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Carboniferous conulariids (Cnidaria: Scyphozoa) from Ukraine

Conuláridos carboníferos (Cnidaria: Scyphozoa) de Ucrania

Viktor V. OHAR & Vitaly S. DERNOV

Abstract: An assemblage of Carboniferous conulariids (Cnidaria) from Ukraine, consisting of *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.*, *P. irregularis* (de Koninck, 1843), *P. kohli* Brew & Beus, 1976, *P. quadrisulcata* (Sowerby, 1821), *P. lata* n. sp., *P.* cf. *crustula* (White, 1880), ?*P.* cf. *subulata* (Hall, 1858), ?*Holoconularia rossica* Van Iten *et al*., 2023, and ?*H. poletaevi* n. sp., is described. Conulariids have been collected from 15 localities, the detailed palaeontological and stratigraphic characteristics of which are summarized here. Nearly all the conulariids were found in the Donets Basin in the Serpukhovian–early Bashkirian and middle–late Moscovian intervals, which are separated from each other by an interval apparently lacking conulariids. Two new species, *Paraconularia lata* n. sp. and ?*Holoconularia poletaevi* n. sp., occur in Moscovian strata. The results of the present study confirm the ability of certain conulariids to withstand major environmental perturbations, as there are no significant changes in species composition across the mid-Carboniferous (Mississippian–Pennsylvanian) boundary. Three species, very similar to species in North America, commonly occur in Carboniferous deposits of Ukraine, namely ?*Paraconularia subulata* (middle Visean), *P. kohli*, and *P.* cf. *crustula* (Moscovian). The discovery of these three species in the Donets Basin of Ukraine underscores the cosmopolitan distribution of at least some conulariids during Carboniferous times.

Resumen: Se describe una asociación de conuláridos (Cnidaria) del Carbonífero de Ucrania, formado por *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.*, *P. irregularis* (de Koninck, 1843), *P. kohli* Brew & Beus, 1976, *P. quadrisulcata* (Sowerby, 1821), *P. lata* n. sp, *P.* cf. *crustula* (White, 1880), ?*P.* cf. *subulata* (Hall, 1858), ?*Holoconularia rossica* Van Iten *et al*., 2023, y ?*H. poletaevi* n. sp. Los conuláridos estudiados proceden de 15 localidades, cuyas características paleontológicas y estratigráficas detalladas se describen en este trabajo. La gran mayoría de los especímenes estudiados se encontraron en los yacimientos de finales del Serpujoviense–principios del Bashkiriense y finales del Moscoviense de la cuenca del Donets (Ucrania oriental), separados por un intervalo significativo sin restos de conuláridos. Dos nuevas especies, *Paraconularia lata* n. sp. Y ?*Holoconularia poletaevi* n. sp., fueron halladas en los yacimientos moscovienses de la cuenca del Donets. Se discute la distribución estratigráfica y algunas características de su filogenia, así como algunos aspectos tafonómicos y paleoecológicos. La considerable resistencia de los conuláridos a los cambios globales queda confirmada por los resultados del estudio de sus restos procedentes de la cuenca del Donets, donde no se registraron cambios significativos en la composición taxonómica cerca del límite medio del Carbonífero (limite Mississippiense–Pennsylvaniense). En los yacimientos carboníferos de Ucrania se han encontrado tres especies comunes y muy similares a las americanas: ?*Paraconularia subulata* (Visiense medio), *P. kohli* y *P.* cf. *crustula* (Moscoviense), lo que puede indicar un cierto grado de cosmopolitismo de al menos algunas especies de conuláridos.

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Palabras-clave:
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Holoconularia
Cuenca de Donets
Depresión de Dnipro-Donets

INTRODUCTION

Conulariids (order Conulariida Miller & Gurley, 1896) are scyphozoan cnidarians (Van Iten *et al*., 2006, 2014) having an organo-phosphatic periderm (theca) and ranging from the terminal Ediacaran to the Late Triassic (Bergström, 1995; Lucas, 2012; Barth *et al*., 2013; Ford *et al*., 2016). Conulariids are usually rare, but in some strata, for example the Ordovician iron-ore beds of the Czech Republic, the Devonian "*Conularia* shales" of Bolivia, and certain Pennsylvanian black shale beds of the North American Midcontinent, they are common (Babcock *et al*., 1987b; Mapes *et al*., 1989).

In Eastern Europe, Carboniferous conulariids have been studied but little and are known only from the Serpukhovian–Moscovian of the Donets Basin and

the Dnipro-Donets Depression (Poletaev, 1974), the Serpukhovian and Moscovian of the Moscow Syneclise (Alekseev, 2001; Van Iten *et al.*, 2023), and the Tournaisian (Torbakova, 1956) and Moscovian (Ogar & Furdui, 2003) of the Urals.

In Ukraine, Carboniferous conulariids are known from the Donets Basin (Poletaev, 1974 and this study), the Dnipro-Donets Depression (Poletaev, 1974 and this study), and the Lviv Palaeozoic Trough (this study). Poletaev (1974) described *Paraconularia inaequicostata* (de Koninck, 1883), *P.* aff. *inaequicostata* (de Koninck, 1883), *P. tubericosta* (Sandberger, 1847), and *P.* cf. *irregularis* (de Koninck, 1843) from Serpukhovian, Bashkirian, and Moscovian deposits in the Donets Basin. A single specimen of *P. inaequicostata* was described by Poletaev (1974) from Bashkirian strata recovered from a borehole (No. 561) drilled near the town of Nizhyn in the Chernihiv Region (Dnipro-Donets Depression). Carboniferous deposits of the Donets Basin have also yielded the organophosphatic, medusozoan cnidarian *Sphenothallus* Hall, 1847 (Aisenverg, 1958, fig. 90, present authors' interpretation of the original specimen, which is stored in the National Museum of Natural History of the NAS of Ukraine, Kyiv; Shulha, 1981, present authors' interpretation; Dernov & Udovychenko, 2019, Fig. 2.1), which occurs as well in the Dnipro-Donets Depression (Dernov, 2023). Finally, conulariids are also known from Ordovician and Silurian deposits of Ukraine (Drygant, 1971), but these fossils require revision.

The present study describes a Carboniferous conulariid assemblage consisting of *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.*, *P. irregularis* (de Koninck, 1843), *P. kohli* Brew & Beus, 1976, *P. quadrisulcata* (Sowerby, 1821), *P. lata* n. sp., *P.* cf. *crustula* (White, 1880), ?*P.* cf. *subulata* (Hall, 1858), ?*Holoconularia rossica* Van Iten *et al.*, 2023, ?*H. poletaevi* n. sp., and Conulariida indet. The conulariids are from the Donets Basin, the Dnipro-Donets Depression, and the Lviv Palaeozoic Trough (Ukraine). New data presented in this study expand the known geographical distribution of certain Carboniferous conulariids and broaden the known taxonomic composition of the Carboniferous sedimentary succession of Ukraine.

GEOLOGICAL SETTING

The studied material was collected at 15 Visean, Serpukhovian, Bashkirian, and Moscovian localities (Middle Mississippian–Middle Pennsylvanian) in the Luhansk, Donetsk, Dnipropetrovs'k, Chernihiv, and Lviv or Volyn regions of Ukraine (Fig. 1).

The Donets Basin and Dnipro-Donets Depression are parts of the northwest-southeast-trending, Pripyat-Dnipro-Donets intracratonic rift that extends from the Baltic to the Caspian Sea across Belarus, Ukraine, and Russia. The rift is located between the Voronezh Anteclise in the north and the Ukrainian Shield in the south, in the southwestern portion of the East European Craton (Izart *et al.*, 1996; Eros *et al.*, 2012; Sachsenhofer *et al.*, 2012; Van Hinsbergen *et al.*, 2015).

The Lviv Palaeozoic Trough is a southeastern extension of the Lublin Trough in Poland, and covers part of the southwestern slope of the East European Craton. Together, the Lviv Palaeozoic Trough and the Lublin Trough form a genetically unified Lviv-Lublin Trough (Basin), that forms much of the Baltic-Dniester pericratonic zone, extending along the western boundary of the East European Craton for over 2000 km and comprising a number of large positive and negative structures (Zinovenko, 1986). The conulariid-bearing localities are described below.

Donets Basin

Zapal-Tyube Hill. Donetsk Region, a hill on the western bank of the Starobesheve reservoir near the village of Voznesenka (47° 46' 40.8" N, 38° 02' 09.1" E). Conulariids occur in a shale bed above the D_3 limestone (1a in Fig. 2: ?*Holoconularia rossica* Van Iten *et al.*, 2023), in a shale between the D_3^1 and D_3^2 limestones (1b: *Paraconularia irregularis* (de Koninck, 1843)), and in a gray mudstone below the D_4 limestone (1c: *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.*) in the Kalmius Formation (Fig. 3).

Zhelvakova Ravine. Donetsk Region, Zhelvakova Ravine near the town of Starobesheve (47° 46' 52.9" N, 38° 00' 18.1" E). Conulariids occur in small rounded calcareous nodules within a 1-m-thick, yellowish gray mudstone above the D_5^7 limestone (2a in Fig. 2: ?*Holoconularia rossica* Van Iten *et al.*, 2023) and in the D_5^8 limestone (2b: *P. inaequicostata* (de Koninck, 1883) *s.l.*) in the Kalmius Formation.

Calcareous nodules measuring 1–7 cm in diameter (see Fig. 6E, 6F) form an interbed (the so-called "nodular horizon" of Aisenverg *et al.* (1987), Poletaev *et al.* (1988), Nemirovskaya *et al.* (1992) and Vdovenko *et al.* (1992)) situated 4 m above the D_5^7 limestone in the Serpukhovian part of the Kalmius Formation. The carbonate "concretions", which may be oncolites or related microbial structures, contain rich and well-preserved marine biota, including cyanobacteria, calcareous algae, foraminifers, corals, bivalves, gastropods, ammonoids, nautiloids, ostracods, conodonts, and fishes (Aisenverg, 1958; Aisenverg *et al.*, 1975, 1987; Popov, 1979; Astakhova, 1983; Brazhnikova & Vdovenko, 1983; Berchenko, 1987; Poletaev *et al.*, 1988; Nemirovskaya *et al.*, 1990, 1992; Vdovenko *et al.*, 1992).

The D_5^8 limestone consists of two interbeds separated from each other by a 4.5-m-thick layer of greenish-grey siltstone. The lower bed (D_5^{8Lower}) is argillaceous, partly brecciated, and contains foraminifers (*Earlandia* sp., *Archaediscus baschkiricus* Krestovnikov & Theodorovich, 1936, *Eostaffella pseudostruvei* (Rauzer-Chernousova & Belyaev in Rauzer-Chernousova *et*

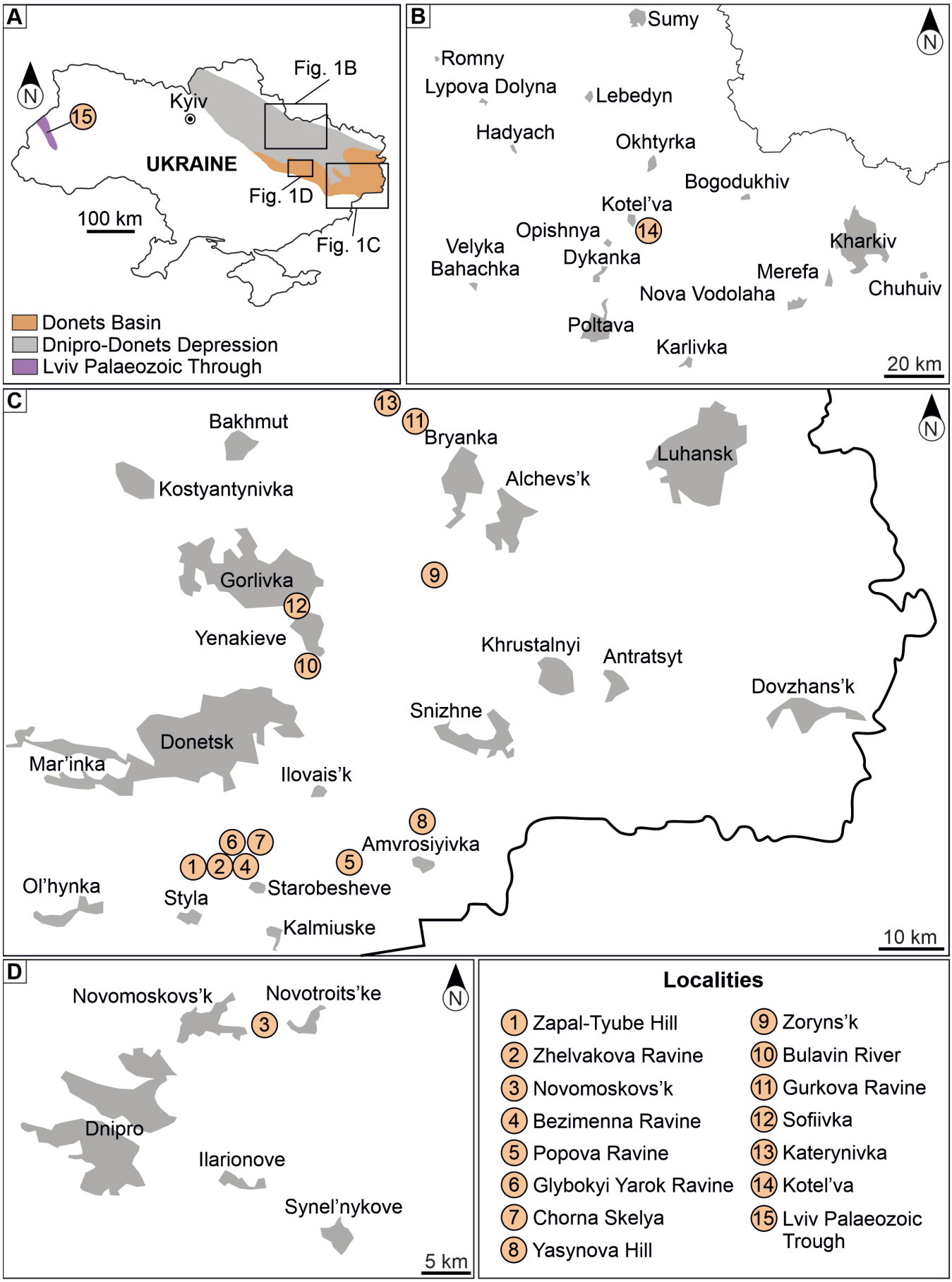

Figure 1. Geographical location of the conulariid-bearing localities.

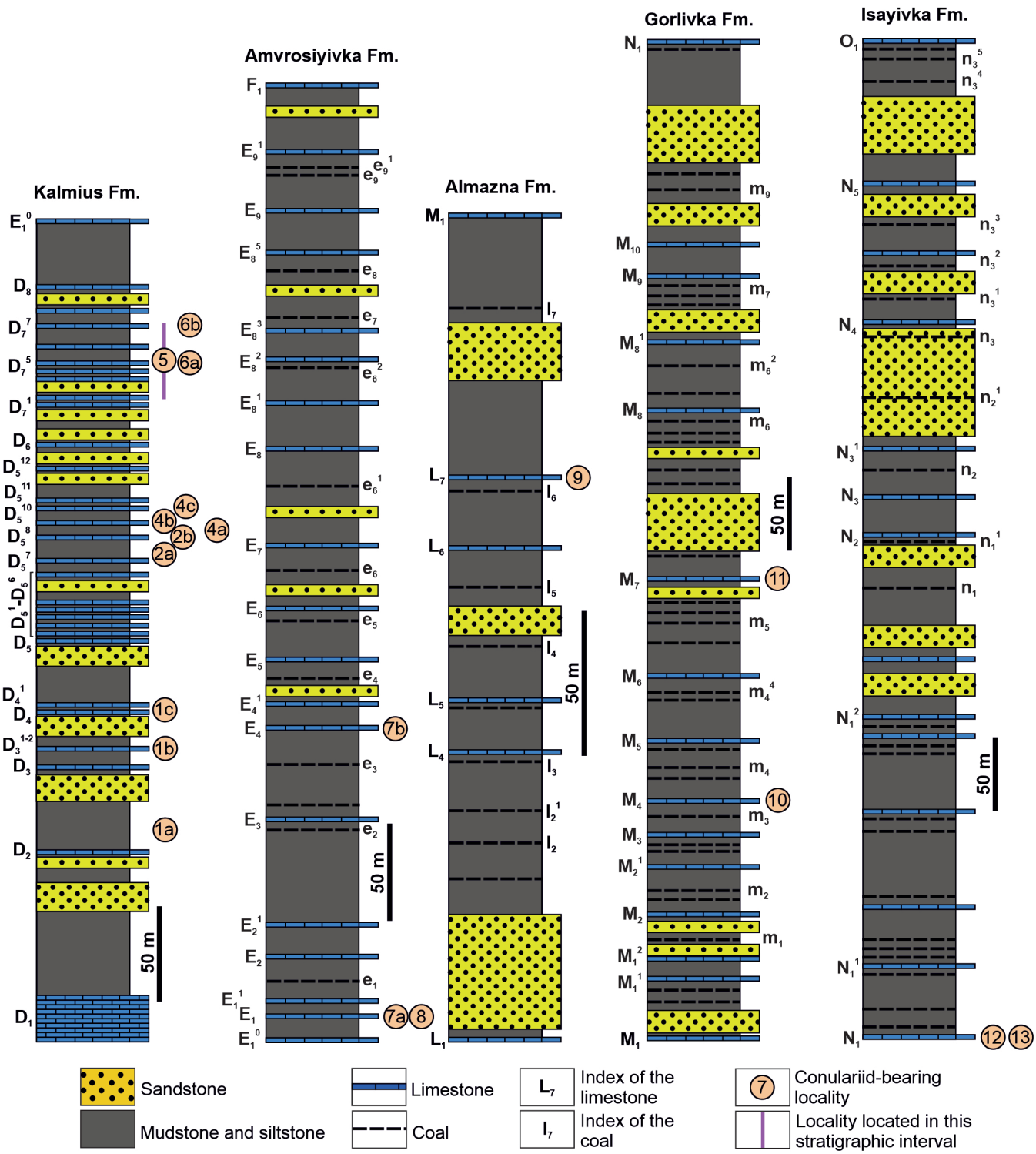

Figure 2. Stratigraphic position of the conulariid localities in the Carboniferous formations of the Donets Basin. Lithological columns modified from Aisenverg *et al.* (1975, figs. 21, 23), Levenshtein & Shirokov (1963, fig. 48) (Kalmius Formation), Levenshtein & Shirokov (1963, fig. 50) (Amvrosiyivka Formation), Levenshtein & Shirokov (1963, fig. 61) (Almazna Formation), Levenshtein & Shirokov (1963, fig. 65) (Gorlivka Formation), and Levenshtein & Shirokov (1963, fig. 66) (Isayivka Formation).

al., 1936), *Ammovertella* aff. *inversa* (Schellwien, 1898), *Loeblichia minima* Brazhnikova, 1962), corals (*Aulina rotiformis* Smith, 1916, *Dibunophyllum bipartitum* M'Coy, 1849, *D. dobroljubovae* Vassilyuk, 1960), brachiopods (*Schizophoria resupinata* (Martin, 1809), *Antiquatonia postinsculpta* (Rotai, 1980), *Gigantoproductus* sp.), gastropods (*e.g.*, *Euphemites urei* (Fleming, 1828)), and conodonts (*Gnathodus bilineatus bollandensis* Higgins & Bouckaert, 1968, and *Paragnathodus mononodosus* (Rhodes *et al.*, 1969)). The upper layer (D_5^{8Upper}) is brownish-grey, clayey, with calcareous algae, bryozoans, brachiopods (*Composita ambigua* (Sowerby, 1822) and ?*Alexenia* sp.), gastropods (*Pseudozygopleura scalaroidea*

System	Subsystem	Stage	Regional stage	Lithostratigraphic unit
CARBONIFEROUS	PENNSYLVANIAN	Gzhelian	Myronivskian	Araukarytova Formation
			Kalynovian	Avilovka Formation
		Kasimovian	Toretzian	Isayivka Formation
		Moscovian	Lomovatkian	Gorlivka Formation
			Lozovian	Almazna Formation
				Kamensk Formation
		Bashkirian	Kayalian	Belaya Kalitva Formation
				Smolyanynivka Formation
				Mospyne Formation
			Mandrykinian	Mandrykyne Formation
			Olmezovian	Amvrosiyivka Formation
	MISSISSIP.	Serpukhovian	Starobeshevian	Kalmius Formation
			Yefremivian	Samara Formation
		Visean		Mezhova Formation
		Tournaisian	Buzyn.+Oleniv.	Mokra Volnovakha Group

Figure 3. Carboniferous stratigraphy of the Donets Basin in eastern Ukraine. Abbreviations: **Buzyn.+Oleniv.** – Buzynivian and Olenivkian, **Mississip.** – Mississippian

(Phillips, 1836), *Platyzona tornatilis* (Phillips, 1836), and conodonts (Poletaev *et al.*, 1988).
Paraconularia cf. *irregularis* (de Koninck, 1843) and *P. inaequicostata* (de Koninck, 1883) were previously described from this locality by Poletaev (1974).

Novomoskovs'k. Dnipropetrovs'k Region, borehole No. 1686 drilled near the town of Novomoskovs'k. *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.* was found in Serpukhovian or early Bashkirian strata recovered at a depth of 202.6–203.7 m.

Bezimenna Ravine. Donetsk Region, the mouth of the Bezimenna Ravine near the town of Starobesheve (47° 47' 41.4" N, 37° 59' 21.1" E). Conulariids occur in a light grey shale between the D_5^8 and D_5^9 limestones (4a in Fig. 2: *Paraconularia irregularis* (de Koninck, 1843)), in the D_5^9 limestone (4b: *Paraconularia quadrisulcata* (Sowerby, 1821)), and in the D_5^{10} limestone (4c: *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.*) in the Kalmius Formation.
The D_5^9 limestone is light grey, argillaceous, bioclastic and oolitic, being massive in the lower part and argillaceous with abundant brachiopods in the upper part. The limestone contains foraminifers (*Eostaffella* ex gr. *pseudostruvei* (Rauzer-Chernousova & Belyaev in Rauzer-Chernousova *et al.*, 1936), *Archaediscus baschkiricus* Krestovnikov & Theodorovich, 1936, *Haplophragmina sarbaica beschevensis* (Brazhnikova in Brazhnikova *et al.*, 1967)), corals, brachiopods, and conodonts (*Rhachistognathus minutus declinatus* (Baeseman & Lane, 1985) and *Declinognathodus noduliferus inaequalis* (Higgins, 1975)) (Poletaev *et al.*, 1988). Rugose corals *Dibunophyllum medium* Fedorowski, 2017 and *Dibunophylloides paulus* Fedorowski, 2017 were described from the D_5^{10} limestone (Fedorowski, 2017).

Popova Ravine. Donetsk Region, Popova Ravine near the village of Yelyzaveto-Mykolaivka (47° 49'2 3.5" N, 38° 20' 08.3" E). ?*Holoconularia rossica* Van Iten *et al.*, 2023 occurs in an unidentified limestone in the stratigraphic interval bounded by the D_7^2 and D_7^7 limestones in the Bashkirian part of the Kalmius Formation. The section here exposes the uppermost part of the Kalmius Formation, which consists of a 35-m-thick succession of terrigenous strata with several limestone interbeds containing calcareous algae, corals, brachiopods (*Rugosochonetes fenia* (Rotai, 1931), *Buxtonia* sp., *Linoproductus* sp.), bivalves, and conodonts (*Declinognathodus noduliferus* Ellison & Graves, 1941, *D. lateralis* (Higgins & Bouckaert, 1968), *Idiognathoides sulcatus* Higgins & Bouckaert, 1968, *Id. sinuatus* Harris & Hollingsworth, 1933, *Hindeodus minutus* Ellison, 1941) (Poletaev *et al.*, 1988).

Glybokyi Yarok Ravine. Donetsk Region, the mouth of the Glybokyi Yarok Ravine near the town of Starobesheve (47° 46' 42.0 "N, 38° 03' 30.2" E). Conulariids occurs in the D_7^5 limestone (6a in Fig. 2: *Paraconularia irregularis* (de Koninck, 1843)) and in the D_7^7 limestone (6b: *Paraconularia quadrisulcata* (Sowerby, 1821) and ?*Holoconularia rossica* Van Iten *et al.*, 2023) of the Kalmius Formation.
The D_7^5 limestone is brown, sandy, and oolitic in the 0.2-m-thick lower part and bluish-grey and massive with microbial nodules and crinoids in the 0.7-m-thick upper part. This limestone contains calcareous algae (*Cuneiphycus aliquantulus* Johnson, 1960, *Berestovia filaris* Berchenko, 1982, *Donezella delicata* Berchenko, 1982, *D. lutugini* Maslov, 1929, etc.), foraminifers (*Archaediscus baschkiricus* Krestovnikov & Theodorovich, 1936, *Archaediscus krestovnikovi* Rauzer-Chernousova, 1948, *Eostaffella pseudostruvei* (Rauzer-Chernousova & Belyaev in Rauzer-Chernousova *et al.*, 1936)), brachiopods (*Schizophoria resupinata* (Martin, 1809)), and conodonts (*Declinognathodus noduliferus inaequalis* (Higgins, 1975), *D. noduliferus noduliferus* (Ellison & Graves, 1941)) (Aisenverg *et al.*, 1987; Poletaev *et al.*, 1988).
The D_7^7 limestone is yellowish-grey, oolitic, and bioclastic in the 0.3-m-thick lower part and brown and clayey in the 0.15-m-thick upper part. The limestone contains calcareous algae (*Berestovia filaris* Berchenko, 1982, *Donezella delicata* Berchenko, 1982, *D. lutugini* Maslov, 1929, etc.), foraminifers (*Archaediscus baschkiricus* Krestovnikov & Theodorovich, 1936, *Archaediscus krestovnikovi* Rauzer-Chernousova, 1948, *Eostaffella pseudostruvei* (Rauzer-Chernousova & Belyaev in Rauzer-Chernousova *et al.*, 1936), *Endothyra pseudobradyi* Brazhnikova, 1956), corals, brachiopods (*Productus* sp., *Buxtonia* sp., ?*Punctospirifer* sp., etc.) and conodonts (*Declinognathodus noduliferus noduliferus* (Ellison & Graves, 1941) and *D. lateralis* (Higgins & Bouckaert, 1968)) (Aisenverg *et al.*, 1987; Poletaev *et al.*, 1988).

Chorna Skelya. Donetsk Region, the mouth of the Berestova River, which flows into the Kalmius River north of the town of Starobesheve (47° 48' 50.1" N, 37° 59' 02.1" E). In this section, the lower part of the Amvrosiyivka Formation consists of a succession of terrigenous rocks with several limestone interbeds (E_1^I–E_4 according to Aisenverg (1958) or D_8–E_3 according to Yefimenko (2006)). In addition to the conulariids *Paraconularia quadrisulcata* (Sowerby, 1821) and ?*Holoconularia rossica* Van Iten *et al.*, 2023 in the E_1^{II-III} limestone (7a in Fig. 2), *Paraconularia irregularis* (de Koninck, 1843) in the E_4 limestone (7b in Fig. 2), this section also contains terrestrial plants, calcareous algae, foraminifers, corals, bryozoans, brachiopods, bivalves, gastropods, nautiloids, ammonoids, crinoids, ostracods, conodonts, and trace fossils (Aisenverg, 1958; Novik, 1968; Popov, 1979; Makarov & Kirichenko, 1982; Aisenverg *et al.*, 1987; Aisenverg & Astakhova, 1987; Yefimenko, 2006, 2013).
Previously, *Paraconularia tubericosta* (Sandberger, 1847) was described by Poletaev (1974) from the E_1 limestone exposed in the Velyka Shyshovka Ravine near the village of Svystuny in the Amvrosiyivka District of the Donetsk Region, or some 50 km north-east of the Chorna Skelya locality.

Yasynova Hill. Donetsk Region, Amvrosyivka District, Yasynova Hill in the Krynka River basin. *Paraconularia irregularis* (de Koninck, 1843) occurs in the E_1^{VII} limestone in the Amvrosiyivka Formation (see Fig. 2).

Zoryns'k. Luhansk Region, right bank of the Lozova River just east of the Nikanor coal mine (48° 26' 26.8" N, 38° 37' 22.2" E). ?*Holoconularia poletaevi* n. sp. co-occurs with abundant brachiopods *Schizophoria resupinata* (Martin, 1809) (see Fig. 6B) in the L_7 limestone in the Almazna Formation (see Fig. 2). The limestone contains corals, bryozoans, brachiopods, bivalves, gastropods, the nautiloid *Ephippioceras clitellarium* (Sowerby, 1840) (unpublished data of VSD), crinoids, trilobites, and fishes. A mudstone bed above the L_7 limestone contains the macroscopic problematicum *Coleolus* sp., the ammonoid *Wiedeyoceras* cf. *cambriense* (Bisat, 1930), the nautiloids *Parametacoceras jongmansi* Delépine, 1937, *Domatoceras* sp., and *Pseudostenopoceras solare* Shimansky, 1967, as well as fish teeth (unpublished data of VSD). *Paraconularia* aff. *inaequicostata* (de Koninck, 1883) was described by Poletaev (1974) from the L_6 limestone exposed near the Avdakovo railway station in the town of Bryanka in the Luhansk Region (approximately 10 km north-east of the town of Zoryns'k).

Bulavin River. Donetsk Region, right bank of the Bulavin River near the village of Ol'khovatka (48° 15' 06.9" N, 38° 24' 21.7" E). *Paraconularia* cf. *crustula* (White, 1880) occurs in the 0.2-m-thick M_4 limestone in the Gorlivka Formation (see Fig. 2). The limestone is dark grey, argillaceous and massive, with foraminifers (*Tetrataxis parviconica* Lee & Chen in Lee *et al.*, 1930 and *Pseudoglomospira elegans* (Lipina, 1949)), brachiopods (*Orthotichia* sp., *Orthotetes* sp., *Kozlowskia* sp.), gastropods (*Euphemites enodis* Sturgeon, 1964), conodonts ("*Streptognathodus*" *dissectus* Kossenko in Kozitskaya *et al.*, 1978, *Idiognathodus* sp.), bryozoans, crinoids, and ostracods (Makarov & Kossenko, 1982).

Gurkova Ravine. Luhansk Region, slopes of the Gurkova Ravine near the town of Sokolohirs'k (48° 36' 48.7" N, 38° 36' 26.0" E). *Paraconularia lata* n. sp. occurs in the 0.6–0.9 m thick M_7 limestone in the Gorlivka Formation (see Fig. 2). This bed contains foraminifers (*Ozawainella pseudoangulata* (Putrya, 1939) and *Fusulinella colaniae* Lee & Chen in Lee *et al.*, 1930), brachiopods, bivalves and conodonts (*Idiognathodus obliquus* Kossenko & Kozitskaya in Kozitskaya *et al.*, 1978, "*Streptognathodus*" *dissectus* Kossenko in Kozitskaya *et al.*, 1978) (Aisenverg *et al.*, 1975; Poletaev *et al.*, 2011; Khodjanyazova *et al.*, 2014).

Sofiivka. Donetsk Region, left bank of the Sadky River near the village of Sofiivka (48° 16' 44.0" N, 38° 11' 05.2" E). ?*Holoconularia poletaevi* n. sp. occurs in the 0.4 m thick N_1 limestone in the Moscovian part of the Isayivka Formation (see Fig. 2). This bed is dark grey, crystalline, massive, and partly argillaceous, with foraminifers (*Hemifusulina bocki* Möller, 1878, *H. graciosa* (Lee, 1937), *Ozawainella nikitovkensis* (Brazhnikova, 1939), etc.), brachiopods (*Neochonetes* sp., *Dictyoclostus donetzianus* (Likharev, 1938), *Brachythyrina* sp. and *Trautscholdia* sp.), bivalves, gastropods (*Euphemites enodis* Sturgeon, 1964, *E.* aff. *multiliratus* Sturgeon, 1964, *E.* cf. *carbonarius* (Cox, 1857), *Platyceras* sp., etc.), trilobites, and conodonts (e.g., *Idiognathodus obliquus* Kossenko & Kozitskaya in Kozitskaya *et al.*, 1978, *I. delicatus* Gunnell, 1931, *Streptognathodus oppletus* Ellison, 1941) (Makarov & Kossenko, 1982).

Katerynivka. Luhansk Region, bank of the Sanzharivka River near the village of Katerynivka (48° 39' 49.2" N, 38° 29' 07.7" E). *Paraconularia kohli* Brew & Beus, 1976 occurs in the N_1 limestone in the Moscovian part of the Isayivka Formation (see Fig. 2).

Dnipro-Donets Depression

Kotelevs'ka-201 borehole. Poltava Region, Kotelevs'ka-201 borehole drilled near the village of Kotel'va (50° 03' 32.2" N, 34° 46' 14.0" E). A single fragment of ?*Paraconularia* cf. *subulata* (Hall, 1858) was found at a depth of 5869.5 m in a middle Visean black shale with brachiopods and crinoids.

Lviv Palaeozoic Trough

Lviv Palaeozoic Trough. A single poorly preserved specimen, here designated as Conulariida indet., was found in a shale bed recovered by the borehole No. 5431 at a depth of 287.5 m. The exact geographical location of this borehole is unknown (Lviv or Volyn Region), and the age of the conulariid is late Visean or early Serpukhovian.

STRATIGRAPHY AND AGES OF THE FAUNAS

The studied conulariids originate mainly from the Kalmius, Amvrosiyivka, Almazna, Gorlivka, and Isayivka formations of the Donets Basin. These are described in some detail below.

Kalmius Formation. The Kalmius Formation consists of a paralic succession of sandstones, siltstones, mudstones, coals (7–11 beds), and limestones (up to 35 layers). The characteristic sandstone beds have been named (*e.g.*, the Feninian sandstone bed) and are used for local correlation of sections. The total thickness of the formation ranges from 530 to 800 m (Aisenverg *et al.*, 1963; Levenshtein & Shirokov, 1963; Feofilova & Levenshtein, 1963; Dunaeva, 1969; Makarov & Kirichenko, 1982; Nemyrovska & Yefimenko, 2013).

The limestones in the interval from the D_1 to D_5 limestone inclusive contain abundant corals (especially in the D_3, D_4, and D_5 limestones). The limestones in the upper part of the Kalmius Formation, in the interval D_5 to E_1, are largely oolitic (especially the D_7 limestone) (Feofilova & Levenshtein, 1963).

The lower boundary of the global Bashkirian Stage lies at the base of the *Homoceras* Genozone or the *Isohomoceras subglobosum* Zone, but the first appearance of *Isohomoceras subglobosum* (Bisat, 1924) in sections in the state of Nevada (USA), where the Global Boundary Stratotype Section and Point (**GSSP**) of the lower boundary of the Bashkirian is located (the Arrow Canyon section), probably lies just below the mid-Carboniferous boundary (Davydov *et al.*, 2012). In the Donets Basin, *Homoceras* first appears in the D_5^{10} limestone in the Kalmius Formation (Astakhova, 1983; Nemirovskaya *et al.*, 1990, 1992). According to Nikolaeva (2022), the surface ornamentation of *Homoceras* sp. from the Donets Basin indicates that the deposits containing it belong to the *H. beyrichianum* Zone of the *Homoceras* Genozone.

Another marker of the mid-Carboniferous boundary, the conodont species *Declinognathodus noduliferus* (Ellison & Graves, 1941), was recorded by Nemyrovska (in Nemirovskaya *et al.*, 1990, 1992) in the D_5^8 limestone in the Kalmius Formation, or about 20 m below the D_5^{10} limestone. Therefore, in the Donets Basin, the lower boundary of the Bashkirian is located at the base of the D_5^8 limestone, and thus the stratigraphic interval between the D_1 and D_5^8 limestones occurs in the *Fayettevillea–Delepinoceras* Genozone (Popov, 1979; Astakhova, 1983).

Amvrosiyivka Formation. The Amvrosiyivka Formation consists of a paralic succession of sandstones, siltstones, mudstones, coals (4–17 seams), and limestones (up to 20 beds). The total thickness of the formation ranges from 250 to 900 m (Aisenverg *et al.*, 1963; Feofilova & Levenshtein, 1963; Levenshtein & Shirokov, 1963; Dunaeva, 1969; Nemyrovska & Yefimenko, 2013).

The formation contains ammonoids of the early Bashkirian *Reticuloceras-Bashkortoceras* Genozone (stratigraphic interval between the E_1 and E_9 limestones) and the *Bilinguites-Cancelloceras* Genozone (the E_9–G_1 limestones) (Popov, 1979; Dernov, 2022). The formation also occurs in the *Idiognathoides sinuatus-Id. sulcatus sulcatus* conodont zone, which correlates with the Krasnopolyanian and Severokeltmenian regional substages of Eastern Europe and with the early–middle Morrowan of North America (Nemyrovska, 2017). The Amvrosiyivka Formation also contains typical Namurian A and B terrestrial plants (Novik, 1968).

Almanza Formation. The Almazna Formation consists of a paralic succession of sandstones, siltstones, mudstones, coals (9 seams), and limestones (5–8 beds). The thickness of the formation varies from 180 m in the NW part of the Donets Basin to 610 m in the SE part of the basin (Aisenverg *et al.*, 1963; Levenshtein & Shirokov, 1963; Dunaeva, 1969; Nemyrovska & Yefimenko, 2013).

Alluvial sandstones are widespread in the lower part of the formation. The upper part of the formation is dominated by marine and lagoonal deposits, many of the sandstones are deltaic in origin (Feofilova & Levenshtein, 1963).

The Almazna Formation corresponds to the Mar'yivkian Horizon (upper half of the Lozovian Regional Stage) of the Regional stratigraphic scheme of the Dnipro-Donets Downwarp (Poletaev *et al.*, 2011; Nemyrovska & Yefimenko, 2013). The formation contains conodonts of the *"Streptognathodus" transitivus-Neognathodus atokaensis* Zone (stratigraphic interval between the K_6 and L_5 limestones) and the younger *Idiognathodus izwaricus* Zone (the L_5–M_1 limestones) (Fohrer *et al.*, 2007; Nemyrovska, 2017). According to conodont studies (Nemyrovska, 2017, text-fig. 2), the Mar'yivkian Horizon of the Donets Basin corresponds to the Kashirian Regional Stage in the historical stratotype section of the Moscovian Stage (Moscow Syneclise).

The Almazna Formation also contains typical Bolsovian (= Westphalian C) terrestrial plants (Novik, 1952, 1974; Fissunenko, 1991, 2000; Boyarina, 2016), nonmarine bivalves (Sergeeva, 1981, 1984), and the ammonoid *Wiedeyoceras* cf. *cambriense* (Bisat, 1930) (unpublished data of VSD). The absolute age of the claystone in the I_3 coal seam, which lies *ca*. 100 m below the L_7 limestone at the Zoryns'k locality, is 312.01±0.08 and 312.18±0.07 My (Davydov *et al.*, 2010).

Gorlivka Formation. The Gorlivka Formation consists of a paralic succession of sandstones, siltstones, mudstones, coals (up to 28 seams), and limestones (20 beds). The thickness of the formation varies from 230 m in the NW part of the Donets Basin to 960 m in the SE part of the basin (Aisenverg *et al.*, 1963; Dunaeva, 1969; Nemyrovska & Yefimenko, 2013).

The limestones in this formation are mostly bioclastic with rich stenohaline fauna, including corals, brachiopods, cephalopods, crinoids, and trilobites.

Some of the limestones are massive, measuring from 3 to 5 m in thickness. A characteristic feature of the lower part of the formation is an exceptionally abrupt transition upsection from limestones rich in marine fauna, including corals and foraminifers, to strata deposited in coal swamps (Feofilova & Levenshtein, 1963).

The Gorlivka Formation corresponds to the Sabivkian Horizon of the Regional stratigraphic scheme of the Dnipro-Donets Downwarp (Poletaev *et al.*, 2011; Nemyrovska & Yefimenko, 2013). The formation contains conodonts of the *Swadelina dissecta* Zone (the stratigraphic interval bounded by the M_1 and M_8 limestones) and the lower part of the *Swadelina gurkovaensis* Zone (the M_8–M_{10}^1 limestones) (Nemyrovska, 2017). According to conodont studies (Nemyrovska, 2017, text-fig. 2), the Sabivkian Horizon of the Donets Basin corresponds to the Podolskian Regional Stage in the historical stratotype section of the Moscovian Stage (Moscow Syneclise).

The Gorlivka Formation also contains typical Asturian terrestrial plants (Novik, 1952, 1974; Fissunenko, 1991, 2000; Boyarina, 2016) and nonmarine bivalves of the *phillipsi* Zone of England (Sergeeva, 1981, 1984). Popov (1979) reported the Westphalian D ammonoid species *Wiedeyoceras cambriense* and *Politoceras* cf. *politum* (Shumard, 1858) from the lower part of the Gorlivka Formation. The absolute age of the claystone in the m_3 coal seam, which occurs in the lower part of the Gorlivka Formation, is 310.55 ± 0.10 My (Davydov *et al.*, 2010).

Isayivka Formation. The Isayivka Formation is a paralic succession of sandstones, siltstones, mudstones, coals (up to 20 seams), and limestones. The thickness of the formation varies from 65 m in the NW part of the Donets Basin to 259 m in the SE part of the basin (Aisenverg *et al.*, 1963; Dunaeva, 1969; Nemyrovska & Yefimenko, 2013).

The Isayivka Formation corresponds to the Sanzharivkian Horizon and the lower part of the Kartanashian Horizon of the Regional stratigraphic scheme of the Dnipro-Donets Downwarp (Poletaev *et al.*, 2011; Nemyrovska & Yefimenko, 2013). Present in the formation are conodonts of the *Swadelina subexcelsa* Zone and the lower part of the *Idiognathodus saggitalis–Idiognathodus* sp. A Zone (Nemyrovska, 2017). According to conodont studies (Nemyrovska, 2017, text-fig. 2), the Sanzharivkian and Kartanashian horizons of the Donets Basin correspond to the Myachkovian and lower part of the Krevyakinian regional stages in the stratotype section of the Moscow Syneclise, and to the uppermost part of the Desmoinesian of the North America Midcontinent.

The Moscovian–Kasimovian boundary in the Donets Basin is currently placed at the base of the N_4 limestone (upper half of the Isayivka Formation) (Shchegolev & Boyarina, 2013; Nemyrovska, 2017, 2022). The Isayivka Formation also contains typical Cantabrian terrestrial plants (Fissunenko, 2000; Boyarina, 2016) and fusulinids (Khodjanyazova *et al.*, 2014) as well as nonmarine bivalves of the *tenuis* and *prolifera* zones of Western Europe (Sergeeva, 1981, 1984). The absolute age of the claystone in the n_1 coal seam in the lower part of the Isayivka Formation is 307.26 ± 0.11 My (Davydov *et al.*, 2010).

PALAEOGEOGRAPHY

Serpukhovian, Bashkirian, and Moscovian coal-bearing strata of the Donets Basin were deposited mainly in a large alluvial-deltaic plain that was flooded periodically by warm epicontinental seas (Fig. 4). The central part of the Donets Basin was characterized by uninterrupted marine sedimentation in the Serpukhovian and Bashkirian. The climate throughout the basin was humid tropical and/or subtropical (Novik, 1952, 1974; Logvinenko, 1953; Fissunenko, 2000). The following depositional environments were present: shallow marine, lagoonal, lacustrine, prodeltaic, deltaic, alluvial, peat swamp, and siliciclastic swamp (Logvinenko, 1953; Feofilova & Levenshtein, 1963; Kozitskaya & Shchegolev, 1993).

The studied conulariids come from two main lithofacies: (1) shales, including black shales, deposited in the proximal-most portions of the epicontinental sea, where

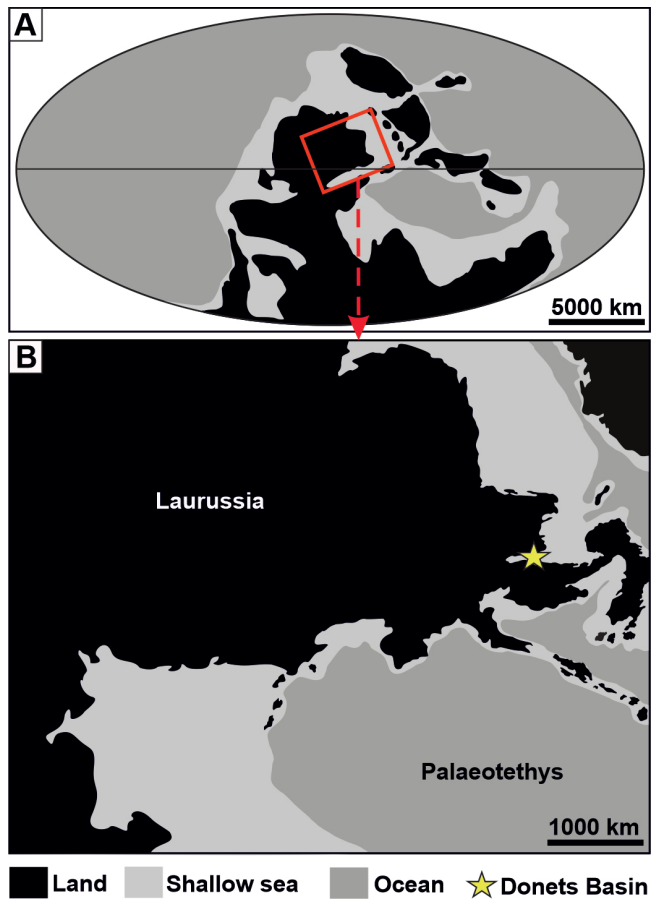

Figure 4. Carboniferous palaeogeography of the world (**A**) and Europe (**B**). Modified from Scotese (2014) and Deep Time Maps (https://deeptimemaps.com).

sedimentation rates were low and the waters dysoxic (*e.g.*, the Zhelvakova Ravine and Kotel'va localities); (2) shallow-water, normal marine limestones (*e.g.*, the Zoryns'k and Bulavin River localities).

MATERIAL AND METHODS

Thirty-three newly collected specimens of mostly moderately well or poorly preserved conulariid thecae were examined in this study (Tab. 1). Most of the conulariids (collection NMNHU-G 8590) were collected by Dr. Vladyslav Poletaev (Institute of Geological Sciences of the National Academy of Sciences of Ukraine, Kyiv; **IGS NASU**), Dr. Nina Vassilyuk (Donetsk Polytechnic), Dr. Vitaly Shulha (IGS NASU), or unknown geologists, all of whom donated fossils for study to the Department of Palaeontology and Stratigraphy of the Palaeozoic Sediments of the IGS NASU. Some of the conulariids were collected by VVO.

Parts of conulariid collections NMNHU-G 1734 and NMNHU-G 2209, previously studied by Poletaev (1974) and Ogar & Furdui (2003), respectively, were also examined. Both collections are housed in the Geological Department of the National Museum of Natural History of the NAS of Ukraine in Kyiv (**NMNHU**). The collection studied by Vladyslav Poletaev consists of 15 specimens (NMNHU-G 1734/01 to NMNHU-G 1734/12 and three uncatalogued specimens; Fig. 5). The conulariids in this collection are represented mainly by deformed thecal fragments, and less often by moulds, that are preserved mainly in carbonate and limonite nodules, less often in limestone or mudstone. The collection studied by Ogar and Furdui (2003) consists of six specimens of compacted thecae in marl-like limestone.

A small collection of *Paraconularia magna* (Ries, 1949) (specimens NMNHU-G 8590/05a to 05j) was kindly provided for study by American geologist R. Erickson at the end of the 1980s. This material was collected from the Missourian rocks at the type locality of this species in the Okfuskee County, Oklahoma, USA.

The present paper uses generally accepted morphological terms presented in Sinclair (1940b), Moore and Harrington (1956), Babcock and Feldmann (1986a), Van Iten (1992) and Van Iten *et al.* (1996) (Fig. 6A). The studied material consists of partial thecae, commonly deformed, and external and internal moulds, some of which do not preserve fine nodes or interspace ridges (Fig. 6B–6F).

In the systematic part below, we adopt a conulariid taxonomy based on the results of the phylogenetic analyses of Van Iten *et al.* (2014, 2016).

SYSTEMATIC PALAEONTOLOGY

Phylum Cnidaria Verrill, 1865
Class Scyphozoa Götte, 1887
Order Conulariida Miller & Gurley, 1896 emended Moore & Harrington, 1956
Genus *Paraconularia* Sinclair, 1940a

Type-species. *Conularia inaequicostata* de Koninck, 1883 from the Tournaisian of Belgium; designated by Sinclair (1940a).

Diagnosis. Transverse ribs moderately strong, sometimes faintly tuberculate, abruptly bent adaperturally at the edges of the corner furrows. Midline on faces indicated only by slight deflection of transverse ribs along it (after Moore & Harrington, 1956, p. F65).

Paraconularia inaequicostata (de Koninck, 1883) *s.l.*

Figure 5A–5C, 5E, 7

1883 *Conularia inaequicostata*; de Koninck, p. 223, pl. 54, figs. 9–11.
1940a *Conularia* (*Paraconularia*) *inaequicostata*; Sinclair, p. 73–74.
1956 *Paraconularia inaequicostata;* Moore & Harrington, p. F65, fig. 50.1.

Table 1. Studied material.

Taxa	Specimens (NMNHU-G 8590/…)	Localities
Paraconularia irregularis (de Koninck, 1843)	06, 09, 10, 17, 23d	Bezimenna Ravine, Yasynova Hill, Zapal-Tyube Hill, Chorna Skelya, Glybokyi Yarok Ravine
Paraconularia quadrisulcata (Sowerby, 1821)	22, 23a, 23b, 23c, 25, 27, 28	Bezimenna Ravine, Glybokyi Yarok Ravine, Chorna Skelya
Paraconularia inaequicostata (de Koninck, 1883) *s.l.*	02, 11–13, 18, 20	Novomoskovs'k, Zhelvakova Ravine, Bezimenna Ravine, Zapal-Tyube Hill
Paraconularia kohli Brew & Beus, 1976	21	Katerynivka
Paraconularia magna (Ries, 1949)	05a–05j	Oklahoma (USA); Missourian (Pennsylvanian)
Paraconularia lata n. sp. paratype	32	Gurkova Ravine
Paraconularia cf. *crustula* (White, 1880)	07	Bulavin River
?*Paraconularia* cf. *subulata* (Hall, 1858)	33	Kotelevs'ka-201 borehole
?*Holoconularia rossica* Van Iten, Mironenko & Vinn, 2023	08, 14–16, 19, 24, 29a, 29b	Zapal-Tyube Hill, Zhelvakova Ravine, Popova Ravine, Glybokyi Yarok Ravine, Chorna Skelya
?*Holoconularia poletaevi* n. sp.	01a, 01b, 04	Zoryns'k, Sofiivka
Conularida indet.	30	Lviv Palaeozoic Trough

v 1974 *Paraconularia inaequicostata;* Poletaev, p. 71, pl. 13, figs. 4, 5.
non 2003 *Paraconularia inaequicostata*; Ogar & Furdui, p. 28, text-figs.1–6.
2009 *Paraconularia inaequicostata*; Sendino, p. 353, pl. 31, figs. 4–7.

Lectotype**.** Specimen MGL6093 in the Lille Natural History Museum (but its presence in this museum requires verification) from the Tournaisian of Belgium. Described and figured by de Koninck (1883, p. 223, pl. 54, figs. 9–11) and Moore and Harrington (1956, p. F65, figs. 50.1a–1c). Plaster duplicate of the lectotype specimen (de Koninck, 1883, pl. 54, fig. 9) figured by Waterhouse (1979, p. 482, figs. 2.6 and 2.7) without indicating the original acronym.

Material. Six specimens (NMNHU-G 8590/02, 11, 12, 13, 18, 20) lacking the apex and aperture from the Zapal-Tyube, Zhelvakova Ravine, Bezimenna Ravine, and Novomoskovs'k localities. Specimen NMNHU-G 8590/12 preserves part of the apertural region of the theca.

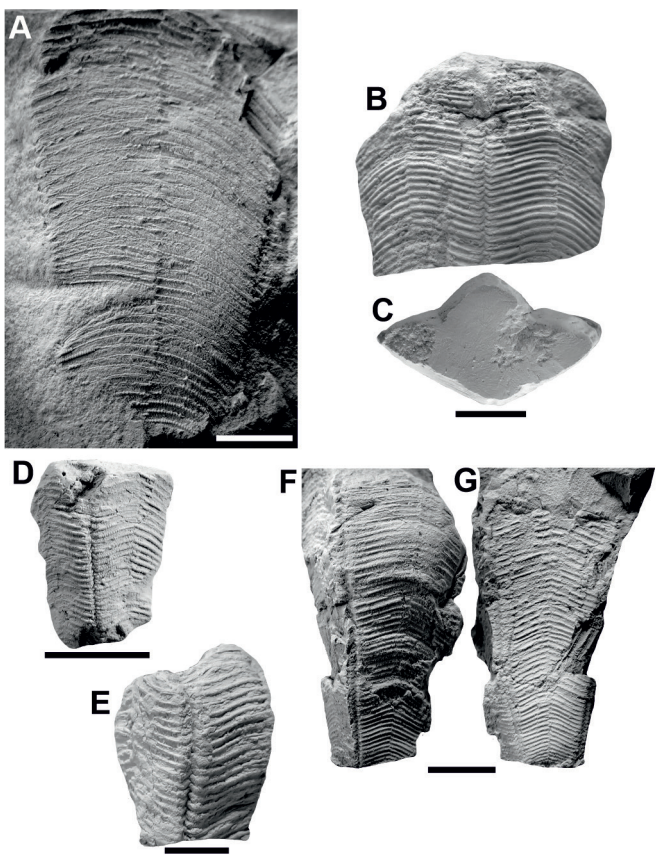

Figure 5. Conulariids from the collection NMNHU-G 1734 (revised definition). **A**–**C, E,** *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.*; **A**, specimen NMNHU-G 1734/09, face view; **B**–**C,** specimen NMNHU-G 1734/08; **B,** corner view; **C,** transverse cross section through the theca; **E,** specimen NMNHU-G 1734/05), corner view; **D,** *?Holoconularia rossica* Van Iten, Mironenko & Vinn, 2023, specimen NMNHU-G 1734/12, corner view; **F**–**G,** *Paraconularia quadrisulcata* (Sowerby, 1821), corner and facial views, respectively (specimen NMNHU-G 1734/01); scale bars = 5 mm.

Diagnosis. Transverse ribs moderately strong, faintly tuberculate, abruptly bent adaperturally at their terminations on the edges of the corner furrows; midline on the faces indicated only by slight deflection of the transverse ribs along it (after Moore & Harrington, 1956, p. F65).

Description. Specimens up to 90 mm in length. Maximum single face width of a specimen with a rhombic section is 18–23 mm; in the case of rectangular sections, the faces differ only slightly in width (20 and 23 mm), probably owing to secondary deformation of the theca. Apical angles 16–20°. Transverse ribs exhibit inflected circular curve style; transverse rib angles 9–16°, decreasing adaperturally; interrib angle 127° in the apical part, increasing to 138–143° adaperturally. Interspaces 2–3 times than the transverse ribs. Density of the transverse ribs in the apical part is 22 to 23 per 10 mm, while in the apertural part it decreases to 10–12 per 10 mm. Transverse ribs interrupted and alternating along the simple midline (Van Iten, 1992a). Transverse ribs bent slightly adaperturally on the shoulders of the shallow corner groove. Nodes rounded or round-oval, bearing an adapertural spine (*e.g.*, Fig. 7B, 7G); 8–12 nodes per 1 mm.

Remarks. In his description of the specimen originally described and illustrated by de Koninck (1883), de Koninck did not mention the presence of nodes on the transverse ribs, a feature included in the diagnosis of Moore and Harrington (1956). However, nodes are clearly visible on the specimens from the Donets Basin (Fig. 7G, 7H). Therefore, until we examine de Koninck's (1883) directly, we are inclined to treat this species as *sensu lato.*

Paraconularia inaequicostata (de Koninck, 1883) *s.l.*, like *Paraconularia quadrisulcata* (Sowerby, 1821), can reach large sizes and is characterized by variation in the shape of the transverse cross section, although the type specimen is regularly pyramidal. The main differences between *P. inaequicostata* (de Koninck, 1883) *s.l.* and *P. quadrisulcata* (Sowerby, 1821) are the inflected gothic curve style of the transverse ribs in *P. quadrisulcata* and the closer spacing of the transverse ribs in this species (from 20 to 36 per 10 mm in *P. quadrisulcata vs* from 10 to 23 per 10 mm in *P. inaequicostata*). In addition, *P. quadrisulcata* has very small nodes measuring *ca*. 0.05 mm in diameter, much smaller than the width of the transverse ribs (see also Sendino, 2009, p. 586–591, pls. 33–36; nodes are clearly visible in pl. 35, fig. 8). In *P. inaequicostata*, by contrast, the nodes are large and as wide as the transverse ribs (compare Figs. 7G and 9B). In our opinion, the most important difference between *P. quadrisulcata* and *P. inaequicostata* is the size of the nodes.

At least in the neotype of *Paraconularia irregularis* (de Koninck, 1843), nodes are absent or inconspicuous and the ends of the transverse ribs merge near the low raised midline (see Sendino, 2009, p. 584, pl. 32, figs. 1–3).

Stratigraphic range. Tournaisian of Belgium (de Koninck, 1883); uppermost Serpukhovian and lowermost Bashkirian of the Donets Basin (see Fig. 16); Bashkirian of the Dnipro-Donets Depression (Poletaev, 1974).

Paraconularia irregularis (de Koninck, 1843)

Figure 8

1843 *Conularia irregularis*; de Koninck, p. 496, pl. 45, figs. 2a–2b.

1956 *Paraconularia irregularis*; Moore & Harrington, p. F65, fig. 50.4.

2009 *Paraconularia irregularis*; Sendino, p. 356, pl. 32, figs. 1–3.

Neotype. Specimen NHM C 19616 in the Natural History Museum of London; Visean of Belgium (Sendino & Domínguez, 2006, p. 176, fig. 1; Sendino, 2009, p. 356, pl. 32, figs. 1–3).

Material. Five specimens (NMNHU-G 8590/06, 09, 10, 17, 23d) lacking the apex and aperture from the Zapal-Tyube Hill, Zhelvakova Ravine, Popova Ravine, Glybokyi Yarok, and Katerynivka localities.

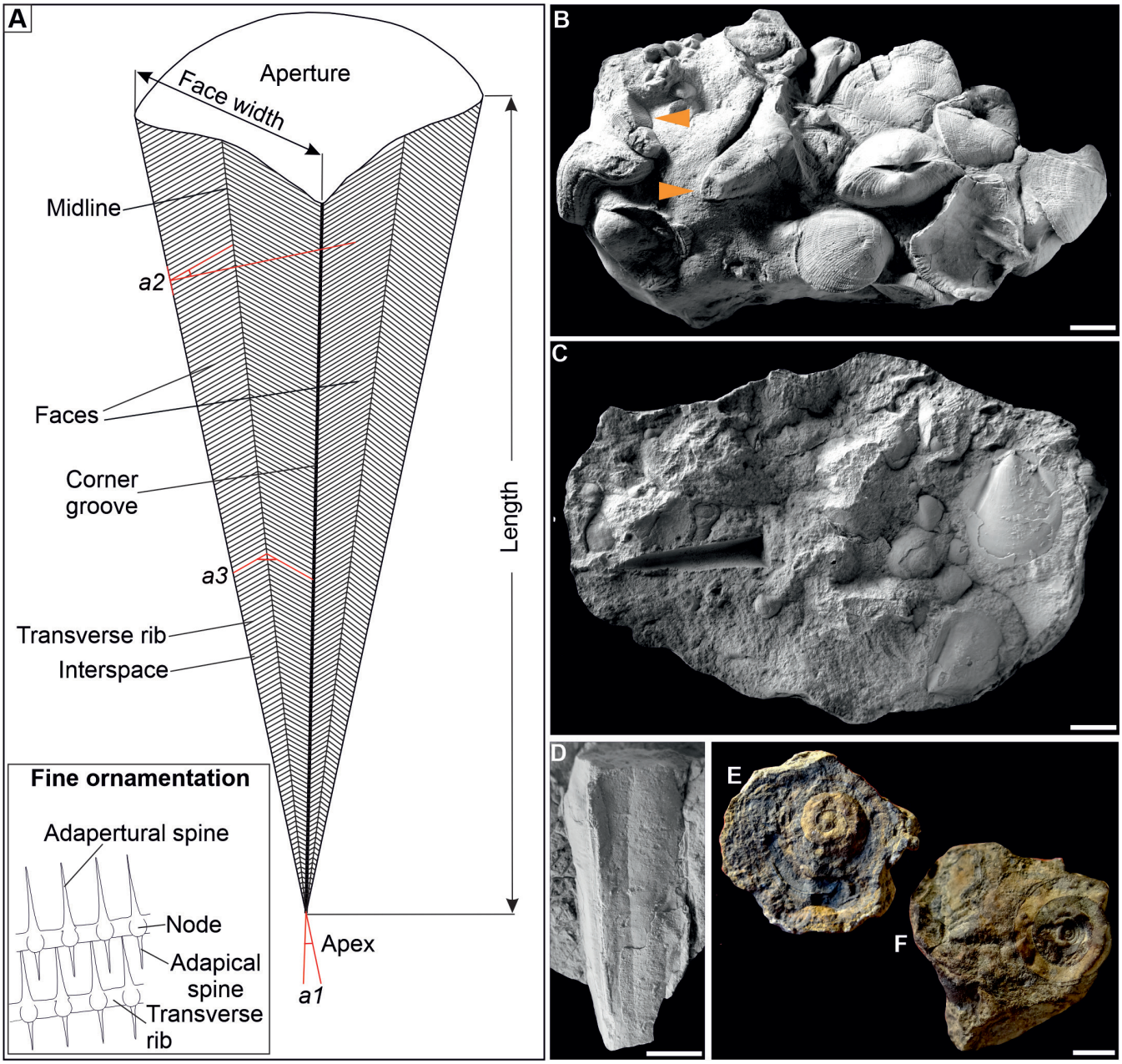

Figure 6. Morphology and taphonomic features of the studied conulariids. **A,** Basic morphological terminology of the conulariid periderm or theca (modified from Babcock & Feldmann (1986a, fig. 1) and Sendino & Bochmann (2021, fig. 5)); **B,** conulariids (arrows) co-occurring with the brachiopods *Schizophoria resupinata* (Martin, 1809) from the Zoryns'k locality; **C,** cluster of brachiopods, orthocerid nautiloids, and the bivalve *Pernopecten carboniferus* (Hind, 1897) in a limestone nodule from the Chorna Skelya locality; **D,** poorly preserved theca of Conulariida indet. (specimen NMNHU-G 8590/30); **E–F,** conulariid-bearing oncolites with ammonoid conchs from the Zhelvakova Ravine locality. Abbreviations: **a1**, apical angle; **a2**, rib angle; **a3**, interrib angle; scale bars = 10 mm (B–F).

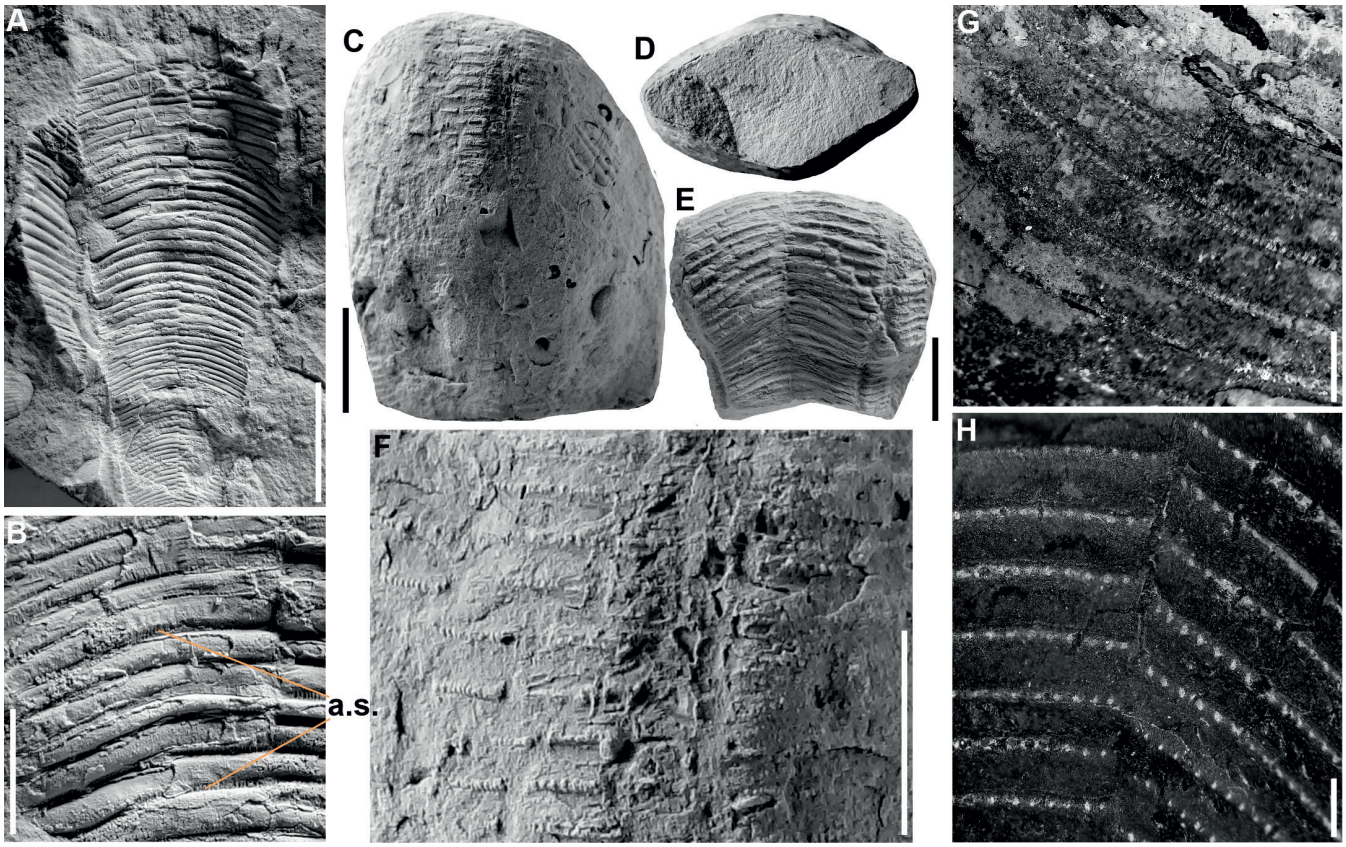

Figure 7. *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.* **A, B, G,** NMNHU-G 8590/11; **A,** general view of two adjacent faces (external mould); **B,** detail of Fig. 7A showing the adapertural spines (termed interspace ridges in Van Iten *et al.*, 1996) (**a.s.**); **G,** detail of Fig. 7A showing closely spaced nodes on the transverse ribs; **C, D, F,** NMNHU-G 8590/20; **C,** general view; **D,** transverse cross-section of the theca; **F,** fragment of the theca showing transverse ribs with nodes (detail of Fig. 7C); **E,** NMNHU-G 8590/12, apertural portion of the theca with partially preserved, lobate apertural lappets; **H,** NMNHU-G 8590/18, fragment of a single face with widely spaced nodes, external mold; scale bars = 10 mm (A, C, D, E), 5 mm (B, F), 1 mm (G, H).

Diagnosis. Thecae with an apical angle increasing from 14º to 23º toward the aperture. Wide and deep corner groove, crossed by transverse ribs that alternate within it. Facial midline marked by alternation of the ends of the transverse ribs and, possibly, by a slight ridge where the transverse ribs meet (after Sendino, 2009, p. 357; translated from the original Spanish).

Description. Specimens measure 18–32 mm long with rhombic or rectangular transverse cross-sections, maximum preserved width 12–14 mm. Apical angles 16–19°. Transverse ribs show gothic arch style, their width ranging from *ca*. 0.1–0.15 mm. Width of the interspaces *ca*. 0.4 mm, or 3–4 times greater than that of the transverse ribs. Transverse ribs number from 18–26 per 10 mm, their size and spacing increasing adaperturally. Rib angles 8–10° to 15°, interrib angles 148–150°, decreasing to 135° towards the aperture. Facial midline marked by a clear linear ridge measuring 0.2–0.3 mm wide and consisting of the thickened ends of transverse ribs that merge and alternate in some places. The height of the interspace ridges is slightly lower than the height of the transverse ribs. Specimen NMNH-G 8590/10 (Fig. 8D) shows a longitudinal, shallow slit that may correspond to an internal midline carina (after Van Iten, 1992a). Nodes mostly absent, faintly developed, interspaces with fine wrinkles in some places. Transverse ribs in the corner groove curved towards the aperture and alternate.

Remarks. In the original description of the species, de Koninck (1883) noted and figured transverse ribs having very small, indistinct nodes (see de Koninck, 1883, pl. 54, fig. 3) and without them (de Koninck, 1883, pl. 54, fig. 7). Therefore, our specimens fully correspond to the description and illustrations of the neotype (Sendino, 2009). The lack of clear nodes on the transverse ribs and the fusion of the transverse ribs on the midline distinguishes this species from similar Pennsylvanian *P. crustula* (White, 1880) and *P. magna* (Ries, 1949). These two species differ from *P. irregularis* in having the transverse ribs more widely spaced (14–18 per 10 mm in *P. crustula* and 14–16 per 10 mm in *P. magna*). In addition, the facial midline in the Pennsylvanian species is indicated by alternation of the transverse ribs. Moreover, examination of *P. crustula* revealed the presence of an internal carina at both the facial midline and the corners (Van Iten, 1992a). Finally, in *P. magna*, small nodes on the transverse ribs are visible in some places (see Fig. 11D).

Stratigraphic range. Visean of Belgium (de Koninck, 1843), upper Serpukhovian and lowermost Bashkirian of the Donets Basin (for details, see Fig. 16).

Paraconularia quadrisulcata (Sowerby, 1821)

Figure 5F, G; 9

1821 C*onularia quadrisulcata;* Sowerby, p. 107, pl. 260, figs. 4–5

v 1974 *Paraconularia* cf. *irregularis;* Poletaev, p. 69, pl. 14, figs. 1a, 1b, 2.

2009 *Paraconularia quadrisulcata*; Sendino, p. 364, pl. 33, figs. 4–8; pl. 34, figs. 1–8, pl. 35, figs. 1–9) *cum syn*.

Neotype. Specimen NHM C 3448 in the Natural History Museum of London; Coal Measures (Lower–Middle Pennsylvanian) of Salop in England. Described and figured by Slater (1907, p. 26, pl. 3, fig. 3). Selected by Sendino (2009, p. 364).

Diagnosis. Small apical angles, averaging 12º. Wide and deep corner groove, with transverse ribs that alternate interlacing. Midline marked by change of direction of transverse ribs. Transverse ribs bent adaperturally in the corner groove. Small nodes on transverse ribs, and more rarely adapertural interspace ridges. Lobate lappets type of closure (after Sendino, 2009, p. 366; translated from the original Spanish).

Material. Seven incomplete specimens (NMNHU-G 8590/22, 23a, 23b, 23c, 25, 27, 28) from the Novomoskovs'k, Popova Ravine, and Glybokyi Yarok Ravine localities. Specimen NMNHU-G 8590/23c preserves portions of the lobate apertural lappets.

Description. Specimens deformed to varying degrees, measuring up to 30 mm long and 14 mm wide (single face) and with rhombic and rectangular transverse cross sections. Apical angles range from 16° (minor faces) to 25° (major faces). Transverse ribs exhibit inflected circular curve style, numbering from 20 to 26 per 10 mm, their size and spacing increasing adaperturally.

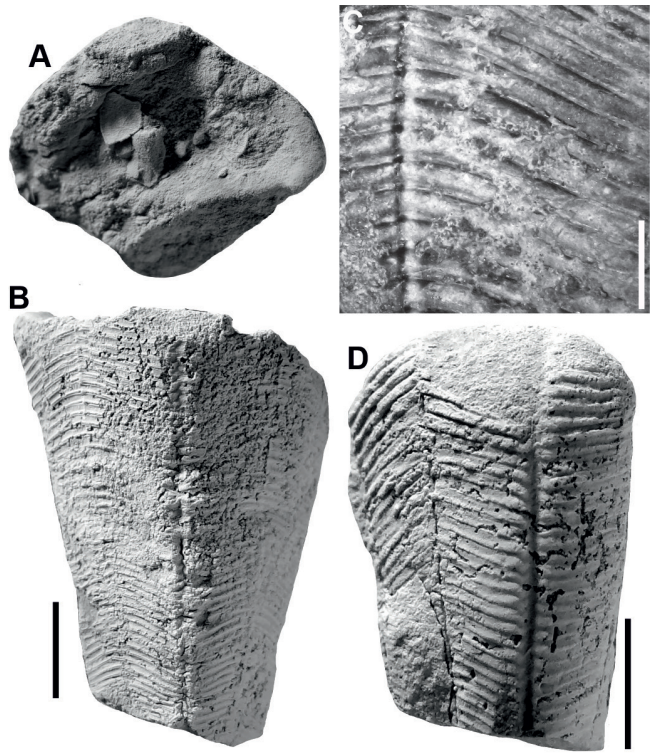

Figure 8. *Paraconularia irregularis* (de Koninck, 1843). **A**–**C**, NMNH-G 8590/06; **A,** corner view; **B,** transverse cross-section near the aperture; **C,** detail of the face showing articulation of the transverse ribs at the midline; **D,** NMNH-G 8590/10; corner view, the midline exhibits a shallow slit-like groove (trace of the single internal carina; Van Iten, 1992a); scale bars = 5 mm (A, B, D), 1 mm (C).

Thickness of the transverse ribs and interspaces *ca*. 0.15 mm and 0.3 mm, respectively. Transverse rib angles 7–14°, interrib angle *ca*. 140°. The midline in the form of alternating transverse ribs and an intermittent low ridge with thickness of 0.1 mm. Transverse ribs in the corner groove bent adaperturally, their ends bring arranged in alternation (Fig. 9D). Transverse ribs bear

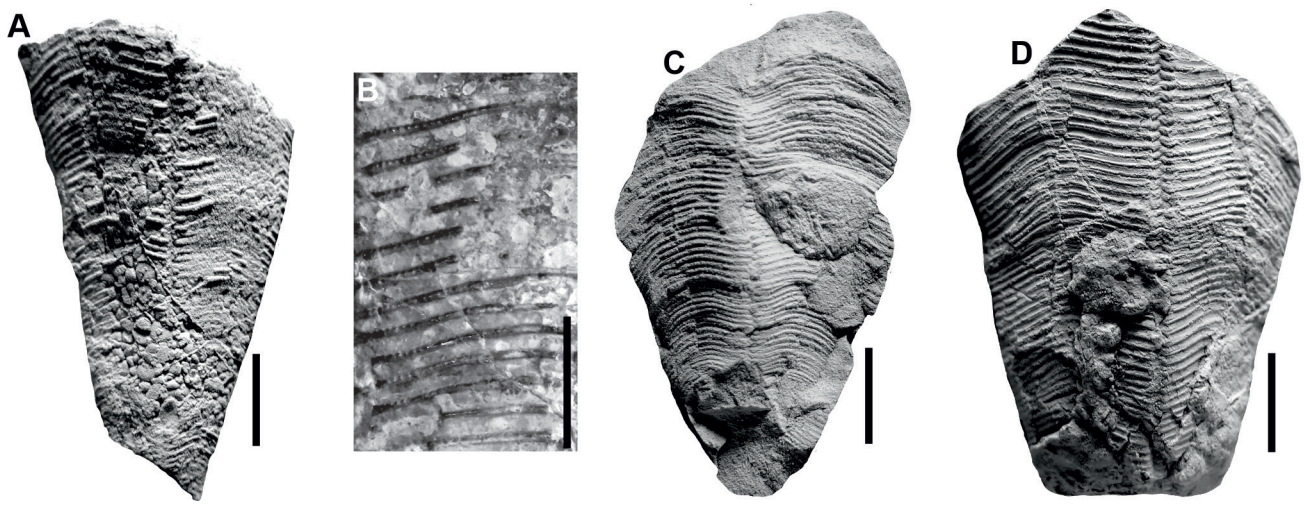

Figure 9. *Paraconularia quadrisulcata* (Sowerby, 1821). **A**–**C,** NMNH-G 8590/22; **A,** corner view; **B,** detail of a face (shown in Fig. A) showing the very small, closely spaced nodes; **C,** NMNH-G 8590/27, corner view; **D,** NMNH-G 8590/23; corner view; scale bars = 5 mm (A, C, D), 1 mm (B).

small, rounded nodes measuring *ca*. 0.05 mm in diameter, or about one third of of the transverse ribs thickness (Fig. 9B). Their density is from 5 to 8–10 per 1 mm. Oblique wrinkles inclined to the facial midline present in the interspaces near the apertural end.

Remarks. As shown in pl. 33, fig. 8 in Sendino (2009), *P. quadrisulcata* from the upper Visean of Bernician Ridsdale in England is similar in ornamentation to the specimens from Ukraine, which exhibit 5 nodes per 2 mm (20–45 per 5 mm; Sendino, 2009, p. 369), or close to the values for the specimens from England. The specimens from Ukraine differ from those from Belgium in being smaller.
Paraconularia irregularis (de Koninck, 1843) exhibits single midline carina and indistinct nodes on the transverse ribs (see above). *Paraconularia* cf. *irregularis*, described by Poletaev (1974, pl. 16, figs. 1, 2; see also Fig. 5F–5G in this paper), differs from our specimens in having a lower density of transverse ribs, namely 14–16 per 10 mm *vs* from 20 to 36 mm per 10 mm, as well as a lower density of small rounded nodes (4–6 per 1 mm *vs* from 5 to 10 per 1 mm).

Stratigraphic range. Upper Devonian to Carboniferous of Great Britain and Ireland (Sowerby, 1821). In the Donets Basin, this species ranges from the upper Serpukhovian to lowermost Bashkirian (see Fig. 16).

Paraconularia kohli Brew & Beus, 1976

Figure 10, 16D

1976 *Paraconularia kohli*; Brew & Beus, 1976, p. 891, pl. 1, figs. 20 and 23.
1977 *Paraconularia kohli*; Tucker & Paukstis, p. 501, text-fig. 1.

Holotype. Specimen ASUX-61 in the Arizona State University; Kohl Ranch section in central Arizona (USA), Naco Formation (Desmoinesian, Middle Pennsylvanian).

Material. One specimen (NMNHU-G 8590/21) without apex and aperture parts from the Gurkova Ravine locality.

Diagnosis. Transverse ribs bend abruptly toward aperture at terminations in corner furrows; adapically directed angle made by transverse ribs at mid-line, 140–150° (after Brew & Beus, 1976, p. 891).

Description. Fragment of the theca measuring 30 mm long, with a maximum single face width of 11 mm. Faces nearly equal in width. Apical angles *ca*. 18–20°. Transverse ribs exhibit inflected circular curve style, numbering 20–22 transverse ribs per 10 mm. Transverse rib angles 14°–16°, interrib angle *ca*. 134°, Transverse ribs and interspaces measure *ca*. 0.2 mm and *ca*. 0.2–0.3 mm wide, respectively. Facial midline marked by alternation of the ends of transverse ribs or by thickening of transverse ribs continue across the simple facial midline. Corner groove with well-

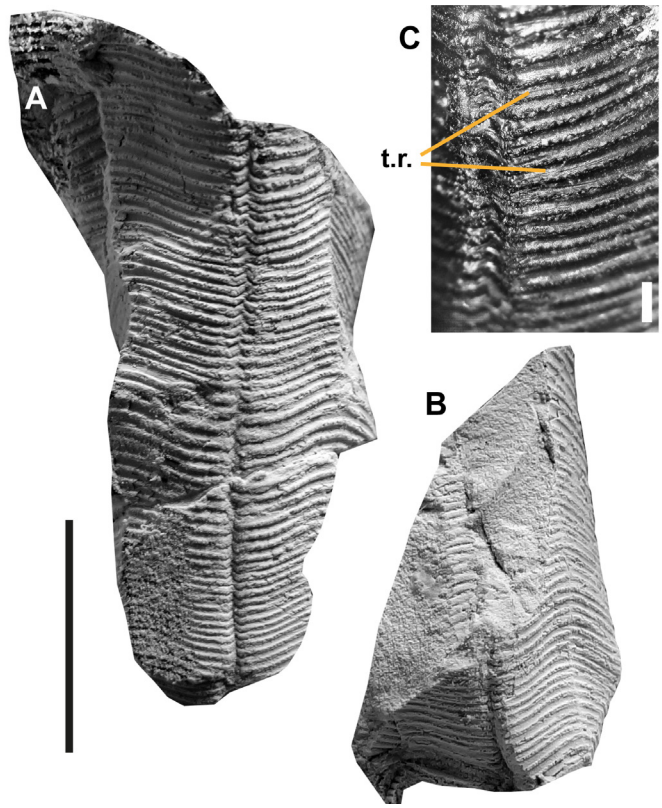

Figure 10. *Paraconularia kohli* Brew & Beus, 1976 (NMNHU-G 8590/21). **A**–**B,** two fragments of the same specimen (corner view); **C,** detail of 10A showing the adaperturally bent transverse ribs in the corner groove, small nodes on the transverse ribs, and thread-like ridges (**t.r.**) in some of the interspaces; scale bars = 5 mm (A, B), 1 mm (C).

defined, alternating thickened ends of transverse ribs bent adaperturally. Faint nodes present in places on the transverse ribs. Thread-like ridges (Brew & Beus, 1976) present in the interspaces (Fig. 10C).

Remarks. The specimen described above is very similar to the holotype of *Paraconularia kohli*. It differs from the similar species *P. irregularis* (de Koninck, 1842) in the expression of the simple facial midline. In addition, *P. irregularis* has narrow transverse ribs that are 3–4 times narrower than the interspaces. *Paraconularia kohli* differs from *P. crustula* (White, 1880) and *P. magna* (Ries, 1949) in having considerably wider transverse ribs. In the Ukrainian specimens, the transverse ribs are almost as wide as the interspaces.

Stratigraphic range. Desmoinesian (Middle Pennsylvanian) of Arizona and Missourian (Upper Pennsylvanian) of Illinois, USA (Brew & Beus, 1976; Tucker & Paukstis, 1977); uppermost Moscovian of the Donets Basin (see Fig. 16).

Paraconularia cf. *crustula* (White, 1880)

Figure 11

Material. Single, slightly deformed theca (NMNHU-G 8590/07) lacking both the apex and the aperture and collected from the Bulavin River locality.

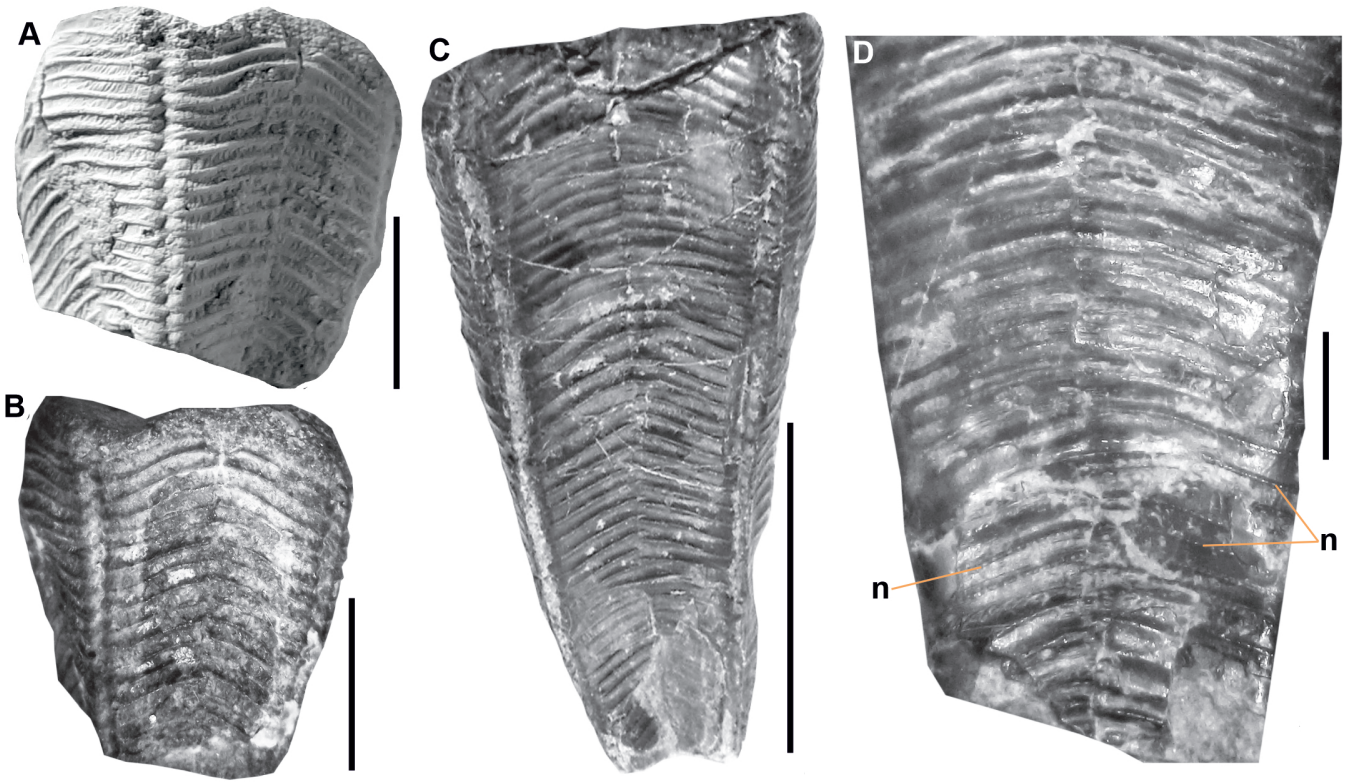

Figure 11. A–B, *Paraconularia* cf. *crustula* (White, 1880), NMNHU-G 8590/07; **A,** corner view; **B,** facial view; **C–D,** *Paraconularia magna* (Ries, 1949), NMNHU-G 8590/5a; **C,** facial view; **D,** detail of Fig. 11A showing small nodes (**n**) on the transverse ribs; scale bars = 10 mm (A–C), 2 mm (D).

Description. Incomplete specimen measuring 5.5 mm long. Maximum width of the major and minor faces 4.0 mm and 3.3 mm, respectively. Transverse cross section rectangular, with apical angles measuring 20° (major faces) and 16° (minor faces). Transverse ribs exhibit inflected gothic arch style. Facial midline marked by frequent alternation of transverse ribs, possibly with an internal carina (linear slits in the upper part of the specimen), interrib angle 135°. Transverse ribs number *ca.* 18 per 10 mm. Transverse ribs and interspaces measure *ca*. 0.2 mm and *ca*. 0.8 mm wide, respectively. Interspaces exhibit prominent, oblique and longitudinal wrinkles.

Remarks. The foregoing description agrees with the diagnosis of *Conularia crustula* White, 1880 *sensu* Shimer and Shrock (1944, p. 79), namely: "Small, with four sides equal; four angles distinctly furrowed, with slender median furrow also". Only the small number of available specimens prevents us from making a definitive identification of the Ukrainian specimens. Girty (1915, fig. 5) described and illustrated specimens bearing nodes; however, Girty's specimens probably belong to *Paraconularia magna* (Ries, 1949). *Paraconularia magna* was first described as *C. crustula* var. *magnus* from the upper shale in the Seminole Formation of Oklahoma (USA). In the holotype of this species, nodes are not always clearly visible (Branson, 1965). They are also not visible in the well-studied topotype specimens from Oklahoma (Mapes *et al.*, 1989). We have ten, well-preserved specimens of *P. magna* (specimens NMNHU-G 8590/5a to 5j) from Missourian strata at the type locality of this species in Okfuskee County, Oklahoma. These conulariids are characterized by convex faces, and just one specimen among them has well-developed, very small nodes (Fig. 11D). Therefore, *P. crustula* and *P. magna* probably are two independent species. *P. crustula* was studied in detail by Van Iten (1992a, 1992b), who demonstrated the presence of an internal carina at both the facial midline and the corners. At least the midline carina is present in the specimen from the Donets Basin.
Among European species, the one most similar to *Paraconularia* cf. *crustula* is *Conularia crustula* from the Namurian of Belgium, described and illustrated by Demanet (1941, p. 242, pl. 16, fig. 28). Of particular note is the presence of wrinkles in the interspaces between the transverse ribs. At the same time, *C. crustula* does not show a clear midline.

Stratigraphic range. Moscovian of the Donets Basin (see Fig. 16). *Paraconularia crustula* described from the Desmoinesian of Oklahoma, USA. "*Conularia crustula*" from the Middle Wewoka Member (Middle Pennsylvanian) of Oklahoma also figured by Sendino *et al.* (2023, text-figs. 1 and 5).

?*Paraconularia* cf. *subulata* (Hall, 1858)

Figure 12

Material. Single specimen (NMNHU-G 8590/33) from the middle Visean black shale at the Kotel'va locality and lacking the apex and aperture.

Description. Small conulariid with a rounded square cross section, 6.5 mm in length, minimum width 1.3–1.4 mm, maximum width 2.5–2.8 mm. Apical angle 12°. Transverse ribs of the gothic arch style extend into the shallow corner groove without bending adaperturally. The ends of the transverse ribs in the corner groove from one face alternate with those from the adjoining face.

Transverse ribs number 6 per 1 mm and 25 per 5 mm, alternating along the simple facial midline. Transverse ribs very thin (*ca*. 0.05 mm), interspaces *ca.* 0.15 mm wide. Transverse rib angle measures 14–15°, interrib angle 140°. Nodes small and inconspicuous.

Remarks. ?*Paraconularia* cf. *subulata* is very similar to the lectotype of *P. newberryi* (Winchell, 1865), which was selected and illustrated by Driscoll (1963, p. 34, pl. 1, figs. 1–8) and then also illustrated by Babcock and Feldman (1986b, figs. 29.2 and 29.3). These illustrations clearly show the absence of adaperture bending of the transverse ribs in the corner groove in the lectotype, as in our specimen. This characeristic disagrees with the original diagnosis of the genus *Paraconularia* (Moore & Harrington, 1956), but is consistent with the diagnosis of this genus by Babcock and Feldman (1986b, p. 412). The latter authors placed *P. newberryi* in synonymy with *P. subulata* (Hall, 1858). Winchell (1865, p. 130) described *P. newberryi* sp. nov. as "*shell very small*…". Driscoll (1963, p. 35) stated that the length of the specimens is greater than 13 mm, with the paratype measuring 75 mm in length. The limited available material does not allow us to identify the Ukrainian specimens with a high degree of confidence. *Paraconularia* cf. *subulata* described from the Mississippian of Mexico by Escalante-Ruiz *et al.* (2014, p. 199, figs. 3M–3R, 4A–4N and 5A–5I) is similar to specimen NMNHU-G 8590/33 but differs from it in having a much lower density of the transverse ribs (5–18 per 10 mm *vs* 50 per 10 mm).

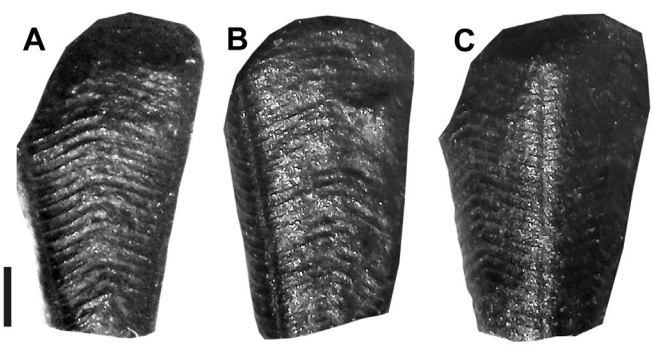

Figure 12. ?*Paraconularia* cf. *subulata* (Hall, 1858), NMNH-G 8590/33. **A,** minor face; **B,** major face; **C,** corner view; scale bar = 1 mm.

Stratigraphic range. Middle Visean of the Dnipro-Donets Depression. *Paraconularia subulata* is known from the Lower Mississippian of Illinois, Indiana, Kentucky, Montana, and Ohio, USA (Babcock & Feldman, 1986b). *Paraconularia* cf. *subulata* is widespread in the upper Tournaisian–upper Visean of Mexico (Escalante-Ruiz *et al.*, 2014). The holotype of *P. newberryi* (Winchell, 1865) is from the Michigan Formation in the Mississippian Waverly Group.

Paraconularia lata n. sp.

Figure 13

v 1974 *Paraconularia* aff. *inaequicostata* (de Koninck, 1883); Poletaev, p. 73, pl. 14, fig. 4a, 4b.

v 2003 *Paraconularia inaequicostata* (de Koninck), 1883; Ogar & Furdui, p. 27, text-figs. 1–6.

Holotype. Specimen NMNHU-G 1734/11 in the Geological Department of the National Museum of Natural History of the NAS of Ukraine, Kyiv; Ukraine, Luhansk Region, town of Kadiyivka (L_6 limestone in the Almazna Formation, Moscovian). Selected here; illustrated by Poletaev (1974, pl. 14, fig. 4a, 4b).

Other material. Syntype NMNHU-G 8590/32 in the Geological Department of the National Museum of Natural History of the NAS of Ukraine, Kyiv; Ukraine, Luhansk Region, town of Sokolohirs'k, Gurkova Ravine (M_7 limestone in the Gorlivka Formation, Moscovian).

Diagnosis. Faces equal in width, length up to 80 mm, apical angles 20–28°. Facial midline marked by the thickened ends of alternating transverse ribs. Nodes rounded and numbering 4–6 per 1 mm.

Etymology. After *latus* (Lat.) – wide (because of the wide faces).

Description. Specimens measure 59–80 mm in length, maximum single face width 28 mm. Apical angles 20–28°. Rib articulation in infected gothic arch style, rib angles 11–15°, interrib angle up to 140°. Simple facial midline marked by alternation of the ends of interrupted transverse ribs and their thickened ends. Transverse ribs number 14–26 (average 18) per 10 mm, their spacing increasing towards the aperture. Width of the transverse ribs *ca*. 0.1–0.15 mm; width of the interspaces *ca*. 0.5 mm. Nodes rounded, numbering 4–5 per 1 mm at a single face width of 23 mm. The ends of the transverse ribs in the corner groove are thickened and bent towards the aperture.

Remarks. Examination of the original material of the Uralian conulariids (collection NMNHU-G 2209) described by Ogar and Furdui (2003) showed that they are conspecific with *Paraconularia lata* n. sp. In both samples, the apical angles range from 20° to 28°, the spacing of the transverse ribs ranges from 12 to 32 per 10 mm, the spacing of nodes is 4–6 per 1 mm, and the

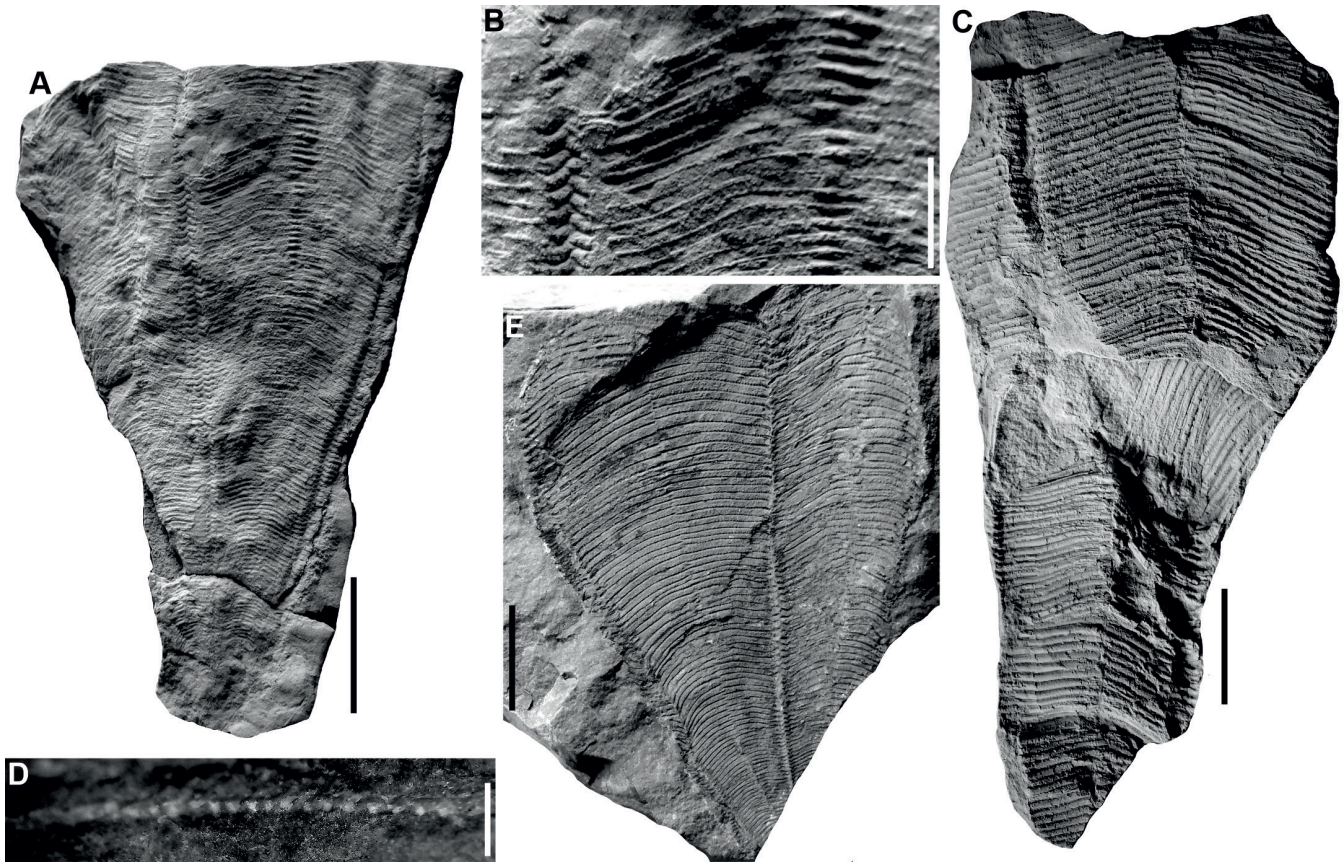

Figure 13. *Paraconularia lata* n. sp. **A**–**B,** NMNH-G 1734/11, holotype, Luhansk Region, town of Kadiyivka, L_6 limestone in the Almazna Formation, Moscovian; **A,** face view; **B,** detail of Fig. 13A showing corner groove with alternating, adaperturally bent transverse ribs, small nodes on the transverse ribs, and the facial midline; **C**–**D,** NMNH-G 8590/32, syntype; **C,** general view of internal (upper part) and external (lower part) moulds; **D,** detail of Fig. 13C showing nodes on a transverse rib (fragment of the periderm); **E,** NMNH-G 2209/5, Southern Urals (Bashkortostan), Zilim River near the village of Tashasty, Zilimian Horizon, Moscovian; external mould of two adjacent faces; scale bars = 10 mm (A, C, E), 5 mm (B), 1 mm (D).

simple facial midline. *Paraconularia lata* n. sp. differs from *P. inaequicostata* (de Koninck, 1883) in having larger apical angles (16–20° in *P. inaequicostata vs* 20–28° in *P. lata* n. sp.) and in the facial midline indicated by frequent alternation of the transverse ribs. Compared with *Paraconularia hollebeni* (Geinitz, 1853) from the Zechstein (Lopingian) of Germany (see Babcock *et al.*, 1987, fig. 7B) and the Kazanian Stage of the Volga-Ural Region and its possible synonyms (for example *Paraconularia kazanensis* Weldon & Shi, 2003), *Paraconularia lata* n. sp. has wider faces (apical angle in *P. kazanensis* only 17°) and a less prominent midline.

Stratigraphic range. Moscovian of the Donets Basin (see Fig. 16) and Southern Urals, Bashkortostan (Ogar & Furdui, 2003).

Genus *Holoconularia* Hergarten, 1985

Type species. *Conularia hummeli* Kegel, 1926 from the Lower Devonian (Pragian) of southern Germany; by original designation.

Diagnosis. Distinctly developed transverse ribs, more or less closely spaced, at the corners curving gently into the well-developed sulcus. Within the corner sulcus the transverse ribs are interrupted and alternate (translated from the original German by Van Iten *et al.* (2023, p. 317)).

?*Holoconularia rossica* Van Iten, Mironenko & Vinn, 2023

Figure 5D, 14, 16A–16C

v 1974 *Paraconularia tubericosta*; Poletaev, p. 74, pl. 14, fig. 3a–3c.
2023 ?*Holoconularia rossica*; Van Iten, Mironenko & Vinn, p. 314, text-figs. 2–5.

Holotype. Specimen PIN 5824/01 in the Borissiak Palaeontological Institute (Moscow). Russia, Kaluga Region, Borshchevsky Quarry (lower Dashkovka Member of the Gurovo Formation, early Serpukhovian).

Material. Eight specimens (NMNHU-G 8590/08, 14–16, 19, 24, 29a, 29b); lobate apertural lappets preserved in the specimens NMNHU-G 8590/14 and NMNHU-G 8590/24.

Diagnosis. Conulariids with finely nodose, trochoidal (longitudinally) transverse ribs numbering 2–6 per 1 mm and terminating within the corner sulcus, with slight or no adapertural bending of their end portions,

and with the end portions from one face alternating with those from the adjoining face; transverse ribs broadly bell-curve-shaped to sub-angulate, continuous across the facial midline or disrupted and arranged in alternation along this feature. Nodes subrectangular, longitudinally elongate, crossed by broadly U-shaped transverse furrows and generally numbering between *ca.* 8 and 20 per 1 mm. Interspaces lack interspace ridges, exhibiting instead irregular transverse, oblique, and longitudinal fine wrinkles (after Van Iten *et al.*, 2023, p. 314).

Description. Narrowly pyramidal thecae with rhombic, rectangular, or nearly square cross-sections. Apertural

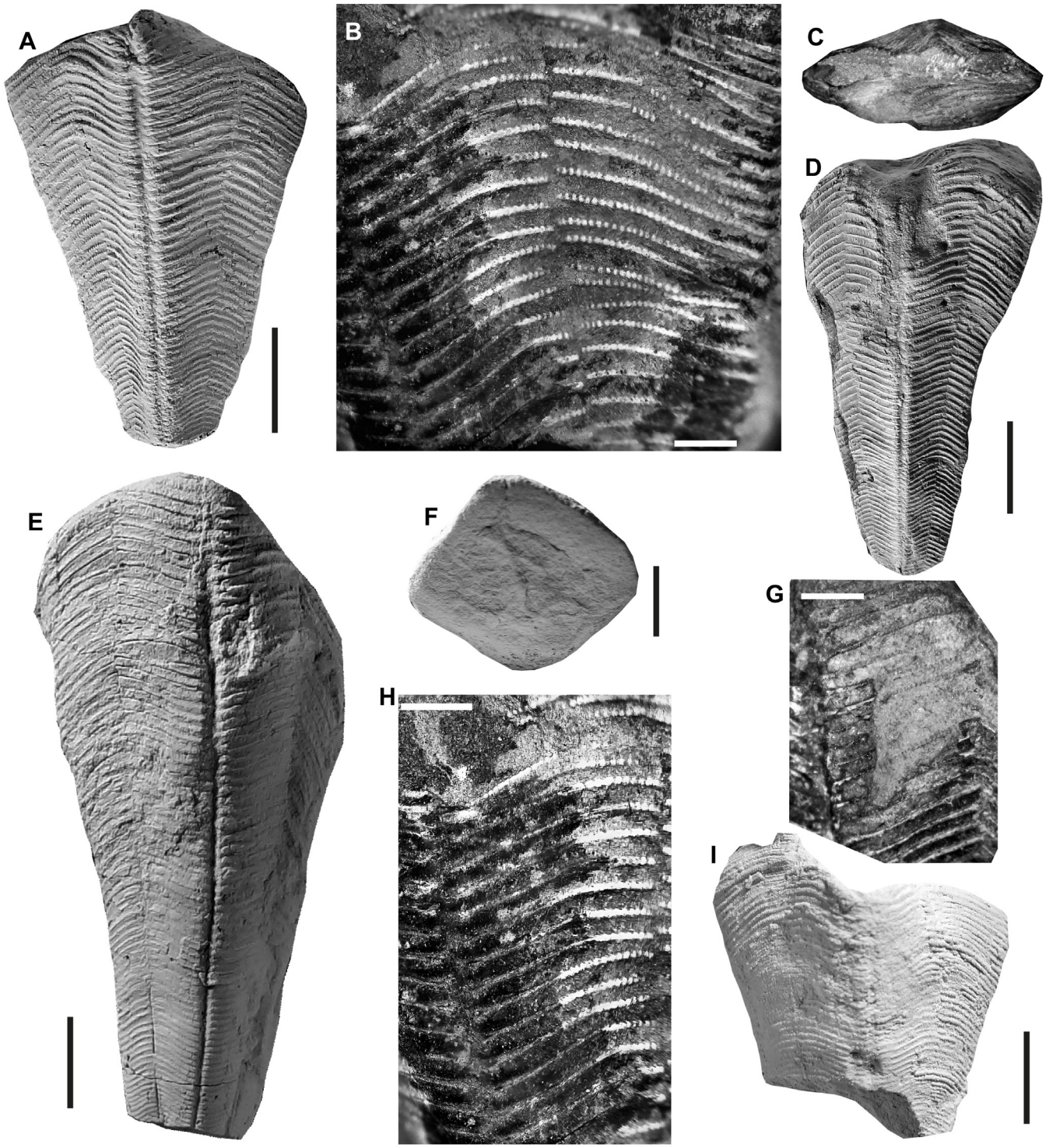

Figure 14. ?*Holoconularia rossica* Van Iten, Mironenko & Vinn, 2023, NMNH-G 8590/14. **A,** corner view with partly preserved lobate lappets in the aperture part; **B,** enlarged from Fig. 14A area showing rectangular nodes on the ribs and midline; **C–D,** NMNH-G 8590/24; **C,** top view, aperture with fragments of lobate lappets; **D,** corner view; **E–H,** NMNH-G 8590/08; **E**, corner view; **F,** top view; **G,** enlarged from Fig. 14E area showing nodes in outer (ectoderm) and inner layers; **H,** enlarged from Fig. 14E area with the corner grove; **I,** NMNH-G 8590/29; corner view; scale bars = 5 mm (A, C–F, I), 1 mm (B, G, H).

lappets semicircular. Specimens from 24 mm (NMNHU-G 8590/24) to 35 mm (NMNHU-G 8590/08) in length, with a maximum single face width of 14 mm. Apical angles 16–24°. Transverse ribs exhibit inflected gothic arch style, with 18–38 transverse ribs per 10 mm, their spacing being smallest near the apical end and greatest near the aperture. Transverse rib angles 9–11°, interrib angles range from 122° to 134°, increasing towards the aperture. Transverse ribs alternate along the facial midline, in the corner groove they do not connect and their ends are slightly adaperturally bent. A thin linear slit (perhaps a trace of the internal carina) is visible in the apical part of specimen NMNH-G 8590/08 (Fig. 14E). Nodes well developed but present only in the outer portion of the theca (see, for example, Fig. 14G). Nodes round-rectangular, elongated perpendicular to the transverse ribs and equal to the transverse ribs in width at *ca*. 0.1 mm. Transverse ribs number *ca*. 7–17 per 1 mm. Interspaces measure 0.3 mm width, often showing obliquely transverse wrinkles.

Remarks. The specimens described above agree well with the diagnosis of the species and with the descriptions of the holotype and paratypes. We did not, however, observe any micropores (Ford *et al.*, 2016; Van Iten *et al.*, 2023), but this may be an artifact of preservation. Specimen NMNHU-G 1734/12, described by Poletaev (1974, p. 74, pl. 14, fig. 3a–3c), exhibits adapertural bending of the ends of some of the transverse ribs in the corner groove, which deflection is a characteristic of the genus *Paraconularia*. However, both in the Ukrainian specimens and in the type material, such bending is not the rule.

Stratigraphic range. Lower Serpukhovian of the Moscow Basin (Russia) and the upper Serpukhovian–lowermost Bashkirian of the Donets Basin (see Fig. 16).

?*Holoconularia poletaevi* n. sp.

Figure 15

Holotype. Specimen NMNHU-G 8590/01a in the Geological Department of the National Museum of Natural History of the NAS of Ukraine, Kyiv; Ukraine, Luhansk Region, town of Zoryns'k, right bank of the Lozova River just east of the Nikanor coal mine (L_7 limestone, Almazna Formation, Moscovian).

Paratypes. Specimen NMNHU-G 8590/01b was found in the same rock sample as the holotype; specimen NMNHU-G 8590/04 from the N_1 limestone in the Isayivka Formation, Moscovian (Donetsk Region, left bank of the Sadky River near the village of Sofiivka).

Etymology. In honour of palaeontologist Dr Vladyslav Poletaev, the first person to describe the Carboniferous conulariids of the Donets Basin.

Diagnosis. Small conulariid up to 15 mm long with equal faces in width, apical angles 18–28°, transverse rib angles up to 17°, interrib angles 138–142°. Gothic arch-type transverse ribs spaced 4–5 per 1 mm, frequently disrupted and arranged in alternation along the facial midline. In the corner groove transverse ribs interrupted and alternate, their end portions being straight or bent slightly towards the aperture. Nodes well developed, subrectangular, numbering 10–12 per 1 mm.

Description. Small conulariid, 10 mm long (holotype) and 13.5–15.0 mm long (paratypes). Maximum width 6–7 mm. Transverse cross-sections nearly square. Apical angles range from 18° to 28°. Transverse ribs gothic arch or inflected gothic arch style. The rib angle 10–11° to 14–17°, transverse ribs angle 138–142°, decreases towards the apical part to 124°. The frequency of transverse ribs 20–26 per 5 mm (4–5 per 1 mm). Nodes well-developed, numbering 10–12 per 1 mm. Their shape is roundly rectangular, with the long side in the direction to the aperture, corresponding to the thickness of the transverse ribs. The thickness of the transverse ribs *ca.* 0.1 mm, interspaces *ca.* 0.3 mm. Striae and wrinkles in the interspaces not observed. Facial midline defined mainly by alternating transverse ribs, as well as by a sharp bend of continuous transverse ribs. Ends of the transverse ribs in the corner groove alternate, being straight or slightly bent adaperturally.

Remarks. ?*Holoconularia mosquensis* (Vorozhbitov & Alekseev in Alekseev, 2001) has a strongly rectangular cross-section, small apical angles (5–7° for the minor faces and 9–13° for the major faces), as well as a much lower density of transverse ribs (1.7–1.9 per 1 mm) and nodes (5–8 per 1 mm). ?*Holoconularia rossica* Van Iten, Mironenko & Vinn, 2023 also has low apical angles (11–19°) and closely spaced transverse transverse ribs (2–6 per 1 mm), but the density of the nodes is high (8–20 per 1 mm compared to 10–12 in ?*Holoconularia poletaevi* n. sp.).

Stratigraphic range. Moscovian of the Donets Basin (see Fig. 16).

Conulariida indet.

Figure 6D

Material. One poorly preserved specimen (NMNHU-G 8590/30); Lviv Palaeozoc Trough locality.

Description. Deformed internal mold with a maximum length of 31 mm without apical part and aperture. Imprints of the side faces in a probably rectangular cross-section make an angle close to a right one. Faces with a maximum width of up to 12 mm, apical angle 15°. The trace of the midline in the form of an indistinct linear depression, placed asymmetrically. The imprint of the midline has a width of 0.5 mm and is manifested in the

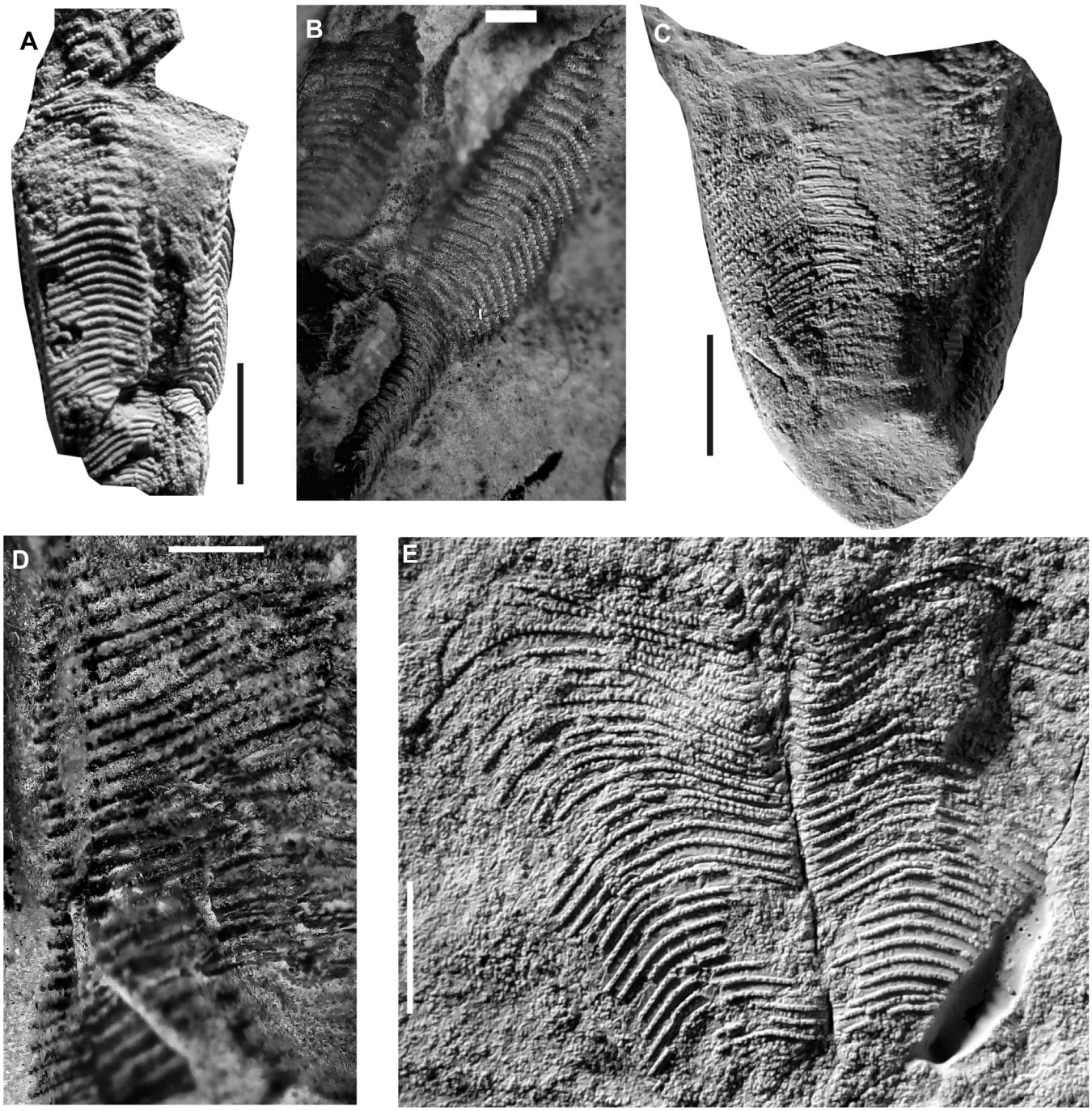

Figure 15. ?*Holoconularia poletaevi* n. sp. **A**–**B,** NMNH-G 8590/01a, holotype, Luhansk Region, the town of Zoryns'k, right bank of the Lozova River just east of the Nikanor coal mine (the L_7 limestone layer, Almazna Formation, Moscovian); **A,** general view; **B,** enlarged from Fig. 15A area showing rectangular nods on the ribs; **C**–**D,** NMNH-G 8590/01b paratype in the same rock specimen; **C,** general view; **D,** corner groove and nodes on the ribs, enlarged from Fig. 15C; **E,** NMNH-G 8590/04, paratype, view of two adjacent faces; scale bars = 5 mm (A, C, E), 1 mm (B, D).

form of a linear furrow, which separates the imprints of two adjacent faces. In some places, indistinct internal impressions of the longithudinal ribs, penetrating into the corner groove, are visible.

Remarks. The described specimen is the first record of a Carboniferous conulariiid in the Lviv Palaeozoic Trough. Poorly preserved specimens of *Paraconularia* sp. (Korejwo, 1986, pl. 1, fig. 1) and *Conularia* cf. *destinezi* Moreels, 1888 (Korejwo & Teller, 1972, pl. 1, figs. 3, 4) were recorded in the Namurian A (Serpukhovian) of the Lublin Basin in Poland. Korejwo (1958, 1960) reported *Conularia* sp. in the Namurian B (early Bashkirian) of the Lublin Basin, but did not describe or figure these fossils. Unfortunately, it is not possible to compare Conulariida indet. described here with the aforementioned conulariids owing to the poor preservation of the available material.

DISCUSSION AND CONCLUDING REMARKS

Summary of the stratigraphic distribution of the conulariids in the Donets Basin

Paraconularia and ?*Holoconularia* occur in two intervals in the Donets Basin (Fig. 16). The first interval comprises the upper Serpukhovian and lower Bashkirian (the Kalmius Formation and the lower part of the Amvrosiyivka Formation), and includes the Mississippian–Pennsylvanian boundary (located in the D_5^{8Upper} limestone based on conodont biozonation (Nemirovskaya *et al.*, 1990, 1992)). Four species occur within these strata, namely *Paraconularia inaequicostata* (de Koninck, 1883) *s.l.*, *P. irregularis* (de Koninck, 1843), *P. quadrisulcata* (Sowerby, 1821), and ?*Holoconularia rossica* Van Iten *et al.*, 2023.

The second stratigraphic interval comprises the upper part of the Moscovian (Almazna, Gorlivka and the lower part of the Isayivka Formation) and contains four conulariid species, two of which are new. These are *Paraconularia kohli* Brew & Beus, 1976, *P.* cf. *crustula* (White, 1880), *P. lata* n. sp., and ?*Holoconularia poletaevi* n. sp.

The portion of the succession between the two conulariid-bearing intervals comprises large parts of the Bashkirian and Moscovian. Likewise, conulariids have not been reported from the Tournaisian, Visean, and a large part of the Serpukhovian (Mississippian), as well as from the Kasimovian and Gzhelian (Upper Pennsylvanian), in spite of extensive sampling by palaeontologists over many years.

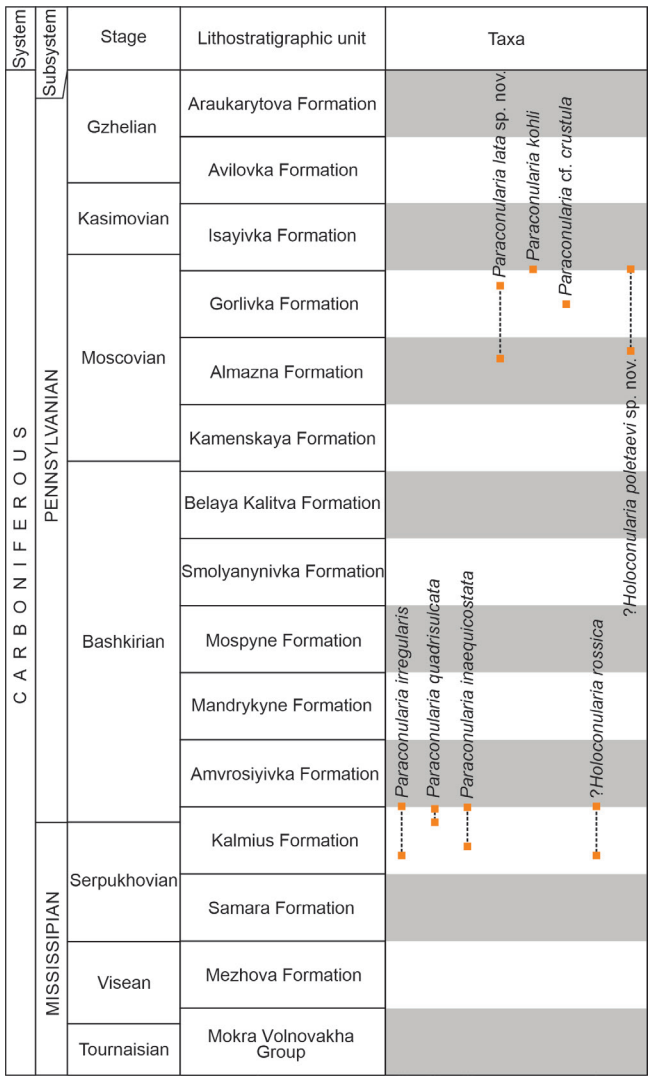

Figure 16. Stratigraphic distribution of the studied conulariid taxa in the Carboniferous succession of the Donets Basin.

Taphonomy, palaeoecology, and palaeobiogeography

Two of the specimens examined here (NMNHU-G 1734/04 and NMNHU-G 8590/24) exhibit possible sublethal injuries consisting of shallow conical pits measuring 0.7–1.0 mm in diameter and located on the faces (Fig. 17). Similar pits were described and figured by Mapes *et al.* (1989) in *Paraconularia magna* (Ries, 1949) from the Pennsylvanian of Oklahoma, USA. Mapes *et al.* (1989) interpreted these pits as sublethal injuries caused by fishes such as species of the genus *Symmorium*. Similar features, interpreted as shell punctures inflicted by cartilaginous fishes, occur on the shells of Pennsylvanian cephalopods from the USA (Mapes & Hansen, 1984).

At present there are no records of fossil fishes from the deposits bearing conulariids showing possible signs of injury, but collections in the Department of Palaeontology and Stratigraphy of the Palaeozoic Sediments (IGS NASU, Kyiv) do contain several

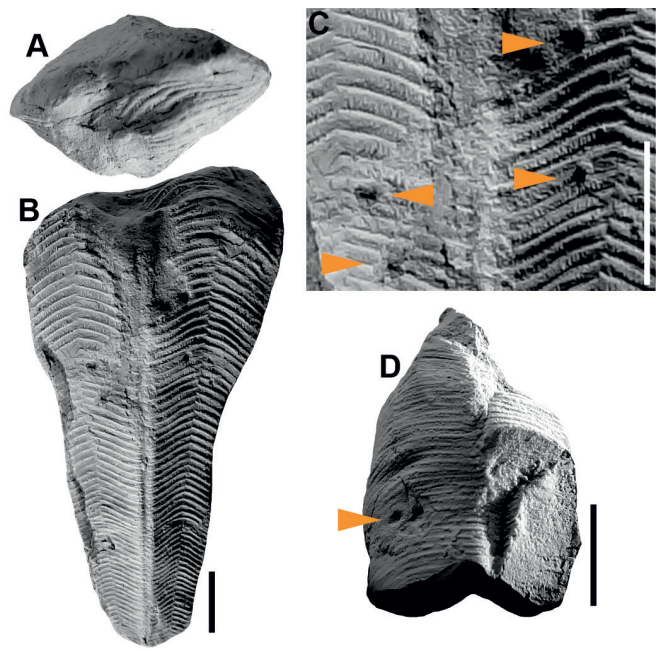

Figure 17. Possible injuries (arrowed) of conulariids. **A–B,** ?*Holoconularia rossica* Van Iten *et al.* 2023, NMNHU-G 8590/24; **A,** apertural view; **B,** corner view; **C,** enlarged part of Fig. 17B; **D,** *Paraconularia kohli* Brew & Beus, 1976 (NMNHU-G 1734/04, corner view); scale bars = 5 mm.

bradyodont dental plates and a fragment of a fin spine similar to the genus *Ctenacanthus* (identification by VSD). However, we cannot confidently attribute the pits on the surface of specimens NMNHU-G 1734/04 and NMNHU-G 8590/24 to lethal attacks by fishes, as the available material is limited. Finally, the surface of specimen NMNH-G 8590/10 (Fig. 8D) has elongate thin holes measuring 0.1–0.3 mm and which may be bioerosion trace fossils.

The observed, uneven stratigraphic distribution of conulariids may reflect peculiar habitat requirements and consequent facies dependence (see also Van Iten *et al.*, 1996). Indeed, the overwhelming majority of conulariids in the Donets Basin occur in argillaceous limestones and marls. This pattern was confirmed by the field observations of the first author (VVO) in the conulariid-bearing Carboniferous deposits on the western slope of the Southern Urals. As in the Donets Basin, *Paraconularia lata* n. sp. in the Southern Urals occurs in a light gray, fine-grained, marl-like limestone. In organogenic and bioclastic limestones, by contrast, conulariids are extremely rare.

Occurrences of the same species of conulariids in Upper Mississippian and Lower Pennsylvanian deposits in the Donets Basin suggest that these organisms were shielded from or able to survive global events which occurred at the Mississippian–Pennsylvanian boundary and brought about substantial changes in the taxonomic composition of most faunal groups (so-called minor mass extinctions).

By conrast, many species and genera of corals, brachiopods, bivalves, ammonoids, and conodonts do not cross the Mississippian–Pennsylvanian boundary in the Donets Basin sections (Popov, 1979; Sergeeva, 1983; Aisenverg & Poletaev, 1983; Astakhova, 1983; Nemirovskaya *et al.*, 1990, 1992; Fedorowski, 2022).

Similarly, the presence of several North American conulariids in the Carboniferous of the Donets Basin and the Dnipro-Donets Depression points to a certain amount of faunal interchange between these parts of Eurasia and the central portions of cratonic North America.

Supplementary information. New taxonomic names proposed in this paper, and the nomenclatural acts it contains, have been registered in ZooBank, the online registration system for the ICZN: https://zoobank.org/References/176860c0-ebd2-4f50-a6ce-5097c4669867.

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