



Weeding the Nettles II: A delimitation of “*Urtica dioica* L.” (Urticaceae) based on morphological and molecular data, including a rehabilitation of *Urtica gracilis* Ait.

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Abstract

The taxonomy of subcosmopolitan *Urtica dioica* L. s.l. is problematic. Recent floras recognize *Urtica dioica* as a subcosmopolitan species ranging throughout the entire holarctic region and also South Africa and New Zealand. Numerous infraspecific taxa have been proposed, especially in western Eurasia. There is only weak character differentiation, with floral and fruit morphology largely uniform, details of leaf morphology and indumentum are therefore primarily used for species delimitation, together with some characters of gender distribution and growth habit. The present study addresses the enigmatic relationships of the infraspecific taxa in *Urtica dioica* with a special emphasis on the monoecious, American representatives of *Urtica dioica* s.l. The study is based on extensive field and herbarium studies, molecular data and the experimental cultivation of all relevant forms. Infraspecific taxa currently assigned to *U. dioica* are retrieved mainly on two separate clades, one comprising the predominantly polygamous western Eurasian and African taxa (all subspecies and varieties sampled), the other comprising the monoecious American taxa. Monoecious American representatives of “*Urtica dioica*” and closely allied taxa (*U. aquatica*, *U. mollis*) are retrieved as a monophyletic group sister to a clade with East Asian and Australasian species, this clade is then retrieved as sister to the western and central Eurasian and African taxa of *U. dioica*. We therefore advocate the removal of the American representatives of this group from *Urtica dioica* and their placement as infraspecific taxa under *Urtica gracilis*. The following new names are consequently proposed: *Urtica gracilis* subsp. *gracilis* (for *Urtica dioica* subsp. *gracilis*), *Urtica gracilis* subsp. *holosericea*, *comb. nov.* (for *Urtica dioica* subsp. *holosericea*), *Urtica gracilis* subsp. *aquatica*, *comb. & stat. nov.* (for *Urtica aquatica*), *Urtica gracilis* subsp. *mollis*, *comb. & stat. nov.* (for *Urtica mollis*). Additionally, we describe a new subspecies from Peru under the name *Urtica gracilis* subsp. *incaica*. The literature report of *Urtica gracilis* (*dioica* subsp. *gracilis*) as an introduced weed in New Zealand is shown to be erroneous – the corresponding specimens belong to Australian *Urtica incisa*. Based on gross morphology close affinities have been proposed between a range of Australasian, Asian, North American and European infraspecific taxa, all of these can be shown to be erroneous.

Key words: *Urtica angustifolia*, monoecy, stinging nettle, phylogeny, chloroplast markers

Introduction

The “Greater Stinging Nettle” *Urtica dioica* Linnaeus (1753: 984) in a wider sense is currently considered as a species of nearly worldwide distribution (Friis 1993). The taxon is morphologically quite plastic and encompasses a large number of named forms on all continents (Geltman 1982, Edmondson 1992, Jiarui *et al.* 2003, Weigend 2005, 2006, Navas 1961, Soraru 1972, Woodland 1982, Juárez 1991, Boufford 1997). *Urtica dioica* is believed to be introduced in both South Africa (Friis & Immelmann 2001) and New Zealand (Webb *et al.* 1988).

Morphologically, the differences between the subspecies and varieties are small and refer largely to details of leaf morphology (narrowly or widely ovate, base cordate or truncate) and indument (density of trichome cover, number of stinging hairs; Edmondson 1992, Woodland 1982, Weigend 2005, 2006, Weigend & Luebert 2009). These characters are, in turn, quite plastic in individual plants (Woodland 1982, Woodland *et al.* 1982, Pollard & Briggs 1982, 1984). The picture is further complicated by the occurrence of different chromosomal races and the possibility of hybridization between different subspecies (Woodland *et al.* 1982, Shannon & Holsinger 2007). In spite of its wide distribution and often extraordinary abundance there has been little systematical progress overall since the classical revisions by Weddell (1856, 1869). Relatively recent and stable classifications are available for North America (Woodland 1982) and Europe (Edmondson 1992). The typical subspecies of *U. dioica* is considered as native to western Eurasia, ranging into Eastern Asia (Jiarui *et al.* 2003). Currently, *Urtica dioica* s.l. is reported as native to Europe (Edmondson 1992) including Mediterranean North Africa (Ghaffor 1977) to China (Jiarui *et al.* 2003), but also from North America (Woodland 1982), South America (Weigend & Luebert 2009) and South Africa (Friis & Immelmann 2001).

The taxonomy of the taxa in *Urtica dioica* of the United States and of Canada has been satisfactorily resolved with regard to the number of taxa that should be recognized: Only two native North American taxa are currently recognized, namely *Urtica dioica* subsp. *gracilis* (Aiton 1789: 341) Selander (1947: 271) and *U. dioica* subsp. *holosericea* (Nuttal 1848: 25) Thorne (1967: 68) (Woodland 1982, Boufford 1997). The taxa of this group in Central and South America, however, remain problematic: The distinctness of Chilean *Urtica mollis* Steudel (1850: 258) from North American *U. dioica* subsp. *holosericea* has been repeatedly questioned (Woodland 1982, Weigend & Luebert 2009) and remains unresolved. Woodland (1982) also questioned the distinctness of these two taxa from western Eurasian *U. dioica* L. subsp. *pubescens* (Ledebour 1833: 240) Domin (1944: 71). North American *Urtica dioica* subsp. *gracilis* has also been widely considered as doubtfully distinct from Scandinavian *Urtica dioica* L. subsp. *sondenii* (Simmons 1910: 78) Hylander in Ahti, T. & Hämet-Ahti (1971: 47) (Nurmi 2000, Woodland 1982) and has been reported as an introduced weed from New Zealand (Webb *et al.* 1988).

Another problem surrounds *Urtica serra* Blume (1856: 140) from Guatemala and Mexico: Weddell (1869) placed this taxon as a synonym under North American *Urtica dioica* L. subsp. *gracilis* (Ait.) Selander, under the name *U. dioica* L. var. *procera* (Muhlenberg ex Willdenow 1805: 353) Weddell (1856: 78). Woodland (1982) argues that *Urtica serra* is conspecific with eastern Asian *Urtica dioica* L. var. *angustifolia* (Fischer ex Hornemann 1819: 107) Ledebour (1833: 241). Boufford (1997) again cites “var. *angustifolia* Schlechtend.” [correct: var. *angustifolia* (Fisch. ex Hornem.) Ledeb.] as a synonym of *Urtica dioica* L. subsp. *gracilis* (Ait.) Selander, thus returning to the interpretation of Weddell (1869). The only recent compilation of *Urtica* in Mexico (Conzatti 1988) reports only *Urtica dioica* L. var. *procera* (Muhl. ex Willd.) Wedd. and *Urtica dioica* L. var. *mollis* (Steud.) Weddell (1869: 78) from this group from the country, mentioning neither *Urtica aquatica* nor *Urtica serra*. However, *U. dioica* var. *procera* is considered as a synonym of *Urtica dioica* subsp. *gracilis*, which is definitely absent from Mexico (Woodland 1982), and *Urtica mollis* is currently considered as restricted to the Southern Cone (Weigend & Luebert 2009) - or possibly identical with subsp. *holosericea* from the southwestern United States, but then also absent from Mexico (Woodland 1982). Additionally, *Urtica aquatica* Liebmann (1851: 291), was described from Mexico, but largely ignored in the literature. To further complicate matters, field studies in Peru yielded material of an *Urtica* very similar to *U. aquatica* from Guatemala and *Urtica serra* from Mexico, but clearly distinct in details of indumentum and leaf shape. No published name appears to be available for this form.

There are thus several levels of problems in the *Urtica dioica*-complex:

It is unclear in how far the American subspecies of *Urtica dioica* are really more closely related to predominantly Eurasian *Urtica dioica* than to the various other American taxa currently recognized at species level such as *U. aquatica* or *U. mollis*, and how these forms can be delimited from each other.

Also, similar and often identically named “forms” are reported from New Zealand, Scandinavia and North America (*U. dioica* ssp. *gracilis* =? *Urtica dioica* ssp. *sondenii*), North and South America plus Western Eurasia (*U. dioica* subsp. *holosericea* =? *U. mollis* =? *U. dioica* subsp. *pubescens*) or northern Central America, Eastern Asia and Western Europe (*Urtica serra* =? *U. aquatica* =? *U. angustifolia* =? = *dioica* var. *angustifolia* Wimmer & Grabowski 1829: 336).

A recent phytochemical and molecular study (Farag *et al.* 2013) showed that the relationships in the *Urtica dioica*-complex are quite different from what the current taxonomy suggests, but also that standard molecular markers are able to provide a well-resolved phylogeny of the genus. Based on this fact, the present study resolves

the relationships in *Urtica dioica* with a special emphasis on western hemisphere taxa. Taxonomically, the re-definition of infraspecific entities as carried out by Woodland (1982) is the starting point. Relationships are clarified for the remaining taxa of the *Urtica dioica*-complex in Central and South America and taxa from other continents that have been associated with them in the literature. Additionally, the question of whether these taxa should be indeed included as infraspecific taxa under *Urtica dioica* is addressed. The confused taxonomic history clearly shows that morphological characters are of limited value in *Urtica*. We therefore address the problem based on a broad morphological and molecular approach, in order to identify the delimitation of *Urtica dioica* and the relationships between the various “forms” assigned to it in the past.

Material and Methods

Plant material

Extensive field collections were carried out in various parts of the globe and extensive herbarium loans were processed from the following herbaria (abbreviations following Holmgren *et al.* 1998 ff): B, BM, BONN, BSB, CHR, CONC, F, FR, FI, E, K, KRAM, LE, LL, M, MO, NY, P, PR, S, SGO, TEX, USM, W. Material included in this analysis was identified both with the current floras and compared to original protologues and type specimens, wherever possible. All relevant forms associated with American taxa from all over the world were included in the analysis, such as Scandinavian *Urtica dioica* ssp. *sondenii*, southern European *Urtica dioica* ssp. *dioica* var. *glabrata*, central European *Urtica dioica* ssp. *dioica* var. *angustifolia*, south-eastern European *Urtica dioica* ssp. *pubescens*, the putative New Zealand populations of North American *U. dioica* ssp. *gracilis*, Chilean *Urtica mollis* and northern Central American *Urtica aquatica*, Mexican and Chinese representatives of *Urtica dioica* and East Asian *Urtica angustifolia*. Representatives of a wide range of “forms” of *Urtica dioica* were taken into cultivation including North American *Urtica dioica* subsp. *gracilis* and *U. dioica* subsp. *holosericea*, *Urtica mollis* from Chile, *U. aquatica* from Guatemala, and a putatively new taxon of this group from Peru (collection *Ch. Schwarzer 14*). In total 75 *Urtica*-accessions were sampled for the phylogenetic analyses, including 36 accessions of *Urtica dioica* in the widest sense. Representatives of *Laportea*, *Nanocnide*, *Obetia* and *Urera* were chosen as outgroup (compare Hadiah *et al.* 2008, Wu *et al.* 2013). A complete vouchers list for the molecular studies, including GenBank accession numbers, is given in Table 1.

TABLE 1. List of *Urtica*-accessions used for the molecular phylogeny, including genbank-numbers for molecular sequences.

Taxon	Country of origin	Herbarium voucher	DNA-Nr	trnL-trnF	trnS-trnG	psbA-trnH	ITS
<i>Laportea canadensis</i> Gaudich.	USA	N. C. Coile 2959 (B)	2028	KF971221	KF971155	KF971254	KF971188
<i>Nanocnide japonica</i> Blume	China	Boufford, D. E. et al. 25403 (E)	2285	KF971223	KF971157	KF971256	KF971190
<i>Nanocnide lobata</i> Wedd.	Japan	Furuse 2091 (K)	29190	KF971222	KF971156	KF971255	KF971189
<i>Obetia carrutheriana</i> (Hiern.) Rendle	Namibia	H. & E. Walter 1112 (B)	2030	KF971220	KF971154	KF971253	KF971187
<i>Urera batesii</i> Rendle	Equatorial Guinea	Carvalho 3412 (B)	2031	KF971219	KF971153	KF971252	KF971186
<i>U. andicola</i> Wedd.	Peru	M. Ackermann & D. Kollehn 276 (BSB)	3081	KF559060	KF559121	KF559000	KF558940
<i>U. angustifolia</i> Fisch. ex Hornem.	Mongolia	Student Group 30 (MO)	2007	KF559022	KF559083	KF558962	KF558902
<i>U. angustifolia</i> Fisch. ex Hornem.	Mongolia	H. H. Hilger 1603 (BSB)	2912	KF971250	KF971184	KF971283	KF971217
<i>U. atrovirens</i> Loisel. ex Poir.	Italy (Sardinia)	M. Weigend 7798 (BSB)	1724	KF559016	KF559076	KF558956	KF558895
<i>U. cannabina</i> L.	Mongolia	M. Weigend 8678 (BSB)	2237	KF559043	KF559104	KF558983	KF558923

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TABLE 1 (continued)

Taxon	Country of origin	Herbarium voucher	DNA-Nr	trnL-trnF	trnS-trnG	psbA-trnH	ITS
<i>U. chamaedryoides</i> Nutt.	Mexico	Rosas R. 299 (BM)	1865	KF971235	KF971169	KF971268	KF971202
<i>U. circularis</i> (Hicken) Soraru	Brazil	M. Weigend 9311 (B)	3091	KF971233	KF971167	KF971266	KF971200
<i>U. dioica</i> L.	China	W. P. Fang 4279 (HUH)	3092	KF971224	KF971158	KF971257	KF971191
<i>U. dioica</i> L.	China	J. F. Rock 14024 (HUH)	3094	KF971226	KF971160	KF971259	KF971193
<i>U. dioica</i> L.	China	T. N. Ho, B. Bartholomew, M. Gilbert 219 (HUH)	3095	KF971225	KF971159	KF971258	KF971192
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>angustifolia</i> Wimm. & Grabowsky	Czech Republic	M. & K. Weigend 5606-C (BSB)	1081	KF559009	KF559069	KF558949	KF558888
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>dioica</i>	Mexico	Ch. Schneider et al. 52a (BSB)	2906	KF559057	KF559118	KF558997	KF558937
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>dioica</i>	Germany	M. & K. Weigend 7807 (B)	2231	KF559039	KF559100	KF558979	KF558919
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>dioica</i>	Germany	E. Zippel 2002/2b (B)	2232	KF559040	KF559101	KF558980	KF558920
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>elegans</i> Chenev.	Switzerland	M. Weigend 8115 (BSB)	3082	KF559061	KF559122	KF559001	KF558941
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>glabrata</i> Clem. ex Visiani	Italy	M. Weigend 7097 (B)	3084	KF971243	KF971177	KF971276	KF971210
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>hispida</i> Wedd.	Switzerland	M. & K. Weigend 8112-C (BSB)	2234	KF559042	KF559103	KF558982	KF558922
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>hispida</i> Wedd.	Switzerland	M. & K. Weigend 8109-C (BSB)	2233	KF559041	KF559102	KF558981	KF558921
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>holosericea</i> Fries	Germany	M. & K. Weigend 8096-C (BSB)	3083	KF559062	KF559123	KF559002	KF558942
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>sarmatica</i> Zapal.	Germany	M. Weigend 9328 (BSB)	3085	KF559063	KF559124	KF559003	KF558943
<i>U. dioica</i> L. subsp. <i>dioica</i> var. <i>sarmatica</i> Zapal.	Germany	M. & K. Weigend 5662 (BSB)	1080	KF559008	KF559068	KF558948	KF558887
<i>U. dioica</i> L. subsp. <i>pubescens</i> (= <i>galeopsifolia</i>)	Italy	M. Weigend 7089-C (B)	2239	KF971244	KF971178	KF971277	KF971211
<i>U. dioica</i> L. subsp. <i>pubescens</i> (Ledeb.) Domin	Italy	G. Parolly, Th. Duerbye, H. H. Hilger, A. Mutallimov 13020 (B)	3071	KF559059	KF559120	KF558999	KF558939
<i>U. dioica</i> L. subsp. <i>sondenii</i>	Norway	T. Alm s.n.-C (BSB)	1722	KF559015	KF559075	KF558955	KF558894
<i>U. dioica</i> L. subsp. <i>subinermis</i> (Uechtr.) Weigend	Germany	M. & K. Weigend 5661 (B)	1093	KF559011	KF559071	KF558951	KF558890
<i>U. dioica</i> L. subsp. <i>subinermis</i> (Uechtr.) Weigend	Austria	M. & K. Weigend 5665 (B)	1095	KF559012	KF559072	KF558952	KF558891
<i>U. dioica</i> L. var. <i>capensis</i> Wedd.	RSA	Moffett 4044 (PRE)	1996	KF971242	KF971176	KF971275	KF971209
<i>U. echinata</i> Benth.	Peru	M. Weigend et al. 9227-C (BSB)	1078	KF559007	KF559067	KF558947	KF558886
<i>U. flabellata</i> Kunth	Peru	M. Weigend et al. 7728 (B)	1560	KF971232	KF971166	KF971265	KF971199
<i>U. gracilentata</i> Greene	Mexico	P. Tonorio et al. 6277 (BM)	1940	KF971234	KF971168	KF971267	KF971201

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TABLE 1 (continued)

Taxon	Country of origin	Herbarium voucher	DNA-Nr	trnL-trnF	trnS-trnG	psbA-trnH	ITS
<i>U. gracilentata</i> Greene	Mexico	T. Wendt & D. Riskind 901 (TEX)	2896	KF971230	KF971164	KF971263	KF971197
<i>U. gracilis</i> Ait. subsp. <i>aquatica</i> Blume	Guatemala	Ch. Schneider et al. 31 (B)	1564	KF971247	KF971181	KF971280	KF971214
<i>U. gracilis</i> Ait. subsp. <i>aquatica</i> Liebm.	Guatemala	M. Weigend 7478 (BSB)	2892	KF559056	KF559117	KF558996	KF558936
<i>U. gracilis</i> Ait. subsp. <i>gracilis</i>	Canada	M. Weigend 9332 (BSB)	2009	KF559023	KF559084	KF558963	KF558903
<i>U. gracilis</i> Ait. subsp. <i>gracilis</i>	USA (California)	Ewan 9916 (K)	22881	KF971249	KF971183	KF971282	KF971216
<i>U. gracilis</i> Ait. subsp. <i>holosericea</i> (Nutt.) Thorne	Mexico (Sonora)	Reina 2002-330 (TEX)	2895	KF971248	KF971182	KF971281	KF971215
<i>U. gracilis</i> Ait. subsp. <i>holosericea</i> (Nutt.) Thorne	USA (California)	L. Ahart 13172 (BSB)	2587	KF559051	KF559112	KF558991	KF558931
<i>U. gracilis</i> Ait. subsp. <i>incaica</i>	Peru	Ch. Schwarzer 14-C (BSB)	1728	KF559017	KF559077	KF558957	KF558896
<i>U. gracilis</i> Ait. subsp. <i>mollis</i> Steud.	Chile	Kalin Arroyo 81901. (CONC)	2886	KF559055	KF559116	KF558995	KF558935
<i>U. gracilis</i> Ait. subsp. <i>mollis</i> Steud.	Chile	H. Gunckel 29.962 (CONC)	2885	KF559054	KF559115	KF558994	KF558934
<i>U. gracilis</i> Ait. subsp. <i>mollis</i> Steud.	Chile	C. Villagrán 53963 (CONC)	2054	KF559029	KF559090	KF558969	KF558909
" <i>U. gracilis</i> subsp. <i>gracilis</i> " New Zealand = <i>U. cf. incisa</i>	New Zealand	Atwood 48288 (CHR)	2265	KF559046	KF559107	KF558986	KF558926
<i>Urtica incisa</i> Poir	New Zealand	Ward CHR 234516A (NZ Landcare Research)	2264	KF971251	KF971185	KF971284	KF971218
<i>U. cf. incisa</i> Poir. New Zealand	New Zealand	M. Weigend 8212 (BSB)	2836	KF559052	KF559113	KF558992	KF558932
<i>U. kioviensis</i> Rogov.	Germany	N. Nürk & J. Devers 333 (BSB)	2240	KF559044	KF559105	KF558984	KF558924
<i>U. kioviensis</i> Rogov.	Germany	M. Ackermann 600 (B)	1864	KF971246	KF971180	KF971279	KF971213
<i>U. kioviensis</i> Rogov. = <i>U. hulensis</i> Feinbr.	Israel	H. Kürschner 7164 (HERB Kürschner)	3087	KF971245	KF971179	KF971278	KF971212
<i>U. lalibertadensis</i> Weigend	Peru	M. Weigend et al. 8018-C (B)	1683	KF559014	KF559074	KF558954	KF558893
<i>U. leptophylla</i> Kunth	Peru	Weigend et al. 7706 (B)	1552	KF559013	KF559073	KF558953	KF558892
<i>U. leptophylla</i> Kunth	Peru	Weigend et al. 7763 (B)	1562	KF971241	KF971175	KF971274	KF971208
<i>U. macbridei</i> Killip	Peru	Ch. Schwarzer 05 (B)	1889	KF559020	KF559080	KF558960	KF558899
<i>U. magellanica</i> Poir.	Argentina	M. Weigend et al. 6809-C (BSB)	2881	KF559053	KF559114	KF558993	KF558933
<i>U. magellanica</i> Poir.	Chile	Jiles 4678 (CONC)	2964	KF971238	KF971172	KF971271	KF971205
<i>U. magellanica</i> Poir.	Chile	Jiles 4741 (CONC)	2966	KF971239	KF971173	KF971272	KF971206
<i>U. magellanica</i> Poir.	Chile	F. Luebert & C. Becker 2912 (SGO)	1997	KF971240	KF971174	KF971273	KF971207
<i>U. magellanica</i> Poir.	Chile	Gunckel 14.883 (CONC)	2965	KF971237	KF971171	KF971270	KF971204
<i>U. membranacea</i> Poir.	Italy	M. Gottschling 1 (BSB)	2229	KF559038	KF559099	KF558978	KF558918
<i>U. mexicana</i> Liebm.	Mexico	Santiz Ruíz 791 (MO)	3114	KF971228	KF971162	KF971261	KF971195

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TABLE 1 (continued)

Taxon	Country of origin	Herbarium voucher	DNA-Nr	trnL-trnF	trnS-trnG	psbA-trnH	ITS
<i>U. morifolia</i> Poir.	Spain (Teneriffa)	M. & K. Weigend 8242 (BSB)	2206	KF559030	KF559091	KF558970	KF558910
<i>U. morifolia</i> Poir.	Spain (Teneriffa)	M. & K. Weigend 8240 (BSB)	2207	KF559031	KF559092	KF558971	KF558911
<i>U. peruviana</i> Geltman	Peru	M. Weigend et al. 7625-C (BSB)	1886	KF559018	KF559078	KF558958	KF558897
<i>U. pilulifera</i> L.	Italy	H H. Hilger s.n. (BSB)	2223	KF559036	KF559097	KF558976	KF558916
<i>U. spirealis</i> Blume	Mexico	Ford Smith M 27 (TEX)	2893	KF971229	KF971163	KF971262	KF971196
<i>U. spirealis</i> Blume	Mexico	McDonald 1819 (TEX)	2894	KF971231	KF971165	KF971264	KF971198
<i>U. subincisa</i> Benth.	Mexico	Pérez-Caliz 459 (MO)	2267	KF971236	KF971170	KF971269	KF971203
<i>U. taiwaniana</i> S. S. Ying	Taiwan	J. N. Chen et al. 00573-C (BSB)	2242	KF559045	KF559106	KF558985	KF558925
<i>U. triangularis</i> Hand- Mazz. subsp. <i>trichocarpa</i> C.J.Chen	China	Ho et al 2807 (MO)	2044	KF971227	KF971161	KF971260	KF971194
<i>U. urens</i> L.	Germany	M. Weigend 5667 (BSB)	1082	KF559010	KF559070	KF558950	KF558889
<i>U. urens</i> L.	Peru	M. Weigend et al. 8317 (BSB)	2220	KF559034	KF559095	KF558974	KF558914

DNA isolation, amplification and sequencing

DNA extraction, amplification, purification, and sequencing followed standard protocols as described in Gottschling & Hilger (2001) and Weigend *et al.* (2010). Samples were sequenced for four genomic regions: the nuclear ribosomal ITS1-5.8S-ITS2 (thereafter ITS), and four plastid regions: the *psbA-trnH* intergenic spacer (IGS), *trnL-F* (including the *trnL* group I intron and the *trnL-F* IGS), and *trnS-G* (including the *trnS-G* IGS and the *trnG* group II intron). Amplicons were sequenced by MacroGen Inc., South Korea (<http://www.macrogen.com>) using the amplification primers, i.e. C and F for *trnL-F* (Taberlet *et al.* 1991), trnS_(GCU) and trn G_(UCC) for *trnS-G* (Hamilton 1999), *psbA* and *trnH* for *psbA-trnH* (Sang *et al.* 1997), and P5 and P4 for ITS (White *et al.* 1990).

DNA sequence alignment & phylogenetic reconstruction

A motif alignment was build using PhyDE® ver. 1 (Müller *et al.* 2005), based on the criteria laid out in Kelchner (2000). Two hairpin associated inversions were observed in the data set, one situated in P8 of the *trnL* intron (compare Borsch *et al.* 2003) and the second approx. 90 nt upstream of the *trnF* gene. As discussed in Quandt *et al.* (2003) and Borsch & Quandt (2009) both inversions were positionally isolated in the alignment and included as reverse complement in the nexus files used for phylogenetic analyses. Each data set was analyzed independently in a Bayesian framework to identify incongruences. As no hard incongruences between the individual data sets were observed, phylogenetic analyses were conducted on a concatenated dataset (ITS, *trnS-G*, *trnH-psbA* and *trnL-F*) employing parsimony as well as maximum likelihood (ML) and Bayesian inference (BI). Calculation of most parsimonious trees (MPTs) was done by using the parsimony ratchet (Nixon 1999) as implemented in PRAP (Müller 2004). Ratchet settings were 20 random-addition cycles of 200 ratchet replicates, and up weighting 25% of the characters. Nodes were evaluated by bootstrapping in PAUP* version 4.0b10 for Windows (Swofford 2002) using 10000 replicates. ML analyses were carried out with the standard settings on the RAxML web server (Stamatakis *et al.* 2008). Node support under ML is based on 1,000 bootstrap replicates. BI analyses were conducted in MrBayes vers. 3.2.2 (Ronquist & Huelsenbeck 2003), with six independent runs of 5,000,000 generations each under the GTR + Γ + I model. Chains were sampled every 1000th generation. Log likelihoods were examined using Tracer v1.5 (Rambaut & Drummond 2009) in order to determine the burn-in and to ensure that an adequate effective sample size (ESS) was attained. The consensus tree and the posterior probability (PP) of clades were calculated based upon the trees sampled after the burn-in set at 500,000 generations. TreeGraph2 (Stöver & Müller 2010) was used for tree drawing.

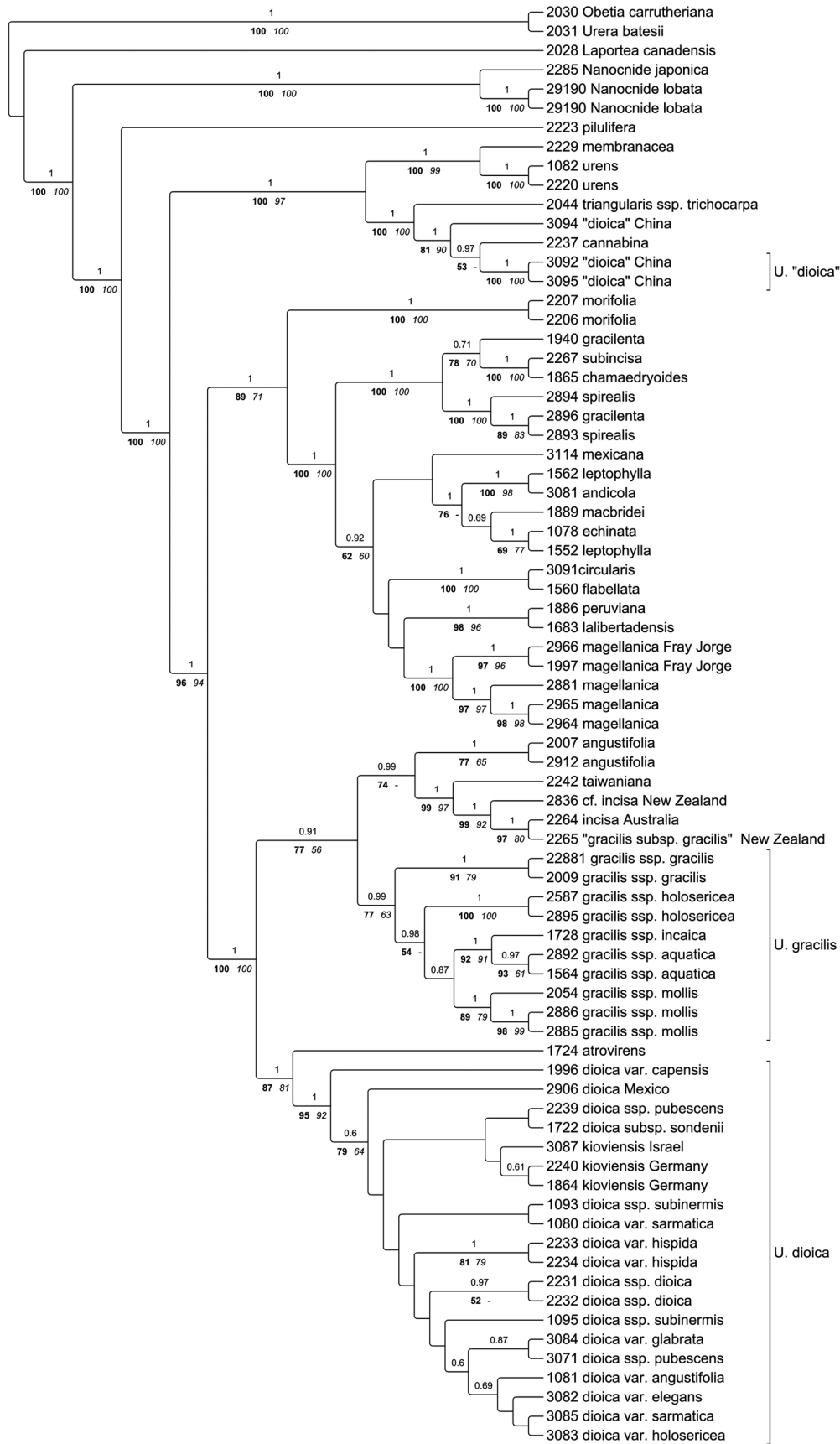


FIGURE 1. Maximum likelihood tree based on the concatenated data set (ITS, *trnL-F*, *trnS-trnG*, *psbA-trnH*). Bayesian posterior probabilities are indicated above branches, while bootstrap support is indicated below. The first value (bold) refers to the bootstrap support under likelihood, and the second (italics) to the parsimony analysis.

Results

Molecular data

A highly resolved phylogeny is retrieved, with Mediterranean *U. pilulifera* L. (1753: 983) the first branching species, followed by a clade comprising two annual Mediterranean species together with several Central and Eastern Asian taxa around *U. cannabina* L. (1753: 984) and the Chinese specimens assigned to *Urtica dioica*. The next branch comprises the bulk of the American species of the genus ranging from North America to Patagonia. “*Urtica dioica*” is retrieved in three major clades: the Chinese specimens are embedded into one Asian clade and show no relationship to the type subspecies or any other group in *U. dioica*. All other “*Urtica dioica*” are retrieved in a crown clade, mixed with several other species: This *Urtica dioica*-clade shows a well-supported sister relationship between a western Eurasian clade and an Asian-American clade. The western Eurasian clade shows a sister relationship between Mediterranean endemic *U. atrovirens* Re. ex. Loiseleur-Deslongchamps (1827: 432) and the—essentially unresolved—western Eurasian *Urtica dioica* in the strict sense. This *Urtica dioica* s.str. includes Scandinavian ssp. *sondenii*, Central European var. *holosericea*, southeastern European ssp. *pubescens*, Eastern European *Urtica kioviensis* Rogowicz (1843: 324), but also southern African var. *capensis* (Weddell 1856: 78) and a presumably introduced *Urtica dioica* from Mexico. The Asian-American clade is retrieved with a sister relationship between an Asian-Australasian subclade and an American subclade. The Asian-Australasian subclade has eastern Asian *U. angustifolia* as first branching taxon, followed by Taiwanese endemic *U. taiwaniana* Ying, Shao Shun (1975: 107) and the Australia-New Zealand accessions. The New Zealand plant referred to *Urtica dioica* ssp. *gracilis* by Webb *et al.* (1988) comes out sister to *Urtica incisa* Poir. in Lamarck (1816: 224) from Australia, this pair is again sister to a taxon called *Urtica incisa* in Cheeseman *et al.* (1925). Conversely, the well-resolved American subclade retrieves temperate North American *Urtica gracilis* ssp. *gracilis* as first branch, ssp. *holosericea* as second branch. The crown clade consists of the newly discovered Peruvian taxon as sister to Guatemalan/Mexican *U. aquatica*, and this pair as sister to Patagonian *U. mollis*.

Morphology

A critical revision of numerous collections including most type collections, and living plants of both the North American subspecies assigned to *Urtica dioica* by Woodland (1982) and the American species of this group, namely *Urtica serra*, *U. aquatica* and *U. mollis*, indicates that all these taxa represent a very homogeneous and closely-knit group of allopatric taxa. However, consistent morphological differences between *U. serra* and *U. aquatica* could not be found. The Peruvian collections (e.g., *Ch. Schwarzer 14*) clearly belong into this complex, but consistently differ in details of the indument. All these forms share essentially unbranched flowering shoots and shortly rhizomatous underground organs. The plants are monoecious, but with both male and female inflorescence branches in varying arrangement on the same shoot.

Discussion

The overall morphological diversity of the relevant characters across the taxa studied is very limited and it is difficult to arrive at an unequivocal interpretation, as evidenced by the highly inconsistent treatment the group has experienced in the past. The molecular data, however, paint a picture of supreme clarity: The Chinese specimens referred to *U. dioica* according to Flora of China (Jiarui *et al.* 2003) are entirely unrelated to *U. dioica*, even in its widest sense, and cluster with the morphologically quite aberrant species *U. cannabina* and *U. triangularis* Handel-Mazetti (1929: 110). A clarification of their taxonomic identity will have to be attempted elsewhere.

Urtica dioica in the wider sense comprises virtually all erect, stoloniferous perennials in the genus and forms a large, paraphyletic group, with very clear geographical sorting. Embedded in the various infraspecific taxa of *Urtica dioica* s.l. are a range of taxa currently recognized at species level, especially in the Australasian subclade. In order to provide a stable and phylogenetically correct classification, two diametrically opposed strategies are available – the reduction of all taxa in *Urtica dioica* s.l. to some infraspecific level, or a further subdivision of *Urtica dioica* and rearrangement of taxonomic levels. The latter process seems to be more appropriate, especially since the phylogenetic data provide a very simple solution: Australasian taxonomy can be completely conserved if the monophyletic America clade is removed from *Urtica dioica* and transferred to *Urtica gracilis*. It seems a

logical extension of the work by Woodland (1982) to remove these taxa completely from *U. dioica* and place them as subspecies into a resurrected *Urtica gracilis* Ait. as the New World-sister to African-Eurasian *U. dioica*. The new Peruvian taxon can then also be placed as a subspecies under that species, so that the following five infraspecific taxa are proposed for *U. gracilis*: *Urtica gracilis* subsp. *gracilis* (for *Urtica dioica* subsp. *gracilis*), *Urtica gracilis* subsp. *holosericea*, *comb. nov.* (for *Urtica dioica* subsp. *holosericea*), *Urtica gracilis* subsp. *aquatica*, *stat. & comb. nov.* (for *Urtica aquatica*), *Urtica gracilis* subsp. *mollis*, *stat. & comb. nov.* (for *Urtica mollis*). Additionally, we describe a new subspecies from Peru under the name *Urtica gracilis* subsp. *incaica*. Moreover, morphological differences between *U. aquatica* and *U. serra* cannot be found and the two taxa should be reduced under the older name *U. aquatica*. Morphologically, this expanded *U. gracilis* can be differentiated by subcircular achenes (versus ovate in *U. dioica* s.str.), unbranched flowering shoots, the formation of short stolons mostly, and the strict monoecy (versus polygamy in *U. dioica* s.str.).

The reports of *U. dioica* subsp. *gracilis* from New Zealand appear erroneous and go back to a misidentification of the Australian taxon *U. incisa*, which is entirely consistent with morphology. Conversely, what is currently considered as *U. incisa* in New Zealand appears to be an undescribed taxon, sister to *U. incisa*. This problem will be resolved elsewhere. Based on the material seen, we cannot confirm the presence of introduced *Urtica dioica* subsp. *gracilis* in New Zealand. The presence of introduced (European) *Urtica dioica* subsp. *dioica* is likely, but was not investigated in this study.

Western Eurasian *Urtica dioica* is here retrieved as well-supported sister to Mediterranean *U. atrovirens*. Resolution of the markers here chosen is clearly insufficient to decide on the monophyly of any of these infraspecific taxa, but it clearly shows that all these forms form a monophyletic group: The various species (*U. kioviensis*), subspecies (e.g. ssp. *subinermis*, ssp. *pubescens*, ssp. *sondenii*) and varieties (var. *holosericea*, var. *glabrata*) are here retrieved on an essentially unresolved clade. In spite of the superficial similarity and contrary to Selander (1947) and Nurmi (2000) North American *U. dioica* ssp. *gracilis* is unrelated to Scandinavian *Urtica dioica* ssp. *sondenii*. Also, contrary to Woodland (1982) North American *U. dioica* subsp. *holosericea* has nothing to do with southeastern European *U. dioica* subsp. *pubescens* or northern European *U. dioica* subsp. *dioica* var. *holosericea* and can be differentiated from South American *U. mollis* both morphologically (see below) and by molecular data. An identity of northern Central American *U. aquatica* with Asian *U. angustifolia* and of both these taxa with Central European *Urtica dioica* var. *angustifolia* (Woodland 1982) is clearly refuted by molecular data.

European *Urtica dioica* is quite variable in appearance, but is polygamous (Heemskerk *et al.* 1998, Weigend 2006) and further differs from *U. gracilis* by the more ovate achenes and the formation of long stolons and usually strongly lateral branches at least late in the season.

Formal Taxonomy

1. *Urtica gracilis* Ait., Hort. Kew 3: 341. 1789. (for type see subsp. *gracilis*)

Erect, perennial herb (0.4–) 1–1.5 (–2.0) m, stems erect, usually unbranched, very rarely with a few branches late in the season, shortly stoloniferous, later shortly rhizomatous. Indumentum of few to many stinging hairs with pluricellular base 1–2 mm overall, and with few to very numerous simple trichomes 0.1–0.2 mm long. Leaf lamina 50–250 × 15–100 mm, ovate-acuminate, oblong-acuminate or lanceolate; surface very densely pubescent with short, simple trichomes 0.1–0.4 mm long and few stinging hairs, adaxially with punctiform cystoliths; leaf base cordate, rounded or cuneate; margins coarsely dentate with 15–25 teeth on each side; leaf apex acute to attenuate; lamina membranaceous to chartaceous; stipules free (4 per node), 2–6 (–8) mm long; petioles (5–) 10–30 (–50) mm long. Plants strictly monoecious. Staminate flowers with tepals ca. 0.5 mm long. Pistillate flowers with short tepals 0.2 mm long and long tepals 0.3 mm long, sparsely pubescent, esetulose. Infructescence (20–) 30–50 mm. Mature fruit with longer tepals 1.5 mm long, achenes subcircular in outline, rounded at base and at the tip, laterally flattened, ca. 1–1.25 × 0.5–0.75 mm.

Urtica gracilis in this definition differs from Eurasian *Urtica dioica* in the strict sense in its strict monoecy (versus polygamy in *U. dioica*), branching of the aerial shoot (very rare in *U. gracilis*, commonly found in *U. dioica* at least late in the season) and the shape of the fruit: Achenes of *U. gracilis* are subcircular in outline and rounded at the base and at the tip, those of *U. dioica* are ovoidal with a narrowed base and apex, widest below the middle.

Key to the subspecies of *Urtica gracilis*.

- 1 Plants subglabrous, with only scattered stinging hairs and very few, scattered, simple trichomes; leaves usually dark green, thinly membranaceous; monoecious, usually with male flowers below and female flowers above (USA, Canada) *Urtica gracilis* subsp. *gracilis*
- Plants more or less pubescent and/or with numerous stinging hairs; leaves yellowish green, or more often whitish from dense pubescence, rarely dark green but then more or less rugose, chartaceous; monoecious, with male flowers below and female flowers above or with a few female nodes followed by several male nodes and then by female nodes at the shoot apex 2
- 2 Plants with numerous, stiffly erect stinging hairs on the stem up to 3.5 mm long; leaves adaxially with stinging hairs, with dense, soft pubescence on stem and adaxially on leaves and fruit; lower nodes on the plant all with male flowers, upper ones with female flowers (Chile, Argentina) *Urtica gracilis* subsp. *mollis*
- Plants with sparse, erect or curved stinging hairs on the stems, these up to 1.5 mm long; leaves adaxially usually without stinging hairs, with or without dense pubescence; lower nodes on the plant with female flowers, followed by males nodes and with female nodes apically 3
- 3 Plants up to 2 m tall; with very dense, white, soft pubescence of simple trichomes ca. 0.5 mm long on stem, fruit and leaves; with scattered, erect stinging hairs on the stem; leaf base cordate to rounded (W USA, NW Mexico) *Urtica gracilis* subsp. *holosericea*
- Plants up to 1(–1.5) m tall; with soft pubescence, but simple trichomes only 0.1–0.3 mm long on stem, fruit and leaves, never appearing white on stem, fruit and leaves; scattered stinging hairs on the stem, many of these acroscopically or basiscopically bent; leaf base subcordate, truncate to rounded 4
- 4 Leaves abaxially with stinging hairs on the larger veins near the leaf base, leaves adaxially dark green, abaxially often flushed red in the living stage; leaf margin always sharply serrate in median and apical leaves (Peru) *Urtica gracilis* subsp. *incaica*
- Leaves abaxially without stinging hairs, leaves adaxially fresh green to yellowish green, abaxially never flushed red in the living state; leaf margin crenate to sharply serrate in median and apical leaves (S-C Mexico, Guatemala) *Urtica gracilis* subsp. *aquatica*

1.1 *Urtica gracilis* Ait. subsp. *gracilis*, Hort. Kew 3: 341. 1789. Fig. 2 A–E, G.

Holotype:—[CANADA: Hudson Bay], Hudson’s Bay [cultivated at Kew Gardens by *W. Aiton*, anno 1782] (BM!).

≡ *Urtica dioica* L. subsp. *gracilis* (Ait.) Selander (1947: 271),

≡ *Urtica dioica* var. *gracilis* (Ait.) Taylor & MacBryde (1977: 434)

= *Urtica procera* Muhl. ex Willdenow (1805: 353). Holotype:—North America, *Muhlenberg* (B-WILLD!). North America, *Muhlenberg s.n.* [B-WILLD # 17405 & B-WILLD # 17406] - photographs: DAO, MTMG; isotype: PH).

= *Urtica dioica* L. var. *procera* (Muhl ex Willd.) Weddell (1856: 78)

= *Urtica lyallii* Watson (1875: 348). Holotype:—[CANADA. British Columbia] in the Cascade Mts. in lat. 49, *Lyll s.n.* (GH!, P).

= *Urtica dioica* L. var. *lyallii* (S.Wats.) Hitchcock (1964: 96)

= *Urtica californica* Greene (1889: 281). Holotype:—[USA. California, San Mateo County] Streamlet below Pt. Peidras, Coast Range in San Mateo County, California, 10 June 1887, *Greene s.n.* (JEPS).

= *Urtica lyallii* S.Wats. var. *californica* (Greene) Jepson, (1901: 147)

= *Urtica dioica* L. var. *californica* (Greene) Hitchcock (1964: 96)

= *Urtica cardiophylla* Rydberg (1897: 191). Holotype:—[USA. Montana, Meagher Co.?] “on a wooded creek bank” near Castle, Montana, *Flodmann 370* (NY).

= *Urtica strigosissima* Rydberg, (1912: 305). Holotype:—[USA. Idaho] Nez Perce County, Forest, *Heller & Heller 3475* (NY, MIN, MO, US).

= *Urtica viridis* Rydberg (1912: 305). Holotype:—[USA, Montana, Park County] Montana, Emigrant Gulch, *Rydberg & Bessey 3935* (NY, F, GH, MONT).

Erect, perennial herb 0.6–1.5 (–2.0) m, unbranched, rarely with a few branches late in season. Plant with very sparse cover of erect stinging hairs ca. 1 mm long, pluricellular base straight and ca. 1/3–1/2 of overall length of the seta, subglabrous with scattered, simple trichomes ca. 0.1–0.4 mm long. Leaf lamina 50–250 × 15–100 mm, broadly

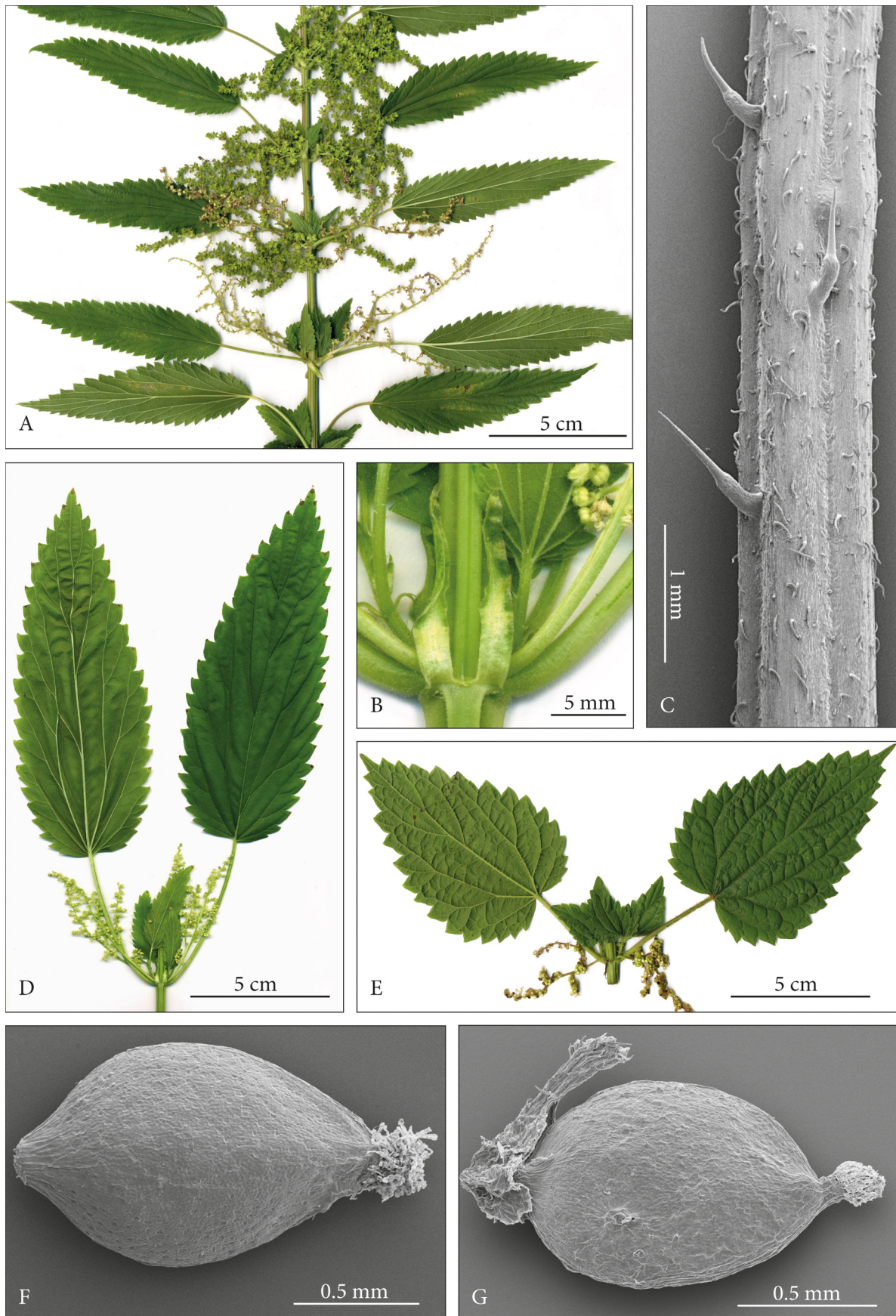


FIGURE 2. *Urtica gracilis* subsp. *gracilis*: (A–D, G: Weigend 9332), A. Habit, B. Node with stipules, C. Stem with scattered simple trichomes and few setae, D–E. Leaf shape variability, D. Narrow leaf pair from Weigend 9332, E. Broader leaves from Liston 1223, F. Ovate achene of *U. dioica* subsp. *dioica* for comparative purposes (Weigend 8102), G. Achene of *U. gracilis* subsp. *gracilis*.

ovate to narrowly ovate-acuminate; subglabrous and without stinging hairs, rarely with individual stinging hairs abaxially; leaf base cordate to rounded; margins coarsely dentate with 15–25 teeth on each side, teeth with proximal side convex and distal side concave or straight; lamina membranaceous, fresh green. Plants monoecious, usually with lowest nodes male, followed by mixed, then female inflorescence branches. Mature fruit ca. 1–1.25 × 0.5–0.75 mm, tepals subglabrous.

Notes:—The typical subspecies of *U. gracilis* is a taxon from mostly moist habitats, often forest edges and clearings, but also from ruderal habitats in the northern USA, usually with subglabrous, thin, dark green leaves (Woodland 1982, Woodland *et al.* 1982). Morphologically, the typical form is quite characteristic, but poorly developed specimens can be easily confused with typical *U. dioica* and, like all more widespread forms of *Urtica*, this ssp. is also quite variable in appearance. Monoecy is often overlooked in this taxon, since the shoots are relatively long and in herbaria often only a shoot portion with either male or female flowers is preserved. Also, male inflorescences may be entirely absent from fruiting plants, because they are shed after anthesis, making the plant apparently female. All plants we raised from two different accessions from Canada and Oregon were consistently monoecious, and we believe this to be a consistent trait as in all other subspecies of *U. gracilis*. This led to a wide range of different taxa being described, which were sorted out by Woodland (1982). This is the first branching taxon of *U. gracilis* as here retrieved by molecular data and the other four subspecies are also morphologically more similar to each other than to ssp. *gracilis*.

This taxon has been confused with ssp. *sondenii* from northern Europe in the past, a classification clearly contradicted by molecular data. Subspecies *sondenii* is similar in its sparse indument and near lack of stinging hairs, but is polygamous like the majority of western Eurasian taxa and not monoecious as ssp. *gracilis*. Also, the achenes of ssp. *gracilis* are subcircular, whereas those of ssp. *sondenii* have the ovate shape typical of *U. dioica* s.str. Thus, strong molecular and weak morphological data clearly show, that the superficial similarity of these two taxa indicates rather a lack of characters than any true affinity.

Representative specimens:—CANADA. **British Columbia:** Vancouver, Point Gray Golf Course, 3 October 1945, *W. Bird 221* (BM); Victoria, Mt. Robson Park, Avalanche slope, 4.5 miles W of Red Pass, 53°01'N, 119°06'W, 1524 m, 14 August 1975, *C.C. Chuang 75/481* (BM); **Saskatchewan:** Prairie Region, Saskatoon, anno 1924, *A.B. Rendle & R. D'O Good 228* (BM); **Manitoba:** Churchill, 40 ft., 27 July 1957, *Eva Beckett 138* (BM); Churchill, Gillam, 30 July 1950, *W.B. Schofield 1288* (BM); **Ontario:** Thunder Bay District, North Shore of Little Pigeon Bay, Lake Superior, Crooks Township, 20 August 1952, *C.E. Garton 2179* (BM); USA. **North Dakota:** Kulm, Aug. 1910, *J.F. Brenckle s.n.* (PR); **Oregon:** July 1883, *T. Howell s.n.* (PR); E. Oregon, mountain streams and bogs, 4000–6000 ft., 4 August 1898, *W.C. Cusick 2070* (PR).

Cultivated in Berlin from source collections: CANADA. **Alberta:** Athabasca, Millenium seed bank 2000 Acc. 147637, *M. Weigend 9332* (B, BONN); USA. **Oregon:** Benton County, 5 miles NW of Corvallis, Oak Creek entrance to McDonald Forest, 21 July 2002, *A. Liston 1223-C* (M, W, LE, KRAM, NY, P, BM, USM, FI, MO).

1.2 *Urtica gracilis* Ait. subsp. *holosericea* (Nutt.) Weigend, *comb. nov.* Fig. 3.

Basionym: *Urtica holosericea* Nuttall (1848: 25). Holotype:—[USA] California, "Near Monterey, Upper California", *Gambel s.n.* (specimen lost). Neotype (designated in Woodland 1982: 287):—USA, California, Monterey Co., on the Salinas Road near Del Monte, "from Type locality", *A. A. Heller 6838* (DS; isoneotypes: E, MO, P, WIS).

≡ *Urtica dioica* L. subsp. *holosericea* (Nutt.) R.F. Thorne (1967: 68),

≡ *Urtica dioica* L. var. *holosericea* (Nutt.) C.L. Hitchcock (1964: 91)

≡ *Urtica gracilis* Ait. var. *holosericea* (Nutt.) Jepson (1909: 367)

= *Urtica dioica* var. *occidentalis* S.Wats. in King (1871: 321). Holotype:—[USA] Nevada, near Carson City, anno 1865, *C.L. Anderson 190* (GH).

= *U. trachycarpa* Weddel, (1856: 95). Holotype: [USA] California, *Beechey s.n.* (G).

= *U. breweri* S.Watson (1875: 348–349). Holotype:—[USA, California, Los Angeles County] Los Angeles, anno 1861, *W.H. Brewer 945* (GH, isotype: US).

= *U. gracilis* Ait. f. *densa* Jepson (1909: 367). Holotype:—[USA] California, "Howell Mts.", Angwin Meadow, Napa River Basin, *W. L. Jepson s.n.* (JEPS).

= *U. gracilis* Ait. f. *greenii* Jepson (1909: 367). Holotype:—[USA] California, Siskiyou County, Etna, *Greene 1028* (not localized).

= *U. gracilis* Ait. var. *greenii* (Jeps.) Jepson (1923: 281)

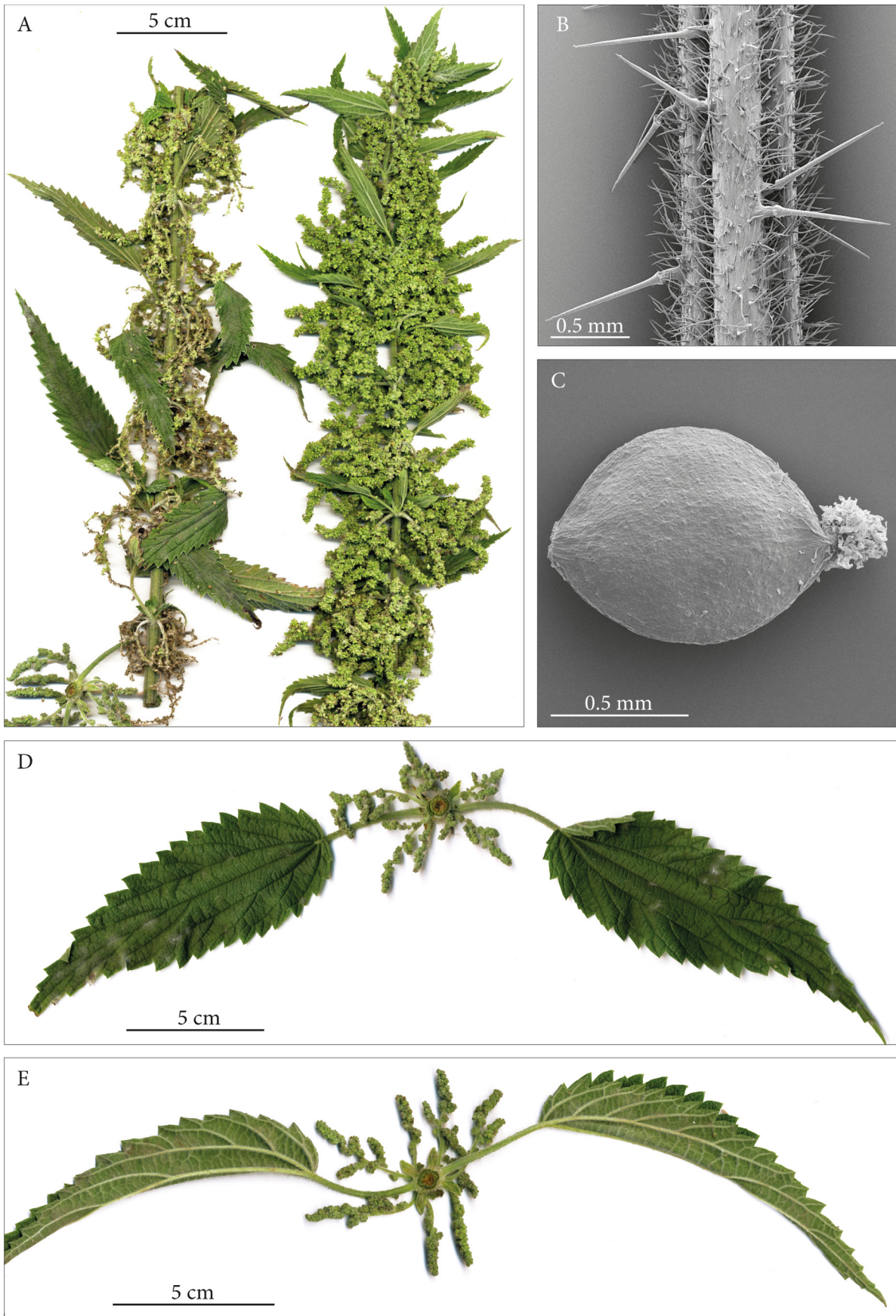


FIGURE 3. *Urtica gracilis* subsp. *holosericea*: (all Ahartt 13535), A. Habit with mixed/male inflorescences in the middle (left) and female inflorescences in the distal parts (right) of the shoot, B. Stem with countless simple trichomes and few erect stinging hairs, C. Mature fruit, D. Node (section) with leaf pair, adaxially, E. Node with leaf pair lateral/abaxial view.

Erect, perennial herb 0.6–1.5 (–2.5) m, unbranched. Plant with sparse cover of erect stinging hairs ca. 1 mm long overall, pluricellular base straight and <1/4 of overall length of the seta, densely pubescent, countless simple trichomes ca. 0.5 mm long. Leaf lamina 50–250 × 15–100 mm, broadly ovate to narrowly ovate-acuminate; densely pubescent especially abaxially and without stinging hairs or with very few stinging hairs abaxially; leaf base cordate to rounded; margins coarsely dentate with 15–25 teeth on each side, teeth with proximal side convex and distal side convex, straight or concave; lamina chartaceous, greyish green. Plants monoecious, with 1–3 lowest nodes female, followed by mixed, then male inflorescence branches, distally with female inflorescence branches. Mature fruit ca. 1–1.25 × 0.5–0.75 mm with tepals densely spreading pubescent with trichomes ca. 1 mm long.

Notes:—This taxon is predominantly western North American and northwestern Mexican. The taxon may grow very tall and reached nearly 250 cm in cultivation in Berlin. Morphologically it is usually immediately recognized by its very dense and very short, whitish to grey pubescence on leaves and stem, including the tepals. There are intermediate forms with ssp. *gracilis* as discussed by Woodland (1982), who also detailed the complex synonymy.

This taxon has been considered as closely allied to or identical with ssp. *mollis* from Chile, which tends to have much broader, more widely crenate leaves, different gender distribution on the shoot and, most easily recognized, much longer, stiffly erect stinging hairs. Molecular data clearly confirm the monophyly of ssp. *holosericea* and also refute any association with Old World ssp. *pubescens*.

Ecologically, the plant is often associated with watercourses or standing water and seasonally flooded areas. At least in cultivation it is sensitive to drought, but seems to require full sunlight for normal development. This makes it quite different from ssp. *gracilis*, which is also moisture loving, but is predominantly a woodland species tolerating strong shading.

Representative specimens:—USA. **California:** Santa Barbara county, Santa Cruz Island, N from Main Ranch along road to Prisoner's Harbour, 100 ft., 10 October 1958, *E.K. Balls 11780* (BM); Los Angeles County, Mesmer, Ballona Creek, 18 August 1902, *Leroy Adams 2958* (BM); Springville, 26 June 1954, *M.J. Groesbeck 195* (BM); Sonoma County, Laguna de Santa Rosa NE of Graton, near Guerneville Road, 17 August 1958, *P. Rubtzoff 3890* (BM); Los Angeles County, Mescal Creek, 1800 m, 2 August 1936, *J.A. Ewan 9916* (K - KEW22881); San Bernardino, May 1880, *G. R. Casey 561* (K); Santa Barbara County, Santa Barbara, August 1902, *A. D. E. Elmer 3864* (K); Butte County, T17N, R1E, southeast 1/4 Section 16, Southwest of Parking Lot 17, Gray Lodge Wildlife Area, freshwater Marsh, ca. 20 m, N 39 19 10,5, W 121 51 20, *Lowell Ahart 13238* (B); Colusa County, T17N, R8W, northwest 1/4 Section 25, Big Springs, on the south side of Letts Lake, ca. 13 miles SW of Stonyford, yellow Pine forest, ca. 1600 m, N 39 18 11,8, W 122 42 46,5, *Lowell Ahart 13535* (B); cultivated from this number in Berlin, *Lowell Ahart 13535-C* (B, E, K, S, W); Colusa County, T17N, R6W, northwest 1/4 Section 24, east side of East Park Reservoir, ca. 1/2 miles N of Lodoga, west of road from Lodoga to Maxwell, ca. 400 m, N 39 18 38,1, W 122 29 12,7, *Lowell Ahart 13172* (B); Nevada: Elko County, near Blaine Post office, 23 August 1913, *A.A. Heller 11124* (K - KEW22880); Reno, 4500 ft., 11 June 1897, *M.E. Jones s.n.* (BM); Indian Creek, 118 13'W, 37 46'N, 27 June 1965, *T. E. Lancaster 862* (BM); Esmeralda County, White Mountains, Chiakovitch Creek, 2600 m, 05 July 1931, *V. Duran 3098* (K);—MEXICO. **Sonora:** El Pintor, 5 km NE of Cucurpe on Rio Dolores, W 110 43, 10, N 30 22 31, 895 m, 16 May 2002, *A. L. Reina G. et al. 2002–330* (TEX); **Baja California:** 15–20 miles from Ensenada to Ojos Negros, 14 September 1929, *Wiggins & Gillespie 4055* (MO).

1.3 *Urtica gracilis* Ait. subsp. *aquatica* (Liebm.) Weigend, *comb. & stat. nov.* Fig. 4.

Basionym: *Urtica aquatica* Liebmann (1851: 291). Holotype:—MEXICO, Puebla, Chinantla, 7000', May 1841, *Liebmann s.n.* (C!; isotypes: K x 2, K000575384!; GH 00015968!).

= *Urtica serra* Blume (1856: 143). Type:—MEXICO, Hidalgo or Tamaulipas, between Tampico and Real del Monte, 17 May 1827, *Cl. Berlandier 340* (W, not seen; BM, BM000593538 pro parte!).

- *Urtica mexicana* Blume (1856: 143), *nom. illeg.* (*non Urtica mexicana* Liebm.). Syntypes:—[Mexico, Federal District,] Toluca, April 1834, *G. Andrieux* [Pl. Mex.] 98 (GH - 00015971!); without precise locality, 24 June 1827, *Cl. Berlandier 432* (BM!, G-DC - microfiche!).

Erect, perennial herb 0.6–1 (–1.5) m, unbranched. Plant with very varying cover of stinging hairs ca. 1.5 mm long, pluricellular base often asymmetrically curved and >1/3rd to 1/2 of overall length of the seta, set with simple trichomes ca. 0.3 mm long. Leaf lamina 50–220 × 15–50 mm, to usually narrowly ovate-acuminate to oblong,

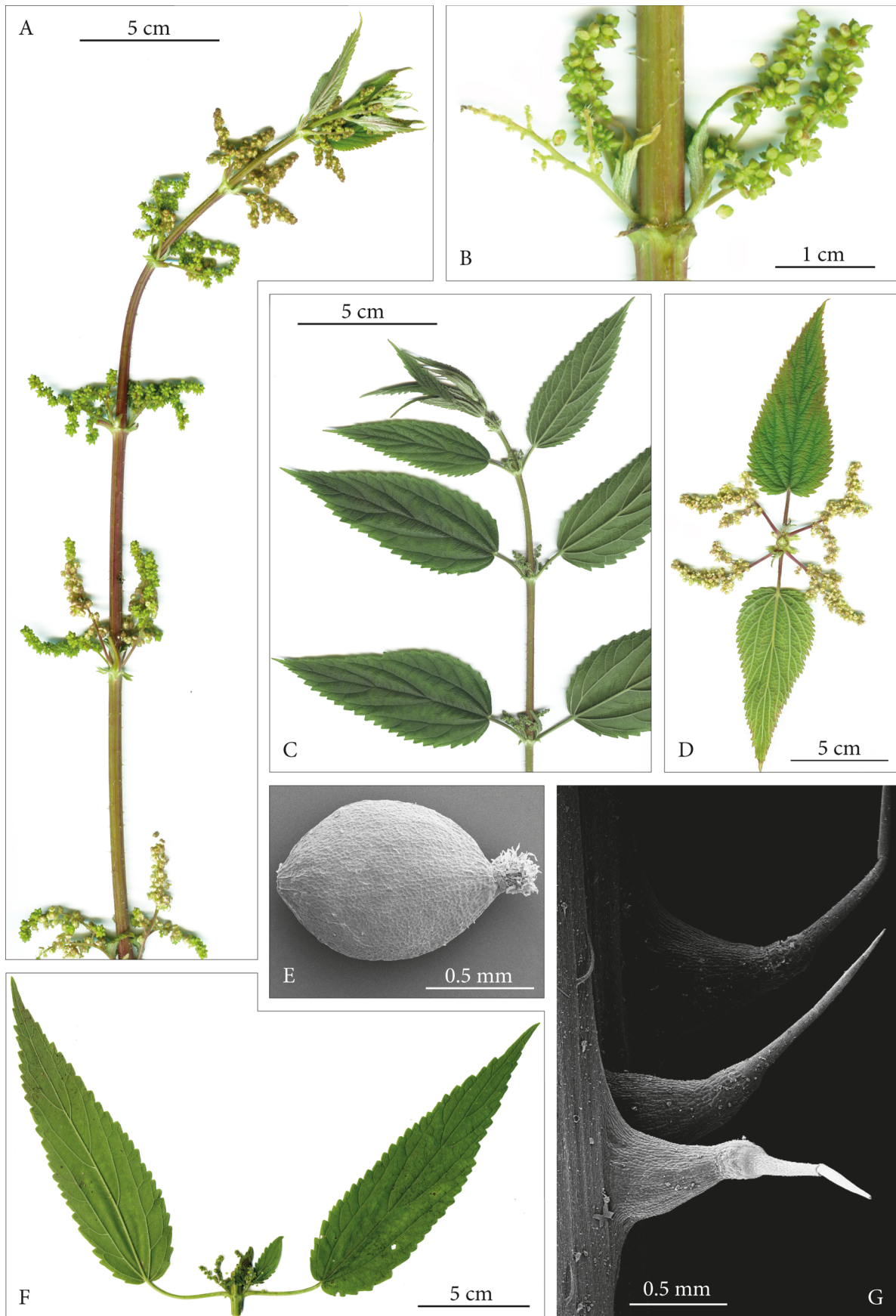


FIGURE 4. *Urtica gracilis* subsp. *aquatica*: (A, C, F: *Schneider s.n.*, all others: *Weigend 7478*), A. Habit with mature inflorescences of both sexes, B. Node with mixed inflorescence, male flowers already shed, female branches with mature fruits, C. Young shoot with immature inflorescences, D. Node (section) with leaf pair with adaxial surface (above) and abaxial surface (below) and male inflorescences, E. Achene, F. Node of *Schneider s.n.* with narrower leaves and female inflorescences, G. Stinging hair with long, curved pluricellular base.

rarely ovate; densely pubescent especially abaxially and without stinging hairs or with only 1–2 stinging hairs abaxially; leaf base rounded to cuneate, rarely cordate in basal leaves; margins coarsely dentate with 15–20 (–25) teeth on each side, teeth with proximal side convex and distal side convex, straight or concave; lamina chartaceous, yellowish green in the living state. Plants monoecious, with 1–3 lowest nodes female, followed by mixed, then male inflorescence branches, distally with female inflorescence branches. Mature fruit ca. 1–1.25 × 0.5–0.75 mm with tepals appressed-pubescent with trichomes ca. 0.1–0.2 mm long.

Notes:—A comparison of the types of *U. serra* Blume, *U. mexicana* Blume and *U. aquatica* Liebm. shows that they are conspecific – there is only one narrow-leaved taxon of this group in Mexico and Guatemala. *Urtica serra* is therefore formally synonymized here, while *Urtica mexicana* Blume is a homonym of *U. mexicana* Liebm. *Urtica aquatica* Liebm. has been considered as “very close to” *Urtica dioica* (Weddell 1856) and subsequently as a synonym of *Urtica dioica* L. var. *angustifolia* (Fisch. ex. Hornem.) Ledebour (1833: 241) (= *Urtica angustifolia* Fisch. ex Hornem., Weddell 1869). However, the present molecular data clearly separate East and Central Asian (polygamous) *Urtica angustifolia* from (monoecious) *Urtica aquatica*, and place the latter firmly in the American *U. gracilis* clade. It is here formally placed as subspecies under that taxon. The association with narrow-leaved European forms is clearly refuted and *U. aquatica* is retrieved as sister to the newly described ssp. *incaica* from Peru (for differences see there).

As the name implies, the species is usually associated with water and is commonly found at the side of streams and water courses, rarely in drier habitats. It is usually found in full sun, but appears to tolerate some degree of shading.

Representative specimens:—MEXICO. **Hidalgo:** Real del Monte, 27 August 1944, *E. Hernández X. 459* (LL); Mexico D.F.: Hidalgo, El Chico, Nov. 1986, *D. Ramos s.n.* (MO); Hidalgo, 21 September 1910, *C. R. Orcutt 4124* (BM); **Mexico D.F.:** Valley of Mexico, 3 June 1896, *C.G. Pringle 6301* (MO, PR); Mpio. Xochimilco, angituguo canal de Cuemanco en Ejido de Xochimilco, 2250 m, N 19 21 02, W 099 06 01, 16 April 2002, *A. Novelo R. 4351* (MO); Tlalpam, ca. 2500 m, 01 August 1924, *G. L. Fisher s.n.* (MO); San Lorenzo, Delegación de Milpa Alta, 2500 m, 10 April 1976, *A. Ventura A. 1305* (MO); Zacayuca, Plantas del Pedregal de San Angel, 01 June 1952, *J. Rzedowski 1073* (TEX); Along banks of canal at Xochimilcho, 11 July 47, *Barkley et al. 17M332* (TEX); Xochimilcho, 25 April 1965, *O. Tapia 48* (TEX); San Gergorio Atlapulco, La Huerta, 2250 m, 06 September 1964, *J. Paez 67* (TEX); Del. Venustiano Carranza, Mercado Sonora – bought on the market, originally from San Salvador Cuautenco in Mexico DF, 13 June 1986, *R. Bye et al. 14588* (TEX); Mpio. Xochimilco, Antiguo canal de Cuemanco en Ejido de Xochimilco, 2250 m, N 19 17 02, W 99 06 01, 16 April 2002, *A. Novelo R. 4351* (MO); Mpio. Texcoco, Poblado San Felipe, 2240 m, 07 May 1983, *R. Muskus 50* (TEX); Valle de Mexico, *Schmitz 142* (BM); **Michoacan:** banks of Rio Angulo, Mpio de Panindicuaro, 1900 m, 08 May 2005, *J. Rzedowski 54142* (TEX); **Oaxaca:** Distrito de Ixtlan, Municipio de Chicomezuchil, 2625 m, *G. J. Martin 604* (BM); Without precise locality, *Graham 308* (BM); **Puebla:** Tescmalaquilla, Mount Orizaba, 3500 m, 18 March 1938, *Balls 5286* (BM); Near Puebla, Manzanilla, 2250 m, 24 November 1908, *B. G. Arsène 1702* (MO); Mpio Cholula, Tlamilolpa, 2450–2500 m, W 98 29–98 30, N 19 04 30–19 05 15, 25. October 87, *M. Tlapa A. & G. Ubierna 1086* (TEX); Mpio Cholula, Santiago Xalitzintla, W 098 31, N 19 04 45, 2580 m, *M. Tlapa A. & G. Ubierna 1961* (TEX); Chinantla, anno 1860, *A. Oersted s.n.* (K); **Veracruz:** near La Banderilla, without date, *D. Schiede 27* (MO); La Banderilla, May 1829, *Schiede & Deppe s.n.* (BM). Without locality, *Schiede s.n.* (P–P00585528); GUATEMALA: **Huehuetenango:** Municipalidad Huehuetenango, road from Todos Santos to Tres Caminos, N 15° 30′ 14″, W 091° 35′ 29″, 2530 m, 07 March 2003, *Ch. Schneider et al. 30* (B); *Ch. Schneider et al. 30a* (B); *Ch. Schneider et al. 31* (B); cultivated at Hannover from Mexican seeds: *anon. s.n.* (MO); Without precise locality: anno 1910, *C. R. Orcutt 4124* (MO).

1.4 *Urtica gracilis* Ait. subsp. *incaica* Weigend, *subspec. nov.* Fig. 5.

Holotype:—PERU: Dept. Huancavelica: Prov. Tayaca. Road from Pampas to Rio Huanchuy, La Colpa, S 12°20′33″, W 74°49′43″, 3207 m, 20 September 2001, *M. Weigend, N. Diané, M. Gottschling, H.H. Hilger, J. Skrabal 5847* (USM; isotypes: BSB, HUT, M).

Erect, perennial herb 0.6–1 (–1.5 m), unbranched. Plant with very varying cover of stinging hairs ca. 1.5 mm long, pluricellular base often asymmetrically curved and >1/3rd to ½ of overall length of the seta, densely pubescent with countless simple trichomes ca. 0.2 mm long. Leaf lamina 60–150 × 15–55, usually narrowly ovate-acuminate to

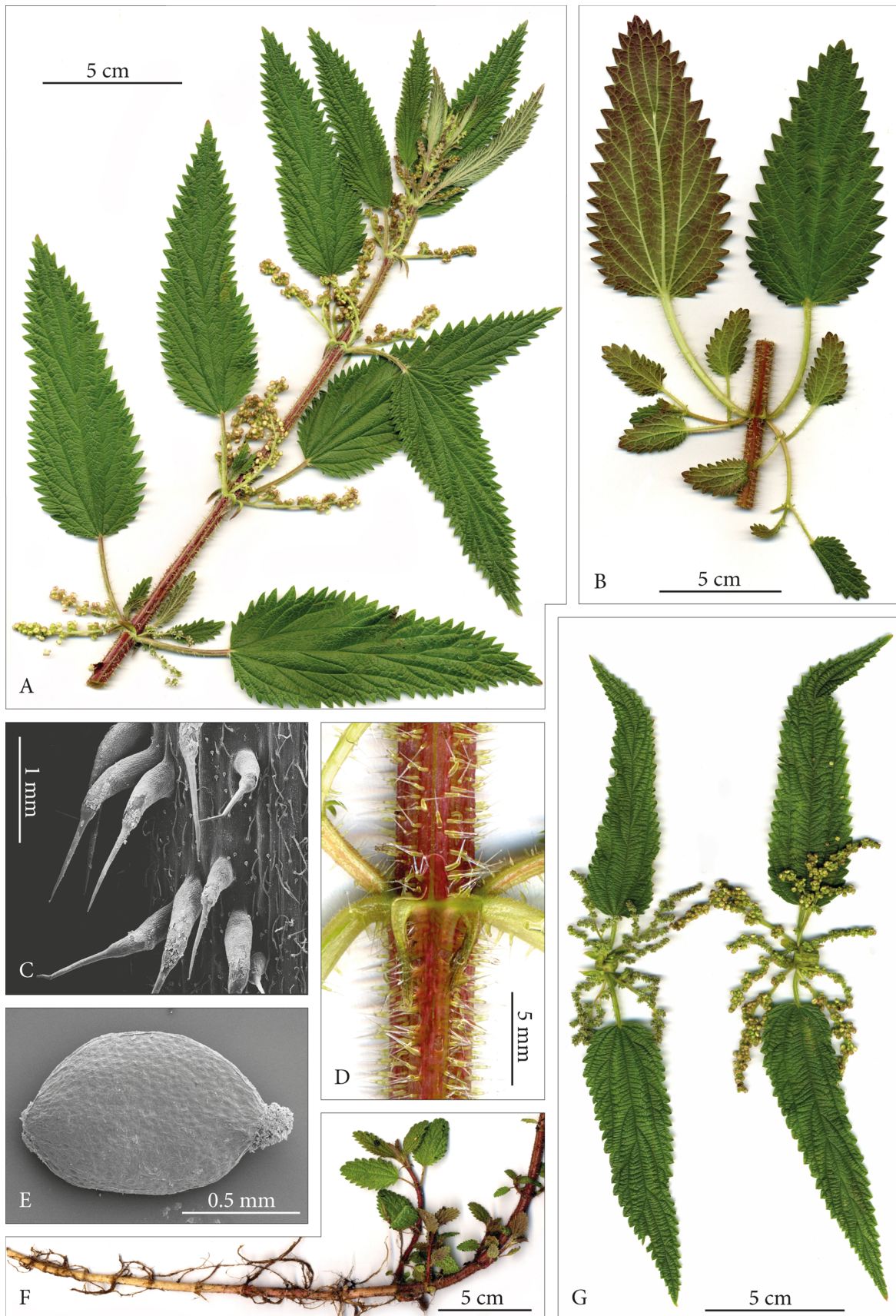


FIGURE 5. *Urtica gracilis* subsp. *incaica*: (All from *Schwarzer 14*), A. Habit of young plant with predominantly male inflorescences, B. Ovate leaves of a young shoot (compare F), note the reddish flushed abaxial surface (left), C. Stem covered with setae with long, asymmetrically curved pluricellular base and numerous simple trichomes, D. Node densely covered with numerous setae, E. Achene, F. Rhizome with young shoots, G. Nodes with leaf pairs and female inflorescences (left) and male inflorescences (right).

oblong, rarely ovate; densely pubescent especially abaxially and without stinging hairs or with 1–2 stinging hairs abaxially; leaf base rounded to cuneate, rarely cordate in basal leaves; margins coarsely dentate with 15–20 (–25) teeth on each side, teeth with proximal side convex and distal side convex, straight or concave; lamina chartaceous, greyish to dark green in the living state, abaxially often flushed with red. Plants monoecious, with 1–3 lowest nodes female, followed by mixed, then male inflorescence branches, distally with female inflorescence branches. Mature fruit ca. 1–1.25 × 0.5–0.75 mm with tepals appressed-pubescent with trichomes ca. 0.1–0.2 mm long.

Notes:—This new taxon has been collected several times in south-central Peru, always at elevations of above 3000 m asl. Molecular data show that it is the sister taxon of subsp. *aquatica* from Guatemala and Mexico, which differs in the absence of stinging hairs on the abaxial leaf surface and the light green leaves (versus leaves abaxially with stinging hairs on the veins and dark green, often reddish green abaxially). Moreover, the plants from Peru are always sparsely pubescent and rough to the touch (leaves adaxially), whereas those from northern Central America (ssp. *aquatica*) are always soft pubescent and velvety to touch. The taxon is probably a lot more widespread and common than here reported, but poorly collected due to the widespread assumption that it is an introduced weed in the Andes.

The type collection came from a seepage area in a pasture, the *Schwarzer 14*-collection is from the *Phragmites*-belt around a high Andean lagoon, so the species is consistently associated with water and lives in fully open, sunny habitats – it is thus ecologically very similar to ssp. *aquatica* and *holosericea*.

Representative specimens:—PERU: **Depto. Apurimac:** Prov. Andahuaylas, Laguna Pacucha near Paccha, near Conpuerta, c. 3125m, 10 July 2004, *Ch. Schwarzer 14* (BSB, USM); specimen prepared from cultivated plants at the Institut für Systematische Botanik, Freie Universität Berlin, specimens prepared in 2005, *Ch. Schwarzer 14-C* (BSB); same collection, specimens prepared in 2006, *Ch. Schwarzer 14-C2* (BSB); **Depto. Cusco:** Prov. Quispicanchis, Dist. Cusipata, Chilliwani, S 13°00' W 71°16', 4700 m, 2 May 2005, *A. Tupayachi 6464* (MO, B); Prov. Paruro, Yaurisque, path Cuczo to Paruro, 3300 m, 7–8 March 1987, *P. Nuñez 7399* (MO); **Depto. Junin:** Prov. Huancayo, Colca, 3250 m, 27 April 1989, *G. Yarupitán 13* (USM); - without locality, [probably Cusco, Prov. Cusco]: *Herrera 2680* (B).

1.5 *Urtica gracilis* Ait. subsp. *mollis* (Steud.) Weigend, *comb. & stat. nov.* Fig. 6.

Basionym: *Urtica mollis* Steudel (1850: 258). Lectotype (designated by Geltman, 1994: 23):—CHILE, Región V., de Valparaíso: “*Urtica*, vulgo Ortiga, flores monoici In ruderatis et sylvaticis ... (illegible)... Quillota”, *Bertero 1382* (P-P00585543!); Duplicates of lectotype (same label): BM!, G-DC!; duplicates of lectotype (different labels): “in ruderatis ad sepes udis Quillota Chili”, October 1829, *Bertero 1382* (HUH!, M!, fragment: L!); Remaining syntypes:—“In ruderatis, ad sepes, in udis Quillota”, October 1829. *Bertero 1383* (mixta cum *U. leptophylla*) (P-P00585544!); “Chili”, *Bertero s.n.* (P!).

= *Urtica diplotricha* Philippi (1864: 234). Holotype:—CHILE, IV Región, Prov. Choapa “Concumen”, January 1863, *Landbeck s.n.* (SGO, fragment: HUH!).

= *Urtica buchtienii* Ross (1905: 466). *syn. nov.* Lectotype (designated in Weigend & Luebert 2009: 10):—CHILE, Región V, Valparaíso, Prov. Los Andes, “Uspallata Pass der chilenischen Hochkordillere (33° s. Breite) zwischen Geröll”, 2200 m, 29 January 1903, *O. Buchtien s.n.*” (M!, isotypes: L!, M!, S, P!, E, G, US).

Erect, perennial herb 0.6–1 (–1.5 m), unbranched. Plant with very varying cover of stinging hairs ca. 2–3.5 mm long, pluricellular base straight and <1/4 of overall length of the seta, densely pubescent with countless simple trichomes ca. 0.2 mm long. Leaf lamina 60–150 × 30–70, usually narrowly ovate-acuminate to oblong, rarely ovate; densely pubescent especially abaxially and without stinging hairs or with 1–2 stinging hairs abaxially; leaf base rounded to cuneate, rarely cordate in basal leaves; margins coarsely dentate with 15–20 (–25) teeth on each side, teeth with proximal side convex and distal side convex, straight or concave; lamina chartaceous, greyish to dark green in the living state, abaxially often flushed with red. Plants monoecious, with 1–7 lowest nodes male, followed by mixed, then female inflorescence branches. Mature fruit ca. 1–1.25 × 0.5–0.75 mm with tepals appressed-pubescent with trichomes ca. 0.1–0.2 mm long.

Notes:—This taxon was considered as a separate species until recently, but doubts were repeatedly voiced about its status. The molecular data now clearly retrieve this taxon nested in *Urtica gracilis* s.l. and separate from North American subsp. *holosericea*, with which it has been associated in the past. The overall plant habit is quite different between these two taxa, but this is impossible to see in the herbarium. However, gender distribution is different, with ssp. *holosericea* showing female nodes at the base, followed by male nodes in the middle and female

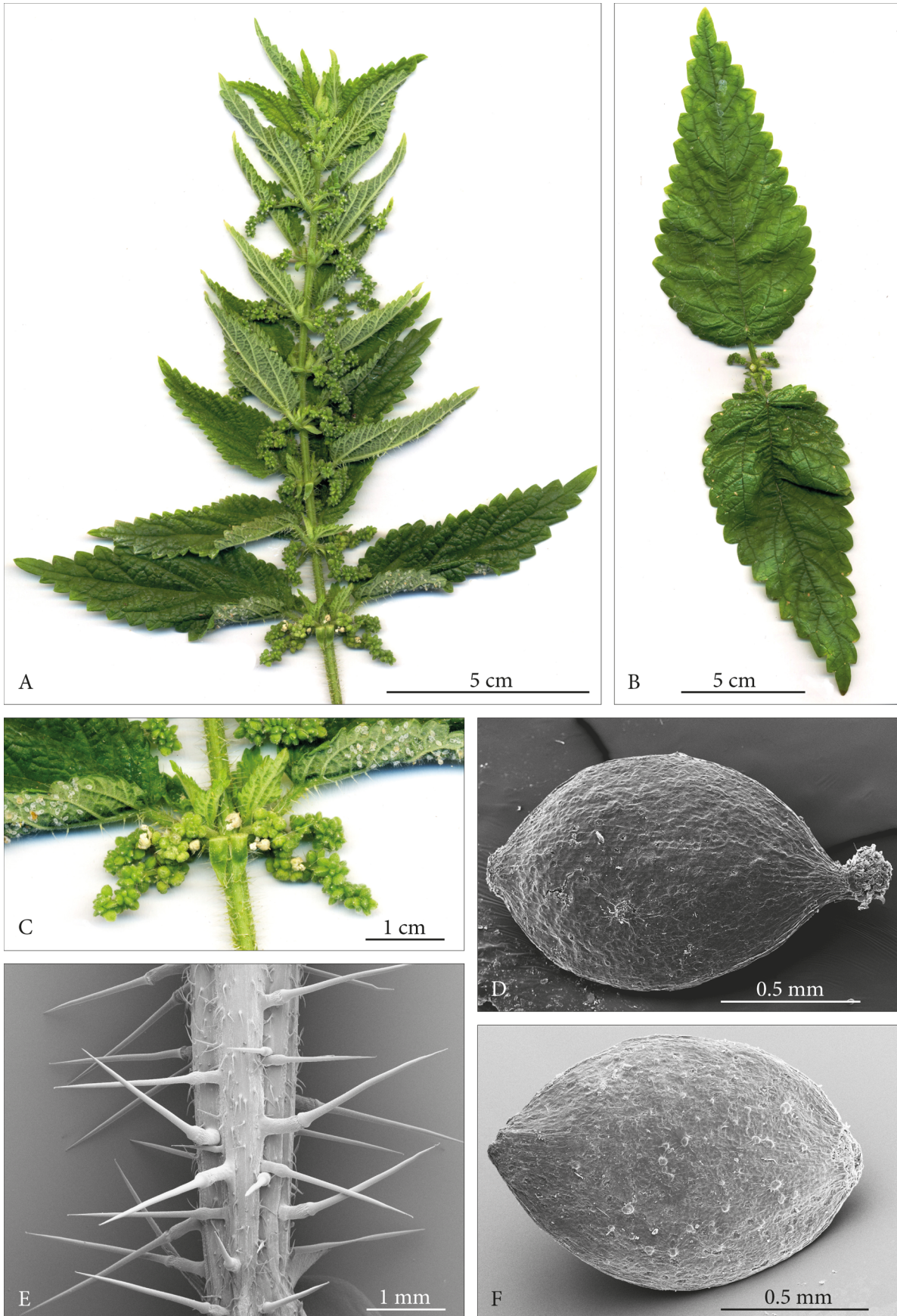


FIGURE 6. *Urtica gracilis* subsp. *mollis*: (D: Ricardi et al. 720, all others: Weigend 9356), A. Habit with mixed inflorescences below and female inflorescence above, B. Node (section) with leaf pair, C. Node from the lower part of the shoot with male flowers, D. Achene from Ricardi et al. 720, E. Stem with numerous long setae and simple trichomes, F. Achene from Weigend 9356.

nodes at the top, whereas ssp. *mollis* has male flowers at the base, followed by female flowers, for further differences see under ssp. *holosericea*. An association of this taxon with Old World ssp. *pubescens* is also clearly refuted.

This taxon is relatively widely distributed in Chile and Argentina, and seems to tolerate relatively dry conditions, unlike all the other subspecies of *U. gracilis*.

Representative specimens:—CHILE. **III Región, Atacama:** Prov. Huasco, Vallenar, 4000 m, January 1924, *E. Werdermann 266* (BM, E, MO); **IV Región, Coquimbo:** Prov. Elqui, margin of Cerro Tapado, 3300 m, 30°12'S, 70°02'W, 07 January 1981, *M. Kalin Arroyo 81901* (CONC); Cerro Hipólito, Embalse La Laguna, 3300 m, 30°16'S, 70°03'W, 06 December 1979, *C. Villagrán et al. 1827* (CONC); Embalse La Laguna, 3350 m, 05 February 1963, *Ricardi et al. 720* (CONC); camino Internacional to San Juan, S side of Embalse La Laguna, entrance to Quebrada Calabozos, 3100 m, 06 January 1967, *Ricardi et al. 1758* (CONC); Prov. Limarí, Depto. Ovalle, 190 m, 30 37 S, *C. Jiles 7119* (M); Cordillera de Ovalle, El Chape, 2650 m, 30°43'S, 70°38'W, 16 January 1949, *C. Jiles 1206* (M); **V Región, Valparaíso:** Prov. San Felipe de Aconcagua, Catemu, 20 April 1989, *O. Zöllner 11869* (MO); **Región Metropolitana, Santiago:** Prov. Cordillera, between Disputada and Pérez Caldera, 3000 m, 28 November 1954, *B. Sparre 11045* (CONC); Pérez Caldera, 3000 m, 27 January 1954, *B. Sparre 10599* (CONC); Prov. Chacabuco, Cuesta de La Dormida, 1160 m, November 1956, *H. Gunckel 29.962* (CONC); Prov. Santiago, Los Cerillos, 550 m, 20 Dezember 1941, *H. Gunckel 18.737* (CONC); Cultivated in Berlin from seed collected in Chile, Región Metropolitana, Parque Mahuida in Santiago, Cerro la Cruz, 13 February 2010, *T. Kern s.n.*, specimens prepared 16 July 2010, *M. Weigend 9356* (B, M, F); without precise locality: *Cuming s.n.* (BM). ARGENTINA. **Prov. Catamarca:** Antofagasta de la Sierra, Cara, 3200 m, 10 February 1912, *F.M. Rodriguez 313* (M); Depto. Ambato, El Rodeo, near Río Ambato, 15–16 December 1971, 1350 m, *L. Ariza 2638* (MO). Depto. Santa Maria, Los Trapiches, 25 April 1948, *A. Reales 1377* (MO); **Prov. Tucuman:** Dept. Tafi del Valle, 16 February 1958, *H.A. Fabris 1550* (M); **Prov. San Juan:** Quebrada de las Vizcachas, Feb. 1960, *H.A. Fabris & J.M. Marchionni 2348* (M); **Prov. Mendoza:** Dept. Tunuyán, Quebrada Capitán Lemes, 1 February 1950, *M.A. Palacios & A. R. Cruzo 4466* (M); Depto. Malargue, 05 January 1893, *F. Kurtz 7484* (MO); Depto. Malargue, 13 January 1885 *F. Kurtz 5790* (MO); Depto. Malargue, 11 February 1893, *F. Kurtz 7664* (MO).

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