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Vascular Cryptogam Plants of the Khoshyeilagh Formation, Northern Shahrud, Eastern Alborz Ranges

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Abstract

Fragmentary, indifferently preserved, and of low diversity plant remains occur in basal part of the Khoshyeilagh Formation, northern Shahrud, eastern Alborz Ranges. The oldest hitherto reported from Iran, the remains are essentially assignable to lycophytes and psilophytes. Additionally, spores retrieved from the Khoshyeilagh Formation with reference to available data on spore-plant relationships denote that Phaeophyta, Rhyniopsida (Rhyniales and Trimerophytales), Zosterophyllopsida, Barinophytopsida (Barinophytales), Filicopsida (Cladoxylales and Zygopteridales), Lycopsida (Drepanophycales), Equisetopsida, and Progymnospermopsida (Aneurophytales and Archaeopteridales) were perhaps the main sources of *sporae dispersae*. Variations in the samples examined of approximate ratio of land-derived to marine palynomorphs, however, evidently support stabilization of marginal marine environments and noticeable modification in complexion of the contemporaneous coastal vegetation upward in the section investigated. Vertical distribution of the plant remains, associated palynofloras, and available faunal indications collectively permit the host strata to be dated as early Middle Devonian (Eifelian). Poor preservation of the plant remains perhaps conveys accumulation during flooding. A river with alternating floods emasculating its bank overtaken by *Protolepidodendron* and *Dawsonites* may be envisaged.

Keywords: Vascular plants; Khoshyeilagh Formation; Palaeobotany; Palaeoecology

Introduction

The first appearance of terrestrial plants is primarily supported by the earliest dispersed spore evidence retrieved from the Llanvirn (mid-Ordovician) strata [58]. It is generally believed that the late Wenlock (mid Silurian) strata host the oldest known fertile axial fossil of embryophytes [22]. Evidently the Late Silurian and earliest Devonian were crucial times in embryophytes evolutionary trends [39], i.e., intervals of the "rhyniophytic phase" [23] or the "eotracheophytic phase" [39] of land plant radiation. It should be noted, nonetheless, that the available fossil record is meager and hence every single documentation of early embryophytes is of significant value in consideration of the derivation and evolution of terrestrial floras. The

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early land plants were generally diminutive and with fairly simple structural organization, i.e., isotomous axis branching and terminally borne sporangia containing isospores [27].

The Trimerophytales, including *Dawsonites*, encompass a number of Devonian vascular plants of variable height (few centimeters to almost a meter) which though superficially resembling the Rhyniales, display some unique features [45]. Although almost certainly paraphyletic, trimerophytes are of great evolutionary interest as including fossils close to the common ancestry of prominent plants such as ferns, progymnosperms, and sphenophytes. Unlike the rhyniophytes, they lack leaves and roots; the plant body mainly consists of branching, photosynthetic stems. Most of the trimerophytes (e.g., *Psilophyton forbesii*) are also pseudomonopodially branched, i.e., axes of different orders forming a main stem with several smaller widely spaced lateral branches [54]. The Trimerophytales are homosporous and their sporangia borne at tips of some branches contain spores almost identical to those of the Rhyniales [45]. The Lepidodendrales, homosporous lycophytes, embrace a group of mostly small herbs known from the Devonian-Mississippian interval. As their name implies they are related to the giant Carboniferous scale trees. Unlike all other lycophytes, nevertheless, the Lepidodendrales bear leaves forked at their tips. The best known protolepidodendroid is *Leclercqia* that is closely related to *Protolepidodendron*. The former is a plant of at least 50cm height bearing unusual leaves each with two forked appendages to their either side (ligules); a feature known in some but not all lycophytes [24]. Existence of ligules implies close relationships among the Protolepidodendrales, Selaginellales, and Isoetales [59]. Protolepidodendrids, extinct by mid-Carboniferous, are known from the pre-Devonian of Aisa, Europe, North America, and Australia.

Notably thick Upper Palaeozoic strata comprising mostly of sandstones, shales, siltstones, and carbonates are generally widespread across Iran [e.g., 56, 5, 1]. These usually host diverse, variably preserved, largely faunal assemblages less frequently associated with miscellaneous palynofloras including microphyto-plankton cysts and spores [34]. Occurrence of plant megafossils in the Iranian Upper Palaeozoic strata, however, is rather meager. In general, fragmentary, poorly preserved Late Palaeozoic plant remains have infrequently been reported from the Alborz Ranges [51, 38, 33, 32, 63, 36], Central Iran Basin [30], and Zagros Ranges [52, 62]. With exception of [52] the other pioneering workers dealing with palaeobotany of Upper Palaeozoic of the Alborz Ranges and Central Iran Basin [i.e., 51, 30] merely alluded to incidence of plant remains in the apposite strata but provided neither description nor any illustration.

The history of palaeobotanical studies of the Iranian Upper Palaeozoic extends back to the early 1940s. Initially [52] described and illustrated comparatively well preserved *Sigillaria persica* from the High Zagros Ranges. Several specimens of the latter variably preserved as impressions and casts recovered from the Chal-i-Sheh Valley were tentatively attributed to the Late Carboniferous-Early Permian. Subsequently, however, [62] illustrated several specimens of *S. persica* from almost the same locality but suggested the host strata (part of the Chaleh Sheh Formation) to be of the Late Devonian-Carboniferous in age. The suggestion was apparently based on their assumption that some of their and in fact Seward's specimens closely resemble such Late Devonian-Carboniferous taxa as *Heleniella*, *Lepidodenropsis*, and *Cyclostigma*. They, furthermore, claimed retrieving seemingly well preserved though unidentified plant megafossils from Lower Permian of the High Zagros Ranges.

Fragmentary, poorly preserved plant remains occurring in uppermost part of the Geirud Formation, central Alborz Ranges which primarily referred to as such by [51] were later proven to be identifiable just at supra-generic level as psilophytes, lycophytes, and sphenophytes by [33, 32, 63, 36] who also provided illustrations. In the eastern Alborz Ranges [38] just mentioned of two early vascular plants, *viz.*, *Psilophyton* sp. and cf. *Dawsonites arcuatus* in lower part of the Khoshyeilagh Formation, northern Shahrud.

Early Late Devonian (Frasnian) flora (lepidophytes, arthrophytes, and filicophytes) associated with rich invertebrate (mostly brachiopods) and vertebrate (mainly Fish) fauna are recorded from Bidu, northern Kerman, southeastern central Iran [30]. The flora comprising essentially of Lepidosigillariaceae (*Heleniella theodori* Zalessky) and *Lepidosigillaria whitei* Kraüsel & Weyland believed to be of similar complexion with the Late Devonian floras of the Urals [64] and that of the Early Carboniferous (Dinantian) of Djado, Eastern Sahara [19, 41].

This study documents Late Devonian plant remains and associated palynofloras of the Khoshyeilagh Formation, northern Mighan, northern Shahrud, eastern Alborz Ranges and attempts to draw palaeophytological and palaeoecological implications accordingly.

Material and Methods

The Iranian geology has been divided by [55] into several distinctive tectonostratigraphic entities. Of

these, the impressive northern Alborz (a.k.a. Elburz) Ranges are subdivided on the basis of notable stratigraphic and structural grounds into three subzones, from west to east, Azerbaijan and western Alborz, central Alborz, and eastern Alborz.

Thick fossiliferous presumably Middle-Upper Devonian sequences of the eastern Alborz Ranges, initially referred to in an unpublished report by Bozorgnia et al., 1970 [cited in 15, p. 9] subsequently defined formally as the Khoshyeilagh Formation [15]. At the type section, it conformably succeeds the presumably Lower Devonian Padeha Formation and precedes the Lower Carboniferous Mobarak Formation. Consisting of basal conglomerates, sandstones, quartzites, basalts, followed upward by alternation of carbonates, shales, and siltstones the Khoshyeilagh Formation yields an exceptionally diverse biota including conodonts, brachiopods, trilobites, algae, bryozoans, corals, Fish, molluscs, plant remains, and palynomorphs [15, 2, 29, 38, 16, 18, 14, 31, 60, 6, 10, 61, 37]. Incongruously, however, age of the Khoshyeilagh Formation's lowermost strata (i.e., four basal beds *sensu* Bozorgnia, 1973) at least at the type section has been subject of much controversy [for details see 6, p. 56, Fig. 3) for decades and as yet surprisingly remains unresolved.

Comprising over 1280m of predominantly marginal marine sediments, the Khoshyeilagh Formation at the Mighan section (base of the rock unit at 55°02´ E and 36°09´N), 30km north of Shahrud and 5km north of Mighan, conformably overlies the presumed Padeha Formation and precedes feature-forming carbonates of the Mobarak Formation (Figs. 1 & 2). There, the Khoshyeilagh Formation yields such miscellaneous biota comparable to those reported from the Khoshyeilagh Formation's type section; collectively indicating a Middle-Late Devonian age [37,38]. Of particular interest at this locality, about 30m above the base, is occurrence of thin-bedded, low-weathering, greenish, medium- to coarse-grained sandstones *ca*. 6 m thick containing the poorly preserved plant remains discussed herein.

The horizon was primarily reported by [38] who simply referred to occurrence of two plant taxa but gave no description/illustration. The plant megafossils documented herein were collected by the author during a field trip to the area in 2002.

Uncovering (dégagement) was the only successful technique in revealing morphological features of the plant remains which were then examined using reflected light microscopy. The specimens were also prepared for palynological investigation utilizing standard acid maceration techniques followed by zinc chloride heavy mineral separation. The residue was finally strew mounted using "Elvacite" as the mounting medium. All the specimens and slides are stored in the Micropalaeontology Laboratory, Department of Geology, Tarbiat Moallem University, Tehran.

Results

Palaeobotany

The plant remains are mostly fragmentary, poorly preserved impressions with virtually no coalified material remaining, occurring on bedding surfaces of the previously mentioned sandstones ascribed to the early Middle Devonian (Eifelian) by [38]. The remains although not unequivocally identifiable systematically embrace few specimens conceivably assignable to the known taxa. The import of the remains lies in the fact that they mark the stratigraphically oldest horizon containing plant megafossils hitherto known from Iran.

Some specimens (Figs. 3A, B) represent parts of lycophytes axes with maximum length and width of, respectively, 30mm and 4mm; one of the stems appears to be dichotomous at its distal end. Fusiform, spirally-arranged, low angle, cushion-like features with overall dimensions of 1x3mm cover the axes. Elliptical-oval ridges resembling cicatrices of the leaves are found on the cushions.

No sign of vascular cicatricules, parichnos scars, and ligules observed. The remains as described are comparable to primitive lycophytes especially the Protolepidodendrales. However, unambiguous generic designation is withheld as characteristic features such as

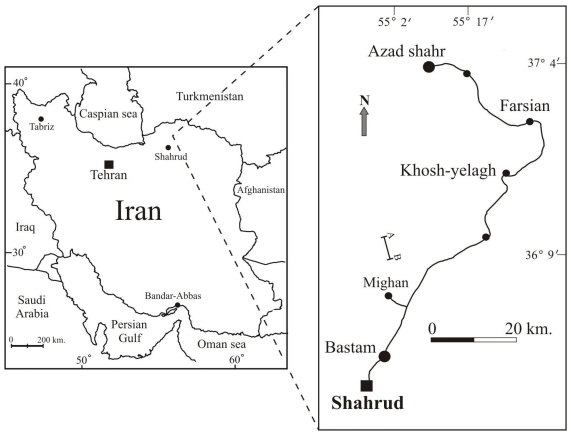

Figure 1. Generalized sketch map of Iran and approximate location of the section studied (A-B), northern Shahrud, eastern Alborz Ranges.

distinctive lycophytes leaves not observed in the material studied. Nonetheless, with reference to overall size and dichotomous branching of the axes as well as the cushion-like features, the specimens could provisionally be attributed to *Protolepidodendron* (Krejci) Potonié & Bernard, 1904.

Other specimens in the assemblage studied are fragments of dichotomous sterile axes of variable length; the most apparently complete of which (Figures 3C, D) is *ca*. 90mm long and about 4mm wide. It bifurcates twice; bifurcation about 30mm apart and at an angle of about 50°.

Width of the first order shootout is *ca*. 3mm and that of the second order measured about 2mm. All over the axes covered with subdued tubercles and near the base rarely with spine-like projections. The specimens appear to be congruent with *Dawsonites* Halle, 1916 and are here termed *D*. sp.

One of the best specimens (Fig. 4) collected from this site is 90mm long, but broken at its proximal part. It shows two very close isotomies, at an angle of 30-50°. Its fertile axes are 2-3mm wide and might show ±triangular emergences but the latter might be artifact of the poor preservation. The specimen bears clusters of paired, re-curved sporangia, i.e., borne terminally on narrowly branching axes. Sporangia are 5mm long, 2mm wide, and most probably fusiform in outline (Figs. 4a, b). Pairs of similar sporangia are also scattered in the host sediments.

Paired fusiform sporangia borne distally on isotomously branched axes are characteristic of *Dawsonites* Halle, 1916 a genus affiliated with the Trimerophytales; specific attribution of the specimen is here provisionally considered as *D*. *arcuatus* Halle, 1916.

Palynology

Small fractions taken from one of the fossiliferous samples (Fig. 4) are analyzed for palynomorphs. The relevant yield, entirely of radiosymmetrical trilete spores (Fig. 5) is very meager and poorly preserved embracing few usually fractured, brown to dark specimens. These include rare representatives of *Retusotriletes* sp. and *Apiculiretusispora plicata* (Allen) Streel, 1967. Additionally, some of the specimens are assignable to *Dibolisporites* on the basis of their biform sculptural elements. It should be emphasized, furthermore, that some samples taken from upper horizons of the Khoshyeilagh Formation (i.e., above the plant megafossils horizon) are palynologically productive containing such distinct marine microphytoplankton cysts as *Cymatiosphaera perimembrana* Staplin, 1961, *Maranhites brasiliensis* Brito, 1965, *Chomotriletes bistchoensis* Staplin, 1961, *Stellinium micropolygonale* (Stockmans & Willière) Playford, 1977 and land-derived spores like *Ancyrospora ancyrea* (Eisenack) Richardson, 1962; *A. parva* de Jersey, 1966; *A. simplex* Guennel, 1963, *A. ampulla* Owens, 1971; *Emphanisporites rotatus* McGregor, 1961, *E. erraticus* (Eisenack) McGregor, 1961, and *Geminospora lemurata* Balme emend. Playford, 1983 [63].

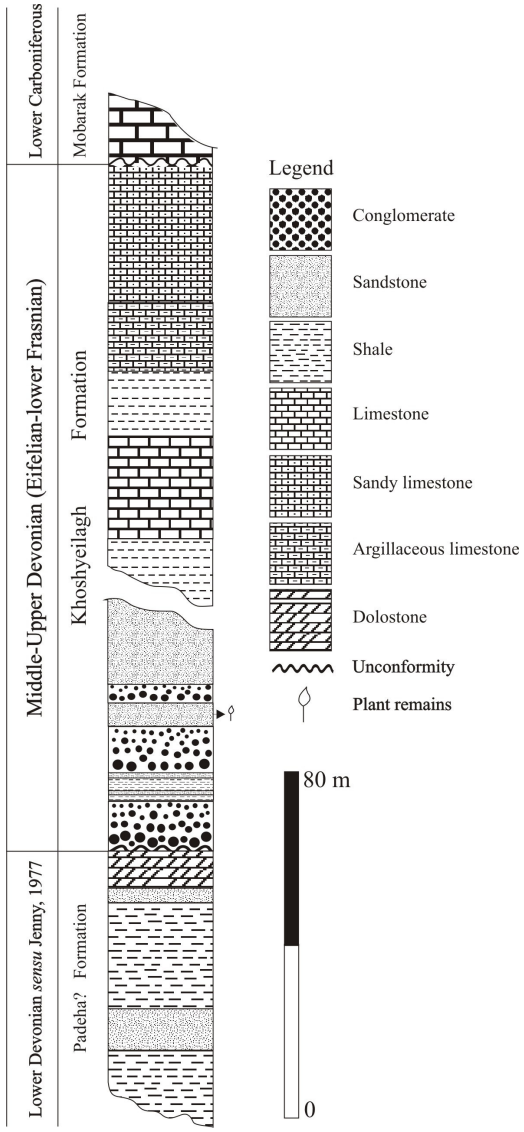

Figure 2. Lithostratigraphic column of the Khoshyeilagh Formation (*partial*), Mighan, northern Shahrud, eastern Alborz Ranges.

Discussion

Inferred Affinity of Plant Microfossils

Spore assemblages documented herein characterize only lower part of the Khoshyeilagh Formation, northern Mighan, while those discussed in [37] represent the whole rock unit at the same locality. The assemblages collectively signify floras that inhabited coastal regions of the eastern Alborz Ranges during the Middle-early Late Devonian interval; the latter is comparable with the *Psilophyton* (upper part), *Hyenia*, *Svalbardia*, and *Archaeopteris* (basal part) Floral Zones of [13].

The palynofloras retrieved from upper part of the Khoshyeilagh Formation were produced by well-speciated coastal floral communities possibly dominated by progymnosperms in particular the cosmopolitan *Archaeopteris* and, perhaps, *Svalbardia*; just possibly also by arborescent lycopods [see, e.g., 46, 11, 17, 44, 12]. However, very little is known about spore-plant relationships of spores occurring in basal part of the Khoshyeilagh Formation including those depicted herein (Fig. 5) and also in [63].

Occurrence in the palynofloras examined of such taxa as *Aneurospora*, *Emphanisporites*, *Dibolisporites*, *Grandispora*, *Retusotriletes*, *Calamospora liquida*, and *Apiculiretusispora plicata* could imply contributions from Phaeophyta, Rhyniopsida (Rhyniales and Trimerophytales), Zosterophyllopsida, Barinophytopsida (Barinophytales), Filicopsida (Cladoxylales and Zygopteridales), Lycopsida (Drepanophycales), Equisetopsida, and Progymnospermopsida (Aneurophytales and Archaeopteridales). Of the spores occurring in upper part of the Khoshyeilagh Formation studied herein, *Apiculiretusispora plicata* (Allen) Streel, 1967 and *Calamospora liquida* Kosanke, 1950 are practically important in spore-plant relationships discussion. *A. plicata* has been compared [43] with *in situ* spores of *Cooksonia crassiparritilis* Yurina, 1964 (Rhyniales) from the Russian Devonian and that of *Pertica dalhousii* (Trimerophytales) Doran et al., 1978 from the Devonian of Canada. Dispersed *C. liquida* has also been associated with *in situ* spores of *Lacoea seriata* Read, 1946 (Noeggerathales of Progymnospermopsida) from the Carboniferous of the U.S.A. [but see 12, p. 182]. Whatever the precise nature of parent plants, the palynological evidence obviously points to a remarkable qualitative change in the coastal forest communities that led to progressive domination in the eastern Alborz Ranges of ferns and archaeopterid progymnosperms during the Middle Devonian time.

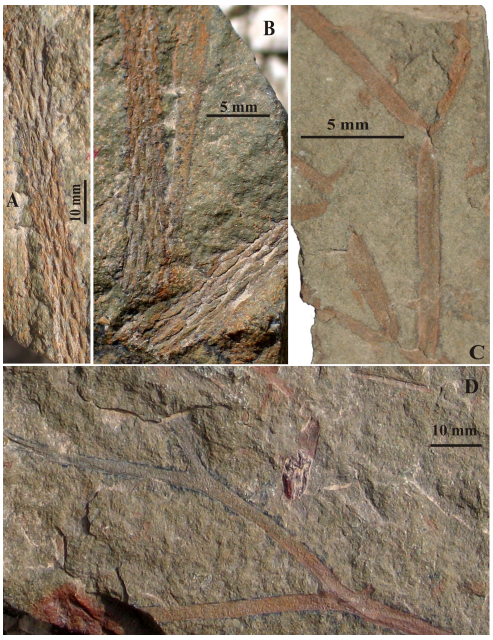

Figure 3. A & B: *Protolepidodendron* sp., note fusiform, spirally-arranged, low-angle features in both A & B and dichotomous axe in B only. C & D: *Dawsonites* sp., featuring well-defined dichotomous stem.

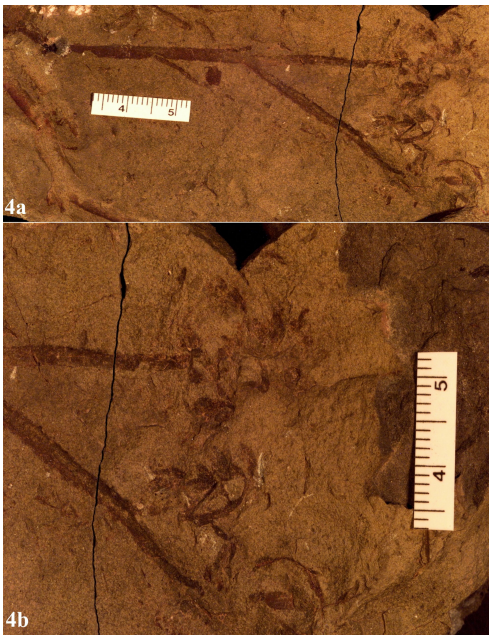

Figure 4. *Dawsonites* sp. cf. *D. arcuatus* Halle, 1916. 4a: General view of a fertile, dichotomous stem. 4b: Enlarged distal part of the specimen depicted in 4a featuring paired, fusiform sporangia borne terminally on narrowly branching axes.

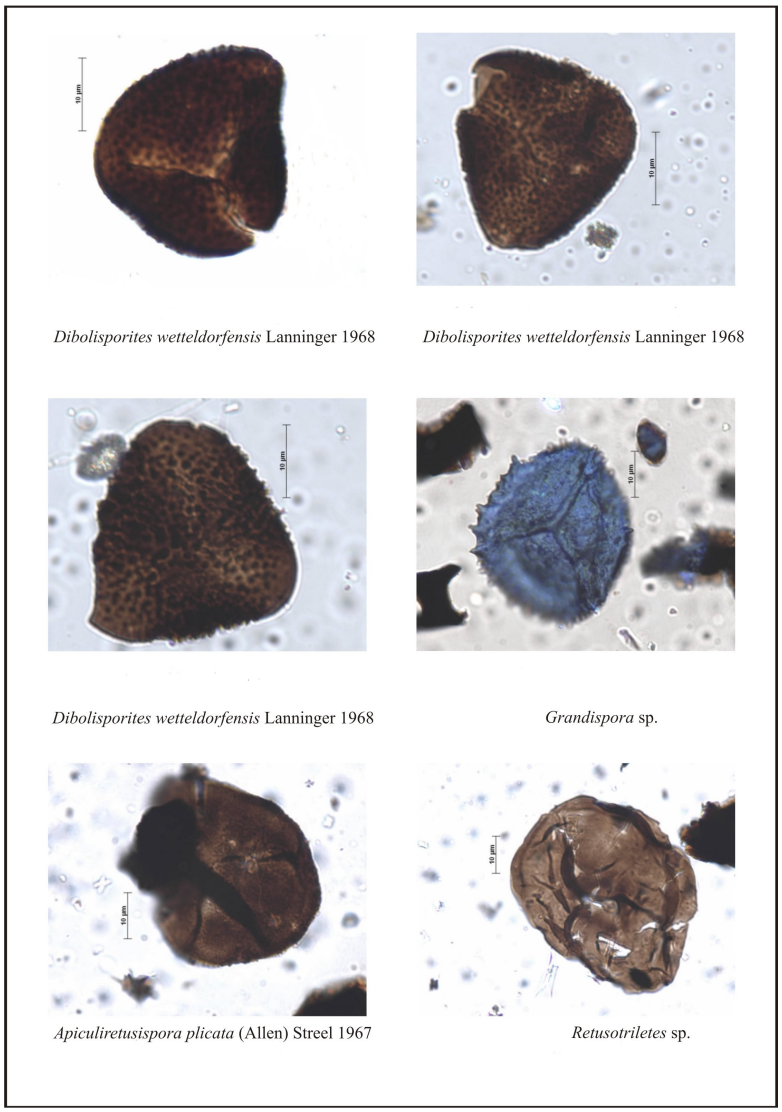

Figure 5. Spores retrieved from the sample shown in Figure 4.

Palaeoecological Considerations

Based on the available palynological data, obviously limited and broad plant macrofossil evidence, and invertebrate fauna of the Khoshyeilagh Formation only generalized comments are possible regarding the palaeoenvironment in which the host sediments accumulated.

The basal layers of Khoshyeilagh Formation at the section investigated generally comprise nonmarine deposits apparently laid down under turbulent conditions. The sedimentary cycle seemingly continued with a widespread westward transgression of the late Middle Devonian Sea. A fluviatile environment can be envisaged for the interbedded shales and plant-bearing sandstones overlying basal conglomerates and sandstones of the Khoshyeilagh Formation. Preservational status of the plant remains probably suggests accumulation during flooding episodes. One might visualize a river with intermittent floods emasculating its bank colonized by coastal vegetation possibly dominated by *Protolepidodendron* and *Dawsonites*. The scenario would satisfactorily justify the rather poor preservational status, fragmentary nature, and different

preservational stages in spore and sporangial developments observed in the material examined.

The emergence and subsequent proliferation of marine fossils mainly corals, bryozoans, crinoids, molluscs, and brachiopods upward in the section studied imply development and stabilization of shallow marine conditions during the Middle Devonian. Total absence in sediments hosting the plant megafossils of marine palynomorphs apparently supports this view.

Geminospora lemurata, *Ancyrospora ampulla*, *A. ancyrea*, *A. parva*, and *A. simplex* are among *sporae dispersae* retrieved from upper part of the Khoshyeilagh Formation of Mighan [37]. *Geminospora lemurata* was produced by archaeopterid trees that had acclimatized to various coastal habitats [42, p. 307]. Several workers [57, 47, 48, 49] have postulated that distribution of some Devonian spores (e.g., *Geminospora* and *Ancyrospora*) could have been ecologically controlled. It is believed that ancyrate forms were produced by plants growing in lowland coastal regions or even in water [20] while *Geminospora* seems to have originated in upland areas.

Age of the Plant Mega-and Microfossil Assemblages

The potential stratigraphic implication of the plant remains is assessed on the basis of previously published records of the fossil plants identified herein, concurrent spores (this study), as well as palynomorphs and invertebrate evidence [38, 37].

Most species allocated to *Protolepidodendron* (Krejci) Potonié & Bernard, 1904 are from the Devonian (particularly Lower and Middle Devonian) worldwide. It should, however, be noted that stratigraphic distribution of other genera within the Protolepidodendrales extends well into the Lower Carboniferous.

Psilophyton is basal within the Euphyllophytina of [40] comprising at least 13 well known species [26]. According to [21] *Psilophyton* occurrences range from uppermost Lockhovian (Lower Devonian) through lowermost Givetian (earliest Middle Devonian). The Givetian occurrence is, nonetheless, uncertain and needs re-examination in light of current knowledge of the genus (Gerrienne, personal communication). Previous records of *Psilophyton* are almost entirely Emsian in age [25] with only one other Gondwanan occurrence of *Psilophyton*-like plants, i.e., two types of *Dawsonites* Halle, 1916 are described by [28] from the lower Emsian (Lower Devonian) of central Morocco. The rather poor preservation of the specimens described here precludes meaningful comparison with the Moroccan material but points to the fact that primitive Euphyllophytina were already present on most of the palaeocontinents during the Early Devonian.

Dawsonites is a form-genus for *Psilophyton*-like clusters of sporangia; the genus has been generally reported from the Devonian (particularly from Lower and Middle Devonian) in a global scale [28].

As indicated earlier, the plant remains are associated with a poorly diversified and indifferently preserved spore association (Fig. 5). More interesting feature of the latter is frequent occurrence of *Dibolisporites wetteldorfensis* Lanninger, 1968 ranging from Pragian (equivalent to Siegenian) up to Emsian [53, 50]. Other spores though having comparatively longer stratigraphic ranges still comply with that of *D. wetteldorfensis*. As previously mentioned, upper part of the Khoshyeilagh Formation at the Might section (i.e., above the plant remains horizon) is palyniferous containing *inter alia* *Geminospora lemurata* Balme emend. Playford, 1983. As part-eponym of Richardson & McGregor's [50] *lemurata-magnificus* Assemblage Zone, *Geminospora lemurata* has been extensively, indeed globally, reported in Givetian-late Frasnian (and perhaps, restrictedly, in Famennian) deposits [for further documentation see 35]. Other terrestrial and marine palynomorphs associated with *G. lemurata* collectively uphold an early Givetian-early Late Devonian (Frasnian) age designation for strata overlying plant remains horizon of the Khoshyeilagh Formation at the section studied [63]. [38] also designated, based on the invertebrate evidence (mostly brachiopods) an early Givetian age for the strata (i.e., Formation 2 of the Khoshyeilagh Group *sensu* 38) immediately overlying the plant remains horizon.

In summary, in absence of direct palaeozoological evidence lower part of the Khoshyeilagh Formation hosting the plant remains is provisionally attributable to early Middle Devonian (late Eifelian) in age. It must be mentioned, nonetheless, that conodonts have been mentioned as occurring in the Khoshyeilagh Formation of Mighan [4] and also in adjacent areas to the east [2, 3, 16, 31, 6, 7, 8, 9, 10]. This is an encouraging sign in that a detailed joint conodont-palynological study could engender more precision in age determination attempts.

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