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Diversity and distribution of Characeae in the Maghreb (Algeria, Morocco, Tunisia)

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Abstract – Characeae are macroscopic green algae present in the Maghreb (Morocco, Algeria, Tunisia) that are known since the 19th century works of Desfontaines (1800) and Braun (1868). Feldmann (1946) published the first regional synthesis, and this study provides a new Maghreb-wide synthesis of all collections made since 1784 (570 observations distributed over 464 sites). Each of the 31 reported species is described in detail with its diagnostic features, ecology and distribution in the three Maghrebian countries. Distribution maps distinguish between the three collection periods: 1780-1939, 1940-1979, and 1980-2016. An illustrated key is provided to help botanists working in the Maghreb to identify the taxa. From a biogeographical perspective, the Characean flora of the Maghreb is dominated by elements originating from northern (European) countries (61.3%) that include regionally very rare species such as *Chara strigosa* and *C. tomentosa*. The Mediterranean-Atlantic element is also well represented (32.3%), with some Mediterranean endemics (*Chara imperfecta*, *C. oedophylla*, *C. vulgaris* var. *gymnophylla*). Finally, two taxa that have an affinity for tropical conditions (*Chara zeylanica* and *Lamprothamnium succinctum*) extend to the southern Sahara. In North Africa, 14 species (7 *Chara*, 2 *Lamprothamnium*, 4 *Nitella* and 1 *Sphaerochara*) are threatened and raise issues about their conservation; three of these are particularly endangered: *Chara imperfecta*, *C. oedophylla* and *Lamprothamnium papulosum*.

Charophytes / Macrophytes / North Africa / identification key / biogeography / distribution

Résumé – Les Characeae sont un groupe d'algues vertes macroscopiques présent au Maghreb, où elles sont connues depuis les travaux anciens de Desfontaines (1800) et Braun (1868). Une première synthèse régionale a été publiée par Feldmann (1946). Le présent travail consiste en une nouvelle synthèse à l'échelle du Maghreb, intégrant toutes les collectes réalisées depuis 1784 (570 relevés répartis dans 464 sites). Chacune des 31 espèces présentes fait l'objet d'une description détaillée, présentant ses caractères diagnostiques, son écologie et sa répartition au Maghreb. Cette dernière est illustrée par une cartographie distinguant trois périodes de collectes : 1780-1939, 1940-1979 et 1980-2016. Dans le but de faciliter l'identification des taxons par les botanistes travaillant au Maghreb, une clé de détermination illustrée est proposée. D'un point de vue biogéographique, la flore des Characeae du Maghreb est dominée par l'élément de souche septentrionale (61,3 %), comprenant des espèces régionalement très rares comme *Chara strigosa* et *C. tomentosa*. L'élément méditerranéen-atlantique est également bien représenté (32,3 %), avec quelques endémiques méditerranéennes (*Chara imperfecta*, *C. oedophylla*, *C. vulgaris* var. *gymnophylla*). Enfin, deux taxons d'affinité tropicale (*Chara zeylanica* et *Lamprothamnium succinctum*) atteignent le sud de la région. Les enjeux conservatoires à l'échelle de l'Afrique du Nord portent sur 14 espèces (7 *Chara*, 2 *Lamprothamnium*, 4 *Nitella* et 1 *Sphaerochara*), parmi lesquelles trois présentent un intérêt conservatoire majeur : *Chara imperfecta*, *C. oedophylla* et *Lamprothamnium papulosum*.

Charophytes / Macrophytes / Afrique du Nord / clé d'identification / biogéographie / répartition

INTRODUCTION

Among green algae, the Characeae are resolved as close ally to the Embryophytes (Leliaert *et al.*, 2012). Their communities play important roles in aquatic ecosystems (water quality control, primary production, housing for invertebrates and fish…) and provide valuable ecological clues to evaluate ecosystem health (e.g. Hargeby *et al.*, 1994; Mouronval *et al.*, 2007; Kufel & Kufel, 2012;

Blindow *et al.*, 2014; Chauvin *et al.*, 2014; Schneider *et al.*, 2015a). The group is poorly diversified, given its age, even though the actual number of species remains a matter of discussion because of divergent taxonomical conceptions. While the lack of complete data on distribution makes the conservation status of some taxa uncertain, the general decline and eutrophication of wetlands constitute major threats to them in numerous regions (e.g. Stewart & Church, 1992; Blaženčić *et al.*, 2006; Auderset Joye *et al.*, 2007). Long neglected by botanists, Characeae recently became a subject of increasing interest for evaluating biodiversity (e.g. Krause, 1997; Cirujano *et al.*, 2008; Bailly & Schaefer, 2010; Mouronval *et al.*, 2015) and as bioindicators of surface water quality (e.g. Zouaïdia *et al.*, 2015). Although the Mediterranean region appears to be important for the family's conservation (Blaženčić *et al.*, 2006; Cirujano *et al.*, 2008), regional data remain deficient, especially in North Africa.

The first published mention of Characeae in the Maghreb was in 1800 by René Louiche Desfontaines after his field mission of 1783-1785 in Algeria and Tunisia, just before he was awarded the Chair of Botany of the King's Garden in Paris. Desfontaines noted the presence of *Chara vulgaris*, and from his collection of 1784, created a new species, *C. squamosa* (Desfontaines, 1800), which is currently considered to be a variety of *C. vulgaris* (var. *gymnophylla*). It was not until 1868 that Professor of Botany Alexander Braun, in Berlin, the first true specialist of the group, published the first synthesis of African Characeae (Braun, 1868) in *Die Characeen Afrika's,* which covered the Characean flora on the continent. Braun's study mainly drew on materials that had been sent to him by eminent naturalists, who, during their fieldtrips, had harvested Characeae. He described 22 taxa for the Maghreb (37 localities recorded): 12 *Chara*, 1 *Lamprothamnium*, 7 *Nitella* and 2 *Tolypella*. Braun's work also refers to earlier finds: In 1819, Philippe Salzmann had discovered *Chara connivens,* a new species near Tangiers and the only Moroccan species that Braun (1868) described. Tunisian collections were first made by Michel Charles Durieu de Maisonneuve in 1840 and by Jean-Louis Kralik in 1854 (Braun 1868), and later completed by Narcisse Théophile Patouillard (Patouillard, 1897). Durieu's collections from Algeria, collected essentially from his 1839-1842 field missions, were the largest by far. To recognize his contribution, Braun dedicated a species to him in his study of North African Characeae, *Chara duriaei*, which is integrated today into *C. galioides*. Later, Ernest Cosson collected Characeae during 8 fieldtrips undertaken between 1852 and 1880. He gave his collections to various botanists and explorers (Benjamin Balansa, Nicolas Bové, Henri-René de la Perraudière, Georges François Reuter, Guillaume Philippe Schimper, Eduard Wilhelm Steinheil) who shared his fieldwork and transmitted most of the species to A. Braun.

In the early 20th century, new explorations were undertaken in Algeria and Morocco by botanists Louis Corbière, Jean Gattefossé, Paul Hariot, Emile Jahandiez, René Maire, Marcellin Mouret and Roger-Guy Werner, and new localities of Characeae were discovered, especially in Algeria. However, few new taxa were discovered (Corbière & Hariot, 1913; Mouret, 1916; Gattefossé, 1932; Maire, 1933; Maire & Werner, 1934; Werner, 1934; Gattefossé & Werner, 1935). We can however note the description by Louis Charles Trabut of *Chara strigosa* var. *myriacantha* (Trabut in Maire & Werner, 1934), no longer distinguished today. Just after the Second World War, Geneviève Feldmann published a synthesis of the collections that had been made since the end of the 19th century in North Africa (Feldmann, 1946), compiling finds from 131 localities and describing 29 taxa (17 *Chara*, 1 *Lamprothamnium*, 8 *Nitella* and 3 *Tolypella-Sphaerochara*). She used numerous unidentified herbarium specimens that were preserved at the French National

Museum of Natural History and at the Faculty of Algiers, and that came from collections of Jules-Aimé Battandier, L.C. Trabut, R. Maire and Augustin Labbe, the zoologist Léon Gaston Seurat and the perfume maker J. Gattefossé. The material collected in Algeria and Tunisia by Lucienne Gauthier-Lièvre in 1924-1930 (Gauthier-Lièvre, 1931) led to the description of two new species: the first from Algeria (*Chara mauretanica*, today considered to be *C. globularis* var. *globularis* f. *mauretanica*), and the second from Tunisia, described as *Chara oedophylla* (Feldmann, 1945). This taxon is considered here to be a species separate from *C. vulgaris* (Soulié-Märsche & Muller, 2016), whereas Wood & Imahori (1965) previously assimilated it to *C. vulgaris* as a variety.

In 1952, G. Feldmann together with Paulette Gayral (who explored Moroccan wetlands for her thesis on phytoplankton) undertook fieldwork in Morocco that allowed her to discover new localities of Characeae, and revealed in particular the abundance of *Tolypella hispanica* in the Middle Atlas (Feldmann, 1953; Gayral, 1954). From the 50s onwards, the interest in North African Characeae essentially focused on Morocco: Several missions by Robert Corillion (Corillion, 1961a, 1962) and Micheline Guerlesquin (Guerlesquin, 1961) led to a better knowledge of Moroccan Characeae. A few years later, within the context of a *Recherche Coopérative sur Programme* (RCP), M. Guerlesquin presented a systematic investigation for 100 sites located largely in northern Morocco and the Middle Atlas (Guerlesquin, 1974, 1978). The highly detailed study distinguished numerous varieties and forms of *Chara vulgaris* (var. *crassicaulis* f. *contraria*, var. *gymnophylla* f. *conimbrigensis* and f. *denudata*, var. *hispidula* and var. *longibracteata*) but treated *Chara mauretanica* as a separate species. 78 localities out of the 100 sites contained *Chara vulgaris* and its affiliated forms, while only 14 sites contained *Nitella* species. No *Tolypella* were identified (Guerlesquin, 1978). More recently, in the 80s and 90s, Najat Elkhiati studied 90 localities in Morocco, corresponding partly to the earlier sites of M. Guerlesquin, and focused particularly on the ecology of some selected sites (Elkhiati, 1987, 1995). She specified the phenology of Characeae, whose maximum biomass appears in February-March with a decline in April and a collapse in May-June (1991-1993).

In 1977, R. Corillion published a synthesis of Tunisian Characeae based on the work of several field missions undertaken by Suzanne Jovet-Ast and Hélène Bischler in 1968 and 1970, and by R. Corillion and M. Guerlesquin in 1973. This resulted in a list of 55 localities and the collection of 12 species and subspecies of Characeae (8 *Chara*, 1 *Lamprothamnium* and 3 *Tolypella*). Part of this material was also the subject of a chromosome study (Guerlesquin, 1977). In Algeria, botanists had abandoned Characeae until Gérard de Bélair's investigations in Numidia noted their occurrence in some 20 sites (De Bélair, 2005), and the doctoral thesis of Hanene Zouaïdia was initiated as part of an Franco-Algerian collaboration and focused on the Characeae of that region (Zouaïdia-Abdelkassa, 2016). Since 2006, other research projects about North African wetlands have been conducted in collaboration with Moroccan (Laïla Rhazi), Tunisian (Amina Daoud-Bouattour, Semia Ben Saad-Limam, Zeineb Ghrabi-Gammar) and Algerian scientists (Mohamed Benslama), extending the investigations to the entire Maghreb (Muller *et al.*, 2008; Daoud-Bouattour *et al.*, 2009; Ferchichi-Ben Jamaa *et al.*, 2010; Bouldjedri *et al.*, 2011; Bouahim *et al.*, 2014; Rouissi *et al.*, 2016; Soulié-Märsche & Muller, 2016). The results of this decade-long research (115 prospected sites; 22 species identified including a new one for the Maghreb) lead us to propose a new synthesis of Maghrebian Characeae. This comes 70 years after Feldmann (1946) and nearly 150 years after Braun (1868). Our synthesis takes into account 570 relevés, which

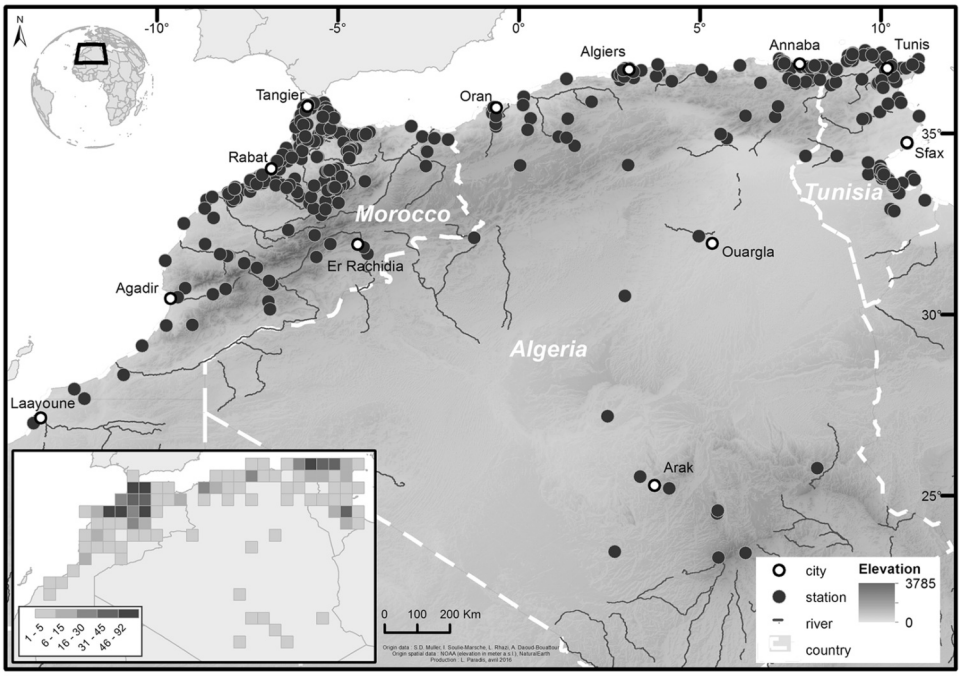


Fig. 1. Localities with Characeae inventoried in the three Maghrebian countries (464 localities). Inlet in the lower left-hand corner indicates the sampling pressure (density of sites per 100 × 100 km).

are to say, all known records since 1784 from 464 localities in Morocco (275), Algeria (108) and Tunisia (81) (Fig. 1; Tab. 1 (page suivante)).

In addition to compiling the data on Maghrebian Characeae, the present paper also aims to do the following: (1) update the nomenclature, based on the more recent works; (2) propose simple, adapted identification keys for botanists working in North Africa; (3) present morphological, ecological and geographical features of each taxon, along with clear illustrations and distribution maps, and (4) conclude with a rapid preliminary analysis of the biogeographic significance and conservation issues concerning Maghrebian Characean communities.

THE CHARACEAE FAMILY

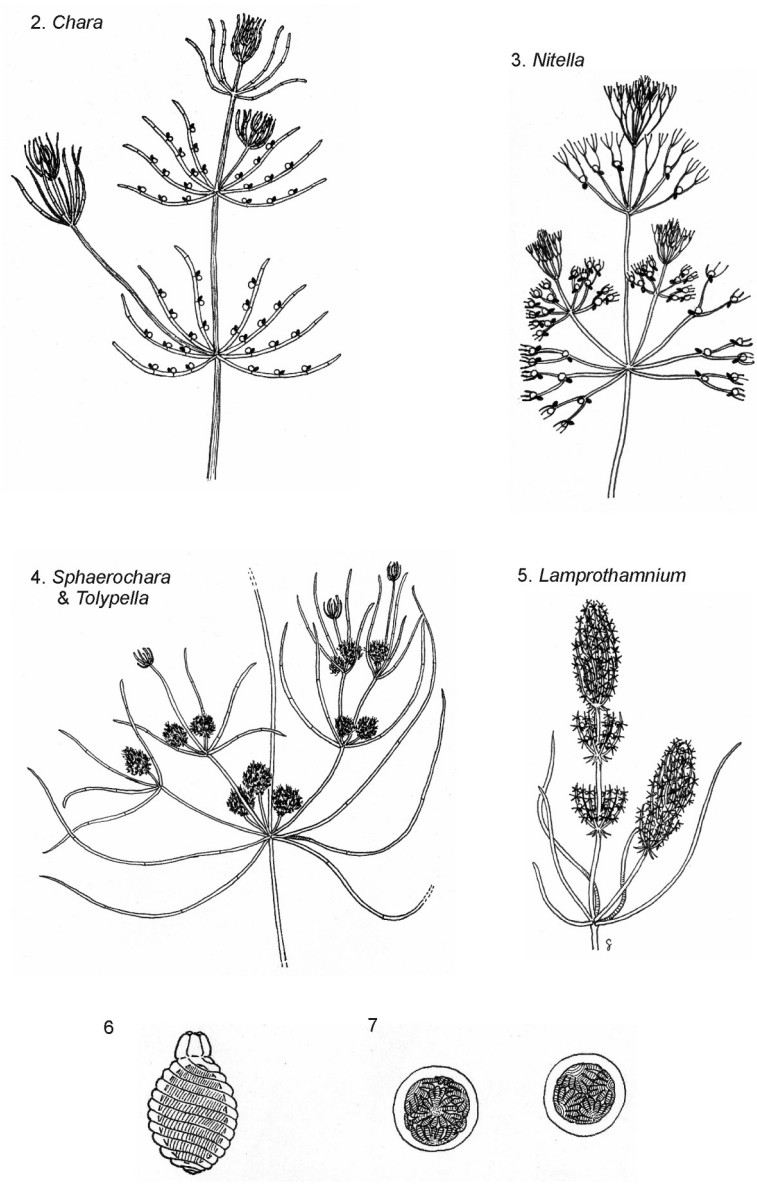
Corillion (1957) describes in detail the systematic position of the Characeae that has long vexed botanists. Since the 15th century, the Characeae were considered to be close to *Equisetum* or *Hippuris*. In the 18th century, Vaillant (1721) grouped them into the genus *Chara*, which was officially created by Linnaeus (1753). Linnaeus included them initially in algae, before moving them into the monoic monostaminate Phanerogames. Thereafter, numerous botanists adopted his point of view (e.g. Adanson, Withering, Hudson, Lamarck, De Candolle and Desfontaines).

Table 1. Number of occurrences of species and sub-species of Characeae in the three countries of Maghreb

Taxon	*Algeria*	*Morocco*	*Tunisia*	*Maghreb*
Chara aspera Deth. *ex* Willd.	12	35	12	59
Chara baltica Bruz.	2	20	7	29
Chara braunii Gmel.	9	1	1	11
Chara canescens Desv. & Lois.	2	5	–	7
Chara connivens Salzm.	17	40	11	68
Chara contraria A.Br. *ex* Kütz.	6	19	1	26
Chara fragifera Dur.	3	–	1	4
Chara galioides DC.	5	7	5	17
Chara globularis Thuill.	15	34	4	53
Chara hispida L.	2	10	1	13
Chara imperfecta A.Br. in Dur.	2	3	–	5
Chara oedophylla Feldmann	–	1	3	4
Chara strigosa A.Br.	–	1	–	1
Chara tomentosa L.	1	3	–	4
Chara vulgaris L. var. *gymnophylla* (A.Br.) Nym.	19	66	12	97
Chara vulgaris L. var. *vulgaris*	25	158	39	222
Chara zeylanica Klein *ex* Willd.	1	–	–	1
Lamprothamnium papulosum (Wallr.) J.Gr.	3	4	5	12
Lamprothamnium succinctum (A.Br. in Asch.) Wood		2		2
Nitella capillaris (Krock.) J.Gr. & B.-W.	5	1	1	7
Nitella confervacea (Bréb.) A.Br. *ex* Leonh.	2	1	–	3
Nitella flexilis (L.) Ag.	–	–	1	1
Nitella gracilis (Smith) Ag.	2	13	–	15
Nitella hyalina (DC.) Ag.	3	13	–	16
Nitella mucronata (A.Br.) Miq.	6	10	1	17
Nitella opaca (Bruz.) Ag.	27	36	7	70
Nitella tenuissima (Desv.) Kützing	8	–	–	8
Nitella translucens (Pers.) Ag.	18	17	5	40
Sphaerochara intricata (Trent. *ex* Roth) Soulié-Märsche	1	–	1	2
Tolypella glomerata (Desv. in Lois.) Leonh.	11	4	9	24
Richness	27	26	21	31
Tolypella hispanica Nordstedt *ex* Allen	5	16	8	29

In the 19th century, Kützing (1849) and Braun (1868) integrated them into algae, and Von Sachs (1882) created the group of Charophytes as an intermediary between thallophytes and bryophytes. Since the first studies of molecular phylogeny, Characeae have been positioned as the sister group of Embryophytes (McCourt, 1995; Huss & Kranz, 1997). They constitute a class (Charophyceae) and an order (Charales) within the paraphyletic group of Charophytes s.l. that also includes Coleochaetales, Zygnematales and Klebsormidiales (Qiu, 2008).

Today, the living Characeae include 7 genera classified in two tribes: *Chareae* (*Chara*, *Lamprothamnium*, *Nitellopsis* and *Lychnothamnus*) and *Nitelleae*



Figs 2-7. Typical habit of the Characean genera recorded in North Africa (2-5) and global aspect of gametangia (6-7). **2.** *Chara*; **3.** *Nitella*; **4.** *Sphaerochara* & *Tolypella*; **5.** *Lamprothamnium*; **6.** Oogonium in lateral view, with spiral cells, coronula and dark oospore inside; **7.** Antheridium composed of 8 triangular shields (apical and lateral view).

(*Nitella*, *Sphaerochara* and *Tolypella*) (Wood, 1962; Soulié-Märsche, 1989; McCourt *et al.*, 1996; Soulié-Märsche & García, 2015). They all present general cladomian architecture structured into main axes with indefinite growth (cladomes) bearing whorls of branchlets or phylloids with definite growth (pleurids) (Figs 2-7). The

basic structure of the plant body (thallus) consists of a succession of internodes and nodes. The tribe of *Chareae* is distinguished by the presence of bract cells on the branchlets, and the genus *Chara* is the only one to develop a cortex of tubular cells forming a sheath around the main cell of axes and branchlets. The particular feature of the Characeae that confused 18th-19th century botanists concerns the unique structure of their reproductive organs carried by gametophytes, which are generally on branchlets. Their complexity recalls the gametangia of Embryophytes, but these reproductive organs are nonetheless gametocysts (Ozenda, 2006). However the term "gametangia" (e.g. Chadefaud & Emberger, 1960; Wood & Imahori, 1965; Corillion, 1975; Krause, 1997) was used for these structures that are in fact evolutive convergences with true gametangia.

The female reproductive organ, or oogonium, is composed of an oocyst surrounded by five long, twisted spiral cells topped by 5 or 10 small cells forming a coronula. After fecundation, the oocyst is surrounded by a resistant dark-colored wall and is then called oospore. In numerous species, the spiral cells surrounding the oospore calcify, and the oospore becomes a gyrogonite, a structure that resists desiccation. Most *Chara* species, as well as *Sphaerochara intricata*, regularly produce gyrogonites (calcified oospores) that may persist for long periods in dry environments. By contrast, *Chara braunii* and *C. canescens* never produce gyrogonites, probably for want of carbonic anhydrase, the enzyme responsible for biomineralization in plants. The more complex male reproductive organ is a structure composed of 8 shield cells that protect numerous spermatocysts (male gametocysts) arranged in filaments. This organ is called an "antheridium", although the term appears incorrect as it usually designates the male gametangium of Embryophytes. Notwithstanding this terminological problem, this paper respects the traditional usage and will employ "gametangia" and "antheridia".

IDENTIFICATION KEYS

The present identification keys focus on the criteria for determining the species encountered to date in the three countries of the Maghreb. Possibly or even probably, more taxa will be discovered, especially in Algeria, which has been poorly investigated for decades. Where relevant, our descriptions of cosmopolitan species takes into account the particular morphology they display in the Mediterranean area.

Classification

Class: Charophyceae Smith
Order: Charales Lindley
Family: Characeae Gray

Key to the genera

1a. Coronula of 5 cells, usually large; axis corticated (except *Lamprothamnium* and *Chara braunii*); generally one secondary axis per axial node; branchlets simple, undivided composed of a variable number of linear cells (segments); branchlet nodes bearing a whorl of 1-celled bract cells, anteriors and posteriors ± developed; gametangia at the inner axil of branchlet nodes 2

1b. Coronula of 10 tiny cells (in 2 tiers); cortex, stipulodes and spine cells absent; branchlets successively divided, furcate; gametangia often clustered in dense "fertile heads"; usually multiple secondary axes at axis nodes 3

2a. Stipulodes simple or double (in 1 or 2 tiers); axis corticated (except *C. braunii*); oogonia above antheridium in monoecious species (Fig. 2) .... *Chara*

2b. Stipulodes in one row; axis ecorticated; oogonium below antheridium; brackish waters (Fig. 5)..... *Lamprothamnium*

3a. Branchlets homogenous, divided several times into similar rays of successive orders, ultimate rays = dactyls; usually two secondary axes per node; gametangia in the forks (Fig. 3); oospores laterally compressed ..... *Nitella*

3b. Branchlets not furcate composed of a main branchlet of linear cells (= rachis) whose nodes form lateral cells (= rays); gametangia on branchlet nodes and at base of whorls; many secondary axes on axial nodes (Fig. 4) 4

4a. Terminal cells all acuminate..... *Sphaerochara*

4b. Terminal cells all obtuse..... *Tolypella*

Key to the species of genus *Chara*

1a. Axes without cortex (ecorticated) (Fig. 8); stipulodes in 1 tiers... *Chara braunii*

1b. Axes corticated; stipulodes in 2 tiers (Fig. 9).....2

2a. Cortex of axes incomplete (Fig. 13)..... *Chara imperfecta*

2b. Cortex of axes complete.....3

3a. Lower-most segment of branchlets ecorticated; tropical species occurring in the Saharan part of the study area..... *Chara zeylanica*

3b. Lower-most segment of branchlets corticated.....4

4a. Cortex haplostichous (Fig. 10); parthenogenetic species, brackish water..... ..... *Chara canescens*

4b. Cortex diplo- or triplostichous 5

5a. Cortex diplostichous (Fig. 11) 6

5b. Cortex triplostichous (Fig. 12) 13

Cortex diplostichous

6a. Dioecious species, often of orange-red colour; cortex strongly tylacanthous (= spine cells on the ridges; Fig. 14); spine cells robust, forming a whorl (Fig. 9); tall plant ..... *C. tomentosa*

6b. Monoecious species; medium to tall plants.....7

7a. Spine cells weakly developed, rudimentary and solitary; bract cells only on the inner (adaxial) side of the branchlet nodes..... *Chara vulgaris*-group 8

7b. Spine cells well developed, predominantly grouped by 2-3 (fasciculate); bract cells as a whorl around branchlet nodes 11

Chara vulgaris-group (8-10)

8a. Antheridia and oogonia on different branchlet nodes; antheridia solitary; 1-3 oogonia arranged vertically on branchlet nodes; 3-4 swollen bract cells on each side of the oogonia .....*Chara oedophylla*

8b. Antheridia and oogonia at the same node; oogonium above antheridium; two rather long bract cells on each branchlet node 9

9a. Cortex tylacanthous (spine cells on protruding cortical tubes)*Chara contraria*
9b. Cortex isostichous (= cortical tubes of same diameter) to aulacanthous (spine cells in furrows) (Fig. 15).....10

10a. Branchlets corticated (at least 3-4 segments corticated followed by 2-3 ecorticated cells); gametangia only on nodes of corticated segments..... .....*Chara vulgaris* var. *vulgaris*
10b. Branchlets devoid of cortication or only the basal segment corticated; gametangia formed on nodes of ecorticated segments..... .....*Chara vulgaris* var. *gymnophylla*

11a. Plant small to medium-sized; axis diameter < 1 mm... *Chara strigosa* pro parte
11b. Plant robust and heavily incrusted; axis diameter 1-3 mm..... ..... *Chara hispida*-group 12

Chara hispida-group (12)

12a. Spine cells solitary; cortex isostichous to tylacanthous (Fig. 14)..... ..... *Chara baltica*
12b. Spine cells 2-3 fasciculate; cortex isostichous to aulacanthous (Fig. 15) ....*Chara hispida*

Cortex triplostichous

13a. Spine cells and stipulodes rudimentary or not developed; freshwater.....14
13b. Spine cells and stipulodes well developed.....16

14a. Monoecious species .....*Chara globularis*
14b. Dioecious species.....15

15a. Branchlets stiff and incurved on male plants; big antheridia (0.6-1.0 mm); branchlets straight on female plants; coronula triangular (connivent)..... ..... *Chara connivens*
15b. Branchlets slender, as long as the internodes; antheridia medium sized (0.5-0.6 mm); presence of bulbils on the rhizoids .....*Chara fragifera*

16a. Monoecious species; very spiny, with fasciculate spine cells; freshwater... ..... *Chara strigosa* pro parte
16b. Dioecious species; spine cells solitary; brackish water.....17

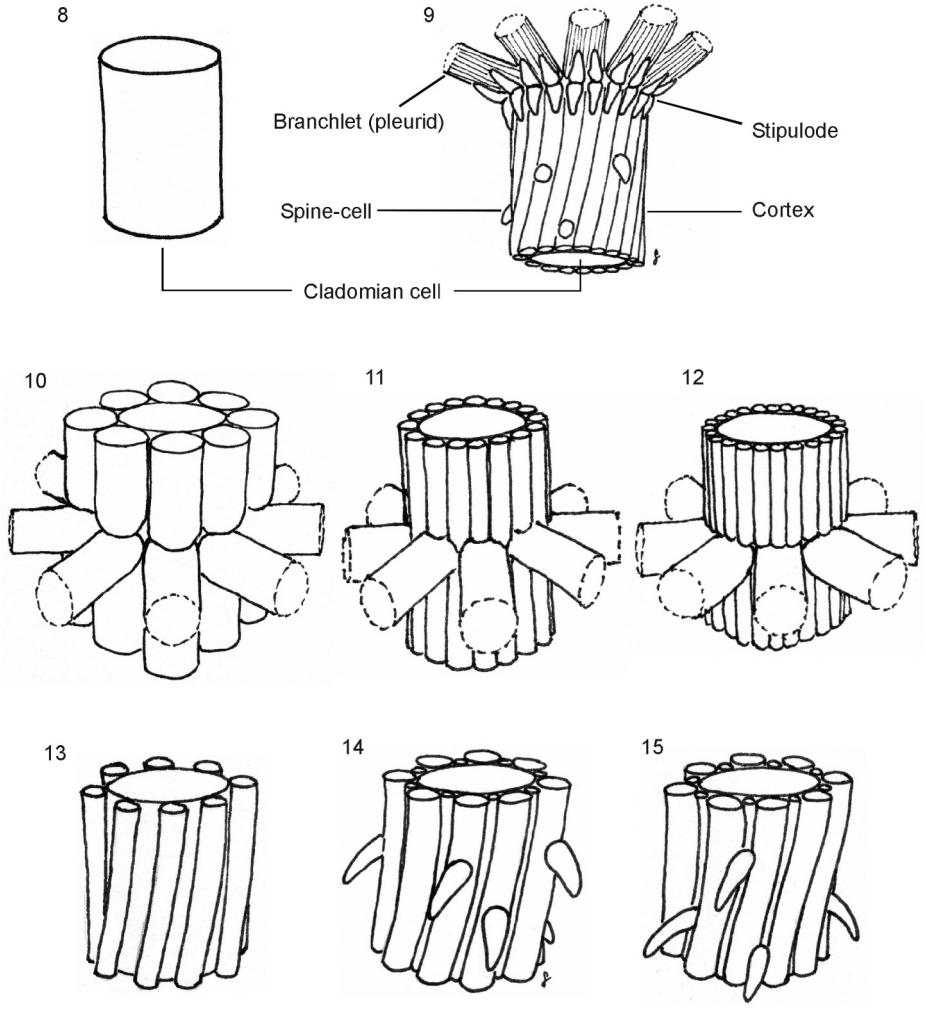
17a. Antheridia < 800 µm ..... *Chara aspera*
17b. Antheridia > 800 µm ..... *Chara galioides*

Key to the species of genus *Lamprothamnium*

1a. Gametangia solely on the branchlet nodes; Atlantico-Mediterranean species..... ..... *Lamprothamnium papulosum*
1b. Presence of additional gametangia (mainly oogonia) at the base of whorls; tropical species present in the Saharan part of the studied area ....*Lamprothamnium succinctum*

Key to the species of genus *Nitella*

1a. Branchlets apparently undivided, composed of one elongated cell with a crown of tiny, void dactyls; robust, tall plant .....*Nitella translucens*
1b. Branchlets furcate; usually delicate plants.....2



Figs 8-15. Diagnostic morphological features in genus *Chara*. **8.** Ecorticated axis; **9.** Stipulodes (here in 2 tiers) located at the base of the branchlets, spine cells on internodes; **10.** Haplostichous cortex (number of cortical tubes equals the number of branchlets); **11.** Diplostichous cortex (cortical tubes = 2 × the number of branchlets); **12.** Triplostichous cortex (cortical tubes = 3 × the number of branchlets; **13.** Incomplete cortex; **14.** Diplostichous tylacanthous cortex (spine cells on the protruding cortical tubes); **15.** Diplostichous aulacanthous cortex (spine cells in the fossae).

2a. Whorls differentiated into long (primary) and short (accessory) branchlets, all furcate and forming mucilaginous heads (*Heteroclemae*)..... *Nitella hyalina*
2b. Branchlets in a whorl all similar (*Homeoclemae*).....3
3a. Unicellular dactyls 4
3b. Pluricellular dactyls (2-5 cells) ending with a sharp, acute terminal cell.....6

Unicellular dactyls

4a. Gametangia surrounded by mucus; dioecious species ..... *Nitella capillaris*
4b. Gametangia without mucus 5

5a. Monoecious species ..... *Nitella flexilis*
5b. Dioecious species ..... *Nitella opaca*

Pluricellular dactyls

6a. Delicate species; axis with long internodes, and regularly spaced, fan-shaped whorls; branchlets divided 2-4 times; gametangia normally absent from the first fork ..... *Nitella tenuissima*
6b. Morphology different; gametangia present on all nodes 7

7a. Robust species, axis diameter > 1 mm; dactyls ending with a tiny cell (mucron) ..... *Nitella mucronata*
7b. Delicate, flexible species, axis diameter < 1 mm 8

8a. Small plant (± 5 cm); whorls forming small fertile heads; gametangia on the first fork of the branchlets ..... *Nitella confervacea*
8b. Absence of fertile heads; gametangia potentially formed on all forks ..... *Nitella gracilis*

Key to the species of genera *Sphaerochara* and *Tolypella*

1a. Terminal cell of branchlets and rays acuminate (*Sphaerochara*); monoecious species ..... *Sphaerochara intricata*
1b. Terminal cell of branchlets and rays rounded, obtuse (*Tolypella*) 2

2a. Dioecious species; brackish water ..... *Tolypella hispanica*
2b. Monoecious species; freshwater to slightly salty water ... *Tolypella glomerata*

MORPHOLOGY, ECOLOGY AND DISTRIBUTION OF SPECIES

Except *Chara oedophylla*, which we consider to be a distinct species (Soulié-Märsche & Muller, 2016), and *Sphaeorochara*, which we distinguish from *Tolypella* (Soulié-Märsche, 1989; Soulié-Märsche & García, 2015), the nomenclature used in the present work follows that of European authors (Corillion, 1975; Krause, 1997; AGCD, 2016) unlike the concept of "macro-species" that has been proposed by Wood & Imahori (1965). The synonymies with taxa used by earlier authors are noted for each species. The new data collected by the authors of the present work are listed Tabs 2 and 3.

Chara aspera Deth. *ex* Willd. **Figs 16-17**

incl. *C. mauritanica* Feldm., *C. desmacantha* (H. & J.Gr.) J.Gr. & B.-W.

Description. Small, bushy plant (20 cm), distinguished by the red colour of the numerous antheridia on male individuals. Appearance delicate but ± incrusted with calcite. Cortex triplostichous with numerous acute spine cells. Spine cells as long as

Table 2. List of new localities explored in the present study. Certain localities correspond to a larger wetland area and comprise several collection sites. Abbreviations: ISM, I. Soulié-Märsche; LR, L. Rhazi; SDM, S.D. Muller. Names in brackets refer to the identification

Locality (code)	*Locality (name)*	*Country*	*Elevation (m)*	*Latitude*	*Longitude*	*Year(s)*	*Number of sites*	*Number of collections*	*Author(s) of collections*
BOU	Boujdayem	Morocco	1202	35,0228	– 5,2067	2010-2013	2	3	SDM, 2010; LR, 2013
BS	Ponds of Ben Slimane	Morocco	222	33,6849	– 7,0769	2009-2013	18	33	SDM, 2009; LR, 2013
CHAO	Ponds of Chaouia	Morocco	218	33,1855	– 7,8735	2013	7	7	LR, 2013
DAY	Dayla	Morocco	1392	35,0188	– 4,9999	2010-2013	2	2	SDM, 2010; LR, 2013
DWA	Dwahriia (iron mine)	Tunisia	300	37,0392	9,2128	2008	1	1	SDM, 2008
EGO	El Gourea	Tunisia	339	36,3353	8,6261	2006	1	1	SDM, 2006
GAM	Gammarth – brackish pond	Tunisia	2	36,9197	10,2794	2006-2016	1	1	SDM, 2006, 2016
GGT	Garâa Guetma	Tunisia	96	37,1331	9,2519	2008-2010	1	3	SDM, 2008
GUE	Guetma	Tunisia	98	37,1269	9,2664	2007-2010	3	4	ISM, 2007
HAM	Hammare	Morocco	1315	35,0308	– 5,0183	2010	1	1	SDM, 2010
HEM	Hank el Menzel	Tunisia	0	35,9800	10,4900	1982	1	1	H.Bismuth (ISM), 1982
ICHR	Ichkeul – stream	Tunisia	20	37,1875	9,6869	2014	1	1	SDM, 2014
LAT	Lake Tonga	Algeria	0	36,8578	8,5008	2013	1	1	H.Zouaïdia (ISM), 2013
MA20	Pond Middle-Atlas 20	Morocco	1894	33,1811	– 5,0647	2013	1	1	LR, 2013
MARZ	Marzine	Morocco	720	35,1006	– 5,3358	2010	1	1	SDM, 2010
MAZ	El Mazarâa	Algeria	693	36,4278	7,9289	2011	1	1	SDM, 2011
MCH	Majen Choucha	Tunisia	445	37,0106	9,2119	2008-2010	1	2	SDM, 2008; ISM, 2010
MGT	Majen el Gtatii	Tunisia	570	36,7294	8,7092	2009	1	1	SDM, 2009
MMA	Majen el Ma	Tunisia	505	36,7811	8,7900	2009	1	1	SDM, 2009
MOZ	Majen el Ouez	Algeria	639	36,4847	8,3197	2012	1	1	SDM, 2012
MZO	M'Zouka	Morocco	24	34,2983	– 6,0028	2009	1	1	SDM, 2009
NEFZ	Dam of Nefza	Tunisia	34	37,0000	9,0700	2010	1	1	ISM, 2010
NOUN	Wady Noun	Morocco	0	29,1372	– 10,4042	2002	1	1	ISM, 2002
OAY	Wady Oulay Ayed	Tunisia	484	36,7722	8,7719	2010	1	1	ISM, 2010
RIF-S7	Temporary pond S7	Morocco	783	35,1284	– 5,4385	2013	1	1	LR, 2013
SBR	Sidi Boughaba	Morocco	13	34,2147	– 6,6894	2009	2	2	P.Grillas, LR, 2009
SEGU	Pond 1, Seguedla	Morocco	20	35,6243	– 5,8769	2013	1	1	LR, 2013
SEJE	Garâa Sejenane	Tunisia	100	37,0833	9,1750	2007-2014	8	9	ISM, 2007, 2010; SDM, 2012-2014
SER	Cap Serrat	Tunisia	1	37,2125	9,2311	2014	2	2	SDM, 2014
SFL	Sidi Freitis	Algeria	14	36,9017	7,2906	2010	1	1	ISM, 2010
THA	Wady Thallet, Tataouine	Tunisia	303	32,8600	10,3700	1992	1	1	E.Schultz (ISM), 1992
ZIA	Wady Ziatine (alder swamp)	Tunisia	10	37,1892	9,2133	2010	1	1	ISM, 2010

Table 3. Occurrence of Characeae species at the localities listed in Table 2

			C.aspera	*C.braunii*	*C.canescens*	*C.connivens*	*C.galtioides*	*C.globularis*	*C.imperfecta*	*C.oedophylla*	*C.vulgaris subsp. gymno.*	*C.vulgaris subsp. vulgaris*	*L.papulosum*	*L.succinctum*	*N.flexxilis*	*N.gracilis*	*N.mucronata*	*N.opaca*	*N.translucens*	*T.glomerata*	*T.hispanica*	*Richness*
BOU	Boujdayem	Morocco																x				1
BS	Ponds of Ben Slimane	Morocco		x		x						x				x		x	x			6
CHAO	Ponds of Chaouia	Morocco										x							x			2
DAY	Dayla	Morocco						x								x		x				3
DWA	Dwahriia (iron mine)	Tunisia				x									x					x		3
EGO	El Gourea	Tunisia									x											1
GAM	Gammarth – brackish pond	Tunisia	x																		x	2
GGT	Garâa Guetma	Tunisia																x	x			2
GUE	Guetma	Tunisia				x				x		x						x		x		5
HAM	Hammare	Morocco							x													1
HEM	Hank el Menzel	Tunisia											x									1
ICHR	Ichkeul – stream	Tunisia										x										1
LAT	Lake Tonga	Algeria																x				1
MA20	Pond Middle-Atlas 20	Morocco										x										1
MARZ	Marzine	Morocco																x				1
MAZ	El Mazarâa	Algeria																x	x			2
MCH	Majen Choucha	Tunisia				x												x	x			3
MGT	Majen el Gtatii	Tunisia																	x			1
MMA	Majen el Ma	Tunisia																	x			1
MOZ	Majen el Ouez	Algeria		x		x												x	x			4
MZO	M'Zouka	Morocco																x				1
NEFZ	Dam of Nefza	Tunisia						x				x										2
NOUN	Wady Noun	Morocco												x								1
OAY	Wady Oulay Ayed	Tunisia																x				1
RIF-S7	Temporary pond S7	Morocco																x	x			2
SBR	Sidi Boughaba	Morocco	x		x		x						x									4
SEGU	Pond 1, Seguedla	Morocco				x																1
SEJE	Garâa Sejenane	Tunisia		x		x				x		x						x				5
SER	Cap Serrat	Tunisia						x				x					x	x	x			5
SFL	Sidi Freitis	Algeria																x	x			2
THA	Wady Thallet, Tataouine	Tunisia						x			x											2
ZIA	Wady Ziatine (alder swamp)	Tunisia										x										1

the axis diameter becoming denser towards the top of the plants. Stipulodes in 2-tiers (two pairs per branchlet) of the same length, thin and acute, well developed. Whorls composed of 8-10 branchlets (phylloides), stiff and short (± 1 cm). Branchlets composed of 6-8 segments, the 2-3 lower ones bearing gametangia (Figs 16-17). Branchlets entirely corticated with the exception of the ultimate cell, which is naked. Bract cells present on all nodes of the branchlets forming a crown of short and acute cells (Figs 16-17). The spine cells are usually single but plants with fasciculate spine cells can occasionally be distinguished as var. *curta*.

Reproduction. Dioecious species. Antheridia 400-600 µm in diameter (Fig. 17); oogonia small to ± 500 µm in height (Fig. 16). Male plants develop earlier than female plants, which corresponds to a phenological time lag. The species shows sexual dimorphism: female plants are dark green with dense close whorls on which the oogonia are difficult to detect and male plants show big antheridia. The sex ratio of the species is very variable among populations. Certain populations appear to have nearly exclusively female plants whereas others appear to contain mostly male plants. In permanent water, the species remains often sterile and reproduces vegetatively, by means of globular bulbils located on rhizoids.

Ecology. Species typical of slightly brackish temporary wetlands (6-8 g/l) but can also develop in freshwater, where it can be found up to 2000 m above sea level.

Distribution. Subcosmopolitan species present in North America, North Africa, Asia, and Europe. Relatively common in countries of the Maghreb (59 localities from 0 to 2100 m a.s.l.; Appendix 1), although recently it has only been observed in Morocco (Elkhiati, 1995), in North-Eastern Algeria (Zouaïdia *et al.*, 2015) and in North-Western Tunisia. Relatively frequent in coastal ponds and marshes of the Maghreb, as well as in temporary ponds of the Middle Atlas (Morocco).

Chara baltica Bruz. **Fig. 18**

Description. Medium-sized plant (20-40 cm) that is very stiff due to strong incrustation (contrary to the plants from the Baltic region). Cortex diplostichous isostichous in the basal part but tylacanthous towards apex. Solitary spine cells shorter or as long as axis diameter, distant from each other on the lower internodes. Stipulodes in 2 tiers, short, obtuse. Very dense whorls composed of 8-10 branchlets, about 2 cm long, bent towards apex, often strongly incrusted (like concrete). Branchlets composed of 3-4 (5) corticated segments followed by 2-3 acorticated cells. Depending on salinity, the penultimate, naked segment can be elongated and inflated (Fig. 18). Bract cells all developed with anteriors (inner) that are longer than the posteriors.

Reproduction. Monoecious species. Antheridia and oogonia are solitary and appear to be small (0.5 mm) compared to plant size and the length of the bract cells (Fig. 18).

Ecology. Typical brackish water species growing in permanent or temporary ponds with 6-8 (12) g/l salinity. The species also occurs in freshwater lakes up to 2000 m a.s.l. When the sediment remains wet, it can regenerate from the spherical bulbils on rhizoids.

Distribution. Species covers disjointed area: Northern Europe (Baltic region) and Mediterranean region. Present in the 3 countries of the Maghreb, especially Morocco and Tunisia (29 localities from 1 to 2180 m a.s.l.; Appendix 2). In Morocco, it was repeatedly observed in mountain lakes of the Middle Atlas and High Atlas. In Lake Tafraout n'Oura (High-Atlas), the highest point at which it was found, it is associated

with *Chara canescens* (Elkhiati, 1995). The surprising presence of these two salt-tolerant species in a freshwater mountain lake could be related to the very mineralized waters, already noted by Gauthier-Lièvre (1930) who also observed *Juncus maritimus* and *Triglochin palustris* in the same site. In Algeria, it was mentioned only in 2 stations (1839, 1841) that are both located in the El-Kala National Park and has not been found again recently despite new exploration (Zouaïdia *et al.*, 2015).

Chara braunii Gmel. **Fig. 19**

= *Charopsis coronata* (Ziz.) A.Br.

Description. Small, rather bushy plant that is 10-20 cm high. Cortex absent, spine cells absent. Stipulodes in a single row 1 per branchlet, in alternate positions. Whorls composed of 6-10 branchlets. Branchlets ecorticated are about as long as the internodes. Bract cells (4-6) are small, tapered, developed on all nodes and on the top of the branchlets, which show 3-6 very small cells (mucrons) (Fig. 19). The main characteristic of *C. braunii* is the presence of only one row of stipulodes. Due to the absence of cortication both on the axis and the branchlets, the plant appears glabrous. However, banded incrustation occurs under high light conditions.

Reproduction. Monoecious species, usually bearing abundant, relatively small gametangia (Fig. 19); geminate or triplate oogonia are frequent. The coronula cells typically taper to a point. *C. braunii* never forms gyrogonites (calcified oospores).

Ecology. C. braunii develops mainly in shallow water (< 1 m) and prefers oligohaline freshwater with a low ionic charge (neutral pH). In calcareous water, it forms banded incrustations in the form of white rings, visible by the alternance at the mm-scale of white and green zones on axes. *C. braunii* tolerates regular drying out of waterbodies but when the substrate remains wet, it can regenerate from the lowest nodes of ancient plants. It is frequent in carp ponds and rice fields (Soulié-Märsche & Vautier, 2004), and in cultivated temporary ponds (L. Rhazi, Table 2).

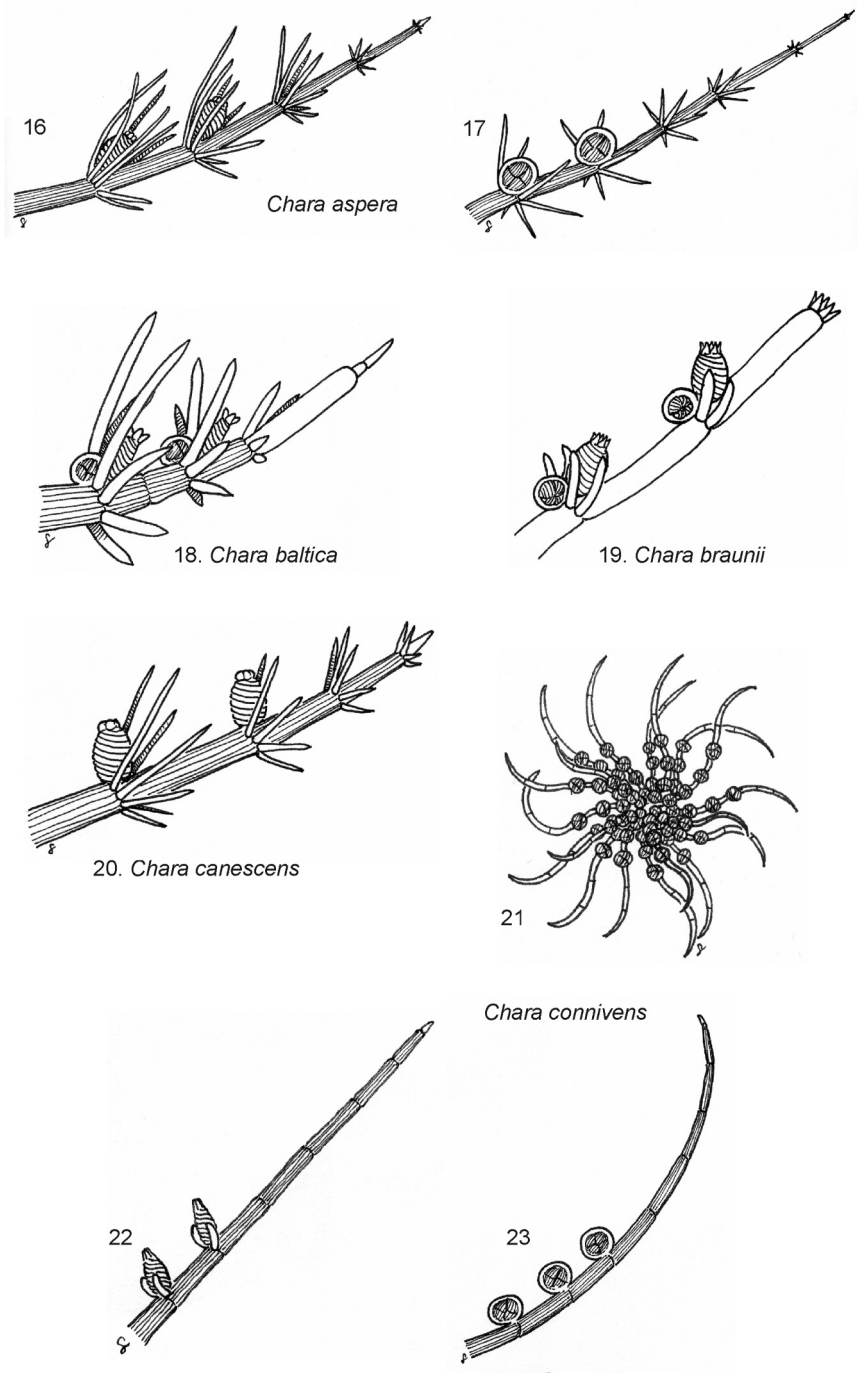
Distribution. Cosmopolitan species widespread in the Northern Hemisphere and relatively rare in countries in the Maghreb (11 localities from 3 to 295 m a.s.l.; Appendix 3). Formerly known in Algeria (8 sites reported between 1839 and 1934), and seen again in 2009 and 2012 in the National Park of El-Kala (Zouaïdia *et al.*, 2015). Recently discovered in Tunisia (Garâa Sejenane, 2007; Rouissi *et al.*, 2016) and in Morocco (plateau de Benslimane, 2013; L. Rhazi, Table 2).

Chara canescens Desv. & Lois. **Fig. 20**

= *C. crinita* Wallr.

Description. Plant erect, 20-30 cm high, appear very spiny due to numerous spine cells all along the axis. Cortex haplostichous. The spine cells acute, grouped 2-3 (fasciculate), form clusters as long or longer than the diameter of axis. Stipulodes in 2 tiers, both upper and lower row elongated and acuminate. Whorls composed of 6-10 branchlets that are distinctly distant from each other, separated by internodes of about the same length. Branchlets show 4-5 corticated segments followed by a small ultimate cell (Fig. 20). Bract cells acuminate, well developed, form a crown around the nodes of the branchlets, thus adding to the spiny appearance of the plant.

Reproduction. Ideally, *C. canescens* is dioecious. However, it is the only species of Characeae capable of developing numerous ripe oospores without fecundation by antheridial sperm (parthenogenetic reproduction). These black oospores never calcify. Most of the finds from Western Europe provided populations composed exclusively of female plants. Careful investigation of sites with *C. canescens* should



Figs 16-23. Morphology of branchlets and bract cells. **16-17.** *Chara aspera*: **16.** Branchlet of a female plant, **17.** Branchlet of a male plant; **18.** *Chara baltica*; **19.** *Chara braunii*; **20.** *Chara canescens*, branchlet of a female plant; **21-23.** *Chara connivens*: **21.** View down on an apex of male plant with very dense whorls with antheridia, **22.** Branchlet of a female plant, **23.** Branchlet of a male plant.

be undertaken, as rare male plants may be discovered among populations as was the case in the dense Characean meadow at Sidi Boughaba (Morocco) where male individuals constituted 28% of the population (L. Rhazi & P. Grillas, Table 2). Isolated male plants were also mentioned in Spain (Comelles, 1986).

Ecology. Typical species of low saline, brackish environments growing in shallow water (0-1 m). *C. canescens* is generally found near the coast or in brackish inland waterbodies.

Distribution. Subcosmopolitan species widespread in the northern hemisphere. Very rare in the Maghreb, where it occurs only in Algeria and Morocco (6 localities from 13 to 2180 m a.s.l.; Appendix 4). In Algeria, it has been collected in only 2 stations near Annaba (1847, 1930) and from the Saharan oasis El Goléa (1902, 1925). In Morocco, 2 previous mentions (Agdal Basin, 1920; Dayet er Roumi, 1952 not seen again in 1973) and 2 recent mentions (Tafraout n'Oura, where it has been known since 1920, and Sidi Boughaba, where it has been known since 1952). It remains abundant in the latter site, especially in its southern part, where it is mixed with *C. aspera* (L. Rhazi & P. Grillas, Table 2).

Chara connivens Salzm. *ex* A.Br. **Figs 21-23**

Chara connivens is easily detected in the field thanks to the very large red antheridia that is visible on male plants. The species displays strong sexual dimorphism especially with regard to the morphology of the branchlets, which are not incurved on the female plants.

Description. Upright medium size plant, 20-40 cm high. Cortex triplostichous, isostichous. Spine cells are absent or reduced to tiny dark green warts. Stipulodes developed as small dots, hardly visible. Whorls show 6-10 branchlets. The sterile whorls in the lower part are distant from each other, the fertile ones are more condensed towards apex. Branchlets are composed of 8-11 segments, totally corticated except the ultimate acute tip (Figs 21-23). Male plants typically show incurved branchlets (connivent) (Fig. 23), whereas female plant branchlets are stiff (Fig. 22). Bract cells are only developed on fertile nodes and present a different morphology: on male plants, they are very short while on female plants they are as long as the height of the oogonium.

Reproduction. Dioecious species. Gametangia usually solitary: Antheridia big (0.6-1.0 mm) (Fig. 22), oogonia up to 1 mm high including the coronula (c. 200 µm) of triangular shape (strongly connivent) (Fig. 23). Ripe plants show large black oospores, which calcify to form gyrogonites. *C. connivens* marks a time lag between the development of male and female plants, with male plants growing earlier in the year. This may render the species vulnerable, as vegetative reproduction by bulbils is unknown.

Ecology. Species of shallow (1-2 m) freshwater, tolerating low salinity (1-5 g/l), frequent in temporary habitats with long hydroperiod.

Distribution. Species discovered in Morocco in 1806 by P. Salzmann (Feldmann, 1946) essentially known in the Mediterranean area. Frequent in Spain and Portugal but rare in southern France (Soulié-Märsche, 2003; Mouronval *et al.*, 2015). Also known in northern Europe (Germany, Netherlands), where it is found in isolated sites and considered to be introduced (Luther, 1979). Frequent in Maghreb (68 localities from 0 to 1050 m a.s.l.; Appendix 5), in particular in the Rif and on the Atlantic coast (Benslimane plateau) of Morocco, in Northeast Algeria (region of Annaba) and in North Tunisia.

Chara contraria A.Br. *ex* Kütz. **Fig. 24**

Description. Plant similar to *C. vulgaris,* from which it differs only by the tylacanthous cortication of the axis. However, the tylacanthous arrangement of the cortex appears mostly on the upper whorls (near the apex) and needs close examination with a binocular microscope. The spine cells form small dark green warts on the producing rows of the axis. Stipulodes in 2 tiers, 2 pairs per branchlet, inconspicuous. Slender whorls composed of 6-9 branchlets. Branchlets form a line of 4-7 segments; the 2-3 terminal branchlets are ecorticated, and usually shorter than in *C. vulgaris* (Fig. 24), *i.e.* the 2-3 ecorticated end-cells represent only a third the length of the branchlet compared to nearly or even more than the half the length of the branchlets in *C. vulgaris*. Anterior (adaxial) bract cells are slightly longer than the oogonium; posteriors papillate.

Reproduction. Monoecious species (Fig. 24). Gametangia conjoined, solitary. Antheridia up to 400 µm in diameter. The oogonia, from 0.7 to 1.0 mm high, are larger than those of *C. vulgaris* (usually 500-800 µm).

Ecology. Species found in various environments, but prefers permanent, meso- to oligotrophic, calcareous water. Can reach depths of 20 m in lakes where it develops long, generally isostichous internodes.

Distribution. Cosmopolitan species mainly distributed in Europe and North America, but rather rare in the Mediterranean region. Infrequent in Maghreb (26 localities from 5 to 2090 m a.s.l.; Appendix 6), where it has only been observed recently in Morocco, mainly in Middle-Atlas (Elkhiati, 1995). Several ancient mentions (prior to 1934) in Algeria, and a unique Tunisian locality (Chenini, at wadi Gabès, 1973) were recorded.

Note. This taxon is close to *C. vulgaris* and has not always been distinguished. For instance, Corillion (1975, p. 82) classified the species within a "complex of taxa" affiliated to *C. vulgaris*. Cirujano *et al.* (2008) following Wood & Imahori (1965) consider it as *C. vulgaris* var. *contraria*.

Chara fragifera Dur. **Figs 26-27**

Description. Small, delicate plant, 10-30 cm high, not incrusted thus flexible. Cortex triplostichous. Spine cells absent. Stipulodes developed as small warts, inconspicuous. Whorls composed of 6-9 branchlets, as long as the internodes of the axis (up to 5 cm long) (Figs 26-27), smooth, undulating in the water. Branchlets corticated except for the ultimate tip. Rudimentary bract cells quasi absent on male plants, less than half the length of the oogonium on female nodes.

Reproduction. Dioecious species (Figs 26-27), scarcely fertile, able to reproduce vegetatively by particular, compound bulbils resembling white raspberries on the rhizoids that develop numerous new sprouts.

Ecology. Oligotrophic species in clear, permanent, shallow water (± 1 m) (Krause, 1997) where it reproduces mainly through its particular bulbils. Often associated with *Nitella* spp.

Distribution. European species with a Mediterranean-Atlantic distribution, known from a few localities near the Atlantic coast and from one single site in Southern France. Very rare in Maghreb, where it is only present in Algeria and Tunisia (4 localities from 3 and 988 m a.s.l.; Appendix 7). It has not been seen for more than a century, which can be attributed either to the lack of investigations or to wetland decline. In Algeria, it was mentioned in 1839 and 1840 in El-Kala region

where it has not been found again during recent investigations (Zouaïdia *et al.*, 2015), and in Chott Khreider (1902). In Tunisia, it was only known at the site of Sidi Boul Baba, close to Gabès (1854).

Chara galioides DC. **Figs 28-29**

incl. *C. duriaei* A.Br.

Description. Plant rather tall (20-40 cm) with robust axis (± 1 mm). Cortex triplostichous. Long internodes separate the whorls, especially on male plants. Spine cells solitary, rare and dispersed in the lower part of the plant, relatively dense on the internodes close to the apex. Stipulodes in 2 tiers, well developed but remaining short. Whorls composed of 6-8 branchlets, often strongly incurved towards the apex. Branchlets entirely corticated, except for the ultimate cell (Figs 28-29). Bract cells are very short on male plants (Fig. 28), a little longer on female nodes.

Reproduction. Dioecious species. Antheridia very big and obvious (0.8-1.1 mm) (Fig. 28). The female plants resemble *C. aspera*. However, in contrast with *C. aspera*, *C. galioides* does not develop bulbils

Ecology. Typical brackish-water species, developing in higher salinity (12-15 g/l) than *C. aspera*. *C. galioides* is thermophilous and develops in shallow, often temporary wetlands (Flor-Arnau *et al.*, 2006). The longer axis and the strong curvature of branchlets, typical for *C. galioides* compared to *C. aspera*, seem to be an adaptative response to strong vertical light, as observed in other *Chara* species (Schneider *et al.*, 2015b).

Distribution. Mediterranean species with a few populations on the French Atlantic coast (Corillion, 1952). Infrequent in the Maghreb (17 localities from 0 to 1050 m a.s.l.; Appendix 8). Recorded again since 1980 in Algeria and Morocco only, located mainly near coasts, with the exception of the Aguelmane Sefrou that is located at 1050 m a.s.l. in the Middle Atlas, Morocco (Guerlesquin 1974).

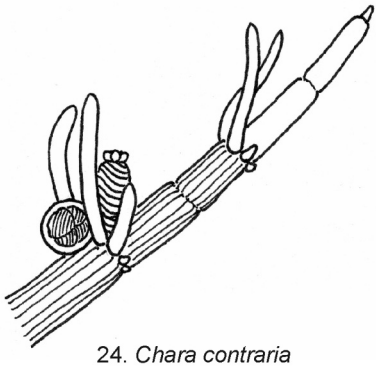
Note. The status of *C. galioides* as a separate species from *C. aspera* has been questioned on many occasions and some uncertainties still persist (Hy, 1913; Corillion, 1957, p. 234). The plant is roughly identical to *C. aspera,* though by definition the distinction is made on the basis of the the diameter of the antheridia: > 600 µm to 1 mm in *C. galioides* against < 600 µm in *C. aspera*. However, both taxa may grow together in the same site and the diameters of the antheridia may overlap (Bonis *et al.*, 1993). In this case, the male plants of *C. galioides* prove more robust and its antheridia more obvious than those of *C. aspera*. The female plants cannot be distinguished based on morphology.

Chara globularis Thuill. **Fig. 25**

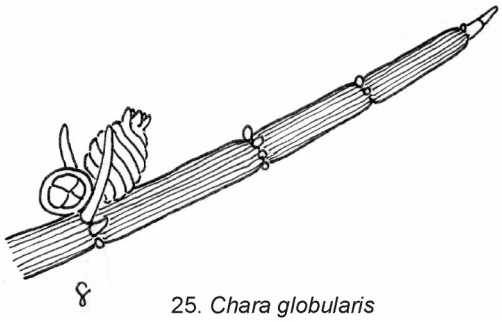
= *C. fragilis* Desv., *C. mauretanica* Feldm.

Description. Plant 20-50 cm high forming delicate, smooth, flexible thalli; bright green in color. Plant usually not or only slightly incrusted and mostly devoid of epiphytes or filamentous algae. Cortex triplostichous. Spine cells absent. Stipulodes represented by small round cells. Whorls are rather distant from each other, covering less than half of the internodes. Since the plants are usually very clean, the cortical

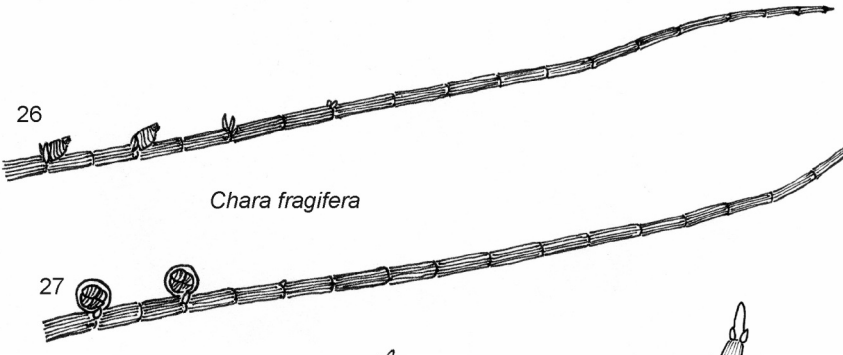
Figs 24-31. Morphology of branchlets and bract cells. **24.** *Chara contraria*; **25.** *Chara globularis*; **26-27.** *Chara fragifera*: **26.** Branchlet of a female plant, **27.** Branchlet of a male plant; **28-29.** *Chara galioides*: **28.** Branchlet of a male plant, **29.** Branchlet of a female plant; **30-31.** *Chara hispida*: **30.** Branchlet, **31.** Fasciculate spine cells. ▶

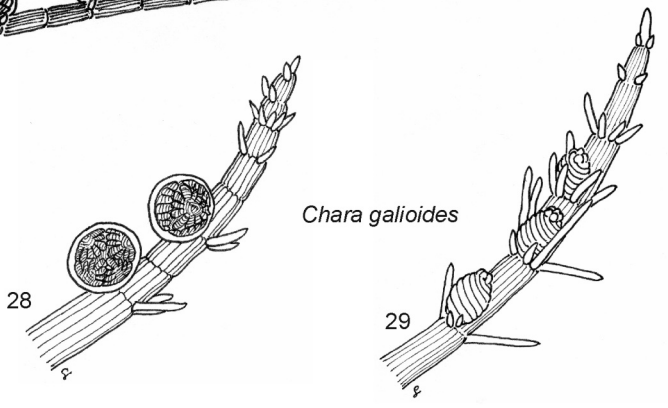


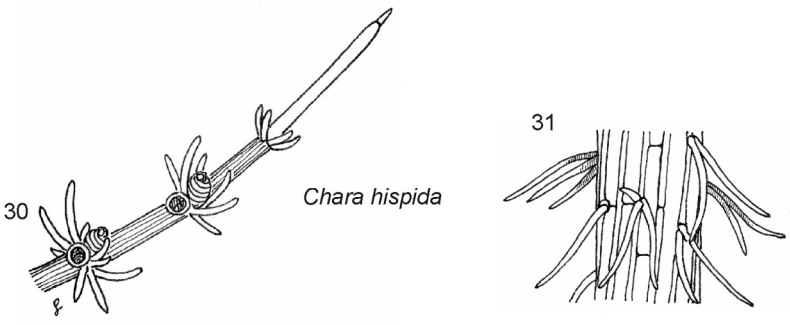
24. *Chara contraria*



25. *Chara globularis*







tubes appear as numerous striae on the internodes. Whorls are short and stiff (like the needles of a pine tree) with 7-9 branchlets forming an angle of about 45° towards the apex. Branchlets composed of 5-6 corticated segments followed by 1-2 very short cells; ultimate tip acuminate (Fig. 25). Bract cells only present on fertile nodes: anteriors short, not longer than the oogonial height; posteriors rudimentary, wart-like, inconspicuous (Fig. 25). Sterile nodes of branchlets never show bract cells (seeming smooth).

Reproduction. Monoecious species. Gametangia regularly formed on the 1-3 lower branchlet nodes. Small antheridia (c. 300 µm); rather large oogonia (700-800 µm) bearing a large coronula.

Ecology. Freshwater species, fructifying later than *C. vulgaris*. As frequent in temporary as in permanent bodies of water (ponds and lake shores), tolerating meso- to eutrophic waters.

Distribution. Cosmopolitan species mainly distributed in the North Hemisphere. After *C. vulgaris*, it is the most frequent species in Europe. Also very frequent in the Maghreb (53 localities from 0 to 2252 m a.s.l.; Appendix 9), but particularly abundant in the Middle Atlas and northern Morocco, Northeastern Algeria and Northern Tunisia.

Chara hispida L. **Figs 30-31**

incl. *C. hispida* var. *major* (Hartmann) Wood, *C. major* Vaillant

Description. Big, robust plant (axis 1-1.3 mm); its height may exceed 1 m depending on water depth; usually heavily incrusted. Cortex diplostichous isostichous on most of the thallus, aulacanthous towards apex. Spine cells grouped by 2-3 (fasciculate) emerging from the furrows on the internodes. Spine cells rather long, delicate and acuminate, pointing up and down (Fig. 31). On the upper internodes, the spine cells are very dense ("hispid") and visible with the naked eye whereas they are sparse or dehiscent on the older parts of the plant. Stipulodes are present in 2 tiers, two pairs below each branchlet, acuminate, similar to the spine cells. Whorls formed by 8-10 long corticated branchlets (c. 5 cm long) that are spread out and culminate in an acuminate naked tip. Bract cells form a crown around the branchlet nodes (verticillate): anterior bracts long or longer than the oogonium; posterior bracts short and rather blunt.

Reproduction. Monoecious species (Fig. 30). Medium-sized antheridia (400-600 µm) barely visible on these large plants. Large oogonia (> 1000 µm) that is often coated in a calcite incrustation containing the calcified gyrogonites after fertilisation.

Ecology. Freshwater species sometimes able to tolerate calcareous, low saline water (4 g/l). It generally develops in greater depths (for instance, 2-9 m at Tigalmamine, in the Middle Atlas, Morocco; Soulié-Märsche *et al.*, 2008). The deep-growing plants (20 m, Cirujano *et al.* 2008) are perennial and often sterile.

Distribution. Euro-Siberian and Mediterranean species, rare in the Maghreb (13 localities from 22 to 2180 m a.s.l.; Appendix 10). The 3 mentions in Tunisia and Algeria date prior to 1902. *C. hispida* seems to be a little more abundant in Morocco (especially in the Middle Atlas), where it is known from 10 sites, including a fossil record (Afourgagh, Middle-Atlas; Détriché *et al.* 2009) and 3 previous observations (Wady Souss, 1934; Tafraout n'Oura, 1934; R. Maire in Feldmann 1946).

Note. Here we characterise *C. hispida* using Krause (1997), Gregor *et al.* (2014) and Schubert *et al.* (2016), who define this species as isostichous aulacanthous. Corillion (1975) considered that this morphology defined the species *C. major* and restricted the name of *C. hispida* to plants with tylacanthous cortex. Although other authors

still rank *C. major* as a species (Bailly & Schaefer, 2010) or a variety (Mouronval *et al.*, 2015), these plants with grouped (fasciculate) spine cells have isostichous cortex most of the time, making it unrealistic to split them into two different taxa.

Chara imperfecta A.Br. *in* Dur. **Figs 32-33**

Description. Small plant 10-20 cm high. Cortex haplostichous disjoined, meaning the cortical tubes of the internodes alternate with naked (ecorticated) spaces. The axis appears like a vertical succession of of light, grey-green striae (1) (representing the incrusted cortical cells) and (2) shiny dark green (the ecorticated spaces). Spine cells absent. Stipulodes rudimentary. Whorls composed of 8-10 short branchlets separated by long internodes. Branchlets totally ecorticated, (exceptionally, traces of cortication were mentioned on the lowermost segment (Guerlesquin, 1962). Branchlets show a rounded tip, thus are unlike most species of *Chara* having an acuminate terminal cell (Figs 32-33). Bract cells of male and female plants are different (sexual dimorphism). The branchlet nodes of male plants show 2-4 short bract cells (Fig. 32). The female plants have 6-8 (3-4 pairs) bract cells positioned as a bundle in front and on the side of the oogonium.

Reproduction. Dioecious species. Male plants are easily visible, whereas the female plants remain inconspicuous as the oogonia are hidden beyond their numerous bract cells. Large antheridia (600-750 µm) mostly geminate (Fig. 32). Oogonia geminate or triplate arranged horizontally (side by side) on the branchlet (Fig. 33).

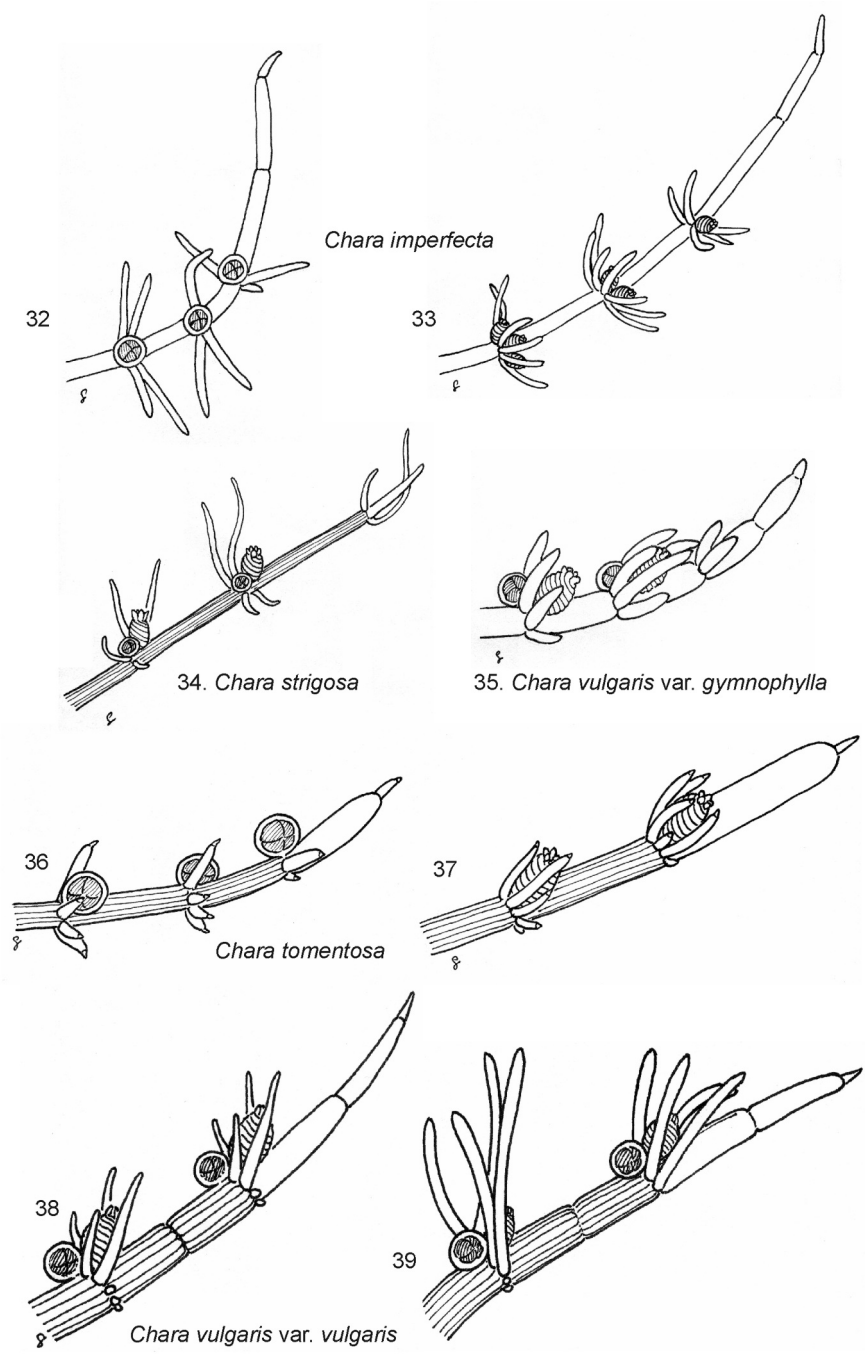
Ecology. Freshwater species developing in both stagnant and running shallow waters. Usually strongly incrusted in calcareous environments; development in early spring (as early as February).

Distribution. Western Mediterranean species discovered in 1845 by M.C. Durieu in Algeria. Very rare and strictly restricted to the Western Mediterranean region. Outside the Maghreb it is known from spring basins at 1600 m a.s.l. in the Iberian Peninsula (Cirujano & Medina, 1994) and in localities recently discovered in southern France (Soulié-Märsche, 2003; Mouronval *et al.*, 2015). Very rare in the Maghreb, where it is only present in Algeria and Morocco (5 localities from 13 to 1390 m a.s.l.; Appendix 3). Not seen for more than a century in Algeria (Tlemcen, 1842; Beni Snouss, 1902). In Morocco, it was collected very recently in the Rif (Merja Hammare, 2010; S.D. Muller, Table 2), and in Lake Sidi Boughaba on the North Atlantic coast, but has not been seen again since 1975 (Guerlesquin, 1978).

Chara oedophylla Feldm. **Figs 40-45**

At a first glance, *Chara oedophylla* could seem to be dioecious because of its remarkable large antheridia, whereas the oogonia are hidden behind large, swollen bract cells. Bract cells inflated, hence the *derivatio nominis* “edemised”. The particular feature of *C. oedophylla* is indeed its sejoined gametangia.

Description. Robust plant 15-30 (60) cm high, often heavily incrusted. Axis diameter 0.8-1.0 mm. Cortex diplostichous, aulacanthous. Spine cells and stipulodes similar to *Chara vulgaris*. Whorls composed of 6-8 branchlets covering more than half the internode of the axis, close to each other near the apex where the internodes become shorter. Branchlets composed of 4-5 corticated segments, followed by one inflated ecorticated cell and a very short ecorticated distal tip. Branchlets mostly incurved (Fig. 44). Bract cells develop differently on male and female plants: the antheridia are accompanied by two short bract cells, not longer than the diameter of the antheridia; oogonia are flanked by a fan of 3-4 pairs of large or relatively large, swollen bract cells (Fig. 42).



Figs 32-39. Morphology of branchlets and bract cells. **32-33.** *Chara imperfecta*: **32.** Branchlet of a male plant, **33.** Branchlet of a female plant; **34.** *Chara strigosa*; **35.** *Chara vulgaris* var. *gymnophylla*; **36-37.** *Chara tomentosa*: **36.** Branchlet of a male plant; **37.** Branchlet of a female plant; **38-39.** *Chara vulgaris* var. *vulgaris*: **38.** Branchlet nodes with short bract cells, **39.** Branchlet nodes with long bract cells.

Reproduction. Monoecious species with sejoined gametangia: antheridia and oogonia developed on different nodes of the branchlets. Antheridia rather big (600-800 µm), mostly solitary; oogonia often grouped by 2-3(4) at the same node, showing a particular vertical arrangement on the branchlet and hidden by inflated bract cells (Fig. 42). The brown oospore calcifies and develops the gyrogonite.

Ecology. C. oedophylla is an annual species growing early in the year in shallow, temporary freshwater ponds and at the edge of semi-permanent lakes (Soulié-Märsche, 2003; Mouronval *et al.*, 2015). Some of the Spanish localities were slightly saline (Comelles, 1981; Cirujano *et al.*, 2008).

Distribution. First described by Feldmann (1945, 1946) from a collection by L. Gauthier-Lièvre in Northern Tunisia (Wadi Tinja, east of Lake Ichkeul, 1926). Distribution restricted to the Western Mediterranean, where it is only known from about 10 localities, in Spain (in 5 provinces), in Southern France (2 sites in Var; Mouronval *et al.*, 2015) and in North Africa (4 localities from 2 and 100 m a.s.l.; Appendix 4). It was regularly found since 2007 in its type region, in the vicinity of Sejenane (2007-2014) (Muller *et al.*, 2008; Daoud-Bouattour *et al.*, 2009; Rouissi *et al.*, 2016) and has been mentioned once in Morocco (Allal-Tazi, 1960).

Note. The taxonomical position of this taxon created by Feldmann (1945) is controversial. Wood (1962) considers it as a simple form of *C. vulgaris*, but Wood & Imahori (1965, p. 115) specify that the only specimen at their disposal seems to be inadequate and that the examinated plants were not mature. Unfortunately, the diagnostic features of this taxon refer precisely to the sejoined position of reproductive organs. Corillion (1957) gives to it the status of subspecies, and considers it as related to the Italian species *C. rabenhorstii* A.Br. Thereafter, several authors reported and described *C. oedophylla* in details, under different taxonomical ranks: as *C. vulgaris* var. *oedophylla* (Comelles, 1981; Cirujano *et al.*, 2008; Mouronval *et al.*, 2015) or as *C. oedophylla* (Soulié-Märsche, 2003). According to Soulié-Märsche & Muller (2016), we opted here to conserve this taxon at the species level because of morphological features that appear specific (sejoined gametangia, edemised fan-like bract cells, oogonia inserted vertically) and constant, even in presence of *C. vulgaris* var. *vulgaris*.

Chara strigosa A.Br. **Fig. 34**

incl. *C. strigosa* var. *myriacantha* Trabut *ex* Maire & Werner

Description. Small, erect plant (5-15 cm high). Cortex irregularly diplostichous to triplostichous. Internodes approximately of same length all along the axis. Numerous fasciculate (2-5) spine cells cover the axis. Stipulodes in 2 tiers, the lower ones short. Whorls composed of 6-8(10) branchlets, regularly spaced. Branchlets short and stiff, composed of 7-8 segments, entirely corticated, except a very short ultimate tip (Fig. 34). Bract cells developed on all branchlet nodes, adaxial (anteriors) longer than abaxial (posterior) ones.

Reproduction. Monoecious species but rarely fructified when growing in permanent water. Antheridia small (300 µm); oogonia 800-900 µm high; oospores strongly calcified forming the gyrogonite (Krause, 1997).

Ecology. Species of cold, clear and calcium-rich water, persisting under winter ice in mountain lakes of the Northern Alps.

Distribution. Arctic-Alpine species, widespread in northern Europe (Scandinavia) and the northern Alps. Very rare in Maghreb, where it is known from one single site, in the Moroccan Middle-Atlas: the Aguelmane Sidi Ali, at 2090 m a.s.l. (Maire & Werner, 1934; Gayral, 1954; Feldmann, 1946; Guerlesquin, 1974, 1978; Appendix 7).

Chara tomentosa L. **Figs 36-37**

= *C. ceratophylla* Wallr., *C. disjuncta* (Nordst.) Trabut *ex* Feldmann

Chara tomentosa, the type species of the genus *Chara*, is very characteristic and easy to recognise by the reddish colour of its thallus (reminding the orange-red colour of corals) due to its large antheridia visible from a distance.

Description. Robust plant exceeding 1.2 m in height; as a rule heavily incrusted; diameter of axis > 1 mm. Cortex diplostichous, usually clearly tylacanthous. Whorls ideally separated by internodes as twice as long as the branchlets. Spine cells solitary or grouped by 2-3, present all along the axis on the protruding cortical cells (tylacanthous), well developed but shorter than the diameter of the axis. Stipulodes in 2 tiers, 2 pairs per branchlet, well developed. Whorls composed of 6-7 branchlets. Branchlets show 3-4 corticated segments followed by a long ecorticated cell, which is typically inflated and topped by an ultimate tip. Bract cells large at the base but acuminate, up to 2 mm long, forming a whorl around the fertile branchlet nodes (Figs 36-37).

Reproduction. Dioecious species. Big antheridia (diameter 0.9-1.2 mm) (Fig. 36) visible from the distance; oogonia c. 1 mm high, bearing a large coronula (Fig. 37). The sex-ratio of this species is very variable from one site to another; populations with abundant male plants are most frequent. At many localities, however, the populations are scarcely fructified and reproduce from sprouts emerging from the lower nodes of ancient plants.

Ecology. Species of freshwater to slightly saline water, growing in lakes and large permanent ponds. Its optimal depth of development is between 2 and 4 m, but it can occur down to 30 m (Krause, 1997) where it remains sterile.

Distribution. Eurasiatic species, with distribution concentrated on the Baltic region and reaching Central Asia (Krause, 1997). In Europe, it extends as far as South Germany and into lakes of the Alps and the Balkans. Ancient mentions in America resulted from erroneous identifications (Corillion, 1957; Wood & Imahori, 1965, p. 70). Very sporadic in the Mediterranean region, and very rare in Maghreb (4 localities from 14 and 1600 m a.s.l.; Appendix 8), where it is only known in Algeria and Morocco. Not seen again for more than a century in Algeria, where it has only been mentioned once (Saïda, 1902), and for more than 60 years in Morocco, where it was known in Middle-Atlas (lake Ouiouane, 1934), Wadi Souss (1934) and Rharb plain (1952).

Note. The ancient mention of *C. tomentosa* at Wadi El Akarit, in Tunisia (coll. L.G. Seurat, in Feldmann, 1946) seems to be due to an error. More recent collections (Corillion, 1977; I. Soulié-Märsche, unpublished data) proved to be *C. vulgaris* whose ecorticated cells were strongly inflated, leading to a look similar to *C. tomentosa*. This abnormal morphology of *C. vulgaris* could be due to the salt content of Wadi El Akarit.

Chara vulgaris **L.**

C. vulgaris var. ***gymnophylla*** (A.Br.) Nym. **Fig. 35**

= *C. gymnophylla* A.Br., *C. squamosa* Desf.

Chara vulgaris is close to *Chara vulgaris* var. *vulgaris*. The distinctive characters consist in its ecorticated branchlets (sometimes just the lowermost segment corticated), and in the presence of gametangia on ecorticated segments (Fig. 35).

Description. Robust plant, heavily incrusted, usually small (± 10 cm, often only 3-5 cm), but also found exceptionally with size up to 50 cm. It has a bushy appearance due to multiple branching on the lower nodes. The plant looks very dense due to very short internodes, thus very tight whorls, suggesting a moss-like appearance (syn. *C. squamosa*, moss-like). Cortex isostichous, aulacanthous. Spine cells solitary, obtuse, and distant from each other along the internodes. Stipulodes in 2 tiers, well developed and obtuse. Whorls composed of 6-8 branchlets, typically acorticated (Fig. 35) or occasionally with one segment corticated. Whorls are flexible often with twisted branchlets. The anterior bract cells are elongated, exceeding by far the height of the oogonia and are formed even on nodes where no gametangia are present. Posterior bract cells are rudimentary.

Reproduction. Monoecious species. In contrast to the var. *vulgaris*, antheridia and oogonia develop on the nodes of ecorticated branchlets. Antheridia 400-600 µm in diameter; oogonia c. 600-800 µm high, bearing a short large coronula.

Ecology. Freshwater species, generally developing in very shallow waters (0.1-0.5 m), in temporary ponds, rivers, thermal springs or seepages of inundated meadows. It can develop practically out of water and takes then the aspect of dense moss-like cushions. It resists well to eutrophication (Zouaïdia *et al.*, 2015).

Distribution. Mediterranean taxon (Corillion, 1957), rare in Europe, where it is only known from a few stations in Italy (Bazzichelli & Abdelahad, 2009; I. Soulié-Märsche, unpublished data), in Spain (Cirujano *et al.*, 2008) and in Southern France (Mouronval *et al.*, 2015); one locality was also described in Israel (Romanov & Barinova, 2012). This variety is, in contrast, much more common in the 3 Maghreb countries (97 localities from 2 to 2174 m a.s.l.; Appendix 11). Besides, the original record, described as *C. squamosa* by R. Desfontaines in 1800, originated from Algeria.

C. vulgaris var. ***vulgaris*** **Figs 38-39**

= *C. foetida* A.Br.*;* incl. *C. boveana* A.Br., *C. crassicaulis* Schl., *C. hispidula* A.Br., *C. longibracteata* Kütz.

Chara vulgaris var. *vulgaris* is by far the most frequent over Maghreb. Mostly, it forms dense meadows and displays a characteristic smell, hence the ancient name of *Chara foetida*. The plants show a greyish-green colour, and have usually a rough touch due to heavy incrustation by calcite crystals. The presence of long bract cells, visible with the naked eye, indicates *C. vulgaris* in contrast to *C. globularis,* which has very short bract cells.

Description. Plants of very variable size (10-50 cm high) depending on water depth, with robust axis, up to 0.75 mm in diameter. Cortex diplostichous, aulacanthous, but isostichous in the lower parts where the spine cells are short to rudimentary. Spine cells near the apex are visible with a field lens. They are always solitary, rather broadly rounded and inserted in the furrows of the cortex. Stipulodes in 2-tiers, short and obtuse, forming one pair below each branchlet. The whorls of 8-10 branchlets are compact, dense and often twisted in the upper part of the plant, whereas they are more spread in the lower parts of the plant. Branchlets composed of 2-5(7) corticated segments followed by 3 long ecorticated cells plus a tiny tip (Figs 38-39). The corticated part represents about half of the length of the branchlet. Only the anterior bract cells (on the inner side, adaxial) are well developed and clearly exceed the height of the oogonium. The posterior bract cells remain as a small wart. It is noticeable that in *C. vulgaris*, the bract cells appear even on sterile nodes. Bract cells are often more than 5 times the height of the oogonium. This morphology has been distinguished as *C. vulgaris* var. *longibracteata* by several authors.

Reproduction. Monoecious species, extremely fertile (Figs 38-39). Antheridia small (250-450 µm); oogonia 500-750 µm high, covered by a short, broad coronula.

Ecology. *C. vulgaris* var *vulgaris* is an opportunistic taxon, with a great capacity of colonisation. Pioneer and ubiquitous, it is able to colonise all types of habitats, with a preference for shallow waters (< 1 m) in temporary or permanent ponds, marshes, waterholes, rivers and spring basins. Well adapted to oligohaline waters (< 5 g/l), it supports also meso- to eutrophic environments (Zouaïdia *et al.*, 2015).

Distribution. Cosmopolitan taxon, the most frequent throughout Europe, from the Polar Circle to the Mediterranean (Krause, 1997). Very common in Maghreb (229 localities from 0 to 2090 m a.s.l.; Appendix 12).

Note. Depending on the authors, *C. vulgaris* is subdivided into numerous varieties and forms. Here we only kept the var. *gymnophylla* and *oedophylla*, the later being re-established as a species. In contrast, we did not consider the var. *crassicaulis* and *longibracteata,* which appear rather to represent only ecotypes. The form *crassicaulis* is characterised by heavy calcite incrustation related to its growth in karstic springs. Due to permanent submersion, these perennial populations remain mostly sterile. The form *longibracteata* has been distinguished because of its extremely elongated bract cells (> 5 times the height of the oogonium). It occurs often in the same habitat together with *C. vulgaris* var. *vulgaris*, the type variety, and appears to be a morphotype linked to high insolation (I. Soulié-Märsche unpublished).

Chara zeylanica Klein *ex* Willd.

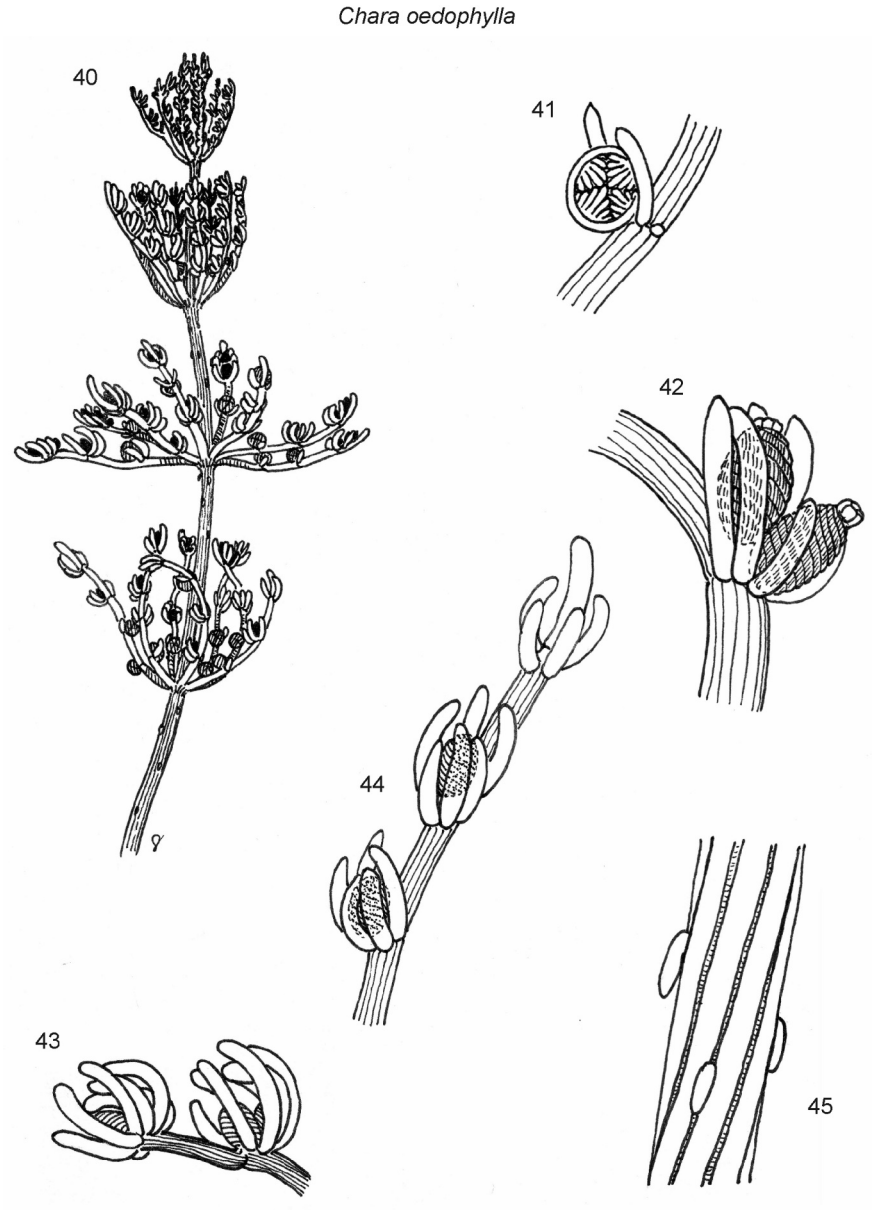
Chara zeylanica is characterised by the absence of cortex on the first (lowermost) branchlet segment, whereas the following segments are corticated. This particular feature is shared by a number of taxa, which do not occur in Europe, and represent a special section of the Characeae, the *Gymnobasalia* (meaning naked base of the branchlets).

Description. Plants erect, straight, about 30-50 cm high. Cortex regularly triplostichous isostichous. Spine cells small, sparse, absent on lower internodes. Stipulodes in 2 tiers, 2 pairs per branchlet, tapering, well developed, mostly as long as the diameter of the axis. Whorls composed of 8-12 branchlets, shorter than the internodes of the axis. Whorls are rather stiff and form an angle of *ca* 45° with the axis. Branchlets composed of 7-11 segments, the lowermost being always ecorticated. This first segment needs attention, as it can be very short. In that case, hidden by the stipulodes, it may be overlooked. The following segments are corticated and the branchlet ends with 1-2 tiny, ecorticated cells. The bract cells form a crown at the branchlet nodes (verticillate) whose length is about the height of the oogonia.

Reproduction. Monoecious species. Antheridia medium-sized (< 500 µm), characterised by the presence of 4 antheridial shields (in contrast to all other species of genus *Chara* which display 8 shields). Oogonia rather big (900-1000 µm), containing an elongated, cigar-shaped oospore inside after fertilisation.

Ecology. Species growing in permanent water (Soulié-Märsche, 1999), but fructifying only at high water temperature (± 25°C) (Corillion & Guerlesquin, 1972).

Distribution. Species of tropical and subtropical regions (Corillion, 1973). Its main populations closest to Maghreb are located in Egypt and Senegal. *C. zeylanica* was cited in Algeria by Maire (1933) in a guelta (Saharan temporary pond) of Hoggar (Appendix 2). This species is likely to appear here and there in Saharan regions.



Figs 40-45. *Chara oedophylla* (from Soulié-Märsche & Muller, 2016). **40.** Habit; **41.** Antheridium with short bract cells; **42.** Geminate oogonia; **43-44.** Branchlet with female nodes and characteristic inflated bract cells, end cell incurved; **45.** Aulacanthous cortex with short obtuse spine cells.

Lamprothamnium papulosum (Wallr.) J.Gr. **Figs 46-47**

= *Chara (Lychnothamnus) alopecuroides* A.Br.

The inverse position of the gametangia compared to *Chara,* and the 1-celled, acute, ultimate branchlet tip make the difference to *C. braunii*. *Lamprothamnium papulosum* is known to form clusters of spherical bulbils.

Description. Small plant, (3)5-15 cm high; colour bright green as a young plant, greyish when incrusted. Both axis and branchlets are ecorticated. Numerous whorls, very close to each other, led to its vernal name of "foxtail stonewort". Cortex absent. Spine cells absent. Stipulodes in 1-tiers (one per branchlet) inserted below the branchlets, well developed, acuminate, longer than the axis diameter and forming a slanting crown downwards the axis, visible with the field lens (Fig. 47). Whorls composed of 6-8 branchlets. Branchlets composed of 4-6 segments ending in an acuminate tip (Fig. 46). Each node shows a crown of 4-6 bract cells. Bract cells short and acuminate, regularly present around both fertile and sterile nodes (Fig. 46). In somewhat deep water, *L. papulosum* can grow up to 40 cm and its branchlets are more spread out, loosing its typical appearance (*e.g.* specimens found in the Rharb; M. Guerlesquin, pers. comm.).

Reproduction. Monoecious species. Antheridia 400-600 µm; oogonia 700-950 µm high. Antheridium situated above the oogonium, the latter being directed downwards (diagnostic feature of the genus (Fig. 46). The gyrogonites (calcified oospores) display a characteristic morphology allowing the distinction of *Lamprothamnium* compared to the other genera (Soulié-Märsche, 1989).

Ecology. *L. papulosum* is the most salt-tolerant species of the European and Mediterranean Characeae. It develops in coastal ponds, between-dunes ponds, ancient salt marshes, as well as salty inland waterbodies (Corillion, 1953; Guerlesquin, 1992). It likes variable-salinity habitats: it effectively needs low salinity (< 20 g/l) for germination, but can remain physiologically active and green in hypersaline waters (50 g/l). Salt content of 40 g/l nevertheless constitutes a threshold for fecundation and oospore formation (Soulié-Märsche, 1998).

Distribution. Cosmopolitan species, uncommon in Europe, where it generally grows near the coasts, from Scandinavia (Blindow & Langangen, 1995) to the Mediterranean (Mouronval *et al.*, 2015). It also colonises endoreic salt lakes, notably in Spain (Cirujano *et al.*, 2008). Although its potential habitats are poorly explored in Maghreb, it seems to be very rare (12 localities from 0 to 480 m a.s.l.; Appendix 13). The single recent locality is the Lake Sidi Boughaba, on the North Atlantic coast of Morocco (L. Rhazi, 2009; Table 2). It has also been mentioned in two other Moroccan localities, Taourirt (1930, not seen again in 1992) and the mouth of Wadi Yquem (1973, 1974). Algerian mentions are all prior to 1940, in Annaba region (1847, 1930) and Ouargla (1930). Finally, in Tunisia, *L. papulosum* is known in 5 stations: Ben Gardane (1930), Madhia (1970), Lake Ichkeul (1972), Aouinet (1973) and Hank el Menzel (1982).

Note. In Maghreb, *L. papulosum* is known as a fossil in 2 sites. In Sebkha Mellala, in Algeria, it marks a Holocene period of strong water dilution (Soulié-Märsche, 2008). In contrast, the abundance of gyrogonites in subfossil sediments of Lake Sidi Boughaba, today characterised by low salinity (5-8 g/l), reveals a period of higher salinity in late Holocene (Elkhiati *et al.*, 2004).

Lamprothamnium succinctum (A.Br. *in* Asch.) Wood **Fig. 48**

Description. Small plant, (5-10 cm high). Morphology in all points identical to *L. papulosum*, except for the presence of additional gametangia at the base of whorls (Fig. 48).

Reproduction. Monoecious species. Antheridia situated above oogonia at the same branchlet node. Additional gametangia (essentially oogonia) occur at the base of whorls. These oogonia are formed at the junction between axis and branchlets. They mostly emerge from an elongated nodal cell (stipitate) that could represent a converted stipulode, and can be directed both upwards and downwards (inside and outside the branchlet node).

Ecology. Like all other *Lamprothamnium*, *L. succinctum* prefers waterbodies with variable salinity, and grows under tropical climate, thus high temperature.

Distribution. Species of tropical origin, at the northern boundary of its distribution in South Morocco, where it was collected in two localities (Appendix 13): Khnifiss (Guerlesquin *et al.*, 1987) and Wadi Noun (Table 2). The type has been described in the Egyptian part of the Lybic Desert (Dahla Oasis; Ascherson, 1878).

Nitella capillaris (Krock.) J.Gr. & B.-W. **Figs 49-50**

= *N. capitata* (Nees) Ag.

The characteristic feature of this early-growing, dioecious species is the presence of mucus in and around the fertile heads.

Description. Delicate, slender plant, about 20-30 cm high, showing at least two secondary axes on each whorl, from the base onwards. Whorls composed of 6-9 branchlets. Sterile and fertile branchlets are quite different: the sterile ones are elongated, rather spread out and divided once; the numerous fertile whorls are condensed as "fertile heads". Branches are divided into 2-3 dactyls, where the central one is longer than the two others and appears like the continuity of the branchlet (Fig. 50). Dactyls are unicellular with an acuminate tip.

Reproduction. Dioecious species, very fertile. Gametangia grouped in dense fertile heads, present also at the base of whorls. Antheridia large (600-750 µm), solitary, in a central position in the forks (like in all *Nitella*) (Fig. 49); oogonia (400-600 µm), often grouped by 2-4 at the same fork (Fig. 50). Presence of mucilage (mucus) especially around the antheridia.

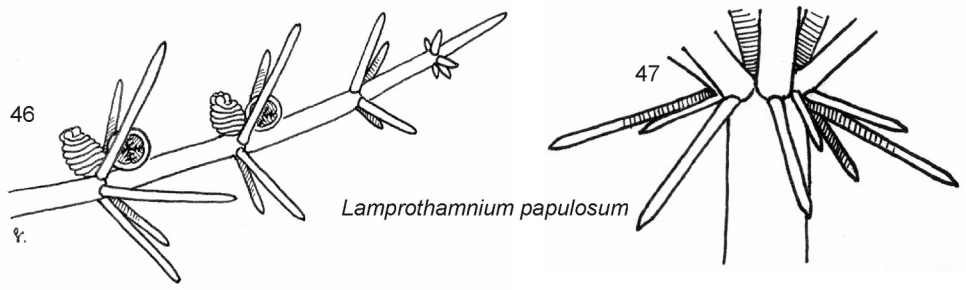
Ecology. This early growing, spring species prefers shallow waterbodies, on acid or slightly alkaline substrate, without concurrence of Spermatophytes. Strictly annual, it decays after its optimum.

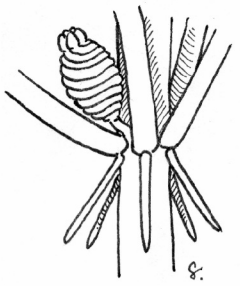
Distribution. Eurasiatic species, present in North Africa, where it is very rare (7 localities from 3 and 450 m a.s.l.; Appendix 14). It has been seen again recently only in Morocco, at Chefchaouen (Elkhiati, 1995). In Algeria, it was known in 5 sites: El-Kala National Park (notably in Lake Oubeira in 1840, where it was not found again during recent investigations; Zouaïdia *et al.*, 2015), near Oran (Djebel Santo, 1853) and near Algiers (Chaiba, 1902; Reghaia, 1902). In Tunisia, it was only known in Garâa Sejenane (Feldmann, 1946), where it was not found again recently (Rouissi *et al.*, 2016).

Nitella confervacea (Bréb.) A.Br. *ex* Leonh. **Figs 51-52**

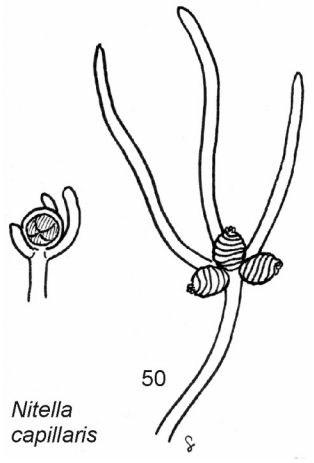
= *N. batrachosperma* (Thuill. acc. Reich.) A.Br. (cf. Gregor *et al.*, 2012)

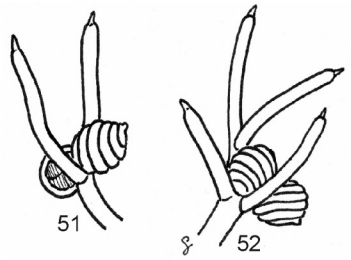
Description. Minute, delicate plant (± 5 cm high) often covered by mud and thus difficult to detect. The whorls are composed of 6-8 branchlets. Several short axes, not more than 3-5 cm high, emerge from the nodes and form a compact dome, similar to the back of a hedgehog (Krause, 1997). Sterile and fertile branchlets different (dimorphism): the sterile branchlets are elongated, spread out and divided (forked) only once; the fertile ones are short and divided twice, forming dense heads.

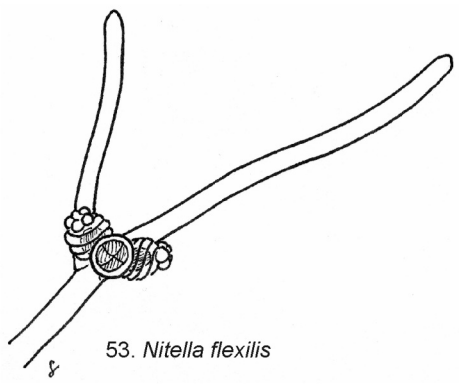




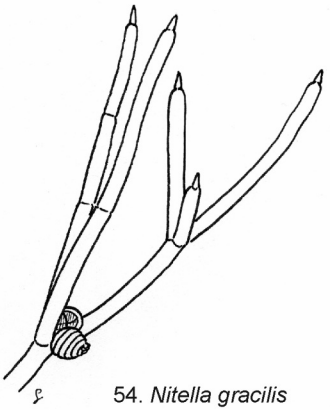
48. *Lamprothamnium succinctum*







53. *Nitella flexilis*



54. *Nitella gracilis*

Dactyls, usually 4, are composed of one elongate cell and a tiny tip (similar to the mucron of *N. mucronata*) (Figs 51-52).

Reproduction. Monoecious species. Gametangia are very small and located at the first division of the branchlets (Figs 51-52). Diameter of the antheridia is ± 200 µm (the smallest among the Characeae); oogonia about 300-400 µm high. This species fructifies late in the year (in summer to autumn).

Ecology. Species forming extended carpets in shallow waters (down to 2 m), often covered by sediment and mud making them hardly discernible. It develops in oligotrophic ponds and lakes, where it can be associated with other *Nitella*.

Distribution. Cosmopolitan species with a discontinuous area. In Europe, it is mainly concentrated in Northern and Western France, and is uncommon in the Mediterranean region. Very rare in Maghreb (3 localities from 4 to 350 m a.s.l.; Appendix 15). Not seen again since 1952 in Morocco (2 ancient mentions: Lake Hadjerin, 1910 and Dayet er Roumi, 1952), but recently discovered in the El-Kala National Park, in Algeria, in a clear freshwater pond far away from human disturbances (Zouaïdia *et al.*, 2015).

Nitella flexilis (L.) Ag. **Fig. 53**

= *N. acuminata* A.Br.

Nitella flexilis is similar to *N. opaca* in sofar the branchlets show 2 unicellular dactyls. The distinctive characters are its bigger size and the fact that it is monoecious and fructifies late in the year.

Description. Slender plant (0,5 to > 1 m high), showing usually typical banded incrustations with alternating white and green spaces on the thallus that give it a zebra look. Axis smooth with long internodes. 1-2 secondary axes at each node. Whorls composed of 6-8 branchlets, flexible and spread out. Branchlets elongated and delicate, divided only once into 2 long, unicellular dactyls whose tip is rounded blunt (like in *N. opaca*) (Fig. 53). The branchlets may lose their delicate dactyls early and thus the branchlet seems undivided (abnormal).

Reproduction. Monoecious species. Usually, each fork bears one antheridium and 1-3 oogonia directed downwards (Fig. 53). The onset of antheridia and oogonia occurs late in the season and mostly with a temporal shift, the oogonia appearing later (protandry). On young whorls, only the antheridia may be present, and may induce the error that the plants belong to a dioecious species. It is recommended to examine whorls at different ripening stages.

Ecology. *N. flexilis* prefers permanent, neutral to acid waters, on siliceous substrate, often associated to *Ranunculus* or *Myriophyllum*. It occurs in rivers with shallow, slowly moving water, lakes and peaty marshes, and forms perennial populations in deep lakes.

Distribution. Cosmopolitan species, widespread in Europe, but becoming rare in the south (Corillion, 1957). In Maghreb, it is known from one single locality in Tunisia,

◀ Figs 46-54. Morphology of branchlets, stipulodes and dactyls. **46-47.** *Lamprothamnium papulosum*: **46.** Fertile nodes with crown of bract cells, **47.** Stipulodes in 1 tier (one row); **48.** *Lamprothamnium succinctum*, oogonium at base of whorl; **49-50.** *Nitella capillaris*: **49.** Antheridium with dactyls (male plant), **50.** Female node with triplate oogonia and dactyls; **51-52.** *Nitella confervacea*: **51.** Fertile node with conjoined gametangia; **52.** Node with geminate oogonia; **53.** *Nitella flexilis*, fertile node with unicellular dactyls; **54.** *Nitella gracilis*, multicellular dactyls.

where it has been recently discovered (2008): the iron mine of Dwahriia, close to Sejenane, at 300 m a.s.l. (Table 2; Appendix 15). This record constitutes an addition to the flora of North Africa.

Nitella gracilis (Smith) Ag. **Fig. 54**

The name of *Nitella gracilis* already suggests delicate plants. The colour is shining green. *N. gracilis* is an excellent coloniser and develops even in small rain puddles given they held water for some weeks.

Description. Small, slender plant, up to 20 cm high, developing only a few delicate secondary axes. Axis smooth, with long internodes. Whorls composed of 5-6 branchlets. Branchlets divided 1-2 times ending with a bundle of 2-3 dactyls each of it presenting a series of 2-3 cells. The first (lower) cell of the dactyls is elongated followed by another shorter cell and a tiny tip (Fig. 54).

Reproduction. Monoecious species. Gametangia are produced at all forks, usually one antheridium and a single oogonium at the same node (Fig. 54). Antheridia small (300 µm); oogonia (*ca* 550 µm). The antheridia may disappear early thus suggesting the plant is dioecious.

Ecology. Calcifuge species developing in poorly mineralised waters. In Central Europe, it develops in ombrotrophic habitats, such as flooded depressions within meadows and crops, and in peatlands where it can produce very dense populations.

Distribution. Cosmopolitan species, however sparse in Europe and in very few localities around the Mediterranean (Iberian Peninsula, France, Italia). Infrequent in Maghreb (15 localities from 1 to 1300 m a.s.l.; Appendix 16), where it is known in Algeria, in the El-Kala National Park (Lake Oubeira; Zouaïdia *et al.*, 2015), and in Morocco, where it is relatively abundant in the north.

Nitella hyalina (DC.) Ag. **Figs 55-56**

Nitella hyalina differs from *N. tenuissima,* which has 6 branchlets of same length at a whorl, by a large number of secondary branchlets of different length, and by the presence of mucus (Fig. 56).

Description. Very bushy plant, up to 40 cm high, smooth and looking shiny green, due to the presence of mucus around the fertile whorls. The whorls differ from those of all other *Nitella*. They are composed of 6-8 primary branchlets (of same length) accompanied by additional numerous secondary branchlets of variable length (Fig. 56). The number of secondary branchlets may be up to 40 at the same node. The branchlets are divided at least once, ending in 4 dactyls made of 2 cells, the total forming a dense cluster. The whorls, especially the young ones, are surrounded by transparent mucus (Fig. 55). In addition, the whorls develop secondary axes of same morphology.

Reproduction. Monoecious species. Antheridia are formed at the 1st and 2nd forks of the branchlets and accompanied by 1-2 oogonia directed downwards (Fig. 55). Antheridia 350-400 µm in diameter; oogonia 500-600 µm high.

Ecology. *N. hyalina* grows mostly in ponds and lakes, from the shoreline downwards to 9 m. It prefers neutral to slightly alkaline pH (in that case, the ends of dactyls are incrusted by lime). It supports the drying out.

Distribution. Cosmopolitan species, present in all Europe, where it is not abundant: for instance, only 3 recent sites known in Germany (Becker, 2016). Sparsely distributed in Southern Europe, essentially in Western France and on the Portuguese

coast. Infrequent in Maghreb (16 localities from 3 to 1650 m a.s.l.; Annexe 17): rare in Algeria (Lake Oubeira, El-Kala National Park; Zouaïdia *et al.*, 2015), and a little more common in northern Morocco.

Nitella mucronata (A.Br.) Mig. **Fig. 57**

= *N. virgata* A.Br. *ex* Vallman

Description. Robust, bushy plant, 15-30 cm high, dark green to bottle-green; slender appearance with elongated whorls. Whorls composed of 6-8 branchlets, as long as the internodes of the axes, widely spread out and forming usually 2 secondary axes. Branchlets c. 5-8 cm long, divided 1-2 times. The lower cell of the branchlet corresponds approximately to the half of the total length of the branchlet. Dactyls composed of one long cell plus a tiny ultimate tip (the mucron) (Fig. 57). This feature is similar to *N. confervacea.*

Reproduction. Monoecious species. Gametangia conjoined on the first and second forks of the branchlets (Fig. 9C). Antheridia and oogonia relatively small, 300 and 400 µm respectively.

Ecology. Species of shallow water (0.5-2 m, exceptionnally known down to 20 m depth); grows on muddy substrate rich in organic matter (peatlands, for instance). The species supports well eutrophic, nutriment-rich waters, and can be associated with *Ceratophyllum* and *Callitriche*.

Distribution. Cosmopolitan species, except Australia, widespread in Europe and in the circum-Mediterranean region. Infrequent in Maghreb (17 localities from 0 to 2100 m a.s.l.; Appendix 18). Previously known in Algeria, where it has not been seen again since 1902, probably because of the lack of investigations. It is sparse in Morocco, where it reaches the altitude of 2100 m (Lake Tamda, High-Atlas) and has been recently discovered in Tunisia, in a coastal wadi of Cap Serrat (Table 2).

Nitella opaca (Bruz.) Ag. **Figs 58-59**

Nitella opaca is an early-growing (vernal) species setting gametangia in February/March in North Africa. It is easily detected from the waters' edge by its red (male plants) or black (female plants) fertile heads.

Description. Plant 10 to 40 cm high. The thallus may present banded incrustation adding a zebra-like appearance (alternate white and green bands) (Fig. 59). Whorls separated by long internodes. Whorls composed of 6-8 branchlets and at least 2 secondary axes. The sterile branchlets are elongated and spread out, the fertile ones are short and condensed into fertile heads. Branchlets (6-8) are divided only once. Dactyls are unicellular, robust and obtuse. The length of the dactyls is different on male and female plants (sexual dimorphism): the forks of the male plants bear 3 rather short dactyls (Fig. 58), whereas the female nodes are divided into 2 elongated and delicate dactyls (Fig. 59).

Reproduction. Dioecious species. Gametangia clustered into either red (male plants) or black (female plants) fertile heads. Antheridia big (700 µm) and solitary. Ripe oogonia with black oospores inside (600-700 µm high) mostly geminate at the same node.

Ecology. *N. opaca* grows mostly in temporary habitats, and occasionally in permanent lakes, down to 12 m depth. It prefers cold waters (for instance, originating from groundwater supply), with pH of 6-8. As a vernal species, it is one of the first plants to germinate at the end of winter and fructifies early and abundantly in February-March. Thereafter, it decays rapidly with increasing water temperature.

Distribution. Cosmopolitan species, present in Europe from the Mediterranean to Scandinavia. Although it was previously considered rare in North Africa (Elkhiati *et al.*, 2002), the recent investigations at the favourable period revealed that it is in fact the most frequent *Nitella* in Maghreb (70 localities from 0 to 1520 m a.s.l.; Appendix 19). It is mainly distributed in Northern and Western Morocco (Bouahim *et al.*, 2014), in northeastern Algeria (Zouaïdia *et al.*, 2015) and in northwestern Tunisia (Rouissi *et al.*, 2016).

Nitella tenuissima (Desv.) Kütz. **Fig. 60**

Description. Small, delicate plant (5-20 cm high); colour greyish green; plant often completely covered by mud. The whorls are very short, compact and regularly spaced on the axis, separated by long internodes. Whorls composed of 6-8 branchlets, each of which is successively divided 3-4 times, every fork producing 3-5 rays. Dactyls composed of 2 cells with an acuminate tip (Fig. 60). Cells of the same order have strictly the same length. The high number of divisions produces a fan-like aspect, characteristic of the species.

Reproduction. Monoecious species. Gametangia are produced at the 2nd and 3rd forks of the branchlets (seldom on the first fork; Krause, 1997). Antheridia very small (< 200 µm); oogonia c. 500 µm (Fig. 9F).

Ecology. *N. tenuissima* develops generally in temporary freshwater wetlands (it can even grows on a few mm of mud deposited on rock), able to form extended carpets in shallow waters or within backwaters of rivers and streams.

Distribution. Subcosmopolitan species, present in Western Europe: Spain, Portugal, Western and Southern France, Rhône and Rhine valleys. Rare in Maghreb, where it has only been found in Algeria between 1852 and 1934 (8 localities from 11 to 1093 m a.s.l.; Appendix 14). One of the last observations of this species was made in the Lake Sidi Freitis (L. Gauthier-Lièvre, 1925 in Feldmann, 1946), where it has not been seen again during recent investigations (I. Soulié-Märsche, unpublished data).

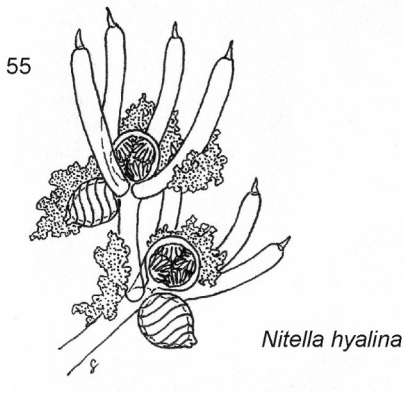
Nitella translucens (Pers.) Ag. **Fig. 61**

incl. *N. brachyteles* A.Br.

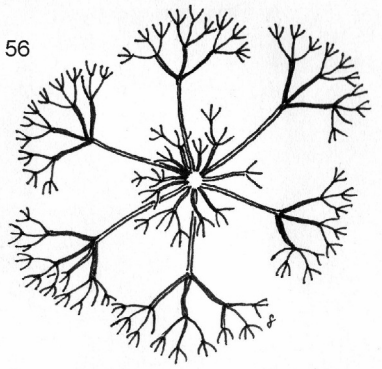
Nitella translucens is an atypical species of *Nitella*, which could be misidentified as *Nitellopsis* because its sterile branchlets are undivided.

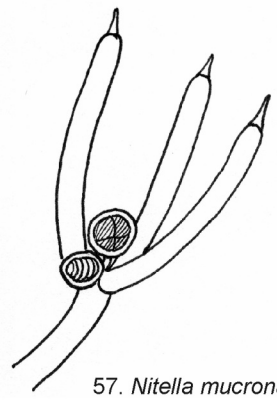
Description. Robust plant, often more than 1 m high, diameter of axis measuring 1-3 mm. Axis with particularly elongated internodes. The whorls of the main axis produce 4-6 (mostly 4) primary branchlets, which consist in a very long (up to 8 cm) cell ending with a crown of 2-4 minute ultimate cells (Fig. 61). Branchlets of the main axis are robust, sterile and appear to be undivided. The nodes of the main axis bear 1-2 secondary axes, which in turn form axes of third order. These adventive axes show also long internodes and end up with a series of very short whorls forming nearly inextricable, dense fertile heads containing the gametangia. Sometimes, the secondary axis remains short and forms a sort of dormant bud inside the whorl of the axis.

Figs 55-61. Morphological features of *Nitella* species. **55-56.** *Nitella hyalina*: **55.** Fertile nodes with bi-cellular dactyls and mucus, **56.** Open view of whorl with primary and secondary branchlets; **57.** *Nitella mucronata,* bicellular dactyls with mucron; **58-59.** *Nitella opaca*: **58.** dactyls of male plant, **59.** dactyls of female plant with banded incrustation; **60.** *Nitella tenuissima*, ultimate fertile node with bicellular dactyls; **61.** *Nitella translucens*, fertile head. ▶

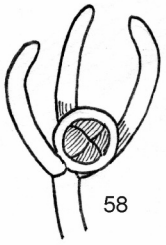


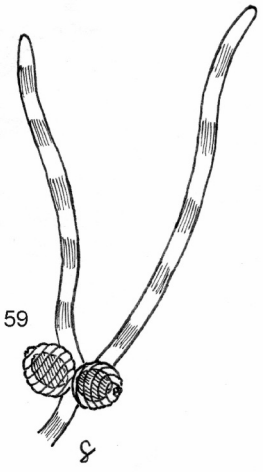
Nitella hyalina



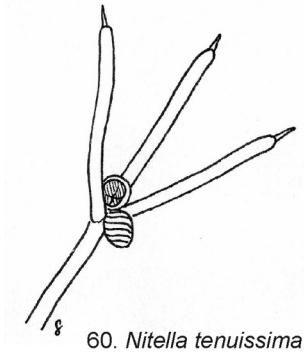


57. *Nitella mucronata*

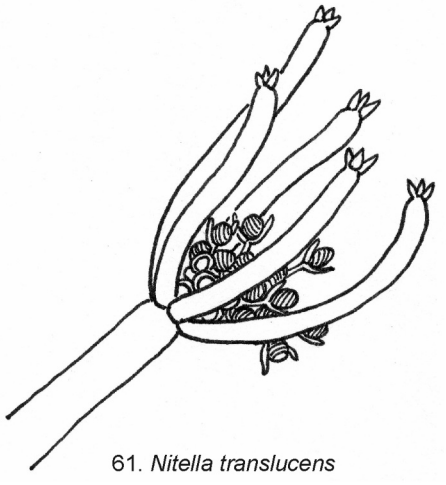




Nitella opaca



60. *Nitella tenuissima*



61. *Nitella translucens*

Reproduction. Gametangia are concentrated at the top of the secondary axes, forming dense fertile heads with minute teminal dactyls (Fig. 61). Antheridia (< 400 µm) accompanied by 2-3 oogonia (< 450 µm). Occasionally, an antheridium occurs on top of a branchlet.

Ecology. *N. translucens* forms mostly perennial populations in freshwaters rich in organic matter, neutral to slightly acid, on siliceous substrate and at water depths of 0.3 to 3 m (Corillion, 1957). In Maghreb, it grows in undisturbed temporary ponds or semi-permanent lakes, often associated to *Callitriche* spp., *Elatine alsinastrum* and *Myriophyllum alterniflorum*.

Distribution. Mediterranean-Atlantic species. Relatively frequent in the 3 Maghreb countries (40 localities from 0 to 1500 m a.s.l.; Appendix 20), where it has been regularly observed since 1992, in particular in Morocco, in Northeastern Algeria and Northwestern Tunisia.

Sphaerochara intricata (Trent. *ex* Roth) Soulié-Märsche **Fig. 62**

= *Tolypella intricata* (Trent. *ex* Roth) Leonh.

Description. Plant 20-50 cm high. The initial internode can be up to 12 cm long with a diameter of nearly 2 mm. The first node then produces numerous secondary axes. The first internode of the secondary axes is equally robust and elongated and already its first node produces numerous axes of third order. Sterile and fertile branchlets are different (dimorphism). The first node of each of the secondary axes bears a whorl of 6-8 rather long, sterile branchlets composed of 3-5 cells. The nodes of the branchlets produce 2-4 short cells (called "rays") ending in an acute tip (Fig. 62D). The sterile branchlets are elongated and divided only once at the first node; they are short on the following whorls. Fertile branchlets are very short, forming dense fertile heads (up to 2 cm in diameter).

Reproduction. Monoecious species, very fertile. Gametangia produced on all branchlets of secondary and higher order as well as at the base of whorls (Fig. 62). Usually, one antheridium of 200-400 µm (often stipitate/stalked) accompanied by 3-7 oogonia at different stages of ripening (thus of different size).

Ecology. Freshwater species, pioneer and colonizer of new habitats. In Europe, it often germinates in autumn, with development during winter and spring, followed by early decay.

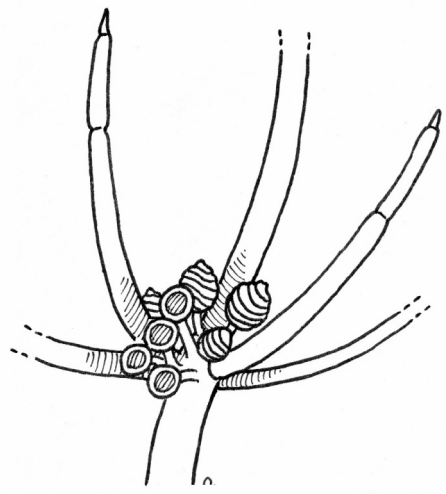
Distribution. Amphi-Atlantic species widespread in Europe (from Scandinavia to Spain and southern France) and in North America. Very rare and maybe extinct in Maghreb, where it was known from only 2 localities (Appendix 21): the spring of Saïda, in Algeria (1852), and the destroyed pond of El Haouaria, on the Cap Bon in Tunisia (1970).

Note. This species was included into the section *Acutifolia* T.F.Allen of the genus *Tolypella*, because of the acute ultimate tip of all terminal cells (Fig. 62). Arguing the presence of distinctive morphological characters of the taxa belonging to this section, they were recently distinguished as a different genus: *Sphaerochara* (Mädler) Soulié-Märsche (Soulié-Märsche, 1989; Soulié-Märsche & García, 2015).

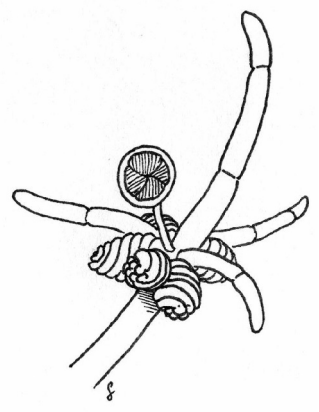
Tolypella glomerata (Desv. in Lois.) Leonh. **Fig. 63**

Tolypella glomerata presents a sort of "stem" that divides starting at the first node. The secondary axes form numerous fertile heads. The protonema is relatively elongated and persisting. All terminal cells are rounded.

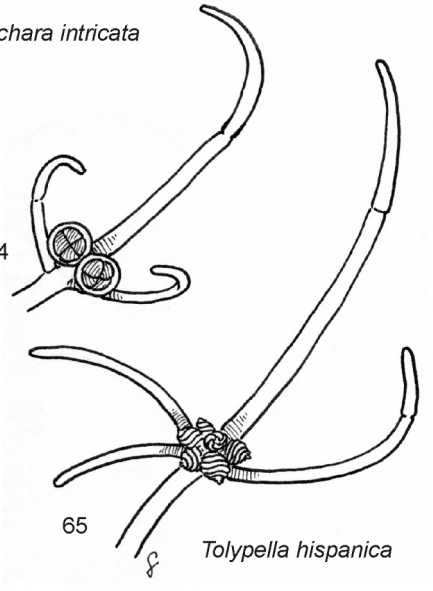
Description. Plant from 5 up to 20(40) cm high; main axis robust, up to 1 mm in diameter. Sterile and fertile whorls are different (dimorphism). The first node of the main axis produces 6 sterile branchlets, and 2-6 secondary axes. The sterile branchlets are undivided and consist in a series of 3-5 elongated cells. The fertile whorls are produced by the secondary axes. They are short and grouped into fertile heads (Fig. 63). The branchlets consist in a central row of cells (the "rachis") that is a succession of internodes and nodes. These nodes produce the gametangia as well as 3 rays of 2-3 cells. All terminal cells are rounded, obtuse (= section *Obtusifolia* Allan).



62. *Sphaerochara intricata*



63. *Tolypella glomerata*



Figs 62-65. Morphology of branchlet nodes in *Sphaerochara* and *Tolypella*. **62.** *Sphaerochara intricata*, branchlet whorl with aggregated gametania; **63.** *Tolypella glomerata*, fertile branchlet node with stalked antheridium; **64-65.** *Tolypella hispanica*: **64.** Branchlet of male plant, **65.** Branchlet of female plant.

Reproduction. Monoecious species, very fertile. Antheridia and oogonia produced at the same node, often provided with an elongated stalk cell (stipitate/stalked) (Fig. 63). Antheridia solitary or geminate, small (< 400 µm); oogonia grouped by 2-6 at the same node (< 500 µm) located below the antheridium and also at the base of the whorls of the secondary axes; unusual at the base of the main axis.

Ecology. Freshwater species, tolerating slight salinity (< 5 g/l). Early-spring species with a short life cycle, able to develop in temporary habitats, even very small ones (tire ruts, boar footprints…), or on the edges of ponds and lakes. It fructifies very early, sometimes in January under ice cover.

Distribution. Subcosmopolitan species, inequally distributed, mainly in Western Europe and in the Mediterranean region. Infrequent in Maghreb (24 localities from 2 to 1600 m a.s.l.; Appendix 21). It has not been seen again in Algeria since 1934, and seems uncommon in Morocco, where it has been recently found in Wadi Jdid-El Houar and in Lake Ras el Maâ, Middle-Atlas (Elkhiati, 1995). Apparently more abundant in Tunisia, where it is known from 8 localities, and where it has been recently found in the Sejenane region (Table 2).

Tolypella hispanica Nordst. **Figs 64-65**

Tolyoella hispanica is easy to recognise with its abundant big red antheridia visible with the naked eye. It differs from all other *Tolypella* in being dioecious (Figs 64-65).

Description. Plant 10-15 cm high. The axis shows a first long internode followed by numerous others, short and close to each other. Branching of the axis starts at the first node, which may show up to 30 secondary axes. Sterile whorls are spread, with a few undivided branchlets, which may be short or long but are particularly elongated (5 cm) on male plants. Fertile branchlets are formed in great number (8-10 per node) on secondary axes. They are very short, forming dense fertile heads. All terminal cells present are obtuse, rounded.

Reproduction. Dioecious species, extremely fertile. Gametangia formed both at the nodes of the branchlets of secondary axes and at the base of these nodes (Figs 64-65). Antheridia 700 µm to 1 mm diameter, visible with the naked eye, often stipitate; oogonia small (*ca* 400 µm), visible as black clusters when ripe.

Ecology. Typical brackish-water species, growing in shallow water (< 50 cm). Depending on precipitations, this early-spring to spring species develops from February to April in temporary waterbodies, and decays afterwards due to increasing temperature or drying out.

Distribution. Mainly a Mediterranean species, present in the South of Europe (from Iberian Peninsula (Cirujano *et al.*, 2013) and southern France (Corillion, 1961b) to Greece) and in North Africa, where it is relatively frequent in the 3 Maghreb countries (29 localities from 2 to 2090 m a.s.l.; Appendix 22). Recently found in Tunisia (Tunis region) (Table 2), and in Morocco in Middle-Atlas (L. Rhazi, unpublished data).

CONCLUSION: BIOGEOGRAPHICAL SIGNIFICANCE AND CONSERVATION ISSUES

The foregoing synthesis of the diversity and distribution of Characeae in the Maghreb revealed the presence of 31 taxa in the area of study. Based on

Corillion's distribution (1958) and data updating it, we are proposing the first biogeographical analysis on the scale of the entire Maghreb. Corillion (1977) already noted the dominance of northern elements (61.3%) and underlined the great similarity between Tunisian communities and the associations observed on the northern Mediterranean shores, which points to the role of glacial-interglacial cycles in establishing Characean flora in North Africa, as well as the influence of long-distance, bird-mediated dispersions during the Holocene. The extension into the Maghreb of a considerable part of European Characean flora suggests that the Mediterranean was not a serious obstacle to the dissemination of species.

The major part of the set of Northern species (14 taxa; 45.2%) presents cosmopolitan to subcosmopolitan distributions with temperate affinities. The distributions of some species are more restricted: Eurasiatic (*C. hispida*, *C. tomentosa*, *Nitella capillaris*), Boreal (*N. flexilis*) and even Arctic-Alpine (*C. strigosa*). Most of these taxa are infrequent to very rare in the Maghreb, particularly *Chara braunii*, *C. canescens*, *C. hispida*, *C. strigosa*, *C. tomentosa*, *Lamprothamnium papulosum*, *Nitella capillaris*, *N. confervacea*, *N. flexilis*, *N. gracilis*, *N. tenuissima*, and *Sphaerochara intricata*. Corillion (1972) also noted that cosmopolitan taxa became increasingly rare towards the south (in Western Africa), where they represent a mere 16% of the Characean flora.

The Mediterranean element, individualised *in situ*, is relatively well represented, particularly if the Mediterranean-Atlantic (*C. fragifera*, *N. translucens*, *T. glomerata*) and Boreal-Mediterranean taxa (*C. baltica*) (10 species; 32.3%) are included. Strictly speaking, it comprises 6 taxa (19.4%), three of which occur thoughout the Mediterranean (*C. connivens*, *C. galioides*, *T. hispanica*), and three of which are restricted to the western Mediterranean basin (*C. imperfecta*, *C. oedophylla*, *C. vulgaris* var. *gymnophylla*). It is worth noting that at least for *C. vulgaris* var. *gymnophylla*, this distribution is clearly focused on the Maghreb while southern European populations are more rare and scarce. Moreover, while Corillion (1978) considered *C. oedophylla* to be endemic to North African before it was discovered in Spain and in France, it is intriguing to note the complete absence of endemic Characean species in the Maghreb. Lastly, the tropical/subtropical element is represented by two species (6.5%) that are found only in the Saharan areas of the Maghreb (*C. zeylanica* and *L. succinctum*). In light of the relative importance of southern elements in the global hydrophytic flora of Numidia (Gauthier-Lièvre, 1931; De Bélair, 2005; Bouldjedri *et al.*, 2011), it is surprising to find so few tropical/subtropical Characeae species in the northern Maghreb.

Although the sampling pressure is very heterogeneous in the territory that was studied, and large parts of Maghreb have been poorly investigated to date, this synthesis nonetheless provides an initial assessment of geographic and taxonomic conservation issues. There is a surprisingly high proportion of rare taxa: 19 taxa (61.3%) were observed in fewer than 20 localities, and 13 (41.9%) were observed in fewer than 10 localities of the 464 sites that were investigated. While these estimations are not strictly based on IUCN criteria, the number nonetheless appears high compared to the IUCN redlist of 24% of the species in North African hydrophytic flora being threatened (Rhazi & Grillas, 2010).

Conservation issues on the scale of North Africa concern 14 species more particularly: 7 *Chara*, 2 *Lamprothamnium*, 4 *Nitella* and 1 *Sphaerochara* (Table 4). Five of these were observed in only one (*C. strigosa*, *C. zeylanica*, *N. flexilis*) or two sites (*L. succinctum*, *S. intricata*), and 6 of them have not been seen for more than 40 years (*C. fragifera*, *C. strigosa*, *C. tomentosa*, *C. zeylanica*, *N. tenuissima*, *S. intricata*). However, two tropical species (*C. zeylanica* and *L. succinctum*) do

reach the northern boundary of their distribution area in the Saharan Maghreb. Due to the diversity and abundance of wetlands, geological substrates, and climates, the Maghreb is of major importance for Characean conservation in general and for three species in particular:

– *Chara imperfecta*, Western-Mediterranean species, very rare in its distribution area (France, Spain, Morocco, Tunisia). Not seen for a century in Algeria and found recently in the Moroccan Rif.
– *Chara oedophylla*, Western-Mediterranean species, very rare in its distribution area (France, Spain, Morocco, Algeria). Previously known from two sites in Morocco and Tunisia; recently observed several times in Tunisia in the Sejenane region.
– *Lamprothamnium papulosum*, cosmopolitan species uncommon in Europe and protected in Britain and in Aquitaine (SW France). Present in the 3 Maghrebian countries but not seen since 1930 in Algeria and since 1982 in Tunisia. The only recent observation was made in 2009 in the area of Lake Sidi Boughaba (Morocco).

To evaluate the current status of these species requires research about their presence in their former localities and in potentially favourable habitats. Such research could well lead to a reevaluation of their rarity, as happened with *Nitella opaca*, which was until recently considered to be very rare in the Maghreb (Elkhiati *et al.*, 2002) whereas it is, in fact, one of the most common species.

From the geographical perspective, certain regions appear particularly rich in Characean species (Fig. 66), which reveals the abundance and diversity of favourable biotopes. Unsurprisingly, these regions are the wettest reliefs and coastal areas: the Middle Atlas, the Rif and the Rharb Plain in Morocco, Numidia in Algeria, and the Kroumiria-Numidia and Gabes Gulf in Tunisia. Within these regions, some emblematic sites and zones are particularly valuable for the conservation of rare species:

– Lake Sidi Boughaba, on the northwestern coast of Morocco, has large populations of *C. canescens* and *L. papulosum*. By contrast, *C. imperfecta* has not been seen

Table 4. Characeae of patrimonial interest in Maghreb

Taxon	*Number of sites*	*Concerned countries*	*Last observation*
Chara canescens	7	Alg, Mor	Sidi Boughaba, Morocco (2009)
Chara fragifera	4	Alg, Tun	Sidi Boul Baba, Tunisia (1854)
Chara imperfecta	5	Alg, Mor	Merja Hammare, Morocco (2010)
Chara oedophylla	4	Mor, Tun	Garâa Sejenane, Tunisia (2014)
Chara strigosa	1	Mor	Aguelmane Sidi Ali, Morocco (1973)
Chara tomentosa	4	Alg, Mor	Rharb, Morocco (1952)
Chara zeylanica	1	Alg	Ahnet, Algeria (1928)
Lamprothamnium papulosum	12	Alg, Mor, Tun	Sidi Boughaba, Morocco (2009)
Lamprothamnium succinctum	2	Mor	Oued Noun, Morocco (2002)
Nitella capillaris	7	Alg, Mor, Tun	Chefchaouen, Morocco (1992)
Nitella confervacea	3	Alg, Mor	Majen Zitoune, Algeria (2009)
Nitella flexilis	1	Tun	Mine de fer Dwahriia, Tunisia (2008)
Nitella tenuissima	8	Alg	In Salah, Algeria (1927)
Sphaerochara intricata	2	Alg, Tun	El Haouaria, Tunisia (1970)

since 1975, when it was observed by M.Guerlesquin (Guerlesquin, 1978). The lake, well known as a stopover of water-fowl, is a biological reserve, and also a Ramsar site. Despite this, farming is expanding, and is irrigated by groundwater pumped from the surrounding dune complex, which directly threatens the lake's hydrological equilibrium on which both birds and aquatic plants depend.

– The El-Kala National Park extends across a vast coastal plain in northeastern Algeria. It includes a diversity of wetlands, some of which are unique at the scale of Africa (peaty alder swamps, lakes, temporary ponds, marshes). A recent inventory of the Characean flora (Zouaïdia *et al.*, 2015) revealed the presence of 12 species, including *N. confervacea*. Being designated as a National Park and a Ramsar site should suffice to ensure the perenity of a habitat, but anthropogenic disturbances (pumping, forest clearing, cultivation, pollution, fire; Samraoui *et al.*, 1992; De Bélair & Samraoui, 1994; Belouahem-Abed *et al.*, 2011) severely threaten the integrity of wetlands.
– Garâa Sejenane is an ancient lake on a vast endoreic plain in northern Tunisia (Mogods). Most of the lake has been drained and cultivated, but prior to the drainage works of the 1960s (Pottier-Alapetite, 1958; Muller *et al.*, 2008; Rouissi *et al.*, 2016), there was an abundance of hydrophytic flora including *N. capillaris*, a species not seen since 1950. The site remains home to a relatively large population of *C. oedophylla*, which was described in a collection of 1927 from the same watershed. Another population was found in a pond a few km from the lake. Lastly, a former iron mine, located on a small hill close to the plain, is home to the only known African population of *N. flexilis*.

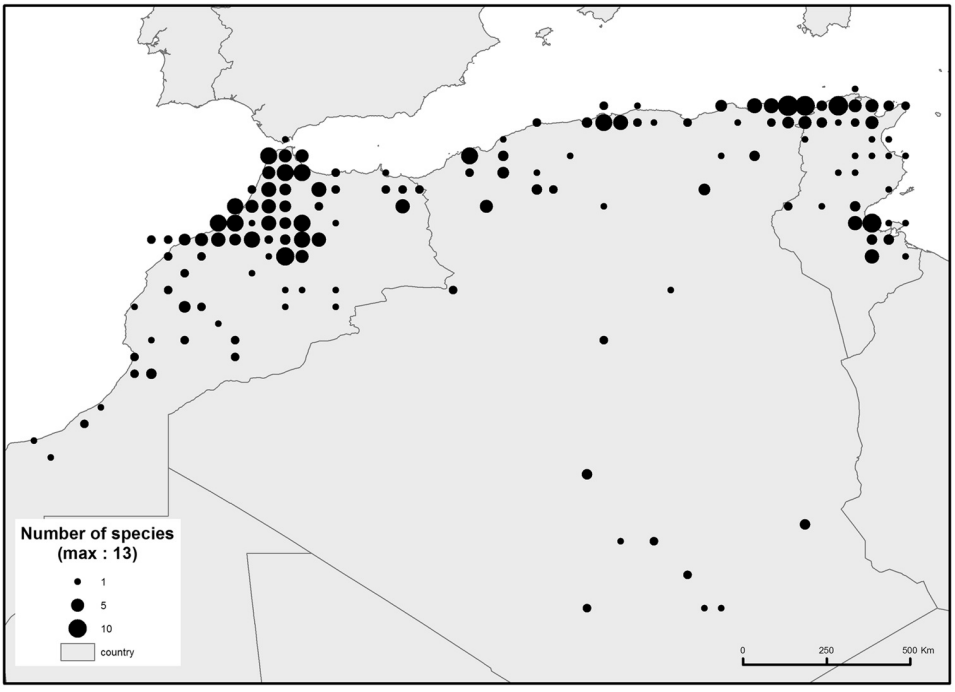


Fig. 66. Distribution frequency of Characeae species on a grid of 50 × 50 km.

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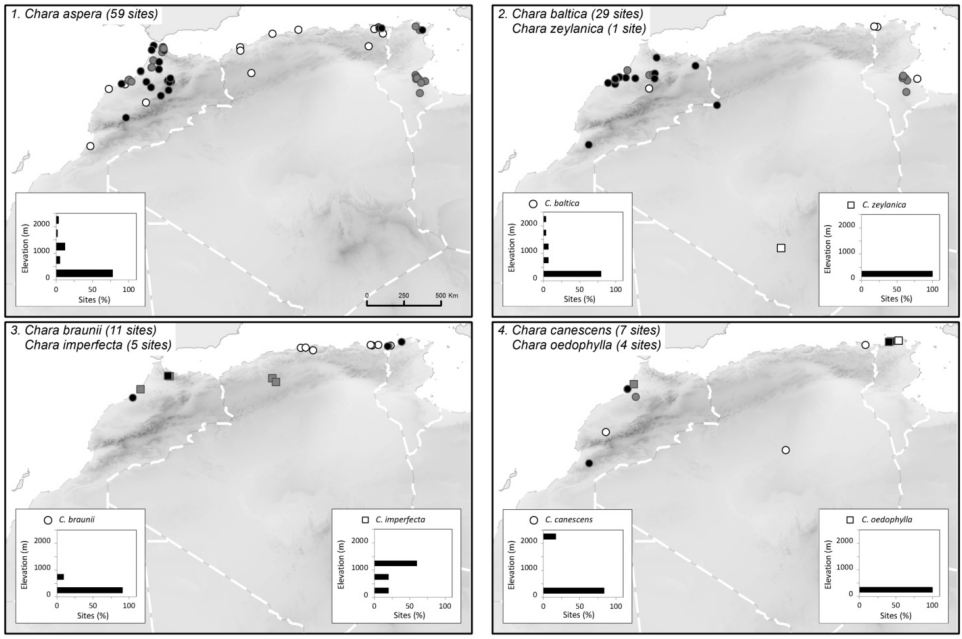
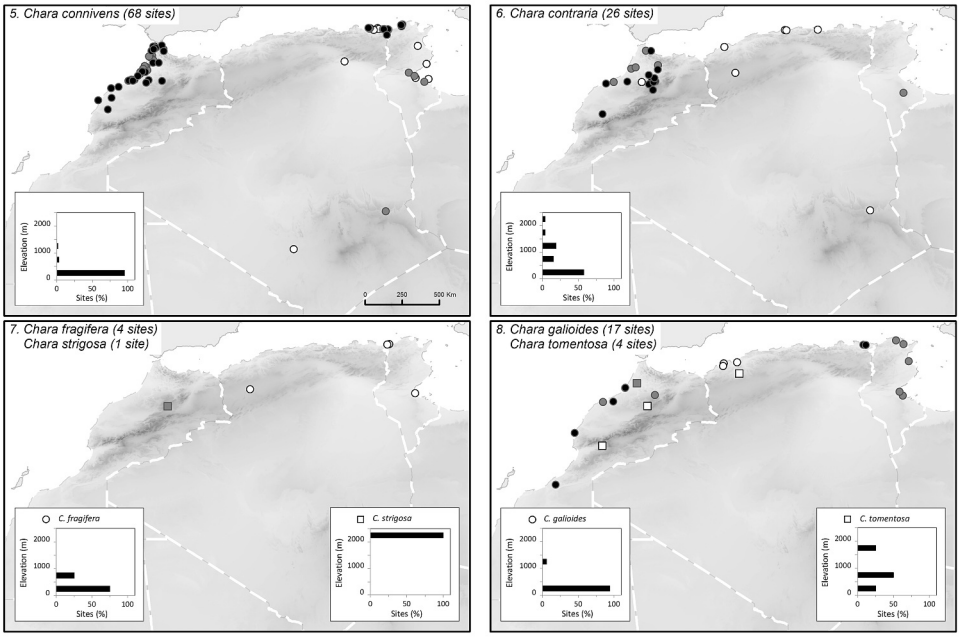
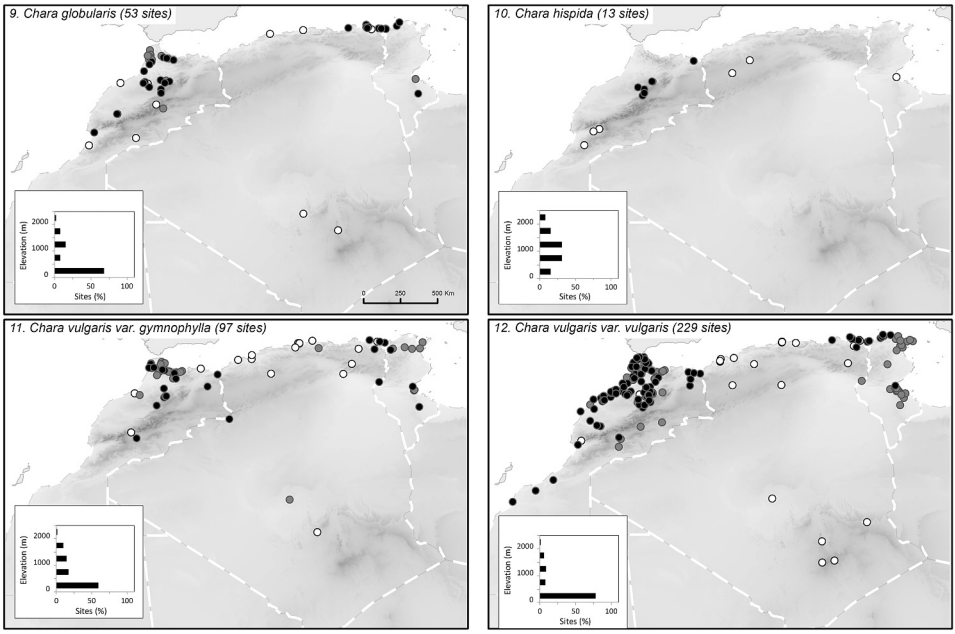
APPENDIXES



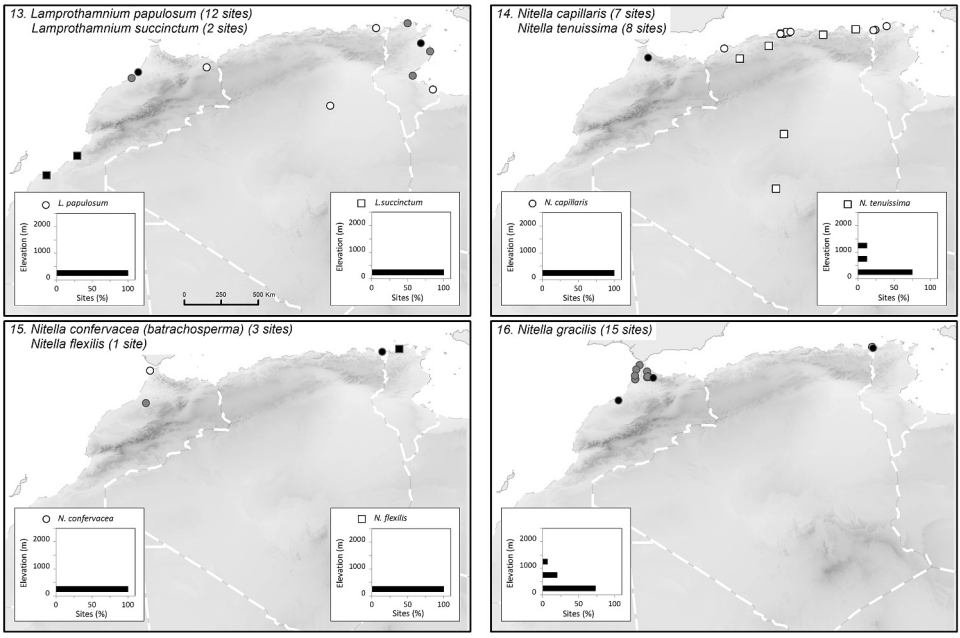
Appendixes 1-4. Distribution and sampling sites of *Chara aspera*, *C. baltica*, *C. braunii*, *C. canescens*, *C. imperfecta*, *C. oedophylla* and *C. zeylanica*. The dates of survey are grouped into three periods, identified with three different colours: 1784-1939 (white), 1940-1979 (gray), 1980-2016 (black).



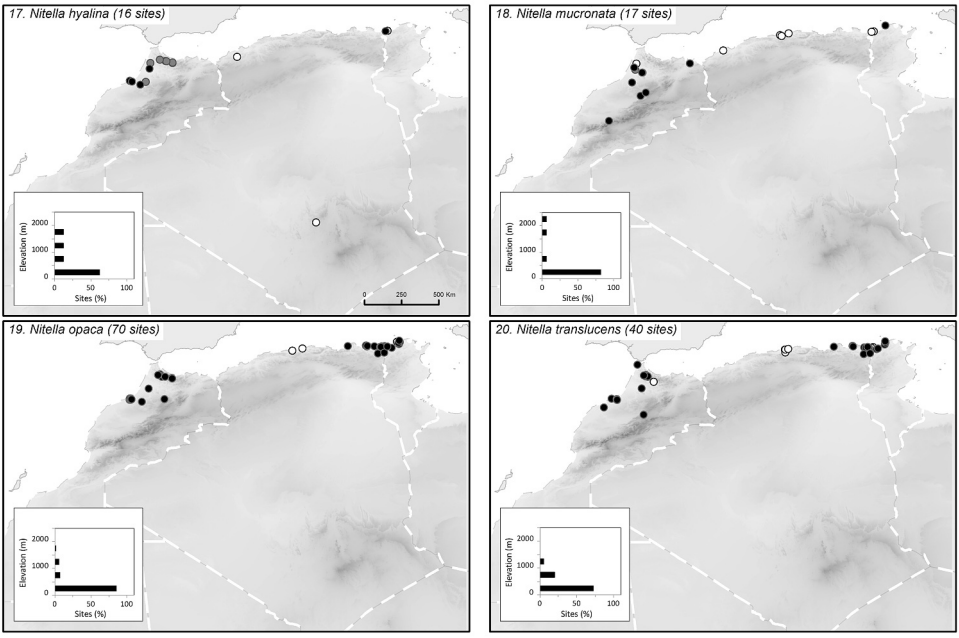
Appendixes 5-8. Distribution of *Chara connivens*, *C. contraria*, *C. fragifera*, *C. galioides*, *C. strigosa* and *C. tomentosa*. The significance of the colour of dots is given in caption to appendixes 1-4.



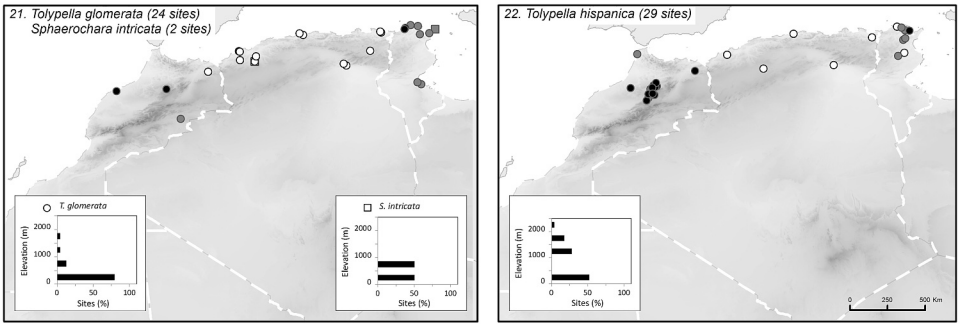
Appendixes 9-12. Distribution of *Chara globularis*, *C. hispida*, *C. vulgaris* var. *gymnophylla* and *C. vulgaris* var. *vulgaris*. The significance of the colour of dots is given in caption to appendixes 1-4.



Appendixes 13-16. Distribution of *Lamprothamnium papulosum*, *L. succinctum*, *Nitella capillaris*, *N. confervacea*, *N. flexilis*, *N. gracilis* and *N. tenuissima*. The significance of the colour of dots is given in caption to appendixes 1-4.



Appendixes 17-20. Distribution of *Nitella hyalina*, *N. mucronata*, *N. opaca* and *N. translucens*. The significance of the colour of dots is given in caption to appendixes 1-4.



Appendixes 21-22. Distribution of *Sphaerochara intricata, Tolypella glomerata* and *T. hispanica*. The significance of the colour of dots is given in caption to appendixes 1-4.