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NEW GADIFORM OTOLITHS FROM THE TERTIARY OF THE NORTH SEA BASIN AND A REVISION OF SOME FOSSIL AND RECENT SPECIES

BY

P. A. M. GAEMERS*

ABSTRACT

Otoliths of 10 new species, including nine Gadidae from different localities in the North Sea Basin (Middle Oligocene – Upper Pliocene) are described: *Gadus parallelus, Trisopterus concavus, T. incognitus, Colliolus parvus, C. johannettae, C. schwarzhansi, Palaeoraniceps regularis, Molva primaeva, Brosme heinrichi* and ? Macruridarum *deurnensis*.

Three new genera are established: *Protocolliolus, Neocolliolus* and *Palaeoraniceps*.

Type material of some fossil otoliths of Gadidae described by Koken (1884, 1891) has been studied; as a result some systematic errors are corrected.

The existence of two recent species of coal-fishes (*Pollachius virens* (L.) and *Pollachius carbonarius* (L.)) is ascertained by study of their otoliths.

INTRODUCTION

Otoliths of new species of the Gadiformes have been discovered from different localities in the North Sea Basin. The material described in this publication comes from West and East Germany, Belgium and the Netherlands. The new species come from various Tertiary deposits ranging from Middle Oligocene to and including Upper Pliocene.

It is necessary to revise the classification of some fossil and recent species of the Gadidae on the ground of their otoliths, because of the new material at my disposal.

SYSTEMATIC DESCRIPTIONS

Phylum PISCES
Superclassis TELEOSTOMI (OSTEICHTYES)
Classis ACTINOPTERYGII
Subclassis TELEOSTEI
Ordo GADIFORMES
Familia GADIDAE Rafinesque, 1810
Subfamilia GADINAE
Genus GADUS Linnaeus, 1758

Gadus parallelus n. sp.
(Pl. I, Figs. 1a, b, 2a, b)

Type. – Holotype: Pl. I, Figs. 1a, b, Coll. RGM 175800.

Locus typicus. – Sand-filled ground of Ford factory, Antwerp-North, Belgium.

Stratum typicum. – Pliocene, upper part.

Derivatio nominis. – Parallèlos (Greek) = parallel. Because the dorsal and ventral rims are nearly parallel.

* Dept. of Stratigraphy and Palaeontology, Geological and Mineralogical Institute, University of Leiden, Garenmarkt 1b, Leiden, the Netherlands.

Diagnosis. – A slender *Gadus* species with a distinct and regular pattern of knobs and furrows. Dorsal rim between predorsal and postdorsal angle long and nearly straight. Otoliths only slightly bent along long axis, thus inner surface somewhat convex and outer surface slightly concave in the direction of the length.

Description. – Otoliths strong and large. Outline oval and elongated. Rather thick ventral rim is weakly and regularly bent and has clearly visible furrows and knobs. Thin and delicate caudal end with a blunt point. Dorsal rim thin; furrows and knobs not as pronounced as on ventral rim. Distinct predorsal and postdorsal angles. Dorsal rim between these angles long and nearly straight. Rostral rim straight and with oblique angle on long axis.

Inner surface slightly convex and curved along long axis. Sulcus acusticus long, wide and almost entirely filled with colliculi. Cauda twice as long as ostium. Rostral end of ostium vague and somewhat bent toward dorsal side. Ostium slightly narrower than cauda. Collum rather short and narrow. Small furrows on dorsal part enter the colliculi; some are furcated. Small furrows on ventral part are distinct but short; they do not traverse large ventral furrow. Area narrow and shallow.

Outer surface slightly concave in lengthwise direction and weakly S-shaped in the direction of the height (ventral part convex, dorsal part somewhat concave). Entire surface highly sculptured, especially ventral part. Medially a cluster of circular knobs. Peripheral knobs in obvious pattern nearly perpendicular to the rims.

L: 12.85 mm, H: 5.09 mm, T: 1.96 mm (holotype)

Caudal end of holotype is slightly eroded, thus true length is somewhat greater.

Material. – 5 sagittas, Pliocene, Ford factory, Antwerp-North, Coll. RGM 175800, 175801, 175802. 3 specimens eroded and without caudal point, 2 broken and

considerably eroded sagittas, basal shell bed of Sands of Kallo, seasluice Kallo, Prov. East Flanders, Belgium, Coll. Gaemers, leg. Vervoenen.

Distribution. – Upper Pliocene, Sands of Kallo.

Discussion. – Variation seems to be mainly restricted to the bend in the ventral rim and the predorsal and postdorsal angles, which can be more or less pronounced.

It is a pity that the best preserved specimen, which has been chosen as holotype, could not be collected stratigraphically. The exact age of this fossil is unknown, but it certainly belongs to the Pliocene; this could be determined by other finds of otoliths in the same sand-filled ground. It cannot be of Pleistocene age because at that time *Gadus morhua* already existed (Gaemers, 1974b). Judging from the preservation of the holotype and the other two specimens, they can derive from the Sands of Kallo or the Sands of Luchtbal, certainly not from the Lower Pliocene Sands of Kattendijk.

Genus POLLACHIUS Bonaparte, 1845

Pollachius virens (Linnaeus, 1758)
(Pl. I, Figs. 3a, b; Pl. II, Figs. 2a, b, 4a, b)

Diagnosis. – A *Pollachius* species with large, elongated and relatively thick otoliths, which are distinctly bent along the long axis. Ventral part conspicuously thicker than dorsal part. Sulcus acusticus wide and straight. Cauda everywhere of nearly equal width. Ventral rim straight to somewhat convex in adult specimens. Caudal part not (and in very old specimens sometimes slightly) twisted perpendicular to the long axis.

L: 21.77 mm, H: 8.91 mm, T: 4.34 mm (L of fish: 89 cm)
L: 18.49 mm, H: 7.68 mm, T: 3.36 mm (L of fish: 64 cm)
L: 18.49 mm, H: 7.42 mm, T: 3.56 mm (L of fish: 66 cm)
L: 18.79 mm, H: 7.00 mm, T: 3.06 mm (L of fish: 63 cm)
L: 16.90 mm, H: 6.24 mm, T: 3.03 mm (L of fish: 56 cm)
L: 15.48 mm, H: 6.38 mm, T: 2.98 mm (L of fish: 49 cm)

Pollachius carbonarius (Linnaeus, 1758)
(Pl. I, Figs. 4a, b, 5a, b, 6a, b)

Diagnosis. – A *Pollachius* species with large, clearly elongated and rather thin otoliths, which are distinctly bent along the long axis. Ventral part only slightly thicker than dorsal part. Sulcus acusticus very wide and bent with convex side toward dorsal rim. Cauda widens distinctly at caudal end. Ventral rim straight to concave in adult specimens. Caudal part of adult specimens conspicuously bent perpendicular to the long axis.

L: 21.27 mm, H: 6.85 mm, T: 2.58 mm (L of fish: 98 cm)
L: 20.88 mm, H: 7.50 mm, T: 3.09 mm (L of fish: 101 cm)
L: 20.74 mm, H: 7.68 mm, T: 3.29 mm (L of fish: 103 cm)
L: 16.50 mm, H: 6.22 mm, T: 2.48 mm (L of fish: 82 cm)
L: 17.78 mm, H: 6.29 mm, T: 2.64 mm (L of fish: 78 cm)

Discussion. – Both species can be easily distinguished by the shape of their otoliths. Length-height and length-thickness ratios rarely overlap, whereas the length-curvature ratio is less distinctive. Moreover, in most cases the ratio of the length of fish to the length of otolith for adult specimens of both species is highly characteristic: *P. virens* has a ratio which ranges between 32 and 45.5, and *P. carbonarius* a ratio which ranges between 44 and 54. When the very clear difference in colour between the black coalfish *P. carbonarius* and the white coalfish *P. virens* is also considered it is clear that Linnaeus was right in differentiating between the two species and that later biologists were wrong in putting the two together in one species.

Genus TRISOPTERUS Rafinesque, 1814

Trisopterus concavus n. sp.
(Pl. II, Figs. 1a, b, 3a, b)

Gadus cf. *spectabilis* Koken, 1891; Leriche 1906, p. 320.
Gadus luscus spectabilis Koken 1891; Weiler, 1942, p. 79, pl. III, figs. 15, 17.
Gadus luscus spectabilis Koken, 1891; Weiler, 1959, p. 97.
Gadus luscus spectabilis Koken, 1891; Zilch, 1965, p. 457.
Gadus luscus spectabilis Weiler, 1942; Gaemers, 1969a, p. 8, pl. I, figs. 7a, b.
Trisopterus luscus spectabilis Weiler, 1942; Gaemers, 1969b, p. 73.
Trisopterus luscus spectabilis Koken, 1891; Gaemers, 1971, p. 242, pl. I, fig. 7; pl. VI, figs. 4, 5.

Type. – Holotype: Pl. II, Figs. 1a, b, Coll. RGM 175822.

Locus typicus. – Miste near Winterswijk, the Netherlands.

Stratum typicum. – Middle Miocene, Hemmoorian.

Derivatio nominis. – Named after the concave caudal part of the dorsal rim.

Diagnosis. – A thick and high *Trisopterus* species of medium size, which is distinctly bent along the long axis. Caudal part of dorsal rim concave. Rostral rim with distinct oblique angle on long axis. Knobs on outer surface of normal size.

Description. – Strong, thick and high otoliths of medium size. Outline elongated. Ventral rim thick, blunt, regularly bent and obviously sculptured. Caudal end clearly and sharply pointed. Dorsal rim much thinner than ventral rim but still rather blunt: dorsal rim s-shaped with a smooth concave part near caudal end and a slightly sculptured convex part near rostral end. Rostral rim with distinct oblique angle on long axis; this rim is nearly straight with two large, low knobs and a shallow depression in between.

Inner surface markedly convex. Sulcus acusticus long, wide and very shallow. Cauda somewhat more than twice as long as ostium. Collum narrow and very short. Sulcus almost entirely filled with colliculi. Cristae very insignificant. Area very shallow and long. Ventral furrow clear. Small furrows and knobs from ventral rim up to ventral furrow.

Outer surface distinctly concave, especially along dorsal rim. Thickest part of otolith near ventral and rostral rims. Ventral part very thick, dorsal part thin. Middle part of otolith s-shaped along height axis. Big knobs and deep furrows over the entire surface and perpendicular to the rims. Medially some central knobs.

L: 9.58 mm, H: 4.41 mm, T: 3.02 mm (holotype)
L: 9.76 mm, H: 4.62 mm, T: 3.28 mm
L: 9.55 mm, H: 4.46 mm, T: 3.07 mm
L: 8.99 mm, H: 3.94 mm, T: 2.91 mm
L: 8.42 mm, H: 3.70 mm, T: 2.36 mm
L: 7.55 mm, H: 3.24 mm, T: 2.08 mm
L: 7.03 mm, H: 3.04 mm, T: 1.90 mm
L: 5.08 mm, H: 2.21 mm, T: 1.26 mm
L: 4.50 mm, H: 1.95 mm, T: 1.04 mm

Material. – 106 sagittas, Miste near Winterswijk, the Netherlands, Miocene, Hemmoorian, Coll. Gaemers, leg. A. F. J. Janssen. 1 sagitta (holotype), Miste, Miocene, Hemmoorian, Coll. RGM 175822. 23 sagittas, 'Flachbohrung 37', Oploo, the Netherlands, Upper Miocene (Langenfeldian), Coll. RGM 175823, 175824, leg. RGD. 2 sagittas, Langenfeldian, Pinneberger Schichten, boring Schenefeld HWW 9, 80 m and 88–90 m, Coll. GLSH. 14 sagittas, bed of Königsbach creek near Königsmühle, Dingden, Western Germany, Dingdener Schichten, Feinsand, Reinbekian, Coll. RGM 175876, leg. A. W. Janssen, 1970.

Distribution. – Miocene: Hemmoorian, Reinbekian and Langenfeldian.

Discussion. – This species resembles *Trisopterus luscus* (L.) very closely. Length-height and length-thickness ratios are almost the same, but nevertheless *T. concavus* appears more slender as far as adult specimens are concerned. *T. concavus* seems to be much less variable than the recent species. Juvenile specimens of *T. luscus* have a very sharp caudal point and a relatively high rostral part. Juvenile specimens of *T. concavus* have a more well-balanced outline and a somewhat more compact appearance than the juvenile otoliths of *T. luscus*.

Remarks. – Up to now this species was confused with *T. spectabilis* (Koken) because the figures in the original publication of Koken (1891) were misleading.

Trisopterus spectabilis (Koken, 1891)
(Pl. II, Figs. 5, 6a, b; Pl. III, Figs. 1a, b–4a, b, c)

Otolithus (Gadus) spectabilis Koken, 1891, p. 94, pl. III, figs. 3a, b, 4.

Type. – Lectotype: Pl. III, Figs. 3a, b, c, Coll. PMHU, Ot. 55, Coll. Koken.

Locus typicus. – Langenfelde, Holstein, Bundesrepublik Deutschland.

Stratum typicum. – Upper Miocene, Langenfeldian.

Paralectotype. – 1 sagitta, *Gadus spectabilis*, Upper Miocene, Langenfelde, Ot. 55, Coll. Koken (PMHU).

Diagnosis. – A very thick and robust *Trisopterus* species. Cauda very wide along entire length and ostium much smaller, especially near collum; thus an obvious jump is visible on the ventral side of the sulcus near the collum. Inner surface markedly convex along long axis. Outer surface in first sketch slightly concave along long axis (in juvenile specimens), but in the adult stage flat because of the presence of large knobs. These knobs are much larger than in other known species.

Description. – Otoliths very thick and robust. Outline oval and elongated. Very thick ventral rim is regularly bent. Thinner, but still rather thick dorsal rim weakly and regularly bent and with distinct predorsal angle. Ventral rim with highly sculptured knobs and furrows. Dorsal rim more or less smooth. Rostral rim straight and with oblique angle on long axis.

Inner surface highly convex along long axis. Bend most pronounced at caudal end. Sulcus acusticus long, wide and straight, almost completely filled with colliculi. Cauda 2 to 2.5 times the length of ostium. Cauda very wide; ostium narrower, especially near collum. Dorsal side of sulcus straight; ventral side with an obvious jump at collum. Collum limited to a narrow groove on dorsal side, somewhat wider on ventral side. Most fully developed cristae along ostium. Area narrow and long. Distinct ventral furrow forms the utmost limit of the small furrows and knobs. Sometimes these furrows are furcated in the middle part of ventral rim.

Outer surface slightly concave along long axis in juvenile specimens but flat in adult ones because of the big knobs; it is convex in the direction of the height. The knobs are few in number but large and very pronounced; they form a rough and rather irregular pattern. On the ventral side knobs are the highest. Thickest part of otoliths often characteristically shifted to caudal part. Few or no central knobs.

L: 9.60 mm, H: 3.88 mm, T: 2.79 mm (Deurne)
L: 7.42 mm, H: 3.07 mm, T: 2.01 mm (Deurne)
L: 7.27 mm, H: 3.03 mm, T: 1.66 mm (Oploo)
L: 7.36 mm, H: 3.02 mm, T: 1.92 mm (Oploo)
L: 8.14 mm, H: 3.47 mm, T: 2.41 mm (Oploo)
L: 9.43 mm, H: 3.89 mm, T: 2.81 mm (Oploo)
L: 9.48 mm, H: 4.01 mm, T: 3.13 mm (Oploo)
L: 9.50 mm, H: 3.98 mm, T: 2.82 mm (Oploo)
L: 9.62 mm, H: 3.90 mm, T: 3.02 mm (Oploo)
L: 9.68 mm, H: 4.11 mm, T: 3.06 mm (Oploo)
L: 9.85 mm, H: 4.12 mm, T: 3.07 mm (Oploo)
L: 10.09 mm, H: 4.25 mm, T: 2.91 mm (Oploo)
L: 10.15 mm, H: 4.70 mm, T: 3.43 mm (Oploo)
L: 10.30 mm, H: 4.56 mm, T: 3.46 mm (Oploo)
L: 10.42 mm, H: 4.71 mm, T: 3.74 mm (Oploo)
L: 9.36 mm, H: 4.55 mm, T: 3.81 mm lectotype (eroded)
L: 8.99 mm, H: 3.89 mm, T: 2.46 mm paralectotype

Material. – 2 sagittas, Upper Miocene, Langenfelde, Coll. Koken (PMHU). 5 sagittas, Upper Miocene, Sands of Deurne, E-3 motorway, Borgerhout near Stenen Brug,

Antwerp, Belgium, Coll. RGM 175837, 175838, 175839. 46 sagittas, Upper Miocene, Langenfeldian, 'Flachbohrung 37', Oploo, eastern part of North Brabant, Netherlands, Coll. RGM 175825, 175826, 175827, leg. RGD, Haarlem. 1 eroded sagitta, Ellewoutsdijk, Westerschelde, Zeeland, Netherlands, Coll. Gaemers, leg. Cadée. 1 sagitta, Langenfeldian, Pinneberger Schichten, boring Schenefeld HWW 9, 88–90 m, Coll. GLSH. 1 sagitta, Langenfeldian–Gramian, Pinneberger Schichten, boring Katharinenhof III near Wedel, 161–164 m, Coll. GLSH.

Distribution. – Upper Miocene: Langenfeldian and Gramian.

Remarks. – The specimen in the Westerschelde is the first evidence of the occurrence of Upper Miocene otoliths in this area. The specimens described as *Gadus luscus spectabilis* Koken by Weiler (1942, 1959), Zilch (1965) and Gaemers (1969a, b, 1971), and as *Gadus* cf. *spectabilis* by Leriche (1906), belong to another *Trisopterus* species, which is described here as the new species *T. concavus*.

Trisopterus luscus (Linnaeus, 1758)
(Pl. III, Figs. 5a, b)

Otolithus (Gadus) anglicus Koken, 1891, p. 94, pl. III, figs. 8, 9. *Trisopterus luscus anglicus* (Koken); Gaemers & Schwarzhans, 1973, p. 210, pl. IV, figs. 6a, b.

Diagnosis. – A thick and high *Trisopterus* species of medium size, which is distinctly bent along the long axis. Caudal part of dorsal rim convex or straight. Rostral rim usually has slightly oblique angle on long axis. Knobs on outer surface of normal size. Inner surface markedly convex along long axis. Outer surface clearly concave to s-shaped along long axis.

L: 11.36 mm, H: 5.38 mm, T: 3.25 mm (Gram)

Material. – 5 sagittas, Gramian, Gram, Coll. RGM 175851, 175852, leg. A. W. Janssen, 13-8-1970. 2 sagittas, Sands of Deurne, Antwerp, Borgerhout near Stenen Brug, Coll. RGM 175840, leg. A. W. Janssen. 1 sagitta, Sands of Deurne, Antwerp, Borgerhout, Foorplein, Coll. RGM 175844, leg. F. J. Janssen. 1 sagitta, Gramian, boring Flensburg-Feldmühle 3, 69–65 m, Coll. GLSH. 13 sagittas, Gramian, boring Pinneberg-Elz, 84–92 m, Coll. GLSH. 1 sagitta, Gramian, boring Flensburg-Bommerlunder, 134–140 m, Coll. GLSH. 3 sagittas, Pinneberger Schichten, Gramian, boring Tornesch II, 19–25 m, Coll. GLSH.

Distribution. – Upper Miocene (Gramian)–Recent.

Discussion. – Otoliths of equal thickness and height, described by Koken (1891) as *Gadus anglicus* can be found among the recent specimens of *T. luscus*. There is no reason therefore to distinguish between two species.

Trisopterus incognitus n. sp.
(Figs. 1a, b, c)

Merlangius cognatus (Koken); Heinrich, 1969, p. 25, pl. XI, fig. 2.

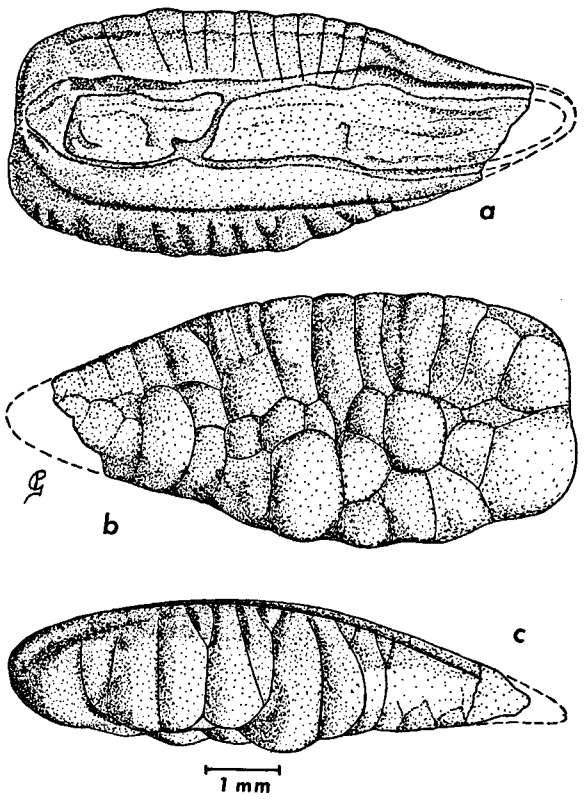

Fig. 1. a. Inner surface, b. Outer surface, c. Ventral side of right sagitta from *Trisopterus incognitus* n. sp. Magnification 10×.

Type. – Holotype: Figs. 1a, b, c, Coll. Heinrich (PMHU); Heinrich (1969): pl. XI, fig. 2.

Locus typicus. – Clay pit, Hohen Woos, Deutsche Demokratische Republik.

Stratum typicum. – Upper Miocene, Langenfeldian (see Heinrich, 1969).

Derivatio nominis. – Incognitus (Lat.) = unknown, unexpected, not recognized. Named for the unexpected occurrence of a new *Trisopterus* species in the Upper Miocene.

Diagnosis. – A thick and high *Trisopterus* species of medium size, which is not or only very slightly bent along the long axis. Distinct postdorsal angle. Part of dorsal rim between predorsal and postdorsal angle long and nearly straight. Rostral rim perpendicular to the long axis. Inner surface somewhat convex along long axis. Outer surface very slightly convex or flat along long axis.

Description. – Strong, thick and high otoliths of medium size. Outline elongated. Ventral rim thick, blunt, regularly bent and distinctly sculptured. Caudal end pointed. Dorsal rim much thinner than ventral rim but still rather blunt. Part of dorsal rim between predorsal and postdorsal angle very long and nearly straight. Part of dorsal rim between postdorsal angle and caudal end slightly concave. Predorsal angle very sharp, postdorsal angle not as fully developed. Rostral rim straight and perpendicular to the long axis.

Inner surface somewhat convex along long axis. Sulcus acusticus long, wide and shallow. Cauda twice as long as ostium. Collum somewhat narrowed and very short. Sulcus almost completely filled with colliculi. Cauda with weak s-shaped bend. Cristae very insignificant. Crista superior somewhat more pronounced than crista inferior. Area shallow and long. Ventral furrow clear and rather far from ventral rim. Small furrows and knobs from ventral rim up to ventral furrow.

Outer surface very slightly convex or flat along long axis. Ventral part of otolith clearly thickest. Big knobs and clear furrows perpendicular to the rims. Middle part of otoliths in particular distinctly sculptured. Medially some central knobs.

L: 7.47 mm, H: 3.55 mm, T: 2.05 mm (holotype)

Caudal end is broken off, thus true length is somewhat greater.

Material. – Several sagittas (mostly fragments), clay pit, Hohen Woos, Upper Miocene, Langenfeldian, Coll. Heinrich (PMHU).

Distribution. – Upper Miocene, Langenfeldian.

Discussion. – The general form of the otoliths of *T. incognitus* indeed resembles that of *Merlangiogadus cognatus* in many respects. Therefore it is not surprising that Heinrich assigned this species to *M. cognatus*. Especially the long straight part between the predorsal and postdorsal angles causes confusion. Nevertheless the entire shape of the sulcus, the straight rostral rim and the great thickness are characteristic for the genus *Trisopterus*. The presence of a postdorsal angle makes it clear that *T. incognitus* is an ancestor of *T. minutus*, which has a somewhat more compact and thicker appearance.

Trisopterus minutus (Linnaeus, 1758)
(Pl. IV, Figs. 2a, b, 4a, b)

Diagnosis. – A thick and high *Trisopterus* species of medium size, which is distinctly bent along the long axis. Distinct postdorsal angle. Part of dorsal rim between predorsal and postdorsal angle short and straight to slightly convex. Rostral rim nearly perpendicular to the long axis. Inner surface markedly convex along long axis. Outer surface slightly concave or s-shaped along long axis.

Distribution. – Upper Pliocene–Recent.

Trisopterus capelanus (Lacepède, 1800)
(pl IV, Figs. 1a, b, 3a, b)

Gadus planatus Bassoli & Schubert, 1906; Chaine & Duvergier, 1928, p. 195, pl. 6, figs. 13, 14.
Gadus cf. *friedbergi* Chaine & Duvergier, 1928; Heinrich, 1969, p. 80, pl. IV, figs. 3a, b.
Trisopterus elongatus Gaemers & Schwarzhans, 1973, p. 210, pl. I, figs. 5, 6a, b, pl. IV, figs. 3a, b.
Trisopterus minutus capelanus (Lacepède, 1800); Svetovidov, 1973, p. 310.

Diagnosis. – A slender, rather thin *Trisopterus* species. Sulcus acusticus wide. Cauda as wide as ostium. Ostium somewhat narrower near collum. Dorsal and ventral rims regularly and weakly bent. Rostral rim nearly straight with oblique angle on long axis. Inner surface convex along long axis. Outer surface slightly concave along long axis, clearly concave in juvenile specimens.

L: 10.79 mm, H: 4.64 mm, T: 2.84 mm (Oploo)
L: 10.57 mm, H: 4.57 mm, T: 2.95 mm (Gram)

Material. – 2 sagittas, Upper Miocene, Gramian, Gram, Denmark, Coll. RGM 175848, 175849. 2 sagittas, Gramian, boring at Pinneberg-Elz, 84–92 m, Coll. GLSH. 3 sagittas, Upper Miocene, Langenfeldian, 'Flachbohrung 37', Oploo, Coll. RGM 175828, 175829, leg. RGD, Haarlem. 1 sagitta, Gramian, Pinneberger Schichten, boring Tornesch II, 19–25 m, Coll. GLSH.

Distribution. – Upper Miocene (Langenfeldian) – Recent.

Discussion. – The specimens of the Gramian cannot be distinguished from recent ones by their shape. Because the otoliths of this species have been differentiated from the branch of *Trisopterus luscus* for a long geological period and since they show even less resemblance to *T. minutus*, *T. capelanus* has to be considered as a separate species and not as a subspecies of *T. minutus*, as stated by Svetovidov (in Hureau & Monod, 1973).

The otoliths of *T. capelanus* of the Langenfeldian from Oploo show a closer similarity to the otoliths from the lineage *T. concavus–T. luscus* than the geologically younger specimens. The splitting of that lineage very probably occurred shortly before the Upper Miocene.

The species *Trisopterus elongatus* Gaemers & Schwarzhans was introduced before I had seen the otoliths of *T. capelanus*. It is not possible to distinguish between the two morphologically.

Genus MERLANGIOGADUS Gaemers, 1973

Merlangiogadus cognatus (Koken, 1891)
(Pl. V, Figs. 1a, b, 2a, b)

Otolithus (Merlangus) cognatus Koken, 1891, p. 89, pl. V, fig. 1 non pl. III, fig. 5.
Merlangus cognatus Koken; Weiler, 1942, p. 79, pl. IX, figs. 7, 8.
Merlangus cognatus Koken; Weiler, 1959, p. 97.
Merlangus cognatus Koken; Brzobohaty, 1964, p. 275.
Merlangus cognatus Koken; Zilch, 1965, p. 461.
Gadus elegans sculptus Koken; Smigielska, 1966, p. 241, pl. XV, fig. 3.
Merlangus? cognatus Koken; Smigielska, 1966, p. 243, pl. XV, fig 4.
Merlangius cognatus (Koken); Weiler, 1968, p. 32.
Merlangius cognatus (Koken); Gaemers, 1969a, p. 8, pl. I, fig. 8.
Merlangius cognatus (Koken); Gaemers, 1969b, p. 74.
Merlangius cognatus (Koken); Gaemers, 1971, p. 244, pl. I, fig. 9 pl. II, fig. 3, pl. V, fig. 5, pl. VI, fig. 1.
Merlangiogadus cognatus (Koken); Gaemers, 1973, p. 63.

Type. – Lectotype: Pl. V, Figs. 1a, b, Coll. PMHU, Ot. 46, Coll. Koken.

Locus typicus. – Langenfelde, Western Germany.

Stratum typicum. – Upper Miocene, Langenfeldian.

Paralectotype. – Pl. V, Figs. 2a, b, Coll. PMHU, Ot. 46, Coll. Koken, same locality and age as lectotype.

Diagnosis. – An elongate, but relatively compact *Merlangiogadus* species. Adult specimens relatively shorter and compacter than juvenile ones.

Material. – 1 sagitta, Upper Miocene, Langenfeldian, 'Flachbohrung 37', Oploo, Coll. RGM 175830, leg. RGD.

Distribution. – Lower Miocene–Upper Miocene.

Remarks. – Very probably the lectotype is the same specimen as shown by Koken (1891, pl. V, fig. 1). Many details agree with this drawing. The only difficulty is that the lectotype is a mirror image of the drawing.

Genus GADICHTHYS Gaemers & Schwarzhans, 1973

Gadichthys undosus Gaemers, 1973

Gadichthys undosus Gaemers, 1973, p. 60, pl. I, figs. 1, 2, 4, Pl. II, fig. 7.
Gadiculus undosus (Gaemers); Gaemers, 1974b, p. 139.

Distribution. – Upper Oligocene.

Remarks. – Up to now this species is the oldest known representative of the *Gadichthys* lineage.

Gadichthys spatulatus (Koken, 1891)
(pl. V, Figs. 3a, b–5a, b)

Otolithus (Merlangus) spatulatus Koken, 1891, p. 89, pl. II, figs. 6, 7, 10.
Otolithus (Merluccius) attenuatus Koken, 1891, p. 85, pl. II, figs. 1, 2.
Merlangius spatulatus (Koken); Heinrich, 1969, p. 61, fig. 11.
Colliolus spatulatus (Koken); Schwarzhans, 1974, p. 101, fig. 74, non figs. 4–7, 13, 14.
Colliolus attenuatus (Koken); Schwarzhans, 1974, p. 102, fig. 75.

Type. – Lectotype: Pl. V, Figs. 5a, b, Coll. PMHU, Ot. 43, Coll. Koken.

Locus typicus. – Germany.

Stratum typicum. – Upper Oligocene or Lower Miocene (Sternberger Gestein).

Paralectotypes. – 1 sagitta, *Merlangus spatulatus*, Sternberger Gestein, Ot. 42, Coll. Koken (PMHU). 2 sagittas, *Merluccius attenuatus*, Sternberger Gestein, Ot. 41, leg. Von Nettelblad (PMHU).

Diagnosis. – A slender and thin *Gadichthys* species with a very sharp caudal point and a rounded to rather pointed rostral end. Sulcus wide and shallow but near the long collum somewhat narrowed and clearly deeper. Dorsal rim variable: nearly straight without indentations to clearly indented half-way between the caudal point and the predorsal angle.

L: 9.79 mm, H: 3.81 mm, T: 1.76 mm (lectotype)
L: 9.18 mm, H: 3.59 mm, T: 1.21 mm (pl. V, Figs. 3a, b)

Distribution. – Upper Oligocene or Lower Miocene.

Discussion. – The drawings of Koken (1891) are misleading for two reasons. Firstly the otoliths of *Merlangus spatulatus* and of *Merluccius attenuatus* are too slender. Secondly the strange indentation has been greatly exaggerated. In reality the otoliths of the two forms distinguished by Koken resemble one another much more than is suggested by Koken's drawings. Also the sulcus of both forms is very similar. A specimen of *G. spatulatus* with a distinctly straight dorsal rim has the pointed rostral end of *Merluccius attenuatus;* this specimen therefore is an intermediate form. The specimen drawn by Schwarzhans (1974, fig. 74) is another intermediate form with a weak indentation in the dorsal rim. Because of these intermediate forms I decided to unite both of Koken's species into one single one.

Gadichthys antwerpiensis (Gaemers, 1971)

Gadus friedbergi Chaine & Duvergier; Weiler, 1942, pl. V, figs. 14a, b.
Merlangus spatulatus (Koken); Weiler, 1942, p. 79, pl. IX, figs. 6, 9.
Merlangius spatulatus (Koken); Gaemers, 1969a, p. 9, pl. I, fig. 9.
Trisopterus antwerpiensis Gaemers, 1971, p. 242, pl. I, fig. 8, pl. V, fig. 3.
Gadichthys antwerpiensis (Gaemers); Gaemers & Schwarzhans, 1973, p. 213.
Gadiculus antwerpiensis (Gaemers); Gaemers, 1974b, p. 139.

Distribution. – Lower–Middle Miocene.

Gadichthys miocenicus (Heinrich, 1969)

Merlangius spatulatus miocenicus Heinrich, 1969, p. 25, pl. V, figs. 1, 2, pl. XVIII, fig. 2, pl. XIX, fig. 1.
Gadichthys miocenicus (Heinrich); Gaemers, 1973, p. 62.
Gadiculus miocenicus (Heinrich); Gaemers, 1974b, p. 139.

Material. – 1 sagitta, Upper Miocene, Langenfeldian, 'Flachbohrung 37', Oploo, Coll. RGM 175831, leg. RGD.

Distribution. – Upper Miocene, Langenfeldian.

Gadichthys benedeni (Leriche, 1926)

Gadus benedeni Leriche, 1926, p. 457, pl. XLI, fig. 10.
Trisopterus benedeni (Leriche); Gaemers, 1971, p. 244.
Gadichthys benedeni (Leriche); Gaemers & Schwarzhans, 1973, p. 213, pl. I, figs. 13–17, pl. VII, fig. 1, non pl. I, figs. 7, 8.
Gadichthys benedeni (Leriche); Gaemers, 1973, p. 62.
Gadiculus benedeni (Leriche); Gaemers, 1974b, p. 139.

Distribution. – Lower Pliocene.

Gadichthys verticalis (Gaemers & Schwarzhans, 1973)

Gadichthys benedeni verticalis Gaemers & Schwarzhans, 1973, p. 214, pl. I, fig. 12, pl. VI, fig. 1.
Gadichthys benedeni verticalis Gaemers & Schwarzhans; Gaemers, 1973, p. 62.
Gadiculus benedeni verticalis (Gaemers & Schwarzhans); Gaemers, 1974b, p. 139.

Distribution. – Upper Pliocene.

Discussion. – In the first instance this species was considered as a subspecies of *G. benedeni*. This was due mainly to the fact that specimens belonging to a *Boreogadus* species were assumed to be juvenile specimens of *G. benedeni*. This fault will be corrected in Gaemers & Schwarzhans (in prep.). All juvenile and adult specimens of *G. benedeni* can now be distinguished from *G. verticalis* and therefore there is no longer any reason to consider the Upper Pliocene otoliths of *Gadichthys* as a subspecies of *G. benedeni*.

Gadichthys thori (Schmidt, 1914)

Gadiculus Thori J. Schmidt, 1914, p. 1, fig. 1.
Gadiculus argenteus thori Schmidt; Svetovidov, 1973, p. 306.
Gadiculus thori Schmidt; Gaemers, 1974b, p. 139.

Distribution. – Recent.

Discussion. – The outline, especially the dorsal rim and the caudal point, of *G. thori* is highly variable. Also the length-height ratio is quite variable. Very probably *G. thori* is a late stage of the *Gadichthys* lineage. Unfortunately, for want of otoliths of this species it is still impossible to reconstruct the diagrams with length-height and length-thickness ratios. When these diagrams become available, the genus identification can be verified. In any case *Gadiculus argenteus* and *Gadichthys thori* are separate species, for the otoliths of both species can always be distinguished.

? Gadichthys venustus (Koken, 1891)
(Pl. V, Figs. 7a, b)

Otolithus (Gadus) venustus Koken, 1891, p. 91, pl. V, figs. 2, 3.
Gadus venustus Koken; Weiler, 1942, p. 77, pl. V, figs. 59, 60.
Gadus venustus Koken; Heinrich, 1969, p. 24, pl. III, figs. 2, 4.
Gadiculus venustus (Koken); Gaemers, 1974b, p. 139.

Distribution. – Upper Miocene, Langenfeldian.

Discussion. – Gaemers (1974b) considered this species to belong to *Gadiculus* Guichenot as the ancestor of *Gadiculus argenteus*. Indeed *?G. venustus* has some characteristics in common with *Gadiculus*. In the first place the otoliths are not bent along the long axis. Secondly the height profile closely resembles that of *Gadiculus*.

The Middle Miocene *Gadiculus ellipticus* Schubert resembles the recent *G. argenteus* so closely that it is highly unlikely that the Upper Miocene *?G. venustus*, which differs in some respects (a very pointed caudal end and a relatively long cauda), is the intermediate form of both *Gadiculus* species.

Possibly *?G. venustus* is the juvenile form of *G. miocenicus*. This is more probable, because both forms are known from the same geological stage (Langenfeldian). Moreover small specimens of *G. miocenicus* and large specimens of *?G. venustus* are unknown. The only difficulty is that specimens with an intermediate size and length-height ratio have not been found up to now.

Should my hypothesis prove to be correct in the future, *G. miocenicus* has to be considered as a junior synonym of *G. venustus*.

Genus GADICULUS Guichenot, 1850

Gadiculus ellipticus (Schubert, 1905)
(Pl. V, Figs. 6a, b; Pl. VII, Figs. 3a, b, 4a, b)

Otolithus (Macrurus) ellipticus Schubert, 1905, p. 622, pl. XVI, figs. 31–33.
Otolithus (Macrurus) excisus Schubert, 1905, p. 623.
Otolithus (Macrurus) ellipticus Schubert; Schubert, 1906, p. 665, pl. V, figs. 8–12.
Glyptorhynchus ellipticus (Schubert); Dieni, 1968, p. 269, pl. III, figs. 4, 5.
Macrurus communis (Procházka); Anfossi and Mosna, 1972, p. 105, pl. IV, fig. 6.

Diagnosis. – A compact, small *Gadiculus* species with indistinct predorsal and postdorsal angles. Postdorsal angle developed most fully in juvenile specimens. Caudal end clearly but not very sharply pointed. Dorsal rim fairly regularly rounded, especially in adult specimens. Highest point of otolith more towards the middle. Ventral rim normally bent in rostral part. Variability is greatest in the dorsal rim.

L: 5.00 mm, H: 3.17 mm, T: 1.04 mm
L: 4.85 mm, H: 3.27 mm, T: 0.99 mm
L: 5.18 mm, H: 3.52 mm, T: 1.06 mm
L: 2.51 mm, H: 1.84 mm, T: 0.56 mm

Material. – 4 sagittas (3 juveniles), Dingdener Schichten, Glimmerton, Middle Miocene, bed of creek near Königsmühle, Dingden, Western Germany, Coll. RGM 175873, 175874, leg. M. van den Bosch. 1 sagitta, same locality and same bed, Coll. Gaemers, leg. Cadée. 1 sagitta, same locality and same bed, Coll. RGM 175872, leg. M. Freudenthal. 1 sagitta, same locality, Dingdener Schichten, Feinsand, Middle Miocene, Coll. RGM 175875, leg. A. W. Janssen.

Distribution. – Middle Miocene–Lower Pliocene.

Remarks. – Possibly the Miocene *Gadus communis* of Procházka (1894) is the same species as *Gadiculus ellipticus* (Schubert). Very probably the specimen shown by Procházka was eroded. This drawing shows a more elongated form than the specimens shown by Schubert, which resemble the material of Dingden very closely.

Gadiculus argenteus Guichenot, 1850

Macrurus sp. Gaemers & Schwarzhans, 1973, p. 218, pl. I, fig. 24.

Diagnosis. – A compact *Gadiculus* species with rather distinct predorsal and postdorsal angles. Predorsal angle most conspicuous. Caudal end clearly but not very sharply pointed. Dorsal rim before predorsal angle, between predorsal and postdorsal angles and behind postdorsal angle straight (except in very large and adult specimens). Highest point of otolith conspicuously toward the front. Ventral rim markedly bent in rostral part. Variability in outline is small and the outline as a whole is very regular.

L: 6.27 mm, H: 4.23 mm, T: 1.54 mm
L: 5.35 mm, H: 3.93 mm, T: 1.16 mm

Distribution. – Upper Pliocene–Recent.

Remarks. – *Macrurus* sp. from boring Ouwerkerk of Upper Pliocene age fits the diagnosis of *G. argenteus* quite well. Although the inner surface is totally destroyed, the outline and the profile of the otolith reveal, that this specimen belongs to this species.

Genus PROTOCOLLIOLUS n. gen.

Species typicus. – *Gadus eocenicus* Frost, 1931.

Diagnosis. – A genus with thick and compact otoliths. Outline oval with rounded rostral end and distinctly pointed caudal end. Predorsal and postdorsal angles moderately pronounced. Parts between caudal point and postdorsal angle and between predorsal and postdorsal angles straight. Sulcus acusticus straight and rather wide, collum short and clearly narrowed. Cauda somewhat less than twice as long as ostium. Sulcus shallow and to a great extent filled with colliculi. Thickest part of otoliths is at the median line or slightly shifted dorsally.

Distribution. – Lower Eocene.
Protocolliolus eocenicus (Frost, 1931) Lower Eocene (Lower Ypresian).

Discussion. – Up to now only one species, *P. eocenicus*, can be placed in the genus *Protocolliolus*. Certainly more finds have to be expected in the future.

Stinton (1965) considers the species *P. eocenicus* to be a member of the genus *Microgadus* Gill, 1863, of which only the recent *Microgadus proximus* Girard is known. Based on otoliths however this latter species is most closely related to *Merlangius*, and to a lesser degree to *Micromesistius*. Most important differences between *Microgadus* and *Protocolliolus* are the following. The otoliths of *Microgadus* are relatively thin with the highest part nearly in the middle; the caudal rim has developed more or less as a straight line (when the sculpturing is not taken into consideration), which forms a sharp angle with the ventral rim and an obtuse angle with the dorsal rim; the sulcus is relatively wide. *Protocolliolus* has thick otoliths; the highest part is definitely towards the caudal end; the caudal rim is rounded; the sulcus is relatively narrow. These characteristics of *Protocolliolus* agree with those of *Colliolus* and *Neocolliolus*. Therefore *Protocolliolus* will be the ancestor of the *Colliolus* lineage.

Genus COLLIOLUS Gaemers & Schwarzhans, 1973

Species typicus. – *Gadus friedbergi* Chaine & Duvergier, 1928.

Diagnosis. – A genus with oval to elongated otoliths. Rostral end rounded and caudal point rather sharp to sharp. Predorsal and postdorsal angles weakly to moderately pronounced. Postdorsal angle sometimes absent. Parts between caudal point and postdorsal angle and between predorsal and postdorsal angles straight to slightly concave. Sulcus acusticus straight and rather narrow, collum rather long and slightly narrowed. Cauda about twice as long as ostium. Sulcus rather deep, colliculi not very thick. Ventral part of otoliths is thickest.

Distribution. – Middle Oligocene–Lower Pliocene.
Colliolus parvus n. sp. Middle Oligocene.
Colliolus sculptus (Koken, 1891) Upper Oligocene–?Lower Miocene.
Colliolus johannettae n. sp. Lower Miocene.
Colliolus friedbergi (Ch. & Duv., 1928) Middle Miocene–Lower Pliocene.
Colliolus schwarzhansi n. sp. Middle Miocene.

Colliolus parvus n. sp.
(Pl. VI, Figs. 1a, b–8a, b)

Type. – Holotype: Pl. VI, Figs. 1a, b, Coll. RGM 175879.

Locus typicus. – Clay pit 'De Vlijt' near Winterswijk, the Netherlands.

Stratum typicum. – Middle Oligocene, Rupelian, top of Brinkheurne Member.

Derivatio nominis. – parvus (lat.) = small. Named after the small size of the otoliths.

Diagnosis. – A small, compact and barely sculptured *Colliolus* species. Ventral rim slightly sculptured. Dorsal rim smooth. Predorsal and postdorsal angles well developed. Caudal end pointed, rostral end angular to pointed. Outer surface with a few thick knobs and deep furrows, especially in the middle part. Not bent along long axis.

Description. – Otoliths thick, small and compact. Outline elongated. Only ventral rim slightly sculptured, otherwise smooth. Ventral rim thick, blunt and regularly bent. Caudal end distinctly pointed. Dorsal rim rather thick and sharper than ventral rim. Predorsal and postdorsal angles well developed. Parts of dorsal rim between ends and angles straight or nearly straight. Postdorsal angle not far from caudal end. Rostral end angular to pointed.

Inner surface slightly convex. Sulcus acusticus long,

rather wide and nearly straight. Cauda straight or very slightly bent with convex side to dorsal rim. Cauda less than twice the length of ostium. Collum deep and narrowest part of sulcus. Distinct colliculi fill sulcus only partly. Cristae insignificant. Area shallow and large. Ventral furrow very indistinct. Weak small furrows and knobs with regular pattern reach ventral furrow.

Outer surface convex, highly sculptured in the middle, nearly smooth at the ends. Relatively big knobs and clear furrows form an irregular pattern.

L: 3.00 mm, H: 1.51 mm, T: 0.64 mm (holotype)
L: 3.07 mm, H: 1.62 mm, T: 0.70 mm
L: 2.72 mm, H: 1.38 mm, T: 0.67 mm
L: 2.88 mm, H: 1.42 mm, T: 0.72 mm
L: 3.08 mm, H: 1.62 mm, T: 0.71 mm
L: 2.47 mm, H: 1.27 mm, T: 0.58 mm
L: 2.13 mm, H: 1.24 mm, T: 0.53 mm

Material. – All sagittas: clay pit 'De Vlijt', Winterswijk, the Netherlands, Middle Oligocene, Rupelian. 460 sagittas, top of Brinkheurne Member, Coll. RGM 175879, 175880, 175881, leg. M. v. d. Bosch, 1973 (new pit). 9 sagittas, Brinkheurne Member, Coll. RGM 85513, leg. De Groot (old pit). 21 sagittas, Brinkheurne Member, Coll. RGM 127064, leg. M. Freudenthal. 13 sagittas, basal deposits of Winterswijk Member, Coll. RGM 175822, leg. M. v. d. Bosch. 29 sagittas, basal deposits of Winterswijk Member, Coll. RGM 175883, 175884.

The otoliths from the Brinkheurne Member are found in the *Serpula septaria – Ancystrocyrinx volgeri* assemblage zone (van den Bosch et al., 1975).

Distribution. – Middle Oligocene, Rupelian.

Discussion. – The shape of the dorsal rim, the caudal and rostral ends and the sculpture on the outer surface are variable. This species can be considered the ancestor of all other *Colliolus* species.

Colliolus johannettae n. sp.
(Pl. VI, Figs. 9a, b, 10a, b)

Trisopterus friedbergi (Chaine & Duvergier, 1928); Gaemers, 1971, p. 242, pl. I, figs. 5, 6; pl. V, fig. 2; pl. VI, fig. 3.
Non *Trisopterus friedbergi* (Chaine & Duvergier); Gaemers, 1971, Sands of Antwerp.

Type. – Holotype: Pl. VI, Figs. 10a, b, Coll. RGM 175855, leg. D. v. d. Mark.

Locus typicus. – Test pit for E-3 tunnel, right bank of Scheldt River, Antwerp, Belgium.

Stratum typicum. – Miocene, Sands of Edegem.

Derivatio nominis. – Named after my wife Johannetta Anje Swen.

Diagnosis. – A very slender but normally thick *Colliolus* species with a very sharp caudal point. Predorsal angle distinct. Generally a rather well developed postdorsal angle; this angle divides dorsal rim between predorsal angle and caudal point into two equal to nearly equal parts, which are straight to slightly concave. Distinctly bent along long axis.

Description. – Otoliths strong and large. Outline highly elongated. Thick and blunt ventral rim is regularly bent, sharpest curve on rostral side. Caudal end with sharp point. Dorsal rim thinner and sharper than ventral rim. Predorsal angle clearly visible. Postdorsal angle usually rather well developed; this angle is located (nearly) midway between two straight to slightly concave parts of the dorsal rim between predorsal angle and caudal end. Dorsal rim before predorsal angle straight to slightly convex.

Inner surface markedly convex, especially in adult specimens. Sulcus acusticus long with average width. Caudal part of cauda slightly bent with convex side toward ventral rim. Sulcus as a whole nearly straight. Cauda nearly twice as long as ostium. Sulcus rather deep, in spite of distinctly developed colliculi. Crista superior sharp and clear, especially along ostium. Crista inferior insignificant. Area wide and large. Weak furrows traverse entire area up to crista superior. Ventral furrow distinct. Small furrows deep, extending to ventral furrow; in juvenile specimens they normally intersect ventral furrow.

Outer surface concave, totally and distinctly sculptured. Medially a low and wide ridge of knobs with the long axis parallel to the height of the otolith. Peripheral knobs perpendicular to the rims.

L: 9.62 mm, H: 3.79 mm, T: 1.74 mm (holotype)
L: 7.04 mm, H: 2.87 mm, T: 1.23 mm (Pl. VI, Figs. 9a, b)

Material. – All sagittas: testpit for E-3 tunnel, Antwerp, Miocene, Sands of Edegem. 133 sagittas, Coll. RGM 175855 (holotype), 175856, 175860, leg. v. d. Mark. 147 sagittas, Coll. RGM 175858. 42 sagittas, Coll. RGM 175859, leg. F. J. Janssen. 93 sagittas, Coll. RGM 175857, leg. Haandrikman. 350 sagittas, Coll. RGM 155176, 155177. 81 sagittas, Coll. Gaemers, leg. Cadée and Coll. Cadée.

Distribution. – Lower Miocene.

Discussion. – Variation is small in most respects. Highest variability noted in dorsal rim. Most specimens have rather distinct predorsal and postdorsal angles, but in some there is a smoothly curved dorsal rim without angles. The length-height and length-thickness ratios show little variability.

Colliolus schwarzhansi n. sp.
(Pl. VI, Figs. 11a, b–13a, b)

Type. – Holotype: Pl. VI, Figs. 12a, b, Coll. RGM 175862, leg. A. W. Janssen, 1970.

Locus typicus. – Bed of the Königsbach Creek near Königsmühle, Dingden, Western Germany.

Stratum typicum. – Middle Miocene, Reinbekian, Dingdener Schichten, Feinsand.

Derivatio nominis. – Named after Werner Schwarzhans, otolith specialist from Berlin, Western Germany.

Diagnosis. – A slender and thin *Colliolus* species. Outer surface and outline distinctly and regularly sculptured. Dorsal rim from predorsal angle up to caudal end straight. A weakly developed postdorsal angle can be present and then the dorsal rim between the predorsal angle and the caudal end is divided into two straight or slightly concave parts. Caudal end sharply pointed. Rostral end angular. Weakly bent along long axis.

Description. – Otoliths thin and large. Outline highly elongated and beautifully sculptured. Rather thick and blunt ventral rim regularly bent. Caudal end with sharp point. Dorsal rim thinner and sharper than ventral rim. Predorsal angle rather well to well developed. A weakly pronounced postdorsal angle divides the dorsal rim between predorsal angle and caudal end into two, nearly equal, straight to slightly concave parts. This part of dorsal rim can also be absolutely straight; then no postdorsal angle exists. Dorsal rim before predorsal angle straight to convex. Rostral end is angular.

Inner surface slightly convex. Sulcus acusticus long and nearly straight. Caudal part of cauda somewhat bent with convex side toward ventral rim. Cauda somewhat more than twice the length of ostium. Sulcus rather shallow. Ostium deeper than cauda. Colliculi clearly developed. Cristae insignificant. Crista superior is traversed by many distinct furrows which cross the wide, large and shallow area. Thus the crista superior is knobbed. Ventral furrow distinct and rather far from ventral rim, which is clearly incised by small furrows. These furrows are usually bifurcated in the middle part of the ventral rim. They cross the ventral furrow many times.

Outer surface slightly concave, totally and distinctly sculptured. Medially an irregular and inconspicuous row of circular to elongated knobs. Peripheral knobs perpendicular to the rims. The highest part of the otolith distinctly shifted towards ventral rim; this characteristic is typical for *Colliolus* species in contrast to *Gadiculus* species, in which the highest part of the otolith is more in the middle.

L: 11.85 mm, H: 4.02 mm, T: 1.48 mm (holotype)
L: 10.62 mm, H: 3.72 mm, T: 1.47 mm
L: 9.43 mm, H: 3.32 mm, T: 1.18 mm
L: 8.45 mm, H: 3.08 mm, T: 1.12 mm
L: 7.62 mm, H: 2.87 mm, T: 0.99 mm
L: 6.36 mm, H: 2.34 mm, T: 0.78 mm
L: 5.45 mm, H: 2.04 mm, T: 0.69 mm
L: 4.14 mm, H: 1.67 mm, T: 0.49 mm

Material. – Bed of creek near Königsmühle, Dingden, Western Germany, Dingdener Schichten, Feinsand, Reinbekian: 165 sagittas, Coll. RGM 175862 (holotype), 175861, 175863, 175864, leg. A. W. Janssen; 35 sagittas Coll. Gaemers, leg. Cadée.

Bank of creek near Königsmühle, Dingden, Western Germany, Dingdener Schichten, Glimmerton, Reinbekian: 123 sagittas, Coll. RGM 175865, 175866, leg. v. d. Bosch; 23 sagittas, Coll. Gaemers, leg. Cadée.

Caudal point of many specimens is broken off.

Distribution. – Middle Miocene, Reinbekian.

Discussion. – Variation is restricted mainly to differences in the shape of the dorsal rim. Postdorsal angle is present or not. Dorsal rim before predorsal angle is convex to straight.

In contrast to other large *Colliolus* species the rostral end is angular; as a result the rostral end of *C. schwarzhansi* appears more robust than in other species of this genus.

C. schwarzhansi and *C. friedbergi* are found together in the 'Dingdener Schichten' of Dingden. They can easily be distinguished from one another because *C. schwarzhansi* is much longer, thinner and less bent along the long axis than *C. friedbergi*. Moreover the juvenile specimens of the two species differ conspicuously. *C. johanettae* can be distinguished from *C. schwarzhansi* because the former is thicker and bends more along the long axis.

Colliolus friedbergi (Chaine & Duvergier, 1928)

Gadus (?)*friedbergi* Chaine & Duvergier, 1928, p. 197, pl. VI, figs. 16–27.
Gadus schuberti Smigielska, 1966, p. 240, pl. XV, figs. 1, 2.

Remarks. – In contrast to the opinion of Smigielska (1966) it can be stated that the length-height and length-thickness ratios for *Gadus schuberti* are exactly the same as those for *C. friedbergi*. The somewhat different predorsal and postdorsal angles as well as the lesser degree of sculpturing of the outer surface fall within the variation of *C. friedbergi*.

The specimens described as *Gadus schuberti* are young specimens of the same species as those adults which are correctly identified as *C. friedbergi*. This can also be deduced from the smaller size and the lesser curvature along the long axis.

Genus NEOCOLLIOLUS n. gen.

Species typicus. – *Gadus Esmarkii* Nilsson, 1855.

Diagnosis. – A genus with slender otoliths. Outline more or less elongated with rounded rostral end and sharply pointed caudal end. Predorsal and postdorsal angles weakly to moderately pronounced. Parts between caudal point and postdorsal angle and between predorsal and postdorsal angles straight. Sulcus acusticus straight and rather wide, collum short and somewhat narrowed. Cauda twice as long as ostium. Sulcus very shallow and almost completely filled with colliculi. Ventral part of otolith is thickest.

Distribution. – Upper Miocene–Recent.

Neocolliolus pliocenicus (Gaemers & Schwarzhans, 1973) Upper Miocene–Lower Pliocene.
Neocolliolus esmarki (Nilsson, 1855) Recent.

Discussion. – Biologists believe that the recent species *Neocolliolus esmarki* belongs to the genus *Trisopterus* (see Svetovidov, 1973) or the genus *Boreogadus* (see Muus, 1966).

The fishes and the otoliths of the recent *Boreogadus saida* differ so greatly from those of *N. esmarki* that the relationship must be very distant. Therefore it is impossible to place *N. esmarki* within the genus *Boreogadus*. The affinity with *Trisopterus* is much greater, but the shape of the fishes as well as their otoliths still show many differences. We will restrict ourselves here to the otoliths alone. The sagittas of *Trisopterus* have a very wide sulcus acusticus, are relatively thick and usually do not have dorsal angles (*Trisopterus minutus* is the only exception; it has a weakly developed postdorsal angle). These properties contrast with those of *N. esmarki*. Other recent genera differ even more.

N. esmarki and *N. pliocenicus* show the closest resemblance to the fossil genus *Colliolus* Gaemers & Schwarzhans. The main differences with this genus are the more compact form and the somewhat wider and shallower sulcus of *Neocolliolus*. Thus we may consider *Colliolus* as the ancestral genus of *Neocolliolus*, which is expressed in the names of these genera.

Neocolliolus pliocenicus (Gaemers & Schwarzhans, 1973)

Gadus elegans Koken, 1884; Smigielska, 1973, p. 6, pl. I, figs. 1a, b.

Remarks. – The specimen shown by Smigielska closely resembles the holotype of *Neocolliolus pliocenicus* (Gaemers & Schwarzhans, 1973; Pl. IV, figs. 4a, b). The shape and depth of the sulcus are equal. The outline of both specimens is very similar. The absence of distinct angles in the Tortonian otoliths of Smigielska is the only difference from the Pliocene holotype.

Subfamilia RANICEPSINAE
Genus PALAEORANICEPS n. gen.

Species typicus. – *Otolithus (Gadi) tuberculosus* Koken, 1884.

Diagnosis. – A genus with thick and compact otoliths. Outline egg-shaped with rounded rostral end and bluntly pointed caudal end. No angles or only very weakly developed dorsal angles. Sulcus acusticus very wide and slightly bent with convex side toward ventral rim. Collum very short and only slightly narrowed. Cauda 1.6 to 2 times as long as ostium. Sulcus very shallow and to a large extent filled with colliculi which have an angular form at the collum. Thickest part of otoliths is slightly ventral.

Distribution. – Lower Oligocene–Lower Miocene. Lower Eocene?

?Palaeoraniceps upnoriensis (Stinton, 1965) Lower Eocene.
Palaeoraniceps tuberculosus (Koken, 1884) Lower Oligocene–Upper Oligocene.
Palaeoraniceps regularis n. sp. Lower Miocene.

Discussion. – The genus *Palaeoraniceps* can easily be distinguished from *Raniceps* by the different form of the sulcus and the colliculi.

Fedotov (1974) describes several skeletons of the Upper Oligocene species *Pseudoraniceps sagus*, established in his publication as a new species belonging to a new genus. Unfortunately otoliths of this species are unknown. Two other Oligocene species, *P. parcus* (Daniltshenko) and *P. oligocaenicus* (Bogatshov), are also known by their skeletons from the Caucasus. It is not known whether one of them is identical with *Palaeoraniceps tuberculosus* of Western Europe. It will be necessary to find either the skeleton of *P. tuberculosus* or the otoliths of the Russian *Pseudoraniceps* species. Perhaps the otoliths are present in situ in the Russian species. It would be exceedingly interesting if they were to be found in these skeletons. With the photograph and description of *Raniceps upnoriensis* Stinton, 1965, it is not possible to determine whether this species belongs to the genus *Palaeoraniceps*. Also other species described by Stinton as *Raniceps* species, namely *R. papillosus* and *R. latidens* from the Lower Eocene London Clay, cannot be placed with certainty in the new genus. The drawings which accompany the descriptions are very rough and thus insufficient. In any case they all cannot be members of the *Raniceps* lineage and have to belong to another genus.

Palaeoraniceps tuberculosus (Koken, 1884)
(Pl. IV, Figs. 5a, b)

Otolithus (Gadi) *tuberculosus* Koken, 1884, p. 540, pl. XI, fig. 1.
Otolithus (Gadidarum) *planus* Koken, 1884, p. 545, pl. XI, fig. 12.
Otolithus (Gadidarum) *latisulcatus* Koken, 1884, p. 545, pl. XI, fig. 5.
Otolithus (*Raniceps*) *tuberculosus* (Koken); Koken, 1891, p. 88.
Otolithus (*Raniceps*) *latisulcatus* (Koken); Koken 1891, p. 86, pl. IV, figs. 4, 4a, Pl. III, figs. 2, 2a.
Otolithus (*Raniceps*) *planus* (Koken); Koken, 1891, pl. III, figs. 7, 7a; pl. IV, figs. 5, 5a.
Macrurus latisulcus (Koken); Leriche, 1910, p. 352, fig. 152.
Raniceps latisulcatus (Koken); Weiler, 1942, p. 83.
Raniceps planus (Koken); Weiler, 1942, p. 83, pl. V, figs. 4a, b, 12, non fig. 10.
Raniceps tuberculosus mut. *supraoligocaena* Weiler, 1942, p. 81, pl. 10, figs. 3–6.
Raniceps tuberculosus (Koken); Weiler, 1942, p. 81, pl. 10, figs. 1, 2.
Raniceps latisulcatus (Koken); Weiler, 1957, p. 137.
Raniceps latisulcatus (Koken); Weiler, 1958, p. 332, pl. 1, figs. 17, 18.
Raniceps planus (Koken); Weiler, 1958, p. 332, pl. 1, fig. 19.
Raniceps latisulcatus (Koken); Martini, 1964, p. 53, fig. 1 (4).
Raniceps planus (Koken); Martini, 1964, p. 53, fig. 1 (5).
Raniceps latisulcatus (Koken); Gaemers, 1972, p. 76, pl. 2, figs. 3a, b.

Type. – Lectotype: Pl. IV, Figs. 5a, b, Coll. PMHU, Ot. 67, Coll. Koken.

Locus typicus. – Süldorf, Germany.

Stratum typicum. – Middle Oligocene.

Paralectotypes. – 2 sagittas, *Raniceps tuberculosus*, Middle Oligocene, Süldorf, ot. 67, Coll. Koken; 3 sagittas, *R. tuberculosus*, Lower Oligocene, Lattorf, ot. 68, Coll. Koken; 7 sagittas, *R. tuberculosus*, Magdeburger Sand, Middle Oligocene, Neustadt near Magdeburg, ot. 69, Coll. Koken; 15 sagittas, *R. planus*, Middle Oligocene, Söllingen, ot.70, Coll. Koken. All specimens: Coll PMHU.

Discussion. – The unique shape of *P. tuberculosus* as shown by Koken (1884) is a very distorted and therefore unserviceable drawing. I have studied Koken's type material of *Raniceps tuberculosus*, *R. latisulcatus* and *R. planus*, which is stored in the Paläontologisches Museum of the Humboldt Universität. It was evident from this material that these three species distinguished by Koken belong to only one species. The specimens of *R. tuberculosus* are all adult forms. The best preserved specimen has been chosen as lectotype and is shown in this publication in the hope that there will no longer be any problems in the future for scientists. The specimens of *R. planus* are all small otoliths except one, which is medium-sized. This otolith cannot be distinguished from the specimens of *R. tuberculosus*. The small specimens are rather variable. They have a flat inner surface and a clearly convex outer surface. The width of the sulcus as well as the length-height ratio of the otoliths is highly variable. There is no doubt that they are juvenile specimens of *P. tuberculosus*. I also have seen the type material of *Raniceps latisulcatus*.

From the drawing and the description (Koken, 1884) it is already clear that these specimens are considerably eroded and therefore not suitable for the description of a new species. These specimens also belong to *P. tuberculosus*.

Palaeoraniceps regularis n. sp.
(Pl. VII, Figs. 1a, b)

Type. – Holotype: Pl. VII, Figs. 1a, b, Coll. RGM 175867, leg. Haandrikman.

Locus typicus. – Test pit for E-3 tunnel, right bank of Scheldt River, Antwerp, Belgium.

Stratum typicum. – Lower Miocene, Sands of Edegem, bed 3 (see Janssen and van der Mark,1968).

Derivatio nominis. – regularis (lat.) = regular. Named after the very regular outline.

Diagnosis. – A highly sculptured and very regularly formed *Palaeoraniceps* species. Weak predorsal angle. Blunt point at caudal end shifted to dorsal rim. Ostium and cauda angular near collum. Rims of cauda straight, rims of ostium slightly bent. Entire sulcus only slightly bent toward ventral side.

Description. – Otoliths strong and medium-sized. Outline egg-shaped. Numerous knobs and furrows all around. Rather thick ventral rim is regularly bent. Caudal end with blunt point, situated more towards dorsal rim. Dorsal rim thinner than ventral rim, regularly bent. Predorsal angle weakly developed.

Inner surface nearly flat, only very slightly convex. Sulcus acusticus long, wide and shallow, somewhat convex towards ventral side. Rims of cauda straight. Rims of ostium slightly curved. Ostium and cauda angular near collum. Cauda 1.5 times as long as ostium. High collum distinctly divides sulcus into ostium and cauda. Colliculi thick and darkly coloured. Cristae low but sharp; crista superior more pronounced than crista inferior. Furrows in dorsal part deeper and usually longer than in ventral part. Nearly entire inner surface sculptured.

Outer surface convex, markedly and totally sculptured. Medially a big cluster of circular to oval knobs. Peripheral knobs perpendicular to the rims.

L: 7.10 mm, H: 3.73 mm, T: 1.66 mm (holotype)
L: 5.27 mm, H: 2.83 mm, T: 1.19 mm (eroded)
L: 3.41 mm, H: 1.78 mm, T: 0.90 mm

Material. – Totally 4 sagittas (one broken and one eroded), Sands of Edegem, bed 3, Miocene, right bank of Scheldt River, test pit E-3 tunnel, Antwerp: 1 sagitta, Coll. RGM 175869; 3 sagittas, Coll. RGM 175867 (holotype), 175868, leg. Haandrikman.

Distribution. – Miocene; Sands of Edegem.

Discussion. – Variability is small. Rims of ostium are more or less curved. Most probably this species is variety èta of *Raniceps latisulcatus* (Koken, 1884) which is mentioned from the black (glauconitic) Miocene Sands of Antwerp. It is a pity that Koken does not show this variety, nor describe it.

Remarks. – Together with specimens of this new species, 2 broken and eroded otoliths of *Raniceps tuberculosus* (Koken, 1884) were found in the Sands of Edegem at Antwerp (Coll. RGM 175871, leg. v. d. Bosch; Coll. RGM 175870, leg. F. J. Janssen). The conservation of these otoliths is very bad and also differs from that of the autochthonous ones. They are darker, more bluish in colour. They originate from the Middle Oligocene Clay of Boom and have survived because of their strength.

Genus RANICEPS Oken, 1817

Diagnosis. – A genus with thick and compact otoliths. Outline egg-shaped with rounded rostral end and bluntly pointed caudal end. No angles. Sulcus acusticus very wide and clearly bent with convex side toward ventral rim. Collum average in length and very narrow. Cauda 1 to 1.3 times as long as ostium. Sulcus very shallow and to a large

extent filled with colliculi which have a rounded oval form. Thickest part of otoliths is slightly ventral.

Raniceps raninus (Linnaeus, 1758)
(Pl. VII, Figs. 2a, b)

Raniceps sp. Gaemers & Schwarzhans, 1973, p. 217, pl. II, fig. 5; Pl. VII, fig. 4.

Diagnosis. – A moderately and irregularly sculptured *Raniceps* species with oval outline. Generally no angles. Ostium and cauda rounded near collum. Rims of ostium and cauda bent. Entire sulcus distinctly bent toward ventral side.

Material. – 1 broken sagitta, Sands of Kallo, Upper Pliocene, basal shell bed, pit for sea sluice near Kallo, Belgium, Coll. Gaemers, leg. Vervoenen.

Distribution. – Upper Pliocene–Recent.

Remarks. – It is not certain that *Raniceps raninus* has lived in the neighbourhood of Antwerp during the formation of the Sands of Kallo. The specimen found is somewhat eroded; moreover there are many fossils in the basal bed of the Sands of Kallo which were transported to this location and which originate from older Pliocene deposits. Of course the minimum age is the age of the Sands of Kallo. The state of preservation of the otolith proves that this fossil comes from the Sands of Kallo or the Sands of Luchtbal.

Subfamily LOTINAE
Genus MOLVA Lesueur, 1819

Molva primaeva n. sp.
(Pl. VII, Figs. 7a, b)

Nemopteryx emarginatus (Koken, 1891); Weiler, 1942, pl. 6, figs. 1a, b.

Type. – Holotype: Pl. VII, Figs. 7a, b, Coll. RGM 175877, leg. A. W. Janssen, 1970.

Locus typicus. – Bed of Königsbach creek near Königsmühle, Dingden, Western Germany.

Stratum typicum. – Middle Miocene, Reinbekian, Dingdener Schichten, Feinsand.

Derivatio nominis. – primaevus, -a (Latin) = in his (her) first youth. Very probably this species represents the first appearance of the genus *Molva*.

Diagnosis. – A small *Molva* species, which is only slightly bent along the long axis. Therefore inner surface is slightly convex, outer surface somewhat concave. No torsion along long axis.

Description. – Elongated, rather thin otoliths. Outline nearly an isosceles triangle with a low height. Ventral rim slightly and regularly bent and somewhat sculptured near rostral and caudal ends; otherwise smooth. Dorsal rim irregularly sculptured with rather big but not very pronounced knobs. Mediodorsal angle clearly developed. Rostral end more sharply pointed than ventral end. All rims sharp and thin.

Inner surface slightly convex. Sulcus acusticus long, wide and shallow. Ratio of the length of ostium to the length of cauda is ca. 3/4. Collum narrow. Sulcus disappears at the rims. Colliculi with oval shape. Cristae distinguishable; crista superior and inferior equally important. Clearly visible area high but not very long. Small furrows short and shallow. Ventral furrow very well developed.

Outer surface slightly concave. Most conspicuous furrows and knobs along dorsal rim and caudal end. Sculpture pattern irregularly radiate. Thickest part of otolith in the middle, just below mediodorsal angle.

L: 8.72 mm, H: 3.59 mm, T: 0.96 mm

Material. – 2 sagittas (1 considerably eroded), bed of Königsbach creek near Königsmühle, Dingden, Western Germany, Middle Miocene, Dingdener Schichten, Feinsand, Coll. RGM 175877 (holotype), 175878, leg. A. W. Janssen, 1970.

Distribution. – Middle Miocene: Hemmoorian and Reinbekian.

Discussion. – This species can be considered as an ancestor of the recent *Molva molva* (Linnaeus) which is much larger with greater curvature. *Molva primaeva* seems to be intermediate between the *Palaeogadus* lineage and *Molva molva* (L.). Therefore it seems very likely that the *Molva* lineage has proceeded from the *Palaeogadus* lineage which has become extinct. *Palaeogadus* species have a much more asymmetrically triangular shape than *Molva* species; moreover curvature is less.

Remarks. – Weiler (1942) shows a definite example of *Molva primaeva* from the Hemmoorian of Hemmoor but he has identified this specimen as *Nemopteryx* (= *Palaeogadus*) *emarginatus*. The close resemblance of these species is demonstrated by this error.

Genus BROSME (Cuvier) Oken, 1817

Brosme heinrichi n. sp.
(Figs. 2a, b, c)

Otolithus (inc. sed.) sp. 4 Heinrich, 1969, p. 46, pl. XI, fig. 3.

Type. – Holotype: Figs. 2a, b, c, Coll. Heinrich (PMHU). Heinrich, 1969: pl. XI, fig. 3.

Locus typicus. – Clay pit, Hohen Woos, Deutsche Demokratische Republik.

Stratum typicum. – Upper Miocene, Langenfeldian (see Heinrich, 1969).

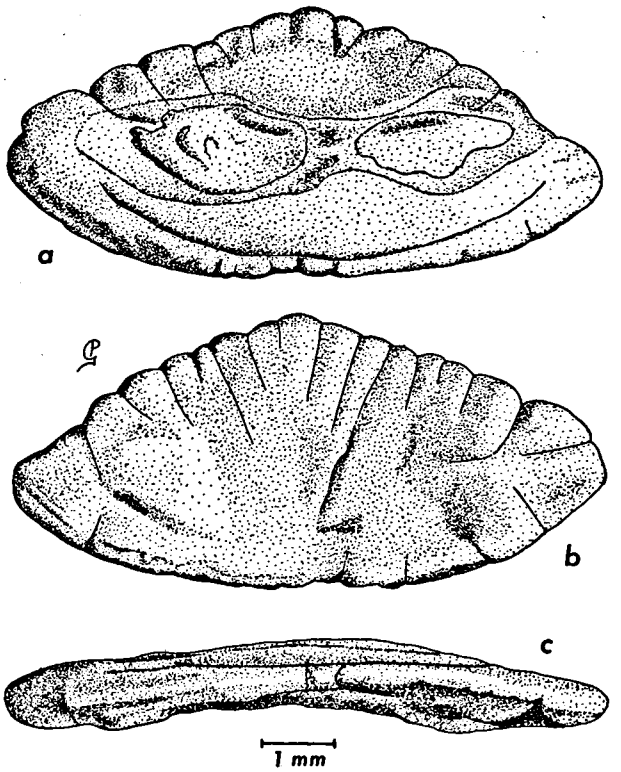

Fig. 2. a. Inner surface, b. Outer surface, c. Ventral side of left sagitta from *Brosme heinrichi* n. sp. Magnification 10×.

Derivatio nominis. – Named after Dr. Wolf-Dieter Heinrich, otolith specialist from Berlin, Eastern Germany, who first found and described this species.

Diagnosis. – A rather small and slender *Brosme* species with a clearly triangular outline which is practically isosceles. Rostral and caudal points both sharp. Middorsal angle distinct. Parts between rostral point and mediodorsal angle and between caudal point and middorsal angle nearly straight. Otolith slightly bent along long axis and without torsion along this axis.

Description. – Rather thin and elongated otoliths. Outline practically like an isosceles triangle. Ventral rim regularly and symmetrically bent and nearly smooth. Dorsal rim somewhat irregularly sculptured with a distinct middorsal angle. Parts of dorsal rim before and behind mediodorsal angle nearly straight. Rostral end a little bit more sharply pointed than caudal end. All rims sharp and thin.

Inner surface slightly convex. Sulcus acusticus very wide and rather long and deep. Ostium a little shorter than cauda. Collum very narrow and long. Sulcus disappears at the rims. Caudal colliculum farther from the rim than ostial colliculum; both are rounded and oval in shape. Cristae not very pronounced; crista superior sharper than crista inferior. Area large but not clearly bordered along the dorsal rim. Ventral furrow far from ventral rim.

Outer surface slightly concave. Most conspicuous furrows and knobs along dorsal rim between mediodorsal angle and caudal point. Sculpture pattern vague.

L: 8.42 mm, H: 3.88 mm, T: 1.06 mm

Material. – 1 sagitta, clay pit, Hohen Woos, Eastern Germany, Upper Miocene, Langenfeldian, Coll. Heinrich (PMHU).

Distribution. – Upper Miocene, Langenfeldian.

Discussion. – The recent species *Brosme brosme* (Ascanius, 1772) has more compact, less pointed otoliths, which have some torsion along the long axis. The part of the dorsal rim before the mediodorsal angle is convex, the part behind the mediodorsal angle concave. The ventral rim is not as regularly bent. On the basis of these differences *B. heinrichi* and *B. brosme* can easily be distinguished from one another.

Familia ?MACRURIDAE

?Macruridarum *deurnensis* n. sp.
(Pl. VII, Figs. 5a, b, 6a, b)

Type. – Holotype: Pl. VII, Figs. 6a, b, Coll. RGM 175847, leg. F. J. Janssen.

Locus typicus. – Foorplein, Antwerp/Borgerhout, Belgium.

Stratum typicum. – Upper Miocene, Sands of Deurne.

Derivatio nominis. – Named after the sands in which the species is found.

Diagnosis. – A species with small and compact otoliths. Inner surface flat. Cauda and ostium equal in length. Collum long. Entire sulcus acusticus clearly depressed. Below collum distinct furrow. Distinct predorsal and postdorsal angles. Ventral furrow far from ventral rim.

Description. – Small, compact and strong otoliths. Outline egg-shaped. Ventral and dorsal rims rather thin and sharp. Ventral rim regularly bent. Dorsal rim consists of straight pieces between caudal and rostral ends, and predorsal and postdorsal angles. Both dorsal angles distinct. Caudal end bluntly pointed. Entire outline sculptured with low and regular knobs and clear small furrows in between.

Inner surface flat. Entire sulcus acusticus distinctly depressed and wide. Ostium and cauda equal in length. Colliculi small and nearly circular. Collum long and somewhat narrower than ostium and cauda. Below collum long and distinct furrow, slightly bent with convex side toward ventral rim. Area unimportant. Ventral furrow very obvious and far from ventral rim.

Outer surface somewhat convex and well-sculptured with a radiate pattern of distinct knobs and furrows. Furrows are shallowest near caudal and rostral ends.

L: 2.51 mm, H: 1.98 mm, T: 0.58 mm (holotype)
L: 2.36 mm, H: 1.70 mm, T: 0.48 mm

Material. – 2 sagittas, Sands of Deurne, Antwerp-

Borgerhout, Foorplein, Coll RGM 175846, 175847, leg. F. J. Janssen.

Distribution. – Upper Miocene, Sands of Deurne.

Discussion. – This species as well as the other small species described as Macruridae from the Middle Miocene and older deposits shows a striking resemblance to the otoliths of *Gadiculus* species. The sulcus acusticus of both groups is nearly the same. Small specimens of *Gadiculus* have a shallower sulcus than the small Macruridae. Ostium and cauda of *Gadiculus* can differ considerably in length, whereas these are usually equally long in the Macruridae.

Properly speaking the most striking difference in the otoliths is their size. The small Macruridae generally do not exceed three millimeters in length, whereas otoliths of *Gadiculus* species often reach a length of 10 millimeters.

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PLATES

PLATE I

Fig. 1a, b. *Gadus parallelus* n. sp., Pliocene, Antwerp, Ford factory, holotype (Coll. RGM 175800) 6×.
Fig. 2a, b. *Gadus parallelus* n. sp., Pliocene, Antwerp, Ford factory, paratype (Coll. RGM 175801) 6×.
Fig. 3a, b. *Pollachius virens* (Linnaeus, 1758), Recent, North Sea (Coll. Gaemers, leg. RIVO) 4×.
Fig. 4a, b. *Pollachius carbonarius* (Linnaeus, 1758), Recent, North Sea (Coll. Gaemers, leg. RIVO) 4×.
Fig. 5a, b. *Pollachius carbonarius* (Linnaeus, 1758), Recent, North Sea (Coll. Gaemers, leg. RIVO) 4×.
Fig. 6a, b. *Pollachius carbonarius* (Linnaeus, 1758), Recent, North Sea (Coll. Gaemers, leg. RIVO) 4×.

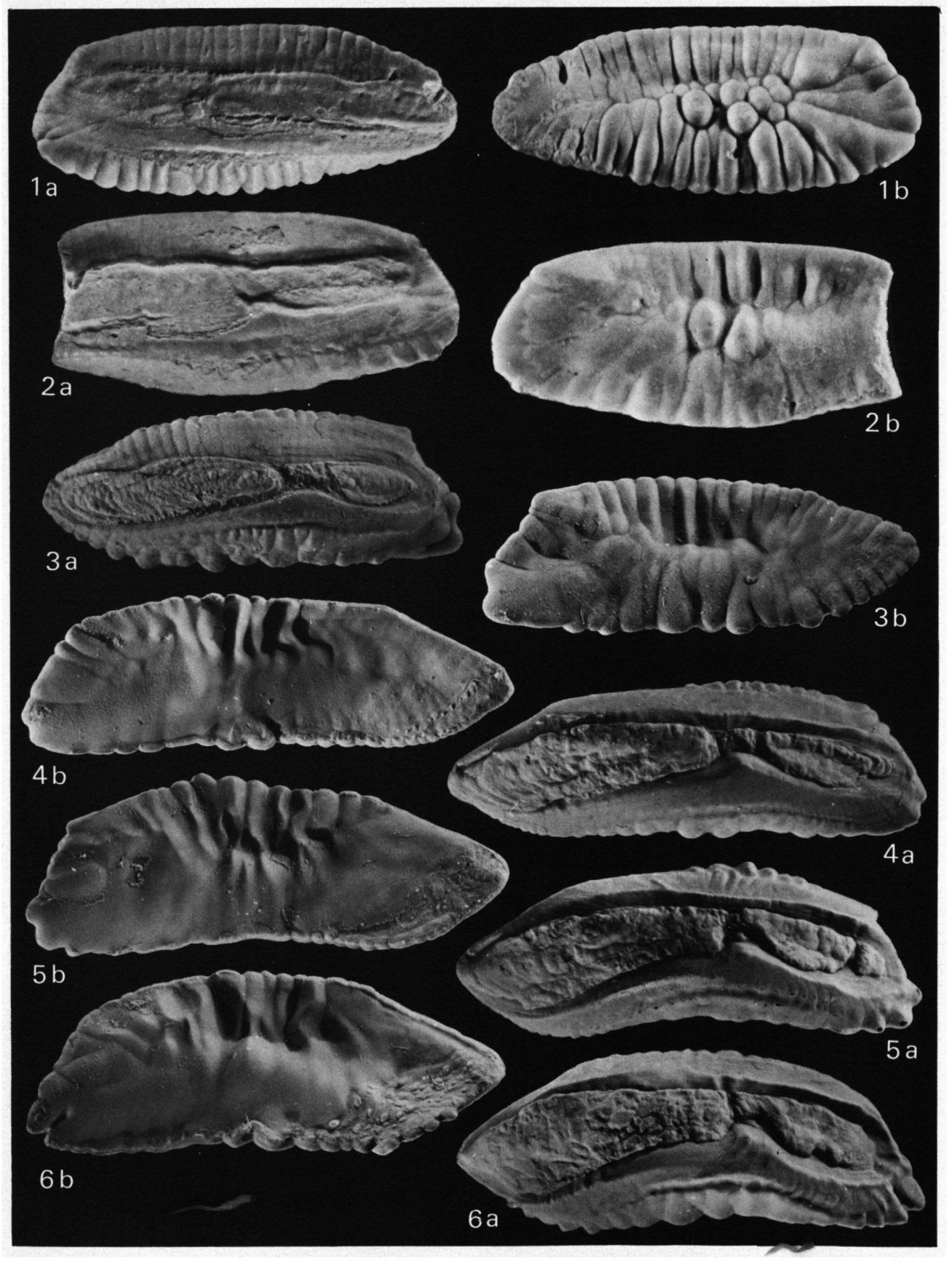
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PLATE II

Fig. 1a, b. *Trisopterus concavus* n. sp., Middle Miocene, Hemmoorian, Miste, holotype (Coll. RGM 175822) 7.5×.
Fig. 2a, b. *Pollachius virens* (Linnaeus, 1758), Recent, North Sea (Coll. Gaemers, leg. RIVO) 4×.
Fig. 3a, b. *Trisopterus concavus* n. sp., Upper Miocene, Langenfeldian, Oploo, paratype (Coll. RGM 175823, leg. RGD) 7.5×.
Fig. 4a, b. *Pollachius virens* (Linnaeus, 1758), Recent, North Sea (Coll. Gaemers, leg. RIVO) 4×.
Fig. 5. *Trisopterus spectabilis* (Koken, 1891), Upper Miocene, Langenfeldian, Oploo (Coll. RGM 175825, leg. RGD) 7.5×.
Fig. 6a, b. *Trisopterus spectabilis* (Koken, 1891), Upper Miocene, Langenfeldian, Oploo (Coll. RGM 175826, leg. RGD) 7.5×.

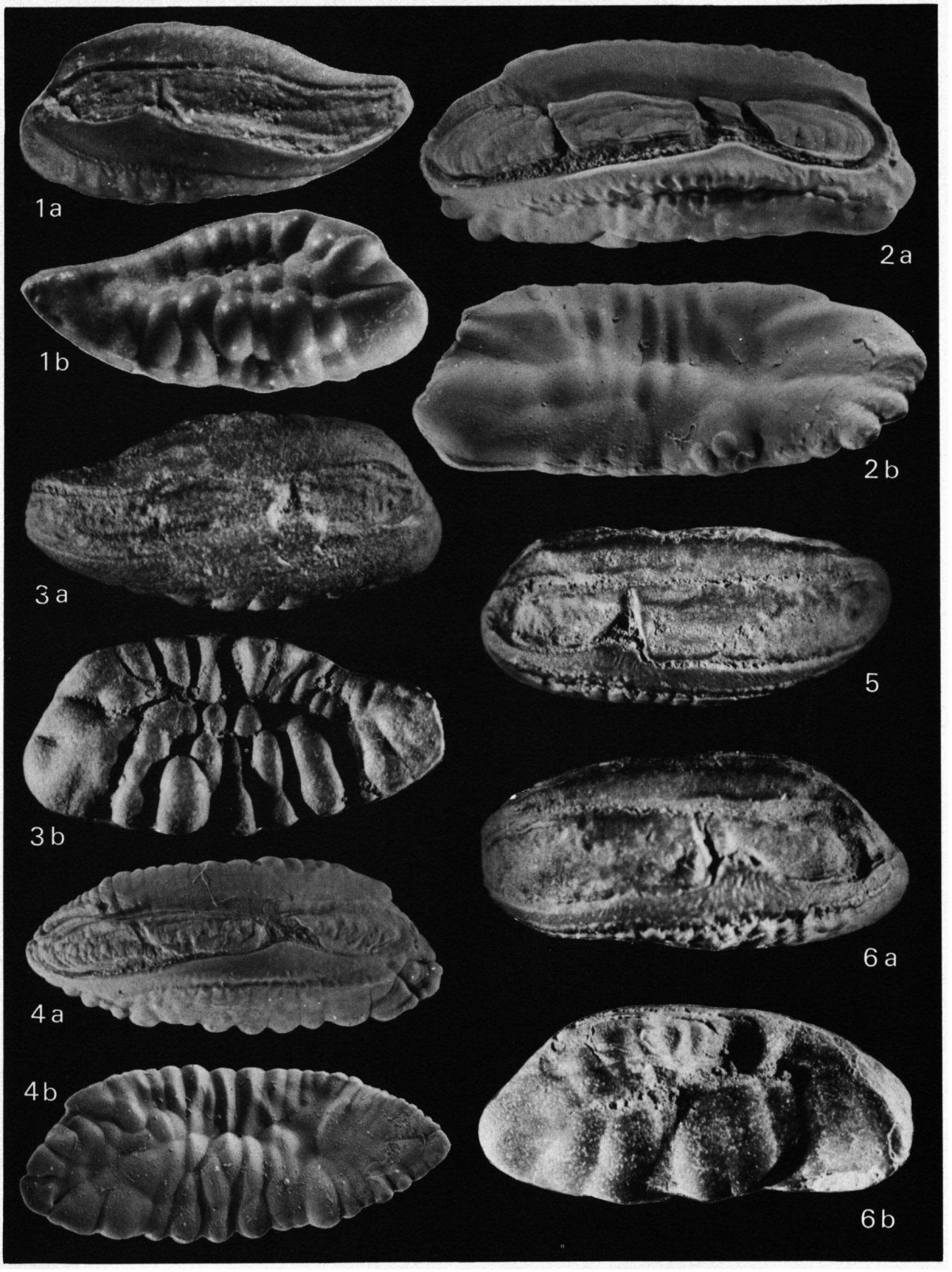
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PLATE III

Fig. 1a, b. *Trisopterus spectabilis* (Koken, 1891), Upper Miocene, Gramian, Sands of Deurne, juvenile specimen (Coll. RGM 175837) 10×.
Fig. 2a, b. *Trisopterus spectabilis* (Koken, 1891), Upper Miocene, Gramian, Sands of Deurne (Coll. RGM 175838) 7.5×.
Fig. 3a, b, c. *Trisopterus spectabilis* (Koken, 1891), Upper Miocene, Langenfeldian, Langenfelde, lectotype (Coll. PMHU, Ot. 55) 7.5×.
Fig. 4a, b, c. *Trisopterus spectabilis* (Koken, 1891), Upper Miocene, Langenfeldian, Langenfelde, paralectotype (Coll. PMHU, Ot. 55) 7.5×.
Fig. 5a, b. *Trisopterus luscus* (Linnaeus, 1758), Upper Miocene, Gramian, Gram (Coll. RGM 175851) 7.5×.

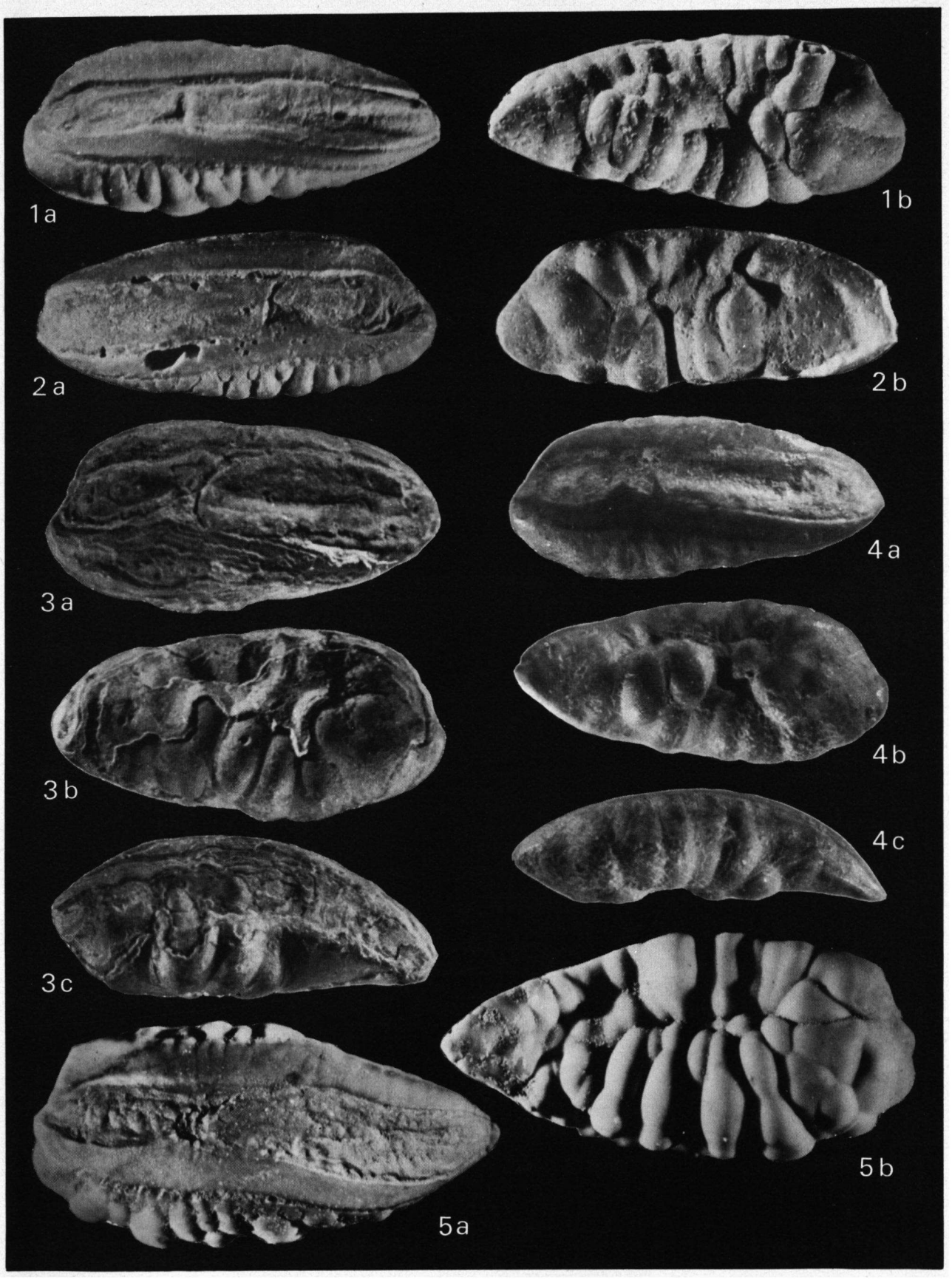
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PLATE IV

Fig. 1a, b. *Trisopterus capelanus* (Lacepède, 1800), Upper Miocene, Langenfeldian, Oploo (Coll. RGM 175828) 7.5×.
Fig. 2a, b. *Trisopterus minutus* (Linnaeus, 1758), Pliocene, Antwerp, Ford factory (Coll. RGM 175808) 10×.
Fig. 3a, b. *Trisopterus capelanus* (Lacepède, 1800), Upper Miocene, Gramian, Gram (Coll. RGM 175849) 7.5×.
Fig. 4a, b. *Trisopterus minutus* (Linnaeus, 1758), Upper Pliocene, Sands of Kallo, sea sluice near Kallo (Coll. Gaemers, leg. Vervoenen) 10×.
Fig. 5a, b. *Palaeoraniceps tuberculosus* (Koken, 1884), Middle Oligocene, Süldorf, lectotype (Coll. PMHU, Ot. 67) 6×.

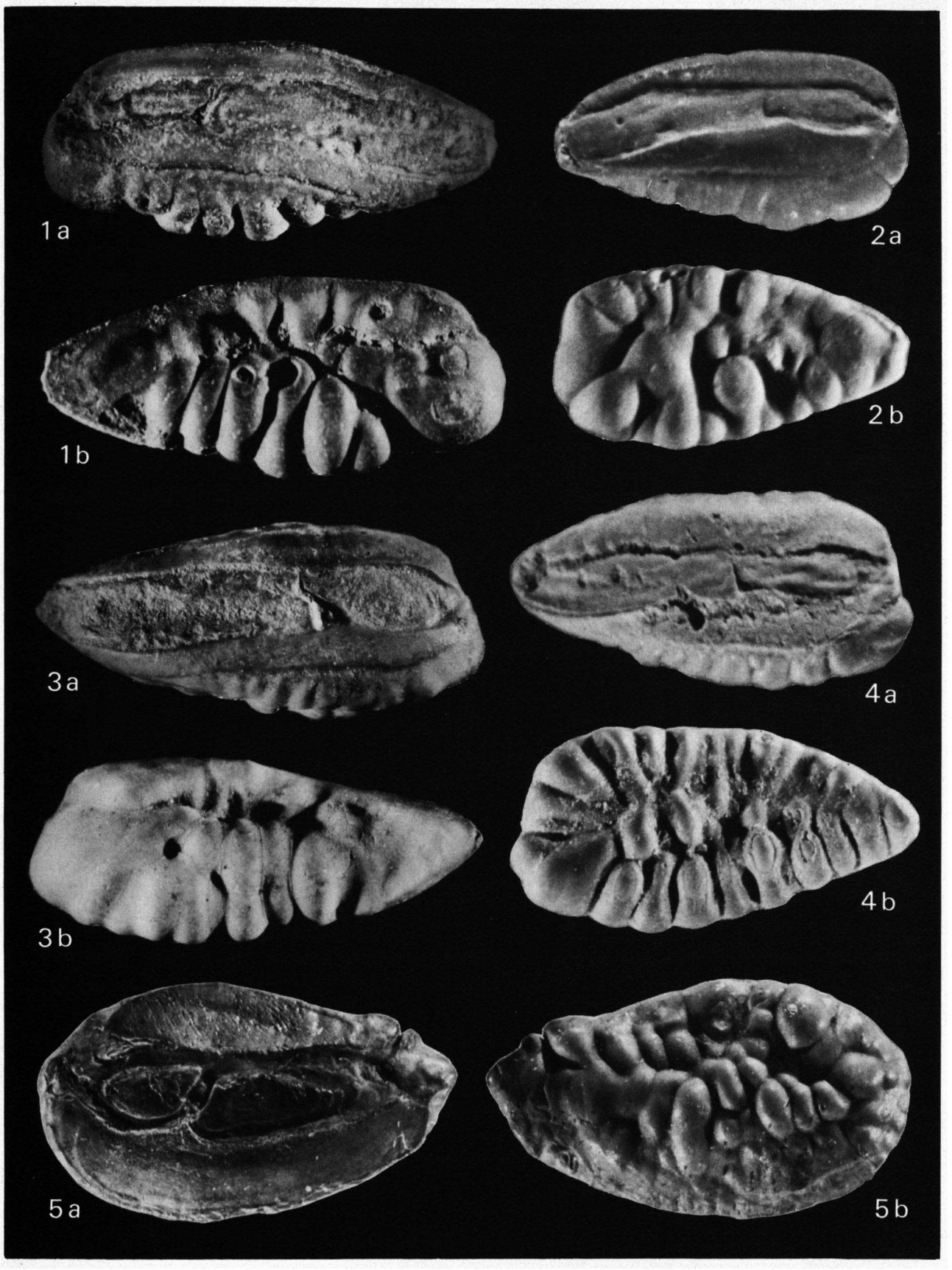
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PLATE V

Fig. 1a, b. *Merlangiogadus cognatus* (Koken, 1891), Upper Miocene, Langenfeldian Langenfelde, lectotype (Coll. PMHU, Ot. 46) 7.5×.
Fig. 2a, b. *Merlangiogadus cognatus* (Koken, 1891), Upper Miocene, Langenfeldian Langenfelde, paralectotype (Coll. PMHU, Ot. 46) 7.5×.
Fig. 3a, b. *Gadichthys spatulatus* (Koken, 1891), Upper Oligocene or Lower Miocene Sternberger Gestein, paralectotype (Coll. PMHU, Ot. 41) 7.5×.
Fig. 4a, b. *Gadichthys spatulatus* (Koken, 1891), Sternberger Gestein, paralectotype (Coll PMHU, Ot. 42) 7.5×.
Fig. 5a, b. *Gadichthys spatulatus* (Koken, 1891), Sternberger Gestein, lectotype (Coll. PMHU Ot. 43) 7.5×.
Fig. 6a, b. *Gadiculus ellipticus* (Schubert, 1905), Middle Miocene, Reinbekian, 'Glimmerton' Dingden (Coll. Gaemers, leg. Cadée) 10×.
Fig. 7a, b. *?Gadichthys venustus* (Koken, 1891), Upper Miocene, Langenfeldian, boring Städt Krankenhaus, Kiel, 96–99 m (Coll. GLSH) 10×.

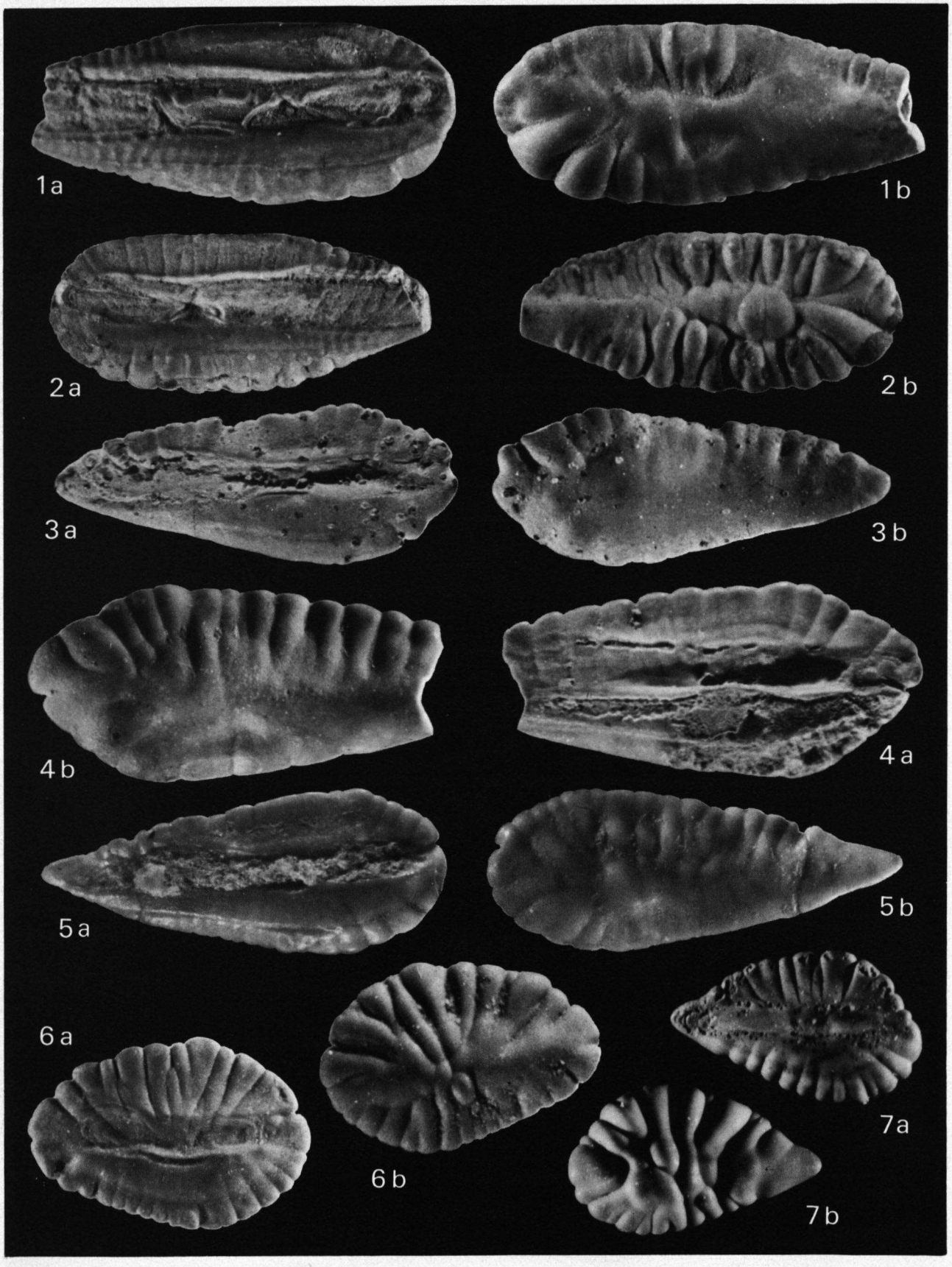
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PLATE VI

Fig. 1a, b. *Colliolus parvus* n. sp., Middle Oligocene, clay pit 'De Vlijt', Winterswijk, holotype (Coll. RGM 175879) 10×.
Fig. 2a, b. *Colliolus parvus* n. sp., Middle Oligocene, clay pit 'De Vlijt', Winterswijk, paratype (Coll. V. van Hinsbergh) 10×.
Fig. 3a, b. *Colliolus parvus* n. sp., Middle Oligocene, clay pit 'De Vlijt', Winterswijk, paratype (Coll. Gaemers, leg. Cadée) 10×.
Fig. 4a, b. *Colliolus parvus* n. sp., Middle Oligocene, clay pit 'De Vlijt', Winterswijk, paratype (Coll. Gaemers, leg. Cadée) 10×.
Fig. 5a, b. *Colliolus parvus* n. sp., Middle Oligocene, clay pit 'De Vlijt', Winterswijk, paratype (Coll. V. van Hinsbergh) 10×.
Fig. 6a, b. *Colliolus parvus* n. sp., Middle Oligocene, clay pit 'De Vlijt', Winterswijk, paratype (Coll. RGM 175880) 10×.
Fig. 7a, b. *Colliolus parvus* n. sp., Middle Oligocene, clay pit 'De Vlijt', Winterswijk, paratype (Coll. V. van Hinsbergh) 10×.
Fig. 8a, b. *Colliolus parvus* n. sp., Middle Oligocene, clay pit 'De Vlijt', Winterswijk, paratype (Coll. V. van Hinsbergh) 10×.
Fig. 9a, b. *Colliolus johannettae* n. sp., Lower Miocene, Sands of Edegem, test pit E-3 tunnel, Antwerp, paratype (Coll. RGM 175856) 7.5×.
Fig. 10a, b. *Colliolus johannettae* n. sp., Lower Miocene, Sands of Edegem, test pit E-3 tunnel, Antwerp, holotype (Coll. RGM 175855) 7.5×.
Fig. 11a, b. *Colliolus schwarzhansi* n. sp., Middle Miocene, Reinbekian, 'Feinsand', Dingden, paratype (Coll. RGM 175861) 7.5×.
Fig. 12a, b. *Colliolus schwarzhansi* n. sp., Middle Miocene, Reinbekian, 'Feinsand', Dingden, holotype (Coll. RGM 175862) 7.5×.
Fig. 13a, b. *Colliolus schwarzhansi* n. sp., Middle Miocene, Reinbekian, 'Feinsand', Dingden, paratype (Coll. RGM 175863) 7.5×.

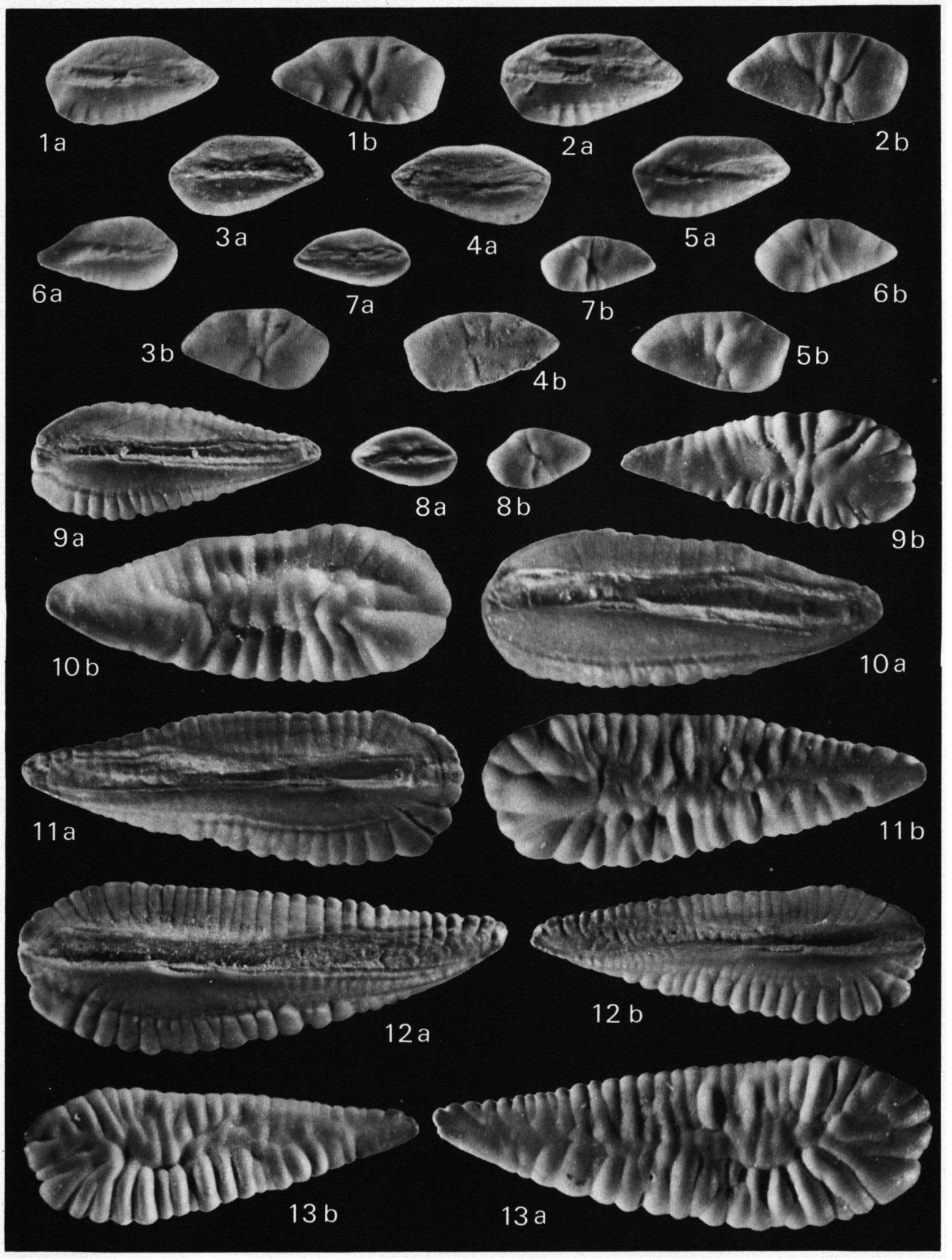
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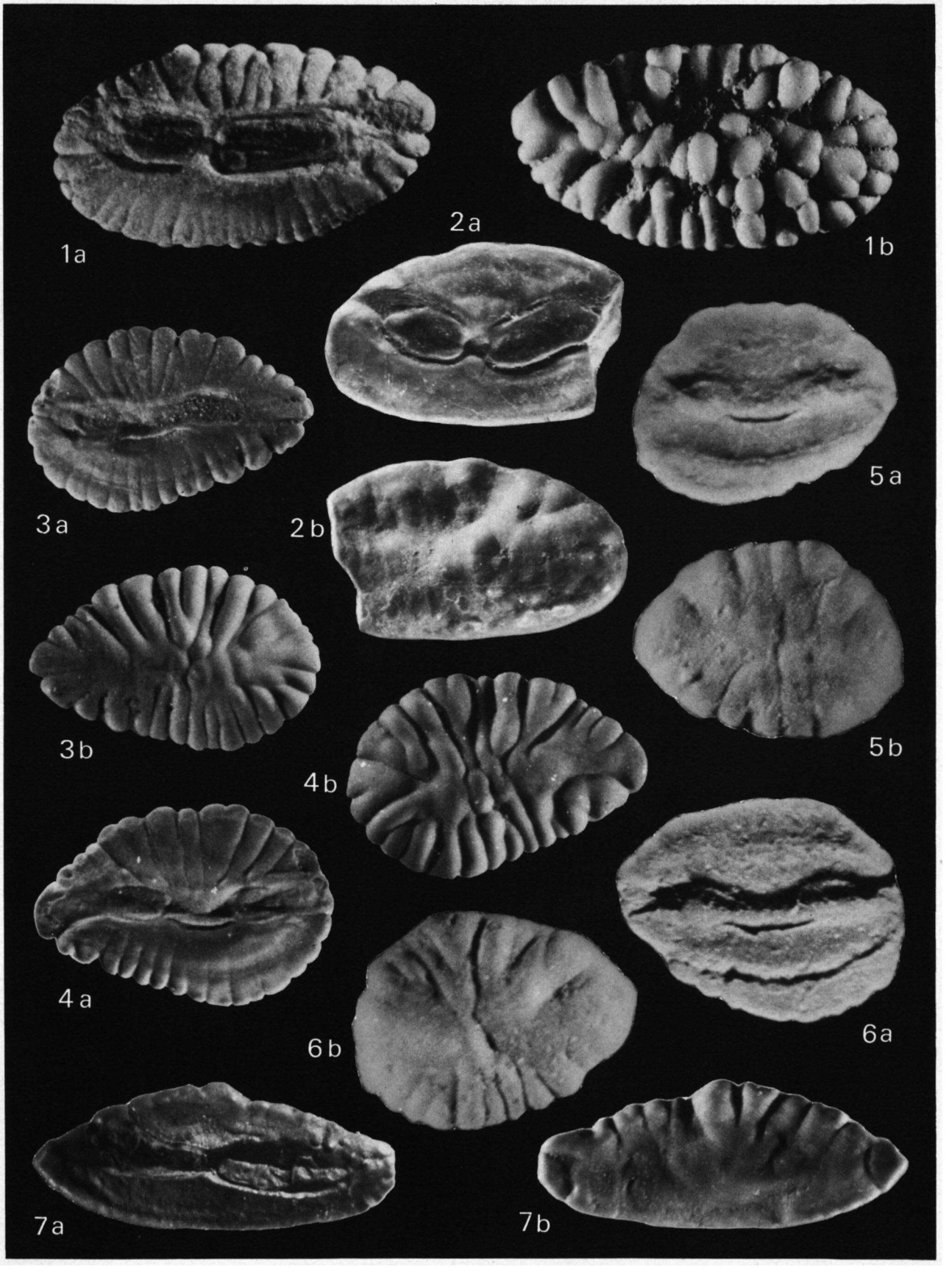
PLATE VII

Fig. 1a, b. *Palaeoraniceps regularis* n. sp., Lower miocene, Sands of Edegem, test pit E-3 tunnel, Antwerp, holotype (Coll. RGM 175867) 10×.
Fig. 2a, b. *Raniceps raninus* (Linnaeus, 1758), Upper Pliocene, Sands of Kallo, basal shell bed, sea sluice near Kallo (Coll. Gaemers, leg. Vervoenen) 7.5×.
Fig. 3a, b. *Gadiculus ellipticus* (Schubert, 1905), Middle Miocene, Reinbekian, 'Glimmerton', Dingden (Coll. RGM 175872) 10×.
Fig. 4a, b. *Gadiculus ellipticus* (Schubert, 1905), Middle Miocene, Reinbekian, 'Glimmerton', Dingden (Coll. RGM 175873) 10×.
Fig. 5a, b. ?Macruridarum *deurnensis* n. sp., Upper Miocene, Gramian, Sands of Deurne, paratype (Coll. RGM 175846) 20×.
Fig. 6a, b. ?Macruridarum *deurnensis* n. sp., Upper Miocene, Gramian, Sands of Deurne, holotype (Coll. RGM 175847) 20×.
Fig. 7a, b. *Molva primaeva* n. sp., Middle Miocene, Reinbekian, 'Feinsand', Dingden, holotype (Coll. RGM 175877) 7.5×.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