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FIRST EVIDENCE OF COLOR PATTERNS ON CONCHS OF THE LOWER MOSCOVIAN (MIDDLE PENNSYLVANIAN) COILED NAUTILOIDS FROM THE DONETS BASIN, UKRAINE

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Abstract. New finds of well-preserved remains of coiled nautiloids from lower Moscovian sediments (Kamenskaya Formation) of the Donets Basin (eastern Ukraine) allowed to describe the color pattern on the conch surface of species of the genera *Parametacoceras, Metacoceras, Coelogasteroceras* and *Ephippioceras*. The conch color pattern of the studied nautiloids is represented by longitudinal light bands along the ventrolateral shoulder (*Parametacoceras* and *Metacoceras*), transverse thin lines on the venter (*Ephippioceras*), and a black spot on the body chamber (*Coelogasteroceras*). Described color patterns represent disruptive coloration. Environmental conditions, e.g. slow sedimentation, absence of agents of mechanical and chemical destruction, dysaerobic conditions and rapid burial were obviously the most important factors for the preservation of coloration on the studied conchs of coiled nautiloids.

Introduction

Color-patterned fossils are of great importance for palaeoecological, palaeogeographic and taxonomic studies (Kobluk & Mapes 1989; Baliński 2010), although the adaptive significance of mollusc shell coloration is denied by some researchers (see discussion in Williams 2016). Therefore, the study of shell colors in fossil molluscs is important for elucidating the evolutionary significance of molluscs skeletal coloration.

The color pattern on the conchs of Carboniferous cephalopods is poorly known, since specific taphonomic conditions are required for the preservation of conch color during fossilization. To date, conch color patterns are known only from species of eight genera of Carboniferous cephalopods: four orthocerid genera (Foerste 1930; Gordon 1964), two genera of coiled nautiloids (Teichert 1964; Niko et al. 2009), and two bactritoid genera (Mapes 1979) (see Table 1 for details). There is no unequivocal evidence for conch color of Paleozoic ammonoids (Mapes & Sneck 1987; Mapes & Larson 2015), which is very strange. The reasons for this phenomenon require further studies. However, Ebbighausen et al. (2007) report a possible color pattern on the conch of the Devonian ammonoid *Tornoceras* sp. from Morocco. If this find, represent-

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Taxa	Localities	Age	Brief description	References
Pseudocyrtoceras acus (Koninck, 1880)	Belgium	Tournaisian, Mississippian	Longitudinal zigzag bands	Koninck 1880; Foord 1888; Newton 1907; Foerste 1930
Campyloceras unguis Phillips, 1836	Belgium	Viséan, Mississippian	Transverse bands	Koninck 1880; Foerste 1930
?*Tripteroceroides* sp.	Arkansas, USA	Imo Fm: Chesterian, Mississippian	Chevron-like bands	Gordon 1964
Arcuatoceras saundersi Niko et al., 2009	Arkansas, USA	Imo Fm: Chesterian, Mississippian	Longitudinal bands	Niko et al. 2009
Angustobactrites saundersi Mapes, 1979	Arkansas, USA	Imo Fm: Chesterian, Mississippian	Longitudinal bands	Mapes 1979
?*Rugobactrites* sp.	Arkansas, USA	Imo Fm: Chesterian, Mississippian	Transverse bands	Mapes 1979
Vestinautilus paucicarinatus (Foord, 1891)	Kork, Ireland	Carboniferous Limestone: Mississippian	Spots or irregular bands	Teichert 1964
?*Michelinoceras dunbari* (Foerste, 1930)	Oklahoma, USA	Ochelata Member: Middle Pennsylvanian	Transverse bands	Foerste 1930
Parametacoceras jongmansi Delépine, 1937	Ukraine	Kamenskaya Fm: early Moscovian	Longitudinal and transverse bands	This study
Metacoceras spp.	Ukraine	Kamenskaya Fm: early Moscovian	Longitudinal bands	This study
Coelogasteroceras coxi Gordon, 1960	Ukraine	Kamenskaya Fm: early Moscovian	Spots	This study
Ephippioceras clitellarium (Sowerby, 1840)	Ukraine	Kamenskaya Fm: early Moscovian	Transverse bands	This study

Tab. 1 - Carboniferous cephalopods with preserved shell coloration.

ed by a single specimen, indeed demonstrates color patterns on the conch, then *Tornoceras* is the earliest ammonoid genus for which conch coloration is known to date (Mapes & Larson 2015). Nevertheless, this problem requires further research, and the find described by Ebbighausen et al. (2007), should be treated with caution.

The so-called "false color patterns" have been described in some cephalopod fossils, e.g. on pyritized steinkerns of Devonian and Mississippian ammonoids (Branson 1964; Mapes & Sneck 1987; Mapes & Davis 1996; Mapes & Larson 2015) and on conchs of Triassic ammonoids (Klug et al. 2007). These different patterns are caused by a variety of different mechanisms, e.g., they may arise where thickening of the conch is present (Mapes & Larson 2015) or at growth halts, where proportionally more melanin was secreted (Klug et al. 2007), and they were seen as darker bands during the life of these animals.

Some conchs of Carboniferous cephalopods bear surface patterns that can be mistaken for coloration, e.g., the innermost layer of conch seemingly with transverse "color" bands resulting from thin extensions of septa to the outer surface of the internal mold in *Solenochilus mcfarlandi* Sturgeon et al., 1982 (Sturgeon et al. 1982: pl. 5, Figs. 3, 4) from the Brush Creek Member (Conemaugh Group, late Desmoinesian–early Virgilian) in Ohio, USA. Apparently the same applies to the specimen of *Solenochilus greenensis* Sturgeon, 1946 from the Allegheny Formation (Middle Pennsylvanian) in Ohio (Sturgeon & Miller 1948: pl. 19).

Previously, Carboniferous cephalopods with preserved conch coloration were not known in Eastern Europe. The only cephalopods with preserved conch color in Ukraine are the Berriasian ammonites from Feodosia in Crimea (Rogov & Perminov 2009). Other fossils with preserved skeletal color from Ukraine were described by Pchelintsev (1925), Baliński (2010), etc.

Here, I describe the color patterns on conchs of the lower Moscovian (Middle Pennsylvanian) coiled nautiloids *Parametacoceras jongmansi* Delépine, 1937, *Metacoceras* spp., *Coelogasteroceras coxi* Gordon, 1960 and *Ephippioceras clitellarium* (Sowerby, 1840) from the Kamenskaya Formation in the northern part of the Donets Basin, eastern Ukraine. The results of the study expand the knowledge about conch color patterns of Paleozoic non-ammonoid cephalopods.

Geological Setting

The studied material was collected in two localities (Fig. 1): (1) the tailings dump and working face of the Lutuhynska-Pivnichna coal mine near Lutuhyne (Ukraine, Luhansk Region; coordinates: 48.42384, 39.20736); (2) the tailings dump of the Cherkas'ka coal mine near Zymohir'ya (Ukraine, Luhansk Region; coordinates: 48.56507, 38.93613).

The examined material comes from the marine roof shale of the k_7^L coal layer (i.e., lower interlayer of the k_7 coal bed) in the upper part of the Kamenskaya Formation (Fig. 2A). The Kamen-

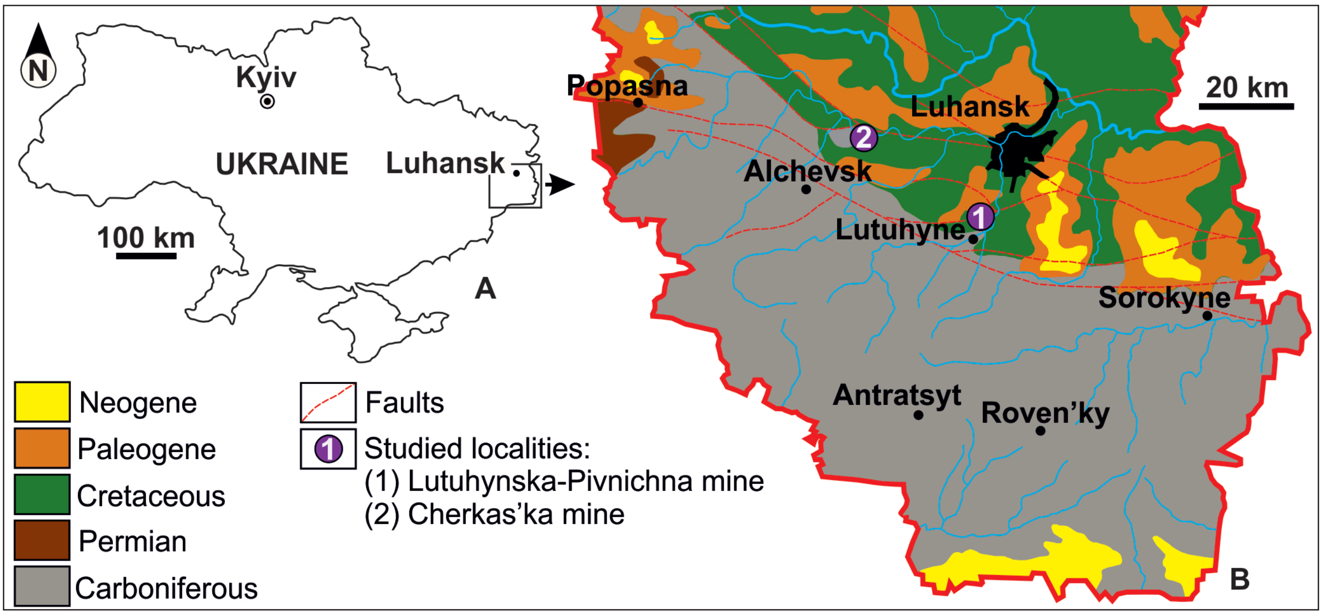

Fig. 1 - Geographic position of the studied localities. A) Study area; B) schematic geological map of the south part of Luhansk Region, showing the geographic location of the studied localities (modified after Fissunenko 2004).

skaya Formation (C_2^5 or K) consists of a sequence of sandstones, siltstones, mudstones, coals and limestones (Fig. 2B). These rocks contain remains of various marine and terrestrial organisms, e.g., foraminifers, chaetetids, corals, brachiopods, bryozoans, bivalves, gastropods, cephalopods, crinoids, echinoids, conchostracans, horseshoe crabs, fishes, macroflora, palynomorphs, calcareous algae, etc. The thickness of the Kamenskaya Formation varies from 300 m in the NW part of the Donets Basin to 1050 m in the SE part of the Donets Basin (Poletaev et al. 2011; Nemyrovska & Yefimenko 2013).

The lower part of the Kamenskaya Formation (stratigraphic interval between the K_1 and K_3 limestone layers) can be ascribed to the uppermost part of the Bashkirian and corresponds to the Krasnodonian Horizon (uppermost part of the Kayalian Regional Stage) of the Regional stratigraphic scheme of the Dnipro-Donets Downwarp; the middle and upper parts of the Kamenskaya Formation (stratigraphic interval between the K_3 and L_1 limestone layers) attributed to the lower Moscovian and corresponds to the Kamenskian Horizon (lower half of the Lozivkian Regional Stage) (Poletaev et al. 2011; Nemyrovska & Yefimenko 2013).

The Kamenskian Horizon roughly corresponds to the Vereian Horizon of the stratotype of the Moscovian Stage (Moscow Syneclise, Russia) (Poletaev et al. 2011; Nemyrovska & Yefimenko 2013). The base of the Moscovian in the Donets Basin is at the base of the K_3 limestone layer (lower part of the Kamenskaya Formation; Fig. 2B) (Poletaev et al. 2011; Nemyrovska & Yefimenko 2013). The absolute age of the volcanic ash interlayer in the k_7 coal bed is 313.16±0.08 Ma (Davydov et al. 2010).

Lutuhynska-Pivnichna coal mine (Fig. 2C)

The fossil-bearing rock is a dark gray, carbonaceous, sometimes pyritized siltstone with large carbonate nodules (Fig. 2D), which is a roof shale of the k_7^L coal layer (Moscovian part of the Kamenskaya Formation). Numerous fossils, such as worm tubes, brachiopods (*Orbiculoidea, Derbyia, Neochonetes, Densepustula*), bivalves (*Paleoneilo*, *Phestia*, *Sanguinolites,* etc.), gastropods, orthocerids (*Pseudorthoceras*), coiled nautiloids (*Gzheloceras*, *Parametacoceras*, *Metacoceras, Temnocheilus, Peripetoceras*, *Coelogasteroceras*, *Ephippioceras*), ammonoids [*Wiedeyoceras clarum* Popov, 1979 (Dernov 2022)], trilobites [*Paladin* cf. *lutugini* (Weber, 1933) (Dernov 2022)], fishes (*Symmorium*, *Venustodus*), and bromalites have been collected from this stratigraphic horizon. Coiled nautiloids *Parametacoceras jongmansi* Delépine, 1937, *Metacoceras* spp., and *Coelogasteroceras coxi* Gordon, 1960 with color patterns were found at this locality. In addition, the shells of some lingulide brachiopods, bivalves and

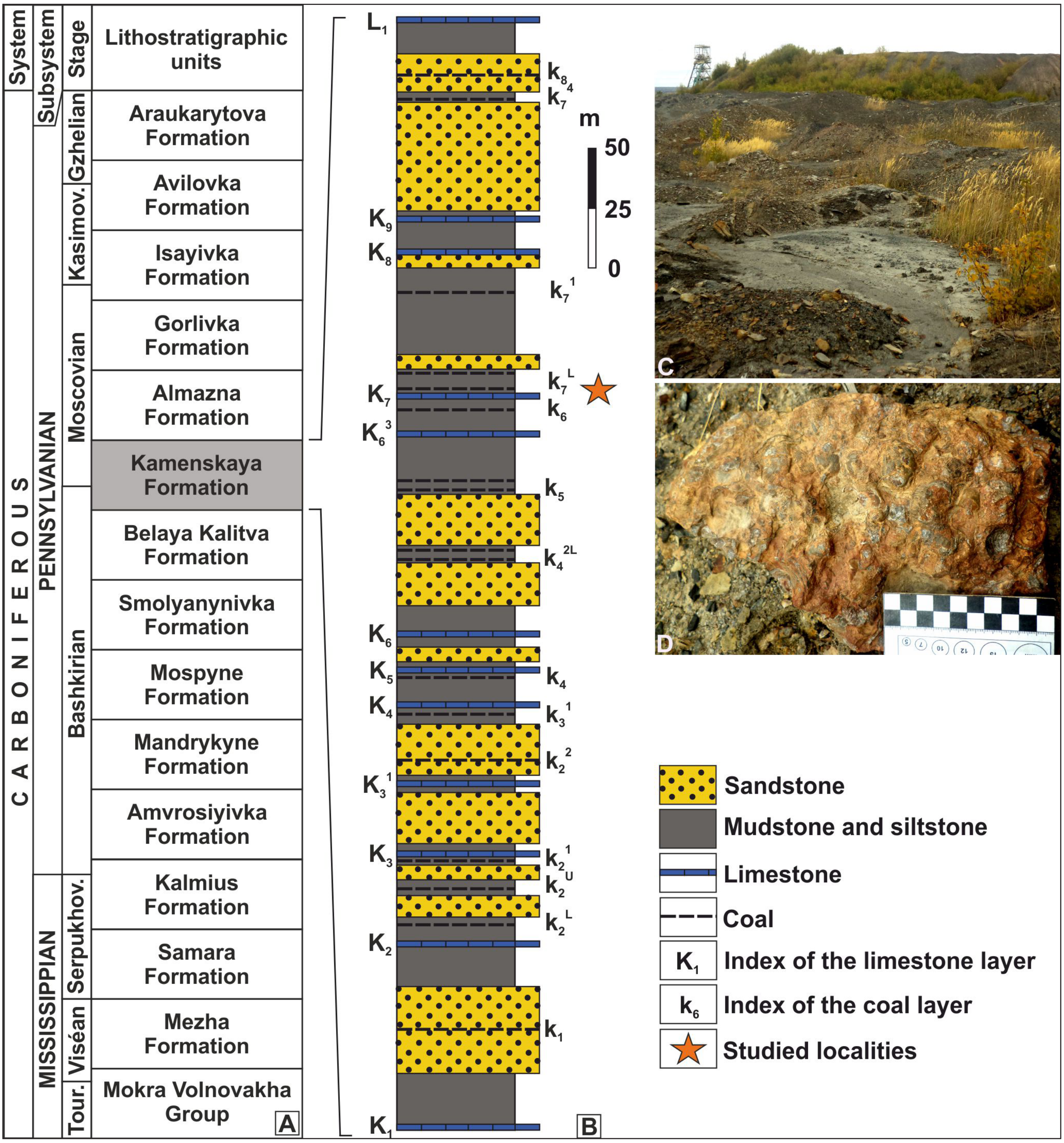

Fig. 2 - Geological setting of the studied sites. A) Stratigraphic position of the Kamenskaya Formation in the Carboniferous succession of the Donets Basin; B) stratigraphic position of the studied localities with nautiloid remains in the Kamenskaya Formation; C) general view of the tailings dump of the Lutuhynska-Pivnichna coal mine; D) carbonate nodule with remains of molluscs and brachiopods from the black shale of the Lutuhynska-Pivnichna coal mine. Abbreviations: Tour. – Tournaisian, Serpukhov. – Serpukhovian, Kasimov. – Kasimovian.

gastropods from this fossil site also bear color patterns (Fig. 3).

Cherkas'ka coal mine

The fossil-bearing rock is dark gray, carbonaceous mudstone with large carbonate nodules (roof shale of the k_7^L coal layer) and remains of bivalves, gastropods, coiled nautiloids, and terrestrial plants. A coiled nautiloid, *Ephippioceras clitellarium* (Sowerby, 1840), with color patterns was found at this locality.

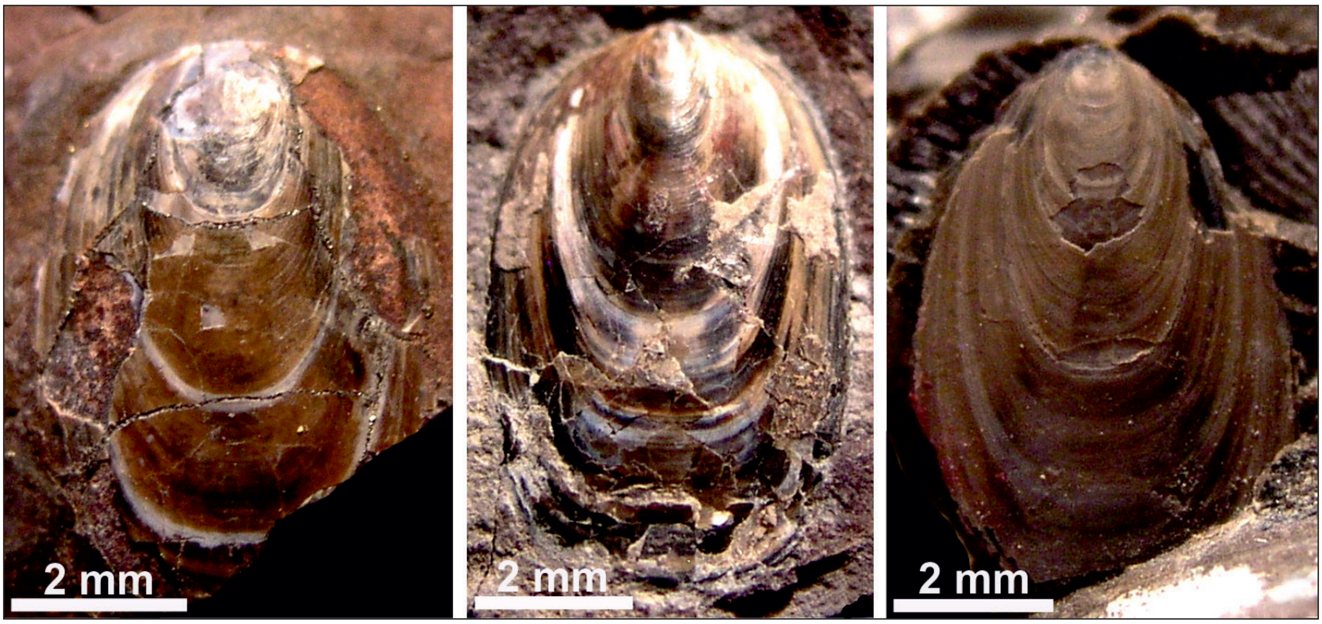

Fig. 3 - Color patterns on lingulide brachiopods valves photographed under daylight from the tailings dump of the Lutuhynska-Pivnichna coal mine (unnumbered specimens from the author's collection stored in IGS NASU).

Material and Methods

In this study, I examined seven specimens of conch fragments (mainly body chambers) of coiled nautiloids with color patterns that belong to *Parametacoceras jongmansi* (two specimens: IGS NASU-4/3174 and IGS NASU-4/6306; body chamber fragments), *Metacoceras* spp. (three specimens: IGS NASU-4/3181, IGS NASU-4/3184, and IGS NASU-4/3262; small conch fragments), *Coelogasteroceras coxi* (one specimen: IGS NASU-4/3160; body chamber fragment), and *Ephippioceras clitellarium* (one specimen: IGS NASU-4/597; fragment of the steinkern with partly preserved shell). *Parametacoceras jongmansi, Metacoceras* spp., and *Ephippioceras clitellarium* were collected from slightly weathered rocks of the coal mine tailings dump; *Coelogasteroceras coxi* was found in the mine working face.

Most specimens were studied and photographed under daylight, because the technique of studying the color patterns on the shells of Mesozoic and Cenozoic and brachiopods by treatment with sodium hypochlorite (NaClO) and observation under ultraviolet (UV) light (Caze et al. 2011; Williams 2016; Gaspard & Loubry 2017; Crippa & Masini 2022) is inadequate for the available material, because sodium hypochlorite (bleach) is a strong oxidant that reacts with the pyritized rock of the fossils matrix. Since the examined material is very rare, I did not risk processing it in this way. In addition, melanin, the most stable of molluscan pigments in fossils, does not fluoresce in UV light (Vinther 2015; Williams 2016). Porphyrins, which can be detected in UV light on the shells of Cenozoic molluscs , are unlikely to be preserved in the shells of Carboniferous molluscs (Williams 2016). Hence, the use of UV light does not make sense.

Only one specimen (IGS NASU-4/3184a) was studied and photographed submerged in water, following the example of Asato et al. (2022). Studies of other specimens immersed in water have not yielded outstanding results, and the wetting of pyritized fossils with water causes the development of pyrite decay, which leads to the destruction of the fossils (Newman 1998; Cavallari et al. 2014; Frank et al. 2014; Becherini et al. 2018).

The studied collection (IGS NASU-4) is stored in the Department of Paleontology and Stratigraphy of the Paleozoic Sediments, Institute of Geological Sciences (National Academy of Sciences of Ukraine, Kyiv).

Description of color patterns

Parametacoceras jongmansi Delépine, 1937

Specimen IGS NASU-4/3174 (Figs. 4A–C)

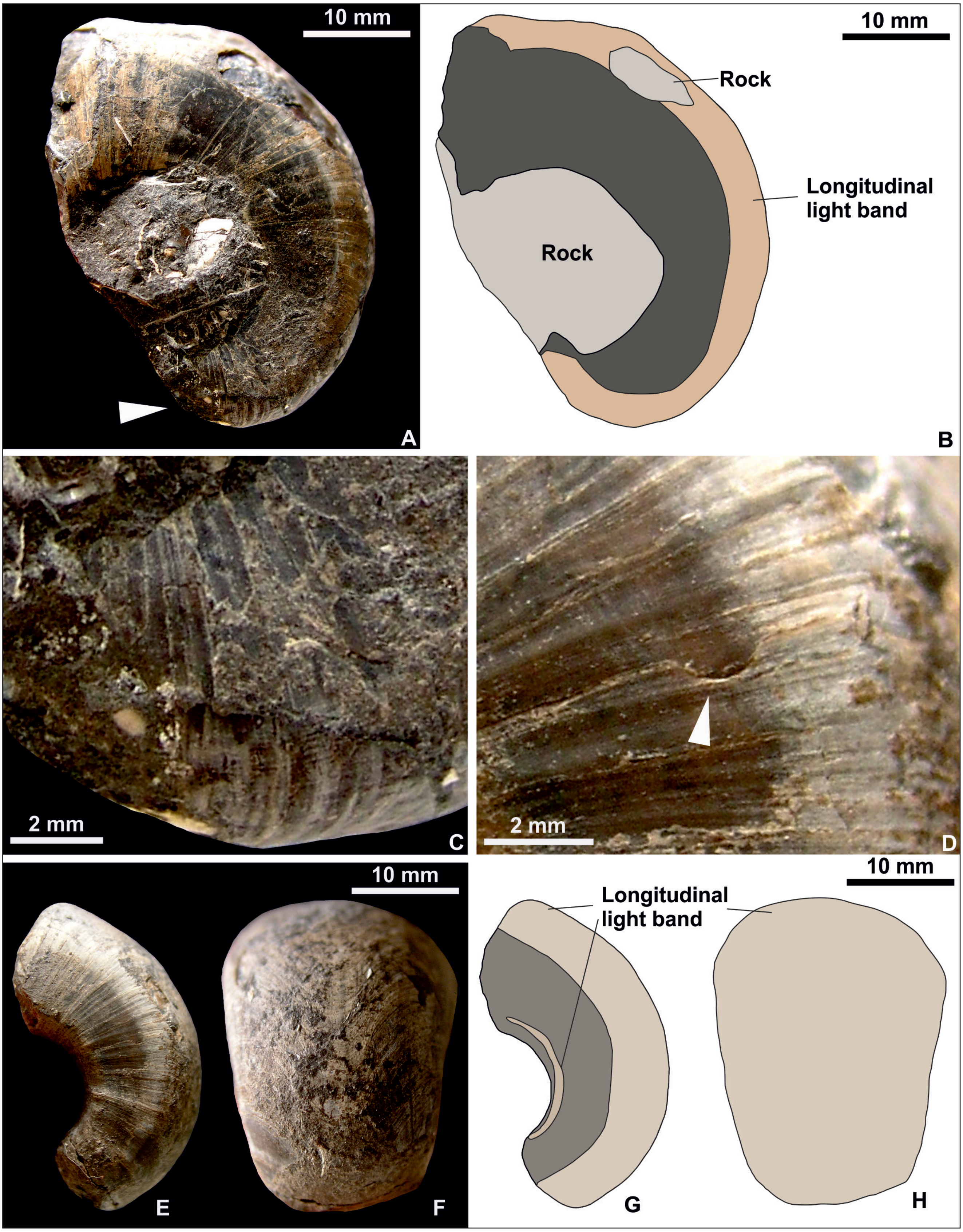

Fig. 4 - Color patterns on the conchs of *Parametacoceras jongmansi* Delépine, 1937. A–C) Specimen IGS NASU-4/3174, A: lateral view (the arrow shows the part of the shell enlarged in Fig. 4C), B: graphic interpretation of Fig. 4A, C: enlarged part of the flank and ventrolateral shoulder of specimen IGS NASU-4/3174; D–H) Specimen IGS NASU-4/6306, D: shell damage on specimen IGS NASU-4/6306, E: lateral view, F: ventral view, G: graphic interpretation of Fig. 4E, H: graphic interpretation of Fig. 4F.

Shell morphology. The specimen consists of a fragment of body chamber with a strongly convex and broad venter; ventrolateral shoulders broadly rounded; flanks flattened and weakly converging to the ventrolateral shoulder. Umbilical margin is angular. The ornamentation consists of thin transverse lirae, which are straight on the flanks and umbilical wall. The specimen has the following dimensions: conch diameter ~ 40.0 mm, whorl height – 17.0 mm, umbilical width – 15.0 mm.

Color patterns. The color pattern on the ventrolateral shoulder of specimen IGS NASU-4/3174 consists of a longitudinal, broad, brown band, c. 3.0 mm in width (Figs. 4A, B). The color of the flank is gray. Light gray, thin (0.2–0.3 mm) transverse bands are located on the anterior part of the body chamber flank (Fig. 4A). The venter is light gray and covered with very narrow (c. 0.5 mm), dark gray transverse bands (Fig. 4C). In summary, the color of specimen IGS NASU-4/3174 is darker than that of specimen IGS NASU-4/6306 (described below), but this may be due to fossilization conditions and to the degree of weathering of the fossil.

Specimen IGS NASU-4/6306 (Figs. 4D–H)

Shell morphology. The specimen consists of the body chamber with rectangular compressed whorl profile and strongly convex and broad venter; ventrolateral shoulders broadly rounded; flanks flattened and weakly converging to the ventrolateral shoulder. Umbilical margin is angular; dorsum is concave and 3–4 times narrower than the venter; the greatest whorl width is at the umbilical margin. The ornamentation consists of coarse transverse lirae, which form a very deep, narrow hyponomic sinus; they are straight on the flanks and umbilical wall. The specimen has the following dimensions: conch diameter – 25.2 mm, whorl height – 13.2 mm, umbilical width – 9.4 mm.

On the flank of the body chamber, near the ventrolateral shoulder, there is a repaired sublethal damage represented by an arc-shaped shallow (1.0 mm) and narrow (1.4 mm) fracture (Fig. 4D). This evidence of trauma is very similar to the non-lethal injuries of Type 1 described in Ward, 1987 on the conchs of the modern nautilid *Nautilus pompilius* Linnaeus, 1758. These injuries were caused by attacks of predators (Keupp 2012: 37).

Color patterns. The color pattern on the ventrolateral shoulder of specimen IGS NASU-4/6306 consist of a longitudinal, broad, light gray band, c. 1.5–3.0 mm in width (Figs. 4E, G). The color pattern on the flank is darker (brownish-gray) than on the ventrolateral shoulder; light gray, thin (0.05–0.1 mm) transverse bands are on the anterior part of the body chamber flank. The umbilical margin is pale, similar in color to that of the band on the ventrolateral shoulder (Figs. 4E, G). The venter is light gray (Figs. 4F, H). The border between the longitudinal stripe on the ventrolateral shoulder and the coloration of the venter is gradual.

Remarks. The species *Parametacoceras jongmansi* was described by Delépine (1937) from the Petit-Buisson marine layer (= Aegir marine layer of the Ruhr Basin in Germany; boundary interval of the Westphalian B and C) in the Netherlands. This species is known only in the Netherlands and eastern Ukraine (Donets Basin) (Delépine 1937 and this study).

Metacoceras **spp.**

Specimen IGS NASU-4/3184 (Figs. 5A, B)

Shell morphology and patterns. The specimen is a conch fragment with elongated nodes on the ventrolateral shoulder. A light gray longitudinal narrow band (c. 2.0 mm in width) is located on the ventrolateral shoulder; the flank of this specimen is dark gray (Figs. 5A, B).

Specimen IGS NASU-4/3262 (Fig. 5I)

Shell morphology and patterns. The specimen is a conch fragment with elongated nodes on the ventrolateral shoulder and a light gray longitudinal narrow band (c. 1.5 mm in width) on the ventrolateral shoulder. The venter is covered with thin (0.3–1.0 mm), frequent dark gray and light gray transverse bands that form a very deep, narrow sinus (Fig. 5I). These transverse bands appear to be a false color pattern as they run parallel to the growth lines.

Specimen IGS NASU-4/3181 (Fig. 5J)

Shell morphology and patterns. The specimen is a fragment of the venter of the conch covered with narrow growth lines, which form a deep, narrow hyponomic sinus. The coloration of the venter is light gray with narrow (c. 0.25 mm) transverse dark gray bands, which have the same form as the growth lines (Fig. 5J).

Remarks. The material of the nautiloid *Metacoceras* spp. belongs to at least two species. This is underlined by variations in the surface ornamentation of the studied fragmentary fossils: different form of nodes on the ventrolateral shoulder, availability of growth lines, etc. Unfortunately, it is not possible to determine the species of these nautiloids due to poor preservation. It is possible that these nautiloids are close to *Metacoceras* aff. *perelegans* Girty, 1915 or *M.* cf. *cornutum* Girty, 1911 of which well-preserved specimens were found in the tailings dump of the Lutuhynska-Pivnichna coal mine.

The specimens IGS NASU-4/3181 and IGS NASU-4/3262 appear to belong to the same species, because the coloration of the venter of their conchs is very similar. Nevertheless, examples of modern nautilids *Nautilus* and *Allonautilus* (Ward et al. 1977, Ward 1987) as well as Silurian nautiloids (Turek & Manda 2011) demonstrate polymorphism of conch coloration of one species.

Coelogasteroceras coxi Gordon, 1960

Shell morphology. The specimen IGS NASU-4/3160 is a fragment of a body chamber of a subglobular conch (Figs. 5E, F) with a slightly depressed whorl profile. The venter is broad, slightly convex, with broad median longitudinal groove; the ventrolateral shoulder is rounded; the flanks are flattened and the umbilical margin is angular. The umbilical wall is vertical and flattened; the umbilicus is wide (uw/dm ~ 0.26). The ornamentation consists of growth lines that form a deep, narrow hyponomic sinus and a low ventrolateral salient; these growth lines are straight on the flanks. The specimen has the following dimensions: conch diameter ~ 40.5 mm, whorl height – 18.4 mm, whorl width ~ 26.0 mm, umbilical width – 10.4 mm.

Color patterns. The conch has the following color pattern (Figs. 5E–H): the anterior part of the body chamber is colored black; the border of this part of the body chamber follows the form of the growth lines, only near the umbilical margin it deviates from them, shifting slightly forward. The posterior part of the body chamber is lighter colored (grayish-brown) than its anterior part. Other non-pyritized body chambers of *Coelogasteroceras coxi* are uniformly yellowish-gray and yellowish-brown in color.

Remarks. The species *Coelogasteroceras coxi* is known from the Early Pennsylvanian of the United States (Gordon 1960) and the early Moscovian of the Donets Basin, eastern Ukraine (this study).

Ephippioceras clitellarium (Sowerby, 1840)

Shell morphology. The specimen IGS NASU-4/597 is a fragment of a subspherical, smooth conch with an extremely depressed whorl profile; the flanks and venter form a single hemispherical surface. Suture line with a V-shaped, narrowly rounded ventral saddle and a broadly rounded lateral lobe (Fig. 5C).

A group (over a hundred) of very shallow small (~ 0.15–0.20 mm in diameter) circular pits (Fig. 5D), which correspond to tubercles on the inner surface of the phragmocone chambers, are located on the steinkern surface of the ventrolateral shoulder of the conch. These depressions are very similar to the "Housean pits" (after Davis & Mapes 1999), especially their Type 2 (*sensu* De Baets et al. 2011), which were tentatively interpreted as deformations of parasitic origin (De Baets et al. 2015). I cannot yet say with certainty that the structures described on the conch of *Ephippioceras clitellarium* are in fact "Housean pits". This problem requires further investigation on more material.

Color patterns. The color pattern is preserved only on the venter of the conch (Fig. 5C), where there are narrow (1.0–1.5 mm) transverse gray bands that run parallel to the septa of the phragmocone chambers. The part of the bands directly in contact with the septa has a darker gray tint (mural band), while the one approaching the aperture has a lighter tint.

Fig. 5 - Color patterns on the conch of *Metacoceras* spp., *Coelogasteroceras coxi* Gordon, 1960 and *Ephippioceras clitellarium* (Sowerby, 1840). A, B) *Metacoceras* sp. (specimen IGS NASU-4/3184), A: ventrolateral shoulder of the conch, B: graphic interpretation of Fig. 5A; C, D) *Ephippioceras clitellarium* (Sowerby, 1840) (specimen IGS NASU-4/597, ventral view), D: possible "Housean pits" on the flank and ventrolateral shoulder of *Ephippioceras clitellarium* (Sowerby, 1840) (specimen IGS NASU-4/597); E–H) *Coelogasteroceras coxi* Gordon, 1960 (specimen IGS NASU-4/3160, E: lateral view (the black arrow indicate the borders of the dark and light parts of the shell color pattern), F: ventral view, G: graphic interpretation of Fig. 5E, H: graphic interpretation of Fig. 5H); I–J) *Metacoceras* spp., I: specimen IGS NASU-4/3262, J: specimen IGS NASU-4/3184a.

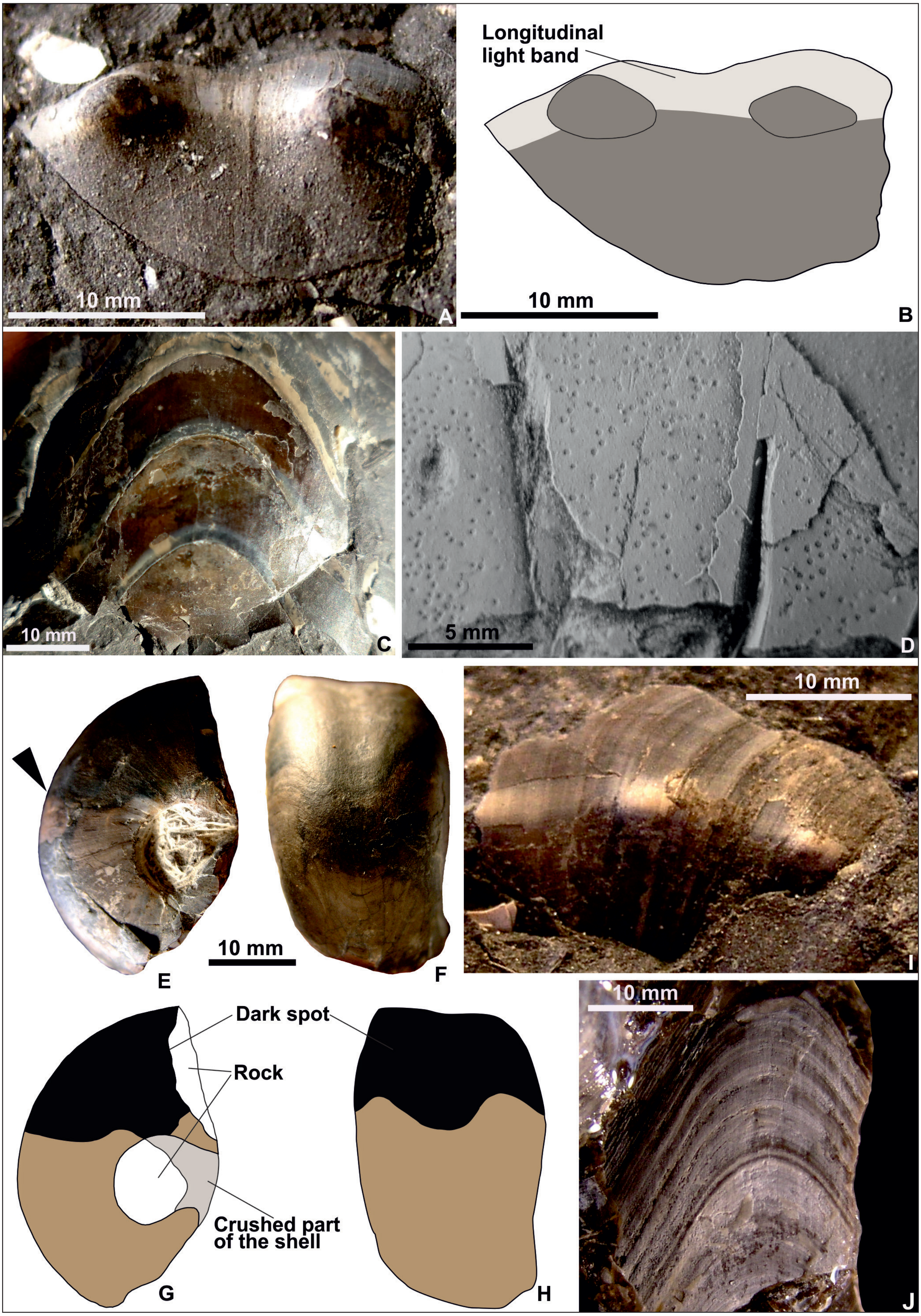
10 mm
A
Longitudinal
light band
10 mm
B
10 mm
C
5 mm
D
10 mm
E
F
10 mm
I
Dark spot
Rock
Crushed part
of the shell
G
H
10 mm
J

Figure 5

Remarks. The color pattern on the conch surface of *Ephippioceras clitellarium* is very similar to the false color patterns on the conchs of *Solenochilus mcfarlandi* and *S. greenensis* (see Introduction), so the transverse stripes on the venter of *Ephippioceras clitellarium* are interpreted here as conch coloration conditionally.

The species *Ephippioceras clitellarium* is known from the Late Mississippian to Late Pennsylvanian in Western Europe, North Africa, central Russia and eastern Ukraine (Shimansky 1967).

Discussion

Of the eight Carboniferous cephalopod genera for which conch coloration has been described, three were found in Europe (Belgium and Ireland) and five occur in the United States (Arkansas and Oklahoma). Most finds of Carboniferous cephalopods with preserved conch color patterns in the United States come from the Serpukhovian Imo Formation in Arkansas (Gordon 1964; Mapes 1979; Niko et al. 2009).

In addition, the Imo Formation also contains numerous gastropod shells with preserved coloration (Jeffery et al. 1994). Sedimentary conditions of this formation appear to have contributed to the preservation of shells coloration. Although ammonoids from this formation and age-matched sediments of the Midcontinent of North America have been described in many works (e.g., Gordon 1965; Saunders 1973; Bond & Saunders 1989), there is no evidence for a color pattern on the conchs of these cephalopods.

The key conditions for the preservation of the color pattern of early Paleozoic cephalopods of the Barrandian Area (Czech Republic) were low oxygen levels on and below the seafloor, rapid burial and lithification (Turek 2009). The depositional environment of the Imo Formation in Arkansas has been interpreted as a relatively shallow-water, low-energy offshore setting with slow deposition of terrigenous clay and periodic deposition of higher-energy carbonate sediments (Webb & Sutherland 1993).

The studied nautiloid conchs with a color pattern were found mainly in thin layers of detrital and bioclastic limestones (tempestites) in black shales; fossil cephalopods are less common in black siltstones and large carbonate nodules. These black siltstones were probably formed in coastal areas of a warm shallow marine basin with low sedimentation rates, below the normal weather wave base but above the storm wave base. This conclusion is supported by the black coloring of the rocks and their siltstone composition, the presence of framboidal pyrite, which is typical of dysaerobic environments, and the evidence of periodic storm action (e.g. intercalations of tempestites). Palaeogeographic data show that during the formation of the roof-shale of the k_7 coal layer, the modern Lutuhynska-Pivnichna fossil site was located within a shallow sea bay (Zhemchuzhnikov et al. 1959).

Large carbonate nodules with clusters of brachiopod and mollusc shells are probably of bacterial origin. Apparently, the depositional conditions of the black shales of the Imo Formation and the roof shale of the k_7^L coal layer of the Kamenskaya Formation were quite similar. Probably, dysoxic conditions and activity of bacterial communities were the reason for the preservation of the nautiloid conch coloration. It should be noted that color patterns were also found on shells of lingulide brachiopods, gastropods, bivalves, and, possibly, orthocerids from the Lutuhynska-Pivnichna coal mine fossil site (see Fig. 3).

Some researchers (e.g. Comfort 1950, 1951) reject the adaptive significance of mollusc conchs coloration, as they believe it is a by-product of the metabolism and/or dietary processes of these animals. However, Hedegaard et al. (2005: 5) disagree with this statement and note that "molluscs have excellent excretory organs, and incorporating waste into structural supports seems implausible, particularly when secretion is episodic and confined to a thin layer at the exterior of the shell". Therefore, it appears that mollusc shell coloration may have an important adaptive function depending on habitat and taxon.

Observations on the color patterns of modern *Nautilus* showed the existence of several coloration polymorphs, but these are not species-specific and do not indicate sex or depth of these cephalopods (Ward et al. 1977; Ward 1987). Cowen et al. (1973) interpreted the color patterns of recent species of *Nautilus* and *Allonautilus* as examples of disruptive camouflage and countershading.

At present, color patterns is known on shells of the following post-Carboniferous coiled nautiloids: *Stenopoceras* from the Cisuralian of Texas, USA (Kemp 1957), ?*Ophinautilus* from the Late Jurassic of Russia (Shimansky 1961, 1962), *Eutrephoceras* from the Early Cretaceous of Russia (Shimansky 1961, 1962) and the Late Cretaceous of South Dakota, USA (Mapes & Evans 1995), *Aturia* from Paleogene and Neogene of France and Italy (Foerste 1930; Teichert 1964). Remarkably, the conch coloration of lower Paleozoic cephalopods is much better known (see Foerste 1930; Balashov 1964; Turek 2009; Turek & Manda 2011, 2020; Manda & Turek 2009, 2015).

The conch coloration of Carboniferous coiled nautiloids differs significantly from that of the modern nautilids of the genera *Allonautilus* and *Nautilus* (Teichert 1964). In addition, the body chamber of modern nautilids is devoid of coloration (at least ventrally), while most of the studied specimens are fragments of body chambers. The presence of injuries on the conchs of *Parametacoceras jongmansi* (Fig. 4D and other undescribed fossils) suggests that nautiloids were attacked by predators.

Based on the studied fossils, it should be noted that representatives of the genera *Parametacoceras* and *Metacoceras* belonging to the family Tainoceratidae have a similar conch coloration consisting of a longitudinal light band along the ventrolateral shoulders. This band cannot be diagenetic in nature and occurs in that part of phragmocone whorls where it overlaps with later whorls, as light bands were observed on body chambers that were not overlapped by later parts of the conch.

The conch coloration of *Parametacoceras* and *Metacoceras* is very similar to the color patterns on the conchs of the Givetian ammonoids *Tornoceras* from Morocco (Ebbighausen et al. 2007: fig. 9), *Leioceras* from the Bajocian of Switzerland (Arkell 1957: fig. 138a), *Cadoceras, Eboriceras, Kosmoceras*, and *Proriceras* from the Callovian of Russia and Poland (Mapes & Larson 2015: fig. 2.5), *Haploceras* from the Berriasian of Crimea in Ukraine (Rogov & Perminov 2009: fig. 1b) and *Beudanticeras, Cleoniceras, Desmoceras* from the Albian of Madagascar (Mapes & Larson 2015: fig. 2.6). All these genera have spiral thin bands on the flanks.

The conch coloration of *Ephippioceras clitellarium* somewhat resembles that of Upper Cretaceous nautilid *Eutrephocerasd dekayi* (Morton, 1834) (Mapes & Evans 1995), Lower Triassic ammonoids *Owenites, Prosphingites* and *Dieneroceras* (Mapes & Sneck 1987), and Callovian and Volgian ammonites *Quenstedtoceras, Kachpurites*, and *Craspedites* (Mironenko 2015). These ammonoids and coiled nautiloids have transverse dark bilaterally symmetrical bands on the venter and flanks.

The color pattern on the studied conchs of lower Moscovian nautiloids possibly may have served as camouflage. As mentioned above, the black roof shale of the k_7^L coal bed were formed at depths below the normal weather wave base but above the storm wave base, i.e., within the euphotic zone, where protective camouflage in the form of color patterns would make sense. Since the Pennsylvanian marine basin of eastern Ukraine was rather shallow, as confirmed by a number of lithological and palaeontological evidence (see Logvinenko 1953; Zhemchuzhnikov et al. 1959; Feofilova & Levenstein 1963; Kozitskaya & Schegolev 1993; Fohrer et al. 2007), apparently its entire water column was in the euphotic zone.

It is likely that the color patterns described above on the conchs of lower Moscovian coiled nautiloids are examples of disruptive coloration, which "is a set of markings that creates the appearance of false edges and boundaries and hinders the detection or recognition of an object's, or part of an object's, true outline and shape" (Stevens & Merilaita 2009: 484).

Examples of disruptive coloration are: (1) differential blending, where at least some markings blend into the background or all markings blend into at least some of the background colors; (2) maximum disruptive contrast, where adjacent patterns have a high contrast; (3) disruptive marginal patterns, where markings touch the outline of the body; (4) disruption of surface, with markings placed away from the body margins creating false edges; (5) coincident disruptive contrast, where markings cross over and join otherwise revealing body parts, such as wings or legs (Stevens & Merilaita 2009). These principles are based on the distraction of a potential enemy's eye by a bright element of color pattern and thereby deforming or disturbing the body contours of the camouflaged animal and/or creating an optical illusion of the plane of a three-dimensional body, which, if successfully realized, thereby making the animal poorly visible against the surrounding environment (Cott 1940).

The differently colored areas of the body chamber of *Coelogasteroceras coxi* apparently made the mollusc less easily visible to a potential predator, regardless of the surrounding background. This also made the silhouette outline of the mollusc's body nearly indistinct; perhaps the darker coloration of the anterior part of the body chamber created a false edge of the nautiloid's conch silhouette. The color patterns on the conchs of the species of *Metacoceras*, *Parametacoceras*, and *Ephippioceras* were apparently multi-purpose and realized as differential blending, maximum disruptive contrast, and disruptive marginal patterns (see above).

Conclusions

(1) Seven specimens of species of four genera of coiled nautiloids (*Parametacoceras, Metacoceras, Coelogasteroceras,* and *Ephippioceras*) from the lower Moscovian strata of the Donets Basin are the first Paleozoic cephalopods from which conch coloration is reported from Ukraine and Eastern Europe in general.

(2) The conch color patterns of studied nautiloids are represented by longitudinal light bands along the ventrolateral shoulder (*Parametacoceras* and *Metacoceras*), transverse thin lines on the venter (*Ephippioceras*), and a black spot on the body chamber (*Coelogasteroceras*).

(3) Environmental conditions were important factors for the preservation of coloration on the conchs of Paleozoic cephalopods, as well as other molluscs. Among these conditions, the most important were slow sedimentation, absence of agents of mechanical and chemical destruction, such as high-energy water activity, encrustation by epibionts, etc., dysaerobic conditions, and rapid burial apparently accompanied by the activity of bacterial communities.

(4) The color patterns on the conchs of lower Moscovian coiled nautiloids *Parametacoceras, Metacoceras, Coelogasteroceras,* and *Ephippioceras* represent disruptive colorations.

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