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Shell injuries in *Densepustula* LAZAREV, 1982, Pennsylvanian productidine brachiopod from the Donets Basin, Ukraine

Vitaly DERNOV [1]

Abstract: Nine injured ventral valves of productidine brachiopods belonging to the genus *Densepustula* LAZAREV, 1982, from the Mospyne, Smolyanynivka, Belaya Kalitva, and Kamensk formations (Upper Bashkirian-lower Moscovian, Lower and Middle Pennsylvanian) of the Donets Basin (eastern Ukraine) were studied. Three morphological types of damage traces have been recognized: Type A) longitudinal, sublongitudinal, and transversal thin straight or sinuous furrows, about 5-7 mm long and 0.5-1.5 mm thick; Type B) rounded and ellipsoidal pits, about 3-4 mm in diameter, located on the umbo, the anterior margin of the ventral valve, and the lateral slopes of the ventral valve; and Type C) irregularly-shaped dimples on the anterior margin and in the sulcus, 2-3 mm in size. These injuries are present on 9 out of 61 (15%) of ventral valves studied, but entirely absent from dorsal valves (0 out of 25). The most likely producers of these damage traces are cartilaginous fishes and parasites of unclear affinity.

Keywords:

- Productida;
- Carboniferous;
- shell injuries;
- palaeoecology

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Résumé : *Lésions de la coquille chez* Densepustula *LAZAREV, 1982, brachiopode productidiné du Pennsylvanien du Bassin du Donetsk, Ukraine.-* Cette étude porte sur neuf valves ventrales endommagées du brachiopode productidiné *Densepustula* LAZAREV, 1982, récoltées dans les formations de Mospyne, Smolyanynivka, Belaya Kalitva et Kamensk (Bashkirien supérieur et du Moscovien inférieur, Pennsylvanien inférieur et moyen) du bassin du Donets (Ukraine orientale). Trois types morphologiques de lésions ont été identifiés : Type A) sillons longitudinaux, sublongitudinaux et transversaux minces, droits ou sinueux, d'environ 5-7 mm de longueur et 0,5-1,5 mm d'épaisseur ; Type B) fosses arrondies et ellipsoïdales, d'environ 3-4 mm de diamètre, situées sur l'umbo, le bord antérieur de la valve ventrale et les pentes latérales de la valve ventrale ; Type C) fossettes de formes irrégulières sur le bord antérieur et dans le sulcus, d'une taille de 2-3 mm. Ces marques sont présentes sur 9 des 61 (15%) valves ventrales étudiées, mais absentes les 25 valves dorsales. Les responsables de ces lésions sont probablement des poissons cartilagineux et des parasites d'affinité systématique incertaine.

Mots-clefs :

- Productida ;
- Carbonifère ;
- lésions de la coquille ;
- paléoécologie

[1] *Institute of Geological Sciences of the NAS of Ukraine, Department of Palaeontology and Stratigraphy of Palaeozoic Sediments, Oles Honchar Str., 55b, Kyiv (Ukraine)*
vitalydernov@gmail.com

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1. Introduction

The study of fossils with abnormalities and malformations is an important source of information about the palaeoecology of organisms, as well as their evolution, distribution patterns, and more (*e.g.*, PEEL, 1984; LINDSTRÖM, 2003; EBBESTAD & HÖGSTRÖM, 2009; ZATOŃ *et al.*, 2015; HOFFMANN *et al.*, 2018; BICKNELL & KIMMIG, 2023). Productidine brachiopods were a significant component of Late Palaeozoic marine ecosystems (LAZAREV, 1990). Their remains are present in marine rocks of different lithologies formed under various depositional conditions (MUIR-WOOD & COOPER, 1960; LAZAREV, 1990, and references therein). Consequently, these brachiopods are well studied among many other groups of Late Palaeozoic marine biota.

The Donets Basin in eastern Ukraine is a key region for studying the Carboniferous marine and terrestrial biota of the Palaeoequatorial belt, particularly the brachiopods, as the Mississippian and Pennsylvanian sequences here are very rich in both animal and plant fossils. Despite the widespread occurrence of productidines in the Carboniferous deposits of the Donets Basin (ROTAI, 1931, 1952, 1980; LIKHAREV, 1938; AISENVERG, 1950, 1951, 1983; AISENVERG *et al.*, 1963), they have not been studied in sufficient detail.

Carboniferous brachiopods with injuries are known from many localities around the world (*e.g.*, SARYTCHEVA, 1949; BRUNTON, 1966; ALEXANDER, 1981; MUNDY, 1982; ELLIOTT & BOUNDS, 1987; ELLIOTT & BREW, 1988), but such fossils have never been recorded in Ukraine. While the Carboniferous biota of Ukraine (*e.g.*, corals, bryozoans, bivalves, gastropods) have been studied in relatively great detail, there is very little data or evidence of lifetime skeletal injuries in animals. Notable mentions of shell injuries include an ammonoid conch and tubeworm *Coleolus* from the Mospyne Formation (Upper Bashkirian, Lower Pennsylvanian) as figured by DERNOV (2022a: Fig. 4g, 2022b: Fig. 4b-d, respectively). DERNOV (2022c, 2023c) also described non-predation injuries to the shells of the non-marine bivalves *Carbonicola rectilinearis* TRUEMAN & WEIR, 1948, *C. limax* WRIGHT, 1934, and *C. acuta* (SOWERBY, 1813) from the lacustrine shales of the Upper Bashkirian Mospyne and Smolyanynivka formations. DERNOV and POLETAEV (2024: Fig. 9l) reported a shell injury on the external and inner surfaces of valves of the spiriferid brachiopod ?*Anthracospirifer* sp. from the Sukha Ravine fossil site of the Mospyne Formation (see the section "Geological setting"). Additionally, DERNOV (2023a: Fig. 4D) figured non-lethal shell injuries in the nautilids *Parametacoceras* from the Upper Bashkirian-lower Moscovian Kamensk Formation.

The author, studying the productidine brachiopods *Densepustula* LAZAREV, 1982, from the Pennsylvanian deposits of the Donets Basin, discovered several injured ventral valves belonging to this genus. This work is devoted to the study of these shell injuries and the investigation of their possible producers.

2. Geological setting

The Donets Basin is part of the northwest-southeast trending deep Pripyat-Dnipro-Donets intracratonic rift, which extends from the Baltic to the Caspian Sea across Belarus, Ukraine, and Russia. This rift is located between the Voronezh Anteclise in the north and the Ukrainian Shield in the south, in the southwestern part of the East European Craton (IZART *et al.*, 1996; EROS *et al.*, 2012; SACHSENHOFER *et al.*, 2012; HINSBERGEN *et al.*, 2015).

Localities

The present material comes from six fossil sites of the Donets Basin (Luhansk and Donetsk regions, Ukraine; Figs. 1-2), from the Upper Bashkirian Mospyne, Smolyanynivka, and Belaya Kalitva formations, as well as from the Upper Bashkirian-lower Moscovian Kamensk Formation. These fossil sites are briefly described below.

1) Sukha Ravine-1 fossil site:

Location: Luhansk Region, Luhansk District, Sukha Ravine, 2 km east of the village of Makedonivka (GPS coordinates: 48°14'28.4"N, 39°20' 06.4"E).

Description: The fossiliferous rock is a brownish-grey, fine-grained, quartz and feldspathic, calcareous, strongly bioturbated sandstone. This layer lies 55 meters below the G_1^2 limestone bed of the Mospyne Formation (Fig. 3.A, C-D).

Fossils: Numerous fossils have been collected from this layer (MYCHKO & DERNOV, 2019; DERNOV, 2021, 2022a; DERNOV & POLETAEV, 2024, and author's unpublished data), including terrestrial plants (*Calamites* and *Sigillaria*), bryozoans, brachiopods [*Angiospirifer* sp., *Brachythyrina* ex gr. *proba* (ROTAI, 1951), *Alphachoristites* (*A.*) *kschemyschensis* (SEMICHATOVA, 1941), *A.* (*A.*) ex. gr. *bisulcatiformis* (SEMICHATOVA, 1941), ?*Anthracospirifer* sp., *Densepustula* sp., ?*Balakhonia* sp., *etc.*], scaphopods, gastropods, bivalves (species of genera *Phestia, Sanguinolites, Palaeoneilo*, *etc.*), orthocerids, coiled nautiloids (*Gzheloceras* sp.*, Planetoceras yefimenkoi* DERNOV, 2021, *Paradomatoceras applanatum* DELÉPINE, 1937, *Megaglossoceras* sp., *etc.*), ammonoids [*Melvilloceras rotaii* (LIBROVITCH in POPOV, 1979), *Gastrioceras angustum* PATTEISKY, 1964, *Branneroceras* sp.], crinoids, trilobites [*Ditomopyge* (*Carniphillipsia*) *kumpani* (WEBER, 1933)], fishes (*Listracanthus*, *Lagarodus*, *etc.*), and trace fossils (*Crescentichnus*, *Planolites*, *Zoophycos*, fish coprolites).

At this site and all those described below, *Densepustula* is one of the dominant brachiopod genera, but brachiopods are a relatively rare faunal group and less numerous than mollusks. In addition to *Densepustula* sp., shell damages from the Sukha Ravine-1 locality were recorded on valves of the spiriferides ?*Anthracospirifer* sp. (DERNOV & POLETAEV, 2024) and *Alphachoristites* spp., as well as the productidines ?*Balakhonia* sp. (author's unpublished data).

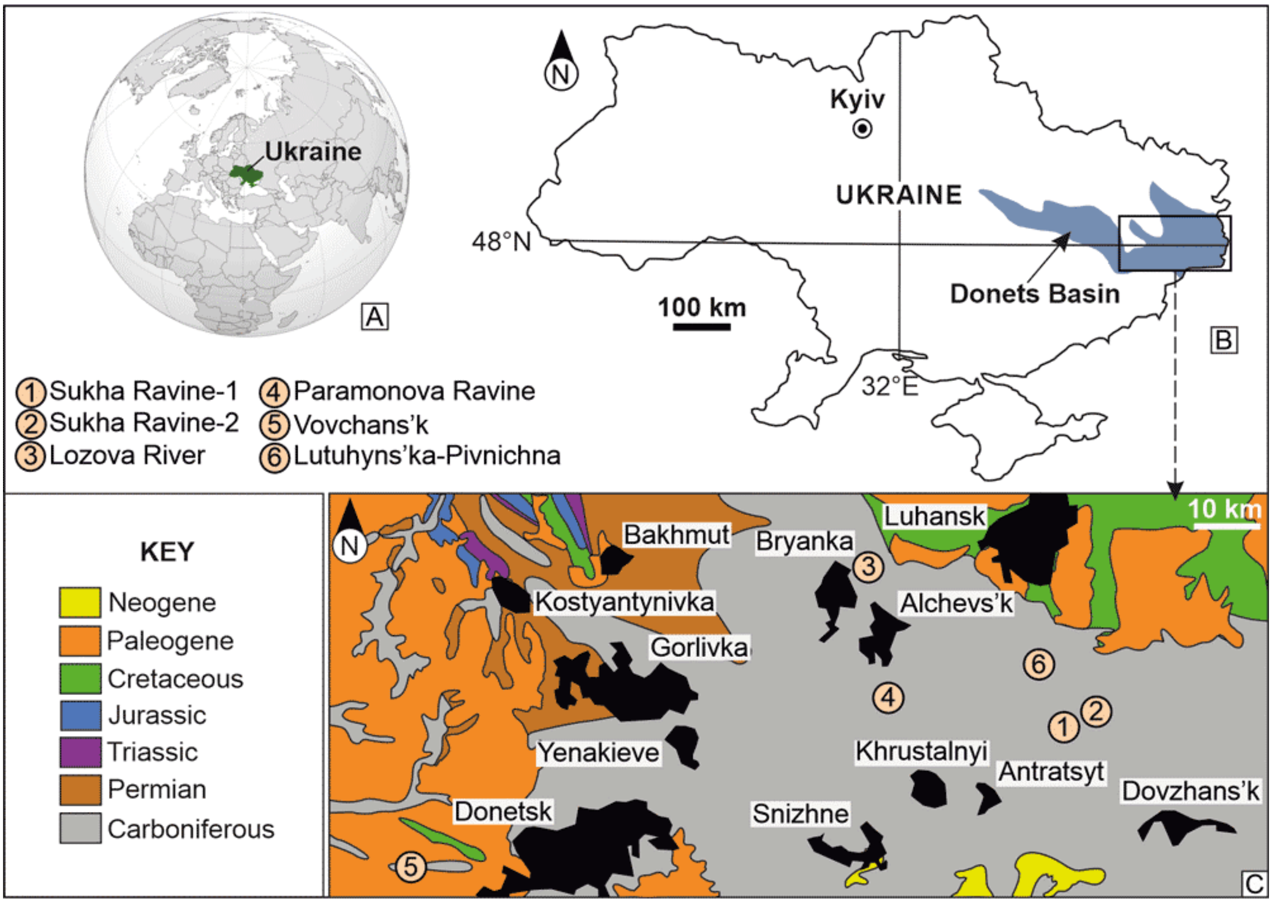


Figure 1: Geographical location of the brachiopod-bearing fossil sites. Geological map in Fig. 1C modified from the Geological Map of the USSR (1:200,000).

2) Sukha Ravine-2 fossil site:

Location: Luhansk Region, Luhansk District, Sukha Ravine 2 km east of the village of Makedonivka (GPS coordinates: 48°14'28.4"N, 39°20' 06.4"E).

Description: The fossil-bearing rock is a dark grey mudstone with siderite nodules below the G_1^2 limestone layer of the Mospyne Formation (Fig. 3.B, F).

Fossils: The mudstone contains very rare rugose corals and the brachiopods (*Lingularia* sp., *Densepustula* sp.), as well as scaphopods, gastropods, bivalves (species of the genera *Phestia*, *Sanguinolites*, *Palaeoneilo*, *Solenomorpha*, *etc.*), orthocerids, coiled nautiloids (*Liroceras* sp., *Metacoceras perelegans* GIRTY, 1911, *Peripetoceras* sp.), ammonoids [*Cymoceras* sp., *Melvilloceras rotaii* (LIBROVITCH in POPOV, 1979), *Branneroceras* spp., *Gastrioceras* sp., *Bisatoceras* sp.], allochtonous terrestrial plants (species of the genera *Calamites*, *Lepidostrobophyllum*, *Lepidodendron*, *Cordaites*), problematics *Coleolus carbonarius* DEMANET, 1938, and trace fossils (*Chondrites*, *Cyclopuncta*, fecal pellets, bromalites) (DERNOV, 2022a, 2022b). The injured tube of *Coleolus* from this locality was figured by the author earlier (DERNOV, 2022b: Fig. 4b-d).

3) Lozova River fossil site:

Location: Luhansk Region, right bank of the Lozova River near the town of Bryanka (GPS coordinates: 48°31'55.1"N, 38°43'34.0"E).

Description: The rock with *Densepustula* sp. is a light grey, clayey limestone (H_6^1 limestone layer, Smolyanynivka Formation).

Fossils: The brachiopods from this locality were studied by AISENVERG (1950), who identified a rich assemblage consisting of about 20 species and approximately 14 genera, which, however, requires revision.

4) Paramonova Ravine fossil site:

Location: Luhansk Region, Alchevs'k District, Paramonova Ravine near the village of Horodysche (GPS coordinates: 48°19'23.0"N, 38°38' 53.2"E).

Description: The fossil-bearing rock is a light grey clayey limestone (H_6^1 limestone layer, Smolyanynivka Formation).

Fossils: Brachiopods from this locality were studied by AISENVERG (1950). However, the taxonomic content of the brachiopod assemblage requires significant revision.

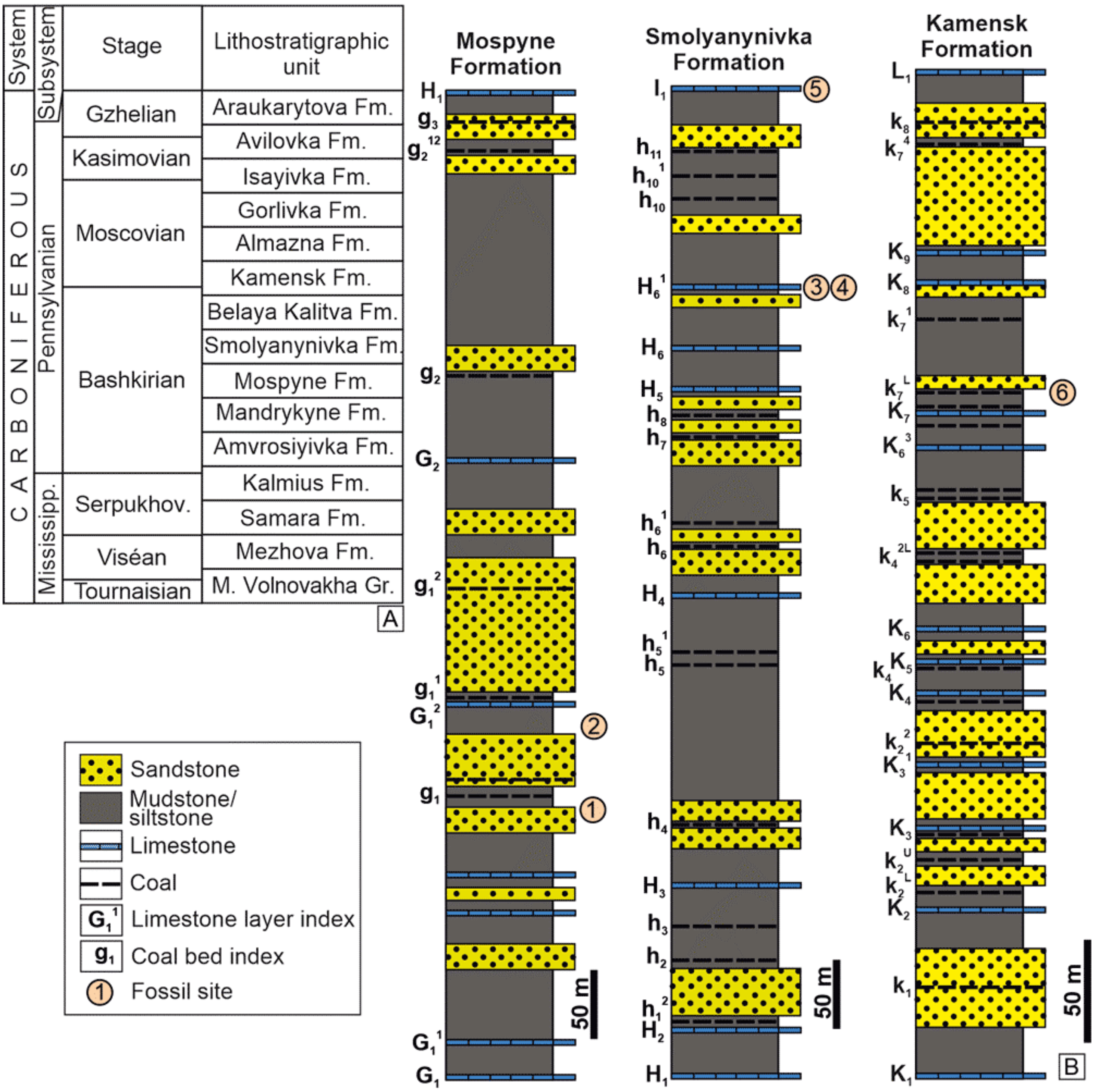


Figure 2: Carboniferous stratigraphy of the Donets Basin. A - stratigraphic scheme of the Carboniferous deposits of the Donets Basin (modified after NEMYROVSKA *et al.*, 2013); B - stratigraphic position of the brachiopod-bearing fossil sites (lithological column modified from POLETAEV *et al.*, 2011). Abbreviations: Mississipp. = Mississippian, M. Volnovakha Gr. = Mokra Volnovakha Group, Serpukhov. = Serpukhovian.

5) Vovchans'k fossil site:

Location: Donetsk Region, Pokrovs'k District, the right bank of the Vovcha River near the town of Vovchans'k (GPS coordinates unknown).

Description and fossils: The fossil-bearing rock is a grey, crystalline, massive limestone (I_1 limestone layer, Belaya Kalitva Formation) with foraminiferans, calcareous algae, and brachiopods (AISENVERG, 1950, 1951).

6) Lutuhyns'ka-Pivnichna mine fossil site:

Location: Luhansk Region, the heap spoil of the Lutuhyns'ka-Pivnichna coal mine near the town of Lutuhyne (GPS coordinates: 48°25' 25.4"N, 39°12'24.9"E).

Description: The *Densepustula*-bearing rock is a dark grey, carbonaceous, sometimes pyritized siltstone with large carbonate nodules and interlayers or lenses of coquina. This siltstone is a roof shale of the k_7^L coal layer (Kamensk Formation).

Fossils: Numerous fossils have been collected from this stratigraphic horizon (DERNOV, 2023a, 2023b), including ?worm tubes, brachiopods [*Orbiculoidea nitida* (PHILLIPS, 1836), *Lingularia mytiloides* (SOWERBY, 1812), *Derbyia* sp., *Neochonetes donetzianus* (AISENVERG, 1950), *Densepustula* sp.], bivalves (species of the genera *Palaeoneilo*, *Phestia*, *Sanguinolites, etc.*), gastropods (species of the genera *Euphemites, Retispira, Bucaniopsis,*

Figure 3: Lithological and palaeontological features of some studied fossil sites. A - sandstone bed of the Sukha Ravine-1 fossil site; B - black shale of the Sukha Ravine-2 fossil site; C - mud cracks on the upper surface of a sandstone bed (Sukha Ravine-1); D - heavy bioturbated sandstone (Sukha Ravine-1); E - Lutuhyns'ka Pivnichna coal mine fossil site; F - cluster of bivalves, gastropods, and cephalopods in a siderite nodule (Sukha Ravine-2; scale bar = 30 mm); G - large carbonate nodule (Lutuhyns'ka-Pivnichna mine).

Naticopsis, Soleniscus), orthocerids, coiled nautiloids (species of the genera *Gzheloceras*, *Parametacoceras*, *Metacoceras, Temnocheilus, Peripetoceras*, *Coelogasteroceras*, *Ephippioceras, etc.*), ammonoids (*Wiedeyoceras clarum* POPOV, 1979, *Winslowoceras* sp.), trilobites [*Paladin* cf. *lutugini* (WEBER, 1933)], fishes (*Symmorium* and *Venustodus*), terrestrial plants (*Calamites* sp.), bromalites and some other trace fossils. The shells of some bivalves, gastropods, and coiled nautiloids from this fossil site bear color patterns (DERNOV, 2023b, 2024a). Shell injury of a coiled nautiloid *Parametacoceras* from this locality has been figured by the author (DERNOV, 2023b: Fig. 4D).

Regional stratigraphy

The Mospyne Formation consists of a succession of sandstones, siltstones, mudstones, coals, and limestones. The thickness of the formation varies from 315 meters in the northwest part of the Donets Basin to 730 meters in its southeast part (AISENVERG *et al*., 1963, 1975; FEOFILOVA & LEVENSTEIN, 1963; DUNAEVA, 1969; NEMYROVSKA & YEFIMENKO, 2013). The Mospyne Formation corresponds to the lower part of the Zuyivkian Horizon (lower half of the Kayalian Regional Stage) of the Regional stratigraphic scheme of the Dnipro-Donets Downwarp (POLETAEV *et al.*, 2011; NEMYROVSKA & YEFIMENKO, 2013). Hereinafter, the transliteration of names of the stratigraphic horizons follows NEMYROVSKA (2017).

The Smolyanynivka Formation consists of a succession of sandstones, siltstones, mudstones, coals, and limestones. This stratigraphic unit is characterized by thick (40-60 meters) beds of coarse-grained alluvial sandstones, which have their own names (*e.g.*, Babakovskyi sandstone bed). This formation is notable for having the highest coal content among the Bashkirian deposits of the Donets Basin. The thickness of the formation varies from 250 meters in the northwestern part of the Donets Basin to 1400 meters in the southeastern part of the basin (AISENVERG *et al*., 1963, 1975; FEOFILOVA & LEVENSTEIN, 1963; DUNAEVA, 1969; NEMYROVSKA & YEFIMENKO, 2013). The Smolyanynivka Formation corresponds to the upper part of the Zuyivkian and Makiivkian horizons (upper half of the Kayalian Regional Stage) in the Regional stratigraphic scheme of the Dnipro-Donets Downwarp (POLETAEV *et al.*, 2011; NEMYROVSKA & YEFIMENKO, 2013).

The Belaya Kalitva Formation consists of a succession of sandstones, siltstones, mudstones, coals, and limestones. A characteristic feature of the Belaya Kalitva Formation in the study area is the presence of beds of so-called "jasper-like rocks". The thickness of the formation varies from 150 m in the northwestern part of the Donets Basin to 650 m in the southeastern part of the basin (AISENVERG *et al*., 1963, 1975; FEOFILOVA & LEVENSTEIN, 1963; DUNAEVA, 1969; NEMYROVSKA & YEFIMENKO, 2013). The Belaya Kalitva Formation corresponds to the uppermost part of the Makiivkian and Krasnodonian horizons (upper half of the Kayalian Regional Stage) of the regional stratigraphic scheme in the Dnipro-Donets Downwarp (POLETAEV *et al*., 2011; NEMYROVSKA & YEFIMENKO, 2013).

The Kamensk Formation consists of a sequence of sandstones, siltstones, mudstones, coals, and limestones, varying in thickness from 300 meters in the northwestern part of the Donets Basin to 1050 meters in the southeastern part of this region (AISENVERG *et al*., 1963, 1975; DUNAEVA, 1969; POLETAEV *et al*., 2011; NEMYROVSKA & YEFIMENKO, 2013). The Kamensk Formation corresponds almost completely with the Kam'iankian Horizon (lower half of the Lozivkian Regional Stage); only the Bashkirian portion of this formation is part of the Krasnodonian Horizon (uppermost part of the Kayalian Regional Stage) in the Regional stratigraphic scheme of the Dnipro-Donets Downwarp (POLETAEV *et al*., 2011; NEMYROVSKA & YEFIMENKO, 2013).

Age

Deposits of the Mospyne and Smolyanynivka formations contain typical Langsettian terrestrial plants (NOVIK, 1952, 1974; FISSUNENKO, 1991; DERNOV & UDOVYCHENKO, 2019b). The nonmarine bivalves, characteristic of the upper part of the *lenisulcata* and *communis* zones, were found in the Mospyne Formation (DERNOV, 2022e); bivalves typical of the *communis* and lower *modiolaris* zones were identified from the Smolyanynivka Formation by SERGEEVA (1984). The Mospyne Formation and almost all of the Smolyanynivka Formation (stratigraphic interval between the G_1 and H_6 limestone layers) belong to the *Gastrioceras-Branneroceras* Genozone (POPOV, 1979; DERNOV, 2022a).

The Belaya Kalitva Formation contains Duckmantian fossil plants (NOVIK, 1952, 1974; FISSUNENKO, 1991). Non-marine bivalves from the upper *modiolaris* and *pulchra+similis* zones were found in the rocks of the Belaya Kalitva and lower part of the Kamensk formations (SERGEEVA, 1984). The Belaya Kalitva Formation and the lower part of the Kamensk Formation (stratigraphic interval bounded by the H_6 and K_2 limestone beds) belong to the *Diaboloceras-Axinolobus* Genozone (POPOV, 1979; DERNOV, 2023a).

The lower boundary of the Moscovian in the Donets Basin is at the base of the K_3 limestone layer (lower part of the Kamensk Formation) (POLETAEV *et al*., 2011; NEMYROVSKA & YEFIMENKO, 2013), but this is somewhat conditional, since the GSSP of this boundary is not defined. Moreover, modern conodont and fusulinid studies (*e.g.*, NEMYROVSKA, 1999, 2017; DAVYDOV, 2009; KHODJANYAZOVA *et al*., 2014; NEMYROVSKA & HU, 2018) indicate the position of this boundary at the base of the K_1 limestone bed, the basal layer of the Kamensk Formation.

The stratigraphic interval containing the k_7^L coal layer was assigned to the early Moscovian *Diaboloceras-Winslowoceras* Genozone by POPOV (1979). Unfortunately, he does not substantiate this assignment, as all ammonoid species described by him do not unambiguously determine the age of the Kamensk Formation. The absolute age of the volcanic ash interlayer in the k_7 coal bed is 313.16±0.08 Ma (DAVYDOV *et al*., 2010).

3. Material and methods

Of the 61 ventral valves of *Densepustula* examined, only nine bear injuries, *i.e.*, approximately 15% of the total number of valves (Table 1). Studied specimens are represented by pyritized and sideritized, moderately and poorly-preserved isolated ventral valves, as well as their external molds. Injuries have also been recorded on shells of other brachiopods from the fossil sites described above, but representatives of the genus *Densepustula* are the most numerous among them. In addition, representatives of this genus have not been previously recorded in the Pennsylvanian of Ukraine.

Table 1: Studied material.

Fossil site	Number of specimens	Specimens
Sukha Ravine-1	1	IGS NASU-11/48
Sukha Ravine-2	2	IGS NASU-11/44, IGS NASU-11/87
Lozova River	2	IGS NASU-11/25, IGS NASU-11/26
Paramonova Ravine	1	IGS NASU-11/61
Vovchans'k	1	IGS NASU-11/84
Lutuhyns'ka-Pivnichna mine	2	IGS NASU-11/01, IGS NASU-11/04

Studied material was collected over the past 50 years by the author, Dr. Mykola I. UDOVYCHENKO (Luhansk Taras Shevchenko National University, Poltava), Dr. Vladyslav I. POLETAEV, and the late Dr. David Ye. AISENVERG (both from the Institute of Geological Sciences of the NAS of Ukraine, Kyiv). The studied collection (IGS NASU-11) is stored in the Department of Palaeontology and Stratigraphy of Palaeozoic Sediments, Institute of Geological Sciences of the NAS of Ukraine.

Although the studied material was collected by different researchers at different times, it can be reasonably assumed that all the fossils identified were collected, not just those that were the most well-preserved or attractive (personal communication with Drs. Vladyslav POLETAEV and Mykola UDOVYCHENKO, January 2022, field notes by Dr. David AISENVERG). The scheme of injuries measurements is shown in Figure 4.BICKNELL & KIMMIG (2023) and BICKNELL *et al*. (2023) used the example of trilobites to review the terminology related to skeletal pathologies, which is also used in this paper. Adapted to brachiopods, this terminology is as follows (modified after BICKNELL & KIMMIG, 2023: p. 201, and BICKNELL *et al*., 2023: p. 4):

- **Injury**: Shell breakage through accidental injury or attack complications;
- **Malformation**: Evidence for injuries, teratologies, or pathologies;
- **Pathology**: Malformed shells resulting from parasitic activity or infections;
- **Teratology**: External expressions of developmental, embryological, or genetic malfunctions.

4. Description of shell injuries

General shell morphology

The studied ventral valves exhibit a convex, rounded, and triangular-elongated outline, with a very shallow median sulcus and overhanging umbo; the ears are very small. The ears bear several rows of small spines spaced about 0.4-0.5 mm apart. Ornamentation on other parts of ventral valves consists of radially arranged, long pustules measuring 0.3-0.4 mm wide, bearing thin, hollow spines 0.3 mm in diameter. Thin rugae present in the lateral part of the umbonal region. Only the best-preserved ventral valves show very delicate growth lines. The internal structure of the ventral valves was not studied due to insufficient quality of material preservation.

Shell injuries

Specimen IGS NASU-11/01 (Fig. 5.B, L) is represented by a pyritized valve with an ellipsoidal pit (concavity; see Fig. 4D) located in the median sulcus area of its anterior part. The pit measures 4.5 mm in length, 1.5 mm in width, and approximately 0.9 mm in depth. It extends along the anterior-posterior direction. The transverse profile of the pit is V-shaped with a slightly pointed bottom and steep walls. The pit edges are sharp and uneven.

Specimen IGS NASU-11/04 (Fig. 5.F-G, O) is represented by a pyritized valve with a sub-triangular, almost rounded pit, 5 mm in longitudinal diameter and 4.5 mm in transverse diameter, located on the lateral slope of the umbonal area. The depth of the pit is 1 mm, and its transverse profile is semi-ellipsoidal with gentle walls and a rounded bottom. The edges of the pit are sharp.

Specimen IGS NASU-11/25 (Fig. 5.C, P) is represented by a limestone external mold of the valve. The injury is characterized by a groove on the outer surface of the valve, positioned at an angle of approximately 130° to its plane of symmetry. The groove measures 6 mm in length and 0.7-0.8 mm in width, gradually decreasing from the posterior to the anterior margin of the valve. The depth of the groove is approximately 0.7 mm, also decreasing gradually from the posterior to the anterior margin. The edges of the groove are quite sharp, with some areas slightly raised above the valve surface. The transverse profile of the groove is V-shaped with steep walls and a narrow bottom.

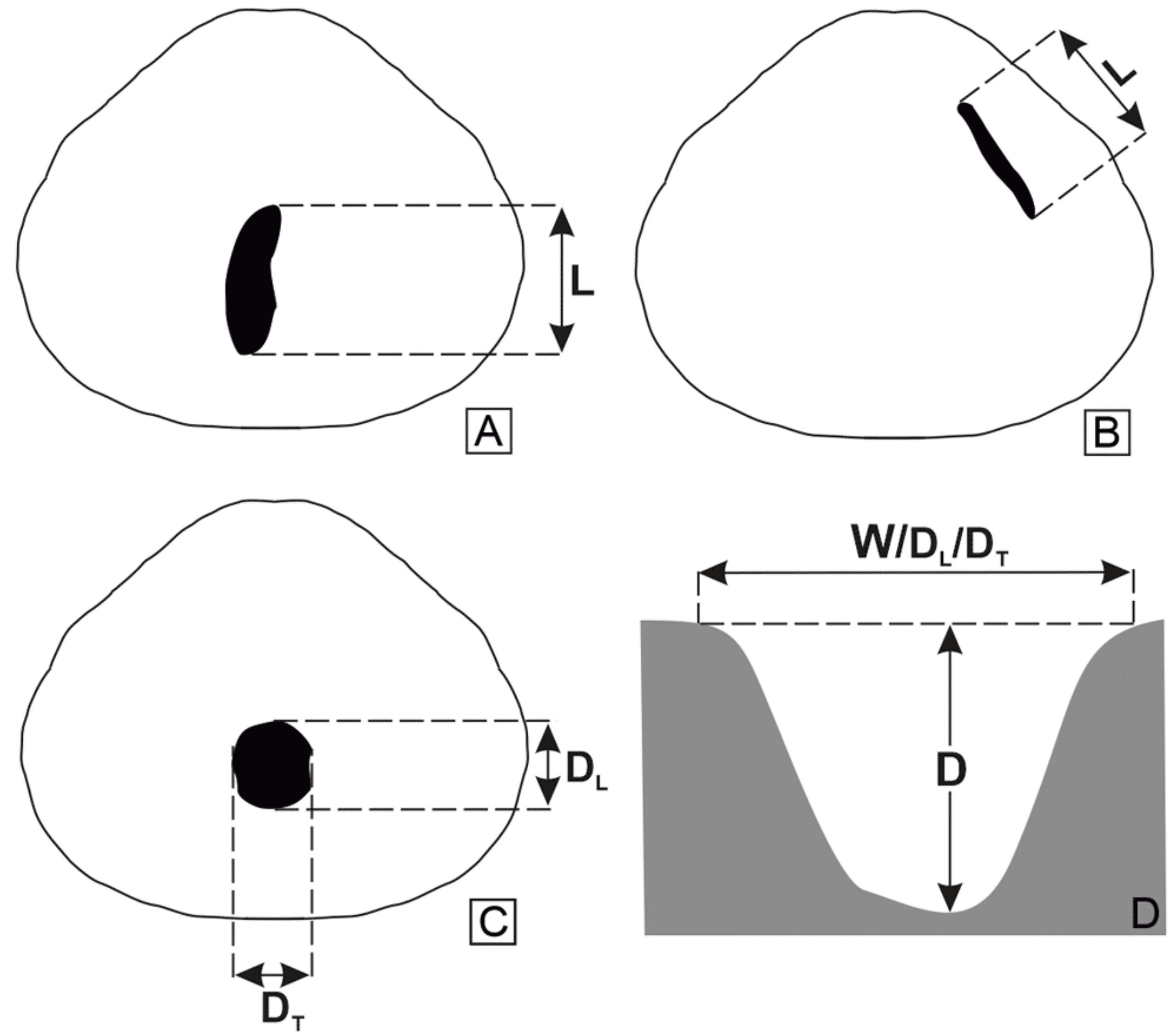


Figure 4: Abstract scheme showing measurements of injuries on valves of *Densepustula* sp. A-B - for elongated injuries, C - for isometric or nearly isometric injuries, D - cross-sectional dimensions of an injury. Abbreviations: D = depth, D_L = longitudinal diamener, D_T = transverse diameter, L = length, W = width.

Specimen IGS NASU-11/26 (Fig. 5.E, N) is represented by a relatively well-preserved undeformed mold of the valve, bearing a small, barely visible pit in its umbonal part. The pit measures 2 mm in length and 2 mm in width, with a depth of approximately 0.4 mm. Its edges are gradual, and its transverse profile is U-shaped.

Specimen IGS NASU-11/44 (Fig. 5.A, Q) is represented by a sideritized valve. The injury is characterized by an ellipsoidal, almost rounded conical pit, measuring 1.9 mm in transverse diameter and 2.05 mm in longitudinal diameter. The pit is slightly elongated in the anterior-posterior direction, with a depth of approximately 0.8 mm. It is located near the anterior margin of the valve, and the edges of the pit are sharp.

Specimen IGS NASU-11/48 (Fig. 5.D, R) is represented by the external mold of a valve. In the sulcus, near the anterior margin, there is an amoeba-shaped shallow pit with a depth of approximately 0.5 mm. The pit measures approximately 3.5 mm in transverse diameter and 2.8 mm in longitudinal diameter, with an uneven bottom and gentle walls.

Specimen IGS NASU-11/61 (Fig. 5.I-J, M, S) is represented by the limestone external mold of a valve, exhibiting two injuries in the umbonal area:

1) an ellipsoidal pit, measuring 4 mm in length and 2 mm in width, located near the medial part of the valve. The pit extends obliquely relative to the symmetry plane of the valve. It has a conical transverse profile and a depth of about 0.8 mm (Fig. 5.J, S);

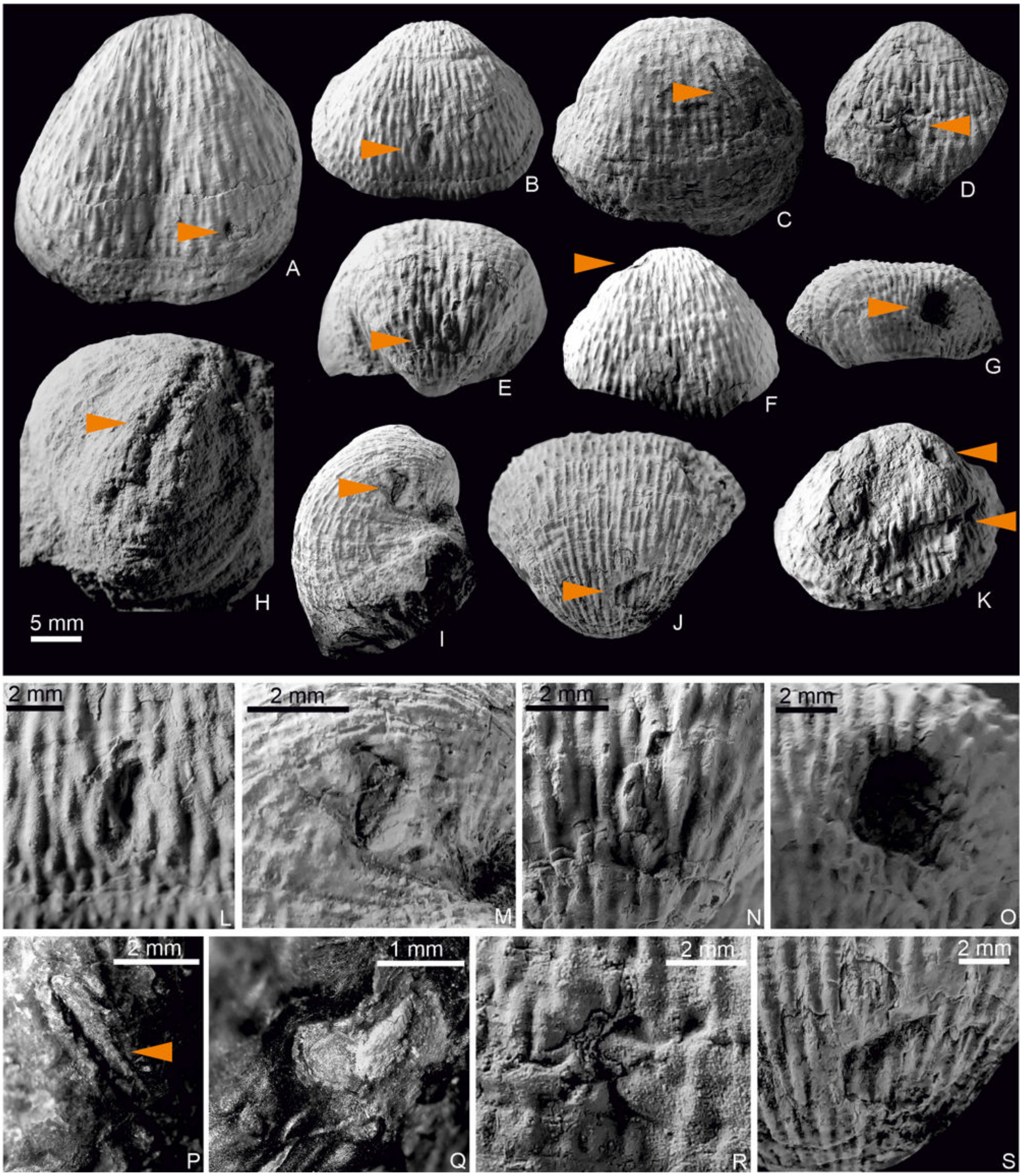


Figure 5: Injured ventral valves of *Densepustula* sp. from the Pennsylvanian of the Donets Basin. A, Q - specimen IGS NASU-11/44 (A – general view of the valve, Q - enlarged part of the valve with the injury; Sukha Ravine-2); B, L - specimen IGS NASU-11/01 (B - general view of the valve, L - enlarged part of the valve with the injury; Lutuhyns'ka-Pivnichna mine); C, P - specimen IGS NASU-11/25 (C - general view of the valve, P - enlarged part of the valve with the injury; Lozova River); D, R - specimen IGS NASU-11/48 (D - general view of the valve, R - enlarged part of the valve with the injury; Sukha Ravine-1); E, N - specimen IGS NASU-11/26 (E - umbonal view of the valve, R - enlarged part of the valve with the injury; Lozova River); F, G, O - specimen IGS NASU-11/04 (F - ventral view of the valve, G - posterior view of the valve, O - enlarged part of the valve with the injury; Lutuhyns'ka-Pivnichna mine); H - specimen IGS NASU-11/87 (Sukha Ravine-2); I, J, M, S - specimen IGS NASU-11/61 (I - lateral view of the valve, J - posterior view of the valve, M, S - enlarged parts of the valve with the injury; Paramonova Ravine); K - specimen IGS NASU-11/84 (Vovchans'k fossil site).

2) an ellipsoidal, almost sub-triangular semi-elliptical pit with a semicircular cross-section profile, measuring 2.5 mm long, 0.7 mm in maximum width, and about 0.9 mm deep. This pit, situated on the lateral slope of the umbonal area, is characterized by very gentle slopes and sharp, uneven edges (Fig. 5.I, M).

Specimen IGS NASU-11/84 (Fig. 5.K) is represented by a poorly preserved external mold of a valve. On its surface, there is an injury in the form of a wide, transversely elongated groove measuring 12 mm in length, 2.0-3.5 mm in width, and about 1 mm in depth. The width of the groove gradually decreases from the edge close to the medial part of the valve to its lateral slope. The transverse profile of the groove varies from U-shaped with a slightly concave wide bottom and wide, steep slopes near the sulcus, to V-shaped with a narrow concave bottom and steep slopes. The edges of the groove are quite sharp, especially those facing the posterior margin of the valve. Additionally, approximately 5.5-6.0 mm posterior to this groove, there is an almost rounded pit measuring about 3 mm in transverse diameter and 3.5 mm in longitudinal diameter. The pit is approximately 0.7 mm deep with a U-shaped transverse profile characterized by steep walls and a wide, almost flat bottom.

Specimen IGS NASU-11/87 (Fig. 5.H) is represented by a sandstone mold of the valve. A longitudinal groove approximately 13 mm in length, 1.5-1.9 mm in width, and about 0.7 mm in depth, preserved between the sulcus and the lateral slope of the valve. The groove exhibits steep slopes and a U-shaped transverse profile: its bottom is uneven and narrow, and its edges are rather sharp. The width and depth of the groove gradually increase from the rear to the anterior margin of the valve. Near the anterior margin of the valve, the groove transitions into an almost rounded pit with diameters of about 3.8 and 3.5 mm. The transverse profile of the pit is W-shaped with a slightly raised central part, about 0.4 mm in diameter. The edges of the pit are rather sharp, especially those facing the lateral slope and the posterior part of the valve.

5. Discussion

Palaeoecology and taphonomy

The author personally collected material from three sites (Sukha Ravine-1, Sukha Ravine-2, and Lutuhyns'ka-Pivnichna mine localities), so taphonomy and palaeoecology can be commented on only in relation to these sites.

Densepustula from the Lutuhyns'ka-Pivnichna coal mine fossil site were discovered within thin interlayers of detrital limestones and large carbonate concretions embedded in black shales. These features developed in nearshore areas of a warm, shallow-marine basin characterized by very low sedimentation rates and locally dysoxic environments (for detailed information, refer to DERNOV, 2023a, 2023b, 2024a). Crinoids and corals are absent in these rocks due to water turbidity hampering the efficiency of crinoid filter-feeding capability and possible photosynthetic symbionts in corals, or due to their inability to live on an unstable substrate. It is likely that irregular storms periodically oxygenated the sediments, oxidizing hydrogen sulfide, and concentrated shelly fauna within local bottom depressions. Consequently, such concentrations, amassed on the seabed surface, formed tempestitic lenses and thin layers of coquina limestone. Palaeogeographic evidence indicate that the Lutuhynska-Pivnichna mine fossil site was situated within a shallow bay during the formation of the k_7 coal layer roof shale (ZHEMCHUZHNIKOV *et al.*, 1959).

Densepustula sp. from the black shales of the Sukha Ravine-2 site existed under similar environmental conditions. However, it should be noted that very rare remains of rugose corals and crinoids, unlike at the Lutuhyns'ka-Pivnichna mine fossil site, occur here. Remains of *Densepustula* sp. are represented by only a few specimens at the Sukha Ravine-2 fossil site, despite more intensive and long-term collecting compared to the Lutuhynska-Pivnichna mine fossil site. This may indicate more unfavorable conditions for the existence of articulate brachiopods, the remains of which were collected from the Sukha Ravine-2 locality. Similarly to the Lutuhynska-Pivnichna mine fossil site, a fairly laterally stable tempestitic bed is present here, represented by bioclastic sandy limestone with pebbles, which consists mainly of fragments of bivalve valves and *Coleolus* tubes.

Densepustula from argillaceous limestones (Lozova River and Paramonova Ravine) and sandstones (Sukha Ravine-1) occurred in the nearshore zones of the shallow marine basin along with other normal marine biota (*e.g.*, calcareous algae, foraminifers, crinoids).

In the Moscow Syneclise region, monospecific assemblages of *Densepustula russiensis* are present in interlayers of the (?) lagoonal sandy limestone and marlstone within the littoral clay and sandstone of the lower Altjutovo Formation, which represents the basal lithostratigraphic unit of the Vereian (Moscovian) (IVANOVA & KHVOROVA, 1955; IVANOVA, 1958). Occasionally, remains of *Densepustula russiensis* are also discovered in shallow marine sandstones and sandy limestones alongside *Balakhonia latiplana* (IVANOV, 1935), *Orthotetes socialis* FISCHER de WALDHEIM, 1850, bellerophontid gastropods, bivalves, fishes, and rare echinoderms (IVANOVA, 1958).

A distinctive feature of *Densepustula* shell ornamentation is its thin spines, the precise function of which remains uncertain and has been speculated to serve various purposes. These include anchoring the brachiopod to hard substrates, stabilizing it on soft substrates, distributing mass to prevent sinking into sediments, deterring epibiont settlement, attracting epibionts for camouflage, housing sensory structures, or providing protection against predation (MUIR-WOOD & COOPER, 1960; GRANT, 1966, 1968; RUD-

WICK, 1970; MCGHEE, 1976; BRUNTON, 1982; BRICE, 1986; BRUNTON & MUNDY, 1988; LEIGHTON, 2000; JOHNSEN *et al.*, 2013; PÉREZ-HUERTA, 2013; HALAMSKI, 2023).

In the case of *Densepustula*, these spines likely primarily served to stabilize the shell on the unstable, semi-liquid clayey substrates and to anchor it in relatively dense sandy and calcareous terrigenous substrate under the influence of high-speed flow. This interpretation is supported by the occurrence of *Densepustula* in various types of sedimentary rocks. In mudstones, such as those found at the Sukha Ravine-2, they are often the sole articulate brachiopods present, suggesting that the unstable substrate may have contributed to the reduced taxonomic diversity of brachiopod communities in such environments. However, further research is necessary to fully understand this phenomenon.

The genus *Parajuresania* LAZAREV, 1982, exhibits morphological similarities to *Densepustula* and is typically found in nearshore areas of ancient basins characterized by substrates such as siliciclastic mud, micritic mud, and biogenic sand (DIEVERT *et al.*, 2021: Fig. 2). *Densepustula* shares a similar habitat preference.

Potential producers of injuries

Shell injuries in the specimens of *Densepustula* sp. under study are represented by longitudinal and sublongitudinal furrows, rounded and ellipsoidal pits, and irregularly shaped dimples. These three morphological types are summarized in Table 2.

The question of why there are no injuries on the dorsal valves of *Densepustula* is not entirely clear. It should be noted that there are 25 dorsal valves in the studied collection. Since 15% of the ventral valves in the studied material bear injuries, it would be natural to expect that about four of the 25 dorsal valves should be injured. However, this is not the case. Perhaps this phenomenon is a taphonomic artifact, in which damaged dorsal valves probably have a lower preservation potential than ventral valves, or it may be due to the influence of the lifetime position of the valves, but it is not yet possible to answer this question unequivocally due to the small amount of material.

The potential agents responsible for injuries of Types A and C include cephalopods (ALEXANDER, 1986a; ELLIOT & BREW, 1988; BRETT, 2003), arthropods (MUNDY, 1982; BRETT, 2003), and fishes (SARYTCHEVA, 1949; BRUNTON, 1966; ALEXANDER, 1981; ELLIOTT & BOUNDS, 1987; BRETT, 2003). These injuries may indicate healed evidence of failed predatory attacks. Numerous coiled nautiloids such as *Gzheloceras, Parametacoceras, Metacoceras, Temnocheilus, Peripetoceras, Planetoceras, Paradomatoceras, Coelogasteroceras, Ephippioceras*, *Megaglossoceras*, *etc.*, orthocerids, ammonoids, and chondrichthian fishes belonging to the genera *Symmorium, Listracanthus*, *Lagarodus*, and *Venustodus* have been found in association with *Densepustula* at fossil sites like Sukha Ravine-1, Sukha Ravine-2, and Lutuhyns'ka-Pivnichna coal mine.

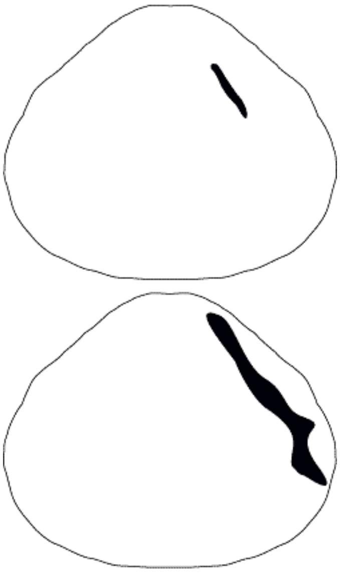
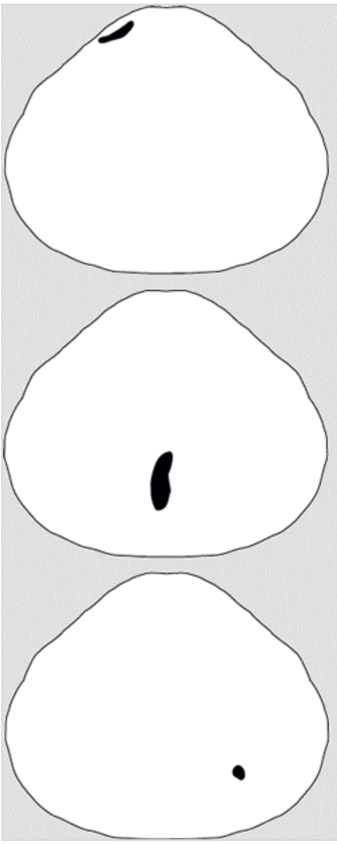
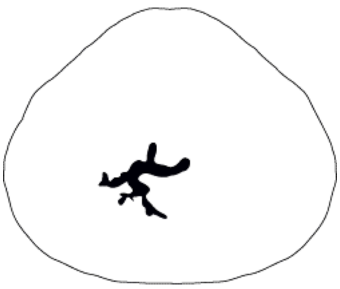
In the Pennsylvanian of the Donets Basin, cephalopods are represented by oncocerids, orthocerids, nautilids, and ammonoids (LIBROVITCH, 1939, 1946; POPOV, 1979; DERNOV, 2018, 2021, 2022a, 2022d, 2023a, 2023b, author's unpublished data). Bactritoids and coleoids have not yet been discovered in this region.

The morphology of the jaw apparatus of Palaeozoic nautiloids is not fully understood due to incomplete and contradictory data (HOLLAND *et al.*, 1978; VOJTÉCH, 1978; EDGECOMBE & CHATTERTON, 1987; HOLLAND, 1987; MAPES, 1987). Palaeozoic ammonoids had weakly mineralized and fragile jaw apparatus (MAPES, 1987; DOGUZHAEVA, 1999; TANABE *et al.*, 2001), which were not suitable for damaging relatively thick-shelled productidine brachiopods. Fossil remains of the ammonoid jaw apparatus found in the mudstones of the Sukha Ravine-2 fossil site (DERNOV, 2022a: Fig. 5) confirm this observation. Additionally, poorly preserved fossils that may represent remains of the jaw apparatus of a coiled nautiloid were discovered inside the body chamber of *Metacoceras* sp. from the Lutuhyns'ka-Pivnichna mine (unpublished author's data), although their interpretation remains ambiguous.

Arthropods are another potential group responsible for predation marks on *Densepustula* (MUNDY, 1982; BRETT, 2003). Trilobite genera such as *Ditomopyge* and *Paladin* are known from the Sukha Ravine-1 and Lutuhynska-Pivnichna mine fossil sites, respectively (MYCHKO & DERNOV, 2019; unpublished author's data). While there are differing views on the feeding habits of trilobites, they are generally considered scavengers, predators, or sediment feeders within their respective taxonomic groups (FORTEY & OWENS, 1999; FORTEY, 2013). However, Carboniferous trilobites from the Donets Basin, which typically did not exceed 3-4 cm in length (WEBER, 1933; MYCHKO & DERNOV, 2019), are unlikely to have caused significant damage to the shells of productidine brachiopods.

Additionally, rare fossils of phyllocarid crustaceans have been found in the black shale of the Sukha Ravine-2. More abundant remains of phyllocarid crustaceans belonging to the genus *Dithyrocaris* have been found in the black shales directly above the sandstones at the Sukha Ravine-1 locality (DERNOV & UDOVYCHENKO, 2019a: Fig. 2.5 and 2.9; DERNOV, 2023d: Fig. 3). Fossil phyllocarids, are known as scavengers/predators, and are documented to feed on small organisms such as mollusks and arthropods, organic particles in sediments (deposit-feeding), or carrion (LIU *et al.*, 2023).

Table 2: Shell injuries of *Densepustula* sp.

Type	Brief description	Sketch	Figures	Possible origin	More examples from the Carboniferous
A	Longitudinal, sublongitudinal and transversal thin straight or sinuous furrows, about 5–7 mm long and 0.5–1.5 mm thick.		Fig. 5.C, H, K	predatory	(1) Sarytcheva, 1949, Pl. 1, fig. 3; (2) Sarytcheva & Sokolskaya, 1952: Pl. 15, fig. 102; (3) Lapina, 1957: Pl. 5, fig. 7a; (4) Brunton, 1966: Pl. 60, fig. 4; (5) Kalashnikov, 1967: Pl. 1, fig. 1; (6) Tyulyandina, 1975: Pl. 2, figs. 1, 8; (7) Kalashnikov, 1980: Pl. 14, fig. 9; (8) Alexander, 1981, Pl. 1, figs. 2, 4; (9) Mundy, 1982: Pl. 4, figs. 1- 2; (10) Elliott & Bounds, 1987: Figs. 2.H- I; (11) Pérez-Huerta, 2007: Fig. 5.16; (12) Lazarev, 2010: Pl. 4, fig. 5; (13) Sun & Baliński, 2011: Fig. $6D_1$, $6D_2$, 6G; (14) Li *et al.*, 2012: Fig. 6.23; (15) Mottequin & Weyer, 2018: Fig. 18.g-h, j.
B	Rounded and ellipsoidal pits, about 3–4 mm in diameter, located on the umbo, anterior margin of the ventral valve and the lateral slopes of the ventral valve.		Fig. 5.A-B, E-G, I-J	? parasitic and/or predatory	(1) Sarytcheva, 1949: Pl. 2, fig. 5; (2) Sarytcheva & Sokolskaya, 1952: Pl. 21, figs. 145, 148; (3) Lapina, 1957: Pl. 5, fig. 7a; (4) Ivanova, 1958: Pl. 16, fig. 2; (5) Monakhova, 1959: Pl. 1, fig. 6b; (6) Kalashnikov, 1967: Pl. 4, fig. 1; (7) Kalashnikov, 1980: Pl. 10, fig. 14a; (8) Mundy, 1982: Pl. 4, figs. 3-4, 7-8; (9) Chen *et al.*, 2005: Fig. 4.27; (10) Pérez-Huerta, 2007: Figs. 5.29, 7.2; (11) Sun & Baliński, 2008: Fig. 8.E; (12) Kucheva, 2010: Pl. 3, fig. 7; (13) El-Shazly, 2011: Pl. 8, figs. 2, 4; (14) Martínez Chacón & Winkler Prins, 2015: Fig. 6.14; (15) Poletaev, 2018: Pl. 28, fig. 4; Pl. 98, fig. 3; (16) Carniti *et al.*, 2022: Fig. 10.N.
C	Irregularly shaped dimples on the anterior margin and in the sulcus, 2–3 mm in size.		Fig. 5.D	predatory	(1) Sarytcheva, 1949, Pl. 1, fig. 2, Pl. 2, fig. 3; (2) Ivanova, 1958: Pl. 3, fig. 3; (3) Beznosova, 1959: Pl. 5, fig. 1a; (4) Böger & Fiebig, 1963: text-fig. 13; (5) Thomas, 1971: Pl. 23, fig. 11b; Pl. 24, figs. 10; (6) Tyulyandina, 1975: Pl. 1, figs. 1, 4, 7; (7) Alexander *et al.*, 1992: fig. 3D; (8) Sun & Baliński, 2011: Figs. $6.E_1$; $6.E_2$, $6.H_1$, $6.H_2$; (9) Poletaev, 2018: Pl. 129, fig. 6.

Among the other marine arthropods likely present in the faunistic communities of the Sukha Ravine-1 site, horseshoe crabs are noteworthy. Their resting traces, identified as the ichnogenus *Crescentichnus* ROMANO & WHYTE, 2015, are frequently found on the bedding planes of the sandstone layer at this locality. In the marine sandstone bed directly beneath the sandstones of the Sukha Ravine-1 site, traces of horseshoe crabs like *Arborichnus* ROMANO & MELÉNDEZ, 1985, and *Selenichnites* ROMANO & WHYTE, 1987, are also common (DERNOV, 2023e).

However, the most likely producers of the shell injuries of *Densepustula* specimens (Fig. 5.C-D, H, K) are holocephalans, specifically species from the genera *Venustodus* or *Lagarodus*. The injuries of Type B observed on *Densepustula* shells (Fig. 5.F-G), similar to injuries on Bashkirian non-marine bivalves *Carbonicola* from of the Donets Basin (DERNOV, 2022c, 2023c), suggest parasitic invasions as potential causes. These injuries also resemble small pits found on fossil cephalopod steinkerns, interpreted as impressions of blister pearls, *i.e.*, a natural defensive reaction of the host organism to foreign body like parasites (DE BAETS *et al*., 2011; BINDER, 2015; LI *et al*., 2016; KHALILI & VINN, 2023). However, the injury in Fig. 5F-G is located on the outer surface of the valve, which precludes it from being a blister pearl (DE BAETS *et al*., 2021).

The producers of rounded drill holes in the skeletons of Late Palaeozoic marine invertebrates, which somewhat resemble the injuries of Type B described above, are usually considered to be platyceratid gastropods (LEIGHTON, 2001; KOWALEWSKI *et al*., 1998; KOWALEWSKI, 2002; KLOMPMAKER *et al*., 2016). Additionally, the producers of these holes may be mysterious soft-bodied animals (CARRICKER & YOCHELSON, 1968; ROHR, 1976; AUSICH & GURROLA, 1979), but it is impossible to verify this assumption. In the Late Palaeozoic, naticid-like drill holes in shells are known, but they cannot be attributed to naticid producers because no skeletal remains of these organisms are preserved with the drilled ichnotaxa. LEIGHTON (2003) reports that the holes produced by platyceratid and naticid gastropods differ in size: the former are up to 1.6 mm in diameter, and the latter are larger than 1.6 mm.

The injuries of Type B differ from the Palaeozoic cylindrical holes, which penetrate shells completely and are attributed by the vast majority of researchers to be traces of gastropod predation (see above) by several important morphological features: 1) the pits described in this paper are not through holes, but concavities on the surface of the valves (some specimens (Fig. 5A) show surviving damaged areas of the valve, and others (Fig. 5G) show very gradual, rounded edges of the pits, *i.e.*, probably show signs of regeneration); 2) the shape of the described pits and drill holes of predatory gastropods is different: the former are conical and semicircular, and the latter are cylindrical in longitudinal section.

In addition, it should be noted that the injuries described above cannot be attributed to bioerosion trace fossils, as it is highly unlikely that bioeroders could have fixed themselves on the ventral valve, which was densely covered with pustules and faced downwards in lifetime position. This was probably not possible even after the death of the brachiopods, as numerous shells from the Sukha Ravine-1, Sukha Ravine-2, and Lutuhyns'ka-Pivnichna coal mine sites show no traces of either lifetime or postmortem bioerosion, with the exception of the ichnogenus *Cyclopuncta*, which was found exclusively on cephalopod shells (Dernov, 2022a; 2024b).

Comparing the described assemblage of injured shells with other records is difficult due to the limited data on shell damage in specimens of the same species.

Furthermore, the amount of material studied is quite limited and may affect the reliability of quantitative results. However, the data reported on the ratio of injured brachiopod shells to intact shells are close to the values obtained in this study. For example, ALEXANDER (1986b) reports that the number of injured brachiopod shells from the Upper Ordovician of the USA (Indiana, Kentucky, and Ohio border area) varies from *c.* 0.5% to *c*. 26.0% for different taxa [median 5.5%, mean 8.0%; own calculations based on data in ALEXANDER (1986b: Table 1)]. A similar number (*c*. 9.5%; 57 specimens) of injured shells of Late Devonian brachiopods from China is given by ZONG & GONG (2022) for a collection consisting of 603 specimens.

Approximately such a significant variation in the number of injured gastropod shells (4.8-35.7%) of two species, *Trochonemella* sp. and *Lophospira trilineata* (HALL, 1858), is given by EBBESTAD and STOTT (2008) for material from the Upper Ordovician of Canada. It should be noted, however, that these two species are represented by a disproportionate number of specimens (28 shells of *Trochonemella* sp. and 207 shells of *Lophospira trilineata*). This circumstance probably strongly influenced the variation in the number of injured shells.

However, this ratio can change significantly towards an increase in the proportion of injured shells. For example, ELLIOTT & BOUNDS (1987) recorded damage to 53.7% of shells (503 out of 935) of the brachiopod *Composita subtilita* (HALL, 1852) from the Middle Pennsylvanian-aged Naco Formation of Arizona, USA. It seems to me that this value is somewhat overestimated, since not all brachiopod specimens with evidence of predator attacks figured by ELLIOTT & BOUNDS (1987) may actually be such. Many of them [*e.g.*, ELLIOTT & BOUNDS (1987: Fig. 2D, K)] are probably signs of diagenetic sediment compression.

LEIGHTON (2003: Fig. 5), using data provided by ALEXANDER (1986b), reports that the frequency of sublethally injured shells of Palaeozoic brachiopods ranges from <1.0% to 9.7%. These values are probably the closest to the real ones, as they are based on the results of studying 14 assemblages of Palaeozoic brachiopods.

6. Conclusion

Three morphological types of shell injuries of the Late Bashkirian and early Moscovian productidines from the Donets Basin are distinguished. Type A is represented by longitudinal, sublongitudinal, and transverse thin straight or sinuous furrows. Type B consists of rounded and ellipsoidal pits located on the umbo, anterior margin of the ventral valve, and the lateral slopes of the ventral valve. Type C is characterized by irregularly shaped dimples on the anterior margin. The most likely producers of Types A and C are cartilaginous fishes, and these injuries are probably evidence of unsuccessful predation. The origins of Type B are likely to be parasitic and/or predatory.

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