PHYSOGALEUS HEMMOORIENSIS (CARCHARHINIDAE, ELASMOBRANCHII) A NEW SHARK SPECIES FROM THE EARLY TO MIDDLE MIOCENE OF THE NORTH SEA BASIN

by

Thomas REINECKE* and Kristiaan HOEDEMAKERS**

SUMMARY

* Hustadtring 28, D-44801 Bochum, Germany, treinecke@web.de,

** Minervastraat 23, B-2640 Mortsel, Belgium, hoedinnig@scarlet.be

Mots-clés: *Physogaleus*, Carcharhinidae, Elasmobranchii, Hemmoorien, Miocene inférieur, bassin de la Mer du Nord, espèce nouvelle.

Key-words: *Physogaleus*, Carcharhinidae, Elasmobranchii, Hemmoorian, Early Miocene, North Sea basin, new species.

Palaeovertebrata, Montpellier, **34** (1-2): 1–25, 3 fig., 1 tabl., 4 pl.
(Publié le 15 Octobre 2006)

ABSTRACT

A new carcharhinid shark species, *Physogaleus hemmooriensis* sp. nov., is described from the Lower Hemmoorian (Behrendorfian, late Burdigalian, early Miocene) of Werder, Lower Saxony, Germany. *P. hemmooriensis* also occurs in the Edegem and Antwerpen Sands Members of the Berchem Formation, Belgium, and in the Miste Bed, Aalten Member of the Breda Formation, The Netherlands, which have an early to middle Miocene age. In the Western Atlantic region, the taxon is present in the early Miocene Calvert Formation of Delaware, U.S.A, which is largely contemporaneous with the Hemmoorian.

RESUME

Une nouvelle espèce de Carcharhinidae, *Physogaleus hemmooriensis* sp. nov., est décrite de l'Hemmoorien inférieur (Behrendorfien, Burdigalien supérieur, Miocène inférieur) de Werder, Basse Saxonie, Allemagne. *Physogaleus hemmooriensis* est également présent dans les "Sands Members" (Berchem Formation) d'Edegem et d'Anvers, Belgique, et dans le "Miste Bed", Membre d'Aalten de la Breda Formation, Pays-Bas, qui ont un âge miocène inférieur à moyen. Dans la région ouest atlantique, le taxon est présent dans la Calvert Formation (Miocène inférieur) du Delaware, U.S.A., qui est en grande partie contemporaine de l'Hemmoorien.

INTRODUCTION

Marine sediments of the early to late Hemmoorian, early to middle Miocene, of the North Sea Basin contain diverse elasmobranch faunas which are incompletely known because of the rarity of fossil remains (teeth, dermal denticles, caudal stings) and surface outcrops. During the 1990s, elasmobranch teeth were recovered by screen washing of large amounts of sediment in a gravel-pit at Werder, near the Weser river, Lower Saxony (fig. 1). Fossil-rich sediments of Hemmoorian age, made up of shelly, glauconitic sands and sandy clays, occur at a depth of about 10-15 m below surface, at the base of the Pleistocene to Holocene filling of the Weser-Aller-Urstrom valley. Mixed with Pleistocene gravel and sand, these were sampled by underwater excavation. Hemmoorian sediments have also been cored in exploration wells a few km to the northwest of Werder (Ludwig, 1965).

The rich invertebrate fauna comprises cephalopods, lamellibranchs, gastropods, bryozoans, echinoids, solitary corals, balanids and decapod remains. Vertebrate fossils include elasmobranch teeth, otoliths (Hoedemakers, in prep.) and skeletal remains of marine mammals and sea turtles. The Werder locality stratigraphically correlates to the *Nassarius cimbricus* zone of the nassariid zonation (Gürs, 2002). The absence of *Nassarius coronatus* (MOSTAFAVI, 1978), the index species of the lowermost Hemmoorian, and the absence of *Nassarius bocholtensis* (BEYRICH, 1854), a common species of the Late Hemmoorian, from the Werder fauna (Gürs, pers. comm.), restricts the depositional age to the late Behrendorfian (early Hemmoorian, late Burdigalian). Micropaleontological data are not yet available. A limited account of the elasmobranch fauna of the early Hemmoorian at Werder, with emphasis on a few taxa, was given by

Reinecke *et al.* (2005). This study describes a new, small carcharhinid species which appears to be characteristic of Hemmoorian shallow-water faunas in the southwestern North Sea Basin.

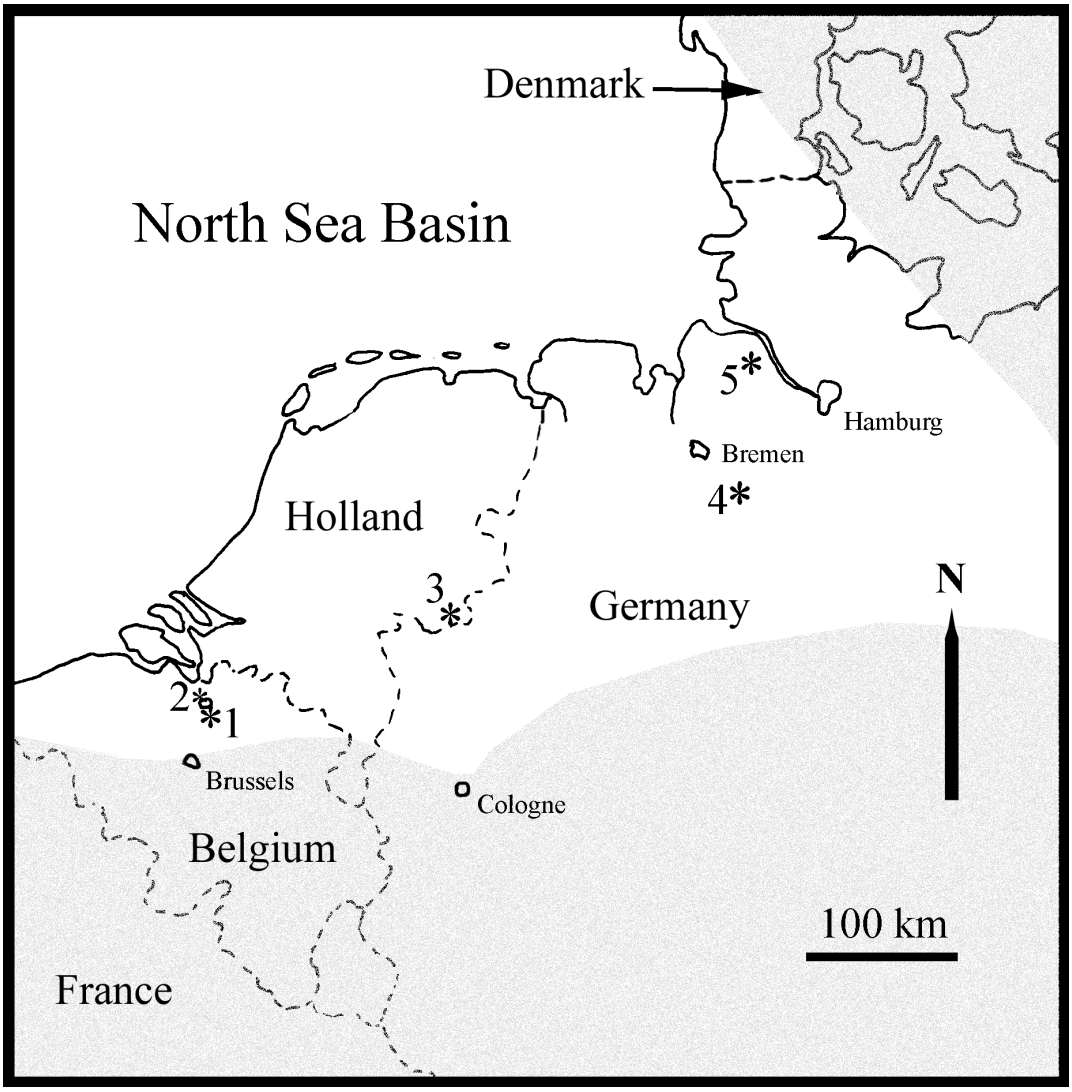


Figure 1.— Sketch map of localities mentioned in the text. 1. Wilrijk, Belgium; 2. City area of Antwerp, Belgium; 3. Winterswijk-Miste, The Netherlands; 4. Werder, Lower Saxony, Germany; 5. Rhaden/Lamstedt, Lower Saxony, Germany. Unshaded area shows the approximate extension of sea during the early to middle Miocene.

SYSTEMATIC PALEONTOLOGY

Order **CARCHARHINIFORMES** COMPAGNO, 1973
Family Carcharhinidae JORDAN & EVERMANN, 1896

Genus ***PHYSOGALEUS*** CAPPETTA, 1980

Sharks of the genus *Physogaleus* existed from the late Palaeocene to middle Miocene in tropical to temperate neritic marine environments. The genus includes several nominal species, with teeth typically ranging from ca. 6 to 15 mm in mesio-distal diameter. The dental characters of *Physogaleus* (type species: *P. secundus* (WINKLER, 1874)) as defined by Cappetta (1987: p. 124-125) are applicable with minor modifications (see below) to all known taxa. Details of crown shape and denticulation may vary considerably in teeth of comparable jaw positions collected from near-isochronous assemblages. These differences can partly be explained by supposed gynandric heterodonty. Perhaps only few of the various nominal species described from Late Palaeocene to Late Eocene deposits, i.e. *P. tertius* (WINKLER, 1876), *P. secundus* (WINKLER, 1876), *P. huberensis* (CASE, 1981), *P. americanus* CASE, 1994, *P. latecuspidatus* MÜLLER, 1999, *P. rosehillensis* CASE & BORODIN, 2000, can be recognized as valid species when a conservative taxonomic approach is adopted. *P. latus* (STORMS, 1894), mainly occurring in the Rupelian, was still present in the Early Miocene. *P. maltzani* (WINKLER, 1875) is presently only known from the Chattian of the North Sea basin (Reinecke *et al*., 2005).

Two species were hitherto described from Miocene sediments: *P. aralensis* KOZLOV, 2001, occurring in the Lower Miocene of the western Aral region, Kasakhstan (KOZLOV, 2001), and *P. singularis* (PROBST, 1878) in the Upper Marine Molasse, Ottnangian, Early Miocene, of southern Germany (Pfeil *in* Barthelt *et al*., 1991). The teeth of both species appear to be very similar to and are perhaps synonymous with *P. latus*.

Ward & Bonavia (2001) synonymized "*Galeocerdo*" *aduncus* AGASSIZ, 1835 with "*Galeocerdo*" *contortus* GIBBES, 1849 and referred it to the genus *Physogaleus*. Reinecke *et al*. (2005: p. 57-59) contradicted Ward & Bonavia´s opinion and assigned only the "*contortus*" morphotype to *Physogaleus*, while the "*aduncus*" morphotype should remain in the genus *Galeocerdo* (tiger sharks). Reinecke *et al*. argued that i) teeth from comparable jaw positions of the two groups have significant differences in some morphological parameters (maximum labio-lingual tooth thickness; apical crown angle; and relative lengths of the mesial and distal root lobes measured from the nutrient groove to the root margins), and ii) the very low abundance of *contortus*-type relative to *aduncus*-type teeth in Rupelian and Chattian and the lack of *contortus*-type teeth along with the common presence of *aduncus*-type teeth in Hemmoorian (Early Miocene) deposits of the North Sea Basin is in conflict with Ward & Bonavia´s (2001, p. 138) assumption "to regard them as either the product of dignathic or gynandric (sexual) heterodonty". If "*Galeocerdo*" *contortus* were correctly assigned to *Physogaleus*, the presence of serrated cutting edges should be included as possible characteristic of the genus.

Physogaleus hemmooriensis sp. nov.

(Pl. 1-4)

.1926 - *Carcharias* (*Scoliodon*) sp. - LERICHE, p. 432, text-fig. 196.

v1975 - *Paragaleus* sp. - VAN DEN BOSCH *et al*., p. 77 (not figured).

v1975 - *Galeorhinus* sp. - VAN DEN BOSCH *et al*., p. 77 (in part, not figured).

.1976 - *Galeorhinus* sp. - DE CEUSTER, p. 137, plate 6, figs 2, 4, 5, *non* 1, 3.

.1976 - *Paragaleus* sp. - DE CEUSTER, p. 140, plate 6, fig. 6.

v1978 - *Paragaleus* sp. - VAN DEN BOSCH, p. 135 (not figured).

.1987 - *Paragaleus* sp. - DE CEUSTER, p. 236, plate 4, fig. 4.

1994 - *Paragaleus* sp. - MENZEL *et al*., p. 13 (not figured).

.1998 - *Paragaleus* sp. - PURDY, p. 133, plate 2, fig. 6, *non* 7-9.

?1998 - *Rhizoprionodon* sp. PURDY, p. 133, plate 2, fig. 12.

Holotype: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main, SMF P9690, plate 2, fig. 1a-c, height: 6.0 mm, width: 5.5 mm.

Paratypes:

1. SMF P9691, plate 2, fig. 2a-c, height: 5.3 mm, width: 6.2 mm.
2. SMF P9692, plate 1, fig. 2, height: 5.1 mm, width: 3.8 mm.
3. SMF P9693, plate 1, fig. 3, height: 5.5 mm, width: 4.3 mm.
4. SMF P9694, plate 1, fig. 5a-d, height: 5.9 mm, width: 4.1 mm.
5. SMF P9695, plate 3, fig. 2a-c, height: 5.0 mm, width: 5.3 mm.
6. SMF P9696, plate 3, fig. 8a-c, height: 4.6 mm, width: 6.3 mm.

Derivatio nominis: after the Hemmoorian stage of the German and Danish part of the Miocene North Sea.

Locus typicus: Gravelpit "Krinke" near Werder, close to the Weser river, ca. 2 km south of Achim, Lower Saxony, Germany.

Stratum typicum: Early Hemmoorian, Behrendorfian, early Miocene, ? NN4.

Additional material: Wilrijk, at University hospital, Belgium, Edegem Sands Member, Berchem Formation: 1 tooth (Coll. Hoedemakers); Antwerp, Schelde tunnel, Belgium, Edegem Sands Member, Berchem Formation: 1 complete tooth (Coll. Naturalis, Leiden, No. 405093); Werder, Lower Saxony, early Hemmoorian: 224 complete and ca. 150 incomplete teeth (Coll. Reinecke); Rhaden, Lower Saxony, late Hemmoorian: 2 incomplete teeth (Coll. Reinecke).

Ticheloven Farm, Eibergen-Loo, The Netherlands, Miste Bed, Aalten Member, Breda Formation, late Hemmoorian: 1 tooth (Coll. Naturalis, Leiden, unnumbered); Winterswijk-Miste, The Netherlands, Miste Bed, Aalten Member: 31 complete and ca. 40 incomplete teeth (Coll. Reinecke); Winterswijk-Miste, Miste Bed: 12 teeth (Coll. Naturalis, Leiden, No. 405605, 405608, 405618); Hemmoorian of the Peel region (borings), The Netherlands: 6 teeth (Coll. Naturalis, Leiden, No. 156163, 156164-156167, 156170); Antwerp-Borgerhout, entry to motorway/Antwerp ringroad, Belgium,

Antwerpen Sands Member, *Cordiopsis/Cyrtodaria* Bed (20 cm above base), Berchem Formation: 9 teeth (Coll. Hoedemakers); Antwerp-Pelikaanstreet, Belgium, Antwerpen Sands Member, *Cordiopsis/Cyrtodaria* bed (20 cm above base), Berchem Formation: 27 teeth (Coll. Hoedemakers); Antwerp-Copernicusstreet-Lange Kievitstreet, Belgium, Antwerpen Sands Member, *Panopea* Bed, Berchem Formation: 2 teeth (Coll. Hoedemakers).

Wilrijk (n = 1)	medial	anterior	upper antero-lateral	lower antero-lateral
height:	-	-	-	2,5
width:	-	-	-	3.9
thickness:	-	-	-	0.9

Werder (n = 209)	medial	anterior	upper antero-lateral	lower antero-lateral
height:	3.2-4.9	3.5-6.8	2.4-7.0	2.1-5.9
width:	2.0-3.7	2.5-5.8	3.2-6.6	2.4-7.7
thickness:	1.2-1.9	1.6-2.9	0.9-2.2	0.7-2.5

Miste (n = 29)	medial	anterior	upper antero-lateral	lower antero-lateral
height:	2,2	3.2-5.2	2.2-4.7	2.5-4.2
width:	1,7	2.2-4.3	3.3-4.9	2.4-4.9
thickness:	0,9	1.0-2.0	0.8-1.6	1.0-1.3

Antwerp (n = 25)	medial	anterior	upper antero-lateral	lower antero-lateral
height:	-	-	3.8-5.8	3.9-5.9
width:	-	-	4.3-6.3	4.0-6.0
thickness:	-	-	1.1-2.3	1.3-1.7

Table1.— Measurements (mm), see fig. 1a-c for teeth from Werder.

Morphological characteristics

Medial teeth

Teeth from medial files are up to 5 mm high and 3.7 mm wide, and have a nearly symmetrical crown with an upright, pointed principal cusp (plate 1, figs 8-10). The cusp is lingually inclined. On the heels, 1-2 or rarely 3 pairs of low, triangular cusplets are present. The labial crown base is almost flat or forms a slightly convex overhang. The root has a pronounced lingual bulge (protuberance), but is rather thin at the marginal heels. Medial teeth tend to be smaller in size (height and width) than anterior and antero-lateral teeth (fig. 2a). Their height-to-width ratio (fig. 2a) and depth-to-width ratio (fig. 2b; depth = maximum labio-lingual diameter perpendicular to tooth height) is similar to that of anterior teeth.

Anterior teeth (without clear assignment to upper or lower jaw)

Teeth with a slender, acute main cusp, narrow to broad heels and a thick root (plate 1, figs 1-7). The labio-lingual diameter of the principal cusp at its base equals or exceeds the mesio-distal diameter. The main cusp is strongly bent lingually and forms an angle of 45-60° with the basal face of the root. The distal inclination of the cusp is variable; it tends to be higher in teeth with a broader root base.

The labial and lingual crown faces are smooth, lacking ornamentation. The labial crown face is convex. The curvature of the lingual face is strong, displaying subparallel marginal faces near the crown base. The basal labial crown overhang is weak. The cutting edges continuously extend from the apex to the margins of the heels, which form high ridges with labio-lingually narrow, convex faces. The cutting edges of the ridges are smooth; they pass into the margins with a convex bow (plate 1, figs 4a, 5a, 7a) or form a broad cusplet on the distal heel (e.g. plate 1, figs 2, 6a). In occlusal view, the distal heel and, less commonly, the mesial heel is recurved lingually. In labial and mesial view, the mesial cutting edge of the main cusp shows a sigmoid, flexuous course. The distal cutting edge is straight to convex; its curvature is less flexuous than the mesial cutting edge.

The root lobes meet at an angle of 180° and are hardly separated. In the most anterior teeth (plate 1, figs 1-4) the root is as wide as labio-lingually thick. In more lateral files (plate 1, figs 5-7) the root width increases, whereas its thickness remains almost unchanged. Generally, the root is asymmetric and has the shape of a distally inclined parallellogram, whose mesial and distal flanks are constricted. The lingual bulge is very thick and salient and forms the solid base of the robust crown (see above).

The basal root face is convex in teeth of the most anterior files (plate 1, fig. 1) and rather flat or irregularly shaped in teeth of more lateral files. The nutrient groove is variably deep and contains one to three larger foramina, sometimes also additional smaller foramina. The paratypes 2, 3 and 4 show the characteristics of anterior teeth.

Anterior teeth tend to show higher height-to-width ratios (fig. 2a) than antero-lateral teeth. Anterior teeth clearly differ from antero-lateral teeth by a higher depth-to-width ratio (fig. 2b) mainly because of their thicker root.

Antero-lateral teeth of the upper jaw

Teeth with a slender, sigmoid principal cusp on a broad base, with low, but distinct cusplets on the distal heel and a moderately thick and low root (plate 2, figs 1-11). The cusp is inclined at 70 to 45° in distal direction. The inclination of the cusp moderately increases while the teeth become lower towards the commissure. The crown faces are smooth and convex, the lingual face being much more convex than the labial one, but not as extreme as in the anterior files. In profile or occlusal view, the teeth show a flexuous labial crown face, characterised by a subcircular bulge at the base, a thin, labially recurved crown tip and a sigmoid bend of the mesial cutting edge (plate 2, figs 1b, 2b, 8b).

The mesial cutting edge runs smoothly from the apex to the outer margin of the mesial heel. Some notches or low cusplets rarely occur at the outer mesial heel. The

distal cutting edge of the cusp is slightly convex, sometimes even straight or sigmoid.

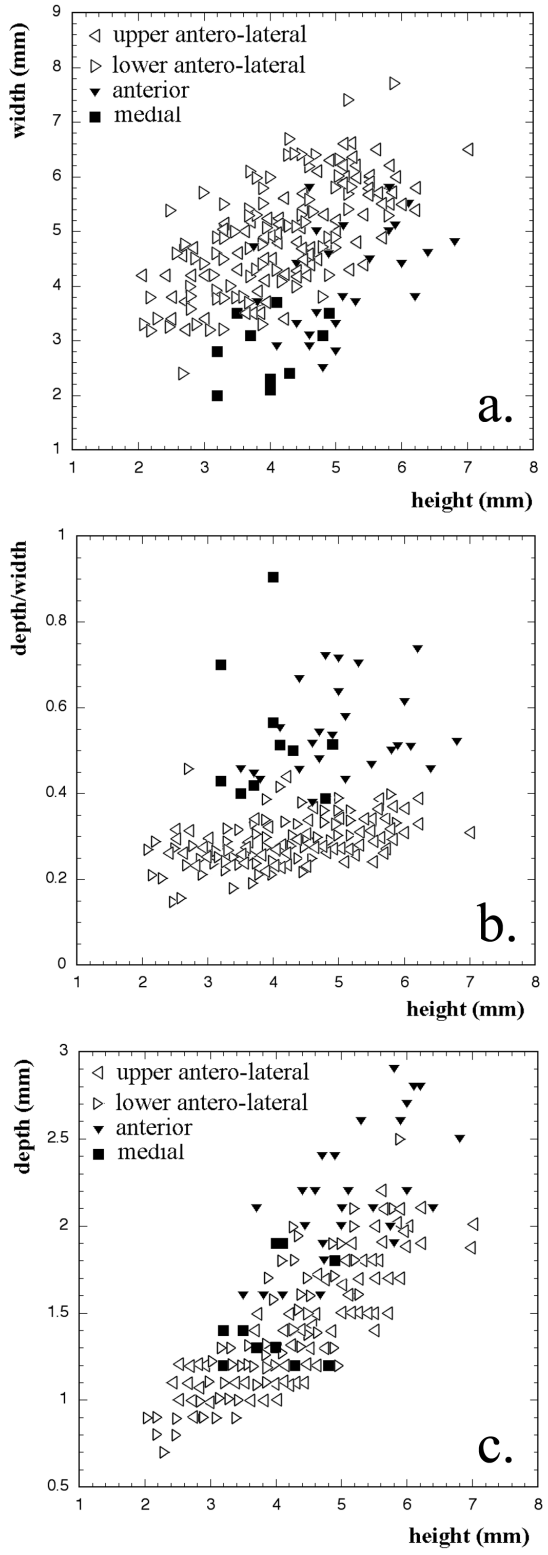


Figure 2.— Tooth dimensions of *Physogaleus hemmooriensis* sp. nov. from Werder, Lower Saxony, Germany. **a.** width versus height, **b.** depth-over-width ratio versus height, **c.** depth (= labio-lingual thickness) versus height.

Separated from the cusp by a concave or acute notch, the distal heel bears two or three (rarely up to five) low cusplets which are distally inclined and decrease in size distally.

The root is only slightly broader than the crown base. It is moderately strong and rather low. Its lingual bulge is less developed than in anterior teeth. Labially, the root is weakly concave, whereas its basal face is almost flat. Lingually, the crown-root junction is marked by a transversal groove. 1-2 foramina join the nutrient groove, which is open and rather flat. Numerous small foramina may also be present along the base of the labial and lingual root faces.

The holotype (plate 2, fig. 1a-c), an upper left antero-lateral tooth, shows a high, narrow cusp that is inclined at an angle of 50° toward the commissure. The mesial cutting edge has a sigmoid outline, whereas the distal cutting edge is straight to slightly convex near the apex. The tooth has broad heels. Three low cusplets, well separated from the main cusp, are present on the distal heel.

Antero-lateral teeth of the lower jaw

The antero-lateral teeth of the lower jaw (plate 3, figs 1-12) resemble the teeth of the upper jaw, except for the following features: the mesial cutting edge is markedly concave and the crown tip is generally directed upward. Some teeth may have a minor bend in the course of the mesial cutting edge (plate 3, fig. 2). The mesial heel is relatively wider and less inclined than in comparable upper teeth. Teeth from very lateral and postero-lateral files have an almost vertical distal cutting edge which in combination with the strongly concave mesial edge gives the teeth a hook-like shape. The cusplets on the distal heel tend to be lower and less regular than in upper files. Rarely, cusplets are lacking and a low, straight or convex enamel board is present on the distal heel. In teeth of the lower jaw the labial crown face is less flexuous than in those of the upper jaw, i.e. the crown tip is straight or only slightly bent in lingual direction. A labial recurvature of the crown tips is only seen in the most anterior files (plate 3, figs 1, 2). The paratypes 5 and 6 are antero-lateral teeth of the lower jaw. Lower und upper antero-lateral teeth have quite similar dimensions (fig. 2a-c).

Differential diagnosis

In the North Sea Basin, the genus *Physogaleus* is present from the Thanetian, late Paleocene (e.g. Smith, 1999) with the following species: *P. secundus* (WINKLER, 1874) in the Paleocene and Eocene, *P. latus* (STORMS, 1894) in the Rupelian, *P. maltzani* (WINKLER, 1875) in the Chattian and *P. hemmooriensis* in the Hemmoorian.

There is a decrease in mean and maximum tooth size (height and width of antero-lateral teeth) from the Rupelian *P. latus* to the Chattian *P. maltzani* and the Hemmoorian *P. hemmooriensis* (fig. 3a, b). The dimensions of *P. secundus* are similar to that of *P. latus.*

Among the three species occurring in the Paleogene, *P. maltzani* is most similar to *P. hemmooriensis*. Anterior antero-lateral teeth of *P. hemmooriensis* have sigmoid cusps similar to those of *P. maltzani*, but their main cusps are normally narrower and

relatively higher (*i.e*. more pointed) than those of *P. maltzani* [compare plate 2, fig. 1 and 3 (upper jaw of *P. hemmooriensis*) and plate 3, figs 1-2 (lower jaw of *P. hemmooriensis*) of this study with plate 42, figs 4-5 (upper jaw of *P. maltzani*, Reinecke *et al*., 2005) and plate 40, fig. 11 (lower jaw of *P. maltzani*; Reinecke *et al*., 2005)]. In *P. maltzani*, distorted teeth with upright to inclined, needle-shaped cusps that are characteristic of the most anterior files in *P. hemmooriensis* (plate 1, figs 1-7) appear to be absent. This is unlikely to be due to an incomplete record of corresponding teeth of *P. maltzani*. We rather conclude that *P. hemmooriensis* developed a more differentiated clutching-cutting-type dentition than the Eocene to Oligocene species of *Physogaleus* which show less pronounced heterodonty (see Reinecke *et al*., 2005: text-fig. 14e-f). Rather long and pointed cusps are present also in the more lateral files of *P. hemmooriensis* (see plate 2, figs 5-6, 8-9 for upper and plate 3, figs 3, 6-8, 10 for lower teeth). They clearly differ from the broader cusps of *P. maltzani* (Reinecke *et al*., 2005: plates 43 and 41) and *P. latus* (Reinecke *et al*., 2001: plates 46 and 47). In the most lateral files close to the commissure, however, the different species cannot be distinguished.

Teeth of *P. secundus* and *P. latus* generally have broader, shorter cusps in a less differentiated gradient-heterodont dentition. Their mesial cutting edge is less concave in lower antero-lateral teeth and slightly convex rather than sigmoid in the first upper antero-lateral files.

Discussion

Comparison of *P. hemmooriensis* with Miocene to Recent taxa of *Sphyrna*, *Galeorhinus*, *Paragaleus*, *Chaenogaleus* and *Scoliodon*:

In the Hemmoorian, small hemigaleid, sphyrnid and triakid teeth are occasionally found together with those of *P. hemmooriensis*. Sphyrnid teeth are commonly present in early to late Hemmoorian sediments. They can be clearly distinguished from *P. hemmooriensis* by their larger size and the smooth, convex cutting edge of the distal heel. Teeth of *Galeorhinus*, morphologically close to the late Miocene *Galeorhinus goncalvesi* ANTUNES, BALBINO & CAPPETTA, 1999 and the extant *G. galeus* (LINNAEUS, 1758), differ from *P. hemmooriensis* by having shorter cusps and a marked overhang of the labial crown base. The hemigaleid genera *Chaenogaleus* and *Paragaleus* are represented in the Hemmoorian by taxa close to *Chaenogaleus affinis* (PROBST, 1878) and *Paragaleus antunesi* BALBINO & CAPPETTA, 2000. Their teeth differ by some morphological features from *P. hemmooriensis*: the relatively shorter and more upright cusp, the higher distal heel (equipped with 4-8 sharp cusplets) in upper antero-lateral files, the more upright cusp, the much stronger basal labial overhang, and occasional mesial cusplets in lower antero-lateral files (compare e.g. Balbino & Cappetta, 2000: plates 1 and 2; Cappetta, 1987: figs 101a-f).

Teeth of the extant *Scoliodon laticaudus* MÜLLER & HENLE, 1838 (Springer, 1964: fig. 3; Compagno, 1988: plates 22b, c and 23b, c; Herman *et al*., 1991: plates 27 and 28) resemble those of *P. hemmooriensis* with respect to morphology and gradient heterodonty, especially in male dentitions. Significant differences are also noticed: the stronger distal inclination of the principal cusp in anterior files, the lack of a clear mesial heel in anterior files and of a distal blade in lower anterior files of males, and the

absence of cusplets on the distal heel of male and female teeth of *S. laticaudus*.

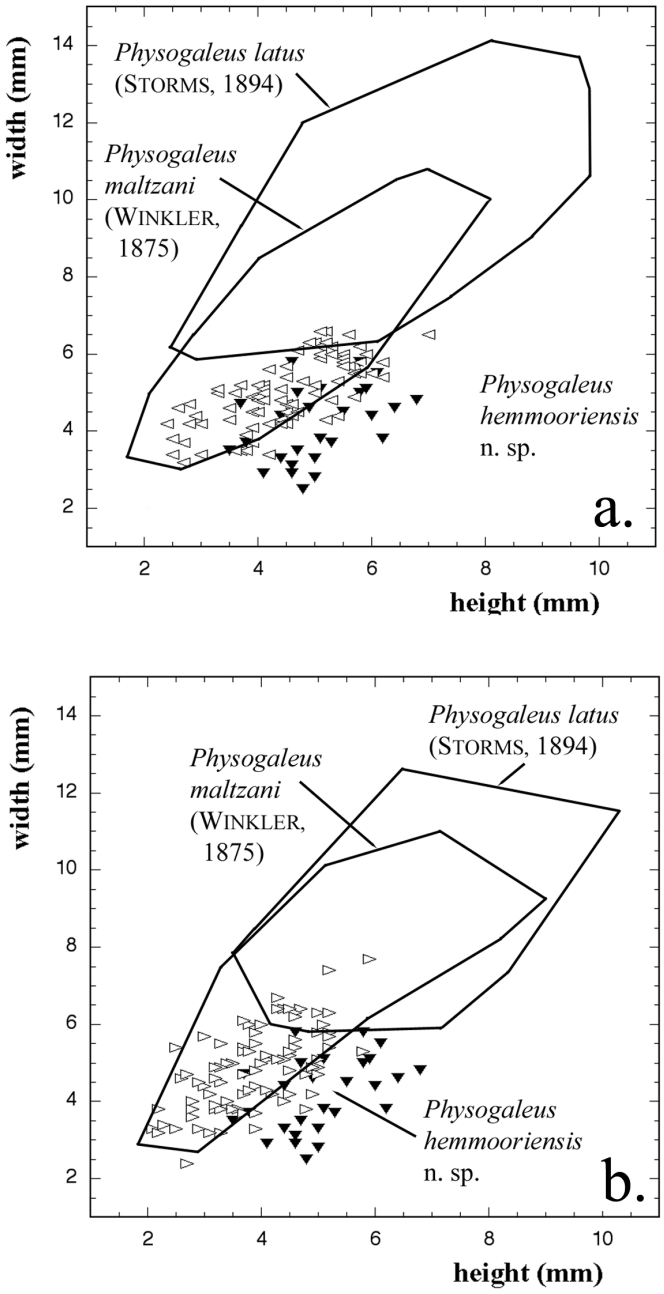


Figure 3.— Tooth dimensions (width versus height) of *Physogaleus hemmooriensis* sp. nov. compared with that of *Physogaleus maltzani* (WINKLER, 1875) (Sternberger Gestein, Sülstorf Beds, Chattian; data from Reinecke *et al*., 2005, text-fig. 14) and *Physogaleus latus* (STORMS, 1894) (Alzey Formation and Boom Clay Formation, Rupelian; data from Reinecke *et al*., 2005: text-fig. 14). **a.** upper antero-lateral and anterior teeth, **b.** lower antero-lateral and anterior teeth. Dimensions of anterior teeth of *P. hemmooriensis* (not attributable to upper or lower dentitions) are shown in a. and b.

Review of Miocene *Scoliodon*, *Physodon*, *Paragaleus*, *Rhizoprionodon* and *Galeorhinus* teeth referable to *Physogaleus hemmooriensis*

Teeth from the Miocene of Central Europe and North America with morphological characteristics similar to *P. hemmooriensis* have been assigned by different authors to *Paragaleus*, *Physogaleus*, *Scoliodon* or *Galeorhinus*. These teeth, however, are sometimes referable to *P. hemmooriensis* based on comparison of teeth from our own and museum collections.

Leriche (1926: p. 432) described a lower lateral tooth as *Carcharias* (*Scoliodon*) sp. from the Antwerpen Sands Member, Hemmoorian. His figure (text-fig. 196) and description closely correspond to our material (compare e.g. plate 3, fig. 8 of this study). The tooth is therefore referred to *P. hemmooriensis*. Leriche pointed out the similarity of the fossil tooth with lower lateral teeth of the extant *Scoliodon laticaudus*, but lacking fossil teeth from other jaw positions he could not present any details.

From the Antwerpen Sands Member at Berchem, Belgium, De Ceuster (1987: plate 4, fig. 4a, b) figured an upper antero-lateral tooth as *Paragaleus* sp., which we refer to *P. hemmooriensis*. According to De Ceuster´s table 1, *Paragaleus* sp. appears to be quite rare in the Antwerpen Sands Member. Among the teeth described by De Ceuster (1976) from the "post Miocene gravel bed" in the Rumst-Terhagen region, south of Antwerp, the complete teeth figured as *Galeorhinus* sp. (plate 6, fig. 4) and *Paragaleus* sp. (plate 6, fig. 6) have to be assigned to *P. hemmooriensis* because of shape and size. In addition, some damaged teeth (plate 6, figs 2, 5) as well as the crown fragment (fig. 7, figured as *Scoliodon taxandriae* LERICHE, 1926) may be referable to the new taxon.

Specimens of *P. hemmooriensis* from the Edegem Sands Member, Berchem Formation, at Wilrijk (plate 4, fig. 9) and the E3 Schelde tunnel in Anwerp, Belgium (coll. Naturalis, Leiden), from the Antwerpen Sands Member, Berchem Formation, collected in the area of Antwerp city (plate 4, figs 5-8), are indistinguishable by morphology and dimensions from the teeth collected at the type locality (plates 1-3).

The unfigured and undescribed teeth of *Paragaleus* sp. and *Galeorhinus* sp. (in part) reported by Van Den Bosch (1978) and Van Den Bosch *et al*. (1975: p. 77) from the Miste Bed, Aalten Member, late Hemmoorian (Oxlundian) at Winterswijk-Miste actually belong to *P. hemmooriensis*. The teeth, now kept in the collections of the Nationaal Natuurhistorisch Museum Naturalis in Leiden, are indistinguishable from our own specimens collected at the same locality (plate 4, figs 1-4) and are within the morphological variation and size range observed in the larger population at Werder.

Menzel *et al*. (1994) reported *Paragaleus* sp. from a clay boulder of late Hemmoorian age found in the open pit of the LECA GmbH at Rhaden/Lamstedt, near Hemmoor, Lower Saxony (fig. 1). Two teeth from Rhaden donated by H. Schieck confirm their identity with *P. hemmooriensis*.

A nominal species with possible relationship to *P. hemmooriensis* was described as *Carcharinus* (*Physodon*) *beckersi* by Van De Geyn (1937: p. 320-321, plate 12, figs 4-11) from the ? late Miocene Elsloo conglomerate, Limburg, The Netherlands. The specimens (Cat. No. 20533) are kept at the Nationaal Natuurhistorisch Museum (Naturalis) in Leiden, except for the two specimens of figs 5 and 9 (holotype) which are

not available and are possibly lost. Morphologically, *Carcharinus* (*Physodon*) *beckersi* has the characteristics of *Physogaleus* CAPPETTA, 1980 and should be assigned to that genus. All teeth are worn and polished (reworked), moreover two of them are damaged at the mesial crown base (figs 4, 6). With a tooth height of 5.6 mm (fig. 8) to 9.1 mm (fig. 10) and a width of 4.9 (fig. 8) to 10.3 mm (fig. 11) teeth of *C. beckersi* are higher and wider than those of *P. hemmooriensis*. Furthermore, the crown and root of *Carcharinus* (*Physodon*) *beckersi* are stouter and labio-lingually thicker than that of *P. hemmooriensis*, even when the larger tooth dimensions are considered. By its chararacters *Carcharinus* (*Physodon*) *beckersi* resembles the Eocene taxon *Physogaleus secundus* (WINKLER, 1876). We conclude that these specific teeth are probably reworked from Eocene strata and hence *Carcharinus* (*Physodon*) *beckersi* is a junior synonym of *Physogaleus secundus*.

Probst (1878: plate 1, figs. 5-6) described two teeth from the Upper Marine Molasse, Ottnangian, Early Miocene, of Baltringen, southern Germany, as *Carcharias (Hypoprion) singularis*. Pfeil *in* Barthelt *et al*. (1991: p. 204) assigned the teeth to *Physogaleus*. In the Probst collection, housed at the Institute of Geological Sciences, University of Tübingen, we found a fragment of the specimen figured in Probst´s fig. 6, whereas the other syntype (fig. 5) is obviously lost. The fragmentary specimen and the figures of Probst (1878) do not show the characters of *P. hemmooriensis*, but appear to be morphologically close to *P. latus* (sensu lato).

Purdy (1998: plate 2, fig. 6) figured a broad-based tooth with a slender, curved cusp from the Cheswold Sands of the early Miocene Calvert Formation at Pollack Farm site, Delaware, which he called *Paragaleus* sp. By size and dental morphology the figured tooth is within the range of upper antero-lateral teeth of *P. hemmooriensis* from the Hemmoorian. Another specimen, called *Rhizoprionodon* sp. (plate 2, fig. 12), may be a lower lateral of *P. hemmooriensis*. Other teeth assigned by Purdy to *Paragaleus* sp. (plate 2, figs 7-8) do not match the gradient heterodonty of *P. hemmooriensis*, and may belong to *Carcharhinus* spp.

The early Miocene Pungo River Formation at Lee Creek Mine, Aurora, North Carolina, has produced teeth, which Purdy *et al*. (2001, pp. 141-142, fig. 45) also identified as *Paragaleus* sp., but clearly have the characters of *Physogaleus*. Among the figured teeth, we do not see the lower lateral morphotype of *P. hemmooriensis* with its slender cusp and concavely curved mesial cutting edge. Superficially, the teeth from Lee Creek Mine with their distorted cusps and distal cusplets are similar to our material, but the photographic views and the description do not permit a detailed comparison. Thus, the specimen from Pollack Farm Site (Purdy, 1998: plate 2, fig. 6) appears to be at present the only reliable record of *P. hemmooriensis* in the Western Atlantic region.

Stratigraphic distribution

At present, we do not know of any teeth of *P. hemmooriensis* from Vierlandian sediments (Vierlandian: lowermost stage of the Danish and German part of the Miocene North Sea, corresponding to the Aquitanian and early Burdigalian; STD, 2002). It appears that this species immigrated into the Miocene North Sea during the early Hemmoorian transgression, as it first occurs in the early Hemmoorian of Werder, Lower

Saxony, and the Edegem Sands Member in the area of Antwerp. The teeth from the Antwerpen Sands Member (De Ceuster, 1987) which has a late Hemmoorian to Reinbekian age (but was largely deposited during late Hemmoorian) and from the Miste Bed, Aalten Member, of the eastern Netherlands indicate the last occurrence of *P. hemmooriensis* in the Miocene North Sea. Van Den Bosch (1978: Table 1, p. 135) did not report *Paragaleus* sp., i.e. *Physogaleus hemmooriensis*, from the Stemerdink Bed, Aalten Member, Reinbekian, overlying the Miste Bed, and the taxon appears to be absent also from all other known Reinbekian to Syltian elasmobranch faunas.

From the Calvert Formation at the Pollack Farm Site, Delaware, Benson (1998) reported a radiolarian assemblage indicative of the late early Miocene (Burdigalian) *Stichocorys wolffii* zone which has an estimated range of 17.3-19.2 Ma. The presence of *P. hemmooriensis* at this site is almost contemporaneous with its occurrence in the Hemmoorian (ca. 15.5 to 19 Ma; STD, 2002) of the North Sea basin.

ACKNOWLEDGEMENTS

We thank Siegfrid Krinke for the permission to enter his gravelpit. Reinier van Zelst and Dr. Lars van den Hoek Ostende at the Nationaal Natuurhistorisch Museum Naturalis in Leiden have kindly shown us the elasmobranch teeth collection and made available the type specimens of *Carcharinus (Physodon) beckersi* Van De Geyn, 1937. We thank Dr. Karl Gürs, LANU Schleswig-Holstein, for biostratigraphic age determination of the Werder molluscan fauna; Dr. Hartmut Schulz, Institute of Geological Sciences, University Tübingen, for giving access to the Probst collection; Dr. Dirk Nolf, IRSNB, Brussels, for allowing us to compare our material with Herman *et al.*´s (1991) material of *Scoliodon laticaudus*; and Dr. Robert Purdy, Smithsonian Institution, for detailed figures of a tooth from Pollack Farm Site. Hartmut Schieck has kindly provided some teeth from Rhaden/Lamstedt. The reviews of the manuscript by David J. Ward, Orpington, and Dr. Henri Cappetta, Montpellier, are much appreciated. Finally, we wish to commemorate our late friend Michael Möller who made his Miste collection available to the first author.

REFERENCES

ANTUNES, M. T., BALBINO, A. C. & CAPPETTA, H., 1999. — A new shark, Galeorhinus goncalvesi nov. sp. (Triakidae, Carcharhiniformes) from the latest Miocene of Portugal. *Tertiary Research*, **19**: 101-106, 3 fig., 1 pl.

BALBINO, A. C. & CAPPETTA, H., 2000. — *Paragaleus antunesi* (Hemigaleidae, Carcharhiniformes) a new shark species from the latest Miocene of Portugal. *Tertiary Research*, **20**: 1-6, 3 fig., 2 pl.

BARTHELT, D., FEJFAR, O., PFEIL, F.H. & UNGER, E., 1991. — Notizen zu einem Profil der Selachier-Fundstelle Walbertsweiler im Bereich der miozänen Oberen Meeresmolasse Süddeutschlands. *Münchner Geowissenschaftliche Abhandlungen*, **19**: 195-208, 3 fig., 4 pl.

BENSON, R. N., 1998. — Radiolarians and diatoms from the Pollack Farm Site, Delaware: marine-terrestrial correlation of Miocene vertebrate assemblages of the middle Atlantic Coastal Plain. In: *Geology and paleontology of the Lower Miocene Pollack Farm fossil site, Delaware* (R.N. BENSON, ed.). *Delaware Geological Survey*, *Special Publications*, **21**: 5-19, 8 fig., 1 tab.

CAPPETTA, H.,1980. — Modification du statut générique de quelques espèces de sélaciens crétacés et tertiaires. *Palaeovertebrata*, **10**: 29-42, 6 fig.

CAPPETTA, H., 1987. — Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. In: *Handbook of Paleoichthyology* (H.-P. SCHULTZE, ed.), 193 p., 148 fig., Gustav Fischer Verlag, Stuttgart.

CASE, G.R., 1981. — Late Eocene Selachians from south-central Georgia. *Palaeontographica*, **A176**: 52-79, 9 fig., 9 pl., 3 tab.

CASE, G.R., 1994. — Fossil fish remains from the Late Palaeocene Tuscahoma and Early Eocene Bashi Formations of Meridian, Lauderdale County, Mississippi. *Palaeontographica*, **A230**: 97-138, 6 fig., 15 pl., 5 tab.

CASE, G.R. & BORODIN, P.D., 2000. — A Middle Eocene Selachian Fauna from the Castle Hayne Limestone Formation of Duplin County, North Carolina. *Münchner Geowissenschaftliche Abhandlungen*, A39, 33-46, 1 fig., 7 pl.

COMPAGNO, L.J.V., 1988. — Sharks of the Order Carcharhiniformes. pp. i-xxii + 1-486, 21 fig., 35 pl., 7 tab., Princeton University Press, Princeton, New Jersey.

DE CEUSTER, J., 1976. — Stratigraphische interpretatie van jong-cenozoische afzettingen bij Rumst (Belgie, Provincie Antwerpen) en beschrijving van de in een post-Mioceen basisgrind aangetroffen vissenfauna. II. Systematische beschrijvingen en conclusies. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, **13**: 119-172, 1 fig., 7 pl., 5 tab.

DE CEUSTER, J., 1987. — A little known odontaspidid shark from the Antwerp Sands Member (Miocene, Hemmoorian) and some stratigraphical remarks on the shark-teeth of the Berchem Formation (Miocene, Hemmoorian) at Antwerp (Belgium). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, **24**: 231-246, 1 fig., 4 pl., 1 tab.

GÜRS, K., 2002. — Miocene Nassariid Zonation - a new tool in North Sea Basin Neogene biostratigraphy. *Northern European Cenozoic Stratigraphy, Proceedings of the 8th Biannual Meeting RCNNS/RCNPS*, Flintbek, pp. 91-106, 2 fig., 3 pl.

HERMAN, J., HOVESTADT-EULER, M. & HOVESTADT, D.C., 1991. — Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. Part A: Selachii. No. 2c: Order Carcharhiniformes, Families Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae. *Bulletin de l´Institut Royal des Sciences Naturelles de Belgique*, *Biologie*, **61**: 73-120, 1 fig., 29 pl.

KOZLOV, V.A., 2001. — Novyi vid carcharhinidnych akul iz niznemiozenovych otlozenii sapadnogo Priaral´ja (in Russian). *Materialy po Stratigrafii i Paleontologii Urala*, **6**: 92-95, 2 pl.

LERICHE, M., 1926. — Les poissons néogènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **32**: 369-472, 228 fig., 15 pl.

LUDWIG, G., 1965. — Untersuchungen zur Geologie, Petrographie und Sedimentologie der Eisenerzlagerstätte von Achim-Horstedt südöstlich von Bremen. *Geologisches Jahrbuch*, **83**: 235-276, 5 fig., 13 pl., 10 tab.

MENZEL, H., GEORGE, P. & SCHIEK, H., 1994. — Eine miozäne Scholle aus der Tongrube in Rhaden bei Lamstedt. *Der Aufschluss*, **45**: 11-25, 2 fig., 4 pl.

MÜLLER, A., 1999. — Ichthyofaunen aus dem atlantischen Tertiär der USA. *Leipziger Geowissenschaften*, **9**/**10**: 1-360, 69 fig., 17 pl., 6 tab.

PROBST, J., 1878. — Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen. Hayfische (Selachoidei A. GÜNTHER). *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **34**: 113-154, 1 pl.

PURDY, R.W., 1998. — The early Miocene fish fauna from the Pollack farm site, Delaware. In: Geology and paleontology of the Lower Miocene Pollack Farm fossil site, Delaware (R.N. BENSON, ed.). *Delaware Geological Survey, Special Publications*, **21**: 133-139, 2 pl.

PURDY, R.W., SCHNEIDER, V.P., APPLEGATE, S.P., MCLELLAN, J.H., MEYER, R.L. & SLAUGHTER, B.H., 2001. — The neogene sharks, rays, and bony fishes from Lee Creek Mine,

Aurora, North Carolina. In: Geology and Paleontology of the Lee Creek Mine, North Carolina (C.E. RAY, D.J. BOHASKA, eds), *Smithsonian Contributions to Paleobiology*, **90**: 71-202, 84 fig., Washington D.C.

REINECKE, T., STAPF, H. & RAISCH, M., 2001. — Die Selachier und Chimaeren des Unteren Meeressandes und Schleichsandes im Mainzer Becken (Rupelium, Unteres Oligozän). *Palaeontos*, **1**: 1-73, 8 fig., 63 pl., 2 tab.

REINECKE, T., MOTHS, H. & GRANT, A. & BREITKREUTZ, H., 2005. — Die Elasmobranchier des Norddeutschen Chattiums, insbesondere des Sternberger Gesteins (Eochattium, Oberes Oligozän). *Palaeontos*, **8**: 1-134, 15 fig., 60 pl., 3 tab.

SMITH, R., 1999. — Elasmobranches nouveaux de la transition Paléocene-Eocène de Dormaal (Belgique). *Bulletin de l´Institut royal des Sciences Naturelles de Belgique*, **69**: 173-185, 2 fig., 2 pl.

SPRINGER, V.G., 1964. — A revision of the carcharhinid shark genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*. *Proceedings of the United States National Museum*, *Smithsonian Institution*, **115**: 559-632, 14 fig., 17 tab.

STD, 2002. — Stratigraphische Tabelle von Deutschland (STD 2002), Karte mit Beiheft, 16 S., Deutsche Stratigraphische Kommission 2002, Geoforschungszentrum Potsdam.

STORMS, R., 1894. — Troisième note sur les poissons du terrain Rupélien. *Bulletin de la Société belge de Géologie, de Paléontologie et d´Hydrologie*, Mémoir VIII: 67-82, 1 pl.

VAN DE GEYN, W.A.E., 1937. — Das Tertiär der Niederlande mit besonderer Berücksichtigung der Selachierfauna. *Leidsche Geologische Mededelingen*, **9**: 177-362, 15 pl., 5 tab.

VAN DEN BOSCH, M., 1978. — On shark teeth and scales from the Netherlands and the biostratigraphy of the Tertiary of the eastern part of the country. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, **15**: 219-136, 1 tab.

VAN DEN BOSCH, M., CADÉE, M.C. & JANSSEN, A.W., 1975. — Lithostratigraphical and biostratigraphical subdivision of Tertiary deposits (Oligocene - Pliocene) in the Winterswijk-Almelo region (eastern part of the Netherlands). *Scripta Geologica*, **29**: 1-167, 36 fig., 23 pl., 10 tab.

WARD , D.J. & BONAVIA, C.G., 2001. — Additions to, and a review of, the Miocene shark and ray fauna of Malta. *The Central Mediterranean Naturalist*, **3**: 131-146, 3 fig., 2 pl.

WINKLER, T.C., 1875. — Beschreibung einiger fossiler Tertiaer-Fischreste, vorzugsweise des Sternberger Gesteins. *Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg*, **29**: 97-129, 3 pl.

WINKLER, T.C., 1876. — Deuxième mémoire sur les dents de poissons fossiles du terrain bruxellien. *Archives du Musée Teyler*, **4**: 16-48, 7 fig., 2 pl.

PLATE 1

IRSNB: Institut royal des sciences naturelles de Belgique, Brussels;

SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main.

Physogaleus hemmooriensis sp. nov., Behrendorfian, Lower Hemmoorian, Werder.

fig. 1: anterior tooth, H = 4.8 mm, W = 2.5 mm, a. labial view, b. profile view, SMF P9698.

fig. 2: ? upper anterior tooth, H = 5.1 mm, W = 3.8 mm, labial view, SMF P9692, paratype 2.

fig. 3: ? upper anterior tooth, H = 5.5 mm, W = 4.3 mm, labial view, SMF P9693, paratype 3.

fig. 4: upper anterior tooth, H = 6.0 mm, W = 4.4 mm, a. labial view, b. mesial view, c. lingual view, SMF P9699.

fig. 5: upper anterior tooth, H = 5.9 mm, W = 5.1 mm, a. labial view, b. mesial view, c. lingual view, SMF P9694, paratype 4.

fig. 6: lower anterior tooth, H = 6.8 mm, W = 4.8 mm, a. labial view, b. mesial view, c. lingual view, SMF P9700.

fig. 7: upper anterior tooth, H = 5.8 mm, W = 5.8 mm, a. labial view, b. mesial view, c. basal view, d. distal view, SMF P9701.

fig. 8: medial tooth, H = 3.5 mm, W = 3.5 mm, labial view, SMF P9702.

fig. 9: medial tooth, H = 3.7 mm, W = 3.1 mm, a. labial view, b. profile view, SMF P9703.

fig. 10: medial tooth, H = 4.1 mm, W = 3.7 mm, labial view, SMF P9704.

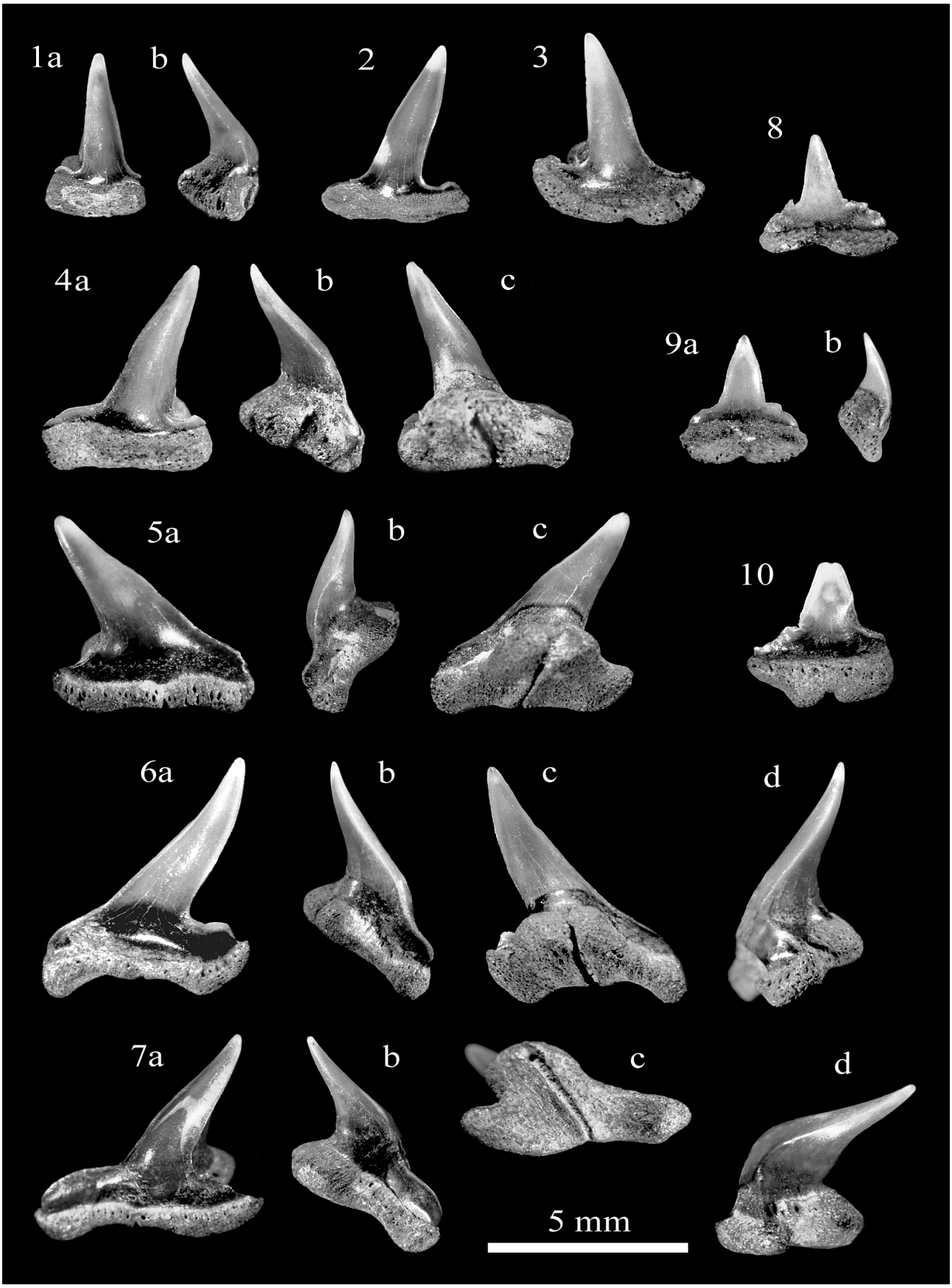

1a
b
2
3
8
4a
b
c
9a
b
5a
b
c
10
6a
b
c
d
7a
b
c
d
5 mm

PLATE 2

Physogaleus hemmooriensis sp. nov., Behrendorfian, Lower Hemmoorian, Werder.

fig. 1: upper antero-lateral tooth, H = 6.0 mm, W = 5.5 mm, a. labial view, b. distal view, c. lingual view, SMF P9690, holotype.

fig. 2: upper antero-lateral tooth, H = 5.3 mm, W = 6.2 mm, a. labial view, b. occlusal view, c. lingual view, SMF P9691, paratype 1.

fig. 3: upper antero-lateral tooth, H = 5.6 mm, W = 5.7 mm, labial view, SMF P9705.

fig. 4: upper antero-lateral tooth, H = 5.1 mm, W = 6.2 mm, labial view, SMF P9706.

fig. 5: upper antero-lateral tooth, H = 4.6 mm, W = 4.6 mm, labial view, SMF P9707.

fig. 6: upper antero-lateral tooth, H = 5.0 mm, W = 5.2 mm, labial view, SMF P9708.

fig. 7: upper antero-lateral tooth, H = 5.3 mm, W = 4.8 mm, a. labial view, b. mesial view, c. lingual view, SMF P9709.

fig. 8: upper antero-lateral tooth, H = 4.9 mm, W = 6.3 mm, a. labial view, b. occlusal view, c. lingual view, SMF P9710.

fig. 9: upper antero-lateral tooth, H = 4.7 mm, W = 6.1 mm, labial view, SMF P9711.

fig. 10: upper latero-posterior tooth, H = 2.4 mm, W = 4.2 mm, a. labial view, b. distal view, c. lingual view, SMF P9712.

fig. 11: upper antero-lateral tooth, H = 2.8 mm, W = 4.7 mm, labial view, SMF P9713.

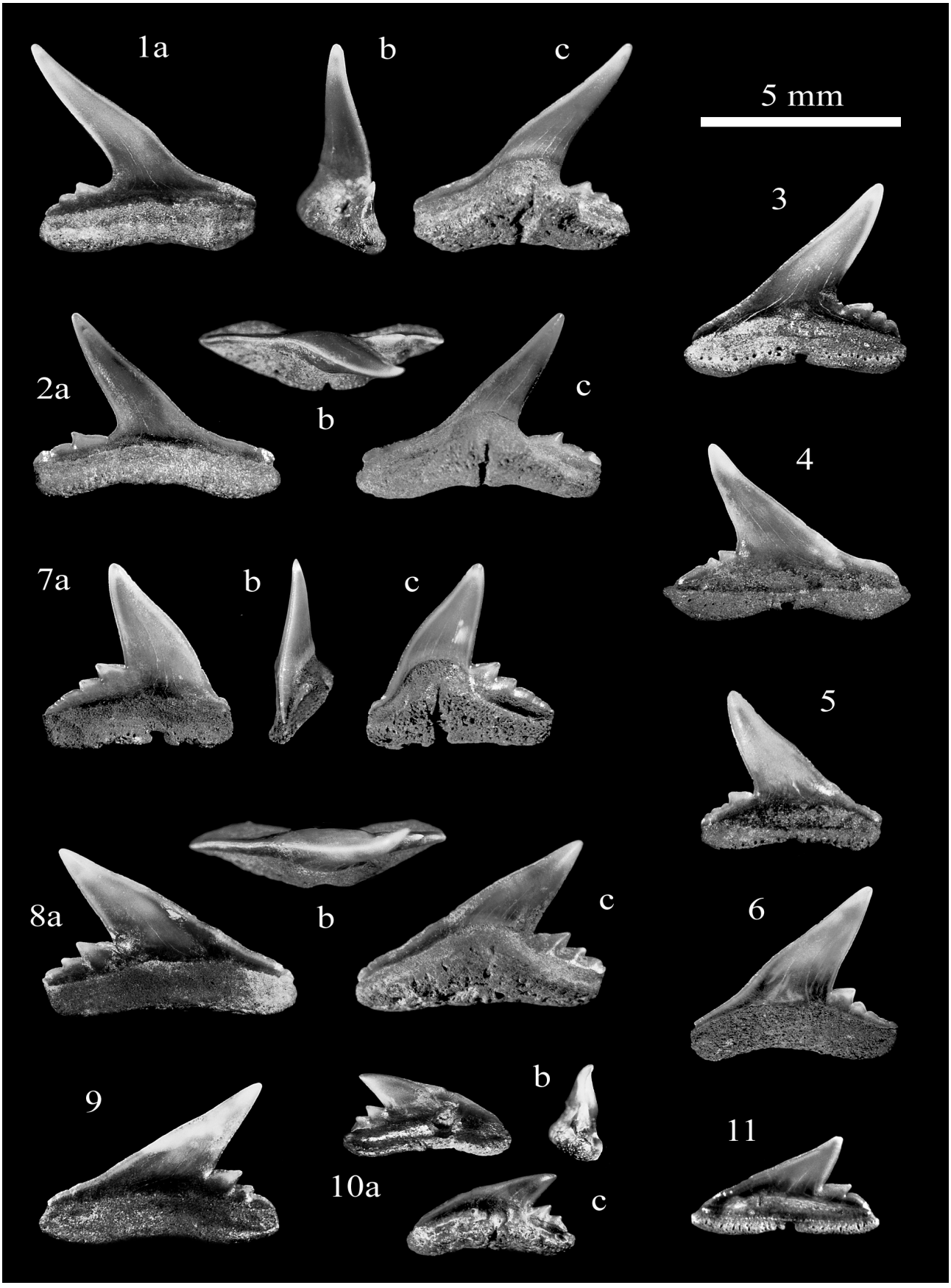

1a
b
c
5 mm
3
2a
b
c
4
7a
b
c
5
8a
b
c
6
9
b
10a
c
11

PLATE 3

Physogaleus hemmooriensis sp. nov., Behrendorfian, Lower Hemmoorian, Werder.

fig. 1: lower antero-lateral tooth, H = 5.8 mm, W = 5.3 mm, a. labial view, b. mesial view, SMF P9714.

fig. 2: lower antero-lateral tooth, H = 5.0 mm, W = 5.3 mm, a. labial view, b. distal view, c. lingual view, SMF P9695, paratype 5.

fig. 3: lower antero-lateral tooth, H = 5.0 mm, W = 5.8 mm, a. lingual view, b. occlusal view, c. labial view, SMF P9715.

fig. 4: lower antero-lateral tooth, H = 5.2 mm, W = 5.8 mm, labial view, SMF P9716.

fig. 5: lower antero-lateral tooth of a subadult specimen, H = 3.3 mm, W = 3.2 mm, labial view, SMF P9717.

fig. 6: lower antero-lateral tooth, H = 4.6 mm, W = 6.2 mm, labial view, SMF P9718.

fig. 7: lower antero-lateral tooth, H = 5.2 mm, W = 7.4 mm, a. lingual view, b. occlusal view, c. labial view, SMF P9719.

fig. 8: lower antero-lateral tooth, H = 4.6 mm, W = 6.3 mm, a. labial view, b. distal view, c. lingual view, SMF P9696, paratype 6.

fig. 9: lower antero-lateral tooth, H = 3.3 mm, W = 5.5 mm, labial view, SMF P9720.

fig. 10: lower antero-lateral tooth, H = 3.9 mm, W = 4.4 mm, labial view, SMF P9721.

fig. 11: lower latero-posterior tooth, H = 2.6 mm, W = 4.6 mm, a. labial view, b. occlusal view, c. lingual view, SMF P9722.

fig. 12: lower latero-posterior tooth, H = 2.7 mm, W = 4.7 mm, a. labial view, b. occlusal view, SMF P9723.

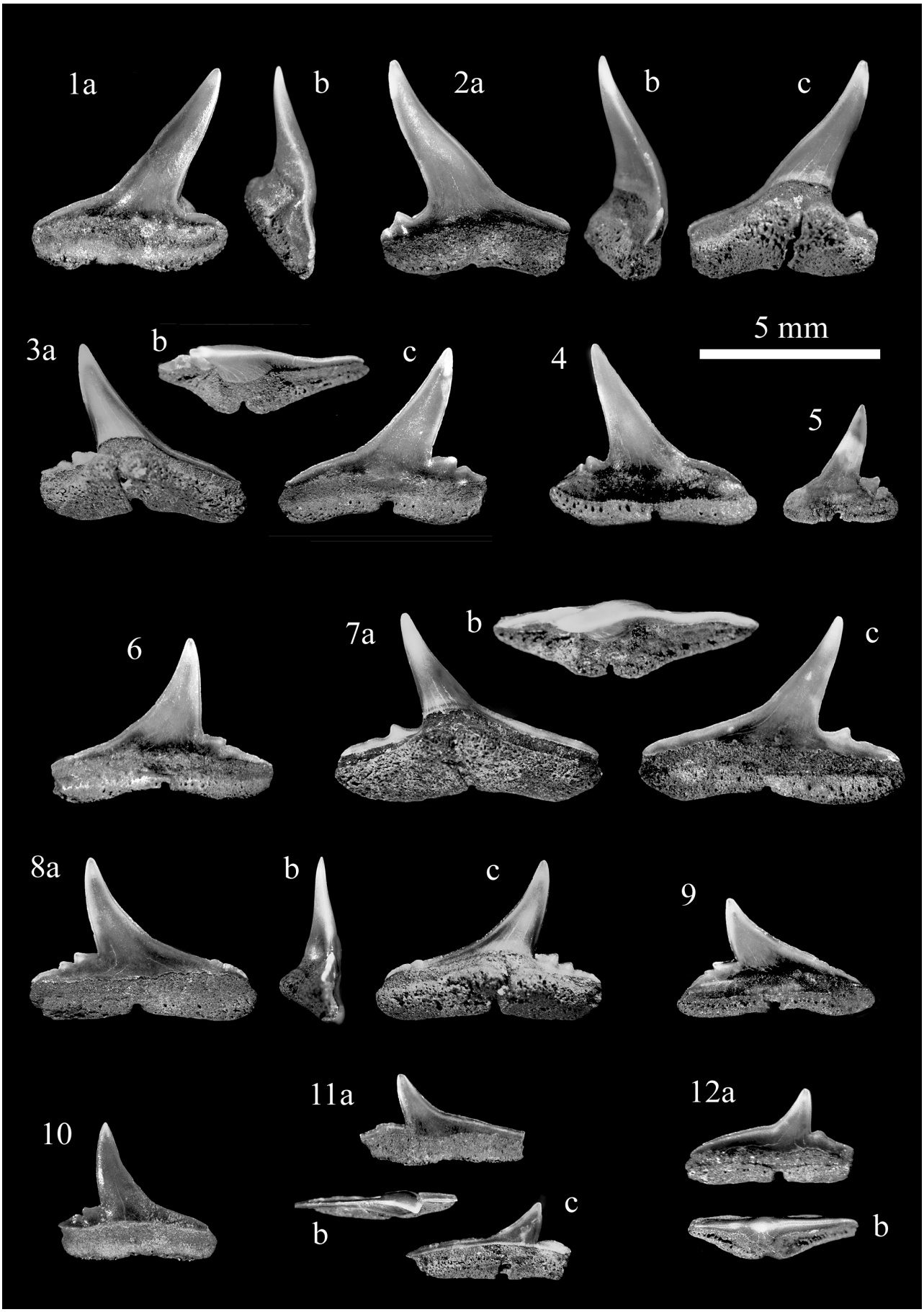

1a
b
2a
b
c
3a
b
c
5 mm
4
5
6
7a
b
c
8a
b
c
9
10
11a
b
c
12a
b

PLATE 4

Physogaleus hemmooriensis sp. nov.

Miste Bed, Aalten Member, Oxlundian, late Hemmoorian, Miste near Winterswijk, The Netherlands.

fig. 1: lower antero-lateral tooth, H = 4.6 mm, W = 4.1 mm, a. labial view, b. mesial view, SMF P9724.

fig. 2: upper antero-lateral tooth, H = 4.5 mm, W = 4.9 mm, a. labial view, b. mesial view, SMF P9725.

fig. 3: lower antero-lateral tooth, H = 3.8 mm, W = 4.2 mm, labial view, SMF P9726.

fig. 4: lower antero-lateral tooth, H = 3.5 mm, W = 4.9 mm, a. lingual view, b. occlusal view, c. labial view, SMF P9727.

Antwerpen Sands Member, *Cardiopsis*/*Cyrtodaria* Bed, Late Hemmoorian.

fig. 5: upper antero-lateral tooth, H = 5.5 mm, W = 5.7 mm, a. lingual view, b. basal view, c. labial view, d. distal view, Antwerp, Pelikaanstreet, IRSNB P8256.

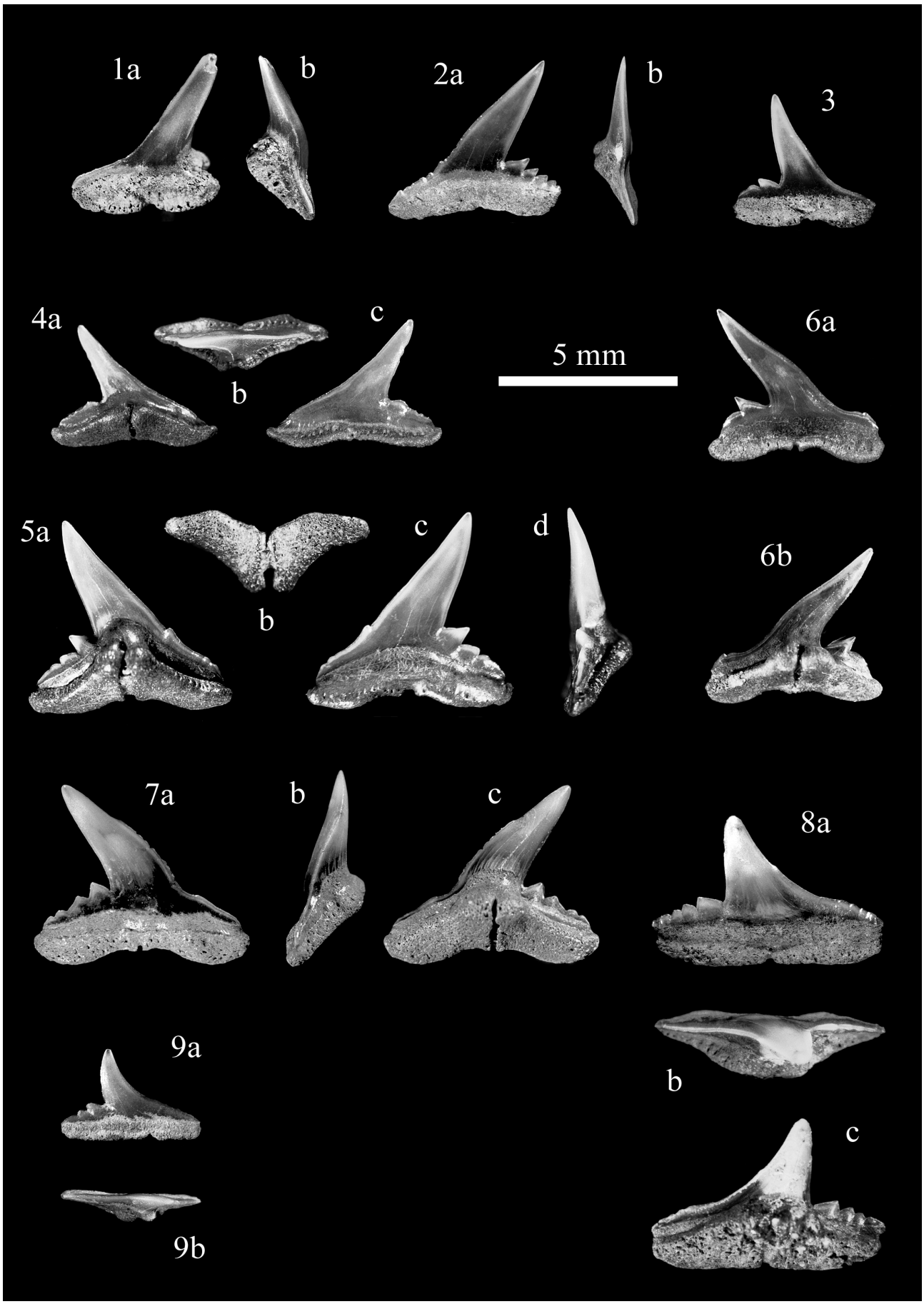
fig. 6: upper antero-lateral tooth, H = 4.3 mm, W = 4.9 mm, a. labial view, b. lingual view, Antwerp, Copernicusstreet-Lange Kievitstreet, IRSNB P8257.

fig. 7: upper antero-lateral tooth, H = 5.1 mm, W = 6.0 mm, a. labial view, b. mesial view, c. lingual view, Antwerp, Pelikaanstreet, IRSNB P8258.

fig. 8: lower antero-lateral tooth, H = 4.3 mm, W = 6.5 mm, a. labial view, b. occlusal view, c. lingual view, Antwerp-Borgerhout, entrance to motorway/ringroad, IRSNB P8259.

Edegem Sands Member, Wilrijk, Lower Hemmoorian.

fig. 9: lower antero-lateral tooth, H = 2.5 mm, B = 3.9 mm, a. labial view, b. occlusal view, IRSNB P8260.


1a
b
2a
b
3
4a
b
c
5 mm
6a
5a
b
c
d
6b
7a
b
c
8a
b
9a
9b
c