Miospores from the Upper Devonian and lowermost Carboniferous strata of the Khoshyeilagh area, northeastern Alborz, Iran

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ABSTRACT
Diverse and well-preserved terrestrial palynomorphs occur in the Padeha, Khoshyeilagh, and Mobarak formations in the Khoshyeilagh area, northeastern Alborz, northern Iran. The spore assemblages consist of 36 species belonging to 24 genera. The data show that assemblages recorded from the Khoshyeilagh section can be correlated with the VCo, LE, LN, and VI Miospore biozones of Europe, Canada, and USA. Many of the palynomorph species, such as Archaeooperisaccus ovalis, Anycyospora ampulla, Diducites macronatus, D. versabilis, Grandispora cornuta, G. echinata, Indotriradites explanatus, Retispora lepidophyta, Retusotriletes incohatus, R. phillipsii, Rugospora flexuosa, Teichertospora torquata, Tumulispora malevkensis, Vallatisporites pusillites, Verrucosisporites bulliferus, and Verrucosisporites nitidus, are closely comparable with coeval assemblages recorded from Belgium, Portugal, Canada, North Africa, South America, and North America. This indicates the close relationship of the Iranian Platform to other parts of the northern Gondwana and southern Laurentian domain during this time interval. Moreover, parent plants of the Late Devonian miospores in the Khoshyeilagh area generally belong to herbaceous Class Rhyniopsida (orders: Rhyniales, Trimerophytales), Zosterophyllopsida, and various classes such as, Lycopsida (herbaceous order: Isoetales, Selaginellales, Padeha, Khoshyeilagh and Mobarak formations, described in detail by Alavi-Naini (1972), Kimyai (1972), Bozorgnia (1973), and references therein. Despite these studies, determination of the exact age of the Upper Palaeozoic succession (the Padeha, Khoshyeilagh, and Mobarak formations), which are exposed in the Khoshyeilagh area, northeastern Alborz Mountains, has long been a matter of controversy.

The main objectives of this paper are to document the Late Devonian terrestrial palynomorphs from the Khoshyeilagh area; to establish a biozonation; to determine absolute number and relative abundances of miospores; to use similarity indices to compare miospore assemblages from north, west, south, and central-east Iran during this interval; to determine the age of the Khoshyeilagh Formation; to identify parent plants of the miospores; and to construct palaeoenvironmental interpretations based on original data.

1. Introduction
The published record of Late Devonian miospores now constitutes a reasonably comprehensive coverage of many parts of Iran. These include Ghavidel-Syooki (2003), Ghavidel-Syooki and Owens (2007), Ghavidel-Syooki et al. (2011), and Taherian et al. (2021) and references therein. Despite these studies, determination of the exact age of the Upper Palaeozoic succession (the Padeha, Khoshyeilagh, and Mobarak formations), which are exposed in the Khoshyeilagh area, northeastern Alborz Mountains, has long been a matter of controversy.

The main objectives of this paper are to document the Late Devonian terrestrial palynomorphs from the Khoshyeilagh area; to establish a biozonation; to determine absolute number and relative abundances of miospores; to use similarity indices to compare miospore assemblages from north, west, south, and central-east Iran during this interval; to determine the age of the Khoshyeilagh Formation; to identify parent plants of the miospores; and to construct palaeoenvironmental interpretations based on original data.

2. Geological setting and stratigraphy
Palaeozoic strata are well exposed in the Khoshyeilagh area, which is located about 5 km west of Khoshyeilagh village, ca. 70 km northeast of Shahrud, northern Iran; 55° 2'E longitude and 36° 45'N latitude (Figure 1). This Palaeozoic succession has been divided, in ascending stratigraphical order, into the Padeha, Khoshyeilagh and Mobarak formations, described in detail by Alavi-Naini (1972), Kimyai (1972), Bozorgnia (1973), and Rafiehe-Oskuei (1992). The Padeha Formation is 492 m thick at its type locality in Ozbak-Kuh (Afshar-Harb 1979), but it is only 268 m thick in the study area (Figure 1). The lower contact of this formation is unconformable with the Soltan Maidan Formation, and its upper contact is gradational with the Khoshyeilagh Formation (Figure 2). The Palaeozoic sequence represents the Ghelli, Soltan Meidan, Padeha, Khoshyeilagh, and Mobarak formations in ascending stratigraphical order. The Ghelli and Soltan Meidan formations were palynologically studied by Ghavidel-Syooki et al. (2011) and assigned to the Upper Ordovician (Katian-Hirnantian)-Upper Silurian (Gorstian), respectively. The Soltan Maidan...
Formation consists of basaltic igneous rocks and based on its stratigraphical position was attributed to the Middle Silurian (Stampfli 1978).

This formation lacks any diagnostic macrofossils at its type locality and, based largely on its stratigraphical position, has been assigned to the Early Devonian (Alavi-Naini 1972). The Khoshyeilagh Formation is 1350 m thick in its type locality (Khoshyeilagh area), but the thickness of this formation varies from place to place. In the study area, its thickness is 820 m. The lower and upper contacts of this formation are gradational, with the underlying Padeha Formation and the overlying Mobarak Formation. This formation consists of fossiliferous limestone, shale, and sandstone (Assereto and Gaetani 1964; Bozorgnia 1973). Ahmadzadeh-Heravi (1975), and Brice et al. (1973) investigated the Khoshyeilagh Formation for brachiopod and conodont faunas in its type locality and assigned an Early–Late Devonian age. The brachiopods of this formation were re-investigated by Brice (1999) and Zaman (2001), and the basal part of the Khoshyeilagh Formation was assigned to the latest Givetian–Frasnian. The Mobarak Formation is 450 m thick at its type locality but only up to 150 m in the study area. This formation consists mainly of limestones with some shale intercalations, which contain both macro- and micro-faunas that suggest an Early Carboniferous age (Stepanov 1971; Bozorgnia 1973; Afshar-Harb 1979). Palynological studies have also been undertaken on the Khoshyeilagh Formation (Coquel et al. 1977; Ghavidel-Syooki 1994a; Taherian et al. 2021), and a broad Late Devonian age was assigned.

3. Materials and methods

Two hundred and seventy surface samples were collected from a measured stratigraphical section of the Khoshyeilagh
area (Figure 2), of which 167 samples were processed and numbered with the prefix TDKh (an abbreviation for Taherian, Devonian, and Khoshyeilagh). Traditional palynological procedures (e.g. Phipps and Playford 1984) were used for the retrieval and concentration of palynomorphs. After a mild surface washing, the samples were crushed, and ca. 60 g was separated and chemically treated in 10% cold hydrochloric acid (HCl) for about 24 hours, followed by treatment with 40% hydrofluoric acid (HF) for 30 hours, and 10% hot (90°C) HCl for 20 minutes. Next, samples were rinsed in water and sieved through 15 μm nylon mesh sieves. Finally, organic residues were separated from the inorganic materials using saturated zinc bromide (ZnBr₂). Then, three slides of each sample were prepared and covered by a coverslip. Selected specimens on all slides were examined extensively via scanning electron and transmitted light microscopy (Olympus DP_12 and Phillips XL30), and photographed.

Figure 2. Biostratigraphy of the studied miospore assemblages in the Khoshyeilagh area.
The biozonation of the studied Devonian section was undertaken on the basis of the ‘first observed occurrence’ (FOO) and the ‘last observed occurrence’ (LOO) of stratigraphically significant terrestrial palynomorph species (Figure 2). In addition, miospores were counted (Tables 2, 3, Appendices C, D; Supplementary Data). In addition, we used the similarity index of Dice (1945) and Sørensen (1948); this is a statistical method used to compare the degree of similarity between two populations or localities. The equation is as follows: Si = 2C/A + B where A = the number of miospore in locality A, B = the number of miospore in locality B, and C = the number of taxa in common between A and B. The index ranges between zero, meaning no common species, and one, meaning total similarity. Finally, using this equation, a comparative table of similarity indices between the Khoshyeilagh area and elsewhere in Iran was prepared and its chart was drawn (Table 1; Figure 3). All samples and slides related to this study are deposited at the Iranian Natural History Museum, Department of Organization Environment (DOE), Islamic Azad University, Tehran, Iran (IR).

### 4. Results

The studied strata in the Khoshyeilagh area contain diverse assemblages of terrestrial palynomorphs. The palynofloras comprise 36 species of spores in 24 genera (Appendix A, Supplementary Data). Selected best-preserved taxa with known stratigraphical distribution and/or persistence were illustrated in Plates 1–3. In addition, the Khoshyeilagh area is one of the few places with abundant marine palynomorphs and other fossils (foraminifera, shelly brachiopods, and corals) which indicates a mainly shallow marine environment (Taherian et al. 2021).

### 4.1. Biostratigraphy

Five local biozones were recognized throughout the Upper Devonian–Lower Carboniferous strata (Padaha, Khoshyeilagh, and Mobarak formations) based on the FOOs and LOOs of selected taxa with known stratigraphical significance and/or persistence throughout the measured section (Figure 2; Table 1 in Appendix B, Supplementary Data). They are described below in ascending stratigraphical order.

#### 4.1.1. BT biozone (bulliferus-torquata biozone)

The Verrucosisporites bulliferus-Teichertospora torquata (BT) Assemblage zone occurs in the upper part of Padaha Formation. It extends through a thickness of ca 33 m (TDKh-145-TDKh-165; Figure 2), and is composed mainly of alternations of limestone and shale with a few dolomite stringers. Its lower boundary is characterized by the FOOs of Archaeoperisaccus ovalis, Cyclogranisporites isostictus, Rhabdosphores langii, Verrucosisporites bulliferus, and Verrucosisporites confirmatus. The upper boundary is characterized by the FOOs of Acinosporites macrospinous, Ancyrospora ampulla, Auroraspora pseudocrista, Grandispora cornuta, Grandispora gracilis, Retusotriletes philippi, Rugospora flexuosa, and Teichertospora torquata (Figure 2). This biozone contains the following species: Archaeoperisaccus scabrat us, Emphasiosporites rotatus, Geminospores lemurata, Retusotriletes distinctus, and Samarisorpetes sp. cf. S. triangulatus (Appendix A; Supplementary Data).

The geological and stratigraphical distribution of miospore species are illustrated in Table 1 (Appendix B; Supplementary Data). Most of the taxa herein have a broad stratigraphical distribution in the Late Devonian (Frasnian–Famennian). Despite this, there are some species with restricted stratigraphical distributions in the Frasnian, such as Acinosporites macrospinous and Cyclogranisporites isostictus (Richardson 1964; Owens and Richardson 1972; McGregor 1977; Balme 1988). Therefore, based on recorded terrestrial palynomorph taxa, a late Frasnian age is suggested for this biozone. Moreover, based on the parent plants of identified miospores, Progymnospermopsida (Archaeopteridales and Aneurophytales), Lycopsida (Selaginellales), Zosterophyllopsida, and Rhynopsida appeared in this biozone (Figure 5). It should be emphasized that the boundary between the Frasnian and Famennian is gradational.

| Localities | Kopet-Dagh | Mighan | Imam-Zadeh Hashem | Geirud | Hassanakdar |
|-----------|-----------|--------|-------------------|--------|-------------|
| Si index: genus level | 0.71 | 0.71 | 0.58 | 0.57 | 0.54 |
| Si index: species level | 0.55 | 0.39 | 0.36 | 0.33 | 0.15 |

Locality: 1. Ghavidel-Syooki and Owens (2007), 2. Ghavidel-Syooki and Taherian (2012), 3. Ghavidel-Syooki (1994a), 4. Vaez-Javadi (1995), 5. Ghavidel-Syooki (1995), 6. Ghavidel-Syooki and Mahdavian (2010), 7. Ghavidel-Syooki (2001), 8. Hashemi and Playford (1998), 9. Ghavidel-Syooki (2003), 10. Hashemi and Nezam-Vapha (2014) (references in Appendix E; Supplementary Data).
This biozone is equivalent to the lower part of acritarch biozone I of Taherian et al. (2021) in this area.

This biozone suggest an assignment to Richardson and McGregor’s Auroraspora torquata-Grandispora gracilis Assemblage zone which is recognized in the latest Frasnian and Early Famennian strata in Europe, Australia and Canada (Richardson and McGregor 1986; Richardson and Ahmed 1988; McGregor and Playford 1992; Streel and Loboziaik 1996).

4.1.2. FF biozone (flexuosa-fruticosa biozone)
The Rugospora flexuosa-Apicipilretusissipora fruticosa (FF) Assemblage zone occurs in the uppermost part of the Padeha Formation and the lowermost part of the Khoshyeilagh Formation and extends through a thickness of 80 m (samples TDKh-165 to TDKh-190; Figure 2), and is composed mainly of alternations of shale, marl, limestone, siltstone, a thick conglomerate, and a thick igneous layer. Its lower boundary is identified by the FOOs of Acinosporites macrospinusos, Ancyrospora ampuilla, Auroraspora pseudocrista, Grandispora cornuta, Grandispora gracilis, Retusotriletes phillipsii, Rugospora flexuosa, and Teichertspora torquata. Its upper boundary is identified by the FOOs of Apicipilretusissipora fruticosa, Diducites mucronatus, Punctatissipores glabrimarginatus Vallatisporites hystricosus, and V. pusillites. In addition, the LOOs of Cyclogranisporites isostictus and Verrucosisporites bulliferus occur in this biozone. All older biozone miospores pass through this biozone. This biozone indicates beginning of the Famennian. This biozone is partly equivalent to the standard versusis-cornuta biozone-VCo zone (Paproth et al. 1983; Richardson and McGregor 1986; Streel et al. 1987; Richardson and Ahmed 1988), and Fa2c biozone in Europe (Clendening et al. 1980) due to the presence of the Late Devonian index miospore Retusotriletes phillipsii. It is notable that from sample TDKh-191 up to TDKh-273, an interval which is 245 m thick, miospores proved extremely sparse. In this interval, the limestones were recrystallized. Thus, no biozone was suggested herein.

4.1.3. LE biozone (lepidophyta-explanatus biozone)
The Retispora lepidophyta-Indotriradites explanatus (LE) Assemblage zone occurs in the middle part of the Khoshyeilagh Formation and extends through a thickness of 255 m (samples TDKh-273 to TDKh-328; Figure 2), and is composed of marl, shale, and limestone with a thick sandstone bed. Its lower boundary is identified by the FOOs of Retispora lepidophyta, Indotriradites explanatus, Denosporites spitsbergenisis, Grandispora echinata, Hystricosporites furcatus, Knoxiosporites sp. cf. K. literatus, and Retispora macroreticulata, and the LOOs of Archaeoperisaccus ovalis and Verrucosisporites confertus. In addition, its upper boundary is identified by the LOOs of Acinosporites macrospinusos, Diducites versabilis, and Hystricosporites furcatus. Based on index miospore taxa, such as Retispora lepidophyta, Indotriradites explanatus, Grandispora echinata, and Hystricosporites furcatus, the Late Famennian is also suggested for the middle part of the Khoshyeilagh Formation. Based on the parent plants of the identified miospores, Selaginellales and Isoetales (Lycopsida) exhibited more diversity and abundance herein. This biozone is equivalent to the LE subzone in the European Ardenne-Rhenish region (Streel et al. 1987; Higgs et al. 1988; Maziane et al. 1999). Moreover, layers of corals, tentaculites and Umbellina microfossils are present in this biozone (Taherian et al. 2021).

4.1.4. LN biozone (lepidophyta-nitidus biozone)
The Retispora lepidophyta-Verrucosisporites nitidus (LN) Assemblage zone occurs in the upper part of the Khoshyeilagh Formation and extends through a thickness of 250 m (samples TDKh-328 to TDKh-368; Figure 2), and is composed of marls and limestones. Its lower boundary is identified by the FOOs of Tumulispora malevkensis and Verrucosisporites nitidus, and its upper boundary is identified by the LOOs of several species such as Retispora lepidophyta, Diducites mucronatus, Grandispora echinata, Indotriradites explanatus, Knoxiosporites sp. cf. K. literatus, Retusotriletes philipsii, Rhabdosporites langii, and Vallatisporites pusillites. Additionally, in sample TDKh-368, Auroraspora pseudocrista, Denosporites spitsbergenisis, Archaeoperisaccus scabatus, Emphanisporites rotatus, Geminospora lemutara, and Punctatissipores glabrimarginatus disappeared. The absence of these miospores indicate that Famennian ended in the upper boundary of this biozone. This biozone is comparable with the LN biozone in Europe (Streel et al. 1987; Higgs et al. 1988; Maziane et al. 1999), suggesting an upper Famennian (Strunian) age for this part of the Khoshyeilagh Formation.

4.1.5. VI biozone (varia-incohatus biozone)
The VI biozone is an assemblage biozone, which occurs in the lower part of the Mobarak Formation and extends through a thickness of 150 m (samples TDKh 368 to TDKh 382; Figure 2), and is composed of shale and fossiliferous limestone. Its lower boundary is characterized by the FOOs of Early Carboniferous miospore species such as Retusotriletes incohatus and Tumulispora varia, and its upper boundary is recognized by the LOOs of Rugospora flexuosa, Retusotriletes distinctus, Tumulispora malevkensis, Vallatisporites hystricosus, and Verrucosisporites nitidus. It should be emphasized that the LOOs of these species represents the end of the sampling interval. Since most Famennian terrestrial miospore taxa were absent in this biozone and based on the stratigraphical potential of Retusotriletes incohatus and Tumulispora varia, an early Tournaisian age is suggested for this part of the Mobarak Formation. This biozone is equivalent to VI strata in Europe (Streel et al. 1987; Higgs et al. 2002).

4.2. Absolute number and relative abundance of miospores
In this study all miospores were counted and their absolute numbers were tabulated (Tables 2, 3; Appendices C, D; Supplementary Data). Similarity index values at the generic and species levels between the miospore assemblages of the Khoshyeilagh area and various localities in Iran were considered. Then, by using the similarity equation of Sørensen (1948), a
comparative table of similarity indices of the Khoshyeilagh area and elsewhere in Iran was prepared (Figure 3; Table 1). Six of the most common and often quantitatively abundant miospore genera, in descending order, are *Geminospora* (Archaeopteridales), *Retusotriletes* (Zosterophyllales), *Teichertospora* (probably Calamostachyales), *Emphasiporites* (Rhyinales), *Grandispora* (Lycopsida), and *Vallatisporites* (Isoetales; Lycopsida), with relative abundances of 48.97, 19.51, 8.5, 3.06, 2.51, and 2.31%, respectively. Six of the most common and relatively abundant miospore species, in descending order, are *Geminospora lemurata*, *Retusotriletes distinctus*, *G. punctata*, *Teichertospora torquata*, and *Ancyrospora ampulla* with percentages of 32.33, 17.8, 16.1, 8.5, 3.1, and 1.56%, respectively. In addition, *Progymnospermopsida*, Zosterophyllods, and Lycopsida were dominant with relative abundances of 48.97, 20.56, and 14.6%, respectively in the Khoshyeilagh area. Rhyniopsida was restricted by a relative abundance of 3.37% during the Frasnian-Famennian.

5. Palaeobotanical affinities

Identifying parent plants of miospore taxa is one of the most useful ways to interpret the palaeoenvironment. Botanical affinities of some taxa have been assigned with varying degrees of confidence, some to more than one major natural group and others more doubtfully assigned. Inferred natural botanical affinities of miospores identified in this study are cited in Table 2 (Appendix A and Appendix E; Supplementary Data) and illustrated in Figures 4 and 5.

*Apiculiretusistinguys* is ascribed to *Cooksonia* (Doran et al. 1978) and *Retusotriletes* is related to *Zosterophyllum* (Gérin 1988) and also to *Archaeopteris* (McGregor and McCutcheon 1988). *Grandispora* was also assigned to *Lycopsida* (Verdoorn and Alston 2013; Gutiérrez and Archangelsky 2014; Mikio Kurita Matsumura et al. 2015). *Rhabdosporites* is attributed to *Tetraxylopteris* (Bonamo and Banks 1967; Wellman 2009) and sometimes to *Protopletridium*. *Rhabdosporites langii* and *Geminospora lemura* were assigned to the Aneurophytales and Archaeopteridiales, respectively. They represent an origin for heterosporous within the progymnosperms (Allen and Marshall 1986; Marshall 1996; Traverse 2007). The progymnosperms arose in the Middle Devonian and reached their acme in the Late Devonian. They declined in the Early Carboniferous. Reproductive structures were essentially cryptogamic with the sporangia borne terminally on lateral branches in the homosporous orders Protopletridiales and Protopletridales, or in association with strobiloid foliar organs in the heterosporous Archaeopteridiales. *Geminospora* and *Rhabdosporites* were almost certainly entirely derived from members of the class *Progymnospermopsida* (Balme 1995; Marshall 1996). The pseudosaccate spore *Auroraspora* was assigned to calcitean cones (Libertin and Bek 2006). *Retispora* belongs to the Order Selaginellales (Lycopsida Therefore, parent plants of the Devonian miospores in the Khoshyeilagh area generally belong to the herbaceous Phylum Rhyniophyta (orders: Rhyinales, Trimerophytales), and various classes such as Lycopsida (herbaceous orders: Isoetales, Selaginellales, *Trimerophytales*), and *Progymnospermopsida* (Order Archaeopteridales and Aneurophytales). Based on miospore vertical distributions and their parent plants in the Khoshyeilagh area, *Progymnospermopsida*, Rhyniopsida and Zosterophyllopsida appeared in the Frasnian, and disappeared in the middle Famennian and late Famennian, respectively. Moreover, at the boundary of the overlying Mobarak Formation, almost all species disappeared. This may be due to a marine transgression in this area during the Early Carboniferous (Figures 4 and 5).

6. Geographical distribution of miospores in Iran and the world

The geographical distribution of the identified miospores in the Khoshyeilagh area was also considered. These miospores were present in Kopet-Dagh (eastern Iran), Mighan (northwestern Shahrud), Imam-Zaideh Hashem, Geirud, Hassanakdar (Central Alborz), Houtrak (Kerman), Chah-e-Risheh (northeastern Esfahan), Cheshmehir (northern Tabas), Tang-e-Zakein (northern Bandar-Abbas), and the Kish Gas field (northern Persian Gulf (Appendices B, F; Supplementary Data). It indicates that there was a relatively high similarity between assemblages in the study area and the Alborz Mountains and the Kerman Basin.

Moreover, the geographical distribution of the miospore assemblages of the Khoshyeilagh area in various Late Devonian–Early Carboniferous localities in the world were considered (Appendices B, G; Supplementary Data). Many of the palynomorph species, such as *Diducites mucronatus*, *Geminospora lemura*, *Grandispora cornuta*, *G. echinata*, *Indotriradites explanatus*, *Retispora lepidophyta*, *Retusotriletes incanthus*, *R. phillipsii*, *Rhabdosporites langii*, *Rugospora flexuosa*, *Teichertospora torquata*, *Tumulispora maleakensis*, *Vallatisporites pusillites*, and *Verrucosisporites nitidus*, are closely comparable with coeval assemblages recorded from Belgium, Portugal, Canada, North Africa, North and South America, and West Asia (Figure 6). By contrast, there is relatively low comparability between the miospore assemblages in the Khoshyeilagh area and the assemblages of the Russian Platform China, Africa, and Australia.
Plate 2. 1. Knoxisporites sp. cf. K. literatus (Waltz) Playford 1963 (Sample TDKh 304), 2. Punctatusporites glabrimarginatus Owens 1971 (Sample TDKh 282), 3. Retusotriletes phillipsii Clendening et al. 1980 (Sample TDKh 190), 4. Retusotriletes phillipsii Clendening et al. 1980 (Sample TDKh 190), 5. Retusotriletes distinctus Richardson 1965 (Sample TDKh 335), 6. Retusotriletes incohatus Sullivan 1964 (Sample TDKh 382), 7. Rhabdosporites langii (Eisenack) Richardson 1960 (Sample TDKh 282), 8. Retispora lepidophyta (Kedo) Playford 1976 (Sample TDKh 328), 9. Retispora macrorniticulata (Kedo) Byvsheva 1985 (Sample TDKh 368), 10. Rugospora flexuosa (Jushko) Strel in Becker et al. 1974 (Sample TDKh 334), 11. Rugospora flexuosa (Jushko) Strel in Becker et al. 1974 (Sample TDKh 335), 12. Teichertospora torquata (Higgs) McGregor and Playford 1990 (Sample TDKh 304), 13. Vallatisporites hystricosus (Winslow) Byvsheva 1985 (Sample TDKh 282), 14. Samarispores sp. cf. S. triangulatus Allen 1965 (Sample TDKh 190), 15. Verrucosisporites bulliferus Richardson and McGregor 1986 (Sample TDKh 190), 16. Teichertospora torquata (Higgs) McGregor and Playford 1990 (Sample TDKh 328), 17. Vallatisporites pusillites (Kedo) Dolby and Neves 1970 (Sample TDKh 282), 18. Tumulispora varia (Kedo) Byvsheva in Avkhimovich et al. 1988 (Sample TDKh 368), 19. Tumulispora malevkensis (Kedo) Tumau 1978 (Sample TDKh 333), 20. Verrucosisporites nitidus (Naumova) Playford 1964 (Sample TDKh 333).
7. Palaeoenvironmental interpretation

The earliest Rhyniales were recovered from the moist and permeable sandy environments in which their primitive roots could live and grow in tidal or delta areas (Richardson 1960, 1964; Richardson and McGregor 1986). Also, the different observed miospores could be transported from the delta areas or further from the land. Recent Selaginella is a cosmopolitan genus and grows in various climate and soil types. Some species grow in very extreme climate such as cool alpine or the Arctic Circle (S. selaginoides, S. rupestris), and also in barren and dry deserts (S. lepidophyta, S. sartorii) (Tryon and Tryon 1982; Zoller 2005), but have their highest diversity in tropical areas (Lellinger et al. 1983). The occurrence of Retispora lepidophyta and Vallatisporites hystericus, indicating ‘downstream’ coastal areas and plant communities near swamps (Streel and Scheckler 1990). The Retispora lepidophyta parent plant was restricted in the coastal environments in East Greenland (Marshall 2021). The palaeoecology of the in situ miospores of Svalbardia (Geminospora) are discussed by Allen and Marshall (1986). They note that ‘Geminospora tends to be more abundant in marginal marine, distal fluviatile and lacustrine environments’.

Based on the relative abundance of miospores in the Khoshyeilagh area, Geminospora and Retusotriletes are the most abundant genera (about 65% of all miospores) and plants of the Order Aneurophytales and Archaeopteridales have been attributed to them (Allen and Marshall 1986; McGregor and McCutcheon 1988). Understanding the habitat of these plants can determine the environment of the Khoshyeilagh Formation. Pepper (1954) found many fragments of land plants, especially Archaeopteris in the sands of the Appalachian region, which belong to a freshwater channel. Teichertospora torquata was inferred to low-latitude positions in Euramerica and Western Australia (Witzke and Heckel 1988; McGregor and Playford 1990).

Taherian (2020) studied the Padeha Formation in the Khoshyeilagh area based on sedimentary evidence and
suggested a fluvial delta with several freshwater channels towards a lagoon and a shallow marine environment for this locality during the early Late Devonian (Figure 7). Taherian et al. (2021) reported various marine fossils such as acritarchs, prasinophytes, chitinozoans, foraminifers, and corals from the Khoshyeilagh area. Moreover, the Khoshyeilagh Formation consists of fossiliferous limestone, shale, and sandstone (Assereto and Gaetani 1964; Bozorgnia 1973). Ahmadzadeh-Heravi (1975) and Brice et al. (1973) investigated this formation for brachiopod and conodont faunas.

Therefore, based on palaeontological evidence, such as parent plant affinities, the presence of Rhyniales, Trimerophytales, Isoetales, Selaginellales, Archaeopteridales, Aneurophytales, Zygopteridiales, Protolepidodendrales, and Marattiales, the absolute number and relative abundance of miospore taxa, marine macrofossils such as brachiopods and corals, and lithological evidence such as several sandstone and limestone layers, and the absence of coal seams in the Khoshyeilagh area, it can be suggested that, during the Late Devonian–Early Carboniferous, there were various environments such as rivers, fluvial deltas with partly sandy tidal flats, lagoons, and a shallow marine environment.

8. Conclusions

Late Devonian–Early Carboniferous terrestrial palynomorphs from the Padeha, Khoshyeilagh, and Mobarak formations are studied herein. The studied stratigraphical succession contains well-preserved miospores in which 36 species (in 24 genera) were identified. The encountered taxa were arranged in five biozones: the Verrucosisporites bulliferus-Teichertospora torquata (BT) Assemblage zone; the Rugospora flexuosa-Apiculiretusispora fruticosa (FF) Assemblage zone; the Retispora lepidophyta-
Indotriradites explanatus (LE) Assemblage zone; and the Retispora lepidophyta-Verrucosisporites nitidus (LN) Assemblage zone, which occur in the upper part of the Khoshyeilagh Formation. The fifth biozone is the Tumulispora varia-Retusotriletes incohatus (VI) Assemblage zone which occurs in lowermost part of the Mobarak Formation, and suggests an early Tournaisian age.

The terrestrial palynomorphs recovered from the identified biozones are closely comparable to those recorded from biozones associated with the Late Devonian–Early Carboniferous strata (the VCo, LE, LN and VI biozones) in North America, Brazil, Argentina, Belgium, and Portugal.

In this study, the absolute number and relative abundances of miospores were studied. The absolute number of Geminispora, Retusotriletes, Teichertspora, Emphanispores, and Grandispora are respectively high. Based on the botanical affinity of miospores, the Progymnospermopsida, Zosterophyllopsida, and Lycopsida were dominant, in the Khoshyeilagh area. The Rhyniopsida were restricted and represent of 3.37% of the miospores during the Frasnian-Famennian.

The similarity indices at generic level between the Khoshyeilagh area with Kopet-Dagh (eastern Iran), Mighan (northwestern Shahroud), Imam-Zadeh Hashem, Geirud, Hassanakdar (Central Alborz), Houtk (Kerman), Chah-e-Riseh (northeastern Isfahan), Cheshmeshir (northern Tabas), Tang-e-Zakeen (northern Bandar-Abbas), and the Kish Gas field (northern Persian Gulf) were studied. Values of Si indicate a relatively strong similarity between the miospore assemblages of the Khoshyeilagh area and those found elsewhere in the Alborz Mountains. In addition, the Khoshyeilagh palynomorph assemblage has a relatively low similarity with assemblages of the Kerman and southwestern areas in Iran.

Figure 5. Chart of the parent plants of the miospores and their taxonomic relations in the Khoshyeilagh area.
Therefore, based on palaeontological evidence, such as parent plant affinity, the presence of Rhyniaceae, Trimerophytales, Isoetales, Selaginellales, progymnosperms, relative abundance of miospore taxa, marine macrofossils (brachiopods, corals), lithological evidence such as, sandstone and fossiliferous limestone layers, and the absence of coal seams in the Khoshyeilagh area, it can be suggested that during the Late Devonian-Early Carboniferous, there were various environments such as rivers, fluvial deltas with partly sandy tidal flats, lagoons, and a shallow marine environment. Additionally, there was an obvious change in the parent plant assemblage over time, in which Rhyniaceae and Zosterophyllales appeared first in the Frasnian. Then, lycopsids and progymnosperms appeared and became dominant in the Famennian. Moreover, in the beginning of the Early Carboniferous most proxies of Rhyniaceae, Aneurophytales, and Selaginellales were absent. In addition, Iran was located along the Palaeo-Tethys Ocean near Gondwanaland in the Southern hemisphere during this interval.

| Miospores                | Botanical affinity      | Age            | Locality                        |
|--------------------------|-------------------------|----------------|---------------------------------|
| Acinosporites             | Lecelercia complexa     | Devonian       | USA                             |
| Ancyrospora               | Thysophyton (Lycopsida) | Devonian       | USA, Ireland, East Greenland, Scotland |
| Apiculiretispora          | Aplaphyton maj.         | Devonian       | Scotland, Russia, Canada        |
| Archaeoisporites          | Khysthovitchina africani (Lycopsida, Selaginellales?) | Devonian       | Russia                          |
| Cyclogranisporites        | Angarakdenon sp.        | Carboniferous   | Russia, Germany, France, USA    |
| Densosporites             | Sporangiostrbus         | Carboniferous   | Spain, Scotland, Spitsbergen    |
| Emphanisporites           | Horneophyton (Rhyiniales) | Devonian       | England                         |
| Geminispora               | Archaeopteris holliana  | Devonian       | USA, Spitsbergen, Scotland, Russia |
| Grandispora               | Haplotasting (Lycopsida) | Devonian       | Argentina, Bolivia              |
| Indotriradites            | Selaginella harrisiana  | Devonian       | Australia                       |
| Punctatissporites         | Discalis longista      | Devonian, Carboniferous | China, Russia, Scotland, France, USA |
| Retispora                 | Selaginellales (Lycopsida) | Late Devonian | China, Eastern European platform, Scotland, Wales, Belgium, Canada, Spitsbergen |
| Retusotilletes            | Asterolyxenacki         | Devonian       | Scotland, Wales, Belgium, Canada, Spitsbergen |
| Rhabdosporites            | Rheillia thomsonii      | Devonian       | USA, Canada, Germany, Russia, Czech Republic, Belgium, Scotland, Russia |
| Vallatisporites           | Omphalophilus           | Devonian-Carboniferous | Russia                          |
| Verrucosisporites         | Sporangiostrbus         | Carboniferous-Permian | Germany, USA, France            |

*Based on data from Abbott (1968), Allen (1980), Allen and Marshall (1986), Avkhimovitch et al. (1993), Balme (1994), Banks et al. (1972), Baxter and Baxendale (1976), Beck (1957), Bek and Leary (2012), Bode (1928), Bonam (1967), Bouron (1964), Broussichine (1983, 1986), Chaloner (1962, 1967), Corvin et al. (2019), Mapes and Schabilion (1979a), McGregor (1969, 1973), Nathorst (1914), Nikitin (1934), Oplustil et al. (2010), Potonie (1962, 1967), Remy (1955), Remy and Remy (1958, 1975), Richardson (1960, 1965), Scott (1897), Serret and Brousmiche (1987), Streel et al. (1987), Taylor (1981), Taylor and Taylor (1993), Townrow (1968), Wellmann (2004), Wellmann et al. (2004), Williamson and Scott (1895) and Yurina (1964).
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The authors declare that they have no conflict of interest.

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