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Intraspecific dental variations in the deep-sea shark *Etmopterus spinax* and their significance in the fossil record

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Abstract

An important character on several taxonomic levels for shark identification is the tooth morphology. Sharks show a variety of highly specialized dentitions reflecting adaptations to their feeding habits. Intraspecific variation of tooth morphology such as sexual or ontogenetic dimorphism is poorly known in many species, even though tooth morphology plays a decisive role in the characterization of the fossil record of sharks, which comprises mostly fossil teeth. Here we analyzed the dentition of 40 jaws of the Velvet Belly Lantern Shark *Etmopterus spinax* and identified ontogenetic and sexual dimorphic characters such as total number of teeth, number of upper teeth, cusplet numbers in upper jaw teeth and width of lower jaw teeth. Dimorphic characters may reduce intraspecific competition for food, as *E. spinax* segregates by sex and size and may allow for identifying the male sex. The lower jaw tooth height, a sexually non-dimorphic character, was used to re-calculate the total length of specimens, which represents the first such approach for a squaliform shark. Results derived from the extant *E. spinax* are subsequently applied to fossil *Etmopterus* sp. teeth (Miocene) to gain individual information such as sex or size, but also characterize the extinct population from the excavation site by a size distribution profile in comparison to data from extant populations. This approach indicates the presence of multiple ontogenetic stages in the extinct population.

Keywords Dentition · Fossil · Shark · Squaliform · Sexual dimorphism · Ontogenetic dimorphism

Introduction

The fossil record of modern sharks (Neoselachii) dates back to the Triassic (Maisey 2012) and the majority of fossil evidence comprises teeth only. While articulated fossils are scarce, numerous dental fossils form a rather detailed fossil record partially documenting the evolutionary history of taxa quite detailed (Maisey 2012). The reason for this lies in the sharks' ability to replace teeth continuously throughout their lifetime (Luer et al. 1990; Overstrom 1991; Reif et al. 1978), depositing numerous organic matter in the environment,

which is ideal for fossilization due to its composition. Contrasting, the cartilage skeleton is less suited for fossilization and is only fragmentary or not at all preserved.

The tooth morphologies of living species are the basis for identifying both extant as well as extinct taxa in the fossil record. Today, 547 described living species contrast 2608 extinct species, which description is mostly based on teeth and therefore dental morphological characters (Pollerspöck and Straube 2020). Intraspecific morphological variation is documented in some living species (e.g. Ellis and Shackley 1995; Moyer and Bemis 2016; Purdy and Francis 2007; Sadowsky 1970; Straube et al. 2008; Taniuchi 1970), however, it is unknown for most, especially in deep-sea sharks (Cullen and Marshall 2019; Martins et al. 2015; Pinchuk and Permitin 1970). The known cases comprise ontogenetic differences (Mello and Brito 2013), which may be due to differences in diet (French et al. 2017; Powter et al. 2010; Raschi et al. 1982; Reif 1976; Schwartz and Hurst 1996; Tomita et al. 2017) as well as seasonal changes due to sexual or population-level differences (Lucifora et al. 2003). Therefore, it is possible that the presence of intraspecific variation

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in tooth morphologies in extant species is more common than documented.

In the fossil record, intraspecific and intraindividual variation in tooth morphology pose a challenge, as multiple fossil teeth found in excavation sites per se do not allow to draw conclusions how many individuals lost these teeth. Further, in case of unknown intraspecific dental morphological variation, which sex(es) and ontogenetic stages were involved or potential morphological congeners.

In this study, we analyze the intraspecific variation of a single deep-sea shark species, *Etmopterus spinax*. *Etmopterus* is the most species rich shark genus, with 44 species described today (Pollerspöck and Straube 2020). *E. spinax* is eponymous for the *E. spinax* clade, one of the four subclades of the genus identified in Straube et al. (2010). Except for adults of a single species, *E. sheikoi*, all other *Etmopterus* species are characterized by a dignathic heterodonty showing multicuspid upper jaw teeth, which are likely used to hold onto prey and single-cusped, overlappingly arranged lower teeth, which form a cutting edge [cutting-clutching type dentition (Cappetta 2012)]. These distinct morphological features allow for identifying a number of fossil forms dating back to the Upper Cretaceous. Using the fossil record to date the divergence times of *Etmopterus* estimated the rise of the genus to the end of the Cretaceous and the divergence of the four subclades to the Eocene, where the different subgroups split in a time frame of approximately 13 million years (Eocene, Oligocene; 37–24 million years) (Straube et al. 2010, 2015). Even though dental characters play a role in some *Etmopterus* species identifications (e.g. Adnet et al. 2006; Chan 1966; Dolganov 1986), little is known on intraspecific variation, except for few studies (e.g. Herman et al. 1989; Straube et al. 2008).

Here we focus on identifying general dental morphological variation of *E. spinax* within single jaws and further identify differences between sexes and different ontogenetic stages. The results are then applied to fossil Miocene *Etmopterus* sp teeth and conclusions are drawn on the former carrier.

Materials and methods

Materials

We analyzed $N = 40$ jaws from the Velvet Belly Lantern Shark *E. spinax*. Please see Supplementary Table 1 for an overview of specimens analyzed and collection information. The specimens were stored frozen and are deposited in the specimen collection of Henrik Glenner's research group, Marine Biodiversity, Department of Biological Sciences (BIO), University of Bergen (see also Rees et al. 2019). The analyzed sample of *E. spinax* specimens comprise 23 male and 17 female individuals of different ontogenetic stages (Supplementary Table 1).

Methods

Frozen specimens were thawed, the total length measured, and the sex determined. Size classes were categorized representing individuals up to 20 cm TL, individuals between 20 and 30 cm TL and individuals > 30 cm TL. Jaws were dissected from frozen specimens and dried for 2–3 h at 45 °C. For further preparation at a later point in time, the jaws were placed for 1–2 min in 95 °C water and thereafter tissue remains were manually removed. For all jaws, where the condition allowed for, the dental formulas were determined, i.e. the number of teeth was determined for the functional row of upper and lower jaws including sub-sectioning in right and left parts of jaws counting from the symphysis.

In total, 148 teeth were dissected from the *E. spinax* jaws for individual analysis. For this preparation step, the jaws were rehydrated in water for 1–2 min and teeth from the right part of jaws manually dissected using needles and tweezers. All teeth were separately cleaned in a 0.6 mol/l KOH solution for 60 min. After KOH digestion, teeth were rinsed with water at room temperature and pasted onto stub-sized stickers usually used for scanning electron microscopy.

Photographic images of teeth were taken under 40× magnification with a Leica ID 80 HD digital camera mounted on a Wild M3 Zoom stereomicroscope. Images were edited using the Leica internal camera software LAS EZ version 3.2.1. Lighting was provided by a light tent and additional LED lighting. Where necessary, stacking was used to create continuous definition of images. Combine Z vers 2010 was used to combine images for stacking. Gimp vers. 2.10.4 was used for final editing steps.

For the upper jaw teeth we counted the number of lateral cusplets (Fig. 1a) in $N = 40$ jaw specimens in the functional rows of teeth. The lower jaw tooth height was measured (Fig. 1b) for a single tooth of $N = 40$ jaw specimens. The tooth was chosen from one of the positions 6–10 of the left lower jaws counting from the symphysis in case the targeted teeth were worn, broken or missing. For specimens 1250 (male) and 1253 (female) all functional row teeth were dissected out and measured. Additionally, the width of the lower jaw teeth was measured in these two specimens, as this can only be done, when teeth are dissected, as in the single lower jaw functional row teeth are overlappingly arranged and connected by a ligament.

For the classification of fossil *Etmopterus* sp. teeth we used 16 lower jaw tooth specimens, ten from Pollerspöck and Straube (2017) and six newly collected for this study as well as a single upper jaw tooth. Fossil teeth newly
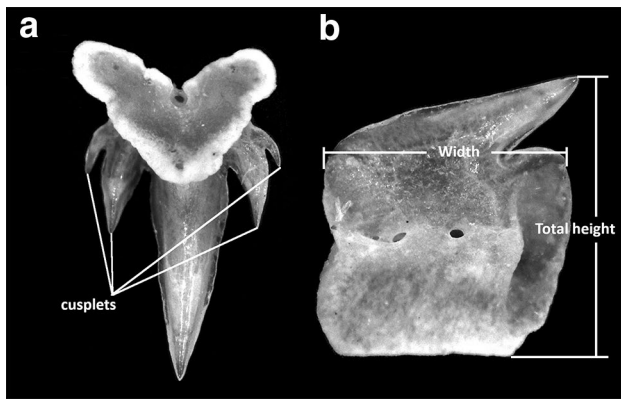
Fig. 1 Morphometric and meristic data collected of *Etmopterus spinax* teeth. **a** Upper jaw tooth. **b** Lower jaw tooth

collected for this study were excavated in 2019 at Mitterdorf (Neuhofener Beds) following the protocol described in Pollerspöck and Straube (2017). Data on the fossil teeth were analoguously collected as for the *E. spinax* teeth (Fig. 1). For estimating the total lengths of specimens based on single lower jaw teeth, we used the equation describing the trendline when plotting lower tooth height against total length of the *E. spinax* specimens as:

$$y \,(\text{tooth height in } \mu) = m \,(\text{gradient}) \, x \,(\text{total length in cm}) \, + \, b \,(y\text{-intercept}).$$

This trendline is characterized by a gradient $m = 39.225$ and a y-intercept $= 113.71$. Thereafter, we solved the equation for x (total length in cm) calculating the total length as:

$$x \,(\text{total length in cm}) = (y \,(\text{tooth height in } \mu) - 113.71)/39.225.$$

As a proof of concept, we used lower jaw tooth heights measured in one jaw half of a single male and a single female *E. spinax* jaw (TL = 35 cm for both specimens, specimens 1250 und 1253; Supplementary Table 1) to recalculate the total length of specimens 1250 (male) and 1253 (female) following the above equation.

Further, we conducted a literature research to collect information on the size distribution of different North East Atlantic and Mediterranean *E. spinax* populations. For that we analyzed data from Neiva et al. (2006), Borges et al. (2002) and Fanelli et al. (2009) and computed the total length distributions (Supplementary Table 1).

We used PAST vers. 3 (Hammer et al. 2001) for performing two sample *t* tests for comparing sexes and three different size groups representing ontogenetic stages (Table 1). The number of cusplets of upper teeth was compared between sexes and the three ontogenetic groups. Excel and PAST were used for graphic analyses of the

data. All specimen details and data are provided in Supplementary Table 1.

Results

Jaws and teeth of *Etmopterus spinax*

On average, an *E. spinax* jaw contained 55 teeth. Twenty-four in upper, 31 in lower jaws. Upper and lower jaw teeth were continuously decreasing in size from the symphysis towards the rears of the mouth (Fig. 2). In upper jaws, there were usually two functional rows of teeth as well as 2–3 replacement rows. See Table 1 for a summary of dental information for the three size groups. Upper jaw teeth were replaced one by one. The number of cusplets in upper jaw teeth varied from 1 to 6 cusplets. Contrasting, there was only a single functional row of teeth in the lower jaws. Lower jaw teeth were connected through a ligament and overlapping areas. The complete functional row was replaced. There were usually 3–4 replacement rows in lower jaws. Lower jaw teeth bore a single cusp only, which was bent distally. Figure 2 illustrates the dental morphological variation between sexes and ontogenetic groups.

Sexual and ontogenetic differences in tooth morphology and meristics

A sexual difference was detected in the total number of teeth between sexes, where males showed an increase in total tooth numbers with increasing size, i.e. male and female specimens of the same body size differed in the number of jaw teeth (Fig. 3a). The difference got more distinct with increasing size (Fig. 3b), which manifested in a significant difference of upper tooth numbers between males and females in the group of specimens with a total length ≥ 30 cm (two sample *t* test; p (same mean) $= 0.01$; Fig. 3b). Given that male specimens showed more teeth at the same size, females seemed to compensate for that by larger teeth. The width of lower teeth was significantly different between specimens 1250 (male) and 1253 (female) (two sample *t* test; p (same mean) $= 0.0001$; Fig. 3c). We further detected a significant difference in the number of cusplets in upper teeth in size groups 2 and 3 (two sample *t* test; p (same mean group 2) $= 0.05$; p (same mean group 2) $= 0.03$). Males developed a larger number of cusplets (Fig. 3d).

Fig. 2 Morphological variation between sexes and ontogenetic groups. *TL* total length in cm. If possible, specimens of similar or same sizes were compared at similar or same tooth positions depending on conditions. *UJ* upper jaw, *LJ* lower jaw, *l* left from symphysis. Further specimen details are given in Supplementary Table 1
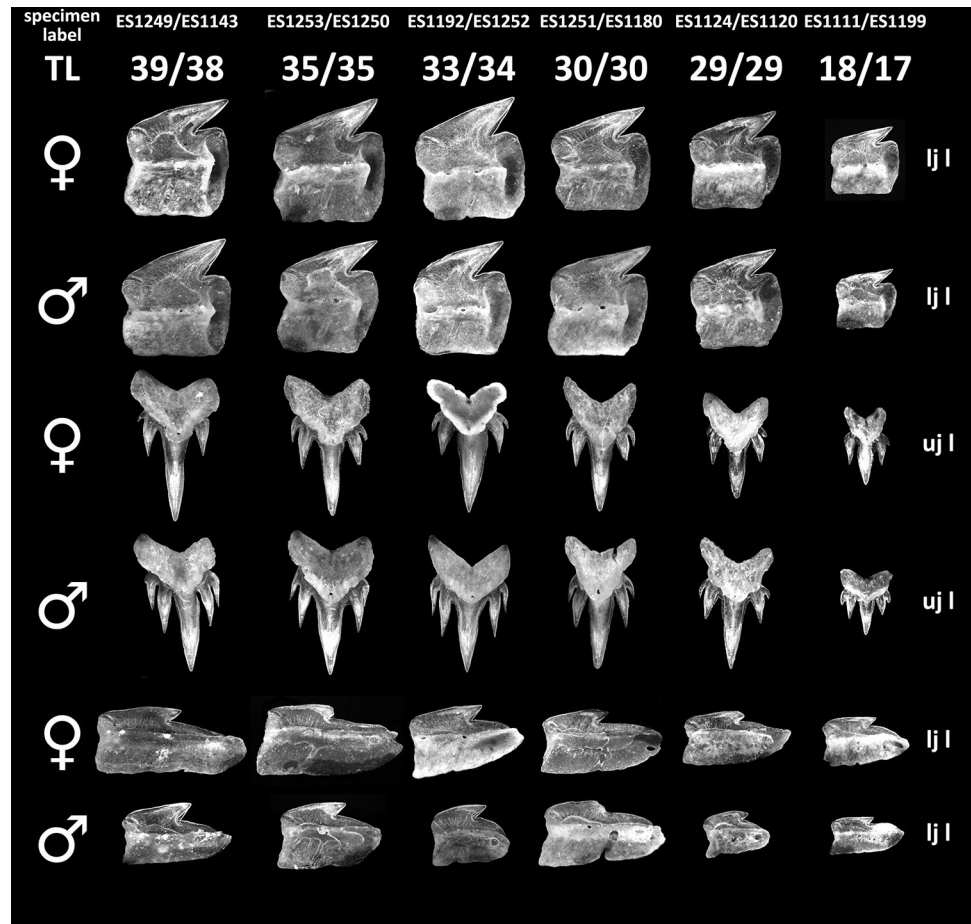
Table 1 Ontogenetic groups and details of tooth numbers of analyzed *Etmopterus spinax* jaws

Size in cm	Upper jaw	Lower jaw	Total	Dental formula
≤ 20 female	22.20	26.60	48.80	20–24/26–27
≤ 20 male	22.67	27.00	49.67	21–26/24–31
> 20 ≤ 30 female	23.67	30.17	53.83	21–26/27–31
> 20 ≤ 30 male	25.17	31.67	56.83	22–26/24–29
> 30 female	23.00	32.67	55.67	20–24/30–35
> 30 male	27.09	33.91	61.00	22–30/30–38
Total female	23.00	30.00	53.00	20–26/26–35
Total male	25.43	31.52	56.96	21–30/24–35

Fossil teeth

Etmopterus spinax upper teeth gradually decreased towards the rears of the mouth. Therefore, any measurements were biased and not suitable to calculate the former total length of the bearer of a fossil tooth. In contrast, the height of the lower teeth remained relatively stable in tooth positions one to ten making them ideal candidates for the estimation of the total lengths of the fossil specimens. Lower jaw teeth from

positions 11 and beyond were also easy to identify due to the distinct change of the root morphology, which gained a trapezoidal shape in the rears of jaws, from tooth position 11 ascending. Results from our approach to re-calculate total lengths of *E. spinax* specimens 1250 (male) and 1253 (female) were widely successful for anterior tooth positions. For male specimen 1250 (male), we were able to recover the total length for tooth positions 1–12 with a variety of 1 cm. Posterior teeth (positions 13–17) showed a larger fluctuation of total length estimates with a variation of 3–11 cm. Commissure teeth (position 16 of ES1253 and position 18 of ES1250) were not considered for measurements due to their distinct morphology (Fig. 2). A similar situation was present in the female specimens. Teeth from positions 1 to 12 showed a variation in re-computed total lengths of 3 cm, while posterior teeth (positions 13–15) showed a variation of 2–10 cm. Posterior lower jaw teeth were therefore not suitable for total length estimations.

Estimating the former total lengths based on the height of lower jaw teeth of 16 fossil *Etmopterus* sp. specimens resulted in two specimens assignable to the size group < 20 cm TL, seven specimens to size group 20–29 cm TL and seven specimens to size group > 30 cm
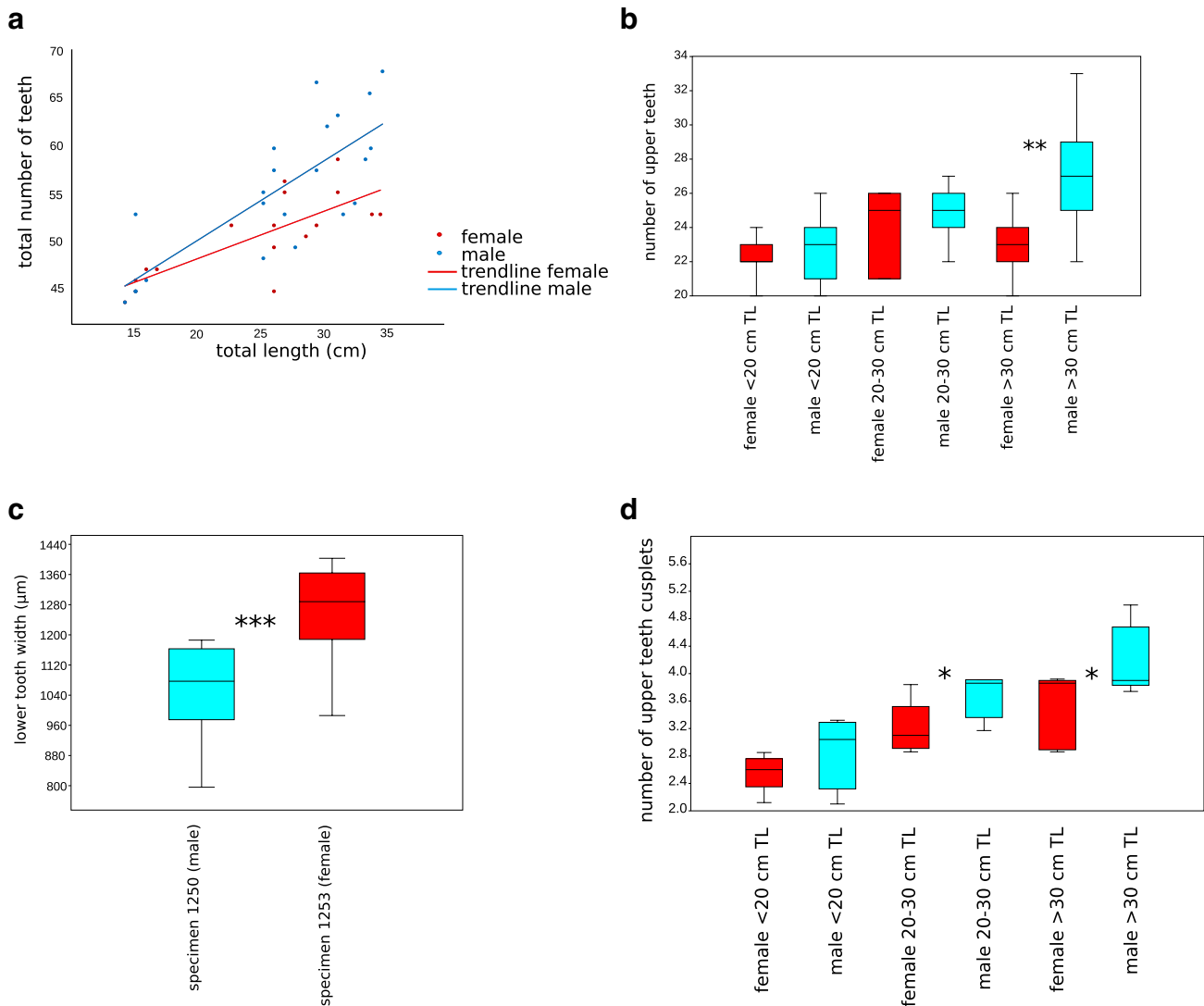
Fig. 3 Sexual and ontogenetic differences in tooth morphology and meristics. *$p < 0.05$; **$p < 0.01$; ***$p < 0.000$. **a** Ontogenetic differences in total number of jaw teeth between sexes of *Etmopterus spinax*. Details on specimens are given in Supplementary Table 1. **b** Boxplots showing the development of upper jaw tooth numbers of *Etmopterus spinax* between sexes of different size groups representing ontogenetic stages. **c** Difference in width of lower teeth of specimens 1250 (male) and 1253 (female). **d** Boxplots showing the development of upper jaw tooth cusplet numbers of *Etmopterus spinax* between sexes of different size groups representing ontogenetic stages

TL. The minimum and maximum estimated sizes were 15 and 36 cm TL (Supplementary Table 1). The lower jaw teeth did not allow for any conclusions on the sexes of the fossils.

Literature research in combination with our sampling allowed us to generate a representative profile of the size distribution of the North East Atlantic and Mediterranean *E. spinax* populations and compare to the findings in the fossil record. Even though the fossil sampling was much smaller, the size distribution profile is similar to the profile derived from data of the extant population (Fig. 4). This approach could therefore be used in continuative studies to draw conclusions on total length distributions in extinct populations.

Discussion

The number of extinct shark species surpasses the number of extant species more than five times. As Purdy and Francis (2007) state, numerous genera and species of extinct sharks have been described in the fossil record lacking detailed knowledge on intraspecific and intraindividual variation of tooth morphologies of extant species. In this study, we contribute to a better understanding of the intraspecific and intraindividual dental variation in *Etmopterus*, hitherto the most diverse extant shark genus (Pollerspöck and Straube 2020). We detected both sexual and ontogenetic dental differences in the total number of
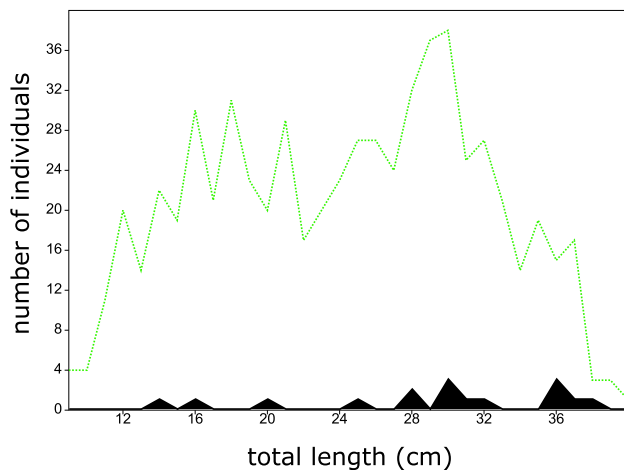
Fig. 4 Size distribution of *Etmopterus spinax* in the North East Atlantic and Mediterrenean (green dotted line) based on literature records (Neiva et al. 2006; Borges et al. 2002; Fanelli et al. 2009) and reconstructed size distribution of *Etmopterus* sp. fossils analyzed (black)

teeth, the number of upper teeth, the number of upper teeth cusplets as well as the width of lower teeth (Fig. 3).

Intraspecific dental variation

As variations documented for *E. spinax* in this study align with variations reported in Straube et al. (2008) for *Etmopterus granulosus* (Günther, 1880), the variability may be typical in other species of the *E. spinax* clade, if not in all species of the genus *Etmopterus*. The variable characters can be summarized to affect total tooth numbers, lower jaw teeth width, number of cusplets in upper teeth, position in jaws and root morphology. We found both ontogenetic and sexual dental differences, which seem to be linked. Ontogenetic differences in the total lengths of *E. spinax* (and other *Etmopterus* species) were the only sexually dimorphic morphological characters known. With increasing size (and age) the differences between males and females get more pronounced and are most prominent in specimens > 30 cm TL (Fig. 3b, d). The size at maturity in *E. spinax* is about 25.3–35 cm TL in males and 30.8–38 cm TL in females (Porcu et al. 2014), we therefore conclude that the dental differences are connected to size at maturity. *E. spinax* is known to segregate by sex and size (Mauchline and Gordon 1983; Massutí and Moranta 2003), the sexually dimorphic dentition may reflect further ecological niche establishment. Stomach content analysis show that *E. spinax* is an opportunistic feeder on a rather low trophic level (Bengil et al. 2019). Its prey items comprise mainly teleosts, cephalopods and crustaceans (Fanelli et al. 2009; Neiva et al. 2006). *E. spinax* undergoes two diet shifts at 15–25 cm TL and 25–45 cm TL (Fanelli et al. 2009; Neiva et al. 2006), the latter falls in the

range of the sexual dental dimorphisms documented herein. However, Neiva et al. (2006) state that the diet shifts are not connected to sex or maturity but size only due to an increase in mouth dimension accompanied by larger flexibility in prey selection. Some sexual variation in diet was explained by depth segregation of sexes after reaching maturity and accompanying food resource differences. Our results may add an ecological segregatory factor, as dentitions may have adapted to different food sources caused by depth segregation for sexes further reducing competition.

Another explanation may be found in a sexual dimorphism related to *E. spinax*' mating behavior. Even though mating has not been observed in the wild for this species so far, a distinct pairing with embrace as in other sharks is assumed (Breder and Rosen 1966). In that, the male shark grabs the female's pectoral fin (base) with its mouth to ease copulation. More and thinner cusplets in upper jaw teeth may be beneficial to hold onto the female. A mating season modification of teeth from flat (for crushing food) to needle-like teeth in males is known from several ray species, for example *Dasyatis americana*, *Urolophus halleri* and *Urotrygon microphthalmum*. This morphological modification of teeth is linked to mating behavior in these species (Chapman et al. 2003; Nordell 1994; Rangel et al. 2016). If similar reasons increase the number of upper tooth cusplets in males of *E. spinax* remain speculative.

Evaluation of fossil etmopterid teeth

Our results showed numerous morphological variations in *E. spinax*, which can be taken into account in studies on fossil etmopterid teeth (Fig. 2). Based on our survey of intraspecific variation, we could extrapolate the former total length of the fossil specimen based on single fossil lower jaw teeth. Even though lower teeth seem to differ between sexes in width (Fig. 3c), the height is stable across sexes and size groups. Therefore, the lower tooth height as measured in Fig. 1b is an adequate character for total length reconstructions (Fig. 4). Total length estimates based on tooth sizes have been conducted on only few shark species so far, mostly lamniform sharks (Applegate 1965; Chavez et al. 2012; Pimiento and Balk 2015; Shimada 2002a, b, 2005, 2006, 2020; Shimada and Seigel 2005). This study is the first such approach for a squaliform shark and can serve as a blueprint for future studies on fossil shark teeth as extant species are the best reference for drawing conclusions on fossil dental morphological variation. Further, our approach is useful in continuative studies on extinct populations or characterization of excavation sites. Given that the size distribution suggests the presence of all ontogenetic stages (Fig. 4), a nursery ground can, therefore, be disregarded. Such interpretations have to be treated with care, however, as the a priori assumption is made that all fossil *Etmopterus* sp. teeth analyzed herein originate from the same species.
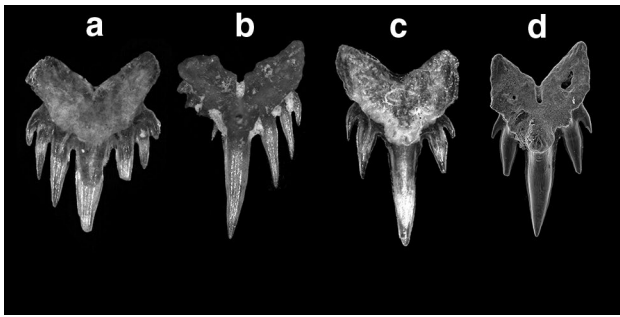
Fig. 5 Comparison of fossil *Etmopterus* sp. upper teeth with *Etmopterus spinax* upper teeth. **a** Adult male upper tooth from specimen ES2020_03 (1st functional row; tooth position 5 counting from symphysis). **b** Potentially adult male fossil upper tooth with increased number of needle-like cusplets (Miocene, Mitterdorf, Neuhofener Beds, Germany). **c** Adult female upper tooth from specimen ES 1253 (1st functional row; tooth position 6 counting from symphysis). **d** Potentially (adult?) female fossil upper tooth with triangular, wider cusplets (from Pollerspöck and Straube 2017, SNSB-BSPG 2015 III 2-21)

Even though we found a significant difference in cusplet numbers of upper teeth between male and female specimens (Fig. 3d), it is difficult to assign a single fossil upper *Etmopterus* tooth to a sex, as the intraindividual variation of cusplet numbers is high (Fig. 2) and a certain number of cusplets does not necessarily indicate the sex due to the large intraindividual variability. However, the shape of cusplets may allow for distinguishing sexes. Male cusplets appear slenderer, bent and hook-like, while female cusplets seem wider and more triangular in shape. Analyzing this character in detail is difficult, as cusplets are often broken and differences diluted by the high variability as also reported in Straube et al. (2008) for *E. granulosus*. A distinction of sex based on cusplet numbers in upper teeth maybe possible in other *Etmopterus* species, however. Straube et al. (2007) report on significant differences in cusplet numbers of two species of the *Etmopterus lucifer* clade. Even though not analyzed in detail, apart from cusplet numbers, the shape of cusplets also seems to differ between sexes. Further, a single pair of first cusplets, which are smaller than subsequent cusplets seems male-specific. Further data of *E. spinax* teeth may allow to identify more sexually dimorphic characters in the future. We speculate that the upper jaw *Etmopterus* sp. teeth shown in Pollerspöck and Straube (2017) are from a female specimen, while the newly analyzed fossil upper *Etmopterus* sp. tooth may originate from a male specimen (Fig. 5).

Compliance with ethical standards

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