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OTOLITH BIOSTRATIGRAPHY AND PALEOECOLOGY OF WELL EIDELSTEDT-1, NORDGETRÄNKE (HAMBURG AREA, F.R.G.), AND COMPARISON WITH SOME OTHER LANGENFELDIAN AND GRAMIAN OTOLITH FAUNAS IN THE NORTH SEA BASIN

by

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The results of the otoliths from well Eidelstedt-1 are given comprising the 129-332 m depth interval which covers the Reinbekian, the Langenfeldian and part of the Gramian. Three new species are described: *Pseudocolliolus eidelstedtensis, P. hinschi* and *Neocolliolus vikingensis*.

Three otolith biozones are recognized: the Pseudocolliolus eidelstedtensis Lineage Zone (c. 159.5-at least 198 m), the Pseudocolliolus hinschi Lineage Zone (c. 133-c. 159.5 m), and the Pseudocolliolus cuykensis Lineage Zone (c. 129-c. 133 m). The first two zones are new. The three key species of these zones are successive members of one rapidly evolving cod lineage. As redefinition of the Langenfeldian/Gramian boundary is proposed the boundary between the *P. eidelstedtensis* and *P. hinschi* zones at c. 159.5 m.

A succession of six otolith communities is described from well Eidelstedt-1, showing a rather shallow shelf sea at the beginning of the Reinbekian which rapidly became deeper. In the later Reinbekian and Early Langenfeldian greatest sea depths (200 m or more) were attained after which the sea gradually became shallower again (to 50 m or somewhat less). Comparisons and correlations are made with localities at Hohen Woos and Gram, and with wells at Assel, Beugen and Cuyk.

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SAMENVATTING

De otolieten van het trajekt 129-332 m uit boring Eidelstedt-1 worden beschreven. Het materiaal is afkomstig uit het Reinbekien, Langenfeldien en een deel van het Gramien. Er werden drie nieuwe soorten gevonden: *Pseudocolliolus eidelstedtensis, P. hinschi* en *Neocolliolus vikingensis*.

Er kunnen drie otolietenzones worden onderscheiden: de Pseudocolliolus eidelstedtensis Lineage Zone (ca 159,5-tenminste 198 m), de Pseudocolliolus hinschi Lineage Zone (ca 133-ca 159,5 m), en de Pseudocolliolus cuykensis Lineage Zone (ca 129-133 m). De twee eerstgenoemde biozones zijn nieuw. De drie gidssoorten van deze zones zijn opeenvolgende leden van één snel evoluerende reeks van een klein kabeljauwengeslacht. Er wordt voorgesteld om de grens Langenfeldien/Gramien te herdefiniëren en te leggen op de grens tussen de P. eidelstedtensis Lineage Zone en de P. hinschi Lineage Zone, welke zich ongeveer op 159,5 m onder maaiveld bevindt.

Van boring Eidelstedt-1 wordt een opeenvolging van zes otolietengezelschappen beschreven, die aantonen dat er een tamelijk ondiepe shelfzee bestond aan het begin van het Reinbekien. De zee werd snel dieper en bereikte in het latere Reinbekien en in het Vroeg-Langenfeldien de grootste zeediepten (200 m of meer). Daarna werd de zee geleidelijk aan weer ondieper (minimaal 50 m of iets minder). Vergelijkingen en correlaties worden gemaakt met de vindplaatsen Hohen Woos en Gram, en met de boringen Assel, Beugen en Cuyk.

INTRODUCTION

The first author who described otoliths from the Late Miocene of northern Germany was Koken (1891). In his pioneer study he introduced various new species of this period, at that time not yet subdivided in stages. Wollemann (1906) mentioned some of Koken's species from the Miocene of the Lüneburg area which apparently belong to the later established Langenfeldian stage, namely *Gadus venustus* Koken, 1891 and *Sciaena holsatica* Koken, 1891. He mentioned also *Morrhua lata* Koken, 1891, *Otolithus* cf. *umbonatus* Koken, 1891 and *Otolithus* (inc. sed.) *lunaburgensis* Koken, 1891, but these otoliths must come from Middle Oligocene deposits, that also crop out in this area. Important progress was made by Weiler in his comprehensive publication of 1942, among other things describing a large number of Late Miocene otoliths from many localities in northern Germany and Denmark. Weiler did not subdivide the Late Miocene material although Staesche (1930) had already introduced the Syltian ("Sylter Stufe") and Langenfeldian ("Langenfelde Stufe") on the basis of different mollusc assemblages. Hinsch (1952) separated the Gramian ("Grammer Stufe") from the Syltian because he could characterize it by means of the mollusc assemblages.

The only study of a comprehensive Langenfeldian otolith fauna available at present is that of Heinrich (1969). The gadids of this fauna were partly revised by Gaemers (1973, 1976b). The only extensive Syltian otolith fauna known to date is that of the type locality of this stage at the Morsum

Cliff (Gaemers & Schwarzhans, 1982; Gaemers, 1983). A comparable study for the Gramian is still missing, but a lot of data implicitly occur in Weiler (1942). A subdivision in Langenfeldian, Gramian, Syltian and other otolith material is given by Menzel (1986), but he found only a small number of species in the Late Miocene. The otolith drawings in his paper unfortunately are of a very poor quality and quite a few species need systematical revision, as I could observe from the material which is at my disposal. A survey of the distribution of gadid otoliths of different northern German regions and other western European areas is given by Gaemers (in press) based on data from the literature and much unpublished material from boreholes and exposures. The situation of the localities from which otoliths are described or mentioned here is given in fig. 1.

The following abbreviations are used: OL: otolith length, OH: otolith height, OT: otolith thickness (all in mm); RGM: Rijksmuseum van Geologie en Mineralogie, Leiden; GLSH: Geologisches Landesamt Schleswig-Holstein, Kiel; NLBF: Niedersächsisches Landesamt für Bodenforschung, Hannover; MB: Museum für Naturkunde der Humboldt-Universität zu Berlin, East Berlin; RGD: Rijks Geologische Dienst, Haarlem.

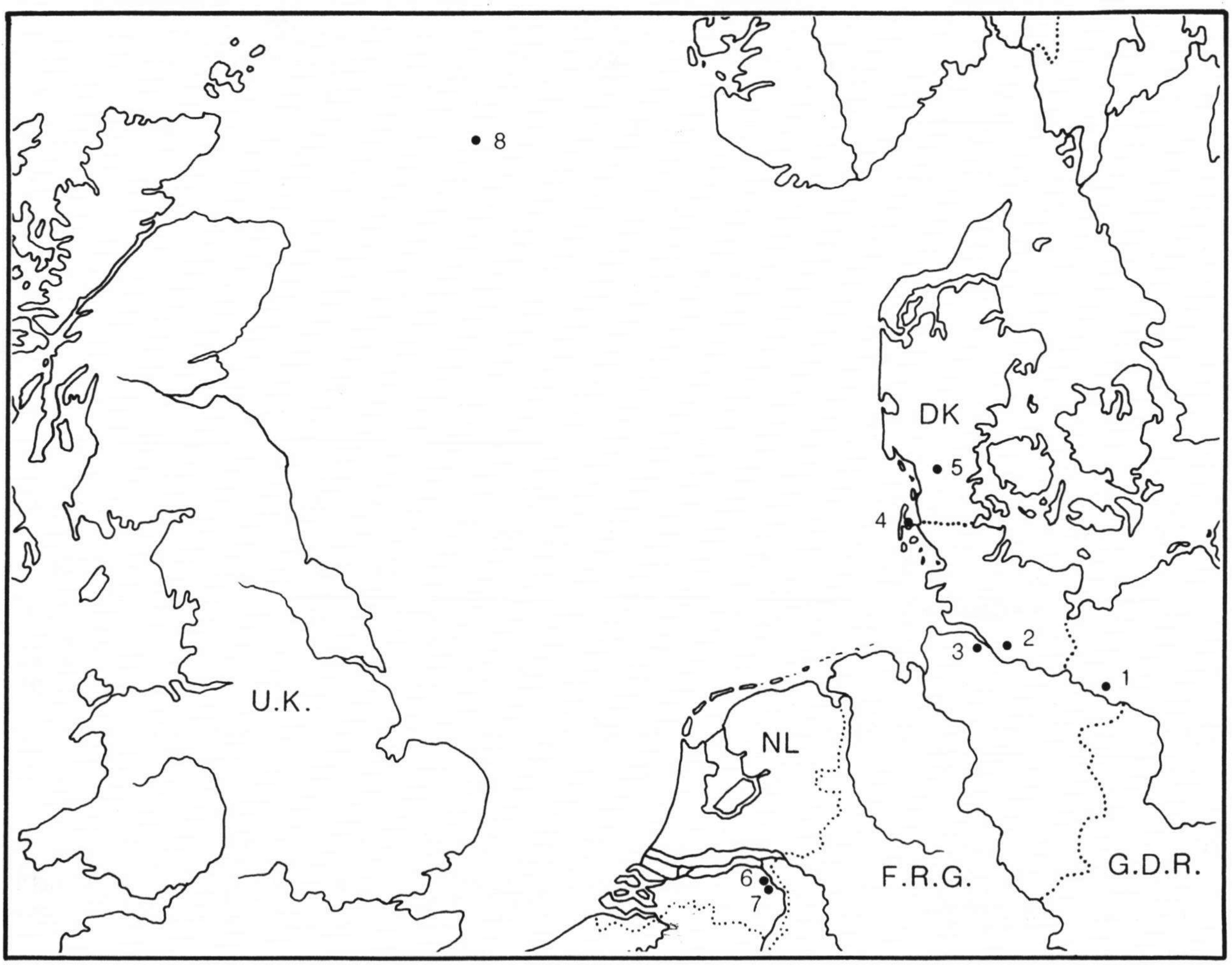


Fig. 1. Map with the localities of otoliths discussed in this paper. 1. Hohen Woos, 2. Eidelstedt-1, Nordgetränke, 3. Assel, 4. Morsum Cliff, Sylt, 5. Gram, 6. Cuyk, 7. Beugen, 8. well 9/18-2, southern part of Viking Graben.

Well 9/18-2 in the Viking Graben (formerly known inofficially as "Boring J") was drilled by Conoco Ltd. more than 10 years ago and is a released well.

Depths in well sections are given in m below surface, unless stated otherwise.

BIOSTRATIGRAPHY OF WELL EIDELSTEDT-1, NORDGETRÄNKE

Well Eidelstedt-1, Nordgetränke was designated as the neostratotype for the Langenfeldian and Reinbekian (Hinsch, 1986b). It is therefore important to know the distribution of otoliths in this well. The available otolith material was identified (see table 1). The relative scarceness of small otoliths compared with otolith faunas from the clay-pits at Hohen Woos (Langenfeldian) and Gram (Gramian) strongly suggest that the Eidelstedt samples originally contained more otoliths than the ones studied in this paper. From this it may be expected that the original frequencies and percentages of many species differed from those in table 1. In spite of the probable incompleteness of the otolith record of this well important conclusions can be drawn. Three otolith biozones can be recognized of which two are described here for the first time.

A few otoliths of *Pseudocolliolus cuykensis* Gaemers, 1978 occur in the samples 135-138 m and 141-143.5 m of well Eidelstedt-1. This species is the key species of the P. cuykensis Lineage Zone (Gaemers, 1978). They occur together, however, with otoliths of its precursor, *Pseudocolliolus hinschi* n. sp., so apparently they have been subjected to caving. The shallowest occurrence of *P. hinschi* is in the sample 132-135 m. One sample higher (129-132 m) has furnished only one poorly preserved otolith, but also a lot of fish bones; above this sample otoliths and molluscs are absent. These observations point to decalcification of these Late Miocene beds, a phenomenon which is for instance well-known from many Late Miocene deposits and localities in the eastern part of the Netherlands (van den Bosch et al., 1975). The good preservation of the *P. cuykensis* otoliths indicates that they must come from the sample 132-135 m, so it can be concluded that the boundary between the P. cuykensis and P. hinschi Lineage Zones occurs within the sample 132-135 m. For convenience this boundary will further be denominated c. 133 m. The upper boundary of the P. cuykensis Lineage Zone probably occurs at 125 m where the boundary between the Syltian and Gramian was drawn (Hinsch, 1987). The thickness of this biozone thus probably amounts to about 8 m. From the Syltian a descendant of *P. cuykensis* is known, *Pseudocolliolus curvidorsalis* Gaemers, 1983. The Syltian belongs to the Doyenneichthys syltensis Range Zone (Gaemers, in press).

Pseudocolliolus hinschi n. sp. is the key species of the lineage zone of the same name. The first occurrence of its precursor, *P. eidelstedtensis* n. sp., is in the sample 159-160 m which also contains *P. hinschi*. Therefore the lower boundary of the P. hinschi Lineage Zone is drawn at 159.5 m. The thickness of this biozone consequently amounts to 26 or 27 m. A downwards decreasing number of *P. hinschi* otoliths was found to a depth of 187 m together with *P. eidelstedtensis*. This simultaneous occurrence can only be explained by downhole caving of the *P. hinschi* specimens. Well Eidelstedt-1 was drilled by means of the air lift method which makes contamination by caving possible. The P. hinschi Lineage Zone lies completely within a sandy interval in which caving is much sooner to be expected than in deeper horizons consisting mainly of mica clays. Initially the caving problem was underestimated, hampering the identification of the *Pseudocolliolus* species. The P. hinschi Lineage Zone is a new otolith zone; its lower boundary is defined by the evolutionary transition of *P. eidelstedtensis* into *P. hinschi*, and its upper boundary by the evolutionary transition of *P. hinschi* into *P. cuykensis*.

Chronostratigraphy (sensu Hinsch, 1986b / sensu Gaemers, this paper)	Gadid otolith zones	depth in m below surface	*Conferencea irregularis* (Gaemers, 1973)	*Neocolliolus vikingensis* Gaemers, n. sp.	*Trisopterus capelanus* (Lacepède, 1800)	*Trisopterus spectabilis* (Koken, 1891)	*Pseudocolliolus hinschi* Gaemers, n. sp.	*Pseudocolliolus cuykensis* Gaemers, 1978	*Colliolus friedbergi* (Chaine & Duvergier, 1928)	*Trisopterus luscus* (Linnaeus, 1758)	*Merlangiogadus cognatus* (Koken, 1891)	*Gadichthys miocenicus* (Heinrich, 1969)	*Trisopterus* sp. indet.	*Merluccius albidus* (Mitchill, 1818)	*Pseudocolliolus eidelstedtensis* Gaemers n. sp.	*Gadichthys venustus* (Koken, 1891)	*Phycis* sp.	Gadinarum *brinki* (Posthumus, 1923)	Gadinarum sp. indet.	*Argyrosomus holsaticus* (Koken, 1891)	*Umbrina* sp.	*Diaphus debilis* (Koken, 1891)	*Diaphus* sp. indet.	*Synagrops teutonicus* (Weiler, 1942)	total number of otoliths
			Gadidae																	Sciaenidae		Myctophidae		other	
GRAMIAN	P. cuykensis Lineage Zone	129-132	1																						1
		132-135	1	1	3	1	2													1	1				10
	Pseudocolliolus hinschi Lineage Zone	135-138	1		1	2	8	2	6	1	1									1					23
		138-141					2		1																3
		141-143.5				1	1	1												1					4
		143.5-144			1																				1
145		145-146.8		1			3																		4
		147-149.5		1	2	3	4		4	1		1	1							5					22
		150-153					2													1					3
		153-154.5					2																		2
		154.5-155		1			2		1																4
		155-156					3																		3
		156-157			1	1	4		3	1				1											11
		157-158				1	1		1	1															4
		158-159					5		4			1								2					12
		159-160				4	10		2						1					1					18
LANGENFELDIAN (159.5)	Pseudocolliolus eidelstedtensis Lineage Zone	160-161					2																		2
		161-162	1		1		3																		5
		162-163					2								1										3
		163-164	2				1																		3
		164-165					1		1																2
		165-166					1		1						1										3
		166-167													1										1
		167-168	1						2						2*				1						6
		168-169										1													1
		169-170					1																		1
		177-178													1										1
		178-179		1																					1
		179-180					1																		1
		180-181							1						1										2
		181-182							1						1				1						3
		185-186	1																1						2
		186-187	1				1		2																4
		187-188							1		1				1				1						4
		192-194				2			1						3										6
		194-195									1														1
		195-196									2				2				1						5
		196-197									1											1			2
		197-198		2					3		1				3				3						12
		201-202	2						1		1					1									5
		202-203							2																2
		206-207				1					1					1			1						4
		207-208									1											1			2
		208-210				1			1		2														4
		212-214															1			1					2
		214-215																				2			2
		218-220							1							3							2		6
		220-222																					1		1
		234-262.5	LÜNEBURGIAN and LEVENSAUIAN substages (no otoliths)																						
REINBEKIAN		307-310																				4		1	5
		324.4-325.1							1									1							2
		327-328							9																9
		328-329							2		1														3
		331-332							3																3

Table 1. Distribution of otoliths in well Eidelstedt-1, Nordgetränke (Hamburg Area). Numbers of otoliths per sample (including countable fragments) are given. One of the two specimens indicated with an asterisc is *P.* aff. *eidelstedtensis*.

The second new otolith zone is the Pseudocolliolus eidelstedtensis Lineage Zone. Its lower boundary lies at least as deep as 198 m, but may be situated even deeper, since no *Pseudocolliolus* otoliths have been found in deeper strata of the well. A higher boundary for this new zone is improbable because caving of *P. eidelstedtensis* otoliths is unlikely due to their occurrence mainly in mica clays. A minimum thickness of 38.5 m consequently can be inferred for this biozone. A still unpublished precursor of this species up to now has only been found in Miocene deposits of Maryland (Atlantic coast of U.S.A.). The lower boundary of the P. eidelstedtensis Lineage Zone thus is defined by the evolutionary transition of the precursor species into *P. eidelstedtensis*, and the upper boundary by the transition of the latter into *P. hinschi*.

CORRELATIONS WITH OTHER LOCALITIES

At Hohen Woos (German Democratic Republic) at least the lowermost 4 m of the c. 6 m high profile of mica clay belongs to the Pseudocolliolus eidelstedtensis Lineage Zone on the basis of the presence of the key species. It is very likely that the whole outcropping section belongs to this zone. On the ground of the thick and high forms of *Colliolus friedbergi* (Chaine & Duvergier, 1928) the section probably correlates with the lower part of the P. eidelstedtensis Lineage Zone in well Eidelstedt-1, because similar forms of this species occur in the same part of this biozone in this well. This agrees very well with Langer's (1963) conclusion, based on Foraminifera, that all strata visible at Hohen Woos belong to the middle part of the Langenfeldian.

In the type locality of the Gramian, the clay pit at Gram (Denmark), *Pseudocolliolus* otoliths are rather common. Seven specimens are measurable and their OL-OT ratios clearly fall within the range of *P. cuykensis*. This means that the clays exposed at Gram belong to the Late Gramian, corresponding with the Winnert Member and only the uppermost few metres of the Pinneberg Member in well Eidelstedt-1 (boundary between these two members at c. 130 m according to Hinsch, 1987). Thus surprisingly enough the *Pseudocolliolus* otoliths show that the clays exposed at Gram correlate (nearly) precisely with the equivalent of the Saed Member in well Eidelstedt-1, whereas one would expect a correlation with the equivalent of the Gram Formation (the boundary between these two lithostratigraphical equivalents in well Eidelstedt-1 lies at 132.5 m according to Hinsch, 1987). Consequently the otolith age determinations demonstrate a diachrony of the Gram Formation and the Saed Member in such a way that these units are younger in Denmark than at Eidelstedt.

In the wells Beugen 46D/220 and Cuyk 46A/147 (The Netherlands) the P. cuykensis and P. hinschi Lineage Zones can be recognized. In well Beugen the P. cuykensis Lineage Zone comprises the interval 71-77 m below surface, correlating with the Late Gramian. Immediately above 71 m the Doyenneichthys syltensis Range Zone occurs. A few otoliths of the key species of the latter zone were found as (apparently) caved specimens in the uppermost samples of the P. cuykensis Zone. The interval 77-82 m contains otoliths of *P. hinschi*, but also of *P. cuykensis*. The number of otoliths per sample is clearly smaller than in the interval 71-77 m. The presence of *P. cuykensis* otoliths can only be explained by caving. Below 82 m no *Pseudocolliolus* otoliths were encountered, so at least the interval 77-82 m belongs to the P. hinschi Lineage Zone and can be placed in the Early Gramian.

In well Cuyk *Pseudocolliolus* otoliths were only found in the interval 78-94 m below surface. The samples between 78 and 87 m contained merely *P. cuykensis*. No *Doyenneichthys syltensis* otoliths were encountered in this well, but the Syltian can be recognized because the Delden Member is present, comprising at least the interval 64-67 m in which phosphorites occur. The Late Gramian P. cuykensis Lineage Zone thus is at least 9 m thick. Between 87 and 94 m a mixture of *P. hinschi* and *P. cuykensis* was found and the number of otoliths per sample is considerably smaller than in the P. cuykensis Lineage Zone. The presence of the latter species again must be a matter of caving. *P. hinschi* was not recognized as a separate species when *P. cuykensis* was described for the first time from this well (Gaemers, 1978), since the number of *P. hinschi* otoliths was limited, most specimens were not complete, and the material was contaminated with *P. cuykensis*. The boundary between the P. hinschi and P. cuykensis Lineage Zones lies at 87 m. The P. hinschi Lineage Zone is at least 7 m thick and represents the Early Gramian.

The occurrence of *P. hinschi* in well UE 123, Assel (Lower Saxony, F.R.G.) demonstrates the presence of the P. hinschi Lineage Zone in this area.

CHRONOSTRATIGRAPHIC ANALYSIS AND PROPOSAL

The original definitions of Tertiary stages in north-western Europe are based upon benthonic mollusc species. The distribution of benthonic fossils however is more strongly influenced and limited by environmental factors than nektonic and pelagic fossils. Moreover the evolutionary lineages of most molluscs are still unknown. Hence the maximum stratigraphic range of many mollusc species is not yet known what applies also to a lot of molluscs used to define stage boundaries. This is often hazardous and leads to equivocal definitions of stage boundaries and to concepts which are unverifiable at other places than the type localities.

In addition the mollusc species defining stages did not always remain the same ones in the course of time. Staesche (1930), who established the Langenfeldian, for instance mentioned the following species as especially characteristic for this stage: *Murex spinicosta* Bronn, *Dolicholathyrus rothi* (Beyrich), *Aquilofusus glabriculus* Philippi, *A. meyni* Semper [= *A. luneburgensis* (Philippi)], *A. gregarius* (Philippi), and *Surcula steinvorthi* (Semper) (see Hinsch, 1958). In his latest papers giving key fossils of stages Hinsch (1986a, b) defines the Langenfeldian as the range zone of *Astarte* (*Carinastarte*) *vetula* Philippi and *Aquilofusus luneburgensis* (Philippi). In addition he mentions six other mollusc species which should have a vertical distribution confined to the Langenfeldian (Hinsch, 1986a). It is not very likely that all these eight species disappeared at the same time at the Langenfeldian/Gramian boundary, therefore the highest occurrences of *Astarte vetula* and *Aquilofusus luneburgensis* are taken as the most critical species for the definition of this boundary. Hinsch (1986b) places the Langenfeldian/Gramian boundary in well Eidelstedt-1 at 145 m, but the highest occurrence of *Astarte vetula* in this well is at 165 m and the highest occurrence of *Aquilofusus luneburgensis* at 155 m below surface (the depths can not be read precisely from the published tables unfortunately, but have been taken from a pers. comm. of Hinsch). The Gramian is defined by Hinsch (1986a, b) as the range zone of *Astarte* (*Carinastarte*) *reimersi* (Semper) and *Aquilofusus semiglaber* (Beyrich). *Astarte reimersi* is lacking in well Eidelstedt-1, but *Aquilofusus semiglaber* occurs in the sample 147-149 m. If the latter occurrence is not caused by caving, it can be concluded that the Langenfeldian/Gramian boundary based on zonal molluscs should lie somewhere between 149 m (or 147 m at the highest) and 155 m. The boundary at 145 m therefore lies too high when the most recent mollusc definition is taken in its most strict sense. The 145 m boundary in well Eidelstedt-1 probably is based on the highest occurrence of *Astarte* (*Nicania*) *gleuei* Wollemann, but this species was neither included in the original definition of the Langenfeldian, nor considered a zone fossil.

As an alternative for the Langenfeldian/Gramian boundary I would like to propose the evolutionary change of *Pseudocolliolus eidelstedtensis* and *P. hinschi* in well Eidelstedt-1, which should be drawn within or at the top of sample 159-160 m. This boundary has several advantages when compared with the molluscan definitions: it occurs in an interval with a continuous record of *Pseudocolliolus* otoliths; it is based on an evolutionary change which can be verified at other places; the occurrence of *Pseudocolliolus* otoliths around this boundary can be expected at many places in NW Europe; the boundary is close to an important lithologic change at about 162 m (boundary between Eidelstedt Formation and Pinneberg Member); it is also close to the probable boundary Serravallian (Middle Miocene) and Tortonian (Late Miocene) at c. 162 m, identified with Foraminifera by Spiegler (see Hinsch, 1987).

PALEOECOLOGY

Although the otolith assemblages of well Eidelstedt-1 probably are not a true reflection of the original percentages of the species because of underrepresentation of smaller otoliths, although caving may sometimes influence the data rather strongly, and although the numbers of otoliths found are usually not large, it is possible to define former sea depths more or less accurately.

Six successive otolith communities can be distinguished and are provisionally named. The oldest assemblage, a *Colliolus* community, comprising about the depth interval 324-332 m below surface, is a poor assemblage of Reinbekian age. Only three species were found, but the presence of *Merlangiogadus cognatus* (Koken, 1891) suggests a sea depth between 50 and 100 m.

One Reinbekian sample (307-310 m) and some Langenfeldian samples (214-222 m) can be reckoned to the *Diaphus* community, characterized by a dominance of lanternfishes of the genus *Diaphus*. A large barren interval occurs in between. At present otolith communities dominated by lanternfishes occur at sea depths of at least 200 m (Wigley & Stinton, 1973). The former sea depth probably was not much greater than c. 200 m because of the presence of *Colliolus friedbergi*. The barren interval might indicate, but not necessarily, a somewhat deeper sea.

Between c. 200 and 214 m below surface a rather rich *Colliolus-Merlangiogadus-Gadichthys-Diaphus* community occurs in which the first two genera seem to dominate. The genus *Gadichthys* is represented by *G. venustus* (Koken, 1891) which on an average is found in deeper assemblages than *G. miocenicus* (Heinrich, 1969). A sea depth of c. 150 m is very likely for this community. A rather poor *Pseudocolliolus-Colliolus-Merlangiogadus* community occurs between about 187 and 198 m below surface. The distribution of *Pseudocolliolus* otoliths in the North Sea Basin suggests a rather shallow to shallow occurrence for this genus. The largest numbers of otoliths of this genus have always been found in shallow shelf areas (see also Gaemers, 1987). This community probably indicates a sea depth of about 100 m.

From about 160 to 187 m a poor *Pseudocolliolus-Colliolus* community is present. In this interval the largest amount of caving could be demonstrated. Both factors make it difficult to interprete sea depth, but this might have been between 50 and 100 m. The presence of *Gadichthys miocenicus* and *Neocolliolus vikingensis* n. sp., if these are no caved specimens, make a shallower depth unlikely.

A rich *Pseudocolliolus-Colliolus-Trisopterus-Argyrosomus* community is present between c. 132 and c. 160 m. This is the interval with the largest number of *Pseudocolliolus* otoliths. The regular occurrence of sciaenids (especially *Argyrosomus*) is striking. These data support the idea of a shallow shelf sea. On the other hand the sea can not have been very shallow because *Neocolliolus*, *Gadichthys miocenicus* and the annelid *Ditrupa* are present. A sea depth of about 50 m therefore seems to be most likely.

The successive otolith communities in well Eidelstedt-1 consequently show a mostly clear picture of the development of the sea depth from the beginning of the Reinbekian to about the middle of the Gramian: it started with a rather shallow sea which rapidly became deeper already early in the Reinbekian. The deepest conditions possibly existed during most of the Reinbekian and the Early Langenfeldian, up to depths greater than those of the present shelves. A gradual shallowing of the sea during the later Langenfeldian and Gramian is very likely, finally resulting in sea depths of somewhat less than 50 m at the top of the otolith-bearing strata.

A rich otolith fauna is known from the Langenfeldian of Hohen Woos containing 14 gadid species. The lanternfish *Diaphus debilis* (Koken, 1891) and *Archaegadiculus labiatus* (Schubert, 1905) are the most frequently occurring species (synonyms of the latter species in Heinrich, 1969 are *Macrourus* aff. *communis*, Macrouridarum *medius* and *Macrourus* cf. *debilis*). Common species are *Colliolus friedbergi* and *Gadichthys miocenicus*. *Pseudocolliolus eidelstedtensis* seems to be less common. *Gadichthys venustus* and other deep living species like *Merluccius albidus, Merlangiogadus cognatus* and *Phycis* sp. are rare. A sea depth of about 125 m seems to be most likely.

A rather rich otolith fauna occurs in the Late Gramian at Gram containing no less than 17 gadid species. The gadids also dominate very strongly in number of individuals. *Archaegadiculus labiatus, Conferencea irregularis* and *Colliolus friedbergi* are abundant, and *Pseudocolliolus cuykensis* is common. *Gadichthys venustus* and *Phycis* sp. are at least in certain horizons rather common. Lanternfishes are rare. Sciaenids are not abundant but do occur. A sea depth of somewhat more than 50 m seems to be most likely.

Pseudocolliolus otoliths strongly dominate the Gramian otolith faunas of wells Beugen and Cuyk. Especially juvenile specimens are very common. Another common species is *Conferencea irregularis*. *Colliolus friedbergi* is rather common, but occurs mainly in the lower part. These faunas belong to the shallowest ones which are known from the Late Miocene of the North Sea Basin, and presumably lived at depths of 15-30 metres. The smaller numbers of *Pseudocolliolus* and the larger numbers of *Colliolus* in the lower part indicate somewhat deeper conditions in the Early Gramian than in the Late Gramian, pointing to the same shallowing of the Late Miocene sea in the SE part of the Netherlands as in north-western Germany and Denmark.

The clearly higher concentration of otoliths and molluscs in the P. cuykensis and P. hinschi Lineage Zones, and the smaller thickness of these zones compared with the P. eidelstedtensis Lineage Zone point to a considerably lower average sedimentation rate for the former two zones.

SYSTEMATIC PART

Genus **Neocolliolus** Gaemers, 1976

Type species — *Gadus Esmarkii* Nilsson, 1855.

Amended diagnosis — A genus of the subfamily Gadinae with rather small to medium-sized, rather elongated otoliths which are slightly to rather strongly bent lengthwise. Rostral end rounded, but sometimes truncated in larger specimens. Caudal end sharply pointed. Predorsal and postdorsal angles weakly to moderately pronounced, postdorsal angle always more strongly developed in larger otoliths. Sulcus acusticus (nearly) straight and wide. Collum long and hardly narrowed; its boundaries are clear due to two kinks in the crista inferior. Collum not covered by caudal colliculum in small otoliths, only its dorsal part covered by this colliculum in larger ones; the uncovered part is large, very deep, and lacking a pseudocolliculum. Ventral rim thicker and more rounded than dorsal rim. Outer surface moderately to weakly ornamented, usually lacking a medial ridge.

Stratigraphic range — Late Miocene (Langenfeldian) - Recent.
Neocolliolus vikingensis n. sp.: Langenfeldian - Gramian.
Neocolliolus esmarki (Nilsson, 1855): Holocene - Recent.

Remarks — In contrast with Gaemers (1976b) the genus *Neocolliolus* can not be considered a descendant of the genus *Colliolus* Gaemers & Schwarzhans, 1973, because important differences exist in various sulcus characteristics. The sulcus in *Colliolus* is narrower, deeper, has a distinct pseudocolliculum, and the caudal colliculum does not extend so far across the collum as in *Neocolliolus*. Sulcus and other characteristics show strongest affinities with *Trisopterus* Rafinesque, 1814. The outline of *Neocolliolus* otoliths resembles that of *Trisopterus minutus* (Linnaeus, 1758) the most, since both have a clear postdorsal angle. Also the external body characteristics of living specimens of *N. esmarki* show more affinities to those of *T. minutus* than to those of the other Recent *Trisopterus* species, *T. luscus* (Linnaeus, 1758) and *T. capelanus* (Lacepède, 1800) (see Svetovidov, 1962). The *Neocolliolus* lineage therefore is considered a descendant of the *Trisopterus minutus* lineage of which the oldest representative is known from the Late Oligocene of the Federal Republic of Germany (unpublished data).

Trisopterus pliocenicus Gaemers & Schwarzhans, 1973, from the Early Pliocene Kattendijk Formation does not belong to *Neocolliolus* as stated by Gaemers (1976). More and better preserved material of this species is available now from the same formation, showing that the otoliths are always (nearly) completely flat. Important differences also exist in the sulcus which is narrower and has a shorter, narrower and shallower collum. *Trisopterus pliocenicus* must be the forerunner of, or is even identical with, ''*Merlangius*'' *pseudaeglefinus* (Newton, 1891).

Neocolliolus vikingensis n. sp.
Plate 1, figs 1, 2

Holotype — Plate 1, fig. 1, leg. C. King, coll. RGM 177 424.

Locus typicus — Well 9/18-2, drilled by Conoco (U.K.) Ltd. in 1975, 59° 28′ N and 01° 32′ E, southern part of Viking Graben, northern North Sea (sea depth c. 109 m).

PLATE 1

Fig. 1a-d *Neocolliolus vikingensis* n. sp. Holotype. Well 9/18-2, Viking Graben, Late Miocene, leg. C. King, coll. RGM 117 424; 12.5 ×.

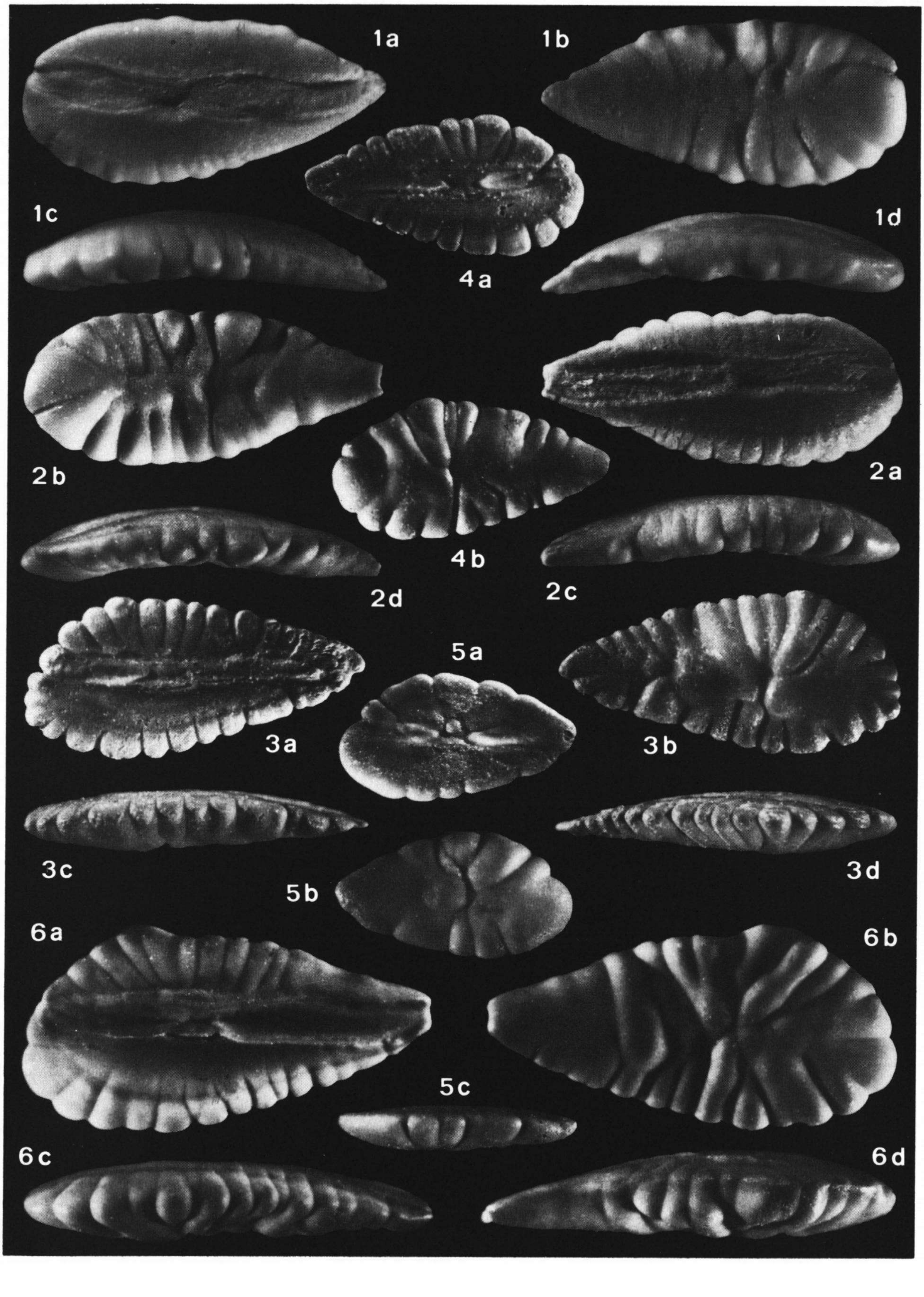
Fig. 2a-d *Neocolliolus vikingensis* n. sp. Paratype. Well Eidelstedt-1, Nordgetränke, 145-146.8 m, Early Gramian, leg. GLSH, coll. RGM 177 428; 12.5 ×.

Fig. 3a-d *Pseudocolliolus* aff. *eidelstedtensis* n. sp. Paratype. Well Eidelstedt-1, Nordgetränke, 167-168 m, Langenfeldian, leg. GLSH, coll. RGM 177 453; 15 ×.

Fig. 4a-b *Pseudocolliolus eidelstedtensis* n. sp. Paratype. Hohen Woos, sample C, 2 m below bottom of clay-pit, Langenfeldian, leg. W.-D. Heinrich, coll. MB Ot. 502; 15 ×.

Fig. 5a-c *Pseudocolliolus eidelstedtensis* n. sp. Paratype. Hohen Woos, sample C, 2 m below bottom of clay-pit, Langenfeldian, leg. W.-D. Heinrich, coll. MB Ot. 503; 20 ×.

Fig. 6a-d *Colliolus friedbergi* (Chaine & Duvergier, 1928). Hohen Woos, Langenfeldian, leg. W.-D. Heinrich, coll. MB Ot. 196; 15 ×.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Stratum typicum — Late Miocene, Langenfeldian or Gramian, Nordland Group, Utsira Formation, 1060-1080 feet below kelly base (= 189-195.1 m below sea floor).

Derivatio nominis — *vikingensis*: named after the Viking Graben.

Diagnosis — A *Neocolliolus* species with small otoliths, which are relatively thin and rather strongly bent lengthwise. Rostral end rounded or slightly truncated. Crista superior sharp, especially in the middle, following an undulating course. Outer surface with relatively strong ornamentation; one or more knobs on the dorsal part have a typical angular crest, which can be the result of one or more dents along the dorsal rim.

Paratypes — Well 9/18-2, Viking Graben, Utsira Formation, Late Miocene (Langenfeldian or Gramian): 1 sagitta, 1080-1100 feet below kelly base (= -KB) (= 195.1-201.2 m below sea floor (= m-SF), coll. RGM 117 423; 8 sagittas, 1060-1080 feet-KB (= 189-195.1 m-SF), col. RGM 177 425; 4 sagittas, 1040-1060 feet-KB (= 182.9-189 m-SF), coll. RGM 177 426; 2 sagittas, 1020-1040 feet-KB (= 176.8-182.9 m-SF), coll. RGM 177 427.

Well Eidelstedt-1, Nordgetränke, Hamburg Area, F.R.G., Eidelstedt Formation, Langenfeldian: 2 sagittas, 197-198 m, coll. GLSH; 1 sagitta, 178-179 m, coll. GLSH.

Well Eidelstedt-1, Nordgetränke, Pinneberg Member, Gramian (Langenfeldian sensu Hinsch): 1 sagitta, 154.5-155 m, coll. GLSH; 1 sagitta, 147-149.5 m, coll. GLSH; 1 sagitta, 145-146.8 m, leg. GLSH, coll. RGM 177 428.

Well Eidelstedt-1, Nordgetränke, Pinneberg Member, Gramian (also Gramian sensu Hinsch): 1 sagitta, 132-135 m, coll. GLSH.

Well Flensburg-Fuchskühle 3, Schleswig, F.R.G., Gramian ?: 1 sagitta, 95-113 m, coll. GLSH.

Well Pinneberg-Etz, Holstein, F.R.G., Gramian: 1 sagitta, 84-92 m, coll. GLSH.

Gram, clay-pit (Gram Teglvaerk), Denmark, Gram Formation, Gramian: 1 sagitta, coll. H. Hein; 1 sagitta, coll. P.A.M. Gaemers.

Hohen Woos, clay-pit, German Democratic Republic, "Glimmerton", Langenfeldian: 1 sagitta, sample 29/32, 2 m below bottom of clay-pit, leg. W.-D. Heinrich, coll. MB Ot. 500.

Beugen, well 46D/220, Noord-Brabant, The Netherlands, Breda Formation, Zenderen Member, Gramian: 1 sagitta, 80-81 m, leg. RGD, coll. RGM 177 429.

PLATE 2

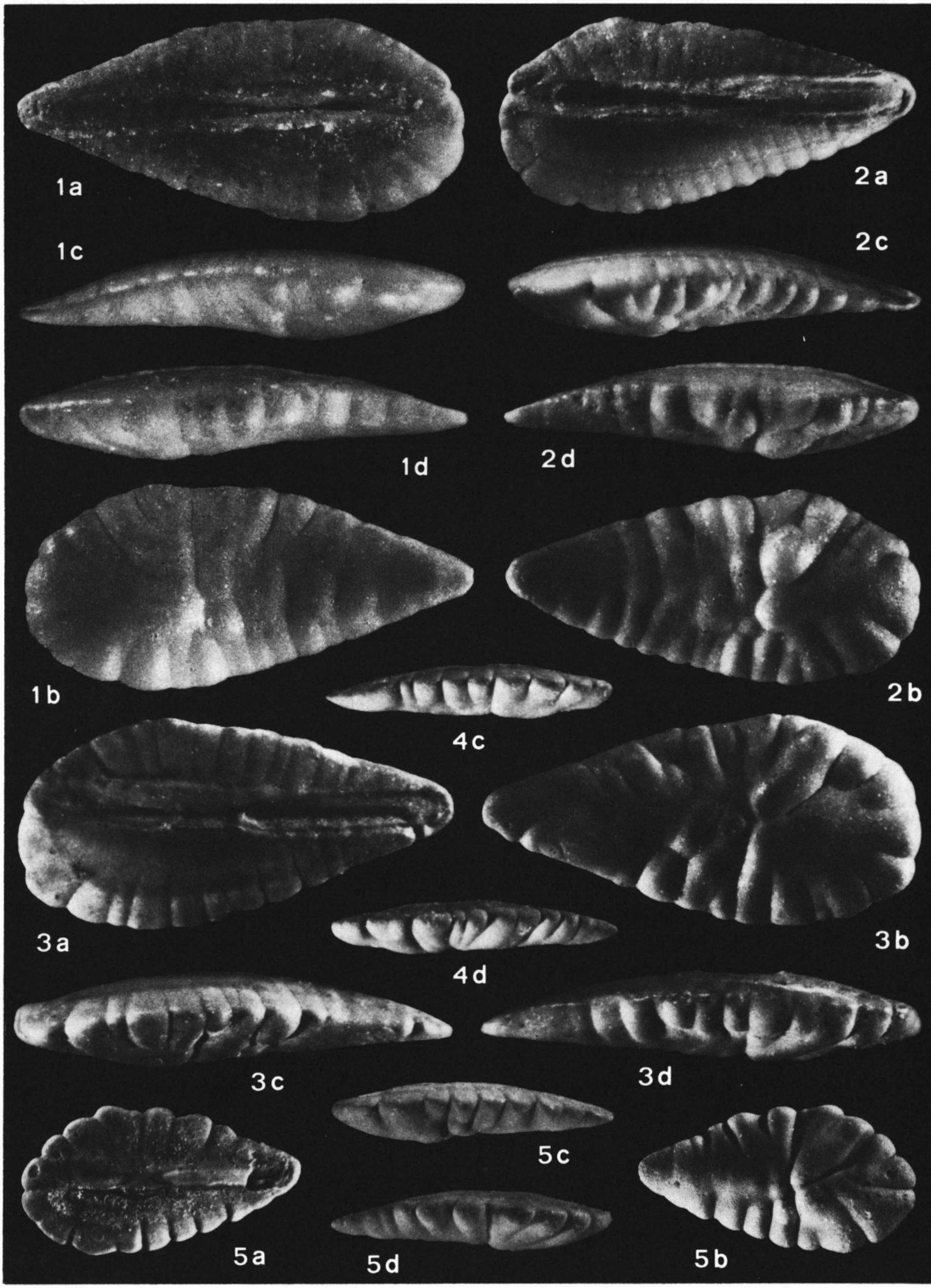
Fig. 1a-d *Pseudocolliolus eidelstedtensis* n. sp. Holotype. Well Eidelstedt-1, Nordgetränke, 162-163 m, Langenfeldian, leg. GLSH, coll. RGM 177 451; 15 × (otolith well-preserved, but difficult to photograph because of its translucency).

Fig. 2a-d *Pseudocolliolus eidelstedtensis* n. sp. Paratype. Well Eidelstedt-1, Nordgetränke, 197-198 m, Langenfeldian, leg. GLSH, coll. RGM 177 452; 15 ×.

Fig. 3a-d *Pseudocolliolus eidelstedtensis* n. sp. Paratype. Hohen Woos, Langenfeldian, leg. W.-D. Heinrich, coll. MB Ot. 197; 15 ×.

Fig. 4c-d *Pseudocolliolus eidelstedtensis* n. sp. Paratype. Hohen Woos, sample C, 2 m below bottom of clay-pit, leg. W.-D. Heinrich, coll. MB Ot. 502; 15 × (figs 4a-b see pl. 1).

Fig. 5a-d *Pseudocolliolus eidelstedtensis* n. sp. Paratype. Hohen Woos, sample 202, 1 m above bottom of clay-pit, leg. W.-D. Heinrich, coll. MB Ot. 501; 15 ×.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Overloon, well 52B/185, Noord-Brabant, The Netherlands, Breda Formation, Zenderen Member, Gramian, leg. RGD: 1 sagitta, 63-64 m, coll. RGM 177 430; 2 sagittas, 62-63 m, coll. RGM 177 431; 3 sagittas, 61-62 m, coll. RGM 177 432; 3 sagittas, 60-61 m, coll. RGM 177 433; 1 sagitta, 59-60 m, coll. RGM 177 434.

Overloon, well 52B/185, Breda Formation, Syltian (reworked from the Gramian), leg. RGD: 5 sagittas, 58-59 m, coll. RGM 177 435; 10 sagittas, 57-58 m, coll. RGM 177 436, 177 437; 3 fragments of sagittas, 56-57 m, coll. RGM 177 438.

Description — Relatively thin, rather elongated and rather small otoliths. Rostral end regularly rounded or slightly truncated. Ventral part of rostral end may or may not be more protruding than dorsal part. Predorsal angle rounded, indistinct, sometimes absent. Postdorsal angle rounded, but larger and more prominent than predorsal angle. If both angles are present they divide the dorsal rim into three (nearly) straight parts. Posterior end clearly pointed. Ventral rim regularly bent. Highest part of otolith at the foremost part of the collum. Otoliths clearly bent lengthwise.

Inner surface strongly convex lengthwise. Sulcus slightly supramedian, wide, and for the larger part shallow. Ostium about one third the length of the sulcus. Ostial colliculum in larger otoliths longer than ostium, covering also the dorsal part of the collum. Caudal colliculum present along (nearly) the whole length of the cauda. Cauda 1.5 times as long as ostium. Ventral part of collum deep, without pseudocolliculum. Crista superior well-developed: sharp and high along most of the sulcus, fading away towards the ends. This crista has an undulating shape with convexities above the ostium and part of the cauda. Crista inferior rounded and hardly or not protruding. Area very long and very wide, with shallow grooves crossing the entire surface. Ventral furrow indistinct, but regularly shaped, running rather far from the ventral rim.

Outer surface clearly convex lengthwise. Sharp furrows and mostly rounded knobs perpendicular to the rims present on the whole surface, but most developed on the central part. The distance between the furrows and size and height of the knobs is rather variable. One or more knobs on the dorsal part possess a typical angular crest perpendicular or parallel to the rim. These crests can be the result of one or more dents along the dorsal rim, which are however not always present. Sometimes a medial longitudinal ridge occurs, consisting of several circular knobs which are more or less connected. Ventral part only slightly thicker than dorsal part.

Ontogeny — Medium-sized otoliths are more slender and thinner than larger ones. From this it can be concluded that the changing ratios between OL and OH, and between OL and OT during growth produce concave allometric curves (Gaemers, 1976a). The same allometric growth has been found in otoliths of the Recent *N. esmarki* (Nilsson, 1855).

Measurements —

OL: 5.36	OH: 2.39	OT: 0.98	OL/OH: 2.24	OL/OT: 5.47	(holotype)
(OL: 5.17)	OH: 2.24	OT: 0.89	OL/OH: c. 2.41	OL/OT: c. 6.07	(pl. 1, fig. 2)
OL: 4.54	OH: 1.80	OT: 0.79	OL/OH: 2.52	OL/OT: 5.75	(Overloon, 57-58 m)
OL: 4.10	OH: 1.78	OT: 0.75	OL/OH: 2.30	OL/OT: 5.47	(Overloon, 58-59 m)

Discussion — The new fossil species is distinguished from the Recent one by its much smaller otoliths, which are thinner and more strongly curved lengthwise. The crista superior is straight and less obvious, and the dents on the outer surface along the dorsal rim are absent in *N. esmarki*.

Genus **Pseudocolliolus** Gaemers, 1978

Type species — *Pseudocolliolus cuykensis* Gaemers, 1978.

Remarks — For the diagnosis of this genus see Gaemers (1987). All known *Pseudocolliolus* species are successive members of one evolutionary lineage. The oldest one is a still undescribed form with the smallest and most compact otoliths known from this lineage. Up to now this species has only been found in the Miocene of the East coast of the U.S.A. (unpublished data). A still smaller and more compact forerunner may exist. The otoliths of the succeeding, new species, *P. eidelstedtensis* and *P. hinschi*, become gradually larger, more slender and thinner. The otoliths of the next species, *P. cuykensis*, attain about the same size as those of *P. hinschi*, but are still thinner and more slender than those of the latter species. *P. cuykensis* has the most slender otoliths of all *Pseudocolliolus* species, so representing phylogenetic stage 3 (Gaemers, 1976a). *P. curvidorsalis* Gaemers, 1983 and *P. redonensis* Gaemers, 1987 are two successive members belonging to phylogenetic stage 4; they are characterized by their relatively slender juvenile otoliths and high adult ones. The otoliths of the latter two species remain relatively thin throughout their ontogeny. Although insufficient measurements of otolith length, height and thickness of all *Pseudocolliolus* species are available yet, they all seem to have a convex allometrical curve for the OL-OH ratio and a concave curve for the OL-OT ratio. The same phylo- and ontogenetic trends can for instance be seen in the various *Colliolus*- and *Gadichthys*-lineages.

Pseudocolliolus cuykensis Gaemers, 1978

Amended diagnosis — A *Pseudocolliolus* species with large thin otoliths. OL/OH growth curve shows strongest allometry of all species of the genus: adult otoliths are very strongly elongated, juvenile ones are high and short. Predorsal angle usually more pronounced than postdorsal one; the latter is often absent. Longitudinal ridge on outer surface absent, or very low and vague. No umbo. Ornamentation strongly developed in large otoliths (deep, sharp grooves and high knobs), less pronounced in juvenile otoliths.

Material — Well Eidelstedt-1, Nordgetränke, Hamburg Area, F.R.G., Pinneberg Member, Gramian: 2 sagittas, 135-138 m below surface, leg. GLSH, coll. RGM 177 439; 1 sagitta, 141-143.5 m below surface, coll. GLSH.

Ontogeny — The measurements of otolith length, height and thickness given in text fig. 2a and 2b were mainly based on type material of well Cuyk 46A/147 (only between 78 and 85 m below surface) and on still unpublished material of a nearby well, Beugen 46D/220 (only between 71 and 76 m below surface). Although smaller otoliths strongly prevail in this material a clear convex growth curve can be constructed for the OL-OH ratio showing strong allometry (text fig. 2a). A concave growth curve for the OL-OT ratio seems more likely than a convex curve (text fig. 2b); more otoliths longer than 3.5 mm are needed for a better definition of this curve.

Pseudocolliolus hinschi n. sp.
Plate 3, figs 2-4

Holotype — Plate 3, fig. 4, leg. Dr W. Hinsch (GLSH), coll. RGM 177 440.

Locus typicus — Well Eidelstedt-1, Nordgetränke, Hamburg Area, F.R.G.; coordinates R ^{35}60 050, H ^{59}43 300, TK 25, map-sheet Niendorf 2325.

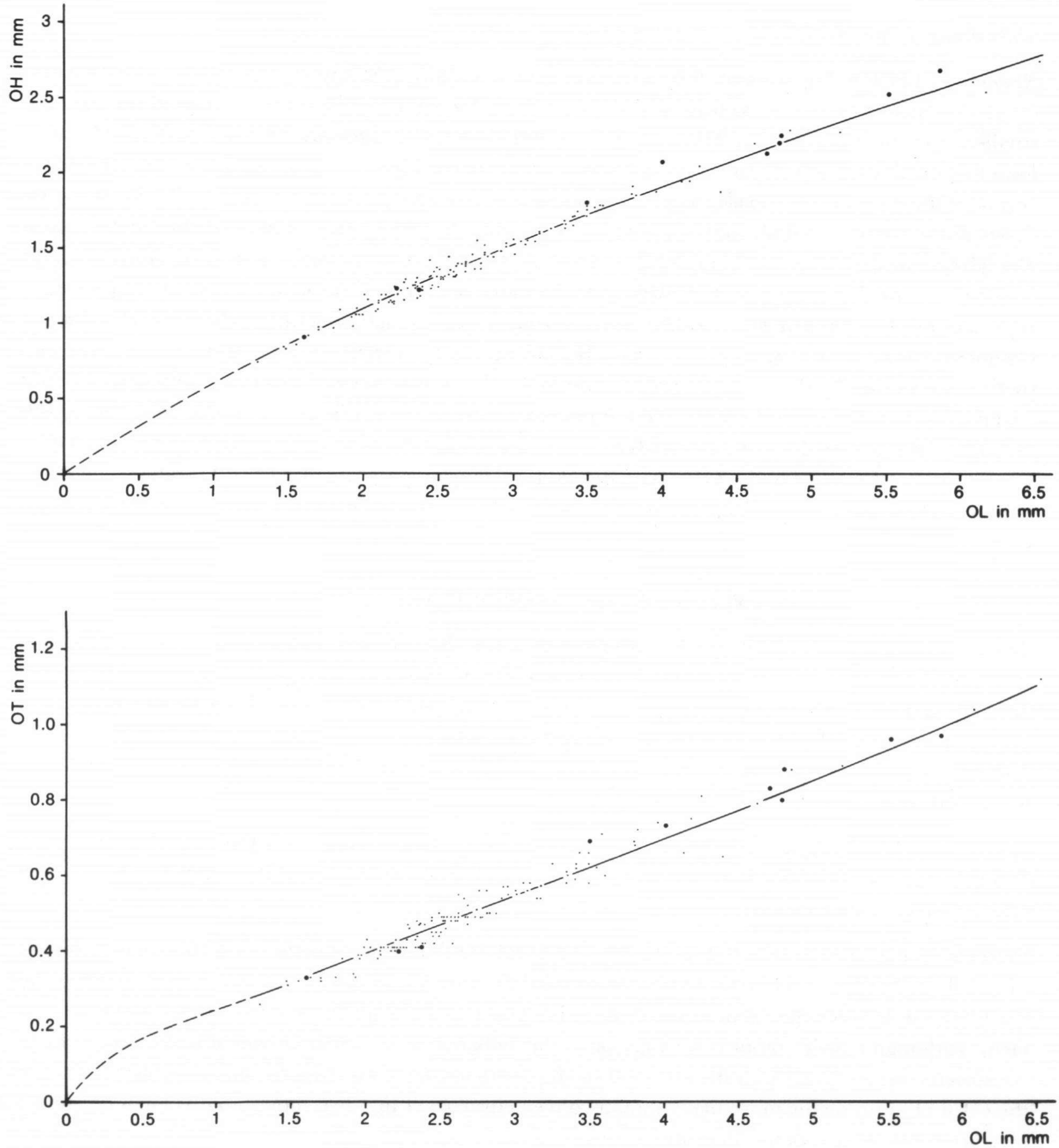


Fig. 2. Scatter diagrams with estimated growth curves of *Pseudocolliolus cuykensis* Gaemers, 1978. Small dots are measurements of otoliths from wells Beugen and Cuyk (n = 123), large dots from the clay-pit at Gram (n = 10). Upper diagram: relation between OL and OH; Lower diagram: relation between OL and OT.

Stratum typicum — Late Miocene, Gramian, Pinneberg Member, 138-141 m below surface.

Derivatio nominis — *hinschi*: named after colleague Dr W. Hinsch, German stratigrapher and paleontologist, who kindly placed otoliths from well Eidelstedt at my disposal.

Diagnosis — A *Pseudocolliolus* species belonging to the *P. cuykensis* lineage, with large, moderately thick otoliths. Large otoliths are clearly elongated. Predorsal angle distinct and rounded, postdorsal angle often absent. Longitudinal ridge on outer surface short, low and wide. Usually no umbo; poorly developed if present. Ornamentation strongly developed with deep, sharp grooves and high knobs.

Paratypes — Well Eidelstedt-1, Nordgetränke, Hamburg Area, F.R.G., Pinneberg Member, Gramian: 1 sagitta, 132-135 m, leg. GLSH, coll. RGM 177 441; 1 sagitta, 132-135 m, coll GLSH; 8 sagittas, 135-138 m, leg. GLSH, coll. RGM 177 442-177 444; 1 sagitta, 138-141 m, leg. GLSH, coll. RGM 177 445; 1 sagitta, 141-143.5 m, coll. GLSH.

Well Eidelstedt-1, Nordgetränke, Pinneberg Member, Gramian (Langenfeldian sensu Hinsch): 3 sagittas, 145-146.8 m, coll. GLSH; 4 sagittas, 147-149.5 m, leg. GLSH, coll. RGM 177 446; 2 sagittas, 150-153 m, coll. GLSH; 1 sagitta, 153-154.5 m, leg. GLSH, coll. RGM 177 447; 1 sagitta, 153-154.5 m, coll. GLSH; 2 sagittas, 154.5-155 m, leg. GLSH, coll. RGM 177 448; 3 sagittas, 155-156 m, coll. GLSH; 4 sagittas, 156-157 m, coll. GLSH; 1 sagitta, 157-158 m, coll. GLSH; 5 sagittas, 158-159 m, coll. GLSH; 10 sagittas, 159-160 m, coll. GLSH.

Well Eidelstedt-1, Nordgetränke, Eidelstedt Formation, Langenfeldian (most, if not all, of these otoliths must come from higher horizons due to caving): 2 sagittas, 160-161 m, coll. GLSH; 3 sagittas, 161-162 m, coll. GLSH; 1 sagitta, 162-163 m, leg. GLSH, coll. RGM 177 449; 1 sagitta, 162-163 m, coll. GLSH; 1 sagitta, 163-164 m, leg. GLSH, coll. RGM 177 450; 1 sagitta, 164-165 m, coll. GLSH; 1 sagitta, 165-166 m, coll. GLSH; 1 sagitta, 169-170 m, coll. GLSH; 1 sagitta, 179-180 m, coll. GLSH; 1 sagitta, 186-187 m, coll. GLSH.

Well UE 123, Assel, map-sheet Stade-Nord, Lower Saxony, F.R.G., Gramian (Langenfeldian sensu Hinsch): 1 sagitta, 99-102 m, coll. NLBF.

Description — Rather thick, rather small to medium-sized, pear-shaped otoliths. Maximum length probably c. 8 mm. Adult otoliths clearly elongated. Anterior rim rounded; its ventral part somewhat more massive than its dorsal part. Predorsal angle distinct and usually rounded, postdorsal angle usually also rounded, but mostly less protruding; the latter is often absent. If both angles are present they divide the dorsal rim into three, not necessarily equally long, straight parts. If the postdorsal angle is absent the dorsal rim behind the predorsal angle is straight or slightly convex. Ventral rim regularly bent; in larger specimens the deepest part of this rim is situated more towards the middle.

Inner surface clearly, but not very strongly convex lengthwise. Sulcus supramedian, rarely median. Sulcus rather wide and deep. Ostial colliculum rather short, covering two-thirds or somewhat less of the length of the ostium. Caudal colliculum long, covering the whole length of the cauda. Caudal colliculum about 2.5 times as long as ostial colliculum. Ventral ridge of pseudocolliculum long and slightly to clearly bent. Crista superior sharp and high along the whole length. Crista inferior rounded, but at least partly protruding. Area very long and wide with clear grooves perpendicular to the dorsal rim crossing its entire surface. In large otoliths the crista superior can even be intersected by the grooves. Ventral furrow distinct and regular, running far from ventral rim in smaller otoliths and closer to this rim in large ones.

Foremost part of outer surface slightly convex lengthwise, hindmost part slightly concave, or whole surface slightly convex lengthwise. Umbo not or only poorly developed. Median or somewhat inframedian longitudinal ridge is usually indistinct, wide and low; in larger otoliths it is sometimes sharply delimited. Ornamentation consisting of a regular pattern of sharp grooves and relatively high knobs, but less strongly developed near posterior point. The distance between the grooves is rather variable.

Ontogeny — Although the number of measurable otoliths is still limited, a distinct allometry can be seen in the OL-OH ratio (text fig. 3a). Larger otoliths are clearly more elongated than smaller ones (convex growth curve). A concave allometric growth curve is highly likely for the OL-OT ratio (text fig. 3b).

Measurements —

(OL: 6.19) = c. 6.33	OH: 2.76	OT: 1.15	OL/OH: c. 2.29	OL/OT: c. 5.50 (holotype)
OL: 5.71	OH: 2.54	OT: 1.04	OL/OH: 2.25	OL/OT: 5.49 (156-157 m)
OL: 5.43	OH: 2.50	OT: 1.06	OL/OH: 2.17	OL/OT: 5.12 (132-135 m)
OL: 4.63	OH: 2.19	OT: 0.89	OL/OH: 2.111	OL/OT: 5.20 (pl. 3, fig. 2)
OL: 4.40	OH: 2.22	OT: 0.89	OL/OH: 1.98	OL/OT: 4.94 (153-154.5 m)
OL: 3.10	OH: 1.66	OT: 0.67	OL/OH: 1.87	OL/OT: 4.63 (154.5-155 m)

Discussion — *Pseudocolliolus hinschi* is an intermediate form between *P. eidelstedtensis* and *P. cuykensis*. The OL-OH ratios of the three species lie close together, so that identifications exclusively based on this characteristic are not trustworthy. There seems to be hardly any overlap in the values of the OL-OT ratios of larger specimens of the three species. Therefore thickness at a given length is important for identification. Other important characteristics to distinguish these species are the presence or absence (and if present the shape) of the umbo and the longitudinal ridge on the outer surface. Ornamentation is more pronounced in *P. hinschi*, in adult otoliths of *P. cuykensis* and in juvenile otoliths of *P. eidelstedtensis*.

Colliolus friedbergi (Chaine & Duvergier, 1928) (see, pl. 1, fig. 6) occurs together with the three successive *Pseudocolliolus* species. Unfortunately it may be difficult to distinguish otoliths of the former from those of *Pseudocolliolus*, as contemporaneous *C. friedbergi* otoliths show a large variability and cover about the same range of OL/OH and OL/OT values as those of *P. hinschi* and *P. eidelstedtensis* together. *P. cuykensis* can always clearly be distinguished from *C. friedbergi*, because it has always much thinner otoliths. The available material of *C. friedbergi* from the Langenfeldian and Gramian furthermore strongly suggest rather dramatic changes in shape when following successive populations through time; these changes might very well be of biostratigraphical importance, but hamper iden-

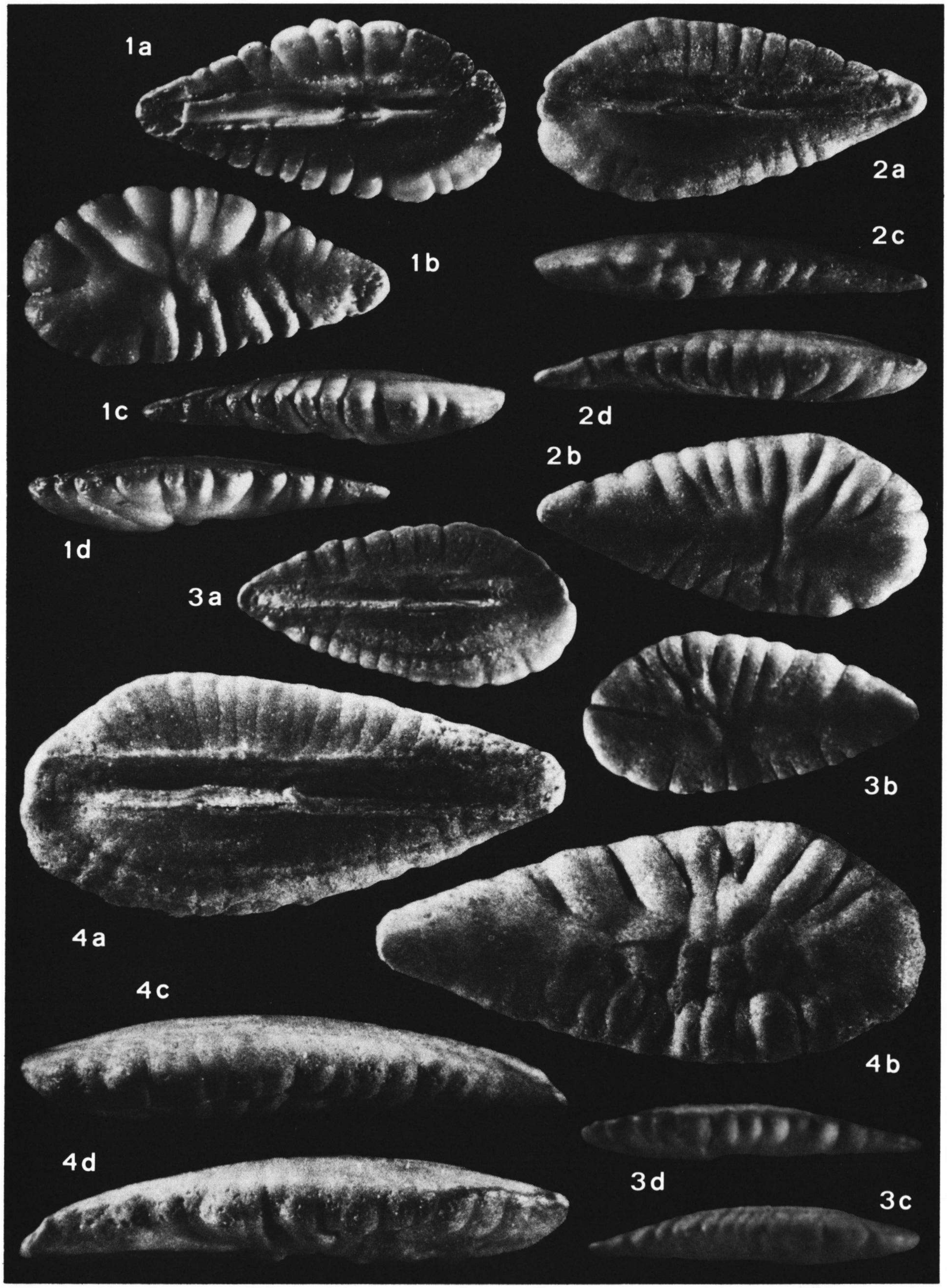
PLATE 3

Fig. 1a-d *Gadichthys miocenicus* (Heinrich, 1969). Well Eidelstedt-1, Nordgetränke, 168-169 m, Langenfeldian, leg. GLSH, coll. RGM 177 454; 15 ×.

Fig. 2a-d *Pseudocolliolus hinschi* n. sp. Paratype. Well Eidelstedt-1, Nordgetränke, 135-138 m, Early Gramian, leg. GLSH, coll. RGM 177 442; 15 ×.

Fig. 3a-d *Pseudocolliolus hinschi* n. sp. Paratype. Well Eidelstedt-1, Nordgetränke, 162-163 m, Langenfeldian (caving from Gramian), leg. GLSH, coll. RGM 177 449; 15 ×.

Fig. 4a-d *Pseudocolliolus hinschi* n. sp. Holotype. Well Eidelstedt-1, Nordgetränke, 138-141 m, Early Gramian, leg. GLSH, coll. RGM 177 440; 15 ×.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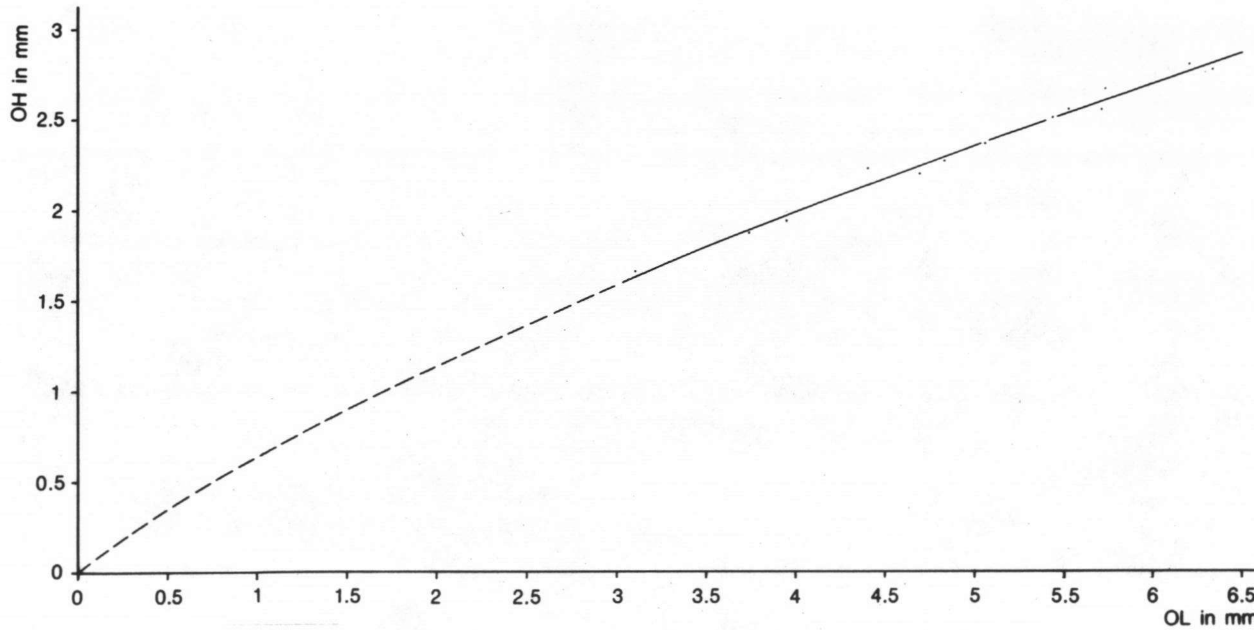

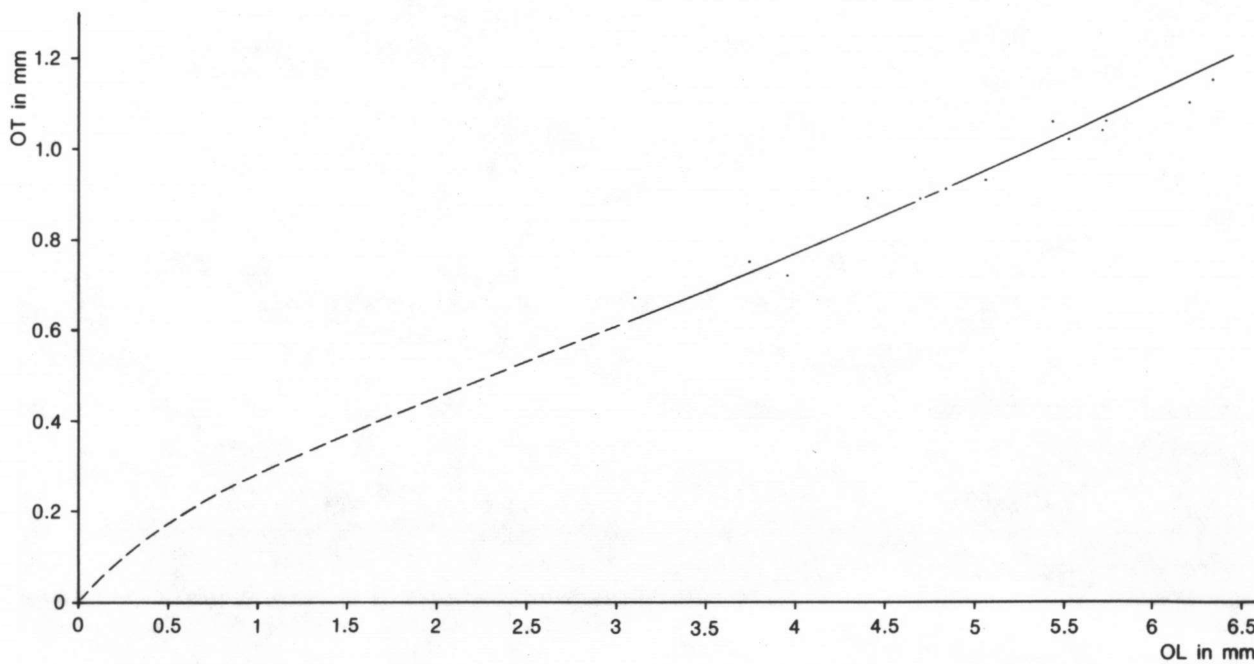

Fig. 3. Scatter diagrams with estimated growth curves of *Pseudocolliolus hinschi* n. sp. All otolith measurements are from well Eidelstedt-1, Nordgetränke (n = 13). Upper diagram: relation between OL and OH; Lower diagram: relation between OL and OT.

tification. The most important characteristics for distinction between otoliths of *Pseudocolliolus* and *Colliolus* appear to be the length of the collum and pseudocolliculum (which is shorter in *Colliolus friedbergi*), the (a)symmetry of the anterior part (more asymmetrical in *Colliolus*, having a more massive, more protruding ventral portion), the (ir)regularity of the dorsal rim (more irregular in *Colliolus*), the (ir)regularity and variability of the ornamentation on the outer surface (more irregular and more variable in *Colliolus*), and the (a)symmetry of the height profile (ventral part usually thicker than dorsal part in *Colliolus*, symmetrical in *Pseudocolliolus*).

Pseudocolliolus eidelstedtensis n. sp.

Plate 1, figs 4, 5; plate 2, figs 1-5

1969 *Gadus friedbergi* Chaine & Duvergier, 1928 - Heinrich (partim), p. 23, pl. 4, fig. 2; non pl. 3, fig. 3 and pl. 4, fig. 3.

Holotype — Plate 2, fig. 1, leg. Dr W. Hinsch (GLSH), coll. RGM 177 451.

Locus typicus — Well Eidelstedt-1, Nordgetränke, Hamburg Area, F.R.G.; coordinates R ^{35}60 050, H ^{59}43 300, TK 25, map-sheet Niendorf 2325.

Stratum typicum — Middle Miocene part of Langenfeldian, upper part of Eidelstedt Formation, 162-163 m below surface.

Derivatio nominis — *eidelstedtensis*: named after the suburb Eidelstedt of the city of Hamburg, where the first specimens were found.

Diagnosis — A *Pseudocolliolus* species belonging to the *P. cuykensis* lineage, with thick, rather large otoliths. Predorsal angle distinct and rounded, postdorsal angle may be absent. Longitudinal ridge on outer surface short and discontinuous, consisting of a small number of uneven knobs. Distinct umbo. Ornamentation strongly developed in juvenile otoliths, rather strongly in adult ones.

Paratypes — Well Eidelstedt-1, Nordgetränke, Hamburg Area, F.R.G., Eidelstedt Formation, Langenfeldian: 1 sagitta, 159-160 m, leg. GLSH, coll. RGM 177 455; 1 sagitta, 165-166 m, coll. GLSH; 1 sagitta, 166-167 m, coll. GLSH; 1 sagitta, 167-168 m, coll. GLSH; 1 sagitta, 177-178 m, coll. GLSH; 1 sagitta, 180-181 m, coll. GLSH; 1 sagitta, 181-182 m, coll. GLSH; 1 sagitta, 187-188 m, coll. GLSH; 3 sagittas, 192-194 m, coll. GLSH; 2 sagittas, 195-196 m, coll. GLSH; 2 sagittas, 197-198 m, coll. GLSH; 1 sagitta, 197-198 m, leg. GLSH, coll. RGM 177 452; 1 sagitta (*P.* aff. *eidelstedtensis*), 167-168 m, leg. GLSH, coll. RGM 177 453.

Hohen Woos, clay-pit, German Democratic Republic, "mica clay", Langenfeldian: 1 sagitta, leg. W.-D. Heinrich, coll. MB Ot. 197; 1 sagitta, sample 202, 1 m above bottom of clay-pit, leg. W.-D. Heinrich, coll. MB Ot. 501; 3 sagittas, sample C, 2 m below bottom of clay-pit, leg. W.-D. Heinrich, coll. MB Ot. 502-504.

Description — Thick, elongated, medium-sized, pear-shaped otoliths with a regular outline. Anterior rim rounded; its ventral part is only slightly more massive than its dorsal part. Predorsal angle distinct and rounded, postdorsal angle also rounded, but usually less protruding; sometimes the latter angle is absent. If both angles are present they divide the dorsal rim into three about equally long straight parts. If the postdorsal angle is absent the dorsal rim behind the predorsal angle is slightly convex. Ventral rim regularly bent, its strongest curvature lying (rather) far to the front. Side view of the rims only slightly curved lengthwise.

Inner surface clearly, but not very strongly convex lengthwise. Sulcus slightly supramedian, or, less commonly, median. Sulcus rather wide and deep. Ostial colliculum rather short, covering about two-thirds to nearly half the length of the ostium. Caudal colliculum long, covering the whole length of the cauda. Caudal colliculum about 2.5 times as long as ostial colliculum. Ventral ridge of pseudo-colliculum long and slightly to clearly bent, never straight. Both cristae are distinct along most of their lengths. Crista superior is mostly a rather high, rather sharp ridge, crista inferior is a lower ridge which is distinct thanks to its sharpness. Area long and very wide with rather clear to clear grooves perpendicular to the dorsal rim crossing its entire surface. These grooves cross the crista superior if ornamentation is very well-developed. Ventral furrow distinct along whole length of otolith, running (rather) far from ventral rim.

Outer surface slightly to clearly convex lengthwise. Otoliths larger than c. 3 mm have a distinct umbo dividing the length profile in a straight or slightly convex foremost part and a straight to slightly concave hindmost part. The centre of the umbo is situated opposite to the foremost part of the collum. Median longitudinal ridge indistinct, consisting of a series of rather distinct, rounded knobs which differ in size and height. Ventral rim always sharp and dorsal rim at least partially blunt. Ornamentation well-developed over most of the surface, usually less strongly developed near posterior point and anterior rim; it consists of a pattern of sharp, straight grooves and low to moderately elevated knobs perpendicular to the rims. The distance between the grooves is highly variable.

Ontogeny — Although the number of measurable otoliths is still limited, a distinct allometry can be seen in the OL-OH and OL-OT ratios. Larger otoliths are clearly more elongate than smaller ones (convex growth curve); large otoliths are also clearly thicker than small ones (concave growth curve). Juvenile otoliths are relatively more strongly ornamented than adult ones. The juvenile otoliths of *P. eidelstedtensis* also have a more pronounced ornamentation than equally large otoliths of *P. hinschi, P. cuykensis*, and *Colliolus friedbergi*.

Measurements —

OL: 5.18	OH: 2.37	OT: 1.06	OL/OH: 2.19	OL/OT: 4.89 (holotype)
OL: 5.43	OH: 2.53	OT: 1.15	OL/OH: 2.15	OL/OT: 4.72 (159-160 m)
OL: 5.12	OH: 2.47	OT: 1.07	OL/OH: 2.07	OL/OT: 4.79 (pl. 2, fig. 3)
OL: 4.76	OH: 2.28	OT: 1.06	OL/OH: 2.09	OL/OT: 4.49 (pl. 2, fig. 2)
OL: 3.35	OH: 1.71	OT: 0.65	OL/OH: 1.96	OL/OT: 5.15 (pl. 1, fig. 4)
OL: 3.28	OH: 1.73	OT: 0.73	OL/OH: 1.90	OL/OT: 4.49 (pl. 2, fig. 5)
OL: 2.14	OH: 1.14	OT: 0.42	OL/OH: 1.88	OL/OT: 5.10 (pl. 1, fig. 5)

P. aff. *eidelstedtensis*:

OL: 4.09	OH: 1.96	OT: 0.74	OL/OH: 2.09	OL/OT: 5.53 (pl. 1, fig. 3)

Discussion — The otoliths of the new species do not seem to grow much larger than about 6 mm, thus remaining somewhat smaller than those of its successors *P. hinschi* and *P. cuykensis*. One otolith was identified provisionally as *P.* aff. *eidelstedtensis* (pl. 1, fig. 3). Its long collum ensures its position in *Pseudocolliolus*, but the ventral part of the anterior rim is rather strongly protruding like in *Colliolus*, although this part is not so massive. Its distinct umbo agrees with *P. eidelstedtensis*, but the otolith is remarkably thin for this species, so it might be a caved specimen of *P. hinschi*.

It may be difficult to distinguish otoliths of *P. eidelstedtensis* from those of *Colliolus friedbergi*. The latter species, however, has otoliths without (clear) umbo, growing to a size twice as long as *P. eidel-*

stedtensis. See discussion of *P. hinschi* for further differences between these species. I had the opportunity to study some of the otoliths from Hohen Woos published by Heinrich (1969) as *Colliolus friedbergi*, as well as a number of still unpublished and unidentified otoliths from the same locality. One of the two of Heinrich's illustrated specimens of *C. friedbergi* in fact does not belong to this species. It is a distinct representative of *P. eidelstedtensis*. The otolith illustrated by Heinrich (1969, pl. 4, fig. 3) as *Gadus* cf. *friedbergi* is a juvenile specimen of *Trisopterus capelanus* (Lacepède, 1800). The otolith material at my disposal from Hohen Woos indicates that *P. eidelstedtensis* and *T. capelanus* are much less common there than *C. friedbergi*.

Gadichthys miocenicus (Heinrich, 1969)
Plate 3, fig. 1

1969 *Merlangius spatulatus miocenicus* Heinrich, p. 25, pl. 5, fig. 1, 2; pl. 18, fig. 2; pl. 19, fig. 1.

Material — Well Eidelstedt-1, Nordgetränke, Hamburg Area, F.R.G., Pinneberg Member, Gramian (Langenfeldian sensu Hinsch): 1 sagitta, 147-149.5 m below surface, coll. GLSH; 1 sagitta, 158-159 m, coll. GLSH.

Well Eidelstedt-1, Nordgetränke, Eidelstedt Formation, Langenfeldian: 1 sagitta, 168-169 m, leg. GLSH, coll. RGM 177 454.

Measurements —

OL: 4.26 OH: 2.10 OT: 0.89 OL/OH: 2.03 OL/OT: 4.79 (pl. 3, fig. 1)

Discussion — Juvenile otoliths of *G. miocenicus* resemble those of *Pseudocolliolus eidelstedtensis* in having a similar OL-OH ratio, a weakly lengthwise bend and an umbo. They can be distinguished from each other by the collum and pseudocolliculum, which are much shorter in *G. miocenicus*, and the longitudinal ridge on the outer surface which is clearly inframedian in *Gadichthys*.

The OL-OH ratio in juvenile otoliths of *G. miocenicus* moreover falls in the same range as that of adult otoliths of *Gadichthys venustus* (Koken, 1891). Therefore otoliths of *G. miocenicus* can easily be misidentified as *G. venustus*, which often occurs in the same beds. All ontogenetic stages of *G. miocenicus* are more slender than equivalent ontogenetic stages of *G. venustus*. Both *Gadichthys* species show a marked allometric growth in the OL-OH ratio, leading to ever more slender otoliths when growing larger.

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