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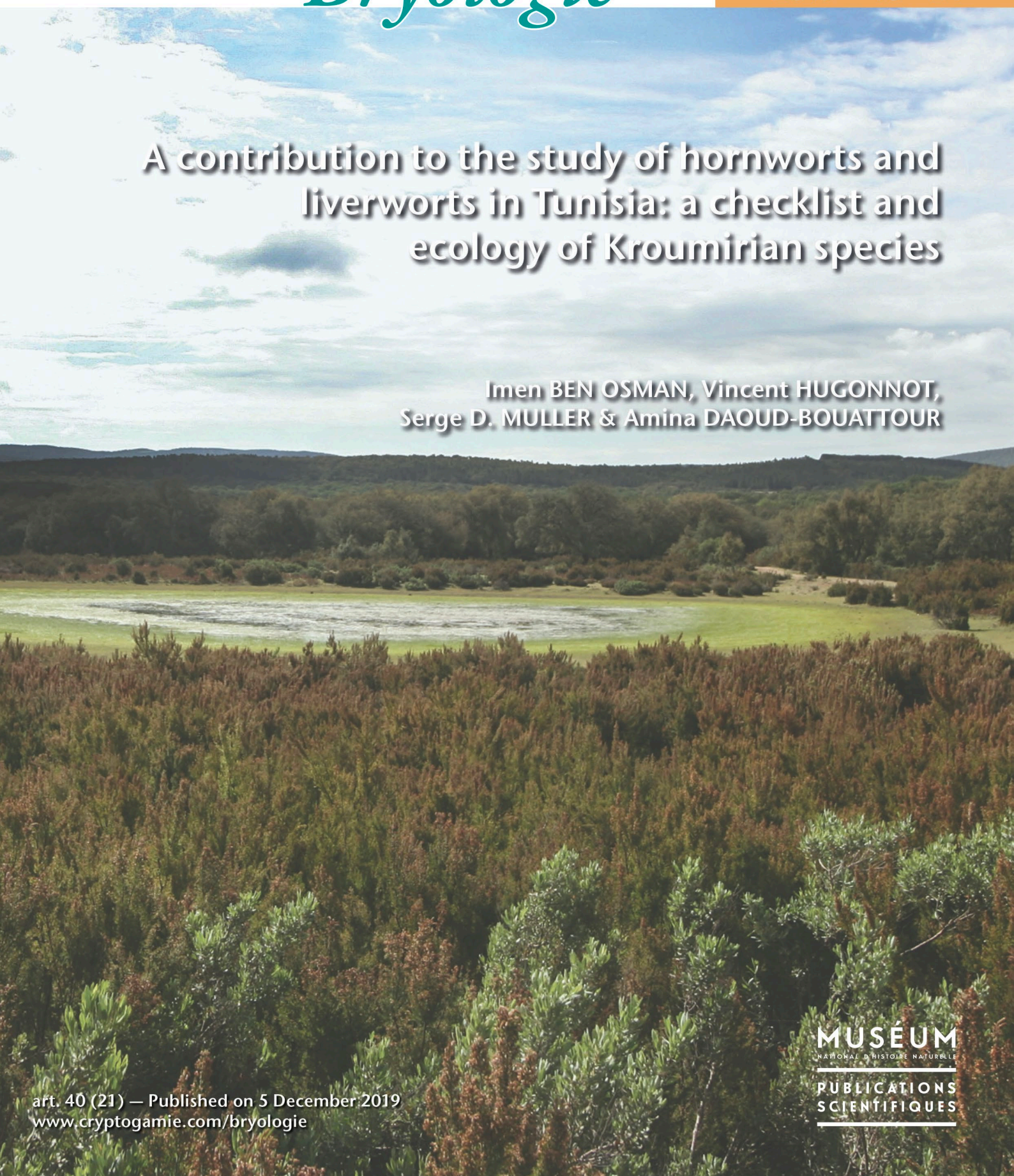

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Mare temporaire à *Riccia perennis* de Majen el Ma en Kroumirie

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Imen BEN OSMAN
Département de Biologie, Faculté des Sciences de Tunis,
Université de Tunis El-Manar, 2092 Tunis (Tunisie)
and LR18ES13 Biogéographie, Climatologie appliquée et Dynamique érosive,
Faculté des Lettres, des Arts et des Humanités de Manouba,
Université de la Manouba, 2010 Manouba (Tunisie)
imanbenosmen@gmail.com (corresponding author)

Vincent HUGONNOT
Le Bourg, F-43380 Blassac (France)

Serge D. MULLER
Université de Montpellier/CNRS, Institut des Sciences de l'Évolution
de Montpellier (ISE-M), case 061, F-34095 Montpellier cedex 05 (France)

Amina DAOUD-BOUATTOUR
Département de Biologie, Faculté des Sciences de Tunis,
Université de Tunis El-Manar, 2092 Tunis (Tunisie)
and LR18ES13 Biogéographie, Climatologie appliquée et Dynamique érosive,
Faculté des Lettres, des Arts et des Humanités de Manouba,
Université de la Manouba, 2010 Manouba (Tunisie)

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ABSTRACT
Studies of the Tunisian bryoflora are disparate and mostly quite outdated. In order to enhance and update our knowledge, a survey of Anthocerotophyta and Marchantiophyta of Kroumiria was carried out in May 1-5, 2017, recording two hornworts and 30 liverworts including *Riccia gougetiana* Durieu & Mont. var. *armatissima* Levier ex Müll.Frib., new to the area. The liverwort and hornwort flora of Kroumiria now stands at 80 reliably recorded taxa, of which 22 species may be threatened. Numerical analyses were used to specify the requirements of the 32 listed taxa for substrate, light, temperature and humidity and to distinguish seven different ecological groups ranging from the hydro-thermo-photophile to the mesohygro-sciaphile.

KEY WORDS
Anthocerotophyta,
biodiversity,
bryoflora,
conservation issues,
Marchantiophyta,
North Africa.

RÉSUMÉ

Contribution à l'étude des anthocérotes et des hépatiques de Tunisie : checklist et écologie des espèces de la Kroumirie.

Les connaissances de la bryoflore tunisienne sont pour la plupart très anciennes et éparses. Afin d'améliorer et d'actualiser nos connaissances, une étude des Anthocérophytes et des Marchantiophytes de Kroumirie a été réalisée du 1 au 5 mai 2017. Deux anthocérotes et 30 hépatiques y sont recensés, dont *Riccia gougetiana* Durieu & Mont. var. *armatissima* Levier ex Müll.Frib., nouvelle pour la région. La flore des hépatiques et des anthocérotes de Kroumirie compte aujourd'hui 80 taxons enregistrés de manière fiable, dont 22 espèces pouvant être menacées. Des analyses numériques ont été utilisées pour spécifier les exigences des 32 espèces recensées vis-à-vis de la nature du substrat, de la lumière, de la température et de l'humidité, et pour distinguer sept groupes écologiques différents, allant du pôle hydro-thermo-photophile au pôle mésohygro-sciaphile.

MOTS CLÉS
Anthocerotophyta, biodiversité, bryoflore, enjeux conservatoires, Marchantiophyta, Afrique du Nord.

INTRODUCTION

Knowledge of the richness, ecology and current distribution of the bryological flora of Tunisia clearly remains insufficient, and as yet no conservation measures have been undertaken nor a Red List established. Our team, therefore, is undertaking a study of the Tunisian bryoflora, in order to enhance and update our knowledge of this flora, and to re-assess the status of species with a view to compiling a Red List and to recommend conservation measures.

This article presents the first results on Anthocerotophyta and Marchantiophyta from Kroumiria, a region chosen for its climate, its diverse habitats favorable to the development of bryophytes, the great bryophytic richness reported in the literature and its conservation interest (biodiversity hotspot, Myers *et al.* 2000; Véla & Benhouhou 2007; Important Plant Area, Radford *et al.* 2011). It aims to: 1) update the current list of Anthocerotophyta and Marchantiophyta of Kroumiria, based on the literature and on new collections; 2) specify the ecological requirements of the identified species; and 3) identify the major ecological groups that have been found. In addition a history of the hepatic and hornwort flora of Tunisia is briefly outlined.

HISTORY OF HEPATICOLOGICAL STUDIES IN TUNISIA

Most of the work on the bryophyte flora in Tunisia is old and scattered. Until the Jovet-Ast & Bischler's (1971) synthesis of liverworts, publications were limited to simple lists of species found during scientific missions devoted mainly to studies of the spermatophyte flora. Bryophyte collections were then made with neither planning nor rigorous method.

The first published works on Tunisia bryophytes were mainly devoted to mosses and they contained only a few liverworts (Bescherelle 1897; Patouillard 1897; Corbière 1899; Thériot 1900; Gillot 1904; Corbière & Pitard 1909). During subsequent exploratory trips made in 1909 by C.-J. Pitard, 40 liverwort and one hornwort species were recorded in the north of the country (Aïn Draham, Tunis, Zaghouan) and eight species of liverwort in the south (Gafsa, Tozeur) (Corbière & Pitard 1909; Pitard 1909; Pitard & Corbière 1909). Among these liverworts, the record of *Riccia crystallina* L. emend. Raddi was later rectified in *R. cavernosa* Hoffm. (Jovet-Ast 1965).

In 1911, L. Trabut noted the presence of two species of *Riella* Mont. in the south of Tunisia. The first, *R. helicophylla* (Bory & Mont.) Mont., collected by Gentner in 1900 in the brackish waters of Chott el Kebir at El Hamma, was later named *R. numidica* Trab. (Trabut 1934). The second, *R. reuteri* Mont., now recognized as *R. notarisii* (Mont.) Mont., was collected in 1909 on the banks of the Sebkha Zarkin in freshwater (Trabut 1911). Later, near Sousse, P. F. Burollet collected *Riccia lamellosa* Raddi and *Southbya nigrella* (De Not.) Henriq. (Potier de la Varde 1924). In 1931, L. Gauthier-Lièvre reported *Riella helicophylla* (Bory & Mont.) Mont. and *Ricciocarpos natans* (L.) Corda (Gauthier-Lièvre 1931). In the next year, a new locality of *Riella notarisii* was discovered around Kairouan (Allorge 1932) and J. Szepesfalvi noted a new site of *Riccia lamellosa* and *Plagiochasma rupestre* (J.R.Forst. & G.Forst.) Steph., a new country record, from the 1927-1930 collections of D. Andreansky (Szepesfalvi 1932; Andreansky 1934). Later, V. Giacomini added *Clevea spathysii* (Lindenb.) Müll.Frib. to the liverwort flora of Tunisia (Giacomini 1940).

In his *Flora of the Hepaticae of North Africa*, L. Trabut added *Riccia nigrella* DC. and *R. spinosissima* Steph. (now recognized as *Riccia ciliata* Hoffm.) to the data of L. Corbière and C. J. Pitard (Corbière & Pitard 1909; Pitard 1909; Pitard & Corbière 1909), and two new localities for *R. lamellosa* (El Jem) and *R. atromarginata* Levier (Kairouan) (Trabut 1941). Müller (1951-1958) indicated on a map the presence of *Trichocolea tomentella* (Ehrh.) Dumort in Tunisia, but this record was later considered to be doubtful (Jovet-Ast & Bischler 1971). The collections of A. Labbe carried out from 1944 to 1952, and identified by R. Potier de la Varde, S. Jovet-Ast and V. Allorge, yielded nine liverwort species (Labbe 1953). Pottier-Alapetite (1953-1954) reported *Anthoceros crispulus* (Mont.) Douin (now considered as *A. agrestis* Paton), a species of hornwort new to the country from the island of Zembra.

From 1949 onwards, F. Jelenc published a synthesis of previously known data concerning bryological flora of North

Africa, updating the nomenclature and reporting for each the synonyms used in the literature, the localities classified according to North African botanical sectors, and some chorological and ecological information. Some new data concerning Tunisia were reported in his treatments (Jelenc 1954, 1955a, b, 1967). At last, De Sloover 1965 reported three species of liverwort new to Tunisia on the basis of M. Coûteaux's collections made in March-April 1963.

Suzanne Jovet-Ast and Hélène Bischler, French specialists in the liverwort and hornwort flora, were the first professional hepaticologists to carry out field investigations in Tunisia with exact objectives and a rigorous methodology. They were the first to publish a synthesis of the records of liverworts and hornworts from the country based on the literature, samples found in herbaria, and the personal collections made during their missions in April 1968 and in March-April 1970 in 229 localities distributed throughout the country. From the 1888 specimens that they collected, they established a list of 60 liverworts and three hornworts using the nomenclature of Müller (1951-1958). For each taxon, they specified localities using a map of distribution, distribution in the Mediterranean and Mediterranean-Atlantic region, the ecological characteristics of the stations, and the influence of ecological factors and human impacts on their distribution. Finally, they described eight groups of liverworts in Tunisia, and discussed their sociological value and reciprocal sociability of taxa (Jovet-Ast & Bischler 1971).

The bryophyte list was updated and published: 1) across North Africa without any taxonomic revision (Ros *et al.* 1999); and 2) across the Mediterranean region, in two separate lists with revised nomenclature: one of the Bryophyta (Ros *et al.* 2013), and the other of the Marchantiophyta and Anthocerotophyta that included four hornworts and 100 liverworts for Tunisia (Ros *et al.* 2007). Finally, Draper *et al.* (2008) listed six epiphytic liverworts collected in 2005 during the work in 11 forests in northern Tunisia.

Most recently, in 2006, the Tunisian scientific community began to take an interest in bryophytes for the first time, and subsequently published a study on the taxonomy and distribution of *Sphagnum* L. species and their plant communities in North Africa (Muller *et al.* 2010, 2011). A 2011 study of liverwort collections from the oak forests of Kroumiria recorded 18 taxa including seven leafy liverworts, describing their life form and specifying their ecological affinities (El Mokni & El Aouni 2011-2012). In 2015, Campisi *et al.* (2015) noted the presence of one hornwort and nine liverworts in the region of Aïn Draham and El Feïja.

STUDY AREA

The Kroumiria region located in north-west Tunisia (Fig. 1) is bordered to the north by the Mediterranean Sea, to the south by the Mejerda Valley (home to Tunisia's main permanent river), to the east by the Mogods hills and to the west by the Algerian-Tunisian border and the coastal El Kala plain. Geologically, the Numidian Flysch clay and sandstone from the Oligocene forms the northern Tunisian Tell, a mountainous massif that ascends to its highest point at Jbel El Ghorra (1203 m) on the Algeria-Tunisia border. Altitudes range between 800 and 900 m above sea level in the region of Aïn Draham (with a summit at 1014 m), descending to around 500 m a.s.l. in the Nefza plain.

Kroumiria is located in the lower humid Mediterranean belt but reaches the upper sub-belt at the highest elevations (INRF 1975). Rainfall in the wettest region of Tunisia ranges between 1000 and 1500 mm/year, and it regularly snows in the mountains from December to February. Annual average temperatures range from 16°C to 20°C, with minimum values between 2°C to 7°C (January), and relatively strong daily, seasonal fluctuations. The prevailing winds come from the north-west and maintain moisture in the region for much of the year (Debazac 1959).

MATERIAL AND METHODS

Fieldwork

We carried out our field survey and bryophyte collections in Kroumiria from May 1-5, 2017 at 18 different locations (14 wetlands, four forest stations) (Fig. 1; Table 1). At each station, we collected all hornworts and liverworts that we found. In preparation for field surveys, we compiled a list of all taxa of the Anthocerotophyta and Marchantiophyta that have been reported from Kroumiria in available bryological literature. This synthesis of previous data formed a basis for our surveys. Nomenclature follows Söderström *et al.* (2016).

Numerical analysis

Univariate analyzes.

We calculated the species richness (SR) for each of the 12 habitat types, and the presence index (Pi) of each species, according to the formula: $Pi = (n/N) \times 100$, with n equal to the number of sites where the species occurs and N the total number of sites.

To calculate the affinity of each species for the four main ecological factors (light, temperature, substrate, wetness), we defined several modalities: 3 for affinity for light (sciaphilous, mesophotophile, photophile), 5 for affinity for temperature based on altitudinal range (highly thermophilous [< 100 m]; thermophilous [100-350 m]; meso-thermophilous [350-600 m]; mesophilous [600-750 m], 75; highly mesophilous [> 750 m]), 5 for affinity for substrate (saxicole, terrico-mineral, corticolous, saprolignicole, terrico-humicolous), and 6 for affinity for wetness (xerophilous, mesoxerophilous, mesohygrophilous, hygrophilous, hydro-hygrophilous, hydrophilous). For each category, the value of the affinity of a species i was calculated according to the formula: $Afi = ni/Ni$, with ni equal to the number of times a species i was found in the concerned modality and Ni the total number of times this species i was found in all sites.

Multivariate analyzes

A Correspondence Analysis (CA; Benzecri 1973) and an Ascendant Hierarchical Classification (AHC; Ward 1963)

TABLE 1. — Studied sites. The sites rated * are part of IPA (Important Plant Areas; Radford *et al.* 2011). The site rated ** is IPA, a nature reserve and a Ramsar site. W, Wetland station; F, Forest station.

Sites	Code	Latitude N	Longitude E	Altitude (m)	Habitat	Substrat
Aïn Jmel Falls*	AJM	36°43'33"	08°42'09"	595	Waterfall (W)	Mineral soil/Dead wood/ Rock
Camp du 18e*	TC18	36°45'15"	08°41'16"	666	*Sphagnum* peat-forming wetland (W)	Organic soil
Dar Fatma**	TDF	36°49'06"	08°46'29"	781	*Sphagnum* peatland (W)	Organic soil
El Mouajène (path)	PMOU	36°43'28"	08°42'07"-08°42'20"	627-647	*Quercus suber* forest (F)	Trunk of *Arbutus unedo* and of *Quercus canariensis*
El Mouajène*	MOU	36°43'32"	08°42'33"	634	Peaty shore of a semi-permanent lake (W)	Organic soil
Majen el Ma*	MMA	36°46'52"	08°47'24"	505	Temporary pond (W)	Mineral soil
Majen Essaf	MESF	36°47'23"	08°47'35"	513	Peat lawn (W)	Organic soil
Majen Sghaïer Channel*	CMSG	36°46'50"	08°47'12"	507	*Quercus suber* riparian forest (W)	Mineral substrate
Majen Sghaïer*	MSG	36°46'52"	08°47'12"	505	Temporary pond (W)	Mineral soil
Source du 18e (path)	SF18	36°45'15"	08°41'21"	650	*Quercus canariensis* forest (F)	Mineral soil
Source du 18e*	TF18	36°45'35"	08°41'28"	750	*Sphagnum* peaty alder (W)	Organic soil
Titria	TIT	36°57'49"	08°57'47"	82	*Quercus suber* forest (F)	Trunk of *Phillyrea angustifolia*
Vallon du Mérij	MER	36°44'51"	08°41'19"	625	*Quercus canariensis* forest (F)	Tronc de *Quercus canariensis*
Vallon du Mérij (Wadi)	OMER	36°45'03"	08°41'17"	612	*Alnus glutinosa* peaty riparian forest (W)	Mineral soil/Organic soil/ Rock
Wadi Hfor Loussif	OHLO	36°49'27"	08°49'85"	355	*Alnus glutinosa* riparian forest (W)	Mineral soil/Dead wood/ Rock
Wadi Titria	OTIT	36°57'51"	08°57'46"	78	*Alnus glutinosa* riparian forest (W)	Mineral soil
Wadi Zen	OZEN	36°46'43"	08°47'29"	511	*Alnus glutinosa* riparian forest (W)	Mineral soill/Trunk of *Quercus suber*
Wadi Zlezel	OZLE	36°49'26"	08°50'17"	355	*Alnus glutinosa* riparian forest (W)	Rocher/Mineral soil

based on the Chord distance were performed on the 32 collected species and their affinity indices (I) for light, wetness, temperature and substrate. The CA and the AHC were respectively realized with XLSTAT and PAST software (Paleontological Statistics; Hammer *et al.* 2001).

To calculate the affinity indexes, we assigned a percentage value 'M_j' for each modality of the different factors:

– light: sciaphilous, 0; mesophotophile, 50; photophile,100;

temperature, based on altitudes: highly thermophilous, 0; thermophilous, 25; meso-thermophilous, 50; mesophilous, 75; highly mesophilous, 100;

– substrate: saxicole, 0; terrico-mineral, 25; corticolous, 50; saprolignicole, 75; terrico-humicolous, 100;

– wetness; xerophilous, 0; mesoxerophilous, 20; mesohygrophilous, 40; hygrophilous, 60; hydro-hygrophilous, 80; hydrophilous, 100.

The value of the affinity index I of a species i was calculated according to the formula: $I = \sum (Mj \times Afj)$, with M representing the value of the modality; Af, its affinity value; and j, the total number of modalities.

Authorships of taxa

All the authorships of taxa are indicated in the Table 4.

RESULTS

Diversity of the liverwort and hornwort flora of Kroumiria

Checklist of taxa

The field surveys produced a collection of 104 specimens corresponding to 32 taxa comprising two Anthocerotophyta in two genera and two families, and 30 Marchantiophyta (15 thallose and 15 leafy liverworts) distributed in 21 families and 22 genera. With seven species and one additional subspecies, *Riccia* is the richest genus. *Calypogeia fissa*, *C. arguta* and *Radula complanata* were the most frequently found species. The associated species were reported in Table 2. The life forms of the 32 recorded liverworts and hornworts comprise 22 (69%) that are mat-forming, 9 (28%) weft-forming and 1 (3%) usually forming short lawns (Table 2). Table 3 gives the surrounding vascular vegetation of each habitat.

Species richness

The hight richness species was found in Aïn Jmel Falls (12 taxa) and the less in El Mouajène and in Titria (1 taxon) (Table 3). Concerning habitats, the riparian alder forest (18 taxa), waterfall (12 taxa) and temporary ponds (8 taxa) presented the richest liverworts and hornworts flora. Other habitats hosted no more than six taxa, with only one in the peaty shore of the semi-permanent lake of El Mouajène, and in *Quercus suber* forest (Fig. 2).

Presence index

Calypogeia fissa, *Radula complanata* and *Riccia canaliculata* are the most frequent taxa (27.78%) (Fig. 3) followed by *Calypogeia arguta*, *Cephaloziella turneri*, *Conocephalum conicum*, *Lejeunea cavifolia*, *Marsupella emarginata* and *Pellia epiphylla* (22.22%).

Ecological features of the liverwort and hornwort flora

Ecological affinities of species

Substrate. The liverworts and hornworts flora consists primarily of terrestrial taxa (88%) that grow mostly on a strictly

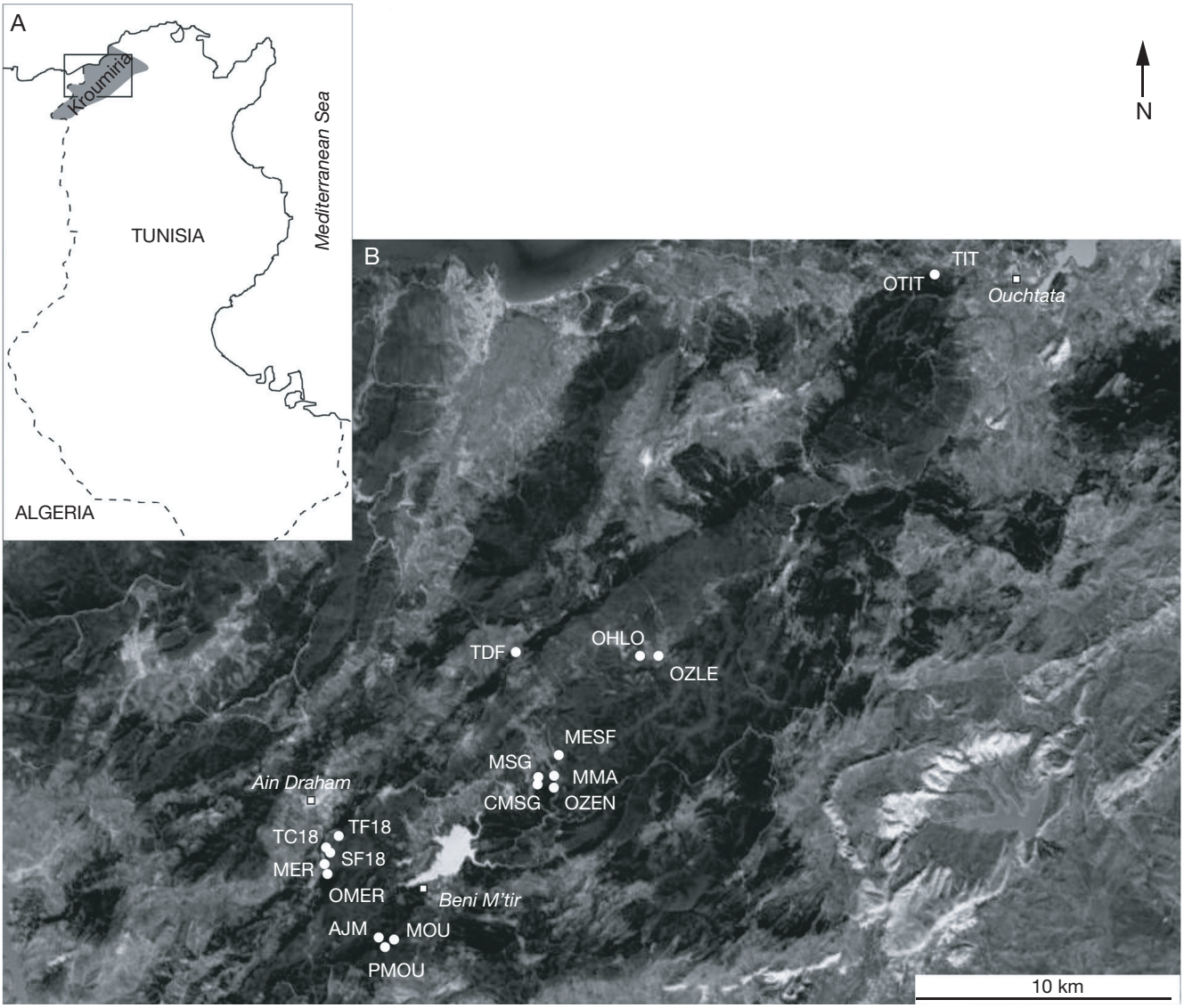

Fig. 1. — Location of Kroumiria region (**A**) and the 18 studied sites (**B**). The site code signification is given in Table 1. Satellite imagery, December 2015, Google Earth.

mineral soil (gravel, silt; 18 taxa, i.e. 58%). Only three species (9%) grow strictly on humus and litter (humicolous): *Cephaloziella divaricata*, *Fossombronia pusilla* and *Riccia beyrichiana*. Four species are adapted to the forest environment, growing on the bark of living or dead wood (corticolous): *Frullania tamarisci*, *Lejeunea cavifolia*, *Porella obtusata* and *Radula complanata*. Lastly, only *Conocephalum conicum* was found on rock (saxicolous) (Fig. 4).

Light. The liverworts and hornworts flora clearly prefers shade (full and partial shade; 75%). *Fossombronia angulosa*, *Frullania tamarisci* and *Lophocolea bidentata* are strictly sciaphilous (9%), while *Cephaloziella divaricata*, *Fossombronia pusilla*, *Riccia macrocarpa*, *R. perennis* and *R. sorocarpa* var. *sorocarpa* develop only in open areas (16%). Lastly, *Calypogeia fissa* tolerates all light conditions (Fig. 4).

Wetness. Most of the taxa that were collected (24 i.e., 75%) are hydro-hygrophilous or hygrophilous, and therefore confined to wet environments. *Frullania tamarisci* is the only mesoxerophilous species that develop solely in dry environments, and *Riccia canaliculata* is probably the most dependent on water since it was the only species that was still submerged in May (Fig. 4).

Temperature. Except for *Lunularia cruciata* and *Mesoptychia turbinata* that show a thermophilous affinity (temperature affinity index of 25 and 0% respectively), the 30 other species have a wide temperature range (index of temperature affinity varying from 50% to 100%), and therefore apparently indifferent to temperature.

Ecological groups

The AHC performed on the complete dataset (four affinity indexes, 32 species) identified seven ecological

TABLE 2. — List of Anthocerotophyta and Marchantiophyta collected for this study. Taxa marked * are new to Kroumiria. Associated species in bold character were not reported in Jovet & Bischler (1971). Life forms (Mägdefrau 1982); **Ni**, total number of times the species was found in all sites.

Taxon	Code	Ni	Life form	Associated species
Anthocerotophyta				
Phaeoceros laevis	Phla	3	Mat	*Lunularia cruciata*
Phymatoceros bulbiculosus	Phbu	2	Mat	–
Marchantiophyta				
Thallose liverworts				
Conocephalum conicum	Coco	4	Mat	–
Corsinia coriandrina	Corsi	1	Mat	–
Fossombronia angulosa	Foan	2	Mat	*Calypogeia arguta*, ***Lophocolea bidentata***
Fossombronia pusilla	Fopu	1	Mat	–
Lunularia cruciata	Lucr	4	Mat	–
Pellia epiphylla	Peep	4	Mat	*Calypogeia fissa*
Reboulia hemisphaerica	Rehe	1	Mat	–
Riccia beyrichiana	Ribe	1	Mat/Annual	–
Riccia canaliculata	Rica	5	Mat/Annual	–
Riccia gougetiana	Rigo	1	Mat/Annual	–
Riccia gougetiana var. *armatissima**	Rigoa	1	Mat/Annual	–
Riccia michelii	Rimi	1	Mat/Annual	–
Riccia macrocarpa	Rima	2	Mat/Annual	–
Riccia perennis	Ripe	1	Mat/Annual	*Riccia sorocarpa var. sorocarpa*
Riccia sorocarpa	Riso	1	Mat/Annual	*Riccia perennis*
Leafy liverworts				
Calypogeia arguta	Caar	8	Weft	*Calypogeia fissa, Fossombronia angulosa, Cephalozia bicuspidata, Cephaloziella turneri, Lunularia cruciata*
Calypogeia fissa	Cafi	10	Weft	*Calypogeia arguta, Cephaloziella turneri, Jungermannia gracillima, Pellia epiphylla*
Cephalozia bicuspidata .	Cebi	3	Weft	*Calypogeia arguta, C. fissa, Jungermannia gracillima*
Cephaloziella divaricata	Cezdi	1	Weft	***Jungermannia gracillima***
Cephaloziella turneri	Ceztu	5	Weft	*Calypogeia arguta, Lejeunea cavifolia*
Frullania tamarisci	Frta	2	Mat	***Radula complanata***
Gongylanthus ericetorum	Goer	2	Mat	–
Jungermannia gracillima	Jugr	5	Weft	*Calypogeia fissa, Cephalozia bicuspidata,* ***Cephaloziella divaricata***
Lejeunea cavifolia	Leca	5	Mat	***Calypogeia arguta, Cephaloziella turneri, Radula complanata, Porella obtusata***
Lophocolea bidentata	Lobi	1	Weft	***Fossombronia angulosa***
Mesoptychia turbinata	Metu	1	Weft	–
Marsupella emarginata	Maem	5	Short turf	***Lejeunea cavifolia, Radula complanata***
Porella obtusata	Poob	4	Mat/Fan	***Lejeunea cavifolia, Radula complanata***
Radula complanata	Raco	7	Mat/Fan	***Frullania tamarisci, Marsupella emarginata, Lejeunea cavifolia, Porella obtusata***
Solenostoma cf. *hyalinum*	Sohy	2	Weft	–

groups, including species with similar ecological requirements (Fig. 5). The CA performed on the same dataset identified and prioritized the factors that are responsible for the distribution of Anthocerotophyta and Marchantiophyta by environmental gradients, and subsequently defined the main environmental groups. Axis 1 (inertia: 56.29%) indicates two gradients: a light gradient that opposes sciaphilous to photophilous groups, and a wetness gradient that isolates mesoxerophilous groups from hygrophilous groups. Axis 2 (inertia: 29.77%) represents a gradient that opposes humicolous groups to inorganic substrate groups (Fig. 6).

The AHC (Fig. 5) and CA (Fig. 6) thus make it possible to distinguish seven ecological groups:

– Ecological Group 1: hydro-hygrophilous highly thermophilous and mesophotophilous taxa growing on mineral substrate requiring relatively high temperatures at low altitudes, show a strong affinity for mineral substrates and a preference for partial shade;

– Ecological Group 2: mesoxerophilous taxa with a sciaphilous tendency growing on an organic substrate show a clear preference for humicolous substrates but are relatively ubiquitous in terms of shade and wetness;

– Ecological Group 3: mesohygrophilous taxa with a sciaphilous tendency growing on a mineral substrate have a clear preference for mineral substrates and tend to develop in shaded, wet habitats;

– Ecological Group 4: mesohygrophilous and very sciaphilous taxa growing on mineral substrate in wet habitats have a strong predilection for darkness and a mineral substrate;

– Ecological Group 5: hygrophilous taxa with a photophilous tendency growing on a mineral substrate develop in wet, partially shaded habitats and present a strong affinity for mineral substrate;

– Ecological Group 6: hydro-hygrophilous and very photophilous taxa growing on a mineral substrate present a strong affinity for light and mineral substrate and are restricted to wet environments;

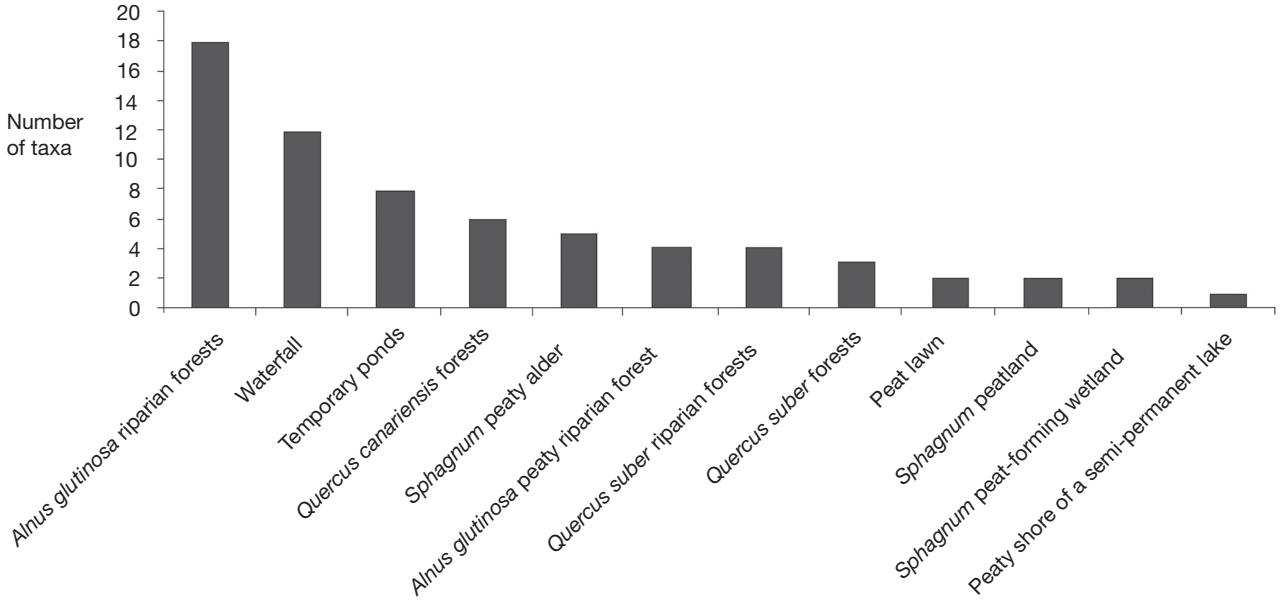

Fig. 2. — Species richness of the studied habitats.

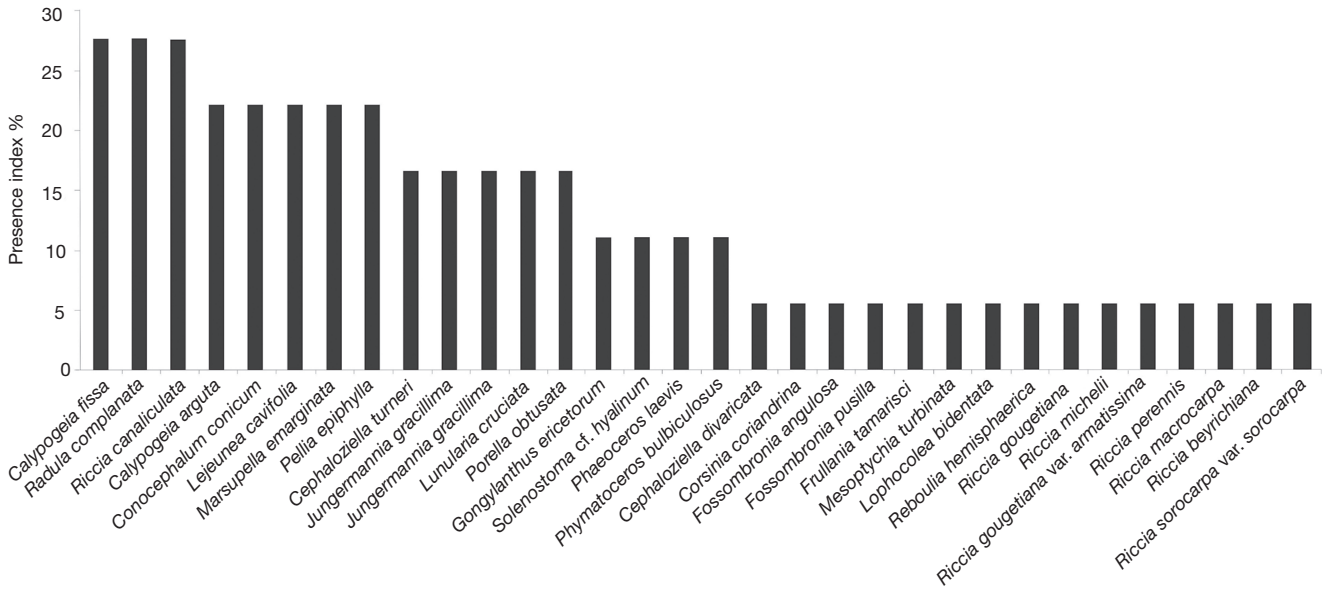

Fig. 3. — Presence index of different taxa in the studied sites.

– Ecological Group 7: hydro-hygrophilous and photophilous taxa growing on organic substrate prefer wet environments to develop and present an affinity for both light and organic substrates.

Synthesis of previous data

A literature search of records of Anthocerotophyta and Marchantiophyta from Kroumiria, together with one addition from the present survey, established a list of 80 taxa: four Anthocerotophyta, belonging to three genera in three families, and 76 Marchantiophyta (39 thallose liverworts and 37 leafy liverworts) in 29 families and 36 genera. This synthesis also made it possible to specify the localities of collection of each taxon (Table 4).

DISCUSSION

Richness of the flora

We collected 32 taxa representing 40% of the known species of the region of Kroumiria (Table 4). This relatively low value can be explained by 1) the paucity of prospected sites (18 compared

TABLE 3. — Liverworts and hornworts flora, and surrounding vegetation of the studied sites. **VC**, vegetation cover (method of Braun-Blanquet 1932): 5, > 75%; 4, 50-75%; 3, 25-50%; 2, 5-25%; 1, 1-5%.

Sites	Taxa	Number of taxa	Vascular vegetation	VC
AJM	*Calypogeia arguta, C. fissa, Cephaloziella turneri, Conocephalum conicum, Fossombronia angulosa, Lejeunea cavifolia, Lophocolea bidentata, Lunularia cruciata, Marsupella emarginata, Pellia epiphylla, Phaeoceros laevis, Solenostoma* cf. *hyalinum*	12	*Acanthus mollis, Adiantum capillus-veneris, Carex elata, Erica arborea, Osmunda regalis, Prunus avium, Quercus canariensis*	5
CMSG	*Gongylanthus ericetorum, Lunularia cruciata, Marsupella emarginata, Phymatoceros bulbiculosus*	4	*Erica arborea, E. scoparia, Quercus suber*	5
MER	*Lejeunea cavifolia, Porella obtusata, Radula complanata*	3	*Erica arborea, Myrtus communis, Quercus canariensis*	5
MESF	*Riccia beyrichiana, R. canaliculata*	2	*Bellis prostrata, Callitriche brutia, Cicendia filiformis, Erica scoparia, Illecebrum verticillatum, Isoetes velata, Juncus heterophyllus, J. pygmaeus, Radiola linoides, Ranunculus hederaceus*	3
MMA	*Riccia canaliculata, R.macrocarpa, R. perennis, Riccia sorocarpa* var. *Sorocarpa*	4	*Crassula decumbens, C. tillaea, Erica arborea, Halimium halimifolium, Juncus capitatus, Plantago coronopus, Pteridium aquilinum, Rumex bucephalophorus*	3
MOU	*Cephalozia bicuspidata*	1	*Arbutus unedo, Erica arborea, Myrtus communis, Phillyrea angustifolia, Quercus canariensis, Q. suber*	5
MSG	*Corsinia coriandrina, Riccia canaliculata, R. gougetiana, R. gougetiana* var. *armatissima, R. michelii*	5	*Erica arborea, E. scoparia, Isoetes velata, Phillyrea angustifolia, Quercus suber*	5
OHLO	*Calypogeia arguta, Cephalozia bicuspidata, Conocephalum conicum, Lejeunea cavifolia, Marsupella emarginata, Porella obtusata, Radula complanata, Solenostoma* cf. *hyalinum*	8	*Alnus glutinosa, Carex pendula, Erica arborea, Selaginella denticulata*	2
OMER	*Calypogeia arguta, C. fissa, Conocephalum conicum, Pellia epiphylla*	4	*Adiantum capillus-veneris, Alnus glutinosa, Athyrium felix-femina, Carex pendula, Osmunda regalis*	5
OTIT	*Lunularia cruciata, Mesoptychia turbinata, Pellia epiphylla*	3	*Alnus glutinosa, Fraxinus angustifolia, Nerium oleander, Phillyrea angustifolia, Ulmus minor*	4
OZEN	*Cephaloziella turneri, Gongylanthus ericetorum, Porella obtusata, Riccia canaliculata*	4	*Arbutus unedo, Erica arborea, Phillyrea angustifolia, Quercus suber*	4
OZLE	*Calypogeia fissa, Conocephalum conicum, Jungermannia gracillima, Phaeoceros laevis, Phymatoceros bulbiculosus, Riccia canaliculata*	6	*Alnus glutinosa, Quercus canariensis*	3
PMOU	*Frullania tamarisci, Lejeunea cavifolia, Radula complanata*	3	*Arbutus unedo, Erica arborea, Quercus canariensis, Q. Suber*	5
SF18	*Cephaloziella turneri, Marsupella emarginata, Radula complanata, Reboulia hemisphaerica*	4	*Erica arborea, Myrtus communis* subsp. *communis, Quercus canariensis*	5
TC18	*Cephaloziella divaricata, Jungermannia gracillima*	2	*Erica scoparia, Juncus effusus, Osmunda regalis*	5
TDF	*Calypogeia fissa, Fossombronia pusilla*	2	*Anagallis crassifolia, A. tenella, Asphodelus ramosus, Carex punctata, Erica scoparia, Potentilla reptans, Solenopsis bicolor*	5
TF18	*Calypogeia arguta, C. fissa, Cephalozia bicuspidata, Jungermannia gracillima, Pellia epiphylla*	5	*Alnus glutinosa, Erica scoparia, Osmunda regalis*	5
TIT	*Radula complanata*	1	*Phillyrea angustifolia, Pistacia lentiscus, Quercus canariensis, Q. coccifera*	5

to more than 80 in the literature); 2) the much smaller area investigated in Kroumiria (excluding western part, for example Aïn Babouch, Feïja; southern part, for example Aïn Zana; and coastal part, for example Tabarka); and 3) the absence of exploration in habitats that are particularly rich in liverworts such as dense oak forests (47 taxa; Jovet-Ast & Bischler 1971). It is also possible that some species have become rarer or even extinct. The explorations carried out by Jovet-Ast & Bischler (1971) twenty years after those of Labbe in exactly the same circuit observed a clear decline in, for example, *Cephalozia connivens*, *Jungermannia gracillima* and *Scapania undulata* in the region of Aïn Draham, and the disappearance of others, including *Chiloscyphus polyanthos*, *Conocephalum conicum*, *Pallavicinia lyellii* and *Riccardia multifida*.

At least 11 species (*Cephaloziella stellulifera*, *Chiloscyphus polyanthos*, *Gymnocolea inflata*, *Lophocolea heterophylla*, *Riccardia chamedryfolia*, *R. latifrons*, *R. multifida*, *Riccia ciliata*, *Scapania compacta*, *S. undulata* and *Southbya tophacea*) were observed several times in the past but were not found recently either by Draper *et al.* (2008), El Mokni and El Aouni (2011-2012) and Campisi *et al.* (2015) or during the present survey, and it is likely that they have declined in the area; 11 other species were formerly found in a single locality (*Cephalozia connivens*, *C. lunulifolia*, *Cephaloziella baumgartneri*, *Cololejeunea minutissima*, *Fossombronia echinata*, *Nardia scalaris*, *Pellia endiviifolia*, *Riccia duplex*, *R. glauca*, *Scapania curta* and *Southbya nigrella*), and were not found during the present survey. These 22 species may be rare and of conservation concern.

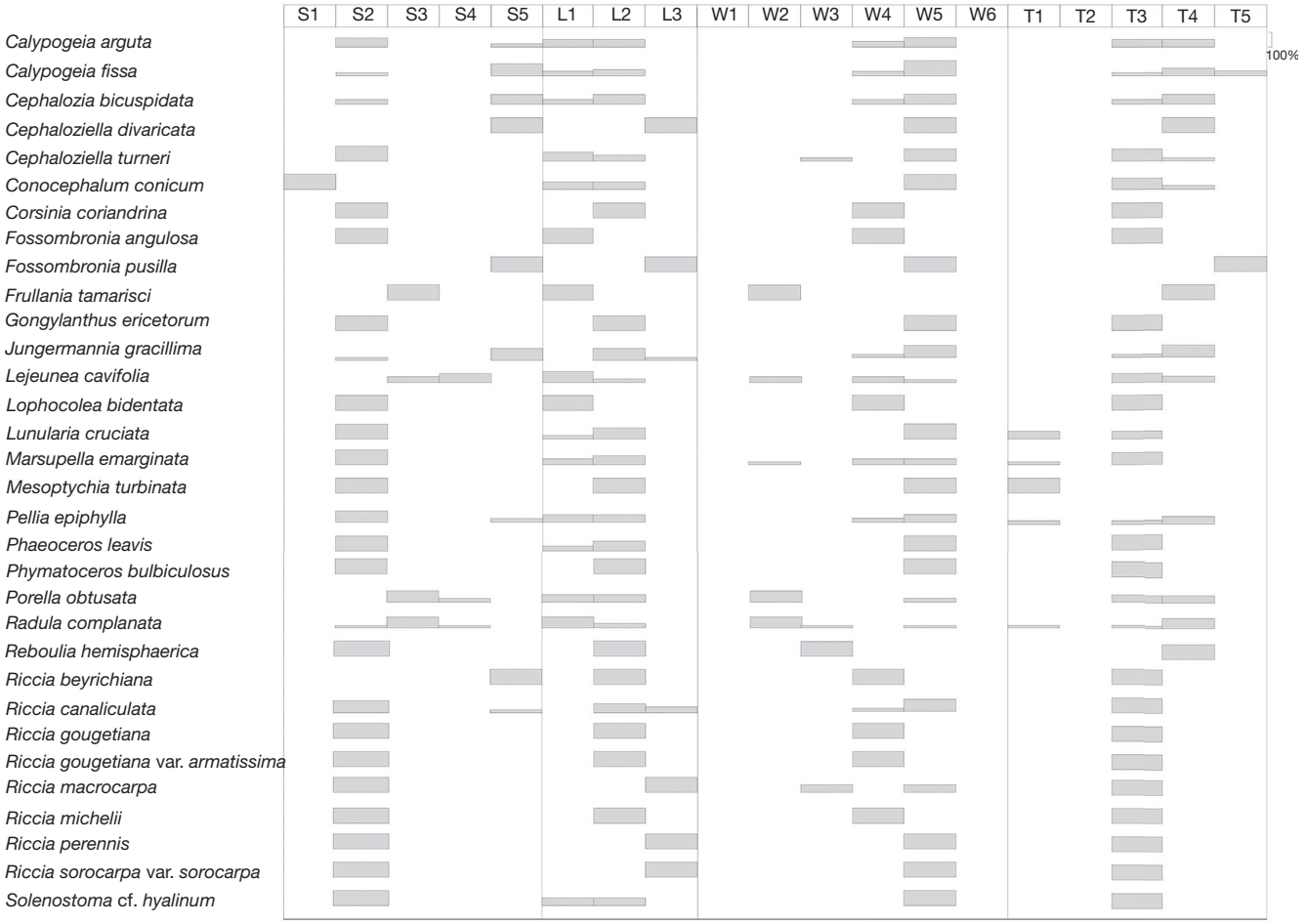

Fig. 4. — Taxa affinity for the nature of the substrate (S), the light (L), the wetness (W) and the temperature (T): **S1**, Saxicole; **S2**, Terrico-mineral; **S3**, Corticolous, **S4**, Saprolignicole, **S5**, Terrico-humicolous; **L1**, Sciaphilous; **L2**, Mesophotophile; **L3**, Photophile; **W1**, Xerophilous; **W2**, Mesoxerophilous; **W3**, Mesohygrophilous; **W4**, Hygrophilous; **W5**, Hydro-hygrophilous; **W6**, Hydrophilous; **T1**, highly thermophilous; **T2**, thermophilous; **T3**, meso-thermophilous; **T4**, mesophilous; **T5**, highly mesophilous.

Futher surveys should be carried out to clarify their status with a view to developing a Red List of Tunisian bryophytes.

Ecology of studied hornworts and liverworts

Specialist/Generalist species

Some species, such as *Calypogeia arguta*, *C. fissa*, *Lejeunea cavifolia*, *Marsupella emarginata* and *Pellia epiphylla*, were collected from several sites from various types of habitat (Fig. 3; Table 3). These species are likely to have wide ecological amplitudes and be considered generalists. Conversely, *Riccia* spp. were collected in temporary ponds (Majen el Ma and Majen Sghaïer) and on a peat lawn (Majen Essaf), with the exception of *R. canaliculata*, a species that is more dependent on water and which also develops on river shores (Table 3). *Riccia* spp. are specialized species of open, low vegetation wetlands with alternating intra-annual dry phases and flooded phases. Like most of the tracheophytes confined to these habitats, *Riccia* spp. are annual and amphibious, which allows them to survive the major changes characterizing them. Their strong affinity for light and low competitive ability also favour their development in open, weakly vegetated habitats (Jovet-Ast 1986; Hugonnot & Hébrard 2004).

Role of environmental factors

Light. Many bryophytes are frugal and energy-efficient (Marschall & Proctor 2004). High level of radiation affects them indirectly by increasing evapotranspiration and reducing ambient wetness (Proctor 1982). High densities of these plants are logically found in forest regions like Kroumiria where shaded areas maintaining wet microclimates are more frequent than in open areas. Yet, some species (14%) are adapted to habitats that are exposed to light (Fig. 4) including the annual species of the genus *Riccia* that develop on the shores of temporary ponds and disappear during the dry season.

Wetness. The majority of the collected taxa (75%) are hydro-hygrophilous or hygrophilous and therefore confined to the very humid conditions that favor the development of bryophytes and illustrates the general dependence of these plants on wetness, which they require for reproduction. However, some other species (mesohygrophilous and mesoxerophilous ones) can withstand more or less significant periods of desiccation, as for example the corticolous leafy liverworts that develop in shady places on the bark of trees that are likely to conserve wetness and certain thallose liverworts such as *Cors-*

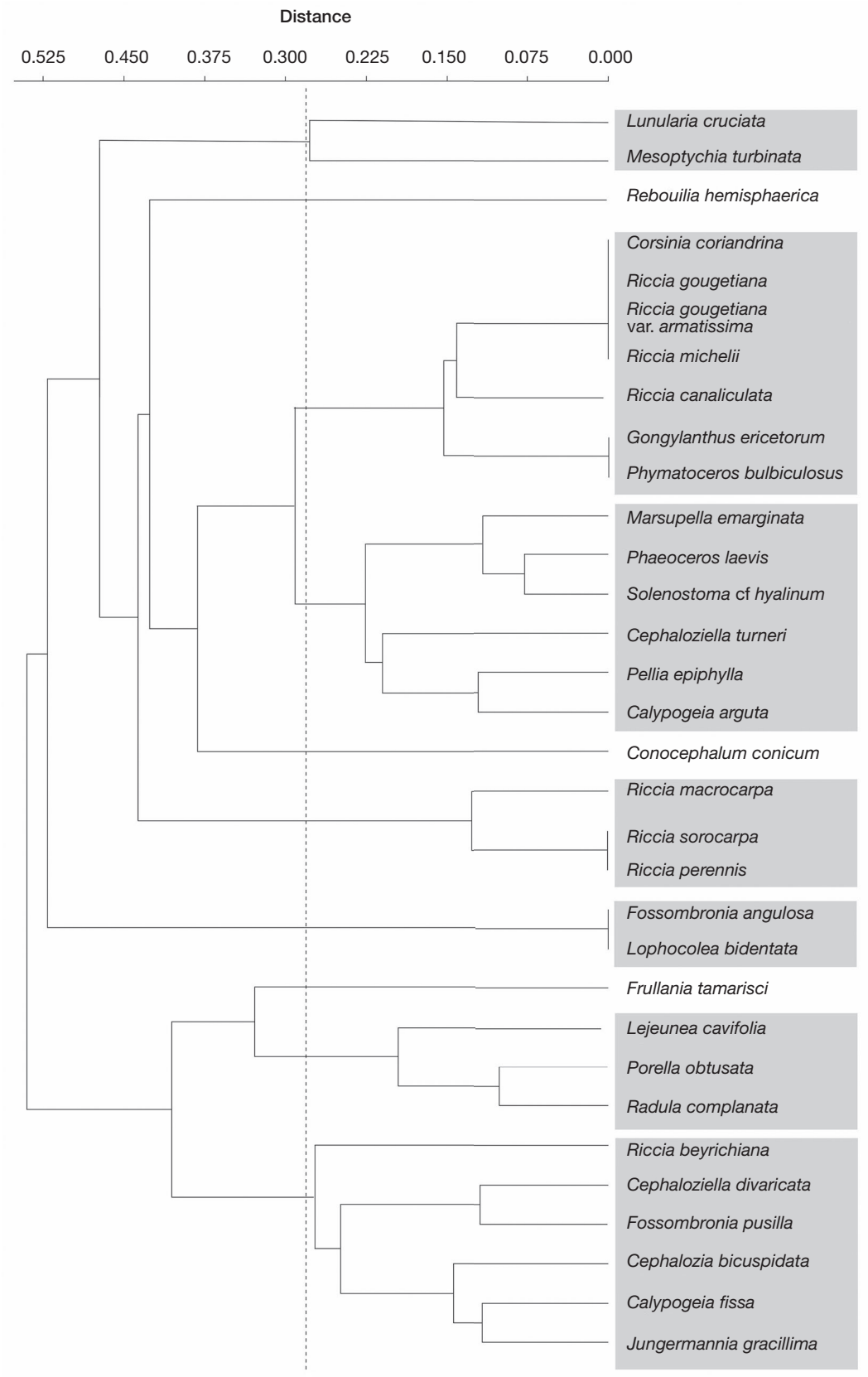

FIG. 5. — Dendrogram obtained by AHC (Ascendant Hierarchical Classification) carried out on the ecological affinity indices of the 32 taxa collected (Chord distance).

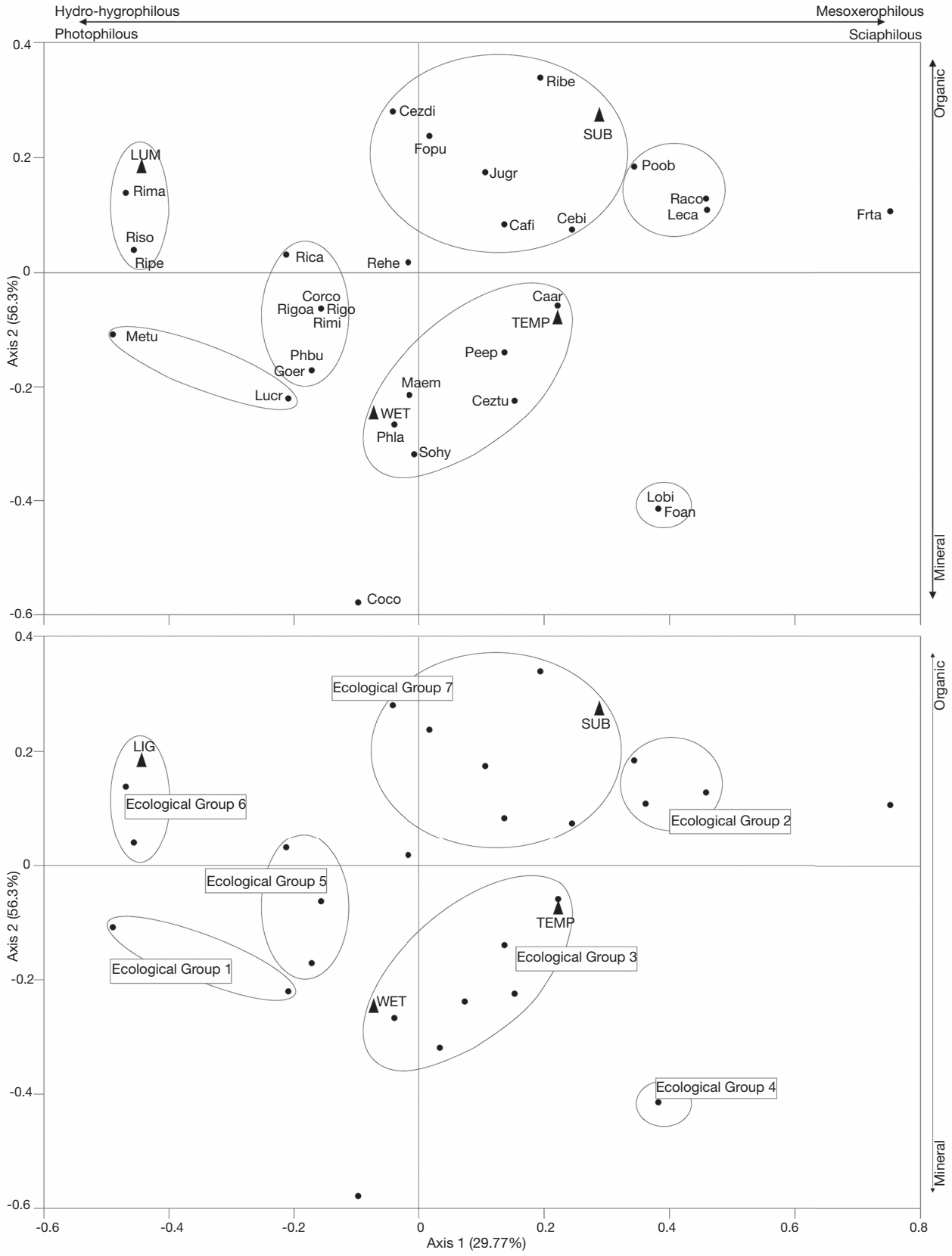

FIG. 6. — Scatterplot of the two first axes of the CA (Correspondence Analysis) performed on four indexes of ecological affinity and 32 taxa. Abbreviations: **LIG**, Light; **SUB**, Substrate; **TEMP**, Temperature; **WET**, Wetness. The taxa code signification is given in Table 2.

TABLE 4. — List of Kroumirian Anthocerotophyta and Marchantiophyta based on published literature and our collections. Taxa recorded during the present survey are indicated in bold and the taxon new to Kroumiria indicated in **bold** and **underlined**. An * indicates that the taxa are mentioned in the literature in Tunisia but no indication of the locality is given. The year indicated corresponds to the last time the species was observed in Kroumiria. Site codes are given in Table 1.

Taxon	Family	Year	Locality	Sources
Anthocerotophyta				
Anthoceros agrestis Paton*	Anthocerotaceae			Ros *et al.* 2007
Anthoceros punctatus L.	Anthocerotaceae	1971	Aïn Draham, Tabarka-Nefza	Jovet-Ast & Bischler 1971
Phaeoceros laevis (L.) Prosk.	Notothyladaceae	2017	Aïn Babouch, Aïn Draham, AJM, Ghardimaou-El Feïja, Oued Dhalma, Tabarka-Nefza, OZLE	Pottier-Alapetite 1954; Jovet-Ast & Bischler 1971; this study
Phymatoceros bulbiculosus (Brot.) Stotler, W.T.Doyle & Crand.-Stotl.	Phymatocerotaceae	2017	Aïn Draham, Aïn Soltane-Ghardimaou, CMSG, Col du vent, Oued Dhalma, Dar Fatma, OZLE	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; this study
Marchantiophyta				
Aneura pinguis (L.) Dumort.	Aneuraceae	2012	Aïn Zana, Mérij	El Mokni & El Aouni 2011-2012
Calypogeia arguta Nees & Mont.	Calypogeiaceae	2017	Aïn Draham, AJM, OHLO, Mérij-Col du vent, OMER, TF18	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; this study
Calypogeia fissa (L.) Raddi	Calypogeiaceae	2017	Aïn Babouch, Aïn Draham, AJM, Béni Mtir, Camp de la santé, Mérij-Col du vent, OMER, TDF, TF18, OZLE	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; Campisi *et al.* 2015; this study
Cephalozia bicuspidata (L.) Dumort.	Cephaloziaceae	2017	Aïn Draham, Béni Mtir, Camp de la santé, Col du vent, Ghardimaou, OHLO, Mérij, MOU	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; this study
Cephalozia connivens (Dicks.) Lindb.	Cephaloziaceae	1971	Mérij-Col du vent	Jovet-Ast & Bischler 1971
Cephalozia lunulifolia (Dumort.) Dumort.	Cephaloziaceae	1967	Mérij	Labbe 1953; Jelenc 1967
Cephaloziella baumgartneri Schiffn.	Cephaloziellaceae	1971	Tabarka-Nefza	Jovet-Ast & Bischler 1971
Cephaloziella calyculata (Durieu & Mont.) Müll.Frib.	Cephaloziellaceae	1971	Aïn Draham, Tabarka-Frontière algérienne	Jovet-Ast & Bischler 1971
Cephaloziella divaricata (Sm.) Schiffn.	Cephaloziellaceae	2017	Aïn Babouch, Aïn Draham, Aïn Soltane-Ghardimaou, Béni Mtir, Feïja-Aïn Soltane, Ghardimaou, Tabarka-Nefza, TC18	Jelenc 1955a; Jovet-Ast & Bischler 1971; this study
Cephaloziella stellulifera (Taylor ex Spruce) Schiffn.	Cephaloziellaceae	1971	Aïn Babouch, Aïn Draham, Camp de la santé, Col du vent-Dar Fatma, Fernana-Aïn Draham, Jbel Bir, J. Bir-Source du 18ème, Tabarka-Nefza	Labbe 1953; Jelenc 1967; Jovet-Ast & Bischler 1971
Cephaloziella turneri (Hook.) Müll. Frib.	Cephaloziellaceae	2017	Aïn Babouch, Aïn Draham, AJM, Béni Mtir, Camp de la santé, Fernana-Aïn Draham, Ghardimaou, SF18, Tabarka-Nefza, OZEN	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; Campisi *et al.* 2015; this study
Chiloscyphus polyanthos (L.) Corda	Geocalycaceae	1955	Aïn Draham, Béni Mtir	Corbière & Pitard 1909; Jelenc 1955a
Cololejeunea minutissima (Sm.) Schiffn.	Lejeuneaceae	1955	Aïn Draham	Corbière & Pitard 1909; Jelenc 1955a
Conocephalum conicum (L.) Dumort.	Conocephalaceae	2017	Aïn Draham, AJM, Béni Mtir, Fernana, OHLO, Mérij, OMER, Oued Zen, OZLE	Corbière & Pitard 1909; Jelenc 1954; Jelenc 1955a; Jelenc 1967; Jovet-Ast & Bischler 1971; El Mokni & El Aouni 2011-2012; Campisi *et al.* 2015; this study
Corsinia coriandrina (Spreng.) Lindb	Corsiniaceae	2017	Aïn Babouch, Aïn Draham, Aïn Soltane-Ghardimaou, Col du vent, El Feïja-Aïn Soltane, Ghardimaou-El Feïja, Mérij, MSG, Tabarka-Nefza	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; this study
Fossombronia angulosa (Dicks.) Raddi	Fossombroniaceae	2017	Aïn Babouch, Aïn Draham, AJM, Aïn Soltane-Ghardimaou, Col du vent, El Feïja-Aïn Soltane, Fernana-Aïn Draham, Ghardimaou, Ghardimaou-El Feïja, Jbel Bir, Mérij, Tabarka, Tabarka-Nefza	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; this study
Fossombronia caespitiformis De Not. ex Rabenh. subsp. *caespitiformis*	Fossombroniaceae	1971	Aïn Babouch, Aïn Draham, Camp de la santé, Dar Fatma, El Feïja-Aïn Soltane, Ghardimaou, Jbel Bir, Mérij-Col du vent, Tabarka-Nefza	Jovet-Ast & Bischler 1971
Fossombronia echinata Macvicar	Fossombroniaceae	1971	Tabarka-Nefza	Jovet-Ast & Bischler 1971

Table 4. — Continuation

Taxon	Family	Year	Locality	Sources
Fossombronia pusilla (L.) Nees	Fossombroniaceae	2017	Aïn Draham, TDF	Corbière & Pitard 1909; Jelenc 1955a; this study
Fossombronia wondraczekii (Corda) Lindb.	Fossombroniaceae	1955	Aïn Babouch, Aïn Draham	Jelenc 1955a
Frullania dilatata (L.) Dumort.	Frullaniaceae	2012	Aïn Babouch, Aïn Draham, Aïn Zana, Béni Mtir, El Feïja, Ghardimaou, Jbel Bir, Mérij, Mérij-Col du vent, Tabarka-Aïn Draham, 10 km à l'est de Tabarka, Tabarka-Nefza	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; Draper *et al* 2008; El Mokni & El Aouni 2011-2012; Campisi *et al.* 2015
Frullania tamarisci (L.) Dumort.	Frullaniaceae	2017	Aïn Babouch, Aïn Draham, Col du vent-Dar Fatma, PMOU	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; this study
Gongylanthus ericetorum (Raddi) Nees	Arnelliaceae	2017	Camp de la santé, CMSG, Col du vent, El Feija-Aïn Soltane, Fernana-Aïn Draham, Jbel Bir, J. Bir-Source du 18ème, Mérij, Tabarka-Nefza, OZEN	Labbe 1953; Jelenc 1967; Jovet-Ast & Bischler 1971; this study
Gymnocolea inflata (Huds.) Dumort.	Lophoziaceae	1955	Aïn Draham, Béni Mtir	Corbière & Pitard 1909; Jelenc 1955a
Jungermannia gracillima Sm.	Jungermanniaceae	2017	Col du vent, Mérij, TC18, TF18, OZLE	Labbe 1953; Jelenc 1967; Jovet-Ast & Bischler 1971; Campisi *et al.* 2015; this study
Jungermannia obovata Nees	Jungermanniaceae	1971	Aïn Draham, Aïn Soltane, Ghardimaou	Jovet-Ast & Bischler 1971
Lejeunea cavifolia (Ehrh.) Lindb.	Lejeuneaceae	2017	Aïn Babouch, Aïn Draham, AJM, Camp de la santé, Dar Fatma, Ghardimaou, OHLO, Jbel Bir, MER, Mérij, Oued El Baghla, O. Zen, PMOU	Corbière & Pitard 1909; Jelenc 1955a; De Sloover 1965; Jelenc 1967; Jovet-Ast & Bischler 1971; Draper *et al* 2008; El Mokni & El Aouni 2011-2012; this study
Lophocolea bidentata (L.) Dumort.	Geocalycaceae	2017	Aïn Babouch, Aïn Draham, AJM, Béni Mtir	Corbière & Pitard 1909; this study
Lophocolea heterophylla (Schrad.) Dumort.	Geocalycaceae	1955	Aïn Babouch, Aïn Draham, Aïn Zana, Béni Mtir, Camp de la santé, Ghardimaou, Jbel Bir, Mérij, Oued Dhalma	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971
Lunularia cruciata (L.) Lindb.	Lunulariaceae	2017	Aïn Babouch, Aïn Draham, AJM, Aïn Soltane, Camp de la santé, CMSG, Col du vent, Dar Fatma, Fernana, Ghardimaou, Ghardimaou-El Feïja, Jbel Bir, Mérij, Tabarka-Nefza, OTIT	Corbière & Pitard 1909; Bizot 1931; Pottier-Alapetite 1952; Jelenc 1967; Jovet-Ast & Bischler 1971; Campisi *et al.* 2015; this study
Marchantia polymorpha L.	Marchantiaceae	2012	Aïn Zana, El Feïja, Mérij	El Mokni & El Aouni 2011-2012
Marsupella emarginata (Ehrh.) Dumort.	Gymnomitriaceae	2017	AJM, CMSG, Col du vent-Dar Fatma, Dar Fatma, OHLO, SF18	Jovet-Ast & Bischler 1971; this study
Mesoptychia turbinata (Raddi) L.Söderstr. & Váňa	Jungermanniaceae	2017	Aïn Babouch, Aïn Draham, Béni Mtir, Col du vent, Mérij, OTIT	Corbière & Pitard 1909; Jelenc 1955a Jovet-Ast & Bischler 1971; this study
Metzgeria conjugata Lindb.	Metzgeriaceae	2012	Aïn Draham, Béni Mtir, Col du vent, Dar Fatma	El Mokni & El Aouni 2011-2012
Metzgeria furcata (L.) Dumort.	Metzgeriaceae	2012	Aïn Babouch, Aïn Draham, Béni Mtir, Jbel Bir	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; Draper *et al* 2008; El Mokni & El Aouni 2011-2012
Nardia scalaris Gray	Jungermanniaceae	1955	Aïn Draham	Corbière & Pitard 1909; Jelenc 1955a
Oxymitra incrassata (Brot.) Sérgio & Sim-Sim	Oxymitraceae	1971	Aïn Draham, El Feïja-Aïn Soltane, Ghardimaou-El Feïja, Jbel Bir, Tabarka-Nefza	Jovet-Ast & Bischler 1971
Pallavicinia lyellii (Hook.) Carruth.	Pallaviciniaceae	2012	Aïn Draham, Aïn Zana, Béni Mtir, Dar Fatma, Mérij	Labbe 1953; El Mokni & El Aouni 2011-2012
Pellia endiviifolia (Dicks.) Dumort.	Pelliaceae	1955	Aïn Draham	Corbière & Pitard 1909; Jelenc 1955a
Pellia epiphylla (L.) Corda	Pelliaceae	2017	Aïn Babouch, Aïn Draham, Aïn Zana, AJM, Col du vent, Mérij, OMER, Source du 18ème, OTIT	Corbière & Pitard 1909; Jelenc 1955a; Jelenc 1967; Jovet-Ast & Bischler 1971 this study
Porella arboris-vitae (With.) Grolle	Porellaceae	2012	Aïn Babouch, Aïn Draham, Béni Mtir, El Feïja, Mérij, Mérij-Col du vent	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; El Mokni & El Aouni 2011-2012
Porella obtusata (Taylor) Trevis.	Porellaceae	2017	Aïn Babouch, Aïn Draham, Col du vent-Dar Fatma, OHLO, Jbel Bir, MER, Mérij, Mérij-Col du vent, OZEN	Jovet-Ast & Bischler 1971; Draper *et al* 2008; this study

TABLE 4. — Continuation

Taxon	Family	Year	Locality	Sources
Porella platyphylla (L.) Pfeiff.	Porellaceae	2012	Aïn Babouch, Aïn Draham, Béni Mtir, Col du vent-Dar Fatma, Dar Fatma, El Feïja, Jbel Bir, Mérij	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; El Mokni & El Aouni 2011-2012; Campisi *et al.* 2015
Preissia quadrata (Scop.) Nees	Marchantiaceae	2012	Aïn Zana, El Feïja, Mérij	El Mokni & El Aouni 2011-2012
Radula complanata (L.) Dumort.	Radulaceae	2017	Aïn Draham, OHLO, Jbel Bir, J. Ghorra, MER, Mérij, PMOU, SF18, TIT	Corbière & Pitard 1909; Jelenc 1955a; Draper *et al* 2008; El Mokni & El Aouni 2011-2012; this study
Radula lindenbergiana Gottsche ex C. Hartm.	Radulaceae	2008	Aïn Babouch, Aïn Draham, Camp de la santé, Col du vent-Dar Fatma, Fernana-Aïn Draham, Ghardimaou, Jbel Bir, 10 km à l'est de Tabarka, Tabarka-Nefza	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; Draper *et al* 2008
Reboulia hemisphaerica (L.) Raddi	Aytoniaceae	2017	Aïn Babouch, Aïn Draham, Camp de la santé, Col du vent-Dar Fatma, El Feïja-Aïn Soltane, Ghardimaou, SF18	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; Campisi *et al.* 2015; this study
Riccardia chamedryfolia (With.) Grolle	Aneuraceae	1955	Aïn Babouch, Aïn Draham, Béni Mtir	Corbière & Pitard 1909; Jelenc 1955a
Riccardia latifrons (Lindb.) Lindb.	Aneuraceae	1955	Aïn Babouch, Aïn Draham, Béni Mtir	Corbière & Pitard 1909; Jelenc 1955a
Riccardia multifida (L.) Gray	Aneuraceae	1955	Aïn Babouch, Aïn Draham, Col du vent, Mérij, Oued Zen	Corbière & Pitard 1909; Jelenc 1955a
Riccia beyrichiana Hampe ex Lehm.	Ricciaceae	2017	Aïn Draham, Ghardimaou, MESF	Jovet-Ast & Bischler 1971; this study
Riccia bicarinata Lindb.	Ricciaceae	1971	Aïn Draham, Tabarka-Nefza	Jovet-Ast & Bischler 1971
Riccia canaliculata Hoffm.*	Ricciaceae	2017	MESF, MMA, MSG, OZEN, OZLE	Jovet-Ast 1986; this study
Riccia ciliata Hoffm.	Ricciaceae	1971	Aïn Babouch, Camp de la santé, Col du vent, Ghardimaou-El Feïja, Mérij, Tabarka-Nefza	Jelenc 1955a; Jovet-Ast & Bischler 1971
Riccia crozalsii Levier	Ricciaceae	1971	Aïn Babouch, Aïn Draham, Aïn Soltane-Ghardimaou, Ghardimaou, Ghardimaou-El Feïja	Jovet-Ast & Bischler 1971
Riccia duplex Lorb.	Ricciaceae	1971	Aïn Draham	Jovet-Ast & Bischler 1971
Riccia glauca L.	Ricciaceae	2012	Fernana	El Mokni & El Aouni 2011-2012
Riccia gougetiana Durieu & Mont.	Ricciaceae	2017	Aïn Babouch, Aïn Draham, Aïn Soltane-Ghardimaou, Col du vent, Dar Fatma, El Feïja-Aïn Soltane, Ghardimaou-El Feïja, Mérij, MSG, Tabarka-Nefza	Jovet-Ast 1986; this study
Riccia gougetiana Durieu & Mont. var. ***armatissima*** Levier ex Müll.Frib.	Ricciaceae	2017	MSG	New for Kroumiria; this study
Riccia lamellosa Raddi	Ricciaceae	1971	Aïn Draham, Jbel Bir-Source du 18ème	Jovet-Ast & Bischler 1971
Riccia macrocarpa Levier	Ricciaceae	2017	Aïn Babouch, Aïn Draham, Béni Mtir, Camp de la santé, Dar Fatma, Jbel Bir, Mérij-Col du vent, MMA, Source du 18ème, Tabarka-Nefza	Jovet-Ast & Bischler 1971; this study
Riccia michelii Raddi	Ricciaceae	1971	Aïn Babouch, Aïn Draham, Aïn Soltane-Ghardimaou, Camp de la santé, Col du vent, Dar Fatma, El Feïja-Aïn Soltane, Ghardimaou, Ghardimaou-El Feïja, Jbel Bir, Mérij-Col du vent, MSG, Source du 18ème, Tabarka, Tabarka-Nefza	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; this study
Riccia nigrella DC.	Ricciaceae	1971	Aïn Babouch, Aïn Draham, Camp de la santé, El Feïja-Aïn Soltane, Ghardimaou-El Feïja, Jbel Bir, Source du 18ème, Tabarka-Nefza	Jovet-Ast & Bischler 1971
Riccia perennis Steph.	Ricciaceae	2017	Aïn Draham, Béni Mtir, Col du vent, Dar Fatma, MMA	Jovet-Ast & Bischler 1971
Riccia sorocarpa Bisch. var***. Sorocarpa***	Ricciaceae	2017	Aïn Babouch, Aïn Draham, Aïn Soltane-Ghardimaou, Camp de la santé, Dar Fatma (piste), El Feïja-Aïn Soltane, Ghardimaou, Ghardimaou-El Feïja, Jbel Bir, Mérij-Col du vent, MMA, Source du 18ème	Jovet-Ast & Bischler 1971
Riella cossoniana Trab. *	Riellaceae	–	–	Ros *et al.* 2007

Table 4. — Continuation

Taxon	Family	Year	Locality	Sources
Scapania compacta (A.Roth) Dumort.	Scapaniaceae	1971	Aïn Babouch, Aïn Draham, Col du vent-Dar Fatma, Dar Fatma, Ghardimaou, Jbel Bir, J. Bir-Source du 18ème, Mérij-Col du vent, Oued Zen	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971
Scapania curta (Mart.) Dumort.	Scapaniaceae	1955	Aïn Babouch	Corbière & Pitard 1909; Jelenc 1955a
Scapania gracilis Lindb.	Scapaniaceae	1955	Aïn Babouch, Aïn Draham	Jelenc 1955a
Scapania nemorea (L.) Grolle	Scapaniaceae	2012	Aïn Zana, El Feïja, Mérij	El Mokni & El Aouni 2011-2012
Scapania undulata (L.) Dumort.	Scapaniaceae	1971	Aïn Babouch, Aïn Draham, Béni Mtir, Camp de la Santé, Col du vent-Dar Fatma, Dar Fatma, Oued Zen	Corbière & Pitard 1909; Jelenc 1954; Jelenc 1955a; Jelenc 1967; Jovet-Ast & Bischler 1971
Solenostoma cf. hyalinum (Lyell) Mitt.	Solenostomataceae	2017	Aïn Draham, AJM, OHLO, Mérij	Corbière & Pitard 1909; Jelenc 1955a; this study
Southbya nigrella (De Not.) Henriq.	Arnelliaceae	1971	Tabarka-Nefza	Jovet-Ast & Bischler 1971
Southbya tophacea (Spruce) Spruce	Arnelliaceae	1955	Aïn Babouch, Aïn Draham, Béni Mtir	Corbière & Pitard 1909; Jelenc 1955a
Sphaerocarpos michelii Bellardi	Sphaerocarpaceae	2012	Aïn Zana, Béni-Mtir, entre Ghardimaou-El Feïja, Ghardimaou, Mérij	Labbe 1953; Jelenc 1967; Jovet-Ast & Bischler 1971; El Mokni & El Aouni 2011-2012
Targionia hypophylla L.	Targioniaceae	1971	Aïn Babouch, Aïn Draham, Col du vent-Dar Fatma, Ghardimaou-El Feïja, Tabarka-Nefza	Corbière & Pitard 1909; Jelenc 1955a; Jovet-Ast & Bischler 1971; Campisi *et al.* 2015

inia coriandrina, *Reboulia hemisphaerica* and *Riccia* spp. that adopt various strategies for tolerating temporarily dry habitats, including thickening and winding the thallus, developing hairs, and a short life cycle (Wood 2007; Glime 2017). Lastly, the hornwort *Phymatoceros bulbiculosus* and the liverwort *Riccia gougetiana* develop ventral tubers that survive in the soil for 9 months after the thallus has deteriorated (Vitt *et al.* 2014), enabling them to tolerate desiccation. The tubers germinate with the first rains and form new plants (Crandall-Stotler *et al.* 2006). Such resistance to desiccation is thought to be due to a large amount of abscisic acid (Hartung *et al.* 1994), a hormone known to induce this tolerance in bryophytes (Pence *et al.* 2005).

Relationships of environmental factors. Our results are in line with the idea that certain factors such as wetness and light offset one other. High ambient humidity would compensate for greater evapotranspiration induced by direct exposure to sunlight. By contrast, shade would allow species to develop in drier situations by strongly reducing evapotranspiration. The richness of the corticoles in the forests perfectly exemplifies this compensation: the same species collected on the bark of trees bordering wadis proliferate in forests whose cover favors significant atmospheric wetness and filter light radiation (Celle *et al.* 2014).

CONCLUSION

This work focuses on liverworts and hornworts, and is based on the collection of 32 taxa, corresponding to 42% of the total richness inventoried in Kroumiria, and probably including its most abundant species. This is the first contribution to the study of the ecology and conservation of Tunisian bryoflora. Of the 44 species that were not found, 27 were either not reviewed recently or only observed once in the past. These species represent more than one third of the liverworts and hornworts of Kroumiria and are likely to present conservation issues. However, further investigations need to be made to verify and clarify the status of these species in order to propose a Red List of Tunisian bryophytes.

This work also identifies seven ecological communities based on the requirements of different species for light, substrate, temperature and wetness, making it possible to better characterize the potential habitats of Anthocerotophyta and Marchantiophyta in northern Tunisia. The results show that these plants prefer wet, shaded microhabitats, but can also colonize open areas. The Maghreb's Mediterranean climate encourages the development of very adapted forms such as annual and photophilous species of the genus *Riccia* that develop especially on temporarily wet depressions and soils (Jovet-Ast 1986; Hugonnot & Hébrard 2004).

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