INTRODUCTION

Upper Carboniferous–Lower Permian biogenic carbonate buildups are widespread throughout the world (Wahlman, 2002). They are numerous on the western slope of the Urals; the most famous of them being the ‘Reef’ massif on the Kozhym River (Subpolar Urals) and biogenic structures in the Southern Urals (called ‘shikhans’), which have been described in the international literature (Antoshkina, 1997; Kossovaya et al., 2013; Vennin et al., 2002; Wahlman &
Konovalova, 2002). In addition to these, there are a large number of other organic buildups, the location and age of some of which are shown in Figure 1. One of the most representative amongst them, although relatively poorly studied, is the Pisanyi Kamen’ section on the Un'ya River, Northern Urals. This section is located in the Verkhnaya Pechora transverse subsidence territory (Timonin, 1998; Yudin, 1983), the tectonic structure of the western slope of the Northern Urals, which in the south and south-west borders with the Polyudov transverse uplift (the south-eastern end of the Timan within the Pre-Urals Foredeep). In the north-west it borders with the Pechora-Kozhva megalithic bank and the southern continuation of the Timaiz transverse uplift. In the Palaeozoic a marine basin existed here, with a sedimentation history somewhat different to that of the northward regions. For example, organic buildups in the Un’ya River basin are of Asselian age (Kalashnikov & Mikhailova, 1971), while the age of northward (Northern and Subpolar Urals) and southward (Southern Urals) buildups are Late Gzhelian–Sakmarian (Antoshkina, 2003; Wahlman, 2002; Wahlman & Konovalova, 2002). Also, the Pisanyi Kamen’ section geographically occupies an intermediate position between the Southern Urals Shikhans, which are considered reefs (Chuvashov et al., 1990; Cuvashov, 2011; Kossoyava et al., 2013; Vennin et al., 2002), and the Upper Gzhelian–Lower Sakmarian buildups in the Subpolar Urals and the Pechora Large Depression (PLD), regarded as skeletal mounds (Antoshkina, 2003; Zhemchugova et al., 2020). There is also no unanimous opinion about the palaeotectonic position of the Lower Permian buildups. Thus, the South Uralian shikhans are confined to the western boundary of the Pre-Uralian Foredeep (Chuvashov, 2011; Chuvashov et al., 1990). The skeletal mounds of the Subpolar Urals and the PLD, according to Antoshkina (2003) and Zhemchugova et al. (2020) developed on the slopes of depressions that appear during the sea floor differentiation (Antoshkina, 2003) associated with the activation of collisional tectonic processes (Puchkov, 2010). These various aspects raise interest for the structure, composition, biota and formation conditions of the Pisanyi Kamen’ reef sequence.

The reefal nature of the exposed rocks was first established by Varsanofieva (1933). Ravikovich (1956) determined the genesis of this organic buildup as a ‘submarine reef’, the top of which was several metres below sea level. It was based on the absence of high energy grainy limestones both in the Pisanyi Kamen’ section itself and in the adjacent sections. Studies of brachiopod and fusulinid assemblages have shown the Pisanyi Kamen’ section to be Asselian in age (Kalashnikov & Mikhailova, 1971). Antoshkina (2003)
suggested the genesis of Upper Carboniferous–Lower Permian buildups as skeletal mounds based on lithological and palaeoecological observations. However, this interpretation of the nature of Northern Urals buildups was based on the descriptions of Ravicovich (1956). Further studies by Sandula (2005) identified several intervals in the lower and middle part of the Asselian portion of the Pisanyi Kamen’ organic buildups that differ from each other by rock texture and predominant fossils. Sandula (2005) assumed that these intervals reflect the developmental stages of this organic buildup. Revision of the previous data and the acquisition of new data provide an opportunity to identify intervals with a different fossil composition in the Pisanyi Kamen’ section, which were repeated in the sequence in a specific way. It was established that this section comprises several organic structures stacked one upon the other, instead of a single one, as previously suggested (Ponomarenko, 2015).

This paper first provides a lithological and palaeoecological description of the Lower Asselian part of the Pisanyi Kamen’ section. Then follows a discussion of the composition and evolution of the palaeocommunity in order to shed light on the buildups history and development.

2 METHODS AND STUDY AREA

In 1930, a Biosphere Reserve was created on the immense territory between the Pechora River and the Ilych River. Vera Aleksandrovna Varsanofieva, the first woman to receive the degree of Doctor of Geology in the USSR, wrote about this area as very remote with a complete absence of roads (Varsanofieva, 1940). Since then little has changed here, in the (from north to south) Ilych River, Pechora River and Un'ya River basins. This area still remains one of the most remote places in the Komi Republic (Russia).

The author studied the Pisanyi Kamen’ section (Figure 1A) in 2009. For practically its entire length (all but the lower 35 km out of 163 km), the Un'ya River displays a mountain river character with numerous rapids. The Pisanyi Kamen’ section is a cliff exposure, partly in the water, and partly in the nearby forest (Figure 2). The dip of the ‘layers’ in these massive rocks was determined by the position of the geopetal fabric: the section climbs stratigraphically from east to west at angles of 85–90°. The section was described from the base of the cliff, when it was possible to step onto land, as well as from a rubber boat when landing was impossible. The cliff exposures in the forest were covered with lichen, making it difficult to observe the rock textures. Where the cliff dropped into the water, the rock composition and textures were clearly visible, but the strong river currents and deep water made describing, sampling and labelling very difficult. Sometimes therefore, ‘layer’ thicknesses were estimated with an error of ±5%. The Lower Asselian interval (140 m) described here was extensively sampled (102 samples). Of these, thin sections and slabs were made for study under petrographic microscope. The collection of specimens and thin sections is kept in the A.A. Chernov museum at the N.P. Yushkin Institute of Geology of the Komi Science Center of the RAS, Syktyvkar (collection No. 714).

3 GEOLOGICAL SETTING

The study region, the Vekhnaya Pechora transverse subsidence, is part of the western slope of the Northern Urals, and belongs to the south-eastern part of the Timan-North Uralian lithosphere block (=Pechora plate) (Pystin et al., 2008). From the west, this area is bordered by the PLD. This location, near the junction of a number of large tectonic structures (Timan in the south and the Pechora-Kozhva megalithic bank in the north), determined the complex character of the Upper Palaeozoic succession.

The Palaeo-Uralian Ocean originated during the Ordovician, and its closure—at the Early to Middle Permian boundary. During the Palaeozoic, the North Urals sedimentary basin was part of the larger megabasin of the north-eastern passive margin of the European continent (Antoshkina et al., 2012).

The Lower Permian organic buildups of the Northern Urals western slope are part of a large Visean-Sakmarian carbonate shelf complex. This complex was formed during active regional tectonic movements against the background of the Gondwana continental glaciations (Antoshkina, 2003; Antoshkina & Ponomarenko, 2014; Wahlman, 2002).

The Early Visean transgression caused terrigenous deposition, which was replaced by carbonate sedimentation during the Middle Visean (Tulian Regional Stage; Eliseev, 1978; Kalashnikov, 1970; Shadrin & Ivanova, 2019; Varsanofieva et al., 1973). Marine carbonate sediments continued to accumulate until the Artinskian (Antoshkina et al., 2011; Eliseev et al., 2006).
The collision of the East European and Kazakhstan continents had a strong influence on sedimentation, which, according to Puchkov (2010), in the northern part (in modern coordinates) of the Palaeo-Uralian Ocean began during Tournesian-Early Visean times. It was accompanied by formation of the Pre-Urals Foredeep, which initially formed on deep bathyal sediments, but, migrating westward, rolled over the shelf edge and entrapped it (Puchkov, 2010). According to Puchkov (2010), the collision was intense during the Late Carboniferous and Early Permian. Such an intensification of collisional processes of the Palaeo-Uralian Ocean active and passive margins was expressed in the Foredeep western flank bottom differentiation, which was encroaching upon the carbonate platform (Antoshkina, 2003; Saldin, 1996). Here, on the slope of this trough, organic buildups were locally developed (Antoshkina, 2003; Antoshkina et al., 2012), one of which now outcrops in the Pisanyi Kamen’ section.

### 3.1 | Stratigraphic framework

In the first half of the 20th century, Varsanofieva (1933, 1940) identified three submeridional zones of Carboniferous deposits in the Northern Urals: western, central and eastern (in modern coordinates). These traditional divisions are used here (Figure 3).

Detailed sequence-stratigraphic analysis of the Northern Urals Carboniferous–Lower Permian deposits was not carried out. This section emphasises only some important sea-level changes, which were noted by the author and his colleagues when studying the Upper Moscovian–Sakmarian deposits of the Northern Urals. Here, in a relatively stable tectonic regime, shallow-water Pennsylvanian (Bashkirian–Middle Kasimovian) deposits accumulated, represented by bioclastic grainstones and packstones, and occasionally by algal boundstones (Antoshkina et al., 2011; Eliseev, 1978; Eliseev et al., 2006; Ponomarenko & Ivanova, 2020). They are characterised by cyclic sequences (especially the Moscovian deposits),
most likely related to the glacioeustatic sea-level oscillations characteristic of this time (Montanez & Poulsen, 2013; Wahlman, 2002). Middle Kasimovian deposits \textit{(Montiparus montiparus zone)} are reliably established only on the Un’ya River (Ponomarenko, 2015) and the Pechora River (Mikhilova, 1974). Northward (the Ilych River basin), the Middle Kasimovian interval was not established, probably indicating a stratigraphic break in sedimentation (Ponomarenko & Ivanova, 2020). Upper Carboniferous (Kasimovian and Gzhelian) deposits were not identified in the western outcrops, which might indicate a stratigraphic unconformity. Instead, here, near the outcrops of the Moscovian deposits, Middle Asselian limestones (Kalashnikov & Mikhailova, 1971) are exposed (TS section in the Utlan River and Svetlyi Rodnik and Pervokamennaya cliffs in the Un’ya River; Figure 3). However, since there are no continuous sections, where the Moscovian rocks would directly underlie the Middle Asselian rocks, the case of local tectonic contact is not excluded.

The next major sedimentation cycle began during the Late Kasimovian (Ponomarenko, 2015; Ponomarenko & Ivanova, 2020) and finished during the Middle Gzhelian (Figure 3). The shallowest deposits are Middle Gzhelian in age \textit{(Daixina sokensis zone)}, and include wavy clotted mudstones (microbial laminites?) and lime breccias (Figure 3). A relative sea-level fall during the Late Gzhelian is also noted within the PLD (Zhemchugova, 2002) and in the Subpolar Urals (Antoshkina, 2003). Northward of the Un’ya River basin, sediments of Gzhelian age are less abundant. On the Pechora River, Upper Gzhelian deposits have not been identified \textit{(Daixina robusta-Daixina bosbytauensis zone)}, and, in the Ilych River basin, Gzhelian deposits are absent.

The next sea-level rise (Timonin, 1998; Zhemchugova, 2002) created a surface, above which the Lower Permian organic buildups of the Northern Urals were developed. During the Early Permian the amplitude of glacioeustatic sea-level fluctuations began to decrease (Wahlman, 2002), but these fluctuations were still quite frequent (Montanez & Poulsen, 2013). Some of them were better developed in the shallower Asselian-Sakmarian sequences of the PLD (Zhemchugova, 2002; Zhemchugova et al., 2020). However, in the Un’ya River Basin, in the Buzgalskiy Kamen’ section (Figure 4), evidence for high-frequency oscillation in the relative sea level is lacking which is probably caused by the ‘subtidal missed beats’ effect (Elrick, 1995; Goldhammer et al., 1990, 1993; Guo et al., 2018; Osleger & Read, 1991), possibly due to deeper sedimentation in the Verkhnaya Pechora sedimentary basin.

However, there is a significant relative sea-level fall at the boundary between the Lower and Middle Asselian. In the south, in the Un’ya River basin, the fall in sea level is expressed by the westward shift in reef facies during the subsequent Middle Asselian transgression (Ponomarenko, 2015). To the north, in the Ilych River basin, at this stratigraphic level in the reef facies there is an erosional surface and a decrease in the thickness to as little as 2 m (compared to a thickness of 22–50 m in the Un’ya River sections). The Middle Asselian transgression was more extensive; thus, after a large probable stratigraphic gap, sedimentation started again in the western zone of the study area (Figures 3 and 5).

In the study area, carbonate sedimentation ends with silicified bryozoan clayey packstones overlapping biohermal limestones in the Pisany Kamen’ section (Figures 3 and 5). No fusulinids are found here and the section has been conditionally attributed to the Upper Asselian (Kalashnikov & Mikhailova, 1971). Further northward, on the Ilych River, similar deposits are dated by Sakmarian fusulinids (Ponomarenko, 2015).

### 3.2 Palaeogeographic setting and facies

The Asselian-aged carbonate sedimentation in the north part of the Urals and the PLD included three common palaeogeographically and lithologically different realms: carbonate shoals, a relatively deep-water depression and organic buildups (Antoshkina, 2003; Antoshkina et al., 2011, 2012; Eliseev, 1978; Eliseev et al., 2006; Ponomarenko, 2015; Zhemchugova et al., 2020).

**Carbonate shoal sediments** are developed in the westernmost part of the studied area, close to the border of the Verkhnaya Pechora depression. On the Un’ya River basin, they are briefly described in the Svetlyi Rodnik and Pervokamennaya sections (Kalashnikov & Mikhailova, 1971; see the schematic map in Figure 3). They were observed here on the Tyagla Creek (TS section in Figure 3).

Here, the Middle to Upper Asselian deposits are represented by grainy (bioclastic) limestones (Table 1). These

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**FIGURE 4** An idealised model of the Lower Permian skeletal mounds of the Northern Urals. After Ponomarenko (2015)
are well-bedded rocks (0.5–1.5 m, rarely up to 2.0 m), which characterise open, normal-marine conditions above and below fair-weather wave base. These microfacies can be arranged in the following deepening-upward sequence: bioclastic packstones/grainstones; bioclastic wackestones/packstones; bioclastic-clotted bindstones; palaeoaplysinid boundstones; phylloid-algal or bryozoan bafflestones. The last three microfacies are associated with bedded units, which allow them to be assessed as biostromes. Northward, in the Ilych River, several erosional surfaces were observed in the westernmost sections of the Middle to Upper Asselian deposits (Ponomarenko, 2015). These surfaces reflect regressive events, possibly those associated with the glacioeustatic sea-level fluctuations characteristic of this time (Montanez & Poulsen, 2013; Wahlman, 2002). However, poor and fragmentary exposures did not allow these deposits to be recognised in the Tyagla Creek section.

Deposits formed in relatively deep-water, typical of the central section, are well exposed in the Buzgal’skiy Kamen’ outcrop on the Un’ya River (Figure 3). These are usually thin-bedded (0.1–0.3 m in thickness) rocks. They are characterised by microbioclastic wackestones/mudstones with nodules, lenses and interlayers of diagenetic cherts (Table 1). Thin layers (0.1–0.3 mm) of bioclastic wackestones/packstones appear here mainly in deposits of Middle Asselian age. The fossil composition is varied and similar to those in Lower Permian organic buildups (see below). Apparently, these fossils were transported from the buildups during sedimentation. Microfacies of microbioclastic wackestones/mudstones and bioclastic wackestones/packstones are depicted at
| Microfacies                          | Thickness (m) | A brief description | Fossil composition                                                                 | Sedimentation conditions                                                                 |
|------------------------------------|---------------|---------------------|-------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------|
| Association of grainy (bioclastic) limestones |                |                     |                                                                                     |                                                                                          |
| Bioclastic pack/grainstones         | 0.5–1.0       | Organic material (80%–95%) from 0.1 to 4.0 mm, cemented with sparite or micrite (up to 10%); patches with microbial clots | Crinoid ossicles are dominant, subordinate bryozoan fragments with rare fusulinids and small foraminifers; occasionally common micritized fragments of palaeoaplysinids and/or Tubiphytes | Shallow-marine conditions, above and/or immediately below fair-weather wave base            |
| Bioclastic wacke/packstones         | 0.5–2.0       | Bioclasts (40%–70%) from 0.3 to 1.5 mm are cemented with micrite (up to 30%) | Crinoid ossicles and tubular green algae (Donezella type) predominate. Fusulinids are common. Red algae, brachiopods, small foraminifera, filamentous cyanobacteria are rare. In rare cases, possibly calcareous sponges | Open normal-marine conditions below fair-weather wave base; quiet waters with bioclastic sedimentation |
| Bioclastic-clotted bindstones       | 0.5–1.5       | Micritic clots (55%–80%) with subordinate small (0.3–1.0 mm, very rare up to 3.0 mm) bioclasts (20%–45%); micrite or sparite cement | Crinoid ossicles and bryozoan fragment are common; fusulinids, small foraminifers, osstracods, red algae (probably Ugdarellaceae) and filamentous cyanobacteria fragments are rare. Sometimes fragments of Tubiphytes and palaeoaplysinids, brachiopod valves and trilobites | Open-marine conditions below fair-weather wave base. Subtidal microbial mats that bind together fine bioclastic material removed from shallower areas of sea bottom |
| Palaeoaplysinid boundstones         | 1.0–1.5       | Palaeoaplysinid plates (up to 60%) are parallel to each other. Bioclastic material (30%) (0.1–2.0 mm) and micrite (10%) are developed between them | Phylloid algae, fusulinids, crinoid ossicles, bryozoans and cyanobacteria filament fragments are observed between abundant Palaeoaplysinid plates | Open-marine normal conditions below fair-weather wave base. Facies of palaeoaplysinid settlements |
| Phylloid-algal or bryozoan bafflestones | 0.7–1.5     | Phylloid algae or bryozoans (up to a few centimetres in size) in growth position. A bioclastic-micrite matrix is developed between them | Bryozoans or phylloid algae predominate; crinoid ossicles, fusulinids, small foraminifers and brachiopods are cited in the interframe cavities | Open-marine conditions below the fair-weather wave base. Facies of algal and bryozoan thickets, bathymetrically lower than palaeoaplysinid settlements |
| Muddy limestones association (Sezym Formation and its analogues) |                |                     |                                                                                     |                                                                                          |
| Microbioclastic wacke/mudstones     | 0.1–1.5       | The bulk mass is represented by micrite (60%–80%) with subordinate fine (<0.1 to 0.5 mm) bioclasts (20%–40%) | Unidentified (<0.1 mm) microbioclasts (up to 80% of fossils) predominate. The subordinate biota is represented by crushed brachiopod shells (up to 3.0 cm), fenestrate bryozoans and crinoid ossicles | Open-marine conditions below the fair-weather wave base, away from bioclastic shoals |
| Bioclastic wacke/packstones         | 0.1–4.5       | Bioclasts (up to 1.0–2.0 mm) prevail (70%–90%); micrite is developed in the intergranular space (10%–30%) | Bryozoan and palaeoaplysinid fragments often predominate. Fusulinids, green phylloid and dasyclasyclad algae fragments, cyanobacterial tangles, Tubiphytes, crinoid ossicles, small foraminifers, brachiopods and pelecypods are common. Some small foraminifers, cyanobacteria filaments, and Tubiphytes encrust some bryozoan fragments | Open normal-marine conditions below fair-weather wave base, away from bioclastic shoals, but closer to the organic builds facies. These layers apparently represent accumulation of organic debris, carried away from the Lower Permian organic builds |

(Continues)
Organic buildups on the Un’ya River constitute the easternmost section type (Figure 3). Unfortunately, it is impossible to determine the structure of such complex formations from one section. Therefore, only after many years of research was it possible to develop an idealised model for the Lower Permian buildups of the Northern Urals (Figure 4). When this idealised model was first drawn (Ponomarenko, 2015), the strikingly similar coeval mounds of Arctic Canada (Beauchamp & Olchowy, 2003) were not considered. The central part of the buildups, mainly represented by biocementstones (this is rock composed of more than 50% bioinduced cements; for details see Section 5.1), as well as the western gentle slope and eastern steep slopes are distinguished here. In the slope facies, in addition to biocementstones, a significant role is played by clotted bindstones and bioclastic packstones and wackestones. They gradually evolve into bedded mudstones with rare brachiopods, fusulinids and crinoids.

In the Pisanyi Kamen’ section in the Lower Asselian interval, the central part of the organic buildups is composed mainly of biocementstones. Eastward, in the Pisanyi Kamen’ section, clotted bindstones with biocementstone lenses and lime mudstones began to form, which are interpreted to represent the eastern margin of skeletal mounds (Ponomarenko, 2015). The central part of the Middle Asselian skeletal mound, composed of biocementstones, crops out in the Chortov Stul’chik section (Kalashnikov & Mikhailova, 1971). In the Buzgal’skiy Kamen’ section, lime mudstones with subordinate packstones were contemporaneous deposits. Mudstones, as background deposits, show the same textures and fauna in both the Lower Asselian and Middle Asselian stages. Subordinate packstones contain abundant clots, cyanobacterial and Tubiphytes fragments, dasyclad green algae and red algae, Palaeoaplysinsids plates, bryozoans, small foraminifers, fusulinids, brachiopods, pelecypod fragments and crinoid ossicles. This assemblage is evidence of an increase in organic material derived from skeletal mounds and suggests that the area where organic buildups form has shifted a little westward.

4 | COMMUNITIES OF THE CENTRAL PART OF THE LOWER PERMIAN ORGANIC BUILDUPS

As noted earlier (Ponomarenko, 2015; Sandula, 2005), at the Lower Asselian stratigraphic level in the Pisanyi Kamen’ section, several intervals are distinguished which differ in lithology and fossil assemblage (Figure 6). A description is given below.

4.1 | Interval I

The deposits of Interval I in the Pisanyi Kamen’ section (10 m thick) are characterised by bioclastic packstones (Figure 7B) in the lower part and by microbial clotted bindstones with irregular areas of biothermal bryozoans biocementstones in the upper part (Figure 7A,C,D). Abundant ramose colonies of bryozoans are characteristic of this interval. Their generic diversity is low and is represented mainly by Fenestella with rare Polypora (Ravikovich, 1956). Locally there are accumulations of free-lying and anchored brachiopods including Chonetes uralicus Moell., Pugnax sp., Dielasma sp. (Kalashnikov & Mikhailova, 1971). Fragments of Tubiphytes, cyanobacteria, crinoids, trilobites and single sponge spicules are found everywhere (Figure 7B).

4.2 | Interval II

Bryozoan biothermal biocementstones are predominant in the lower part of Interval II (Figure 7E; total extent 8.5 m thick). Bryozoans are mainly represented by net-like growth forms. In the upper part, phylloid-algal biocementstones are more abundant. Phylloid algae are dominant among the algae although higher in the sequence they are replaced by dasyclad algae (Figure 7F,G). At the top of Interval II, small foraminifers, fusulinids, fragments of Palaeoaplysina, crinoid ossicles, fenestellid bryozoans and cyanobacterial tangles (Girvanella?) appear. All of these fossils are rimmed by 0.5–2 mm thick synsedimentary
| Microfacies of phylloid-algal and palaeoaplysinid biocementstones are also rare here; a brief description is given in the next part of the table, since they are widespread in the facies of the central part of the Lower Permian buildups |

### TABLE 2  Common microfacies of the Asselian organic buildups

| Microfacies                        | Thickness   | A brief description                                                                 | Fossil composition                                                                 | Sedimentation conditions                      |
|-----------------------------------|-------------|-------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------|-----------------------------------------------|
| Biohermal limestones association  |             |                                                                                     |                                    |                                               |
| Western gentle slope zone facies  |             |                                                                                     |                                    |                                               |
| (2–4 on Figure 4)                 |             |                                                                                     |                                    |                                               |
| Bioclastic mud/packstones         | 0.1–1.0 m, rare up to 5.0 m | Unsorted bioclasts (10%–80%) in a micrite matrix (20%–90%) | Fragments of *Tubiphytes*, phylloid algae, palaeoaplysinids, and fenestrate bryozoans; rare fusulinids and small foraminifers, crinoid ossicles, brachiopod and gastropod shells | Open shallow-marine environments below the fair-weather wave base |
| Foraminiferal-cyanobacterial      | 0.2–3.8 m   | The rocks are composed of cyanobacteria colonies (0.5–0.7 mm) and small attached foraminifers, connected by biologically induced cements. Small interframe cavities are filled with sparite cements, micrites and/or bioclasts | Cyanobacteria (*Girvanella* type), small foraminifers, bioclasts of green (dasyclad) and red algae, bryozoans, crinoids and fusulinids in interframe cavities | Open shallow-marine environments below the fair-weather wave base |
| biocementstones                   |             |                                                                                     |                                    |                                               |
| Bryozoan and *Tubiphytes*         | 1.0–1.2 m in facies 2, as well as 0.7–7.5 m in facies 3 | Rocks consist of fenestrate bryozoans (35%–40%) and *Tubiphytes* (up to 20%), and biologically induced cements. Micrite and sparite in small interframe cavities, forming geopetal fabric | Fenestrate bryozoans, *Tubiphytes*, sometimes various brachiopods. Rare crinoid ossicles, green phylloid and dasyclad algae. In interframe cavities, small foraminifers, gastropod and fusulinid shells are sometime additionally noted | Open shallow-marine environments below the fair-weather wave base |
| Bromazoan-bryozoan biocementstones|             |                                                                                     |                                    |                                               |
| Bioclastic biocementstones        | 2.0–5.0 m   | Rocks are composed of bioclastic material (40%–50%) with biologically induced cements and sparite calcites | Fossils are very diverse; fragments of palaeoaplysinids, *Tubiphytes*, bryozoans, green (phylloid and dasyclad) and red algae, small foraminifers and fusulinids, crinoid ossicles, brachiopods, gastropods | Open shallow-marine environments, at or immediately above the fair-weather wave base |
| Clotted bindstones                | 1.0–12.6 m  | The rock is composed of small (up to 0.1 mm) micritic clots (60%–80%), which are often linked in small (up to 0.5 mm) clusters; a small sparite calcite is developed between them. Thin cement crusts are sometimes noted | Mostly microbial clots. Fragments of whole fossils are rare, they are represented by almost all types characteristic of the Lower Permian buildups | Open shallow-marine environments below the fair-weather wave base |

(Continues)
zonned calcite crusts. Framework voids are usually filled with either sparry calcite or clotted bindstones with rare bioclasts.

4.3 | Interval III

This interval (50.5 m thick) is dominated by bioclastic biocementstones. In the lower part, among the bioclastic material, there are numerous fragments of green dasyclade algae, *Palaeoaplysina*, *Tubiphytes*, crinoids, fusulinids, small foraminifers and cyanobacterial tangles (Figure 8B). In the upper part, Palaeoaplysinid fragments begin to predominate (Figure 8A). Larger fragments of their plates (7–12 cm) are oriented, but small fragments (1–5 cm) are not. All fossil fragments are encrusted by zoned fibrous calcite. This fact underlines the crucial importance of the synsedimentary biologically induced cements in the Pisanyi Kamen’ carbonate skeletal mounds; without this cementation, these rocks would be just bioclastic grainstones or rudstones. Instead, a bioclastic biocement-supported framework is observed, defined in structural classification terms (sensu Riding, 2002) as a segment-cement. In framework cavities clotted bindstones with rare bioclasts are present.

4.4 | Interval IV

The deposits of this interval (68.9 m thick) are mainly represented by phylloid-algal biocementstones (Figure 8C–E); rare
Palaeoplysinids appear only in its terminal part. Among algae, phylloid Anchicodium sp. with subordinate Eugonophyllum sp. and Epimastopora sp. are dominant. Algae thalli are encrusted with Girvanella threads and small foraminifers Tolypammina sp., Glomospira sp., Palaeonubecularia sp., Syzrania sp., Tubertina sp. and others (Ponomarenko & Ivanova, 2010). The phylloid algae thalli are cemented by zoned biologically induced calcite crusts up to 1.0 cm in thickness. In this interval, two types of phylloid algae biocementstones can be recognised (Figure 8C–E): (a) dark-gray crusts with thin, small algal thalli; and (b) light-gray crusts with larger thalli. In the first case, the cement colour is caused by the high micrite content which occurs both between individual zones of crust and between calcite fibers (Figure 8D). The change in lithology may indicate a change between quiet sea water conditions and some more active environments, and/or alternation of cloudy and cleaner waters. It is possible, however, that these two factors could act together. In small framework cavities, clotted bindstones with low amounts of small foraminifers Globivalvulina sp., Ammodiscus sp., Tetrataxis sp., fusulinids Schubertella sp., Eoschubertella sp. and Triticites sp., also problematic Tubiphytes obscursus Masl., are observed (Ponomarenko & Ivanova, 2010).

Except for a few intervals, green algae (i.e. phylloid algae with subordinate Dasycladaceae) are widespread in the Pisanyi Kamen’ section. This composition sharply distinguishes them from other deposits in the Urals, which are characterised by abundant Tubiphytes and bryozoans. Organic buildups of the Northern and Subpolar Urals (Antoshkina, 2003; Ponomarenko, 2015; Wahlman & Konovalova, 2010).

FIGURE 6 Structure of the Lower Asselian organic buildups in the Pisanyi Kamen’ section
2002) are distinguished by the absence of coral and stromatolites, which are noted in the South Uralian shikhans (Kossovaya et al., 2013; Wahlman, 2002), and they also lack Archaeolithophyllum, which are common contributors to the Lower Permian buildups around the world.

5 | DISCUSSION AND INTERPRETATIONS

5.1 | Buildups type in the Pisany Kamen’ section

A number of different methods have been used to study ancient reefs resulting in: (a) the appearance of new terms; (b) a change in the meaning of pre-existing terms, and; (c) a noticeable difference in the understanding of some terms. For example, the term ‘reef’ has at least two meanings: (a) a reef (sensu lato) as the most general concept covering all organic structures (Flügel & Flügel-Kahler, 1992; Riding, 2002; Wood, 1998); (b) a reef (sensu stricto) as a structure with depositional relief where the top is above wave base and the slopes are made up of reworked sediment or, more precisely, a rock association, which constitutes a facies set of the reef complex (Antoshkina, 2003; James, 1978; James & Bourque, 1992). But even in the latter case, the term ‘reef’ may have different meanings depending on the point of view (landscape-morphological, ecological, geological, etc.). Some of the most comprehensive reef-related reviews are given in Riding (2002) and Antoshkina (2003). Here, the author uses the definition of Antoshkina (2003) of reef as “…a large complex structure on the shallow

FIGURE 7  The main types of rocks in Interval I (A–D) and Interval II (E–G). (A) Areas of bryozoan biothermal biocementstones in the bryozoan-clotted bindstone. Sample P-Un28/152-2009. Polished slab. (B) Bioclastic bryozoan wackestone. The lime muddy matrix contains numerous fragments of bryozoans (Bry) with rarer fragments of ostracods (O), brachiopods (Br) and sponge spicules (S). Thin-section P-Un 28/156-2009. (C) The clotted bindstone with areas of bryozoan biocementstones (Cl—clots; Bry—bryozoan fragments; Cem—cement crusts). Thin-section P-Un28/151-2009. (D) A small bryozoan colony rimmed by the early diagenetic calcite. Thin-section P-Un28/151-2009. (E) Bryozoan biocementstone with net-like bryozoans (Bry). Single fragments of gastropods (Ga) are noted. Thin-section P-Un28/147-2009. (F) A phylloid algae thalli fragment rimmed by thick fibrous cement crusts. Thin-section P-Un28/143-2009. (G) Dasyclad algae colony fragment (Da, oblique section) in the biocementstone. Thin-section P-Un28/140-2009
shelf margin, having a primary biogenic framework of climax stages of the ecological succession and presenting a tectonically-controlled eco-sedimentary barrier that separates the back-reef and fore-reef areas that are different in their hydro-physical-chemical properties” (Antoshkina, 2003, p. 26).

Another well-known type of organic buildup—carbonate mud mounds—was popularised by Wilson (1975). Later, James (1978) introduced the term ‘reef mound’ for organic buildups that grew below the fair-weather wave base. Further, James and Bourque (1992) simplified the matter by referring to ‘mounds’, distinguishing among them mud mounds, microbial mounds and skeletal mounds. Bosence and Bridges (1995, p. 4) introduced biodetrital mud mounds in which “… the dominant composition is broken and transported skeletal debris”.

A comparison of the Lower Permian buildups of the Northern Urals (Ponomarenko, 2015) with the shallow-water reefs which crop out in this area (Upper Ordovician, Upper Silurian and Lower Devonian: Antoshkina, 2003; Ponomarenko, 2018a; Shmelyova, 2016, 2018, 2020), establishes a number of differences:

1. Shallow-water reefs are composed of highly diverse communities dominated by organisms which develop large and massive colonial forms, while the Lower Permian buildups are composed chiefly of sessile, delicate and small fossils.

2. In the Upper Ordovician–Lower Devonian reefs, landscape and facies zones (reef crest, reef-flat, intra-reef lagoons) are established, but they are not distinguished in the Lower Permian buildups.

3. Reef complexes include back-reef facies and elastic deposits of fore-reef facies. The Lower Permian buildups are surrounded by carbonate and clayey-carbonate mudstones (Ponomarenko, 2015) without reworked carbonates.

4. A larger number of the reef breccias are contained within reef structures, when lime mud is common in the Lower Permian buildups, occurring both in interframe cavities and in the form of separate lenses and interlayers, and often also inside abundant synsedimentary biologically induced cement crusts.
The idealised model depicted in Figure 4 resembles the reef mound of James (1978, fig. 11). However, such reef mounds “…consisting of poorly sorted bioclastic lime mud with minor amounts of organic boundstone” are not typical of the Lower Permian frameworks which are, instead, dominated by biocementstones. The Biodetrital Mud Mounds of Bosence and Bridges (1995) are also not similar to the Lower Permian organic structures of the Northern Urals. They more closely approximate the ‘skeletal mounds’ of James and Bourque (1992), which are made up of small delicate skeletons such as bryozoans, delicate branching or solitary corals and stromatoporoids, skeletal algae (dasyclads and others), phylloid algae and others.

The growth of the Lower Permian skeletal mounds of the Northern Urals is limited by the fair-weather wave base, and not by sea level, as is typical for reefs. This fact is supported by the absence of carbonate breccias, which are common in shallow-marine reefs. The Lower Permian skeletal mounds are surrounded by microbioclastic lime wackestone/mudstones (Ponomarenko, 2015), and also often contain an abundance of muddy materials, a consequence of their growth in quiet water conditions and confirms the conclusions of previous workers (Antoshkina, 2003; Eliseev, 1978; Ravikovich, 1956; Sandula, 2005).

An important detail of the Lower Permian organic build-ups of the Northern Urals is the widespread development of cement crusts. An understanding of the significance of submarine cementation in reef structures came in the second half of the 1960s (Ginsburg et al., 1967; Macintyre et al., 1968). Usually, thick fans and isopachous crusts strengthen and stabilise skeletons and sediment and provide substrates for further skeletal growth (Riding, 2002). Tsien (1981) introduced the term ‘bioceementstone’ for carbonate rocks “in which the original components are organically bound together during deposition by vagrant organisms which cement debris and sediments.” But this term identified organisms as cementing agents. Further, Webb (1996, p. 949) described the bioceementstone framework as “…consisting of delicate, small and/or poorly calcified organisms contained within abundant, localized, biologically induced cement”. The discovery of organic matter in the Lower Permian cement crusts of the Urals and the study of these crusts by electron spin resonance spectroscopy allowed them to be identified as a result of the synsedimentary calcification associated with microbial activity (Antoshkina & Ponomarenko, 2014). Thus, bioceement-frameworks are defined here as structures formed by small or thin skeletal or non-skeletal organisms covered by microbial films/crust which induced precipitation of synsedimentary carbonate cements. According to Antoshkina and Ponomarenko (2014), the framework of these biothermal rocks was formed only due to rapid synsedimentary biologically induced cementation, since these small, fragile, sessile organisms alone could not build the framework.

Very rapid cementation is indicated by the following facts:

1. Phylloid algae cementation occurred before the post-mortem disintegration of their thalli. For comparison, the post-mortem disintegration of the modern analogs Halimeda and Udotea occurs from 8 hr to 19 days after death (Clifton & Clifton, 1999; Forsythe et al., 2002).
2. Palaeoaplysinsids plate fragments bound by bioinduced cements contain an increased Sr content (from 0.2% to 0.43%), while the Sr content of cements varies between 0.029% and 0.056% (Ponomarenko, 2018b). This difference in Sr composition supports a primary aragonite composition for the Palaeoaplysinsid skeleton. However, it is also evidence of the ‘closed diagenesis effect’ (Yudovich et al., 1980, and references therein), in which Sr does not go back into the near-bottom water. Since aragonite is a very unstable mineral under surface temperatures and pressures, it dissolves in very shallow near-surface environments (Flügel, 2010, and references therein). The high Sr contents therefore indicate that, when aragonite was dissolved, the Palaeoaplysinsid skeletons were already covered with bioinduced crusts that prevented Sr from leaching and leaving near-bottom water.

5.2 | Is there an ecological succession?

As can be seen from Section 4, at the Lower Asselian stratigraphic level in the Pisanyi Kamen’ section, several intervals are noted, characterised by different lithologies and different sets of fossils. Is this an ecological succession?

The ecological succession principle was actively applied to the ancient reefs described in the 1970–1980s. In subsequent years, however, interest in ecological succession in ancient reefs, with rare exceptions, faded away. However, this principle received an unexpected boost in Russian-language literature. A number of authors, specialists in ancient and modern reefs, concluded, while analysing Phanerozoic organic buildups, that the ecological succession still exists on reefs (Ivanovskiy et al., 1997). However, their view of ecological succession differs from an earlier understanding, which postulates that succession was largely determined by the community (see, for example, Walker & Alberstadt, 1975, and discussion and references therein). Indeed, the ecological relationships between organisms and the environment are a multi-level and multifactorial system, which is often very difficult to understand. Changes in reef communities can be affected by such different factors as changes in the relative sea level, water temperature, nutrient flux, terrigenous material input, etc. At the same time, it is worth remembering that communities themselves can influence the environment. For example, in shallow-water reefs, the community of organisms forms a geomorphological barrier with a trail of
consequences for sedimentation (Antoshkina, 2003; Zavarzin & Rozhnov, 2011).

Ivanovskiy et al. (1997) highlighted widely divergent views on the driving forces and mechanisms of ecological succession. An attempt to test different concepts, both in the natural environment and experimentally, have shown that different driving forces and mechanisms can replace each other over time, or can act simultaneously, which leads to synthesis of processes, rather than division (Ivanovskiy et al., 1997).

In this work, the term ‘ecological succession’ is used as a natural change of biocenoses with time, not those associated with evolutionary changes in species (Zhuravleva et al., 1990). At the same time, ecological succession turns into a convenient tool for describing vertical changes in reef rocks and communities, that is, the development of individual reefs and other organic buildups through time. Use of this tool made it possible to identify unified (very similar in fabric) intervals in shallow reefs of different ages (Antoshkina, 2003; Ivanovskiy et al., 1997; Shmelyova, 2016; Walker & Alberstadt, 1975). This does not mean a formal approach to identifying and describing an ecological succession: each change should be discussed separately.

5.3 | Vertical succession

In the carbonate skeletal mounds development in the Lower Asselian interval of the Pisanyi Kamen’ section, seven events, caused by biotic and abiotic factors are distinguished (Figure 6).

5.3.1 | Stabilisation of the soft sea floor by bryozoans and heterotrophic microbes

Interval I began with the accumulation of lime mud in the quiet water conditions below fair-weather wave base. The presence of fragments of cyanobacterial threads indicates the euphotic zones and primary production in this area. However, the abundance of suspension-feeders requires sufficient nutrients in the water column, which may indicate their external source. Bryozoans and Tubiphytes were baffling and trapping. Tubiphytes are organisms of an uncertain systematic affinity (see references in Riding & Guo, 1992; Senowbari-Daryan, 2013). According to samples from the Pisanyi Kamen’ section, these organisms were attached and not restricted to the photic zone (Figure 9). This fact excludes a primary cyanobacterial or algal origin. Overall, this organic structure of Interval I resembles the Sakmarian Tubiphytes-bryozoan buildups of the Canadian Arctic Archipelago (Beauchamp, 1989), but with significantly less sponge spicules.

The appearance of microbial clots in the upper part of Interval I dramatically changes both the lithological and palaeoecological picture. Currently, clots are interpreted as a product of heterotrophic bacterial calcification of extracellular polymeric substances and other cellular products (Dupraz et al., 2009; Monty, 1995; Pratt, 1995; Riding, 2011). Rapid microbial calcification completes the stabilisation of the sea floor. Interval I is similar to the pioneer stabilisation stage in terms of ecological succession (Antoshkina, 2003; James & Bourque, 1992; Walker & Alberstadt, 1975) and characterises the stabilised sea floor.

5.3.2 | Colonisation of the hard sea floor by bryozoans and the appearance of abundant biologically induced cements

The hard sea floor was subsequently inhabited by fenestellid bryozoans. After death, colonies were covered with microbial films inducing rapid cementation (Antoshkina & Ponomarenko, 2014). In terms of ecological succession, this interval characterises the pioneer colonisation stage.

5.3.3 | Displacement of bryozoans by phylloid algae community

The bryozoan biocementstones of Interval II were very quickly replaced by phylloid-algal biocementstones. Anchicodium algae are edifice-builders (sensu lato:...
organisms whose activity creates or seriously changes the environment). Phylloid algae had an erect, cyathiform and leaf-like growth form and grew in clear waters below the fair-weather wave base (Beauchamp et al., 1989; Breuninger et al., 1989; Enpu et al., 2007; Morin et al., 1994; Samankassou & West, 2002; and others). The low diversity of the Upper Pennsylvanian–Lower Permian phylloid algae communities (see references in Enpu et al., 2007) is also seen in Intervals II and IV of the Pisanyi Kamen’. A high generic diversity of small foraminifers is recorded here (Ponomarenko & Ivanova, 2010). However, genera such as Tubertina, Bisphaera, Pachysphaera and Archaeosphaera are characteristic of the Upper Devonian. During the Early and Middle Carboniferous, they were common inhabitants of unfavourable environments. Their co-existence with phylloid algae and the almost complete absence of other Metazoa groups are evidence of adverse conditions (Ponomarenko & Ivanova, 2013), apparently created by Anchicodium sp. Thus, Wilson (1975) attributed a high density of algal populations to adverse conditions. Enpy et al. (2007) speculated that phylloid algae, like some modern algae, produced poisonous substances, which allowed them to keep other organisms away from areas that they rapidly colonised. Despite the logic, the modern specimens of diatoms, dinoflagellates and cyanobacteria belong to the toxin-producing algoflora (Falconer, 1993). Among green algae, toxic species are unknown. Forsythe et al. (2002) showed that phylloid algae produced short-lived populations that reached reproductive maturity after 6 months or 2 years, but then massively died during a spawning of a new generation. Such synchronous reproduction is often accompanied by mass death in modern algae Halimeda and Udotea (Forsythe et al., 2002), with which phylloid algae are often associated. Ponomarenko and Ivanova (2013) proposed a possible scenario that could lead to the development of low diversity in the phylloid algae community suggesting a similar phenomenon to algal blooms, which is probably analogous to episodic changes in water conditions in modern marine environments (Chernova et al., 2017).

5.3.4 Appearance of higher community diversity

The rapid growth of phylloid algae compensated and exceeded the rate of immersion of the basin bottom, therefore, the carbonate skeletal mounds community in the Pisanyi Kamen’ section began to approach fair-weather wave base. This fact led to an increase in oxygen in the water column and allowed other groups of organisms to compete successfully with the phylloid algae. Here cyanobacteria, abundant green dasyclade algae, crinoids, fusulinids and palaeoaplysinids began to appear.

5.3.5 Reaching of fair-weather wave base

In typical Palaeozoic reefs of the northern part of the Urals (Antoshkina, 2003), reaching the fair-weather wave base usually led to the formation of a highly diverse community capable of resisting wave activity. At the climax diversification stage of the reef ecosystem, the number of the main frame-building groups usually increases; therefore, the diversity of adaptive growth forms is extended (Antoshkina, 2003; Ivanovskiy et al., 1997; James & Bourque, 1992; Walker & Alberstadt, 1975). With an increase in the species diversity belonging to different reef guilds (Fagerstrom & Weidlich, 1999; Flügel, 2010), the number of new landscape associations of biota increases (Antoshkina, 2003; James & Bourque, 1992). This, in turn, leads to the formation of fore-reef, reef crest, reef-flat with sandy-pebble shoals and back-reef facies. However, none of the above environments were observed in the carbonate skeletal mound in the Pisanyi Kamen’ section. Apparently, during the Early Permian biota had a low frame-building potential and were not able to build resistant structures.

On reaching fair-weather wave base, important taphonomic changes occurred. The green algae thallus (predominantly dasycladaceans), Palaeoaplysinids plates, fusulinids, bryozoans and others, strongly fragmented by wave action, are enclosed in synsedimentary zoned fibrous cements. These accumulations of fossils after diagenesis would probably represent grainstones and rudstones without rapid post-mortem biologically induced cementation. However, taking into account all biotic and abiotic factors, a very specific type of bioclastic-cemented framework was formed (see Section 4.3).

These major differences do not allow the standard climax stages of a reef ecosystem to be determined in Interval III. Features diagnostic of the destruction stage, when the environment predominated, were identified and these led to the collapse of the ecosystem, which was never able to develop into a typical reef.

5.3.6 Collapse of the ecosystem

The relative biological diversity of Interval III before the beginning of the destruction stage was gradually, but relatively rapidly, replaced by a community dominated by Palaeoaplysinids. The systematic position of these organisms is unclear. For more than a century, they have been variously regarded as sponges (Krotov, 1888), hydroids (Breuninger, 1976; Davies, 1971; Davies & Nassichuk, 1973; Ponomarenko et al., 2014; Ryabinin, 1955), or stromatoporoids (Chuvashov, 1973). Over the past few decades, there has been a tendency to compare them with algae. Recently, Palaeoaplysinids were assigned to red algae on
the basis of the similarity of the cellular tissue with the Late Palaeozoic red alga *Archaeolithophyllum* thallus (Anderson & Beauchamp, 2014; Vachard & Kabanov, 2007). The specific taxonomic affinity of these fossils will not be discussed here, rather the palaeoecologic interpretations.

Over the past several decades, palaeoaplysinids have been considered to be indicators of colder water conditions (Bensing et al., 2008; Nakazawa et al., 2011; Wahlman, 2002), partly based on the composition of associated skeletal grains, a promising tool for microfacies research (Beauchamp, 1994; Beauchamp & Desrochers, 1997; Flügel, 2010; James, 1997). In any case, whether palaeoaplysinids were red algae or hydactinoids, their presence does not exclude the colder temperatures of the surrounding waters. Studies by Kossovaya et al. (2013) on the influence of climate on the Permian reef biota of the East European Platform established the development of cold-water reef fauna only in the Upper Artinskian sediments. Wahlman (2002), however, noted that the Upper Gzehlian–Lower Sakmarian organic buildups in the Subpolar Urals and the Southern Urals include an extensive *Tubiphytes*-bryozoan skeletal association, indicating, in his opinion, cooler-water sediments. However, based on the example of skeletal mounds in the Pisanyi Kamen’ section (Ponomarenko, 2015), a typically warm-water association of green phylloid algae is found almost throughout the Asselian. Palaeoaplysinids are also present at several levels. This could be interpreted in terms of climate fluctuations, but palaeoaplysinids appeared in different sections of the Northern Urals at different stratigraphic levels (Ponomarenko, 2015). Moreover, in the biostromes of Kasimovian age, Palaeoaplysinids and phylloid algae often replaced each other laterally (Ponomarenko, 2020). If the temperatures of the surrounding waters are being analysed, these observations could only be explained by the presence of a hypothetical complex network of cold and warm currents. The author does not say that the analysis of photozoan and heterozoan assemblages is wrong, but in the case of fossils with problematic affinity, it must be treated with great caution. In order to prove that palaeoaplysinids were cooler-water organisms, additional lithological, mineralogical and/or geochemical evidence is needed. Such example would be the Middle Ordovician (Darrinvillean) terrigenous-carbonate deposits of the Northern Urals, containing a heterozoan assemblage of grains (Ponomarenko, 2019), together with chamosite ooids which indicate a temperate climate (Antoshkina et al., 2017; Yudovich et al., 1981). Conversely, the Upper Ordovician (Sandbian, Katian) deposits are characterised by photozoan assemblages (Antoshkina, 2003; Antoshkina et al., 2017; Shmelyova, 2016, 2020). These warm-water carbonate deposits are contemporaneous with evaporates developed within the Verkhnaya Pechora depression (Rasskazova, 1988; Timonin, 1998). Unfortunately, no such analogy is given for the Lower Permian rocks containing Palaeoaplysinidae.

However, hydrodynamics were a more important force in the Pisanyi Kamen’ section. With a strong and long-term influence, current and wave action excluded those erect and ramose organisms that were unable to resist it. Palaeoaplysinids had a tabular growth form that was more adapted to active environments.

### 5.3.7 Recurrent colonisation of the hard sea floor by the phylloid algae community

The intense influence of active hydrodynamics on the carbonate skeletal mound in the Pisanyi Kamen’ section strongly slowed, or stopped, the further development of the reef ecosystem. Consequently, compensation for the slow sea floor deepening ceased, and when the level fell below the fair-weather wave base, the top of the skeletal mound was again colonised by the phylloid algae community. Interval IV (referred to stabilisation stage 2 in ecological succession terms) has a greater thickness than Interval II. Walker and Alberstadt (1975) stated that pioneer stages are usually of reduced thickness, a characteristic of Intervals I and II. The greater thickness of Interval IV may result from stronger subsidence of the sea floor, when even their rapid growth (‘catch-up growth’ sensu Ivanovskiy et al., 1997) could not reach the fair-weather wave zone. Noteworthy here is the alternation of the two types of phylloid-algal biocementstones (see Section 4.4 for details). Apparently, these were the very same glacioeustatic fluctuations seen in the relative sea level (Montanez & Poulsen, 2013; Wahlman, 2002). However, as we can see from the section, they did not exert any strong influence on the benthic ecosystem of the deeper skeletal mounds in the Pisanyi Kamen’ section, probably representing little more than background ‘noise’ in the terms of Beauchamp and Olchowy (2003).

The palaeoecological and succession analysis presented above shows, in general, the bathymetric dependence of the vertical replacement of communities. Where the development of Early Permian organisms depends on the depth of the surrounding waters (Breuninger et al., 1989; Morin et al., 1994), then this ‘bathymetric triad of fossils’ of bryozoans, green phylloid algae and palaeoaplysinids is mentioned. The surrounding water temperatures probably played a subordinate role: the deepest-water communities (bryozoans, *Tubiphytes*, brachiopods, microbes; Interval I) could have been somewhat cooler, but they were quickly replaced by a photozoan warm-water assemblage (Interval II) in the Pisanyi Kamen’ section. The communities themselves could also contribute indirectly to changing the environment. Thus, rapid microbial calcification could stabilise the
soft muddy sea floor at the initial stages of skeletal mound development. The supposed rapid growth of green phylloid algae also appears to have an impact on the environment. One such consequence could be the top of the skeletal mound reaching fair-weather wave base.

The skeletal mound community in the Pisanyi Kamen’ section did not reach the classical climax stages of an ecological succession (Antoshkina, 2003; James & Bourque, 1992; Walker & Alberstadt, 1975), when the assemblage itself separates into two sedimentation realms (fore-reef and back-reef), which differ greatly in their physicochemical characteristics (Antoshkina, 2003; Zavarzin & Rozhnov, 2011). That is, this community did not develop into one adapted to the environment anisotropy (Marfenin, 2010) and capable of resisting active hydrodynamic forces. Instead, the skeletal mound community began to rapidly degrade, reaching the fair-weather wave base. Therefore, the destruction stage was identified. At the same time, based on changes in the vertical assemblage, we can clearly see how the community was striving for diversity near the lower boundary of the fair-weather wave base. However, under environmental influence, community diversity has decreased and become dominated by a tabular growth form (Palaeoaplysinidae) better adapted to active hydrodynamics than green phylloid algae with erect or cautiform growth (Samankassou & West, 2002).

This interpretation confirms the words of Odum (1986, p. 165) that “...ecological succession is a directed and, therefore, predictable process”. A predictable desire for diversity is noted both in the Lower Palaeozoic shallow-water reefs (Antoshkina, 2003; Shmelyova, 2016, 2020) and in the Lower Permian skeletal mounds of the Northern Urals.

Recovery and repetition of some communities (as well as their successions) in a vertical section indicated that at Pisany Kamen’ skeletal mounds are observed stacking atop each other, similar to situations noted in other parts of the world (see review Wahlman, 2002).

6 | CONCLUSION

The lithological and palaeoecological analysis of the Lower Permian communities characteristic of the central part of the skeletal mounds in the Pisanyi Kamen’ section identified the following facts and interpretations:

1. The Lower Permian organic buildups in the Pisanyi Kamen’ section on the Un’ya River, the Northern Urals, were classified as skeletal mounds. They formed on the slopes of a depression resulting from deformation of the sea floor at the margin of the carbonate platform during activation of Palaeo-Uralian collisional processes. Skeletal mounds developed in quiet water conditions with growth slowing dramatically once fair-weather wave base was reached.

2. The entire section of the Pisanyi Kamen’ section is not one buildup, but is formed by a series of buildups stacked one upon the other. Here, at the Lower Asselian stratigraphic level, a section of the central part of two skeletal mounds was observed. At the Middle and Upper Asselian level, the eastern slope facies are developed, probably consisting of several skeletal mounds.

3. In general, along the section (with the exception of some intervals), green phylloid algae are dominant, which distinguishes the skeletal mounds in the Pisanyi Kamen’ section from their more southern and northern analogues, characterised by well-developed bryozoans and Tubiphytes.

4. A detailed description of the central part of the skeletal mounds at the Lower Asselian stratigraphic level made it possible to establish four intervals that differ in lithology and fossils. These intervals have been interpreted in terms of ecological succession. This interpretation showed that in the vertical section of the central part of the studied Lower Permian skeletal mounds, only pioneer stages are distinguished. Climax stages in the classical understanding of ecological succession are absent here. Their position is occupied by the destruction stage, which corresponds to the degradation the community experiences after the fair-weather wave base is reached. At the same time, it should be noted that one of the predictable properties of the ecosystems, namely, the desire for diversity, is also expressed here.

5. Seven changes in the benthic community were identified in the vertical succession of the central part of the skeletal mounds: (a) stabilisation of the soft sea floor by bryozoans and microbes; (b) colonisation of hard sea floors with bryozoans; (c) replacement of bryozoans by phylloid algae; (d) the emergence of a more highly diverse community; (e) fragmentation of organisms as they reach the fair-weather wave base; (f) an impoverished community dominated by organisms with lamellar growth forms; (g) new colonisation of the hard sea floor by phylloid algae.

6. Water depth was a significant influence on the distribution of the floral and faunal assemblage (‘bathymetric triad of community’ of bryozoans, phylloid algae and Palaeoaplysinids), but it is also possible that the communities themselves played a role. For example, the rapid growth of phylloid algae could be one of the reasons the fair-weather wave base was reached.

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