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On the occurrence of *Riella affinis* M. Howe & Underwood (Marchantiopsida, Sphaerocarpales) in the Sahara Desert (Africa)

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Abstract – A small population of *Riella affinis* M. Howe *et* Underwood, a rare aquatic liverwort species belonging to the subgenus *Trabutiella*, has been located in the Tassili n'Ajjer (Algeria, central Sahara desert). This is the first confirmed record of this disjunct tropical species from North Africa. The study of living material shows that its reproductive biology seems especially well adapted to stochastic habitats found in seasonal pools. Although it is likely to be of Gondwanic origin, the present distribution of *R. affinis* is, at least in some cases, best explained by events of dispersal favoured by strong winds. Its presence in the Sahara desert is probably a relic from biome shifts associated with wetter periods of the Holocene.

***Riella* / *Riella affinis* / Sphaerocarpales / Sahara / Biogeography / Disjunct distribution / Dispersal mechanisms**

Résumé – Une population isolée de *Riella affinis* M. Howe *et* Underwood, une hépatique aquatique rare appartenant au sous-genre *Trabutiella*, a été observée au Tassili n'Ajjer (Algérie, Sahara Central), ce qui représente la première localité de ce taxon en Afrique du Nord. L'étude des spécimens vivants a montré que sa biologie reproductive semble bien adaptée aux petites mares saisonnières occasionnelles dans le désert. Bien que ce taxon ait sans doute une origine Gondwanéenne, sa distribution actuelle peut, au moins dans quelques cas, s'expliquer comme le résultat d'une dispersion favorisée par le vent. Sa présence au Sahara est probablement une relique des fluctuations des biomes associés aux périodes plus humides de l'Holocène moyen.

***Riella* / *Riella affinis* / Sphaerocarpales / Sahara / Biogéographie / Disjonction / Mécanismes de dispersion**

INTRODUCTION

Riella is a specialised genus of winter-spring annuals of delicate and short-lived aquatic liverworts living in seasonal ponds of clear and cool waters in warm and semi-arid regions worldwide. Gametophytes develop quickly during

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winter or spring, and complete their life cycle in a few months while water remains (Schuster, 1984), resting in the form of spores during the adverse dry season. It is known that spores retain viability over long periods, often for several years. According to Schuster 1992, the main areas of diversity for *Riella* are South Africa and the Mediterranean region. The majority of species of *Riella* are dioicous (Schuster, 1992), with only two species: *R. affinis* M. Howe *et* Underwood and *R. cossoniana* Trabut, monoicous. Together with *R. cossoniana* and *R. garmundiae* Hassel de Menéndez, *R. affinis* belongs to the subgenus *Trabutiella* A.E. Porsild, characterised by winged archegonial involucres.

Recently, we detected the presence of a conspicuous population of *R. affinis* in a small rock pool located in the Tassili n'Ajjer mountain massif in Southeast Algeria (central Sahara). This is the first confirmed record of this taxon in North Africa. Although Trabut (1942) previously included this species in the area, no specific locality was indicated; Jelenc (1955) included this species with a comment "sine loco". Later Jelenc (1957) stated that *R. affinis* was able to grow in North Africa, but did not present any proof of this assertion. Schuster (1992) in his revision on the world distribution of *Riella* did not confirm the presence of the taxa in the area, and Ros *et al.* (1999) incorrectly cited this species, according to Jelenc (1955). Finally, Söderström *et al.* (2002) considered that its presence in North Africa was doubtful.

The Sahara is the largest desert in the world (Ezcurra, 2006); it extends over 4.6 million km^2 from the Atlantic coasts in the West to the Red Sea, that is, 10 percent of the African continent. The Red Sea separates the Sahara from the mountains and the deserts of the Arabian Peninsula; at present, its climate is one of the hottest and most hyper-arid in the world.

The Tassili n'Ajjer range is a vast region of 80,000 km^2 located in the Southeast corner of Algeria. The massif is made up of Cambrian-Ordovician and Silurian materials deposited on a granite base of pre-Cambrian origin (Julivert, 2003), and shows unique geo-morphologic structures of barren gravel plains and NW-SE-oriented stone plateaus. Together with the Hoggar located in South Algeria, the Aïr massif in Northern Niger and the Tibesti massif in Northern Chad, all belong to the Saharan Montane Xeric Woodlands ecoregion (WWF, 2001; Olson *et al.*, 2001). Currently these Saharan mountains have a cool and moister climate than the low-elevation surrounding desert, conditions that have allowed a refuge for a notable relict and endemic flora of Mediterranean affinities of great biogeographical interest, like the Duprey cypress or "tarout" (*Cupressus dupreziana* A. Camus), the wild olive (*Olea laperrinei* Battand & Trabut) and the Saharan myrtle (*Myrtus nivellei* Battand & Trabut) (Ozenda, 1977; Ezcurra, 2006).

The climate there is continental with heavy daily and seasonal fluctuations, including freezing weather in winter. In the nearest village of Djanet (1100 m), the mean annual temperature is 22ºC and rainfall, which is highly irregular from year to year, is less than 100 mm per year (Ozenda, 1977). The area is drained by a complex network of dry riverbeds ("wadis") which create several spectacular narrow yet deep gorges to the South. In these steep-walled canyons, small permanent or seasonal rock pools are common (Villiers & Hirtle, 2002). These rock pools, locally known as "gueltas", are often surrounded with *Nerium oleander,* and are sometimes colonised by a macrophyte flora of *Potamogeton* and *Chara.* Ecologically, these "gueltas" play a critical ecological role during periods of severe droughts as they allow the survival of domestic cattle and wild fauna. Our population of *R. affinis* grew in one of these rock pools which was deprived of any other type of macrophyte vegetation.

The region is highlighted by its biota, the beauty of the desert landscapes and its cultural interest, and it preserves one of the world's best collections of Neolithic paintings and engravings. The whole area is considered a World Heritage site by UNESCO, and is included in the Algerian Tassili n'Ajjer National Park.

RESULTS

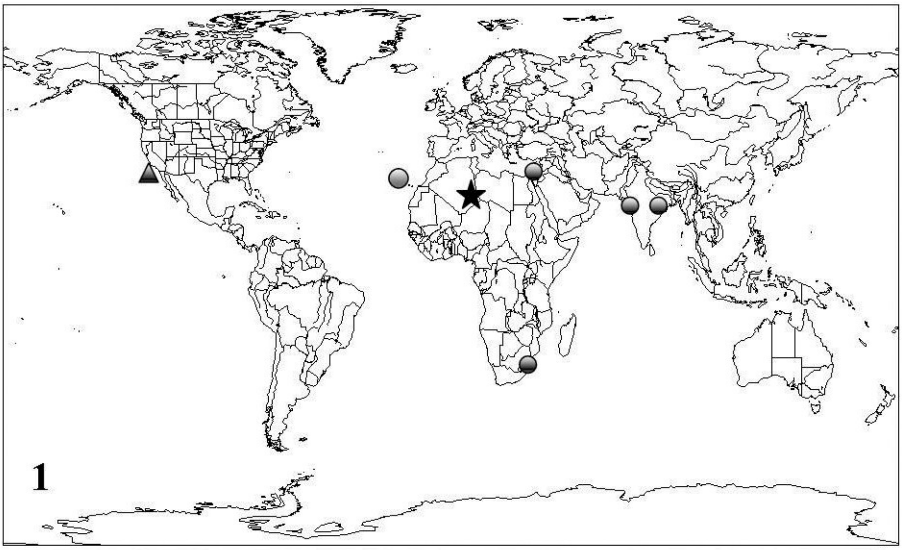
Material examined. **Algeria**: Tassili n'Ajjer, Tafilalet canyon, in a seasonal rock pool with a surface of around 10 m^2 on very fine mud from the surface to 1 m depth (Fig. 2). 24º36'05''N, 9º37'26''E, 1600 m. altitude. *Boisset, F.* 13/01/2007, VAL-Briof. 7.372. The water was cool and clear, and plants were fertile. Living material was cultured at the laboratory with natural light and under controlled conditions with 12/12 light/darkness at 18ºC/10ºC.

***Riella affinis* M. Howe *et* Underwood**, *Bull. Torrey Bot. Club* 30: 214-224. 1903.
Description: Plants 1.8-4.2 cm (Fig. 3), caespitose, unbranched or branched sparingly, shoot apex falciform. Axis slight flattened 0.5-0.6 mm wide. Dorsal wing 2-3 mm wide (Fig. 5), margin entire, marginal wing cells 45-57 × 28-40 µm; wing cells near axis 47-50 × 27-32 µm; oil cells 17.5-22,5 × 20-22.5 µm, oil bodies 15-20 µm spherical. There are two types of scales along the axis, they are linear some enlarged at the top in the upper part of the thallus, 300-500 × 60-120 µm; there is also another type of scales with a panduriform shape in the older parts of the thallus (Fig. 10). Monoicous, proterandrous, antheridia 4-6, in sinus of the blade, antheridial body 200-250 × 120-150 µm (Fig. 4). Archegonial involucre ovoid 1.5-2 × 1-1.3 mm, with 8 lamellae of 150-200 µm wide in the upper part with a margin that is entire or undulate-sinuate (Fig. 6). Sporophyte with seta of 0.2-0.4 mm (Fig. 5), capsule globose 0.6-1 mm in diameter (Fig. 6). Spores ovoid, 80-100 µm (Fig. 8), distal face with spines 9-12 µm, with apices truncate slightly dilatate (Fig. 9), occasionally acute, surface of spines striate, surface between spines almost smooth, basal membranes of spines sometimes forming a few imperfect areola; proximal face with short spines to 5 µm, obtuse or truncate or with small protuberances as tubercles, surface of projections and between them irregular striate, and basal membranes are absent.

After several months, cultured plants showed a gradual tendency to senescence. Over several months, however, new plants arose from both the basal parts of the thallus and the gametophytic tissues located in the vicinity of the sporophytes. Growth from spores in culture was not observed.

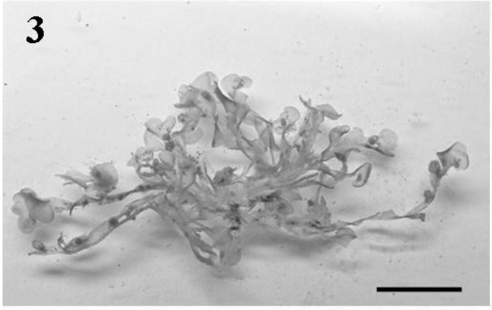
DISCUSSION

The genus *Riella* is traditionally included in the order Sphaerocarpales, and represents an early diverging lineage of Marchantiopsida (Boisselier-Dubayle *et al.*, 2002; Forrest & Crandall-Stotler, 2005; Heinrichs *et al.* 2005, 2007; He-Nygrén *et al.*, 2006), and it probably evolved in the Paleozoic, where it was seemlingly restricted to warm and continental areas of Pangea (Schuster, 1992).



Figs 1-2. **1.** Global distribution of *Riella affinis,* ★: new location; ●: previously known locations, ▲: introduced population. **2.** Aspect of population of *R. affinis* in a small rock pool or "guelta", located in the Tassili n'Ajjer, Algeria (central Sahara).

Figs 3-10. **3.** Habit of a plant (scale bar: 1 cm). **4.** View of distal part of thallus showing dorsal lamina with gametangia, arrow: group of antheridia, arrowhead: archegonium (scale bar: 250 µm). **5.** View in median part of thallus with several sporophytes inside involucres (scale bar: 0.5 mm). **6.** Upper view of the winged involucres (scale bar: 200 µm). **7.** Capsule deprived of involucres with spores located inside (scale bar: 0.5 mm). **8.** Distal face of spore, distal face (scale bar: 25 µm). **9.** Detail of spines on spore distal face (scale bar: 5 µm). **10.** Pandurate scale, arrow: oil cells (scale bar: 100 µm).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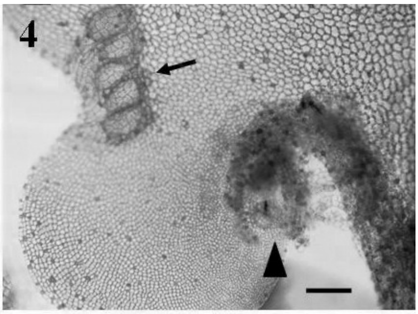
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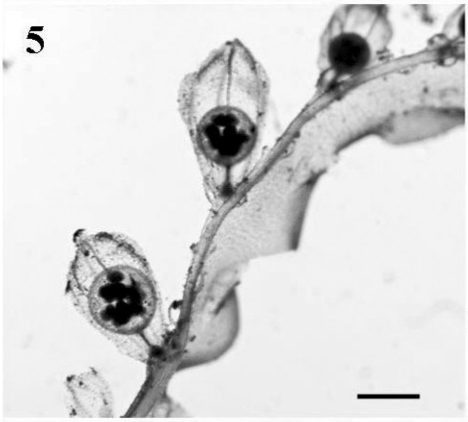
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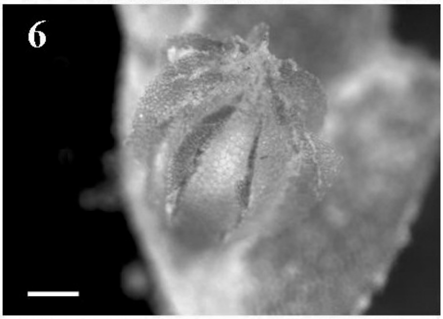
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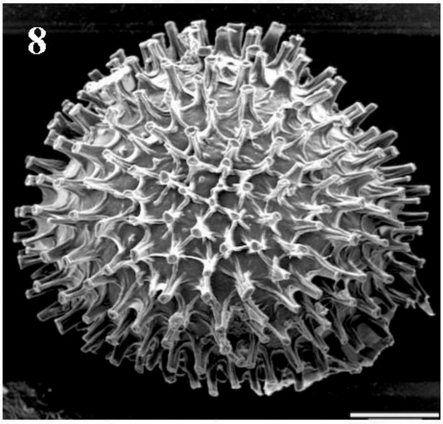
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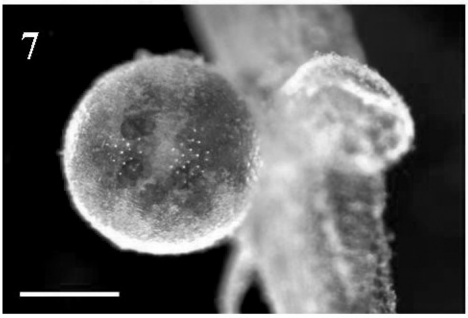
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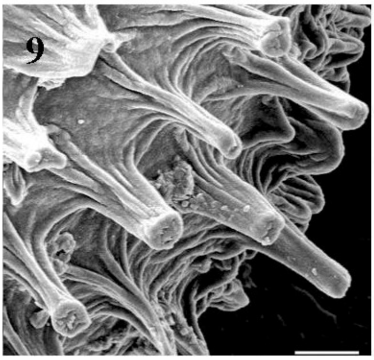
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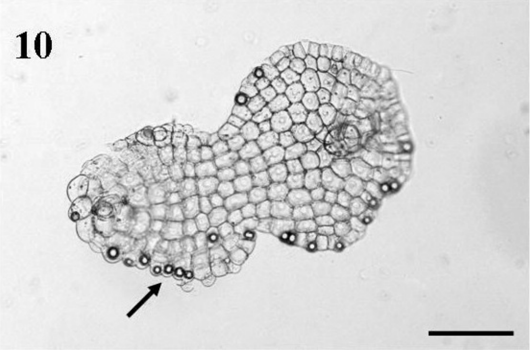
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Although *Riella* specimens are rarely included in the recent molecular analysis, the near basal position of the Sphaerocarpales (3 genera, less than 30 species) in Marchantiopsida seems well based.

Characteristically of the genus, *R. affinis* presents large and long-lived spores (70-100 µm) that presumably remain dormant in the spore bank during the long drought intervals, and germinate after a flash flood replenishes the pool. The reproductive strategy of *R. affinis* seems to adjust to the model of a short-lived species (annual shuttle species), developing in spatially rare patches with a high temporal variation and a low frequency of favourable years (During, 1992, 1997; Söderström & Herben, 1997). A high vegetative growth rate combined with an active sexual and asexual reproduction assures life in temporary habitats. This strategy can be interpreted as a trade-off between local survival in the spore bank and dispersal (During, 1977). Monoecy, a rare reproductive character in the genus only shared with *R. cossoniana,* can be interpreted as a successful strategy if the foundations of new colonies are rare events based on few spores (Schuster, 1983, 1992). At least theoretically, even a single spore can be the inoculum of a clonal population. Our laboratory observations suggest that once the plants have been established and there are no other competitive organisms, the plants can persist asexually for several months at least. In this time, sexual reproduction, probably intragametophytic self-fertilisation, and the gradual ripening of the sporophytes, allow the formation of a perdurable spore bank. As previously indicated for other species of *Riella* (Schuster, 1992), we observed no germination of spores in these cultures, which suggests that they are genotypically conditioned to withstanding several months, or even years, in drought conditions before germination. In summary, in the ephemeral and unpredictable "gueltas" habitat, large spores assure longevity in the seed bank and, at least theoretically, their drought resistance may also enhance the ability for colonising new localities (Söderström & Herben, 1997).

In Africa, the genus *Riella* shows a marked bipolar distribution (Schuster, 1992), (Fig. 1). In Austral Africa, the genus is represented by five species: *R. echinospora* Wigglesworth, *R. purpureospora* Wigglesworth, *R. alatospora* Wigglesworth, *R. capensis* Cavers and *R. affinis*. Seven species are present in Mediterranean Africa, which is a relatively well explored area (Schuster, 1992; Ros *et al*., 1999; 2007): *R. bialata* Trabut, R. *cyrenaica* Maire, *R. cossoniana*, *R. helicophylla* (Bory *et* Montagne) Montagne, *R. notarisii* (Montagne) Montagne, *R. parissi* Gottsche, *R. sersuensis* Trabut. The Atlas range acts as a biogeographical barrier, separating the Sahara from North Africa, with a Mediterranean climate and biota.

R. affinis is a rare species with a highly disjunct distribution which is scattered in a small number of localities around the world. Initially described from the Canary Islands (Howe & Underwood, 1903), the species was indicated later in North America (Thomson, 1940; Schuster, 1992; Bartholomew-Began, 2002), South Africa [Proskauer (1955), India (Pandé *et al*., 1954; Pattel, 1977) and Israel (Ros *et al*., 2007)]. In North America, it seems that the population of California was introduced at the Stanford University campus, perhaps by D.H. Campbell (Bartholomew-Began, 2002). Meanwhile, the citation of Argentina that was attributed to Hässel de Menéndez (1959) in Schuster (1992) is not correct (Perold, 2000). In India, the species was initially described as *R. vishwanathai* Pandé, Misra et Srivastava, from material found in Uttar Pradesh near Banares (Pandé *et al*., 1954). Later, Patel (1977) found it in the shallow areas of Lake Kanewal (Gujarat). Proskauer (1955) considered that the characters employed for describing the first species were highly variable and, consequently concluded that all the Indian material was conspecific with *R. affinis.*

During the Pleistocene and Holocene, the Saharan climate presented several pluvial periods which allowed the formation of numerous lakes and wetlands, including an expanded Lake Chad (Hoelzman *et al.*, 1998). The change in climate favoured the shifting of biomes and the repeated isolation and (re)connection of aquatic flora. During the last mid-Holocene humid period (8500-5500 yr BP), the Sahara desert was drastically reduced and the Sahelian vegetation belts (*i.e.* steppe, xerophytic woods/scrub, tropical dry forest) shifted northwards (Prentice *et al.*, 2000). During this period, wild fauna was typical of the African savannah, and human Neolithic settlements were common. So, it appears to be very likely that the presence of *R. affinis* in the Sahara is a relic of the last wetter climatic conditions. In this sense, other isolated populations may still be present on some of the other massifs of the Sahara, or even the Arabian Peninsula. From the mid-Holocene (6000 yr BP) onwards, a sudden transition occurred to the more arid conditions that are prevalent today (Adams *et al.*, 1999). In the near future, the current global warming scenario of higher temperatures will probably increase the potential for more severe, longer-lasting droughts in the deserts of the world (Herrmann & Hutchinson, 2006).

Although the species of Marchantiopsida with relatively large spores have a priori a limitation in their dispersal capabilities, and long-range dispersal seems unlikely at first sight, we consider that the mechanism of wind dispersal (During, 1997) may explain the findings of new populations in the case of *R. affinis,* and probably in other species of *Riella*. Recently, molecular dating of lineage divergences in a wide variety of taxa has favoured the resurrection of oceanic dispersal over tectonic vicariance to explain disjunct distributions (Lomolino *et al.*, 2006: Queiroz, 2005). It is important to remember that the Sahara has long been acknowledged as the major source of aeolian dust in the world with an annual production of 400-700 Tg per year (Washington *et al.*, 2003). The winds that blow over the desert show different trajectories during the year, and can be very energetic and transport dust over long distances (Middleton & Goudie, 2001). The characteristic particle size of Saharan dust sampled in a few storms within hundreds of kilometres from the source indicates a median diameter of 72-74 µm (Coudé-Gaussen, 1981; McTainsh & Walker, 1982), similar to spores sizes. It has recently been confirmed that these dust events also carry microorganisms and pollen. In this way, they act as long-distance dispersal mechanisms of global transcontinental transport (Kellogg & Griffin, 2006). The hypothesis that episodic events of heavy winds act as a dispersal vehicle over long distances for cryptogams (mosses, liverworts and lichens) has been also recently shown in the Southern Hemisphere (Muñoz *et al.*, 2004).

It is interesting to note that strong winds originating in South Algeria often blow over the Canary Islands and the Middle East (Middleton & Goudie, 2001). Dust rains in South Europe are also a relatively common phenomenon. It seems highly plausible that if *R. affinis* was more common in the Sahara in the mid-Holocene, a colonisation of the Canary Islands and Israel would have been facilitated by dust plumes, favouring its dispersal to these localities. In the first case, all the islands were formed in the past 20 million years (Ma) by volcanic eruptions and currently have a subtropical climate strongly influenced by the humid trade winds from the northeast. Winds that with the sea currents have favoured the transport of colonizers from neighbouring North Africa and the Iberian Peninsula (Juan *et al.*, 2000). On the other hand, their presence in the Sahara, Israel and India suggests a certain continuity in the vast arid area of the Saharo-Sindien deserts.

Finally, the presence of South African populations of *R. affinis* could be alternatively explained as a relic from Gondwana or as the result of more recent colonisations facilitated by the existence of an arid tract or corridor in East Africa from the Miocene (Van Zinderen Bakker, 1975; Coetzee, 1983). This corridor has been proposed to account for the disjunctions between South and North Africa in arid-adapted pteridophyte genera (De Winter, 1971; Aldasoro *et al*., 2004), *Androcymbium* (Caujapé-Castells *et al*., 2001; Del Hoyo & Pedrola-Monfort, 2006), and to also explain the colonisation of Africa by taxa of an Eurasian origin, like Borraginaceae (Raven & Axelrod, 1974) and *Erica (*McGuire & Kron, 2005). In any case, a more precise interpretation of the patterns and processes in the highly disjunct biogeographical pattern of *R. affinis* will only be possible when more data will be collected in the framework of future molecular phylogeographical studies.

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