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OLIGOCENE TO RECENT CETORHINIDAE (VERTEBRATA, BASKING SHARKS); PROBLEMATICAL FINDS OF TEETH, DERMAL SCALES AND GILL-RAKERS

by

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Teeth, dermal scales and gill-rakers of Recent and fossil Cetorhinidae were investigated. In Recent *Cetorhinus* two types can be distinguished with respective body lengths to c. 450 cm and 1000 to 1200 cm. These two types are assumed to represent two species.

Fossil Cetorhinidae are known from the interval between Late Tongrian/Early Rupelian and Early Pliocene. In Early Pliocene deposits a *Cetorhinus* type is found which is related to one of the Recent types. In other deposits teeth, scales and gill-rakers are never found in connection, so only gill-rakers are with certainty recognizable as Cetorhinidae. Teeth of presumed Cetorhinidae can be divided into three types. A fourth type of which scales and a tooth are known may also belong to this family. These four types are of Oligocene and Miocene age.

Gill-rakers have hardly any specific characteristics. Mean values of measurements of stratigraphically arranged populations show differences, but there is a wide overlap. In fossil gill-rakers three, maybe four types can be distinguished. *Cetorhinus parvus* Leriche, 1908 includes at least two of these types.

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Contents:

SAMENVATTING

Onderzocht werden tanden, schubben en kieuwaanhangsels van recente en fossiele Cetorhinidae. Hieraan bestond grote behoefte, omdat de collectie van het RGM te Leiden vele problematica bevat, die mogelijk tot deze groep kunnen behoren. Verder dan een inventarisatie met kritische kanttekeningen is het echter niet gekomen; de kennis van met name recente *Cetorhinus* is buitengewoon incompleet. Deze publicatie is dan ook bedoeld als discussiestuk en draagt geen nieuwe, met zekerheid te stellen oplossingen aan.

Bij recente *Cetorhinus* blijken twee typen te bestaan, *Cetorhinus* sp. type 1 met individuen tot ca. 450 cm en *Cetorhinus* sp. type 2 met individuen tot 1000 à 1200 cm. Zowel de tanden als de kieuwaanhangsels vertonen zoveel onderlinge verschillen, die per type constant zijn, dat het bestaan van twee recente soorten vermoed kan worden. Studie van aanvullend materiaal zal dat definitief aan moeten tonen. Alleen van type 1 konden ook schubben worden bestudeerd; van type 2 zijn die niet voorhanden, zodat die vergelijking niet gemaakt kan worden. Welke van de twee typen tot *Cetorhinus maximus* (Gunnerus, 1765) behoort, wordt in deze publicatie niet uitgemaakt.

Fossiel materiaal is bekend vanaf het jongste Tongrien/oudste Rupelien (Oligoceen) tot in de Zanden van Kattendijk (ouder Plioceen). Een type dat met zekerheid tot *Cetorhinus* behoort komt voor in Miocene en Pliocene afzettingen. Hiervan zijn tanden en kieuwaanhangsels in connectie aangetroffen in de Zanden van Kattendijk (Herman, 1979). Het wordt in deze publicatie aangeduid als *Cetorhinus* sp. type 3. De tanden hiervan zijn verwant aan type 2 en de kieuwaanhangsels nagenoeg identiek.

Van het overige fossiele materiaal, uit Oligoceen en Mioceen, kunnen feitelijk alleen de kieuwaanhangsels met zekerheid als Cetorhinidae worden beschouwd. Samen met de pliocene exemplaren zijn de fossiele kieuwaanhangsels na meting volgens figuur 67a in drie of vier typen te verdelen (fig. 67b): na stratigrafische rangschikking ontstaat per type steeds een ander gemiddelde in de grafiek. In het Oligoceen zijn zo Cetorhinidae type α en type β te onderscheiden. Een groot deel blijkt echter niet soortkarakteristiek te zijn, omdat de metingen elkaar overlappen. *Cetorhinus parvus* Leriche, 1908 uit het Rupelien heeft betrekking op zeker twee typen kieuwaanhangsels. De metingen toonden herhaaldelijk aan dat de plaats in de grafiek niet wordt bepaald door de grootte van de exemplaren. Er blijkt dus geen vormverandering te ontstaan naar gelang het groeistadium van de individuen. Zolang van de oudere typen Cetorhinidae nog geen tanden, schubben en kieuwaanhangsels in connectie gevonden zijn, kan van de tanden en schubben alleen worden vermoed dat zij tot de Cetorhinidae behoren.

In Oligoceen en Mioceen bestaan 3 typen tanden van vermoedelijk Cetorhinidae, die nauw verwant aan elkaar zijn. Het betreft Cetorhinidae type A uit het jongste Tongrien en oudste Rupelien, Cetorhinidae type B uit het Rupelien en Cetorhinidae type C uit het Midden-Mioceen. De verwantschap van deze reeks met *Cetorhinus* sp. type 2 en 3 is vrij gering en met type 1 is die er helemaal niet. Voorts bestaat er in Oligoceen en Mioceen nog een vierde type, dat mogelijk tot Cetorhinidae behoort, Cetorhinidae type D. Hiervan zijn veel schubben, maar ook een tand bekend, die veel vormgelijkenis vertoont met *Cetorhinus* sp. type 1.

Duidelijk is wel dat de recente en fossiele Cetorhinidae een veel grotere groep van soorten omvat dan alleen de beschreven *Cetorhinus maximus* (Gunnerus, 1765) en *Cetorhinus parvus* Leriche, 1908. Uitgaande van de tanden bestaan er 6, mogelijk 7 typen of soorten, waarvan de verwantschap in drie groepen (genera?) te verdelen is.

INTRODUCTION

The collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (RGM) contains quite a few problematical finds that might belong to the Cetorhinidae. A critical investigation of this material, comprising teeth, dermal scales and gill-rakers, resulted in this paper which is an inventory without final conclusions on systematics and nomenclature. The formal status of both well-known species *Cetorhinus maximus* (Gunnerus, 1765) and *C. parvus* Leriche, 1908 are brought up for discussion. Due to a very considerable lack of well-documented material of Recent Cetorhinidae representing various growth stages and both sexes final solutions appeared to be unattainable yet.

Close cooperation of Dr H. K. Loose (RGM) and Mr A. W. Janssen, editor of this periodical, in the completion of the manuscript is gratefully acknowledged.

Abbreviations used in this paper:

RGM - Rijksmuseum van Geologie en Mineralogie, Leiden
RMNH - Rijksmuseum van Natuurlijke Historie, Leiden
NMR - Natuurhistorisch Museum, Rotterdam
BM(NH) - British Museum (Natural History), London.

RECENT CETORHINIDAE, TEETH AND DERMAL SCALES

In the RGM collection a number of problematica from Tertiary deposits are stored that may be presumed to belong to Cetorhinidae (basking sharks). To confirm this possibility solid parts of Recent Cetorhinidae (teeth, dermal scales and gill-rakers) were examined.

To obtain an impression as reliable as possible material of both sexes and of various growth stages should be included in this study and of each individual teeth, dermal scales and gill-rakers should be inspected. This, however, turned out to be next to impossible, as these three components have been collected and documented only very rarely from one and the same specimen.

Recent specimens are always identified as *Cetorhinus maximus* (Gunnerus, 1765). During this study, however, two different types could be distinguished, teeth and scales of which are described here. The gill-rakers will be dealt with in a separate chapter.

Cetorhinus sp., type 1
Figs 1-17

1948 *Cetorhinus maximus* (Gunnerus) 1765 - Bigelow & Schroeder, p. 148, figs 23c-e (teeth and dermal scales of an individual with a length of 12 feet from Fire Island, New York).

Remarks - Recent material occasionally washing ashore on North Sea beaches and specimens sometimes caught by fishermen in the North Sea presumably all belong to this small form, indicated here as *Cetorhinus* sp., type 1.

Van Deinse & Adriani (1953) mention several specimens from the Dutch coast and from the North Sea, males as well as females, with lengths between 337 and 620 cm. Redeke (1941) mentions *Cetorhinus* from Dutch coastal waters with lengths in between 330 and 375 cm. These measurements

contrast strongly with specimens from outside the North Sea, varying in total length from 1000 to 1200 cm.

From a few of the specimens regarded as juveniles by Redeke (1941) some material (teeth and gill-rakers) is still available. Dermal scales could be studied from a male with a length of 340 cm washed ashore at Terheijde (The Netherlands) in 1973.

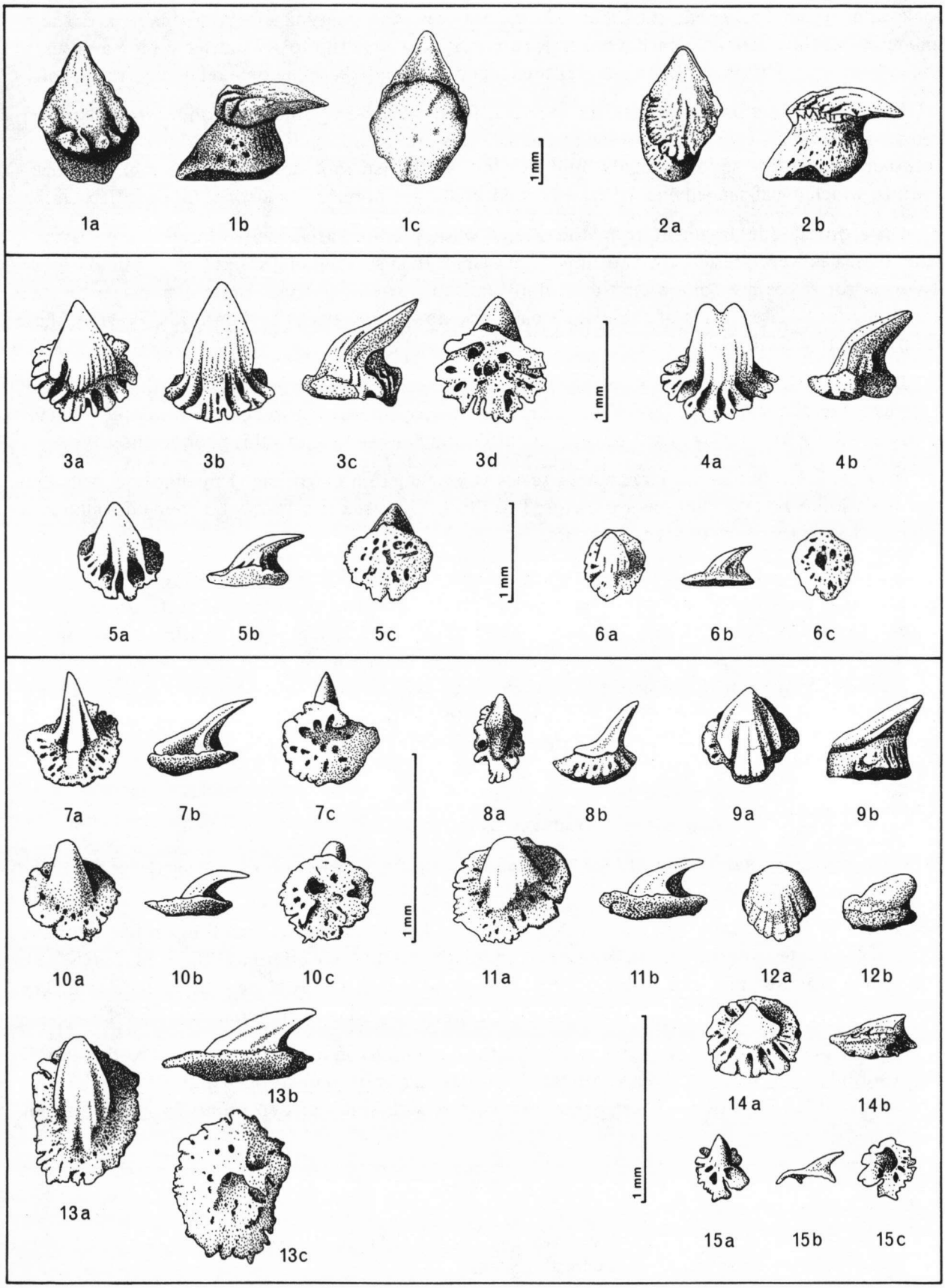
Teeth were seen from several *Cetorhinus* specimens with lengths up to 450 cm. These agree without exception with the teeth represented here in figs 1 and 2. The tooth of fig. 1 belonged to a male, length 421 cm, captured East of Aberdeen. Jaws of this specimen are present in the RMNH collection. Two halves of these jaws are illustrated on pl. 1 and 2.

In fig. 2 a tooth is represented from a female animal with a length of 344 cm. The crown of this tooth is small (2-3 mm at the most) and placed on its root at an angle of c. 90°. The lower part of the crown has a distinct cauliflower-like structure, that may differ from specimen to specimen (compare figs 1 and 2). The crown has a sharp cutting edge, changing downwards into the irregular structure just mentioned, never reaching the base of the crown. The root is more or less conical. Its basal side has a very weak furrow (fig. 1c), suggesting a separation into two root branches (compare also pl. 3, fig. 1). All inspected jaws of this *Cetorhinus* type have teeth conform this description. There are no discrete differences between anterior, lateral and commissural teeth, except for some variation in the length/width-ratios of the crown. Due to insufficient material the presence of sexual dimorphism could not be established. Teeth of specimens with lengths up to 450 cm demonstrate no distinct changes in form correlated with the size of the animals.

Dermal scales belonging with certainty to *Cetorhinus* are known from a male specimen washed ashore near Terheijde in 1973. This shark was transported to the RMNH at Leiden where it was dissected for the alcohol collection. From remaining fragments some pieces of skin were collected by the author, from the dorsal side of the animal as well as from the ventral side and also from the pharynx. Unfortunately the exact position of these skin parts could not be determined. Partly these skin samples were kept in the dry collection (pl. 3, fig. 2), another part was macerated to obtain isolated dermal scales (figs 7-15, 17). Teeth of this specimen were of the same type as represented here in figs 1 and 2. Consolidated gill-rakers were not present. From a jaw fragment of a female specimen with a length of 344 cm (a tooth of which is represented in fig. 2) some oral scales could be prepared (figs 3-6). Further material was not available. Bigelow & Schroeder (1948, p. 148) give schematical drawings of *Cetorhinus* scales, also from a small individual and of the same type as described here.

The illustration of the scales (figs 3-15) need only a short explanation. Scales from the dorsal side of the animal (figs 7-9) have a projecting spine, usually slender and sharp, but sometimes wide and blunt (fig. 9). Those from the ventral side (figs 10-14) have a flatter, blunt spine; sometimes the

Figs 1-15. *Cetorhinus* sp., type 1; 1. Male, length 421 cm, caught East of Aberdeen, 14 October 1937; about hindmost lateral tooth from left lower jaw. Coll. RMNH 496 (16516). Compare also pls 1, 2, and pl. 3, fig. 1, a: top view; b: lateral view; c: basal view; 2. Female, length 355 cm, 't Horntje, Texel, 2 June 1947; tooth, coll. RMNH 496, a: top view; b: lateral view; 3-6. Same specimen; oral scales, 3a, 4a, 5a, 6a: top views; 3b: front view; 3c, 4b, 5b, 6b: lateral views; 3d, 5c, 6c: basal views; 7-9. Male, length 340 cm, washed ashore at Terheijde, breakwater nr 11, 16 October 1973; collection M. van den Bosch. Dorsal scales, 7a, 8a, 9a: top views; 7b, 8b, 9b: lateral views; 7c: basal view; 10-14. Same specimen. Ventral scales, 10a, 11a, 12a, 13a, 14a: top views; 10b, 11b, 12b, 13b, 14b: lateral views; 10c, 13c: basal views; 15. Same specimen. Scale from the pharynx, a: top view; b: lateral view; c: basal view. Bar length represents 1 mm.


1a
1b
1c
1mm
2a
2b
3a
3b
3c
3d
1 mm
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4b
5a
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6b
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1 mm
11a
11b
12a
12b
13a
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13c
1 mm
14a
14b
15a
15b
15c

scales are broadly rounded stubs (fig. 12). Scales from the pharynx are very small (c. 0.3 mm) and resemble those from the back. Oral scales are relatively large (up to 1.2 mm) and have a different shape (figs 3-6). Striking in these scales is the erect arrowhead-like spine on a relatively small root.

The scales of *Cetorhinus* as described here differ from those of other Selachii by their flattened, rounded or oval root on which a spine is present. This principal form is also found in some Batoidei. In other Selachii the scale is usually built up from a ramified root, sometimes resembling a duck's foot, to which a leaf-shaped enamel scale is connected by a more or less distinct intermediate stalk.

On a dorsal skin fragment from the animal washed ashore at Terheijde locally very scattered pairs of scales were present, two to three times larger than surrounding scales (fig. 17; pl. 3, fig. 2). These larger scales are somewhat tuberculous and an obvious cavity is present between the two components. Isolated parts of these scale pairs resemble the beaks of certain birds. Possibly these are particular sense-organs.

Bigelow & Schroeder (1948, p. 165) illustrated such a large pair of scales from the species *Alopias superciliosus* (Lowe, 1840). These drawings are copied here in figs 16a-b. From other Selachii such scale pairs are unknown, but possibly no attention has been paid to this phenomenon.

Material resembling such large paired scales is known from Oligocene (Rupelian) deposits, but also from Miocene and Pliocene sediments. For illustrations see figs 18-22. Further information is given in the explanations of these drawings.

Especially the Oligocene specimens are strongly curved. The scales are large (1-2 mm) and smooth. It is improbable that these specimens represent aberrant (? distorted) teeth forms, as the material available demonstrates a constant morphology. A relation with the large scale pairs as found in the Recent specimen seems reasonable. It is not clear, however, to what Selachii these fossil scales could belong. Considering their size they may be expected to belong to a large species, which does not exclude Cetorhinidae, but any further evidence for their belonging to this family is not available. Specimens with a completely preserved root have not yet been found.

Cetorhinus sp., type 2

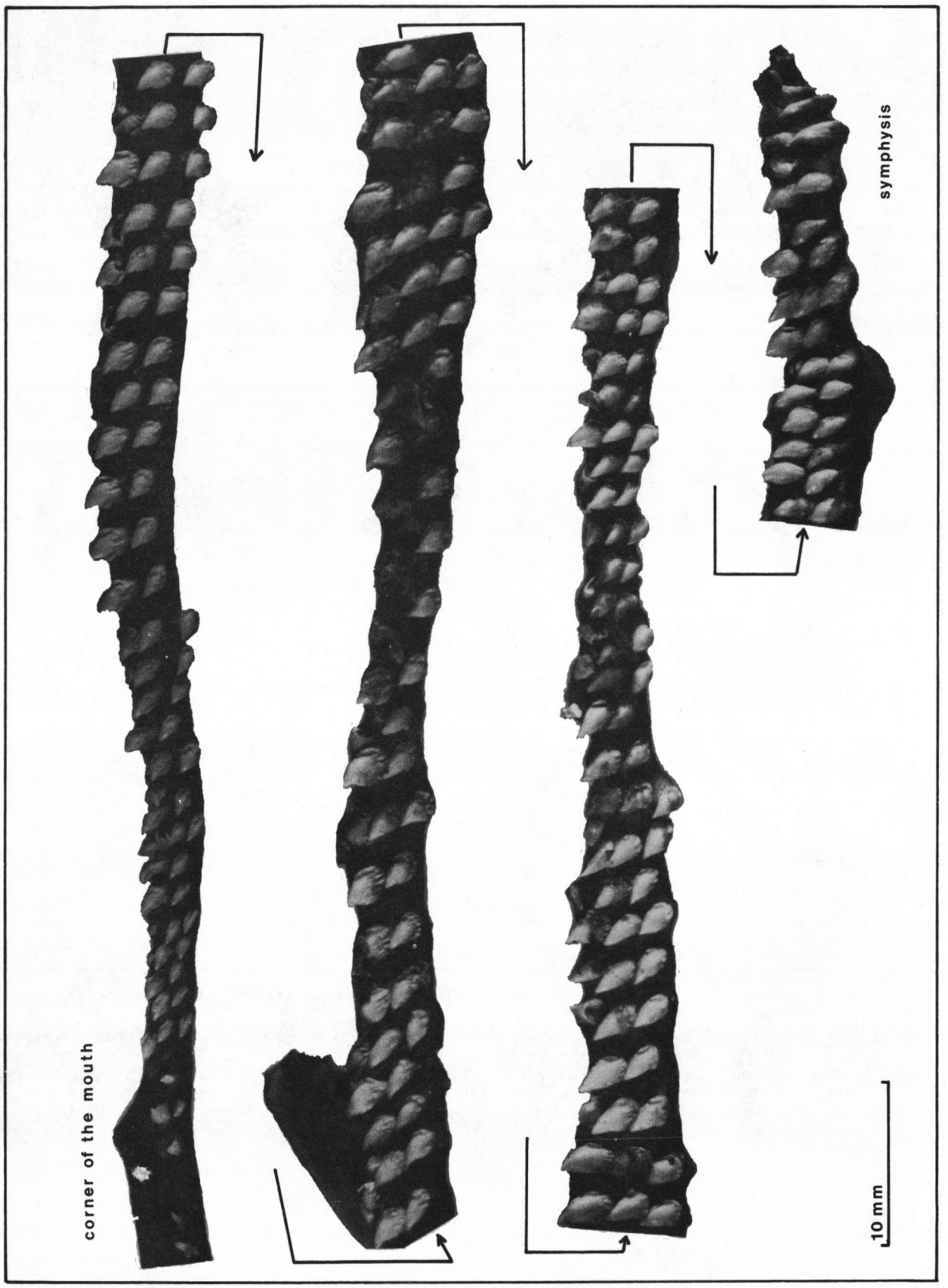
1979 *Cetorhinus maximus* (Gunnerus) 1765 - Herman, pl. 2, figs 8-9 (teeth of a full-grown female specimen from the Irish coast, 1934)

Remarks - In these teeth, with a crown height of 3 to 4 mm, the irregular cauliflower-like structure at the base of the crown is absent, only some undulations are visible (Herman, 1979, pl. 2, figs 8-9). The crown is more erect and slightly curved to one side. The root is somewhat dibranchiate. The shape of the teeth resembles Miocene and Pliocene specimens, illustrated here in figs 23-34.

Further descriptions of jaws and teeth of large *Cetorhinus* individuals belonging to this type 2 are not available in literature. Scales of this form have never been mentioned and, as far as I know, not preserved in collections. Therefore a comparison with scales of *Cetorhinus* sp., type 1 is not

Plate 1. *Cetorhinus* sp., type 1, left upper jaw.
Male, 421 cm, North Sea, East of Aberdeen, 14 October 1937. Coll. RMNH 497 (16516).
Deformation of the object is caused by desiccation.

Plate 1



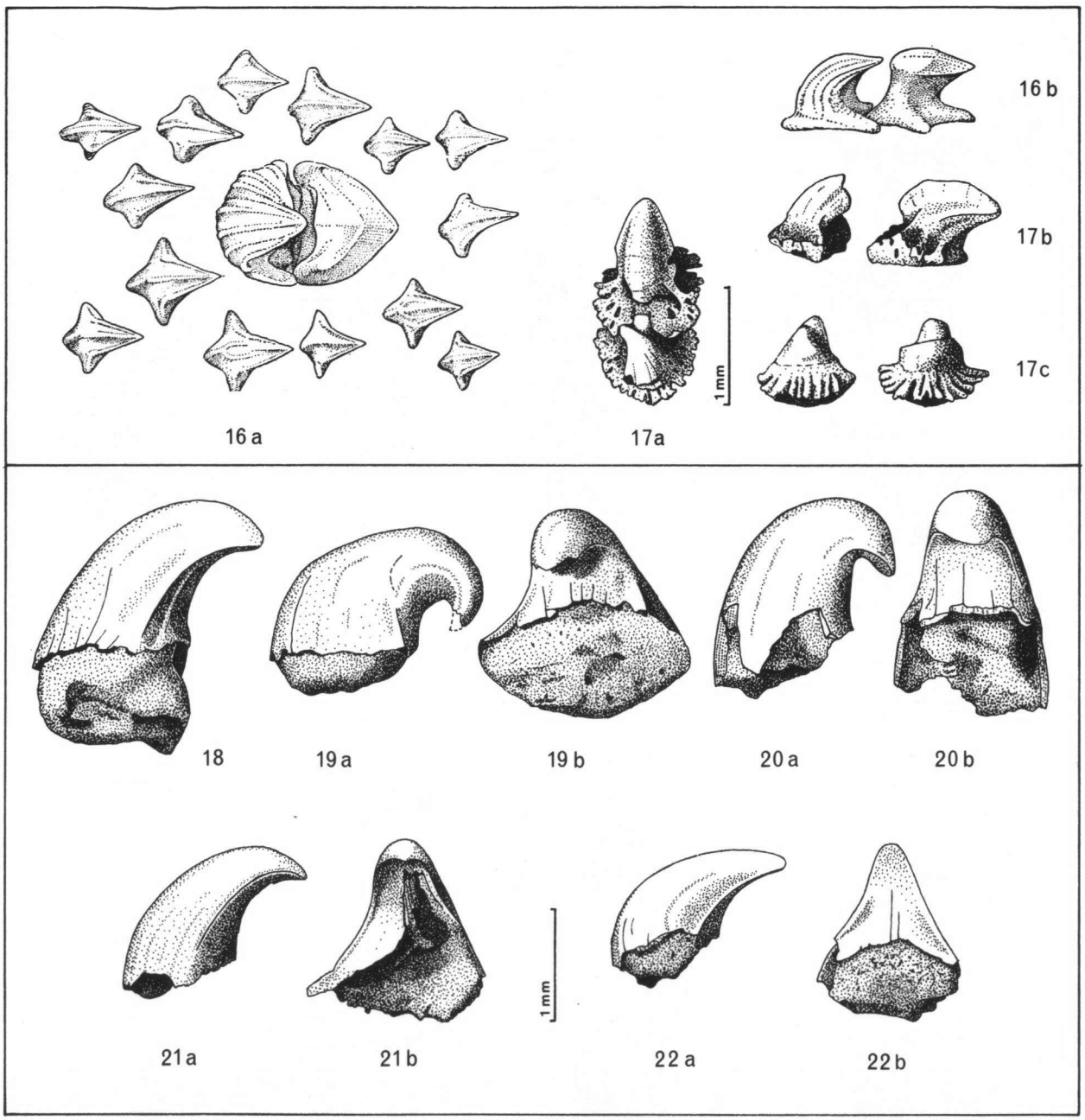


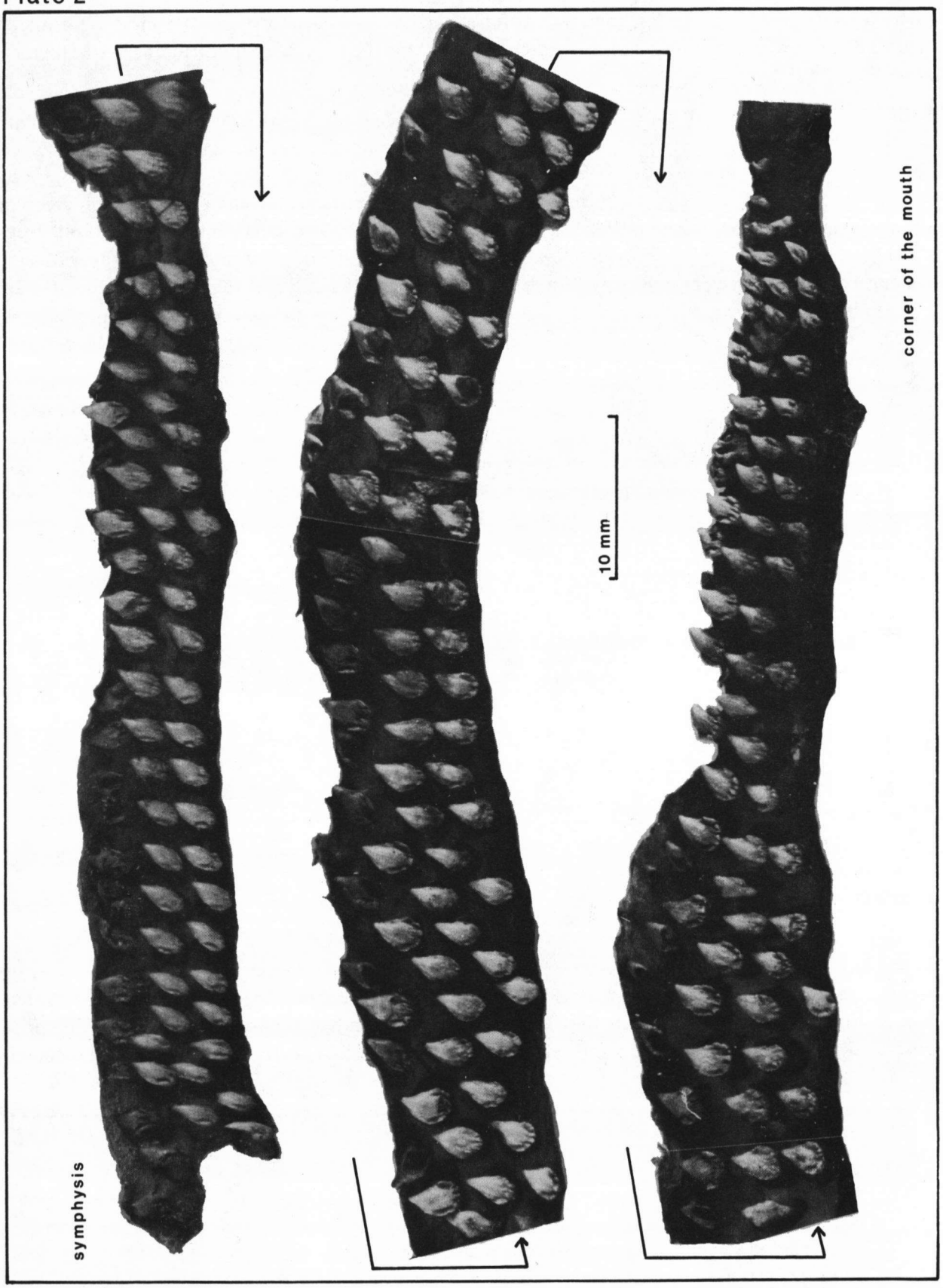
Fig. 16. *Alopias superciliosus* (Lowe, 1840). Male, length 129 cm. Scales with two large paired scales (after Bigelow & Schroeder, 1948, p. 165). Cuba. Magnification 130 X, a: top view; b: lateral view of the large paired scales.

Fig. 17. *Cetorhinus* sp., type 1. Male, length 340 cm, same as figs 7-15. Large paired scales from the dorsal side, exact position unknown, compare pl. 3, figs 2 a-b, a: top view; b: lateral view; c: back of the two scales.

Figs 18-22. Supposed fossil parts of large paired scales of Elasmobranchii (Selachii). 18. Lateral view. Berg Sands, Kleine Spouwen, Belgium. Oligocene, Rupelian. Coll. RGM 176 237; 19. Same locality, coll. RGM 176 238, a: lateral view; b: back view; 20. Base of Boom Clay Formation, clay-pit at St. Niklaas, Belgium. Oligocene, Rupelian. Coll. RGM 176 239, a: lateral view; b: back view; 21. Sylt Stufe, Morsum Cliff, Sylt, F.R.G. Miocene/Pliocene (Syltian). Coll. RGM 176 240, a: lateral view; b: back view; 22. Equivalents of Zenderen or Delden Member. Well 52B.185 at Overloon, depth 57-58 m. Miocene/Pliocene. Coll. RGM 176 241, a: lateral view; b: back view.

Plate 2. *Cetorhinus* sp., type 1, left lower jaw.
Data as in Plate 1.

Plate 2



possible. The teeth of type 2, however, differ strongly from those of type 1: compare Herman's figures 8 and 9 with figs 1 and 2 in the present paper. Also the gill-rakers are different, see below.

As far as it can be decided now *Cetorhinus* sp., type 2 seems to conform with the large individuals with lengths between 800 and 1200 cm, as regularly observed on the Irish and Norwegian coast, but also elsewhere. It was generally accepted that these large animals are adult specimens of *Cetorhinus* sp., type 1. This, however, is not confirmed by the morphology of the teeth. The differences are so substantial that it is unlikely that the large morphological changes are the result of a progressing growth. Bigelow & Schroeder (1948) also assume that smaller and larger individuals (25-40 feet) belong to one species, viz. *Cetorhinus maximus* (Gunnerus, 1765), but they do not provide any conclusive proof. For comparison with a specimen of more than 26 feet they illustrate the head of a juvenile individual with a length of 12 feet. This head differs strongly in shape from the large specimen and considering its teeth it belongs to type 1 (Bigelow & Schroeder, 1948, p. 148; compare figs 23-23a).

Although there are strong indications that *Cetorhinus* sp., type 1 and type 2 belong to separate species, occupying different geographical areas, this cannot be proven with absolute certainty. Too little well-documented material is available, preventing a sound investigation of growth stages and sexual dimorphism, especially concerning teeth and dermal scales. On the other hand the differences observed can hardly be interpreted as ontogenetical changes. The presence of gill-rakers is typical for Cetorhinidae, it is no proof that it always concerns *C. maximus*.

The question which of the two types represents typical *Cetorhinus maximus* is avoided in the present paper. If really two species are present in the Recent fauna it might be necessary to settle the matter by designation of a neotype.

FOSSIL CETORHINIDAE, TEETH AND SCALES

Cetorhinus sp., type 3
Figs 23-34

1974 *Cetorhinus maximus* (Gunner, 1765) - Herman, p. 23, pl. 1, fig. 7 (tooth from the Kattendijk Sands near Antwerp).

1979 *Cetorhinus* cf. *maximus* (Gunner, 1765) - Herman, p. 365, pl. 2, fig. 1-7 (teeth from the Kattendijk Sands near Antwerp).

Remarks - Among the fossil material described here *Cetorhinus* sp., type 3 is the only form of which it is known with certainty that it belongs to the Cetorhinidae. Teeth of this type, illustrated here in figs 24-34, were found in the Early Pliocene Kattendijk Sands near Antwerp. This find, described by Herman (1979), comprised both a large number of teeth and also the gill-rakers, all

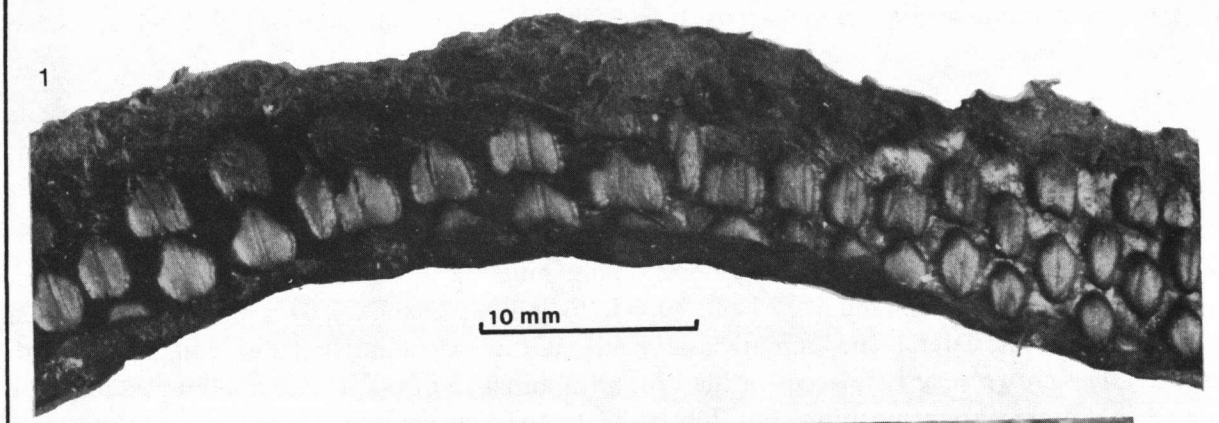
Plate 3. *Cetorhinus* sp., type 1

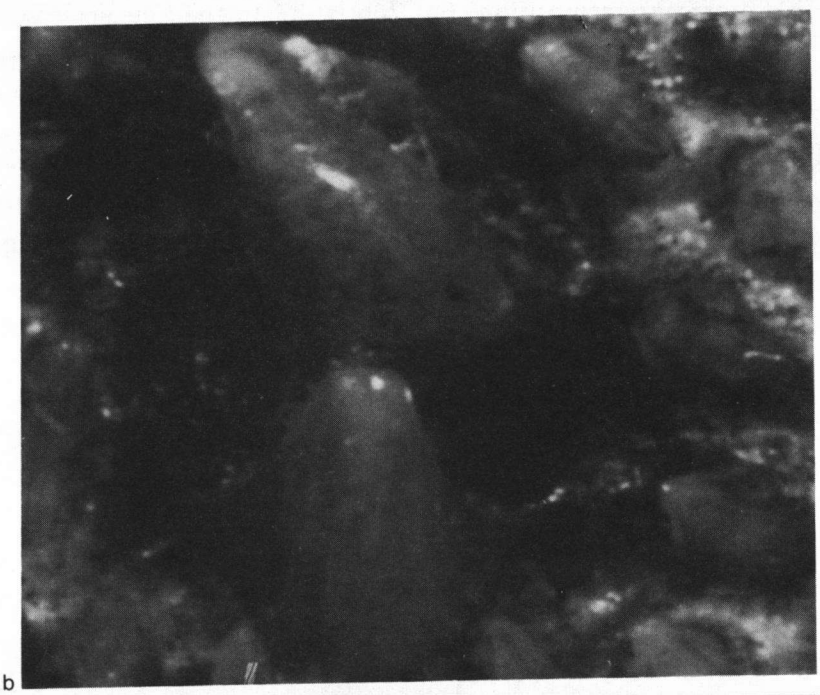
Fig. 1. Root part of teeth from the left lower jaw. Data as in Pl. 1.

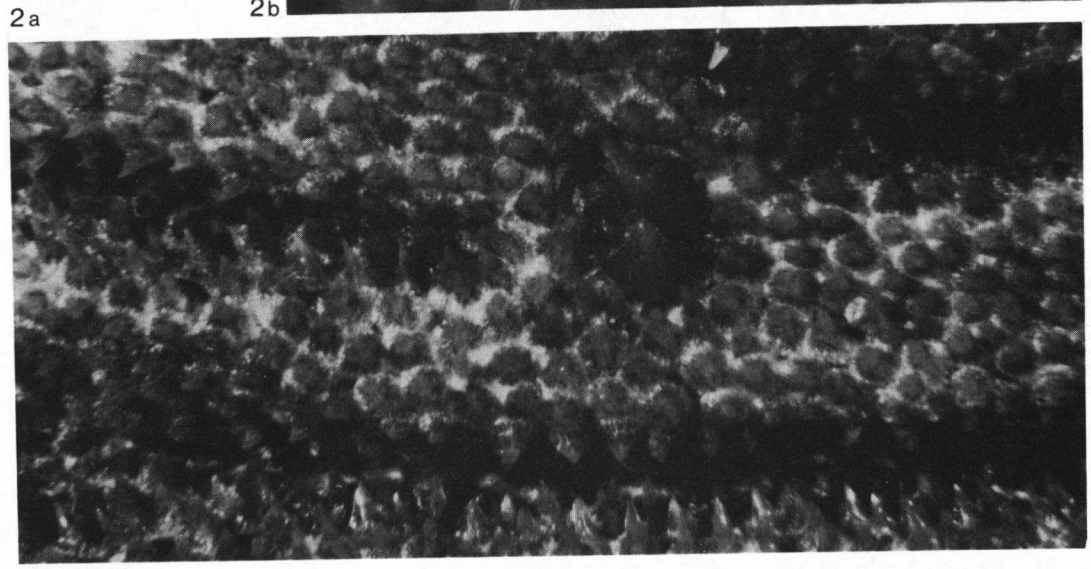
Fig. 2. Part of the skin from the dorsal side with scales and large paired scales. Male, 340 cm, Terheijde, washed ashore, 16 October 1973. Coll. van den Bosch.

Fig. 3. Detail of fig. 2, large paired scales.

Plate 3







from one individual. Unfortunately the finest sediment fractions were not inspected, so the dermal scales, of which hundreds of thousands must have been present, remain unknown. Still this specimen is of great importance.

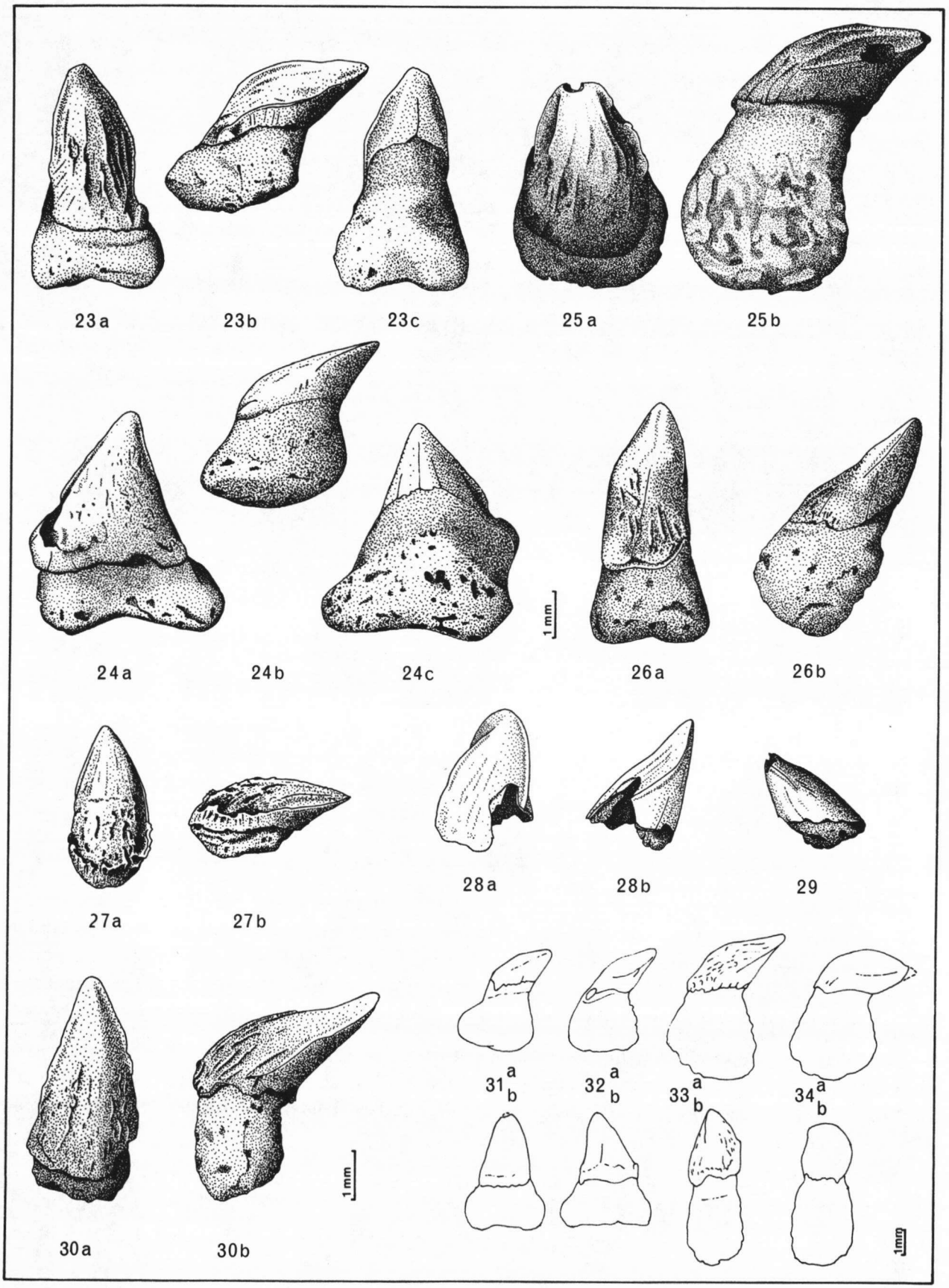
Teeth of type 3 have one feature in common, viz. the irregular wrinkles on the crown, as visible in figs 23a, 24a, 26a and 30a. Only the tooth represented in fig. 27a-b is somewhat different in this respect. Here the wrinkles show a very strong development, resulting in the presence of irregular sharp carinae.

The jaw of this representative of the Cetorhinidae must have contained several types of teeth, compare figs 23 and 31, 24 and 32, 25 and 30, 33, 26 and 28, 27 and 34. This material is supposed to include anterior, lateral and commissural teeth, but these cannot yet be distinguished with certainty. The crown may be placed on the root with an angle of 90° (fig. 34a), but also it can be situated in a more upright position (figs 26b, 30b). In the latter case the root is narrow and long. Striking is the form of fig. 24. It resembles teeth of the genus *Alopias*, as was already pointed out by Herman (1979). For comparison a number of commissural teeth of *Alopias vulpinus* Bonaterre, 1788 are illustrated here (figs 35-39). Though similarities are present, there are also fundamental differences: in *Alopias* the branches of the root are distinctly separated and the sharp cutting edge of the crown reaches to the base. This is not the case in Cetorhinidae.

Beyond any doubt there is a relationship between the teeth of the Recent *Cetorhinus* sp., type 2 and the fossil *Cetorhinus* sp., type 3, as described here. This is especially expressed by the size and the outline of the teeth. Still, some distinguishing features may be noted: in type 3 the crown of the teeth is always wrinkled to a higher or lesser degree. These wrinkles are absent in type 2, but they possess some undulations or folds. The particular tooth form represented in figs 24 and 32 is less convincingly present in type 2. These characteristic differences, constant in the fossil material, justify the presumption that this material belongs to another, now extinct species. Further investigation of *Cetorhinus* sp., type 2 teeth material will be necessary for a final decision.

Teeth of *Cetorhinus* sp., type 3 are known from the Kattendijk Sands (Early Pliocene) in the Antwerp area, Belgium (figs 23-24), the Delden Member (Late Miocene/Early Pliocene) in the eastern and northern parts of the Netherlands (figs 25-28, 31-34) and the Sylt Stufe (Syltian) from the Morsum Cliff at Sylt, F.R.G. (fig. 29). A much older specimen is known from the Dingdener Schichten (= Aalten Member, Reinbekian) at Dingden near Bocholt, F.R.G. This latter specimen is represented here in fig. 30.

Figs 23-34. *Cetorhinus* sp., type 3. 23. Tooth. Kattendijk Sands, 4.20 m above base, construction-pit at Kallo near Antwerp, Early Pliocene. Coll. RGM 176 242, a: front view; b: lateral view; c: back view; 24. Tooth (compare fig. 32). Base of Kattendijk Sands, Deurne near Antwerp, temporary exposure near cemetery, Early Pliocene. Coll. RGM 176 243, a: front view; b: lateral view; c: back view; 25. Tooth. Base of Delden Member, outcrop in forest 't Klooster near Aalten, Miocene/Pliocene. Coll. RGM 176 244, a: top view; b: lateral view; 26. Tooth. Same locality as fig. 25. Coll. RGM 156 209, a: front view; b: lateral view; 27. Tooth with defective root. Well NAM De Wijk-19, depth 195-205 m minus RT, Miocene/Pliocene. Coll. RGM 176 245, a: top view; b: lateral view (compare fig. 34a); 28. Disconnected crown of tooth. Same locality as fig. 27, depth 220-227,50 m minus RT, Miocene/Pliocene. Coll. RGM 176 246, a: front view; b: lateral view (compare fig. 26b); 29. Disconnected crown of tooth, morphological type as in fig. 26. Aporrhais Level, Sylt Stufe, Morsum Kliff, Sylt, F.R.G., Miocene/Pliocene. Coll. RGM 176 247; 30. Tooth. Dingdener Schichten (= Aalten Member, Stemerdink Bed), Feinsand, Dingden, Königsmühle, F.R.G., Middle Miocene (Reinbekian). Coll. RGM 176 248, a: top view; b: lateral view; 31-34. Various types of teeth. Delden Member, same locality as fig. 25. Coll. M. C. Cadée. 31a-34a: lateral views; 31b-34b: front views.


23a
23b
23c
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25b
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1mm
26a
26b
27a
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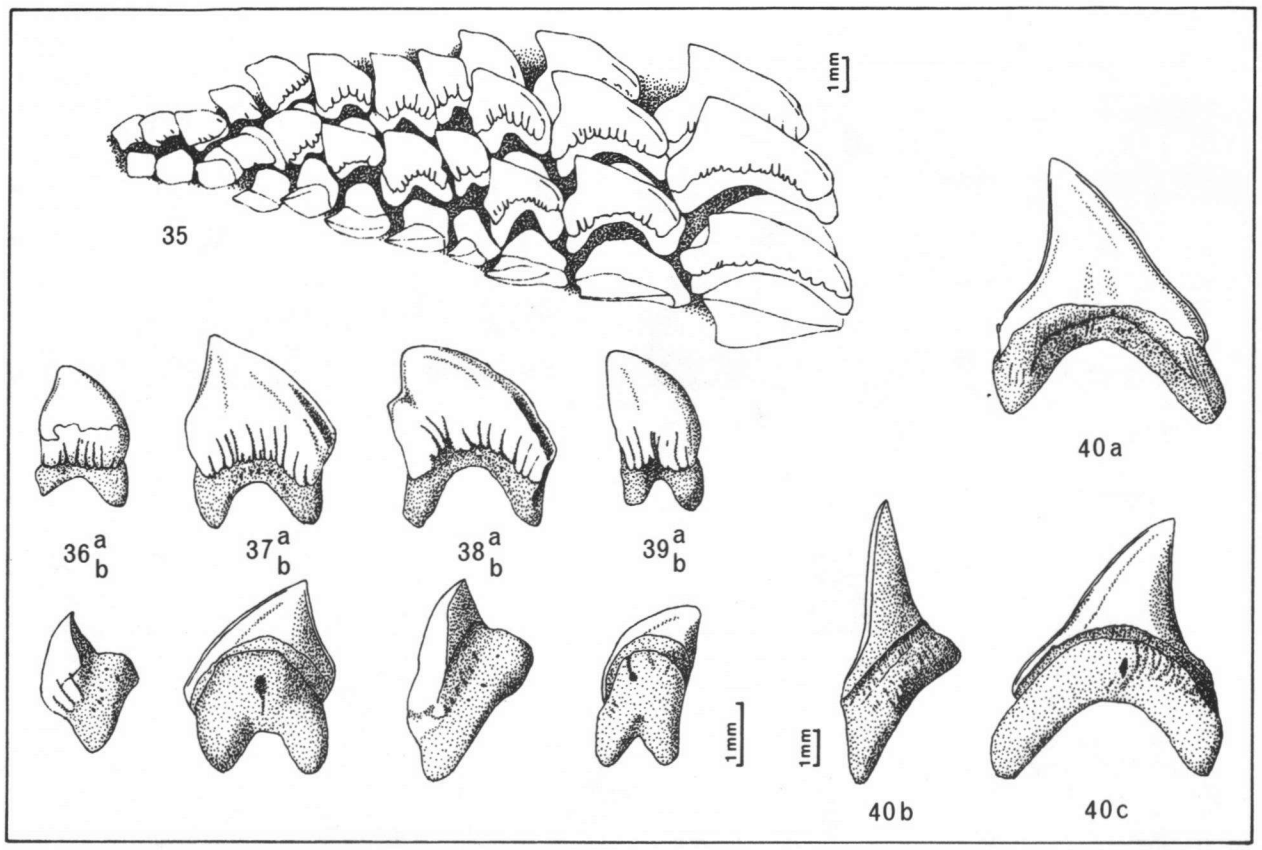
29
30a
30b
1mm
31 a b
32 a b
33 a b
34 a b
1mm



Figs 35-40. *Alopias vulpinus* Bonnaterre, 1788. Recent, length 400 cm, caught 2 miles off Scheveningen, September 1958. Coll. M. van den Bosch; 35. Commissural teeth left upper jaw, 14th to 24th row of teeth; 36-39. Various commissural teeth from the left upper jaw, 17th to 24th row, compare figs 24 and 32. 36a-39a: external views; 36b, 38b: lateral views; 37b, 39b internal views; 40. First lateral tooth (4th row) from the left upper jaw. a: external view; b: lateral view; c: internal view.

Cetorhinidae, type A
Figs 41-43

Remarks - Of this type only some crowns of teeth without roots are known from the Bassevelde Sands at Ruisbroek, Belgium, and from the Ratum Member in the eastern part of the Netherlands. Possibly a similar form occurs in the basal deposits of the Winterswijk Member in clay-pit "De Vlijt" at Winterswijk, eastern part of the Netherlands. These occurrences indicate an age of oldest Rupelian, but its presence in younger Rupelian deposits is not excluded.

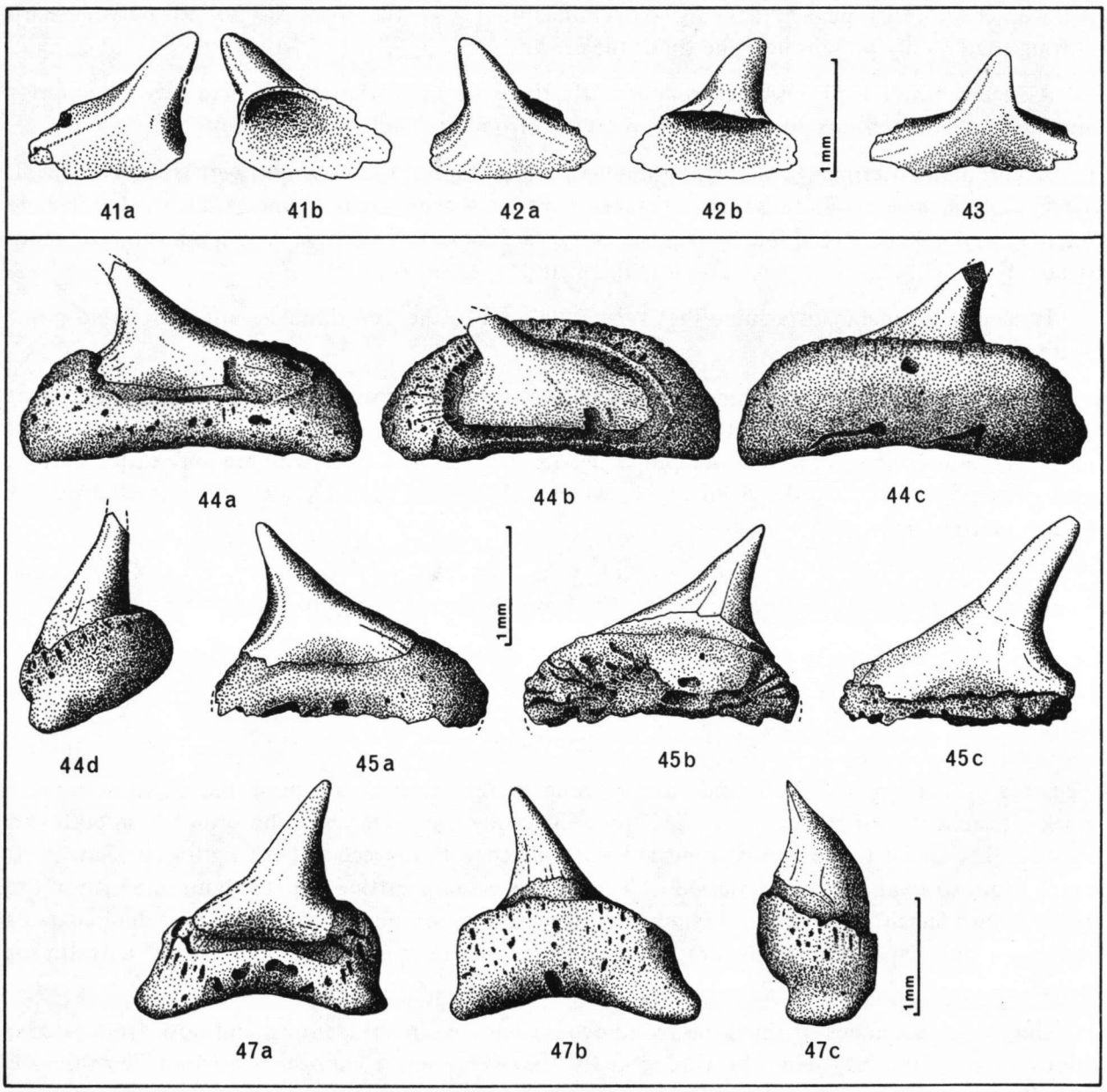
The shape of the crown roughly agrees with Cetorhinidae, type B, described below. Contrary to type B the crowns of type A are externally flattened and the sharp cutting edges reach to about half the height of the crown. Also these teeth are slightly less slender than those of type B and the base of the crown may be strongly expanded (fig. 43).

It cannot be excluded with certainty that type A remains within the range of variability of type B, but it is striking that all finds in older Rupelian sediments exclusively belong to type A. These deposits also yield Cetorhinidae gill-rakers. Together these belong to the oldest known Cetorhinidae.

Cetorhinidae, type B
Figs 44-47

1979 *Cetorhinus parvus* Leriche, 1908 - Herman, p. 366, pl. 3, figs 1-2 (teeth from the Boom Clay Formation at Steendorp and reworked material from Kallo near Antwerp).

Remarks - The shape of the teeth is very characteristic: a wide and long root (fig. 44b) without



Figs 41-43. Cetorhinidae, type A; 41-42. Southern part of construction-pit of Rupel tunnel, Ruisbroek, Belgium, Bassevelde Sands, Oligocene, earliest Rupelian/"Tongrian sup.". 41. Crown of tooth, coll. RGM 176 249. 42. Crown of tooth, coll. RGM 176 250, a: external view; b: internal view; 43. Well 34G.2-8, Haaksbergen, depth 27.01-28.01 m, Ratum Formation, Oligocene, Rupelian. Coll. RGM 176 251.

Figs 44-47. Cetorhinidae, type B. 44-46. Clay-pit "De Vlijt", Winterswijk, 41E-3-143, depth 2.30-2.55 m, base of Winterswijk Member, Oligocene, Rupelian; 44. Tooth, coll. RGM 176 252, a: external view; b: top view; c: internal view; d: lateral view; 45. Tooth, root incomplete, coll. RGM 176 253. a: external view; b: internal view; 46. Tooth, root broken; external view. Coll. RGM 176 254; 47. Tooth, Well NAM De Wijk-19, depth 250-257.50 m minus RT, lower part of Boom Clay Formation, Oligocene, Rupelian. Coll. RGM 176 255, a: external view; b: internal view; c. lateral view.

obvious branches (figs 44a, 47a), carrying a rather oblique, pointed crown, sloping to one side (figs 45a, 47a), with a widely expanded crown base (figs 44a-b, 45a, 46, 47a).

The crown is smooth, externally convex, internally swollen. Only close to the tip sometimes a sharp cutting edge is present (fig. 47c). Around the base of the crown a slightly projecting edge of the root is present, only visible in completely preserved specimens (figs 44a, 44b, 47a, 47c). Obvious bone structures are frequently visible in the roots (fig. 45b) as numerous small holes and pits in the surface. The tooth represented in fig. 47 reminds of *Alopias* (compare figs 36-39), but the sharp cutting edge is only present near the tip of the crown.

All teeth have a similar shape, so apparently there are no obvious differences between anterior and lateral teeth, contrary to *Cetorhinus* sp., type 3 from Mio- and Pliocene deposits.

According to Herman (1979) Cetorhinidae type B belongs to *Cetorhinus parvus* Leriche, 1908. This taxon, however, was based on gill-rakers. Up to now there are now finds available that include teeth and gill-rakers of one individual, as was the case for *Cetorhinus* sp., type 3. As will be demonstrated below gill-rakers cannot be used to distinguish between species.

It seems reasonable to assume that type B belongs to the Cetorhinidae, but there is no proof that it belongs to *C. parvus*.

Material from Oligocene sediments are Weinheim-Neumühle (Mayence Basin) contains abundant gill-rakers of "*C. parvus*" (coll. RGM), but distinct Cetorhinidae teeth were not found there. Most teeth mentioned here, however, were collected from the basal Winterswijk Member in the eastern part of the Netherlands (20 specimens), in which gill-rakers are relatively rare. These observations justify a critical approach.

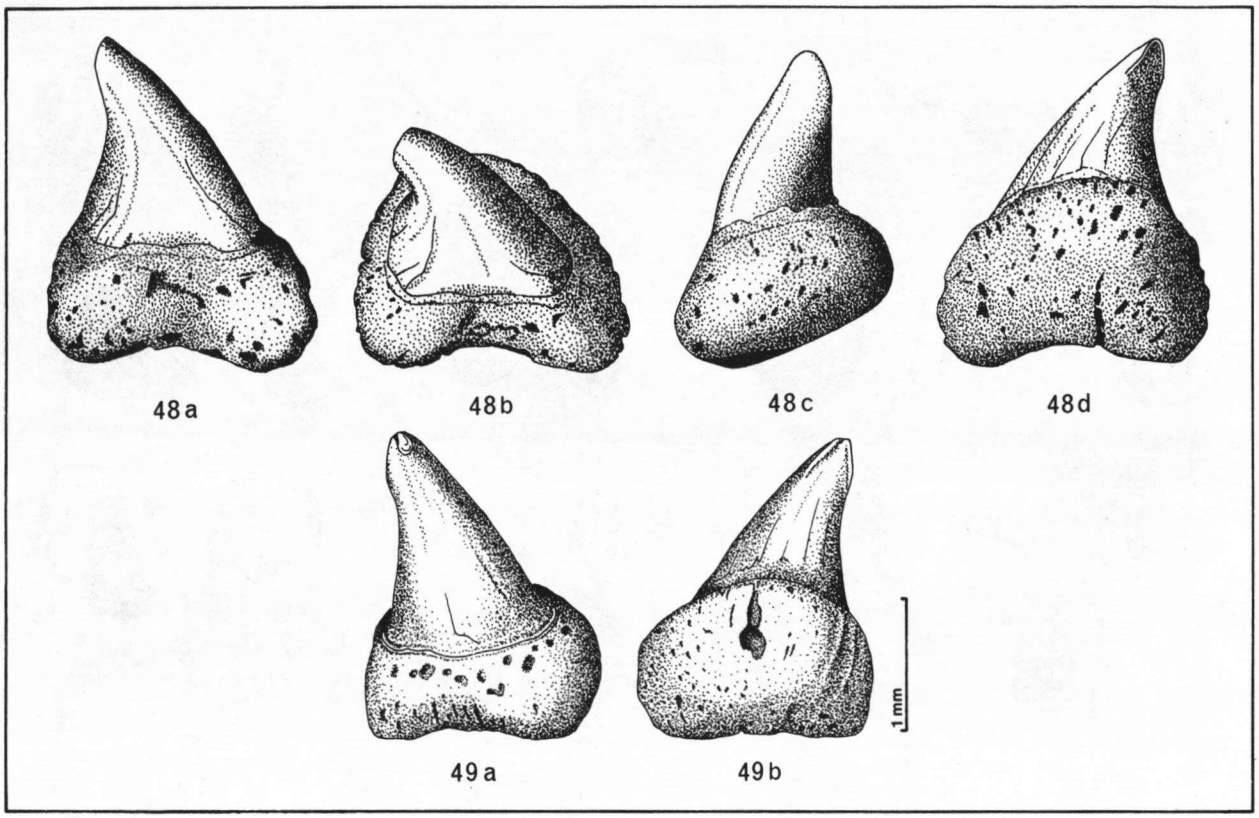
Finds of Cetorhinidae type B are restricted to the Brinkheurne Formation (= Boom Clay Formation s. str.) and the lower part of the Winterswijk Member (Oligocene, Rupelian).

Cetorhinidae, type C
Figs 48-49

Remarks - Shape of the teeth and size are roughly the same as in type B, but the root is more thick-set, almost oval in top view (fig. 48b). Internally and externally the crown is smooth and swollen. The tip of the crown is truncated and twisted with respect to the length axis of the root, much more so than in type B (fig. 48d). The tip has a sharp cutting edge to about one fifth of the entire crown height. The crown has a rather upright position on the root. The root demonstrates numerous holes and pits. A distinct ramification of the root is absent, only a slight curvature is present.

Only two specimens of this type are known. They are almost identical and both from Middle Miocene (Hemmoorian) deposits. Undoubtedly they represent a younger relative of Cetorhinidae type B.

Cetorhinidae type C individuals must have lived at the same time or almost the same time as *Cetorhinus* sp., type 3 specimens, considering the presence of this latter form in the Dingdener Schichten (also Middle Miocene) (fig. 30). This renders a close relationship of these two types unlikely. If really types A, B and C belong to the Cetorhinidae, at least they would have developed differently with regard to *Cetorhinus* sp. types 1 and 2.



Figs 48-49. Cetorhinidae, type C. 48. Tooth. Temporary exposure at Winterswijk-Miste, Aalten Member, Miste Bed, Middle Miocene (Hemmoorian). Coll. RGM 176 256, a: external view; b: top view; c: lateral view; d: internal view; 49. Tooth. Well Langenklint, depth 92,40 m, Schleswig-Holstein, F.R.G., Middle Miocene (Hemmoorian, Oxlundian), Lentidium Horizon. Coll. Geologisches Landesamt Schleswig-Holstein, Kiel, a: external view; b: internal view.

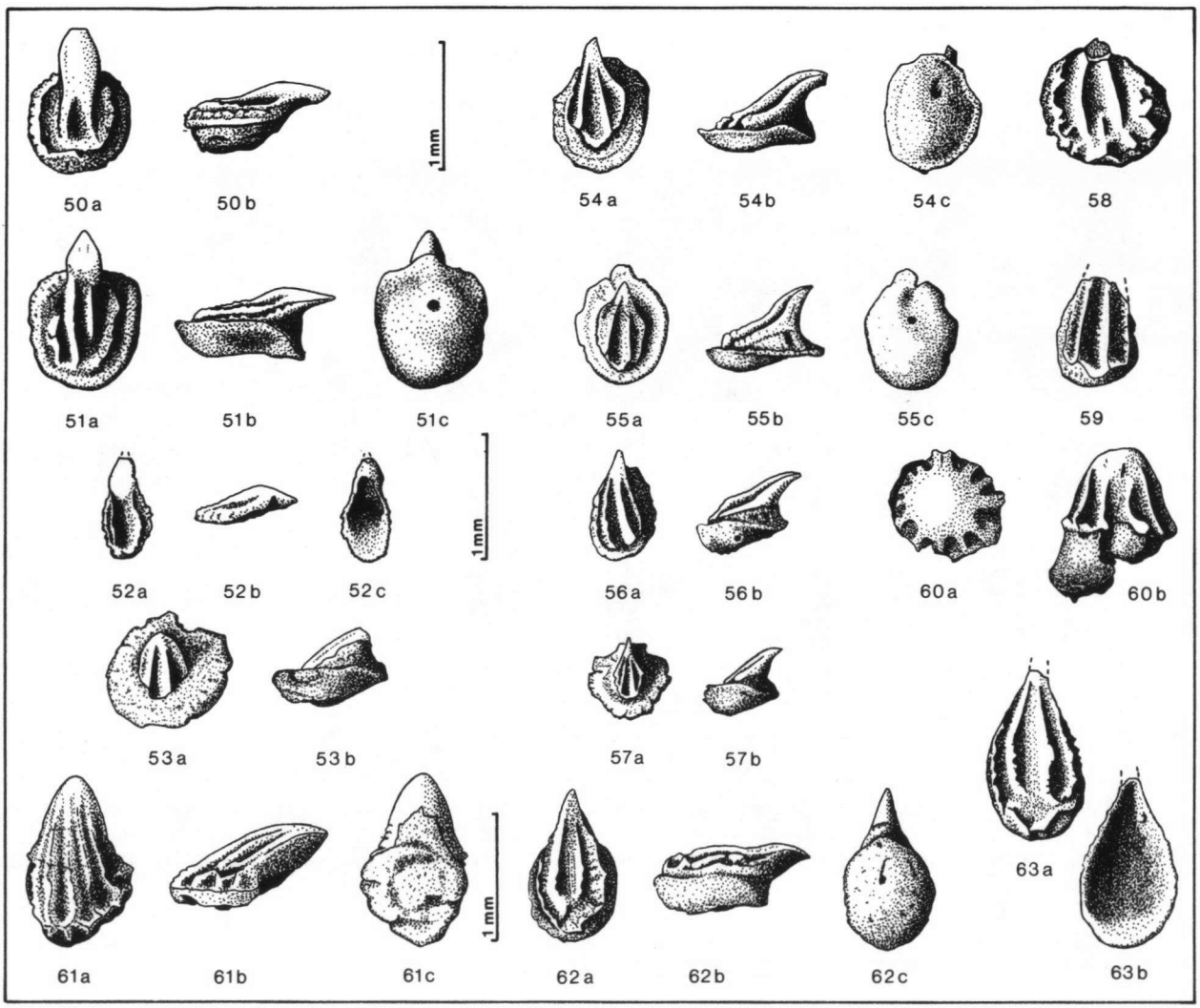
? Cetorhinidae, type D
Figs 50-66

Remarks – Finds of this type almost always concern dermal scales of very characteristic form. Their size varies from c. 0.5 to over 1 mm. As in *Cetorhinus* sp., type 1 the scales are built up from a more or less roundish root with a rather convex, perforated base. This root carries a small, widely based spine, ornamented with a number of distinct and sharp riblets or carinae.

A comparison with *Cetorhinus* sp., type 1 enables very well the distinction of dorsal and ventral scales in this fossil material. Scales from the ventral side have a rather blunt spine, somewhat arrow-head-like shaped, not erect, but in a backward direction. Compare figs 10-11 with figs 50-51. Also ventral scales are present with only a small and blunt spine, as is the case in *Cetorhinus* sp., type 1, compare figs 14 and 53.

Dorsal scales have a slender spine in rather upright position, in which the carinae are present almost to the tip, compare figs 7-8 with figs 54-57.

Furthermore the material contains larger scales with relatively a small root, illustrated in figs 58, 59, 62 and 63. These could be oral scales, but it is quite difficult to be certain in this respect, see figs 3-5. Also some hollow spines occur, without roots; compare figs 52 and 63.



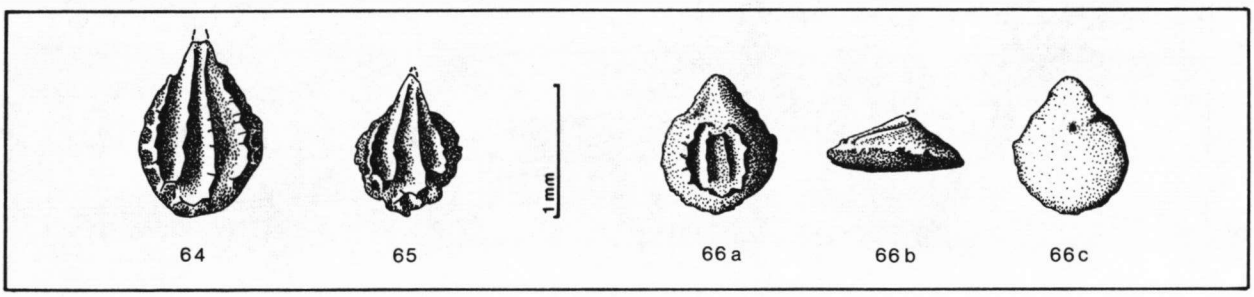
Figs 50-63. ? Cetorhinidae, type D; 50. Ventral scale. Southern part of construction-pit of Rupel tunnel at Ruisbroek, Belgium; Bassevelde Sands, Oligocene, Rupelian/"Tongrien sup.", coll. RGM 176 257, a: top view; b: lateral view; 51-57. Clay-pit "De Vlijt", Winterswijk, 41E3-143, depth 2.30-2.55 m; base of Winterswijk Member, Oligocene, Rupelian. 51-53. Ventral scales, resp. coll. RGM 176 258, 176 259 and 176 260. 54-57. Dorsal scales, resp. coll. RGM 176 261, 176 262, 176 263 and 176 264, a: dorsal views; b: lateral views; c: basal views; 58. Scale, same locality as fig. 50, coll. RGM 176 265, top view; 59. Defective scale. Well 60C.899, Beek airport, South-Limburg, depth 62.50-63.50 m. Equivalent of Woold Member, Oligocene, Rupelian. Coll. RGM 176 266. Top view; 60. Scale. Same locality as figs 51-57. Coll. RGM 176 267, a: top view; b: lateral view (root damaged); 61. Tooth ? Same locality as fig. 59, depth 56.50-57.50 m. Coll. RGM 176 268, a: External view; b: lateral view; c: basal view (root damaged); 62-63. Dorsal or oral scales? Same locality as figs 51-57, resp. coll. RGM 176 269 and 176 270, 62a: top view; 62b: lateral view; 62c: basal view. 63a: top view; 62b: basal view (hollow crown, root is absent).

The significance of the roundish, mushroom-like scale represented in fig. 60 is unclear. Its form is very aberrant from the other scales, but considering the presence of a sculpture with obvious ribs it may belong in the type D series.

The general shape of these scales agrees with that of *Cetorhinus* sp., type 1. Scales of type 2 are unknown. As noted above there are no other Elasmobranchs, as far as known, having scales with a similar shape and construction. Therefore it seems reasonable to regard these scales as Cetorhinidae, but it cannot be demonstrated with certainty. It would be obvious to consider type D scales as belonging to the same animals from which the teeth were described as types A, B and C. This

cannot be excluded, but a find from boring Beek renders this supposition doubtful. This specimen, illustrated in fig. 61, can hardly be called a scale, it could be a tooth. Especially its shape in lateral view (fig. 61b), showing a strongly inclining crown with a sharp cutting edge to half its height, resembles strongly teeth of the Recent *Cetorhinus* sp., type 1, as illustrated in figs 1 and 2. This problem seems to be quite complicated and it cannot be solved at present.

Type D spines are not uncommon in Rupelian deposits. They were found in Bassevelde Sands at Ruisbroek, Belgium (figs 50 and 58), the Boom Clay Formation (Woold Member) (figs 59 and 61) and the basal Winterswijk Member (figs 51-57, 62, 63). Also specimens from younger Tertiary deposits are known. They appear to be not rare in the Breda Formation (Edegem Sands, compare Janssen, 1971) in a well at Haamstede, the Netherlands (figs 64-65) and finally one specimen is known from the Sylt Stufe in the Morsum Cliff at Sylt, F.R.G. (Miocene to Pliocene) (fig. 66).



Figs 64-66 ? Cetorhinidae, type D; 64. Scale, top view. Well 42B.20-3, Haamstede airport, depth 149-150 m, Edegem Sands, Middle Miocene. Coll. RGM 176 271; 65. Dorsal scale. Same locality as fig. 64, depth 154-155 m. Coll. RGM 176 272. Top view; 66. Dorsal scale, spine broken. Morsum Cliff, Sylt, F.R.G., Sylt Stufe, Miocene/Pliocene (Syltian). Coll. RGM 176 273, a: top view, b: lateral view; c: basal view.

GILL-RAKERS OF CETORHINIDAE, FOSSIL AND RECENT

Cetorhinidae gill-rakers are found in Tertiary deposits from the Bassevelde Sands (Oligocene, earliest Rupelian, marine facies of the so-called "Tongrien supérieur", see Gaemers, 1984 and van den Bosch & Hager, 1984) until the Kattendijk Sands (Early Pliocene). They are most common during the late Rupelian and the Early Pliocene, in intermediate deposits they are much less frequent.

Measurements were taken from a large number of gill-rakers to obtain an insight into the morphological variability. Comparisons between Recent and fossil material, however, offer some problems. Fossil material always contains a random selection of gill-rakers from all parts of the gill-arches. In the scanty Recent material often only the central part of the gill-arches is preserved in dry collections. It was not allowed to prepare dry specimens for measurements from complete gill-arches kept in alcohol collections. Therefore inevitably measurements of Recent material are biassed.

Measurements can only be taken from completely preserved gill-rakers (see fig. 67a). The angle α between the straight lines c and d is measured and plotted on the vertical axis (fig. 67b). The ratio a : b is calculated and plotted on the horizontal axis. In this way a fair approach to the characteristic form is obtained. Less favourable results are obtained by comparing the ratios a : b and a : c. All available Recent and fossil material was measured in this way and recorded in fig. 67b.

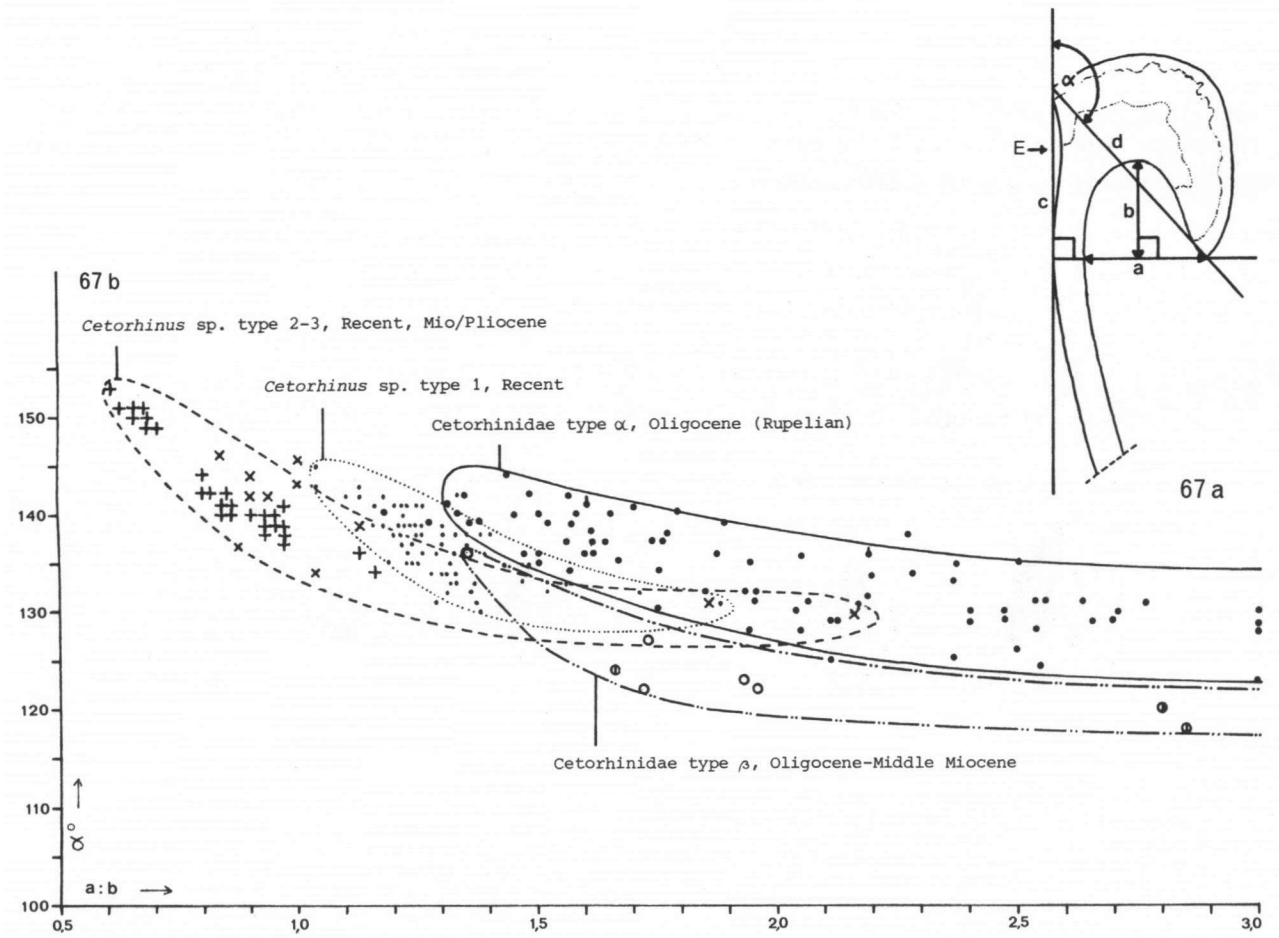


Fig. 67b. Cetorhinidae gill-rakers; survey of measurements according to text-fig. 67a

Cetorhinus sp. type 1 (Recent).
Male, 421 cm, East of Aberdeen, 14.10.1937; coll. RMNH 496 (16516) (compare txt-fig. 1).
Male, 360 cm, North Sea near Doggersbank, 19.10.1951; coll. NMR reg. nr. P. 123.

\+ *Cetorhinus* sp. 2 (Recent)
Large individual, Galley Head, England, 14.5.1914; coll. BM (NH).
Male, 600 cm, Morro Bay, California, U.S.A., June 1976; coll. Los Angeles County Museum of Natural History, California, U.S.A.

x *Cetorhinus* sp. type 3 (Middle Miocene/Early Pliocene)
Specimens from Dingden, F.R.G. (Middle Miocene, Dingdener Schichten = Aalten Member, Miste Bed), from Antwerp, Belgium (Early Pliocene, Kattendijk Sands) and material depicted by M. Leriche (1926).

● Cetorhinidae type α (Oligocene, Rupelian)
Specimens from Weinheim-Neumühle, Mayence Basin, F.R.G. (Oligocene, Rupelian, Unteres Meeressand), coll. RGM.

◖ Cetorhinidae type α (Oligocene, Rupelian)
Specimens from the Rupel area, Belgium (Oligocene, Rupelian, Boom Clay Formation), depicted by Leriche (1910)

● Cetorhinidae type β (Middle Miocene)
Specimens from the Haamstede well, the Netherlands, and from Antwerp, construction-pit for Kennedy tunnel (E3) (Middle Miocene, Hemmoorian, Behrendorfian, Edegem Sands), coll. RGM.

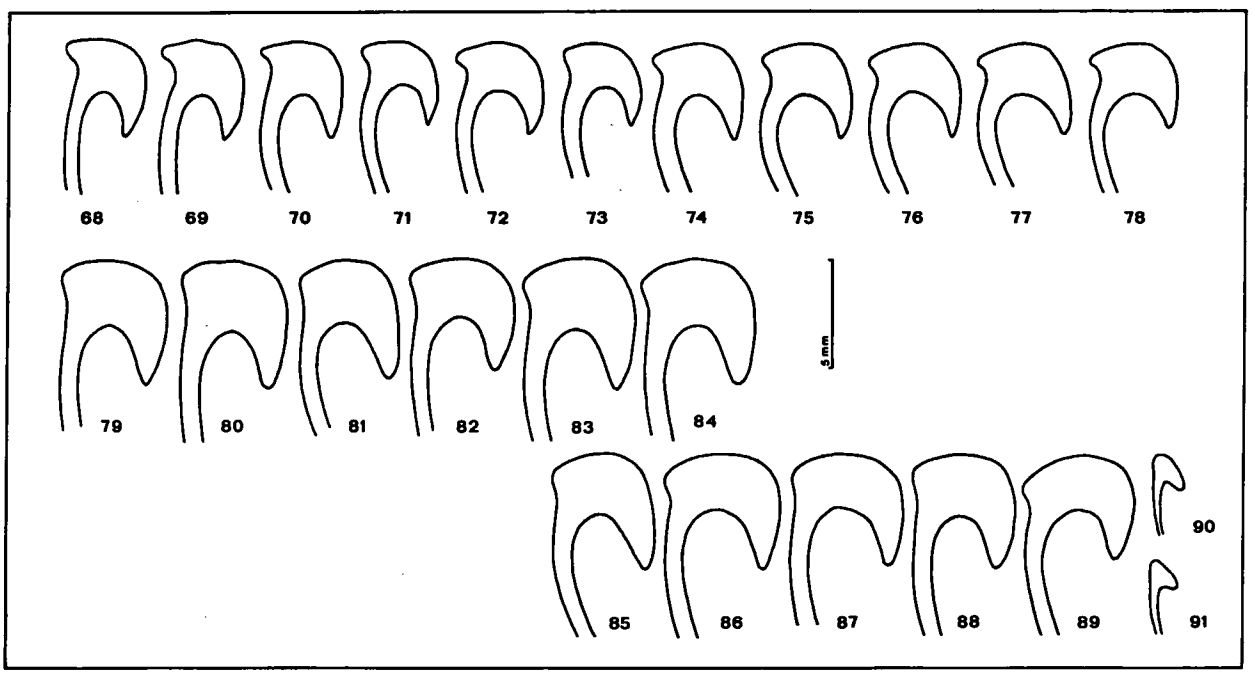
o Cetorhinidae type β (Oligocene, Rupelian)
Material depicted by Leriche (1910) from the Rupel area, Belgium (Oligocene, Rupelian, Boom Clay Formation) and from the eastern part of the Netherlands (Oligocene, Rupelian, Brinkheurne Formation), coll. RGM.

The distribution of the measurements in fig. 67b demonstrates that most of the collected gill-rakers have no specific characteristics; the centre of the graph demonstrates an overlap of the various types of gill-rakers. However, if the finds are arranged stratigraphically, it is possible to distinguish four different types. These will be discussed below.

Cetorhinus sp., type 1
Figs 68-91

Remarks – Measurements could be taken from two individuals, in both cases however the extreme lateral parts of the gill-arches are missing. It was impossible to measure these without destruction of the material.

Measured were gill-rakers of a male (length 360 cm) from the North Sea (figs 68-78) and a male (length 421 cm), also from the North Sea (figs 79-91). From this latter specimen also some gill-rakers from the extreme lateral parts of the gill-arches are depictured (figs 90-91), but these could not be measured.



Figs 68-91. *Cetorhinus* sp., type 1; gill-rakers, Recent; 68-78. Male, length 360 cm. North Sea Doggersbank, 19 October 1951, coll. NMR St. P. 123; 79-91. Male, length 421 cm. North Sea, East of Aberdeen, 14 October 1937, coll. RMNH 496 (16516).

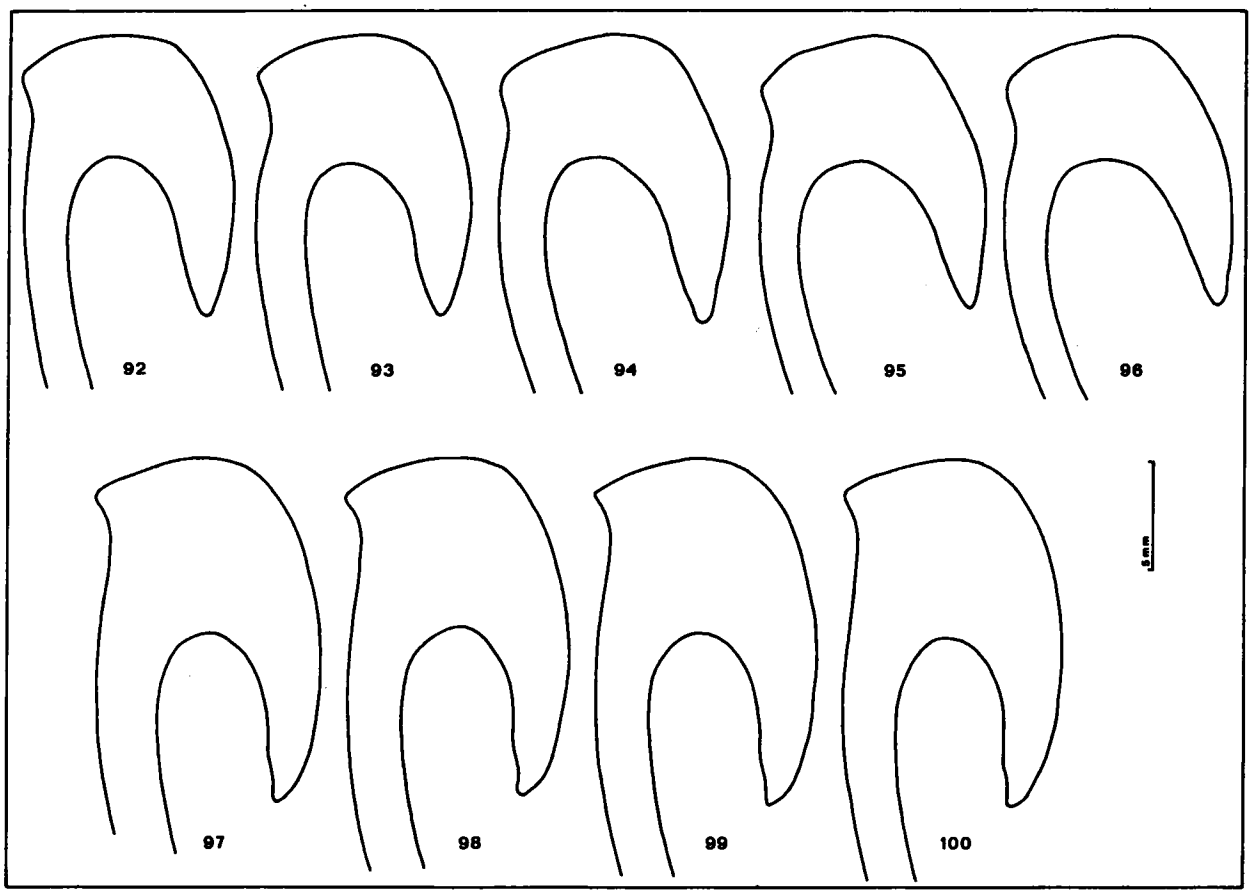
The drawings are arranged according to increasing values of the angle α, which coincides with the distribution from upper left to lower right in fig. 67b. Morphological variation is expressed in this way by the vertical distribution of the various points. It is a constant in the two individuals. Also the difference in size of the two specimens is manifest but this does not influence the measurements: in spite of the differences in size the form remains identical.

It is striking that the indentation along the straight line c near point E (fig. 67a) is much more expressed in the specimen with a length of 360 cm (figs 68-78) than it is in the specimen with length 421 cm (figs 79-89). This feature was also found in other types and may well be considered to be an individually determined natural variable.

Cetorhinus sp., type 2
Figs 92-100

Remarks - In this type also it was possible to take measurements from two individuals, but in both cases only gill-rakers from the exact middle part of the gill-arches were available. Therefore the morphological variation in the measured material is restricted.

Striking is the size of the gill-rakers. The male with a length of 600 cm (figs 92-96) has gill-rakers of which the root is more than twice as long as those in the *Cetorhinus* type 1 with a length of 421 cm. It seems unlikely that this is the result of an advanced growth stage; this would mean an extra increase of 1,5 times with respect to the body lengths. As the root parts in type 2 are longer the measurements shift to upper left in the graph (fig. 67b).



Figs 92-100. *Cetorhinus* sp., type 2; gill-rakers, Recent; 92-96. Male, length 600 cm. Morro Bay, California, U.S.A., June 1976. Coll. Los Angeles County Museum of Natural History, L.A., California, U.S.A.; 97-100. Large individual, stranded at Galley Head, England, 14 May 1914. Coll. BM(NH).

Cetorhinus sp., type 3
Figs 101-109

1926 *Cetorhinus maximus* Gunner, 1765 - Leriche, pl. 38, figs 2-5.

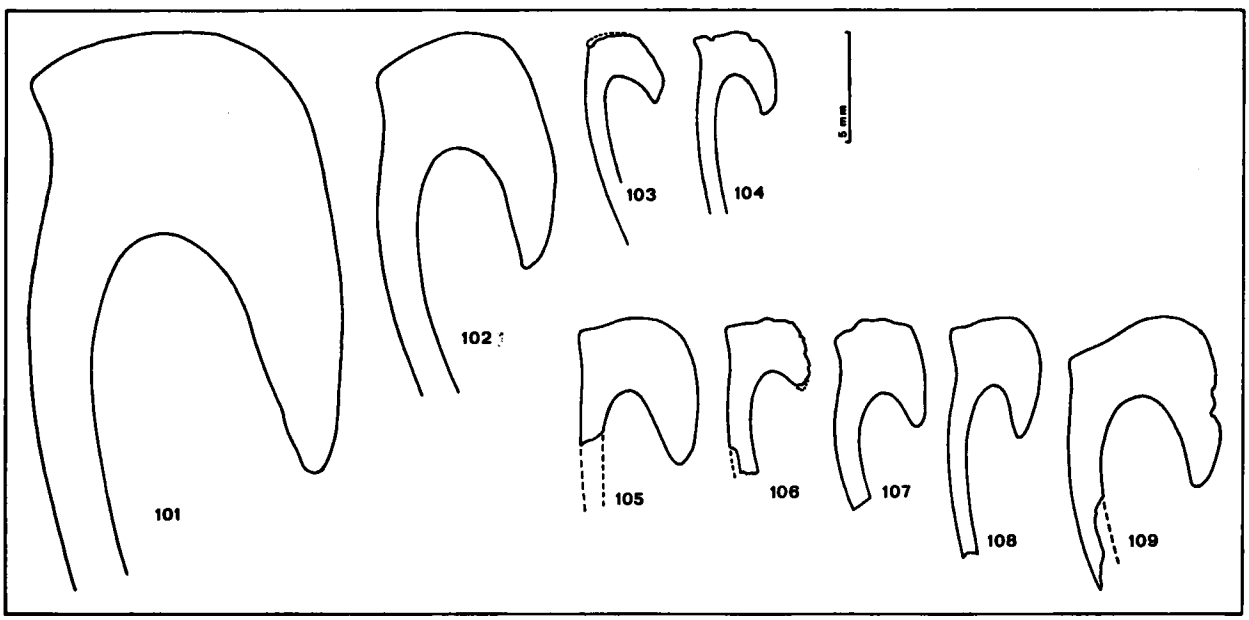
Remarks - Gill-rakers of type 3, undoubtedly belonging to the same individuals to which the teeth of type 3 belong (see above), completely agree with those of type 2 and differ only in their strati-

graphical distribution. Contrary to the teeth gill-rakers of types 2 and 3 have no specific characteristics.

As may be expected in fossil material gill-rakers are also found originating from the extreme lateral parts of the gill-arches (figs 103, 104, 106).

In Pliocene deposits very large specimens occur (fig. 101), presumably belonging to individuals with lengths to over 1000 cm. But the measurements again do not deviate from other points of this type. Again it can be established that gill-rakers increase in size during growth of the animal, but that they do not change their form. The larger specimens illustrated by Leriche (1926) match this picture very well.

Middle Miocene specimens are smaller, but considering the find of a large tooth (fig. 30) this may be coincidence. Material is scant, finds of well-preserved gill-rakers of Cetorhinidae in Middle Miocene deposits are very rare. Specimens from these deposits are represented in figs 105-109.



Figs 101-109. *Cetorhinus* sp., type 3, gill-rakers, fossil; 101. Very large specimen. Kattendijk Sands, Quay nr. 271, Antwerp, Belgium. Coll. RGM 176 274; 102. Kattendijk Sands, connection 5th Dock with Amerikadock, Antwerp, Belgium. Coll. RGM 176 275; 103. Specimen from the extreme lateral part of the gill-arch. Kattendijk Sands, construction pit for sea sluice at Kallo near Antwerp, Belgium. Coll. RGM 176 276; 104. Kattendijk Sands, construction pit at Schijnpoort, Antwerp, Belgium. Coll. P.A.M. Gaemers, Leiden; 105. Dingdener Schichten, Feinsand (= Aalten Member, Stemerdink Bed), Dingden, Königsmühle, F.R.G. Coll. RGM 176 277; 106. Specimen from the extreme lateral part of the gill-arch. Aalten Member, Miste Bed, Ticheloven near Eibergen, The Netherlands. Coll. RGM 176 278; 107-109. Aalten Member, Miste Bed, Miste near Winterswijk, The Netherlands. Respectively coll. RGM 176 279 to 281.

Cetorhinidae, type α
Figs 110-134

1910 *Cetorhinus parvus* Leriche, 1908 - Leriche, p. 294, text-fig. 91, ? 92, 94.

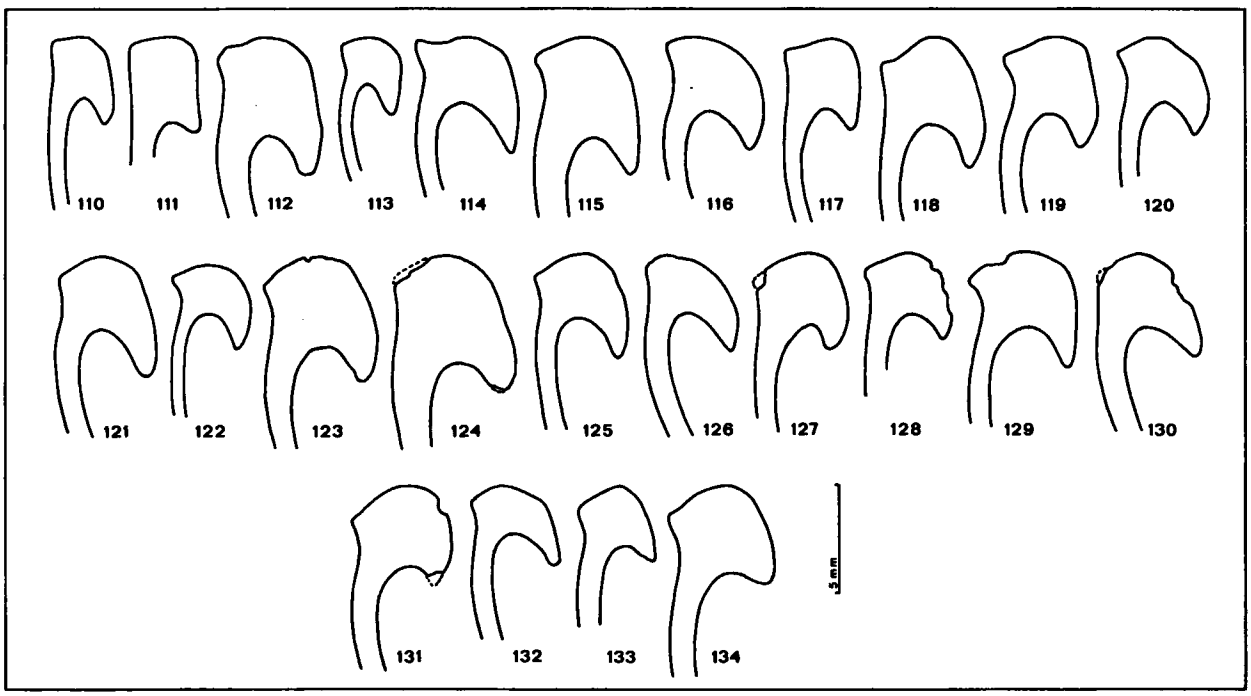
Remarks - The many well-measurable gill-rakers collected at Weinheim-Neumühle in the Mayence Basin (Oligocene, Rupelian, Unteres Meeressand) belong to this type. They constitute a curious wide assemblage in the graph of fig. 67b, overlapping the other types in part. In fact gill-rakers as

illustrated in figs 110, 114, 120 etc. cannot be distinguished from those of *Cetorhinus* sp., type 1. Others, like those represented in figs 111, 124, 127, 134 etc. differ so strongly in outline that a confusion with type 1 gill-rakers is out of the question, even without measurements. It is possible therefore that the material comprises two species. If so, however, they cannot be separated in the graph because of the large overlap. Compare figs 126 and 132 with figs 118, 127 and 131.

The measurements demonstrate distinctly that the size of the gill-rakers has no influence on their form. In the entire assemblage in fig. 67b larger and smaller specimens are equally distributed.

From the Weinheim-Neumühle locality no teeth are known that belong with certainty to the Cetorhinidae (RGM collection), so any correlation is impossible here.

Gill-rakers falling within the type α measurement distribution are also found in the Boom Clay Formation, viz. Leriche (1910, text-figs 91 and 94).

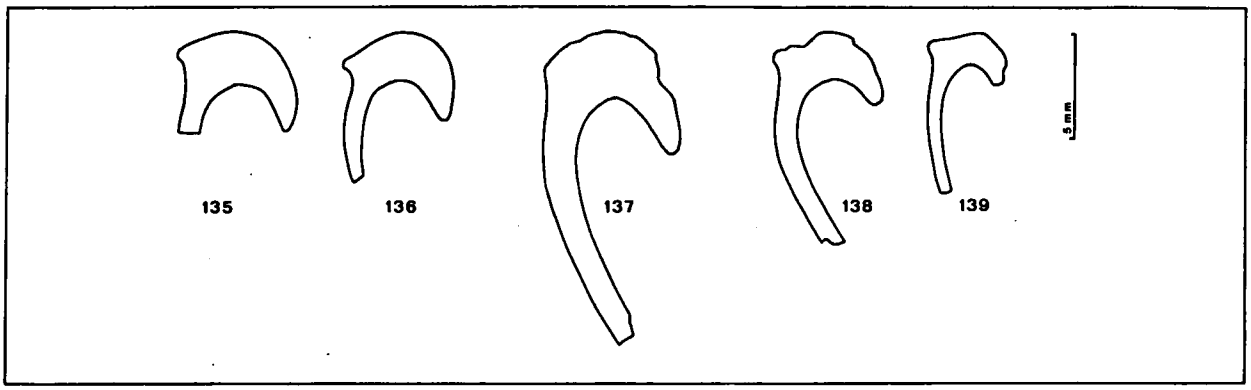


Figs 110-134. Cetorhinidae, type α, gill-rakers. Weinheim-Neumühle, Mayence Basin, F.R.G. Unteres Meeressand (Oligocene, Rupelian). Coll. RGM 176 282.

Cetorhinidae, type β
Figs 135-139

1910 *Cetorhinus parvus* Leriche, 1908 - Leriche, p. 294, text-fig. 93.

Remarks – In the Boom Clay Formation/Brinkheurne Formation gill-rakers are found with a slender, strongly curved root (figs 135-136). Among these a few measurable specimens demonstrate a constant picture. The measurements do not coincide with those of the rich Weinheim-Neumühle material. Apparently this form is absent at Weinheim-Neumühle, so it is reasonable to assume that it represents a different species. In the Boom Clay Formation/Brinkheurne Formation this type is presumably the dominating form.



Figs 135-139. Cetorhinidae, type β, gill-rakers; 135-136. Winterswijk, clay-pit "De Vlijt", The Netherlands. Brinkheurne Formation, Woold Member (Oligocene, Rupelian). Coll. M. C. Cadée, Leiden: 137. Haamstede, Well Haamstede airport, The Netherlands, depth 132-135 m. Edegem Sands, Breda Formation (Miocene, Hemmoorian, Behrendorfian). Coll. RGM 176 283); 138-139. Antwerp, construction pit for E 3 Kennedy tunnel, Belgium. Edegem Sands (Miocene, Hemmoorian, Behrendorfian). Coll. RGM 176 284 to 285.

It cannot be decided whether or not this form is related to the teeth of Cetorhinidae type B or the scales of type D. It cannot be assigned with any certainty to Leriche's *Cetorhinus parvus* since no type specimen was designated and no illustrations are joined to the original publication. In 1910 Leriche illustrated both types as *Cetorhinus parvus* Leriche, 1908.

Type β gill-rakers were also found in older Middle Miocene deposits, see figs 137-139. It cannot be excluded that this same type is still present in Middle Miocene sediments. Some specimens from Winterswijk-Miste are indicative in this respect, but they are too strongly damaged for measurements, the only way to obtain a sound identification.

SUMMARY OF CONCLUSIONS

In Recent *Cetorhinus* material two types can be distinguished: a smaller type with body lengths to 450 cm or slightly more (*Cetorhinus* sp., type 1) and a larger type with body lengths up to 1000 to 1200 cm (*Cetorhinus* sp., type 2). It is assumed that these types represent two different species. Considerable differences are demonstrated in the morphology of teeth and gill-rakers. These differences cannot be explained sufficiently as the result of continuing growth: gill-rakers and presumably also teeth do not change their form during ontogeny.

Scales could only be studied in *Cetorhinus* sp., type 1. The question which of the two types represents typical *Cetorhinus maximus* (Gunnerus, 1765) is avoided in this paper. Possibly a continued research will necessitate the designation of a neotype for this taxon.

Among the fossil material only one type is found of which teeth and gill-rakers are known that certainly belong to the same individuals. These are the remains of very large animals of Late Miocene and Early Pliocene age, but the same type is already known in Middle Miocene deposits. This type is indicated here as *Cetorhinus* sp., type 3. Presumably it is closely related with *Cetorhinus* sp. type 2. Type 2 and type 3 gill-rakers cannot be distinguished (fig 67b). Teeth, however, demonstrate considerable differences, especially in the sculpture of the crown. This is not regarded to represent a normal range of variability. The fossil material is very uniform.

Gill-rakers of fossil Cetorhinidae mostly have no specific characteristics. Their measurements demonstrate a wide overlap. Only if the various populations are separated according to their stratigraphical origin the mean values show a different position in the graph (fig. 67b).

Apart from the teeth of type 3, gill-rakers are the only proof for the occurrence of fossil Cetorhinidae. They are known from Early Rupelian to Middle Miocene, a period from which no finds are known of teeth, scales and gill-rakers in connection. Teeth and scales can therefore only be presumed to belong to Cetorhinidae.

In Rupelian deposits two, perhaps even three different types of gill-rakers are present, resulting in the impression that they represent different geographical distributions. The rich material of Weinheim-Neumühle (Mayence Basin) might comprise two types, but this is insufficiently demonstrable by the wide range of variability in the measurements. The Weinheim material is indicated here as Cetorhinidae, type α. In the Rupelian of Belgium and the Netherlands, but also in lower Miocene deposits, furthermore another type is found (Cetorhinidae, type β) of which the measurements deviate from those of the Weinheim material; compare figs 110-134 with figs 135-139. Especially the material of Weinheim-Neumühle demonstrated that the size of the gill-rakers is not decisive for their location in the graph.

It is impossible to decide which of the two, maybe three types of Rupelian gill-rakers represents the typical *Cetorhinus parvus* Leriche, 1908. Illustrations given by Leriche (1910) indicate that both type α and type β were included in the original description.

One may wonder if it is justified to introduce species solely on their gill-rakers, since largely these appear to have no specific characterics. Introduction of species based on teeth seems to be more reliable, but in fossil material it is uncertain if certain teeth really belong to Cetorhinidae when they are not found in connection with gill-rakers.

In Oligocene and also in Miocene deposits teeth are found that presumably belong to Cetorhinidae. Three types can be distinguished, that are very probably closely related: Cetorhinidae type A in lower Rupelian deposits, Cetorhinidae type B in Rupelian sediments and Cetorhinidae type C in the Middle Miocene. Up to now Late Oligocene and Early Miocene deposits have yielded no Cetorhinidae teeth. If types A to C indeed belong to the Cetorhinidae (which is probable but not yet certain), it cannot be decided which type of gill-rakers belong to which type of teeth. Teeth of Cetorhinidae types A to C demonstrate only a slight resemblance with *Cetorhinus* sp. types 2 and 3. Certainly there is no relationship with *Cetorhinus* sp. type 1.

A fourth type (? Cetorhinidae type D) is frequently found in Oligocene and Early Miocene deposits, of which it is difficult to prove that it really belongs to the Cetorhinidae. These finds mainly concern scales and possibly also a tooth the outline of which shows similarities with Cetorhinidae type 1 teeth. Further material will be necessary to obtain a better insight in this matter.

Summarizing it may be obvious that Recent and fossil Cetorhinidae comprise a much larger group of species than the two described *C. maximus* and *C. parvus*. Based on teeth the occurrence of six, maybe seven types or species may be assumed. These can be arranged in three groups or genera.

In fig. 140 the results of the observations are summarized. Relations between gill-rakers, teeth and stratigraphical distribution are indicated.

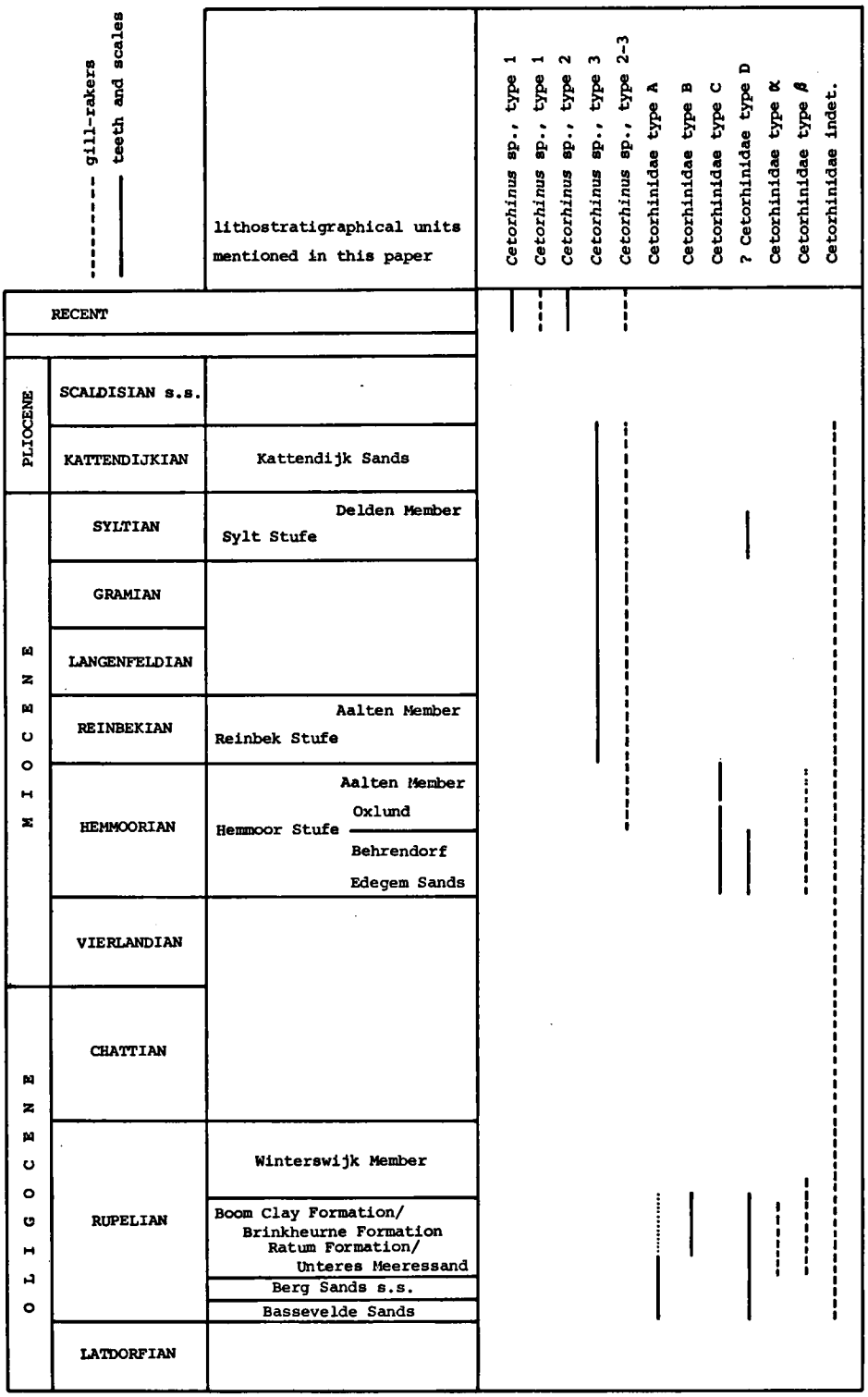


Fig. 140. Stratigraphical distribution of Cetorhinidae.

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