Attempts to predate on gadid fish otoliths demonstrated by naticid gastropod drill holes from the Neogene of Mill-Langenboom, The Netherlands

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Incomplete drill holes produced by naticid snails are occasionally found in late Cenozoic gadid otoliths from the North Sea Basin. Among the Neogene otoliths found at Mill-Langenboom naticid drill holes are relatively common. Their occurrence is linked to strata that formed under reduced rates of sedimentation and/or that reflect non-sedimentation and erosion. The Upper Miocene–Upper Pliocene deposits at Mill-Langenboom (province of Noord-Brabant, the Netherlands) constitute a condensed sequence comprising most North Sea Basin stages of this interval from the Gramian to the end of the Pliocene, as demonstrated by index taxa amongst gadid otoliths, with a considerable hiatus between Miocene and Pliocene strata. The lag deposit at the base of the Pliocene yields otoliths that were reworked from eroded Upper Miocene, and Lower and Middle Pliocene sedimentary rocks. Smaller hiatuses exist within the Pliocene. Under such conditions, isolated otoliths can occur in sufficient numbers on the sea floor or just below it, where naticids live and search for prey. The drill holes occur exclusively in otoliths of relatively small, locally abundant extinct species of cod. Most of these otoliths originate from individuals that must have been eaten by larger predators. Overall otolith shape more or less resembles the shell of tellinid bivalves. It is evident that the naticids have become aware of their mistake prior to finishing their drilling, because drilling never exceeded depths more than half the otolith thickness. This is the first published record of drill holes in otoliths.

Contents

Introduction

The Mill-Langenboom locality in the south-east Netherlands has yielded an unu-sually large number of incomplete drill holes by gastropods in fossil otoliths. Although the senior author has noted some examples of such from various localities over the years, these observations have not been published to date.

Drill holes of extant gastropods are well documented in the literature. Pioneer studies in this field are those by Boettcher (1930), Ankel (1937), Carriker (1943, 1961, 1981) and Ziegelmeier (1954). Important summaries on Recent gastropod and other drill holes have been provided by Kabat (1990), Walker (2007) and Modica & Holford (2010).

Drill holes produced by gastropods and other organisms are also well known from the fossil record. A growing number of papers have appeared during the last two dec-ades, inclusive of numerous detailed case studies. Currently, the best overviews of fossil drill holes are those by Kowalewski (1993, 2002) and Kelley & Hansen (2001, 2003). At Mill-Langenboom drill holes produced in particular by naticid gastropods occur abundantly in bivalves, gastropods, scaphopods, serpulid worms and decapod crustaceans; these have been described in a series of papers by Klompmaker (2008, 2009, 2011a, b, 2012) and Klompmaker et al. (2013).

Geological setting and stratigraphy

The former 'De Kuilen' subaquaceous sandpit at Mill-Langenboom in the north-east of the province of Noord-Brabant (Fig. 1) is renowned for its rich faunas which comprised numerous previously unrecorded extinct genera and species. Many inver-tebrate groups are represented in addition to bony fish, sharks, rays, marine birds and whales, and some species of turtle, seal and other mammals (see for example, De Vos & Wijnker, 2006; Foekens, 2008; Koretsky & Peters, 2008; Van Bakel et al., 2009; Wijnker & Olson, 2009; Formanoy & Ahrens, 2010; Mol et al., 2011; Peters & De Vos, 2012a, b, 2013). Wijnker et al. (2008) were able to take fresh underwater samples of Pliocene and Miocene sedimentary rocks by scuba diving, and described and interpreted the entire subaquaceous section (Fig. 2).

In the Late Miocene and Pliocene North Sea, sedimentation rates in the wider envi-rons of Mill-Langenboom were low; the Peel Horst there underwent much less subsid-ence than the adjoining grabens, that is, the Roer Valley Graben to the south-west and the Venlo Graben to the north-east. As a result, the total thickness of Pliocene deposits does not exceed 8 m (Wijnker et al., 2008), compared to up to 200 m in other parts of the Netherlands. A distinct unconformity is present at -15 m, accompanied with a sudden change in lithology that documents a large hiatus comprising a considerable portion of the Late Miocene and the earlier part of the Pliocene. The base of the Pliocene sedimen-tary rocks is a lag deposit, a concentration of fossils reworked from various strati-graphic horizons, as demonstrated by the occurrence of gravel, numerous shells, many abraded shark and ray teeth, bones and teeth of whales and other marine mammals, and some bird bones (Wijnker et al., 2008). Various Late Miocene vertebrates from the 10-30 cm thick basal gravel of the Pliocene support the existence of this hiatus, as do several Late Miocene otolith taxa which can only have originated from this lag deposit.
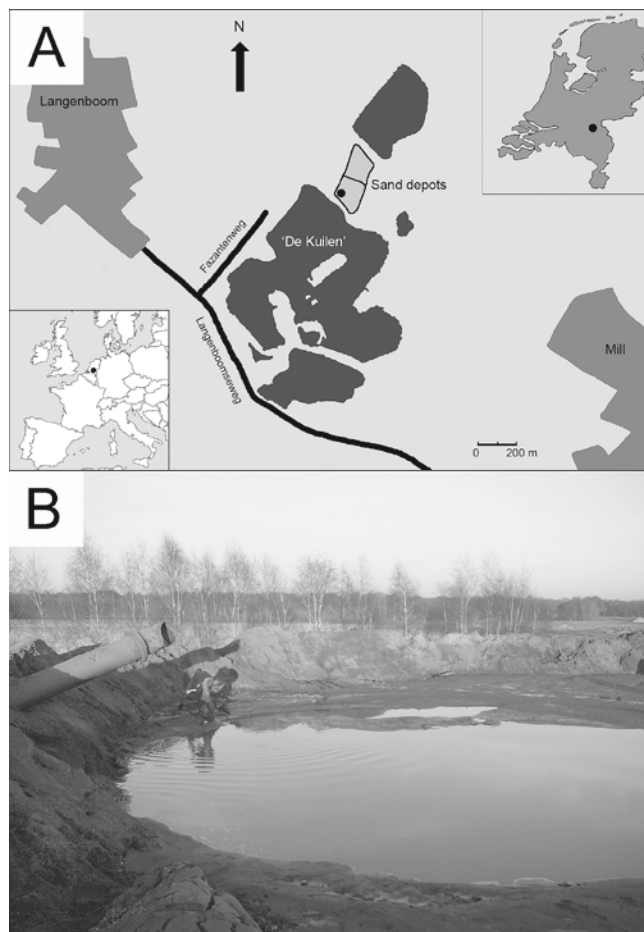
Fig. 1. Study area. A) Location of the sandpit at Mill-Langenboom and location where the samples were taken (black dot). B) The Langenboom site. The northernmost of the two depots has just been filled with sediments pumped out of the southern lake (after Klompmaker, 2009).

These have a polished, glossy surface as a result of transport and attrition; such specimens almost invariably are of a dark-bluish or blackish colour due to mineral infiltration with reduced iron. Such does not occur in fossils originating from deposits with continuing sedimentation. The index gadid otolith taxa of the Syltian (*Miogadiculus syltensis* (Gaemers & Schwarzhans, 1982)), and the Gramian (*Pseudocolliolus cuykensis* Gaemers, 1978), as well as evolutionary stages of Syltian and Gramian otoliths of the small cod genus *Conferencea*, have been collected from sediment residues at Mill-Langenboom. Thus, at least a large portion of the Gramian, all Syltian and perhaps Elbian deposits must have been eroded here, and only gravel and gravel-sized and larger fossils formed a condensed lag deposit. The Miocene sands (4-6 m thick) exploited below this lag deposit are therefore most likely of Gramian and/or late Langenfeldian age. Wijnker *et al.* (2008) dated the Late Miocene deposits at Mill-Langenboom as early-middle Tortonian, which seems to be in agreement with otolith age determinations.

Wijnker *et al.* (2008) found otoliths and other calcareous fossils exclusively in the interval between 15 and 12 m below the water level of the lake. Sediments below and
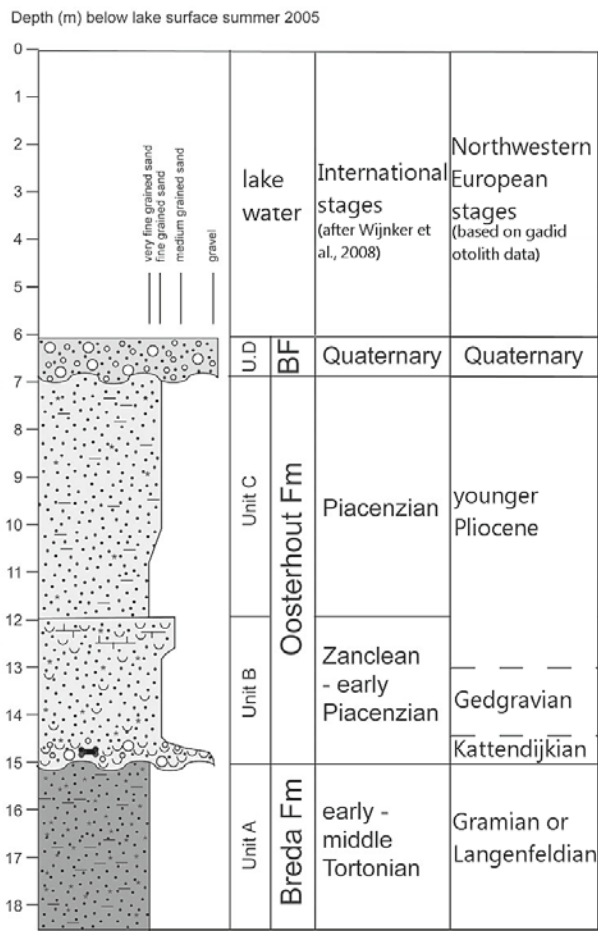
Fig. 2. The stratigraphy of the Mill-Langenboom locality based on samples and observations by scuba divers. U.D = unit D; BF = Beegden Formation; a = gravel; b = sand; c = silt; d = glauconite; e = carbonate cement; f = shells; g = bones. Northwestern European stages determined with Gadidae otolith biozonation (Gaemers, 1978, 1993, 2001). Modified and extended after Wijnker *et al.* (2008).

above this interval are (near-)entirely decalcified. Most Lower Pliocene (Kattendijkian), Middle Pliocene (Gedgravian) and a fair number of supra-Middle Pliocene otoliths from Mill-Langenboom also are polished, and a larger or smaller number of them are dark-bluish or blackish in colour, indicating erosion and transportation. However, perfectly preserved Lower Pliocene and many higher Pliocene otoliths also occur at this locality; these are indicative of *in situ* preservation of sediments of various Pliocene ages. At least three, but probably four or five, different intra-Pliocene ages can be recognized on the basis of gadid otoliths within Unit B (3 m thick) of Wijnker *et al.* (2008), between -15 and -12 m depth. Moreover, they observed worn mollusc shells and rounded shell grit in all successive strata of this interval. From all these data it can be concluded that this interval cannot possibly be comprised of a single depositional sequence as those authors suggested. Thus, at least two hiatuses, of lesser magnitude than that at the base of the Pliocene deposits, due to non-sedimentation and erosion, must exist within this calciferous interval.

Otoliths of *Gadichthys benedeni* (Leriche, 1926), the index of the Lower Pliocene (Kattendijkian), constitute the commonest bony fish taxon in the lowermost sample (-15 m). The Lower Pliocene (Kattendijkian = Zanclean) sediments are represented only within the lag deposit, judging from otolith taxa listed by those authors. We assume the Middle Pliocene (Luchtbal Member of Lillo Formation = Coralline Crag Formation = Gedgravian) to be restricted to the lag deposit as well, because Middle Pliocene otoliths show the same preservational state (colour and polishing) as those of the Kattendijkian. These data show that the base of the Piacenzian should be placed lower than suggested by Wijnker *et al*. (2008). Their stratigraphic conclusions, based on dinocysts, deviate from those based on otoliths to some extent. Some Lower Pliocene otoliths are so well preserved that it is likely that, somewhere in the (vicinity of the) Mill-Langenboom sandpit, unreworked Kattendijkian strata occur.

The chronostratigraphic conclusions based on the gadid otolith biozonation can be tied to the northwest European stages (Gaemers, 1978, 1993, 2001; see Fig. 2). The boundary between the Kattendijkian–Gedgravian complex and the higher Pliocene is shown as a dashed line, because its precise position is still unknown to us; possibly it could be defined after restudy of the otoliths listed by Wijnker *et al*. (2008). The international stages used by those authors are based on type sections in Italy. It is still impossible to correlate them accurately with the north-west European stages, on account of large climatic differences between the Mediterranean and the North Sea, and the resultant faunal and floral differences, also in the geological past.

Methods

Fossiliferous sands were suction dredged commercially at Mill-Langenboom, passed through a pipe and dumped near the lake. The junior author has processed sands from these dumps on a 1-mm mesh sieve and handpicked residues. Amongst otoliths the first four specimens with circular drill holes were recognized by the junior author. Later, the senior author screened other collections of otoliths from Mill-Langenboom for drill holes, yielding a total of four (J. Boes Collection), plus 24 (in the collections of Oertijdmuseum De Groene Poort (W. Vergoossen, 20; C. de Visser, 4)). These otoliths were also collected from residues sampled with 1-mm mesh sieves. The senior author identified the species of all otoliths, measured (with *c.* 0.01 mm precision) their length and the drill holes by means of a Wild M5 binocular microscope at the largest possible magnification for each specimen. To remove sediment from most of the drill holes, otoliths were treated in an ultrasonic bath. Unfortunately, this led to damage of the floor of some drill holes, making them deeper than the original hole. (The early stages of otoliths, toward their centre, are much more vulnerable than the outer parts, because the inner portion contains more organic material and less calcium carbonate). Photographs were taken by the senior author at the Naturalis Biodiversity Center, Leiden, using a digital multifocal camera (Leica MZ16A) with accompanying software coupled to a PC. Literature data on extant animals that produce drill holes were screened, leading to the conclusion that, with the exception of a single specimen, all drill holes in the otoliths must have been produced by naticids.
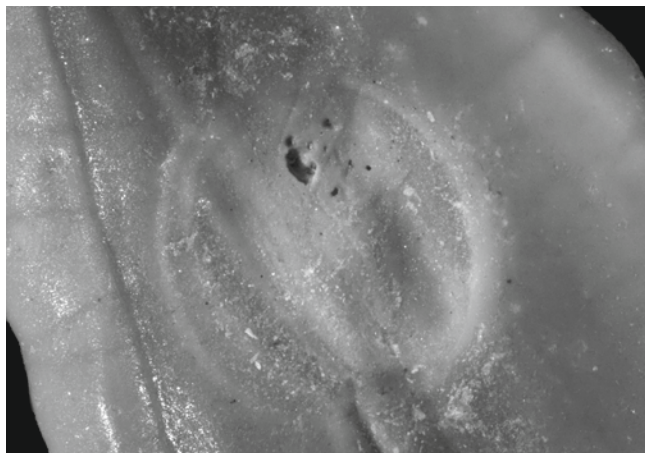
Fig. 3. Enlargement of the drill hole of a large otolith of *Doyenneichthys verticalis* (Gaemers & Schwarzhans, 1973) with large drill hole diameter of 1.40 mm, coll. MAB 4648, leg. B.W. Langeveld.

Material

Thirty-two otoliths from Mill-Langenboom exhibit drill holes (Tables 1, 2); all have been transferred to the collections of the Oertijdmuseum De Groene Poort (registration numbers: MAB 4648-4680), Boxtel, the Netherlands. Eighteen examples are found on the inner otolith surface and fourteen on the outer. Two drill holes occur in broken otoliths, that is, a young adult and a late juvenile of *Colliolus friedbergi* (Chaine & Duvergier, 1928), the commonest species of the lower Middle Miocene (Oxlundian) to the uppermost Upper Miocene (Elbian). A single drill hole occurs in the inner surface of a strongly eroded and somewhat broken, fully-grown otolith of *Pseudocolliolus cuykensis* Gaemers, 1978, the index taxon of the Gramian (Upper Miocene). Three drill holes were found in an almost fully-grown adult otolith and two smaller-sized adult otoliths of *Gadichthys benedeni* (Leriche, 1926), the index of the Lower Pliocene (Kattendijkian).

The remaining 26 drill holes were found in otoliths of *Doyenneichthys verticalis* (Gaemers & Schwarzhans, 1973), which is characteristic of the Upper Pliocene (Fig. 3; Pl. 1, figs. 1-8, 10, 11; Pl. 2 figs. 1-5). The state of preservation of the otoliths varies strongly from (near-) perfect (Pl. 1, figs. 1, 3) to strongly eroded and polished (Pl. 2, fig. 1).

It is interesting to compare instances of drill holes in the collections studied; unfortunately, otoliths contained in the W. Vergoossen and C. de Visser collections could not be counted separately, because part of their material was put together prior to our study. For that reason, only the J. Boes and B. Langeveld collections were counted (see Table 3). The vast majority of otoliths belong to *D. verticalis*. In the larger Boes Collection, one in 1,900 otoliths of this species in this assemblage has a drill hole, whereas a much higher rate is found in the Langeveld Collection, that is, one in 515 specimens. Drill holes in otoliths of other, far less numerous cod species are few, thus minimizing the chances of finding one. The same applies to the subsets of Upper Miocene otoliths within these collections, which both consist of a mere 1.7 per cent of the otolith faunas. The high rate found in the Miocene subset of the Langeveld Collection, namely one in 35 specimens, does not represent an average figure, for the larger Miocene subset in the Boes Collection does not contain any drilled otoliths.

Table 1. Naticid drill holes from Mill-Langenboom in otoliths of *Doyenneichthys verticalis* (Gaemers & Schwarzhans, 1973). Dimensions of the otoliths and the outer diameter of their drill holes, location of the drill holes, and state of preservation of the otoliths. One measurement of the diameter of two otoliths (MAB 4679 and MAB 4651) is not reliable and is therefore put between brackets: in the first specimen it is too small due to a size exceeding the width of the otolith, in the second one it is too large due to erosion.

Registration number	Otolith Length (mm)	Outer Hole Diameter (mm)	Location	Otolith Preservation	Illustration	Collector
MAB 4656	5.50	0.80 x 0.77	inner surface	slightly eroded		Vergoossen
MAB 4648	5.23	1.40 x 1.25	inner surface	well preserved	Pl. 1, fig. 1	Langeveld
MAB 4671	5.13	0.49 x 0.48	inner surface	slightly eroded		De Visser
MAB 4657	5.13	0.39 x 0.37	inner surface	well preserved	Pl. 1, fig.3	Vergoossen
MAB 4672	4.82	0.59 x 0.59	inner surface	slightly eroded		De Visser
MAB 4652	4.75	0.65 x 0.63	outer surface	eroded	Pl. 1, fig. 10	Boes
MAB 4649	4.73	0.72 x 0.70	inner surface	well preserved	Pl. 1, fig. 2	Langeveld
MAB 4680	±4.50	0.58 x 0.54	outer surface	slightly eroded, broken		Vergoossen
MAB 4660	±4.20	0.75 x 0.67	outer surface	slightly eroded, broken	Pl. 2, fig. 5	Vergoossen
MAB 4659	4.18	0.50 x 0.47	outer surface	medium eroded	Pl. 2, fig. 2	Vergoossen
MAB 4658	4.18	0.79 x 0.78	inner surface	slightly eroded	Pl. 1, fig. 5	Vergoossen
MAB 4663	±4.17	0.95 x 0.95	inner surface	well preserved, broken	Pl. 1, fig. 8	Vergoossen
MAB 4669	4.17	0.97 x 0.90	inner surface	slightly eroded		Vergoossen
MAB 4668	4.15	1.00 x 0.98	inner surface	strongly eroded		Vergoossen
MAB 4653	4.07	0.78 x 0.78	outer surface	strongly eroded	Pl. 2, fig. 1	Boes
MAB 4666	4.04	0.62 x 0.56	outer surface	well preserved		Vergoossen
MAB 4670	±4.00	0.63 x 0.62	outer surface	well preserved, broken		Vergoossen
MAB 4679	3.99	1.94 x (1.67)	inner surface	medium eroded	Pl. 1, fig. 7	Vergoossen
MAB 4667	3.99	0.38 x 0.38	outer surface	slightly eroded		Vergoossen
MAB 4673	3.86	0.50 x 0.47	inner surface	slightly eroded		De Visser
MAB 4650	3.85	0.53 x 0.53	inner surface	slightly corroded	Pl. 1, fig. 6	Langeveld
MAB 4665	3.77	0.50 x 0.47	outer surface	medium eroded		Vergoossen
MAB 4661	3.66	0.94 x 0.90	outer surface	slightly eroded	Pl. 2, fig. 3	Vergoossen
MAB 4651	3.61	0.69 x (0.87)	inner surface	eroded	Pl. 1, fig. 4	Boes
MAB 4662	3.46	0.91 x 0.72	outer surface	medium eroded	Pl. 1, fig. 11	Vergoossen
MAB 4664	±3.45	0.31 x 0.31	outer surface	medium eroded	Pl. 2, fig. 4	Vergoossen

Table 2. Naticid drill holes from Mill-Langenboom in otoliths of *Gadichthys*, *Colliolus* and *Pseudocolliolus*. Dimensions of the otoliths and the outer diameter of their drill holes, location of the drill holes, and state of preservation of the otoliths. Otolith lengths are estimated because all caudal ends are broken.

Species	Registration number	Otolith Length (mm)	Outer Hole Diameter (mm)	Location	Otolith Preservation	Illustration	Collector
G. benedeni	MAB 4654	± 8.60	1.20 x 1.41	inner surface	well preserved	Pl. 2, fig. 7	Boes
G. benedeni	MAB 4675	± 7.25	0.95 x 0.90	inner surface	moderately eroded		Vergoossen
G. benedeni	MAB 4676	± 6.60	0.85 x 0.81	outer surface	strongly eroded		De Visser
C. friedbergi	MAB 4677	± 6.45	0.84 x 0.73	outer surface	well preserved	Pl. 2, fig. 8	Vergoossen
P. cuykensis	MAB 4678	± 7.80	1.40 x 1.29	inner surface	strongly eroded		Vergoossen

Table 3. Statistics for otoliths and drill holes in the J. Boes and B.W. Langeveld collections.

Numbers and percentages of otoliths, and rates of drill holes		Boes Colln	Langeveld Colln
Total number of fish otoliths		6,919	2,015
Total number of fish species		54	35
Number of *D. verticalis* otoliths		5,700	1,546
Percentage of *D. verticalis* otoliths		82.4 %	76.7 %
Rate of drill holes in *D. verticalis* otoliths		1/1,900	1/515
Number of *G. benedeni* otoliths		506	207
Percentage of *G. benedeni* otoliths		7.3 %	10,3 %
Rate of drill holes in *G. benedeni* otoliths		1/506	zero
Number of all other otoliths (Pliocene & Miocene)		713	262
Percentage of all other otoliths (Pliocene & Miocene)		10.3%	13.0 %
Rate of drill holes in all other otoliths (Plio/Miocene)		zero	1/262
Subset	number of Late Miocene otoliths	121	35
	percentage of Late Miocene otoliths	1.7 %	1.7 %
	rate of drill holes in Late Miocene otoliths	zero	1/35

About the otoliths and the palaeobiology of the fish species

All four fossil fish species represent small extinct cods (Gadidae) more closely related to the two modern species of silvery pout, *Gadiculus argenteus* Guichenot, 1850, and *Gadiculus thori* J. Schmidt, 1914, than to other modern cod taxa. The presence of a distinct collum with a pseudocolliculum on the sulcus acusticus in the fossil otoliths clearly shows this (see Gaemers, 1989, fig. 5b).

Today, silvery pouts are the smallest living cod species; *G. thori* attains total lengths of up to 17 cm (corresponding to a standard length of 15 cm according to Svetovidov *in* Whitehead *et al*. 1986), while *G. argenteus* remains smaller, up to 15 cm. During the Cenozoic, however, many closely related small cods lived in the North Atlantic, the North Sea, the Mediterranean and the Paratethys. These were commonly (much) smaller than the Recent taxa. This is easily seen when comparing maximum otolith sizes. A comparison of otolith size in *D. verticalis* and in modern silvery pouts allows the maximum total length of the former to be estimated at *c*. 13 cm. Otoliths of the former are the commonest in the material from Mill-Langenboom, and *D. verticalis* undoubtedly was the favourite prey of many larger fish species and other predators in the North Sea during the Middle and Late Pliocene, because of their small size and large numbers. The mortality rate of small cod and other small fish species may be assumed to have been very high; much less than 50 % of all individuals survive beyond their first year (see, for example, Biagi *et al*., 1992), and the same holds true for the second and following years. The vast majority of these fossil otoliths thus must have come from fishes that were eaten by larger sea creatures. Subsequently, these otoliths went through the digestive tract of the predators, were excreted and settled on the sea floor (Gaemers, 1977). They became buried by ongoing sedimentation. Not yet fully-grown otoliths certainly originate from fishes that were eaten by predators, for they did not get the chance to complete their whole life cycle. But, also, otoliths from fully-grown specimens probably came from individuals that were preyed upon. There is no reason to assume that most (if not all) individuals died because of illnesses or physical abnormalities.

The two modern-day species of *Gadiculus* are mesopelagic to benthopelagic, and live in large schools in the deeper part of the shelf and above the continental slope at depths between 100 and 1,000 m, but mainly between 200 and 600 m (Cohen *et al.*, 1990). Otoliths of *Gadiculus* exhibit the closest resemblance with those of the extinct genus *Gadichthys* Gaemers & Schwarzhans, 1973; the genus *Gadiculus* is assumed to be derived from *Gadichthys*. It is no coincidence that *Gadichthys* occurs most frequently in the deeper parts of the Cenozoic North Sea. The abundant occurrence of otoliths of *D. verticalis* in the shallow part of the Middle and Late Pliocene North Sea shows that this species must have had a different life habit, and inhabited much shallower water. Yet they would also have occurred in large schools. The more elongated, pyriform otoliths with a shorter collum and pseudocolliculum distinguish the extinct genus *Doyenneichthys* Gaemers, 1983, from *Gadiculus*. The former genus most closely resembles otoliths of the older fossil genus *Pseudocolliolus* Gaemers, 1978, which is assumed to have been its precursor (Gaemers, 2001). Like *Doyenneichthys*, fishes of the genus *Pseudocolliolus* were more abundant in shallower water than representatives of the genus *Gadichthys*. The inferred habitat depths of *Doyenneichthys* and *Pseudocolliolus* match the similarities of their otoliths and the phylogenetic relationships gleaned from them.

The maximum total length of the fish species *Gadichthys benedeni* probably matched that of the Recent *Gadiculus thori* as determined from similar otolith lengths, that is, about 17 cm. The large number of otoliths in Lower Pliocene deposits in the North Sea Basin indicates that it must have been a species that lived in large schools as well. Otoliths of *Pseudocolliolus cuykensis* attain nearly the same size, while those of *Colliolus friedbergi* could grow slightly larger, so that their maximum fish length can be estimated to have been between 20 and 25 cm. These somewhat larger, yet still small, gadid species will undoubtedly also have been eaten by many different species of larger predators.

Description of drill holes

All drilled otoliths show regularly formed, (near-)completely circular, small to large incomplete holes; deviations of perfectly round diameters are mostly due to the uneven surface relief of the otolith. This rules out the possibility that these holes resulted from dissolution during fossilization, because such are always variable and irregular in shape. Uncommonly, a pseudo-hole is observed on the outer otolith surface, in the form of a peculiar depression in the ornament (Pl. 1, fig. 9). Such a pseudo-hole is easily distinguished from genuine drill holes because it has smooth, convex rims. No scratch marks were observed under the microscope within the holes, not even at the largest available magnification of x 62.5.

Otoliths of *Doyenneichthys* do not show a clear relationship between otolith length and outer diameter of drill holes (Table 1). A medium-sized specimen reveals the largest drill hole (Pl. 1, fig. 7); its overall size even surpasses otolith width in some places. The second largest specimen assigned to *Doyenneichthys* has the second largest drill hole (Fig. 3; Pl. 1, fig. 1). The outer diameter at the surface of the otolith ranges between 1.25 and 1.40 mm; the inner diameter between 0.94 and 1.09 mm. This hole slightly resembles a small tea cup (Cadée, 1998; Cadée & Wesselingh, 2005; Klompmaker, 2009). The diameter of the hole gradually decreases downward (that is, countersunk), where-
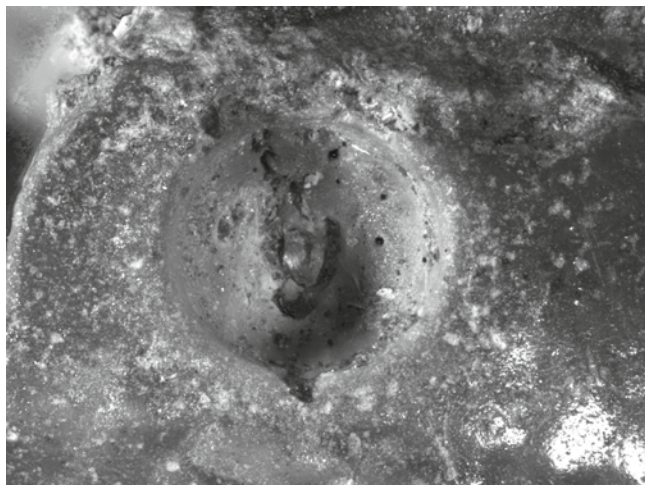
Fig. 4. Enlargement of the drill hole of the broken otolith of a young adult of *Colliolus friedbergi* (Chaine & Duvergier, 1928) with a drill hole diameter of 0.97 mm, coll. MAB 4655, leg. B.W. Langeveld.

as the wall of the upper part gradually becomes steeper. Near the centre is a weakly developed elevation that gradually passes into the somewhat lower surrounding bottom of the hole. Another specimen, however, only 0.1 mm shorter, reveals a small drill hole measuring 0.39 x 0.37 mm. The smallest otolith of the same species has the smallest hole, with an outer diameter of 0.31 mm, but another specimen of *c.* one-fifth of a millimetre longer (3.66 mm) has a hole that is three times larger in diameter (0.90 x 0.94 mm).

The shape of many drill holes is countersunk, but a central boss or elevation is often lacking. The hole in an otolith of *Gadichthys benedeni* (Pl. 2, fig. 7) shows a similar elevation to that in the largest otolith of *Doyenneichthys* (Pl. 1, fig. 2). The length of the former well exceeds that of the latter, yet both specimens have near-equal sized, large holes. One otolith has a drill hole with a low elevation at the bottom, situated at about the half of the radius of the hole (Pl. 1, fig. 11).

The coloration of the otolith inside the drill hole commonly is lighter than that of the unaffected surface. In the best example (Pl. 2, fig. 2), the surface is impregnated by bivalent iron giving it a somewhat bluish colour, whereas the deeper part of the drill hole is whitish. Other otoliths (Pl. 1, fig. 1; Pl. 2, fig. 3) also clearly show a lighter colour within the drill hole.

The hole in a broken otolith of *C. friedbergi* (Pl. 2, fig. 6) differs markedly from the others in being perfectly circular with a diameter (measured along the flat part of the otolith surface) of 0.97 mm. Close below the surface the hole at first widens on one side, whereas the wall on the other side is perpendicular to the otolith surface. From this it can be concluded that the hole was not drilled in a completely vertical orientation. The hole narrows semi-spherically close to its deepest point, while its floor is damaged slightly in its central part, mainly as a result of the activity of another, smaller boring organism (Fig. 4). The otolith surface is well polished, yet only slightly eroded, and shows small, sharp-edged pock-marks due to slipping and bumping during post-mortem transport, but initial narrowing of the hole near the surface is absent. Instead, a circular rim (diameter 1.45-1.49 mm) surrounds the hole that is 0.22 to 0.26 mm in

width. This rim is fairly clearly delimited from the remainder of the otolith surface, being characterized by a fairly regular micro-relief with tiny rounded pits and ledges. The rim is slightly lower than the rest of the otolith surface and is interpreted as an etched surface.

This drill hole lies entirely below the sulcus acusticus, below the collum and somewhat below the central portion of the cauda. This is a relatively thick part of the otolith, yet not the thickest; this is found just below the transition of collum and ostium in this particular taxon.

Damaged floors to several holes can be explained by the weaker innermost structure of otoliths. Larval and early juvenile growth increments consist of more organic matrix and less calcium carbonate (aragonite) than more outward portions of otoliths, so that the inner part is always weaker and more vulnerable to dissolution. In broken fossil otoliths it has frequently been observed that the innermost layers have disappeared completely by chemical dissolution, leaving a central cavity.

Recent drilling predation

Various groups of organisms produce drill holes – What kind of organism produced these drill holes? To date, a large number of drilling organisms are known (Carriker, 1961; Kabat, 1990; Kowalewski, 1993, 2002), inclusive of gastropods, octopods, nematodes (roundworms), and platyhelminths (flatworms). The size and/or shape of the drill holes produced by organisms other than gastropods are different (Kowalewski, 1993), apart from some octopod drill holes (personal communication Mark A. Wilson), and need not be considered further. Confusion with circular holes originating from post-mortem marine fungal degradation is unlikely as well because such holes are diminutive (Reyment & Elewa, 2003).

An increasing number of gastropod families are known to produce drill holes. Such activity is widely distributed in most, if not all, species of the Naticidae and Muricoidea (Muricidae and Thaididae). Other gastropod taxa that are known to drill include species of the Buccinidae, Capulidae, Cassidae, Eulimidae, Marginellidae, Nassariidae, Ranellidae, nudibranchs and pulmonates (Helicidae, Oleacinidae) (Walker, 2007).

Muricoidean drill holes are cylindrical with a (near-)constant diameter; this type is referred to as *Oichnus simplex* by Bromley (1981). One Australian buccinid species is known to produce cylindrical holes (Peterson & Black, 1995), while capulids also drill cylindrical holes, but leave attachment scars around them. Cassids and other tonnaceans make irregular holes, mainly in echinoderms. Some members of the Ranellidae (subfamily Cymatiinae) have been reported to drill into mussels, creating large holes (Taylor, 1998). The post-larvae of a single nassariid species, *Nassarius festivus* Powys, 1835, are known to drill holes in shells of conspecific post-larvae, but the adults apparently do not drill; this species produces holes of various shapes ranging from elongate slits to countersunk circular holes (Morton & Chan, 1997). Eulimids are small molluscs parasitic on echinoderms and create small holes in their hosts. Pulmonates are freshwater species and, as such, they need not be considered here.

Naticids produce drill holes that are easily recognized by their shape, which is different from those of snails of most other families; the diameter decreases downward

(countersunk), whereas the wall of the upper part of the hole gradually becomes steeper. This type of drill hole was named *Oichnus paraboloides* by Bromley (1981), in view of the fact that the vertical cross section of the hole has a nearly parabolic shape. It is interesting to note that the ratio between inner and outer borehole diameter in different naticid species can be very different. Grey *et al.* (2005) did experiments with live individuals of three American species, *Euspira heros* (Say, 1822), *E. lewisii* (Gould, 1847) and *Neverita duplicata* (Say, 1822), that showed this clearly. The consequence of this feature is that the steepness of the drill hole markedly varies amongst different species; in extreme cases even vertical walls exist. At least one naticid species, *Naticarius intricatoides* (Hidalgo, 1873), is known to drill cylindrical holes in the venus clam *Chamelea gallina* (Linnaeus, 1758), as noted by Guerrero & Reyment (1988) in laboratory experiments. It will be difficult – if not impossible – to distinguish such drill holes from those produced by muricaceans. On the other hand, Herbert & Dietl (2002) found some Recent muricids that produced borings indistinguishable from those of naticids (Bromley, 2004). Finally, it must be remarked that drill holes of the *Oichnus paraboloides* type are already known from the Cambrian onwards (Bromley, 2004). This is long before the existence of the naticids which probably originated in the Late Campanian, Cretaceous; up to now it is a mystery which animals made these earlier drill holes (Kase & Ishikawa, 2003).

Two marginellid species of *Austroginella*, in south-east Australia have been recorded to drill holes that are similar to those of the Naticidae (Ponder & Taylor, 1992); however, this genus does not occur in the North Sea. The parabolic holes of nudibranchs are very small and cannot be confused with those of naticids.

Recent observations of predation by naticids – Moon snails prefer to plough through the upper layers of the sea floor (Ziegelmeier, 1954; Trueman, 1968); the large muscular foot and its foremost part, the propodium, enable them to burrow into the sediment. They can also slide on or bulldoze through the sea-bed (Huelsken *et al.*, 2008). They live in and on sandy or muddy bottoms, and are often seen ploughing in the sand searching for prey. The recorded maximum depth below sediment surface is about 5 cm (calculated by Van Schooten, 1998; observed by Huelsken *et al.*, 2008). Depending on the species, naticids occur at a great variety of depths, from the intertidal zone to thousands of metres. These gastropods are carnivorous and feed mostly on bivalve molluscs, but they also attack other shelled molluscs such as scaphopods and other gastropods, even including other moon snails (Huelsken *et al.*, 2008), and shells of the serpulid worm *Ditrupa* (Klompmaker, 2012). They are thus fairly opportunistic and even cannibalistic; they often eat conspecifics and confamilials (Carriker, 1951; Kitchell *et al.*, 1981; Kabat, 1990; Kelley & Hansen, 2006). They are not known to eat carrion under normal circumstances, unlike dog whelks (Nassariidae). Naticids have a characteristic mode of catching prey by enveloping it with their large foot; after having drilled a hole into a shell they can reach the soft parts of their victims with their proboscis (Huelsken *et al.*, 2008). Most naticid species prefer to hunt for infaunal species, but some also look for epifaunal prey (Berry, 1982) and are also able to drag prey living on the sea floor into the sediment. Proof of epifaunal naticid prey in the fossil record was documented by Dietl (2003). Naticids bore holes through the shell of their victims using their radula as a mechanical tool, and the accessory boring organ situated under the tip of the pro-

boscis for secretion of acid and possibly other chemical agents (Carriker, 1981). They must be very persevering while drilling because it takes many hours to days in order to drill through shells. For example, Ziegelmeier (1954) observed that it took the common necklace shell *Euspira nitida* (Donovan, 1804) four hours to bore through a 0.1 mm thick shell of *Fabulina fabula* (Gmelin, 1791). Once the shell is bored through, the proboscis is used to consume the flesh of the prey.

Incomplete naticid drill holes from the present and the past are well known, and are usually interpreted as failed attacks due to the effectiveness of prey defensive adaptations. Thick shells of the prey and a relatively small size of the predator (inferred from a small drill hole diameter) are usually linked to incomplete drilling (Kelley, 1989; Harper & Skelton, 1993). A well-developed ornamentation like prominent spines or thick ridges is also seen as a cause for incomplete drilling, but Allmon *et al*. (1990) and Harper & Skelton (1993) did not find a good correlation with increased failure of the predator. Experimental research in aquaria, however, clearly shows that competition between naticids leads to incomplete drill holes, whereas isolated naticids always made complete, successful holes (Hutchings & Herbert, 2013). These authors also found that the percentage of incomplete drill holes became significantly higher the greater the competition between the naticids.

Fossil drilling predation in otoliths

Naticid predation at Mill-Langenboom – The drill holes in most otoliths from Mill-Langenboom are *Oichnus paraboloides*. It is reasonable to assume that the less well-preserved examples belong to the same type. The elevation in the largest drill hole in *Doyenneichthys* and in that in *G. benedeni* is not so conspicuous as the boss illustrated in a bivalve example by Fretter & Graham (1962, p. 243, fig. 129), but this may have been caused by the relatively great differences in otolith relief at the places of the drill hole; for example, the crista inferior (that is, the ventral rim of the sulcus) still can be seen as a ledge in the drill holes. Moreover, the illustration in Fretter & Graham (1962) is not a photograph, but a line drawing, so that the boss might have been exaggerated. Furthermore, a conspicuous boss probably is not typical for naticid drill holes at all. Kitchell *et al*. (1981, fig. 5) illustrated cross-sections of Recent naticid drill holes that only show weak central elevations or hardly any elevation at their bottom. More research on this topic is necessary, because such data are usually completely lacking in the literature. The low eccentric elevation on the floor of one hole (Pl. 1, fig. 11) might indicate that a boss or elevation disappears in the course of the drilling process. Kitchell *et al*. (1981) also convincingly showed that the angle of boring becomes steeper as the drilling goes deeper and that the countersunk character of the upper part of the drill hole may become very weak.

In several instances, a boss cannot be seen as a result of damage or partial dissolution of the floor of the drill holes. In spite of the absence of a central elevation in several examples, we are confident in identifying the holes in otoliths of *Gadichthys*, *Pseudocolliolus* and *Doyenneichthys*, and in one specimen of *Colliolus*, as drill holes produced by moon snails. This is not a surprise because naticids are abundant in the Pliocene of Mill-Langenboom, whereas other gastropod families that produce drill holes are either rare or altogether absent and/or drill other types of holes. This matches results pre-

sented by Klompmaker (2009), who found only a single aberrant drill hole among 347 holes in Pliocene bivalves and an unspecified number of holes in Pliocene gastropods from this locality. All other holes are of the *O. paraboloides* type and, according to Klompmaker (2012), were drilled by naticids.

Investigation of the position of the drill holes on the otoliths shows a certain degree of preference. On the inner surfaces only four (of 17) specimens with naticid drill holes have a hole on the dorsal side (Pl. 1, figs. 5, 8), and three have a hole precisely medially (Pl. 1, figs. 6, 7). Thus, a good majority of 11 specimens has the hole more or less extremely on the ventral side of the otolith. All four large otoliths of *Gadichthys* and *Pseudocolliolus* have naticid drill holes that occupy a clear ventral position, mainly or completely below the sulcus. The ventral part of all fossil gadid otoliths is invariably thicker than the dorsal part and the thickest part lies medially or somewhat ventrally. There is a majority of 11 (of 14) otoliths of *Doyenneichthys* with the hole on a substantial part of the sulcus between the posterior part of the ostium and the anterior part of the cauda, thus never far from the thickest portion of the otoliths. From these data we may conclude that most naticids that drilled the inner surface of the otolith were successful in finding a spot not far from the thickest point of the otolith.

Fourteen specimens were drilled on the outer surface, eight of them having the hole in a (near-) medial position, and ten (four of which not included in the former eight) have the hole not far from the thickest point. Thus, also on this side, naticids showed a preference to drill not very far from the thickest point of the otolith, although the preference is somewhat less strong than on the inner surface. This may be due to the fact that the outer otolith surface is more convex, whereas the inner is nearly flat. It is perhaps more difficult for naticids to drill in the outer surface; the apparent shift during drilling on an outer surface, which resulted in the most elliptical hole (length 0.91 mm, width 0.72 mm; see Table 1), might indicate this (Pl. 1, fig. 11).

A preferential, so-called stereotypic position of naticid drill holes on the same prey species and even on different, related species was observed by Berg & Nishenko (1975), who studied drill holes in a Recent species of *Nassarius* from the Atlantic coast of Massachusetts and a Late Pleistocene congener from the Pacific coast of California. Recent naticids manipulate their prey at capture when positioning it for drilling (Berg & Nishenko, 1975). Złotnik (2001) observed that larger naticids displayed more site selectivity than smaller ones. Apparently, naticids 'learn' how to find the best place on a specific prey species in the course of their life. A stereotypic position of drill holes on shelled prey is not so common among Muricoidea as it is in the Naticidae and is absent in several species (Kabat, 1990; Urrutia & Navarro, 2001; Kowalewski, 2004; Modica & Holford, 2010). The tendency of a preferential position of holes in the fossil otoliths is another argument that naticids produced these. Some of the smallest holes in the fossil otoliths have a more aberrant position (Pl. 1, fig. 3; Pl. 2, fig. 4), which is in agreement with Złotnik's (2001) observations of Recent specimens that the smaller naticids were less apt at selecting the theoretically best site to drill into.

It is understandable that small moon snails can drill only small holes. The larger the moon snail, the larger its drill hole will be. Kingsley-Smith *et al.* (2003) demonstrated that diameters of naticid drill holes correlated with predator size. They also observed that larger individuals of the naticid species *Polinices pulchellus* (Risso, 1826) selected larger cockles as prey. Many other authors have observed that larger naticids

consume larger prey (see, for example, Berry, 1982; Złotnik, 2001). Drill hole size in the fossil otoliths in general, however, does not correlate well with otolith size, yet the size of the otoliths of *Gadichthys*, *Colliolus* and *Pseudocolliolus* with holes is larger than that of *Doyenneichthys*. It is remarkable that the former never have very small holes (compare Tables 2 and 3). This perhaps reflects that larger naticids attacked larger prey items, in this case otoliths.

Furthermore, it is noteworthy that the distribution of drill hole sizes in the inner and outer surfaces of the otoliths is not random. Drill holes in otoliths of *Doyenneichthys* predominantly occur on the outer surfaces at otolith lengths between 3.45 and 4.10 mm (8 out of 12). Otoliths with lengths between 4.10 and 5.50 mm have holes with a clear preference for the inner surfaces (10 out of 14), whereas otoliths in excess of 4.80 mm reveal holes only on their inner surface. An explanation for this clear tendency might be found in changes in shape and/or ornament during otolith growth.

There is no reason to suppose that drilling predation in otoliths should cause a change in preservation potential of the otoliths. Yanes & Tyler (2009) observed on an average a poorer preservation of limpet shells that were drilled through by the muricoid gastropod *Nucella* compared to undrilled shells. They distinguished five taphonomic features, namely fragmentation, colour preservation, corrosion, bioerosion and encrustation. We did not observe bioerosion and encrustation on otolith surfaces, colour preservation is not applicable to otoliths that are originally white, it is very unlikely that naticids drill holes in fragments of otoliths and fractures do not cross drill holes. Erosion or corrosion of otolith surfaces took place before drilling and did not affect the fossilization potential of the otoliths which are still solid fossils even in that condition.

Unknown drilling predator at Mill-Langenboom – It is not certain which gastropod type produced the differently shaped drill hole in one of the otoliths of *Colliolus friedbergi* (Fig. 4; Pl. 2, fig. 6), which is nearly cylindrical. A naticid origin is unlikely, although at least one species of naticid, *Naticarius intricatoides* (Hidalgo, 1873), is known to drill such holes (Guerrero & Reyment, 1988). Most likely, the drill hole was produced by a muricacean gastropod because they drill cylindrical holes. The age of this drill hole is also debatable; *C. friedbergi* is a long-ranging form (Oxlundian to the latest Miocene). The oldest otoliths at Mill-Langenboom are of Gramian age. If the hole was made during the Gramian or younger Late Miocene, a different mollusc fauna occurred in the area, related to a more equable climate. More subtropical species can thus be expected to be represented and the number of gastropod families that drill may easily have been higher than during the Pliocene. We are confident that the polished otolith of *C. friedbergi* originates from the lag deposit at the base of the Pliocene. The drill hole was therefore made sometime during the Gramian-Middle Pliocene interval. Breakage of the otolith occurred in the geological past, because it is an old fracture, most likely during the formation of the lag deposit at the base of the Pliocene. It is unlikely that this otolith was drilled in its broken stage because the hole is close to the broken edge and the snail would probably have found out that there was nothing edible. The chance that the drill hole was made during the Pliocene is negligible and a Late Miocene age can be assumed, also in view of the greater chance of the occurrence of other drilling gastropod families in this period.

Drill holes from other localities – Drilled otoliths are uncommonly found in Cenozoic fish faunas at other localities and of different stratigraphic ages, for example in the Miocene (Oxlundian) at Miste near Winterswijk (province of Gelderland, the Netherlands). These strata formed, at least in part, at low sedimentation rates. The most common larger otolith taxon is the small cod *Colliolus friedbergi* (Chaine & Duvergier, 1928); the senior author observed only a few specimens with unfinished drill holes amongst many tens of thousands of otoliths. The genus *Colliolus* is also more closely related to *Gadiculus* than to other Recent genera, similar to other drilled otoliths. Another example was found in the Lower Miocene (Behrendorfian) glauconitic Edegem Sands of borehole Haamstede (province of Zeeland, the Netherlands); the drill hole occurs on the outer surface of an otolith of *Colliolus johannettae* Gaemers, 1976.

Relationship between drill holes and low sedimentation rates

Why would a moon snail drill a hole in an otolith? These otoliths must have remained on the sea floor for a considerable length of time or, even more likely, slightly below it, otherwise the snails could not have found the otoliths. This means that the sedimentation rate must have been low, at least periodically so. Alternatively, sedimentation came to a halt for some period and/or erosion occurred, and a lag deposit consisting of the coarser-grained fraction was all that remained.

Thanks to the low sedimentation rate, and periods of non-sedimentation and erosion at Mill-Langenboom, more otoliths (and, of course, also more mollusc shells and other skeletal remains) were left on the sea floor or closely below it at different times. Thus, there was an increased chance that moon snails happened to encounter isolated otoliths. Evidently, these snails initially took this to be a shell with flesh inside, and began to drill. Larger otoliths, especially those referable to the cod family, are relatively more massive than equally large mollusc shells.

By enveloping their prey, moon snails apparently have a (probably coarse, but sufficient) perception of size and shape of the whole body (including the shell) of a bivalve or otolith. When drilling into an otolith, nothing edible can be found in it; the moon snails obviously became aware of their mistake before finishing their drilling because none of the otoliths have been drilled completely through to the other side. Among the 31 otoliths with naticid drill holes, the depth of most holes equals half of the otolith thickness, never more than that. The snails thus gave up and left the otoliths in search for better prey. Moon snails apparently are able to estimate when they are halfway and conclude that the rest of the object must also be skeletal material, so that further drilling cannot provide food and is senseless. This is a useful trait because drilling holes is an energetically very costly, lengthy process requiring many hours or even days. In three cases drilling stopped well before reaching half of the otolith thickness, leaving only a shallow circular depression (Pl. 1, figs. 8, 11). Perhaps such drillings were made by naticids that had undertaken a previous fruitless attempt or that were disturbed. The fairly large size of these shallow depressions in any case shows that they were produced by larger (that is, older) moon snails. Taken together, all observations suggest that a completely drilled fossil otolith probably will never be found.
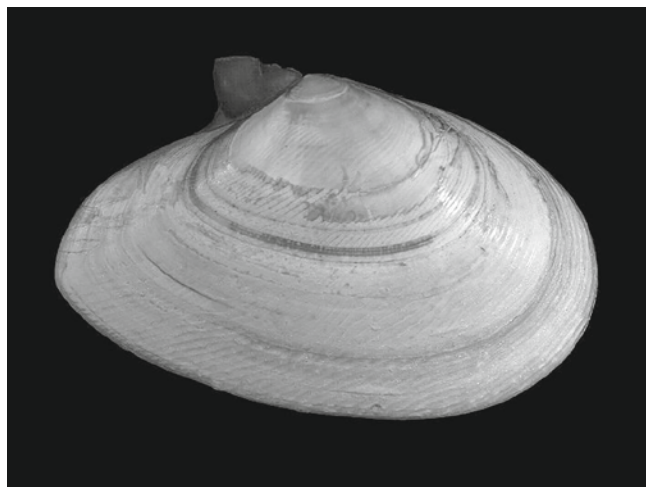
Fig. 5. Right valve of *Fabulina fabula* (Gmelin, 1791), the bean tellin, an example of the Tellinidae for comparison with the shape of the gadid otoliths (after Hans Hillewaert, Wikipedia).

Concluding remarks

To date, we are not aware of drilled otoliths in fish families other than the Gadidae. It is understandable that the chances of moon snails drilling into gadid otoliths in the North Sea Basin are far greater because these predominate in otolith assemblages in this area, and are relatively large and massive. A very small or thin otolith probably will not be seen as a potential food item. After all, otoliths with drill holes are rare and lacking from most otolith faunas. Usually many tens of thousands of otoliths from a suitable stratum at a suitable locality need to be collected and screened in search of a single hole. Thus, moon snails and other drilling snails erred only on rare occasions. The mistake in drilling otoliths of gadid species very likely was enhanced by an overall similarity in shape with shells of the bivalve family Tellinidae, which are a common prey item for naticids (see Fig. 5). Being infaunal, many tellinids are oriented horizontally in the sediment, lying on their left side, whereas most other infaunal molluscan species live in a vertical position. Otoliths deposited in sediment layers usually also will have a horizontal orientation, as this is their most stable position. This is probably an additional factor that naticids will drill holes in these otoliths more easily. From this the conclusion can be drawn that naticids are only able to discern rough forms.

The presence of naticid drill holes in fossil otoliths indicates that these snails sometimes are unable to distinguish between live and dead objects as their prey. Unsuccessful drill holes in otoliths thus may help to explain why more than one naticid drill hole can be found in some shells (Klompmaker, 2008). Naticids are known to prey mostly on living organisms and rarely eat carrion. Preying on dead objects is not yet known from observations on recent naticids, but apparently they attack sometimes even dead, inedible objects such as otoliths. So why should moon snails not occasionally also, by accident, drill a hole in empty molluscan shells? About this, however, we can never be completely sure with only fossil examples available; this can only be proved by direct observation in the living world. A more likely possibility for the existence of more than

one complete drill hole in any molluscan shell is that the mollusc was not killed and eaten during an earlier drilling attempt. Important observations were made by Hutchings & Herbert (2013). They found multiple drill holes in shells when naticids were competing with one another due to their large numbers per surface unit. Not only did they find one complete drill hole and one or more incomplete ones, but also two or more complete drill holes in one shell. Apparently, the second naticid that pushed aside the first one after it finished a complete hole without having the chance to eat its prey, could not find and use the first drill hole, and started the time consuming process anew. This, again, is a strong argument that naticids can only discern rough forms. Overcrowding of naticids resulting in competition may be an additional reason for drilling holes in otoliths. It would, therefore, be interesting to investigate the number of multiple drill holes of naticids in molluscan shells from the Mill-Langenboom locality. High competition, though, between naticids cannot explain why no otolith has been drilled through completely, for Hutchings & Herbert (2013) found up to 21.3% incomplete drilling with high competition. Thus, even in such cases the majority of drill holes were complete.

Acknowledgements

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Plate 1

Figs. 1-11. Otoliths of *Doyenneichthys verticalis* (Gaemers & Schwarzhans, 1973), Late Pliocene. Figs. 1-8, 10-11. Unfinished drill holes. Fig. 9. Otolith with pseudo-hole, coll. MAB 4674, leg. W. Vergoossen.
Figs. 1, 2, 6. Drill holes on inner surfaces, coll. MAB 4648-4650, leg. B.W. Langeveld.
Figs. 4, 10. Drill hole on inner surface (Fig. 4), drill hole on outer surface (Fig. 10), coll. MAB 4651-4652, leg. J. Boes.
Figs. 3, 5, 7, 8, 11. Leg. W. Vergoossen. Drill holes on inner surfaces: Figs. 3 (coll. MAB 4657), 5 (coll. MAB 4658), 7 (coll. MAB 4679), 8 (coll. MAB 4663). Drill hole on outer surfaces: Figs. 11 (coll. MAB 4662).

All otoliths are from the locality Mill-Langenboom and are illustrated at the same magnification, indicated by the bar. All specimens are in the collection of the Oertijdmuseum De Groene Poort in Boxtel (MAB registration numbers).
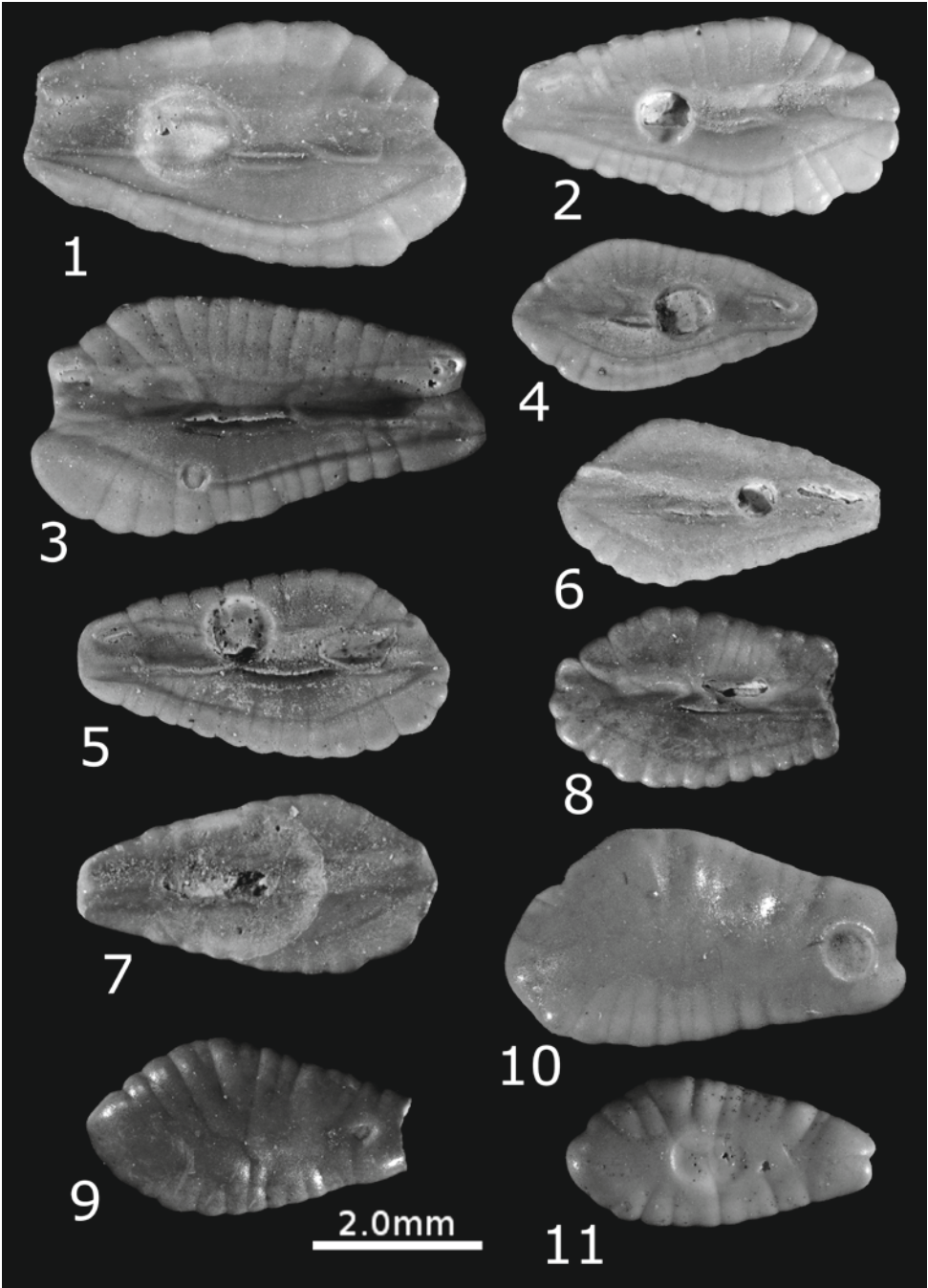
Plate 2

Figs. 1-5. Otoliths of *Doyenneichthys verticalis* (Gaemers & Schwarzhans, 1973), Late Pliocene.
Fig. 1. Drill hole on outer surface, coll. MAB 4653, leg. J. Boes.
Figs. 2-5. Leg. W. Vergoossen. Drill holes on outer surfaces, coll. MAB 4659, 4661, 4664, 4660, respectively.
Fig. 6. Broken otolith of a young adult of *Colliolus friedbergi* (Chaine & Duvergier, 1928) from the Late Miocene with an unfinished drill hole on its inner surface, coll. MAB 4655, leg. B.W. Langeveld. Length of this incomplete specimen is 5.45 mm.
Fig. 7. Incomplete otolith of an almost fully-grown adult of *Gadichthys benedeni* (Leriche, 1926) from the Early Pliocene with an unfinished drill hole on its inner surface, coll. MAB 4654, leg. J. Boes.
Fig. 8. Incomplete otolith of *Colliolus friedbergi* (Chaine & Duvergier, 1928) from the Late Miocene with an unfinished drill hole on its outer surface coll. MAB 4677, leg. W. Vergoossen.

All otoliths are from the locality Mill-Langenboom and are illustrated at the same magnification, indicated by the bar. All specimens are in the collection of the Oertijdmuseum De Groene Poort in Boxtel (MAB registration numbers).