpals, phalanges and ossicles) and cartilages of adult specimens of *C. australis* ($n = 2$) were also studied through a clearing technique with double staining. Clearing and staining protocols were performed at the Laboratorio Histología, Instituto de Investigaciones Marinas y Costeras (IIMyC, CONICET-UNMdP). We used Alcian Blue 8GX staining for cartilage and Alizarin Red S staining for bone, following the procedures described in Supporting Information Appendix S1A. The cleared and stained material was photographed using an Olympus E-620 digital camera connected to a binocular stereo microscope Olympus SZ6. We focused on articulations and bony structures related to the thenar pad. The staining and clearing method used in this study has the advantage that all bones are retained in their original position and there is no chance of losing small bones or wrongly identifying similar bones (Green, 1952).

Musculotendinous system

We examined the muscles – and tendons – associated to the thenar pad in adult specimens of *C. talarum* ($n = 2$) and *C. australis* ($n = 8$). Dissections were carried out under a binocular stereo microscope Olympus SZ6. We recorded the general features and the location on the forearm skeleton of the origin and insertion areas of each muscle. The anatomical nomenclature used was based on Rinker (1954), Diogo & Abdala (2010), which is currently used for the comparative myology of vertebrates. We also include a table with the synonyms of the Nómina Anatómica Veterinaria (2005), which includes the most used names for mammals (Appendix S1B). We used the abbreviation 'm.' for muscle (pl. 'mm.'), while for tendons, the nomenclature coincided with that of the corresponding muscle, but without this abbreviation preceding it.

Histology of the thenar pad

Two adult male specimens of *C. talarum* were used for the histological description. The rest of the animals were frozen for dissection and anatomical description of the forepaws.

For the histological description, the forepaws were removed, fixed in formaldehyde buffer for 48 h and immersed in a decalcifying solution (Decalcifier Plus, Biopack) for 17 days. Samples were routinely processed for the inclusion of bone material in paraffin (Montuenga et al. 2014). Histological sections 7- μ m-thick were cut by microtome and then treated with Hematoxylin-Eosin and Masson's trichrome techniques for morphology (Montuenga et al. 2014).

Functional analysis of the gripping action

Animal capture and housing conditions

Two adult males of *C. talarum* were captured on April 2018 in Estancia San Manuel (37° 47' S, 57° 28' W, Buenos Aires province, Argentina) using wire mesh live traps (10 cm in diameter) located at burrow entrances. All animals were housed in individual plastic cages (25 × 32 × 42 cm) provided with wood shavings. Food was provided *ad libitum* and consisted of carrots, sweet potatoes, lettuce, corn, mixed grasses and sunflower seeds. The temperature in the animal room remained constant (25 ± 1 °C) and a 12 : 12-h light : dark cycle was maintained. Once observations finished, animals were returned to the capture site.

Observational procedure

To investigate the ability of tuco-tucos to manipulate food items, individuals were filmed at 300 fps using a Casio Exilim Pro EX-F1 camera while foraging on two different food items inside a transparent glass box of 7.0 cm wide × 20 cm long × 20 cm high. The offered items differed in size and type: the larger item consisted of panic-grass (*Panicum racemosum*) stems (5 cm long), and the smaller item of corn kernels (*Zea mays*). The used grass is part of the natural diet of *C. talarum* (Comparatore et al. 1995) and is one of the most preferred among the plants consumed annually by adults (del Valle et al. 2001).

To determine whether the thenar pad compensates for the lack of prehensile abilities in *Ctenomys* hand, we focused on its motor capabilities, especially, its ability to adduct or abduct independently. We investigated the gripping action in detail and determined the relationship between structures to clarify whether the thenar pad acts as an opposable 'sixth digit' and whether this palmar pad can act as a pincer-like apparatus.

Results

A photograph of a forepaw of *C. talarum* in palm view is presented in Fig. 1. The figure illustrates the position of the most developed palmar pads, the thenar and the hypothenar (TP and HP, respectively), which are separated by a short sulcus. The palm shows a marked flexion crease that runs ulnarly from the insertion area of the thumb (Fig. 1).

Hand bones

The analysis of clarified and double-stained forepaws showed that the TP is supported by an elongated and paddle-shaped bone, which passes to the lower two-thirds of the TP, and continues distally in a cartilaginous triangular-shaped structure (Fig. 2A). In a lateral-medial view, it is flattened, such as the cartilage on its distal extreme (Fig. 2B).

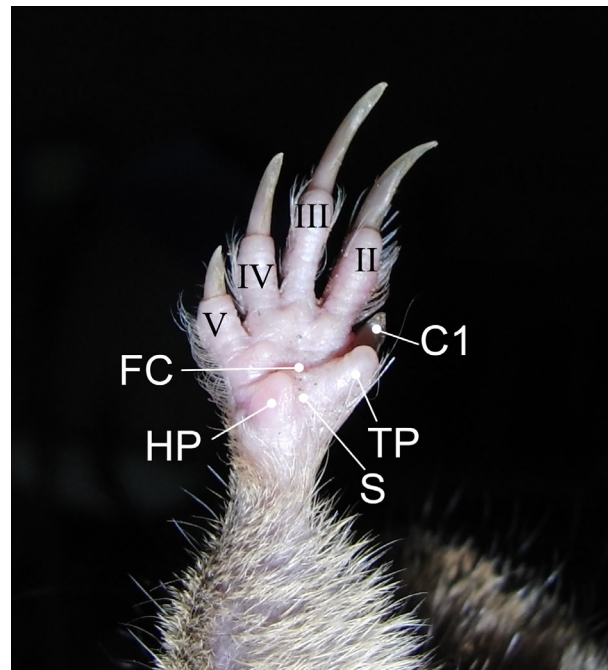


Fig. 1 Palmar view of the right forepaw of *Ctenomys talarum*. S, sulcus; TP, thenar pad, C1, claw of the thumb; FC, flexion crease; HP, hypothenar pad. Black roman numerals indicate the number of each digit.

Both structures, the bone and the distal cartilage, are hooked-shaped (in lateral-medial view) and they are dorsally displaced towards the external face of the TP (Fig. 2B). In a palmar-dorsal view (with the TP resting on the DI, forming a pincer-apparatus), the bone is convex (with the concave facet facing the DI) and slightly displaced towards the radial side of the TP (Fig. 2C). Three *C. talarum* specimens displayed a small triangular-shaped bone, dorso-palmarly flattened, located close to the distal edge – ulnar side – of the main bone (Fig. 2D).

In the radiographs (Fig. 3) it could be observed that the main bone reaches the level of the joint between the first metacarpal and the proximal phalanx of the thumb, and articulates proximally with a protrusion of the scapholunate bone. The dorsal displacement towards the external face of the main bone and its cartilaginous distal extreme can be clearly observed in the Fig. 3.

Musculotendinous system

Limb muscles that govern thenar pad movement in *Ctenomys* belong to two anatomic groups: extrinsic muscles (reside within the forearm and connect to skeletal structures in the forepaw via long tendons) and intrinsic muscles (both the muscles and tendons located within the forepaw). Muscles associated with the thenar pad are described below.

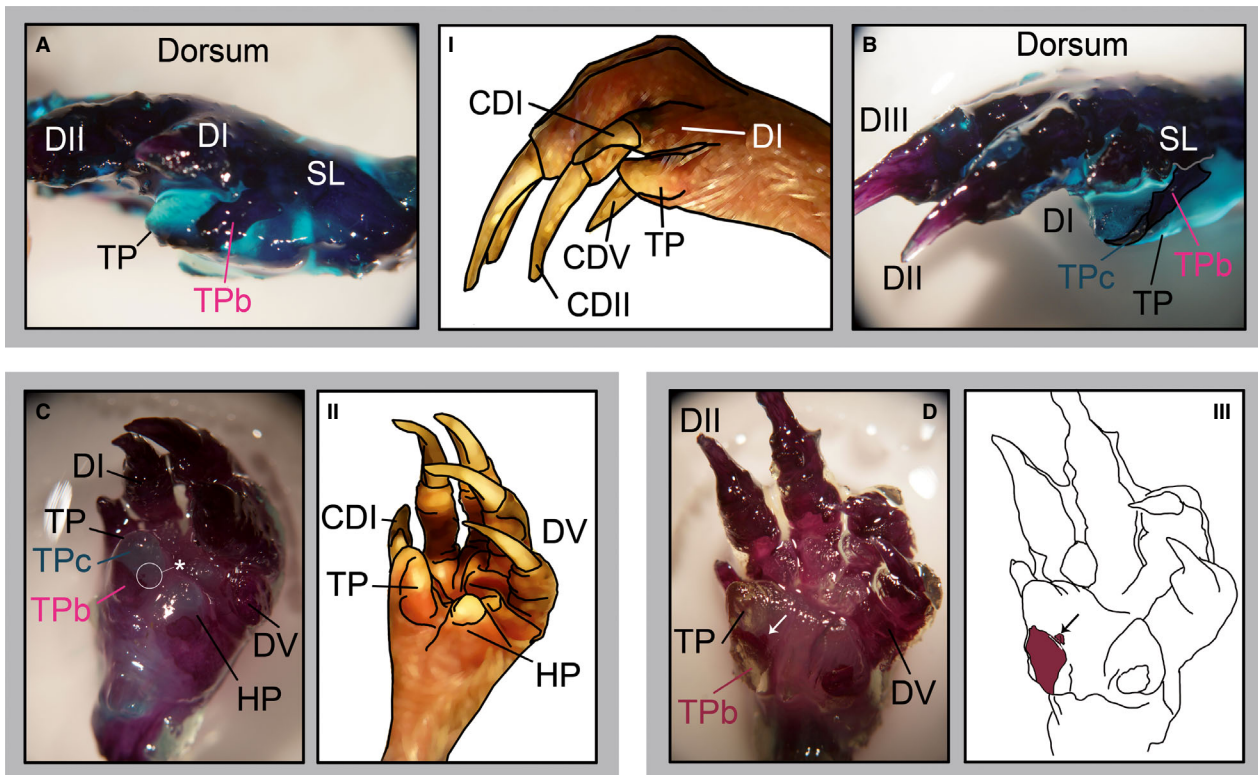


Fig. 2 Right (A,B) and left hands (C,D) of *Ctenomys talarum* (adults) cleared and double-stained with Alizarin red and Alcian blue. (A) Radial, (B) dorso-radial, (C,D) palmar views. We included illustrations of the hands in the shown positions (i-ii); in (D), we included an illustration of the photography (iii) to clarify the location of the described distal bone (marked with arrows in D, and with a white asterisk in C). DI, digit I (thumb); DII, digit II; DIII, digit III; DV, digit V; CDI, claw of DI; CDII, claw of DII; CDV, claw of DV; TP, thenar pad; TPb, TP main bone; TPc, TP cartilage; HP, hypothenar pad; SL, scapholunate bone.

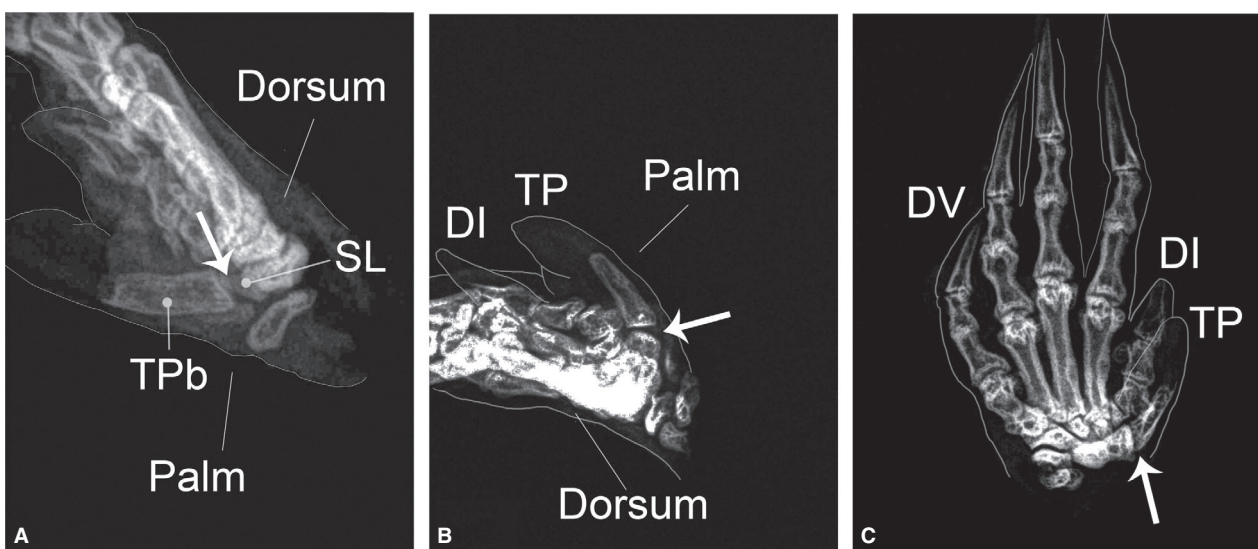


Fig. 3 Radiographic images of a right (A,C) and a left (B) hand of *Ctenomys australis*. (A,B) Radial aspect, (C) palmar aspect. TPb, thenar pad bony support; SL, scapholunate bone; TP, thenar pad; DI, digit I (thumb); and DV, digit V. The white arrow marks the articulation between the scapholunate and the bony support of the thenar pad. (A) The scapholunate protrusion where the TPb articulates.

Extrinsic muscles

M. palmaris longus

This is a large, approximately fusiform and flat, well-defined muscle located on the radial side of the volar surface of the antebrachium. This extrinsic muscle belongs to the flexor group of the forearm. It arises from the medial epicondyle of the humerus, passing to the lower two-thirds of the radius, and blends with the proximal portion of the *m. flexor carpi ulnaris*, another extrinsic flexor muscle. The insertion tendon passes superficial to the flexor retinaculum, and its fibers continue into the hand and attach to the palmar aponeurosis which inserts onto the proximal borders – under the cornified layers – of the thenar (TP) and hypothenar (HP) pads, specifically, on the ulnar half of the TP and on the radial half of the HP; respectively. In *C. australis*, the palmar aponeurosis showed two shapes: Y-shaped or funnel-shaped. In the case of a funnel-shaped aponeurosis, the central tendon fibers also insert on the central area between pads, called the intertorical area (Ade & Ziekur, 1999). In some specimens, the palmar aponeurosis showed at least two layers, a superficial one, corresponding to the commonly described layer, and an inner or dorsal layer, in which resistance lines formed by thinner tendons were observed. Moreover, the main tendon may continue distally in two thinner tendons that insert onto DIII and DIV.

M. abductor pollicis longus

This originates from the ulna and radius and is clearly distinguishable as its fibers are obliquely located in the dorsum of the antebrachium, and its insertion tendon reaches the point of bifurcation between the DI and the TP. A narrow ribbon-like muscle runs from the bifurcation in the base of the TP and inserts distally onto its skeletal support, which can be identified as the *m. abductor pollicis brevis*.

Intrinsic muscles

Mm. flexores breves profundi

These muscles originate from the distal carpal corresponding to each digit. The *m. flexor brevis profundus* that inserts on the thumb (DI) originates from the trapezium. They all insert onto the sesamoids at the metacarpophalangeal joints of each digit.

There is a massive muscular complex between the thumb (DI) and the skeleton of the TP. Although the limits of each muscle are indistinguishable, for topology it can be inferred that the complex is composed by the *m. abductor pollicis brevis*, *m. flexor pollicis brevis* and *m. adductor pollicis brevis* (Figs 4 and 5).

M. abductor pollicis brevis

This originates from the proximal border of the skeletal support of the TP and inserts onto the radial side of the metacarpal of digit I (Fig. 4).

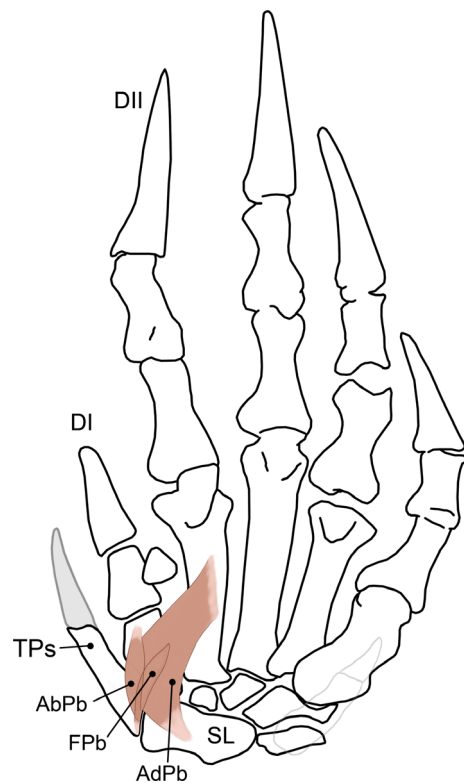


Fig. 4 Origin and insertion areas of the three muscles that integrate the massive muscular complex located between the thumb and the skeleton of the TP in *Ctenomys australis*. DI, thumb; DII, digit II; TPs, skeletal support of the thenar pad; SL, scapholunate bone; AbPb, abductor pollicis brevis muscle; FPb, flexor pollicis brevis muscle; AdPb, adductor pollicis brevis muscle. The light gray structure in the distal extreme of the TPs corresponds to the cartilaginous axis of the thenar pad. The light gray bones at the ulnar side of the hand represent the pisiform (i.e. skeletal support of the hypothenar pad) that locates above the illustrated bones.

M. flexor pollicis brevis

This originates from the base of the skeletal support of the TP and inserts onto the base of the metacarpal of digit I (Fig. 4).

M. adductor pollicis brevis

This originates from the common deep palmar ligament between the scapholunate bone and incorporates to the complex connecting the TP, the DI and the DII (Fig. 4).

Histology of the thenar pad

In a longitudinal section of the TP, it was observed that the skeletal support and its distal cartilaginous axis were located near the external face of the thenar pad (Fig. 5). Moreover, the stratum corneum, composed of keratin (a key structural material making up claws), was more developed in the external face (Fig. 5). A thick epidermis is observed, with its highly developed stratum corneum. The

underlying dermis is mostly dense (fibrous) connective tissue. Immersed in the dermis are moderate amount of eccrine glands, bundles of striated muscle and white adipose tissue. Laterally, there is hyaline cartilage, thickened at its base (proximal end), and associated with the dense connective tissue of the dermis (Figs. 5 and 6A,D).

In greater detail, the epidermis is differentiated in four layers: cornified, granular, espinous and basal (Fig. 6C). Thick collagen fibers from the dermis connect with the cartilage at one end and to the muscle at the opposite end (Fig. 6A,D). The transverse orientation of the muscle fibers predominates. There are abundant adipocytes (Fig. 6E), as well as nervous tissue (Fig. 6F).

Functional analysis of the gripping action

Tuco-tucos adopted two different body positions for eating. The most common was crouched, but they also foraged sitting on their haunches. For all of the food items, the strategy used for reaching was first to sniff the food by bringing the snout in contact with it and next picking up by mouth. They manipulated the food into their mouths with the paws as eating progressed.

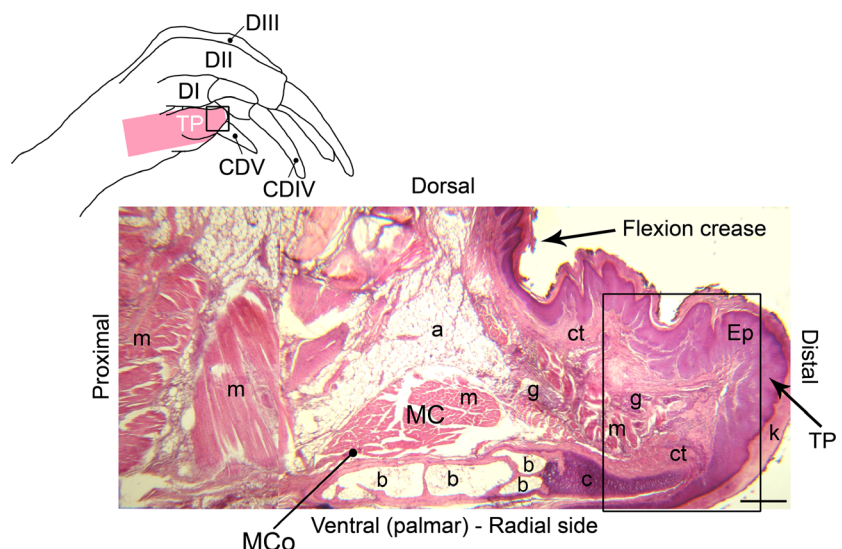
Unilateral prehension

Once the animal grasped the item, it retrieved the food in its mouth, reaching it forward with a single limb to take the food item from the mouth and hold it with one paw. To do this, the animal first lifts the paw from the ground, then brings the forearm to the midline of the body (i.e. adducts) while raising it (Fig. 7A,B). As the paw approaches the food item, the elbow moves closer to the midline of the body. In the case of small items (corn kernels in this study), the paw is supinated when reaching the item (i.e. semi-pronated posture), so its palm faces it with the digits extended

(Fig. 7B). For corn kernels, the grasping pattern included holding the kernel mainly between digits DI–DIV – and their respective claws (CI–CIV) – and peeling it by pulling down the pericarp (or hull) with the TP tip, CI and DII. During this grasping pattern, the DV remained extended or flexed with the kernel resting on its claw (CV). To push the kernel into the mouth, the animals flexed the TP, move it toward to the DII (being between the middle of both, the claw of DI) and pushing up the kernel from below. Frequently, the animals took out the kernel from the mouth, moving it close to the nose and sniffed it. While eating the kernel, animals alternated the paw with which they manipulated it. To do this, first they released the item, leaned the paw on the ground and grasped the item with the opposite paw. Another strategy used to manipulate and to push the kernel into the mouth was to grasp it with the TP placed under the item, the digit II curling above, and the claws III and IV holding and supporting the distal extreme of the item. Both claws (CIII and CIV) were also used to push the kernel into the mouth.

Typically, when holding a long food item, such as the stems of *P. racemosum*, tuco-tucos used a variety of hand and digit postures, many of which are illustrated in Fig. 8. Animals extended all the digits and the TP, opening the hand to reach the item grasped in the mouth. The paw was supinated if necessary to hold the item. The food could be held with a power grip (Napier, 1956); i.e. all the digits (and their respective claws) curling around the stem, that was clasped against the palm (particularly, against the flexion crease), with the TP acting as an opposable thumb. Sometimes, the animals supinated the forearm and the hand, rotating the paw along with the food item, 180°. This movement was made while moving the food towards the mouth, until it was held between the incisors. Seemingly to improve the grip, the digits could be held quite close together, so that claws II and IV remain locked under claw

Fig. 5 Longitudinal section of the thenar pad (left forepaw) of an adult male of *Ctenomys talarum*. The pink colored area in the scheme of the hand indicates the location of the longitudinal section illustrated. a, adipocytes; b, bone; c, cartilage; ct, connective tissue; Ep, epidermis; g, eccrine glands; k, keratin; m, muscle; TP, thenar pad; DI, digit I (thumb); DII, digit II; DIII, digit III; CDIV, claw of digit IV; CDV, claw of digit V; MCo, proximal border of the TP skeleton, where the muscles integrated to the muscular complex originate; MC, massive muscular complex between the thumb (DI) and the skeleton of the TP. Scale bar: 400 μ m.



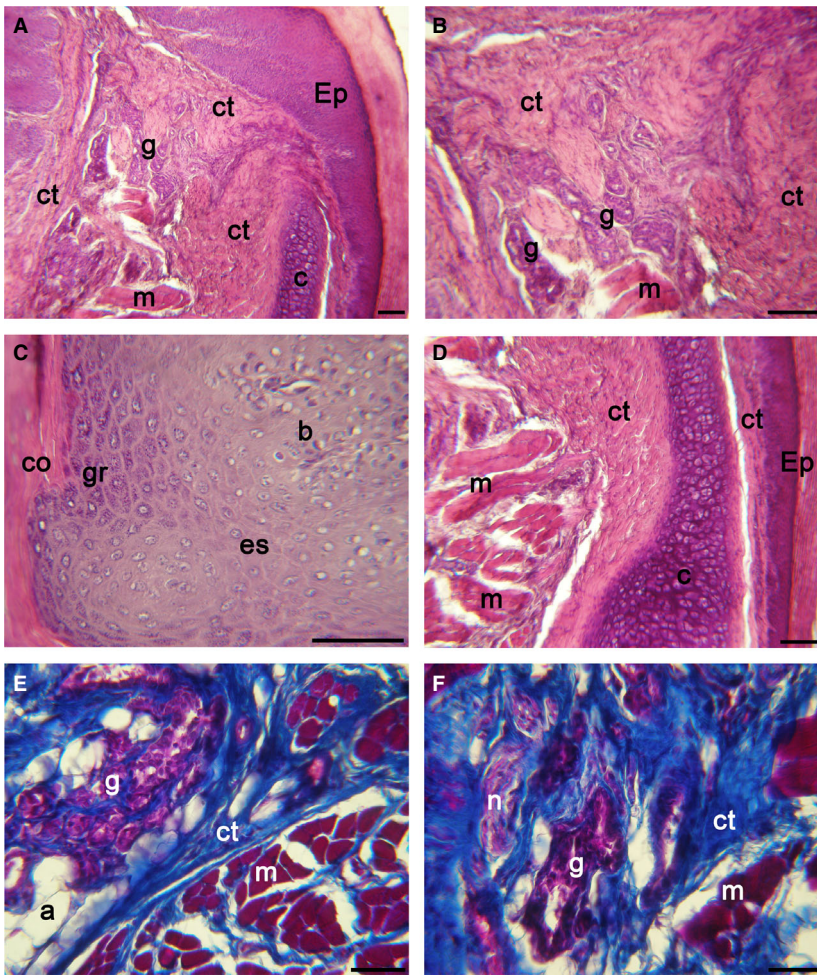


Fig. 6 Longitudinal sections of a thenar pad (left forepaw, distal extreme) of an adult male of *Ctenomys talarum* (see Fig. 5, insets). (A-D) Sections were stained with Hematoxylin-Eosin. (E,F) Masson trichrome. Scale bars: (A, B,D) 100 μm , (C,E,F) 50 μm . a, adipocytes; b, basal layer; c, cartilage; co, cornified layer; ct, connective tissue; Ep, epidermis; es, epinuous layer; g, eccrine glands; gr, granular layer; m, muscle; n, nervous tissue.

III, and claw V remains below claw IV. Both digit postures were used for peeling the cataphylls using their incisors. To do this, animals separated the digits while they moved the hand in the direction of the free end of the stem, and they held the digits closer to push the stem in the direction of the mouth while peeling the cataphylls.

Eventually, animals could grasp the food mainly with digits II, III and IV (which were held more tightly together) curling on the stem, which was supported by the 'thenar pad', and digits I and V. The food could also be held with an intermediate grip (Feix et al. 2016); i.e. a pincer-like apparatus formed by the 'thenar pad' and digits II and I.

Discussion

This study was performed with the aim of assessing the functional morphology and identity of the thenar pad (TP) in *Ctenomys* using multiple sources of evidence. From a functional perspective, our data indicate that the TP is the structure that actively performs the movements needed in the power and intermediate grasp, intensively used during feeding in *Ctenomys*, as the first digit is atrophied. Tuco-tucos use a range of complex forelimb and forepaw

movements for food handling despite the specializations that the limbs and paws have undergone to adapt to the subterranean lifestyle. Particularly, the adaptations related to scratch-digging behavior are mainly found in the hand (Hildebrand, 1985; Hildebrand & Goslow, 2001; Kley & Kearney, 2007); given the characteristics of these adaptations, it would be natural to expect a mechanical constraint imposed on paw and digit use during food handling in this genus. For example, when we analyze the pad pattern on the palmar face of the *Ctenomys* hand, there is a lack of distinct distal pads accompanied by strongly developed proximal pads. This pad pattern is similar to that observed in other fossorial rodents (all Spalacinae occurring at least in Europe; several bathyergids: *Georychus*, *Cryptomys* and *Bathyergus*; *Pedetes capensis*–Pedetidae; Geomyidae and the dipodine *Juculus*; for references see Ade & Zieker, 1999). According to Ade & Zieker (1999) this morphology of the palms indicates that the animals can dig by using their paws in a hoe or scraper-like manner, since digits II-III-IV-V project ventrally and the flexed palm forms a kind of scraper or hoe. The complexity of the hand would have promoted the emergence of adaptations beyond its primary specializations related to digging behavior. In particular, its

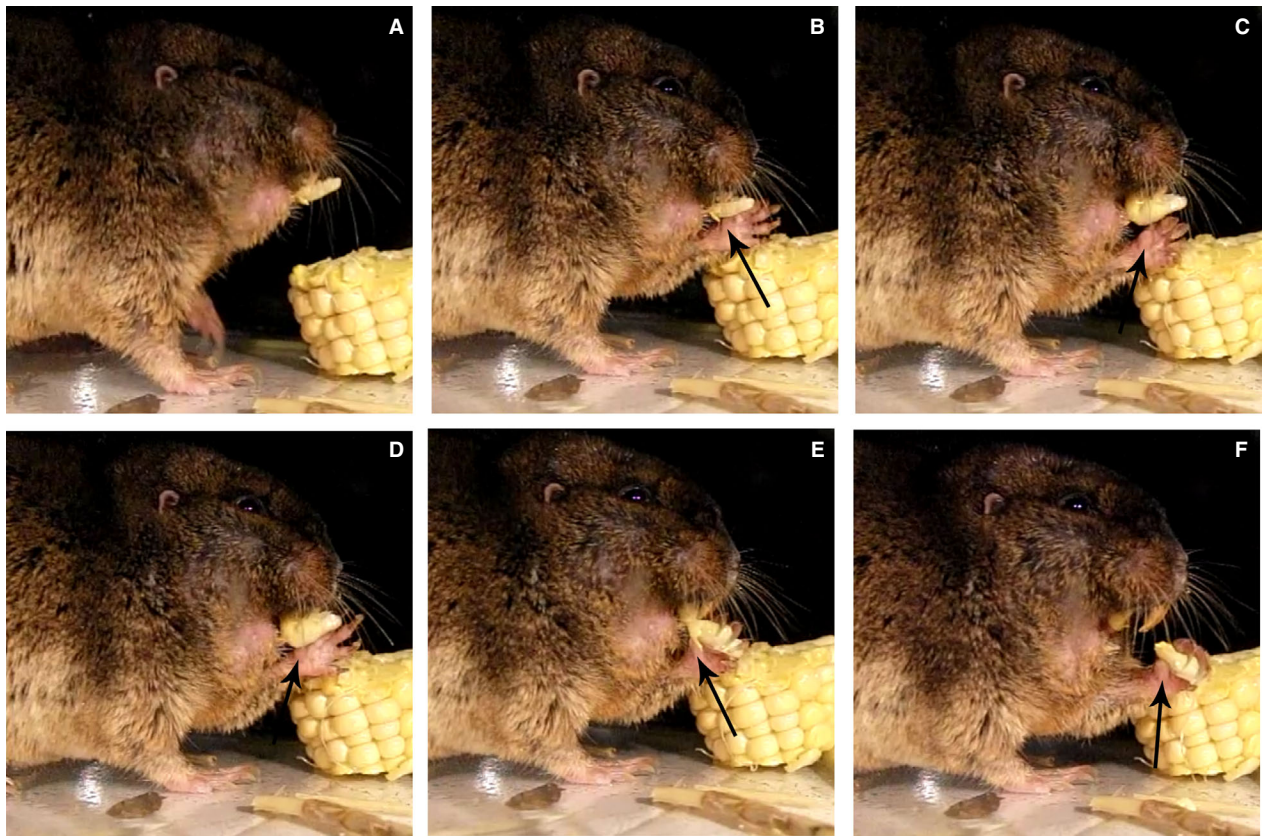


Fig. 7 Unilateral prehension by a tuco-tuco (*Ctenomys talarum*) foraging on a small food item (corn kernel, *Zea mays*). The animal sniffs the food item and next picks it up by mouth (A), the forepaw is supinated when reaching towards the item (B), the digits (I, II) and the thenar pad are used to push the food into the mouth (C), the palm faces the item with the digits extended (D), the digits curl around the item, and the thenar pad acts like an opposable real thumb (E,F). Black arrows indicate the thenar pad.

design (palm, pad pattern, digits and claws) may have led to a separation of the functions of scratch-digging and food-handling (e.g. grasping), and this functional duality seems more accentuated in the TP. The alignment of the thumb with the rest of the digits – together with short and robust carpals and metacarpals – broadens the palm, and broader palms are adaptations to transport loosened substratum more effectively. In turn, this configuration of the digits does not allow the thumb to be opposable, and food handling would be reduced to grabbing the food with both hands; i.e. rudimentary – not skilled – movements (see Napier, 1980). However, our results showed that this constraint seems to be compensated by the TP, strongly developed and digitiform, topologically located in the position of an opposable thumb (in a common pentadactyl model of a tetrapod hand) and with the ability to perform independent movements. In a resting position, the TP skeleton stays parallel to the first digit, closing the gap with the other digits in a position similar to the power grip. When the hand is being used, the TP remains mostly rigid, abduction being its main movement, to adjust the TP to the food in the power or intermediate grip. The joint between the protrusion of the scapholunate bone and the skeletal base

of the TP is probably active when the TP abduction is performed. Our observations suggest that the TP has intrinsic movements but, contrary to our initial hypothesis, it was found that its repertoire is limited, basically, abduction probably guided by the extrinsic muscles of the hand, with adduction being controlled by the intrinsic muscles of digit I, modified in the complex that includes the TP. In the case of pandas (giant panda *Ailuropoda melanoleuca*, red panda *Ailurus fulgens*), both extant species use digits and wrist bones with remarkable dexterity when manipulating food, and this has led to the interpretation of the radial sesamoid as an opposable 'sixth digit' (Davis, 1964; Gould, 1980). However, in more recent studies (e.g. Endo et al. 1999a, 1999b, 2001) the gripping action was reinterpreted as a 'double pincer-like apparatus'; i.e. the radial sesamoid is not seen as an independent digit, but as part of a mechanism that allows food items and objects to be grabbed between the digits and the radial sesamoid and pisiform bones (Endo et al. 2001).

Taken together, our data suggest that the TP acts as a false-thumb, with a skeletal morphology very different to a sesamoid, except for its location, over most carpal joints because of the protrusion of the scapholunar. Traditionally,

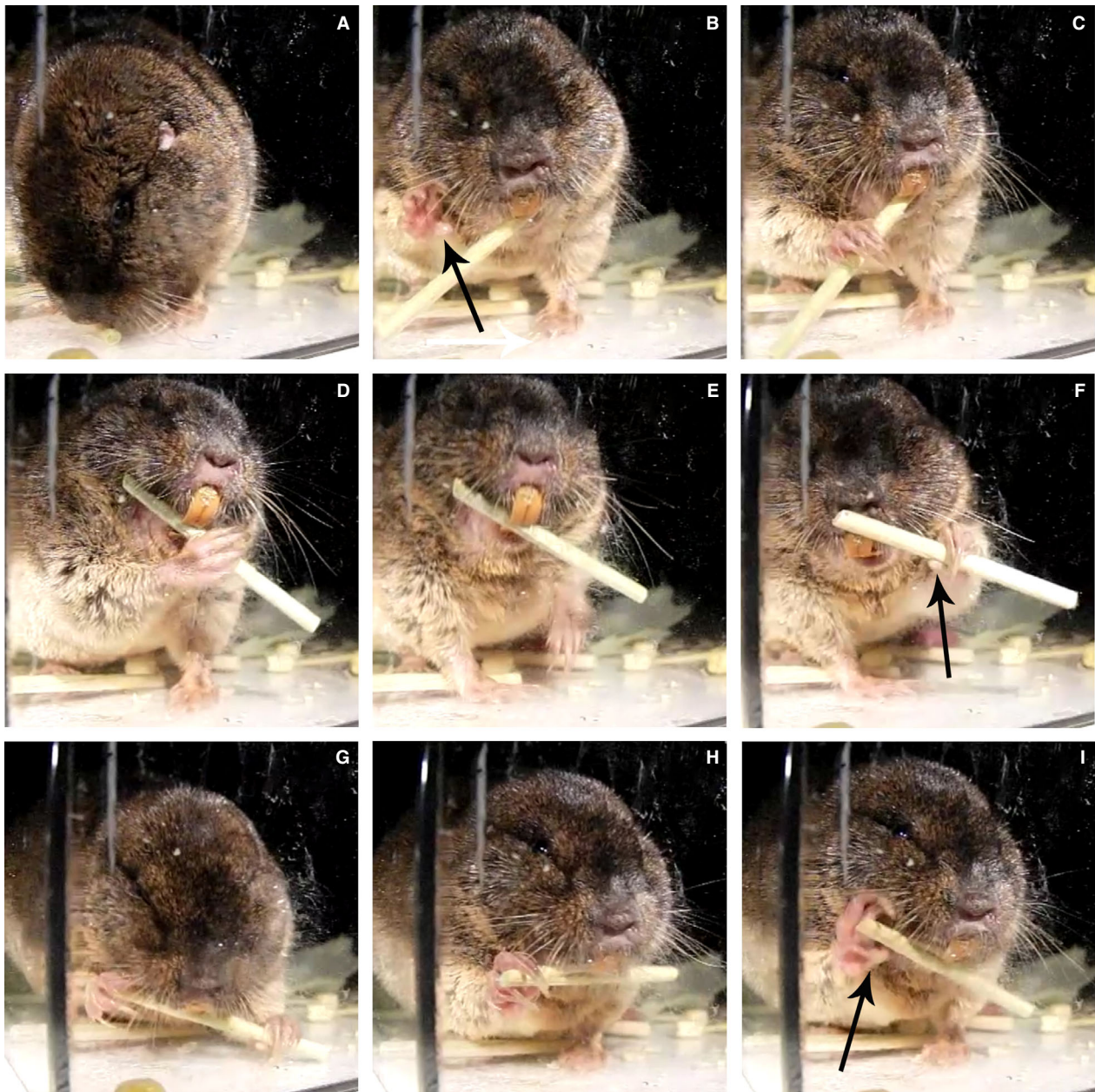


Fig. 8 Unilateral prehension by a tuco-tuco (*Ctenomys talarum*) foraging on a long food item (grass stem, *Panicum racemosum*). The animal sniffs the food item (A), the forepaw is lifted and aimed, with all the digits and the palmar pads extended (B), the digits and the thenar pad grasp the food (C), the forepaw can be rotated and supinated to change the position of the food in the mouth (D), the animal holds the food between the incisors with change of active forepaw (E), the food is grasped between the digits and the thenar pad, which acts like an opposable real thumb (F), the animal grabs the food with both forepaws (G), the digits and the thenar pad act as a pincer-like apparatus (H), the digits are extended (forepaw opened) while the food is held in the mouth, and after this the animal grasps the food using all the digits and the thenar pad while rotating and peeling the stem (I). Black arrows indicate the thenar pad.

this structure was described as an enlarged palmar pad supported by a ‘palmar ossicle’ (Woods, 1972), or ‘prepollex’ (Ubilla & Altuna, 1990; Morgan & Verzi, 2011) and a cartilaginous axis (Ubilla & Altuna, 1990). Particularly, Ubilla & Altuna (1990) and Altuna et al. (1998) suggested a prehensile function for this structure; however, they did not investigate it in detail. The results obtained in our study confirm

the important role of the TP during food handling, and shed light on the characteristics of its skeletal support, associated muscles and functional capabilities. Sánchez-Villagra & Menke (2005) (see also Bickelmann et al. 2012; Mitgutsch et al. 2012) described the number and arrangement of carpal bones in talpids (Talpidae), a taxa with a great diversity of lifestyles, including strictly subterranean, semifossorial

and semiaquatic species. They pointed out the extremely enlarged prepollex, which corresponds to the radial sesamoid – os falciforme – to which a functional adaptive meaning was attributed. For example, according to these authors, in *Talpa* the presence of an enlarged prepollex increases hand surface, important for propulsion during locomotion. In giant pandas the ‘false-thumb’, also interpreted as the radial sesamoid, constitutes a part of a double pincer-like, manipulative functional apparatus in which the hand flexes around the scapholunar and the unciform so as to grasp objects between the true digits and both the radial sesamoid and the pisiform (Endo et al. 1999a, 1999b, 2001; Antón et al. 2006). Schmitt et al. (2009) mentioned recently a similarly enlarged prepollex and prehallux in the giant mole-rat, *Fukomys mechowii*, and interpreted them also as an adaptation for its digging lifestyle. Thus, the most accepted perspective is that the prepollex in these mammal taxa would be the radial sesamoid (for an alternative interpretation of the identity of a predigit in anurans see Hayasi et al. 2015). A closer look at the anatomy of this structure in *Ctenomys* allows us to stress that this sesamoid underwent a radical change on its morphology in this genus.

A sesamoid is any organized, intratendinous/intraligamentous structure, including those composed of fibrocartilage associated to a joint (Haines, 1969; Vickaryous & Olson, 2007; Tsai & Holliday, 2011; Regnault et al. 2017; Abdala et al. 2018; Amador et al. 2018). Our data on the TP skeleton, muscles, tendon insertions and epithelium suggest a highly complex anatomical structure. Sesamoids commonly do not participate in joints; they are associated with them but as periarticular structures, usually within the tendon surrounding the joint. The TP skeleton is served by the same muscles as those of digit I; e.g. mm. abductor pollicis longus and adductor pollicis brevis (Fig. 4). It receives the insertion tendon of m. palmaris longus and m. abductor pollicis longus; however, sesamoids are generally not served by muscles (but see Chadwick et al. 2014). Although there are sesamoids on the bases of the thumb and hallux in the mammalian limb attached to the short flexor and short adductor digital muscles, these muscles convey digit movement instead of sesamoid movement. Sesamoids generally do not have intrinsic movement, they rather move along with the tendons they are embedded into (but see Chadwick et al., 2014). However, there is no tendon embedding the TP skeleton. Another interesting anatomical finding to consider is that the distal area of the skeletal support of the TP is covered by skin with keratin, a typical claw tissue. Report of skin modifications associated with the presence of sesamoids are rather scarce, for example that related to the ossicones on the head of okapis and giraffes (Hall, 2015).

Sesamoids have been proposed as a source of skeletal variability (Parsons, 1904, 1908; Eyal et al. 2015, 2019; V. Abdala, M. C. Vera, L. I. Amador, G. Fontanarrosa, J. Fratani & L. Ponssa, in prep.) and it could be inferred that

they even can give rise to a digit-like structure (see e.g. Hutchinson et al. 2011). Developmental data have shown that the patella sesamoid arises from a distinct pool of progenitor cells similar to the development of bony eminences, which modularly attach onto the main body of the bone (Blitz et al. 2013; Eyal et al. 2015, 2019). It would be very interesting to test whether the progenitor cells of the TP are similar to those of other sesamoids, which would confirm these structures as those mainly responsible for the plasticity of the patterning of vertebrate skeleton. Diogo et al. (2015) proposed the topology model to account for the link between muscles and skeleton: identity and attachment of the limb tendons/muscles is settled by topological position of digits on which they insert, regardless of the anlage or developmental identity of digits. The distal insertion of tendons such as the abductor pollicis longus suggests that the first digit and the TP are so closely related that tendons interpret the information as if there were a single digit (Danforth, 1947; Crowley et al. 2018), in line with Diogo et al. (2015) proposal. The relation of this skeletal structure (the radial sesamoid) with the anatomical digit I elements could have driven its transformation in a digit-like structure.

The presence of this complex skeletal structure in *Ctenomys*, similar to the grasping structure of sigmodontines (e.g. Abella et al. 2016) and to the climber pad of *Rhipidomys* (Rivas et al. 2010), is a reflection of the flexibility of morphological evolution, which can thus lead to anatomical innovations that secondarily allow to face different environmental and ecological challenges. In conclusion, the results of this study suggest that the TP could actually be considered a ‘false-thumb’, probably the result of a radical transformation of the radial sesamoid, with the capacity to manipulate food with relative skill. Further investigation (development, gene expression) is required to advance settlement of the identity of a structure that has fascinated researchers for centuries.

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Author contributions

This study was conceived by all the authors. A.I.E. designed research, collected specimens and morphological data from

dissections (gross anatomy), performed bone radiographs, data interpretation. V.A. performed muscle dissections and data interpretation. M.V.L. carried out the histological analyses and data interpretation. A.I.V. collected specimens. Drafting of the manuscript was performed by A.I.E., V.A. and M.V.L., and all authors critically revised it.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary Material.