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Biometric analysis of the teeth of fossil and Recent hexanchid sharks and its taxonomic implications

SYLVAIN ADNET

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A biometric analysis of the lower teeth of Recent cow sharks (Hexanchidae) investigates the ontogenetic and phylogenetic aspects of the dental characters employed by many ichthyologists and palaeontologists. The dental characters currently used to separate two extant species of sixgill sharks (*Hexanchus griseus* and *H. nakamurai*) are analysed and the fossil record of their relatives reviewed. The main results suggest that the cusp number ratio (number of cusps per mm) is preferable to width of the lower tooth for inference of total body size, at least in species of *Hexanchus*. The presence of a serrated edge or an enlarged acrocone appears to depend on ontogeny and care must be taken when using these as taxomomic characters. Three Eocene species of *Hexanchus*, *H. collinsonae*, *H. hookeri*, and *H. agassizi*, and a new assemblage of fossil teeth from the late Ypresian/early Lutetian (Early/Middle Eocene) of south-western France, are also analysed. The first two of these species may be ontogenetic states of *H. agassizi*. *Hexanchus agassizi*, belonging to the vituliform lineage and closely related to the living *H. nakamurai*, is considered here to be the only species of *Hexanchus* in the Lower to Middle Eocene. A brief overview of Palaeogene *Hexanchus*, suggests no evidence of the grisiform group (closely related to living *H. griseus*) before the Late Eocene.

Key words: Elasmobranchii, Hexanchidae, shark teeth, biometry, Eocene.

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Introduction

In Recent oceans, hexanchid or cow sharks are one of the less diverse shark groups. Only three living genera and four species belong to the family Hexanchidae. The most conspicuous diagnostic features of these sharks are the presence of six or seven gill slits, only one dorsal fin and antero-lateral lower teeth with a sawblade-like (most commonly described as comb-like) appearance (Bigelow and Shroeder 1948; Compagno 1973, 1977; Kemp 1978; Cadenat and Blache 1981). Fossil species of the Hexanchidae are more numerous and have a long stratigraphic range extending back to the Lower Jurassic (Beaumont 1960). Taxa are mainly based on isolated teeth, particularly lower teeth. However, fossils are relatively sparse, especially before the Upper Cretaceous, and are often limited to fragmentary material. This has led to debates about the systematics of the group (Ward and Thies 1987; Cappetta 1987, 1990; Long et al. 1993). Fossil remains from the Upper Cretaceous and Cenozoic are better known, generally more numerous and include among others the three extant genera.

Following the palaeontological work of Ward (1979), two morphological types of lower teeth are usually considered to be present in Cenozoic *Hexanchus*: grisiform and vituliform (Ward 1979). The separation of these two "modern lineages" since the Early Eocene is based on the observation of discrete variation in the shape of the lower antero-lateral teeth between the two living species, the great blunt nose sixgill shark, *H. griseus* (Bonnaterre, 1788), and the smaller big eyed sixgill shark, *H. nakamurai* Teng, 1962. Included in the synonymy of this last species is *H. vitulus* Springer and Waller, 1969 (Taniuchi and Tachikawa 1991, Compagno 1999). Kemp (1978) and Welton (1979) pointed out taxonomic difficulties caused by the ontogenetic development of the lower teeth in Recent *Hexanchus*. Nevertheless, slight differences in antero-lateral tooth morphology have been regarded as key diagnostic characters allowing distinction between the two living species in many handbooks (Whitehead et al. 1984; Compagno 1984). Cione and Reguero (1994) subsequently suggested that most of the dental features were too variable to be employed for separation of the two living species, whereas Herman et al. (1994) considered that there were three living species within the genus *Hexanchus* based on odontological characters. Other Palaeogene fossils of *Hexanchus* have been found since the work of Ward (1979) and it is sometimes difficult to assign them to a particular species. This ambiguity arises because dental variations were never fully analysed in living *Hexanchus* before their employment as taxonomic characters (Cappetta 1980) and it is clear that analysis of ontogenetic variability is required.

The purpose of this paper is to examine ontogenetic and individual variations between the extant and extinct species of sharks of the family Hexanchidae, especially *Hexanchus*.

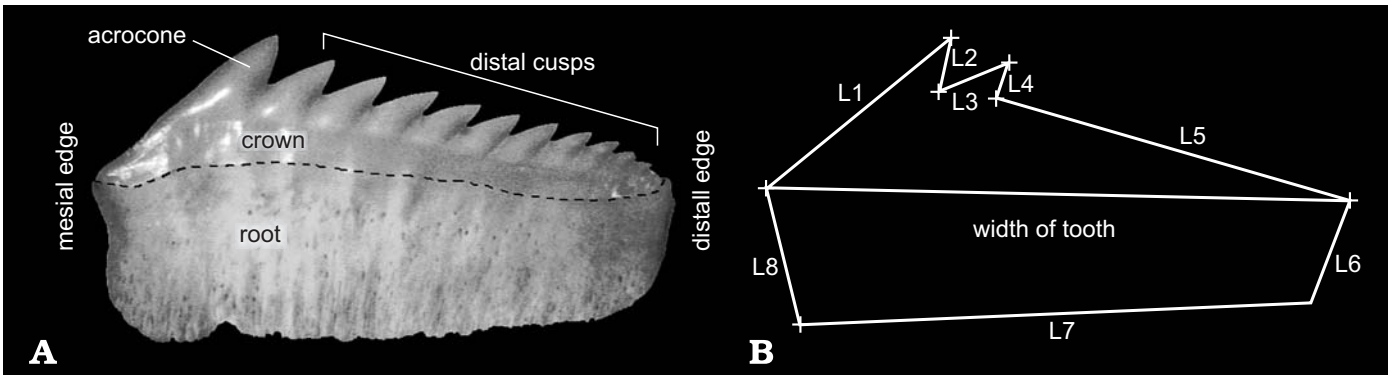


Fig. 1. **A**. Simplified terminology of a *Hexanchus* lower tooth (*Hexanchus griseus*, 4th right file, >300 cm total length, UMC-REC204bM). **B**. Schematic drawing of measurements (homologuous points and intermediate distances) discussed in the text.

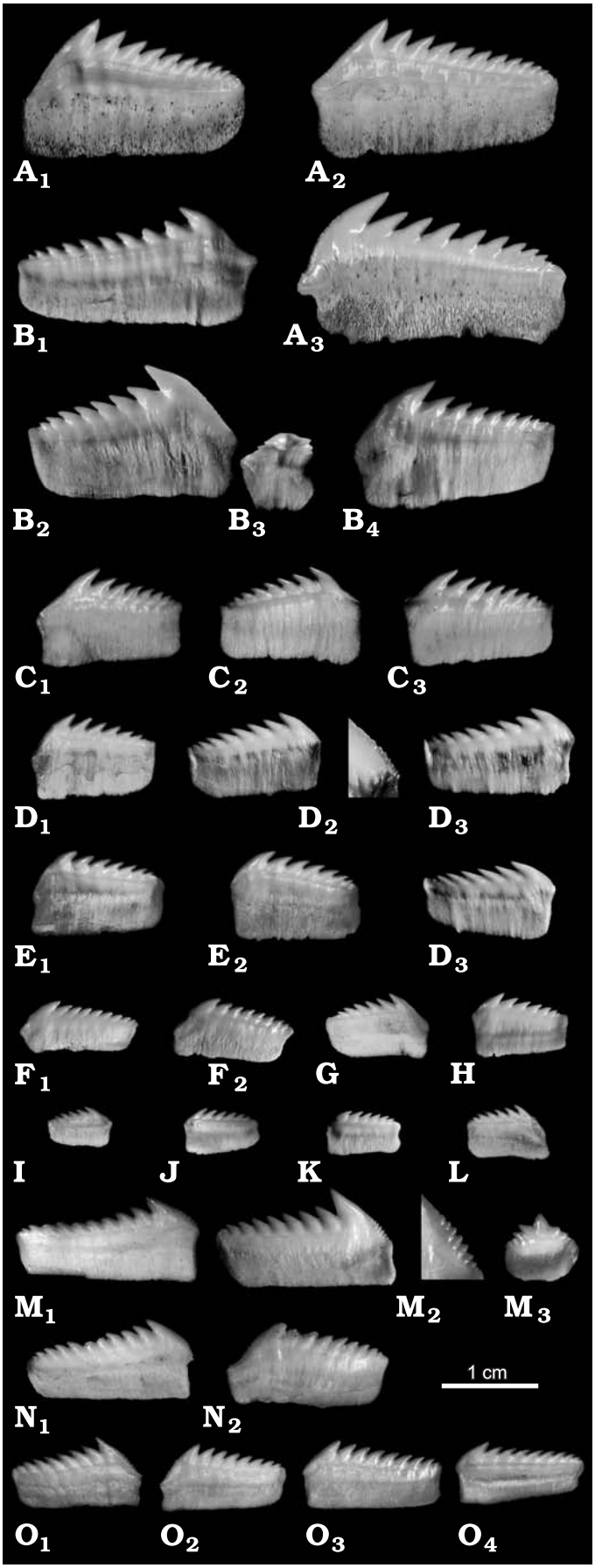
Analysis was first carried out on Recent *Hexanchus* and then extended to Palaeogene specimens, particularly a large new collection of isolated lower teeth from the late Ypresian/early Lutetian of south-western France. This has allowed reassessment of the significance of the supposedly diagnostic characters traditionally used in hexanchid taxonomy (e.g., width of tooth, cusp number, the presence of serration on acrocone and presence of erected symphysial tooth), and clarification of whether the splitting of the two Recent lineages of *Hexanchus* took place before the Lutetian.

Institutional abbreviations.—UMC, University of Montpellier, France; UMC-SG, collection of fossil shark teeth from the Saint-Geours-d'Auribat quarry at UMC; UMC-REC, collection of Recent shark teeth at UMC.

Material and methods

The characters used to describe hexanchid teeth, particularly in the genus *Hexanchus*, are usually based on general size and sometimes on qualitative variations in morphology (e.g., degrees of cusp serration and root enlargement). However, few studies on specific variation have been undertaken when describing Recent or fossil teeth of hexanchids (Welton 1979; Herman et al. 1994; Kaneko et al. 1997). Variation in tooth morphology within selachian species is usually termed heterodonty (Compagno 1970; Cappetta 1986, 1987), with several subdivisions (e.g., ontogenetic and gynandric heterodonty) according to its effect or its cause. In addition to ontogenetic heterodonty, two other types of heterodonty occur in hexanchid species, monognathic heterodonty (variation of tooth morphology along each half jaw) and dignathic heterodonty (variation of tooth morphology between upper and lower jaws). In fact, three major dental morphologies may be recognised on hexanchid jaws: upper anterior teeth with hook-like shapes, upper lateral teeth and antero-lateral lower teeth with sawblade-like or comb-like shapes, and commissural lower and upper teeth with similar pavement-like morphologies. Only antero-lateral lower teeth are studied here for two reasons. First, the highly variable morphology of the upper teeth and the scarcity in the fossil record of commissural teeth restrict their value in taxonomy. Secondly, fossil Hexanchidae have been described essentially using lower antero-lateral teeth.

Dental terminology (Fig. 1A) has been taken from numerous works (Applegate 1965; Kemp 1978; Cappetta 1976; Welton 1979; Ward 1979). In the present study, each antero-lateral lower tooth has been analysed independently. Eight metric distances and their respective angles have been measured between eight points considered as homologous (for L1–L5) and directly taken on the labio-lingual view of the tooth (Fig. 1B) or calculated from line intersections (for L6–L8) using graphics tablet software. The width of the lower teeth has been computed from other metric measurements. A total of 217 complete lower teeth (UMC-REC) of Recent *Hexanchus griseus* (Bonnaterre, 1788) (e.g., Fig. 2) were measured using a graphics tablet under an enlarger. For Recent material, the position of the tooth on the lower jaw (named file), as well as the sex and total length of the shark, were recorded for each measured tooth. Also on Recent and on well preserved fossil teeth, the number of cusps was recorded, and in all cases, the presence or absence of serration on the mesial edge of the acrocone (the first mesial cusp) was noted. Each lower tooth contains up to 20 quantitative and qualitative variables: inter-point distances (L1–L8) and angles (A1–A8); width of crown; total length of the fish, tooth position on the jaw (named file); number of cusps; sex of fish; and presence/absence of serration on the mesial edge of the first cusp. Because of difficulties in obtaining fresh hexanchid jaws, all species have not been equally sampled. Therefore, *Hexanchus griseus* is represented by 150 teeth in young and subadult fishes, whereas *H. nakamurai*, *H. perlo*, and *Notorynchus cepedianus* are represented respectively by 26, 24, and 27 lower teeth from sub-adult to adult fishes. Material, all collected during the three last decades, is housed in the Palaeontology Department, University of Montpellier II, France. To complement

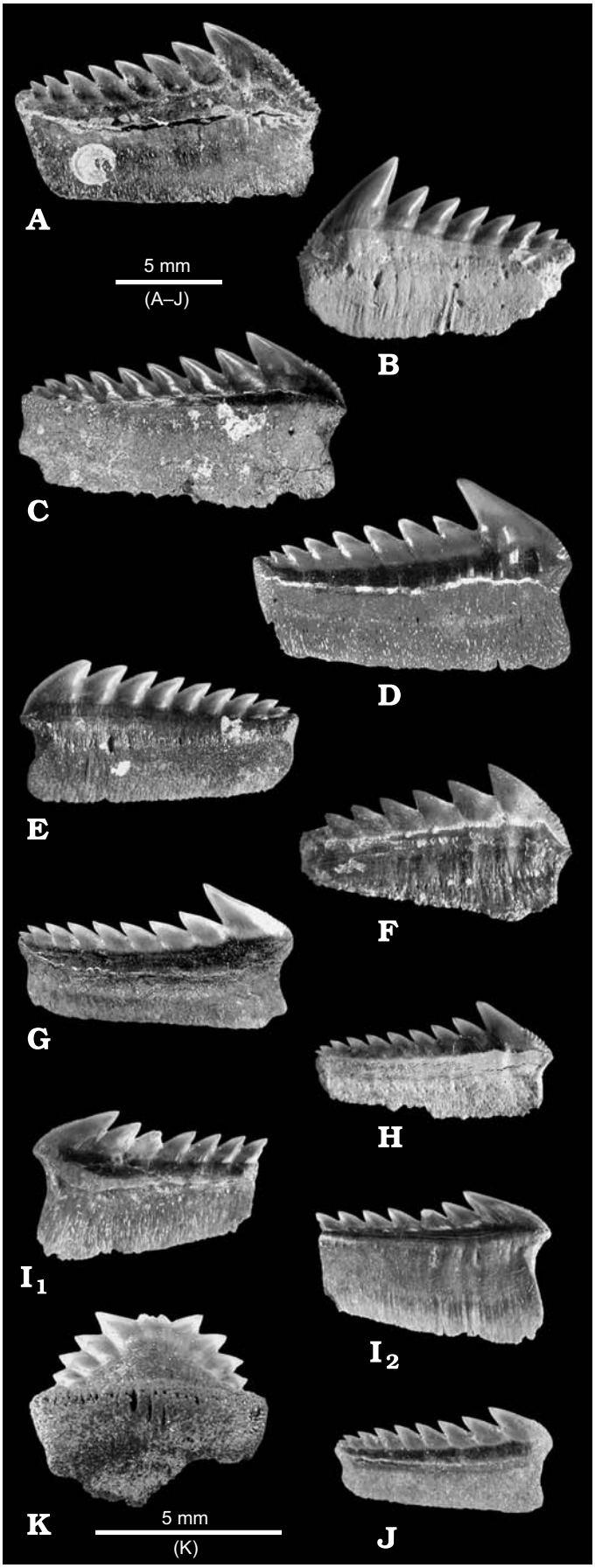


the database of Recent species, measurements were taken from Welton (1979, table 12), Kaneko et al. (1997: table 1) and from the figures of Kemp (1978: pl. 12: 5; 1991: pl. 6: A1) with respective information on body length, sex and tooth position. The same measurements have been made on available and well preserved fossil *Hexanchus* teeth. Comparative measurements (Appendix 1) were made on fossil material or directly on figured specimens of Palaeogene *H. agassizi* (Cappetta 1976), *H. collinsonae*, *H. hookeri* (Ward 1979), *H. microdon* (Arambourg 1952) and on the new material from south-western France (see below) using the same protocols.

New Eocene material from south-western France

Eocene material from south-western France represents one of the largest known collections of Palaeogene *Hexanchus*. It is composed of more than 100 teeth ranging from 0.7 cm to 1.55 cm in width. This material was obtained by surface collecting and screening-washing of more than 1000 kg of blue marls of the "Donzacq marls" Formation (Sztrakos 1996) from the working quarry at Saint-Geours-d'Auribat, east Dax, Landes. Contemperaneous exploited levels were formerly dated as Late Ypresian (Platel 1990) or Early Lutetian (Boulanger 1968; Steurbaut in Nolf 1988), but are now regarded as late Ypresian/early Lutetian [?P9–P10, NP14] (Sztrakos et al. 1998; Adnet 2000, Nolf et al. 2002). A large fossil selachian fauna, including fragmentary teeth of species of *Heptranchias*, is under study or published in part (Adnet et al. 2006). Using current taxonomic criteria, each level contains lower teeth from both the vituliform and grisiform *Hexanchus* groups (Fig. 3).

Fig. 2. Overview of dental variations in lower teeth of living species of *Hexanchus*. Labial view of some lower teeth of *Hexanchus griseus* (**A**–**L**) and *Hexanchus nakamurai* (**M**–**O**). **A**. ♀uncertain (UMC-REC204bM), >300 cm TL; 1st left file (A_1), 3rd (uncertain) left file (A_2), and lateral left file (A_3). **B**. ♂ (UMC-REC204M), 300 cm TL; 3rd right file (B_1), 1st right file (B_2), symphysial file (B_3), and 1st left file (B_4). **C**. ♂ (UMC-REC162M), 223 cm TL; 1st left file (C_1), 2nd right file (C_2), and 3rd left file (C_3). **D**. ♂ (UMC-REC175M), 195 cm TL; 1st left file (D_1), 3rd left file with enlargement on the mesial serrated cutting edge of the first cusp (D_2), 4th left file (D_3), and 5th left file (D_4). **E**. ♀ (UMC-REC161M), 191 cm TL; 1st left file (E_1) and 3rd left file (E_2). **F**. ♂ (UMC-REC611M), 1.08 cm TL; 1st left file (F_1), 4th left file (F_2). **G**. ♀ (UMC-REC163M), 114 cm TL, 1st right file. **H**. ♀ (UMC-REC164M), 117 cm TL, 3nd left file. **I**. Unsexued (UMC-REC201M), 58 cm TL 2nd right file. **J**. Unsexued (UMC-REC172M), 72 cm TL, 2nd left file. **K**. Unsexued (UMC-REC173M), 75 cm TL, 1st left file. **L**. ♂ (UMC-REC174M), 80 cm TL, 1st right file. **M**. ♀ uncertain (UMC-REC197M), 148 cm TL; 4th rigth file (M_1), 1st right file with enlargement on the mesial serrated cutting edge of the first cusp (M_2), symphysial file (M3). **N**. ♂ uncertain (UMC-REC192M), 145 cm TL; 3rd right file (N_1) and 1st left file (N_2). **O**. Sex undetermined (UMC-REC196M), 1 m TL, 1st right file (O_1), 1st left file (O_2), 3rd lateral file (O_3), and 4th lateral file (O_4). A–D and F–O are respectively at the same magnification (vertical white bars). Abbreviation: TL, total length.



Results

Recent *Hexanchus griseus* (Bonnaterre, 1788)

To test the quality of the measurements, multiple analyses of variance on all measured values for living species were undertaken. The results indicate no significant differences between the right and left rows of lower jaws. Mean values, standard deviations and other parameters are given in Appendix 1 for all analysed specimens.

Width of tooth and growth of shark.—In the large species *H. griseus*, the length of the body (total length according to Compagno 1984) and width of the tooth of each file are well correlated ($R = 0.95$ to 0.98, $p < 0.001$). A simple linear regression equation expressing the relationship between the width of lower teeth and the body length of the shark can be calculated: length of shark (in cm) = 111 × width of tooth (in cm) + 3.9 ($R = 0.97$, $p < 0.001$; $N = 243$). The three other smaller species were also analysed. The width of the lower teeth of *N. cepedianus* shows the same relationship to body length as *H. griseus*, whereas *H. perlo* teeth are closer to the relationship seen in *H. nakamurai* where shark length (in cm) = 65.1 × width of tooth (in cm) + 23.1 ($R = 0.91$, $p < 0.001$; $N = 27$). *H. griseus* and *N. cepedianus* possess six lower teeth (per half jaw) compared to the five present in *H. perlo* and *H. nakamurai.* This seems to indicate that the widening of the lower jaw teeth follows the growth of the shark, with a relationship which depends on the lower dental formula in hexanchids.

Cusp number.—Lower teeth of available *Hexanchus griseus* specimens have between 4 and 11 cusps (including the first mesial cusp, the acrocone), according their position on the jaw and the size of the shark. If the entire population is considered, the number of cusps appears to vary slightly with file position (with minimum values for the first and sixth files and maximum for the third file) and shark size. When each file is considered independently, the number of cusps increases slowly with the body length of the shark, with a mean increase of 1 cusp for 80 cm of length. However, the ratio between the number of cusps and tooth width (number of cusps per centimetre) decreases with the body size of the shark. Consequently, as Welton (1979) noted, if the adult cow sharks possess lower teeth with a greater number of cusps than the juveniles, then the second ones have lower teeth with relatively more cusps than the first ones (see Fig. 2I–L).

Fig. 3. Fossil *Hexanchus* sp. lower teeth from the Donzacq Formation of Saint-Géours-d'Auribat (late Ypresian/early Lutetian, south-western France). **A**. UMC-SG13, antero-lateral file, labial view. **B**. UMC-SG130, antero-lateral file, lingual view. **C**. UMC-SG15, lateral file, labial view. **D**. UMC-SG14, antero-lateral file, labial view. **E**. UMC-SG131, lateral file, lingual view. **F**. UMC-SG132, antero-lateral file, lingual view. **G**. UMC-SG17, lateral file, labial view. **H**. UMC-SG133, lateral file, labial view. **I**. UMC-SG134, broken lateral lower tooth with peculiar deep root, labial (I_1) and lingual (I_2) views. **J**. UMC-SG135, lateral file, labial view. **K**. UMC-SG12, symphysial file, lingual view.

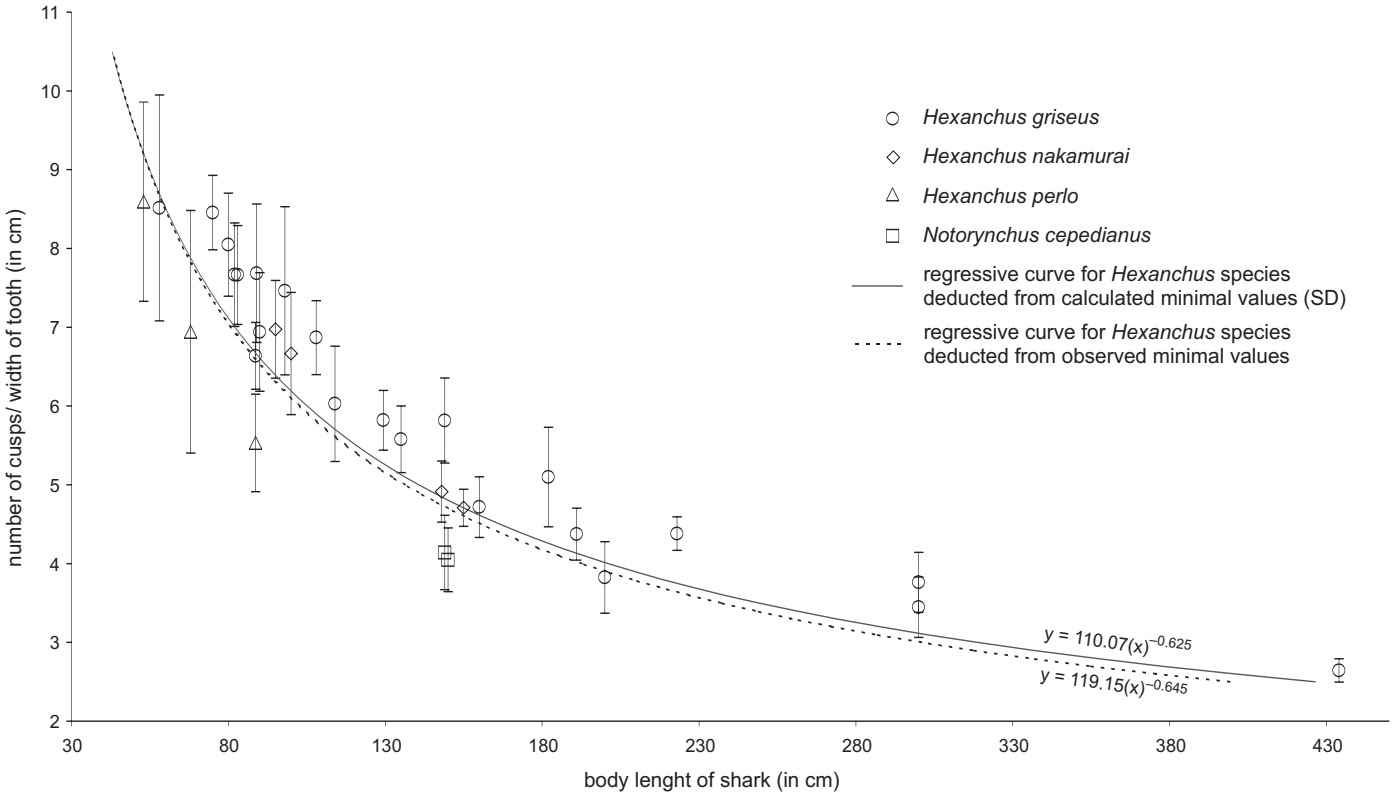


Fig. 4. Relationship between the number of cusps per tooth width (vertical axis) and total body length (horizontal axis) in Recent hexanchid species. Variation of values along the jaw for each specimen are shown by the mean values (symbol) and the standard deviations (vertical bar).

Other hexanchid species were also analysed and placed on the same bivariate plot (Fig. 4). At equal body size, *H. nakamurai* shows lower teeth with the same ratio as *H. griseus*. *N. cepedianus*, and to a lesser degree *H. perlo*, possess lower teeth with a smaller ratio which allows easily separation from other hexacanthid species. Finally, the ratio of number of cusps/width of the tooth appears to be better correlated in the group than tooth width which depends more on available jaw space available (and thus dental formulation). As the body size of cow sharks is inversely correlated with this ratio, one can apply it *a posteriori* to deduce the size of the shark from its teeth. To minimise aberrant values and consider individual variability, only the minimal values for each data set (per specimen) are considered. Regression analyses have been made for the minimal values for each calculated distribution (mean value minus one standard deviation; $R = 0.97$, $p < 0.001$; $N = 26$; continuous line on Fig. 4) and from observed minimal values for each data set of *Hexanchus* ($R = 0.96$, $p < 0.001$; $N = 26$; dashed line on Fig. 4), which show no significant difference.

Acrocone morphology.—Quantitative variables in the teeth of Recent *Hexanchus griseus* and other species have been studied using PCA. No qualitative distinction (specific or sexual groups) is evident from the two resulting major axis which explain 70% of the variability. The first principal axis explains only overall shark size. This is essentially composed of the nine distance variables (L1–L8 and tooth width). The evolution of the size of the first cusp (acrocone) size is a particular focus of interest because of its taxonomic importance. One approach is to compare the sizes of its mesial (L1) and distal (L2) edges with those of the second distal cusp (e.g., ratios L1/L3, L2/L4, L1/L4, and L2/L3; see Fig. 1B). Dependence tests and regression analyses between each ratio and the tooth width, sex and body size have been computed. In all cases, these ratios increase with the width of the tooth and with body size, suggesting an increase of acrocone size compared to that of the second cusp as the sharks grow.

The relative increase in acrocone size appears to be similar in the two species of *Hexanchus* despite a difference in growth rate. The distribution of L2 values compared to L3 values (Fig. 5) illustrates this difference in growth rate because it reflects the importance of the acrocone compared to the second cusp. Several logarithmic regressions can be computed with the same confidence between L2 and L3 values for *H. griseus* and the choice has been to keep the simplest one. One of the better regressions appears to follow an exponential equation ($R = 0.94$, $p < 0.001$; $N = 151$). Despite a smaller sample size, a similar equation can be applied to the L2/L3 values of *H. nakamurai* ($R = 0.73$, $p < 0.01$; $N = 26$). No formula has been calculated for *N. cepedianus* or *H. perlo* because of the lack of a significant regression ($R<0.7$). Regression curves and L2/L3 values have been drawn and distinctions made between teeth with serrated and non-serrated acrocones (Fig. 4). For the

lower teeth of *Hexanchus*, increase in acrocone size compared to the second cusp appears to be non-linear and reveals allometric growth. Differences in the speed of development (growth rate) of the acrocone between the two species of *Hexanchus* may be explained by the fact that *H. griseus* reaches a total length in excess of 480 cm (Castro 1983; Compagno 1984), possibly larger (Clark and Kristof 1990; Celona et al. 2005), compared to the maximum length of 180 cm in *H. nakamurai* (Compagno 1984). Even though the largest mature *H. griseus* and the smallest juvenile *H. nakamurai* are lacking in the data set used here, L2/L3 regression curves are very distinct for these two living species (Fig. 5). This is particularly interesting in the context of discriminating between teeth of juvenile *H. griseus* and those of adult *H. nakamurai*, two sharks which have very similar body sizes and tooth widths. Indeed, the two living species of *Hexanchus* seem to possess a similar pattern of acrocone growth, with various parameters attesting to the difference of growth rate between the large and the small sixgill sharks.

New Eocene material of a *Hexanchus*

Size reconstitution.—The material studied from the late Ypresian/early Lutetian of south-western France comprises lower teeth from 0.7 to 1.55 cm in width, showing 7–8 cusps per crown and a serrated acrocone (Fig. 3). Measured parameters are reported in Appendix 1. The calculated minimum values of distribution (mean minus one standard deviation) for the cusp number ratio (number of susp per width of tooth) indicate a maximum size of shark around 110 cm in total length, with an error range of 0.2 m.

Biometric analysis.—As a first step, all the available variables calculated from measurements of fossil teeth were analysed along with those of the two living species of *Hexanchus*. As for the samples of Recent species, no qualitative distinction (specific or sexual groups) is evident from the PCA. L2/L3 values of fossil teeth have been plotted on a bivariate graph which also contains the previous regression curves and/or plots from teeth of living *Hexanchus* species (Fig. 6). The abundance of material allows a regression curve to be calculated as for the living species ($N = 75$; $R = 0.87$).

As one would expect, the distribution of values and regression equation parameters are close to those of living *Hexanchus* and more particularly to *H. nakumurai,* despite the number of cusps and absolute values of L2 and L3 being slightly lower. ANOVA performed on the L2/L3 ratio confirms the lack of species differentiation between *H. nakamurai* and the fossil sample from Landes ($F = 2.92$, ns), whereas *H. griseus* and the Landes sample are significantly different ($F = 29.8$, $p < 0.001$). This result shows that variation of acrocone size in the fossil sample compares well with that of modern *Hexanchus* species such as *H. nakamurai*. Indeed, all *Hexanchus* fossil teeth from south-western France seem to belong to a unique species of the vituliform group of Ward (1979). Differences in tooth morphology within this sample can be considered as ontogenetic.

Discussion

Tooth width and shark size

Generally speaking, all observed morphological and biometric tooth characters are more or less correlated with the overall growth of the shark. For the four living hexanchid species, the width of the lower teeth increases proportionally to body size at two different rates (estimated from the regression coefficients) that depend more on dental formula than species affiliation. Moss (1967: 324) obtained a similar regression curve for lemon shark teeth: size of shark (in cm) = 128 to 135 × width of tooth (in cm) according to file, 14–17 files of tooth per half lower jaw. Similar regression coefficients have been computed from Hubbell's data (1996) on white sharks: size of shark (in cm) = 127 × width of tooth (in cm) + 41 on the first upper tooth with 12–13 files of tooth per half upper jaw. Although unverified, all of these coefficients seem to increase with the number of teeth per half jaw in different shark species and may indicate that the width of the teeth is more constrained by the amount of free space in the jaw than phylogenetic affiliation or dental strategy. Application to fossils seems to be very limited because of the lack of information concerning the dental formulae of fossil sharks which are generally known from isolated teeth. Using the ratio length of acrocone/height of root on lower teeth, Kaneko et al. (1997) inferred the dental formula in isolated *Hexanchus* teeth from the Miocene of Japan. Application of the same ratio in Recent teeth does not support their results. Though the width of the tooth appears to depend on dental formula, the ratio between the number of cusps and tooth width correlates more with generic affiliation and appears to be more appropriate in extrapolating the general size of shark (see Fig. 4).

Hexanus vitulus/*H. nakamurai*/*H. griseu*s debate

Lower symphysial teeth.—The presence of a median erect cusp on the crown of the lower symphysial tooth has been used to separate *H. nakamurai* from *H. griseus* (Welton 1978). Despite the incorrect representation in Compagno (1984), living *H. griseus* always seems to possess a lower symphysial tooth lacking a median erect cusp (see Fig. $2B_3$), as seen in the seven gill shark *Notorynchus cepedianus*. Erect cusps (Fig. $2M_3$) appear to characterise *Heptranchias perlo* and *H. nakamurai* (or *H. vitulus* and *H. nakamurai* sensu Herman et al. 1994), although their absence has been often seen in the last of these species (personal observations). If we consider only the genus *Hexanchus*, the presence of a lower median tooth with an erect cusp may indicate a vituliform group. However, its absence is not diagnostic.

Development and serration of the acrocone.—Although this dental character has never been quantified, since Ward's work (1979) many fossil *Hexanchus* teeth have been placed in grisiform or vituliform groups according to

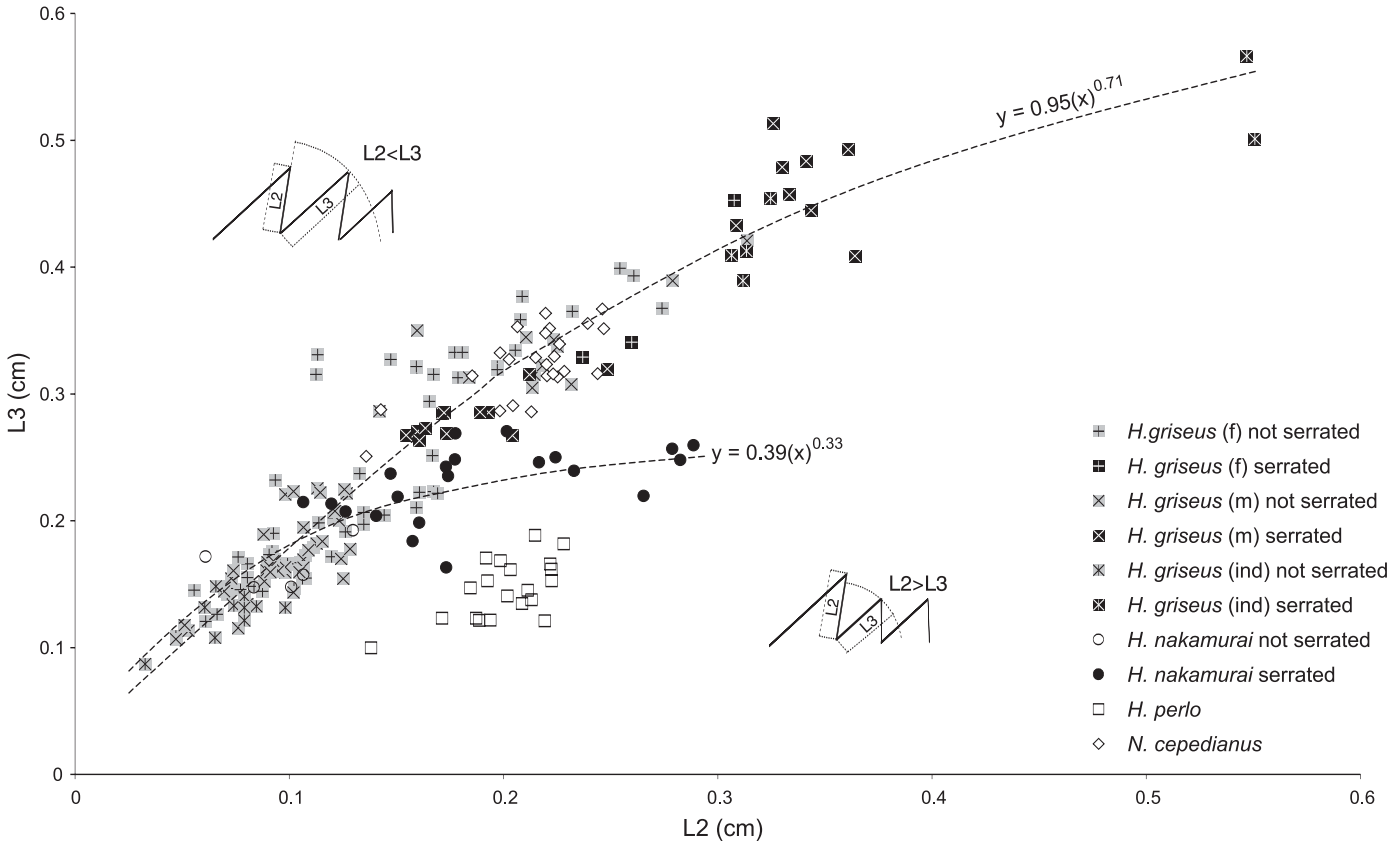


Fig. 5. Acrocone shape of lower teeth in Recent hexanchid species. Small pictures illustrate the changes in acrocone size according to the L2/L3 values. Interrupted lines are regression curves from data for the two living *Hexanchus* species. For *H. griseus*, different symbols have been used to indicate the sex of the sharks (m, male; f, female; ind, indeterminate).

the size of the acrocone. In fact, the greater development of the acrocone in comparison to the second distal cusp of the lower antero-lateral teeth has been used to separate the two living nominal species *H. griseus* and *H. vitulus* (see Fig. 2). Unfortunately, figures of the teeth from dried jaws (USNM 110900) in the original description of *H. vitulus* (Springer and Waller 1968: fig. 2) and from a paratype (USNM 200765) (Herman et al. 1994: text-fig. 2) do not show this last character. Based on this contradiction, Herman et al. (1994) suggested in an *addendum* to their previous paper (Herman et al. 1987) that two species could be recognised within the common small *Hexanchus* material: *H. nakamurai* with a low acrocone, and *H. vitulus* with a high acrocone. As discussed below, this point of view must be considered. The new results presented here suggest that a well developed acrocone is the first sign of maturity in species of *Hexanchus*. As with the presence of a serrated mesial edge on the acrocone and cusp number, the development of an acrocone may indicate only that the shark has reached a large size or a state of maturity (see Fig. $2A_3$, B_1, B_2, B_4 for *H. griseus*, and Fig. $2M_1$, M_2 for *H. nakamurai*). For these reasons, the use of such characters by Herman et al (1994) to distinguish between *H. vitulus* and *H. nakamurai* must be questioned. In fact, in the work of these authors, *H. vitulus* is represented only by mature males (>1.48 m) and *H. nakamurai* by young sub-adults (<1.17 m) and one adult female (1.57 m). Such sexual and ontogenetic differences between samples explain the reasons why Taniushi and Tachikawa (1991) considered *H. vitulus* to be a synonym of *H. nakamurai*.

Concerning serration of the acrocone and contrary to the odontological criteria to identify *Hexanchus* species by Herman et al. (1994: 151, 155: "mesial serration absent on lower lateral teeth of acrocone in *H. griseus*"), acrocones with serrated mesial cutting edges have been often observed (e.g., Fig. 2A, B) on lower teeth of *H. griseus* (Welton 1979). This serration has been illustrated in the previous analysis (Fig. 5). It appears, for example, that larger individuals of *H. griseus* show a mesial serration on the lower teeth (sometimes on the upper teeth too) which increases with growth (Welton 1979). The presence of serrations appears to be dependant on shark growth because they begin to appear on the first file when the shark has reached 160 cm in total body length (e.g., Fig. $2D_2$). With an increase in size, serration of the acrocone extends to the lateral files. Sexual dimorphism has been sometimes thought to explain observed differences (Cappetta 1980; Kent 1994) but this has not been tested because of a lack of samples. Despite this, as males reach maturity before

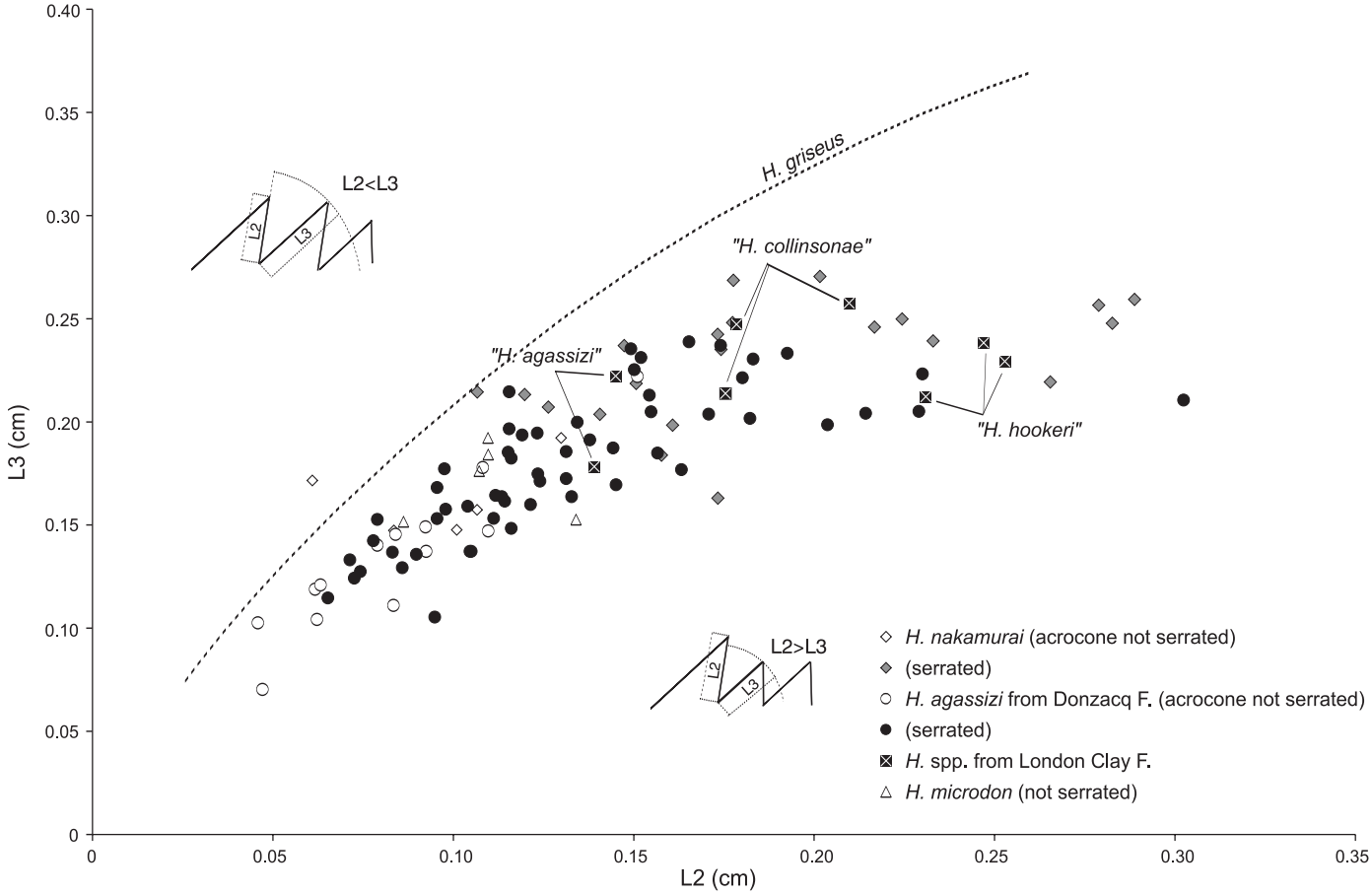


Fig. 6. Acrocone shape of lower teeth in Late Eocene (Early Lutetian) *Hexanchus agassizi* from south-western France. Bivariate plot constructed as in Fig. 4. Data for Recent *Hexanchus* species are indicated by symbols for *H. nakamurai* teeth but only by regression lines for *H. griseus* teeth. Holotypes, paratypes and figured teeth of the fossil species from the work of Ward (1979) are distinguished on the graph. Some *H. microdon* specimens (Paleocene - early Eocene) have been added for comparison.

females in terms of total length (3.25 m and 4.21 m, respectively, see Ebert 1986), the development of a serrated acrocone may begin earlier in terms of absolute tooth width for males.

The use of these last characters for identification allows an overview of the maturity states of all of the populations studied. Without body size (or maturity state) information, lower teeth of the two valid species, *H. griseus* and *H. nakamurai*, are hardly distinguishable, especially from the lower teeth of juvenile or sub-adult specimen of both species.

The main problem with small samples of isolated Recent or fossil teeth is that observed differences in terms of size and shape can be interpreted either as the presence of several species or as ontogenetic variations in a single species. Kemp (1978: 66) suggested that "allometric growth patterns would enable the differentiation of a tooth of a juvenile *H. griseus* from a tooth of an adult *H. vitulus*, for example there would be more crownlets on the *H. vitulus* tooth than on the similar-sized *H. griseus* specimen." In reality, *H. nakamurai* and *H. griseus* seem to possess the same pattern of dental development, but with a delay in time produced by the different maturity ages in terms of size (different parameters of the L2/L3 regression equation). Such heterochronic development may lead to a persistence of a "juvenile shaped" tooth (unserrated acrocone, lower value of L2/L3) in *H. griseus* compared to *H. nakamurai*.

Implications for fossil determination and Palaeogene history

In 1976, Cappetta described a new fossil species of *Hexanchus*, *H. agassizi*, from material previously attributed to *Notidanus* (Woodward 1889) from the London Clay Formation. Ward (1979) reviewed the systematic affiliation of *Hexanchus* teeth from the London Clay based on new material and named two new species, *H. collinsonae* and *H. hookeri.* The three contemporaneous species, which occur at the same two localities in southern England (Burnham on Crouch and Sheppey), possess lower teeth with a similar width, a similar number of cusps (7 or 8) and an acrocone more or less serrated. However, *H. agassizi* and *H. collin-*

sonae have been placed in grisiform groups and have been distinguished from *H. hookeri* (vituliform group) by the less developed acrocone. In the grisiform group, *H. agassizi* has been separated from *H. collinsonae* by its lower teeth showing relatively wider and shallower roots and weaker mesial serrations on the acrocone.

Values of L2 and L3 for the holotypes and paratypes of *H. agassizi*, *H. hookeri*, and *H. collinsonae* teeth have been plotted long with values of fossil *Hexanchus* teeth from south-western France (Fig. 4 and Appendix 1). On the basis of acrocone shape, the three London Clay species cannot be differentiated from the range of dental morphologies seen in the new French material of *Hexanchus*. Indeed, the dental differences described between *H. agassizi*, *H. hookeri*, and *H. collinsonae* could be reinterpreted as three different maturity states within a single species belonging to the vituliform group of Ward (1979). There is no evidence from acrocone morphology that more than one species is present in the Ypresian of England or the late Ypresian/early Lutetian of France. The new material from south-western France is therefore referred to *H. agassizi* Cappetta 1976 (non pl. 1: 6). This fossil species belongs to the vituliform group and is only distinguishable from the living species *H. nakamurai* by its slightly smaller size (absolute tooth width and number of cusps per cm of tooth width) and more serrated acrocone. Considering tooth width, *H. agassizi* may be more advanced in terms of maturity than *H. nakamurai*. The inference that *H. hookeri* and *H. collinsoni* are ontogenetic variations of *H. agassizi* must be tested by additional analyses, at least for *H. collinsoni* which seems to possess lower teeth with noticeably deeper roots than the other species (David J. Ward personal communication, 2004). However, the results here lead to rejection of an Early Eocene divergence between the grisiform and vituliform lineages.

While the assignment of *Hexanchus* teeth from the Cretaceous–Palaeocene to the single species *H. microdon* has appeared suspect (Ward 1979; Cappetta 1987; Siverson 1995), most Eocene *Hexanchus* teeth have been placed in three species (and sometimes in other questionable new species) without careful consideration. From a brief examination of Palaeocene–Eocene *Hexanchus* teeth worldwide (Appendix 1), most of the Early and Middle Eocene fossils may belong to *H. agassizi* and not to several contemporaneous species with identical geographical distributions, and very similar sizes and probably diets.

According to calculations of body size (Appendix 1), species of *Hexanchus* species did not exceed 1 metre in total length during the Palaeocene and 1.9 metres during the Early to Middle Eocene, the maximum size also observed for the living *H. nakamurai*. The first large form comes from the Late Eocene of Antarctica (Cione and Reguero 1994) with a size exceeding 2 metres (see Appendix 1). This size contrast, never observed in living *H. nakamurai*, is perhaps the first step in a trend towards larger forms of *Hexanchus* belonging to the grisiform group which are better known in later faunas. Size increase is perhaps a response to a global change in the environment and in food resources (e.g. marine mammals), as observed in the living *H. griseus* when individuals reach a threshold size of 2 metres in length (Ebert 1994).

Conclusions

Results show that the two Recent species of *Hexanchus* have a similar dental development but with a different rate of growth. This fact implies that for the same tooth width, *H. griseus* retains a "young" morphology compared to *H. nakamurai* (e.g., a weak serration on the mesial edge of the acrocone, lower acrocone and a crown with fewer cusps). The dental separation of these two species is currently limited to the presence, in some individuals, of a vertical median cusp on the symphysial tooth in *H. nakamurai* and a different dental formula.

In *Hexanchus* species, the stable ontogenetic relationship between total body length and tooth cusp number ratio (number of cusps/width of tooth) allows one to reconstruct with confidence the size of fossil sharks using an allometric equation.

Biometric analyses of new and abundant material of fossil *Hexanchus* shows that *H. hookeri* and *H. collinsonae* may be ontogenetic states of the previously described fossil species *H. agassizi*. The size of the teeth and the regression curve for acrocone size (L2/L3) allows these species to be placed in the vituliform group. No clear evidence of the grisiform lineage has been found prior to the Middle Eocene. A brief examination of Palaeogene species of *Hexanchus* reveals that some fossil teeth from the end of this time begin to show a greater width (more than 20 mm) with few cusps in the lower teeth (small cusp number ratio), which suggests a body size exceeding 2 metres. This trend could herald the rise of a new group of large *Hexanchus*, perhaps the first representatives of the extant grisiform lineage better known in Neogene and Recent oceans. Only a wider study on all fossil hexanchids (particularly on the large specimens from the Oligocene–Miocene) will permit a better understanding of the history of hexanchids and may explain the significant differences in the distribution and abundance between the two Recent species (*H. griseus* and *H. nakamurai*) and their Palaeogene relatives.

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References

Adnet, S. 2000. *Les Elasmobranches fossiles du Paléogène des Landes (Sud-Ouest, France). Implications dans la connaissance des communautés d'élasmobranches d'eaux profondes. Evolution des Squaliformes et paléoécologie*. 211 pp. Unpublished Ph.D. thesis, Université des Sciences et Techniques du Languedoc, Montpellier.

Adnet, S., Cappetta, H., and Reynders, J. 2006. Nouveaux genres de Squaliformes (Chondrichthyes) du Paléogène des Landes (Sud-Ouest de la France). *Paläontologische Zeitschrift* 80: 60–67.

Applegate, S.P. 1965. A confirmation of the validity of *Notorhynchus pectinatus*; the second record of the Upper Cretaceous cowshark. *Bulletin of the Southern California Academy of Science* 64: 122–126.

Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc–Algérie–Tunisie). *Notes et Mémoires du Service géologique du Maroc* 92: 1–372.

Bigelow, H.B. and Schroeder, W.C. 1948. Sharks. *In*: J. Tee-Van, C.M. Breder, S.F. Hildebrand, A.E. Parr, and W.C. Schroeder (eds.), *Fishes of the western North Atlantic, Sears Foundation for Marine Research Memoir* 1: 59–543.

Beaumont, G. de 1960. Contribution à l'étude des genres *Orthacodus* Woodward et *Notidanus* Cuvier (Selachii). *Mémoire Suisse de Paléontologie* 77: 4–36.

Bonnaterre, J.P. 1788. *Tableau encyclopédique et méthodique des trois règnes de la nature. Ichthyologie*. 215 pp. Chez Panckoucke, Paris.

Boulanger, D. 1968. *Révision du Nummulitique de la Chalosse, du Béarn et du Bas-Adour (Landes et Basses-Pyrénées)*. 338 pp. Unpublished Ph.D. thesis, Faculté des Sciences de Paris, Paris.

Cadenat, J. and Blache, J. 1981. Requins de Méditerranée et d'Atlantique (plus particulièrement de la côte occidentale d'Afrique). *Collection Faune Tropicale* 21: 1–330. ORSTOM, Paris.

Cappetta, H. 1976. Sélaciens nouveaux du London Clay de l'Essex (Yprésien du Bassin de Londres). *Geobios* 9: 551–575.

Cappetta, H. 1980. Les Sélaciens du Crétacé supérieur du Liban. I. Requins. *Palaeontographica A* 168: 69–148.

Cappetta, H. 1986. Types dentaires adaptatifs chez les sélaciens actuels et post-paléozoïques. *Palaeovertebrata* 16: 57–76.

Cappetta, H. 1987. Mesozoic and Cenozoic Elasmobranchii, Chondrichthyes. *In*: H.-P. Schultze (ed.), *Handbook of Paleoichthyology, 2, 3B*, 1–193. Gustav Fischer Verlag, Stuttgart.

Cappetta, H. 1990. Hexanchiforme nouveau (Neoselachii) du Crétacé inférieur du Sud de la France. *Palaeovertebrata* 20: 33–54.

Carvahlo, M.R. 1996. Higher-level Elasmobranch Phylogeny, Basal Squaleans, and Paraphyly. *In*: M.L.J. Stassny, L.R. Parenti, and G.D. Jonhson (eds.), *Interrelationships of Fishes 3*, 35–62. Academic Press, New York.

Case, G.R. 1996. A new selachian fauna from the Lower Hornestown Formation (Early Paleocene/Montian) of Monmouth County, New Jersey. *Palaeontographica A* 242: 1–14.

Castro, J.I. 1983. *The Sharks of North American Waters*. 180 pp. Texas A and M University Press, College Station.

Celona, A., De Maddalena, A., and Romeao, T. 2005. Bluntnose sixgill shark, *Hexanchus griseus* (Bonnaterre, 1788) in the eastern north Sicilian waters. *Bollettino del Museo Civico di Storia Naturale di Venezia* 56: 137–151.

Cione, A.L. and Reguero, M. 1994. New records of the sharks *Isurus* and *Hexanchus* from the Eocene of Seymour Island, Antarctica. *Proceedings of the Geologists' Association* 105: 1–14.

Clark, E. and Kristof, E. 1990. Deep-sea elasmobranchs observed from submersibles off Bermuda; Grand Cayman, and Freeport, Bahamas. *In*: H.L. Pratt, S. Gruber Jr., and T. Taniuchi (eds.), *Elasmobranchs as Living Resources: Advances in Biology, Ecology, Systematics and the Status of the Fisheries*, 269–284. NOAA Technical Report NMFS 90.

Compagno, L.J.V. 1970. Systematics of the genus *Hemitriakis* (Selachii: Carcharhinidae), and related genera. *Proceedings of the California Academic Sciences* 38: 63–97.

Compagno, L.J.V. 1973. Interrelationships of living elasmobranchs. *In*: P.H. Greenwood, R.S. Miles, and C. Patterson (eds.), Interrelationships of Fishes. *Zoological Journal of the Linnean Society* 53 (Supplement 1): 15–61.

Compagno, L.J.V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* 17: 303–322.

Compagno, L.J.V. 1984. *FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes*. 249 pp. FAO Fisheries Synopsis, Rome.

Compagno, L.J.V. 1999. Checklist of living elasmobranchs. *In*: W.C. Hamlett (ed.), *Sharks, Skates, and Rays: the Biology of Elasmobranch Fishes*, 471–498. John Hopkins University Press, Maryland.

Ebert, D.A. 1986. Biological aspects of the sixgill shark, *Hexanchus griseus*. *Copeia* 1: 131–135.

Ebert, D.A. 1994. Diet of the sixgill shark *Hexanchus griseus* off southern Africa. *South African Journal of Marine Science* 14: 213–218.

Glickman, L.S. [Glikman, L.S.] 1964. *Akuly paleogena i ih stratigrafičeskoe značenie*. 229 pp. Nauka, Moskva.

Herman, J., Hovestadt-Euler, M., and Hovestadt, D.C. 1987. Part A: Selachii. N° 1. Order: Hexanchiformes. Family: Hexanchidae. Commissural teeth. *In*: M. Stehmann (ed.), Contributions to the Study of the Comparative Morphology of Teeth and Other Relevant Ichthyodorulites in Living Supraspecific Taxa of Chondrichthyan Fishes. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique* 57: 43–56.

Herman, J., Hovestadt-Euler, M., and Hovestadt, D.C. 1994. Addendum to Part A, N° 1. Order: Hexanchiformes-Family: Hexanchidae. Odontological results supporting the validity of *Hexanchus vitulus* Springer and Waller, 1969 as the third species of the genus *Hexanchus* Rafinesque, 1810, and suggesting intrafamilial reordering of the Hexanchidae. *In*: M. Stehmann (ed.), Contributions to the Study of the Comparative Morphology of Teeth and Other Relevant Ichthyodorulites in Living Supraspecific Taxa of Chondrichthyan Fishes. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique* 64: 147–163.

Hubbell, G. 1996. Using Tooth Structure to determine the Evolutionary History of the White Shark. *In*: A.P. Klimley and D.G Ainley (eds.), *Great White Sharks. The Biology of Carcharodon Carcharias*, 9–18. Academic Press, San Diego.

Kaneko, M., Fujii, K., Takayama, Y., and Sakamoto, O. 1997. Analysis of Dental Formula based on 315 Fossil Teeth of *Hexanchus* sp. from the Miocene in the Chichibu basin, Central Japan. *Bulletin of the Saitama Museum of Natural History* 15: 17–32.

Kemp, N.R. 1978. Detailed comparisons of the dentitions of extant Hexanchid sharks and tertiary Hexanchid teeth from South Australia and Victoria, Australia (Selachii: Hexanchidae). *National Museum, Victoria. Memoirs* 39: 61–83.

Kemp, N.R. 1991. Chondrichthyans in the Cretaceous and Tertiary of Australia. *In*: P. Vickers-Rich, J.M. Monaghan, R.F. Baird, and T.H. Rich (eds.), *Vertebrate Palaeontology of Australasia*, 497–568. Pioneer Design Studio, Melbourne.

Kent, B.W. 1994. *Fossil Sharks of the Chesapeake Bay Region*. 146 pp. Egan Rees and Boyer, Inc., Columbia, Maryland.

Kent, B.W. 1999. Part 2. Sharks from the Fisher/Sullivan Site. *In*: R.E. Weems (ed.), Fossil Vertebrates and Plants from the Fisher/Sullivan Site (Stafford County): A Record of Early Eocene Life in Virginia. *Virginia Division of Mineral Resources* 152: 11–37.

Long, D.J., Murphy, M.A., and Rodda, P.U. 1993. A new world occurrence of *Notidanodon lanceolatus* (Chondrichthyes, Hexanchidae) and comments on hexanchid evolution. *Journal of Paleontology* 67: 655–659.

Moss, S.A. 1967. Tooth replacement in the Lemon Shark, *Negaprion brevirostis*. *In*: P.W. Gilbert, R.F Mathewson, and D.P. Rall (eds.), *Sharks, Skates and Rays*, 319–330. Johns Hopkins University Press, Baltimore.

Nolf, D. 1988. Les otolithes de téléostéens éocènes d'Aquitaine (sud-ouest de la France) et leur intérêt stratigraphique. *Mémoire de l'Institut Royal des Sciences Naturelles de Belgique* 19: 1–147.

Nolf, D., Steurbaut, E., and Cahuzac, B. 2002. Progrès récents dans la connaissance des gisements cénozoïques en Aquitaine méridionale (Chalosse, Béarn et Bas-Adour; SW France. *Revue de Micropaléontologie* 45: 169–194.

Platel, J.P. 1990. *Carte Géologique de la France B 1/50000, TARTAS*. 51 pp. BRGM 950, Paris.
Pledge, N.S. 1967. Fossil elasmobranch teeth of South Australia and their stratigraphic distribution. *Transactions of the Royal Society of South Australia* 91: 135–160.
Reinecke, T. and Engelhard, P. 1997. The selachian fauna from Geschiebe of the Lower Selandian basal conglomerate (Thanetian, Late Paleocene) in the Danish subbasin (Sealand, Scania, Western Baltic Sea). *Erratica* 2: 3–45.
Shirai, S. 1992. *Squalean Phylogeny: a New Framework of "Squaloid" Sharks and Related Taxa*. 151 pp. Hokkaido University Press, Sapporo.
Siverson, M. 1995. Revision of the Danian cow sharks, sand tiger sharks, and goblin sharks (Hexanchidae, Odontaspididae, and Mitsukurinidae) from southern Sweden. *Journal of Vertebrate Paleontology* 15: 1–12.
Springer, S. and Waller, R.A. 1969. *Hexanchus vitulus*, a new sixgill shark from the Bahamas. *Bulletin of Marine Science* 19: 159–174.
Sztrakos, K. 1996. Le Thanétien supérieur et l'Yprésien du Bassin de l'Adour (Aquitaine, France). Stratigraphie et paleoenvironnement. Etude des foraminifères. *Cahier de Micropaléontologie* 10: 25–63.
Sztrakos, K., Gély, J.-P., Blondeau, A., and Müller, C. 1998. L'Eocène du Bassin sud-aquitain: lithostratigraphie, biostratigraphie et analyse séquentielle. *Géologie de France* 4: 57–105.
Taniuchi, T. and Tachikawa, H. 1991. *Hexanchus nakamurai*, a senior synonym of *H. vitulus* (Elasmobranchii), with notes on its occurrence in Japan. *Japanese Journal of Ichthyology* 33: 57–60.
Teng, H.T. 1962. *Classification and Distribution of the Chondrichthyes of Taiwan*. 9 pp. Ogawa Press, Maizuru.
Ward, D.J. 1979. Additions to the fish fauna of the English Palaeogene. 3. A review of the Hexanchid sharks with a description of four new species. *Tertiary Research* 2: 111–129.
Ward, D.J. and Thies, D. 1987. Hexanchid shark teeth (Neoselachii, Vertebrata) from the Lower Cretaceous of Germany and England. *Mesozoic Research* 1: 89–106.
Welton, B.J. 1979. Late Cretaceous and Cenozoic Squalomorphii of the Northwest Pacific Ocean. *Unpublished PhD Thesis*. 553 pp. University of Califonia, Berkeley.
Whitehead, P.J.P., Bauchot, M.-L, Hureau, J.-C, Nielsen, J., and Tortonese, E. 1984. *Fishes of the North-eastern Atlantic and the Mediterranean. Vol. 1*. 510 pp. UNESCO, Paris.
Woodward, A.S. 1889. *Catalogue of the Fossil Fishes in the British Museum (Natural History) Part. I.* 474 pp. British Museum (Natural History), London.
Zhelesko, V.I. and Kozlov, V.A. 1999. Elasmobranchii and Paleogene biostratigraphy of Transural and Central Asia. *Russian Academy Sciences, Urals Branch* 3: 1–323.

Appendix 1

Abbreviations: max, maximum value; min, minimum value; med, median; M, mean; SD, standard deviation; N, sample size; er.med. C, erect median cusp; *presence of erect medial cusp in one of three fishes; **according to Cione and Reguero on a broken tooth (2.4 cm width); ***previously figured by Pledge (1964) and Kemp (1978); ****questionable new attribution.

Species	References	Age	Size of fish (in cm)	Sex of fish	Number of cusps	Mesial edge of acrocone	Width of tooth (in cm)	Number of cusp per width of tooth	L2/L3 ratio	Lower symphyseal tooth morphology
Hexanchus griseus	Collections H. Cappetta (Univ. Montpellier)	Recent	M = 137 max = 300 N = 14	both sex	med = 6 (4–11) N = 150	Principally no serrated	M = 1.26 SD = 0.68 max = 3.45 N = 149	M = 6.04 SD = 1.95 min = 2.89 N = 149	M = 0.61 SD = 1.15 N = 151	without er. med. C
	Welton (1979: 172, table 12)	Recent	M = 163.3 max = 434 N = 8	both sex	med = 7 (5–11) N = 92	Principally no serrated	M = 1.48 SD = 1 max = 4.64 N = 94	M = 5.87 SD = 1.62 min = 2.43 N = 92		without er.med.C
	Kaneko et al. (1997: pl. 1)	Recent	300? N = 1	undet.	med = 8 (7–8) N = 6	undet.	M = 2.1 SD = 0.27 max = 2.2 N = 6	M = 3.76 SD = 0.27 min = 3.49 N = 6		without er. med. C
Hexanchus nakamurai	Collections H. Cappetta (Univ. Montpellier)	Recent	M = 131 max = 148 N = 3	uncertain	med = 9 (8–11) N = 26	principally serrated	M = 1.58 SD = 0.32 max = 2.29 N = 26	M = 5.87 SD = 1 min = 4.35 N = 26	M = 0.78 SD = 0.21 N = 26	both types*
	Kemp (1978: pl. 12: 5)	Recent	155 N = 1	male	med = 9 (8–10) N = 5	exclusively serrated	M = 1.91 SD = 0.08 max = 1.95 N = 5	M = 4.7 SD = 0.23 min = 4.57 N = 5		with er. Med. C
	Kaneko et al. (1997: pl. 2)	Recent	95 N = 1	female	med = 8 (8–9) N = 5	undet.	M = 1.18 SD = 0.05 max = 1.22 N = 5	M = 6.97 SD = 0.62 min = 6.53 N = 5		without er. med. C
Hexanchus perlo	Collections H. Cappetta (Univ. Montpellier)	Recent	M = 60.5 max = 68 N = 3	both sex	med = 6 (4–8) N = 27	exclusively serrated	M = 0.76 SD = 0.14 max = 1 N = 27	M = 8.09 SD = 1.42 min = 4.26 N = 27	M = 1.34 SD = 0.18 N = 27	with er. Med. C
Notorynchus cepedianus	Collections H. Cappetta (Univ. Montpellier)	Recent	148 and 150 N = 2	both sex	med = 5 (5–6) N = 24	exclusively serrated	M = 1.28 SD = 0.11 max = 1.48 N = 24	M = 4.09 SD = 0.43 min = 3.36 N = 24	M = 0.66 SD = 0.66 N = 24	without er. med. C

Species	References	Age	Size of fish (in cm)	Sex of fish	Number of cusps	Mesial edge of acrocone	Width of tooth (in cm)	Number of cusp per width of tooth	L2/L3 ratio	Lower symphyseal tooth morphology
Hexanchus sp.	Siverson (1995: 3, fig. 2F)	Early Palaeocene	62 estimated		8 N = 1	serrated	0.96	8.3		
Hexanchus microdon	Case (1996: pl. 11: 3, 4)	Early Palaeocene	80 estimated		8 and 8 N = 2	weakly serrated	0.95 and 1.125	8.4 and 7.11		with er.med.C
Hexanchus sp.	Reinecke and Engelard (1997: pl. 1: 1–4)	Late Palaeocene	65 estimated		6 N = 1	no serrated	0.74	8.12		
Hexanchus microdon	Arambourg (1952: pl. 1: 30–48)	Late Palaeocene	97 estimated		med = 8 (7–10) N = 8	no or weakly serrated	M = 1.18 SD = 0.17 max = 1.5 N = 8	M = 7.15 SD = 0.84 min = 6 N = 8		without er.med.C
Hexanchus "*microdon*"	Collections H. Cappetta (Univ. Montpellier)	Late Palaeocene	82 estimated		med = 8 (8) N = 2	serrated	1.07 and 1.14	7.45 and 6.99	M = 0.64 SD = 0.13 N = 5	
Hexanchus sp.	Case (1996: pl. 11: 5)	Late Palaeocene	68 estimated		8 N = 1	serrated	1.02	7.84		
Hexanchus agassizi	Glickman (1964: pl. 6: 5)	Eocene	155 estimated		8 N = 1	undet.	1.7	4.7		
"*Hexanchus. casieri*"****	Zhelezko and Kozlov (1999: pl. 67: 2)	Eocene	68 estimated		10 N = 1	no serrated	1.4	7.85		
"*Hexanchus tusbairicus*"****	Zhelezko and Kozlov (1999: pl. 67: 1, 3, 4)	Eocene	101 estimated		8 N = 1	weakly serrated	1.3	6.15		
Hexanchus microdon	Arambourg (1952: pl. 2: 54–56)	Early Eocene	155 estimated		med = 8 (8–9) N = 3	no or weakly serrated	M = 1.38 max = 1.7 N = 3	M = 6.21 min = 4.7 N = 3		
Hexanchus "*microdon*"	Collections H. Cappetta (Univ. Montpellier)	Early Eocene	179 estimated		9 N = 1	serrated	2.1	4.3	0.98	
Hexanchus sp.	Kent (1999: pl. 2.1: B)	Early Eocene	170 estimated		8 N = 1	serrated	1.8	4.44		with er. Med. C
Hexanchus sp.	from Nanjemoy Form. (personal observation)	Early Eocene	190 estimated		8 N = 2	serrated	1.81 and 1.193	4.42 and 4.14	0.97 and 1.28	
Hexanchus agassizi, *Hexanchus collinsonae*, *Hexanchus hookeri*	Ward (1979: pl. 1: 1–8; pl. 2: 1, 2)	Early Eocene	146 estimated		med = 7 (7–8) N = 8	exclusively serrated	M = 1.32 SD = 0.17 max = 1.43 N = 8	M = 5.74 SD = 0.85 min = 4.32 N = 8	M = 0.87 SD = 0.17 N = 8	
Hexanchus agassizi	from Donzacq Form. (present study)	Middle Eocene	112 estimated		med = 8 (7–8) N = 30	principally serrated	M = 1.04 SD = 0.3 max = 1.55 N = 27	M = 8.43 SD = 2.68 min = 5.19 N = 27	M = 0.71; SD = 0.16; N = 75	principally with er. Med. C.
Hexanchus agassizi	Kemp (1991: pl. 7: J, L***)	Middle–Late Eocene	141 estimated		9 and 11 N = 2	weakly serrated	1.73 and 2.2	5.2 and 5	1.28 and 0.97	
Hexanchus sp. 1	Kemp (1991: pl. 7: N***)	Late Eocene	121 estimated		11 N = 1	serrated	2	5.5		
Hexanchus sp.	Cione and Reguero (1994: 5, fig. 4)	Late Eocene	228** estimated		10 N = 1	possibly serrated	2.7**	3.7**		