



# Effects of Sex and Breeding Status on Skull Morphology in Cooperatively Breeding Ansell's Mole-Rats and an Appraisal of Sexual Dimorphism in the Bathyergidae

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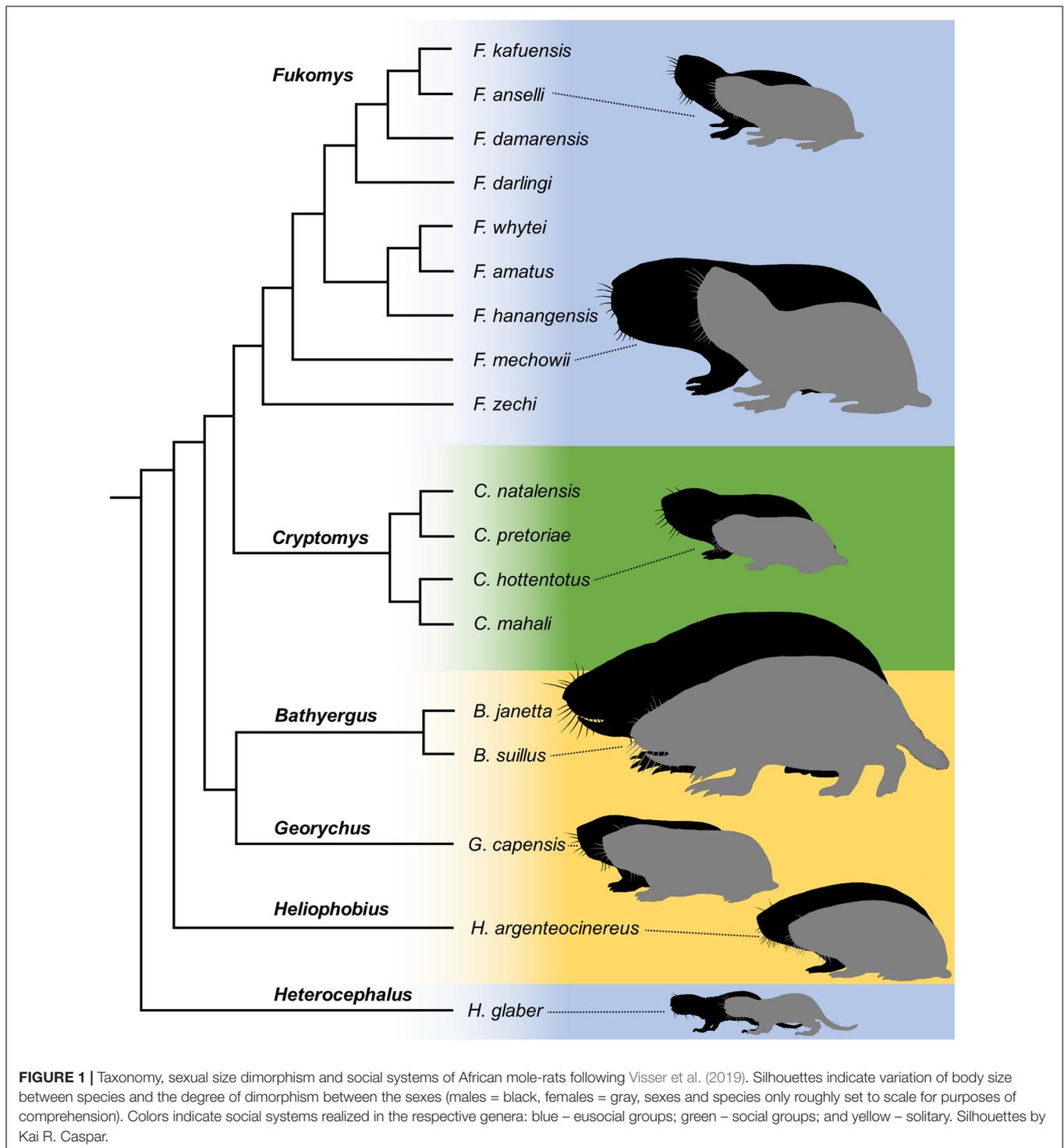
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African mole-rats of the genus *Fukomys* (Northern common mole-rats) combine a monogamous mating system and pronounced sexual size dimorphism; a pattern highly untypical for mammals. At the same time, they live in cooperatively breeding groups composed of reproductive and non-reproductive members of both sexes. How and to which degree sex and breeding status influence morphofunctional characters in eusocial mole-rats is not well characterized but essential to come to a comprehensive understanding of their peculiar social system. Here, we explore patterns of morphological differentiation in skulls of Ansell's mole-rats (*Fukomys anselli*) by means of multivariate analysis of linear skull measurements combined with a 2D shape analysis of cranium and mandible. Compared to females, males display larger skulls relative to body size and show an expansion of the facial portion of the cranium, while reproductive status did not have an effect on any of the traits studied. We also show that species of *Fukomys* mole-rats display a scaling of relative sexual body size dimorphism in compliance to Rensch's rule, which is deemed indicative of intense male intrasexual competition. For the bathyergid family as a whole, results of scaling analyses were more ambiguous, but also indicative of Rensch's rule conformity. In line with genetic field data, our results point to a greater role of male-male conflicts in *Fukomys* than is traditionally assumed and support the notion that reproductive status does not correlate with morphofunctional segregation in these unusual rodents.

**Keywords:** Bathyergidae, Rensch's rule, shape analysis, osteology, geometric morphometrics

## INTRODUCTION

African mole-rats (Bathyergidae) are a speciose group of sub-Saharan rodents which are renowned for their superb adaptation to life underground (Gomes Rodrigues et al., 2016). Despite their ecological uniformity and specialization, bathyergids encompass species with strongly contrasting social systems (Figure 1). The genera *Bathyergus* (dune mole-rats), *Georchus* (Cape mole-rat), and *Heliophobius* (silvery mole-rat) lead strictly solitary lives, while the sister genera *Cryptomys* (Southern common mole-rats) and *Fukomys* (Northern common mole-rats) as well as the basalmost branching



bathyergid genus *Heterocephalus* (naked mole-rat), live in cooperatively breeding groups. These families typically comprise only a single breeding female in all social genera, while the number of simultaneously active reproductive males varies.

In *Fukomys*, the reproductive female is typically monogamous (Burland et al., 2002; Šumbera et al., 2012; Patzenhauerová

et al., 2013). When applying the term monogamy, it is important to differentiate between social monogamy (living and raising offspring with a single partner) and genetic monogamy (exclusively mating and producing offspring with such partner). Many socially monogamous mammals are not genetically monogamous (Cohas and Allainé, 2009). However,

current evidence suggests that *Fukomys* indeed exhibits strict social and predominant sexual monogamy, the latter fluctuating in frequency between populations (Burland et al., 2002; Patzenhauerová et al., 2013). While staying faithful to their current mate for prolonged periods (Bappert et al., 2012; Begall et al., 2021), *Fukomys* may experience serial changes in partners over their lifetime (Burland et al., 2002; Šumbera et al., 2012; Patzenhauerová et al., 2013). Different mating systems are expressed in the other two social bathyergid genera. The breeding female in *Heterocephalus* families may mate with two (seldom more) males at a time (Braude et al., 2020) and in *Cryptomys* it often has multiple partners (Bishop et al., 2004). In *Heterocephalus* as well as in *Fukomys*, more than six generations of pups overlap in average family groups and the majority of offspring remains with their parents and assist in provisioning their siblings instead of reproducing themselves (Burda et al., 2000; Torrents-Ticó et al., 2018). Because of this high degree of philopatry in combination with partitioning of reproductive labor and cooperative breeding, these genera have at times been characterized as eusocial mammals (Burda et al., 2000). In *Cryptomys*, levels of philopatry and male reproductive skew are notably lower than in the other social genera (Bishop et al., 2004; Ingram et al., 2004) so that they are generally not considered to be eusocial. Less is known about the mating systems of solitary genera, but morphological, genetic and behavioral evidence suggests that they are either polygynous or promiscuous (Patzenhauerová et al., 2010; Bray et al., 2012; Visser et al., 2017).

In social mole-rats such as *Fukomys*, non-reproductive individuals are believed to reduce the workload of the breeding female, granting a fitness benefit (Burda et al., 2000). Empirical evidence in support of this assumption has been provided for *Fukomys damarensis*, the Damaraland mole-rat. In captivity, the fecundity of *F. damarensis* breeding females as well as the time they spend resting and feeding correlates positively with the number of non-reproductive helpers (Houslay et al., 2020) and in the wild, breeders spend significantly less time foraging than helpers (Francioli et al., 2020). Although at times stated differently, mole-rat helpers do not show developmentally fixed patterns of task specialization (Lacey and Sherman, 1991; Zöttl et al., 2016; Thorley et al., 2018b; Van Daele et al., 2019), meaning that no helper casts dedicated to specific tasks (e.g., foraging, pup raising, and nest defense) exist, as it is the case in many social insects. Rather than that, an individual's age influences the frequency in which it engages in specific helping behaviors (Zöttl et al., 2016), with differences in the contributions of male and female helpers being negligible (Thorley et al., 2018b).

Due to the differing social and mating systems among bathyergids, it would be predicted that mole-rat genera display varying patterns of sexual size dimorphism (SSD) and sexually selected weaponry directly linked to their mating system (Heske and Ostfeld, 1990; Schulte-Hostedde, 2007). In the solitary genera, one would predict pronounced SSD since access to partners is contested and individual males can gain a reproductive advantage by mating with multiple females via the monopolization of defendable resources. Fitting this assumption, pronounced SSD is found in many solitary subterranean rodents that belong to diverse evolutionary lineages (Daly and

Patton, 1986; Mauk et al., 1999; Su et al., 2018). A conjoint prediction would be that males in these species evolve more formidable weapons, in case of mole-rats more powerful and robust jaws and incisors, to solve this task. More subtle or absent sexual dimorphism would be expected in the social genera, particularly so in monogamous *Fukomys*, where physical breeding competition is low for prolonged periods once a pair-bond is established (Patzenhauerová et al., 2013). Among the few non-bathyergid social subterranean rodents, monogamy and a lack of SSD is for instance evident in the Northern mole vole (*Ellobius talpinus*; Moshkin et al., 2001). On the other hand, it might be expected that these social genera display differences in functional morphology that relate to reproductive status, for example more strongly developed weaponry in breeders of both sexes to defend their status against challengers (Young and Bennett, 2013). Such hypotheses appear reasonable, since at least female breeders in *Fukomys* and *Heterocephalus* show marked changes in their postcranial skeletal anatomy when attaining breeding status (Dengler-Crish and Catania, 2007; Thorley et al., 2018a), indicating a notable degree of developmental plasticity. So far, such differences are not evident in the skulls of female mole-rats (Thorley et al., 2018a) but precise methods such as geometric morphometrics have not yet been employed to differentiate between reproductive status groups and male mole-rats were never studied at all in this respect.

Surprisingly, SSD expression does not appear to correlate with social systems or phylogeny among bathyergids (Burda, 1990, **Figure 1**). Although these patterns are inconsistent and counterintuitive, the phenomenon received only little scientific attention and is seldom comparatively assessed: The solitary *Bathyergus* and at least most species of eusocial *Fukomys* are highly sexually dimorphic in body size with adult males being the larger sex with more massive skulls (Hart et al., 2007; Chimimba et al., 2010; Young and Bennett, 2013). Nevertheless, potential dimorphism in skull shape unrelated to size remains essentially unaddressed in these genera (but see Faulkes et al., 2017 for *Fukomys*). Within the remaining groups of African mole-rats, available studies suggest that skulls are not sexually dimorphic (Taylor et al., 1985; van Rensburg et al., 2004; Barčiová et al., 2009) and that differences in body size are variably expressed. Solitary *Heliophobius* are notably dimorphic in mass (Šumbera et al., 2003). For male-biased SSD in social *Cryptomys*, contradictory results have been published, but studies relying on data from multiple family groups agree that it is indeed present to varying degrees (Spinks et al., 2000; van Rensburg et al., 2004). Finally, eusocial *Heterocephalus* as well as solitary *Georychus* are assumed to lack SSD (Brett, 1991; Jarvis and Bennett, 1991; Bennett et al., 2006, see also Thomas et al., 2012).

If no clear relationship with sociality is evident, what factors underly the expression of SSD in African mole-rats? In many animal groups, SSD scales with body mass, a phenomenon most prominently described by Rensch's rule (Abouheif and Fairbairn, 1997). Rensch's rule posits that among closely related species, SSD grows with increasing general body size when males are the larger sex (Rensch, 1950) and *vice versa* when the opposite is the case (Rensch, 1960, but see Webb and Freckleton, 2007). However, it is commonly assumed that Rensch's rule can only be observed

among socially polygynous or polygamous species (Dale et al., 2007; Bidau and Martínez, 2016) so that bathyergids and even more so *Fukomys* species would not be expected to comply to it. In other subterranean rodents studied so far, the polygynous South American tuco-tucos (*Ctenomys*) and Central Asian zokors (*Eospalax* and *Myospalax*), Rensch's rule is not in effect (Martínez and Bidau, 2016; Su et al., 2018), and notable SSD appears to be rare among small-bodied mammals in general (Lu et al., 2014). Finding Rensch's rule among bathyergids would be unexpected and could indicate so far unappreciated social dynamics acting across the boundaries of social systems in this group.

In this exploratory study, we focus on patterns of sexual dimorphism and correlates of breeding status in *Fukomys anelli*, the Ansell's mole-rat. *F. anelli* is a typical representative of its genus in displaying the puzzling combination of pronounced SSD in conjunction with prolonged sexual monogamy and cooperative breeding (Burda and Begall, 1998; Patzenhauerová et al., 2013). Besides employing craniometric methods to assess morphological differentiation, we also quantify differences in relative skull size between the sexes. This phenomenon received little study in mammals (but see Young and Bennett, 2013) but is well investigated in squamate reptiles, where it is prominently discussed as an indicator for intrasexual competition (e.g., Baird, 2013). To place sexual dimorphism in the Ansell's mole-rat into its phylogenetic context, we further compile a dataset on body mass in the sexes of various bathyergid species and test for SSD scaling conforming to Rensch's rule. By combining these different approaches, we aim to arrive at a comprehensive characterization of sexual dimorphism in cooperatively breeding *Fukomys* mole-rats, which is a crucial step to understand the interplay between monogamous mating systems and pronounced SSD found in these animals.

## MATERIALS AND METHODS

### SSD and the Validity of Rensch's Rule in the Bathyergidae

We conducted a literature search for information on sex-specific body mass in the Bathyergidae and concluded with a dataset spanning 18 species from all six extant genera, which cover almost the complete spectrum of body sizes found in the family, including size extremes (Table 1). The genus *Fukomys* is represented by nine species. Species were included when data for at least five specimens per sex and species corresponding to wild adult animals were available. Data from pregnant females were excluded, whenever provided by the respective sources. Following Ingram et al. (2004), we refer to populations of *Cryptomys* (*C. hottentotus*, *C. mahali*, *C. natalensis*, and *C. pretoriae*) as full species, since the age of these lineages as well as their genetic divergence exceeds that of many *Fukomys* populations which are differentiated at the species level.

We tested for the validity of Rensch's rule in both bathyergids in general and in *Fukomys* by employing two established methods to investigate SSD scaling. If both were to yield comparable outcomes, the respective results could be assumed to be robust. First, we employed phylogenetic

reduced major axis (pRMA) regression, a widely accepted method to study scaling in SSD (Abouheif and Fairbairn, 1997; Fairbairn, 1997; Bidau and Martínez, 2016; Martínez and Bidau, 2016), by utilizing the *phytools* package in R (Revell, 2012). For such interspecific comparisons, phylogenetic relationship must be accounted for to address the non-independence of species data points due to shared ancestry. Based on the bathyergid phylogeny of Visser et al. (2019; see Figure 1), we calculated pRMA regressions of  $\log_{10}(\text{male body mass})$  on  $\log_{10}(\text{female body mass})$  to estimate whether SSD in bathyergids scales with body mass in compliance with Rensch's rule. The rule is in effect when the coefficient  $\beta$  of said regressions is significantly greater than the expected value 1 (Abouheif and Fairbairn, 1997; Martínez and Bidau, 2016). Clark's T statistic with adjusted degrees of freedom was employed to assess the deviation of the slope from the expectation (Bidau and Martínez, 2016).

Second, we calculated phylogenetic linear regression models based on modified Lovich-Gibbons' ratios (two-step LG ratio) on  $\log_{10}(\text{female body mass})$  as recommended by Smith (1999). The two-step LG ratio is calculated as follows: If the mean body mass of males is higher than that of females: M/F; if the mean body mass of females is higher than that of males: 2-F/M. Smith (1999) recommends the application of the two-step LG ratio for typical mammalian data sets where male-biased SSD is prevalent. Linear regression models were corrected for phylogeny by using phylogenetic independent contrasts. According to this method, Rensch's rule is in effect when the coefficient  $\beta$  of the regression line is significantly greater than 0.

### Skull Morphometrics of *Fukomys anelli*

All morphometric data was collected blindly with the researchers taking measurements being unaware of sex and reproductive status of the specimen concerned. All analyses, if not otherwise indicated, were carried out in R Studio for Mac Version 1.3.1093 (RStudio Team, 2020).

### Material

Skulls of 40 adult *Fukomys anelli*, representing ten non-breeders and ten breeders of either sex were extracted from ethanol-fixed or frozen animals from the research collection of the Department of General Zoology, University of Duisburg-Essen (Supplementary Table 1). Respective individuals were kept and often bred in the laboratories of the University but genealogically derive from animals captured close to the type locality of the species in the Lusaka area of Central Zambia. Relying on captive subjects allowed for an unequivocal determination of an individual's reproductive status, as breeding was closely monitored in the laboratory. Only captive-born individuals that never reproduced were classified as non-breeders, while breeders were required to have produced at least one offspring. All skulls derived from animals that were at least 30 months old at the time of death and therefore fully mature. *F. anelli* is full grown at an age of approximately 12 months (Burda and Begall, 1998). Mean age for breeders was 111.2 months (=9.3 years; SD: 41.4 months), while mean age for helpers was 57.9 months (=4.8 years; SD: 36.3 months). This stark discrepancy is largely explained by the bimodal aging pattern in the genus *Fukomys*,

**TABLE 1** | Mean body mass (BM, g) and sexual size dimorphism (SSD, male:female) based on BM in African mole-rats.

Species	<i>n</i> <sub>males</sub>	<i>n</i> <sub>females</sub>	BM <sub>males</sub>	BM <sub>females</sub>	SSD	References
<i>Bathyergus janetta</i>	100	106	429.4	330.4	1.30	Herbst et al., 2004
<i>Bathyergus suillus</i>	87	100	955.2	778.5	1.23	Bennett et al., 2009
<i>Cryptomys hottentotus</i>	31	19	77	57	1.35	Jarvis and Bennett, 1991
<i>Cryptomys mahali</i>	8	8	131	92.1	1.42	van Jaarsveld et al., 2019
<i>Cryptomys natalensis</i>	106	95	108.8	77.3	1.41	Oosthuizen, 2008
<i>Cryptomys pretoriae</i>	96	184	100.5	90.7	1.11	van Rensburg et al., 2004
<i>Fukomys amatus</i>	9	5	71.6	65.2	1.10	Scharff, 1998
<i>Fukomys anselli</i>	87	86	63	52.9	1.19	Sichilima et al., 2011
<i>Fukomys damarensis</i>	290	281	165	141.5	1.17	Bennett and Jarvis, 2004
<i>Fukomys darlingi</i>	23	20	69.5	63.5	1.10	Bennett et al., 1994; Gabathuler et al., 1996
<i>Fukomys hanangensis</i> *	12	5	89.7	78.2	1.15	Faulkes et al., 2017
<i>Fukomys kafuensis sensu lato</i> *	5	12	89.8	75.6	1.19	Van Daele et al., 2019, reclassified according to Visser et al., 2019
<i>Fukomys mechowii</i>	79	76	570.7	391.8	1.46	Sichilima et al., 2008
<i>Fukomys whytei</i> *	11	11	131.1	107.3	1.22	Burda et al., 2005; Faulkes et al., 2017
<i>Fukomys zechi</i>	28	29	234.1	202.2	1.16	Yeboah and Dakwa, 2002
<i>Georchus capensis</i>	189	277	193.1	195.8	0.99	Bennett et al., 2006; Thomas et al., 2012; Visser et al., 2017
<i>Heliophobius argenteocinereus</i>	70	74	190.1	162.1	1.17	Šumbera et al., 2003
<i>Heterocephalus glaber</i>	<i>n</i> <sub>total</sub> = 651		34.1	36.5	0.93	Brett, 1991

In case that data were pooled from different studies, weighted means have been calculated. Data presented refer to adult animals measured in the wild (age class assignment followed respective references). \*only unequivocally sexed specimens with body masses equal to or above 50 g were considered and, if applicable, those in adult dental age categories as assigned by the respective authors. The two-step Lovich-Gibbons' ratios (Smith, 1999) were identical with SSD values to the second decimal place.

with breeders reaching on average two times the age of helpers in captivity (Dammann and Burda, 2006). However, mean ages of males (7.8 years; SD: 49.2 months) and females (6.3 years; SD: 44 months) did not differ significantly (Student's *t*-Test,  $p > 0.2$ ). Each specimen derived from a different litter and for the most part from different families. Only two pairs of different aged siblings were sampled, all of the respective individuals being non-breeders.

## Multivariate Skull Morphometrics

A set of 24 linear measurements from cranium and mandible (Table 2) were collected with digital calipers (fixpoint® model 77001). Measurements were taken by a single observer (KRC) to 0.1 mm from either the sagittal plane or the right side of the skull (see Table 2 and Supplementary Table 1) and are visualized in Figure 2. In case relevant structures of the right side of the skull were damaged, measurements were taken from the left one (11 measurements = 1.1% of total measurements). Missing measurements [10 measurements = 1% of total measurements ( $n = 950$ ), see Supplementary Table 1] were estimated using the *LOST* package (Arbour and Brown, 2020). Hindfoot length was chosen as a proxy for body size to assess its influence on cranial measurements. Foot length is a common metric in small mammal research that is insensitive to changes in body condition and was measured to the nearest 0.1 mm excluding claws, following Ansell (1965).

Measurements were log-transformed and analyzed using principal component analysis (PCA). Subsequently, leave-one-out cross-validated linear discriminant function analysis (LDA)

was performed on the principal components (PC) generated by the PCA to estimate how well sexes and breeding status groups could be differentiated based on cranial measurements. One-tailed exact binomial tests were used to check whether correct assignment rates differed significantly from chance level. Suitability of PC covariance for LDA was tested with Box's *M* test. The assumption of multivariate normality was tested using the Shapiro-Wilk multivariate normality test. A MANOVA was used to test for the effects of body size, sex, and reproductive status as well as their interaction on skull morphology. Comparisons of each linear measurement between the respective groups of specimens were performed by employing Welch's two sample *t*-test for normally distributed measurements and Wilcoxon rank sum test for non-normally distributed ones, respectively, controlling for alpha error accumulation via Bonferroni correction. This resulted in an adjusted significance level of  $\alpha_{\text{adjusted}} = 0.002$ .

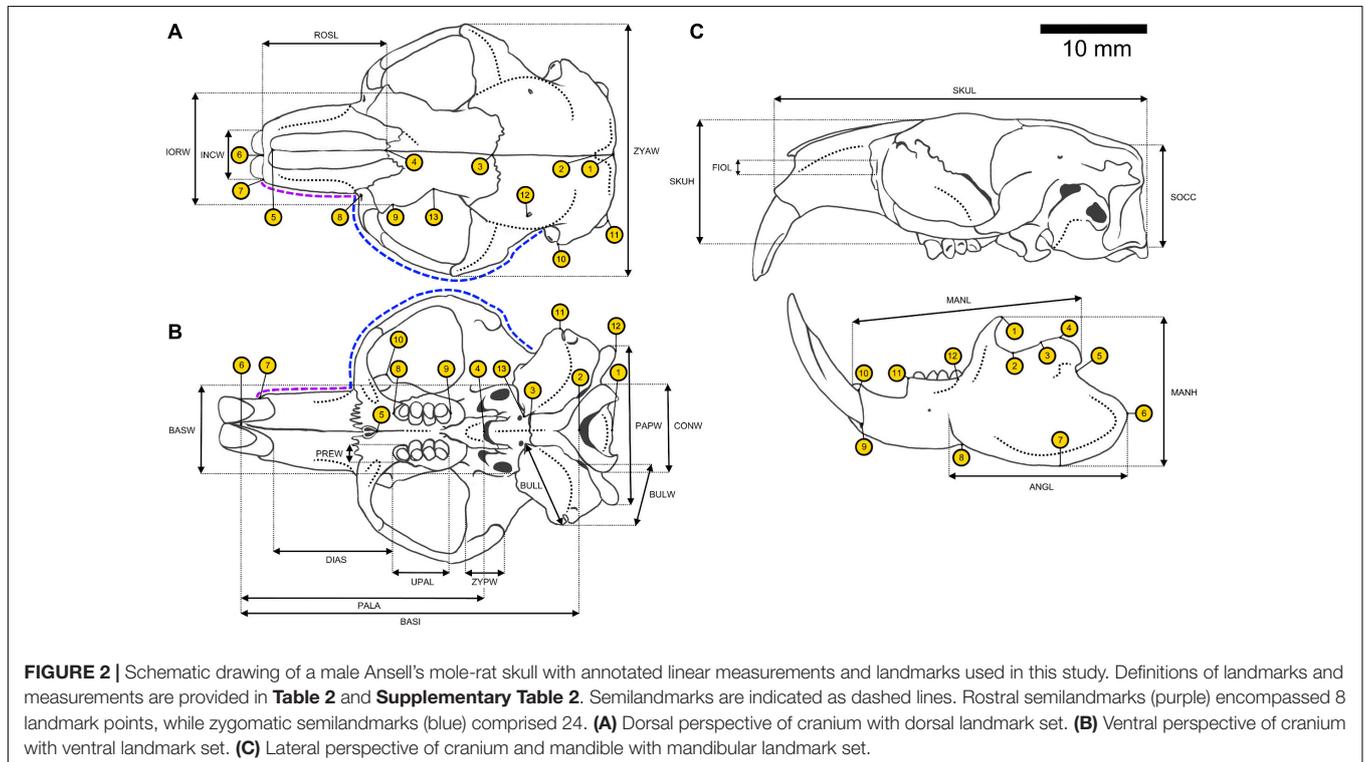
## 2D Geometric Morphometrics of Cranium and Mandible

Size-independent differences in skull shape were analyzed by employing a 2D landmark approach. Crania were photographed with a Canon EOS 200D reflex digital camera in a standardized fashion from dorsal and ventral perspectives. Mandibles were photographed from a lateral perspective. Specimens were placed on a checkered mat with squares of 1 cm edge length that was used to provide spatial orientation and acted as a size reference. The inclination of the crania was adjusted with a piece of plasticine. The camera focus was adjusted on the molars

**TABLE 2 |** Summary of linear cranial measurements collected for multivariate morphometric analysis.

Measurement	Abbreviation	Description
Length of diastema	DIAS	Distance between alveoli of the upper incisor and premolar.
Palatilar length	PALA	Distance between staphylion and the alveoli of the upper incisors
Length of upper alveolar row	UPAL	Length of upper tooth row, measured at the alveolar margins.
Width of premolar	PREW	Breadth of upper premolar, measured at the alveolar margin
Length of bulla	BULL	Length of bulla measured from styliform process to the external auditory meatus
Width of bulla	BULW	Width of bulla measured from the jugular foramen to the external auditory meatus
Basilar length	BASI	Distance between the anterior margin of the foramen magnum and the anterior margin of the incisor alveoli
Greatest length of skull	SKUL	Distance between the premaxillary tip and the posteriormost extension of the occipital in the sagittal plane
Interorbital width	IORW	Smallest distance between the outer margins of the frontals at the reduced bony orbits
Width of posterior portion of zygomatic arch	ZYPW	Width of squamosal portion of zygomatic arch measured in parallel to the sagittal plane
Width of zygomatic arches	ZYAW	Maximum width of zygomatic arches measured at the anterior tips of the squamosals
Width of skull base	BASW	Minimal distance between squamosals measured ventrally
Width of skull at paroccipital processes	PAPW	Maximum width of cranium measured at paroccipital processes
Size of infraorbital foramen	FIOL	Maximum extension of the infraorbital foramen
Width of processus zygomaticus maxillaris	PZMW	Width of the processus zygomaticus maxillaris at the infraorbital foramen
Width of incisors	INCW	Width of upper incisors measured at the alveolar margins
Length of rostrum	ROSL	Distance between alveolar margins of incisors and the nasofrontal suture.
Height of cranium	SKUH	Distance between anterior alveolar margin of the premolar and the nasofrontal suture.
Width of condyle	CONW	Greatest width of condyle
Height of occiput	SOCC	Greatest length of the supraoccipital bone (including skull crests, if present)
Mandible length	MANL	Length of the ramus mandibulae measured from condyle to the incisors' alveolar margin
Total height of mandible	MANH	Distance between tip of coronoid process and the ventral margin of the angular process
Height of coronoid process	CONH	Distance between tip of coronoid and ventral margin of the mandibular ramus
Length of angular process	ANGL	Greatest length of angular process

Measurements were adopted and modified from Van Daele et al. (2013).



for both ventral cranium and mandible photos and on the interfrontal suture of the skull roof for pictures taken from the dorsal perspective. Unilateral sets of 13 landmarks for the dorsal and ventral cranium and 12 landmarks for the mandible were

selected and analyzed independently from each other (**Figure 2**; definitions are listed in **Supplementary Table 2**). Dorsal and ventral sets were amended by two lateral semilandmarks. The first one consisted of 8 semilandmark points and was set

along the rostrum from the incisor to the zygomatic arch. The second one comprised 24 landmark points and demarcated the zygomatic arch (Figure 2). Bending energy was used as criterion to optimize landmark positioning during sliding. Landmarks' digitization and scaling of photographs was achieved in TPSDig2 version 2.31 (Rohlf, 2018) and done by a single researcher for each landmark set (JM: dorsal/ventral; KRC: mandible). The geomorph package (Adams et al., 2020) was employed to analyze shape data. Occasional damage to the coronoid process led to missing landmarks (6 landmark points = 1.25%) in the mandible dataset, which were estimated and replaced by aid of the *LOST* package (Arbour and Brown, 2020). Landmarks were Procrustes superimposed to allow for subsequent analysis. Allometry was assessed by an ANOVA, regressing shape variables against centroid size, which is a measure of overall size in superimposed landmark datasets. PCA and LDA were employed with procedures analogous to those used in the analysis of linear cranial measurements and served the same purpose. However, the mandible dataset was not normally distributed. Therefore, statistical differences in measurements for sexes and reproductive status groups as well as interaction effects were assessed via MANOVA for dorsal and ventral cranial datasets and via a PERMANOVA for the mandibular one, respectively. Since LDA requires normal distribution of data as well, the randomForest method was used as an alternative classification procedure for mandibular landmark data (Liaw and Wiener, 2002).

## Sex Differences in Relative Skull Dimensions

The greatest lengths of the skull (SKUL) and zygomatic arch width (ZYAW) were chosen to represent skull length and width, respectively, while hindfoot length was again used as a proxy for body size. Differences in hindfoot length between sexes and reproductive status groups were assessed in a linear regression model with hindfoot length as the dependent variable and sex and breeding status as predictors. Subsequently, the influence of body size and sex on skull size was tested the same way with either skull length or width as the dependent and hindfoot length as well as sex as predictor variables. Based on results from our previous morphometric analyses, the influence of breeding status on these parameters was not tested. Data were inspected visually for biasing outliers, linearity, normality, and homogeneity of variances in diagnostic plots. The latter two aspects were also assessed through Shapiro–Wilk and Levene tests, respectively, and found to be suitable for linear regression. Values for Cohen's *d* were derived from models' *t* statistics to provide a measure of effect size.

## RESULTS

### Occurrence and Scaling of SSD in the Bathyergidae

We found large differences in SSD among bathyergids and within the most speciose genus, *Fukomys* (Table 1). Lowest SSD values

indicating sexual monomorphism were recovered for *Georychus* and *Heterocephalus*. All other bathyergids show a male-biased SSD which is pronounced in *Fukomys mechowii*, the giant mole-rat, and in the small-bodied genus *Cryptomys*. There was only a modest correlation between  $\log_{10}$  female body mass and SSD in the Bathyergidae in general (Pearson correlation:  $r = 0.3$ ;  $t = 1.26$ ; and  $p = 0.23$ ) but a strong one among *Fukomys* species (Pearson correlation:  $r = 0.76$ ;  $t = 3.1$ ; and  $p = 0.017$ ).

Analyses of body mass data via pRMA models (Table 3 and Figure 3) recovered that bathyergids as a whole show a trend to follow Rensch's rule of SSD scaling ( $\beta = 1.072$ ,  $p = 0.079$ ) while *Fukomys* species clearly comply to it ( $\beta = 1.102$ ;  $p = 0.021$ ). For both groups a strong phylogenetic signal associated with SSD was found ( $\lambda = 0.999$ ), indicating a tight correlation between the expression of SSD and phylogenetic affiliation in bathyergids. Results of the regression models on two-step LG ratios did only partially align with the ones of the pRMA models. The former found bathyergids to comply to Rensch's rule ( $\beta = 0.2214$ ;  $p = 0.01$ ) while the data for *Fukomys* is approaching significance ( $\beta = 0.2611$ ;  $p = 0.05$ ).

### Multivariate Skull Morphometrics

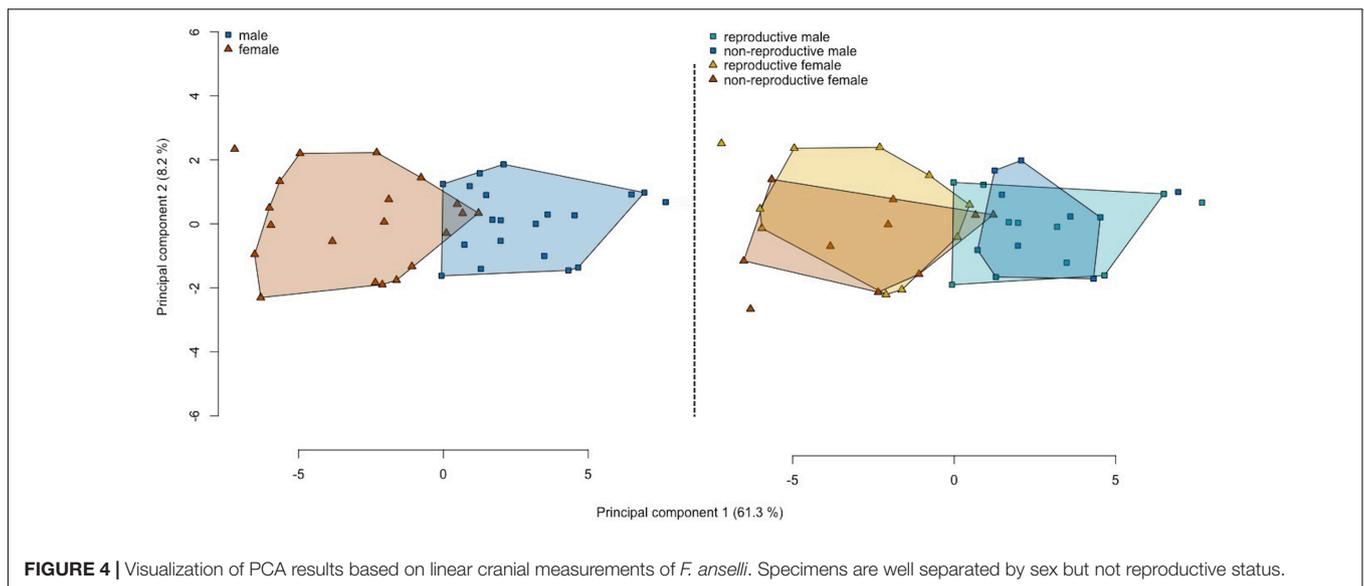
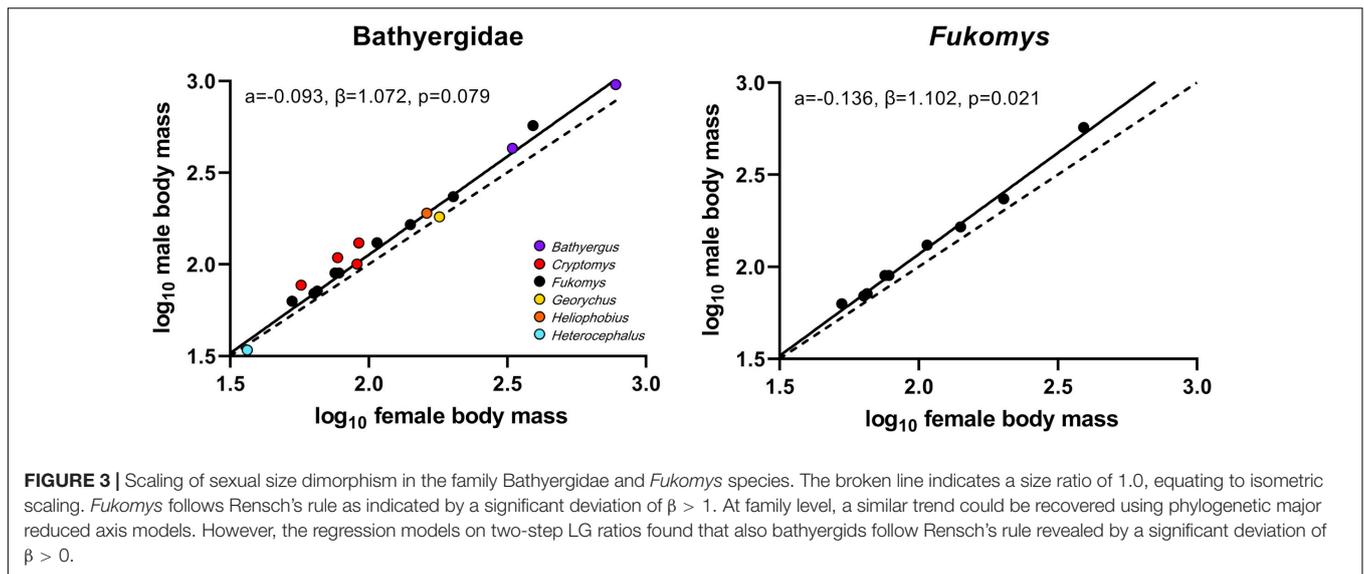
Male and female *F. anselli* were recovered as almost completely separated in the PCA morphospace based on linear cranial measurements, while reproductive groups were not discernible from each other (Figure 4 and Table 4). Further analyses provided results consistent with this finding. MANOVA indicated a strong influence of sex on cranial morphometrics ( $F = 12.13$ ,  $p \ll 0.001$ ) but none of reproductive status ( $F = 0.63$ ,  $p = 0.74$ ) or the interaction between both ( $F = 0.34$ ,  $p = 0.84$ ). Hindfoot length was a strong general predictor of cranial morphology ( $F = 7.33$ ,  $p < 0.001$ ), but not among individuals of the same sex ( $F = 0.40$ ,  $p = 0.8$ ), and irrespective of their reproductive status ( $F = 0.1$ ,  $p = 0.98$ ). While males (90%) and females (80%) could be reliably classified in the linear measurement LDA ( $p < 0.01$ ), individuals of the same sex were randomly assigned to reproductive status groups ( $p > 0.1$ , Table 5).

For the linear measurements, PCA computed 24 principal components, the first four of which had eigenvalues  $> 1$  and explained 79.9% of total variance in the sample (Table 4). The most important measurements for group separation in PC1 were indicators of overall skull size, but particularly of its facial portion: mandibular length (MANL: 6.35%), basilar

**TABLE 3** | Results from phylogenetic major reduced axis models investigating the relationship between male and female body mass in African mole-rats.

Group	N	$\lambda$	$r^2$	$\alpha$	$\beta$	$p$
Bathyergidae	18	0.999	0.979	-0.093	1.072	0.079
<i>Fukomys</i>	9	0.999	0.993	-0.136	1.102	0.021

*N* gives the number of analyzed species in the respective group. Northern common mole-rats (*Fukomys* sp.) obey Rensch's rule, while the family in total does not, according to this method. Different from that, the regression models on two-step LG ratios suggest that bathyergids follow Rensch's rule as well ( $\beta = 0.2214$ ;  $p = 0.01$ ).



length (BASI: 6.35%), and zygomatic arch width (ZYAW: 6.29%). However, PC1 factor loadings were to a large extent evenly distributed over the measurements, excluding several measurements concerned with dental characters and the skull base, which were of specific relevance to PC2. Width of skull base (BASW: 22.04%), width of premolar (PREW: 21.43%), and upper tooth row length (UPAL: 15.9%) contributed most to PC2 (Table 4).

The comparison of individual measurements between sexes and reproductive groups supported results of other analyses in showing distinct sexual dimorphism and the absence of cranial differences between breeders and non-breeders (Table 5). All but six variables differed significantly between the sexes ( $p_{adjusted} < 0.002$ ). Non-significant variables primarily encompassed measurements relevant to the dentition and skull base. They related to the upper cheek dentition (PREW,

UPAL), condyle (CONW) and paroccipital processes (PAPW), infraorbital foramen size (FIOL) and the width of the tympanic bulla (BULW). Differences between breeders and non-breeders of the same sex were consistently non-significant.

### Sex Differences in Relative Skull Dimensions

Hindfoot length, approximating body size, was not found to differ intrasexually within reproductive status groups ( $t = -0.355$ ,  $p > 0.7$ , and  $d = 0.12$ ), but between the sexes ( $t = 2.626$ ,  $p = 0.012$ , and  $d = 0.88$ ). Skull length as well as width was found to increase proportionally with body size without significant differences among regression slopes between the sexes (skull length:  $t = 1.543$ ,  $p = 0.131$ , and  $d = 0.51$ ; skull width:  $t = 1.773$ ,  $p = 0.085$ , and  $d = 0.59$ ; Figure 5). However, relative skull length and width was greater in males compared to females as

**TABLE 4 |** Results of PCA based on linear cranial measurements in *F. ansellii*.

Variable	PC1		PC2		PC3		PC4	
	EV: 14.70	Var. expl. 61.3%	EV: 1.95	Var. expl. 8.2%	EV: 1.44	Var. expl. 6.0%	EV: 1.09%	Var. expl. 4.55%
DIAS*	5.44%	0.23	2.82%	0.17	0.12%	-0.04	0.27%	0.05
PALA*	6.26%	0.25	0.16%	0.04	0.12%	0.04	0.11%	-0.03
UPAL	0.54%	0.07	15.90%	-0.40	5.65%	0.24	1.36%	-0.12
PREW	0.10%	0.03	21.53%	-0.46	2.78%	0.17	27.81%	-0.53
BULL*	4.68%	0.22	1.53%	0.12	9.76%	-0.31	0.58%	-0.08
BULW	3.49%	0.19	3.75%	0.19	10.98%	-0.33	0.08%	-0.03
BASI*	6.35%	0.25	0.56%	0.07	0.25%	0.05	0.02%	0.02
SKUL*	6.11%	0.25	0.16%	0.04	0.20%	0.04	0.32%	0.06
IORW*	5.56%	0.24	0.77%	0.09	0.94%	0.10	1.86%	-0.14
ZYPW*	3.86%	0.20	0.92%	-0.10	5.02%	-0.22	3.08%	-0.18
ZYAW*	6.29%	0.25	0.43%	0.07	0.14%	0.04	0.30%	0.05
BASW*	0.12%	0.04	22.04%	-0.47	0.35%	-0.06	37.99%	0.62
PAPW	3.34%	0.18	5.77%	-0.24	0.60%	-0.08	3.05%	0.17
FIOL	0.92%	0.10	9.37%	-0.31	22.05%	-0.47	8.46%	-0.29
PZMW*	3.78%	0.19	2.11%	-0.15	11.14%	0.33	0.15%	0.04
INCW*	5.55%	0.24	0.96%	0.10	2.55%	0.16	1.53%	0.12
ROSL*	5.19%	0.23	0.73%	0.09	0.32%	0.06	5.48%	-0.23
SKUH*	5.44%	0.23	1.21%	0.11	0.02%	0.01	0.05%	0.02
CONW	1.97%	0.14	5.09%	-0.23	11.35%	-0.34	0.05%	0.02
SOCC*	3.00%	0.17	0.41%	0.06	14.21%	0.38	2.59%	-0.16
MANL*	6.35%	0.25	0.36%	0.06	0.32%	-0.06	0.02%	0.01
MANH*	5.42%	0.23	0.37%	-0.06	0.01%	0.01	1.32%	0.11
CONH*	4.69%	0.22	2.91%	-0.17	0.98%	0.10	0.83%	0.09
ANGL*	5.54%	0.24	0.13%	-0.04	0.15%	0.04	2.72%	0.16

\*indicates measurements that differed significantly ( $p_{adjusted} < 0.002$ ) between the sexes. See **Table 2** for abbreviations of linear measurements; EV, eigenvalue; Var. expl., percentage of explained variance.

**TABLE 5 |** Correct assignment rates (%) of *F. ansellii* skulls based on sex and reproductive status according to discriminant function analyses (based on LDA or in the case of mandibular landmarks on randomForest).

Sex ( $n = 20$ )	Linear measurements				Dorsal landmarks				Ventral landmarks				Mandibular landmarks			
	♂♂		♀♀		♂♂		♀♀		♂♂		♀♀		♂♂		♀♀	
	<b>90</b>	<b>80</b>	<b>90</b>	<b>85</b>	<b>95</b>	<b>85</b>	<b>70</b>	<b>65</b>								
Breeding status ( $n = 10$ )	<i>R</i>	NR	<i>R</i>	NR	<i>R</i>	NR	<i>R</i>	NR	<i>R</i>	NR	<i>R</i>	NR	<i>R</i>	NR	<i>R</i>	NR
	30	20	60	50	40	50	50	50	40	60	50	50	60	70	50	60

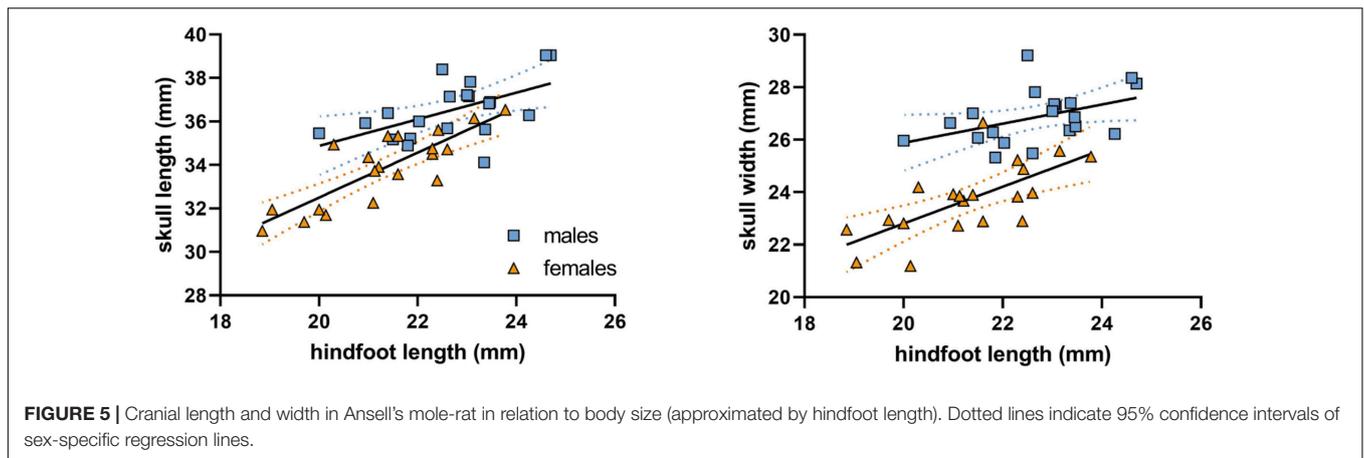
Bold numbers indicate correct assignments significantly different from chance ( $p < 0.05$ , one-tailed exact binomial test). NR, non-reproductive, R, reproductive.

indicated by significantly different regression constants (skull length:  $t = 3.849$ ,  $p < 0.001$ , and  $d = 1.27$ ; skull width:  $t = 6.665$ ,  $p < 0.001$ , and  $d = 2.19$ ). There was a mean sex difference of 1.5 mm (SD: 0.39) in skull length and 2.4 mm (SD: 0.36) in width at equal body size, conforming to 4.4 and 10.1% of mean female skull length and width, respectively.

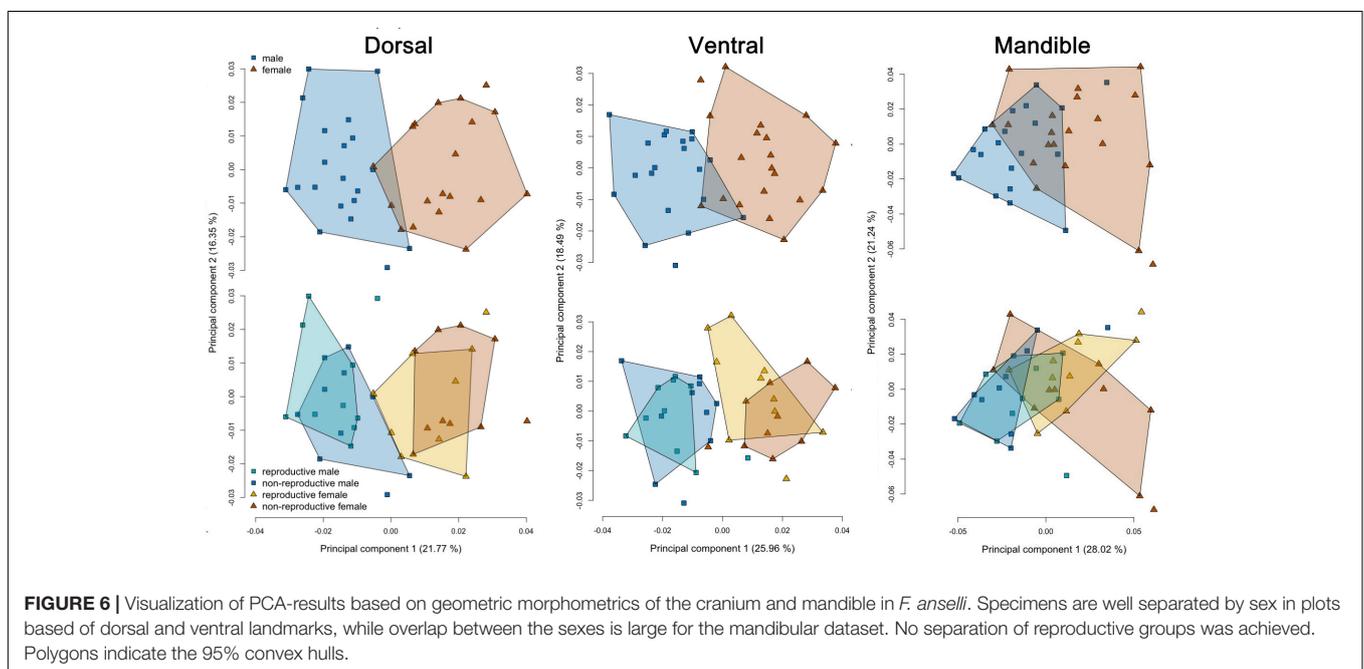
## 2D Geometric Morphometrics of Cranium and Mandible

Analyses on the two landmark sets corresponding to dorsal and ventral cranium yielded similar results, while the mandibular dataset deviated from the latter ones in some respects, being less

sensitive to influences of sex and skull size. In the dorsal and ventral cranial datasets, the PCA was able to separate specimens well regarding sex but not breeding status. However, the first two principal components encompassed only a fraction of total variance (38.1 and 44.8%, respectively; **Figure 6**), indicating high overall morphological variability. A similar pattern was recovered for the mandibular dataset, although morphospace overlap between the sexes as well as the variance explained by the first two PCs (49.3%) was greater compared to the other ones (**Figure 6**, see below). Accordingly, only sex was recovered to significantly influence the shape of the dorsal ( $F = 6.36$ ,  $p = 0.001$ ) and ventral cranium ( $F = 5.32$ ,  $p = 0.001$ ) as well as mandibular shape ( $F = 4.82$ ,  $p = 0.001$ ). Reproductive status or the combined



**FIGURE 5** | Cranial length and width in Ansell's mole-rat in relation to body size (approximated by hindfoot length). Dotted lines indicate 95% confidence intervals of sex-specific regression lines.



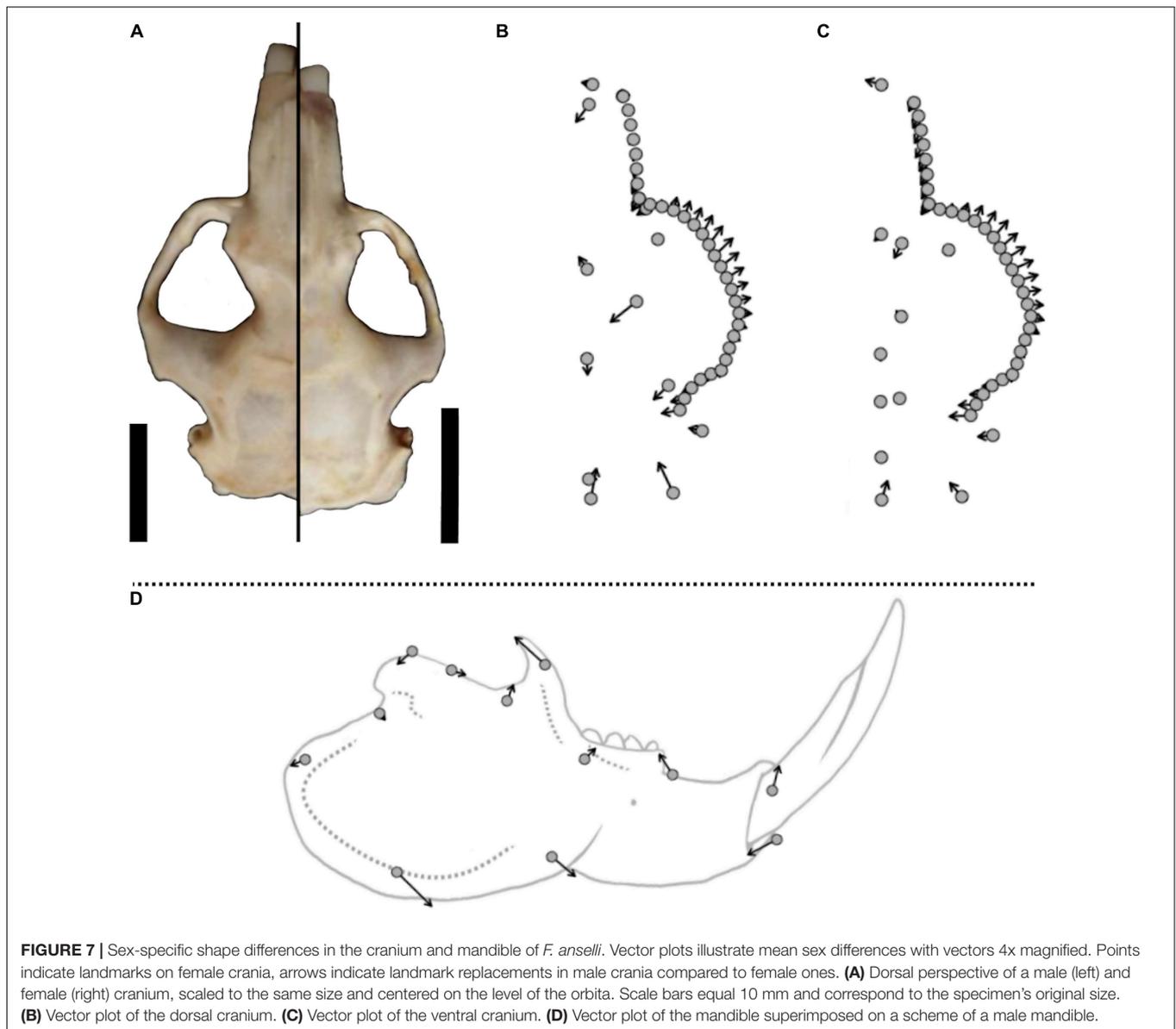
**FIGURE 6** | Visualization of PCA-results based on geometric morphometrics of the cranium and mandible in *F. anselli*. Specimens are well separated by sex in plots based of dorsal and ventral landmarks, while overlap between the sexes is large for the mandibular dataset. No separation of reproductive groups was achieved. Polygons indicate the 95% convex hulls.

effect of sex and breeding status had no significant effect on these traits ( $p > 0.1$ ). Shape allometry was detected for the dorsal ( $F = 3.80$ ,  $p = 0.001$ ) and ventral ( $F = 3.17$ ,  $p = 0.001$ ) cranium, but not for the mandible ( $F = 1.97$ ,  $p = 0.06$ ). However, since males had almost consistently larger skulls than females (**Figure 6**), this result is trivial. No pattern of allometry was found among specimens of the same sex in either landmark dataset (dorsal:  $F = 0.69$ ,  $p = 0.25$ ; ventral:  $F = -0.44$ ,  $p = 0.66$ ; and mandible:  $F = 1.1$ ,  $p = 0.40$ ).

Compared to females, the facial portion of the skull in males is enlarged, with longer rostra and widened zygomatic arches, which flare out more anteriorly (**Figure 7**). When scaled to the same size, the braincase and occipital region of male skulls therefore appear notably compressed compared to those of females. **Figure 7** visualizes shape differences between male and female *F. anselli* in a vector plot, highlighting relevant shape differences. Shape variable contributions and eigenvalues of PCs can be derived from **Supplementary Table 3**. Male mandibles

were found to display a deeper and slightly more elongated processus angularis (landmark 6: 7.8% of PC1 variance, 16.9% of PC2 variance; landmark 7: 41.2% of PC1 variance, 22.7% of PC2 variance) thicker lower incisors (landmark 9: 23.2% of PC1 variance, 14% of PC2 variance) and a longer, more sickle shaped coronoid process (landmark 1: 14.4% of PC1 variance, 12% of PC2 variance), when compared to females (**Figure 7**). However, sex differences in the shape of the lower jaw were altogether less pronounced than the ones in cranial shape. This was indicated by a more pronounced morphospace overlap and markedly higher error rates for assignments of individuals to one sex based on mandibular compared to cranial shape (**Table 5**, see below).

Cranial shape was found to be highly diagnostic for the sexes in *F. anselli*, but more so for males than for females mirroring the results from linear measurements (**Table 5**). LDA assigned 90% of males and 85% of females correctly based on dorsal cranial shape, while the ventral dataset allowed to classify 90% of males and 85% of females correctly. In both cases, these proportions



differed significantly from random assignments ( $p \leq 0.001$ ). The mandibular shape yielded less definite results: 70% of males and 65% of females were assigned to the correct categories, rates that did not significantly deviate from chance levels ( $p > 0.05$ ). All intrasexual assignments based on reproductive status were randomized ( $p > 0.1$ ).

## DISCUSSION

### Occurrence and Scaling of SSD in the Bathyergidae

Regression analyses based on both pRMA and two step LG ratios found Rensch's rule expressed in the monogamous mole-rat genus *Fukomys*, while only the latter did so for the bathyergid clade as a whole. The evidence for *Fukomys* following Rensch's

rule is therefore robust, while its validity for bathyergids might still be questioned. However, although the pRMA regression did not reveal bathyergid SSD scaling significantly deviating from an isometric trajectory, a statistical trend ( $p < 0.1$ ) emerged. If this is considered together with the positive results from the LG ratio based regression, one could therefore tentatively assume that Rensch's rule could apply to bathyergids on family level as well. Differences in the clarity of analytical outcomes between the two studied groups (*Fukomys* versus all bathyergids) might result from more uniform intrasexual selection pressures in *Fukomys*, when compared to other genera, which encompass a greater diversity of mating systems (compare Bray et al., 2012; Visser et al., 2017; Braude et al., 2020). Still, with the exception of *Heterocephalus*, aggressive competition between males, deduced either from direct observations (see below for *Fukomys* and, e.g., Jarvis and Bennett, 1991 for *Bathyergus* and Oosthuizen, 2008

for *Georychus*) or from morphological correlates such as sexual dimorphism, is evident throughout the bathyergid radiation. As such, it could underly the prevalence and scaling of SSD in these different taxa.

It is, however, important to point at the limitations of our dataset: Various studies have shown that intraspecific variation in bathyergid SSD (as approximated by body mass) can correlate with geographic provenance (*Cryptomys hottentotus* – Spinks et al., 2000; *Fukomys mechowii* – Scharff, 1998) and season of the year (*Georychus capensis* – Oosthuizen, 2008), factors for which we did not and could not control. Additionally, as we only included adult animals as assigned by the respective studies, we have to expect inconsistencies in the assignment of somatic maturity by the various authors we drew data from (see below). We must therefore consider a certain bias to our dataset. However, since most recovered rates of SSD correspond well to general reporting in the literature, we do not see the validity of our results compromised in that regard. Still, a more comprehensive dataset would have been desirable, especially regarding *Fukomys* species occurring North to the equator and for unambiguously localized populations of the solitary bathyergid genera, which might encompass significantly more species than currently recognized (Visser et al., 2019). However, biometric information on these mole-rats is currently unavailable.

Smaller-bodied species in our dataset (<150 g) are more variable regarding the expression of dimorphism than larger ones, where marked male-biased SSD is prevalent (Table 1). Among the small species, SSD is particularly pronounced in *Cryptomys*, in which male reproductive competition can be intense since multiple breeding males are regularly cohabiting a burrow and high incidences of extra-group paternity are common (Bishop et al., 2004). Bathyergids with strongly expressed SSD such as *Cryptomys* ssp. and *F. mechowii* are even among the most dimorphic of all rodents (Schulte-Hostedde, 2007), pointing to a crucial biological relevance of SSD in these animals. The latter must be especially emphasized for the genus *Fukomys*, where SSD scaling unambiguously follows Rensch's rule.

It appears that if at all, only modest SSD should be considered the ancestral condition in the Bathyergidae. Notable SSD is predominately found in derived bathyergids and is missing in the most basal genus *Heterocephalus* as well as among the closely allied rodent taxa Thryonomyidae and Petromuridae (Adu et al., 2002; Rathbun and Rathbun, 2006). Still, future studies might try to retrace the evolution of SSD in African hystricognaths in detail to eventually solve this question. Clarifying the matter might be specifically relevant to add to our understanding of the independent evolution of eusociality in *Fukomys* and *Heterocephalus*, which apparently derived from ancestors that strongly differed in SSD. In any case, some bathyergid SSD patterns will remain challenging to explain (compare Figure 1). The lack of SSD in *Georychus* appears to be secondarily acquired and is unexpected in an aggressively territorial solitary species. Not only are other non-social bathyergids, including its sister genus *Bathyergus*, dimorphic, but well-developed SSD is found in the majority of solitary subterranean rodents (Ctenomyidae –

Martínez and Bidau, 2016; Geomyidae – Daly and Patton, 1986; Mauk et al., 1999; and Spalacidae – Su et al., 2018). On the other hand, the presence of pronounced SSD in at least several of the monogamous *Fukomys* species is surprising: their social system is commonly assumed to result in monomorphic sexes, and compliance to Rensch's rule could not be expected *a priori*. Possible explanations for this trait combination based on male-biased dynamic replacement of breeders will be discussed below.

## Effects of Breeding Status on Skull Morphology in *F. anselli*

None of our analyses recovered significant differences between breeding and non-breeding mole-rats of the same sex, while sexual dimorphism was found to be pronounced within both groups. An important caveat to our analysis is the limited sample size of only ten individuals per status group and sex, especially in light of the high morphological variability we recover. However, since none of the different datasets we compared indicated even a trend of morphological segregation, we are reasonably confident that our findings reflect the actual conditions. Additionally, although our study is the first to explicitly address potential differences in skull morphology between mole-rats of different reproductive status, previous publications have already alluded to the lack of status-dependent cranial differentiation in *Fukomys* (Thorley et al., 2018a). Still, there surely is the possibility that future studies relying on more refined methods, such as 3D geometric morphometrics, may show detectable differences between mole-rat status groups. Nevertheless, even if such disparities would eventually be demonstrated, respective traits will be far more subtle than general sex-specific skull characteristics.

The uniformity of cranial characters contrasts with the pronounced differences in postcranial skeletal anatomy of breeding and non-breeding females in this genus (Thorley et al., 2018a) and points to similar functional demands to the skull among reproductive and non-reproductive mole-rats. Although there is evidence that non-reproductive *Fukomys* mole-rats are generally more active (Šklíba et al., 2016; Van Daele et al., 2019; Francioli et al., 2020; Houslay et al., 2020), both breeders and helpers engage in the same set of tasks, resulting in quantitative rather than qualitative differences in behavior, which could explain the lack of cranial divergence between them. Our results suggest that breeders do not develop more formidable weaponry or experience further somatic growth (safe for already documented allometric changes in breeding females' postcranium – Thorley et al., 2018a) after acquiring their status. Still, having more powerful jaws or greater body size might enhance the chances of becoming a breeder in the wild (compare Young and Bennett, 2013).

Field studies reported reproductives (excluding pregnant females) to be significantly heavier than helpers in *F. anselli* (Sichilima et al., 2011). de Bruin et al. (2012) even describe breeders (males:  $81.45 \pm 13.71$  g,  $n = 18$ ; females:  $63.87 \pm 11.39$  g,  $n = 19$ ) to be on average roughly two times as heavy as helpers (males:  $39.80 \pm 18.97$  g,  $n = 49$ ; females:  $33.47 \pm 11.78$  g,  $n = 64$ ). However, there are several problems with status assignment

in these studies. First, the authors assume a very early onset of maturity, classifying individuals  $\geq 35$  g as adults, whereas laboratory results suggest that this species reaches adulthood at approximately two times this body mass (Burda and Begall, 1998). We consider this difference to be too extreme to simply derive from the likely higher growth rates in provisioned captive animals. The assumption of such an early onset of maturity will strongly skew the results toward lower weights in non-reproductive animals. This way, a certain fraction of immature individuals will be counted as adult helpers since diagnostic traits of breeders are missing. Such practices will also bias estimations of SSD (see above). Unfortunately, precise aging of mole-rats in the wild is not possible offhand. Second, typically employed phenotypical criteria to assign breeding status in wild *F. anselli* males (and some congeneric species), such as testes size estimated by palpation or perioral secretions, are ambiguous. The latter frequently occur in non-reproductive males, at least in captivity (pers. obs.) and apart from the difficulty of assessing testes size by touch, contradicting findings have been published on testes volume differences between reproductive groups (de Bruin et al., 2012; Garcia Montero et al., 2016). Therefore, the reliability of available field data on weight distributions, especially for males can be questioned.

In case significant intrasexual differences in both sexes are confirmed, it needs to be clarified whether wild *F. anselli* might attain breeding status because of elevated body mass or develop it after succeeding to do so. Since body size is typically only approximated by mass in field studies, findings of intrasexual size differences might simply result from the allocation of limited resources in combination with lower activity levels of breeders in the wild (compare Francioli et al., 2020). In provisioned captive families, no such deviation in body mass is apparent (pers. obs., see Thorley et al., 2018a for *F. damarensis*) and even the opposite pattern might occur (Schielke et al., 2017). In any case, data on captive animals from this study and others demonstrate that attaining permanent breeding status *per se* does not go along with an isometric increase in body size (which would affect both hindfoot and cranial measurements, see Figure 5) or body mass in this species.

On a different note, our findings of uniform skull morphology in *F. anselli* status groups are relevant to *Fukomys* taxonomy, indicating that missing information about a specimen's reproductive history does not bias outcomes of anatomical studies.

## Effects of Sex on Skull Morphology in *F. anselli*

In contrast to reproductive status, sex importantly influences both skull size and shape in *F. anselli*. In fact, *F. anselli* was also recovered as one of the more dimorphic small (<200 g) *Fukomys* species in regard to body mass, with males being roughly 20% heavier than females in the wild (Sichilima et al., 2011, but see above for problems with this estimate), with data from captive animals indicating even 40% higher body mass in males (Burda and Begall, 1998). Detected cranial differences are profound and not only point to a larger relative skull size in males but also to

greater robustness of the male jaw apparatus. In light of this, it is surprising that a previous landmark analysis of the dorsal and ventral skull in sexually dimorphic *F. anselli*, *F. hanangensis* and *F. whytei* (compare Table 1) found no sex specific shape patterns (Faulkes et al., 2017). However, this study included immature specimens, which could have led to biased results.

Sex-specific cranial differences in *F. anselli* emerge due to hypertrophy of the facial portion of the skull in males (compare Figure 7), while several measurements of the skull base vary little between the sexes (Table 4). When scaled to the same size, males display wider as well as thicker zygomatic arches and larger angular processes than females which permit the development of a more voluminous musculus masseter, the most important masticatory muscle (Cox et al., 2020). Shape analysis also revealed a higher coronoid process in male mandibles, which together with more pronounced sagittal crests in males (pers. obs.) indicates a more strongly developed musculus temporalis, another jaw adductor (Cox et al., 2020). We therefore predict higher bite forces in male *F. anselli* compared to females relative to body mass (but see Van Daele et al., 2019 reporting equal bite forces in a small sample of a similar-sized *Fukomys* species). Apart from that, males can be expected to display a wider gape, since their rostra and mandibles are more elongated than the ones of females (Table 4). Still, there appears to be no noteworthy sex difference in cheek dentition, indicating that masticatory demands do not drive the sex-specific differentiation in the facial skeleton. The incisors on the other hand, which represent the most important weapons of African mole-rats, are hypertrophied in males, indicating adaptation to combat (Young and Bennett, 2013). This sex-specific trait was not only recovered herein but has already been noticed by Burda (1990) for *F. anselli* and by Young and Bennett (2013) for *F. damarensis*.

Sexual size dimorphism in relative skull size has been seldomly studied in mammals, but its occurrence was reported for *F. damarensis* (Young and Bennett, 2013). Our results agree with the respective study, in which head width (cranium and adhering soft tissues) in anesthetized *F. damarensis* was measured and males were found to have significantly wider heads than females relative to their body size. Unfortunately, head dimensions were only approximated by that single measure and raw data were not communicated, so that no further comparison with our findings on *F. anselli* can be drawn.

Clues to what underlies relative skull size SSD in mole-rats might derive from comparisons with reptiles, since the phenomenon has been intensively researched in lizards, subterranean amphisbaenians, and snakes, where exaggerated relative male head size is a common trait (Shine, 1991; Gienger and Beck, 2007; Martín et al., 2012; Baird, 2013). In fact, squamate reptiles and mole-rats differ little in that jaw and gape dimensions rather than other physical characteristics can decide conflicts with conspecifics. Just as male-biased body mass SSD in general, it is commonly assumed that enlarged heads in reptiles are intrasexually selected traits (Baird, 2013). Alternatively, ecological niche divergence between sexes could underlie this anatomical difference (Shine, 1991, but see Baird, 2013), a factor also hypothesized to explain SSD in some monogamous mammals (e.g., Hillis and Mallory, 1996). However, the peculiar

lifestyle and foraging behavior of mole-rats argues against ecological influences on dimorphic head dimensions and again points to males combating competitors. There is also no evidence that male and female *Fukomys* differ in distances or mode of dispersal (above ground or underground) when leaving their natal family (Finn, 2017), so that an influence of this factor can also be ruled out (compare Young and Bennett, 2013). Instead, all the cranial traits discussed beforehand as well as the pattern of SSD scaling in *Fukomys* indicate a pronounced role of male-male combat in the social life of this genus. But how does that comply with the monogamous mating strategy of these mole-rats?

## Socioecological Implications of Sexual Dimorphism in *Fukomys* Mole-Rats

Mammals exhibiting social and/or sexual monogamy are not expected to show pronounced SSD (compare Bidau and Martinez, 2016), so that the patterns found in *Fukomys* are surprising. Field studies employing microsatellite data demonstrated that reproductive skew in wild *Fukomys* is indeed extremely high. In *F. anseli*, only a single resident breeder of each sex is present and juveniles are sired almost exclusively by the established breeding male ( $n_{\text{families}} = 13$ ; 96.4% – Patzenhauerová et al., 2013). At the same time, the number of immigrants into established colonies is very small ( $n_{\text{non-breeders}} = 85$ ; 3.5%) but it is yet unclear whether these data are representative for *Fukomys* in general. In *F. damarensis*, a similar field study found the number of immigrants to be higher, at 7.5%, and the rate of extra-pair paternity was increased compared to *F. anseli* [up to 16% (31.9% if two outlier families are included); Patzenhauerová et al., 2013 referring to Burland et al., 2002]. These results do not challenge the assumption that both social and sexual monogamy is predominant in *Fukomys* but suggest that the latter may become compromised under specific circumstances.

However, although mating partners stay mostly faithful to each other and do so over long periods of time, once formed pairs can still be disrupted. This process appears to be mediated by male intrusion into established families. Shorter tenure length in reproductive males compared to females has been demonstrated by several genetic and capture-recapture studies (Young and Bennett, 2013, see below), indicating sex-biased social dynamics compliant with asymmetric reproductive competition and male-male combat. Genetic relatedness levels in males compared to females in wild *F. damarensis* groups also suggest that males do more frequently invade foreign groups and take over a breeding position (Burland et al., 2002). In case a breeder succession happens, or when a foreign male joins a group which lost its male breeder, a “patchwork family” with offspring of mixed descent can be established. Breeding male turnovers by intruders appear not to be rare (but see Torrents-Ticó et al., 2018), as all parentage studies on wild *Fukomys* found evidence for it in at least one family group analyzed (*F. anseli* – Patzenhauerová et al., 2013; *F. damarensis* – Burland et al., 2002; and *F. mechowii* – Šumbera et al., 2012).

Established wild *Fukomys* groups therefore exhibit high reproductive skew, experience at least some degree of immigration pressure and can tolerate the replacement of male breeders. The extreme, cooperatively enacted xenophobia

found in laboratory-housed *Fukomys* appears to be an artifact of captivity (compare Bishop et al., 2004 for a similar pattern in *Cryptomys*). We suggest that the increased rate of male compared to female breeder turnover in the wild might be an unappreciated indication for stronger male intrasexual competition in *Fukomys* with major implications for SSD. Given the degree of SSD in *Fukomys* and the cranial adaptations described herein, it is likely that these replacements follow violent attacks. Still, such interactions are not documented so far. The reproductive benefit of securing a reproductive female, a burrow system and even a number of helpers for potentially several years must be extreme and might explain why SSD in *Fukomys* is more strongly expressed than in many polygynous or polygamous rodents, where mating associations are shorter-lived.

But there are several caveats to this hypothesis. First, it must be explained why such reproductive competition would occur in *Fukomys* and not in other cooperatively breeding rodents with slow life histories that occupy self-constructed defensible home ranges, such as mole-voles (*Ellobius* spp.), beavers (*Castor* spp.) and most importantly, *Heterocephalus*. It could also be argued that low documented rates of male group takeovers (Torrents-Ticó et al., 2018) could not create a sufficient selective pressure to explain the observed sexual dimorphism. Besides, faster male turnovers might not be provoked by intrasexual combat but by males facing higher mortality risks, for example increased predation pressure. For this, however, one would expect differences in the activity and ranging patterns of males and females, which is so far not apparent in wild *Fukomys* (*F. damarensis* – Francioli et al., 2020). A final potential caveat is the lack of intraspecific combat adaptations in *Fukomys* that are found in other bathyergids: Even large-bodied *Fukomys* lack defensive dermal shields, a trait found in the dune mole-rats of the genus *Bathyergus* (Jarvis and Bennett, 1991), which might be expected to evolve convergently in both genera in case males commonly experience violent encounters with competitors.

## CONCLUSION

Our study provides a comprehensive description of the well-developed sexual dimorphism in the skull of *F. anseli*, which points to a significant role of male competition in the social life of mole-rats belonging to this cooperatively-breeding genus. *Fukomys* might best be characterized as serially monogamous rodent genus, in which males stay faithful to their partners for prolonged time but have to regularly engage in conflicts with same-sex rivals to secure their mate. That assumption is further supported by the recovery of SSD scaling conforming to Rensch's rule among *Fukomys* species, indicating violent monopolization of breeding females by males. At the same time, we show that no morphological differentiation in the cranium of breeders and non-breeders exists, indicating a lack of morpho-functional caste specialization beyond characters relevant to reproduction. The currently available data can only be considered a starting point regarding efforts to understand the evolutionary pressures influencing sexual dimorphism in social mole-rats. Future studies might address the following

questions to characterize the evolutionary pressures behind these morphological findings: How frequent are attempts to take over groups by foreign males in the wild and how do invaded family groups react? Why do helpers accept unrelated male breeders within the “patchwork family” scheme? To which degree do *Fukomys* species differ in respect to this behavior and how do they compare to *Cryptomys* and *Heterocephalus*? What factors underly the varying expression of SSD in the three solitary bathyergid genera?

Solving these questions will importantly contribute to fully unravel the remarkable diversity of social patterns found within the Bathyergidae and the factors that shaped it.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**; further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

KRC conceived the study and its methodology with input from SB. KRC and SB prepared the skulls, took linear measurements, and prepared the figures. JM photographed the skulls and compiled landmark datasets of the dorsal and ventral skull. KRC collected landmark data on the mandibles. SB and JM analyzed the data with input from KRC. All authors interpreted the findings. KRC wrote the first draft, which was reviewed by SB and JM. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.638754/full#supplementary-material>

**Supplementary Table 1** | Linear skull measurements and hindfoot lengths of *Fukomys ansellii* specimens used in this study. Yellow mark: Measurement was taken from the left side of the skull. Red mark: Measurement was estimated using the LOST package (Arbour and Brown, 2020).

**Supplementary Table 2** | Overview and definitions of point landmarks used to characterize skull traits in *Fukomys ansellii*.

**Supplementary Table 3** | Variable contributions (%) and eigenvalues of principal components computed for the shape of the dorsal and ventral cranium as well as for the mandible of *Fukomys ansellii*.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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