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Original Scientific Paper

New finds of *Chara oedophylla* Feldmann in Tunisia: significance of sejoined gametangia

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ABSTRACT: *Chara oedophylla* was established as a new species after examination of specimens collected by L. Gauthier in Tunisia in 1926, which were kept at the herbarium of Paris. Subsequently, several scientists considered it to be a variety of *Chara vulgaris.* During fieldwork in northern Tunisia, we found the species close to its type locality (Mogods region). Detailed examination of abundant populations of these plants revealed their particular, specific morphology. *Chara oedophylla* is characterised by a sejoined arrangement of the gametangia (on different nodes), whereas they are conjoined in *C. vulgaris*. The antheridia are very large, as is usually the case in dioecious species. In contrast to *C. vulgaris*, where geminate oogonia are side by side, they are vertically geminated in *C. oedophylla.* The female nodes bear numerous swollen bract cells, hence the etymology of the species name.

Here we provide an emended diagnosis that highlights the differences compared to *C. vulgaris* in order to maintain *C. oedophylla* as a valid species. The significance of sejoined gametangia with respect to speciation is discussed.

KEYWORDS: Characeae, temporary habitat, North Africa, monoecism, dioecism

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INTRODUCTION

During investigations of the wetland flora of northern Tunisia (Mogods region) conducted between 2007 and 2014, we found several populations of a poorly known taxon of the genus *Chara*, so-called *Chara oedophylla*. The plants formed dense monospecific populations on silty-clay substrate, in drainage ditches and pits dug along side paths, among inundated crops and in a natural wady. They showed the particular morphology of *C. oedophylla*, established as a new species by FELDMANN (1945) based on herbarium specimens collected in 1926 by L. Gauthier from northern Tunisia. On the basis of Feldmann's description and examination of a herbarium specimen, the taxon was later considered to be a variety of *Chara vulgaris* L. (WOOD 1962). However, WOOD & IMAHORI (1965) specify that they only had an inadequate immature specimen at hand, implying that they did not see any fresh material. GUERLESQUIN (1960) undertook a detailed examination of some specimens from Morocco that she subsequently attributed to *C. oedophylla* (GUERLESQUIN 1961). Only in the 80s, during PhD investigations in Spain, was this particular morphology identified again, described and illustrated in detail (COMELLES 1981, 1982). Finally, one of us discovered and surveyed for three successive years two new populations of the species in southeastern France (SOULIÉ-MÄRSCHE 2003). One of these populations was seen again in 2015 (MOURONVAL *et al*. 2015).

Our recent finds in the type region, as well as the previous collects and observations from France, show that the morphology of *C. oedophylla* has persisted for a long time and appears stable for successive years when settled in a habitat, even in the presence of *C. vulgaris*. The aim of the present paper is to argue that *C. oedophylla* fulfils the criteria to be considered a separate species, which we define herein with an emended diagnosis.

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EMENDED DIAGNOSIS, DISTRIBUTION AND HABITAT

Chara oedophylla Feldmann emend. Soulié-Märsche

≡ *Chara oedophylla* Feldmann 1945, Bull. Soc. Hist. Nat. Afr. Nord 36: 168-171, fig. 1.

≡ *Chara vulgaris* L. var. *oedophylla* (Feldmann) R.D. Wood 1962, Taxon 11: 8.

Emended diagnosis. Plant monoecious with sejoined gametangia (antheridia and oogonia on different nodes of the branchlets), seeming to be dioecious because of big antheridia flanked by two short bract cells, whereas the oogonia are hidden behind 3-4 pairs of large, swollen bract cells. Oospores without basal cage. Cortex diplostichous.

Typus: coll. L. Gauthier 1926, (PC- Herbarium of Paris) vide Feldmann 1945.
Type locality: Oued Tinja, northern Tunisia (37°10’14”N; 09°45’44”E). The type locality is a pond close to a small watercourse (wadi) that connects Lake Ichkeul to the Lake of Bizerte.

The emended diagnosis was established from material collected by the authors at two other sites in northern Tunisia within and close to the Garâa Sejenane depression, about 30 km west of Lake Ichkeul (Rouissi *et al.* 2016):

(1) Garâa Sejenane (37°05’00”N; 09°10’30”E): artificial pit and drainage ditches. Coll. dates: 2007/05/05; 2010/04/25; 2014/05/09 (Fig. 1).

(2) Guetma (37°07’29”N; 09°16’25”E): inundated agricultural field and Sejenane River. Coll. dates: 2008/04/20; 2010/04/22.

The largest population (in an artificial pond in Garâa Sejenane) was found in 2007, and it was observed again in 2014, in a pit dug along a track on the Garâa Sejenane plain. A dense carpet of *C. oedophylla* filled the pond completely, occupying *ca.* 10 m^2 to a maximum water depth of 2 m. The specimens were collected by hand in ± 1 m of water depth all around the pond, and with a hook in deeper water. Collected plants were transported in plastic bags and kept cold in a portable cooler and refrigerator until examination. Others were directly preserved in alcohol (60%). Fresh and dry material was examined in detail with a binocular microscope, and compared with collections from localities in southern France described earlier (Soulié-Märsche 2003).


Fig. 1. Artificial pit dug at Garâa Sejenane (upper) showing dense monospecific population of *Chara oedophylla* (lower) (April 25, 2007).

Description (Fig. 2**).** Plant robust, 15-30 (60) cm high. Axis 0.8-1.0 mm in diameter, heavily incrusted. Internodes short towards the apex. Phylloids (branchlets) 6-8 in a whorl, short (1.0-1.5 cm long), incurved towards the axis. Phylloids typically composed of four corticate segments followed by one inflated ecorticate cell and a very short ecorticate distal tip. Lateral bract cells and bracteoles mostly short, inflated; posterior bracts not developed. Cortex, spine cells and stipulodes similar to *C. vulgaris*. Cortex diplostichous and aulacanthous (secondary cells protruding), isostichous in the lower part. Spine cells sparse, solitary, obtuse or elongate, but shorter than diameter of the axis, absent on lower internodes. Stipulodes in two tiers, inconspicuous.

Reproductive structure. Antheridia and oogonia predominantly on different nodes of the phylloids. The normal antheridium position below the oogonium is extremely rare (3-5% of all fertile nodes). The studied

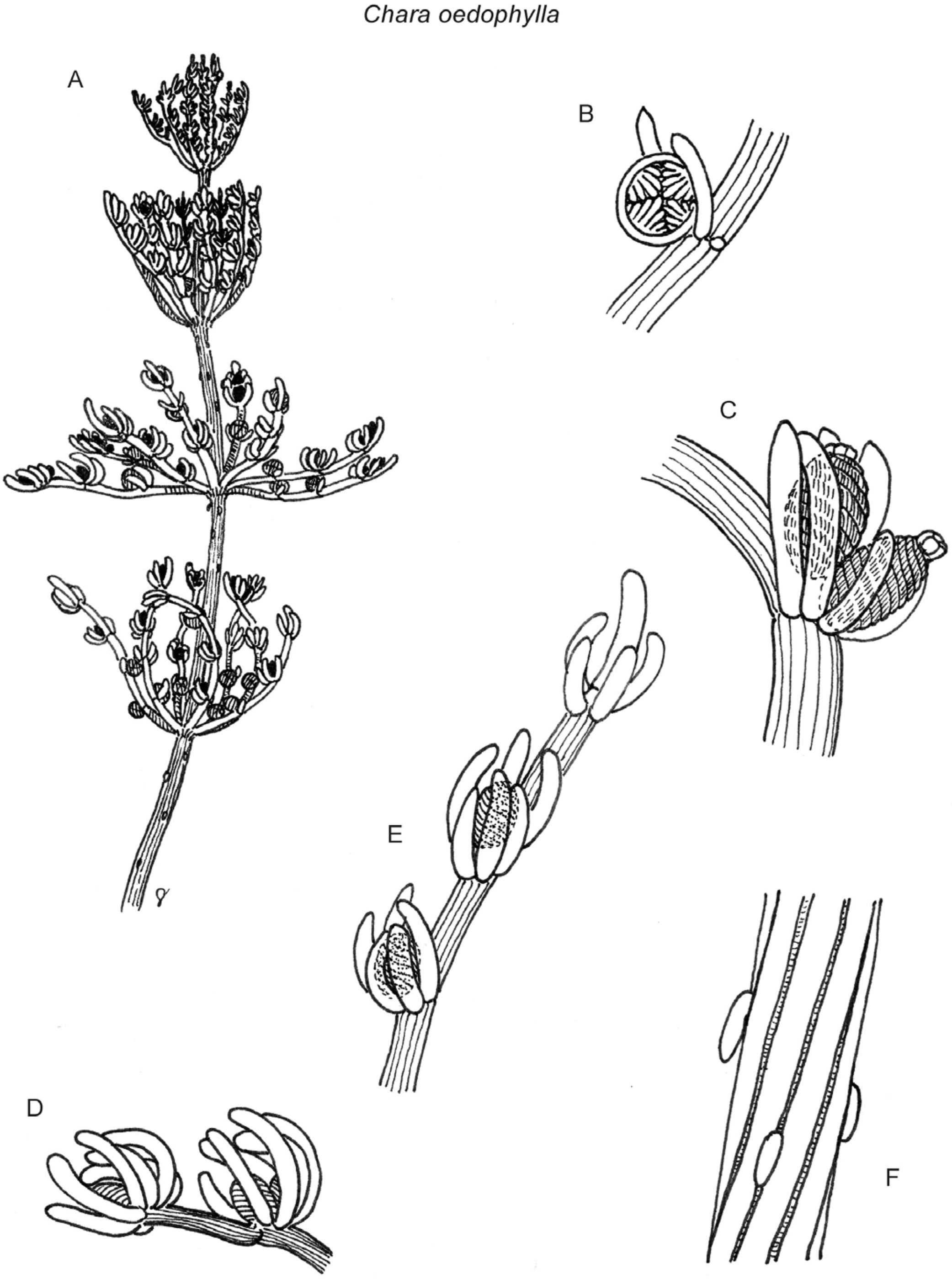

Fig. 2. *Chara oedophylla.* A) Habit of the plant; B) antheridium; C) geminate oogonia; D-E) characteristic inflated bract cells including those at the tip of phylloids; F) aulacanthous cortication (drawings SD Muller).

Fig. 3. Typical features of *Chara oedophylla* from Garâa Sejenane: big antheridia with very short bract cells, vertically geminated oogonia accompanied by 3-4 pairs of inflated bract cells, and last node of the phylloids equally fertile.

material usually showed four nodes fructified, either with one antheridium or with 1-3 (rarely four) oogonia. The distal node of the phylloid showed bract cells even when not fructified. Antheridia mostly solitary, rarely geminate and accompanied by a single pair of bracts, equal to or a little longer than diameter of the antheridium (Fig. 2B). Oogonia mostly in groups of 2-3 (four) at the same node. All geminate and triplate oogonia display a particular, characteristic position of being aligned vertically on the phylloid (Fig. 3). Female nodes bear 3-4 swollen, obtuse «oedemised» pairs of lateral bract cells forming a fan on each side. Short but swollen bracteoles are present below the lowermost of the geminate oogonia. The brown oospore calcifies and develops the gyrogonite.

Morphometric measurements.

Oogonia. Length: 600-800 µm (average 700 µm); Width: 440-560 µm (average 500 µm).

Coronula. Height: 100 µm; Width: 225 µm; Bract cells at their base: 262 µm wide.

Antheridia. Diameter: 600-800 µm.

Oospores. Colour: brown; No basal cage (claws) present (Fig. 4A).

Gyrogonites. Measurements of 50 gyrogonites indicate a size range of 640-760 µm (mean 707 ± 9 µm) for length, and 420-540 µm (mean 493 ± 6 µm) for width with an isopolarity index (100 x L/w) in the range of 123.1-154.2 (mean 143.5 ± 1.8) (Table 1). The shape of the gyrogonites is regularly, perfectly ellipsoidal with 10-12 convolutions visible in lateral view separated by very thin and delicate spiral crests. Spiral cell calcification remains always concave. The apex is slightly pointed; the base is rounded (Fig. 4B-D).

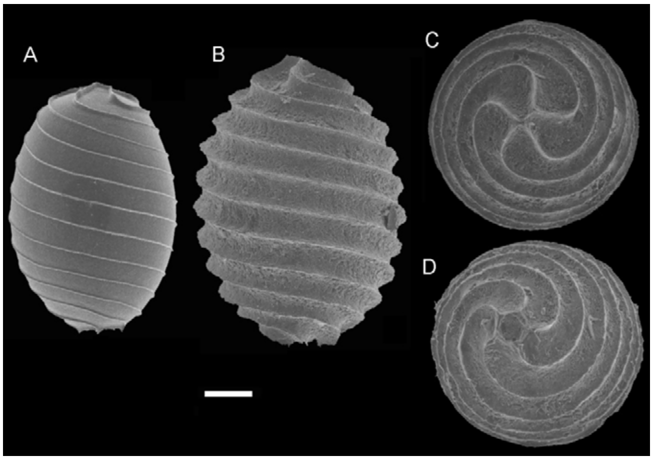

Fig. 4. *Chara oedophylla*. A) Oospore; B) gyrogonite; C) apical view of the gyrogonite; D) basal view of the gyrogonite. Scale bar = 100 µm.

Remarks. The gyrogonite population recovered from Garâa Sejenane (> 1000 specimens) revealed itself to be extremely homogenous with the size range extending only over 120 µm. Compared to *C. vulgaris*, the gyrogonites of *C. oedophylla* are a little bigger: their average size is 700 x 500 µm against 550 x 350 µm for *C. vulgaris* (see Soulié-Märsche 1989, figs. 31-33). Further, *C. vulgaris* gyrogonites very often display a truncate basal column, whereas this feature is completely absent in *C. oedophylla* gyrogonites, which are characterised by a rounded basal pole.

Distribution. North Africa (Morocco, Tunisia) and southwestern Europe (France, Spain). In Tunisia, *C. oedophylla* occurs in Wadi Tinja (between the Lake of Bizerte and Lake Ichkeul) and in the Sejenane region (Mogods). In Morocco, it was only recorded in the Allal Tazi wetland (34°31'34"N; 06°19'07"W; Corillion 1961; Guerlesquin 1961). In Spain, the species is rare and only known from five dispersed finds from southern provinces (Comelles 1982; Cirujano *et al.* 2007; Cirujano *et al.* 2008), i.e., Laguna del Tarja, Cadix (36°32'09"N; 06°03'24"W; Comelles 1981). In southern France, *C. oedophylla* was found at two sites classified as "Natura 2000" (Soulié-Märsche 2003): Lake Bonne Cougne (43°20'36"N; 6°15'34"E; alt. 253 m) and lake Gavoti (43°20'22"N; 6°11'25"E; alt. 260 m). Collected at both sites every year from April 2000 to April 2003, the species was still present in Lake Bonne Cougne in the spring of 2015 and had kept its characteristic features since the year 2000 (Mouronval *et al.* 2015).

Habitat. *Chara 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 1982; Cirujano *et al.* 2008).

Table 1. *Chara oedophylla*, biometrical data of the extant gyrogonites from Garâa Sejenane (Tunisia).

	Length (μm)	Width (μm)	ISI
N	50	50	50
Mean	707 ± 9	493 ± 6	143.5 ± 1.8
Conf. int.	698 – 716	487 – 499	141.6 – 145.3
Min.	640	420	123.1
Max.	760	540	154.2
Variance	1006	532	43.8
Var. index	4.5%	4.7%	4.6%

ISI - Isopolarity index = L/w x 100; N - number of measurements; Mean - mean value of the measured sample; Conf. int. - confidence interval at 95% = 196 x $\sigma/\sqrt{(n)}$; Min. - lowest value; Max. - highest value; Variance - variance = σ^2; Var. Index - variation index = 100 x σ/mean.

DISCUSSION

On the basis of the original description, established on fragmentary specimens (Feldmann 1945, p. 169), Feldmann (1945) and Corillion (1957, 1961) noted the morphological affinity of *Chara oedophylla* with *C. rabenhorstii* A.Br. and *C. crassicaulis* Schleich. Applying the macrospecies concept, Wood (1962) assigned *C. oedophylla* to *C. vulgaris* as a variety. This nomenclatural status was maintained in subsequent papers that reported finds of the species in Spain, but did not focus on taxonomy (Comelles 1981, 1982; Espinar *et al.* 1997, 2002; García Murillio *et al.* 2006; Cirujano *et al.* 2008).

Examination of large populations of fresh material from the type region allows us to highlight a number of notable features that are unique to *C. oedophylla* and sufficiently significant to re-establish the taxon as a separate species. The main differences compared to *C. vulgaris* are:

- A large majority (97%) of sejoined gametangia;
- The big size (600-800 μm) of the antheridia, corresponding to that usually observed for dioecious species;
- Vertically geminated oogonia, even when only two oogonia are present;
- The presence of 6-8 lateral bract cells on female nodes of the phylloids.

Despite the fact that its cortication is indeed like that of *C. vulgaris,* the plant as a whole looks different owing to the presence of big clearly visible solitary antheridia and oogonia "hidden" by numerous swollen bract cells. These features clearly give the impression that the plant is dioecious. Vertically geminate oogonia, already noted both by Feldmann (1946) and by Comelles (1982), are a constant feature in all of the finds, but were not given the significance they deserve as a unique feature of *C. oedophylla*. The "normal" position of antheridia and oogonia occurs very rarely, and can be considered a relictual morphological feature. Thorough counts on a number of plants from Morocco (the Allal Tazi site) revealed only 3-5% of nodes bearing conjoined gametangia (Guerlesquin 1960), and detailed counts on the Spanish material showed that antheridia were always solitary (Comelles 1982).

Aside from the "macrospecies concept" of Wood (1962), the presence of sejoined gametangia in Characeae is usually considered species-specific and grounds for separation of the concerned taxa at the species level. For instance, *C. sejuncta* A.Br., with antheridia and oogonia at different nodes of branchlets, is considered distinct from *C. zeylanica* Klein ex Willd., whose antheridia occur at the base of (i.e., below) oogonia (Ophel 1952). Similarly, Alix & Scribailo (2011) distinguish *C. drouetii* Wood from *C. zeylanica* because of its sejoined gametangia, in contrast to the taxonomic rank given by Wood (1962), who considered it to be a simple form (*C. zeylanica* var. *sejuncta* f. *drouetii* Wood). The evolutionary significance of this character has not been definitely elucidated, but it could represent an intermediate state between monoecy and dioecy. Although Wood (1962) did not recognise the taxonomic value of the arrangement of gametangia in Characeae, unsuccessful hybridisation attempts between close monoecious and dioecious taxa (McCracken *et al.* 1966; Proctor 1975) show it to be a good character for discriminating species.

Proctor (1971, 1980) expressed the conjecture that for the Characeae "dioecious taxa are ancestral to monoecious species". He based this hypothesis on his interpretation, under the prism of evolutionary biogeography, that species with a more limited distribution are ancestral to those with a cosmopolitan distribution. Consequently, the fact that dioecious charophyte species are most diversified in the southern hemisphere, while monoecious ones display more cosmopolitan distributions, would mean that the former are ancestral.

Indeed, as an example we can cite *Lamprothamnium papulosum* (Wallr.) J.Gr., which is largely cosmopolitan, whereas *L. heraldii* A. García & M.T. Casanova, its dioecious counterpart, is restricted to Australia. Similarly, the dioecious *Nitella congesta* (R.Br.) A.Br. is rare and endemic in Australia compared to its monoecious cosmopolitan counterpart, *N. hyalina* (DC.) Ag. Arguing that Characeae evolved from the former Gondwana flora, whose relicts correspond to the landmasses of the southern hemisphere, Proctor (1980) concluded that the numerous dioecious taxa from this palaeocontinent would have constituted the original stock of the living Characeae.

The biogeographic pattern with 2/3 of all taxa being monoecious (Khan & Sarma 1984) leads us to question this hypothesis. Indeed, monoecy has an advantage for long-distance dispersal since one single dispersal event (generally dispersal by water birds) would be sufficient for colonising new territories, whereas at least two events leading to the contemporaneous development of a male plant and a female plant are needed to produce fertile populations of dioecious species. One could moreover argue that the "older" characean flora of the southern hemisphere had more time in millions of years to spread over other continents as monoecious plants, and to evolve locally from monoecy to dioecy. According to this alternative view, the monoecious taxa would represent the ancestral form, the dioecious ones having evolved over millions of years in the southern hemisphere through mutations from the original genetic stock. The dioecious characean species would thus be less frequent in Eurasia (of Laurasian origin) because the originally introduced monoecious taxa would have had less time to produce dioecious forms since the beginning of the Mesozoic (245 Ma), when Gondwana started to split. This is consistent with the concept of the evolution of dioecy in angiosperms, in which dioecious species are also much less numerous than monoecious ones (Bawa 1980; Charlesworth 1999; Barrett 2002).

As an exception, one could point to the dioecious *Nitellopsis obtusa* (Desv.) J.Gr., recently introduced to North America (Mann *et al.* 1999) and considered an invasive species today (Pullmann & Crawford 2010). However, its success as a coloniser is due to strong vegetative multiplication through particular stellate bulbils, since for the moment it seems that all populations in the USA were constituted of only male plants (Brown 2014). Thus, without the vegetative reproduction that counterbalances its dioecism, *N. obtusa* would not have been able to spread in the Great Lakes region unless it "met" a female plant.

Recent analyses of the historical biogeography of fossil clavatoracean charophytes (phylogeny detailed in Martín-Closas 1996) provide examples of the very early worldwide expansion of monoecious taxa attested by the exceptional preservation of antheridial imprints on utricles of *Atopochara trivolvis* (Martín-Closas & Wang 2008), and suggest that such monoecious species are ancestors of dioecious ones, which are characterised by more limited distribution areas (Martín-Closas 2015).

Nevertheless, the palaeobiogeography of fossil *Nitellopsis* as studied by Sanjuan & Martín-Closas (2015) showed that, in the long run, dioecy did not represent a limitation for long-distance spread, but just resulted in lower migration rates compared to monoecious species.

These considerations lead us to suggest that *Chara oedophylla* represents a separate species that is splitting from the monoecious *C. vulgaris* and in the process of evolving towards a dioecious state. This highlights existence of the "hot spot" for biodiversity and evolution represented by the Mediterranean region and more particularly by its temporary wetlands, which can be considered "evolutionary pools".

CONCLUSION

The characteristic features of *Chara oedophylla* prove constant in time and space, and support the view that the species should be recognised as taxonomically distinct from the species complex of *C. vulgaris*. The presence of sejoined gametangia in *C. oedophylla* can be considered a step of evolution from monoecy towards dioecy, as well as from cosmopolitanism towards endemism.

Chara oedophylla appears to be a typical Mediterranean species linked to high light intensity and alkaline water. Altogether, only 10 sites (located in North Africa, Spain and southern France) are known at present. Further investigations should lead to the discovery of new occurrences of this rare taxon, at least in the western Mediterranean (notably in Algeria), but also possibly in eastern Mediterranean regions as well.

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Botanica SERBICA

REZIME

Novi nalazi vrste *Chara oedophylla* Feldmann u Tunisu: značaj odvojenih gametangija

Ingeborg Soulié-Märsche i Serge D. Muller

Chara oedophylla je ustanovljena kao nova vrsta nakon istraživanja primeraka sakupljenim od strane L. Gauthiera u Tunisu 1926.godine, a koji se čuvaju u Herbarijumu u Parizu. Kasnije je ona smatrana od strane više naučnika varijetetom vrste *Chara vulgaris*. Tokom terenskih istraživanja u severnom delu Tunisa, našli smo ovu vrstu blizu njenog tipskog nalazišta (Mogods region). Detaljna istraživanja brojnih populacija ove vrste otkrila su njihovu specifičnu morfologiju. *C. oedophylla* se karakteriše odvojenim gametangijama (na različitim pršljenima), dok su kod *C. vulgaris* one spojene. Anteridije su veoma velike, kao što je to slučaj kod dvodomih vrsta. Za razliku od *C. vulgaris* gde su udvojene oogonije jedna pored druge, kod *C. oedophylla* su one udvojene vertikalno. Ženski pršljeni nose brojne naduvene ćelije listova, te otuda i poreklo naziva vrste. Ovde dajemo izmenjenu dijagnozu koja ističe razlike u odnosu na *C. vulgaris* u cilju održavanja *C. oedophylla* u statusu vrste. Razmatra se i značaj odvojenih gametangija sa aspekta specijacije.

Ključne reči: Characeae, privremena staništa, Severna Afrika, jednodomost, dvodomost