Chapter 3
Digging Up Convergence in Fossorial Rodents: Insights into Burrowing Activity and Morpho-Functional Specializations of the Masticatory Apparatus

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Abstract Fossorial habits are tightly related to digging abilities in vertebrates and the most extreme fossorial specialization is being restricted to conducting the entire life underground. Many mammals, especially rodents, show behavioural, morphological and physiological adaptations to fossorial life, mainly for gaining access to sources of food and escaping predators and extreme climatic fluctuations. Adaptations to fossorial life are found in more than ten families of extant and extinct rodents, on most continents. Examples are Eurasian mole voles (Cricetidae), African mole-rats (Bathyergidae) and root-rats, Asian zokors and bamboo rats (Spalacidae), North American pocket gophers (Geomyidae) and mountain beavers (Aplodontidae), and South American tuco-tucos (Ctenomyidae) and cururos (Octodontidae). The constraints imposed by digging and living underground have led to strong behavioural and morphological convergences, notably involving the functioning of the rodent masticatory apparatus. Whereas most mammals use their claws for digging, rodents are unique in that some species use their ever-growing incisors for this purpose, with most subterranean species having become chisel-tooth

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diggers. Here, we review examples of convergence found in the main morphological and functional components of the rodent digging apparatus in relation to burrowing activity. We first present the different modes of digging in rodents, focusing on the chisel-tooth digging mechanisms and their associated burrowing behaviours. Following this, several morphological specializations of the skull and the main jaw adductor muscles are described in relation to their associated contribution to biting efficiency. Specialized incisors allow subterranean rodents to dig in hard soil and to consume hard subterranean parts of plants, and their morphological and structural characteristics are considered in the last part of this chapter. Data on incisor bite force of fossorial rodents are also compiled to highlight the enhanced efficacy of the masticatory apparatus of chisel-tooth digging species. Despite the different cranial and muscular morphotypes in rodents, we underscore the fact that multiple modifications of the different components of the masticatory apparatus have led to similar overall morphologies and functions, overcoming phylogenetic inheritance. This remarkable example of convergence needs further scrutiny at both the micro- and macroevolutionary level to more fully understand how different rodent families evolved to deal with such external constraints.

Keywords Chisel-tooth digging activity · Cranial specializations · Masticatory muscles · Incisor procumbency · Bite force

3.1 Introduction

Fossorial mammals (that is, mammals adapted for digging) spend most of their life burrowing and transporting excavated soil. Although burrowing is energetically very costly (see Zelová et al., 2010 for an overview), many vertebrate taxa have adapted to the subterranean environment as it provides microclimatic stability, a relatively stable food supply, and a low risk of predation (Nevo, 1979, 1999; Burda et al., 2007). Many lineages of mammaliaforms and mammals, especially rodents, have independently colonised this environment at different times since the Mesozoic (e.g. Nevo, 1979; Cook et al., 2000; Luo & Wible, 2005). Life in subterranean burrow systems and the need to dig for large part of the day have stimulated the independent, but repeated evolution of many genetic, morphological, behavioural, and physiological adaptations (e.g. Nevo, 1979; Lacey et al., 2000; Partha et al., 2017). These specializations make underground mammals one of the best animal models for studying convergent evolution, rivalling traditional textbook examples such as aquatic or flying vertebrates.

Among mammals, rodents show numerous examples of convergent evolution toward fossorial life (e.g. Ellerman, 1956; Nevo, 1979; Stein, 2000). Specializations to both fossorial life and life in burrows have been observed in more than ten families of extant (e.g. Aplodontidae, Bathyergidae, Cricetidae, Ctenomyidae, Echimyidae, Geomyidae, Muridae, Octodontidae Sciuridae, Spalacidae) and extinct rodents (e.g. Cylindrodontidae, Mylagaulidae, Tsaganomyidae; see Fig. 3.1). Due to the independent origin and different timelines of colonisation of subsurface

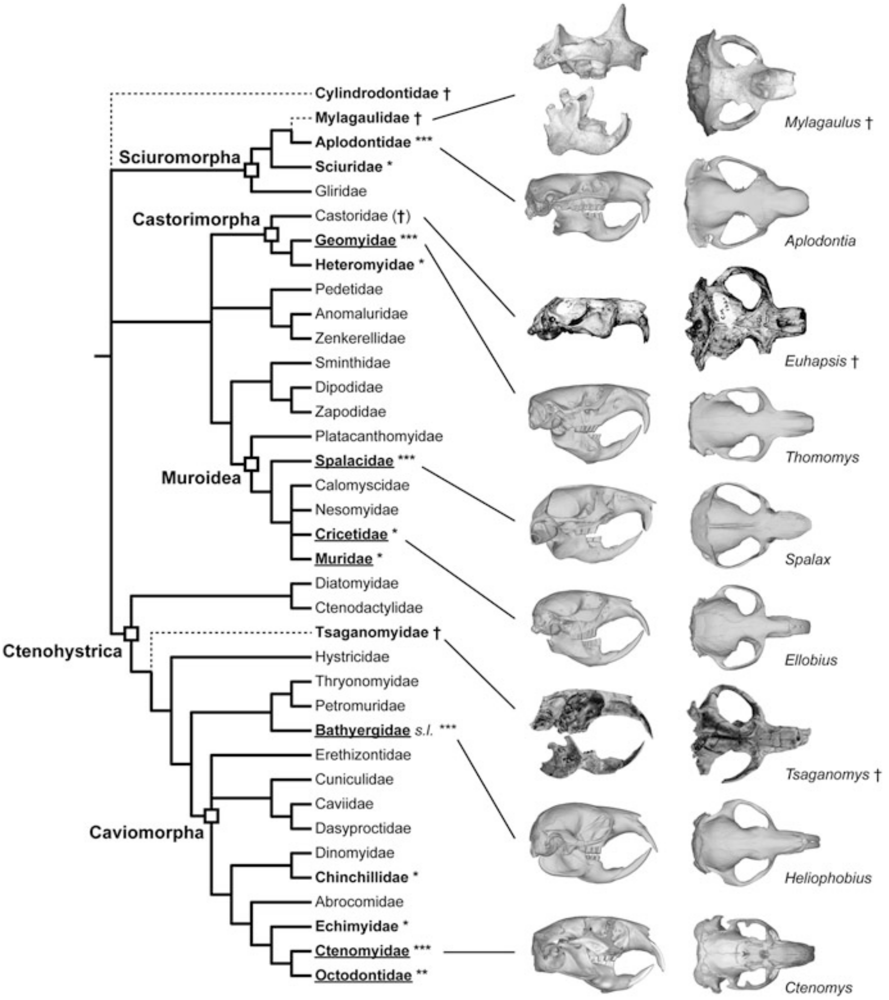
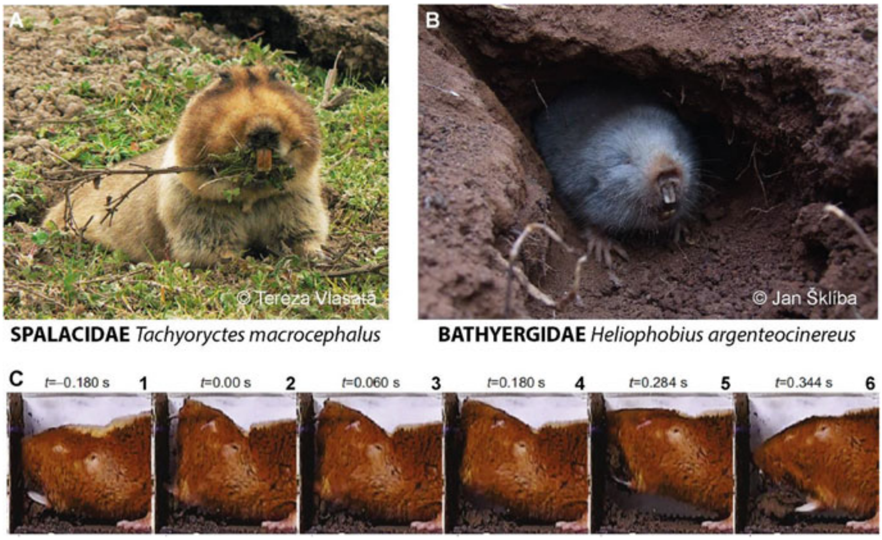


Fig. 3.1 Phylogeny of rodents (d'Elia et al., 2019) showing the main extant fossorial groups (in bold) and their associated convergent skull morphologies (in lateral and dorsal views). The number of asterisks indicates the proportion of fossorial species in each family (*< 30%; 30% < ** < 70%; 70% < ***). Scratch digging behaviour is present in all fossorial families, and underlined names indicate the presence of chisel-tooth digging species. Skull imaging results from X-ray microtomography (*Aplodontia rufa*, MNHN.ZM.MO1981–683; *Thomomys bottae*, BMNH.98.3.1.131; *Spalax* sp., BMNH.10.3.12.10; *Ellobius talpinus*, BMNH.34.2.11.30; *Heliophobius argenteocinereus*, ID13; imaging of *Ctenomys* species is modified from Korbin et al., (2020), except for *Mylagaulus cornusaulax* (modified from Czaplewski, 2012), *Euhapsis platyceps* [modified from Samuels and van Valkenburgh (2009)], and *Tsaganomys altaicus* [modified from Wang (2001)]. †, extinct taxa



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SPALACIDAE *Tachyoryctes macrocephalus*

BATHYERGIDAE *Heliophobius argenteocinereus*

Fig. 3.2 (**a**, **b**) Examples of chisel-tooth digging rodents in the vicinity of their burrow. The protruding incisors can be observed. (**c**) Kinematics of chisel tooth digging in *Fukomys micklemi* (Bathyergidae; modified from Van Wassenbergh et al., 2017). Video frames show: 1. the start of nose-up cranial rotation, 2. reaching maximum gape, 3. initial soil penetration by the incisors, 4. mouth closing mainly by the lifting of the lower incisors, 5. nose-down cranial rotation bringing the grasped soil parcel down, and 6. release of the soil

environments, together with particular ecological conditions of habitats occupied by particular taxa, different degrees of adaptation to subterranean life are observed among fossorial rodents (Fig. 3.2a, b). Fossorial species feeding regularly on the surface can be distinguished from highly specialized fossorial forms that are adapted exclusively for life below ground and categorized as "subterranean" (e.g. Nevo, 1999; Begall et al., 2007; Šumbera, 2019). The most iconic cases of convergent adaptations to subterranean conditions are observed in the naked mole-rat, *Heterocephalus* (Heterocephalidae *sensu* Patterson and Upham, 2014, considered in the present study as included in the Bathyergidae *s.l.*), and the blind mole-rat, *Spalax/Nannospalax* (Spalacidae), both of which have evolved tolerance to hypoxia, exhibit extensive longevity (i.e. live more than 20 years), and resistance to cancer (e.g. Kim et al., 2011; Manov et al., 2013; Fang et al., 2014; Kirby et al., 2018).

Fossorial rodents also display a high number of morphological convergences, primarily those related to digging (Ellerman, 1956; Hildebrand, 1985) but also secondarily to life underground (e.g. fusiform body shape, reduced eyes and pinnae; Nevo, 1979; Stein, 2000). Two main ways of breaking and loosening soil have evolved, relying upon two types of digging tools. Scratch diggers alternate flexion and extension of their forelimbs endowed with enlarged claws, whereas chisel-tooth diggers are characterized by an increase in incisor procumbency, which is suggested to be combined with specific head movements in a few cases (Hildebrand, 1985; Laville et al., 1989; Stein, 2000). The degree of adaptation to a subterranean life and

Table 3.1 Ecological and geographical information for fossorial rodents that mainly use incisors for digging

Family	Subfamily	Genus or species	Modes of digging	Geographic range
Geomyidae	Geomyinae	*Thomomys*	Chisel-tooth/scratch	North America
Spalacidae	Spalacinae	*Spalax*	Chisel-tooth (with head)	Eurasia
	Spalacinae	*Nannospalax*	Chisel-tooth (with head)	Eurasia, Africa
	Rhizomyinae	*Cannomys*	Chisel-tooth, scratch	Asia
	Rhizomyinae	*Rhizomys*	Chisel-tooth, scratch	Asia
	Rhizomyinae	*Tachyoryctes*	Chisel-tooth, scratch	Africa
Cricetidae	Arvicolinae	*Ellobius*	Chisel-tooth (with head?)	Eurasia
	Arvicolinae	*Arvicola scherman*	Chisel-tooth, scratch	Europe
Muridae	Murinae	*Bandicota bengalensis*	Chisel-tooth	Asia
	Murinae	*Nesokia indica*	Chisel-tooth	Africa, Asia
Bathyergidae *s.l.*	Bathyerginae	*Fukomys*	Chisel-tooth	Africa
	Bathyerginae	*Cryptomys*	Chisel-tooth	Africa
	Bathyerginae	*Georychus*	Chisel-tooth	Africa
	Bathyerginae	*Heliophobius*	Chisel-tooth	Africa
	Heterocephalinae	*Heterocephalus*	Chisel-tooth	Africa
Ctenomyidae	Ctenomyinae	*Ctenomys*	Chisel-tooth/scratch	South America
Octodontidae	Octodontinae	*Spalacopus*	Chisel-tooth	South America

the frequency and length of surface forays thus depend on digging mode and performance. These different degrees of specialization provide striking cases of morphological convergence in the limbs and skull (Agrawal, 1967; Nevo, 1979; Stein, 2000), which remain to be more fully explored from both morphological and functional viewpoints.

The aim of the present chapter is to highlight the main adaptations of skull morphology and muscular anatomy in relation to chisel-tooth digging in rodents (Table 3.1). In order to better define fossorial adaptations of the masticatory apparatus, we review the morphological convergences in light of functional aspects and structural constraints, as previously suggested (e.g. Agrawal, 1967; Cook et al., 2000; Lessa, 2000). We first detail the burrowing activity of the most fossorial rodents and compare it to the morphological specializations of the masticatory apparatus. Then, we focus on the characteristics of the main digging tool, the incisors, and the associated bite force, for which new data are provided. This study allows us to link digging behaviours with the morphology and function of the masticatory apparatus for tracing the steps leading to convergent evolution for fossorial life during the evolutionary history of rodents.

3.2 A Brief Overview of Burrowing in Rodents

3.2.1 Extensive Burrowing Activity

Burrowing is a crucial activity for fossorial mammals for finding food, selecting a stable microclimate, locating sexual partners, or simply dispersing (Nevo, 1979). The biomass of food in the form of the subterranean parts of plants (e.g. bulbs, roots, and tubers) is generally less than that of plant parts above the surface. Consequently, solitary species that feed exclusively below ground need to build very large burrow systems of several tens or even hundred metres (e.g. the bathyergid *Heliophobius* and *Bathyergus*; the spalacids *Tachyoryctes* and *Spalax*; Jarvis & Sale, 1971; Cuthbert, 1975; Heth, 1989; Šumbera et al., 2003). The Cape dune mole-rat *Bathyergus suillus* is able to move 13.5 kg of sand in less than one hour and excavate up to five metres of burrows per day with its claws (Cuthbert, 1975). In social species such as the octodontid cururos *Spalacopus cyanus* (Begall & Gallardo, 2000) and chisel-tooth digging bathyergids, such as the naked mole-rat *Heterocephalus glaber* (Brett, 1991), Ansell's mole-rat *Fukomys anselli* (Šklíba et al., 2012), the giant mole-rat *Fukomys mechowii* (Šumbera et al., 2012), and the Damaraland mole-rat *Fukomys damarensis* (Jarvis et al., 1998), burrows can reach several hundred metres or even kilometres in length. Building such extensive burrow systems imposes strong selective pressures on digging efficiency. The silvery mole-rat *Heliophobius argenteocinereus* (Bathyergidae) is able to dig about one metre of burrow per day during the dry season when the soil is as hard as concrete (Šklíba et al., 2009). Based on the weight of material deposited in mounds and burrow diameter data it was estimated that a family of 87 individuals of the naked mole-rat excavated between 2.3 and 2.9 km of burrows in 2 years (Brett, 1991). Similarly, a family of 16 individuals of the Damaraland mole-rat, together weighing 2.2 kg, excavated and moved 2.6 tonnes of soil in less than 2 months (Jarvis et al., 1998). In fact, these values are probably considerable underestimates since excavated soil can also be deposited below ground, especially during the dry season. Burrow systems of fossorial rodents, especially those of subterranean species, do not constitute stable or rigid structures, but are instead dynamic, with new burrows being continuously opened and old ones filled in, especially at the periphery of the burrow system (Jarvis et al., 1998; Šumbera et al., 2003; Šklíba et al., 2009).

Burrowing through substrate requires the application of large forces to the soil, so that soil characteristics and food distribution are the main determinants of burrowing success. Apart from the geo-mechanical quality of the soil, the body mass of the burrow inhabitants also seems to influence burrow characteristics such as diameter and depth (Carotenuto et al., 2020). Many, if not all, subterranean mammals have primary and secondary digging modes (see Stein, 2000), as in pocket-gophers

(Geomyidae, Nevo, 1979; Marcy et al., 2016) and in tuco-tucos (Ctenomyidae; Giannoni et al., 1996; Becerra et al., 2014), which can be used alternatively depending on the characteristics of the soil. Different digging modes are also observed in closely related bathyergid species. Spalacids also comprise very different clades (i.e. Spalacinae, Myospalacinae and Rhizomyinae), for which repeated adaptations to a fossorial life-style are hypothesized (Fournier et al., 2021). As a result, morphological and behavioural variation among rodents does not only reflect phylogenetic relationships. The variation in digging apparatus must rather be viewed as an outcome of complex interactions between phylogenetic history, soil types, and the duration, frequency and nature of surface activities, which have led to convergent behavioural and morphological adaptations (Lessa & Thaeler, 1989; Stein, 2000).

3.2.2 Burrowing Modes and Behaviours

Burrowing is the process of the breaking of soil from the substrate, moving loosened soil below (or along) the body, moving it through the burrow, and finally depositing dirt either above ground into mounds, or backfilling unused burrows. Due to independent colonisations of the subterranean environment, this activity can be realised in different or convergent ways (see Nevo, 1979; Stein, 2000). Scratch digging is widely distributed among mammals. In fossorial rodents, this digging mode is known for most geomyids and ctenomyids, as well as for *Bathyergus* (Bathyergidae), *Myospalax/Eospalax* (Spalacidae), and *Prometheomys* (Cricetidae) among others. Contrastingly, chisel-tooth digging has evolved only in rodents, and is observed in bathyergids (except *Bathyergus*), spalacine and rhizomyine genera (Spalacidae), *Spalacopus* (Octodontidae), *Ellobius* (Cricetidae) and in some species of *Ctenomys* (Ctenomyidae), *Thomomys* (Geomyidae), *Arvicola* (Cricetidae), *Nesokia* and *Bandicota* (Muridae, see Table 3.1). Chisel-tooth digging rodents loosen soil mainly by using their incisors and, as for most scratch diggers, move the soil below the body and kick it vigorously through and out of the burrow. Soil can be loosened by both the incisors and the feet in tuco-tucos (*Ctenomys*) and pushed backward with the feet. After removing soil, some diggers may turn around (180°) and push soil face-first using their head, breast, forefeet, and chin (Airoldi et al., 1976; Stein, 2000).

Only a few studies have thoroughly investigated the digging behaviour and kinematics of fossorial rodents, all of them involving captive specimens (e.g. Jarvis & Sale, 1971; Cuthbert, 1975; Gasc et al., 1985; Lessa, 1987; Laville, 1989; Laville et al., 1989; Gambaryan & Gasc, 1993; Camin et al., 1995; Giannoni et al., 1996; Van Wassenbergh et al., 2017). Apart from data on scratch-diggers, these studies also provide important information regarding the use of incisors during digging and feeding, with different roles being suggested for upper and lower incisors. In *Fukomys micklemi* (Bathyergidae; see Van Wassenbergh et al., 2017), the upper incisors usually remain stationary and play an anchoring role during both digging and gnawing (Fig. 3.2c). In contrast, the lower incisors show upward movements to cut away the soil or to scrape food, and can contribute up to three quarters of the excavating work (Fig. 3.2c). These behaviours were also observed in other bathyergids, such as *Heliophobius*, *Heterocephalus*, and to a lesser extent *Georychus*, as well as in the spalacid *Tachyoryctes* and the cricetid *Arvicola scherman* (Jarvis & Sale, 1971; Cuthbert, 1975; Laville, 1989). In some social mole-rats, such as *Heterocephalus* and *Fukomys*, individual workers can work independently to remove the soil or unite to form so-called digging chains (Jarvis & Sale, 1971; Lacey & Shermann, 1991, RS unpublished observation).

Even if convergence in digging movements has been observed between the fossorial *Arvicola scherman* (Cricetidae) and *Nannospalax ehrenbergi* (Spalacidae; Laville et al., 1989), some differences are evident in the use of incisors and head. The blind mole-rat (*Nannospalax*) scrapes the floor with its incisors, although putatively in combination with its head that is used to push soil up to compact it, which is not the case for *Arvicola* (Gasc et al., 1985; Laville, 1989; Laville et al., 1989; Gambaryan & Gasc, 1993). Head lifting, defined as the "*use of incisors in concert with skull to form a powerful drill and shovel combination that is capable of loosening and removing soil*" (Hildebrand, 1985; Stein, 2000 and references therein) is often considered as the third burrowing type in rodents. However, if the blind mole-rats do use their broad and flat head and nose in effective bulldozing of soil out of burrows, the actual use of the head during digging remains debatable (Zuri et al., 1999; and RS personal observations). Then, pending further evidence, we consider that this digging mode should, rather, be considered as chisel-tooth digging combined with a quite unusual way of soil removal. Some taxa, such as the mole vole *Ellobius* (Cricetidae), often considered as a head lifter, might rather represent typical chisel-tooth diggers that use only their incisors to remove soil (Novikov pers. communication). Head lift digging has, nonetheless, also been reported for zokor *Myospalax* (Spalacidae), and for other mammals, such as the golden mole *Chrysochloris* and the marsupial mole *Notoryctes*, despite these latter species not using incisors for digging (Nevo, 1979; Hildebrand, 1985).

Both modes of digging and their repeated evolution across rodent lineages seem to be strongly related to soil characteristics. The digging mode usually changes depending on the hardness of the soil, with scratch diggers generally being restricted to sandy soils, while chisel-tooth diggers are present in a broader range of soils, as observed in the different species of pocket gophers (Geomyidae) and tuco-tucos (Ctenomyidae; Lessa & Thaeler, 1989; Giannoni et al., 1996; Mora et al., 2003; Marcy et al., 2016; Echeverría et al., 2017). This is particularly well illustrated in the Western Cape region of South Africa where three species of African mole-rats (Bathyergidae) occur sympatrically, but with a microallopatric distribution (Reichman & Jarvis, 1989). The largest species, the Cape dune mole-rat *Bathyergus suillus*, inhabits sandy dune habitats and is a scratch digger, whereas the Cape mole-rat *Georychus capensis* and the common mole-rat *Cryptomys hottentotus* prefer more consolidated soils and are both typical chisel-tooth diggers (Cuthbert, 1975). In these highly specialized rodents, these diverse digging behaviours are strongly associated with morphological adaptations reflecting not only the nature of the soil, but also the modes of digging and removal of soil, and are suggested to drive the repeated evolution of morphological and functional fossorial patterns.

3.3 A Highly Specialized Skull with Massive Masticatory Muscles

3.3.1 Cranial and Mandibular Convergences

Many studies have pinpointed morphological convergences in the skulls of fossorial rodents (e.g. Bekele, 1983; Lessa & Thaeler, 1989; Stein, 2000; Samuels & van Valkenburgh, 2009; Gomes Rodrigues et al., 2016; McIntosh & Cox, 2016a, b; Fournier et al., 2021). Alongside anterior projection of the incisor tips, corresponding to procumbency, all fossorial rodents are characterized by short, flat, but also deep and broad skulls, in association with enlarged zygomatic arches and temporal areas (see Figs. 3.1 and 3.3 for more details). Such cranial similarities

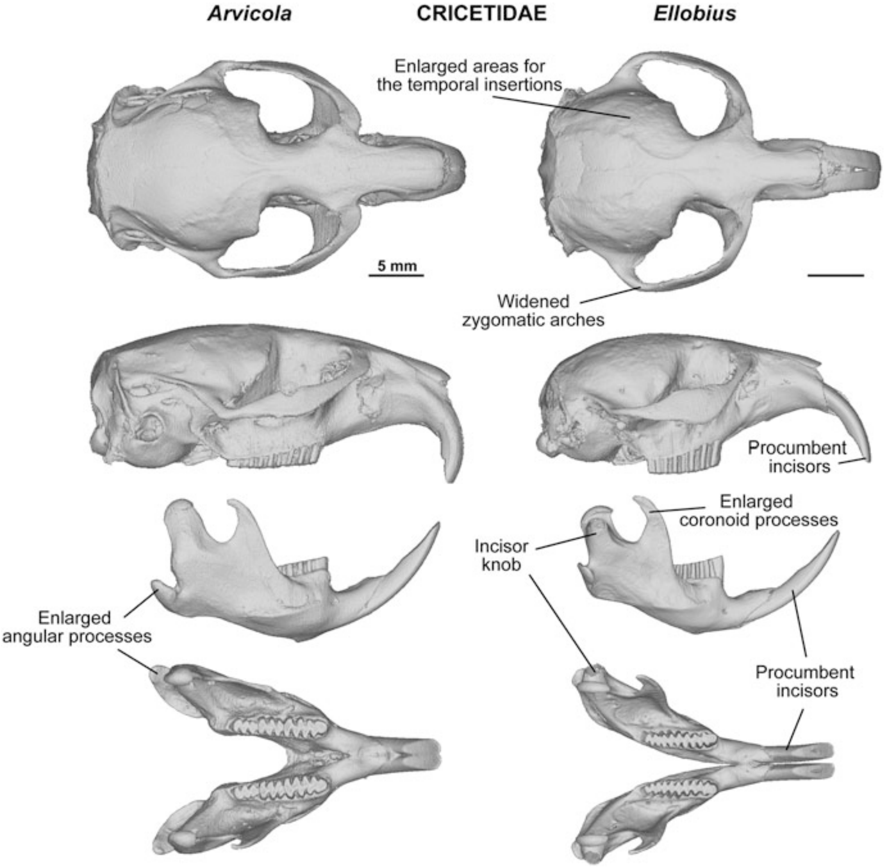

Fig. 3.3 Comparison of skull morphology between a non-fossorial species (*Arvicola amphibius*, BMNH.1937.3.22.48) and a highly specialized chisel-tooth digger (*Ellobius talpinus*, BMNH.34.2.11.30; with the right zygomatic arch partly reconstructed) of the family Cricetidae

are linked to the development of massive and powerful masticatory muscles necessary to enhance incisor biting while digging. These two anatomical and functional aspects are discussed further below. These massive muscles require large areas of attachment on the zygomatic and temporal regions of the skull, as well as on the mandible. All these specializations are the result of successive modifications leading to repeated adaptations to fossorial lifestyles, especially for chisel-tooth digging. Several authors suggested that these adaptive changes toward fossoriality were generally preceded by behavioural changes, since some non-fossorial cricetid and octodontid species (e.g. *Pitymys*, *Octodon*, and *Tympanoctomys* frequently defined as being semi-fossorial), are able to dig complex burrows without significant morphological adaptations for this purpose (Casinos et al., 1983; Lessa et al., 2008). According to the fossil record, such behavioural changes (i.e. digging without morphological adaptations) could be related to the opening of the environment from 40 Ma onward in different areas across the globe (e.g. North American Great Plains, Mongolian Plateau), the need to find new resources, and also the requirement to find alternative shelters for avoiding being preyed upon (Nevo, 1999; Jardine et al., 2012; but see Rodríguez-Serrano et al., 2008 for alternate hypotheses). Morphological specializations are observed in the oldest rodent fossorial lineages, the Cylindrodontidae and Tsaganomyidae (Bryant & MacKenna, 1995), as well as in the Castoridae, Geomyidae, and Aplodontoidea in the last 30 Ma. In contrast, other extant families did not evolve any specific fossorial characteristics prior to 20 Ma (Cook et al., 2000; Hopkins, 2005; Samuels & van Valkenburgh, 2009; Jardine et al., 2012; He et al., 2020; Fournier et al., 2021).

Because of the strong influence of chisel-tooth digging on the morphology of the entire masticatory apparatus, morphological convergences are also evident between species belonging to different genera, which are not exclusively fossorial. The best examples are found among bandicoot rats (Muridae), *Nesokia* and *Bandicota*, species of which show a wide array of behavioural habits, from aquatic to fossorial life (Agrawal, 1967; Kryštufek et al., 2016). Both genera include fossorial species that display similar cranial and mandibular specializations for chisel-tooth digging (Fig. 3.4a; see Kryštufek et al., 2016). Their crania are broad with enlarged zygomatic arches, as well as a wide and short rostrum, when compared to non-fossorial species (Fig. 3.4a, PC2). Their mandibles show the strongest morphological changes, with short and laterally-oriented angular processes, enlarged coronoid processes, as well as prominent alveolar processes at the root of the incisor, forming a knob at the level of the angular process (see Fig. 3.4b, PC1). In general, the mandible shows the strongest ecological imprint, because of its simple morphology consisting of a single bone, the dentary (on each side). Similar morphotypes are also observed in Cricetidae (Durão et al., 2019; Fig. 3.3) and in the Ctenohystrica (Gomes Rodrigues et al., 2016; Fig. 3.4b).

All these morphological characteristics can be found at the intrageneric levels and also at the intraspecific level, although less pronounced, depending on the nature of the soil. When the soil is harder, rodents more frequently use their incisors for digging, which implies similar skull modifications (e.g. short skull with enlarged zygomatic arches, procumbent incisors), as observed in different species of

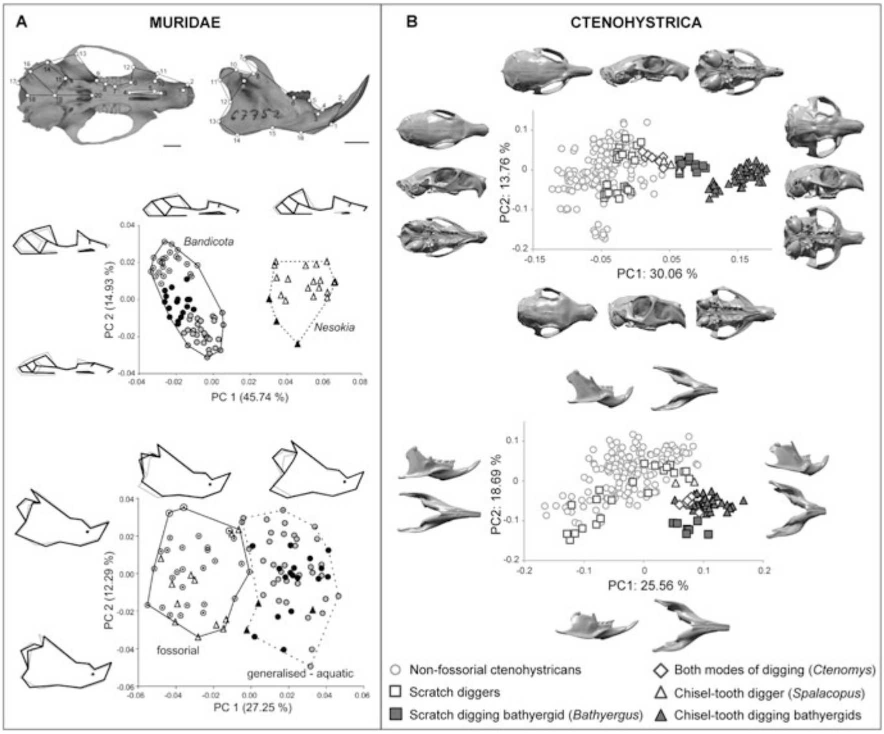

Fig. 3.4 (**a**) Quantification and comparison of cranial and mandibular morphology between convergent fossorial bandicoot rat species (*Bandicota bengalensis* and *Nesokia indica*; open symbols) and non-fossorial species (*Bandicota indica*, *Bandicota savilei*, and *Nesokia bunni*; filled symbols) using geometric morphometric methods (modified from Kryštufek et al., 2016; scale bars: 5 mm). (**b**) Quantification and comparison of cranial and mandibular morphology between fossorial scratch digging, chisel-tooth digging and non-fossorial ctenohystrican rodents using geometric morphometric methods (modified from Gomes Rodrigues et al., 2016)

Tachyoryctes (Beolchini & Corti, 2004), in *Heliophobius argenteocinereus* (Barčiová et al., 2009) and in *Thomomys bottae* (Lessa & Thaeler, 1989). In contrast, soil hardness does not seem to have strongly influenced the skull morphology of *Spalacopus* (Bacigalupe et al., 2002) and *Ctenomys* (Echeverría et al., 2017). At a higher taxonomic level, most chisel-tooth digging species present the above-mentioned specializations in comparison to scratch digging and non-fossorial species. These convergences have been highlighted in a number of geometric morphometric studies dealing either with rodents as a whole (Samuels & van Valkenburgh, 2009; McIntosh & Cox, 2016b) or focusing on specific taxa [e.g.; ctenomyids and octodontids in Becerra et al. (2014) and by Gomes Rodrigues et al. (2016) also focusing on bathyergids; geomyids in Marcy et al. (2016); spalacids in Fournier et al. (2021)].

The use of the head for digging, or to push and pack soil, also implies strong but additional cranial adaptations compared to other chisel-tooth diggers. In fossorial taxa that use their head as a shovel (whether for digging or removing soil), the upper incisors are not necessarily highly procumbent. They differ from other chisel-tooth diggers by exhibiting short crania with broader frontal and nasal bones, and have a very broad posterior face due the presence of an enlarged and anteriorly-tilted occipital plate for the insertion of massive neck muscles. These characteristics are evident in *Spalax/Nannospalax* and *Myospalax/Eospalax* (Spalacidae; Fournier et al., 2021), in some extinct taxa (Mylagaulidae, Castoridae; Hopkins, 2005; Samuels & van Valkenburgh, 2009; Fig. 3.1), and in a few other mammals, such as golden moles (Afrosoricida; Hildebrand, 1985). Such a high degree of morphological specialization, repeatedly resulting from selection during the evolution of rodents, is important from an evolutionary viewpoint. It allows us to confidently infer fossorial adaptations in extinct species (e.g. Hopkins, 2005; Mein & Pickford, 2008; Flynn, 2009; Samuels & van Valkenburgh, 2009) and notably to infer a precocious adaptation to chisel-tooth digging in the evolutionary history of rodents, as suggested for the Tsaganomyidae and Cylindrodontidae (Bryant & MacKenna, 1995).

3.3.2 Prominent Adductor Muscles

Although rodents present a wide array of skull morphologies that have been traditionally arranged into four main muscular morphotypes (Wood, 1965), the constraints of fossorial life, especially chisel-tooth digging, are strong enough to have influenced the morphological evolution of the masticatory apparatus. These functional constraints have led to extensive modifications of both the skull structure and anatomy of masticatory muscles, mainly involving the size of the adductor muscles rather than their structural organization (e.g. Lessa & Stein, 1992; Cox et al., 2020). Muscle size is the main factor influencing bite force (Becerra et al., 2014). In rodents, the masseter muscles, especially the superficial and deep layers, and, to a lesser extent, the temporal and pterygoid muscles constitute the most dominant part of the masticatory musculature (Fig. 3.5). In a detailed comparative study, Morlok (1983) described the muscular anatomy in the main fossorial rodent families (Spalacidae, Bathyergidae, Geomyidae, Cricetidae, and Ctenomyidae). However, although the large size of the masseter and temporalis muscles was mentioned, convergent adaptations between families were not discussed with regard to differences in digging modes. These adductor muscles were shown to be very prominent in subterranean rodents, such as bathyergids (Van Daele et al., 2009; Cox et al., 2020), and also in ctenomyids, when compared to less or non-fossorial sister taxa such as the Chinchillidae and Octodontidae (Fig. 3.5; see Becerra et al., 2014). Differences in the size of the musculature are also observed at the intraspecific level in *Thomomys bottae,* depending on the hardness of soils occupied (Lessa & Thaeler, 1989). Specimens found in rocky, clay soils showed larger adductor muscles than those found in sandy soils.

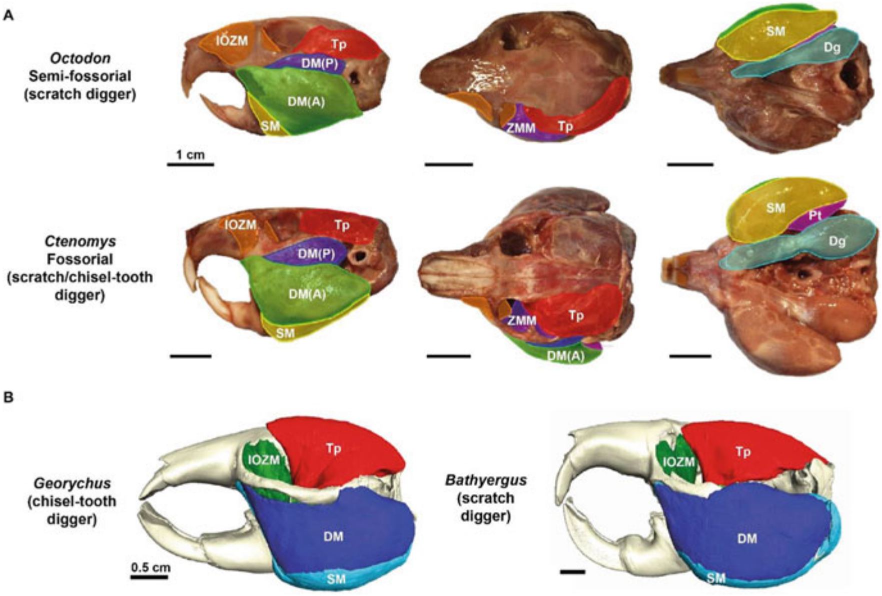

Fig. 3.5 (**a**) Comparison of the anatomy of the masticatory muscles after dissection of a semi-fossorial and a fossorial ctenohystrican rodent in lateral, dorsal, and ventral views (modified from Becerra et al., 2014). (**b**) Anatomy of masticatory muscles in the Bathyergidae (lateral views). Virtual dissection after iodine-based contrast-enhanced microCT imaging (modified from Cox et al., 2020). Abbreviations—*SM* superficial masseter, *DM* deep masseter—(*A*) anterior and (*P*) posterior parts, *ZMM* zygomaticomandibular masseter, *IOZM* infraorbital part of the zygomaticomandibular masseter, *Tp* temporal, *Pt* pterygoid, *Dg* digastric muscle

Among the adductor muscles, the temporal muscle generally consists of several layers; it is highly involved in the jaw-closing motion and, depending on its size, high output force can be produced at the level of the incisors during both feeding and digging (Hiiemae, 1971; Van Daele et al., 2009; McIntosh & Cox, 2016a). This muscle is generally more voluminous in chisel-tooth digging rodents than in scratch diggers, with an attachment closer to the sagittal plane on the cranium, and an insertion on the enlarged coronoid process of the mandible, as shown in some caviomorphs (*Ctenomys vs Octodon*, Becerra et al., 2014, Fig. 3.5a). However, the relative size of the temporal muscle is reduced in ctenomyids (15% of the total mass of masticatory muscles), whereas it reaches approximately 30% in most chisel-tooth digging rodents, such as bathyergids, spalacids, and cricetids (e.g. Morlok, 1983; Cox et al., 2020). Non chisel-tooth diggers, such as *Aplodontia*, *Bathyergus*, and *Castor*, also exhibit a temporal muscle of relatively large size (Druzinsky, 2010; Cox & Baverstock, 2016; Cox et al., 2020) in relation to morphological characteristics inherited from their putative chisel-tooth digging ancestors or to other mechanically-demanding activities (Hopkins, 2005; Samuels & van Valkenburgh, 2009; Gomes Rodrigues et al., 2016). While rarely used for digging, the incisors of non-chisel-tooth diggers are still used to gnaw hard food items, such as geophytes, tubers or tree bark, which can explain why the inherited morpho-functional properties of their masticatory apparatus are conserved. The head-lift digging spalacids, *Spalax*/*Nannospalax,* show the greatest relative size of the temporal muscle (45%) among the described musculature of fossorial rodents (Morlok, 1983), although this is not associated with procumbent upper incisors but rather with highly procumbent lower incisors. This temporal characteristic, combined with powerful neck muscles (splenius and rhomboideus; Nevo, 1999), might be involved in improving the loosening and removing of soil (Laville et al., 1989), as proposed for extinct aplodontoids and castorids, and, to a lesser extent, for other spalacids (*Myospalax*) and, putatively, for cricetids (e.g. *Ellobius*; see Krapp, 1965).

In highly specialized fossorial rodents, the superficial and deep masseters are massive muscles with large areas of origin on the zygomatic arches and rostrum. They have been shown to contribute extensively to the generation of high bite forces at the level of both the incisors and cheek teeth (Becerra et al., 2014; Cox & Faulkes, 2014). Nonetheless, the superficial masseter generally has an insertion area that is more limited in the posterior part of the mandible in different chisel-tooth digging species, due to its reduced angular process (see Figs. 3.3, 3.4 and 3.5b). This is not the case for tuco-tucos (Ctenomyidae), probably because the incisors are not necessarily the main digging tools in the various species (Becerra et al., 2014; Echeverría et al., 2017). This muscle is considered to be the main protractor of the mandible (Hiiemae, 1971), but its role during the power stroke of the jaw remains to be ascertained. It has been assumed that its limited amount of insertion on the posterior part of the mandible of chisel-tooth diggers might favour a wide gape (McIntosh & Cox, 2016a), so that the temporal muscle can produce a higher output force during incisor biting at the expense of the biomechanical advantage of the superficial masseter (Gomes Rodrigues et al., 2016). The infraorbital part of the zygomaticomandibular masseter is peculiar to rodents and is only present in two “masticatory morphotypes”, characterized by their enlarged infra-orbital foramina (Wood, 1965). Interestingly, this muscle tends be less voluminous and less anteriorly expanded in chisel-tooth digging rodents, such as some ctenomyids (Becerra et al., 2014), and more importantly in bathyergids, in which the foramina are highly reduced and the muscle is mostly confined to the orbital region (Morlok, 1983; Gomes Rodrigues et al., 2016; Cox et al., 2020; Fig. 3.5b). This reorganisation is likely related to the reduction of the snout and favours a wider gape, which optimizes incisor output force (McIntosh & Cox, 2016a, b; Cox et al., 2020). More studies on the masticatory musculature of rodents are needed to better understand the anatomical and functional characteristics of each of these muscular layers, as well as their precise contribution during gnawing and incisor-biting and for different digging stages.

3.4 The Incisors: A Powerful Tool for Digging

3.4.1 *Highly Specialized Incisors*

If the masticatory muscles and skull constitute the machinery producing the energy necessary for gnawing or digging, incisors represent the main tool for the accomplishment of these tasks. Incisors coupled with cheek teeth constitute one of the main functional components of the masticatory apparatus of rodents. All subterranean rodents have convergently evolved high-crowned cheek teeth to cope with high wear resulting from the unintentional ingestion of abrasive particles (i.e. grit and dust) during digging and feeding (Stein, 2000; Gomes Rodrigues, 2015; Gomes Rodrigues & Šumbera, 2015). The most extreme case is observed in the silvery mole-rat, *Heliophobius* (Bathyergidae), which presents a continuous and horizontal replacement of its molars, working like a conveyor belt, assumed to be related to its important digging activity (Gomes Rodrigues et al., 2011). Incisors are ever-growing in rodents and are covered only on their labial surface with enamel for resisting bending stresses. In many rodent species, this enamel layer is enriched with iron oxides, which reinforces the enamel and is responsible for the orange colour of the incisors (mainly the upper incisors; see Fig. 3.2a). This characteristic is, however, not specific to fossorial species as it is observed in many non-fossorial taxa; it can also be absent in some fossorial ones (e.g. Bathyergidae; Gomes Rodrigues, 2015; Fig. 3.2b). This oxide enrichment might be biomechanically linked with procumbency since the upper incisors are usually less coloured when highly procumbent. This observation has been made for the Spalacidae, Geomyidae, Ctenomyidae and Cricetidae (see Stein (2000) for more details).

The deficiency in oxide enrichment of incisors of some chisel-tooth digging rodents can be paralleled by a reinforcement of their enamel microstructure. Previous studies of enamel microstructure have shown that the enamel layer is generally thicker in fossorial rodents, especially the outer enamel layer of the upper incisors. This is nicely exemplified in chisel-tooth digging species such as spalacids, cricetids, geomyids, and the extinct ctenomyids (~35–55% and ~40–60% of the total enamel thickness of the lower and upper incisors respectively; e.g. Flynn et al., 1987; Kalthoff, 2000; Vieytes et al., 2007). Such a difference between fossorial and non-fossorial rodents was also observed between species of *Arvicola*, with the fossorial *Arvicola scherman* showing thicker enamel than the semi-aquatic *A. amphibius and A. sapidus* (Marcolini et al., 2011). This adaptation compensates for high dental wear due to the intense use of incisors during digging. In addition, compared to non-fossorial taxa, fossorial species, such as blind mole rats (Spalacidae), naked mole-rats (Bathyergidae) and pocket-gophers (Geomyidae; Manaro, 1959; Hildebrand, 1985; Zuri et al., 1999; Berkovitz & Faulkes, 2001), exhibit higher growth rates of the incisors, especially the lower ones that are more importantly used during digging. This rate is higher in chisel-tooth diggers than in scratch diggers, as observed for pocket-gophers (scratch digging *Geomys*: 0.35 mm/

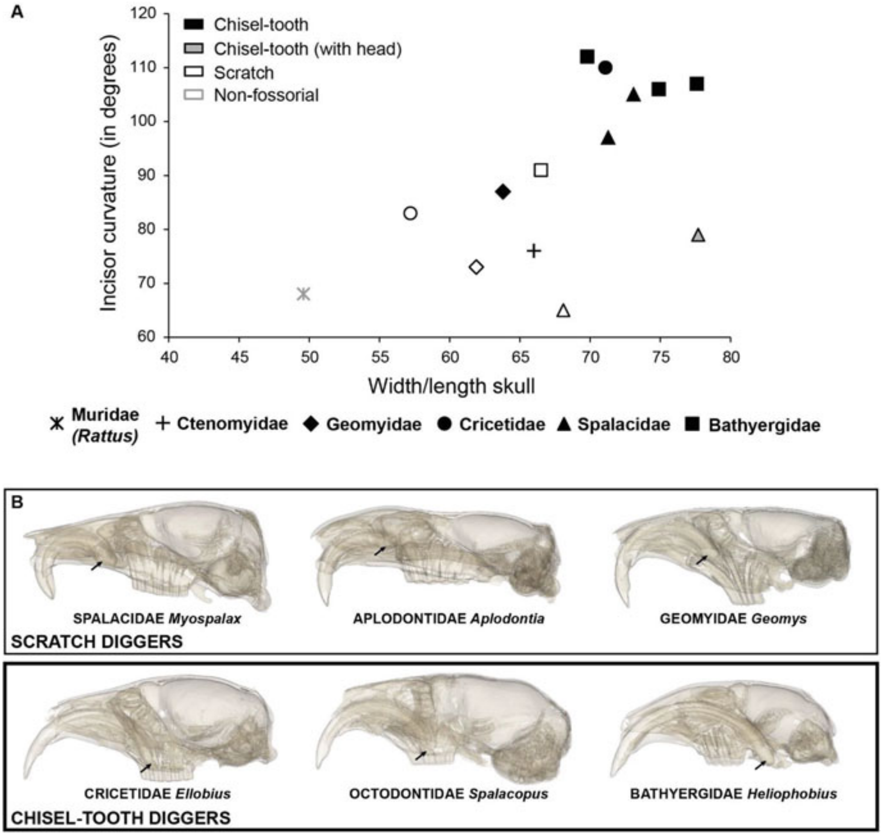

Fig. 3.6 (**a**) Biplot of the width/length ratio of the cranium and incisor curvature in different fossorial rodents (data compiled from Morlok 1983). (**b**) Comparison of incisor root insertion location and procumbency between scratch digging and chisel-tooth digging rodents using translucent X-ray microtomographic reconstruction of the cranium (*Myospalax* sp. BMNH.9.1.1.206; *Aplodontia rufa*, MNHN.ZM.MO1981-683; *Geomys pinetis floridanus*, MNHN.ZM2007-233; *Ellobius talpinus*, BMNH.34.2.11.30; *Spalacopus cyanus*, BMNH.98.1.8.5; *Heliophobius argenteocinereus*, BMNH.68.93)

day *versus* chisel-tooth digging *Thomomys*: 0.5 mm/day; Miller, 1958; Manaro, 1959).

The external protrusion of the upper incisors constitutes one of the main characteristics of fossorial rodents, especially chisel-tooth diggers (see Fig. 3.2). Incisor procumbency is generally greater than 90° relative to the rostral plane in the latter taxa (e.g. *Ellobius*, *Tsaganomys*, *Heliophobius* and *Ctenomys* in Figs. 3.1 and 3.3; Marcy et al., 2016), which defines proodonty (Thomas, 1919; Landry Jr., 1957). The corresponding values of the angle of incisor curvature (or protrusion here) in chisel-tooth digging taxa are always greater than those for scratch diggers and non-fossorial species (Fig. 3.6; Morlok, 1983; Van der Merwe & Botha, 1998; McIntosh & Cox, 2016b). As for the proportion of the skull and the associated mass of main adductor muscles, procumbency tends to increase in relation to soil hardness and to the degree of adaptation to chisel-tooth digging, as observed in several families (Fig. 3.6a) and in different species of *Thomomys* (Geomyidae; Marcy et al., 2016). Incisor procumbency also involves the lower incisors, but to a lesser degree (Van der Merwe & Botha, 1998). This is notably observable in sciurognathous rodents, which are characterized by the absence of lateralization of the angular process of the mandible. In the sciurognathous spalacids, cricetids, murids and geomyids (Figs. 3.1, 3.3 and 3.4a), the incisor root inserts posteriorly and protrudes laterally from the mandible to form a knob close to the articular condyle. The role of the upper incisors is mainly for anchorage to the substrate, whereas the lower incisors are mainly used as a shovel (Jarvis & Sale, 1971; Laville et al., 1989; Van Wassenbergh et al., 2017). Incisor procumbency associated with wide gaping during digging enables rodents to obtain a more effective angle of attack, with the incisor tip always being in contact with the soil (Mora et al., 2003; McIntosh & Cox, 2016b). The external protrusion of the tips of the upper incisors, in addition to the development of protecting folds of the lips, also helps to prevent soil from entering the mouth and nostrils (Agrawal, 1967). More generally, procumbent incisors allow for an increase of mechanical efficiency during digging (Landry Jr., 1957; McIntosh & Cox, 2016b). The lower incisors also serve as manipulators of soil and food, which is also facilitated by the independent movements of the hemi-mandibles, thanks to the presence of an unfused symphysis in most fossorial rodents. These alternate movements are particularly pronounced in bathyergids and spalacids (Landry Jr., 1957; Gomes Rodrigues et al., 2016).

3.4.2 Procumbency and Mechanical Efficiency of the Incisors

Procumbent incisors result in a more efficient bite, but also impose greater biomechanical constraints resulting from important stresses and pressures. Increasing procumbency means increasing the radius of curvature of the incisor, which is generally associated with an enlargement of the incisor, (e.g.; Landry Jr., 1957; McIntosh & Cox, 2016b). An allometric relationship between rostral size and incisor procumbency was emphasized by Lessa and Patton (1989). They noted that incisor procumbency increases with the enlargement of the rostrum, involving an increase of incisor length in many pocket-gophers (Geomyidae), in which the incisor root is inserted in front of the cheek teeth. They also mentioned the occurrence of this allometric pattern related to incisor procumbency in root-rats *Tachyoryctes* (Spalacidae), and it was then generalized to most rodents by Lessa (2000). Incisor procumbency was also suggested to be independent of rostral size, as in ctenomyids (Echeverría et al., 2017), but more specifically in bathyergids, in which the incisor root is inserted behind the molars in chisel-tooth digging genera (e.g. *Heliophobius* in Fig. 3.6b; Landry Jr., 1957; McIntosh & Cox, 2016b). Such a departure from allometric “constraints” is also observed in more specialised chisel-tooth digging cricetids, octodontids and spalacids (e.g. *Ellobius*, *Spalacopus*, *Cannomys*) that all display a posterior insertion of the upper incisors at the level of the molars (see Fig. 3.6b). This pattern notably favours incisor lengthening in small-sized subterranean rodents and it contributes to the dissipation of forces during biting (Becerra et al., 2012; McIntosh & Cox, 2016b). It is worth noting that both allometric and non-allometric trends related to procumbency can be observed in the same family and can also depend on the nature of the soil (see Marcy et al. (2016) on species of *Thomomys* for more details).

These structural adjustments may also contribute to the optimization of digging motions and the increase of bite force. Increasing body size is associated with greater muscular strength due to enlarged muscles, a longer rostrum and thus a more proodont incisor, and a resulting higher bite force. This might explain why harder soils are generally inhabited by larger species in a given family, as noticed for instance in the Geomyidae (Marcy et al., 2016), even if this relationship can be more complex when taking into account the burrow architecture (Carotenuto et al., 2020). If this configuration implies greater in-lever arms (i.e. distance from the condyle or fulcrum to the point of muscle attachment), the out-lever arms (distance from the condyle to the incisor tip) are also greater due to procumbent incisors and an enlarged rostrum, which reduces the force applied at the incisors (Bekele, 1983). In rodent species showing a posterior insertion of the incisors and a shortened rostrum, the associated reduction of the out-lever arm would produce a greater bite force owing to a higher mechanical advantage of the temporal muscle. This is typically the case for most chisel-tooth digging ctenohystricans (Gomes Rodrigues et al., 2016), especially bathyergids (McIntosh & Cox, 2016a, b). Different biomechanical configurations may improve bite force, depending on digging mode: from *Thomomys* showing both allometric and non-allometric architectural possibilities (Marcy et al., 2016) to *Ctenomys* showing a combination of an increase of both the adductor muscle size and procumbency without significant shortening or lengthening of the rostrum (Becerra et al., 2014; Echeverría et al., 2017).

3.4.3 Absolute Incisor Bite Force

To sum up, an increase of bite force in rodents is favoured by procumbent incisors combined with the great enlargement of the masticatory muscles and a wide and deep skull, permitting the combination of this force with the wide gape needed for digging (McIntosh & Cox, 2016a, b). Absolute bite force was demonstrated to be correlated to body mass in rodents (e.g. Freeman & Lemen, 2008; Van Daele et al., 2009, 2019; Becerra et al., 2014). Fossorial rodents, especially chisel-tooth diggers, were assumed to have higher bite forces than non-fossorial taxa. For instance, estimated bite force is higher for the fossorial species of *Arvicola* compared to its non-fossorial relatives (Durão et al., 2019). However, this hypothesis was never tested on a large dataset. In order to test whether fossoriality has a convergent impact on bite force in rodents we compiled literature data on absolute bite force (Freeman & Lemen, 2008; Van Daele et al., 2009; Williams et al., 2009; Becerra et al., 2011, 2013, 2014; Kerr et al., 2017; Ginot et al., 2018; Hite et al., 2019). We then gathered data for 456 individuals belonging to 25 species, for which maximal *in vivo* bite forces were available (Table 3.2). In addition, we collected data for two species of fossorial rodent, *Spalacopus cyanus* ($N = 7$) and *Spalax galili* ($N = 36$). In brief, we used an isometric Kistler force transducer connected to a charge amplifier [for details of the experimental setup, see Herrel et al. (1999)]. Animals were taken from their cages, restrained, and allowed to bite the transducer five times. The highest bite force was then retained as an estimate of maximal bite performance.

We found that all fossorial rodents differ significantly from non-fossorial species (see Table 3.2) and have a higher bite force for their body mass according to the ANCOVA ($F_{1,38} = 10.23$, $P = 0.003$; see Fig. 3.7), as previously observed for a few species (e.g. Freeman & Lemen, 2008; Van Daele et al., 2009; Hite et al., 2019). Extensive comparison between chisel-tooth digging and scratch digging species could not be realized since only one scratch digger (*Geomys*) was considered in the analysis and did not significantly differ from the other fossorial species. Among octodontids, the degu (*Octodon*) is a non-specialized scratch digger, which does show a lower bite force than the chisel-tooth digging cururo (*Spalacopus*; Table 3.2). Improvement of the use of incisors and their resistance to bending stresses enable subterranean species not only to generate the high bite force used for digging, but also that needed for the consumption of a wide range of hard geophytes (Van Daele et al., 2009; McIntosh & Cox, 2016b; Vassallo et al., 2021). The high bite force value observed for the non-fossorial squirrel *Sciurus niger* (Table 3.2) was probably similarly related to the gnawing of hard items, such as nutshells (Freeman & Lemen, 2008), and to the large temporal muscles generally observed in sciuromorphous rodents (Ball & Roth, 1995; Cox et al., 2020). By measuring greater resistance to stresses in the skull of chisel-tooth digging caviomorphs and bathyergid species, several studies using finite element analyses (McIntosh & Cox, 2016c; Buezas et al., 2019; Vassallo et al., 2021) have demonstrated that the morpho-functional characteristics of their masticatory apparatus not only allow them to produce high bite forces, but also to be able to sustain them over long periods of time without structural failure (Van Daele et al., 2009; Vassallo et al., 2021).

3.5 Conclusion

From a morpho-functional point of view we demonstrate that fossorial life imposes strong constraints on the rodent skull, especially when the masticatory apparatus is involved in digging through the deployment of powerful incisor biting. This finding alone is sufficient for explaining why the evolution of the masticatory apparatus in fossorial rodents constitutes one of the most striking cases of morphological and functional convergence in mammals. Whereas fossorial and subterranean behaviours might be induced by the opening of landscapes and the search for new shelters and food resources, the main drivers of the evolution of chisel-tooth digging might be related to both the consumption of hard geophytes and living in harder soils. The

Table 3.2 Data on incisor bite force gathered for both fossorial and non-fossorial rodents

Species	*N*	Family	Life style	Method	Body mass (g)	Bite force (N)	References
Apodemus sylvaticus	103	Muridae	Non-fossorial	Piezo	20.4	9.1	Ginot et al. (2018)
Apodemus sylvaticus	11	Muridae	Non-fossorial	Piezo	25.9	9.6	Kerr et al. (2017)
Chinchilla lanigera	10	Chinchillidae	Non-fossorial	Strain gauge	570.0	23.5	Becerra et al. (2014)
Ctenomys australis	10	Ctenomyidae	Fossorial	Strain gauge	360.0	68.7	Becerra et al. (2014)
Ctenomys talarum	15	Ctenomyidae	Fossorial	Strain gauge	146.6	31.7	Becerra et al. (2011)
Ctenomys tuconax	3	Ctenomyidae	Fossorial	Strain gauge	520.0	74.9	Becerra et al. (2013)
Dipodomys ordii	11	Heteromyidae	Non-fossorial	Flexiforce	63.0	14.0	Freeman and Lemen (2008)
Fukomys mechowii	73	Bathyergidae	Fossorial	Piezo	105.6	32.3	Modifed from Van Daele et al. (2009)
Fukomys micklemi	11	Bathyergidae	Fossorial	Piezo	75.9	21.8	Modifed from Van Daele et al. (2009)
Fukomys whytei	8	Bathyergidae	Fossorial	Piezo	82.6	23.0	Modifed from Van Daele et al. (2009)
Geomys bursarius	5	Geomyidae	Fossorial	Flexiforce	153.0	50.6	Freeman and Lemen (2008)
Heterocephalus glaber	10	Bathyergidae *s.l.*	Fossorial	Flexiforce	56.1	21.1	Hite et al. (2019)
Microtus ochrogaster	10	Cricetidae	Non-fossorial	Flexiforce	34.0	12.9	Freeman and Lemen (2008)
Mus spretus	35	Muridae	Non-fossorial	Piezo	13.7	8.3	Ginot et al. (2018)
Neotoma floridana	15	Cricetidae	Non-fossorial	Flexiforce	321.0	30.3	Freeman and Lemen (2008)
Octodon degus	10	Octodontidae	Non-fossorial	Strain gauge	240.0	21.9	Becerra et al. (2014)
Onychomys leucogaster	2	Cricetidae	Non-fossorial	Flexiforce	34.0	11.5	Freeman and Lemen (2008)
Onychomys leucogaster	10	Cricetidae	Non-fossorial	Strain gauge	49.9	13.5	Williams et al. (2009)
Perognathus flavescens	1	Heteromyidae	Non-fossorial	Flexiforce	6.5	4.6	Freeman and Lemen (2008)
Peromyscus leucopus	10	Cricetidae	Non-fossorial	Flexiforce	23.0	10.0	Freeman and Lemen (2008)

(continued)

Table 3.2 (continued)

Species	*N*	Family	Life style	Method	Body mass (g)	Bite force (N)	References
Peromyscus maniculatus	10	Cricetidae	Non-fossorial	Strain gauge	21.2	8.5	Williams et al. (2009)
Peromyscus maniculatus	4	Cricetidae	Non-fossorial	Flexiforce	21.0	8.8	Freeman and Lemen (2008)
Reithrodontomys megalotis	3	Cricetidae	Non-fossorial	Flexiforce	11.5	7.7	Freeman and Lemen (2008)
Sciurus niger	22	Sciuridae	Non-fossorial	Flexiforce	588.0	73.0	Freeman and Lemen (2008)
Sigmodon hispidus	6	Cricetidae	Non-fossorial	Flexiforce	105.0	19.9	Freeman and Lemen (2008)
Spalacopus cyanus	7	Octodontidae	Fossorial	Piezo	96.0	25.7	This study
Spalax galili	36	Spalacidae	Fossorial	Piezo	161.4	43.1	This study
Spermophilus tridecemlineatus	4	Sciuridae	Non-fossorial	Flexiforce	144.0	21.1	Freeman and Lemen (2008)
Zapus hudsonius	1	Zapodidae	Non-fossorial	Flexiforce	24.5	7.6	Freeman and Lemen (2008)

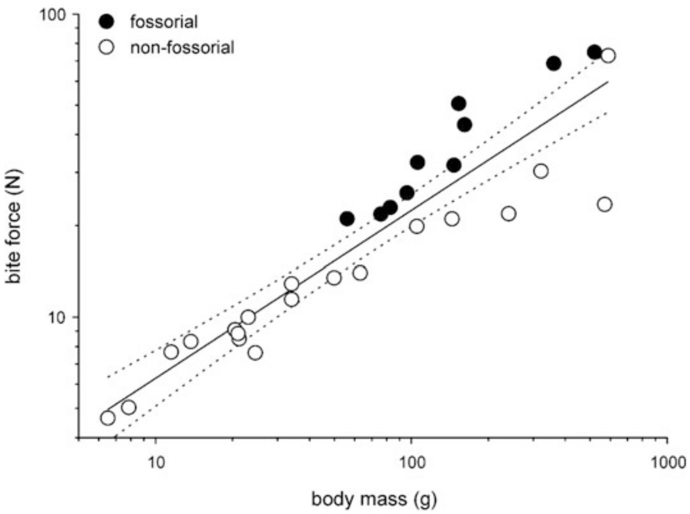

Fig. 3.7 Biplot showing the regression of the body mass against bite force measured in fossorial and non-fossorial rodents

constraints imposed by life underground are such that the whole masticatory apparatus is impacted and such adaptations are evident across different continents. The subsequent specializations are the result of many possible adjustments of the different components of the masticatory apparatus (e.g. skull and adductor muscle architecture, incisor shape and insertion), which in the end lead to similar overall morphologies and functions.

Although these fossorial patterns are now fairly well understood and recognized in different rodent families, the way in which the different muscular morphotypes accommodate such constraints to produce efficient biting and digging motions remains to be more thoroughly assessed. A study of importance investigating intraspecific variation in different fossorial species in relation to the physical properties of the ingested food and soil could be particularly revealing in this respect (e.g. Lessa & Thaeler, 1989; Bacigalupe et al., 2002; Beolchini & Corti, 2004; Barčiová et al., 2009). Ontogenetic aspects should also be more effectively integrated to better capture allometric effects (e.g. Cubo et al., 2006; Durão et al., 2019; Vassallo et al., 2021). Palaeontological and macroevolutionary studies will also play a key role in characterizing the main events leading to fossorial specializations and for defining the main extrinsic drivers (e.g. environment, climate, competition) of their convergent adaptations (see Nevo, 1979; Cook et al., 2000).

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