Dental structure of the Giant lantern shark *Etmopterus baxteri* (Chondrichthyes: Squaliformes) and its taxonomic implications

Nicolas Straube · Ulrich Schliewen · Jürgen Kriwet

Abstract Dogfish sharks (Squaliformes) are a highly diverse group of neoselachians occurring in a wide range of marine environments and are common members of deep-sea faunas. The order Squaliformes comprises six families with approximately 98 extant species. The dentition of most squaliforms is characterized by a strong dignathic heterodonty and dental variation yielding a suite of potential tooth characters that could be used for taxonomic and systematic purposes. So far, no detailed study has been carried out to analyse the use of tooth morphologies in reconstructing the phylogeny of squaliforms. Also, the degree of characteristics of intraspecific variability of tooth morphologies is still unclear. Here, we analysed the dental differences between juveniles and adults and between the sexes of the Giant lantern shark, *Etmopterus baxteri*, and tested these dental characters for taxonomic purposes employing different statistical procedures. The results show that upper teeth of adult females and males differ morphologically in that those of females are bigger and display a lanceolate central cusp, whereas male specimens have thin and needle-like central cusps. Upper teeth of males have a higher number and a more pronounced variability of lateral cusplets than those of females. Moreover, an ontogenetic heterodonty might be developed in male specimens with sexually immature males displaying similar dental morphologies to those of adult females. Lower teeth, conversely, do not differ morphologically between the sexes. Results indicate that tooth morphologies of squaliform sharks bear high potential for phylogenetic purposes if tooth variations are considered, but have to be treated with care, if no variation is analysed.

Keywords *Etmopterus baxteri* · Sexual dimorphism · Dignathic heterodonty · Tooth morphology · Shape analysis

Introduction

Dogfish sharks (''squaloids'') are a highly diverse group of neoselachians occurring in coastal and oceanic, cool temperate and deep tropical waters in both the northern and southern hemisphere (Compagno 1999; Musick et al. 2004). They include common members of deep-sea faunas. Most species are benthic but many mesopelagic forms undertake nightly vertical migrations in search for food. Currently, six families (Squalidae, Centrophoridae, Etmopteridae; Somniosidae, Oxynotidae, Dalatiidae)

N. Straube (✉) · J. Kriwet
Museum für Naturkunde der Humboldt Universität
zu Berlin, Invalidenstr. 43, 10115 Berlin, Germany
e-mail: nicolas.straube@museum.hu-berlin.de

U. Schliewen
Zoologische Staatssammlung München, Münchhausenstr. 21, 81247 Munich, Germany

with approximately 98 extant species are recognized within the order Squaliformes. The monogeneric family Echinorhinidae is excluded from the squaliforms based on odontology (Pfeil 1983; Herman et al. 1989), skeletal features (Shirai 1992; Carvalho 1996), and molecular evidence (Bernardi and Powers 1992).

Generally, sharks can be identified by features of their teeth such as shape, arrangement of nutritive foramina, form of root, and number of tooth rows (e.g., Herman et al. 1989; Adnet and Cappetta 2001). Some sharks can even be identified to species level by these characters. Due to their cartilage skeleton, fossilised bodies are rarely recovered contrary to fossil teeth consisting of highly mineralised material, which fossilizes more easily. Hence, teeth are the most important skeletal elements for reconstructing past diversity patterns of sharks and to explore their systematic position and evolutionary traits. Most extant and fossil squaliform shark species possess a rather high degree of dental variation, inter- as well as intraspecifically. These differences permit the recognition of a suite of characters that can be analysed with phylogenetic methods. However, odontological features of most fossil and extant taxa remain incompletely documented and the intra- and interspecific as well as the sexual and ontogenetic variation of tooth morphologies is not yet established for any squaliform species. The intention of this paper is to (1) analyse intraspecific dental differences between juveniles and adults, (2) between the sexes of the Giant lantern shark, *Etmopterus baxteri*, and (3) test suitability of dental characters for taxonomic purposes employing different statistical procedures.

Material and methods

Specimens of *Etmopterus baxteri* (Garrick 1957) that form the focus of this study were caught in 1979 southeast off New Zealand in the south-west Pacific basin, in a depth between 200 m and 1000 m by the German research vessel ''FSM Wesermünde''. The material is housed in the Bavarian State Collection of Zoology (ZSM) since 1981 and specimens are kept in 75% ethanol. Hundred-fifteen specimens of *E. baxteri* in total, 70 of which are male, 45 female, were analysed. Specimens were identified with the help of a morphological key by Compagno and Niems

(1998). *Etmopterus baxteri* and *E. granulosus* were confused in the past because both share very similar character combinations. However, *E. granulosus* is confined to South America, whereas *E. baxteri* occurs off Australia and New Zealand and probably off South Africa (Compagno et al. 2005). The validity of both species will hopefully be clarified with the help of molecular analyses in the near future.

The approximate total length (TL), the average length of the claspers (CL) of males (calculated from the means of each pair of claspers), and the cusplet number of upper teeth in the first functional series of the upper jaw for each gender were determined. The TL is the sum of three lengths (snout tip to origin of the first dorsal fin spine plus the distance from origin of the first dorsal fin spine to the origin of the second plus origin of the second dorsal fin spine to the tip of the tail fin). The direct total length was measured prior to fixation of the material after capture in 1979. We calculated the length consisting of three individual measurements during this project to compare the original results, because the condition of the preserved specimens averted measurements of the total lengths.

Teeth are morphologically very dissimilar throughout the jaws. Consequently, grouping into anterior, lateral, and posterior positions is artificial and represent the most labial (positions 1–4) and most distal positions (positions 12–16) with lateral teeth in between (positions 5–11).

The number of cusplets in the first functional upper tooth series was counted. There was sometimes a high variation in the number of cusplets within one jaw. The mean values of the cusplet number were calculated for further statistical analyses.

Upper teeth were gently removed from the jaw cartilages with a scalpel or soft tweezers to avoid damaging of teeth. The lower teeth were cut out with a scalpel along the edge of the jaw cartilage and separated. Remaining soft tissues covering the teeth were tried to be removed with 15% hydrogen peroxide, which was unsuccessful as was an ultrasonic bath.

All teeth were digitally documented with a LEO 1430 VP scanning electron microscope (SEM). Therefore, the teeth were mounted on SEM stubs and coated with gold in a POLARON SEM COATING SYSTEM for 120 s. The images were processed with the software package Photoshop 7.0.

Upper teeth from presumably homologous positions (2nd, 7th, and 12th tooth row) of 20 jaws (10 male and 10 female jaws) were extracted. If teeth in these positions were damaged, teeth of positions right next to the damaged ones or to the next functional tooth in the row were processed. *E. baxteri* possesses 2–3 functional rows of upper teeth and all teeth were fully calcified and verified this approach. The following distances were measured (Fig. 1a): height of teeth (h), height of crowns (hc), height of roots (hr), width of teeth (wt), and width of central cusps (wc). The height of teeth, h was measured from the upper margin of the basal concavity to the apex of the central cusp, hc was measured from the crown/root junction to the apex of the central cusp, hr from the tip of the root lobes to the crown/root junction. Following this, means of both root lobe lengths were calculated. Wt is the distance between the outermost cusplets. Due to the fact that many central cusps were aborted, wc was measured 1 mm from the basis of the cusp. This was possible for every tooth. The original length of broken cusps was acquired by flanking the cusp with two direct lines and to follow these lines till they intersected. This was done for ten individuals of each gender. Upper teeth were divided into three groupings: anterior (positions 1–4), lateral (positions 5–9), and posterior teeth (positions 10–18) of the upper left half of the jaw and then analysed separately. Data were analysed with a Mann–Whitney U test to search for significant differences of upper teeth. Linear regression models were employed to analyse, if significant size differences are referred to differences in body size.
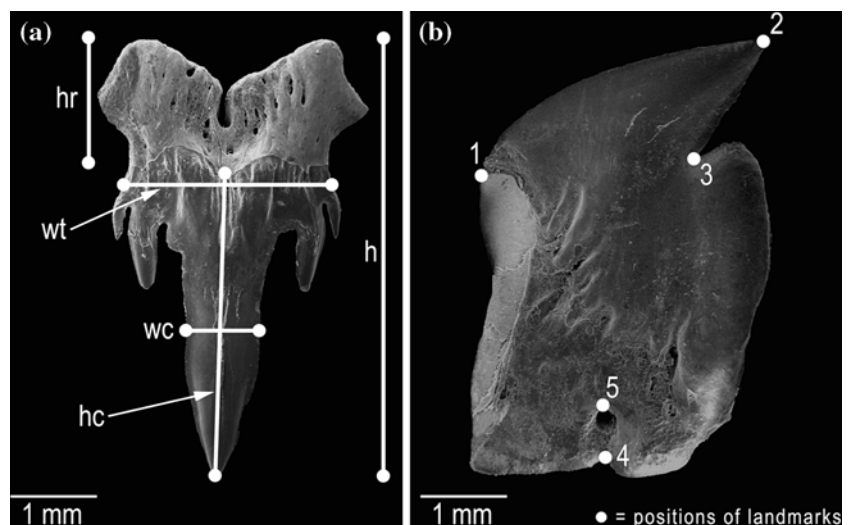
Teeth of positions 2, 7, and 14 of the left lower jaws were extracted, if these teeth were available. Alternatively, positions next to missing ones were chosen.

Morphometric techniques based on landmarks were employed to analyse differences between male and female specimens. The TPS software package was subsequently used to create TPS files and to set landmarks on digitalized images of lower teeth (Fig. 1b). TPSUTIL version 1.20 (Rohlf 2003) was used to create TPS files from images.

With the help of the TPSdig2-software, only five landmarks were set on the SEM images because identifying additional homologous sites on teeth is quite difficult. To ensure homologous positions of landmarks in every picture, the landmarks were positioned at points, which could be found in every SEM image. The first landmark was set at the mesial side of the cusp, the second at the apex of the cusp, the third at the distal side of the cusp, where the cusp separates from the crown basis, the fourth at the end of the basal concavity, and the fifth at the apex of the lower axial foramen (Fig. 1b).

Then, the morphometric landmark data were analysed with the IMP (Integrated Morphometrics

Fig. 1 Distance measurements of upper teeth (**a**) and landmarks set on SEM images of lower teeth (**b**). Three teeth of 10 specimens of each sex of *E. baxteri* were measured (anterior, lateral and posterior positions)

Package) software package, which allows a statistical analysis of landmark based geometric morphometric data (Zelditch et al. 2004). The Generalised Procrustes Analysis (Rohlf 1990; Rohlf and Slice 1990) integrated into the program CoordGen6f was used to remove non-shape variation by scaling all specimens to unit size, translating them to a common location and rotating them to their corresponding landmarks line up as closely as possible. CoordGen6f was used to transform the data files into CS-data format, needed for subsequent analyses with the IMP software package.

In a next step, a principal component analysis (PCA) of significant differences in a given group was executed with the PCAGen6 software package. The two groups then were compared employing two different methods: the CVAGen6j software enables a canonical variates analysis (CVA) of the landmark data, which was tested with a Bartlett's test, and the TwoGroup6h software package conducts Goodall's *F*-test as an analytical analysis and bootstrapped *F*-tests as resampling tests.

Taxonomy of *Etmopterus baxteri*

Etmopterus baxteri, which forms the focus of this study, is member of the Etmopteridae (Lantern sharks), which are inhabitants of the deep sea occurring in depths of 200 to more than 2500 m at continental shelves or seamounts. Numerous characters all reflecting their adaptation to the deep sea conditions, e.g., large eyes, a very effective tapetum lucidum, and bioluminescence, readily identify them. Another important character are the specialized teeth. Upper teeth of *Etmopterus* are multicuspid with 2–8 cusplets flanking a central cusp (Compagno et al. 2005). In contrast, the lower teeth are single-cusped with the cusp being distally bent. These teeth are overlapping each other forming a continuous blade-like structure. Generally, upper teeth of female specimens of *Etmopterus* are assumed to have fewer lateral cusplets than those of males (Ledoux 1970), while the lower teeth of both sexes are considered to be morphologically identical.

Etmopterus baxteri is one of the largest representatives of the Etmopteridae. Adults reach sizes between 70 cm and 88 cm total length. The trunk is dark brown to blackish with a very rough-textured skin and a short, blunt snout (Compagno et al. 2005). Light organs occur on the underside of the snout and the trunk. The second dorsal fin and its spine are noticeably longer and larger than the first, the second spine being significantly curved caudally.

Etmopterus baxteri occurs off south New Zealand, Tasmania, and southern Australia, as well as South Africa. They prefer depths between 800 m and 1300 m and deeper at upper insular slopes on or near the bottom (Wetherbee 1996). The orange roughy, *Hoplostethus atlanticus*, forms a major part of its food and is often found in stomachs of caught specimens (Wetherbee 1999).

The females are ovoviviparous and give birth to 6–16 pups per litter. Maturity is reached at a length of about 63 cm, in contrast to the males, which mature at about 54 cm (Compagno et al. 2005). Age estimates suggest *E. baxteri* to be a long-living and late-maturing species based on growth band counts of the external surface of the second dorsal-fin spine (Irvine et al. 2006).

There exists still some discussion, if *E. baxteri* is a synonym of the Southern lantern shark, *E. granulosus* (Günther 1880) (e.g., Tachikawa et al. 1989). Garrick (1957) described the holotype of *E. baxteri* based on a single female specimen of 74.2 cm total length. He illustrated the upper teeth as multicuspid with up to four small cusplets flanking the central cusp with the first pair of cusplets being smaller than the accompanying ones. One male specimen out of the 115 analysed specimens also displays such a dentition, but a second (or third) bigger cusplet appears irregularly. In this case, one side shows a second cusplet, which is larger than the first, the other side, conversely, has no additional cusplet. This aligns with the conditions of the other studied male specimens. Generally, males show high degrees of variability in single teeth concerning the sides next to the central cusp. No female specimen bears this high number of cusplets and no specimen, except the one mentioned before, had lateral cusplets with the first pair being smaller than the second one.

The problem is further complicated by the fact that the holotype of *E. granulosus* is a sexually immature male specimen showing just one pair of cusplets next to the central cusp. Here, molecular analyses might add to clarifying the taxonomic status of *E. baxteri* and *E. granulosus*.

Results

Morphology of teeth

The total number of teeth varies between the investigated specimens from 15 to 18 in the upper jaws and 20–24 in the lower jaws counting from the symphysis towards the rears.

In contrast to the lower jaws, the upper jaws show 2–3 functional rows of teeth, the teeth are not interlocked (Fig. 2a). A main character of the upper teeth of *E. baxteri* is the central or principal cusp, which is flanked by 1–4 cusplets on each side (Garrick 1957). The crown's profile is triangular forming a tool to grab and hold onto prey. The central cusp is erect; the cusplets are always smaller than the central cusp and can reach at most half the height of the central cusp. The lateral cusplets are broadly united with the principle cusp but well-defined. The base of the crown is quite high. Labially, there are numerous vertical ridges, which are confined to the

crown shoulder. They do not reach beyond the basis of the central cusp. The crown/root junction is centrally concave (Fig. 3).

The two lobes of the root are well developed with the basal concavity being distinct. The teeth are not interlocked. Figure 3 shows an upper tooth of an adult female specimen with two mesial and three distal cusplets; the central cusp is noticeably formed lanceolate. Neither principle cusp nor cusplets are serrated. The first pair of cusplets reach a height of one third of the central cusp. The second pair of cusplets does not reach much further than the beginning of the central cusp. The single third distal cusplet reaches hardly any further than the second distal cusplet. The cusplets are lanceolate.

Lower teeth are always interlocked (Fig. 2b) and show an inner distal and outer mesial depression. The overlapping surface is well developed and high covering almost the complete height of the root. The crown lacks any lateral cusplets, the principle cusp is triangular, smooth-edged, and sharply inclined distally (between 45° and 90°) to form a blade-like tool to cut prey (Herman et al. 1989). The basal concavity of the root is less distinct and the lobes are therefore shorter. Ridges only occur along the transitions of the crown and root, which are arranged bevelled pointing towards the apex of the teeth, and form an irregular crown/root junction. Two axial foramina (lower and upper) are present on the labial face of upper and lower teeth (Fig. 3).
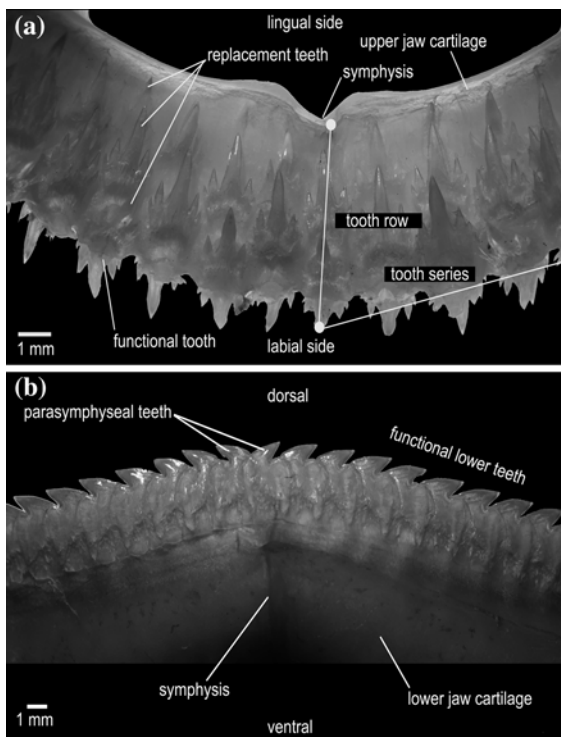

Fig. 2 Jaws and dentition of *E. baxteri*. (**a**) Lingual view of upper jaw. Explanation of terms used for the upper jaw. (**b**) Labial view of lower jaw displaying the functional row
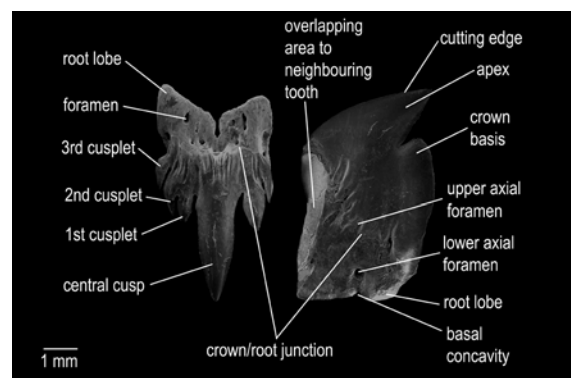

Fig. 3 SEM images of upper (left) and lower (right) teeth with terminology used in this study. Teeth were extracted of jaws of an adult female specimen of *E. baxteri*. Note the widening of the central cusp of the upper tooth

Statistical analyses of upper teeth

We performed a number of statistic tests to analyse the ontogenetic and sexual variations of upper and lower tooth morphologies of *E. baxteri*.

According to the tests, no significant differences of measurements of upper teeth (Fig. 1a) between both gender were found using non-parametrical Mann–Whitney U, Kolmogorov–Smirnov, and Wald–Wolfowitz tests after calculating the linear regressions. Upper teeth of females are morphologically characterized by a lanceolate and wider central cusp, whereas the central cusps of upper male teeth appear to be slender and needle-like. However, these morphologic differences between female and male upper teeth turned out not to be statistically significant when comparing the width of the central cusps (wc, Fig. 1a).

We counted the number of lateral cusplets of the upper functional series to establish differences between both genders. In males, the mean of lateral cusplet numbers flanking the central cusp is 2.058 for 70 male specimens and 1.814 for 45 female specimens (Fig. 4). Male and female specimens differ in the cusplet numbers significantly (Table 1). Correlation tests did not reveal any significant connection
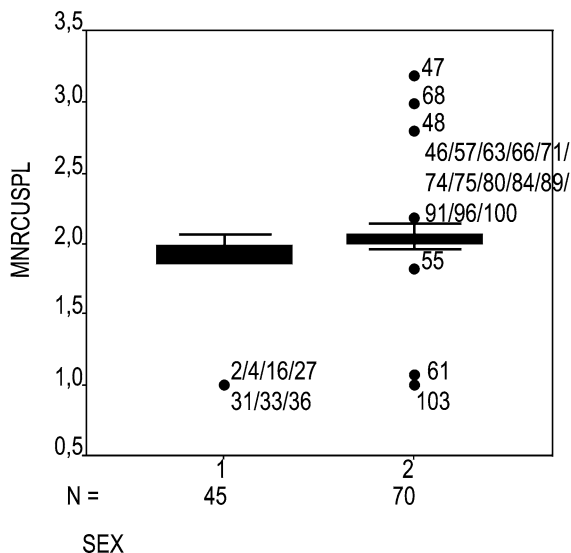
Table 1 Statistics for Mann–Whitney U test, including test factor U and the exact probability of error (P), which is in field of high significance and therefore supports a difference in cusplet numbers of upper teeth between the sexes

Initial value	Number of cusplets
Mann–Whitney U	879.000
Exact significance (P; 2-sided)	<0.001

$N = 60$, 30 upper teeth of male and 30 upper teeth of female specimens of *E. baxteri*

between cusplet numbers and body size, water depth and water temperature, or occurrences.

Procrustes analyses of lower teeth

Figure 5 shows Procrustes superimpositions for the landmark data of both sexes, which were set on digitalized SEM images of lower teeth (Fig. 1b). Hardly any difference between females and males can be noticed, because Procrustes of sexes overlap broadly. A principal component analysis (PCA) of the Procrustes superimpositions showed that both groups were homogeneous.

Subsequently, a canonical variates analyses (CVA) was conducted to look for significant differences between sexes. The results of the CVA are shown in Fig. 6. The scatterplot of scores shows no spatial separation and therefore no significant differences between both genders. The Bartlett's test also reveals no canonical variates between all tested specimens.
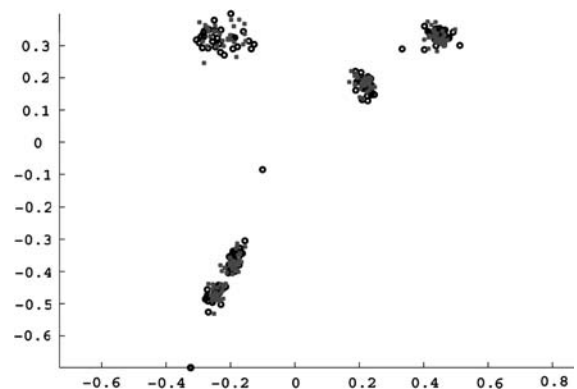

Fig. 4 Boxplot showing means of cusplet numbers (mnrcuspl) for the sexes (1 = male, 2 = female specimens). $N = 115$, 45 female, 70 male specimens. Males show a significant wider range in the cusplet numbers of upper teeth as females do. Dots mark single outliers in cusplet numbers of upper teeth

Fig. 5 Procrustes superimposition of landmarks set on SEM images of lower teeth of male and female specimens of *E. baxteri*. Note the overlapping of Procrustes, pointing towards minimal differences between the sexes. $N = 60$, 30 lower teeth of female, 30 lower teeth of male specimens
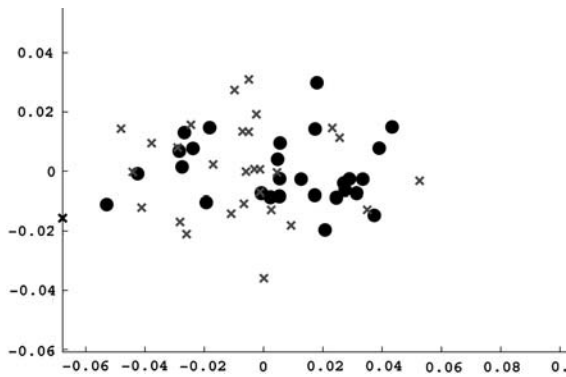
Fig. 6 CVA plot of male and female specimens of *E. baxteri* calculated from the Procrustes superimpositions. Dots equal male, crosses female specimens. The *x*-axis shows CV1, the *y*-axis shows CV2

Fig. 7 Means of Procrustes of both sexes of *E. baxteri*. Triangles equal female, stars male specimens. Note the small distances between the means of both groups. $N = 60$, 30 lower teeth of female and 30 lower teeth of male specimens

In a next step, the Procrustes of both sexes (Fig. 5) were analysed with a *F*-test, which does not display any characteristic separation between scatterplots of landmarks. The Procrustes of males and females are nearly identical. The conducted statistical tests support these observations. The Goodall's *F*-test also does not reveal any significant differences between female and male lower teeth ($P = 0.22$).

The bootstrapped *F*-test shows similar results as Goodall's *F*-test. Values of the probability of error (P) are not in range of significance. Increasing the number of bootstrap steps does not increase the level of significance. Conversely, P increases if the bootstrap values are increased and therefore moves away from significant values ($P = 0.21$ up to $P = 0.24$ with increasing bootstrap steps).

Due to the fact that results of both tests are not in any range of significance, the other factors such as degrees of freedom and distance between means were not interpreted.

Minimal differences become obvious when comparing the means of Procrustes of both groups (Fig. 7). Both analyses did not reveal any differences of lower teeth between the sexes.

Discussion

Size differences of upper teeth between the sexes are assumed to depend on differences in body size in general. Calculated regression models could not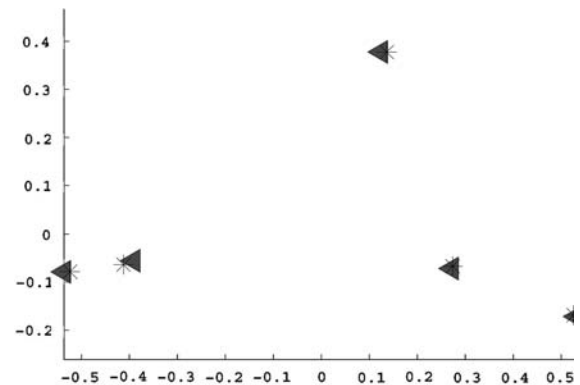 assert that upper teeth of male and female specimens are actually different in size for similar body sizes, whereas the size of the teeth is correlated with the body size, which was to be expected.

The morphologic difference in the shape of the central cusp could not be statistically acquired by comparing the width of it (Fig. 1a). Therefore, the shape of the central cusp is not a reliable character to identify genders.

The average values in cusplet numbers show that this feature is significantly sexually dimorphic for adult specimens although exceptions may exist. It varies from 1 to 4 for males, whereas upper teeth of females vary from 1 to 2. Some females display a greater number of later cusplets, which are too rare to be of any statistical importance. Similar phenomenons were described for *E. pusillus* and *E. bigelowi* by Shirai and Tachikawa (1993). These authors also state that this morphological change occurs with maturation. The teeth of all immature specimens studied here showed a constant number of two pairs of cusplets next to the central cusp. However, the sample size of juveniles is very limited and it thus is not possible to support Shirai's theory, but it could not be refused either. Only upper teeth of adult specimens show remarkable differences regarding the number of cusplets, which might be related to differences in the diet or simply represents phenotypical plasticity. The latter might be indicated by the fact that most upper teeth of both sexes display two pairs of cusplets flanking the central cusp.

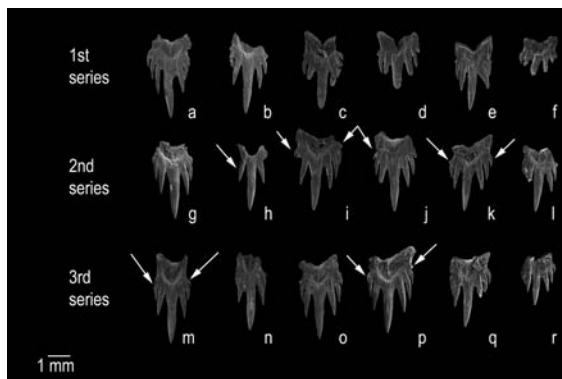Surprisingly, there is a high variation in the number of cusplets of upper teeth within one jaw,

Fig. 8 Upper tooth shapes of anterior, lateral and posterior region within one jaw of a male specimen of *E. baxteri*, SEM images, labial views. Arrows indicate morphological differences between the teeth (see text). Also note the missing of a widening of the central cusp compared to the upper teeth of females shown in Fig. 3

which should exemplify the difficulties to use the character ''number of cusplets'' to describe species. Figure 8 shows rows and series of teeth within one male jaw. Comparing, for example, teeth shown in Fig. 8h, m, j, and i, the number of cusplets varies between one (h) and four (i). The 3rd and 4th pairs of cusplets develop differently. For instance, tooth k has a very reduced third cusplet, whereas tooth j reveals a fully developed third cusplet. Hence, not just the number of cusplets varies, but also their appearance, which makes the teeth look very different from each other, although coming from the same jaw and even row. Another criterion is the variation and development of cusplets on the mesial and distal sides of the central cusp respectively. Tooth i has four distal cusplets, the fourth cusplet is reduced. Conversely, there are three well-developed cusplets (mark: the second cusplet is damaged) mesially to the cusp. Another example is tooth k. Its central cusp is flanked by three pairs of cusplets on both sides, but the third mesial cusplet is not fully developed in contrast to the third distal cusplet. Consequently, the number of cusplets does not follow any regularities in a given male upper jaw. Moreover, neither rows nor series of teeth follow any pattern. Conversely, females do not have such variations except for very few teeth.

Lower teeth were analysed with landmark data because of the simplicity of tooth morphologies resulting in less available data. The analysis of five landmarks set on SEM images of lower teeth did not reveal any biologically meaningful differences

between male and female specimens, neither within the sexes, nor between the sexes. Figure 6 shows explicitly the overlapping of the sexes for the canonical variates analysis (CVA). The analysis with the TwoGroup6h software shows similar results. The means of Procrustes in Fig. 7 reveal overlapping of average values or very small distances between the means, which are too small, to find significant differences between male and female specimens.

Conclusions

We have presented a series of tests to determine possible relationships between tooth shape and other parameters such as body length, ontogeny or gender to determine dental features that can be used for taxonomic and systematic purposes. Due to the fact that specimens of *Etmopterus* display a very pronounced dignathic heterodonty (teeth in upper and lower jaws are different), upper teeth were measured and analysed. Lower teeth, conversely, were subject to a landmark data analysis.

According to the results derived from these analyses, upper teeth of adults are sexually dimorphic. Although a significant difference in upper tooth size was not noted, upper teeth of females might be larger than those of males due to the sexual dimorphism of body sizes. Additionally, they differ morphologically in displaying a lanceolate central cusp, whereas male specimens have thin and needle-like central cusps. Males also show a higher number and a more pronounced variability of cusplets than females. An ontogenetic heterodonty might be developed in male specimens, but more material is required, to support this hypothesis. Sexually immature males show similar dentitions to those of adult females. No significant correlations between any dental characters were found. However, teeth of adult females and males differ morphologically in the shape of the central cusp and most importantly, in the number of lateral cusplets, which always is more variable and higher in males.

The analysis of landmarks set on SEM images of lower teeth did not reveal any differences between females and males. Specimens analysed herein show pronounced variations in dental morphology that are difficult to assess. The application of the morphological traits identified in extant *E. baxteri* on fossil

records requires the assumptions that tooth shape and variation is the same in fossil *Etmopterus* species as it is in living forms and that fossil taxa are distinguishable by their tooth morphologies. Given the fact that the fossil record of squaliform sharks is quite good and the general dental appearance of fossil *Etmopterus* species did not change too much over time, we assume that the characters of living female and male specimens identified herein can be applied to fossil taxa. Moreover, these features may help clarifying the taxonomic status of fossil taxa assigned to *Etmopterus*, which possibly may in some cases represent different gender of the same species.

References

Adnet S, Cappetta H (2001) A palaeontological and phylogenetical analysis of squaliform sharks (Chondrichthyes: Squaliformes) based on dental characters. Lethaia 34:235–248

Bernardi G, Powers DA (1992) Molecular phylogeny of the prickly shark, *Echinorhinus cookei*, based on a nuclear (18S rRNA) and a mitochondrial (Cytochrome b) gene. Mol phylogenet evol 2:161–167

De Carvalho MR (1996) Higher-level Elasmobranch phylogeny, basal Squaleans, and paraphyly. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes, 1st edn. Academic Press, San Diego

Compagno LJV (1999) Checklist of living Elasmobranchs. In: Hamlett WC (ed) Sharks, Skates and Rays–the biology of living Elasmobranchs, 1st edn. The Johns Hopkins University Press, Baltimore

Compagno LJV, Niems VH (1998) Squalidae. Dogfish sharks. In: Carpenter KE, Niem VH (eds) FAO identification guide for fishery purposes. The living marine resources of the Western Central Pacific. FAO, Rome, pp 1213–1232

Compagno LJV, Dando M, Fowler S (2005) A field guide to the sharks of the world. Harper Collins Publishers Ltd., London

Garrick JAF (1957) Studies on New Zealand Elasmobranchii. Part VI: Two new species of *Etmopterus* from New Zealand. Bull Museum competitive Zool 116:171–190

Günther A (1880) Report on the shore fishes procured during the voyage of H.M.S. Challenger in the years 1873–1876. In: Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876. Zool 1:1–82

Herman J, Hovestadt-Euler M, Hovestadt DC (1989) Contribution to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. Part A: Selachii. No 3: Order: Squaliformes—families: Echinorhinidae, Oxynotidae and Squalidae. Bulletin de l'Institut Royal de Sciences Naturelles de Belgique, Biologie 59:101–157

Irvine SB, Stevens JD, Laurenson LJB (2006) Comparing external and internal dorsal spine bands to interpret the age and growth of the giant lantern shark, *Etmopterus baxteri* (Squaliformes, Etmopteridae). Environ Biol Fish 77:253–264

Ledoux JC (1970) Les Dents des Squalides de la mediterranee occidentale et de l'Atlantique nord-ouest Africain. Extrait de ''Vie et Milieu'' Serie A: Biologie Marine 2A:309–362

Musick MA, Harbin MM, Compagno LJV (2004) Historical zoogeography of the Selachii. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, 1st edn. CRC Press, Boca Raton

Pfeil FH (1983) Zahnmorphologische Untersuchungen an rezenten und fossilen Haien der Ordnungen Chlamydoselachiformes und Echinorhiniformes. Palaeoichthyologica 1:1–315

Rohlf FJ (1990) Rotational fit (Procrustes) methods. In: Proceedings of the Michigan morphometrics workshop, The Univ. Michigan Mus. Zool., Ann Arbor, pp 227–236

Rohlf FJ (2003) Bias and error in estimates of mean shape in morphometrics. J Hum Evol 44:665–683

Rohlf FJ, Slice D (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst Zool 39:40–59

Shirai S (1992) Squalean phylogeny: a new framework of ''squaloid'' sharks and related taxa. Hokkaido University Press, Sapporo

Shirai S, Tachikawa H (1993) Taxonomic resolution of the *Etmopterus pusillus* species group (Elasmobranchii, Etmopteridae) with description of *E. bigelowi*, n. sp. Copeia 2:483–495

Tachikawa HT, Taniuchi T, Arai R (1989) *Etmopterus baxteri*, a junior synonym of *E. granulosus* (Elasmobranchii, Squalidae). Bull Natl Sci Museum Tokyo 15:235–241

Wetherbee BM (1996) Distribution and reproduction of the southern lantern shark from New Zealand. J Fish Biol 49:1186–1196

Wetherbee BM (1999) Assemblage of deep-sea sharks on Chatham Rise, New Zealand. Fishing Bull 98:189–198

Zelditch M, Swiderski DL, Sheets DH, Fink WL (2004) Geometric morphometrics for biologists. Elsevier Academic Press, San Diego