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A striking convergence in conchological morphology between Oligocene-Miocene lottiids (Mollusca, Patellogastropoda) from the North Sea Basin and the Paratethys

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The protoconch and teleoconch morphology of *Patella compressiuscala* Karsten, 1849 (North Sea Basin, Chattian - Langhian) is described and illustrated. The new genus *Boreoblinia* is established for this species which is characterized by a protoconch indicative of a lecithotrophic type of early development, lacking even a short free-swimming larval stage. The distinctness of *Boreoblinia* gen. nov. from other Patellogastropoda such as *Tectura*, *Patella*, and *Helcion* exhibiting the typical patellogastropod protoconch types is supported also by its unusual shell structure. An amazing heterochronous convergence of both protoconch and teleoconch morphology between the new species from the North Sea Basin and Miocene *Flexitectura subcostata* (Sinzow, 1892) from the Sarmatian of the Paratethys is shown. Detailed descriptions and SEM images of species involved are presented.

KEY WORDS – Gastropoda, Lottidae, Miocene, Europe, protoconch, new genus

Introduction

Oligocene and Miocene patellogastropods from the Mediterranean and Paratethys as well as from the North Sea Basin have usually been classified in different families, such as Patellidae Rafinesque, 1815, Acmaeidae Carpenter, 1857, or Tecturidae Gray, 1847. The small-shelled representatives of this group occur regularly but not abundantly in various shallow to deeper marine and brackish water habitats and were studied by many authors (Eichwald, 1830-1853; Karsten, 1849; von Koenen, 1882; Sinzov, 1892; Friedberg, 1928); Kolesnikov, 1935; Jekelius, 1944; Anderson, 1959; Bałuk, 1975; Janssen, 1984; Il'ina, 1993; Anistratenko, 2000, 2001; Harzhauser and Kowalke, 2002).

Correct taxonomic identification of these species is sometimes difficult because the restricted number of conchological characters available and insufficient knowledge of the range of intraspecific morphological variation. Furthermore, few data on protoconch morphology and type of early development of these gastropods have been obtained so far (*e.g.*, Anistratenko *et al.*, 2006; Anistratenko & Anistratenko, 2007).

Protoconch ornamentation and shape are now generally accepted as useful taxonomic characters, particularly in marine gastropods with a planktotrophic larva in their ontogeny (*e.g.*, Bandel, 1982, 1991; Sasaki, 1998; Kaim, 2004). The characters of embryonic, larval, and juvenile shells can be used to reconstruct the phylogeny of some gastropods. In the case of the patellogastropods the protoconch characters can reveal the size of the eggs and the mode of embryonic development, *e.g.*, the presence of a free swimming larva.

For the first time a comparative study is presented between the minute *Patella*-like *Patella compressiuscala* Karsten, 1849 that lived in the North Sea Basin from Chattian until Langhian time (Late Oligocene – Middle Miocene), and similar species known from the later Badenian and Sarmatian (Middle Miocene) from the Paratethys. The former exhibits an unusual type of protoconch, which indicates a lecithotrophic type of early development. This type of protoconch has been discovered before only in several species of Sarmatian lottiids from the Paratethys (see Anistratenko & Anistratenko, 2007). We also present and discuss new data on the shell structure of the studied species.

For the Oligocene/Miocene species the new genus name *Boreoblinia* is proposed. Although the generic level of taxonomic attribution of the patellogastropods investigated here requires further confirmation we assign them to the family Lottiidae Gray, 1840 (for more detailed discussion see below under "Taxonomy").

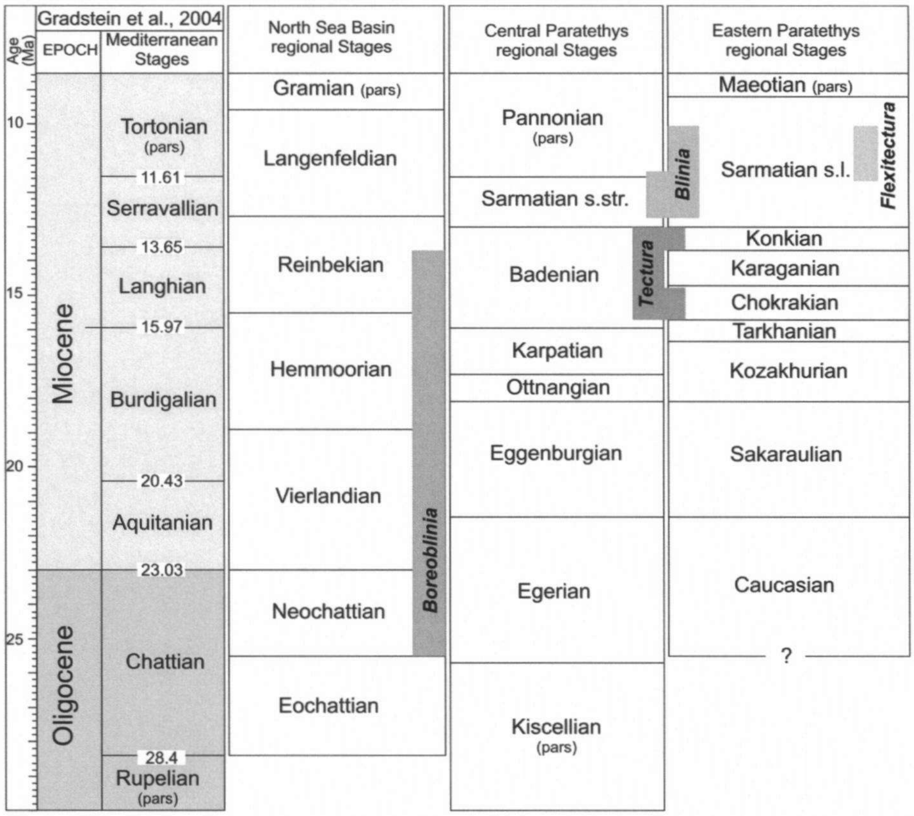

Figure 1. Stratigraphic correlation chart of the standard scale (Mediterranean Stages) with local stages of the North Sea Basin, the Central and the Eastern Paratethys (Mediterranean Stages after Gradstein *et al.*, 2004; Central Paratethys regional Stages after Harzhauser & Mandic, 2008). The time ranges of Patellogastropods with a different type of protoconch shown in vertical lines.

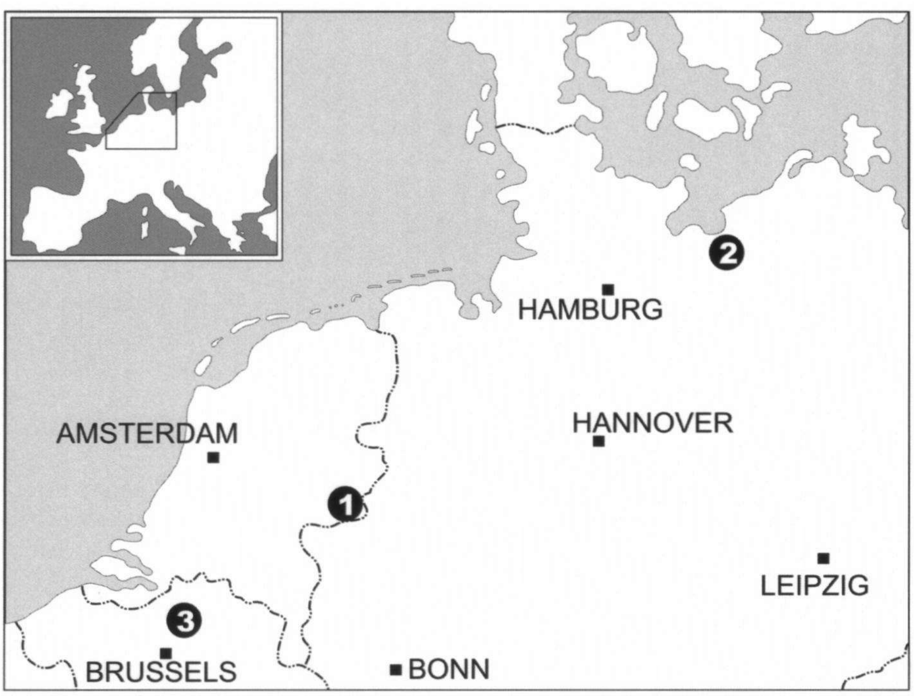

Figure 2. Localities, where studied materials were collected. **1** – Miste, near Winterswijk, the Netherlands (local stage Hemmoorian, lower part of the Langhian); **2** – Pinnow, in the neighborhood of Schwerin, Germany ("Sternberger Gestein", Neochattian); **3** – Heist-op-den-Berg, located between Antwerp and Aarschot, Belgium (Zonderschot Sands, late Hemmoorian, early Langhian).

Material and methods

Our study is based on material from three localities in the North Sea Basin (Figures 1, 2):

1. Miste near Winterswijk (Gelderland province, the Netherlands). It concerns a Middle Miocene fauna (local stage Hemmoorian, lower part of the Langhian) from the Breda Formation that is described by Janssen (1984). At this locality a lot of pits have been made especially for fossil collecting. Six specimens came from the pit, made in 1968; the other six come from several pits, dug between 1968 and 1977. All provided by A.W. Burger.
2. Six specimens of *Patella compressiuscala* from the Neochattian "Sternberger Gestein" kindly provided by mr A.F.J. Jansen could be studied, collected near Pinnow in the neighborhood of Schwerin (Schleswig-Holstein, Germany).
3. Also provided by mr A.F.J. Jansen were 18 specimens from Heist-op-den-Berg (Brabant Province, Belgium), where also several pits have been dug for fossil collecting. The material originates from the Zonderschot Sands, also of late Hemmoorian (early Langhian) age.

Adult shell characters were studied with an optical stereomicroscope. Standard dimensions for shell characters were used. Morphological features of protoconchs such as shape, size, sculpture and character of boundary with the teleoconch were examined by means of scanning electron microscope (SEM). Altogether thirty-six specimens of *Patella compressiuscala* were analysed. Four specimens were partially broken for SEM examination of the shell microstructure.

Most of the SEM images were obtained in the Institute of Geological Sciences National Academy of Sciences of the Ukraine (Kiev, Ukraine). Shells were mounted on stubs, sputter-coated with gold and then documented using a JSM-6490 Scanning Electron Microscope. A few additional SEM micrographs of shell structure were performed in the Geological-Paleontological Institute and Museum of the University of Hamburg (Germany); here the digital SEM LEO 1455 VP was used. All figured specimens are housed at the Institute of Geological Sciences National Academy of Sciences of the Ukraine (Kiev, Ukraine), abbreviated as IGS NANU.

Morphological terms for the shell description used in text (Figure 3):

AP – apex position, *i.e.* distance of apex from frontal edge, DP – greater diameter of a protoconch, HS – height of shell, LS – length of shell, WS – width of shell.

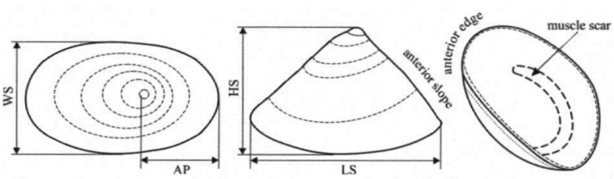

Figure 3. A sketch of studied lottiid shell (schematic); muscle scar on the inner surface indicated by arrow. See explanation for measurements in the text.

Nomenclatural notes and taxonomy

Originally the species discussed was described as *Patella compressiuscala* and subsequently has been attributed to different genera: *Acmaea* Eschscholz in Rathke, 1833 (*e.g.* Kautsky, 1925), *Scurria* Gray, 1840 (*e.g.* Anderson, 1959), *Lepetella* Verrill, 1880 (*e.g.*, Janssen, 1984). According to Warén (1972) the species belongs to the Cocculinacea and not to the Acmaeidae. In our opinion *Patella compressiuscala* Karsten, 1849 should be assigned to the family Lottiidae Gray, 1840 as it is characterized by the same type and morphology of protoconch as *Blinia* Anistratenko, Bandel & Anistratenko, 2006 and *Flexitectura* Anistratenko, 2000 (more details see below).

Since the publication of Karsten (1849) the incorrect spelling "*compressiuscula*" has been generally used (*e.g.* Kautsky, 1925; Anderson, 1959; Janssen, 1984; Wienrich, 2001), although the correct original spelling is "*compressiuscala*" (Karsten, 1849: 12), and there is no nomenclatural reason to change it. Moreover, in this case the risk of homonymy with *Pileopis compressiuscula* Eichwald, 1830 (though it is attributed to another genus – *Tectura*) is fortunately removed.

The distinct similarity of the protoconch and teleoconch of *P. compressiuscala* with *Flexitectura subcostata* (Sinzov, 1892) from the Middle Sarmatian of Ukraine and Moldova might be considered as evidence for their congenerity or even conspecifity. However, there are some strong arguments against this attribution. First of all this Middle Sarmatian lottiid with a pancake-like protoconch is assumed to be derived from the Early Sarmatian "*Tectura*" and might represent one of a large group of endemic mollusc genera of the Middle Sarmatian Paratethys basin (Kolesnikov, 1935; Paramonova, 1994; Harzhauser & Kowalke, 2004; Ionesi *et al.*, 2005; Anistratenko & Anistratenko, 2007). Noteworthy, the Early Sarmatian basin was already landlocked and immigrants from the Mediterranean or the North Sea Basin could not penetrate. The last occurrence of *P. compressiuscala* in the North Sea Basin predates the first occurrence of *Blinia* and *Flexitectura* about 2.5 Ma. If *P. compressiuscala* from the North Sea Basin and *F. subcostata* would be attributed to a single genus the monophyly of the genus *Flexitectura* would become questionable. Hence, in spite of a striking resemblance we treat the similarities between *Patella compressiuscala* and *Flexitectura subcostata* as a convergence, and we suggest for the Oligocene/Miocene lottiid from the North Sea Basin a new genus name: *Boreoblinia*.

Shell microstructure characters and its taxonomic implications

Some patellogastropod taxa are characterized by having both calcitic and aragonitic shell layers and this is interpreted as the most primitive gastropod shell structure. Calcitic layers in patellogastropod shells include foliated and homogeneous structures; aragonitic layers are predominantly crossed-lamellar. Some families *e.g.*, Patellidae, possess both foliated and crossed - lamellar structures,

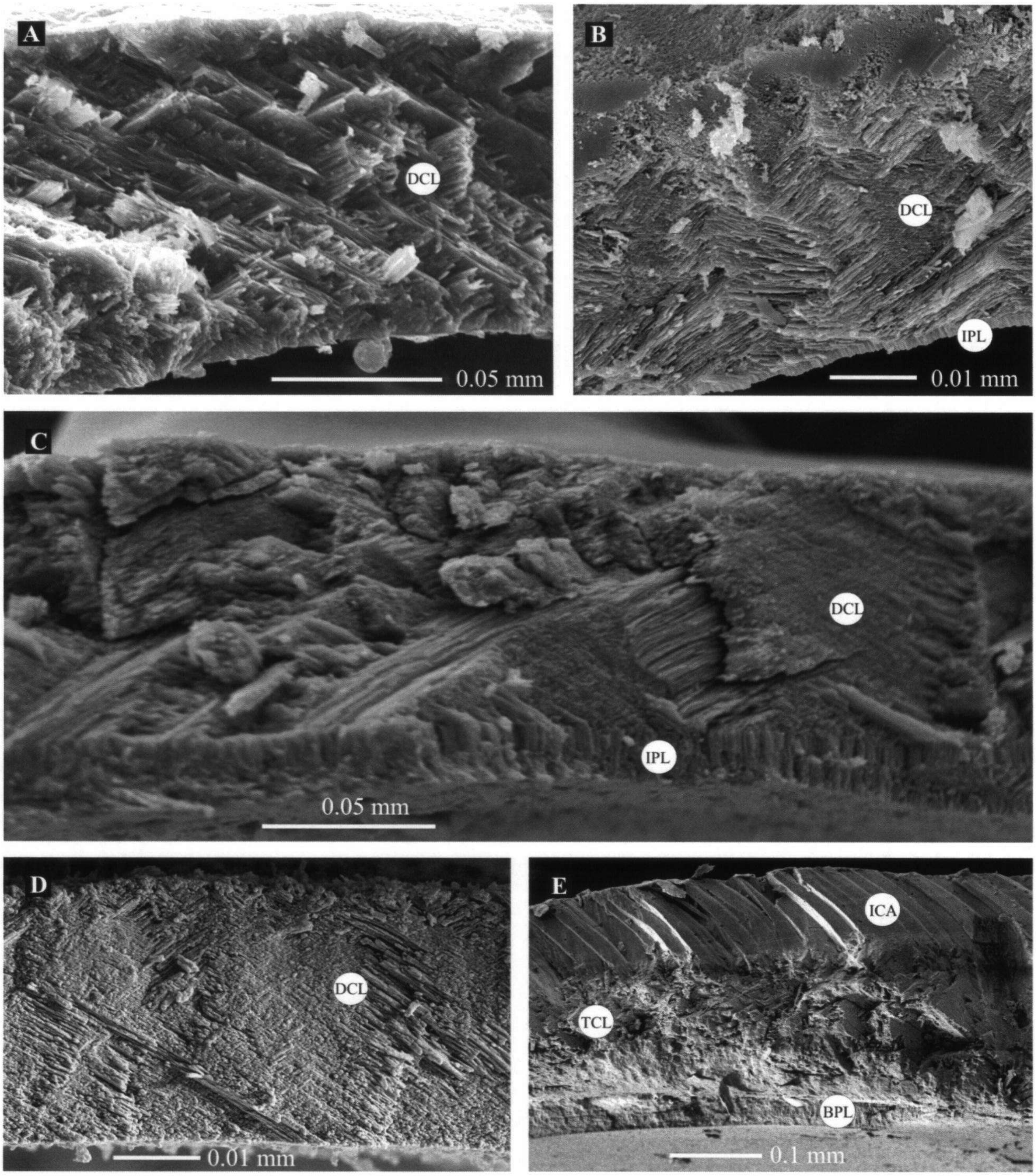

Figure 4. The shell structure of patellogastropods discussed in the text. **A, B.** *Boreoblinia compressiuscala* (Karsten, 1849). **A** – Specimen (IGS NANU, Miste_1977-4/2008) from the Langhian. Cross-section, showing the dissected aragonitic crossed lamellar structure (DCL) and the aragonitic porous outer layer of the shell. **B** – Specimen (IGS NANU, Heist-op-den-Berg_2001-3/2009) from the Langhian. The same aragonitic crossed lamellar structure as in the specimen of fig. 4A and also the inner prismatic layer (IPL) are visible. **C.** *Tectura zboroviensis* (Friedberg, 1928). Specimen (IGS NANU, 18/2003) from the Chokrakian of Yurkino (Crimea peninsula, Ukraine), reveals a similar composition with crossed lamellar layer (DCL) and inner prismatic layer (IPL). **D.** *Blinia* sp. Specimen (IGS NANU, 34/2004) from the middle Sarmatian of Letichev, West Ukraine. Section showing the aragonitic crossed lamellar structure (DCL) and more rough sets of the inner crossed lamellar layers of the shell, compared with *B. compressiuscala*. **E.** *Tectura virginea* (Müller, 1776). Recent specimen from the North Sea, Doggerbank, (private collection of Dr. Jens Hartmann) shows developed inner shell layer as aragonitic basal prismatic layer (BPL), middle shell layer composed of transversally fractured, aragonitic crossed lamellar layer (TCL), and outer calcitic layer of inclined sheets (ICA).

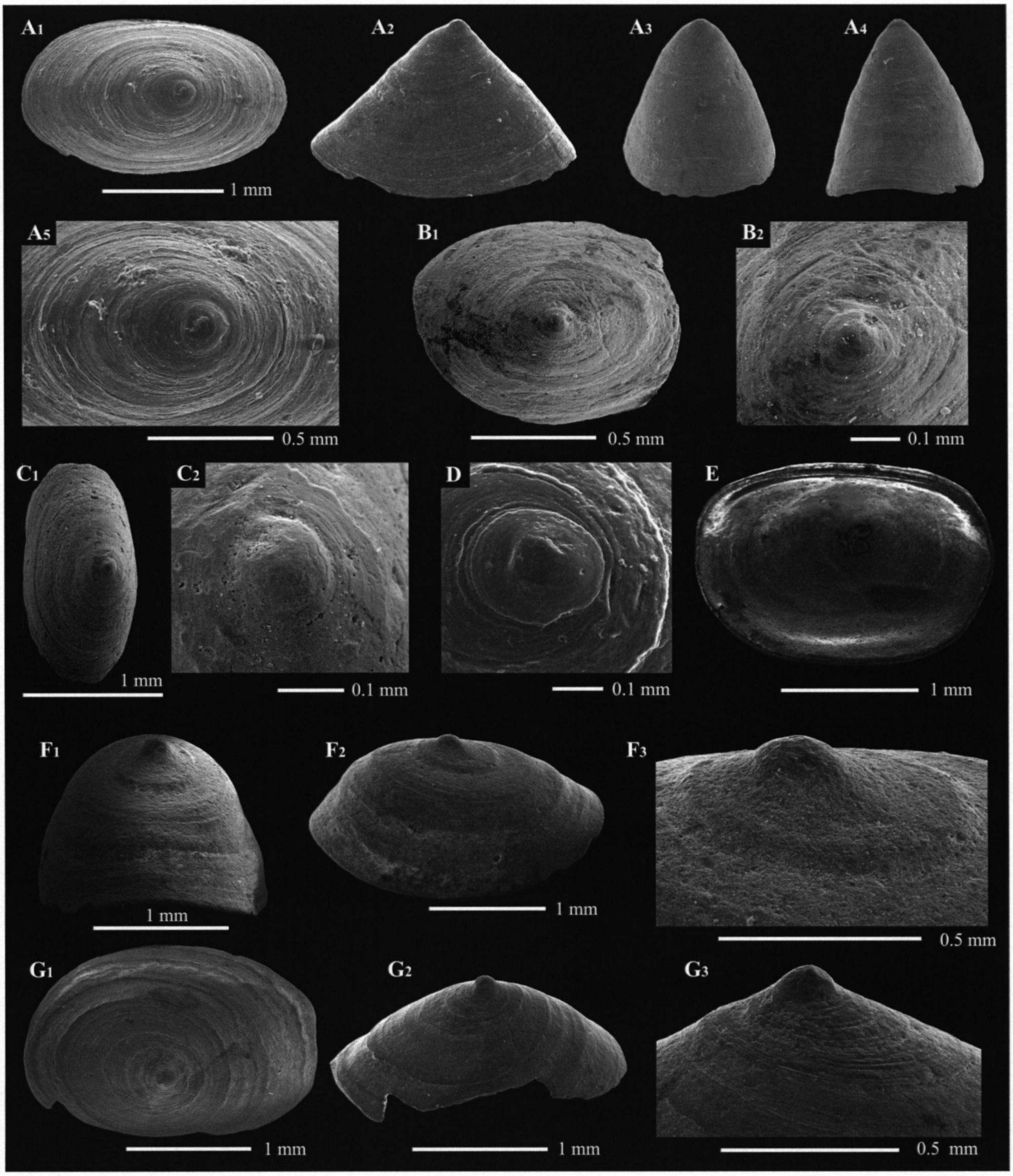

Figure 5. A-G. *Boreoblinia compressiuscala* (Karsten, 1849). **A** – IGS NANU, Miste_1968-4/2008, Langhian; A1 – apical view; A2 – right lateral view; A3 – anterior view; A4 – posterior view; A5 – details of apical view of the shell. **B** – IGS NANU, Heist-op-den-Berg_2001-3/2009, Langhian; B1 – apical view; B2 – details of apical view of the embryonic shell. **C** – IGS NANU, Heist-op-den-Berg_2001-2/2009, Langhian; C1 – apical view; C2 – details of apical view of the embryonic shell.**D** – IGS NANU, Miste_1968-5/2008, Langhian; apical view of the embryonic shell; the clear demarcation between the protoconch and early teleoconch is visible. **E** – IGS NANU, Schwerin-1/2008, Chattian; apertural view, the muscle scars are visible as gentle expressive tracts. **F** – IGS NANU, Schwerin-2/2008, Chattian; F1 – posterior view; F2 – left lateral view; F3 – apical part of the shell viewed from the left. **G** – IGS NANU, Schwerin-3/2008, Chattian; G1 – apical view; G2 – right lateral view; G3 – apical part of the shell viewed from the left.

whereas Lottiidae have shells with thin outer calcitic homogeneous layers underlain by aragonitic crossed-lamellar layers (MacClintock, 1967; Lindberg, 1988).
The shell structure of *Boreoblinia* is characterized by a simple type of aragonitic crossed-lamellar structure, the same as is known from the Chokrakian "*Tectura*" *zboroviensis* (Friedberg, 1928) and Sarmatian *Blinia* from the Paratethys (Anistratenko *et al.*, 2006). In all these cases most of the shell is composed of one layer of crossed lamellae in which the needles of the two directions of lamellae of the first order commonly intersect (Figure 4). A similar structure is known from the Triassic patellid *Scutellastraea costulata* (Münster, 1841) from the St Cassian Formation of the Alps, and from a patellogastropod species of similar shape from the Paleocene of Alabama (Bandel, 1982). The sets of crossed lamellae are more delicate in *Blinia*'s shell wall than in *Boreoblinia* and "*Tectura*" *zboroviensis*.
The outer layer of *Boreoblinia* also resembles that of the *Blinia* shell – it is thin and porous, and also aragonitic. These characters distinguish both *Boreoblina* and *Blinia* clearly from *Patella* and its relatives, which have a calcitic outer layer with a characteristic layered structure that is usually quite thick and has a rather complex structure (Figure 4).
Hence, the structure of the *Boreoblinia* shell is characterized as follows: the outer layer is thin, porous and aragonitic (1), most of the shell has an aragonitic crossed-lamellar structure, composed of a single layer of coarse crossed lamellae (2) and a thin inner prismatic layer exists (3), though it is often peeled off, and the inner surface of most of the adult individuals appears to be lacking this specific layer.

Systematic paleontology

Class Gastropoda Cuvier, 1797
Order Patellogastropoda Lindberg, 1986
Family Lottiidae Gray, 1840
Genus *Boreoblinia* nov.

Type species — *Patella compressiuscala* Karsten, 1849. Late Oligocene (Chattian) – Middle-Miocene (Langhian) of the Netherlands, Belgium, NW Germany and Denmark.

Etymology of the name — Derived from "*Borealis*" (Latin, northern) and "*Blin*" (Russian, pancake) for the general shape of the protoconch that is like a thick pancake.

Diagnosis — Conical, relatively small patellogastropods with high-conical, laterally compressedshell and "pancake"–like protoconch. Teleoconch ornament of concentric growth ribs; aperture elongated in shape, anterior and posterior edges have distinct flexures.

Differentiation — Differs from Sarmatian *Blinia* with similar type of protoconch mainly in having larger protoconch and more rough sets of the inner crossed lamellar layers of the shell, whereas the organization of these layers in both taxa is similar. The outer layer of the *Boreoblinia* (as well as of the *Blinia*) shell is thin and porous, both are aragonitic. That distinguishes both genera from *Patella* and its relatives, which have a calcitic outer layer that is usually thick and has a complex structure. The shell structure of *Boreoblinia* and *Blinia* is similar in general to that of the Sarmatian "*Tectura*" *zboroviensis*, but the first two differ from the latter as well as from all other known patellogastropods (except for *Flexitectura* and *Squamitectura*) in having a "pancake"–like protoconch. The new genus differs from *Blinia* in larger and more globular shape of the protoconch, which has no expressed sculpture, wrinkles or other specific ornamentation or pit on its surface.

Description — The shell is small to moderate in size, thin-walled, high-conical in shape without marginal slit, apical hole or internal septum. It measures up to 4 mm in length, up to 2 mm in width and up to 2 mm in height. The apex is situated eccentric and slightly tilted forward. The lateral edges of the shell are almost parallel to each other. The teleoconch surface has numerous concentric lines. The protoconch is round to oval "pancake"-like in shape, quite bulbous and measures from 0.18 mm to 0.25–0.28 mm in maximum diameter. The protoconch surface is apparently smooth, perhaps the ornamentation is not preserved. The transition from the embryonic shell to the teleoconch is usually clearly marked by a constriction.

Discussion — The more or less cap–like or semi globe-shaped embryonic shell of *Patella compressiuscala* indicates a lecithotrophic type of early development and the absence of any short free–swimming larval stage following the yolk–rich embryogenesis (*e.g.*, Bandel (1982)). The shape and proportions of a "pancake"–type of protoconch may suggest the brooding of young snails in the maternal adult individuals (as it is in the modern *Erginus moskalevi* (Golikov and Kussakin, 1972) illustrated by Sasaki (1998, fig. 21a–c). The imprints on the inner surface of the shell of *Boreoblinia*, which we interprete as the muscle scars, are horseshoe–like, gentle expressive tracts (Figure 3). The impressions were SEM–documented as well (Figure 5e). The combination of shell structure features and the protoconch morphology support that the Oligocene/Miocene lottiid from the North Sea Basin discussed here should be considered as belonging to an independent genus.

Boreoblinia compressiuscala (Karsten, 1849)
(Figure 5)

1849 *Patella compressiuscala* n. sp?; Karsten, p. 12.
1868 *Patella compressiuscula* Karsten; Koch & Wiechmann, p. 562, pl. 12, fig. 12.
1876 *Patella compressiuscula* Karsten; Koch, p. 165.
1882 *Patella compressiuscula* KARSTEN; von Koenen, p. 323.
1925 *Acmaea compressiuscula* Karsten; Kautsky, p. 55.
1959 *Scurria compressiuscula* (Karsten, 1849) [non Eichwald]; Anderson, p. 45-46, pl. 2, fig. 2a, b.
1984 *Lepetella compressiuscula* (Karsten, 1849); Janssen, p. 121, pl. 44, fig. 2a-c.
2001 *Lepetella compressiuscula* (Karsten, 1849); Wienrich, p. 394-395, pl. 63, fig. 2a-d.

Diagnosis — See diagnosis for genus.

Material — Twelve specimens from the Langhian of Miste, Holland, IGS NANU, Miste_1968-1/2008-6/2008 (ex coll. A.W. Burger); IGS NANU, Miste_1977-1/2008-6/2008 (ex coll. A.W. Burger); six specimens from the Chattian of Schwerin, Germany, IGS NANU, Schwerin-1/2008-6/2008 (ex coll. A.F.J. Jansen); eighteen specimens from the Langhian of Heist-op-den-Berg, Belgium, IGS NANU, Heist-op-den-Berg_2001-1/2009-18/2009 (ex coll. A.F.J. Jansen).

Description — Shell small, high-conical, with lateral edges subparallel. The apex is eccentric, slightly tilted forward. The apical angle (measured from the front view) varies, usually about 55-65° in different specimens. The anterior and posterior slopes are straight or slightly convex; the anterior and posterior edges with distinct flexures. Aperture oval. The muscle scars are horseshoe–like and are usually clearly visible as gentle expressive tracts (Figures 3, 5). The protoconch is "pancake"-like to semi globe-shaped, apparently smooth. The teleoconch surface is covered by coarse concentric growth lines alternating with fine ones. The transition from the embryonic shell to the teleoconch is usually marked by a constriction or a rim.

Measurements — See Table 1.

No	LS	HS	WS	AP	DP
IGS NANU, Schwerin_					
1/2008	2.2	1.2	1.5	1.2	~0.18
2/2008	2.55	1.2	1.6	1.3	0.23-0.25*
3/2008	2.25	1.0	~1.6	1.3	0.18-0.19*
4/2008	2.75	1.5	1.4	1.6	~0.15
5/2008	2.9	1.7	1.76	1.5	0.20
6/2008	2.7	1.45	1.7	1.25	-
IGS NANU, Miste_					
1968-1/2008	1.9	1.15	1.1	0.9	~0.16
1968-2/2008	2.5	1.45	1.4	~1.0	0.19
1968-4/2008	2.3	1.45	1.45	0.95	0.18-0.20*
1968-5/2008	2.35	1.5	1.4	0.95	0.24-0.25*
IGS NANU, Miste_					
1977-1/2008	2.75	1.85	1.65	1.2	0.28
1977-2/2008	-	-	-	-	~0.18
1977-3/2008	-	-	-	-	0.23-0.27*
IGS NANU, Heist-op-den-Berg_					
2001-1/2009	1.7	0.8	1.2	0.8	0.13
2001-2/2009	2.6	1.4	1.3	1.1	0.18
2001-3/2009	3.9	1.8	1.9	1.7	0.16
2001-4/2009	1.8	1.4	1.75	0.8	0.12

Table 1. Measurements of *Boreoblinia compressiuscala.* All measurements in mm. The asterisk denotes two measurements (biggest and smallest) of a protoconch.

Remarks — Specimens of *Boreoblinia compressiuscala* both from the Chattian and the Langhian differ from the Middle Sarmatian *Flexitectura subcostata* in its larger and more globular not inflated protoconch. The Langhian *B. compressiuscala* differs from the Chattian specimens in a more eccentricic position of the apex. The protoconchs of *B. compressiuscala* from the Heist-op-den-Berg are generally a little bit smaller than those of specimens from all other localities (see Table 1).

Concerning the shell variability a few notes should be presented here. We examined more than fifteen specimens and the limits of dimensions' variability and shape of shell are restricted. The protoconch in *Blinia* can be with or without pit (a small depression in the central part of the protoconch surface: Anistratenko & Anistratenko, 2007) whereas the protoconch in all studied *Boreoblinia* specimens has no expressed sculpture, wrinkles or other specific ornamentation or pit on its surface.

The specimens from the studied material generally correspond well to the original description of *Patella compressiuscala* (Karsten 1849). Unfortunately, the original description contains no illustration, whereas the shape, proportions and ornament of specimens of this species, described and illustrated by Janssen (1984, 121, pl. 44, fig. 2a-2c), correspond fully to the "*compressiuscala*" specimens studied here. Due to corrosion, the protoconch-teleoconch transition is sometimes not clearly visible even in SEM images of adult specimens. Morphologically, specimens from the Chattian "Sternberger Gestein" are almost indistinguishable from the Langhian specimens and they should be considered as a single species with a stratigraphic range of at least 25 -15 Ma. There are other species known which have been living as long as this species – many modern taxa in the Mediterranean and Atlantic persist from the Late Miocene or even Oligocene (*e.g., Cocculina rathbuni* Dall, 1882; *Epitonium clathrus* (Linnaeus, 1758), *Bittium reticulatum* (Da Costa, 1778), *Cerithium vulgatum* Bruguière, 1792, *Alvania montagui* (Payraudeau, 1826)).

Stratigraphic and geographic range — This species has been recorded in fully-marine deposits of the North Sea Basin from Late Oligocene (Chattian) until Early Serravallian, where it occurs mostly in low numbers (*e.g.*, Karsten, 1849; Janssen, 1984).

Palaeoecological implications

As it is suggested, the modifications in protoconch morphology of the Badenian/Sarmatian lottiids from a planktotrophic to a lecithotrophic one, could have been triggered by decreasing salinities of the water (Anistratenko *et al.*, 2006; Anistratenko & Anistratenko, 2007). What was a key reason for the change in ontogenetic strategy occurring in the Late-Oligocene in fully marine circumstances in the North Sea Basin?

It is possible, that already in the Early-Oligocene predessesors of *Boreoblinia* existed with the same type of protoconch. However that only puts the problem further back in time. One of the possible reasons could be, that properties of bottom waters changed during the Oligocene, caused by changes in the palaeogeography, also influenced by the development of a stronger seasonality. Was it really an independent development in the North Sea Basin, that was repeated during the Sarmatian of the Paratethys, or is there a possibility, that these groups could have a common development?

The time-gap between the last occurrence of *Boreoblinia compressiuscala* and the first occurrence of patellogastropods with a pancake-like protoconch in the Paratethys (*Blinia, Flexitectura* and *Squamitectura*), suggest there is no direct relation between both developments. But it seems possible that there existed a, perhaps short-lived, connection between the North Sea Basin and the Paratethys during the Middle-Miocene highstand along the southern border of Poland, of which the deposits have been removed by subsequent uplift and erosion. In that case, there is a possible closer relationship between *Blinia, Flexitectura* and *Boreoblinia*, and the time-gap becomes artificial. Unfortunately no paleogeographic evidence is known for such a connection yet. On the other hand it could be hypothesized that a faunal interchange between mentioned basins existed earlier, *e.g.* during the Late-Oligocene (Chattian) since the main connection of the Paratethys with the open sea was in the west, towards the North Sea Basin (*e.g.* Báldi, 1986; Popov *et al.,* 2004). In this case forerunners of the Badenian "*Tectura*" *zboroviensis* and Sarmatian *Blinia* probably branched off from a common ancestor of *Boreoblinia* and immigrated into the Paratethyan Basin. And the resemblance in structure of the shell in *Boreoblinia, Blinia* and "*Tectura*" *zboroviensis* seems to support this idea.

Acknowledgements

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