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## The genus *Heteromera* (*Compositae*, *Anthemideae*)

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**Abstract:** A comprehensive treatment of the N African genus *Heteromera* Pomel (*Compositae*, *Anthemideae*) is presented. Morphological, anatomical and karyological features as well as distribution maps are reported. The analysis of nrDNA and cpDNA sequence variation reveals the close relationship of the two species, with *H. philaenorum* exhibiting little variation and being well separated from a more diverse *H. fuscata*. The chromosome numbers of *H. fuscata* and *H. philaenorum* are reported for the first time. *Heteromera philaenorum* Maire & Weiller, *Chrysanthemum fuscatum* f. *pubescens* Trotter and *Chrysanthemum fuscatum* f. *subcanescens* Trotter are lectotypified and *H. philaenorum* is reported as new for the flora of Algeria and Tunisia.

**Key words:** *Anthemideae*, *Asteraceae*, chromosome numbers, *Compositae*, *Heteromera*, nomenclature, North Africa, taxonomy, typification

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## Introduction

The genus *Heteromera* Pomel was established by Auguste Pomel (1874) to include the N-African species *Chrysanthemum fuscatum* Desf. (Desfontaines 1799) and – with reservations – *Pyrethrum macrocarpum* Coss. The latter taxon is today placed in the genus *Endopappus* Sch. Bip. as *E. macrocarpus* (Coss.) Sch. Bip. *Heteromera* is characterized by achenes with non-valecular resin ducts or sacs in the upper part of the ribs, a characteristic also found in *Aaronsohnia* Warb. & Eig, *Matricaria* L. and *Daveaua* Mariz, which led Bremer & Humphries (1993) to include *Heteromera* in the subtribe *Matricariinae* sensu Bremer & Humphries (1993). However, molecular phylogenetic studies by Oberprieler & Vogt (2000) and Oberprieler & al. (2007, 2009) demonstrated that the subtribal classification of the tribe proposed by Bremer & Humphries (1993) contained a number of non-

monophyletic subtribes and that especially their subtribe *Matricariinae* suffered from being highly polyphyletic.

Renato Pampanini (1914a, 1914b) was the first to report a certain variability within the genus. His *Chrysanthemum fuscatum* var. *tripolitanum* Pamp. from Tarhunah in Libya was characterized and separated from the typical form by a dense pubescence and small size of stems and leaves. It was René Maire and Marc Weiller (1939) who additionally noticed the deviating achene morphology and size of these plants and consequently described the taxon at specific rank as *Heteromera philaenorum* Maire & Weiller. Aside other differences in achene morphology and anatomy the most striking difference is the expression of a pappus. In *H. fuscata* (Desf.) Pomel, the apex of the disc floret achenes is formed by characteristic membranous scales, while in *H. philaenorum* it is expressed as a short and continuous, basally callose rim.

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The present paper contributes a formal taxonomic treatment of the genus *Heteromera* and addresses the question of species identity based on molecular sequence analyses of nuclear (nrDNA ITS/ETS) and plastid markers (cpDNA *petN-psbM* and *trnQ-rps16* intergenic spacer regions). While in Wagner & al. (2019) the two species of *Heteromera* were already included in a molecular phylogenetic study, only a single individual for each species was analysed and, therefore, no assessment of the genetic variation throughout their geographical range was possible.

## Material and methods

The present study is based on cultivated material and field studies as well as herbarium specimens held at the following institutions [abbreviations according to Index herbariorum (Thiers 2008+)]: AMD, B, B-W, BC, BM, E, FI, FI-W, G, K, L, M, MA, MPU, MSB, P, P-Desf., PAD, PORUN, RAB, RNG, S, UPS, W, WAG, WU and the private collection of C. Oberprieler. In addition, the virtual herbaria of MPU, P, RB and US were consulted.

Seed material and living plants were collected during field trips by the authors to Tunisia organized by the Botanic Garden and Botanical Museum Berlin-Dahlem in 1994 and 2009. Living plants were cultivated in the greenhouses of the Botanic Garden Berlin. Vouchers are deposited at B.

Information on plant material used in the molecular analysis based on nrDNA ITS/ETS and cpDNA sequences is given in Table 1. We have tried to sample the two species throughout their distribution ranges; however, we did not include old or defective specimens in our analysis. DNA was extracted from herbarium specimens following the CTAB protocol described by Doyle & Doyle (1987) and Doyle & Dickson (1987). For the amplification of nrDNA ITS, primers 18SF and 26SR (Rydin & al. 2004) were used if ITS1, 5.8S and ITS2 were amplified in one stretch, or with the additional primers P2 (White & al. 1990) and ITS-D (Blattner 1999) for ITS1 and ITS2, respectively. PCR amplification of nrDNA ETS and the two chloroplast markers *petN-psbM* and *trnQ-rps16* were carried out with primers L-ETS/18S-ETS (Lee & al. 2002; Baldwin & Markos 1998), *petN1/psbM2R* (Lee & Wen 2004) and *trnQ2/rps16x1* (Shaw & al. 2007), respectively. PCR products were purified using the AmliClean™ Magnetic Bead PCR Clean-up Kit (NimaGen, Nijmegen, The Netherlands) and sequenced by Macrogen Inc. (Amsterdam, The Netherlands). If necessary (nrDNA ITS in accession A1177), PCR products were cloned with the CloneJET PCR Cloning Kit (Thermo Fisher Scientific) and inserts sequenced after colony-PCR with the above-mentioned primer combinations. Sequences were edited manually with ChromasLite v.2.01 (Technelysium Pty Ltd, 1998–2015) and multiple sequence alignments (Supplementary Material files 1 and 2) were performed

using BioEdit v. 3.2.6 (Hall 1999). Parsimony-based ribotype (nrDNA) and haplotype (cpDNA) networks were constructed by the TCS (Clement & al. 2002) option in the PopART software package (<http://popart.otago.ac.nz>).

Chromosome numbers were obtained from somatic mitoses of root tips of plants raised from seed. Root tips were pre-treated with hydroxyquinoline (0.002 molar aqueous solution) for 2 hours, fixed in 96% ethanol/glacial acetic acid (3:1) and refrigerated. Hydrolysis was carried out with 1–2N hydrochloric acid for 10–15 minutes at 60°C. For chromosome staining, root tips were squashed in aceto-orcein. Chromosome counts were made for several plants of a common seed origin. Five to ten metaphase stages were examined for every plant.

SEM images of indumentum, flowers, achenes and pollen grains were taken with a Philips SEM 515 in the Botanical Museum Berlin after the objects had been coated with a gold-palladium layer in a Polaron sputter coater.

The descriptions are based on measurements made on dried plants. The cited variation ranges cover the total observed variation exhibited by a particular taxon. Extreme values have been placed in parentheses.

In the lists of specimens, seen localities are given country-wise in the following order: Algeria, Tunisia and Libya. Within each country, administrative districts (Algeria: Wilaya; Tunisia: Gouvernorat; Libya: Shabiyah) are listed in alphabetical order. Within each district, specimens are listed from north to south. Most of the specimens are given with the longitude and latitude of the collecting locality, written as stated by the collector(s), or taken from various maps or online resources and then cited in square brackets. Distribution maps were generated using QGIS (QGIS Development Team) and extraction of information on the mean annual precipitation (BioClim variable BIO12) for the two species was based on data supplied by the WorldClim database (<https://www.worldclim.org/>).

## Results and Discussion

### Systematic position of *Heteromera*

In their cladistic analysis of *Compositae–Anthemideae* based on morphological and anatomical evidence, Bremer & Humphries (1993) assigned the genus *Heteromera* (being unispecific in their interpretation due to the alleged synonymy of *H. philaenorum* with *H. fuscata*) to their subtribe *Matricariinae*. This subtribe, however, was found to be a highly polyphyletic assemblage of genera by subsequent molecular phylogenetic analyses (e.g. Oberprieler & Vogt 2000). Comprehensive analyses of the whole tribe based on nuclear and chloroplast markers (Oberprieler & al. 2007, 2009) allowed for a new subtribal classification of the *Anthemideae*. It revealed the close relationship of *Heteromera* to subtribe *Leucanthemiinae* without sharing, however, the characteristic achene

Table 1. *Heteromera* populations sampled for the present molecular analyses with information on localities, voucher specimens and GenBank accession numbers for the two nuclear and the two chloroplast markers.

Population	Taxon	Locality	Coordinates	Collectors	Voucher specimen	GenBank nrDNA ITS	GenBank nrDNA ETS	GenBank cpDNA <i>petN-psbM</i>	GenBank cpDNA <i>trnQ-rps16</i>
A0072	<i>H. fuscata</i>	Tunisia, Gouvernorat Gafsa, road C 122 c. 9 km N of Métaoui, 500 m	34°22'42"N, 08°26'04"E	R. Vogt 12689 & C. Oberprieler 6994	B100673071	MZ668668	MZ668685	MZ668702	MZ668657
A0796	<i>H. fuscata</i>	Tunisia, Gouvernorat Tozeur, road C 106 between Kariz and road P 3 (Tozeur–Gafsa), oued c. 2 km S of junction with road P 3, 65 m	34°03'12"N, 08°14'10"E	R. Vogt 16585, C. Oberprieler 10528 & C. Gstöttl	B100216212	MZ668669	MZ668686	MZ668703	MZ668658
A0937	<i>H. fuscata</i>	Tunisia, Gouvernorat Gabès, road C 104 between Médenine and Matmata, c. 10 km WNW of Toujane, 469 m	33°29'08"N, 10°03'36"E	R. Vogt 16547, C. Oberprieler 10490 & C. Gstöttl	B100673058	MZ668670	MZ668687	MZ668704	MZ668659
A0939	<i>H. fuscata</i>	Tunisia, Gouvernorat Kasserine, road P 15 between Fériana and Gafsa, track between Fériana and Sidi Aïch, 810 m	35°51'04"N, 08°32'32"E	R. Vogt 12612 & C. Oberprieler 6917	B100673049	MZ668671	MZ668688	MZ668705	MZ668660
A0940	<i>H. fuscata</i>	Tunisia, Gouvernorat Gafsa, road C 201 between Moularès and Redeyef, sandy plains of Oued Selja, c. 7 km S of Moularès, 400 m	34°27'01"N, 08°13'12"E	R. Vogt 12694 & C. Oberprieler 6999	B100673055	MZ668672	MZ668689	MZ668706	MZ668661
A0941	<i>H. fuscata</i>	Tunisia, Gouvernorat Tozeur, road P 16 between Tamerza and Chbika, 350 m	34°21'31"N, 07°54'08"E	R. Vogt 12785 & C. Oberprieler 7090	B100673056	MZ668673	MZ668690	MZ668707	MZ668662
A1169	<i>H. fuscata</i>	Algeria, Wilaya Biskra, 8 km N of Biskra, Col de Sfa, 800 m	34°50'N, 05°35'E	D. A. Sutton & S. J. Sutton 590	RNG	MZ668676	MZ668693	MZ668710	MZ668665
A1170	<i>H. fuscata</i>	Algeria, Wilaya Bordj Bou Arréridj, 50 km NW of Bordj Bou Arréridj, Chaîne des Bibans, 750 m	36°10'N, 04°25'E	D. A. Sutton & S. J. Sutton 535	RNG	MZ668677	MZ668694	MZ668711	MZ668666
A1177	<i>H. fuscata</i>	Algeria, Wilaya M'Sila, 27 km SW of Bou-Saâda on road to Djelfa, 920 m	35°04'N, 03°58'E	D. Podlech 37201	MSB003481	MZ668678– MZ668684	MZ668695– MZ668701	MZ668712	MZ668667
A0944	<i>H. philaenorum</i>	Tunisia, Gouvernorat Tataouine, road P 19 between Tataouine and Remada, c. 4.5 km S of Bir Thlethine, 420 m	32°39'N, 10°19'E	R. Vogt 13007 & C. Oberprieler 7312	B100673044	MZ668674	MZ668691	MZ668708	MZ668663
A1166	<i>H. philaenorum</i>	Libya, Shabiyah Al Jabal al Gharbi, Gebel Nefoussa, 27 km SE of Giado, 650–700 m	31°49'N, 12°10'E	P. Davis 49629	RNG	MZ668675	MZ668692	MZ668709	MZ668664

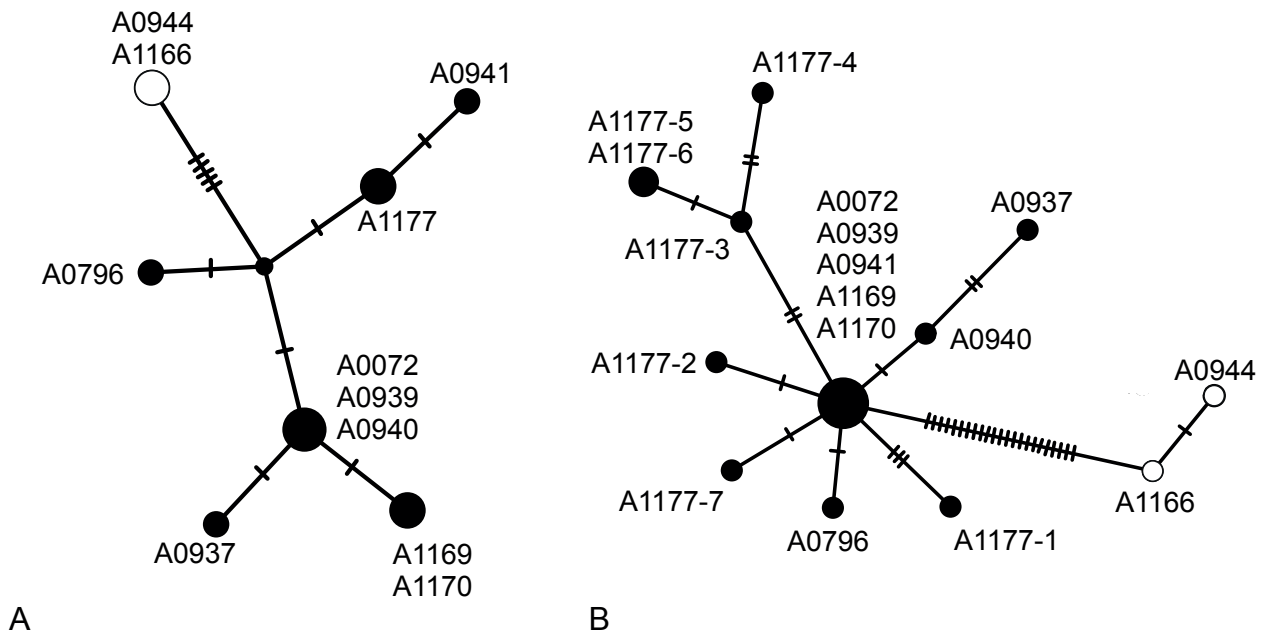


Fig. 1. Phylogenetic networks of cpDNA haplotypes (A) and nrDNA ribotypes (B) based on accessions of *Heteromera fuscata* (●) and *H. philaenorum* (○) described in Table 1. Numbers A1177-1 through A1177-7 refer to different ribotype sequences from this specimen after cloning of PCR products. The size of haplotype and ribotype dots corresponds to the number of sequences collapsed into a single haplo- or ribotype, with the smallest one (in A) representing a hypothetical one. Tick marks refer to the number of mutations separating haplo- or ribotypes (nucleotide substitutions or indels).

anatomy (vallecular resin ducts and myxogenic cells along ribs) with its closely-knit generic members *Chlamydo-phora* Less., *Chrysanthoglossum* B. H. Wilcox & al., *Co-leostephus* Cass., *Glossopappus* Kunze, *Leucanthemum* Mill, *Mauranthemum* Vogt & Oberpr., *Plagius* DC. and *Rhodanthemum* B. H. Wilcox & al. (the *Leucantheminae* s.str.). Based on single individuals representing the two *Heteromera* species, a molecular phylogenetic study using sequence information for four nuclear markers and three plastid loci carried out by Wagner & al. (2019) revealed the well-supported sister-group relationship of *H. fuscata* and *H. philaenorum* in a species-tree reconstruction of the subtribe *Leucantheminae* of *Compositae–Anthemideae*. The genus was found to be nested among the genera *Dave-aea* Mariz and *Otospermum* Willk. and the *Leucanthemi-nae* s.str.; however, no statistically trustworthy closer relationship to one of these has been revealed.

The chloroplast haplotype and nuclear ribotype networks presented here (Fig. 1) support the close relationship between the two *Heteromera* species, with the two representatives of *H. philaenorum* (A0944 from Tunisia and A1166 from Libya) showing some molecular uniformity and a distinct phylogenetic separation from the genetically more diverse *H. fuscata*. However, this genetic uniformity of the former species may be also attributable to the restricted sampling of this taxon (two populations vs. nine populations of *H. fuscata*). An accession of the latter species (A1177) provided no readable nrDNA ITS sequence in the direct sequencing procedure and the PCR product had to be cloned, resulting in six different ribotypes. Owing to the multi-copy nature of the nuclear

ribosomal repeat (Álvarez & Wendel 2003), this could be best explained by the non-homogenization of this marker, which is often seen when this region is cloned. The clustering of cloned sequences from specimen A1177 with ribotypes from all other accessions of *H. fuscata* argues for a non-hybridogenic origin of this variation. Since polyploidy is very rare in annual members of the *Compositae–Anthemideae* (Oberprieler & al. 2009), we also think that ribotype variation observed in accession A1177 is also no indication of genome duplication in this specimen.

#### Key to the species

1. Achenes of disc florets < 2.5 mm long, resin sacs visible in ribs apically, pappus of 5 or 6 distinct scales  
..... *H. fuscata*
- Achenes of disc florets > 3 mm long, resin canals in ribs not visible, pappus a basally callose and apically narrow, scarious corona ..... *H. philaenorum*

#### Taxonomy

*Heteromera* Pomel in Bull. Soc. Sci. Phys. Algérie 11: 60. 1874 (Nouv. Mat. Fl. Atl.: 60. 1874). – **Lectotype (designated here):** *Heteromera fuscata* (Desf.) Pomel (≡ *Chrysanthemum fuscatum* Desf.).

*Description* — Annual herbs. Indumentum of basifixed hairs. Stems erect or ascending-erect. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate, heterogamous. Involucre meniscoid to hemispheric. Phyllar-

ies (involucral bracts) in 3 or 4 imbricate rows, with light brown to brown, scarious margins. Receptacle convex to conic, epaleate. Florets heteromorphic. Ray florets female, fertile or sterile; limb white. Disc florets hermaphrodite, fertile; corolla apically 5-lobed, yellow or basally reddish. Stamens glabrous; filament collar enlarged; anthers rounded at base, apical anther appendages ovate and blunt; pollen tricolporate, spiny. Style terete, slightly swollen at base, set in a conspicuous nectary, style branches truncate-penicillate at tips. Achenes cylindrical to obovoid, straight or slightly curved, 3–5-ribbed, circular or dorsiventrally flattened in cross-section; apex with an adaxially longer scarious corona or auricle, with a short, basally callose corona, or with 5–9 obovate scales (pappus); pericarp with myxogenic cells along ribs and on abaxial surface, with 3–5 resin canals or apical resin sacs in ribs.

*Chromosome number* — Basic chromosome number  $x = 9$ . Ploidy level:  $2x$ .

*Distribution* — Two species in North Africa, in Algeria, Tunisia and Libya (Fig. 5).

***Heteromera fuscata*** (Desf.) Pomel in Bull. Soc. Sci. Phys. Algérie 11: 60. 1874  $\equiv$  *Chrysanthemum fuscatum* Desf., Fl. Atlant. 2: 283. 1799  $\equiv$  *Pyrethrum fuscatum* (Desf.) Willd., Sp. Pl. 3: 2156. 1803  $\equiv$  *Matricaria fuscata* (Desf.) Poir. in Lam. & Poir., Encycl. Suppl. 3, 2: 602. 1814  $\equiv$  *Tripleurospermum fuscatum* (Desf.) Sch. Bip. in Bonplandia 8: 369. 1860. – Ind. loc.: “Habitat in agris incultis prope Tunetum”. – Holotype: *Chrysanthemum fuscatum* (P-Desf.); isotype: ex Herb. Desfontaines (FI-W [FI006519 image!]).

*Note* — The plant in the upper part of the holotype specimen in the “Herbier de la Flore Atlantique” (P-Desf.) served as a template for t. 237 of *Flora atlantica* (Desfontaines 1799). Desfontaines’s handwritten draft diagnosis is attached to the specimen.

= *Chrysanthemum fuscatum* f. *pubescens* Trotter in Nuov. Giorn. Bot. Ital., ser. 2, 22: 358. 1915. – Ind. loc.: “Bu Gheilan nel Gharian (24. IV. 913, Pamp., 18. III. 914 Trotter), Uadi Rumia nel Geb. Iefren (20. III. 914), Uadi Mellha ad occ. di Nalut (6. IV. 914)”. – **Lectotype (designated here)**: “Plantae Tripolitanae a R. Pampanini anno 1913 lectae, n. 3618”, Garian, Bu Gheilan, 24 Apr 1913, R. Pampanini (FI! [FI063907]). – Remaining syntypes: Gebel Gharian, Bugheilan–Gasr Gharian, 18 Mar 1914, A. Trotter (PORUN [image!]); Nalut, Uadi Melha, 6 Apr 1914, A. Trotter (PORUN [image!]).

*Note* — The plant material cited in the protologue of *Chrysanthemum fuscatum* f. *pubescens* (Trotter 1915) is heterogeneous and comprises both specimens of *Heteromera fuscata* and of *H. philaenorum*. While the first-cited specimen, which was collected by Pampanini on 24 April 1913 in “Garian, Bu Gheilan”, represents *H. fuscata*, two further specimens

from the original material (collected by Trotter on 18 March 1914 and 6 April 1914) belong to *H. philaenorum*. In accordance with Jeffrey’s assignment of *C. fuscatum* f. *pubescens* to *H. fuscata* in *A check-list of the Libyan flora* (Boulos 1979), Pampanini’s gathering kept in FI is designated here as the lectotype.

- *Pyrethrum fuscatum* “forma *gigantea*” J. Gay in sched. (B [B100673149], G [G00163362, G00163363], G [without barcode], MPU [MPU243276, MPU243278], P [P02813822, P02813914, P02813917], S [S11-13800], UPS).
- *Pyrethrum fuscatum* “forma *uberior*” Coss. in sched. (P [P00729944, P00729945, P00729949]).

*Illustrations* — Desfontaines, *Flora atlantica* 2: t. 237. 1799; Jafri & El-Gadi, *Flora of Libya* 107: 147, fig. 41. 1983; Ozenda, *Flore et Végétation du Sahara*, ed. 3: 439, fig. 163. 1991; Pottier-Alapetite, *Flore de la Tunisie*: 1005, fig. 1461. 1981. – Fig. 2A–I.

*Exsiccata* — Plantae de Tunisie, no. 144 (sub *Pyrethrum fuscatum*); Plantae Saharae algeriensis, no. 54 (sub *Chrysanthemum fuscatum*); Plantae Saharae algeriensis, no. 54a (sub *C. fuscatum*); Plantae Saharae algeriensis, no. 54bis (sub *C. fuscatum*); B. Balansa, Pl. D’Algérie, 1853, no. 782 (sub *P. fuscatum*); E. G. Paris, Iter boreali Africanum, no. 459 (sub *P. trifurcatum* (Desf.) Willd.); P. Jamin, Pl. d’Algérie, 1852, no. 275 (sub *P. fuscatum*); Fragmenta Florae Algeriensis exsiccata, no. 144 (sub *P. fuscatum*); J.-A. Battandier et L. Trabut, Pl. d’Algérie, no. 161 (sub *P. fuscatum*); Société Française pour l’échange des plantes vasculaires – Exsicc. B. de Retz, Fascicule n° 12 (1964–1966), no. 5014 (sub *Heteromera fuscata* var. *fuscata*); L. Kralik, Pl. Tunetanae, no. 86 (sub *P. fuscatum*); L. Kralik, Pl. Tunetanae, no. 86a (sub *P. fuscatum* “forma *gigantea*” J. Gay); Plantae de Tunisie, no. 408 (sub *P. fuscatum*); E. Bourgeau, Pl. d’Algérie, 1856, no. 192 (sub *P. fuscatum*); Dr. R. Maire et M. Weiller – Iter Libycum, 1938, no. 852 (sub *C. fuscatum*).

*Description* — Plants annual. Indumentum of up to 0.5 mm long, basifixed, white hairs. *Stems* herbaceous, erect or ascending-erect, 2–15(–30[–50]) cm long, solitary and with 1 capitulum or branched in lower part and with 2–5(–10) capitula, densely leafy in lower part, sulcate, green or greyish, sparsely hairy. *Leaves* alternate, green, sparsely hairy, distal part pinnatisect with linear, minutely mucronate lobes, proximal part linear, entire, basally slightly broadened, uppermost cauline leaves undivided, linear. *Capitula* terminal, pedunculate, solitary, 1.2–3(–5) cm in diam. (measured from pressed specimens), heterogamous and radiate. *Involucre* hemispheric, 0.8–1.5(–2) cm in diam. (measured from pressed specimens). *Involucral bracts* imbricate, in 3(or 4) layers, herbaceous, light green, apically sometimes slightly reddish, with broad, pale to brown, scarious margins, with central resin canals; outer bracts triangular to ovate, abaxially

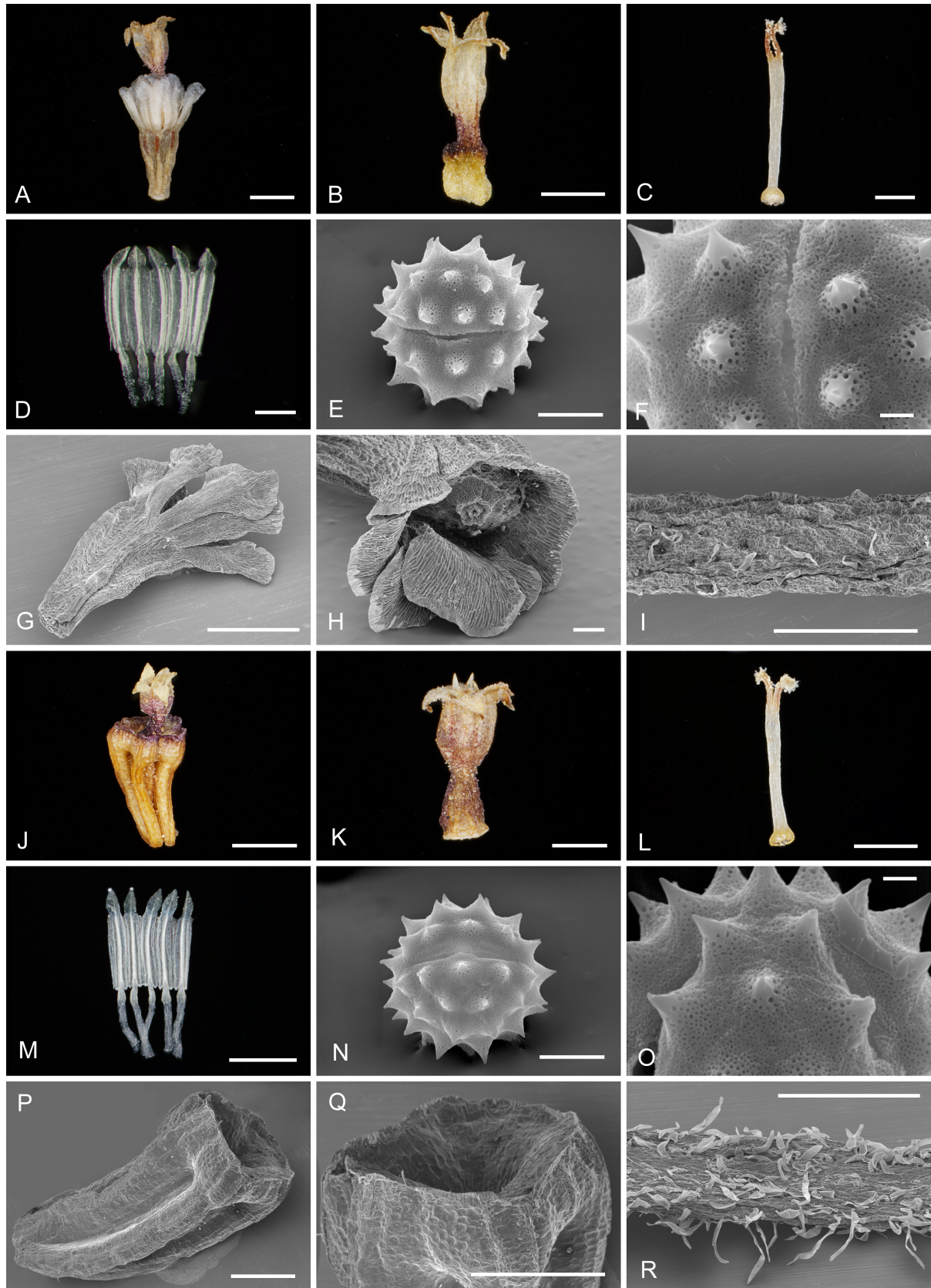


Fig. 2. Light microscope and SEM micrographs from A–I: *Heteromera fuscata* (Vogt 12847 & Oberprieler 7152) and J–R: *H. phyllaenorum* (Vogt 13007 & Oberprieler 7312). – A: disc floret; B: corolla of disc floret; C: style; D: stamens; E: pollen grain; F: detail of pollen grain; G: achene; H: apical part of achene; I: hairs on leaf; J: disc floret; K: corolla of disc floret; L: style; M: stamens; N: pollen grain; O: detail of pollen grain; P: achene; Q: apical part of achene; R: hairs on leaf. – Scale bars: A, B, G, I, K–M, P–R = 1 mm; C, D = 500  $\mu$ m; E, N = 10  $\mu$ m; F, O = 2  $\mu$ m; H = 200  $\mu$ m.



Fig. 3. *Heteromera philaeorum*. Lectotype in MPU (MPU004064). – Image © and by courtesy of the Université de Montpellier – DCSPH, reproduced with permission.

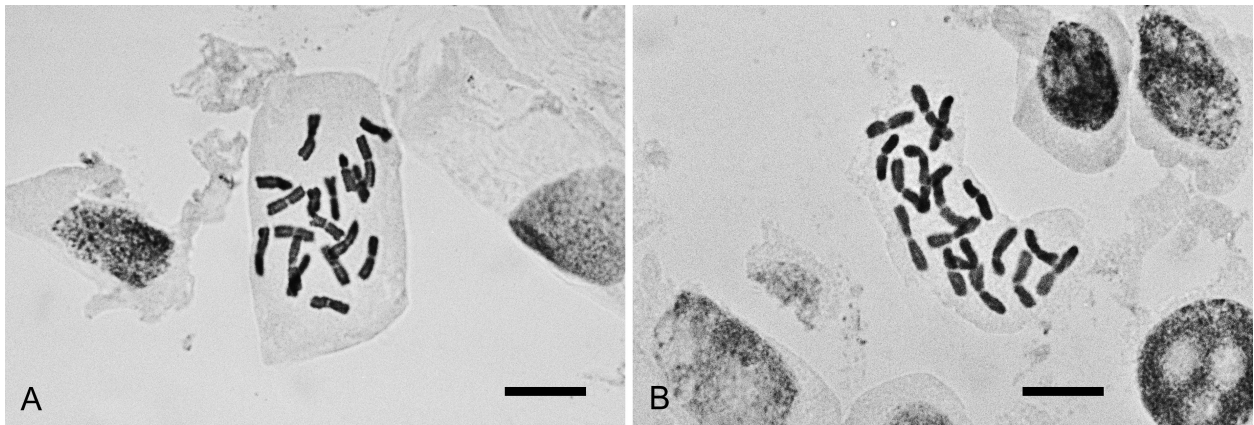


Fig. 4. Metaphase plates in *Heteromera*. – A: *H. fuscata*,  $2n = 18$  (Vogt 12800 & Oberprieler 7105); B: *H. philaenorum*,  $2n = 18$  (Vogt 13007 & Oberprieler 7312). – Scale bars = 10  $\mu\text{m}$ .

hairy; middle ones oblong to obovate, 4.5–6 mm long, 2–3 mm wide, abaxially hairy; innermost ones oblong to narrow obovate, glabrous or abaxially sparsely hairy. *Receptacle* convex to conic, epaleate. *Florets* heteromorphic. *Ray florets* hermaphrodite, fertile; limb white, elliptic to oblong, 4–12(–20) mm long, 2–4.5(–7) mm wide, apically rounded or 3-dentate, tubular part 1–1.2(–2 mm long. *Disc florets* hermaphrodite, fertile; corolla 2.5–3.5 mm long, apically 5-lobed, lobes dorsally with an appendage, yellow, tube basally expanded and sometimes reddish. *Fertile achenes of ray florets* cylindric to obovoid, straight or slightly curved, dorsiventrally slightly flattened, (1.5–)2–2.5 mm long, 1–1.2 mm wide, 3(–5)-ribbed; pappus a 1.5–2.5 mm long, membranous, adaxially longer corona; pericarp with myxogenic cells along ribs and on abaxial surface, with 3(–5) resin sacs apically in ribs. *Achenes of disc florets* obovoid, slightly curved, dorsiventrally slightly flattened, 1.5–2.5 mm long, 1–1.2 mm wide, 5-ribbed with 1 ventral, 2 lateral and 2 weaker dorsal ribs; pappus of 5–9 up to 1–1.5 mm long, adaxially longer, membranous, obovate-spatulate scales; pericarp with myxogenic cells along ribs and on abaxial surface, with 5 resin sacs apically in ribs.

**Chromosome number** —  $2n = 18$  chromosomes. *Heteromera fuscata* has previously not been examined karyologically. Plants from three populations in Tunisia were studied (Fig. 4A). As discussed above, we do not think that the ribotype variation observed in specimen A1177 is due to polyploidy, but rather the consequence of non-homogenization of the nuclear ribosomal repeat, which is often observed for this molecular marker (Álvarez & Wendel 2003).

#### New chromosome counts

$2n = 18$ : Tunisia, Gouvernorat Gabès, Tunisie du Sud, Monts de Matmata, road C 104 between Médenine and Matmata, c. 2.5 km NW of Toujane, stony slopes, 590 m, 33°28.350'N, 10°07.477'E, 15 May 1994, R. Vogt 13240 & C. Oberprieler 7545 (B [B100673048, B100673076], Herb. Oberprieler).

$2n = 18$ : Tunisia: Gouvernorat Tozeur, Tunisie du Sud, Chott Er Rahim, road P 16 between Chbika and Tozeur, c. 10 km SE of Chbika, 0 m, 34°14.973'N, 07°52.953'E, sand, 10 May 1994, R. Vogt 12800 & C. Oberprieler 7105 (B [B100673051, B100673077], Herb. Oberprieler). – Fig. 4A.

$2n = 18$ : Tunisia: Gouvernorat Tataouine, Tunisie du Sud, Monts de Matmata, road C 207 between Tataouine and Chenini, c. 5 km W of turn-off to Ghomrassen, 390 m, 32°55.619'N, 10°20.841'E, sandy plains, 14 May 1994, R. Vogt 13115 & C. Oberprieler 7420 (B [B100273213], Herb. Oberprieler); ibidem, cult. Hort. Bot. Berlin-Dahlem, 25 Jul 1996, R. Vogt s.n. & C. Oberprieler (B [B100273230, B100673053]).

**Flowering period** — (January–)March–May.

**Distribution and habitat** — *Heteromera fuscata* is restricted to N Africa, where it is native to Algeria, Tunisia and Libya (Fig. 5). The indication of this species for Morocco in Med-Checklist (Greuter & Raab-Straube 2008), Euro+Med PlantBase (Euro+Med 2006+) and Plants of the World Online (POWO 2019+), based on an alleged indication in Ozenda (1977), has not been confirmed and was already questioned by Ibn Tattou (Fennane & al. 2014).

*Heteromera fuscata* is reported to grow on sandy plains, stony slopes and in dry riverbeds, on road embankments and along field margins from sea level up to 800 m.

**Common names** — “Baïaoua” (Quézel & Santa 1963).

**Etymology** — The epithet “*fuscata*” refers to the brown-bordered involucre bracts of the capitula.

***Heteromera philaenorum*** Maire & Weiller in Bull. Soc. Hist. Nat. Afrique N. 30: 283. 1939  $\equiv$  *Tripleurospermum philaenorum* (Maire & Weiller) Alavi in Jafri & El-Gadi, Fl. Libya 107: 148. 1983. – Ind. loc.: “In pascuis aridis lapidosis litoris Magnae Syrteos inter



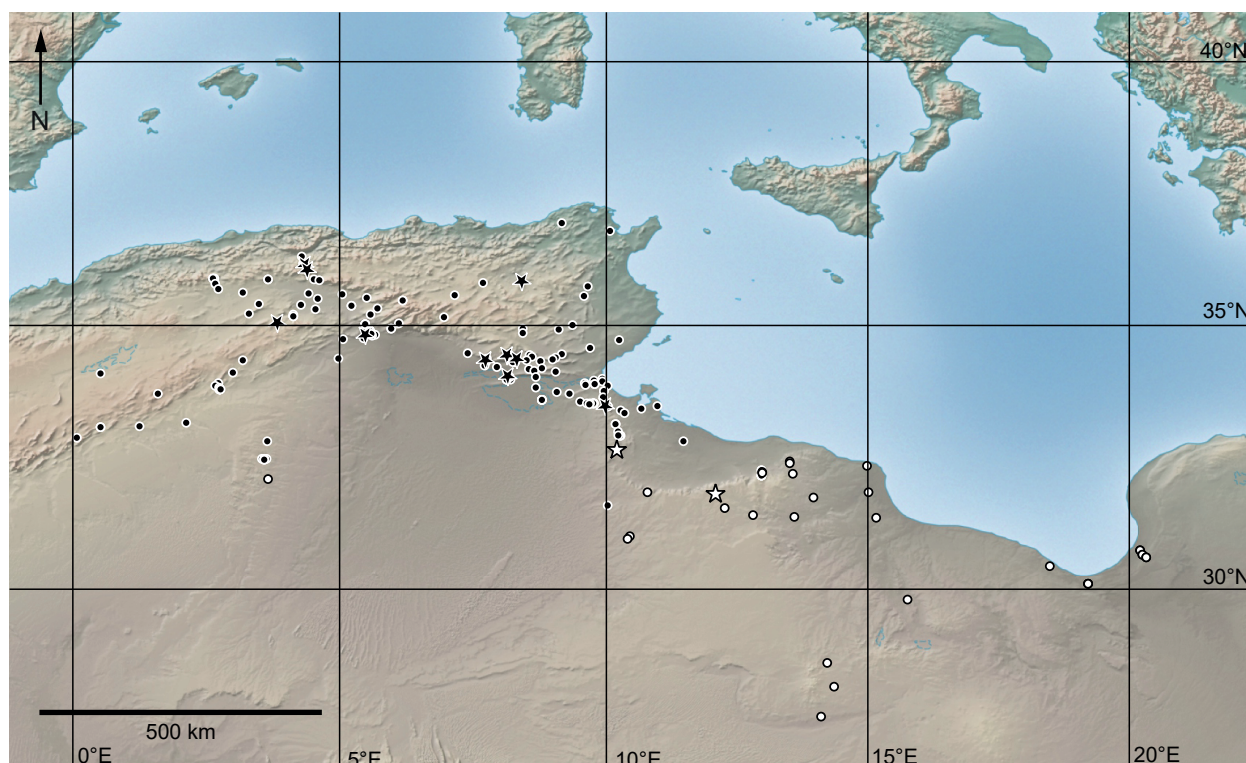


Fig. 5. Distribution of *Heteromera fuscata* (●) and *H. philaenorum* (○) in N Africa according to revised material. Asterisks (★) indicate populations studied in the molecular analysis.

Aras Philaenorum et Diversorium” and “Cyrénaïque: pâturages pierreux du littoral de la Grande Syrte entre la Casa Ristoro et l’Arc de Triomphe des Philènes (n° 853)”. – **Lectotype (designated here):** “Dr. R. Maire et M. Weiller – Iter Libycum, 1938, no. 853”, Cyrenaica, in aridis lapidosis litoris Magnae Syrteos prope Casa Ristoro prope Aras Philaenorum, 29 Apr 1938, *R. Maire & M. Weiller* (MPU! [MPU004064]; isolectotype: P! [P02088603]).

*Note* — As in many other cases (e.g. Vogt & Oberprieler 1996; Vogt 2005), the type specimen of *Heteromera philaenorum* was cut up after Maire’s herbarium was moved from Algiers to Montpellier, one part being passed on to Paris. In the case of the type of *H. philaenorum*, the lower part of the original sheet from Maire’s collection with the original label remains in MPU (lectotype, Fig. 3), while the upper part with two plants and the label “Herbier Maire” is now housed in P (isolectotype).

= *Chrysanthemum fuscatum* var. *tripolitanum* Pamp. in Bull. Soc. Bot. Ital. 1914: 19. 1914 (& Pl. Tripol.: 256. 1914) ≡ *Chrysanthemum tripolitanum* (Pamp.) Le Houérou in Bull. Soc. Bot. France 116: 282. 1969 (Turland & al. 2018: Art. 41.8(c)). – Ind. loc.: “(N. 1996)” [& “Tarhuna, Uadi Tenziua sul Ras Maader, 1.4. (n. 1996)”. – Holotype: “Plantae Tripolitanae a R. Pampanini anno 1913 lectae, n. 1996”, Tarhuna, Uadi Tenziua sul Ras Maader, 1 Apr 1913, *R. Pampanini* (FI! [FI001205]).

*Note* — Alavi in his treatment of the *Compositae* for *Flora of Libya* (Alavi 1983) incorrectly included

*Chrysanthemum fuscatum* var. *tripolitanum* in *Tripleurospermum fuscatum* (≡ *Heteromera fuscata*).

= *Chrysanthemum fuscatum* f. *subcanescens* Trotter in Nuov. Giorn. Bot. Ital., ser. 2, 22: 358. 1915. – Ind. loc.: “Reg. merid. del Tarhuna: Tenziua sul Ras Maader (1. IV. 913. Pamp.), Uadi el Maader nel Tarhuna (13. V. 913. Trotter), a sud del Gharian tra Ghedama e Uadi Gani (23. IV. 914), bacino del Sofeggín presso la carovaniera tra Melga e Nesma (2. V. 914) e tra Tininai e Scemmàch (5. V. 914)”. – **Lectotype (designated here):** “Ar... sassosi a Uadi el Maader / Tarhuna”, 13 May 1913, *A. Trotter* (PORUN [image!]). – Remaining syntypes: “Plantae Tripolitanae a R. Pampanini anno 1913 lectae, n. 1996”, Tarhuna, Uadi Tenziua sul Ras Maader, 1 Apr 1913, *R. Pampanini* (FI! [FI001205]); Gebel Gharian, Gasr Gharian–Tercia, 23 Apr 1914, *A. Trotter* (PORUN [image!]); Presso la carovaniera Melga Sofegin Nesna, 2 May 1914, *A. Trotter* (PORUN [image!]); Presso la carovaniera da Bir Tininai a Scemeg, 5 May 1914, *A. Trotter* (PORUN [image!]).

*Note* — Jeffrey, in his treatment of the *Compositae* for *A check-list of the Libyan flora* (Boulos 1979), included *Chrysanthemum fuscatum* f. *subcanescens* in *Heteromera fuscata*, although Trotter (1915) cited in the protologue of *H. fuscata* the type material of *C. fuscatum* var. *tripolitanum*, which Jeffrey on the other hand included in *H. philaenorum*. Antonio de Natale (PORUN) kindly supported the verification of the identity of the type material of *C. fuscatum* f. *sub-*

*canescens* by providing close-up images of the relevant achene characters.

*Illustrations* — Fig. 2J–R.

*Exsiccata* — Dr. R. Maire et M. Weiller – Iter Libycum, 1938, no. 853 (sub *Heteromera philaenorum*).

*Description* — Plants annual. Indumentum of up to 0.6 mm long, basifixed, white hairs. *Stems* herbaceous, erect or ascending-erect, 3–10(–20) cm long, solitary with 1 capitulum or branched in lower part and with 2(–4) capitula, densely leafy in lower part, sulcate, green or greyish, sparsely to densely hairy. *Leaves* alternate, green or greyish, sparsely to densely hairy, distal part pinnatisect/tripartite with linear, minutely mucronate lobes, proximal part linear, entire, basally slightly broadened, uppermost cauline leaves undivided, linear. *Capitula* terminal, pedunculate, solitary, 2–3.5(–5) cm in diam. (measured from pressed specimens), heterogamous and radiate. *Involucre* hemispheric, 1.2–1.8 cm in diam. (measured from pressed specimens). *Involucral bracts* imbricate, in 3(or 4) layers, herbaceous with broad, pale to brown, scarious margins; outer bracts triangular to ovate, abaxially densely hairy; middle ones ovate to oblong, 5–7.5 mm long, 2–3 mm wide, abaxially densely hairy; innermost ones oblong to narrow obovate, glabrous or abaxially sparsely hairy. *Receptacle* convex to conic, epaleate. *Florets* heteromorphic. *Ray florets* hermaphrodite, fertile; limb white, elliptic to oblong, 8–15(–20) mm long, 4–7.5(–9) mm wide, apically rounded or 3-dentate, tubular part 1.2–1.5(–2 mm long. *Disc florets* hermaphrodite, fertile; corolla 3–3.5 mm long, apically 5-lobed, lobes dorsally with an appendage, yellow, tube basally expanded. *Fertile achenes of ray florets* cylindrical to obovoid, straight or slightly curved, dorsiventrally flattened, 3–4 mm long, 1.5–2 mm wide, 4(or 5)-ribbed; pappus a 0.5–1 mm long, basally callose, apically membranous and often adaxially somewhat longer corona; pericarp with myxogenic cells along ribs, with resin canals in ribs. *Achenes of disc florets* cylindrical to obovoid, straight or slightly curved, circular in cross-section, (3–)3.5–4 mm long, 1.7–2.2 mm wide, 5-ribbed, ribs conspicuous protruding and thick; pappus a 0.5–0.8 mm long, basally strongly callose, apically narrowly membranous corona; pericarp with myxogenic cells along ribs, with resin canals in ribs.

*Chromosome number* —  $2n = 18$  chromosomes (Fig. 4B). *Heteromera philaenorum* has previously not been investigated karyologically.

*New chromosome count*

$2n = 18$ : Tunisia, Gouvernorat Tataouine, Tunisie du Sud, road P 19 between Tataouine and Remada, c. 4.5 km S of Bir Thlethine, 420 m, 32°39'N, 10°19'E, sandy plains and fields E of road, 13 May 1994, R. Vogt

13007 & C. Oberprieler 7312 (B [B100673044, B100673046], MA [MA586902], Herb. Oberprieler); ibidem, cult. Hort. Bot. Berlin-Dahlem, 17 Aug 1995, R. Vogt s.n. & C. Oberprieler (B [B100673047], M, MA). – Fig. 4B.

*Flowering period* — (February–)March–May.

*Distribution and habitat* — *Heteromera philaenorum* is endemic to the desertic southern regions of Algeria, Tunisia and Libya (Fig. 5), where it is reported to grow on sandy plains and in dry riverbeds, on road embankments, along field margins and on stony slopes from the littoral up to 700 m above sea level.

In terms of mean annual precipitation, *Heteromera philaenorum* is found in considerably drier habitats than its sister-species. While the latter prefers habitats with 180–210 mm (95% confidence interval) annual precipitation, the former is adapted to annual precipitation values of 100–160 mm (WorldClim variable BIO12 gained from QGIS analysis with all georeferenced occurrence data). In correspondence with statistical analyses in the flora of California (Baker 1972) and with experiments performed with the Sonoran annual *Dithyrea californica* Harv. (*Brassicaceae*; Larios & al. 2014), which found advantages for species or individuals with larger seed sizes in desert communities with higher likelihoods of drought stress compared to their mesic counterparts, the distinctively larger size of achenes in *H. philaenorum* may be due to an adaptation to these extremely dry habitats in S Algeria, Tunisia and Libya.

*Note* — *Heteromera philaenorum* was not previously reported from Algeria and Tunisia.

*Etymology* — The epithet “*philaenorum*” refers to the ancient *Arae Philaenorum* (Altars of the Philaeni) located near Ras Lanuf near the possible borders between Carthage and Cyrene. Until 1970, the area was marked by a monumental arch (Marble Arch, Arch of the Philaeni, al-Gaus) erected in 1937 during the period of Italian colonization in Libya.

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## References

- Alavi S. A. 1983: *Compositae*. – Pp. 1–455 in: Jafri S. M. H. & El-Gadi A. (ed.), *Flora of Libya* **107**. – Tripolis: Al Faateh University, Faculty of Science, Department of Botany.
- Álvarez I. & Wendel J. F. 2003: Ribosomal ITS sequences and plant phylogenetic inference. – *Molec. Phylogen. Evol.* **29**: 417–434.
- Baker H. G. 1972: Seed weight in relation to environmental conditions in California. – *Ecology* **53**: 997–1010.
- Baldwin B. G. & Markos S. 1998: Phylogenetic utility of the external transcribed spacers (ETS) of 18S–26S rDNA: congruence of ETS and ITS trees of *Calyca-denia* (*Compositae*). – *Molec. Phylogen. Evol.* **10**: 449–463.
- Blattner F. R. 1999: Direct amplification of the entire ITS region from poorly preserved plant material using recombinant PCR. – *BioTechniques* **27**: 1180–1186.
- Boulos L. 1979: A check-list of the Libyan flora 3. *Compositae* (by C. Jeffrey). – *Candollea* **34**: 307–332.
- Bremer K. & Humphries C. J. 1993: Generic monograph of the *Asteraceae–Anthemideae*. – *Bull. Brit. Mus. (Nat. Hist.), Bot.* **23**: 71–177.
- Clement M., Snell Q., Walker P., Posada D. & Crandall K. 2002: TCS: estimating gene genealogies. – *Parallel and Distributed Processing Symposium, International Proceedings* **2**: 184.
- Desfontaines R. 1798–1799: *Flora atlantica, sive historia plantarum, quae in Atlante, agro tunetano et algeriensis crescunt* **2**. – Parisiis: L. G. Desgranges.
- Doyle J. J. & Dickson E. E. 1987: Preservation of plant samples for DNA restriction endonuclease analysis. – *Taxon* **36**: 715–722.
- Doyle J. J. & Doyle J. S. 1987: A rapid DNA isolation procedure for small quantities of fresh leaf tissue. – *Phytochem. Bull. Bot. Soc. Amer.* **19**: 11–15.
- Euro+Med 2006+ [continuously updated]: Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. – Published at <http://ww2.bgbm.org/EuroPlusMed/> [accessed 30 Jan 2019].
- Fennane M., Ibn Tattou M. & El Oualidi J. (ed.) 2014: *Flore pratique du Maroc* 3. – *Trav. Inst. Sci., Sér. Bot.* **40**: I–XI, 1–793.
- Greuter W. & Raab-Straube E. von (ed.) 2008: *Med-Checklist – a critical inventory of vascular plants of the circum-mediterranean countries. 2 Dicotyledones (Compositae)*. – Palermo, Genève, Berlin: OPTIMA.
- Hall T. 1999: BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – *Nucl. Acids Symp. Ser.* **41**: 95–98.
- Ibn Tattou M. & Fennane M. 2009: *Flore vasculaire du Maroc, inventaire et chorologie* **2**. – *Trav. Inst. Sci. Univ. Mohammed V, Sér. Bot.* **39**: 1–398.
- Larios E., Búrquez A., Becerra J. X. & Venable D. L. 2014: Natural selection on seed size through the life cycle of a desert annual plant. – *Ecology* **95**: 3213–3220.
- Lee J., Baldwin B. G. & Gottlieb L. D. 2002: Phylogeny of *Stephanomeria* and related genera (*Compositae–Lactuceae*) based on analysis of 18S–26S nuclear rDNA ITS and ETS sequences. – *Amer. J. Bot.* **89**: 160–168.
- Lee C. & Wen J. 2004: Phylogeny of *Panax* using chloroplast *trnC–trnD* intergenic region and the utility of *trnC–trnD* in interspecific studies of plants. – *Molec. Phylogen. Evol.* **31**: 894–903.
- Maire R. & Weiller M. 1939: *Contributions à l'étude de la Flore de la Libye* [Maire R., Contributions à l'étude de la Flore de l'Afrique du Nord, Fascicule 27]. – *Bull. Soc. Hist. Nat. Afrique N.* **30**: 255–314.
- Murbeck S. 1897: *Contributions à la connaissance de la flore du Nord-Ouest de l'Afrique et plus spécialement de la Tunisie, I. Ranunculaceae – Cucurbitaceae*. – *Acta Univ. Lund.* **33(12)**: [I]–VI, [1]–126, t. 1–6.
- Oberprieler C., Himmelreich S. & Vogt R. 2007: A new subtribal classification of the tribe *Anthemideae* (*Compositae*). – *Willdenowia* **37**: 89–114.
- Oberprieler C., Himmelreich S., Källersjö M., Vallès J., Watson L. E. & Vogt R. 2009: Tribe *Anthemideae* Cass. – Pp. 631–666 in: Funk V. A., Susanna A., Stuessy T. F. & Bayer R. J. (ed.), *Systematics, evolution, and biogeography of the Compositae*. – Washington, DC: IAPT.
- Oberprieler C. & Vogt R. 2000: The position of *Castrilanthemum* Vogt & Oberprieler and the phylogeny of Mediterranean *Anthemideae* (*Compositae*) as inferred from nrDNA ITS and cpDNA *trnL/trnF* IGS sequence variation. – *Pl. Syst. Evol.* **225**: 145–170.
- Ozenda P. 1977: *Flore du Sahara, ed. 2*. – Paris: Centre National de la Recherche Scientifique.
- Pampanini R. 1914a: *Piante nuove della Tripolitania settentrionale*. – *Bull. Soc. Bot. Ital.* **1914**: 10–20.
- Pampanini R. 1914b: *Plantae tripolitanae ab auctore anno 1913 lectae et repertorium florum vascularis Tripolitaniae*. – Firenze: Stabilimento Pellas.
- Pomel A. 1874: *Nouveaux matériaux pour la flore atlantique*. – *Bull. Soc. Sci. Phys. Algérie* **11**: 1–260.
- Pottier-Alapetite G. 1981: *Flore de la Tunisie, Angiospermes-Dicotyledones, Gamopétales* **3**. – Tunis: Imprimerie Officielle de la République Tunisienne.
- POWO 2019+ [continuously updated]: *Plants of the World Online*. Facilitated by the Royal Botanic Gardens, Kew. – Published at <http://www.plantsoftheworldonline.org/> [accessed 31 Mar 2020].

- QGIS Development Team [continuously updated]: 'QGIS Geographic Information System'. Open Source Geospatial Foundation Project. – Published at <https://qgis.org/en/site/> [accessed 15 Feb 2021].
- Quézel P. & Santa S. 1963: Nouvelle Flore de l'Algérie et des régions désertiques méridionales **2**. – Paris: Centre National de la Recherche Scientifique.
- Rydin C., Pedersen K. R. & Friis E. M. 2004: On the evolutionary history of *Ephedra*: Cretaceous fossils and extant molecules. – Proc. Natl. Acad. Sci. U.S.A. **101**: 16571–16576.
- Shaw J., Lickey E. B., Schilling E. E. & Small R. L. 2007: Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. – Amer. J. Bot. **94**: 275–288.
- Thiers B. (ed.) 2008+ [continuously updated]: Index herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's virtual herbarium. – Published at <http://sweetgum.nybg.org/science/ih/> [accessed 31 Mar 2020].
- Trotter A. 1915: Nuovi materiali per una flora della Tripolitania. – Nuov. Giorn. Bot. Ital., ser. 2, **22**: 319–364.
- Vogt R. 2005: Lectotypification of twenty-one names in *Rhodanthemum* (*Compositae*, *Anthemideae*). – Taxon **54**: 479–484.
- Vogt R. & Oberprieler C. 1996: The genus *Nivellea* B. H. Wilcox, K. Bremer & Humphries (*Compositae*, *Anthemideae*). – Bot. J. Linn. Soc. **122**: 123–135.
- Wagner F., Ott T., Zimmer C., Reichart V., Vogt R. & Oberprieler C. 2019: 'At the crossroads towards polyploidy': genomic divergence and extent of homoploid hybridization are drivers for the formation of the ox-eye daisy polyploid complex (*Leucanthemum*, *Compositae*–*Anthemideae*). – New Phytol. **223**: 2039–2053.
- White T. J., Bruns T., Lee S. & Taylor J. 1990: Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. – Pp. 315–322 in: Innis M., Gelfand D., Sninsky J. & White T. (ed.), PCR protocols: a guide to methods and application. – San Diego: Academic Press.
- leuses de l'Oued à Barika, [35°23'N, 05°17'E], 23 Mar 1930, A. Dubuis (MPU [MPU358165]); Terres argileuses de l'Oued à Barika, [35°23'N, 05°17'E], 12 Apr 1931, A. Dubuis (MPU [MPU358164], P [P04087274]); El Kantara, Sahar., c. 580 m, [35°14'N, 03°21'E / 05°21'E?], in petrosis et campis argillosis, 22–23 May 1870, E. G. Paris (FI [FI063908], G [G00426996], US [US01822913]); El Kantara, [35°13'N, 05°42'E], Apr 1886, J.-A. Battandier & L. Trabut (G [G00163360, G00431770], L [L3653749], UPS); Aurès, Ghoufi, [35°03'N, 06°10'E], Apr 1936, J. Clastrier (MPU [MPU401431]). — Wilaya **BISKRA**: El Outaya, cercle de Batna, province de Constantine, [35°02'N, 05°35'E], 27 May 1853, H. de la Perraudière (RAB); El Outaya, [35°02'N, 05°35'E], Jun 1910, H. Burgeff (M [M0155754]); El Outaia, sud de la province de Constantine, [35°02'N, 05°35'E], 30 Mar 1858, E. Cosson (P [P02813883]); El Outaia, entre Batna et Biskra, province de Constantine, [35°02'N, 05°35'E], 27 May 1853, E. Cosson (P [P02813888]); Mshûnish gorge [M'chouneche], Gebel Aurès, [34°57'N, 06°00'E], 15 Apr 1937, A. H. G. Alston & N. D. Simpson 37288a (BM [BM001010380]); Basman(?), Gebel Aurès, [34°57'N, 06°00'E], 15 Apr 1937, A. H. G. Alston & N. D. Simpson 37288b (BM [BM001010381]); Pentes rocailleuses du Col de Sfa, près de Biskra, [34°55'N, 05°41'E], 11 Apr 1933, L. Faurel (MPU [MPU358161], P [P04087280]); Col de Sfa (Aurès) près Biskra, [34°55'N, 05°41'E], Apr 1936, Herb. M. Gerot Nicot (P [P02813857]); Pentes rocailleuses du col de Sfa près de Biskra, [34°55'N, 05°41'E], 12 Apr 1931, A. Dubuis (MPU [MPU358163], P [P04087275]); Alluvions graveleuses de l'oued Biskra, à Biskra, [34°52'N, 05°40'E], 10 Apr 1933, L. Faurel (MPU [MPU358162], P [P04087281]); Biskra, auf lehmigem Sand gegen das Hammam, [34°52'N, 05°40'E], 1914, O. Renner (M [M0155753]); Biskra, fontaine chaude, [34°52'N, 05°40'E], 13 Jun 1902 & 10 May 1904, L. Chevallier (P [P02813910]); Biskra, in alveis siccis rivulorum prope Ain Salahin, [34°52'N, 05°40'E], 13 Jun 1902, L. Chevallier (US [US01822774]); Prope Hammam es Salahin, [34°52'N, 05°40'E], 27 Apr 1912, T. J. Stomps (AMD [AMD34120]); Hammam Salahin près Biskra, [34°52'N, 05°40'E], 6 Apr 1903, S. Murbeck (UPS); Collines arides près des fontaines chaudes à Biskra, [34°52'N, 05°40'E], 3 Apr 1856, C. Schmitt (BM [BM001010375], K, MPU [MPU243250, MPU243253, MPU243254, MPU243265], P [P02813819, P02813826, P02813859, P02813887, P02813889], RB [RB00777781], S [S11-13793], US [US01822912]); Biskra, [34°51'N, 05°43'E], 9 Feb 1901, O. Juel (UPS); Biskra, sur les collines incultes, [34°51'N, 05°43'E], 19 Apr 1853, B. Balansa (B [B100673067], BM [BM001010371], FI [FI063909], G [G00163367, G00163368], G, P [P00729971, P02813821], S [S11-13795], UPS, WAG [WAG1443121]); Biskra, [34°51'N, 05°43'E], Apr 1890, L.-A. Girod (G [G00163369]); Biskra, sud de la province de Constantine, [34°51'N, 05°43'E], 5 Apr 1858, Herb. Schultz Bip. (P [P00729946]); Biskra, [34°51'N, 05°43'E], 15 Mar 1852, A. Hénon (MPU [MPU242860]); Biskra, [34°51'N, 05°43'E], Herb. Battandier (MPU [MPU242861]); Biskra, [34°51'N, 05°43'E], Herb. Miergues (P); Biskra, [34°51'N, 05°43'E], Feé (P [P02813886]); Environs de Biskra, les sables, [34°51'N, 05°43'E], Mar 1853, V. Jamain (P [P02813810]); Biskra, in al-

## Appendix 1: specimens examined

### *Heteromera fuscata* (Desf.) Pomel

**ALGERIA:** Wilaya **BATNA:** Eluagg(?), N'gaous, [35°32'N, 05°37'E], 1903, A. Joly (MPU [MPU242857]); Arch de Batna, province de Constantine, [35°29'N, 06°15'E], 26 May 1859, E. Cosson (P [P02813925]); El Kantara, Cercle de Batna, province de Constantine, [35°29'N, 06°15'E], 26 May 1853, E. Cosson (MPU [MPU243252], P [P02813884]); Les Tamarins, Cercle de Batna, province de Constantine, [35°20'N, 05°51'E], 25 May 1853, H. de la Perraudière (MPU [MPU243257]); Terres argi-

- luvion amnis, ad margines agrorum, [34°51'N, 05°43'E], Apr / May 1896, *L. Chevallier* (B [B100673072], FI [FI063910], G [G00163359, G00431772], P [P04296510, P02813901, P02813902, P02813907, P02813924, P04296510], WU, WAG [WAG1443119]); Biskra, lit de l'oued en amont de la ville, [34°51'N, 05°43'E], 27 Apr 1893, *L. Chevallier* (P [P02813904]); Biskra, Oued Biskra, [34°51'N, 05°43'E], 16 Apr 1937, *N. D. Simpson* 37294 (BM [BM001010372]); Department Aures, rocailles au Col de Sfa, au nord de Biskra, [34°54'N, 05°41'E], 5 May 1963, *A. Dubuis & L. Faurel* (L [L1308039], MPU [MPU358155, MPU208113], MSB [MSB119894], P [P04431351, P04431352, P04087276]); 8 km north of Biskra, Col de Sfa, 800 m, 34°54'N, 05°41'E, shallow soils on slate, 23 Apr 1976, *D. A. Sutton & S. J. Sutton* 590 (RNG); 8 km N of Biskra, Col de Sfa, 800 m, 34°54'N, 05°41'E, shallow soils on slate, 23 Apr 1976, *D. A. Sutton & S. J. Sutton* 582 (RNG); Sables près l'oasis de Chettma, environs de Biskra, [34°50'N, 05°48'E], 24 Feb 1852, *P. Jamin* (G [G00163370], G, K, MPU [MPU242855], P [P02813820, P02813881]); Oasis de Biskra, Constantine, [34°49'N, 05°44'E], Mar 1890, *J. Garrigues* (B [B100673066]); Rochers a Biskra, [34°51'N, 05°43'E], Feb 1933, *M. Weiller* (MPU [MPU370994]); Biskra, [34°51'N, 05°43'E], 1869, *Coste* (MPU [MPU444031]); In pascuis deserti inter Vescera (Biskra) et Tolga, [34°46'N, 05°33'E], 23 Mar 1933, *R. Maire* (MPU [MPU243255], P [P02813890]); Entre Biskra y Bou-Saâda, inmediaciones del cruce hacia Ouled-Djellal, [34°45'N, 05°06'E], 1 Apr 1986, *A. Aparicio & J. García Rowe* (SEV [SEV211158]); Oued Djedida, haut-plateau de la province de Constantine, [34°23'N, 05°00'E], 20 Apr 1863, *A. Letourneux* (P [P02813883]). — Wilaya **BORDJ BOU ARRÉRIDJ**: Les Portes de Fer, [36°11'N, 04°23'E], 4 Jun 1914, *G. Hibon* (P [P02813906]); Portes de Fer [36°11'N, 04°23'E], *L. Trabut* (MPU [MPU242859]); 50 km NW of Bordj Bou Arreridj, Chaîne des Bibans, 750 m, 36°10'N, 04°25'E, shale scree slopes, 23 Apr 1976, *D. A. Sutton & S. J. Sutton* 535 (RNG); Mansoura to El Mehiri station, Bouira to Bordj Bou Arreridj, 580–650 m, [36°04'N, 04°28'E], 24 May 1975, *P. Davis* 58258 (BM [BM001010373]); Sables de Midjez au nord de M'Sila, province de Constantine, [35°53'N, 04°37'E], Jul 1885, *V. Reboud* (P [P02813880]); In rupestribus calcareis aridis ad radice montium Maadid prope Medjez, [35°52'N, 04°44'E], 18 May 1925, *R. Maire* (MPU [MPU243249]). — Wilaya **BOUIRA**: Beni Mansour, [36°19'N, 04°21'E], Herb, Battandier (MPU [MPU242856]). — Wilaya **EL DJELFA**: Dhaga prope Birin, [35°38'N, 03°13'E], May 1882, *A. Letourneux* (K, P [P02813923]); Emplacements de campements près de l'Aïn-Feka au nord du Zahrez Chergui, [35°25'N, 03°34'E], 30 Mar 1936, *de Ager* (MPU [MPU358159], P [P04087278]); Aïn el Ibel, sud de la province d'Alger, [34°21'N, 03°13'E], 17 Jun 1856, *E. Cosson* (P [P02813888]); Hauts Plateaux, vers les Zahrez, *J.-A. Battandier* (MPU [MPU243261]); Zahrez, Apr 1883, *A. Letourneux* (BM [BM001010359]), G [G00426994]). — Wilaya **EL BAYADH**: Sables à Khadra, [34°06'N, 00°34'E], 2 May 1865, *A. Warion* (P [P-02813926]); Environs de Sidi Tifour, Djebel Amour, [33°43'N, 01°40'E], 15 May 1880, *A. Roux* (MPU [MPU243251]); O.[Oran], Brezina, [33°06'N, 01°16'E], 27 Apr 1862, Herb. Pomel (MPU [MPU243264]); Pente du Djebel Lembah près Bou-Semiroum [Bou Semghoun], [32°53'N, 00°03'E], 7 Feb 1865, *A. Warion* (P [P02813926]). — Wilaya **GHARDAÏA**: Oued Bir en dessous de Berrian dans le M'zab, sud de la province d'Alger, [32°49'N, 03°45'E], 24 May 1858, *E. Cosson* (P [P02813927]); Sahara, El Ateuf, ravin à l'entree de l'Ergoub, [32°29'N, 03°44'E], 7 Apr 1899, *L. Chevallier* (P [P02813903]); El Ateuf prop. Ghardaïa, in glareosis, [32°29'N, 03°41'E], 7 Apr 1899, *L. Chevallier* (FI [FI063911]); M'zab, Ghardaïa, [32°29'N, 03°38'E], Apr 1921, *F. Recroix* (MPU [MPU242858]); El Ateuf, dans le M'zab, sud de la province d'Alger, [32°29'N, 03°41'E], 17 May 1858, *E. Cosson* (P [P00729947, P02813817, P02813825, P02813879]); Beni Isguen [Isguen], M'zab, [32°28'N, 03°41'E], 3 May 1902, *L. Chevallier* (P [P02813909]); M'zab, [32°28'N, 03°41'E], *A. Letourneux* (MPU [MPU242863]); Environs de Ghardaïa–M'zab, [32°28'N, 03°41'E], Mar 1883, *A. Letourneux* (FI [FI058777]); In collibus saxosis inter Beni Isguen et Metlili, [32°22'N, 03°39'E], Mar 1883, *A. Letourneux* (G [G00426993]). — Wilaya **KHENCHELA**: M'chounech, Oued el Abiad, Aurès Mts., [35°10'N, 07°00'E], 15 Apr 1937, *A. H. G. Alston & N. D. Simpson* 37288 (BM [BM001010363]). — Wilaya **LAGHOUAT**: Sidi Makhelouf, sud de la province d'Alger, [34°07'N, 03°00'E], 16 Jun 1856, *E. Cosson* (P [P02813878]); Fissures des rochers des crêtes, partie sud du Djebel Milok vers 1150 m, près de Laghouat, [33°55'N, 02°50'E], 7 Apr 1955, *L. Faurel* (MPU [MPU358156], P [P04087277]); Environs de Laghouat, [33°48'N, 02°51'E], 2 Jun 1858, *H. de la Perraudière* (MPU [MPU242862]); Djebel Milagh près Laghouat, sud de la province d'Alger, [33°52'N, 02°46'E], 2 Jun 1858, *E. Cosson* (P [P00729948, P02813877]); Alluvion de l'oued Mzi à Ras el Aïoum près Laghouat, sud de la province d'Alger, [33°50'N, 02°51'E], 6 Jun 1858, *E. Cosson* (P [P00729944, P00729945, P00729949, P02813827, P02813828, P02813880, P02813921]); Sahara desert, El Aghuat, [33°48'N, 02°52'E], 31 Mar 1873, *G. Maw* (K); Sahara, Laghouat, [33°48'N, 02°52'E], Apr 1897, *L. Chevallier* (P [P02813911]); Laghouat, [33°48'N, 02°52'E], May 1918 (P, RAB); El Aghuat, sud de la province d'Alger, [33°48'N, 02°52'E], 13 Jun 1856, *E. Cosson* (P [P02813927]); Laghouat, Sahara, semi-desert conditions, [33°48'N, 02°52'E], 23 Mar 1931, Herb. R. Meinertzhagen (BM [BM001010366]); Rochers à Laghouat, sahara algérien, [33°48'N, 02°52'E], 3 May 1856, *V. Reboud* (P [P02813816, P02813889]); Laghouat, [33°48'N, 02°52'E], 3 May 1854, *V. Reboud* (MPU [MPU243256], P [P02813926], UPS); Laghouat, [33°48'N, 02°52'E], 1854, *V. Reboud* (G [G00426992]); Laghouat, Algerian Sahara, moist ground, [33°48'N, 02°52'E], 23 Mar 1931, Herb. R. Meinertzhagen (BM [BM001010361]); Alluvions caillouteuses ou sablonneuses de l'Oued Zergoun, au sud-ouest de Laghouat (Sud-algérois), [33°10'N, 02°08'E], 26 Mar 1946, *L. Faurel* (MPU [MPU358158], P [P04087283]); O.[Oran], Hauts Plateaux, M. Kraoula, [33°48'N, 02°53'E], 17 Jun 1860, *A. Pomel* (MPU [MPU243266]). — Wilaya **MEDEA**: Lieux incultes sur les rives de l'oued Cheliff près de Boghari, [35°54'N, 02°45'E], 5 May 1857, *O. Debeaux* (P [P02813887]); Bords de ravins au dessous de Boghari, [35°54'N, 02°43'E], 12 May 1857, Herb. O. Debeaux (P [P02813818]); Bord du torrents dans le Haut-Cheliff, cercle de Boghari, [35°54'N, 02°43'E], 12

May 1856, *O. Debeaux* (P [P03436984]); Pentes rocheuses du Djebel El Guettar près de Boghari, Dept. d'Alger, [35°48'N, 02°46'E], 12 Apr 1933, *A. Dubuis* (MPU [MPU358160], P [P04087282]); In ...ludosis inter Dhages el Banyan et Bou Guezoul [Bougzoul], [35°42'N, 02°50'E], Apr 1883, *A. Letourneux* (FI [FI063912]). — Wilaya **M'SILA**: Bou-Saâda, Moulin Ferrero, [35°11'31"N, 04°09'57"E], calizas, 2 Apr 1986, *A. Aparicio & J. García Rowe* (B [B100673060], SEV); Reç. le long de la route d'Aumale à Bou-Saâda de Sidi Aïssa, [35°53'N, 03°46'E], 24 Apr 1859, Herb. Alcide Charoy (P [P02813883]); Entre Baniou et Bou-Saâda, sud de la province de Constantine, [35°53'N, 03°46'E], 28 May 1865, *V. Reboud* (P); Sud de M'sila, province de Constantine, [35°37'N, 04°30'E], 24 May 1865, *V. Reboud* (P [P02813879]); Algérie, a 8 km de Magra, 680 m, [35°36'N, 05°05'E], 11 Jun 1990, *C. Benedi, A. Romo 5498 & P. Vives* (B [B100715346]); Hodna, province de Constantine, [35°31'N, 04°42'E], *Dukerley* (P); Baniou, [35°24'N, 04°20'E], May 1882, *A. Letourneux* (FI [FI063913]); Rive Sud du Chott Hodna, près de Bir el Mogari, (Sud algérois), [35°19'N, 04°39'E], 20 May 1953, *A. Dubuis* (MPU [MPU358157], P [P04087279]); Oued Bou-Saâda, sud de la province de Constantine, [35°13'N, 04°10'E], 1865, *V. Reboud* (P [P02813879, P02813926]); Dj. Kerdada près Bou-Saâda, sud de la province de Constantine, [35°11'N, 04°10'E], 15 May 1865, *V. Reboud* (P [P02813880]); Bou-Saâda, rocailles calcaires de Dj. Kerdada, [35°11'N, 04°10'E], 23 May 1921, *R. Maire* (MPU [MPU243268], P [P02813896]); Sahara-Atlas, 27 km SW Bou-Saâda an der Straße nach Djelfa, 920 m, 35°04'N, 03°58'E, 12 Apr 1982, *D. Podlech 37201* (M [M0155755], MSB [MSB003481]). — Wilaya **NAÂMA**: Pente pierreuse du Djebel Nzira près Arba Tatani [Arbaouats], sud de la province d'Oran, [33°05'N, 00°34'E], 18 May 1856, *L. Kralik* (BM [BM001010374], FI [FI063914], G [G00163366, G00163365], G, MPU [MPU243262, MPU243263], P [P02813817, P02813885], UPS, WAG [WAG1443120]); Arba Tahtani [Arbaouats], sud de la province d'Oran, [33°05'N, 00°34'E], 18 May 1856, *E. Cosson* (P [P02813887]). — Wilaya **ŌUM EL BOUAGHI**: Ad ripas Oued Mellag, [35°49'N, 07°51'E], 11–12 Jul 1863, *A. Letourneux* (P [P02813882]); Guerrah El Tarf, [35°35'N, 07°14'E], May 1883, *J. Reboud* (P [P02813922]). — **WITHOUT EXACT INDICATION**: Entre Boghar et Laghouat, province d'Alger, 1854, *Geslin?* (P [P02813878]); Union Agricole du Sig, province d'Oran, printemps, champs du Bois des Tamaris, 1852, *G.-L. Durando* (G [G00163371]). — Wilaya **TEBESSA**: Negrin, "Mission des Chott", [34°29'N, 07°31'E], 23–28 Mar 1875, *H. Duveirier 1537* ([P02813823]). — **WITHOUT EXACT INDICATION OR NOT LOCATED**: Djebel Rezahl nördl. Biskra, 400 m, 6 Mar 1908, *J. Braun-Blanquet* (MPU [MPU701990]); Oued Beiada/Hadnaf(?), province de Constantine, Jul 1859[?], *V. Reboud* (P [P02813878]); Beida, bords du Chot Iharf(?), May 1883, *A. Julien* (RAB; P [P03824809]); Oran, *A. Chabert* (FI [FI058776]); Algerie, *F. Schlumberger 311* (G [G00426995]). — **TUNISIA**: Gouvernorat **BIZERTE**: Bazina, in collibus ad basion Djebel Cherb ech Chergui, [36°57'N, 09°16'E], 22 Mar 1886, *A. Letourneux* (P [P02813833, P02813916]). — Gouvernorat **GABÈS**: Mélaoui, [34°19'N, 08°24'E], Apr 1911, *M. Bursaux* (G [G00163358]); Mélaoui, [34°19'N, 08°24'E], 4 Apr 1938, *N. D. Simpson 38148a* (BM [BM001010383]); Area around Ae Nouha oasis c. 20 miles northwest of Gabès, dry sandy soil, [34°00'N, 10°00'E], Apr 1968, *R. Young 92* (BM [BM001010357]); Oudref, [33°58'N, 09°58'E], lieux arides désertiques, Mar 1907, *C. J. Pitard* (BC, AMD [AMD36541], E [E00585616], G [G00163376]); Gobernación de Gabès, Mélaoui, gorges de Seldja, 34°20'03"N, 08°20'21"E, 200 m, pastos y matorral, substrato arenoso, 25 Mar 2009, *A. Herrero 3799 & al.* (B [B100550819], MA [MA797099]); Ksar El Maya, [33°57'N, 10°00'E], Herb. Pomel ([MPU243267]); In collibus aridis Djebel Keroua prope Gabès, [33°55'N, 09°46'E], 27 Apr 1854, *L. Kralik* (BM [BM001010368], E [E00585619], FI [FI063915], G [G00163364], G, MPU [MPU243271], P [P02813835, P02813858, P02813913, P02813918], RAB); Gabès, Dissa, in collibus aridis, [33°54'N, 09°59'E], Feb 1907, *C. J. Pitard* (B [B100673147], G [G00163372, G00163377], L [L3653748], MA [MA128814], MPU [MPU243273], US [US 01822911], WAG [WAG1443117]); Dj. Dissa pr. Gabès, [33°54'N, 09°59'E], 9 Apr 1896, *S. Murbeck* (BM [BM001010376], WU); El Hamma prope Gabès, [33°53'N, 09°47'E], 26 May 1884, *A. Letourneux* (P [P02813830]); In alluviae exsiccata Oued Gabès, [33°52'N, 10°07'E], 1 May 1854, *L. Kralik* (B [B100673149], G [G00163363, G00163362], G, MPU [MPU243276, MPU243278], P [P02813822, P02813914, P02813917], S [S11-13800], UPS); El Hamma–Tozeur, [33°50'N, 08°51'E], 7 Apr 1912, *H. Humbert* (MPU [MPU243272], RAB); Champs près Djebel Gafsa, route de Gabès à Matmata, [33°46'N, 10°02'E], 19 Apr 1909, *L. Chevallier* (P [P02813905], P); Gabès, montagnes de Matmata, calcaire, 400–500 m, [33°46'N, 10°02'E], Apr 1909, *R. Maire* (P [P04231627]); In convallibus et praeruptis Djebel Tebaga / Dj. Aziza prope El Hamma, [33°43'N, 09°26'E], 26 May 1884, *A. Letourneux* (P [P02813900]); Bordj Toulal, [33°39'N, 10°01'E], 9 Apr 1909, Herb. Meslin (P [P02813894]); Piste n. 104 zwischen Tamezret und Kebili, c. 18 km W Tamezret, Ränder eines Djessour, 100 m, [33°34'N, 09°40'E], 27 Mar 1998, *C. Oberprieler 9822* (B [B101154210]; S; Herb. Oberprieler); ibidem, cult. Hort. Bot. Berlin-Dahlem, 19 Aug 2002, *M. Cubr 40018* (B [B100017887]); Gerlán supra vicum Matmata, ad rupes, [33°32'N, 09°58'E], 22 Apr 1884, *A. Letourneux* (P [P02813928]); Matmata, [33°32'N, 09°57'E], 500 m, 2 Apr 1912, *H. Humbert* (MPU [MPU243275]); Matmata, [33°32'N, 09°57'E], Herb. Battandier (MPU [MPU243274]); Gabès, Dahar-Bergland, Segetalflur bei Matmata, 500 m, [33°32'N, 09°58'E], 9 Apr 1997, *M. Staudinger* (W [W-2006-19852]); Matmata, [33°32'N, 09°57'E], 23 Apr 2007, *E. Emanuelsson 3398* (S [S07-13263]); Djebel Matmata, [33°32'N, 09°53'E], 20 Apr 1884, *A. Letourneux* (P [P02813892, P02813919]); Road C 104 between Tamesret and Kebili, c. 5 km W of Tamesret, 312 m, 33°32'01.7"N, 09°48'43.6"E, oued and stony slopes, 19 Mar 2009, *R. Vogt 16512, C. Oberprieler 10455 & C. Gstöttl* (B [B100216208]); Bei Tamezret, [33°31'N, 09°52'E], 9 Mar 1968, *H. Leippert 7064* (B [B100673070]); Road C 104 between Médenine and Matmata, c. 10 km WNW of Toujane, 469 m, 33°29'08.6"N, 10°03'36.2"E, stony slopes, 21 Mar 2009, *R. Vogt 16547, C. Oberprieler 10490 & C. Gstöttl* (B [B100673058, B100216207], Herb. Oberprieler); ibidem,

- cult. Hort. Bot. Berlin-Dahlem, 27 Jul 2011, *M. Cubr 48064* (B [B100342901]); Road C 104 between Médenine and Matmata, c. 2 km N of Toujane, 539 m, 33°29'07.7"N, 10°07'05.4"E, stony plain, 21 Mar 2009, *R. Vogt 16545*, *C. Oberprieler 10488* & *C. Gstöttl* (B [B100216209]); Tunisie du Sud, Monts de Matmata, road C 104 between Médenine and Matmata, c. 2.5 km NW of Toujane, 590 m, 33°28'21"N, 10°07'28"E, stony slopes, 15 May 1994, *R. Vogt 13240* & *C. Oberprieler 7545* (B [B100673076, B100673048], Herb. Oberprieler). — Gouvernorat **GAFSA**: Gafsa, Sened, [34°28'N, 09°16'E], in aridis deserti, Apr 1909, *C. J. Pitard 1737* (G [G00163381]); Moularès, [34°28'N, 08°16'E], Mar 1948, Herb. A. Cuénod (G [G00163357]); Südtunesien, NW Gafsa, Südabdachung des Djebel Ben Younes, c. 250 m, [34°27'N, 08°43'E], felsige Hänge und Wadirand, Halbwüste, 18 Apr 1968, *G. Wagenitz 1326* (B [B100673068]); Tunisie du Sud, road C 201 between Moularès and Redeyef, sandy plains of Oued Selja, c. 7 km S of Moularès, 400 m, 34°27'01"N, 08°13'12"E, 9 May 1994, *R. Vogt 12694* & *C. Oberprieler 6999* (B [B100673078, B100673055], Herb. Oberprieler); Gafsa, autour de l'oasis, [34°25'N, 08°46'E], 10 Mar 1884, *Robert* (P [P02813915]); Gebel Orbata near Gafsa, [34°24'N, 09°08'E], 5 Apr 1938, *N. D. Simpson 38148b* (BM [BM001010384]); El Guettar, Djebel Orbata S, 420 m, [34°22'N, 09°04'E], Hangfuß, Halbwüste, Sandstein, Mar 1987, *J. P. Gruber*, cult. Hort. Bot. Berlin-Dahlem, 7 Jun 1989, *Schwerdtfeger 24960* (B [B100673065, B100673064]), 21 Jun 1989, *Schwerdtfeger 25049* (B [B100673063, B100673062, B100673061]); Tunisie du Sud, road C 122 between Métlaoui and Moularès, c. 9 km N of Métlaoui, 500 m, 34°22'42"N, 08°26'04"E, road embankments, 8 May 1994, *R. Vogt 12689* & *C. Oberprieler 6994* (B [B100673071, B100673073, B100673050], BM [BM001010370], RNG, Herb. Oberprieler); 18 km SW von Gafsa an der Straße nach Tozeur, 140 m, Gipssteppe, 34°21'N, 08°39'E, 10 Apr 1980, *D. Podlech 34213* (M [M0309962], MSB [MSB006440]); Gafsa, El Guettar, [34°20'N, 08°57'E], in aridis deserti, Apr 1909, *C. J. Pitard 1736* (G [G00163375, G00163380]); Gafsa, in arenosis deserti, Apr 1908, *C. J. Pitard* (BM [BM001001021], E [E00585617], FI [FI063916], G [G00163378, G00163373], K, L [L3653746, L3653747], M [0155757], MA [MA128813], MPU [MPU361089], RNG, WAG [WAG1443118]); 5 km N of Métlaoui, SW of Gafsa, 350 m, [34°20'N, 08°24'E], rocky desert hills in gullies, 7 May 1975, *P. Davis 57440* & *J. Lamond* (BM [BM001010362], RNG); 6 km SW von Metlaoui (46 km SW Gafsa) an der Straße nach Tozeur, 140 m, sandig-steinige Fläche, 34°19'N, 08°21'E, 10 Apr 1980, *D. Podlech 34201* (M [M0309961], MSB [MSB006439]); Djebel Berda, [34°12'N, 08°59'E], 29 May 1884, "Mis. scient. Tun. 1884", *N. Doûmet-Adanson & E. Bonnet* (P [P02813806]); Djebel Attigue [Djebel Hattig], [34°11'N, 08°42'E], 17 May 1884, "Mis. scient. Tun. 1884", *N. Doûmet-Adanson & E. Bonnet* (P [P02813809]); Bir Oum el Jaf... à l'extrémité occidentale du Dj. Berda, SE de Gafsa, [34°09'N, 08°49'E], 1 May 1886, *Thomas* (P [P02813920]); Djebel Oum-Ali, [34°08'N, 09°08'E], 26 May 1884, "Mis. scient. Tun. 1884", *N. Doûmet-Adanson & E. Bonnet* (P [P02813811]). — Gouvernorat **KAIROUAN**: Fondouk el Aouareb, [35°34'N, 09°45'E], 26 Mar 1969, *J. Timbal* (MPU [MPU341970]). — Gouvernorat **KASSERINE**: Tunisie Centrale, road P 15 between Fériana and Gafsa, track between Fériana and Sidi Aïch, 810 m, 35°51.067'N, 08°32.547'E, stony slopes, 8 May 1994, *R. Vogt 12612* & *C. Oberprieler 6917* (B [B100673075, B100673049], BC [BC871621], Herb. Oberprieler); Halfgrasebene zwischen Oued Kebir und Fériana, [34°57'N, 08°34'E], am Straßenrand bei den Pflanzlöchern für *Eucalyptus*, 24 Oct 1968, *H. Walter & E. Walter 105* (B [B100673069]); Halfsteppe südl. Fériana, [34°52'N, 08°34'E], Mar 1930, *G. & J. Braun-Blanquet* (MPU [MPU115325]). — Gouvernorat **KEBILI**: Oasis Keberita "Mission des Chotts", [34°02'N, 08°51'E], May 1879, *F. E. Roudaire* (P [P02813807]); Tunisie du Sud, road P 16 between Kebili and Gabès, c. 10 km E of Limaguess, 150 m, 33°44.927'N, 09°09.442'E, palm grove and sandy slopes, 11 May 1994, *R. Vogt 12847* & *C. Oberprieler 7152* (B [B100673150]); Arad et Nefzaoua, Kanzeria, prope Gabès, [33°36'N, 08°59'E], in aridis deserti, Mar 1913, *C. J. Pitard 2903* (G [G00163382]); Arad et Nefzaoua, Raz el Oued, ad Gabès, [33°36'N, 08°59'E], in aridis, Mar 1913, *C. J. Pitard 2904* (G [G00163383]); Gabès, Nefzaoua, in aridis deserti, [33°36'N, 08°59'E], Mar 1913, *C. J. Pitard* (P [P02813912]); In collibus Djebel Nefzaoua prope Kebili, [33°36'N, 08°59'E], 30 May 1884, *A. Letourneux* (P [P02813899]); Piste n. 16 zwischen Douz und Kebili, 14.4 km NW Douz [33°35'51"N, 09°00'33"E], 29 Mar 1998, *C. Oberprieler 9836* (B [B101154211], FI [FI063917], Herb. Oberprieler). — Gouvernorat **MEDÉNINE**: Zarzis, [33°29'N, 11°03'E], 11–15 May 1884, *A. Letourneux* (P [P02813897, P02813898, P02813928]); Sebkh el Mehabend, S des Golfe de Bou Gara, zwischen Medénine und Zarzis, 33°26'N, 10°51'E, 20 Apr 1994, *Ullmann* (MSB [MSB003482]); Djebel Tadjera, [33°24'N, 10°24'E], 280 m, 6 May 1884, *A. Letourneux* (P [P02813891, P02813919]); Mednine, [33°21'N, 10°29'E], 3 Feb 1907, *A. Joly* (MPU [MPU243277]). — Gouvernorat **SFAX**: Bir Arrach, [34°44'N, 10°22'E], 19 Apr 1884, "Mis. scient. Tun. 1884", *N. Doûmet-Adanson & E. Bonnet* (P [P02813812]). — Gouvernorat **SIDI BOU ZID**: Sidi bou Sid, [35°01'N, 09°30'E], 20 Feb 1963, *F. Zednik* (W [W-1979-10102]); Oued Leben, [34°35'N, 09°53'E], 22 Apr 1884, "Mis. scient. Tun. 1884", *N. Doûmet-Adanson & E. Bonnet* (P [P02813814]); El Hafay, [34°56'N, 09°12'E], 25 Apr 1896, *S. Murbeck* (S [S11-13788]). — Gouvernorat **TATAOUINE**: Road C 207 between Ghomrassen and Beni Kheddache, c. 5 km N of Ksar Hadada, 398 m, 33°08'35.2"N, 10°17'29.7"E, stony slopes, 22 Mar 2009, *R. Vogt 16570*, *C. Oberprieler 10513* & *C. Gstöttl* (B [B100216211]); Tunisie du Sud, Monts de Matmata, track C 207 between Ghomrassen and Beni Kheddache, c. 8 km N of Ksar Hadada, 470 m, 33°08.407'N, 10°17.206'E, stony slopes and rocks, 14 May 1994, *R. Vogt 13143* & *C. Oberprieler 7448* (B [B100673080, B100673057], BM [BM001010369], RNG, Herb. Oberprieler); Tunisie du Sud, Monts de Matmata, road C 207 between Tataouine and Ghomrassen, c. 8 km S of Ghomrassen, 340 m, 32°59.952'N, 10°20.524'E, road embankments and stony slopes, 14 May 1994, *R. Vogt 13127* & *C. Oberprieler 7432* (B [B100673074]); Road C 207 between Tataouine and Ghomrassen, c. 5 km NW of Tataouine, 275 m, 32°55'22.5"N, 10°23'51.2"E, 22 Mar 2009, *R. Vogt 16558*, *C. Oberprieler*

10501 & *C. Gstöttl* (B [B100216210]); Dahar-Gebirge, Piste n. 207 zwischen Beni Kheddache und Ghomrassen, c. 17.7 km S Beni Kheddache [33°07'35"N, 10°17'36"E], steinige Hänge, trockenes Bachbett, 26 Mar 1998, *C. Oberprieler 9796* (B [B101154212]; FI [FI063918]; S; Herb. Oberprieler); Douiret à l'W de Tataouine, route de Tataouine à env. 4 km du village, c. 450 m, [32°55'N, 10°23'E], friche au pied des collines gréseuses à végétation steppique-subdésertique, 9 Apr 1999, *J. Lambinon 99/Tu/140* & *J. Margot* (MA [MA693913], RNG); Tunisie du Sud, Monts de Matmata, road C 207 between Tataouine and Chenini, c. 5 km W of turn-off to Ghomrassen, 390 m, 32°55.619'N, 10°20.841'E, sandy plains, 14 May 1994, *R. Vogt 13115* & *C. Oberprieler 7420* (B [B100673052]; RAB; Herb. Oberprieler); ibidem, cult. Hort. Bot. Berlin-Dahlem, 25 Jul 1996, *R. Vogt s.n.* & *C. Oberprieler* (B [B100273230 B100673053]); Djeneien–Bir Zar, [31°36'N, 10°07'E], 14 May 1957, *H.-N. LeHouérou 150457* (P [P02813860]). — Gouvernorat **TOZEUR**: Tamerza in humidis ad aqua fontan., [34°23'N, 07°56'E], 6 May 1887, *A. Letourneux* (P [P02813920]); Tunisie du Sud, road P 16 between Tamerza and Chbika, 350 m, 34°21'31"N, 07°54'08"E, limestone rocks, 9 May 1994, *R. Vogt 12785* & *C. Oberprieler 7090* (B [B100673081, B100673056], Herb. Oberprieler); Chott el Gharsa, Straße n 16 zwischen El Hamma du Djeid und Tamerza, c. 20 km NW El Hamma du Djerid [34°09'31"N, 08°03'58"E], 29 Mar 1998, *C. Oberprieler 9839* (B [B101154213]; MA; Herb. Oberprieler); Oberhalb der Oase Chbika bei Tamerza, [34°19'N, 07°55'E], c. 400 m, alpinen Felshang, trocken, südl., kalkhaltiger Boden, 22 Mar 1999, *G. Geisler* (W [W-2000-00135]); Tunisie du Sud, Chott Er Rahim, road P 16 between Chbika and Tozeur, c. 10 km SE Chbika, 0 m, 34°14'58"N, 07°52'57"E, sand, 10 May 1994, *R. Vogt 12800* & *C. Oberprieler 7105* (B [B100673077, B100673051]; Herb. Oberprieler); Tunisie du Sud, Chott Er Rahim, road P 16 between Chbika and Tozeur, c. 14 km SE of Chbika, c. 0 m, 34°13'19"N, 08°00'06"E, sandy plains, oued, 10 May 1994, *R. Vogt 12819* & *C. Oberprieler 7124* (B [B100673079, B100673054]); Road C 106 between Kariz and road P 3 (Tozeur–Gafsa), oued c. 2 km S of junction with road P 3, 65 m, 34°03'12.7"N, 08°14'10.5"E, oued and sandy plain, 23 Mar 2009, *R. Vogt 16585*, *C. Oberprieler 10528* & *C. Gstöttl* (B [B100216212, B100673059], Herb. Oberprieler); In collibus lapidosis supra Kriz (Djerid), [34°00'N, 08°15'E], 2 Jun 1884, *A. Letourneux* (P [P02813829, P02813916]); Kriz, [34°00'N, 08°15'E], Mar 1930, *G. & J. Braun-Blanquet* (MPU [MPU701991]); Prope Cedada, [34°00'N, 08°14'E], 9 Jun 1884, *A. Letourneux* (P [P02813831]); El Oudiane, [33°59'N, 08°13'E], in aridis deserti, Mar 1908, *C. J. Pitard 1271* (G [G00163374, G00163379]); S-Tunesien, N-Rand des Schott-el-Djerid, c. 3 km südöstlich der Oase Cedada, an der Piste Tozeur–Kebili, [33°59'N, 08°18'E], Halbwüste, 8–20 Apr 1968, *H. Hertel 8480* (M [M0155756]); Gobernación de Jerid, Cedada, Sidi Arbes Bouhel, 34°01'56"N, 08°16'56"E, 65 m, pastos y matorral, calizas y areniscas intercaladas, 25 Mar 2009, *A. Herrero 3940* & al. (MA [MA795178]); Degach in depressis arenosis, [33°59'N, 08°13'E], 30 May 1887, *A. Letourneux* (P [P02813832, P02813920]). — Gouvernorat **TUNIS**: Habitat in agris incultis prope Tunetum, [36°48'N, 10°10'E] (FI

[FI006519], P-Desf.). — Gouvernorat **KEBILI & TOZEUR**: Tozeur, Arad et Nefzaoua [33°36'N, 08°59'E], El Oudiane [33°59'N, 08°13'E], in aridis deserti, 1909, *C. J. Pitard* (MA [MA128815]). — **WITHOUT EXACT INDICATION OR NOT LOCATED**: Tunisie, Apr 1912, Herb. Viguier (P); Tunis, Herb. G. Curling Joard. (US [US01822914]); Aïn Temran, 2 May 1884, *A. Letourneux* (P [P02813834; P02813928]); Oued Hedj [Eddedj], 24 Apr 1884, "Mis. scient. Tun. 1884", *N. Doûmet-Adanson & E. Bonnet* (P [P02813813]); Djebel Djegeiga [Cheguieïga], 28 May 1884, "Mis. scient. Tun. 1884", *N. Doûmet-Adanson & E. Bonnet* (P [P02813808]); Redir Timiat, 25 May 1884, "Mis. bot. Tun. 1884", *N. Doûmet-Adanson & E. Bonnet* (P). — **LIBYA**: Shabiyah **AL JABAL AL GHARBI**: Garian, Bu Gheilán, [32°16'N, 13°01'E], 24 Apr 1913, *R. Pampanini 3618* (FI [FI063907]); Bu-Gheilán, [32°16'N, 13°01'E], 1923/1924, *F. Cavara* (NAP); Tripolitaine, sous Garian vers pied du Djebel, [32°10'N, 13°01'E], 1 May 1938, *R. Maire & M. Weiller* (FI [FI063919]); Tripolitania, in lapidosis calcareis infra Garian, 400–600 m, [32°10'N, 13°01'E], 1 May 1938, *R. Maire & M. Weiller* (MPU [MPU243259], P [P02813895, P02813908]); near Garian, 300', [32°10'N, 13°01'E], rocky hillside, north facing, 28 Dec 1969, *D. Maitland* (K); Garian, escarpment, rocky hillside, 1500 ft, [32°10'N, 13°01'E], 12 Feb 1949, *G. F. Johnson 67* (BM [BM001010367]). — Shabiyah **AN NUQAT AL KHAMS**: S. of El Asa, ["El Assa", 32°49'N, 11°37'E], 4 Mar 1955, *K. M. Guichard 601* (BM [BM001010358]). — **CULTIVATED**: Jardin de Durieu, graines reçues de Bouçada en Algérie, 13 Jun 1853, Herb. J. Gay (K); Jardin de Valleyres [Switzerland], ex Algeria, Biskra (G [G00427002]); Jard. de Valleyres [Switzerland], ex Algeria, Biskra, 1854 (G [G00426997]); Jardin de Valleyres [Switzerland], 1859 (G [G00427000, G00427001]); Hort. Genev. [Switzerland], ex Tunetano, Kralik, Jul 1857 (G [G00426999]); Hort. Genev. [Switzerland], ex Algeria (G [G00426998]).

### *Heteromera philaeorum* Maire & Weiller

**ALGERIA**: Wilaya **GHARDAÏA**: Between El Golea and Ghardaïa, 180 km from El Golea, Mar 1967, [32°06'N, 03°46'E], *E. Hultén* (S [S11-13804]). — **TUNISIA**: Gouvernorat **TATAOUINE**: Tunisie du Sud, road P 19 between Tataouine and Remada, c. 4.5 km S of Bir Thlethine, 420 m, 32°39'N, 10°19'E, sandy plains and fields E of road, 13 May 1994, *R. Vogt 13007* & *C. Oberprieler 7312* (B [B100673046, B100673044], MA [MA586902], Herb. Oberprieler); ibidem, cult. Hort. Bot. Berlin-Dahlem, 17 Aug 1995, *R. Vogt & C. Oberprieler s.n.* (B [B100673047], M, MA). — **LIBYA**: Shabiyah **AL JABAL AL GHARBI**: Gebel Gharian, Gasr Gharian–Tercia, [32°14'N, 13°02'E], 23 Apr 1914, *A. Trotter* (PORUN); Gebel Gharian, Bugheilán–Gasr Gharian, [32°13'N, 13°02'E], 18 Mar 1914, *A. Trotter* (PORUN); T[ripolitania], Gebel Nefoussa, 27 km SE of Giado, 650–700 m, [31°49'N, 12°10'E], sandy hammada near barley field, 16 Mar 1970, *P. Davis 49629* (E [E00585618], K, RNG); T[ripolitania], Gebel Nefoussa, 60 km SE of Giado, 675 m, [31°33'N, 12°22'E], sandy hammada, 16 Mar 1970, *P. Davis 49617* (K); Presso la carovaniera Melga Sofegin Nesna, [31°25'N, 12°59'E], 2 May 1914, *A. Trotter* (PORUN). —



Shabiyah **AL MURGUB**: Tripolis, Tarhuna, [32°26'N, 13°38'E], [Jan–Mar 1844], *A. von Lorent* (P [P00729941]); Plantae Tripolitanae a R. Pampanini anno 1913 lectae, n. 1996 [= Tarhuna, Uadi Tenziua sul Ras Maader, 1 Apr 1913] [32°12'N, 13°42'E] (FI [FI001205]); Ar... sassosi a Uadi el Maader / Tarhuna, [32°24'N, 13°38'E], 13 May 1913, *A. Trotter* (PORUN). — Shabiyah **AL WAHAT**: Cyrenaica, desert between Agedabia [Adschdabiya] and Wadi Zaregh, [30°45'N, 20°13'E], 30 Mar 1939, *N. Y. Sandwith* 2179 (K); Cirenaica, Saumnu a nord-est di Agedabia, [30°45'N, 20°13'E], 10 Apr 1934, *R. Pampanini* 8592 & *R. Pichi-Sermolli* (FI [FI063920]); Cirenaica, Shabi, Saniet-el-Hamar, a sud est di Agedabia [Adschdabiya], [30°40'N, 20°16'E], 9 Apr 1934, *R. Pampanini* 8593 & *R. Pichi-Sermolli* (FI [FI063921], G [G00163356], L [L3036653]); Cirenaica, Saniet-el-Hamar, a sud est di Agedabia [Adschdabiya], [30°40'N, 20°16'E], 12 Mar 1933, *R. Pampanini* 8588 (FI [FI063922], W [W-1961-19453]); in barley in desert on Gâlo track, c. 20 miles south of Agedabia [Adschdabiya], Benghazi Province b. 5 miles, [30°37'N, 20°21'E], 30 Mar 1939, *N. Sandwith* 2179 & *N. D. Simpson* 39081a (BM [BM001010379]); in barley in desert on Gâlo track, c. 20 miles south of Agedabia [Adschdabiya], Benghasi Province b. 5 miles, [30°37'N, 20°21'E], 30 Mar 1939, *N. Sandwith* 2179 & *N. D. Simpson* 39081b (BM [BM001010378]); Cyrenaica, in aridis lapidosis litoris Magnae Syrteos prope Casa Ristoro prope Aras Philaenorum, [30°27'N, 18°33'E], 29 Apr 1938, *R. Maire & M. Weiller* (MPU [MPU004064], P [P02088603]); Cirenaica, Tra el-Agheila e Maaten Giofer, [30°07'N, 19°14'E], 15 Mar 1933, *R. Pampani-*

*ni* 8589 (FI [FI063923]); Cirenaica, el-Agheila: Uadi Faregh, Maaten Giofer, [30°07'N, 19°14'E], 15 Mar 1933, *R. Pampanini* 8590 (FI [FI063924]); Cirenaica, Uadi Faregh, Maaten Giofer, [30°07'N, 19°14'E], 8 Apr 1934, *R. Pampanini* 8591 & *R. Pichi-Sermolli* (FI [FI063925]). — Shabiyah **MISRATAH**: Um el Gharaniq, Syrtica, Misurata Province, [32°21'N, 15°01'E], 17 Apr 1939, *N. D. Simpson* 391241 (BM [BM001010382]); Beni-Oulid [Ulid, Waled] entre Tripoli et Bondjem, [31°45'N, 14°00'E], Jan 1879, *G. Rohlfs & A. Stecker* (P [P00729942]); Presso la carovaniera da Bir Tininai a Scemeg, [31°23'N, 13°44'E], 5 May 1914, *A. Trotter* (PORUN); Libya, 22 miles S of Gheddahia, small sandy wadi, [31°22'N, 15°13'E], 3 Feb 1952, *K. M. Guichard* 62 (BM [BM001010377]). — Shabiyah **NALUT**: Nalut, Uadi Melha, [31°51'N, 10°59'E], 6 Apr 1914, *A. Trotter* (PORUN); Sinaouen [Sinawin], [31°01'N, 10°36'E], 1958, *H.-N. Le Houérou* (P [P00729943]); Tripolitania, Se... a sud di Sinauen [Sinawin], [30°58'N, 10°33'E], 28 Mar 1934, *S. Zenari* (PAD). — Shabiyah **SABHA**: Fezzan, Wadi Ziz-zah, [27°36'N, 14°10'E], 26 Oct 1981, *D. Turner* 6/83 (BM [BM001010364]). — Shabiyah **SURT**: Tripolitaniën, Südwestrand des Hongrabens, c. 80 km N Hon, [29°49'N, 15°54'E], 28 Jan 1972, *B. Gabriel* (B [B100673045]). — Shabiyah **WADI AL SHATHI**: Fezzân septentrionale, tra Bir el Ghelania [B'ir al Ghilaniyah] e Brach [Birak, Biraq], presso l'U.[Uadi] Issa, [28°37'N, 14°18'E], 14 Feb 1934, *R. Corti* 384 (FI [FI063926]); Fezzân septentrionale, tra Brach [Birak, Biraq] e l'U.[Uadi] Masauda, [28°10'N, 14°27'E], 19 Apr 1933, *R. Corti* 386 (FI [FI063927]).

## Supplemental content online

See <https://doi.org/10.3372/wi.51.51207>

Supplementary File S1. Gap-coded cpDNA alignment in NEXUS format.

Supplementary File S2. Gap-coded nrDNA ITS+ETS alignment in NEXUS format.

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