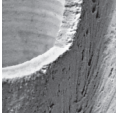


Late Eocene (Priabonian) coleoid cephalopods from the Mandrykivka Beds of the city of Dnipro, Ukraine

VITALY DERNOV & VICTOR DEMIANOV



A low-diverse coleoid cephalopods assemblage consisting of *Beloptera belemnitoidea* de Blainville, 1825, *B. cf. longa* Naef, 1922 and *Belosaepia blainvillei* (Deshayes, 1835) from the Priabonian Mandrykivka Beds of the Konzentrations-Lagerstätte Rybalsky Quarry in the city of Dnipro, central Ukraine, is described and diagnoses of these species are clarified. The study results show that *Belosaepia blainvillei* from the Mandrykivka Beds is the latest record of this genus in the fossil record; previously, this genus was thought to be distributed in the Ypresian to Bartonian strata (Eocene). The Rybalsky Quarry is the easternmost locality of the Paleogene coleoids in the Paratethyan Realm (*i.e.*, in the so-called Beloglinian Basin or Subparatethys); here, these cephalopods probably came from the palaeobasin of the modern Western Europe by sublatitudinal sea currents. Here, the sepiid genus *Belosaepia* probably existed in seagrass meadows along with other animals such as bivalves, gastropods, and ostracods. • Key words: Ukraine, Priabonian, coleoid cephalopods, *Beloptera*, *Belosaepia*.

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Vitaly Dernov, Department of Paleontology and Stratigraphy of the Paleozoic sediments, Institute of Geological Sciences of the NAS of Ukraine, Kyiv, Ukraine; vitalydernov@gmail.com • Victor Demianov, independent researcher, Dnipro, Ukraine

Paleogene rocks are widespread in Ukraine and are represented by all three series of this system (Zosimovich & Shevchenko 2015 and references there). Paleogene sections are composed of different rocks: from deep-water flysch strata to extremely shallow marine and even continental sedimentary rocks (Zosimovich & Shevchenko 2015). A rich biota, including taxonomically diverse mollusk assemblages, is known from the Paleogene marine rocks (Sokolov 1894, 1905; Korobkov 1962; Makarenko 1970; Amitrov 1993; Berezovsky 2016, *etc.*) as well as terrestrial (lacustrine) deposits (Dykan *et al.* 2018) of Ukraine.

Paleogene cephalopods in Ukraine are represented almost exclusively by nautilid species of the genera *Eutrechoceras*, *Pseudocenoceras*, *Deltoidonautilus*, *Aturia* and rhyncholites *Rhyncholite danicus* Shimansky & Alekseev, 1975 (Slodkevich 1928; Makarenko 1956, 1970; Korobkov 1971, 1975; Shimansky 1975, 1979; Shimansky & Alekseev 1975; Dernov & Udovychenko 2016; and unpublished data of the first author). Data on the Paleogene coleoid cephalopods from Ukraine is scarce; Sokolov (1894) briefly described and figured the spirulid *Beloptera aff. belemnitoidea* de Blainville, 1825 from the “lower Oligocene” sands exposed near Ekaterinoslav (modern city of Dnipro) in central Ukraine. These sands were later dated to the late Eocene (see discussion in

“Geological setting”) and named Mandrykivka Beds (Mamyuk 2014). Korobkov (1962) reported the presence of *Beloptera belemnitoidea* de Blainville, 1825 in the Kyiv Formation (late Lutetian–Bartonian) of southern Ukraine, but did not describe or illustrate this fossil.

The aim of this paper is to describe a new coleoid fauna consisting of *Beloptera belemnitoidea* de Blainville, 1825, *B. cf. longa* Naef, 1922 and *Belosaepia blainvillei* (Deshayes, 1835) from the upper Eocene (Priabonian) Mandrykivka Beds exposed in the Rybalsky Quarry, city of Dnipro. Obtained data significantly expand our knowledge on the Paleogene coleoid cephalopods of Eastern Europe and supplement data on the palaeontology of the upper Eocene sedimentary sequence in central Ukraine. Apparently, finds of the species of the genus *Belosaepia* Voltz, 1830 in the Priabonian of the Rybalsky Quarry are the latest record of this genus in the fossil record; previously, this genus was thought to be distributed in the Ypresian to Bartonian strata (Eocene) (Košťák *et al.* 2013: fig. 11).

Material and methods

In this study, we investigated six specimens of mostly poorly preserved apical parts of the sheath of *Belosaepia*

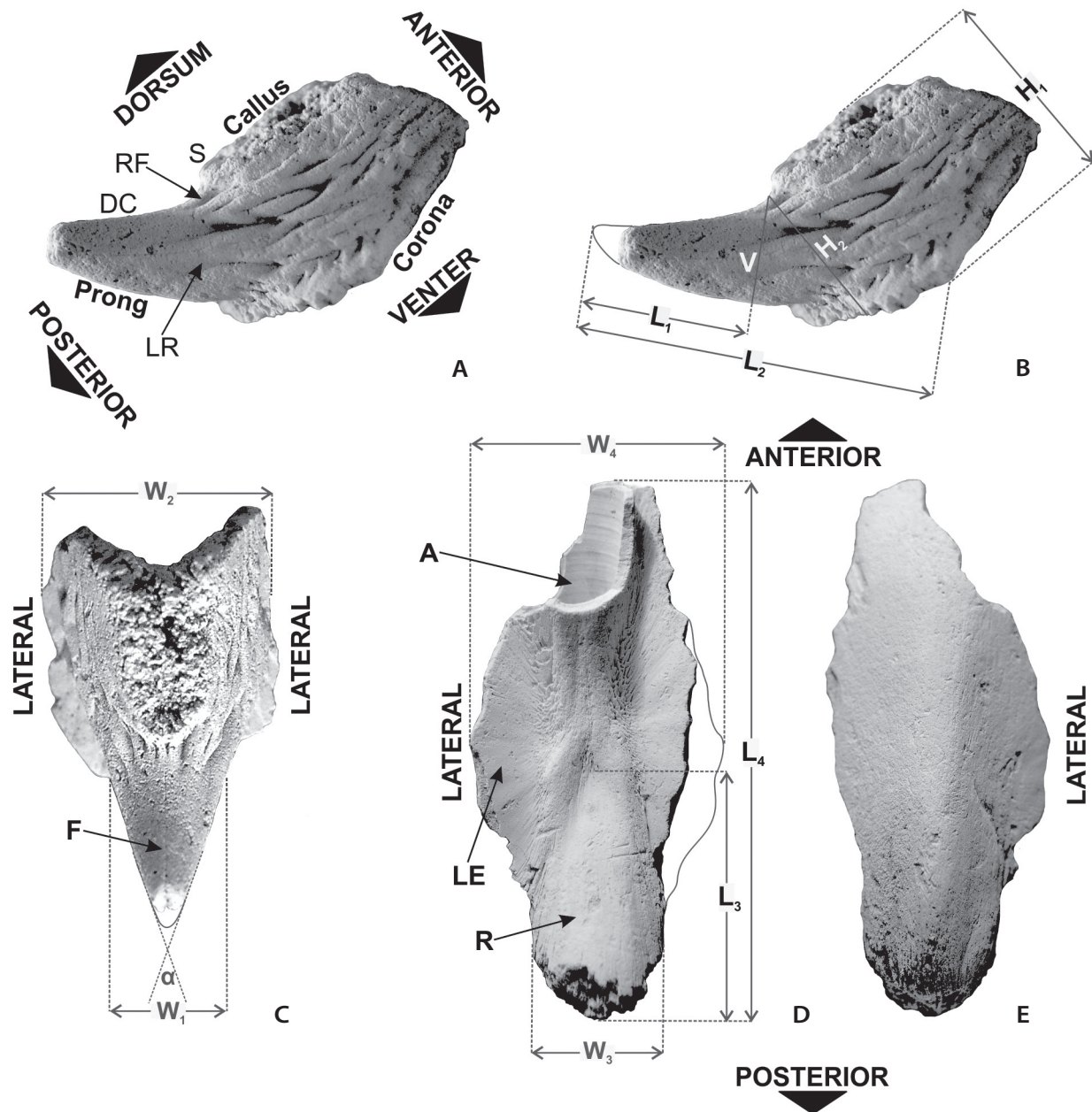


Figure 1. Basic morphological terminology and the scheme of dimensions of the studied coleoid remains. • A–C – *Belosaepia blainvillei* (Deshayes, 1835) (A, B – lateral view, C – dorsal view). • D, E – *Beloptera belemnnoidea* de Blainville, 1825 (D – ventral view, E – dorsal view). Abbreviations of morphological elements: A – alveole; DC – dorsal carina; F – fissure; LE – lateral expansion; LR – lateral rib; R – rostrum; RF – rill field; S – shoulder. Abbreviations of dimensions: α – apical angle of the prong; H_1 – incomplete height of the guard; H_2 – height of the prong between base of shoulder and ventral portion of prong in life position; L_1 – length of the prong; L_2 – length from the apex to base of corona; L_3 – length of the rostrum; L_4 – length of the sheath; V – height of the prong at junction with shoulder; W_1 – maximum width of the prong; W_2 – maximum width of the guard; W_3 – width of the rostrum; W_4 – width of the sheath.

and guard-like sheaths of *Beloptera*. The studied material was collected by the second author (Victor Demianov) in the Rybalsky Quarry in the eastern part of the city of Dnipro during the past 30 years. Studied specimens (IGS NASU-15/01 to IGS NASU-15/06) are housed in the Department of Paleontology and Stratigraphy of the

Paleozoic sediments, Institute of Geological Sciences of the National Academy of Sciences of Ukraine (Kyiv).

The examined material was collected by visual searches of the quarry slopes and sieving sand on a sieve with a mesh diameter of 5 mm. There is not known specific outcrop within the Rybalsky Quarry where specimens

IGS NASU-15/03 to IGS NASU-15/06 were found, because the find site was not documented in a timely manner; specimen IGS NASU-15/01 comes from sands of the Mandrykivka Beds exposed by the ravine near a stream on the southern side of the Rybalsky Quarry (“Outcrop B” described by Berezovsky 2016: p. 19), and the specimen IGS NASU-15/02 was found in glauconitic sands of the Mandrykivka Beds with numerous scaphopods and well-preserved gastropods, exposed by a ditch on the southern side of the Rybalsky Quarry approximately 350 m east from the “Outcrop B” described by Berezovsky (2016).

The basic morphological terminology (after Naef 1922, Dauphin 1985, Yancey *et al.* 2010, Košťák & Hoşgör 2012, Košťák *et al.* 2013, and Goolaerts *et al.* 2022) and the scheme of dimensions (modified from Košťák *et al.* 2013 for *Belosaepia*) are presented in Fig. 1.

Geological setting

All available specimens come from the Mandrykivka Beds (Priabonian, late Eocene: 37.71–33.9 Ma, International Chronostratigraphic Chart 2023), which are widely known because of the numerous and well-preserved fossils of the marine biota, consisting of *c.* 450 gastropod species, about 200 bivalve species, about 40 coral species, and many other excellent preserved fossils that have been found here (Berezovsky & Demianov 2022). It is one of the most taxonomically diverse Paleogene mollusk assemblages in Europe (Berezovsky 2016).

About one hundred works by various authors have been devoted to the study of the fossil biota from the Mandrykivka Beds. However, the fossil fauna and flora from the Mandrykivka Beds of the Rybalsky Quarry and some other lost fossil sites (*e.g.*, the village of Mandrykivka and Shevchenko Park in the city of Dnipro) are unevenly studied: the most investigated are corals (Berezovsky & Satanovskaya 2019, 2020, *etc.*), gastropods and bivalves (Sokolov 1894, 1905; Amitrov 1993; Berezovsky 2011, 2016; Berezovsky & Demianov 2022; Berezovsky *et al.* 2022; *etc.*). Dinoflagellates, spores and pollen, calcareous nannoplankton, infusorians, foraminifers, sponges, brachiopods, scaphopods, polyplacophorans, ostracodes and fishes are less studied; worms, bryozoans, echinoids, barnacles, crabs and tetrapods are almost or completely unexplored. Based on the huge concentration of well-preserved hard skeletal remains, the outcrop of the Mandrykivka Beds in the Rybalsky Quarry may be considered to be a Konzentrat-Lagerstätte.

The lithological composition of the Mandrykivka Beds varies considerably laterally from the weakly cemented coquina and sands with numerous calcareous microbialite nodules (Fig. 2C) to calcareous fine-grained detrital (coral and shelly) sands (Fig. 2B, D), but in general these rocks

are presented by the yellowish to light gray, sometimes light brown detrital weakly clayey calcareous fine-grained sands (Stefanskyi 2015a, b; see Fig. 2A, E). Boulders of crystalline rocks and sandstones with attached bivalves, gastropods *Vermetus* and corals sometimes occur in the lower part of the detrital sand bed (Stefanskyi 2015a, b).

The only modern outcrop of the Mandrykivka Beds is situated in the Rybalsky Quarry (coordinates: 48.449760, 35.141527; see Fig. 3B, C), located on the left bank of the Dnipro River in the eastern part of the city of Dnipro (Manyuk 2014, Stefanskyi 2015a). Here, the Mandrykivka Beds, 3–6 m thick (Bratishko 2009, Stefanskyi 2015a, Zosimovich & Shevchenko 2015), are uncovered by the quarry wall and small ravines crossing the sides of the quarry (Manyuk 2014, Stefanskyi 2015a) (Fig. 3D).

The Mandrykivka Beds are locally distributed in the southern and eastern parts of the city of Dnipro (Nesterenko 1960, Veselov *et al.* 1974, Shirokov *et al.* 1986, Stefanskyi 2014), filling a depression in the Precambrian crystalline basement, measuring 9 km by 3 km (Berezovsky 2016). In most of the Rybalsky Quarry, the Mandrykivka Beds are overlain by the Quaternary alluvial and fluvio-glacial sands and clays (Manyuk 2014; Stefanskyi 2014, 2015a) and underlain by the Precambrian crystalline rocks or kaolin weathering crust (Stefanskyi 2015a).

The Mandrykivka Beds are an extremely shallow water age analogue of the Obukhiv Formation (Priabonian) developed elsewhere in eastern, central and northern Ukraine (Zosimovich & Shevchenko 2015 and references there; Fig. 3A). The rocks exposed in the Rybalsky Quarry belong to the calcareous nannoplankton zone NP19 and the base of zone NP20 (Martini & Ritzkowski 1970); the dinoflagellate zones DP10 and DP11 were identified in the Mandrykivka Beds by Savytska (1996).

Analysis of the Mandrykivkian faunal community indicates the origin of the fossil-bearing rocks in the coastal zone (0 to 10–20 m depth) of a warm-water normally saline paleobasin with good oxygenation and active water dynamics (Amitrov 1993, Stefanskyi 2015b). The bulk of the calcareous sands are thought to have been formed by the erosion of a nearby coral reef (Stefanskyi 2015a, b).

The distribution of the fossils in the Rybalsky Quarry is uneven, showing evidence of mechanical destruction of skeletal remains by waves and bioeroders, *e.g.*, drilling sponges, predatory gastropods and sclerophagous fishes (Stefanskyi 2015a, b). The presence of mollusk shells and detritus with polished or even rounded surface and perfectly preserved shells of the same species, as well as co-occurring of whole thin-walled and large thick-walled broken shells is characteristic for the Mandrykivka Beds (Stefanskyi 2015a, b). Some mollusk shells from the Mandrykivka Beds bear color patterns that are clearly visible in ultraviolet light (Pacaud 2017).

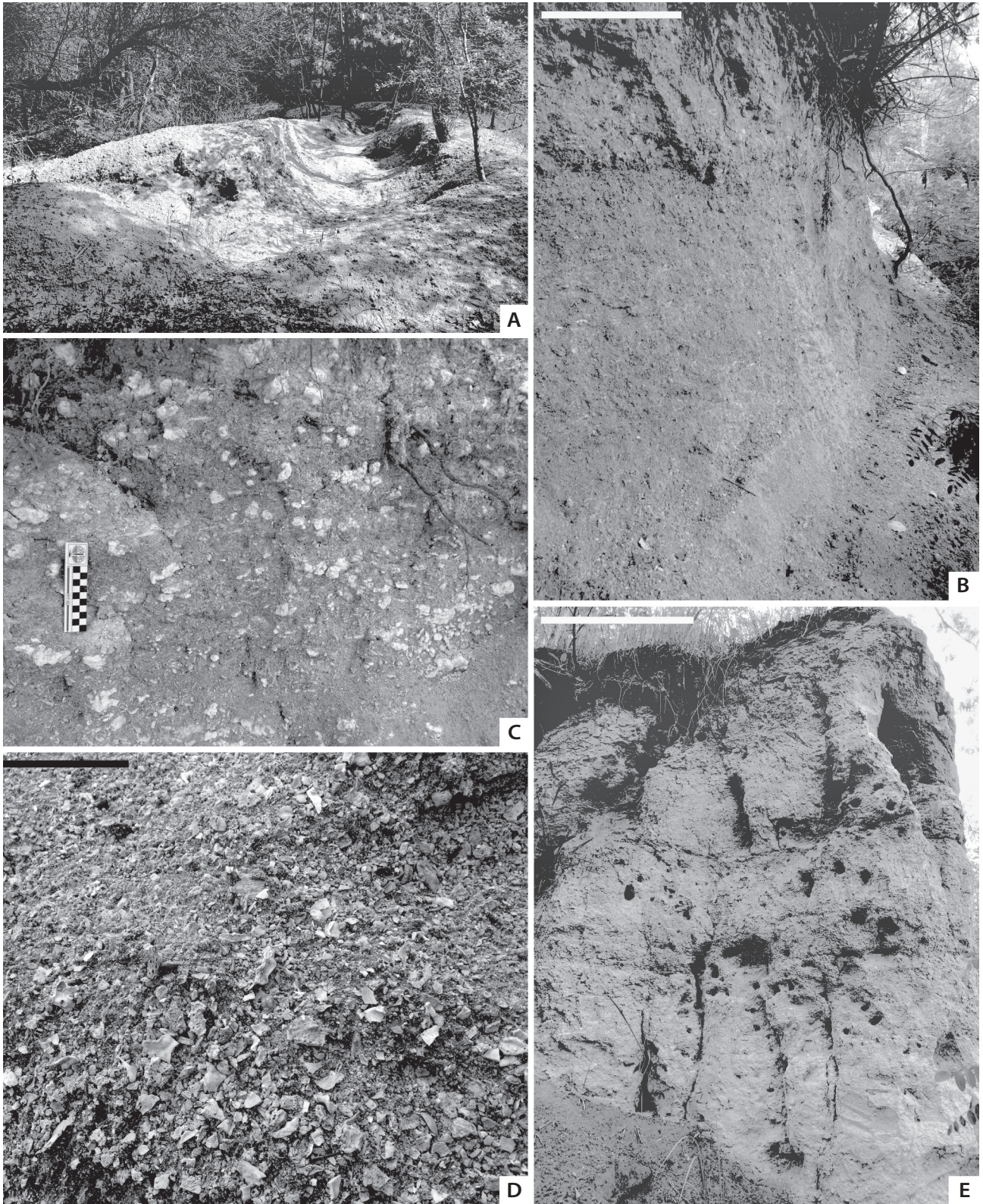


Figure 2. Geological settings of the Rybalsky Quarry fossil site. • A, E – calcareous detrital fine-grained sands of the Mandrykivka Beds in the southern part of the Rybalsky Quarry; A – a ditch on the southern side of the Rybalsky Quarry; E – the ravine near a stream on the southern side of the Rybalsky Quarry (= “Outcrop B”, described by Berezovsky 2016: p. 19). • B, D – calcareous fine-grained detrital sands of the Mandrykivka Beds in the upper level of the Rybalsky Quarry. • C – sands of the Mandrykivka Beds with numerous calcareous microbialite nodules (upper level of the Rybalsky Quarry). Scale bars are 5 cm (D) and 50 cm (B, E).

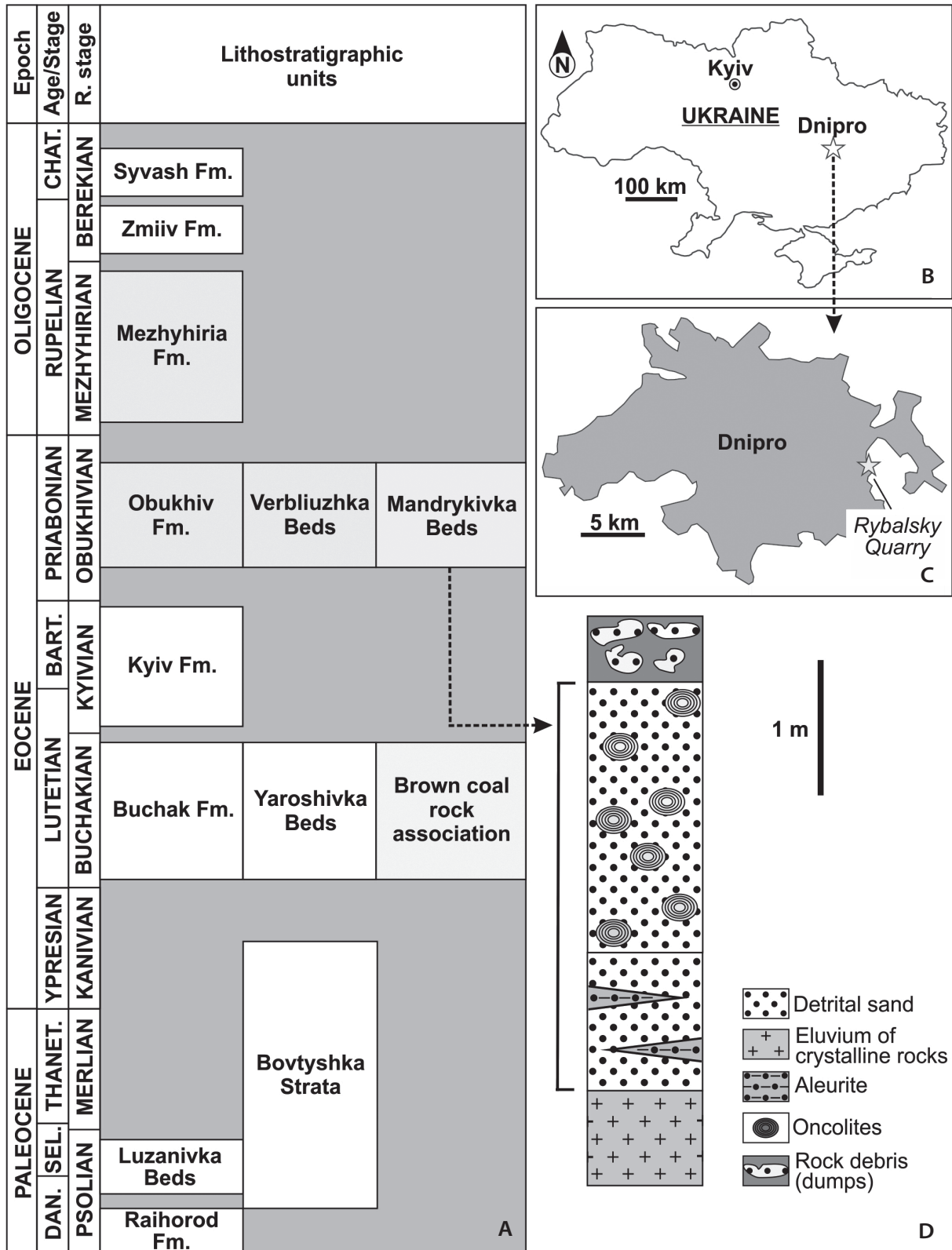


Figure 3. Geological setting of the studied site. • A – Paleogene stratigraphy of the central part of the Ukrainian Shield (after Zosimovich & Shevchenko 2015: tabs 1, 2). • B, C – maps showing general and detailed location of the Rybalsky Quarry. • D – lithological column of the Mandrykivka Beds in the SE part of the Rybalsky Quarry (after Stefanskyi 2014: fig. 2). Abbreviations: Bart. – Bartonian; Chat. – Chattian; Dan. – Danian; Fm. – formation; R. stage – regional stage; Sel. – Selandian; Thanet. – Thanetian.

Shallow short scratch marks are found on the ventral surface of the guard-like sheath of *Beloptera belemnoidea* de Blainville, 1825 (see Fig. 5A). These damages may be collecting artefacts, e.g., spade or hammer marks, although similar postmortem scratches caused by birds have been observed on the cuttlebones of the modern cuttlefish *Sepia officinalis* Linnaeus, 1758, discarded on the beaches of the North Sea in the Netherlands (Jongbloed *et al.* 2016). The origin of the scratch marks on the skeletal remains of *Beloptera belemnoidea* is unclear, but their postmortem occurrence is beyond doubt.

The dorsal surface of the sheath of *Beloptera belemnoidea* (specimens IGS NASU-15/03 figured in Fig. 5A–C and IGS NASU-15/01 in Fig. 6F–H) is rough due to mechanical impact of waves, as in many other shells from the Mandrykivka Beds (Stefanskyi 2015a, b). The surface of two other specimens of *Beloptera belemnoidea* (IGS NASU-15/04 and IGS NASU-15/05) is glossy, and only in some places the guard-like sheath of the specimen IGS NASU-15/04 is slightly rough. It should be noted that the specimen of *Beloptera cf. longa* Naef, 1922 (IGS NASU-15/02) preserved the glossy surface of the sheath, as it is likely that the burial of these remains occurred in conditions of much lower water activity (glauconite sands with shell detritus and perfectly preserved gastropod shells) compared to the detrital sands of the Mandrykivka Beds, in which, for example, the specimen of IGS NASU-15/01 was found. The only examined specimen of *Belosaepia blainvillei* (Deshayes, 1835) (IGS NASU-15/03) has a broken prong apex and the ventral corona margin.

No bioerosion traces were found on the surface of the studied fossils, although many other fossils from the Rybalsky Quarry bear borings of sponges and predatory gastropods (see, for example, Demianov 2018: fig. 7a, b), *etc.* On the ventral surface of the specimen IGS NASU-15/02, in the area between the base of the alveole and the base of the rostrum, there is an enigmatic circular impression, c. 15 mm in diameter, bounded by a very narrow (c. 0.5 mm) groove (see Fig. 6E).

Systematic palaeontology

Class Cephalopoda Cuvier, 1797
 Subclass Coleoidea Bather, 1888
 Order Sepiida Gray, 1849
 Family Belosaepiidae Dixon, 1850

Genus *Belosaepia* Voltz, 1830

Type species. – *Beloptera sepioidea* de Blainville, 1825; original designation.

Diagnosis. – See Garvie 1996: p. 121.

Belosaepia blainvillei (Deshayes, 1835)

Figure 4

- 1835 *Sepia Blainvillii* sp. nov.; Deshayes, p. 758, pl. 101, figs 12–15.
- 1838 *Belosepia Blainvillii* (Deshayes). – Bronn, p. 1128.
- 1848 *Belosepia Blainvillii* (Deshayes). – Bronn, p. 1133.
- 1849 *Belosepia sepioidea* var. *Blainvillii* (Deshayes). – Edwards, p. 29, pl. 1, fig. 1g–i.
- 1850 *Belosepia Blainvillii* (Deshayes). – Sowerby in Dixon, pp. 109, 193, pl. 9, figs 16, 17.
- 1866 *Belosepia Blainvillii* (Deshayes). – Deshayes, p. 616.
- 1882 *Belosepia Blainvillei* (Deshayes). – Vasseur, pl. 1, figs 1–4, pl. 2, fig. 1.
- 1881–1885 *Belosepia Blainvillei* (Deshayes). – Zittel, p. 514, figs 707, 708.
- 1887 *Belosepia Blainvillei* (Deshayes). – Fischer, p. 358, fig. 135.
- 1894 *Belosepia Blainvillei* (Deshayes). – Newton & Harris, p. 122.
- 1895–1898 *Belosepia Blainvillei* (Deshayes). – Cossmann, p. 166, pl. 1, figs 7–9.
- 1900 *Belosepia Blainvillei* (Deshayes). – Cossmann & Pissarro, p. 4, pl. 1, figs 1, 2.
- 1912 *Belosepia Blainvillei* (Deshayes). – Pompeckj, p. 296, fig. 58.
- 1913 *Belosaepia Blainvillei* (Deshayes). – Cossmann & Pissarro, pl. 60, figs 2–4.
- 1915 *Belosaepia blainvillei* (Deshayes). – Zittel, p. 686, fig. 1331.
- 1920 *Belosaepia Blainvillei* (Deshayes). – von Bülow-Trummer, p. 242.
- 1952 *Belosaepia blainvillei* (Deshayes). – Roger, fig. 80.
- 2012 *Belosaepia blainvillei* (Deshayes). – Lebrun *et al.*, pl. 1, fig. 29.

For a more detailed synonymy, see Vincent (1901), Bülow-Trummer (1920) and Riegraf *et al.* (1998).

Material. – One poorly preserved specimen (IGS NASU-15/06) from the Priabonian Mandrykivka Beds of the Rybalsky Quarry, Dnipro, Ukraine.

Diagnosis. – *Belosaepia* with a narrow slightly dorsally curved and elongated prong (spine in other terminologies), which has a slightly oval cross section, a fissure near the apex and a rounded dorsal carina. Lateral surfaces of the prong with one longitudinal wide weakly visible rib, and ventral and dorsal surfaces of the prong are smooth, except for a very thin striae and small short ribs on the rill field area; the lateral surfaces of the guard below the callus are covered with small ridges and elongated pits.

Description. – The specimen IGS NASU-15/06 is a well preserved posterior sheath consisting of a flattened callus,

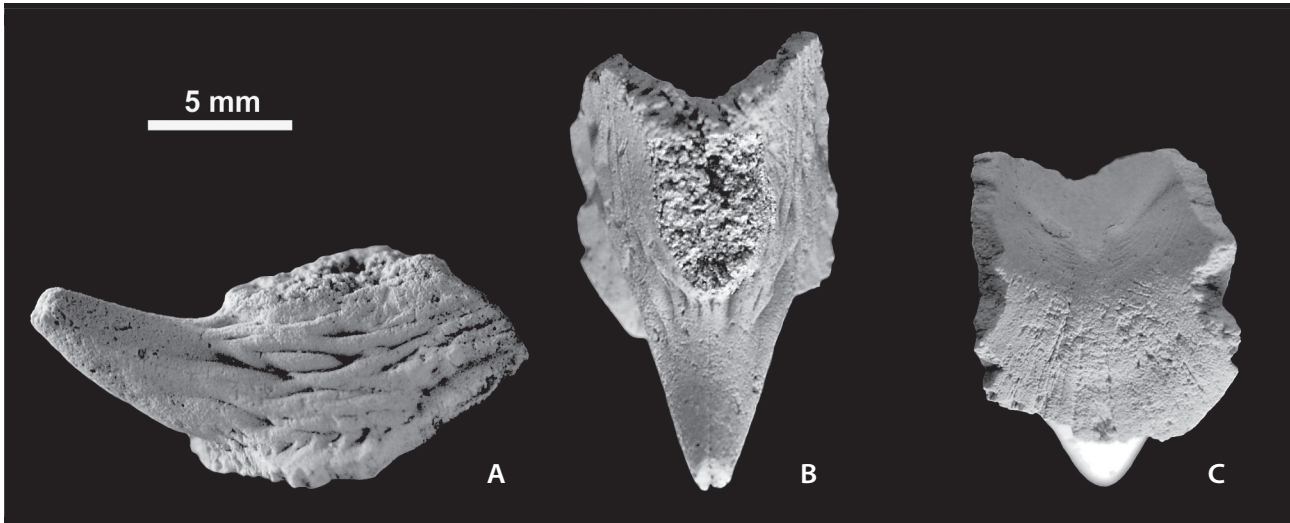


Figure 4. *Belosaepia blainvillei* (Deshayes, 1835) from the Priabonian Mandrykivka Beds of the Rybalsky Quarry (specimen IGS NASU-15/06); A – lateral view; B – dorsal view; C – ventral view.

a narrow, slightly dorsally curved and elongated (conical in the dorso-ventral aspect and slightly curved conical in the lateral aspect) prong length 6.5 mm with a rounded dorsal carina, and remains of the ventral corona (ventral process in other terminologies). The callus is flattened. The cross section of the prong is slightly oval (almost circular), wider than height and rounded on the ventral and dorsal sides. The lateral surfaces of the prong bearing one longitudinal wide, weakly visible rib, *c.* 1 mm wide at the base, tapering to the apex; the ventral and dorsal surfaces of the prong are smooth, except for the very thin striae and small short ribs on the rill field area. The fissure is developed and well visible near the apex of the prong. The ventral corona is apparently arched outline, but partly preserved (lateral width 9.6 mm, incomplete ventral-dorsal height *c.* 8.0 mm) with a weakly concave surface covered by thin radial ribs and attached to the base of the prong. The lateral surfaces of the guard below the callus are covered with small ridges and elongated pits (the so called “reticulated field”).

Table 1. Dimensions (in mm, except α value) of *Belosaepia blainvillei* (Deshayes, 1835).

Specimen	L ₁	L ₂	H ₁	H ₂	W ₁	W ₂	α
IGS NASU-15/06	6.5	12.0	8.0	5.8	5.3	9.6	35°

Remarks. – The specimen of *Belosaepia blainvillei* figured by Roger (1952: fig. 80 and photo in the digital images repository of the Muséum National d’Histoire Naturelle, Paris) is better preserved than the material we studied. The prong of the specimen IGS NASU-15/06 is straighter than that in the Roger’s specimen, but the callus of the Roger’s specimen is higher; the ornamentation of the lateral surfaces of the guard below the callus is coarser in the specimen IGS NASU-15/06, but the ornamentation

of the ventral corona is coarser in Roger’s specimen. The specimen IGS NASU-15/06 is very similar to the specimen of *Belosaepia blainvillei* figured by Cossmann (1895–1898: pl. 1, figs 7–9), but the ornamentation of the lateral surfaces is apparently more delicate in the Cossmann’s specimen.

Belosaepia blainvillei differs from *B. ungula* Gabb, 1860, figured by Yancey *et al.* (2010: fig. 1) and Weaver *et al.* (2010: fig. 5f) in massive ribs and elongate furrows on the lateral area below the callus and very narrow longitudinal lines on the dorsal carina. *Belosaepia blainvillei* differs from *B. incurvata* Cossmann & Pissarro, 1909 and *B. stenzeli* Allen, 1968 in its narrower and longer prong. *Belosaepia blainvillei* is distinguished from *B. veatchi* Palmer, 1937 by the shorter and thicker prong, as well as massive ribs and elongate furrows. *Belosaepia blainvillei* and *Belosaepia sepioidea* distinguished by the coarse ornamentation of the lateral surfaces of the guard below the callus and the longer prong in *B. blainvillei* and the sharp dorsal carina in *B. sepioidea*. *Belosaepia blainvillei* differs from *B. tricarinata* (Watelet, 1851) in the longer prong and apparently the smooth lateral surfaces below the callus.

Occurrence. – Ypresian–Priabonian (early and middle Eocene) of England, Lutetian and Bartonian (middle Eocene) of France and Belgium, Priabonian of Ukraine.

Order Spirulida Haeckel, 1866
Family Belopterae Fischer, 1887

Genus *Beloptera* de Blainville, 1825

Type species. – *Beloptera belemnoides* de Blainville, 1825; original designation.

Diagnosis. – The entire posterior part of the guard-like sheath and especially its narrowed rounded end is deflected ventrally in relation to the phragmocone. The flanks have well-developed wing-like expansions (after Krymholz 1958: p. 165).

***Beloptera belemnoida* de Blainville, 1825**

Figures 5, 6F–H

- 1825 *Beloptera belemnoida* sp. nov.; de Blainville, p. 622.
- 1827 *Beloptera belemnitoidea* de Blainville. – de Blainville, p. 111, pl. 1, fig. 3.
- 1827 *Beloptera belemnitoidea* de Blainville. – de Blainville, pl. 11, fig. 8.
- 1829 *Beloptera belemnitoidea* de Blainville. – Sowerby, p. 183, pl. 591, fig. 2.
- 1830 *Beloptera belemnitoidea* de Blainville. – Voltz, p. 20.
- 1835 *Beloptera belemnitoidea* de Blainville. – Deshayes, p. 761, pl. 100, figs 4–6.
- 1835–1848 *Beloptera belemnitoidea* de Blainville. – de Férussac & d’Orbigny, p. 296, pl. 3, figs 7–9, pl. 24, figs 11, 12.
- 1837 *Beloptera belemnitoidea* de Blainville. – Bronn, pl. 42, fig. 18.
- 1838 *Beloptera belemnitoidea* de Blainville. – Bronn, p. 1129.
- 1843 *Beloptera belemnitoidea* de Blainville. – Nyst, p. 612, pl. 46, fig. 2.
- 1844 *Beloptera belemnitoidea* de Blainville. – Knight, fig. 2585.
- 1845 *Beloptera belemnitoidea* de Blainville. – Pictet, p. 316, pl. 14, fig. 2.
- 1845 *Beloptera belemnitoidea* de Blainville. – d’Orbigny, p. 172, pl. 8, figs 1–4.
- 1846 *Beloptera belemnitoidea* de Blainville. – d’Archiac, p. 216.
- 1846 *Beloptera belemnitoidea* de Blainville. – Quenstedt, p. 472, pl. 30, fig. 38.
- 1848 *Beloptera parisiensis* de Blainville. – Bronn, p. 166.
- 1850 *Beloptera belemnitoidea* de Blainville. – Sowerby in Dixon, p. 109, pl. 9, fig. 18.
- 1856 *Beloptera parisiensis* d’Orbigny. – Bronn, p. 599, pl. 42, fig. 18.
- 1862 *Beloptera belemnitoidea* de Blainville. – Le Hon, p. 825.
- 1866 *Beloptera belemnitoidea* de Blainville. – Deshayes, p. 619.
- 1868 *Beloptera belemnitoidea* de Blainville. – Nyst in Dewalque, p. 401.
- 1873 *Beloptera belemnitoidea* de Blainville. – Vincent & Lefèvre, p. 70.
- 1879 *Beloptera belemnitoidea* de Blainville. – Vincent & Rutot, p. 139.
- 1880 *Beloptera belemnitoidea* de Blainville. – Woodward, p. 177, pl. 2, fig. 7.
- 1881 *Beloptera belemnitoidea* de Blainville. – Vasseur, pl. 1, fig. 7.
- 1883 *Beloptera belemnitoidea* de Blainville. – Vincent & Rutot, p. 196.
- 1883 *Beloptera belemnitoidea* de Blainville. – Tryon, p. 48, pl. 29, fig. 80.
- 1881–1885 *Beloptera belemnitoidea* de Blainville. – Zittel, p. 509, fig. 700.
- 1885 *Beloptera belemnitoidea* de Blainville. – Quenstedt, p. 607, pl. 47, fig. 34.
- 1887 *Beloptera belemnitoidea* de Blainville. – Fischer, p. 359, pl. 2, fig. 7.
- 1894 *Beloptera belemnitoidea* de Blainville. – Newton & Harris, p. 122.
- 1895–1898 *Beloptera belemnitoidea* de Blainville. – Cossman, p. 165, pl. 1, figs 1, 2.
- 1896 *Beloptera belemnitoidea* de Blainville. – Couturieaux, p. 27.
- 1900 *Beloptera belemnitoidea* de Blainville. – Cossman & Pissarro, p. 21, pl. 1, fig. 4.
- 1901 *Beloptera belemnitoidea* de Blainville. – Vincent, p. 3, pl. 1, figs 1–4.
- 1901 *Beloptera belemnitoidea* var. *excentrica* de Blainville. – Vincent, p. 6, pl. 1, figs 5–8.
- 1910–1913 *Beloptera belemnitoidea* de Blainville. – Cossman & Pissarro, pl. 61, fig. 3.1.
- 1916 *Beloptera belemnitoidea* de Blainville. – Abel, p. 143, figs 58, 59.
- 1920 *Beloptera belemnitoidea* de Blainville. – von Bülow-Trummer, p. 235.
- 1922 *Beloptera belemnitoidea* de Blainville. – Naef, p. 56.
- 1922 *Beloptera angusta* de Blainville. – Naef, p. 59.
- 1938 *Beloptera belemnitoidea* de Blainville. – Glibert, p. 157.
- 1952 *Beloptera belemnitoidea* de Blainville. – Roger, p. 728, fig. 67.
- 1958 *Belopterina levesquet* (d’Orbigny). – Krymholz, pl. 70, fig. 5.
- 1985 *Beloptera belemnitoidea* de Blainville. – Dauphin, fig. 3a–d.
- 2006 *Beloptera* sp. – Fuchs, pl. 5, figs c, d.
- 2014 *Beloptera belemnitoidea* de Blainville. – Fuchs & Lukeneder, fig. 1c.
- 2016 *Beloptera belemnitoidea* de Blainville. – Fuchs & Košťák, fig. 4b, c.

For a more detailed synonymy, see Vincent (1901), Bülow-Trummer (1920), Naef (1922) and Riegraf *et al.* (1998).

Material. – Four poorly preserved specimens (one guard-like sheath of an adult specimen and three young specimens: IGS NASU-15/01 and IGS NASU-15/03 to IGS NASU-15/05) from the Priabonian Mandrykivka Beds of the Rybalsky Quarry.

Diagnosis. – *Beloptera* with an elongate and nearly elliptical guard-like sheath, slightly curved ventrally and with lateral expansions inclined towards the venter and gives a convex form to the dorsal surface and a corresponding concavity to the venter. The ventral surface covered with very small elongate pits at the base of the lateral expansions and very fine radial grooves on the

circular in cross-section rostrum. Most of the dorsal surface is smooth.

Description. – The specimen IGS NASU-15/03 (Fig. 5A–C) is a poorly preserved elongated and nearly elliptical ($L_4/W_4 = 2.25$) slightly curved ventrally guard-like sheath, 45 mm in length, with lateral expansions inclined towards

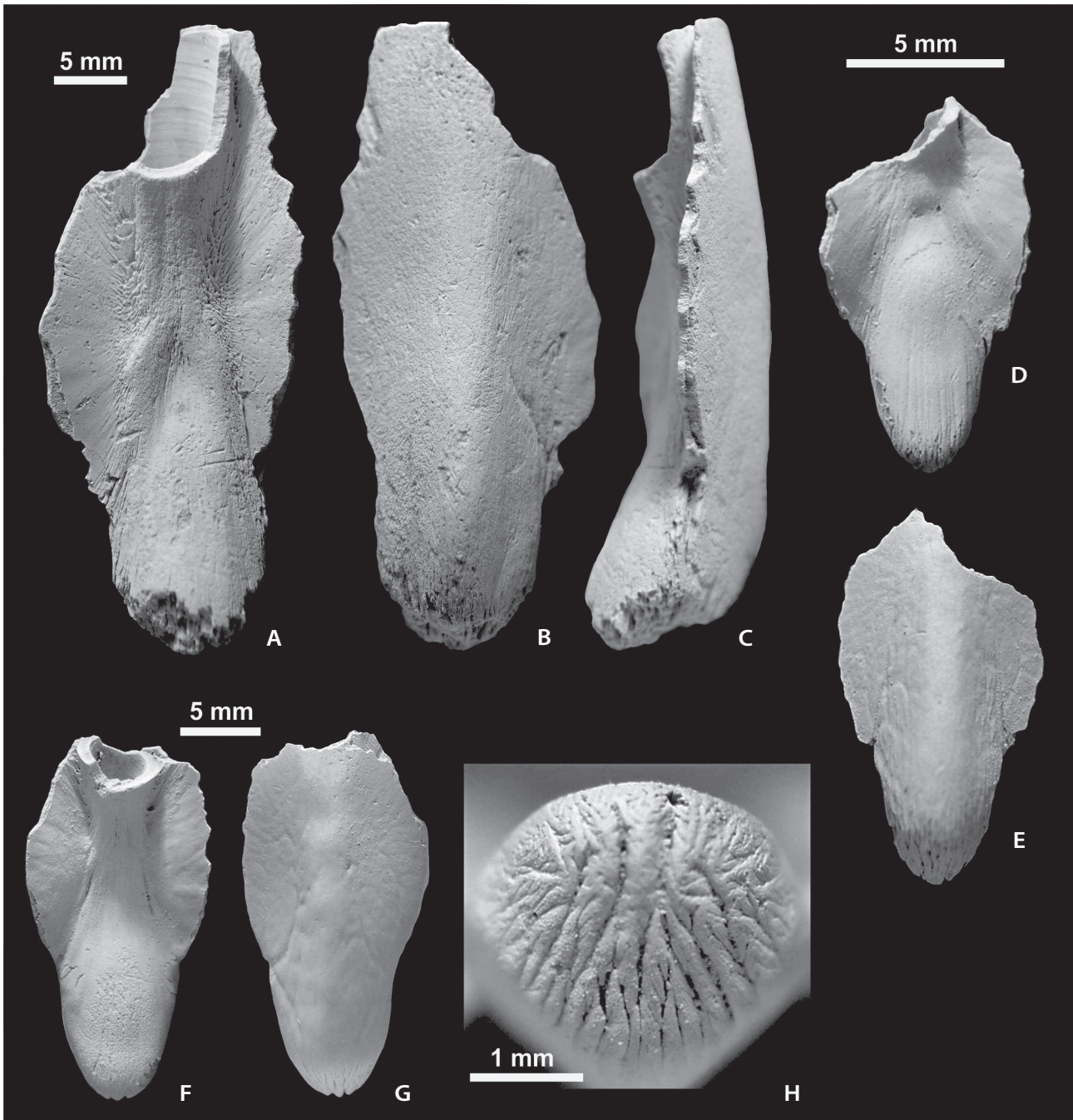


Figure 5. *Beloptera belemnoides* de Blainville, 1825 from the Priabonian of the Rybalsky Quarry; A–C – specimen IGS NASU-15/03 (A – ventral view, B – dorsal view, C – lateral view); D, E – specimen IGS NASU-15/05 (D – ventral view, E – dorsal view); F–H – specimen IGS NASU-15/04 (F – ventral view, G – dorsal view, H – ornamentation of the rostrum apex: the ventral surface of the rostrum is turned upwards).

Table 2. Dimensions (in mm) of *Beloptera belemnoidea* de Blainville, 1825.

Specimen	L ₃	L ₄	W ₃	W ₄	L ₄ /W ₄
IGS NASU-15/03	20.0	45.0	11.0	20.0	2.25
IGS NASU-15/01	11.5	15.0	4.7	6.8	2.20
IGS NASU-15/04	11.0	21.0	7.0	11.0	1.91
IGS NASU-15/05	5.5	11.0	3.2	5.8	1.90

the venter and gives a convex form to the dorsal surface and a corresponding concavity to the venter. The lateral expansions are thick at the articulation area of the rostrum and sheath and become gradually thinner to the periphery; their margins (one of which is broken) form a protrusion at the posterior part of the lateral expansion and the notch area at their anterior part. The ventral surface is covered with very small elongate pits at the base of the lateral expansions and very fine radial grooves on the rostrum. The circular in the cross-section rostrum gradually enlarges, but its apex is broken and its shape cannot be observed; the rostrum is slightly curved ventrally and the guard-like sheath is somewhat arched longitudinally. At the base of the rostrum there is a triangular depression about 5 mm in size. The most of the dorsal surface is smooth, only shallow marks of blood vessel occur on the preserved lateral expansion.

The specimen IGS NASU-15/04 (Fig. 6F–H) is a poorly preserved elongate and nearly elliptical ($L_4/W_4 = 1.91$) slightly curved ventrally guard-like sheath, 21 mm in length, with semi-elliptical lateral expansions inclined towards the venter and gives a convex form to the dorsal surface and a corresponding concavity to the venter; the ventral surface is almost smooth, only with longitudinal very narrow ribs at the base of the rostrum; the dorsal surface is almost smooth, only shallow grooves (marks of blood vessels) are on the lateral expansions. The rostrum is slightly curved ventrally and the sheath is somewhat arched longitudinally and gradually enlarges and then diminishes towards the posterior end, which is nearly conical in form and covered with narrow furrows (Fig. 5H).

The specimen IGS NASU-15/01 (Fig. 6F–H) is a poorly preserved elongate and nearly elliptical ($L_4/W_4 = 2.35$) greatly curved ventrally guard-like sheath, 16 mm in length, with semi-elliptical small lateral expansions inclined towards the venter and gives a very convex form to the dorsal surface and a corresponding concavity to the venter; the ventral surface is almost smooth, only with very fine radial grooves on the rostrum; the dorsal surface is smooth. The dorsal surface with a raised narrow medial zone, which is present only on the rostrum part of the dorsal surface. The nearly triangular in cross-section rostrum is slightly curved ventrally and the sheath is

somewhat arched longitudinally and gradually enlarges and then diminishes towards the posterior end, which is nearly conical in form and covered with narrow furrows.

The specimen IGS NASU-15/05 (Fig. 5D, E) is a poorly preserved small, elongated and nearly elliptical ($L_4/W_4 = 1.90$) guard-like sheath with a length of 11.0 mm. This specimen does not differ morphologically from the specimen IGS NASU-15/04.

Remarks. – De Blainville (1825) did not select the holotype of *Beloptera belemnoidea*. He noted that his specimen belongs to the collection of Deshayes in Lyon, France, but the illustrated specimen has not been found there (personal communication from Dirk Fuchs). Later, as far as we know, the neotype was also not specified. So a study of a topotypic material by researchers with access to the new or historical collections is necessary to select the neotype. The same applies to the problem with the holotype of *Belosaepia blainvillei*.

The specimens of *Beloptera belemnoidea* described here do not differ morphologically from the specimens of *Beloptera belemnoidea* illustrated, for example, by Fuchs & Košťák (2016: fig. 4b), Dauphin (1985: fig. 3a–d) and earlier authors (e.g., Vincent 1901: pl. 1, fig. 2; Roger 1952: fig. 67). There are some morphological differences with the specimen of *Beloptera belemnoidea* described by Vasseur (1880–1917): compared with our material, the specimen described by Vasseur is wider, its rostrum more massive, and the guard-like sheath is more strongly curved ventrally. *Beloptera belemnoidea* and *B. brevilata* Doncieux, 1908 are distinguished by the laterally wider sheath, the narrower rostrum, and the more curved sheath in *Beloptera belemnoidea*.

Vincent (1901) considered *Beloptera curta* Cossmann, 1896 to be an “anomaly” of *Beloptera belemnoidea*, probably referring to the manifestation of intraspecific, probably sexual, dimorphism of *Beloptera belemnoidea* specimens. However, *Beloptera belemnoidea* significantly differs from *B. curta* in the longer and less massive rostrum, as well as an elliptical outline guard-like sheath.

Occurrence. – Ypresian–Lutetian (early and middle Eocene) of England, Lutetian and Bartonian (middle Eocene) of France and Belgium, Priabonian of Ukraine.

***Beloptera cf. longa* Naef, 1922**

Figure 6A–E

Material. – One poorly preserved specimen (IGS NASU-15/02) from the Priabonian Mandrykivka Beds of the Rybalsky Quarry, Dnipro.

Description. – The specimen IGS NASU-15/02 is a poorly preserved elongated and nearly elliptical ($L_4/W_4 \sim 2.0$)

Table 3. Dimensions (in mm) of *Beloptera cf. longa* Naef, 1922.

Specimen	L ₃	L ₄	W ₃	W ₄	L ₄ /W ₄
IGS NASU-15/02	20.4	39.3	10.0	~19.6	~2.0

greatly curved ventrally guard-like sheath (Fig. 6A–C), 39.3 mm in length, with lateral expansions inclined

towards the venter and gives a very convex form to the dorsal surface and a corresponding concavity to the venter. The lateral expansions are almost broken. The dorsal surface is roof-like with a raised narrow medial zone and steep slopes gradually turning into lateral expansions. The ventral surface is covered with very small elongate pits at the base of the lateral expansions and very fine radial grooves on the rostrum. The nearly triangular in cross-

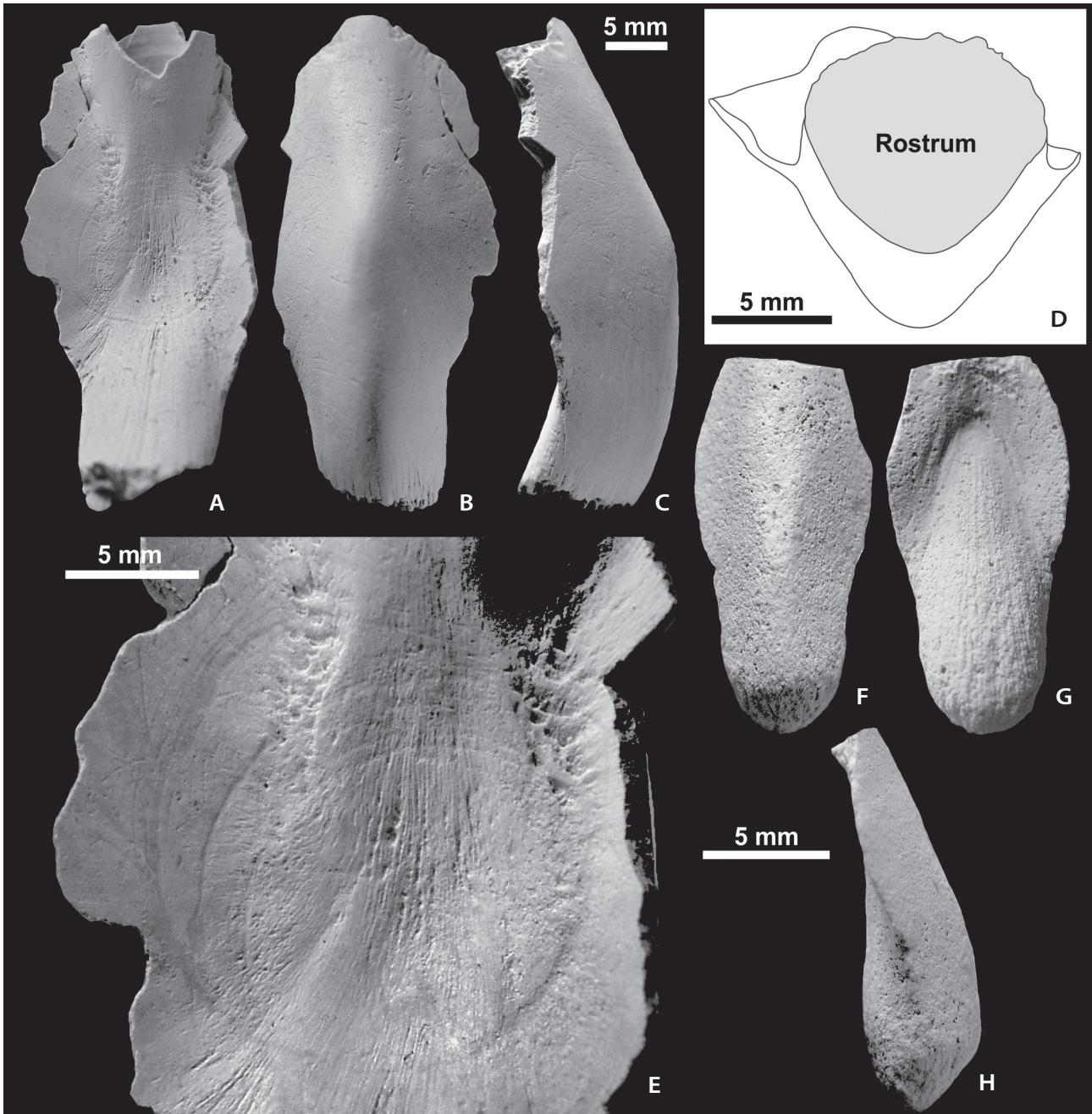


Figure 6. *Beloptera cf. longa* Naef, 1922 (A–E) and *Beloptera belemnnoidea* de Blainville, 1825 (F–H) from the Priabonian of the Rybalsky Quarry; A–E – specimen IGS NASU-15/02 (A – ventral view, B – dorsal view, C – lateral view, D – sketch of the rostrum cross section, E – enlarged part of the venter surface with problematic circular impressions); F–H – specimen IGS NASU-15/01 (F – dorsal view, G – ventral view, H – lateral view).

section rostrum (Fig. 6D) gradually enlarges, but its apex is broken and its shape cannot be observed; the rostrum is slightly curved ventrally and the guard-like sheath is somewhat arched longitudinally. The dorsal surface is smooth.

Remarks. – The described specimens differ from the specimen of *Beloptera longa*, figured by Edwards (1849: pl. 2, fig. 1) and Naef (1922: fig. 18a–g) by the more curved ventrally sheath. *Beloptera* cf. *longa* Naef, 1922 differs from the most morphologically similar species *Beloptera belemnoides* in the following morphological features: (1) a very convex smooth dorsal surface; (2) a greatly curved ventrally guard-like sheath; (3) a nearly triangular in the cross-section rostrum.

Occurrence. – Bartonian (middle Eocene) of England, Priabonian (late Eocene) of Ukraine.

Discussion

The first record of Sepiida is at about 68–70 Ma (Maastrichtian, Late Cretaceous), but they are very rare in the Paleogene (Košťák *et al.* 2013). The earliest Paleogene sepiids are the genera *Ceratisepia* Hewitt & Jagt, 1999 and *Belocurta* Avnimelech, 1958 from the Danian (early Paleocene) strata at Vigny, Val-d’Oise (France), and the “Montian” (= middle Danian) of Israel and Belgium, respectively (Avnimelech 1958, Hewitt & Jagt 1999). Note that the genus *Ceratisepia* survived extinction at the Cretaceous–Paleogene boundary, as finds of its representatives are known in the Maastrichtian (Gronsveld Member of the Netherlands) and Danian (Calcaire de Vigny Formation of France) (Meyer 1993, Hewitt & Jagt 1999).

Košťák *et al.* (2013) reported the representatives of the genera *Aegyptosaepia* Košťák *et al.*, 2013 and *Anomalosaepia?* Weaver & Ciampaglio, 2003 from the Garra Formation (late Paleocene) in the Western Desert, Egypt. This genus is considered by Košťák *et al.* (2013) as a transitional taxon between the *Belocurta*-like sepiids without a prong but with a well-developed corona and *Belosaepia*. The family Belosaepiidae Nyst, 1843 is usually considered a stem lineage of the recent genus *Sepia* Linnaeus, 1758, which separated from belosaepiids during the middle Eocene (Jeletzky 1969, Hewitt & Jagt 1999, Haas 2003, Košťák & Hoşgör 2012).

Belosaepiids, in particular the well-studied genera *Belosaepia* Voltz, 1830 and *Hungarosaepia* Doyle, Donovan & Nixon, 1994 were reported from the Eocene strata of Europe and Asia Minor (Newton & Harris 1894, Szórényi 1934, Bone *et al.* 1991, Fornaseiro & Vicariotto 1995, Tracey *et al.* 1996, Hewitt & Jagt, 1999, Košťák

& Hoşgör 2012, Košťák *et al.* 2013), but the European belosaepiid species are need of great taxonomic revision (Košťák & Hoşgör 2012).

Coleoid statoliths *Sepia boletzkyi* Neige *et al.*, 2016 and *Sepia? pira* Neige *et al.*, 2016 were recorded from the middle Lutetian (middle Eocene) of the Paris Basin in France by Neige *et al.* (2016). An interesting and somewhat mysterious fact is that statoliths are not known in Cretaceous rocks, although they are recorded in the Jurassic and Paleogene strata (however only in the middle Eocene) (see tab. s1 in Neige *et al.* 2016); this fact may be a taphonomic or collecting artefact (Neige *et al.* 2016).

In North America, *Belosaepia pennae* Garvie, 1996 and *Belosaepia* sp. were recorded from the Marquez Shale Member of the Reklaw Formation (Ypresian, lower Eocene) of Texas (Garvie 1996) and Hatchetigbee Bluff Formation (Ypresian) of Alabama (Toulmin 1977), respectively. From the younger rocks in Alabama (Lisbon Formation, Lutetian, middle Eocene) were reported the species *Belosaepia alabamensis* Palmer, 1937, *B. harrisi* Palmer, 1937, *B. saccaria* Palmer, 1937, *B. uncinata* Palmer, 1937 and *B. veatchi* Palmer, 1937 (Palmer 1937). Another middle Eocene species, *Mississaepia mississippiensis* Weaver, Dockery & Ciampaglio, 2010 was recorded from the Moodys Branch Formation of Mississippi (Weaver *et al.* 2010).

Belosaepia ungula Gabb, 1860 was described from the Crockett Formation, Bartonian (middle Eocene) of Mississippi, Alabama and Texas (Yancey *et al.* 2010); several *Belosaepia* species (*B. alabamensis*, *B. harrisi*, *B. uncinata*, *B. vokesi*) were reported from the Bartonian Gosport Sand Formation in Alabama (Palmer 1937, Palmer & Brann 1965, Allen, 1968). *Belosaepia uncinata*, *B. ungula*, *B. veatchi*, *B. stenzeli* and *B. jeletzkyi* were described from the Cook Mountain Formation (Bartonian) of Texas and Louisiana (Palmer & Brann 1965, Allen 1968) and *Anomalosaepia* Weaver & Ciampaglio, 2003 was recorded from the Bartonian Castle Hayne Limestone in North Carolina (Weaver & Ciampaglio 2003).

In Africa, *Beloseapia sepioidea* were recorded from the Ameki and Ilaro formations (Lutetian, middle Eocene) in Nigeria (Newton 1922) and *B. arabica* Cuvillier, 1930 were described from the Bartonian of Egypt (Cuvillier 1930). *Belosaepia incurvata* Cossman & Pissaro, 1909 was described from the Ranikot Formation (Thanetian, early Eocene) of India (Cossman & Pissaro 1909).

Košťák & Hoşgör (2012) and Košťák *et al.* (2013) suggest that belosaepiids might have originated in the Tethyan Realm (*e.g.*, modern India, Türkiye, Egypt) near the Cretaceous–Paleogene boundary. In the early and middle Eocene, belosaepiids underwent a significant divergence and several genera appeared, including *Sepia*, *Pseudosepia*, *Beloseapia*, and *Belosepiella* (Neige *et al.* 2016).

Based on the data of Košťák *et al.* (2013: fig. 11), we can make a cautious assumption that *Belosaepia blainvillei* from the Mandrykivka Beds was the first representatives of the genus *Belosaepia* recorded in the Priabonian strata. This means that the genus *Belosaepia* existed together with its presumed descendant, the genus *Sepia*, in the Priabonian (see Košťák *et al.* 2013: fig. 11; Neige *et al.* 2016). This conclusion correlates well with the data of Neige *et al.* (2016), according to which the genus *Sepia* existed already in the Lutetian.

In the late Eocene, the study area (south-eastern slope of the Ukrainian Shield) was a part of the so-called Subparatethys (*sensu* Zosimovich *et al.* 1989), an interregional zone of peculiar intraplateform sedimentogenesis covering the area from NW Europe to the South Urals and generally oriented parallel to the marine and brackish basins of the Central and Eastern Paratethys (Zosimovich 2007). In the Priabonian, the part of the Subparatethys bounded by the Carpathians in the west and the Fergana Depression (eastern Uzbekistan, Kyrgyzstan and Tajikistan) in the east was referred to as the so-called Beloglinian Basin (Popov *et al.* 2001). Benthic animals of this basin were moderately thermophilic and belonged to the so-called Latdorffian type fauna (Popov *et al.* 2001).

As can be seen from Fig. 7, the distribution of the coleoid fauna probably occurred from west to east in accordance with sea currents, which is generally consistent with the geographical and stratigraphic distribution of the coleoid cephalopods *Belosaepia blainvillei*, *Beloptera belemnoides* and *B. cf. longa* described above. As far as we know, no remains of representatives of the genera *Belosaepia* and *Beloptera* are known from the Paratethys to the east of Ukraine.

Modern sepiids inhabit temperate and tropical basins of the western Pacific, Indian Ocean, and eastern Atlantic (Reid 2016, Neige 2021, Lupše *et al.* 2023). The habitats inhabited by sepiids are generally restricted to coastal

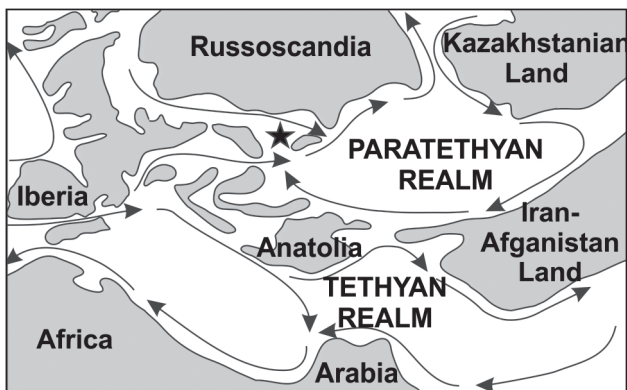


Figure 7. Paleogeographic map of western Eurasia and northern Africa in the Priabonian with the location of the Rubalsky Quarry fossil site (showed by the asterisk). Black arrows show sea currents. Modified from Popov *et al.* (2001: figs 5, 6); Fuchs & Košťák (2016: fig. 2).

waters, although some modern species occur at depths of up to 1000 m (Neige 2021).

Many of the Paleogene sepiid-bearing fossil sites have indirect evidence of seagrass meadows (IPSI – Indirect paleo-seagrass indicators *sensu* Reich *et al.* 2015) as a habitat for cuttlefish (see Forsey 2019 for details). Such indirect criteria, in addition to the cuttlefish already mentioned above, are: (1) the specific benthic foraminifer assemblages (*i.e.*, presence of epiphytic foraminifers); (2) the specific composition and growth morphology of crustose coralline red algae, bryozoans, ostracods and mollusks; (3) the presence of hydroids, lucinid bivalves and other chemosymbiotic bivalves, as well as some sharks, sirenians, sea snakes, specific echinoderms, gastropods and ostracods (*e.g.*, genera *Loxoconcha*, *Xestoleberis* and *Aurila*); (4) occurrence of Pinnidae in the life position and otoliths of juvenile sciaenids (Eva 1980; Domning 1981; van der Heide *et al.* 2012; Vélez-Juarbe 2013; Di Martino & Taylor 2014; Reich *et al.* 2014, 2015; Forsey 2016, 2018, 2019; Tomás *et al.* 2016; Mariani *et al.* 2022; *etc.*).

Fishes, sirenians, and sea snakes, the remains of which not found in the Mandrykivka Beds, cannot confirm the presence of seagrass meadows during the formation of these rocks in the area of the modern city of Dnipro. However, hydroids, bivalves, gastropods, cuttlefish, ostracods seem to confirm the presence of seagrass meadows as a habitat for these organisms.

Conclusions

Three species of coleoid cephalopods, *Belosaepia blainvillei* (Deshayes, 1835), *Beloptera belemnoides* de Blainville, 1825 and *B. cf. longa* Naef, 1922 are described from the Mandrykivka Beds of the Rybalsky Quarry in the city of Dnipro. The research results show that the genus *Belosaepia* is not extinct on the Bartonian–Priabonian boundary. The Rybalsky Quarry is the easternmost locality of the Paleogene coleoids in the Paratethyan Realm. Described coleoids probably came in the modern territory of Ukraine from the paleobasin of modern Western Europe by sublatitudinal sea currents, *i.e.*, there were no significant barriers between these paleobasins. Apparently, the sepiid genus *Belosaepia* probably existed in seagrass meadows along with other animals such as bivalves, gastropods, and ostracods.

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