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Article

The otoliths from the middle Paleocene of Luzanivka (Cherkasy district, Ukraine)

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With 15 figures and 1 table

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Abstract: Fish otoliths are described from the middle Paleocene (Selandian) from temporary outcrops at Luzanivka, Cherkasy district, Central Ukraine. A total of 26 species are described, 15 as newly established and 5 in open nomenclature. This is the first record of Paleocene otoliths from the Ukraine and the central Ukrainian Basin, which formed the most westward extension of the Caspian Basin during early Tertiary times. As a consequence the fauna from Luzanivka shows a considerable regional differentiation from the better known Paleocene otolith-based fish faunas of central and western Europe, which is expressed in the high amount of new species. The location is on the fringes of the basin, on the stable Ukrainian shield south of the deep Dnjeper graben in a shallow, near shore environment with coral patches. The first fossil occurrence of a relative of the recent 'garden eels' is remarkable in this respect (*Heteroconger astroblematicus* n. sp.). Of particular interest from a phylogenetic point of view are certain gadiform otoliths (genus Merlucciidarum *antiquus* n. sp. and *Maorigadus ukrainicus* n. sp., the latter probably related to the basal gadiform family Muraenolepididae) and very plesiomorphic percoid otoliths (genus Epigonidarum *tyassminensis* n. sp., genus Sparidarum *spatiatus* n. sp., genus Haemulidarum *gullentopsi* and genus Haemulidarum *makarenkoi* n. sp.). Further new taxa described are: *Chlorophthalmus udovichenkoi* n. sp., *Arius subtilis* n. sp., *Fierasferoides bucculentus* n. sp., *Gadophycis serratus* n. sp., *Ogilbia luzanensis* n. sp., genus Bythitidarum *rozenbergi* n. sp., *Centroberyx anguinicauda* n. sp., genus Holocentridarum *ryabchuni* n. sp. and genus Leiognathidarum *tashlikensis* n. sp.

Key words: Teleostei, otoliths, Paleocene, Selandian, taxonomy, paleogeography, Ukraine.

1. Introduction

The location of the rich Paleocene fauna near the village Luzanivka in the Cherkasy district of Ukraine (Fig. 1) was first discovered by V. K. Ryabchun in 1959 (Ryabchun 1970). The location soon became an object of intense paleontological and stratigraphical research. The sandy deposits at the "Lyisa gora" artificial outcrop on the left bank of the Syiroy Tashlik river (coordinates: 49°03'45''N, 31°55'35''E) are particularly rich in bivalves and gastropods. Amitrov (1993) considered the mollusk-fauna as one of most divers and richest of the Eurasian Paleogene and attributed Montian age to it, a term not longer used in international chronostratigraphy and replacing Selandian (in *sensu strico* sense and including Danian to various parts in *sensu lato* sense). Earlier, Makarenko (1970) also considered the mollusk-fauna as of Montian age, but noted their similarity with Selandian of Denmark, then considered a regional stage only. Further studies of mollusks from Luzanivka were published by Korobkov (1964) and Moroz & Soloviak-Krukovskiy (1993),

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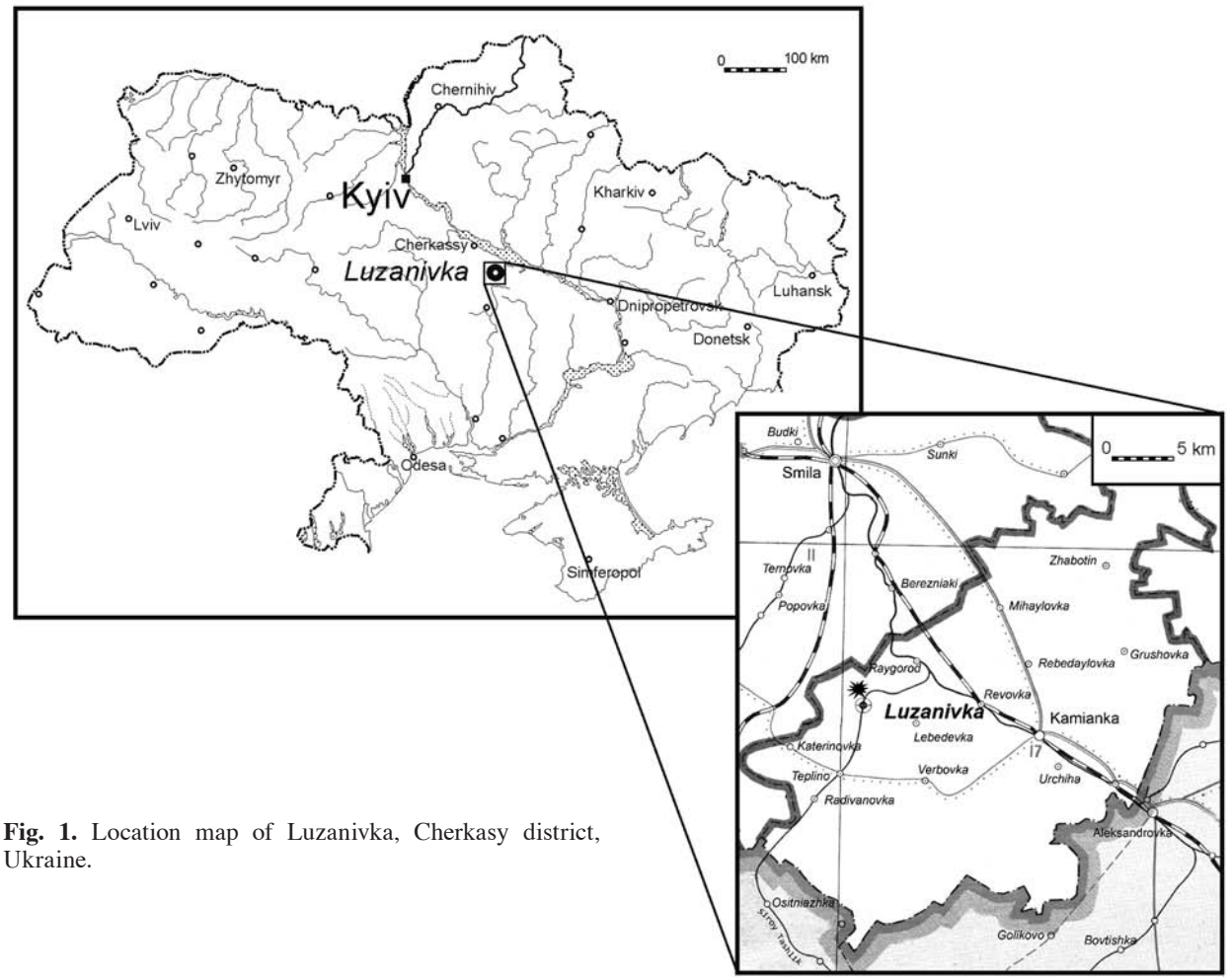

Fig. 1. Location map of Luzanivka, Cherkasy district, Ukraine.

sharks teeth were studied by GLIKMAN and ZHELEZKO, ostracods by SHEREMETA (1968), who also interpreted them as of Montian age. Other fossil remains recovered are foraminifera, corals, sea-urchins, fossil fish bones and otoliths (see MAKARENKO 1970).

The stratigraphical scheme of Paleogene deposits of Ukraine (ANONYMUS 1993; see also MAKARENKO et al. 1987), showed the Paleocene strata near Luzanivka as the "Luzanovskaya Series" (= Luzanovka Group – Fig. 2), a now widely used regional term.

MOROZ and SOVYAK-KRYKOVSKIY (1993) identified two successive Paleocene deposits near Luzanivka, the "Makartitskaya Suite" (= Makartit Formation) and the "Tashlikskaya Suite" (= Tashlik Formation) on the basis of analyses of nannoplankton, foraminifera, dinocysts, palynoflora, mollusks, sea-urchins and corals. The Makartit Fm. was placed in the Danian, the Tashlik Fm. was correlated with the Selandian and Thanetian (Fig. 2). The sandy level with the rich molluskfauna was interpreted as of Selandian age (NP5–NP6, as defined by Luljewa and Kalinichenko, see MASLUN & IVANIK, 2009).

A rich otolith assemblage of about 1100 specimens was obtained from the upper part of the Luzanovka Gr. / lower Tashlik Fm. while sieving the sediments for shark teeth together with N.I. UDOVICHENKO. An artificial outcrop of two meters deep was dug out and otoliths were collected from the rich mollusk layer (about 1 m thickness.). Following MAKARENKO (1970) the following two levels can be distinguished from bottom to top (Fig. 2):

Level 1: Sand, light greenish-grey, medium-grained, calcareous, glauconitic, compacted. The upper section contains a thin band (1-2 cm) of hard sandstone. Mollusks are rare. Thickness = 30 cm.
Level 2: Sand, dark greenish-grey, fine-grained, glauconitic, calcareous, few interlayers of discrete coquina beds (8-12 cm) with some gravel and pebbles. Thickness = 60 cm.

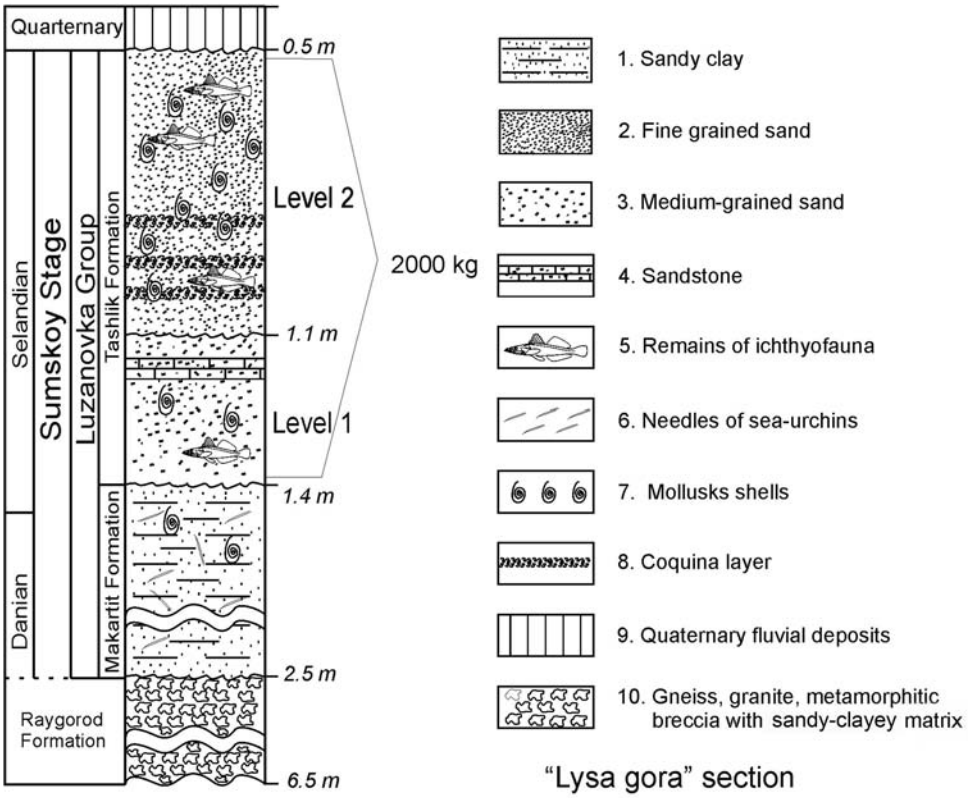

Fig. 2. Stratigraphic position of the sampled strata at Luzanivka.

The sequence is capped by alluvial deposits of probable Quaternary age.

A total of 2000 kg of sand was washed and sieved (Fig. 2). Despite the many paleontological studies of the sequence at Luzanivka over more than 50 years and its wealth in fossils, its ichthyofauna has remained poorly investigated. This is the case for the teleost otoliths described in the following as well as remains (teeth) of the Selachii, which are being studied by N.I. Udovichenko.

Previous records of fossil otoliths are still sparse in the Ukraine, comprising work on Eocene and Early Oligocene associations (Müller & Rozenberg 2003a, b; Bratishko 2009 and Shevchenko & Bratishko 2008).

2. Systematic palaeontology

All illustrated specimens and all holotypes and paratypes are deposited at the geological museum of Luhansk Taras Shevchenko National University, Ukraine and are indicated with the prefix ULUZ 2. All other specimens remain in the collections of Andriy Bratishko, except for a small number of comparative specimens made available for the private collection of Werner Schwarzhans. Comparative material has been available from the Natural History Museum, London (BMNH), the Institute Royale des Science Naturelles, Belgique (IRSNB), the Senckenberg Museum, Frankfurt am Main (SMF) and the Western Australian Museum, Perth (WAM).

The taxonomic description of the otoliths and the morphological terminology follow that of Koken (1884) with amendments proposed by Weiler (1942) and Schwarzhans (1978). Open generic nomenclature is used for species of uncertain generic position and follows the recommendations made by Nolf (1985).

For the purpose of this publication established otolith based genera are used where found appropriate and assumed valid, but we have refrained from establishing new fossil otolith based genera -see also Schwarzhans (2007, 2010a).

The classification used here follows Nelson (2006) except for Pterothrissidae and Rancipitidae in family ranking.

Synonymy listings are restricted to primary citations, important revisions relevant to the described species or new or updated synonymizations.

Each species is accompanied with a short description (except for poorly preserved specimens) complementing the figures and with the aim to optimize future identification of similar collections.

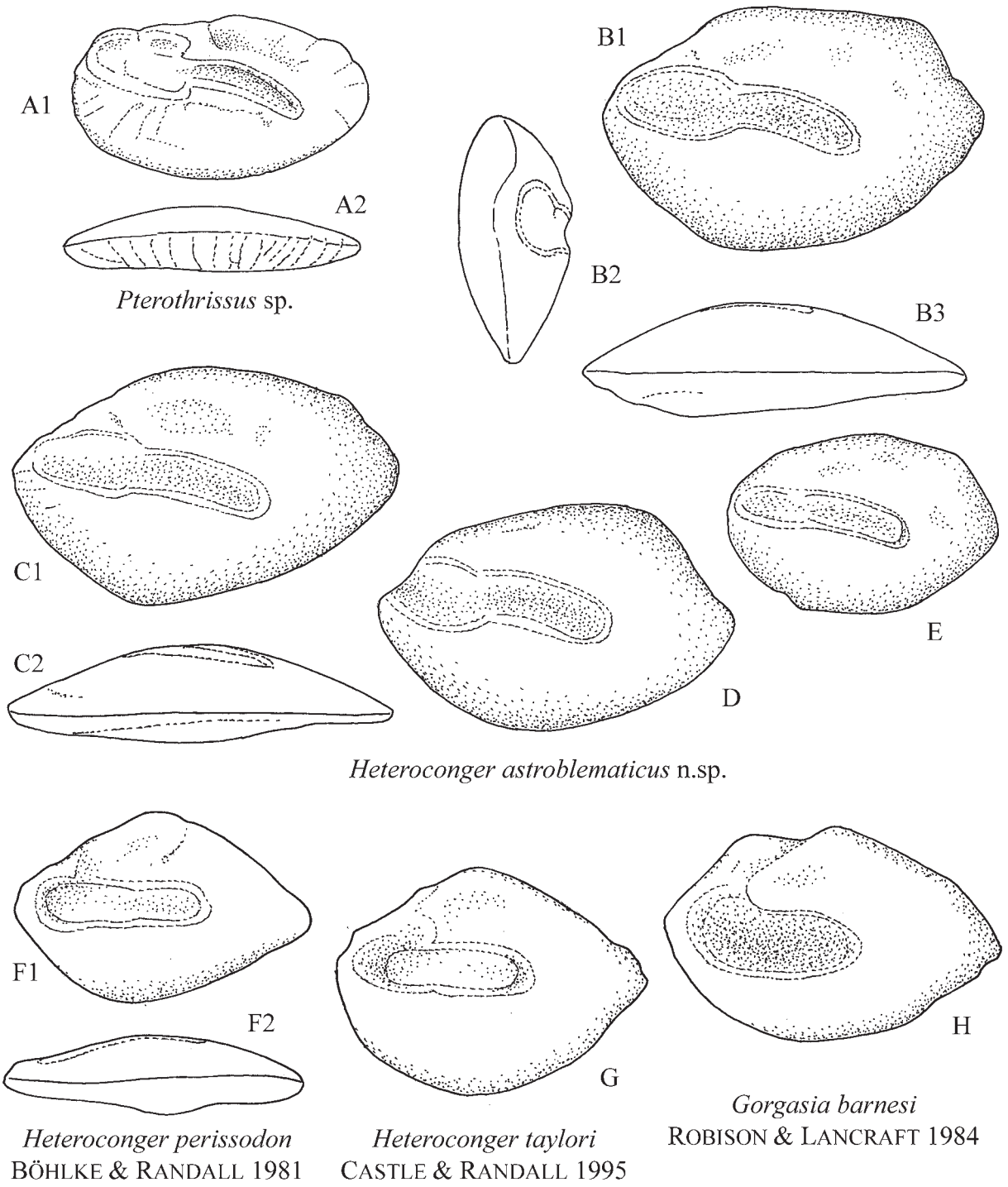

Fig. 3. A. *Pterothrissus* sp. (mirror imaged), ULUZ 2/075. **B-E.** *Heteroconger astroblematicus* n. sp., B: holotype (mirror imaged), ULUZ 2/062, C-E: paratypes (C and E mirror imaged), ULUZ 2/058, ULUZ 2/061, ULUZ 2/059. **F.** *Heteroconger perissodon* BÖHLKE & RANDALL, 1981, Recent, 05°50'N, 95°17'E, WAM 32765-001. **G.** *Heteroconger taylori* CASTLE & RANDALL, 1995, Recent, 02°10'N, 128°13'E, WAM 32981-001. **H.** *Gorgasia barnesi* ROBISON & LANCRAFT, 1984, Recent, 04°02'S, 134°13'E, WAM 32805-003. - 20 x.

Explanation for abbreviations used: otolith length = OL, otolith height = OH, otolith thickness = OT; sulcus length = SuL, sulcus height = SuH, ostium length = OsL, cauda length = CaL, ostium height = OsH, cauda height = CaH, ostial colliculum length = OCL, caudal coliculum length = CCL, ostial colliculum height = OCH, caudal coliculum height = CCH, colliculum length (in case of single colliculum) = CL, colliculum height (in case of single colliculum) = CH; affinity = aff.; versus = vs; synonymous = syn.

All measurements are given in mm.

All figures show otoliths from the right side, or mirror imaged as if from the right side, in order to better facilitate comparison.

Order Albuliformes Nelson, 1973
Suborder Albuloidei Jordan, 1923
Family Pterothrissidae Gill, 1893
Genus *Pterothrissus* Hilgendorf, 1877

Pterothrissus sp.
Fig. 3A

Material: 3 juvenile specimens, ULUZ 2/075, Luzanivka, Selandian.

Short description: Small, juvenile otoliths of about 2.5 mm length with a slightly convex inner face and a nearly flat outer face. OL:OH = 1.8. Outline typical of a juvenile otolith of the genus *Pterothrissus*, smooth, oval, elongate, without major angles but an expanded postdorsal region. Sulcus diagonally on the inner face with a wide, ventrally and dorsally widened ostium and a narrow, slightly swung cauda. CaL:OsL = 1.1; OsH:CaH = 2.3. Outer face intensely ornamented, typical for juvenile *Pterothrissus* otoliths.

Comparison: The strongly dorsally widened ostium and the slightly swung cauda is different from the known *Pterothrissus* of the European Paleocene and Eocene, such as *P. angulatus* (Stinton, 1966) and *P. conchaeformis* (Koken, 1885) and suggest that these specimens may represent another yet undescribed species.

Order Anguilliformes Regan, 1909
Suborder Congroidei Regan, 1909
Family Congridae Kaup, 1856
Genus *Heteroconger* Bleeker, 1868

Heteroconger astroblematicus n. sp.
Figs. 3B-E, 15A

Holotype: Figs. 3B, 15A, ULUZ 2/062; Luzanivka, Selandian.

Paratypes: 6 specimens, Fig. 3C-E, ULUZ 2/058, ULUZ 2/061, ULUZ 2/059, same location.

Etymology: Referring to the nearby asteroid crater of Boltysh of terminal Cretaceous / early Paleocene times.

Diagnosis: Small otoliths up to slightly over 3 mm length, roundish, thick; OH:OT = 2.2-2.4. Inner face strongly convex. Sulcus inclined; ostium widened and deepened, anteriorly closed near to anterior tip of otolith and without ostial channel. No or very weak dorsal depression.

Description: Moderately elongate, oval otoliths with moderately pointed, median anterior and posterior tips and variably extended postdorsal region, sometimes with postdorsal angle; rims otherwise smooth and without angles. Sulcus on convex inner face distinctly inclined at angle of 10° to 15°, somewhat deepened, particularly ostium. Cauda short, slightly bent, with rounded tip. Ostium widened, reaching close to anterior tip of otolith but anteriorly closed, without ostial channel dorsally. Ostial and caudal colliculi undivided, entirely filling sulcus. OL:SuL = 1.6; CaL:OsL = 1.0-1.2. No or weak dorsal depression. No ventral furrow. Outer face flat to slightly convex, smooth.

Comparison and discussion: *Heteroconger astroblematicus* is the first otolith based fossil record of a "garden eel". *Heteroconger* otoliths are characterized by the deepened sulcus with the widened ostium reaching close to the anterior rim of the otolith. Most recent species show some form of an ostial channel dorsally and a variable expression of the dorsal depression ranging from weak to moderate. Otoliths of the related genus *Gorgasia* Meek & Hildebrand, 1923, another "garden eel", are characterized by the much deeper and shorter sulcus. Otoliths of the genus *Gnathophis* Kaup, 1860, with which *H. astroblematicus* could possibly be confused, always show an ostial channel and its ostium is not widened and terminates at some distance from the anterior rim of the otolith. Recent otoliths of *Heteroconger* and *Gorgasia* are figured for comparison in Fig. 3 below.

Order Siluriformes Cuvier, 1817
Family Ariidae Günther, 1864
Genus *Arius* Cuvier & Valenciennes, 1840

Arius danicus Koken, 1891
Fig. 4A-E

1891 *Arius danicus*. – Koken, p. 81, fig. 1.
1930 *Arius germanicus* Koken, 1891. – Roedel, p. 52.
1930 *Arius rotundus*. – Roedel, pl. 1, fig. 17
?1993 genus Ariidarum sp. 1. – Nolf & Dockery, pl. 2, figs. 5-6.
2003 *Arius danicus* Koken, 1891. – Schwarzhans, fig. 11J-K.
2004 *Arius danicus* Koken, 1891. – Schwarzhans, fig. 3A-F.

Material: 44 specimens, ULUZ 2/106, ULUZ 2/014, ULUZ 2/012, ULUZ 2/107, ULUZ 2/015, Luzanivka, Selandian.

Description: *Arius danicus* otoliths are lapilli, which are easily recognized by the almost regular rounded outline, except for a mild postdorsal projection. Otolith size up to 4.5 mm at Luzanivka, but elsewhere known from specimens up to 5.5 mm length. OL:OH = 1.2-1.35; OH:OT = 2.5-2.8. In-

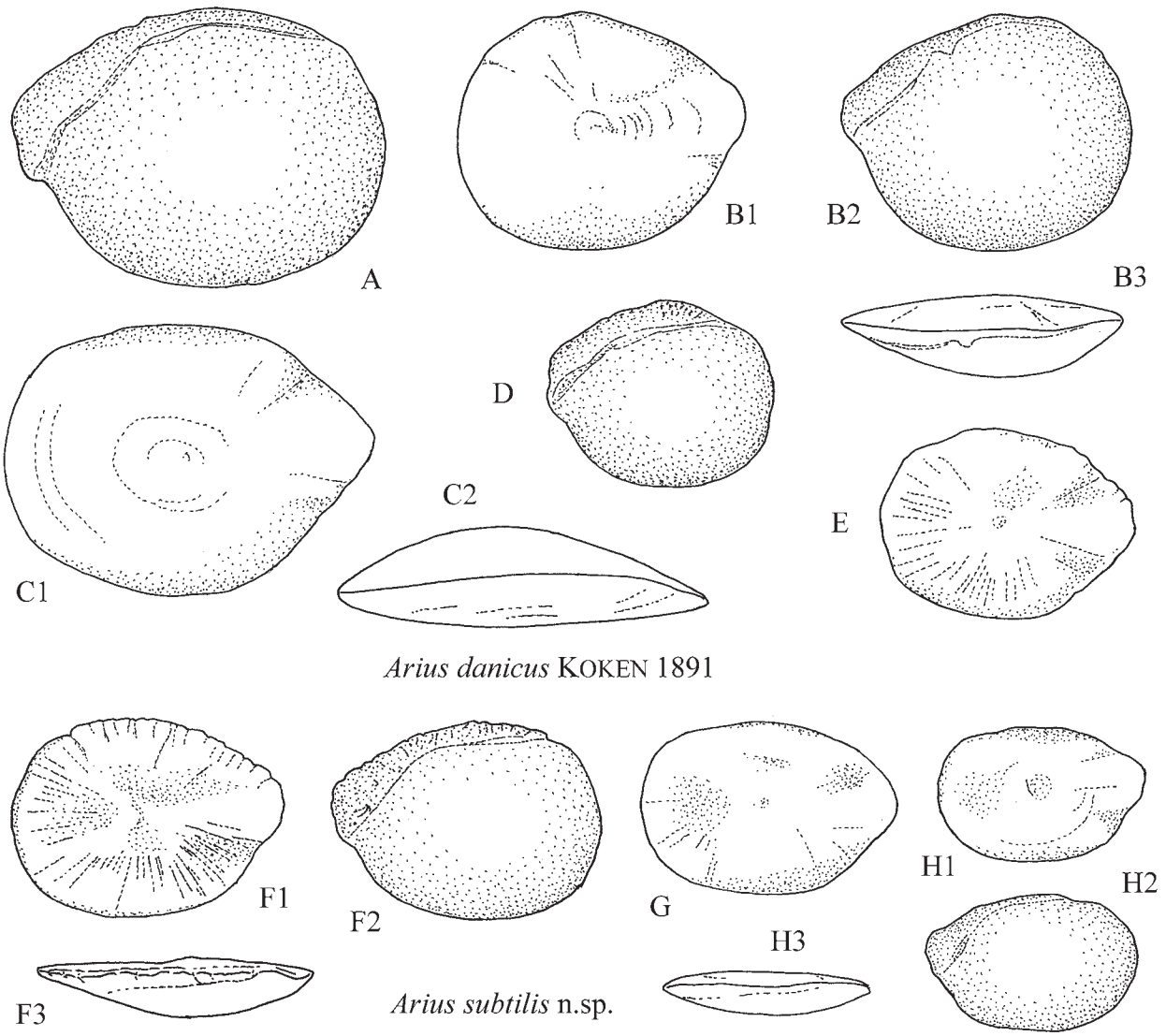

Fig. 4. A-E. *Arius danicus* KOKEN, 1891 (A, C-E mirror imaged), ULUZ 2/106, ULUZ 2/014, ULUZ 2/012, ULUZ 2/107, ULUZ 2/015. **F-H.** *Arius subtilis* n. sp., F: holotype, ULUZ 2/145, G-H: paratypes, ULUZ 2/108, ULUZ 2/107. - 12 x.

ner face convex, smooth with faint sulcus-like feature along the dorsal rim, widening towards postdorsal projection and merely separated by faint groove. Outer face flat with some faint radial furrows.

Distribution: This species appears to be widely distributed during Paleocene times and has been recorded from Western Greenland through the North Sea Basin to Bavaria (unpublished data) and the Ukraine, and possibly also from the U.S.A.

Arius subtilis n. sp.
Figs. 4F-H, 15B

Holotype: Fig. 4F, ULUZ 2/145; Luzanivka, Selandian.

Paratypes: 10 specimens, Figs. 4G-H, 15B, ULUZ 2/108, ULUZ 2/107, same location.

Further material: 32 specimens and 2 poorly preserved tentatively assigned specimens, same location.

Etymology: Subtilis (Latin) = thin-bodied.

Diagnosis: Regular oval outline with mild postdorsal projection. OL:OH = 1.35-1.5; OH:OT = 3.2-3.5.

Description: Lapilli with regular rounded, oval outline, ex-

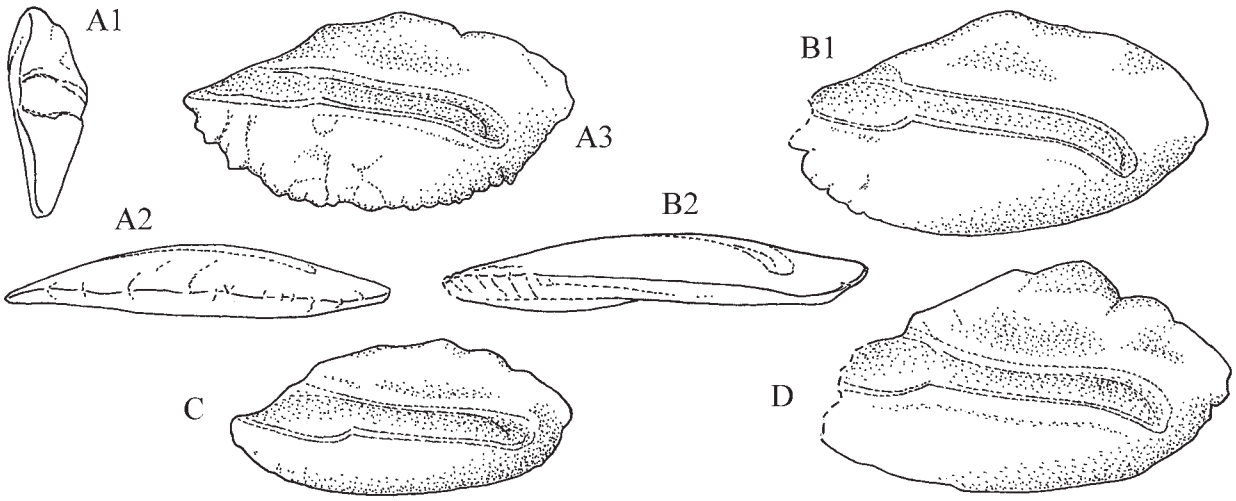

Fig. 5. A-D. *Chlorophthalmus udovichenkoi* n. sp., A: holotype (mirror imaged), ULUZ 2/053, B-D: paratypes, ULUZ 2/109, ULUZ 2/101, ULUZ 2/110. - 20 x.

cept for mild postdorsal projection. Otolith size up to slightly above 3 mm at Luzanivka, but unpublished data from Bavaria reach up to over 5 mm length. Inner face mildly convex, smooth with faint sulcus-like feature along the dorsal rim, widening towards postdorsal projection and merely separated by faint groove. Outer face flat with some faint radial furrows.

Comparison: Otoliths of *A. subtilis* closely resemble those of the contemporaneous species *A. danicus*, except for the more thin appearance and the slightly more elongate shape.

Order Aulopiformes Rosen, 1973
Family Chlorophthalmidae Jordan, 1923
Genus *Chlorophthalmus* Bonaparte, 1840

Chlorophthalmus udovichenkoi n. sp.
Figs. 5A-D, 15C

Holotype: Figs. 5A, 15C, ULUZ 2/053; Luzanivka, Selandian.

Paratypes: 4 specimens, Fig. 5B-D, ULUZ 2/109, ULUZ 2/101, ULUZ 2/110, same location.

Etymology: In honour of N. I. Udovichenko (Luhansk) for his contribution to the knowledge of fossil sharks from the Ukraine.

Diagnosis: Elongate otolith with undulating dorsal rim and slight twist of inner face towards outwards posteriorly. Sulcus long, narrow, distinctly inclined at angle of about 10°. Cauda slightly downturned with pointed tip reaching close to postdorsal rim of otolith.

Description: Small, elongate otoliths up to 3 mm length. OL:OH = 1.95-2.25; OH:OT = 2.5-3.0. Ventral rim gently curved, sometimes delicately crenulated, deepest anteriorly; dorsal rim irregularly undulating, highest at its middle. Anterior tip moderately pointed; posterior tip more massive, dorsally shifted. Inner face convex, slightly twisted along long axis. Sulcus inclined, somewhat deepened. Ostium rather narrow, much shorter than cauda; cauda narrow, long with slightly downturned and tapering tip terminating close to postventral rim. CaL:OsL = 1.5-1.8. Small dorsal depression; no ventral furrow. Outer face flat to slightly concave, rather smooth.

Comparison: Otoliths of *C. udovichenkoi* differ from those of *C. tortus* (Schwarzhans, 2003) (as *Aulopus tortus*) from the Danian of Denmark in the higher dorsal rim and the thinner appearance and from *C. deflecticauda* Schwarzhans, 2007 from the Eocene of Germany likewise in the higher dorsal rim, its much thinner appearance, the less inclined sulcus and the different caudal tip. Otoliths of the recently established genus *Paraulopus* Sato & Nakabo, 2002 differ in the lack of the twist of the inner face, the shorter, more straight cauda and the dorsally expanded ostium. To this genus belongs the widespread Paleocene species *P. postangulatus* (Nolf & Dockery, 1993) (previously in *Chlorophthalmus*), which is lacking from Luzanivka, and its successor in the European Eocene, *P. davisi* (Frost, 1925).

Order Gadiformes Goodrich, 1909
Family indet. near Muraenolepididae
Genus †*Maorigadus* Schwarzhans, 1980

Remarks: The fossil otolith-based genus *Maorigadus* was originally established by Schwarzhans from the Eocene of New Zealand as representing an extinct genus of the Mac-

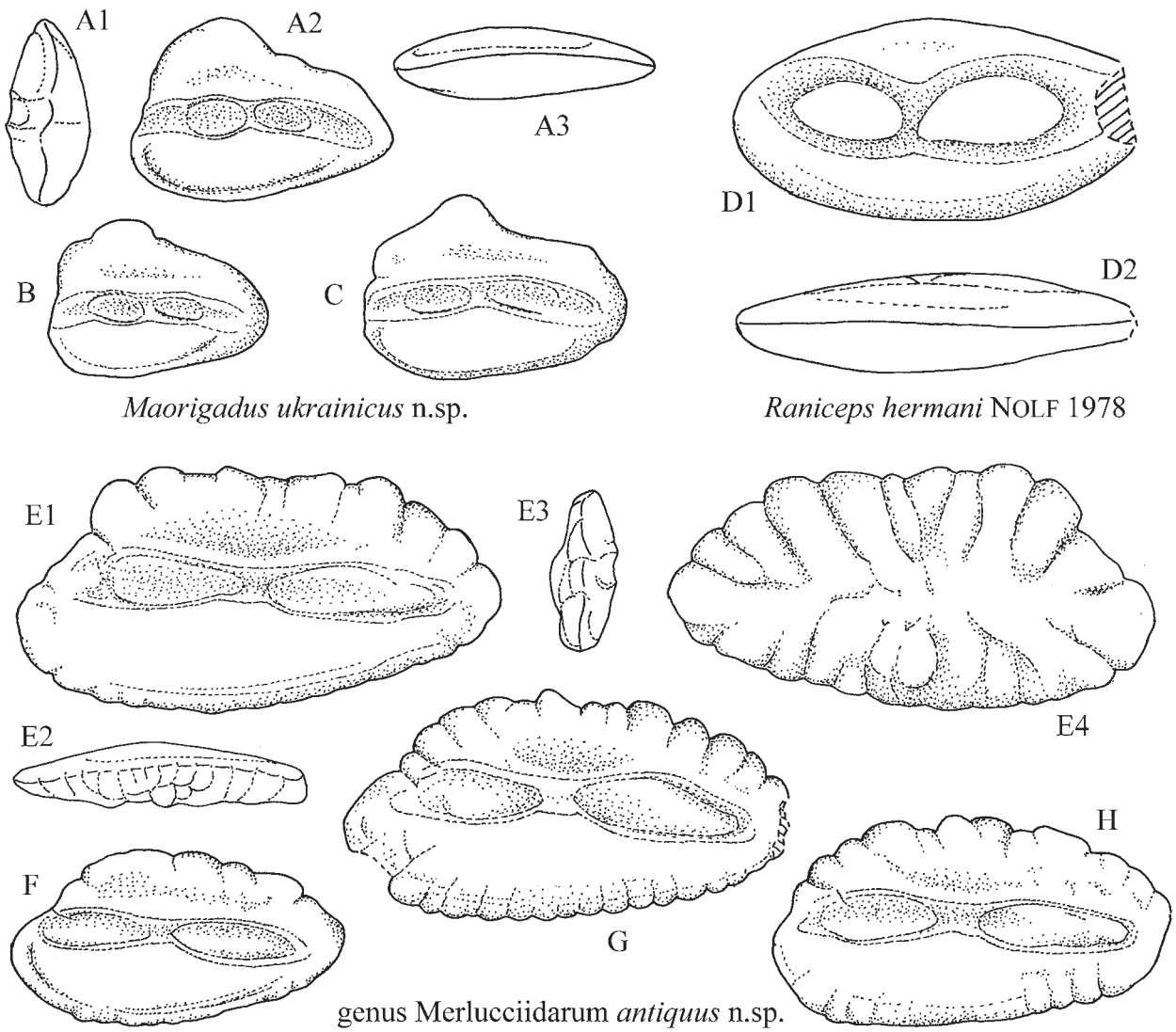

Fig. 6. A-C. *Maorigadus ukrainicus* n. sp., A: holotype, ULUZ 2/087, B-C: paratypes, ULUZ 2/088, ULUZ 2/086. - 20 x. **D.** *Raniceps hermani* NOLF, 1978, ULUZ 2/066. - 8 x. **E-H.** genus Merlucciidarum *antiquus* n. sp., E: holotype (mirror imaged), ULUZ 2/ 067, F-H: paratypes (mirror imaged), ULUZ 2/068, ULUZ 2/110, ULUZ 2/069. - E1, E4, F-H: 20 x; E2-E3: 12 x.

rouridae, based on superficial resemblance with otoliths of the recent *Hymenogadus gracilis* GILBERT & HUBBS, 1920. However, the short, narrowly positioned colliculi without pseudocolliculum in between and the downward bending of the sulcus towards its anterior and posterior tips are quite distinctive features not found in Macrouridae, but in Muraenolepididae, a family considered endemic to the Southern Ocean, chiefly the Antarctic, until a recent yet unpublished find off the Canaries (J. NIELSEN, personal communication). The distinct predorsal lobe, however, separates *Maorigadus* from Muraenolepididae.

Maorigadus ukrainicus n. sp.
Figs. 6A-C, 15D

Holotype: Figs. 6A, 15D, ULUZ 2/087; Luzanivka, Selandian.

Paratypes: 2 specimens, Fig. 6B-C, ULUZ 2/088, ULUZ 2/086, same location.

Etymology: Named after Ukraine.

Diagnosis: Small, otoliths not exceeding 2 mm length. Predorsal projection rounded. Posterior tip rounded. Colliculi

narrowly placed, no pseudocolliculum. Sulcus bent downward anteriorly and posteriorly.

Description: Small otoliths with nearly triangular outline. OL:OH = 1.4; OH:OT = 2.6. Ventral rim smooth, shallow, regularly curved; dorsal rim with irregularly rounded broad predorsal projection and slight concavity behind. Anterior tip blunt, inframedian; posterior tip moderately pointed to rounded, inframedian. Inner face slightly convex with central, convex up, moderately deepened sulcus. OsL:CaL about 1.0. Colliculi small, narrow placed, no pseudocolliculum. Small dorsal depression; distinct ventral furrow close to rim of otolith. Outer face slightly convex, smooth.

Comparison: *Maorigadus ukrainicus* is the second species of the genus after *M. anarchicus* Schwarzhans, 1980 (with *M. delicatulus* Schwarzhans, 1980 as junior synonym) from the Early Eocene of New Zealand from which it differs in the rounded predorsal projection (vs angular with flat top), the rounded posterior tip (vs pointed) and the not specifically deepened colliculi (vs deepened).

Family Ranicipitidae Markle, 1989
Genus *Raniceps* Oken, 1817

Raniceps hermani Nolf, 1978
Fig. 6D

1978 *Raniceps hermani*. – Nolf, pl. 1, fig. 5.
2003 *Raniceps hermani* Nolf, 1978. – Schwarzhans, fig. 19A-D.

Material: A single large nearly 7 mm long incomplete and somewhat eroded specimen from Luzanivka, Seelandian, ULUZ 2/066.

Remarks: A typical *Raniceps* otolith with its large, narrowly positioned colliculi. The slender shape identifies the specimen as *R. hermani* despite its incompleteness, a species well known from the Thanetian of Belgium and the Selandian of Denmark.

Family Merlucciidae Gill, 1884
Genus indet.

genus Merlucciidarum *antiquus* n. sp.
Figs. 6E-H, 15E

Holotype: Fig. 6E, 15E, ULUZ 2/ 067; Luzanivka, Selandian.

Paratypes: 10 specimens, Fig. 6F-H, ULUZ 2/068, ULUZ 2/110, ULUZ 2/069, same location.

Further material: 41 specimens and 3 poorly preserved tentatively assigned specimens, same location.

Etymology: Antiquus (Latin) = old, referring to the old age of the species.

Diagnosis: Elongate oval otolith with intensely crenulated rims. OL:OH = 1.9-2.0. Sulcus narrow; ostium about as long as cauda. CaL:OsL = 1.0-1.1. No pseudocolliculum.

Description: Small, elongate, oval otoliths up to about 3.5 mm length. OH:OT about 2.5. Dorsal rim intensely crenulated, with rounded predorsal angle; ventral rim less intensely crenulated, regularly curved, deepest anterior of the middle. Anterior rim broadly rounded, its tip inframedian; posterior tip rounded, median. Inner face convex with narrow, moderately deepened, slightly supramedian sulcus divided into nearly equal sized ostium and cauda. Colliculi long, narrow placed; no pseudocolliculum. Dorsal depression above collum; mostly indistinct ventral furrow cose to ventral rim of otolith. Outer face flat, intensely ornamented with many furrows positioned vertically on the otolith margins.

Comparison: Otoliths of g. M. *antiquus* resemble those of g. M. *papillosus* (Stinton, 1966) and differ mainly in the narrower sulcus, the index CaL:OsL of 1.0-1.1 (vs 1.2-1.4) and the presence of a moderate predorsal lobe (vs predorsal region rounded). Another similar otolith is *Archaemacruroides ornatus* Stinton, 1965 from the Thanetian of England and the Selandian of Western Greenland, which however has more compressed otoliths (OL:OH = 1.7) and small colliculi which are reduced in length towards the anterior and posterior otolith tips.

Order Ophidiiformes Berg, 1937
Family Carapidae Jordan & Fowler, 1902
Genus †*Fierasferoides* Schwarzhans, 1981

Fierasferoides bucculentus n. sp.
Figs. 7E-F, 15F

Holotype: Figs. 7E, 15F, ULUZ 2/112; Luzanivka, Selandian.

Paratype: 2 specimens, Fig. 7F, ULUZ 2/023, same location.

Further material: 1 poorly preserved tentatively assigned specimen, same location.

Etymology: Bucculentus (Latin) = plump, chubby, referring to the compressed, somewhat plump appearance of these otoliths compared to other species of the genus.

Diagnosis: Compact otoliths. OL:OH = 1.6. Moderate predorsal lobe. Inner face convex, smooth, with level sulcus. OCL:CCL = 2.8-3.4. OL:SuL = 1.8-1.9.

Description: Small, compact otoliths up to about 2.5 mm length. OH:OT = 2.5. Dorsal rim with rounded predorsal lobe; ventral rim more shallow, smooth, regularly curved. Anterior tip broadly rounded; posterior tip rounded to slightly pointed. Inner face convex, smooth. Sulcus small, shallow, completely filled with ostial and caudal colliculi, which meet very closely. Indistinct, small dorsal depression; indistinct ventral furrow very close to ventral rim of otolith. Outer face nearly flat, smooth.

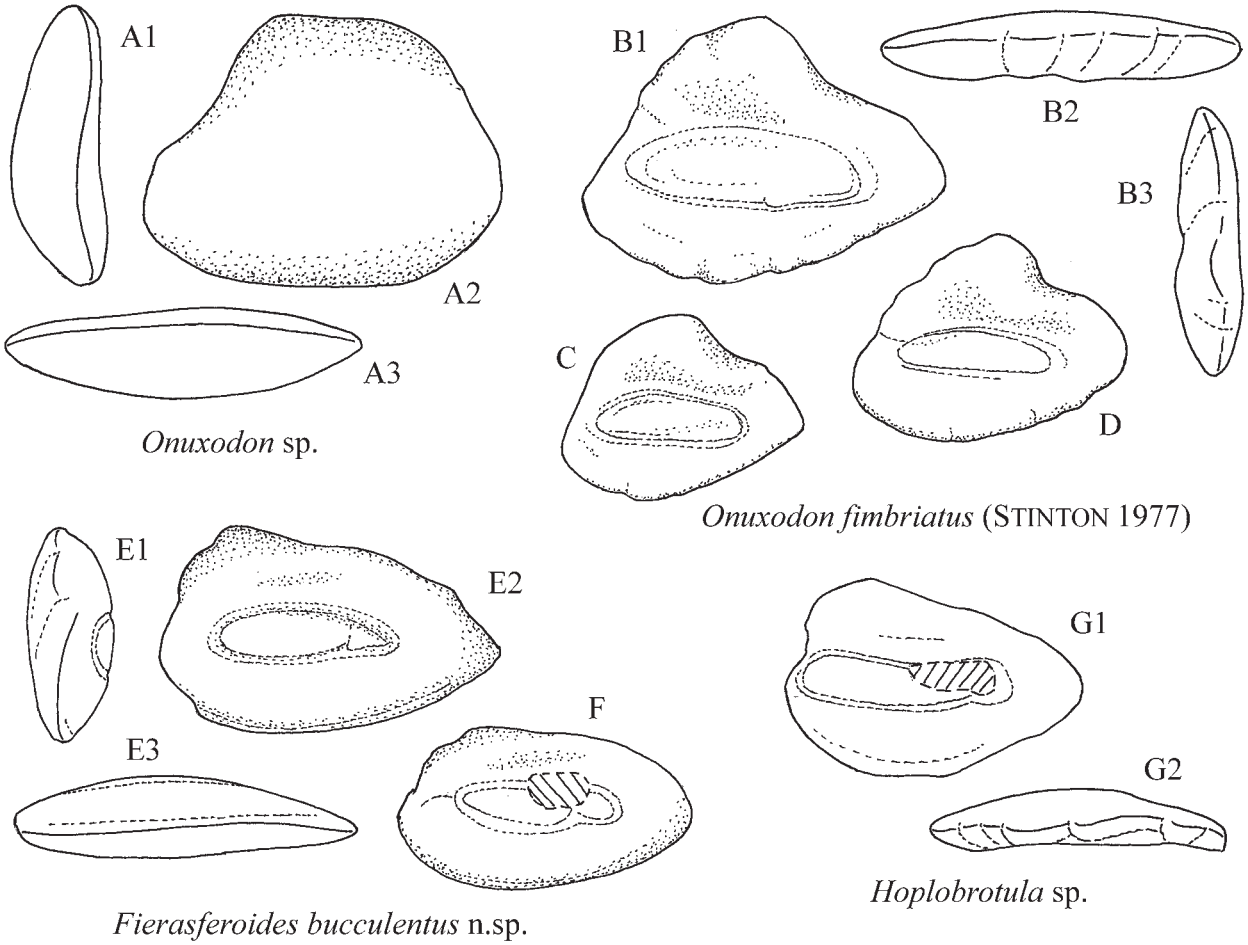

Fig. 7. A. *Onuxodon* sp. (mirror imaged), ULUZ 2/114. - 20 x. **B-D.** *Onuxodon fimbriatus* (STINTON, 1977) (mirror imaged), Barton, England, Bartonian, Late Eocene, BMNH P. 23588. - 15 x. **E-F.** *Fierasferoides bucculentus* n. sp., E: holotype, ULUZ 2/112, F: paratype (mirror imaged), ULUZ 2/023. - 20 x. **G.** *Hoplobrotula* sp., ULUZ 2/113. - 8 x.

Comparison: *Fierasferoides bucculentus* is the most compressed and earliest species of this fossil otolith-based genus, which could be interpreted as a very plesiomorph carapid. *Fierasferoides subregularis* (SCHUBERT, 1916) and *F. longissimus* (NOLF, 1980) from the Eocene are both more elongate and show a smaller index OL:SuL.

Genus *Onuxodon* SMITH, 1955

Onuxodon sp.
Fig. 7A

Material: A single, small otolith with completely eroded inner face, ULUZ 2/114, Luzanivka, Selandian.

Remarks: Similar otoliths are known from the Early Oligocene – *O. coheni* NOLF, 1980 – and the Late Eocene – *O. fimbriatus* (STINTON, 1977). The later was originally described by specimens with eroded inner face as *Hymenocephalus fimbriatus*, but review of material at the British Museum collection revealed a few well preserved specimens (Fig. 7B-D). Their outline differs in the pointed predorsal lobe and the extended posterior tip from the Ukrainian specimen, which certainly represents an undescribed species. More similar, with a flat predorsal lobe, is another otolith figured by STINTON (1977, pl. 7, fig. 11) from the Middle Eocene, also with an eroded inner face.

Family Ophidiidae RAFINESQUE, 1810
Subfamily Neobythitinae RADCLIFFE, 1913
Genus *Hoplobrotula* GILL, 1863

Hoplobrotula sp.
Fig. 7G

Material: A single large otolith with eroded inner face, ULUZ 2/113, Luzanivka, Selandian.

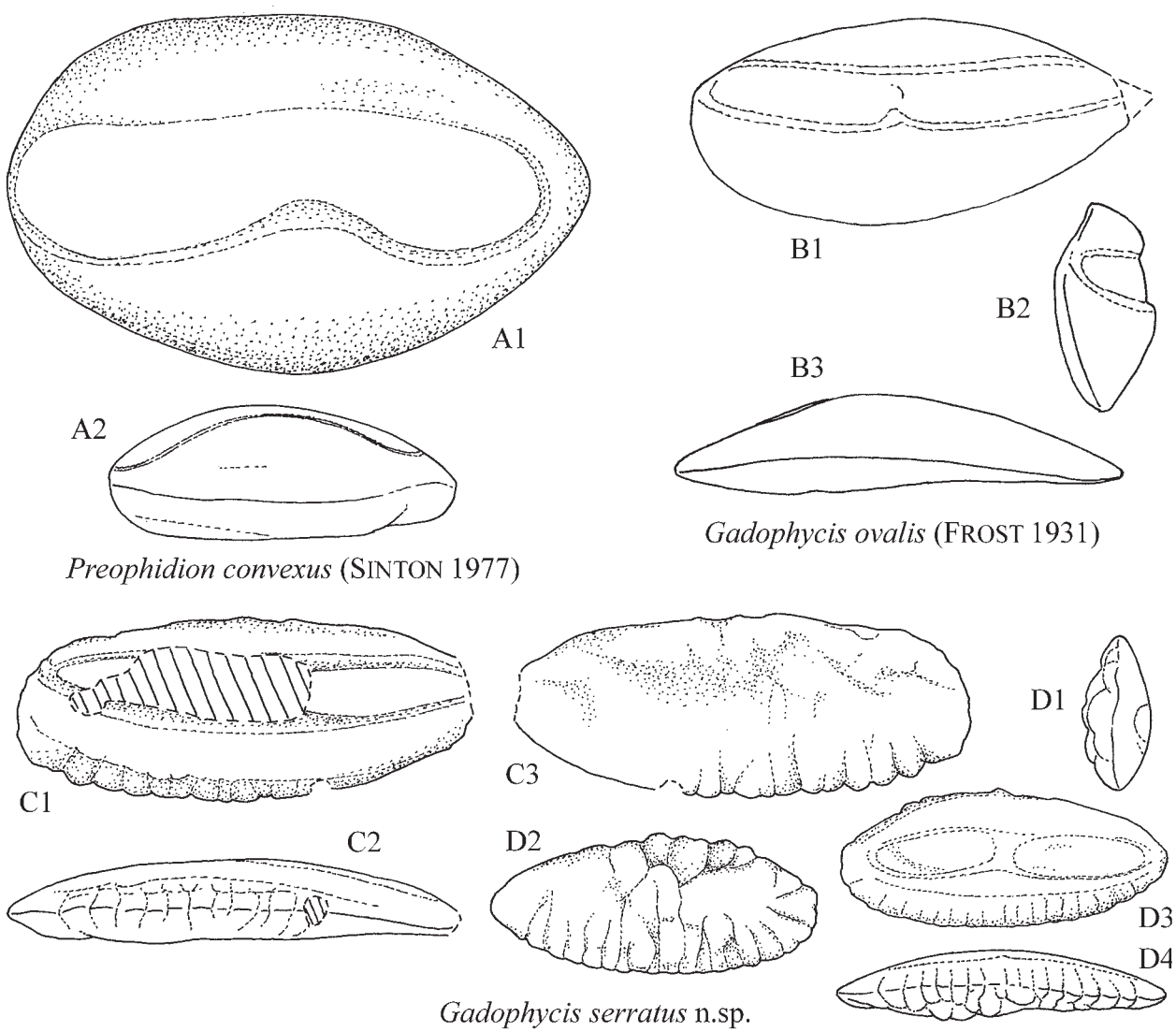

Fig. 8. A. *Preophidion convexus* (STINTON, 1977) (mirror imaged), ULUZ 2/103. - A1: 20 x; A2: 12 x. **B.** *Gadophycis ovalis* (FROST, 1931) (mirror imaged), Abbey Wood, Kent, England, Blackheath Beds, Ypresian, Early Eocene, BMNH P. 15293. - 5 x. **C-D.** *Gadophycis serratus* n. sp., D: holotype (mirror imaged), ULUZ 2/105, C: paratype (mirror imaged), ULUZ 2/073. - 12 x.

Remarks: An unidentifiable *Hoplobrotula* otolith of about 5 mm length characterized by a massive predorsal lobe, an index OL:OH of about 1.5, an index OH:OT of about 3.5 and a flat outer face.

Subfamily Sirembinae GILL, 1863
Genus †*Gadophycis* STINTON, 1965

Gadophycis serratus n. sp.
Figs. 8C-D, 15G

Holotype: Figs. 8D, 15G, ULUZ 2/105; Luzanivka, Selandian.

Paratypes: 3 specimens, Fig. 8C, ULUZ 2/073, same location.

Further material: 1 poorly preserved tentatively assigned specimen, same location.

Etymology: Serratus (Latin) = serrated, after the expression of the ventral rim.

Diagnosis: Elongate, thin otoliths; OL:OH = 2.35-2.55. Dorsal and ventral rim shallow, regularly curved; ventral rim intensely serrated. Distinct ventral furrow away from ventral rim of otolith.

Description: Elongate otoliths up to at least 5.5 mm length. OH:OT = 2.0-2.2. Dorsal rim very shallow, gently curved, somewhat undulating; ventral rim shallow, very regularly curved, intensely serrated. Anterior rim broadly rounded; posterior tip slightly more pronounced than anterior tip. Inner face moderately strong convex with distinctly supramedian, wide, shallow sulcus, filled with two about equally long colliculi. No dorsal depression; ventral field distinct ventral furrow at some distance from ventral rim of otolith. Many furrows leading from serrated ventral rim up to ventral furrow on inner face. Outer face flat, with many vertical furrows, particularly ventrally.

Comparison and discussion: *Gadophycis serratus* is now the fourth species of this enigmatic fossil otolith based genus. It is easily distinguished from the other three species by the presence of a distinct ventral furrow on the inner face. *Gadophycis thulei* (Schwarzhans, 2004) from the Selandian of Western Greenland differs further in the lack of the serration of the ventral rim. *Gadophycis ovalis* (Frost, 1931) (Fig. 8B shows an eroded specimen used by Stinton 1965) from the Thanetian and Ypresian of England and Belgium has a deeper ventral rim and smooth rims, and *G. bramscheensis* Schwarzhans, 2007 from the Lutetian of Germany differs further in the expanded postventral region. A similar, more compressed, massive otolith-based genus with nearly fused colliculi is *Palaeomorrhua* Gaemers & Schwarzhans, 1973 with two species – *P. bulbus* Nolf, 1978 from the Thanetian of Belgium and *P. faba* Koken, 1884 from the Oligocene of the North Sea Basin. The placement of the genus group, which further contains the fossil otolith-based genus *Symmetrosulcus* Schwarzhans, 1981, to the Ophidiiformes has recently been discussed by Rozenberg, 2003, who described otoliths in situ from the skeleton-based fossil genus *Protobrotula* Danilchenko, 1960 (from the type species *P. sobijevi* (Danilchenko, 1953)), and identified the fossil otolith-based genus *Ensigadus* Gaemers, 1978 as a junior synoym. However, according to Rozenberg's discussion, the placement with the Ophidiiformes was questioned and an association with the Phycidae of Gadiformes may in our opinion represent a more viable alternative indeed. Further detailed combined osteological and otolith studies are required.

Genus *Preophidion* Dante & Frizzell, 1965

Preophidion convexus (Stinton, 1977)
Fig. 8A

1977 *Sirembo convexus*. – Stinton, pl. 8, figs. 12-13.
2007 *Preophidion convexus* (Stinton, 1977). – Schwarzhans, fig. 18I-K.

Material: 5 specimens, ULUZ 2/063, ULUZ 2/064, ULUZ 2/065, ULUZ 2/102, ULUZ 2/103, Luzanivka, Selandian.

Short description: Moderately elongate and thick otoliths up to 5 mm length. OL:OH = 1.6-1.9; OH:OT about 2. Dorsal rim thickened; all rims gently curving and smooth. Inner face strongly convex with large, shallow sulcus. Ostium and cauda of similar length filled by single undivided colliculum, ventrally contracted at collum. Outer face flat.

Distribution: Selandian of Ukraine, Lutetian and Bartonian of England, Belgium, Germany and France.

Family Bythitidae Gill, 1861
Subfamily Bythitinae Gill, 1861
Genus indet.

genus Bythitidarum *rozenbergi* n. sp.
Figs. 9G-I, 15I

Holotype: Figs. 9G, 15I, ULUZ 2/144; Luzanivka, Selandian.

Paratypes: 2 specimens, Fig. 9H-I, ULUZ 2/143, ULUZ 2/021, same location.

Further material: 2 poorly preserved tentatively assigned specimens, same location.

Etymology: In honour of A. Rozenberg (Leipzig) for his contribution to the knowledge of fossil otoliths from the Ukraine.

Diagnosis: Elongate otoliths with moderately pointed anterior and posterior tips and regularly curved dorsal and ventral rims. OL:OH = 2.15-2.25. Inner face flat along horizontal axis, bent along vertical axis. OL:SuL = 1.8-2.2.

Description: Elongate, moderately thick otoliths up to 4.5 mm length. OH:OT about 2.2. Dorsal rim regularly curved, shallow, without angles; ventral rim slightly deeper, deepest anterior of its middle, very regularly curved. Anterior and posterior tips median, moderately pointed. Inner face smooth, rather flat except for outward bent dorsal field and region close to ventral rim. Single undivided, long, oval colliculum within poorly defined sulcus, shallow. Sulcus not inclined. Ventral furrow faint. Outer face slightly convex, smooth.

Comparison: Most bythitid otoliths exhibit a very generalized outline and a reduced sulcus morphology, which makes distinction of genera very difficult, like in this case, and also of species. Main useful characters for specific differentiation relate to details of the outline, curvature of inner and outer faces, inclination and size of sulcus. The most similar species to g. B. *rozenbergi* is probably g. B. *pseudoacuminatus* (Sulc, 1932) from the Late Eocene of the Aquitaine Basin in France, from which it differs mainly in the longer sulcus (OL:SuL = 1.8-2.2 vs 2.6-2.9).

Subfamily Dinematichthyinae Whitley, 1928
Genus *Ogilbia* Jordan & Evermann, 1898

Ogilbia luzanensis n. sp.
Figs. 9A-F, 15H

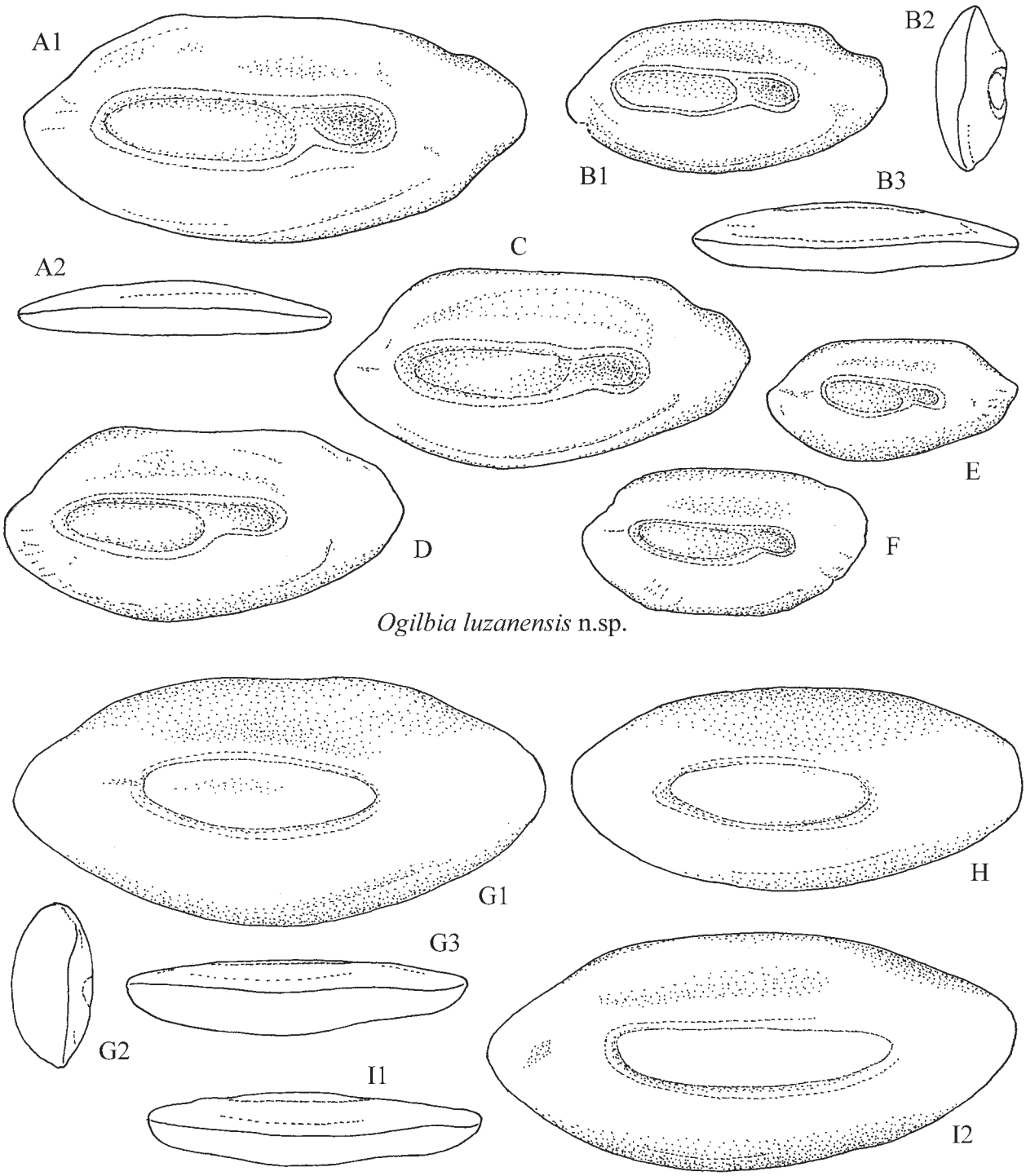

Fig. 9. A-F. *Ogilbia luzanensis* n. sp., B: holotype (mirror imaged), ULUZ 2/139, A, C-F: paratypes (C, E-F mirror imaged), ULUZ 2/020, ULUZ 2/019, ULUZ 2/141, ULUZ 2/140, ULUZ 2/142. - 20 x; A2: 12 x. **G-I.** genus Bythitidarum *rozenbergi* n. sp., G: holotype, ULUZ 2/144, H-I: paratypes, ULUZ 2/143, ULUZ 2/021. - G1, H, I2: 20 x; G2-G3, I1: 12 x.

2003 *Bidenichthys lapierrei* (Nolf, 1978). – Schwarzhans, fig. 29A-J (non Nolf 1978)
2004 *Bidenichthys lapierrei* (Nolf, 1978). – Schwarzhans, fig. 9C-F (non Nolf 1978)

Holotype: Fig. 9B, ULUZ 2/139; Luzanivka, Selandian.

Paratypes: 10 specimens, Figs. 9A, C-F, 15H, ULUZ 2/020, ULUZ 2/019, ULUZ 2/141, ULUZ 2/140, ULUZ 2/142, same location.

Further material: 9 specimens and 21 poorly preserved and tentatively assigned specimens, same location.

Etymology: Named after the type-locality Luzanivka, Ukraine.

Diagnosis: Elongate, thin otoliths; OL:OH = 1.9-2.2; OH:OT = 2.0-2.5. Dorsal rim with concavity behind postdorsal angle. Inner face slightly convex; outer face flat. Sulcus clearly divided into longer ostium and shorter, deepened cauda.

Description: Elongate otoliths up to about 4 mm length. Dorsal rim with rounded pre- and postdorsal angles and often distinct concavity behind postdorsal angle; stretch in between straight. Ventral rim regularly curved, deepest in front of its middle. Anterior tip pointed; anterior rim curved below tip and straight, inclined above. Posterior tip broad, dorsally shifted. Inner face slightly convex with median sulcus. OL:SuL = 1.7-2.0; OCL:CCL = 2.6-2.8; OCH:CCH = 1.5-1.8. Dorsal depression moderately distinct, narrow; ventral furrow close to ventral rim of otolith. Outer face flat, smooth.

Comparison and discussion: Detailed drawings of the holotype (IRSNB P 2703) and a paratype (IRSNB P 2704) of *O. lappierrei* from the Thanetian of Belgium kindly made available by Nolf revealed that these otoliths exhibit a rather flat inner face and a convex outer face and overall are more thickset than those of *O. luzanensis*. Therefore, the position proposed by Schwarzhans (2003, 2004) is maintained no longer, who related *Ogilbia*-otoliths from the Selandian and Danian of Denmark and Western Greenland to *O. lappierrei*. Together with the Selandian specimens from Ukraine these otoliths are now placed in the new species *O. luzanensis*. Another aspect of uncertainty is the relation with certain plesiomorphic genera of the Brosmophycinae Gill, 1862 (Dinematichthyinae here regarded as the sister group in the same ranking), such as *Bidenichthys* Barnard, 1934, since both genera, *Bidenichthys* and *Ogilbia* are probably very basal, plesiomorphic representatives of their respective clades. The overall appearance of the otoliths of *O. lapierrei* and *O. luzanensis* are typical for dinematichthyins, particularly their dorsal rim with the straight inclined anterior portion and the concave posterior region as well as the shape of the posterior tip.

Distribution: Danian of Denmark, Selandian of Western Greenland, Denmark and Ukraine.

Order Beryciformes Regan, 1909
Suborder Berycoidei Regan, 1909
Family Berycidae Lowe, 1843
Genus *Centroberyx* Gill, 1862

Centroberyx anguinicauda n. sp.
Figs. 11D-F, 15J

2004 *Centroberyx* sp. – Schwarzhans, fig. 12F-H

Holotype: Figs. 11D, 15J, ULUZ 2/116; Luzanivka, Selandian.

Paratypes: 2 specimens, Fig. 11E-F, ULUZ 2/074, ULUZ 2/115, same location.

Further material: 3 poorly preserved specimens, same location.

Etymology: Combination of anguinis (Latin) = snake-like and cauda, referring to the narrow and slightly swung cauda.

Diagnosis: Shape elongate, oval; OL:OH = 1.4. Inner face markedly convex. Dorsal field narrow. Cauda narrow, markedly swung.

Description: Moderately elongate otoliths of somewhat variable thickness up to 5 mm length. OH:OT = 2.5-3.5. Dorsal rim shallow, without prominent angles. Ventral rim deep, regularly curved, smooth. Inner face markedly convex along horizontal axis, much less so along vertical axis. Sulcus distinctly supramedian, divided into wide, shallow, moderately short ostium and narrow, swung, somewhat deepened cauda terminating very close to postdorsal rim. CaL:OsL = 1.2-1.3; OsH:CaH about 2. Dorsal depression small; no ventral furrow. Outer face flat to slightly concave, smooth.

Comparison: The strongly convex inner face, the shallow dorsal rim without prominent angles and the curiously swung cauda distinguish *C. anguinicauda* from contemporaneous species of the genus *Centroberyx*.

Centroberyx fragilis Schwarzhans, 2003
Figs. 10A-I, 15K

2003 *Centroberyx fragilis*. – Schwarzhans, fig. 34A-J.
2004 *Centroberyx fragilis* Schwarzhans, 2003. – Schwarzhans, fig. 12A-E.

Material: 157 specimens, ULUZ 2/119, ULUZ 2/123, ULUZ 2/001, ULUZ 2/120, ULUZ 2/121, ULUZ 2/122, ULUZ 2/010, ULUZ 2/007, ULUZ 2/082, Luzanivka, Selandian.

Description: Moderately compressed otoliths up to 9 mm length. OL:OH = 1.2-1.35, increasing with size; OH:OT = 3.5-3.9. Dorsal rim highest anterior of the middle often with

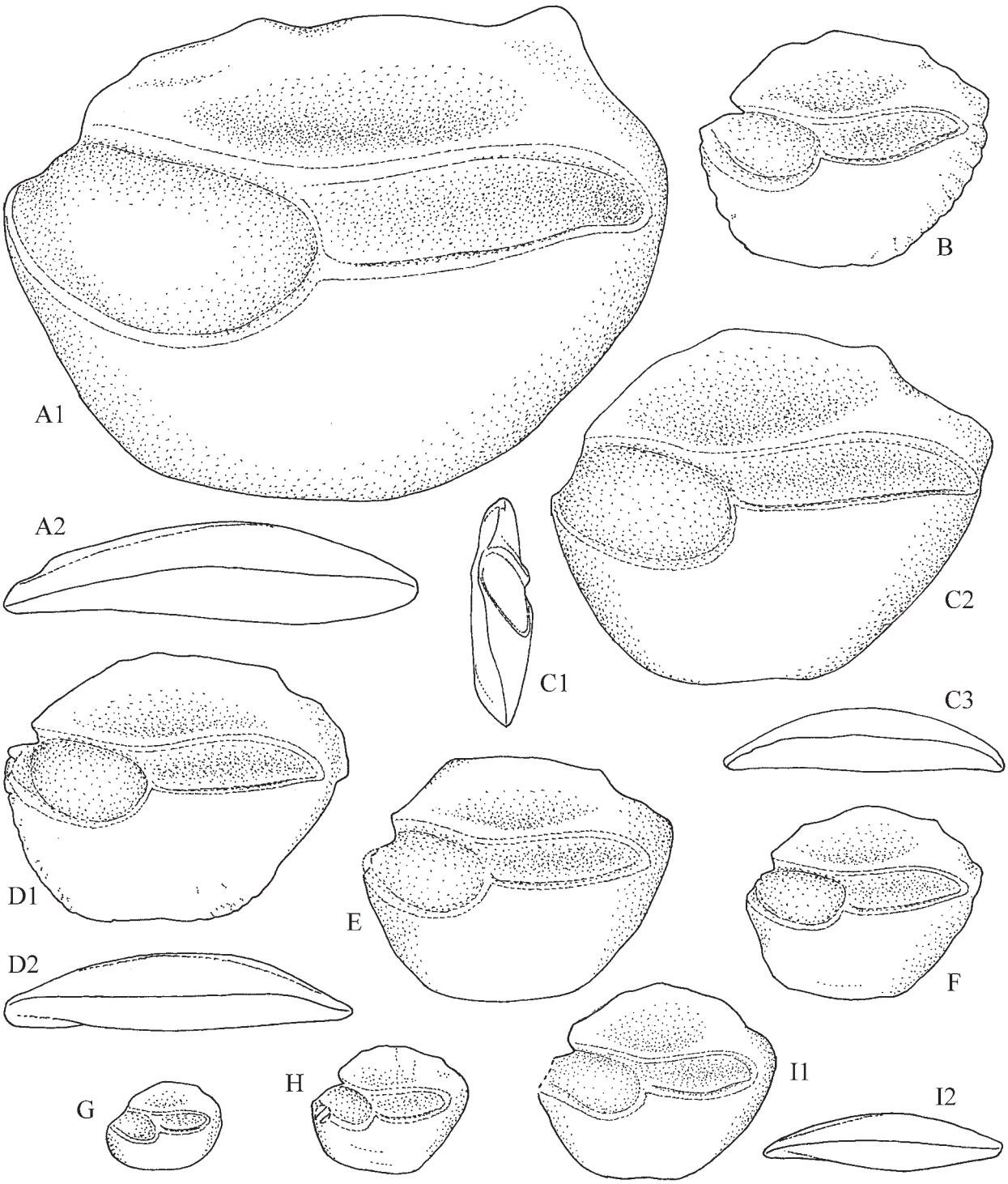

Fig. 10. A-I. *Centroberyx fragilis* SCHWARZHANS, 2003 (A mirror imaged), ULUZ 2/119, ULUZ 2/123, ULUZ 2/001, ULUZ 2/120, ULUZ 2/121, ULUZ 2/122, ULUZ 2/010, ULUZ 2/007, ULUZ 2/082. - 12 x; A2, C1, C3: 8 x.

shallow postdorsal concavity and more or less sharp angle just before (sharp in large specimens). Ventral rim deep, with rounded pre- and postdorsal angles; its medioventral portion rather short. Rostrum massive, short, blunt; posterior tip angular positioned above caudal tip. Rims delicately crenulated in juveniles, smooth in adults. Inner face moderately convex with long, slightly supramedian sulcus. Ostium wide, slightly turned upwards; cauda narrow, also slightly turned upwards, with a pointed tip, very slightly bent in large specimens, terminating close to posterior tip of otolith. CaL:OsL = 1.1-1.3; OsH:CaH about 1.7. Dorsal depression moderately large; no ventral furrow. Outer face flat, ornamented in juveniles, smooth in adults.

Comparison: See *C. anguincauda* and *C. integer* (Koken, 1885).

Distribution: Danian and Selandian of Denmark, Selandian of Western Greenland and Ukraine.

Centroberyx integer (Koken, 1885)
Figs. 11A-C, 15L

1885 Otolithus (Apogonidarum) *integer.* – Koken, pl. 5, fig. 27
2003 *Centroberyx integer* (Koken, 1885). – Schwarzhans, fig. 33A-J

Material: 43 specimens, ULUZ 2/124, ULUZ 2/125, ULUZ 2/126, Luzanivka, Selandian.

Comparison: Otoliths of *C. integer* differ from those of the contemporaneous *C. fragilis* mainly in the slightly more compressed appearance (OL:OH = 1.1-1.25 vs 1.2-1.35), the thicker appearance (OH:OT = 2.6-3.3 vs 3.5-3.9) and the lack of a bent at the caudal tip.

Distribution: Danian and Selandian of Denmark and Selandian of Ukraine, in both instances less common than *C. fragilis.*

Centroberyx sp.
Fig. 11G-H

Material: 6 small specimens, of which only one is well preserved, ULUZ 2/117, ULUZ 2/118, Luzanivka, Selandian.

Remarks: These small specimens of less than 3 mm length differ from the other three species in the combination of a rather flat inner face, a high index OL:OH of 1.4-1.45, the thin appearance and the unusually inclined ostium, particularly its ostial colliculum. They likely represent a further yet undescribed species, but the available specimens are not adequate for such description.

Suborder Holocentroidei Johnson & Patterson, 1993
Family Holocentridae Richardson, 1864
Genus indet.

genus Holocentridarum *ryabchuni* n. sp.
Figs. 12A-C, 15M

Holotype: Fig. 12A, ULUZ 2/048; Luzanivka, Selandian.

Paratypes: 10 specimens, Figs. 12B-C, 15M, ULUZ 2/050, ULUZ 2/047, same location.

Further material: 20 specimens and 3 poorly preserved tentatively assigned specimens, same location.

Etymology: In honour of V.K. Ryabchun (Kyiv), who was the first geologist to discover the fossil location Luzanivka in 1959.

Diagnosis: Thin, rounded, oval otoliths. OL:OH = 1.5. Inner face markedly convex, smooth. No ventral furrow, but dorsal furrow. Ostium regularly and gradually widened dorsally and ventrally. Cauda slightly bent at tip. Outer face concave.

Description: Oval otoliths up to nearly 5 mm length with very thin and sharp rims. Outline perfectly oval, without major angles or distinguished rostrum. Dorsal rim highest postdorsally in a broadly pronounced area; ventral rim deepest at its middle. Rounded anterior tip median; posterior tip slightly supramedian. Inner face strongly convex, with smooth surface except for slightly deepened sulcus. Ostium spatulate, opening anteriorly, continuously widening from collum both dorsally and ventrally, shallow; cauda narrow, slightly deepened, slightly bent at tip, terminating close to postventral rim of otolith. CaL:OsL = 1.2-1.4; OsH:CaH = 1.7-1.9. No or very indistinct dorsal depression, but with marked dorsal furrow above; no ventral furrow. Outer face concave, smooth.

Comparison: Holocentrid otoliths are difficult to be distinguished from otoliths of the many percoid fishes. Possible characters of distinction could be the lack of a ventral furrow (and the occasional occurrence of a dorsal furrow instead) and the peculiar spatulate shape of the ostium, but the assignment of g. H. *ryabchuni* remains tentative.

Order Perciformes Bleeker, 1859
Suborder Percoidei Bleeker, 1859
Family Epigonidae Johnson, 1984
Genus indet.

genus Epigonidarum *tyassminensis* n. sp.
Figs. 12D-M, 15N

Holotype: Fig. 12D, ULUZ 2/128; Luzanivka, Selandian.

Paratypes: 30 specimens, Figs. 12E-M, 15N, ULUZ 2/029, ULUZ 2/031, ULUZ 2/028, ULUZ 2/127, ULUZ 2/129, ULUZ 2/131, ULUZ 2/032, ULUZ 2/130, ULUZ 2/033, same location.

Further material: 148 specimens, same location.

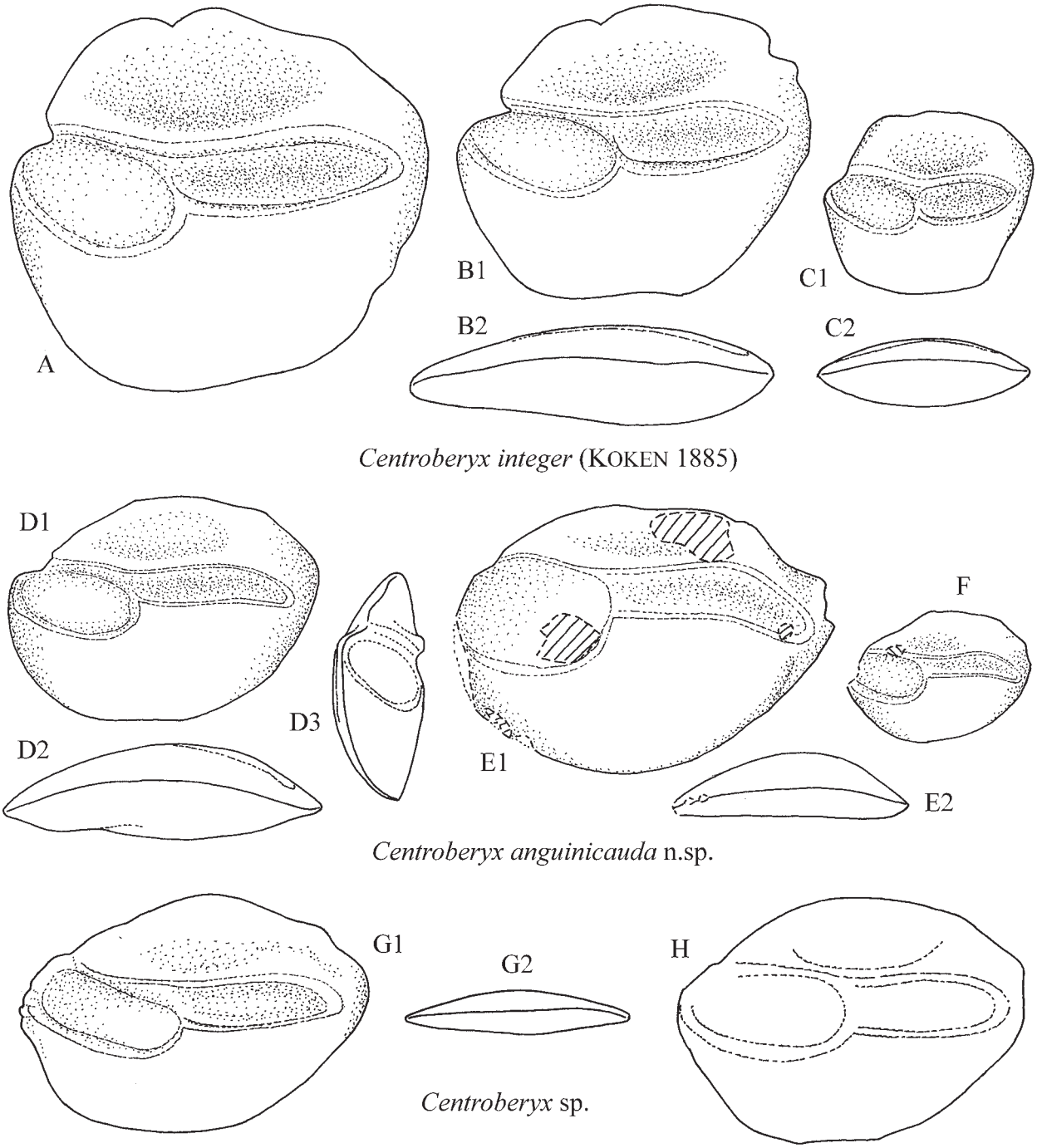

Fig. 11. A-C. *Centroberyx integer* (KOKEN, 1885) (C mirror imaged), ULUZ 2/124, ULUZ 2/125, ULUZ 2/126. - 12 x. **D-F.** *Centroberyx anguinicauda* n. sp., D: holotype, ULUZ 2/116, E-F: paratypes (E mirror imaged), ULUZ 2/074, ULUZ 2/115. - 12 x; E2: 8 x. **G-H.** *Centroberyx* sp. (mirror imaged), ULUZ 2/117, ULUZ 2/118. - G1, H: 20 x; G2: 12 x.

Etymology: Named after the river Tyassmin, which forms the main drainage system of the area.

Diagnosis: Small, oval, elongate otoliths. OL:OH = 1.6-1.85. Dorsal rim irregularly undulating, shallower than ventral rim. CaL:OsL = 1.3-1.5; OsH:CaH = 1.6-1.8. Cauda only slightly bent at tip.

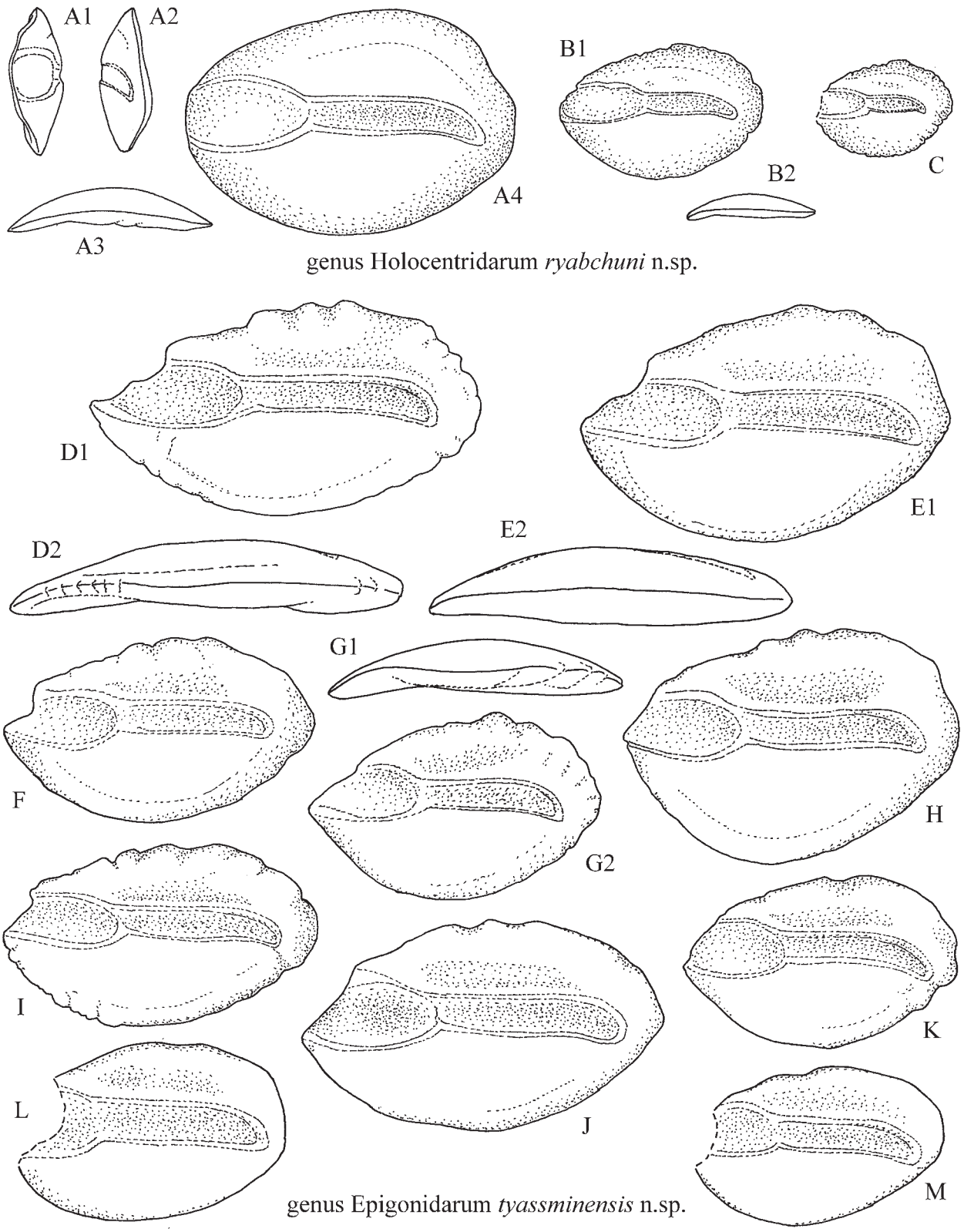

Fig. 12. A-C. genus Holocentridarum *ryabchuni* n. sp., A: holotype, ULUZ 2/048, B-C: paratypes (B mirror imaged), ULUZ 2/050, ULUZ 2/047. - A4, B1, C: 12 x; A1-A3, B2: 8 x. **D-M.** genus Epigonidarum *tyassminensis* n. sp., D: holotype (mirror imaged), ULUZ 2/128, E-K: paratypes (E, G, H, K, M mirror imaged), ULUZ 2/029, ULUZ 2/031, ULUZ 2/028, ULUZ 2/127, ULUZ 2/129, ULUZ 2/131, ULUZ 2/130, L-M: tentatively assigned specimens, , ULUZ 2/029, ULUZ 2/031, ULUZ 2/028, ULUZ 2/127, ULUZ 2/129, ULUZ 2/131, ULUZ 2/032, ULUZ 2/130, ULUZ 2/033. - 20 x.

Description: Thin, elongate otoliths up to about 3.5 mm length. OH:OT = 3.0-3.2. Dorsal rim shallow, irregularly undulating, postdorsally pronounced; ventral rim deeper than dorsal rim, gently curved and mostly smooth, deepest anterior of the middle. Anterior tip with moderately sharp rostrum, shallow excisura and indistinct antirostrum; posterior tip rounded, above caudal tip. Inner face moderately convex with slightly supramedian, long sulcus. Ostium widened and deepened; cauda narrower, similarly deepened, its tip only slightly and terminating close to the posterior rim of the otolith. Dorsal depression narrow; dorsal field occasionally with few radial furrows; ventral furrow weak, close to ventral rim of otolith. Outer face flat, moderately ornamented.

Variability: The variations observed in the otoliths of this species are rather pronounced. This is particularly true for the index OL:OH, which varies more than in most other species and irrespective of the ontogenetic stage. The far end of the index OL:OH variation is depicted in the elongate specimens of Fig. 12D (holotype) and 12F and the more compressed specimens of Fig. 12E and 12H. In addition there are also specimens with a conspicuously wider cauda and smooth otolith rims (Fig. 12L, M), which however are too poorly preserved to allow further analysis.

Comparison: Otoliths of g. E. *tyassminensis* are inconspicuous in appearance. The small size and regular outline indicate a plesiomorphic character status. They resemble best those of the Eocene g. E. *selsiensis* (Stinton, 1978) (see Schwarzhans 2007), but are more elongate and with a comparatively longer cauda. Because of the elongate shape, its placement with the Epigonidae has to be regarded as preliminary.

Family Haemulidae Richardson, 1848
Genus indet.

genus Haemulidarum *gullentopsi* Nolf, 1978
Figs. 13A-B, 15O

1978 genus Pomadasyidarum *gullentopsi*. – Nolf, pl. 2, figs. 14-15.

Material: 18 specimens, ULUZ 2/036, ULUZ 2/037, ULUZ 2/038, ULUZ 2/039, ULUZ 2/138, Luzanivka, Selandian.

Description: Moderately compressed otoliths up to more than 3.5 mm length. OL:OH = 1.5-2.6; OH:OT about 4. Dorsal rim shallow, with broad postdorsal angle; ventral rim deep, regularly curved, deepest anterior of the middle. All rims somewhat undulating, dorsal rim more than ventral rim. Posterior tip with short rostrum; no excisura or antirostrum; posterior tip blunt, rounded, dorsally pronounced. Inner face convex with slightly supramedian and slightly deepened sulcus. Ostium longer and wider than cauda; cauda slightly inclined, somewhat bent at tip and terminating close to postventral rim. CaL:OsL = 1.4; OsH:CaH = 1.8. Dorsal depression narrow, indistinct; ventral furrow feeble or absent. Outer face concave, slightly ornamented.

Comparison: Genus Haemulidarum *gullentopsi* is interpreted as one of those early haemulid otoliths with a plesiomorphic morphological state characterized best by the moderately bent cauda, like also g. H. *pulcher* (Frost, 1934) (see Schwarzhans 2007) from the Eocene. The compressed shape distinguishes it from contemporaneous percoid otoliths at Luzanivka.

Distribution: Thanetian of Belgium and Selandian of Ukraine.

genus Haemulidarum *makarenkoi* n. sp.
Figs. 13C-J, 15P

Holotype: Fig. 13C, ULUZ 2/132; Luzanivka, Selandian.

Paratypes: 10 specimens, Figs. 13D-J, 15P, ULUZ 2/133, ULUZ 2/040, ULUZ 2/041, ULUZ 2/136, ULUZ 2/135, ULUZ 2/042, ULUZ 2/134, same location.

Further material: 43 specimens and 18 poorly preserved tentatively assigned specimens, same location.

Etymology: In honour of D.E. Makarenko (Kyiv), who described many fossils from Luzanivka in his monograph of 1970 and was also the first to mention otoliths from the location.

Diagnosis: OL:OH = 1.7-2.0. Dorsal rim shallow with feeble or no mediodorsal angle. Rims of posterior half of otolith delicately crenulated, anterior half nearly smooth. Ostium shallow, with horizontal and parallel ventral and dorsal rims.

Description: Elongate otoliths up to 4.5 mm length. OL:OH mostly 1.8-1.9 (one specimen 1.6; Fig. 13J), increasing with size; OH:OT = 2.5-2.8. Dorsal rim shallow with broad, indistinct or no mediosorsal angle and variably pronounced postdorsal region. Ventral rim regularly curved, shallow, deepest anterior of the middle. Anterior rim with median, long, but rounded rostrum; no excisura or antirostrum. Posterior tip rounded in juveniles, angular in adults. Rims delicately crenulated at posterior part of otolith. Inner face strongly convex, with slightly supramedian sulcus. Ostium shallow, spatulate, with flat, parallel ventral and dorsal rims after widening at the collum. Cauda narrow, deepened, slightly bent downward at its pointed tip, terminating closer to the postventral rim than the posterior tip. CaL:OsL = 1.0-1.2; OsH:CaH = 1.7-1.8. Dorsal depression narrow, indistinct; ventral furrow indistinct. Outer face concave, intensely ornamented near rims.

Comparison: The combination of the lack of an excisura, the shape of the shallow ostium and the caudal tip characterize the otoliths of g. H. *makarenkoi* as representatives of the family Haemulidae, although most recent species show a more strongly downturned caudal tip, indicating that g. H. *makarenkoi* is still a plesimorphic otolith morphology. Stinton (1965) described a similar otolith as *Isacia sylvestris* from the Early Eocene (Ypresian) of England and later

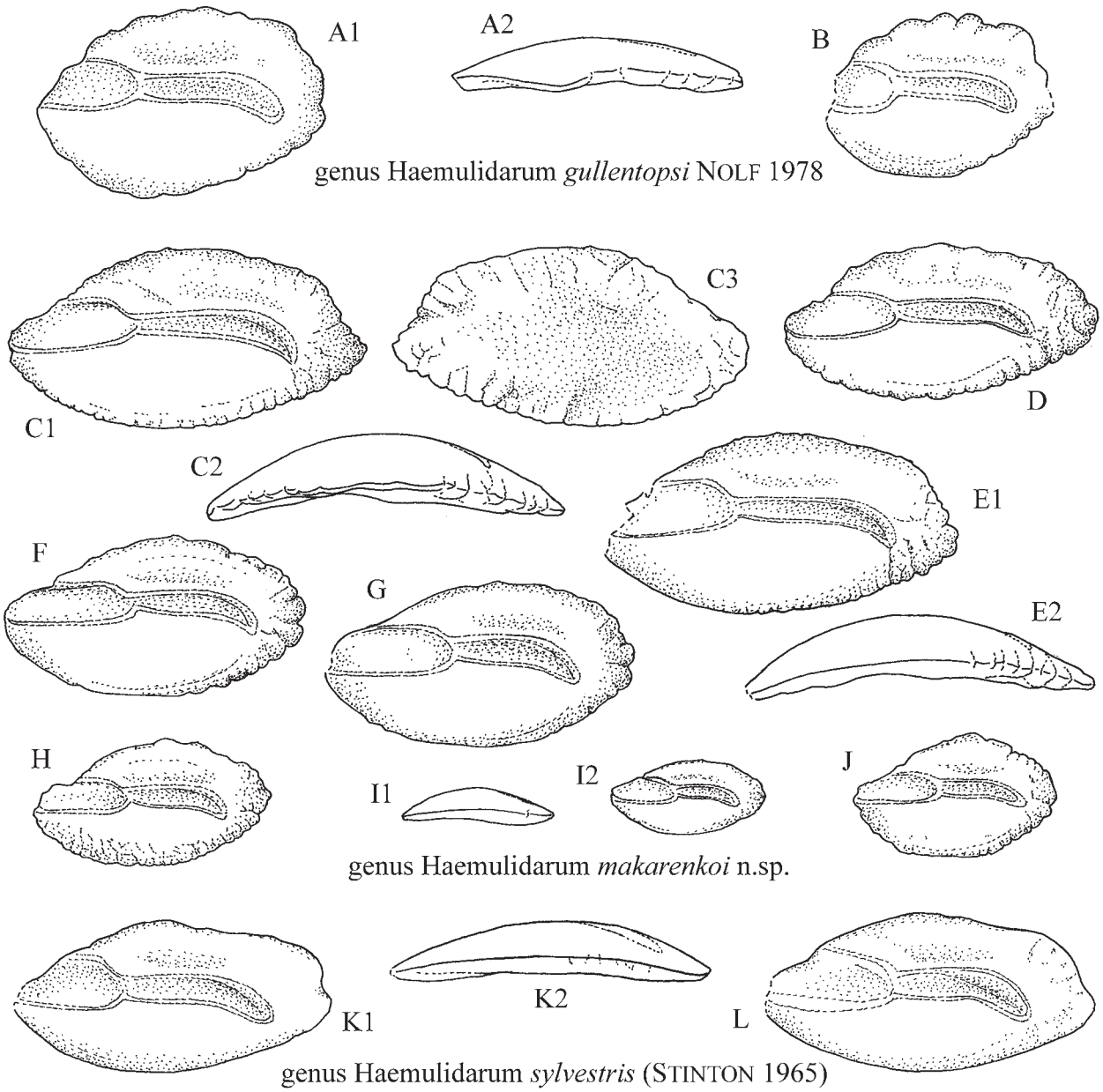

Fig. 13. A-B. genus Haemulidarum *gullentopsi* NOLF, 1978 (A mirror imaged), ULUZ 2/039, ULUZ 2/138. **C-J.** genus Haemulidarum *makarenkoi* n. sp., C: holotype, ULUZ 2/132, D-J: paratypes (E, F, G, I, J mirror imaged), ULUZ 2/133, ULUZ 2/040, ULUZ 2/041, ULUZ 2/136, ULUZ 2/135, ULUZ 2/042, ULUZ 2/134. **K-L.** genus Haemulidarum *sylvestris* (STINTON, 1965), paratypes (L mirror imaged), Lower Upnor, Kent, England, Oldhaven Beds, Ypresian, Early Eocene, SMF P. 3686. - 12 x.

a new as *Acanthochaetodon longirostris* STINTON, 1966 (placed in *Pomacanthus* in STINTON, 1984). Genus Haemulidarum *makarenkoi* differs from the younger g. H. *sylvestris* in the more compressed appearance (OL:OH = 1.7-2.0 vs 2.0-2.2), the more shallow dorsal rim, the shallow cauda (vs slightly deepened) and the horizontal and parallel rims of the ostium (vs the upper rim of the ostium slightly inclined upward / anteriorly). Also, otoliths of g. H. *makarenkoi* appear generally more intensely crenulated than those of g. H. *sylvestris*. Both species are probably closely related. Two paratypes of g. H. *sylvestris* are figured for comparison (see Fig. 13K, L). A further unspecified haemulid with a more strongly bent caudal tip and an inclined ostial / caudal joint has been described from the Selandian of western Greenland (SCHWARZHANS 2004).

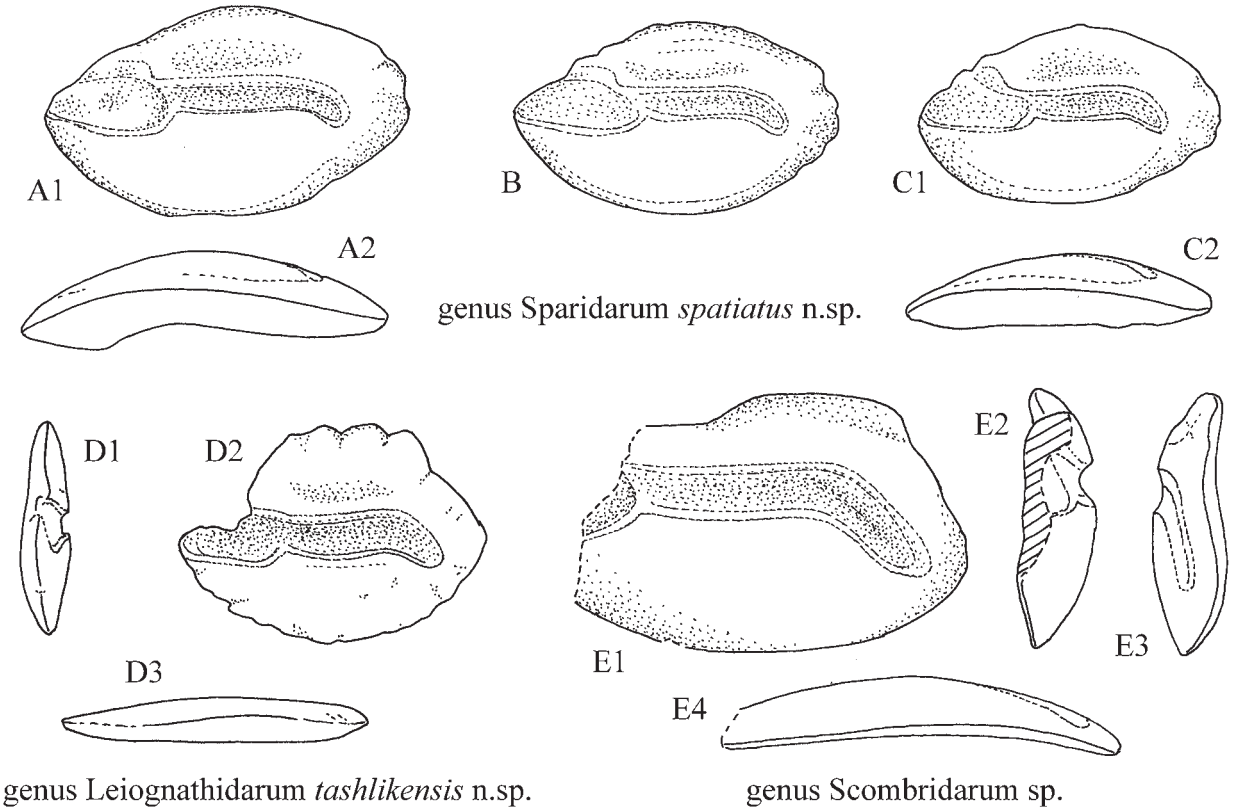

Fig. 14. A-C. genus Sparidarum *spatiatus* n. sp., A: holotype, ULUZ 2/096, B-C: paratypes, ULUZ 2/043, ULUZ 2/137. - 12 x. **D.** genus Leiognathidarum *tashlikensis* n. sp., holotype, ULUZ 2/054. - 20 x. **E.** genus Scombridarum sp., ULUZ 2/100. - 12 x.

Family Sparidae Bonaparte, 1832
Genus indet.

genus Sparidarum *spatiatus* n. sp.
Fig. 14A-C, 15Q

Holotype: Figs. 14A, 15Q, ULUZ 2/096; Luzanivka, Selandian.

Paratypes: 20 specimens, Fig. 14B-C, ULUZ 2/043, ULUZ 2/137, same location.

Further material: 88 specimens and 8 poorly preserved tentatively assigned specimens, same location.

Etymology: Spatiatus (Latin) = gap, referring to the diagnostic gap between the upper margin of the ostial colliculum and the upper margin of the ostium.

Diagnosis: Elongate, oval otoliths. OL:OH = 1.7. Dorsal rim mediodorsally pronounced. Ostium dorsally much widened with gap between ostium rim and dorsal rim of ostial colliculum. Cauda short, its tip slightly bent, rounded.

Description: Small elongate and moderately thin otoliths up to 4 mm length. OH:OT = 2.5-2.8. Dorsal rim gently curved with broad mediodorsal angle and shallow postdorsal area without angle. Ventral rim regularly curved, smooth, deepest at its middle. Anterior tip with blunt rostrum, no distinct excisura or antirostrum. Posterior tip median, rounded, somewhat undulating. Inner face convex with nearly median, moderately deepened sulcus. Ostium short, widened, dorsally as much as ventrally, but widened area shifted anteriorly. Ostial colliculum not as much widened dorsally. Cauda narrow, only slightly bent towards rounded tip, terminating at some distance from posterior and postventral rims. CaL:OsL = 1.15-1.35; OsH:CaH = 2.0-2.2. Dorsal depression moderately large and distinct; ventral furrow moderately distinct, very close to ventral margin of otolith. Outer face slightly concave to flat, smooth.

Comparison: A very inconspicuous otolith, which is however still well recognized by the peculiar gap between the ostial colliculum and the dorsal margin of the ostium. All other characters including the gently curved caudal tip, the regular outline and the short, blunt rostrum result in a very generalized plesiomorphic otolith morphology.

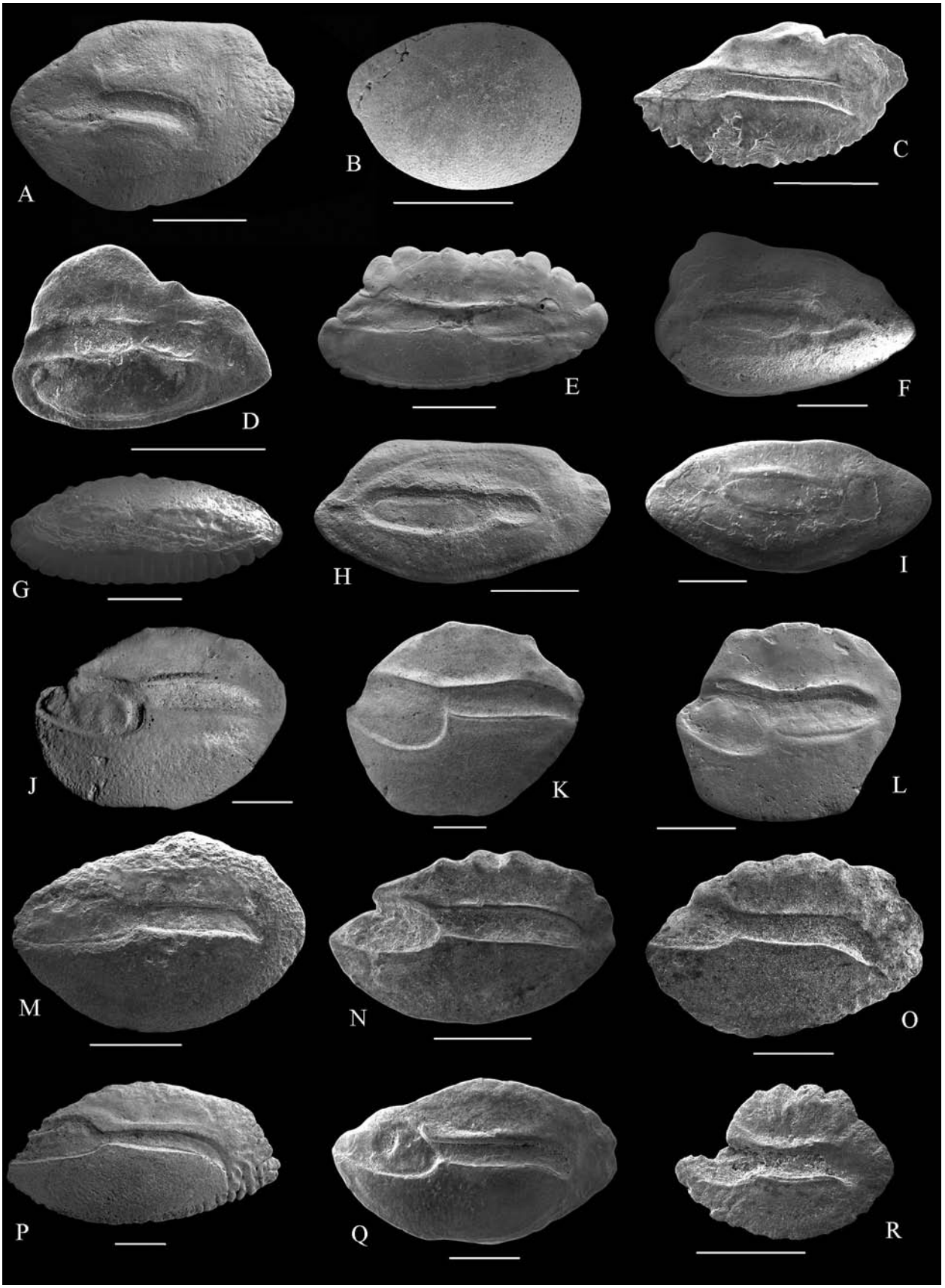

Fig. 15

Family Leiognathidae Jordan, 1923
Genus indet.

genus Leiognathidarum *tashlikensis* n. sp.
Figs. 14D, 15R

Holotype: Figs. 14D, 15R, ULUZ 2/054; Luzanivka, Selandian.

Etymology: Named after the river Tashlik passing by the locality at Luzanivka.

Diagnosis: Compressed otolith with rather flat inner face. OL:OH = 1.4. Rostrum long, excisura broad. Dorsal rim as high as ventral rim deep. Ostium dorsally not widened.

Description: A single well preserved, thin otolith of about 2 mm length. OH:OT nearly 5. Dorsal rim high, short, with obtuse pre- and postdorsal angles and flat in between, broadly serrated. Ventral rim very regularly curved, deepest at its middle, irregularly undulating. Anterior tip with median, long rostrum, broad excisura, but no antirostrum. Posterior rim broadly rounded with median angular tip. Inner face nearly flat with rather deep sulcus. Ostium only slightly widened ventrally, not dorsally. Cauda moderately wide, slightly bent towards rounded tip and dorsally widened at bent. CaL:OsL = 1.5; OsH:CaH = 1.4. Dorsal depression small; no ventral furrow. Outer face flat, rather smooth.

Comparison: A very distinct otolith both in shape as well as expression of the sulcus which is tentatively placed with the Leiognathidae.

Suborder Scombroidei Bleeker, 1859
Family Scombridae Rafinesque, 1815
Genus indet.

genus Scombridarum sp.
Fig. 14E

Material: A single otolith lacking the anterior portion with ostium and rostrum; ULUZ 2/100, Luzanivka, Selandian.

Remarks: The single incomplete specimen of more than 4 mm length is characterized by the reduced dorsal rim with the postdorsal lobe, the shallow ventral rim and the deep cauda with the long downturned portion at about 45° in a distinct kink. The ostium is largely missing, except for a small portion at the collum indicating only a moderate ventral widening. The inner face is convex, the outer face concave and the otolith thin with sharp rims. There is no dorsal depression or ventral rim. All in all this is a typical plesiomorphic scombroid otolith not unlike genus Gempylidarum *merus* Schwarzhans, 2003 from the Danian of Denmark, but less elongate and with a much broader postdorsal lobe, which is more typical for otoliths of the family Scombridae.

3. Faunal evaluation

3.1. Palaeoecology

The otoliths from Luzanivka have been obtained from the Tashlik Formation of Middle Paleocene, Selandian age (NP5 - NP6) representing the last cycle of a continuous sedimentation from Maastrichtian through the Danian Makartite Formation and interrupted by the Boltysh astroblem event at the Cretaceous / Tertiary boundary (Valter & Plotnikova 2003). The sediments of the Tashlik Formation were deposited on the southern fringes of the wide Central Ukrainian Paleogene Basin in very shallow water with coral patches (Makarenko 1970). This aspect is reflected in the faunal composition of fishes as represented by otoliths. Otoliths of deep water or epipelagic fishes are not observed in Luzanivka, like they are in the Danish Selandian (Argentinidae and Macrouridae) (Schwarzhans 2003) or the (unpublished) Paleocene otoliths from Bavaria (i.e. Gonostomatidae, Myctophidae). Instead, the Luzanivka fauna is dominated by shallow water neritic elements such as the Ariidae, Dinematichthyinae, Holocentridae and certain Percoidei like the Haemulidae and Sparidae. Other groups which are now occurring in the outer neritic zone from 50 to 200 m water depth could have been living in shallower waters (as well) during the Paleocene (Schwarzhans 2003), for instance the Merlucciidae, the genus *Centroberyx* of the Berycidae or the Epigonidae, which are related to the inshore fishes of the Apogonidae. The occur-

Fig. 15. Photo-plate of otoliths. **A.** *Heteroconger astroblematicus* n. sp., holotype. **B.** *Arius subtilis* n. sp., paratype. **C.** *Chlorophthalmus udovichenkoi* n. sp., holotype. **D.** *Maorigadus ukrainicus* n. sp., holotype. **E.** genus Merlucciidarum *antiquus* n. sp., holotype. **F.** *Fierasferoides bucculentus* n. sp., holotype. **G.** *Gadophycis serratus* n. sp., holotype. **H.** *Ogilbia luzanensis* n. sp., paratype. **I.** genus Bythitidarum *rozenbergi* n. sp., holotype. **J.** *Centroberyx anguinicauda* n. sp., holotype. **K.** *Centroberyx fragilis* Schwarzhans, 2003. **L.** *Centroberyx integer* (Koken, 1885). **M.** genus Holocentridarum *ryabchuni* n. sp., paratype. **N.** genus Epigonidarum *tyassminensis* n. sp., paratype. **O.** genus Haemulidarum *gullentopsi* Nolf, 1978. **P.** genus Haemulidarum *makarenkoi* n. sp., paratype. **Q.** genus Sparidarum *spatiatus* n. sp., holotype. **R.** genus Leiognathidarum *tashlikensis* n. sp., holotype. Bar length 1 mm.

rence of a representative of the 'garden eel' genus *Heteroconger* (Congridae) is of particular interest not only because it is the first such find in fossil otoliths, but also because their recent distribution (Allen et al. 2003) would connect well with the shallow water coral patch environment of Luzanivka. It is, however, uncertain, whether these fishes did maintain the same mode of living during the Paleocene as today.

3.2. Paleogeography

In the Paleocene, the Central Ukrainian Basin formed a marginal basin of the Caspian Basin, to which it was connected in the East (Ziegler 1988). During the Selandian it was neither connected north-westwards to the North Sea Basin, nor westwards to the Prealpine basins nor southwards to the Crimean Basin of the Black Sea. It is thus not surprising that the otolith association at Luzanivka located on the southern shores of the Central Ukrainian Basin shows relatively little correspondence to age equivalent faunal associations known from the North Sea Basin (Nolf 1978; Schwarzhans 2003) or the Bavarian Basin (unpublished), although differences in paleonvironment / paleo-water depth have certainly played a supportive role. The closest relation is to the Selandian of Denmark (Schwarzhans 2003) with 5 species conspecific and 2 belonging to the same genus / genus group (in the case of open generic nomenclature) as species from Luzanivka and hence are considered related. The degree of similarity is 23% (with the 'related species' valued as 'half count') of the association of Luzanivka. The Selandian association of West Greenland (Schwarzhans 2004) also shows a high degree of similarity (23%, 4 species conspecific, 4 related with species in Luzanivka) and likewise from Bavaria (21%, 3 species conspecific, 5 related with species in Luzanivka) (see Table 1). The few faunal associations known from the Danian of Denmark and the Thanetian of Belgium relate slightly worse with ranges of 17% to 19%; the Thanetian and Ypresian from the London Basin (Stinton, 1965, 1966) still worse with 8%. Surprisingly, the correlation with the Lutetian of the North Sea Basin (Schwarzhans 2007) again is higher, with 21%, but only 1 species is conspecific with a species from Luzanivka (*Preophidion convexus*) whereas 9 other species represent the same genus / genus group and are considered related (see above). This effect is interpreted as being caused by the much better knowledge of the Lutetian otolith associations as compared to those of the Paleocene or the early Eocene.

The most common group by means of specimens is the genus *Centroberyx* of Berycidae - and in this case also by means of species – followed by genus Epigonidarum *tyassminensis*, genus Haemulidarum *makarenkoi*, *Ogilbia luzanensis* and the two species of the genus *Arius*. Of these *Centroberyx fragilis*, *C. integer*, *Ogilbia luzanensis* and *Arius danicus* are widely distributed in the European Paleocene and are usually common (Schwarzhans 2003, 2004). Genus Epigonidarum *tyassminensis* is restricted so far to Luzanivka, *Arius subtilis* is shared with Bavaria (unpublished) and genus Haemulidarum *makarenkoi* probably is closely related to genus Haemulidarum *sylvestris* (Stinton, 1965) from the Ypresian of England. Representatives of Ophidiiformes other than *Ogilbia luzanensis* are rare, although quite a number of species are recorded (7) (Stinton 1965, 1966; Nolf 1978; Schwarzhans 2003). This is in agreement with other European Paleocene faunas. It appears that otoliths of the Ophidiiformes only become the dominant faunal element in Eocene times. Another common group in the Paleocene are chlorophthalmid otoliths (Schwarzhans 2003 and unpublished data). Interestingly, it is not the ubiquitous *Paraulopus postangulatus* (Nolf & Dockery, 1993), but a representative of the genus *Chlorophthalmus*, *C. udovichenkoi*, which is related to *C. tortus* (Schwarzhans, 2003) from the Danian of Denmark. An interesting find is the basal gadiform near Muraenolepididae, *Maorigadus ukrainicus*, since *Maorigadus* so far was only known from the early Eocene of New Zealand. Its find in Ukraine indicates a much wider distribution than originally expected.

3.3. Otolith-biostratigraphy

Paleocene otolith assemblages are still not well enough known to allow significant biostratigraphic conclusions. Still, the best correlation is with Selandian assemblages of other European localities (see Table 1), for instance in respect to *Arius*, *Ogilbia* and *Centroberyx* species. Seven species from Luzanivka are also known from other Selandian locations of Europe and Greenland (Schwarzhans 2003, 2004), although never more than five in any of them. Three species are already present in the Danian (Schwarzhans 2003) and similarly three in the Thanetian (Nolf, 1978), but both stratigraphic intervals are not as well studied for otoliths as the Selandian. However, there are also a notable exceptions: genus Haemulidarum *gullentopsi* has hitherto only been known from the Thanetian and *Preophidion convexus* only since Lutetian (Nolf 1978; Schwarzhans 2007).

Table 1. Otolith species list from the Paleocene of Luzanivka and correlation plate. Dark grey = same species; light grey = related species.

Seelandian of Luzanivka, Ukraine	Danian	Selandian			Thanetian		Ypresian	Lutetian
	Denmark	W-Greenl.	Denmark	Bavaria	Belgium	England	England	N-Sea
Pterothrissidae								
Pterothrissus sp.								
Congridae								
Heteroconger astroblematicus								
Chlorophthalmidae								
Chlorophthalmus udovichenkoi								
Ariidae								
Arius danicus								
Arius subtilis								
Gadiformes near Muraenolepididae								
Maorigadus ukrainicus *New Zealand								
Ranicipitidae								
Raniceps hermani								
Merlucciidae								
gen. Merlucciidarum antiquus								
Carapidae								
Fierasferoides bucculentus								
Onuxodon sp.								
Ophidiidae								
Gadophycis serratus								
Preophidion convexus								
Hoplobrotula sp.								
Bythitidae								
Ogilbia luzanensis								
gen. Bythitidarum *rozenbergi*								
Berycidae								
Centroberyx anguinicauda								
Centroberyx fragilis								
Centroberyx integer								
Centroberyx sp.								
Holocentridae								
gen. Holocentridarum *ryabchuni*								
Epigonidae								
gen. Epigonidarum *tyassminensis*								
Haemulidae								
gen. Haemulidarum *gullentopsi*								
gen. Haemulidarum *makarenkoi*								
Sparidae								
gen. Sparidarum *spatiatus*								
Leiognathidae								
gen. Leiognathidarum *tashlikensis*								
Scombridae								
gen. Scombridarum sp.								
Same species	**3**	**4**	**5**	**3**	**3**	**0**	**0**	**1**
Related species	**3**	**4**	**2**	**5**	**4**	**4**	**4**	**9**
Degree of similarity	**17%**	**23%**	**23%**	**21%**	**19%**	**8%**	**8%**	**21%**

3.4. Evolutionary interpretation

SCHWARZHANS (1996, 2003) and (2010b) expanded on the evolutionary significance of otolith finds from the Maastrichtian and the Paleocene concluding that these finds can be associated with certain principle morpho-logic-evolutionary categories. These categories, as described in the following, also fit well the characterization of the Luzanivka otolith assemblage.

Category 1: persistent taxa: Otoliths with morphologies that have not altered significantly since

Paleocene times and thus can reasonably be assigned to living genera. Such living genera represented in Luzanivka comprise *Pterothrissus* (Pterothrissidae), *Heteroconger* (Congridae), *Chlorophthalmus* (Chlorophthalmidae), *Arius* (Ariidae), *Raniceps* (Ranicipitidae), *Hoplobrotula* (Ophidiidae), *Ogilbia* (Bythitidae) and *Centroberyx* (Berycidae). *Onuxodon* of Carapidae is not counted until positively tested by adequate finds. Also not counted is genus Bythitidarum *rozenbergi*, which cannot be allocated to a living genus mainly because of the very simple, reduced otolith morphology found in the Bythitinae. These are all families that have yielded similar or the same species and genera from other European Paleocene locations and hence are established in this category. The only exception is the congrid genus *Heteroconger*, while the Congridae are known from other extant genera for instance in the Danish Selandian. In total 12 (possibly 14) species belong in the category of persistent taxa corresponding to 46% to 54% of the total fauna (45% in the Paleocene of Denmark).

Category 2: extinct early specialized taxa: Otoliths with highly specialized morphologies without apparent affinities to living taxa. Such otoliths are interpreted to represent extinct taxa that were either inherited from late Cretaceous times or are indigenous to the early Tertiary. Only three species belong to that category – *Maorigadus* hitherto only known from the early Eocene of New Zealand, an extinct gadiform possibly related to the family Muraenolepididae, *Gadophycis* an enigmatic Ophidiidae and genus Holocentridarum *ryabchuni*, which represents a group carried over from Late Cretaceous times (the fossil otolith-based genus *Holocentronotus* Schwarzhans 2010b). With three species and about 12% this category is small, but in the similar range as in Denmark (14%).

Category 3: extinct plesiomorphic taxa: Otoliths with generalized morphologies interpreted to represent a plesiomorphic character status, which are attributable to extant families. Representatives of this category in Luzanivka are *Fierasferoides* a supposed primitive Carapidae and *Preophidion* of the Sirembiniae of the Ophidiidae. Again, this is a small group with only two species or about 8% of the fauna, significantly less than the 21% observed in Denmark.

Category 4: 'missing links': This informal heading contains certain other generalized otolith morphologies, which are interpreted as of plesiomorphic character status. These otolith morphologies are characterized by low level or few synapomorphies of the families or higher taxa in which they are placed and therefore are interpreted to be situated near major dichotomical events of the phylogeny of such higher taxa. This category is not very sharply defined and with a fluent transition to category 3 and always subject to increasing knowledge of fossil otoliths. In Luzanivka, all 5 percoid and the single scombroid records are interpreted as belonging to this category (see respective descriptions), thus amounting to 26% of the fauna. Similar observations have been made in the Paleocene of Denmark (Schwarzhans 2003) and the Maastrichtian and Paleocene of Bavaria (Schwarzhans 1996, 2010b). The high amount of primitive, generalized percoid otolith morphologies combined with their generally small size is particularly notable. Such findings can be characteristic for an early evolutionary phase, when early plesiomorphic 'blue prints' have evolved from which the subsequent perciform radiation derived (Alfaro et al. 2009; Friedman 2009, 2010). It likely is an expression of the uprising of the perciform dominated teleost fauna of the Tertiary and the Recent as compared to the beryciform dominated fauna of the Late Cretaceous (Patterson 1964, 1993). And it may also serve as an indication that not much wealth of fossil Percoidei can be expected prior to the Tertiary. The presence of a very basal scombroid otolith in Luzanivka, together with a similar find in the Danian of Denmark and finds of stromateoid otoliths in the Paleocene of Denmark indicate though that certain sister-groups of the Percoidei were already established in Paleocene times (see also Friedman 2009). A basal perciform radiation – as far as can be supported by monophyly – therefore likely was of late Pre-Tertiary origin.

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seum in Perth (WAM), H. Wilkens of Zoological Museum of the University of Hamburg (ZMH) and P. Møller and J. Nielsen of the Zoological Museum of Copenhagen (ZMUC). B. Reichenbacher (München) and R. Brzobohaty (Brno) are thanked for their constructive reviews of the manuscript.

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