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Taxonomic revision and new elasmobranch records from the Wemmel Sand and Asse Clay members, base of the Maldegem Formation (middle Lutetian, southern North Sea Basin)

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Dr Jacques Herman (former staff member of the Belgian Geological Survey, †2022) documented and sampled the temporary outcrop studied herein and preserved the recovered fossils, including the elasmobranch teeth. This paper is dedicated to his memory in recognition of his lifetime contributions to elasmobranch palaeontology and his enduring passion for the Belgian Palaeogene.

ABSTRACT

The elasmobranch fauna of the middle Lutetian Asse Clay Member (the lower part of the Maldegem Formation) has been updated and complemented with new material from a temporary outcrop at Papenboskant (Wolvertem), about 20 km north of Brussels. This faunal assemblage, which exclusively comes from its coarse-grained glauconitic base, traditionally known as the *bande noire*, comprises 22 taxa. Fourteen are mentioned for the first time in this horizon, including *Abdounia lapierrei*, which has never been recorded in Belgium before, and *Casierabatis* spp. The latter comprises dental morphologies deviating from these of the two nominal *Casierabatis* species known to date, although it is currently unclear if these reflect intraspecific variability or represent taxonomic novelties. The new records from Papenboskant consist predominantly of small-toothed taxa, mainly batoids, which are absent from the historical handpicked museum collections of the Wemmel Sand and Asse Clay members reviewed in this study. The composition of the elasmobranch fauna indicates that during the middle Lutetian, the area north of Brussels was covered by a tropical to warm-temperate shallow sea with sandy to muddy bottoms and an open connection to deeper waters. The pronounced similarities between the assemblages of the Belgian, Hampshire, and Paris basins indicate that, during the middle and late Lutetian, these three subareas of the southern North Sea remained interconnected and maintained marine exchange with the Atlantic Ocean, not only through the northern seaway but also via the southwestern English Channel. Virtually all of the newly recovered elasmobranch taxa existed over a considerable period of time and were reported from several Ypresian and/or Lutetian deposits across the North Sea Basin. *Abdounia lapierrei* appears to possess biostratigraphic significance, being so far confined to Lutetian strata. This may also apply to certain representatives of the *Casierabatis* species group, although this remains to be confirmed. The single tooth of *Notorynchus* figured in Leriche (1905) and recovered from the Wemmel Sand Member at Neder-Over-Heembeek is re-examined and refigured. This specimen represents the first occurrence of *Notorynchus kempi* in Belgium.

KEYWORDS

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1. Introduction

The Belgian Basin is well suited for palaeobiodiversity and palaeoenvironmental studies of Eocene strata because of the numerous fairly complete sections with well-documented integrated sequence stratigraphy and often abundant fossil content (e.g. Steurbaut, 1998; Vandenberghe et al., 2004; Iserbyt & De Schutter, 2012; Steurbaut & Nolf, 2021). Many of these focused on the Ypresian (Dupuis et al., 1991; Steurbaut, 2006; Steurbaut & King, 1994, 2017), which is renowned for its rich and highly diversified elasmobranch fauna, resulting from extensive sampling over the last decades (e.g. Casier, 1946, 1950; Nolf, 1972; Herman, 1975, 1977, 1979, 1982a, 1982b, 1984, 1986; Smith et al., 1999; Iserbyt & De Schutter, 2012; Migom et al., 2021; Reinecke et al., 2024). Among the most thoroughly investigated localities for shark tooth collecting in the Ypresian are the Marke clay pit (several levels within the Roubaix Clay Member; Steurbaut & King, 2017, figs 6 a, b, c) and the Egem sandpit (base of the Egemkapel Clay Member and several levels in the overlying Egem Sand Member; Steurbaut, 1998, 2006, 2015) (Fig. 1).

Elasmobranch faunas from overlying middle and upper Eocene strata of Belgium are less understood, except these from some exceptionally rich levels within the middle Lutetian. Steurbaut & Nolf (2021) recently recalibrated the onset of the Lutetian as the result of high-resolution correlations between the historical Lutetian stratotype in the Paris Basin and a series of well-dated sections across NW Europe. The Ypresian–Lutetian boundary sensu Steurbaut & Nolf (2021), dated at 49.11 Ma, predates the GSSP-defined base of the Lutetian Stage—initially dated at 47.84 Ma (Molina et al., 2011), but recently recalibrated to 48.07 Ma (Speijer et al., 2020; Cohen et al., 2024)—by approximately 1.1 to 1.3 Myr. As a consequence, Steurbaut & Nolf (2021) suggested redefining the Lutetian of Belgium to include the top of the Aalter Sand Formation, the Brussel Sand and Lede Sand formations, and the lower part of the Maldegem Formation (Fig. 1).

The early Lutetian Brussel Sand Formation (calcareous nannofossil Zone NP14) and the middle Lutetian Lede Sand Formation (base Zone NP15) revealed to be exceptionally rich in selachian remains (e.g. Burtin, 1784; Winkler, 1873, 1874b; Leriche, 1905, 1906, 1951; Casier, 1949; de Meijer, 1973a, b; Nolf, 1973, 1988; Herman, 1975, 1982a; Taverne & Nolf, 1979; Cappetta & Nolf, 2005; Mollen, 2008; Van Den Eeckhaut & De Schutter, 2009). The younger Lutetian shark faunas, which are poorly represented in the historical museum collections of Belgium, and have received little attention to date (Leriche, 1905, 1906, 1939; Casier, 1966), are reviewed herein. However, the main focus of this paper lies on the exceptionally rich elasmobranch fauna of Papenboskant, recovered from the glauconitic base of the middle Lutetian Asse Clay Member, traditionally known as the *bande noire* (literally the black band).

2. Locality and material

The material studied in this paper was collected by the late Dr Jacques Herman in early 1998 in a temporary exposure dug out by Distrigas (now Eni Gas & Power NV/SA) at Papenboskant (see Supplementary material for an overview of the excavation activities). This site is located on the hamlet of Nerom (village of Wolvertem, now municipality of Meise, Vlaams-Brabant, northern Belgium), about 50 m from the highway A12 Brussel–Antwerpen and approximately 12 km NE of Asse (x = 146.350, y = 185.300; WGS84 coordinates 50°58'40.57" N, 4°19'0.41" E; Fig. 2). It is registered at the Belgian Geological Survey (BGS) as 73W324. The material figured was collected from the glauconitic base of the Asse Clay Member. Approximately 1200 kg of this horizon was screen-washed using a sieve with 0.5 mm mesh. It is deposited in the collections of the Institute of Natural Sciences (Brussels) under registration numbers IRSNB P 10774–10796. The remaining fossils (the non-figured elasmobranch teeth, teleost otoliths and molluscs) are registered under IG 34940.

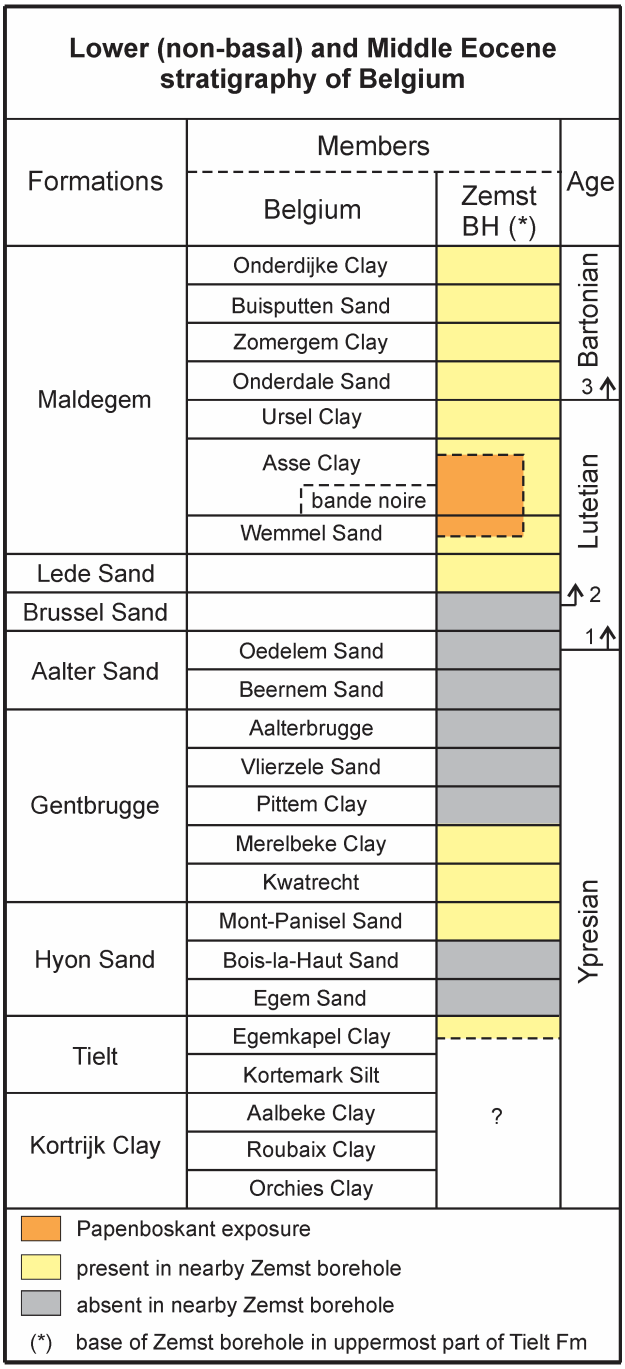

Figure 1. Stratigraphic position of the Papenboskant exposure relative to the nearby Zemst borehole (after Steurbaut et al., 2015). (1) = Ypresian–Lutetian boundary sensu Steurbaut & Nolf (2021); (2) = GSSP-defined base of the Lutetian Stage according to Molina et al. (2011); (3) = base of the Bartonian according to De Coninck (1995). Basal Ypresian units omitted; Kortrijk Clay Formation grades laterally in central Belgium into a sandy succession, the upper part of which represents the Mons-en-Pévèle Sand Formation (Steurbaut et al., 2017). Abbreviations: BH, borehole; Fm, Formation.

3. Lithology and stratigraphy of the studied section

Four units were recognised by J. Herman in the almost 5 m deep temporary excavation at the Papenboskant in Nerom (Wolvertem) (see Table 1), among which the Wemmel Sand Member (Vincent & Lefèvre, 1872) and the overlying Asse Clay Member (sensu Jacobs, 1978; before, the Asse Clay included the Ursel Clay, e.g. Conseil géologique, 1929) (Figs 2–3). Both represent the lower part of the Maldegem Formation (Jacobs & Sevens, 1993), a marine sandy-clayey succession of middle Lutetian to latest Bartonian age (e.g. Steurbaut, 2006; King, 2016) (Fig. 1).

The excavation at Papenboskant terminated in glauconitic clayey sand containing nummulites and rare *Lentipecten*, attributed to the Wemmel Sand Member (Table 1). A comparative analysis of coeval records (e.g. Kaasschieter, 1961; Jacobs, 1978; Steurbaut et al., 2015) shows that these clayey sands correlate with the upper part of the Wemmel Sand Member. Its presence at Papenboskant is not surprising as the highly fossiliferous Wemmel Sand Member has been systematically documented in the area between Asse and Zemst, north of Brussels, over the last 150 years (e.g. figuring in many publications from Vincent & Rutot, 1879 up to Steurbaut et al., 2015), yielding rich and highly diversified mollusc faunas (Glibert, 1936, 1938) and remarkable fish remains (Storms, 1896). It is presently interpreted as a single depositional sequence, assigned to the middle part of Zone NP15 and of middle Lutetian age (Steurbaut et al., 2015).

At Papenboskant, as elsewhere between Asse and Zemst (Fig. 2), the Wemmel Sand Member is overlain by a 5 to 10 cm thick highly glauconitic coarse-grained sand (authigenic glauconite locally comprising up to 50% of the sand fraction; unit 2 of Table 1, Fig. 3). This horizon, which represents the base of the Asse Clay Member, has been identified throughout the Belgian Basin, from the Mont-des-Récollets in the SW (Lyell, 1852), through the area between Gent and Brugge (Delvaux, 1886; Hacquaert, 1936; Jacobs, 1978) to the Zemst area, north of Brussels (Steurbaut et al., 2015). The *bande noire* is exceptionally fossiliferous at Papenboskant (a wide variety of invertebrate taxa was recorded by J. Herman, commented on and illustrated in Supplementary material) and particularly rich in nummulites and molluscs, dominated by *Lentipecten* and *Ostrea*. Sixty-five identifiable elasmobranch teeth were retrieved through bulk sampling and screen-washing and are studied herein. The overlying interval, presenting a fining upward trend from silty glauconitic sands to silty clays with decreasing glauconite content, was attributed to the Asse Clay Member (unit 3 of Table 1). This interpretation is in line with earlier data from the type locality Asse (Jacobs, 1978; Steurbaut, 1986), the Balegem outcrop (Jacobs & Sevens, 1994), respectively about 12 km and 37 km west, and the recent investigation of the Zemst borehole, about 10 km east of the Papenboskant section (Steurbaut et al., 2015). According to Steurbaut et al. (2015), the Asse Clay Member, including the *bande noire*, and the overlying Ursel Clay Member (Steurbaut et al., 2015) form part of a single depositional sequence. Microfossil investigations (Steurbaut, 1986; De Coninck, 1995), especially the identification of Zone NP15 and the base of NP16, revealed that this sequence does not belong to the Bartonian, as thought up to the late 1970s (surprisingly maintained in Maréchal, 1994), but is of middle to late Lutetian age (Steurbaut, 2006; Steurbaut & Nolf, 2021) (Fig. 1).

4. Taxonomic notes on elasmobranchs of the Asse Member

4.1. Preliminary remarks

As virtually all of the elasmobranch taxa from Papenboskant have been thoroughly described from many lower and middle Lutetian deposits in the southern North Sea Basin, only the most relevant information is given in the present paper. It includes technical data, such as the available material and collection numbers, and, obviously, a general discussion on the criteria used for species delimitation and assignment. When necessary, comments on taxonomic updates and distribution patterns are added.

Systematics, morphological tooth terminology and tooth measurements follow Cappetta (2012) for the selachians and Reinecke et al. (2024) for the batomorph genera. The reader is referred to the latter for an extensive description and iconography of several batomorph species encountered in the present study. Author and publication dates of higher taxonomic levels up to species level are taken from Cappetta (2012). These data are not included in the reference list.

Several species cited by Leriche (1905, 1906) do not figure in the species list compiled in the present paper (Table 2) as they are considered synonymous with other taxa. *Physodon tertius* (Winkler, 1874b) and *Galeorhinus minor* (Agassiz, 1843) are placed in synonymy with *Physogaleus secundus* (Winkler, 1874b) (e.g. Cappetta, 1980, 2012). *Lamna* (*Odontaspis*) *hopei* Agassiz, 1843 represents *Hypotodus verticalis* (Agassiz, 1843), following Cappetta & Nolf (2005) and *Isurolamna inflata* (Leriche, 1905) represents *Isurolamna affinis* (Casier, 1946), a species not yet recognised at the time of Leriche. The genus *Jaekelotodus* Menner, 1928 is assigned to the family Jaekelotodontidae as originally defined by Glückman (1964) and subsequently adopted by Iserbyt & De Schutter

Units	Depth	Lithologic description	Lithostratigraphy
4	0.00–1.05 m	Loess sediments, clayey, grey-brown to reddish-brown	Quaternary
3	1.05–3.95 m	grey-green to grey, highly glauconitic sandy silt with upward-increasing clay and decreasing glauconite content	Asse Clay Member
2	3.95–4.00 m	coarse back-green, highly glauconitic sands with abundant nummulites and molluscs, dominated by *Lentipecten*	“bande noire” (glauconitic base of the Asse Clay Member)
1	4.00–4.80 m	fine grey-green, clayey and glauconitic sands with nummulites and sporadic *Lentipecten*	Wemmel Sand Member (base not attained)

Table 1. Lithology and stratigraphic interpretation of the Papenboskant section (extract of J. Herman’s field notebook dating back to 1998).

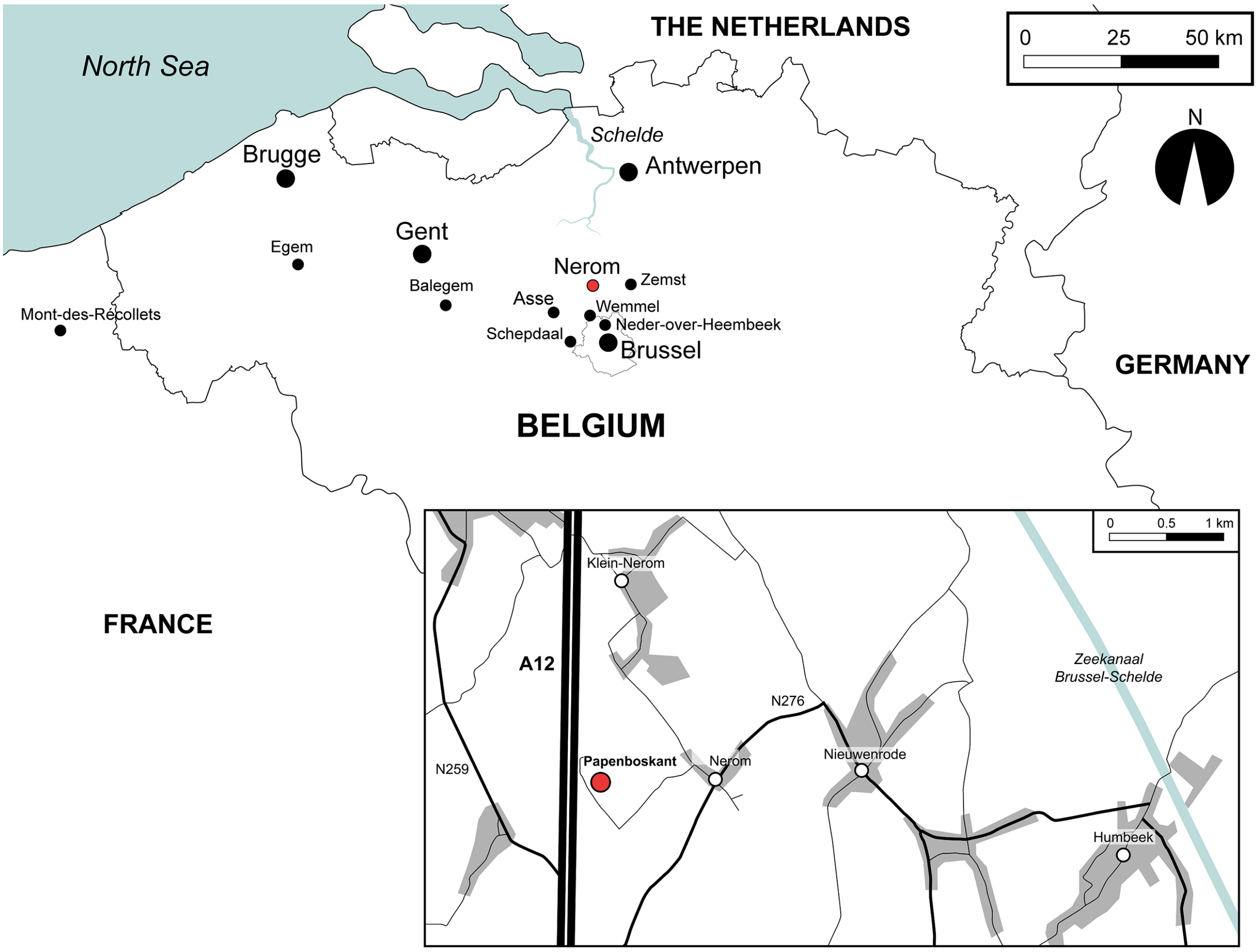

Figure 2. Location of the temporary exposure of the Asse Clay Member at Papenboskant (hamlet Nerom, village of Wolvertem).

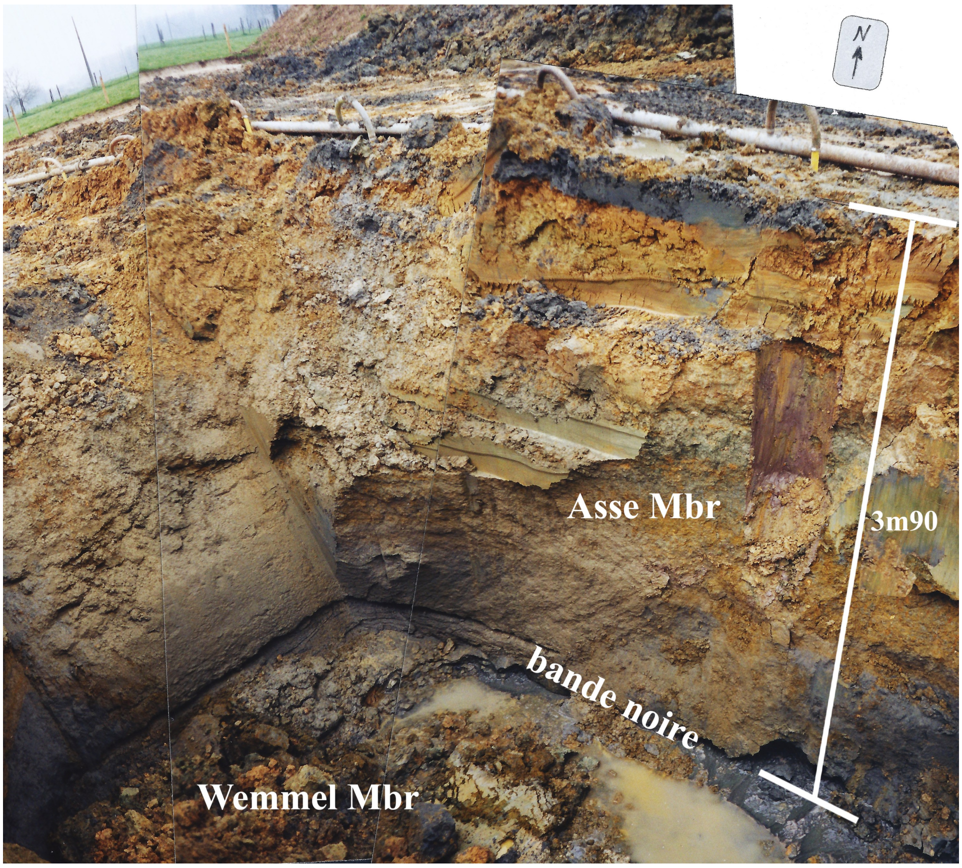

Figure 3. Photograph of the Papenboskant exposure taken in 1998 by J. Herman, showing stratigraphic details. Abbreviation: Mbr, Member.

(2012) and Ebersole et al. (2024). The genus *Striatolamia* is assigned to the family Carchariidae, as first proposed by Cunningham (2000) and subsequently adopted by Adolfssen & Ward (2015). The use of quotation marks, before and after generic names, as proposed by Reinecke et al. (2024) (e.g. '*Pseudobatos*' *steurbauti* and '*Rhynchobatus*' *vincenti*) is adopted herein. Quotation marks (' ') are used in taxonomy around a genus-group (or species-group) for specifying that the name is obsolete or for indicating that the species is thought to belong to a related genus or to a new genus, related to the named genus, but that the available material is insufficient for making formal decisions (Bengtson, 1988). Their use by Reinecke et al. (2024) refers to the latter. The single tooth, erroneously attributed to *Notidanus primigenius* Agassiz, 1843 by Leriche (1905), represents the first record of *Notorynchus kempi* Ward, 1979 in Belgium.

Sixty-five teeth have been identified to at least genus level (Table 2), belonging to 17 taxa, including 14 nominal species, and two species and one species complex in open nomenclature. According to Herman's report ('Archives SGB 73W324' in the file catalogue of the BGS, which is available as Supplementary material), around 20 not fully grown teeth were additionally collected from the sieve residue, but these seem to have been lost.

4.2. Order Carcharhiniformes

Abdounia minutissima (Winkler, 1873)
(Pl. 1.6)

Two teeth, including IRSNB P 10774, are attributed to *Abdounia minutissima* (Winkler, 1873) by the presence of a principal pair of cusplets, well separated from the main cusp, faint folds on the labial crown base and a vestigial secondary pair of cusplets, which may occur on these teeth (e.g. Leriche, 1905, pl. 5, fig. 40).

Abdounia beaugei (Arambourg, 1935)
(Pl. 1.7)

A single tooth, IRSNB P 10775, is attributed to *Abdounia beaugei* (Arambourg, 1935) by its large size, smooth crown surface and less high crown. Among the additional characteristics are the presence of a principal pair of diverging cusplets, attached to the main cusp, and the presence of a marginal secondary pair.

Abdounia lapierrei Cappetta & Nolf, 1981
(Pl. 1.5)

Two teeth, including IRSNB P 10776, are attributed to *Abdounia lapierrei* Cappetta & Nolf, 1981 by their tall and elongated crown marked by a single pair of sharp cusplets and by their mesio-distally compressed root. Teeth of *A. lapierrei* are similar to those of *Abdounia enniskilleni* (White, 1956), but they are smaller in size, have higher and sharper cusplets and a smooth crown surface (Cappetta & Nolf, 1981).

Physogaleus secundus (Winkler, 1874b)
(Pl. 1.3)

A single tooth, IRSNB P 10777, is attributed to *Physogaleus secundus* (Winkler, 1874b) by the smooth mesial cutting edge and limited number of distal cusplets (Ebersole et al., 2019). As already mentioned above, *Physogaleus tertius* (Winkler, 1874b), listed by Leriche (1905, 1906), is regarded as junior synonym of *P. secundus* (e.g. Cappetta, 1980; Kent, 1999). As both morphologies are typically found together, they might well be the result of sexual dimorphism or ontogenetic change.

Rhizoprionodon ganntourensis (Arambourg, 1952)
(Pl. 1.9)

Two teeth, including IRSNB P 10778, are attributed to *Rhizoprionodon ganntourensis* (Arambourg, 1952), the only valid Eocene member of the genus, showing a nearly circumglobal distribution in the middle Eocene (Ebersole et al., 2023). Iserbyt & De Schutter (2012) recognised the species from the lower Ypresian Roubaix Clay Member (Kortrijk Clay Formation) at Marke, representing the stratigraphically oldest *R. ganntourensis* find in the published record. The species is also present in the slightly younger middle Ypresian Egemkapel Clay Member (Tielt Formation) and Egem Sand Member (Hyon Sand Formation) at Egem (De Schutter, pers. obs.).

Pachyscyllium gilberti (Casier, 1946)
(Pl. 2.2–4)

Three teeth, IRSNB P 10779–10781, are confidently assigned to *Pachyscyllium gilberti* (Casier, 1946) (e.g. Cappetta & Nolf, 1981) because of the presence of a tall and sharp cusp, two pairs of well-developed cusplets (even a third marginal distal cusplet on one specimen) and vertical folds on the labial crown base and at the height of the cusplets on the lingual side. This species, which previously has been allocated to the genus *Premontreia* (e.g. Noubhani & Cappetta, 1997; Cappetta, 2006), was transferred to the genus *Pachyscyllium* (Cappetta, 2012, p. 267), mainly because of differences in root morphology.

Foumtizia sp.
(Pl. 2.1)

One well preserved tooth (IRSNB P 10782) and two incomplete teeth can be attributed to the genus *Foumtizia*. The single complete specimen recovered from Papenboskant is mesio-distally elongated and measures 3 mm in width. It has a tall, erect but basally broad cusp, flanked by two pairs of low, rudimentary lateral cusplets, well separated from the main cusp. The crown's cutting edge is complete, extending across the lateral cusplets. The labial crown base possesses coarse vertical folds on a prominent horizontal crest overhanging the root. The ornamentation does not extend to the crown face. The lingual crown face is equally smooth. The size of this specimen is fairly large for the genus, and markedly larger than the specimens of *Foumtizia pattersoni* (Cappetta, 1976) from the Ypresian of Egem (De Schutter, pers. obs.). This single well-preserved specimen is left in open nomenclature because the available material is insufficient for a confident species assignment, and certainly inappropriate for the formal erection of a new species.

4.3. Order Lamniformes

Striatolamia macrota (Agassiz, 1843)
(Pl. 1.2)

A single (juvenile) tooth, IRSNB P 10783, is assigned to *Striatolamia macrota* (Agassiz, 1843) by the typical strong folds on the lingual crown surface. This shark is easily the most common larger species recorded in Eocene strata worldwide (e.g. Cappetta, 2012).

***Jaekelotodus trigonalis* (Jaekel, 1895)**
(Pl. 1.1)

A single tooth, IRSNB P 10784, is attributed to *Jaekelotodus trigonalis* (Jaekel, 1895). Its dentition consists of three upper anterior teeth followed by at least a single file of intermediate teeth, identical to that of its ancestor *Jaekelotodus robustus* (Leriche, 1921). The single *J. trigonalis* tooth recorded in the Asse Clay Member corresponds to an upper intermediate tooth position. This species is permanently occurring in the elasmobranch assemblages of the later part of the Eocene (e.g. Ward, 1980; Zhelezko & Kozlov, 1999; Trif et al., 2019, fig. 6 as *J. robustus*). *Jaekelotodus robustus*, which is still present in the Wemmel Sand Member (Leriche, 1905, 1921; Casier, 1966), seems to have disappeared in the overlying Asse Clay Member. Its successor, *J. trigonalis* occurs throughout both members.

4.4. Order Squaliformes

***Squalus minor* (Daimeries, 1888)**
(Pl. 1.10)

Two teeth, including IRSNB P 10785, correspond well with the type specimens of *Squalus minor* (Daimeries, 1888), figured in Leriche (1902) and originating from the Selandian Orp Sand Member (Heers Formation). According to Migom et al. (2021), this species is identical to *Squalus smithi* Herman, 1982a and a senior synonym of the latter. However, teeth of extant species of *Squalus* are very difficult to differentiate, even when complete sets are available. This demonstrates the difficulty in identifying fossil species, when only isolated teeth are available (Cappetta et al., 2016; Engelbrecht et al., 2017).

***Isistius trituratus* (Winkler, 1874b)**
(Pl. 1.8)

One complete tooth, IRSNB P 10786, and two incomplete teeth are attributed to *Isistius trituratus* (Winkler, 1874b), a species occurring throughout the entire Lutetian. It has been reported from the Brussel Sand Formation and Lede Sand Formation (e.g. Leriche, 1905; Van Den Eeckhaut & De Schutter, 2009; Hovestadt & Steurbaut, 2023) and, according to the present data, persists into the base of the Asse Clay Member. *Isistius trituratus* is common in the sand-dominated sediments of the Ypresian Mons-en-Pévèle Sand Formation (De Schutter, pers. obs.) and in the outer neritic London Clay Formation (Casier, 1966; Rayner et al., 2009), but seems to be very rare in the nearshore slightly younger Ypresian deposits from Egem (one specimen recorded to date, found in bed IV at the base of the Egemkapel Clay Member sensu Steurbaut, 1998, fig. 11) (Migom et al., 2021, p. 20) (Fig. 1).

4.5. Order Squatiniformes

***Squatina* cf. *prima* (Winkler, 1874a)**
(Pl. 1.11)

Eocene angel shark teeth have usually been assigned to *Squatina prima* (Winkler, 1874a), which type specimens came from the Selandian Orp Sand Member (Heers Formation) (e.g. Winkler, 1874a; Leriche, 1905, 1906; Casier, 1946, 1966; Nolf, 1988). *Squatina crassa* Daimeries, 1889, described from Ypresian and Lutetian strata, has smaller sized teeth than *S. prima*, and are more robust with a thick root. The single specimen in our sample, IRSNB P 10787, has a very slender and fragile morphology, leaning much more towards *S. prima* than *S. crassa*. However, as Squatinids present a very conservative (tooth) morphology and the taxonomy of extinct Squatinids is very problematic (e.g. Cappetta, 2012; Mollen et al., 2016), our specimen from Papenboskant is left in open nomenclature.

4.6. Order Rhinopristiformes

'*Pseudobatos*' *steurbauti* (Cappetta & Nolf, 1981)
(Pl. 2.5–6)

These rhinobatoid teeth are easily recognisable by their small size, reaching a maximum height of 1 to 2 mm and by the presence of a globular crown with a well-developed central uvula. The anterior teeth possess barely marked lateral uvulae and their height is greater than their width. The two well-preserved teeth from the Asse Clay Member, IRSNB P 10788–10789, are similar to those of the upper Lutetian (Zone NP16) *Sables d'Auvers* in the Paris Basin, originally described as *Rhinobatos steurbauti* Cappetta & Nolf, 1981. They are also identical to the Ypresian teeth recently described from the Egem and Marke quarries, tentatively denoted as '*Pseudobatos*' *steurbauti* (Cappetta & Nolf, 1981) (Reinecke et al., 2024). The Papenboskant find is only the second published record of the species in Belgium.

'*Rhynchobatus*' *vincenti* Jaekel, 1894
(Pl. 2.8)

Six rhinid teeth, including IRSNB P 10790, are assigned to '*Rhynchobatus*' *vincenti* Jaekel, 1894 because of their extreme width, which may exceed 3 mm and by the typical characteristics of the crown. The latter presents a large central uvula, but lacks lateral uvulae. Some irregular pitting occurs around the edges of the crown, which has a slightly globular or, when worn, flattened apical part.

***Glaucopristis bruxelliensis* (Jaekel, 1894)**
(Pl. 2.7)

Three complete teeth, including IRSNB P 10791, and ten incomplete specimens are attributed to *Glaucopristis bruxelliensis* (Jaekel, 1894). These teeth measure around 2 mm in height. They are smaller sized than those of '*Rhynchobatus*' *vincenti* and often wider than high. They are furthermore characterised by a thick, rather long, central uvula and prominent, laterally diverging, lateral uvulae. *Rhinobatos bruxelliensis* Jaekel, 1894 was transferred to the recently created genus *Glaucopristis* (Reinecke et al., 2024). It is by far the most common rhinopristiform species in the Ypresian and Lutetian of Belgium (e.g. Leriche, 1905; Casier, 1946; Smith et al., 1999; Van Den Eeckhaut & De Schutter, 2009; Iserbyt & De Schutter, 2012).

4.7. Order Myliobatiformes

***Casierabatis* spp.**
(Pl. 2.9–12)

Reinecke et al. (2024) recently erected the genus *Casierabatis* to accommodate teeth of *Casierabatis lambrechtsi* Reinecke et al., 2024 from the Belgian Ypresian and those previously attributed to *Dasyatis jaekeli* (Leriche, 1905), originally described from the Lutetian (Hovestadt & Steurbaut, 2023, p. 94). Teeth of *C. lambrechtsi* have a labial crown surface covered with small and larger depressions and a very small secondary pitting. To the contrary, teeth of *C. jaekeli* lack the secondary pitting, and only possess a finely scarred surface with some irregular short folds and shallow pits. For an extensive description and iconography of both species the reader is referred to Reinecke et al. (2024).

Sixteen specimens from the Asse Clay Member, including IRSNB P 10792–10795, present dental morphologies which match the general characteristics of *Casierabatis*, but cannot be reliably assigned to the two nominal species known to date and miss the necessary characteristics to serve as references for new species. Therefore, they are kept in open nomenclature and denoted as *Casierabatis* spp. Most of them (e.g. IRSNB P 10792–10793, Pl. 2.9–10) present a coarser labial crown ornamentation than that observed in *C. lambrechtsi* and miss the small-scaled secondary pitting typical of this species, but at the same time, do not show the finely scarred surface of *C. jaekeli*. These specimens are provisionally left in open nomenclature, because it is still unclear whether these differences fall within the intraspecific variability of the nominal *Casierabatis* species or if they justify the erection of a new taxon or not. One specimen (IRSNB P 10794, Pl. 2.11) has a flat, strongly abraded crown and is too poorly preserved to allow an identification to species level. One specimen (IRSNB P 10795, Pl. 2.12) is fairly atypical for the genus *Casierabatis*, being very large, measuring 3.5 mm in height, and having a split crown. Such teeth with a split crown are considered pathological (Reinecke et al., 2024, p. 72) and cannot be designated as a reference for a new species, new genus or some other taxon. Hence, this aberrant tooth from the Asse Clay Member is also left in open nomenclature.

‘*Myliobatis*’ sp.
(Pl. 1.4)

Batoid dental plates, similar to IRSNB P 10796, have traditionally been identified as *Myliobatis dixoni* (Agassiz, 1843). Cappetta (2012), based on the labial and lingual crown ornamentation, suggested an affiliation with the extant genus *Aetomylaeus* Garman, 1908. However, Hovestadt & Hovestadt-Euler (2013) and Reinecke et al. (2024) noted the high variability within the dentition of extant Myliobatid species and the extreme difficulty of confidently identifying isolated fossil myliobatid teeth. This partial dental plate, IRSNB P 10796, and five isolated lateral teeth are, therefore, denoted as ‘*Myliobatis*’ sp. A major revision of the entire family is needed to resolve the problem.

5. First record of *Notorynchus kempi* Ward, 1979 in Belgium

A single tooth of *Notorynchus* (IRSNB P 650), originating from the Wemmel Sand Member and figured by Leriche (1905, p. 207, text-fig. 62) as *Notidanus primigenius* Agassiz, 1843, was re-examined and refigured herein (Fig. 4). This specimen (IRSNB P 650), collected in the 19th century at Neder-Over-Heembeek (Fig. 2), represents the first published record of *Notorynchus kempi* Ward, 1979 in Belgium.

Although the identification of *Notorynchus* species is primarily based on isolated lower antero-lateral teeth, and on somehow variable and rather subjective dental characters (Bor et al., 2012), the single upper antero-lateral tooth available, can be attributed to *N. kempi* by its large size (17.9 mm wide), fine mesial cusplets and curved, distally directed, distal cusplets. This species was originally described from the Bartonian of England (Highcliffe Member, NP 17, see King, 2016). Our specimen differs from the early and middle Eocene teeth of *N. serratissimus* (Agassiz, 1843) by its larger size, by an apico-basally deeper root with a larger lingual protuberance and by finer and evenly sized mesial cusplets on the principal cusp. The principal cusp and the three distal cusplets are all distally oriented. In addition, the distal cusplets diminish in size away from the principal cusp (Ward, 1979). The Oligocene–Miocene *N. primigenius* (Agassiz, 1843) has larger teeth, especially in the Oligocene (e.g. Leriche, 1910), and coarser mesial cusplets. The principal cusp and distal cusplets are relatively larger and more robust, more pointed and less distally directed (Ward, 1979).

6. Palaeobiodiversity and palaeoenvironmental considerations

6.1. Composition of the elasmobranch fauna of the Maldegem Formation

The elasmobranch fauna of the Maldegem Formation currently consists of 26 taxa. It is exclusively originating from the Wemmel Sand Member and the base of the Asse Clay Member (traditionally known as the *bande noire*) and includes the historical collections studied by Leriche (1905,1906), additional


60 PISC. TERT. I
Nom *Notidanus primigenius* Agass.
Terr. ÉOCÈNE
Etage BARTONIEN
Loc. *Neder-over-Humbeek*
Dét. LERICHE *1903*
I.G. *6115* [650]

Figure 4. An upper antero-lateral tooth of *Notorynchus kempi* Ward, 1979 (IRSNB P 650) collected from the Wemmel Sand Member at Neder-over-Heembeek, district of Brussels. Lingual (A) and labial (B) views. Scale bar = 5 mm.

Table 2. Overview of the Elasmobranch assemblages from the Wemmel Sand Member and the base of the Asse Clay Member (lower part of the Maldegem Formation, middle Lutetian), based on Leriche (1905, 1906), Casier (1966) and the present paper (* see Section 5).

	Papenboskant (present study)	Leriche (1905, 1906)	Leriche (1905, 1906) Casier (1966)
	Asse Member (*bande noire*)	Asse Member (*bande noire*)	Wemmel Member
Striatolamia macrota (Agassiz, 1843)	1	+	+
Brachycarcharias lerichei (Casier, 1946)		+	+
Isurolamna affinis (Casier, 1946)		+	+
Hypotodus verticalis (Agassiz, 1843)		+	+
Jaekelotodus trigonalis (Jaekel, 1895)	1	+	+
Jaekelotodus robustus (Leriche, 1921)			+
Otodus auriculatus (Blainville, 1818)			+
Notorynchus kempi Ward, 1979			+*
Macrorhizodus praecursor (Leriche, 1905)			+
Physogaleus secundus (Winkler, 1874b)	1		+
Pristis lathami Galeotti, 1837		+	+
Isistius trituratus (Winkler, 1874b)	3		+
Abdounia lapierrei Cappetta & Nolf, 1981	2		
Abdounia beaugei (Arambourg, 1935)	1		
Abdounia minutissima (Winkler, 1873)	2		+
Rhizoprionodon ganntourensis (Arambourg, 1952)	2		
Pachyscyllium gilberti (Casier, 1946)	3		
Squalus minor (Daimeries, 1888)	2		
***Foumtizia* sp.**	3		
Squatina* cf. *prima (Winkler, 1874a)	1		+
Aetobatus irregularis (Agassiz, 1843)		+	+
‘*Myliobatis*’ sp.	5 + 1	+	+
***Casierabatis* spp.**	16		
‘*Pseudobatos*’ *steurbauti* (Cappetta & Nolf, 1981)	2		
Glaucopristis bruxelliensis (Jaekel, 1894)	13		
‘*Rhynchobatus*’ *vincenti* (Jaekel, 1894)	6		

material listed by Casier (1966) and the material collected by J. Herman at Papenboskant in 1998, first studied herein. The identified taxa are summarized in Table 2, taking into account the taxonomic updates commented on in Section 4.

The faunal assemblage of the Wemmel Sand Member yields 16 taxa, 11 of which were listed by Leriche (1905, 1906) and 5 were subsequently added by Casier in his monograph on the London Clay (1966, p. 273, table IV), although without any descriptions or figures. Five additional species (*Eostegostoma angustum* (Nolf & Taverne) in Herman, 1977; *Nebrius thielensi* (Winkler, 1873); *Palaeorhincodon wardi* Herman, 1975; *Archaeomanta melenhorsti* Herman, 1979; and *Mustelus* sp.) were described by Herman (1977, 1979, 1982b) from the base of the Wemmel Sand Member at Schepdaal. At the time of sampling in 1976, Herman, noting the exceptional preservation of the teeth and lacking awareness of comparable Ypresian faunas, considered the assemblage to be autochthonous. Subsequent study, however, led him to correctly interpret the material as reworked from underlying Lutetian and Ypresian strata (Herman, 2010, personal notes, file 87E8” of the Belgian Geological Survey). Consequently, this material is not included in Table 2.

Twenty-two taxa are recorded from the base of the Asse Clay Member, 17 of which from the Papenboskant locality. Eight of these 22 taxa were already known by Leriche (1905, 1906) and 14 are listed here for the first time, among which the first published record of *Abdounia lapierrei* in Belgium (Table 2). All taxa from the base of the Asse Clay Member reported by Leriche have been recorded in the historical collections of the Wemmel Sand Member.

The number of taxa in both the Wemmel Sand Member and the base of the Asse Clay Member is too limited for far-reaching conclusions. However, there are differences between the material taken from the base of the Asse Clay Member at Papenboskant and that from the historical collections from the Wemmel Sand and Asse Clay members. Taxa with small teeth (maximum tooth length <5 mm) are under-represented or nearly absent in the historical ‘Leriche – Casier’ material, which contains only one (*Squatina* cf. *prima*) of the nine small-toothed taxa recorded at Papenboskant. This discrepancy is essentially due to differences in sampling methodology. At Papenboskant, a 0.5 mm mesh sieve was used, allowing the recovery of very small specimens (74% of the total number of teeth are less than 5 mm long), whereas the material from historical collections was largely handpicked, favouring the collection of larger teeth. Interestingly, most taxa recovered from the Wemmel Sand Member, which are predominantly large-toothed taxa (main tooth length >1 cm), such as *Hypotodus verticalis* (Agassiz, 1843), *Isurolamna affinis* (Casier, 1946), *Otodus auriculatus* (Blainville, 1818) and others, are absent from the Papenboskant assemblage. This probably reflects the rarity of elasmobranch remains in the lower members of the Maldegem Formation (less than one specimen per 20 kg sediment at Papenboskant) where the recovery of each additional taxon requires the processing of a tremendous amount of sediment.

6.2. Taphonomic, palaeoenvironmental and palaeobiogeographic results

The elasmobranch assemblage from Papenboskant exclusively consist of isolated teeth of benthic and neritic taxa, which apparently accumulated on the seafloor as the result of normal physiologic processes, essentially tooth shed. The presence of not fully grown shark teeth, however, shows that at least one, and probably more, dead animals contributed to the formation of this assemblage. The natural mix of small-sized and large-sized teeth, similar to the size distribution in the other fossil invertebrate groups (unpublished data by Herman, commented on in the Supplementary material), seems to exclude strong selective sediment transport and sorting, suggesting feeble wave action and little or no lateral displacement. This suggests that the *bande noire* at this locality is not a beach deposit, but formed slightly deeper, along the lower shoreface, just below fair-weather wave base. The reduced sand fraction, as well as the abundance of glauconite, much of which is coarse-grained, and the abundance of nummulites, corroborate with this depositional model, as medium- to coarse-grained glauconite and nummulites proliferate in areas with low sediment supply and few or no turbulence, conditions which are met with on the lower shoreface.

Members of the families Pristidae, Myliobatidae, Dasyatidae, and small Carcharhiniformes, are well represented in the assemblage and are all indicative of tropical and warm-temperature areas with a preference for shallow waters (Compagno, 1984, 2001; Carpenter & Niem, 1999). The majority of the batoids of the assemblage belong to the myliobatiform *Casierabatis*, abundantly present in the inner neritic deposits at Egem, confirming their preference for shallow marine habitats (Reinecke et al., 2024). This also applies to *'Pseudobatos' steurbauti* (Cappetta & Nolf, 1981), which is absent in the outer neritic London Clay Formation, but common at Egem (Reinecke et al., 2024). Most Myliobatiformes are also benthic predators that evolved a flattened morphology allowing them to cover themselves in soft-bottom environments (Ferry-Graham et al., 2002). Similarly, extant *Squatina* are often found hiding in muddy or sandy bottoms, feeding on a variety of small invertebrates and small bony fish, caught by ambush attack (e.g. Compagno, 1984; Mollen et al., 2016). Smaller shallow-water predatory sharks, represented by *Physogaleus*, *Abdounia* and *Rhizoprionodon*, are presumably somewhat generalist feeders on small active prey such as bony fishes (Underwood et al., 2011). As is typical for Eocene selachian assemblages, multiple species of the genus *Abdounia* (Cappetta, 1980) coexisted. Additionally, the presence of large open-water predators like *Jaekelotodus*, and some pelagic Squalidae and Dalatiidae, indicate a connection with the Atlantic Ocean. Supporting this view is *Isistius*, a tropical oceanic shark 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 optimal temperature range (Compagno, 1984).

The Elasmobranch fauna of the lower part of the Maldegem Formation has many species in common with the fauna of the *Sables d'Auvers* in the Paris Basin (75% of the taxa in these sands are recorded at Papenboskant; Cappetta & Nolf, 1981) and with the fauna of the Selsey Formation in the Hampshire Basin (especially the many in common subtropical to warm-temperate large open water and oceanic taxa, such as *Jaekelotodus trigonalis* (Jaekel, 1895), *Isistius trituratus* (Winkler, 1874b), *Macrorhizodus praecursor* (Leriche, 1905), *Notorynchus kempi* Ward, 1979 and *Otodus auriculatus* (Blainville, 1818) (Kemp et al., 1990; Ward, 2016). This suggests that during the middle and late Lutetian (Biochron late NP15 to Biochron early NP16) these three subareas of the southern North Sea were still interconnected and opened to the Atlantic Ocean, not only through the north but also via the English Channel to the southwest.

6.3. Biostratigraphic remarks

A close inspection of existing literature data reveals that most of the recorded taxa from the Papenboskant section are fairly common in middle Ypresian to upper Lutetian–lower Bartonian deposits of the North Sea Basin (e.g. Casier, 1946, 1966; Cappetta, 1976; Ward, 1980; Nolf, 1988; Smith et al., 1999; Cappetta & Nolf, 2005; Van Den Eeckhaut & De Schutter, 2009; Ward, 2016). Some of these existed over a very long period of time, dating back to the middle Paleocene (e.g. Smith et al., 1999, table III), while others (e.g. *Striatolamia macrota* (Agassiz, 1843), *Jaekelotodus trigonalis* (Jaekel, 1895), *Isistius trituratus* (Winkler, 1874b), etc.) persisted up in the earliest Bartonian (Ward, 2016). *Abdounia lapierrei* Cappetta & Nolf, 1981, which in Belgium is only known from the middle Lutetian Asse Clay Member, appears to be restricted to the Lutetian. It has been reported from the lower Lutetian Earnley Formation up to the uppermost Lutetian–basal Bartonian Elmore Member in the Hampshire Basin (Kemp et al., 1990; Ward, 2016) and from the upper Lutetian *Sables d'Auvers* in the Paris Basin (Cappetta & Nolf, 1981). Some representatives of the *Casierabatis* species group may also have biostratigraphic relevance, although this still needs further confirmation.

7. Conclusions

The stratigraphic investigation and bulk sediment sampling of the *bande noire* at the base of the Asse Clay Member at Papenboskant (Wolvertem), 20 km north of Brussels, led to the following conclusions:

1. The Papenboskant excavation resulted in the discovery of the richest and most diversified invertebrate fauna ever recovered from the *bande noire* horizon and from the Asse Clay Member *tout court*. This is also true for the elasmobranch fauna studied herein, which consists of 22 taxa, 14 of which have never been recorded from this middle Lutetian horizon before.
2. The elasmobranch fauna of the *bande noire* horizon is dominated by benthic batoid taxa, several of which prefer hiding in the soft fine-grained sea bottom sediment. It also includes several neritic tropical to warm-temperate small predatory sharks, essentially feeding on small bony fish, and some large open-water predators and pelagic taxa. Some of the open-water taxa undertake daily migrations to deeper waters, like *Isistius*, the sole oceanic taxon recorded.
3. The elasmobranch data reveal that, during middle

Lutetian times, the area north of Brussels was covered by a tropical to warm-temperate shallow sea, with sandy to muddy bottoms and an open connection to deeper waters. The palaeontological and sedimentological context suggests that sedimentation took place along the lower shoreface, just below main wave base, in an area with very low sediment supply, initiating the formation and accumulation of coarse-grained glauconite, fossil shell beds and nummulite-rich layers.

4. The strong similarities between the elasmobranch assemblages of the Belgian, Hampshire and Paris basins suggest that during the middle and late Lutetian, these three subareas of the southern North Sea were still interconnected and opened to the Atlantic Ocean, not only through the north but also via the southwestern English Channel.

5. Virtually all of the recovered elasmobranch taxa existed over a considerable period of time and were reported from other Ypresian and/or Lutetian deposits across the North Sea Basin. *Abdounia lapierrei* Cappetta & Nolf, 1981 appears to possess biostratigraphic significance, being so far restricted to Lutetian strata. Certain representatives of the *Casierabatis* species group may likewise be limited to the basal part of the Asse Clay Member, pending confirmation.

6. The re-examination of Leriche's historical museum collections, which was carried out within the scope of the present paper, revealed that the single tooth of *Notorynchus* recovered from the Wemmel Sand Member (Leriche, 1905) represents the first occurrence of *Notorynchus kempi* in Belgium.

7. This study highlights the need for caution when interpreting historical elasmobranch museum collections, as they were largely handpicked and under-represent small-toothed taxa that dominate recent sieved assemblages.

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Author contribution

PDS performed the taxonomic analysis of the elasmobranch material, collected by Jacques Herman in 1998, and designed the figures and plates. PDS and ES wrote the manuscript.

Data availability

All studied specimens are housed in official repositories guaranteeing their long-term safekeeping and availability to other researchers for future studies.

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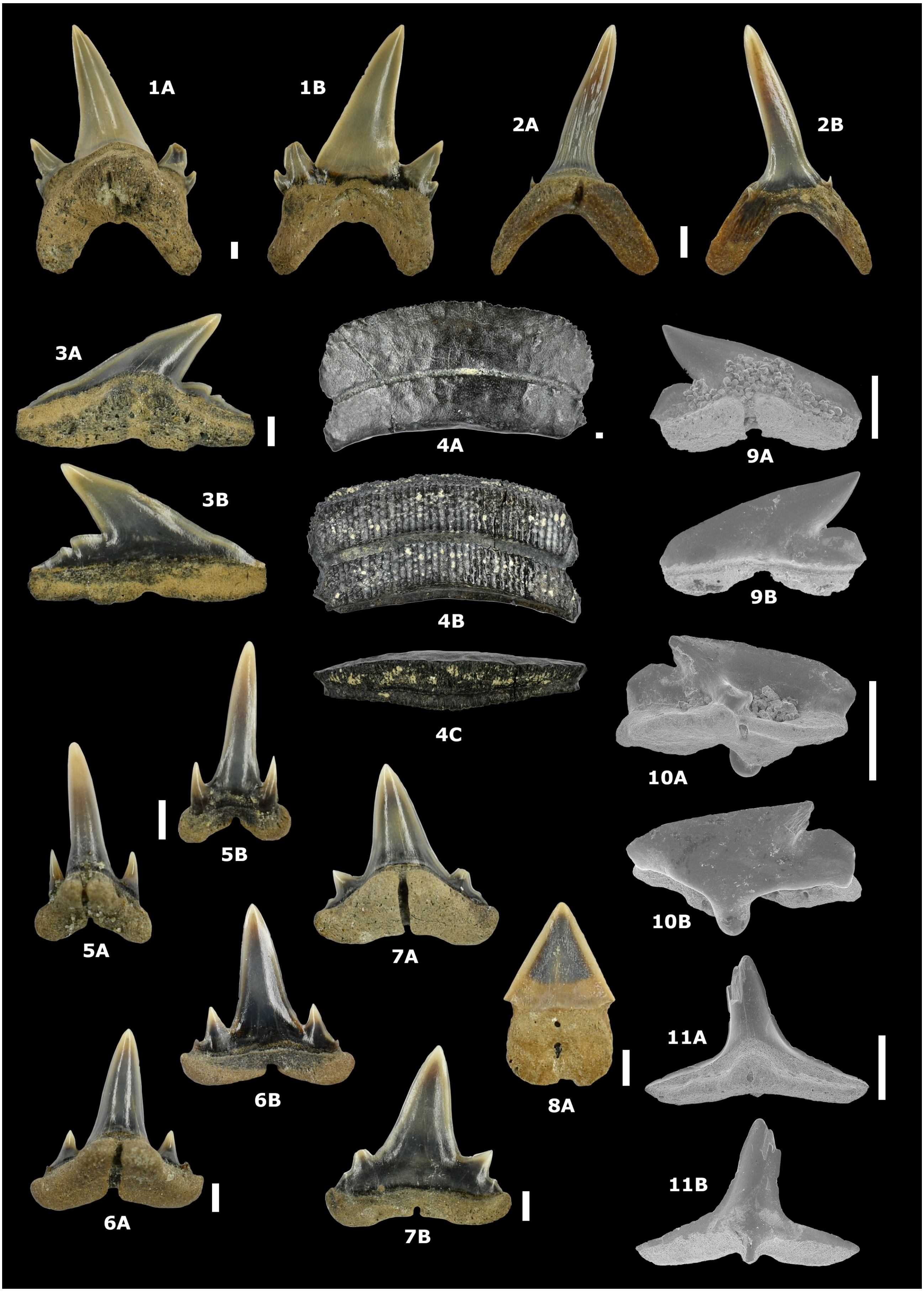

Plate 1. Elasmobranch teeth, base of the Asse Clay Member, Papenboskant (Wolvertem). Scale bar = 1 mm. 1–3, 5–11: Lingual (A) and labial (B) views. 4: Occlusal (A), basal (B) and profile (C) views. **1A–B.** *Jaekelotodus trigonalis* (Jaekel, 1895), IRSNB P 10784. **2A–B.** *Striatolamia macrota* (Agassiz, 1843), IRSNB P 10783. **3A–B.** *Physogaleus secundus* (Winkler, 1874b), IRSNB P 10777. **4A–C.** *'Myliobatis'* sp., IRSNB P 10796. **5A–B.** *Abdounia lapierrei* Cappetta & Nolf, 1981, IRSNB P 10776. **6A–B.** *Abdounia minutissima* (Winkler, 1873), IRSNB P 10774. **7A–B.** *Abdounia beaugei* (Arambourg, 1935), IRSNB P 10775. **8A.** *Isistius trituratus* (Winkler, 1874b), IRSNB P 10786. **9A–B.** *Rhizoprionodon ganntourensis* (Arambourg, 1952), IRSNB P 10778. **10A–B.** *Squalus minor* (Daimeries, 1888), IRSNB P 10785. **11A–B.** *Squatina* cf. *prima* (Winkler, 1874a), IRSNB P 10787.

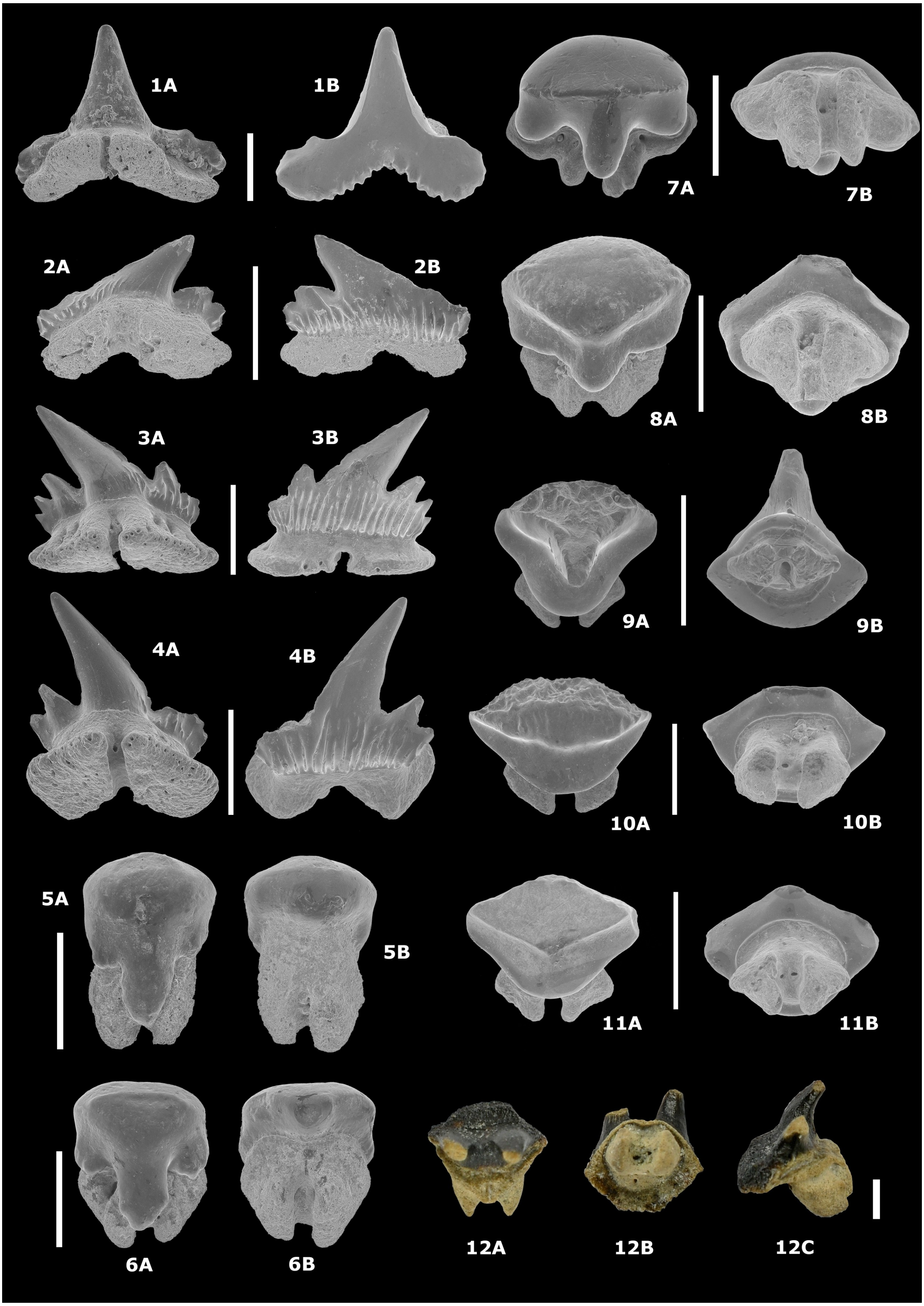

Plate 2. Elasmobranch teeth, base of the Asse Clay Member, Papenboskant (Wolvertem). Scale bar = 1 mm. 1–4: Lingual (A) and labial (B) views. 5–12: Occlusal (A), basal (B) and profile (C) views. **1A–B.** *Foumtizia* sp., IRSNB P 10782. **2A–B to 4A–B.** *Pachyscyllium gilberti* (Casier, 1946), IRSNB P 10779-10781. **5A–B**, **6A–B**. *'Pseudobatos' steurbauti* (Cappetta & Nolf, 1981), IRSNB P 10788-10789. **7A–B.** *Glaucopristis bruxelliensis* (Jaekel, 1894), IRSNB P 10791. **8A–B.** *'Rhynchobatus' vincenti* (Jaekel, 1894), IRSNB P 10790. **9A–B to 12A–C.** *Casierabatis* spp., IRSNB P 10792-10795.