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Quantitative analysis of Elasmobranch assemblages from two successive Ypresian (early Eocene) facies at Marke, western Belgium

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ABSTRACT. Temporal patterns in biodiversity are affected largely by changes in environmental conditions. Sea level fluctuations rank amongst the major factors that affect marine biodiversity or community structure on a local or regional scale, as confirmed by numerous case studies relating lithology with fossil assemblages in order to reconstruct palaeoenvironmental conditions. However up to now, few studies quantified selachian and batoid faunas (Elasmobranchii) in such a context. In the present study, we compare elasmobranch teeth from two successive facies of Ypresian (Early Eocene) age, as exposed at the Marke clay pit in the southern part of the Belgian Basin. We present a significant link between the difference in lithology of these levels and elasmobranch community structure. In general, selachians are notably more common in clayey levels, while batoids predominate in sandy levels. Following the principle of uniformitarianism, such a link indicates that the recognised patterns in elasmobranch diversity depend mainly on the preferred sea level and/or habitat requirements by a species or a species group, in analogy to what is seen in modern communities. Additional notes on the palaeoenvironment are presented, as well as a list of 36 elasmobranch taxa from Marke, including a number of new recorded taxa for the Ypresian of Belgium.

KEYWORDS: Elasmobranchii, Belgium, biodiversity, ecological community, Ypresian, habitat requirements, sea level fluctuations

1. Introduction

Amongst the most popular ecological research issues currently ranks the study of changes in local and global biodiversity or community composition (Loreau et al., 2001; Hooper et al., 2005). Not all ecological communities comprise the same number of species and are influenced by combinations of numerous factors (Currie, 1991; Fraser & Currie, 1996). Of such factors, local evolutionary history, climate and disturbance events are the most important; they jointly act in shaping local biodiversity and ecosystem functioning (Krebs, 2001). Any changes in environmental conditions, ranging from competition and predation to climatic changes and resource availability, will consequently have an impact on the local community structure (Hooper et al., 2005). Therefore, communities are best viewed as open, non-equilibrium systems. This has also been confirmed by palaeoecological data which demonstrate conclusively that communities change dramatically over time, and that community stability is never reached, not even on a short-time scale (e.g. Whitehead, 1981; Jackson et al., 2000).

Sea level fluctuations are amongst the more important changes in marine ecosystems. Such fluctuations are caused mainly by climatic changes or tectonic activity (Blum & Tornqvist, 2000; Siddall et al., 2003; Church et al., 2004) and result in cycles of transgressions and regressions. During transgressions, the coastline moves landwards and the shelf area enlarges (Cattaneo & Steel, 2003). With this comes the tendency for more and larger grain-sized sediment to be trapped in the alluvial and coastal plain environments, while finer-grained material is deposited in the basin. Evidently, local sediment texture varies according to sea level and ultimately to palaeoenvironment or community structure (Peron et al., 2005). Previous studies have linked lithology with fossil assemblages, allowing exact positioning of successive units, high-resolution stratigraphy and reconstructions of palaeoenvironmental conditions (Dupuis et al., 1991; Steurbaut, 1998). Although remains of Elasmobranchii (selachians and batoids) are common in the fossil record, few studies quantified such fossils as indicator taxa in this context.

The Belgian Basin is well suited for palaeoenvironmental studies of Eocene strata because of its fairly complete sections with integrated sequence stratigraphy (Steurbaut, 1998; Vandenberghe et al., 2004). Moreover, these strata often yield abundant fossil material and the elasmobranch faunas of the Belgian Ypresian were first described in detail by Casier (1946). Casier (1950), Nolf (1972), Herman (1974, 1982a, 1982b, 1984, 1986), Herman & Crochard (1977, 1979), Herman et al. (1989), Van Simaeys (1994) and Smith et al. (1999) subsequently presented updates. In the present study, we compare the elasmobranch faunas of two successive facies of Ypresian age along the southern margin of the North Sea Basin (Steurbaut, 2006), with the lithological differences of these levels likely reflecting different palaeoenvironmental conditions (for a discussion, see Willems & Moorkens, 1991 and Steurbaut, 2006). We predict that there is a close link between lithology and diversity and composition of elasmobranch communities, comparable to what has been recorded for other taxa (e.g. Steurbaut & Nolf, 1991). Similar to present-day observations, this would imply that former environmental conditions, such as sea level and local deposition, at least in part determine local biodiversity. This would furthermore confirm the principle of uniformitarianism, also referred to as the principle of actualism, which states that never-changing mechanisms underlie biological and geological phenomena (Baker, 1998). In addition, the present paper provides a list of 36 elasmobranch taxa from Marke, including some species that were not recorded previously from the Belgian Ypresian. Several taxa are in urgent need of revision, in particular the Carcharhinidae and Myliobatidae (see also Adnet & Cappetta, 2008; Underwood et al., 2011).

2. Stratigraphy

During the Ypresian, the epicontinental sea which flooded present-day Belgium, underwent numerous major and minor sea level changes, as a result of the interplay between changes in the earth's astronomical parameters and local subsidence (Steurbaut, 2006; Vanhove et al., 2011). During transgressions and regressions siliciclastic particles in the basin were redistributed into a series of alternating clay and sand layers (Steurbaut, 1998; Vandenberghe et al., 1998). The elasmobranch remains in the present study were collected at a former clay pit near Marke (western Belgium; coordinates N 50° 48' 15" – E 3° 13' 06"), a site especially famous for its crustacean faunas (Iserbyt & Christiaens, 2004). It is situated in an area with numerous outcrops of Ypresian strata (Steurbaut 2006), about 30 km south of the well-known Egem quarry. Particularly at Marke, most of the section exposed is assignable to the Roubaix Clay Member, with the base of the Aalbeke Clay Member overlying it (Steurbaut & Jacobs, 1993; Steurbaut, 1998). Both units belong to the Kortrijk Clay Formation, of early Ypresian age. Throughout the section, elasmobranch teeth appear to be concentrated at specific levels, such as sequence boundaries or transgressive surfaces (Steurbaut, 2006). We collected teeth from two of such concentrations, both within the Roubaix Clay Member, but with less than 100 kyr between them (E. Steurbaut, personal communication). It has been postulated that both levels were deposited in well-oxygenated infralittoral settings, at depths of 50 to 100 m (Steurbaut, 2006). The first level, described as 'layer 7' by Steurbaut & Jacobs (1993) and Steurbaut (1998), is a silty clay of 2.6 m in thickness, with scattered molluscs, and a 5 cm-thick level (layer Y) in the middle of it, containing numerous black oysters, *Turritella* and bony fish otoliths. The other level sampled (‘layer 4’) is a 1.3 m thick, heavily bioturbated sandy silt with some phosphatic nodules and shell impressions (oysters at the base, *Turritella* near the top). A markedly bioturbated layer of silty sand (thickness 20 cm) occurs near the middle of this level. Below, we shall be referring to levels 7 and 4 as the ‘clay’ and ‘sand’ level, respectively. Both investigated levels clearly differ in sea depth (Vandenberghe et al., 2004; Vanhove et al., 2011), with the ‘clay’ level being indicative of a deeper sea than the ‘sand’ level. It should be noted that both levels differ from layer 6, which yields few teeth, but which is especially well known for its abundant phosphatic nodules with crustacean remains (see Iserbyt & Christiaens, 2004).

3. Material and methods

Samples from both levels were taken between 2001 and 2007, sieved on a 1-millimetre mesh after which the residu was handpicked. In total, the ‘clay’ and ‘sand’ levels yielded 1594 and 551 teeth, respectively (Table 1). Given the fact that some teeth could not be identified to the species level, due to poor preservation, uncertainties about their dental position or unresolved taxonomic matters, we restricted our quantitative analyses to the family level (see Table 1). Systematics follow Cappetta (2006).

We calculated the frequency of occurrence (%) for each family and stratigraphic level, by dividing the number of teeth

Order	Family	Species	n_c - n_s	χ^2, *d.f.* = 1	*p*
►Squaliformes					
	• Squalidae		3 - 0	1.78	0.18
		- ***Squalus smithi* Herman, 1982**			
	• Dalatiidae		58 - 0	34.99	**<0.001**
		- ***Isistius trituratus* (Winkler, 1874)**			
►Squatiniformes					
	• Squatinidae		8 - 3	0.01	0.9
		- *Squatina prima* (Winkler, 1874)			
►Heterodontiformes					
	• Heterodontidae		6 - 1	0.54	0.46
		- ***Heterodontus* sp.**			
►Orectolobiformes					
	• Ginglymostomatidae		1 - 0	0.59	0.44
		- *Nebrius thielensi* (Winkler, 1873)			
	• Parascyllidae		0 - 1	2.72	0.099
		- ***Pararhincodon ypresiensis* Cappetta, 1976**			
►Lamniformes					
	• Odontaspididae		305 - 66	15.62	**<0.001**
		- **cf. *Palaeohypotodus rutoti* (Winkler, 1874)**			
		- *Brachycarcharias lerichei* (Casier, 1946)			
		- ***Hypotodus verticalis* (Agassiz, 1843)**			
		- *Odontaspis winkleri* Leriche, 1905			
		- *Striatolamia macrota* (Agassiz, 1843)			
		- *Sylvestrilamia teretidens* (White, 1931)			
	• Jaekelotodontidae		3 - 1	0.00	0.97
		- ***Jaekelotodus robustus* (Leriche, 1921)**			
	• Otodontidae		1 - 0	0.59	0.44
		- *Otodus obliquus* Agassiz, 1843			
	• Lamnidae		5 - 2	0.03	0.86
		- *Isurolamna affinis* (Casier, 1946)			
	• *Incertae sedis*		1 - 1	0.54	0.46
		- ***Parotodus pavlovi* (Menner, 1928)***			
►Carcharhiniformes					
	• Carcharhinidae		653 - 183	10.49	**0.001**
		- *Abdounia beaugei* (Arambourg, 1935)			
		- *Abdounia minutissima* (Winkler, 1873)			
		- *Abdounia recticona* (Winkler, 1873)			
		- *Physogaleus secundus* (Winkler, 1874)			
		- ***Rhizoprionodon* aff. *ganntourensis* (Arambourg, 1952)***			
	• Scyliorhinidae		35 - 11	0.08	0.78
		- *Premontreia (Premontreia) degremonti* Cappetta, 1992			
		- *Premontreia (Oxyscyllium) gilberti* (Casier, 1946)			
		- *Microscyliorhinus burnhamensis* (Cappetta, 1976)			
	• Triakidae		191 - 54	1.98	0.16
		- *Galeorhinus ypresiensis* (Casier, 1946)			
		- ***Galeorhinus duchaussoisi* Adnet & Cappetta, 2008***			
		- *Pachygaleus lefevrei* (Daimeries, 1891)			
	• Carcharhiniformes indet.		28 - 6	1.27	0.26
		- *Foumtizia pattersoni* (Cappetta, 1976)			
		- ***Foumtizia* sp. nov.***			
►Pristiformes					
	• Pristidae		1 - 0	0.59	0.44
		- *Pristis lathami* (Galeotti, 1837)			
►Rajiformes					
	• Rhinobatidae		8 - 8	4.35	**0.037**
		- *Rhinobatos bruxelliensis* (Jaekel, 1894)			
►Myliobatiformes					
	• Myliobatidae		266 - 170	47.58	**<0.001**
		- *Aetobatus irregularis* (Agassiz, 1843)			
		- *Myliobatis* spp.			
	• Mobulidae		5 - 7	5.73	**0.017**
		- ***Burnhamia daviesi* (Woodward, 1889)**			
	• Dasyatidae		16 - 37	46.54	**<0.001**
		- *Dasyatis jaekeli* (Leriche, 1905)			
		- *Dasyatis* spp.			

Table 1. Results of the Chi-square tests comparing both levels studied for frequency of collected teeth within each family. Number of teeth collected in the ‘clay’ and ‘sand’ level is presented (n_c - n_s) and significant differences are indicated by bold *p*-values. Total number of collected teeth in both layers is n = 1594 and n = 551, respectively. Names of taxa illustrated in Plates 1 and 2 are shown in bold.
* New records for the Belgian Ypresian.

collected per family by the total number of teeth collected per level. To test whether or not, overall elasmobranch community diversity and composition differed between both levels, we first conducted a generalised linear model with a Poisson error structure and a log link function. Stratigraphic level, family and their interaction, were added to the model as categorical explanatory variables. Next, we analysed in more detail whether the frequency of occurrence of each family differed between both levels or not, using Chi-square tests (see also Bennington & Bambach, 1996). All analyses were performed in SAS 9.2 (SAS Institute Inc, Carry, NC, USA) and were two-tailed with a significance level of $p < 0.05$.

4. Results

We distinguished at least 36 taxa, assigned to 20 families and 9 orders. Four of these are new for the Belgian Ypresian (see Table 1). For reasons mentioned above, we restricted our analyses to the family level. The Carcharhinidae, Myliobatidae and Odontaspididae were in both layers the most frequently collected groups, representing over 75% of all teeth collected (Fig. 1). In contrast, there are 11 rare families that together make up only about 2% of all teeth. Five families are confined to the 'clay' statum, namely the Squalidae, Dalatiidae, Ginglymostomatidae, Otodontidae and Pristidae, while Parascyllids are found exclusively in the 'sand' level (Table 1). This clearly indicates that both levels vary in faunal diversity, but apparently also the community composition differs (Table 1; Fig. 1). This is confirmed by a highly significant level*family interaction ($\chi^2 = 109.2$; *d.f.* = 15; $p < 0.0001$) indicating overall differences between both levels in occurrence frequency of collected teeth per family. In general, selachians are more present in the 'clay' level (81.4%) compared to the 'sand' level (59.7%). More specifically, the families Dalatiidae, Carcharhinidae and Odontaspididae were significantly more common in the 'clay' level. Heterodontidae and Squalidae follow the same tendencies. The reverse was observed for all batoid families, i.e. Myliobatidae, Dasyatidae, Rhinobatidae and Mobulidae, which were significantly more common in the 'sand' level (see Table 1) and make up 40.3% of all collected teeth in this level (compared to 18.6% in the 'clay' level). The following species are recorded for the first time in the Ypresian of Belgium: *Parotodus pavlovi* (Menner, 1928), *Rhizoprionodon* aff. *ganntourensis* (Arambourg, 1952), *Galeorhinus duchaussoisi* Adnet & Cappetta, 2008 and *Foumtizia* sp. nov. Several teeth of *Rhizoprionodon* aff. *ganntourensis* are found (Plate 2J-K). Despite being incomplete, the abundant occurrence of this species at the Egem quarry, from the base of the Egemkapel Clay Member going up the sequence, supports this identification. These new species for the Ypresian of Belgium, among others, are presented in two plates.

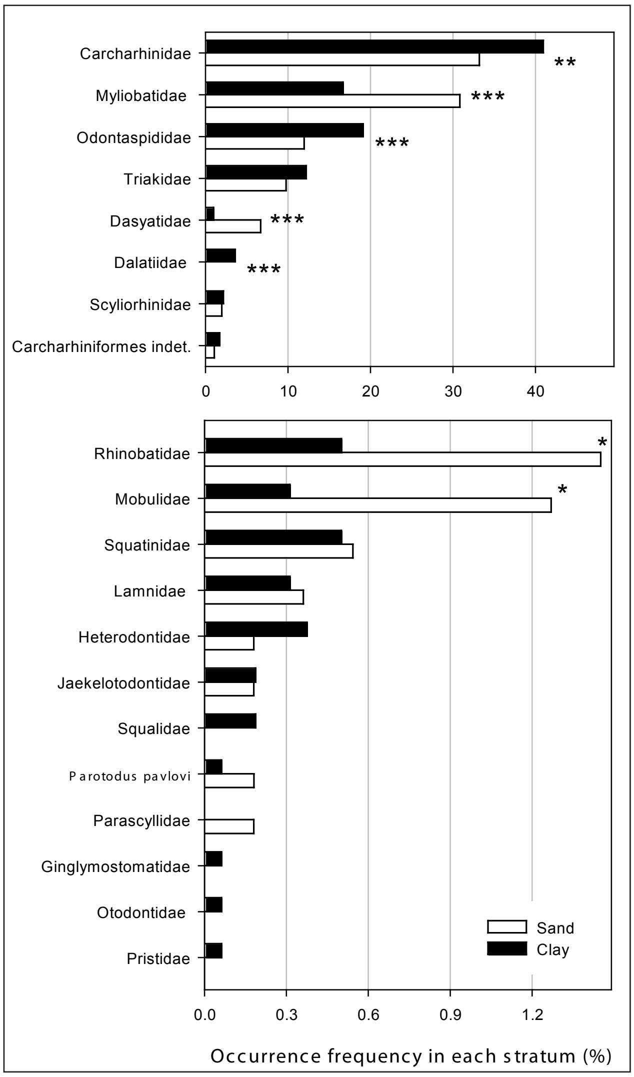

Figure 1. Graphical comparison between both levels in occurrence frequency of collected teeth within each family. Significant differences are indicated (* p<0.05; ** p<0.01; *** p<0.001).

5. Discussion

Earlier studies of microfossil assemblages have resulted in the exact positioning of successive units within the Belgian Basin and to a detailed resolution of Ypresian stratigraphy (Steurbaut & Nolf, 1986; Dupuis et al., 1991; Steurbaut, 1998). In addition, we here provide rare quantitative evidence that elasmobranch community diversity and composition also correlates with lithology. Our general results indicate that selachian families are more commonly observed in, or are even restricted to the studied clayey level, while batoids are more clearly linked to the sandy level. Both levels were deposited in an inner shelf area, the 'clay' level being indicative of a deeper sea than the 'sand' level (Steurbaut, 1998; Vandenberghe et al., 2004). Such sea level fluctuations alter local deposition, which comes along with the potential to affect community diversity and composition (Krebs, 2001; Hooper et al., 2005), as observed in the present case study.

Thus the local presence of a species or species group, depends largely on its multiple habitat requirements, such as intertwined effects of sea level and the abundance of suitable prey items (Krebs, 2001). Interestingly, a central theme in the radiation of elasmobranchs is the behavioural and morphological evolution of different prey-capture mechanisms in accordance to a wide variety of habitats (Motta, 2004; Wilga et al., 2007). In general, elasmobranchs feed on a large variety of prey, ranging from zooplankton to the largest marine mammals (Motta & Wilga, 2001). Indeed, a clear difference exists in feeding behaviour between benthic and pelagic species. Benthic elasmobranchs usually are mechanistic suction-feeding specialists, while most epibenthic and pelagic forms are generalists which use ram, suction and biting, or a combination of these, to catch a wide range of prey (Wilga et al., 2007). Together, a species or species group is characterised by both habitat requirements (e.g. sea level and abundance of prey) and behavioural, morphological and dental adaptations to catch prey.

The majority of taxa identified in the present study are fairly common in the Ypresian of the North Atlantic (e.g. Casier, 1946, 1966; Cappetta, 1976; 1992; Ward, 1980; Ward & Wiest, 1990; Van Simaeys, 1994; Smith et al., 1999; Adnet & Cappetta, 2008). The section at Marke reflects a carcharhinid-dominated ecosystem, although lamniforms (Odontaspididae) were still abundant. This is in accordance with the replacement of lamniform-dominated ecosystems by carcharhinid-dominated ones during the Eocene, as demonstrated by e.g. Adnet et al. (2007) and Underwood et al. (2011). In general, both community structures presented herein suggest a relatively shallow-marine environment, with rich invertebrate and fish faunas. The occurrence of members of the families Heterodontidae, Ginglymostomatidae, Pristidae, Myliobatidae and Dasyatidae, and the predominance of small Carcharhiniformes are all indicative of a littoral habitat at tropical latitudes (Compagno, 1984, 2001; Carpenter & Niem, 1999). Smaller shallow-water predatory sharks are represented by common genera such as *Physogaleus, Abdounia* and *Galeorhinus* (Plate 2C-F), all presumably somewhat generalist feeders on small active prey such as bony fishes (Underwood et al., 2011). Various benthic invertebrate feeders occur also, for instance *Heterodontus* (Plate 1E-F), *Dasyatis, Rhinobatos* and *Myliobatis,* whereas open-water predators like *Jaekelotodus* (Plate 1J-M), *Otodus* and *Parotodus* (Plate 1A-D) are poorly represented (Table 1). However, significant differences in community structure between both levels studied remain, which is most likely related to former sea level and its correlated effects of, for instance, depositional regimes.

In detail, we found significantly more batoid teeth in the 'sand' level, compared with the deeper marine environment of the 'clay' level. The majority of batoids that we observed were Myliobatiformes, which are in general restricted to tropical and warm-temperature areas with a preference for shallow waters (Carptenter & Niem, 1999). Most Myliobatiformes are also benthic predators and evolutionary specialists that evolved a flattened morphology allowing them to cover themselves in soft-bottom environments (Ferry-Graham et al., 2002). They use suction and blowing to fluidise the sediment and extract prey concealed therein (Sasko et al., 2006). Thus sandy substrates and low sea levels may be a more favourable environment for such benthic taxa. However, the few observed teeth of Heterodontidae (Plate 1E-F), Pristidae and Ginglymostomatidae in the 'clay' and not in the 'sand' level may contradict this pattern, given that these latter taxa are also typically benthic with a preference for shallow water (Compagno, 1984, 2001; Carpenter & Niem, 1999). Also the single tooth found of the pelagic *Pararhincodon* was assigned to the 'sand' layer, contrasting our expectations. Nonetheless, the scarcity in the 'sand' level of open-water species and the absence of deeper-water taxa suggest the body of water to have been either shallow, within a bay or behind a barrier.

Furthermore, the presence and abundance in the 'clay' level of large predators [Odontaspididae (Plate 1N-Q; Plate 2G-H), Otodontidae and Jaekelotodontidae (Plate 1J-M)] and some pelagic forms [Squalidae (Plate 2A-B) and Dalatiidae (Plate 2L-M)] is suggestive of a better connection with the Atlantic. Supporting this view is *Isistius*, a tropical oceanic shark genus, characterised by highly specialised foraging tactics and the necessity to migrate to greater depths during daytime (Papastamatiou et al., 2010). *Squalus* also needs to retreat into deeper water to stay within their optimum temperature range (Compagno, 1984). At Marke, both these squaliform sharks are confined to the 'clay' level and thus confirm our hypothesis.

In contrast to the base of the Egemkapel Clay Member (layer IV; Steurbaut, 1998, 2006), the genera *Xiphodolamia*, *Hexanchus* and *Macrorhizodus* are missing at Marke. However, these taxa are also quite rare in the shallower water deposits from Egem (Steurbaut, 2006), given their preference for deep and/or open water habitats (Compagno, 1984; Adnet et al., 2009; Underwood et al., 2011). At Marke, water depth may have been greater (50 to 100 m; Steurbaut, 2006), but still not presenting a favourable environment for these taxa. However, a sample bias can neither be ruled out here, in view of the scarcity of these taxa and the larger sample efforts at Egem over recent years. Furthermore, Casier (1946) compared presence and absence of Eocene elasmobranch taxa throughout the entire North Sea Basin. We note that these results should be treated with care, as numerous taxa were overlooked at that time and many taxa have more recently been reclassified, though still in serious need for revision (cf. Adnet & Cappetta, 2008; Underwood et al., 2011). Direct comparison with our study is therefore nearly impossible. However, we highlight the importance of future quantitative studies in order to reconstruct palaeoenvironmental conditions.

In summary, our data indicate that: (1) as expected, elasmobranch community structure and lithology are correlated, (2) that communities change considerably over time and that community stability is never reached, not even over short geological time spans (< 100 kyr). In addition (3), elasmobranch diversity and composition may largely depend on the preferred environmental conditions by a species or species group, in analogy to what is seen in modern communities and thus confirms the principle of uniformitarianism. Lastly (4), in order to reconstruct palaeoenvironmental conditions within a lithostratigraphical unit, it is recommended to quantify all essential parameters (including biodiversity) for all strata.

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Plate 1.
Elasmobranchs from the Ypresian at Marke clay pit, western Belgium.
All teeth belong to AI collection, unless noted otherwise. Collection registration numbers are provided between brackets. Scale bar = 5 mm.

A-D. ***Parotodus pavlovi*** (Menner, 1928) - ‘clay’ level (AI-Ma01L7)
Lingual (A), labial (B), lateral (C) and basal (D) views.

E-F. ***Heterodontus* sp. -** ‘sand’ level (AI-Ma01L4)
Lateral (E) and occlusal (F) views.

G-I. ***Burnhamia daviesi*** (Woodward, 1889) - ‘sand’ level (AI-Ma02L4)
Basal (G), occlusal (H) and labial (I) views.

J-M. ***Jaekelotodus robustus*** (Leriche, 1921) - ‘clay’ level
Lingual (J), labial (K), lateral (L) and basal (M) views.
Theo Lambrechts collection.

N-Q. ***Hypotodus verticalis*** (Agassiz, 1843) - ‘sand’ level (AI-Ma03L4)
Lingual (N), labial (O), lateral (P) and basal (Q) views.


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Plate 2.
Elasmobranchs from the Ypresian at Marke clay pit, western Belgium.
All teeth belong to AI collection and collection registration numbers are provided between brackets. Scale bar = 1 mm.

A-B. ***Squalus smithi*** Herman, 1982 - 'clay' level (AI-Ma02L7)
Lingual (A) and labial (B) views.

C-D. ***Galeorhinus duchaussoisi*** Adnet & Cappetta, 2008 - 'clay' level (AI-Ma03L7)
Lingual (C) and labial (D) views.

E-F. ***Galeorhinus duchaussoisi*** Adnet & Cappetta, 2008 - 'sand' level (AI-Ma04L4)
Lingual (E) and labial (F) views.

G-H. **cf. *Palaeohypotodus rutoti*** (Winkler, 1874) - 'sand' level (AI-Ma05L4)
Lingual (G) and labial (H) views.

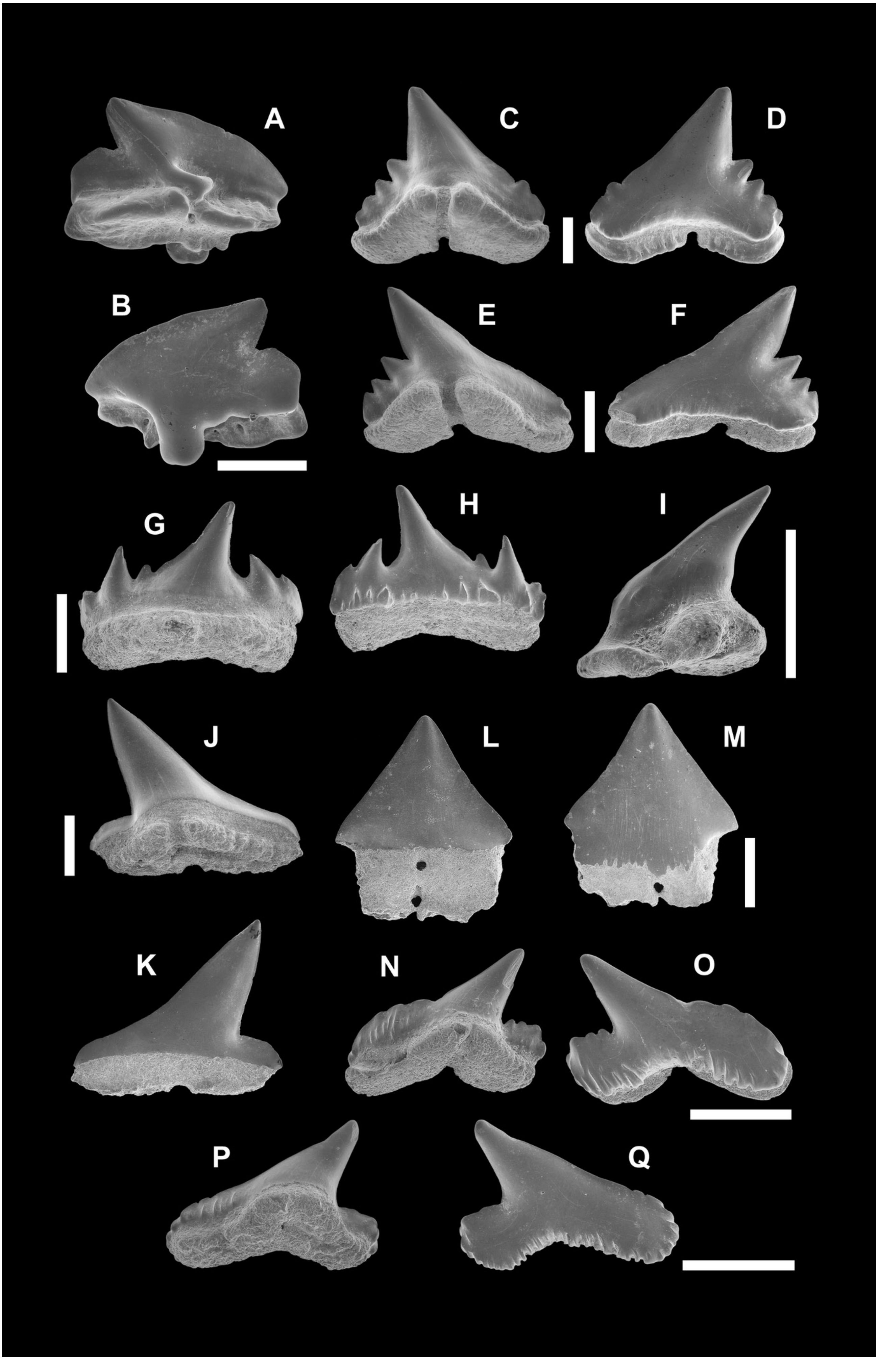
I. ***Pararhincodon ypresiensis*** Cappetta, 1976 - 'sand' level (AI-Ma06L4)
Lateral view.

J-K. ***Rhizoprionodon* aff. *ganntourensis*** (Arambourg, 1952) - 'sand' level (AI-Ma07L4)
Lingual (J) and labial (K) views.

L-M. ***Isistius trituratus*** (Winkler, 1874) - 'clay' level (AI-Ma04L7)
Lingual (L) and labial (M) views.

N-O. ***Foumtizia* sp. nov. -** 'clay' level (AI-Ma05L7)
Lingual (N) and labial (O) views.

P-Q. ***Foumtizia* sp. nov. -** 'clay' level (AI-Ma06L7)
Lingual (P) and labial (Q) views.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