Teaser text

The scale-eating cichlid fish *Perissodus microlepis*, from Lake Tanganyika in Africa, is an excellent model for studying animal lateralization. However, how environmental factors shape this pronounced asymmetry remains unclear. Here, we investigated changes in craniofacial morphology under different foraging conditions to assess the impact of phenotypic plasticity on left–right mandibular differences. By comparing individuals reared on granulated feed with those that foraged on fish scales, we provide direct evidence that feeding experience influences mandibular asymmetry. These findings offer new insights into the interplay between behaviour, morphology, and ecological adaptation, shedding light on the mechanisms underlying lateralized traits in cichlids.

Abstract

Phenotypic plasticity, in which traits change in response to environmental conditions, is closely related to predator–prey interactions and speciation. The scale-eating cichlid fish *Perissodus microlepis* exhibits marked left–right differences in predatory behaviour and mouth morphology. While phenotypic plasticity is hypothesized to contribute to the formation of laterality, direct evidence remains scarce. We examined how plasticity shapes laterality by analysing the predatory behaviour and mandibular changes under different foraging conditions: picking granulated feed (non-scale-eating) and tearing scales from prey fish. During the predation experiment, the number of attacks increased over time. Behavioural analysis revealed the mean inter-individual distance from scale-eater to prey gradually decreased, whereas mean swimming activity increased. Morphological analysis of the mandible showed elongation of the dentary bone along the anterior–posterior axis in the scale-eating groups compared to the non-scale-eating group. Furthermore, mandible height was significantly greater on the dominant side, with the degree of asymmetry increasing with scale-eating experience. This strongly suggests that phenotypic plasticity contributes to the enhancement of laterality and promotes disruptive selection of lateral morphs. This study advances our understanding of the unique adaptation in *P. microlepis* and highlights the importance of feeding experience in shaping

adaptive traits within the cichlid lineage.

Keywords: phenotypic plasticity, cichlids, morphometrics, asymmetry, polymorphism, predation

Introduction

Phenotypic plasticity—the ability of an individual organism to alter its phenotype in direct response to environmental changes— plays diverse roles in ecology and evolution. These roles range from enabling populations to persist in new and changing environments to contributing to the evolutionary origins of novel phenotypes (Agrawal et al., 1999; Pigliucci & Hayden, 2001; Dewitt & Scheiner, 2004). Many species exhibit phenotypic changes that enhance their ability to avoid predation or make available underutilized resources (reviewed by Pfennig & Pfennig, 2012). In a predator–prey relationship, both predator and prey can undergo morphological changes. For example, the mollusc *Thais lamellosa* thickens its shell and develops denticles at the aperture when exposed to water containing the predator crab *Cancer productus* (Palmer, 1985). Couch's spadefoot toad (*Scaphiopus couchii*) develops shorter guts when fed shrimp—a novel diet for this species—compared to its typical detritus diet (Ledon-Rettig et al., 2008; 2010; Levis et

al., 2018). Similarly, *Scaphiopus holbrookii* exhibits diet-dependent plasticity in several traits characteristic of the carnivore morph in *Spea* tadpoles, including in gut length, denticle rows, and mouthparts (Levis et al., 2018). Thus, organisms can modify their morphology, physiology, and behaviour in response to environmental conditions during ontogeny (Svanback & Bolnick, 2007; Svanbäck et al., 2008).

Phenotypic plasticity in feeding morphology, particularly in response to food quality and quantity, is an area of ongoing experimental investigation (Mori & Vincent, 2008; Segall et al., 2016). Brecko et al. (2011) found evidence of differences in head size and shape of dice snakes (*Natrix tessellate*) with those that consumed fish having narrower heads—an adaptation likely advantageous for capturing prey in water—compared to snakes that fed on frogs. The mechanical effects of diet on occlusion and mastication may drive morphological differences in the cranial skeleton within a species. The vertebrate skeleton, which has plastic characteristics, can change in size and shape depending on external influences. For example, diet consumption during development has been linked to morphological features of the skull in grizzly bears (*Ursus arctos*) (Mowat & Heard, 2006). Additionally, Amur tigers (*Panthera tigris altaica*) exhibit differences in skull shape, such as in the sagittal crest, skull width, and rostral height, between captive and wild individuals (Cooper et al., 2022). High forces will be exerted

on this predator's cranial traits as it chews through the tough skin, muscle, and hard bones of its prey. Therefore, cranial traits are likely to be affected by a plastic response to the demands of catching and consuming prey, influenced by factors such as prey size, hardness, mobility, and abundance encountered during ontogeny. This diversification of feeding modes is a significant driver of species diversity and has been recognized in several large-scale adaptive radiations, including Darwin's finches, Hawaiian honeyeaters, and cichlids.

The cichlid fishes of South American and African lakes are a valuable model of rapid adaptive radiation, demonstrating extraordinary species diversity and ecological specialization. Their dietary preferences that correspond closely to the morphology of their mouthparts, with both interspecific and intraspecific variations observed (Fryer & Iles, 1972). Cichlids have also long served as a model for studying phenotypic plasticity, with well-documented plastic responses in morphological traits such as craniofacial structure, oral jaws, and pharyngeal jaws (Meyer, 1987; Muschick et al., 2011; Gunter et al., 2013; Parsons et al., 2014; Singh et al., 2017). In Malawi cichlids, including *Tropheops sp.*, differences in foraging conditions have been shown to induce plastic changes in trophic morphology. Recent studies have further investigated the molecular mechanisms of this plasticity, revealing that the response is mediated by

83 mechanosensitive pathways involving hedgehog signalling (Parsons et al., 2016; Hu &
84 Albertson, 2017; Navon, 2020; Tetrault et al., 2023; 2024).

85 Another intriguing aspect of cichlid mouthpart morphology is the left–right
86 difference in the mandible (Hori et al., 2017). Individuals with a larger right mandible
87 open their mouths to the left when viewed dorsally, while those with a larger left mandible
88 open their mouths to the right. This asymmetry varies in degree depending on diet, with
89 those scale-eating fish that forage prey fish by tearing their scales off showing the most
90 pronounced left–right difference (Takeuchi et al., 2019). Morphometric analysis of the
91 mandibles in the genus *Perissodini*, a known group of scale-eating fish from Lake
92 Tanganyika, revealed that *P. microlepis* exhibits particularly large left–right differences
93 (Stewart & Albertson, 2010). In *P. microlepis*, individuals with greater mandibular
94 asymmetry were found to have more scales in their stomachs, indicating that this
95 asymmetric trait enhances feeding efficiency (Takeuchi et al., 2016). The mechanical
96 demands of tearing and consuming the hard scales on the lateral side of prey would
97 asymmetrically affect the mandible and skull, leading to distorted morphological changes.
98 Since the fish shift from a plankton to a scale diet during their growth, as their body size
99 increases, the left–right asymmetry of the mandibles becomes more pronounced
100 (Nshombo et al., 1985; Takeuchi et al., 2016). This suggests that diet-dependent

101 phenotypic plasticity may play a crucial role in the development of mandibular
102 asymmetry in scale-eating cichlids.

103 In this study, we quantitatively examined changes in mandibular morphology under
104 different foraging conditions to assess the effect of phenotypic plasticity on left–right
105 differences in the mandibles of the scale-eating fish *Perissodus microlepis*. To our
106 knowledge, previous studies have focused on the plasticity of feeding morphology in
107 response to food resources, but few have specifically investigated its impact on skeletal
108 left–right differences. By analysing the individuals within genetically similar
109 backgrounds, we aimed to assess the effects of phenotypic plasticity. Additionally,
110 previous studies (Takeuchi et al., 2022; Takeuchi, 2023) demonstrated that scale-eating
111 fish acquire attack-side preference through scale-eating experience during early
112 development. However, other details of changes in predatory behaviour still remain
113 obscure. Therefore, we also measured changes in predatory behaviour associated with
114 scale-eating experiences. Such body asymmetry and behavioural laterality are widespread
115 among vertebrates and appear to have emerged early in their evolutionary history (Rogers
116 et al. 2013). A fundamental organizational plan is shared across diverse animals: left-right
117 asymmetry in the nervous system serves as a general principle, forming the basis for a
118 wide range of lateralized behaviours (Rogers 2015; Vallortigara & Vitiello 2024). This

119 study will contribute to our understanding on how phenotypic lateral variation within a
120 species can be shaped and evolve through interactions with the external environment,
121 such as individual experience.
122
123 **Materials and Methods**
124 **Subjects**
125 The scale-eaters used in our study were bred in our laboratory with help of the World
126 Freshwater Aquarium Aquatotto Gifu in Japan. Broodstock were collected from Lake
127 Tanganyika (Cameron Bay, Zambia; 8°29′S, 30°27′E) and transported to Japan by a fish
128 dealer. Offspring from a single wild-caught pair were used in the experiments, and thus
129 were assumed to exhibit low genetic diversity. Prey 2, Prey 1, and Non-scale-eating
130 groups were siblings, respectively. The fish were maintained at 27℃, pH 8.3, and a 12
131 h:12 h light:dark photoperiod with light provided by a 32 W fluorescent light.
132
133 **Predation experiments**
134 We prepared three groups of specimens with different levels of scale-eating experience
135 (Fig. 1A). First, a control group with no scale-eating experience was isolated in small
136 tanks (25 × 8 × 15 cm) after hatching and reared on artificial feed only until 8 months old

(hereafter referred to as “Non-scale-eating group”; standard length (SL): 51.5 ± 0.6 mm, $N = 29$). The other scale-eating fish were fed only granulated artificial feed twice daily in a rearing tank (90 × 45 × 45 cm) from hatching to 4 months old. Scale-eating fish group at 4 months old reached roughly SL 35 mm. This body size corresponds to the size at which they begin scale-eating in the field (Nshombo et al., 1985; Takeuchi et al., 2016). One prey fish, a goldfish (50–60 mm SL), was introduced into the rearing tank of that scale-eating fish for 10 minutes every day for the following 4 months, during which time the fish was allowed to feed freely (hereafter, “Prey 1 group”; SL: 48.8 ± 0.7 mm, $N = 21$). For 10 minutes after the introduction of the prey fish, the predation events were recorded from the side of the tank with a digital video camera (HDR-XR550V, SONY, resolution: 1920 × 1080 pixels, 30 frames/second) (Fig. 1B). The prey fish was captured 10 minutes after its introduction and returned to the home tank. A new prey fish was introduced each time. In addition, at 4 months old, another group was fed two prey fish for 10 minutes daily up to 8 months old (hereafter referred to as the “Prey 2 group”; SL: 49.9 ± 0.6 mm, $N = 23$, Fig. 1A). The predation experiments were conducted daily for 127 days from the start, and predation was recorded every few days with a video camera; 32 videos of the Prey 1 group and 29 videos of the Prey 2 group were obtained. We counted the number of attacks during a 10-minute period based on video data. When a

scale-eating fish attacked and came into contact with a prey fish, the prey fish responded C-bend of its body and swam away quickly, so we could accurately determine whether the predation was a success or failure.

Analysis of behavioural change using image-processing and deep-learning methods

To detect the position of each scale-eating fish and prey fish in the tank, we fine-tuned the pre-trained neural network YOLO v3 (Redmon, 2018) on our dataset taken from the predation experiment. For making the training dataset, we recorded the predation experiment for about 30 seconds and split this video into frames. For every four frames, 122 scenes were selected, and all scale-eating fish and prey fish were tagged using the software for annotation, VoTT (Fig. 1C). The 122 annotated scenes were split into training (75%) and validation (25%) data. Using this dataset, the fine-tuning of the neural network was performed for 100 epochs with default hyperparameter settings. We ran inference on 72 videos using the fine-tuned network, outputting the coordinates of each scale-eating fish and prey fish in the tank for each frame of each video. To determine changes in predation behaviour with scale-eating experience, we took the coordinates during the first minute after the introduction of prey and calculated the inter-individual distance between them.

Moreover, using optical flow, we calculated the swimming activity of scale-eating fish, defined as the total swimming distance of the fish in the movie. Optical flow is an image-processing technique that calculates the differences in bright patterns between consecutive video frames, representing the direction and magnitude of movement of objects, surfaces, and edges across captured images. If only optical flow is applied to video frames, the movements of structures in the water tank other than the fish, such as aquatic plants, and aeration bubbles will be captured. In this study, we applied optical flow to the coordinates of scale-eating fish inferred by our fine-tuned neural network and succeeded in visualizing only the movements of scale-eating fish in the tank (Fig. 1D). The swimming activity of prey fish was also analysed using the same method.

The detection of positions of scale-eating fish and prey fish and the calculations concerning the swimming activity of scale-eating fish were performed on Windows 10 and WinPython 3.7.41. For training and inference by YOLO v3, the necessary packages were installed through the keras-yolo3 repository (https://github.com/qqwweee/keras-yolo3). To calculate optical flow, we used the OpenCV package and adopted the Shi–Tomasi and Lucas–Kanade methods implemented in this package. To analyse the relationship between the number of experimental days and inter-individual distance or swimming activity of scale-eater, we divided the experimental period into three phases

191 (1–50 days, 51–90 days, and 91–127 days) and assessed the trend using Spearman's rank
192 correlation.
193
194 **Morphometric analysis of the lower jawbone**
195 To assess the morphological features of the mouth of *P. microlepis*, we performed a
196 geometric morphometric analysis on the lower jawbone. At 8 months old, fish in the three
197 scale-eating groups described above were killed by an overdose of 0.2% tricaine
198 methanesulfonate (MS-222; Sigma-Aldrich, St. Louis, MO, USA). The lower jawbones
199 of specimens were carefully denuded of any adhering soft tissue according to Takeuchi et
200 al. (2016). We took digital photographs of the left and right lower jawbones using a digital
201 microscope with image analysis software (VHX-2000; Keyence, Osaka, Japan). We
202 plotted nine landmarks for each lower jawbone using the software tpsUtil and tpsDig2
203 (Rohlf, 2009, 2010) (Fig. 2). Landmarks were standardized among individuals via
204 Procrustes analysis (Rohlf & Slice, 1990) using MorphoJ software (version 2.0,
205 Klingenberg, 2011), and then a principal component analysis (PCA) was conducted on
206 those morphometric data to calculate the values of the first principal component (PC1)
207 and the second principal component (PC2) of each sample. To visualize the differences
208 between the three groups on PC1 and PC2 axes, we created a wireframe.

The geometric morphometric data were subjected to a Generalized Procrustes Analysis (GPA; Goodall, 1991) using the geomorph package (Adams & Otárola-Castillo, 2013) in R version 4.5.0 (R Core Team, 2021). GPA decomposes organismal form into two components, size and shape, removing non-shape variation due to differences in position, orientation, and scale. This process was performed by gpagen function, and centroid size and Procrustes coordinates were generated. Centroid size was calculated as the square root of the sum of squared distances from each landmark to the centroid, representing overall size (Zelditch et al., 2004). To assess the effect of foraging conditions (e.g., Prey 2, Prey 1, Non-scale-eating), laterality (dominant vs. non-dominant), and individual on shape variation, we conducted a Procrustes ANOVA on Procrustes coordinates, using procD.lm function. To assess potential influence of allometry on shape, log-transformed centroid size (logCS) was also added in the Procrustes ANOVA model. Pairwise comparisons of Procrustes coordinates among foraging conditions were performed using functions from the RRPP package (Collyer & Adams, 2018).

Furthermore, we measured the length of the entire posterior dimension of each lower jaw (referred to as mandibular height, Fig. 2). The asymmetry index was quantified using the formula:

$$(Height\ R\ -Height\ L)/((Height\ R + Height\ L) \div 2) \times 100$$

227 Thus, fish with an index > 0 were designated as righties (i.e., the right lower jawbone is
228 larger than the left lower jawbone), and those with an index < 0 were designated as lefties
229 (the left lower jawbone is larger than the right lower jawbone). Morphological features
230 can be asymmetrical in three ways, namely, fluctuating asymmetry (FA), directional
231 asymmetry (DA), and antisymmetry (AS) (Palmer & Strobeck, 1986). We performed
232 model selection to determine which of these was most like the asymmetry seen in mouth
233 morphology and to generate an index of asymmetry distribution (Package “IASD” in R,
234 detailed in Hata et al. 2013). The FA model assumes that the data have a normal
235 distribution with a mean of zero ($\mu = 0$) and a standard deviation ($\pm$ SD), whereas the DA
236 model assumes a non-zero mean ($\mu \neq 0$) $\pm$ SD. The AS model is based on a bimodal
237 distribution composed of an unequally weighted mixture of two normal distributions with
238 means $\pm \mu$ ($\neq 0$) $\pm$ SD. In these three models, μ, SD, and the fraction of righties or lefties
239 were calculated using maximum likelihood estimation. We applied Akaike's information
240 criterion (AIC) to each of the three models (FA model, DA model, and AS model) to
241 identify the model with the lowest AIC, which is considered the best distribution type.
242 Moreover, the deviation of each distribution from a normal distribution was examined
243 using the Shapiro–Wilk test. Finally, we compared the absolute values of the asymmetry
244 index in the Non-scale-eating, Prey 1, and Prey 2 groups using the Tukey–Kramer HSD

245 test. Using the same methods, left–right differences in mandibular height were measured
246 in cichlids collected in Lake Tanganyika (wild-caught fish) and in breeding cichlids in the
247 laboratory with no scale-eating experience (isolated-rearing fish), and these two groups
248 were compared (see Supplemental text).

249 All experimental procedures were approved by the Toyama University Committee
250 on Animal Research (Approval # A2021MED-21), and the experimental methods were
251 carried out in accordance with the approved guidelines.

252

253 **Results**

254 **Changes in predation behaviour related to scale-eating experience**

255 *P. microlepis* exhibited predatory behaviour, removing scales from prey fish in the tank
256 similarly to their behaviour in the field. The median inter-individual distance between
257 scale-eater and prey fish was analysed in relation to the number of experimental days,
258 excluding data from the first to the fifth day of the experiment due to the minimal number
259 of attacks during this period (Fig. 3A). In both Prey 1 and 2 groups, the inter-individual
260 distance decreased over the experimental days (Spearman's rank correlation, Prey 1
261 group: $\rho = -0.439$, $P = 0.014$; Prey 2 group: $\rho = -0.503$, $P = 0.008$). This indicates that
262 as the scale-eating fish gained experience, they were prepared to swim progressively

263 closer to their prey fish in the early stages leading up to an attack. Moreover, the
264 swimming activity of scale-eating fish, measured via optical flow analysis, increased
265 steadily throughout the experimental period (Fig. 3B, Spearman's rank correlation, Prey
266 1 group: $\rho = 0.702$, $P < 0.001$; Prey 2 group: $\rho = 0.703$, $P < 0.001$). During the initial 50
267 days, no difference in the mean swimming activity was observed between the Prey 1 and
268 Prey 2 groups (Wilcoxon rank sum test, $z = 0.945$, $P = 0.345$). However, from day 51 to
269 90, the swimming activity of the Prey 2 group was significantly higher than that of the
270 Prey 1 group ($z = 2.340$, $P = 0.019$), and this trend continued during days 91–128 ($z =$
271 2.654, $P = 0.008$). Similarly, goldfish exhibited increased swimming activity over the
272 experimental days in both groups (Fig. S1). During the 10-minute period described above,
273 the number of attacks increased for both groups, starting around 10 days and reaching a
274 plateau around day 40 for the Prey 1 group and day 50 for the Prey 2 group (Fig. 3C).
275 Notably, focusing on the number of attacks in the first minute of the experiment, both
276 groups showed a linear increase over time. This suggests that the predation behaviour
277 immediately after the start of the experiment was strongly influenced by feeding
278 experience (Fig. 3D).
279
280 **Morphological changes in the mandible and increase in left–right differences related**

to scale-eating experience

Geometric morphometrics revealed significant differences on jaw shape among the groups with varying scale-eating experiences. Procrustes ANOVA showed significant effect of foraging conditions, laterality, individuals and log-transformed centroid size (logCS) (Table 1). The significant effect of logCS indicates that the jaw shape had allometry and our Procrustes ANOVA model accounts for the allometric effect. The subsequent pairwise comparison showed that significant morphological differences were detected between all groups (Prey 2 vs. Prey 1, Prey 2 vs. Non-scale-eating, and Prey 1 vs. Non-scale-eating; Table 2).

These results were visualized by PCA analysis, which showed a clear separation of the mandibular shape between different foraging conditions along the PC1 axis (Fig. 4A). The wireframe representation coordinate changes for different PC1 values highlighted the most prominent alterations in the distance between landmarks 1 and 3, corresponding to the length of the dentary. Additionally, the depth at the distal end of the denticles, represented by the distance between landmarks 1 and 9, was largely increased. The lower jawbone of the Prey 2 group exhibited elongation in the dentary bone, especially along the anterior–posterior axis, in comparison to the Non-scale-eating group (Fig. 4B). Differences in PC2 were observed between the dominant and non-dominant sides (Fig.

299 4A). The most pronounced change involved the distance between landmarks 3 and 6,
300 representing the mandibular height (the distance from the upper end of the dentary bone
301 to the lower end of the posterior articular bone). This distance was greater on the dominant
302 side compared to the non-dominant side (Fig. 4B).

303 Next, we quantified the left–right differences in mandibular height across the three
304 groups of specimens. Frequency distributions of the asymmetry index revealed a distinct
305 bimodal distribution in all groups, which best fit the AS model (Fig 5A). Furthermore,
306 this distribution significantly deviated from a unimodal distribution (Shapiro–Wilk test:
307 Non-scale-eating group: $W = 0.914$, $P = 0.022$; Prey 1 fish group: $W = 0.895$, $P = 0.028$;
308 Prey 2 fish group: $W = 0.897$, $P = 0.022$). When comparing the absolute values of the
309 asymmetry index among the three groups, the left–right difference between the Prey 1
310 and 2 groups was significantly greater than in the Non-scale-eating group (Tukey HSD
311 test, $P < 0.05$, Fig. 5B). These results suggest that feeding experience increases the left–
312 right difference in the mandible. To further test this hypothesis, we compared the
313 mandibles of wild-caught fish, presumed to have extensive scale-eating experience, with
314 those of isolated-rearing fish, which had no scale-eating experience. The left–right
315 difference in wild-caught fish was approximately three times larger than that of isolated-
316 rearing fish (Fig. S2). Taken together, our anatomical analyses indicate that mandible

shape is plastic, both in functionally relevant bone lengths and in whole shape of mandible.

Discussion

In this study, we investigated how predatory behaviour and mandibular morphology change with scale-eating experience to assess the role of phenotypic plasticity in the laterality of *P. microlepis*. Four-month-old individuals from three sibling groups, each bred from different parents, were reared for four additional months under different feeding conditions; one group was fed granulated food (Non-scale-eating group), and the other two groups foraged on scales from prey fish (Prey 1 group and Prey 2 group). Behavioural analysis revealed the following findings: (1) the inter-individual distance between the scale-eating fish and the prey lessened over time, indicating improved efficiency in approaching the prey; (2) the swimming activity of both the scale-eaters and the prey increased progressively, reflecting dynamic interactions between predator and prey; (3) the number of attacks during the 10-minute experiment increased in both scale-eating groups, with a particularly dramatic increase in the first minute of the experiment, suggesting that scale-eating fish hone their predatory behaviour to optimize feeding opportunities over time. Geometric morphometrics of mandibles revealed significant differences in the anterior–posterior axis length of the dentary bone among the three

groups with different feeding experience. Additionally, notable left–right differences in mandibular morphology were observed between the dominant and non-dominant side. Specifically, two key landmarks—upper end of dentary bone (landmark 3) and posterior end of posterior articular bone (landmark 6)—exhibited significant positional differences. Lengthening of the tooth-bearing region of the dentary bone may increases contact with the prey fish's body in predation, allowing more scales to be torn off. Measurement of mandible height showed that the asymmetry of the Prey 1 and 2 groups was significantly greater than that of the Non-scale-eating group. The distance between the two abovementioned key landmarks (landmark 3 and landmark 6) corresponds to a key metric used in previous studies (Takeuchi et al., 2016; Takeuchi et al., 2022), confirming that this measurement adequately captures left–right differences in the lower jawbone. Environmental stimuli, such as feeding experience, may drive the development of asymmetric traits in scale-eating fish.

Cichlids, known for their extraordinary species diversity, display significant variation in mouth morphology across the group (Stiassny et al., 2007). The type and availability of food resources are thought to drive morphological variation in some cichlid species (Parsons et al., 2016; Hu & Albertson, 2017; Navon, 2020; Tetrault et al., 2023; 2024). Feeding conditions can influence the morphological appearance of the mouthparts

353 in *P. microlepis* (van Dooren et al. 2010). In this study, we not only corroborated findings
354 from previous studies, but also further demonstrated that scale-eating experience
355 amplifies mandibular asymmetry in scale-eating fish. This mandibular asymmetry is
356 believed to improve individual fitness by influencing the direction and strength of mouth
357 opening, which is linked to enhanced feeding efficiency (Hori et al., 2007). Although
358 genetic factors are involved in determining the laterality of *P. microlepis* (Stewart &
359 Albertson, 2010; Raffini et al., 2017; Raffini et al., 2018), since this study is used in the
360 offsprings of the same lineage with low genetic diversity, the differences in morphology
361 here can be attributed to environmental conditions rather than genetic differences. This
362 finding suggests that phenotypic plasticity enhances laterality and may facilitate the
363 disruptive selection underlying lateral morph (Rueffler et al.2006; Takeuchi et al. 2016;
364 Indermaur et al. 2018).

365 One study examining left–right differences in head morphology across all 62 orders
366 of fish showed that the degree of asymmetry tends to cluster phylogenetically. Ancient
367 fish exhibit larger left–right differences, while "modern" fishes, such as Perciforms,
368 display a smaller degrees of asymmetry (Hori et al., 2017). However, *P. microlepis*,
369 despite being Perciform, demonstrates one of the most pronounced cases of asymmetry
370 among fishes (Hata et al., 2013). In contrast, other cichlids with differing feeding habits,

371 such as the algal feeder *Variabilichromis moorii* from Lake Tanganyika (Hori et al., 2007),
372 the shrimp eater *Neolamprologus fasciatus* from Lake Tanganyika (Takeuchi & Hori,
373 2008), and the fin biter *Genyochromis mento* from Lake Malawi (Takeuchi et al., 2019),
374 show relatively little asymmetry compared to that of *P. microlepis*. This suggests a strong
375 correlation between feeding habits and the degree of left–right differences in mandibular
376 morphology. Taken together, the scale-eating strategy may require pronounced left–right
377 differences, and this appears to develop during ontogeny through a combination of plastic
378 responses and potential genetic factors. At an early developmental stage (juveniles), *P.*
379 *microlepis* exhibits levels of mandibular asymmetry comparable to those of other
380 Perciforms, but the mandibular asymmetry becomes significantly amplified as the fish
381 grows (Takeuchi et al., 2016). Our results provide insights into the mechanisms
382 underlying the development of specialized morphology and represent an important
383 advance in our understanding of the evolutionary processes promoted by laterality.

384 The mandible shape of scale-eating fish shifted to an acutorostral shape in response
385 to scale-eating experience (Fig. 5). While the granulated food fed to the Non-scale-eating
386 group can be consumed with slow and relatively effortless movements, the scale-eating
387 experienced groups must actively pursue their escaping prey, attack the side of their prey's
388 body, and tear off scales. This morphological change to the jaw may enhance the

389 efficiency of scale capture and consumption. Although differences in nutrients between
390 scales and artificial feed could potentially influence these morphological changes, no
391 significant difference in body size was observed across the three groups. The relationship
392 between feeding experience and change of the cranial skeleton has been reported in
393 various animals. For instance, tiger snakes (*Notechis scutatus*) exhibit elongated
394 mandibular bones when experimentally fed on large victims (Aubret et al., 2004).
395 Similarly, wild continental tigers (*Panthera tigris tigris*) were found to have mandibles
396 with higher angular projections compared to those of captive individuals that were fed on
397 animal carcasses (Cooper et al., 2022); this higher angular projection supports the
398 development of a larger and more effective temporalis muscle, enabling a stronger bite
399 force. The mechanical load of predation—such as prey pursuit, prey handling, and
400 masticatory movements—is likely to induce phenotypic plasticity in skeletal
401 morphology; that is, phenotypic plasticity plays a major role in predator–prey
402 relationships (e.g., Miner et al., 2005; Kishida et al., 2014). The findings of our study
403 shed light on predator-specific feeding movements and how mechanical loads contribute
404 to bone remodelling. This hypothesis is further supported by comparisons of mandibular
405 height between rearing and wild-caught individuals of *P. microlepis* (Fig. S2). Scale-
406 eating is a rare and highly specialized feeding strategy among fishes, with relatively few

407 competitors exploiting the same resources. However, this feeding mode imposes
408 significant ecological demands, requiring specialized morphology and behaviour, which
409 are likely shaped by selection pressure within a nutrient-poor environment (Keenleyside,
410 2012; Martin & Wainwright, 2013). The ability of *P. microlepis* to respond flexibly to
411 environmental challenges through phenotypic plasticity likely plays a central role in
412 meeting these demands.

413 The molecular mechanisms regulating the phenotypic plasticity that confers
414 predation advantage remain a compelling avenue for exploration. In other cichlids, recent
415 research has revealed that upregulation of the hedgehog gene (Hh signal) and the function
416 of primary cilia play a pivotal role in driving plastic morphological changes in the oral
417 jaw skeleton (Navon et al., 2020; Gilbert et al. 2021). Hh signalling may influence bone
418 deposition rates, allowing a change in mouth morphology. Thus, it would be highly
419 valuable to investigate the relationship between Hh signalling and the mandible
420 asymmetry observed in *P. microlepis*. Specifically, it would be critical to determine if
421 asymmetric bone growth on the dominant side is mediated by localized upregulation of
422 Hh pathway genes and whether this pathway operates differently in lefty and righty
423 morphs, potentially linking molecular signalling with behavioural laterality. Interestingly,
424 the scale-eating experience in *P. microlepis* has been shown to alter attack side preference

425 only during the early developmental stage (Takeuchi et al., 2022). This suggests that
426 developmental-stage-dependent constraints may limit the plasticity of mandibular
427 asymmetry. Moreover, while our findings indicate a unidirectional change in mandibular
428 morphology—from weak to strong asymmetry—with scale-eating experience, it remains
429 unclear whether this asymmetry is reversible. For instance, reverting to a diet of
430 granulated food may potentially reduce or shift mandibular asymmetry. Testing this
431 hypothesis would provide critical evidence on whether plastic traits, such as mandibular
432 asymmetry, can be reversed or if they become fixed over time. These insights could have
433 implications for understanding how environmental change drives phenotypic plasticity
434 and contributes to evolutionary diversification in vertebrates (Conith & Albertson, 2021;
435 Zogbaum et al., 2021).

436 In conclusion, we have here demonstrated that plasticity contributes to predatory
437 behaviour and the formation of morphological asymmetry in scale-eating fish. As
438 individuals with greater mandibular asymmetry exhibit higher predation success in scale-
439 eating fish, the effects of plasticity are likely to extend beyond individual fitness to
440 influence community dynamics and resource utilization (Takeuchi et al., 2016).
441 Phenotypic plasticity is thought to facilitate adaptation, promote diversification, and drive
442 evolutionary innovation, particularly in response to changing ecological conditions

(Nijhout, 2003; Wund, 2012). Our findings offer insights into the evolutionary mechanisms underlying laterality, emphasizing the complex interplay between plastic responses and adaptive traits.

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626
627
628
629

630

Fig. 1

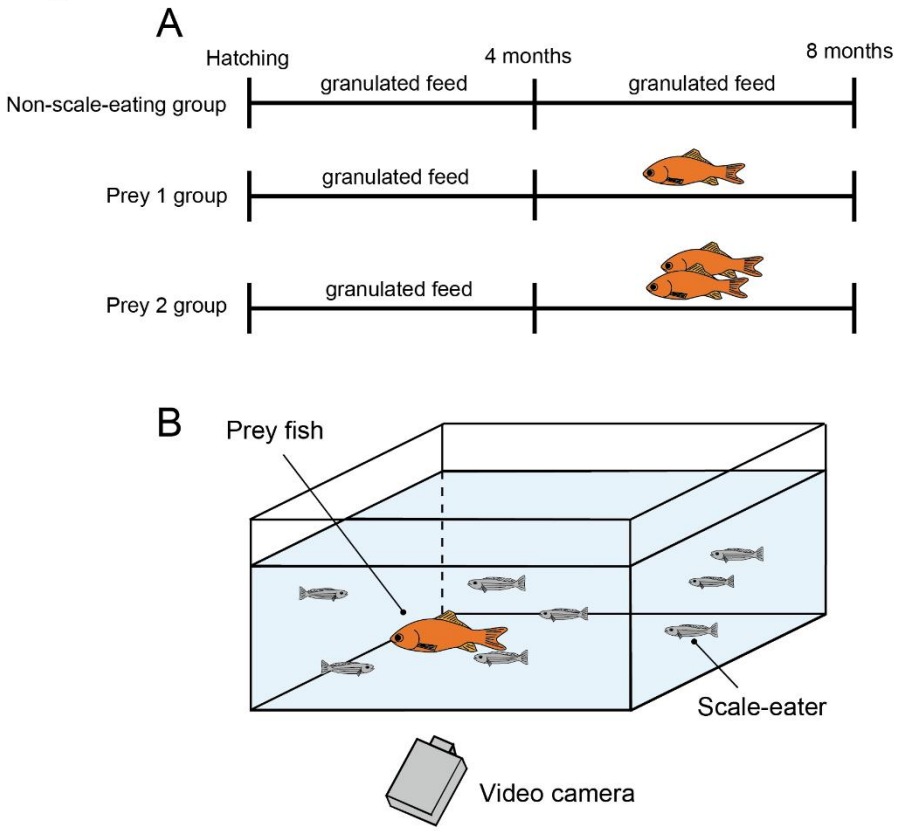
A
Hatching
4 months
8 months
Non-scale-eating group
granulated feed
granulated feed
Prey 1 group
granulated feed
Prey 2 group
granulated feed
B
Prey fish
Scale-eater
Video camera
C
cichlid
kingyo
D

Fig. 1 Predation experiments (A) Schedule of experiments. The “Non-scale-eating group” was given artificial granulated food from hatching to 8 months old (i.e., the end of the experiment). The “Prey 1 group” was fed on granulated food until 4 months old, and from then until 8 months old, one prey fish (goldfish) was introduced into the home tank of a scale-eating fish for 10 minutes daily, and scale-eating fish were allowed to forage freely. The “Prey 2 group” was fed on granulated food until 4 months old, and from then until 8 months old, two prey fish were simultaneously placed in the home tank. (B) Schematic diagram of predation experiments. Fish behaviour was filmed with a digital video camera from the side of the tank. (C) Annotation of recorded images for training the neural network YOLO v3. Green and red boxes indicate the location of scale-eating fish and prey fish, respectively. (D) Optical flow of scale-eating fish. The length of the trajectory indicates the amount of swimming. The total swimming distance across the image was defined as the swimming volume.

Alt text: Illustrations and photographs show the time-course of the predation experiment and behavioral analysis by Yolo.

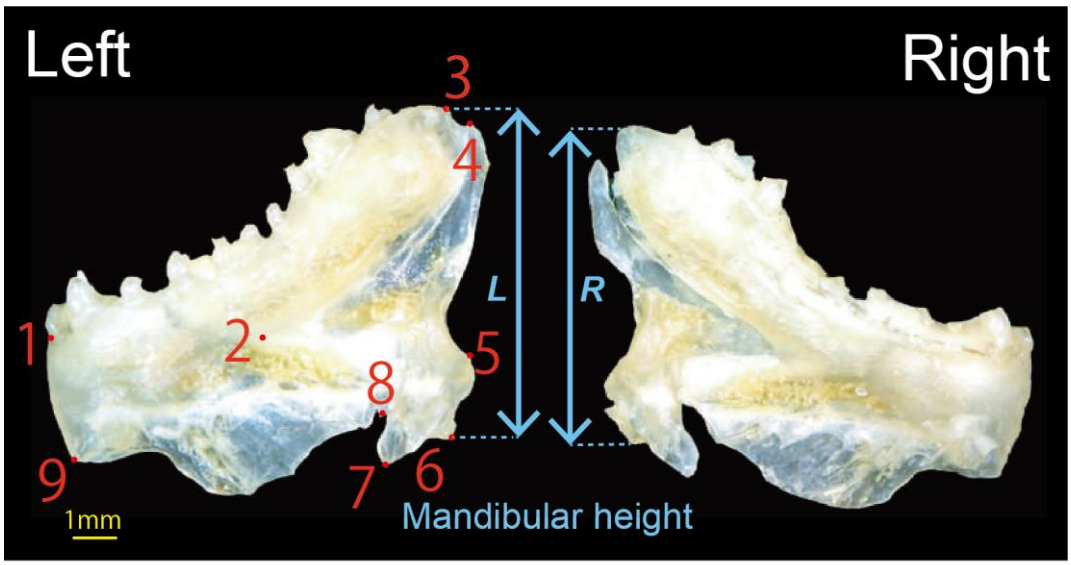

Fig. 2

647

648 **Fig. 2 Lower jawbone landmarks and mandibular height** The locations of nine

649 landmark characters were determined on the mandible. The arrows indicate the distance

650 between the two points on the upper end of the dentary bone and the lower end of the

651 posterior articular bone (referred as mandibular height). “L” and “R” refer to the left and

652 right sides of the lower jawbone. This specimen was a lefty individual.

653 **Alt text**: Photographs show landmarks and mandibular height in the lower jawbone.

654

655

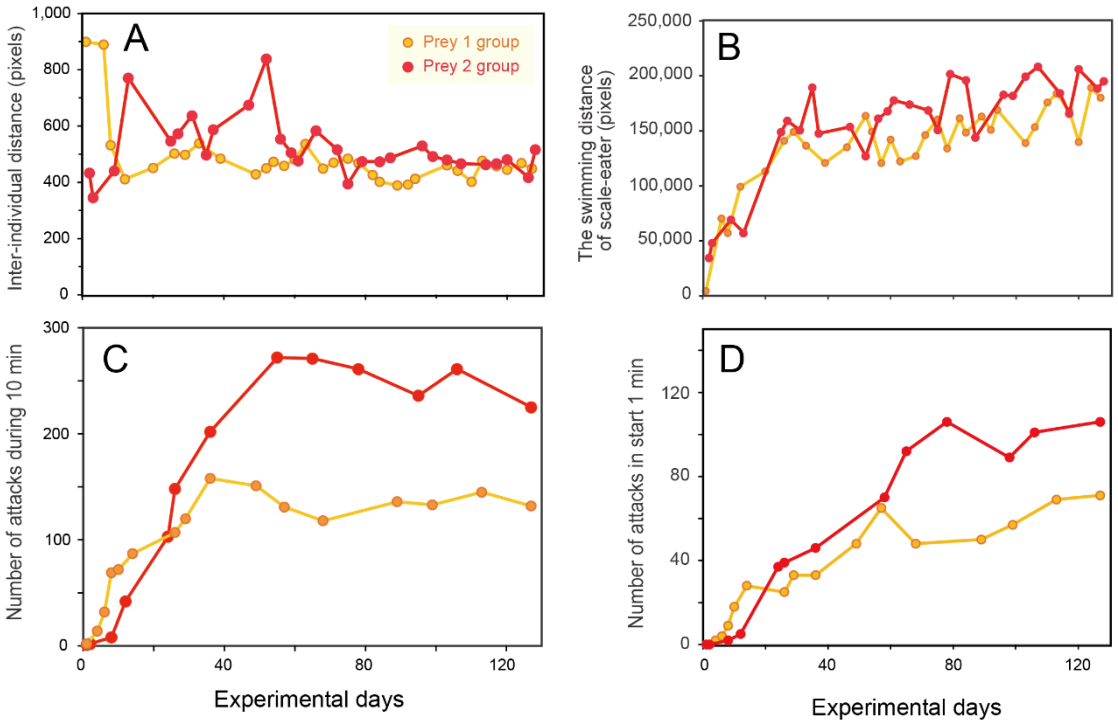

Fig. 3

Fig. 3 Influences of scale-eating experience on predation behaviour (A) Relationship between the number of experimental days and inter-individual distance between scale-eating fish and prey fish. Orange dots represent the Prey 1 group and red dots indicate the Prey 2 group. (B) Relationship between the number of experimental days and the swimming distance of scale-eater. Swimming activity was positively correlated with the number of experimental days in both groups. (C) Relationship between the number of experimental days and the number of attacks in the experimental 10-minute period. (D) Change over time in the number of attacks in the first minute of the experiment.

664 **Alt text**: Graph showing temporal changes in predation behavior of scale-eating fish.

665

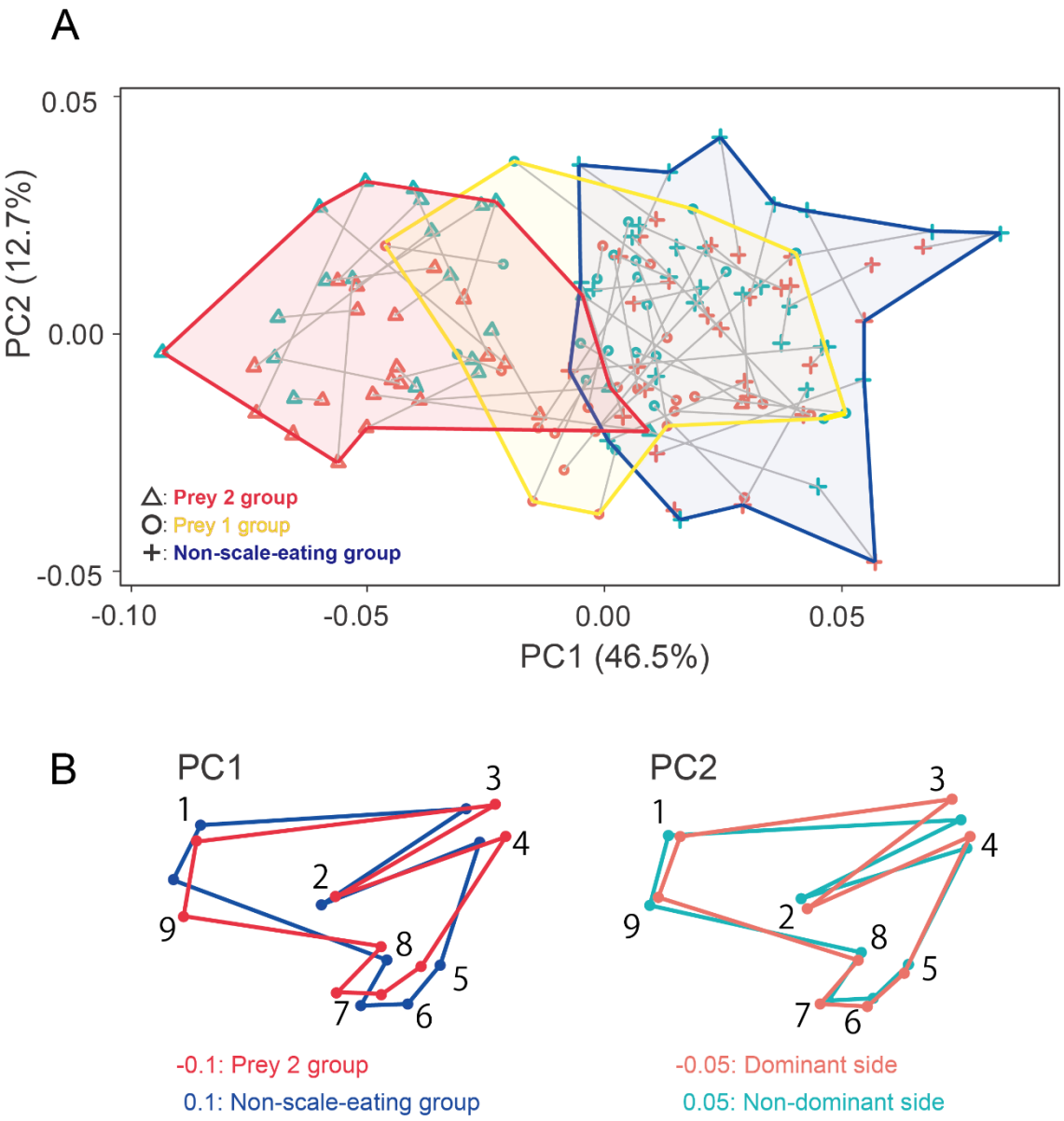

Fig. 4

666 **Fig. 4 Shape differences of lower jawbones** (A) Scatter plots of PC1 and PC2 from

667 principal component analysis of the lower jawbone. The blue frame shows the Non-scale-

668 eating group, the yellow frame shows the Prey 1 group, and the red frame shows the Prey
669 2 group, respectively. Coral and jade colours represent the dominant and non-dominant
670 sides of jaws. (B) Variations in jawbone shape that correspond to PC1 and PC2 are shown.
671 Lower jawbone wireframes denote morphologies at either end of the correlational axis.
672 Numbers refer to landmarks illustrated in Figure 2. PC1 showed the greatest change in
673 distance between landmarks 1 and 3. PC2 showed the greatest change in distance between
674 landmarks 3 and 6.
675 **Alt text**: Scatterplot and data showing differences in mandibular shape between foraging
676 conditions.

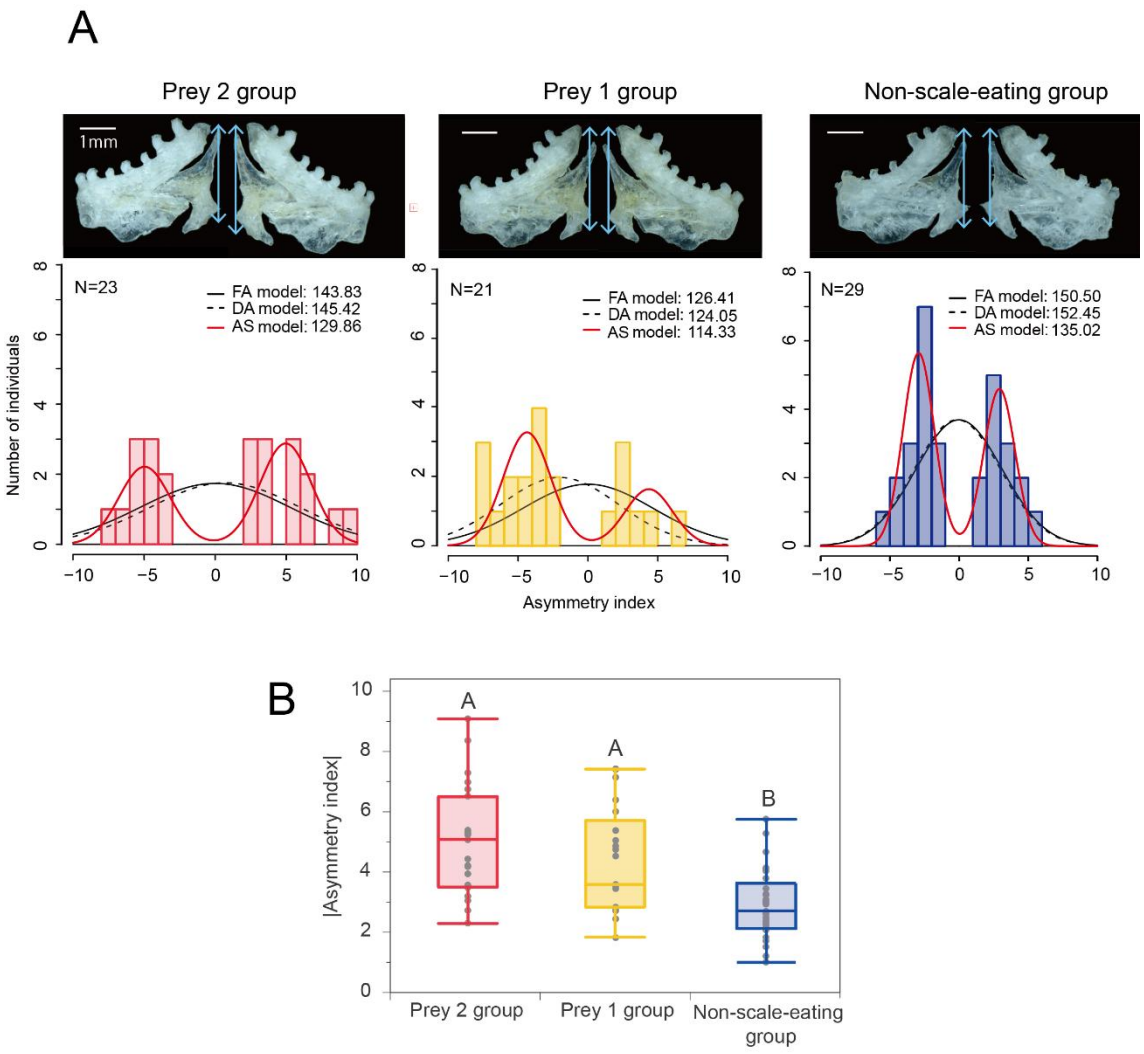

Fig. 5

677

678

679 **Fig. 5 Left–right differences in the lower jawbone** (A) Photographs of the lower

680 jawbones of righty individuals from three groups (Prey 2, Prey 1, and Non-scale-eating)

681 and frequency distributions of the asymmetry index of mandibular height. The arrow

682 indicates the mandibular height. In the frequency distributions, the red columns represent
683 the Prey 2 group, yellow columns represent the Prey 1 group, and blue columns represent
684 the Non-scale-eating group. The lines show probability curves obtained from three
685 models: the FA model (solid black line), the DA model (broken line), and the AS model
686 (solid red line). For each experimental groups, we calculated the Akaike information
687 criterion (AIC) of the three models. The model with the lowest AIC value was selected as
688 the best explanation for the observed asymmetries. (B) Comparison of absolute values of
689 the asymmetry index. Different letters above the bars represent significant differences of
690 pairwise comparisons (Tukey HSD test, $P < 0.05$).
691 **Alt text**: Photographs and graphs show mandible height of the jawbone for each foraging
692 condition.
693

694 **Table 1.** Results of Procrustes ANOVA of lower jaws on the effects of variables.

Factors	df	Sum Sq	Mean Sq	R Sq	*F*	*z*	*P*
Foraging conditions	2	0.118	0.059	0.313	66.738	7.64	< 0.001
Laterality	1	0.009	0.009	0.023	9.974	4.802	< 0.001
logCS	1	0.029	0.029	0.077	32.661	4.907	< 0.001
individual	67	0.161	0.002	0.427	2.718	11.294	< 0.001
Residuals	68	0.060	0.001	0.160			

695

696 **Table 2.** Results of Pairwise test among foraging conditions.

Comparisons	d	UCL (95%)	*z*	*P*
Prey 2 vs. Prey 1	12.929	7.115	4.452	< 0.001
Prey 2 vs. Non-scale-eating	12.247	7.251	8.649	< 0.001
Prey 1 vs. Non-scale-eating	6.786	6.32	2.11	0.024

697 Note: d, pairwise standardized distances between means