

ORIGINAL ARTICLE

Functional and morphological divergence in the forelimb musculoskeletal system of scratch-digging subterranean mammals (Rodentia: Bathyergidae)

Germán Montoya-Sanhueza¹  | Nigel C. Bennett²  | Radim Šumbera¹ 

¹Department of Zoology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

²Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

Correspondence

Germán Montoya-Sanhueza, Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 1760, České Budějovice 37005, Czech Republic.
Email: g.montoya.sanhueza@gmail.com

Abstract

Whether the forelimb-digging apparatus of tooth-digging subterranean mammals has similar levels of specialization as compared to scratch-diggers is still unknown. We assessed the scapular morphology and forelimb musculature of all four solitary African mole rats (Bathyergidae): two scratch-diggers, *Bathyergus suillus* and *Bathyergus janetta*, and two chisel-tooth diggers, *Heliophobius argenteocinereus* and *Georychus capensis*. Remarkable differences were detected: *Bathyergus* have more robust neck, shoulder, and forearm muscles as compared to the other genera. Some muscles in *Bathyergus* were also fused and often showing wider attachment areas to bones, which correlate well with its more robust and larger scapula, and its wider and medially oriented olecranon. This suggests that shoulder, elbow, and wrist work in synergy in *Bathyergus* for generating greater out-forces and that the scapula and proximal ulna play fundamental roles as pivots to maximize and accommodate specialized muscles for better (i) glenohumeral and scapular stabilization, (ii) powerful shoulder flexion, (iii) extension of the elbow and (iv) flexion of the manus and digits. Moreover, although all bathyergids showed a similar set of muscles, *Heliophobius* lacked the m. tensor fasciae antebrachii (aiding with elbow extension and humeral retraction), and *Heliophobius* and *Georychus* lacked the m. articularis humeri (aiding with humeral adduction), indicating deeper morphogenetic differences among digging groups and suggesting a relatively less specialized scratch-digging ability. Nevertheless, *Heliophobius* and *Bathyergus* shared some similar adaptations allowing scratch-digging. Our results provide new information about the morphological divergence within this family associated with the specialization to distinct functions and digging behaviors, thus contributing to understand the mosaic of adaptations emerging in phylogenetically and ecologically closer subterranean taxa. This and previous anatomical studies on the Bathyergidae will provide researchers with a substantial basis on the form and function of the musculoskeletal system for future kinematic investigations of digging behavior, as well as to define potential indicators of scratch-digging ability.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Authors. *Journal of Anatomy* published by John Wiley & Sons Ltd on behalf of Anatomical Society.

KEYWORDS

African mole-rats, chisel-tooth digger, convergence, fossorial adaptations, muscle anatomy, scapula, scratch-digger

1 | INTRODUCTION

Morphological convergence among fossorial and subterranean mammals is mainly the result of similar functional demands associated with the construction of burrow systems for either shelter and/or foraging (Gomes Rodrigues et al., 2023; Hildebrand, 1985; Nevo, 1979, 1999). However, mammals have evolved multiple digging strategies to build burrows and exploit the subterranean ecotone, including forelimb digging (e.g. scratch-digging, hook-and-pull digging, humeral rotation) and head digging (e.g. chisel-tooth digging, head-lifting) (Gambaryan & Gasc, 1993; Gomes Rodrigues et al., 2023; Hildebrand, 1985; Nakai & Fujiwara, 2023). Consequently, subterranean mammals have specialized their digging apparatus to maximize excavation according to the different selective pressures and functional regimes associated with each digging mode (e.g. Fournier et al., 2021; Hildebrand, 1985). African mole-rats (Bathyergidae) are an excellent group of mammals to assess the adaptive processes behind such functional diversification, especially because they possess highly specialized morphological and physiological adaptations to build extensive burrow systems in a wide range of habitats with varying soil hardnesses (e.g. from sandy to highly compacted: Bennett & Faulkes, 2000; Lövy et al., 2012). The members of this family use two main digging modes to break up soils. The genus *Bathyergus*, composed of two species, the Cape dune mole-rat *Bathyergus suillus* and the Namaqualand dune mole-rat *Bathyergus janetta*, are predominantly scratch-diggers that use their long foreclaws to break up soils, while the other five genera (*Heliophobius*, *Georychus*, *Cryptomys*, *Fukomys*, and *Heterocephalus*) are chisel-tooth diggers (hereafter tooth-diggers) that use their highly procumbent incisors to break-up soils (Bennett & Faulkes, 2000). Nevertheless, all members of this family use both their fore and hindlimbs for removing and transporting soil (Cuthbert, 1975; Genelly, 1965; Jarvis & Sale, 1971; Van Wassenbergh et al., 2017).

Considerable morpho-functional divergence has been detected in the craniodental and muscular anatomy between tooth- and scratch-digging bathyergids: the former presents higher levels of procumbency (i.e. anterior projection of the incisors), as well as short, flat, but also deep and broad skulls, in association with enlarged zygomatic arches and temporal areas, all features associated with the development of massive and powerful masticatory muscles necessary to enhance bite force (e.g. Cox et al., 2020; Fournier et al., 2021; Gomes Rodrigues et al., 2016, 2023; McIntosh & Cox, 2016a, 2016b). Accordingly, computational modeling data comparing the gape performance of the cranium of the giant mole-rat *Fukomys mechowii*, and *B. suillus* suggests that the cranium of *F. mechowii* is stiffer than that of *B. suillus*, making it more efficient at converting muscle forces into bite forces (McIntosh & Cox, 2016b). This pattern has been recently supported by *in vivo* measurements of bite force among all

bathyergid genera showing that tooth-diggers have larger bite forces than scratch-diggers (Kraus et al., 2022), which is probably linked to the exploitation of harder and more compacted soils (Gomes Rodrigues et al., 2023; Kraus et al., 2022; McIntosh & Cox, 2016a).

Whether the appendicular musculoskeletal system of bathyergids has experienced similar levels of morphological specialization during their evolutionary history is still not fully understood, principally because of the limited information about their postcranial adaptations. Particularly, the forelimb musculature of bathyergids is poorly known, and only a few species (along with reduced sample sizes) have been studied. Regarding the myology of the Bathyergidae, a major emphasis has been placed on their cranial musculature (Cain et al., 2019; Cox et al., 2020; Cox & Faulkes, 2014; Van Daele et al., 2009), with only a few studies describing their limb musculature. The taxonomically broad and early study of Parsons (1896) on the myology of rodents included only two bathyergid specimens, one *B. suillus* and one Cape mole-rat, *Georychus capensis*. Later, Cuthbert (1975) assessed the cranial and forelimb musculature of the same two species, although such descriptions remain unpublished. More recently, Sahd et al. (2019, 2020) assessed the effects of hind-foot drumming in the hindlimb musculature of three bathyergids, *B. suillus*, *G. capensis*, and the common mole-rat *Cryptomys hottentotus hottentotus*, while Doubell et al. (2020) and Sahd et al. (2023) assessed differences in the forelimb musculature, muscle architecture and fiber-type composition of *B. suillus* and the naked mole-rat *Heterocephalus glaber*. The latter studies reported skeletal and myological differences between such species and attributed them to their distinct digging modes, i.e., the forelimb of *B. suillus* has relatively larger and additional forelimb muscles with higher muscle mass percentage and more robust bones in comparison to *He. glaber*, suggesting a higher specialization for scratch-digging (Doubell et al., 2020; Sahd et al., 2023). However, such comparison, based on two of the most morphologically and ecologically divergent species within the family (see below), raises several questions, such as whether such differences reflect true morphological adaptations to their digging strategies or rather represent differences in other aspects of their biology (e.g. social organization; disparate body size) and/or phylogenetic history.

Recently, a series of comprehensive studies on the long bone anatomy of the Bathyergidae, including all six genera, have reported that (i) mole-rats (except *He. glaber*) possess a set of morphological features to maximize scratch-digging in their humerus, ulna, femur, and tibia-fibula, regardless of digging mode, and (ii) that tooth-diggers can sometimes exhibit even higher indices of morpho-functional specialization than scratch-diggers (Montoya-Sanhueza, Bennett, et al., 2022; Montoya-Sanhueza, Šaffa, et al., 2022). Such results demonstrate comparable limb scratch-digging specializations in the silvery mole-rat *Heliophobius argenteocinereus* and *B. suillus*, for example (Montoya-Sanhueza, Bennett, et al., 2022), the former being a medium-sized

mole-rat that reaches up to 360g, has short foreclaws and burrows in very hard soils (Šumbera et al., 2007). Those unexpected findings could be explained by the fact that tooth-diggers usually exploit more compacted soils than the soft substrates that scratch-diggers use, which would drive the selection of enhanced robustness of their appendicular skeleton for body support and forward (propulsive) force generation during tooth-digging (Montoya-Sanhueza, Bennett, et al., 2022; Montoya-Sanhueza, Šaffa, et al., 2022).

Additionally, although the long bones of most bathyergids are represented by a set of similar synapomorphies associated with increased fossoriality, *He. glaber* stands out by its unique phenotype lacking several of the typical skeletal adaptations that characterizes this family, e.g., a deltoid tuberosity in the humerus and tibio-fibular fusion (Montoya-Sanhueza, Bennett, et al., 2022; Montoya-Sanhueza, Šaffa, et al., 2022). Such a divergent and 'less specialized' skeletal phenotype suggests significantly reduced limb specializations in *He. glaber* as compared with other tooth-diggers of the same family, as well as with other subterranean rodents, such as tuco-tucos, cururos, and blind mole rats (Montoya-Sanhueza, Šaffa, et al., 2022). This evidenced that the appendicular system of *He. glaber* is not representative of the typical bathyergid tooth-digging form, and also differs from other subterranean mammals. For this reason, it has been hypothesized that its disparate limb phenotype might not reflect distinctly functional adaptations to a specific digging mode, and that other phylogenetic, developmental and/or ecological factors may also be involved (Montoya-Sanhueza, Šaffa, et al., 2022). In fact, numerous

studies have reported the remarkable intraspecific variation and phenotypic plasticity of *He. glaber* (see Montoya-Sanhueza, Šumbera, et al., 2022, and references therein). Consequently, two-species comparisons including naked mole-rats must consider such biases before making direct functional correlations and interpretations between digging mode and morphological specialization (or lack of it).

Considering these latter studies, the limb musculature of some bathyergid tooth-diggers should reflect accordingly similar levels of specialization as scratch-diggers. However, deductions on structure and function in this family are not straightforward (see Doubell et al., 2020; Montoya-Sanhueza, Bennett, et al., 2022). Increasing our knowledge on the musculoskeletal system of bathyergids will greatly help understand their morphological patterns, as well as unravel how fossorial adaptations have evolved in this family. The main goal of this study is to determine the phenotypic differences in the forelimb musculoskeletal system of scratch-digging and tooth-digging bathyergids using a broader phylogenetic sample than previous studies, and analyze such diversity in light of the recent morpho-functional investigations of their cranial and postcranial anatomy, and digging behavior (Figure 1).

2 | MATERIALS AND METHODS

The forelimb musculature of all four solitary bathyergids was investigated: *B. suillus* ($n = 5$), *B. janetta* ($n = 5$), *H. argenteocinereus* ($n = 7$),

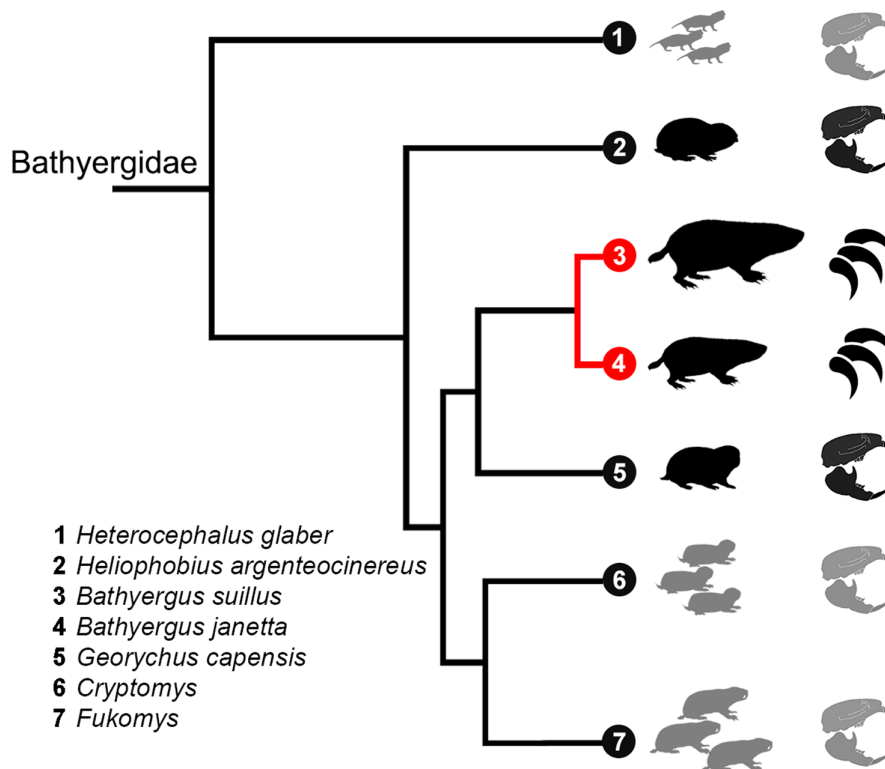


FIGURE 1 Simplified phylogeny of Bathyergidae including all six genera and the four species studied here (black shades). Social species are indicated by group symbols, and solitary species are indicated by a single mole-rat symbol. The emergence of scratch-digging taxa is indicated by red branches. Tree modified from Uhrová et al. (2022).

and *G. capensis* ($n = 5$) (Table 1). As *Heliophobius* and *Georychus* are monotypic genera, they are henceforth referred to by their genus name. *Bathyergus suillus* is endemic to sandy soils of the southern and southwestern coastal regions of South Africa (Bennett et al., 2009), whereas *B. janetta* inhabits the arid and sandy regions of Namaqualand and the southwestern coast of Namibia (Herbst & Bennett, 2006). *Georychus* has a disjunct distribution across South Africa in coastal dunes and sandy deposits along rivers and intermontane valleys of the Western Cape, southwestern KwaZulu-Natal, and in Mpumalanga (Visser et al., 2017). *Heliophobius* inhabits a wide range of habitats in East Africa, including those with seasonally very hard soils to those with light farmland soils, being one of the most widely distributed bathyergids, occurring in southern Kenya, Tanzania, southeast D. R. Congo, eastern Zambia, Malawi, and northern Mozambique (Bryja et al., 2018; Šumbera et al., 2007). The inclusion of *Heliophobius* into our analysis, which represents the second split in the bathyergid phylogeny after the basal *He. glaber* is of special relevance because recent studies have suggested that the synapomorphies associated with increased fossoriality in this family (i.e. fully fossorial appendicular skeleton) may have appeared in the ancestors leading to this genus and the remaining mole-rats (Montoya-Sanhueza, Šaffa, et al., 2022). Additionally, the postcranial anatomy of *Heliophobius* has been largely overlooked.

Specimens were obtained from the collections of the Department of Zoology (University of South Bohemia, České Budějovice, Czech Republic) and the University of Pretoria (Pretoria, South Africa). All specimens came from the wild (Table 1), although some of them were kept in captivity after their collection. The adult status was determined based on body mass, using the minimum mass reported for female adults of each species: 589 g for *B. suillus* (Bennett et al., 2009); 271 g for *B. janetta* (Herbst & Bennett, 2006); 118 g for *H. argenteocinereus* (Šumbera et al., 2007) and 121 g for *G. capensis* (Visser et al., 2017). Thus, the musculature of most adults was studied, and only two specimens (BJ005 and HAM001) were slightly below the minimum mass reported for an adult, whereby they were considered subadults (see Table 1). Although both sexes were analyzed, no sexual dimorphism was assessed in this study.

We studied the main muscles of the shoulder, arm, and forearm involved in parasagittal scratch-digging behavior, as well as some of the most superficial (extrinsic) neck muscles (Table 2). The muscles of the pectoral region (e.g. mm. pectorales) were not examined, since several of our specimens were used in previous studies that destroyed considerably their ventral region, including their thoracic muscles. The musculoskeletal anatomy was described following the traditional terminology used for rodents, e.g. Parsons (1894, 1896), Greene (1935), Klingener (1964) and Woods (1972), and contrasted primarily with recent studies dealing with bathyergids (Doubell et al., 2020), cavioids (García-Esponda et al., 2021) or general hystricomorph myology (Gambaryan et al., 2013). We tried to follow as much as possible the myological scheme of the *Nomina Anatomica Veterinaria* (Gasse et al., 2017) and Böhmer et al. (2021), the latter of which condenses the limb myology of a wide diversity of

mammalian species. A list of different muscle names (synonyms and non-synonyms) used by other authors is also provided in the Results section to facilitate comparison among different sources. Origin and insertion attachments were determined for all forelimb muscles, except for the most extrinsic muscles connecting the shoulder and neck regions (e.g. m. latissimus dorsi, m. trapezius pars thoracica), because some specimens (e.g. *G. capensis*, *H. argenteocinereus*) had torn muscles due to decapitation. Muscle maps for the origin and insertion of each muscle were generated for each species. The muscle attachment on a bone that is less movable for action was termed origin (usually the most proximal attachment relative to the joint crossed), and the attachment on a bone that is more movable was its insertion (usually the most distal attachment relative to the joint crossed) (Böhmer et al., 2021; Howell, 1965). Because the function of each muscle slightly varies according to species and digging mode, a purported (hypothesized) action for bathyergids was determined comparing different sources including a wide diversity of scratch-digging fossorial mammals, such as pocket gophers (Holliger, 1916), badgers (Moore et al., 2013), armadillos (Marshall et al., 2021; Olson et al., 2016), and marsupials (Jenkins & Weijs, 1979; Warburton et al., 2014), as well as by manual estimation of their actions during dissection. Muscle names, functions, and abbreviations are presented in Table 2.

Dissections were performed on either the right or left limb following standard techniques and equipment (e.g. Marshall et al., 2021). All specimens were stored in 70% ethanol, although some of them were previously stored in 5% formalin. Forelimbs were skinned, and muscles were systematically dissected from proximal to distal beginning, starting from the extrinsic muscles of the neck to the innermost intrinsic muscles of the antebrachium and hand. Muscle bellies were identified along with the documentation of their origins, insertions and estimation of their actions. During dissections, muscles were regularly hydrated with phosphate-buffered saline (PBS) solution to prevent desiccation. The musculature was examined with the naked eye and using a binocular stereomicroscope (Arsenal STM 802). Several photographs were taken for each muscle location and belly using an Olympus E450 digital camera, and which were used to construct muscle maps and illustrations of forelimb muscle topography.

We also included a detailed description of relevant skeletal material (scapula and ulna). A description of the humerus (and other long bones) of all bathyergid genera is reported elsewhere (Montoya-Sanhueza, Bennett, et al., 2022; Montoya-Sanhueza, Šaffa, et al., 2022). After dissecting all muscles, the scapula, humerus and ulna were prepared and skeletonized for osteological comparison, and used as the basis for the illustrations. Forelimb bones of two additional individuals of *B. suillus* (BS286, BS287), two individuals of *Georychus* (GC291, GC292), and two individuals of *Heliophobius* (HAM010, HAM011) were also skeletonized and added to the osteological comparisons (Table 1). We follow the updated skeletal nomenclature of recent studies (Montoya-Sanhueza, Bennett, et al., 2022; Montoya-Sanhueza, Šaffa, et al., 2022, and references therein). Due to the complex scapular morphology found

TABLE 1 Morphological and behavioral characteristics of the Bathyergidae analyzed here, including digging mode, sex and body mass (BM).

Common name	Species	ID	Digging mode	Sex	BM (g)
Cape dune mole-rat	<i>Bathyergus suillus</i>	BS282	Scratch-digging	Female	603
Cape dune mole-rat	<i>Bathyergus suillus</i>	BS284	Scratch-digging	Male	1201
Cape dune mole-rat	<i>Bathyergus suillus</i>	BS285	Scratch-digging	Female	658
Cape dune mole-rat	<i>Bathyergus suillus</i>	BS288	Scratch-digging	Female	665
Cape dune mole-rat	<i>Bathyergus suillus</i>	BS547	Scratch-digging	Male	964
Cape dune mole-rat	<i>Bathyergus suillus</i>	BS286*	Scratch-digging	Female	697
Cape dune mole-rat	<i>Bathyergus suillus</i> (S)	BS287*	Scratch-digging	Female	524
Namaqua dune mole-rat	<i>Bathyergus janetta</i>	BJ003	Scratch-digging	Male	356
Namaqua dune mole-rat	<i>Bathyergus janetta</i>	BJ004	Scratch-digging	Female	442
Namaqua dune mole-rat	<i>Bathyergus janetta</i> (S)	BJ005	Scratch-digging	Female	242
Namaqua dune mole-rat	<i>Bathyergus janetta</i>	BJ006	Scratch-digging	Male	448
Namaqua dune mole-rat	<i>Bathyergus janetta</i>	BJ007	Scratch-digging	Male	690
Silvery mole-rat	<i>Heliophobius argenteocinereus</i> (S)	HAM001	Chisel-tooth digging	Female	113
Silvery mole-rat	<i>Heliophobius argenteocinereus</i>	HA244	Chisel-tooth digging	Male	207.5
Silvery mole-rat	<i>Heliophobius argenteocinereus</i>	HA476	Chisel-tooth digging	Male	137.6
Silvery mole-rat	<i>Heliophobius argenteocinereus</i>	HA622	Chisel-tooth digging	Female	214.3
Silvery mole-rat	<i>Heliophobius argenteocinereus</i>	HA713	Chisel-tooth digging	Female	214.8
Silvery mole-rat	<i>Heliophobius argenteocinereus</i>	HA718	Chisel-tooth digging	Female	162.6
Silvery mole-rat	<i>Heliophobius argenteocinereus</i>	HA733	Chisel-tooth digging	Male	185.4
Silvery mole-rat	<i>Heliophobius argenteocinereus</i>	HA010*	Chisel-tooth digging	Female	120
Silvery mole-rat	<i>Heliophobius argenteocinereus</i>	HAM011*	Chisel-tooth digging	Female	202
Cape mole-rat	<i>Georychus capensis</i>	GC005	Chisel-tooth digging	Female	245
Cape mole-rat	<i>Georychus capensis</i>	GC008	Chisel-tooth digging	Female	182
Cape mole-rat	<i>Georychus capensis</i>	GC011	Chisel-tooth digging	Female	145
Cape mole-rat	<i>Georychus capensis</i>	GC014	Chisel-tooth digging	Male	150
Cape mole-rat	<i>Georychus capensis</i>	GC018	Chisel-tooth digging	Female	148
Cape mole-rat	<i>Georychus capensis</i>	GC291*	Chisel-tooth digging	Female	248
Cape mole-rat	<i>Georychus capensis</i>	GC292*	Chisel-tooth digging	Male	202

Note: The skeletal material was obtained from the individuals marked with an asterisk (*). Only three subadults (S) were included in this study.

among bathyergids, a schematic representation of this bone showing its most relevant structures is also presented in Figure 2. All schematic representations including muscle maps and other anatomical structures, were made and edited in Photoshop (Adobe Inc., 2015).

3 | RESULTS

3.1 | Skeletal anatomy

Scapula (Figures 2, 3). All species have a triangular scapula, although the scapula of *Heliophobius* and *Georychus* is slender and more elongated with smaller supraspinous and infraspinous fossae as compared to that of *Bathyergus*, which is more robust and equilateral, i.e. the vertebral border of *Bathyergus* is as long as the caudal border, while the caudal border of tooth-diggers is longer than the vertebral border. In all species, the supraspinous fossa is smaller than

the infraspinous fossa, although this is much more pronounced in *Heliophobius* and *Georychus*. The cranial, vertebral, and caudal borders of all species are thickened, allowing a larger surface area for muscle attachment. Also, the lateral surface of the scapula of all species is divided by a well-developed scapular spine, which develops close to the vertebral border, and projects prominently around the center of the scapula in *Heliophobius* and *Georychus*, and more closer to the scapular neck in *Bathyergus* (see below). The projection of the scapular spine is robust in all species, particularly in *Bathyergus* allowing a wide surface area for the attachment of m. trapezius pars cervicalis, m. trapezius pars thoracica and m. deltoideus pars scapularis, although the thickness of the spine can also vary considerably in *Heliophobius* (Figure 3c).

One of the most conspicuous morphological differences among species is the proximal tip of the scapular spine, which consists of a simplified acromion process (AP) in *Bathyergus*, while it is divided into an AP and a metacromion process (MP) in *Heliophobius* and

TABLE 2 Muscles analyzed in this study, including its origin, insertion, and proposed function in African mole-rats: *Bathyrergus suillus* (Bs), *Bathyrergus janetta* (Bj), *Heliophobius argenteocinerus* (Ha) and *Georychus capensis* (Gc).

Species	Muscle	Acronym	Origin	Insertion	Main function
Extrinsic muscles					
Bs, Bj, Ha, Gc	Trapezius pars thoracica	TT	*Spines of the thoracic and lumbar vertebrae (T4-L3)	Proximal tip of projection of scapular spine (angle)	Scapular retractor/elevator/stabilizer
Bs, Bj	Rhomboideus cervicis + Rhomboideus thoracis	RC+RT	*From the spinous processes of cervical and thoracic vertebrae (C1-C5 and C1-C2, respectively)	Middle of vertebral border, sometimes reaching the teres major process region.	Neck elevator, shoulder extension, scapula adduction/protraction/stabilizer
Ha, Gc	Rhomboideus cervicis + Rhomboideus thoracis	RC+RT	*From the spinous processes of cervical and thoracic vertebrae (C1-C5 and C1-C2, respectively)	Distal vertebral border, always reaching the teres major process region.	Neck elevator, shoulder extension, scapula adduction/protraction/stabilizer
Bs, Bj, Ha, Gc	Rhomboideus capitis	RCP	*Laterodistal part of the lambdoid suture (dorsal to the ear region)	From vertebral angle to scapular spine, sometimes extending to infraspinous fossa	Neck elevator, shoulder extension, scapula adduction/protraction/stabilizer
Intrinsic Shoulder muscles					
Bs, Bj, Gc	Deltoides pars scapularis	DS	Caudal border of projection of scapular spine and fascia of ISP	Deltoid tuberosity of humerus, proximo-lateral side	Shoulder flexion, humeral abductor/lateral rotator
Ha	Deltoides pars scapularis	DS	Caudal border of projection of scapular spine	Deltoid tuberosity of humerus, proximo-lateral side	Shoulder flexion, humeral abductor/lateral rotator
Bs, Bj, Ha	Deltoides pars acromialis	DA	Acromion process (sometimes clavicle tip)	Deltoid tuberosity of humerus, craniolateral side	Shoulder flexion, humeral abductor/lateral rotator
Gc	Deltoides pars acromialis	DA	Acromion process (sometimes clavicle tip), and ventral side of metacromion	Deltoid tuberosity of humerus, craniolateral side	Shoulder flexion, humeral abductor/lateral rotator
Bs, Bj, Ha, Gc	Deltoides pars clavicularis	DC	Great part of the clavicle (ventrally), sometimes reaching the acromion	Deltoid tuberosity of humerus, medial side	Shoulder flexion, humeral adductor/medial rotator
Bs, Bj	Supraspinatus	SSP	Supraspinous fossa (up to the scapular neck) and scapular spine	Greater and lesser tubercles of humerus	Shoulder extension, humeral stabilizer
Ha, Gc	Supraspinatus	SSP	Supraspinous fossa (up to the scapular neck), scapular spine and acromion	Greater tubercle of humerus	Shoulder extension, humeral stabilizer
Bs, Bj, Ha, Gc	Infraspinatus	ISP	Infraspinous fossa and scapular spine	Greater tubercle of the humerus (proximal to TMN)	Shoulder flexion, humeral stabilizer

(Continues)

TABLE 2 (Continued)

Species	Muscle	Acronym	Origin	Insertion	Main function
Bs, Bj, Ha, Gc	Subscapularis	SUB	Subscapular fossa (until the scapular neck and coracoid process) including almost all borders of scapula	Lesser tubercle of humerus	Scapular adduction, humeral stabilizer
Bs, Bj, Ha, Gc	Teres minor	TMN	Caudal border of scapula, from glenoid fossa up to the beginning of teres minor process	Greater tubercle of the humerus (distal to ISP)	Shoulder flexion, humeral stabilizer, lateral humeral rotator
Bs, Bj, Ha, Gc	Teres major	TMJ	Caudal border and caudal angle of scapula, at the teres major process	Caudomedial side of teres tuberosity, proximal to deltoid tuberosity and distal from humeral head (lesser tubercle)	Shoulder flexion
Brachium					
Bs, Bj, Ha, Gc	Triceps brachii caput longum	TBLO	Caudal border of scapula, from scapular neck (teres minor facet) to the center of the same caudal border	Caudomedial tip of olecranon	Shoulder flexion, elbow extension
Bs, Bj, Ha, Gc	Triceps brachii caput laterale	TBLA	Greater tubercle, distal to TMN, and extending caudally around the distal part of humeral head	Lateral side of olecranon process	Shoulder flexion, elbow extension
Bs, Bj, Ha, Gc	Triceps brachii caput mediale	TBM	Caudomedial humeral diaphysis, in teres tuberosity	Medial side of olecranon process	Elbow extension
Bs, Bj, Ha, Gc	Anconeus	ANC	Distal caudal side of humeral diaphysis, along lateral epicondyle	Cranial surface of olecranon and anconeal processes	Elbow extension
Bs, Bj, Ha, Gc	Triceps brachii caput medial accessorium anconeus	TBMAA	Caudomedial epicondyle of humerus	Medial side of olecranon process	Elbow extension
Bs, Bj, Gc (absent in Ha)	Tensor fasciae antebrachii	TFA	Fascia of the insertion region of m. latissimus dorsi	External fascia of the olecranon process (medially)	Elbow extension, humeral retractor/adductor
Bs, Bj, Ha, Gc	Biceps brachii	BB	Two parts: long part (tendon) in the supraglenoid tubercle in scapula; and short part in coracoid process (ventrally)		Shoulder extension, elbow flexion
Bs, Bj, Gc	Brachialis (external part)	BCHe	Proximal caudolateral humeral diaphysis and humeral head neck	Medial surface of proximal ulna (close to coronoid process)	Elbow flexion, forearm pronator
Ha	Brachialis (external part)	BCHe	Proximal caudolateral humeral diaphysis and humeral head neck	Medial surface of proximal ulna (close to coronoid process), sometimes in radius	

TABLE 2 (Continued)

Species	Muscle	Acronym	Origin	Insertion	Main function
Bs, Bj, Ha, Gc	Brachialis (internal part)	BCHI	Distal to deltoid tuberosity (cranial humeral surface)	Cranial surface of the ulna (close to coronoid process)	Elbow flexion
Bs, Bj (absent in Ha, Gc)	Articularis humeri	AH	Coracoid process, deep to m. biceps brachii	Teres tuberosity (superficial to TMJ), towards deltoid tuberosity level (cranio-medially)	Humeral adduction
Antebrachium					
Bs, Bj, Ha, Gc	Pronator teres	PT	Proximal craniomedial epicondyle of humerus	Midshaft of radius (medially)	Forearm pronation
Bs, Bj, Ha, Gc	Flexor carpi radialis	FCR	Medial epicondyle of humerus (distal to PT)	Proximal end of metacarpal III	Wrist flexion
Bs, Bj, Ha, Gc	Flexor carpi ulnaris caput ulnare + humerale	FCU	Medial side of olecranon process and medial epicondyle	Accessory carpal bone and palmar aponeurosis	Wrist flexion
Bs, Bj, Gc	Palmaris longus	PL	Distal tip of medial epicondyle, and distal tip of olecranon (proximal to FCU)	Superficial layer of palmar aponeurosis	Wrist and digital flexion
Ha	Palmaris longus	PL	Cranial tip of medial epicondyle	Superficial layer of palmar aponeurosis	Wrist and digital flexion
Bs, Bj, Ha, Gc	Flexor digitorum superficialis	FDS	Most distal part of medial epicondyle (deep to FCU), mostly extending caudally and ventrally	Middle phalanx of digits II-IV (ventrally)	Wrist and digital flexion
Bs, Bj, Gc	Flexor digitorum profundus	FDP	Medial epicondyle of humerus, medial aspect of olecranon, medial and lateral ulnar diaphysis, and proximal radius	Distal phalanges of digits II-V (ventrally)	Wrist and digital flexion
Ha	Flexor digitorum profundus	FDP	Medial epicondyle of humerus, medial aspect of olecranon, medial and lateral ulnar diaphysis	Distal phalanges of digits II-V (ventrally)	Wrist and digital flexion
Bs, Bj, Gc	Extensor carpi radialis longus + brevis	ECRL/B	Proximalateral side of humeral epicondyle (deepest extensor)	Bases of metacarpals II and III	Wrist and digital extension
Ha	Extensor carpi radialis longus + brevis	ECRL/B	Proximalateral side of humeral epicondyle (deepest extensor)	Bases of metacarpals II and III, sometimes a third tendon inserted carpal bones	Wrist and digital extension
Bs, Bj, Ha	Extensor digitorum communis	EDC	Lateral epicondyle of humerus, and proximal tip of radius	Middle and distal phalanges of digits II-V	Wrist and digital extension
Gc	Extensor digitorum communis	EDC	Lateral epicondyle of humerus	Middle and distal phalanges of digits II-V	Wrist and digital extension

(Continues)

TABLE 2 (Continued)

Species	Muscle	Acronym	Origin	Insertion	Main function
Bs, Bj, Ha, Gc	Extensor digitorum lateralis	EDL	Lateral side epicondyle of humerus, olecranon, trochlear notch and radius (most superficial extensor)	Distal phalanges of digits IV-V	Wrist and digital extension
Bs, Bj, Ha	Extensor carpi ulnaris	ECU	Olecranon (lateral), humeral epicondyle (inferior part and deep to EDL), ulnar fossa almost to the midshaft	Base of metacarpal V (ventrally)	Wrist and digital extension, wrist supination
Gc	Extensor carpi ulnaris	ECU	Olecranon (lateral), humeral epicondyle (distal part and deep to EDL), ulnar fossa below trochlear notch	Base of metacarpal V (ventrally)	
Bs, Bj, Ha, Gc	Supinator	SUP	Lateral epicondyle of humerus	Cranio-medial surface of radius	Forearm supination
Bs, Bj, Ha, Gc	Pronator quadratus	PQ	Medial surface of ulna	Cranio-medial surface of radius	Forearm pronation
Bs, Bj, Gc	Extensor digiti 1	ED1	Lateral ulnar and radial mid-diaphysis (interosseous ligament) (inferior to AD1L)	Distal phalanx of digit I (medially)	Wrist and digital extension
Ha	Extensor digiti 1	ED1	Lateral ulnar mid-diaphysis (inferior to AD1L)	Distal phalanx of digit I (medially)	Wrist and digital extension
Bs, Bj, Ha, Gc	Abductor digiti 1 longus	AD1L	Trochlear notch, proximal cranio-lateral ulna, caudolateral radius, and interosseous ligament (superior to ED1)	Base of metacarpal of the digit I (medially)	Wrist and digital extension

Note: (*) The asterisk indicates the origin of the extrinsic muscles for *B. suillus* and *G. capensis*, obtained from Doubell et al. (2020) and Parsons (1896).

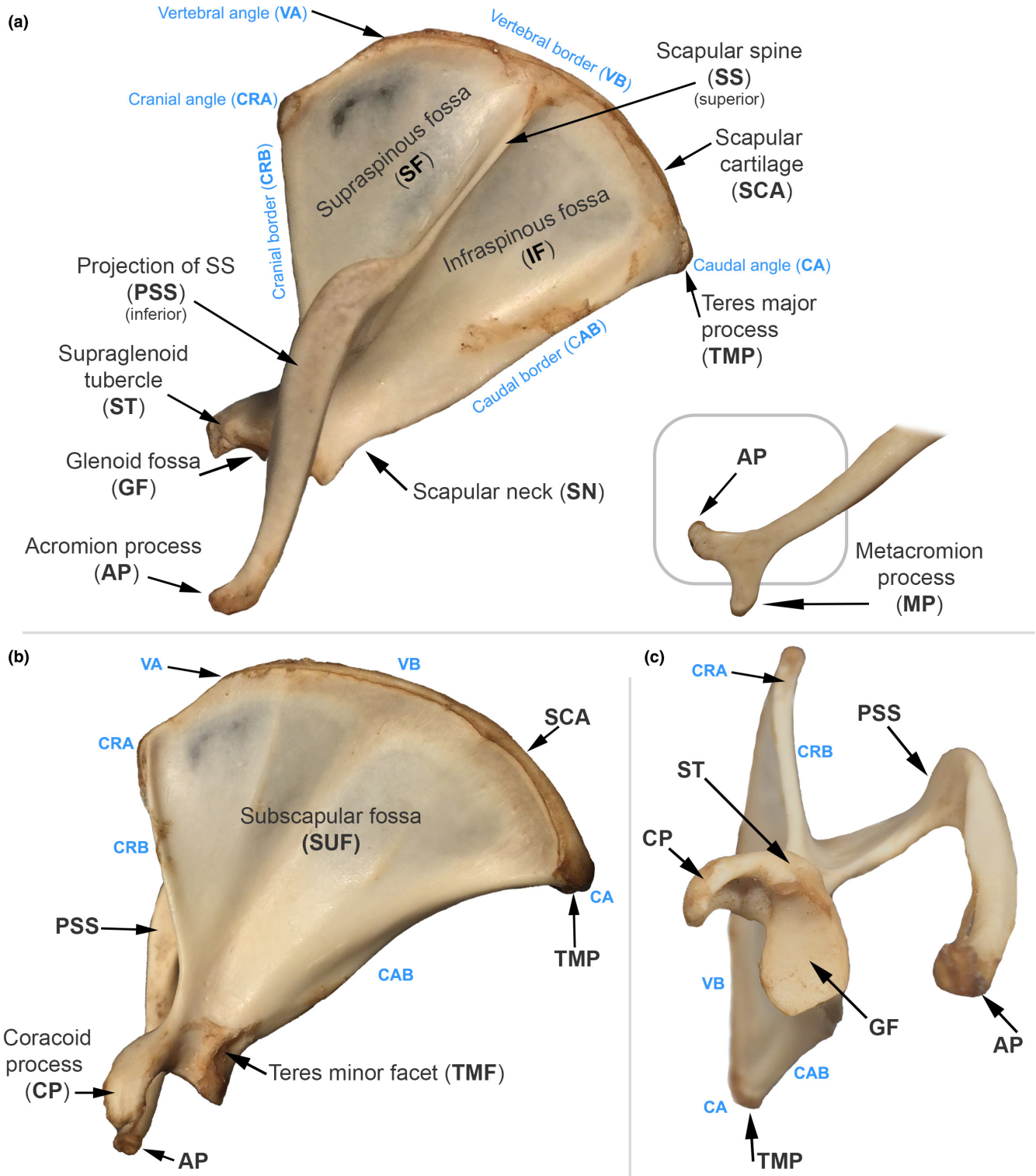


FIGURE 2 Anatomy of the scapula of *Bathyergus suillus* in lateral (a), medial (b), and cranial (c) view. The illustration showing the metacromion process (MT) corresponds to *Heliophobius argenteocinereus*.

Georychus (elsewhere referred as hamate and suprahamate processes, respectively, see Doubell et al., 2020; Onwuama et al., 2015). Some individuals of *Heliophobius* showed a variable degree of division of the AP and MP (Figure 3c), while the individuals of *Georychus* have a less defined MP (Figure 3d). Our observations agree with previous reports for *B. suillus* having a simple AP (Doubell et al., 2020).

Thus, the tip of the scapular spine of *Bathyergus* is considerably less robust than that of *Heliophobius* and *Georychus*.

The projection of the scapular spine also surpasses the glenoid fossa in all species. Such distance appears to be quite similar between *B. suillus* and *Georychus* (Cuthbert, 1975). The teres major process (TMP) is well-developed in all species, clearly projecting

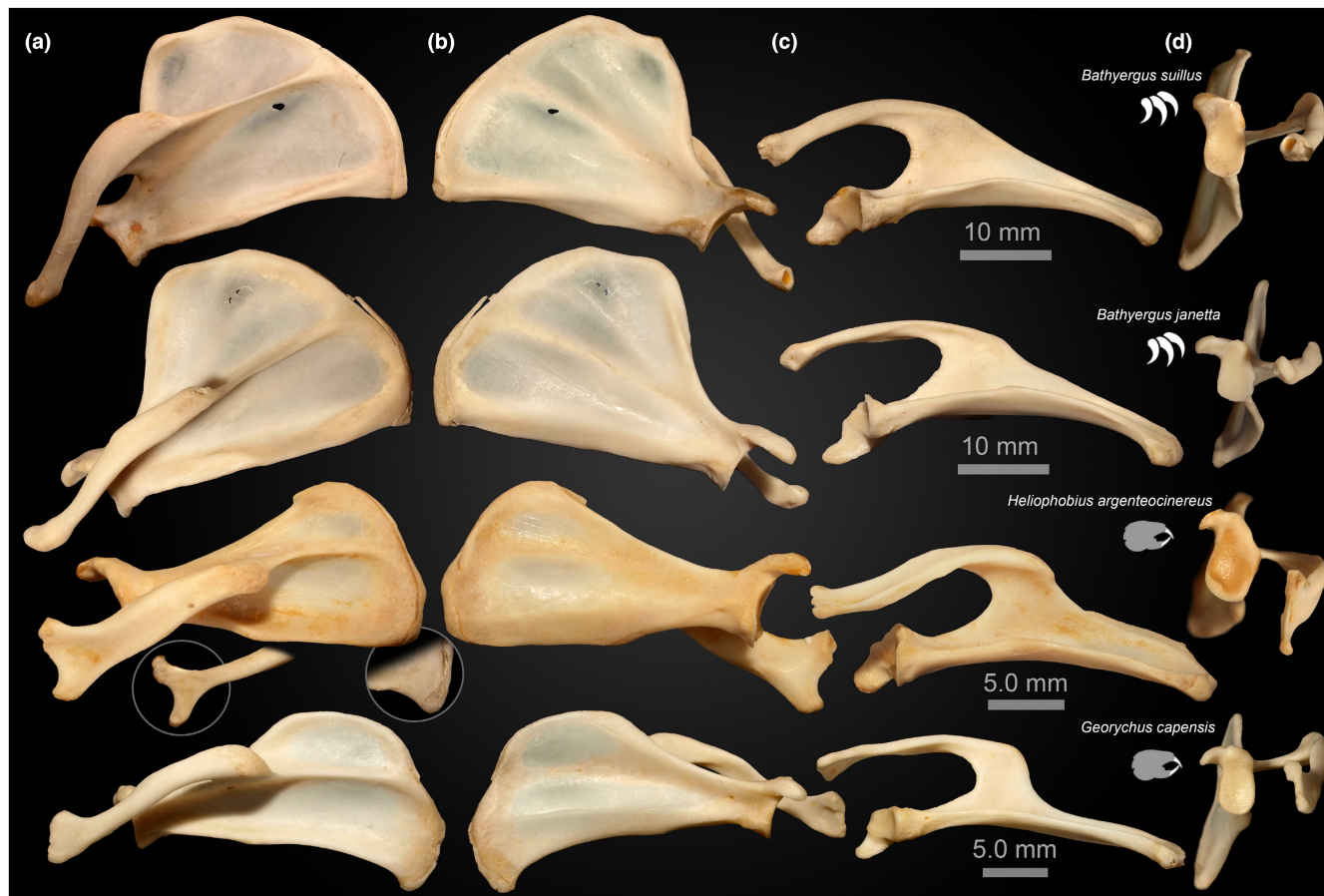


FIGURE 3 Scapula of solitary bathyergids in lateral (a), medial (b), ventral (c), and cranial (d) view.

ventrally from the caudal angle of the scapula, although some individuals of *Heliophobius* showed a less conspicuous TMP. In the middle of the caudal border, a protuberance was observed in all species, although this appears more developed in some individuals than in others (Figure 2a,b). Similarly, the vertebral border of the scapula of *Bathyergus* and *Heliophobius* exhibits an additional protuberance that forms the vertebral angle (Figure 2a,b), although this is poorly distinguished in *Georychus*. A similar protuberance, but even more developed than in bathyergids has been observed in armadillos, e.g. *Chaetophractus villosus* and *Zaedyus pichiy* (Acuña et al., 2017; Marshall et al., 2021). On the medial side of the scapula, the subscapular fossa is relatively flat and similar among all four species. The entire scapula is slightly concave (medially) in all four species. Overall, the scapula of *Bathyergus* resembles the general shape of some armadillos's scapula (Marshall et al., 2021; Miles, 1941).

In ventral view, it is possible to observe that the projection of the scapular spine of *Bathyergus* forms a broad base covering a wide area in the centroproximal region of the scapula, almost reaching the glenoid region, while in *Heliophobius* and *Georychus* it is narrower and restricted to the center of the scapula (Figure 3c). Such protracted origin of the scapular spine in *Bathyergus* makes its scapular neck appearing shorter, but more robust than in the other taxa.

In cranial view, the scapular spine of *Bathyergus* appears to be less oriented downwards as compared to *Heliophobius* and *Georychus* (Figure 3d). All species have a relatively similar ellipsoidal glenoid fossa (dorso-ventrally) and a conspicuous coracoid process, which extends cranio-medially. The size of the coracoid process in *B. suillus* and *Georychus* appears to be quite similar (Cuthbert, 1975). Also, the cranial border of the scapula, close to the cranial angle, widens in *Bathyergus* and *Heliophobius* (and only slightly in *Georychus*) allowing a larger area for the attachment of the muscles of this region (e.g. m. supraspinatus).

Ulna (Figure 4). All species exhibited a similar ulna in terms of overall proportions and morphology; quite elongated, straight and particularly thick below the trochlear notch. Despite all species showing a straight ulna without major curvatures in its diaphysis, the olecranon process (OP) of *Bathyergus* is notably oriented medially, thus increasing its overall "apparent" curvature and line of action for certain muscles. Another conspicuous difference among species was the development of a triangular and wide cranial surface area in the OP of *Bathyergus*, which considerably increases the area for the insertion of the m. anconeus and mm. triceps brachii. The OP of *Heliophobius* and *Georychus* is more rectangular and elongated, although some specimens of *Heliophobius* also showed a wide dorsal area. Additionally, the cranial surface of the ulnar diaphysis (around the midshaft) of *Heliophobius*

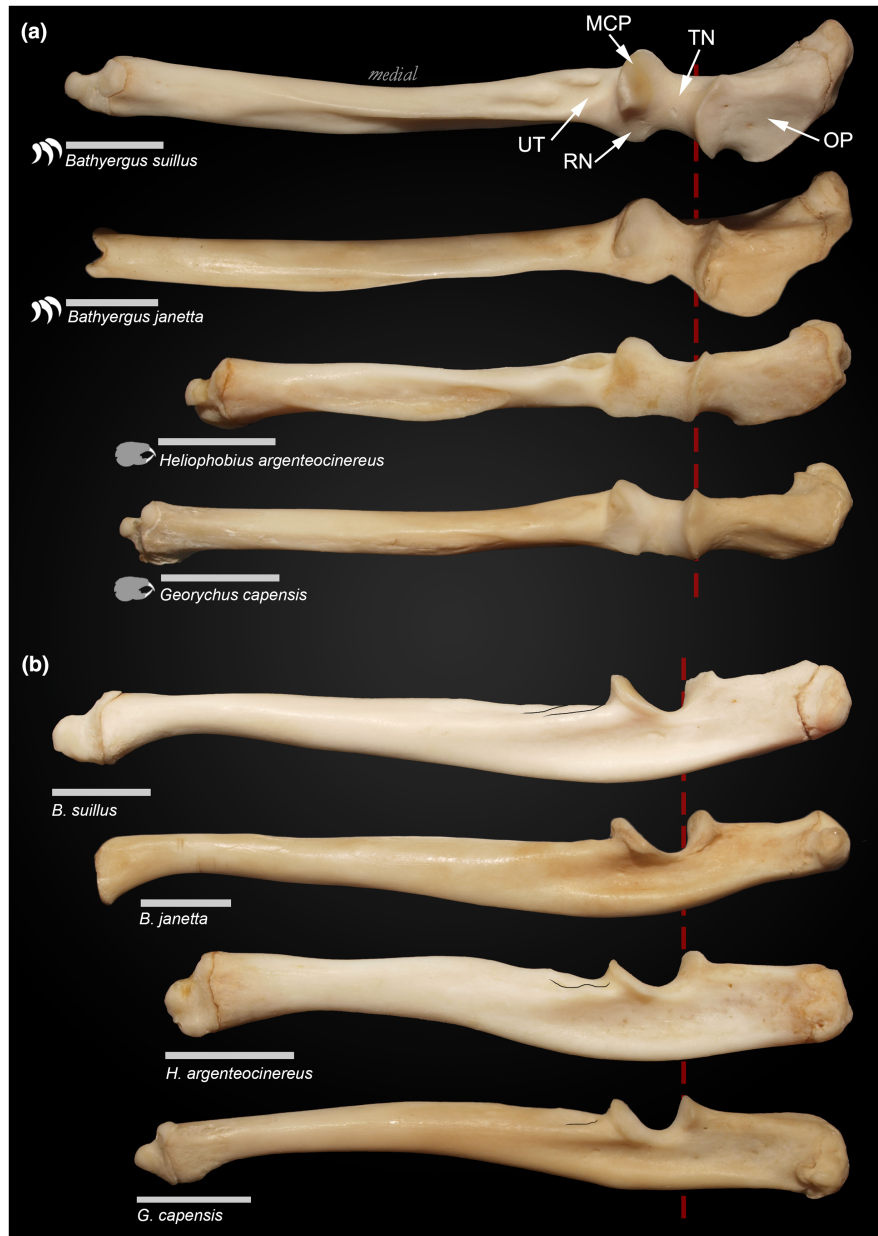


FIGURE 4 Ulna of solitary bathyergids in cranial (a) and medial (b) view. Close to the ulnar tuberosity (UT) two sulci (outlined as black lines in “b”) for the attachment of the *m. biceps brachii* and *m. brachialis* are observed in *Bathyergus*, while tooth-diggers showed a single and less differentiated sulcus. MCP, Medial coronoid process; OP, olecranon process; RN, radial notch; TN, trochlear notch. Scales: 5 mm.

and *Georychus* has a large contact zone with the caudal surface of the radius, with some individuals showing a flat surface due to the proximity/connection with the radius (Figure 4a). This level of bone–bone contact is not observed in *Bathyergus*, where such bones are quite separated. *Bathyergus* has a more laterally protuberant radial notch as compared to *Heliophobius* and *Georychus*, indicating that the radius of *Bathyergus* protrudes more than in the tooth-diggers (Figure 4a). The medial coronoid process is also more pronounced (elevated) in *Bathyergus* (Figure 4b). On the cranial surface of the ulna, close to the ulnar tuberosity, two marked sulci indicate the independent insertions

for the *m. biceps brachii* and *m. brachialis* in *Bathyergus*, while tooth-diggers showed a less marked and single sulcus (Figure 4a).

3.2 | Muscle anatomy

More than 640 muscles corresponding to 37 different neck and forelimb muscles including their corresponding parts were dissected and examined (Table 2). Fused muscles are described together, e.g. *m. rhomboideus cervicis* + *m. rhomboideus thoracis*.

3.3 | Extrinsic muscles

3.3.1 | M. Trapezius pars thoracica (TT) (Figure 5)

(M. dorso-scapularis, inferior posterior trapezius; trapezius inferior; trapezius pars thoracis; trapezius pars ascendens trapezius inferior; trapezius thoracis)

This is an elongated triangular but thin muscle covering a great part of the lumbar and lateral thoracic region. This muscle has a similar organization among species: it originates from the spines of the thoracic and lumbar vertebrae (Parsons, 1896) and inserts onto the tip of the projection of the scapular spine (caudally), in close association with the pars cervicalis. In all species, a thin auricular strip separates from the TT, running ventrally and inserting laterally onto a more superficial muscle the m. cutaneus trunci (=m. cutaneus maximus). The latter muscle is composed by a band of extrinsic muscles running laterally in the body and inserted onto the shoulder (Woods, 1972), where attaches to both the acromion and metacromion in *Heliophobius* and *Georychus*, while only to the acromion in *Bathyergus*. The auricular slip is also present in other rodents (Klingener, 1970; Woods, 1972), variably associated to fascial muscles, and probably acting as a cheekpouch retractor, although in bathyergids it may have a different function due to its insertion onto the extrinsic muscle responsible of retracting the shoulder (Klingener, 1970). Interestingly, the auricular slip is present in *Thryonomys* but absent in *Petromus* (Woods, 1972).

3.3.2 | M. Rhomboideus

This muscle is composed of a variable number of parts in mammals along with several modifications to their origins and insertions (e.g. Böhmer et al., 2021; Ercoli et al., 2015; Marshall et al., 2021; Thorington et al., 1997; Warburton et al., 2014). This group of muscles is found in the dorsal-to-lateral regions of the neck (deep to the m. trapezius pars cervicalis) and usually having a flat and band-like morphology. We follow the nomenclature of Gasse et al. (2017), describing three main parts in mammals: m. rhomboideus cervicis, m. rhomboideus thoracis and m. rhomboideus capitis. The two first parts are generally inserted onto the dorsomedial vertebral border of the scapula and have been suggested to be variably fused and continuous at its origin in the nuchal ligament in most hystricomorphs (Woods, 1972), including bathyergids (Parsons, 1896) and other subterranean rodents such as the zokor *Myospalax* (= *Siphneus*) and the pocket gopher *Thomomys bottae* (Holliger, 1916; Milne-Edwards & Milne-Edwards, 1868; Woods, 1972).

3.3.3 | M. Rhomboideus cervicis (RC) + m. rhomboideus thoracis (RT) (Figure 6)

(RC, M. rhomboideus minor; rhomboideus anterior; rhomboideus cervicis; rhomboideus principal) (RT, M. rhomboideus major; rhomboideus posterior; rhomboideus accesorium)

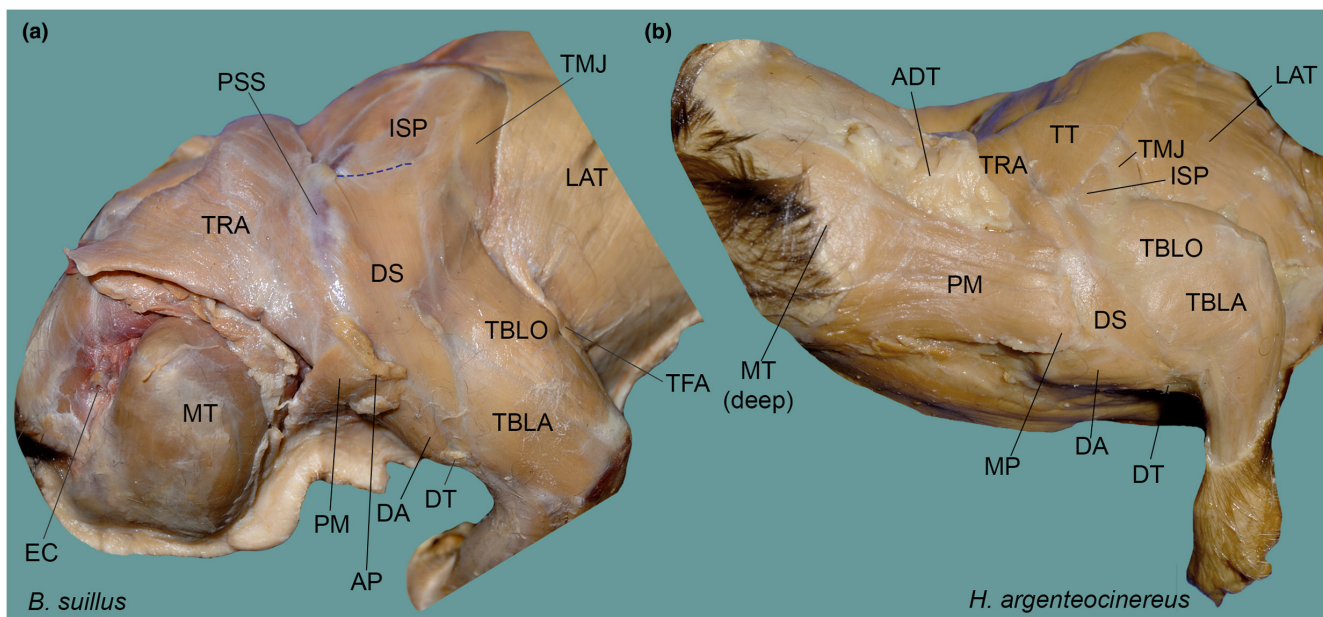


FIGURE 5 Comparative anatomy of superficial neck and forelimb muscles of *Bathyergus suillus* (a) and *Heliophobius argenteocinereus* (b) (in lateral view). The dotted line indicates the extended origin of the m. deltoideus pars scapularis on the surface of the m. infraspinatus in *B. suillus*. See the main abbreviations in Table 2. ADT, adipose tissue; DT, deltoid tuberosity; EC, ear canal; LAT, m. latissimus dorsi; MT, m. masseter; MP, region of the metacromion process; PM, m. platysma myoides TRA, m. trapezius; TT, m. trapezius pars thoracica.

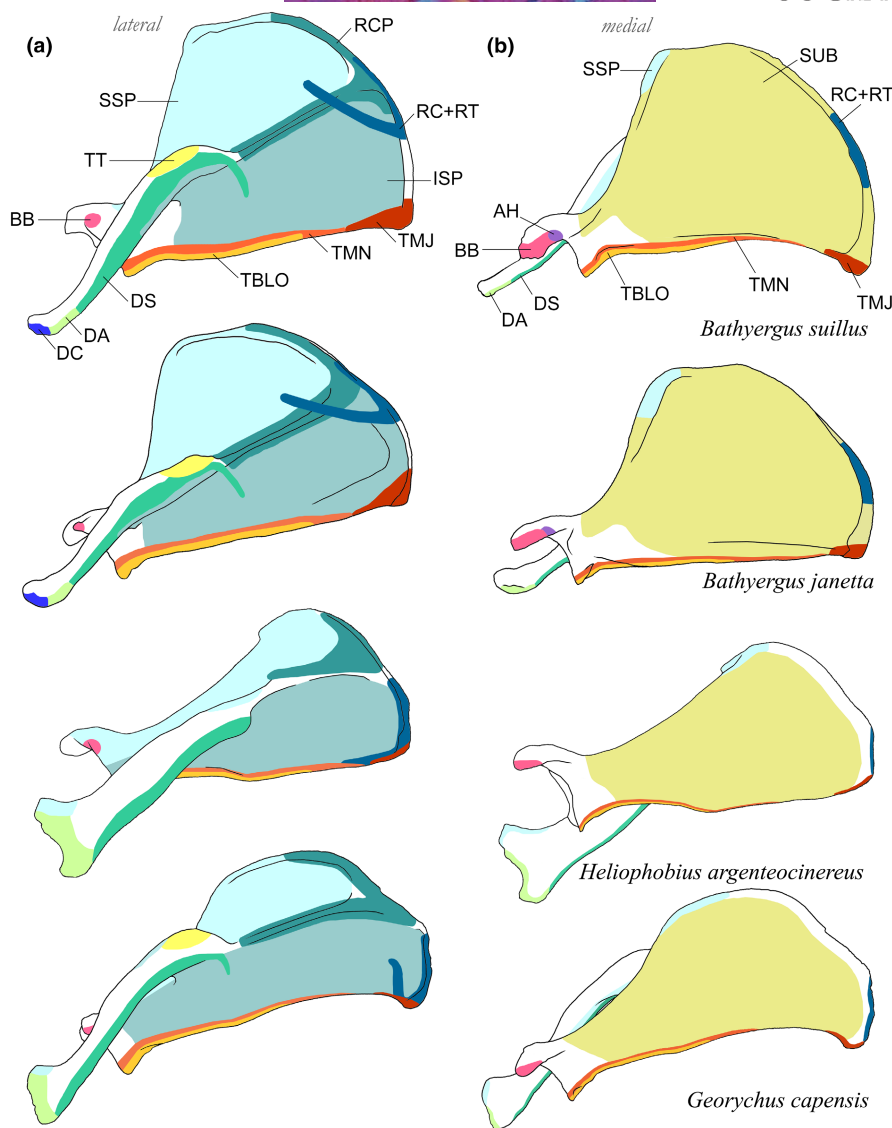


FIGURE 6 Muscle maps of the scapular attachments of solitary bathyergids in lateral (a) and medial (b) view. See the main abbreviations in Table 2 and Figure 5.

These muscles are continuous in their origin and fused at their insertion, and they are also superficial to m. rhomboideus capitis. The cranial part corresponds to the RC, which is considerably larger and well-developed than the caudal part corresponding to RT. Both muscles are continuous at their origins (nuchal ligament) but separable from each other. They are fused at their insertion (around the center of the vertebral border), where both parts are hardly distinguishable. However, the belly of RC is quite large in *Bathyergus* and inserts onto the lateral side of the scapula, forming a U-shaped attachment around the vertebral border, which extends from the vertebral angle to the origin of the scapular spine. This insertion and attachment shape agrees with that of Doubell et al. (2020) for *B. suillus*. In some specimens of *Bathyergus* this insertion extends to the distal part of the vertebral border. This attachment covers (by fascia) a great part of the m. rhomboideus capitis, m. supraspinatus and m. infraspinatus. These muscles have

a different insertion in *Heliophobius* and *Georychus*, onto the caudal part of the vertebral border, from the origin of the scapular spine to the TMP. In *Heliophobius*, the insertion extends along the caudal border, while in *Georychus* it goes vertically crossing superficially the m. infraspinatus. The RT part is smaller but fused to the RC at the insertion, which occurs onto the more medial side of the vertebral border in all species, but more distally in *Heliophobius* and *Georychus*. Parsons (1896) does not specify the insertion of these muscles, although Milne-Edwards & Milne-Edwards (1868) report a medial attachment for the RC in *Myospalax* (= *Siphneus*), whereas Holliger (1916) mentions the attachment of RC and RT onto the medial side of the vertebral border of the scapula in *T. bottae*. Thus, the RC in other rodents and mammals is usually described as having a medial insertion. The different (more lateral) insertion of the RC observed in our specimens may have important consequences for scapular functionality.

3.3.4 | M. Rhomboideus capitis (RCP) (Figure 6)

(M. occipitoscapularis; rhomboideus occipitalis; rhomboideus capitalis; levator scapulae dorsalis; levator scapulae minor)

Large, elongated, and flat muscle originated in the laterodistal part of the lambdoid suture (dorsal to the ear region), which also extends behind the m. masseter. The muscle extends from the neck area to the scapula, specifically to the scapular spine and vertebral angle. In all species, it appears clearly distinct from the m. rhomboideus cervicis, which agrees with the observations of Parsons (1896) for *Bathyergus* and *Georychus*, as well as for other rodents such as geomyids, *Chinchilla*, *Aplodontia*, and squirrels (Gambaryan et al., 2013; Thorington, 1997; Woods, 1972). In all bathyergids, it inserts (laterally) onto the vertebral border, around the vertebral angle and the proximocaudal part of the scapular spine, forming a U-shaped attachment that covers (by fascia) the most caudal part of the m. supraspinatus. The insertion of the RCP is deep to the insertion of m. rhomboideus cervicis. Such insertion was also reported by Parsons (1896) for *Bathyergus* and *Georychus*. This muscle can also cover the dorsal part of the m. infraspinatus, as observed in other rodents (e.g. *Chinchilla*, Gambaryan et al., 2013).

This muscle is well-developed in all species, although slightly larger in *Bathyergus*. However, some specimens of *B. suillus* and *B. janetta* showed a relatively separated muscle along the ventral portion, which was also evident at their insertion onto the scapula. This configuration has not been normally reported for other rodents (but see below), and it may correspond to a distinct muscle, the m. rhomboideus profundus observed in some carnivores (e.g. *Galictis cuja*, Ercoli et al., 2015) and some armadillos (e.g. *Tolypeutes matacus*, Marshall et al., 2021). In *Ga. cuja*, the m. rhomboideus profundus is located ventral to RCP and originates from the caudomedial wing of the atlas, inserting via fascia onto the lateral surface of the m. supraspinatus (Ercoli et al., 2015). Recently, Böhmer et al. (2021) reported four rhomboids for the caviomorph *Octodon degus*, with the m. rhomboideus profundus having a similar attachment configuration to that of *Ga. cuja*. Our specimens did not show an attachment to the atlas, but the unusual insertion of the RCP onto the lateral side of the scapula (superficial to m. supraspinatus) may indicate the presence of fused elements forming a single muscle, as has been reported in armadillos forming the m. rhomboideus profundus et capitis (see Marshall et al., 2021, and references therein). Whether the RCP of bathyergids (and other rodents) is represented by a fusion of such muscles it is unknown, and it deserves additional examination of the entire complex muscular system of the neck and of developmental data.

3.4 | Intrinsic muscles

3.5 | Shoulder region

3.5.1 | M. Deltoideus (Figures 5, 6)

A relatively large muscle composed of three parts (Gasse et al., 2017). In Bathyergidae, we identified the m. deltoideus pars scapularis (DS),

which is clearly distinguishable and separated from m. deltoideus pars acromialis (DA), but the latter is more difficult to separate from m. deltoideus pars clavicularis (DC). This agrees with Parsons (1896), who noted that the three parts are quite fused and hardly distinguishable in Myomorpha, a condition which differs from most of the Hystricomorpha where the parts are more separated, except in *B. suillus* and *Georychus*. The origin of these muscles slightly varies among bathyergids, although its three parts are clearly inserted onto the deltoid tuberosity. This classification varies from recent proposals, which synonymise the pars clavicularis with the m. cleidobrachialis (= m. clavobrachialis, Böhmer et al., 2021), which has a different insertion onto the distal humeral diaphysis, a configuration not observed in bathyergids.

The DS (M. deltoideus pars spinalis, spinodeltoideus) is a triangular muscle occupying the most lateral side of the shoulder and strongly attached (and originated) from the caudal portion of the projection of the scapular spine: in *Bathyergus* and *Georychus* it also attaches by fascia to the most cranial part of the insertion of the m. trapezius thoracica, and over a large area on the m. infraspinatus. Such attachment over the m. infraspinatus was also reported in other rodents, including *Erethizon*, *Thryonomys*, and *Petromus* (Parsons, 1894; Woods, 1972). This is the largest muscle of the deltoideus, especially in *Bathyergus*. A similar size pattern is observed in Myomorpha (Parsons, 1894), where the pars scapularis predominates, although this is usually the smallest of the deltoideus among Hystricomorpha (Woods, 1972). In *Georychus*, it passes over the metacromion process before attaching to the deltoid tuberosity. It inserts onto the proximal side of the deltoid tuberosity (laterally), where it is strongly fused to pars acromialis. The pars scapularis and pars acromialis are comparatively more fused in *Bathyergus* and *Georychus* than in *Heliophobius*.

The DA (M. deltoideus pars acromialis, acromiodeltoideus) is an elongated muscle and usually the smallest of the deltoid group in bathyergids. This contrasts with other mammals, where it represents the largest of the group (e.g. armadillos, Marshall et al., 2021). Located between the pars clavicularis (medial) and pars scapularis (lateral), it originates from the acromion process in *Bathyergus* and *Heliophobius* and both acromion and metacromion (including ventral region) in *Georychus*, covering a small portion of the tip of the clavicle in some specimens. It inserts onto the tip (cranial region) of the deltoid tuberosity, in some specimens more associated with the medial side of the tuberosity. In some individuals, this muscle is hardly distinguishable from the other two parts, particularly closer to the insertion point. Such fusion to pars clavicularis is also mentioned by Doubell et al. (2020) for *B. suillus*.

The DC (M. deltoideus pars clavicularis, m. cleidobrachialis, m. clavobrachialis, m. clavodeltoideus) is an elongated muscle with subtriangular shape, usually larger than pars acromialis, but smaller than pars scapularis. It originates in the ventral distal half (lateral) of the clavicle in *Bathyergus* (in close contact with the acromion in some specimens), while it covers almost the entire clavicle (ventrally) in *Heliophobius* and *Georychus*. It widely inserts onto the proximal medial border of the deltoid tuberosity in all species.

3.5.2 | M. Supraspinatus (SSP) (Figures 6, 7)

One single thick and triangular muscle, occupying most of the supraspinous fossa. It originates from the cranial border throughout the vertebral border and scapular spine. There are some differences among species, especially regarding the robustness of the muscle. It is relatively large with a wide origin in the fossa and the superior aspect of the scapular spine in *Bathyergus*, while covering a smaller area of the fossa and not reaching completely the cranial and vertebral border in *Heliophobius* and *Georychus*. The muscle appears more developed in *Heliophobius* than in *Georychus*. *Bathyergus* and *Heliophobius* cover part of the medial side of the cranial border, resulting in a broader attachment to the scapula. The muscle is strongly inserted by tendinous tissue onto the greater tubercle and part of the acromion (ventrally). The attachment is wider (extending towards the lesser tubercle) and more developed in *Bathyergus* as compared to the other taxa which has a more restricted insertion.

3.5.3 | M. Infraspinatus (ISP) (Figures 6, 7)

A relatively large muscle that occupies the infraspinous fossa. In all species, this muscle does not completely cover the infraspinous fossa, not

reaching the vertebral border, and neither reaches the TMP region. In *Heliophobius* and *Georychus*, it passes under the projection of the scapular spine, close to the acromion and metacromion, while it only covers the scapular spine and the middle part of the ventral surface of its projection in *Bathyergus*. This is probably an effect of the more ventrally oriented scapular spine of *Heliophobius* and *Georychus*. It is inserted onto the greater tubercle, proximal to the attachment of the m. teres minor.

3.5.4 | M. Subscapularis (SUB) (Figure 6)

A large muscle located on the subscapular fossa. In *Bathyergus* it is a large triangular muscle, while in *Heliophobius* and *Georychus* it is smaller and elongated, following the narrow shape of the scapula. In all four species, the origin covers almost all borders of the scapula, including the cranial, vertebral and caudal borders, and actually it extends further on the caudal border, where is strongly associated with the m. infraspinatus, thus covering a larger surface area than the actual fossa. Only a part of the muscle is attached to the scapular neck and at some extent the coracoid process, especially in *Heliophobius* and *Georychus*. This muscle is strongly attached to the fossa, contrasting markedly with the lesser degree of attachment of the m. supraspinatus and m. infraspinatus. This muscle is sometimes not fully attached



FIGURE 7 Comparative anatomy of forelimb muscles of Bathyergidae in lateral (a) and medial (b) view. See abbreviations in Figure 2 and Table 2.

to the vertebral border (around the cranial angle) of all species, probably because of the wide attachment of the m. supraspinatus in both lateral and medial sides of this border. The muscle is very small and thin in *Georychus* and large in *Bathyergus*, while *Heliophobius* has an intermediate size. The insertion is onto the lesser tubercle, with large and fleshy attachments in *Bathyergus* and a smaller insertion area in the other species. Along the caudal border, it is also continuous to the m. teres major. At its insertion, and in all species, it is semi-connected to the origin of the m. triceps brachii caput longum. The more caudal fibers of m. subscapularis are very well attached to the m. teres minor. Some fibers of this muscle are also associated with the ventral side of the coracoid process by the coracoclavicular ligament. The insertion is superficial to the origin of m. coracobrachialis in *Bathyergus*.

3.5.5 | M. Teres minor (TMN) (Figures 6–8)

The elongated muscle is located on the caudal border of the scapula. In *Bathyergus*, the origin extends from the scapular neck (close to the glenoid fossa) throughout the caudal border of the scapula, which is slightly fused to the ventral portion of the m. infraspinatus, to finally reach the border with m. teres major. The attachment to the caudal border is thicker on the lateral side of the scapula, with only a small area attached to the medial side. In all species, it is inserted onto the greater tubercle of the humerus just distal to the insertion of the m. infraspinatus.

3.5.6 | M. Teres major (TMJ) (Figure 5–8)

This is an elongated, flattened muscle located in the caudal border of the scapula. It originates from the TMP in all four species and is considerably larger in *Bathyergus*, with a wide and fleshy origin covering a large part of the TMP (on both lateral and medial sides). The origin in *Georychus* is more tendinous than in *Bathyergus* and *Heliophobius* and covers a more restricted area of the process. On the lateral side, it appears associated ventrally with the m. infraspinatus, whereas the medial side is adhered to the m. subscapularis. It is inserted onto the medial side of the humerus, on the teres process in all four species, although in *Heliophobius* and *Georychus*, it appears more proximally inserted (close to the humeral head), while it is more distally inserted in *Bathyergus*. The muscle insertion is wider and fleshier in *Bathyergus* than in the other genera, which have a more tendinous insertion. The ventral region of the muscle, close to the insertion, is quite fused to m. latissimus dorsi in all species.

3.6 | Brachium region

3.6.1 | M. Triceps brachii

In mammals, the triceps can be composed of 2–6 parts: two in the opossum and up to six well-defined parts in mustelids and armadillos

(Ercoli et al., 2015; Marshall et al., 2021). In rodents, it is usually consisting of 3–4 parts: caput longum, caput laterale, caput mediale, and caput accessorium (Klingener, 1964; Thorington et al., 1997; Woods, 1972). The three first parts are considerably large and occupy most of the caudal part of the humeral diaphysis and olecranon process, while the medial accessorium is a short muscle covering a reduced part of the epicondylar region.

3.6.2 | Caput longum (TBLO) (Figures 5–8)

(M. anconeus longus)

It is a conspicuously large muscle in all four species and has a relatively similar origin and insertion in all of them. It originates from the caudal border of the scapula, extending from the scapular neck (associated with the teres minor facet) to the center of the caudal border (superficial to the m. infraspinatus), thus covering a great part of the caudal border of the scapula. It appears formed by two parts, which in *Bathyergus* and *Heliophobius* are tightly fused along their bellies (and start to differentiate at their attachments), while in *Georychus*, they are usually separated. The cranial part of TBLO is more associated with the medial side of the scapula (teres minor facet), while the more caudal part is associated with the lateral side of the scapula. Such “dual” configuration was also reported by Gambaryan et al. (2013) for *Ctenodactylus*, with one medial part being more tendinous and attached to the proximal part of the caudal border of the scapula and a second more fleshy part situated laterally. This is similar to our specimens, although the attachment closer to the neck region of the scapula is more tendinous in *Bathyergus* and *Heliophobius* only. In all species, TBLO inserts onto the caudal tip of the olecranon toward its medial side.

3.6.3 | Caput laterale (TBLA) (Figures 5–8)

(M. anconeus lateralis; anconeus laterale)

The thick, elongated muscle occupies the caudolateral side of the humeral diaphysis, cranial to the caput longum. Originates from the humeral neck (under the greater tubercle), inferior to the m. teres minor. This muscle is located just deep and distal of the AP in *Bathyergus* and MP in *Heliophobius* and *Georychus*, and it extends downwards around the distal and lateral part of the humeral diaphysis. *Bathyergus* and *Heliophobius* have large muscles with a tendinous origin. In some specimens of *B. suillus*, the muscle is also superficially attached to the lateral side of the deltoid tuberosity. In all four species, it inserts onto the lateral side of the OP, covering a wide area, from the lateral epicondyle and anconeal process of the ulna to the tip of the OP. We did not find any part of the muscle attached to the scapula, as reported by Doubell et al. (2020), although the muscle is continuous with the caput longum.

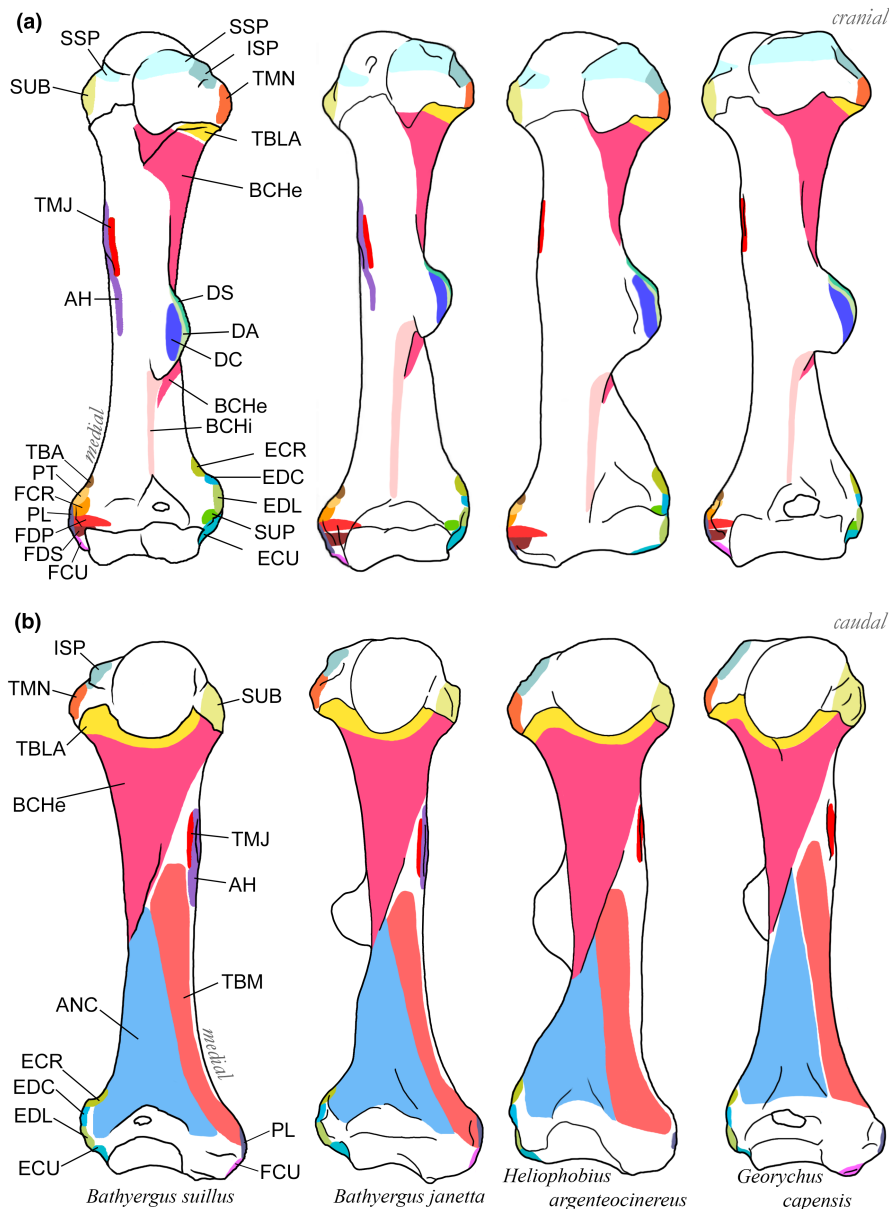


FIGURE 8 Muscle maps of the humeral attachments of solitary bathyergids in cranial (a) and caudal (b) views. Note that although the m. deltoideus pars scapularis and m. deltoideus pars acromialis have a more lateral and craniomedial position in the deltoid tuberosity, respectively, they were included to show its relative position regarding the m. deltoideus pars clavicularis. See abbreviations in Table 2.

3.6.4 | Caput mediale (TBM)+ m. anconeus (ANC) (Figures 6–8)

(TBM, M. anconeus posterior; anconeus medialis; caput profundum; inner head) (ANC, M. anconeus externus; epitrochleoanconeus lateralis)

The TBM is a large muscle present in all species and is fused to the ANC. These muscles were separated only in some individuals of *B. suillus* and *Georychus*, where the medial part (most likely the TBM) is slender than the lateral part (most likely representing the ANC) (e.g. Böhmer et al., 2021). TBM originates in the caudomedial and distal part of the humeral shaft, at the level of the teres process (and deep to caput longum and m. teres major), running down the

diaphysis and reaching the medial epicondyle (superficially). ANC originates and fuses to the TBM belly from the caudolateral part of the humerus (distal to the deltoid tuberosity) along the lateral side of the diaphysis and covers a large surface area. The fusion of these muscles forms a broad attachment area in the caudal part of the diaphysis, thus reflecting the relevance of these muscles for the extension of the elbow, particularly in *B. suillus* and *Heliophobius*, since these muscles are slightly smaller in *B. janetta* and *Georychus*. The TBM inserts rather in the medial side of the OP, while the ANC inserts on the entire dorsal surface of the OP, reaching the anconeal process and covering the supratrochlear region.

Our observations agree with previous authors, who mention that the inner head of the triceps (=TBM) rises from the greater

part of the caudal surface of the humerus and is continuous with ANC and that the latter muscle is attached to the lateral side of the olecranon (Böhmer et al., 2021; Parsons, 1894). Moreover, Parsons (1894) mentions that the ANC is especially well-marked and inseparable from TBM. However, Doubell et al. (2020) briefly report a small and medially inserted “m. anconeus” in *B. suillus*. Our observations corroborate the early descriptions of Parsons in bathyergids and other rodents (Parsons, 1894, 1896) that these muscles (TMB and ANC) are fused and that ANC is a well-developed muscle in bathyergids, not reduced and restricted to the medial side as suggested by the descriptions of Doubell et al. (2020). Based on different authors suggesting that the ANC originates in the lateral side of the humerus in mammals, we provide further support to the myological organization of this muscle in bathyergids so that the “ANC” of Doubell et al. (2020) must correspond to another muscle (see below).

3.6.5 | Caput mediale accesorium anconeus (TBMAA) (Figures 7, 8)

(M. articularis cubiti; epitrochleoanconeus; epitrochleoanconeus medialis; anconeus internus)

Very small muscle dissected in almost all specimens. It originates from the distal caudomedial side of the epicondyle, and is inserted onto the medial side of olecranon. Due to its small size and relatedness to the muscles of the olecranon (caput mediale + m. anconeus), it was sometimes not clearly differentiated. This muscle would correspond to the “m. anconeus” reported by Doubell et al. (2020) for *B. suillus*.

3.6.6 | M. Tensor fasciae antebrachii (TFA) (not observed in *H. Argenteocinereus*) (Figure 9)

(M. dorso-epitrochlearis; tensor fasciae antebrachii; omo-anconeus; epitrochleoanconeus; extensor antibrachii longus; extensor parvus antibrachii)

The TFA is an elongated muscle located in the caudal region of all specimens studied here but not observed in any specimen of *Heliophobius*. Some specimens of *Bathyergus* exhibited a shorter muscle, but it was always present. It originates from fleshy fibers in a central part of the m. latissimus dorsi in *Bathyergus*, and from a ventral border of the same muscle in *Georychus* around the level of the proximal humerus, inserting medially onto the external fascia of the OP. The insertion area in the olecranon is wider in *Bathyergus* as compared to *Georychus*, extending towards the medial epicondyle of the humerus, and sometimes united to the m. triceps brachii caput longum, a condition which is also found in semifossorial marsupials, such as the southern brown bandicoot and greater bilby (Warburton et al., 2014), but also in non-fossorial rodents, such as *Cricetomys* (Parsons, 1896), *Laonastes* and *Ctenodactylus* (Gambaryan et al., 2013). Similar origin in the

external fascia of the m. latissimus dorsi has been reported for many other hystricomorph rodents, e.g. *Chinchilla* (Gambaryan et al., 2013). The insertion of *B. suillus* onto the medial side of the olecranon contrasts with the dorsal insertion onto the olecranon reported by Doubell et al. (2020). The latter is unlikely because the m. tensor fasciae antebrachii is a superficial muscle, and the dorsal part of the olecranon is occupied entirely by the m. triceps brachii caput mediale and m. anconeus (see above).

3.6.7 | M. Biceps brachii (BB) (Figures 6–9)

(M. biceps brachii caput longum and breve; biceps cubiti)

Elongated muscle occupying all the cranial aspect of the humerus (medial to the deltoid tuberosity), originating from the scapula, and variably inserted proximally onto the forearm bones. It is divided into two parts at its origin, which unite around the middle of the muscle belly length, just near the position of the deltoid tuberosity. In all species, the medial fleshy part (short head) originates ventrally from the coracoid process of the scapula, while the more tendinous cranial part (long head), which passes through the intertubercular groove of the humeral head, originates from the supraglenoid tubercle. The attachment of the short head is very fleshy in *Bathyergus* and more tendinous in *Heliophobius*, with *Georychus* being intermediate. In *Bathyergus*, the origin of the short head is in common with the deeper origin of the m. articularis humeri. The long part inserts medially onto the ulna, while the short head inserts onto the caudomedial part of the radius in *Bathyergus* and *Georychus* and only to the radius in *Heliophobius* (although some specimens also showed a very close attachment to the ulna). The ulnar insertions are clearly marked as sulci in the ulna (Figure 4).

Among rodents, the insertion can be onto the radius, ulna, or both bones, and there is considerable variation within a single family and even within one species (Parsons, 1896, 1894). In *Erethizon* (and other rodents, such as *Cricetus* and *Myoxus*), it is inserted largely onto the radius, although in *Hystrix* (and other rodents, such as *Rhizomys*) onto the ulna (Parsons, 1896, 1894). Our results agree with Parsons (1896), who reported that the insertion in *B. suillus* and *Georychus* goes to both bones, although this disagrees with the findings of Doubell et al. (2020) for *B. suillus*, who reported insertion onto the ulna uniquely, without providing further details about the attachment.

3.6.8 | M. Brachialis (BCH) (Figures 6–9)

(M. brachialis anticus)

This is a large muscle comprised of two parts. The most superficial, thick, and elongated part (BCHe) is located along the caudolateral aspect of the humeral diaphysis, arising in all species from the neck of the humeral head (under the greater tubercle) and curves caudally around the midshaft, thus covering a great part of the proximal caudolateral humeral diaphysis, including the lateral side of the

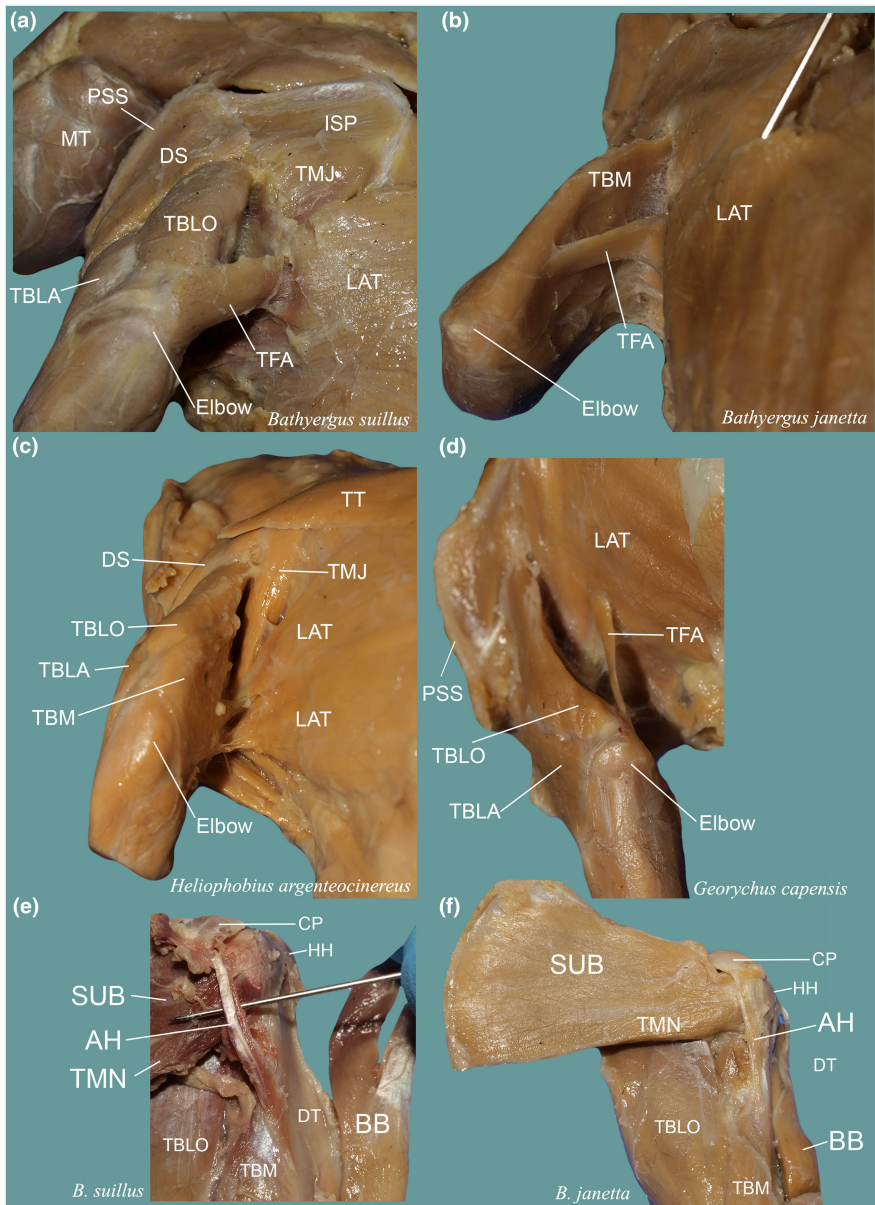


FIGURE 9 Detail of the superficial m. tensor fasciae antebrachii observed in *Bathyergus* and *Georychus* only, but not in *Heliophobius* (caudolateral view, a–d), and the deep m. articularis humeri observed in *Bathyergus* only (medial view, e, f). HH, humeral head. See additional abbreviations in Figure 2 and Table 2.

deltoid tuberosity. It is inserted onto the craniomedial surface of the ulna only, close to the coronoid process, and passing (along with the m. biceps brachii) between forearm muscles (m. extensor carpi radialis and m. pronator teres). The fibers of BCH and m. biceps brachii are quite fused at the insertion point in the ulna, although it is possible to see the BCH fibers attaching between the two insertions of the m. biceps brachii (to ulna and radius). Some specimens of *Heliophobius* also show some fibers inserted into the radius. The second part (BCHi) is considerably smaller and also located cranially but deep to the first part, and originates in all species from the distal tip of the deltoid tuberosity, inserting onto the cranial surface of the ulna, in close association with the coronoid process (proximal to the insertion of BCHe and m. biceps brachii). Both parts are sometimes fused

at the insertion (along with the m. biceps brachii), a condition also reported for *T. bottae* (Holliger, 1916) and for *Myomorpha* in general (Parsons, 1894). Our observations agree with Parsons (1894), who also describes *B. suillus* as having a clear distinction between the parts, although nothing is mentioned by this author for *Georychus*.

3.6.9 | M. Articularis humeri (AH) (Figure 10)

(M. coracobrachialis; coracobrachialis brevis; coracobrachialis profundus)

This is a very thin and relatively long muscle located in the proximal part of the humerus (deep to m. biceps brachii) observed only in

Bathyergus. It is very fibrous and originates as a thin tendon from the dorsal aspect of the coracoid process in connection with the short head of the *m. biceps brachii*, and inserts broadly onto the proximal part of the humeral diaphysis, around the *teres process* region, extending (craniomedially) to the level of the *deltoid tuberosity*.

This muscle has often been described as *m. coracobrachialis*, which can be composed of 2–3 heads (Parsons, 1896, 1894; Woods, 1972), although all three parts are seldom present together (Parsons, 1894). This muscle has been described for several mammals, including fossorial marsupials, carnivores (*Ga. cuja*) and *Thomomys bulbivorus* (Ercoli et al., 2015; Hill, 1937; Warburton et al., 2014), as well as non-fossorial mammals, such as *Laonastes*, *Ctenodactylus* and *Chinchilla* (Gambaryan et al., 2013). All heads appear to originate from the same point in the scapula, with their insertions varying across taxa. The short head is restricted to the proximomedial region of the humerus, while the long part shows a rather extensive insertion onto the medial side of the humerus, reaching the medial epicondyle (Hill, 1937; Holliger, 1916; Parsons, 1896, 1894; Woods, 1972). Woods (1972) mentions that this muscle and *m. biceps brachii* arise from a common tendon from the coracoid process of the scapula, and the *coracobrachialis* derives some fibers from the extensor surface of the short head of *m. biceps brachii*. Thus, the muscles in *Bathyergus* are more similar in position and origin to the short head than to the long head. Assuming that the second part of the *coracobrachialis* described by Parsons (1896) for *B. suillus* corresponds to the AH, our observations would confirm his descriptions for these species, which states that this muscle is present only in *B. suillus* and lacking in *G. capensis*. However, he does not specify the insertion of this muscle. This muscle was absent in *He. glaber* (Doubell et al., 2020), although these authors briefly described its presence in *B. suillus*, proposing a quite different size (rather big) and insertion for this muscle onto the medial border of the proximal ulna.

We did not find a muscle with such topography in our dissections of *Bathyergus*.

3.7 | Antebrachium region

3.7.1 | M. Pronator teres (PT) (Figures 8, 10)

(*M. pronator radii teres*, *pronator teres radii*; *pronator teres caput humerale*; *pronator teres caput ulnare*)

This is a relatively short and triangular muscle originating proximally in the craniomedial epicondyle and superficial to all other flexors. It is inserted widely onto the midshaft (medial side) of the radius, although in some specimens of *Georychus*, it occupies a narrower area in the proximal part of the radius. In *B. suillus*, we did not find an origin in the olecranon, as reported by Doubell et al. (2020).

3.7.2 | M. Flexor carpi radialis (FCR) (Figures 8, 10)

Elongated muscle originating in the craniomedial epicondyle, deep and distal to *m. pronator teres*. In *Bathyergus* and *Georychus*, it is strongly fused with *m. flexor digitorum profundus* in its origin, but not so fused in *Heliophobius*. Its tendon is attached to the distal radius by a fibrous pulley and inserts onto the proximal end of the metacarpal III.

3.7.3 | M. Flexor carpi ulnaris (FCU) (Figures 8, 10)

Large elongated muscle found in the ventral part of the forearm, and consisting of two closely fused but distinguishable parts, *caput*

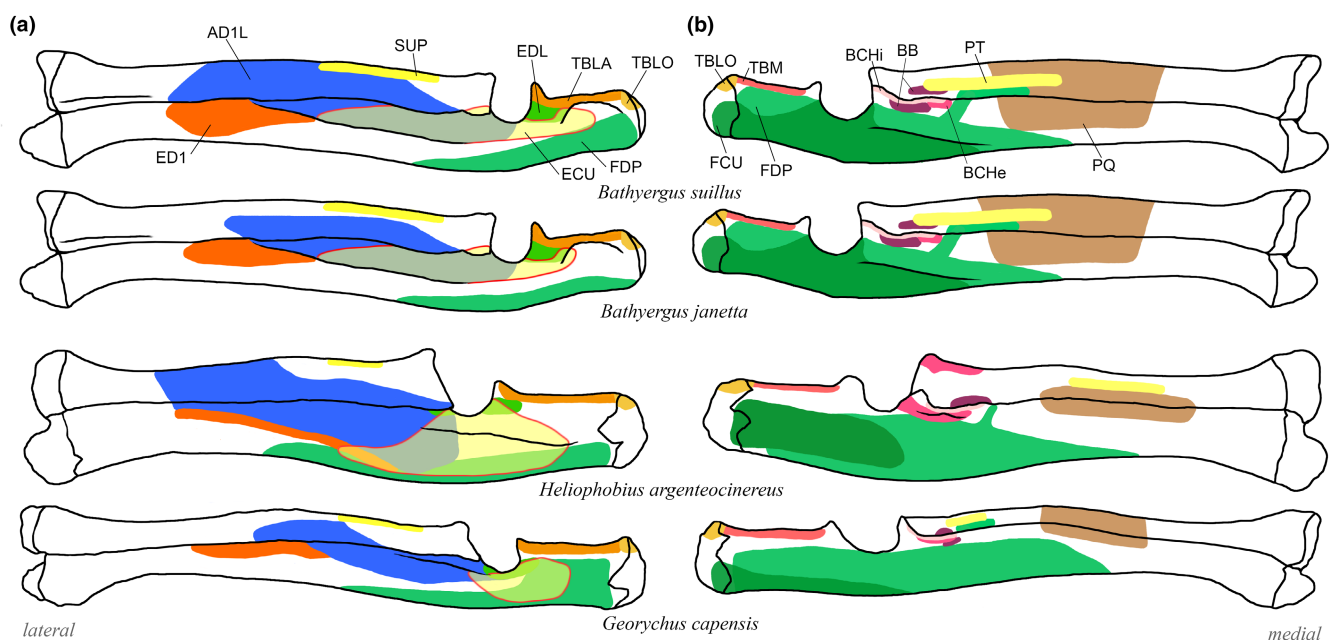


FIGURE 10 Muscle maps of the ulnar attachments of bathyergids in lateral (a) and medial (b) view. See abbreviations in Table 2.

ulnare (FCUU) and caput humerale (FCUH). These muscles are covered by a thick fascia, which covers several muscles, including m. flexor carpi radialis and m. flexor digitorum profundus. The FCUU is the largest of both, and originates from the olecranon and medial epicondyle, mostly covering the caudal and ventral part of the epicondyle, and the base of the olecranon. FCUU is united to the FDP (caput ulnare) in the caudal side of the ulna. The FCUU is superficial and distal to FCUH. The FCUH originates from a more central part of the medial epicondyle, cranial to the FCUU. In *Heliophobius*, the origin of the FCU is restricted to only the ventral tip of the epicondyle, but it has a wide attachment area in the olecranon. These muscles are small and not completely fused in *Georychus*, while they are larger and quite fused in *Bathyergus* and *Heliophobius*. *Bathyergus* develops only one tendon to the manus, *Georychus* can have one or two tendons, while *Heliophobius* has two tendons. In any case, the tendons are inserted into the accessory carpal bone and palmar aponeurosis of the hypothenar pad.

3.7.4 | M. Palmaris longus (PL) (Figures 8, 10)

(M. flexor digitalis superficialis; flexor sublimis digitorum)

Elongated muscle located in the medial side of the forearm. This muscle is variable in relative size among the species; it has a large belly in *Bathyergus* and a smaller belly in *Heliophobius*, with *Georychus* showing an intermediate size. The arrangement of this muscle also varies among species: it is highly fused in its origin to m. flexor carpi ulnaris (inferiorly) in *Bathyergus* and *Georychus*, while it is an independent muscle in *Heliophobius*. The origin spans from the olecranon to the cranial side of the medial epicondyle in *Bathyergus* and *Georychus* while originating directly from the cranial side of the medial epicondyle in *Heliophobius*. In the latter species, the muscle belly is also quite short, and the tendon is quite long. In all four species, it is superficial and relatively proximal to m. flexor carpi ulnaris. In all species, the tendon passes below the tendon of the m. flexor carpi ulnaris, where both muscles insert at the same level, but into different structures. The PL inserts onto the superficial layer of the palmar aponeurosis (palmar fascia) of the hypothenar pad in all species, continuous to the insertion of the m. flexor carpi ulnaris.

Parsons (1896) described this muscle inserted into the palmar cartilage or ossicle, and into the fascia of the palm in *B. suillus* and *G. capensis* (and other rodents as well). The description of Böhmer et al. (2021) synonymizes PL with the m. flexor digitorum superficialis (the latter not presented individually by them), and state that the insertion of PL can be either onto the second phalanges of digits II–V or the palmar aponeurosis. However, an insertion onto the distal phalanges of digits II–V agrees more with the insertion typically ascribed to m. flexor digitorum superficialis (e.g. Greene, 1935). In other taxa, such as armadillos it has been suggested to be fused with m. flexor digitorum superficialis (see Marshall et al., 2021, and references therein). The m. flexor digitorum superficialis is often well-defined and superficial to m. flexor digitorum profundus, and

inserted onto digits. Therefore, the synonymy made by Böhmer et al. (2021), with two possible insertion sites for PL needs further evaluation, since this muscle is also often a well-defined muscle superficial to the flexors of the digits. Most importantly, when PL is present, it is associated with the palm or carpals (Gambaryan et al., 2013; Greene, 1935; Parsons, 1896) but not with digits. For example, Parsons (1894) mentions that this muscle is liable to great individual variation in rodents and in humans, but such variation in mammals has not been associated with the digits.

3.7.5 | M. Flexor digitorum superficialis (FDS) (Figures 8, 10)

(M. flexor digitalis superficialis; flexor sublimis digitorum; flexor digitorum sublimis)

Elongated muscle is superficial to m. flexor digitorum profundus, which originates from the most distal and internal part of the medial epicondyle, in close association with the m. flexor digitorum profundus. It divides into two large tendons in *Bathyergus* and three tendons in *Heliophobius* and *Georychus*, which pass superficial to the tendon of m. flexor digitorum profundus before reaching the manus. Each tendon inserts in the ventral part of the middle phalanx of digits II–IV. We did not find a tendon sent to digit V, as reported by Doubell et al. (2020) for *B. suillus*. Our observations support the description of Parsons (1896) for this muscle (=flexor sublimis digitorum), as well as the insertion onto only three digits in other hystricomorphs (e.g. *Ctenodactylus* and *Chinchilla*, Gambaryan et al., 2013).

3.7.6 | M. Flexor digitorum profundus (FDP) (Figures 8, 10)

(M. flexor profundus digitorum)

Large and elongated muscle composed of four parts (deep to FCR) and covering an extensive part of the medial ulnar fossa. In all four species, the FDP is composed of two superficial heads (medial and lateral) originating from the medial epicondyle (FDPHM and FDPHL, which are continuous) and of two deep heads originating from the medial surfaces of the radius and ulna (FDPR and FDPU). FDPHM and FDPHL are relatively small muscles compared to the other two parts and originate in the cranial part of the epicondyle, with FDPHL lateral to FDPHM. FDPR is thick and attached to the proximal medial surface of the radius, while the FDPU attaches to the dorsal side of the ulna, near the insertions of m. biceps brachii and m. brachialis. FDPU is the largest head in the group and the deepest flexor muscle in the proximal part of the ulna, having a wide attachment area in the distal olecranon and along the medial ulnar fossa (below the trochlear notch). Some fibers of this muscle cross to the lateral side of the ulna ventrally, thus covering a greater part of the diaphyseal surface (proximal, medial, ventral, and lateral) and continuous with

m. flexor carpi ulnaris. The only difference among the species is the level of attachment of the FDP to the radius, which is quite broad in *Bathyergus*, reduced in *Georychus* (with some individuals lacking such attachment), and absent in *Heliophobius*. The latter taxon also exhibits a more reduced attachment area of FDP to the most caudal part of the olecranon. Four tendons arise from FDP, reaching each of the ventral parts of the distal phalanges of digits II–V. Overall, our observations support the description of Parsons (1896) for bathyergids and Greene (1935) for rats, although we did not find a tendon sent to digit I as reported by Doubell et al. (2020) for *B. suillus*.

3.7.7 | M. Extensor carpi radialis longus (ECRL)+brevis (ECRB) (Figures 8, 10)

(ECRL, M. extensor carpi radialis longior) (ECRB, M. extensor carpi radialis brevior)

In all species, these muscles (hereafter ECR) are fused at their origin, although they can be distinguishable (separable) in *Bathyergus* along its belly. In all species, they are elongated and originate from the proximal craniolateral epicondylar area (distal to m. brachialis, as well as proximal and deep to m. extensor digitorum communis). This corresponds to the deepest extensor attached to the humeral epicondyle. Generally, the ECRB (inferior to ECRL) is the largest of the two. Two tendons appear from these muscles, longus (thinner) and brevis (thicker), which pass together under the tendon of the m. extensor digiti 1 and m. abductor digiti 1 longus, and inserts onto the base of metacarpal II and base of metacarpal III, respectively. However, *Heliophobius* showed considerable variation, with some specimens having only one tendon (inserted in metacarpal II), others having one tendon that only divides close to the insertion, and others having three tendons (the third inserting onto the most proximal carpal bone close to the metacarpal II (most likely the trapezoid)).

3.7.8 | M. Extensor digitorum communis (EDC) (Figures 8, 10)

(M. extensor communis digitorum; extensor digitorum; extensor digiti minimi)

This is an elongated muscle, originating from the craniolateral epicondylar area (distal and superficial to m. extensor carpi radialis), although in *Georychus* it also covers a small area of the tip of the radius. Generally, four tendons ultimately emerge from this muscle in all the species analyzed, which inserts onto distal phalanges of digits II–V. However, *B. suillus* can show a variable tendon organization. One specimen showed three main tendons, two thick tendons inserted onto digits II and III, and the third inserted also onto digit III, but distally subdivided and inserted in digit V as well. Another specimen showed very developed tendons inserting mainly in digit V, with a small portion inserting in digit IV. Thus, only *Bathyergus*

appears to send a slip to the digit V, which contrasts with the reports of Parsons (1896), mentioning that none of his specimens (of *B. suillus* and *G. capensis*) had a slip given to the digit V. Our observations agree with the findings of Doubell et al. (2020) of insertion onto digits II–V in *B. suillus*.

3.7.9 | M. Extensor digitorum lateralis (EDL) (Figures 8, 10)

(M. extensor digiti lateralis; extensor minimi digiti; extensor digiti quarti; extensor digiti quinti proprius)

Elongated muscle originating from the lateral epicondylar area (distal to m. extensor digitorum communis), which also covers the trochlear notch and the closer regions of the olecranon and radius (particularly in *Bathyergus*). This corresponds to the most superficial extensor of the forearm, and it is quite attached to the m. extensor digitorum communis in its origin. This muscle runs along the lateral ulnar fossa (below the trochlear notch), a concavity that is accentuated due to the superior position of the radius, thus creating a deeper fossa to accommodate the muscles. All species showed two tendons inserted onto distal phalanges of digits IV–V: in *Bathyergus* and *Heliophobius* the tendons are of different sizes (the smaller tendon going to digit IV), whereas in *Georychus* the tendons are of similar size.

3.7.10 | M. Extensor carpi ulnaris (ECU) (Figures 8, 10)

Elongated muscle originating from the lateral side of the olecranon, distal tip of the epicondyle (deep and continuous to m. extensor digitorum lateralis) and running along the lateral fossa of the ulna from the trochlear notch to almost the midshaft in *Bathyergus* and *Heliophobius*, except in *Georychus* where it is limited to the olecranon region, epicondylar region and trochlear notch only. This is one of the extensors with the broadest attachment area in its origin (with the exception of *Georychus*). In all species, it is inserted onto the base of the metacarpal V (ventrally).

3.7.11 | M. Supinator (SUP) (Figures 8, 10)

(M. supinator longus; supinator brevis)

This is a relatively short and triangular muscle originating from a tendinous attachment in the lateral epicondyle (proximal part). In *Bathyergus* it is evidently larger as compared to *Heliophobius* and *Georychus*. In all species, it inserts onto the craniomedial surface of the proximal radius (slightly distal to the insertion of the m. pronator teres in the medial side): covering an extensive area in *Bathyergus* (almost to the middle of the diaphysis), while covering a reduced area in *Heliophobius* and *Georychus*. This muscle is deep to m. extensor carpi radialis and other extensors.

3.7.12 | M. Pronator quadratus (PQ) (Figures 8, 10)

This is a relatively small and deep medial muscle reinforcing the connection between the ulna and radius. It originates in the craniomedial surface of the ulna, with a wide extension in *Bathyergus*, and a more reduced attachment area in *Georychus*, and a very small area in *Heliophobius*. The insertion is onto the medial surface of the radius, from dorsal to ventral, although this area is quite reduced in *Heliophobius*, being restricted to only the ventral region.

3.7.13 | M. Extensor digiti 1 (ED1) (Figures 8, 10)

(M. extensor secundi internodii pollicis; abductor pollicis; abductor pollicis longus; extensor pollicis longus)

Elongated muscle originating from the cranio-lateral mid-diaphysis of the ulna, and closely related to the interosseous ligament and caudal part of the radius in *Bathyergus* and *Georychus*. In *Heliophobius*, it is more restricted to the ulna only. The attachment area is quite extensive in *Bathyergus* and *Heliophobius*, although wider and extending to the distal portion of the ulna in the former and rather elongated in the latter. The attachment in *Georychus* is more centralized and reduced in size. In all species, it is inserted onto the base of the distal phalanx of digit I (medially). This insertion in *B. suillus* differs from that of Doubell et al. (2020) in the proximal phalanx of digit I.

3.7.14 | M. Abductor digiti I longus (AD1L) (Figures 8, 10)

(M. ossis metacarpi pollicis; extensor pollicis brevis)

Large and elongated muscle originating from the trochlear notch to the cranio-lateral proximal mid-diaphysis of the ulna and caudoproximal diaphysis of the radius, also covering the interosseous ligament. The muscle is proximal and larger than m. extensor pollicis longus, and strongly attached to it. *Bathyergus* and *Heliophobius* have a wider attachment area as compared to *Georychus*, particularly in the radius, although in *Heliophobius* the attachment does not surpasses caudally the trochlear notch. In all species, the tendon is inserted into the medial base of the metacarpal of digit I. The insertion in *B. suillus* also differs from that of Doubell et al. (2020) in the distal phalanx of digit I.

4 | DISCUSSION

Scratch-digging kinematics implies considerable muscular and skeletal specialization of each section of the forelimb, which in synergy each part contributes to generate greater muscle moment arms and increased power stroke during parasagittal scratch-digging (Hildebrand, 1985; Lehmann, 1963; Nakai & Fujiwara, 2023). Our results support the hypothesis that the forelimb phenotype of scratch-diggers differs from that of tooth-diggers: *Bathyergus* has a more specialized forelimb musculature with corresponding divergent

adaptations in the scapula and ulna as compared to *Heliophobius* and *Georychus*. Nonetheless, some of such specializations were not exclusive to the *Bathyergus* lineage and are also shared by the other taxa, thus confirming previous findings of certain forelimb similarity between tooth- and scratch-diggers. The functional implications of such divergences are discussed in light of the new evidence.

Solitary bathyergids showed in general a similar set of muscles (Table 2), and relatively similar skeletal anatomy (see also Montoya-Sanhueza, Bennett, et al., 2022; Montoya-Sanhueza, Šaffa, et al., 2022), although most of the differences among bathyergids were detected in the pectoral girdle region and forearm. The neck and shoulder of *Bathyergus* are considerably more robust than in the two other genera and composed of well-developed m. rhomboideus, m. supraspinatus and m. subscapularis. These muscles are widely inserted onto a relatively enlarged scapula, with large supraspinous and subscapular fossae and a long vertebral border (Figure 3a,b). In mammals, the pectoral girdle is strongly influenced by factors facilitating shoulder stabilization, limb mobility, and neck elevation (Fischer et al., 2002; Jenkins & Weijs, 1979; Morgan, 2015). Similarly, the muscles of the head-neck-shoulder transition have multiple functions (see Table 2), so their actions are quite complex to be simplified into a unique single function (Holliger, 1916). Hildebrand (1985) suggests that the scapula of fossorial mammals has a greater influence on shoulder movement and stabilization, although no distinction between scratch- or tooth-diggers is further commented. In this study, the larger scapula of *Bathyergus*, having longer vertebral borders, allows a broader attachment of the mm. rhomboidei, which are involved in anterior rotation and lifting of the scapula, thus contributing to scapular adduction/retraction and neck elevation (Holliger, 1916; Morgan, 2015). The most distinctive characteristic found in *Bathyergus* was the more central insertion of the m. rhomboideus cervicis and m. rhomboideus thoracis onto the scapula, while *Heliophobius* and *Georychus* showed a more caudal insertion (Figure 6). Such differences are probably related to the distinct digging mechanisms of such species, where neck elevation and scapular stability are essential for all of them but probably specialized for different digging mechanisms, i.e., scratch-diggers may have developed more efficient scapular stabilization mechanisms, while tooth-diggers a more rotational scapula. *Bathyergus* lives in soft sandy soils where the roof and walls of burrows tend to collapse more frequently than in dryer environments with compacted soils. To avoid this, *B. suillus* elevates the head (and nose) to the top of the tunnel to brace itself during digging persistently with one or both forelimbs (Cuthbert, 1975). It is probable that this behavior may require a higher degree of shoulder and neck stabilization (less free rotation), which may differ from the more dynamic nature of the head and neck of tooth-diggers, which is required for generating strong and repeated bites for loosening the soil of walls and roof (Cain et al., 2019; Cuthbert, 1975; Gambaryan & Gasc, 1993; Jarvis & Sale, 1971; Van Wassenbergh et al., 2017). In this sense, it has been suggested that social tooth-diggers such as *Fukomys micklei*, benefit from greater rotational mobility of

the head-neck to generate a high-leverage effect against hard soils (similar to rotating a shovel after sticking it into the ground) (Van Wassenbergh et al., 2017). The same authors also suggested that muscular modifications allowing the independent stabilization of forelimbs and the shoulder to remain fixed in a position to efficiently provide forward force during digging would also be expected (Van Wassenbergh et al., 2017). If our previous hypothesis is further confirmed (with kinematic assessments), a similar distal muscular arrangement should be expected for social tooth-digger species of this family. In fact, Doubell et al. (2020) illustrated a similar caudal insertion of *m. rhomboideus cervicis* and *m. rhomboideus thoracis* onto the vertebral border of the scapula of *He. glaber* (and a central position for *B. suillus*), although they do not provide detailed descriptions and interpretations for such arrangement. Therefore, the more central and broad insertion of *m. rhomboideus cervicis* and *m. rhomboideus thoracis* in *Bathyergus* appears to prioritize shoulder stability and restrict rotation of the scapula, while the more caudal insertion of such muscles in the tooth-diggers may increase their line of action, thus playing an important role in increasing mechanical advantage and scapular rotation, and probably neck elevation to generate forward forces (see below). In this sense, Sahd et al. (2023) found that *B. suillus* had greater force outputs and low-contraction velocity of the *m. subscapularis* and *m. teres major*, which may indicate a stabilization function of the shoulder joint rather than fast movements. Such stabilization function of the shoulder was also further reflected in the significantly lower percentage of MHC II fibers in *B. suillus* as compared to *He. glaber* (Sahd et al., 2023). Similar to our interpretations, Sahd et al. (2023) also reported that *He. glaber* have powerful limb retractors and scapular elevators/stabilizers, suggesting a stabilization function of the shoulder and increased leverage of the head/neck/jaw to produce enough forward force to bite the soil with their incisors in combination with a downward thrust of the elbow extensors.

Such increased shoulder stabilization in *Bathyergus*, along with the digging with only one arm (*pers. obs.* GMS) may result in decreased digging speeds (and lower level of scapular rotation). In fact, Cuthbert (1975) mentions that the digging behavior of *G. capensis* is more active (faster) than *B. suillus*, which is also supported by our observations in the field and laboratory (*unpublished data*). Along with the *m. rhomboideus*, other muscles such as the *m. supraspinatus*, *m. infraspinatus*, and *m. subscapularis* were also conspicuously more robust in *Bathyergus* than in *Heliophobius* and *Georychus*, showing a more extensive attachment onto the scapular surface, up to the vertebral border in *Bathyergus*, and limited to the fossa in the other taxa (Figure 6). This also suggests better glenohumeral and scapular stabilization in *Bathyergus*.

Similarly, in the shoulder, the presence of a simplified acromion process in the scapular spine of *Bathyergus* contrasts with the condition observed in *Heliophobius* and *Georychus*: the latter taxa exhibiting both an acromion and a metacromion process. A metacromion was also previously reported for *He. glaber* (Hamilton, 1928; Doubell et al., 2020; and *pers. obs.* GMS), and for the closest relatives of the

Bathyergidae, *Thryonomys swinderianus*, *Hystrix africae australis*, *Hy. cristata* and *Petromus typicus* (Mpagike & Makungu, 2023; Onwuama et al., 2015). Therefore, the tooth-diggers of the family exhibit high phenotypic similarity, most likely as a result of plesiomorphy, which does not necessarily reflect a unique functional relationship with digging behavior in mammals. In our study, we observed a well-developed superficial muscle attached to the shoulder region of *Bathyergus* and *Heliophobius* (including the metacromion), which runs directly to the head region behind the ear, most likely representing the *m. platysma myoides* (Figure 5). This muscle appears relatively smaller in *Bathyergus*, but it was not possible to observe it in *Georychus*. Recently, Cain et al. (2019) described the superficial neck musculature of *He. glaber*, and briefly mentioned that the superficial *m. platysma myoides* has an important role in lateral movement of the lower incisor and hemi-mandible in this species, thus facilitating independent movement of the lower incisors laterally. These authors briefly mention that the origin is on the dorsal scapula, with its insertion along the ventral extent of the mandible (Cain et al., 2019), although they do not provide precise anatomical details about the origin of this muscle and its topography on the scapula. However, this arrangement is in general similar to the attachments reported for *Georychus* by Parsons (1896, p. 173): "the *m. platysma myoides* is very strong and rises from the angle of the mouth and from the median raphe running back from the symphysis menti, it runs backward and upward to be lost over the region of the shoulders, though some of the more caudal fibers are attached to the metacromial process". The latter description supports the finding of a metacromion in *Georychus*, although it does not provide information for *B. suillus*. Another superficial muscle inserted in the metacromion of *He. glaber*, as well as in other mammals, is the *m. omotransversarius* (Böhmer et al., 2021), which originates from the transverse process of the atlas and inserts onto the metacromion (Doubell et al., 2020). The *m. omotransversarius*, not described in the species of our study, acts as a lateral neck rotator/elevator and limb (scapular) protractor/elevator (Böhmer et al., 2021; Marshall et al., 2021). It is important to note that despite the small size of naked mole-metacromionrats, they possess the largest (size-corrected) bite force among bathyergids (Kraus et al., 2022), even surpassing the predictions for its body size (Hite et al., 2019). It is probable that such extended metacromion in tooth-diggers increases the attachment area of the shoulder, thus favoring the leverage and rotation of the jaw. Therefore, the shoulder region and its metacromial extension in tooth-diggers represent an important attachment site for multiple superficial jaw, neck, and thoracic muscles, yet a poorly understood system (Gambaryan & Gasc, 1993; Van Wassenbergh et al., 2017).

Skeletal variation in the scapular spine was also noted among fossorial mammals by Hildebrand (1985), although not further documented. An extended scapular spine (i.e. beyond the glenoid fossa) has been suggested to be a common feature of fossorial animals, mainly to restrict the lateral movement of the humerus and to alleviate the tendency of the humeral head to dislocate from the glenoid fossa (Lehmann, 1963), as well as to accommodate enlarged deltoids (Stein, 2000). Nevertheless, a long, slender, and caudally projected metacromion in the scapula of many small mammals,

such as lagomorphs, elephant shrews, and most cavioid rodents (Morgan, 2009, 2015), has been regarded as an osteological correlate of locomotor specialization (Salton & Sargis, 2008; Seckel & Janis, 2008). Such structure and morphology have been suggested to be particularly important in rapid half-bounding small to medium-sized (cursorial) mammals to increase the moment arm of some muscles (e.g. m. trapezius pars cervicalis) and, therefore, increasing the stabilization and resistance of the scapula to ground reaction forces during the landing phase onto a single forelimb (Seckel & Janis, 2008). Although the metacromial morphology of such cursorial taxa does not exactly fit with the morphology of the taxa studied here (*Heliophobius* and *Georychus*, and other bathyergids), its general morphology and caudal orientation may result in similar functional correlates to stabilize the glenohumeral articulation during tooth-digging, by providing additional surface area for the attachment of important superficial muscles associated with jaw, neck and thoracic movement, e.g. m. platysma myoides, m. trapezius and m. latissimus dorsi. Because the m. rhomboideus appears to increase the mechanical advantage and rotation of the scapula in tooth-diggers (see above), an increased stabilization of the glenohumeral articulation, now acting as a pivot for its rotation would also be required to facilitate such movement. The presence of a metacromion process and the muscles attached onto it would allow tooth-diggers an increased stabilization of the glenohumeral region for a more effective rotation.

Although scratch-diggers such as *Bathyergus* are expected to experience higher reaction forces in their shoulders than tooth-diggers mainly due to their vigorous scrapping of the soil, such loading could also be expected in tooth-diggers by burrowing harder soils with their heads, i.e. the shoulder region represents a convergent point receiving the reaction forces applied with either the skull or forelimbs. The relatively slower digging of soft substrates of scratch-diggers (see above) may also reduce the impact on the shoulder girdle. The scapular spine of *Bathyergus* seems not to be unique among subterranean mammals since the pocket gophers *Thomomys* and *Geomys*, other highly specialized scratch-diggers that build burrows in soft soils (Marcy et al., 2016; Orcutt, 1940), also lacks a metacromion in the scapular spine, along with having a triangular scapular shape similar to *Bathyergus* (Hill, 1937; Holliger, 1916). This suggests a convergent scapular morphology between *Bathyergus* and geomyids, which further supports our hypothesis of morphological differentiation between digging modes, and that the metacromion in subterranean species may represent a specific adaptation of specialized tooth-diggers.

Another scapular specialization observed in *Bathyergus* was the wider base of the scapular spine when it projects from the blade as compared to *Heliophobius* and *Georychus* (Figure 3c). Cuthbert (1975) found a similar pattern, where the width of the spine at this rising point of the blade is proportionately thicker in *B. suillus* than in *G. capensis* (1.3:1.0). This would increase the robustness of the spine and scapular neck of *Bathyergus* to resist high impact reaction forces transmitted throughout the glenohumeral joint, but also to increase the resistance of the scapula when is flexed against the arm (see below).

These results show that the neck region plays a fundamental role in tooth-diggers, where neck mobility, strength and shoulder stabilization are fundamental synergic components to powering the dual phase-pattern of tooth-digging, i.e. forward force generation and head rotation (Van Wassenbergh et al., 2017). Overall, the larger and more robust scapula of *Bathyergus* appears to represent a divergent feature within the family Bathyergidae (probably an autapomorphy), while the scapular morphology of tooth-diggers may represent an ancestral condition for the family. Additionally, the presence of a bifurcated scapular spine in other non-fossorial small mammals, as well as in bathyergids would not necessarily represent a lack of fossorial specialization but most likely a homologous character adjusted to different functions and complex kinematics carried out by the scapula in tooth-diggers (see Gambaryan & Gasc, 1993; Jarvis & Sale, 1971).

The muscles contributing to powerful shoulder flexion and scapular adduction, such as m. infraspinatus and m. subscapularis were also relatively more robust and occupied a larger surface area in the scapula of *Bathyergus*. These muscles are well-developed in scratch-diggers and favor the adduction and retraction of the arm (Olson et al., 2016). For example, Thewissen and Badoux (1986) report considerable rotation and strong adduction of the forelimb by the scapular muscles in the aardvark. Powerful shoulder flexion in *Bathyergus* was also improved by having a more developed m. teres major, correspondingly broader attachment area in the teres major process, and a more distal insertion of this muscle onto the teres tuberosity in the humerus as compared to the other species (Figure 6), thus increasing the (perpendicular) distance of the line of action from the joint center of rotation. The m. teres minor was distinct and quite similar among all species, although it was documented fused to the m. subscapularis in *He. glaber* (Doubell et al., 2020). In our specimens, such muscles were continuous but not fused.

Three deltoids were observed in all species, although its parts are more distinct in *Heliophobius*, and variably fused in the other genera: the deepest parts, the pars acromialis and pars clavicularis are more difficult to separate in *Bathyergus* and *Georychus*. Doubell et al. (2020) mention that these two parts were fused in all their specimens of *B. suillus*, while the three parts are distinct and easily separable in *He. glaber*, thus resembling the condition of *Heliophobius* of our study. Doubell et al. (2020) also describe a separate insertion of the pars scapularis (=spinalis) and pars acromialis on the opposite sides of the deltoid tuberosity in *B. suillus*, and proposes that the actions of these two heads are in opposition. Such configuration and interpretation are unlikely for *B. suillus*, since in our study these two parts are associated with the scapula and acromion, and inserted on the lateral and cranial side of the tuberosity, respectively, while the clavicular part (more internal) is inserted onto the medial side of the tuberosity. Despite some of our specimens showed certain association of the pars acromialis with the medial side of the tuberosity, this would not involve totally opposed actions. In this sense, the "pars acromialis" described by Doubell et al. (2020) could correspond to the pars clavicularis. Although the deltoids were more developed in *Bathyergus*, all the species showed a prominent and distally located deltoid tuberosity. This bony configuration increases the line

of action of deltoids allowing stronger shoulder flexion and forelimb retraction, whereas regulation of forelimb adduction and abduction (Hildebrand, 1985; Lessa & Stein, 1992; Stein, 2000). Among these muscles, the pars scapularis of *Bathyergus* has a wider surface area of origin as compared to the other genera, covering a large part of the m. infraspinatus and thus suggesting an increased ability to flex the shoulder in this taxon.

The muscles that allow a powerful extension of the elbow were quite similar among species, although the muscles of *Bathyergus* were slightly more robust. The m. triceps brachii was enlarged in all species studied here, although the caput longum, caput laterale, and caput mediale were relatively less developed in *Georychus*. For example, the caput longum is larger and more fused in *Bathyergus* and *Heliophobius*, while *Georychus* has a smaller (and elongated) muscle, which sometimes has two easily separable parts. The caput mediale was fused to the m. anconeus, which forms a broad insertion onto the dorsal surface of the olecranon process, thus being one of the most important muscles for the extension of the elbow. In this sense, *Bathyergus* showed a dorsally wider olecranon (Figure 10) in comparison to the other species, which allows a better attachment and larger size of the m. anconeus and m. triceps brachii. This is not unexpected for a scratch-digger, but *Heliophobius* also showed a well-developed olecranon, particularly in comparison to *Georychus*. Such morpho-functional similarities between *B. suillus* and *H. argenteocinereus* were also previously reported by Montoya-Sanhueza, Bennett, et al. (2022). For example, the index of fossorial ability (IFA: proportional length of the olecranon in relation to the total length of the ulna) is similar between *B. suillus* (IFA=0.313, Montoya-Sanhueza et al., 2019) and *H. argenteocinereus* (IFA=0.306), and both more developed than in *G. capensis* (IFA=0.276; Montoya-Sanhueza, Bennett, et al., 2022). In the same study, *Heliophobius* also showed the most distally located deltoid tuberosity and the thickest relative craniocaudal diameter of the ulna among bathyergids (Montoya-Sanhueza, Bennett, et al., 2022). Such adaptations in the humerus and ulna of *Heliophobius* appear more developed than in other tooth-diggers of the family, such as *Fukomys* and *Cryptomys*, suggesting increased mechanical advantage and power-stroke (flexion/retraction) of the forearm, extension of the elbow, and bending resistance of the ulna (Montoya-Sanhueza, Bennett, et al., 2022). This information, along with the well-developed muscles of *Heliophobius*, suggests an important mechanical advantage for scratch-digging behavior.

The m. biceps brachii was quite similar in all bathyergids studied, having a dual origin from the coracoid process and the supraglenoid tubercle. It is probable that given the “secondary” contribution of this muscle for scratch-digging behavior (aiding with recovery stroke), it may not experience considerable morphological specialization in bathyergids. This muscle was inserted onto both forearm bones in *Bathyergus* and *Georychus*, while only to the radius in *Heliophobius*, thus suggesting a broader insertion and, therefore, a better distal specialization for stronger elbow flexion in the former taxa. Doubell et al. (2020) also reported a single insertion in *He. glaber*, but onto the ulna. Deep to this muscle, and only in *Bathyergus*, was the m. articularis humeri (Figure 9e,f), which is a very thin and relatively

long muscle located in the proximal part of the humerus, aiding with extension and adduction of the forelimb. Because of its small size in other subterranean rodents, such as *T. bottae* it has been regarded as an unimportant adductor of the arm (Holliger, 1916). The absence of the m. articularis humeri in *Heliophobius* and *Georychus* confirm the findings of Parsons (1894), who stated its absence in *Georychus*. This muscle was also absent in *He. glaber* (Doubell et al., 2020), suggesting that it might be exclusive to the *Bathyergus* lineage, although further assessment of other members of the family (*Fukomys* and *Cryptomys*) is needed to corroborate this hypothesis. Parsons (1894) mentions that this muscle was not located in one of the specimens of *B. suillus* studied by Milne-Edwards & Milne-Edwards (*vide in* Parsons, 1894), whereby intraspecific variation could be present in this species. Similarly, Marshall et al. (2021) carried out a myological study of the armadillo *Zaedyus pichiy* demonstrating its presence in most specimens, except by one animal, which lacked such muscle. This indicates that intraspecific variation for this muscle is present in a wide range of mammalian species. The absence of this muscle in the tooth-diggers is unlikely to be the result of intraspecific variation, because our representative number of individuals including both sexes. Its absence in the basal member of the family *He. glaber* (Doubell et al., 2020) would rather suggest an early modification (probably lost) within the family. Another muscle contributing to antebrachial pronation was the m. pronator teres, which showed similar development in *Bathyergus* and *Heliophobius*, but more reduced in *Georychus*.

One remarkable difference among species was the presence of the m. tensor fasciae antebrachii in *Bathyergus* and *Georychus*, but its absence in *Heliophobius* (Figure 9a–d). This is a superficial muscle aiding with elbow extension and limb retraction (Böhmer et al., 2021), which is normally present in many hystricomorphs and rodents in general (Gambaryan et al., 2013; Parsons, 1896, 1894). It rises from the belly of m. latissimus dorsi and inserts onto the medial side of the olecranon (Parsons, 1894). It is generally small and fleshy, although specially well-developed in semiaquatic forms, such as *Castor* (Parsons, 1894). In some hystricomorphs (e.g. *Chinchilla*; Gambaryan et al., 2013), and fossorial xenarthrans (Olson et al., 2016), it originates from the external fascia of the m. latissimus dorsi. Therefore, this muscle seems to be very plastic, with a high degree of intraspecific and interspecific variation among mammals (e.g. Gambaryan et al., 2013; Greene, 1935; Warburton et al., 2014). In *Bathyergus*, the m. tensor fasciae antebrachii originates from a central part of the m. latissimus dorsi, while in *Georychus* from the most ventral border of the same muscle, close to its ventral insertion (Figure 9a–c). This muscle was also absent in *He. glaber* (Doubell et al., 2020), whereby its absence in both most basal members of the family *Heliophobius* and *Heterocephalus* may represent a plesiomorphic feature of the group. In fact, this muscle is present in many other rodents including basal hystricomorphs (e.g. *Laonastes* and *Ctenodactylus*) suggesting a loss in the basal Bathyergidae (see Gambaryan et al., 2013), while its origin in *Bathyergus* and *Georychus* may be an evolutionary novelty. Because this muscle attaches onto the m. latissimus dorsi and the olecranon, its function as an additional limb retractor and elbow joint

extensor becomes evident, since it pulls the elbow internally against the body and/or backwards by the conjoined action of the *m. latissimus dorsi* (e.g. Warburton et al., 2014). This is particularly true for *Bathyergus*, where the *m. tensor fasciae antebrachii* is quite thick, although its presence in *G. capensis* is intriguing since this species shows comparatively more reduced scratch-digging specializations. It is probable that the development of this muscle in *Bathyergidae* responded to increased scratch-digging demands in the ancestors that gave rise to both *Bathyergus* and *Georychus*, whereby it could be hypothesized a potential scratch-digging mode for the fossil ancestors of these genera. Further clarification of such a scenario will require additional examinations of superficial and thoracic muscles among bathyergids (e.g. *m. latissimus dorsi*, *mm. pectorales*), as well as the inclusion of developmental data and a larger sample of individuals of different ontogenetic stages. It is important to note that the lack of the *m. articularis humeri* and *m. tensor fasciae antebrachii* in *Heliophobius* and *Heterocephalus* probably does not reflect adaptations for tooth-digging, as suggested by Doubell et al. (2020) for the latter taxon. Such interpretation is premature, since in our study *m. tensor fasciae antebrachii* was found in *Georychus*, and is known to be present in many other non-fossorial rodents (Gambaryan et al., 2013; Parsons, 1896). Most importantly, the lack of a muscle hardly would indicate adaptation, but rather its presence would do it.

In general, the carpal and digital flexors of *Bathyergus* were also more robust, tightly attached to bone surfaces (e.g. epicondyle, olecranon, medial and lateral fossae of the ulna) and usually covering wider bone surface areas than in *Heliophobius* and *Georychus* (Figure 10). Moreover, *Bathyergus* usually showed fused muscles and tendons. The *m. flexor carpi radialis* in *Bathyergus* and *Georychus* are quite fused to *m. flexor digitorum profundus*. Similarly, the *m. flexor carpi ulnaris* is well-developed and also fused in *Bathyergus* and *Heliophobius*. The belly of the *m. flexor digitorum superficialis* divides into two thick tendons inserting onto the hand, while *Heliophobius* and *Georychus* show three tendons. The *m. flexor digitorum profundus* is similar among species, although the radial part has a broader attachment in *Bathyergus*, is reduced in *Georychus* (with some individuals lacking such attachment), and absent in *Heliophobius*. The *m. pronator quadratus* is considerably larger in *Bathyergus* than in *Heliophobius* and *Georychus*. This is probably related to the lesser degree of connection between the radius and ulna in *Bathyergus*, so that this muscle is larger to keep these bones together, while the surfaces of the ulna and radius of *Heliophobius* and *Georychus* are much more connected, precluding the development of a larger muscle to keep such connection. Thus, the forearm muscles of *Bathyergus* appear more specialized to generate larger forces with their forefeet and digits as compared to *Heliophobius* and *Georychus*, which is ultimately evidenced by the long foreclaws of *Bathyergus* (Montoya-Sanhueza, Bennett, et al., 2022). Larger and stronger flexors were also reflected in the anatomical features of the ulna. Among these, the ulna of *Bathyergus* (and to some extent also of *Heliophobius*) showed considerable medial orientation of the olecranon, which contributes to an increased curvature of the bone and therefore increases the (perpendicular) distance of the line of action of the

flexors, suggesting a greater functional efficiency to flex the wrist and digits in comparison to *Georychus*. A similar curved morphology has been observed in other scratch-diggers (Hildebrand, 1985; Vassallo, 1998). Such curvature determines the line of action of digital and carpal flexor muscles, so that a greater ulnar curvature will provide greater effective forces for muscles which originate in the olecranon and in the medial epicondyle of the humerus (Fernández et al., 2000).

Overall, our results show the better specialized musculoskeletal system of *Bathyergus* allowing to perform stronger and efficient parasagittal scratch-digging. The fact that several muscles in *Bathyergus* were tightly continuous (often fused), demonstrates clear adaptations to increase muscle size and strength. Additionally, our analysis indicates that most functional requirements needed for maximizing scratch-digging behavior are concentrated in the shoulder (scapula) and the elbow (olecranon) joints, which are fundamental pivots for generating greater out-forces. Nevertheless, the morphological similarity between *B. suillus* and *H. argenteocinereus* may explain why previous comparative studies of energy expenditure among tooth-diggers found that the latter taxon digs more efficiently (spending less energy for burrowing per distance burrowed in the same soil type) than the social *F. mechowii* (Zelová et al., 2010), despite both occupy habitats with similar soil and food characteristics (Šumbera et al., 2012). These data seems to conform to the fact that *Heliophobius* appears as the least forceful biter among all tooth-digger genera in the family, having quite similar values to *B. suillus* (Kraus et al., 2022). If this is further confirmed, digging performance and energy expenditure may have been reduced due to morphological specializations in the forelimb of *Heliophobius*. However, as the latter authors mention, other factors including low sample size and old age of the specimens of *Heliophobius* may also affect such bite force estimations (Kraus et al., 2022). Moreover, the morphological similarities in the appendicular system among the solitary bathyergids, particularly the low variation in the muscles and muscle attachments in the arm (humerus, Figure 8) also highlights the overall processes of limb convergence in the family for burrow construction (Montoya-Sanhueza, Bennett, et al., 2022; Montoya-Sanhueza, Šaffa, et al., 2022). In this way, fossorial adaptations in bathyergids have a modular nature, where certain features (e.g. humerus) appear similarly optimized for multiple functions while others (e.g. scapula and ulna) experience more dramatic changes to maximize its functionality according to different digging demands. Therefore, it is clear that tooth-diggers develop a similar set of adaptations as scratch-diggers (Hildebrand, 1985), although marked differences can also be detected among these digging groups (Doubell et al., 2020; and our study). Specifically, skeletal similarity between these two digging groups appears to be associated with variation of continuous characters (e.g. width, length, surface area, etc.), while the differences observed at the myological level appears not to be only related to continuous characters but also with discrete characters (e.g. presence or absence of certain muscles), probably implying deeper phenotypic modifications at morphogenetic level throughout their phylogenetic history. The evolution and loss of both superficial and

deep muscles among bathyergids suggests strong but differential selective pressures acting among these highly specialized mammals, involving not only phylogenetic, ecological and physiological factors (Nevo, 1979) but also functional and behavioral.

In summary, this study improves considerably our understanding of the morphological diversity of the family Bathyergidae, as well as the morphological and functional divergence of the forelimb musculoskeletal system of rodents. Additionally, the inclusion of all solitary species within the family allowed us to reduce the potential confounding effects that social organization (e.g. effect of cooperative foraging) and considerably disparate phenotypes (e.g. *He. glaber*) may have on our observations. A strong functional relationship is found in the neck muscles and the scapular shape, which revealed the somehow overlooked role of their complex interaction for forward force production for breaking-up soils in tooth-diggers. In this sense, although morphological changes in the scapula of other fossorial rodents (e.g. *Ctenomys* and *Spalacopus*) have been disregarded as indicators of fossorial specialization (Morgan, 2015), our findings suggest the contrary: modifications in the arrangement of the m. rhomboideus and the corresponding morphological changes of the scapula of *Bathyergus* are potential indicators of specific digging abilities in this family. Our results also show that despite the clear scratch-digging specialization of *Bathyergus*, the tooth-digger *Heliophobius* also showed some degree of forelimb specialization. Whether such scratch-digging specialization reflects truly augmented forefoot scrapping capabilities it is unknown, so that in addition to fine analyses of the neck musculature and scapular morphology of bathyergids, other studies integrating kinematics assessments of digging behavior and locomotion in these strictly subterranean mammals are needed, e.g. to know the magnitude of scratch-digging behavior in tooth-diggers, kinematics of the head-neck-shoulder system and potential differences between solitary and social taxa. Additionally, we increased considerably the number of specimens and taxa analyzed for the family as compared to previous studies, which allowed us to clarify several misunderstandings about the presence, absence, origin and insertion of their muscles. This and previous anatomical studies on the Bathyergidae will provide researchers a substantial basis on form and function of the musculoskeletal system for future kinematic investigations of digging behavior, as well as for paleobiological inferences in the fossil record.

ACKNOWLEDGEMENTS

We thank to Jennifer Jarvis and Kate Cuthbert for kindly granting us access to specimens and data of the mole-rat species analyzed here. Discussions and suggestions on mammalian muscle anatomy made by M. Butcher, O. Zherebtsova and C. García-Esponda greatly contributed to improve the quality of this manuscript. I am also very grateful for the constant help and support of Lucie Montoya Sanhueza and Felipe Ruedlinger in completing the large number of dissections of this work. Many thanks to J. Okrouhlik and M. Lovy for their kind help during this project. This project was supported by the Czech Science Foundation project GAČR (20-10222S). Open access publishing

facilitated by Jihočeská Univerzita v Českých Budejovicích, as part of the Wiley - CzechELib agreement.


CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data supporting our findings are available in the present study in the form of tables and figures.

ORCID

Germán Montoya-Sanhueza  <https://orcid.org/0000-0002-3363-2827>

Nigel C. Bennett  <https://orcid.org/0000-0001-9748-2947>

Radim Šumbera  <https://orcid.org/0000-0001-8658-9378>

REFERENCES

- Acuña, F., Sidorkewicz, N.S., Popp, A.I. & Casanave, E.B. (2017) A geometric morphometric study of sex differences in the scapula, humerus and ulna of *Chaetophractus villosus* (Xenarthra, Dasypodidae). *Iheringia Série Zoologia*, 107, e2017010.
- Adobe Inc. (2015) Adobe Photoshop. Available from: <https://www.adobe.com/products/photoshop.html>
- Böhmer, C., Theil, J.-C., Fabre, A.-C. & Herrel, A. (2021) *Atlas of terrestrial mammal limbs*, 1st edition. Boca Raton, FL: CRC Press.
- Bennett, N.C. & Faulkes, C.G. (2000) *African mole rats: ecology and eusociality*. Cambridge, UK: Cambridge University Press.
- Bennett, N.C., Faulkes, C.G., Hart, L. & Jarvis, J. (2009) *Bathyergus suillus* (Rodentia: Bathyergidae). *Mammalian Species*, 828, 1–7.
- Bryja, J., Konvičková, H., Bryjová, A., Mikula, O., Makundi, R., Chitaukali, W.N. et al. (2018) Differentiation underground: range-wide multilocus genetic structure of the silvery mole-rat does not support current taxonomy based on mitochondrial sequences. *Mammalian Biology*, 93, 82–92.
- Cain, B.W., Reynolds, T. & Sarko, D.K. (2019) Superficial, suprahyoid, and infrahyoid neck musculature in naked mole-rats (*Heterocephalus glaber*): relative size and potential contributions to independent movement of the lower incisors. *Journal of Morphology*, 280, 1185–1196.
- Cox, P.G. & Faulkes, C.G. (2014) Digital dissection of the masticatory muscles of the naked mole-rat, *Heterocephalus glaber* (Mammalia, Rodentia). *PeerJ*, 2, e448.
- Cox, P.G., Faulkes, C.G. & Bennett, N.C. (2020) Masticatory musculature of the African mole-rats (Rodentia: Bathyergidae). *PeerJ*, 8, e8847. Available from: <https://doi.org/10.7717/peerj.8847>
- Cuthbert, K. (1975) *Burrowing and the associated modifications in the mole-rats Bathyergus suillus and Georchus capensis - a comparative study*. Cape Town, South Africa: Zoology Honours Project, University of Cape Town.
- Doubell, N.S., Sahl, L. & Kotzé, S.H. (2020) Comparative forelimb morphology of scratch-digging and chisel-tooth digging African mole-rat species. *Journal of Morphology*, 281, 1029–1046.
- Ercoli, M.D., Álvarez, A., Stefanini, M.I., Busker, F. & Morales, M.M. (2015) Muscular anatomy of the forelimbs of the lesser grison (*Galictis cuja*), and a functional and phylogenetic overview of Mustelidae and other Caniformia. *Journal of Mammalian Evolution*, 22, 557–591.
- Fernández, M.E., Vassallo, A.I. & Zárate, M. (2000) Functional morphology and palaeobiology of the Pliocene rodent *Actenomys* (Caviomorpha: Octodontidae): the evolution to a subterranean mode of life. *Biological Journal of the Linnean Society of London*, 71, 71–90.

- Fischer, M.S., Schilling, N., Schmidt, M., Haarhaus, D. & Witte, H. (2002) Basic limb kinematics of small therian mammals. *Journal of Experimental Biology*, 205, 1315–1338.
- Fournier, M., Hautier, L. & Gomes Rodrigues, H. (2021) Evolution towards Fossoriality and morphological convergence in the skull of Spalacidae and Bathyergidae (Rodentia). *Journal of Mammalian Evolution*, 28, 979–993.
- Gambaryan, P.P. & Gasc, J.-P. (1993) Adaptive properties of the musculoskeletal system in the mole-rat *Myospalax myospalax* (Mammalia, Rodentia), cinefluorographical, anatomical and biomechanical analyses of the burrowing. *Zoologische Jahrbuch, Anatomie*, 123, 363–401.
- Gambaryan, P.P., Zherebtsova, O.V. & Perepelova, A.A. (2013) Comparative analysis of forelimb musculature in *Laonastes aenigmamus* (Rodentia: Diatomyidae). *Proceedings of the Zoological Institute RAS*, 317(3), 226–245.
- García-Esponda, C.M., Calanocce, A.R. & Candela, A.M. (2021) Brachiocephalic muscular arrangements in cavioid rodents (Caviomorpha): a Functional, anatomical, and evolutionary study. *Journal of Mammalian Evolution*, 28, 529–541.
- Gasse, H., Van Den Broeck, W., Egerbacher, M., Staszuk, C., Budras, K.-D., Constantinescu, G.M. et al. (2017) *Nomina Anatomica Veterinaria*, 6th edition. Hanover: International Committee on Veterinary Gross Anatomical Nomenclature.
- Genelly, R.E. (1965) Ecology of the common mole-rat (*Cryptomys hottentotus*) in Rhodesia. *Journal of Mammalogy*, 46, 647–665.
- Gomes Rodrigues, H., Šumbera, R. & Hautier, L. (2016) Life in burrows channelled the morphological evolution of the skull in rodents: the case of African mole-rats (Bathyergidae, Rodentia). *Journal of Mammalian Evolution*, 23, 175–189. Available from: <https://doi.org/10.1007/s10914-015-9305-x>
- Gomes Rodrigues, H., Šumbera, R., Hautier, L. & Herrel, A. (2023) Digging up convergence in fossorial rodents: insights into burrowing activity and Morpho-functional specializations of the masticatory apparatus. In: Bels, V.L. & Russell, A.P. (Eds.) *Convergent Evolution*. Springer, Cham: Fascinating Life Sciences.
- Greene, E.C. (1935) The anatomy of the rat. *Transactions of the American Philosophical Society*, 27, 1–370.
- Hamilton, W.J., Jr. (1928) *Heterocephalus*, the remarkable African burrowing rodent. *The Museum of the Brooklyn Institute of Arts and Sciences*, 3(5), 173–191.
- Herbst, M. & Bennett, N.C. (2006) The burrow architecture and burrowing dynamics of the endangered Namaqua dune mole-rat, *Bathyergus janetta* (Rodentia: Bathyergidae). *Journal of Zoology*, 270, 420–428.
- Hildebrand, M. (1985) Digging of quadrupeds. In: Hildebrand, M., Bramble, D., Liem, K. & Wake, D.B. (Eds.) *Functional vertebrate morphology*. Massachusetts and London: The Belknap Press of Harvard University Press, pp. 89–109.
- Hill, J.E. (1937) *Morphology of the pocket gopher mammalian genus Thomomys*, Vol. 42. Berkeley: University of California Publications in Zoology, pp. 81–171.
- Hite, N.J., Germain, C., Cain, B.W., Sheldon, M., Perala, S.S.N. & Sarko, D.K. (2019) The better to eat you with: bite force in the naked mole-rat (*Heterocephalus glaber*) is stronger than predicted based on body size. *Frontiers in Integrative Neuroscience*, 13, 70.
- Holliger, C.D. (1916) Anatomical adaptations in the thoracic limb of the California pocket gopher and other rodents. *Zoology, University of California Publications*, 13, 447–494.
- Howell, B. (1965) *Speed in mammals, their specialization for running and leaping*. New York and London: Hafner Publishing Company.
- Jarvis, J. & Sale, J. (1971) Burrowing and burrow patterns of east African mole-rats *Tachyoryctes*, *Heliophobius* and *Heterocephalus*. *Journal of Zoology*, 163, 451–479.
- Jenkins, P.A. & Weijs, W.A. (1979) The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). *Journal of Zoology*, 188, 379–410.
- Klingener, D. (1964) The comparative myology of four dipodoid rodents (Genera *Zapus*, *Napaeozapus*, *Sicista*, and *Jaculus*). *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 124, 1–100.
- Klingener, D. (1970) Superficial Facial Musculature of Aplodontia. *Journal of Mammalogy*, 51(1), 35–41.
- Kraus, A., Lövy, M., Mikula, O., Okrouhlik, J., Bennett, N.C., Herrel, A. et al. (2022) Bite force in the strictly subterranean rodent family of African mole-rats (Bathyergidae): the role of digging mode, social organization and ecology. *Functional Ecology*, 36, 2344–2355.
- Lövy, M., Šklíba, J., Burda, H., Chitaukali, W.N. & Šumbera, R. (2012) Mole-rat habitat characteristics. *Journal of Zoology*, 286, 145–153.
- Lehmann, W.H. (1963) The forelimb architecture of some fossorial rodents. *Journal of Morphology*, 113, 59–76.
- Lessa, E.P. & Stein, B.R. (1992) Morphological constraints in the digging apparatus of pocket gophers (Mammalia, Geomyidae). *Biological Journal of the Linnean Society*, 47(4), 439–453.
- Marcy, A.E., Hadly, E.A., Sherratt, E., Garland, K. & Weisbecker, V. (2016) Getting a head in hard soils: convergent skull evolution and divergent allometric patterns explain shape variation in a highly diverse genus of pocket gophers (Thomomys). *BMC Evolutionary Biology*, 16, 207.
- Marshall, S.K., Superina, M., Spainhower, K.B. & Butcher, M.T. (2021) Forelimb myology of armadillos (Xenarthra: Cingulata, Chlamyphoridae): anatomical correlates with fossorial ability. *Journal of Anatomy*, 238, 551–575.
- McIntosh, A.F. & Cox, P.G. (2016a) Functional implications of craniomandibular morphology in African mole-rats (Rodentia: Bathyergidae). *Biological Journal of the Linnean Society*, 117, 447–462.
- McIntosh, A.F. & Cox, P.G. (2016b) The impact of gape on the performance of the skull in chisel-tooth digging and scratch digging mole-rats (Rodentia: Bathyergidae). *Royal Society Open Science*, 3, 160568.
- Miles, S.T. (1941) The shoulder anatomy of the armadillo. *Journal of Mammalogy*, 22, 157–169.
- Milne-Edwards, H., Huet, L., Mesnel, A., Milne-Edwards, A. & Severeys, G. (1868) Recherches pour servir à l'histoire naturelle des mammifères: comprenant des considérations sur la classification de ces animaux. Available from: <https://doi.org/10.5962/bhl.title.59889>
- Montoya-Sanhueza, G., Bennett, N.C., Chinsamy, A. & Šumbera, R. (2022) Functional anatomy and disparity of the postcranial skeleton of African mole-rats (Bathyergidae). *Frontiers in Ecology and Evolution*, 10, 857474. Available from: <https://doi.org/10.3389/fevo.2022.857474>
- Montoya-Sanhueza, G., Šaffa, G., Šumbera, R., Chinsamy, A., Jarvis, J.U.M. & Bennett, N.C. (2022) Fossorial adaptations in African mole-rats (Bathyergidae) and the unique appendicular phenotype of naked mole-rats. *Communications Biology*, 5, 526.
- Montoya-Sanhueza, G., Šumbera, R., Bennett, N.C. & Chinsamy, A. (2022) Developmental plasticity in the ossification of the proximal femur of *Heterocephalus glaber* (Bathyergidae, Rodentia). *Journal of Mammalian Evolution*, 29, 663–675.
- Montoya-Sanhueza, G., Wilson, L.A.B. & Chinsamy, A. (2019) Postnatal development of the largest subterranean mammal (*Bathyergus suillus*): Morphology, osteogenesis, and modularity of the appendicular skeleton. *Developmental Dynamics*, 248, 1101–1128.
- Moore, A.L., Budny, J.E., Russell, A.P. & Butcher, M.T. (2013) Architectural specialization of the intrinsic thoracic limb musculature of the American badger (*Taxidea taxus*). *Journal of Morphology*, 274(1), 35–48.
- Morgan, C.C. (2009) Geometric morphometrics of the scapula of South American caviomorph rodents (Rodentia: Hystricognathi): form, function and phylogeny. *Mammalian Biology*, 74, 497–506.
- Morgan, C.C. (2015) The postcranial skeleton of caviomorphs: morphological diversity, adaptations and patterns. Ch 5. *SAREM Series A - Mammalogical Research*, 1, 167–198.
- Mpagike, F.H. & Makungu, M. (2023) Osteology and radiographic anatomy of the thoracic limb of the greater cane rat (*Thryonomys swinderianus*). *Anatomia, Histologia, Embryologia*, 52(3), 393–402.

- Nakai, D. & Fujiwara, S. (2023) Fossorial mammals emphasise the forelimb muscle moment arms used for digging: new indices for reconstruction of the digging ability and behaviours in extinct taxa. *Journal of Anatomy*, 242, 846–861.
- Nevo, E. (1979) Adaptive convergence and divergence of subterranean mammals. *Annual Review of Ecology and Systematics*, 10, 269–308.
- Nevo, E. (1999) *Mosaic evolution of subterranean mammals: regression, progression and global convergence*. Oxford: Oxford University Press.
- Olson, R.A., Womble, M.D., Thomas, D.R., Glenn, Z.D. & Butcher, M.T. (2016) Functional morphology of the forelimb of the nine-banded armadillo (*Dasypus novemcinctus*): comparative perspectives on the myology of Dasypodidae. *Journal of Mammalian Evolution*, 23, 49–69.
- Onwuama, K.T., Adeniyi, O.S., Olajide, H.J., Tavershima, D. & Sulaiman, S.O. (2015) Macro-anatomical and morphometric studies of the Grasscutter (*Thryonomys winderianus*) forelimb skeleton. *International Journal of Veterinary Sciences and Animal Husbandry*, 2(1), 6–12.
- Orcutt, E.E. (1940) Studies on the muscles of the head, neck, and pectoral appendages of *Geomys bursarius*. *Journal of Mammalogy*, 21, 37–52.
- Parsons, F.G. (1894) On the myology of the sciuriform and hystricomorphine rodents. *Proceedings Zoological Society of London*, 18, 251–297.
- Parsons, F.G. (1896) Myology of rodents –part II. An account of the myology of the Myomorpha, together with a comparison of the muscles of the various suborders of rodents. *Journal of Zoology*, 64, 159–192.
- Sahd, L., Bennett, N.C. & Kotzé, S.H. (2019) Hind foot drumming: morphological adaptations of the muscles and bones of the hind limb in three African mole-rat species. *Journal of Anatomy*, 235, 811–824.
- Sahd, L., Bennett, N.C. & Kotzé, S.H. (2020) Hind foot drumming: Morphofunctional analysis of the hind limb osteology in three species of African mole-rats (Bathyergidae). *Journal of Morphology*, 281, 438–449.
- Sahd, L., Doubell, N., Bennett, N.C. & Kotzé, S.H. (2023) Muscle architecture and muscle fibre type composition in the forelimb of two African mole-rat species, *Bathyergus suillus* and *Heterocephalus glaber*. *Journal of Morphology*, 284, e21557.
- Salton, J.A. & Sargis, E.J. (2008) Evolutionary morphology of the Tenrecoidea (Mammalia) forelimb skeleton. In: Sargis, E. & Dagosto, M. (Eds.) *Mammalian evolutionary morphology, a tribute to Frederick S. Szalay*. Dordrecht: Springer Netherlands, pp. 51–72.
- Seckel, L. & Janis, C. (2008) Convergences in scapula morphology among small cursorial mammals: an osteological correlate for locomotory specialization. *Journal of Mammalian Evolution*, 15, 261–279.
- Stein, B. (2000) Morphology of subterranean rodents. In: Lacey, E.A., Patton, J. & Cameron, G.N. (Eds.) *Life underground: the biology of subterranean rodents*. Chicago: The University of Chicago Press, pp. 19–61.
- Šumbera, R., Chitaukali, W.N. & Burda, H. (2007) Biology of the silvery mole-rat (*Heliophobius argenteocinereus*). Why study a neglected subterranean rodent species? In: *Subterranean rodents: news from underground*. Berlin Heidelberg New York: Springer-Verlag, pp. 220–236.
- Šumbera, R., Mazoch, V., Patzenhauerová, H., Lövy, M., Šklíba, J., Bryja, J. et al. (2012) Burrow architecture, family composition and habitat characteristics of the largest social African mole-rat: the giant mole-rat constructs really giant burrow systems. *Acta Theriologica*, 57(2), 121–130.
- Thewissen, J.G.M. & Badoux, D.M. (1986) The descriptive and functional myology of the fore-limb of the aardvark (*Orycteropus afer*, Pallas 1766). *Anatomischer Anzeiger*, 162, 109–123.
- Thorington, R.W., Darrow, K. & Betts, A.D.K. (1997) Comparative myology of the forelimb of squirrels. *Journal of Morphology*, 234, 155–182.
- Uhrová, M., Mikula, O., Bennett, N.C., van Daele, P., Piálek, L., Bryja, J. et al. (2022) Species limits and phylogeographic structure in two genera of solitary African mole-rats *Georchus* and *Heliophobius*. *Molecular Phylogenetics and Evolution*, 167, 107337.
- Van Daele, P.A., Herrel, A. & Adriaens, D. (2009) Biting performance in teeth-digging African mole-rats (*Fukomys*, Bathyergidae, Rodentia). *Physiological and Biochemical Zoology*, 82(1), 40–50. Available from: <https://doi.org/10.1086/594379>
- Van Wassenbergh, S., Heindryckx, S. & Adriaens, D. (2017) Kinematics of chisel-tooth digging by African mole-rats. *Journal of Experimental Biology*, 220(23), 4479–4485.
- Vassallo, A.I. (1998) Functional morphology, comparative behaviour, and adaptation in two sympatric subterranean rodents genus *Ctenomys* (Caviomorpha: Octodontidae). *Journal of Zoology*, 244, 415–427.
- Visser, J.H., Bennett, N.C. & Jansen van Vuuren, B. (2017) Distributional range, ecology, and mating system of the cape mole-rat (*Georchus capensis*) family Bathyergidae. *Canadian Journal of Zoology*, 95(10), 713–726.
- Warburton, N.M., Lea, G., Sandra, J. & Camille, F. (2014) Adaptations for digging in the forelimb muscle anatomy of the southern brown bandicoot (*Isodon obesulus*) and bilby (*Macrotis lagotis*). *Australian Journal of Zoology*, 61, 402–419.
- Woods, C.A. (1972) Comparative myology of jaw, hyoid and pectoral appendicular regions of new and Old World Hystricomorph rodents. *Bulletin of the American Museum of Natural History*, 147, 115–198.
- Zelová, J., Šumbera, R., Okrouhlík, J. & Burda, H. (2010) Cost of digging is determined by intrinsic factors rather than by substrate quality in two subterranean rodent species. *Physiology and Behavior*, 99(1), 54–58.

How to cite this article: Montoya-Sanhueza, G., Bennett, N.C. & Šumbera, R. (2024) Functional and morphological divergence in the forelimb musculoskeletal system of scratch-digging subterranean mammals (Rodentia: Bathyergidae). *Journal of Anatomy*, 245, 420–450. Available from: <https://doi.org/10.1111/joa.14058>