A new genus of patellogastropod with unusual protoconch from Miocene of Paratethys

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The protoconch and teleoconch morphology of *"Tectura" angulata*, *"Tectura" pseudolaevigata* from the Sarmatian and *"Tectura" zboroviensis* from the Badenian of the Eastern Paratethys have been studied in detail for the first time. The new genus *Blinia* is established for Sarmatian species which are characterized by a protoconch indicative of lecithotrophic type of early development lacking even a short free-swimming larval stage. In contrary the protoconch of Badenian *"Tectura" zboroviensis* demonstrates features of the shell typical for planktonic larva. The shape and proportions of a pancake-like protoconch in *Blinia* species suggest the development of young snails in brood pouch in the mantle cavity of maternal individual. The independence of *Blinia* gen. nov. from other Patellogastropoda such as *Tectura*, *Patella*, and *Helcion* is supported also by characteristics of shell structure. Typical patellogastropod protoconchs are present in the Badenian and the first half of the early Sarmatian and the protoconchs indicating lecithotrophic development are observed in patellogastropods only from the younger half of early Sarmatian and middle Sarmatian deposits. The change in ontogenetic strategy occurred during time of lowered salinity in the Paratethys. We suggest that the snails' reproductive strategy was modified and free larval life was suppressed to cope with salinity change in the ambient water.

Key words: Patellogastropoda, *Tectura*, protoconch morphology, ontogeny, Sarmatian, Paratethys.

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Introduction

Miocene patellogastropods of the Paratethys have been classified in different families, such as Patellidae Rafinesque, 1815, Acmaeidae Carpenter, 1857, or Tecturidae Gray, 1847. These snails represent not abundantly occurring but widely distributed components of the Miocene gastropod fauna of the Paratethys and they were subject of extensive studies by several authors (Eichwald 1853; Sinzov 1892; Friedberg 1911–1928; Kolesnikov 1935; Zhizhchenko 1936; Jekelius 1944; Bałuk 1975; Anistratenko 2000a, b, 2001). Small, *Patella*-like species of Badenian to Sarmatian age have usually been attributed to the genus *Tectura* Gray, 1847 or *Acmaea* Eschscholtz in Rathke, 1833 of which representatives were widespread both in the Central and Eastern Paratethys (e.g., Strausz 1966; Švagrovský 1971; Il'ina 1993; Anistratenko 2000a; Harzhauser and Kowalke 2002). Identification of these species is sometimes difficult because the limits of their morphological diversity and the range of variation are not sharply defined yet (e.g., Anistratenko 2000a, b). Few data on protoconch morphology and type of early development of these gastropods have been obtained so far. Living representatives can be distinguished by features of anatomy, the form and arrangement of the teeth in the radula, the features of the respiratory structures and of the shape and arrangement of pallial tentacles (e.g., Ponder and Lindberg 1997; Lindberg 1998). These characters are not available in the fossil species and only their shells can be compared with those of the living species, though muscle scars can be used to reconstruct some anatomical aspects.

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; Riedel 1993; Kaim 2004). The characters of embryonic, larval, and juvenile shells can be used to reconstruct the phylogeny of some gastropods. In case of the patellogastropods the protoconch can reveal the size of the eggs and the mode of embryonic development, e.g., the presence of a free swimming larva. Larval shells of patellogastropods (and vetigastropods) differ significantly from larval shells of remaining marine gastropods, since their veligers do not feed in the plankton. Study of shell structure also is considered helpful in interpretation of systematic relationship among Patellogastropoda (e.g., Bandel 1982).

We present new data on the protoconch and teleoconch morphology of two Sarmatian and one Badenian *Patella*-like species that inhabited the Eastern Paratethys. An unusual type of protoconch, which indicates a lecithotrophic type of

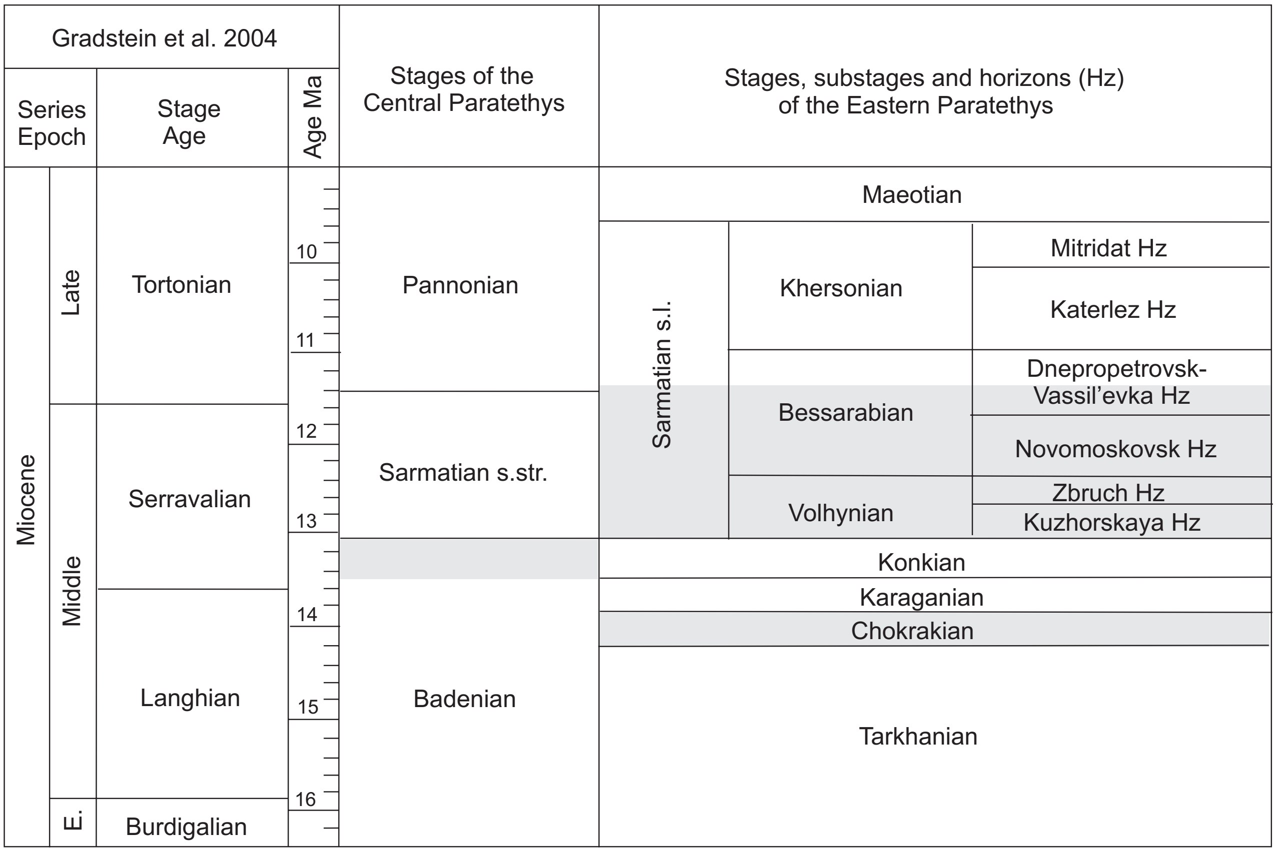


Fig. 1. Stratigraphic correlation chart of the standard scale with the Central Paratethys and the Eastern Paratethys (after Rögl 1988). The oldest horizon from which study material in East Paratethys came from is indicated with lower grey belt; the upper one shows youngest strata in East Paratethys (Sarmatian); the middle belt indicates the Central Paratethyan strata (Varovtsy locality). E., Early.

early development, has been discovered in at least two species of Sarmatian *"Tectura"*; for these species a new genus name *Blinia* is proposed.

The protoconch indicative of planktonic development was common among the limpet-like patellogastropods of the Miocene Paratethys Basin. We recorded this type of early ontogeny in "*Tectura*" *zboroviensis* Friedberg, 1928 from the Badenian of Western Ukraine and from the Chokrakian of Kerch Peninsula of the Crimea.

We also present and discuss new data on shell structure of the studied species. Analysis of shell variability, species distribution, their relationships, taxonomy and nomenclatural problems of the other Miocene "*Tectura*" will be discussed elsewhere. Nevertheless, a few notes should be presented here. We examined more than forty specimens and the limits of dimensions' variability and shape of shell's apical part are rather restricted. The protoconch in *Blinia* can be smooth with or without pit and wrinkled with or without pit. No specific characters in this regard have been observed.

We provisionally accept here the genus name *Tectura* Gray, 1847 (based on *Patella virginea* Müller, 1776 from Northern Atlantic) as a valid generic name for the Badenian and early Sarmatian limpets that have the typical patellogastropod-like protoconch morphology as characterized by Bandel (1982).

Material and methods

Our study is based on material collected by the authors from several natural outcrops of early to middle Sarmatian and Chokrakian (correlated with middle Badenian in the Central Paratethys) deposits in West and South Ukraine and the Kerch Peninsula (Crimea) between 1996 and 2004 (Figs. 1, 2). Also several specimens were used from the collection of the late Dr. Valentin Ya. Didkovski; they were collected in the 1980s from the Badenian of the Varovtsy locality in West Ukraine (Fig. 2). Altogether more than 300 specimens of "*Tectura*" are identified in these materials. Shells from the Romanian locality Soceni (Banat) from our own collections obtained in 2003 aided in understanding the data of Jekelius (1944) for the Sarmatian deposits from that locality.

Adult shell characters were studied with an optical stereomicroscope. Standard dimensions for shell characters were used. Morphological features of protoconchs were examined with aid of the scanning electron microscope (SEM) with special reference to shape, size, sculpture, and character of boundary with the teleoconch. At least ten specimens of each species were observed and documented. Several specimens were broken for SEM examination of the shell microstructure and its composition. The analysis of shell structure was

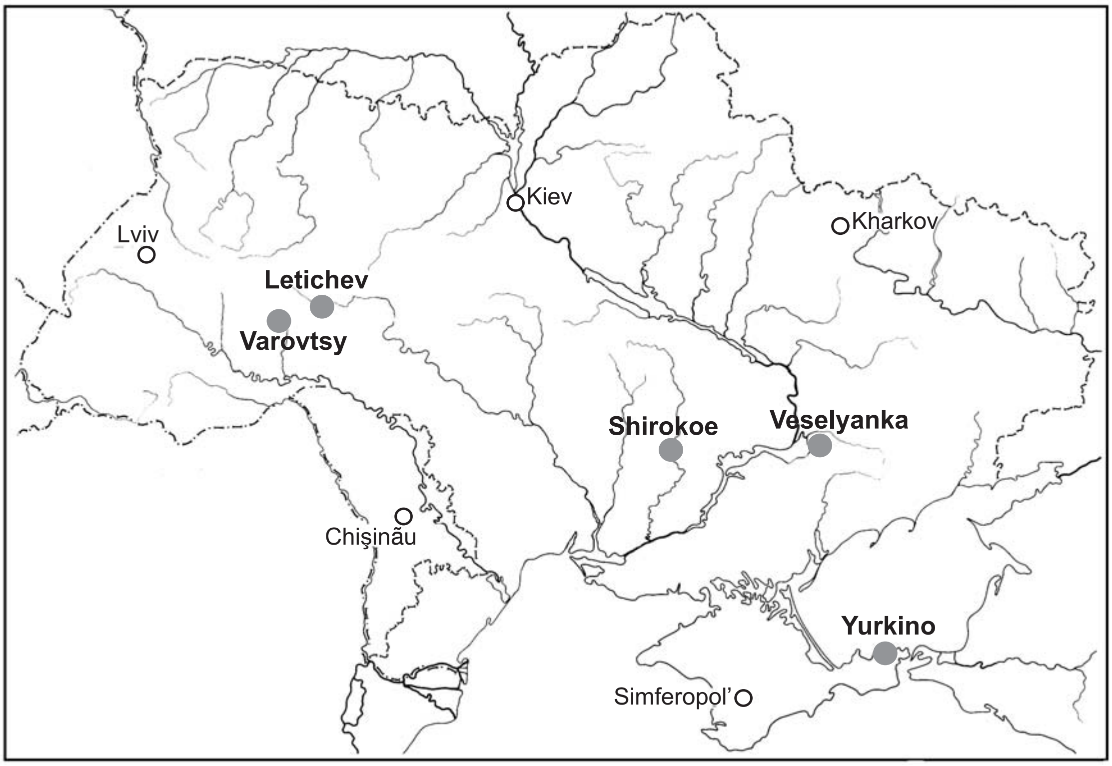


Fig. 2. *Blinia*-bearing localities in west and south Ukraine and in Crimea. Varovtsy, outcrop in the vicinity of Varovtsy village, Gorodok district, Khmelnitsky region (late Badenian); Letichev, quarry 1.5 km NE of Letichev town, Khmelnitsky region (middle Sarmatian); Shirokoe, outcrop in the vicinity of Shirokoe village about 35 km SW of Krivoyi Rog town, Dnepropetrovsk region (Zbruchian horizon of early Sarmatian); Veselyanka, outcrop near Veselyanka village, Zaporozh'e region (Kuzhorian horizon of early Sarmatian); Yurkino, outcrop in the vicinity of Yurkino village about 15 km NW of town Kerch (Crimea) (Chokrakian).

done by X-ray analysis and morphological comparison of the ultratructure is based on the study by Bandel and Geldmacher (1996).

The SEM images were obtained in the Geological-Paleontological Institute and Museum of the University of Hamburg (Germany). Shells were mounted on stubs, sputter-coated with gold and then documented using the digital Scanning Electron Microscope LEO 1455 VP.

Institutional abbreviation.—All figured specimens are housed at the Institute of Geological Sciences National Academy of Sciences of the Ukraine (Kiev, Ukraine), abbreviated IGS NANU.

Systematic paleontology

Class Gastropoda Cuvier, 1797

Order Patellogastropoda Lindberg, 1986

Family uncertain

Genus *Blinia* nov.

Type species: *Helcion angulata* d'Orbigny, 1844 in Hommaire de Hell (1844): 470, table 4, figs. 13–15. Middle Sarmatian of Volhyno-Podolia and Kerch Peninsula (Kolesnikov 1935).

Derivation of the name: "Blin" is Russian for pancake, and the general shape of the protoconch of *Blinia* is like a pancake.

Diagnosis.—Conical, relatively small patellogastropods with the smooth or wrinkled "pancake"-like protoconch; ornament of axial ribs; aperture oval. The new genus differs from *Tectura* mainly in regard to the outer layer of the shell whereas the organization of the inner crossed lamellar layers in both taxa is more or less similar. The outer layer of the shell of *Blinia* is characterized by a simple type of aragonitic in construction crossed lamellar structure while *Tectura* has a calcitic one. *Blinia* differs from *Helcion* in the same characteristics of composition and structure of the outer layer as from *Tectura*, while the inner crossed lamellar layer is similar. From all other known patellogastropods *Blinia* differs by having a round "pancake"-like protoconch.

Description.—The shell is small to moderate in size, has a thin wall, and approximately conical shape without marginal slit, apical hole or internal septum. It measures up to 13.5 mm in length (exceptionally—up to 20 mm), up to 11 mm in width and up to 6.5 mm in height. The apex lies out of the center and is tilted forward or backward. The anterior end of the shell is narrower than its posterior end. The surface has numerous radiating ridges crossed by concentric lines, which lie usually parallel to the apertural plane.

The protoconch has round to oval "pancake"-like shape, is quite flat and measures from 0.13 mm to 0.16–0.18 mm in maximum diameter; the lesser diameter is up to 0.11–0.12

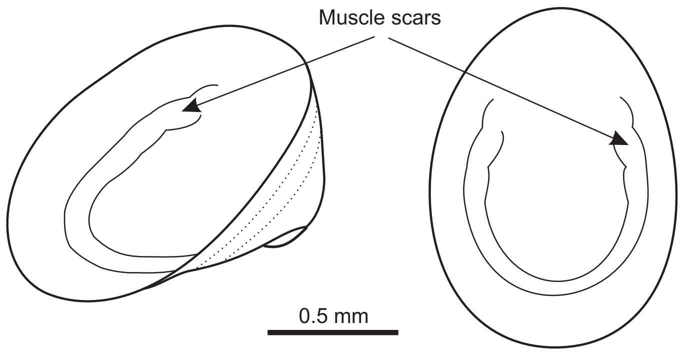


Fig. 3. A sketch drawing of the inner shell surface of *Blinia* sp. with muscle scars indicated by arrows. Specimen (IGS NANU 88/2004) from the middle Sarmatian of Letichev. Anterior edge of a shell is on the top.

mm. The protoconch surface is smooth or wrinkled; sometimes with a small pit on top of embryonic shell. The transition from the embryonic shell to the teleoconch is usually clearly marked by a constriction or a rim and change in ornament.

Discussion.—The more or less bulbous embryonic shell of *Blinia* species indicates a lecithotrophic type of early development and the absence of any short free-swimming larval stage following the yolk-rich embryogenesis. The young started its independent life as a crawling animal. The shape and proportions of "pancake"-type of protoconch may suggest the brooding of young snails in the maternal adult individuals.

The new genus is established for at least two Sarmatian species, which have been usually attributed to *Tectura* or *Acmaea* (Acmaeidae). The teleoconch characteristics (rather than the shell structure, see below) support a relationship of *Blinia* with those two genera.

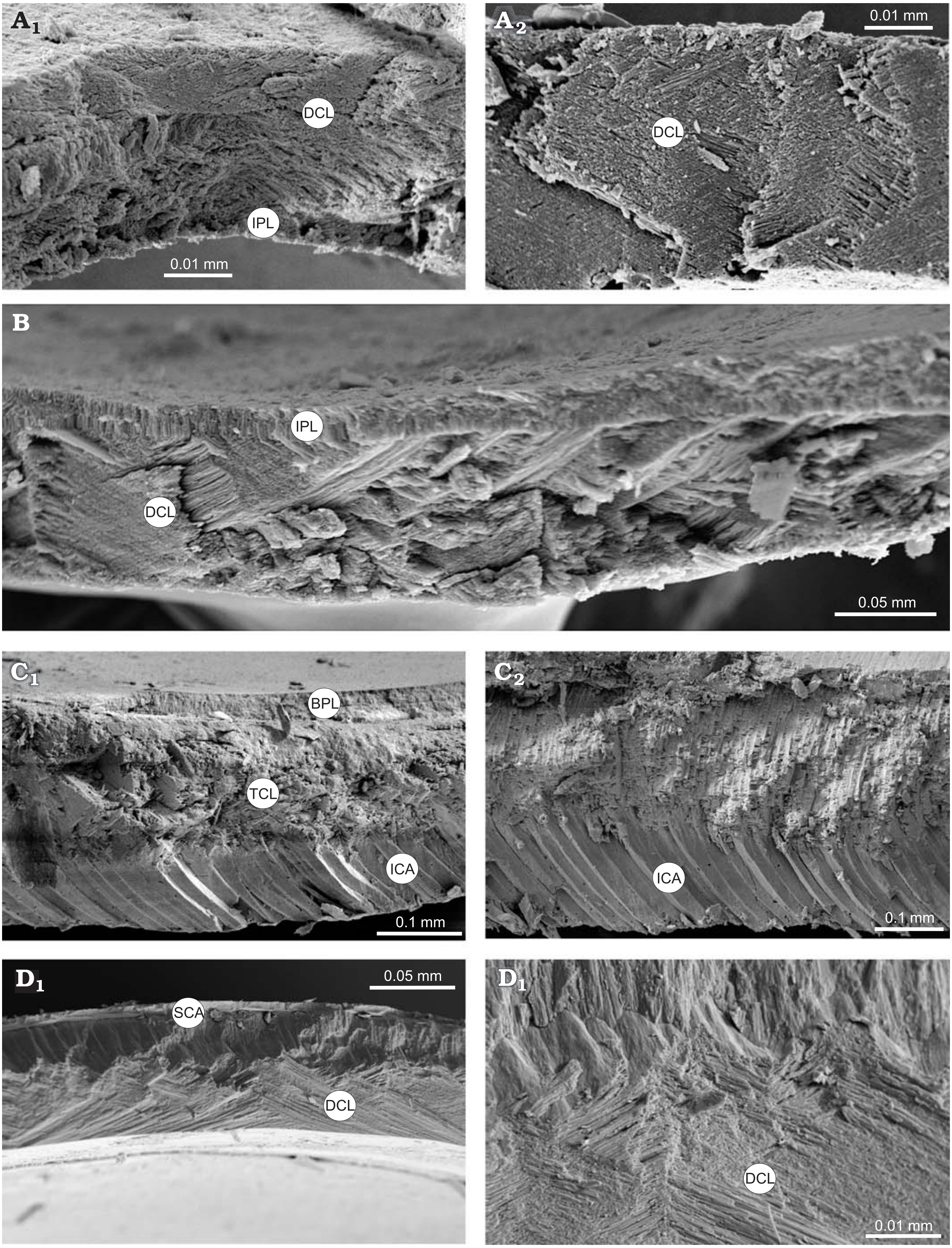
The shell shape and the muscle scars of *Blinia* resemble those known among patellogastropods (Lindberg 1998). The imprints on the inner surface of the shell of *Blinia*, we interpret as the muscle scars, are horseshoe-like, gently expressive tracts (Fig. 3). The impressions were not SEM-documented as they appear usually as regions of different shade that is not recognizable after coating of the specimens. In some cases even under the light microscope it is difficult to recognize whether the edge of these horseshoe-shaped scares is opened. At the same time their protoconch morphology indicates a clearly lecithotrophic embryonic development and suggest that they should be considered an independent genus. Moreover, the position of apex in some representatives of *Blinia* is quite distinctive. In contrast to a forward-tilted apex in *Patella*, *Acmaea*, *Tectura*, and majority of other patellids, some *Blinia* (e.g., *Blinia pseudolaevigata*) have an apex that is tilted backwards, as in *Propilidium ancyloides* (Forbes, 1840) (Lepetidae) and also in the slit bearing *Emarginula* Lamarck, 1801 (Fissurellidae). The family assignment of *Blinia* is uncertain. Comparison with other Patellogastropoda and *Patella*-like gastropods as a whole indicates that general shape and morphology of a protoconch may tell us practically nothing about systematic position. Ornamentation can rarely help in this respect, but shape and size of the protoconch can indicate the size of the eggs and the mode of embryonic development (Bandel 1982).

The shell structure of *Blinia* is characterized by a composition predominated by a simple type of crossed lamellar structure (Fig. 4A). Such aragonitic crossed lamellae are known from the oldest well preserved patellid species *Scutellastraea costulata* (Münster, 1841) from the Triassic St Cassian Formation of the Alps and could also be found in a patellogastropod species of very similar shape from the Paleocene of Alabama (Hedegaard et al. 1997; personal observations). The outer layer of the *Blinia* shell is thin and porous, and also aragonitic in construction. That distinguishes *Blinia* clearly from *Patella* and its relatives, which have a calcitic outer layer, usually quite thick and commonly with rather complex structure (Bandel and Geldmacher 1996). In case of *Blinia* 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, giving in perpendicular section an almost spherulitic appearance.

The shell structure (see Fig. 4) of *Blinia pseudolaevigata* is similar to that of *"Tectura" zboroviensis* but differs substantially from that of *Patella virginea* Müller, 1776 (type species of *Tectura*) and from *Helcion pellucidus* (Linnaeus, 1758) of the family Patellidae. *Tectura* as well as *Helcion* have a calcitic outer layer of the shell of characteristic layered structure that is absent in *Blinia* and "*Tectura*" *zboroviensis*.

In *Tectura virginea* (Müller, 1776) from the North Sea shell structure is quite different from that of *Blinia*. The outer shell layer is formed by a calcitic layer of coarse inclined prismatic appearance of its elements (Fig. 4C). The inner crossed lamellar layer is well organized in lamellae of first, second, and third order, with needles of the first order usually not intersecting. The shell of *Helcion pellucidus* (Linnaeus, 1758) from holdfasts on brown algae of the intertidal zone of the Bretagne (France) also has a thick outer layer composed of inclined sheets, massive in the outermost layer and spherulitic below (Fig. 4D). The crossed lamellar layer forming

Fig. 4. The shell structure of patellogastropods discussed in the text. **A**. *Blinia* sp. Specimen (IGS NANU, 34/2004) from the middle Sarmatian of Letichev. → Longitudinal section (A_1) showing the dissected aragonitic crossed lamellar structure (DCL) and inner prismatic layer (IPL) and (A_2) magnification of the dissected aragonitic crossed lamellar structure (DCL). **B**. *Tectura zboroviensis* (Friedberg, 1928). Specimen (IGS NANU, 19/2003) from the Chokrakian of Yurkino reveals basically the same composition with inner prismatic layer (IPL) and crossed lamellar layer (DCL). **C**. *Tectura virginea* (Müller, 1776). Modern specimen from the North Sea, Doggerbank, Germany (private collection of Dr. Jens Hartmann) shows (C_1) developed inner shell layer as aragonitic basal prismatic layer (BPL), middle shell layer composed of transversally fractured, well-developed, aragonitic crossed lamellar layer (TCL), and outer calcitic layer of inclined sheets (ICA) well visible at higher magnifications (C_2). **D**. *Helcion pellucidus* (Linnaeus, 1758). Modern specimen from the North Sea (collection of Prof. Klaus Bandel). Sections (D_1 and D_2) show the calcitic outer layer with structure of spherulitic shape (SCA) and the aragonitic dissected crossed lamellar layer (DCL) better visible at higher magnifications (D_2).


A1
DCL
IPL
0.01 mm
A2
0.01 mm
DCL
B
IPL
DCL
0.05 mm
C1
BPL
TCL
ICA
0.1 mm
C2
ICA
0.1 mm
D1
0.05 mm
SCA
DCL
D1
DCL
0.01 mm

most of the inner shell is similar to that of *Blinia* with crossed lamellae intersecting the individual needles.

The combination of features of the shell layers in *Blinia* closely resembles that of a patellogastropod limpet of similar shell morphology from the Paleocene of Alabama (personal observations by KB), but that species has a typical patellid protoconch, resembling that of *Tectura zboroviensis* described here.

Descriptions and illustrations of all species studied viz. *Blinia angulata* (d'Orbigny, 1844), *Blinia pseudolaevigata* (Sinzov, 1892), and *Tectura zboroviensis* (Friedberg, 1928) are presented below to demonstrate the differences between their protoconchs and corresponding inferred types of early ontogeny.

Blinia angulata (d'Orbigny in Hommaire de Hell, 1844)

Fig. 5A.

1844 *Helcion angulata* sp. nov.; d'Orbigny in Hommaire de Hell 1844: 470, pl. 4: 13–15.

1935 *Acmaea angulata* (d'Orbigny, 1844); Kolesnikov 1935: 128–129, pl. 19: 12–15.

2000 *Tectura* (*Tectura*) *angulata* (d'Orbigny, 1844); Anistratenko 2000a: 33–39, pl. 2: 1a, 1b.

Type material: Repository unknown.

Material.—Twenty one specimens from middle Sarmatian of Letichev locality (IGS NANU 1/2004–17/2004), and lower Sarmatian of Shirokoe locality (IGS NANU 1/1999– 4/1999), Ukraine.

Description.—The shell is moderate in size, thin, low conical in lateral profile and oval to egg-shaped in dorsal view. The apex is subcentral, somewhat tilted forwards. The apical angle measured in anterior view varies from 120° to 140°. Posterior and anterior slopes are straight or slightly convex. Sculpture consists of numerous, weak but clearly visible radial ribs crossed by concentric lines of growth. The outer, thin, sculptured layer of a shell is often peeled off, and in that case the surface of teleoconch appears to be totally smooth. The aperture is egg-shaped to broadly oval.

The protoconch is round to oval, pancake-like, almost flat and smooth. The greater diameter of the embryonic shell (i.e., "pancake") measures about 0.16 mm; symmetrically located in the sagittal axis of the teleoconch. The protoconch-teleoconch transition is usually sharp, marked by a clear constriction or rim.

Dimensions.—Length of shell (of material studied)—up to 13.5 mm; width of shell—up to 11.0 mm; height of shell—up to 6.5 mm.

Discussion.—*Blinia angulata* differs from *Blinia pseudolaevigata* by having a larger and relatively lower shell with a somewhat mammillated apex.

Stratigraphic and geographic range.—This species represents the most abundant and widespread *Blinia* species in Sarmatian deposits of the Eastern Paratethys (d'Orbigny in Hommaire de Hell 1844; Sinzov 1892; Friedberg 1911–1928; Kolesnikov 1935; Anistratenko 2000a).

Blinia pseudolaevigata (Sinzov, 1892)

Fig. 5B.

1892 *Acmaea pseudolaevigata* sp. nov.; Sinzov 1892: 63, pl. 3: 11–12.

1935 *Acmaea pseudolaevigata* (Sinzov, 1892); Kolesnikov 1935: 128, pl. : 8–11.

1944 *Acmaea soceni* sp. nov.; Jekelius 1944: 42, pl. 2: 4–6 [partim, non figs. 1–3].

2000 *Tectura pseudolaevigata* (Sinzov, 1892); Anistratenko 2000a: 33–39, pl. 2: 4a–4d.

Type material: The type material is not present in the collection of Museum of Odessa University where it was deposited by Sinzov (1892) and most probably lost.

Material.—Forty five specimens from middle Sarmatian of Letichev locality (IGS NANU 41/2004–60/2004) and lower Sarmatian of Shirokoe locality (IGS NANU 32/1999–58/1999), Ukraine.

Description.—The shell is small, thin, relatively tall-conical in all lateral views, oval in dorsal view. The apex is subcentral, tilted well backward, thus of sometimes hook-like appearance. The apical angle in anterior view varies from 60° to 70°. The posterior slope is straight to slightly concave, the anterior slope usually somewhat convex. Sculpture consists of numerous, weak but clear radial ribs crossed by concentric lines of growth. The outer sculptured layer of a shell is usually peeled off so that the surface of teleoconch appears to be totally smooth. The aperture is moderately to broadly oval.

Specimens of *Blinia pseudolaevigata* from the middle Sarmatian of western Ukraine (Letichev) and the lower Sarmatian of southern Ukraine (Shirokoe) are characterized by round to oval pancake-like and almost flat protoconchs. The greater diameter of the embryonic shell (i.e., "pancake") measures about 0.13–0.15 mm; it is situated symmetrically in the sagittal axis of the teleoconch. The surface of a protoconch may be smooth or wrinkled. Some specimens have a small pit in the top of their embryonic shell. The protoconch—early teleoconch transition is usually sharp, marked by a well-developed constriction or rim (Fig. 5B$_3$).

Dimensions.—The shells studied measure up to 2.8 mm in length and up to 1.9–2.0 mm both in height and width. According to Kolesnikov (1935) the shells of *Blinia pseudolaevigata* can reach a larger size—up to 11.0 mm in length, 8.0 mm in width and 7.0 mm in height.

Discussion.—*Blinia angulata* differs by a lower shell and no backward tilt of the apex.

Two specimens of, perhaps, *Blinia pseudolaevigata* under the name *Acmaea soceni* Jekelius, 1944 have also been recorded by Harzhauser and Kowalke (2002: 62, pl. 12: 1–3) from the Sarmatian of St. Margarethen in the Vienna Basin (*Potamides disjunctus* assemblage). The authors reported that the protoconch of the shell illustrated is separated from the teleoconch by a marked constriction and measures 0.3 mm in height (rather in diameter as shown by the figures and scale bar). Unfortunately the actual protoconch is not well preserved in their samples and can be identified with our material of *Blinia pseudolaevigata* with

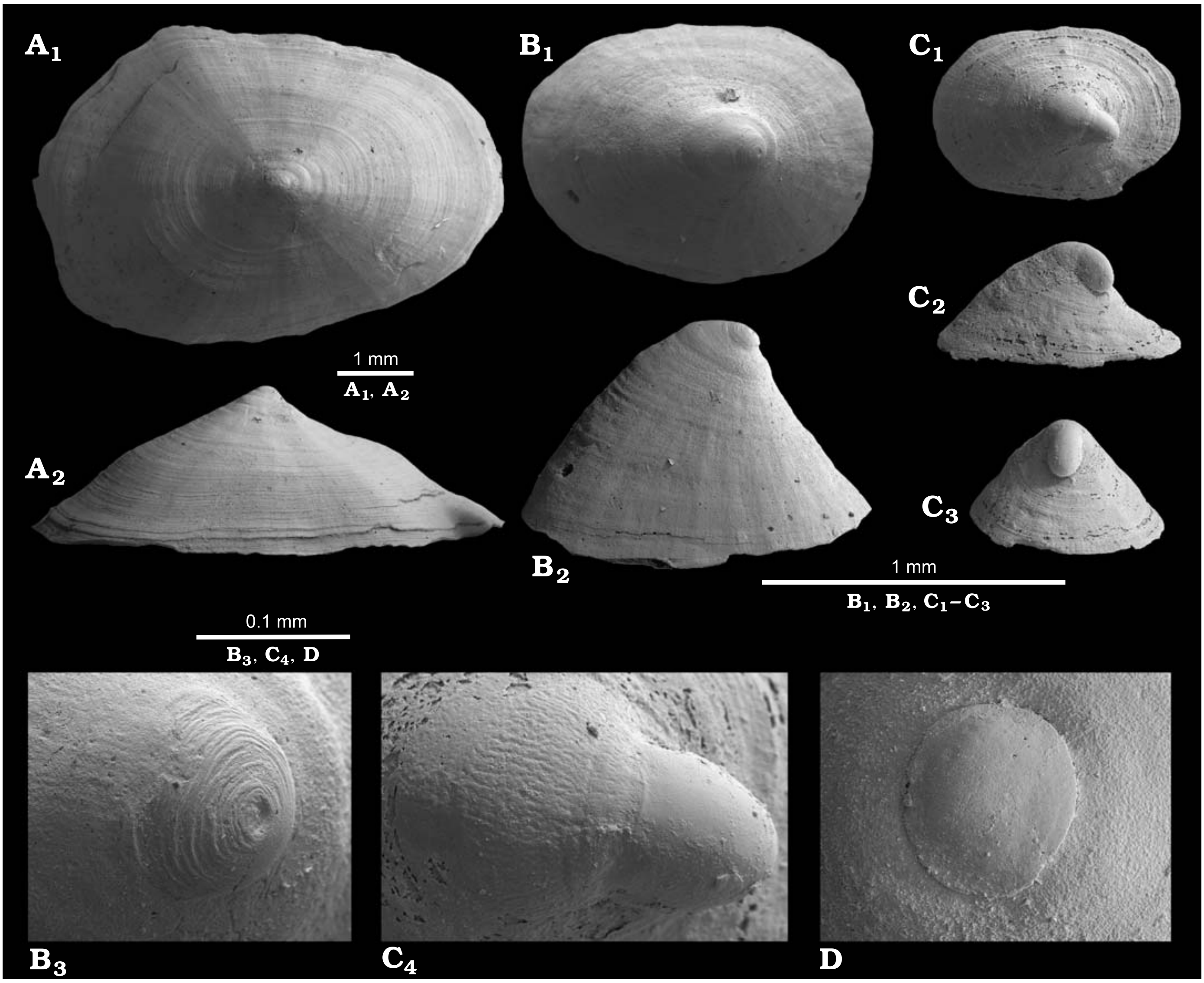


Fig. 5. *Blinia* gen. nov. and *Tectura* Gray, 1847 from Miocene of Ukraine. **A**. *Blinia angulata* (d'Orbigny, 1844). Specimen (IGS NANU 1/2004) from the middle Sarmatian of Letichev, apical view (A_1). Lateral view of the same specimen (A_2). **B**. *Blinia pseudolaevigata* (Sinzov, 1892). Specimen (IGS NANU 41/2004) from the middle Sarmatian of Letichev, apical view (B_1). Lateral view of the same specimen (B_2). Detailed apical view of the embryonic shell and juvenile teleoconch of the same specimen as in B_1 (B_3). The embryonic shell is ornamented by fine concentric wrinkles and pit on the apex. **C**. *Tectura zboroviensis* (Friedberg, 1928). Specimen (IGS NANU 18/2003) from the Chokrakian of Yurkino, apical view (C_1). Lateral and frontal views of the same specimen (C_2, C_3). Detailed apical view of the embryonic shell and juvenile teleoconch of the same specimen as in C_1 (C_4). The onset of juvenile teleoconch is ornamented by fine spiral threads. **D**. *Blinia* sp. Specimen (IGS NANU 4/2004) from the middle Sarmatian of Letichev. Detailed apical view of the embryonic shell and juvenile teleoconch.

some doubts only. Moreover the dimensions of *Blinia* protoconchs in our material are smaller. Likewise the specimen of *Acmaea soceni* illustrated by Jekelius (1944) appears slightly higher in lateral view than that illustrated by Harzhauser and Kowalke (2002). Protoconchs of *Acmaea soceni* collected from the same locality as those described by Jekelius (1944) were documented. They are of the type as in *Blinia* and therefore *Acmaea soceni* is considered here as *Blinia pseudolaevigata*.

Stratigraphic and geographic range.—*Blinia pseudolaevigata* is a typical (in some localities abundant) and widespread species of early and middle Sarmatian sediments of the Eastern Paratethys viz. Ukraine, Moldova, Romania, Central Sub-Caucasus to the Central Paratethys and its eastern shore at Soceni in Romania (Kolesnikov 1935; Jekelius 1944; Anistratenko 2000a). It also perhaps is found in synchronous deposits of the western Central Paratethys (e.g., Švagrovský 1971; Harzhauser and Kowalke 2002).

Tectura zboroviensis Friedberg, 1928

Fig. 5C.

1928 *Tectura zboroviensis* sp. nov.; Friedberg 1928: 536, pl. 35: 8a, 8b.

Type material: Three specimens from the late Badenian of Zborów, Ukraine (Friedberg 1911–1928). The material is stored in the Geological Museum of the Institute of Geological Sciences PAS (Kraków, Poland).

Material.—Sixteen specimens from the Chokrakian of Yurkino locality (IGS NANU 18/2003–34/2003); seventeen specimens from the late Badenian of Varovtsy locality (IGS NANU 1/1980–17/1980); nine specimens apparently of this species have been found in early Sarmatian deposits of Veselyanka locality (IGS NANU 1/2003–17/2003), Ukraine.

Description.—Specimens of *Tectura zboroviensis* from the late Badenian of western Ukraine (Varovtsy) have a limpet-like moderately high shell. The apex in adult specimens is positioned almost centrally, but in juvenile individuals it is somewhat tilted backward, the apical angle (measured from the front view) varies about 70–80° in different specimens. Sculpture consists of numerous (up to 20) but rather fine radial ribs crossed by the growth lines. The outer sculptured layer is often peeled off and the surface of teleoconch in most adult individuals appears smooth. The aperture is broad oval (Fig. $5C_1$–C_3).

The studied specimens of *Tectura zboroviensis* from the Chokrakian of the Kerch region and early Sarmatian of the southern Ukraine (Veselyanka) are characterized by elongated, cup-shaped, ventrolaterally inflated protoconchs. They measure from 0.08 mm to 0.10 mm in length and about 0.10 mm in width, and are situated in an asymmetrical position relative to the sagittal axis of the teleoconch. The surface of the protoconch is smooth (Fig. $5C_4$). The transition from the embryonic shell to the early teleoconch is usually quite distinct, defined by a small constriction or by a rim of the aperture of the protoconch shell. This feature may have formed when the veliger was ready to settle for benthic life and begin construction of the teleoconch with adult sculpture. The later, relatively extended part of the juvenile teleoconch reaches up to 0.2 mm in width and is covered by fine lines parallel to the axis of the protoconch.

The protoconch shape, dimensions and proportions indicate indirect development including a free swimming, but non-feeding, veliger larva.

Dimensions.—The studied shells measure up to 2.8 mm in length, 1.8 mm in width and 1.3 mm in height. Friedberg (1928) has presented similar data for *Tectura zboroviensis* from the type locality (Zborov town, Lviv region, Ukraine): up to 2.6 mm in length, 2.0 mm in width and 1.5 mm in height.

Discussion.—Modern representatives of *Tectura* (sometimes included in *Acmaea*) from the Mediterranean Sea and from the North Atlantic are characterized by a protoconch morphology similar to *Tectura zboroviensis*. One specimen of *Tectura virginea* (Müller, 1776) from the Mediterranean Sea has been documented but not published yet by Anders Warén (Swedish Museum of Natural History, Stockholm) who kindly provided SEM photo of that specimen. This Recent form has nearly the same protoconch dimensions as *Tectura zboroviensis*, but it is distinguished by a more bulbous embryonic shell.

Stratigraphic and geographic range.—*Tectura zboroviensis* was originally described from the late Badenian of the Central Paratethys (Friedberg 1928). It was encountered recently in our material from Chokrakian of the Eastern Paratethys (coeval with middle Badenian of the Central Paratethys).

Bałuk (1975: 20–30, figs. 9, 10) documented *Acmaea (Tectura) friedbergi* Bałuk, 1975 from the Lower Badenian of Poland, and Strausz (1966) found *Acmaea* sp. from Hungary. But these authors noted that a more detailed comparison between these and others described forms or species is not possible. Judging from the similar shell shape and also their occurrence in beds of the same or similar stratigraphical age (that is Badenian) it is quite possible that *Acmaea friedbergi* represents a species with the same type of protoconch as *Tectura zboroviensis*.

Discussion and conclusions

The protoconch shape and structure found among species of the order Patellogastropoda (e.g., Patellidae, Acmaeidae, Lottiidae), and some Orthogastropoda (e.g., Cocculinidae and Lepetellidae) usually are typical of patellogastropods. All species of these limpets of which the protoconch has been illustrated apparently had planktonic development including a free living, but non-feeding larval stage (e.g., Bandel 1982; Sasaki 1998). Lecithotrophic development has not been known for the limpet gastropods of the Paratethys basin so far.

According to data obtained the small limpets (most commonly classified to *"Tectura"*) from the Chokrakian and late Badenian sediments in the Eastern Paratethys (Kerch and Varovtsy localities) have typical patellid protoconch morphology. Apparently they had a planktonic development including a free-swimming but non-feeding larval stage.

From the lower half of early Sarmatian sediments (Kuzhorskaya horizon, Veselyanka locality) forms with the same type of protoconch as in the Badenian have been noted. But in the second half of Early Sarmatian (Zbruchian horizon, Shirokoe locality) and in the middle Sarmatian there occur only forms with the flat pancake-like protoconch which suggests a lecithotrophic type of early development without even a very short free-swimming larval stage following the yolk-rich embryogenesis.

The protoconch of *Blinia* from the Middle Sarmatian has a unique, flat, cap-like and round outline compared with most known patellogastropods. A similar oval shield-like protoconch has been illustrated only by Sasaki (1998: fig. 21a–c) in the modern *Erginus moskalevi* (Golikov and Kussakin, 1972) of the Lottiidae Gray, 1840. This species is interpreted as brooding the young snails within the pallial cavity of the parent, but without indicating the exact site of their metamorphosis to miniature crawling limpets.

Only development with large evidently lecithotrophic eggs can result in a cap-like protoconch and a pancake-like shape (e.g., Bandel 1982). Shell mineralization is retarded until after the point of development when the shell becomes coiled. This occurs in patellogastropods usually at the end of embryonic development, and in case of species with a free swimming larval stage when they are ready to metamorphose to benthic life.

The shape and proportions of the “pancake”-type of protoconch in *Blinia angulata* and *B. pseudolaevigata* implies brooding of young snails in the shelter of the mantle cavity of the adult past embryonic and larval stages to the benthic, postlarval form.

Assemblages of the Eastern Paratethys in Badenian time have yielded abundant pectinids, echinoderms, calcareous algae and other taxa, indicating normal marine conditions. They indicate that the basin had wide connection with the open Ocean (e.g., Muzylev and Golovina 1987; Rögl 1998). On the contrary, the early Sarmatian basin had a very restricted connection with the open sea and developed into a brackish semi-marine basin with particular composition of saline (Kolesnikov 1935; Steininger 1963; Nevesskaya 1971; Nevesskaya et al. 1986; Roshka 1987; Goncharova 1989; Rögl 1998; Il’ina 1998; Anistratenko 2000a). During the middle Sarmatian the water of the basin was even less salty (no more than 15‰) than previously (e.g., Nevesskaya et al. 1986; Muzylev and Golovina 1987).

For gastropods of the Paratethys, the clearly lecithotrophic type of early ontogeny is now reported for the first time. It characterizes the limpet gastropods only from the late part of early Sarmatian and the whole middle Sarmatian. We suggest that this drastic change in the early development of *Blinia* from ancestors with the usual type of embryonic development and a free swimming larval stage not only coincided in time with decreased salinity but was actually triggered by this change of environmental conditions. Although we cannot present more direct evidence a similar phenomenon was also observed in the middle Sarmatian (versus Badenian) nassariids (Harzhauser and Kowalke 2004).

The discussed small patellogastropod limpet that probably lived on algae with round fronds, such as brown algae of the *Sargassum* type, reacted to the change in salinity by brooding its young instead of releasing eggs into the sea or egg masses from which veligers hatched. In this way a difficult time of early ontogeny was overcome and young hatched as more robust and larger individuals fit for life in a sea with variable environmental conditions. Life on at least periodically drifting brown algae could enable *Blinia* to live in most of the Paratethys Sea. This was apparently at least from the Vienna Basin, along the island chain of the Carpathians to the Kerch Island region. A model for the substrate preference of *Blinia* can be the living *Helcion*, which is usually found on brown algae in the eastern North Atlantic (Bandel 1982).

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