Eleven species belonging to ten genera, i.e. Discradisca Stenzel, 1964, Novocrania Lee & Brunton, 2001, Terebratulina d’Orbigny, 1847, Megathiris d’Orbigny, 1847, Argotheca Dall, 1900, Bronnothyris Popiel-Barczyk & Smirnova, 1978, Joania Álvarez, Brunton & Long, 2008, Megerlia King, 1850, Platidia Costa, 1852, and Lacazella Munier-Chalmas, 1880 have been identified in the Upper Eocene (Priabonian) deposits of Dnipropetrovsk, eastern Ukraine. Two species, Bronnothyris danaperensis sp. nov. and Joania ukrainica sp. nov. are described as new. The genera Discradisca, Novocrania, Megathiris, Joania, Megerlia and Platidia are reported for the first time from the Eocene of Ukraine. Additionally, the occurrence of Joania and Megerlia extends their stratigraphical range from the Oligocene to the Eocene. The fact that megathyridids and thecideides make up more than 90% of the material indicates that the fauna was living in a warm, shallow-water environment. • Key words: Brachiopoda, Late Eocene, Priabonian, Ukraine, taxonomy, gastropod drilling predation.

Eocene brachiopods, although not diverse, have a widespread distribution throughout Europe and have been reported from many localities in Ukraine (Zelinskaya 1962, 1970, 1975, 1977; Makarenko 1974). Recently Systerova (2012) briefly summarized what is known of Paleogene brachiopods from this area. In earlier reports that need modern revision, Zelinskaya (1975, 1977) described more than 30 species and Makarenko (1974) described a new craniid species.

The aim of this paper is to describe a new brachiopod fauna from Upper Eocene deposits exposed in the Rybalsky Quarry at Dnipropetrovsk, eastern Ukraine (Fig. 1). Although rich in specimens, this fauna has never been fully described, although it was mentioned by Systerova (2012, 2014).

Geological setting

The Upper Eocene deposits cropping out in the Rybalsky Quarry, situated on the left bank of the Dnieper River at Dnipropetrovsk (Fig. 1), lie unconformably on Precambrian granites of the Ukrainian Shield (Müller & Rozenberg 2003). They are represented by yellowish, light grey detrital sands up to 5 m thick, interpreted as shallow-water facies. The lower part (1.5 m) of the exposed section is composed of calcareous sands with rare macrofossils and common red-algal nodules. The upper part (3.5 m) contains a rich fauna of corals, sponge spicules, molluscs, brachiopods, byzozoans and fish otoliths (Müller & Rozenberg 2003; Amitrov & Zhegallo 2007; Armitrov 2008; Berezovsky 2014, 2015; Sirenko & Dell’Angelo 2015). Based on the calcareous nannoplankton those deposits were assigned to zone NP 19, corresponding to the Priabonian, Late Eocene. For detailed geological description, see Müller & Rozenberg (2003).

Material and methods

The material described herein was collected at the Rybalsky Quarry in Dnipropetrovsk (Fig. 1). Apart from 12 specimens donated by T.A. Stefanska (Dnipropetrovsk), the specimens were picked from five large (about 100 kg each) bulk samples (UDR1 to UDR5 in Müller & Rozenberg 2003), taken by the junior author in 1999 and washed on a 0.5 mm mesh sieve. For details of sampling see Müller & Rozenberg (2003, pp. 362–364). Among 1356 specimens, 269 were articulated and 1087 were separate valves. The
preponderance of disarticulated valves suggests a high-energy environment and/or post-mortem transport, but if so, the good state of preservation indicates short distance transport.

Specimens selected for scanning electron microscopy were mounted on stubs, coated with platinum and examined using Philips XL-20 microscope at the Institute of Paleobiology, Warszawa. The majority of the collection is housed at the University of Leipzig, Germany under the catalogue numbers UDB 147-216. Twelve specimens donated by T. Stefanska are kept at the Institute of Paleobiology, Polish Academy of Sciences, Warszawa, under collection number ZPAL Bp.82.

**Systematic palaeontology**

Order Lingulida Waagen, 1885  
Superfamily Discinoidea Gray, 1840  
Family Discinidae Gray, 1840  

**Genus Discradisca Stenzel, 1964**

*Type species.* – *Orbicula antillarum* d’Orbigny, 1845, by original designation of Stenzel (1964, p. 627).

*Discradisca* sp.  
Figure 2A, B

*Material.* – Four poorly preserved fragments of dorsal valves.

*Remarks.* – This is the first record of discinid brachiopods from the Eocene of Ukraine. The ribbed neatic shell (Fig. 2B) allows attribution to the genus *Discradisca* (see discussion in Bitner & Cahuzac 2013). The larval (protegulum) shell is smooth without growth lines, reaching about 0.5 mm, while the postlarval (brephic) shell is smooth but sculptured by numerous growth lines (Fig. 2A).

*Occurrence.* – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine. Several species of *Discradisca* have been recognized in the Paleogene and Neogene of Europe (see Bitner & Cahuzac 2013; Dulai 2013, 2015; Bitner & Müller 2015; Bitner & Motchurova-Dekova 2016).

Order Craniida Waagen, 1885  
Superfamily Cranioidea Menke, 1828  
Family Craniidae Menke, 1828  

**Genus Novocrania Lee & Brunton, 2001**

*Type species.* – *Patella anomala* Müller, 1776, by original designation of Lee & Brunton (1986, p. 150).

*Novocrania cf. anomala* (Müller, 1776)  
Figure 2C–E

*cf. 2013a Novocrania anomala* (Müller). – Bitner *et al.*, p. 584, fig. 2a–d (cum syn.).  
*cf. 2014a Novocrania anomala* (Müller). – Robinson, fig. 5c–f.
cf. 2016 Novocrania anomala (Müller). – Bitner & Motchurova-Dekova, p. 10, fig. 2c–g.

Material. – Six dorsal valves.

Remarks. – The specimens closely resemble Novocrania anomala (Müller, 1776), but because the ventral valves are missing and the material is limited we prefer to leave them in open nomenclature. The shell is small with maximum observed length 5.2 mm, subcircular in outline, slightly conical with a subcentral to posteriorly directed apex. The outer surface is usually worn but irregular growth lines are visible. Posterior adductor muscle scars are subcircular, widely separated, lying near the margin. The anterior adductor muscle scars are oval to kidney-shaped, moderately elevated. Brachial retractors are small but distinct, separated from the adductor scars (Fig. 2E). Brachial protractor is indistinct. In a larger specimen mantle canals are observed in the anterior half of the valve.

Studying craniid musculature and its function Robinson (2014a) concluded that brachial retractor muscles are misnamed and an appropriate name should be support structure as given by Blochmann (1892). In addition, a new name has been proposed for brachial protractor muscles, small anterior muscles.

The separation of support structure from adductors used to be considered as an important distinguishable character between Novocrania anomala and N. turbinata (Poli, 1795) (see Logan & Long 2001, Kroh et al. 2008, Hiller 2011). According to Emig (2014) those differences fit within the intraspecific variability and both species are synonymous. However, in the opinion of Robinson (2015) N. anomala and N. turbinata are confirmed to be separate species based on morphology of the ventral valve. Interestingly, molecular studies seem to support the separation of those two species, nevertheless, the sequence analyses were made without close examination of shell morphology (Cohen et al. 2014).

The specimens described by Makarenko (1974) as a new craniid, Crania belokrysi are much larger than those from the Rybalsky Quarry, reaching up to 20 mm. Based on the published illustrations and description it is difficult to determine if Makarenko’s material also represents Novocrania anomala. Moreover, Makarenko (1974) wrongly attributed some of his specimens to ventral valves; all his illustrated specimens represent dorsal valves.

Occurrence. – Late Eocene (Priabonian) of Dnipropetrovsk, eastern Ukraine. Novocrania anomala was reported from the Upper Oligocene of France (Bitner et al. 2013a) and is common in the Miocene of Europe (Bitner & Motchurova-Dekova 2016). Today this species lives in the Mediterranean Sea and the eastern North Atlantic from 3 to 1665 m (Logan 1979, Logan & Long 2001).
Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Cancellothyridoidea Thomson, 1926
Family Cancellothyrididae Thomson, 1926
Subfamily Cancellothyridinae Thomson, 1926

Genus *Terebratulina* d’Orbigny, 1847

Type species. – *Anomia retusa* Linnaeus, 1758, by subsequent designation of Brunton *et al.* (1967, p. 176).

*Terebratulina tenuistriata* (Leymerie, 1846)

Figure 3

1894 *Terebratulina planicosta* v. Koenen; Koenen, p. 1343, pl. 97, figs 7–10.
1894 *Terebratulina tenuicosta* v. Koenen; Koenen, p. 1346, pl. 97, fig. 6.
1894 *Terebratulina asperula* v. Koenen; Koenen, p. 1347, pl. 97, figs 2–5.
1975 *Terebratulina parisiensis* (Deshayes). – Zelinskaya, p. 111, pl. 11, fig. 7.
1975 *Terebratulina tenuilineata* (Baudon). – Zelinskaya, p. 113, pl. 11, fig. 8.
1975 *Terebratulina asperula* Koenen. – Zelinskaya, p. 114, pl. 12, figs 1, 2.
1975 *Terebratulina tenuicosta* Koenen. – Zelinskaya, p. 115, pl. 12, fig. 3.
1975 *Terebratulina planicosta* Koenen. – Zelinskaya, p. 122, pl. 13, figs 1, 2.
2005 *Terebratulina sp. cf. T. tenuistriata* (Leymerie). – Bitner & Boukhary, p. 396, fig. 3a–f.
2008 *Terebratulina tenuistriata* (Leymerie). – Bitner & Dulai, p. 33, fig. 4.1–8.
2009 *Terebratulina tenuistriata* (Leymerie). – Bitner & Dulai, p. 185, pl. 3, figs 1–11.
Figure 4. *Megathiris detruncata* (Gmelin, 1791), Upper Eocene, Dnipropetrovsk, Ukraine. • A–D – dorsal views of complete specimens; A – juvenile specimen, no. UDB 163; B – no. UDB 164; C – no. UDB 165; D – no. UDB 166. • E–I – dorsal valves, visible three septa; E, F – interior and oblique views, no. UDB 167; G – interior view, no. UDB 168; H, I – interior and oblique views, no. UDB 169. • J–L – interior of ventral valves; J – no. UDB 170; K – no. UDB 171; L – no. UDB 172. All SEM.

2011 *Terebratulina tenuistriata* (Leymerie). – Bitner et al., p. 122, fig. 3a–c.
2012 *Terebratulina tenuistriata* (Leymerie). – Bitner & Boukhary, fig. 2c, d.
2016 *Terebratulina tenuistriata* (Leymerie). – Bitner et al., p. 3, figs 2.4–6.

**Material.** – 82 articulated specimens plus 9 ventral and 6 dorsal valves.

**Remarks.** – The species *Terebratulina tenuistriata* has been reported from the Eocene of Ukraine, but under several different names (Zelinskaya 1975). Here this species is relatively common. In shell outline and ornamentation the specimens closely resemble those from other localities (e.g. Bitner 2000; Bitner et al., 2011, 2016; Bitner & Müller 2015). The shell is of medium size (maximum observed length = 16.2 mm), elongate oval and biconvex. Its surface is covered with numerous, fine ribs.

**Occurrence.** – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine. This species is well known in the Eocene of Europe, and is also reported from Egypt and the United Arab Emirates (see fig. 3 in Bitner & Boukhary 2012). Recently it was recognized in the Lower Oligocene of Central Germany (Bitner & Müller 2015).

Suborder Terebratellidina Muir-Wood, 1955
Superfamily Megathyridoidea Dall, 1870
Family Megathyrididae Dall, 1870

**Genus Megathiris d’Orbigny, 1847**

**Type species.** – *Anomia detruncata* Gmelin, 1791, by subsequent designation of Dall (1920, p. 331).

**Megathiris detruncata** (Gmelin, 1791)

Figure 4

1864 *Argiope multicostata* n. spec.; Bosquet, p. 3, figs 1–5.
1894 *Argiope multicostata* Bosquet. – von Koenen, p. 1357, pl. 98, figs 16–17.
1900 *Megathiris detruncata* (Gmelin). – Bitner, p. 135, text-figs 3, 4, pl. 3, figs 1–8, pl. 6, figs 1–7 (cum syn.).
1900 *Megathiris detruncata* (Gmelin). – Popiel-Barczyk & Barczyk, p.175, text-figs 10, 11, pl. 6, figs 6–11, pl. 7, figs 1–13.
2003 *Megathiris detruncata* (Gmelin). – Bitner & Moissette, p. 473, fig. 6g, h.
2008 *Megathiris detruncata* (Gmelin). – Bitner & Dulai, p. 35, fig. 5.1–4.
2009 *Megathiris detruncata* (Gmelin). – Bitner & Schneider, p. 127, fig. 6a–c.
2010 *Megathiris detruncata* (Gmelin). – Dulai, p. 26, pl. 3, fig. 1a, b.
2010 *Megathiris detruncata* (Gmelin). – Dulai et al., p. 186, pl. 2, fig. 4.
2011 *Megathiris detruncata* (Gmelin). – Dulai, p. 305, fig. 8a, b.
2012 *Megathiris detruncata* (Gmelin). – Zágoršek et al., p. 27, fig. 6d, e.
2013a *Megathiris detruncata* (Gmelin). – Bitner et al., p. 586, fig. 3a–m.
2013b *Megathiris detruncata* (Gmelin). – Bitner et al., p. 83, fig. 3j–l.
2016 *Megathiris detruncata* (Gmelin). – Bitner & Motchurova-Dekova, p. 10, fig. 3a–l.

**Material.** – 47 articulated specimens, 70 ventral valves, 153 dorsal valves.

**Remarks.** – This species is one of the most common in the investigated assemblage and this is the first record of any representative of the genus *Megathiris* from the Eocene of Ukraine. Specimens assigned to *Megathiris* by Zelinskaya (1962, 1975) undoubtedly belong to *Argyrotheca* (see below).

*Megathiris detruncata* is characterized by its small, transversely elongate to subpentagonal shell ornamented by a few broad, rounded ribs. The foramen is large, subtriangular. This species can be easily distinguishable from other megathyridids by the presence of three septa on the interior of the dorsal valve.

**Occurrence.** – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine. *Megathiris detruncata* has a long stratigraphical range from the Eocene to the Holocene. Today it lives in the Mediterranean Sea and the north-eastern Atlantic with a depth range from 5 to 896 m (Logan 2007).

**Genus Argyrotheca Dall, 1900**

**Type species.** – *Terebratula cuneata* Risso, 1826, by original designation of Dall (1900, p. 44).

**Argyrotheca lunula** (von Koenen, 1894)

Figure 5

1894 *Argiope lunula* v. Koenen; Koenen, p. 1360, pl. 98, figs 6–10.
1894 *Argiope lunula* var. percostata v. Koenen; Koenen, p. 1361, pl. 98, figs 11–13.
1962 *Megathyris lunula percostata* (Koenen). – Zelinskaya, p. 109, text-fig. 2, pl. 6, figs 9–11.


**Figure 5.** *Argyrotheca lunula* (von Koenen, 1894), Upper Eocene, Dnipropetrovsk, Ukraine. • A–F – dorsal valves; A, B – interior and oblique views, no. UDB 173; C – interior view, no. UDB 174; D, E – interior and oblique views, no. UDB 175; F – interior view, no. UDB 176. • G–I – interior of ventral valves; G – no. UDB 177; H – no. UDB 178; I – no. UDB 179. • J–M – dorsal views of complete specimens; J – young individual, no. UDB 180; K – no. UDB 181; L – no. UDB 182; M – no. UDB 183. All SEM.
1987 *Argyrotheca lunula* (Koenen). – Popiel-Barczyk & Barczyk, p. 98, text-fig. 5, pl. 2, figs 1–3.

**Material.** – 61 articulated specimens, 45 ventral and 113 dorsal valves.

**Description.** – Shell small (maximum observed length 4.9 mm), thick, variable in outline from transversely elongate to subrectangular with maximum width at hinge line, ventribiconvex. Shell surface with up to 15 rounded ribs; in juvenile specimens delicate ribs visible only on the anterior part (Fig. 5J). Foramen large, triangular, hypothyrid, flanked by narrow deltoidal plates. Lateral commissures straight, anterior commissure rectimarginate.

Ventral valve interior with long, narrow teeth lying parallel to the hinge margin. Pedicle collar well-developed, supported by a septum. Dorsal valve interior with narrow but massive inner socket ridges. Cardinal process distinct. Hinge plates attached to the septum forming a broad trough. Crura very short. Loop attached to valve floor and anteriorly to septum. Septum high, triangular in profile; serrations present in young specimens, in adult they are overgrown (Fig. 5D, E).

**Remarks.** – This species, originally described from West
Germany (von Koenen 1894), was reported from the Eocene of Ukraine by Zelinskaya (1962, 1975), who wrongly assigned it to the genus *Megathiris*, a brachiopod characterized by the presence of three septa on the dorsal valve, a feature observed neither in the original material from Germany (von Koenen 1894) nor in the specimens from Ukraine (Zelinskaya 1975, pl. 14, figs 9, 10). The lateral ridges on the ventral valve reported by Zelinskaya (1962, 1975) are not diagnostic characters for *Megathiris*.

*Argyrotheca lunula* is one of the most common species in the material under study. In shell outline and ornamentation the specimens from the Rybalsky Quarry are consistent with those hitherto described, differing only in larger size.

**Occurrence.** – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine. Apart from Ukraine this species was also recorded from the Upper Eocene/Lower Oligocene of West Germany (von Koenen 1894) and Upper Eocene of southern Poland (Popiel-Barczyk & Barczyk 1987).

*Argyrotheca megapora* Zelinskaya, 1975

**Figure 6**

1975 *Argyrotheca megapora* Zelinskaya; Zelinskaya, p. 132, pl. 16, fig. 1.

**Material.** – 38 articulated specimens, 14 ventral and 26 dorsal valves.

**Description.** – Shell thin, small, weakly biconvex, smooth or covered with poorly defined ribs. Hinge line straight, long. Foramen large, triangular, hypothyrid, bordered by raised deltidial plates. Pedicle collar wide, supported by a slender septum. Dorsal valve with narrow but thick inner socket ridges and prominent cardinal process. Hinge plates attached to valve floor. Loop not preserved. Dorsal median septum high, triangular in profile with 4 serrations.

**Remarks.** – This species is relatively common in the Dnipropetrovsk assemblage. Externally, in outline and poorly defined ribs it resembles somewhat *Joania cordata* (Risso, 1826) but differs strongly internally by the lack of marginal tubercles (Logan 1979; Bitner 1990, 1993; Bitner et al. 2013a; Bitner & Motchurova 2016).

**Occurrence.** – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine. *Argyrotheca megapora* seems to be endemic to the Eocene of Ukraine.

**Genus Bronnothyris** Popiel-Barczyk & Smirnova, 1978

**Type species.** – *Terebratula bronnii* Roemer, 1841 by original designation of Popiel-Barczyk & Smirnova (1978, p. 41).

**Brunnothyris danaperensis** sp. nov.

**Figure 7**

**Types.** – Holotype no. UDB 193 figured in Fig. 7D, paratypes no. UDB 194–201 figured in Fig. 7B, C, E–N.

**Type locality.** – Rybalsky Quarry, Dnipropetrovsk, eastern Ukraine.

**Type horizon.** – Priabonian, Late Eocene.

**Etymology.** – After Danaper, the Latin name of the Dnieper River.

**Diagnosis.** – *Brunnothyris* with smooth surface and hinge line equal to maximum width; foramen large, hypothyrid with narrow pedicle collar; hinge plates fused forming a broad, coherent platform; dorsal median septum high with short septal flanges.

**Material.** – 24 articulated specimens, 38 ventral and 148 dorsal valves.

**Measurements.** – in mm.

<table>
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<th>Specimen</th>
<th>Length</th>
<th>Width</th>
<th>Thickness</th>
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<td>5.7</td>
<td>2.0</td>
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<td>Paratype UDB 194</td>
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<td>2.1</td>
</tr>
<tr>
<td>Paratype UDB 195</td>
<td>2.6</td>
<td>4.4</td>
<td>1.9</td>
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</table>

**Description.** – Shell small, thick, subrectangular to transversely oval in outline, wider than long, ventribiconvex. Shell surface smooth with numerous, distinct growth lines. Anterior commissure rectimarginate, lateral commissures straight. Beak low, suberect with sharp beak ridges. Interarea narrow transversely striated. Beak and area can be eroded, suggesting a short pedicle. Foramen, substrangular, hypothyrid, bordered by two narrow deltidial plates, often poorly defined. Hinge line straight, equal to maximum width.

Ventral valve interior with short but wide teeth parallel to hinge margin (Fig. 7N). Sometimes teeth are strongly reduced (Fig. 7L). Pedicle collar narrow, supported by a median septum extending to about mid-valve. Shallow depressions to accommodate serrations of dorsal septum visible.

Dorsal valve interior with short, widely divergent socket ridges occupying most of valve width. Rough surface between ridges most probably served as cardinal process. Outer and inner hinge plates very broad, fused to form a single coherent platform. Crura very short or absent. Crural processes medianly directed, massive. Loop attached to valve floor and septum (Fig. 7F–H). Short septal flanges extend ventrally from the septum (Fig. 7H, K). Septum triangular in profile, high, with 3 serrations.
Remarks. – The genus Bronnothyris was established based on the presence of septal flanges extending from the dorsal septum, the feature not observed in other megathyridids (see Popiel-Barczyk & Smirnova 1978, Bitner & Kroh 2011). This feature is also displayed in the specimens under study, supporting their attribution to Bronnothyris. 

In its fused hinge plates forming a single, broad platform the newly established species, Bronnothyris danaparensis sp. nov. is most similar to the Early Oligocene B. subradiata (Sandberger, 1862) from the Mainz Basin, differing, however, externally; B. subradiata has a high beak and shell surface covered with up to 10 ribs (Bitner & Kroh 2011). The fused hinge plates are also observed in the Late Cretaceous species, B. coniuncta (Steinich, 1965), however, in that species the plates are much narrower and it differs in having strongly transversely elongate outline and ribbed surface (Steinich 1965).

The newly described species also displays similarities to Argyrotheca wansinensis Vincent, 1923 from the Upper Paleocene of Belgium (Vincent 1923), however, insufficient description and illustrations as well a major stratigraphical and geographical gap prevent any further conclusions (see also discussion in Bitner & Kroh 2011).

Systerova (2014) also recognized the genus Bronnothyris in the material from the Rybalsky Quarry. However, the three species proposed in this paper should be treated as nomen nudum according to the ICZN (1999) rules. There are no descriptions, insufficient illustrations, and no designation of holotypes. Additionally, the species were presented in the local conference materials as nomen provisorium, a form that does not exist in the ICZN. There is no doubt that all three Systerova’s (2014) species are conspecific with B. danaparensis sp. nov. fitting within the intraspecific variability.

Occurrence. – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine.

Genus Joania Álvarez, Brunton & Long, 2008

Type species. – Terebratula cordata Risso, 1826 by original designation of Álvarez et al. (2008, p. 400).

Jania ukrainica sp. nov.

Figure 8

Types. – Holotype no. UDB 203 figured in Fig. 8B–F, paratype no. UDB 202 figured in Fig. 8A.

Type locality. – Rybalsky Quarry, Dnipropetrovsk, eastern Ukraine.

Type horizon. – Priabonian, Late Eocene.

Etymology. – After Ukraine, the country of origin. Gender feminine.

Diagnosis. – Small Joania with wide, rounded ribs up to 12; teeth wide, parallel to hinge margin, cardinal process distinct.

Material. – 3 articulated specimens, 2 ventral and one dorsal valves.

Measurements. – in mm.

<table>
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<th>Specimen</th>
<th>Length</th>
<th>Width</th>
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</tr>
<tr>
<td>Paratype UDB 202</td>
<td>2.2</td>
<td>2.6</td>
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Description. – Shell small (maximum observed length 2.4 mm), thin, wider than long, subrectangular in outline, weakly biconvex. Shell surface with 10 to 12 single, broad, rounded ribs with narrow grooves between them; median rib thinner and shorter. Growth lines indistinct. Hinge line wide, straight to slightly curved. Beak erect with sharp beak ridges and narrow interarea. Foramen large, triangular, hypothyrid, bordered by two narrow, disjunct deltoidal plates. Lateral commissures straight. Anterior commissure rectimarginate with a very shallow, median sulcus in both valves.

Ventral valve interior with wide, short teeth parallel to hinge margin. Pedicle collar wide, supported by a slender septum extending to about mid valve. Ovoid depressions to accommodate dorsal septum serrations present.

Dorsal valve interior with well-developed, narrow inner socket ridges. Hinge plates fused with valve floor. Cardinal process distinct. Crura very short; crural processes relatively long, directed medianly. Descending branches posteriorly curved, united quickly with valve floor; loop emerges anteriorly to attach to a dorsal median septum. Septum high, triangular in profile, sloping towards the anterior margin with 5 serrations. Elongated tubercles on inner margin of both valves.

Remarks. – The presence of marginal tubercles, an important diagnostic character of the genus Joania (see Álvarez...
196; F–H – interior and oblique views, and enlargement tilted (H) of median septum to show extended septal flanges of dorsal valves, no. UDB 197; I–K, interior and oblique views, and enlargement (K) of median septum with extended septal flanges, no. UDB 198; • L–N – interior of ventral valves, paratypes; L – no. UDB 199; M – no. UDB 200; N – no. UDB 201. All SEM.
et al. 2008), indicates attribution to this genus. By its ornamentation Joania ukrainica sp. nov. is easily distinguishable from the type species J. cordata (Risso, 1826) whose shell is subtriangular in outline and smooth or covered with imperceptible costae (Logan 1979; Bitner 1990, 1993; Bitner & Kaim 2004; Álvarez et al. 2008; Bitner & Motchurova 2016).

Although similar in size and outline, the specimens from Dnipropetrovsk differ markedly from the Late Oligocene species from the Aquitaine Basin, Joania peyrerensis Bitner, Lozouet & Cahuzac, 2013 in character of ribs; in J. peyrerensis ribs are fewer, narrow, with large spaces between them (Bitner et al. 2013a). Also in J. ukrainica teeth are wide and short, while those in J. peyrerensis form a small triangular plate.

Another ribbed Joania species, J. ageriana (Taddei Ruggiero, 1993) from the Lower Pleistocene of Italy shows significant differences in shell size and nature of ribbing. It is much larger than the Eocene species, reaching 7 mm in length, and ornamented by numerous (up to 18), fine ribs (Taddei Ruggiero 1993).

**Occurrence.** – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine.

Superfamily Platidioidea Thomson, 1927
Family Platidiidae Thomson, 1927
Subfamily Platidiinae Thomson, 1927

**Genus Platidia Costa, 1852**

**Type species.** – Orthis anomioides Scacchi & Philippi, 1844, by original designation of Costa (1852, p. 47).

**Platidia sp.**

Figure 9A

**Material.** – 3 articulated specimens, one broken.

**Remarks.** – Platidia is rare in the material under study. The specimens are small, hardly exceeding 2 mm. Their shell is smooth, subcircular in outline with a short, straight hinge line and a large, amphihtyrid foramen.

In size and outline the specimens from the Rybalsky Quarry are similar to those described by Dulai (2011) as Platidia anomioides from the Upper Eocene of Austria. Our material, however, precludes any assignment at species level.

**Occurrence.** – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine. Platidia is very common in the Miocene of the Central Paratethys (Bitner 1990, Popiel-Barczyk & Barczyk 1990, Bitner & Dulai 2004, Bitner et al. 2013b, Bitner & Motchurova-Dekova 2016). It is also widespread in modern oceans, having a very wide depth range from 8 m to more than 2000 m (Logan 2007).
Superfamily Kraussinoidea Dall, 1870
Family Kraussinidae Dall, 1870
Subfamily Megerliinae Hiller, MacKinnon & Nielsen, 2008

Genus *Megerlia* King, 1850

*Type species.* – *Anomia truncata* Linnaeus, 1767, by the original designation of King (1850, p. 145).

*Megerlia* sp.
Figure 9B–H

*Material.* – Nine ventral valves.

*Remarks.* – *Megerlia* is rare in the investigated material and represented only by ventral valves. The shell is transversely oval, wider than long, reaching up to 11 mm length and 14 mm in width. The shell surface is covered with numerous, fine, nodulose ribs; concentric growth lines are distinct. The foramen is large with a narrow pedicle collar. The teeth are widely separated, without dental plates. A short, low septum is present in the posterior part.

All the characters mentioned above support attribution to the genus *Megerlia*, however, missing dorsal valves prevent attribution to species level and/or description of a new species. This is the first record of this genus from the Eocene, extending its stratigraphical range. So far the oldest occurrence of *Megerlia* has been from the Lower Oligocene of Germany (Müller 2011). The specimens described by von Koenen (1894) as *Argiope? squamulosa* most probably represent the genus *Megerlia* based on description and illustrations.

*Occurrence.* – Late Eocene (Priabonian) of Dnipropetrovsk, Ukraine.

Order Thecideida Elliott, 1958
Superfamily Thecideoidea Gray, 1840
Family Thecideidae Gray, 1840
Subfamily Lacazellinae Backhaus, 1959

Genus *Lacazella* Munier-Chalmas, 1880

*Type species.* – *Thecidea mediterranea* Risso, 1826, by original designation of Munier-Chalmas (1880, p. 279).

*Lacazella mediterranea* (Risso, 1826)
Figure 10

1894 *Thecidiwm mediterraneum* L. var. *Lattorfense* Davidson. – v. Koenen, p. 1364, pl. 97, figs 11–16.
1970 Lacazella mediterranea (Risso). – Pajaud, p. 128, text-figs 50, 52, pl. 1, fig. 4, pl. 5, fig. 4, pl. 7, fig. 3, pl. 10, figs 1–6; pl. 11, fig. 3, pl. 12, fig. 2, pl. 16 (cum syn.).


1979 Lacazella mediterranea (Risso). – Logan, p. 73, text-fig. 22, pl. 10, figs 1–8.


2005 Lacazella mediterranea (Risso). – Bitner & Dieni, p. 109, fig. 4i–k.

2008 Lacazella mediterranea (Risso). – Bitner & Dulai, p. 40, fig. 5.7–8.

2010 Lacazella mediterranea (Risso). – Dulai, p. 28, pl. 3, fig. 3a, b.


2012 Lacazella sp. – Systerova, fig. 1.

2013a Lacazella mediterranea (Risso). – Bitner et al., p. 595, fig. 9a–l.

Material. – 11 articulated specimens, 64 ventral and 379 dorsal valves.

Remarks. – This is the second record of Lacazella mediterranea from the Eocene of Ukraine (Zelinskaya 1977). This species is the commonest brachiopod in the assemblage from the Rybalsky Quarry. Its shell is small (maximum observed length 5.2 mm), subtriangular in outline, with a strongly convex ventral valve and almost flat dorsal one. The beak is high, without foramen; the delthyrium is closed by a convex, triangular pseudodeltidium for which Logan & Baker (2013) propose the name rugideltidium. The hemispondylium, supported by a small median septum, projects as two prominent prongs (Fig. 10I, G). A trifurcating dorsal median septum is characteristic for Lacazella (Fig. 10A–E). Margins of both valves are papillose.

Occurrence. – Lacazella mediterranea has a very wide stratigraphical range, being first noted from the Upper Palaeocene of Spain (Pajaud & Plaziat 1972). In the Eocene this species is widespread in Europe (see Bitner & Dieni 2005, Bitner & Dulai 2008). Today L. mediterranea is considered as neoendemic (Logan et al. 2004), being known from the western part of the Mediterranean Sea at depths of 1–110 m (Logan 2007, Emig 2016).

Palaeoecological remarks

The detrital sands cropping out in the Rybalsky Quarry at Dnipropetrovsk contain an abundant and diverse Late Eocene fauna of corals, sponges, bivalves, gastropods, brachiopods, bryozoans and fish otoliths. The brachiopods are rich in specimens but of low diversity; eleven species have been identified. Apart from two species cemented to the substrate by the ventral valve, Novocrania cf. anomalata and Lacazella mediterranea, all species have a functional pedicle opening and lived attached by a pedicle to a hard substrate. Dominance of megathyridids and thecideides indicate a warm, shallow-water environment (Logan 1977, 1979; Álvarez et al. 2005) which is supported by the associated molluscs and fish otoliths (Müller & Rozenberg 2003, Amitrov 2008).

Drilling predation

Gastropod drilling predation on invertebrate shells, including brachiopods is of great interest and has been subject of many reports. However, in the Cenozoic drilling predation on brachiopods was only occasionally intense (e.g. Baumiller & Bitner 2004; Harper 2005, 2011; Baumiller et al. 2006; Tuura et al. 2008), usually traces of drill holes are infrequent, often in barely 1% of specimens (Taddei Ruggiero & Bitner 2008, Bitner et al. 2013a, Bitner & Müller 2015, Bitner & Motchuurova-Dekova 2016). At Dnipropetrovsk the frequency of drill holes in brachiopods is relatively high; 130 drilled specimens (9.6%) were found among 1356 specimens examined (Fig. 11, Table 1). Drillings were observed on Terebratulina tenuistriata, Megathiris detruncata, Argyrotheta lunula, A. megapora, Bronnothyris danaperensis, Joania ukrainica, Megerlia sp., and Lacazella mediterranea. No drill holes were observed on Di-scradisca sp., Novocrania cf. anomalata, and Platidia sp. The much higher drilling frequencies among the representatives of Megathyrididae may suggest taxonomic selectivity. We also observe valve selectivity; the dorsal valve was drilled at a higher frequency. Drill holes occur on 40 ventral and 91 dorsal valves, in one case on both valves (Table 1). Contrary to thecideides whose ventral valve is cemented to the substrate, the dorsal valve preference is difficult to explain in the megathyridids as their shell is oriented in a vertical position with both valves equally exposed. However, such preference for the dorsal valve was also recognized in other Cenozoic populations (e.g. Bitner et al. 2013a, Bitner & Müller 2015). Additionally, in the ribbed brachiopods, such as M. detruncata and A. lunula, preferential drill hole siting is observed. Drill holes are very often situated between ribs (Fig. 11 E–G, L–N) where the shell can be up to half as thick on ribs.

On some specimens failed drill holes are visible (Fig. 11K–M). According to Robinson (2014b) some abandoned drill holes can be unrecognized, repaired drill holes. Predatory drilling by gastropods is usually fatal, but brachiopods that survive attacks are capable of repairing their shells (Alexander et al. 1992, Hiller 2014, Robinson...
Figure 10. *Lacazella mediterranea* (Risso, 1826), Upper Eocene, Dnipropetrovsk, Ukraine. • A–E – dorsal valves; A – interior view of juvenile specimen, no. UDB 147; B – interior view, no. UDB 148; C – interior view, no. UDB 149; D, E – interior and oblique views, no. UDB 150. • F–H – ventral valves; F, G – interior view and enlargement tilted view of posterior part to show hemispondylium, no. UDB 151; H, I – interior and tilted views, no. UDB 152. • J–M – dorsal views of complete specimens, and enlargement of umbilical part to show pseudodeltidium; J, K – no. UDB 153; L, M – no. UDB 154. All SEM.
Terebratulina tenuistriata

Among terebratulides there are representatives of four fa-
species is the most common in the studied assemblage.

have only one representative, 

Novocrania cf.

are represented by the discinid 

The brachiopod fauna collected from the Priabonian sands 

r-8 species. Four species, Megathiris detruncata, Argyro-
then the section brachiopods are less numerous, represented by 

Conclusions

The brachiopod fauna collected from the Priabonian sands 

in the Rybalsky Quarry at Dnipropetrovsk, eastern Ukraine 

that part brachiopods are also most abundant; about 800 

2014b) and in the investigated assemblage some evidence 

have been recognized: Megathiris detruncata, two species of 

have only one representative, 

Lacazella mediterranea, this species is the most common in the studied assemblage. 

Megathiris detruncata, two species of 

Argyrotheca megapora

Bromnothyris danaparensis

Joania ukrainica

Platidia sp.

Megerlia sp.

Lacazella mediterranea

Drill hole data for the Late Eocene brachiopods from Dnipropetrovsk.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number undrilled</th>
<th>Number drilled (% drilled)</th>
<th>Drilled on ventral</th>
<th>Drilled on dorsal</th>
<th>Drilled on both valves</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discradisca sp.</td>
<td>4</td>
<td>0 (0.0%)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Novocrania cf. anomalua</td>
<td>6</td>
<td>0 (0.0%)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Terebratulina tenaistritata</td>
<td>92</td>
<td>5 (5.2%)</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Megathiris detruncata</td>
<td>238</td>
<td>32 (11.8%)</td>
<td>14</td>
<td>18</td>
<td>0</td>
</tr>
<tr>
<td>Argyrotheca lunula</td>
<td>192</td>
<td>27 (12.3%)</td>
<td>11</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>Argyrotheca megapora</td>
<td>75</td>
<td>3 (3.8%)</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Bromnothyris danaparensis</td>
<td>167</td>
<td>43 (20.5%)</td>
<td>5</td>
<td>37</td>
<td>1</td>
</tr>
<tr>
<td>Joania ukrainica</td>
<td>5</td>
<td>1 (16.7%)</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Platidia sp.</td>
<td>3</td>
<td>0 (0.0%)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Megerlia sp.</td>
<td>8</td>
<td>1 (11.1%)</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lacazella mediterranea</td>
<td>436</td>
<td>18 (4.0%)</td>
<td>1</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>1226</td>
<td>130 (9.6%)</td>
<td>39</td>
<td>90</td>
<td>1</td>
</tr>
</tbody>
</table>

Figure 11. Drilled brachiopods, Upper Eocene, Dnipropetrovsk, Ukraine. • A–D – Lacazella mediterranea (Risso, 1826); A, B – ventral valve and a close-up image of drill hole (B), no. UDB 207; C – exterior of dorsal valve, no. UDB 208; D – exterior of dorsal valve, no. UDB 209. • E–G – Megathiris detruncata (Gmelin, 1791); E – exterior of dorsal valve, no. UDB 210; F – exterior of ventral valve, no. UDB 211; G – dorsal view of complete specimen, no. UDB 212. • H–K – Bromnothyris danaparensis sp. nov.; H–J – exterior and interior views of ventral valve, and a close-up image (I) of partially re-

2014b) and in the investigated assemblage some evidence 

have only one representative, 

Novocrania cf.

are represented by the discinid 

The genera Discradisca, Novocrania Megathiris, 

Joania, Megerlia and Platidia are reported for the first time 

from the Eocene of Ukraine. Additionally, there are the
oldest occurrences of Joania and Megerlia, extending their stratigraphical range from the Oligocene to the Eocene.

Although many Eocene species have a very wide geographical distribution throughout the whole of Europe, such as T. tenuistrata, M. detruncata, and L. mediterranea described here, the Dnipropetrovsk fauna displays greater similarity (having five species in common) to that of the Latdorf basin of northern Germany (von Koenen 1894) than to any sample from southern Europe (Bitner 2000, Bitner & Dieni 2005, Bitner & Dulai 2008, Dulai et al. 2010, Bitner et al. 2011, Dulai 2011). The molluscan fauna from the Rybalsky Quarry is also most similar to the fauna from Latdorf (Amitrov 2008).

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