

# Minute patellogastropods (Mollusca, Lottiidae) from the Middle Miocene of Paratethys

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## ABSTRACT:

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The protoconch and teleoconch morphology of lottiid patellogastropods that inhabited the Central and Eastern Paratethys in the Badenian and Sarmatian are described and illustrated. Eleven species belonging to the genera *Tectura*, *Blinia*, *Flexitectura* and *Squamitectura* are considered as valid: *Tectura laevigata* (EICHWALD, 1830), *T. compressiuscula* (EICHWALD, 1830), *T. zboroviensis* FRIEDBERG, 1928, *T. incognita* FRIEDBERG, 1928, *Blinia angulata* (D'ORBIGNY, 1844), *B. pseudolaevigata* (SINZOV, 1892), *B. reussi* (SINZOV, 1892), *B. sinzovi* (KOLESNIKOV, 1935), *Flexitectura subcostata* (SINZOV, 1892), *F. tenuissima* (SINZOV, 1892), and *Squamitectura squamata* (O. ANISTRATENKO, 2001). The type material of species introduced by W. FRIEDBERG (1928) is revised and lectotypes are designated for *T. zboroviensis* and *T. incognita*. The taxonomic status and position of this group of species is discussed. Data on palaeogeographic and stratigraphic distribution, variability and the relationships of Middle Miocene Lottiidae GRAY, 1840 are presented.

**Key words:** Patellogastropoda, Lottiidae, *Tectura*, *Flexitectura*, *Blinia*, Shell morphology, Taxonomy, Miocene, Paratethys.

## INTRODUCTION

Minute patellogastropods, albeit not occurring abundantly, settled various shallow to deeper normal marine and brackish water habitats in the Badenian and Sarmatian of the Paratethys and were studied by many authors (e.g. EICHWALD

1830-1853; FRIEDBERG 1928; JEKELIUS 1944; KRACH 1951, 1981; STRAUZ 1966; ŠVAGROVSKÝ 1971; BAŁUK 1975; IL'INA 1993).

The small-shelled representatives of this group have usually been classified in different families, such as Patellidae RAFINESQUE, 1815, Acmaeidae CARPENTER, 1857 or Tecturidae

GRAY, 1847. Although the exact taxonomic attribution of the patellogastropods investigated here requires further confirmation we assign them provisionally to the family Lottiidae GRAY, 1840 (for more detailed discussion see below under "Taxonomy").

Over ten nominal species of these minute limpet gastropods are known from the Miocene of the Paratethys (e.g. ZHIZHCHEKO 1936; SIMIONESCU & BARBU 1940; IONESI & *al.* 2005); most of them were described from the eastern part of the basin, particularly from west and south Ukraine and Moldova (SINZOV 1892; KOLESNIKOV 1935; JEKELIUS 1944; ANISTRATENKO 2000a, b; 2001).

The identification of lottiid species is quite difficult because their range of variability is not yet sharply defined. Also, very few data on protoconch morphology and type of early development of these gastropods have been obtained so far (e.g. HARZHAUSER & KOWALKE 2002; ANISTRATENKO & *al.* 2006).

The additional complication with the taxonomy of fossil species is that they cannot be diagnosed by anatomical features, and only their shells can be compared with those of living species. On the other hand, muscle scars (if preserved, and observable) can be used to reconstruct some anatomical characters; some features of the protoconch can also be utilized as useful taxonomic characters, particularly in marine gastropods with a planktotrophic larva in their ontogeny (e.g. BANDEL 1982; RIEDEL 1993; KAIM 2004). 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. Study of shell microstructure characters is also considered helpful in the interpretation of systematic relationships, particularly among Patellogastropoda (e.g. MACCLINTOCK 1967; BANDEL 1982; PONDER & LINDBERG 1997).

Recently, based on the protoconch and teleoconch morphology of several "*Tectura*" from the Badenian and Sarmatian of the Paratethys, the new genus *Blinia* has been established for Sarmatian species (ANISTRATENKO & *al.* 2006). These species are characterized by an unusual "pancake"-like protoconch that indicates a lecithotrophic type of early development without even a very short free-swimming larval stage, whereas the Badenian "*Tectura*" demonstrates the

usual planktonic one. The independence of *Blinia* from other Patellogastropoda is also supported by differences in shell structure (for more details see below).

The present contribution aims to present additional data on the diversity, taxonomy and shell morphology of lottiids that inhabited the Central and Eastern Paratethys Seas in the Middle Miocene (Badenian and Sarmatian regional stages). Herein we describe in detail eleven recognized (i.e. considered as valid) species attributed to four genera and discuss the taxonomic position and status of these taxa. The available data on geographic and stratigraphic distribution, variability and the relationships of Middle Miocene Lottiidae are also provided and discussed.

## MATERIAL AND METHODS

The present study is based mainly on material collected by the authors from several natural outcrops of Early and Middle Sarmatian (Volhynian–Bessarabian substages) and Chokrakian (the latter stage of the Eastern Paratethys regional scale is correlated with the Middle Badenian in the Central Paratethys) deposits in west and south Ukraine and the Kerch Peninsula (Crimea) between 1996 and 2004 (Text-figs 1, 2). Several specimens were used from the collection of the late Dr. V. Ya. DIDKOVSKI, Institute of Geological Sciences NAS, Kiev (Ukraine); they were collected in the 1980s from the Badenian of the Varovtsy locality in west Ukraine (Text-fig. 2). A few specimens were discovered in a lot from the Early Sarmatian of Ślasków Mały, Poland, kindly provided by Dr. Ewa STWORZEWICZ, Institute of Systematics and Evolution of Animals PAS, Kraków (Poland). Altogether more than 300 specimens of lottiids are identified in these materials deposited at the Institute of Geological Sciences National Academy of Sciences of the Ukraine (Kiev, Ukraine).

Additional material came from large collections of Prof. W. FRIEDBERG, and Prof. W. KRACH housed in the Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków (Poland). The FRIEDBERG collection includes 52 specimens of "*Tectura*" shells from the Badenian and Early Sarmatian of eastern Poland and western Ukraine (Text-fig. 2), collected

between 1905 and the 1930s. The “*Tectura*” in this collection were attributed to four species of which two were described by FRIEDBERG (1928) as new. The material from the W. KRACH collection comprises 121 specimens of “*Acmaea*”, attributed originally to seven species, collected in 1936–1937 from the Badenian of eastern Poland and the Badenian and Sarmatian of western Ukraine (Text-fig. 2). The material of these collections formed the basis for the monographs of FRIEDBERG (1911–1928) and KRACH (1951, 1981) but has never been revised, in spite of the fact that the taxonomical approach and methodology used by malacologists at that time has long been obsolete (see Appendix).

Additionally, material in the large collections of Prof. I.F. SINZOV and Prof. V.P. KOLESNIKOV, housed in the Central Museum of VSEGEI, St.-Petersburg (Russia), has been examined, including the type series of six “*Acmaea*” species, described by these authors.

The shell characters were studied with an optical stereomicroscope and standard dimensions were measured. Additionally, the apical angle (measured from the frontal view) was used as a simple and easy measurable species-diagnostic parameter (Text-fig. 3).

Morphological features of protoconchs were examined with the aid of a scanning electron microscope (SEM) with special reference to shape, size, sculpture and character of the boundary with the teleoconch. No less than ten specimens of each species were observed and documented (except for *Tectura incognita*, which is represented by a few specimens only).

Most of 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”.

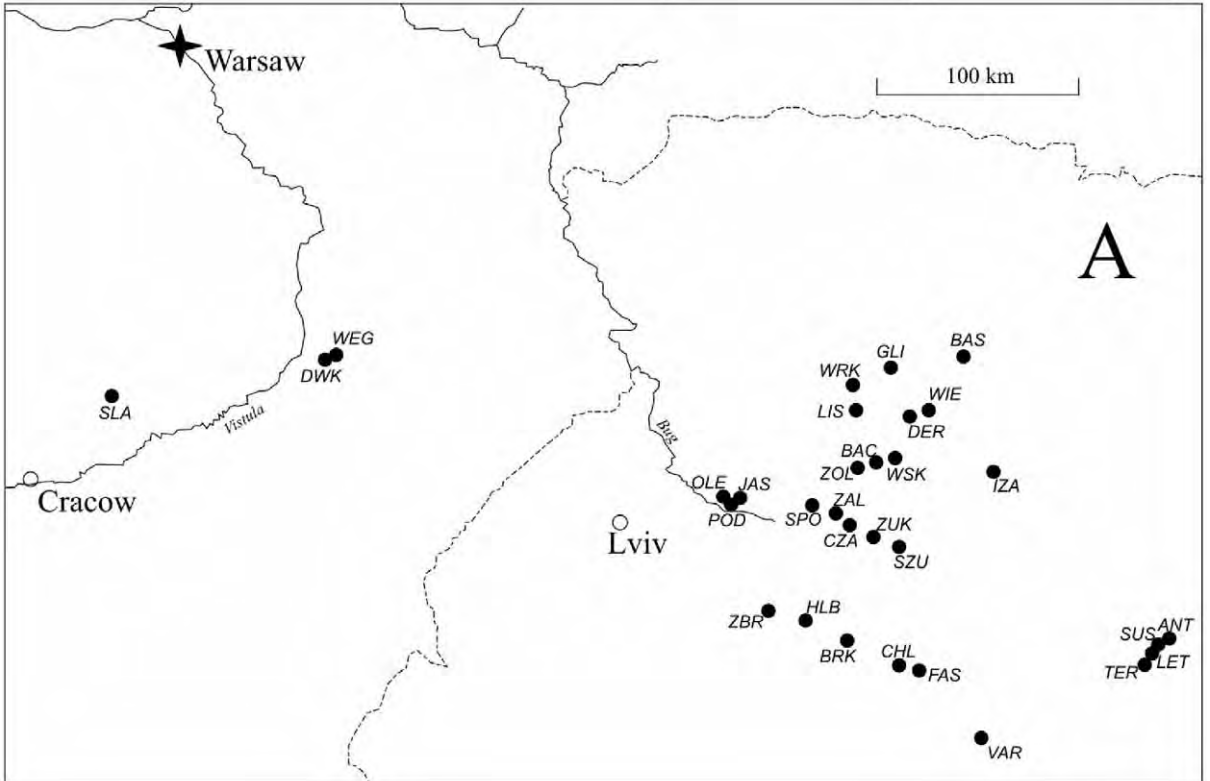
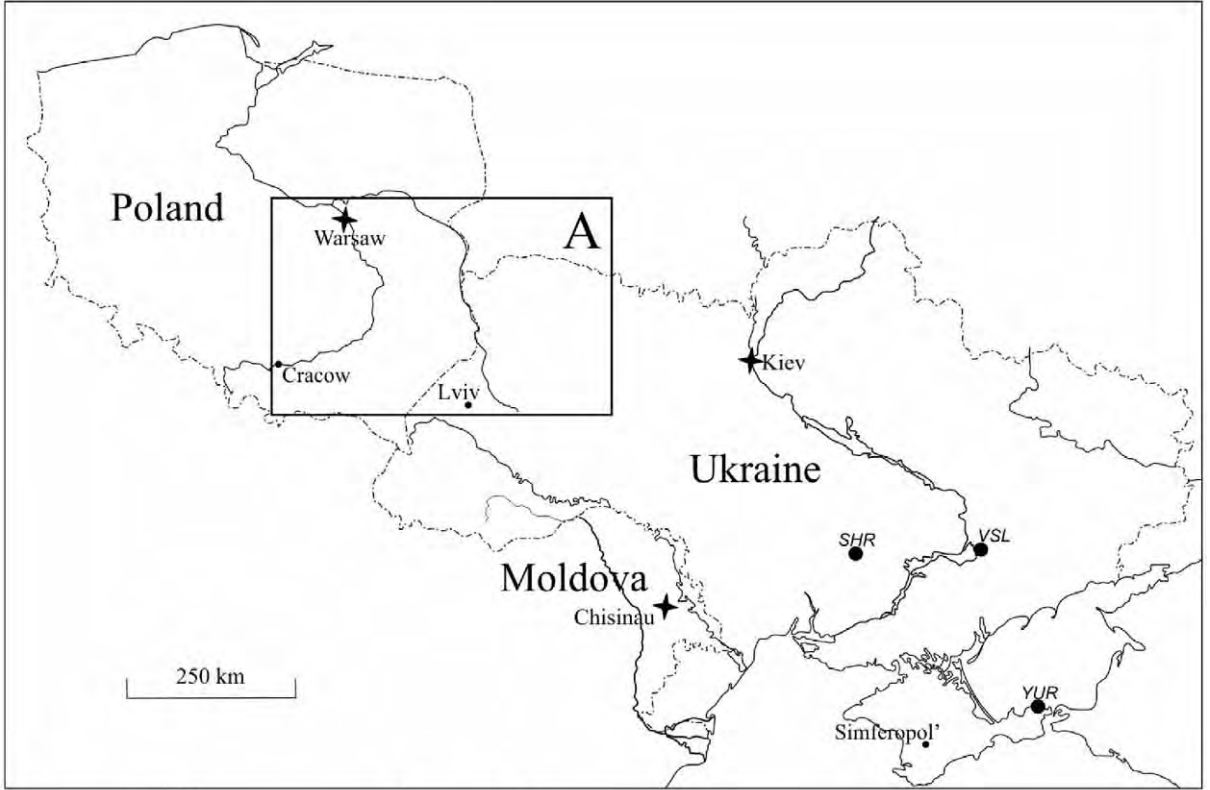
Some additional scanning electron micrographs

Gradstein et al. 2004			Central Paratethys Stages	Eastern Paratethys Stages, substages and horizons (Hz)		
Series	Epoch	Stage Age		Age Ma		
Miocene	Late	Tortonian	Pannonian	Sarmatian s.l.	Maeotian	
					Khersonian	Mitridat Hz
	Katerlez Hz					
	Serravalian	Sarmatian s.str.	Bessarabian		Dnepropetrovsk-Vassil'evka Hz	
					Novomoskovsk Hz	
	Middle	Langhian	Badenian		Volhynian	Zbruch Hz
				Kuzhorskaya Hz		
	E.	Burdigalian		Konkian		
				Karaganian		
				Chokrakian		
			Tarkhanian			

Fig. 1. Stratigraphical correlation chart of the standard scale with the Central Paratethys and the Eastern Paratethys (after RÖGL 1988). The horizons from which the study material came are indicated with grey belts

of specimens from FRIEDBERG's collection were performed in the Laboratory of Field Emission Scanning Electron Microscopy and Microanalysis, Institute of Geological Sciences, Jagiellonian

University, Kraków (Poland). Here the shells were mounted on stubs, coated with carbon and then photographed using a Hitachi S-4700 scanning electron microscope.



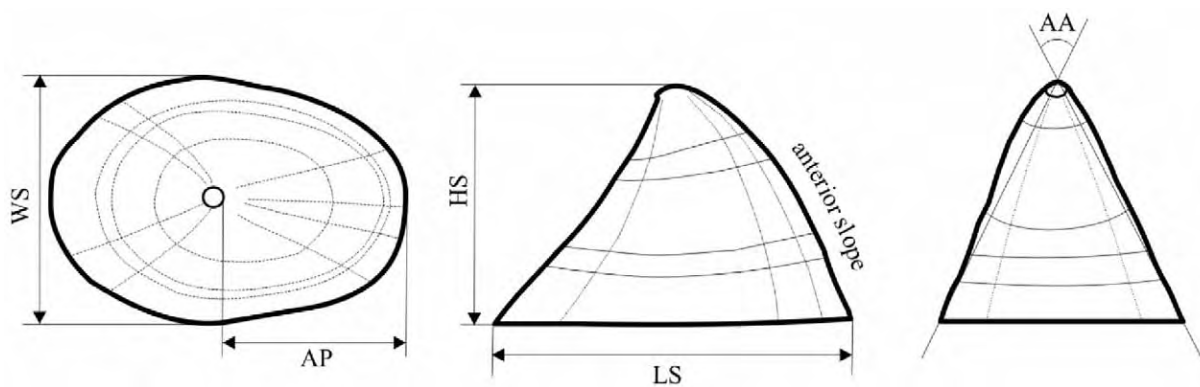


Fig. 3. A sketch of lottiid shell (schematic). See explanation for measurements in the “Abbreviations”

ABBREVIATIONS

Abbreviations and repositories:

IGS NANU – Institute of Geological Sciences, National Academy of Sciences of the Ukraine, Kiev (Ukraine).

ZNG PAN – Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków (Poland); the collection of Prof. W. FRIEDBERG is registered under the catalogue number A-I-50; the material of Dr. W. KRACH under the catalogue numbers A-I-87 and A-I-95.

Morphological terms for the shell description used in text (see Text-fig. 3): AA – apical angle; AP – apex position, i.e. distance of apex from frontal edge; AE – apex eccentricity, i.e. the AP/LS ratio, HS – height of shell, LS – length of shell, WS – width of shell, No – number of lots according to the Museum Catalogue.

NOMENCLATURAL NOTES AND TAXONOMY

We accept here the genus name *Tectura* GRAY, 1847 (based on *Patella virginea* O. F. MÜLLER, 1776 from the Northern Atlantic) as a valid name for the Badenian and Sarmatian lottiids that have the typical protoconch structure seen in *Patella virginea*. However, there is some uncertainty in this attribution since these Middle-Miocene “*Tectura*” differ substantially from *P. virginea* in having an aragonitic outer shell layer, whereas the latter has a calcitic one (also see below).

The majority of authors considered the name *Tectura* GRAY, 1847 either as a synonym of *Acmaea* ESCHSCHOLTZ in RATHKE, 1833 (*Acmaea* ESCHSCHOLTZ, 1828 is a nomen nudum), or as a subgenus of the genus *Acmaea* (e.g. KNIGHT & al. 1960; BAŁUK 1975). GOLIKOV & STAROBOGATOV (1975) considered *Tectura* as a separate genus and

Fig. 2. Localities in Poland and Ukraine mentioned in this paper, with abbreviations used (alphabetically). ANT – the Middle Sarmatian of Antonovka, Ukraine; BAC – the Sarmatian of Bakaj, Ukraine; BAS – the Middle Sarmatian of Baszyna, Ukraine; BRK – the Late Badenian of Borki Wielkie, Ukraine; CHL – the Early Sarmatian of Chlebów, Ukraine; CZA – the Sarmatian of Czajczyńce, Ukraine; DER – the Middle Sarmatian of Dermań, Ukraine; DWK – the Sarmatian of Dwikozy, Poland; FAS – the Late Badenian/Sarmatian of Faszczówka, Ukraine; GLI – the Sarmatian of Glińsk, Ukraine; HLB – the Late Badenian of Hluboczek Wielki, Ukraine; IZA – the Early/Middle Sarmatian of Iziaslav, Ukraine; JAS – the Late Badenian of Jasionów, Ukraine; LET – the Middle Sarmatian of Letichev, Ukraine; LIS – the Sarmatian of Listwin, Ukraine; OLE – the Late Badenian of Olesko, Ukraine; POD – the Late Badenian of Podhorce, Ukraine; TER – the Middle Sarmatian of Terlovka; SHR – the Early Sarmatian (Zbruchian horizon) of Shirokoe, Ukraine; SLA – the Early Sarmatian of Ślădków Mały, Poland; SPO – the Late Badenian of Stary Poczajów, Ukraine; SUS – the Early/Middle Sarmatian of Suslovtsy, Ukraine; SZU – the Late Badenian/Sarmatian of Szuszkowce, Ukraine; VAR – the Late Badenian of Varovtsy, Ukraine; VSL – the Early Sarmatian (Kuzhorian horizon) of Veselyanka, Ukraine; WEG – the Badenian of Węglińek, Poland; WIE – the Middle Sarmatian of Wierzchów, Ukraine; WOL – the Sarmatian of unknown location, Wołyń, Ukraine; WRK – the Middle Sarmatian of Warkowicze, Ukraine; WSK – the Sarmatian of Wańkowce, Ukraine; YUR – the Chokrakian of Yurkino, Crimea, Ukraine; ZAL – the Late Badenian/Sarmatian of Zalesce, Ukraine; ZBR – the Late Badenian of Zborów, Ukraine; ZOL – the Sarmatian of Żołobki, Ukraine; ZUK – the Late Badenian/Sarmatian of Żukowce, Ukraine

suggested using “Tecturidae GRAY, 1847” for the name of family instead “Acmaeidae CARPENTER, 1857” because the former has priority. Originally, we also attributed the species studied from the Sarmatian to the family Tecturidae (ANISTRATENKO 2000a, b; 2001) but, according to modern systematics, the genus *Tectura* belongs in the Acmaeoidea and the family Lottiidae (e.g. SASAKI 1998).

Recently, a new genus *Blinia* O. ANISTRATENKO, BANDEL & V. ANISTRATENKO, 2006, with a protoconch morphology unusual for patellogastropods, was described from the Sarmatian of the Paratethys. Originally the genus comprised two species and it was uncertain to which family it should be assigned (ANISTRATENKO & *al.* 2006). In the present investigation it was discovered that many Middle Miocene patellogastropods considered previously as *Tectura* or *Acmaea* (e.g. FRIEDBERG 1928; JEKELIUS 1944; KRACH 1951, 1981; HARZHAUSER & KOWALKE 2002; ANISTRATENKO 2000a, b; 2001) are actually characterised by the same type and morphology of protoconch as *Blinia*. Naturally all these species should be removed from the genus *Tectura*. This particularly concerns the representatives of the recently established subgenera *Tectura* (*Flexitectura*) and *Tectura* (*Squamitectura*) (ANISTRATENKO 2000a, 2001), which are considered here as taxa of generic rank. The species of the latter two genera differ from each other and from *Blinia* in the sculpture and/or shape of the teleoconch (see more detailed *Systematic palaeontology*).

The patellogastropods considered here are attributed to four genera: *Tectura*, *Blinia*, *Flexitectura* and *Squamitectura*.

The taxonomic position of *Tectura* species from the Badenian and *Blinia* (together with *Flexitectura* and *Squamitectura*) from the Sarmatian of the Paratethys is still quite a complicated problem. Theoretically, it is even questionable that these taxa belong to the order Patellogastropoda LINDBERG, 1986. This is because the species of e.g. *Blinia* lack two characteristics that are considered as important synapomorphies of Patellogastropoda. Patellogastropods share asymmetrical protoconch growth, while the protoconch of *Blinia* species is symmetrical; all patellogastropods have a calcitic outer shell layer (e.g. MACCLINTOCK 1967; LINDBERG 1988; PONDER & LINDBERG 1997), whereas the outer layer of *Blinia* is aragonitic. The same shell structure is possessed by *Tectura* (e.g. *T. zboroviensis*)

though the species of this genus have a typical patellogastropod protoconch (ANISTRATENKO & *al.* 2006).

In order to examine the taxonomic position and, in particular, the family assignment of the Middle Miocene patellogastropods discussed here, it is necessary to review details of the shell structure, and of the protoconch morphology in the context of early ontogeny.

### Shell microstructure characters and taxonomic position of the species studied

Within the patellogastropods some 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. In some taxa there may be as many as five distinct layers, excluding the myostracum (MACCLINTOCK 1967).

It was shown that e.g. Patellidae have both foliated and crossed-lamellar structures, whereas Lottiidae have shells with thin outer calcitic homogeneous layers underlain by aragonitic crossed-lamellar layers, similar to the pattern in the more derived gastropod clades (MACCLINTOCK 1967; LINDBERG 1988).

According to ANISTRATENKO & *al.* (2006), the shell of *Blinia* has predominantly a simple type of aragonitic crossed-lamellar structure. A similar structure is 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 (BANDEL 1982). The outer layer of the *Blinia* shell is thin and porous, and also aragonitic in composition. That distinguishes *Blinia* clearly from *Patella* and its relatives, which have a calcitic outer layer that is usually quite thick, with commonly a rather complex structure (BANDEL & GELDMACHER 1996). In the 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 an almost spherulitic appearance in perpendicular section.

The shell structure of *Blinia* is similar to that of *Tectura zboroviensis* (see ANISTRATENKO & *al.* 2006)

but differs substantially from that of *Patella virginea* (type species of *Tectura*) and from *Helcion pellucidus* (LINNAEUS, 1758) of the family Patellidae. Modern *Tectura* as well as *Helcion* have a calcitic outer shell layer with a characteristic layered structure that is apparently absent from *Blinia* and *Tectura zboroviensis*.

#### Reproduction, type of protoconch and early development

It is considered that, within the Gastropoda, ancestral taxa have external fertilization and pelagic, non-feeding larvae, whereas more derived taxa have internal fertilization, the addition of a non-pelagic phase (within the egg capsule or brood pouch), and feeding larvae (e.g. PONDER & LINDBERG 1997).

According to data of many authors (e.g. FRETTER & GRAHAM 1962; HICKMAN 1992) most patellogastropods and vetigastropods have pelagic development following external fertilization, but some derived representatives in both subclades have independently evolved copulatory structures and internal fertilization. Particularly striking examples of the latter case occurred (GOLIKOV & KUSSAKIN 1972) within the patellogastropod family Lottiidae.

The protoconch of *Blinia* (as well as of *Flexitectura* and *Squamitectura*) has an unusual “pancake”-like outline (from almost flat to hemispherical) compared with that of most known patellogastropods. The more or less bulbous embryonic shell of these species evidently indicates a lecithotrophic type of early development and the absence of even a very short free-swimming larval stage following the

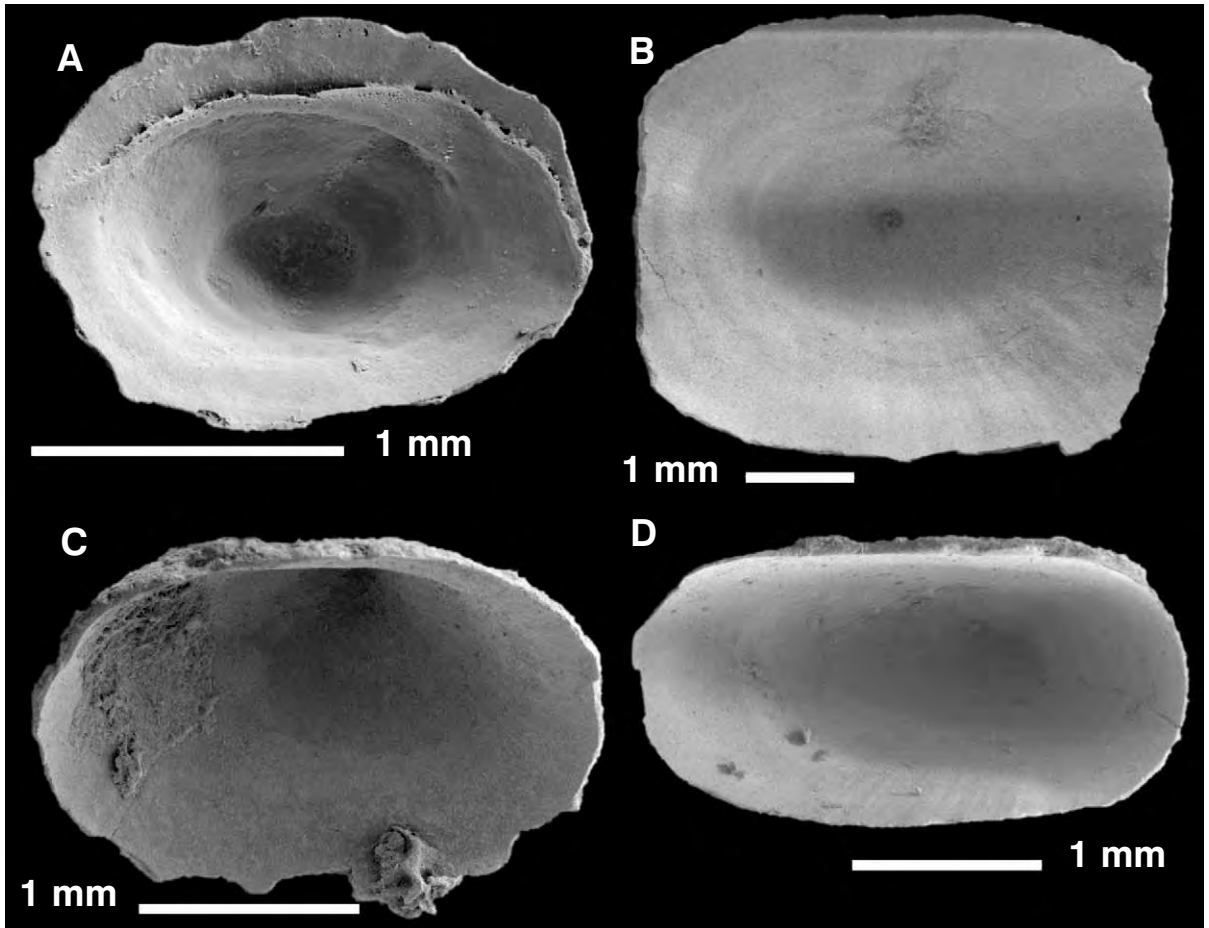


Fig. 4. The inner shell surface of some Middle Miocene lottiids with muscle scars. A – *Tectura zboroviensis* FRIEDBERG, 1928, IGS NANU, 19/2003, Chokrakian, Yurkino, Ukraine. B – *Blinia angulata* (D’ORBIGNY, 1844), IGS NANU, 51/2000, Middle Sarmatian, Antonovka, Ukraine. C – *Blinia sinzovi* (KOLESNIKOV, 1935), IGS NANU, 37/2000, from the same locality as previous. D – *Flexitectura subcostata* (SINZOV, 1892), IGS NANU, 25/2000, from the same locality as previous

yolk-rich embryogenesis. Only development with large, evidently lecithotrophic, eggs can result in a cap-like protoconch and a pancake-like shape (e.g., BANDEL 1982). The young snail evidently started its independent life crawling. The shape and proportions of the “pancake”-type of protoconch may also suggest the brooding of young snails in the mantle cavity of the parents (ANISTRATENKO & *al.* 2006). It is clear that we cannot provide any direct and definitive evidences to argue for that assumption and it is still just supposition based on analogy. Thus, a similar oval shield-like protoconch has been discovered only in the modern *Erginus moskalevi* (GOLIKOV & KUSSAKIN, 1972) of the Lottiidae. This species, illustrated by SASAKI (1998, fig. 21a-c), is interpreted as brooding the young snails within the pallial cavity of the parent. For more detailed comparison of the studied taxa with other patellogastropods see “Discussion and conclusions”

It should be noted that the term “lecithotrophic” is used here as an alternative to “planktotrophic”; it means that the larvae of lottiid species with the “pancake”-type of protoconch did not have a planktonic phase and that their juveniles were probably actually brooded. However, we do not use the term “brooding” (though it is suggested) because only lecithotrophy may be proven on the basis of protoconch morphology, the proof of brooding requiring direct observations on living material.

The data presented show the uncertainty of the attribution of the patellogastropods studied. The shell microstructure characters suggest that *Blinia* and related taxa constitute a not insignificant grouping within the patellogastropods. At the same time, the commonly used teleoconch characteristics undoubtedly support a relationship between *Blinia*, *Tectura*, *Acmaea* and other orthodox patelloids. The shell shape and the characters of the muscle scars suggest that *Blinia* is at least a patellogastropod. The muscle scars in *Blinia* (see ANISTRATENKO & *al.* 2006) and in other lottiids look like weakly expressed horseshoe-shaped tracts on the inner surface of the shell, as in other “normal” patellogastropods (Text-fig. 4). The scars are usually preserved though sometimes it is difficult to recognize even the edge where this horseshoe-shaped scar is opened.

There is no doubt that the protoconch morphology of *Blinia* and related taxa (i.e., *Flexitectura* and *Squamitectura*) is quite unusual for patellogastropods (i.e., *Patella virginea*) in indicating a lecithotrophic embryonic development, perhaps

even with brooding of juveniles in the mantle cavity of the adult. Moreover, the position of the apex in some representatives of *Blinia* is quite distinctive. In contrast to a forward-tilted apex in *Tectura*, *Acmaea*, *Patella* and the majority of other patelloids, some *Blinia* (e.g. *Blinia pseudolaevigata*) have an apex that is tilted backwards, as in *Propilidium ancyloide* (FORBES, 1840) (Lepetidae DALL, 1869) and also in the slit-bearing *Emarginula* LAMARCK, 1801 (Fissurellidae FLEMING, 1822).

All those features suggest that the Sarmatian patellogastropods with a pancake-like protoconch should be considered as a separate lottiid branch albeit one directly connected to the Badenian *Tectura*. This is because no other morphologically similar patellogastropods are known during that period (Badenian/Sarmatian) either from the basins studied or from the Mediterranean. Additionally, *Blinia* replaces *Tectura* in the deposits with practically no gap in time (see more details below).

Finally, it is suggested that all the genera with a pancake-like protoconch discussed herein (*Blinia*, *Flexitectura* and *Squamitectura*) should be assigned to the family Lottiidae, i.e. to the same family that includes the genus *Tectura*. One argument is the fact that lottiid shells have thin outer calcitic homogeneous layers underlain by aragonitic crossed-lamellar layers, which probably are not preserved in *Blinia*. Moreover, the protoconch morphology of *Blinia* and the related taxa mentioned is most similar to that of some lottiids, e.g. *Erginus moskalevi* (see e.g. SASAKI 1998).

## SYSTEMATIC PALAEOLOGY

Class Gastropoda CUVIER, 1797  
Order Patellogastropoda LINDBERG, 1986  
Family Lottiidae GRAY, 1840

*Tectura* GRAY, 1847

TYPE SPECIES: *Patella virginea* O.F. MÜLLER, 1776, Northern Atlantic and Mediterranean Sea.

DIAGNOSIS: Conical, small patellogastropods characterized by elongated, cup-shaped, ventrolaterally inflated protoconch with smooth or ornamented surface. Protoconch positioned asymmetrically relative to sagittal axis of teleoconch and



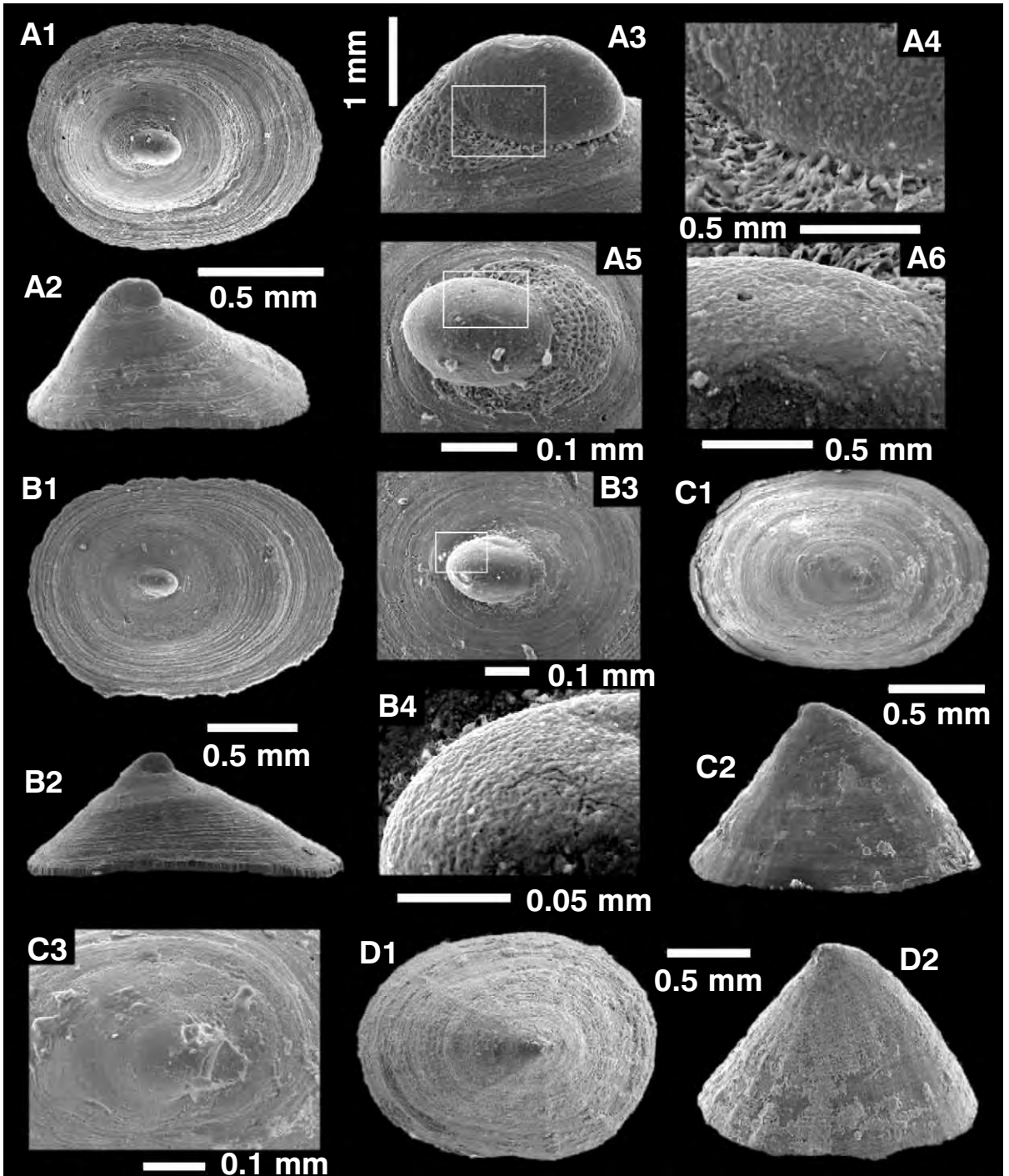


Fig. 5. **A, B.** *Tectura laevigata* (EICHWALD, 1830). A – ZNG PAN A-I-50/1796.1, Late Badenian/Sarmatian; Zalesce, Ukraine; A1 – apical view; A2 – lateral (left-side) view; A3 and A5 – details of the apical part of the shell viewed from the left and top, respectively; A4, A6 – close-up of the embryonic shell; the fine irregular reticulate pattern on the surface of the embryonic shell and “waffle” ornamentation on the initial part of teleoconch are seen. B – ZNG PAN A-I-50/1798, Late Badenian, Stary Poczajów, Ukraine; B1 – apical view; B2 – left lateral view; B3 – detail of the apical part of the shell viewed from the top; B4 – close-up of the embryonic shell; the fine irregular reticulate pattern on the surface of the embryonic shell is visible. **C, D.** *Tectura compressiuscula* (EICHWALD, 1830). C – ZNG PAN A-I-50/1787, Late Badenian, Podhorce, Ukraine; C1 – apical view; C2 – right lateral view; C3 – details of the apical part; the scar where the protoconch has broken off is visible. D – ZNG PAN A-I-50/1790.1, Late Badenian/Sarmatian, Zalesce, Ukraine; D1 – apical view; D2 – right lateral view

always directed backward; aperture oval. The apex usually tilted backward – rarely forward (*Tectura laevigata*). Differs from *Blinia*, *Flexitectura* and *Squamitectura*, with “pancake”-like protoconch, in having typical patellogastropod protoconch morphology, indicating indirect development, including a free-swimming veliger larva.

**DESCRIPTION:** The anterior end of the shell is narrower than its posterior end. The protoconch surface is usually covered by fine reticulate ornament. The transition from the embryonic shell to the teleoconch is usually clearly marked by a change in ornament.

*Tectura laevigata* (EICHWALD, 1830)  
(Text-figs 5A, B, 6A)

1830. *Pileopsis laevigata* n. sp.; EICHWALD, p. 214.

1850. *Acmaea laevigata* (EICHWALD); EICHWALD, pl. 6, fig. 18a-c.

1928. *Tectura laevigata* (EICHWALD); FRIEDBERG, p. 535, pl. 35, fig. 7.

**TYPE MATERIAL:** Repository unknown.

**MATERIAL:** One specimen from the Late Badenian of Hluboczek Wielki, Ukraine, ZNG PAN A-I-50/1792; two specimens from the Late Badenian of Podhorce, Ukraine, ZNG PAN A-I-50/1793; one specimen from the Late Badenian of Jasionów, Ukraine, ZNG PAN A-I-50/1794; twenty-three specimens from the Badenian/Sarmatian of Zalesce, Ukraine, ZNG PAN A-I-50/1796 (ten specimens), A-I-95/3d.1-13 (thirteen specimens); two specimens from the Early Sarmatian of Chlebów, Ukraine, ZNG PAN A-I-50/1797; two specimens from the Late Badenian of Stary Poczajów, Ukraine, ZNG PAN A-I-50/1798 (one specimen), A-I-95/li (one specimen); eight specimens from the Badenian of Żukowce, Ukraine, ZNG PAN A-I-50/1799 (six specimens.), A-I-95/3e (two specimens.); one specimen from the Late Badenian/Sarmatian of Szuszkowce, Ukraine, ZNG PAN A-I-50/1800; fourteen specimens from the Badenian of Węglinek, Poland, ZNG PAN A-I-87/75.1-14; one specimen from the Late Badenian of Varovtsy, Ukraine, IGS NANU, 18/1980; eight specimens from the Early Sarmatian of Zwerzyniec, Poland, IGS NANU, 1/1996 – 8/1996;

(?) one specimen from the Early Sarmatian (Zbruchian horizon) of Shirokoe, Ukraine, IGS NANU, 5/1999; four specimens from the Early Sarmatian of Dwikozy, Poland, IGS NANU, 1/2001 – 4/2001; thirty-nine specimens from the Early Sarmatian of Ślasków Mały, Poland, IGS NANU, 1/2002 – 39/2002.

**DESCRIPTION:** The shell is small, relatively thick-walled, low conical in lateral profile and oval in apertural view. The anterior slope is usually somewhat concave; the posterior is more or less convex (Text-figs 5A, B, 6A). The apex in both juvenile and adult specimens is somewhat tilted forward, the apical angle (measured from the front view) varies, usually about 65–80° in different specimens. The protoconch is directed backwards, elongated, cup-shaped, positioned asymmetrically relative to the sagittal axis of the teleoconch.

The surface of the protoconch is apparently smooth, but at higher magnifications the fine irregular reticulate pattern on the surface of the embryonic shell and “waffle” ornamentation on the initial part of the teleoconch are sometimes clearly visible; the transition from the embryonic shell to the early teleoconch is usually sharply defined.

The sculpture consists of numerous very fine concentric growth lines; axial ornamentation is absent, only the initial part of the teleoconch is covered by a fine “waffle” pattern (Text-fig. 5A, B). The muscle scars are sometimes visible under the light microscope (e.g. Text-fig. 6A).

**MEASUREMENTS** (in mm):

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-50/1793.1	2.96	2.35	1.30	1.13	0.38	83
ZNG PAN A-I-50/1794	1.65	1.22	0.70	0.61	0.37	82
ZNG PAN A-I-50/1796.1	1.13	0.87	0.61	0.48	0.42	69
ZNG PAN A-I-50/1796.2	2.70	2.00	1.39	0.96	0.36	71
ZNG PAN A-I-50/1797.1	1.74	1.39	0.44	0.52	0.30	115
ZNG PAN A-I-50/1797.2	2.00	1.65	1.04	0.70	0.35	76
ZNG PAN A-I-50/1798	1.63	1.07	0.67	0.43	0.41	75
ZNG PAN A-I-50/1799.1	3.04	2.26	1.39	1.13	0.37	77
ZNG PAN A-I-50/1800	2.26	1.65	1.04	0.70	0.31	76
ZNG PAN A-I-87/75.1	3.48	2.61	1.57	1.04	0.30	79
ZNG PAN A-I-95/li	2.87	2.09	1.39	0.96	0.33	75
ZNG PAN A-I-95/3d.1	4.35	3.30	2.26	1.57	0.36	72
ZNG PAN A-I-95/3d.2	4.26	3.57	1.65	1.48	0.35	94
ZNG PAN A-I-95/3d.3	2.87	2.26	1.74	0.96	0.34	65

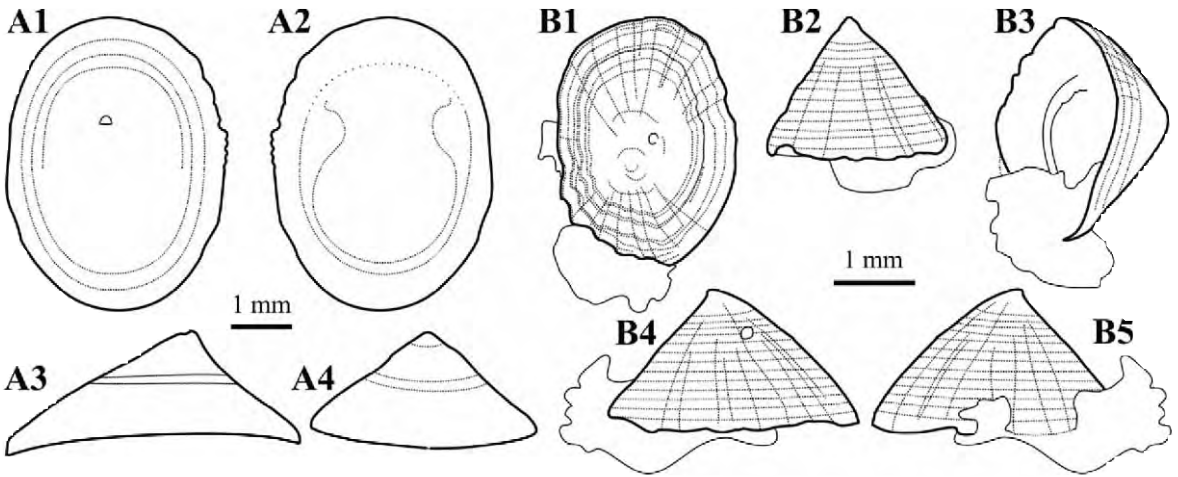


Fig. 6. *A. Tectura laevigata* (EICHWALD, 1830), ZNG PAN A-I-95/3d.2, Late Badenian, Zalesce, Ukraine; A1 – apical view; A2 – apertural view; A3 – right lateral view; A4 – anterior view; muscle scars are visible. **B. Tectura zboroviensis** FRIEDBERG, 1928 (= FRIEDBERG 1928, p. 536, pl. 35, figs 8a, 8b), paralectotype, ZNG PAN A-I-50/1801, Late Badenian, Zborów, Ukraine; B1 – apical view; B2 – anterior view; B3 – apertural view; B4 – right lateral view; B5 – left lateral view; muscle scars are visible

REMARKS: Several lots of the KRACH collection contain *T. laevigata* under different names (see Appendix). According to our observations on the growth lines, the parietal train in the *Tectura laevigata* shell, in contrast to that of other *Tectura* considered here, grows much faster than the outer lip of the aperture. Because of this, the shell apex and the protoconch are tilted forward (i.e. to the anterior edge), which is clearly visible in juvenile shells (Text-fig. 5A, B). The sharply tilted position of the apex in *T. laevigata* remains the same in adult individuals (Text-fig. 6A), whereas in mature individuals of other *Tectura* it becomes positioned more or less centrally (e.g., Text-fig. 5C, D). This mode of shell growth perhaps also explains the original onychoid (=unguiculate) shape of the *T. laevigata* shell, which is revealed in the presence of “lateral gaping” i.e. the shell is not tightly attached by the middle part of both lateral sides to the substrate.

The specimens from FRIEDBERG’s and KRACH’s collections correspond well with the original illustration of *Acmaea laevigata* provided by EICHWALD (1850, tab. 6, fig. 18a-c). *T. laevigata* differs from all other *Tectura* in having a forward-tilted apex and in “lateral gaping” of the shell; the adult shells of *T. laevigata* really accord with the species name and are usually almost completely smooth or show only weak growth lines.

DISTRIBUTION: The data recently obtained show that *Tectura laevigata* is one of the most com-

monly occurring lottiids in both the Badenian of Central Paratethys and the Early Sarmatian of Eastern Paratethys (e.g. eastern Poland and the Volhynian-Podolian region of Ukraine). It was also recorded from the Early Sarmatian (Zbruchian horizon) of Shirokoe in southern Ukraine (ANISTRATENKO 2000a) and it occurs rarely in the Konkian of the Transcaspien (IL’INA 1993).

*Tectura compressiuscula* (EICHWALD, 1830)  
(Text-fig. 5C, D)

- 1830. *Pileopsis compressiuscula* n. sp.; EICHWALD, p. 214.
- 1850. *Acmaea compressiuscula* (EICHWALD); EICHWALD, pl. 6, fig. 19a-c.
- 1928. *Tectura compressiuscula* (EICHWALD); FRIEDBERG, p. 534, pl. 35, fig. 6.

TYPE MATERIAL: Repository unknown.

MATERIAL: One specimen from the Late Badenian/Sarmatian of Faszczówka, Ukraine, ZNG PAN A-I-50/1785; one specimen from the Late Badenian of Borki Wielkie, Ukraine, ZNG PAN A-I-50/1786; one specimen from the Late Badenian of Podhorce, Ukraine, ZNG PAN A-I-50/1787; two specimens from the Badenian of Szuszkowce, Ukraine, ZNG PAN A-I-50/1788; four specimens from the Late Badenian of Jasionów, Ukraine, ZNG PAN A-I-50/1789; four specimens from the

Late Badenian/Sarmatian of Zalesce, Ukraine, ZNG PAN A-I-50/1790; one specimen from the Late Badenian of Olesko, Ukraine, ZNG PAN A-I-50/1791; one specimen from the Badenian of Węgliń, Poland, ZNG PAN A-I-87/75.15.

**DESCRIPTION:** Shell limpet-like, small, moderately high. The apex in adult specimens is positioned almost centrally or somewhat tilted backward; the apical angle (measured from the front view) varies between 60° and 75° in different specimens. The aperture is moderately broad oval. The protoconch is directed backward, elongated, and positioned asymmetrically relative to the sagittal axis of the teleoconch. The transition from the embryonic shell to the early teleoconch is distinct. The sculpture consists of numerous fine concentric growth lines crossed by radial ribs, producing the “waffle” ornamentation (Text-fig. 5D). The outer sculptured layer is commonly peeled off and the surface of the teleoconch in most adult individuals appears smooth, or at least lacks the radial ribs (Text-fig. 5C).

#### MEASUREMENTS (in mm):

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-50/1787	1.56	1.04	0.98	0.90	0.58	77
ZNG PAN A-I-50/1788.1	1.74	1.30	1.04	0.87	0.50	63
ZNG PAN A-I-50/1788.2	2.09	1.48	1.30	1.30	0.62	58
ZNG PAN A-I-50/1789.1	1.74	1.22	1.04	0.96	0.55	61
ZNG PAN A-I-50/1790.1	1.47	0.96	0.73	0.73	0.50	68

**REMARKS:** This species is deposited in KRACH’s collection under different names (see Appendix). The specimens from FRIEDBERG’s collection correspond fairly well to the original illustration of *T. compressiuscula* (EICHWALD 1850, tab. 6, fig. 19a-c). Due to corrosion, the scar where the protoconch has broken off is sometime clearly visible only in SEM images of adult specimens (e.g. Text-fig. 5C, D). *Tectura compressiuscula* differs from *T. zboroviensis* in having a comparatively higher shell (ratio HS/LS is about 0.6), which is also compressed laterally, whereas the latter species is characterised by a clear broad oval outline of the aperture.

**DISTRIBUTION:** The material studied shows that *Tectura compressiuscula* is found in the Badenian of Central Paratethys and the Early Sarmatian of Eastern Paratethys (i.e. eastern Poland and the

Volhynian-Podolian region of Ukraine). The species was also recorded from the Badenian and Sarmatian reef facies of Moldova (JANAKEVITCH 1987; IONESI & *al.* 2005).

#### *Tectura zboroviensis* FRIEDBERG, 1928 (Text-fig. 4A, 6B, 7A-C)

1928. *Tectura zboroviensis* n. sp.; FRIEDBERG, 536, pl. 35, figs 8a, 8b

**TYPE MATERIAL:** Three specimens from the Late Badenian of Zborów, Ukraine, ZNG PAN A-I-50/1801 (one specimen), 1802 (two specimens).

**MATERIAL:** Two specimens from the Late Badenian of Borki Wielkie, Ukraine, ZNG PAN A-I-50/1803; five specimens from the Late Badenian of Zalesce, Ukraine, ZNG PAN A-I-50/1804; one specimen from the Late Badenian of Stary Poczajów, Ukraine, ZNG PAN A-I-50/1805; one specimen from the Badenian of Szuszkowce, Ukraine, ZNG PAN A-I-95/3c; seventeen specimens from the Late Badenian of Varovtsy, Ukraine, IGS NANU, 1/1980 - 17/1980; one specimen from the Late Badenian of Satanov, Ukraine, IGS NANU, 21/1981; five specimens from the Early Sarmatian of Dwikozy, Poland, IGS NANU, 5/2001 - 9/2001; twenty-seven specimens from the Early Sarmatian of Ślasków Mały, Poland, IGS NANU, 40/2002 - 66/2002; nine specimens from the Early Sarmatian (Kuzhorian horizon) of Veselyanka, Ukraine, IGS NANU, 1/2003 - 9/2003; sixteen specimens from the Chokrakian of Yurkino, Crimea, Ukraine, IGS NANU, 18/2003 - 34/2003.

**DESCRIPTION:** Shell limpet-like, small, moderately high. The apex in adult specimens is positioned almost centrally, but in juvenile individuals it is clearly tilted backward, the apical angle (measured from the front view) varies between 60° and 80° in different specimens. The sculpture consists of numerous (up to 20) rather fine radial ribs crossed by the growth lines, producing the “waffle” ornamentation sometimes clearly visible on the initial part of the teleoconch (Text-fig. 7B). The outer sculptured layer is often peeled off and the surface of the teleoconch in most adult individuals appears smooth. The aperture is broad oval (e.g. Text-fig. 7C). The muscle scars are sometimes visible under

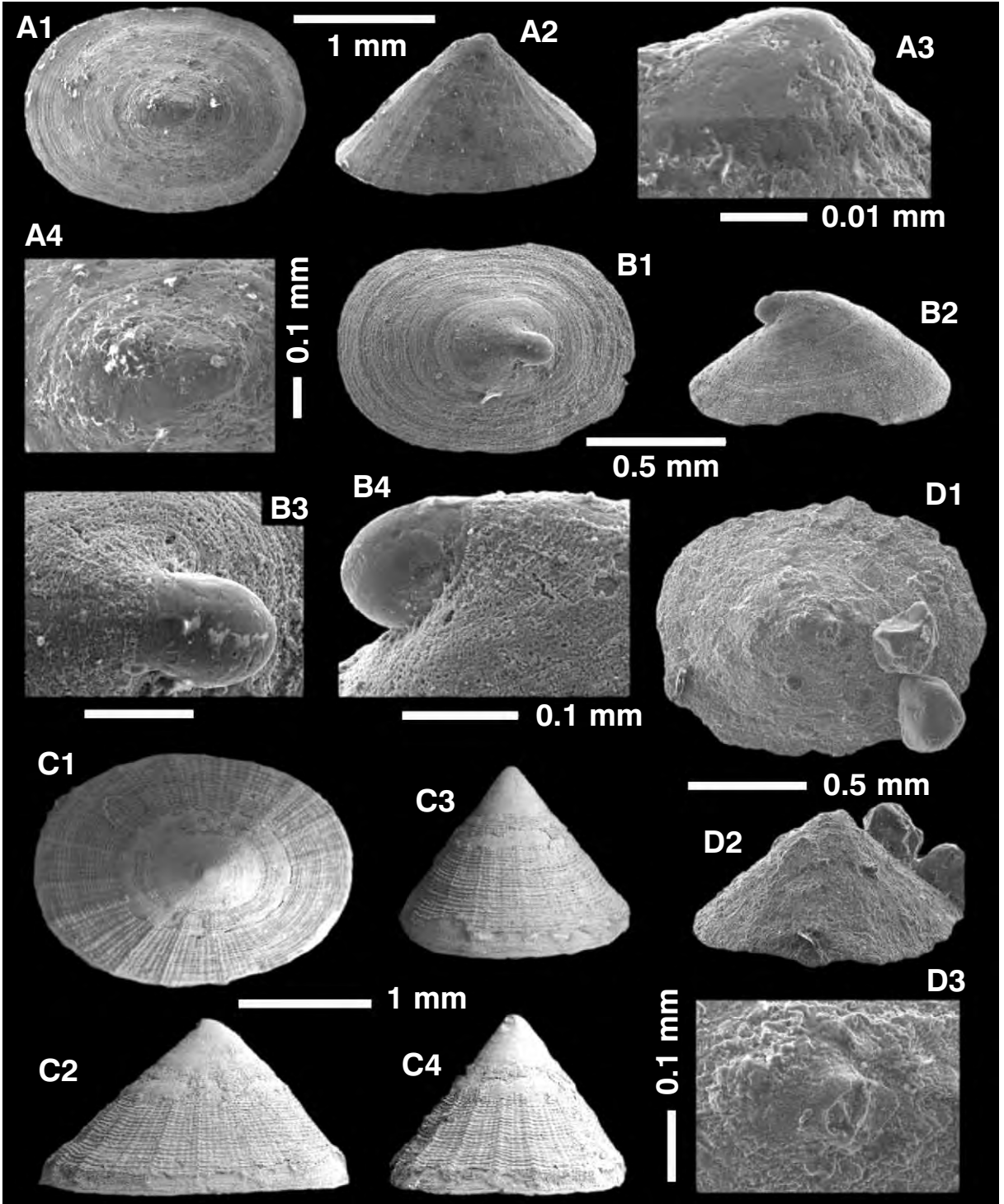


Fig. 7. A-C. *Tectura zboroviensis* FRIEDBERG, 1928; A – ZNG PAN A-I-50/1802.1, lectotype, Late Badenian, Zborów, Ukraine; A1 – apical view; A2 – left lateral view; A3-A4 – details of apical part of the shell viewed from the left and top respectively; remnants of the fine “waffle” pattern on the initial part of teleoconch are seen. B – ZNG PAN A-I-50/1804.2, Late Badenian, Zalesce, Ukraine; B1 – apical view; B2 – right lateral view; B3-B4 – details of apical part of the shell viewed from the top and right respectively; the fine “waffle” ornamentation and radial ribs on the initial part of teleoconch are clearly visible. C – IGS NANU 9/1980, Late Badenian, Varovtsy, Ukraine; C1 – apical view; C2 – right lateral view; C3 – anterior view; C4 – posterior view; the teleoconch sculptural pattern and the scar where the protoconch has broken off are clearly visible. D – *Tectura incognita* FRIEDBERG, 1928, lectotype, ZNG PAN A-I-50/1806.1, Late Badenian, Borki Wielkie, Ukraine; D1 – apical view; D2 – left lateral view; D3 – details of apical part of the shell from the top; the scar where the protoconch has broken off is visible

the SEM or even under the light microscope (e.g. Text-fig. 4A, 6B).

The protoconch is elongated, cup-shaped, inflated ventrolaterally. It measures from 0.08 mm to 0.10 mm in length and about 0.10 mm in width, situated in an asymmetrical position relative to the sagittal axis of the teleoconch and always directed backward.

The surface of the protoconch is apparently smooth (Text-fig. 7B); the transition from the embryonic shell to the early teleoconch is usually sharply 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 the adult sculpture. The later, relatively extended part of the juvenile teleoconch reaches up to 0.2 mm in width and is covered by fine radial ribs. The scar where the protoconch has broken off is sometimes clearly visible (e.g. Text-fig. 7C).

#### MEASUREMENTS (in mm):

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-50/1802.1 (the lectotype)	1.87	1.33	0.87	0.93	0.50	79
ZNG PAN A-I-50/1801 (the paralectotype)	2.61	1.91	1.65	1.30	0.50	60
ZNG PAN A-I-50/1803.1	1.57	1.22	0.70	0.70	0.45	82
ZNG PAN A-I-50/1803.2	1.22	0.83	0.70	0.70	0.57	61
ZNG PAN A-I-50/1804.1	0.87	0.67	0.40	0.47	0.53	80
ZNG PAN A-I-50/1804.2	0.80	0.53	0.40	0.53	0.66	68
ZNG PAN A-I-95/3c	2.61	2.09	1.04	1.04	0.40	83
IGS NANU 1/1980	2.50	1.79	1.05	1.15	0.46	85
IGS NANU 2/1980	2.35	1.68	1.25	1.15	0.49	70
IGS NANU 3/1980	1.92	1.40	1.15	0.92	0.48	67
IGS NANU 4/1980	2.11	1.65	0.95	1.02	0.48	82
IGS NANU 5/1980	2.24	1.60	1.40	1.05	0.49	60
IGS NANU 6/1980	2.05	1.38	1.05	1.06	0.52	69
IGS NANU 7/1980	2.25	1.60	1.29	1.10	0.49	65
IGS NANU 8/1980	2.12	1.50	1.11	1.00	0.47	70
IGS NANU 9/1980	2.42	1.77	1.36	1.14	0.47	70
IGS NANU 10/1980	3.45	2.50	2.10	1.55	0.45	75
IGS NANU 11/1980	3.01	2.12	1.99	1.60	0.53	70
IGS NANU 12/1980	2.85	2.15	1.80	1.39	0.49	71
IGS NANU 13/1980	2.08	1.45	1.30	1.00	0.48	75
IGS NANU 21/2003	0.86	0.62	0.44	0.55	0.64	72
IGS NANU 22/2003	0.86	0.57	0.37	0.48	0.56	75

REMARKS: The type series of *Tectura zboroviensis* consists of three specimens collected from the Late

Badenian of Zborów, Ukraine (ZNG PAN A-I-50/1801, 1802). One of these specimens (ZNG PAN A-I-50/1801) was originally illustrated in FRIEDBERG'S work (FRIEDBERG 1928, p. 536, pl. 35, figs 8a, 8b), the drawing of it is presented in Text-fig. 6B. One of the syntypes from another lot (ZNG PAN A-I-50/1802.1) is designated here as lectotype of *Tectura zboroviensis* FRIEDBERG, 1928 and the SEM images of it are presented in Text-fig. 7A. The two remaining specimens (ZNG PAN A-I-50/1801 and 1802.2) are the paralectotypes (ICZN Art. 74). The reason for the lectotype designation is that in the Middle Miocene of the Central and Eastern Paratethys several more or less similar but distinct species of *Tectura* occur. Designation of a lectotype will allow confident identification of *T. zboroviensis*. Our observations show that the growth of the parietal train in *Tectura zboroviensis* is slower than that of the outer lip of the aperture. Therefore, the shell apex with protoconch tilted backward (i.e. to posterior edge) is clearly shown in juvenile individuals (Text-fig. 7B) but in mature individuals it becomes more or less centrally positioned (e.g. Text-fig. 7C).

*Tectura zboroviensis* differs from the similar *T. compressiuscula* in having a relatively lower shell (ratio HS/LS is about 0.45). Modern representatives of *Tectura virginea* from the Mediterranean Sea and from the North Atlantic are characterized by a protoconch with shape and dimensions similar to those of *T. zboroviensis* (ANISTRATENKO & *al.* 2006). This recent species is distinguished from *T. zboroviensis* by a slightly more bulbous embryonic shell.

DISTRIBUTION: *Tectura zboroviensis* was originally described from the Late Badenian of the Central Paratethys (FRIEDBERG 1928). It was also encountered recently in our material from the Chokrakian of the Eastern Paratethys (coeval with the middle part of the Badenian of the Central Paratethys) and from the Early Sarmatian of the Eastern Paratethys (see the *Material*).

#### *Tectura incognita* FRIEDBERG, 1928 (Text-fig. 7D)

1928. *Tectura incognita* n. sp.; FRIEDBERG, p. 536, pl. 35, fig. 9.

? 1975. *Acmaea (Tectura) friedbergi* n. sp.; BALUK, p. 29, pl. 2, figs 9, 10.

**TYPE MATERIAL:** Two specimens from the Late Badenian of Borki Wielkie, Ukraine, ZNG PAN A-I-50/1806. Originally the type series consisted of three specimens but only two of them have survived in the collection; unfortunately, the specimen illustrated by FRIEDBERG (1928, pl. 35, fig. 9) is lost.

**MATERIAL:** One specimen has been studied from the Badenian of Zaleśce, Ukraine, ZNG PAN A-I-95/3d.14.

**DESCRIPTION:** The shell is small, low conical (height about half the width) and broad oval in apertural view. The apex in adult specimens is positioned almost centrally, or slightly tilted forward, the apical angle (measured from the front view) varies from 80° to 85°. The protoconch is directed backward, elongated, and positioned asymmetrically relative to the sagittal axis of the teleoconch. The transition from the embryonic shell to the early teleoconch is usually sharply defined. The scar where the protoconch has broken off is sometimes clearly visible (e.g., Text-fig. 7D). The sculpture on the surface of the teleoconch consists of 12–14 fine radial ribs crossed by the growth lines.

**MEASUREMENTS (in mm):**

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-50/1806.1 (the lectotype)	1.30	1.04	0.52	0.65	0.50	83
ZNG PAN A-I-50/1806.2 (the paralectotype)	1.30	1.09	0.52	0.52	0.40	85
ZNG PAN A-I-95/3d.14	2.87	2.61	1.30	1.22	0.43	83

**REMARKS:** The type series of *Tectura incognita* comprises two specimens collected from the Late Badenian of Borki Wielkie, Ukraine (ZNG PAN A-I-50/1806). One of the syntypes is designated here as lectotype of *Tectura incognita* FRIEDBERG, 1928 and the SEM micrographs of it are presented in Text-fig. 7D. The remaining, rather damaged specimen is the paralectotype (ICZN Art. 74). The reason for the lectotype designation here is the same as for the designation of a lectotype for *T. zboroviensis* (see above). One lot of the KRACH collection contains *T. incognita* under the name *T. laevigata* (see Appendix).

BALUK (1975, p. 29, pl. 2, figs 9, 10) described the new species *Acmaea (Tectura) friedbergi* from the Early Badenian of Korytnica, Poland. The author mentioned that specimens documented by FRIEDBERG (1928, p. 534, tab. 35, fig. 6) as *Tectura compressiuscula* (EICHWALD, 1830) did not accord with EICHWALD's concept of the species and should be attributed to his new species *A. friedbergi* (BALUK 1975, p. 29). Comparative analysis shows that the described and illustrated specimens of *A. friedbergi* do not really correspond to *T. compressiuscula* in EICHWALD's original interpretation, whereas the material of *T. compressiuscula* sensu FRIEDBERG (1928) agrees fairly well with EICHWALD's concept of this species (see EICHWALD 1850, tab. 6, fig. 19a-c). The specimens figured by BALUK actually agree well with the type specimens of *Tectura incognita* e.g., lectotype (Text-fig. 7D) and are considered here as *T. incognita* FRIEDBERG, 1928. They also fall in all respects, including the ratios of the measurements, within the range of variability of *T. incognita* in the concept proposed here.

*Tectura incognita* differs from *T. zboroviensis* in being comparatively lower in lateral view and in being broader in frontal view. It should be noted that sometimes low-conical *T. zboroviensis* occur, but nevertheless they differ clearly in having significantly more numerous radial ribs (up to 20) whereas *T. incognita* is characterised by no more than 12–14 ribs on the surface of the teleoconch.

**DISTRIBUTION:** It is difficult to discuss the palaeogeography of *Tectura incognita* since occurrences are restricted to only a few localities of the Late Badenian of western Ukraine and probably the Early Badenian of eastern Poland (Korytnica) – see above. *Acmaea* sp. was recorded from the Chokrakian of the Kerch Peninsula (e.g. ZHIZHCENKO 1936) but without figures or description. Records by IL'INA (1993) of rare occurrences of *T. incognita* from the Chokrakian of the Western Sub-Caucasian suggest that these records of *Acmaea* sp. from Kerch also belong to *Tectura incognita*.

*Blinia* O. ANISTRATENKO, BANDEL &  
V. ANISTRATENKO, 2006

**TYPE SPECIES:** *Helcion angulata* D'ORBIGNY, 1844, by original designation. Sarmatian of west

and south Ukraine, the Kerch Peninsula of the Crimea, Moldova, the Banat of Romania and western Central Paratethys (Vienna Basin).

**DIAGNOSIS:** Conical, relatively small patellogastropods with smooth or wrinkled “pancake”-like completely symmetrical protoconch; ornament of axial ribs; aperture oval. The apex off-centre and tilted forward or backward. Differs from *Flexitectura* and *Squamitectura*, with similar type of protoconch, in having aperture tightly attached to substrate with no clearance, while both *Flexitectura* and *Squamitectura* have distinct flexures in both anterior and posterior shell edges (see below). From all other known patellogastropods *Blinia* differs in having a round “pancake”-like protoconch, indicating a lecithotrophic type of early development and the absence of even a very short free-swimming larval stage.

**DESCRIPTION:** The anterior end of the shell is usually narrower than its posterior end (except *Blinia angulata*). The teleoconch surface has numerous radiating ridges crossed by concentric lines, which lie usually parallel to the apertural plane. The protoconch has a round to oval “pancake”-like shape. It 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 mm. The protoconch surface is smooth or wrinkled; sometimes with a small pit on top of the 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.

*Blinia angulata* (D’ORBIGNY, 1844)  
(Text-fig. 4B, 8A)

1844. *Helcion angulata* n. sp.; D’ORBIGNY, p. 470, pl. 4, figs 13-15.
1935. *Acmaea angulata* (D’ORBIGNY); KOLESNIKOV, p. 128, pl. 19, figs 12-15.
1935. *Acmaea enikalensis* n. sp. KOLESNIKOV, p. 129, pl. 19, figs 18-21.
- 2000a. *Tectura (Tectura) angulata* (D’ORBIGNY); ANISTRATENKO, p. 37, pl. 2, figs 1a, 1b.
- 2000a. *Tectura (Tectura) enikalensis* (KOLESNIKOV); ANISTRATENKO, p. 37, pl. 2, figs 2a-2c.
2006. *Blinia angulata* (D’ORBIGNY); O. ANISTRATENKO, BANDEL & V. ANISTRATENKO, p. 160, fig. 5a.

**TYPE MATERIAL:** The syntype of *Helcion angulata* D’ORBIGNY, 1844 is deposited in the National Museum of Natural History, Paris (France), coll. D’ORBIGNY, R64466. Three syntypes of *Acmaea enikalensis* KOLESNIKOV, 1935 are deposited in the Central Museum of VSEGEI, St.-Petersburg (Russia), coll. V.P. KOLESNIKOV, 107-109/11126.

**MATERIAL:** Seven specimens from the Middle Sarmatian of Wierzchów, Ukraine, ZNG PAN A-I-95/1.1-7; one specimen from the Middle Sarmatian of Glińsk, Ukraine, ZNG PAN A-I-95/1a.1; one specimen from the Middle Sarmatian of Dermań, Ukraine, ZNG PAN A-I-95/3b; one specimen from the Sarmatian of unknown location in Wołyń, Ukraine, ZNG PAN A-I-95/6c.6; four specimens from the Early Sarmatian (Zbruchian horizon) of Shirokoe, Ukraine, IGS NANU, 1/1999 - 4/1999; eleven specimens from the Middle Sarmatian of Antonovka, Ukraine, IGS NANU, 46/2000 - 56/2000; five specimens from the Middle Sarmatian of Terlovka, Ukraine, IGS NANU, 57/2000 - 60/2000, 61/2004; one specimen from the Middle Sarmatian of Suslovtsy, Ukraine, IGS NANU, 63/2000; thirty-eight specimens from the Middle Sarmatian of Letichev, Ukraine, IGS NANU, 1/2004 - 17/2004, 62/2004 - 84/2004.

**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 80° to 120° in different specimens.

Posterior and anterior slopes are straight or slightly convex. The 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 the teleoconch appears to be totally smooth. The aperture is egg-shaped to broadly oval. The muscle scars are sometimes indistinct (Text-fig. 4B). The protoconch is round to oval, pancake-like, smooth, and usually shiny. The greater diameter of the embryonic shell (i.e., “pancake”) measures about 0.16 mm; the protoconch is symmetrically located in the sagittal axis of the teleoconch. The protoconch-teleoconch transition is usually sharp, marked by a distinct constriction or rim.



## MEASUREMENTS (in mm):

No	LS	WS	HS	AP	AE	AA
IGS NANU 46/2000	4.80	3.05	1.75	1.85	0.39	84
IGS NANU 47/2000	10.82	8.70	4.19	6.00	0.56	95
IGS NANU 48/2000	12.81	10.51	5.79	6.01	0.47	85
IGS NANU 49/2000	12.02	9.70	5.25	5.81	0.48	90
IGS NANU 50/2000	5.68	4.63	1.86	2.81	0.50	121
IGS NANU 57/2000	7.85	5.61	2.60	3.70	0.47	102
IGS NANU 58/2000	4.05	3.20	1.13	1.73	0.43	112
IGS NANU 59/2000	1.40	1.12	0.55	0.60	0.43	90
IGS NANU 60/2000	3.92	3.23	1.62	1.80	0.46	100
IGS NANU 63/2000	3.55	2.45	1.52	1.92	0.54	82
IGS NANU 11/2004	11.60	9.70	5.42	5.31	0.46	90
IGS NANU 12/2004	6.08	4.15	2.15	2.92	0.48	88

REMARKS: Several lots of the KRACH collection contain *B. angulata* under different names (see Appendix). Into the synonymy of *Blinia angulata* we include *Acmaea enikalensis* KOLESNIKOV, 1935 since the description and illustrated specimens of this species (KOLESNIKOV 1935, p. 129, pl. 19, figs 18-21) accord well with the material of *B. angulata* in the concept accepted here.

*Blinia angulata* differs well from all other known *Blinia* species in the size of the adults, and in the massive and relatively low, stocky shell with a somewhat mammillated apex.

DISTRIBUTION: This species is one of the most abundant and widespread *Blinia* species in Sarmatian deposits of the Eastern Paratethys (D'ORBIGNY 1844; SINZOV 1892; FRIEDBERG 1911-1928; KOLESNIKOV 1935; IONESI & *al.* 2005; ANISTRATENKO & *al.* 2006).

*Blinia pseudolaevigata* (SINZOV, 1892)  
(Text-fig. 8B, C)

1892. *Acmaea pseudolaevigata* n. sp.; SINZOV, p. 63, pl. 3, figs 11-12.

1944. *Acmaea soceni* n. sp.; JEKELIUS, p. 42, pl. 2, figs 4-6 [typus: fig. 4].

2000a. *Tectura (Tectura) pseudolaevigata* (SINZOV); ANISTRATENKO, p. 37, pl. 2, figs 4a-4d.

2006. *Blinia pseudolaevigata* (SINZOV); O. ANISTRATENKO, BANDEL & V. ANISTRATENKO, p. 160, fig. 5b.

TYPE MATERIAL: Three syntypes of *Acmaea pseudolaevigata* SINZOV, 1892 are deposited in the

Central Museum of VSEGEI, St.-Petersburg (Russia), coll. I.F. SINZOV, 99-101/11126.

MATERIAL: Two specimens from the Middle Sarmatian of Wierzchów, Ukraine, ZNG PAN A-I-95/1.8 (one specimen), 7.4 (one specimen); one specimen from the Middle Sarmatian of Glińsk, Ukraine, ZNG PAN A-I-95/1a.2; twenty specimens from the Middle Sarmatian of Dermań, Ukraine, ZNG PAN A-I-95/1b (seventeen specimens), 5.1-3 (three specimens); three specimens from the Sarmatian of Bakaj, Ukraine, ZNG PAN A-I-95/1c; one specimen from the Sarmatian of Żołobki, Ukraine, ZNG PAN A-I-95/1d; six specimens from the Sarmatian of Wańskowce, Ukraine, ZNG PAN A-I-95/1f; five specimens from the Middle Sarmatian of Warkowicze, Ukraine, ZNG PAN A-I-95/1g.4-8; one specimen from the Sarmatian of Czajczyńce, Ukraine, ZNG PAN A-I-95/1h; two specimens from the Sarmatian of unknown location, Wołyń, Ukraine, ZNG PAN A-I-95/6c.4,5; twenty seven specimens from the Early Sarmatian (Zbruchian horizon) of Shirokoe, Ukraine, IGS NANU, 32/1999 – 58/1999; fifty-nine specimens from the Middle Sarmatian of Letichev, Ukraine, IGS NANU, 41/2004 – 60/2004, 85/2004 – 123/2004.

DESCRIPTION: The shell is small, thin, relatively high-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 50° to 65°. The posterior slope is straight to slightly concave, the anterior slope usually distinctly convex. The sculpture consists of numerous, weak but distinct radial ribs crossed by concentric lines of growth. The outer, sculptured shell layer is usually peeled off so that the surface of the teleoconch appears to be totally smooth. The aperture is moderately to broadly oval.

The protoconch is characterised by a round to oval, pancake-like shape; it is smooth, and usually shiny.

The greater diameter of the embryonic shell (i.e. the “pancake”) measures about 0.13-0.15 mm; it is situated symmetrically in the sagittal axis of the teleoconch. The surface of the 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 (Text-fig. 8C4).

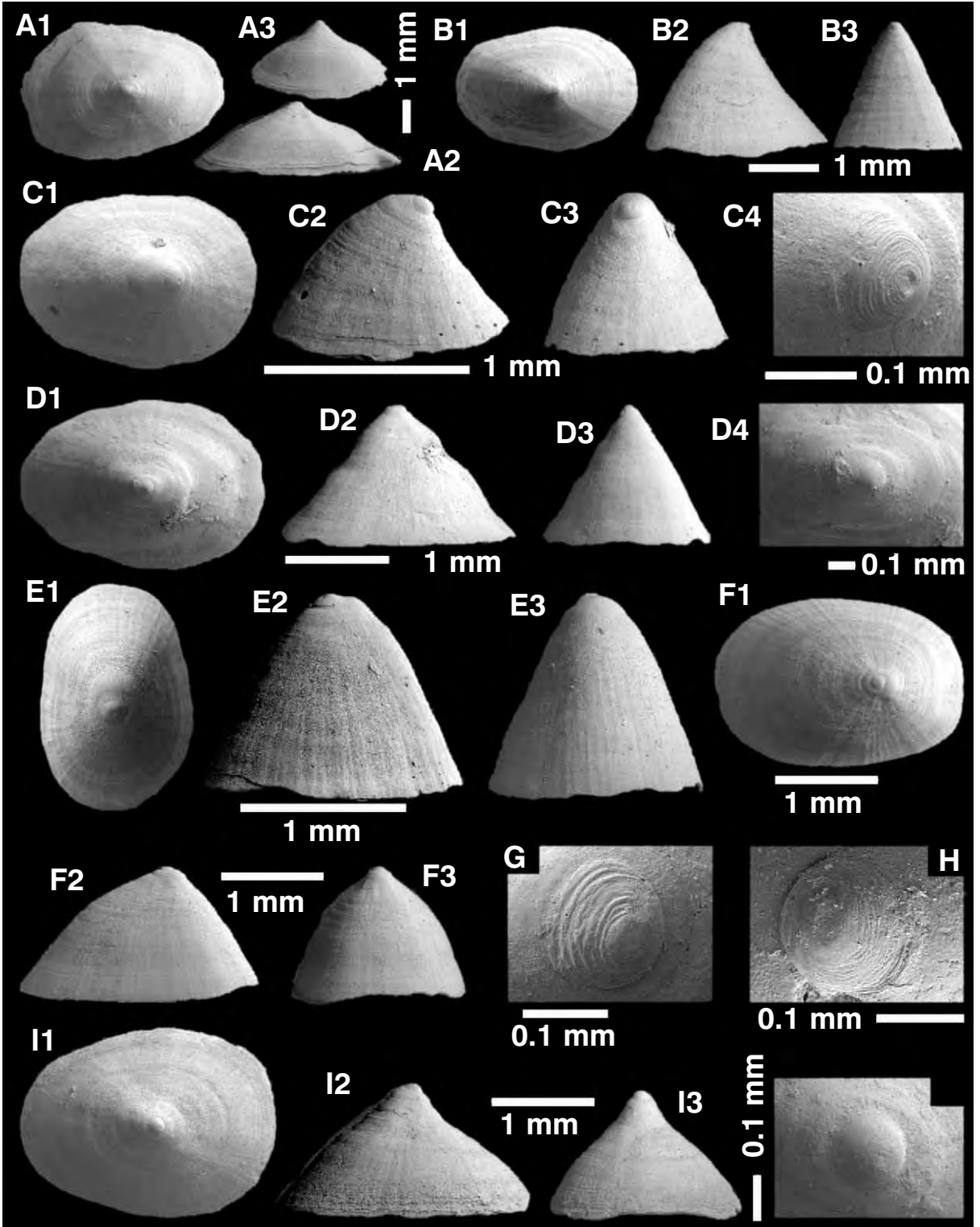


Fig. 8. **A.** *Blinia angulata* (D'ORBIGNY, 1844), IGS NANU, 1/2004, Middle Sarmatian, Letichev, Ukraine; A1 – apical view; A2 – right lateral view; A3 – posterior view. **B, C.** *Blinia pseudolaevigata* (SINZOV, 1892); B – IGS NANU, 42/2004, Middle Sarmatian, Letichev, Ukraine; B1 – apical view; B2 – left lateral view; B3 – posterior view. C – IGS NANU, 41/2004, Middle Sarmatian, Letichev, Ukraine; C1 – apical view; C2 – left lateral view; C3 – posterior view; C4 – details of apical view of the embryonic shell and juvenile teleoconch; the embryonic shell is ornamented by fine concentric wrinkles and there is a pit on the apex. **D, E.** *Blinia reussi* (SINZOV, 1892); D – IGS NANU, 40/2000, Early/Middle Sarmatian, Suslovtsy, Ukraine; D1 – apical view; D2 – left lateral view; D3 – anterior view;

## MEASUREMENTS (in mm):

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-95/1b.1	2.26	1.48	1.39	1.39	0.62	54
ZNG PAN A-I-95/1b.2	1.30	0.87	0.78	0.87	0.67	59
ZNG PAN A-I-95/1b.3	1.13	0.70	0.70	0.70	0.62	52
ZNG PAN A-I-95/5.1	2.70	2.00	1.74	1.39	0.52	58
ZNG PAN A-I-95/5.2	2.17	1.48	1.22	1.13	0.52	61
IGS NANU 41/2004	1.20	0.88	0.82	0.75	0.63	55
IGS NANU 42/2004	2.83	1.92	2.03	1.50	0.53	62
IGS NANU 85/2004	1.60	1.20	1.15	1.00	0.63	55
IGS NANU 86/2004	1.20	0.91	0.60	0.73	0.61	65
IGS NANU 87/2004	2.10	1.60	1.45	1.40	0.67	55
IGS NANU 88/2004	1.10	0.75	0.75	0.70	0.64	50
IGS NANU 89/2004	4.12	2.91	2.65	2.50	0.61	57
IGS NANU 90/2004	4.00	2.89	2.70	2.60	0.65	57
IGS NANU 91/2004	2.60	1.88	1.85	1.60	0.62	55
IGS NANU 116/2004	2.55	1.90	1.7	1.6	0.63	57

REMARKS: *Blinia pseudolaevigata* is deposited in KRACH's collection under different names (see Appendix). Probably it has sometimes been confused with *B. reussi* or other *Blinia* species. This species differs from *B. angulata* in a higher shell and the backward tilt of the apex. The specimens of *Acmaea soceni* described and illustrated by JEKELIUS (1944, p. 42, pl. 2, figs 4-6) are very similar to *B. pseudolaevigata* in the concept accepted here. Protoconchs of *A. soceni* collected from the same locality as those described by JEKELIUS (1944) are fully concordant with those documented for *B. pseudolaevigata* and therefore *Acmaea soceni* is considered (ANISTRATENKO & al. 2006) as a synonym of *Blinia pseudolaevigata*.

Two specimens of, most probably, *Blinia pseudolaevigata* were recorded by HARZHAUSER & KOWALKE (2002, p. 62, pl. 12, figs 1-3) from the middle part of the Sarmatian of St. Margarethen in the Vienna Basin (*Potamides disjunctus* assemblage) under the name *Acmaea soceni* JEKELIUS, 1944. However, this record can only be identified with our material of *B. pseudolaevigata* with reservation due to the relatively poor preservation of the protoconch figured by these authors

The shells in our material of *B. pseudolaevigata* measure up to 4.12 mm in length and up to 2.9 mm in height (see measurements). 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.

DISTRIBUTION: *Blinia pseudolaevigata* is a typical (in some localities even abundant) and most widespread species of *Blinia* occurring in Early and Middle Sarmatian sediments (Bessarabian substage) of the Eastern Paratethys viz. Ukraine, Moldova, Romania, Central Sub-Caucasus to the Central Paratethys and its eastern shore at Soceni in Romania (e.g. KOLESNIKOV 1935; JEKELIUS 1944; ŠVAGROVSKÝ 1971; HARZHAUSER & KOWALKE 2002; IONESI & al. 2005; ANISTRATENKO 2000a; ANISTRATENKO & al. 2006).

*Blinia reussi* (SINZOV, 1892)  
(Text-fig. 8D, E)

1892. *Acmaea (Scurria) reussi* n. sp.; SINZOV, p. 60, pl. 3, figs 3-5.

1944. *Acmaea soceni* n. sp.; JEKELIUS, p. 42, pl. 2, fig. 3 (partim).

2000a. *Tectura (Tectura) reussi* (SINZOV); ANISTRATENKO, p. 37, pl. 2, figs 5a-e.

TYPE MATERIAL: One syntype of *Acmaea reussi* SINZOV, 1892 is deposited in the Central Museum of VSEGEI, St.-Petersburg (Russia), coll. I.F. SINZOV, 106/11126.

MATERIAL: Three specimens from the Middle Sarmatian of Warkowicze, Ukraine, ZNG PAN A-I-95/1g.1-3; three specimens from the Middle Sarmatian of Dermań, Ukraine, ZNG PAN A-I-95/5.4-6; three specimens from the Sarmatian of Listwin, Ukraine, ZNG PAN A-I-95/6b.1-3; sixteen specimens from the Early Sarmatian (Zbruchian horizon) of Shirokoe, Ukraine, IGS NANU, 27/1999 - 31/1999, 59/1999 - 69/1999; one specimen from the Early Sarmatian of Izyaslav, Ukraine, IGS

D4 – details of apical view of the embryonic shell and juvenile teleoconch. E – IGS NANU, 126/2004, Middle Sarmatian, Letichev, Ukraine; E1 – apical view; E2 – right lateral view; E3 – anterior view. F-I. *Blinia sinzovi* (KOLESNIKOV, 1935). F – IGS NANU, 150/2004, Middle Sarmatian, Letichev, Ukraine; F1 – apical view; F2 – right lateral view; F3 – anterior view. G – IGS NANU, 159/2004, Middle Sarmatian, Letichev, Ukraine; detailed apical view. H – IGS NANU, 165/2004, Middle Sarmatian, Letichev, Ukraine; detailed apical view. I – IGS NANU, 34/2000, Middle Sarmatian, Antonovka, Ukraine; I1 – apical view; I2 – left lateral; I3 – posterior view; I4 – details of apical view

NANU, 62/2000; seven specimens from the Early/Middle Sarmatian of Suslovtsy, Ukraine, IGS NANU, 38/2000 - 44/2000; two specimens from the Middle Sarmatian of Terlovka, Ukraine, IGS NANU, 45/2000, 144/2004; twenty specimens from the Middle Sarmatian of Letichev, Ukraine, IGS NANU, 124/2004 - 143/2004.

**DESCRIPTION:** The shell is small, high-conical, compressed from lateral sides, oval in apertural view. The apex is positioned almost centrally. The apical angle varies from 55° to 70°. The posterior and anterior slopes are usually straight. The sculpture consists of numerous radial ribs crossed by fine concentric lines of growth. The outer, sculptured layer of the mature shells is usually peeled off so that the surface of the teleoconch appears to be totally smooth. The aperture is moderately to broadly oval.

The protoconch is characterised by a round to oval, pancake-like shape; it is smooth or wrinkled and usually shiny. The greater diameter of the embryonic shell (i.e. the “pancake”) measures from 0.13 mm to 0.16-0.18 mm; it is situated symmetrically in the sagittal axis of the teleoconch. Some specimens have a small pit in the top of their embryonic shell. The transition from protoconch to early teleoconch is usually sharp, marked by a well developed constriction or rim (Text-fig. 8D4).

#### MEASUREMENTS (in mm):

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-95/1g.1	2.78	2.00	1.74	1.48	0.53	58
ZNG PAN A-I-95/5.4	4.43	2.78	2.17	2.44	0.55	64
IGS NANU 38/2000	3.10	2.09	1.16	1.80	0.58	68
IGS NANU 39/2000	3.25	2.35	2.00	1.70	0.52	65
IGS NANU 40/2000	2.37	1.70	1.44	1.18	0.50	81
IGS NANU 124/2004	2.45	1.60	1.50	1.09	0.45	55
IGS NANU 125/2004	2.51	1.59	1.60	1.00	0.40	55
IGS NANU 126/2004	1.43	0.95	1.05	0.73	0.51	60
IGS NANU 144/2004	4.85	3.50	3.21	2.48	0.52	57

**REMARKS:** This species is deposited in KRACH’s collection under different names (see Appendix). Probably it has sometimes been confused with *B. pseudolaevigata* or other *Blinia* species. *Blinia reussi* is characterised by the relatively highest shell among all known *Blinia*. From the similar *Blinia sinzovi* it differs in having straight slopes and in the smaller apical angle.

**DISTRIBUTION:** *Blinia reussi* is recorded from Early and Middle Sarmatian in Western Ukraine and Middle Sarmatian of South Ukraine and Moldova (e.g. KOLESNIKOV 1935; SIMIONESCU & BARBU 1940; ANISTRATENKO 2000a; IONESI & *al.* 2005).

#### *Blinia sinzovi* (KOLESNIKOV, 1935) (Text-fig. 4C, 8F-I)

1935. *Acmaea sinzovi* n. sp., KOLESNIKOV, p. 129, pl. 19, figs 16-17.

2000a. *Tectura (Tectura) sinzovi* (KOLESNIKOV); ANISTRATENKO, p. 37, pl. 2, figs 6a, 6b.

**TYPE MATERIAL:** One syntype of *Acmaea sinzovi* KOLESNIKOV, 1935 is deposited in the Central Museum of VSEGEI, St.-Petersburg (Russia), coll. V.P. KOLESNIKOV, 106/11126.

**MATERIAL:** Nine specimens from the Sarmatian of Listwin, Ukraine, ZNG PAN A-I-95/1e; three specimens from the Middle Sarmatian of Dermań, Ukraine, ZNG PAN A-I-95/5.7-9; twenty-one specimens from the Middle Sarmatian of Letichev, Ukraine, IGS NANU, 145/2004 – 165/2004; twenty one specimens from the Early Sarmatian (Zbruchian horizon) of Shirokoe, Ukraine, IGS NANU, 6/1999 – 26/1999; five specimens from the Middle Sarmatian of Terlovka, Ukraine, IGS NANU, 30/2000, 31/2000, 64/2000, 166/2004, 167/2004; six specimens from the Middle Sarmatian of Antonovka, Ukraine, IGS NANU, 32/2000 – 37/2000.

**DESCRIPTION:** Shell small, relatively high, helmet-shaped, and oval to egg-shaped in apertural view. The muscle scars are sometimes indistinct (Text-fig. 4C). The apex is positioned almost centrally or slightly tilted forward. The apical angle varies from 60° to 80°. The posterior and anterior slopes are convex. The sculpture consists of numerous radial ribs crossed by fine concentric lines of growth. The outer sculptured layer is usually peeled off so that the surface of teleoconch appears smooth.

The protoconch is characterised by a round to oval pancake-like shape and is smooth (Text-fig. 8F, I) or wrinkled (Text-fig. 8G, H) and usually shiny. The embryonic shell (i.e. the “pancake”) is situated symmetrically in the sagittal axis of the teleoconch.

Some specimens have a small pit in the top of their embryonic shell. The transition from protoconch to early teleoconch is usually sharp, marked by a well developed constriction or rim.

MEASUREMENTS (in mm):

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-95/5.7	5.48	3.57	2.78	2.78	0.51	60
IGS NANU 30/2000	6.80	5.30	4.31	3.92	0.58	70
IGS NANU 31/2000	5.11	3.94	2.65	2.40	0.47	77
IGS NANU 32/2000	7.48	5.70	4.80	3.19	0.43	63
IGS NANU 33/2000	3.42	2.42	2.48	1.91	0.56	62
IGS NANU 34/2000	2.72	2.09	1.49	1.31	0.63	82
IGS NANU 64/2000	3.09	2.30	1.60	1.34	0.44	75
IGS NANU 145/2004	2.35	1.70	1.49	1.30	0.55	61
IGS NANU 149/2004	5.02	3.80	2.72	2.61	0.52	70
IGS NANU 150/2004	2.43	1.63	1.37	0.77	0.31	65
IGS NANU 157/2004	6.71	4.61	4.20	3.31	0.49	60
IGS NANU 158/2004	1.35	0.92	0.57	0.45	0.33	73
IGS NANU 159/2004	1.45	1.08	0.72	0.66	0.46	70
IGS NANU 166/2004	8.01	6.03	4.90	4.00	0.50	60
IGS NANU 167/2004	4.35	3.04	2.32	2.20	0.51	66

REMARKS: This species is deposited in the KRACH collection under different names (see Appendix). From the similar *Blinia reussi* it differs in the relatively lower and helmet-shaped shell.

DISTRIBUTION: *Blinia sinzovi* is known from the Early Sarmatian of south Ukraine and from the Middle Sarmatian of western and south Ukraine, and Moldova (e.g. KOLESNIKOV 1935; ANISTRATENKO 2000a; IONESI & *al.* 2005).

*Flexitectura* O. ANISTRATENKO, 2000 (as subgenus *Tectura* (*Flexitectura*))

TYPE SPECIES: *Acmaea (Scurria) tenuissima* SINZOV, 1892, by original designation. Early and Middle Sarmatian of west Ukraine, Middle Sarmatian of the Kerch Peninsula of the Crimea, and Moldova (ANISTRATENKO 2000a).

DIAGNOSIS: Conical, relatively small or tiny patellogastropods with high-conical, laterally compressed shell; the “pancake”-like protoconch smooth or wrinkled. Aperture oval in shape, anterior and posterior edges have distinct flexures; teleoconch ornament of axial ribs or threads. The apex is almost

central or slightly tilted forward. Differs from *Blinia*, with similar type of protoconch, in having anterior and posterior edges with distinct flexures. From *Squamitectura* differs in lack of scalloped and scaly radial ribs on the teleoconch sculpture. From *Tectura* and other known patellogastropods differs in having a “pancake”-like protoconch.

DESCRIPTION: The lateral edges of the shell are usually almost parallel to each other. The teleoconch surface has numerous radiating ridges crossed by concentric lines. The protoconch is round to oval, “pancake”-like, with a smooth or wrinkled surface; sometimes with a small pit on top of the embryonic shell. The transition from the embryonic shell to the teleoconch is usually clearly marked by a constriction or a rim.

*Flexitectura subcostata* (SINZOV, 1892)  
(Text-fig. 4D, 9A, B)

1892. *Acmaea (Scurria) subcostata* n. sp.; SINZOV, p. 61, pl. 3, figs 6-7.

1892. *Acmaea (Scurria) striato-costata* n. sp.; SINZOV, p. 62, pl. 3, figs 8-10.

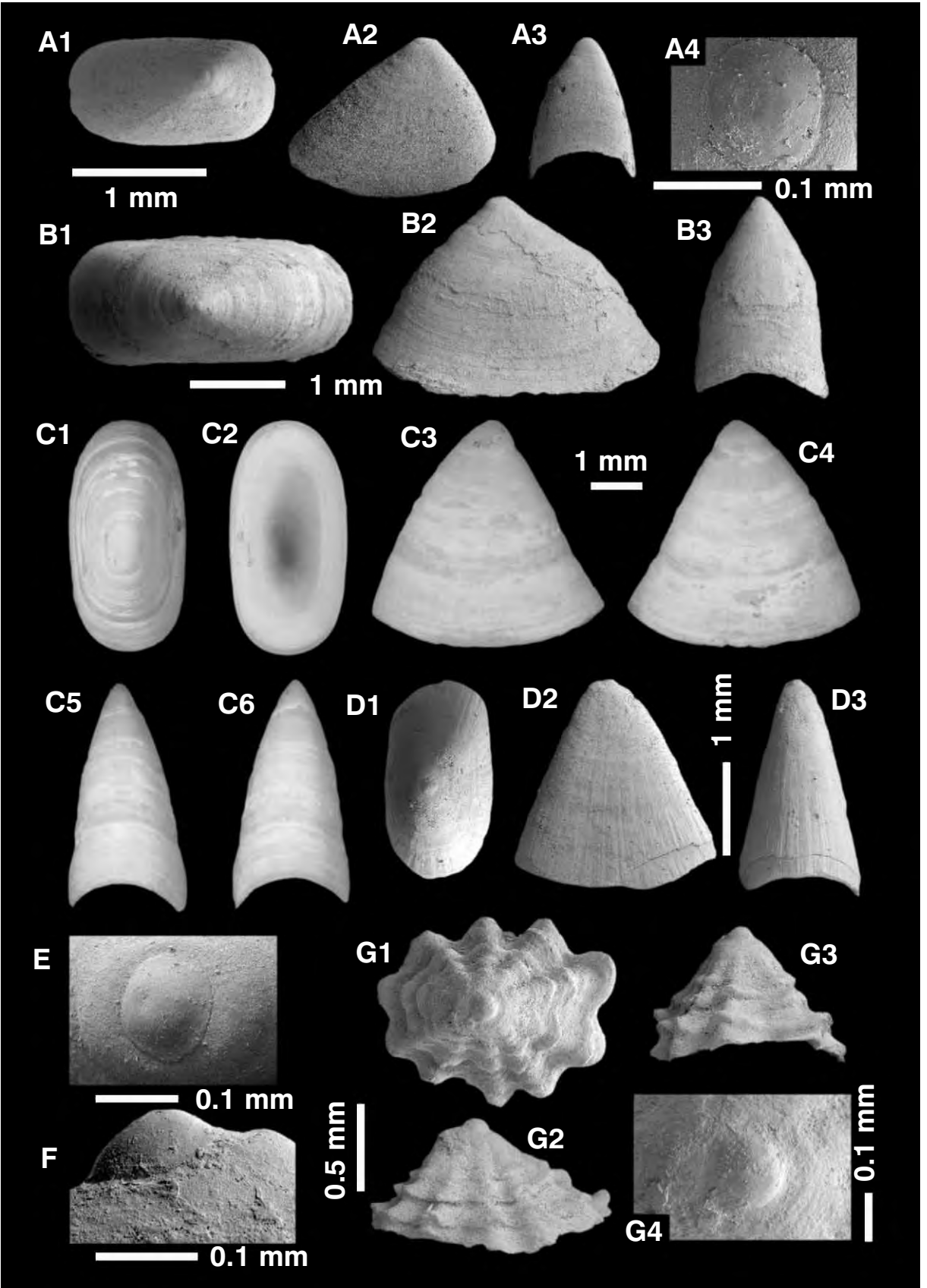
2000a. *Tectura (Flexitectura) subcostata* (SINZOV); ANISTRATENKO, p. 38, pl. 2, figs 7a-c.

2000a. *Tectura (Flexitectura) striatocostata* (SINZOV); ANISTRATENKO, p. 38, pl. 2, figs 11a-c.

2000b. *Tectura (Flexitectura) matvei* n. sp.; ANISTRATENKO, p. 85, figs a-c.

TYPE MATERIAL: Two syntypes of *Acmaea subcostata* SINZOV, 1892 are deposited in the Central Museum of VSEGEL, St.-Petersburg (Russia), coll. I.F. SINZOV, 110, 111/11126.

MATERIAL: Five specimens from the Middle Sarmatian of Dermań, Ukraine, ZNG PAN A-I-95/6; two specimens from the Middle Sarmatian of Warkowicze, Ukraine, ZNG PAN A-I-95/6a; one specimen from the Sarmatian of Listwin, Ukraine, ZNG PAN A-I-95/6b.4; three specimens from the Sarmatian of unknown location, Wołyń, Ukraine, ZNG PAN A-I-95/6c.1-3; one specimen from the Middle Sarmatian of Letichev, Ukraine, IGS NANU, 1/2000; nine specimens from the Middle Sarmatian of Antonovka, Ukraine, IGS NANU, 20/2000 - 28/2000; one specimen from the Early/Middle Sarmatian of Suslovtsy, Ukraine, IGS



NANU, 29/2000; twenty-eight specimens from the Middle Sarmatian of Letichev, Ukraine, IGS NANU, 168/2004 - 195/2004.

**DESCRIPTION:** Shell small, high-conical, with lateral edges subparallel. The apex is almost central or slightly tilted forward. The apical angle usually varies from 35° to 50°. The anterior and posterior slopes are usually convex; the anterior and posterior edges always have distinct flexures. Aperture oval-quad-rangular. The muscle scars in mature specimens are sometimes indistinct (Text-fig. 4D), but in juveniles they are usually clearly visible. The protoconch is “pancake”-like, smooth or wrinkled, sometimes with a small pit on the top of the embryonic shell. The teleoconch surface is covered by numerous radiating ribs or threads crossed by fine concentric lines. The transition from the embryonic shell to the teleoconch is usually marked by a constriction or a rim.

**MEASUREMENTS (in mm):**

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-95/6.1	1.57	0.96	1.22	0.70	0.45	40
ZNG PAN A-I-95/6.2	1.22	0.87	0.96	0.44	0.31	46
ZNG PAN A-I-95/6a.1	2.17	1.30	1.65	1.13	0.52	42
ZNG PAN A-I-95/6a.2	2.09	1.30	1.57	1.04	0.50	44
IGS NANU 1/2000	1.89	1.45	1.25	0.91	0.48	70
IGS NANU 20/2000	4.10	1.85	2.80	2.01	0.49	36
IGS NANU 21/2000	3.43	1.55	2.25	1.50	0.44	35
IGS NANU 22/2000	3.15	1.75	2.38	1.50	0.48	40
IGS NANU 23/2000	3.30	2.11	2.30	1.40	0.42	47
IGS NANU 24/2000	2.32	1.35	1.32	1.10	0.47	51
IGS NANU 25/2000	3.12	1.36	2.18	1.36	0.44	36
IGS NANU 26/2000	2.00	1.11	1.33	0.87	0.44	55
IGS NANU 27/2000	2.41	1.45	1.25	1.20	0.50	60
IGS NANU 28/2000	3.12	1.60	2.16	1.57	0.50	45
IGS NANU 168/2004	2.40	1.21	1.62	1.11	0.46	40
IGS NANU 169/2004	3.11	1.50	1.75	1.40	0.45	46
IGS NANU 183/2004	1.60	0.95	0.99	0.47	0.29	54
IGS NANU 184/2004	1.57	0.83	1.22	0.49	0.31	40

**REMARKS:** From *F. tenuissima* it differs in the significantly lower shell (ratio HS/LS is 0.6-0.8 in adult specimens). From the similarly high-conical *Blinia reussi* it differs in having distinct flexures in the anterior and posterior edges.

**DISTRIBUTION:** *Flexitectura subcostata* is known from the Middle Sarmatian of western Ukraine, the Kerch Peninsula and Moldova (SINZOV 1892; KOLESNIKOV 1935; ANISTRATENKO 2000a, b).

*Flexitectura tenuissima* (SINZOV, 1892)  
(Text-fig. 9C-F)

1892. *Acmaea (Scurria) tenuissima* n. sp.; SINZOV, p. 61, pl. 3, figs 1-2.

1940. *Acmaea pseudolaevigata* SINZOV; SIMIONESCU & BARBU 1940, p. 10, pl. 6, fig. 101.

1944. *Acmaea soceni* n. sp.; JEKELIUS, p. 42, pl. 2, fig. 1, 2 (partim).

2000a. *Tectura (Flexitectura) tenuissima* (SINZOV); ANISTRATENKO, p. 38, pl. 2, figs 8a-e.

2000 b. *Tectura (Flexitectura) kolesnikovi* n.sp.; ANISTRATENKO, p. 86, figs d-f.

**TYPE MATERIAL:** Three syntypes of *Acmaea tenuissima* SINZOV, 1892 are deposited in the Central Museum of VSEGEI, St.-Petersburg (Russia), coll. I.F. SINZOV, 114-116/11126.

**MATERIAL:** Three specimens from the Middle Sarmatian of Wierzchów, Ukraine, ZNG PAN A-I-95/7.1-3; two specimens from the Middle Sarmatian of Baszyna, Ukraine, ZNG PAN A-I-95/7a; two specimens from the Middle Sarmatian of Terlovka, Ukraine, IGS NANU, 2/2000, 3/2000; eight specimens from the Middle Sarmatian of Antonovka, Ukraine, IGS NANU, 4/2000 - 12/2000; four specimens from the Early/Middle Sarmatian of Izyaslav, Ukraine, IGS NANU, 13/2000 - 16/2000; three

Fig. 9. **A, B.** *Flexitectura subcostata* (SINZOV, 1892). A – IGS NANU, 184/2004, Middle Sarmatian, Letichev, Ukraine; A1 – apical view; A2 – right lateral view; A3 – anterior view; A4 – details of apical view of the embryonic shell. B – IGS NANU, 25/2000, Middle Sarmatian, Antonovka, Ukraine; B1 – apical view; B2 – left lateral view; B3 – posterior view. **C-F.** *Flexitectura tenuissima* (SINZOV, 1892). C – IGS NANU, 3/2000, Middle Sarmatian, Terlovka, Ukraine; C1 – apical view; C2 – apertural view; C3-C4 – left lateral and right lateral views respectively; C5 – anterior view; C6 – posterior view. D – IGS NANU, 203/2004, Middle Sarmatian, Letichev, Ukraine; D1 – apical view; D2 – left lateral view; D3 – posterior view. E – IGS NANU, 26/2000, Middle Sarmatian, Letichev, Ukraine; apical view. F – IGS NANU, 16/2000, Early/Middle Sarmatian, Izyaslav, Ukraine; details of apical part of the shell viewed from the right. **G.** *Squamitectura squamata* (O. ANISTRATENKO, 2001), IGS NANU, 8/2000, Middle Sarmatian, Letichev, Ukraine; G1 – apical view ; G2 – left lateral view; G3 – posterior view; G4 – details of apical view of the protoconch and juvenile teleoconch

specimens from the Early/Middle Sarmatian of Suslovtsy, Ukraine, IGS NANU, 17/2000 - 19/2000; forty-three specimens from the Middle Sarmatian of Letichev, Ukraine, IGS NANU, 196/2004 - 238/2004.

**DESCRIPTION:** Shell small, high-conical, laterally compressed, i.e. lateral edges of the shell are almost parallel to each other. The apex is practically central, deviating only insignificantly from this position (see Measurements). The apical angle varies from 30° to 40°. The anterior and posterior slopes are straight or slightly convex; the anterior and posterior edges always have distinct flexures. The aperture is oval-quadrangular. The protoconch is “pancake”-like, smooth or wrinkled, sometimes with a small pit on the top of the embryonic shell. The teleoconch surface is covered by numerous fine radial threads crossed by concentric growth lines. The transition from the embryonic shell to the teleoconch is distinct, marked by a constriction or a rim.

#### MEASUREMENTS (in mm):

No	LS	WS	HS	AP	AE	AA
ZNG PAN A-I-95/7.1	2.09	1.22	1.65	0.96	0.46	40
ZNG PAN A-I-95/7.2	1.65	0.87	1.39	0.70	0.42	35
IGS NANU 4/2000	4.37	1.35	5.10	2.30	0.53	25
IGS NANU 5/2000	3.55	2.10	3.70	1.80	0.51	28
IGS NANU 6/2000	2.90	1.85	2.85	1.55	0.53	35
IGS NANU 7/2000	2.80	1.41	2.03	1.30	0.46	45
IGS NANU 8/2000	3.82	1.10	3.21	1.85	0.48	30
IGS NANU 9/2000	2.54	1.29	2.24	1.20	0.47	32
IGS NANU 16/2000	2.40	1.30	2.22	1.21	0.50	34
IGS NANU 17/2000	1.78	0.87	1.40	0.95	0.53	36
IGS NANU 18/2000	1.50	0.72	1.10	0.70	0.47	35
IGS NANU 196/2004	3.01	1.70	3.50	1.71	0.57	28
IGS NANU 197/2004	2.00	1.25	1.73	0.95	0.48	37
IGS NANU 203/2004	2.20	1.20	2.21	1.11	0.51	30
IGS NANU 204/2004	2.80	1.61	3.20	1.50	0.54	30
IGS NANU 205/2004	3.20	1.60	3.42	1.60	0.50	27
IGS NANU 206/2004	2.90	1.60	2.61	1.50	0.52	33
IGS NANU 207/2004	2.40	1.42	2.40	1.20	0.50	33
IGS NANU 208/2004	2.59	1.70	2.50	1.40	0.54	39

**REMARKS:** This species is deposited in the KRACH collection under different names (see Appendix).

From *F. subcostata* it differs in the significantly higher shell (ratio HS/LS is 0.8-1.2 in adult specimens).

**DISTRIBUTION:** *Flexitectura tenuissima* is known from the Middle Sarmatian of western Ukraine and Moldova (SINZOV 1892; KOLESNIKOV 1935; ANISTRATENKO 2000a, b).

*Squamitectura* O. ANISTRATENKO, 2001 (as subgenus *Tectura* (*Squamitectura*))

**TYPE SPECIES:** *Tectura* (*Squamitectura*) *squamata* O. ANISTRATENKO, 2001, by original designation. Middle Sarmatian of west Ukraine.

**DIAGNOSIS:** Shell minute conical, slightly compressed laterally with smooth “pancake”-like protoconch. Aperture oval, anterior and posterior edges have distinct flexures; sculpture of ten strong scalloped and scaly radial ribs. From *Blinia* and *Flexitectura*, with similar type of protoconch, differs in its distinctive teleoconch sculpture.

**DESCRIPTION:** The edge of the shell is scalloped. The teleoconch surface covered by wide radial ribs, covered by scales. The protoconch is round and “pancake”-like; the transition from the embryonic shell to the teleoconch is clearly marked by a rim and the beginning of adult ornamentation.

*Squamitectura squamata* (O. ANISTRATENKO, 2001)  
(Text-fig. 9G)

2001. *Tectura* (*Squamitectura*) *squamata* n. sp.; O. ANISTRATENKO, p. 94, fig. 1a-d.

**TYPE MATERIAL:** The holotype, from the Middle Sarmatian of Letichev, Ukraine, IGS NANU, 8/2000.

**MATERIAL:** The holotype.

**DESCRIPTION:** The shell is tiny, low-conical in all lateral views, ovoid in dorsal view. The apex is subcentral, tilted slightly forward. The apical angle in anterior view is 83°. The anterior and posterior slopes are almost straight; the anterior and posterior edges have distinct flexures. The sculpture consists of ten strong, wide, scalloped radial ribs covered by thick-edged scales. The space between the ribs is approximately the same as their width. The scales are arranged in concentric lines which accord



to the shape of the apertural edge. The aperture is ovoid and scalloped. The inner surface is smooth, porcelain-like and shiny, with radial depressions corresponding to radial ribs on the outer surface. The muscle scars are visible under high magnification, best seen when lit from the side. The protoconch is oval, pancake-like, apparently smooth, shiny. The transition between the protoconch and the early teleoconch is sharply marked by a well developed constriction.

MEASUREMENTS (in mm): Holotype only:

No	LS	WS	HS	AP	AE	AA
IGS NANU, 8/2000	1.46	1.23	0.85	0.58	0.40	83

REMARKS: From all known *Blinia* and *Flexitectura*, with a similar type of protoconch, it differs in its distinctive teleoconch sculpture.

DISTRIBUTION: This species is known only from the type locality – the Middle Sarmatian deposits of Letichev (Khmelnitsky region) in western Ukraine.

## DISCUSSION AND CONCLUSIONS

### Variability, Comparative shell morphology and Relationships

The identification of some lottiids described here is difficult due to the wide range of their shell variability, reflected e.g. in the wide variation of the apical angle (see Measurements). The other most variable character of the lottiid shell is the degree of axial rib development – sometimes these are sharp and strong but at other times weak and/or almost absent, albeit the number of axial ribs on the teleoconch of *Tectura* and *Blinia* is constant. A smooth surface of the shell is usually the result of the peeling off of the outermost layer.

Since the shell shape is variable in all the species studied, the more reliable diagnostic characters are those of protoconch morphology, particularly dimensions. However, there is also variability in protoconch dimensions, e.g. the larger diameter of the embryonic shell (“pancake”) in *Blinia reussi* ranges from 0.13 mm to 0.16–0.18 mm.

The more or less wide variability of all the features mentioned is the reason for not considering as reliable diagnostic characters based on only one or

two of them. The most reliable diagnosis requires using the complex of all available characters and dimensions.

Comparison of the Mid Miocene lottiids described above with other patellogastropods is confined mainly to taxa which lived in the pre-existing Badenian Basin, i.e. *Patella*, *Tectura*, *Propilidium* and some others. It is pointless to compare them with groups absent from that basin and/or definitely unrelated to taxa discussed here (for example, fissurellids). Some comparative remarks on *Erginus* and *Lottia* are provided since they are morphologically similar and, presumably, more or less closely related to *Tectura* and *Blinia-Flexitectura*.

It is known that species of *Patella* actively throw off the protoconch after sealing the interior with a septum (e.g. SMITH 1935, WARÉN 1988). The larval shell of *Lottia tenuisculpta* SASAKI & OKUTANI, 1994 is similar in shape and proportions to those of Recent *Patella* and Badenian *Tectura* spp. (Text-figs 5A3, A5, 7B3), and is also usually rejected in adult individuals. The place where it was attached is marked by a distinct scar with a large pore, sealed with a calcareous plug (septum), as figured by SASAKI (1998, fig. 21, d-h). Behind the scar, a more or less distinct impression or concavity is present, formed by the overhanging part of the larval shell (WARÉN 1988, figs 12-14). The shells of *Tectura* from the Badenian and the first half of the Early Sarmatian usually have a similar scar (generally clearly marked even in adult individuals – see Text-figs 5C3, D, 7C4) and a small impression behind it. That agrees in a general way with the scenario of the larval/early postlarval development of *Patella*, *Lottia* and some other patellogastropods (e.g. SMITH 1935, MARSHALL 1985, WARÉN 1988, SASAKI 1998).

The similarity of the Badenian *Tectura* to recent *Lottia tenuisculpta* is sufficiently significant (similar protoconch and almost the same type of teleoconch sculpture) to consider them as not only belonging to the same family, but to suspect their close relationship. At the same time, it must be emphasized that type of development (taken as a character in isolation) has usually nothing to do with phylogenetic relationships or taxonomy.

The protoconch of Badenian *Tectura* species (in contrast to those of e.g. *Patella* and *Lottia*) falls off, with no adjacent part of the initial teleoconch attached. Therefore the plane of the scar in *Tectura* is almost perpendicular to the apertural plane,

whereas these planes are usually parallel in most patellogastropods. Those characteristics show that the *Tectura* spp. studied should not be considered as congeneric with either *Patella* or *Lottia*, albeit the latter genus exhibits a remarkable morphological similarity to the Badenian lottiids.

The shell shape, structure of protoconch and sculpture of the Recent *Tectura virginea* (type species of *Tectura*) concord well with those of the Badenian lottiids studied. The latter differ mainly in finer sculpture, smaller shell size and a slightly less bulbous embryonic shell. The last feature could be judged from a SEM image of a specimen of *T. virginea* from the Mediterranean (kindly provided by Dr. Anders WARÉN). Besides these small but clear differences, the existence of a huge time-gap between the recent *T. virginea* and Badenian *Tectura* species prevents us from considering them to be conspecific. Moreover, the shell structure of fossil *Tectura* differs substantially from that of *T. virginea* (see ANISTRATENKO & al. 2006).

As has been described above, the apex in the Badenian *Tectura* is positioned either somewhat tilted forward (*T. laevigata*) or almost centrally (*T. compressiuscula*), but in juvenile individuals it is clearly tilted backward; the protoconch is always directed backward (Text-figs 5A2, B2, C2; 7B2, C2). The recent *Propilidium ancyloide* (family Lepetidae) is similar to the Badenian *Tectura* in shell shape but differs significantly in having the apex tilted in the same direction as the protoconch (i.e., forward) and also in less regular sculpture. The apex in *P. ancyloide* is tilted well forward, sometimes producing a hook-like appearance, similar to that of some Sarmatian *Blinia* (e.g. Text-fig. 8C), but differs in having a spirally coiled protoconch.

The *Tectura* studied agree well with the Badenian *Propilidium circulare* BOETTGER, 1901 and *P. oblongum* BOETTGER, 1906 described from Kosteĵ in Transylvania. The type specimens of these two lepetids, figured by ZILCH (1935) and, particularly, specimens of *P. circulare* recently recorded and figured by BAŁUK (2006) from Korytnica, exhibit a very similar shape of shell, and sculpture. They differ, however, in the tilting direction of the apex and protoconch; in *Propilidium* both the apex and protoconch are tilted in the same direction whereas they are tilted in different direction in the *Tectura*.

The shell outline of *Tectura* discussed here is similar to that of some Badenian cocculinids, e.g. *Cocculina miocaenica* BOETTGER, 1901 and

*Cocculina unica* BAŁUK, 2006, which have recently been recorded from the famous Badenian locality Korytnica in Poland (BAŁUK 2006). The former species was known before from Kosteĵ in Transylvania (BOETTGER 1901). Both *Cocculina* species are similar in shape and type of sculpture but differ from *Tectura* in having an anteriorly placed apex. In describing *C. unica*, the author remarked that the convex protoconch, situated left of the apex, lacked spiral coiling (BAŁUK, 2006). That means that the protoconch is asymmetrically positioned relative to the sagittal axis of the teleoconch (as in *Tectura laevigata*) and should be spirally coiled but, due to poor the poor preservation of the shell used for description, this character has not been detected. In addition, the sculptural elements of *C. unica* – riblets composed of pearl-like tubercles and slightly arched leftwards – are completely atypical of the *Tectura* studied here.

The absence of a scar from the protoconch, and the bowl-shaped apex, make some *Blinia* and *Flexitectura* similar to recent monoplacophoran, namely *Neopilina goesi*, which was described and figured sufficiently well (WARÉN 1988, figs 2-7) to allow comparison with the species discussed here. However, it is obvious that the similarity is only superficial and due to convergence (the shell structure of the fossils studied is quite different from that in Monoplacophora), probably caused by a similar early ontogenetic scenario. In any case, the ecological conditions of the Sarmatian Sea were unsuitable for Monoplacophora at that time.

The lepetelloid *Bathysciadium xylophagum* WARÉN & CARROZZA, 1996 is also similar in general shape of the shell and its apex to *Blinia* and *Flexitectura*. However, it differs in having a scar and a flat septum (WARÉN 1996, fig. 9a-d) at the point where the spirally coiled protoconch broke off – visible in juvenile specimens (WARÉN 1996, fig. 2b) – whereas neither *Blinia* nor *Flexitectura* have a scar or septum.

Our observations show that the concentric sculpture of the protoconch in *Blinia* and *Flexitectura* is never covered by the outer layers of the adult shell. Moreover, an elevated hem around their larva's aperture is always situated on top of the early teleoconch (i.e. covering it as a cap) but never on the inside as in e.g. *Patella*, *Lottia* or any other patellogastropods having a zone of larval shell breakage (WARÉN 1988, figs 12-14; SASAKI 1998, fig. 21, d-h). This shows that the apical part of

the *Blinia-Flexitectura* shell (see Text-figs 8 and 9) represents a protoconch, but not a secondary septum as in e.g. *Lottia* and that the ‘wrinkles’ (the concentric sculpture) are not secondarily deposited.

Judging from our extensive scanned material (dozens of juveniles), the “pancake” may either have wrinkles or be devoid of wrinkles. There may also be either a pit on the top of the “pancake” or no pit. The pit, therefore, should not be considered as the remains of the pore (like in e.g. *Patella* or *Lottia*), though they are both situated in a similar position.

The origin of the concentric sculpture (‘wrinkles’) observed on some “pancake”-like protoconchs is still uncertain. Prof. Klaus BANDEL (personal communication) considers that initially (before hatching) the larval shell in these individuals was probably soft, with a smooth surface, and susceptible to creasing. The ‘wrinkles’ represent traces of creasing of this soft larval shell before calcification and the development of callosity were completed (Text-fig. 8G, H). It is suggested that creasing of a shell might have occurred during hatching when something hampered the hatching of the larva, such as a narrow space in the brood sac. Although no proof for this supposition can be provided as yet, this ‘mental picture’ could nevertheless perhaps be considered as a reasonable working hypothesis.

The distinctly concave base of the Sarmatian lottiids should be commented on briefly. The majority of patellogastropods have a plane aperture and thus differ markedly from *Flexitectura* and *Squamitectura*, which are characterized by the presence of distinct flexures in both the anterior and posterior edges of the shell (Text-fig. 9).

It has been indicated before (e.g. ANISTRATENKO 2000a) that, besides the flexures in the anterior and posterior edges, the shells of *Flexitectura* and *Squamitectura* species are also laterally compressed. Additionally, these two genera never occurred outside the bryozoan reefs. Since these two characteristics always coincide, it may be suggested that the ‘flexured’ lottiids were specialized forms adapted to crawling through the ‘micro-relief’ in bryozoan buildups or even to being attached to bryozoan branches. Such a kind of environment should trigger some change in shell morphology and, perhaps also in early ontogeny.

Species of the genus *Erginus* (as mentioned above) brood the developing embryos in the pallial

cavity and they hatch as crawling limpets (GOLIKOV & KUSSAKIN 1972). Their larval shell is apparently slightly more convex than those usually documented in *Blinia* and *Flexitectura* (Text-figs 8 and 9) albeit the fossil shells sometimes show a bowl-like protoconch (Text-figs 8I, 9F) very similar to that of *Erginus moskalevi* (see SASAKI 1998, fig. 21a, b). Although the differences between *E. moskalevi* and *Blinia* or *Flexitectura* show that a direct relationship is out of the question, nevertheless the similarity of these taxa supports us in the assignment of the fossils discussed here to the same family (Lottiidae) as *Erginus*.

Lottiids surviving in the Badenian and in the first half of the Early Sarmatian (Volhynian substage) were represented by *Tectura* spp., which were then replaced by *Blinia* and *Flexitectura*, i.e., lottiids with a pancake-like protoconch. According to the stratigraphic occurrences, the representatives of *Tectura* should be considered as the initial group to the ‘pancake’-bearing lottiids discussed here. It makes sense to assume a direct relationship between the Badenian and Sarmatian lottiids. In fact, the lecithotrophic forms were more probably descended from the planktotrophic one than vice versa (see above). Sarmatian *Blinia*, as well as *Flexitectura* and *Squamitectura*, are considered here as lottiid branches closely related to the Badenian *Tectura*, since no other more morphologically similar patellogastropods are known from these basins that could be regarded as ancestral stock. Additionally, in the Early Sarmatian basin was already landlocked and immigrants from the Mediterranean had no chance to penetrate.

### Palaeogeography and Palaeoecology

The available data show that all the species described here were irregularly distributed in both space and time. The western part of the Eastern Paratethys (notably localities in western Ukraine) was inhabited by more than half of all the known lottiids recognized (Table 1). Southern Ukraine (e.g. the Shirokoe locality) and Moldova are characterized by significant lottiid diversity as well, albeit less than in the previous region. In contrast, the majority of localities from the Central Paratethys (e.g. Korytnica, eastern Poland) as well as the most south-eastern of the regions studied (e.g. in the Kerch Peninsula and Western Sub-Caucasian) exhibit very few species of lottiids.

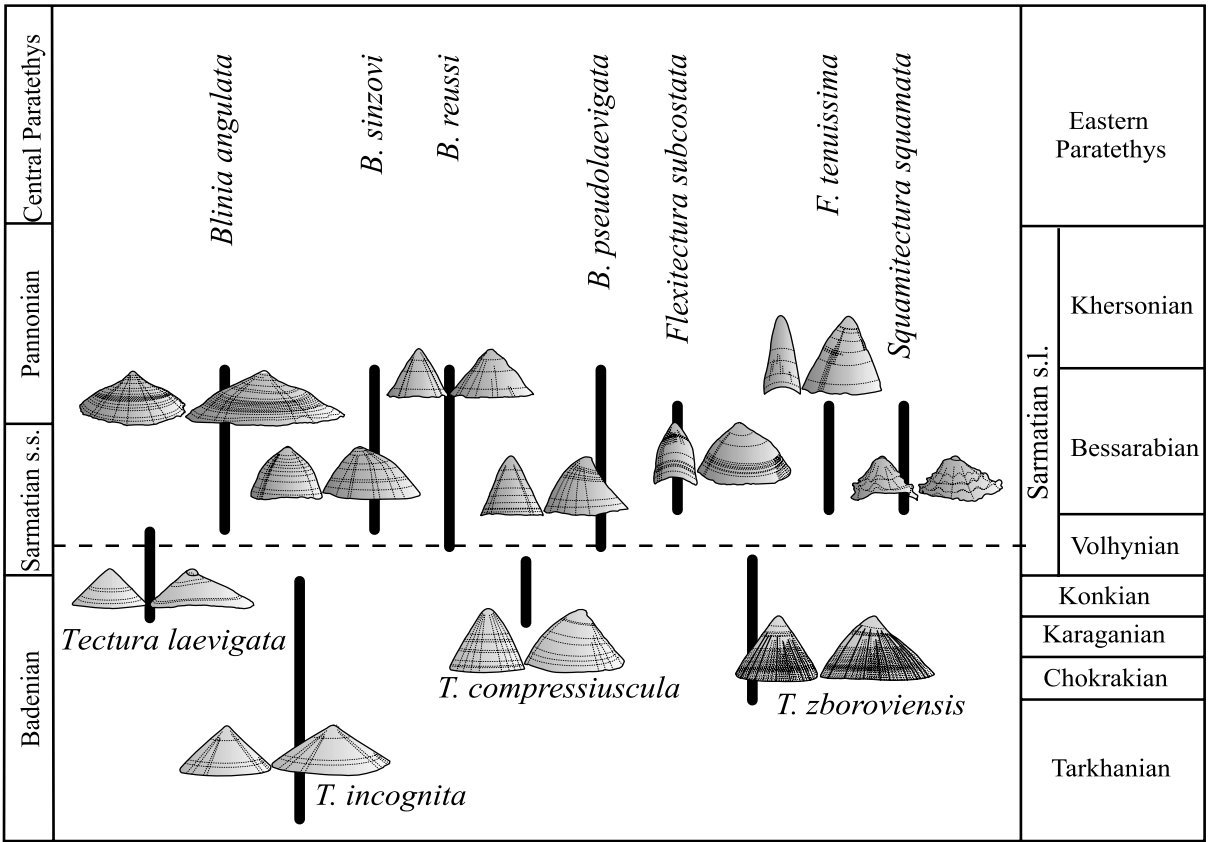


Fig. 10. Stratigraphical distribution of Lottiidae in the Middle Miocene of Paratethys. Note the time-border between the lottiids with typical patellogastropod protoconch morphology (*Tectura*) and lecithotrophic development (*Blinia*, etc.) is located in the mid-Early Sarmatian (Volhynian)

The material studied shows that *Blinia pseudolaevigata* and *B. reussi* are the two most frequently occurring and abundant species of *Blinia* in the Sarmatian deposits. The remaining species of *Blinia* are represented almost equally in the localities studied. The commonest and most widely ranging *Tectura* was *T. laevigata*. *T. incognita* appears to be rare (although the material is unrepresentative) while *T. compressiuscula* and *T. zboroviensis* are almost equally represented in fossil material.

The richest lottiid fauna occurred in the Middle Sarmatian (Volhynian-Bessarabian), the lottiid faunas are less rich in the Badenian and are particularly poor in the Early Sarmatian (Table 1). A drastic change in lottiid protoconch morphology took place in the Early Sarmatian (see below).

According to data obtained in the Badenian of the Central Paratethys, and in the Chokrakian of the Eastern Paratethys, only lottiids with “typical” patellogastropod protoconch morphology occurred. At least four species of *Tectura* appar-

ently had a planktotrophic development, including a free-swimming larval stage. In the lower half of the Lower Sarmatian (Kuzhorskaya horizon, Volhynian substage – i.e. below the demarcation shown in Text-fig. 10), lottiids with the same type of protoconch as in the Badenian have been noted. However, starting from the upper half of the Lower Sarmatian (Zbruchian horizon, Volhynian substage) and in the middle Sarmatian (Bessarabian) – i.e. above the demarcation shown in Text-fig. 10 – no lottiids with a protoconch of the type in Badenian *Tectura* (Text-fig. 5A, B) were found. The lottiids at these levels possessed a pancake-like protoconch, evidencing a lecithotrophic development, supposedly without even a very short free-swimming larval stage (ANISTRATENKO & *al.* 2006). No transitions or so-called intermediate morphological forms have been registered.

The boundary between the Badenian and Sarmatian was characterized by a substantial

change in basin conditions, resulting in significant faunal changes. The Badenian Basin in the Central Paratethys (as well as the Chokrakian Basin in the Eastern Paratethys) were widely connected with the open ocean (e.g. RÖGL 1998) and were characterized by an exceptionally rich molluscan fauna indicating normal marine conditions (e.g. BAŁUK 1975; KOWALKE & HARZHAUSER 2004). At the Badenian/Sarmatian boundary, there was a marked decrease in molluscan diversity, with the disappearance of polyhaline groups, suggesting that significant freshening took place. In contrast to the Badenian Basin, the Early Sarmatian Basin had a very restricted connection with the open sea and developed into a brackish semi-marine, low-salinity basin (e.g., KOLESNIKOV 1935; RÖGL 1998). In spite of brief and local connections with the Mediterranean assumed to have occurred in the Early Sarmatian, immigration was very limited and no incursions of new patellogastropods have been recorded. The Middle Sarmatian (Bessarabian) Basin is considered to have had even lower salinities – no more than 15‰ (see e.g., MUZYLEV & GOLOVINA 1987); it remained landlocked up to the end of the Bessarabian substage, marked by a major extinction of all faunas of marine origin.

At the beginning of the Volhynian substage in the Subcarpathian Basin – namely, in Galician Bay (west Ukraine), a significant freshening has been demonstrated based on geochemical data (e.g. GAŚIEWICZ & CZAPOWSKI 2005). The Galician Bay was inhabited by a very rich, apparently brackish fauna. Certainly, being a huge basin, the Sarmatian Basin would have had local zones with different conditions, e.g. hypersalinity, as was argued by BELOKRYŚ (1967) for the Borysthenian Bay (South Ukraine) or by PILLER & HARZHAUSER (2005) in the case of the Vienna Basin.

The problem of the existence in the Sarmatian Basin of zones of hypersalinization, as well as zones with brackish conditions, requires to be discussed in more detail elsewhere. In view of the vast size and long duration of the basin, it can be supposed that the Sarmatian Sea was locally hypersaline, but that most of its eastern half was most likely a semi-marine basin at least in Middle Sarmatian (Bessarabian) time.

It has been demonstrated that the larval shell morphology changed significantly in some Badenian/Early Sarmatian nassariids (HARZHAUSER & KOWALKE 2004) and rissoids (ANISTRATENKO 2005).

These major changes in early development coincided each time with supposedly decreasing salinities in the Paratethys basins. The same obtained in the Maeotian stage, when the rissoids, basically inhabiting marine conditions, had a planktotrophic larva, whereas brackish-water sediments contain lecithotrophic forms, e.g. *Coelacanthia* (e.g. ANISTRATENKO 2004).

In view of these precedents, and our unpublished data, we suggest that the modifications in protoconch morphology of the Badenian/Sarmatian lottiids are evidence of alteration (“switching”) of their early ontogeny type from a planktotrophic to a lecithotrophic one, triggered by decreasing salinities of the water (ANISTRATENKO & ANISTRATENKO 2005, 2006 a, b; ANISTRATENKO & *al.* 2006).

As previously noted, the change in ontogenetic strategy occurred during a time of lowered salinity in the Paratethys. We suggest that the reproductive strategy in the case of *Tectura-Blinia* was modified and that free larval life was suppressed to cope with salinity change in the ambient water (ANISTRATENKO & *al.* 2006).

Based on these data, it has been hypothesized that lecithotrophic development in some Miocene gastropods was probably a biological response to decreasing salinities below a physiological barrier (presumably about 13-15 ‰). The patellogastropods discussed here provide the most detailed illustration so far that this evolutionary process of changing reproductive strategies has occurred several times (ANISTRATENKO & ANISTRATENKO 2006 a, b).

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## Appendix

The List of Badenian to Sarmatian occurrences of *Tectura*, *Flexitectura* and *Blinia* species deposited in the Geological Museum of the IGS PAS (Kraków, Poland) collections of W. FRIEDBERG and W. KRACH.  
Total amount 173 samples in 51 lots.

Number of lots according to Museum Catalogue	Species name according to FRIEDBERG (1928) and KRACH (1951, 1981)	Pages, No of Tables and figures in the appropriate monograph			Locality	Number of specimens	Species name, recognized in the present paper (number of specimens in parenthesis)
		Page	Table	Figure			
A-I-50/ 1785	<i>Tectura compressiuscula</i> (Eichw.)	534-535	35	6	Faszczówka	1	<i>Tectura compressiuscula</i>
A-I-50/ 1786	“-“	-	-	-	Borki Wielkie	1	<i>Tectura compressiuscula</i>
A-I-50/ 1787	“-“	534-535	-	-	Podhorce	1	<i>Tectura compressiuscula</i>
A-I-50/ 1788	“-“	-	-	-	Szuszkwowce	2	<i>Tectura compressiuscula</i>
A-I-50/ 1789	“-“	534-535	-	-	Jasionów	4	<i>Tectura compressiuscula</i>
A-I-50/ 1790	“-“	-	-	-	Zaleśce	4	<i>Tectura compressiuscula</i>
A-I-50/ 1791	“-“	-	-	-	Olesko	1	<i>Tectura compressiuscula</i>
A-I-50/ 1792	<i>Tectura laevigata</i> (Eichw.)	535-536	35	7	Hluboczek Wielki	1	<i>T. laevigata</i>
A-I-50/ 1793	“-“	535-536	-	-	Podhorce	2	<i>T. laevigata</i>
A-I-50/ 1794	“-“	535-536	-	-	Jasionów	1	<i>T. laevigata</i>
A-I-50/ 1795	“-“	-	-	-	Korytnica	1	<i>Fissurellidea clypeata</i> (Grateloup, 1927)
A-I-50/ 1796	“-“	535-536	-	-	Zaleśce	10	<i>T. laevigata</i>
A-I-50/ 1797	“-“	535-536	-	-	Chlebów	2	<i>T. laevigata</i>
A-I-50/ 1798	“-“	-	-	-	Stary Poczajów	1	<i>T. laevigata</i>
A-I-50/ 1799	“-“	535-536	-	-	Żukowce	6	<i>T. laevigata</i>
A-I-50/ 1800	“-“	-	-	-	Szuszkwowce	1	<i>T. laevigata</i>
A-I-50/ 1801	<i>Tectura zboroviensis</i> Friedb.	536	35	8	Zborów	1	<i>T. zboroviensis</i>
A-I-50/ 1802	“-“	536	-	-	“-“	2	<i>T. zboroviensis</i>
A-I-50/ 1803	“-“	536	-	-	Borki Wielkie	2	<i>T. zboroviensis</i>
A-I-50/ 1804	“-“	-	-	-	Zaleśce	5	<i>T. zboroviensis</i>
A-I-50/ 1805	“-“	-	-	-	Stary Poczajów	1	<i>T. zboroviensis</i>
A-I-50/ 1806	<i>Tectura incognita</i> Friedb.	536-537	35	9	Borki Wielkie	2	<i>T. incognita</i>
A-I-87/75	<i>Acmaea laevigata</i> (Eichw.)	42-43	12	15-17	Węglinek	15	<i>T. laevigata</i> (14), <i>T. compressiuscula</i> (1)
A-I-95/1	<i>Acmaea compressiuscula</i> (Eichw.)	6-7	-	-	Wierzchów	8	<i>Blinia angulata</i> (7), <i>B. pseudolaevigata</i> (1)
A-I-95/1a	“-“	6-7	-	-	Glińsk	2	<i>B. angulata</i> (1), <i>B. pseudolaevigata</i> (1)
A-I-95/1b	“-“	6-7	-	-	Dermań	17	<i>B. pseudolaevigata</i>
A-I-95/1c	“-“	6-7	-	-	Bacaj	3	<i>B. pseudolaevigata</i>
A-I-95/1d	“-“	6-7	-	-	Żołobki	1	<i>B. pseudolaevigata</i>
A-I-95/1e	“-“	6-7	-	-	Listwin	9	<i>B. sinzovi</i>
A-I-95/1f	“-“	6-7	-	-	Waśkowce	6	<i>B. pseudolaevigata</i>
A-I-95/1g	“-“	6-7	-	-	Warkowicze	8	<i>B. pseudolaevigata</i> (5), <i>B. reussi</i> (3)
A-I-95/1h	“-“	-	-	-	Czajczyńce	1	<i>B. pseudolaevigata</i>
A-I-95/1i	“-“	-	-	-	Stary Poczajów	1	<i>T. laevigata</i>
A-I-95/2	<i>Acmaea</i> an n. sp.	7	1	1-4	Waśkowce	-	material absent
A-I-95/2a	“-“	7	1	1-4	Krugolec	-	material absent
A-I-95/2b	“-“	7	1	1-4	Dermań	-	material absent
A-I-95/3	<i>Acmaea laevigata</i> (Eichw.)	7	1	5, 6	Wierzchów	-	material absent
A-I-95/3a	“-“	7	1	5, 6	Warkowicze	-	material absent
A-I-95/3b	“-“	-	-	-	Dermań	1	<i>B. angulata</i>
A-I-95/3c	“-“	-	-	-	Szuszkwowce	1	<i>T. zboroviensis</i>
A-I-95/3d	“-“	-	-	-	Zaleśce	14	<i>T. laevigata</i> (13), <i>T. incognita</i> (1)
A-I-95/3e	“-“	-	-	-	Żukowce	2	<i>T. laevigata</i>
A-I-95/4	<i>Acmaea</i> cf. <i>angulata</i> (d’Orb.)	7-8	1	7	Spasów	-	material absent
A-I-95/4a	“-“	7-8	1	7	Dermań	-	material absent

A-I-95/5	<i>Acmaea pseudolaevigata</i> Sinz.	8	1	8-11	Dermań	9	<i>B. pseudolaevigata</i> (3), <i>B. reussi</i> (3), <i>B. sinzovi</i> (3)
A-I-95/6	<i>Acmaea subcostata</i> Sinz.	8	1	12-14	Dermań	5	<i>Flexitectura subcostata</i>
A-I-95/6a	-“-	8	1	12-14	Warkowicze	2	<i>F. subcostata</i>
A-I-95/6b	-“-	8	1	12-14	Listwin	4	<i>F. subcostata</i> (1), <i>B. reussi</i> (3)
A-I-95/6c	-“-	-	-	-	? Wołyń	6	<i>F. subcostata</i> (3), <i>B. pseudolaevigata</i> (2), <i>B. angulata</i> (1)
A-I-95/7	<i>Acmaea reussi</i> Sinz.	9	1	15, 16	Wierzhów	4	<i>B. pseudolaevigata</i> (1), <i>F. tenuissima</i> (3)
A-I-95/7a	-“-	9	1	15, 16	Baszyna	2	<i>F. tenuissima</i>