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Fissidens fontanus (Bach.Pyl.) Steud. and allies: aquatic bryophytes of the Asir granite highlands (Arabian Peninsula)

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Abstract: Two aquatic bryophytes of Northern character, *Fissidens fontanus* and *Leptodictyum riparium*, are reported for the first time from the Arabian Peninsula. A synthesis based on new field observations and a review of the literature provides an overview of the aquatic bryoflora of the Peninsula. The five species forming this exceptional assemblage in Arabia are mapped. They are restricted to wadis (dry riverbed that flows only after rain) carved into granite bedrock that efficiently channel and concentrate rainfall runoff – particularly under the influence of the monsoon – into localized zones of persistent moisture. The conservation status of these species is briefly discussed.

Keywords: aquatic bryophytes; impluvium; Asir mountains; *Fontinalis hypnoides*; *Leptodictyum riparium*; *Rhynchostegium riparioides*.

Introduction

Bryophytes, particularly aquatic species, are closely dependent on water for their reproduction and physiological functions. Unlike vascular plants, they lack true roots and conducting tissues, absorbing water directly through their surfaces (Oliver et al. 2005). Their sexual reproduction requires the presence of water on plant surface, allowing flagellated sperms to swim to the archegonia (Glime 2007). Amphibious and aquatic bryophytes differ in their level of specialization to aquatic immersion. Amphibious species inhabit hydrologically unstable environments, such as rocky areas or riverbanks subject to regular flooding, and exhibit a tolerance to temporary

submersion while requiring emerged phases for growth and reproduction (Dierßen 2001; Stream Bryophyte Group 1999). In contrast, aquatic species are restricted to permanently or near-permanently submerged habitats, such as rivers and ponds, and develop specific morphological and anatomical traits, such as thin leaves, reduced supporting structures, and the absence of a cuticle, to optimize gas exchange in saturated environments (Glime 2007). This ecological gradient, ranging from amphibious to strictly aquatic species, reflects a progressive adaptation to hydric conditions, with specialization closely linked to the duration and frequency of immersion (Glime & Vitt 1984; Rimac et al. 2022).

In the Arabian Peninsula, where a hyper-arid climate prevails and perennial rivers are virtually absent (Glennie 1987; Vincent 2008), surface water occurs only intermittently in wadis, ephemeral streambeds that flow briefly after intense rainfall events. Under such conditions, the occurrence of aquatic bryophytes is highly unexpected. The discovery of *Fontinalis hypnoides* Hartm. at Jabal Ibrahim, Saudi Arabia – a truly aquatic species typically confined to stable river systems – was therefore remarkable (Kürschner 1989). This article reports some new populations of several strictly aquatic species, among which *Fissidens fontanus* (Bach. Pyl.) Steud. and *Leptodictyum riparium* (Hedw.) Warnst.. It includes an updated review of the literature on aquatic bryophytes of the Arabian Peninsula, incorporating recent contributions.

Material and Methods

Aquatic species were selected based on the BET (Bryophytes of Europe Traits) trait database (Van Zuijlen et al. 2023), with amphibious taxa, which are more numerous than aquatic ones in the Arabian Peninsula, excluded from the analysis. In cases of ambiguity, we relied on the habitat observed in the field in Saudi Arabia, and only species that were fully and persistently submerged were considered (*Cratoneuron filicinum* (Hedw.) Spruce, *Vesicularia montagnei* (Bél.) Broth. were not further considered). Species not mentioned in Van Zuijlen et al. (2023) were systematically reviewed to assess their ecological affinities, drawing primarily on literature such as Kürschner's regional studies.

Field surveys were carried out between January and March 2024 & 2025 in the Asir Mountains of Saudi Arabia, to document noteworthy or previously unrecorded bryophyte taxa in the Arabian Peninsula – a region where the bryoflora remains relatively underexplored. Site selection was guided by geological and topographical maps, and prioritized areas with potential moisture sources such as wadis, springs, and wetlands. Accessibility was also considered, favouring locations reachable within a 5 km walk via existing trails.

For *Fissidens fontanus*, reproductive structures (gametangia and sporophytes) were systematically searched for both in the field and in the laboratory, using specimens collected during the surveys. To facilitate the observation of fertile buds, leaves have been removed with forceps. These specimens are now preserved in the authors' bryological herbarium.

Study sites

All known populations of aquatic bryophytes in Saudi Arabia are confined to the Asir Mountains, one of the highest and most biologically diverse regions of the Arabian Peninsula, along with the Yemeni Highlands. The Asir range, composed predominantly of Precambrian granite and granodiorite, forms part of the Arabian Shield. These mountains rise sharply to elevations between 2,400 and 2,600 meters above sea level, creating a dramatic escarpment along the Red Sea to the west, while gradually descending eastward toward the Arabian Platform (Sayed & Masrahi 2023).

The region's geology, marked by its extensive granitic bedrock, influences both hydrology and soil development, creating habitats that support specialized bryophyte communities. The climate of Asir is classified as semi-humid and montane, with average annual temperatures ranging from 16 to 18 °C. It is characterized by a bimodal rainfall pattern, with primary precipitation peaks occurring in winter and spring, and a secondary peak during the summer months (July–August) due to the influence of the southwestern monsoon. Annual rainfall varies considerably with elevation and exposure but averages around 500 mm (for more details see Vincent 2008). This relatively high and seasonally distributed precipitation supports a more mesic vegetation cover compared to the surrounding arid lowlands.

Results

Five strictly aquatic bryophyte species are now known to occur in the Arabian Peninsula (Tab. 1). *Fissidens fontanus*, *Leptodictyum riparium*, *Rhynchostegium riparioides* and *Fontinalis hypnoides* have been observed on several occasions in Saudi Arabia. The new localities are listed in the following:

Fissidens fontanus (Bach.Pyl.) Steud.: SAUDI-ARABIA, 2025/03/13, 2,6 km SSE Ash Shafa, 1980 m, 21°3'5"N, 40°19'43"E; 2025/03/13, 4 km S Ash Shafa, 1810 m, 21°1'59"N, 40°19'8"E; 2025/03/13, 4,5 km SSW Ash Shafa, 1650 m, 21°2'6"N, 40°18'15"E; 2024/03/02, 1,6 km S Jabal Ibrahim, 2150 m, 20°24'22"N, 41°8'16"E.

Fontinalis hypnoides Hartm.: SAUDI-ARABIA, 2024/03/23, 7 km N Tanomah, Jabal Ibrahim, 2300 m, 18°59'42"N, 42°11'7"E.

Leptodictyum riparium (Hedw.) Warnst.: SAUDI-ARABIA, 2024/03/10, 1,5 km SW Jidanah Wadi Shora, 2200 m, 19°46'27"N, 41°43'1"E; 2024/03/14, 3,1 km NE Alhumaid, 1910 m, 19°52'2"N, 41°41'58"E; 2024/03/19, Alsharaf Park, 4,5 km NW Tanomah, 2460 m, 18°57'8"N, 42°8'32"E; 2024/03/02, 1,6 km S Jabal Ibrahim, 2150 m, 20°24'22"N, 41°8'16"E; 2024/03/23, 7 km N Tanomah, 2300 m, 18°59'42"N, 42°11'7"E.

Rhynchostegium riparioides (Hedw.) Cardot: SAUDI-ARABIA, 2024/03/16, 2,7 km E Bani Sar, 2030 m, 20°6'12"N, 41°28'29"E; 2024/03/20, 5,6 km N Tanomah, 2610 m, 18°58'42"N, 42°11'22"E; 2025/03/13, 4 km S Ash Shafa, 1810 m, 21°1'59"N, 40°19'8"E; 2024/03/19, Alsharaf Park, 4,5 km NW Tanomah, 2460 m, 18°57'8"N, 42°8'32"E.

The average elevation of the observed populations is 2,138 meters. All these species have a Northern biogeographical character, being mostly temperate species (Van Zuijlen et al. 2023).

Oxyrrhynchium speciosum (Brid.) Warnst. (incl. var. *angustifolium* P.Størmer) has not been observed but was mentioned previously in Saudi Arabia (Kürschner 1989) and in Yemen (Kürschner et al. 2015).

From an ecological point of view, all observed populations are located in wadis (Fig. 1, 2) that collect runoff water from extensive smooth granite slabs (Fig. 3).

The known distribution of the five aquatic bryophyte species is provided (Fig. 4). Overall, the populations of aquatic bryophytes are all located between 16,5°N in Yemeni Highlands and 20,5°N in Saudi Arabian Asir. *Fontinalis hypnoides* has the most restricted distribution, being known from only a single population, recorded at Jabal Ibrahim for around forty years (Kürschner 1989). *Oxyrrhynchium speciosum* and *Rhynchostegium riparioides* have the widest distributions within the Asir Mountains, extending into the highlands of Yemen. *Fissidens fontanus* and *Leptodictyum riparium* appear to be more confined to the central elevations of Saudi Arabian Asir.

No sporophytes of *Fissidens fontanus* could be found in Saudi Arabia populations. However, male and female branches were present and abundant in all the populations studied (Fig. 5).

Discusion

Fissidens fontanus has a broad global distribution, occurring in North and Central America, as well as in Europe, where it ranges northward to Scandinavia, eastward to Ukraine, and includes Macaronesia (Blockeel et al. 2014). In Africa, it is recorded in Morocco (Gattefossé & Werner 1932; Maire & Werner 1934; Jelenc 1955), Algeria (Jelenc 1955; Ahayoun et al. 2007), Egypt (El-Saadawi et al. 2015) and Chad (Pursell 1987; O'Shea 2006). It is replaced by *F. bessouensis* Corb. in Equatorial west Africa and *F. palmifolius* (P. Beauv.) Broth. in southern Africa (note that many ancient African collections are erroneously attributed to *Fissidens fontanus*). *Fissidens fontanus* (as well as *Leptodictyum riparium*) is newly recorded for the entire Arabian Peninsula (Kürschner & Frey 2020). The nearest population is the single one of Israel (Heyn & Herrnstadt 2004), located at 1200 km North, and that of south-east Turkey (Yayintaş & Allen 2009), at 2000 km North, both populations being highly localized. In the Mediterranean region, the nearest populations are found in the Maghreb, Italy (Dickson et al. 2021), Slovenia (Jakob et al. 2024) and Montenegro (Anđić et al. 2018). The significant cluster in the southwestern Arabian Peninsula is therefore clearly isolated.

The Arabian Peninsula is often perceived as a uniformly arid region, yet it displays great geological and geomorphological diversity, with a variety of habitats, some of which are humid. Nevertheless, the discovery of an aquatic species is surprising, given the rarity of such species reported so far from the Peninsula. In the Asir

Tab. 1 Aquatic bryophyte species in the Arabian Peninsula (SA: Saudi Arabia; Ye: Yemen)**.**

	SA	Ye
Fissidens fontanus (Bach.Pyl.) Steud.	new	x
Fontinalis hypnoides Hartm.	x	x
Leptodictyum riparium (Hedw.) Warnst.	new	x
Oxyrrhynchium speciosum (Brid.) Warnst.	x	x
Rhynchostegium riparioides (Hedw.) Cardot	x	x

Fig. 1 Aquatic bryophyte community with *Fissidens fontanus* and *Fontinalis hypnoides* in Jabal Ibrahim (Saudi Arabia) (photograph taken in March 2025).

Fig. 2 Colony of *Fissidens fontanus* in a wadi near Taif (photograph taken in March 2025).

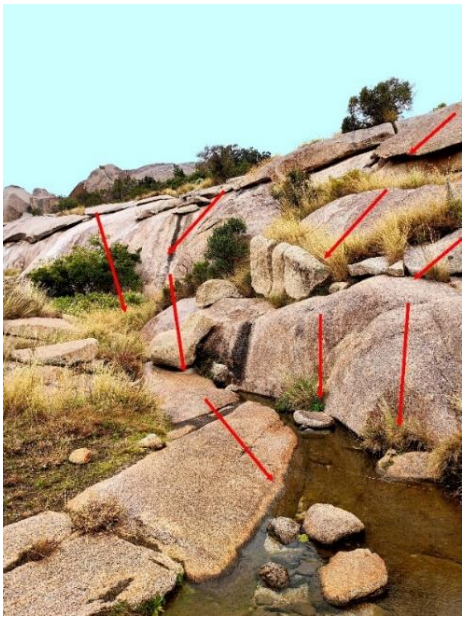

Fig. 3 Presumed runoff of water over smooth granite slabs in Jabal Ibrahim (Saudi Arabia) (photograph taken in March 2025).

Mountains of the Arabian Peninsula, small catchment areas developed on granitic bedrock can feed wadi systems that host aquatic bryophytes, sometimes even in a semi-permanent manner. While granite is impermeable in its solid form, it is often heavily fractured and jointed, allowing some infiltration. However, in these environments, surface runoff plays a particularly crucial role. During episodes of orographic rainfall – often enhanced by the influence of the Indian monsoon – water rapidly flows over exposed granite slabs and among large blocks and boulders. These surfaces, often smoothed and compacted, generate efficient runoff, especially when soils are thin or absent. In small basins, the topography and arrangement of these surfaces create natural impluviums – areas where water collects and converges – leading to the formation of permanent or semi-permanent streams and seepages (Fig. 3). If the catchment is favourably oriented (for example, north-facing) and benefits from shading by topography or vegetation, evaporation is reduced, further enhancing water persistence in the landscape. These hydrological dynamics can support microhabitats that remain moist for extended periods, allowing aquatic bryophytes to thrive even in an otherwise arid environment.

The phytosociological approach appears of limited relevance for aquatic bryophyte communities in Saudi Arabia. Assemblages are often reduced to one or two dominant species, making it difficult to identify meaningful species associations or apply existing European syntaxa. Yet, the bryological assemblages associated with *Fissidens fontanus* are always remarkable, even if generally sparse and inconspicuous. *Fissidens fontanus*, and the other strictly aquatic species, are occasionally also accompanied by amphibious species of high heritage conservation value (*Cratoneuron filicinum*, *Fissidens crassipes* Wilson ex Bruch & Schimp., *Hydrogonium bolleanum* (Müll. Hal.) A. Jaeger, *Philonotis hastata* (Duby) Wijk & Margad.).

No sporophytes of *Fissidens fontanus* could be found in Saudi Arabia. However, male and female branches were present and abundant in all the populations studied. In Italy, Dickson et al. (2021) found that the small capsules are caducous and considered to be the main dispersal unit, rather than the shed spores. However, the occurrence and caducity of the sporophytes have yet to be confirmed in Saudi Arabia especially since no old female branches were located (from where caducuous sporophytes would have originated). Certainly, as argued by the same authors, vegetative propagules, along with stem and leaf fragments, also contribute to the species' dispersal. The question of the origin of the Arabian population remains open. Given the presence of large, well-established populations located several hundred kilometers apart, the species can be considered native and an integral part of the aquatic bryophyte assemblages of the Arabian Peninsula. The occurrence of sterile populations of *Fissidens fontanus* in the Asir granite mountains may be explained by long-range or chance dispersal, particularly through vegetative propagules transported by migratory water birds. This migration route, which connects Eastern Europe and Turkey to the Arabian Peninsula and Africa, could

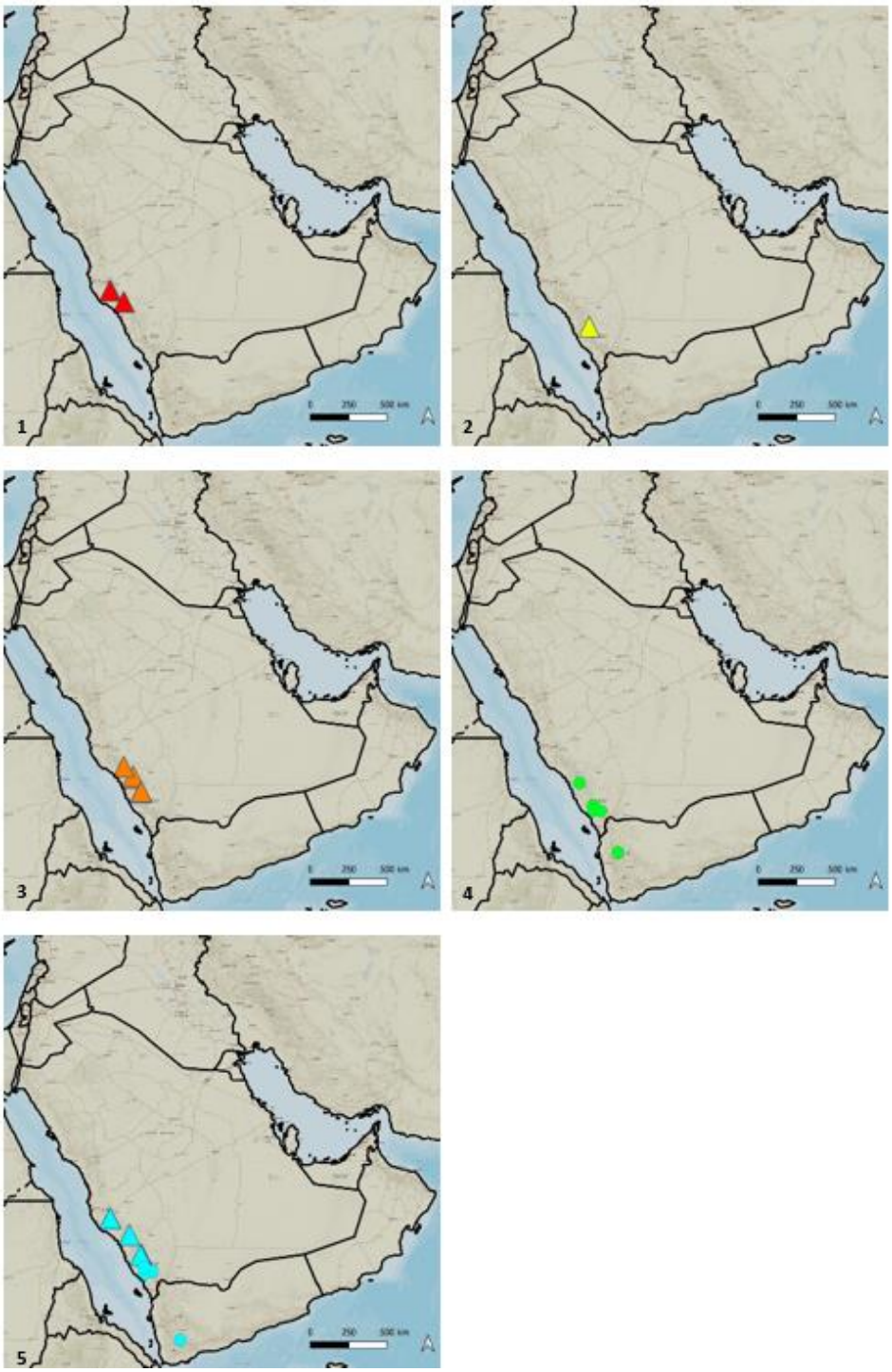

Fig. 4 Arabian Peninsula distribution of 1: *Fissidens fontanus* (Bach. Pyl.) Steud.; 2: *Fontinalis hypnoides* Hartm.; 3: *Leptodictyum riparium* (Hedw.) Warnst.; 4: *Oxyrrhynchium speciosum* (Brid.) Warnst.; 5: *Rhynchostegium riparioides* (Hedw.) Cardot (triangle: new data; circle: bibliographical data).

facilitate episodic introductions of aquatic bryophytes into isolated habitats such as those found in the Asir region (Green & Elmberg 2014; Hahn et al. 2009).

All these wadis are entirely natural, often without any notable hydrological developments, although some may include water abstraction for agricultural use. The species does not appear to be locally threatened, although the anthropogenic transformation of watercourses could become a concern in the medium term. Furthermore, as water resources are extremely limited in the region, and in light of ongoing climate change and increasingly severe droughts, there is concern that growing pressure may be exerted on the watercourses hosting these aquatic bryophyte communities. Detailed surveys would be necessary to determine demographic trends of *Fissidens fontanus* populations and other aquatic bryophyte species.

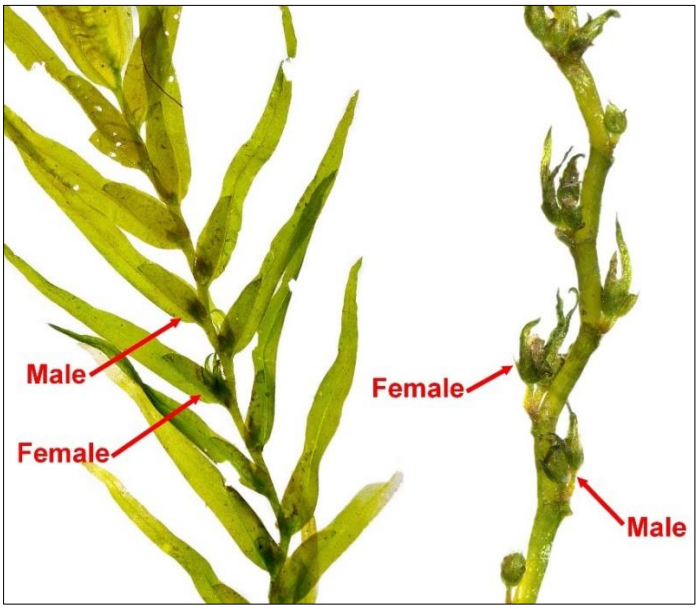

Fig. 5 Male and female branches of *Fissidens fontanus* (Bach.Pyl.) Steud. (note that the species is monoicous; leaves have been removed from the left shoot).

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