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# The intraspecific diversity of tooth morphology in the large-spotted catshark *Scyliorhinus stellaris*: insights into the ontogenetic cues driving sexual dimorphism

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Teeth in sharks are shed and replaced throughout their lifetime. Morphological dental changes through ontogeny have been identified in several species, and have been correlated to shifts in diet and the acquisition of sexual maturity. However, these changes were rarely quantified in detail along multiple ontogenetic stages, which makes it difficult to infer the developmental processes responsible for the observed plasticity. In this work, we use micro-computed tomography and 3D geometric morphometrics to describe and analyze the tooth size and shape diversity across three ontogenetic stages (hatchling, juvenile, and sexually mature) in the large-spotted catshark *Scyliorhinus stellaris* (Linnaeus, 1758). We first describe the intra-individual variation of tooth form for each sex at each ontogenetic stage. We provide a tooth morphospace for palatoquadrate and Meckelian teeth and identify dental features, such as relative size and number of cusps, involved in the range of variation of the observed morphologies. We then use these shape data to draw developmental trajectories between ontogenetic stages and for each tooth position within the jaw to characterize ontogenetic patterns of sexual dimorphism. We highlight the emergence of gynandric heterodonty between the juvenile and mature ontogenetic stages, with mature females having tooth morphologies more similar to juveniles' than mature males that display regression in the number of accessory cusps. From these data, we speculate on the developmental processes that could account for such developmental plasticity in *S. stellaris*.

## KEYWORDS

geometric morphometrics, gynandric heterodonty, monognathic heterodonty, ontogenetic trajectory, scyliorhinids

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## 7 1 | INTRODUCTION

8 The fantastic diversity of shark tooth shapes has been  
 9 studied in relation to the evolutionary history and eco-  
 10 logical traits of this iconic group (Bazzi et al., 2018).  
 11 Functionally convergent tooth shapes between the bon-  
 12 nethead sharks *Sphyrna tiburo* (Sphyrnidae) and horn  
 13 sharks (Heterodontidae) were associated with the hard  
 14 prey they feed on (Wilga and Motta, 2000). On the other  
 15 hand, a strong phylogenetic signal arose from the analy-  
 16 sis of the whole dentition of Lamniforms, which have a  
 17 unique symphyseal to commissural tooth-type pattern-  
 18 ing (Shimada, 2002, 2005). For this reason, tooth shape  
 19 is one of the main supports for establishing taxonomic  
 20 groups and phylogenetic relationships between fossil  
 21 and extant elasmobranchs (sharks and batomorphs) (Shi-  
 22 mada, 2002, 2005; Cappetta, 2012). One issue in this  
 23 matter arises from the fact that an elasmobranch is  
 24 rarely characterized by a single tooth type (molariform,  
 25 unicuspidate, multicuspidate) within the jaw but by a  
 26 continuum of different tooth shapes along the jaw axis  
 27 (monognathic heterodonty) and often displays differ-  
 28 ences between the palatoquadrate (upper) and Mecke-  
 29 lian (lower) teeth (dignathic heterodonty). The continu-  
 30 ous and lifelong replacement of teeth in elasmobranchs  
 31 makes this variation dynamic in time (ontogenetic het-  
 32 erodonty), their tooth types being replaced, linked to di-  
 33 etary shifts (Luer et al., 1990; Powter et al., 2010) and re-  
 34 productive status (Reif, 1976; Springer, 1979; Gottfried  
 35 and Francis, 1996; Motta and Wilga, 2001; Purdy and  
 36 Francis, 2007; Powter et al., 2010; French et al., 2017).

37 In elasmobranchs, tooth replacement occurs at var-  
 38 ious rates and following different patterns, depending  
 39 for instance on tooth imbrication and water temper-  
 40 ature, and may also differ between jaws (Strasburg,

41 1963; Luer et al., 1990; Correia, 1999; Moyer and Be-  
 42 mis, 2016; Meredith Smith et al., 2018). Gynandric het-  
 43 erodonty (sexual dimorphism in teeth) is very common  
 44 in elasmobranchs (Feduccia and Slaughter, 1974; Tani-  
 45 uchi and Shimizu, 1993; Kajiura and Tricas, 1996; Ge-  
 46 nizz et al., 2007; Gutteridge and Bennett, 2014; Under-  
 47 wood et al., 2015; French et al., 2017) and affects spe-  
 48 cific tooth files (reported in Dasyatidae, Carcharhinidae,  
 49 and Leptochariidae) to the whole dental set at vari-  
 50 ous degrees during the sexually mature stage (Cappetta,  
 51 1986). The higher and sharper mature male teeth are  
 52 indeed assumed to function in grasping females and  
 53 consequently to facilitate clasper introduction during  
 54 copulation (Springer, 1966; McEachran, 1977; McCourt  
 55 and Kerstitch, 1980; Cappetta, 1986; Ellis and Shackley,  
 56 1995; Kajiura and Tricas, 1996; Pratt, Jr. and Carrier,  
 57 2001; Litvinov and Laptikhovskiy, 2005; Gutteridge and  
 58 Bennett, 2014). This feature has been recorded as a sea-  
 59 sonal variation in the Atlantic stingray *Dasyatis sabina*  
 60 (Kajiura and Tricas, 1996), while it is assumed to be a  
 61 fixed-in-time feature in other elasmobranch species for  
 62 which it has been described (Gutteridge and Bennett,  
 63 2014; de Sousa Rangel et al., 2016). Gynandric het-  
 64 erodonty has also been only described at sexually ma-  
 65 ture stages, suggesting that sex hormone signals trigger-  
 66 ing the reproductive activity may also be involved in the  
 67 development of the observed dental sexual dimorphism  
 68 (McEachran, 1977; Cappetta, 1986; Snelson et al., 1997;  
 69 Powter et al., 2010).

70 Shark tooth shapes have been mostly evaluated  
 71 through semi-quantitative studies based on asymmetry,  
 72 number, sharpness, and relative bending or size of cusps  
 73 (Cappetta, 1986; Frazzetta, 1988). Moreover, studies  
 74 that performed morphometrics on extant species mainly  
 75 focused on tooth crown dimensions (height, width, and  
 76 angle) of specific teeth (small-spotted catshark *Scyliorhi-  
 77 nus canicula* (Linnaeus, 1758) (Ellis and Shackley, 1995),  
 78 Lamniforms (Shimada, 2002), and Port Jackson shark  
 79 *Heterodontus portusjacksoni* (Meyer, 1793) (Powter et al.,  
 80 2010)). These approaches mainly base the tooth shape  
 81 analysis on main cusp dimensions, which do not cap-  
 82 ture complex heterodonty patterns (Whitenack and Got-  
 83 tfried, 2010). Recent publications, however, have fo-

84 cused on quantitative tooth traits in sharks by using  
 85 geometric morphometrics (Marramà and Kriwet, 2017;  
 86 Soda et al., 2017; Cullen and Marshall, 2019), providing  
 87 more subtle information on tooth size and shape quan-  
 88 titative variation. These comparative studies allow to  
 89 infer developmental and phylogenetic hypotheses and  
 90 refine our knowledge about the inter- and intraspecific  
 91 tooth shape variation in several shark species. Overall,  
 92 the authors highlight the benefits of a quantitative in-  
 93 vestigation of complete tooth shape patterns in sharks  
 94 to understand ontogenetic and evolutionary shifts.

95 Scyliorhinids are emerging models for shark studies  
 96 (Coolen et al., 2008) and among them, *S. canicula* tooth  
 97 morphologies have been the most studied. Mature *S.*  
 98 *canicula* specimens display gynandric heterodonty that  
 99 has been qualitatively described (Brough, 1937; Ellis and  
 100 Shackley, 1995; Erdogan et al., 2004; Debais-Thibaud  
 101 et al., 2015; Soares and Carvalho, 2019) but quantifi-  
 102 cation of scyliorhinids dental variation is still fragmen-  
 103 tary. In particular, the nursehound *Scyliorhinus stellaris*  
 104 (Linnaeus, 1758) is a phylogenetically close relative of *S.*  
 105 *canicula* (Iglésias et al., 2005; Vélez-Zuazo and Agnars-  
 106 son, 2011) and has mostly been studied for physiological  
 107 aspects (Piiper et al., 1977; Heisler and Neumann, 1980).  
 108 To our knowledge, the study of Soldo et al. (2000) is  
 109 the only one focusing on *S. stellaris* tooth shape patterns.  
 110 However, this study did not test the impact of ontogeny  
 111 on tooth morphology and did not detect sexual dimor-  
 112 phism although gynandric heterodonty is known to be  
 113 a common feature to Scyliorhinidae (Cappetta, 1986;  
 114 Soldo et al., 2000; Soares and Carvalho, 2019).

115 Here, we provide the first detailed description of  
 116 *S. stellaris* tooth form (shape and size) using microCT  
 117 images and quantitative 3D geometric morphometrics.  
 118 We characterize the ontogenetic and sexually dimor-  
 119 phic trajectories of tooth shapes and highlight the emer-  
 120 gence of gynandric heterodonty with sexual maturation.  
 121 We also describe intra-individual tooth morphological  
 122 variation and we discuss the developmental hypotheses  
 123 that could be involved in the observed tooth diversity of  
 124 *S. stellaris*.

## 2 | MATERIALS AND METHODS 125

### 2.1 | Biological material 126

In total, 33 specimens of *S. stellaris* (16 females, 17  
 127 males; 2,467 teeth) were analyzed. Total length (TL, in  
 128 cm) was used to define the groups of same ontogenetic  
 129 stages. Female *S. stellaris* are considered sexually mature  
 130 at 79 cm TL and males at 77 cm TL (Fischer et al., 1987;  
 131 Musa et al., 2018) but longer mature specimens were  
 132 chosen to avoid biases due to potential later maturation.  
 133 Juveniles were twice shorter than the mature specimens  
 134 and hatchling specimens were chosen as close as possi-  
 135 ble from hatching (Musa et al., 2018) although umbilical  
 136 scars were never observed. We cannot evaluate how  
 137 these time points are distributed along the ontogeny of  
 138 the specimens because we have no information on the  
 139 age of each specimen, and no growth curve has been  
 140 published for this species beyond the hatchling stage  
 141 (Musa et al., 2018). Growth rates may be sex-specific in  
 142 elasmobranchs (Hale and Lowe, 2008) so we may expect  
 143 age differences between males and females of similar to-  
 144 tal length. Hatchling specimens were  $17.7\text{cm} \pm 3.3\text{cm}$   
 145 TL (7 females, 5 males), juveniles were  $57.7\text{cm} \pm 3.2\text{cm}$   
 146 TL (5 females, 5 males) and mature ones were  $102.7\text{cm}$   
 147  $\pm 7.2\text{cm}$  TL (4 females, 7 males) (Table 1). Dried jaws  
 148 were provided by the Institute of Evolution Sciences of  
 149 Montpellier (France) and jaws preserved in ethanol were  
 150 provided by the Aquarium du Cap d'Agde (France). 151

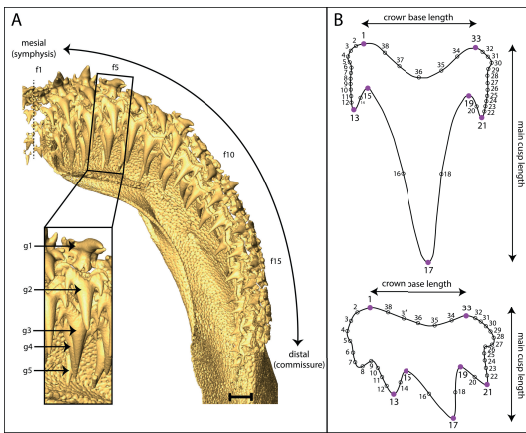
### 2.2 | MicroCT scans 152

Jaws were microCT scanned using a Phoenix Nanotom S  
 153 with voxel sizes ranging from  $(10.7\mu\text{m})$  to  $(30.0\mu\text{m})$  and  
 154 3D volumes were reconstructed using the correspond-  
 155 ing phoenix datos x2 reconstruction software (v2.3.0). 156

### 2.3 | Tooth selection 157

For each specimen, all 3D teeth were isolated from  
 158 the right palatoquadrate and Meckelian cartilages with  
 159 Amira software (v6.2.0) (Stalling et al., 2005). Each tooth  
 160 was identified within a file (or family) along the mesio-  
 161

162 distal axis and by the generation within a tooth file (Fig.  
 163 1A). Within each tooth file, we analyzed 1 to 4, func-  
 164 tional but not worn, generations.



**FIGURE 1** Tooth identification within a jaw and landmarking. A) microCT image of a right Meckel's cartilage of a juvenile female *S. stellaris*, dorsal view. f, file as defined from the symphysis (dotted line) to the commisure; g, generation. Scale bar represents 2.5mm for the jaw and 1mm for the zoomed teeth; B) Mesial (top) and distal (bottom) examples of landmark (purple) and semilandmark (empty dots) setting.

165 The teeth were not clustered into classically used  
 166 tooth-type denominations (e.g., symphyseal, parasym-  
 167 physeal, lateral, commissural) (Reif, 1976; Lucifora et al.,  
 168 2001) on purpose since we did not visually identify  
 169 abrupt tooth shape or size change along the mesio-distal  
 170 axis, except for the symphyseal teeth on the lower jaw  
 171 (Fig. 1A). These symphyseal teeth are located between  
 172 the right and left Meckelian cartilages and are not lo-  
 173 cated above jaw cartilages, contrary to all other teeth.  
 174 All subsequent analyses were performed under the hy-  
 175 pothesis of homology between tooth files of different  
 176 specimens, which for example means that the most sym-  
 177 physeal Meckelian tooth file of a given hatchling male is  
 178 considered equivalent to the most symphyseal Mecke-  
 179 lian tooth file of a mature female.

## 2.4 | Geometric morphometrics

180 Seven 3D landmarks and 31 semilandmarks were placed  
 181 on the cutting edge of each tooth (Fig. 1B) with the  
 182 Landmark software (v3.0.0.6) (Wiley et al., 2005) and  
 183 the data were preprocessed with Scyland3D (v1.1.0)  
 184 (Berio and Bayle, 2020). The semilandmark density was  
 185 made higher in the lateral sides of the teeth because  
 186 gynandric heterodonty in scyliorhinids is known to in-  
 187 volve the addition of lateral accessory cusps (Gosztonyi,  
 188 1973; Ellis and Shackley, 1995; Debais-Thibaud et al.,  
 189 2015; Soares and Carvalho, 2019). Our form compari-  
 190 son analyses will be interpreted in light of this choice:  
 191 the centroid size and shape parameters will be more af-  
 192 fected by variations in the lateral zones (with higher den-  
 193 sity of semilandmarks) than in the main cusp and crown  
 194 base zones. All analyses were performed separately for  
 195 Meckelian and palatoquadrate teeth.

196  
 197 Crown base width was computed based on the distance  
 198 between landmarks 1 and 33 (d1-33, Fig. 1B), while  
 199 main cusp height was the mean of the distances be-  
 200 tween the main cusp and each side of the tooth (mean  
 201 of d1-17 and d17-33, see Fig. 1B). We also used these  
 202 measures to generate a ratio between main cusp height  
 203 and crown base width, later referred to as the cusp-  
 204 crown ratio. Tooth symmetry was measured by the ratio  
 205 between d1-17 and d17-33 and a value of 1 implies a  
 206 symmetric tooth.

207 A Generalized Procrustes Superimposition (GPA) was  
 208 performed (Bookstein, 1991) during which the semiland-  
 209 marks were slid based on minimizing bending energy  
 210 (Bookstein, 1997). The tooth size patterns were investi-  
 211 gated using centroid sizes computed based on the GPA  
 212 and the tooth shape variation was displayed with princi-  
 213 pal component analyses (PCAs). In order to reduce the  
 214 high dimensionality of the aligned coordinates, the data  
 215 were reduced prior to multivariate analyses of variance  
 216 (MANOVAs) to the axes containing 95% of the total vari-  
 217 ation (14 and 13 PCA axes for Meckelian and palato-  
 218 quadrate teeth respectively, out of 114 available axes).  
 219 We defined the random variable as the tooth generation  
 220 within a given tooth file, in a specimen. We used these  
 221 generations as internal replicates from which we gen-

erated an average tooth shape per tooth file, for each specimen. One-Way analyses of variance (ANOVAs) and MANOVAs were then computed on tooth mean centroid size and tooth shape for each tooth position, each sex, at each ontogenetic stage, to avoid biases due to unbalanced sampling between tooth files (from one to four sampled teeth within one tooth file). Two-way ANOVAs and MANOVAs were subsequently used on tooth mean centroid size and shape to test the interaction between sex, stage, and tooth position along the jaw. Within each jaw, inter-group differences in shape were first investigated between sexes without considering ontogenetic stages nor tooth positions. The differences due to sex and tooth position within the jaw were subsequently tested within given ontogenetic stages.

Trajectory analyses were performed to evaluate the developmental tooth shape changes within each tooth position. The trajectories were computed and compared i) between sexes and ii) between two consecutive ontogenetic stages within sexes (e.g., from hatchling to juvenile, and juvenile to mature). The statistical tests were performed on the length, direction, and shape of the trajectory in the morphospace (Adams and Otárola-Castillo, 2013).

Geometric morphometric superimposition and analyses were carried out in R (v3.4.3) with the geomorph library (v3.2.1) (Adams and Otárola-Castillo, 2013).

## 3 | RESULTS

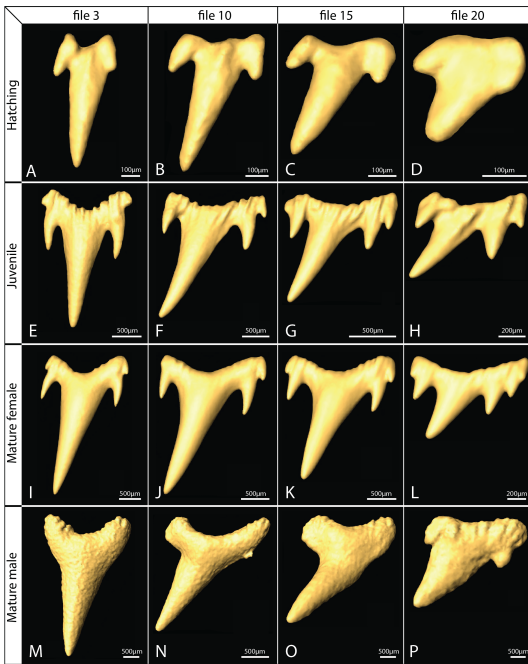
### 3.1 | Visual inspection of tooth morphology

There were no symphyseal teeth on the palatoquadrate, but one symphyseal file on the Meckelian cartilage (for 41% of the specimens). Although the second Meckelian tooth file is partially located above the Meckelian mesial edge, the teeth display size and morphological similarities to the symphyseal ones (for 59% of the specimens). We report no significant difference in tooth file counts between right and left sides of the jaw within each ontogenetic stage for each sex (Wilcoxon matched-pairs signed rank tests,  $p\text{-val} > 4.60e^{-2}$  for all

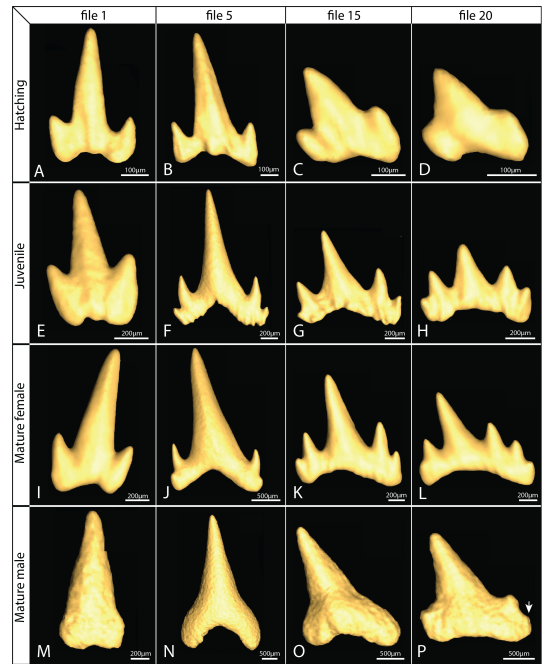
tests; we observed a maximum difference of two tooth files between the right and left jaws, in 13/51 comparisons). Palatoquadrate number of tooth files does not differ significantly between ontogenetic stages in males and in females (One-Way permutation ANOVAs,  $p\text{-vals} > 5.00e^{-2}$ ). Conversely, in both sexes, there are significantly more Meckelian tooth files in juvenile and mature specimens compared to hatchling ones (One-way permutation ANOVAs,  $p\text{-vals} < 5.00e^{-2}$ ), but no difference was detected between the juvenile and mature ontogenetic stages. Moreover, there is no significant difference in tooth file counts between males and females (Wilcoxon tests,  $p\text{-val} > 3.10e^{-1}$  for all tests).

A graded decrease of tooth size is observed along the mesio-distal axis of the jaw, except for the symphyseal teeth which are smaller than parasymphyseal ones (see Fig. 1, Fig. 2E, and Fig. 3E and I). In all sexes and stages, there is a graded increase of lateral bending of teeth from the symphysis to the commissure, producing asymmetric teeth (Fig. 2 and 3). Teeth of male and female hatchlings are visually similar in shape with tricuspid teeth in both jaws (Fig. 2A to D and Fig. 3A to D).

Juvenile female and male teeth display little variability in cusp number along the jaw: mesial palatoquadrate teeth (Fig. 2E) often display one main cusp and four accessory cusps while the more distal ones have four to five cusps and often more accessory cusps in the mesial than in the distal part of the crown (Fig. 2E to H). A similar pattern is observed in Meckelian teeth (Fig. 3E to H), except for tricuspid symphyseal ones. Mature female teeth are similar in shape to those of juveniles except at the most distal positions where they exhibit up to six cusps (Fig. 2I to L and Fig. 3I to L). Mature male mesial teeth are always un-bent and unicuspidate while more distal teeth undergo an addition of one to two accessory cusps (Fig. 2M to P and Fig. 3M to P). Mature male teeth rarely display more than two accessory cusps (Fig. 2M to O and Fig. 3M to P), however a small third accessory cusp was detected on the distalmost teeth of some specimens (see arrow on Fig. 3P).



**FIGURE 2** Palatoquadrate tooth shape diversity in *S. stellaris*. A-D) Hatchling female teeth; E-H) Juvenile female teeth; I-L) Mature female teeth; M-P) Mature male teeth. Symphyseal (mesial) pole to the left.



**FIGURE 3** Meckelian tooth shape diversity in *S. stellaris*. A-D) Hatchling female teeth; E-H) Juvenile female teeth; I-L) Mature female teeth; M-P) Mature male teeth. Symphyseal (mesial) pole to the left.

## 3.2 | Morphometric analyses

### 3.2.1 | Tooth size patterns

To support and quantify visual observations, morphometric measurements were performed and ratios of the main cusp height and the crown base width were computed. Ratio values are higher than 1, showing that the main cusp is higher than the crown base is wide (Fig. 4A and D).

In all groups, this ratio decreases along the mesio-distal axis of the jaw (Fig. 4A and D), with exceptions in the distalmost positions in Meckelian teeth of mature males and juvenile females (Fig. 4A and D). The variation of this ratio follows the gradual decrease of both measures, although stronger decrease is observed in the main cusp height (Additional figure). At each position, the measured cusp-crown ratio is very comparable between ontogenetic stages, but in the palato-

quadrate teeth of hatchling specimens we report higher ratios (1.5-fold increase), with a minimum of 1.6 along the mesio-distal axis (see position 19 in hatchling males in Fig. 4D). The raw data on main cusp height and crown base width show that hatchling palatoquadrate teeth are different from Meckelian teeth because of their smaller crown base (Additional figure, A and B). Overall, these observations point to similar developmental constraints on the overall geometry of teeth at all ontogenetic stages on Meckelian teeth and to a transition of these developmental constraints between the hatchling and juvenile ontogenetic stages in palatoquadrate teeth.

### 3.2.2 | Tooth asymmetry

Teeth of *S. stellaris* undergo a global increase of bilateral asymmetry from the symphysis to the commissure al-

336 though we also report a sudden fall of asymmetry values  
 337 in the distalmost tooth files (Fig. 4B and E). In Meckel-  
 338 elian teeth, the tooth asymmetry values of all groups  
 339 (ontogenetic stages) are overlapping until the 15<sup>th</sup> tooth  
 340 file, but female teeth distal to this position tend to dis-  
 341 play higher asymmetries than teeth of other groups (Fig.  
 342 4B). A similar pattern is observed in the palatoquadrate:  
 343 asymmetry values of all groups are very similar until the  
 344 14<sup>th</sup> tooth file (Fig. 4E). However, contrary to Mecke-  
 345 lian teeth, asymmetry patterns of hatchling teeth distal  
 346 to the 14<sup>th</sup> tooth file are distinct from those of juveniles  
 347 with lower asymmetry values (Fig. 4E). Mature males  
 348 display teeth whose symmetry values are in between  
 349 those of hatchling and juvenile specimens (Fig. 4E). As  
 350 for Meckelian teeth, mature female teeth are the most  
 351 asymmetrical (Fig. 4E) with maximum values between  
 352 the 19<sup>th</sup> and 23<sup>rd</sup> files (Fig. 4B). In the palatoquadrate,  
 353 these maxima are reached between the 22<sup>nd</sup> and 24<sup>th</sup>  
 354 tooth files in all groups (Fig. 4E). We also highlight that  
 355 the anteriormost teeth (1<sup>st</sup> file in the palatoquadrate  
 356 and up to the 3<sup>rd</sup> file in the Meckelian cartilage) are  
 357 close to bilateral symmetry (Fig. 4B and E). These mea-  
 358 surements highlight similar tooth mesio-distal asymme-  
 359 try patterns within hatchling and juvenile specimens and  
 360 higher asymmetry values in mature females compared  
 361 to all other groups (Fig. 4B and E).

### 362 3.3 | Geometric morphometric analyses

363 In the previous two morphometric analyses, the mesio-  
 364 distal variation of tooth shape could be discriminated in  
 365 terms of relation of cusp height and crown width and in  
 366 terms of asymmetry for juvenile and mature teeth. How-  
 367 ever, no strong difference of these parameters could be  
 368 seen between sexes in either jaws of all three ontoge-  
 369 netic stages. In the following, we established the tooth  
 370 centroid size patterns of variation along the mesio-distal  
 371 jaw axis for each group.

372 *Meckelian teeth.* Both sexes show similar tooth cen-  
 373 troid size patterns along the mesio-distal axis of the  
 374 jaw at hatchling and juvenile stages (Fig. 4C). Hatchling  
 375 males and females display very little tooth centroid size  
 376 variation along the jaw (Fig. 4C), as opposed to juvenile

377 and mature specimens that share a maximum tooth cen-  
 378 troid size in file 5 or 6 (Fig. 4C): values for juvenile teeth  
 379 are intermediate between the hatchling and mature val-  
 380 ues. Overall, the mesio-distal tooth centroid size pat-  
 381 tern is similar between juvenile and mature specimens  
 382 (Fig. 4C) but mature males display an exacerbated tooth  
 383 size pattern compared to mature females, except at the  
 384 symphyseal tooth positions (Fig. 4C).

*Palatoquadrate teeth.* Similar to the Meckelian teeth,  
 385 palatoquadrate tooth centroid sizes do not differ be-  
 386 tween sexes at hatchling or juvenile stages, centroid  
 387 size increase with ontogeny, and mature males display  
 388 higher values compared to females (Fig. 4F). Juvenile  
 389 males and females have two local maximum tooth cen-  
 390 troid sizes at the 3<sup>rd</sup> and 12<sup>th</sup> and 4<sup>th</sup> and 10<sup>th</sup> files  
 391 respectively, and a minimum centroid size at file 7 (Fig.  
 392 4F). Mature specimens display a clear bimodal tooth cen-  
 393 troid size pattern from the symphysis to the commissure,  
 394 with local maximum values in the 3<sup>rd</sup> and 10<sup>th</sup> files and  
 395 a local minimum value in the 7<sup>th</sup> file (Fig. 4F). Topologi-  
 396 cally, the Meckelian file 5 (maximal value in adult males)  
 397 faces the palatoquadrate file 7 (local minimum in adult  
 398 males) which suggests functional constraints for these  
 399 variation of tooth size along the mesio-distal axis. 400

401 Our statistical tests corroborated the observation  
 402 that tooth centroid size varies according to the ontoge-  
 403 netic stage in both cartilages (One-Way ANOVAs, p-vals  
 404  $< 2.00e^{-16}$ , Table 2). Within all ontogenetic stages, the  
 405 Meckelian and palatoquadrate tooth mesio-distal posi-  
 406 tion also significantly impacts the tooth centroid size  
 407 (One-Way ANOVAs, p-vals  $< 9.37e^{-4}$ , Table 2). The  
 408 Meckelian and palatoquadrate tooth centroid size of  
 409 mature specimens is also significantly impacted by sex  
 410 (One-Way ANOVAs, p-vals  $< 1.54e^{-2}$ , Table 2). We fi-  
 411 nally report a significant interaction between sex and on-  
 412 togenetic stage in the Meckelian and palatoquadrate full  
 413 datasets (Two-Way ANOVAs, p-vals  $< 3.24e^{-3}$ , Table 2),  
 414 as well as between ontogenetic stage and tooth mesio-  
 415 distal position in Meckelian teeth (Two-Way ANOVA, p-  
 416 val  $< 2.49e^{-3}$ , Table 2).



### 3.4 | Developmental trajectories

We performed independent PCAs in each jaw, and the extreme shapes on the PC1 and PC2 axes illustrate how similar shape parameters generate the main Meckelian and palatoquadrate variations of tooth shapes. This first observation highlights the fact that, although we treated them separately, teeth of the upper and lower jaw show similar shape variations along the first PCs. In both cases, the main axis of tooth shape variation relates to the main cusp proportions, and to the variation in the number of lateral accessory cusps (Fig. 5A and 5B). The second axis of variation seems to relate to the size of lateral cusps relative to the main cusp size (Fig. 5A and 5B).

The shape of Meckelian and palatoquadrate teeth of *S. stellaris* is mostly impacted by ontogenetic stage (One-Way MANOVAs,  $p$ -vals <  $2.20e^{-16}$ ,  $3.04e^1$  <  $F$  approx <  $4.58e^1$ , Table 3) although the sex of the specimens and the tooth position along the mesio-distal axis of the jaw also significantly impact the tooth shape (One-Way MANOVAs, Sex:  $p$ -val <  $6.13e^{-8}$ ,  $5.39$  <  $F$  approx <  $7.61$ ; Tooth position:  $p$ -val <  $3.12e^{-14}$ ,  $1.80$  <  $F$  approx <  $1.89$ , Table 3). Within ontogenetic stages, the mesio-distal position of a tooth significantly impacts the tooth shape of juveniles (One-Way MANOVAs,  $p$ -vals <  $1.16e^{-4}$  for both jaws, Table 3) and palatoquadrate teeth of hatchling specimens (One-Way MANOVA,  $p$ -val <  $2.28e^{-6}$ , Table 3). Conversely, for both jaws and within each ontogenetic stage, a sexual dimorphism of tooth shape was detected (One-Way MANOVAs,  $p$ -vals <  $5.37e^{-3}$ , Table 3). We finally report that the sexual dimorphism differs between stages and tooth mesio-distal positions for Meckelian and palatoquadrate teeth (Two-Way MANOVAs,  $p$ -vals <  $1.02e^{-2}$ , Table 3).

*Comparison of developmental trajectories between sexes.* The full shape developmental trajectories (from hatchling to juvenile, and to mature stage) differ between sexes for most of the palatoquadrate tooth files that are distal to the 3<sup>rd</sup> file and for all Meckelian tooth files distal to the 8<sup>th</sup> file ( $p$ -vals <  $1.60e^{-2}$ , Tables 4 and 5). These differences arise from divergent juvenile-to-mature developmental directions between males and fe-

males (45/46 significant  $p$ -values,  $p$ -vals <  $3.10e^{-2}$ , Tables 4 and 5). Significant differences between males and females for juvenile-to-mature trajectory lengths are also reported for most tooth files and always involve longer trajectories in males than females ( $p$ -vals <  $3.40e^{-2}$ , Tables 4 and 5). We report no such differences between male and female hatchling-to-juvenile trajectory lengths and angles (Tables 4 and 5). This pattern highlights a shift between male and female tooth shape developmental trajectories only after the juvenile stage.

*Comparison of developmental trajectories within sexes.* Significant differences were observed for all tooth files of both jaws between the hatchling-to-juvenile and the juvenile-to-mature trajectory angles within sexes ( $p$ -vals <  $1.20e^{-2}$ , Additional tables 1 and 2), showing that whatever the mesio-distal position of a tooth, the shape modifications between juvenile and mature stages cannot be considered a prolongation of the hatchling-to-juvenile modifications. Significant differences in trajectory lengths are reported for most female palatoquadrate files (19/25 significant  $p$ -values, Additional table 1) and for female Meckelian files distal to the 8<sup>th</sup> file ( $p$ -vals <  $4.40e^{-2}$ , Additional table 2). In all these cases, the hatchling-to-juvenile trajectory is longer than the juvenile-to-mature one (Additional tables 1 and 2), showing that, in females, tooth shapes generated at sexual maturation are less dissimilar to juveniles than in males. In contrast, male trajectory lengths significantly differ only in a few tooth files (6/46 significant  $p$ -values, Additional tables 1 and 2,  $p$ -vals <  $4.60e^{-2}$ ).

## 4 | DISCUSSION

### 4.1 | Capturing the intra-individual and ontogenetic-stage variations of tooth shape in *Scyliorhinus stellaris*

In this study, we generated 3D images and collected 3D coordinates of landmarks and semilandmarks on the cutting edge of the tooth surface. Despite the 3D nature of the surface data, the described tooth outline finally includes very little information in the third dimension.

499 While the use of 2D data would have probably been  
500 less time-consuming, working on 3D data avoids biases  
501 due to parallax (Mullin and Taylor, 2002; Fruciano, 2016).  
502 Moreover, 3D surfaces can provide insights into topo-  
503 logical aspects such as ornamentations, which can be of  
504 interest for future studies.

505 From our analyses, we described the wide range  
506 of blade-shaped to crown-shaped teeth in *S. stellaris*,  
507 which we characterized through classical and geomet-  
508 ric morphometric analyses. In *S. stellaris*, we quantified  
509 how classical tooth shape parameters (asymmetry and  
510 cusp-crown ratio) vary in a gradual and linear way along  
511 the mesio-distal axis of both jaws, with extreme vari-  
512 ations at the mesial-most and distal-most tooth posi-  
513 tions. Also, we captured a higher cusp-crown ratio for  
514 palatoquadrate hatchling teeth compared to other on-  
515 togenetic stages. Because the lack of asymmetry is a  
516 shared feature of hatchling teeth and symphyseal teeth  
517 of older specimens, we show that palatoquadrate and  
518 Meckelian teeth undergo similar transition in their devel-  
519 opment (asymmetry) once the hatching stage is passed,  
520 to the exception of the symphyseal teeth. According to  
521 visual observations, the palatoquadrate and Meckelian  
522 teeth of *S. stellaris* are very similar in shape (dignathic ho-  
523 modonty or weak dignathic heterodonty), which is con-  
524 sistent with previous works on scyliorhinids (Herman  
525 et al., 1990; Ellis and Shackley, 1995; Soares and Car-  
526 valho, 2019). As opposed to Scyliorhinidae, dignathic  
527 heterodonty is very common in other shark groups, such  
528 as in Hexanchidae and most Squaliformes. The tooth-  
529 type discrepancies between palatoquadrate and Mecke-  
530 lian teeth have been correlated with different functions  
531 in feeding: upper grasping teeth might help catching  
532 and holding a prey, whereas blade-shaped lower teeth  
533 might function in tearing a prey to pieces (Cappetta,  
534 1986; Frazzetta, 1988; Cappetta, 2012). Beyond ecol-  
535 ogy, dignathic heterodonty might also convey a phylo-  
536 genetic signal: sharks from distinct taxonomic groups  
537 might have overlapping trophic habits (especially in the  
538 case of opportunistic behavior) and, however, display  
539 different dignathic heterodonty patterns that diet alone  
540 cannot explain. Regarding whether the gynandric het-  
541 erodonty follows similar patterns between both jaws,

the data gathered hitherto on sharks are insufficient to  
answer.

Our results notably suggest a developmental transi-  
tion between hatchlings and juveniles, especially on the  
palatoquadrate, that involves a global increase of the  
crown size. Note that asymmetry and cusp-crown ra-  
tio poorly discriminate between the three ontogenetic  
stages because they are corrected for size. As expected,  
the variation of tooth centroid size strongly discrimi-  
nates between ontogenetic stages (Table 2) and shape  
analyses also recover growth stage significant differ-  
ences (Table 3).

## 4.2 | The ontogenetic tempo and pattern of gynandric heterodonty

In previous works, classical shape parameters did not  
discriminate sex-dependent variation of tooth shape  
in *S. stellaris*, although gynandric heterodonty is well-  
known in scyliorhinids (Gosztanyi, 1973; Ellis and Shack-  
ley, 1995; Cappetta, 2012; Debais-Thibaud et al., 2015;  
Soares and Carvalho, 2019). In our geometric morpho-  
metric analyses of *S. stellaris* teeth, we detected no  
significant centroid size differences between sexes at  
hatching and juvenile ontogenetic stages, while we ob-  
served such difference at mature stages with male tooth  
centroid sizes being larger than female ones. Centroid  
size is, per construction, a feature with little sensitivity  
to shape. However, because we weighted tooth zones  
by positioning the majority of semilandmarks in the lat-  
eral sides and in the crown base of the teeth (see Mate-  
rial and Methods, and Fig. 1B), the abovementioned dif-  
ferences in centroid size might be marginally affected by  
differences in tooth shape at these locations (Webster  
and Sheets, 2010). For most specimens, these crown  
sides and bases include lateral cusps (between land-  
marks 1-13 and 21-33, Fig. 1), but also other aspects of  
tooth shape such as the labial notch where two succes-  
sive teeth can be in contact (between landmarks 33-1,  
Fig. 1). Statistical analyses supported the observed sex-  
ual dimorphism of the centroid size and shape among  
mature specimens, as well as a visually undetected sex-  
ual dimorphism in tooth shape at hatching and juvenile

583 stages (Table 2 and Table 3).

584 We generated developmental trajectories between  
585 the three ontogenetic stages at all tooth positions in  
586 order to compare the shape transitions along jaws and  
587 ontogeny. Our analyses were performed under the hy-  
588 pothesis of homology (equivalence between compared  
589 structures) between tooth files of different specimens,  
590 to allow the developmental comparisons of forms over  
591 the lifetime of specimens of a given sex. However, the  
592 biological support for this hypothesis is questionable  
593 as the number of tooth files is not a fixed parameter  
594 over time. In *S. stellaris*, we also observed variation in  
595 the number of tooth files between specimens of simi-  
596 lar total length. We chose to accept this hypothesis of  
597 homology based on the fact that newly formed tooth  
598 files are generally considered to be added at the jaw dis-  
599 tal extremity in elasmobranchs (see Smith (2003); Smith  
600 et al. (2009); Underwood et al. (2016) for sharks and  
601 Underwood et al. (2015) for batoids). However, they  
602 also might be inserted between already existing tooth  
603 files (Reif, 1976, 1980; Smith et al., 2013), which would  
604 skew the continuity of tooth file numbering over time  
605 (see Underwood et al. (2015); Smith et al. (2013) for simi-  
606 lar remarks on batoids). Finally, we want to highlight  
607 that this homology (comparability) hypothesis is based  
608 under the assumption that the genesis of a tooth bud  
609 happens from a defined and continuous source, which is  
610 a strongly mammal-centered view of tooth morphogen-  
611 esis. In contrast, tooth bud initiation in elasmobranchs  
612 is considered to happen through self-organisation of the  
613 dental lamina, the invaginated epithelial fold from which  
614 new teeth develop (Reif, 1982; Rasch et al., 2016). For  
615 all these reasons, we interpreted our results as trends  
616 along the mesio-distal axis of a jaw but never under a  
617 strict homology hypothesis that would allow the compar-  
618 ison of a single given file between specimens, to the  
619 exception of the developmental trajectory analyses that  
620 necessitate a one-to-one comparison.

621 Over the time of sexual maturation, the juvenile-  
622 to-mature tooth shape developmental trajectories di-  
623 verged between males and females at all tooth positions.  
624 In both sexes, these juvenile-to-mature developmental  
625 trajectories differed from the hatchling-to-juvenile ones

(Tables 4 and 5). However, this deviation is increased  
626 in mature males ("angle cor" values are higher in males  
627 than in females in Tables 4 and 5). In males, mature  
628 tooth morphogenesis is characterized by an elongation  
629 of the main cusp and a reduction of the number of ac-  
630 cessory cusps, generating unicuspid to tricuspid teeth  
631 similar to hatchling ones (Fig. 2 and 3). In contrast, ma-  
632 ture female tooth shape patterns resemble those of ju-  
633 veniles although the most distal teeth of mature females  
634 can reach a maximum of six accessory cusps (Fig. 2 and  
635 3). As a conclusion, during sexual maturation, all tooth  
636 files in *S. stellaris* are affected by a slighter (females) or  
637 stronger (males) modification of developmental trajec-  
638 tories, compared to their hatchling-to-juvenile trajec-  
639 tories.  
640

641 On the one hand, it is tempting to speculate on die-  
642 tary differences between sexes that would correlate  
643 with morphological differences in teeth. It was reported  
644 that *S. stellaris* juvenile and mature specimens mostly  
645 feed on cephalopods and, to a lesser extent, on teleosts  
646 and crustaceans (Capapé, 1975). Juvenile females were  
647 reported to feed more on crustaceans than males and  
648 mature females (Capapé, 1975). These observations do  
649 not fit with any of the morphological shifts in tooth  
650 shape described in this study, so we cannot discuss any  
651 putative link between *S. stellaris* trophic ecology and  
652 tooth shape variation. On the other hand, the gynan-  
653 dric heterodonty of mature *S. stellaris* is consistent with  
654 reports on the role of teeth during copulation in elasm-  
655obranchs (Springer, 1967; McEachran, 1977; Kajiura and  
656 Tricas, 1996; Pratt, Jr. and Carrier, 2001; Gutteridge and  
657 Bennett, 2014). The increased main cusp height of ma-  
658 ture male teeth might indeed enhance gripping, as com-  
659 pared to teeth with more accessory cusps and smaller  
660 main cusp. However, this remains speculative as there  
661 is no experimental data on comparative gripping effi-  
662 ciency for shark teeth, only a few studies that compared  
663 flat *versus* cuspidate teeth in batoids (Kajiura and Tricas,  
664 1996; Gutteridge and Bennett, 2014).

### 4.3 | Developmental cues linked to tooth development plasticity

Our analyses highlight features linked to tooth developmental plasticity in several ontogenetic dimensions. The notion of developmental plasticity classically refers to the building of distinct phenotypes from the expression of a same genome in different environments (Moczek, 2015). Here, we want to use a modified version of this concept and apply it to tooth shape variation: (i) of different teeth at the intra-individual level and (ii) of comparable teeth between successive ontogenetic stages. First, the intra-individual variation points to developmental plasticity which is here dependent on the mesio-distal position of the tooth bud, and which we could name “positional developmental plasticity”. Second, the comparison between different ontogenetic stages —although an extrapolation of a situation with constant genome— questions developmental plasticity in the temporal dimension, assuming comparable tooth files between successive ontogenetic stages. We name this process “successive developmental plasticity”, generated through tooth successional replacement. Here we have quantified a peculiarity of successive developmental plasticity: the divergence of its developmental trajectory between males and females during sexual maturation.

From these observations, we want to speculate on the potential developmental mechanisms that might generate these developmental plasticities, considering the physical and molecular cues acting on tooth bud growth within the dental lamina. To our knowledge, there are very scarce genetic data available on tooth morphogenesis in *S. stellaris* (Rasch et al., 2016) but gene regulatory networks involved in elasmobranch tooth development have been investigated in *S. canicula*. The expression of classical developmental genes was characterized in tooth buds (Debiais-Thibaud et al., 2011, 2015; Martin et al., 2016; Rasch et al., 2016), including the well-known signaling factor *Shh* that acts as both a tooth bud initiation signal and a proliferation signal during tooth morphogenesis (Berio and Debiais-Thibaud, 2019; Hosoya et al., 2020). Data on the physical features that could constrain tooth bud growth within the

dental lamina are even scarcer although previous studies on mammals emphasized that a modification of the tooth bud physical environment can modify the final shape of a tooth (Renvoisé et al., 2017). Several observations of the jaw morphology may still help discuss how these physical constraints can be linked to tooth development. Of course, these genetic and physical cues acting on tooth development should not be considered as acting independently of one another on tooth development: it is likely that developmental signaling pathways impact morphogenesis by modifying physical parameters at the cellular level, while geometrical and physical constraints at the jaw cartilage or dental lamina levels can induce differential diffusion of molecules (Salazar-Ciudad, 2008; Renvoisé et al., 2017; Calamari et al., 2018). The parameters of this complex system that may be relevant for specific aspects of tooth morphology and its variational properties in time or space are essentially unknown. However, from our results in *S. stellaris*, we wish to draw three main discussion points on the putative sources of: (1) mesio-distal patterning, (2) asymmetry, and (3) gynandric heterodonty.

(1) *Sources of the mesio-distal patterning.* The graded variation of cusp-crown ratio is a shared feature of all ontogenetic stages and both jaws: this observation suggests the occurrence of a graded signal along the mesio-distal axis of a jaw at all developmental stages. This signal may be of two non-mutually exclusive origins: a gradient of physical constraints, and a gradient of molecular signals along the jaw.

Very little is known on the potential variation of the shape, thickness, and curvature of the dental lamina at any developmental stage. However, previous observations of catshark jaws showed that hatchling tooth buds develop very close to the Meckel's cartilage surface (observations in *S. canicula* in Debiais-Thibaud et al. (2015)), suggesting the gradient of dental lamina invagination is weak or nonexistent at this stage, contrary to older specimens whose dental lamina is more deeply invaginated. Therefore, the physical constraints on the dental lamina do not seem to explain the observed gradients of cusp-crown ratios. The overall jaw geometry may also be considered as another potential driver of the mesio-distal

750 patterning. As for the dental lamina, its effects on the  
751 mesio-distal patterning may however be non-linear: the  
752 sexually dimorphic heads in mature scyliorhinids would  
753 also affect the shape of jaw cartilages (Ellis and Shack-  
754 ley, 1995; Soares, 2019; Soares and Carvalho, 2019).  
755 This would suggest a sexual dimorphism in the gradient  
756 of cusp-crown ratio by affecting differently the labial-  
757 lingual local curvature of the dental lamina where the  
758 tooth buds develop. However, this is not obvious from  
759 our observations, although mature males tend to have a  
760 higher cusp-crown ratio in Meckelian teeth than females  
761 do, and compare best to juveniles in that respect.

762 On the other hand, the mesio-distal patterning of  
763 jaws by developmental genes was demonstrated in  
764 model organisms (Van Otterloo et al., 2018) and molec-  
765 ular signaling is known to generate the mesio-distal  
766 gradient in tooth morphology in mouse (reviewed in  
767 Cobourne and Sharpe (2003)). The genes involved in  
768 jaw patterning and tooth morphogenesis of mammals  
769 are also expressed in *S. canicula* (Debiais-Thibaud et al.,  
770 2013, 2015; Rasch et al., 2016). Yet, there is no avail-  
771 able empirical evidence about how this signaling gra-  
772 dient may change during the ontogeny of scyliorhinids  
773 and whether it does correlate with the cusp-crown ratio  
774 gradient.

775 (2) *Sources of asymmetry*. The first generation of tooth  
776 buds in embryos or just hatched specimens of *S. canic-  
777 ula* develops very close to the surface of the jaw epithe-  
778 lium, within a superficial dental lamina (Debiais-Thibaud  
779 et al., 2011, 2015; Rasch et al., 2016). In addition, given  
780 the topology of the jaw symphysis (without underlying  
781 cartilage), we speculate that the situation is similar for  
782 symphyseal teeth. We therefore consider the possibility  
783 of tooth asymmetry as being correlated with the depth  
784 and topology of the dental lamina invagination. Some of  
785 our preliminary tests on modeling tooth development in  
786 sharks suggest that the mechanical stresses exerted on  
787 a tooth bud by the surrounding tissues (the dental lam-  
788 ina and the underlying cartilage) may be key to breaking  
789 the symmetry of the tooth morphology. We speculate  
790 that the deeper the dental lamina, the higher the likeli-  
791 hood of an asymmetry in the boundary conditions of the  
792 growing tooth bud reflecting into its final shape.

(3) *Sources of gynandric heterodonty*. Sex-related tooth  
793 shape dimorphism is visually detectable only in mature  
794 specimens. This dimorphism stands strongly in the rela-  
795 tive size of the main cusp versus accessory cusps (higher  
796 in males), and in the number of accessory cusps (higher  
797 in females). Previous studies and modeling of mam-  
798 malian tooth morphogenesis have recovered patterns  
799 of covariation between main cusp sharpness and the  
800 number and spacing of accessory cusps (Jernvall, 2000;  
801 Salazar-Ciudad and Jernvall, 2010). Although highly  
802 speculative to infer mammalian developmental patterns  
803 to sharks, the 2D-tooth shapes computed in this case  
804 study are very similar to the *S. stellaris* lateral teeth (es-  
805 pecially those of the ringed seal *Phoca hispida*) (Salazar-  
806 Ciudad and Jernvall, 2010). In this case study, the au-  
807 thors have interpreted the observed relationship be-  
808 tween the height of the main cusp and the height of ac-  
809 cessory cusps as a product of the enamel knot signaling  
810 center spacing: the closer the secondary enamel knots  
811 as compared to the primary enamel knot, the higher  
812 and the more blunt the accessory cusps (Jernvall, 2000;  
813 Salazar-Ciudad and Jernvall, 2010). Conversely, when  
814 the distance between primary and secondary enamel  
815 knots is greater, sharper teeth with fewer and smaller  
816 accessory cusps develop (Jernvall, 2000; Salazar-Ciudad  
817 and Jernvall, 2010). The successive activation of enamel  
818 knots and their spacing is strongly regulated by the dif-  
819 fusion rate of signaling molecules such as Shh and Fgfs  
820 (Thesleff and Mikkola, 2002; Du et al., 2017). Another  
821 developmental parameter in which variation was associ-  
822 ated with this shape relationship is epithelial growth rate  
823 (Salazar-Ciudad and Jernvall, 2010), e.g., the rate of cell  
824 division in the tooth bud that is growing from the den-  
825 tal lamina. Finally, the dental lamina characteristics (act-  
826 ing on diffusion rates and cell division rate) might exhibit  
827 sexual dimorphism, as a consequence of sexually dimor-  
828 phic head dimensions in Scyliorhinidae (Ellis and Shack-  
829 ley, 1995; Soares, 2019). The longer and narrower jaw  
830 in males compared to females at mature stage is actually  
831 a recurrent feature in elasmobranchs and gives support  
832 to this hypothesis (Ellis and Shackley, 1995; Braccini and  
833 Chiamonte, 2002; Erdogan et al., 2004; Geniz et al.,  
834 2007; Soares et al., 2016; Soares, 2019). Labial curva-  
835

836 ture of the jaw cartilages may then impact the physi- 877  
 837 cal constraints on dental lamina. A second hypothetical 878  
 838 source, which might interact with the previous one, is 879  
 839 based on the sex-hormone dependence of the molecu- 880  
 840 lar signalisation involved in tooth bud growth. This is 881  
 841 supported by previous identification of a sex-hormone 882  
 842 dependency for *Shh* expression in vertebrates, including 883  
 843 elasmobranchs (Ogino et al., 2004; Chew et al., 2014; 884  
 844 O'Shaughnessy et al., 2015). Gene regulatory networks 885  
 845 involved in elasmobranch tooth development have been 886  
 846 most extensively investigated in *S. canicula*, where the 887  
 847 expression of classical developmental genes was charac- 888  
 848 terized (Debiais-Thibaud et al., 2011, 2015; Martin et al., 889  
 849 2016; Rasch et al., 2016). If the situation in *S. stellaris* is 890  
 850 comparable to what was observed in *S. canicula*, then a 891  
 851 modification of balance between developmental genes 892  
 852 (e.g., *Shh*) under the reception of sex-hormone signals 893  
 853 in mature specimens could modify the balance between 894  
 854 cell proliferation and differentiation that impacts the fi- 895  
 855 nal shape of a tooth. 896

856 As discussed here, a variety of hypothetical physi- 897  
 857 cal and molecular factors might be involved in the 898  
 858 generation of tooth shape plasticity in elasmobranchs. 899  
 859 To test these influences, morpho-anatomical and func- 900  
 860 tional studies are still necessary although they are diffi- 901  
 861 cult to realize in non-model and threatened species such 902  
 862 as most elasmobranchs. We expect that our extensive 903  
 863 description of the actual tooth form diversity in *S. stel- 904  
 864 laris* will help to orientate the hypotheses to be further 905  
 865 tested to identify the sources of heterodonty in elasmobranchs. 906

#### 867 4.4 | Conclusion

868 Teeth are involved in two main functions in elasmobranchs: feeding and reproduction. Although ontogenetic shifts in tooth morphologies have been reported in different shark orders, very few studies focused on the changes from an embryonic to a mature dentition in males and females separately. Here we gave a description of the wide, natural, and intraspecific variation of tooth shapes in *S. stellaris*. We detailed the tooth form transitions between three ontogenetic stages and

877 focused on: (i) graded variation of several morphometric parameters along the mesio-distal axis of a jaw, only starting during the juvenile stage and on (ii) gynandric heterodonty at mature stage generated by a stronger change in developmental trajectory for males (unicuspid to tricuspid teeth) than for females (addition of lateral cusps). We hope that the detailed morphospaces we provide here for *S. stellaris* teeth will be extended in an interspecific framework to challenge hypotheses on the developmental mechanisms that generate the known elasmobranch tooth shape diversity. 887

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 905 The authors declare no conflict of interest. The datasets generated and analyzed in the current study are not publicly available due to ongoing other project but are available from the corresponding author on reasonable request. 906  
 907  
 908  
 909

## 6 | AUTHOR'S CONTRIBUTIONS 910

911 FB generated and analyzed the data; FB and AE designed the statistical analyses; FB, NG and MDT designed the experimental setup; FB and MDT drafted the manuscript. 912  
 913  
 914

## References

- 915 **References**
- 916 Adams, D. C. and Otárola-Castillo, E. (2013) geomorph: an  
917 R package for the collection and analysis of geometric  
918 morphometric shape data. *Methods in Ecology and Evolution*, **4**, 393–399.  
919
- 920 Bazzi, M., Kear, B. P., Blom, H., Ahlberg, P. E. and Campione,  
921 N. E. (2018) Static dental disparity and morphological  
922 turnover in sharks across the end-Cretaceous mass extinction.  
923 *Current Biology*, **28**, 2607–2615.e3.
- 924 Berio, F. and Bayle, Y. (2020) Scyland3D: Processing 3D  
925 landmarks. *Journal of Open Source Software*, **5**, 1262.
- 926 Berio, F. and Debais-Thibaud, M. (2019) Evolutionary developmental  
927 genetics of teeth and odontodes in jawed  
928 vertebrates: a perspective from the study of elasmobranchs.  
929 *Journal of Fish Biology*.
- 930 Bookstein, F. L. (1991) *Morphometric tools for landmark data: geometry and biology*. Cambridge: Cambridge University Press.
- 933 – (1997) Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Medical Image Analysis*, **1**, 225–243.
- 936 Braccini, J. M. and Chiaramonte, G. E. (2002) Intraspecific variation in the external morphology of the sand skate. *Journal of Fish Biology*, **61**, 959–972.
- 939 Brough, J. (1937) On certain Secondary Sexual Characters in the Common Dogfish (*Scyliorhinus caniculus*). *Journal of Zoology*, **107**, 217–223.
- 942 Calamari, Z. T., Hu, J. K.-H. and Klein, O. D. (2018) Tissue mechanical forces and evolutionary developmental changes act through space and time to shape tooth morphology and function. *BioEssays*, **40**, 1800140.
- 946 Capapé, C. (1975) Contribution à la biologie des Scyliorhinidae des côtes tunisiennes. IV *Scyliorhinus stellaris* (Linné, 1758). Régime alimentaire. *Archives de l'Institut Pasteur de Tunis*, **52**, 383–394.
- 950 Cappetta, H. (1986) Types dentaires adaptatifs chez les séla-ciens actuels et post-paléozoïques. *Palaeovertebrata*, **16**, 57–76.
- 953 – (2012) *Handbook of Paleichthyology, Vol 3E: Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth*. Munich: Verlag Dr. Friedrich Pfeil.
- 956 Chew, K., Pask, A., Hickford, D., Shaw, G. and Renfree, M. (2014) A dual role for SHH during phallus development in a marsupial. *Sexual Development*, **8**, 166–177.
- Cobourne, M. T. and Sharpe, P. T. (2003) Tooth and jaw: molecular mechanisms of patterning in the first branchial arch. *Archives of Oral Biology*, **48**, 1–14.
- Coolen, M., Menuet, A., Chassoux, D., Compagnucci, C., Henry, S., Lévêque, L., Da Silva, C., Gavory, F., Samain, S., Wincker, P., Thermes, C., D'Aubenton-Carafa, Y., Rodriguez-Moldes, I., Naylor, G., Depew, M., Sourdain, P. and Mazan, S. (2008) The dogfish *Scyliorhinus canicula*: A reference in jawed vertebrates. *CSH protocols*, **2008**, pdb.emo111.
- Correia, J. P. (1999) Tooth loss rate from two captive sandtiger sharks (*Carcharias taurus*). *Zoo Biology*, **18**, 313–317.
- Cullen, J. A. and Marshall, C. D. (2019) Do sharks exhibit heterodonty by tooth position and over ontogeny? A comparison using elliptic Fourier analysis. *Journal of Morphology*, **280**, 687–700.
- de Sousa Rangel, B., Santander-Neto, J., Rici, R. E. G. and Lessa, R. (2016) Dental sexual dimorphism and morphology of *Urotrygon microphthalmum*. *Zoomorphology*, **135**, 367–374.
- Debais-Thibaud, M., Chiori, R., Enault, S., Oulion, S., Germon, I., Martinand-Mari, C., Casane, D. and Borday-Birraux, V. (2015) Tooth and scale morphogenesis in shark: an alternative process to the mammalian enamel knot system. *BMC Evolutionary Biology*, **15**, 292.
- Debais-Thibaud, M., Metcalfe, C. J., Pollack, J., Germon, I., Ekker, M., Depew, M., Laurenti, P., Borday-Birraux, V. and Casane, D. (2013) Heterogeneous Conservation of *Dlx* Paralog Co-Expression in Jawed Vertebrates. *PLoS ONE*, **8**, e68182.
- Debais-Thibaud, M., Oulion, S., Bourrat, F., Laurenti, P., Casane, D. and Borday-Birraux, V. (2011) The homology of odontodes in gnathostomes: insights from *Dlx* gene expression in the dogfish, *Scyliorhinus canicula*. *BMC Evolutionary Biology*, **11**, 307.
- Du, W., Hu, J. K. H., Du, W. and Klein, O. D. (2017) Lineage tracing of epithelial cells in developing teeth reveals two strategies for building signaling centers. *Journal of Biological Chemistry*, **292**, 15062–15069.
- Ellis, J. R. and Shackley, S. E. (1995) Ontogenetic changes and sexual dimorphism in the head, mouth and teeth of the lesser spotted dogfish. *Journal of Fish Biology*, **47**, 155–164.

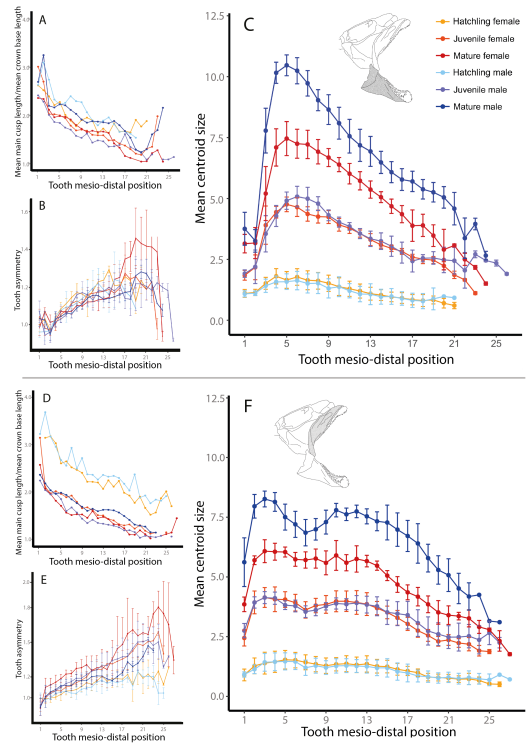
- 1003 Erdogan, Z., Koc, H., Cakir, T., Nerlović, V. and Dulčić, J. 1045  
 1004 (2004) Sexual dimorphism in the small-spotted catshark 1046  
 1005 *Scyliorhinus canicula* from the Edremit Bay (Turkey). *Se-* 1047  
 1006 *ries Historia Naturalis*, **14**, 165–170. 1048
- 1007 Feduccia, A. and Slaughter, B. H. (1974) Sexual dimorphism 1049  
 1008 in skates (Rajidae) and its possible role in differential 1050  
 1009 niche utilization. *Evolution*, **8**, 164–168. 1051
- 1010 Fischer, W., Bauchot, M.-L. and Schneider, M. (1987) Fiches 1052  
 1011 FAO d'identification des espèces pour les besoins de la 1053  
 1012 pêche (Révision 1). Méditerranée et Mer Noire. Zone de 1054  
 1013 pêche 37. Vertébrés. *FAO*, **2**, 761–1530. 1055
- 1014 Frazzetta, T. H. (1988) The mechanics of cutting and the 1056  
 1015 form of shark teeth (Chondrichthyes, Elasmobranchii). 1057  
 1016 *Zoomorphology*, **108**, 93–107. 1058
- 1017 French, G. C. A., Stürup, M., Rizzuto, S., van Wyk, J. H., Ed- 1059  
 1018 wards, D., Dolan, R. W., Wintner, S. P., Towner, A. V. and 1060  
 1019 Hughes, W. O. H. (2017) The tooth, the whole tooth 1061  
 1020 and nothing but the tooth: tooth shape and ontogenetic 1062  
 1021 shift dynamics in the white shark *Carcharodon carcharias*. 1063  
 1022 *Journal of Fish Biology*, **91**, 1032–1047. 1064
- 1023 Fruciano, C. (2016) Measurement error in geometric mor- 1065  
 1024 phometrics. *Development Genes and Evolution*, **226**, 1066  
 1025 139–158. 1067
- 1026 Geniz, J., Nishizaki, O. and Perez, J. (2007) Morphological 1068  
 1027 variation and sexual dimorphism in the California skate, 1069  
 1028 *Raja inornata* Jordan and Gilbert, 1881 from the Gulf of 1070  
 1029 California, Mexico. *Zootaxa*, **1545**, 1–16. 1071
- 1030 Gosztonyi, A. E. (1973) About sexual and secondary 1072  
 1031 dimorphism of *Halaelurus bivius* (Muller & Henle, 1841) 1073  
 1032 Garman 1913 (Elasmobranchii, Scyliorhinidae) in 1074  
 1033 Patagonian-Fueguinas waters. *Physis A*, **32**, 317–323. 1075
- 1034 Gottfried, M. D. and Francis, M. P. (1996) Developmental 1076  
 1035 changes in white shark tooth morphology: implications 1077  
 1036 for studies on fossil sharks. *Journal of Vertebrate Paleon-* 1078  
 1037 *toLOGY*, **16**. 1079
- 1038 Gutteridge, A. N. and Bennett, M. B. (2014) Functional impli- 1080  
 1039 cations of ontogenetically and sexually dimorphic den- 1081  
 1040 tition in the eastern shovelnose ray, *Aptychotrema ros-* 1082  
 1041 *trata*. *The Journal of experimental biology*, **217**, 192–200. 1083
- 1042 Hale, L. F. and Lowe, C. G. (2008) Age and growth of the 1084  
 1043 round stingray *Urobatis halleri* at Seal Beach, California. 1085  
 1044 *Journal of Fish Biology*, **73**, 510–523. 1086
- Heisler, N. and Neumann, P. (1980) The role of physico- 1087  
 chemical buffering and of bicarbonate transfer pro- 1088  
 cesses in intracellular pH regulation in response to 1089  
 changes of temperature in the larger spotted dogfish 1090  
 (*Scyliorhinus stellaris*). *Journal of Experimental Biology*, **85**, 1091  
 99–110. 1092
- Herman, J., Hovestadt-Euler, M. and Hovestadt, D. C. (1990) 1093  
 Contributions to the study of the comparative morphol- 1094  
 ogy of teeth and other relevant ichthyodorulites in liv- 1095  
 ing supraspecific taxa of Chondrichthyan fishes. Part 1096  
 A: Selachii. No. 2b: Order: Carcharhiniformes - Family: 1097  
 Scyliorhinidae. *Bulletin de l'Institut Royal des Sciences Na-* 1098  
*turelles de Belgique*, **60**, 181–230. 1099
- Hosoya, A., Shalehin, N., Takebe, H., Shimo, T. and Irie, 1100  
 K. (2020) Sonic Hedgehog signaling and tooth devel- 1101  
 opment. *International Journal of Molecular Sciences*, **21**, 1102  
 1587. 1103
- Iglésias, S. P., Lecointre, G. and Sellos, D. Y. (2005) Exten- 1104  
 sive paraphyly within sharks of the order Carcharhini- 1105  
 formes inferred from nuclear and mitochondrial genes. 1106  
*Molecular Phylogenetics and Evolution*, **34**, 569–583. 1107
- Jernvall, J. (2000) Linking development with generation of 1108  
 novelty in mammalian teeth. *Proceedings of the National* 1109  
*Academy of Sciences of the United States of America*, **97**, 1110  
 2641–2645. 1111
- Kajiura, S. N. and Tricas, T. C. (1996) Seasonal dynamics of 1112  
 dental sexual dimorphism in the Atlantic stingray *Dasy-* 1113  
*atis sabina*. *Journal of Experimental Biology*, **199**, 2297– 1114  
 2306. 1115
- Litvinov, F. F. and Laptikhovsky, V. V. (2005) Methods of in- 1116  
 vestigations of shark heterodonty and dental formulae's 1117  
 variability with the blue shark, *Prionace glauca* taken as 1118  
 an example. In *ICES CM*, **15**. 1119
- Lucifora, L. O., Menni, R. C. and Escalante, A. H. (2001) Anal- 1120  
 ysis of dental insertion angles in the sand tiger shark, 1121  
*Carcharias taurus* (Chondrichthyes: Lamniformes). *Cy-* 1122  
*bium*, **25**, 23–31. 1123
- Luer, C. A., Blum, P. C. and Gilbert, P. W. (1990) Rate of tooth 1124  
 replacement in the nurse shark, *Ginglymostoma cirratum*. 1125  
*Copeia*, **1990**, 182–191. 1126
- Marramà, G. and Kriwet, J. (2017) Principal component and 1127  
 discriminant analyses as powerful tools to support taxo- 1128  
 nomic identification and their use for functional and phy- 1129  
 logenetic signal detection of isolated fossil shark teeth. 1130  
*PLoS ONE*, **12**, e0188806. 1131



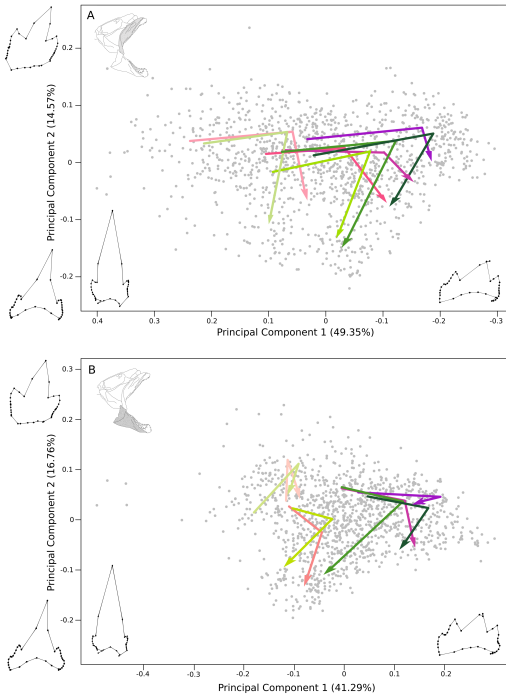
- 1090 Martin, K., Rasch, L. and Cooper, R. (2016) Sox2+ progen- 1135  
 1091 itors in sharks link taste development with the evolu- 1136  
 1092 tion of regenerative teeth from denticles. *PNAS*, **113**, 1137  
 1093 14769–14774. 1138
- 1094 McCourt, R. and Kerstitch, A. (1980) Mating behavior and 1139  
 1095 sexual dimorphism in dentition in the stingray, *Urolophus*  
 1096 *concentricus*, from the Gulf of California. *Copeia*, **1980**,  
 1097 900–901.
- 1098 McEachran, J. D. (1977) Reply to “Sexual dimorphism in  
 1099 skates (Rajidae)”. *Evolution*, **31**, 218–220.
- 1100 Meredith Smith, M., Underwood, C., Clark, B., Kriwet, J.  
 1101 and Johanson, Z. (2018) Development and evolution of  
 1102 tooth renewal in neoselachian sharks as a model for  
 1103 transformation in chondrichthyan dentitions. *Journal of*  
 1104 *Anatomy*, **232**, 891–907.
- 1105 Moczek, A. P. (2015) Developmental plasticity and evolu-  
 1106 tion—*quo vadis?* *Heredity*, **115**, 302–305.
- 1107 Motta, P. J. and Wilga, C. D. (2001) Advances in the study  
 1108 of feeding behaviors, mechanisms, and mechanics of  
 1109 sharks. In *The behavior and sensory biology of elasmobranch fishes: an anthology in memory of Donald Richard Nelson*, 131–156. Dordrecht: Springer.
- 1112 Moyer, J. K. and Bemis, W. E. (2016) Tooth microstruc-  
 1113 ture and replacement in the gulper shark, *Centrophorus*  
 1114 *granulosus* (Squaliformes: Centrophoridae). *Copeia*, **104**,  
 1115 529–538.
- 1116 Mullin, S. K. and Taylor, P. J. (2002) The effects of parallax  
 1117 on geometric morphometric data. *Computers in Biology*  
 1118 *and Medicine*, **32**, 455–464.
- 1119 Musa, S. M., Czachur, M. V. and Shiels, H. A. (2018)  
 1120 Oviparous elasmobranch development inside the egg  
 1121 case in 7 key stages. *PLoS ONE*, **13**, e0206984.
- 1122 Ogino, Y., Katoh, H. and Yamada, G. (2004) Androgen depen-  
 1123 dent development of a modified anal fin, gonopodium,  
 1124 as a model to understand the mechanism of secondary  
 1125 sexual character expression in vertebrates. *FEBS Letters*,  
 1126 **575**, 119–126.
- 1127 O’Shaughnessy, K. L., Dahn, R. D. and Cohn, M. J. (2015)  
 1128 Molecular development of chondrichthyan claspers and  
 1129 the evolution of copulatory organs. *Nature Communica-*  
 1130 *tions*, **6**, 6698.
- 1131 Piiper, J., Meyer, M., Worth, H. and Willmer, H. (1977) Res-  
 1132 piration and circulation during swimming activity in the  
 1133 dogfish *Scyliorhinus stellaris*. *Respiration Physiology*, **30**,  
 1134 221–239.
- Powter, D. M., Gladstone, W. and Platell, M. (2010) The in- 1135  
 fluence of sex and maturity on the diet, mouth morphol- 1136  
 ogy and dentition of the Port Jackson shark, *Heterodon-* 1137  
*tus portusjacksoni*. *Marine and Freshwater Research*, **61**, 1138  
 74. 1139
- Pratt, Jr., H. L. and Carrier, J. C. (2001) A Review of Elas- 1140  
 mobranch Reproductive Behavior with a Case Study on 1141  
 the Nurse Shark, *Ginglymostoma cirratum*. *Environmental* 1142  
*Biology of Fishes*, **60**, 157–188. 1143
- Purdy, R. W. and Francis, M. P. (2007) Ontogenetic develop- 1144  
 ment of teeth in *Lamna nasus* (Bonnaterre, 1758) (Chon- 1145  
 drichthyes: Lamnidae) and its implications for the study 1146  
 of fossil shark teeth. *Journal of Vertebrate Paleontology*, 1147  
**27**, 798–810. 1148
- Rasch, L. J., Martin, K. J., Cooper, R. L., Metscher, B. D., Un- 1149  
 derwood, C. J. and Fraser, G. J. (2016) An ancient dental 1150  
 gene set governs development and continuous regen- 1151  
 eration of teeth in sharks. *Developmental Biology*, **415**, 1152  
 347–370. 1153
- Reif, W.-E. (1976) Morphogenesis, pattern formation and 1154  
 function of the dentition of *Heterodontus* (Selachii). 1155  
*Zoomorphology*, **83**, 1–47. 1156
- (1980) A mechanism for tooth pattern reversal in sharks: 1157  
 the polarity switch model. *Wilhelm Roux’s archives of de-* 1158  
*velopmental biology*, **188**, 115–122. 1159
- (1982) Evolution of Dermal Skeleton and Dentition in Ver- 1160  
 tebrates: The Odontode Regulation Theory. In *Evolu-* 1161  
*tionary Biology* (eds. M. K. Hecht, B. Wallace and G. T. 1162  
 Prance), chap. 7, 287–368. New York: Plenum Press. 1163
- Rennois , E., Kavanagh, K. D., Lazzari, V., H kkinen, T. J., 1164  
 Rice, R., Pantalacci, S., Salazar-Ciudad, I. and Jernvall, 1165  
 J. (2017) Mechanical constraint from growing jaw facili- 1166  
 tates mammalian dental diversity. *Proceedings of the Na-* 1167  
*tional Academy of Sciences of the United States of America*, 1168  
**114**, 9403–9408. 1169
- Salazar-Ciudad, I. (2008) Tooth morphogenesis in vivo, in 1170  
 vitro, and in silico. *Current Topics in Developmental Biol-* 1171  
*ogy*, **81**, 341–371. 1172
- Salazar-Ciudad, I. and Jernvall, J. (2010) A computational 1173  
 model of teeth and the developmental origins of mor- 1174  
 phological variation. *Nature*, **464**, 583. 1175
- Shimada, K. (2002) Dental homologies in lamniform sharks 1176  
 (Chondrichthyes: Elasmobranchii). *Journal of Morphol-* 1177  
*ogy*, **251**, 38–72. 1178

- 1179 – (2005) Phylogeny of lamniform sharks (Chondrichthyes: 1224  
1180 Elasmobranchii) and the contribution of dental charac- 1225  
1181 ters to lamniform systematics. *Paleontological Research*, 1226  
1182 **9**, 55–72.
- 1183 Smith, M. M. (2003) Vertebrate dentitions at the origin of 1227  
1184 jaws: when and how pattern evolved. *Evolution and De-* 1228  
1185 *velopment*, **5**, 394–413.
- 1186 Smith, M. M., Fraser, G. J., Chaplin, N., Hobbs, C. and Gra- 1229  
1187 ham, A. (2009) Reiterative pattern of sonic hedgehog ex- 1230  
1188 pression in the catshark dentition reveals a phylogenetic 1231  
1189 template for jawed vertebrates. *Proceedings of the Royal* 1232  
1190 *Society B: Biological Sciences*, **276**, 1225–33.
- 1191 Smith, M. M., Johanson, Z., Underwood, C. and Diekwisch, 1235  
1192 T. G. H. (2013) Pattern formation in development of 1236  
1193 chondrichthyan dentitions: a review of an evolutionary 1237  
1194 model. *Historical Biology*, **25**, 127–142.
- 1195 Snelson, F. F., Rasmussen, L., Johnson, M. R. and Hess, D. L. 1238  
1196 (1997) Serum concentrations of steroid hormones dur- 1239  
1197 ing reproduction in the Atlantic stingray, *Dasyatis sabina*. 1240  
1198 *General and Comparative Endocrinology*, **108**, 67–79.
- 1199 Soares, K., Gomes, U. and De Carvalho, M. (2016) Taxo- 1241  
1200 nomic review of catsharks of the *Scyliorhinus haecke-* 1242  
1201 *lii* group, with the description of a new species (Chon- 1243  
1202 drichthyes: Carcharhiniformes: Scyliorhinidae). *Zootaxa*, 1244  
1203 **4066**, 501–534.
- 1204 Soares, K. D. A. (2019) Sexually dimorphic body proportions 1245  
1205 in the catshark genus *Scyliorhinus* (Chondrichthyes: Car- 1246  
1206 charhiniformes: Scyliorhinidae). *Journal of Fish Biology*, 1247  
1207 **95**, 683–685.
- 1208 Soares, K. D. A. and Carvalho, M. R. D. (2019) The catshark 1248  
1209 genus *Scyliorhinus* (Chondrichthyes: Carcharhiniformes: 1249  
1210 Scyliorhinidae): taxonomy, morphology and distribution. 1250  
1211 *Zootaxa*, **4601**, 1–147.
- 1212 Soda, K., Slice, D. and Naylor, G. (2017) Artificial neural 1251  
1213 networks and geometric morphometric methods as a 1252  
1214 means for classification: A case-study using teeth from 1253  
1215 *Carcharhinus sp.* (Carcharhinidae). *Journal of Morphology*, 1254  
1216 **278**, 131–141.
- 1217 Soldo, A., Dulčić, J., Cetinic, P. and Cetinic, P. (2000) Con- 1255  
1218 tribution to the study of the morphology of the teeth 1256  
1219 of the nursehound *Scyliorhinus stellaris* (Chondrichthyes: 1257  
1220 Scyliorhinidae). *Scientia Marina*, **64**, 355–356.
- 1221 Springer, S. (1966) A review of western Atlantic cat sharks, 1258  
1222 Scyliorhinidae, with descriptions of a new genus and five 1259  
1223 new species. *Fishery Bulletin*, **65**, 581–624.
- (1967) Social organization of shark populations. In *Sharks,* 1260  
*Skates and Rays* (eds. P. W. Gilbert, R. F. Mathewson and 1261  
D. P. Rall), 149–174. Baltimore: Johns Hopkins Press.
- (1979) A revision of the catsharks, family Scyliorhinidae. 1262  
*Tech. rep.*, US Department of Commerce. 1263
- Stalling, D., Westerhoff, M. and Hege, H. C. (2005) Amira: 1264  
A highly interactive system for visual data analysis. *The* 1265  
*visualization handbook*. 1266
- Strasburg, D. W. (1963) The diet and dentition of *Isistius* 1267  
*brasilensis*, with remarks on tooth replacement in other 1268  
sharks. *Copeia*, 33–40. 1269
- Taniuchi, T. and Shimizu, M. (1993) Dental sexual dimor- 1270  
phism and food habits in the stingray *Dasyatis akajei* 1271  
from Tokyo Bay, Japan. *Nippon Suisan Gakkaishi*, **59**, 53– 1272  
60. 1273
- Thesleff, I. and Mikkola, M. (2002) The role of growth fac- 1274  
tors in tooth development. *International Review of Cytol-* 1275  
*ogy*, **217**, 93–135. 1276
- Underwood, C., Johanson, Z. and Smith, M. M. (2016) Cut- 1277  
ting blade dentitions in squaliform sharks form by mod- 1278  
ification of inherited alternate tooth ordering patterns. 1279  
*Open Science*, **3**, 160385. 1280
- Underwood, C. J., Johanson, Z., Welten, M., Metscher, B., 1281  
Rasch, L. J., Fraser, G. J. and Smith, M. M. (2015) De- 1282  
velopment and evolution of dentition pattern and tooth 1283  
Order in the skates And rays (Batoidea; Chondrichthyes). 1284  
*PLoS ONE*, **10**, e0122553. 1285
- Van Otterloo, E., Li, H., Jones, K. L. and Williams, T. (2018) 1286  
AP-2 $\alpha$  and AP-2 $\beta$  cooperatively orchestrate homeobox 1287  
gene expression during branchial arch patterning. *Devel-* 1288  
*opment*, **145**. 1289
- Vélez-Zuazo, X. and Agnarsson, I. (2011) Shark tales: A 1290  
molecular species-level phylogeny of sharks (Selachi- 1291  
morpha, Chondrichthyes). *Molecular Phylogenetics and* 1292  
*Evolution*, **58**, 207–217. 1293
- Webster, M. and Sheets, H. D. (2010) A Practical Introduc- 1294  
tion to Landmark-Based Geometric Morphometrics. *The* 1295  
*Paleontological Society Papers*, **16**, 163–188. 1296
- Whitenack, L. B. and Gottfried, M. D. (2010) A morphomet- 1297  
ric approach for addressing tooth-based species delimita- 1298  
tion in fossil mako sharks, *Isurus* (Elasmobranchii: Lam- 1299  
niformes). *Journal of Vertebrate Paleontology*, **30**, 17–25. 1300

- 1266 Wiley, D., Amenta, N., Alcantara, D., Ghosh, D., Kil, Y., Del-  
 1267 son, E., Harcourt-Smith, W., Rohlf, F., St. John, K. and  
 1268 Hamann, B. (2005) Evolutionary Morphing. In *Proceed-*  
 1269 *ings of the IEEE International Conference on Visualization,*  
 1270 431–438. Minneapolis: Institute of Electrical and Elec-  
 1271 tronics Engineers (IEEE).
- 1272 Wilga, C. D. and Motta, P. J. (2000) Durophagy in sharks:  
 1273 feeding mechanics of the hammerhead *Sphyrna tiburo*.  
 1274 *The Journal of Experimental Biology*, **203**, 2781–2796.



**FIGURE 4** Tooth dimensions of *S. stellaris* right Meckelian and palatoquadrate teeth. A and D) Morphometric measure of the ratio between main cusp height and crown base width; B and E) Deviation to tooth bilateral symmetry: difference between the tooth tip and each crown base extremity distances. C and F) Tooth centroid sizes. At each tooth position, mean values are computed among all tooth generations (internal replicates), before being computed among all specimens. Error bars are standard deviations among replicates and specimens.



**FIGURE 5** 2D representation (PC1xPC2) of tooth developmental trajectories in *S. stellaris*. A) 2D trajectories for palatoquadrate tooth files 3, 10, 15 and 20; B) 2D trajectories for Meckel's tooth files 1, 5, 15, and 20. The trajectory representations are drawn between the mean shape of hatchling (starting point), juvenile, and mature (arrow tip) specimen teeth. Purple and green shades are for females and males trajectories respectively. Mesial to distal files appear in light to deep shades.

1275 **7 | SUPPLEMENTARY MATERIAL**

**ADDITIONAL FIGURE** Tooth main cusp height and crown base width in *S. stellaris*. A) Meckelian teeth of hatchlings; B) Palatoquadrate teeth of hatchlings; C) Meckelian teeth of juveniles; D) Palatoquadrate teeth of juveniles; E) Meckelian teeth of matures; F) Palatoquadrate teeth of matures. The main cusp values are the mean lengths between the mesial-most landmark of the tooth and the main cusp tip, and the distal-most landmark of the tooth and the main cusp tip (d1-17 and d17-33). The crown base values are the lengths between the mesial-most and the distal-most landmarks on the tooth (d1-38).

**ADDITIONAL TABLE 1** Developmental trajectory values within sexes for palatoquadrate teeth. Significant p-values after Benjamini & Hochberg correction are in bold. Due to the difference in total tooth file number between stages, some comparisons could not be done (NAs). -, difference; dL, delta length; HJ, hatchling-to-juvenile; JM, juvenile-to-mature.

File	Females	Males	Females	Males
	dL (JM-HJ) (p-val)	dL (JM-HJ) (p-val)	angle cor (p-val)	angle cor (p-val)
1	$-5.11e^{-2}$ ( $5.40e^{-2}$ )	$1.70e^{-3}$ ( $9.54e^{-1}$ )	1.21 ( <b><math>1.00e^{-3}</math></b> )	1.83 ( <b><math>1.00e^{-3}</math></b> )
2	$-4.70e^{-2}$ ( $1.59e^{-1}$ )	$-5.33e^{-2}$ ( <b><math>4.60e^{-2}</math></b> )	1.76 ( <b><math>1.00e^{-3}</math></b> )	1.99 ( <b><math>1.00e^{-3}</math></b> )
3	$-8.42e^{-2}$ ( <b><math>3.20e^{-2}</math></b> )	$2.08e^{-2}$ ( $5.40e^{-1}$ )	1.62 ( <b><math>1.00e^{-3}</math></b> )	1.96 ( <b><math>1.00e^{-3}</math></b> )
4	$-1.00e^{-1}$ ( <b><math>5.00e^{-3}</math></b> )	$-5.00e^{-4}$ ( $9.88e^{-1}$ )	1.41 ( <b><math>1.00e^{-3}</math></b> )	2.00 ( <b><math>1.00e^{-3}</math></b> )
5	$-3.93e^{-2}$ ( $1.77e^{-1}$ )	$3.60e^{-2}$ ( $2.40e^{-1}$ )	1.29 ( <b><math>1.00e^{-3}</math></b> )	2.10 ( <b><math>1.00e^{-3}</math></b> )
6	$-5.88e^{-2}$ ( <b><math>2.60e^{-2}</math></b> )	$1.45e^{-2}$ ( $6.84e^{-1}$ )	1.25 ( <b><math>1.00e^{-3}</math></b> )	2.20 ( <b><math>1.00e^{-3}</math></b> )
7	$-4.40e^{-2}$ ( $7.10e^{-2}$ )	$-2.18e^{-2}$ ( $4.56e^{-1}$ )	1.08 ( <b><math>1.00e^{-3}</math></b> )	2.11 ( <b><math>1.00e^{-3}</math></b> )
8	$-7.89e^{-2}$ ( <b><math>1.10e^{-2}</math></b> )	$-6.10e^{-3}$ ( $8.30e^{-1}$ )	1.26 ( <b><math>1.00e^{-3}</math></b> )	2.13 ( <b><math>1.00e^{-3}</math></b> )
9	$-8.76e^{-2}$ ( <b><math>2.00e^{-3}</math></b> )	$-2.71e^{-2}$ ( $9.70e^{-1}$ )	1.56 ( <b><math>1.00e^{-3}</math></b> )	2.01 ( <b><math>1.00e^{-3}</math></b> )
10	$-5.10e^{-2}$ ( $6.10e^{-2}$ )	$-2.69e^{-2}$ ( $4.59e^{-1}$ )	1.36 ( <b><math>1.00e^{-3}</math></b> )	2.06 ( <b><math>1.00e^{-3}</math></b> )
11	$-8.35e^{-2}$ ( <b><math>1.50e^{-2}</math></b> )	$-2.70e^{-3}$ ( $9.30e^{-1}$ )	1.83 ( <b><math>1.00e^{-3}</math></b> )	1.97 ( <b><math>1.00e^{-3}</math></b> )
12	$-1.26e^{-1}$ ( <b><math>3.00e^{-3}</math></b> )	$-1.86e^{-2}$ ( $5.70e^{-1}$ )	1.56 ( <b><math>2.00e^{-3}</math></b> )	2.00 ( <b><math>1.00e^{-3}</math></b> )
13	$-9.78e^{-2}$ ( <b><math>1.10e^{-2}</math></b> )	$-4.97e^{-2}$ ( $2.08e^{-1}$ )	1.74 ( <b><math>3.00e^{-3}</math></b> )	2.03 ( <b><math>1.00e^{-3}</math></b> )
14	$-1.45e^{-1}$ ( <b><math>3.00e^{-3}</math></b> )	$-1.83e^{-2}$ ( $6.13e^{-1}$ )	1.56 ( <b><math>1.00e^{-3}</math></b> )	2.15 ( <b><math>1.00e^{-3}</math></b> )
15	$-1.18e^{-1}$ ( <b><math>4.00e^{-3}</math></b> )	$-2.78e^{-2}$ ( $4.32e^{-1}$ )	1.18 ( <b><math>1.00e^{-3}</math></b> )	2.11 ( <b><math>1.00e^{-3}</math></b> )
16	$-1.58e^{-1}$ ( <b><math>2.00e^{-3}</math></b> )	$-2.93e^{-2}$ ( $3.20e^{-1}$ )	1.53 ( <b><math>1.00e^{-3}</math></b> )	2.20 ( <b><math>1.00e^{-3}</math></b> )
17	$-1.55e^{-1}$ ( <b><math>1.00e^{-3}</math></b> )	$-6.93e^{-2}$ ( $5.90e^{-2}$ )	1.40 ( <b><math>1.00e^{-3}</math></b> )	1.98 ( <b><math>1.00e^{-3}</math></b> )
18	$9.58e^{-2}$ ( <b><math>2.10e^{-2}</math></b> )	$-5.08e^{-2}$ ( $1.08e^{-1}$ )	$9.81e^{-1}$ ( <b><math>1.00e^{-3}</math></b> )	2.09 ( <b><math>1.00e^{-3}</math></b> )
19	$-1.34e^{-1}$ ( <b><math>4.00e^{-3}</math></b> )	$-9.68e^{-2}$ ( <b><math>5.00e^{-3}</math></b> )	$8.51e^{-1}$ ( <b><math>3.00e^{-3}</math></b> )	2.05 ( <b><math>1.00e^{-3}</math></b> )
20	$-1.66e^{-1}$ ( <b><math>1.00e^{-3}</math></b> )	$-1.06e^{-1}$ ( <b><math>1.90e^{-2}</math></b> )	1.56 ( <b><math>1.00e^{-3}</math></b> )	2.26 ( <b><math>1.00e^{-3}</math></b> )
21	$-1.66e^{-1}$ ( <b><math>1.00e^{-3}</math></b> )	$-1.23e^{-1}$ ( <b><math>1.30e^{-2}</math></b> )	1.55 ( <b><math>1.00e^{-3}</math></b> )	2.29 ( <b><math>1.00e^{-3}</math></b> )
22	$-1.86e^{-1}$ ( <b><math>1.00e^{-3}</math></b> )	$-1.42e^{-1}$ ( <b><math>9.00e^{-3}</math></b> )	1.54 ( <b><math>1.00e^{-3}</math></b> )	2.49 ( <b><math>1.00e^{-3}</math></b> )
23	$-1.13e^{-1}$ ( $4.00e^{-2}$ )	$-9.82e^{-2}$ ( $1.11e^{-1}$ )	1.43 ( <b><math>1.00e^{-3}</math></b> )	2.32 ( <b><math>7.00e^{-3}</math></b> )
24	$-1.14e^{-1}$ ( <b><math>2.50e^{-2}</math></b> )	NA	1.45 ( <b><math>3.00e^{-3}</math></b> )	NA
25	$-1.95e^{-1}$ ( <b><math>1.00e^{-2}</math></b> )	NA	1.71 ( <b><math>1.20e^{-2}</math></b> )	NA

**ADDITIONAL TABLE 2** Developmental trajectory values within sexes for Meckelian teeth. Significant p-values after Benjamini & Hochberg correction are in bold. Due to the difference in total tooth file number between stages, some comparisons could not be done (NAs). -, difference; dL, delta length; HJ, hatchling-to-juvenile; JM, juvenile-to-mature.

File	Females	Males	Females	Males
	dL (JM-HJ) (p-val)	dL (JM-HJ) (p-val)	angle cor (p-val)	angle cor (p-val)
1	$4.75e^{-3}$ ( $8.40e^{-1}$ )	$3.22e^{-2}$ ( $1.40e^{-1}$ )	2.38 ( <b><math>4.00e^{-3}</math></b> )	1.84 ( <b><math>1.00e^{-3}</math></b> )
2	$1.23e^{-2}$ ( $6.64e^{-1}$ )	$1.25e^{-1}$ ( <b><math>1.00e^{-2}</math></b> )	2.17 ( <b><math>9.00e^{-3}</math></b> )	2.27 ( <b><math>1.00e^{-3}</math></b> )
3	$-7.49e^{-4}$ ( $9.78e^{-1}$ )	$1.99e^{-2}$ ( $4.35e^{-1}$ )	1.82 ( <b><math>1.00e^{-3}</math></b> )	1.99 ( <b><math>1.00e^{-3}</math></b> )
4	$-7.83e^{-3}$ ( $6.50e^{-1}$ )	$8.41e^{-3}$ ( $7.00e^{-1}$ )	1.74 ( <b><math>1.00e^{-3}</math></b> )	2.13 ( <b><math>1.00e^{-3}</math></b> )
5	$-5.86e^{-3}$ ( $8.00e^{-1}$ )	$1.22e^{-2}$ ( $5.85e^{-1}$ )	1.71 ( <b><math>1.00e^{-3}</math></b> )	2.07 ( <b><math>1.00e^{-3}</math></b> )
6	$-3.00e^{-3}$ ( $9.12e^{-1}$ )	$4.08e^{-2}$ ( $1.17e^{-1}$ )	1.85 ( <b><math>1.00e^{-3}</math></b> )	2.21 ( <b><math>1.00e^{-3}</math></b> )
7	$3.85e^{-3}$ ( $8.60e^{-1}$ )	$1.55e^{-2}$ ( $5.85e^{-1}$ )	1.55 ( <b><math>1.00e^{-3}</math></b> )	2.17 ( <b><math>1.00e^{-3}</math></b> )
8	$-6.65e^{-3}$ ( $7.65e^{-1}$ )	$2.73e^{-2}$ ( $3.13e^{-1}$ )	1.84 ( <b><math>2.00e^{-3}</math></b> )	2.23 ( <b><math>1.00e^{-3}</math></b> )
9	$-4.47e^{-2}$ ( <b><math>2.30e^{-2}</math></b> )	$1.80e^{-2}$ ( $4.97e^{-1}$ )	1.67 ( <b><math>1.00e^{-3}</math></b> )	2.19 ( <b><math>1.00e^{-3}</math></b> )
10	$-4.92e^{-2}$ ( <b><math>4.40e^{-2}</math></b> )	$5.72e^{-2}$ ( $5.40e^{-1}$ )	1.56 ( <b><math>2.00e^{-3}</math></b> )	2.04 ( <b><math>1.00e^{-3}</math></b> )
11	$-5.60e^{-2}$ ( <b><math>1.40e^{-2}</math></b> )	$8.30e^{-3}$ ( $7.63e^{-1}$ )	1.73 ( <b><math>1.00e^{-3}</math></b> )	2.12 ( <b><math>1.00e^{-3}</math></b> )
12	$-5.02e^{-2}$ ( <b><math>3.80e^{-2}</math></b> )	$2.43e^{-2}$ ( $3.11e^{-1}$ )	1.57 ( <b><math>1.00e^{-3}</math></b> )	2.03 ( <b><math>1.00e^{-3}</math></b> )
13	$-6.95e^{-2}$ ( <b><math>4.00e^{-3}</math></b> )	$1.73e^{-2}$ ( $6.30e^{-1}$ )	1.61 ( <b><math>1.00e^{-3}</math></b> )	2.22 ( <b><math>2.00e^{-3}</math></b> )
14	$-8.06e^{-2}$ ( <b><math>1.00e^{-3}</math></b> )	$1.12e^{-3}$ ( $9.77e^{-1}$ )	1.59 ( <b><math>1.00e^{-3}</math></b> )	2.19 ( <b><math>1.00e^{-3}</math></b> )
15	$-8.27e^{-2}$ ( <b><math>8.00e^{-3}</math></b> )	$3.86e^{-2}$ ( $3.04e^{-1}$ )	1.51 ( <b><math>1.00e^{-3}</math></b> )	2.25 ( <b><math>2.00e^{-3}</math></b> )
16	$-9.22e^{-2}$ ( <b><math>1.00e^{-3}</math></b> )	$1.86e^{-2}$ ( $5.42e^{-1}$ )	1.66 ( <b><math>1.00e^{-3}</math></b> )	2.17 ( <b><math>1.00e^{-3}</math></b> )
17	$-1.11e^{-1}$ ( <b><math>1.00e^{-3}</math></b> )	$4.87e^{-2}$ ( $1.91e^{-1}$ )	1.53 ( <b><math>3.00e^{-3}</math></b> )	2.01 ( <b><math>1.00e^{-3}</math></b> )
18	$-1.27e^{-1}$ ( <b><math>1.00e^{-3}</math></b> )	$-2.11e^{-2}$ ( $4.39e^{-1}$ )	1.41 ( <b><math>1.00e^{-3}</math></b> )	2.17 ( <b><math>1.00e^{-3}</math></b> )
19	$-1.51e^{-1}$ ( <b><math>1.00e^{-3}</math></b> )	$-4.49e^{-2}$ ( $1.90e^{-1}$ )	1.20 ( <b><math>1.00e^{-3}</math></b> )	2.08 ( <b><math>1.00e^{-3}</math></b> )
20	$-1.49e^{-1}$ ( <b><math>6.00e^{-3}</math></b> )	NA	2.39 ( <b><math>2.00e^{-3}</math></b> )	NA
21	$-8.47e^{-2}$ ( <b><math>1.40e^{-2}</math></b> )	NA	1.08 ( <b><math>1.00e^{-3}</math></b> )	NA

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**TABLE 1** Scanned *Scyliorhinus stellaris* specimens. etOH, 70% ethanol; F, female; Hat, hatchling stage; Juv, juvenile stage; M, male; Mat, mature stage; Mc, Meckel cartilage; Pq, palatoquadrate.

Specimen	Sex	Stage (TL, cm)	Cartilage	Preservation	Scanning resolution ( $\mu\text{m}$ )
100418A	F	Hat (22)	Both	etOH	13.18
100418B	F	Hat (21)	Both	etOH	13.18
100418D	F	Hat (14)	Both	etOH	8.64
100418E	M	Hat (17.5)	Both	etOH	13.00
100418F	M	Hat (14)	Both	etOH	9.41
100418G	F	Hat (14)	Both	etOH	9.41
100418H	M	Hat (17)	Both	etOH	14.26
160118B	F	Hat (17)	Both	etOH	10.88
160118C	F	Hat (17)	Both	etOH	11.16
160118D	F	Hat (17.5)	Both	etOH	11.40
160118E	M	Hat (16.5)	Both	etOH	10.51
230918A	M	Hat (24.5)	Both	etOH	10.00
000000B	F	Juv (64)	Pq	Air	16.61
000000C	M	Juv (56)	Pq	Air	16.61
UM REC0371M	M	Juv (53)	Pq	Air	15.60
UM REC0778M	M	Juv (59)	Both	Air	19.17
UM REC1068M	F	Juv (55)	Both	Air	16.56
UM REC1073M	M	Juv (60)	Both	Air	14.29
UM REC1074M	F	Juv (57)	Both	Air	18.33
UM REC1075M	F	Juv (59)	Both	Air	12.50
UM REC1076M	F	Juv (55)	Both	Air	16.00
UM REC1077M	M	Juv (59)	Both	Air	21.28
UM REC0185M	M	Mat (112)	Mc	Air	26.93
UM REC0187M	M	Mat (106)	Mc	Air	26.93
UM REC0188M	M	Mat (113)	Pq	Air	26.93
UM REC0189M	F	Mat (93)	Both	Air	26.93
UM REC0353M	F	Mat (95)	Mc	Air	18.52
UM REC1312M	M	Mat (98)	Both	Air	30.00
UM REC1496M	M	Mat (102)	Both	Air	29.75
UM REC1497M	M	Mat (105)	Both	Air	30.00
UM REC1498M	M	Mat (110)	Both	Air	30.00
UM REC1499M	F	Mat (94)	Both	Air	25.00
UM REC1500M	F	Mat (102)	Both	Air	30.00



**TABLE 2** ANOVA results on centroid sizes. Significant p-values after Benjamini & Hochberg correction are in bold.

Meckelian teeth					
	All	Hatchling	Juvenile	Mature	
	F value (p-val)	F value (p-val)	F value (p-val)	F value (p-val)	F value (p-val)
Sex	2.37 (1.26e <sup>-1</sup> )	1.47e <sup>-1</sup> (7.04e <sup>-1</sup> )	4.00e <sup>-2</sup> (8.42e <sup>-1</sup> )	6.33 (1.54e <sup>-2</sup> )	
Stage	1.03e <sup>2</sup> (< 2.00e <sup>-16</sup> )	-	-	-	
ToothMD	1.09 (3.61e <sup>-1</sup> )	2.43e <sup>1</sup> (2.67e <sup>-10</sup> )	1.48e <sup>1</sup> (4.69e <sup>-9</sup> )	5.39 (5.77e <sup>-5</sup> )	
Sex:Stage	5.99 (3.24e <sup>-3</sup> )	-	-	-	
Sex:ToothMD	2.20e <sup>-2</sup> (1.00)	-	-	-	
Stage:ToothMD	2.14 (2.49e <sup>-3</sup> )	-	-	-	
Palatoquadrate teeth					
	All	Hatchling	Juvenile	Mature	
	F value (p-val)	F value (p-val)	F value (p-val)	F value (p-val)	F value (p-val)
Sex	2.83 (9.48e <sup>-2</sup> )	4.52e <sup>-1</sup> (5.04e <sup>-1</sup> )	1.00e <sup>-3</sup> (9.70e <sup>-1</sup> )	1.48e <sup>1</sup> (3.32e <sup>-4</sup> )	
Stage	2.24e <sup>2</sup> (2.00e <sup>-16</sup> )	-	-	-	
ToothMD	8.29e <sup>-1</sup> (7.03e <sup>-1</sup> )	1.91e <sup>1</sup> (3.44e <sup>-11</sup> )	2.72e <sup>1</sup> (1.33e <sup>-12</sup> )	3.56 (9.37e <sup>-4</sup> )	
Sex:Stage	1.59e <sup>1</sup> (5.48e <sup>-7</sup> )	-	-	-	
Sex:ToothMD	1.50e <sup>-2</sup> (1.00)	-	-	-	
Stage:ToothMD	1.33 (1.28e <sup>-1</sup> )	-	-	-	

**TABLE 3** MANOVA results on shape data. Significant p-values after Benjamini & Hochberg correction are in bold. MD, mesio-distal.

Meckelian teeth						
	All	Hatchling	Juvenile	Mature		
	F approx (p-val)	F approx (p-val)	F approx (p-val)	F approx (p-val)	F approx (p-val)	F approx (p-val)
Sex	5.39 ( <b>6.13e<sup>-8</sup></b> )	4.02 ( <b>9.54e<sup>-4</sup></b> )	1.86e <sup>1</sup> ( <b>5.72e<sup>-12</sup></b> )	2.67e <sup>1</sup> ( <b>5.39e<sup>-14</sup></b> )		
Stage	3.04e <sup>1</sup> ( <b>&lt; 2.20e<sup>-16</sup></b> )	-	-	-		
ToothMD	1.80 ( <b>3.12e<sup>-14</sup></b> )	1.09 (2.36e <sup>-1</sup> )	1.50 ( <b>1.16e<sup>-4</sup></b> )	1.03 (4.12e <sup>-1</sup> )		
Sex:Stage	1.05e <sup>1</sup> ( <b>&lt; 2.20e<sup>-16</sup></b> )	-	-	-		
Sex:ToothMD	8.73e <sup>-1</sup> (9.33e <sup>-1</sup> )	-	-	-		
Stage:ToothMD	1.18 ( <b>1.02e<sup>-2</sup></b> )	-	-	-		
Palatoquadrate teeth						
	All	Hatchling	Juvenile	Mature		
	F approx (p-val)	F approx (p-val)	F approx (p-val)	F approx (p-val)	F approx (p-val)	F approx (p-val)
Sex	7.61 ( <b>2.67e<sup>-11</sup></b> )	2.88 ( <b>5.37e<sup>-3</sup></b> )	4.84 ( <b>7.58e<sup>-5</sup></b> )	5.99e <sup>1</sup> ( <b>&lt; 2.20e<sup>-16</sup></b> )		
Stage	4.58e <sup>1</sup> ( <b>&lt; 2.20e<sup>-16</sup></b> )	-	-	-		
ToothMD	1.89 ( <b>3.36e<sup>-16</sup></b> )	1.65 ( <b>2.28e<sup>-6</sup></b> )	1.52 ( <b>9.56e<sup>-5</sup></b> )	1.17 (7.37e <sup>-2</sup> )		
Sex:Stage	7.32 ( <b>&lt; 2.20e<sup>-16</sup></b> )	-	-	-		
Sex:ToothMD	8.63e <sup>-1</sup> (9.53e <sup>-1</sup> )	-	-	-		
Stage:ToothMD	1.50 ( <b>4.16e<sup>-9</sup></b> )	-	-	-		

**TABLE 4** Developmental trajectory values between sexes for palatoquadrate teeth. Significant p-values after Benjamini & Hochberg correction are in bold. Due to the difference in total tooth file number between stages, some comparisons could not be done (NAs). -, difference; dL, delta length; F, females; M, males.

File	All stages		Juvenile to mature stage		hatching to juvenile stage		MF angle cor (p-val)
	M/F shape (p-val)	dL (M-F) (p-val)	MF angle cor (p-val)	dL (M-F) (p-val)	MF angle cor (p-val)		
1	3.08e <sup>-1</sup> (6.10e <sup>-2</sup> )	7.39e <sup>-2</sup> ( <b>3.00e<sup>-3</sup></b> )	1.21 ( <b>1.00e<sup>-3</sup></b> )	2.12e <sup>-2</sup> (4.89e <sup>-1</sup> )	6.57e <sup>-1</sup> (1.20e <sup>-2</sup> )		
2	1.13e <sup>-1</sup> (5.90e <sup>-1</sup> )	4.14e <sup>-2</sup> (9.60e <sup>-2</sup> )	1.04 ( <b>1.00e<sup>-3</sup></b> )	4.77e <sup>-2</sup> (1.97e <sup>-1</sup> )	4.90e <sup>-1</sup> (3.10e <sup>-2</sup> )		
3	3.34e <sup>-1</sup> (3.20e <sup>-2</sup> )	7.05e <sup>-2</sup> ( <b>1.70e<sup>-2</sup></b> )	9.63e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	-3.45e <sup>-2</sup> (4.05e <sup>-1</sup> )	3.35e <sup>-1</sup> (1.23e <sup>-1</sup> )		
4	3.86e <sup>-1</sup> ( <b>1.40e<sup>-2</sup></b> )	6.29e <sup>-2</sup> ( <b>3.40e<sup>-2</sup></b> )	9.19e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	-3.66e <sup>-2</sup> (3.64e <sup>-1</sup> )	4.24e <sup>-1</sup> (2.40e <sup>-2</sup> )		
5	4.41e <sup>-1</sup> ( <b>2.00e<sup>-3</sup></b> )	6.58e <sup>-2</sup> ( <b>2.90e<sup>-2</sup></b> )	1.05 ( <b>1.00e<sup>-3</sup></b> )	-9.50e <sup>-3</sup> (7.45e <sup>-1</sup> )	6.44e <sup>-1</sup> (2.30e <sup>-2</sup> )		
6	4.95e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	7.13e <sup>-2</sup> ( <b>1.10e<sup>-2</sup></b> )	1.03 ( <b>1.00e<sup>-3</sup></b> )	-2.10e <sup>-3</sup> (9.45e <sup>-1</sup> )	4.35e <sup>-1</sup> (1.90e <sup>-2</sup> )		
7	4.58e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	6.88e <sup>-2</sup> ( <b>5.00e<sup>-3</sup></b> )	1.22 ( <b>1.00e<sup>-3</sup></b> )	4.67e <sup>-2</sup> (1.44e <sup>-1</sup> )	3.64e <sup>-1</sup> (1.90e <sup>-2</sup> )		
8	4.54e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	7.85e <sup>-2</sup> ( <b>5.00e<sup>-3</sup></b> )	9.69e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	5.60e <sup>-3</sup> (8.51e <sup>-1</sup> )	3.37e <sup>-1</sup> (1.07e <sup>-1</sup> )		
9	2.93e <sup>-1</sup> (4.60e <sup>-2</sup> )	7.64e <sup>-2</sup> ( <b>3.00e<sup>-3</sup></b> )	7.97e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	1.59e <sup>-2</sup> (6.25e <sup>-1</sup> )	2.74e <sup>-1</sup> (1.17e <sup>-1</sup> )		
10	3.32e <sup>-1</sup> ( <b>1.20e<sup>-2</sup></b> )	5.17e <sup>-2</sup> (6.60e <sup>-2</sup> )	1.04 ( <b>1.00e<sup>-3</sup></b> )	2.76e <sup>-2</sup> (3.66e <sup>-1</sup> )	3.47e <sup>-1</sup> (8.30e <sup>-2</sup> )		
11	3.14e <sup>-1</sup> (3.50e <sup>-2</sup> )	9.38e <sup>-2</sup> ( <b>3.00e<sup>-3</sup></b> )	6.26e <sup>-1</sup> ( <b>4.00e<sup>-3</sup></b> )	1.30e <sup>-2</sup> (7.25e <sup>-1</sup> )	3.07e <sup>-1</sup> (2.20e <sup>-2</sup> )		
12	4.11e <sup>-1</sup> ( <b>3.00e<sup>-3</sup></b> )	1.02e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	8.38e <sup>-1</sup> ( <b>2.00e<sup>-3</sup></b> )	-5.80e <sup>-3</sup> (8.75e <sup>-1</sup> )	3.47e <sup>-1</sup> (1.00e <sup>-2</sup> )		
13	2.55e <sup>-1</sup> (1.82e <sup>-1</sup> )	8.29e <sup>-2</sup> ( <b>1.20e<sup>-2</sup></b> )	6.53e <sup>-1</sup> ( <b>2.60e<sup>-2</sup></b> )	3.48e <sup>-2</sup> (4.18e <sup>-1</sup> )	3.68e <sup>-1</sup> (1.80e <sup>-2</sup> )		
14	4.76e <sup>-1</sup> ( <b>5.00e<sup>-3</sup></b> )	1.23e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	1.06 ( <b>1.00e<sup>-3</sup></b> )	-3.50e <sup>-3</sup> (9.46e <sup>-1</sup> )	3.59e <sup>-1</sup> (4.00e <sup>-3</sup> )		
15	4.85e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	1.25e <sup>-1</sup> ( <b>2.00e<sup>-3</sup></b> )	1.22 ( <b>1.00e<sup>-3</sup></b> )	3.48e <sup>-2</sup> (3.43e <sup>-1</sup> )	3.05e <sup>-1</sup> (2.00e <sup>-2</sup> )		
16	4.88e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	1.17e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	8.27e <sup>-1</sup> ( <b>3.00e<sup>-3</sup></b> )	-1.13e <sup>-2</sup> (7.59e <sup>-1</sup> )	2.90e <sup>-1</sup> (2.60e <sup>-2</sup> )		
17	3.68e <sup>-1</sup> ( <b>1.20e<sup>-2</sup></b> )	1.09e <sup>-1</sup> ( <b>1.00e<sup>-3</sup></b> )	1.15 ( <b>1.00e<sup>-3</sup></b> )	2.40e <sup>-2</sup> (5.14e <sup>-1</sup> )	3.63e <sup>-1</sup> (1.20e <sup>-2</sup> )		
18	4.63e <sup>-1</sup> ( <b>2.00e<sup>-3</sup></b> )	6.49e <sup>-2</sup> ( <b>3.30e<sup>-2</sup></b> )	1.38 ( <b>1.00e<sup>-3</sup></b> )	1.99e <sup>-2</sup> (5.33e <sup>-1</sup> )	3.45e <sup>-1</sup> (6.90e <sup>-2</sup> )		
19	4.41e <sup>-1</sup> ( <b>2.00e<sup>-3</sup></b> )	9.03e <sup>-2</sup> ( <b>4.00e<sup>-3</sup></b> )	1.58 ( <b>1.00e<sup>-3</sup></b> )	5.27e <sup>-2</sup> (2.07e <sup>-1</sup> )	2.60e <sup>-1</sup> (1.18e <sup>-1</sup> )		
20	3.54e <sup>-1</sup> ( <b>4.00e<sup>-3</sup></b> )	8.28e <sup>-2</sup> ( <b>1.00e<sup>-3</sup></b> )	1.17 ( <b>3.00e<sup>-3</sup></b> )	2.24e <sup>-2</sup> (5.34e <sup>-1</sup> )	3.25e <sup>-1</sup> (3.40e <sup>-2</sup> )		
21	3.36e <sup>-1</sup> ( <b>9.00e<sup>-3</sup></b> )	8.08e <sup>-2</sup> ( <b>1.00e<sup>-3</sup></b> )	1.08 ( <b>1.00e<sup>-3</sup></b> )	3.72e <sup>-2</sup> (2.54e <sup>-1</sup> )	2.26e <sup>-1</sup> (7.50e <sup>-2</sup> )		
22	3.31e <sup>-1</sup> (3.90e <sup>-2</sup> )	4.88e <sup>-2</sup> ( <b>1.90e<sup>-2</sup></b> )	1.25 ( <b>9.00e<sup>-3</sup></b> )	4.20e <sup>-3</sup> (9.16e <sup>-1</sup> )	2.95e <sup>-1</sup> (2.50e <sup>-2</sup> )		
23	3.77e <sup>-1</sup> (1.14e <sup>-1</sup> )	3.16e <sup>-2</sup> (2.44e <sup>-1</sup> )	1.37 ( <b>2.00e<sup>-3</sup></b> )	1.71e <sup>-2</sup> (7.15e <sup>-1</sup> )	3.29e <sup>-1</sup> (2.00e <sup>-2</sup> )		
24	NA	NA	NA	2.44e <sup>-2</sup> (5.69e <sup>-1</sup> )	5.88e <sup>-1</sup> (4.00e <sup>-3</sup> )		
25	NA	NA	NA	2.63e <sup>-2</sup> (7.13e <sup>-1</sup> )	8.04e <sup>-1</sup> (2.20e <sup>-2</sup> )		

**TABLE 5** Developmental trajectory values between sexes for Meckelian teeth. Significant p-values after Benjamini & Hochberg correction are in bold. Due to the difference in total tooth file number between stages, some comparisons could not be done (NAs). -, difference; dL, delta length; F, females; M, males.

File	All stages		Juvenile to mature stage		hatching to juvenile stage		MF angle cor (p-val)
	M/F shape (p-val)	dL (M-F) (p-val)	MF angle cor (p-val)	dL (M-F) (p-val)	MF angle cor (p-val)	MF angle cor (p-val)	
1	3.30e <sup>-1</sup> (7.20e <sup>-2</sup> )	4.88e <sup>-2</sup> (2.10e <sup>-2</sup> )	1.14 (1.00e <sup>-3</sup> )	2.14e <sup>-2</sup> (3.11e <sup>-1</sup> )	9.65e <sup>-1</sup> (1.10e <sup>-2</sup> )	9.65e <sup>-1</sup> (1.10e <sup>-2</sup> )	
2	3.11e <sup>-1</sup> (2.56e <sup>-1</sup> )	1.54e <sup>-1</sup> (1.00e <sup>-3</sup> )	1.49 (1.00e <sup>-3</sup> )	4.04e <sup>-2</sup> (1.04e <sup>-1</sup> )	9.16e <sup>-1</sup> (3.00e <sup>-3</sup> )	9.16e <sup>-1</sup> (3.00e <sup>-3</sup> )	
3	1.11e <sup>-1</sup> (7.19e <sup>-1</sup> )	5.95e <sup>-2</sup> (8.00e <sup>-3</sup> )	7.61e <sup>-1</sup> (3.00e <sup>-3</sup> )	3.88e <sup>-2</sup> (1.86e <sup>-1</sup> )	7.27e <sup>-1</sup> (5.00e <sup>-3</sup> )	7.27e <sup>-1</sup> (5.00e <sup>-3</sup> )	
4	2.07e <sup>-1</sup> (1.19e <sup>-1</sup> )	5.46e <sup>-2</sup> (3.40e <sup>-2</sup> )	5.05e <sup>-1</sup> (2.40e <sup>-2</sup> )	5.40e <sup>-2</sup> (6.00e <sup>-3</sup> )	7.63e <sup>-1</sup> (1.00e <sup>-3</sup> )	7.63e <sup>-1</sup> (1.00e <sup>-3</sup> )	
5	1.98e <sup>-1</sup> (2.19e <sup>-1</sup> )	5.20e <sup>-2</sup> (9.70e <sup>-2</sup> )	7.55e <sup>-1</sup> (1.30e <sup>-2</sup> )	3.39e <sup>-2</sup> (1.02e <sup>-1</sup> )	6.32e <sup>-1</sup> (1.70e <sup>-2</sup> )	6.32e <sup>-1</sup> (1.70e <sup>-2</sup> )	
6	2.44e <sup>-1</sup> (1.54e <sup>-1</sup> )	8.06e <sup>-2</sup> (1.40e <sup>-2</sup> )	6.96e <sup>-1</sup> (8.00e <sup>-3</sup> )	3.71e <sup>-2</sup> (1.54e <sup>-1</sup> )	6.41e <sup>-1</sup> (1.50e <sup>-2</sup> )	6.41e <sup>-1</sup> (1.50e <sup>-2</sup> )	
7	3.14e <sup>-1</sup> (5.20e <sup>-2</sup> )	6.35e <sup>-2</sup> (3.00e <sup>-2</sup> )	7.71e <sup>-1</sup> (3.10e <sup>-2</sup> )	5.19e <sup>-2</sup> (1.07e <sup>-1</sup> )	6.76e <sup>-1</sup> (2.90e <sup>-2</sup> )	6.76e <sup>-1</sup> (2.90e <sup>-2</sup> )	
8	2.52e <sup>-1</sup> (1.78e <sup>-1</sup> )	9.04e <sup>-2</sup> (4.00e <sup>-3</sup> )	7.58e <sup>-1</sup> (1.70e <sup>-2</sup> )	5.65e <sup>-2</sup> (2.10e <sup>-2</sup> )	7.69e <sup>-1</sup> (8.00e <sup>-3</sup> )	7.69e <sup>-1</sup> (8.00e <sup>-3</sup> )	
9	4.01e <sup>-1</sup> (1.60e <sup>-2</sup> )	1.01e <sup>-1</sup> (1.00e <sup>-3</sup> )	8.20e <sup>-1</sup> (1.00e <sup>-2</sup> )	3.85e <sup>-2</sup> (2.20e <sup>-1</sup> )	6.42e <sup>-1</sup> (1.10e <sup>-2</sup> )	6.42e <sup>-1</sup> (1.10e <sup>-2</sup> )	
10	4.82e <sup>-1</sup> (6.00e <sup>-3</sup> )	1.15e <sup>-1</sup> (1.00e <sup>-3</sup> )	9.85e <sup>-1</sup> (3.00e <sup>-3</sup> )	8.46e <sup>-3</sup> (7.74e <sup>-1</sup> )	5.45e <sup>-1</sup> (5.70e <sup>-2</sup> )	5.45e <sup>-1</sup> (5.70e <sup>-2</sup> )	
11	3.76e <sup>-1</sup> (1.40e <sup>-2</sup> )	1.03e <sup>-1</sup> (1.00e <sup>-3</sup> )	9.61e <sup>-1</sup> (4.00e <sup>-3</sup> )	3.86e <sup>-2</sup> (1.84e <sup>-1</sup> )	4.83e <sup>-1</sup> (2.10e <sup>-2</sup> )	4.83e <sup>-1</sup> (2.10e <sup>-2</sup> )	
12	3.88e <sup>-1</sup> (1.60e <sup>-2</sup> )	1.05e <sup>-1</sup> (1.00e <sup>-3</sup> )	8.80e <sup>-1</sup> (2.00e <sup>-3</sup> )	3.01e <sup>-2</sup> (2.92e <sup>-1</sup> )	4.74e <sup>-1</sup> (5.10e <sup>-2</sup> )	4.74e <sup>-1</sup> (5.10e <sup>-2</sup> )	
13	4.97e <sup>-1</sup> (2.00e <sup>-3</sup> )	1.23e <sup>-1</sup> (1.00e <sup>-3</sup> )	8.04e <sup>-1</sup> (1.00e <sup>-3</sup> )	3.61e <sup>-2</sup> (2.20e <sup>-1</sup> )	3.94e <sup>-1</sup> (1.00e <sup>-1</sup> )	3.94e <sup>-1</sup> (1.00e <sup>-1</sup> )	
14	4.72e <sup>-1</sup> (4.00e <sup>-3</sup> )	1.43e <sup>-1</sup> (1.00e <sup>-3</sup> )	1.02 (1.00e <sup>-3</sup> )	6.14e <sup>-2</sup> (4.20e <sup>-2</sup> )	4.14e <sup>-1</sup> (1.20e <sup>-2</sup> )	4.14e <sup>-1</sup> (1.20e <sup>-2</sup> )	
15	5.51e <sup>-1</sup> (2.00e <sup>-3</sup> )	1.33e <sup>-1</sup> (1.00e <sup>-3</sup> )	1.02 (1.00e <sup>-3</sup> )	1.19e <sup>-2</sup> (7.40e <sup>-1</sup> )	2.78e <sup>-1</sup> (2.43e <sup>-1</sup> )	2.78e <sup>-1</sup> (2.43e <sup>-1</sup> )	
16	5.11e <sup>-1</sup> (2.00e <sup>-3</sup> )	1.07e <sup>-1</sup> (1.00e <sup>-3</sup> )	1.01 (1.00e <sup>-3</sup> )	-3.27e <sup>-3</sup> (9.17e <sup>-1</sup> )	3.68e <sup>-1</sup> (1.39e <sup>-1</sup> )	3.68e <sup>-1</sup> (1.39e <sup>-1</sup> )	
17	5.99e <sup>-1</sup> (2.00e <sup>-3</sup> )	1.15e <sup>-1</sup> (1.00e <sup>-3</sup> )	1.17 (3.00e <sup>-3</sup> )	-4.49e <sup>-2</sup> (2.42e <sup>-1</sup> )	7.78e <sup>-1</sup> (2.90e <sup>-2</sup> )	7.78e <sup>-1</sup> (2.90e <sup>-2</sup> )	
18	5.02e <sup>-1</sup> (1.00e <sup>-3</sup> )	9.26e <sup>-2</sup> (6.00e <sup>-3</sup> )	1.23 (5.00e <sup>-3</sup> )	-1.33e <sup>-2</sup> (7.28e <sup>-1</sup> )	3.75e <sup>-1</sup> (1.42e <sup>-1</sup> )	3.75e <sup>-1</sup> (1.42e <sup>-1</sup> )	
19	4.43e <sup>-1</sup> (1.00e <sup>-3</sup> )	5.94e <sup>-2</sup> (1.50e <sup>-2</sup> )	1.47 (3.00e <sup>-3</sup> )	-4.71e <sup>-2</sup> (1.78e <sup>-1</sup> )	3.93e <sup>-1</sup> (2.30e <sup>-2</sup> )	3.93e <sup>-1</sup> (2.30e <sup>-2</sup> )	
20	NA	4.02e <sup>-2</sup> (1.42e <sup>-1</sup> )	9.81e <sup>-1</sup> (1.09e <sup>-1</sup> )	NA	NA	NA	
21	NA	4.10e <sup>-3</sup> (8.47e <sup>-1</sup> )	1.57 (1.00e <sup>-3</sup> )	NA	NA	NA	
22	NA	7.71e <sup>-2</sup> (5.40e <sup>-2</sup> )	1.18 (2.80e <sup>-2</sup> )	NA	NA	NA	
23	NA	-5.97e <sup>-2</sup> (3.12e <sup>-1</sup> )	2.21 (1.00e <sup>-3</sup> )	NA	NA	NA	

**FIGURE 1** Tooth identification within a jaw and landmarking. A) microCT image of a right lower jaw of a juvenile female *S. stellaris*, dorsal view. f, file as defined from the symphysis (dotted line) to the commissure; g, generation. Scale bar represents 5mm for the jaw and 3mm for the zoomed teeth; B) Examples of landmark (purple) and semilandmark (empty dots) setting on mesial (top) and distal (bottom) teeth of a juvenile female.

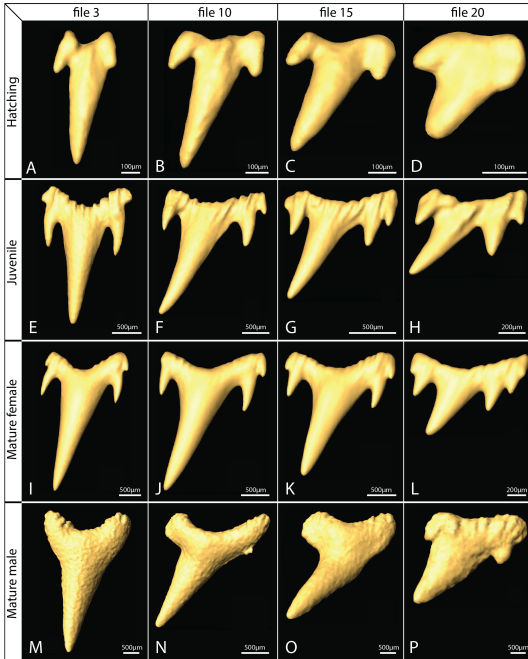
**FIGURE 2** Palatoquadrate tooth shape diversity in *S. stellaris*. A-D) Hatchling female teeth; E-H) Juvenile female teeth; I-L) Mature female teeth; M-P) Mature male teeth. Symphyseal (mesial) pole to the left.

**FIGURE 3** Meckelian tooth shape diversity in *S. stellaris*. A-D) Hatchling female teeth; E-H) Juvenile female teeth; I-L) Mature female teeth; M-P) Mature male teeth. Symphyseal (mesial) pole to the left.

**FIGURE 4** Tooth dimensions of *S. stellaris* right Meckelian and palatoquadrate teeth. A and D) Morphometric measure of the ratio between main cusp height and crown base width; B and E) Deviation to tooth bilateral symmetry: difference between the tooth tip and each crown base extremity distances. C and F) Tooth centroid sizes. At each tooth position, mean values are computed among all tooth generations (internal replicates), before being computed among all specimens. Error bars are standard deviations among replicates and specimens.

**FIGURE 5** 2D representation (PC1xPC2) of tooth developmental trajectories in *S. stellaris*. A) 2D trajectories for palatoquadrate tooth files 3, 10, 15 and 20; B) 2D trajectories for Meckel's tooth files 1, 5, 15, and 20. The trajectory representations are drawn between the mean shape of hatchling (starting point), juvenile, and mature (arrow tip) specimen teeth. Purple and green shades are for females and males trajectories respectively. Mesial to distal files appear in light to deep shades. Wireframes depict extreme deformations of the mean shape at the positive and negative extremities of the PC1 and PC2 axes.

## GRAPHICAL ABSTRACT



This study uncovers the wide intraspecific diversity of tooth form in the large-spotted catshark *Scyliorhinus stellaris* using micro-computed tomography and 3D geometric morphometrics. We characterize the emergence of sexual dimorphism along ontogenetic stages using sex-specific ontogenetic trajectories. We discuss the physical and chemical parameters acting on tooth morphogenesis that may generate the described developmental plasticity in elasmobranchs.