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The Impact of Food Properties on Jaw Movements in Rodents: A Comparison Between Myomorphous and Hystricomorphous Species

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ABSTRACT

Rodents can be divided into three major morphological groups (myomorphy, sciuromorphy, and hystricomorphy; additionally, protogomorphy can be found in only one recent species) based on the configuration of the skull and jaw muscles. These three morphotypes have been suggested to be adapted to different food types and allow for different chewing movements. Previous authors have postulated that the masticatory grinding movements should occur mostly in the antero-posterior direction, but other studies have suggested that different degrees of antero-posterior movement may occur across the rodent tree of life and in response to differences in food properties. Here, we use 3D reconstructed movements from X-Ray videos to show that both morphology and food type influence masticatory movements in two myomorphous and two hystricomorphous rodents. Yet, while hystricomorphs do not change the frequency of their masticatory movements in response to different food items, myomorphs do so. Additionally, myomorphs and hystricomorphs that exhibit propalinal chewing movements tend to possess a relatively lower mandibular condyle. Overall, our data suggest that molar morphology, in connection with dietary habits, directly influences masticatory movements. These results show that relatively small differences in a relatively conserved *bauplan* can have a large impact on jaw movements.

1 | Introduction

While not entirely restricted to mammals, mastication is a key feature of the group, in part made possible by their heterodont dentition (Herring 1985; Hiiemäe and Crompton 1985; Strait 1997; Hiiemäe 2000; Schwenk 2000; Schwarz et al. 2026). Traditionally, mastication is separated into three different chewing types or sequences, while in rodents a fourth, the characteristic gnawing is present (Hiiemäe 1967; Turnbull 1970; Schwartz et al. 1989; Gerstner et al. 2010). During the preparatory chews, the food is mainly transported backward to the molars and tooth–tooth contact occurs only rarely. During the subsequent reduction series food is crushed between the molars. Lastly, the pre-swallowing series are the longest cycles during which the crushed food is transformed into a bolus and transported toward the pharynx (Schwartz et al. 1989; Gerstner et al. 2010). Reduction series bites typically consist of distinct phases: (1) fast close (FC) at the end of which tooth-food contact is achieved; (2) slow close (SC), where the teeth are in contact with the food, but the mandible still moves

a considerable amount toward the cranium; (3) followed by the power stroke (PS) where the food reduction actually takes place; (4) slow opening (SO) during which the food is set free allowing the tongue to move the food particles within the oral cavity; (5) and fast opening (FO) where the mandible moves again toward the ventral-most position. Some species also exhibit an additional second SO phase (SO2) during which tongue-food contact is achieved (Gerstner et al. 2010; Da Cunha 2024).

The jaw morphology of rodents has long been a focus of research. Per jaw, all rodents possess two ever growing incisors, no canines, and a varying number of premolars and molars with diverse morphologies (Ryder 1878; Butler 1980; Butler 1985; Nowak 1999; Meng and Wyss 2005; Lazzari et al. 2008). The trough-like glenoid fossa of the mandibular joint allows rodents to actively switch between the characteristic gnawing at the incisors, involving simple up-and-down movements of the mandible and chewing at the cheek teeth which involves moving the jaw in a propalinal direction (i.e., directed antero-posteriorly; Ryder 1878; Fox 1965; Turnbull 1970). Three derived morphotypes of craniomandibular organization can be recognized among rodents, the sciuromorphous type (e.g., beavers and squirrels), considered most efficient at gnawing at the incisors; the hystricomorphous type (e.g., Guinea pigs and Capybaras), considered most efficient during at the chewing at the molars; and the myomorphous type (e.g., mice and hamsters), being a generalist type, efficient at both gnawing and chewing (Cox et al. 2012). While hystricomorph and myomorph refer to the phylogenetic group, hystricomorphous and myomorphous refer to the craniomandibular morphological condition. In the hystricomorphous type, the zygomaticomandibularis muscle originates on the snout of the animal and its deeper part extends posteriorly through the orbit and an enlarged infraorbital foramen (Figure 1B,D,F,H; Wood 1965; Turnbull 1970; Cox and Jeffery 2011; Da Cunha et al. 2024). The myomorphous configuration is mainly characterized by an enlarged infraorbital foramen and zygomatic arch. The deep masseter originates on an enlarged zygomatic plate, while the zygomaticomandibularis originates on the rostrum via the enlarged infraorbital foramen (Figure 1A,C,E,G; Wood 1965; Turnbull 1970; Cox and Jeffery 2011). The presence of a trough-like glenoid fossa has led to the assumption that masticatory movements in rodents mainly occur in a propalinal direction (i.e., directed antero-posteriorly; Ryder 1878; Fox 1965).

It has been hypothesized that rodents use their trough-like glenoid fossa not only for switching between chewing and gnawing but also for allowing grinding movements in an antero-posterior direction typical of rodents. These movements are called propalinal movements opposing the typical mediolateral grinding, or oblique, movements as seen in ungulates, for example (Ryder 1878; Fox 1965). Propalinal masticatory movements likely evolved at least two times independently in the Muroidea, three times in the Octodontoidea and at least once in the extinct Theridomyidae (Vassallo and Verzi 2001; Olivares et al. 2004; Lazzari et al. 2008; Hautier et al. 2010). Historically, it has been hypothesized that propalinal chewing evolved gradually within rodents (Butler 1980, 1985). Based on the morphology of molars' cusps and crests, Butler (1980) argued that Sciuromorpha and Hystricomorpha do not show propalinal chewing movements, while Muroidea practice propalinal chewing. Microwear studies in muroids showed that propalinal jaw movements are associated with specialized tooth morphologies, some allowing for propalinal movements, while others do not (Lazzari et al. 2008). However, since microwear only occurs during the PS, observations of tooth wear are likely not a reliable feature to describe the full jaw motion (Gordon 1984; Hylander et al. 1987; Teaford and Byrd 1989; Olivares et al. 2004).

Generally, myomorphous and hystricomorphous rodents have a broad variety of masticatory movements, with discrepancies between different studies being possibly due to methodological differences. However, the general consensus is that the movement patterns are different between myomorphous and hystricomorphous rodents (Hiiemäe and Ardran 1968; Weijs 1975; Gorniak 1977; Byrd 1981; Da Cunha 2024). Methods like (X-ray) cinematography can describe the whole range of motion of the jaws and not only the direction of the PS as captured by tooth wear studies. Nonetheless, results may vary depending on the filming method used, possibly due to differences in frame rate or differences in the food items used. For example, while some studies did not observe propalinal movements in *Rattus norvegicus* (Hiiemäe and Ardran 1968), others did (Weijs 1975; Weijs and Dantuma 1975; McParland et al. 2024). In another study on the myomorph *Mesocricetus auratus*, propalinal movements were (Gorniak 1977) observed contradicting microwear studies (Lazzari et al. 2008). Hystricomorphous rodents also seem to display varying degrees of propaliny. While *Octodon degus* does not appear to show propalinal movements (Da Cunha 2024), *Mycastor* and *Plagiodontia* show a mix of propalinal and oblique chewing (Woods 1976), and *Capromys* and springhares show a completely propalinal PS (Woods 1976; Offermans and de Vree 1990). For *Cavia*, some studies suggest a completely propalinal PS (De Vree 1977, 1979) while others did not find evidence for propaliny (Byrd 1981; Da Cunha 2024).

Studies comparing the influence of different food items on mastication have mostly been conducted on primates, including humans (Takada et al. 1994; Hiiemae et al. 1996; Thexton and Hiiemae 1997; Filipić and Keros 2002; Pereira et al. 2006; Montuelle et al. 2018; Montuelle et al. 2020). Generally, the range of motion appears reduced while feeding on harder compared to softer foods (Filipić and Keros 2002; Montuelle et al. 2020). Only few studies have investigated differences in kinematics while chewing different food types in rodents. Although no differences were observed in the chewing kinematics of rats when eating soft or hard food (Hiiemäe and Ardran 1968), some differences were noted in *Cavia* (De Vree 1977; Byrd 1981). For example, *Cavia* shows shorter chewing cycles and a shorter PS when fed with carrot compared to pellets (De Vree 1977; Byrd 1981). Additionally, the range of chewing movements is larger in all directions for carrots than for pellets (Byrd 1981).

The aim of the present study was to compare the three-dimensional movements among two myomorphous and two hystricomorphous species. Since propalinal masticatory movements evolved independently in myomorphs and hystricomorphs, we examine whether morphological differences in muscle organization between the two groups result in differences in motion patterns (Vassallo and Verzi 2001; Olivares

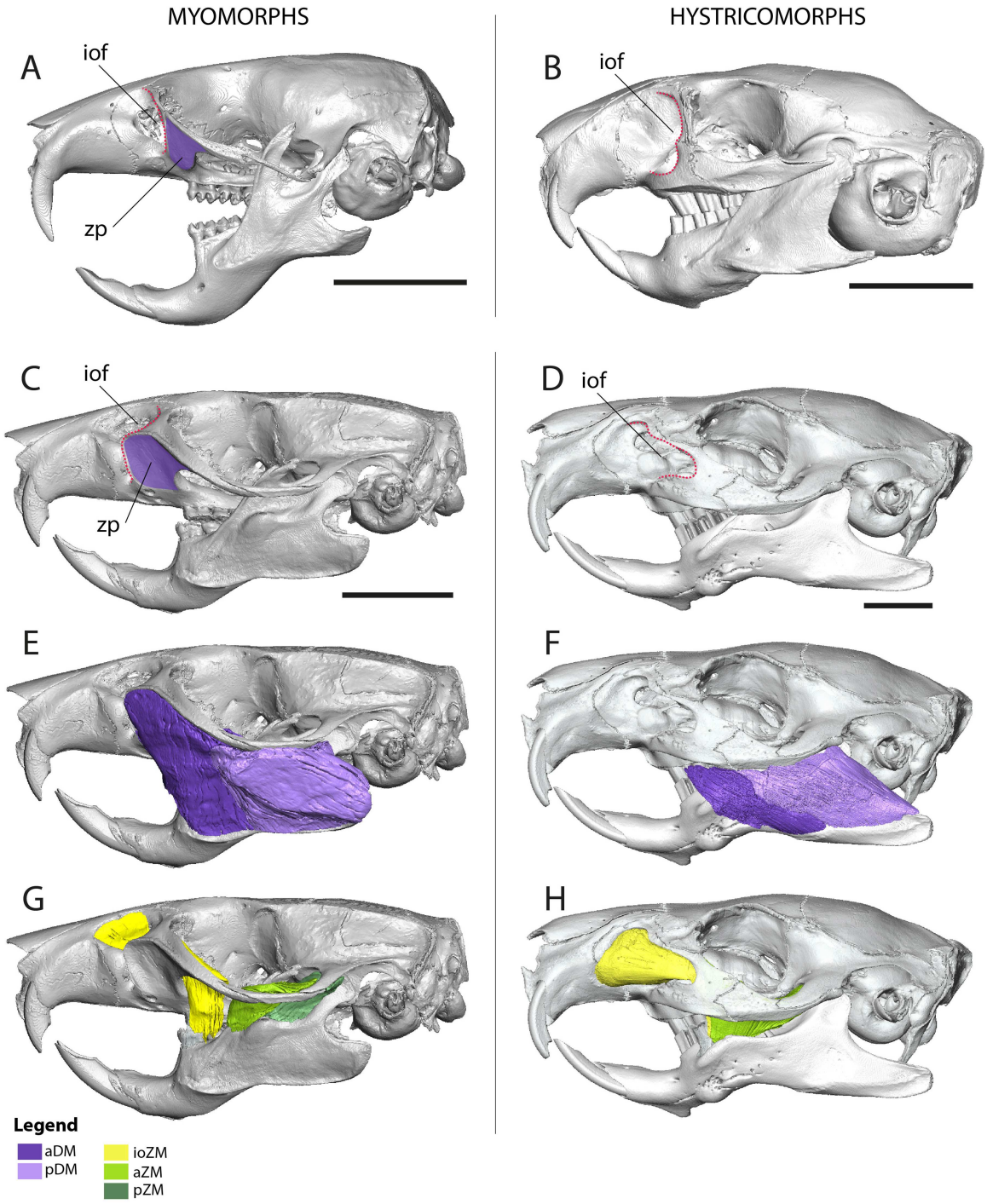

FIGURE 1 | Morphological differences between myomorphous and hystricomorphous morphotypes. Left lateral view of the CT-scanned skulls of *Mesocricetus auratus* (A), *Octodon degus* (B), *Rattus norvegicus* (C), and *Cavia porcellus* (D). 3D reconstructions of the masticatory musculature of *Rattus norvegicus* (E, deep masseter; G, zygomaticomandibularis) and *Cavia porcellus* (F, deep masseter; H, zygomaticomandibularis). Scale bars are 10 mm long. aDM, anterior deep masseter; aZM, anterior part of the zygomaticomandibularis; iof, infraorbital foramen; ioZM, infraorbital part of the zygomaticomandibularis; pDM, posterior deep masseter; zp, zygomatic.

et al. 2004; Lazzari et al. 2008). The two hystricomorphous species (*Cavia porcellus* L., 1758, "Guinea pig", and *O. degus* Molina, 1782, "Degu") are morphological extremes within the hystricomorphous type (cavioid and octodontoid, respectively) allowing us to assess the influence of a different muscle configuration, and mandibular and cranial morphology on masticatory movements within a single group (Vassallo and Verzi 2001; Hautier et al. 2011). The cavioid configuration is characterized by a more anterior-posterior muscle organization compared to the more medio-lateral muscle organization exhibited by the octodontoid type (Vassallo and Verzi 2001, Hautier et al. 2011). For the myomorphous rodents, we selected *R. norvegicus* Berkenhout, 1769 (Brown rat), and *M. auratus* Waterhouse, 1839 (Golden hamster), which differ not only in their muscular, mandibular, and cranial morphologies, but also in their molar morphology (Satoh and Iwaku 2004; Lazzari

et al. 2008; Miljutin 2011). *Mesocricetus* is characterized by a relatively higher mandibular condyle compared to *Rattus* and the molars are more interlocking in *Mesocricetus* (Satoh and Iwaku 2004; Lazzari et al. 2008; Miljutin 2011). By selecting these species, it should be possible to link changes in the masticatory movements to differences in morphology and to interpret the results in the context of rodent evolution, as well as their diverse ecologies. Specifically, we aim to link morphological differences to variation in propalinal movements. Additionally, we compare the influence of the consistency of different food items on the masticatory movements and masticatory phases. We hypothesize that: (i): the movement patterns are linked to morphology with a pronounced difference between species with a myomorphous or hystricomorphous organization of the jaw system; (ii): food type influences the composition of the masticatory phases, where we expect that harder foods lead to reduced gape but a longer PS; (iii): both groups should modulate their chewing kinematics. We expect them to be modulated in different ways in response to the food type, given the known differences in morphology.

2 | Materials and Methods

2.1 | Specimens

Three individuals each of *C. porcellus* L., 1758, *O. degus* Molina, 1782, *R. norvegicus* Berkenhout, 1769, and *M. auratus* Waterhouse, 1839 were used in the study. The animals were obtained from the pet trade. *Cavia* and *Octodon* are part of the monophyletic group of Caviomorpha and belong to the hystricomorphous type (Wood 1965; Cox and Jeffery 2011). *Rattus* and *Mesocricetus* both belong to the Muroidea parvorder and show a myomorphous morphology (Cox et al. 2012). Morphometric and sex data for each individual is provided in Supplementary Table S1.

2.2 | Surgical Implantations and Animal Care

All animals were anesthetized with a mixture of Ketamine and Medetomidine (Supporting Information S1: Table S2). While under anesthesia, they were implanted with six radio-opaque, cylindrical, lead markers of around 1 mm in length. Due to the small size of the animals, the markers were placed at the side of the bone by means of hypodermal injection needles. Three markers were placed on the cranium, the remaining three on the mandible. Three markers were placed on each side of the head with the anterior cranial and mandibular markers that were analyzed being on the right side (Figure 2). After implantation, marker position was reviewed using X-ray imaging, while the animals were still anesthetized. For recovery, the animals were injected with a reversal agent (Atipamezole, intramuscular injection at two to five times the dose of medetomidine depending on the species and its weight, see Supporting Information S1: Table S2) and remained in a temperature-controlled recovery box until fully awake. Animals were left to recover for 1 week after surgery. Water and food were available *ad libitum*. Before the recording sessions, the animals were deprived of food for 24 h to ensure feeding during the trials. All experiments were approved by the Ethics committee of the Muséum national d'histoire naturelle (MNHN, Comité Cuvier, protocol number 068).

2.3 | Three-Dimensional (3D) Imaging and Reconstruction

To visualize morphological differences between the myomorphous and the hystricomorphous morphotypes, individuals of *R. norvegicus* (UM ZOOL-3105) and *C. porcellus* (UM 499 V) were selected for diceCT, a method of contrast-enhanced microcomputed tomography (microCT) using Lugol iodine (I2KI) (Figure 1C–H). These specimens belong to the collection of the University of Montpellier. Specimens were placed in sealed containers filled with 5% I2KI solution, with sufficient volume to facilitate the diffusion process. The duration of staining varied depending on the size of the sample: *C. porcellus* required three, while *R. norvegicus* required 2 weeks. Each specimen was scanned twice - before and after contrast enhancement - on an EasyTom 150 X-ray microtomograph at the *Institut des Sciences de l'Évolution de Montpellier*, University of Montpellier (MRI; ISE-M, Montpellier, France; Da Cunha et al. 2024). Independent imaging of bone and muscle facilitated skull segmentation from bone-optimized scans and automatic alignment with muscle-optimized scans using the "Magic Wand" tool and the "Register Images" module of the Avizo software (Avizo.Lite 2019.4; Thermo Fischer Scientific), respectively. Image data and pre-segmented muscle slices were imported into Biomedisa (Lösel et al. 2020) with the "all axes" parameter selected in the label field. The final segmentation was obtained by selecting the cleaned and smoothed parameters, with minor adjustments to correct errors from the semi-automatic image segmentation. The skulls of *M. auratus* (NHMUK 1992.42) and *O. degus* (UM 506 V), from the collections of the Natural History Museum of London and the University of Montpellier, respectively, were also CT scanned for comparison (Figure 1A,B). Implanted specimens were CT scanned at a voxel size of 51.5 µm, at the end of the experiment, using a Quantum GX3 CT scanner at the UMR7179-MECADEV to visualize marker position (Figure 2). This allowed us to verify that marker position had not changed over time.

2.4 | Data Acquisition

The imaging system consisted of two custom X-ray systems (RST Medical, Netherlands) with 38 cm image intensifiers (Koninklijke Philips N.V., The Netherlands). The X-ray sources (Philips Super 50CP with Philips SRM 1550 ROT350 tubes) and image intensifiers were placed in an angle of approximately 90° to one another; one vertically, the other horizontally. On each of the image intensifiers, a high-speed camera (Phantom Miro model R311, AMETEK, Berwin, PA, USA) was mounted.

For imaging, a 120 × 20 × 20 cm plexiglass container was placed on the image intensifier of the vertical X-ray system, parallel to the horizontal imaging system. The animals were placed in the plexiglass container, and the food item was placed in the field of view of both image intensifiers. Videos were taken for 6 s at 400 fps at a resolution of 1200 × 800 pixels. For camera control and video manipulation, the Phantom Camera Control (PCC) software V. 3.6 (Vision Research Inc., USA) was used. X-rays were produced from 45 to 60 kV and 50 to 94 mA for the vertical system, and from 54 to 75 kV and 80 to 140 mA for the horizontal system. Videos were taken for soft (namely, pieces of apple) and hard food items (sunflower seeds). For *Cavia* and

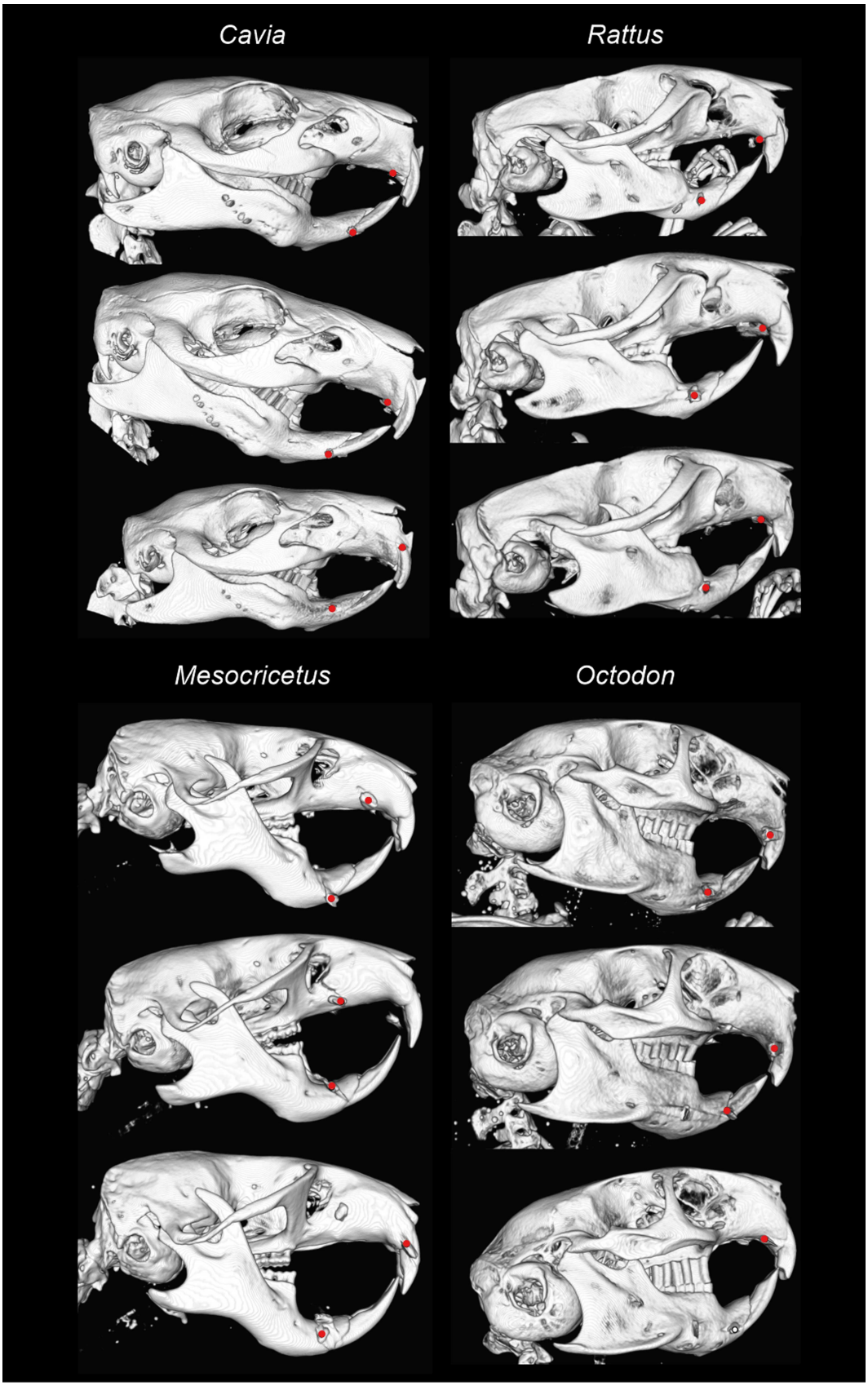

FIGURE 2 | Marker position on the heads of all animals. Right lateral view of CT-scanned skulls of all the animals used in this study. The markers used for the analysis (the anterior-most ventral and dorsal markers) are marked with red dots.

Octodon videos for feeding on sunflower seeds were obtained for only two specimens. Whenever the setup was changed it was calibrated and corrected for distortion. For the calibration of the three-dimensional space between the two image intensifiers, a custom-made calibration object was imaged. Additionally, a grid to correct for image distortion was placed on each of the image intensifiers and filmed to perform image retro-deformation.

For tracking, the videos were exported in shorter sequences with the PCC software in AVI format. The tracking of the markers was done with the XMALAB software (Version 1.5.5; Knörlein et al. 2016). The same software was used for calibration and image retro-deformation. All six markers were tracked whenever feasible but only data from the anteriormost mandibular and cranial marker were used. Markers were tracked with the automatic function but corrected manually where needed. A sequence of at least five consecutive bites was analyzed for each video. The tracked data was exported from XMALAB as 3D coordinates.

To get a better understanding of the videos, one sequence for *Rattus* and for *Cavia* can be found in the supplements (Movies S1, S2). For both animals, the dorso-ventral and lateral view were filmed simultaneously.

2.5 | Data Analysis

The 3D coordinates were imported into R (Version 4.3.1, R Core Team 2023) using RStudio (Version 2023.6.1.524; Posit team 2023). The *tidyverse* (Version 2.0.2; Wickham et al. 2019) environment was used for data transformation and manipulation. Descriptive analysis of the masticatory movements was performed by producing 3D plots of the anterior-most mandibular marker using the *plotly* package (Version 4.10.4; Sievert 2020). The video material was further visually examined to interpret the obtained plots. The movement of the anteriormost mandibular marker was corrected for head movement by subtracting the coordinates of the anteriormost cranial marker from the coordinates of the marker used for the analysis. Consequently, our kinematic data only describe the movement of the mandible relative to the cranium to account for size difference.

The gape distance was calculated as the distance between the anterior-most cranial and mandibular markers and was corrected for inter-marker distance by subtracting the minimal distance between both markers. Cycle duration (CY) was calculated as the time between two maximal gape distances. We defined a cycle as a jaw movement starting at the ventral-most position at maximum gape, followed by a closing phase, where the food is crushed and an opening movement at which the jaw is brought back to the ventral-most position at maximum gape (Hiiemäe 1978). The classification of the types of cycles followed Byrd (1981). The different phases of a masticatory cycle were extracted in a semiautomatic manner. To discriminate between the different masticatory phases the points with maximum and minimal gape distance, as well as the points of maximum and minimal acceleration, were plotted onto the two-dimensional graph of the gape distance (Figure 3). These points were plotted onto the three-dimensional trajectories, and modified and selected manually as start points, one for each phase, following a modified

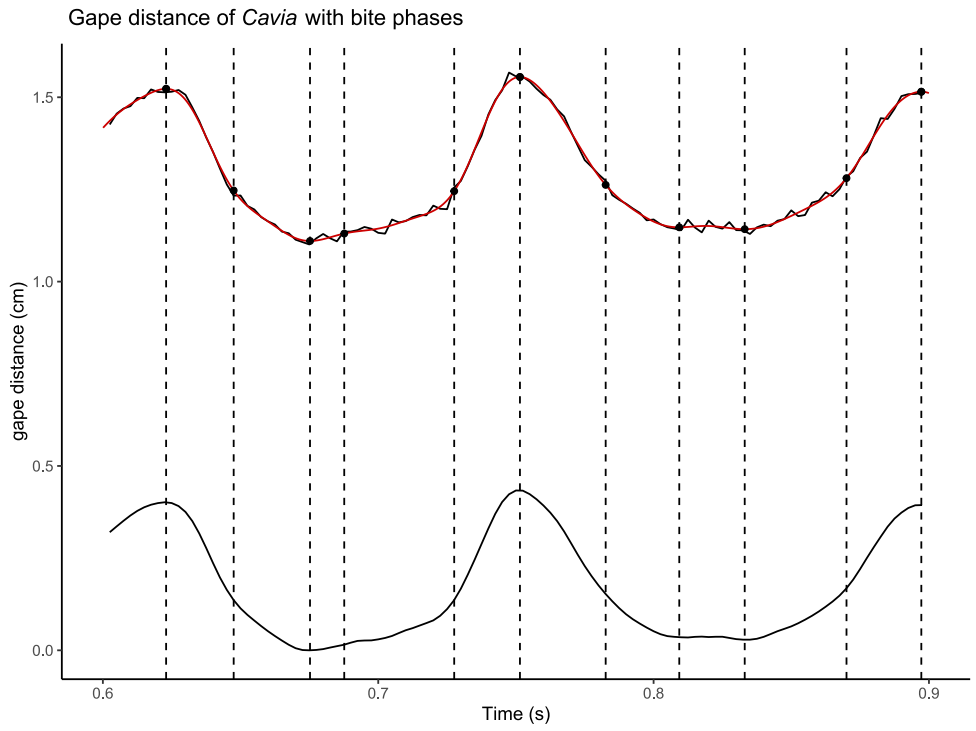

FIGURE 3 | Example of phase discrimination based on gape distance in *Cavia*. The upper black line shows the raw gape distance. The red line overlain shows the fitted general additive model (GAM). The black dots show the points used for phase discrimination. The lower black line shows the GAM model corrected for inter-marker distance. Two masticatory cycles are shown, the first does not show a power stroke but does have a slow open 2 phase, while the second does show a power stroke but not a slow open 2 phase.

definition from Montuelle et al. (2018, 2020). The FC starts at maximum gape distance and lasts until the start of the SC phase. The SC starts with a change in acceleration after the gape gets significantly reduced. If a PS was present, it was characterized as starting at minimum gape distance and by a visible grinding movement in the 3D plots. The slow open one (SO1) either starts at minimum gape (if no PS is present) or with a change in acceleration at the end of the grinding movement (if a PS is present). If a SO2 is present, it is associated with another change in acceleration and a plateau in the 3D plots. The FO starts with a change in acceleration and most of the opening movement occurs during this phase. The phase delimitations based on acceleration and inter marker distance can be seen in Figure 3 and Supporting Information S1: Figure S1. For the calculation of starting and ending points of each phase, the gape distance was modeled with a general additive model (GAM) with gape distance as the response variable and time as the predictor, using the *mgcv* package (Version 1.9.1, Wood 2011; Figure 3, Supporting Information S1: Figure S1). We used a GAM since it is the most flexible model, allowing for multiple peaks. These points were calculated with the help of the *changepoint* (Version 2.2.4; Killick et al. 2024), *splus2R* (Version 1.3.5; Constantine and Hesterberg 2024) and *manipulate* (Version 1.0.1; Allaire 2014) packages. To create the 3D plots, the data were low-pass filtered using a Butterworth filter with the help of the *signal* (Version1.8.1; Signal Developers 2023) package. The final 3D plots were obtained by removing both ends of the graph showing edge effects introduced by the low pass filtering and by rotating. In the final plots, the plane between the medio-lateral and anterior-posterior axis is parallel to the plane of the upper molars surface. The dorso-ventral axis was perpendicular to this plane.

2.6 | Statistical Analyses

Differences between both food types were analyzed for each species and each phase with Wilcoxon–Mann–Whitney tests. The same was done for differences in maximum gape distance. Differences between the phases for all food types were tested with Kruskal–Wallis tests, followed by pairwise comparisons with Bonferroni correction. The same was done for differences between species for each phase and food type. Finally, to test whether the effect of food type was the same for the two morphotypes, a two-way analysis of vairance (ANOVA) was performed with food type and morphology as the categorical variables and the times of each phase as the response variable. Even if in some cycles the slow open 2 (SO2) phase was absent, we referred to the slow open phase as slow open 1 for consistency.

3 | Results

A total of 211 cycles were tracked for this study, with 115 for the myomorphous species and 96 for the hystricomorphous species (see details in Supporting Information S1: Table S3). For feeding on apple, 133 cycles were recorded and 78 cycles were recorded for feeding on sunflower seeds (Supporting Information S1: Table S3).

3.1 | Descriptive Analysis of Movements

When *Cavia* feeds on apple, the masticatory cycles typically alternate bilaterally, meaning that they switch sides between each cycle (Figure 4A). Occlusion movements are directed toward the center with a slight anterior movement (Figure 4A,C,E). During the PS, the mandible moves to the opposite site of the head. The slow open 1 phase starts with a sharp movement in medial direction, while during the FO phase the mandible moves again to a more lateral position (Figure 4A,C,E). The propalinal component of the movement is very limited (Figure 4C,E). Additionally, unilateral cycles were recorded where maximum gape is reached at a medial instead of a lateral position (Supporting Information S1: Figure S2). Occlusion then occurred more laterally. Unilateral cycles showed less propaliny. Closing started medially toward a more dorso-lateral position. During the PS the mandible shifts laterally across the midline toward the opposite side creating a transverse griding motion. During opening, the mandible is again brought into a more medial position (Figure 4A,C,E). *Octodon* feeding on apple shows even less propalinal movement than *Cavia* (Figure 5C,E). Generally, movements look similar to those observed in *Cavia*; however, the lateral movements during the PS are more pronounced (Figures 4A,C,E and 5A,C,E). The lateral movements are also more pronounced during the slow open phase when compared to *Cavia*. Additionally, the transition between the PS and slow open phases is less smooth than in *Cavia*. The unilateral cycles occur more often than in *Cavia* but look very similar (Figure 5; Supporting Information S1: Figure S2).

While feeding on sunflower seeds, masticatory movements in *Cavia* look different from the ones observed during feeding on apple (Figure 4). The cycles also alternate between both sides, but instead of starting at a lateral position they start at a medial position (Figure 4B). During occlusion, the mandible moves to a posterio-lateral position (Figure 4B,D,F). During the PS, the mandible remains lateral and moves anteriorly with a more pronounced propalinal movement (Figure 4D,F). Opening occurs toward a posterio-medial direction, before closing again toward the opposite site (Figure 4B,D). We call cycles of this type unilateral central cycles. In *Octodon* feeding on sunflower seeds cycles look similar to the ones observed for feeding on apple (Figure 5). However, there is some increase in the propalinal component of the movement as well as in the lateral movements during the PS (Figure 5A–D). Cycles resembling the alternating bilateral type were not observed as frequently during mastication on sunflower seeds compared to apple (Figure 5A,B). They always occurred isolated from similar cycles on the opposite side by medial cycles (Figure 5A).

While feeding on apple *Mesocricetus* shows bilaterally alternating cycles (Figure 6A). Occlusion starts at the lateralmost point and a slightly medial movement occurs (Figure 6A,C). During the PS, the mandible moves latero-posterially to the opposite side (Figure 6C,E). During opening phases, the mandible moves to a slightly more lateral position with a slight anterior curve (Figure 6A,C). In *Rattus*, the masticatory movements also occur as bilaterally alternating cycles, which look similar to those in *Mesocricetus* (Figures 6A,C,E and 7A,C,E). While the movement patterns are generally similar across the two species, *Rattus* shows more pronounced propalinal

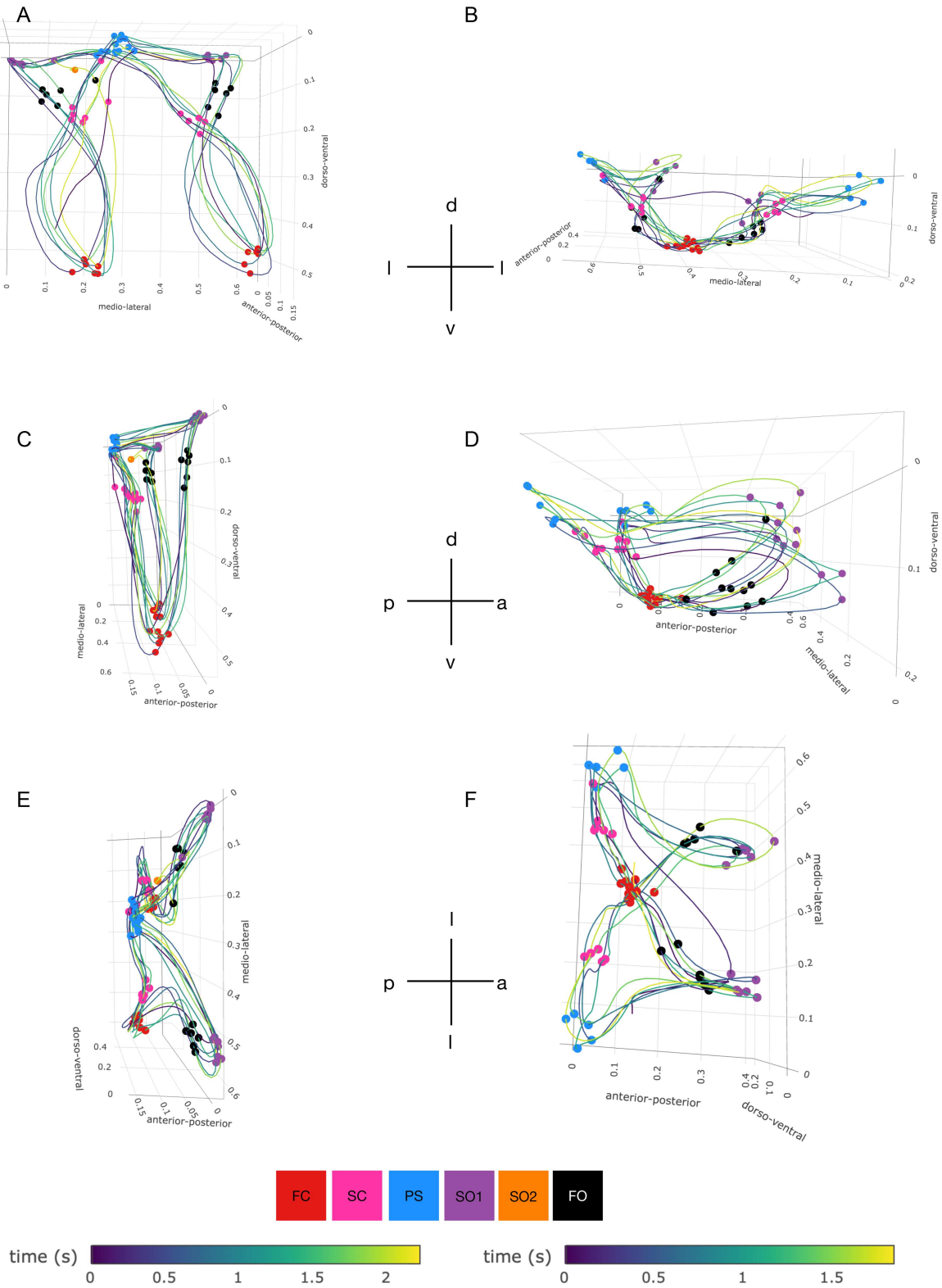

FIGURE 4 | Masticatory movements of *Cavia*. (A, C, E) Masticatory movements of the mandible while feeding on apple. (B, D, F) Masticatory movements while feeding on sunflower seeds. (A, B) Frontal view; (C, D) lateral view; (E, F) dorsal view. The crosses indicate the relative directions with respect to the center of the head: a, anterior; d, dorsal; l, lateral; p, posterior; v, ventral. The points indicate the start or end of the masticatory phases. Please note that FC phase start and FO phase end are, by definition, the same points. The shift in the masticatory pattern between the soft and hard food is clearly visible. This shift is not visible in the other hystricomorphous species, *Octodon* (Supporting Information S1: Figure S2). Please note that the numbers on the axis represent relative distances and do not have units.

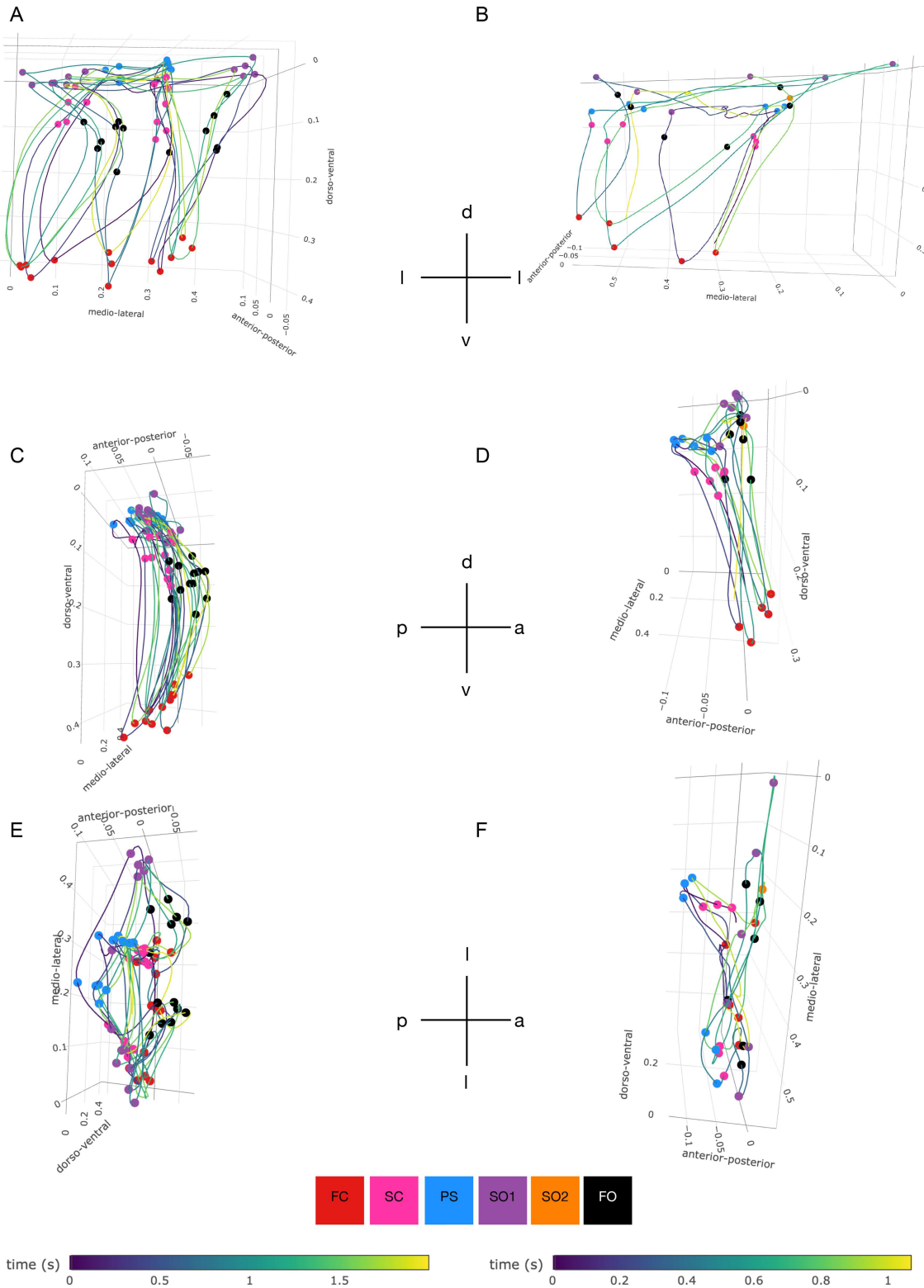

FIGURE 5 | Masticatory movements of *Octodon*. (A, C, E) Masticatory movements while feeding on apple. (B, D, F) Masticatory movements while feeding on sunflower seeds. (A, B) Frontal view; (C, D) lateral view; (E, F) dorsal view. The crosses indicate the relative directions with respect to the center of the head: a, anterior; d, dorsal; l, lateral; p, posterior; v, ventral. The points indicate the start or end of the masticatory phases. Please note that FC Start and FO end are by definition the same points. The increase in the range of motion in the harder food is visible. Please note that the numbers on the axis represent relative distances and do not have a unit.

movements (Figures 6C,E and 7C,E). Additionally in *Rattus*, a larger proportion of the lateral movements occurs during the FC and FO phases compared to the SC and slow open phases (Figure 7A,C,E).

During the mastication of sunflower seeds, *Mesocricetus* movements look similar to those for apple in (Figure 6). However, some key differences are noticeable. While the occlusion movements are very similar, the PS starts with a small

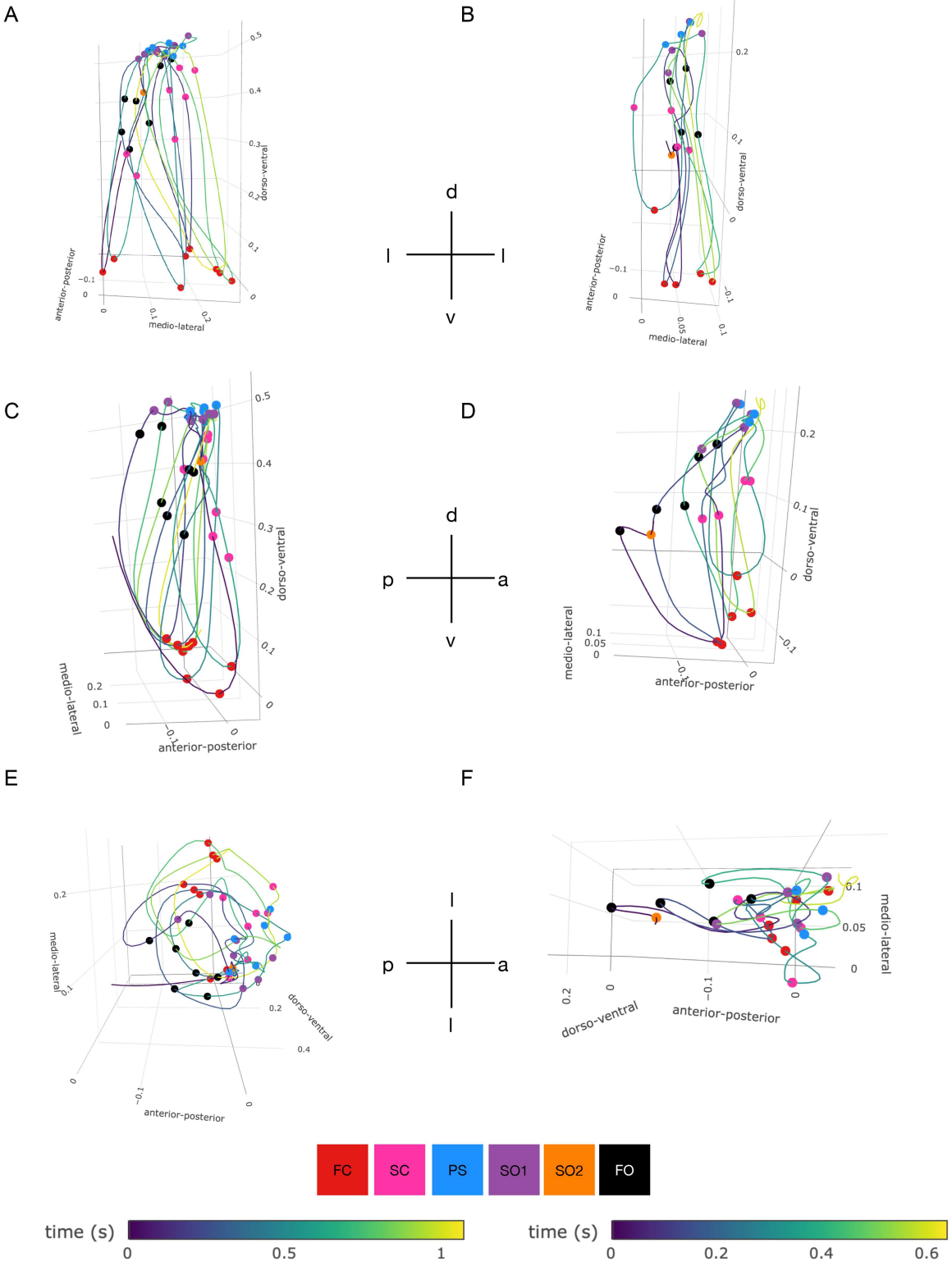

FIGURE 6 | Masticatory movements of *Mesocricetus*. (A, C, E) Masticatory movements while feeding on apple. (B, D, F) Masticatory movements while feeding on sunflower seeds. (A, B) Frontal view; (C, D) lateral view; (E, F) dorsal view. The crosses indicate the relative directions with respect to the center of the head: a, anterior; d, dorsal; l, lateral; p, posterior; v, ventral. The points indicate the start or end of the masticatory phases. Please note that FC phase start and FO phase end are, by definition, the same points. Medial starting cycles as observed in the hystricomorphous species are not visible (Figure 4, Supporting Information S1: Figure S2). While feeding on harder food *Mesocricetus* shows less propalinal movement than *Rattus* (Supporting Information S1: Figure S3). Please note that the numbers on the axis represent relative distances and do not have units.

propalinal forward movement (Figure 6C,D), after which the mandible is moved laterally (Figure 6F). At the end of the PS, the mandible moves posteriorly before opening starts again. *Rattus* also shows alternating bilateral cycles while feeding on sunflower seeds (Figure 7). In comparison to movements while chewing on apple, propalinal movements are stronger (Figure 7E,F). During occlusion the mandible moves dorsally and slightly medially. During the PS the mandible has a more

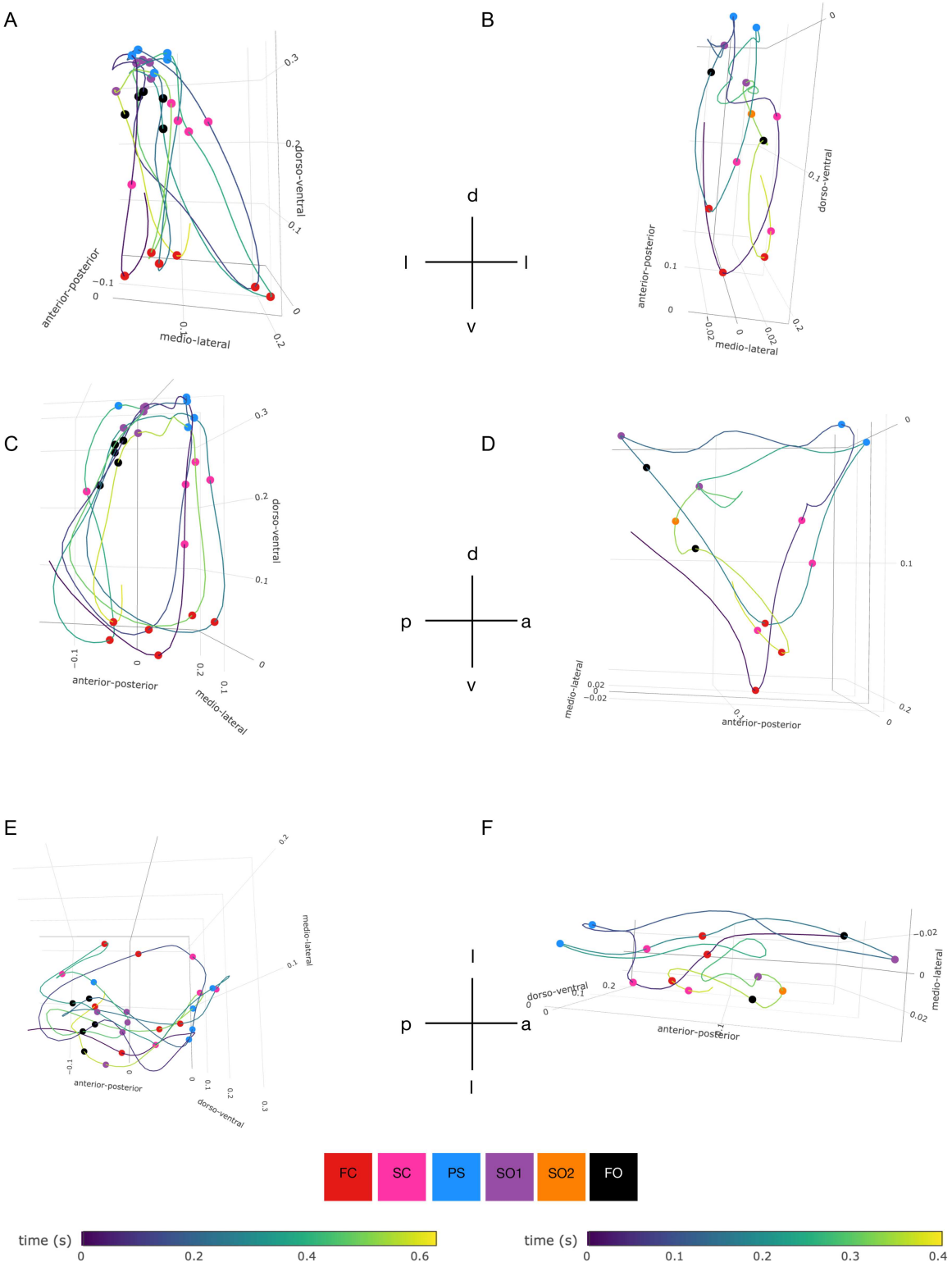

FIGURE 7 | Masticatory movements of *Rattus*. (A, C, E) Masticatory movements while feeding on apple. (B, D, F) Masticatory movements while feeding on sunflower seeds. (A, B) Frontal view; (C, D) lateral view; (E, F) dorsal view. The crosses indicate the relative directions with respect to the center of the head: a, anterior; d, dorsal; l, lateral; p, posterior; v, ventral. The points indicate the start or end of the masticatory phases. Please note that FC Start and FO end are by definition the same points. The increase in the propalinal movement in the hard food is visible. Please note that the numbers on the axis represent relative distances and do not have a unit.

pronounced forward movement. The opening movements are directed in a posterior and slight lateral direction toward the opposit side after which closing starts (Figure 7D).

3.2 | Differences in the Gape Distance

Wilcoxon-Mann-Whitney tests revealed that the maximum gape distance in *Cavia*, *Mesocricetus,* and *Octodon* is significantly larger while feeding on apple compared to sunflower seeds ($p < 0.01$; Supporting Information S1: Figure S3). In *Rattus*, the difference is not significant ($p > 0.05$; Supporting Information S1: Figure S3). Kruskal–Wallis tests did not find a significant difference in the gape distance between the species for both food types separately ($p > 0.05$; Supporting Information S1: Figure S3). However, the pairwise comparisons revealed that the gape distance while feeding on apple is significantly smaller in *Rattus* compared to the other species ($p < 0.01$; Supporting Information S1: Figure S3). Additionally, the gape distance is significantly larger in *Mesocricetus* compared to *Octodon* when feeding on apple ($p < 0.01$; Supporting Information S1: Figure S3). While feeding on sunflower seeds, the gape distance is significantly smaller in *Cavia* compared to all other species, and in *Rattus* compared to *Mesocricetus* and *Octodon* ($p < 0.001$; Supporting Information S1: Figure S3).

3.3 | Occurrence and Relative Duration of Masticatory Phases

The FC, SC, and FO phases occur in every masticatory cycle, while the slow open 1 phase occurs in 81-100% of the cycles across all species and both food types (Supporting Information S1: Table S3). In *Cavia,* a clear PS occurs in 77%–84% of the cycles (Supporting Information S1: Table S3) but in 85-92% of the masticatory cycles in *Octodon* (Supporting Information S1: Table S3). In the myomorph species, the occurrence of the PS ranges from 42% in *Mesocricetus* feeding on apple to 80% in *Rattus* feeding on apple (Supporting Information S1: Table S3). While the slow open 2 phase is present in 25% of cycles in *Octodon* (Supporting Information S1: Table S3) it only occurs in one out six cycles in *Cavia* (Supporting Information S1: Table S3). *Mesocricetus* performs the slow open 2 phase in 42%–45% of the cycles (Supporting Information S1: Table S3). *Rattus* has an occurrence of the slow open 2 phase of 30% while feeding on apple, while it is present in only 15% of the cycles when feeding on sunflower seeds (Supporting Information S1: Table S3).

While feeding on apple, the relative durations of the FC and FO are similar across all species (Figure 8H; Supporting Information S1: Table S3). The SC is relatively shorter in *Octodon* compared to the other species, while the PS is shortest in *Mesocricetus* (Figure 8H; Supporting Information S1: Table S3). The slow open phases are relatively shorter in *Cavia* compared to the other species while feeding on apple (Figure 8H; Supporting Information S1: Table S3). In comparison to apple, the relative duration of the PS increases in all species when chewing sunflower seeds except for *Mesocricetus*. The relative increase is strongest in *Octodon*. All other phases are consequently relatively shorter in *Octodon* when feeding on sunflower seeds, compared to apple (Figure 8H; Supporting Information S1: Table S3). The FC is relatively shorter in *Rattus* when feeding on sunflower seeds compared to apple. However, the relative duration of the FO is relatively stable across all species and food types, except for *Octodon* (Figure 8H; Supporting Information S1: Table S3).

3.4 | Differences Between Food Types

In *Cavia,* the slow close phase is significantly longer when chewing apple compared to sunflower seeds, while the PS is significantly shorter for apple compared to sunflower seeds (Table 1; Figure 8C,D). The cycle duration, the PS and the FC, and the slow open 2 phases are longer in *Mesocricetus* when feeding on apple compared to feeding on sunflower seeds (Table 1; Figure 8A,B,D,F). For *Octodon* the FC and the slow open 1 phases are longer when chewing apple compared to sunflower seeds (Table 1; Figure 8B,E). However, the PS is longer while feeding on sunflower seeds compared to apple slices (Table 1; Figure 8D). In *Rattus,* the cycle duration, and the FC and the FO phases are longer when chewing apple compared to sunflower seeds (Table 1; Figure 8A,B,G).

3.5 | Differences in Duration Between the Phases

The Kruskal–Wallis tests revealed that the duration of the phases only differed significantly to each other in *Cavia* feeding on apple ($p > 0.05$). The pairwise comparisons revealed more differences. For *Cavia*, when feeding on soft food, the FC and FO phases are significantly longer than the slow open 1 and 2 phases (Table 2; Figure 8B,E–G). The PS is significantly longer than the slow open 1, slow open 2, and the FO phases, while the SC phase is longer than the slow open 1 (Table 2; Figure 8C–G). The other species and *Cavia* feeding on sunflower seeds showed only significant differences in the pairwise comparisons (Table 2). When feeding on sunflower seeds the slow open 1 is significantly shorter than the FC, the PS, and the FO phase, while the PS is significantly longer than the FC, the SC and the FO phases in *Cavia* (Table 2; Figure 8B–E,G).

In *Octodon,* the PS is significantly longer than the FC, the SC, the slow open 1, and the FO phases when feeding on sunflower seeds and also longer compared to the slow open 1 phase when feeding on apple (Table 2; Figure 8B–E,G). Additionally, the slow open 1 is significantly shorter than the FC and the FO for sunflower seeds (Table 2; Figure 8B,E,G).

For *Rattus* feeding on apple, the slow open 1 phase is significantly shorter than the FC, the SC, the PS, and the FO phase (Table 2; Figure 8B–E,G). Moreover, the slow open 2 is significantly shorter than the FO phases (Table 2; Figure 8F,G). While feeding on sunflower seeds, the PS is significantly longer than the FC and slow open 1 phases (Table 2; Figure 8B,D,E).

3.6 | Differences Between the Species

Kruskal-Wallis tests did not find significant differences between the species for the single phases ($p > 0.05$). Pairwise comparisons, however, revealed that while feeding on apple the cycle

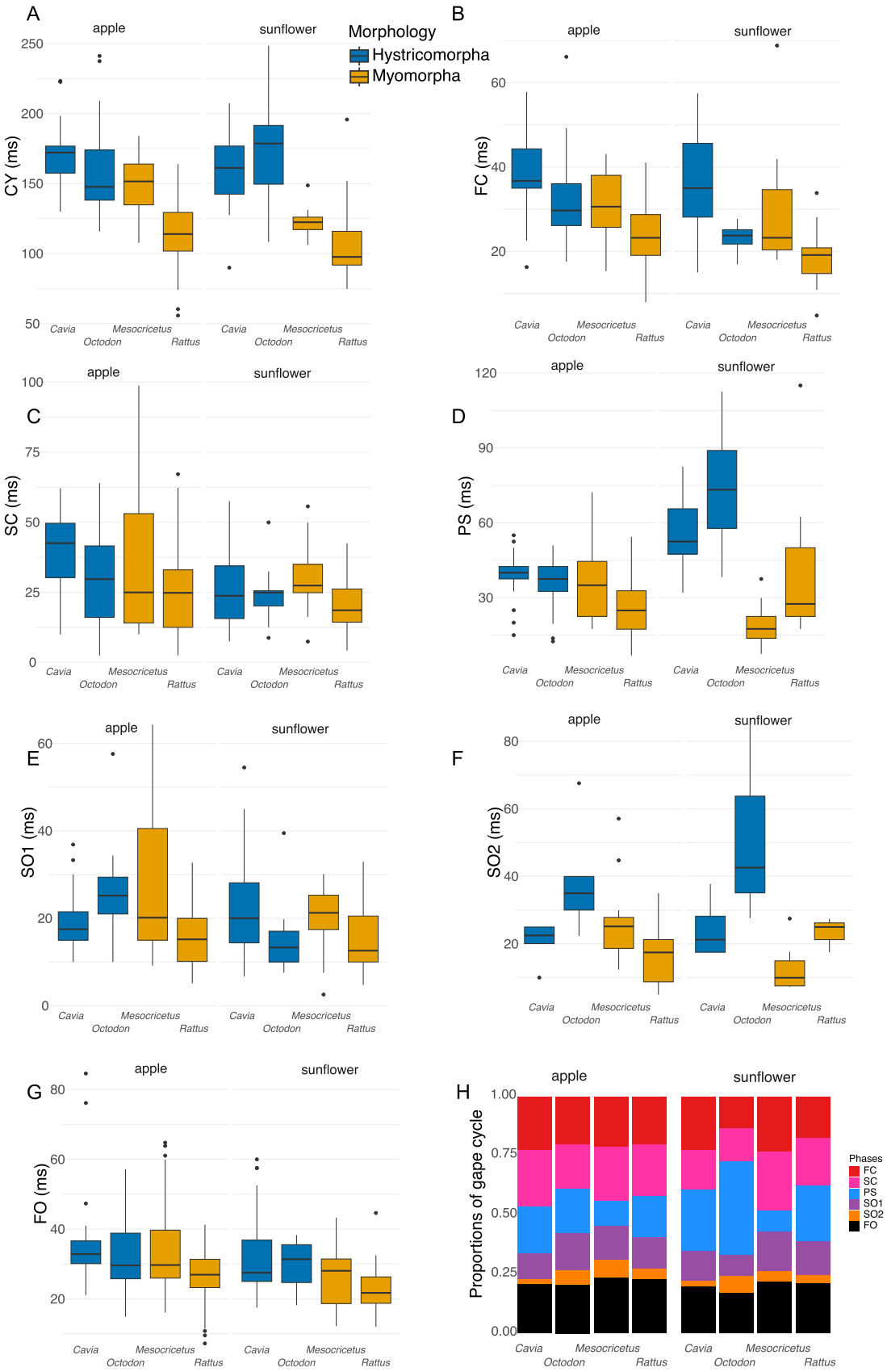

FIGURE 8 | Boxplots showing the differences in cycle duration and the masticatory phases. The color indicates the morphological group. The sample size for each phase can be found in Supporting Information S1: Table S2. The central line indicates the median; box edges indicate the 25th and 75th percentiles; whiskers extend to the most extreme values within 1.5 × IQR from the box; points beyond whiskers represent outliers. (A) Total cycle duration (CY); (B) fast close (FC); (C) slow close (SC); (D) power stroke (PS); (E) slow opening 1 (SO1); (F) slow opening 2 (SO2); (G) fast opening (FO); (H) Relative duration of the masticatory phases for each species and both food types. The colors code for the different phases.

TABLE 1 | Results of Wilcoxon–Mann–Whitney tests for the total duration, masticatory phase durations, and gape distance (GP). The test compared the differences in the durations between soft and hard food.

	Cavia		*Mesocricetus*		*Octodon*		*Rattus*	
	W	***P***	**W**	***P***	**W**	***P***	**W**	***p***
CY	487	0.181	464	< 0.001	116	0.169	670	0.018
FC	439	0.569	352	0.043	258	0.003	688	0.009
SC	607.5	0.001	245	0.750	195	0.323	547	0.371
PS	108	< 0.001	113	0.004	10	< 0.001	166	0.066
SO1	319.5	0.373	228	0.648	274	< 0.001	491	0.732
SO2	9	0.900	86	0.004	6	0.383	13	0.301
FO	503.5	0.109	334	0.103	180.5	0.584	658.5	0.026
GP	744	< 0.001	383	0.006	298	< 0.001	576	0.149

Abbreviations: CY, total duration of a masticatory cycle; FC, fast close; FO, fast opening; *p*, *p*-value; PS, power stroke; SC, slow close; SO1, slow opening 1; SO2, slow opening 2; W, sum of ranks.

duration is significantly shorter in *Rattus* compared to any other species (Table 3; Figure 8A). In *Cavia,* the cycle duration is significantly longer than for *Mesocricetus* (Table 3; Figure 8A). The FC phase is significantly shorter in *Rattus* while feeding on apple compared to any other species (Table 3; Figure 8B). Additionally, the FC phase is longer in *Cavia* compared to *Mesocricetus* and *Octodon* (Table 3; Figure 8B). When feeding on apple, the SC phase is significantly longer in *Cavia* compared to *Rattus* (Table 3; Figure 8C). The PS is significantly shorter for *Rattus* compared to *Cavia* and *Octodon*, when feeding on apple (Table 3; Figure 8D). The slow open 1 phase is significantly longer in *Octodon* compared to *Rattus* and *Cavia* when feeding on apple (Table 3; Figure 8E). Additionally, the slow open 2 phase is significantly shorter in *Rattus* compared to *Octodon* (Table 3; Figure 8F). In the case of apple, the FO phase is longer for *Cavia* compared to *Rattus* (Table 3; Figure 8G).

While chewing sunflower seeds, the cycle duration is significantly shorter in *Rattus* than in any other species (Table 3; Figure 8A). Additionally, the cycle duration is significantly shorter in *Mesocricetus* compared to both hystricomorph species (Table 3; Figure 8A). The FC phase, when feeding on sunflower seeds, is significantly shorter for *Rattus* compared to the other species (Table 3; Figure 8B). In *Cavia*, the FC phase is significantly longer than in *Mesocricetus* and *Octodon* (Table 3; Figure 8B). The PS is significantly longer in *Octodon* while feeding on hard food, compared to the other species (Table 3; Figure 8D). Additionally, the PS is longer in *Cavia* compared to *Mesocricetus* and *Rattus* (Table 3; Figure 8D). In *Rattus*, the PS is significantly longer than in *Mesocricetus* (Table 3; Figure 8D). The FO phase is significantly longer in *Cavia*, feeding on sunflower seeds, compared to *Rattus* (Table 3; Figure 8G).

3.7 | Influence of Morphology Versus Food Type

The morphology has a highly significant influence on the duration of the cycle duration, the FC, the slow open 2, FO phases as well as the PS (Table 4). The food type significantly influences the duration of the cycle time, the FC, the SC, the PS, the slow open 1, and the FO (Table 4). However, the interaction between food type and morphology is significant only for the PS (Table 4), suggesting that the effect of food type is similar for the different morphotypes except for the PS.

4 | Discussion

Previous studies investigating rodent mastication mostly focused on a single species and a singular food type (Hiiemäe and Ardran 1968; Weijs 1975; Weijs and Dantuma 1975; Gorniak 1977; De Vree 1977, 1979; Byrd 1981; McParland et al. 2024), making it difficult to understand how anatomical differences between species impact the kinematics of chewing and how this interacts with variation in food properties. Our study aimed to close this knowledge gap by investigating masticatory movements in four different species of rodents from two different morphological groups and with two different food types. By doing so we, attempt to link differences in the masticatory movements to differences in the morphology of the masticatory apparatus and the different ecologies of the species. We provide evidence that relatively small differences within the conserved rodent cranial *bauplan* can lead to relatively large changes in masticatory movements. Not only the jaw movements, but also the composition of the phases differed between morphotypes (i.e., myomorphous and hystricomorphous groups) suggesting differences in control strategies. Although differences in the trajectories of the masticatory movements were not evaluated directly, differences between the two morphological groups and the two food types are clearly visible (Figures 4–7). In this study, hystricomorphous and myomorphous species can be easily distinguished with the latter species showing less medio-lateral movement during mastication. An additional difference is the absence of unilateral medial cycles in myomorphous species in our dataset.

4.1 | Gape Distance Reduces With Food Hardness

While chewing hard food, the maximum gape distance is smaller compared to feeding on softer foods and only the medio-lateral and propalinal movements increase. However, the difference in gape distance is not significant in *Rattus* (Figures 4–7; and Supporting Information S1: S3; Table 1). This difference in gape distance might be primarily caused by the

TABLE 2 | *p*-Values for the pairwise comparison with Bonferroni correction of the different phases after Kruskal–Wallis test. The tests assed the differences between the phases for each species between soft and hard food.

Food	Species	Phase	FC	SC	PS	SO1	SO2
Apple	*Cavia*	SC	1.00				
		PS	1.00	1.00			
		SO1	< 0.001	< 0.001	< 0.001		
		SO2	0.026	0.079	0.037	1.00	
		FO	0.190	0.241	0.013	< 0.001	0.033
	Mesocricetus	SC	1.00				
		PS	1.00	1.00			
		SO1	1.00	1.00	1.00		
		SO2	1.00	1.00	1.00	1.00	
		FO	1.00	1.00	1.00	0.34	0.29
	Octodon	SC	1.00				
		PS	1.00	1.00			
		SO1	0.280	1.00	0.005		
		SO2	1.00	1.00	1.00	0.202	
		FO	1.00	1.00	1.00	0.110	1.00
	Rattus	SC	1.00				
		PS	1.00	1.00			
		SO1	< 0.001	0.02275	0.00012		
		SO2	0.210	0.95194	0.27683	1.00	
		FO	0.632	1.00	1.00	2.7e-08	0.02417
Sunflower	*Cavia*	SC	0.075				
		PS	< 0.001	< 0.001			
		SO1	< 0.001	1.00	< 0.001		
		SO2	1.00	1.00	0.087	1.00	
		FO	1.00	1.00	< 0.001	0.026	1.00
	Mesocricetus	SC	1.00				
		PS	0.071	0.056			
		SO1	0.371	0.022	1.00		
		SO2	< 0.001	0.005	1.00	0.169	
		FO	1.00	1.00	0.277	0.334	0.006
	Octodon	SC	1.00				
		PS	< 0.001	0.001			
		SO1	0.013	0.336	0.001		
		SO2	0.132	0.543	1.00	0.256	
		FO	0.363	1.00	0.001	0.011	1.00
	Rattus	SC	1.00				
		PS	0.024	0.113			
		SO1	1.00	1.00	0.009		
		SO2	1.00	1.00	1.00	1.00	
		FO	0.901	1.00	0.386	0.192	1.00

Abbreviations: FC, fast close; FO, fast opening; PS, power stroke; SC, slow close; SO1, slow opening 1; SO2, slow opening 2.

different size of the food items. However, it should be noted that all animals typically took bites out of the apple slices using their incisors, reducing the size before mastication. A reason why *Rattus* did not show differences might be because it is an omnivore and adapted to many different food items (Dews et al. 2022). Previous studies have found varying results concerning the impact of food hardness on the range of motion. For both *Cavia* and humans, the largest movements were recorded with relatively hard and ductile items like carrots (Hiiemae et al. 1996; Byrd 1981; Filipić and Keros 2002). Brittle food items, such as pellets or biscuits, might break apart faster. This could potentially reduce the need for larger opening movements, as demonstrated by Byrd (1981) and Hiiemae et al. (1996).

TABLE 3 | *p*-Values for the pairwise comparison with Bonferroni correction for the different species after Kruskal–Wallis test. The tests assed the differences between the duration of each phase for each species for both soft and hard food.

Food	Phase		*Cavia*	*Mesocricetus*	*Octodon*
Apple	CY	*Mesocricetus*	0.004		
		Octodon	0.212	1.00	
		Rattus	< 0.001	< 0.001	< 0.001
	FC	*Mesocricetus*	0.032		
		Octodon	0.042	1.00	
		Rattus	< 0.001	< 0.001	0.005
	SC	*Mesocricetus*	1.00		
		Octodon	0.090	1.00	
		Rattus	< 0.001	1.00	1.00
	PS	*Mesocricetus*	1.00		
		Octodon	1.00	1.00	
		Rattus	< 0.001	0.171	0.003
	SO1	*Mesocricetus*	1.00		
		Octodon	0.003	1.00	
		Rattus	0.530	0.057	< 0.001
	SO2	*Mesocricetus*	1.00		
		Octodon	0.137	0.333	
		Rattus	1.00	0.322	0.006
	FO	*Mesocricetus*	1.00		
		Octodon	1.00	1.00	
		Rattus	0.003	0.182	0.165
Sunflower	CY	*Mesocricetus*	< 0.001		
		Octodon	1.00	< 0.001	
		Rattus	< 0.001	0.004	< 0.001
	FC	*Mesocricetus*	0.032		
		Octodon	0.001	1.00	
		Rattus	< 0.001	0.007	0.036
	SC	*Mesocricetus*	1.00		
		Octodon	1.00	0.689	
		Rattus	0.917	0.093	1.00
	PS	*Mesocricetus*	< 0.001		
		Octodon	0.041	< 0.001	
		Rattus	0.036	0.025	0.013
	SO1	*Mesocricetus*	1.00		
		Octodon	0.15	0.09	
		Rattus	0.22	0.39	1.00
	SO2	*Mesocricetus*	0.321		
		Octodon	0.650	0.055	
		Rattus	1.00	0.600	0.600
	FO	*Mesocricetus*	1.00		
		Octodon	1.00	1.00	
		Rattus	0.017	0.645	0.080

Abbreviations: CY, total duration of a masticatory cycle; FC, fast close; FO, fast opening; PS, power stroke; SC, slow close; SO1, slow opening 1; SO2, slow opening 2.

4.2 | Range of Motion Increases With Harder Food

Although the gape distance is mostly smaller when chewing on harder food, there is a relative increase in the range of motion, especially during the PS. This increase is unlikely caused by a larger food bolus size, since a larger bolus size should increase the gape distance which was not observed. The increase in movement seems to be larger in the hystricomorphous species (Figures 4–7) suggesting that they might not be as well adapted to consuming harder foods as myomorphs. While myomorphs might be adapted better to harder food. Outside of rodents, an

TABLE 4 | Results of the two-way-ANOVA assessing the influence of the food type and morphology on the duration of a masticatory cycle and the masticatory phases.

Phase		*F*-value	*p*
CY	Food	9.995	< 0.001
	Morphology	127.830	< 0.001
	Food: Morphology	3.285	0.071
FC	Food	3.478	0.032
	Morphology	43.105	< 0.001
	Food: Morphology	0.011	0.918
SC	Food	3.703	0.026
	Morphology	3.701	0.056
	Food: Morphology	1.849	0.175
PS	Food	23.64	< 0.001
	Morphology	50.78	< 0.001
	Food: Morphology	18.75	< 0.001
SO1	Food	9.198	< 0.001
	Morphology	2.625	0.107
	Food: Morphology	0.155	0.694
SO2	Food	0.293	0.747
	Morphology	12.172	< 0.001
	Food: Morphology	2.095	0.153
FO	Food	4.082	0.018
	Morphology	13.532	< 0.001
	Food: Morphology	0.572	0.450

Abbreviations: CY, total duration of a masticatory cycle; FC, fast close; FO, fast opening; PS, power stroke; SC, slow close; SO1, slow opening 1; SO2, slow opening 2.

increase in the range of motion during the tooth–food–tooth contact has been also described in pigs (Montuelle et al. 2020). In this case, movements were similar across the food types although there was considerable variation.

The general pattern of masticatory movements during chewing of soft food is consistent across hystricomorphs and aligns with existing literature (Byrd 1981; Vassallo and Verzi 2001; Olivares et al. 2004). However, this changes when chewing on harder foods. In *Octodon*, the predominant cycle type shifts from bilateral alternating to unilateral central while eating sunflower seeds. The cycles resembling the bilateral alternating type are probably performed to switch the direction of the unilateral medial cycles since the bilateral alternating cycles only occur isolated from one another (Figure 5B). In *Cavia*, the masticatory movements while feeding on harder food items do not resemble the ones described in the literature (Byrd 1981), but rather those observed in *Pedetes* with a strong propalinal PS (Figure 4B,D,F; Offermans and de Vree 1990).

4.3 | Food Hardness Influences Phase Durations

Despite some differences, both hystricomorphous species exhibited an increase in the range of motion primarily during the PS when chewing on harder foods. While *Octodon* increases the range motion of the PS in lateral direction, *Cavia* increases the range of motion in a propalinal manner (Figures 4 and 5). An increase in the range of motion in response to harder food has already been described in the literature (Byrd 1981), and is probably caused by the different food properties of the apple slices versus the sunflower seeds as discussed above. This is supported by the fact that both species increase the duration of the PS while feeding on hard food, yet keep a stable cycle duration (Figure 8A,H).

More generally, both hystricomorphous species show the same pattern for the phase durations while feeding on sunflower seeds. Not only is the PS longer than the other phases but also the slow open 1 is shorter than the FC and FO phases (Figure 8B,C,E,G). This indicates that, despite the vastly different movement pattern between both species, they both modify the composition of the masticatory phases in the same way in response to a harder, less favorable food item. Since there are great differences for the FC and PS phases between species, they seem to be species-specific but further research is needed to test this (Figure 8; Supporting Information S1: Table S2). In particular, the FC phase might be used to modulate the total duration of a masticatory cycle, compensating for differences in the other phases, to maintain chewing frequency.

Both myomorphs generally show the same pattern in their masticatory movements which largely aligns with the literature (Figures 4 and 5; Weijs 1975; Weijs and Dantuma 1975; Lazzari et al. 2008; McParland et al. 2024). However, one key difference from previous studies is that occlusion starts in a more lateral position in *Mesocricetus* (Figure 6A; Gorniak 1977). Additionally, not all studies found a change in the degree of propaliny depending on food type (Figure 7C–F; Hiiemäe and Ardran 1968). The greater increase in the propalinal movements during the PS in *Rattus*, while feeding on sunflower seeds, is linked to a longer PS duration in *Rattus* compared to *Mesocricetus* (Figures 5C–F, 7C–F, 8D). However, the comparatively longer PS in *Rattus* does not result in a longer masticatory cycle duration as proposed by Weijs (1975). Together with the prolonged duration of the slow open 2 phase while feeding on apple in *Mesocricetus*, this indicates that *Mesocricetus* may be better adapted to chew hard foods.

Contrary to Weijs' (1975) findings, results from the hystricomorphous species and other mammals, myomorphous species reduce the cycle duration when chewing on harder food items (see Figure 8A; Reed and Ross 2010; Iriarte-Díaz et al. 2011; Montuelle et al. 2018). While the reduced cycle time might be the result of an adaptation toward gnawing in myomorphs, allowing them to break down foods more efficiently at the incisors (Cox et al. 2012), there are also some modifications of the masticatory phases. *Mesocricetus* achieves the shortening of chewing by reducing the duration of the FC, the PS, and the slow open 2 phases, similar to what was observed in macaques, showing similarities across different mammalian groups (Figure 8B,D,F; Thexton and Hiiemae 1997). In contrast to pigs, where the cycle time is prolonged when chewing harder food through longer FC and FO phases (Montuelle et al. 2020), *Rattus* reduces its cycle duration when chewing on harder food by shortening both the FC and FO phases, compared to softer food. Generally, *Rattus* has the shortest cycle and individual phase durations and is able to achieve this by its relatively

simple movements (Figures 7 and 8). The different modification of the masticatory phases, in response to differing food hardness, is likely caused by differences in masticatory trajectories; which in turn are caused by differences in jaw and muscle morphology in *Rattus* and *Mesocricetus* (Satoh and Iwaku 2004; Miljutin 2011).

4.4 | Phase Distribution Is Less Fixed in Myomorphs Than in Hystricomorphs

The occurrence of different masticatory phases appears to be species-specific among hystricomorphous species as there is little variation on how each one performs on either food type (Supporting Information S1: Table S3). As the SO2 phase involves moving the food within the oral cavity, it occurs less frequently than the other phases (Supporting Information S1: Table S3; Gerstner et al. 2010; Da Cunha 2024). In myomorphous species, the occurrence of masticatory phases appears to be less consistent (Supporting Information S1: Table S3). These differences may also be due to the different types of cycles. The unilateral central cycles and the bilateral alternating cycles with more pronounced lateral movements in Hystricomorpha may not allow much variation in the phase occurrence. Hystricomorpha may not allow much variation in the phase occurrence; which is the opposite to what the relatively simpler cycles do in myomorphs.

4.5 | Morphology and Ecology Influence Masticatory Modulation

The differences in the motion patterns between and within the two morphogroups are best explained by synergies of specific morphologies and ecologies. Ecologically, our hystricomorphous species are both herbivorous, feeding mostly on relatively soft herbaceous plants (Edwards 2009; Veiga et al. 2019). Although *Mesocricetus* also feeds on herbaceous plants when available, they are known to hoards seeds for times of reduced food availability whereas *Rattus* is a typical omnivore (Lanier et al. 1974; Dews et al. 2022; Gavril et al. 2023). These differences in food preference may explain why *Mesocricetus* is the species that increases the range of the PS the least and even reduces its duration while feeding on harder foods. These ecological differences are also reflected in the differences between molar morphologies (Lazzari et al. 2008). Hystricomorphs have flatter teeth which enable them to grind down herbaceous plants. Together with their more medio-lateral muscle organization, this may allow them to perform more complex masticatory movements, resulting in longer phase durations (Turnbull 1970; Woods and Boraker 1975; Cox and Jeffery 2011; Böhmer 2015; Álvarez and Pérez 2019; Boivin et al. 2022). In contrast, the molars of myomorphs present cusps and crest, not allowing for the same freedom of movement in hystricomorphs. The cusps and crests of the murine rodents (i.e., *Rattus*) facilitate strong propalinal movements, whereas the molar morphology of *Mesocricetus* does not (Lazzari et al. 2008). Moreover, these morphological differences might be linked to the diversity in muscle architecture and the relatively higher mandibular condyle in the Cricetinae; which further supports the differences in propaliny and medio-lateral jaw movements between *Rattus* and *Mesocricetus* (Satoh and Iwaku 2004; Hautier et al. 2010; Hautier et al. 2011; Miljutin 2011; Álvarez and Pérez 2019).

Similarly, the shift from a medio-lateral to a propalinal PS in *Cavia* can be explained by a relatively lower mandibular condyle in comparison to *Octodon*, together with a more anterior-posterior muscle organization (Greaves 1980; Vassallo and Verzi 2001; Hautier et al. 2011; Álvarez and Pérez 2019). These morphological differences allow *Cavia* to efficiently change their direction of the PS from medio-lateral to propalinal, since a lower mandibular condyle in combination with a more anterior-posterior muscle organization facilitates propalinal jaw movements (Greaves 1980; Hautier et al. 2010). *Octodon* with its more medio-lateral muscle organization and higher mandibular condyle is able to sufficiently increase the range of the PS in lateral direction in response to harder foods. Generally, hystricomorphs exhibit longer masticatory cycles and cycles with longer durations for their individual phases compared to the myomorphs (Figure 8). This might be partially caused by allometric differences, since as smaller animals have generally higher chewing frequencies than larger ones (Druzinsky 1993). However, there also seems to be differences caused by the morphology, since the size of *Rattus* is intermediate between *Cavia* and *Octodon* (Supporting Information S1: Table S1). One explanation might be that the movements of myomorphs are less complex allowing for faster movements.

Even though there are differences in phase duration between species within a morphogroup that can be explained by morphological and ecological differences, the ANOVA suggests, that these differences in phase duration between both groups are important (Table 4). Differences in cranial morphotypes appear to be a better predictor for the duration of phases than for the food type, except for the SC and slow open 1 phases. These two phases are positioned directly before and after the PS, or they represent the main phase for tooth-food-tooth contact when the PS is absent (Table 4). Perhaps both, soft and hard food items, require similar handling within the oral cavity before and after being crushed. However, the interaction between food type and morphology is only a reliable predictor for the PS which is crucial for crushing food and depends on molar morphology (Olivares et al. 2004; Lazzari et al. 2008; Gerstner et al. 2010; Boivin et al. 2022). Since microwear patterns are formed during the PS, the types of food the animals consumed are important for interpreting these patterns (Hylander et al. 1987; Olivares et al. 2004). This is particularly true for omnivorous species or species with seasonal changes in their diets (Robinet et al. 2020; Robinet et al. 2022).

4.6 | Limitations

The most obvious limitation of our study is the fact that sciuromorphous rodents were not included. Another limitation is that, in the species in our study, myomorphy and hystricomorphy evolved within monophyletic groups, even though both conditions have independently evolved multiples times (Wood 1965; Huchon et al. 2002; Adkins et al. 2003; Blanga-Kanfi et al. 2009; Luckett and Hartenberger 2013). Additionally, we only investigated two species of each group, restricting our

assumptions. Both points should be addressed in future studies. Whereas differences between previous studies and our current analysis may be due to differences in frame rates, filming at 400 fps enabled us to achieve a sufficient temporal resolution of masticatory movements, which should, thus, accurately represent the motion of the mandible in these species. Yet, phase discriminations are an issue for all studies of masticatory movements, since methodological differences may impede comparability. For example, in many studies no method for phase discrimination is mentioned, rendering comparisons more difficult and subjective (Thexton et al. 1980; Offermans and de Vree 1990; Yamada and Yamamura 1996; Thexton and Hiiemae 1997). Montuelle et al. (2018, 2020) developed a protocol for phase discrimination based on changes in acceleration, gape distance, and jaw yaw (rotation of the mandible around a dorsoventral axis). They categorized mastication into four phases: FC, SC, SO, and FO. We adopted this protocol because it is the most objective and reproducible. However, we had to alter it due to the presence of the PS and SO2 phases in our data. Additionally, because of the extensive propalinal movements, especially in *Cavia* feeding on sunflower seeds, we had to manually check and correct the phase discriminations. We recommend that future studies should use the phase separation protocol developed by Montuelle et al. (2018, 2020) and alter it where needed.

5 | Conclusion

Our first hypothesis, linking movement patterns to morphology was confirmed. In contrast to hystricomorphs, myomorphs do not show unilateral central cycles in the here studied species. Additionally, both groups modify their masticatory patterns differently in response to different food items. The three main ways in which the rodents studied here modify their chewing in response to different food items were: (i) minor changes of the movement pattern, similar chewing frequency and modulation of the masticatory phases as observed in *Octodon*; (ii) minor changes of the movement pattern, modified chewing frequency and modulation of the masticatory phases as observed in the two myomorph rodents studied here; and (iii) great changes in the movement pattern, similar chewing frequency and modulation of the masticatory phases as observed in *Cavia*. Our second hypothesis, which stated that the composition of masticatory phases changes in response to the food type was also confirmed. In hystricomorph species, however, different food items altered the composition of the masticatory cycles in different ways, alongside large differences in the movement patterns, also confirming our third hypothesis. Additionally, we inferred that, contrary to ungulates, propalinal jaw movements are associated with a lower mandibular condyle in the species studied here. Future work should therefore expand the dataset to include other myomorph and hystricomorph species, particularly those from distant clades. Sciuromorphous species should also be included to provide a fuller picture of masticatory movements in rodents, further linking anatomical differences to movement patterns.

Author Contributions

Simon Sommerfeld: visualization, writing – review and editing, writing – original draft, formal analysis, investigation. **Lea Da Cunha:** investigation, writing – review and editing, visualization. **Lionel Hautier:** writing – review and editing, supervision, conceptualization, visualization. **Anthony Herrel:** conceptualization, writing – original draft, writing – review and editing, supervision, visualization.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Table S1: Morphometric data of the animals used.

Table S2: Dosages of the anesthesia. Dosages of the two drugs used for anesthesia and of the reversal agent for each species.

Table S3: Absolute and relative occurrence of the masticatory phases per cycle as well as mean duration and standard deviation of the durations.

Movie S1: *Rattus norvegicus* feeding. Video of *Rattus* feeding, first dorso-ventral view, second lateral view.

Movie S2: *Cavia porcellus* feeding. Video of *Cavia* feeding, first dorso-ventral view, second lateral view.