



## Benthic foraminiferal morphogroups from the Paleogene of the Republic of Macedonia – characterization and paleoecological significance

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## Бентосни фораминиферни морфогрупи от Палеогенската система в Република Македония – характеристика и палеоеколожко значение

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**Abstract.** Benthic foraminiferal assemblages belonging to clayey-carbonate-sandy successions of Late Eocene-Early Oligocene age from seven sedimentary basins of central (Vardar Zone) and eastern part (Serbian-Macedonian Massif) of the Republic of Macedonia were analyzed. The foraminiferal data, obtained from 13 sections (146 samples studied), allowed the definition and illustration of 11 morphological groups (morphogroups or morphotypes) based on the test shape and the nature of test coiling (i.e. chamber addition): rounded trochospiral (RT), plano-convex trochospiral (PT), biconvex trochospiral (BT), milioline (M), rounded planispiral (RP), lenticular (L), tapered and cylindrical (T/C), spherical (S), flattened tapered (FT), tube-shaped (T), and heteromorphous (H). The present article aims to expand the paleoenvironmental analysis by combining of the morphological features with inferred life-style (epifaunal, shallow infaunal and deep infaunal) and feeding strategy (suspension feeder, deposit feeder, herbivores, etc.) of the foraminifera. Comparison of our morphogroup system to modern and fossil ones is outlined accordingly. Generally, the investigated assemblages are slightly dominated by morphogroups characteristic for shallow (shelf) environment.

**Keywords:** benthic foraminifers, morphogroups, paleoecology, Paleogene, Republic of Macedonia.

**Резюме.** Анализирани са бентосни фораминиферни асоциации от глинесто-карбонатно-песъчливи последователности с къснооценско-раноолигоценска възраст от 7 седиментни басейна от централната (Вардарска зона) и източната част (Сръбско-Македонски масив) на Република Македония. Фораминиферните данни, получени от 13 разреза (146 анализирани пробы), позволиха дефинирането и илюстрирането на 11 морфологични групи (морфогрупи или морфотипове) въз основа на формата на черупиха и начина на завиването ѝ (т. е. добавянето на нови камери): закръглена коничноспирална, плоскоизпъкната коничноспирална, двойноизпъкната коничноспирална, милиолидна, закръглена плоскоизпъкната, лещовидна, заострена и цилиндрична, сплесната заострена, тръбеста и хетероморфна. Настоящата статия има за цел да разшири палеоеколожкия анализ чрез комбиниране на морфологичните характеристики с предполагаемия начин на живот (епифауна, плитка инфауна и дълбока инфауна) и начина на хранене (придълни биофилтратори, тинеяди, растителнодядни и др.) на фораминиферите. Предложената схема е съпоставена с описани съвременни и фосилни асоциации. Като цяло, изучените асоциации са доминирани слабо от морфогрупи, характерни за плитководна (шelfова) обстановка.

**Ключови думи:** бентосни фораминифери, морфогрупи, палеоекология, Палеоген, Република Македония.

## Introduction

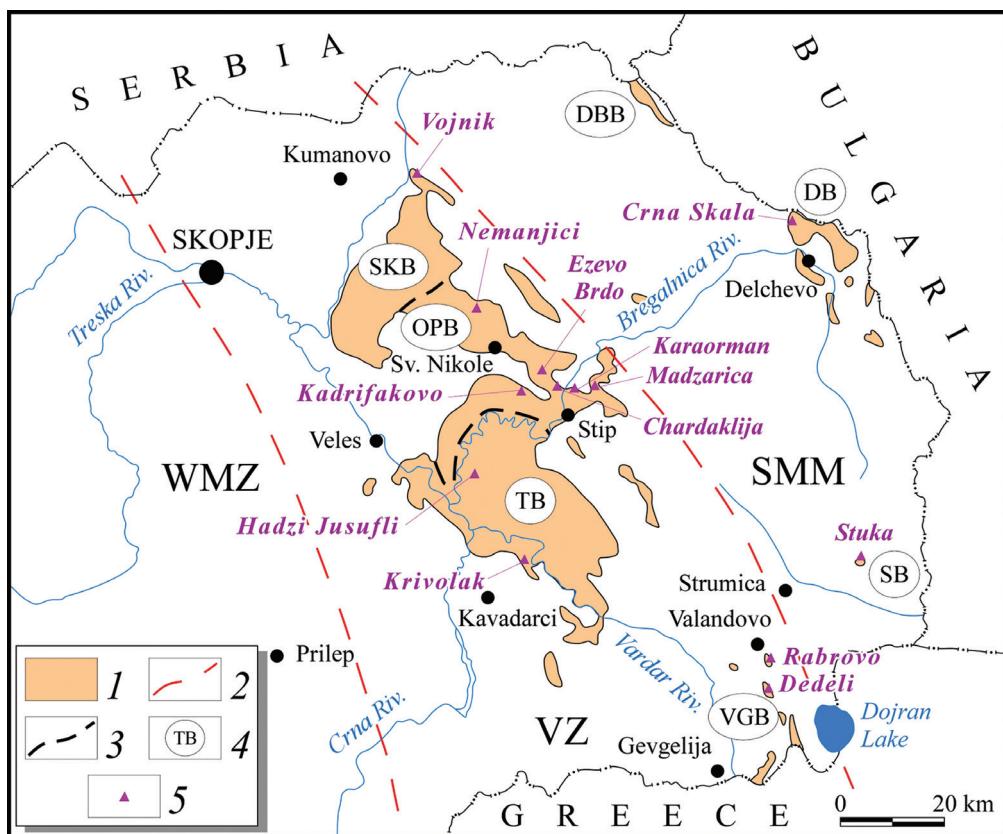
It is widely known that benthic foraminifers are one of the most useful fossil groups for interpretation of ancient marine environment. Attempts to use these microfossils for paleoenvironmental conclusions have been made since the end of the 19th century when agglutinated foraminifers from the Carpathians were involved in the studies (Grzybowski, 1898), but the real initial steps in the elucidating of the paleoeco-

logical significance of foraminiferal test morphology are dated from the 60s, 70s and 80s of the 20th century (Bandy, 1960, 1964; Chamney, 1976; Severin, 1983). After that various articles, concerning mainly the depth influence, were published (see Boltovskoy et al., 1991; Murray, 1991, 2006). The morphogroup concept was introduced by Jones and Charnock (1985) and further developed in great number of works based both on modern and fossil assemblages (e.g. Corliss, 1985, 1991; Bernhard, 1986; Corliss, Chen, 1988;

Koutsoukos et al., 1990; Nagy, 1992; Tyszka, 1994; Khare et al., 1995; Nagy et al., 1995, 2009; Bąk et al., 1997; Bąk, 2004; Szydło, 2005; Reolid et al., 2008; Motamedalshariati et al., 2010; Alperin et al., 2011, and others) by involving data about parameters like temperature, salinity, oxygen levels, carbonate dissolution, substrate, nutrition, dissolved oxygen, illumination, pollution, life-style and feeding strategies.

The Paleogene sedimentary rocks (Upper Eocene–Lower Oligocene – Maksimović et al., 1954; Mitrovič-Petrović et al., 1990; Stojanova, 2008; Stojanova et al., 2011, 2012, 2013; Stojanova, Petrov, 2012) of the Republic of Macedonia, cropping out in the central and eastern part of the country, and divided into 7 sedimentary basins in 2 tectonic zones (Fig. 1), contain diverse benthic foraminiferal microfauna (the studied specimens have been obtained from 13 sec-

tions: Vojnik, Nemanjici, Ezevo Brdo, Kadrifakovo, Chardaklija, Karaorman, Madzarica, Hadzi Jusuflı, Krivolak, Rabrovo, Dedeli, Crna Skala, and Stuka, as their lithology, fossil content and age have been discussed in the works of Maksimović et al., 1954; Stojanova, 2008; Stojanova et al., 2011, 2012, 2013; Stojanova, Petrov, 2012). A total of 65 species (picked up from 146 samples) have been recorded and described taxonomically previously (Džuranov et al., 1999; Valchev et al., 2013a, b). This high taxonomic diversity led us to do the first step for estimating the paleoecological significance of the foraminiferal assemblages – a definition of eleven groups of tests based on characteristic features of their morphology (Valchev, Stojanova, 2014). The present article aims to expand the paleoenvironmental analysis by combining of the morphological features with inferred life-



**Fig. 1. Sketch with the location of the Paleogene basins in Republic of Macedonia and the studied sections (after Dumurdzanov et al., 2005, modified by Valchev et al., 2013b, with new data)**

1 – распространение на палеогенските седиментни скали; 2 – тектонска граница (WMZ – Западномакедонска зона, VZ – Вардарска зона, SMM – Сръбско-Македонски масив); 3 – басейнова граница; 4 – басейни (SKB – Скопско-Кумановски, OPB – Овчеполски, TB – Тиквешки, VGB – Валандово-Гевгелийски, DBB – Девебаирски, DB – Делчевски, SB – Струмички); 5 – разрез

**Фиг. 1. Скица с разпространението на палеогенските басейни в Република Македония и изучените разрези (по Dumurdzanov et al., 2005, с изменения от Valchev et al., 2013b и нови данни)**

1 – разпространение на палеогенските седиментни скали; 2 – тектонска граница (WMZ – Западномакедонска зона, VZ – Вардарска зона, SMM – Сръбско-Македонски масив); 3 – басейнова граница; 4 – басейни (SKB – Скопско-Кумановски, OPB – Овчеполски, TB – Тиквешки, VGB – Валандово-Гевгелийски, DBB – Девебаирски, DB – Делчевски, SB – Струмички); 5 – разрез

style (epifaunal, shallow infaunal and deep infaunal) and feeding strategy (suspension-feeders, deposit-feeders, herbivores, etc.) of the foraminifera. Comparison of our morphogroup system to modern and fossil ones is going to be outlined accordingly.

## Description of the morphogroups

A morphogroup is an aggregation of forms with similar test morphology, independent of systematic relationships (Murray, 1973, 2006). According to several authors (e.g. Nagy, 1992; Reolid et al., 2008, and others) using morphological categories in paleoenvironmental analyses may be preferred over the use of formal species identifications because: 1) the morphological approach enables reliable comparisons to be made among assemblages of different ages, reducing the effect of taxonomical divergence caused by biological evolution, 2) identifications of species are not required, and 3) using a small number of morphogroups instead of a large number of species reduces the amount of data to be analyzed.

On the basis of external test morphology (test shape) and the nature of test coiling (i.e. chamber addition), we have already (Valchev, Stojanova, 2014) defined 11 morphological groups (morphogroups or morphotypes). In this article they are described and illustrated in details (see Plates I–III). Additional data about their inferred life-style and feeding strategy (based on published data from modern and fossil assemblages, e.g. Jones, Charnock, 1985; Corliss, 1985, 1991; Corliss, Chen, 1988; Nagy et al., 1995; Reolid et al., 2008; Alperin et al., 2011; Murray et al., 2011, etc.) are given here.

1) Rounded trochospiral morphogroup (RT). It includes species with trochospiral mode of coiling and broadly rounded periphery (Plate I, 1–7): *Baggina subconica* (Terquem), *Valvulineria jacksonensis* Cushman, *Anomalinoides acutus* (Plummer), *A. danicus* (Brotzen), and *A. welleri* (Plummer). This morphogroup comprises epifaunal active herbivores, detritivores, omnivores and bactrivores. It corresponds to rounded trochospiral morphogroup of Corliss and Chen (1988) and morphogroup M2 (partly) of Szydło (2005).

2) Plano-convex trochospiral morphogroup (PT). It is represented by examples with trochospiral tests, having flat spiral side and narrowly rounded to sharp periphery (Plate I, 8–19): *Cibicides carinatus* (Terquem), *C. lobatulus* (Walker and Jakobs), *C. tallahatensis* Bandy, *C. ungerianus* (d'Orbigny), *C. cf. westi* Howe, *Cibicides* sp., *Gyroidinoides soldanii* (d'Orbigny), *Pararotalia audouini* (d'Orbigny), and *P. subinermis* Bhatia. The listed taxa are epifaunal grazing herbivores; primary weed fauna. This morphogroup is similar to plano-convex morphogroup of Severin (1983), Corliss and Chen (1988), morphogroups G of Reolid et al. (2008) and CM1 of Motamedalshariati et al. (2010).

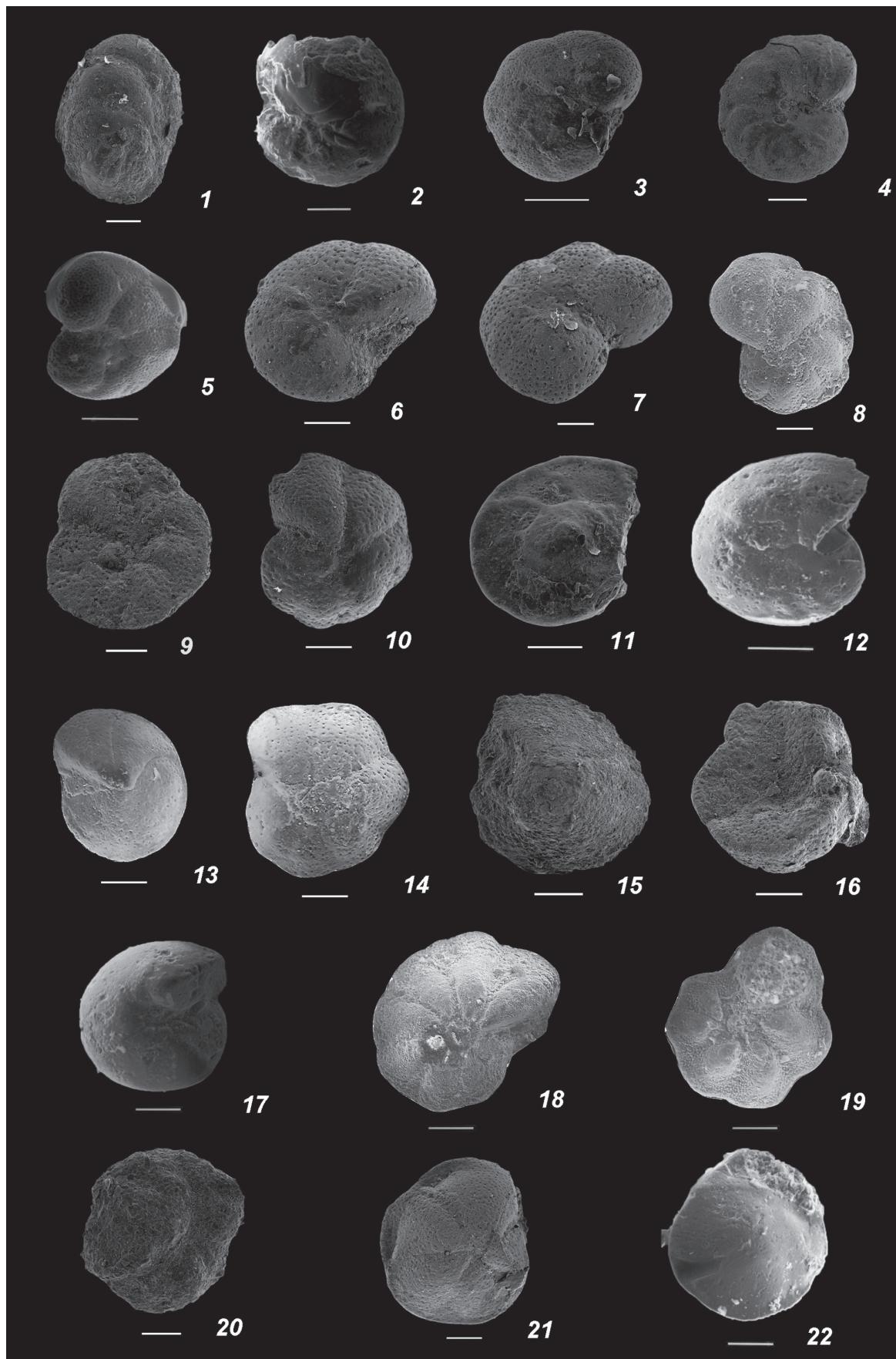
3) Biconvex trochospiral morphogroup (BT). It contains species with trochospiral mode of coiling and biconvex morphology, characterized by sharply angled to narrowly rounded periphery (Plate I, 20–22, Plate II, 1–6): *Trochammina deformis* Grzybowski, *Eponides minima* Cushman, *Eponides* sp., *Cibicidoides* sp., *Heterolepa dutemplei* (d'Orbigny), and *H. perlucida* (Nuttall). Epifaunal active herbivores, detritivores and omnivores are included here. Our morphogroup corresponds to the morphogroup of the same name of Corliss and Chen (1988), morphogroups D (partly) of Jones and Charnock (1985), A-4 (partly) of Tyszka (1994), 4-a (partly) of Nagy et al. (1995), D (partly) of Reolid et al. (2008), D1 (partly) of Nagy et al. (2009).

4) Milioline morphogroup (M). It consists of species with flattened tests, elliptical outline and milioline chamber arrangement (Plate II, 7–12): *Spiroloculina communis communis* Cushman et Todd, *Quinqueloculina juleana* d'Orbigny, *Quinqueloculina* sp., *Triloculina angularis* d'Orbigny, *T. gibba* d'Orbigny, *Hauerina* sp., and *Pyrgo bulloides* (d'Orbigny). The representatives of this morphogroup are epifaunal active deposit-feeders, detritivores and herbivores. It could be correlated to milioline morphogroup of Corliss and Chen (1988), as well as morphogroup I of Reolid et al. (2008).

5) Rounded planispiral morphogroup (RP). It includes compact tests with planispirally arranged chambers and broadly rounded periphery (Plate II, 13–17): *Nonion graniferum* (Terquem), *Nonionella winniana* Howe, *Mellonis affine* (Reuss), and *Pullenia quinqueloba* (Reuss). Shallow infaunal active deposit-feeders and detritivores are included in this morphotype. This morphogroup is similar to the morphogroups of the same name of Severin (1983) and Corliss and Chen (1988), and partly to flattened ovoid morphogroup of Corliss and Chen (1988).

6) Lenticular morphogroup (L). Species from this group display biconvex morphology with sharply angled or keeled periphery (Plate II, 18–20): *Lenticulina* cf. *wilcoxensis* (Cushman, Ponton), *Lenticulina yagutensis* (Bermudez), and *Lenticulina* sp. This morphogroup is represented by epifaunal to deep infaunal (predominantly the second one), active deposit-feeders and grazing omnivores. It corresponds to morphogroups B (partly) of Jones and Charnock (1985), C8 of Tyszka (1994), M6 of Szydło (2005), K of Reolid et al. (2008), flattened multilocular morphotypes of Nagy et al. (2009), CM3 of Motamedalshariati et al. (2010).

7) Tapered and cylindrical morphogroup (T/C). It is represented by forms with round, oval or triangular cross section, and parallel or subparallel sides (Plate II, 21–26, Plate III, 1–7). Rectilinear and straight uniserial, biserial and triserial tests are included in this morphogroup: *Marssonella indentata* (Cushman et Jarvis), *Textularia bronniiana* (d'Orbigny), *Textularia minuta* Terquem, *Nodosaria ewaldi* Reuss, *Nodosaria* sp., *Glandulina ovula* d'Orbigny, *Bulimina sculptilis*



## PLATE I

### Rounded trochospiral morphogroup (RT)

- 1, 2. *Baggina subconica* (Terquem, 1882): 1, Delchevo basin, Crna Skala section, upper flysch unit, sample 5, SEMx150; 2, Ovche Pole basin, Nemanjici section, upper flysch unit, sample 7, SEMx180.
3. *Valvulineria jacksoensis* Cushman, 1933: Delchevo basin, Crna Skala section, upper flysch unit, sample 24, SEMx270.
4. *Anomalinoidea acutus* (Plummer, 1926): Delchevo basin, Crna Skala section, upper flysch unit, sample 24, umbilical view, SEMx180.
5. *Anomalinoidea danicus* (Brotzen, 1940): Ovche Pole basin, Nemanjici section, upper flysch unit, sample 13, umbilical view, SEMx280.
- 6, 7. *Anomalinoidea welleri* (Plummer, 1926): Tikvesh basin, Krivolak section, upper flysch unit, sample 3: 6, spiral view, SEMx150; 7, umbilical view, SEMx190.

### Plano-convex trochospiral morphogroup (PT)

8. *Cibicides carinatus* (Terquem, 1882): Ovche Pole basin, Chardaklija section, upper flysch unit, sample 1, umbilical view, SEMx126.
- 9, 10. *Cibicides lobatulus* (Walker and Jakobs, 1798): Tikvesh basin, Hadzi Jusuflji section, upper flysch unit, sample 7: 9, spiral view, SEMx180; 10, umbilical view, SEMx160.
- 11, 12. *Cibicides ungerianus* (d'Orbigny, 1846): 11, Delchevo basin, Crna Skala section, upper flysch unit, sample 24, spiral view, SEMx200; 12, Ovche Pole basin, Nemanjici section, upper flysch unit, sample 3, umbilical view, SEMx160.
13. *Cibicides tallahatensis* Bandy, 1949: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 3, umbilical view, SEMx143.
14. *Cibicides cf. westi* Howe, 1939: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 3, umbilical view, SEMx150.
- 15, 16. *Cibicides* sp.: Tikvesh basin, Krivolak section, upper flysch unit, sample 6: 15, umbilical view, SEMx160; 16, spiral view, SEMx180.
17. *Gyroidinoides soldanii* (d'Orbigny, 1826): Ovche Pole basin, Madzarica section, upper flysch unit, sample 12, umbilical view, SEMx220.
18. *Pararotalia audouini* (d'Orbigny, 1826): Ovche Pole basin, Chardaklija section, upper flysch unit, sample 2, SEMx143.
19. *Pararotalia subinermis* Bhatia, 1955: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 4, SEMx203.

### Biconvex trochospiral morphogroup (BT)

20. *Trochammina deformis* Grzybowski, 1898: Delchevo basin, Crna Skala section, upper flysch unit, sample 2, SEMx150.
21. *Eponides minima* Cushman, 1933: Valandovo-Gevgelija basin, Rabrovo section, upper flysch unit, sample 2, umbilical view, SEMx170.
22. *Eponides* sp.: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 10, spiral view, SEMx200.

## ТАБЛИЦА I

### Закръглена коничноспирална морфогрупа

- 1, 2. *Baggina subconica* (Terquem, 1882): 1 – Делчевски басейн, разрез Црна скала, горна флишка задруга, проба 5, SEMx150; 2 – Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 7, SEMx180.
3. *Valvulineria jacksoensis* Cushman, 1933: Делчевски басейн, разрез Црна скала, горна флишка задруга, проба 24, SEMx270.
4. *Anomalinoidea acutus* (Plummer, 1926): Делчевски басейн, разрез Црна скала, горна флишка задруга, проба 24, умбиликална страна; SEMx180.
5. *Anomalinoidea danicus* (Brotzen, 1940): Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 13, умбиликална страна; SEMx280.
- 6, 7. *Anomalinoidea welleri* (Plummer, 1926): Тиквешки басейн, разрез Криволак, горна флишка задруга, проба 3: 6 – спирална страна, SEMx150; 7 – умбиликална страна, SEMx190.

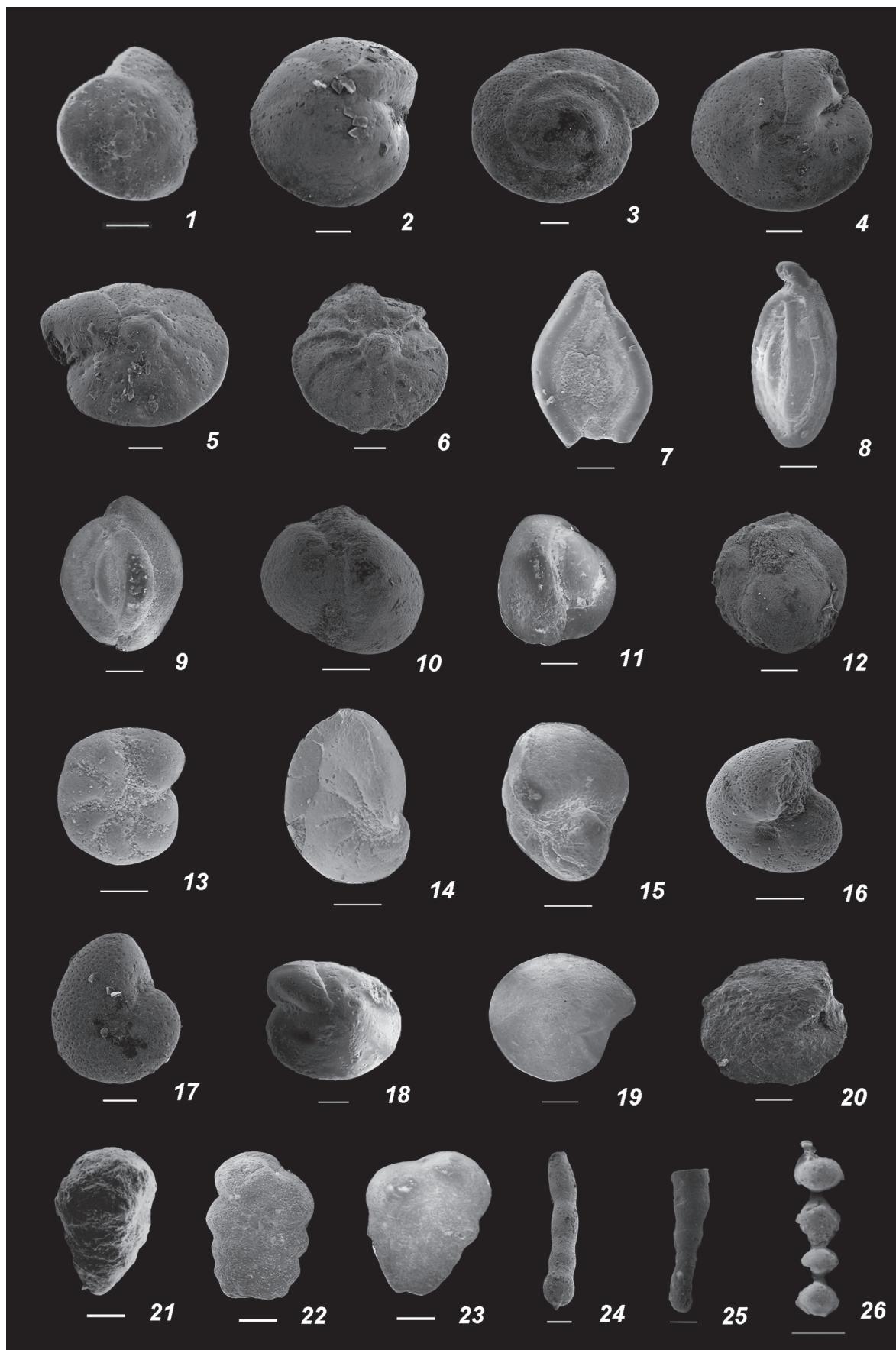
### Плоскоизпъкната коничноспирална морфогрупа

8. *Cibicides carinatus* (Terquem, 1882): Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 1, умбиликална страна, SEMx126.
- 9, 10. *Cibicides lobatulus* (Walker and Jakobs, 1798): Тиквешки басейн, разрез Хаджи Юсуфли, горна флишка задруга, проба 7: 9 – спирална страна, SEMx180; 10 – умбиликална страна, SEMx160.
- 11, 12. *Cibicides ungerianus* (d'Orbigny, 1846): 11 – Делчевски басейн, разрез Црна скала, горна флишка задруга, проба 24, спирална страна, SEMx200; 12 – Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 3, умбиликална страна, SEMx160.
13. *Cibicides tallahatensis* Bandy, 1949: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 3, умбиликална страна, SEMx143.
14. *Cibicides cf. westi* Howe, 1939: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 3, умбиликална страна, SEMx150.
- 15, 16. *Cibicides* sp.: Тиквешки басейн, разрез Криволак, горна флишка задруга, проба 6: 15 – умбиликална страна, SEMx160; 16 – спирална страна, SEMx180.
17. *Gyroidinoides soldanii* (d'Orbigny, 1826): Овчеполски басейн, разрез Маджарица, горна флишка задруга, проба 12, умбиликална страна, SEMx220.
18. *Pararotalia audouini* (d'Orbigny, 1826): Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 2, SEMx143.
19. *Pararotalia subinermis* Bhatia, 1955: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 4, SEMx203.

### Двойноизпъкната коничноспирална морфогрупа

20. *Trochammina deformis* Grzybowski, 1898: Делчевски басейн, разрез Црна скала, горна флишка задруга, проба 2, SEMx150.
21. *Eponides minima* Cushman, 1933: Валандово-Гевгелийски басейн, разрез Раброво, горна флишка задруга, проба 2, умбиликална страна, SEMx170.
22. *Eponides* sp.: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 10, спирална страна, SEMx200.

Scale bar – 100 µm



## PLATE II

### Biconvex trochospiral morphogroup (BT)

- 1, 2. *Cibicidoides* sp.: 1, Ovche Pole basin, Nemanjici section, upper flysch unit, sample 4, spiral view, SEMx200; 2, Tikvesh basin, Krivolak section, upper flysch unit, sample 3, umbilical view, SEMx140.  
3, 4. *Heterolepa dutemplei* (d'Orbigny, 1846): Delchevo basin, Crna Skala section, upper flysch unit, sample 5: 3, spiral view, SEMx120; 4, umbilical view, SEMx130.  
5, 6. *Heterolepa perlucida* (Nautall, 1932): Valandovo-Gevgelija basin, Rabrovo section, upper flysch unit, sample 15: 5, umbilical view, SEMx150; 6, spiral view, SEMx180.

### Milioline morphogroup (M)

7. *Spiroloculina communis communis* Cushman et Todd, 1942: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 1, SEMx137.  
8. *Quinqueloculina juleana* d'Orbigny, 1846: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 3, SEMx137.  
9. *Quinqueloculina* sp.: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 5, SEMx115.  
10. *Triloculina angularis* d'Orbigny, 1850: Delchevo basin, Crna Skala section, upper flysch unit, sample 6, SEMx180.  
11. *Triloculina gibba* d'Orbigny, 1846: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 3, SEMx150.  
12. *Pyrgo bulloides* (d'Orbigny, 1826): Tikvesh basin, Hadzhi Jusufl section, upper flysch unit, sample 3, SEMx180.

### Rounded planispiral morphogroup (RP)

13. *Nonion graniferum* (Terquem, 1882): Ovche Pole basin, Chardaklija section, upper flysch unit, sample 4, SEMx287.  
14, 15. *Nonionella winniana* Howe, 1939: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 4: 14, SEMx126; 15, SEMx203.  
16. *Mellonis affine* (Reuss, 1851): Valandovo-Gevgelija basin, Rabrovo section, upper flysch unit, sample 15, spiral view, SEMx230.  
17. *Pullenia quinqueloba* (Reuss, 1851): Delchevo basin, Crna Skala section, upper flysch unit, sample 16, spiral view, SEMx140.

### Lenticular morphogroup (L)

18. *Lenticulina cf. wilcoxensis* (Cushman and Ponton, 1932): Ovche Pole basin, Kadrifakovo section, upper flysch unit, sample 6, SEMx340.  
19. *Lenticulina yagutensis* (Bermudez, 1949): Ovche Pole basin, Chardaklija section, upper flysch unit, sample 3, SEMx170.  
20. *Lenticulina* sp.: Tikvesh basin, Krivolak section, upper flysch unit, sample 2, SEMx180.

### Tapered and cylindrical morphogroup (T/C)

21. *Marssonella indentata* (Cushman et Jarvis, 1928): Ovche Pole basin, Nemanjici section, upper flysch unit, sample 3, SEMx200.  
22. *Textularia bronniiana* (d'Orbigny, 1846): Ovche Pole basin, Chardaklija section, upper flysch unit, sample 4, SEMx156.  
23. *Textularia minuta* Terquem, 1882: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 4, SEMx178.  
24. *Nodosaria ewaldi* Reuss, 1851: Valandovo-Gevgelija basin, Dedeli section, upper flysch unit, sample 6, SEMx65.  
25. *Nodosaria* sp.: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 6, SEMx200.  
26. *Siphonodosaria adolphina* (d'Orbigny, 1846): Ovche Pole basin, Nemanjici section, upper flysch unit, sample 16, SEMx110.

## ТАБЛИЦА II

### Двойноизпъкната коничноспирална морфогрупа

- 1, 2. *Cibicidoides* sp.: 1 – Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 4, спирална страна, SEMx200; 2 – Тиквешки басейн, разрез Криволак, горна флишка задруга, проба 3, умбиликална страна, SEMx140.  
3, 4. *Heterolepa dutemplei* (d'Orbigny, 1846): Делчевски басейн, разрез Црна скала, горна флишка задруга, проба 5: 3 – спирална страна, SEMx120; 4 – умбиликална страна, SEMx130.  
5, 6. *Heterolepa perlucida* (Nautall, 1932): Валандово-Гевгелийски басейн, разрез Раброво, горна флишка задруга, проба 15: 5 – умбиликална страна, SEMx150; 6 – спирална страна, SEMx180.

### Милиолидна морфогрупа

7. *Spiroloculina communis communis* Cushman et Todd, 1942: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 1, SEMx137.  
8. *Quinqueloculina juleana* d'Orbigny, 1846: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 3, SEMx137.  
9. *Quinqueloculina* sp.: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 5, SEMx115.  
10. *Triloculina angularis* d'Orbigny, 1850: Делчевски басейн, разрез Црна скала, горна флишка задруга, проба 6, SEMx180.  
11. *Triloculina gibba* d'Orbigny, 1846: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 3, SEMx150.  
12. *Pyrgo bulloides* (d'Orbigny, 1826): Тиквешки басейн, разрез Хаджи Юсуфли, горна флишка задруга, проба 3, SEMx180.

### Закъръглена плоскоспирална морфогрупа

13. *Nonion graniferum* (Terquem, 1882): Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 4, SEMx287.  
14, 15. *Nonionella winniana* Howe, 1939: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 4: 14 – SEMx126; 15 – SEMx203.  
16. *Mellonis affine* (Reuss, 1851): Валандово-Гевгелийски басейн, разрез Раброво, горна флишка задруга, проба 15, спирална страна, SEMx230.  
17. *Pullenia quinqueloba* (Reuss, 1851): Делчевски басейн, разрез Црна скала, горна флишка задруга, проба 16, спирална страна, SEMx140.

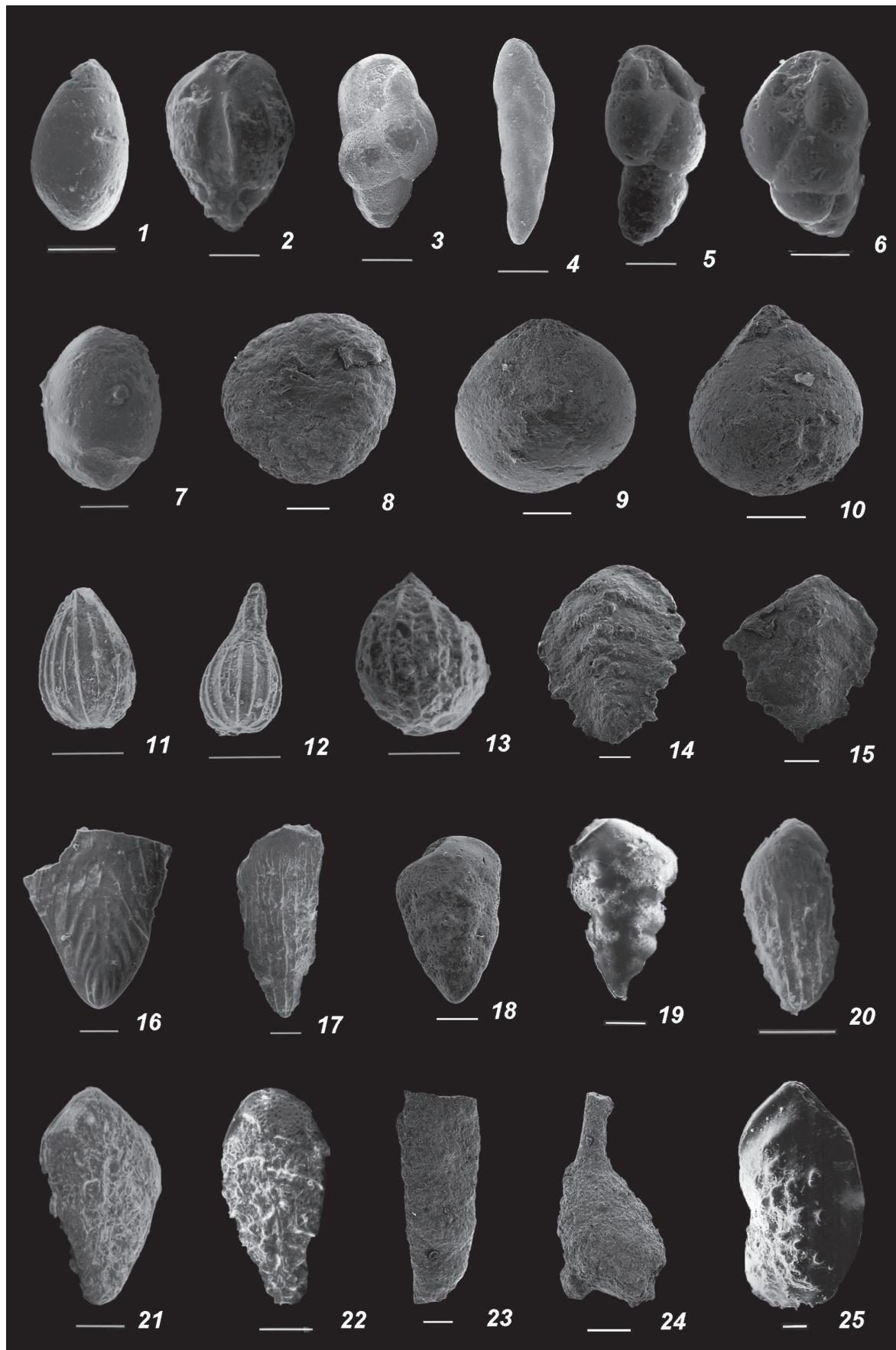
### Лещовидна морфогрупа

18. *Lenticulina cf. wilcoxensis* (Cushman and Ponton, 1932): Овчеполски басейн, разрез Кадрифаково, горна флишка задруга, проба 6, SEMx340.  
19. *Lenticulina yagutensis* (Bermudez, 1949): Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 3, SEMx170.  
20. *Lenticulina* sp.: Тиквешки басейн, разрез Криволак, горна флишка задруга, проба 2, SEMx180.

### Заострена и цилиндрична морфогрупа

21. *Marssonella indentata* (Cushman et Jarvis, 1928): Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 3, SEMx200.  
22. *Textularia bronniiana* (d'Orbigny, 1846): Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 4, SEMx156.  
23. *Textularia minuta* Terquem, 1882: Овчеполски басейн, разрез Чардаклия, горна флишка задруга, проба 4, SEMx178.  
24. *Nodosaria ewaldi* Reuss, 1851: Валандово-Гевгелийски басейн, разрез Дедели, горна флишка задруга, проба 6, SEMx65.  
25. *Nodosaria* sp.: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 6, SEMx200.  
26. *Siphonodosaria adolphina* (d'Orbigny, 1846): Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 16, SEMx110.

Scale bar – 100 µm



### PLATE III

#### Tapered and cylindrical morphogroup (T/C)

1. *Glandulina ovula* d'Orbigny, 1846: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 5, SEMx400.
2. *Bulimina sculptilis* Cushman, 1923: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 6, SEMx300.
3. *Bulimina trigona* Terquem, 1882: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 4, SEMx186.
4. *Furstenkoina dibollensis* (Cushman et Applin, 1926): Ovche Pole basin, Chardaklija section, upper flysch unit, sample 3, SEMx101.
5. *Caucasina eocenica* Chalilov, 1958: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 6, SEMx240.
6. *Caucasina tenebricosa* Pishvanova, 1960: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 14, SEMx300.
7. *Chilostomelloides balkhanensis* (Dain et Chalilov, 1952): Ovche Pole basin, Nemanjici section, upper flysch unit, sample 3, SEMx250.

#### Spherical morphogroup (S)

8. *Saccammina placenta* (Grzybowski, 1898): Tikvesh basin, Hadzi Jusuflj section, upper flysch unit, sample 1, SEMx150.
9. *Globulina gibba* d'Orbigny, 1826: Tikvesh basin, Krivolak section, upper flysch unit, sample 7, SEMx170.
10. *Guttulina irregularis* (d'Orbigny, 1846): Tikvesh basin, Krivolak section, upper flysch unit, sample 5, SEMx200.
11. *Lagena humifera* Bandy, 1949: Ovche Pole basin, Chardaklija section, upper flysch unit, sample 4, SEMx221.
12. *Lagena striata* (d'Orbigny, 1839): Ovche Pole basin, Chardaklija section, upper flysch unit, sample 4, SEMx221.
13. *Favulinia hexagona* (Williamson, 1848): Ovche Pole basin, Nemanjici section, upper flysch unit, sample 5, SEMx340.

#### Flattened tapered morphogroup (FT)

14. *Spiroplectinella carinata* (d'Orbigny, 1846): Valandovo-Gevgelija basin, Dedeli section, upper flysch unit, sample 12, SEMx120.
15. *Spiroplectinella dentata* (Alth, 1850): Tikvesh basin, Hadzi Jusuflj section, upper flysch unit, sample 3, SEMx130.
16. *Palmula budensis* (Hantken, 1875): Ovche Pole basin, Nemanjici section, upper flysch unit, sample 5, SEMx180.
17. *Bolivina cf. antegressa* Subbotina, 1953: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 8, SEMx140.
18. *Bolivina cf. cookei* Cushman, 1922: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 8; SEMx250.
19. *Bolivina gracilis* Cushman and Applin, 1926: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 6, SEMx185.
20. *Bolivina nobilis* Hantken, 1875: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 12, SEMx325.
21. *Bolivina reticulata* Hantken, 1875: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 12, SEMx250.
22. *Bolivina scalprata* Schwager, 1883: Ovche Pole basin, Nemanjici section, upper flysch unit, sample 10, SEMx250.

#### Tube-shaped morphogroup (T)

23. *Bathysiphon* sp.: Tikvesh basin, Krivolak section, upper flysch unit, sample 1, SEMx110.
24. *Hyperammina* sp.: Tikvesh basin, Hadzi Jusuflj section, upper flysch unit, sample 2, SEMx150.

#### Heteromorphous morphogroup (H)

25. *Percultazonaria fragaria* (Gümbel, 1868): Ovche Pole basin, Nemanjici section, upper flysch unit, sample 10, SEMx110.

### ТАБЛИЦА III

#### Заострена и цилиндрична морфогрупа

1. *Glandulina ovula* d'Orbigny, 1846: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 5, SEMx400.
2. *Bulimina sculptilis* Cushman, 1923: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 6, SEMx300.
3. *Bulimina trigona* Terquem, 1882: Овчеполски басейн, разрез Чардаклија, горна флишка задруга, проба 4, SEMx186.
4. *Furstenkoina dibollensis* (Cushman et Applin, 1926): Овчеполски басейн, разрез Чардаклија, горна флишка задруга, проба 3, SEMx101.
5. *Caucasina eocenica* Chalilov, 1958: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 6, SEMx240.
6. *Caucasina tenebricosa* Pishvanova, 1960: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 14, SEMx300.
7. *Chilostomelloides balkhanensis* (Dain et Chalilov, 1952): Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 3, SEMx250.

#### Сферична морфогрупа

8. *Saccammina placenta* (Grzybowski, 1898): Тиквешки басейн, разрез Хаджи Јусуфли, горна флишка задруга, проба 1, SEMx150.
9. *Globulina gibba* d'Orbigny, 1826: Тиквешки басейн, разрез Криволак, горна флишка задруга, проба 7, SEMx170.
10. *Guttulina irregularis* (d'Orbigny, 1846): Тиквешки басейн, разрез Криволак, горна флишка задруга, проба 5, SEMx200.
11. *Lagena humifera* Bandy, 1949: Овчеполски басейн, разрез Чардаклија, горна флишка задруга, проба 4, SEMx221.
12. *Lagena striata* (d'Orbigny, 1839): Овчеполски басейн, разрез Чардаклија, горна флишка задруга, проба 4, SEMx221.
13. *Favulinia hexagona* (Williamson, 1848): Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 5, SEMx340.

#### Спленснато-заострена морфогрупа

14. *Spiroplectinella carinata* (d'Orbigny, 1846): Валандово-Гевгелијски басейн, разрез Дедели, горна флишка задруга, проба 12, SEMx120.
15. *Spiroplectinella dentata* (Alth, 1850): Тиквешки басейн, разрез Хаджи Јусуфли, горна флишка задруга, проба 3, SEMx130.
16. *Palmula budensis* (Hantken, 1875): Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 5, SEMx180.
17. *Bolivina cf. antegressa* Subbotina, 1953: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 8, SEMx140.
18. *Bolivina cf. cookei* Cushman, 1922: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 8, SEMx250.
19. *Bolivina gracilis* Cushman and Applin, 1926: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 6, SEMx185.
20. *Bolivina nobilis* Hantken, 1875: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 12, SEMx325.
21. *Bolivina reticulata* Hantken, 1875: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 12, SEMx250.
22. *Bolivina scalprata* Schwager, 1883: Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 10, SEMx250.

#### Тръбеста морфогрупа

23. *Bathysiphon* sp.: Тиквешки басейн, разрез Криволак, горна флишка задруга, проба 1, SEMx110.
24. *Hyperammina* sp.: Тиквешки басейн, разрез Хаджи Јусуфли, горна флишка задруга, проба 2, SEMx150.

#### Хетероморфна морфогрупа

25. *Percultazonaria fragaria* (Gümbel, 1868): Овчеполски басейн, разрез Неманци, горна флишка задруга, проба 10, SEMx110.

Scale bar – 100 µm

Cushman, *B. trigona* Terquem, *Fursenkoina dibolensis* (Cushman et Applin), *Caucasina eocaenica* Chalilov, *C. tenebricosa* Pishvanova, *Siphonodosaria adolphina* (d'Orbigny), and *Chilostomelloides balkanensis* (Dain and Chalilov). The morphogroup includes shallow to deep infaunal deposit-feeders, detritivores and bacterial scavengers and could be correlated to elongate-flattened and tapered morphogroup of Severin (1983), tapered/cylindrical one of Corliss and Chen (1988), morphogroups B (partly) of Jones and Charnock (1985), 3-b (partly) of Nagy (1992) and Nagy et al. (1995), A-8 of Tyszka (1994), M4 (partly) of Szydło (2005), C3 (partly) and J1 (partly) of Reolid et al. (2008) and Nagy et al. (2009), CM2 (partly) and AGM2 (partly) of Motamedalshariati et al. (2010).

8) Spherical morphogroup (S). It contains species of unilocular and inflated planispiral or trochospiral multilocular tests (Plate III, 8–13): *Saccammina placenta* (Grzybowski), *Lagena humifera* Bandy, *Lagena striata* (d'Orbigny), *Globulina gibba* d'Orbigny, *Guttulina irregularis* (d'Orbigny), and *Favulina hexagona* (Williamson). The foraminifera, included here, are shallow infaunal detritivores or deposit-feeders. The S-morphogroup is close to spherical morphogroup of Corliss and Chen (1988), morphogroups B (partly) of Jones and Charnock (1985), 2-a (partly) of Nagy (1992), A3 of Bąk et al. (1997), M3 (partly) of Szydło (2005), B (partly) of Nagy et al. (2009).

9) Flattened tapered morphogroup (FT). This group includes uniserial, biserial and palmate tests, with ovate to compressed in cross section, and parallel to subparallel sides (Plate III, 14–22). It is represented by *Spiroplectinella carinata* (d'Orbigny), *S. dentata* (Alth), *Palmula budensis* (Hantken), *Bolivina cf. antegressa* Subbotina, *B. cf. cookei* Cushman, *B. gracilis* Cushman and Applin, *B. nobilis* Hantken, *B. reticulata* Hantken, and *B. scalprata* Schwager. This morphogroup is characterized by shallow infaunal detritivores and scavengers and it is correlated to the morphogroup of the same name of Corliss and Chen (1988), morphogroups 3-b of Nagy et al. (1995), A5 of Bąk et al. (1997).

10) Tube-shaped morphogroup (T). This group combines examples with simple morphology – straight or curved single tubes having flattened or rounded cross section (Plate III, 23, 24), and agglutinated wall (e.g. *Bathysiphon* sp., and *Hyperammina* sp.). Epifaunal suspension-feeders are represented here. Our morphogroup corresponds to morphogroups A of Jones and Charnock (1985), 1-a of Nagy (1992) and Nagy et al. (1995), A-1 of Tyszka (1994), A1 of Bąk et al. (1997), A of Reolid et al. (2008).

11) Heteromorphous morphogroup (H). It includes forms showing two or more types of chamber arrangement (Plate III, 25): *Percultazonaria fragaria* (Gümbel). Shallow infaunal active deposit-feeders and grazing omnivores correlated here to morphogroups M5 of Szydło (2005) and J2 of Reolid et al. (2008).

## Distribution of the morphogroups

The morphogroups, described above, does not demonstrate uniform distribution in the studied area (Fig. 2). Only two of them – milioline (M) and tapered and cylindrical (T/C), are presented in all sections, while the heteromorphous (H) (established in Nemanjici section only) and the tube-shaped morphogroup (T) (recorded in Hadzi Jusuflı and Krivolak sections) are the rarest ones. The other morphogroups were found in at least six sections. The greatest variety of test morphologies is observed in Nemanjici and Krivolak sections, where 10 and 9 morphogroups respectively were described. On the other hand, Karaorman and Stuka sections (two and three morphogroups respectively) are with lowest variety of test morphology. The other studied sections include 5 to 8 morphogroups.

As could be seen from the distribution of the morphogroups along the sections (Figs. 3–9) there is no strongly dominating one. For example the most characteristic morphotypes in Nemanjici section (the most diverse one from test morphology point of view) are tapered and cylindrical (T/C), plano-convex trochospiral (PT) and flattened tapered (FT) morphogroup, which are recorded in all samples. Krivolak section represents structure with lower abundance of specimens and main contributors milioline (M), flattened tapered (FT) and plano-convex trochospiral (PT) morphogroups. Ezevo Brdo, Madzarica and Kadrifakovo sections are dominated by plano-convex trochospiral (PT), tapered and cylindrical (T/C) and milioline (M) morphogroups, but with low specimen abundance, while in the other studied sections the morphogroups are represented mainly by single specimens and therefore there is no dominating one.

## Discussion

The dominating morphogroups from the most representative sections – Nemanjici (T/C, PT, FT) and Krivolak (M, FT, PT), are recorded predominantly in shallow-water environments in modern (e.g. Corliss, Chen, 1988; Khare et al., 1995; Alperin et al., 2011, and others) and ancient seas (e.g. Szydło, 2005; Reolid et al., 2008; Setoyama et al., 2011, and others). For example, PT-morphogroup is typical for inner to middle shelf conditions, FT-morphogroup maximum abundance ranges from middle to outer shelf. M-morphogroup is composed entirely of porcelaneous tests also characteristic for inner to middle shelf. The peak of T/C-morphogroup is in the upper bathyal realm, but it is abundant on the shelf as well.

The epifaunal-infaunal data shows that both groups of tests are equally presented in the Paleogene of the Republic of Macedonia. Such a ratio is characteristic for inner to middle shelf conditions.

Generally, the low specimen abundance in the majority of the sections is an obstacle to make interpreta-

Basin and section	SKB	OPB					TB		VGB		DB	SB
		Vojnik	Nemanjici	Ezevo Brdo	Kadrifakovo	Madzarica	Chardaklja	Karaorman	Hadzi Jusufli	Krivolak		
Morphogroup												
Rounded trochospiral (RT)		●	●									
Plano-convex trochospiral (PT)	●	●	●	●	●	●	●		●	●	●	●
Biconvex trochospiral (BT)		●	●			●	●		●	●	●	●
Milioline (M)	●	●	●	●	●	●	●	●	●	●	●	●
Rounded planispiral (RP)	●	●	●	●	●	●	●		●	●	●	●
Lenticular (L)		●	●	●	●	●	●				●	
Tapered and cylindrical (T/C)	●	●	●	●	●	●	●		●	●	●	●
Spherical (S)	●	●	●	●	●	●	●		●	●	●	
Flattened tapered (FT)		●			●				●	●	●	●
Tube-shaped (T)									●	●		
Heteromorphous (H)		●										

Fig. 2. Distribution of the morphogroups in the studied sections

Фиг. 2. Разпространение на морфогрупите в изучените разрези

tion about parameters like temperature, salinity, oxygen levels, carbonate dissolution, substrate, nutrition, dissolved oxygen, illumination, and pollution.

The occurrence of planktonic foraminiferal specimens in the investigated sections is very rare and uneven – totally 110 specimens in eight sections (Stojanova et al., 2013), as despite Nemanjici section, where planktonics occur in almost all samples, in the other seven sections they are represented by single specimens only. Thus, the ratio of planktonic/benthic foraminifera (P/B ratio) is very low (<5%) and it is typical for inner shelf environment.

Additional data for the paleoenvironmental conditions during the Late Eocene–Early Oligocene could be obtained from the preservation of the foraminiferal specimens as well as the presence of larger foraminifera and macrofauna. As a whole, the majority of the foraminiferal tests is badly preserved and deformed, which is typical for littoral to sublittoral conditions or due to turbidity flow. On the other hand, nummulitids, corals, shallow-water molluses – *Crassatella*, *Pecten*, *Natica*, etc. (Maksimović et al., 1954; Čanović,

1968f<sup>1</sup>, 1969f<sup>2</sup>, 1970f<sup>3</sup>; Kemenci, 1968f<sup>4</sup>), and echinids (Mitrović-Petrović et al., 1990) have been previously found. This fact is another proof for inner shelf environment.

## Conclusions

In the Paleogene sedimentary rocks (Upper Eocene–Lower Oligocene) from the central and eastern part of

<sup>1</sup> Čanović, M. 1968f. *Mikrobiostatigrافsko proučavanje sedimentne serije u profilu bušotine Kurjačka Reka -1 (Makedonija)*. Nafta Gas, Sector za istraživanje, Novi Sad, 19 p.

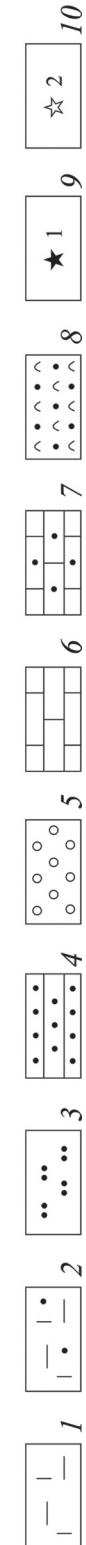
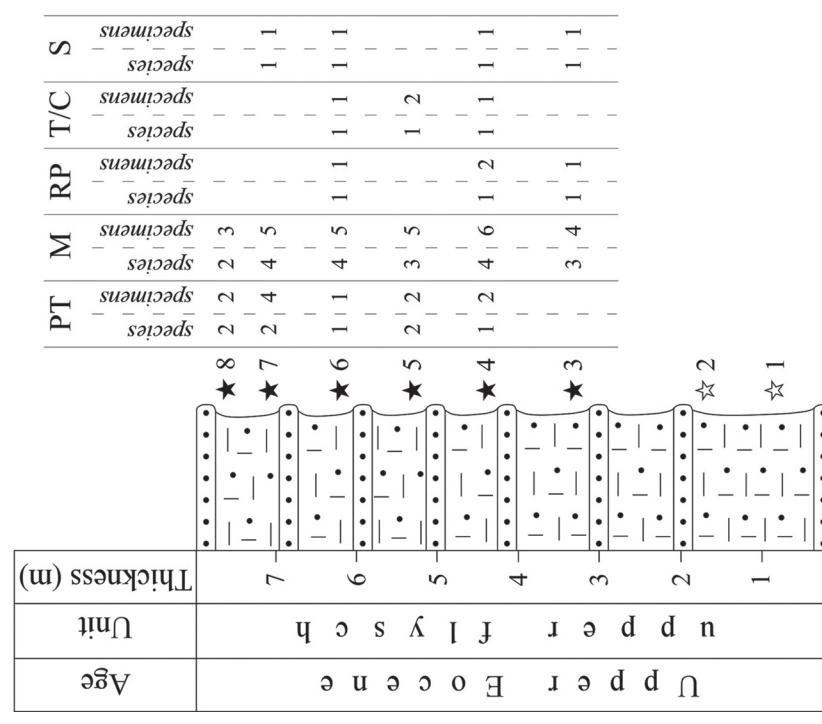
<sup>2</sup> Čanović M. 1969f. *Rezultati od mikropaleontoloških ispitivanja sedimentne serije u bušotini Ovče Polje-1 (Makedonija)*. Nafta Gas, Sector za istraživanje, Novi Sad, 38 p.

<sup>3</sup> Čanović, M. 1970f. *Rezultati mikropaleontoloških ispitivanja iz bušotine TV-1 (Makedonija)*. Nafta Gas, Sector za istraživanje, Novi Sad, 11 p.

<sup>4</sup> Kemenci, R. 1968f. *Izveštaj o sedimentaloškim ispitivanjima jezgrovanih naslaga iz bušotine KR-1 (Makedonija)*. Nafta Gas, Sector za istraživanje, Novi Sad, 17 p.

## Vojnik Section

## Nemanjici Section

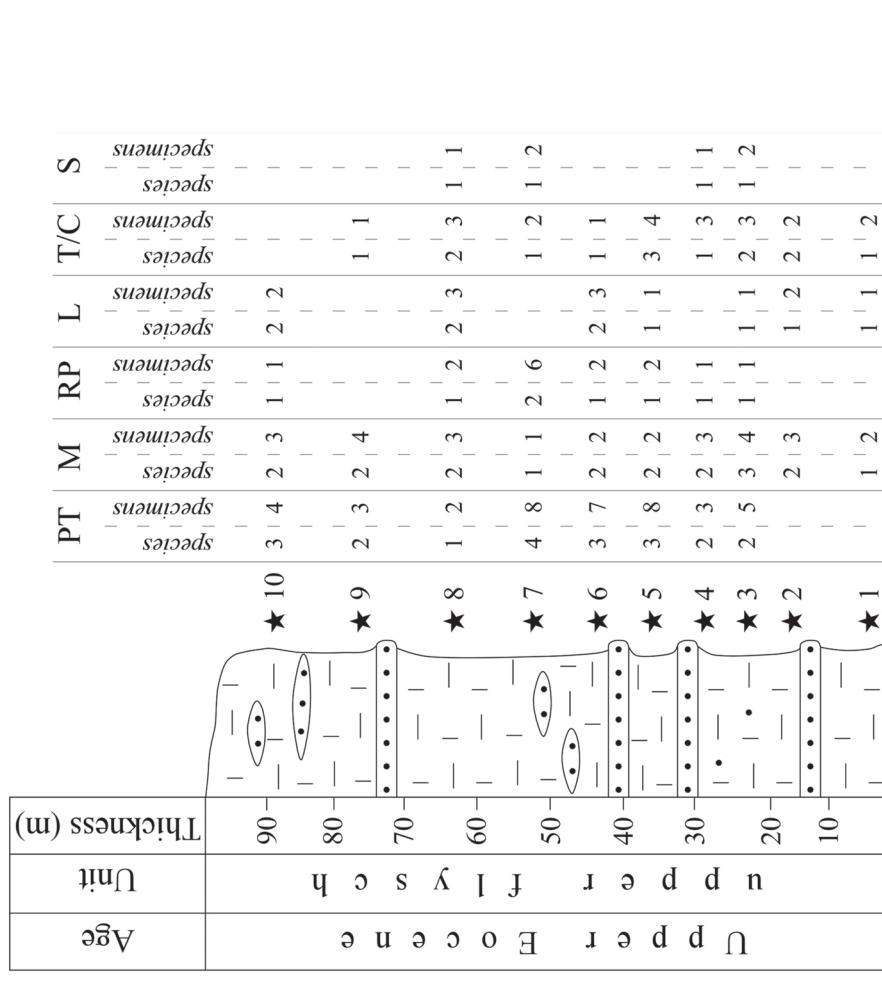
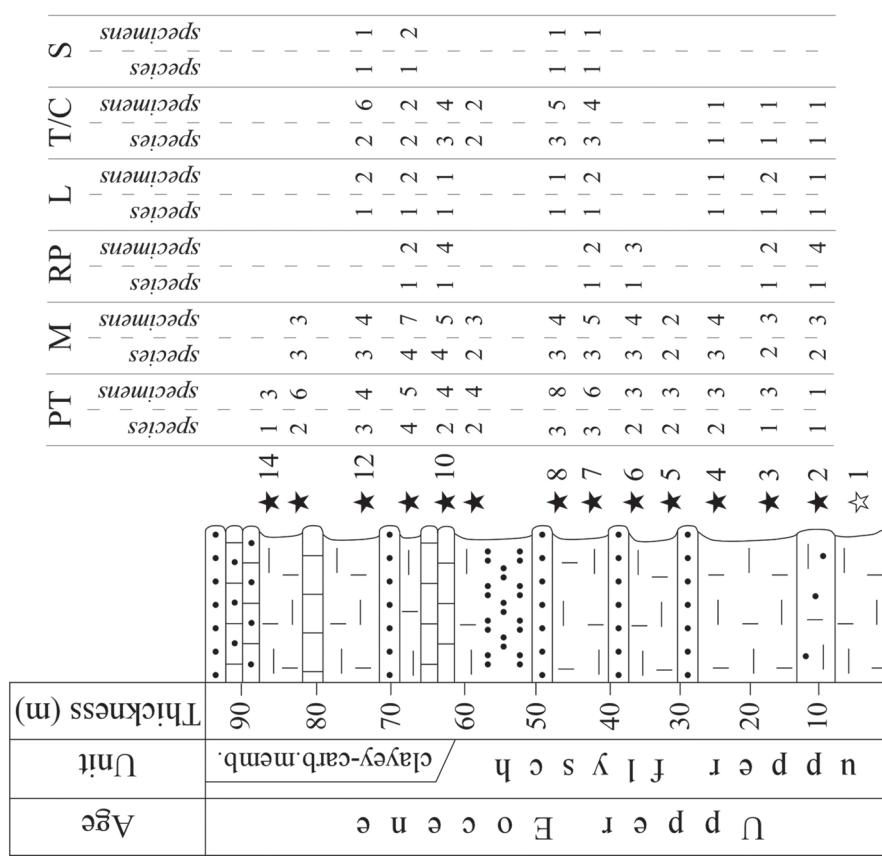


**Fig. 3. Разпространение на установените морфогрупи в разрези Войник и Неманџици (възрастовите определения на фиг. 3–9 са по данни от planktonни и бентосни фораминифери на Stojanova, 2008; Stojanova et al., 2011, 2012, 2013; Stojanova, Petrov, 2012)**  
 I – глинесто-карбонатни седименти; 2 – глинокластови пистъчници; 3 – алверолити; 4 – тънкокластови седименти; 5 – конгломерати; 6 – варовици; 7 – песъчливи варовици; 8 – туфи; 9 – проба, съдържаща хиалинни екземпляри; 10 – проба без хиалинни екземпляри

**Фиг. 3. Развръщане на установените морфогрупи в разрези Войник и Неманџици (възрастовите определения на фиг. 3–9 са по данни от planktonни и бентосни фораминифери на Stojanova, 2008; Stojanova et al., 2011, 2012, 2013; Stojanova, Petrov, 2012)**  
 I – глинесто-карбонатни седименти; 2 – глинокластови пистъчници; 3 – алверолити; 4 – тънкокластови пистъчници; 5 – конгломерати; 6 – варовици; 7 – песъчливи варовици; 8 – туфи; 9 – проба, съдържаща хиалинни екземпляри; 10 – проба без хиалинни екземпляри

### Ezevo Brdo Section

### Kadrifakovo Section



**Fig. 4. Distribution of the morphogroups established in Ezevo Brdo and Kadrifakovo sections (legend on Fig. 3)**

**Фиг. 4. Разпространение на установените морфогрупти в разрез Езево бърдо и Кадрифаково (легенда на фиг. 3)**

### Madzarica Section

### Chardaklija Section

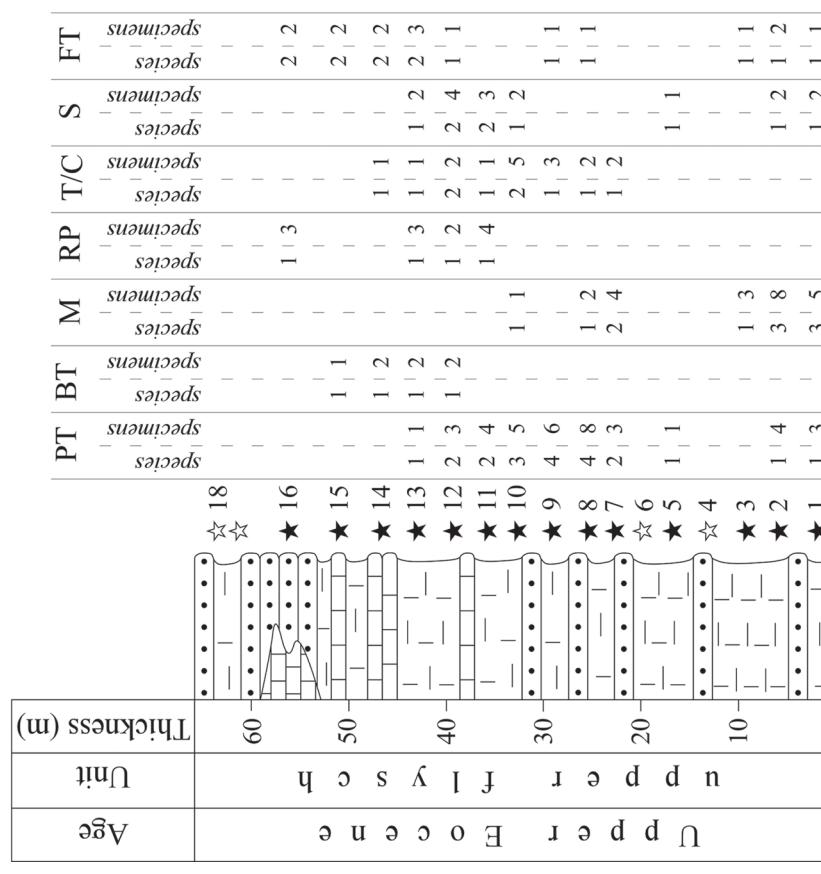


Fig. 5. Distribution of the morphogroups established in Madzarica and Chardaklija sections (legend on Fig. 3)

Фиг. 5. Разпространение на установените морфогрупти в разрези Маджарцица и Чардаклия (легенда на фиг. 3)

## Karaorman Section

## Hadzi Jusufli Section

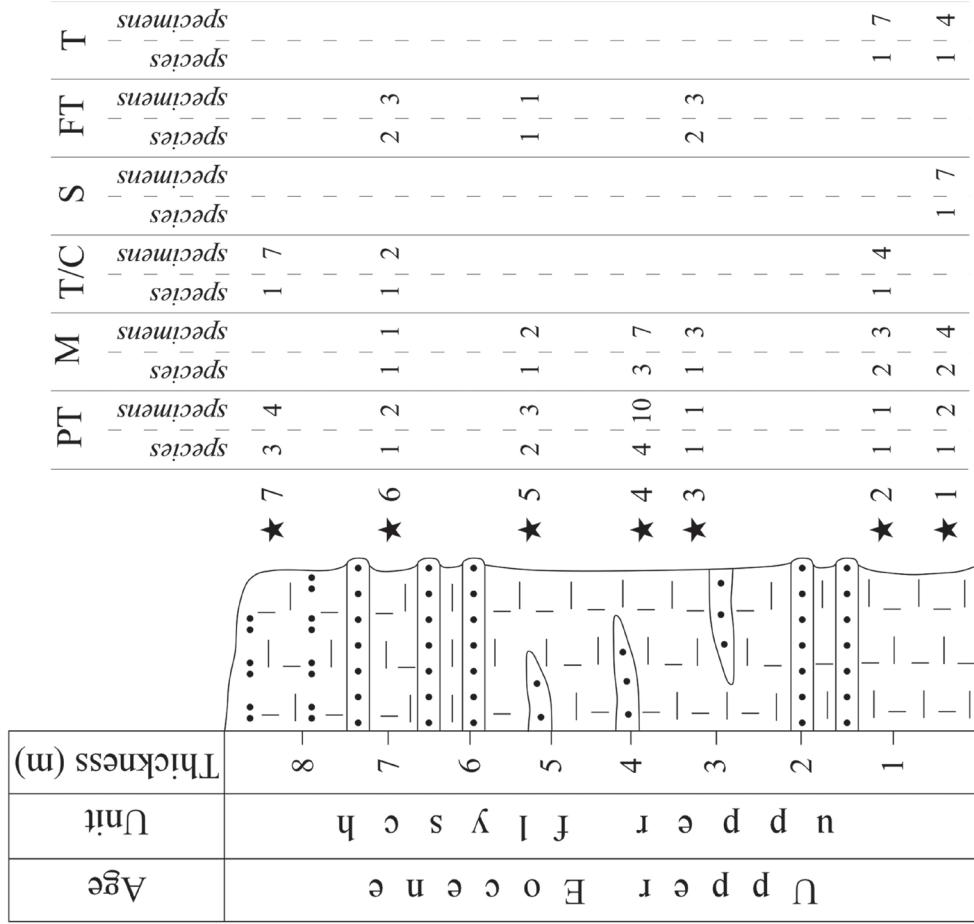
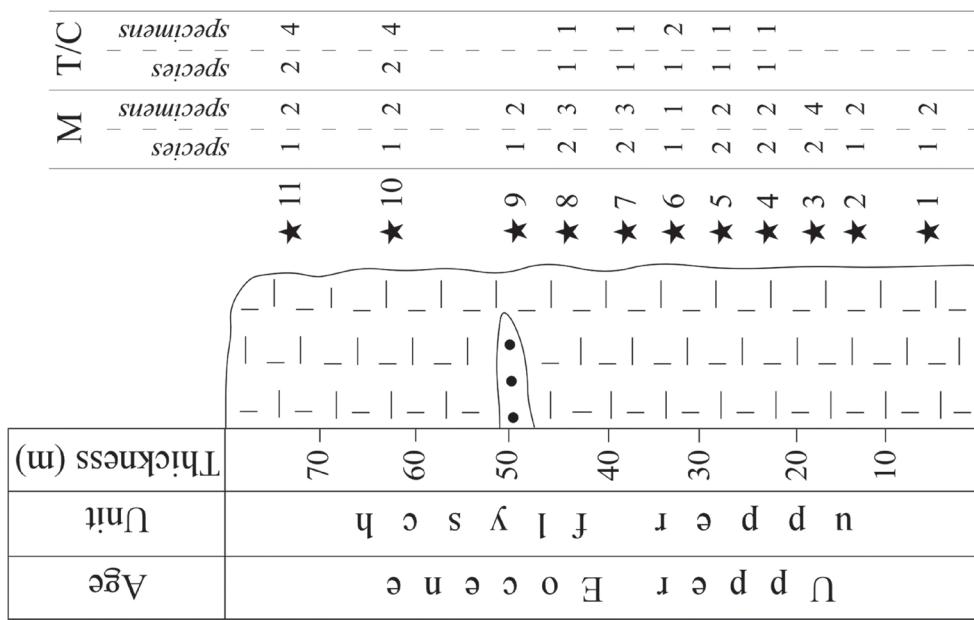
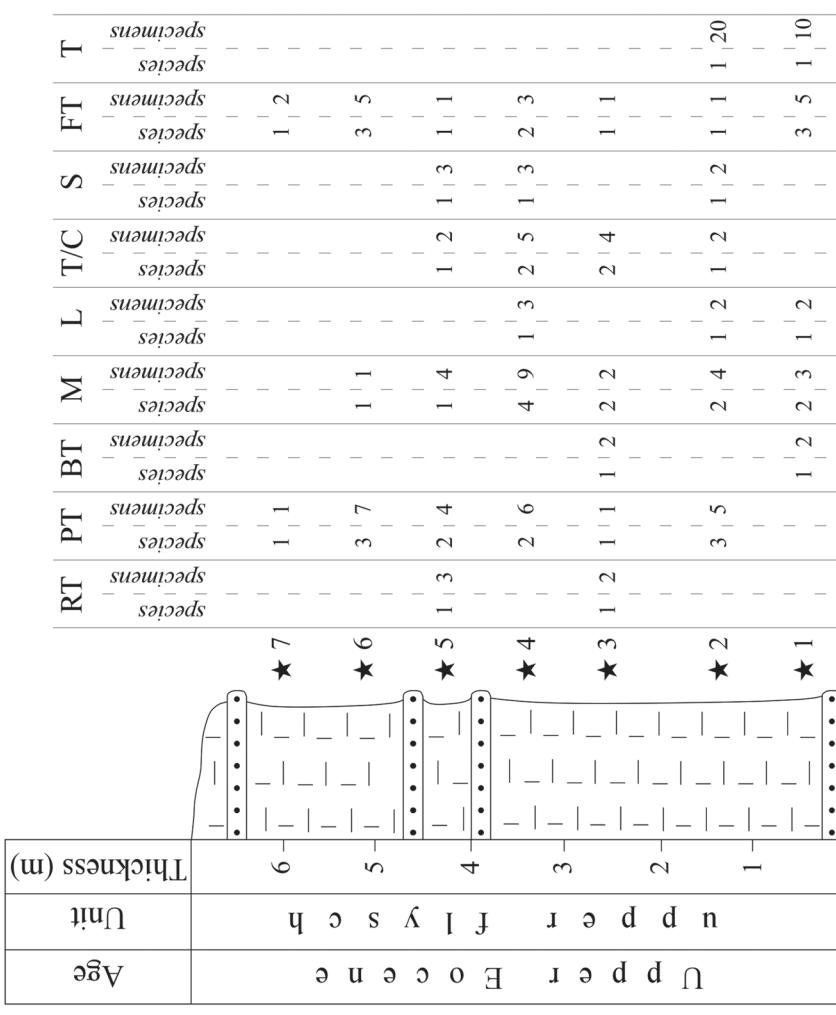


Fig. 6. Distribution of the morphogroups established in Karaorman and Hadzi Jusufli sections (legend on Fig. 3)

Фиг. 6. Разпространение на установените морфогрупи в разрези Караорман и Хаджи Юсупли (легенда на фиг. 3)

### Krivolak Section



### Rabrovo Section

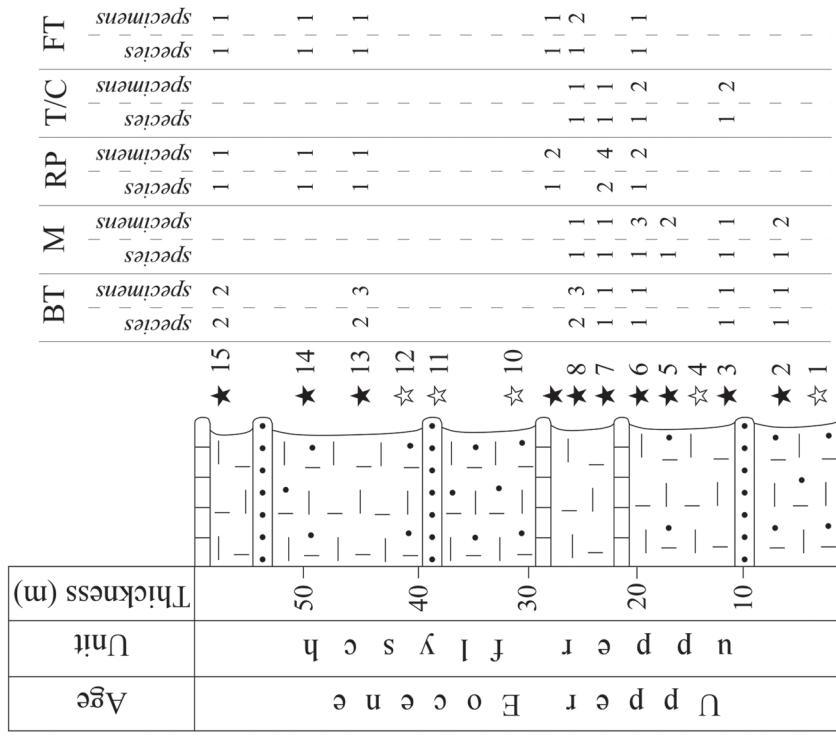
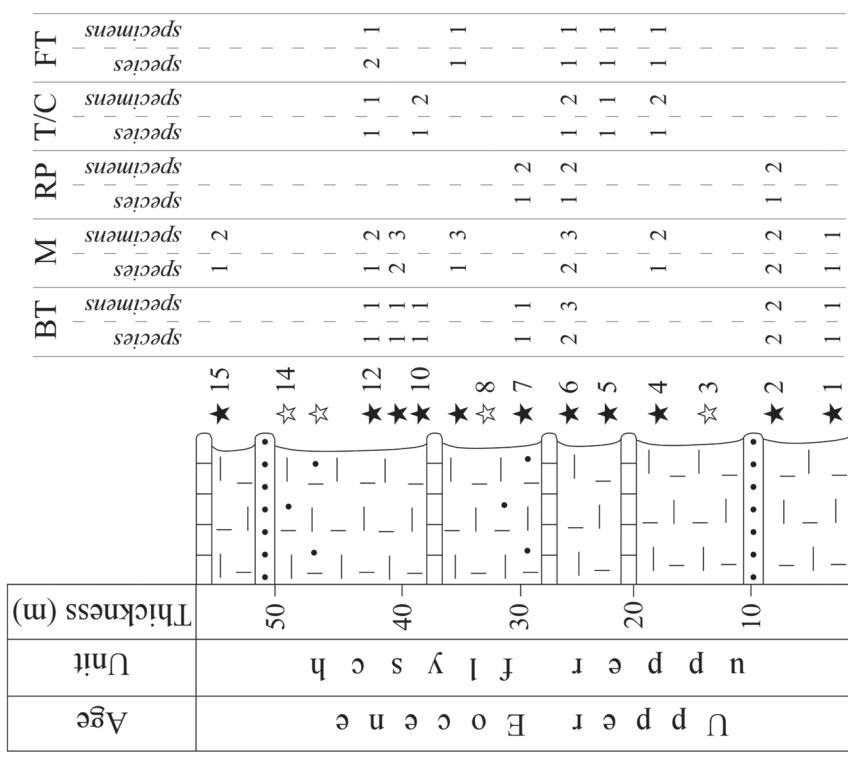


Fig. 7. Distribution of the morphogroups established in Krivolak and Rabrovo sections (legend on Fig. 3)

Фиг. 7. Разпространение на установените морфогрупи в разрези Криволак и Раброво (легенда на фиг. 3)

### Dedeli Section



### Crna Skala Section

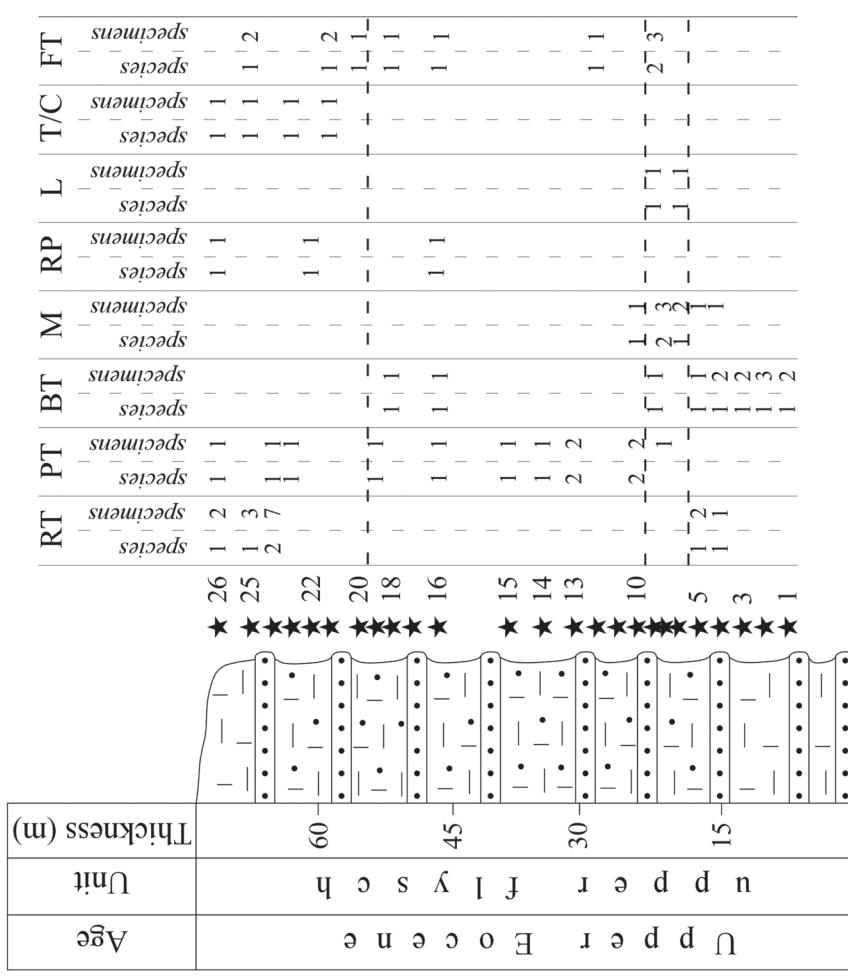


Fig. 8. Distribution of the morphogroups established in Dedeli and Crna Skala sections (legend on Fig. 3)

Фиг. 8. Разпространение на установените морфогрупи в разрези Дедели и Црна скала (легенда на фиг. 3)

## Stuka Section

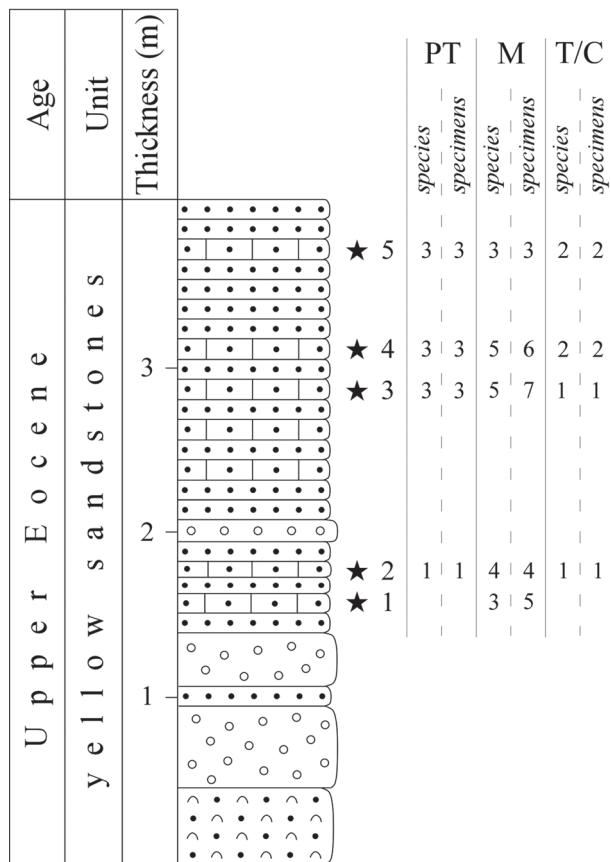


Fig. 9. Distribution of the morphogroups established in Stuka section (legend on Fig. 3)

Фиг. 9. Разпространение на установените морфогрупи в разрез Щука (легенда на фиг. 3)

the Republic of Macedonia we defined and illustrated eleven morphogroups by arranging taxa according to morphological features (external test morphology – test shape and the nature of test coiling – chamber addition), combined with microhabitats (epifaunal, shallow infaunal and deep infaunal) and feeding strategies (suspension-feeders, herbivores, bacterivores, omnivores, etc.). Generally, the investigated assemblages are slightly dominated by morphogroups characteristic for shallow (inner shelf) environment, but the low specimen abundance led us to the conclusion that the foraminiferal data yielded from the majority of the sections are not reliable for paleoecological implications. Therefore, additional foraminiferal data (preservation of benthic foraminiferal tests, P/B ratio) as well as data from other fossil groups have been used to confirm our results.

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