

# Convergent Traits in Mammals Associated with Divergent Behaviors: the Case of the Continuous Dental Replacement in Rock-Wallabies and African Mole-Rats

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**Abstract** The study of convergences in mammals is crucial to understand the evolutionary processes underlying the origin of shared traits. A classic example is the independent evolution in the pygmy rock-wallaby, the silvery mole-rat, and manatees of continuous dental replacement to compensate for high dental wear. The origins of continuous dental replacement in mammals remain unresolved. As the functional study of a trait may permit pinpointing the adaptive nature of its independent evolution, we aimed at comparing first the morpho-functional characteristics of the masticatory apparatus between the pygmy rock-wallaby and their closest relatives, and then with some published data on the silvery mole-rat. 3D geometric morphometric and biomechanical analyses were complemented by

dental microwear analyses. Our results showed that the pygmy rock-wallaby clearly departs from its relatives in having a wider skull, a shorter snout, and a dentition situated more distally. These cranial modifications, previously observed in the silvery mole-rat, are probably linked with a neotenic development. Because of higher developmental constraints on marsupial skulls, such adjustment in the pygmy rock-wallaby may have improved the force generated by adductor muscles at molars for comminution of tough and abrasive plants. In contrast, the strong attrition combined with the ingestion of dust during high activity of digging and feeding might contribute to both molar damage and high wear in the silvery mole-rat. Our results stress the importance of combining morphological, developmental, and functional data to show that different behaviors related to ecology can explain the convergent occurrence of continuous dental replacement in mammals.

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## Introduction

The study of convergence is fundamental in evolutionary biology to understand the mechanisms involved in the independent origins of similar traits, as well as their putative adaptive nature (Arendt and Reznick 2008; Losos 2011; Wake et al. 2011). Mammals underwent numerous events of diversification that resulted in spectacular examples of morphological convergences. These convergent traits are generally associated with similar modes of life in response to very similar environmental conditions, as is the case for gliding, fossorial, ant-eating, or carnivorous species (McGhee 2011). The study of convergent traits in mammals is thus appropriate to investigate underlying biological mechanisms (i.e. functional,

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phylogenetic, and developmental constraints) and to understand the core of convergent evolutionary processes.

Teeth are intimately associated with obtaining or processing of food items, and generally play a major role in defining the ecology of mammals (Ungar 2010). Investigating an exceptional feature such as the continuous replacement of teeth is a highly promising case for examining convergent evolution. Continuous dental replacement (CDR) corresponds to the continuous addition of molars at the back of the jaw, which then migrate toward the front of the jaw to replace heavily worn teeth (Domning and Hayek 1984; Janis and Fortelius 1988; Sanson 1989; Gomes Rodrigues et al. 2011; Fig. 1a). Manatees (*Trichechus* sp., Sirenia, Placentalia) and the pygmy rock-wallaby (*Petrogale concinna*, Macropodiformes, Marsupialia) have CDR, which might allow them to withstand intense dental wear resulting from highly abrasive diets, involving mainly grasses (Domning 1982; Sanson et al. 1985). CDR has also recently been described in the silvery mole-rat (*Heliophobius argenteocinereus*, Bathyergidae, Placentalia), which is a subterranean rodent (Gomes Rodrigues et al. 2011). It has been hypothesized that CDR could be related to the solitary and intensive chisel-tooth digging activity of this mole-rat, because it continuously rebuilds its burrow system for foraging and dispersion (Škliba et al. 2009), which could imply high dental wear (Gomes Rodrigues et al. 2011, 2016). However, the evolutionary origin of CDR in both placentals and marsupials remains to be explained.

Although morphological dental convergences are widespread among mammals, placentals and marsupials show disparate cranial and dental patterns and ontogenies (Clark and Smith 1993; Smith 1997; Cifelli and Muizon 1998; Luo et al. 2004; Sánchez-Villagra et al. 2008). Permanent anterior teeth (incisor and canines) show a delayed eruption in marsupials while the deciduous teeth remain in a vestigial state, and only the distal-most (third) premolar is replaced. This is probably due to the prolonged lactation necessitating a period of fixation of the young to maternal nipple soon after birth (Luckett 1993; Van Nievelt and Smith 2005). In contrast, all the teeth but molars are replaced in many placentals, which are not similarly constrained during early development. Early suckling also leads to a precocious ossification of facial bones in marsupials (Clark and Smith 1993; Smith 1997; Sánchez-Villagra et al. 2008). After quantification of cranial morphospaces, Bennett and Goswami (2013) concluded that such a developmental sequence has limited the number of possible evolutionary pathways in marsupials compared with placentals. Because the development of the masticatory apparatus is constrained early during the ontogeny of marsupials, we aim to determine first how CDR can be interpreted at the functional level in the pygmy rock-wallaby, by comparing the morpho-functional characteristics of the masticatory apparatus between the pygmy rock-wallaby and its closest relatives (other rock-wallabies).

Following the proposal of Losos (2011) in order to understand the multiple occurrences of convergent traits, the study of the functional consequences of CDR is required to assess the adaptive nature of the convergent evolution of this unique developmental pattern in mammals. Consequently, we compared the morpho-functional characteristics of the masticatory apparatus of the pygmy rock-wallaby with those of the silvery mole-rat, by using 3D geometric morphometrics, biomechanical estimations, and dental microwear analyses. The characteristics of this mole-rat have been recently published and compared with its closest relatives (Gomes Rodrigues et al. 2016). The case of rock-wallabies and mole-rats is interesting because they both show a diprotodont masticatory apparatus (i.e., two lower front teeth combined with a large diastema between incisor and cheek teeth), but a very different evolutionary background including distinct developmental constraints on the masticatory apparatus. Such a comparison will be a key route to better understand the functional origins of CDR in mammals. More generally, we aimed to assess to what extent and under which conditions convergent morphological traits can occur in mammals that are distantly related.

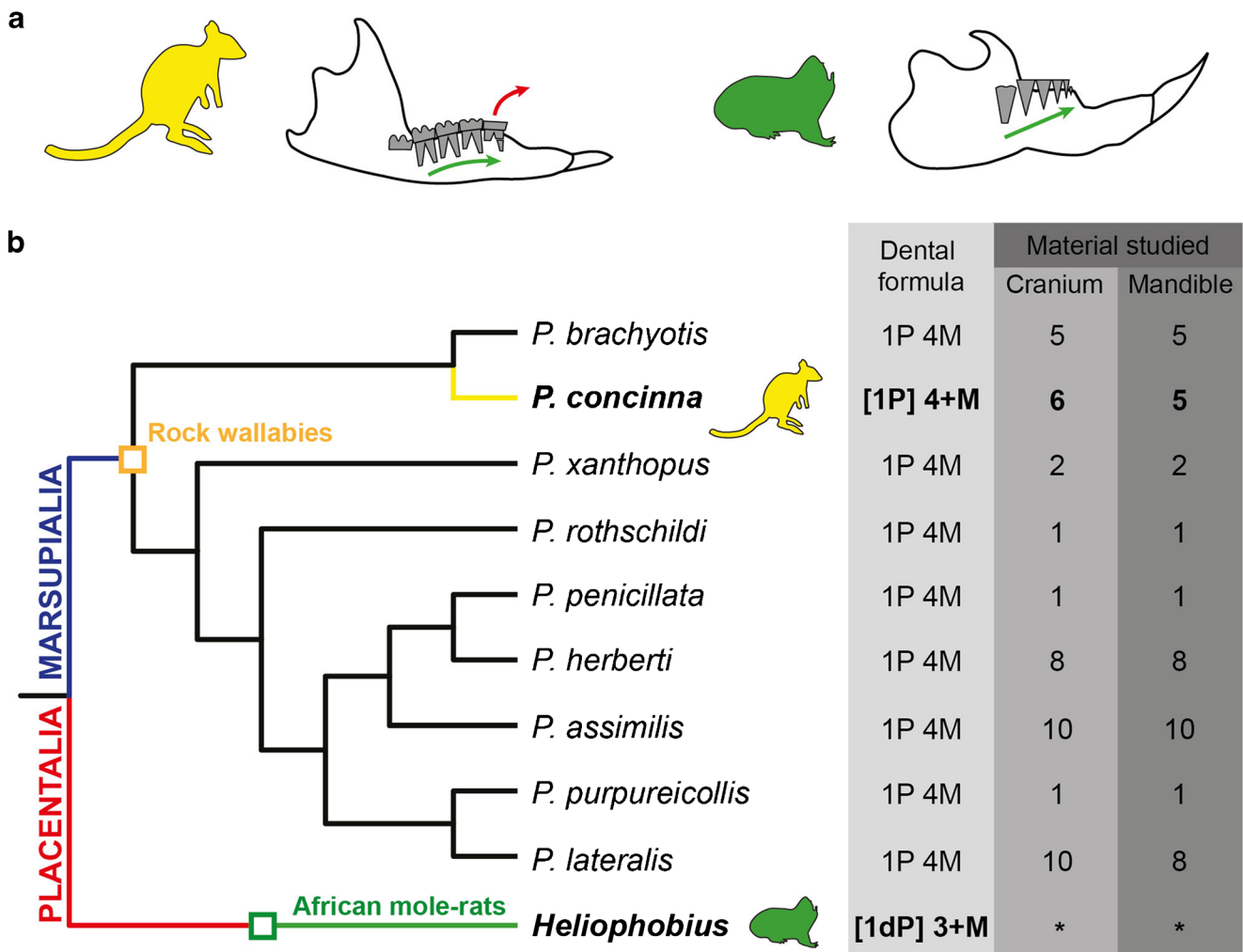
## Material and Methods

### Sample Composition

We analyzed 41 mandibles and 44 crania belonging to both sexes, and representing nine species of rock-wallabies for geometric morphometrics (Fig. 1, Online resource 1) housed in the mammal collections of the Natural History Museum, London (NHM; United Kingdom), and including one specimen from the University Museum of Zoology, Cambridge (UMZC; United Kingdom) and one specimen from Museum Victoria, Melbourne (MV; Australia). This sample notably includes *Petrogale concinna* and its sister species, *P. brachyotis*, which live in sympatry. Biomechanical analyses were limited to the six species for which more than one specimen was available for study. Dental casts of 11 *Petrogale concinna*, nine *Petrogale brachyotis*, and 15 specimens of *Heliophobius argenteocinereus* were sourced from the Western Australian Museum, Perth (WAM; Australia) and the Royal Museum for Central Africa, Tervuren (RMCA; Belgium).

### Geometric Morphometric Methods

The mandibular and cranial forms were quantified with 11 and 61 anatomical landmarks, respectively (Fig. 2 and Online resource 2). Digital data of all specimens were acquired using a Microscribe 3-D digitizer. One skull of *Petrogale brachyotis* was scanned using Xradia Versa 520 XRM at energy of 120 kV with a cubic voxel of 46.4  $\mu\text{m}$ , in order to visualize



**Fig. 1** (a) Diagrams of mandible showing patterns of continuous dental replacement (green arrows: mesial drift; red arrows: shed tooth) in the pygmy-rock wallaby and the silvery mole-rat. (b) Phylogeny of rock-wallabies (from Potter et al. 2012), also including the silvery mole-rat,

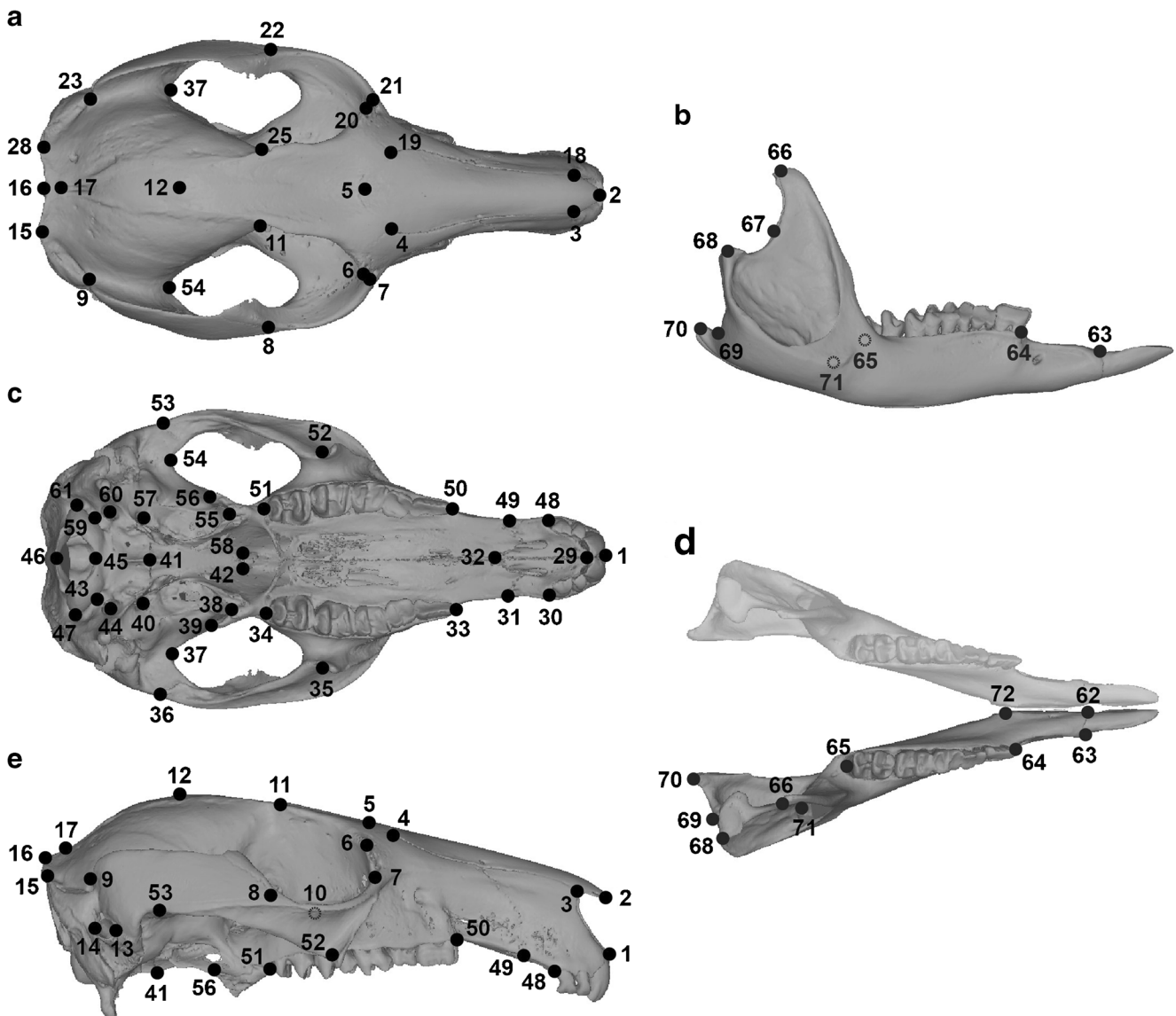
and showing the adult dental formula (dP: deciduous premolars, P: permanent premolars, M: molars, [teeth rapidly shed]) and the number of specimens studied for geometric morphometric analyses. \* data from Gomes Rodrigues et al. (2016)

virtual deformations within the *Petrogale* dataset. Because the mandible of *Petrogale* is constituted by a dentary bone of relatively simple shape, most of the landmarks taken on the dentary were of type 2 (e.g., *maxima* of curvature - Fig. 2; Bookstein 1991). All configurations (sets of landmarks) were superimposed using the Procrustes method of generalized least squares superimposition (see Gomes Rodrigues et al. 2016 for more details). Shape variability of the cranium and mandible was analyzed by principal components analysis (PCA) of shape (Fig. 3). Analysis and visualization of patterns of shape variation were performed with the interactive software package MORPHOTOOLS (Specht et al. 2007; Lebrun et al. 2010). A multivariate regression of the first PCs representing 95 % of the variance (15 PCs for the mandibles and 30 PCs for the crania) on size, estimated by the logarithm of the centroid size, allowed us to take into account the potentially confounding effects of allometry on shape. Multivariate regressions were performed with PAST 2.06 (Hammer et al. 2001). To account for

the potentially confounding effects of size allometry on shape of rock-wallabies, size-corrected shapes were obtained as follows: PCres corresponds to principal components of a PCA performed on shape data corrected for allometry (i.e. centroid size; Fig. 4). Additionally, univariate regressions were undertaken using the first two principal components and the logarithm of the centroid size of each specimen (Fig. 5). Younger (i.e. last molars not erupted, or premolars still present for *P. concinna*) and older specimens (i.e. last molars fully erupted, or premolars missing for *P. concinna*) of *Petrogale* were shown on univariate regressions.

### Biomechanical Analyses

The quantification of the mechanical advantage of each adductor muscle (temporalis, superficial masseter, and deep masseter) allows the measurement of force transmitted from the muscle to the bite point (cheek teeth). The mechanical

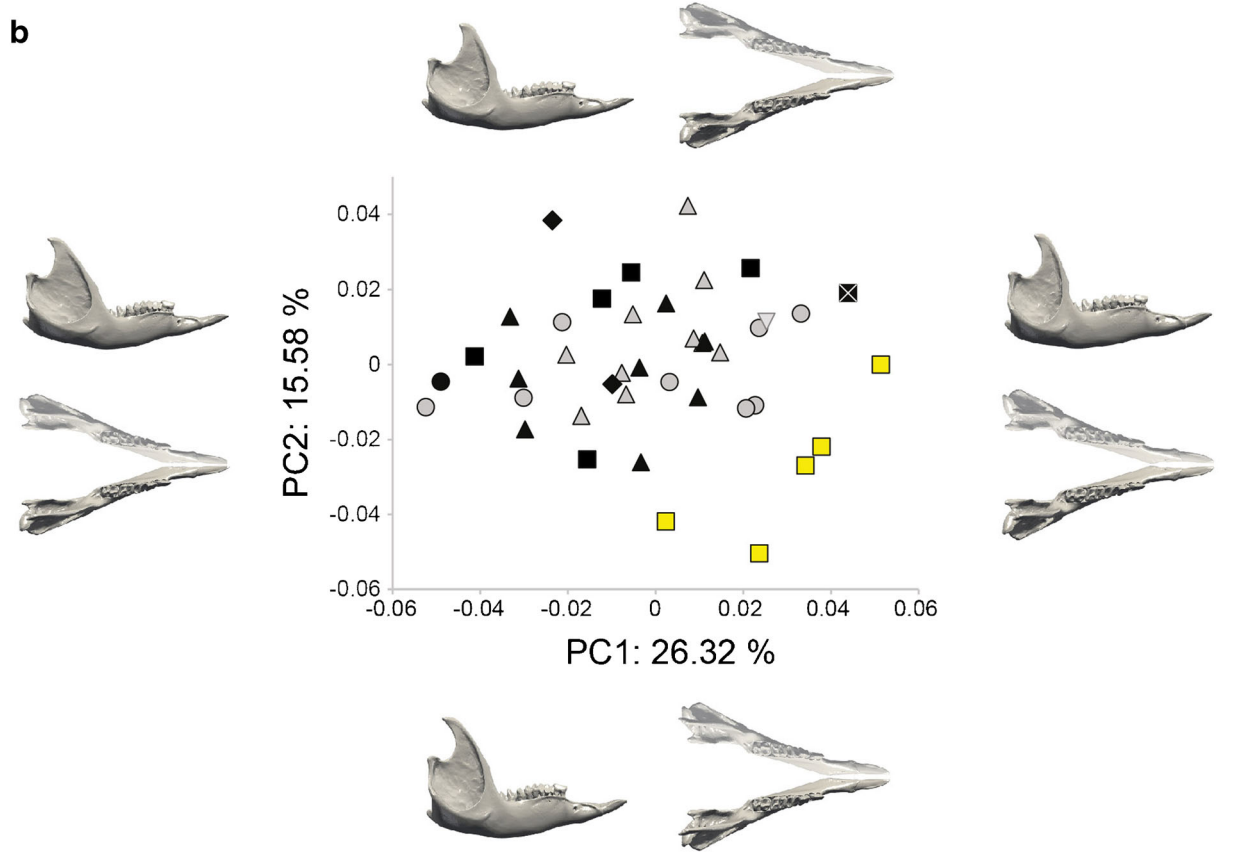
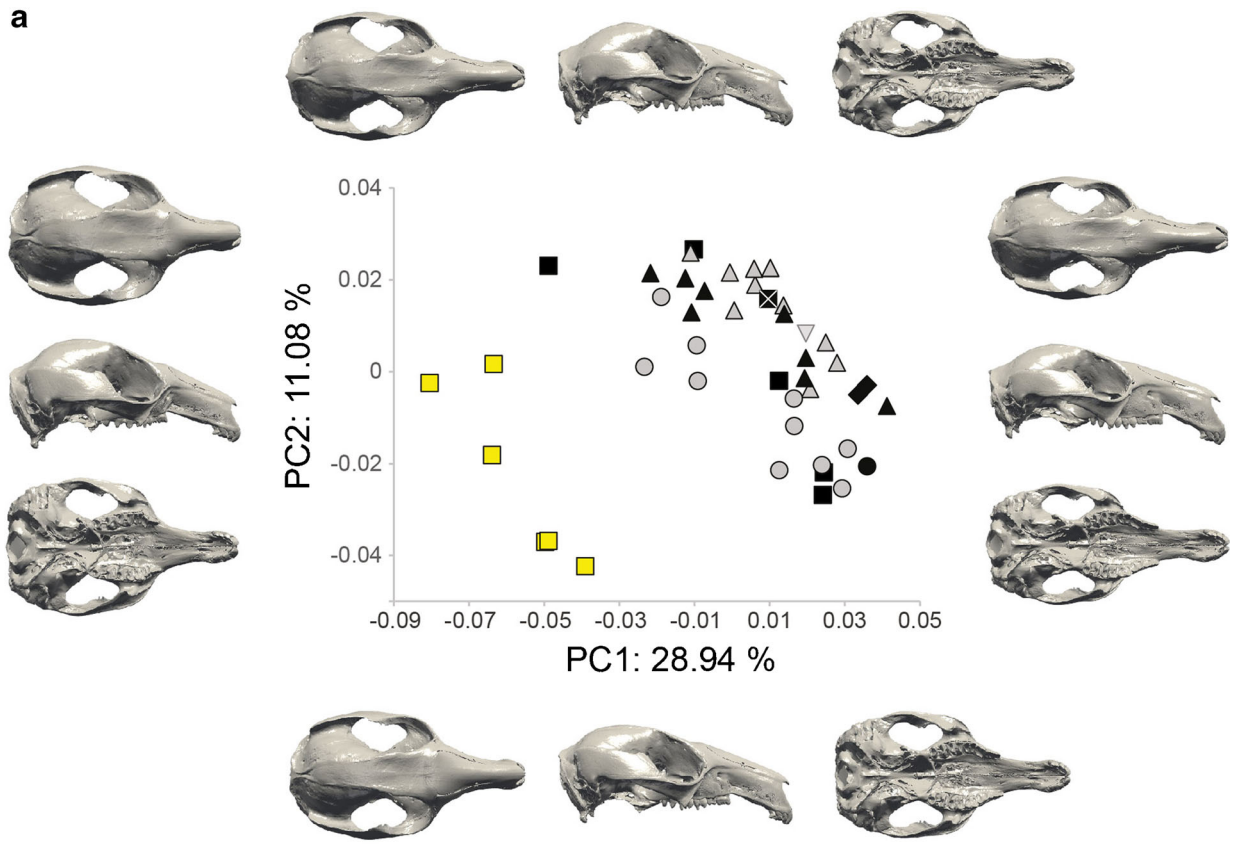


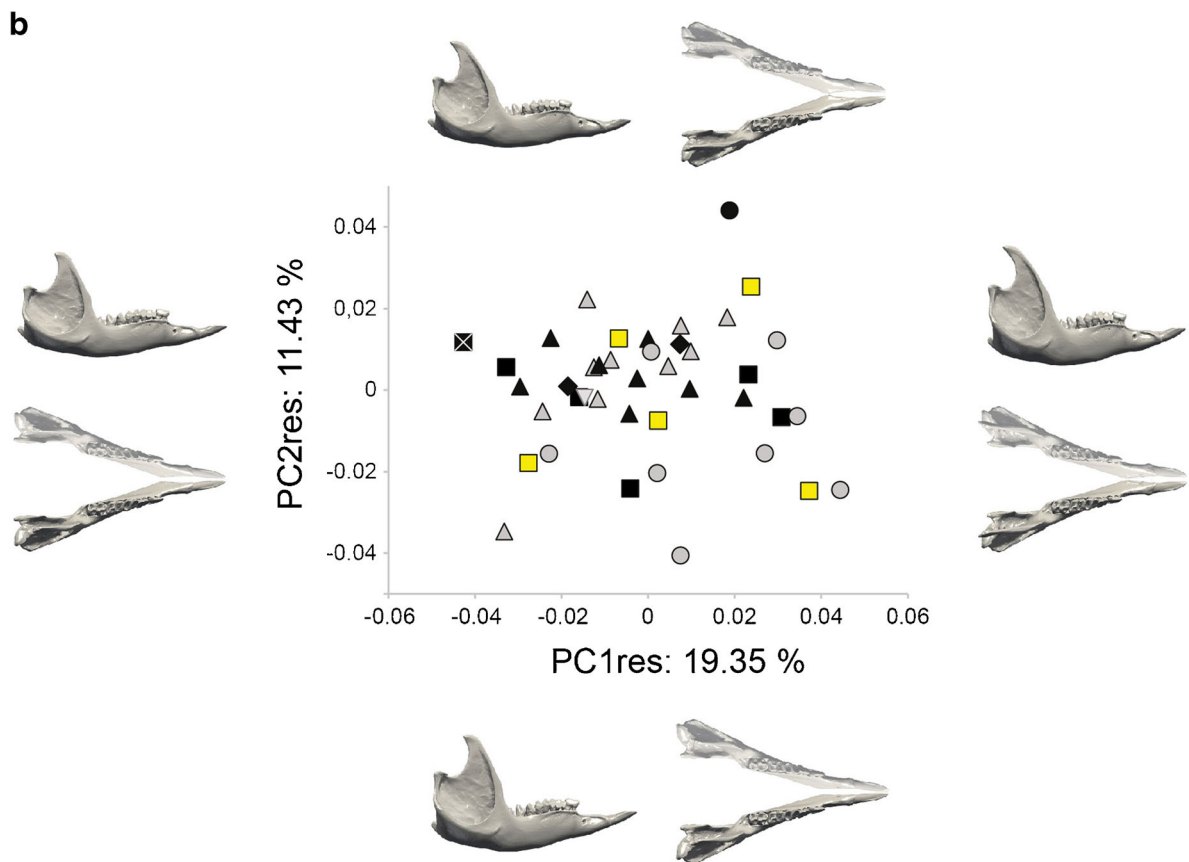
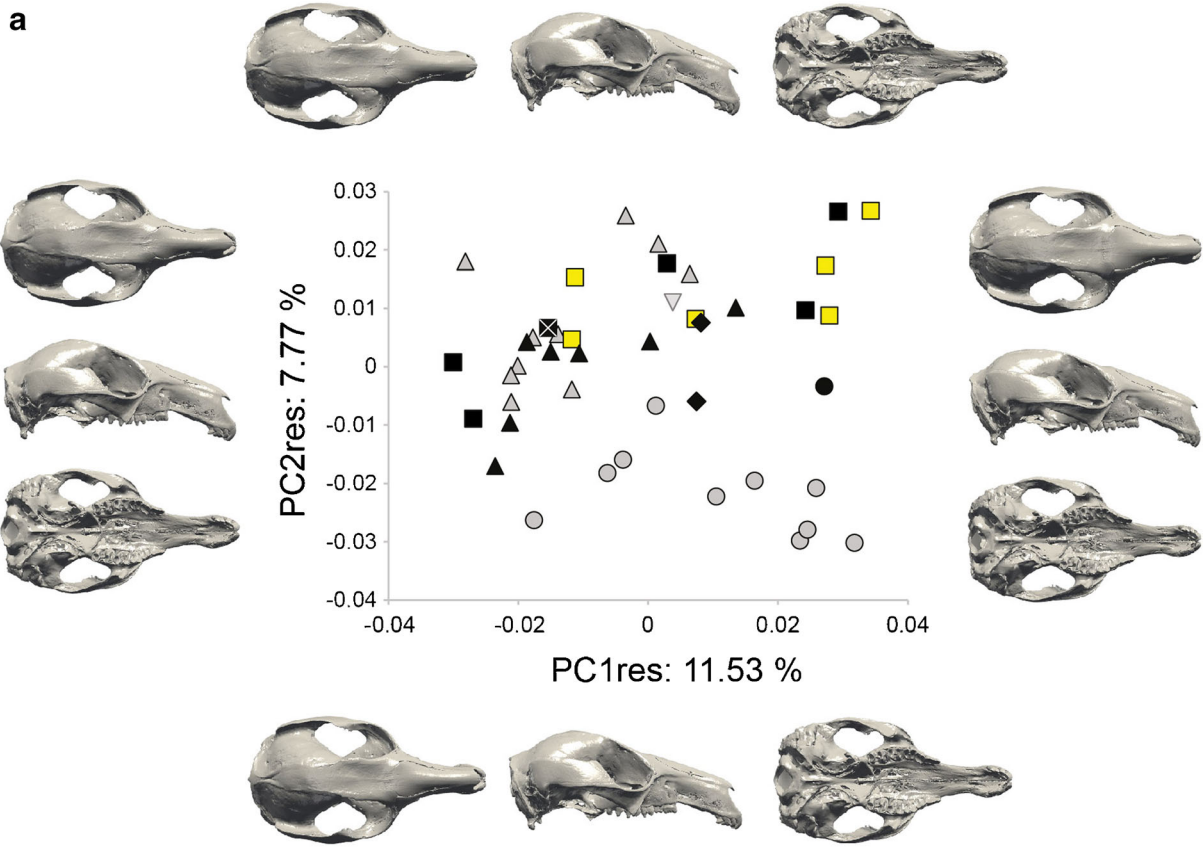
**Fig. 2** Landmarks digitized on the cranium (**a**, dorsal view, **c**, ventral view, **e**, lateral view) and the mandible (**b**, lateral view, **d**, occlusal view) of *Petrogale brachyotis* rendered from laboratory X-ray microtomographic imaging

advantage can be estimated as the ratio of the estimated in-lever (distance from the condyle or fulcrum to the point of muscle attachment) and the out-lever (distance from the condyle to the bite point; Hiiemae 1971). Three adductor muscles have been considered for in-levers: the temporalis, which attaches along the coronoid process (landmark 66); the superficial masseter, which attaches along the angular part of the mandible (landmark 69), and the deep masseter, which attaches in the masseteric fossa (landmark 71; Warburton 2009; Fig. 6). Only cheek teeth are considered as the bite point, and not incisors, which are less relevant here because our study focuses on cheek teeth replacement. The middle point of cheek tooth row (between landmarks 64 and 65) was measured as the bite point for the out-lever. Three estimates of biomechanical advantage (in-lever/out-lever) were

thus considered for a given mandible (following Thorington and Darrow 1996; Gomes Rodrigues et al. 2016):  $TvsCT$  (temporalis/cheek teeth),  $SMvsCT$  (superficial masseter/cheek teeth), and  $DMvsCT$  (deep masseter/cheek teeth). Differences between rock-wallabies in the in-lever/out-lever ratios were tested using post-hoc multiple mean comparison tests: the Fischer's Least Significant Difference test (LSD) and the Tukey's Honestly Significant Difference

**Fig. 3** Principal component analyses for **(a)** crania and **(b)** mandibles of *Petrogale* species and associated virtual deformations on the extreme sides of each axis. Symbols used: *P. assimilis* ( $\Delta$ ), *P. brachyotis* ( $\blacksquare$ ), *P. concinna* ( $\blacksquare$ ), *P. herberti* ( $\blacktriangle$ ), *P. lateralis* ( $\circ$ ), *P. penicillata* ( $\nabla$ ), *P. purpureicollis* ( $\bullet$ ), *P. rothschildi* ( $\otimes$ ), *P. xanthopus* ( $\blacklozenge$ )





◀ **Fig. 4** Principal component analyses for (a) crania and (b) mandibles of *Petrogale* species with shape data corrected for allometry, and associated virtual deformations on the extreme sides of each axis. Symbols used: *P. assimilis* (△), *P. brachyotis* (■), *P. concinna* (□), *P. herberti* (▲), *P. lateralis* (○), *P. penicillata* (▽), *P. purpureicollis* (●), *P. rothschildi* (⊗), *P. xanthopus* (◆)

test (HSD), the latter being less sensitive but more conservative than the former.

### Dental Microwear Analysis

Dental microwear mainly results from abrasion (i.e. tooth-food contact), and its analysis permits reconstruction of the last diet items ingested by an animal prior to its death (Walker et al. 1978), involving the physical properties of the ingested matter. The protocol used here combines transmitted light stereomicroscopy and high resolution photographs (see Merceron et al. 2004). We use the method adapted to small mammals by Gomes Rodrigues et al. (2009), using translucent upper molar casts at  $\times 100$  magnification and a  $0.01\text{mm}^2$  square at the center of dental facets to quantify dental microwear features (see Fig. 7). Three variables were used for quantification: the numbers of fine scratches (*Nfs*), wide scratches (*Nws*), and large pits (*Nlp*). Both *Nws* and *Nlp* have a width exceeding  $5\ \mu\text{m}$ . A high *Nfs* likely indicates an abrasive and tough component (e.g. consumption of either graminoids including small silica phytoliths and/or plants from the herbaceous stratum covered by dust); a high *Nws* indicates intake of coarse and tough to brittle material (e.g. fruits with hard shells, nuts) and a high *Nlp* likely indicates ingestion of hard material (e.g. exoskeleton of invertebrates, bones of vertebrates, dust and grit). Direct comparisons are possible between marsupials and placentals, because we only wanted to infer and compare the physical properties of material ingested by *P. concinna* and *Heliophobius*, and not the particular type of food items (Christensen 2014).

### Results

According to both PCAs performed on the crania and mandibles (Online resource 3), *P. concinna* can be clearly differentiated from other *Petrogale*. The crania of *P. concinna* are clearly separated along the negative end of the first principal component (PC1, Fig. 3a), which shows a shortened snout, an increase in skull width with widened zygomatic arches, an elevation of the cranial roof, and a distal and reduced dental row. In contrast, in the positive values, most *Petrogale* species show a more gracile skull, enlarged snout with enlarged nasal bones and premaxillae, and a more mesial and enlarged dentition. Most of the specimens of *P. concinna* cluster together in

the negative values of PC2 where specimens show a wider snout, but a reduced anterior part of premaxillae and a narrower posterior part of the braincase. The mandibles of *P. concinna* are clearly discriminated from those of other *Petrogale* species in the morphospace defined by the first two principal components (Fig. 3b). Negative PC1 correlates with mandibles characterized by a larger ascending ramus relative to the horizontal ramus, with a mesial dental row, whereas the tooth row is more distally located on the positive values, with mandibles showing a reduced ascending ramus compared to the horizontal ramus even if processes and condyle are slightly more expanded. PC2 displays variation in the height and width of the ascending ramus. The negative values characterize *P. concinna*, which show a mandible with an elevated condyle, an elongated and slender coronoid process projecting backward, and an angular process more lingual than the condyle.

A multivariate regression of the shape component on size, estimated by the logarithm of centroid size, was highly significant (cranium:  $F = 49.66$ ,  $p = 2.38 \times 10^{-9}$ ,  $df = 30$ ; mandible:  $F = 6.712$ ,  $p = 1.74 \times 10^{-5}$ ,  $df = 15$ ). Then, we observed less differentiation with shape data corrected for allometry (Fig. 4), especially in the mandible dataset. Specimens of *P. concinna* do not set apart from other *Petrogale* for both the cranium and mandible, which indicates that the differences in shape are related to its difference in size. However, on the negative side of PC2res for crania, *P. lateralis* differs from other *Petrogale* in having a larger braincase, a gracile snout with enlarged nasal bones, while the fronto-sphenoid part is reduced (Fig. 4a). Regressions of the first cranial and mandibular principal components on centroid size (Fig. 5; crania:  $r^2 = 0.82$ ;  $p = 2.09 \times 10^{-17}$ ; mandible,  $r^2 = 0.340$ ;  $p = 5.71 \times 10^{-5}$ ) show a clear allometric trends, with small specimens, including *P. concinna* and younger *Petrogale*, displaying wide crania, with a reduced snout, and a relatively shortened mandibular ramus, and a dental row distally located. However, even if regressions of the second principal component on centroid size are less obvious, although significant, for crania ( $r^2 = 0.10$ ;  $p = 0.0325$ ), and mandibles ( $r^2 = 0.29$ ;  $p = 2.91 \times 10^{-4}$ ), the specimens are not randomly distributed on the graph. It seems to highlight ontogenetic series of *Petrogale* species, in which older specimens tend to have a wider snout but a reduced anterior part of premaxillae, a narrower posterior part of the braincase, and a dental row slightly displaced mesially (Fig. 5b). It is notably expressed in *P. concinna*, and, to a lesser extent, in *P. brachyotis*, *P. lateralis*, and *P. purpureicollis*.

Estimates of biomechanical advantage for adductor muscles revealed that *P. concinna* present the highest values for the temporalis, the superficial masseter and the deep masseter among the reduced sample of *Petrogale* species (Fig. 6, Online resources 4 and 5). It significantly differs from other *Petrogale* species, including *P. brachyotis*, which show low values. *Petrogale lateralis* is also characterized by high

values, especially for the masseters, while *P. xanthopus* tends to have the lowest values for all muscles but the deep masseter.

Dental microwear analyses showed that *P. concinna* displays a high proportion of fine scratches, likely indicating an ingestion of abrasive and tough material, and shows no significant differences with *P. brachyotis*. *Heliophobius* has a higher proportion of large pits than rock-wallabies, which is probably linked to coarse and hard elements (Fig. 7, Online resource 6).

## Discussion

### Heterochrony and Skull Development in the Pygmy Rock-Wallaby

The pygmy rock-wallaby has been frequently assigned to the monotypic genus *Peradorcas*, even in recent studies (Nowak 1999; Meredith et al. 2009), because of its unique mode of dental replacement, which is unknown in other *Petrogale* species. Such generic discrimination could be also substantiated by the strong cranial and mandibular morphological differentiations of *P. concinna* compared to its relatives. Nonetheless, we have shown that the wide but short skull of *P. concinna* is clearly related to its small size and is reminiscent of the overall morphology observed in young *Petrogale* specimens. As a result, *P. concinna* likely displays a neotonic morphology compared to other *Petrogale* (Fig. 6), as attested by the strong allometric relationships of skull shape in *Petrogale*, especially the cranium (Fig. 5). As a matter of fact, a young specimen of its closest relative *P. brachyotis* resembles the specimens of *P. concinna* in some aspects (see negative side of PC1 on Fig. 5a). The reduced snout of *P. concinna* and young *Petrogale*, especially in its posterior part, combined with the distal location of a shorter dentition can clearly be considered as juvenile characters because the elongation of the rostrum involves a more mesial and enlarged cheek tooth row in adults. During the prolonged growth of kangaroos and wallabies (Cockburn and Johnson 1988), there is a mesial progression of the dentition, which can be either attributed to dental shift or drift (Lentle and Hume 2010). Dental drift corresponds to the migration of teeth inside the bone, as it is continuously observed from the rear to the front of the jaw of *P. concinna* (Fig. 1a). It can be defined as moderate (following Gomes Rodrigues et al. 2012) in most kangaroos, which can lose their premolars completely, whereas it should be considered as slight in most *Petrogale*, because only tipping of premolars has been observed without dental loss (Lentle and Hume 2010). Consequently, such a mesial progression of the dentition is mainly attributed to mesial shift in rock-wallabies (Lentle et al. 2003b), which corresponds to virtual displacement of teeth due to bone apposition during growth, especially at the rear of the jaw. All these observations concur

**Fig. 5** Regression of the first and second principal components on the centroid size of (a, b) crania and (c, d) mandibles of *Petrogale* species, and associated virtual deformations. Symbols used: *P. assimilis* (△), *P. brachyotis* (■), *P. concinna* (□), *P. herberti* (▲), *P. lateralis* (○), *P. penicillata* (▽), *P. purpureicollis* (●), *P. rothschildi* (⊗), *P. xanthopus* (◆). Open symbols and the cross represent younger specimens

with the fact that *P. concinna* is a small rock-wallaby that retained a juvenile morphology, probably like the smallest rock-wallaby *P. burbidgei* (Kitchener and Sanson 1978), which could not be investigated here.

### A Developmental Adjustment toward an Increase of the Masticatory Efficiency?

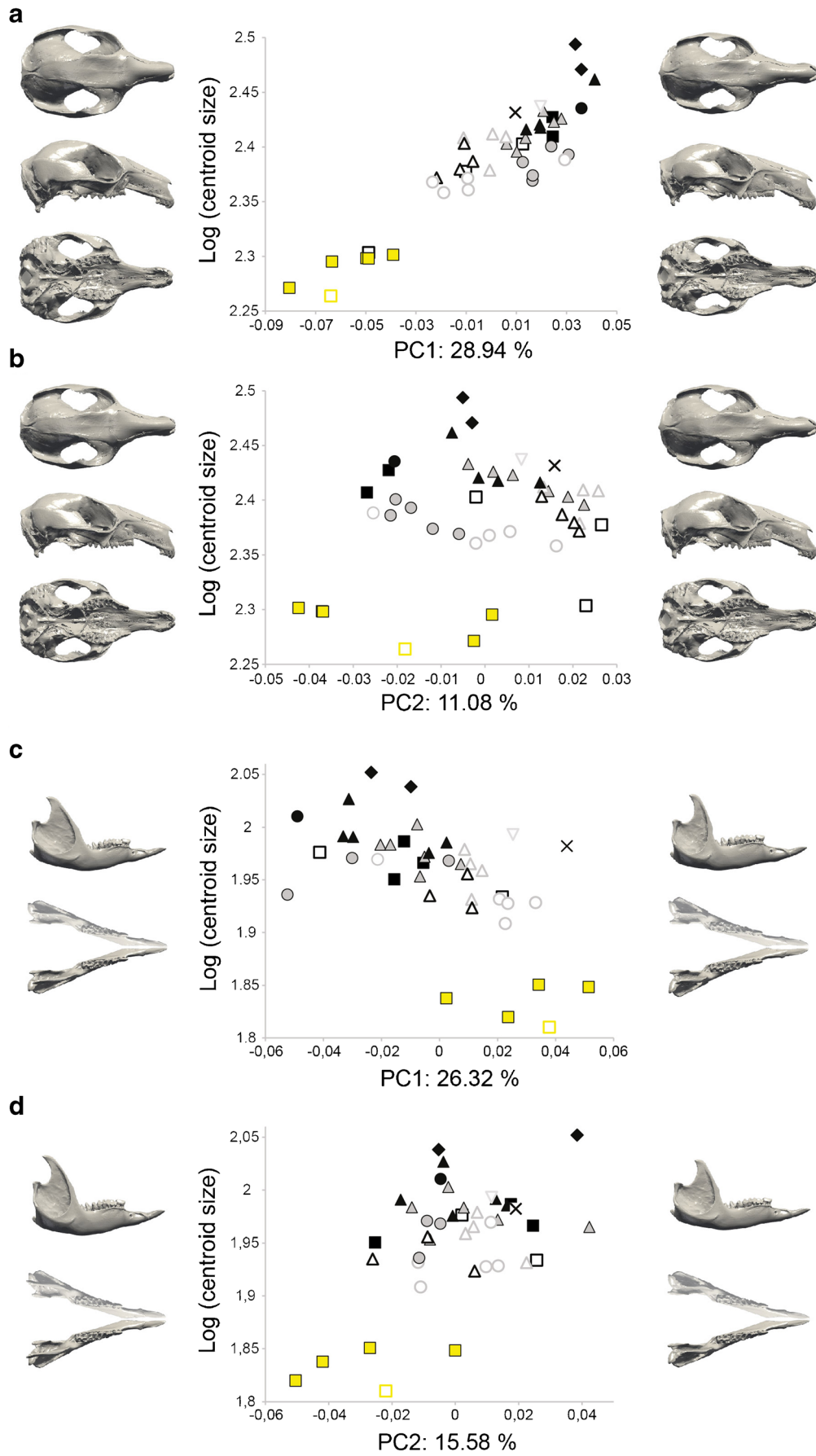
The muscular anatomy of the masticatory apparatus of rock-wallabies remains poorly studied (Parsons 1896). We showed that, despite its small size, *P. concinna* displays widened zygomatic arches, higher mandibular condyles, enlarged but slender coronoid processes, and more lingual angular processes (Fig. 3). All these modifications may be associated with larger areas of insertion for adductor muscles (temporalis, superficial masseter, deep masseter, and medial pterygoid). The developmental constraints on the oral region during the early development of marsupials are likely to limit morphological changes compared to placentals (Bennett and Goswami 2013). The pedomorphic nature of the skull of *P. concinna* might represent a suitable adjustment to improve the efficiency of the masticatory apparatus. Such an assertion is evidenced by the values obtained for the biomechanical advantages of the adductor muscles, which are the highest for *P. concinna* compared to other *Petrogale* species, especially its sister species *P. brachyotis*. The distal position of the tooth row in *P. concinna* induces a decrease of the out-lever and, as a consequence, an increase of the output force at the cheek teeth level.

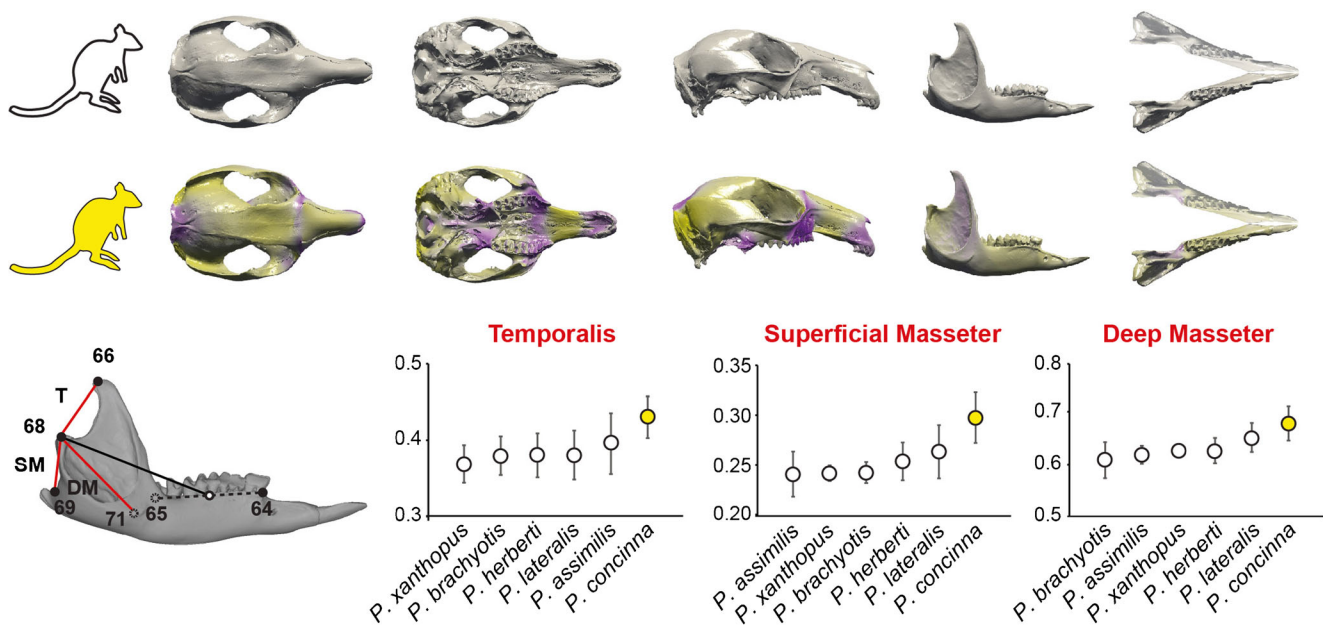
The pygmy rock-wallaby has larger insertion for adductor muscles, especially for the temporalis because of a slightly enlarged coronoid processes (Fig. 6). In kangaroos and wallabies, the temporalis permits an efficient cutting of plant materials with incisors, particularly in browsers (Lentle et al. 2003a; Warburton 2009). *Petrogale concinna* seems to be highly prone to grazing and seasonally feeds on abrasive ferns found in floodplains during the dry season (Sanson et al. 1985). The putative enlargement of the temporalis in *P. concinna* linked to the development of the coronoid process could also confer to this species a more efficient cutting of highly fibrous plant material.

### Morphological Convergences and Masticatory Disparities between Rock-Wallabies and Mole-Rats

Similarly, most African mole-rats show a cranial configuration characterized by a wide cranium with a short snout (Gomes







**Fig. 6** Mean cranial and mandibular reconstruction for the whole sample of rock-wallabies compared to *P. concinna*. Yellow and violet code for increases and decreases in surface area, respectively. Measures of in-levers (red lines), and out-levers (black lines) between landmarks

digitized are indicated on the mandible. T: Temporalis; SM: Superficial Masseter; DM: Deep Masseter. Graphs represent the different mean in-lever/out-lever ratio with corresponding standard deviations for rock-wallabies

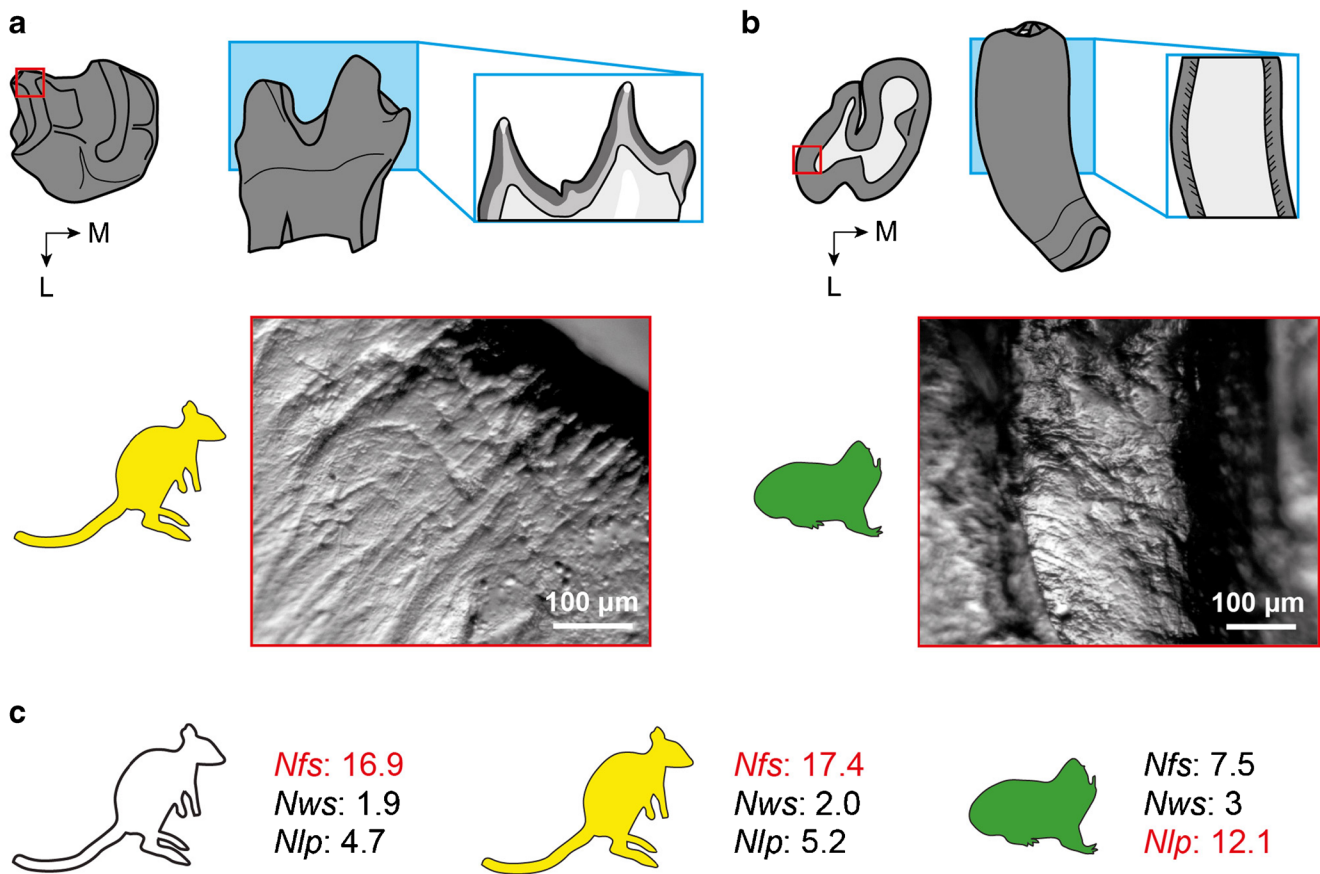
Rodrigues et al. 2016), which is associated with massive adductor muscles (temporalis, superficial masseter, and deep masseter) used for digging with incisors (Cox and Faulkes 2014). They are also considered as forceful biters among mammals, especially at the level of molars (Van Daele et al. 2009). The temporalis is highly developed and greatly contributes to the jaw closing motion (Cox and Faulkes 2014), which might increase the output force at the level of both incisors and molars in these rodents (Gomes Rodrigues et al. 2016; McIntosh and Cox 2016). Interestingly, the pygmy rock-wallaby and the silvery mole-rat show similar overall morphological trends in having larger insertions for adductor muscles, especially for the temporalis.

However, the morphological convergences observed between these animals, which could be attributed to the occurrence of the CDR, do not actually reflect similar adaptations but rather an ecological differentiation. Even if the silvery mole-rat shows high values, it has lower biomechanical advantage of adductor muscles for molar bite than most of its relatives (Gomes Rodrigues et al. 2016), contrary to the pygmy rock-wallaby. Differences in the direction of the power stroke should also be integrated when considering morpho-functional aspects. Distinct orthal and transverse phases of mastication are observed in kangaroos and wallabies, contrasting with the sole efficient transverse motion noticed in most placental herbivores (Crompton et al. 2008). In kangaroos and wallabies, the insertion of the deep masseter on the mandible protrudes anteriorly in the masseteric fossa. In addition, the extended lingual angular process allows for a greater insertion of the superficial masseter and for a widening of the pterygoid

fossa involving a developed medial pterygoid (Tomo et al. 2007; Crompton et al. 2008; Warburton 2009). All these characteristics are not present in most mole-rats, which have a reduced angular process potentially limiting the force generated by the superficial masseter during mastication (Gomes Rodrigues et al. 2016). In kangaroos and wallabies, the superficial masseter and the medial pterygoid greatly contribute to the orthal phase of shearing food between high transverse lophs of molars, and more importantly to the transverse phase of crushing food on interlophine links (Sanson 1980, 1989; Crompton et al. 2008; Crompton 2011; see Fig. 7). Shearing and crushing actions could be hypothesized as improved in the pygmy rock-wallaby because of its larger angular process for the insertion of the superficial masseter, as well as its wider pterygoid fossa, but this remains to be tested. The process of mastication is far less known in the African mole-rats. The main component of their mastication was assumed to be propalinal (Landry 1957). But, they more likely have a significant oblique component associated with precocious flat occlusal dental surface, due to very low cusps associated with enamel free areas present before eruption (Fig. 7).

### Mosaic of Morpho-Functional Characters Associated with CDR

Alternative mechanisms preventing high dental wear and allowing a sustained function of the dentition, such as high-crowned teeth, are less common among extant marsupials (i.e., only wombats) than in placentals (e.g., “ungulates”, xenarthrans, rodents). However, *P. concinna* displays a tooth



**Fig. 7** Dental characteristics of the pygmy rock-wallaby (a) and the silvery mole-rat (b). Details of occlusal surface (M: mesial, L: lingual) and enamel microstructure (pale grey corresponds to dentine and dark grey to enamel, which includes a softer outer layer and a translucent inner layer in the pygmy rock-wallaby, modified from Palamara et al., 1984 and Koenigswald, 2004) of erupting upper molars are represented with

diagrams (not to scale). Photographs of dental microwear are also shown (squares indicate the facets analysed on upper molar occlusal surface). (c) Comparison of dental microwear data between *P. brachyotis*, *P. concinna*, and *Heliophobius* (Nfs: number of fine scratches, Nws: number of wide scratches, Nlp: number of large pits)

row more curved than other *Petrogale*, which more importantly limits the number of functional teeth and maintains the efficiency of the dentition throughout its lifetime (Sanson 1989). This is coupled to a reduced dental length compensated by the presence of CDR, and which facilitates dental drift. It also has a molar enamel microstructure with a soft outer layer, which is opaque, hypomineralized, and shows a high number of voids contrary to other macropodids, such as *Macropus* and *Wallabia* (other *Petrogale* were unfortunately not considered; Palamara et al. 1984). Such a feature might favour rapid wear at the tip of cusps, and would be appropriate to maintain precise occlusal relationships during dental drift and to limit malocclusion issues (Palamara et al. 1984). In contrast, a softer enamel would decrease the molar efficiency more rapidly, so the presence of CDR becomes an advantage (Sanson 1989), especially considering the tough and highly abrasive components of their feeding habits revealed by dental microwear analyses. However, it might not be relevant here to link the acquisition of CDR only with differences in feeding habits. This is challenged by our microwear study indicating that

sympatric *P. brachyotis* and *P. concinna* might eat abrasive material or plants, such as grasses, in similar proportions, as noticed by Telfer and Bowman (2006), even if data on fern consumption are lacking in their study. Moreover, other *Petrogale* species, such as *P. xanthopus* and *P. assimilis*, are known to significantly feed on grasses (Arman and Prideaux 2015), but their masticatory apparatus does not show higher mechanical advantages for adductor muscles than most of the investigated *Petrogale* species. None of these observations take into account the potential effect of the incidental ingestion of dust deposited in the lower stratum of plant cover depending on the environment and habitat, and the fact that comminution of highly fibrous plant may involve longer chewing sequences and could lead to higher dental wear, especially due to the combined ingestion of abrasive mineral particles. The putative differences of feeding behavior (i.e. diet and mastication) and habitat (rock-habitat specialist vs. generalist) between *P. concinna* and *P. brachyotis*, could have led to niche partitioning (Telfer et al. 2008). Variations in size and dental replacement might be the consequences of

such an ecological partitioning probably at the origin of vicariant speciation.

In comparison with the pygmy rock-wallaby, the masticatory apparatus of the silvery mole-rat is not especially predisposed to a more efficient use of cheek teeth compared to its relatives. In fact, the skull of *Heliophobius* is mainly constrained by its subterranean mode of life, and specifically adapted to chisel-tooth digging like other African mole-rats (Gomes Rodrigues et al. 2016; McIntosh and Cox 2016). This does not mean that the masticatory apparatus of *Heliophobius* is less efficient than that of the wallaby, because it shows relatively higher biomechanical advantages for molars than for incisors (Gomes Rodrigues et al. 2016), which however need high output force for digging. *Heliophobius* displays precocious flat occlusal surfaces; its high-crowned cheek teeth are likely efficient for grinding (Schmidt-Kittler 2002), but the incisors are mainly used for cutting and shearing the underground part of plants (tubers and bulbs), as well as digging. No difference in enamel microstructure was observed in comparison with other mole-rats (Koenigswald 2004), and most of them show high dental wear with apparent traces of damage, apart from dental microwear which could only be investigated in *Heliophobius*. One can legitimately wonder why this species developed a CDR, while it already has high-crowned teeth to withstand dental wear, which is generally associated with the ingestion of abrasive matter (Janis and Fortelius 1988; Koenigswald 2011; Madden 2015). It has been recently noted that high-crowned teeth enable improved anchorage of teeth during dental drift, which in turn can contribute to the setting up of CDR (Gomes Rodrigues and Šumbera 2015). Dental microwear analyses confirmed this assertion and revealed that strong attrition is probably combined with the ingestion of dust and grit because of high activity of digging and feeding, which leads to strong molar damages and intense wear compensated by CDR. Paradoxically, the ingestion of mineral particles associated with flat and simplified dental occlusal surface might enhance the mechanical reduction of underground part of plants, and represent an alternative to shearing crests (Madden 2015).

### On the Origins of CDR and Convergent Traits in Mammals

Understanding the origins of CDR in mammals is highly challenging from evolutionary and functional points of view. It might be directly associated with the feeding behavior in the pygmy rock-wallaby, whereas it might be tightly related to the fossorial activity of the silvery mole-rat, which surely has a significant impact on dental wear. More generally, if developmental, phylogenetic and ecological constraints could have limited the acquisition of CDR in mammals, its scarce occurrence is surely a contingent phenomenon. On the one hand, different constraints do not necessarily prevent the occurrence

of similar traits: for instance, CDR is combined with developmental adjustments for the skull in a marsupial, and superimposed on a digging-adapted skull in a placental. On the other hand, similar phylogenetical backgrounds do not hinder opposite evolutionary trends, as exemplified by sirenians for different types of plant comminution: manatees have a CDR, dugong has a degenerate but high-crowned dentition associated with enlarged horny pads, and the extinct Steller's sea cow only had horny pads without teeth (Domning 1982; Lanyon and Sanson 2006). Consequently, and even if prerequisites are required for the setting of CDR (e.g., mesial drift; Gomes Rodrigues et al. 2011), only infrequent genetic processes could explain the evolution of supernumerary teeth in very distant phylogenetical taxa such as marsupials and placentals. Only then this mechanism could have been positively selected in response to environmental pressures, which vary from one group to another (i.e. food-related abrasiveness, life underground), but of which the consequences are in the end the same (i.e., high dental wear).

In conclusion, these results show that if convergent features occur in mammals, they may sometimes reflect different adaptive natures. The study of adaptation constitutes an important cornerstone of evolutionary biology, but defining an adaptation is not an easy task (Curio 1973; Gould and Lewontin 1979; Gould and Vrba 1982; Krimbas 1984; Reeve and Sherman 1993). Biological adaptation can only be built upon available variation, and evolutionary plasticity is in part limited by phylogenetic constraints and the general rules of construction of a structure. While variation is widely available in nature, the general rules of structural construction are not infinite as they depend on the preservation of the integration between different body parts, which directly reflects the dictates of past adaptations (Lessa 2000; Arthur 2001). Adaptationist hypotheses consider morphological variation as mainly reflecting adaptation in relation to organismal survival. In contrast, the structuralist viewpoints aim to understand the general rules of construction of a morphological feature (Seilacher 1970; Raup 1972; Cubo et al. 2008). In practice, these two schools of thought are not mutually exclusive. The convergent evolution of CDR in distant mammalian clades gives us an opportunity to separate the effect of ecological and developmental constraints on the morphological evolution of the skull. The difficulty lies in assessing the relative importance of constraints and selection, as well as the potential confounding effects of ecological factors that can channel morphological variation into a main direction by the acquisition of CDR. The adaptationist program is based on the observation that an adaptive balance, derived from natural selection, will lead a structure to align itself with a function. However, we showed that the analysis of this dual relationship must be set into a functional, developmental, and phylogenetic context in order to better understand the notions of convergences and adaptation as well as the respective roles played by

environmental conditions and other factors susceptible to interact with selection.

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### Compliance with Ethical Standards

**Conflict of Interest** The authors declare that they have no conflict of interest.

**Human and Animal Rights** This article does not contain any studies with human participants or animals performed by any of the authors.

**Informed Consent** Informed consent was obtained from all individual participants included in the study.

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