

**Systematics, taxonomy and biogeography of species-rich
groups of the genus *Carex* (Cyperaceae)**

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**For E. in deep love,
admiration and gratitude**

***“Nothing in biology makes sense
except in the light of evolution”***

Theodosius Dobzhansky (1900–1975)

List of abbreviations

aff.	related to, affinity with or to (<i>affinis</i> , lat.)
Art.	article (of the ICN; see also under this abbreviation)
c.	around, about, approximately (<i>circa</i> , lat.)
cf.	compare (literally), or uncertain identification (<i>confer</i> , lat.)
cm	centimeter (for measurements, e.g., plant height, spike length)
Co.	county (administrative division, e.g., ‘Autu Co., China’)
comb. nov.	a new (taxonomic) combination (<i>combinatio nova</i> , lat.)
E	east, -ern (cardinal directions, geographically, e.g., ‘E China’)
e.g.	for example, for instance (<i>exempli gratia</i> , lat.)
esp.	especially, particularly, or specially
Ex.	example (of the ICN; see also under this abbreviation)
Fig., Figs.	figure (sing, singular), figures (pl, plural)
Herb.	herbarium (refers to private collections, e.g., Herb. Rösler)
ICN	International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)
i.e.	that is (<i>id est</i> , lat.)
ILS	incomplete lineages sorting (evolutionary, genetically)
ind. loc.	type locality (<i>indicatio locotypica</i> , <i>locus classicus</i> , lat.)
in prep.	in preparation, under processing
lat.	Latin (language)
LDD	long distance dispersal (biogeographically)
m	meter (for measurements, e.g., elevation, altitude, plant height)
mm	millimeter (for measurements, e.g., utricle length, leaf width)
Mt., Mts.	mount (single peak, sing), mountains, mountain range (pl)
N, NE, NW	north, -ern; northeast, -ern; northwest, -ern (cardinal directions)
NGS	next generation sequencing (molecular method)
nom. cons.	conserved name (<i>nomen conservandum</i> , lat.)
nom. illeg.	illegitimate (taxonomic) name (<i>nomen illegitimum</i> , lat.)
nom. inval.	invalid (taxonomic) name (<i>nomen invalidum</i> , lat.)
nom. nov.	new (taxonomic) name (<i>nomen novum</i> , lat.)
nom. nud.	invalid name, invalidly published name (<i>nomen nudum</i> , lat.)
nom. rej.	rejected name (<i>nomen rejiciendum</i> , lat.)
nom. superf.	a superfluous (taxonomic) name (<i>nomen superfluum</i> , lat.)
PJM	Pedro Jiménez-Mejías, PhD (Seville, Spain)

List of abbreviations (continued)

pers. comm.	personal communication
pers. obs.	personal observation (e.g., SG & PJM, pers. obs.)
p.p.	in part, partly (<i>pro parte</i> , lat.)
Pref., pref.	prefecture (administrative divisions, e.g., 'Ilan Pref., Japan')
Prov., prov.	province (administrative divisions, e.g., 'Sichuan Prov., China')
RadSeq	restriction site-associated DNA sequencing (molecular method)
S, SE, SW	south, -ern; southeast, -ern; southwest, -ern (cardinal directions)
s.coll.	without (name of) collector (<i>sine collectore</i> , lat.)
s.d.	without a (collection) date (<i>sine diem</i> , lat.)
sect., sectt.	section (sing), -s (pl)
SG	Sebastian Gebauer, MSc (author of this thesis; Halle, Germany)
s.l.	in a (taxonomically) broad sense (<i>sensu lato</i> , lat.)
s.loc.	without a (collection) place (<i>sine locus</i> , lat.)
s.n.	without a (collection) number (<i>sine numero</i> , lat.)
SNPs	single-nucleotide polymorphisms (pl)
spp.	species (pl)
s.str.	in a (taxonomically) narrow sense (<i>sensu stricto</i> , lat.)
stat. nov.	a new (taxonomic) status (<i>status novus</i> , lat.)
subg.	subgenus (sing)
subsp., subspec.	subspecies (sing)
subsect., subsectt.	subsection (sing), -s (pl)
tab.	table (sing), -s (pl)
unpubl. data	unpublished data, preliminary data
var.	variety (<i>varietas</i> , lat.)
viz.	namely, in particular (<i>videlicet</i> , lat.)
W	west, -ern (cardinal directions)
1n	haploid chromosome number (count, e.g., 1n = 24)
2n	diploid chromosome number (count)
>	larger than (for measurements, e.g., utricle beak > 1.5 mm long)
<	smaller than (for measurements)
±	more or less, plus-minus (literally; for measurements)
=	heterotypic (taxonomic) synonym ('subjective synonym', see ICN)
≡	homotypic (nomenclatural) synonym ('objective synonym', see ICN).

Errata & corrigenda

CHAPTER4:

Page 72, *C. atrata*:

The reported occurrence of *C. atrata* from NW Turkey (Mt. Uludağ) is misleading. Re-investigation of this collection revealed that it represent *C. aterrima* Hoppe subsp. *medwedewii* (Leskov) T.V.Egorova with yellowish instead of dark-purplish utricles. Thus, the SE range limit of *C. atrata* is located in C Greece. The occurrence of subsp. *medwedewii* in NW Turkey forms at the same time the W limit of this subspecies of *C. aterrima*. The collection of *C. atrata* from C Greece further contain a single stem of *C. aterrima* subsp. *aterrima*, forming its southernmost European record!

Page 87, *C. gracilenta*:

The specimen from W Nepal (*H. Ikeda et al. 20911125*, Bajhang distr., E 00509831!) has since been re-identified as a depauperate individual of *C. psychrophila* Nees. Thus, the only chromosome count ($2n = 52$) for *C. gracilenta* by Yano et al. (2010) actually refers to the latter species!

Page 124, *C. psychrophila*:

Chromosome count ($2n$): 52 (Yano et al. 2010 [as *C. gracilenta*]); see comment above!

APPENDIX:

Page 221, *C. bijiangensis*:

The specimen “CHINA. SICHUAN: Daocheng Xian, road [...] from Litang to Sandui [...], 4605 m [...], *D. E. Boufford et al. 37409*, A!” has been re-identified as *C. kansuensis* Nelmes. As a result, no evidence for the occurrence of *C. bijiangensis* in Sichuan is found (see page 74)!

Page 227, *C. gracilenta*:

The specimen “NEPAL. MECHI: Bajhang distr., around Dhahidunga Kharka, 3281 m [...], *H. Ikeda et al. 20911125*, E!” has been re-identified as *C. psychrophila* Nees (see comment above)!

Note: The present PhD thesis “Systematics, taxonomy and biogeography of species-rich groups of the genus *Carex* (Cyperaceae)” is submitted as a **monographic doctoral thesis** (non-cumulative).

It comprises three chapters resulting from research of the author (SG). **Chapter 2** is based on Gebauer et al. (2014): *Organisms, Diversity and Evolution* 14: 247–258, and **Chapter 3** is based on Gebauer et al. (2015): *Systematic Botany* 40: 433–447. **Chapter 4** is an unpublished original work by the author. Submission of this last chapter for publication (which was written in manuscript form), with PJM as co-author, is planned for the future.

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SUMMARY

The present thesis deals with the systematics, taxonomy and biogeography of two selected species-rich sections of genus *Carex*, one of the three largest angiosperm genera with about 126 sections and > 2,000 species. Both sections, i.e. *C. sect. Racemosae* and *C. sect. Vesicariae*, have a rather complicated and often controversial taxonomic history.

Phylogenetic analyses were performed using molecular data from chloroplast and nuclear DNA sequences, complemented by morphological data, ecology, biogeography, and, partly, karyological information. For the molecular phylogenetic analyses the plastid *trnK–matK* gene region and *rps16* intron, and the nuclear ITS and ETS 1f regions were chosen. In *C. sect. Vesicariae*, special attention was paid to the boreal-arctic taxa and comparative study of a putative parallel and convergent diversification in the Arctic and adjacent boreal zone. For this purpose, the data of a previous study in *C. sect. Phacocystis* (Dragon & Barrington 2009) were used, re-analyzed, and supplemented by additional morphological and ecological data. In *C. sect. Racemosae*, the present thesis focuses on clarification of its phylogenetic relationships, further subdivision (i.e. subsections), and biogeography (e.g., geographic vicariance). Another focus was on its Old World taxa with the aim of a revised taxonomy and preparation of an identification key. This thesis represents, compared with previous studies, the most comprehensive and taxonomically representative molecular phylogenetic analyses of both sections.

The phylogenetic results corroborate previous suggestions on the non-monophyly of *C. sect. Vesicariae*. The taxa from the section are dispersed in a clade with representatives from sections *Carex*, *Lupulinae*, *Paludosae*, and *Pseudocypereae*. Subsequent studies and preliminary data suggest that this clade (i.e. ‘Hirta clade’) also includes sections *Squarrosae* p.p. and *Anomalae* p.p. as well as a large number of further taxa, which makes it one of the largest clades of the genus (c. 110 taxa). Taxonomic conclusions regarding the ‘Hirta clade’, which is named according *Carex hirta*, the type species of the genus, subgenus *Carex*, as well as *C. sect. Carex*, appear premature, and it is in need of further investigation. Most species of the section form a core *Vesicariae* clade that is further divided into a boreal-arctic and a non-arctic lineage (‘Northern’ and ‘Mixed’ clades). A similar pattern is found in *C. sect. Phacocystis*. Boreal-arctic lineages of both sections showed a lower genetic divergence compared to non-arctic lineages. Only a few reproductive traits indicate morphological divergence between boreal-arctic lineages of both sections, suggesting them section-specific or phylogenetically constrained. A clear ecological differentiation between these lineages of both sections was not detected. This parallel pattern in lineages of both sections suggests its rather recent diversification within

the Arctic and adjacent boreal regions. Thus, a rare case of a northern replicative adaptive radiation is reported in boreal to arctic habitats with parallel diversification and ecological convergence. An ongoing diversification in a sub-clade of *C. sect. Phacocystis* further suggest that such replicative adaptive radiations may only be a transitional state in the diversification of species.

The phylogenetic analyses revealed that *C. sect. Racemosae* is monophyletic, with the exclusion of a few taxa. Its subdivision into subsections has been largely refuted. Previous assumptions on a geographic vicariance between North American (*C. nelsonii*, *C. nova*) and Asian (*C. melanocephala*, *C. oligantha*) taxa were not corroborated. This as well as the proposed subsections resulted from extreme morphological homoplasy, as shown in this study. The study gives evidence that the disjunct South American species (e.g., *C. atropicta*, *C. malmei*) clearly belong to the section as suspected on morphological reasons. Its possible relationships with other species of the group remain unresolved and require further investigation, as suggested by a subsequent study. Biogeography of some major clades suggests that colonization of high-mountains and subsequent diversification has played an important role for the evolution and species richness of the group.

The morphological revision of the Eurasian taxa of *C. sect. Racemosae* carried out in this study resulted for the first time in a revised taxonomic treatment for entire Eurasia, complemented by an identification key. In the result of the revision, 45 taxa (i.e. 39 species and 6 subspecies) were accepted within the Old World. The morphology and difficulties of species delimitation and identification are discussed in detail. For each species, the most important synonyms are listed and information on the distribution range, habitats, altitudinal distribution, and known chromosome numbers is provided. Finally, all accepted taxa are illustrated in detail, some taxa for the first time.

As a result of the analyses and taxonomic revision described above, the following taxonomic changes were proposed: The new section *Carex sect. Stylosae*, stat. et comb. nov., and the species *Carex kangchengyaoensis*, nom. et stat. nov., were introduced, and the new combination *Carex duthiei* subsp. *longistolonifera*, comb. nov., was made. Furthermore, typifications were made for 33 taxonomic names, 12 of them for accepted species.

1 GENERAL INTRODUCTION

1.1 INTRODUCTION

Cyperaceae Juss. — The relationships between the genera of the Cyperaceae (c. 105 genera; Goetghebeur 1998; Stevens 2001+; Govaerts et al. 2018+) have been more or less well elucidated in the last decades (Bruhl 1995; Muasya et al. 1998; Simpson et al. 2007; Muasya et al. 2009a, b; Hinchliff & Roalson 2013; L veill -Bourret et al. 2014). With regard to the infrageneric and biogeographic relationships of its genera including *Carex* (see below) there are still considerable uncertainties in terms of their systematics and taxonomy. Most of the complete taxonomic treatments of genera are morphology-based and were performed in the past century (e.g., K kenthal 1909, 1935–1936, 1949, 1950, 1951, 1952). For some genera recent molecular studies became available [*Cyperus* L.: Larridon et al. 2011a, 2013, 2014; Bauters et al. 2014; *Eleocharis* R.Br.: Hinchliff et al. 2010; Roalson et al. 2010; *Isolepis* R.Br.: Muasya et al. 2001; *Rhynchospora* Vahl: Thomas et al. 2009; *Schoenoplectus* (Rchb.) Palla s.l.: Shiels et al. 2014; *Scirpus* L. s.l.: Jung & Choi 2010, 2011; *Scleria* P.J.Bergius: Bauters et al. 2013].

***Carex* L.** — The genus *Carex* (Cyperaceae) is one of the world’s most species-rich (c. 2,000 species) genera of vascular plants (Reznicek 1990; Goetghebeur 1998; Govaerts et al. 2018+). It has almost worldwide distribution in a variety of habitats with its center of species richness and distribution in the Northern Hemisphere (Reznicek 1990; Goetghebeur 1998; Stevens 2001+; Global *Carex* Group 2015). In addition, the genus is of particular environmental and economic importance (Simpson & Inglis 2001), especially in the wetlands of the Northern Hemisphere. These range from the temperate zone to the boreal coniferous forest belt and subarctic areas to the Arctic, as well as in subalpine and alpine regions of high mountains. Within these regions, representatives of *Carex* often have a dominant character, and contribute significantly to the local biomass and formation of natural vegetation (Ball & Reznicek 2002; Mishra et al. 2016).

Taxonomy of the genus *Carex*. — The genus *Carex*, placed in the subfamily Cyperoideae Beilschm., formed for a long time together with the monotypic genus *Cymophyllus* Mack. and genera *Kobresia* Willd., *Schoenoxiphium* Nees and *Uncinia* Pers. the tribe Cariceae Nees (see below). *Carex* has been divided into the subgenera *Psyllophora* (Degl.) Peterm. (= *Primocarex* K k.), *Vignea* (P.Beauv. ex Lestib.) Peterm., *Vigneastra* (Tuck.) K k. (= *Indocarex* K k.), and *Carex* (= *Eucarex* K k.). The further subgenera *Altericarex* H.St. John & C.S.Parker, introduced to delimitate *C. concinnoides* Mack. with four stigmata and four-sided nutlets (St. John & Parker 1925), as well as

Kreczetoviczia T.V.Egorova, which was established to unite all distigmatic taxa of subg. *Carex* [e.g., sectt. *Phacocystis* Dumort., *Graciles* (Tuck. ex Kük.) Ohwi, and *Abditispicae* G.A.Wheeler], however, remained largely ignored. Another subgenus, i.e. subg. *Vesicarex* Steyermark (Steyermark 1951; Cleef 1982; Bruhl 1995), was based only on immature material and is referable to *C.* sect. *Abditispicae* (see above; Mora-Osejo 1982; Wheeler 1989; Reznicek 1990).

The current systematics and taxonomy, i.e. the division of *Carex* into several subgenera (see above) and about 126 recognized sections (and subsections), are largely based on the last and only worldwide monograph published by Kükenthal (1909). Kükenthal's (1909) segregation of genera within tribe Cariceae, and subgenera in *Carex*, was mostly based on a few reproductive features. These were, e.g., the inflorescence structure, morphology of cladophylls, whether perigynia were open or closed in form of a utricle, and presence and morphology of the rachilla (reviewed in Global *Carex* Group 2015; Jiménez-Mejías et al. 2016a). Further subdivision of *Carex*, which is still used today, was mainly based on utricle morphology and indumentum, arrangement of spikes, and sex distribution of the spikelets (Kükenthal 1909). The taxonomic (and floristic) treatments published after Kükenthal (1909) were mostly limited to geographically defined groups of species, for example, North America (Mackenzie 1931–1935; Flora of North America Editorial Committee 2002), Europe (Chater 1980; Schultze-Motel 1980), Russia and the states of the former Soviet Union (Kreczetovicz 1935b; Kozhevnikov 1988; Malyshev 1990; Egorova 1999), China (Flora of China Editorial Committee 2010), Japan (Akiyama 1932; Ohwi 1965; Hoshino et al. 2011), Nepal (Koyama 1978a), Taiwan (Koyama 1978b; Koyama et al. 2000), Bhutan (Noltie 1994), *Flora Karakorumensis* (Dickoré 1995), *Flora Iranica* area (Kukkonen 1998), Pakistan (Kukkonen 2001), Mongolia (Grubov 2001; Nyambayar 2009), Scandinavia (e.g., Kukkonen et al. 1998; Elven et al. 2005) or Great Britain (e.g., Jermy et al. 2007).

Molecular phylogenetics of the genus *Carex*. — Since publication of Kükenthal's fundamental work (1909) it became soon apparent that some of his groups were non-monophyletic and rearrangements in the classification were necessary. Regionally different taxonomic concepts further complicate a comprehensive treatment of the genus. Frequent homoplasy (i.e. convergent evolution) of morphological characters, which has often led to incorrect taxonomic conclusions, is another challenging issue (Naczi 2009; Escudero et al. 2010). The difficulties arising from these above-mentioned points, as well as the frequently difficult access to rare species (i.e. endemics, sub-endemics) complicate the understanding

regarding possible evolutionary pathways and tendencies. Furthermore, they have largely prevented extensive phylogenetic and biogeographic studies using molecular phylogenetic methods with respect to the entire genus (see Waterway & Starr 2007).

First molecular studies on *Carex* addressed the infrageneric divisions (i.e. subgenera, sections; Roalson et al. 2001; Hendrichs et al. 2004a, b). For this purpose, the sampling focused on more or less representative species from different sections, including the other genera of tribe Cariceae (i.e. *Cymophyllus*, *Kobresia*, *Schoenoxiphium*, and *Uncinia*; Roalson et al. 2001; Starr et al. 2004). Other molecular studies focus on smaller and morphologically well-defined sections (see Starr et al. 1999; Roalson et al. 2004a, b). The studies by Starr et al. (2004), Starr & Ford (2009), and Gehrke et al. (2010) confirmed the implications of the aforementioned works, revealing *Kobresia* as para- or polyphyletic, and that all genera of tribe Cariceae (see above) should be included in a broadly circumscribed genus *Carex*. Furthermore, these studies have shown that most of the proposed subgenera of *Carex* are non-monophyletic, so that they will no longer be maintained as distinct subgenera in some cases without further adjustments.

Further molecular studies focused on the phylogenetic relationships of individual subgenera (i.e. subg. *Carex*: Hendrichs et al. 2004a; subg. *Vignea*: Hendrichs et al. 2004b; Ford et al. 2006; King & Roalson 2008; Ford et al. 2012), between the sections (Hendrichs et al. 2004a, b; Waterway & Starr 2007; Gehrke & Linder 2009; Waterway et al. 2009), or individual sections [e.g., sectt. *Acrocystis* Dumort.: Roalson & Friar 2004a, b; *Ovales* Kunth: Hipp et al. 2006; Hipp 2007; Hipp et al. 2007; *Phacocystis* Dumort.: Dragon & Barrington 2008, 2009; Jiménez-Mejías et al. 2011; *Phyllostachys* Tuck. ex Kük.: Ford et al. 2008; *Spirostachyae* Drejer ex L.H.Bailey: Escudero et al. 2008; Escudero & Luceño 2009; Escudero et al. 2009; *Ceratocystis* Dumort.: Jiménez-Mejías et al. 2012; *Vesicariae* (Heuff.) J.Carey: Shekhovtsov et al. 2012; *Siderostictae* Franch. ex Ohwi s.l.: Yano et al. 2014]. Interestingly, these studies have shown that most of the species studied actually belong to certain taxonomic groups that largely correspond to their existent sectional classification. However, there are always individual taxa that are unexpectedly placed within these or other groups, regardless of their previous sectional affiliations. These circumstances are a challenge regarding the future morphological circumscription of these natural groups. Another important result with respect to the putative East Asian origin of the genus (i.e. diversification center) was the identification of a monophyletic group consisting of representatives from subgenera *Vigneastra* and *Carex* (i.e. the *Siderostictae*

group). This group is found early branching at the base of the genus *Carex* (see Waterway et al. 2009; Jung & Choi 2013; Yano et al. 2014; see below).

Evolution of the genus *Carex*. — Evolution of the genus *Carex* (and tribe Cariceae), i.e. character evolution and its polarization, has been the subject of much controversy (Kükenthal 1909; Nelmes 1951a, b; Reznicek 1990; Egorova 1999; reviewed in Starr & Ford 2009). Kükenthal's (1909) division into four subgenera (see above) suspected an evolutionary progression from simple to more complex (compound) inflorescences, and from 2-stigmatic to 3-stigmatic flowers (but see Reznicek 1990; Egorova 1999). However, the artificial character of this subdivision was revealed by the first molecular studies on the genus (see above; reviewed in Starr & Ford 2009).

An East Asian origin of the genus was early suspected (e.g., Nelmes 1951a). The early-diverged East Asian *Siderostictae* group (see above) further supports this hypothesis. Its representatives share the lowest chromosome numbers within *Carex* (e.g., *C. siderosticta* Hance: $2n = 12$; *Siderostictae* group: $2n = 12-24$; entire genus: $2n = 12-124$; reviewed in Roalson 2008; Escudero et al. 2012; Yano et al. 2014). This underlines their potential importance for further understanding of the evolution of the entire genus (see Tanaka 1939, 1940; Roalson 2008; Waterway et al. 2009; Yano et al. 2014). The holocentric (= holokinetic) chromosomes of the agmatoploid (= [agmato-]pseudopolyploidy; Battaglia & Boyes 1955; Battaglia 1956) genus *Carex* and its rapid diversification in the Northern Hemisphere have been repeatedly studied. Its discontinuous evolution, i.e. high rates of chromosomal rearrangement via fission, fusion, and translocation during meiosis, may be a driver of diversification, especially in cold-temperate climates (Hipp 2007; Escudero et al. 2012; Escudero & Hipp 2013). This is possibly accompanied with 'polyploidy' (see above; Lipnerová et al. 2013). A shift to higher diversification rates during periods of global cooling in the late Eocene and Oligocene, as well as the late Tertiary, has been suggested. This shift seems to be accompanied by a transition in diploid chromosome number, usually to higher numbers (Escudero et al. 2012).

Towards a new classification of the genus *Carex*. — As a result of these studies, of new insights and implications, a global scientific collaboration, i.e. the Global *Carex* Group, has emerged. With the goal of a future reclassification of the genus, this scientific network intends to synthesize the existing molecular, morphological, anatomical, and physiological data. In addition, the synthesis and assembly of a representative number of

taxa should achieve a first comprehensive genus phylogeny. This objective continues through the promotion and support of further molecular studies and taxonomic revisions.

A first necessary step was the taxonomic reassessment of the genus *Carex* and its segregate genera of tribe Cariceae (viz., *Cymophyllus*, *Kobresia*, *Schoenoxiphium*, *Uncinia*; see above). With the aim of a stable nomenclature and in the partial absence of clear synapomorphies, and avoiding the further splitting of the genera *Carex* and *Kobresia*, this could be achieved by the inclusion of all segregate genera into a broadly defined genus *Carex* in a monotypic tribe Cariceae (see Global *Carex* Group 2015).

***Carex* sect. *Vesicariae* (Heuff.) J.Carey.** — Traditionally, *C.* sect. *Vesicariae* (type species: *C. vesicaria* L.) is placed in in subg. *Carex* (Kükenthal 1909; Mackenzie 1931–1935; Chater 1980; Schultze-Motel 1980; Egorova 1999; Reznicek & Ford 2002; [Dai et al. 2010b as *C.* sect. *Physocarpae* Drejer ex L.H.Bailey]). Depending on the taxonomic treatment, it comprises about 20–55 species and subspecies (Mackenzie 1931–1935; Egorova 1999; Reznicek & Ford 2002; Dai et al. 2010b; for its morphological description see **Chapter 2**). The taxa are mainly distributed in the extratropical regions of both hemispheres with a distribution center in the cooler regions of the Holarctic (Fig. 1). A few taxa also occur in the Tropics (Egorova 1999; Reznicek & Ford 2002; Dai et al. 2010b; Gehrke 2011). Its representatives can be found in various types of wetlands, for example, riparian areas of standing and flowing waters, on stream edges, in wet forests and swamps, as well as peat bogs and wet tundra (Kreczetovicz 1935b; Egorova 1999; Reznicek & Ford 2002; Reznicek & González-Elizondo 1995). The group seems to date back to the Miocene or even the late Oligocene, and its representatives already showed these ecological niche requirements, as fossils remains are typically associated with freshwater deposits (reviewed in Jiménez-Mejías et al. 2016b).

Apart from Kükenthal (1909) and some regional treatments (see above), only a few taxonomic studies, except for a few geographically or morphologically defined taxa, have so far been performed on *C.* sect. *Vesicariae* (Ford et al. 1991; Ford & Ball 1992; Ford et al. 1993; Reznicek & González-Elizondo 1995). In contrast to other species-rich sections (e.g., *Aulocystis* Dumort., *Mitratae* Kük., *Racemosae* G.Don), no subsectional divisions have been proposed (Egorova 1999; Reznicek & Ford 2002; Dai et al. 2010b; but see Kreczetovicz 1935b). On morphological reasons, the closer relationship to other sections has been suggested, i.e. *Pseudocypereae* Tuck. ex Kük. (included in *C.* sect. *Vesicariae* by most North American authors; see Reznicek & Ford 2002), *Carex*, *Paludosae* G.Don (=

Tumidae Meinsh. *sensu* Egorova 1999), *Lupulinae* Tuck. ex J.Carey, *Rostrales* Meinsh., and *Squarrosae* J.Carey (Kükenthal 1909; Kreczetovicz 1935b; Nilsson 1985; Kukkonen 1998). Occasionally, individual species were brought into closer relationship with species of sections *Pseudocypereae* or *Carex* (Kreczetovicz 1935b). A broadened sectional circumscription including all the taxa of *Carex*, *Paludosae*, *Pseudocypereae*, and *Vesicariae* in one *C. sect. Carex* was proposed by Hylander (1966), Nilsson (1985) and Kukkonen (1998). Kreczetovicz (1935b) proposed an alternative but invalidly published treatment merging *C. sect. Vesicariae* together with *Carex*, *Pseudocypereae*, and *Rostrales* into his large *C. sect. Pompholyx* V.I.Krecz. (*nom. inval.*; ICN, Art. 39.1; Turland et al. 2018). This section was subdivided into the ‘cycles’ (i.e. equivalent to subsections) *Ampullaria* V.I.Krecz. (*nom. inval.*; ICN, Art. 39.1) and *Vesicularia* V.I.Krecz. (*nom. inval.*; ICN, Art. 39.1). However, subsequent authors ignored these systematic ideas. A similar inclusive grouping, which also went unnoticed, was proposed by Savile & Calder (1953) based largely on evidence from smut parasitism (i.e. genus *Cintractia* Cornu, Anthracoideaceae Denchev). Savile & Calder (1953) recognized this species assemblage as the new subgenus *Kuekenenthalia* Savile & Calder (type: *C. vesicaria*).

Based on morphology, two informal species groups within the section were proposed (Ford et al. 1991; Ford & Ball 1992). Namely, the short-beaked (*C. membranacea* Hook., *C. rotundata* Wahlenb., and *C. saxatilis* L.) and the long-beaked taxa (*C. rostrata* Stokes, *C. utriculata* Boott, and *C. vesicaria*). However, this division was not supported by allozyme studies with the short-beaked taxa being more closely related to two different long-beaked species. Thus, Ford et al. (1993) concluded that the initially proposed groups are not monophyletic.

First molecular studies confirmed the close relationship of the sections *Vesicariae*, *Pseudocypereae*, *Carex*, *Lupulinae*, and *Paludosae* (= *Tumidae sensu* Egorova 1999, excluding the type species of section *Paludosae*, *C. acutiformis* Ehrh.) (Roalson et al. 2001; Hendrichs et al. 2004a). Subsequent studies with a more representative taxonomic sampling confirmed these results (Waterway & Starr 2007; Gehrke & Linder 2009; Waterway et al. 2009). The only molecular study specifically dealing with *C. sect. Vesicariae* remained largely confined to the Siberian representatives, and most taxa related to the section were disregarded (Shekhovtsov et al. 2012). However, Shekhovtsov et al. (2012) assumed an existing sister group relationship with *C. sect. Pseudocypereae*, which was used as outgroup. They observed a very low sequence divergence between the taxa of the section. Furthermore, a separation into two main groups was found, which partly

corresponds to the invalid treatment of Kreczetovicz (1935b). A comprehensive study that includes a representative number of the remaining taxa of *C.* sect. *Vesicariae* and related groups in a molecular phylogenetic framework is still missing. Such a study should also consider the western Holarctic, Neotropical, Afrotropical, and Australasian taxa suspected of belonging to *C.* sect. *Vesicariae* (or related groups) (Kükenthal 1899, 1909, 1925; Werdermann 1929; Mackenzie 1931–1935; Chermezon 1937; Barros 1947, 1969; Gordon-Gray 1995; Reznicek & González-Elizondo 1995; Wheeler 1996; Lye 1997; Reznicek & Ford 2002; Verdcourt 2010; Gehrke 2011). These taxa have not yet been studied in detail or only insufficiently molecularly or biogeographically (Gehrke & Linder 2009).



FIG. 1: Distribution of *Carex* sect. *Vesicariae sensu* Egorova (1999) in the Northern Hemisphere. Based on own data and information adopted from Clarke (1908), Kükenthal (1909), Mackenzie (1931–1935), Kreczetovicz (1935b), Grossgejm (1940), Meusel et al. (1965), Egorova (1966), Hylander (1966), Hultén (1968), Chater (1980), Hultén & Fries (1986), Kristinsson (1987), Kozhevnikov (1988), Malyshev (1990), Noltie (1994), Dickoré (1995), Fu (1995), Gubanov (1996), Kukkonen (1998), Kukkonen et al. (1998), Egorova (1999), Kukkonen (2001), Reznicek & Ford (2002), Sekretareva (2004), Elven et al. (2005), Egorova (2006), Aiken et al. (2007), Jermy et al. (2007), Luceño (2008), Malyshev (2008), Nyambayar (2009), Dai et al. (2010b), Amini Rad (2011), Elven et al. (2011), Hoshino et al. (2011), Koopman (2011), Assyov et al. (2012), Krasnoborov (2012), Chang et al. (2014).

In the course of an ongoing study, which focuses on a revised taxonomy of *C.* sect. *Vesicariae* (Gebauer et al., in prep.), an interesting molecular and biogeographic pattern is suspected with respect to its boreal to arctic species. The section includes a relatively high proportion of presumably closely related taxa with mainly boreal to arctic distribution

ranges (Egorova 1966, 1999; Reznicek & Ford 2002; Aiken et al. 2007; Elven et al. 2011). Initial molecular data (see also Shekhovtsov et al. 2012) suggest a geographical differentiation in two sister lineages, i.e. one involving the boreal to arctic taxa, the other mainly taxa with more southern ranges. In addition to this geographical pattern, these lineages also show a certain morphological differentiation (e.g., rhizome growth, utricle shape) (Kreczovicz 1935b; Egorova 1999; Reznicek & Ford 2002; SG, pers. obs.). Such a pattern of differentiation has recently been reported by Dragon & Barrington (2009) in the closely related *C. sect. Phacocystis* (see above). Two sister lineages identified (i.e. the ‘*C. aquatilis* Wahlenb.’ and ‘*C. lenticularis* Michx.’ lineages) were also divergent with respect to their biogeography and morphology. Dragon & Barrington (2009) further suggested a rather recent (and ongoing) diversification in the ‘*C. aquatilis* lineage’. Species of both sections represent important vegetation components in northern regions, especially the Arctic, and frequently co-occur (Kozhevnikov 1978; Matveyeva 1998; CAVM Team 2003; Kade et al. 2005; Reynolds et al. 2005; Yurtsev et al. 2010). This obvious parallel pattern suggests that both sections may represent a case of parallel diversification and ecological convergence within the Arctic and adjacent boreal regions. Inevitably, the question arises if this putative convergent and parallel evolution in niche requirements as well as putatively existing functional or lineage-specific morphological traits could explain their sympatric occurrence.

***Carex sect. Racemosae* G.Don.** — Section *Racemosae* [syn. sect. *Microrhynchae* (Drejer) L.H.Bailey, *Atratae* (Heuff.) H.Christ, *Loxaniza* (Rafin.) V.I.Krecz.; sectional type species: *C. atrata* L.] is traditionally placed in subg. *Carex* (Kükenthal 1909; Mackenzie 1931–1935; Chater 1980; Schultze-Motel 1980; Egorova 1999; Murray 2002a; Liang & Koyama 2010a; for its morphological description see **Chapters 3** and **4**). It is one of the larger sections of the genus, and comprises about 60 taxa. The species are mainly distributed in temperate to arctic regions of the Northern Hemisphere (see references above; Fig. 2). Three further species form a disjunct South American distribution range that extends from the southern Andes to Tierra del Fuego (Wheeler 1990). Its representatives show a wide range of habitats ranging from drier locations to various types of wetlands, as well as the Arctic lowland tundra to the high alpine grassland communities (Kükenthal 1909; Chater 1980; Egorova 1999; Murray 2002a; Liang & Koyama 2010a). There are two diversity centers of the section, each comprising about 20 spp. (including some endemics). One of them is located in the high mountains of Central Asia surrounding the Tibetan Plateau and Tarim Basin (i.e. Karakoram, Himalayas, Hengduan Mountains

and adjacent mountain ranges of Central China; Noltie 1994; Dickoré 1995; Kukkonen 1998; Liang & Koyama 2010a). Another center can be observed in western North America (i.e. Rocky Mountains, Cascades, Sierra Nevada; Murray 1969; Murray 2002a; Reznicek & Murray 2013).

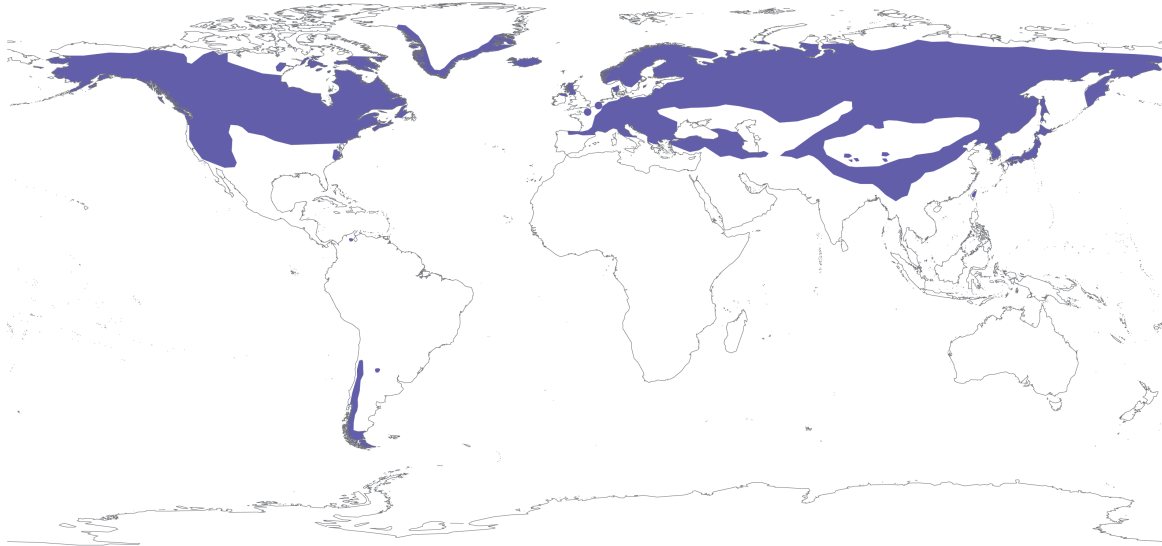


FIG. 2: Distribution of *Carex* sect. *Racemosae* s.str. Based on own data and information adopted from Clarke (1908), Mackenzie (1931–1935), Kreczetovicz (1935b, c), Grossgejm (1940), Kreczetovicz (1941), Kalela (1944), Barros (1947), Popova (1950), Hultén (1958), Polyakov (1958), Kreczetovicz (1963), Ohwi (1965), Meusel et al. (1965), Raymond (1965), Egorova (1966), Hylander (1966), Hultén (1968), Barros (1969), Murray (1969), Stewart (1972), Koyama (1975), Egorova (1976a, b, c), Galushko (1978), Koyama (1978a, b), Scoggan (1978), Kitagawa (1979), Chater (1980), Porsild & Cody (1980), Schultze-Motel (1980), Hooper (1985), Hultén & Fries (1986), Kristinsson (1987), Kozhevnikov (1988), Malyshev (1990), Wheeler (1990), Hartvig (1991), Noltie (1994), Dickoré (1995), Fu (1995), Gubanov (1996), Srivastava (1996), Kukkonen (1998), Kukkonen et al. (1998), Egorova (1999), Koyama et al. (2000), Liang (2000), Chandjian (2001), Grubov (2001), Kukkonen (2001), (Murray 2002a), Dai et al. (2003), Sekretareva (2004), Elven et al. (2005), Egorova (2006), Aiken et al. (2007), Jermy et al. (2007), Luceño (2008), Malyshev (2008), Nyambayar (2009), Liang & Koyama (2010a, b), Amini Rad (2011), Elven et al. (2011), Hoshino et al. (2011), Koopman (2011), Assyov et al. (2012), Krasnoborov (2012), Zika (2012), Chang et al. (2014), Liao (2014), Koopman et al. (2015), Bartók et al. (2016), Jiménez-Mejías et al. (2018), Kaplan et al. (2018).

Apart from the last global revision by Kükenthal (1909), only a few studies have dealt with the systematics and taxonomy of *C. sect. Racemosae* (Kalela 1944; Murray 1969; Egorova 1985; Wheeler 1990; Reznicek & Murray 2013). Most taxonomic (and floristic) accounts were limited to geographically defined regions (or sets of species), or only checklists (Kreczetovicz 1935b; Raymond 1965; Koyama 1975; Koyama 1978a, b; Nilsson 1985; Malyshev 1990; Gubanov 1996; Grubov 2001; Koyama et al. 2000).

The taxonomic history of *C. sect. Racemosae* is quite complicated. This concerns both the relationships with other taxa usually placed in other sections, as well as the further subdivision into subsections (see Table 1 in **Chapter 3**). For example, Kreczetovicz (1935b) affiliated the taxa in his *C. sect. Loxaniza* V.I.Krecz. (*nom. inval.*; ICN, Art.

39.1). This section was further divided into ‘cycles’ (see above) and ‘series’ (i.e. rank below subsections). Kreczetovicz’s (1935b) treatment also incorporated the species traditionally placed in *C. sect. Scitae* Kük. (Kükenthal 1909; Murray 2002b), which was partly followed by later authors (Mackenzie 1931–1935; Malyshev 1990). *Carex bicolor* All. has been sometimes affiliated with the section by Eurasian botanists (Kreczetovicz 1935b; Chater 1980; Egorova 1999). Later, it was placed in the monotypic subsect. *Bicolores* Tuck. ex Kük. by Egorova (1985, 1999; see below). However, it was placed in *C. sect. Bicolores* (Tuck. ex L.H.Bailey) Rouy by North American authors (e.g., Ball 2002a). A first sub-sectional division of the section was proposed by Kalela (1944). Kalela (1944) placed a number of morphologically similar taxa in the new subsect. *Alpinae* Kalela (*nom. inval.*; ICN, Art. 39.1; = subsect. *Alpinae* Kalela ex T.V.Egorova). Egorova (1985) adopted Kalela’s (1944) treatment, proposing a further subdivision into nine subsections (see **Chapter 3**). Several taxa from outside Russia and neighboring states of the former Soviet Union were also assigned to these subsections (Egorova 1985, 1999). Most recently, Wheeler (1990) proposed the subsect. *Atropictae* G.A.Wheeler, which includes the three South American representatives of *C. sect. Racemosae*. However, these subdivisions went unnoticed by other authors (Kukkonen 1998, 2001; Murray 2002a; Liang & Koyama 2010a; Hoshino et al. 2011).

Regarding the biogeography of *C. sect. Racemosae*, geographic vicariance between extremely similar taxa distributed in North America (*C. nova* L.H.Bailey, *C. nelsonii* Mack.) and Asia (*C. melanocephala* Turcz., *C. oligantha* Steud.) has been discussed in subsect. *Alpinae*. These taxa have occasionally been considered synonymous by North American taxonomists (Holm 1903; Murray 1969, 2002a; Weber 2003). However, this presumed vicariant taxa have never been studied molecularly. As a result of some morphological studies, several new species have recently been described in the section, viz., *C. bijiangensis* S.Yun Liang & S.R.Zhang and *C. obliquitruncata* Y.C.Tang & S.Yun Liang from China (Liang & Zhang 2006) and *C. orestera* Zika from North America (Zika 2012). The revision of the ‘*Carex parryana* Dewey complex’ resulted in the recent description of further North American taxa (*C. holmgreniorum* Reznicek & D.F.Murray, *C. utahensis* Reznicek & D.F.Murray; Reznicek & Murray 2013). These morphological studies point to the general importance and necessity of taxonomic revisions, even in seemingly well-circumscribed but taxonomically difficult groups, such as *C. sect. Racemosae*.

First molecular studies, which also included taxa of *C. sect. Racemosae*, suggested the monophyly of the section (Roalson et al. 2001; two taxa sampled), with the exclusion of *C. bicolor* (Hendrichs et al. 2004a; eight taxa sampled, including the type species *C. atrata*). In the latter, *C. bicolor* was found nested in a clade composed by species from sectt. *Bicolores* (*sensu* Ball 2002a), *Laxiflorae* (Kunth) Mack. (Bryson & Naczi 2002), and *Paniceae* G. Don (Egorova 1999; Rothrock & Reznicek 2002). In contrast, Waterway & Starr (2007) and Waterway et al. (2009) showed that two taxa currently placed in *C. sect. Racemosae* (*C. mertensii* Prescott ex Bong., *C. stylosa* C.A.Mey.) are closely related to the sections *Phacocystis* and *Scitae* (note: only two or three taxa each sampled out of approximately 97 and 140 species, respectively). Later, Gehrke & Linder (2009) and Jung & Choi (2013) confirmed the previous studies regarding the placements of *C. bicolor*, *C. mertensii*, and *C. stylosa*. In both studies, the remaining taxa of the section resolved in a well-supported monophyletic clade.

Despite these findings, the section must be regarded as molecular-phylogenetically insufficiently studied, since so far only a small fraction of its taxa has been taken into account. Thus, a comprehensive molecular study that accounts for a representative number of taxa from the section, taking into account its biogeography, the vicarious taxa, and potential diversification centers, is lacking. This also applies to the disjunct South American taxa, whose affiliation to *C. sect. Racemosae* has also not yet been investigated molecularly.

1.2 QUESTIONS ADDRESSED IN THIS THESIS

As mentioned above, the genus *Carex* has a rather complicated taxonomic history, often resulting in contradictory views on its systematics and taxonomy, as well as the inter- and infrageneric circumscription (reviewed in Global *Carex* Group 2015). This applies to a much greater extent to the further subdivision into numerous sections (and subsections). The delimitations and suspected phylogenetic relationships of the sections are based almost exclusively on morphological evidence and their interpretations (Kükenthal 1909; Egorova 1999; see above). The aim of the present thesis is therefore to elucidate the phylogeny and systematics of two selected species-rich sections of the genus, i.e. *C. sect. Racemosae* and *C. sect. Vesicariae*. It also aims to explore some issues related to their general evolution and biogeography, as well as to clarify some existing taxonomic and nomenclatural problems (see below). Thus, this thesis also wants to make an important contribution to the general understanding of the evolution, systematics and taxonomy as well as biogeography of the genus *Carex*.

For *C. sect. Vesicariae* (and allies), to which **Chapter 2** is devoted, the most recent morphological treatments by Egorova (1999) and Reznicek & Ford (2002) are important starting points. These are complemented by the findings from previous molecular studies (Hendrichs et al. 2004a; Gehrke & Linder 2009; Waterway et al. 2009; Shekhovtsov et al. 2012; see above). These studies have already suggested that the section is non-monophyletic in its current taxonomic circumscription (*sensu* Egorova 1999; Reznicek & Ford 2002). Although a close relationship has also been shown to representatives from other sections (e.g., *Carex*, *Lupulinae*, *Paludosae*, *Pseudocypereae*), *C. sect. Vesicariae* and its related groups have been insufficiently sampled in molecular studies. The previous studies left unanswered questions regarding the delineation of the section in its narrowest sense (*sensu* Egorova 1999), as well as the relationships with and between related groups. The biogeographical pattern suggested by Shekhovtsov et al. (2012) and preliminary data and the alleged parallel diversification concerning boreal to arctic taxa of the section, compared with *C. sect. Phacocystis* (Dragon & Barrington 2009), have never been studied. For the first time, a representative taxonomic sampling from *C. sect. Vesicariae* and related groups will be considered in a broader molecular-phylogenetic framework. Considering all boreal-arctic taxa in this framework, the present study focuses on the comparative study of the suspected parallel and convergent evolution in lineages of sections *Vesicariae* and *Phacocystis*. In addition to the molecular data, which are also analyzed with regard to their

differentiation, reproductive and vegetative morphological traits and ecophysiological information will also be taken into account.

The following specific questions were addressed in **Chapter 2** of the present thesis: (1) Does the section represent a non-monophyletic entity as suggested by previous studies (see above), or is it monophyletic in a rather narrow sense, considering existing and divergent treatments (see Egorova 1999; Reznicek & Ford 2002)? (2) Does the section show a comparable or possibly convergent and parallel diversification and differentiation pattern compared to *C. sect. Phacocystis* studied by Dragon & Barrington (2009)? (3) Is there a comparable molecular and morphological differentiation of both sections between and within Arctic and non-Arctic lineages? (4) Are these lineages of similar age? (5) Which morphological features are convergent, even considering the common co-occurrence of the species of both sections? (6) Which features may be functionally related to Arctic vegetation, and which are lineage-specific?

Chapters 3 and **4** deal with the systematics and taxonomy of *C. sect. Racemosae*. The taxonomic treatments by Chater (1980), Wheeler (1990), Egorova (1999), and Murray (2002a) are the starting points. These are supplemented by initial molecular findings (Roalson et al. 2001; Hendrichs et al. 2004a; Waterway & Starr 2007; Gehrke & Linder 2008; Waterway et al. 2009; Jung & Choi 2013). Except for Hendrichs et al. (2004a) and Gehrke & Linder (2009), none of these studies included a representative number of taxa from the section. However, the two latter studies rely only on analyses of a single nuclear marker (ITS), or one nuclear (ITS) and one plastid (*trnL-trnF* region) marker each. These studies suggest the monophyly of the section, excluding individual taxa whose affiliation has already been partially controversial (e.g., *C. bicolor*). All South American, as well as the majority of its North American and Asian representatives have not yet been studied molecularly. Thus, *C. sect. Racemosae* has been insufficiently sampled, particularly with respect to further subdivisions proposed on morphological reasons (i.e. subsections), and a phylogenetic hypothesis is missing. The aim of this study is to investigate the section for the first time molecular-phylogenetically using a comprehensive taxonomic sampling and additional molecular markers to provide a first phylogenetic hypothesis. This sampling will take into account previous findings, its morphological variation, proposed subdivisions (Kalela 1944; Egorova 1985; Wheeler 1990; Egorova 1999), and its biogeography (e.g., vicarious taxa). In this phylogenetic framework, the morphological variation of the considered taxa and possibly resulting taxonomic conclusions will be discussed in detail (**Chapter 3**). The only recent major treatments are those for Russia and the neighboring

states within the borders of the former Soviet Union (Egorova 1999) and the Flora of China (Liang & Koyama 2010a). The section, which is considered to be taxonomically rather difficult and often confusing, lacks a comprehensive taxonomic treatment, including an identification key covering Eurasia. Such a treatment (and key) seems useful in the context of mostly regional and often conflicting taxonomic views on the status or delineation of individual taxa. Therefore, the present thesis also aims to obtain such a taxonomic treatment and key resulting from extensive morphological revisions of the section throughout Eurasia (**Chapter 4**). This also includes recent findings (Global *Carex* Group 2016; Massatti et al. 2016), preliminary molecular data (Gebauer et al., unpubl. data), and the results presented in **Chapter 3**. Thus, the taxonomic synopsis and key for the Eurasian species of *C. sect. Racemosae* should provide a relevant contribution in terms of nomenclatural stability, taxonomic integrity, and reliable species identification.

In **Chapter 3**, the following specific questions have been addressed: (1) Is subsect. *Bicolores* (= *C. sect. Bicolores sensu* Ball 2002a) distinct from *C. sect. Racemosae* as suggested by previous molecular studies or should all species be unified under section *Racemosae* s.str. as suggested by Chater (1980) and Egorova (1999)? (2) Is *C. sect. Racemosae* monophyletic? (3) Is the classification of subsections proposed by previous morphological treatments (Egorova 1985; Wheeler 1990; Egorova 1999) supported by the molecular phylogeny? And, (4) which clades of *C. sect. Racemosae* are resolved by the molecular phylogenetic tree and how do they relate to morphology and distribution?

The morphological revision presented in **Chapter 4** deals with the proposal of a uniform taxonomically revised circumscription of *C. sect. Racemosae* within the borders of Eurasia. As part of this process, necessary taxonomic conclusions, such as changes in nomenclature or taxonomic ranks, as well as exclusion or inclusion of taxa, are carried out. If necessary, typifications are also made. Information (and discussion) on the distribution and ecology, as well as known karyology (i.e. chromosome counts) is drawn. Finally, all taxa are listed with relevant information, including the most important synonymous names. The taxonomic synopsis will be supplied by a dichotomous identification key, which takes into account all accepted Eurasian taxa.

CHAPTER 2

**Parallel and convergent diversification in two northern
hemispheric species-rich *Carex* lineages (Cyperaceae)**

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**Parallel and convergent diversification in two northern hemispheric species-rich
Carex lineages (Cyperaceae)**

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ABSTRACT

Carex species are dominant and abundant plants in boreal and arctic landscapes, typically covering large wetland areas. Most of these vegetation-characteristic species are from *Carex* sections *Phacocystis* and *Vesicariae*, frequently growing together, but also forming monodominant stands. Here we study these species in a phylogenetic framework to infer whether this co-occurrence pattern results from convergent evolution. In both sections, we observed a Northern clade consisting only of arctic to boreal species, a Mixed clade of northern and more southerly distributed species and a Southern grade of species mainly from temperate or further southern zones. The species of the Northern clades of both sections that are the focus of the study may be of similar young age and are rather equally diversified in terms of molecular divergence and morphology, suggesting a replicate adaptive radiation in boreal to arctic habitats. Morphological characters possibly linked with functional importance are not significantly different between the respective clades of the two sections, whereas reproductive structures may be phylogenetically constrained. The evolution of salt tolerance and ongoing diversification in the Northern clade of sect. *Phacocystis* suggests that the observed replicate adaptive radiation might be a transitional state in the diversification of species and may explain why such radiations are so rarely documented.

KEY WORDS: Replicate adaptive radiation, phylogeny, evolution, Arctic, vegetation, wetlands.

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CHAPTER 3

**Molecular phylogeny of the species-rich *Carex* sect. *Racemosae*
(Cyperaceae) based on four nuclear and chloroplast markers**

Sebastian Gebauer, Martin Röser & Matthias H. Hoffmann
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Molecular phylogeny of the species-rich *Carex* sect. *Racemosae* (Cyperaceae) based on four nuclear and chloroplast markers**Gebauer, S.¹, Röser, M.¹ & Hoffmann, M. H.¹**¹Institute of Biology, Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 3, 06108 Halle (Saale), Germany.

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ABSTRACT

Carex is one of the most species-rich genera of the world and an important component of vegetation, particularly in colder regions. One of its larger groups is *C.* sect. *Racemosae* with almost 60 species, which are distributed mainly in mountains of the Northern Hemisphere as well as in the Andes of South America. To address the systematics and evolution of this section and related groups we sampled nearly 80% of the species from all morphological groups previously recognized in the section and estimated their phylogenetic relationships using maximum parsimony, maximum likelihood and Bayesian analyses on a combined nuclear (ITS, ETS 1f) and chloroplast (*trnK–matK*, *rps16*) DNA sequence dataset. We observed incongruence only between the chloroplast *trnK–matK* and the nuclear ETS 1f data and attribute this to a putative parallelism in the chloroplast data set. Our results indicate that *C.* sect. *Racemosae* is not monophyletic in its traditional circumscription. Most species, however, belong to a well-supported clade that is sister to clades consisting of all other sampled species from *Carex* sections *Bicolores*, *Paniccae*, *Phacocystis*, and *Scitae*. We recognize eight major clades within the *Racemosae*, most of them supported by morphological and, in part, geographical data. Previously suggested vicariant distribution patterns between western North American and Eurasian species could not be corroborated. The phylogenetic tree suggests that whereas single morphological characters are highly homoplasious, combinations of characters are nevertheless suitable to recognize clades.

KEY WORDS: ETS, geography, homoplasy, ITS, *rps16*, sectional classification, *trnK–matK* region.

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CHAPTER 4

**A revised taxonomic synopsis and key for the species-rich and
predominantly high mountain sedge group *Carex* section
Racemosae G.Don (Cyperaceae) in Eurasia**

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A revised taxonomic synopsis and key for the species-rich and predominantly high mountain sedge group *Carex* section *Racemosae* G.Don (Cyperaceae) in Eurasia

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ABSTRACT

Carex sect. *Racemosae*, comprising c. 60 species, belongs to *Carex* subg. *Carex* (Cyperaceae) and is mainly found in high mountain and boreal habitats of the Northern Hemisphere. The extreme overall morphological similarity and often only minor differences between not closely related taxa, together with the lack of recent comprehensive treatments, have caused considerable problems in terms of taxonomic delimitation, species identification and actual distribution of the different species. As a result of an extensive revision of herbarium material, and considering previous insights based on molecular data, we present a revised taxonomic synopsis and a determination key that takes into account all Eurasian species. We consider a total of 39 species and six subspecies. *Carex atrata* var. *glacialis* is raised to species rank and described as *Carex kangchengyaoensis*, nom. et stat. nov. *Carex giraudiasii* and *C. schneideri* proved to agree with the type of the largely neglected *C. atrata* subsp. *longistolonifera*, which is treated as a subspecies of *C. duthiei* (*C. duthiei* subsp. *longistolonifera*). The morphologically and geographically distinct East Asian *C. apodostachya* and *C. japonalpina* are split from the mainly Western Palearctic *C. atrata*. *Carex decaulescens* subsp. *alsia* is reduced to synonymy with *C. popovii* subsp. *popovii*, and *C. minxianensis* and *C. montis-wutaii* are considered as synonyms of *C. moorcroftii* and *C. hancockiana*, respectively. *Carex atrofuscoides* and *C. psychrophila*, previously placed in *Carex* sect. *Aulocystis*, are transferred to *Carex* sect. *Racemosae*. Finally, all accepted Eurasian taxa are illustrated, with some rare and poorly known species being pictured for the first time.

KEY WORDS: alpha-taxonomy, determination key, Eurasia, *Carex kangchengyaoensis*, *Carex* sect. *Racemosae*, Cyperaceae, Flora of China, Old World, Palearctic, revision, species identification, taxonomic treatment, typification.

4.1 INTRODUCTION

Carex section *Racemosae* G.Don [type: *Carex atrata* L.] is one of the largest sections within the genus *Carex* L. In its narrowest concept (see below) the section comprises c. 60 species (see below), which are mainly found in Eurasia and North America. Three additional species are disjunctly distributed in South America in the temperate southern Andes, south of Tierra del Fuego (Wheeler 1990); a fourth species — the circumboreal *C. buxbaumii* — was recently reported from the northern Andes (Jiménez-Mejías et al. 2018). The section seems to be naturally absent in Africa and Oceania. Species in *Carex* sect. *Racemosae* occupy diverse habitats, from dry pastures to wetlands, and from lowland tundra in the Arctic to high-mountain alpine grasslands, mainly linked to cold or cold-temperate environments (Kükenthal 1909; Mackenzie 1931–1935; Kreczetovicz 1935b; Murray 1969; Chater 1980; Egorova 1999; Murray 2002a; Liang & Koyama 2010a; Gebauer et al. 2015; Koopman 2015; Więćław et al. 2016). Moreover, in some particular areas as Central Asia, representatives of *Carex* sect. *Racemosae* constitute important elements of various types of high-altitude vegetation (e.g., Egorova 1967; Dickoré 1995). Two main diversity centers with a particularly high number of species (c. 20 spp. each), including a number of endemisms, can be easily identified: one in the mountain ranges of Inner Asia (i.e. Hindukush, Karakoram, Himalayas, and mainly the Hengduan Mountains region including adjacent mountainous regions of China; 20 spp.), and another in western North America (i.e. Rocky Mountains, Cascades, and Sierra Nevada; 23 spp.) (Murray 1969; Noltie 1994; Dickoré 1995; Kukkonen 1998, 2001; Murray 2002a; Liang & Koyama 2010a; Reznicek & Murray 2013; SG & PJM, pers. obs.).

There are two studies that have addressed the systematic relationships within *Carex* sect. *Racemosae* using DNA markers: Gebauer et al. (2015) and Massatti et al. (2016). In addition, a number of phylogenies have included a variable number of taxa of the section (Hendrichs et al. 2004; Waterway & Starr 2007; Waterway et al. 2009; Global *Carex* Group 2016). These data show that, in its broad traditional conception, *Carex* sect. *Racemosae* was not monophyletic. The DNA-based phylogenies, together with the morphological insights that they newly reveal, suggest the exclusion of a number of taxa, narrowing the section down to the monophyletic group of approximately 60 spp. dealt with in this taxonomic synopsis (Global *Carex* Group 2016; Gebauer et al., in prep.). Among the excluded taxa, most of them are more closely related to *Carex* sect. *Phacocystis* rather than to *Carex* sect. *Racemosae*. This is especially true for *C. apoiensis* Akiyama, *C. augustinowiczii*, *C. curvicollis* Franch. & Savat., *C. hongyuanensis*, *C. macrostigmatica*

Kük., *C. mertensii*, *C. meyeriana*, *C. stylosa*, *C. tatjanae* Malyshev, and *C. urostachys* Franch. Some of them have already been formally transferred to the new section *Stylosae* (T.V.Egorova) S.Gebauer & M.H.Hoffm. (viz., *C. hongyuanensis*, *C. meyeriana*, and *C. stylosa*; Gebauer et al. 2015). The future taxonomic affiliations concerning the taxa *C. macrostigmatica* and *C. tatjanae*, which are also excluded here from *Carex* sect. *Racemosae*, will be published elsewhere (Benítez-Benítez et al. 2018; Gebauer et al., in prep.). It seems that the presence of three stigmata instead of two (as typical in section *Phacocystis*), as well as an overweighting of the presence of auricles (see below) has misled most authors to formerly place all of these species within *Carex* sect. *Racemosae* (e.g., Chater 1980; Malyshev 1990; Egorova 1999; Murray 2002a; Liang & Koyama 2010a; Hoshino et al. 2011).

On the contrary, a few taxa previously included in other sections must be transferred to *Carex* sect. *Racemosae*. This holds true for the East Asian *C. heterostachya*, formerly placed in *Carex* sect. *Paludosae* (Dai & Koyama 2010), found to be nested within *Carex* sect. *Racemosae* (Global *Carex* Group 2016; SG et al., unpubl. data). This also applies to *C. atrofuscoides* and *C. psychrophila*, which are usually placed in the apparently polyphyletic *Carex* sect. *Aulocystis* (Liang & Koyama 2010b), but confirmed to belong to *Carex* sect. *Racemosae* by recent molecular results (SG et al., unpubl. data). The characters of these species, apparently deviant characters from the typical morphological conception of *Carex* sect. *Racemosae*, motivated their placement in different groups, as we explain below in the synopsis.

A few authors have made attempts of subdividing *Carex* sect. *Racemosae* into several subsections (Kalela 1944; Egorova 1985; Wheeler 1990; Egorova 1999). However, these infrasectional partitions have been largely refuted by molecular phylogenies (Gebauer et al. 2015; Massatti et al. 2016; Global *Carex* Group 2016), as well as their putative synapomorphies not fully supported by morphological studies (Zhang et al. 2010; Więclaw et al. 2016). Only two of these proposed subsections have been found to be monophyletic, i.e. subsect. *Papilliferae* T.V.Egorova (“*C. buxbaumii* group”) and subsect. *Sabulosae* T.V.Egorova (“*C. sabulosa* group”) (Gebauer et al. 2015; Massatti et al. 2016). Strikingly, the prominent subsect. *Alpinae* Kalela ex T.V.Egorova (“*C. norvegica* group”), which used to combine all taxa with capitate inflorescences and trigonous perigynia, was found to be non-monophyletic (Gebauer et al. 2015; Massatti et al. 2016; Global *Carex* Group 2016). The phylogenies suggest an evolutionary scenario for *Carex* sect. *Racemosae* where the reduction of taxonomically important characters has led to frequent morphological

transitions between states, and thus multiple morphological homoplasies and apparently labile morphological limits between taxa. Such situation can certainly be transferred to most sections of the genus *Carex* (reviewed in Global *Carex* Group 2016).

A comprehensive summary of *Carex* sect. *Racemosae* species in a global perspective has been missing since Kükenthal's (1909) global monograph. Revisions have been so far restricted to regional treatments or checklists (Kreczetowicz 1935b; Ohwi 1965; Raymond 1965; Egorova 1967, 1976, 1985, 1999; Koyama 1978a; Chater 1980; Nilsson 1985; Malyshev 1990; Noltie 1994; Dickoré 1995; Gubanov 1996; Grubov 2001; Kukkonen 1998, 2001; Liang & Koyama 2010a; Hoshino et al. 2011; Koopman 2015). The most comprehensive account for Eurasia is that provided by Flora of China (Liang & Koyama 2010a), as the area covered by this treatment contains the highest number of *Racemosae* species for a single modern country, including several endemics (see below).

In the course of the revision of herbarium materials for two different projects, a series of inconsistencies were found in the treatment of *Carex* sect. *Racemosae* in the Flora of China (Liang & Koyama 2010a) independently by the two authors of this publication. Since then, we have worked together for a better taxonomic understanding of this difficult group of sedges. As result of extensive herbarium research and literature survey, we present a revised taxonomic account of *Carex* sect. *Racemosae* in the Old World, including an identification key and specific comments in particular cases. A few taxonomic changes are also proposed. In addition, some rare and largely unknown (including recently described) species are here depicted for the first time. Relevant features, important for the use of the identification key and the general understanding of the species variation, are also illustrated.

With this work, we intend to address a first step towards a global revision of the section, with the particular intention of stimulating the interest of other botanists on this exciting group of beautiful *Carex* species of the Eurasian high mountains and the Arctic.

4.2 MATERIALS & METHODS

We performed an extensive revision of specimens deposited in the following 29 herbaria: A, B, BM, BOZ, DOV, E, GJO, GZU, H, HAL, HNWP, IRAN, JE, K, LE, M, MOR, MSB, MW, NY, P, SOM, TARI, TBI, TIAE, TUS, UPOS, US, WU (abbreviations according to Thiers 2018+), High Asia Project Herbarium Marburg (MR, private collection of G. Miehe, Philipps University Marburg, Germany), and private collections of the first

author (Herb. Gebauer, Halle, Germany), M. H. Hoffmann (Herb. Hoffmann, Halle, Germany), M. Röser (Herb. Röser, Halle, Germany), A. Strid (Herb. Strid, Ørbæk, Denmark), and N. Tkach (Herb. Tkach, Halle, Germany; see Appendix 2). In addition, we also studied high-resolution images or detailed photographs that were kindly provided by curators or accessible through respective databases of the following herbaria: ALTB, B, BM, C, CAN, CAS, DAO, DOV, E, ERE, GFW, GH, GLM, H, K, KB, KH, KUN, KYO, L, LD, LE, LINN, MO, MT, MW, NSK, OKAY, P, PE, PEY, S, SOM, TAIF, TASH, TI, TIAE, TRH, UPS, US, W, WU, Z, and ZT.

We have made every effort to include all relevant literature on the Eurasian species of *Carex* sect. *Racemosae*. The main taxonomic treatments used as references in our survey were Kükenthal's global revision (1909), Flora of Bhutan (Noltie 1994), *Flora Karakorumensis* (Dickoré 1995), Egorova's monograph for the former USSR (1999), Flora of North America (Murray 2002a), and Flora of China (Liang & Koyama 2010a), without detriment of using additional specialized literature in particular cases (see additional citations under "Taxonomic Synopsis" in the Discussion section).

Terminology used for the last-order inflorescence prophylls (utricles vs. perigynia) follows the suggestions made by Jiménez-Mejías et al. (2016a). The term "auricle(s)" refers to the dark purplish to blackish ear-like glumaceous appendages present at the base of the inflorescence bracts, mainly on the lowermost one.

This revisionary work also takes fully into consideration preliminary molecular data (SG et al., unpubl. data), especially when pointing to conspecificity and when unequivocally indicating polyphyly.

4.3 RESULTS & DISCUSSION

We accept in this revision a total of 39 species of *Carex* sect. *Racemosae* occurring in Eurasia (see Table 1). *Carex atrata* var. *glacialis* is the only taxon here upranked as a new species (*C. kangchengyaoensis*; see Taxonomic Synopsis). We consider infraspecific subdivisions only for *C. aterrima* (subspec. *aterrima* and subspec. *medwedewii*), *C. duthiei* (subspec. *duthiei* and subspec. *longistolonifera*), and *C. popovii* (subspec. *popovii* and subspec. *brunneola*). Four taxa, namely *C. decaulescens*, *C. minxianensis*, *C. montis-wutaii*, and *C. schneideri*, considered in recent treatments are here dismissed as synonyms of other *Racemosae* species (see below). In the future minor changes might be possible after a better study of some of the rare taxa (see below).

Morphological account of section *Racemosae*: characters and variability. — Despite most taxa of *Carex* sect. *Racemosae* share a particular set of morphological characters, the section itself is quite morphologically variable, and intra-specific variability is not rare. Here we describe the most important taxonomic characteristics of *Carex* sect. *Racemosae* species and comment their variability:

(1) *Rhizomes*: Although a few species display creeping rhizomes with long internodes (e.g., *C. adelostoma*, *C. buxbaumii*, *C. heterostachya*, *C. moorcroftii*, *C. polymascula*; Fig. 1: A), the majority of species is more or less caespitose, with rhizomes with short internodes, although specimens where the rhizomes are slightly elongated are not rare (see, for example, Fig. 1: B).

(2) *Inflorescence*: The inflorescences typically bear between two and eight spikes. Unispicate specimens with inflorescences reduced to a single spike are rare among the Eurasian representatives of the section, but occasionally occur in almost all species. The inflorescences have been traditionally characterized either as racemose (Supplemental Fig. S1: e.g., A–D, F–L, N–P; see Appendix 1) or capitate (Fig. S2: e.g., R, U, AA, AC, AE). Racemose inflorescences are looser and typically display clear internodes at least between the 1–2 lowermost spikes, which are usually long-peduncled and pendent to spreading. Capitate inflorescences are denser, ranging from a set of apparently clustered sessile or subsessile spikes separated by short internodes, to a very congested raceme where the individual spikes are hardly noticeable (Figs. S2: Y, AF; S3: AK, AL). Intermediate cases are not very rare (Figs. S1: M; S2: X, Z, AB; S3: AM–AO), which hamper the use of most published identification keys that tend to overweight the importance of those two states. This is especially true for species with capitate inflorescences, where sometimes the lowermost spike might be a bit separated by a more or less conspicuous internode and bears an elongated peduncle (Figs. S1: M; S2: Z; S3: AO). But in the later case, the spike is almost always erect or a bit inclined at most.

(3) *Proximal bract*: The proximal bract ranges from leaf-like or setaceous, although in small specimens of species with capitate inflorescences it can sometimes be glumaceous. Typically, the bract in *Carex* sect. *Racemosae* has been regarded as sheathless or at most provided with a very short sheath. This character has been traditionally considered as definatory of the section. However, after the inclusion of species formerly placed in other groups, the section now also contains a few species that often display a short but more or less conspicuous sheath at the base of the bract (e.g., *C. atrofuscoides*, *C. heterostachya*; Fig. S1: P). The presence of auricles (Fig. 4: H–J; Figs. S1: A; S2: AC, AE, U), a pair of

glume-like appendages present at the base of the bract blade is a typical character for species in *Carex* sect. *Racemosae*. Auricles are typically membranaceous and dark purplish to black in color, rarely whitish-hyaline on margin, exceptionally – if at all – entirely decoloured. This character is shared with representatives of *Carex* sect. *Phacocystis* and its closely allied groups (e.g., Jiménez-Mejías et al. 2014a), although the auricles in these species tend to be less conspicuous than those of species in *Carex* sect. *Racemosae*.

(4) *Sex distribution*: The spikes display a variety of cases regarding the arrangement of male and female flowers. Spikes are typically either entirely male (Figs. S1: I, P; S3: AH), gynaeandrous (male flowers at base and female ones at top; usually the terminal spike; Fig. S1: A–B, H, J, N) or entirely female (i.e. the lateral ones; Fig. S1: A, F, i, N, P). Very rarely some species might develop androgynous spikes (female flowers at base and male ones at top; Fig. S3: AN). Male flowers, whose anthers are usually lost early and not preserved in herbarium specimens, can be recognized by the remnants of the filaments (Fig. S1: A, F, H, J, P). Between the male and female glumes also occur usually slight differences in shape, color and their dimensions. Entirely male spikes are typically narrowly lanceolate or fusiform, while spikes containing female flowers range from short cylindrical or oblong to ovate, elliptic or globose. In a few species where the gynaeandrous spikes have a significant number of male flowers at base, the spike becomes noticeably clavate (e.g., *C. buxbaumii*, *C. hancockiana*, *C. hartmaniorum*, *C. peiktusani*).

(5) *Terminal spike*: The majority of species has a gynaeandrous terminal spike. Some species always have an entirely male terminal spike (e.g., *C. heterostachya*, *C. holostoma*, *C. moorcroftii*, *C. polymascula*; Figs. S1: P; S2: AB; S3: AH; in *C. holostoma* concealed and overtopped by the lateral spikes, and thus usually not visible; Fig. S1: Q). Only *C. polymascula*, and sometimes *C. heterostachya*, might bear more than one entirely male spike at the top of the inflorescence. We have observed that a few species with a usually gynaeandrous terminal spike might develop with more or less frequency a male one instead (e.g., *C. adelostoma*, *C. caucasica*, *C. obscura*, *C. parviflora*, *C. psychrophila*; Fig. S1: i). This transition has been also observed in aberrant specimens of species with the terminal spike typically gynaeandrous (e.g., *C. aterrima* s.l., *C. hartmaniorum*, *C. norvegica*; Cajander 1935; SG, pers. obs.) implying that this transition might also happen in other species. But in these rare cases, the specimens with a terminal male spike are the exception among the majority of specimens with a gynaeandrous one.

TABLE 1: List of taxa accepted in our revised synopsis of *Carex* sect. *Racemosae* in Eurasia and their distribution. The numbers in front of the species name refer to the respective number of the species listed alphabetically in the ‘Taxonomic Synopsis’ (1/3).

Taxon	Distribution
1. <i>Carex adelostoma</i> V.I.Krecz.	Subarctic to arctic Eurasia & North America, also mountains of S Norway (<i>circumpolar</i>)
2. <i>Carex apodostachya</i> Ohwi	<i>Taiwanese</i> (Zhongyang Range) (<i>endemic</i>)
3. <i>Carex aristulifera</i> P.C.Li	<i>SW Chinese</i> (NW Yunnan) (<i>endemic</i>)
4. <i>Carex aterrima</i> Hoppe	Temperate & boreal Eurasia (see below)
4a. subsp. <i>aterrima</i>	Central European Mts., and widely distributed throughout Siberia (southwards to Tian Shan, Altai–Sayan region, Mongolia, NW China: Xinjiang) (<i>European–Siberian</i>)
4b. subsp. <i>medwedewii</i> (Leskov) T.V.Egorova	SW Asia (Caucasus and adjacent mountains) (<i>mainly Caucasian</i>)
5. <i>Carex atrata</i> L.	N Europe, W, Central, E & SE European Mts., partly W & SW Asia (NW Siberia: Polar Urals; NW Turkey: Mt. Uludağ); disjunct in S Greenland (<i>amphi-Atlantic</i> , but mainly European)
6. <i>Carex atrofuscooides</i> K.T.Fu	<i>Central Chinese</i> (N & W Sichuan, NE Tibet, Qinghai, Shaanxi)
7. <i>Carex bijiangensis</i> S. Yun Liang & S.R.Zhang	<i>Sino–Himalayan</i> (SE Tibet, SW Sichuan, NW Yunnan, Bhutan, Sikkim, E Nepal)
8. <i>Carex buxbaumii</i> Wahlenb.	Boreal & temperate Eurasia, North America (scattered in temperate regions & E Asia) (<i>circumboreal</i>), disjunct in N South America, apparently introduced in Australia
9. <i>Carex caucasica</i> Steven	E Europe, SW Asia (Caucasus and adjacent regions), Central Asia (Altai, Alatau, Tian Shan, NW China: Xinjiang), ± disjunct in W Siberia, N Central Asia, S Siberia (<i>E European–W Asian</i>)
10. <i>Carex duthiei</i> C.B.Clarke	<i>Sino–Himalayan</i> (see below)
10a. subsp. <i>duthiei</i>	<i>Sino–Himalayan</i> (from N Pakistan to SW China: S & SE Tibet, W Sichuan, NW Yunnan)
10b. subsp. <i>longistolonifera</i> (Kük.) S.Gebauer & Jim.Mejías, comb. nov.	<i>Central–N Central Chinese</i> (E Tibet, Sichuan, NW Yunnan, E & NE Qinghai, S Gansu)

Table 1: 2/3 (continued).

Taxon	Distribution
11. <i>Carex gmelinii</i> Hook. & Arn.	<i>E Asian</i> (NE China: Jilin; Korea, Japan, Far East, E Siberia), also present in NW North America (<i>amphi-Pacific</i>)
12. <i>Carex gracilentata</i> Boott ex Boeckeler	<i>Central & E Himalayan</i> (Nepal to Bhutan), SW China (S & SE Tibet, W & SW Sichuan, NW Yunnan), rather humid regions
13. <i>Carex hancockiana</i> Maxim.	<i>S Central & SE Siberian–E Asian</i> , Mongolia, NW to NE China (Xinjiang, Qinghai to Jilin), Korea
14. <i>Carex hartmaniorum</i> A.Cajander	Central Europe, W Siberia, SW Asia (Caucasus region) (<i>European–W Siberian</i>)
15. <i>Carex heterostachya</i> Bunge	<i>E Asian</i> (N Central, N & NE China, Korea)
16. <i>Carex holostoma</i> Drejer	Arctic to subarctic Eurasia (<i>circumpolar</i>)
17. <i>Carex infuscata</i> Nees	<i>W Central Asian</i> (NE Afghanistan to Pamiro-Alai region), W Himalayas (Pakistan to Uttarakhand, eastwards to westernmost Nepal)
18. <i>Carex japonalpina</i> (T.Koyama) T.Koyama	<i>E Asian</i> (NE China: Jilin; Korea, S Far East, Japan) (<i>sub-endemic</i>)
19. <i>Carex jisaburo-ohwiana</i> T.Koyama	<i>Taiwanese</i> (mainly Hsuehshan Range) (<i>endemic</i>)
20. <i>Carex kangchengyaoensis</i> S.Gebauer, Jim.Mejías & Noltie, nom. et stat. nov.	<i>E Central Himalayan</i> (E Nepal, Sikkim, Bhutan), S Tibet, distribution insufficiently known (<i>endemic</i>)
21. <i>Carex kansuensis</i> Nelmès	<i>Central Chinese</i> (E & SE Tibet, NW Yunnan, W Sichuan, N & E Qinghai, S Gansu, SW Shaanxi)
22. <i>Carex lehmannii</i> Drejer	<i>Sino–Himalayan–E Asian</i> ; from the Central & E Himalayas (Nepal to Bhutan) throughout SW, Central & E China to Korea & Japan
23. <i>Carex media</i> R.Br.	Boreal Eurasia & North America, in the Old World southwards to Central Mongolia, N & NE China (<i>circumboreal</i>)
24. <i>Carex melanantha</i> C.A.Mey.	Mainly Central Asia, also in S Siberia (Altai–Sayan & Baikal regions, Mongolia), ± disjunct in SW Asia (N & E Caucasus, N Iran: Elburz Mts.) (<i>Central Asian–S Siberian</i>)

Table 1: 3/3 (continued).

Taxon	Distribution
25. <i>Carex melananthiformis</i> Litv.	<i>S Siberian–Mongolian</i> (Altai–Sayan & Baikal regions, N & W Mongolia), with a few occurrences in the Dzungarian Alatau & Tian Shan
26. <i>Carex melanocephala</i> Turcz.	<i>S Siberia–N Central Asian</i> (Altai–Sayan & Baikal regions, Mongolia, NW China: Xinjiang)
27. <i>Carex moorcroftii</i> Falc. ex Boott	Mainly <i>Qinghai–Tibetan</i> Highlands, also in E Karakoram, Himalayas, SW & NW China (W Sichuan, S Gansu)
28. <i>Carex norvegica</i> Retz.	N & Central Europe, N Eurasia (N boreal to arctic regions), also in N North America (\pm <i>circumpolar</i>), but scattered in N Central Siberia
29. <i>Carex obscura</i> Nees	<i>Sino–Himalayan</i> (from N Pakistan to S & SE Tibet, NW Yunnan, W Sichuan)
30. <i>Carex oligantha</i> Steud.	<i>SW Asian–Caucasian</i> (Caucasus and adjacent mountains), reaching Europe on Mt. Elbrus (<i>sub-endemic</i>)
31. <i>Carex parviflora</i> Host	W, Central & E European mountains (<i>European</i>)
32. <i>Carex peiktusani</i> Kom.	<i>E Asian</i> (N & E China, Korea, Japan, S Far East)
33. <i>Carex polymascula</i> P.C.Li	<i>SW Chinese</i> (restricted to W Sichuan) (<i>endemic</i>)
34. <i>Carex popovii</i> V.I.Krecz.	<i>W Central & SW Asian</i> (see below)
34a. subsp. <i>popovii</i>	W Central Asia (NE Iran, N Afghanistan to S Kazakhstan); mainly Pamiro–Alai regions
34b. subsp. <i>brunneola</i> (Kukkonen) Amini Rad	SW Asia (N Iran: Elburz Mts.) (<i>endemic</i>)
35. <i>Carex praeclara</i> Nelmes	<i>Tibetan Plateau</i> ; also N Sikkim & NW Yunnan
36. <i>Carex pseudobicolor</i> Boeckeler	<i>W Himalayan</i> (NE Afghanistan to N India: Himachal Pradesh, Uttarakhand)
37. <i>Carex psychrophila</i> Nees	<i>Sino–Himalayan</i> (NE Afghanistan to Bhutan), SW China (S Tibet, W Sichuan), mostly scattered
38. <i>Carex sabulosa</i> Turcz. ex Kunth	N Asia (boreal to arctic NE Siberia, southwards to Altai–Sayan region, Mongolia, NW China: Xinjiang), mostly scattered; disjunct in NW North America (\pm <i>Siberian–Beringian disjunct</i>)
39. <i>Carex serreana</i> Hand.-Mazz.	<i>N Central & N Chinese</i> (NE Qinghai, Gansu, Hebei, Shanxi), mostly scattered (<i>sub-endemic</i>)

The association of a terminal gynaecandrous spike as a key character that defines the entire *Carex* sect. *Racemosae* has been the source of misclassification of specimens with a terminal male spike, which are not uncommon in herbarium collections (mostly confused with species from *Carex* sect. *Phacocystis*, e.g., *C. orbicularis* Boott s.l.).

(6) *Lateral spikes*: Most species have usually entirely female lateral spikes (see above). In a few species (viz., *C. aristulifera*, *C. atrofuscoides*; Fig. S1: C–G) the distal lateral spikes are typically gynaecandrous, more rarely all of them. This is sometimes hardly noticeable, as the almost entirely female spike just bears 1–few male flowers at the base (e.g., *C. bijiangensis*, *C. duthiei* s.l., *C. kansuensis*; Figs. S1: H, J–K; S2: V). Lateral androgynous spikes are more rarely found, and almost exclusively in specimens that also bear a terminal male spike (e.g., *C. melanantha*, *C. moorcroftii*).

(7) *Glumes*: Glumes are typically broadly or narrowly ovate to lanceolate, rarely orbicular-ovate, with apex usually acute or attenuated into a more or less elongated acuminate tip, more rarely obtuse and, in a few species, mucronate (e.g., *C. adelostoma*, *C. heterostachya*; Figs. S4: A; S5: Q) or aristate (e.g., *C. aristulifera*, *C. buxbaumii*, *C. gmelinii*; Figs. S4: C; S5: I, M). The color in the vast majority of the species is blackish or dark-purplish, which gives the typically dark appearance to the inflorescences of many species of the group, although in some species the glumes are typically brownish (e.g., *C. heterostachya*, *C. praeclara*). Other species display a more or less developed hyaline margin. All the species bear a 1–3-veined single midrib on the glume (character quite variable even within species) that can be paler in color, but other times concolored with the glume and hardly noticeable. As pointed above, there are slight but yet noticeable differences in shape and size between male and female glumes.

(8) *Utricle shape*: As in the vast majority of *Carex* species, in *Carex* sect. *Racemosae* the perigynium that encloses the nutlet has its margins closed and only opens at the top through the so-called beak, constituting what is properly denominated an utricle (Jiménez-Mejías et al. 2016a). The outline can be ovate, obovate, elliptic, oblong or suborbicular, rarely rhombic or lanceolate. The cross-section of the utricles is particularly relevant in *Carex* sect. *Racemosae* taxonomy. For taxonomic purposes, five types of utricles (A–E; listed below) can be defined attending to their cross-section when fully ripe: (A) *Compressed-trigonous*: the adaxial side completely flat, and the abaxially one flattened at margins and upper parts, being shallowly convex only in the lower portion that contains the nutlet, which usually fills less than $\frac{1}{2}$, at the most $\frac{1}{3}$, utricle length (e.g., *C. atrofuscoides*, *C. bijiangensis*, *C. kansuensis*; Figs. S4: G–H; S6: W–W’); in some

species where the nutlet is very small compared to the rest of the utricle body, this might be perceived simply as flat (e.g., *C. popovii* s.l.; Fig. S7: A10–A11). (B) *Trigonous*: forming a three-dimensional trigonous body, as the utricle is usually almost filled by the enclosed nutlet (e.g., *C. media*, *C. norvegica*, *C. oligantha*; Fig. S6: Y–Y', A4, A6). (C) *Inflated*: utricles terete or nearly so in cross-section, especially distally. These utricles are primarily trigonous proximally because they envelope more or less tightly the nutlet (e.g., *C. gracilentata*, *C. lehmannii*, *C. pseudobicolor*; Figs. S5: N; S6: X; S7: A13). (D) *Planoconvex*: the adaxial surface is flat, while the abaxial side is prominently convex (e.g., *C. aterrima* s.l., *C. atrata*, *C. japonalpina*; Figs. S4: D–F; S6: T). (E) *Narrowly biconvex*: the utricle is flattened but both the adaxial and the abaxial surfaces are slightly convex, similar in cross-section to a lentil (e.g., *C. caucasica*, *C. duthiei* s.l., *C. infuscata*; Figs. 2: A–D, J–M; S5: J–L; S6: S). Of course, these categories are not perfect, and transitions between one to another must be expected as part of the variation within a same species.

(9) *Utricle ornamentation*: The utricle wall varies from thin and membranous or papery to (sub-)coriaceous. The presence of nerves is a character of taxonomic value, while it might be sometimes difficult to evaluate. While some species display conspicuously raised nerves that run from the base of the utricle to almost the beak (e.g., *C. hancockiana*, *C. peiktusani*, *C. serreana*; Figs. S5: O; S7: A8, A16), others have mostly nerves only noticeable as lines and are primarily marked proximally. Indeed, it is not rare that species with utricles typically considered nerveless, display 1–few short nerves towards the base of the utricles. The ornamentation of the epidermis ranges from smooth to papillose, with a few taxa also having short prickles on the upper half margins (e.g., *C. obscura*, also occasionally *C. bijiangensis*, *C. kansuensis*; Figs. 1: F; S6: W; S7: A5). Many species bear more or less elevated papillae at the top. Only species previously grouped in subsection *Papilliferae* (e.g., *C. adelostoma*, *C. buxbaumii*, *C. hartmaniorum*) have utricles entirely densely covered by high papillae (Figs. 1: C; S4: A; S5: I, P).

(10) *Utricle beak*: The beak is usually short, rarely elongated and prominent (e.g., *C. atrofusoides*, *C. moorcroftii*, *C. psychrophila*, *C. sabulosa*; Figs. S4: G; S6: A3; S7: A14–A15), smooth or ± prickly at the margins of the opening (orifice), although in a few cases the utricle can be almost beakless (e.g., *C. duthiei* s.l., *C. pseudobicolor*; Figs. 2: A–D, partly J–M; S5: K; S7: A13). It might be truncate, emarginate or bidentate (when deeply bidentate referred as bifid), rarely obliquely truncate (see comments about aberrant utricles under '*C. obliquitruncata*-type' paragraph; Fig. 1: G [right utricle], H).

(11) *Style*: The species typically bear a deciduous style with three stigmata. However, aberrant specimens with two stigmata can occasionally be found among typical tristigmatic flowers (e.g., *C. aterrima* subsp. *medwedewii*, *C. hancockiana*, *C. kansuensis*, *C. parviflora*; Kitagawa 1979; SG & PJM, pers. obs.).

(12) *Nutlets*: The fruit is typically smaller than the utricles and in most cases loosely enclosed by them. Sometimes the nutlets are clearly noticeable from the outside. However, in species with trigonous utricles, those are almost completely filled by the nutlets, especially in its basal part. The nutlets are trigonous in cross-section (Figs. 3: A, H; 4: K–L; S8: A–B), very rarely compressed-trigonous (e.g., *C. kansuensis*; Fig. S8: F–G), often tipped by the short-cylindrical remnant of the style base, and usually constricted proximally forming a sub-stipitate base. The presence of a true carpophore (a peduncle softer than the achene and jointed to the base of it) is usually obscure, although it might be noticeable in some samples.

According to the above-mentioned variation, the morphological account of *Carex* sect. *Racemosae* after its re-definition needs to consider combinations of characters as the only possible synapomorphies to morphologically characterize the group. Previous works have considered the following characters as a unique synapomorphic combination for *Carex* sect. *Racemosae*: bracts sheathless or very shortly sheathed, with auricles at the base of the blade, utricles ascending, and nutlets much smaller than the utricle, loosely enclosed by it (e.g., Egorova 1999; Murray 2002a; Liang & Koyama 2010a). However, these characters are shared also with those species recently excluded from the section (i.e. *Carex* sect. *Phacocystis* s.l.; see Introduction). It has been suggested that the search for additional, often non-traditional, morphological features and especially their combination appears to be advantageous in the reworking of newly resolved groups in *Carex* (e.g., Gebauer et al. 2015; Massatti et al. 2016; Míguez et al. 2018; reviewed in Global *Carex* Group 2016). Further efforts including also the American species of the group would be needed for the eventual finding of a unique combination of morphological characters that might be diagnostic for the whole *Carex* sect. *Racemosae*.

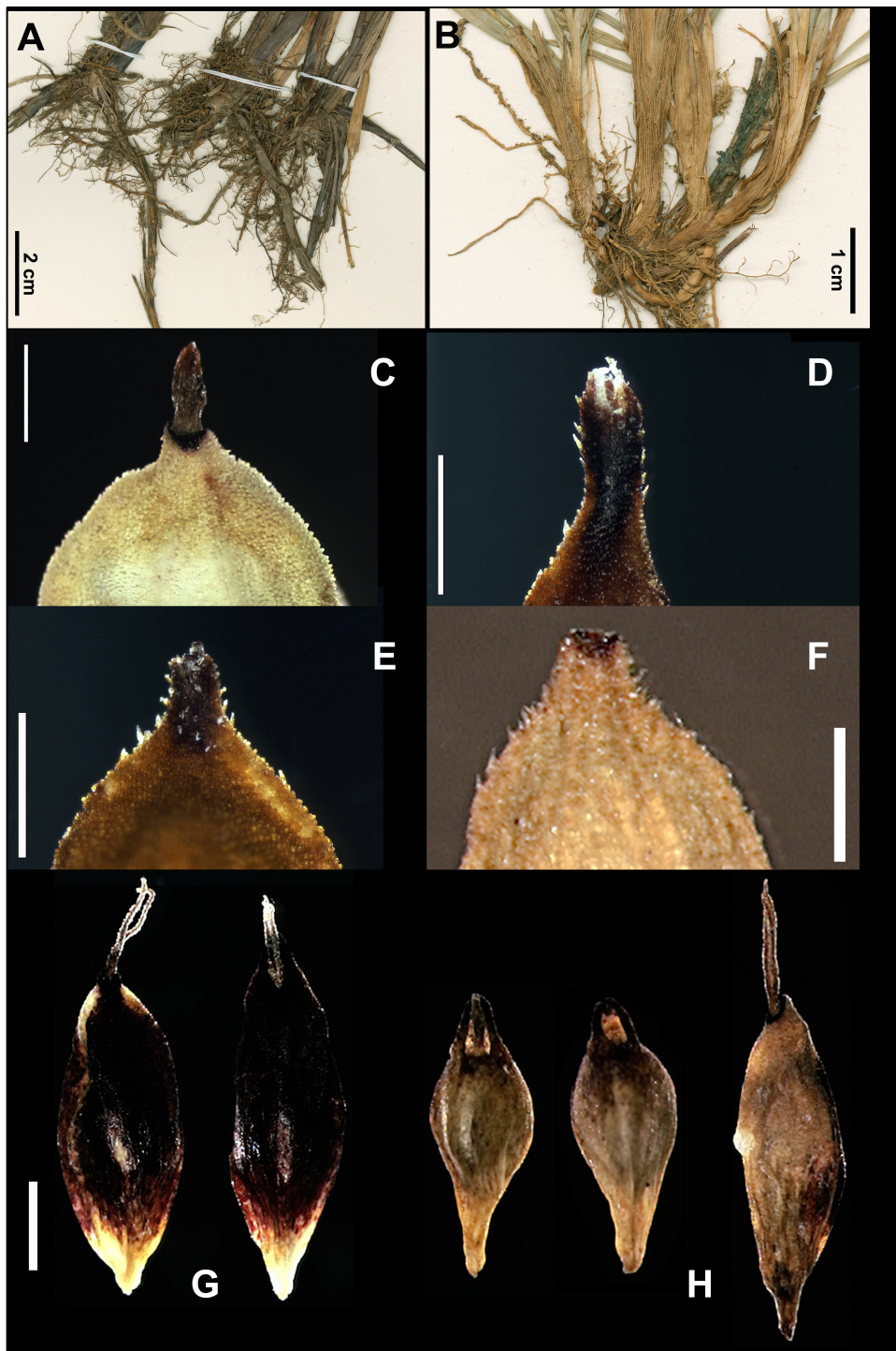


FIG. 1: A–H, Detailed images of relevant morphological features, and aberrant utricles of Eurasian taxa of *Carex* sect. *Racemosae*. A–B: basal parts, A, rhizomatous growth with elongated, long-creeping rhizome in *C. buxbaumii* (Furuse 6009; NY!), scale bar = 2 cm; B, cespitose growth with short, but slightly spreading rhizome in *C. gracilentia* (ACE 111; K!), scale bar = 1 cm; C–F: utricles and beak surface, scale bar = 0.5 mm; C, entire surface densely high papillose (elongated papillae), with very short utricles beak, *C. adelostoma* (Höller, s.n.; M!); D, utricles papillose in the apical part, and utricles beak rather long and ± scabrous in *C. melanocephala* (Heuchert B32; HAL!); E, utricles papillose in the upper part, and utricles beak short and ± scabrous in *C. norvegica* (Gebauer 14085; Herb. Gebauer); F, utricles ± smooth (epapillose), but prickly to densely hispidulous on upper margins in *C. obscura* (Dickoré 10982; MSB!); G–H: aberrant utricles of *C. duthiei* subsp. *duthiei* with obliquely truncate beak orifice (*C. obliquitruncata*-type), scale bar = 1 mm; G: Watson et al. 146 (E!); H: Farille 81-535 (E!).

Distribution and biogeography of *Carex* section *Racemosae* in Eurasia. — *Carex* sect. *Racemosae* in the Old World is almost entirely distributed within the Palearctic, with a few species entering the mountains of SE China and the island of Taiwan. We confirmed that there are no naturally occurring species in Africa or Australasia. *Carex buxbaumii* has been reported as a locally naturalized alien in southeastern Australia (Wilson 1996), although given the frequent long-distance dispersal events involving *Carex* species even between Earth Hemispheres (Villaverde et al. 2017b), it would be desirable to perform additional studies to elucidate the true status of these Australian populations. There is also a report of *C. buxbaumii* from Algeria (Hultén 1958; Meusel et al. 1965) that seems to be highly doubtful, as the taxon was not reported in Maire's (1957) exhaustive compilation for North Africa. As mentioned above, there is a clear diversity center in the mountains of Inner Asia (see above; 20 spp.), surrounding the much drier Tibetan Plateau and Tarim Basin.

The distribution of the group draws a clearly Arctic-alpine pattern, with species occurring in lowland at high latitudes, but restricted to mountains in the lower ones. The only species occurring at relatively low altitudes in temperate climates is the western Eurasian *C. hartmaniorum*, that displays a rather nemoral ecology (Cajander 1935; Hultén & Fries 1986; Gebauer et al. 2015). Most species are more or less restricted to a few sets of mountain ranges, although sometimes extending through vast areas. On the contrary, there are a number of species that are rare narrow endemics (e.g., *C. apodostachya*, *C. aristulifera*, *C. jisaburo-ohwiana*, *C. kangchengyaoensis*). A few others are 'sub-endemics', which are only distributed in a few closely connected single-mountain ranges, but still have quite small distribution areas (e.g., *C. oligantha*, *C. serreana*). In addition, there are a few widespread species that are present in both, Eurasia and North America, following a distribution pattern that can be Circumpolar (*C. adelostoma*, *C. holostoma*, ± *C. norvegica*), Circumboreal (*C. buxbaumii*, *C. media*), amphi-Atlantic (*C. atrata*), amphi-Pacific (*C. gmelinii*), or ± Siberian–Beringian disjunct (*C. sabulosa*).

Two species (*C. moorcroftii*, *C. praeclara*) are reported at extreme altitudes (c. 5700 m), which place them among the mountain-dwelling vascular plants occurring at highest altitudes. Among *Carex*, they seem to be only surpassed by the reports of *C. deasyi* (C.B. Clarke) O. Yano [= *Kobresia schoenoides* (C.A. Mey.) Steud.; Global *Carex* Group 2015] at 5800 m (e.g., Dai et al. 2010).

Taxonomic problems. — Taxonomy of *Carex* sect. *Racemosae* has been found to be more complicated than previous works accounted, with some species not closely related

showing extreme resemblance, while others resulting rather polymorphic. As mentioned above, this synopsis has been prepared through studying herbarium specimens, but fully taking into account the results derived from published (Gebauer et al. 2015; Massatti et al. 2016; Global *Carex* Group 2016) and unpublished molecular data (SG et al., unpubl. data). Accordingly, the taxonomic changes regarding rank or synonymy that we present in this work are not the mere result of whimsical opinion, but derived from a careful evaluation that integrates our observations from morphological data with the available molecular insights. This is the case of taxa usually treated as synonyms, subspecies or varieties of other species, that we have upranked as ‘good’ species (viz., *C. apodostachya*, *C. japonalpina*, *C. kangchengyaoensis*, usually treated under *C. atrata*; and *C. jisaburo-ohwiana*, often considered a subspecies of *C. caucasica*). The subordinate status of these taxa was in most cases an erroneous interpretation of strong morphological resemblance as a sign of true phylogenetic convergence, which has been disregarded by the genetic studies.

A particularly recurrent problem that we detected when preparing the identification key was the finding of dwarf specimens associated to high altitude habitats. Those forms are depauperate plants that indeed belong to a number of different species. Their superficial resemblance is probably the result of further morphological reduction as a consequence of the harsh environments they inhabit, as found in other groups of high mountain *Carex* (Jiménez-Mejías et al. 2017, 2018). Those similar-looking plants might be correctly identified at species level after careful evaluation of the utricle morphology, and whether possible comparing with additional materials of other species co-occurring in the region.

Despite we consider our account of 39 species and 6 subspecies for Eurasia to be fairly accurate, the actual number might still change in the future. On the other hand, a number of new taxa have been recently described in *Carex* sect. *Racemosae* (e.g., Liang & Zhang 2006; Zika 2012; Reznicek & Murray 2013), which might indicate that some species might still remain cryptic.

Special mention deserves the problems found in the Flora of China (Liang & Koyama 2010a) account. As mentioned above, the two authors of this paper found independently the same inconsistencies in the treatment. Some of the nomenclatural and taxonomic considerations, as well as the constraints imposed by the character choice for the key, were causing confusion and thus difficulties in the practical application of the Flora of China treatment. That was probably due to the limited amount of materials that the authors were

able to study to prepare their synopses. Our more focused effort and broader geographical coverage allowed us to uncover the roots of those problems. In particular, we found a few Chinese endemic taxa (*C. atrata* subsp. *longistolonifera*, *C. minxianensis*, *C. montis-wutaii*, and *C. obliquitruncata*; see below) to be the result of taxonomic overvaluation of deviant characters. These taxa were based only on their types or on a few collections. In addition, the morphological synopses provided seemed to mostly rely on previous accounts. Thus, the lack of critical comparison with other taxa led to the persistence of these names in the literature. Further confusion was caused by a few cases of misapplication or neglect of names (*C. angarae*, *C. atrata* subsp. *pullata*, *C. duthiei*, and *C. giraudiasii*; see comments below).

Putative hybrids. — There is little information available about the existence of hybrids between *Carex* sect. *Racemosae* species beyond pure speculation.

Carex × *candrianii* Kneuck. (syn. *C.* × *sarntheinii* J. Vetter), a putative hybrid between *C. atrata* and *C. norvegica* described from the Swiss Alps, is also reported from northern Europe (Kneucker 1899; Vetter 1907; Kukkonen et al. 1998; Elven et al. 2005). The suspected hybrid combination between *C. atrata* and *C. aterrima* was also described as *C.* × *binensis* Kneuck. from the Swiss Alps (Kneucker 1899), and further suggested by intermediate plants from the Carpathians and Sudetes (Egorova 1999; Kaplan et al. 2018). *Carex* × *montanoaltaica* Zolot. of suggested hybrid origin from the parents combination *C. melanocephala* × *C. aterrima* subsp. *aterrima*, was described from the Altai (Zolotuchin 1984; Egorova 1999).

The morphological intermediacy of *C. melananthiformis* between *C. melanantha* and *C. sabulosa* has been suggested as a sign of an introgressive origin for *C. melananthiformis* (Egorova 1999). However, most hybrids reported needs to be taken with caution, since recent molecular evidence suggests that seeming morphological intermediacy in *Carex* might be just the result of punctual malformations within a single species and that the hybrid account for the genus as a whole could be overestimated (see Řepka et al. 2014).

Other more occasional hybrid products already suggested are *C. adelostoma* × *C. buxbaumii* (Elven et al. 2005), *C. atrata* × *C. buxbaumii*, *C. atrata* × *C. media*, *C. buxbaumii* × *C. hartmaniorum* (Koopman 2011), *C. media* × *C. norvegica* (Egorova 1999), *C. melanantha* × *C. moorcroftii*, and *C. melanantha* × *C. obscura* (Dickoré 1995). Two additional putative hybrids, viz., *C. buxbaumii* × *C. elata* All. (*Carex* sect. *Phacocystis*) and *C. parvi-*

flora × *C. sempervirens* Vill. (*C.* × *salisiana* Brügger; *Carex* sect. *Aulocystis*), seem to be extremely doubtful (Koopman 2011).

Indeed, our own observations suggest that some intermediate specimens might actually involve hybridization between species (e.g., *C. aterrima* subsp. *aterrima* × *C. atrata*, *C. aterrima* subsp. *aterrima* × *C. japonalpina*, *C. bijiangensis* × *C. kansuensis*, and *C. gracilentata* × *C. infuscata*). Further discussion about these possible hybrid plants is provided under the corresponding paragraphs of the different species involved.

In any case, additional studies using alternative approaches would be desirable to confirm the true nature of these abovementioned putative hybrid plants.

Key to Eurasian taxa of *Carex* sect. *Racemosae*: notes on use. — To facilitate taxonomic identification in this taxonomically difficult group of sedges we have designed this key as a practical tool making the possible choices in the most straightforward way possible. Thus, to minimize the number of characters to be evaluated in every step, we decided to key out multiple times the taxa that showed the widest morphological variation. Accordingly, despite we placed morphologically similar species together, the key does not intend to set any phyletic order, so that closely related species (in relation to the DNA-based data above-mentioned) are not necessarily grouped together.

Given that the overall similarity between certain species of *Carex* sect. *Racemosae* can sometimes be extreme, the species can usually only be identified unambiguously on the basis of fully developed individuals with ripe fruits. Furthermore, depauperate and aberrantly grown, as well as immature individuals often remain indeterminable and cannot be confidently assigned to a specific taxon. Examination of several inflorescences is also highly advisable to accurately evaluate intrapopulational variation, since some characters may be particularly variable, as the number of stigmata, the exact distribution of female and male flowers, or the length of spike peduncles. In the case of strictly endemic species, we also provide a distribution note to help discard deviant specimens of more widely distributed taxa.

Measurements for the length of the utricles include the beak and, if present, the basal stipe. Similarly, the dimensions given for the length of the nutlets also include, if present, the remnant of the style-base as well as the basal sub-stipitate base.

For additional interpretations of the variation in inflorescence, spikes and utricles, the reader is referred to the Morphological Account of the *Carex* sect. *Racemosae* paragraph, including Figs. 1–4, and Supplemental Figs. S1–S9 (see Appendix 1).

The numbers in front of the species name within the key refer to the corresponding number of the species listed alphabetically in the Taxonomic Synopsis (see also Table 1), where also further information on the possible or even frequent confusion with other species, as well as on the distribution and habitats can be found.

Key to *Carex* section *Racemosae* in Eurasia

1. Female glumes (8)9–10 mm long, with conspicuous wide hyaline margins; inflorescence capitate, head-like, with all the spikes congested and hardly apparent; dwarf plants of high elevations (4500–5700 m) ... 35. *C. praeclara*
 - Female glumes less than 8 mm long (excluding arista if present), variously colored; inflorescence diverse, spikes congested or separate, apparent or not ... 2
2. Utricles densely high-papillose on the entire surface, pale green, grayish green, greenish to whitish, yellowish green, or brownish and blackish above ... 3
 - Utricles mostly epapillose, smooth or minutely punctate, or papillose only distally and very sparsely so below, greenish, yellowish, stramineous, purplish, brownish or blackish ... 7
3. Terminal spike entirely male; female glumes obtuse, acute or sometimes with a short mucro < 0.5 mm long; utricles pale green, greenish whitish or brown and blackish above ... 4
 - Terminal spike gynaeandrous, rarely androgynous or male; female glume apex subulate to acuminate, mostly with a long linear tip > 0.5 mm long; utricles grayish green, greenish, yellowish green, or yellowish brown (utricles pale green or greenish whitish and female glumes acute or acuminate with mucro usually < 0.5 mm long in *C. adelostoma*, 4, 5) ... 5
4. Inflorescence often > 3.5 cm long, rarely shorter, rather loose; female glumes ovate-lanceolate, without hyaline margin, acute or acuminate; utricles pale green or greenish whitish, sometimes brown-purplish spotted; Subarctic plants (southwards to mountains of S Norway; see also 5) ... 1. *C. adelostoma* (in part)
 - Inflorescence usually < 3.5 cm long, rather dense (male spike concealed and overtopped by the lateral spikes); female glumes ovate, with or without hyaline margins, acute to obtuse; utricles brownish, blackish above; Arctic plants ... 16. *C. holostoma*
5. (3) Female glumes acute or shortly acuminate, then with a very short mucro < 0.5 mm long, usually shorter than mature utricles; inflorescence often < 5 cm long; utricles pale green or greenish whitish, almost beakless or with short beak < 0.2 mm long; Subarctic plants (southwards to mountains of S Norway; see also 4) ... 1. *C. adelostoma* (in part)
 - Female glumes aristate, with a mucro > 0.5 mm long, usually overtopping mature utricles; inflorescence usually 5–10 cm long, rarely shorter; utricles grayish green, greenish to yellowish green, or yellowish brown, usually with short beak > 0.2 mm long, rarely nearly beakless ... 6
6. Terminal spike cylindrical, rarely narrowly clavate; 3–6 lateral spikes, 4–6(7) mm wide, lowermost one usually > 2.5 cm long, cylindrical; utricles 2–3(3.5) mm long, conspicuously veined, with rather small and fine papillae, beak distinctly bifid, with teeth straight; leaves usually green or dark green, flat ... 14. *C. hartmaniorum*

- Terminal spike clavate, rarely oblong-ovoid; 2–3(4) lateral spikes, (5)6–10 mm wide, up to 2.5 cm long, ovoid, rarely oblong; utricles (2.5)3–4.5 mm long, obscurely to conspicuously veined, with rather large and coarse papillae, beak shallowly to distinctly bifid, with the teeth usually somewhat divergent, rarely utricles nearly beakless; leaves usually glaucous or greyish green, flat or with margins involute ... 8. *C. buxbaumii*
- 7. (2) Upper spike(s) entirely male and proximal female spikes conspicuously pedunculate, usually on > 20 mm long, slender peduncles, pendent... 8
 - Upper spike gynaeandrous, with the female part usually longer than the male one, or male; if upper spike(s) male, then the female spikes sessile or subsessile, erect (rarely only the lowermost pedunculate and pendent, see 27) ... 9
- 8. Upper 1–4 spikes entirely (or almost entirely) male; utricles suborbicular to broadly ovate, 2.3–3(3.2) mm long, veinless; rhizome thickened, elongated, long creeping; plants endemic to W Sichuan ... 33. *C. polymascula*
 - Upper spike male, remaining spikes entirely female; utricles obovate to obovate-elliptic, 3.5–4 mm long, abaxial side faintly (2)3–5-veined at base; rhizome short, plants cespitose (see also 28, 82) ... 9. *C. caucasica* (in part)
- 9. (7) All spikes gynaeandrous or only the lowermost entirely female (male flowers at the base of each spike may be easily overlooked) ... 10
 - Terminal spike gynaeandrous or male, rarely androgynous, and all lateral spikes entirely female, rarely androgynous ... 15
- 10. Leaf blades 1.5–2(3) mm wide; female glumes aristate, with a narrow but conspicuous green or yellowish midrib; plants slender; plants endemic to NW Yunnan (Gongshan, Gaoligongshan) ... 3. *C. aristulifera*
 - Leaf blades (2)3–10 mm wide; female glumes acute, if long acuminate, then the midrib inconspicuous, dark brown to dark purplish or almost blackish, very rarely greenish or yellowish; plants rather stout ... 11
- 11. Lowermost bract with a short sheath up to 4 mm long, shortly bladed, filiform or setaceous, shorter to slightly longer than inflorescence; lateral spikes globose or ovate to short-elliptic, ± clavate, (8)10–15(18) mm long, with the glumes from the lower half spreading; utricles gradually attenuated into the beak ... 6. *C. atrofusoides*
 - Lowermost bract sheathless, usually leaf-like, with ± well-developed blade, not filiform, rarely setaceous, slightly shorter to largely exceeding inflorescence; lateral spikes cylindrical, obovate or oblong, 10–35 mm long, with all the glumes erect, rarely the lowermost ones slightly spreading; utricles rounded at top, abruptly constricted or attenuated into a short beak or utricles beakless ... 12
- 12. Utricles narrowly biconvex, obscurely or conspicuously veined, rarely veinless, nearly beakless or with a very short beak 0.1–0.3(0.4) mm long (rarely the apex ± acuminate, not forming a beak), with the orifice usually emarginate or ± horizontally truncate, without prickles on upper margin ... 13
 - Utricles compressed-trigonous, plano-convex or strongly flattened, veinless, with a distinct beak > 0.3 mm long, with the orifice ± horizontally truncate, emarginate or shallowly bidentate, often with a few prickles on upper margin ... 14

- 13.** Mature utricles yellowish to golden-yellowish, sometimes brownish, often dark purplish punctate above, obovate-elliptic to oblong-elliptic, \pm rounded at apex, abruptly constricted at apex into a short beak 0.1–0.2(0.3) mm long, sometimes nearly beakless; nutlet obovate to obovate-elliptic (see also **48, 73, 83, 91**) ... 10a. *C. duthiei* subsp. *duthiei* (in part)
- Mature utricles entirely yellowish green or yellowish, elliptic-lanceolate to obovate-elliptic, \pm cuneate at apex, gradually attenuated or slightly constricted into a short beak 0.2–0.3(0.4) mm long; nutlet elliptic to elliptic-obovate (see also **48, 83, 91**) ... 10b. *C. duthiei* subsp. *longistolonifera* (Kük.) S.Gebauer & Jim.Mejías, comb. nov. (in part)
- 14.** (12) Female glumes 4–4.5(5) mm long; utricles broadly elliptic to suborbicular, stramineous, often yellowish-brown or dark purplish punctate above at maturity (rarely almost entirely dark purplish punctate), thin-walled, papery, usually translucent at early stages, abruptly constricted into the beak, the orifice slightly bifid or emarginate; nutlet oblong or obovate-oblong, the maximum width near the middle, \pm compressed-trigonous (see also **89**) ... 21. *C. kansuensis* (in part)
- Female glumes (4)4.5–6(6.5) mm long; utricles elliptic or obovate-elliptic, yellowish at base, the remaining parts uniformly dark purplish or purplish black tinged at maturity (rarely stramineous or almost purplish black), \pm subcoriaceous, usually not translucent even at early stages, gradually or abruptly constricted into the beak, the orifice truncate or emarginate; nutlet narrowly obovate, the maximum width near the apex, trigonous (see also **51, 88**) ... 7. *C. bijiangensis* (in part)
- 15.** (9) Female glumes with broad white-hyaline margins (usually more than $\frac{1}{3}$ the width between the midvein and the glume margin) and lowermost bract shorter or as long as the inflorescence ... **16**
- Female glumes with narrow white-hyaline margins or margins not differentially colored, if with broad hyaline margins, then lowermost bract longer than the inflorescence (see also **28**; rarely shorter, see also **75**) ... **21**
- 16.** Female glumes ovate, with a scabrous long arista (0.5)1–3 mm long (rarely only the lower glumes long-aristate); terminal spike gynaeandrous or male (both expressions sometimes on the same tuft); utricles smooth or with a few papillae above, thin-walled, \pm papery (see also **28, 51**) ... 11. *C. gmelinii* (in part)
- Female glumes broadly ovate, oblong-ovate or ovate-lanceolate, apex acute to acuminate, without a scabrous long arista, at most with a short mucro < 0.5 mm long; terminal spike male or gynaeandrous (rarely androgynous); utricles densely papillose above (\pm smooth in *C. heterostachya*, **17, 31**), coriaceous ... **17**
- 17.** Uppermost 1–2(3) spikes entirely or almost entirely male; lowest bract sheathless or with a short 2–4 mm long sheath; utricles entirely brownish (see also **31**) ... 15. *C. heterostachya* (in part)
- Terminal spike male or gynaeandrous, remaining spikes entirely female, rarely androgynous but then the female part as long as or longer than the male one; lowest bract sheathless; utricles yellowish green and ferruginous-brown to purplish blackish above, sometimes almost purplish blackish ... **18**
- 18.** Utricles entirely yellowish green or ferruginous-brown to reddish purple above, rarely dark purplish at the upper part, usually contrasting with the darker glumes, with the apex \pm cuneate and attenuated into a (0.3)0.4–1.2 mm long beak with the orifice bidentate ... **19**

- Utricles yellowish green at base, dark purplish to purplish blackish in its entire upper half, rarely only at the apex below the beak (sometimes almost purplish blackish in *C. melanantha*, **20**, **23**), not contrasting with the glumes, with the apex \pm rounded (rarely \pm cuneate in *C. melanantha*, **20**, **23**), and thus abruptly constricted into a (0.1)0.2–0.3(0.5) mm long beak, with the orifice usually truncate, sometimes emarginate (rarely bidentate, but then with a beak $<$ 0.3 mm long) ... **20**
- 19.** Terminal spike male, rarely gynaeandrous or androgynous; leaves flat, straight and stiff, pointy; utricles yellowish green, ferruginous-brown to reddish purple above, rarely dark purplish at the upper part, (2.5)3–3.5(4) mm long with a beak (0.3)0.4–0.5 (very rarely up to 0.9) mm long (see also **32**) ... **27. C. moorcroftii** (in part)
- Terminal spike gynaeandrous, rarely male; leaves slightly convolute, \pm flexuous; utricles entirely yellowish-green, only the beak sometimes reddish purple, 4–5(6) mm long with a beak (0.5)0.7–1.2 mm long (see also **54**) ... **38. C. sabulosa** (in part)
- 20. (18)** Inflorescence very dense, the spikes tightly compacted and the boundaries between individual spikes indistinct, rarely the lowermost spike a bit distant, but the internode usually shorter than the spike and thus much overlapping with the rest of the inflorescence; terminal spike male, rarely gynaeandrous or androgynous; utricles (2.5)3–3.5 mm long, ovate, elliptic or obovate, with a short (0.1)0.2–0.3(0.4) mm long beak; leaf blades (2.5)3–6(7) mm wide, the apex abruptly narrowed into a \pm acuminate tip (see also **23**) ... **24. C. melanantha** (in part)
- Inflorescence dense, the spikes compacted but the individual spikes usually \pm distinct, the lowermost spike usually separated, with the internode often as long as or longer than the spike, thus it shortly overlapping with the rest of the inflorescence; terminal spike usually gynaeandrous, more rarely male or androgynous; utricles 2–3(3.3) mm long, broadly obovate, broadly elliptic or suborbicular, with a short (0.1)0.2–0.3(0.5) mm long beak; leaf blades (2)2.5–3(5) mm wide, apex gradually narrowed (see also **23**, **54**) ... **25. C. melanthiformis** (in part)
- 21. (15)** Spikes very congested at the top of the inflorescence, so crowded that sometimes the individual spikes cannot be easily distinguished, only the 1(2) lowermost spikes sometimes a bit distant; glumes blackish to purplish black, rarely dark reddish brown, \pm not contrasting with the also dark-colored utricles (at least in their upper part); plants cespitose with rhizome short or only slightly elongated or with thickened, long-creeping rhizome ... **22**
- Spikes distant or approximate, if approximate then all the individual spikes can be easily distinguished; glumes from black to ferruginous-brown, contrasting or not in color with the utricles; plants cespitose or with elongated rhizomes; if plants with rhizomes long-creeping and inflorescence \pm congested, then utricles contrasting in color with the glumes ... **25**
- 22.** Female glumes (3.8)4–6 mm long, oblong-ovate, usually much longer than the utricles, usually several with a \pm conspicuous broad white-hyaline tip; plants with thickened long-creeping rhizome ... **23**
- Female glumes 2–3(3.2) mm long, ovate or broadly ovate to oblong, shorter to slightly shorter than the utricles, without or with a narrow white-hyaline tip; plants densely to loosely cespitose, with rhizomes short or slightly elongated ... **24**
- 23.** Inflorescence very dense, the spikes tightly compacted and the boundaries between individual spikes indistinct, rarely the lowermost spike a bit distant, but the internode usually shorter than the spike

- and thus much overlapping with the rest of the inflorescence; terminal spike male, rarely gynaeandrous or androgynous; utricles (2.5)3–3.5 mm long, ovate, elliptic or obovate, with a short (0.1)0.2–0.3(0.4) mm long beak; leaf blades (2.5)3–6(7) mm wide, the apex abruptly narrowed into a ± acuminate tip (see also **20**) ... 24. *C. melanantha* (in part)
- Inflorescence dense, the spikes compacted but the individual spikes usually ± distinct, the lowermost spike usually separated, with the internode often as long as or longer than the spike, thus it shortly overlapping with the rest of the inflorescence; terminal spike usually gynaeandrous, more rarely male or androgynous; utricles 2–3(3.3) mm long, broadly obovate, broadly elliptic or suborbicular, with a short (0.1)0.2–0.3(0.5) mm long beak; leaf blades (2)2.5–3(5) mm wide, apex gradually narrowed (see also **20, 54**) ... 25. *C. melananthiformis* (in part)
- 24. (22)** Utricles (3)3.5–4(4.5) × 1–1.3(1.5) mm, oblong-elliptic or narrowly elliptic, rarely obovate-elliptic; female glumes ovate to oblong, (2)2.2–3.2 × 1–1.5 mm, apex acute; plants densely cespitose, rhizomes short (see also **66, 68, 71**) ... 26. *C. melanocephala* (in part)
- Utricles (2.7)3–3.7 × 1.2–1.9 mm, elliptic or obovate-elliptic; female glumes broadly ovate, (2.2)2.4–3 × 1.4–1.9 mm, apex acute or rounded; plants rather loosely cespitose, the rhizomes slightly spreading (see also **66, 68, 71**) ... 30. *C. oligantha* (in part)
- 25. (21)** Terminal spike male ... **26**
- Terminal spike gynaeandrous ... **34**
- 26.** Spikes ± distant, separated along the upper part of the stem, usually the lowermost ones not overlapping, only the uppermost spikes approximate and somewhat overlapping; lower spikes usually on long peduncles > 20 mm long, rarely shorter, ± pendent (see also **82**) ... **27**
- Spikes approximate at the top of the stems, usually all them somewhat overlapping; peduncles very short or spikes sessile, only the lowermost spike sometimes on a well-developed peduncle < 20 mm long, from ± erect to spreading ... **29**
- 27.** Utricle shape elliptic to rhomboid-elliptic, (2.5)3–4(5) × (0.8)1–1.5 mm, ± cuneate at apex and attenuated or scarcely constricted into a rather long beak (0.5)0.7–1.2(2) mm long, often scabrous and ± bent, with the orifice bidentate; utricule veins conspicuous, often running into the beak; female glumes (1.7)2–3(3.3) mm long, acute, sometimes with a mucro < 0.5 mm long (see also **29, 56, 80**) ... 37. *C. psychrophila* (in part)
- Utricle shape obovate, elliptic-obovate or elliptic, 3.5–5 × 1.8–3 mm, rounded at apex and abruptly constricted into a rather short beak 0.1–0.4(0.6) mm long, ± smooth except sometimes around the orifice, straight, with the orifice truncate or emarginate; utricule veins restricted to the lower half, not running into the rather short beak, or utricles nerveless; female glumes 3.5–5 mm long, acute to acuminate, or with a scabrous long arista (0.5)1–3 mm long ... **28**
- 28.** Female glumes with body 4–5 mm long and a scabrous long arista, (0.5)1–3 mm long (rarely only the lower glumes long-aristate), the midrib broad and light in color, conspicuously contrasting with the rest of the glume; utricles 3.5–5 × 2–3 mm, with a beak 0.2–0.3 mm long (see also **16, 51**) ... 11. *C. gmelinii* (in part)
- Female glumes 3.5–4 mm long, acute to acuminate, the midrib usually inconspicuous, pale but very thin or concolored with the rest of the glume; utricles 3.5–4 mm × 1.8–2.4 mm, with a beak 0.3–0.4(0.6) mm long (see also **8, 82**) ... 9. *C. caucasica* (in part)

- 29. (26)** Utricles elliptic to rhomboid-elliptic, yellowish green, with walls thin, membranous, with a rather long beak, (0.5)0.7–1.2(2) mm long, often scabrous and ± bent, with the orifice bidentate (see also **27, 56, 80**) ... 37. *C. psychrophila* (in part)
- Utricles obovate, elliptic, or suborbicular, yellow, brownish, purplish or almost black, usually with a rather short beak, < 0.5 mm long, smooth or scabrous and usually straight, with the orifice truncate, emarginate or bidentate ... **30**
- 30.** Utricles 1.7–2.5(2.7) mm long, at least some of them prickly to densely hispidulous on the upper margins, pale greenish, yellowish or golden-yellowish, rarely brownish (see also **35, 55**) ... 29. *C. obscura* (in part)
- Utricles (2.5)3–4(4.5) mm long, smooth on the upper margins, or only slightly and sparsely scabrous above, brownish, yellowish green, greenish ferruginous, yellowish brown, golden-brownish or mostly blackish or blackish purple, if with a few ± prominent prickles, then utricles almost entirely blackish or blackish purple ... **31**
- 31.** Female glumes ferruginous-brown with margins hyaline; utricles ± homogeneously brownish; rhizome clearly elongated, long-creeping (see also **17**) ... 15. *C. heterostachya* (in part)
- Female glumes black, purplish black, or dark reddish brown, with or without narrow hyaline margins; utricles yellowish green, greenish ferruginous, yellowish brown, golden-brownish or mostly blackish or blackish purple; rhizomes elongate or not ... **32**
- 32.** Rhizomes clearly elongated, long-creeping; utricles broadly trigonous (± obtusely-trigonous in cross-section), often slightly inflated; leaves stiff, pointy (see also **19**) ... 27. *C. moorcroftii* (in part)
- Rhizomes short, sometimes slightly spreading, but not creeping; utricles plano-convex, compressed-trigonous or almost flat; leaves herbaceous, not stiff and pointy ... **33**
- 33.** Utricles compressed-trigonous to almost flat, the enclosed nutlet contrasting from the outside with the flattened margins, greenish ferruginous, yellowish brown or golden-brownish, dark brown to blackish at the beak, broadly elliptic to suborbicular, somewhat glossy, ± strongly flattened; female glumes acuminate, dark reddish brown (see also **62, 87**) ... 34a. *C. popovii* subsp. *popovii* (in part)
- Utricles plano-convex, almost entirely blackish or blackish purple, paler on the upper edges, broadly ovate or obovate, dull; female glumes acute, ± blackish (see also **58**) ... 31. *C. parviflora* (in part)
- 34. (25)** Lowermost bract leaf-like, much longer than the inflorescence ... **35**
- Lowermost bract glumaceous, setaceous or leaf-like, shorter, equaling or slightly longer than inflorescence ... **50**
- 35.** At least some utricles prickly to densely hispidulous on the upper margins (see also **30, 55**) ... 29. *C. obscura* (in part)
- Utricles smooth on the upper margins, or only slightly and sparsely scabrous above or only at the beak orifice ... **36**
- 36.** Glumes with conspicuous white-hyaline margins ... **37**
- Glumes without white-hyaline margins ... **44**
- 37.** Inflorescence dense, all spikes approximate and conspicuously overlapping; lateral spikes ± erect, nearly sessile, or lowermost one on a short stout peduncle < 10 mm long, usually erect ... **38**

- Inflorescence loose, racemose, the lowermost spike distant and often not or scarcely overlapping; lateral spikes erect to spreading, the lowermost one \pm pendent on a slender peduncle > 10 mm long ... **41**
- 38.** Female glumes 1.4–2.5 mm long, ovate, rarely oblong-ovate, apex acute, shorter than to almost equaling the utricles; mature utricles 1.8–3(3.5) mm long, \pm trigonous or biconvex, sometimes \pm inflated; lateral spikes 4–12 \times 3–5(6) mm; plants slender ... **39**
- Female glumes 3–4(4.5) mm long, oblong-ovate, apex acute to acuminate, usually longer than utricles; mature utricles 3–3.8(4) mm long, \pm flattened, from compressed-trigonous to plano-convex; lateral spikes (8)10–30 \times (5)6–10 mm; plants rather stout ... **40**
- 39.** Plants loosely cespitose; leaves rather soft, from $\frac{1}{2}$ to as long as the stems; utricles (2.2)2.5–3.5 mm long, pale green or whitish, becoming yellowish or brownish greenish to golden-yellowish, rarely brownish, usually \pm shiny, faintly veined or veinless, usually smooth above, beak smooth or sparsely prickly; female glumes about $\frac{1}{2}$ as long as the utricles (see also **77**) ... 23. *C. media* (in part)
- Plants densely cespitose; leaves rather rigid, about $\frac{1}{2}$ as long as the stems; utricles 1.8–2.5(3) mm long, greenish, becoming olive brown or dark brown, dull, usually veinless, usually slightly sparsely scabrous above, beak usually conspicuously and densely prickly; female glumes about $\frac{3}{4}$ as long as the utricles, rarely slightly shorter or only $\frac{1}{2}$ as long as the utricles (see also **75**) ... 28. *C. norvegica* (in part)
- 40. (38)** Inflorescence blackish brown to blackish, rarely dark brown; female glumes acute to acuminate, blackish or dark blackish-brown, sometimes dark purplish brown; mature utricles yellowish to ferruginous-yellowish, rarely yellowish brown, densely purplish punctate above, at base more or less broadly cuneate and attenuating into a short stipe; nutlet obovate to elliptic-obovate; culms smooth above (see also **43, 45, 64, 94**) ... 5. *C. atrata* (in part)
- Inflorescence dark reddish or purplish brown to dark brown; female glumes acuminate, dark reddish to purplish brown or dark brown; mature utricles yellowish brown, brownish to reddish or purplish brown, without or with irregular purplish spots, \pm rounded at base and constricted into a short stipe or stipeless; nutlet elliptic to elliptic-obovate; culms smooth or scabrous above (see also **43, 45, 64, 94**) ... 18. *C. japonalpina* (in part)
- 41. (37)** Mature utricles biconvex to inflated, not flattened, greenish, grayish green or yellowish green, with an often \pm somewhat bent, usually bidentate beak yellowish green to somewhat purplish; inflorescence greenish to pale or light brown; female glumes pale- to light-brown or pale ferruginous, sometimes purplish brown, \pm pale greenish in the middle ... **42**
- Mature utricles \pm flattened, from compressed-trigonous to plano-convex, yellowish, brownish, reddish, or purplish brown, \pm veinless, with a short, straight, usually truncate to emarginate beak dark purplish brown to purplish black; inflorescence dark brownish, reddish to purplish brown or blackish; female glumes dark brown, dark reddish or purplish brown to dark blackish brown or blackish, \pm with the same color in the middle as the body, rarely light-brown to yellowish brown ... **43**
- 42.** Terminal spike conspicuously clavate (male part $\frac{1}{3}$ – $\frac{2}{3}$ of the length), strongly contrasting in shape from the cylindrical lateral spikes; female glumes acuminate, with a subulate tip 0.5–1.5 mm long;

- utricles adpressed-ascendent at maturity, cuneate at apex and \pm gradually attenuated into the beak (see also 47) ... 32. *C. peiktusani* (in part)
- Terminal spike elliptical to broadly elliptical (male part often $< \frac{1}{3}$ of the length), usually not strongly contrasting in shape from the lateral spikes; female glumes acute to acuminate, with a subulate tip up to 0.5(1) mm long; utricles spreading or slightly ascendent at maturity, \pm rounded at apex and thus abruptly contracted into the beak (see also 49) ... 13. *C. hancockiana* (in part)
43. (41) Inflorescence blackish brown to blackish, rarely dark brown; female glumes acute to acuminate, blackish or dark blackish brown, sometimes dark purplish brown; mature utricles yellowish to ferruginous-yellowish, rarely yellowish brown, densely purplish punctate above, at base more or less broadly cuneate and attenuating into a short stipe; nutlet obovate to elliptic-obovate; culms smooth above (see also 40, 45, 64, 94) ... 5. *C. atrata* (in part)
- Inflorescence dark reddish or purplish brown to dark brown; female glumes acuminate, dark reddish to purplish brown or dark brown; mature utricles yellowish brown, brownish to reddish or purplish brown, without or with irregular purplish spots, \pm rounded at base and constricted into a short stipe or stipeless; nutlet elliptic to elliptic-obovate; culms smooth or scabrous above (see also 40, 45, 64, 94) ... 18. *C. japonalpina* (in part)
44. (36) Mature utricles flattened, from compressed-trigonous to plano-convex ... 45
- Mature utricles not flattened, \pm trigonous or narrowly biconvex, sometimes \pm inflated ... 46
45. Inflorescence blackish brown to blackish, rarely dark brown; female glumes acute to acuminate, blackish or dark blackish brown, sometimes dark purplish brown; mature utricles yellowish to ferruginous-yellowish, rarely yellowish brown, densely purplish punctate above, at base more or less broadly cuneate and attenuating into a short stipe; nutlet obovate to elliptic-obovate; culms smooth above (see also 40, 43, 64, 94) ... 5. *C. atrata* (in part)
- Inflorescence dark reddish or purplish brown to dark brown; female glumes acuminate, dark reddish to purplish brown or dark brown; mature utricles yellowish brown, brownish to reddish or purplish brown, without or with irregular purplish spots, \pm rounded at base and constricted into a short stipe or stipeless; nutlet elliptic to elliptic-obovate; culms smooth or scabrous above (see also 40, 43, 64, 94) ... 18. *C. japonalpina* (in part)
46. (44) Utricles elliptic, narrowly elliptic or elliptic-lanceolate ... 47
- Utricles obovate-elliptic, obovate, or oblanceolate ... 49
47. Terminal spike conspicuously clavate (male part $\frac{1}{3}$ - $\frac{2}{3}$ of the length), strongly contrasting in shape from the cylindrical lateral spikes; utricle beak yellowish green, the orifice deeply bidentate, with teeth > 0.1 mm long (see also 42) ... 32. *C. peiktusani* (in part)
- Terminal spike oblong-lanceolate or broadly elliptical (male part often $< \frac{1}{3}$ of the length), not strongly contrasting in shape from the lateral spikes; utricle beak dark purplish-red, the orifice truncate or emarginated and then the teeth < 0.1 mm long ... 48
48. Mature utricles yellowish to golden-yellowish, sometimes brownish, often dark purplish punctate above, obovate-elliptic to oblong-elliptic, \pm rounded at apex, abruptly constricted at apex into a short beak 0.1–0.2(0.3) mm long, sometimes nearly beakless; nutlet obovate to obovate-elliptic (see also 13, 73, 83, 91) ... 10a. *C. duthiei* subsp. *duthiei* (in part)

- Mature utricles entirely yellowish-green or yellowish, elliptic-lanceolate to obovate-elliptic, \pm cuneate at apex, gradually attenuated or slightly constricted into a short beak 0.2–0.3(0.4) mm long; nutlet elliptic to elliptic-obovate (see also **13, 83, 91**) ... 10b. *C. duthiei* **subsp. longistolonifera** (Kük.) S.Gebauer & Jim.Mejías, comb. nov. (in part)
- 49. (46)** Utricles 2.5–3(3.5) mm long, oblanceolate to narrowly obovate-elliptic, yellowish green or grayish green, spreading or slightly ascendent at maturity, faintly nerved to nerveless, beak (0.2)0.3–0.5 mm long, often \pm somewhat bent, the orifice deeply bidentate, rarely emarginate; plant base reddish purplish (see also **42**) ... 13. *C. hancockiana* (in part)
- Utricles (1.8)2–2.5(3) mm long, broadly obovate to broadly obovate-elliptic, yellowish-green, becoming golden-brown or orange-brown, spreading at maturity, conspicuously nerved, with raised veins, beak < 0.2 mm long, straight, orifice shallowly emarginate to truncate; plant base dark purplish brown ... 22. *C. lehmannii*
- 50. (34)** Female glumes with a scabrous long (0.5)1–3 mm long arista at apex, or long-acuminate with a scabrous-papillose subulate tip \pm 1–1.5 mm long, the glume body 4–6(6.5) mm long; plants with rhizomes short or only slightly elongated ... **51**
- Female glumes without a scabrous long arista at apex or with a mucro < 0.5(1) mm long, if subulate tip longer and \pm scabrous, then the glume body usually < 4.5 mm long (see also **89!**); if > 4.5 mm long, then the glumes oblong-ovate with apex acute or obtuse, and plants with thickened, long-creeping rhizomes (in *C. melananthiformis*, **20, 23, 54**, *C. sabulosa*, **19, 54**) ... **52**
- 51.** Female glumes with body 4–5 mm long and a scabrous long arista \pm (0.5)1–3 mm long, the midrib conspicuously lighter colored; utricles veined, entirely yellowish green, turning pale brown to brown at maturity, the beak shallowly emarginate, with a broad obtuse sinus between teeth; nutlet compressed-trigonus (see also **16, 28**) ... 11. *C. gmelinii* (in part)
- Female glumes with body (4)4.5–6(6.5) mm long, long-acuminate, with a subulate often scabrous-papillose tip 1–1.5 mm long, midrib inconspicuous; utricles veinless, yellowish green at base, dark purplish above, sometimes almost entirely dark purplish at maturity, rarely entirely stramineous, the beak truncate or very shallowly emarginate; nutlet trigonus (see also **14, 88**) ... 7. *C. bijiangensis* (in part)
- 52. (50)** All spikes sessile or subsessile, \pm erect, very densely approximated, forming a contiguous, \pm capitate inflorescence, rarely the lowermost spike conspicuously pedunculated, but then it is \pm erect too ... **53**
- At least the lowermost spike conspicuously pedunculated, from pendent to \pm spreading, rarely erect, forming a \pm loosely disposed racemose inflorescence ... **78**
- 53.** Female glumes (3.8)4–6 mm long, (if 3.8–4 mm long, then the glumes > $\frac{1}{3}$ longer than the mature utricles; in *C. melananthiformis*, **20, 23, 54!**), the apex acute or obtuse, usually at least several of them with an \pm conspicuous broad white-hyaline tip; plants with thickened, long-creeping rhizomes ... **54**
- Female glumes < 4.5 mm long (if close to 4.5 mm long, then the glumes only slightly to < $\frac{1}{3}$ longer than the mature utricles, and the apex usually acuminate), without or only a few with a narrow white-hyaline tip; plants without thickened rhizomes, rhizomes short or only slightly elongated ... **55**

- 54.** Utricles 4–5(6) mm long, yellowish or yellowish-green, elliptic to oblong-obovate, with a beak (0.5)0.7–1.2 mm long, orifice distinctly bidentate; leaves slightly convolute, ± flexuous (see also **19**)... **38. *C. sabulosa*** (in part)
- Utricles 2–3(3.3) mm long, yellowish green, dark purplish or purplish black in the uppermost part below the utricle beak, broadly obovate, broadly elliptic or suborbicular, with a short beak (0.1)0.2–0.3(0.5) mm long, orifice truncate, rarely emarginate or short-bidentate; leaves flat, ± straight or somewhat curved, but not flexuous (see also **20, 23**) ... **25. *C. melananthiformis*** (in part)
- 55. (53)** At least some utricles prickly to densely hispidulous on the upper margins, pale greenish, yellowish or golden-yellowish, rarely brownish (see also **30, 35**) ... **29. *C. obscura*** (in part)
- Utricles smooth or slightly and sparsely scabrous above, variously colored, if conspicuously scabrous then utricles ± dark purplish or purplish black at least above or entirely dark olive brown to brown ... **56**
- 56.** Utricles elliptic to rhomboid-elliptic, yellowish-green, conspicuously veined, ± cuneate at apex and attenuated or scarcely constricted into a rather long beak (0.5)0.7–1.2(2) mm long, ± bent, with the orifice bidentate (see also **27, 29, 80**) ... **37. *C. psychrophila*** (in part)
- Utricles elliptic, obovate, oblanceolate, or suborbicular, veined or veinless, usually rounded at apex and ± abruptly constricted into a rather short beak, often < 0.5 mm long, straight, with the orifice truncate or emarginate, rarely shallowly bidentate ... **57**
- 57.** Mature utricles ± conspicuously flattened, from compressed-trigonous to plano-convex or strongly flattened; stems rather stout ... **58**
- Mature utricles not flattened, ± trigonous or biconvex, sometimes ± inflated, if utricles ± flattened, then the section is conspicuously biconvex; stems slender or stout ... **69**
- 58.** Utricles dark purplish black or nearly blackish above, margined with conspicuous upper paler edges, ovate or obovate, rounded at the top thus abruptly contracted into a beak 0.1–0.3(0.5) mm long, the upper margins often ± scabrid or with very elevated papillae on the edges (see also **33**) ... **31. *C. parviflora*** (in part)
- Utricles ± uniformly colored, if purplish, reddish or blackish above, then the edges are not distinctly paler or they are very narrowly and inconspicuously so, oblong, elliptical, ovate or obovate, rounded or cuneate at the top, thus abruptly or gradually contracted into a beak 0.2–0.7(1) mm long, the upper margins smooth or scabrid ... **59**
- 59.** Utricles ± rounded at the top, thus abruptly contracted into the beak, with the margins smooth, rarely scabrous ... **60**
- Utricles ± cuneate at the top, thus gradually attenuated into the beak, with the margins scabrous, rarely smooth ... **68**
- 60.** Mature utricles yellowish, ferruginous-yellowish, greenish ferruginous, yellowish brown, brownish, golden-brownish to reddish or purplish brown, often ± purplish punctate above, usually strongly contrasting by color from the darker female glumes; female glumes oblong-ovate, rarely ovate, apex acute to acuminate, slightly shorter to longer than utricles, rarely much shorter ... **61**
- Utricles only greenish to yellowish or brown at base, becoming almost dark purplish reddish or entirely blackish in all its upper half at maturity, thus usually not contrasting or slightly contrasting

- by color from the female glumes; female glumes ovate or broadly ovate, rarely oblong-ovate, apex acute or obtuse, usually much shorter than the utricles, rarely slightly shorter than them ... **65**
- 61.** Mature utricles broad elliptic to suborbicular, \pm strongly flattened, greenish ferruginous, yellowish, yellowish brown or golden-brownish, only dark brown to blackish at the beak; female glumes acuminate; plants of Central & SW Asia ... **62**
- Mature utricles elliptic to obovate-elliptic or ovate, \pm compressed-trigonous to plano-convex, yellowish, ferruginous-yellowish, brownish to reddish- or purplish-brown, often purplish punctate above; female glumes acute to acuminate; plants of N Europe, European Arctic, W Siberia (Subpolar Urals), W, Central, E & SE European mountains, NW Turkey, and E Asia (E China: Jilin, Japan, Korea, Russian Far East: S Ussuri region), and Taiwan ... **63**
- 62.** Leaves (1)2–3(4) mm wide; inflorescence rather dark, almost blackish or blackish brown; terminal spike usually gynaeandrous, sometimes entirely male; utricles (2.5)3–3.5(4.5) mm long, the beak 0.2–0.3(0.4) mm long (see also **33, 87**) ... 34a. *C. popovii* subsp. *popovii* (in part)
- Leaves (1.5)3–4(5) mm wide; inflorescence paler, \pm brownish; terminal spike always gynaeandrous; utricles (2.8)3–3.5(4) mm long, the beak (0.2)0.3–0.5 mm long; plants endemic to Iran (Elburz Mountains; see also **87**) ... 34b. *C. popovii* subsp. *brunneola* (in part)
- 63. (61)** Utricle beak (0.6)0.7–1 mm long, orifice emarginate to shallowly bidentate; female glumes slightly shorter than utricles, 2.7–3(3.5) mm long, ovate to oblong-ovate, apex acute to shortly acuminate; plants endemic to mountains of Taiwan (see also **86**) ... 2. *C. apodostachya* (in part)
- Utricle beak 0.3–0.5(0.6) mm long, orifice truncate to emarginate; female glumes longer than utricles, rarely slightly shorter, 3–4(4.5) mm long, oblong-ovate to narrowly oblong-ovate, apex acute to acuminate ... **64**
- 64.** Inflorescence blackish brown to blackish, rarely dark brown; female glumes acute to acuminate, blackish or dark blackish brown, sometimes dark purplish brown; mature utricles yellowish to ferruginous-yellowish, rarely yellowish brown, densely purplish punctate above, at base more or less broadly cuneate and attenuating into a short stipe; nutlet obovate to elliptic-obovate; culms smooth above (see also **40, 43, 45, 94**) ... 5. *C. atrata* (in part)
- Inflorescence dark reddish or purplish brown to dark brown; female glumes acuminate, dark reddish to purplish brown or dark brown; mature utricles yellowish brown, brownish to reddish or purplish brown, without or with irregular purplish spots, \pm rounded at base and constricted into a short stipe or stipeless; nutlet elliptic to elliptic-obovate; culms smooth or scabrous above (see also **40, 43, 45, 94**) ... 18. *C. japonalpina* (in part)
- 65. (60)** Mature utricles at least of the lower spikes \pm clearly horizontally patent or spread downwards, narrowly elliptic, oblong-elliptic or elliptic to obovate-elliptic, its maximum width near the middle, greenish to yellowish at base, dark purplish reddish or purplish blackish above or densely purplish spotted at maturity (rarely almost blackish in *C. melanocephala*, **24, 66, 68, 71**), (2.7)3–4(4.5) \times 1–1.9 mm, smooth to scabrous above (including beak); utricule beak 0.4–0.7 mm long ... **66**
- Mature utricles not spreading, \pm adpressed, broad ovate or broad obovate, its maximum width near the top or the base, entirely purplish black to blackish at maturity, (3.5)4–5(5.6) \times 1.7–2.5 mm, usually smooth above or only the beak sometimes slightly scabrous; utricule beak 0.2–0.4(0.8) mm long ... **67**

- 66.** Utricles (3)3.5–4(4.5) × 1–1.3(1.5) mm; utricle beak scabrous, rarely smooth; female glumes dark purplish black or blackish, ovate to oblong, apex acute; plants densely cespitose, rhizomes short (see also **24, 68, 71**) ... 26. *C. melanocephala* (in part)
- Utricles (2.7)3–3.7 × 1.2–1.9 mm; utricle beak smooth or scabrous; female glumes dark reddish brown, broadly ovate, apex acute or rounded; plants rather loosely cespitose, the rhizomes slightly spreading (see also **24, 68, 71**) ... 30. *C. oligantha* (in part)
- 67. (65)** Inflorescence (2.5)3.5–5 cm long; lowest spike with peduncle (0.5)1–3 cm long; stems rather stout, sharply trigonous, strongly scabrous above (see also **93**) ... 4a. *C. aterrima* subsp. *aterrima* (in part)
- Inflorescence (0.8)1.5–3.5 cm long; lowest spike with peduncle (0.2)0.5–1.5 cm long; stems less strong, trigonous, smooth or slightly scabrous above (see also **93**) ... 4b. *C. aterrima* subsp. *medwedewii* (in part)
- 68. (59)** Utricles (3)3.5–4(4.5) × 1–1.3(1.5) mm, oblong-elliptic or narrowly elliptic, rarely obovate-elliptic; plants densely cespitose, rhizomes short (see also **24, 66, 71**) ... 26. *C. melanocephala* (in part)
- Utricles (2.7)3–3.7 × 1.2–1.9 mm, elliptic or obovate-elliptic; plants rather loosely cespitose, the rhizomes slightly spreading (see also **24, 66, 71**) ... 30. *C. oligantha* (in part)
- 69. (57)** Utricles conspicuously dark purplish, dark purplish reddish, purplish blackish or nearly blackish above, veinless or obscurely veined; beak scabrous, rarely smooth, 0.3–0.8 mm long; stems rather stout, ± erect ... **70**
- Utricles entirely yellowish to whitish or greenish olivaceous to golden or olive brown, sometimes purplish punctate above, veined or veinless; beak smooth or scabrous, 0.1–0.8 mm long, rarely nearly beakless; stems rather slender, often somewhat curved ... **72**
- 70.** Utricles 1.8–2.5 × 0.5–0.8(1) mm, veinless, beak rather scabrous, 0.2–0.6 mm long; female glumes equaling or slightly longer than utricles, lanceolate, apex acuminate; culms 4–18(20) cm; dwarf plants of high elevations (4300–5200 m); plants endemic to E Nepal (Ramthang Valley, Kanchenjunga), N Sikkim (Dongkya range), Chumbi Valley (S Tibet, W Bhutan) ... 20. *C. kangchengyaoensis* S.Gebauer, Jim.Mejías & Noltie, nom. et stat. nov.
- Utricles (2.7)3–4.5 × 1–2 mm, veinless or obscurely veined, beak scabrous or smooth, 0.4–0.8 mm long; female glumes shorter than utricles, ovate, apex acute or rounded; culms 10–40 cm ... **71**
- 71.** Utricles (3)3.5–4(4.5) × 1–1.3 mm, oblong-elliptic or narrowly elliptic, cuneate at the apex thus gradually contracted into the beak, rarely obovate-elliptic and then ± rounded at apex and abruptly contracted into the beak; beak scabrous, rarely smooth; female glumes ovate to oblong, apex acute; plants densely cespitose, rhizomes short (see also **24, 66, 68**) ... 26. *C. melanocephala* (in part)
- Utricles (2.7)3–3.7 × 1.2–1.9 mm, elliptic or obovate-elliptic, rounded to cuneate at the apex thus gradually or abruptly contracted into the beak; beak smooth or scabrous; female glumes broadly ovate, apex acute or rounded; plants rather loosely cespitose, the rhizomes slightly spreading (see also **24, 66, 68**) ... 30. *C. oligantha* (in part)
- 72. (69)** Utricles nearly beakless or very short-beaked, the beak when present 0.1–0.2 mm long ± mammillate to short-cylindric; plants from the Himalayas ... **73**
- Utricles distinctly beaked, the beak > 0.2 mm long, ± cylindric ... **74**

73. Utricles $1.8\text{--}2.5 \times (0.8)0.9\text{--}1.1$ mm, obovate, golden-yellowish to golden-brownish, \pm beakless, the beak when present mammillate, $0.1(0.2)$ mm long, the orifice, horizontally truncate; female glumes ovate, apex acute or obtuse, slightly to much shorter than mature utricles; plants \pm loosely tufted, rhizomes slightly spreading; lower leaf sheaths \pm yellowish brown to brownish, \pm dull ... 36.
C. pseudobicolor
- Utricles $(2)2.2\text{--}3 \times (1)1.1\text{--}1.4$ mm, obovate-elliptic to obovate, yellowish or golden-yellowish, sometimes brownish, often dark purplish punctate above, usually with a short cylindric beak, $0.1\text{--}0.2$ mm long, rarely nearly beakless, the orifice \pm horizontally truncate or emarginate; female glumes \pm lanceolate, acuminate, usually slightly longer than the mature utricles, rarely slightly shorter; plants \pm densely tufted with rhizome short; lower leaf sheaths \pm dark brownish or reddish to purplish black, \pm shining (see also 13, 48, 83, 91) ... 10a. *C. duthiei* subsp. *duthiei* (in part; dwarf form from high elevations)
74. (72) Utricle sides usually with several veins conspicuously raised, the raised veins almost reaching the beak, rarely \pm obscurely veined; utricles narrowly elliptic or obovate-elliptic, $(2.7)3\text{--}3.5 \times 1\text{--}1.2$ mm, yellowish green, becoming yellowish and often bronze at base; lowest spike with a short peduncle > 0.5 cm long, rarely shorter or spike sessile (see also 80) ... 39. *C. serreana* (in part)
- Utricles veinless or if sides veined, veins usually not raised and not reaching the utricule top, rarely 1–few veins raised part of their length at utricule base; utricule shape and color diverse, $1.8\text{--}3.7 \times 0.9\text{--}1.5$ mm; lowest spike sessile or with a short peduncle < 0.5 cm long ... 75
75. Utricles sparsely scabrous above, the beak conspicuously and densely prickly, dull, usually veinless (rarely with a few faint veins at base); plants densely cespitose; female glumes about $\frac{3}{4}$ as long as the utricles, rarely slightly shorter or only $\frac{1}{2}$ as long as the utricles (see also 39) ... 28. *C. norvegica* (in part)
- Utricles smooth, the beak smooth or sparsely prickly, dull or somewhat glossy, veined to veinless, if beak densely prickly then utricule \pm veined; plants densely to loosely cespitose; female glumes from about $\frac{1}{2}$ as long as the utricles to equaling or slightly surpassing them ... 76
76. Utricles narrowly biconvex, both the adaxial and abaxial sides convex, conspicuously veined, narrowly elliptic to obovate-conical, at maturity yellowish or sometimes pale brownish at base; plants densely cespitose, rhizomes short ... 17. *C. infuscata*
- Utricles \pm trigonous, often \pm inflated towards the apex, veinless or veined, ovate, oblong-ovate to obovate-elliptic or rhombic, at maturity becoming yellowish or brownish greenish to golden-yellowish or olive brown, sometimes purplish punctate; plants loosely cespitose, rhizomes slightly elongated ... 77
77. Utricles rhombic-elliptic to obovate-elliptic, $2\text{--}2.5(3) \times 1.2\text{--}1.5$ mm, greenish to yellowish, becoming olive brown, often purplish punctate, \pm dull (see also 85) ... 12. *C. gracilentia* (in part)
- Utricles ovate to oblong-ovate or obovate-elliptic, $(2.2)2.5\text{--}3.5 \times 1\text{--}1.5$ mm, pale green or whitish, becoming yellowish or brownish greenish to golden-yellowish, usually \pm shiny (see also 39) ... 23. *C. media* (in part)
78. (52) Utricles with conspicuously raised veins ... 79
- Utricles nerveless or faintly nerved, with veins not raised ... 84

- 79.** Proximal spike with a peduncle 0.5–1.2(4.5) cm long, ± erect to somewhat spreading; utricule beak 0.3–1.2(2) mm long, orifice bidentate, rarely emarginate ... **80**
- Proximal spike with a peduncle (0.5)1.5–5(14) cm long, ± spreading to conspicuously pendulous, rarely ± erect; utricule beak 0.1–0.4(0.6) mm long, sometimes nearly beakless, truncate or short-emarginated ... **81**
- 80.** Utricles narrowly-elliptic or obovate-elliptic, (2.7)3–3.5 × 1–1.2 mm, yellowish green, becoming yellowish and often bronze at base, ± papillose above; utricule beak 0.3–0.4(0.5) mm long, straight; stems slender (see also **74**) ... 39. *C. serreana* (in part)
- Utricles rhomboid-elliptic, (2.5)3–4(5) × (0.8)1–1.5 mm, yellowish green, ± smooth or somewhat papillose above; utricule beak (0.5)0.7–1.2(2) mm long, often ± bent; stems slender or stout (see also **27, 29, 56**) ... 37. *C. psychrophila* (in part)
- 81.** (79) Female glumes often acute, sometimes short-acuminate, at least some of them with narrow white-hyaline margins, rarely without hyaline margins; utricles compressed-trigonous to plano-convex, sometimes slightly narrowly biconvex; leaves as long as or shorter than culms (always > 2/3 of the stem length); peduncle of proximal spike usually clearly > 2 cm long, very rarely shorter; plants of easternmost Europe, SW & Central Asia (including Caucasus region), W Siberia, and Taiwan ... **82**
- Female glumes long-acuminate, without white-hyaline margins; utricles narrowly biconvex; leaves shorter than culms, rarely as long as culms; peduncle of proximal spike usually < 2 cm long, sometimes up to 4.5 cm, and very rarely longer (up to 14 cm); plants of the Himalayas (including the Karakoram), mountains of S & Central China ... **83**
- 82.** Leaf blades 4–8 mm wide; female glumes reddish brown to purplish black; utricles 3.5–4 mm long, yellowish greenish to golden-yellowish, often irregularly purplish or ferruginous tinged, abaxial side faintly (2)3–5-veined, the veins not reaching the middle length of the utricule, the beak 0.3–0.4(0.6) mm long; nutlets obovate to obovate-elliptic, (1.8)2.1–2.5 mm long (see also **8, 28**) ... 9. *C. caucasica* (in part)
- Leaf blades 3–5 mm wide; female glumes purplish black to almost blackish; utricles 3–3.5(3.8) mm long, yellowish greenish at base, almost entirely dark purplish to purplish black tinged above, abaxial side conspicuously 5–9-veined, the veins reaching the upper half of the utricule, the beak 0.1–0.3 mm long; nutlets elliptic, 1.9–2.1 mm long; plants endemic to Taiwan ... 19. *C. jisaburo-ohwiana*
- 83.** (81) Mature utricles yellowish to golden-yellowish, sometimes brownish, often dark purplish punctate above, obovate-elliptic to oblong-elliptic, ± rounded at apex, abruptly constricted at apex into a short beak 0.1–0.2(0.3) mm long, sometimes nearly beakless; nutlet obovate to obovate-elliptic (see also **13, 48, 73, 91**) ... 10a. *C. duthiei* subsp. *duthiei* (in part)
- Mature utricles entirely yellowish green or yellowish, elliptic-lanceolate to obovate-elliptic, ± cuneate at apex, gradually attenuated or slightly constricted into a short beak 0.2–0.3(0.4) mm long; nutlet elliptic to elliptic-obovate (see also **13, 48, 91**) ... 10b. *C. duthiei* subsp. *longistolonifera* (Kük.) S.Gebauer & Jim.Mejías, comb. nov. (in part)
- 84.** (78) Female glumes 2–3(3.5) mm long; female spikes usually 4–15(20) mm long, very rarely up to 25 mm long... **85**

- Female glumes (3)3.5–6(6.5) mm long; female spikes usually (15)20–35 mm long, very rarely only 10 mm long ... **88**
- 85.** Mature utricles rhombic-elliptic to obovate-elliptic, inflated-trigonous towards the apex, 2–2.5(3) mm long; plants of Central and E Himalayas, W & SW Sichuan, NW Yunnan, S & SE Tibet (see also **77**) ... 12. *C. gracilentata* (in part)
- Mature utricles ± flattened, from compressed-trigonous to plano-convex or ± strongly flattened, ovate, elliptic or broad elliptic to suborbicular, (2.5)3–3.5(4.5) mm long; plants of Central & SW Asia, and Taiwan ... **86**
- 86.** Mature utricles ovate to elliptic, (3)3.5–4 mm long, with a beak (0.6)0.7–1 mm long; plants endemic to Taiwan (see also **63**) ... 2. *C. apodostachya* (in part)
- Mature utricles broad elliptic to suborbicular, (2.5)3–3.5(4.5) mm long, with a beak 0.2–0.5 mm long; plants of Central & SW Asia ... **87**
- 87.** Leaves (1)2–3(4) mm wide; inflorescence rather dark, almost blackish or blackish brown; utricles (2.5)3–3.5(4.5) mm long, beak 0.2–0.3 mm long (see also **33**, **62**) ... 34a. *C. popovii* subsp. *popovii* (in part)
- Leaves (1.5)3–4(5) mm wide; inflorescence paler, ± brownish; utricles (2.8)3–3.5(4) mm long, beak (0.2)0.3–0.5 mm long; plants endemic to Elburz Mountains (Iran (see also **62**)) ... 34b. *C. popovii* subsp. *brunneola* (in part)
- 88. (84)** Female glumes (4)4.5–6(6.5) mm long, long acuminate into a subulate, often papillose-scabrous tip 1–1.5 mm long (see also **14**, **51**) ... 7. *C. bijiangensis* (in part)
- Female glumes (3)3.5–4.5(5) mm long, acute, if acuminate then the subulate tip usually < 1 mm long, very rarely longer ... **89**
- 89.** Utricles broad elliptic to suborbicular, compressed-trigonous, usually stramineous, sometimes brownish or purplish punctate above, the beak horizontally truncate; female glumes 4–4.5(5) mm long; some lateral spikes usually with several male flowers at base which can be easily overlooked (see also **14**) ... 21. *C. kansuensis* (in part)
- Utricles narrowly oblong, obovate-elliptic, or ovate, from ± flattened and compressed-trigonous or plano-convex to narrowly biconvex, yellowish green, ferruginous-yellowish, golden-yellowish, brownish, dark brown or purplish black, often conspicuously dark brown to purplish above, rarely entirely yellowish, the beak obliquely or horizontally truncate or emarginate; female glumes (3)3.5–4(4.8) mm long; lateral spikes usually entirely female (if with several male flowers at base then utricles ± narrowly biconvex) ... **90**
- 90.** Mature utricles not flattened, ± narrowly biconvex, with a short beak, 0.1–0.3(0.4) mm long, sometimes nearly beakless (if apex acuminate, not forming a distinct beak, then orifice obliquely truncate); female glumes lanceolate, long-acuminate ... **91**
- Mature utricles ± flattened, from compressed-trigonous to plano-convex, with a beak 0.2–0.8 mm long; female glumes ovate to oblong-ovate, acute to acuminate ... **92**
- 91.** Mature utricles yellowish to golden-yellowish, sometimes brownish, often dark purplish punctate above, obovate-elliptic to oblong-elliptic, ± rounded at apex, abruptly constricted at apex into a short beak 0.1–0.2(0.3) mm long, sometimes nearly beakless; nutlet obovate to obovate-elliptic (see also **13**, **48**, **73**, **83**) ... 10a. *C. duthiei* subsp. *duthiei* (in part)

- Mature utricles entirely yellowish green or yellowish, elliptic-lanceolate to obovate-elliptic, \pm cuneate at apex, gradually attenuated or slightly constricted into a short beak 0.2–0.3(0.4) mm long; nutlet elliptic to elliptic-obovate (see also **13, 48, 83**) ... 10b. *C. duthiei* subsp. *longistolonifera* (Kük.) S.Gebauer & Jim.Mejías, comb. nov. (in part)
- 92. (90)** Utricles (3.5)4–5(5.6) mm long, purplish black to blackish above, often almost entirely purplish black, rarely dark brownish (occasionally yellowish in plants from S Siberia and Russian Far East); female glumes ovate, sometimes \pm oblong-ovate, apex acute, usually shorter than mature utricles, not differing by color from them ... **93**
- Utricles 3–3.8(4) mm long, ferruginous-yellowish, sometimes brownish to purplish, dark purplish or purplish above, rarely entirely yellowish; female glumes oblong-ovate to narrowly oblong-ovate, apex acute to acuminate, usually longer than mature utricles, rarely slightly shorter, usually somewhat contrasting by color from them ... **94**
- 93.** Inflorescence (2.5)3.5–5 cm long; lowest spike with peduncle (0.5)1–3 cm long; stems rather stout, sharply trigonous, strongly scabrous above (see also **67**) ... 4a. *C. aterrima* subsp. *aterrima*
- Inflorescence (0.8)1.5–3.5 cm long; lowest spike with peduncle (0.2)0.5–1.5 cm long; stems less strong, trigonous, smooth or slightly scabrous above (see also **67**) ... 4b. *C. aterrima* subsp. *medwedewii* (in part)
- 94. (92)** Inflorescence blackish brown to blackish, rarely dark brown; female glumes acute to acuminate, blackish or dark blackish brown, sometimes dark purplish brown; mature utricles yellowish to ferruginous-yellowish, rarely yellowish brown, densely purplish punctate above, at base more or less broad cuneate and attenuating into a short stipe; nutlet obovate to elliptic-obovate; culms smooth above (see also **40, 43, 45, 64**) ... 5. *C. atrata* (in part)
- Inflorescence dark reddish- or purplish brown to dark brown; female glumes acuminate, dark reddish to purplish brown or dark brown; mature utricles yellowish brown, brownish to reddish or purplish brown, without or with irregular purplish spots, \pm rounded at base and constricted into a short stipe or stipeless; nutlet elliptic to elliptic-obovate; culms smooth or scabrous above (see also **40, 43, 45, 64**) ... 18. *C. japonalpina* (in part)

Taxonomic synopsis. — The accepted names are presented here in alphabetical order, including the indication of their types and taxonomic notes. Given the large amount of names involved and difficulty in finding type collections for many of them, the nomenclatural account does not intend to be exhaustive. Instead, we present the accepted name for each taxon, and the most common synonyms, including those used in the accounts of Egorova (1999) and Flora of China (Liang & Koyama 2010a, b). We provide ecological and chorological notes based on published data as well as our own observations based on fieldwork experience and the study of herbarium material.

Carex sect. ***Racemosae*** G.Don in J.C.Loudon, Hort. Brit. [ed. 2]: 376 (1830).

Lectotype: Carex atrata L., designated by Reznicek (2001: 455).

≡ *Carex* sect. *Atratae* Fr. ex Pax in A.Engler & K.Prantl, Nat. Pflanzenfam. 2(2): 125 (1888).

≡ *Carex* [unranked] *Atratae* Kunth, Enum. Pl. 2: 431 (1837), *nom. nud.*

≡ *Carex* [unranked] *Atratae* Heuff., Magyar Orv. Termész. Nagy Gyül. Munk. 4: 116 (1844) et Flora 27(31): 531 (1844).

≡ *Carex* ***Cyrtostomae* ε *Atratae* Fr. [unranked], Summa Veg. Scand. 1: 71 (1845), *nom. nud.*

≡ *Carex* sect. *Atratae* Fr. ex H.Christ, Bull. Soc. Roy. Bot. Belgique 24(2): 15 (1885), *nom. nud.*

Type: *Carex atrata* L. (ICN, Art. 10.8).

≡ *Carex* sect. *Loxaniza* (Raf.) V.I.Krecz. in V.L.Komarov, Fl. URSS 3: 246 (1935).

≡ *Loxaniza* Raf., Good Book.: 25 (1840). (Basionym).

Lectotype: Carex atrata L., designated by Mackenzie (1931: 9).

≡ *Carex* sect. *Microrhynchae* (Drejer) L.H.Bailey, Proc. Amer. Acad. Arts. Sci. 22: 76 (1886), *pro parte.*

Lectotype: Carex atrata L., designated by Egorova (1999: 373).

Note: There is some ambiguity regarding the correct citation of *C.* sect. *Atratae*, its authors, description and validity. The name ‘*Atratae*’ was first introduced by Kunth (1837), without a morphological description and valid diagnosis of its rank. Later, Heuffel (1844a, b) used this name for the same taxa providing a morphological description, but without referring to Kunth (1837) and lacking a valid diagnosis of its taxonomic rank. The same applies to the name published by Fries (1845). At sectional rank, the name ‘*Atratae*’ was introduced by Christ (1885), only with reference to Fries (1845). However, Christ neither provided a valid description nor referred to Heuffel (1844a, b). Thus, the citations as section *Atratae* (Heuff.) H.Christ, *Atratae* (Heuff.) Fr. ex H.Christ, or *Atratae* Fr. ex H.Christ are incorrect, and partly based on inadequate nomenclatural interpretations (e.g., Chater 1980; Kukkonen 1998; Reznicek 2001; Murray 2002a; Gebauer et al. 2015; Więclaw et al. 2016). These names are *nomina nuda* (*nom. nud.*; ICN, Art. 38.1), except for Heuffel’s unranked name (see above). The sectional name has been validated by Pax

(1888), who has provided a German diagnosis with reference to Fries (see above), as *C. sect. Atratae* Fr. ex Pax (see also Malyshev 1990; Egorova 1999).

1. *Carex adelostoma* V.I.Krecz., in V.L.Komarov (ed.), Fl. URSS 3: 603 (1935).

(Figs. 1: C, S1: A, S4: A).

Holotype: RUSSIA. MURMANSK OBLAST: Kola Peninsula, Aleksandrovsk, Tyva-guba, on the banks of the river, 23 Jun 1921, *M. I. Naearov* 7762 (LE 01039494, digital image!).

= *Carex buxbaumii* Wahlenb. subsp. *alpina* (Hartm.) Liro, Ann. Acad. Sci. Fenn., Ser. A, IV, Biologica 42: 523 (1938).

≡ *Carex buxbaumii* Wahlenb. var. *alpina* Hartm., Kongl. Vetensk. Acad. Handl. 1818: 160 (1818).

Lectotype (designated here): NORWAY. NORD-TRØNDELAG: In subalpinis jugi Norv. prope Snaasen Norv., [1813], *C. J. Hartman*, s.n. (UPS-V 896293, digital image!).

Note: No type of *C. buxbaumii* var. *alpina* has been indicated by Hartman (1820). The specimen selected here as the lectotype has already been suggested by Cajander (1935: 85, 89) as an authentic specimen (see also Isoviita 1977).

= *Carex morrisseyi* A.E.Porsild, Sargentia 4: 21 (1943).

Holotype: CANADA. NEWFOUNDLAND & LABRADOR: Labrador, Cutthroat Harbor, south of Cape Mugford, 57° 30' N., 62° W., low granite Island, wet, marshy places, 26 Aug 1937, *A. E. Porsild* 173 (CAN 24357, digital image!; *isotypes*: C 10010071, digital image!; S-G 9523, digital image!; US 00087239, digital image!).

= *Carex buxbaumii* Wahlenb. subsp. *mutica* (Hartm.) Isoviita, Ann. Bot. Fenn. 14: 208 (1977).

≡ *Carex buxbaumii* Wahlenb. var. *mutica* Hartm., Handb. Skand. Fl. [ed. 1]: 40 (1820).

Lectotype (designated here): NORWAY. NORDLAND: Norska Nordland vid Sörfoldbotten, 22 Jul 1807, *G. Wahlenberg*, s.n. (UPS-V 156433 [specimen on the left], digital image!).

Note: No type of *C. buxbaumii* var. *mutica* has been indicated by Hartman (1820). The specimen selected here as the lectotype has already been suggested by Cajander (1935: 85, 89) as an authentic specimen (see also Isoviita 1977).

Habitat: Moist to wet minerotrophic to mesotrophic places, often on alkaline, sandy to gravelly soils, in meadows, marshes, swamps, riverbanks, streams, lakes shores and tideland, shrub tundra, and along forest edges and thickets; from subarctic tundra at higher latitudes, to forest or grasslands in mountains at its southernmost locations; 0–500(1350) m

(Kreczetovicz 1935b; Egorova 1966; Löve 1970; Egorova 1976a; Chater 1980; Kozhevnikov 1988; Malyshev 1990; Kukkonen et al. 1998; Egorova 1999; Elven et al. 2005).

Distribution: Circumpolar; scattered from N Europe (Fennoscandia, Kola Peninsula, Karelia), throughout Siberia to the Russian Far East (Okhotsk Sea), southwards to the mountains of S Norway, N of Altai (Kurkuli), Lena-Kolyma region, and Lake Baikal (Egorova 1966; Chater 1980; Hultén & Fries 1986; Kozhevnikov 1988; Malyshev 1990; Egorova 1999; Elven et al. 2005; 2011); also occurring in subarctic North America (Murray 2002a).

Chromosome count (2n): 106 (Roalson 2008 and references therein; Rotreklová et al. 2011; Lipnerová et al. 2013), c.106 (Cayouette 1997: Canada).

2. *Carex apodostachya* Ohwi, Jap. J. Bot. 7: 188 (1934).

(Figs. 3: H–M, S1: B, S4: B).

≡ *Carex atrata* L. subsp. *apodostachya* (Ohwi) T.Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 8(4): 149 (1962).

Holotype: TAIWAN. TAICHUNG: Formosa in Mt. Nanko-taisan, Jul 1933, *J. Ohwi* 4182 (KYO 00022137, digital image!; *isotypes*: F 1464064, digital image!, K 000961019!);

Paratypes: Formosa in Mt. Nanko-taisan, Jul 1933, *J. Ohwi* 4053 (KYO 00022138, digital image!; NY! [not databased]), Formosa in Mt. Nanko-taisan, Jul 1933, *N. Fukuyama* 4054 (KYO 00022139, digital image!; NY! [not databased]).

Habitat: Dry to moist or seasonally wet places, in mountain grasslands and scrublands, and also in the margins of upper *Abies* mountain forest at the tree line; 3000–3800 m (Ohwi 1936; Koyama 1978b; Liang 2000; Koyama et al. 2000; Liang & Koyama 2010a; Liao 2014).

Distribution: E Asian—Taiwanese endemic; only known from the mountain ranges of Taiwan, where it is mainly found in the Zhongyang Range (Liang 2000; Koyama et al. 2000; Liao 2014).

Chromosome count (2n): Unknown.

Notes: *Carex apodostachya* was originally described as a distinct species endemic from Taiwan by Ohwi (1934). However, its independence has been largely ignored by subsequent authors who have considered this species as a subspecies of *C. atrata* (Koyama 1962, 1978b; Liang 2000) or simply placed it as a mere synonymy of *C. atrata* (Koyama et

al. 2000; Liang & Koyama 2010a). This unfortunate assimilation led to the merge of *C. apodostachya* together with *C. jisaburo-ohwiana* under the synonymy of a very broadly conceived *C. atrata* in the latest comprehensive study on Taiwanese sedges (Liao 2014). It is possibly because of the study of an insufficient number of specimens of these rare and poorly known taxa. Recent molecular data also support the independent character of *C. apodostachya* (SG et al., unpubl. data). The species is a Taiwanese endemic known only from a few herbarium collections (Koyama et al. 2000; Liao 2014; SG & PJM, pers. obs.). It has been recently discovered at three additional locations in the Chilai Mountains (C.-K. Liao, pers. comm.) suggesting that it has might have been overlooked in other Taiwanese mountain areas.

Carex apodostachya is easily distinguished from the superficially similar *C. atrata* and *C. japonalpina* by its longer beaks and shorter female glumes, which are usually much shorter than the mature perigynia, apart from the other characters mentioned in the key.

3. *Carex aristulifera* P.C.Li, Acta Bot. Yunnan. 12: 141 (1990).

(Figs. S1: C, S4: C).

Holotype: CHINA. YUNNAN: Gongshan Xian, Mons Gaoligongshan, Doshaofang, ad rupes in fructibus prati alpini, alt. 3500 m, 24 Jul 1982, *Exped. Qinghai–Xizang 8539* (PE 00030575, digital image!; *isotype*: PE 00030576, digital image!).

Habitat: Poorly known; based on the literature and the few collections seen, it seems a species of dry to moist loamy or sandy, often rocky soils over granite or marble, on subalpine to alpine grasslands and scrublands, often along streams; 3200–3500(3980) m (Liang 2000; Dai et al. 2003; Liang & Koyama 2010a).

Distribution: S Central Chinese endemic; only known from the S Hengduan Mountains (Gongshan, Gaoligongshan) in NW Yunnan (Liang 2000; Dai et al. 2003; Liang & Koyama 2010a).

Chromosome count (2n): Unknown.

Notes: Some materials previously affiliated to this species have been confused with taxa of *C. sect. Praelongae* (Kük.) Nelmes (e.g., *C. gologongshanensis* P.C.Li: A [HUH-GH] 00269359!, A [HUH-GH] 00269389!; SG, pers. obs.).

4. *Carex aterrima* Hoppe, Caric. Germ.: 53 (1826) et Denkschr. Königl.-Baier. Bot. Ges. Regensburg 1(1): 159–167, tab. 3, fig. o, p, q (sin. nom. spec.) (1815).

≡ *Carex atrata* L. subsp. *aterrima* (Hoppe) Hartm., Sv. Norsk Exc.-Fl.: 131 (1846).

≡ *Carex atrata* L. var. *aterrima* (Hoppe) Boott, Ill. Carex 3: 114 (1862).

Lectotype (designated by Egorova 1999: 396): [icon in] Hoppe, Denkschr. Königl.-Baier. Bot. Ges. Regensburg 1(1): tab. 3, fig. o, p, q (1815).

Distribution: European–Siberian; widely distributed in mountains of Central and E Europe, and throughout temperate and boreal Asia (Siberia), the Caucasian region, and some mountain ranges of Central Asia (see below).

4a. *Carex aterrima* subsp. *aterrima*

(Figs. S1: D, S4: D).

= *Carex perfusca* V.I.Krecz. in V.L.Komarov (ed.), Fl. URSS 3: 600 (1935).

Holotype: RUSSIA. ALTAI KRAI: Sibiria, prov. Tomsk, distr. Zmeinogorsk, in partibus superioribus fluminum Czernovaja et Birjuska, in Tundra alpina, 04 Aug 1910, M. P. Fomin 355 (LE 01006944, digital image!; *isotype*: LE 01006945, digital image!).

Habitat: Moist to wet places on nutrient-rich, humose loam and clay soils, in grasslands, thickets in open forests, and margins of water bodies, often along springs and streams; from about sea level at its northernmost limit in arctic Siberia up to subalpine and alpine environments at more southern locations (3200(3450) m in Central Asia (e.g., Tian Shan); (800)1200–2300(2500) m in European Mountains (Kreczetovicz 1935b; Popova 1950; Polyakov 1958; Egorova 1966, 1967, 1976a, b, c; Chater 1980; Schultze-Motel 1980; Kozhevnikov 1988; Malyshev 1990; Grubov 2001; Nyambayar 2009; Krasnoborov 2012; Kaplan et al. 2018).

Distribution: European-Siberian; mountains of Central and E Europe (Alps, Carpathians, and Sudetes), widely distributed throughout Siberia, southwards to Tian Shan, NW China (Xinjiang), Altai-Sayan and Transbaikal regions, and Mongolia, and eastwards to the Russian Far East (Chater 1980; Kozhevnikov 1988; Malyshev 1990; Egorova 1999; Nyambayar 2009; Liang & Koyama 2010a; Koopman 2011; Kaplan et al. 2018), bordering the Arctic in N Siberia at the lower reaches of Yenisei River (Egorova 1966; Malyshev 1990; Elven et al. 2011). Reports from the eastern Pyrenees seem to be erroneous, although further confirmation would be desirable (Luceño 2008; M. Luceño, pers. comm.).

Chromosome count (2n): 52 (Rotreklová et al. 2011; Lipnerová et al. 2013: Siberia), 54 (Hadač & Hašková 1956; Kochjarová 1992; Májovský et al. 2000: E Europe), c.54 (Krogulevicz 1971: Siberia). Some reports of 2n = 48–52 (Sokolovskaya and Strelkova

1948a) ascribed to *C. atrata* (see also Roalson 2008), but from outside its accepted range (Siberia, Altai), most probably refer to *C. aterrima* subsp. *aterrima*.

Notes: Problematic specimens with light-colored utricles from eastern Siberia and the Russian Far East might constitute introgressive forms with *C. japonalpina*. Confusion with *C. atrata* is also frequent in herbaria (see comments under that species). Intermediate specimens that are morphologically transitional to *C. atrata* are sometimes found in the overlapping ranges of both species (e.g., Carpathians, Sudetes), which may also represent introgressive forms (Egorova 1999; Kaplan et al. 2018; SG, pers. obs.). Rarely sterile plants have been reported from the Sudetes (Krkonosé, Hrubý Jeseník Mts.), which may represent true hybrids of *C. aterrima* subsp. *aterrima* and *C. atrata* (Kaplan et al. 2018).

4b. *Carex aterrima* subsp. *medwedewii* (Leskov) T.V.Egorova, *Novosti Sist. Vyssh. Rast.* 22: 54 (1985).

(Figs. S1: E, S4: E).

≡ *Carex medwedewii* Leskov, *Zhurn. Russk. Bot. Obshch.* 16(1): 70 (1931).

Holotype: RUSSIA. ADYGEJA: Caucasus occidentalis, distr. Maikop, ad fontes fl. Belaja, in prato subalpino ad mont. Abago, 16 Aug 1929, A. I. Leskov, s.n. (LE 01042919, digital image!).

= *Carex aequivoca* V.I.Krecz. in V.L.Komarov (ed.), *Fl. URSS* 3: 600 (1935).

Lectotype (designated by Egorova 1999: 398): GEORGIA. MTSKHETA-MTIANETI: Prov. Tiflis, distr. Gori (Cartalinia), in declivio occid. mont. Tskhra-Tskharo, 01–02 Jul 1916, P. N. Krylov & E. I. Steinberg, s.n. (LE 01042921, digital image!; *isolectotype*: LE 01042920, digital image!); *Syntypes*: Transcaucasica, Cartalinia, in prato alpino montis Tskhra-Tskharo, 12 Jun 1907, E. Bordzilowski, s.n. (LE 01042922, digital image!; LE 01042923, digital image!; E 00353983, photo!).

= *Carex kukkonenii* Ö.Nilsson in P.H.Davis (ed.), *Fl. Turkey* 9: 622 (1985).

Holotype: TURKEY. HAKKÂRI: Cilo Dağ [Buzul Dağı], 10 km W. of Cilo Tepe, 3140 m, 09 Aug 1954, P. H. Davis & O. Polunin, *D.* 24141 (E 00021628!).

Habitat: Dry to moist or wet places on gravelly slopes, rock ledges and moraines, in mountain grasslands and scrublands, as well as along the tree line, even reaching subnival regions; 2000–3400 m (Kreczetovicz 1935b; Grossgejm 1940; Galushko 1978; Hooper 1985; Nilsson 1985; Kukkonen 1998; Chandjian 2001; SG, pers. obs.).

Distribution: Mainly Caucasian; widely distributed in the Greater and Lesser Caucasus (SW Russia, Georgia, Azerbaijan), the Armenian highlands, and the adjacent mountains of NE Turkey (Anatolia), extending further south to the Zagros Mountains in SE Turkey, N Iraq, and NW Iran, with isolated occurrences in the Anatolian Taurus Mountains in the West (Hooper 1985; Nilsson 1985; Kukkonen 1998; Egorova 1999; Chandjian 2001; Egorova 2006; Amini Rad 2011).

Chromosome count (2n): 32 (Gvinianidze & Avazneli 1982; Chandjian 2001), 46 (Kharadze et al. 1973, 1977; Egorova 1999).

Notes: This taxon is often treated as a separate species endemic from the Caucasus (as *C. medwedewii*; Grossgejm 1940; Galushko 1978; Chandjian 2001). However, the close relationship to *C. aterrima* has been already demonstrated by molecular-phylogenetic studies (Gebauer et al. 2015; Massatti et al. 2016; SG, unpubl. data), as previously proposed by Egorova (1985, 1999).

Carex aterrima subsp. *medwedewii* has been a rather problematic taxon. It seems extremely morphologically variable in comparison to *C. aterrima* subsp. *aterrima*, which is rather uniform throughout its much wider range (see Gebauer et al. 2015; Więclaw et al. 2016). It has resulted in the description of additional taxa for morphological variants of *C. aterrima* subsp. *medwedewii* (viz., *C. aequivoca*, *C. kukkonenii*) of no taxonomic value (Egorova 1985, 1999).

The variability of *C. aterrima* subsp. *medwedewii* has also led to confusion with other species. Specimens that display densely approximate, capitate inflorescences have been confused with *C. oligantha* (see Gebauer et al. 2015; see also below). For example, most specimens of *C. atrata* s.l. cited in the treatment for Flora of Turkey (Nilsson 1985) have been here re-classified as *C. aterrima* ssp. *medwedewii* (SG, pers. obs.; for records from NW Turkey: NW Anatolia see comments under *C. atrata*) as already indicated by Egorova (2006). The source of this confusion seems to rely on the variability of the utricles of *C. aterrima* subsp. *medwedewii*, which can range from glossy to dull, bear papillae above or not, but especially, be very rarely ferruginous-yellowish instead of the usually almost purplish black (SG, pers. obs.).

The taxonomic situation of *C. aterrima* subsp. *medwedewii* becomes especially complicated in the Zagros Mountains and adjacent regions (SE Turkey, NW Iran, NE Iraq), where morphologically deviant plants can be found with rather elliptical or narrowly ovate utricles, smaller spikes, and occasionally unispicate inflorescences (M. Amini Rad, pers. comm.; SG, pers. obs.). Those plants are in need of further investigation.

5. *Carex atrata* L., Sp. Pl.: 976 (1753).

(Figs. 3: A–G, S1: F, S4: F).

Ind. loc.: “Habitat in Alpibus Europae”.

Lectotype (designated by Kukkonen 1980: 155): s.loc., s.d., *G. Clifford, s.n.* (Herb. *G. Clifford*) (BM 000647360, digital image!).

Habitat: Dry to moist-wet places, on base-rich to siliceous, gravelly loam or clay soils, in tundra, alpine grasslands and scrublands, or along the tree line in mountains or at taiga regions, often along springs and streams, also on high mountain rocky habitats; from lowland at the northern limit of its distribution (0–2000 m; N Europe, Arctic), to mountains at more southern locations ((950)1500–3100 m; W, Central and E European Mountains) (Kreczetovicz 1935b; Egorova 1966, 1976a, b; Chater 1980; Schultze-Motel 1980; Kristinsson 1987; Kukkonen et al. 1998; Elven et al. 2005; Jermy et al. 2007; Luceño 2008; Kaplan et al. 2018).

Distribution: Amphi-Atlantic (mainly European); an arctic-alpine species mainly distributed from the mountains of W, Central and E Europe (Cantabrian Mountains, Pyrenees, Alps, Carpathians, Sudetes) to N Europe (British Isles, Fennoscandia, Iceland, N European Russia), and NW Siberia (NW Russia, Polar and N Urals) (Egorova 1966; Hultén & Fries 1986; Egorova 1999; Sekretareva 2004; Koopman 2011; Kaplan et al. 2018). Southwards to mountains of Central Greece (S Pindus Mts.: Mt. Vardousia) (Hartvig 1991; Dimopoulos et al. 2013; A. Strid, pers. comm.; SG, pers. obs.). The records from SW Asia located in NW Turkey (NW Anatolia: Mt. Uludağ) constitute the southeasternmost limit of its known distribution (Nilsson 1985; SG, pers. obs.). Disjunct in southern Greenland (Murray 2002a; Elven et al. 2011; SG, pers. obs.).

Chromosome count (2n): 54 (Roalson 2008 and references therein; Rotreklová et al. 2011; Lipnerová et al. 2013). Rare reports of 2n = 52 from E Europe (Druskovic 1982, 1995) may be related to *C. aterrima* subsp. *aterrima*. Reports of 2n = 48–52 (see Sokolovskaya & Strelkova 1948) from Siberia, and 2n = 56 (Tanaka 1948) from Japan, are from outside of its accepted range, and refer to other species (see comments under *C. aterrima* subsp. *aterrima* and *C. japonalpina*). The low numbers ranging from 2n = 18 to 2n = 26 from Slovakia (Hadač & Hašková 1956) seems erroneously and may belong to other species.

Notes: The taxonomy and biogeography of the type species of *Carex sect. Racemosae* have been controversially discussed, and it is still in need of a deeper critical revision (e.g., Kukkonen 1998; Gebauer et al. 2015). Due to the complicate taxonomy of the section,

C. atrata has been regarded as a widespread arctic-alpine species with circumboreal distribution (see Meusel et al. 1965; Hultén & Fries 1986). This confusion is partly due to the fact that the name *C. atrata* has been widely used to refer to different members of *C. sect. Racemosae* in early works, especially relatively large taxa with pendent spikes. This confusion is not rare in *Carex*, as other names have also been applied to generally refer to allied species (e.g., *C. cespitosa* L.; Jiménez-Mejías et al. 2014b). More comprehensive treatments (Egorova 1966, 1999; Murray 2002a; Elven et al. 2011) suggest that *C. atrata* is largely confined to arctic-alpine environments of Europe (including Iceland and Northern Urals) and southern parts of Greenland (i.e. amphi-Atlantic; see Hultén 1958), as further supported also by ongoing molecular studies (SG et al., unpubl. data). Reports from Southern and Eastern Turkey seem to refer to *C. aterrima* subsp. *medwedewii* (see above). Citations from Sino-Himalayan regions (Noltie 1994; Srivastava 1996; Kress et al. 2003) belong to a number of other species (SG & PJM, pers. obs.; see below). Specimens with rather brownish utricles, which sometimes occur, have been frequently confused with *C. aterrima* subsp. *aterrima* in herbaria (Kaplan et al. 2018; SG, pers. obs.). Such plants can be distinguished from *C. aterrima* subsp. *aterrima* by its short to long-acuminate female glumes, which are usually longer than the utricles, and its shorter utricles (see key). Intermediate specimens as well as putative hybrids of both species were also reported (see comments under *C. aterrima* subsp. *aterrima*).

Several taxa sometimes treated within *C. atrata* (viz., *C. apodostachya*, *C. aterrima*, *C. atrata* var. *glacialis*, *C. duthiei*, *C. japonalpina*) are here treated as separate species as suggested by previous studies or more recent morphological and molecular data (Gebauer et al. 2015; Global *Carex* Group 2016; SG et al., unpubl. data).

6. *Carex atrofusoides* K.T.Fu, Fl. Tsinlingensis 1(1): 446 (1976).

(Figs. S1: G, S4: G).

Holotype: CHINA. SHAANXI: Tai-pai Shan, Pao-ma-liang, alt. 3400 m, marshy ground on high ridge, 08 Aug 1959, *K. T. Fu 8514* (WUK? [not seen!]); *Paratype*: Tai-pai Shan, Hwei-ling-sze, alt. 3400 m, 08 Aug 1959, *K. T. Fu 8514* (WUK? [not seen!]).

Habitat: Moist to wet places in alpine grasslands and scrublands; 3400–4700(4900) m (Dai et al. 2000; Liang & Koyama 2010b; SG, pers. obs.).

Distribution: Central Chinese endemic; *Carex atrofusoides* is restricted to the mountain ranges of Central China (E Tibet, Sichuan, E Qinghai, Shaanxi; ?Gansu) (Dai et al. 2000; Liang & Koyama 2010b).

Chromosome count (2n): Unknown.

Notes: This central Chinese endemic species has been usually placed in *Carex* sect. *Aulocystis* due to its superficial resemblance to *C. atrofusca* Schkuhr, and the relatively long-beaked utricles (Liang & Koyama 2010b). The species can only be distinguished from *C. atrofusca* in the field by the reduced proximal bract that is either shortly bladed or setaceous with a short sheath up to 4 mm long (vs. proximal bract leafy, with 5–30 mm long sheath), and its larger glumes, 5.5–6 mm long, that are apparently spreading from the lower half of the spike (vs. 4–5 mm long and not spreading) (Liang & Koyama 2010b; SG, pers. obs.).

Unexpectedly, recent molecular data have revealed that the species belongs to *C. sect. Racemosae* (SG et al., unpubl. data). Within *C. sect. Aulocystis*, *C. atrofusoides* was the only species whose all spikes are invariably gynaeandrous, a feature that is also observed in certain species of *C. sect. Racemosae* (Li 1990; Liang & Zhang 2006; Liang & Koyama 2010a, b; SG & PJM, pers. obs.). *Carex atrofusoides* is the only Eurasian representative of the *Carex sect. Racemosae*, whose populations also regularly contain unispicate individuals (SG, pers. obs.).

Carex atrofusoides is a clear example of the remarkable morphological convergence that might happen between representatives of non-closely related groups of genus *Carex* (Global *Carex* Group 2016).

7. *Carex bijiangensis* S.Yun Liang & S.R.Zhang, Novon 16: 364 (2006).

(Figs. S1: H, S4: H, S8: A–E).

Holotype: CHINA. YUNNAN: Mt. Biluo Shan, Bijiang, 4000 m, 18 Aug 1934, *H. T. Tsai* 58022 (PE 01862974, digital image!); *Paratypes:* CHINA. YUNNAN: Bijiang, Che-tse-lo, 4000 m, 22 Aug 1934, *H. T. Tsai* 58093 (PE 00030626, digital image!; PE 00030627, digital image!).

Habitat: Moist to wet places on rocky to gravelly soils, in mountain grasslands and scrublands and along the tree line, typically on margins of streams and bogs; 3100–4600(4880) m (Liang & Zhang 2006; Liang & Koyama 2010a).

Distribution: S Central Chinese–E Himalayan; from NW Yunnan, SW Sichuan, and SE Tibet across Bhutan and Sikkim to E Nepal (Liang & Zhang 2006; Liang & Koyama 2010a; SG & PJM, pers. obs.).

Chromosome count (2n): Unknown.

Notes: This species was recently described from NW Yunnan (Liang & Zhang 2006). Examination of herbarium specimens during the course of ongoing molecular studies performed by both authors (Global *Carex* Group 2016; SG et al., unpubl. data) revealed that specimens from the E Himalayas previously treated under *C. atrata* (Noltie 1994; Kress et al. 2003), as well as some specimens identified as *C. duthiei* and *C. kansuensis* from SW Sichuan and SE Tibet, actually represented *C. bijiangensis*. The confusion arose from the too narrow concept of *C. bijiangensis* presented in Flora of China (Liang & Koyama 2010a), whose description was probably based on a small number of specimens. It led to the overweight of certain characters (female glume shape and length) as diagnostic of the species, leaving behind part of the morphological variation of the species (SG & PJM, pers. obs.). As consequence, these materials ended classified as other taxa. The reevaluation of the newly detected material revealed that *C. bijiangensis* has female glumes (4)4.5–6(6.5) mm long, rather long acuminate with a 1–1.5 mm long subulate and often somewhat scabrous tip, instead the suggested 6–6.5 mm glumes with a long scabrous awn (Liang & Zhang 2006; Liang & Koyama 2010a). We also detected that the vast majority of the specimens possess gynaeandrous lateral spikes with a few male flowers at base.

Carex bijiangensis seems to be very closely related to *C. kansuensis*, and the range of both species overlap in SE Tibet and SW Sichuan. Their separation often appears to be difficult, and both species may occasionally hybridize as intermediary specimens suggest (SG, pers. obs.). Whether only subspecific ranks of a single polymorphic species should be regarded for both taxa can only be conclusively clarified by further extensive studies. In our opinion, the further occurrence of *C. bijiangensis* in other neighboring regions of the E Himalayas (i.e. NE India and N Myanmar) seems quite possible.

8. *Carex buxbaumii* Wahlenb., Kongl. Vetensk. Acad. Nya Handl. 24: 163 (1803).

(Figs. 1: A, S3: P, S5: I).

Ind. loc.: “Hab. in paludosis Sveciæ, ex gr. in Stormossan ad Östhammar, & in Lapponia ubique”.

Lectotype (designated by Moberg & Nilsson 1991: 291): SWEDEN. NOT LOCATED. In Sueciae paludosis, s.d., *G. Wahlenberg, s.n.* (UPS-THUNB 21771, digital image!).

Note: The type conflict between Moberg & Nilsson’s (1991) and Egorova’s (1999) typifications regarding *C. buxbaumii* Wahlenb. was recently clarified by Jiménez-Mejías et al. (2018).

= *Carex polygama* Schkuhr, Besch. Riedgräs. 1: 84 (1801), *nom. illeg.*, non J.F.Gmelin, Syst. Nat. ed. 13[bis]: 145 (1791).

Ind. loc.: “[...] aus der Barbyer, als auch [...] Hallischen Flora, [...] aus Seeland [...]”.

Lectotype (designated by Egorova 1999: 389): DENMARK. ZEALAND: In uliginosis Siallandiae, Jul 1799, *M. Vahl, s.n.* (HAL 0103626!).

Note: Egorova’s (1999) typification of material deposited in Halle (HAL 0103626!) was in fact the lectotypification of *C. polygama* Schkuhr (see Jiménez-Mejías et al. 2018). Interestingly, two sheets verified by Schkuhr (1801) as original material of *C. polygama* (Germany, Saxony-Anhalt, Delauer Heide [= Halle (Saale), Dölauer Heide], *leg. Kroker, s.n., [ex Herb. C. Schkuhr]*; HAL 0107553!, HAL 0107556!) revealed to actually represent another species, namely *C. hartmaniorum* A.Cajander (SG, pers. obs.).

= *Carex tarumensis* Franch. [“*tarunensis*”], Bull. Soc. Philom. Paris sér. 8, vii: 87 (1895).

Ind. loc.: “Japon: île d’Yéso, plaine de Kushiro; Tarunai (*Faurie*)”.

Lectotype (designated by Egorova 1999: 389): JAPAN. HOKKAIDO: Tarumai, bord des marais, 18 Jun 1893, *U. J. Faurie 10093* (P 00280539, digital image!; *isolectotypes*: 6724702, digital image!; P 00280540, digital image!; P 00280541, digital image!; P 00280542, digital image!; P 00280543, digital image!; K 000960735, digital image!); *Syntype*: Tarumai, bord des marais, 18 Jun 1893, *U. J. Faurie 10063* (K 000960737, digital image!).

Habitat: Moist to mostly wet or swampy places on moderately nutrient-rich soils, predominantly in open places at forested altitudes, or on wetland edges; from the sea-level at the northern limit of its distribution to colline-montane regions at more southern locations, less often reaching the subalpine belt (0–1500(1750) m) (Cajander 1935; Kreczetovicz 1935b; Grossgejm 1940; Polyakov 1958; Ohwi 1965; Egorova 1966, 1976b; Chater 1980; Schultze-Motel 1980; Kozhevnikov 1988; Kukkonen et al. 1998; Elven et al. 2005; Liang & Koyama 2010a; Hoshino et al. 2011; Elven et al. 2011; Krasnoborov 2012).

Distribution: Circumboreal, from nemoral to N boreal (i.e. boreo-montane; Elven et al. 2011). Very scattered in Eurasia. Its range is more or less continuous from Central Europe north to Fennoscandia. Eastwards its distribution enters Siberia, and loosens up into several disjunct localities in NE Asia, reaching the Russian Far East, NE China (Jilin), Korea, and Japan in the East (Hultén & Fries 1986; Egorova 1999; Elven et al. 2005; Chang et al. 2014; Hoshino et al. 2011; Koopman 2011). Westwards, it reaches the northern slopes of the Pyrenees (Sulmont & Duhamel, 2002). Present in the Arctic in Fennoscandia and NW Russia (Egorova 1966, 1999; Sekretareva 2004; Elven et al. 2011). More widespread in North America, where the species reaches more southern locations on mountains (Murray 2002a). Disjunct in the northern Andes in South America (Colombia-Venezuela; Jiménez-Mejías et al. 2018).

Chromosome count (2n): 100 (Egorova 1999; Rotreklová et al. 2011; Lipnerová et al. 2013: Central Europe), c.100 (Löve and Löve 1961: N Europe), 105±1 (Engelskjon & Knaben 1971), 106 (Löve & Löve 1981; Cayouette 1997; both reports from Canada). Reports of 2n = 74 (cf. Heilborn 1924; Egorova 1999) from Sweden (Jämtland) seem doubtful.

Notes: The name *C. tarumensis* has sometimes been applied to *C. buxbaumii* populations from East Asia in some of the major works in *Carex* taxonomy (Egorova 1999; Liang & Koyama 2010a). However, the presumably distinguishing features between *C. tarumensis* and *C. buxbaumii*, such as the venation of the utricles, shape of the utricle beak, and lateral spike length, largely overlap, and specimens that might be determinable as *C. tarumensis* are not rare in other parts of the range of *C. buxbaumii* (SG & PJM, pers. obs.). This seems to have been a case of regional overemphasizing of putative taxonomic differences (see Global *Carex* Group, 2016). The alleged differences between *C. tarumensis* and *C. buxbaumii* get diluted when the whole circumboreal range of *C. buxbaumii* is taken into account (SG & PJM, pers. obs.). Accordingly, and as previous authors already suggested (see also Ohwi 1965; Hoshino et al. 2011), *C. tarumensis* is here considered a synonym of *C. buxbaumii*.

9. *Carex caucasica* Steven, Mémoires de la Société Impériale des Naturalistes de Moscou 4: 68 (1813).

(Figs. S1: i, S5: J).

≡ *Carex atrata* L. var. *caucasica* (Steven) Boott, Ill. Carex 3: 114 (1862).

≡ *Carex atrata* L. subsp. *caucasica* (Steven) Kük., Pflanzenr. (Engler) IV. 20(Heft 38): 400 (1909).

Ind. loc.: “In alpe Schahdagh, specimen in Ossetia iberica circa Tschala ab Gueldenstaedio lectum [...], 1810, *Steven*”.

Lectotype (designated by Egorova 1985: 47): AZERBAIJAN. QUBA-XAÇMAZ: Juchari-basch, Jun 1810, *C. Steven*, s.n. (H 1301663, digital image!).

= *Carex pseudoatrata* Meinsh., Trudy Imp. S.-Peterburgsk. Bot. Sada 18: 346 (1901).

Ind. loc.: “In den kaukasischen Provinzen [...] Tindal, monte Bogos 5000’–7000’ (*von Ruprecht ex pl.*) [...]; im Ural, Jurma (*Lessing*); Turkestan, in den Bergen am Aryslyn (*A. Regel*)”.

Lectotype (**designated here**): RUSSIA. DAGESTAN: Caucas. orient., Tindal [Tindi], montes Bogos, in reg. silvat. m. Antschabala, 10–1300 hex., Jul 1861, *F. J. I. Ruprecht*, s.n. (LE 01042936, digital image! [E 00326525, photo!]; *isolectotype*: LE 01042937, digital

image!); *Syntypes*: CHINA. XINJIANG: Bach Nilki am Kasch 7000', 08 Jun 1879, *E. A. von Regel*, *s.n.* (K 000960579!, K 000960580!).

Note: The description of *C. pseudoatrata* comprised three different collections without indication of a type. Therefore, one of the sheets corresponding to the first mentioned collection (LE 01042936!) is chosen as the lectotype.

= *Carex urbis-malorum* Popov, *Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. n.s.* 44: 131 (1935).

Ind. loc.: "Hab. ad. riv. Almatinka minor prope urb. Alma-ata. Ad fonts riv. Batareika et Kazaktschy, 10, 28 Jul 1933 (*Rubtsov*)".

Lectotype (designated by Egorova 1999: 393): KAZAKHSTAN. ALMATY: Zailiysky Alatau [E Tian Shan, Ile-Alatau], on the river Batareyki [Batareika], 10 Jul 1933, *N. I. Rubtsov*, *s.n.* (AA! [not seen!] according to Egorova 1999).

= *Carex karacolica* Polozhij, *Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kuybysheva* 79–80: 11 (1956).

Holotype: RUSSIA. ALTAI REPUBLIC: Altai, Karakol lake, wetlands, 17 Jul 1947, *A. V. Polozhij*, *s.n.* (TK! [not seen!] according to Egorova 1999); *Paratype*: RUSSIA. ALTAI REPUBLIC: Altai, the mouth of the Karakol river, waterlogged, 13 Jul 1947, *A. V. Kuminova & G. P. Pavlova*, *s.n.* (TK! [not seen!] according to Egorova 1999).

Habitat: Moist to mostly wet or swampy meadows and pastures, on humose to loamy or gravelly soils, from open montane forest to mountain grasslands, less often on rocky places; (1500)1800–2700(3000) m (Kreczetovicz 1935b, c; Grossgejm 1940; Popova 1950; Polyakov 1958; Egorova 1967, 1976a, b, c; Galushko 1978; Chater 1980; Nilsson 1985; Malyshev 1990; Liang & Koyama 2010a; SG, pers. obs.).

Distribution: E European–W Siberian–Caucasian–Central-SW Asian; mainly distributed in the Caucasus and adjacent regions in NE Turkey, Armenia and N Iran, with disjunct range parts in E European Russia, W and S Siberia (Volga-Kama and Dvina-Pechora regions, S Urals, Altai), and Central Asia (Dzungarian Alatau, Tian Shan, NW China: Xinjiang) (Chater 1980; Nilsson 1985; Egorova 1999; Liang & Koyama 2010a; Amini Rad 2011).

Chromosome count (2n): 52 (Egorova 1999), 54 (Heilborn 1939; Egorova 1999; Hayirlioğlu-Ayaz et al. 2001).

Notes: There is some confusion between *C. caucasica* and *C. popovii*, as these two taxa co-occur in a vast region of SW and Central Asia. Indeed, the specimen of *C. caucasica* cited and illustrated by Kukkonen (1998) from NE Afghanistan (Panshir valley, above Mukeni,

Hedge & Wendelbo 5266, E 00353981!) – the only record of this species from that region – actually corresponded to *C. popovii* subsp. *popovii*. *Carex caucasica* is often reported to invariably have a long-peduncled and usually pendulous lowermost spike (Kreczetowicz 1935b; Galushko 1978; Egorova 1999, 2006). However, studied collections of *C. caucasica* from Tian Shan (Kazakhstan, NW Tian Shan, Trans-Ili Alatau, *Hilpold & Schönschwetter, s.n.*, BOZ!; Kyrgyzstan, N Central Tian Shan, Terskey Alatau, *Zhiryakov, s.n.*, MW 0811147!) displayed a rather dense inflorescence, with short ellipsoid lateral spikes on short peduncles, 9–20 mm long. Such deviant specimens of *C. caucasica* can be distinguished from *C. popovii* only by the characteristics of the utricles and female glumes, i.e. utricle shape obovate-elliptic to broadly obovate-elliptic (vs. broadly elliptic to suborbicular), utricles compressed-trigonous to narrowly biconvex (vs. strongly flattened), utricles with several short but raised veins in the lower half (vs. veinless), and larger female glumes, usually > 3.5 mm long (vs. usually < 3.5 mm long). Where and how often such deviating specimens occur throughout the range of *C. caucasica* and are being mistaken with *C. popovii* is unknown and requires further investigation, especially in the Tian Shan and Pamiro-Alai regions.

10. *Carex duthiei* C.B. Clarke, in J.D. Hooker, Fl. Brit. India 6: 731 (1894).

Holotype: INDIA. UTTARAKHAND: Brit. Garhwál, above Bhowámi, 13–14,000 ft, 16 Sep 1885, *J. F. Duthie 4499* (K 000998994, digital image!; *isotype*: K 000998995, digital image!).

Distribution: Sino–Himalayan; from the W Himalayas (N Pakistan) east to Sikkim, Bhutan, SE Tibet, and Central China (NW Yunnan, W Sichuan) (Egorova 1967; Noltie 1994; Dickoré 1995; Srivastava 1996; Kukkonen 1998, 2001; Liang 2000; Liang & Koyama 2010a; SG & PJM, pers. obs.). Reports on the occurrence of *C. atrata* in Myanmar (Kachin region; cf. Kress et al. 2003) may refer in part to *C. duthiei*, but should be considered with caution, as four specimens seen from Myanmar (i.e. *Forrest 26989*, NY [not barcoded], two sheets!; US 1378065 [barcode: 00619589], digital image!; *Forrest 26994*, US 1378067 [barcode: 00619590], digital image!) have been confused with species from *C. sect. Aulocystis*, namely *C. haematostoma* Nees and *C. nivalis* Boott (SG, pers. obs.).

Notes: In this treatment we consider two subspecies of *C. duthiei*, the western subspec. *duthiei* and the eastern subspec. *longistolonifera*, comb. nov. Although traditionally treated as separate species (see below), both entities can often not be easily separated from each

other (see key), and intermediate individuals are not rare. Their ranges widely overlap in eastern Tibet, NW Yunnan and SW Sichuan (Liang & Koyama 2010a; SG & PJM, pers. obs.). The first molecular results show very little or no divergence between sequences of the two taxa (SG et al., unpubl. data), suggesting that both should have split rather recently and their divergence is incomplete, and that they might be better treated as subspecies under the prior *C. duthiei*.

The name *C. duthiei* was misapplied to *C. gracilentata* in Flora of China treatment (Liang & Koyama 2010a), whereas *C. duthiei* s.str. was treated under the synonymous name *C. atrata* subsp. *pullata* as has already been clarified in previous works (Noltie 1994; Dickoré 1995; Kukkonen 2001). Recent molecular data (Global *Carex* Group 2016; SG et al., unpubl. data) further suggest that *C. duthiei* is not closely related to *C. atrata*, thus it should not be treated as a subspecies of the latter.

10a. *Carex duthiei* subsp. *duthiei*

(Figs. 1: G–H, 2: A–I, S1: K, S5: K).

= *Carex atrata* L. subsp. *pullata* (Boott) Kük., Pflanzenr. (Engler) IV. 20(Heft 38): 400 (1909).

≡ *Carex atrata* L. var. *pullata* Boott, Ill. Carex 3: 114, tab. 364 (1862).
(Basionym).

Ind. loc.: “from Lachen and Yeumtung, 12–15,000 feet, from *Dr. Hooker*”.

Lectotype (designated here): Boott, Ill. Carex 3: tab. 364.

Note: No specimen that corresponds to *Carex atrata* var. *pullata* Boott could be detected. Therefore, the detailed illustration in Boott (1862: tab. 364) is lectotypified here (ICN, Art. 9.3, 9.4).

= *Carex nigerrima* Nelmes, Bull. Misc. Inform. Kew 1939(4): 200.

Holotype: PAKISTAN. GILGIT-BALTISTAN: India, Kashmir, Barzil [Burzil], 11,300 ft, 28 Jul 1876, *C. B. Clarke* 29722 (K 000496379!).

= *Carex obliquitruncata* Y.C.Tang & S.Yun Liang, Novon 16(3): 364 (2006).

Holotype: CHINA. YUNNAN: Gongshan, grassy slopes, *T. T. Yü* 22740 (PE 00031496, digital image!); **Paratypes:** CHINA. YUNNAN: Che-tse-lo, 4000 m, top of Pi-lo-Shan [Mt. Biluo Shan], 27 Aug 1934, *H. T. Tsai* 28237 (PE 00031498, digital image!); CHINA. YUNNAN: Changputong, Gongshan, 3600–3800 m, 20 Sep 1940, *K. M. Feng* 7863 (PE 01862991, digital image!).

Habitat: Moist to wet rocky to gravelly soils, in montane open forest and mountain grasslands and scrublands; from the upper montane to alpine and subnival belts (2700–

4800(5182) m) (Koyama 1978a; Noltie 1994; Srivastava 1996; Kukkonen 1998, 2001; Liang 2000; Dai et al. 2003; Liang & Koyama 2010a).

Distribution: Sino–Himalayan; from the W Himalayas (N Pakistan) east to Sikkim, Bhutan, SE Tibet, and S Central China (NW Yunnan, SW Sichuan) (Egorova 1967; Koyama 1978a; Noltie 1994; Dickoré 1995; Srivastava 1996; Kukkonen 1998, 2001; Liang 2000; Liang & Koyama 2010a).

Chromosome count (2n): Unknown.

Notes: The western subspecies of *C. duthiei* is extremely variable regarding plant size, arrangement of spikes and their dimensions, as well as size and venation of the utricles (Noltie 1994; SG, pers. obs.). Dwarfed specimens from high elevations of E Nepal and Sikkim have been confused with the sympatrically occurring *C. kangchengyaoensis* (see below). Similar specimens from the Central Himalayas (e.g., Nepal), with almost beakless utricles can also be easily confused with *C. pseudobicolor* (see key).

Deviant plants from Yunnan, resembling *C. duthiei* s.l. were recently described as *C. obliquitruncata* (Liang & Zhang 2006). Two features were reported as exclusive of this species: (1) the obliquely truncate orifice of the utricles, which seemed to be unique among *C. sect. Racemosae*; and (2) the occurrence of a sterile bract (not subtending any spike), that is however a feature that can be occasionally observed in several other species of the section. Contradictorily, the study of a high-resolution image of the holotype revealed that normally shaped utricles (resembling those of *C. duthiei*, with a short beak, 0.1–0.2 mm long, and orifice horizontally truncate), are intermingled with the obliquely truncate ones. Interestingly, similar *C. duthiei* subsp. *duthiei* plants from Central Nepal (*M. A. Farille 81-535*, E 00198994!; *M. F. Watson et al. 146*, E 00576599!), far from the alleged range of *C. obliquitruncata*, are a perfect morphological match of this latter (Fig. 1: G–H). These individuals also have some normally shaped utricles, as described above, but also several strongly deformed utricles, suggesting that the deviant characters might be teratogenetic or due to infection by smut fungi. The holotype of *C. obliquitruncata* was collected in NW Yunnan, where the two subspecies of *C. duthiei* (subspec. *duthiei*, and subspec. *longistolonifera*) overlap (see above). As the specimen is malformed, we cannot completely rule out an affiliation with subsp. *longistolonifera*. In principle, the normally formed utricles of the holotype seems to be a much better match of subsp. *duthiei*, as they are brownish instead yellowish or golden-yellowish, as in typical specimens of subsp. *giraudiasii*. For these reasons we placing *C. obliquitruncata* under synonymy of *C. duthiei* subsp. *duthiei*.

10b. *Carex duthiei* subsp. *longistolonifera* (Kük.) S. Gebauer & Jim. Mejías, comb. nov.
(Figs. 2: J–Q, S1: J, S5: L).

≡ *Carex atrata* L. subsp. *caucasica* (Steven) Kük. var. *longistolonifera* Kük.,
Pflanzenr. IV, 20(38): 400 (1909). (Basionym).

≡ *Carex atrata* L. subsp. *longistolonifera* (Kük.) S. Yun Liang, Fl. Reipubl. Popul.
Sin. 12: 114 (2000).

Ind. loc.: “Ostt Tibet [Eastern Tibet], Tongolo, Olong che, *Soulié n. 2997*”.

Lectotype (designated here): CHINA. SICHUAN: Thibet oriental, [Tagong] Olong che, 09
Aug 1894, *J. A. Soulié n. 2997* (P 00277752, digital image!; *isolectotype*: P 00283483,
digital image!).

Note: Two sheets representing original material were found in Paris, and one of them (P 00277752!) is
chosen as the lectotype.

= *Carex giraudiasii* H. Lév., *Repert. Spec. Nov. Regni Veg.* 12: 288 (1913).

Ind. loc.: “Yun-Nan: Pâturages de Ta-Hai, 3200 m, juill. 1912 (*E. E. Maire*)”.

Lectotype (designated here): CHINA. YUNNAN: Yun-Nan, Pâturages de Ta-Hai, alt. 3200
m, Jul 1912, *E. E. Maire, s.n.* (P 00277786, digital image!; *isolectotypes*: E 00386819!; P
00697826, digital image!); *Syntype*: CHINA. YUNNAN: Graminée des pâturages hauts
plateau de Ta-hai, alt. 3300 m, 13 Jul 1913, *E. E. Maire, s.n.* (E 00881111!).

Note: Three collections representing original material were found. One sheet deposited in Paris (P 0027776!)
is selected as the lectotype.

= *Carex atrata* L. subsp. *pullata* (Boott) Kük. var. *subgracilentata* Kük., *Acta Horti Gothob.*
5: 43 (1930).

Ind. loc.: “Sze-ch’uan bor., Dongrergo, in prato herboso-fruticoso, 4200 m, 9 Aug 1922,
Smith n. 3157 et in prato nivali, 4400 m, 9 Aug 1922, *Smith n. 3454*”.

Lectotype (designated here): CHINA. SICHUAN: Sze-ch’uan, reg. bor., Dongrergo
[Songpan], in prato herboso-fruticoso, 4200 m, 9 Aug 1922, *Smith n. 3157* (UPS-V
044014, digital image!); *Syntype*: CHINA. SICHUAN: Sze-ch’uan, reg. bor., Dongrergo
[Songpan], in prato nivali, 4400 m, 9 Aug 1922, *Smith n. 3454*, UPS-V 044015, digital
image!).

Note: Kükenthal (1930) listed two collections without selection of a type. Thus, the first mentioned one
(UPS-V 044014!) is selected as the lectotype.

= *Carex schneideri* Nelmes, *Bull. Misc. Inform. Kew* 1939(4): 201 (1939).

Holotype: CHINA. YUNNAN: Yunnan, near Lichiang, in alpine meadows of the snow
mountains, c. 3800 m, 06 Aug 1914, *C. Schneider 2138* (K 000960994, digital image!;

isotype: A [HUH-GH] 00027540, digital image!); *Paratypes*: CHINA. SICHUAN: Szechwan, Sungpan Hsien, in thickets, 08 Aug 1928, W. P. Fang 4053 (E 00881141, digital image!; PE 00031528, digital image!, PE 00031530, digital image!; US 1509651 [barcode: 02143868], digital image!); CHINA. SICHUAN: North Szechwan, Dongrergo [Songpan], in an alpine meadow, 4300–4700 m, 20 Jul 1922, H. Smith 3818 (UPS-V 044013, digital image!).

Habitat: Moist to wet gravelly or rocky soils, in open forests and mountain grasslands and scrublands; from the upper montane to alpine and subnival belts; (2225)2900–4480(4875) m (Liang 2000; Dai et al. 2003; Liang & Koyama 2010a; SG, pers. obs.).

Distribution: Central Chinese; from E Tibet (Xizang) east to Yunnan, Sichuan, NE Qinghai, and S Gansu (Liang 2000; Liang & Koyama 2010a; SG, pers. obs.). However, we saw no collections from E Tibet (Xizang). The reports of *C. duthiei* from Qinghai cited by Egorova (1967) were incorrectly localized and actually originated from Gansu and representing several different species; only one of these collections from the Min Shan range in S Gansu (*R. C. Ching* 989, A Chüan [Archuen], T'ao Chou Hsien, US 1245986 [barcode: 02143864]!) can be treated under the eastern subspec. *longistolonifera*. As newly revealed by our revisions, the northernmost limit of its known distribution is located in NE Qinghai (E Qilian Mountains: Datong Shan, Daban Shan; SG, pers. obs.).

Chromosome count (2n): Unknown.

Notes: The eastern *C. duthiei* subsp. *longistolonifera* was treated in Flora of China (Liang & Koyama 2010a) as *C. schneideri*. The latter was originally described by Nelmes (1939) from southern China (Yunnan, Sichuan), and later cited from Xizang (Tibet; Liang & Koyama 2010a). Our revisions revealed that it is identical with the type specimen of *C. atrata* subsp. *longistolonifera* (see below), and with *C. giraudiasii* – a largely neglected name – also described from Yunnan.

The type specimen of *C. duthiei* subsp. *longistolonifera* was treated in the Flora of China treatment (Liang & Koyama 2010a) as *C. atrata* subsp. *longistolonifera*, reported as endemic to W Sichuan (Tongolo [Dong'eluo, Tagong], Olong che). Its original description as *C. atrata* subsp. *caucasica* var. *longistolonifera*, was mainly motivated by the presence of an alleged prolonged long-creeping stoloniferous rhizome (see Kükenthal 1909).

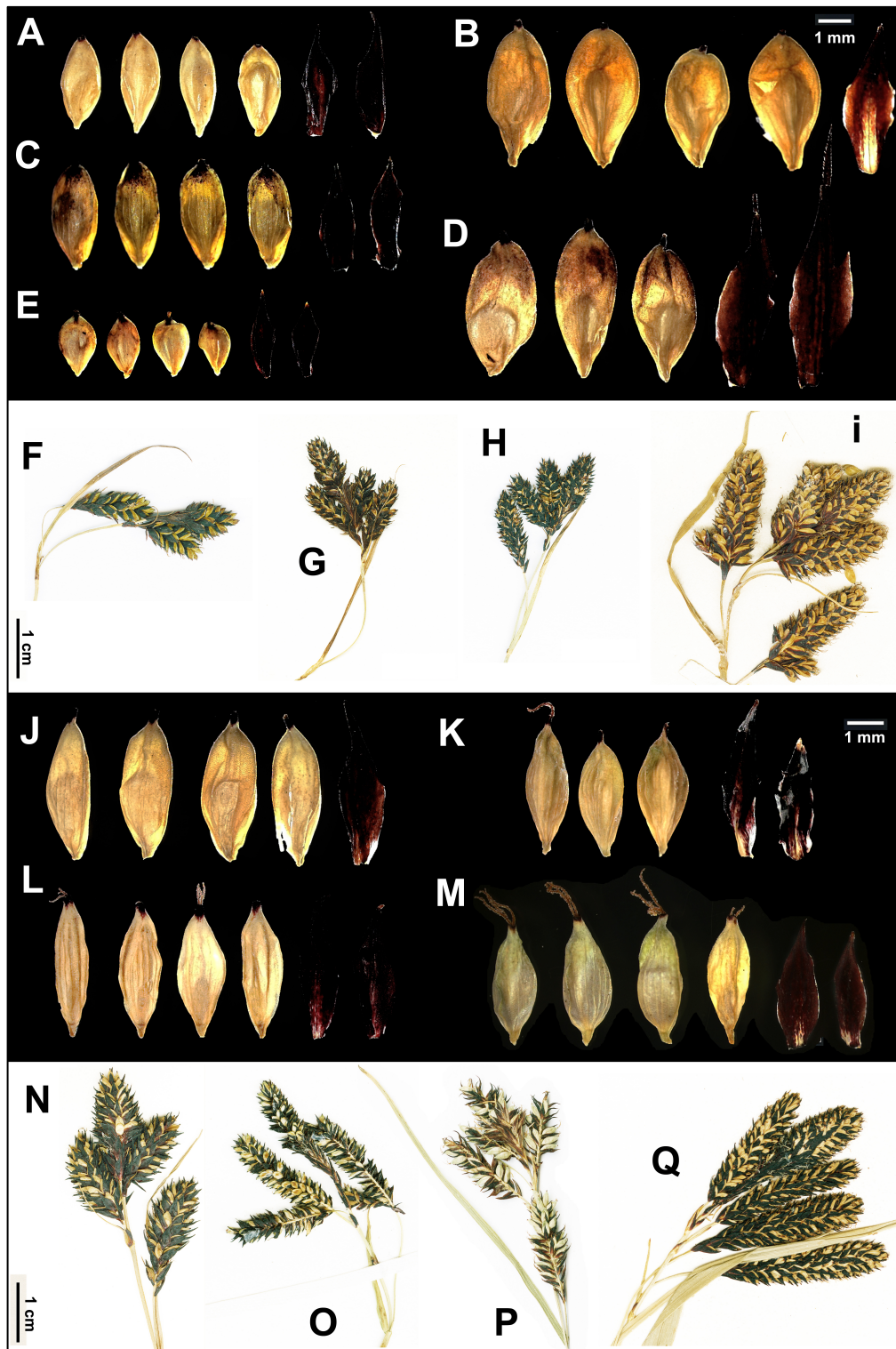


FIG. 2: A–Q, Detailed images of *Carex duthiei* subsp. *duthiei* and *Carex duthiei* subsp. *longistolonifera* (Kük.) S. Gebauer & Jim. Mejías, comb. nov. A–I, *C. duthiei* subsp. *duthiei*: A–E: utricles and female glumes, scale bar = 1 mm; F–i: inflorescences, scale bar = 1 cm; J–Q, *C. duthiei* subsp. *longistolonifera*: J–M: utricles and female glumes, scale bar = 1 mm; N–Q: inflorescences, scale bar = 1 cm; A: Rock 5245 (E!); B, i: Clarke 29722 (K, Type! of *C. nigerrima*); C, F: Miehe et al. 04-134-05 (MR!); D: Rock 11987 (E!); E, H: Miehe et al. 00-265-22 (MR!); G: Long et al. 335 (E!); J, N: Maire, s.n. (E, Type! of *C. giraudiasii*); K: Chung & Li 24-1 (MOR!); L, Q: Rock 16562 (E!); M, P: Miehe et al. 94-433-17 (MR!); O: Boufford et al. 34025 (A!).

However, the examination of the high-resolution image of the type collection (*J. A. Soulié* 2997, P 00277752!) showed that the rhizome does not appear to be as much elongated as indicated in the original diagnosis, and that this feature was obviously overemphasized by Kükenthal (1909). This name seems to have persisted in the taxonomic literature, without a critical revision of the type, and subsequent authors recording it (Liang & Koyama 2010a) seem to have simply reproduced Kükenthal's view. In our opinion, the type collection of *C. atrata* subsp. *longistolonifera* is identical to *C. giraudiasii* and *C. schneideri*. A recent morphologically similar collection (*G. Miehe et al.* 94-433-17, Chola Shan, Dege-Garze; MR!) from NW Sichuan, only about 300 km north-west of the type locality of *C. atrata* subsp. *longistolonifera*, supports this assumption as well, since this specimen has been confirmed by molecular data to be identical to other specimens of *C. schneideri* (SG et al., unpubl. data). Kükenthal's *C. atrata* subsp. *caucasica* var. *longistolonifera* represents the first name for the present taxon used at subspecies rank (*C. atrata* subsp. *longistolonifera*) and has, therefore, priority (ICN, Art. 11.2, 11.4, Ex. 16), and we reduce *C. giraudiasii* and *C. schneideri* to synonymy with *C. duthiei* subsp. *longistolonifera*. Studying detailed images of the type collections of *Carex atrata* subsp. *pullata* var. *subgracilentata* described by Kükenthal (1930) from N Sichuan has shown that it is also identical to *C. duthiei* subsp. *longistolonifera*, and we therefore place it under synonymy of the latter.

11. *Carex gmelinii* Hook. & Arn., Bot. Beechey Voy.: 118, tab. 27 (1832).

(Figs. S1: L, S5: M).

Lectotype (designated here): RUSSIA. KAMCHATKA KRAI: Avatshka [Avacha] Bay, Kamchatka, *Beechey, s.n.* (E 00021629, digital image!; *isolectotype*: K 001079025, digital image!); **Lectosyntypes:** U.S.A. ALASKA: Kotzebue Sound, *Beechey, s.n.* (E 00021630, digital image!; K 001079024, digital image!).

Note: Several collections corresponding to *Beechey's* voyage and representing original material of *C. gmelinii* were found in E and K, but only two of them refers to Kamchatka. In the lectotype selected here, 'Avatshka Bay' is additionally mentioned (E 00021629!). On this sheet, a syntype (Alaska, Kotzebue Sound; E 00021630!) is mounted together with the lectotype, as well as another collection of *C. gmelinii* without type status (Canada, Clemenity Harbour, Sea Ohne, *W. F. Tolmie* 79; K 00107923!).

= *Carex acrolepis* Ledeb., Denkschr. Königl.-Baier. Bot. Ges. Regensburg 3: 56 (1841).

Ind. loc.: "*Carex* species seminalibus brevius pedunculatis crassiusculis aristatis marem tenuem contingentibus... *Carex acrolepis* m.!".

Holotype: RUSSIA. KAMCHATKA: *Carex* species seminalibus brevius pedunculatis crassiusculis aristatis marem tenuem contingentibus, Stirp. Sib. 77 pag. 139. Tab. XXX, f. 1. *Gmelin* (LE 01006659, digital image!).

= *Carex laticuspis* Franch., Bull. Soc. Philom. Paris VIII, 7: 38 (1895).

Ind. loc.: “Japon sept.: Yéso, falaises des Barauta (*Faurie*)”.

Lectotype (designated here): JAPAN. HOKKAIDO: Falais des Barauta, 11 Jul 1892, *U. J. Faurie* 8294 (P 00283681, digital image!; *isolectotype*: K 000960726, digital image!).

Note: Both collections listed above represent original material of *C. laticuspis* bearing the handwriting of *A. R. Franchet*, whereby the sheet in Paris (P 00283681!) is chosen as the lectotype. The lectotype has been erroneously databased as ‘*Carex halophila* F.Nyl.’, a non-related taxon from the Kola Peninsula (see Väre 2007).

Habitat: Dry to wet, sandy to gravelly, often saline soils, on open grassy places along coastal sands, less often on cliffs and outcrops; 0–200 m (Kreczetovicz 1935b; Ohwi 1965; Kozhevnikov 1988; Fu 1995; Liang 2000; Takahashi et al. 2006; Liang & Koyama 2010a; Hoshino et al. 2011; SG, pers. obs.).

Distribution: Amphi-Pacific; from NE China (Jilin), N Korea, and Japan eastwards to the Russian Far East (e.g., Chukotka, Kamchatka, Sakhalin and Ussuri region, penetrating punctually into the Arctic), reaching NW North America (Alaska and British Columbia) (Kozhevnikov 1988; Egorova 1999; Murray 2002a; Sekretareva 2004; Liang & Koyama 2010a; Elven et al. 2011; Hoshino et al. 2011; Chang et al. 2014).

Chromosome count (2n): c.50 (Kozhevnikov et al. 1986: Russian Far East), 58 (Zhukova 1965: Chukotka), c.60 (Harling 1945: Kamchatka), >60 (Yurtsev & Zhukova 1978: Chukotka), 62 (Yurtsev & Zhukova 1978: Chukotka), c. 62 (Moore & Calder 1964: Alaska).

Notes: The only taxon of the section regularly associated to subsaline environments.

12. *Carex gracilentia* Boott ex Boeckeler, *Linnaea* 41: 185 (1877).

(Figs. 1: B, S1: M, S5: N).

Ind. loc.: “Sikkim, Lachen, alt. 11–14,000 ft, Herb. *J. D. Hooker*”.

Lectotype (designated here): INDIA. SIKKIM: Lachen, alt. 11–12,000 ft, s.d., *Herb. J. D. Hooker*, s.n. (K 000998969, digital image!); *Lectosyntype*: INDIA. SIKKIM: Lachen, 14,000 ft, s.d., *Herb. J. D. Hooker*, s.n., K 000998970, digital image!).

Note: The sheet in K contains three collections of *C. gracilentia*, with two of them constituting original material of *J. D. Hooker*. The collection K 000998969! is chosen as the lectotype. The name ‘*C. gracilentia*

Boott ex [apud] Strachey' (Cat. Pl. Kumaon: 73. 1854) has been used on different ranks by some authors (e.g., Kükenthal 1909; Koyama 1958; Liang 2000), but lacks a valid description or illustration.

Habitat: Moist to wet soils, rarely on dryer place, in mountain grasslands and along the tree line, often associated to streams and rivers, relatively common on yak-grazed places; from the upper forest belt to alpine regions (2350)2700–3800(4480) m (Noltie 1994; Dickoré 1995; Srivastava 1996; Liang 2000; Liang & Koyama 2010a; B. Dickoré, pers. comm.; SG pers. obs.).

Distribution: Sino-Central & E Himalayan; mainly distributed from the rather moist Central and E Himalayas (NE Nepal, Sikkim, Bhutan) reaching to S Central China (SE Tibet, NW Yunnan, SW and W Sichuan) (Kükenthal 1909; Noltie 1993, 1994; Dickoré 1995; Srivastava 1996; Liang 2000; Liang & Koyama 2010a; SG, pers. obs.).

Chromosome count (2n): 52 (Yano et al. 2010: W Nepal; *C. infuscata* × *gracilentata*?, SG, pers. obs.; see below).

Notes: This species was erroneously synonymized to *C. duthiei* and treated under this name in the Flora of China (Liang & Koyama 2010a).

Carex gracilentata is often a small-sized taxon that might be easily confused with other similar high-altitude dwelling species of the section (e.g., *C. infuscata*, *C. duthiei*). *Carex gracilentata* is substituted at the western limit of its range by the W Himalayan *C. infuscata*, on which are undoubtedly based the reports of *C. gracilentata* from this region (Koyama 1958; Raymond 1965; Stewart 1972). Immature individuals of both species are almost indistinguishable, while mature specimens are usually more easily told apart. The boundaries of the distribution ranges of *C. gracilentata* and *C. infuscata* seem to overlap partially in Nepal are not well known yet (Dickoré 1995; SG, pers. obs.). One collection from W Nepal (*H. Ikeda et al.* 20911125, Bajhang distr., E 00509831!), which could be affiliated with *C. gracilentata*, appears somewhat intermediate between both taxa (SG, pers. obs.), thus occasional hybridization may be suspected within the putative contact area. On the other hand, *C. gracilentata* is ecologically replaced in N Central (NE Qinghai, Gansu) and NE China (Hebei, Shanxi) by the morphologically similar *C. serreana* (Handel-Mazzetti 1936; Liang & Koyama 2010a; SG, pers. obs.).

13. *Carex hancockiana* Maxim., Bull. Soc. Imp. Naturalistes Moscou 54(1): 66 (1879). (Figs. S1: N, S5: O).

Lectotype (designated by Egorova 1985: 50): CHINA. HEBEI: Fl. Pekin., Po-hua-shan, Jun 1877, Dr. [E. V.] Bretschneider, s.n. (LE 01012338, digital image!).

= *Carex montis-wutaii* T.Koyama, Jap. J. Bot. 25: 172 (1956).

Holotype: CHINA. SHANXI: Mt. Wutai-shan, Shanxi, 06 Jul 1942, *M. Takahashi, s.n.* (TI 00010160, digital image!; *isotype*: TI 00010161, digital image!).

= *Carex komaroviana* A.I. Baranov & Skvortsov, Quart. J. Taiwan Mus. 18: 229 (1965).

Holotype: CHINA. NEI MONGOL: ? (? [not seen!] see note below!).

Note: *Carex komaroviana* (type specimen not seen), described from NE China (Nei Mongol), was placed under synonymy of *C. hancockiana* by Kitagawa (1979), which was also accepted by later authors (e.g., Egorova 1999; Chang et al. 2014).

Habitat: Moist to wet places mostly on gravelly to stony or rocky soils, in open places in forests and thickets, and forest steppes, often along rivers and streams; from the forest belt to alpine regions (400–2350(2700) m) (Kreczetovicz 1935b; Egorova 1967; Malyshev 1990; Liang 2000; Grubov 2001; Nyambayar 2009; Liang & Koyama 2010a; Krasnoborov 2012; SG, pers. obs.).

Distribution: S Siberian–E Asian; from the Altai-Sayan (including the Chinese part in N Xinjiang) and Transbaikal regions to Mongolia, N Central (Qinghai, Gansu) and E China (Nei Mongol and Shaanxi to Jilin), and N Korea in the East (Egorova 1999; Nyambayar 2009; Liang & Koyama 2010a; Chang et al. 2014).

Chromosome count (2n): Unknown.

Notes: *Carex montis-wutaii* was described from NE China (Wutai Shan Mts.) by Koyama (1956b). Examination of its description, the detailed illustration, as well as high-resolution images of the type material (Yano et al. 2017) showed a rather loose inflorescence instead of spikes being approximate, as noted by Liang & Koyama (2010a). Only the uppermost spikes were somewhat approximated, with pendulous proximal spikes on long slender peduncles up to 50 mm long. In our opinion, the type specimens fit well into the variation of *C. hancockiana*. The lectotype chosen for *C. hancockiana* (Egorova 1985) was collected near Shanxi, only about 170 km east of the Wutai Shan Mts. Additionally, one collection from NE Qinghai, initially identified as *C. montis-wutaii* using Liang & Koyama's (2010a) key, was also confirmed as *C. hancockiana* by molecular data (SG et al., unpubl. data). A numerical taxonomic study of *C. sect. Racemosae* in China by Zhang et al. (2010) also placed *C. montis-wutaii* close to *C. hancockiana* and *C. peiktusani*, although these authors recognized the species as being distinct. Therefore, we consider *C. montis-wutaii* as a synonym of *C. hancockiana*, whose variation was taken into account in the present key.

The contradictory indications of Liang & Koyama (2010a) regarding inflorescence morphology of *C. montis-wutaii* (rather loose vs. approximated) seem to be due to an unfortunate confusion with specimens of *C. serreana*. Indeed, the type material of *C. serreana* (see under this species) was identified as *C. montis-wutaii* by Koyama himself. The inflorescence of *C. hancockiana* is usually rather lax and racemose, composed of approximated upper spikes, whereas the lateral spikes are well separated and pendulous on 10–50 mm long slender peduncles. In *C. serreana* the entire inflorescence is dense, sometimes capitate, with lateral spikes usually sessile or subsessile. We have confirmed a few deviant specimens of *C. serreana* with rather lax inflorescences (but then with the lowermost spike sessile) or the lowermost spike long peduncled (but then it is erect instead of pendulous), characters that seem to have been overemphasized in *C. montis-wutaii*, what might have contributed to the persistence of the name in the taxonomic literature.

The ranges of *C. hancockiana* and *C. peiktusani* (see below) overlap in E China and N Korea (e.g., Hebei, Shanxi, and Jilin), so that confusion of both species, especially in the past, cannot be completely ruled out (Liang 2000; Liang & Koyama 2010a; Chang et al. 2014; SG, pers. obs.).

14. *Carex hartmaniorum* A.Cajander [*‘hartmanii’*], Ann. Bot. Soc. Zool.-Bot. Fenn. "Vanamo" 5(5): 23 (1935).

(Figs. S1: O, S5: P).

Lectotype (designated by Egorova 1976a: 195, 1999: 388): SWEDEN. GOTLAND: Gotland, Ardre, Helgmyr, 14 Jun 1931, *B. Englund, s.n.* (H 1003478, digital image!; *isolectotype*: H 1003479, digital image!).

Note: Butler (2017) and Koopman (2018) recently clarified that *‘hartmaniorum’* is the correct species epithet instead of *‘hartmanii’* (ICN, Art. 60.8, Note 4) since dedicated to *A. K. Cajander* (father; author standard form *‘Cajander’*) and *A. A. A. Cajander* (son; author standard form *‘A.Cajander’*; after 1935 changed in *A. Kalela* with author standard form *‘Kalela’*).

= *Carex emasculata* V.I.Krecz. in V.L.Komarov (ed.), Fl. URSS 3: 604 (1935).

Lectotype (**designated here**): RUSSIA. ST. PETERSBURG: Ingria, Sestroretsk–Dubki, in silvis frondosis solo humoso, -fin. Iun., 03 Jul 1888, *C. Meinshausen, s.n.* (LE 00018196, digital image!; *isolectotypes*: LE 00018197, digital image!; LE 00018198, digital image!).

Note: The lectotype selected for *C. emasculata* is the only specimen of its collections that bears Kreczetovicz’s handwriting, which ensures its condition of being original material.

Habitat: Moist to wet moderately nutrient-rich soils, in open places associated to deciduous forests and thickets; the only typically nemoral species among the Eurasian

species of *Carex sect. Racemosae*. Predominantly on lowlands and the colline belt, but occasionally in mountains (0–1500(2230) m) (Cajander 1935; Kreczetovicz 1935b; Polyakov 1958; Egorova 1976a; Chater 1980; Schultze-Motel 1980; Kukkonen et al. 1998; Elven et al. 2005; Koopman et al. 2015; SG & PJM, pers. obs.).

Distribution: European–W Siberian; mostly scattered throughout the lowlands from Central Europe to W Siberia, northwards to S Fennoscandia, NW Russia and the Baltic region, southwards to the Balkan Peninsula and Caucasian region (Nilsson 1985; Hultén & Fries 1986; Egorova 1999; Koopman 2011). In European mountains usually limited to the valleys and upper montane belt (Schultze-Motel 1980), reaching in its southern range also alpine regions (Grossgejm 1940; Koopman et al. 2015).

Chromosome count (2n): 68 (Lipnerová et al. 2013).

Notes: In the past often not treated separately from *C. buxbaumii*, and many older reports on both taxa must be considered with caution. At locations with disturbed water balance and overgrazed or frequently mowed wet meadows, individuals can be found with smaller spikes, as well as a narrowly clavate terminal spike, which are very similar to *C. buxbaumii*. The determination of such plants often causes considerable problems. Such individuals can be distinguished from the latter by usually smaller utricles, which have rather small and fine papillae, straight beak teeth, and coloration of the leaves (see key; SG, pers. obs.). Plants with terminal male spikes occasionally occur in such over-dried habitats (cf. Więclaw et al. 2016).

15. *Carex heterostachya* Bunge, Enum. Pl. China Bor.: 69 (1833).

(Figs. S1: P, S5: Q).

Ind. loc.: “*Hab. in pratis prope Pekinum haud rara*”.

Lectotype (**designated here**): CHINA. BEIJING: Chin. bor., 1831, A. A. von Bunge, s.n. (P 00710333, digital image!; *isolectotype*: H 1304061, digital image!).

Note: The collection P 00710333 with a label referring to *Bunge* and, additionally, to his Enum. Pl. China Bor., indicated by the abbreviation ‘Chin. bor.’, corresponding with the label of a duplicate deposited at Helsinki, is designated as lectotype.

≡ *Carex bungeana* Debeaux, Actes Soc. Linn. Bordeaux 33: 68 (1879), *nom. superf.*

= *Carex haematostachys* H.Lév. & Vaniot, Bull. Acad. Int. Géogr. Bot. 11: 305 (1902).

Holotype: KOREA, N. PYONGYANG: In tumulis Pyeng Yang [Pyongyang], Jun 1901, U. J. Faurie 926 (P 00284054, digital image!; *isotypes*: P 00284055, digital image!; P 00284056, digital image!; P 00284057, digital image!).

Habitat: Dry, usually sandy and loose soils, in open places, occasionally on human-modified habitats like roadsides, wastelands, and parks (often planted in the latter); 300–1000 m (Fu 1995; Dai et al. 2000; Dai & Koyama 2010).

Distribution: E Asian; mainly occurring in NE China from Shaanxi to Heilongjiang, and Korea (Fu 1995; Dai et al. 2000; Dai & Koyama 2010; Chang et al. 2014). Previous reports from SW Asia (Caucasus region), Mongolia and the Russian Far East (Kreczetovicz 1935b; Egorova 1967, Kitagawa 1979; Koopman 2011) were mainly based on confusion with *C. songorica* Kar. & Kir. and *C. gotoi* Ohwi (Kozhevnikov 1988; Malyshev 1990; Egorova 1999). Locally introduced in North America (Fell 1956; Reznicek 1993; Reznicek & Catling 2002).

Chromosome count (2n): Unknown.

Notes: Formerly classified as a member of *C. sect. Paludosae* (Dai & Koyama 2010) because of its elongate inflorescence with erect cylindric mostly unisexual spikes, pale glumes, and coriaceous bidentate utricles, *C. heterostachya* is indeed a morphologically deviant taxon within *C. sect. Racemosae*. Its true relationships were unexpectedly revealed by Global *Carex* Group (2016) and further confirmed by additional molecular data (SG et al., in prep.). A closer examination of the specimens revealed that, however, the taxon displays some of the typical features of *C. sect. Racemosae*, as a pair of dark auricles at the base of the bract, a character rarely observed in taxa traditionally placed in *C. sect. Paludosae* and allied groups.

16. *Carex holostoma* Drejer, Naturhist. Tidsskr. 3: 447 (1841).

(Figs. S1: Q, S5: R).

Ind. loc.: “Grönland, Vahl”.

Lectotype (**designated here**): GREENLAND. AVANAATA [QAASUITSUP]: Grönland, s.d., J. L. M. Vahl, s.n. (C 10006042, digital image!); *Syntypes*: Umanak, s.d., J. L. M. Vahl, s.n. (C 10006041, digital image!); in locus humidis ad ped. alpium sinus Pakitsok Groenlandiae, Aug 1833, J. L. M. Vahl, s.n. (P 00305542, digital image!; C 10006128, digital image!).

Note: Several collections in different herbaria constitute original material of *C. holostoma*. The label of the sheet here selected as the lectotype (C 10006042!) exactly matches the indicatio locotypica of the protologue of *C. holostoma* given by Drejer (1841).

Habitat: Moist to wet, often inundated and acidic places, like bogs, marshes, springs, lakeshores, as well as along rivers and streams, less often on dry tundra or rocky mountain places; from sea-level and the upper birch–larch forest belt in the Arctic to lower alpine regions at southern locations (0–1000 m) (Kreczetowicz 1935b; Egorova 1966; Kozhevnikov 1988; Malyshev 1990; Kukkonen et al. 1998; Elven et al. 2005).

Distribution: Circumpolar, but mostly scattered and often overseen; in the Arctic it seems to be more frequent in NW and NE Siberia; outside the Arctic it reaches the mountains and larger river basins of Fennoscandia, Kola Peninsula, Chukotka, and the Russian Far East (Egorova 1966; Hultén & Fries 1986; Kozhevnikov 1988; Malyshev 1990; Kukkonen et al. 1998; Egorova 1999; Elven et al. 2005, 2011). The occurrence on Iceland (Löve 1970) is not confirmed by Kristinsson (2008). Entirely confined to the Arctic in North America (Murray 2002a; Aiken et al. 2007; Elven et al. 2011).

Chromosome count (2n): 54 (Yurtsev and Zhukova 1982: NE Siberia; Malyshev 1990: Siberia), c.54 (Krogulevich 1971: E Siberia), 56 (Zhukova & Tikhonova 1971; Zhukova 1980: Chukotka; Dalgaard 1989: Greenland), 58–60 (Engelskjön & Knaben 1971: Fennoscandia), 60 (Jørgensen et al. 1958: Greenland; Zhukova & Petrovsky 1975: W Chukotka; Löve & Löve 1981: Canada).

17. *Carex infusata* Nees, in R. Wight, Contr. Bot. India: 125 (1834).

(Figs. S2: R, S6: S).

Ind. loc.: “*Nepalia* [...] *Royle 123*” (see notes for further clarification).

Lectotype (designated by Egorova 1999: 406): INDIA. HIMACHAL PRADESH: Pungee in Kunawur [Kinnaur], *J. F. Royle 123* (K 000998959, digital image!).

= *Carex trispiculata* Boeckeler, Beitr. Cyper. 1: 45 (1888).

Ind. loc.: “*Himalaya occid., prov. Garhwal, alt. 10,000–10,600 ped., Herb. Schlagintweit no. 10056*”.

Holotype: INDIA. UTTARAKHAND: Western Himalaya, Prov. Garhvál [Garhwal], 10000–10600 ft, 01–31 Aug 1855, *Herb. A. von Schlagintweit 10056* (BM! [not seen!] according to Kukkonen 1998, 2001).

= *Carex atrofurfur* T. Koyama, Acta Phytotax. Geobot. 16: 166 (1956).

Holotype: ?PAKISTAN. GILGIT-BALTISTAN: Karakoram, Oltali Chish, 2400 m, 10 Jun 1955, *S. Nakao, s.n.* (KYO 00024258, digital image!).

Note: *Carex atrofurfur*, described from the Karakoram (Oltali Chish; Koyama 1956b), is placed here under synonymy of *C. infuscata* following the suggestions by previous authors (Egorova 1967; Dickoré 1995; Egorova 1999) and confirmed by our own observations on a high-resolution image of the type.

Habitat: Moist to wet places, in meadows and thickets, less often in open birch-pine forest, mountain steppes, and semi-deserts, typically associated to springs, streams and rivers; in the middle montane belt up to high-alpine regions (2000–3600(4000) m) (Kalela 1944; Polyakov 1958; Raymond 1965; Dickoré 1995; Kukkonen 1998, 2001; SG, pers. obs.).

Distribution: Central Asian–W Himalayan; from the Pamiro-Alai and Hindukush to the Karakoram and W Himalayas, eastwards to Uttarakhand (Garhwal) and W Nepal (Koyama 1958, 1978a; Egorova 1967, 1999; Dickoré 1995; Kukkonen 1998, 2001; SG, pers. obs.).

Chromosome count (2n): 54 (Sokolovskaya & Strelkova 1939; Egorova 1999: Pamir).

Notes: The indicatio locotypica stated “Nepalia, *Royle 118 et 123; Wallich 3381*”. The specimen *Royle 118* corresponds to *C. obscura*. The number *Wallich 3381* is indeed the type of *C. lehmannii*. Thus, Egorova’s (1999) typification seems the only valid choice to preserve the current use of the name. The locality (“Kunawur”, very probably Kinnaur) does not seem to be in today’s Nepal, but NW India (Himachal Pradesh).

For confusion and possible hybridization with *C. gracilentia* see notes under that species (see above). Reports on its occurrence in China (Qinghai, Nanshan Mts.) by Egorova (1967) are, in our opinion, due to confusion with *C. serreana* (see below).

18. *Carex japonalpina* (T.Koyama) T.Koyama [*japonoalpina*], Acta Phytotax. Geobot. 16: 154 (1956). (Figs. 3: H–M, S2: S, S6: T).

≡ *Carex atrata* L. var. *japonalpina* T.Koyama, J. Jap. Bot. 30: 313 (1955). (Basionym).

≡ *Carex perfusca* V.I.Krecz. var. *japonalpina* (T.Koyama) Kitag., Fl. Manshur.: 134 (1979).

Holotype: JAPAN. HONSHU: Mt. Kitadake, 2600 m, 15 Aug 1924, *H. Matsuda, s.n.* (TI 00010005, digital image!).

Habitat: Moist to wet places, in open-forest and mountain grasslands and scrublands, often along rivers and streams; from the upper forest belt near the tree line to the alpine zone (1800–3100 m) (Ohwi 1936, 1965; Fu 1995; Liang 2000; Liang & Koyama 2010a; Hoshino et al. 2011; SG, pers. obs.).

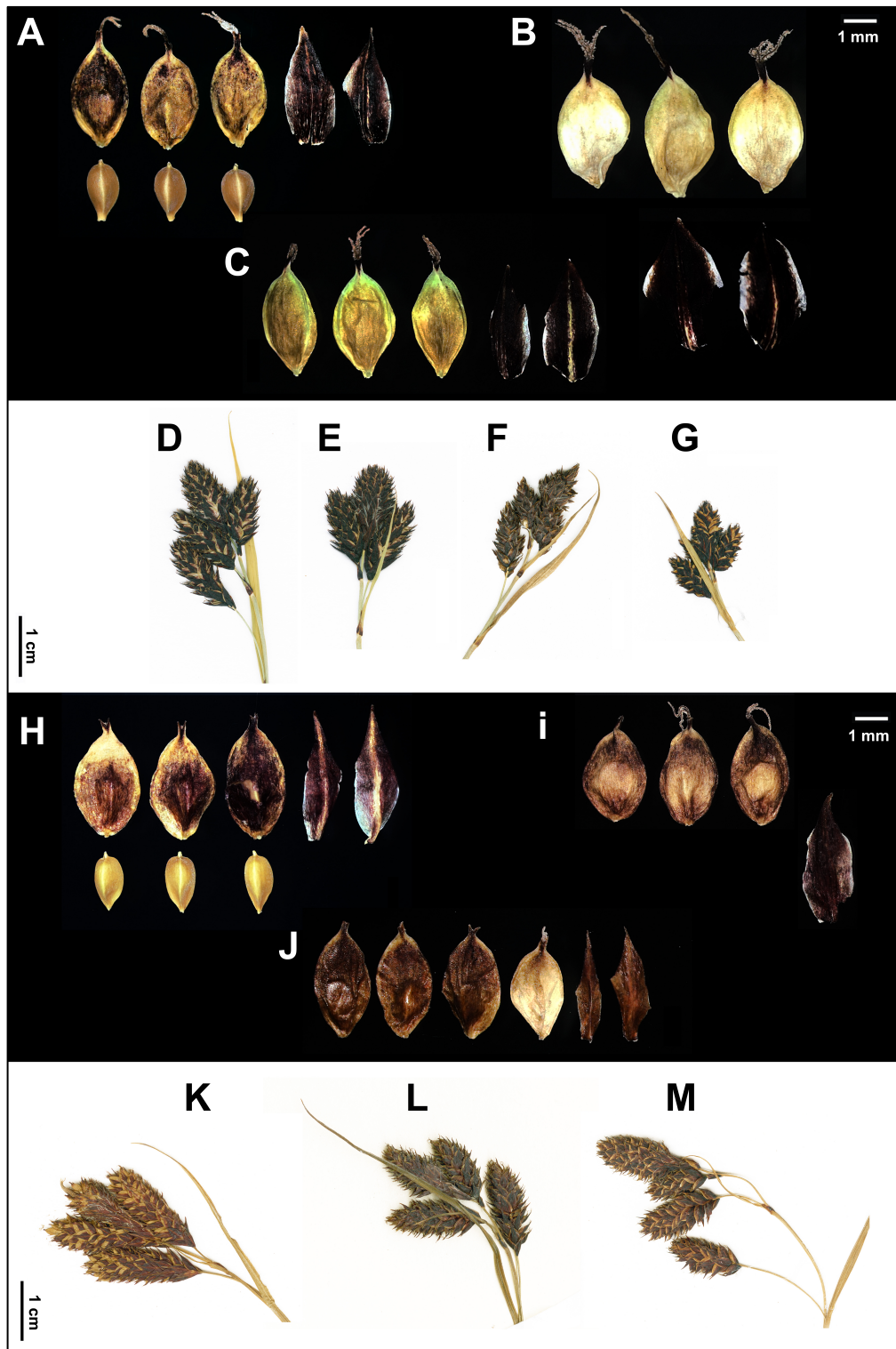


FIG. 3: A–M, Detailed images of *Carex atrata* and *Carex japonalpina*. A–G, *C. atrata*: A–C: Utricles, female glumes, and nutlets, scale bar = 1 mm; D–G: Inflorescences, scale bar = 1 cm; H–M, *C. japonalpina*: H–J: Utricles, female glumes, and nutlets, scale bar = 1 mm; K–M: Inflorescences, scale bar = 1 cm; A: Gebauer 140872 (Herb. Gebauer); B: Hoffmann a117 (Herb. Hoffmann), C: Hoffmann a128 (Herb. Hoffmann); D, E: Gebauer 140816 (Herb. Gebauer); F: Hoffmann, s.n. (HAL!); G: Frahm, s.n. (B!); H, M: Ohwi, s.n. (NY!); i, L: Hermann, s.n. (M!); J: Koidzumi 60202 (NY!); K: Furuse 47902 (K!).

Distribution: E Asian; exhibiting a relatively restricted distribution range from NE China (S Jilin) and Korea to Japan (Honshu), and the S Russian Far East (N Ussuri region) (Koyama 1955; Ohwi 1965; Kitagawa 1979; Egorova 1999; Liang & Koyama 2010a; Hoshino et al. 2011; SG & PJM, pers. obs.). Erroneously reported from NE Mongolia (Khentii Mts.) by Egorova (1999), but without detailed explanations (all *C. atrata*-like plants studied by us from Mongolia represented *C. aterrima* subsp. *aterrima*).

Chromosome count (2n): 54 (Okuno 1939, 1940 as *C. atrata* [cited in Yano et al. 2008 as *C. atrata* var. *japonalpina*]), 56 (Tanaka 1948 as *C. atrata*).

Notes: *Carex atrata* and *C. japonalpina* are two closely related species that can be distinguished by using the characters highlighted in the key. In consequence of these separating features, the obvious allopatric ranges of both taxa, and their weak but still present molecular divergence (SG et al., unpubl. data), we consider the East Asian plants as a separate species, revalidating the name *C. japonalpina* (T.Koyama) T.Koyama.

East Asian plants from E China, N Korea and Japan (Honshu) resembling *C. atrata* and *C. aterrima* have caused much confusion regarding their taxonomic identity (Koyama 1955, 1956a; Kitagawa 1979; Kozhevnikov 1988; Fu 1995; Liang & Koyama 2010a; Hoshino et al. 2011). First described by Koyama (1955) as a variety of *C. atrata* L. and later treated by him as a separate species (Koyama 1956a), this taxon is mostly considered identical with *C. atrata* and placed under its synonymy (Fu 1995; Liang & Koyama 2010a; Hoshino et al. 2011; but see Kitagawa 1979; Egorova 1999), or as a variety of *C. atrata* (Ohwi 1965).

Remarkably, Kozhevnikov (1988) pointed out the need of further research on *C. aterrima* in the Russian Far East, which he characterized as a polymorphic species most likely because of the inclusion by him of all *C. atrata*-like plants (i.e. *C. japonalpina*). Accordingly, two examined Russian Far Eastern collections (N Ussuri region, Tardoki-Yani, Charkevich et al. 939a and 939b, two sheets, NY!), which were previously determined as *C. aterrima*, are treated here under *C. japonalpina* as well. We cannot discard completely that introgression between the two taxa may occur.

19. *Carex jisaburo-ohwiana* T.Koyama, Jap. J. Bot. 15: 176 (1956).

(Figs. S2: T, S6: U).

≡ *Carex caucasica* Steven subsp. *jisaburo-ohwiana* (T.Koyama) T.Koyama, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 8(4): 197 (1962).

Holotype: TAIWAN. TAICHUNG: Formosa, Mt. Niitaka, 06 Jul 1933, *J. Ohwi* 3671 (KYO 00024255, digital image!); *Paratypes*: Formosa, Mt. Niitaka, 06 Jul 1933, *J. Ohwi* 3707 (KYO 00024256, digital image!; P 00282530, digital image!); Formosa, Taityû, inter Niitaka-syuzan et Hattûkwan [Mt. Niitaka], 17 Aug 1934, *M. Tagawa* 444 (KYO 00024257, digital image!; NY [not databased!]).

Habitat: Poorly known, described from, presumably moist to wet, alpine grasslands; 3200–3884 m (Ohwi 1936; Koyama 1956c, 1978b; Koyama et al. 2000; Liang 2000; Liang & Koyama 2010a; Liao 2014).

Distribution: E Asian–Taiwanese endemic; mainly confined to the Hsuehshan Range, but possibly overlooked in other mountain ranges or confused with *C. apodostachya* (Koyama 1956c, 1978b; Koyama et al. 2000; Liang 2000; Liang & Koyama 2010a; Liao 2014).

Chromosome count (2n): Unknown.

Notes: This largely undervalued taxon has mostly been treated at subspecific rank within the predominantly W and Middle Asian species *C. caucasica*, or placed under its synonymy (Koyama et al. 2000) due to the morphological resemblance between the two species. Furthermore, the species has been, together with *C. apodostachya* (see above), confused with *C. atrata* by Liao (2014). The differences mentioned in the key, which demonstrate an obvious morphological separation of both taxa and their clear geographical separation as well as first molecular insights (SG et al., unpubl. data) clearly suggest the independence of the Taiwanese plants from both *C. atrata* and *C. caucasica*. Accordingly we treat them here as an independent species.

20. *Carex kangchengyaoensis* S.Gebauer, Jim.Mejías & Noltie, nom. et stat. nov.

(Figs. 4: A–L, S2: U, S6: V).

≡ *Carex atrata* L. var. *glacialis* Boott, Ill. Carex 3: 114, tab. 365 (1862).

Ind. loc.: “Himalaya/N. Sikkim, alt. 15–17,000 ft., *J. D. Hooker* (*Herb. Hooker*)”.

Lectotype (**designated here**): INDIA. SIKKIM: Kinchinjhow [Mt. Kangchengyao], 17,000 ft., 14 Sep 1849, *J. D. Hooker*, s.n. (*Herb. Hooker*) (K 000998998!).

≡ *Carex duthiei* C.B. Clarke var. *glacialis* (Boott) C.B. Clarke, in *J.D. Hooker*, Fl. Brit. India 6: 732 (1894).

Note: The sheet selected here as the lectotype of *C. atrata* var. *glacialis* (K 000998998!) is the only collection found during our studies that seems to constitute original material corresponding to Boott’s (1862) nomenclatural name (see also comments below).

Habitat: Poorly known due to the few available collections and mostly missing habitat descriptions, seemingly on the gravel of damp moraines and screes with low vegetation at high altitudes, mainly between 4300–5200 m (Noltie 1994; Srivastava 1996; SG & PJM, pers. obs.).

Distribution: Known only by a few collections, the species seems to be endemic to a small area of the rather humid central Himalayas, stretching from easternmost Nepal at the upper Ramthang Valley and the Kanchenjunga massif across the Dongkya Range in northern Sikkim to the Chumbi Valley in the Tibetan Himalayas on the border between the Tibet Autonomous Region of China (Xizang) and western Bhutan in the east (Noltie 1994; Srivastava 1996). It can be assumed that the species has often been overlooked or confused with other species of *Carex* sect. *Racemosae* and may be more widespread, especially in eastern Nepal and Bhutan.

Morphological diagnosis: *Carex kangchengyaoensis* shows a basically overall similarity to other members of *Carex* sect. *Racemosae* like most of the other species of the group. The new species can be distinguished from almost any other species of *Carex* sect. *Racemosae* occurring in the Himalayas and Central Asia by the unique morphology of the utricles: small (1.8–2.5 mm long), narrowly elliptic, and trigonous in cross section, becoming dark purplish to almost purplish-black at maturity, subcoriaceous, generally veinless, cuneate at the apex and \pm attenuated into a distinct 0.2–0.6 mm long scabrous beak, with the orifice conspicuously white-hyaline, emarginate to slightly bidentate.

Carex kangchengyaoensis morphologically resembles the most some dwarf high-altitude specimens of *C. duthiei* subsp. *duthiei*, which also co-occur in the same region. But in particular, *C. duthiei* subsp. *duthiei* has utricles (2)2.2–3 \times (1)1.1–1.4 mm, obovate to obovate-elliptic, narrowly biconvex, yellowish to golden-yellowish, sometimes brownish, only dark purplish punctate above, membranous, obscurely to strongly veined, rarely veinless, rounded at apex and abruptly contracted into a very short, 0.1–0.2 mm long, smooth beak, with the orifice not differentially colored, truncate, rarely emarginate. Additional differences between these two taxa are the auricles, prominent and conspicuously clasping in *C. kangchengyaoensis*, vs. smaller and not clasping in *C. duthiei* subsp. *duthiei*, and the leaves, usually about $\frac{1}{2}$ the culms length and stiff in *C. kangchengyaoensis*, vs. usually about as long as the culms and much weaker in *C. duthiei* subsp. *duthiei*.

Boott (1862) considered it a variety of *C. atrata*, which according to our findings (SG et al., unpubl. data) does not occur in the central Himalayan region and adjacent areas (see

comments under this species). *Carex kangchengyaoensis* is distinguished from *C. atrata* by the smaller size of most vegetative and generative plant parts, and especially by the significantly different color, shape and dimensions of the utricles (see Figs. 3: A–C, 4: K–L, S4: F, S6: V), the proximal bract (setaceous-filiform to glumaceous vs. leaf-like, occasionally setaceous, but then not filiform) and the auricles (dark purplish black to almost blackish, larger and conspicuous clasping vs. dark purplish brown to blackish brown, smaller and not clasping).

Description: Perennial; caespitose or loosely tufted, with rhizomes short, sometimes slightly spreading. *Fertile culms* 3–18(20) cm long, (0.5)1–1.2 mm wide at its middle length, usually much longer than the leaves, rather stout, \pm erect, only slightly curved below the inflorescence, trigonous, with narrowly winged margins, smooth. Basal sheaths scale-like, up to 1.5 cm long, yellowish brown, becoming dark reddish to purplish brown. *Leaves* usually shorter than $\frac{1}{2}$ of the length of the fertile stems, rarely up to $\frac{2}{3}$ of the stem length in dwarfed specimens, blades 1.5–9 cm long \times 1–3(4.5) mm wide, flat or slightly folded, more conspicuously V-shaped towards its base, pale grayish green to yellowish green when dry, stiff, straight to outcurved, the midrib more prominent abaxially than the remaining nerves, the margins slightly revolute, smooth or slightly scabrous distally, gradually narrowing into a long-acuminate tip; ligule 0.5–1.2 mm long, shorter than wide, the apex \pm rounded, obtuse or subacute, the margins greenish to brownish, with reddish or purplish spots. *Inflorescence* 1.1–2.7(3.3) \times 0.8–1.7 cm (measured from the base of the proximal bract to the apex of the terminal spike), with (2)3–4(5) spikes, \pm capitate, the spikes densely approximate, erect or proximal ones slightly spreading; *Proximal bract* glumaceous to setaceous, shorter than the inflorescence and often than its subtending spike, the blade filiform, 0.3–2 cm long, yellowish green to greenish, with prominent clasping blackish auricles at its base, 1.2–2 mm wide at its widest point; terminal spike gynaeceandrous, 9–13(16) \times 4–5(6) mm, clavate to short-cylindrical, the staminate portion $< \frac{2}{3}$ of the spike length, sessile; lateral spikes entirely pistillate, (5)7–12(14) \times 4–5(7) mm, subglobose to elliptic or short-cylindric, with a stiff peduncle 3–9(10) mm long, the distal-most ones \pm sessile, all overlapping or the proximal-most one somewhat distant. *Staminate glumes* (3)3.2–4.5 \times 0.7–1.2 mm, lanceolate, acute to acuminate, dark purplish brown to almost blackish, the midrib inconspicuous and \pm of the same color as the glume body, the margins sometimes narrowly white-hyaline and almost always towards the tip, sometimes with a short mucro up to 0.2 mm long. *Pistillate glumes* (3)3.2–4 \times 0.8–1.3 mm, usually exceeding the mature utricles, lanceolate, acuminate, the midrib inconspicuous and \pm of the

same color as the glume body, occasionally slightly lighter, sometimes with the margin narrowly white-hyaline, more often towards the tip. *Utricles* 1.8–2.5 × 0.5–0.8(1) mm (including the beak and the basal stipe), narrowly elliptic, trigonous, slightly inflated, almost completely filled by the nutlet, subcoriaceous, yellowish green at base, the upper parts dark purplish, becoming almost dark purplish brown to purplish black at maturity, cuneate at apex and ± gradually attenuated into the beak, somewhat papillose above, with a short but prominent stipe at base, 0.2–0.4 mm long; *Beak* 0.2–0.6 mm long, ± straight, dark purplish blackish to black, papillose, scabrous, the orifice conspicuously white-hyaline, emarginate to slightly bidentate. Stigmata 3, reddish brown, long protruding from the utricle beak, papillose, promptly deciduous. *Nutlets* 1.4–1.7 × 0.5–0.9 mm (measured including remnant of the style-base and the basal stipe), elliptic, the faces slightly concave, yellowish to yellowish brown, usually with a short-cylindrical up to 0.1 mm long remnant of the style-base at the top, with a short basal stipe 0.1–0.2 mm long. *Anthers* c. 1.5–1.7 mm long.

Etymology: The species epithet “*kangchengyaoensis*” refers to the Mount Kangchengyao (= Kinchinjhow, Kangchenjau), a 6889 m a.s.l. high summit of the Dongkya range in the north of the Indian state of Sikkim, which forms the border with the Tibet Autonomous Region of China (Xizang). The species was first collected in 1849 by Joseph D. Hooker in the area of the glacier southeast of the summit.

Phenology: Plants with ripe fruits were collected from end of July to October (Noltie 1994; Srivastava 1996; SG & PJM, pers. obs.).

Chromosome count (2n): Unknown.

Notes: Usually treated as variety under *C. atrata* (*C. atrata* var. *glacialis*; Boott 1862; Kükenthal 1909; Noltie 1994). In the description of *C. atrata* var. *glacialis*, Boott (1862) did not mention a precise geographic reference, citing only “[...] Himalaya, 15–17,000 feet, Dr. Hooker”. Clarke (1894) later specified the locality to be “N. Sikkim; alt. 15–17,000 ft., J. D. H[ooker]”. The voucher we have located at Kew (K 000998998) bear a Clarke’s revision label indicating the study of the specimen for Hooker’s Flora of British India, as well as an additional label handwritten by Clarke himself, which refers to Boott’s (1862) description and illustration of *C. atrata* var. *glacialis*.

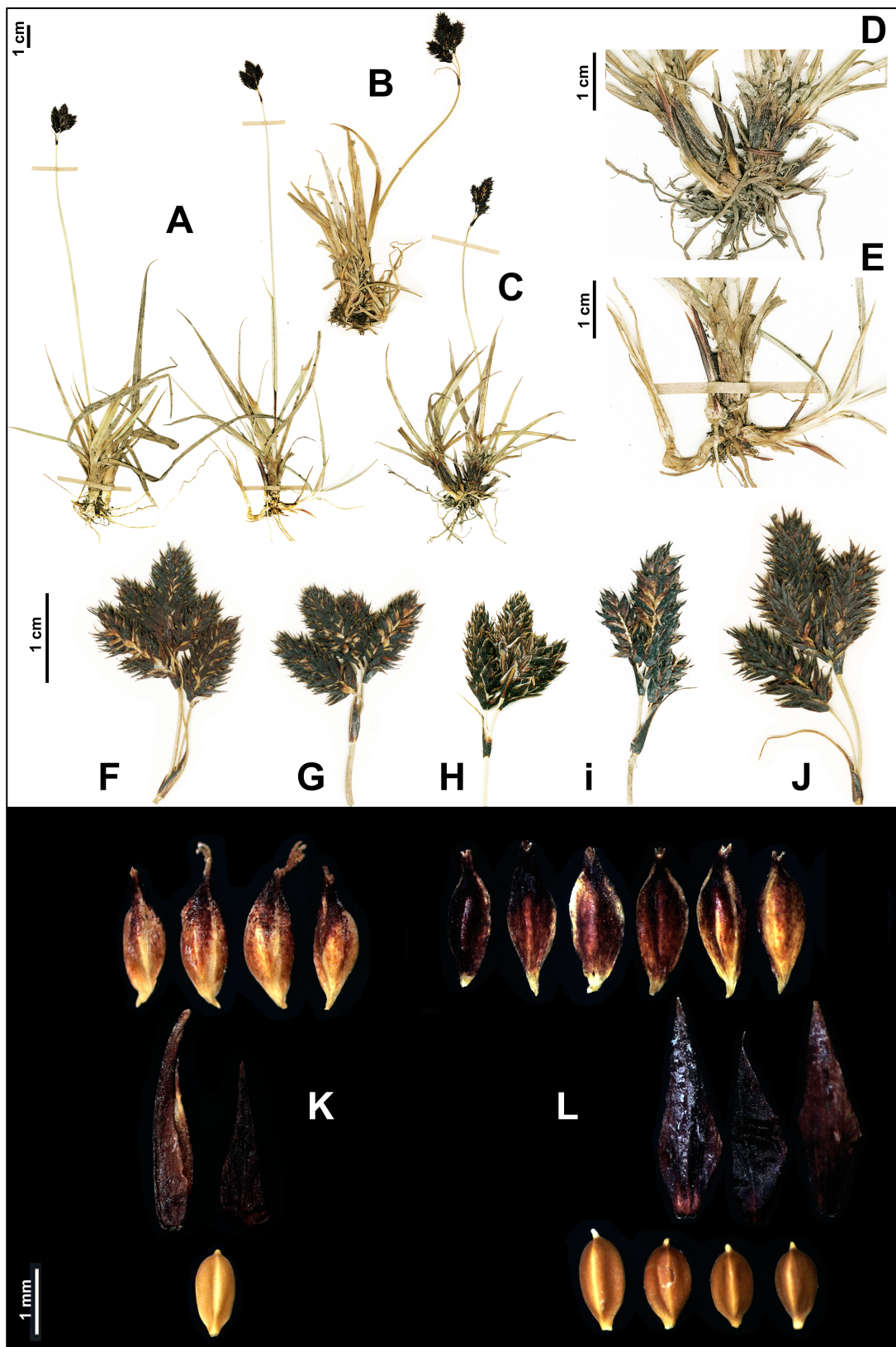


FIG. 4: A–L, Detailed images of *Carex kangchengyaoensis* S.Gebauer, Jim.Mejías & Noltie, nom. et stat. nov. A–C: General habit, scale bar = 1 cm; D–E: Basal parts, scale bar = 1 cm; F–J: Inflorescences, scale bar = 1 cm; K–L: Utricles, female glumes, and nutlets, scale bar = 1 mm; A, E, H, Long & Noltie 388 (E!); B, F–G, J, L, Hooker, s.n. (K, Type!); C–D, i, KEKE 531 (E!); K, Gould 1495 (K!).

However, Hooker's typical print label is missing. Together with the material of *C. atrata* var. *glacialis* (left), a collection of *C. obscura* (right; K 000998999) is also mounted on this sheet, bearing Hooker's print label and a handwritten note with the collection data, whose handwriting is identical to that of the former (Hooker's handwriting). The specimens of *C. atrata* var. *glacialis* appear identical to the ones in Boott's (1862) illustration (tab. 365). Since the handwritten label refers to "Kinchinhow" (= Mt. Kangchengyao, Kangchenjau, Kangchen Jau, Khangchen-chho) located in Sikkim (Hooker 1855), it seems to us, along with the above-mentioned hints, that there is no doubt that this is Hooker's collection and thus original material of *C. atrata* var. *glacialis*. To avoid further confusion and fix a consistent use of the name, the left collection is designated here as the lectotype of *C. atrata* var. *glacialis*.

Interestingly, the specimens initially classified under this taxon represented a mixture of two taxa. Some collections actually were dwarfed high-altitude specimens of the rather polymorphic *C. duthiei* (SG, pers. obs.). This is most likely also the case of the reports of *C. atrata* var. *glacialis* from Sichuan (see Kükenthal 1909). However, other collections (including type specimens annotated by Clarke during preparation of the Flora of British India) clearly differ from *C. atrata* and co-occurring species by the characters mentioned in the key.

Due to its distinct morphology, Noltie (1994) already pointed out that *C. atrata* var. *glacialis* should merit taxonomic recognition at specific rank, which is further supported by first molecular insights (SG et al., unpubl. data). Accordingly, here we uprank this variety as a new species.

21. *Carex kansuensis* Nelmes, Bull. Misc. Inform. Kew 1939: 201 (1939).

(Figs. S2: V, S6: W–W', S8: F–I).

Holotype: CHINA. GANSU: Western Kansu, 10 Jul 1918, *E. Licent* 4232 (K 000961006, digital image!; *isotypes*: BM 000797617, digital image!; PE 01842048, digital image!); *Paratypes*: CHINA. SICHUAN: Sze-ch'uan, reg. bor.-occid.: Merge, c. 50 km austr.-occid., versus, in prato humido, c. 3500 m, 03 Sep 1922, *H. Smith* 4312 (UPS-V 044008, digital image!; PE 00030605, digital image!).

Habitat: Moist to wet soils, in mountain grasslands and scrublands and open forest; from upper forest to high-alpine belt (3400–4600(4820) m) (Liang 2000; Dai et al. 2003; Liang & Koyama 2010a; SG, pers. obs.).

Distribution: Central Chinese endemic; the distribution reaches from SE Tibet and NW Yunnan in southern Central China to NE Qinghai, W Sichuan, Gansu, and SW Shaanxi (Nelmes 1939; Egorova 1967; Liang 2000; Liang & Koyama 2010a).

Chromosome count (2n): Unknown.

Notes: For confusion with *C. bijiangensis* and possible hybridization with it see comments under that species (see above).

22. *Carex lehmannii* Drejer, Symb. Caric.: 13 (1844).

(Figs. S2: W, S6: X).

Ind. loc.: “Napalia, Wallich 3381”.

Lectotype (designated here): NEPAL. NOT LOCALIZED: Napalia, 1831 [1821?; see comment below], *N. Wallich 3381* (K 000998976, digital image!; *isolectotypes*: Nepal: E Napalia, 1821, *N. Wallich 3381* (NY 00011542, digital image!; Napalia, 1821, s.coll., n. 3381 (K 000998977, digital image!; LE 00010262, digital image!); s.loc., ex *Herb. Wallich 3381* (K 000998973, digital image!)).

Note: There are several collections of ‘Wallich 3381’ deposited in different herbaria. These specimens that constitute the original material of *C. lehmannii* share a unique collector number but bear two different dates (1821 and 1831). The confusion seems to come from a mistake in the transcription of the labels. According to the annotations in NY specimen, the actual collection date is 1821, while 1831 seems to be the year the exsiccata was distributed. One sheet (K 000998976) is selected as the lectotype.

Habitat: Moist to wet gravelly and rocky soils, often on shady environments or along rivers and streams, occasionally on boggy places, in diverse kinds of forests, and in mountain grasslands and scrublands; 2800–4150 m (Ohwi 1965; Noltie 1994; Dickoré 1995; Srivastava 1996; Kukkonen 2001; Liang & Koyama 2010a; Hoshino et al. 2011; SG, pers. obs.).

Distribution: Sino–Himalayan–E Asian; reaching from the W Himalayas (Kashmir) throughout Nepal and Bhutan to Central and E China (from SE Tibet to Shanxi), and Korea and Japan in the East (Egorova 1967; Koyama 1975, 1978a; Noltie 1994; Dickoré 1995; Kukkonen 2001; Liang & Koyama 2010a; Hoshino et al. 2011; Chang et al. 2014).

Chromosome count (2n): Unknown.

23. *Carex media* R.Br., in J. Richardson, Bot. App., in J. Franklin, Narr. Journ. Polar Sea: 750 (1823).

(Figs. S2: X, S6: Y–Y’).

Ind. loc.: “[...] the wooded country from latitude 54° to 64° north”.

Lectotype (designated here): CANADA. NOT LOCALIZED: s.loc., s.d., *Dr. Richardson, s.n.* (K 000501844, digital image!).

Note: Egorova (1999) already mentioned a putative type in K, but no barcode was mentioned to identify it. The sheet (K 000501844!) found in this study corresponding to *C. media* R.Br. is, therefore, designated as lectotype.

= *Carex alpina* Sw. ex Lilj. var. *inferalpina* Wahlenb., Fl. Lapp.: 241 (1812).

≡ *Carex norvegica* Retz. subsp. *inferalpina* (Wahlenb.) Hultén, Acta Univ. Lund., 2, 38(1): 348 (1942).

Ind. loc.: “Hab. praecipus β. in graminosis humifuscus inferalpinis per Nordlandiam vulgatissime et Finmarkiam totam usque ad Utsjoki passim”.

Neotype (designated by Moberg & Nilsson 1991: 296): NORWAY. SØR-TRØNDELAG: *Carex alpina*, Norska Nordland vid Sörfoldbotten d. 21 Jul 1807 (Wahlenberg’s handwriting) (UPS-V 050217, digital image!).

= *Carex angarae* Steud., Syn. Pl. Glumac. 2: 190. 1855.

Ind. loc.: “Ad fluv. Angara et Lena Sibir [= lect. *J. Gmelin*]”.

Lectotype (mentioned by Buzunova et al. 2010: 106): RUSSIA. IRKUTSK. “*Carex* spiculis subrotundis ternis, in summo culmo se contingentibus, breviforme pedunculatis. Stirp. Sib. n. 86. p. 146”, “Specimina a Gmelin lecta. V.I.Kreczetovicz” (sub *Carex vahlii* Cam. determ. 1842) (LE 01006692, digital image!).

Carex brachylepis Turcz. ex Besser, Flora 17(1 Beibl.): 26 (1834), *nom. nud.*

= *Carex angarae* Steud. subsp. *brachylepis* Kalela, Ann. Bot. Soc. Zool.-Bot. Fenn. “Vanamo” 19(3): 7 (1944).

Ind. loc.: “In arenosis ad thermas Turkenses, 1829, *Turczaninow* (in “Plantae exsiccatae” sub nomen *Carex brachylepis*)”.

Lectotype (designated here): RUSSIA. ?BURYATIA: Baikal, in lapidosis subalpinis, 1829, *N.S. Turczaninow, s.n.* (P 00292523, digital image!).

Note: The only sheet found in this study representing original material, is designated here as lectotype.

= *Carex mimula* V.I.Krecz. in V.L.Komarov (ed.), Fl. URSS 3: 603 (1935).

Holotype: RUSSIA: ALTAI REPUBLIC: Altai, reg. Bijsk, in parte superior fl. Anui Niger, in tundra muscoso-lichenosa cacuminis Talitski bielok, 12 Jul 1928, *E. G. Pobedimova 118b* (LE 01006898, digital image!; *isotype*: LE 01006899, digital image!).

Habitat: Moist to wet or swampy places on gravelly to peaty soils, in forests, thickets, meadows, riverbanks and bogs.; predominantly a boreal species of the forest belt, reaching punctually the Arctic at its northernmost limit and the subalpine to alpine regions in the southern part of its distribution (0–2150(2520) m) (Kreczetovicz 1935b; Kalela 1944, 1950; Popova 1950; Polyakov 1958; Egorova 1966, 1976a, b, c; Chater 1980; Kozhevnikov 1988; Malyshev 1990; Kukkonen et al. 1998; Grubov 2001; Elven et al. 2005; Nyambayar 2009; Liang & Koyama 2010a; Krasnoborov 2012; M. H. Hoffmann, pers. comm.).

Distribution: Circumboreal; widely distributed in boreal Eurasia and North America, penetrating the Arctic mainly along large river basins, southwards to the mountains of NE Central Asia and S Siberia (i.e. Altai-Sayan Mts., Mongolia) (Meusel et al. 1965; Egorova 1966, 1999; Hultén & Fries 1986; Murray 2002a; Liang & Koyama 2010a; Elven et al. 2011). The reports of *C. norvegica* from Korea (Chang et al. 2014) most likely refer, in our view, to *C. media*.

Chromosome count (2n): 54 (Löve & Löve 1961 and references therein: Fennoscandia), 56 (Roalson 2008 and references therein: Fennoscandia, Alaska, and Canada).

Notes: The generally rather weak morphological differentiation between *C. media* and *C. norvegica*, their often sympatric occurrence, especially in northern Eurasia (Elven et al. 2011), and reports of hybrids (Egorova 1999) give rise to legitimate doubts concerning their status as distinct species, which we only provisionally accept here. Only targeted molecular, morphological, as well as phylogeographical studies involving extensive comprehensive sampling across the entire distribution area of both species (including their segregates) could clarify whether they might only represent morphotypes with local climatic or site-specific adaptations of a single polymorphic species with a remarkable post-glacial history.

The name *C. angarae* was recorded as an accepted name in Flora of China treatment (Liang & Koyama 2010a). This name was already considered a synonym of the circumboreal *C. media* in previous works (Kalela 1950; Egorova 1999; Murray 2002a). At higher altitudes and towards the Arctic the utricles of *C. media* often turn brown at maturity (usually brownish-greenish, yellowish or golden-yellowish), resembling *C. norvegica* (Egorova 1999; SG, pers. obs.). These forms are often difficult to distinguish from this latter species (SG, pers. obs.). Such plants also appear a bit more compact and less slender than usual for *C. media* (SG, pers. obs.). In our opinion, this circumstance has led to

contradictory statements regarding the occurrence of *C. norvegica* in N Central Asia, S and SE Siberia (Egorova 1999; Malyshev 2008; Nyambayar 2009; Krasnoborov 2012), which we do not accept here and therefore consider such plants as belonging to the rather widespread *C. media* (see also Malyshev 1990; Elven et al. 2011).

24. *Carex melanantha* C.A.Mey., in C.F. von Ledebour, Fl. Altaic. 4: 216 (1833).

(Figs. S2: Y, S6: Z, S9: A–G).

Ind. loc.: “Hab. In summo monte circa fontes fl. Tscharysch, in monte crucis prope Riddersk, in insulis fl. Koksun [*Ledebour*] et Tschuja [*Bunge*]”.

Lectotype (designated by Egorova 1999: 399): RUSSIA. ALTAI REPUBLIC: Ad Tscharysch, *Herb. K. F. von Ledebour* 455 (LE 01006880, digital image!).

= *Carex regelii* C.B. Clarke ex O. Fedtsch., Fl. Pamira: 71 (1903).

Lectotype (designated here): INDIA. JAMMU & KASHMIR: Kashmir, Mussid Valley, 13,000 ft, 26 Jul 1893, *J. F. Duthie* 13256 (K 000998990, digital image!).

Note: The only collection found to correspond to *C. regelii* C.B. Clarke ex O. Fedtsch., is designated here as lectotype. No specimens were found in LE (I. Illarionova, pers. comm.).

Habitat: Moist to wet, usually gravelly to sandy soils, occasionally on somewhat salty places, in diverse open mountain habitats, like *Juniperus* forests, scrublands, steppes, meadows, swamps, riverbanks and along springs and streams; from the mountain-steppe and upper forest boundary to the nival zone ((1250)2000–4820(5030) m) (Kreczetovicz 1935b, 1941, 1963; Polyakov 1958; Egorova 1967, 1976c; Dickoré 1995; Kukkonen 1998, 2001; Grubov 2001; Nyambayar 2009; Liang & Koyama 2010a; Krasnoborov 2012).

Distribution: Central Asian—(Irano–Turanian)—S Siberian; from the Caucasus range and N Iran (Elburz Mts.), the Hindukush, Karakoram and Pamiro-Alai to the W Himalayas (Jammu and Kashmir, Himachal Pradesh) in the East, northwards to the Altai Mts., Mongolia, and, very isolatedly, the Eastern Sayan Mts. (Egorova 1967, 1999; Dickoré 1995; Kukkonen 1998, 2001; Amini Rad 2011; SG, pers. obs.).

Chromosome count (2n): 52 (Sokolovskaya & Strelkova 1939; Egorova 1999: Pamir), 78 (Sokolovskaya & Strelkova 1948a; Egorova 1999: Altai [erroneous?]); (1n): 24 (Mehra & Sachdeva 1975: Jammu and Kashmir).

Notes: *Carex melanantha* is widespread in Central Asia and S Siberia, and distinguished from its close relatives *C. melananthiformis* and *C. moorcroftii* mainly by its usually densely approximate and overlapping spikes (Raymond 1965; Egorova 1967, 1999; Liang

& Koyama 2010a). Although morphologically quite uniform across most of its distribution range, *C. melanantha* shows greater variability in the western Himalayas (i.e. SW Karakoram and adjacent areas). In addition to typical individuals, there are sometimes plants that have rather loose inflorescences, smaller spikes, narrower and less firm leaves, which are often as long as the fertile culms, and more slender stems. Such plants have been sometimes separately treated as *C. regelii* (see Dickoré 1995). Otherwise, the glumes and utricles of such plants are typically for *C. melanantha*. Dickoré (1995) discussed a possible introgression from *C. obscura* into *C. melanantha* in connection with *C. regelii*.

The exact delimitation of the ranges of *C. melanantha* and the closely related *C. moorcroftii* within the western Himalayas is still not clear, especially in the northern Karakoram (Yarkand) and throughout the upper Indus valley (Jammu and Kashmir), where intermediate individuals of putative hybrid origin have been found (Dickoré 1995; SG & PJM, pers. obs.). There, both taxa can occasionally be found growing close to each other (see Dickoré 1995; M. H. Hoffmann, pers. comm.).

The reports of *C. melanantha* from Nepal (e.g., Koyama 1978a) seem to entirely refer to *C. moorcroftii* (see below). Rare Caucasian plants formerly assigned to *C. melananthiformis* (see Egorova 1967, 1999, 2006) are treated under *C. melanantha* based on the shape of the inflorescences, as well as the shape and dimensions of the utricles (see below).

25. *Carex melananthiformis* Litv., Trudy Bot. Muz. Imp. Akad. Nauk 7: 90 (1910).

(Figs. S2: Z, S6: A1, S9: H–N).

Ind. loc.: “Siberiae prov. Irkutsk. In humidis sabulosis ad fl. Irkut prope Mondam, anno 1830 leg. *Turczan*. Nec non prope limites rossicas, in Mongolia chinensi ex adverso Monda 1830 (*Turcz.*)”.

Lectotype (designated by Egorova 1999: 399): RUSSIA. BURYATIA: In humidis sabulosis ad fl. Irkut prope Mondam [Mondy], 1830, *N.S. Turczaninow*, *s.n.* (LE 01006885, digital image!; *isolectotype*: H 1305796, digital image!); *Lectosyntype*: MONGOLIA. KHÖVSGÖL: In Mongolia Chinensi, prope limites Rossicas ex adverso Mondae [Mondy], 1830, *N.S. Turczaninow*, *s.n.* (H 1305797, digital image!).

Habitat: Moist to wet, sandy or sandy-silty to loamy soils, in swampy meadows, sedge marshes, lakesides, riverbanks, and steppe depressions, less commonly on drier mountain-steppe slopes; from the upper forest belt to the alpine zone (100–2500(2800) m) (Egorova 1967, 1976c; Grubov 2001; Liang & Koyama 2010a; Krasnoborov 2012; M. H. Hoffmann, pers. comm.; SG, pers. obs.).

Distribution: Mainly Mongolian–S Siberian; the main distribution reaches from the Altai region in the West to N Mongolia, the Sayan Mts., and the Transbaikal region east of Lake Baikal (Egorova 1967, 1976c; Grubov 2001; Krasnoborov 2012; SG, pers. obs.). The species is further reported from a few other locations in Central Asia (e.g., Tian Shan; Polyakov 1958; Egorova 1999; Liang & Koyama 2010a). Plants from the Caucasus affiliated with *C. melananthiformis* (see Egorova 1967, 1999, 2006) are treated here under *C. melanantha* (see below).

Chromosome count (2n): Unknown.

Notes: Quite similar to *C. melanantha* and often regarded to be conspecific with it (Malyshev 1990; Gubanov 1996). *Carex melananthiformis* might also resemble *C. sabulosa* in some leaves and utricles characters, a taxon with which it has also been sometimes misidentified (Egorova 1999; SG, pers. obs.). The first molecular insights made contradictory suggestions regarding its relationship to other species of the *Carex sabulosa* group, being shown in some studies to be more closely related to *C. sabulosa* (Gebauer et al. 2015) and in others to *C. melanantha* (Massatti et al. 2016). However, further evidence is still needed, as confusion with the two taxa has been evidenced to happen frequently (see also Kukkonen 1998; Egorova 1999; SG & PJM, pers. obs.). Based on these observations and the fact that both *C. melanantha* and *C. sabulosa* have a sympatric occurrence within the main distribution range of *C. melananthiformis* in S Siberia, it can not be completely ruled out that the latter is a fertile introgressive product of the aforementioned species, which requires further investigation.

Regarding the disjunct occurrence of *C. melananthiformis* in the Caucasian region (Egorova 1967, 1999, 2006) it seems difficult to make a clear statement, since we could study only a few herbarium specimens from this region. However, these specimens showed, albeit mostly with a gynaeandrous terminal spike, rather elliptic to obovate utricles, (2.5)3–3.5 mm long, and densely approximated, overlapping spikes typical of *C. melanantha*. Furthermore, *C. melanantha* is also known from northern Iran (Elburz Mts., cit. in Kukkonen 1998; Amini Rad 2011, pers. comm.), and it displays a much more variable morphology at the edge of its distribution range, with less densely arranged spikes and often narrower leaves (see above). Since a biogeographic link between the Caucasus and Central Asia via the northern Iranian mountains is a well-known floristic pattern (i.e. Irano-Turanian region; e.g., Takhtajan 1986) also observed in other species of *Carex* sect. *Racemosae* (e.g., *C. caucasica*, *C. oligantha*–*C. melanocephala*) and considering the specimens seen, we treat the Caucasian *C. melananthiformis* plants as *C. melanantha*.

26. *Carex melanocephala* Turcz., Bull. Soc. Imp. Naturalistes Moscou 28(1): 334 (1855).
(Figs. 1: D, S2: AA, S6: A2–A2’).

Ind. loc.: “In alpinis Baicalensibus Urgudei, Schibet, ad. fl. Tessa et caet.”:

Lectotype (designated by Egorova 1999: 406): RUSSIA. BURYATIA: In alpinis Schibet et Urgudei, 1829, *N. S. Turczaninow, s.n.* (LE 01006886, digital image!; *isolectotypes*: LE 01006887, digital image!; LE 01006888, digital image!; LE 01006889, digital image!); *Lectosyntypes*: In alpinis Schibet et Urgudei, 1823, *N. S. Turczaninow, s.n.* (H 1054871, digital image!); In alpinis Schibet et Urgudei, 1829, *N. S. Turczaninow, s.n.* (H 1054872, digital image!); RUSSIA. ?TRANSBAIKAL: In humidis transbaicalensibus, 1829, *N. S. Turczaninow, s.n.* (P 00292521, digital image!; P 00292520, digital image!).

Habitat: Moist to wet, often swampy, open places, on gravel, slate and granite floors, in mountain grasslands and scrublands, typically along rivers, streams and springs, also in bogs and lakeshores; 1600–2700(2950) m (Kreczetovicz 1935b; Polyakov 1958; Egorova 1967, 1976c; Grubov 2001; Malyshev 1990; Nyambayar 2009; Liang & Koyama 2010a; Krasnoborov 2012; M. H. Hoffmann, pers. comm.).

Distribution: Central Asian–S Siberian; mainly occurring in the Altai–Sayan Mountains, spreading from E Tian Shan (China: Xinjiang) and E Kazakhstan (W Altai Mts.) in the West, eastwards to Central Mongolia, the E Sayan and S Lake Baikal regions (Polyakov 1958; Egorova 1999; Malyshev 1990; Nyambayar 2009; Liang & Koyama 2010a). An isolated occurrence is reported from the Udokan range northeast of Lake Baikal (Malyshev 1990; Egorova 1999).

Chromosome count (2n): 52 (Sokolovskaya & Strelkova 1948a; Egorova 1999: Altai).

27. *Carex moorcroftii* Falc. ex Boott, Proc. Linn. Soc. London 1: 288 (1846).

(Figs. S2: AB, S6: A3).

Holotype: INDIA. JAMMU & KASHMIR: In Indiâ Orientali, ad ripas fluv. Indi in planitie elatâ Tibetanâ, “Tibet Grass of Moorcroft”, *H. Falconer, s.n.* (K 000998993, digital image!).

= *Carex minxianensis* S. Yun Liang, Fl. Reipubl. Popularis Sin. 12: 520 (2000).

Holotype: CHINA. GANSU: Minhsien [Minxian], Suehloshan, 3000 m, damp place in valley, *T. P. Wang 4805* (PE 01842059, digital image!; *isotype*: PE 0184060, digital image!).

Habitat: Dry to wet sandy high-altitude steppes and grasslands, usually along streams or associated to chionophilous plant communities, occasionally on somewhat salty soils;

3000–5700 m (Egorova 1967; Noltie 1994; Dickoré 1995; Liang 2000; Liang & Koyama 2010a; M. H. Hoffmann, pers. comm.; SG, pers. obs.).

Distribution: Tibetan–(Sino–Himalayan); Mainly occurring on the (Qinghai–)Tibetan Plateau. Its distribution reaches the Karakoram Range and Kashmir in the West, and Central China (W Sichuan, E Qinghai, and S Gansu) in the East (Egorova 1967; Noltie 1994; Dickoré 1995; Liang 2000; Liang & Koyama 2010a).

Chromosome count (2n): Unknown.

Notes: *Carex minxianensis* was considered a species endemic of southern Gansu (Minxian) in Flora of China treatment (Liang & Koyama 2010a). Rare specimens of *C. moorcroftii* with darker inflorescences because of female glumes with narrow or wanting white-hyaline margin sometimes occur especially in the eastern limit of the distribution range of the species. Such plants were the basis for the description of *C. minxianensis*, which was allegedly separated from *C. moorcroftii* mainly by the female glumes without or with a narrow white-hyaline margin (vs. broad white-hyaline) and a rather loose inflorescence (vs. rather dense; see Liang & Koyama 2010a). Since these features can vary to a certain extent within *C. moorcroftii*, and the type locality of *C. minxianensis* directly adjoins occurrences of *C. moorcroftii* in E Qinghai and NW Gansu (SG & PJM, pers. obs.), we see no reason to consider *C. minxianensis* as a distinct entity. Accordingly, we treat it as a synonym of *C. moorcroftii*.

In the western distribution area (e.g., Jammu and Kashmir, Nepal) *C. moorcroftii* specimens with dark inflorescences can be found that approach *C. melanantha* (SG & PJM, pers. obs.). A hybridogenous origin of these specimens has been suggested (Dickoré 1995). Records of *C. melanantha* from Nepal very probably belong to *C. moorcroftii*. Other deviant specimens with rather loose inflorescence (i.e. the proximal spike somewhat distant) occasionally occur throughout its range (SG & PJM, pers. obs.).

28. *Carex norvegica* Retz., Fl. Scand. Prodr.: 179 (1779), nom. cons.

(Figs. 1: E, S2: AC, S6: A4).

Type (designated by Jørgensen & Elven 2012: 1324): NORWAY. NORDLAND: Rana, Stormdalen, in. Tverrelva, 12 Aug 1976, 660 m a.s.l., B. Berre, E. Forbord & S. E. Odden, s.n. (TRH-V 174383, digital image!), *typ. cons.*

= *Carex halleri* Gunnerus, Fl. Norveg. 2: 106 (1766), *nom. rej.*

Lectotype (designated by Jørgensen 2012: 1089): [icon in] Oeder, Fl. Dan. 3(7): tab. 403 (1768)—*Epitype* (designated by Jørgensen 2012: 1089): NORWAY. NORDLAND: Rana, Stormdalen, in. Tverrelva, 12 Aug 1976, 660 m a.s.l., B. Berre, E. Forbord & S. E. Odden, s.n. (TRH-V 174383, digital image!).

= *Carex alpina* Sw. ex Lilj., Svensk Fl. ed. 2: 26 (1789), *nom. illeg.*, non Schrank, Baier. Fl. 1: 298 (1789), nec Honck, Syn. Pl. Germ. 1: 374 (1792).

Ind. loc.: “i Torneå Lappm.”.

Lectotype (designated here): SWEDEN. NORRBOTTEN: Alp. T[orne] L[appmark], s.d., s.coll. [ex Herb. S. Liljeblad] (UPS [not databased], digital image!).

Note: The only specimen found to correspond to this name is here chosen as the lectotype (UPS [not databased]!). A single specimen deposited at the Linnean Society of London Herbarium (LINN-HS 1441-91, digital image!) collected and verified by O. Swartz himself with unknown locality seems to actually represent *C. media* R.Br. (SG, pers. obs.).

= *Carex vahlii* Schkuhr, Besch. Riedgräs. 1: 87 (1801).

Holotype: NORWAY. NOT LOCALIZED: [Norwegische Alpen] In alpinis Lapponicis, s.d., G. C. E. Oeder, s.n. [ex Herb. M. Vahl] (HAL 0103647!).

= *Carex norvegica* Retz. subsp. *conicorostrata* Kalela, Ann. Bot. Soc. Zool.-Bot. Fenn. “Vanamo” 19(3): 30 (1944).

Lectotype (designated here): RUSSIA. CHUKOTKA: An der Beringsstrasse: Luetke-Hafen, am Strande, 10 Aug 1881, A. & A. Krause 213a (LE 01006918, digital image!).

Note: Egorova (1999) already referred to its intermediary morphology and discussed the rare subsp. *conicorostrata* as a possible fertile hybrid of *C. media* and *C. norvegica*, which is here provisionally placed under synonymy of the letter (e.g., Malyshev 1990; Egorova 1999; Elven et al. 2011). With the exception of the sheet in LE that has been suggested an isotype by Egorova (1999), no putative type material could be found in any other herbaria, including Berlin (R. Vogt, pers. comm.), which might have been destroyed in the WWII. Accordingly, the LE specimen (LE 01006918!) is designated as lectotype (ICN, Art. 9.3, 9.11).

= *Carex norvegica* Retz. subsp. *inserrulata* Kalela, Ann. Bot. Soc. Zool.-Bot. Fenn. “Vanamo” 19(3): 25 (1944).

Lectotype (designated here): CANADA. NEWFOUNDLAND & LABRADOR: Torngat region, north shore of Duck Bight, 1 km north of Ryan’s Bay, 24 Aug 1926, R. H. Woodworth 103 (C 10010073, digital image!; *isolectotype*: NY 02308966, digital image!).

Note: Two collections that correspond to this name were found, and Kalela (1944) has not indicated a type and where it has been deposited. Thus, one of them is chosen as the lectotype.

= *Carex norvegica* Retz. subsp. *pusteriana* (Kalela) Á.Löve & D.Löve ex Chater, Bot. J. Linn. Soc. 76(4): 365 (1978). [see note below!]

≡ *Carex norvegica* Retz. subsp. *pusteriana* (Kalela) Á.Löve & D.Löve, Opera Bot. 5: 86 (1961), *non rite public*.

≡ *Carex angarae* Steud. subsp. *pusteriana* Kalela, Ann. Bot. Soc. Zool.-Bot. Fenn. "Vanamo" 19(3): 4 (1944).

≡ *Carex media* R.Br. subsp. *pusteriana* (Kalela) W.Schultze-Motel, in G.Hegi, Ill. Fl. Mitt.-Eur. [ed. 3], 2(1): 168 (1969).

Lectotype (designated by Wallnöfer 2004: 414): AUSTRIA. TYROL: Tirolia orientalis, Pustaria. In udis lapidosis alpinis et subalpinis ad Innervillgraten, solo schistoso, 1600–2300 m.s.m., s.d., leg. Gander, s.n., Flora exsiccata austro-hungarica, Nr. 1062 (WU 0029367, digital image!; *isolectotypes*: B 100296437!; GZU 000006126!; GZU 000006128!; NY 00743271, digital image!).

Note: There is confusion regarding the authorship of the name of *C. norvegica* subsp. *pusteriana*. The combination at subspecies rank of *C. norvegica* was introduced by Löve & Löve (1961), but considered as insufficiently published ('*non rite public*') by Chater (1978), who repeated the combination, whereby Chater (1978) misspelled the name as 'subspec. *pusterana*'. Since we agree with Chater (1978), the combination 'Á.Löve & D.Löve ex Chater' is proposed.

Habitat: Moist to wet, and often boggy, open places, on basic to acidic grounds, in tundra and mountain grasslands and scrublands, usually associated to bogs, springs and streams, less common in dry to moist stony pastures, often on N-exposed slopes, (Kalela 1944; Egorova 1966; Löve 1970; Egorova 1976a, b; Chater 1980; Schultze-Motel 1980; Kristinsson 1987; Kozhevnikov 1988; Kukkonen et al. 1998; Elven et al. 2005; Jermy et al. 2007; Wallnöfer 2004; SG, pers. obs.). In northern Europe (Iceland, Fennoscandia) and subarctic to arctic Eurasia from the edge of the forest belt and the tundra to the summits of the fells and mountains (0–1600(2000) m), in the Scottish Highlands at 550–900(1095) m, and in the Alps from 1500 to 2700 m (Schultze-Motel 1980; Kukkonen et al. 1998; Elven et al. 2005; Jermy et al. 2007; Wallnöfer 2004; SG, pers. obs.).

Distribution: Circumpolar; an arctic-alpine species with partly disjunct occurrences in the Eastern and Central Alps, the British Islands (Scottish Highlands), Northern Europe (including Iceland), and NW Siberia (Polar Urals Mts.) (Egorova 1966, 1976a, b; Schultze-Motel 1980; Kristinsson 1987; Egorova 1999; Elven et al. 2005; Jermy et al. 2007). The species is further reported from subarctic to arctic regions of northeastern Siberia and the Chukotka Peninsula (Egorova 1966; Kozhevnikov 1988; Sekretareva 2004; Elven et al. 2011), which is provisionally accepted here.

Chromosome count (2n): 56 (Roalson 2008 and references therein: Fennoscandia, Greenland [including subsp. *inserrulata*], Iceland, NE Siberia). Some of these reports can not be unambiguously assigned to *C. norvegica* or *C. media*, as they were published under the broader names *C. alpina* and *C. halleri*, and were not distinguished between both taxa. Rare reports of 2n = 54 (see Zhukova & Petrovsky 1980; Egorova 1999; Roalson 2008) from NE Siberia have sometimes been assigned to *C. media* (e.g., Elven et al. 2011). Reports of 2n = 66 (Tanaka 1942, 1948) seem erroneous and may refer to other species (see also Elven et al. 2011).

Notes: This species is often divided into several usually weakly differentiated subspecies, sometimes including *C. media* (syn. *C. norvegica* subsp. *inferalpina*), which has been treated separately here (Kalela 1944; Chater 1980; Murray 2002a). Plants from the E Alps have been treated as *C. norvegica* subsp. *pusteriana* but no clear separation has been found either by molecular (Gebauer et al. 2015) nor quantitative morphological data (Wallnöfer 1988, 2004; Więclaw et al. 2016; SG, pers. obs.).

Carex norvegica is rather variable with respect to the indument of the upper part of the utricles (smooth or serrulate), the transition from the body into the beak (abruptly or gradually), as well as the length of the female glumes in relation to the utricles (e.g., Kalela 1944; Egorova 1966, 1999; Murray 2002a), which is sometimes observed even within the same individual (SG, pers. obs.). Some of these characters have been used for delineation of further subspecies, i.e. *C. norvegica* subsp. *inserrulata* from NE North America and W Greenland and *C. norvegica* subsp. *conicorostrata* from Behringia (Kalela 1944; but see Egorova 1999), which are included here under a broadly circumscribed *C. norvegica* (see Egorova 1999; Murray 2002a). Egorova (1999) discussed the putative hybridogenous origin of *C. norvegica* subsp. *conicorostrata*, which is only known from the Chukot Peninsula, suggesting it to be resulting from the cross between *C. norvegica* and *C. media*.

Most reports from east of the Ural Mountains, especially from Central Asia, should be considered with caution, because *C. norvegica* has been frequently confused with the rather widespread *C. media* (Malyshev 1990; Gubanov 1996; Elven et al. 2011; Gebauer et al. 2015). In addition, we follow Malyshev (1990) by treating the Central Asian, S and SE Siberian plants, which were treated by some authors as *C. norvegica*, under *C. media* (including *C. mimula* that is reduced to synonymy with *C. media*; see also comments under this species).

29. *Carex obscura* Nees, in R. Wight, Contr. Bot. India: 126 (1834).

(Figs. 1: F, S2: AD, S7: A5).

Ind. loc.: “Nepalia; *Royle 112*”.

Lectotype (designated here): ?NEPAL. NOT LOCALIZED: Thalma, s.d., *J. F. Royle 112*’ (K 000998978, digital image!; *isolectotype*: K 000998981, digital image!).

Note: Two sheets in K correspond to *C. obscura* Nees and ‘*Royle 112*’. Only one sheet (K 000998978!) directly refers to a geographic location, and is, therefore, chosen as the lectotype.

= *Carex obscura* Nees var. *brachycarpa* C.B. Clarke in J.D. Hooker, Fl. Brit. India 6: 731 (1894).

Ind. loc.: “Himalaya, alt. 10–12,000 ft., from Simla, *Duthie*, to Sikkim, *J. D. Hooker, &c.*”.

Lectotype (designated here): INDIA. SIKKIM: Sikkim, Kankola, 12,000 ft., 22 Aug 1849, *J. D. Hooker, s.n.* (K 000061660, digital image!; *isolectotype*: K 000998984, digital image!).

Note: There are two sheets in K corresponding to the name that also bear the handwritings of C. B. Clarke (listed above). Since no type specimen is indicated, one of them (K 000061660!) is chosen as the lectotype. It is mounted together with another collection of this species (Lachen, 11 Jun 1849, 11,000ft, *J. D. Hooker, s.n.*; K 000998983).

= *Carex souliei* Franch., Bull. Soc. Philom. Paris VII, 7: 35 (1895).

Ind. loc.: “Chine occid.: marais á Tatsienlou, prov. de Su-tchuen (*Farges*)”.

Lectotype (designated here): China. Sichuan: Tatsienlou [Kangding], Thibet oriental, Tongolo (Principauté du Kiala), 30 Jul 1893, *J. A. Soulié 412* (P 00292649, digital image!; *isolectotype*: E 00386820, digital image!).

Note: No collection by P. G. Farges, which corresponds to the indicatio locotypica and the name *C. souliei* Franch., was found. However, both collections listed above correspond to the protologue and they further bear handwritings of the nomenclatural name by A. R. Franchet (see also Marhold et al. 2015). Thus, we consider these collections as original material, which A. R. Franchet has been provided for his description, and one of them (P 00292649!) is designated as lectotype.

Habitat: On moist to wet, often peaty soils, in clearings of coniferous forests, along riverbanks and streams, and other wet places like bogs or wet meadows; from the upper montane forest belt to above tree line (2500–4100(4380) m) (Koyama 1975, 1978a; Noltie 1994; Kukkonen 1998, 2001; Liang 2000; Dai et al. 2003; Liang & Koyama 2010a; SG, pers. obs.).

Distribution: Sino–Himalayan; from N Pakistan to W Sichuan and NW Yunnan (Koyama 1975, 1978a; Noltie 1994; Dickoré 1995; Kukkonen 1998, 2001; Liang 2000; Dai et al. 2003; Liang & Koyama 2010a).

Chromosome count (2n): 56 (Yano et al. 2015: W Nepal).

Notes: This widely distributed Sino-Himalayan species is often divided into two varieties, namely a western var. *obscura* and an eastern var. *brachycarpa* (Koyama 1975, 1978a; Noltie 1994; Dickoré 1995; Kukkonen 1998, 2001; Liang & Koyama 2010a). Such division was mainly based on minor differences in the utricle shape, i.e. almost beakless (var. *obscura*) vs. short beaked (var. *brachycarpa*) (e.g., Clarke 1894; Srivastava 1996). The studies of herbarium materials (including high-resolution images of types) showed that this character seems to be unstable, and that almost beakless as well as short-beaked utricles were found indistinctly in the western and eastern Himalayas, and even within a single individual (SG, pers. obs.). Therefore, *C. obscura* is treated here in a broader concept, without division into any infraspecific taxa.

30. *Carex oligantha* Steud., Syn. Pl. Glumac. 2: 203 (1855).

(Figs. S2: AE, S7: A6).

Ind. loc.: “In paludibus alpinis Caucasi occidentalis (alt. 1300–1450 hexap.)”.

Lectotype (designated by Egorova 1991: 1743): RUSSIA. KABARDINO-BALKAR: In paludibus alpinis Caucasi occidentalis, 1829, 1830, d[et.] 13 Jul 1831, *C. A. Meyer 189* (LE 01039495, digital image!; *isolectotypes*: LE 01039496, digital image!, P 00292522, digital image!); *Syntype*: In paludosis alpinis Caucasi occidentalis, 1831, *C. A. Meyer, s.n.* (H 1060626, digital image!).

Note: The misspelling of the name ‘*C. pauciflora* C.A.Mey.’ by Steudel (1855) instead of ‘*C. parviflora* Host’, with which Meyer (1831) initially affiliated the Caucasian plants with a question mark (Verzeichn. Pfl. Cauc. Casp.: 30), has already been demonstrated by Egorova (1991). Later, Kükenthal (1909) treated the species as ‘*C. parviflora* C.A.Mey.’, placing the Central Asian–Southern Siberian *C. melanocephala* Turcz. in its synonymy, which has long persisted in the literature, but especially on herbarium labels. Kükenthal (1909) further affiliated some specimens seen by him from the Caucasus to *C. nigra* Bellardi ex All. (= *C. parviflora* Host) and treated the name ‘*C. oligantha* Steud.’ separately as *species dubia*, which may have contributed to the long-lasting confusion regarding *C. oligantha* Steud., *C. parviflora* Host, and *C. melanocephala* Turcz.

Habitat: On wet open alpine habitats, like damp grasslands and scrublands, bogs, wet moraines, or along riverbanks, springs and streams; 2200–2600(3400) m (Kreczetovicz 1935b; Grossgejm 1940; Galushko 1978; Nilsson 1985; Kukkonen 1998; Egorova 1999; Chandjian 2001; SG, pers. obs.).

Distribution: A Caucasian endemic rare throughout its entire range. It spans from the Caucasus (Greater and Lesser Caucasus ranges) in the North, through E Turkey, to the mountain ranges of S Armenia (Nilsson 1985; Kukkonen 1998; Egorova 1999; Chandjian

2001; Egorova 2006). Interestingly, most herbarium specimens were collected in the Russian part of the northern Greater Caucasus along a line from Teberda (Karachay-Cherkess Republic) across the Mt. Elbrus area (Kabardino-Balkar) to Akhsau (North Ossetia-Alania), where the species seems more abundant (Grossgejm 1940; Galushko 1978; SG, pers. obs.). Indications about its occurrence in NW Iran (Nilsson 1985) need confirmation (M. Amini Rad, pers. comm.; SG, pers. obs.).

Chromosome count (2n): 52 (Sokolovskaya & Strelkova 1948b: Central Caucasus), 82 (Hayirlioğlu-Ayaz et al. 2001: NE Anatolia [erroneous?]).

Notes: *Carex oligantha* is similar to the N Central Asian–S Siberian *C. melanocephala* (Kreczetowicz 1935b; Egorova 1999; Gebauer et al. 2015), and it has also been often confused with *C. aterrima* subsp. *medwedewii* in the Caucasus (Gebauer et al. 2015; see above). As a consequence of its striking rarity and the scarce number of collections available, the morphological variation of *C. oligantha* does not appear to be well established (see also Nilsson 1985). The utricles seem to vary in cross-section from usually trigonous or biconvex to compressed-trigonous (J. Koopman, pers. comm.; SG, pers. obs.); the same variation is sometimes also found in *C. melanocephala* (SG, pers. obs.). This variation was also taken into account in the present key to facilitate their identification.

31. *Carex parviflora* Host, Icon. Descr. Gram. Austriac. 1: 64, t. 87 (1801).

(Figs. S2: AF, S7: A7).

Ind. loc.: “In alpium Judenburgensium praecipitiis”.

Lectotype (designated here): AUSTRIA. STYRIA: Habitat in alpius Styria, s.d., *N. T. Host, s.n.* (Herb. Willdenow) (B-W 17186-010!).

Note: No type of *C. parviflora* Host has ever been designated. The majority of Cyperaceae in Host’s herbarium was destroyed during the WWII, so that no corresponding specimen in the remaining’s of the Herbarium Host neither in W (E. Vitek, pers. comm.) nor in B (R. Vogt, pers. comm.; SG, pers. obs.) could be found. However, one specimen in Willdenow’s herbarium deposited in Berlin (B-W 17186-010!) seems to represent original material of Host, since it corresponds to the protologues and clearly refers to ‘Host. W[ien = Vienna]’, and is selected here as the lectotype.

= *Carex nigra* Bellardi ex All., Fl. Pedem. 2: 267 (1785), *nom. illeg.*, non (L.) Reichard, Fl. Moeno-Francof. 2: 96 (1778).

Ind. loc.: “In summis alpius Pedemontii, & Sabaudiae non rara *Cl. Bellardi*”.

Holotype: ?ITALY: PIEDMONT: Piedmont, s.d., leg. *C. A. L. Bellardi* (TO? [not seen!]).

Note: Usually cited as ‘*C. nigra* All.’ (e.g., Govaerts et al. 2018+), we propose to use the author spelling ‘Bellardi ex All.’ as it was regularly overlooked that the description of this (and 22 other) species and related

information in C. Allioni's *Flora Pedemontana* was prepared by C. A. L. Bellardi (see Perry & McNeill 1986; A. Selvaggi, pers. comm.). In his *Flora Pedemontana*, Allioni acknowledged Bellardi's contributions in the preface of *Flora Pedemontana* (Allioni 1785, vol. 1: IV) and consequently cited Bellardi for the locality information (ind. loc.), marking the new species of which he received information from him with a “†”. Thus, correction of the authorship to ‘*C. nigra* Bellardi ex All.’ seems necessary (ICN, Art. 46.2) to take this often overlooked fact into account (A. Selvaggi, pers. comm.).

= *Carex pirinensis* (Acht.) Acht., Gen. Carex Bulgar.: 65 (1957).

≡ *Carex nigra* Bellardi ex All. var. *pirinensis* Acht., Izv. Carsk. Prir. Inst. Sofija 11: 72 (1938). (Basionym).

Holotype: BULGARIA. BLAGOEVGRAD: In graminosis alpinis sub cac Eltepe mt. pirini, 2000–2350 m.s.m., solo granitico, 24 Aug 1936, B. Achtarov, s.n. (SOM 000009859, digital image!).

Habitat: On dry to wet, mesotrophic, usually fine-grained loam and clay soils over calcareous or dolomitic rocks, but also on granite, in meadows, screes, rock crevices, and along meltwater streams; typical plant of chionophilous, plant communities of the subalpine and alpine belts; 1800–3200 m (Chater 1980; Schultze-Motel 1980; Luceño 2008; Bartók et al. 2016; SG & PJM, pers. obs.).

Distribution: European; from the northern Iberian Peninsula (Cantabrian Mountains, Pyrenees) in the west, throughout the Alps to the NW Dinarids and the central Apennines (Abruzzi), and from the Carpathians (e.g., Tatra Mts., Bucegi Mts., Făgăraș Mts.) to the Balkan Peninsula (Pirin Mts.) (Chater 1980; Schultze-Motel 1980; Luceño 2008; Koopman 2011; Assyov et al. 2012; Bartók et al. 2016 and references therein; Bartolucci et al. 2018).

Chromosome count (2n): 54 (Roalson 2008 and references therein); (1n): 27 (Dietrich 1972).

Notes: Egorova (1999) compared *C. pirinensis* with *C. aterrima* subsp. *medwedewii*. The examination of the type material clearly reveals it is *C. parviflora*. Egorova's confusion might be probably due by the fact that *C. parviflora* is a European endemic entirely absent from Russia, so she probably did not know very well the variation of this species.

32. *Carex peiktusani* Kom. [*‘peiktusanii’*], Trudy Imp. S.-Peterburgsk. Bot. Sada 18: 445 (1901).

(Figs. S2: AG, S7: A8).

≡ *Carex hancockiana* Maxim. var. *peiktusani* (Kom.) Kük., Pflanzenr. (Engler) IV, 20(38): 395 (1909).

Lectotype (designated by Egorova 1999: 383): KOREA, N., RYANGGANG: In paludibus planitiei elevata Peischan vel Peiktusan, ad trajectum Abuzsa kogar, Korea Septentr. phov. Kensong, 21 Jun 1897, *V.L. Komarov, s.n.* (LE 01001919, digital image!); *Syntype*: In paludibus herbosis et ad ripas rivulorum in planitiei elevate Pei schan ad trajectum Abuzsa kogar, Korea Septentr., 12 Jun 1897, *V.L. Komarov, s.n.* (LE 01001920, digital image!).

Habitat: Calcareous, along forests, riversides and rock crevices; the lower and middle forest belt to subalpine regions ((800)950–1700 m) (Kreczetovicz 1935b; Ohwi 1936, 1965; Kozhevnikov 1988; Egorova 1999; Liang 2000; Liang & Koyama 2010a; Hoshino et al. 2011).

Distribution: East Asian; from NE China (E Shanxi, S Hebei, E Shandong, S Liaoning, S Jilin, and S Heilongjiang) and Korea to the Russian Far East (S Ussuri region), as well as Japan (Central Honshu) (Kreczetovicz 1935b; Ohwi 1936, 1965; Kozhevnikov 1988; Egorova 1999; Liang 2000; Liang & Koyama 2010a; Hoshino et al. 2011).

Chromosome count (2n): Unknown.

33. *Carex polymascula* P.C.Li, Acta Bot. Yunnan. 12: 140 (1990).

(Figs. S3: AH, S7: A9).

Holotype: CHINA. SICHUAN: Xiangchen, Mons Wumingshan, alt. 3800 m, in abietetis, 07 Aug 1983, *Grup. Veget. Exped. Qinghai-Xizang 4855* (PE 00030573, digital image!);

Paratype: Xiangchen, Mons Wumingshan, alt. 4200 m, in declivitatibus, 07 Aug 1983, *L. Kai-yong et al. 2639* (PE 00030572, digital image!).

Habitat: Gravelly to sandy and dry to moist soils, in alpine and subalpine grasslands and scrublands or in open upper montane coniferous forests; 3700–4460(4650) m (Li 1990; Liang 2000; Liang & Koyama 2010a; SG, pers. obs.).

Distribution: Endemic to S Central China; NE Hengduan Mountains (W Sichuan) (Li 1990; Liang 2000; Liang & Koyama 2010a).

Chromosome count (2n): Unknown.

34. *Carex popovii* V.I.Krecz., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 181 (1935).

Holotype: UZBEKISTAN. SURXONDARYO: Kugitang [Köytendag] Mts., near the village Kempyr-tube [Kampyrtepa], 29 Apr 1915, *M.G. Popov 301bis* (TAK!, transferred to TASH 0000145, digital image!);

Topotypes: Kugitang [Köytendag] Mts., near the village Kempyr-tube [Kampyrtepa], 28 Apr 1915, *M.G. Popov 284* (LE 00050393, digital

image!); Kugitang [Köýtendag] Mts., near the village Kempyr-tube [Kampyrtepa], 28 Apr 1915, *M.G. Popov 300* (LE 00050394, digital image!).

Distribution: SW Asian–Central Asian; N Iran (Elburz Mts., subspec. *brunneola*) and NE Iran (Khorasan, Mt. Binaloud), S Turkmenistan to NE Afghanistan (Hindukush) and N Pakistan (Chitral, Darkot), the Pamiro-Alai (Uzbekistan, Tajikistan) to the southern and western Tian Shan (subspec. *popovii*) (Kreczetovicz 1935a, b, c, 1941; Raymond 1965; Stewart 1972; Egorova 1976c, 1999; Kukkonen 1984, 1998, 2001; Amini Rad 2007, 2008, 2011; SG, pers. obs.).

Notes: Kreczetovicz (1935a, b) introduced the names *C. popovii* (Kreczetovicz 1935a: 181, in Byull. Sredne-Aziatsk. Gosud. Univ.) and *C. decaulescens* (Kreczetovicz 1935b: 477, in Fl. URSS) nearly simultaneously for plants from Central Asia. Later, Kreczetovicz (1941) noted the great similarity between both taxa and tried to reveal distinctions between them (e.g., appearance of the lowest proximal bract, size of the utricles, or proportion and length of the female glumes compared to the utricles). Egorova (1976c) did not find clear differences after the examination of the type specimens of the two names, and reduced *C. popovii* to synonymy with *C. decaulescens*. While working on her monograph, Egorova (1999) noted that the name *C. popovii* had priority, as it was published a month earlier than *C. decaulescens*, thus she consequently inverted the synonymy. However, this remained largely unnoticed (Kukkonen 2001; Govaerts et al. 2016), and the name *C. decaulescens* remained in use.

Kukkonen (1984) proposed two further infraspecific taxa within *C. decaulescens*: *C. decaulescens* subsp. *alsia* (Raymond) Kukkonen from Pakistan (Karakoram) and *C. decaulescens* subsp. *brunneola* Kukkonen from N Iran (Elburz Mts.). Both taxa are known only from a few collections, and thus their true morphological variation remains largely non-established, resulting in differing views on their taxonomic value to the point of rejection (Raymond 1965; Kukkonen 1984; Dickoré 1995; Egorova 1999; Kukkonen 2001). Recently, populations from NW Iran (Tehran, Elburz Mountains, Tochal Mt.) were rediscovered, and the combination *C. popovii* subsp. *brunneola* (Kukkonen) Amini Rad was proposed (Amini Rad 2007, 2015). Examination of collections of these Iranian populations showed strong similarity with *C. popovii* from Central Asia, but also confirmed the distinctive features provided in the key and stated by Kukkonen (1984) in his infraspecific treatment (SG, pers. obs.). On the contrary, the critical examination of the protologue and additional herbarium specimens of the Pakistani subspec. *alsia* revealed that the morphological features suggested for distinguishing it from the Central Asian

C. popovii s.str. showed considerable overlapping (SG, pers. obs.). Therefore, *C. decaulescens* subsp. *alsia* is treated here under *C. popovii*.

Carex popovii seems to be rather polymorphic with respect to some of the characters used to delineate the above mentioned infraspecific units (i.e. the size of the utricles, proportion and ratio of the female glumes compared to the utricles, plant height, and appearance of the lowest proximal bract; Kreczetovicz 1935a, b, c, 1941; Egorova 1976c, 1999; Kukkonen 1984; SG pers. obs.). The situation is further complicated by the confusion with other sympatric species, as *C. caucasica* (see above).

34a. *Carex popovii* subsp. *popovii*

(Figs. S3: AJ, S7: A11).

= *Carex caucasica* Steven var. *abbreviata* Litv., Trudy Bot. Muz. Imp. Akad. Nauk 7: 88 (1910).

Ind. loc.: “Prov. Fergana, in valle Alaj, ad torrentem Kulduk, in ripis, 10.000’, 27 Junii 1895 fr. (*Korshinsky*). Ibid. ad torrentem Kok-ssu, in ripis muscosis, 10.000’, 2 Julii 1905 fr. (*Korshinsky*)”.

Lectotype (designated here): KYRGYZSTAN. ?OSH: Prov. Fergana, in valle Alaj, ad torrentem Kulduk, in ripis, 10.000’, 27 Jun 1895, *S. I. Korshinsky, s.n.* (LE 00050494, digital image!); **Syntype:** Prov. Fergana, in valle Alaj, ad torrentem Kok-ssu, in ripis muscosis, 10.000’, 2 Jul 1905, *S. I. Korshinsky, s.n.* (LE 00050493, digital image!).

Note: Two different collections were mentioned in the protologue without specification of a type. The first collection (LE 00050494!) is chosen as the lectotype, here.

= *Carex caucasica* Steven var. *bracteata* Litv., Trudy Bot. Muz. Imp. Akad. Nauk 7: 89 (1910).

Holotype: KYRGYZSTAN. ?OSH: Prov. Fergana, in valle Alaj, in ripis torrentis Kulduk, 10.000’, 27 Jun 1895, *S. I. Korshinsky, s.n.* (LE 00050495, digital image!).

= *Carex decaulescens* V.I.Krecz. in V.L.Komarov (ed.), Fl. URSS 3: 599 (1935).

Holotype: KYRGYZSTAN. NOT LOCALIZED: Tian-Schan occidentalis, ad. riv. Andaulgan, infra confluvionem, 23 Jul 1897, *B. Fedtschenko, s.n.* (LE 00050395, digital image!); **isotype:** LE 00050395, digital image!).

= *Carex decaulescens* V.I.Krecz. subsp. *alsia* (Raymond) Kukkonen, Ann. Bot. Fenn. 21: 387 (1984).

≡ *Carex alsia* Raymond, Biol. Skr. 14(4) (Symb. Bot. Afghanicae 6): 23 (1965).
(Basionym).

Lectotype (designated here): PAKISTAN. GILGIT-BALTISTAN: Chitral, Khot An, N of Mastuj, between Turikho and Mastuj rivers, 13000 ft, on rock ledges, 11 Jul 1958, *J. D. A. Stainton* 2839 (BM 000574309!).

Note: The putative type in Vienna cited by Kukkonen (1984) could not be found there (H. Rainer, pers. comm.). Kukkonen (1984) himself has apparently only seen the BM specimen (marked as an isotype with question mark). Therefore, the specimen BM 000574309! is hereby designated as lectotype (ICN, Art. 9.3, 9.11).

Habitat: Moist to wet soils on mountain environments, in grasslands, riverbanks, along streams, springs and rivulets, and also on rocky habitats; (2000)2400–3960 m (Kreczetovicz 1935a, b, c, 1941; Raymond 1965; Egorova 1976c; Kukkonen 1984, 1998; Egorova 1999; Kukkonen 2001; Amini Rad 2008, 2011; M. H. Hoffmann, pers. comm.; SG, pers. obs.).

Distribution: Central Asian (mainly Pamiro-Alai and Tian Shan ranges); from NE Iran (Khorasan, Mt. Binaloud) and S Turkmenistan southwards to NE Afghanistan (Hindukush) and N Pakistan (Chitral, Darkot) through the Pamiro-Alai (Uzbekistan, Tajikistan) to the southern and western Tian Shan (Kyrgyzstan, Kazakhstan) (Kreczetovicz 1935a, b, c, 1941; Raymond 1965; Stewart 1972; Egorova 1976c, 1999; Kukkonen 1984, 1998, 2001; Amini Rad 2008, 2011; SG, pers. obs.).

Chromosome count (2n): 54 (Sokolovskaya and Strelkova 1939; Egorova 1999: Pamir).

Notes: A single collection from Afghanistan (Panshir valley, above Mukeni, *Hedge & Wendelbo* 5266, E 00353981!) previously affiliated with *C. caucasica* by Kukkonen (1998) corresponded to *C. popovii* subsp. *popovii*. The careful study of the shape and the size of the utricles and female glumes showed that they differ considerably from *C. caucasica*, and were a fairly good match of *C. popovii* subsp. *popovii* (SG, pers. obs.).

34b. *Carex popovii* subsp. *brunneola* (Kukkonen) Amini Rad, Iran. *J. Bot.* 21: 87 (2015).

(Figs. S3: AH, S7: A10).

≡ *Carex decaulescens* V.I.Krecz. subsp. *brunneola* Kukkonen, *Ann. Bot. Fenn.* 21: 388 (1984).

Holotype: IRAN. TEHRAN: Persia, Teheran, in declivibus ad pedes Montium Elburz supra vicum Darband et declivia montis Kuhha-ye Touchal, 2000–3800 m, in pratis montanis, 29 Apr 1973, *J. Soják* 7079 (PR! [not seen!] according to Kukkonen 1984).

Note: The type in Prague seen and cited by Kukkonen (1984) that was required for a loan by us could not be found at the moment (O. Šida, pers. comm.) and was therefore not seen by us. Inquiries in other herbaria

related to the work on the *Flora Iranica* project (i.e. H, W, and WU) were also unsuccessful (H. Rainer, pers. comm.; W. Till, pers. comm., H. Väre, pers. comm.). If the type is not found in the near future, designation of a neotype would be needed, which we have refrained from doing here.

Habitat: Poorly known; moist alpine meadows; 2500–3000 m (Kukkonen 1984, 1998; Amini Rad 2007, 2011).

Distribution: Endemic to N Iran (Elburz Mountains); known only from the type locality at Mt. Tochal (Kukkonen 1984, 1998; Amini Rad 2007, 2011).

Notes: Further collections of *C. popovii* subsp. *brunneola* are needed to better understand the morphological variation of this rather isolated taxon. This would also allow molecular studies concerning a possibly stronger differentiation from *C. popovii* subsp. *popovii*.

35. *Carex praeclara* Nelmes, Hooker's Icon. Pl. 35: tab. 3403 (1940).

(Figs. S3: AK, S7: A12).

Holotype: CHINA. XIZANG: Tibet, Salween–Tsangpo divide, 16,000–17,000ft, 30 Sep 1933, *F. Kingdon-Ward 10878* (BM 000797620, digital image!; *isotype*: K 000999211, digital image!).

Habitat: Open sandy places or turf between scree, frequently on cushions of *Carex parvula* O.Yano [= *Kobresia pygmaea* (C.B. Clarke) C.B. Clarke; Global *Carex* Group 2015]; belonging to high-altitudinal periglacial vegetation, between (4500)4800–5700 m (Nelmes 1940; Noltie 1994; Dickoré 1995; Srivastava 1996; Liang 2000; Dai et al. 2003; Liang & Koyama 2010a; SG, pers. obs.).

Distribution: Endemic to S and SE Tibet (Xizang), with a few occurrences in N Sikkim and NW Yunnan (Nelmes 1940; Noltie 1994; Srivastava 1996; Liang 2000; Dai et al. 2003; Liang & Koyama 2010a).

Chromosome count (2n): Unknown.

36. *Carex pseudobicolor* Boeckeler, Beitr. Cyper. 1: 44 (1888).

(Figs. S3: AL, S7: A13).

Ind. loc.: “Himalaya occident., coll. *Schlagintweit no. 8643*”.

Lectotype (designated here): INDIA. UTTARAKHAND: Western Himalaya, Prov. Garhvál [Garhwal], 10350–13800 ft, 01–31 Aug 1855, *Herb. A. von Schlagintweit 8643* (LE 00010622, digital image!).

Note: The type in B (cited by Kükenthal 1909) mentioned by Kukkonen (1998) with a question mark could not be found there (R. Vogt, pers. comm.) and may have been destroyed during the WWII. Therefore, a duplicate specimen of ‘*Schlagintweit 8643*’ (LE 00010622!) is hereby selected as the lectotype.

= *Carex alpina* Sw. ex Lilj. subsp. *infuscata* var. *erostrata* (Boott) Kük., Pflanzenr. (Engler) IV, 20(38): 386 (1909), *pro parte* [see note below!].

≡ *Carex infuscata* Nees var. *erostrata* (Boott) T.Koyama, Acta Phytotax. Geobot. 17(4): 97 (1958), *pro parte* [see note below!].

≡ *Carex alpina* Sw. ex Lilj. var. *erostrata* Boott, Ill. Carex 1: 71, t. 194, fig. 2 (1858). (Basionym).

Ind. loc.: “In Himalaya alpina, ad Kumaon, *Royle, n. 61*, et ad Gugu, alt. 14,500–15,500 ped., *Strachey et Winterbottom*”.

Lectotype (designated here): INDIA. HIMACHAL PRADESH: Lippa in Kunawur [Kinnaur], s.d., *J. F. Royle 61* (K 000998964, digital image!; *isolectotype:* K 000998967, digital image!).

Note: Two corresponding sheets were located in Kew, and one of them (K 000998964) is, therefore, designated as lectotype. The treatment of *C. pseudobicolor* by some authors as a variety of *C. infuscata* (Kükenthal 1909; Koyama 1958), which is treated here separately, is confusing since most of the specimens affiliated under ‘var. *erostrata*’ were reported from outside the actual distribution range of *C. pseudobicolor* (see Kükenthal 1909; Koyama 1958; see also below), most probably resulting from confusion with *C. infuscata* s.str. and *C. gracilentata*.

Habitat: Moist to wet mountain open habitats, like in snow-patches, meltwater-streams and rivulets, moraines, and alpine meadows; chionophilous (often with co-occurring *Carex nivalis* Boott, *C. ovoidispica* O.Yano [= *Kobresia nitens* C.B.Clarke; Global *Carex* Group 2015]), between 2700–4420(5000) m (Stewart 1972; Dickoré 1995; Kukkonen 1998; Dickoré & Nüsser 2000; Kukkonen 2001; Haq et al. 2011, 2012; SG, pers. obs.).

Distribution: W Himalayan; from E Afghanistan and N Pakistan to NW India (Jammu and Kashmir, Himachal Pradesh, Uttarakhand) (Stewart 1972; Dickoré 1995; Kukkonen 1998, 2001; Haq et al. 2011, 2012; pers. obs.). Reports from the Tibet Autonomous Region of China (Kukkonen 1998, 2001) and the Pamir region (see Koyama 1958; cited as *C. infuscata* var. *erostrata*) seems erroneous or need confirmation (e.g., Egorova 1967).

Chromosome count (2n): Unknown.

Notes: For confusion with *C. gracilentata* see notes under the latter name.

37. *Carex psychrophila* Nees, in R. Wight, Contr. Bot. India: 127 (1834).

(Figs. S3: AM, S7: A14).

Ind. loc.: “Nepalia, Royle n. 113”.

Lectotype (designated here): INDIA. UTTARAKHAND: Kedarkanta [Kedarkantha], Ind. orient., s.d., *J. F. Royle 113* (K 000999035, digital image!; *isolectotypes*: s.loc., s.d., *Herb. Royle n. 113* (K 000999036, digital image!; K 000999037, digital image!)).

Note: There are several sheets deposited in K corresponding to ‘Royle 113’ and the name *C. psychrophila* Nees. The lectotype designated here (K 000999035!) is the only one that also contains geographic information.

= *Carex asperula* Nees, in R. Wight, Contr. Bot. India: 124 (1834).

Ind. loc.: “Nepalia, Royle n. 111”.

Lectotype (designated here): ?INDIA. HIMACHAL PRADESH: s.loc., s.d., *J.F. Royle 124* (K 000999038, digital image!; *isolectotype*: K 000999041, digital image!).

Note: There are two sheets of ‘Royle 124’ found in K. Thus, one (K 000999038) is chosen as the lectotype.

= *Carex parvibracteata* Nees, in R. Wight, Contr. Bot. India: 125 (1834).

Ind. loc.: “Nepalia, Royle n. 124”.

Holotype: ?INDIA. HIMACHAL PRADESH: Seran ni Kunawur [Kinnaur], s.d., *J.F. Royle 124* (K 000999040, digital image!).

= *Carex celsa* Boott, Ill. Carex 3: 108 (1862).

Ind. loc.: “In Nipalia, *Herb. Wallich, n. 3393*”.

Lectotype (designated here): NEPAL. NOT LOCALIZED: Nipal, 1821, *N. Wallich 3393* (*Herb. Wallich Cat. No. 3393*) (K 000999042, digital image!; *isolectotypes*: K 000767927, digital image!; K 001119309, digital image!).

Note: The lectotype designated here is the only one that bears Boott’s handwriting. The other Wallich’ specimens (K 000999042, K 000767927) are mounted on the same sheet, and seem to further contain a depauperate specimen of another unidentified species, which was already noted by C. B. Clarke.

Habitat: Damp to marshy soils on mountain slopes; (1500)2700–3660 m (Raymond 1965; Noltie 1994; Dickoré 1995; Srivastava 1996; Kukkonen 1998, 2001; Liang & Koyama 2010b; Haq et al. 2011, 2012).

Distribution: Sino-Himalayan; from E Afghanistan and the Jammu and Kashmir region in the west across the entire, but primarily the more humid outer Himalayas to southern Central China (S Tibet, Sichuan) in the east (Raymond 1965; Noltie 1994; Dickoré 1995; Srivastava 1996; Kukkonen 1998, 2001; Liang & Koyama 2010b; Haq et al. 2012; SG, pers. obs.).

Chromosome count (2n): Unknown.

Notes: This species was previously placed in the apparently polyphyletic *C. sect. Aulocystis* (Global *Carex* Group 2016; SG et al., unpubl. data), but its sectional affiliation was based entirely on phenetic affinities (Kükenthal 1909; Dickoré 1995; Kukkonen 1998, 2001; Liang & Koyama 2010b). However, the affinity of this species to *C. sect. Racemosae* was already emphasized by previous authors, some as early as Drejer (1844) and Clarke (1908). More recently, Noltie (1994) also referred to its similarity with *C. duthiei*, with which *C. psychrophila* can also occasionally be confused.

According to our own observations, *C. psychrophila* is in fact more similar to the representatives of *C. sect. Racemosae* than to those of *Carex sect. Aulocystis*, with perhaps the exception of its usually conspicuously long-beaked utricles, whose beaks are often somewhat bent and scabrous above (Noltie 1994; Kukkonen 1998, 2001; Liang & Koyama 2010a, b; SG & PJM, pers. obs.). First molecular insights have unequivocally demonstrated its affiliation to *C. sect. Racemosae* instead to any of the subgroups of the highly polyphyletic *C. sect. Aulocystis* s.l. (SG et al., unpubl. data).

38. *Carex sabulosa* Turcz. ex Kunth, Enum. Pl. 2: 432 (1837).

(Figs. S3: AN, S7: A15).

≡ *Carex melanantha* C.A.Mey. var. *sabulosa* (Turcz. ex Kunth) Kük., Pflanzenr. (Engler) IV, 20(38): 392 (1909).

Ind. loc.: “Alpes Baicalenses?”.

Lectotype (designated by Egorova 1999: 400): RUSSIA. BURYATIA: In sabulosis ad Baicalem prope Turcam, 1829, *N.S. Turczaninow*, s.n. (LE 01006995, digital image!; *isolectotypes*: LE 01006996, digital image!; LE 01006997, digital image!; LE 01006998, digital image!).

= *Carex sabulosa* Turcz. ex Kunth subsp. *leiophylla* (Mack.) A.E.Porsild, Natl. Mus. Canada Bull. 216: 20 (1966).

≡ *Carex leiophylla* Mack., N. Amer. Fl. 18(6): 365 (1935). (Basionym).

Holotype: CANADA. YUKON: Carcross [Upper Yukon Valley], 16 Jul 1914, A. Eastwood 725a (US 538796 [barcode: 00087222], digital image!; *isotypes*: CAS 0032457, digital image!; GH 00027300, digital image!).

Habitat: Mainly on moist to dry sandy soils, in steppes, riverbanks, dunes, and dry meadows, and in the southern part of its distribution range mainly in mountain forest-

steppe areas; 100–2000(2500) m (Egorova 1967; Malyshev 1990; Grubov 2001; Murray 2002a; Nyambayar 2009; Liang & Koyama 2010a; SG, pers. obs.).

Distribution: ± Siberian–Beringian disjunct (primarily Siberian–American); N Central Asia (?China: Xinjiang; Mongolia) and S and SE Siberia (E Altai region [Krasnoyarsk: Yenisei River]; Baikal-Sayan region), NE Siberia (Lower Lena region), also present in north-western North America (Yukon, Alaska) (Egorova 1967, 1999; Malyshev 1990; Grubov 2001; Murray 2002a; Nyambayar 2009; Liang & Koyama 2010a).

Chromosome count (2n): Unknown.

39. *Carex serreana* Hand.-Mazz., Oesterr. Bot. Z. 85: 225 (1936).

(Figs. S3: AO, S7: A16).

Ind. loc.: “Tschili: Ta-Wutai-schan, Gipfel des Peitai, 14 Jul 1925, *Chanet & Serre 469*”.

Lectotype (**designated here**): CHINA. SHANXI: Shan Si, Ou T'ai Shan, Pic Nord, Sommet, 14 Jul 1925, *L. Chanet & J. H. Serre [A]469* (P 00520984, digital image!; *isolectotype*: PE 01842107, digital image!); *Topotype*: Shan Si, Ou T'ai Shan, Pic Nord, Pente nord, 14 Jul 1925, *L. Chanet & J. H. Serre [A]468* (P 00520983!).

Note: There are two sheets corresponding to the protologue and *Chanet & Serre 469* (P 00520984, PE 01842107). Further suspected specimens in Vienna (W, WU) could not be found (H. Rainer, pers. comm.; W. Till, pers. comm.). The sheet deposited in Paris (P 00520984!), which includes several inflorescences in comparison to the one in PE, is, therefore, selected as the lectotype.

= *Carex wenchenii* F.T. Wang & Tang, Acta Phytotax. Sin. 1: 134 (1951).

Holotype: CHINA. HEBEI: Hsilingshan, 06 Aug 1933, *C. W. Wang 60671* (PE 00031553, digital image!).

Habitat: Damp soils, in subalpine and alpine open scrublands and grasslands and along the treeline, mostly on shady places amongst *Rhododendron* scrub, mainly on N-facing slopes; 2100–3530 m (Liang 2000; Liang & Koyama 2010a; SG, pers. obs.).

Distribution: N Central–NE Chinese endemic; distributed in the mountain ranges of N Central (NE Qinghai, Gansu) and NE China (Shanxi, Hebei) (Liang 2000; Liang & Koyama 2010a).

Chromosome count (2n): Unknown.

Notes: A little known and seemingly often overlooked or otherwise confused species in whose populations sometimes unispicate individuals with a single terminal gynaeandrous spike occur (SG, pers. obs.). For confusion with *C. hancockiana* see under that name.

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5 MAIN RESULTS AND DISCUSSION

Molecular markers. — The phylogenetic analyses conducted in this study are based on (mostly concatenated) molecular datasets of the plastid *trnK–matK* region and *rps16*, the nuclear ribosomal ITS, and, in the case of *C. sect. Racemosae*, ETS 1f regions.

The plastid regions. — The 5'-*trnK* intron, the *matK* gene (usually the 3'-gene fragment), as well as the *rps16* intron have been widely used in systematic and molecular studies of numerous plant groups (Johnson & Soltis 1994, 1995; Hilu & Liang 1997; Oxelman et al. 1997; Hidalgo et al. 2004; Döring et al. 2007; Soreng et al. 2007; Döring 2009; Schneider et al. 2009, 2011, 2012; Blaner et al. 2014; Wölk & Röser 2014; Hochbach et al. 2015; Wölk & Röser 2017; Hochbach et al. 2018). In the Cyperaceae they were used at the genus and species level (Gilmour et al. 2013; Lévillé-Bourret et al. 2014, 2015; Glon et al. 2017; Reid et al. 2017), as well as in genus *Carex* (Escudero & Luceño 2009; Escudero et al. 2009; Jiménez-Mejías et al. 2012; Shekhovtsov et al. 2012; Villaverde et al. 2015a; Waterway et al. 2015; Global *Carex* Group 2016; Benítez-Benítez et al. 2017; Jiménez-Mejías et al. 2017; Villaverde et al. 2017a). These markers were also suitable for regional barcoding (Starr et al. 2009; Le Clerc-Blain et al. 2010; Burgess et al. 2011; Kuzmina et al. 2012; Saarela et al. 2013), albeit with limited success. They were also used in phylogeographical studies on *Carex* (Escudero et al. 2010; Villaverde et al. 2012, 2015a, b; Márquez-Corro et al. 2017; Villaverde et al. 2017a).

Unlike the above studies, the present thesis includes the entire *matK* gene, including the non-coding 5'-*trnK* intron, as well as a small portion (about 200 nucleotides) of the 3'-*trnK* intron. Although the *matK* gene has been widely used (see above), the non-coding DNA regions of the entire region exhibit higher evolutionary rates compared to the coding regions (*matK* gene, *trnK* exon). This resulted in a higher percentage of potentially parsimony-informative characters that are more powerful for studying lower taxonomic levels, e.g., on genus or sectional ranks (Small et al. 2004). However, compared to the nuclear DNA datasets (see below), the plastid *trnK–matK* region, as well as *rps16*, were less informative. Nevertheless, the phylogenetic analyses of the plastid regions (esp. *trnK–matK* region) show an often better resolved backbone and strongly supported lineages for the internal early-branching lineages and major groups found in comparison to the nuclear DNA regions.

The nuclear gene regions. — As part of the ribosomal 18S–5.8S–26S rDNA cistron, which is arranged in tandem arrays at a single or several chromosomal loci, the internal transcribed spacer (ITS) region consists of the respective intergenic spacer regions

(Baldwin et al. 1995; Álvarez & Wendel 2003). Since ribosomal genes occur in hundreds to thousands of copies, they are easily accessible for DNA isolation (Baldwin et al. 1995; Blattner 1999; Small et al. 2004). Thus, the ITS region has become one of the most frequently used nuclear markers for addressing phylogenetic questions. It is characterized by its simple amplification also from herbarium material, its high mutation rate, and its relatively small size (Baldwin et al. 1995; Starr et al. 1999; King & Roalson 2008; reviewed in Poczai & Hyvönen 2010). The ETS 1f is part of the external transcribed spacers (ETS) situated within the intergenic spacer (IGS) region. The IGS separates the repetitive 18S–5.8S–28S ribosomal gene blocks (see above). It evolves with higher rates than the ITS region (Baldwin et al. 1995; Starr et al. 2003; reviewed in Poczai & Hyvönen 2010). Besides the ITS, the ETS 1f region became one of the most commonly used markers in genus *Carex* (Starr et al. 2004, 2007; Starr & Ford 2009; Waterway & Starr 2007; Waterway et al. 2009; Maguilla et al. 2015; Waterway et al. 2015; Global *Carex* Group 2016; Maguilla et al. 2018).

The nuclear ribosomal DNA is arranged in multiple tandem repeats of the 26S subunit, ITS1, 5.8S subunit, ITS2, 18S subunit; and the large IGS which contains the 5' and 3' ends of the ETS of hundreds to thousands copies. It is assumed for the purposes of species level phylogenies that all copies within an individual evolve concertedly, thereby maintaining each repeat as an identical copy (i.e. concerted evolution; Hillis & Dixon 1991; Hillis et al. 1991; Small et al. 2004; King & Roalson 2008). However, several studies found paralogous or non-functional (pseudogene) copies sometimes co-existing within individuals (see King & Roalson 2008). This can result in incorrect phylogenies, especially if only one of these paralogues is sequenced (i.e. single-specimen per species phylogenies), as is common in many studies (Sanderson & Doyle 1992; Doyle & Davis 1998; Bailey et al. 2003; Small et al. 2004; King & Roalson 2008). Additionally, concerted evolution may be incomplete, which can lead to problems caused by evolutionary dynamics of DNA sequences, such as incomplete lineage sorting (ILS), hybridization, or recombination (chimerization) within the spacer region. These processes often cause considerable difficulties for accurate inference of phylogenetic relationships of the taxa studied (reviewed in King & Roalson 2008).

Taxonomy of *Carex* sect. *Vesicariae*. — The non-monophyly of *C.* sect. *Vesicariae*, even in a broader sense (i.e. inclusion of *C.* sect. *Pseudocypereae* by North American botanists; Reznicek & Ford 2002), is shown by the present thesis. Thus, previous suggestions (Hendrichs et al. 2004a; Waterway & Starr 2007; Gehrke & Linder 2009;

Waterway et al. 2009; Jung & Choi 2013) were confirmed by a more representative taxonomic sampling and using additional molecular markers.

The molecular studies revealed a complex relationship of taxa from different sections, i.e. the sections *Vesicariae*, *Pseudocypereae*, *Carex*, *Lupulinae*, *Paludosae* (= *Tumidae sensu* Egorova 1999), and, partly, *Squarrosae* J.Carey. *Carex hirta*, the type species of the genus, subgenus *Carex*, as well as *C. sect. Carex*, is consistently found as belonging to this clade (Waterway et al. 2015; Global *Carex* Group 2016). Consequently, this circumstance should be considered, and this clade (i.e. ‘*Vesicariae* alliance’; see also Hoffmann & Gebauer 2016), should be hereinafter referred to as the ‘*Hirta* clade’. The clade is named according *C. hirta* (see above) without further taxonomic conclusions that appear premature. Based on the molecular findings and new morphological observations, at least about 110 taxa may belong to this clade (Gebauer et al., in prep.; Global *Carex* Group, in prep.).

The core *Vesicariae* clade. — Most of the traditional taxa of *C. sect. Vesicariae* were nested in a single clade. The further subdivision into two sister lineages (see below) is also observed in later studies (Global *Carex* Group 2016; Hoffmann & Gebauer 2016; Gebauer et al., in prep.). The ‘Northern clade’ consists of mostly boreal to arctic species (i.e. *C. jacutica*, *C. membranacea*, *C. mollissima*, *C. rhynchophysa*, *C. rostrata*, *C. rotundata*, ‘*C. stenolepis*’, and *C. utriculata*). Some are circumboreal (*C. rhynchophysa*, *C. rostrata*) or circumpolar species (*C. membranacea*, *C. rotundata*). The ‘Mixed clade’ is geographically variable, i.e. consisting of taxa that may have a northern distribution, but the majority is non-arctic and more southerly distributed (i.e. *C. exsiccata*, *C. pamirica* s.l., *C. saxatilis* s.l., *C. vesicaria*, and *C. vesicata*). The sampled specimen of ‘*C. stenolepis*’ need now to be named as *C. ×saamica* T.M.Pedersen & Elven, a stabilized hybrid taxon resulting from the hybridization of *C. rostrata* × *C. rotundata* (see Pedersen et al. 2016; Elven et al. 2017). This explains its unexpected phylogenetic position, because it was considered a hybrid between *C. saxatilis* and *C. vesicaria* (Elven et al. 2017).

Both clades, i.e. ‘*C. rostrata* group’ (Northern clade) and ‘*C. vesicaria* group’ (Mixed clade) largely coincide with the concept proposed by Kreczetovicz (1935b), especially in relation to the Holarctic species. Morphologically, the Northern clade includes these species whose utricles have a rather abrupt transition into the beak, as well as a loosely cespitose to colonial growth with long-creeping rhizomes. The utricles of the species of the

Mixed clade are rather gradually beaked, and the species have short rhizomes and a rather densely cespitose growth pattern (Egorova 1999; Reznicek & Ford 2002; pers. obs.).

The boreal to arctic Eurasian *C. rhynchophysa* (e.g., Chater 1980; Egorova 1999; Elven et al. 2011), which has sometimes been considered identical with *C. utriculata* that was earlier described from North America (Ford et al. 1993; Reznicek & Ford 2002) is almost inseparable by morphological features (but see Mackenzie 1931–1935; Hultén 1968; Scoggan 1978). However, it shows minor molecular divergence compared to the latter (including sequences from other studies deposited at GenBank). It might be a cryptic species, but taxonomic conclusions appear premature.

The circumpolar species *C. saxatilis* and its segregates (i.e. subspec. *laxa*, *C. miliaris*, *C. physocarpa*), whose taxonomic identity were discussed often controversial (Egorova 1999; Reznicek & Ford 2002; Elven et al. 2011, 2017), cluster in a single branch, supporting the conclusions made by Ford et al. (1991) and Ford & Ball (1992) treating *C. saxatilis* and its segregates as a single polymorphic species or as a set of cryptic species.

The Eastern North American temperate to boreal species *C. tuckermanii* Boott, with a slightly different morphology in terms of the utricle shape and the transition into the beak (e.g., Reznicek & Ford 2002), was suggested as belonging to the *C. vesicaria* group (Mixed clade) in subsequent molecular studies (Global *Carex* Group 2016; Gebauer et al., in prep.). The rather temperate *C. schweinitzii* Dewey ex Schwein., which is restricted to Eastern North America (e.g., Reznicek & Ford 2002), was found either as sister to the *C. rostrata* group (Northern clade) (Global *Carex* Group 2016) or as a single branch, together with both above-mentioned groups, in a polytomy (Gebauer et al., in prep.). In terms of morphology, it has some intermediate features that appear transitional between the species of the *C. vesicaria* group and the species traditionally placed in *C. sect. Pseudocypereae* (Kükenthal 1909; Mackenzie 1931–1935; Reznicek & Ford 2002; pers. obs.). The extinct Korean species *C. nakasimae* Ohwi (Son et al. 2017) also belongs to the *C. vesicaria* group (Global *Carex* Group 2016).

The remaining taxa of the ‘Hirta clade’. — The phylogenetic position of the East Asian *C. dickinsii* Franch. & Sav., traditionally placed in *C. sect. Vesicariae* (Egorova 1999; Dai et al. 2010b), with intermediate morphology (transitional to *C. sect. Lupulinae* and the *C. lurida* group; see below), remains unresolved (*incertae sedis*). The species was found nested without clear relationship in the ‘Hirta clade’ (Gebauer et al., in prep.).

The North American species *C. oligosperma* (*Vesicariae*) and *C. intumescens* (*Lupulinae*) revealed as early-branching lineages in the present study. The same branching pattern was found in other studies (Waterway & Starr 2007; Waterway et al. 2009, 2015; Global *Carex* Group 2016; Gebauer et al., in prep.). Later studies further place the Eastern North American *C. grayi* J.Carey (*Lupulinae*) to these early-branching lineages, sister to *C. intumescens* (Global *Carex* Group 2016; Gebauer et al., in prep.). Their previous affiliations to species of the core *Vesicariae* clade (see above; i.e. *C. oligosperma*) or the apparently polyphyletic *C. sect. Lupulinae* (i.e. *C. grayi*, *C. intumescens*) seems to be caused by parallel evolution (i.e. morphological homoplasy) (Reznicek 2002; Reznicek & Ford 2002).

The North American *C. bullata* Willd. (*Vesicariae*) was found recently as sister to a clade consisting of species traditionally placed in *C. sect. Pseudocypereae* (Global *Carex* Group 2016; Gebauer et al., in prep.). These studies places further species (e.g., *C. capricornis* Meinsh. ex Maxim. [East Asia], *C. cognata* Kunth, *C. congolensis* Turrill [Eastern and Southern Africa], *C. insularis* Carmich. [South Atlantic: Tristan da Cunha], *C. mcvaughii* Reznicek [Central America: Mexico], and *C. thurberi* Dewey ex Torr. [Southwestern North America, Mexico, and Caribbean]) in this clade, which appears also in the present study (i.e. part of the ‘Southern grade’; see **Chapter 2**). These studies revealed a rather complicated intercontinental biogeography, especially regarding the Neotropical and African sub-Saharan and Madagascan species. The Neotropical species of this clade need revision (Jiménez-Mejías et al. 2018; Jiménez-Mejías et al., in prep.; pers. obs.).

The arrangement of the clade that includes two taxa of the apparently polyphyletic North American *C. sect. Lupulinae* (*C. gigantea*, *C. lupulina*) and *C. retrorsa* (*Vesicariae*) was confirmed by recent studies (Global *Carex* Group 2016; Gebauer et al., in prep.). However, the latter remains unresolved in a polytomy involving the above-mentioned clade (i.e. *C. bullata*, taxa of *C. sect. Pseudocypereae*) and some species of *C. sect. Lupulinae* (additionally *C. lupuliformis* Sartwell ex Dewey, *C. louisianica* L.H.Bailey) in the first study (Global *Carex* Group 2016).

The South Australian *C. alsophila* F.Muell., usually placed in *C. sect. Anomalae* J.Carey (e.g., Global *Carex* Group 2016), revealed to be closely related to species of the ‘Southern grade’ by a recent study (Waterway et al. 2015). Morphologically, the species

appears somewhat intermediate between species traditionally placed in *C. sect. Pseudocypereae* and the *C. vesicaria* group (pers. obs.).

The remaining species of the ‘Southern grade’ consist also of species previously affiliated to *C. sect. Vesicariae* (i.e. *C. baileyi*, *C. lurida*). The clade formed by *C. baileyi* and *C. lurida* revealed to also include the Neotropical taxa *C. durangensis* Reznicek & S.González, *C. longiligula* Reznicek & S.González, and *C. setigluma* Reznicek & S.González (Global *Carex* Group 2016; Gebauer et al., in prep.). All these species were referred to the so-called ‘*C. lurida* group’ by Reznicek & González-Elizondo (1995). Another Mexican species affiliated to the group, *C. rzedowskii* Reznicek & S.González, has not yet been molecularly studied. The relationships of this clade with respect to the other groups discussed remain unresolved, since its phylogenetic placement differs among all previous studies (see Hendrichs et al. 2004a; Global *Carex* Group 2016; Gebauer et al., in prep.). With respect to the morphology, the species of this clade also appear somewhat intermediate between the species of the clade including the ‘*C. rostrata*’ and ‘*C. vesicaria* groups’, as well as of the species traditionally placed in *C. sect. Pseudocypereae* (i.e. shape and venation of the utricles, the rather densely approximated spikes, and the conspicuously awned pistillate and staminate glumes; Reznicek & González-Elizondo 1995; Egorova 1999; Reznicek & Ford 2002; Reznicek & González-Elizondo 2001; pers. obs.).

The close relationship between the representatives of the sections *Carex* and *Paludosae* (= *C. sect. Tumidae sensu* Egorova 1999) has been repeatedly demonstrated, although with markedly differences in terms of statistical support (Global *Carex* Group 2016; Gebauer et al., in prep.; see also references above). The placement of several species (i.e. *C. congdonii* L.H.Bailey, *C. latisquamea* Kom., *C. sartwelliana* Olney, *C. vestita*) apart from the clade that includes the majority of species from *C. sect. Paludosae* (see below) has been repeatedly shown (Waterway & Starr 2007; Waterway et al. 2009; Jung & Choi 2013; Global *Carex* Group 2016; Gebauer et al., in prep.). This also applies to its type species, *C. acutiformis* (Waterway et al. 2009; Global *Carex* Group 2016; Gebauer et al., in prep.). However, most sampled representatives of *C. sect. Paludosae* were found nested in a subclade of the ‘Hirta clade’ (Waterway et al. 2009, 2015; Global *Carex* Group 2016; Gebauer et al., in prep.), largely corresponding to the treatment by Egorova (1999). Egorova (1990, 1999) united the Eurasian species, except for *C. acutiformis*, under *C. sect. Tumidae* (type species: *C. riparia*). *Carex riparia* was also consistently found nested in the same clade by other studies as suggested here (Waterway et al. 2009, 2015; Global *Carex* Group 2016; Gebauer et al., in prep.).

The placement of *C. songorica* in this clade together with species from *C. sect. Paludosae* was not corroborated by a recent study of the Global *Carex* Group (2016), where it was nested among species of *C. sect. Carex*. However, in the study by Gebauer et al. (in prep.) it resolves in a similar clade consisting of species from *C. sect. Paludosae*. Incongruence between gene trees was detected for ITS and cpDNA, where *C. songorica* is, together with *C. pumila*, nested among species traditionally placed in *C. sect. Carex* with strong support (Gebauer et al., in prep.). In the phylogenetic trees of the cpDNA and combined (nrDNA + cpDNA) datasets *C. songorica* is, however, nested together with *C. pumila* in a clade with representatives of *C. sect. Paludosae*. *Carex songorica* and *C. pumila* are morphologically very similar and share the adaptation to saline soil conditions (Egorova 1999; Reznicek & Catling 2002; Dai & Koyama 2010).

The rare North American endemic *C. houghtoniana* appears also problematic with regard to its placement, because the phylogenetic position differs among molecular studies. It is found either on a basal position of a clade consisting of the sub-clades of both sections (present study) or on a rather basal position in a *C. sect. Carex* clade (Gebauer et al., in prep.). In a recent study by the Global *Carex* Group (2016) it was nested unresolved in a large polytomy, together with clades of *C. sect. Carex* and two species of *C. sect. Squarrosae*. This incongruence may be another indication of ILS or ancestral hybridization between both lineages, which needs further investigation. The sister group relationship between sections *Carex* and *Paludosae* has been either confirmed (present study: *trnK–matK* region, *rps16*, ITS; Waterway et al. 2009: *trnL–trnF* region, ITS, ETS 1f; Gebauer et al., in prep.: resolved as sister without statistical support, *trnK–matK* region, *rps16*, ITS, ETS 1f) or rejected (Jung & Choi 2013: *trnL–trnF* region, *rbcL*, ITS; Global *Carex* Group 2016: *matK*, ITS, ETS 1f) depending on the respective combination of molecular markers used.

Parallel diversification of the *Vesicariae* and *Phacocystis* lineages. — A similar branching and distribution pattern is found in sectt. *Phacocystis* (Dragon & Barrington 2009) and *Vesicariae* lineages (this study). The lineages of both sections display a clear biogeographic differentiation into a ‘Northern clade’ and a ‘Mixed clade’, as well as a more heterogeneous ‘Southern grade’ mostly composed of more southerly distributed lineages (see **Chapter 2**).

Dragon & Barrington (2009) suggested an early Pleistocene origin (c. 1.89–1.07 mya) of the ancestor of the Northern (c. 0.76–0.64 mya) and Mixed clade (1.50–1.11) of the

Phacocystis lineages by molecular dating. Despite the lack of suitable fossil evidence, this molecular clock approach was possible due to the presence of several Hawaiian endemics, using island formation as calibration points (Dragon & Barrington 2009). These dates fit well with the geological appearance of the Arctic (Matthews 1979; Matthews & Ovenden 1990), which suggests their diversification within the Arctic and adjacent boreal regions. The period of global cooling during the late Tertiary and Quaternary (Gradstein et al. 2004) has been demonstrated as generally important with respect to the recent diversification within genus *Carex* (Escudero et al. 2012). A comparable dating of the corresponding *Vesicariae* lineages was not possible due to different molecular markers and the lack of such ideal calibration points. However, the lower molecular differentiation of the species of the *Vesicariae* lineages compared to those of *C. sect. Phacocystis* suggests that they may be of similar age or even younger (see Table 3 in **Chapter 2**).

In terms of their molecular differentiation (i.e. nucleotide diversity, number of segregating sites), lower genetic divergence of species from the boreal-arctic lineages ('Northern clades') of sectt. *Phacocystis* and *Vesicariae* were detected in both sections compared to non-arctic lineages ('Mixed clades' and 'Southern grades').

The morphological differentiation between the boreal-arctic lineages of both sections (and compared to the non-arctic lineages) is very low. Only reproductive traits (e.g., utricle length, number of female spikes) indicated a divergence between the boreal-arctic lineages of both sections. This suggests that these generative features may be section-specific and phylogenetically constrained. No clear ecological differentiation could be detected; although the evolution of salt tolerance in some species of the boreal-arctic lineage of *C. sect. Phacocystis* was not paralleled in *C. sect. Vesicariae*. The biogeographical structure of the *Vesicariae* lineages, their molecular divergence, habitat preferences, and vegetative, but above all, reproductive characteristics are paralleled to the corresponding lineages of *C. sect. Phacocystis*. Considering the corresponding boreal-arctic lineages of both sections, a northern replicative adaptive radiation (Losos 2010) could be documented in boreal to arctic habitats with parallel diversification and ecological convergence. Further evidence (i.e. ongoing diversification in the Northern clade of *C. sect. Phacocystis*) suggest that this replicative adaptive radiation may be a transitional state in the diversification of species, which may explain why such radiations are so rarely reported (see **Chapter 2**).

Taxonomy of *Carex* sect. *Racemosae*. — The monophyly of *C. sect. Racemosae*, which excludes a few taxa previously treated as members of the group (see below), is

highly supported by the present study. The majority of the taxa traditionally affiliated to the section, including the sectional type species, were found in a strongly supported clade. This outcome was also revealed by subsequent studies, with almost identical topologies (Global *Carex* Group 2016; Massatti et al. 2016).

Taxa to be excluded. — Some species (e.g., *C. augustinowiczii*, *C. mertensii*) typically treated as members of the section revealed to be closely related to *C. sect. Phacocystis* s.l. (see also Global *Carex* Group 2016; Massatti et al. 2016), as partly suggested by previous studies (e.g., Waterway & Starr 2007; Waterway et al. 2009). The species transferred to the newly proposed *C. sect. Stylosae* (e.g., *C. meyeriana*, *C. stylosa*), which was also resolved in recent molecular studies (Waterway et al. 2015; Massatti et al. 2016: Appendix S4), should also no longer be considered as members of the section. Based on morphology, *C. hongyuanensis* is also treated in *C. sect. Stylosae*. The exclusion of *C. bicolor*, which is clearly nested in a ‘*Bicolores-Laxiflorae-Paniceae* clade’ (Waterway et al. 2015; see below), has already been discussed by previous authors (Ball 2002a). Massatti et al. (2016) further demonstrated that *C. curvicollis* should also be excluded from *C. sect. Racemosae*.

Sister group relationships. — The clade that includes species traditionally placed in *C. sect. Paniceae* and *Bicolores* (including *C. bicolor*) is suggested as the sister group of *C. sect. Racemosae* in the present thesis. This relationship was also found in recent molecular studies (Waterway et al. 2015; Global *Carex* Group 2016; Massatti et al. 2016). This clade additionally includes species typically treated in *C. sect. Laxiflorae* (Waterway et al. 2015; Global *Carex* Group 2016; = ‘*Bicolores-Laxiflorae-Paniceae* clade’). The placement of *C. williamsii* Britton, which resolved as sister to this clade in the study by Massatti et al. (2016), was not corroborated by other large phylogenies with more representative taxon sampling (Waterway et al. 2015; Global *Carex* Group 2016). This taxon is usually placed in *C. sect. Chlorostachyae* Tuck. ex Meinsh. (e.g., Egorova 1999; Ball 2002b). A single branch composed of the Eurasian *C. arnellii* Christ ex Scheutz and the North American *C. sprengei* Dewey ex Spreng. was further found at the base of the *C. sect. Racemosae* s.str. clade by Waterway et al. (2015) and the Global *Carex* Group (2016). The sectional affiliation of both taxa has been often controversial [e.g., Chater 1980; Egorova 1999; Waterway 2002; Dai et al. 2010a; mostly affiliated to *C. sect. Hymenochlaenae* (Drejer) L.H.Bailey]. Both taxa are strikingly different from *C. sect. Racemosae* with respect to its general habit and morphology (Egorova 1999; Waterway 2002; pers. obs.). For example, its basal sheaths are densely fibrous (vs. not fibrous), and the

utricle beak is rather long, pronounced, and narrowly tubular (vs. usually short, and short-cylindrical to largely absent). Both species represent typical elements of rather dry to mesic forest steppes, which is rarely observed in *C. sect. Racemosae* whose forest steppe species are associated with rather hydric soils (e.g., *C. hancockiana*, *C. media*; Egorova 1999; pers. obs.). However, this alleged relationship disappeared with the addition of taxa in the genus phylogeny (P. Jiménez-Mejías, pers. comm.).

***Carex sect. Racemosae s.str.* — The South American taxa (subsect. *Atropictae*).** — The South American species placed in subsect. *Atropictae* (i.e. *C. atropicta*, *C. malmei*; Wheeler 1990) resolved as an early-branching lineage sister to the remaining species of the section in the present study (clade 4 in **Chapter 3**). The identical placement was found in the recent genus phylogeny (see Global *Carex* Group 2016; *C. atropicta* included). The only incongruence detected between individual gene trees (i.e. *trnK–matK* vs. *rps16*, ITS, ETS 1f) concerned these two taxa, suggesting molecular homoplasy, i.e. parallel mutations in the chloroplast genome (see Table 3 in **Chapter 3**), resulting from stochastic variation or different evolutionary processes (Sullivan 1996; Johnson & Soltis 1998; Wendel & Doyle 1998). The study by Massatti et al. (2016) suggests a close relationship (*C. atropicta* included) to the species of the western North American ‘*Carex parryana* complex’ (*C. idahoensis*, *C. parryana*, *C. serratodens*; Murray 2002a; Reznicek & Murray 2013).

The taxa of subsect. *Atropictae* exhibit some morphological peculiarities that are unique within *C. sect. Racemosae*, i.e. narrowly winged utricles with \pm prominent ciliate-scabrous margins, lenticular nutlets that are \pm prominently stipitate, and generally 2-stigmatic styles (rarely with a few 3-stigmatic flowers). Further, the flattened utricles are only filled by the nutlet in their basal parts (Wheeler 1990; Egorova 1999; Murray 2002a; pers. obs.). The species of the ‘*Carex parryana* complex’ differ by the usually 3-stigmatic styles; with some of them (e.g., *C. specuicola*, *C. utahensis*) share an admixture with 2-stigmatic flowers, whereby the 3-stigmatic ones always predominate (pers. obs.). The generally wingless utricles are usually \pm trigonous and almost filled by the sessile to short-stipitate, trigonous nutlets (rarely not almost filled; e.g., *C. aboriginum*, *C. specuicola*, *C. utahensis*) (Murray 2002a; Reznicek & Murray 2013; pers. obs.). Reduction of the lateral spikes towards unispicate inflorescences, which is otherwise quite uncommon in the section (e.g., *C. atrofusoides*, *C. serreana*; pers. obs.), is found in both groups (e.g., *C. malmei*, *C. monodynamis* [South America]; *C. hallii*, *C. idahoensis* [North America]). However, if possessing more than a single spike, the inflorescences of the South American taxa are more condensed with densely approximated, overlapping spikes (e.g.,

C. atropicta), whereas the spikes of the North American species are rather distantly arranged (Wheeler 1990; Reznicek & Murray 2013; pers. obs.). Besides some similarities, a few morphological characters or their combinations are unique to either group, clearly separating them. Thus, the noticeable discordance regarding the phylogenetic position of the South American species between the above-mentioned studies may be explained by different taxon sampling and the phylogenetic inference methods used.

Migration or dispersal from North to South America was suspected by Wheeler (1990). This hypothesis seems not unlikely in the light of the phylogenetic trees of the present study and that by Massatti et al. (2016). The bipolar disjunction in the section may be further explained either by long-distance dispersal (LDD) or Cordilleran migration and extinction of intermediate populations. Interestingly, LDD is the more frequent explanation instead of migration via the mountain chains of the Americas ('mountain-hopping'), as suggested by studies on extant bipolar *Carex* species (reviewed in Villaverde et al. 2017b). Further, north-to-south dispersal as the prevalent direction in bipolar LDD events between both hemispheres has repeatedly reported in bipolar *Carex* species (reviewed in Villaverde et al. 2017b). South-to-north LDD was only suggested in the bipolar *C. macloviana* d'Urv. (cf. Márquez-Corro et al. 2017).

Subsect. *Papilliferae*. — The monophyly and early-branching of subsect. *Papilliferae* (i.e. *C. adelostoma*, *C. buxbaumii*, and *C. hartmaniorum*) are shown for the first time by the present study (clade 5 in **Chapter 3**). The arctic *C. holostoma*, previously treated in the monotypic subsect. *Holostomae* (Egorova 1985, 1999), was found nested in the subsect. *Papilliferae* clade as sister to the subarctic–arctic species *C. adelostoma*. Later molecular studies by the Global *Carex* Group (2016) and Massatti et al. (2016) found a similar pattern. Morphologically, *C. holostoma* was separated from subsect. *Papilliferae* by its more slender growth, the smaller and densely approximated lateral spikes, and the male terminal spike (Egorova 1985). However, it shares all the typical features of subsect. *Papilliferae*, such as long-creeping rhizomes and utricles that are obtusely trigonous in cross-section, whose entire surface is densely covered by elongated papillae (Chater 1980; Egorova 1999; Murray 2002a; pers. obs.). The weak molecular divergence found between the morphologically well-separated *C. adelostoma* and *C. holostoma* may be explained either by the lack of variation in the markers, a rather recent diversification, or introgression between both often co-occurring taxa. Another explanation may be the hybrid origin of one of these species. *Carex adelostoma* appears morphologically somewhat intermediate between *C. holostoma* and the remaining species, particularly

C. buxbaumii (pers. obs.). This intermediacy is evident by the sex distribution of its terminal spike (either staminate or gynaecandrous) and the coloration of the mature utricles (pale green or greenish whitish, but often dark-purplish to purple-blackish tinged). The arrangement of the spikes continues this (ranging from rather loose to approximated) (Chater 1980; Egorova 1999; Murray 2002a; pers. obs.). Densely approximated spikes, a generally terminal staminate spike, and dark purple-blackish to almost blackish colored utricles are only found in *C. holostoma*. Rather loosely arranged inflorescences, gynaecandrous terminal spikes, and utricles without such dark coloration occur in the circumboreal *C. buxbaumii* and the rather nemoral *C. hartmaniorum* (Chater 1980; Egorova 1999; Murray 2002a; pers. obs.). Furthermore, *C. adelostoma* shows more similarities to the latter two species in terms of its general appearance and growth (plant height, sizes of vegetative and reproductive organs) than to *C. holostoma* (Chater 1980; Egorova 1999; Murray 2002a; pers. obs.). This intermediate character of *C. adelostoma* could thus indicate a possible hybrid origin of the species.

Subsect. *Sabulosae*. — The morphologically well-defined subsect. *Sabulosae* is resolved as monophyletic for the first time by the present study (clade 7 in **Chapter 3**). This was later also found in subsequent studies by the Global *Carex* Group (2016) and Massatti et al. (2016). The first study further includes the mainly Tibetan *C. praeclara* as previously suggested (Egorova 1999). The clade seems rather recently derived (Massatti et al. 2016), and the species delimitation is often obscured by the frequent co-occurrence, largely overlapping distribution ranges, as well as their extreme overall-similarity (pers. obs.). There are slight differences in the respective topologies of the clade, especially regarding the placement of *C. melananthiformis* (see also Massatti et al. 2016; Global *Carex* Group 2016). *Carex melananthiformis* was found sister to *C. sabulosa* in the present study, whereas sister to *C. melanantha* by Massatti et al. (2016). *Carex melananthiformis* is morphologically intermediate between *C. melanantha* and *C. sabulosa* (e.g., Egorova 1999; pers. obs.). Further, it is often considered conspecific to the widely distributed *C. melanantha* (Malyshev 1990; Kukkonen 1998). Morphological investigations in the course of the taxonomic revision performed revealed frequent misidentifications of herbarium specimens, especially between the taxa *C. melanantha*, *C. melananthiformis*, and *C. sabulosa*. Morphologically intermediate specimens further suggest recent introgression or hybridization between them (pers. obs.). In the result of the revision, taking into account preliminary molecular data (Gebauer et al., unpubl. data), *C. melananthiformis* is provisionally accepted, although its morphological intermediary

may indicate a possible introgressive origin (Egorova 1999), which may explain its divergent placements.

The Central Asian–Sino-Himalayan clade. — A clade mostly composed of species distributed in high mountains of Asia (i.e. mostly Central Asian and Sino-Himalayan species; Noltie 1994; Dickoré 1995; Kukkonen 1998; Egorova 1999; Kukkonen 2001; Liang & Koyama 2010a) was established for the first time in the present study (e.g., *C. infuscata*, *C. pseudobicolor*; clade 10, see **Chapter 3**). Later, this clade was also found by Massatti et al. (2016) and, partly, the Global *Carex* Group (2016). These studies demonstrate the inclusion of further Asian taxa (e.g., *C. duthiei* s.l., *C. kansuensis*, *C. lehmannii*, and *C. polymascula*). The clade is morphologically rather heterogeneous. It combines very different taxa (see **Chapter 4**) previously treated in the apparently polyphyletic subsectt. *Alpinae* p.p. (e.g., *C. infuscata*), *Aterrimae* p.p. (e.g., *C. caucasica*, *C. kansuensis*), and *Longibracteatae* p.p. (i.e. *C. lehmannii*) (Kalela 1944; Egorova 1985, 1999). Since not all of the putatively associated Asian taxa have been molecularly studied yet (see below), statements on the possible species-specific relationships of that clade (e.g., sister species, smaller internal groups) are rather difficult to address. The grouping of these morphologically different taxa previously placed in different subsections, also highlights the importance of biogeography for the general understanding of the group, apart from previous morphology-based considerations. Most species of this clade are confined to regions within one of the two diversification centers of *C. sect. Racemosae* in the high mountains of Inner Asia (Egorova 1967; Kukkonen 1998; Egorova 1999; Kukkonen 2001; Liang & Koyama 2010a).

The Western North American (Nearctic) clade. — This clade, firstly described in the present study (clade 11 in **Chapter 3**), is also found in later studies (Global *Carex* Group 2016; Massatti et al. 2016). Species of this clade have previously been associated with subsectt. *Alpinae* p.p. and *Aterrimae* p.p. (Kalela 1944; Egorova 1985, 1999). The clade is also morphologically heterogeneous and includes species with rather loose, racemose inflorescences (e.g., *C. chalciolepis*, *C. heteroneura*), as well as with rather dense, capitate inflorescences (e.g., *C. nelsonii*, *C. nova*) (Kalela 1944; Egorova 1999; Murray 2002a). Massatti et al. (2016) suggests *C. albonigra*, whose placement remains unresolved in the present study, as belonging to this clade. The recently described Californian endemic *C. orestera* has so far been considered only in the present study, which suggests that it also belongs to the western Nearctic clade. Previous morphology-based affiliation of some Nearctic taxa (*C. nelsonii*, *C. nova*, and *C. pelocarpa*) to

apparently non-related Asian taxa (*C. melanocephala*, *C. oligantha*; Holarctic clade; see below) in subsect. *Alpinae* was essentially caused by homoplasy (i.e. convergent evolution). The western North American *C. helleri* and *C. raynoldsii* placed in a polytomy (clade 9 in **Chapter 3**) were suggested as sister to this clade (Massatti et al. 2016; but see Global *Carex* Group 2016). The western North American *C. atosquama* also nested in a polytomy was also suggested as belonging to this clade (Massatti et al. 2016: Appendix S4; but see Global *Carex* Group 2016). A possible sister group relationship of this clade to the Holarctic clade (see below) is further suggested by Massatti et al. (2016); both clades are situated, together with the Central Asian–Sino-Himalayan clade (see above), in a large polytomy in the present study.

The Holarctic clade. — This clade, revealed for the first time, also includes species from several subsections (i.e. *Alpinae* p.p., *Aterrimae* p.p., and the monotypic *Longiaristatae*; Egorova 1985, 1999; sub-clades 13 and 14, and *C. gmelinii* in **Chapter 3**). The type species of *C. sect. Racemosae*, *C. atrata*, is also included. The Holarctic clade is mainly composed of circumboreal (e.g., *C. media*) or boreo-alpine (*C. aterrima* s.l., *C. stevenii*) to arctic-alpine (e.g., *C. atrata*, *C. norvegica*) species. Some of them are confined to either North America (*C. atratiformis*, *C. stevenii*) or Eurasia (*C. aterrima* s.l., *C. melanocephala*) (Kalela 1944; Hultén 1958; Meusel et al. 1965; Murray 1969; Chater 1980; Porsild & Cody 1980; Hultén & Fries 1986; Egorova 1999; Murray 2002a; Elven et al. 2011; see also **Chapter 4**). The clade with almost similar biogeographical composition was also found by later studies (Global *Carex* Group 2016; Massatti et al. 2016). The clade is biogeographically characterized by taxa that are rather confined to (cold-)temperate and boreal to arctic regions, with southernmost occurrences in the Caucasian region (e.g., *C. aterrima* subsp. *medwedewii*), northern Central Asia (e.g., *C. aterrima* subsp. *aterrima*, *C. melanocephala*), East Asia (e.g., *C. gmelinii*), and the southern Rocky Mountains (*C. stevenii*) (see references above). A possible relationship of the remaining species of subsect. *Longibracteatae* (*C. hancockiana*, *C. peiktusani*; clade 12 in **Chapter 3**) to this clade, as suggested by the present study (without statistical support), was also found with weak support by Massatti et al. (2016). The affiliation of *C. oligantha* endemic to the Caucasian region to this clade is supported by preliminary molecular data (Gebauer et al., unpubl. data).

Taxa with unclear relationships. — The phylogenetic placements of some species remain, even taking into account the studies by Massatti et al. (2016) and the Global *Carex* Group (2016), unresolved (e.g., *C. albonigra*, *C. atosquama*, both discussed above;

C. parviflora). The isolated position of the European alpine *C. parviflora* in the present study may be affected by incomplete taxon sampling. Massatti et al. (2016: Appendix S4) suggests *C. parviflora*, albeit without statistical support, as related to the Holarctic clade (see above) that includes the remaining European and often sympatric alpine taxa (e.g., *C. atrata*, *C. norvegica*; Chater 1980; Egorova 1999). Morphologically, *C. parviflora* is most similar to the species *C. aterrima* and *C. atrata* (Chater 1980; Egorova 1999; pers. obs.). On the other hand, this high similarity could be the result of convergent evolution. The East Asian *C. heterostachya*, so far studied only by the Global *Carex* Group (2016), is suggested as related to species usually placed in subsect. *Sabulosae* (see above). However, this putative relationship based on the barcoding markers *matK*, ITS, and ETS 1f, needs further clarification. Morphologically, the species shares the obtusely trigonous utricles and a rather thickened, long-creeping rhizome with the taxa of this group (Dai & Koyama 2010; Liang & Koyama 2010a; pers. obs.). Thus, their phylogenetic relationship cannot be completely ruled out. The clade- and species-specific placements and relationships of further taxa affiliated with the section, which have not yet been molecularly investigated in any published study, remain unclear. Their membership to *C. sect. Racemosae* is essentially based on morphological studies (or preliminary molecular data) (Ohwi 1934; Koyama 1955, 1956a, b; Ohwi 1965; Kukkonen 1984; Li 1990; Noltie 1994; Dickoré 1995; Kukkonen 1998; Egorova 1999; Liang & Koyama 2010a; Kukkonen 2001; Gebauer et al., unpubl. data; for exceptions and clarifications see **Chapter 4**).

Revised taxonomy of *C. sect. Racemosae* in Eurasia (synopsis and key). — The revised taxonomic synopsis (and key) of Eurasian taxa of the section has taken into account all of the above molecular phylogenetic studies discussed above, as well as other recent findings from ongoing studies (Benítez-Benítez et al. 2018; Gebauer et al., unpubl. data), and continues to be based on extensive studies on herbarium specimens.

45 taxa, i.e. 39 species and 6 subspecies, are accepted as occurring within Eurasia (see Table 1 in **Chapter 4**). 11 species are not considered as belonging to the section, and were therefore excluded (viz., *C. apoiensis*, *C. augustinowiczii*, *C. bicolor*, *C. curvicollis*, *C. hongyuanensis*, *C. macrostigmatica*, *C. mertensii*, *C. meyeriana*, *C. stylosa*, *C. tatjanae*, and *C. urostachys*). *Carex heterostachya* is transferred from *C. sect. Paludosae* (see above) to the section based on molecular (Global *Carex* Group 2016; Gebauer et al., unpubl. data) and morphological findings (e.g., presence of dark auricles). Two further species usually placed in *C. sect. Aulocystis*, i.e. *C. atrofuscoides* and *C. psychrophila*, are also placed in the section. *Carex atrofuscoides* from Northern Central China has been placed in *C. sect.*

Aulocystis due to its superficial resemblance to *C. atrofusca*; however, its invariably gynaeandrous spikes do not occur further in *C. sect. Aulocystis*, but is also observed in some species of *C. sect. Racemosae* (e.g., *C. aristulifera*; Li 1990; Liang & Zhang 2006; Liang & Koyama 2010a, b; pers. obs.). Its affiliation to the section studied here is further suggested by molecular data (Gebauer et al., unpubl. data). Thus, its *C. atrofusca*-like appearance seems a further example of a remarkable morphological convergence between non-closely related groups of genus *Carex* (see Global *Carex* Group 2016). The Sino-Himalayan *C. psychrophila* has been previously affiliated with *C. sect. Aulocystis* mainly by its long-beaked utricles (Kükenthal 1909; Dickoré 1995; Kukkonen 1998, 2001; Liang & Koyama 2010b), although other authors have noticed its greater similarity or confusion with representatives of the section studied here (Drejer 1844; Clarke 1908; Noltie 1994). First molecular sequence data of an ongoing study support its placement in *C. sect. Racemosae* (Gebauer et al., unpubl. data).

Four key morphological features appear to be of particular importance with regard to the taxa previously affiliated to the *C. sect. Racemosae* (see above), which are excluded in the present study: the presence of (1) 2-stigmatic vs. 3-stigmatic flowers, (2) strikingly purple-blackish to blackish auricles at the base of the proximal bract, (3) often dark purplish to blackish utricles, and (4) terminal staminate vs. gynaeandrous spikes. All of these features occur in both *C. sect. Racemosae* and *Phacocystis*, but are weighted differently in taxonomic treatments (Egorova 1999; Murray 2002a; Liang & Koyama 2010a). *Carex sect. Racemosae* is traditionally characterized by the presence of usually 3-stigmatic flowers, the mostly gynaeandrous terminal spikes, and the dark auricles, whereas *C. sect. Phacocystis* is circumscribed by its 2-stigmatic flowers and the male terminal spikes (Egorova 1999). However, these only seemingly section-specific features occur, albeit to varying degrees, regularly in individual species or even only occasionally in single individuals of both sections (Egorova 1999; Shekhovtsova 2010; Reznicek & Murray 2013; pers. obs.), which has obviously resulted in misled conclusions regarding the correct taxonomic affiliation of these species (see also below).

Carex tatjanae from southern Siberia was placed in the section by previous treatments (see Malyshev 1990; Egorova 1999). Despite morphologically similar to *C. orbicularis* Boott s.l. (*Phacocystis*), the taxon shows some features that appear intermediate between the sections *Phacocystis* and *Racemosae*. Thus, it has been discussed as a locally established intersectional hybrid (Egorova 1999; Shekhovtsova 2010). This assumption was based on the occurrence of 3-stigmatic flowers among 2-stigmatic ones, and a rather

scabrous utricle beak (Egorova 1999). Egorova (1999) noted that the type collections have generally sterile utricles, and suggested *C. orbicularis* subsp. *altaica* (Gorodkov) T.V.Egorova and *C. media* (*Racemosae*) as the putative parents. However, preliminary molecular data (including an isotype) suggests that *C. tatjanae* is identical to *C. orbicularis* subsp. *altaica* (Benítez-Benítez et al. 2018; Gebauer et al., unpubl. data; I. Shekhovtsova, pers. comm.). Consequently, *C. tatjanae* is excluded from the section. Flowers with 3-stigmatic styles occasionally occur in several species of *C. sect. Phacocystis* (e.g., *C. aquatilis* s.l., *C. middendorffii* F.Schmidt) and the polymorphic *C. orbicularis* s.l. (Shekhovtsova 2010). The Siberian endemic *C. macrostigmatica* has also been affiliated to *C. sect. Racemosae* (see Kükenthal 1903, 1909; Malyshev 1990; Egorova 1999). Studying the type (and only known specimen) showed a remarkable intermediacy between taxa from the sections *Scitae* and *Phacocystis* instead of species from *C. sect. Racemosae*. Shape and coloration of the pistillate glumes, shape of the utricles, including the short, entire beak, and the lenticular nutlets are typical for *C. sect. Phacocystis* (Chater 1980; Egorova 1999; Jiménez-Mejías & Martinetto 2013). The 3-stigmatic styles occur, however, in *C. sect. Scitae* (Egorova 1999; Murray 2002b; *Scitae* nested in *Phacocystis* s.l.: Global *Carex* Group 2016; Benítez-Benítez et al. 2018; see also **Chapter 3**). Since the type of *C. macrostigmatica* has three inflorescences of different sex distribution with respect to the terminal spike (i.e. either staminate, gynaeandrous, or pistillate) and most of the utricles are sterile, a hybrid origin has been discussed by Egorova (1999). Morphologically, due to these ambiguous features, the type does not permit a reliable determination. In case of a hybrid origin, *C. elata* All. subsp. *omskiana* (Meinsh.) Jalas, *C. nigra* (L.) Reichard, or *C. orbicularis* s.l. (*Phacocystis*), and *C. podocarpa* R.Br. (*Scitae*) could be involved as putative parent species (pers. obs.). On the other hand, *C. macrostigmatica* may represent a malformed 3-stigmatic form of one of the afore-mentioned taxa from *C. sect. Phacocystis* s.l., analogous to *C. tatjanae* discussed above. Two sequence fragments (*matK*, *ETS 1f*) support its affiliation with *C. sect. Phacocystis* s.l. (Benítez-Benítez et al. 2018; Gebauer et al., unpubl. data). However, due to the usually weak molecular divergence between the species of this group, both fragments are not suitable as barcoding markers that would allow identification. Hybridization (and hybrid speciation) occurs frequently, and seems to be an important driver of diversification in *C. sect. Phacocystis*, making analysis of the few molecular data even more difficult (P. Jiménez-Mejías, pers. comm.). Regardless of its true taxonomic identity, *C. macrostigmatica* is no longer considered as belonging to *C. sect. Racemosae*. As a main conclusion, previous treatments seem to have been influenced by

the overestimation or differential weighting of some morphological features that occur independently (i.e. homoplasy) in both sections. As a result, in these and other groups of *Carex*, this has led to frequent incorrect taxonomic conclusions, which becomes increasingly clear through the use of molecular biological approaches (see also Global *Carex* Group 2016).

The treatment of the polymorphic Sino-Himalayan *C. duthiei* combines the often contradictory regional views that have led to descriptions of further taxa, as well as misapplication or neglect of names (Kükenthal 1909, 1930; Nelmes 1939; Noltie 1994; Dickoré 1995; Srivastava 1996; Kukkonen 1998, 2001; Liang & Zhang 2006; Liang & Koyama 2010a). A western (subspec. *duthiei*) and an eastern (subspec. *longistolonifera*) subspecies were proposed. The type of *C. atrata* subsp. *longistolonifera* is identical with *C. giraudiasii* (Léveillé 1913: 288) and *C. schneideri* (Nelmes 1939: 201) and predates the latter names in the rank of a subspecies of *C. duthiei*. Consideration as a subspecies is supported by the often insufficient morphological separation, especially in the overlapping zone in eastern Tibet, northwestern Yunnan and western Sichuan (pers. obs.). Furthermore, both taxa showed an almost complete lack of molecular differentiation (Gebauer et al., unpubl. data). Their rather recent split and molecular divergence still seem incomplete. The recently described *C. obliquitruncata* (Liang & Zhang 2006), which seems only based on aberrant plants with malformed utricles, is considered synonymous with *C. duthiei* subsp. *duthiei*. The morphological peculiarities and possible independence of *C. atrata* var. *glacialis* have been discussed previously (Noltie 1994; H. Noltie, pers. comm.). It was also sometimes treated under *C. duthiei* (Clarke 1908; Kükenthal 1909). However, it is clearly different from *C. duthiei* and all other species of the section occurring in the Central Himalayan region by the smaller size of most vegetative parts and the dimensions and shape of its utricles (Noltie 1994; pers. obs.). Therefore, *C. atrata* var. *glacialis* is considered in the rank of a species, as *C. kangchengyaoensis*. This treatment is further supported by first molecular data (Gebauer et al., unpubl. data). The fact that the Central Asian *C. popovii* and *C. decaulescens* represent the same species, with the first has priority, was already recognized by Egorova (1985), which is also followed in the present study. Consequently, Amini Rad (2015) recently proposed the combination of *C. decaulescens* subsp. *brunneola* under the first name. *Carex popovii* has been studied very rarely and never comparatively with regard to the regionally described subspecies, as in the present taxonomic synopsis (Kreczetovicz 1935a, b, c, 1941; Raymond 1965; Kukkonen 1984; Dickoré 1995; Kukkonen 1998; Egorova 1999; Amin Rad 2007, 2008,

2011, 2015; M. Amin Rad, pers. comm.). *Carex decaulescens* subsp. *alsia* was delineated from the type species by small differences in the width of the spikes, length of the female glumes, the glume/utricle ratio, and width of the utricles by Kukkonen (1984). The comparison of several specimens of *C. popovii* and the type of subspec. *alsia* showed, however, that both taxa significantly overlap in these characteristics. It was also observed that *C. popovii* is more variable, especially with regard to the glume/utricle ratio, so that the latter is regarded as conspecific with *C. popovii*. The same applies to *C. popovii* subsp. *brunneola*. However, the rather brownish inflorescence (vs. blackish-brown to blackish) and longer utricule beaks (0.3–0.5 mm vs. 0.2–0.3 mm), as well as the geographical separation allow the recognition as a subspecies (Kukkonen 1984, 1998; SG, pers. obs.). *Carex montis-wutaii* is recognized as identical with *C. hancockiana* widely distributed in the same region (Egorova 1967, 1985; Liang & Koyama 2010a) and considered synonymous. In the original description, it was compared with *C. lehmannii* (Koyama 1956b) similar with both taxa. The occurrence of *C. hancockiana* in the same region was apparently unknown to Koyama (1956b). The separating features mentioned also distinguish *C. hancockiana* from *C. lehmannii* (Egorova 1967; Kukkonen 2001; Liang & Koyama 2010a; SG, pers. obs.). *Carex minxianensis* was delineated from *C. moorcroftii* mostly by the absence of the broad white-hyaline margin of the female glumes and a rather loose inflorescence (vs. rather densely approximate) (Liang 2000: 520). However, such plants are also found throughout the distribution range of the latter, especially in the eastern limit close to the *locus classicus* of *C. minxianensis* (pers. obs.). Consequently, *C. minxianensis* is treated as synonymous with *C. moorcroftii*. *Carex atrata*, which is regarded as a Western Palearctic species, has long been treated as a collective species, especially by European botanists studying Asian plants and comparing them with *C. atrata* known from Europe (Clarke 1908; Kükenthal 1909). *Carex apodostachya*, originally described as a distinct species (Ohwi 1934), was often considered synonymous with *C. atrata* or a sub-species of it (Koyama 1962, 1978b; Koyama et al. 2000; Liang & Koyama 2010a). However, *C. apodostachya* is easily distinguished from *C. atrata* (and *C. japonalpina*; see below) by its shorter female glumes and the longer utricule beaks (pers. obs.). Its separation is further supported by molecular data (Gebauer et al., unpubl. data). Further East Asian plants resembling *C. atrata* are also often considered conspecific with the latter (Fu 1995; Liang & Koyama 2010a; Hoshino et al. 2011). These were sometimes treated as a variety of *C. atrata* or as a distinct species, *C. japonalpina* (Koyama 1956a). Both taxa were considered closely related, but the color of the inflorescences and utricles,

and the shape of the utricles and the nutlets can separate them (Koyama 1955, 1956a; pers. obs.). Their allopatric distribution ranges (Koyama 1955) and initial molecular data also support their separation, so that the East Asian plants are considered here as *C. japonalpina*. Some Taiwanese plants were treated as *C. caucasica* subsp. *jisaburo-ohwiana* (Koyama et al. 2000; Liang & Koyama 2010a), although originally described as a species (Koyama 1956c). Study of the type material of *C. jisaburo-ohwiana* has made clear that it seems not closely related to *C. caucasica* and should be considered as a distinct species (pers. obs.). Its separation is further supported by first molecular data (Gebauer et al., unpubl. data).

In order to prevent confusions of similar and polymorphic species, these were placed several times in the key, taking into account the known morphological variation. Although this approach makes the key significantly longer compared with other treatments (Chater 1980; Egorova 1999; Liang & Koyama 2010a), it offers the advantage of an increased likelihood of correct species identification in this difficult group.

General aspects on biogeography. — Biogeographically, the study of both selected groups in the present thesis suggests that the origins of arctic species and lineages are to be found in different regions. For example, a high mountain origin of arctic species that are placed in a clade composed of boreal to arctic, or arctic-alpine taxa (e.g., *C. aterrima* subsp. *aterrima*, *C. atrata*, *C. atratiformis*, and *C. norvegica* s.l.) in *C. sect. Racemosae* can be assumed (see **Chapters 3** and **4**). The arctic taxa of the northern radiations ('Northern clades') in *C. sectt. Vesicariae* and *Phacocystis* (see Dragon & Barrington 2009; **Chapter 2**), as well as a few species belonging to *C. sect. Racemosae* may rather be of lowland origin (*C. adelostoma*, *C. holostoma*). Multiple places of origin for arctic taxa have previously been inferred in other angiosperms, which include various types of wetlands (*Ranunculus* L.: Hoffmann et al. 2010), high mountains (*Pedicularis* L.: Tkach et al. 2014; *Saxifraga* L.: DeChaine et al. 2013), boreal forests (*Pedicularis*: Tkach et al. 2014), and more rarely steppes (*Artemisia* L.: Tkach et al. 2008a, b). Furthermore, *in situ* evolution of some Arctic species is suggested in both northern radiations (e.g., *C. membranacea*, *C. rotundata*, *C. subspathacea*) and *C. sect. Racemosae* (e.g., *C. holostoma*). *In situ* evolution in the Arctic has also been reported in other genera (*Artemisia*: Tkach et al. 2008a, b; *Cerastium* L.: Scheen et al. 2004; *Douglasia*: Schneeweis et al. 2004; *Draba* L.: Grundt et al. 2006; *Pedicularis*: Tkach et al. 2014; *Ranunculus*: Hoffmann et al. 2010; and *Saxifraga*: Brochmann et al. 1998; Jørgensen et al. 2006). The species of both studied sections mostly occur in various types of wetlands in lowlands or high mountains (Egorova

1999; Murray 2002a; Reznicek & Ford 2002; Liang & Koyama 2010a), which have also been demonstrated as important sources of the Arctic flora by a recent biogeographical study on genus *Carex* (see Hoffmann et al. 2017).

High rates of endemism and regional species richness occur in *C. sect. Racemosae*. The highest number of endemics (as well as species) is found in the high mountain ranges of western North America and Inner Asia. In North America, the Rocky Mountains and the Pacific mountain system (including the Cascades and Sierra Nevada) are of particular importance that houses, especially in its southern areas, some narrow endemics (e.g., *C. aboriginum*, *C. orestera*, or *C. specuicola*) (Murray 1969, 2002a; Zika 2012; Reznicek & Murray 2013). In Inner Asia, high species richness is found in the high mountain ranges surrounding the Tibetan Plateau and the Qaidam and Tarim Basins. Highest species richness is observed in the Hengduan Mountain region, where most of the endemic taxa occur (e.g., *C. aristulifera*, *C. bijiangensis*, or *C. polymascula*) (Liang & Koyama 2010a). The exceptional diversity and endemism of the Hengduan Mountains have been widely documented, and the region is considered one of the most important biodiversity hotspots of the temperate zone (López-Pujol et al. 2011; Sun et al. 2017; Xing & Ree 2017). Two endemics occur in Taiwan (*C. apodostachya*, *C. jisaburo-ohwiana*; Koyama et al. 2000), which is also well known for its exceptional plant endemism (Myers et al. 2000). Some species exhibit quite small ranges, being rather restricted to a few closely connected single-mountain ranges. Such taxa can be considered ‘sub-endemic’ (e.g., *C. oligantha*, *C. serreana*) (Kukkonen 1998; Egorova 1999; Liang & Koyama 2010a; pers. obs.).

General aspects on morphology. — It has been shown that several morphological characters, particularly those related to reproductive structures that have been selected *a priori* as being of taxonomic value for classification, are influenced by homoplasy. This is of particular importance in *C. sect. Racemosae*, especially regarding some qualitative morphological features (**Chapters 3 and 4**). Many other examples of such homoplasy have been reported by phylogenetic studies on the genus (Roalson et al. 2001; Ford et al. 2006; Hipp et al. 2006; Ford et al. 2012; Jiménez-Mejías et al. 2012; Maguilla et al. 2015; Molina et al. 2015; Global *Carex* Group 2016). Thus, reexamination of morphological variation may help to identify morphological characters, which can be used to define taxa that are congruent with phylogenetic lineages, and thus natural groups (Global *Carex* Group 2016). The combination of qualitative and quantitative generative, reproductive and vegetative features has been found very useful during preparation of the present taxonomic synopsis and key of *C. sect. Racemosae* in Eurasia. This particularly concerned the

delineation of very similar species, as well as to circumscribe the section, taking into account the recent molecular phylogenetic insights. Character combinations used to define groups (e.g., sections) in future classifications to circumvent the confounding effects of homoplasy if a few characters are considered independently (Maguilla et al. 2015; Global *Carex* Group 2016) have also been suggested by recent studies (Hipp et al. 2006; Molina et al. 2015). Further, consideration of non-traditional characters as sources of variation, i.e. anatomical and micromorphological (Roalson et al. 2001; Naczi 2009; Proctor & Bradshaw 2013, 2014a, b, 2015a, b), carpological (Jiménez-Mejías & Martinetto 2013; Martinetto et al. 2014; Jiménez-Mejías et al. 2016) and vegetative (see above), helps developing future taxonomic schemes. This has already been demonstrated for other large and taxonomically complex groups (Larridon et al. 2011b; Zamora et al. 2014; reviewed in Global *Carex* Group 2016). The morphological circumscription of natural groups is not only of systematic or taxonomic relevance, since it also promotes reliable identification and understanding of taxa. Thus, it also has implications for other fields of biology, such as ecology, conservation biology, and biodiversity research. It has also an impact on the field of amateur botanists and thus also gains importance for the general public and the long-term synthesis of global biodiversity knowledge (reviewed in Global *Carex* Group 2016).

6 CONCLUSION

The present thesis focused on the systematics, taxonomy and biogeography of two species-rich groups of genus *Carex*, (1) *Carex* sect. *Vesicariae* and allied groups (i.e. the ‘Hirta clade’), and (2) *Carex* sect. *Racemosae*. Molecular sequence data from three to four DNA regions (plastid *trnK–matK*, *rps16*; nuclear ITS [both sections], ETS 1f [only in *C.* sect. *Racemosae*]), were used. These were partly combined with morphological, ecological, chorological, and karyological data.

It was shown that *C.* sect. *Vesicariae* is non-monophyletic even in its broadest sense (Egorova 1999; Reznicek & Ford 2002). Its representatives are nested in a large clade (‘Hirta clade’) that includes most sampled taxa from sections *Carex*, *Lupulinae*, *Paludosae* (= *Tumidae sensu* Egorova 1999), and *Pseudocypereae* (Gebauer et al., in prep.; also *Squarrosae* p.p.: Waterway et al. 2015; Global *Carex* Group 2016; *Anomaliae* p.p.: Waterway et al. 2015). These findings suggest the ‘Hirta clade’ one of the largest groups of the entire genus. The majority of species previously affiliated to *C.* sect. *Vesicariae* were found nested in a clade that is further divided into two sister lineages. The present study found a similar topology and biogeographic pattern in these lineages of *C.* sect. *Vesicariae* (‘Northern’ and ‘Mixed clades’) as reported for *C.* sect. *Phacocystis* (Dragon & Barrington 2009). A similar pattern was observed for the molecular and morphological differentiation between and within the corresponding lineages of both sections and their niche requirements. Thus, a rare case of rather recent and rapid parallel diversification and ecological convergence (i.e. replicated adaptive radiation; Losos 2010) in boreal to arctic environments in both sections is reported. The inclusion of the type species of the genus, subgenus *Carex*, and *C.* sect. *Carex* (*C. hirta*) in the ‘Hirta clade’ is important regarding the future reclassification and subdivision of the genus. The sectional name ‘*Carex*’ would have priority if the ‘Hirta clade’ is considered a section in the future. Morphologically intermediate taxa (e.g., *C. lurida* group, *C. oligosperma*, *C. schweinitzii*), homoplasmy (e.g., *Lupulinae*, *Vesicariae*), and discordant placements of a few taxa (e.g., *C. songorica*) suggest patterns of ILS, ancestral hybridization, or introgression in the ‘Hirta clade’, which needs further investigations. Subsequent studies should include ‘candidate-species’ that may be related to this clade based on current findings and observed morphological similarities.

It is shown that *C.* sect. *Racemosae* s.str. is monophyletic. The majority of sampled species, including the type species (*C. atrata*), were found in a strongly supported monophyletic clade. Several taxa previously assigned to the section must be excluded. Three species were newly included in the section. The majority of the proposed sub-

sections were not confirmed. It is shown that previous suggestions on the relationships of morphologically similar taxa (i.e. subsectional division, vicariant species) resulted from the exceptional homoplasy in the group. The revised taxonomic treatment proposed for the Eurasian taxa consequently dispenses with further subdivision into subsections. The present study gives evidence that biogeography of some major clades better explains the associated taxa than morphological considerations (e.g., Central Asian–Sino-Himalayan clade, Nearctic clade). Colonization of high-mountain regions followed by subsequent diversification may have played an important role for the evolution and species richness of the group. Unexplored diversity (e.g., cryptic species) might be expected in some lineages, particularly within the group's diversity centers in western North America (R. Massatti, pers. comm.) and Inner Asia. This is evidenced by recent descriptions of species in the group (Li 1990; Liang & Zhang 2006; Zika 2012; Reznicek & Murray 2013; this study). The present taxonomic synopsis and identification key for the Eurasian species enable for the first time reliable identification and comparison across national borders. It can also provide the impetus for a worldwide revision of this species-rich group.

The present study provides with the first comprehensive phylogenetic hypotheses new and important insights into the evolution, systematics and taxonomy as well as biogeography of the two studied sections. Like many other studies, it further points to a rather complicated phylogenetic history of the entire genus *Carex* and the traditionally circumscribed various sections. Its results and implications thus represent a fundamental basis for further studies, even in other groups of the genus. However, some questions remain unresolved regarding the biogeographic history or some clade- or species-specific relationships in these rather recently diverged groups. Thus, detailed biogeographical analyses could be interesting to resolve the migration history in, e.g., *C.* sect. *Racemosae* to better understand its recent distribution. Datasets using multiple single- or low-copy genes or loci from anchored hybrid enrichment approaches have proven to be useful in recently diverged lineages, particularly due to possible different evolutionary histories of single markers, as well as presence of ILS, introgression, or hybridization (Faircloth et al. 2012; Lemmon et al. 2012; Zhang et al. 2012; Mendoza et al. 2015; Schmickl et al. 2016; Stoughton et al. 2018). Thus, next-generation sequencing (NGS) would be appropriate for studying such multiple single- or low-copy genes or other loci (including SNPs from RadSeq data; Eaton & Ree 2013; Massatti et al. 2016) in rather recently diverged and taxonomically difficult plant groups.

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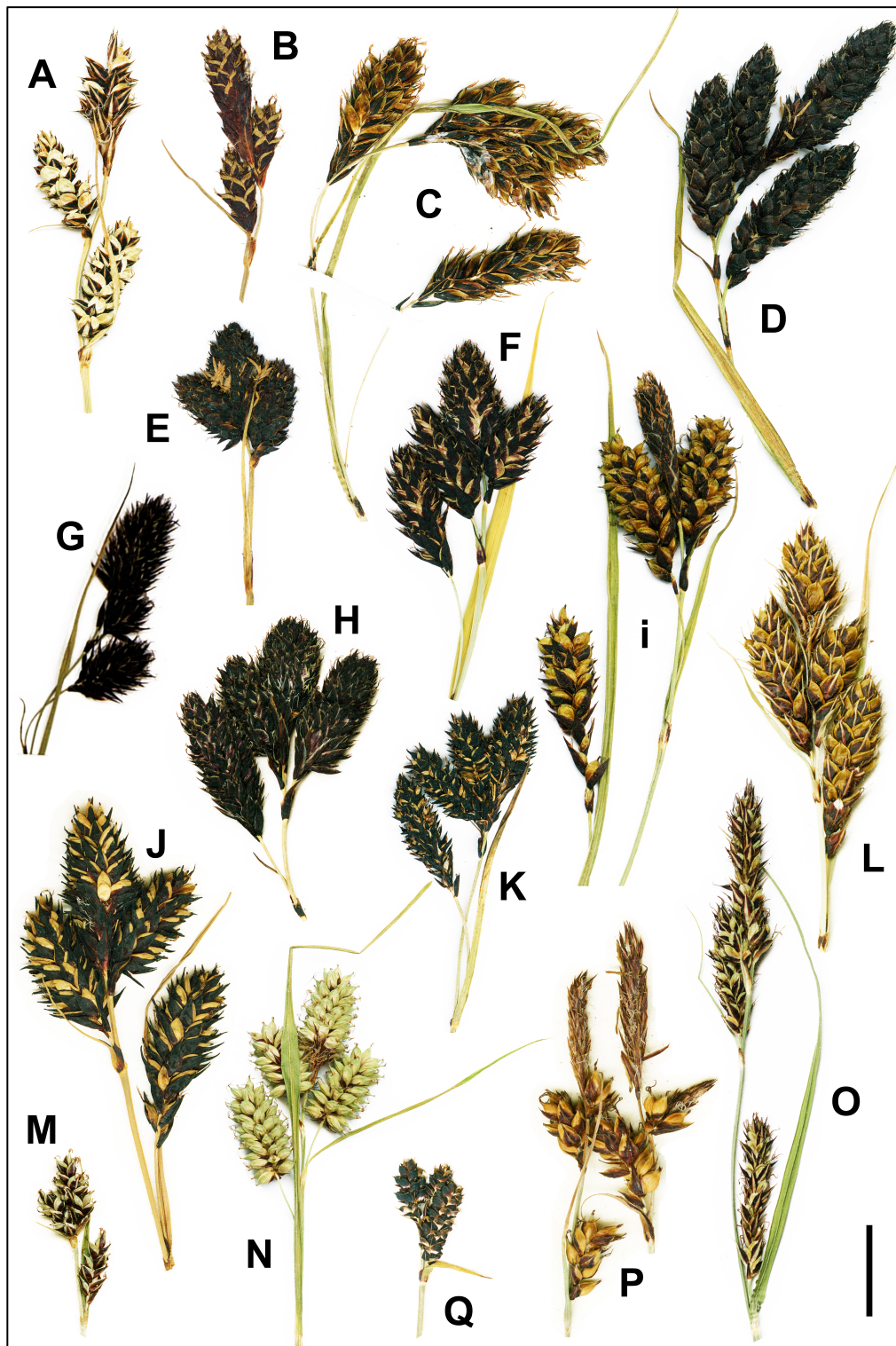
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8 APPENDIX

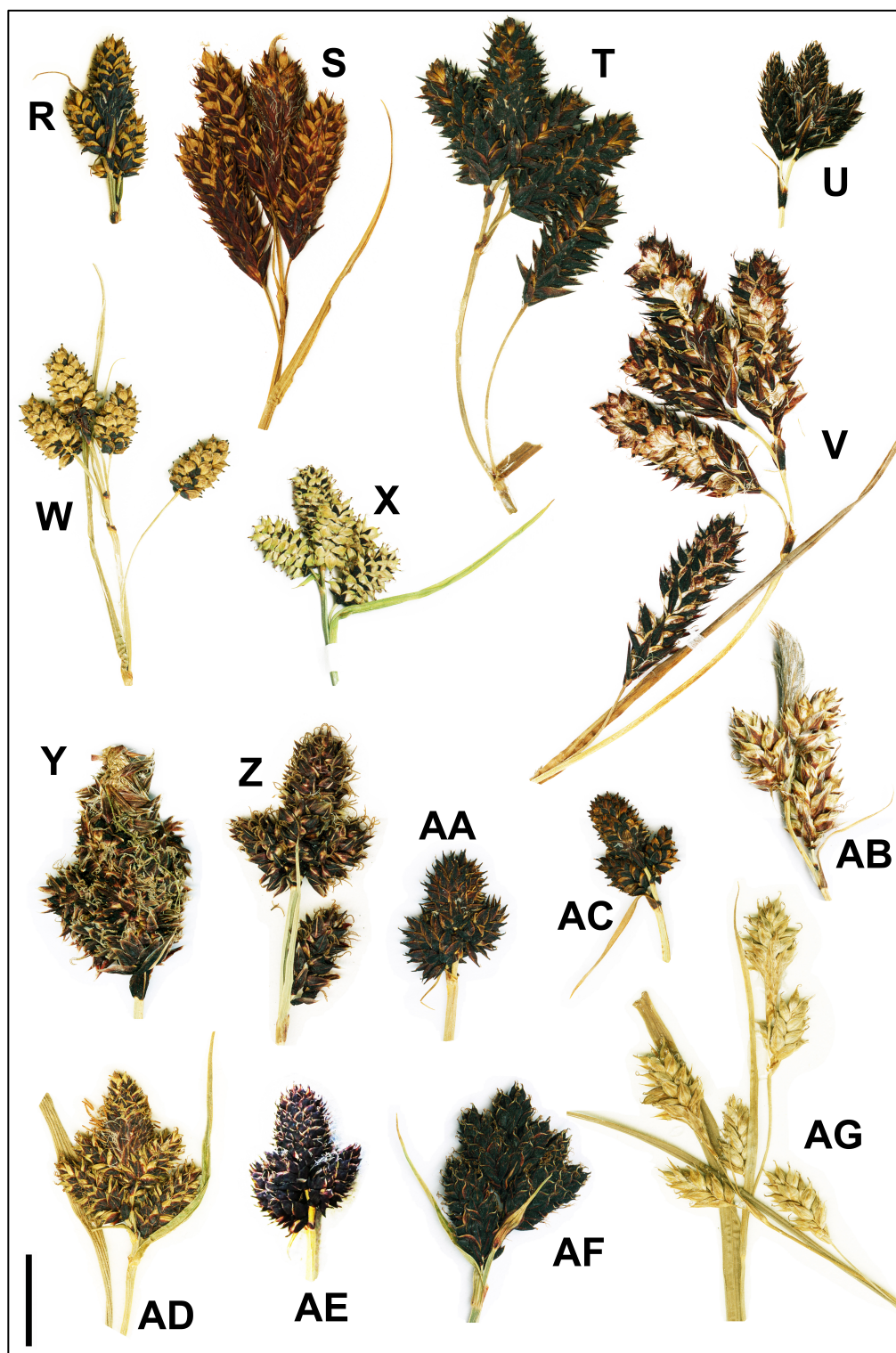
APPENDIX: CHAPTER 4

A revised taxonomic synopsis and key for the species-rich and predominantly high mountain sedge group *Carex* section *Racemosae* G.Don (Cyperaceae) in Eurasia, Gebauer, S. & Jiménez-Mejías, P.*, unpublished Manuscript (*co-author for planned submission).

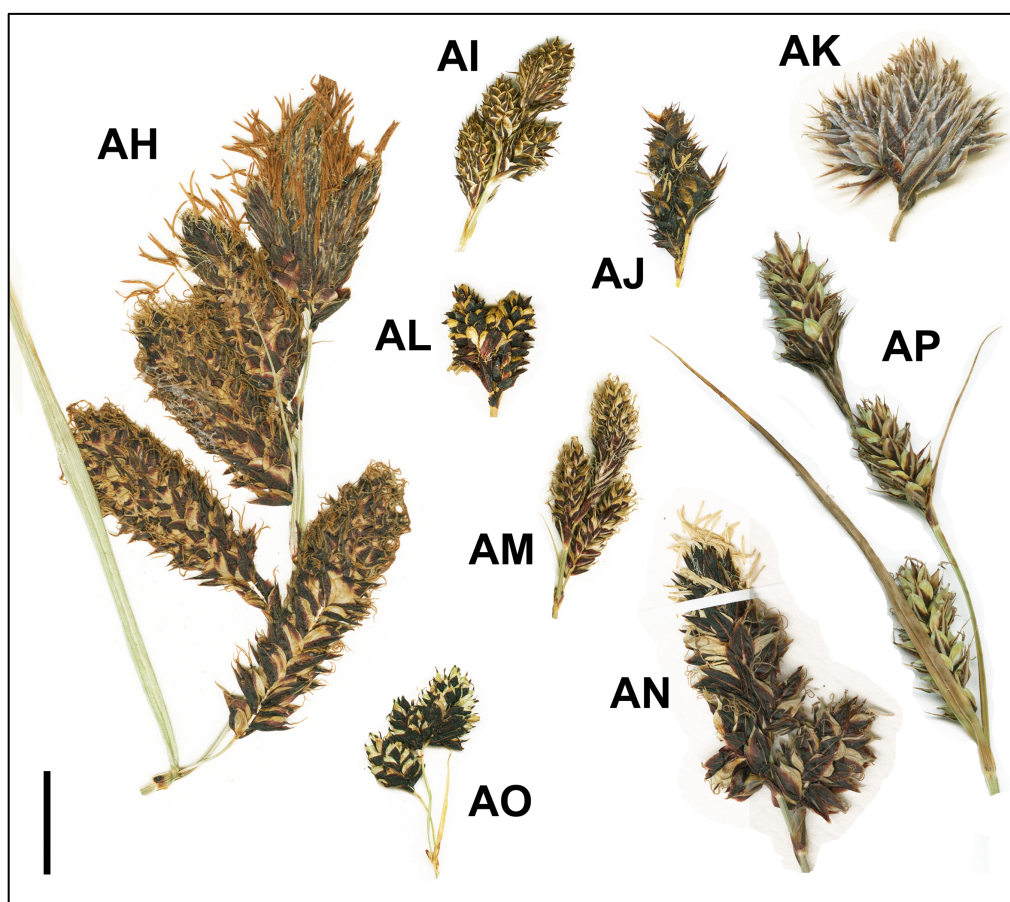
Appendix 1 (Supplemental Figures S1–S9)



SUPPLEMENTAL FIG. S1: A–Q. Inflorescences of Eurasian taxa of *Carex* sect. *Racemosae* (scale bar = 1 cm). A: *C. adelostoma* (Schneider, s.n.; HAL!); B: *C. apodostachya* (Ohwi 4053; NY, Type!); C: *C. aristulifera* (Heng et al. 32179; A!); D: *C. aterrima* subsp. *aterrima* (Hilpold et al., s.n.; BOZ!); E: *C. aterrima* subsp. *medwedewii* (Gebauer 130752; Herb. Gebauer); F: *C. atrata* (Gebauer 140816; Herb. Gebauer); G: *C. atrofusoides* (Elumeeva, s.n.; MW!); H: *C. bijiangensis* (Long & Noltie 374; E!); i: *C. caucasica* (Gebauer 130720; Herb. Gebauer); J: *C. duthiei* subsp. *longistolonifera* (Maire, s.n.; E, Type! of *C. giraudiasii*); K: *C. duthiei* subsp. *duthiei* (Miehe et al. 00-265-22; MR!); L: *C. gmelinii* (Gage & Semsrott BS0017; NY!); M: *C. gracilentia* (Dickoré 9784; MSB!); N: *C. hancockiana* (Hoffmann M02:218; Herb. Hoffmann); O: *C. hartmaniorum* (Hoffmann 1432; Herb. Hoffmann); P: *C. heterostachya* (Hertel 23290; M!); Q: *C. holostoma* (Læggaard, s.n.; B!).



SUPPLEMENTAL FIG. S2: R–AG, Inflorescences of Eurasian taxa of *Carex* sect. *Racemosae* (scale bar = 1 cm). **R**: *C. infusata* (Anders 5136; MSB!); **S**: *C. japonalpina* (Furuse 47902; K!); **T**: *C. jisaburo-ohwiana* (Sasaki, s.n.; NY!); **U**: *C. kangchengyaoensis* (Long & Noltie 388; E!); **V**: *C. kansuensis* (Miehe et al. 04-165-08; MR!); **W**: *C. lehmannii* (Polunin 572; NY!); **X**: *C. media* (Jäger, s.n.; HAL!); **Y**: *C. melanantha* (Heuchert B43; HAL!); **Z**: *C. melananthiformis* (Mirkin, s.n.; HAL!); **AA**: *C. melanocephala* (Heuchert B32; HAL!); **AB**: *C. moorcroftii* (Miehe & Miehe 03-052-09; MR!); **AC**: *C. norvegica* (Tribsch, s.n.; WU!); **AD**: *C. obscura* (Stewart & Stewart 5939; NY!); **AE**: *C. oligantha* (Bysh & Bysh, s.n.; TBI!); **AF**: *C. parviflora* (Gebauer 140870; Herb. Gebauer); **AG**: *C. peiktusani* (Ohwi 2701; NY!).



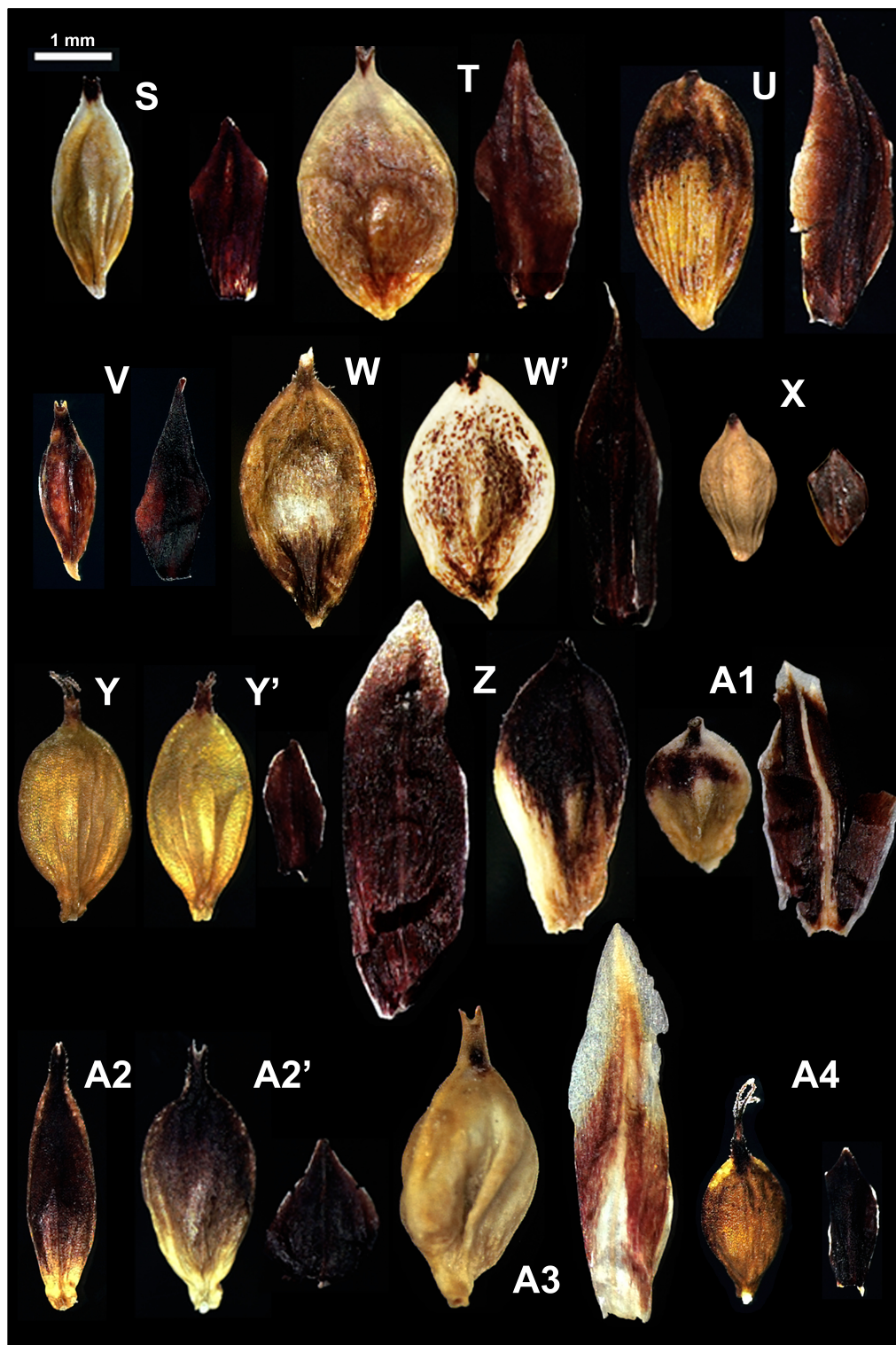
SUPPLEMENTAL FIG. S3: AH–AO, Inflorescences of Eurasian taxa of *Carex* sect. *Racemosae* (scale bar = 1 cm). AH: *C. polymascula* (Boufford et al. 28634; A!); AI: *C. popovii* subsp. *brunneola* (Amini Rad & Torabi, s.n.; IRAN!); AJ: *C. popovii* subsp. *popovii* (Hoffmann T547; Herb. Hoffmann); AK: *C. praeclara* (Dickoré 3831; MSB!); AL: *C. pseudobicolor* (Stewart 20127; NY!); AM: *C. psychrophila* (Dobremez 2133; NY!); AN: *C. sabulosa* (Petrovsky, s.n.; JE!); AO: *C. serreana* (Long et al. 1045; E!); AP: *C. buxbaumii* (Hoffmann a197; Herb. Hoffmann).



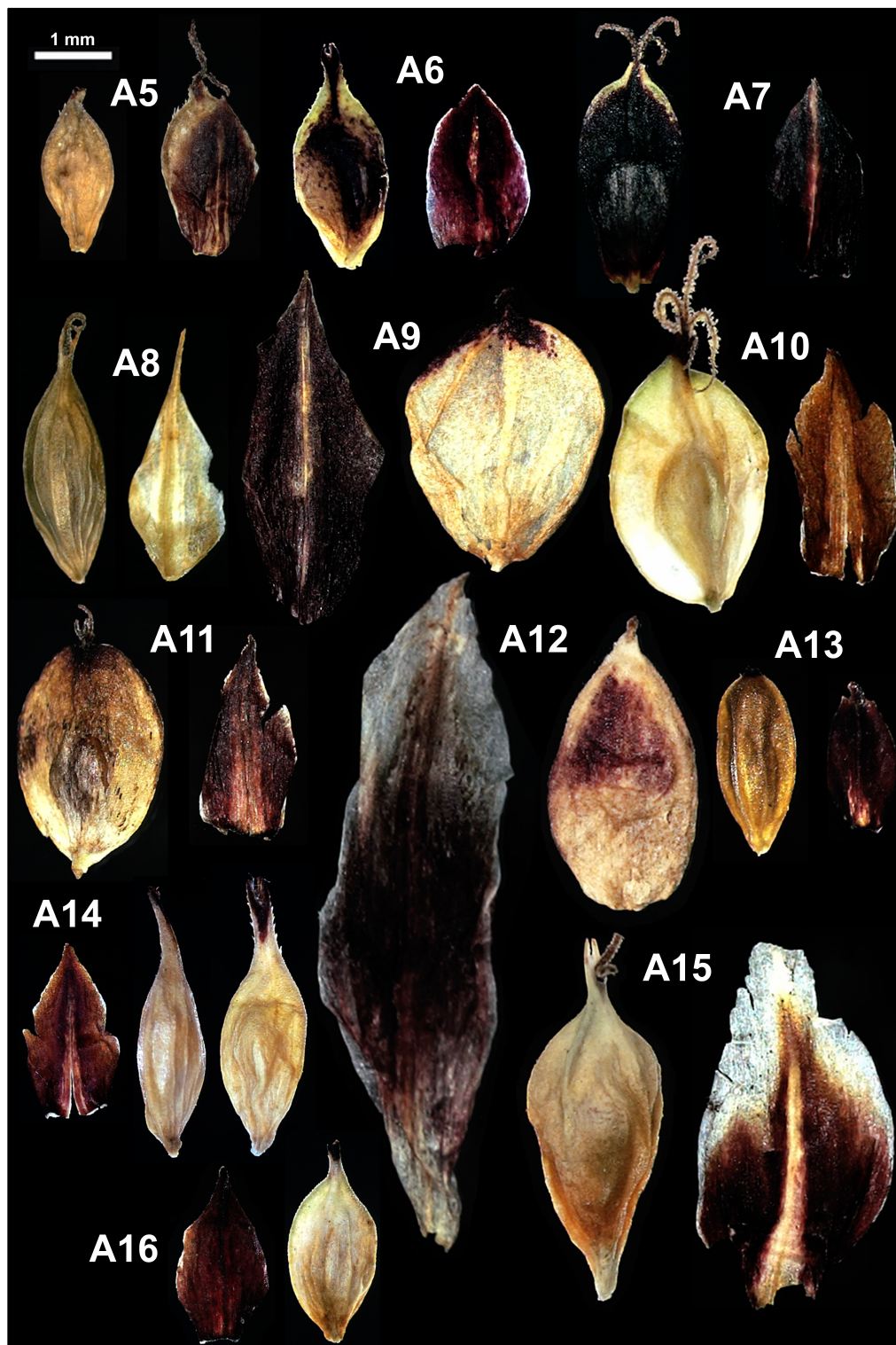
SUPPLEMENTAL FIG. S4: A–H, Utricles and female glumes of Eurasian taxa of *Carex* sect. *Racemosae* (scale bar = 1 mm). **A:** *C. adelostoma* (Hoffmann a245; Herb. Hoffmann); **B:** *C. apodostachya* (Liao & Tien-Tsai, s.n.; TAIE!); **C:** *C. aristulifera* (Heng et al. 32179; A!); **D:** *C. aterrima* subsp. *aterrima* (Heuchert B28; HAL!); **E:** *C. aterrima* subsp. *medwedewii* (Stainton & Henderson 6175; E!); **F:** *C. atrata* (Gebauer 140872; Herb. Gebauer); **G:** *C. atrofuscoides* (Elumeeva, s.n.; MW!); **H:** *C. bijiangensis* (Deng 05234; MOR!).



SUPPLEMENTAL FIG. S5: *I–R*, Utricles and female glumes of Eurasian taxa of *Carex* sect. *Racemosae* (scale bar = 1 mm). *I*: *C. buxbaumii* (Hoffmann a197; Herb. Hoffmann); *J*: *C. caucasica* (Gebauer 130727; Herb. Gebauer); *K*: *C. duthiei* subsp. *duthiei* (Clarke 29722; K, Type! of *C. nigerrima*); *L*: *C. duthiei* subsp. *longistolonifera* (Maire, s.n.; E, Type! of *C. giraudiasii*); *M*: *C. gmelinii* (Gage 7129; NY!); *N*: *C. gracilentia* (Miehe & Miehe 00-290-08; MR!); *O*: *C. hancockiana* (Hoffmann M02:218; Herb. Hoffmann); *P*: *C. hartmaniorum* (Gebauer 120617; HAL!); *Q*: *C. heterostachya* (Kung 1372; NY!); *R*: *C. holostoma* (Løgaard, s.n.; B!).



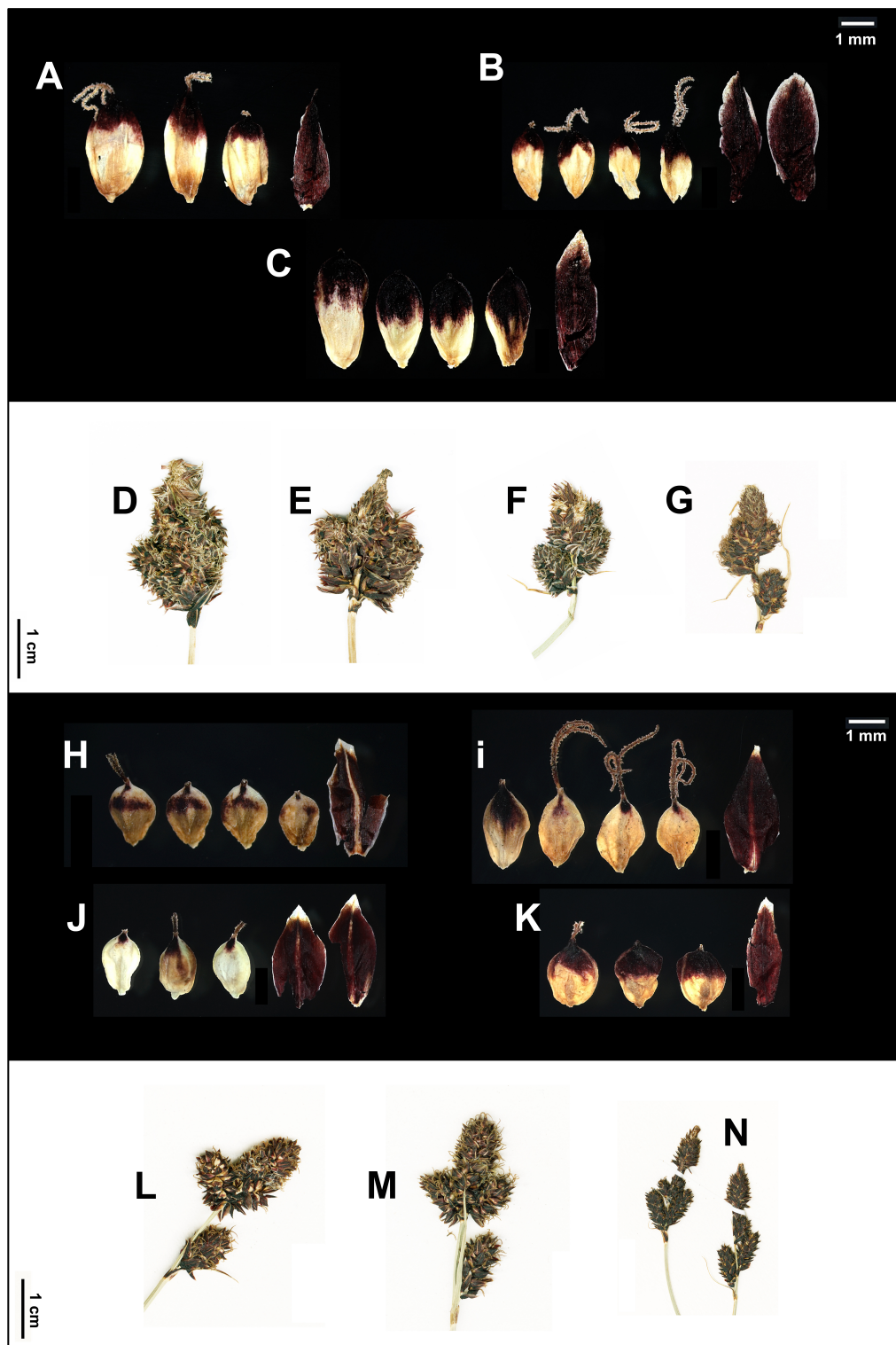
SUPPLEMENTAL FIG. S6: S–A4, Utricles and female glumes of Eurasian taxa of *Carex* sect. *Racemosae* (scale bar = 1 mm). **S:** *C. infusata* (Kerstan 948a; HAL!); **T:** *C. japonalpina* (Koidzumi, s.n.; NY!); **U:** *C. jisaburo-ohwiana* (Tagawa 444; NY, Type!); **V:** *C. kangchengyaoensis* (Hooker, s.n.; K, Type!); **W:** *C. kansuensis* (Miehe et al. 94-408-18; MSB!); **W':** *C. kansuensis* (Miehe et al. 04-165-08; MR!); **X:** *C. lehmannii* (Dickoré 10600; MSB!); **Y:** *C. media* (Elias & Murray 11269; NY!); **Y':** *C. media* (Heuchert B53; HAL!); **Z:** *C. melanantha* (Hoffmann T466; Herb. Hoffmann); **A1:** *C. melananthiformis* (Neyfeld & Dereka, s.n.; JE!); **A2:** *C. melanocephala* (Heuchert B32; HAL!); **A2':** *C. melanocephala* (Schischkin et al., s.n.; NY!); **A3:** *C. moorcroftii* (Koelz 9863; NY!); **A4:** *C. norvegica* (Hoffmann a243; Herb. Hoffmann).



SUPPLEMENTAL FIG. S7: A5–A16, Utricles and female glumes of Eurasian taxa of *Carex* sect. *Racemosae* (scale bar = 1 mm). A5: *C. obscura* (Stewart 5603; NY!); A6: *C. oligantha* (Shcherbakov & Filonov, s.n.; MW!); A7: *C. parviflora* (Gebauer 140810; Herb. Gebauer); A8: *C. peiktusani* (Ohwi 2701; NY!); A9: *C. polymascula* (Boufford et al. 28634; E!); A10: *C. popovii* subsp. *brunneola* (Amini Rad & Torabi, s.n.; IRAN!); A11: *C. popovii* subsp. *popovii* (Hoffmann T547; Herb. Hoffmann); A12: *C. praeclara* (Dickoré 3853; K!); A13: *C. pseudobicolor* (Koelz 1209; NY!); A14: *C. psychrophila* (Thomson, s.n.; M!); A15: *C. sabulosa* (Pavlov 41; NY!); A16: *C. serreana* (Miehe 9220/07; MR!).



SUPPLEMENTAL FIG. S8: A–I, Detailed images of *Carex bijiangensis* and *C. kansuensis*. A–E, *C. bijiangensis*: A–B: utricles, female glumes, and nutlets, scale bar = 1 mm; C–E: inflorescences, scale bar = 1 cm; F–I, *C. kansuensis*: F–G: utricles, female glumes, and nutlets, scale bar = 1 mm; H–I: inflorescences, scale bar = 1 cm; A: Deng 05234 (MOR!); B, D: Dickoré 9852 (MSB!); C, E: Long & Noltie 374 (E!); F, H: Miehe et al. 04-165-08 (MR!); G, I: Miehe et al. 94-408-18 (MSB!).



SUPPLEMENTAL FIG. S9: A–N, Detailed images of *Carex melanantha* and *C. melananthiformis*. A–G, *C. melanantha*: A–C: utricles and female glumes, scale bar = 1 mm; D–G: inflorescences, scale bar = 1 cm; H–N, *C. melananthiformis*: H–K: utricles and female glumes, scale bar = 1 mm; L–N: inflorescences, scale bar = 1 cm; A: Vasilczenko & Vassiljeva, s.n. (NY!); B: Günther et al. 305 (JE!); C: Hoffmann T466 (Herb. Hoffmann); D–E: Heuchert B43 (HAL!); F: Hilpold & Schönswetter, s.n. (BOZ!); G: Stewart 19923 (NY!); H: Hoffmann j96 (Herb. Hoffmann); I, N: Neyfeld & Dereka, s.n. (JE!); J: Hoffmann j103 (Herb. Hoffmann); K: Rodin 601 (NY!); L–M: Mirkin, s.n. (HAL!).

APPENDIX: CHAPTER 4

A revised taxonomic synopsis and key for the species-rich and predominantly high mountain sedge group *Carex* section *Racemosae* G.Don (Cyperaceae) in Eurasia, Gebauer, S. & Jiménez-Mejías, P.^{*}, unpublished Manuscript (*co-author for planned submission).

Appendix 2 (Additional specimens studied)

List of additional specimens studied. Abbreviations for herbaria in brackets follow Thiers (2018+; continuously updated); “MR” refers to the High Asia Project Herbarium deposited at the Philipps University Marburg, Germany. Private collections are also listed in parentheses with the name of the respective collectors as explained in the Materials and Methods section (see above).

1. *Carex adelostoma* V.I.Krecz.:—FINLAND. LAPLAND: Kemi Lapland, Savukoski, Ruuvaaja, Sotataival—*S. Vuokko* 82 (H, HAL). Perä-Pohjanmaa, Rovaniemi rural comm. E of road to Niesi (220 m)—*T. Ulvinen, s.n.* (HAL). Enontekiö, Kilpisjärvi, Possujoki (600 m)—*U. B. Segerman* 8066 (BR, digital image!).—**NORWAY. SØR-TRØNDELAG:** In uliginosis Dovrefield—*s. coll.* (HAL). Dovrefjell, Knutshø, between Hjerskinn and Kongsvoll/Drivdalen (1041 m)—60° 34.291' N 17° 52.764' E. *M. H. Hoffmann* a245 (Herb. Hoffmann). Dovrefjell, Oppdal—cultivated at Botanical Garden Halle from seeds of Botanical Garden Ringve, Trondheim—*s. coll.* (HAL).—**TROMS:** Troms fylke, Bardu herad, Bardu, lower slopes of Storfjellet—*K. & U. Laine, s.n.* (JE). Bardu Herred (370 m)—68° 65' N 18.5° E. *J. Höller, s.n.* (M). Bardu Herred (370 m)—68° 65' N 18.5° E. *J. Höller, s.n.* (M). Troms fylke, Nordreisa Herred, Reisendal W of Vinnelys (100 m)—*J. Höller, s.n.* (M). Troms fylke, Nordreisa Herred, Straumtjorden S tip (5 m)—*J. Höller, s.n.* (M). Kvaenangen Herred, Battereidet (100 m)—*J. Höller, s.n.* (M).—**RUSSIA. Krasnoyarsk:** W Taimyr, Putorana plateau, near W part of lake Gloubokoïe—69° 17' 22.1" N 89° 51' 50.9" E. *I. N. Pospelov* 15-0244 (MW, digital image!).—**MURMANSK OBLAST:** Peninsula Kolaënsis, Montes Chibiny, in palude—21 Jul 1925. *D. Litwinow, s.n.* (LE; MW, digital image!). Maiwaltajok valley—*K. Schneider, s.n.* (HAL). Kola distr., area of upper Tuloma reservoir, ridge between mountains Mutkaselka and Chiltada, E macroslope—68.228027° N 31.006638° E. *K. B. Popova* M-795 (MW, digital image!). Kandalshky distr., Luevenga, Louveng tundra mts.—67.1315000° N 32.75852° E. *M. N. Kozhin* M-07-019 (MW, digital image!). Kandalaksha distr., neighborhood of the village Luevenga, Louvain tundra mts.—*E. A. Gryaznova* M-2209 (MW, digital image!). Kandalaksha distr., neighborhood of the village Luevenga, Louvain tundra mts.—67.15438° N 32.76527° E. *M. N. Kozhin* M-1990 (MW, digital image!). Terski distr., White Sea, Porya Guba, Bol'shoj Pedun Isl. (SW part)—66.7092° N 33.64227° E. *M. N. Kozhin* M-2291 (MW, digital image!).—**SWEDEN. LAPPLAND:** swamp places above Vassijaure—*H. Meusel, s.n.* (HAL, two sheets).

2. *Carex apodostachya* Ohwi:—TAIWAN. HUALIEN: Hoping Hsian, Mt. Nanhutashan, Taosweifeng peak (3450 m)—24° 21' 35" N 121° 27' 11" E. *W. C. Leong et al., s.n.* (DOV, digital image!).—**TAICHUNG:** Formosa—21 Jul 1932. *S. Sasaki, s.n.* (mixed with *C. jisaburo-ohwiana* T.Koyama) (NY). Ilan Hsien,

Taroko N.P., just below Nanhutashan from Nanhu Camp, loop on shale slopes above camp (3480 m)—24° 22' N 121° 26' E. *W. L. Wagner 6534* (US). Mt. Nan-hu (3550 m)—24° 22' 44" N 121° 26' 23" E. *C. Liao & C. Tien-Tsai, s.n.* (TAIE). Mt. Nan-hu (3385 m)—24° 21' 59" N 121° 26' 53" E. *C. Liao & C. Tien-Tsai, s.n.* (TAIE). Hsuehshan (3500 m)—*S.-Y. Lu 19984* (as *C. atrata* subsp. *apodostachya*) (TAIF, digital image!). Hoping Hsiang, Hsuehshan (3600–3884 m)—*S.-P. Li 176* (as *C. atrata* subsp. *apodostachya*) (TAIF 153179, digital image!).—**YILAN:** Pref. Ilan, Mt. Nanhuta-shan, between Kamibajin and Bunakkei (3000–3300 m)—*M. Tamura et al., s.n.* (KUN, digital image!). Nanhu cirque (3600 m)—24° 21' N 121° 26' E. *S.-Y. Lu, s.n.* (as *C. atrata* subsp. *apodostachya*) (TAIF, digital image!). Nanhu cirque, Mt. Nanhuta (3400 m)—*T.-C. Hsu 199* (as *C. atrata*) (TAIF, digital image!). Nanhutashan (3400–3700 m)—*H.-J. Lai 615* (as *C. atrata*) (TAIF, two sheets, digital image!).

3. *Carex aristulifera* P.C.Li:—CHINA. YUNNAN: Gongshan: Cikai, Near Yipsaka lake, E side of Gaoligong Shan (3450 m)—27° 45' 18.1" N 98° 27' 21" E. *Heng et al. 32179* (A). Gongshan: Bingzhongluo, E side of Gaoligong Shan (3880 m)—27° 59' 14" N 98° 28' 23.8" E. *Heng et al. 31311* (as *C. atrata*) (A).

4. *Carex aterrima* Hoppe:—4a. *Carex aterrima* subsp. *aterrima*:—AUSTRIA. TYROL: St. Jakob (2200 m)—*Flecke, s.n.* (HAL).—**VORARLBERG:** close to the Ulm hut (Ulmer Hütte) (c. 2100 m)—*G. Kükenthal 257* (HAL). Bregenzer Wald, S of Furka ridge, W crest of Pfrondhorn Mt. (1900–1950 m)—*M. Röser 5779* (Herb. Röser).—**GERMANY. BAVARIA:** Berchtesgaden Alps, Feldalm—*A. Buhl 4442* (HAL). Berchtesgadener Alps, Hanauerlaubsattel (1866 m)—*A. Buchholz K109* (M).—**KAZAKHSTAN. ALMATY:** Tian Shan, Trans-Ili Alatau, peak SW third Kolsay lake, northeastern slope (3200–3450 m)—42° 53' 30" N 78° 19' 42" E. *A. Hilpold et al., s.n.* (BOZ).—**EAST KAZAKHSTAN:** Montes Saur (Tarbagatai)—*N. Gontscharova & A. Borissova 509* (as *C. atrata* L.) (NY).—**KYRGYZSTAN. ISSYK KUL:** Tian Shan, Terskey Alatau, Pereval Zyndan (3000–3200 m)—*N. Tkach 98* (Herb. Tkach).—**MONGOLIA. KHENTII:** Daba-Tui, E slope—*N. & V. Ikonnikov-Galitzky 468* (as *C. atrata* L.) (NY). Montes Kentei (Khentei-Khan), NE slope—*N. & V. Ikonnikov-Galitzky 497* (as *C. atrata* L.) (NY). Montes Kentei (Khentei-Khan), SE declivity—*N. & V. Ikonnikov-Galitzky 920* (as *C. atrata* L.) (NY). Oyuta Mt., E slope—*N. & V. Ikonnikov-Galitzky 2043* (as *C. atrata* L.) (NY). 'Mongolia'—*N. & V. Ikonnikov-Galitzky 3176* (as *C. atrata* L.) (NY).—**RUSSIA. ALTAI KRAI:** Altai Mts., above Tigirek—*V. Titov, s.n.* (NY).—**ALTAI REPUBLIC:** Gorno-Altaysk, Syeminsky pass (1760 m)—*T. S. Elias et al. 4267* (as *C. perfusca* V.I.Krecz.) (NY). Altai Mts., Ajgulakskij plateau, N of Aktasch, near Ozero Uzukjol lake (2000–2150 m)—50° 28' N 87° 37' E. *B. Heuchert B28* (HAL). Ongudaysky distr., Seminskij Pereval (1762 m)—51.042498° N 85.635520° E. *M. H. Hoffmann j183* (Herb. Hoffmann).—**BURYATIA REPUBLIC:** S Lake Baikal, N macroslope of Khamar-Daban, river Neva (503 m)—51.4935° N 105.2238° E. *N. Gamowa BR-0478* (MW, digital image!).—**IRKUTSK:** S Siberia, Lake Baikal region, N slope of Khamar-Daban range, upper reaches of Slyudyanka River valley, 10–14 km SSW of Slyudyanka (900–1850 m)—51° 33'–35' N 103° 36'–38' E. *H. H. Iltis et al. 990, 954a* (as *C. perfusca* V.I.Krecz.) (NY, two sheets).—**KHABAROVSK:** Tuguro-Chumikansky distr., Dzhugdzhur, Perevalny valley (744 m)—55.64248 N 134.42968 E. *S. V. Dudov 78* (MW, digital image!).—**KRASNOYARSK KRAI:** SE Putoranskiy plateau—*V. Kuvaev & A. Laearev 77-1* (MW, digital image!). Evenkia, Baikit distr., lower reaches of river Kochumdek—*S. S. Shcherbina, s.n.* (MW, digital image!). SW Taimyr, W Putoranskiy plateau—69° 18' 52.0" N 90° 09' 22.2" E. *N. I. Pospelov 15-0122* (MW, digital

image!).—**MAGADAN OBLAST:** Tenkinka highway (km 168) from the village Palatka—61° 00' N 149° 40' E. *I. M. Krasnoborov & A. N. Berkutenko 404* (MW, digital image!).—**TUVA REPUBLIC:** Mongun-Taiginsky distr., Pereval Buguzun (2585 m)—50.184895° N 89.411116° E. *M. H. Hoffmann j132* (Herb. Hoffmann).—**SLOWAKIA. PREŠOV:** High Tatras Mts., 1 km W of Vyšné Kôprovské pass—*H. Dörfelt, s.n.* (HAL).—**SWITZERLAND. GRISONS:** Upper Engadine, NE Pontresina, Bernina pass, above Lago Bianco (2261 m)—46.404707° N 10.004041° E. *S. Gebauer 140878* (Herb. Gebauer).—**4b. *Carex aterrima* subsp. *medwedewii* (Leskov) T.V.Egorova:**—**ARMENIA. ARAGAZOTN:** Ashtarak distr., in declivibus austro-orientalis montis Aragac (3100–3400 m)—*V. Vašák, s.n.* (as *C. caucasica*) (B, two sheets). Ashtarak distr., Mt. Aragats—*A. P. Khokhryakov 480* (MW, digital image!).—**ARARAT:** Davagez gorge [Ughtuakunk], SW Adgad spur [Spitaksar], Gegamskiy ridge—*Akhverdov, s.n.* (MOR).—**SHIRAK:** Artik distr., N side of Aragats Mt., valley above Mantash reservoir (2627 m)—40° 32' 30" N 44° 06' 34" E. *M. Oganesyanyan et al. 05-2651* (MSB).—**SYUNIK:** Kapan distr., Kajaran pass, side valley W of pass, c. 3–5 km from top of pass (2700–2890 m)—39° 06' 17" N 46° 07' 23" E. *G. Fayvush et al. 05-1774* (MSB).—**GEORGIA. IMERETI:** Iri distr., Radchinskij khrebet ridge, Tagverulla Mt. (2400 m)—*J. Čuba, s.n.* (M, NY).—**MTSKHETA-MTIANETI:** South Ossetia, Liakvha, Bibil'ti-vtseg pass, Chaparykh side (2380 m)—*E. & N. Bysh, s.n.* (as *C. aequivoca*) (E). SE of Mutso village, SW of Tebulo massif (3000–3200 m)—42° 35' 14.4" N 45° 15' 55.0" E. *H.-J. Züendorf 24130* (Herb. Gebauer, JE). Dzhuta valley, 2.5 km above Juta village (2264 m)—42° 35' 24.7" N 44° 46' 18.2" E. *S. Gebauer 130734* (Herb. Gebauer). Dzhuta valley, SE slopes of Kvibishi massif (2748 m)—42° 36' 51.4" N 44° 46' 39.4" E. *S. Gebauer 130737* (Herb. Gebauer). Dzhuta valley, 1.5 km NE of Juta village (2267 m)—42° 35' 24.9" N 44° 46' 20.5" E. *S. Gebauer 130750* (Herb. Gebauer). Veshattskaro valley, rise to Arkhotistavisghele (2981 m)—42° 35' 40.6" N 44° 50' 22.5" E. *S. Gebauer 130752-1* (Herb. Gebauer). Tsakorostavi, tributary valley, beneath Kalotanisghele (2935 m)—42° 37' 23.0" N 44° 58' 01.0" E. *S. Gebauer 130778* (Herb. Gebauer). Kalotanisghele, below the pass (2935 m)—42° 36' 15.5" N 44° 57' 58.0" E. *S. Gebauer 130783* (Herb. Gebauer). Source area of Tsirtslovnistskali below Bogovachisgele (2890 m)—42° 35' 33.0" N 44° 53' 18.0" E. *J. Hentschel & F. Petzke Hb01293* (Herb. Gebauer, JE). Upper Tsirtslovnistskali Valley, c. 5.6 km S of Akhieli village (2290 m)—42° 36' 28.0" N 44° 54' 35.0" E. *J. Hentschel Hb012945* (Herb. Gebauer, JE).—**SAMTSKHE-JAVAKHETI:** Didi Abuli massif, W of Paravani lake (2300–2500 m)—*H.-J. Züendorf et al. 22170* (Herb. Gebauer, JE).—**RUSSIA.—DAGESTAN REPUBLIC:** Rutulsky distr., wet places—*G. Kulikova, s.n.* (MW, digital image!).—**KABARDINO-BALKAR:** Ad fontes fluminis Baksan, mons Elbrus—*A. L. Ivanov, s.n.* (as *C. oligantha*) (Herb. Gebauer).—**KARACHAY-CHEKES REPUBLIC:** E Teberda Nature Reserve, crest of Malaya Khatipara (2450 m)—*V. Pavlov 315* (MW, digital image!).—**KRASNODAR KRAI:** Sochi distr., S cliff of Mt. Kogot (2360–2380 m)—43.69085° N 40.39381° E. *M. N. Kozhin Kr-1047* (MW, digital image!). Gora Ajgba, S of Krasnaja Poljana (2067 m)—43.641510° N 40.256356° E. *M. H. Hoffmann j205* (Herb. Hoffmann).—**NORTH OSSETIA-ALANIA:** S of Ardon, S slope of Tseyskiy gorge—*N. Shvedchikova, s.n.* (MW, digital image!). Basin of Ardon river, crest of Tsey range—*N. Shvedchikova, s.n.* (as *C. melananthiformis*; mixed with *C. melanantha*) (MW).—**TURKEY. ARTVIN:** Ardanuç: Kordevan Dağı (Yalnizçam Dağları) (2700 m)—*P. H. Davis & I. C. Hedge D30398* (as *C. atrata* subsp. *atrata*) (E). Otingöl (2000 m)—*A. Stainton & D. Henderson 5970* (as *C. atrata* subsp. *atrata*) (E).—**BAYBURT:** Trabzon: Bayburt, of 3 km N of pass top (2400 m)—*A. Stainton & D. Henderson 6175* (as *C. atrata* subsp. *atrata*) (E).—**GİRESUN:** Karagöl Dağ [Karagöl Dağı] (2600 m)—*C. Tobey 1454* (as *C. atrata* L. coll.) (E).—**HAKKÂRI:** Sat Dağı [Buzul Dağı], between Varegöz [Çayır] and Sat

Gölu [İkiyaka] (2600 m)—*P. H. Davis 45667* (as *C. kukkonenii*) (E).—**İĞDIR:** d. Aralık, Büyük Ağrı Dağı [Ararat Mt.] above Serdar Bulak (3000 m)—*P. H. Davis 46983* (as *C. atrata* subsp. *atrata*) (E).—**NIĞDE:** Bulghar Magara—*W. Siehe 294* (as *C. kukkonenii*) (E).—**RIZE:** İkizdere distr., Vercinin Tepe (3100 m)—*P. H. Davis 21147* (as *C. atrata* subsp. *atrata*) (K). İkizdere–İspir W of top of pass (3000 m)—*A. Stainton & D. Henderson 6213* (as *C. atrata* coll.) (E). İkizdere distr., Ovid Dağı pass (2670 m)—40° 37.546' N 40° 46.861' E. *T. Gregor & L. Meierott 7037* (as *C. norvegica*) (M).—**TUNCELI:** Munzur dağ, above Ovacik (2400 m)—*P. H. Davis & I. C. Hedge D31341* (as *C. kukkonenii*) (E).—**VAN:** Satak [Çatak], Kavussahap Dag [Kavuşşahapdağı Tepe] (2740 m)—*P. H. Davis 23068* (as *C. kukkonenii*) (E).

5. *Carex atrata* L.:—AUSTRIA. NOT LOCALIZED: [Styria/Upper Austria] Dachsteingebiet—*C. von Ettingshausen, s.n.* (mixed with *C. parviflora*) (GZU).—**CARINTHIA:** Großglockner Mts., below the Glocknerhouse (c. 2100 m)—*M. H. Hoffmann 42* (HAL).—**LOWER AUSTRIA:** Limestone Alps, Schneeberg Mts., S & SW slope of Waxriegel Mt. (1800–1875 m)—*M. Röser 5125* (Herb. Röser).—**STYRIA:** Seetaler Alpen, Lavant-See (1859 m)—*Anonymous, s.n.* (GZU). Hochschwab, auf dem Schwabenboden (c. 2150 m)—*P. Conrath, s.n.* (mixed with *C. parviflora*) (GZU). Wölzer Tauern, Hochwart bei Oberwölz (2300 m)—*E. Echsler, s.n.* (mixed with *C. parviflora*) (GZU). Hochschwab, Ebenstein (2124 m)—*W. Möschl, s.n.* (mixed with *C. parviflora*) (GZU).—**BULGARIA. SOFIA:** Rila Mts., upper Musala lake, below Musala Mt. (2500 m)—*E. Jäger, s.n.* (HAL).—**CZECHIA. HRADEC KRÁLOVÉ:** Krkonoše Mts.—*Örtel, s.n.* (HAL).—**FINLAND. NOT LOCALIZED** [?LAPLAND]: Lapponia peetsamoensis, Kalastajasaarento, Pummanki, Haminanperä, in prato—*A. Cajander, s.n.* (BR, digital image!).—**FRANCE. OCCITANIA:** Pyrenees, Dept. Haute-Garonne, S of Bagnères-du-Luchon, Hospice de France (1895 m)—42° 42.375' N 00° 38.862' E. *M. H. Hoffmann a117* (Herb. Hoffmann). Pyrenees, Dept. Haute-Pyrénées, S of Bagnères-du-Luchon, Hospice de France, below Col Venasque (1983 m)—42° 42.375' N 00° 38.862' E. *M. H. Hoffmann a128* (Herb. Hoffmann).—**GERMANY. BAVARIA:** Allgäu Alps, Egg-Alp (1360 m)—*A. Buchholz [04/]K29* (M).—**GREECE. CENTRAL GREECE:** Sterea Ellas. Prov. Fokidos. Distr. Doridos. Mt. Vardousia, summit area of Korax (2000–2200 m)—*C. Baden et al., A. Strid 765* (Herb. Strid).—**ICELAND. NORÐURLAND EYSTRÁ:** Laxá River outlet of Mývatn lake—*G. Frahm, s.n.* (B). Mývatn lake, Skútustaðir (c. 280 m)—65° 34' 25" N 17° 02' 00" W. *A. Buhl 27252* (HAL, two sheets).—**NORWAY. TROMS FYLKE:** Lyngen herad, Lyngenfjord, Furufalten, upper course of Lyngselva river—*I. Kause, s.n.* (JE).—**SØR-TRØNDELAG:** Dovrefjell, Knutshø, between Hjerskinn and Kongsvoll/Drivdalen (941 m)—62° 16.878' N 09° 36.204' E. *M. H. Hoffmann a226* (Herb. Hoffmann). Dovrefjell, Knutshø, between Hjerskinn and Kongsvoll/Drivdalen (1056 m)—62° 17.080' N 09° 37.729' E. *M. H. Hoffmann a235b* (Herb. Hoffmann).—**ROMANIA. HUNEDOARA:** Retezat Mts., E of Gura Zlata, between Taul Gemeenele lake and Poarta Bucurei (pass) (1950–2050 m)—*M. Röser 9587* (Herb. Röser).—**MARAMUREŞ:** Rodna Mts., Prislop Pass, path from Prislop Pass to Gărgălaş Pass (1933 m)—47° 34' 24.34" N 24° 47' 43.94" E. *M. H. Hoffmann s88* (somewhat transitional to *C. aterrima* subsp. *aterrima*) (Herb. Hoffmann).—**PRAHOVA:** Bucegi Mts., W of Azuga, summit of Bucşoiu Mt. (2492 m)—*A. Buhl 15373* (HAL).—**SIBIU:** Făgăraş Mts., Transfăgăraş Highway, Lacul Bălea (1982 m)—45° 36' 22.33" N 24° 37' 19.4" E. *M. H. Hoffmann s67* (somewhat transitional to *C. aterrima* subsp. *aterrima*) (Herb. Hoffmann).—**SLOWAKIA. BANSKÁ BYSTRICA:** Lower Tatra Mts., Lajštroch (c. 1600 m)—*J. Friedrich 2745* (HAL).—**ŽILINA:** Lower Tatra Mts., N slope of Chopok Mt.—*A. Buhl 11271* (HAL; seven sheets).—**SPAIN. HUESCA:** Formigal, estación de esquí, subida al Ibón de Anayet (2200 m)—*S.*

Martín-Bravo 565SMB05 (UPOS).—**LLEIDA:** Tredós, entre el Puerto de Colomers y el lago del Port de Colomers (2510 m)—*E. Maguilla 38EMS12* (UPOS). Valle de Arán, Portilla de la Roterá, 2570 m, 42° 36' 25" N 0° 57' 50" E—*M. Luceño 3309ML*.—**SWEDEN. LAPLAND:** Kopparåsen, S of Betuletum station—*H. Meusel, s.n.* (HAL).—**NORRBOTTEN:** Torne Lappmark, Kiruna, surroundings of Tornetrusk lake, Gearevággi (Kärkevaggi) valley (510–830 m)—68° 26' N 18° 19' E to 68° 23' N 18° 21' E. *H. Hertel 33.063* (M).—**SWITZERLAND. GRISONS:** Upper Engadine, NE Pontresina, Piz Languard, below Lej Languard (2550 m)—46° 29' 10.55" N 09° 56' 14.73" E. *S. Gebauer 14087* (Herb. Gebauer, two sheets). Upper Engadine, NE Pontresina, Piz Languard, below Lej Languard (2622 m)—46° 28' 33.85" N 09° 57' 05.41" E. *S. Gebauer 140816* (Herb. Gebauer, two sheets). Upper Engadine, SE Pontresina, Bernina Pass, above Lej Pitschen (2230 m)—46° 25' 11.86" N 10° 00' 10.61" E. *S. Gebauer 140832* (Herb. Gebauer, two sheets). Upper Engadine, SE Pontresina, Bernina Pass, above Lago Bianco, Val da Cambrena (2257 m)—46° 24' 25.62" N 10° 00' 23.30" E. *S. Gebauer 140872* (Herb. Gebauer, two sheets).—**TURKEY. BURSA:** Vilayet Bursa: Uludağ (Bithynian Olympus), between the summits of Kusuklikaya and Uludağ zirve (2200–2400 m)—*A. Strid 14372* (Herb. Strid).

6. *Carex atrofusoides* K. T. Fu:—**CHINA. QINGHAI:** Huangnan Xian, Maixiu Linchang [Maixiu] Baizang Gou—*B.-Z. Guo 26123* (as *C. kansuensis*) (HNWP). Gande (Gadê) Xian, Gande (Gadê) Shan, Shanggongma Xiang, on road from Dari (Darlag) to Gande (Gadê) (4400 m)—33° 55' 46" N 99° 44' 36" E. *T. N. Ho et al. 914* (as *C. atrofusca*) (A). W Anyi Machen Shan, along road S205, c. 6 km NW of Jiaguocun (4692 m)—34° 49' 34.5" N 99° 02' 29.2" E. *S. Gebauer et al., SG-CN-027* (HAL, HNWP, Herb. Gebauer, three sheets). E Anyi Machen Shan, above road S101 between Qingzhen Xian and Golog (4413 m)—34° 14' 02.1" N 100° 13' 56.4" E. *S. Gebauer et al., SG-CN-033* (HAL, HNWP, Herb. Gebauer, three sheets).—**SICHUAN:** Serxu Xian, NW of Shiqu (Serxu), vicinity of Anbala Shan at Ya Kou (Ya Pass) (4560–4875 m)—33° 08' 24" N 97° 29' 53" E. *D. F. Boufford et al. 33538* (A). Batang Xian, road from Litang to Batang, glacial lake on S side of pass at Haizi Shan (4500–4600 m)—30° 18' 13" N 99° 33' 27" E. *D. F. Boufford et al. 36062* (A). Kaka Gou, Shuijing village, Songpan Co. (3930 m)—32° 59' 02.76" N 103° 40' 07.38" E. *T. G. Elumeeva, s.n.* (MW, two sheets). W of Tianhuashi (pass on road X120), between Chuanzhusi and Huanglong, NE of Songpan (4032 m)—32° 44' 32.6" N 103° 43' 58.9" E. *S. Gebauer et al., SG-CN-050* (HAL, KUN, Herb. Gebauer, three sheets). NW of Balang Shan La (pass on road S303), 12 km SE of Rilong (4500 m)—30° 54' 33.4" N 102° 53' 25.5" E. *S. Gebauer et al., SG-CN-062* (HAL, KUN, Herb. Gebauer, three sheets).

7. *Carex bijiangensis* S. Yun Liang & S. R. Zhang:—**BHUTAN. GASA:** Tangey, lower Tsorim Chu (4880 m)—28° 03' N 90° 13' E. *G. & S. Miehe 00-383-08* (as *C. atrata*) (MR).—**THIMPHU:** Lemcheng (4620 m)—27° 57' N 89° 27' E. *G. & S. Miehe 00-226-16* (as *C. atrata*) (MR).—**CHINA. SICHUAN:** Daocheng Xian, road (highway 217) from Litang to Sandui, NNE of Sandui, Haizi Shan (4605 m)—29° 27' 28" N 100° 11' 33" E. *D. E. Boufford et al. 37409* (as *C. kansuensis*) (A).—**XIZANG:** Linzhi Xian, Huijila Shan (4400 m)—*B.-Z. Guo & W.-Y. Wang 21792* (as *C. kansuensis*) (HNWP). Linzhi Xian, Huijila Shan Dong po (4320 m)—*B. Qingzang 751053* (as *C. kansuensis*) (HNWP). Cuona Xian, ?Shankou (4500 m)—*Z.-Y. Wu et al. 75-986* (as *C. kansuensis*) (HNWP). S Tibet, Tibetan Himalaya N of Bhutan, Kuru Chu, Hill SW of Lhozak Valley junction (4440 m)—28° 18' N 90° 51' E. *B. Dickoré 9852* (as *C. duthiei*) (MSB). SE Tibet, from Longzi Co. to Zha-ri village, Longzi Co. (4606 m)—28° 40.8754' N E 93° 02.1130' E. *M. Deng DM05232*,

DM05234 (MOR, two sheets).—**YUNNAN**: Lotueshan, mountains of Labako (Lijiang Co.)—*J. F. Rock 9557* (as *C. atrata* var. *pullata*) (E, two sheets). Chao-ü Shan, Mekong–Jangtse divide (3960 m)—27° 09' N 99° 35' E. *G. Forrest 25708* (as *C. giraudiasii*) (E).—**INDIA. SIKKIM**: N Sikkim, SE side of Lasha Chhu, below Sebu La (4560 m)—27° 56' 13" N 88° 38' 30" E. *D. G. Long & H. J. Noltie 374* (as *C. atrata* var. *atrata*) (E).—**NEPAL. JANAKPUR**: Nagaon to Choralba, Dolakha distr. (4300 m)—*K. R. Rajbhandari & B. Roy 1887* (NY).

8. *Carex buxbaumii* Wahlenb.—**ESTONIA. LÄÄNE**: Haapsalu, Nuemöisa—*H. Aasamaa, s.n.* (JE, two sheets).—**FINLAND. KAINUU**: Sotkamo, marshy edges of SE shore of Lauttalampi pond, Korholanmäki village—*K. Alho & U. Laine, s.n.* (JE).—**LAPLAND**: Kittilä, Kiistala, Kuortisoja, SW of Rajalompolo (260 m)—*A. Kurtto & S. Vuokko 1837* (HAL).—**FRANCE. GRAND EST**: Prairies tourbeuses entre l'Ill et le Rhin, près de Benfeld—*N. Nicklès, s.n.* (HAL).—**GERMANY. BRANDENBURG**: [probably in today's Poland!] Karauschen b. Bademeusel, b. Forst—*Groß, s.n.* (GLM, digital image!).—**MECKLENBURG-WESTERN POMERANIA**: Torgelow, Ferdinandshof—*J. Bisse, s.n.* (JE, two sheets). Ferdinandshof—*K. Helmecke, s.n.* (HAL).—**THURINGIA**: Erfurt, Alperstedter Ried—*S. Rauschert, s.n.* (HAL). Sömmerda, Alperstedter Ried—*K. Schubert, s.n.* (JE). Alperstedt, Alperstedter Ried (c. 155 m)—*A. Buhl 27162* (HAL, two sheets).—**JAPAN. HOKKAIDO**: Nambuto, Nemuro—*S. Akiyama 119* (NY). Iburi Province, Benten, Tomakomai-shi—*M. Furuse 6009* (as *C. tarumensis*) (NY).—**HONSHU**: Nagano Pref., Minamisaku-gun, Nobeyama, near Sangan-chaya—*T. Ikeda, s.n.* (TUS).—**KAZAKHSTAN. KYZYLORDA**: Middle part of Karsakpayskiy rayon, E slopes of Ulutau—*N. Schipczinsky 449* (NY).—**LATVIA. LIEPĀJA**: 2 km N of Liepāja, E shore of the lake Tosmares—*N. Shvedchikova, s.n.* (MW, digital image!).—**MADONA**: Krustkalny Reserve, Pen. of the lake (Svetes) Dreyman—*N. Shvedchikova, s.n.* (MW, digital image!).—**POLAND. LUBUSZ VOIVODESHIP**: Waldmoor zwischen Forst und Pforthen [Brody]—*Groß, s.n.* (GLM, digital image!).—**RUSSIA. ALTAI KRAI**: Altai Reserve, S part of Teletskoye, left bank of river Kygy near the mouth—*N. Shvedchikova, s.n.* (MW, two sheets, digital image!).—**BASHKORTOSTAN REPUBLIC**: Salavatskiy distr., surroundings of Arkaulovo, valley of river Yuryuzan—*N. Shvedchikova, s.n.* (MW, two sheets, digital image!).—**IRKUTSK**: Balagansky distr., Bashiewsky—*N. I. Maltsev, s.n.* (LE, NY).—**KARELIA REPUBLIC**: Loukhsky distr., E coast of lake Vorobyov—*A. B. Shipunov, s.n.* (MW, digital image!). Loukhsky distr.—*A. B. Shipunov, s.n.* (MW, digital image!).—**MURMANSK OBLAST**: 20–25 km to the S of Khibiny—*V. Novikov & K. Kiseleva, s.n.* (as *C. adelostoma*) (MW, digital image!).—**TATARSTAN REPUBLIC**: Busk distr., 4 km SE of Bolozhinov, near Angelovka—*A. Zelenchuk, s.n.* (MW, digital image!). Sokalsky distr., 2 km SE of Khlevchans Volitsky Reserve—*A. Zelenchuk, s.n.* (MW, digital image!).—**TOMSK OBLAST**: W Siberia, S Vasyugane—*Efimova & Dombrovskaya, s.n.* (MW, digital image!).—**ZABAYKALSKY KRAI**: Barguzinsky distr., Kuchegyr—*V. Siplivsky, s.n.* (MW, digital image!).—**SWEDEN. UPPSALA LÄN**: Uppland—*H. Jungetadt, s.n.* (JE). Sikhjälma Hamn (8 m)—*M. H. Hoffmann a197* (Herb. Hoffmann).—**UNITED KINGDOM. SCOTLAND**: Highland distr., East Inverness & Nairn, Loch na Ba Ruaidhe, near Drumnadrochit (237 m)—*McHaffie et al. 31, 33, 34* (E, three sheets, digital images!).

9. *Carex caucasica* Steven—**ARMENIA. GEGHARKUNIK**: NE shore of Sevan lake, first gorge Tak-Agach—*O. Polyanskaya, s.n.* (NY).—**AZERBAIJAN. QUBA-XAÇMAZ**: In pratis montanis, q. n. 'Gilskie polia' Kub u Bakin (2438 m)—*V. I. Kreczetovicz, s.n.* (MW, two sheets, digital images!).—**YUXARI**

QARABAĞ: Transcaucasia, Nagorno-Karabakh, Lysogorsk—*I. Shukin & N. Shukina, s.n.* (MW, digital image!). Regio autonoma Karabagh [Nagorno-Karabakh]—*V. A. & I. P. Petrov, s.n.* (MW, two sheets, digital images!).—**CHINA. XINJIANG:** Zhaosu Xian north (1950 m)—*D. Xinjiang 956* (as *C. kansuensis*) (HNWP).—**GEORGIA. MTSKHETA-MTIANETI:** Above confluence of rivers Dzhuta and Kura, below Juta village (2091 m)—42° 34' 27.8" N 44° 44' 13.1" E. *S. Gebauer 130720, 130727* (Herb. Gebauer). Dzhuta valley, 0.8 km NE Juta village (2206 m)—42° 35' 11.0" N 44° 45' 16.4" E. *S. Gebauer 130748* (Herb. Gebauer).—**SHIDA KARTLI:** South Ossetia, Ermany, right side of middle Ermany canyon (2600 m)—*V. Ya. Darbin, s.n.* (NY). South Ossetia, Erman, right bank of river Ermani-Don (2000 m)—*E. Gogina, s.n.* (MW, digital image!). South Ossetia, Erman, right bank of river Ermani-Don (2000 m)—*V. Surova, s.n.* (MW, digital image!).—**IRAN. MAZANDERAN:** On service road bypassing main tunnel on Karaj-Chalus hwy.—*N. Jardine 899B* (E).—**TEHRAN:** 4 km Shemshak to Dizin, Tal-Tange (2700 m)—*M. Amini Rad & Eskandari* (H, HAL, IRAN).—**KAZAKHSTAN. ALMATY:** Tian Shan, Trans-Ili Alatau, left Talgar valley, next to camping area (2250 m)—43° 07' 13" N 77° 09' 08" E. *A. Hilpold & P. Schönswetter, s.n.* (as *C. popovii*) (BOZ).—**KYRGYZSTAN. ISSYK KUL:** Tian Shan, Terskey-Alatau range, basin of Chon-Kysyl-Su river (2600 m)—*Zhiryakov, s.n.* (as *C. popovii*) (MW).—**RUSSIA. CHELYABINSK OBLAST:** S Urals, Katav-Ivanovskiy rayon, Lesoseka, Mt. Iremel (810 m)—*V. Kuvaev et al. 174* (MW, digital image!).—**DAGESTAN:** About 25 km N of Botlikh (1800–2000 m)—*A. K. Skvortsov, s.n.* (NY).—**KABARDINO-BALKAR:** Sukan river source, Sukan-bashi-thifi (2400 m)—*E. & N. Bysh, s.n.* (NY). Tyrnyaus distr., Donguz-orunkel lake W of Cheget Mt. (2400–2600 m)—*V. Vašák, s.n.* (NY). Baksanskiy Rayon, Adyl-su (2700 m)—*Y. L. Meinitskiy et al. 8* (LE).—**KARACHAY-CHEKKESS REPUBLIC:** Stavropol territory, Karachay-Cherkess autonomous area, reg. Teberdinsky ascent to Chuchhor—*Anonymous, s.n.* (MW, digital image!). Stavropol territory, Teberdinsky Reserve, Alibek, slopes of Semen-bashi (2300 m)—*V. G. Onipchenko, s.n.* (MW, digital image!).—**KRASNODAR KRAI:** Abago (1800 m)—*P. Smirnov, s.n.* (MW, digital image!). Sochi distr., W slope of Mt. Aishkh (2110 m)—43.65828° N 40.43994° E. *M. N. Kozhin et al. Kr-1050* (MW, digital image!). Gora Ajgba, S of Krasnaja Poljana (2076 m)—43.238050° N 40.238050° E. *M. H. Hoffmann j207* (Herb. Hoffmann).—**NORTH OSSETIA-ALANIA:** In Birkenwäldern an den Quellen des Ardon bei dem Passe Mamisson in Imeretien im kaukasischen Gouvernement Kutais (c. 2700 m)—*B. Markovicz, s.n.* (E, digital image!; LE). Ossetia, in silvis betulinis in regione subalpino—*B. Markovicz, s.n.* (P, two sheets, digital images!).—**SVERDLOVSK OBLAST:** S Urals, Karpinsky rayon (540 m)—*V. Kuvaev 349-6* (MW, digital image!).—**TURKEY. BAYBURT:** Soğanlı Geçidi (c. 1750 m)—*E. Pasche H+P 77/11A* (E, digital image!).

10. *Carex duthiei* C.B. Clarke:—10a. *Carex duthiei* subsp. *duthiei*:—BHUTAN. BUMTHANG: Dzoling to Ra La [Ura La] (3658 m)—*B. J. Gould 575* (K).—**GASA:** Limithang, above Bekei (4630 m)—28° 04' N 89° 35' E. *G. & S. Miehe 00-265-22* (MR). Rodophu (4280 m)—28° 02' N 89° 47' E. *G. & S. Miehe 00-296-05* (MR).—**CHINA. SICHUAN:** NW Sichuan, Upper Yalong basin, Chola Shan, Dege–Garze, Manigango (4100–4250 m)—31° 52' N 99° 07' E. *G. Miehe et al. 94-401-07* (MR).—**XIZANG:** S Tibet, Natula [Nathu La] (4359 m)—*N. L. Bor & Kirat Ram 20662* (K). SE Tibet, Gyala Peri N, ridge W of Gyala Peri-N Glacier (above High Camp 15) (4650 m)—29° 54' N 94° 52' E. *B. Dickoré 11393* (as *C. gracilentia*) (MSB). SE Tibet, Kawang Karpo, E slope (4250 m)—28° 31' N 98° 43' E. *G. Miehe et al. 04-134-05* (MR). Shannan, Cuona Xian, MamaGou Yakou (4509 m)—27° 55' 36.8" N 91° 52' 42.6" E. *J. Luo & S.-L. Wang LiuJQ11XZ032* (HNWP). Jilong Xian, Rucheng Lamamiao Shan (3700 m)—*s. coll. 317* (as *C. atrata* subsp.

pullata; one sheet mixed with *C. psychrophila* (HNWP, two sheets). Jilong Xian, Tuo dang bei to Xia pu heng (3500 m)—*s. coll.* 557 (HNWP). Milin Xian, Xialong Gou (4500–4800 m)—*s. coll.* 4022 (HNWP). SE Tibet, Gyala Peri W, Pass Nyingchi–Dongjuk (4500 m)—29° 35' N 94° 38' E. *G. Miehe & U. Wündisch 94-182-40* (MR). SE Tibet, Gyala Peri N, ridge W of Gyala Peri-N Glacier (above High Camp 15) (4650 m)—29° 54' N 94° 52' E. *B. Dickoré 11393* (as *C. gracilentia*) (MSB). SE Tibet, Kawang Karpo, E slope (4250 m)—28° 31' N 98° 43' E. *G. Miehe et al. 04-134-05* (MR).—**YUNNAN**: Yangtse watershed, Likiang [Lijiang] distr., E slopes of Likiang Snow Range [Xueshan]—*J. F. Rock 5245* (as *C. atrata* subsp. *pullata* var. *subgracilentia*) (E). Zhongdian, N of Napa Hai, N of Zhongdian (3910 m)—27° 55' N 99° 34' E. *B. Aldén et al. 1406* (E). Zhongdian, Geza, Summit pass of Little Snow Mountain (3830 m)—28° 19' 24" N 99° 45' 80" E. *Alpine Garden Society Expedition to China (1994) ACE 523* (E). Deqen, Beima Shan (4322 m)—28° 22' N 99° 02' E. *Alpine Garden Society Expedition to China (1994) ACE 742* (as '*C. duthiei* var. [= *C. atrata* subsp. *pullata* var. *subgracilentia*']') (E, K). Zhongdian, Deqen, Beima Shan (4675 m)—28° 32' 16" N 99° 00' 80" E. *Alpine Garden Society Expedition to China (1994) ACE 1291* (somewhat transitional to *C. duthiei* subsp. *longistolonifera*) (E). Nujiang Lisu Aut. Pref., Gongshan Co., W side of ridge near Dong Shao Fang on track from Qi Qi to Dulongjiang (3700 m)—27° 41' 30" N 98° 27' 25" E. *Gaoligong Shan Expedition (1996) GSE 7772* (as *C. obliquitruncata*) (E).—**INDIA. HIMACHAL PRADESH**: Kukti pass, Chamba (4267 m)—*W. Koelz 8617* (as *C. nigerrima*) (NY).—**JAMMU & KASHMIR**: Khilanmarg, above Gulmarg—*R. R. Stewart 8595* (as *C. atrata*) (NY). Khilanmarg, above Gulmarg—*R. R. Stewart 8595a* (as *C. nigerrima*) (K).—**SIKKIM**: Hab. Sikkim, ?Timgu (3353–5182 m)—*J. D. Hooker, s.n.* (K). Dzongri (c. 4000 m)—*B. N. Starling et al. (AGSES) 291* (K). N Sikkim, North distr., S of Thanggu (3760 m)—27° 52' 28" N 88° 32' 31" E. *D. G. Long & H. J. Noltie 275* (E). N Sikkim, North distr., SE side of Lasha Chhu, below Sebu La (4560 m)—27° 56' 13" N 88° 38' 30" E. *D. G. Long & H. J. Noltie 375* (as *C. atrata* var. *glacialis*) (E). N Sikkim, North distr., Lakes on SE side of Sebu La (5040 m)—27° 55' N 88° 39' E. *D. G. Long & H. J. Noltie 410* (as *C. aff. duthiei*) (E). N Sikkim, West distr., Jamlinghang, Chhurong Chhu valley below Dzongri (3700 m)—27° 28' 20" N 88° 09' 14" E. *D. G. Long et al. 188* (E).—**NEPAL. BAGMATI**: Chhulema, Dolakha distr. (3800 m)—*K. R. Rajbhandari & B. Roy 1659* (NY). Rasuwa distr., Jaisuli Kund (4250 m)—Paldol Base Camp (4300 m)—28° 13' N 85° 12' E. *F. Miyamoto et al. 40066* (as *C. infuscata*) (E). Sindhupalchok distr., Bhairab Kund area (4160 m)—27° 59' 07" N 85° 52' 47" E. *M. F. Watson et al. 146* (as *C. cf. obliquitruncata*) (E).—**GANDAKI**: Shiar Khola (4114 m)—*P. C. Gardner 1325* (NY). Rambrong, Lamjung Himal. (3505 m)—*J. D. A. Stainton et al. 6001* (NY). Rambrong, Lamjung Himal. (4267 m)—*J. D. A. Stainton et al. 6162* (NY). Thinigaon, N of Tukucha (4267 m)—*J. D. A. Stainton et al. 8044* (NY). Manang distr., N slope Lamjung Mt. (?Namun Bhanjyan) (3700–4000 m)—*M. A. Farille 81-535* (as *C. cf. obliquitruncata*) (E).—**JANAKPUR**: Chobuk, Dolakha distr. (4450 m)—*K. R. Rajbhandari & B. Roy 1956* (NY).—**KARNALI**: Maharigaon, 5 mi NE (4267 m)—*O. Polunin et al. 273* (NY). Bhurchula Lekh, near Jumla (3810 m)—*O. Polunin et al. 4675* (NY).—**KOSHI**: Arun Vy., Barun Khola, N of Num (3810 m)—*J. D. A. Stainton 552* (NY). Milke Danda (3962 m)—*L. W. Beer 10165* (NY). Thudam (3400 m)—*H. Kanai et al. 720760* (NY). Sankhuwasabha distr., Shipton La, S slope of highest pass (4020 m)—27° 40' N 87° 13' E. *D. G. Long et al. 335* (E).—**MECHI**: Kangrang La (3657 m)—27° 25' N 88° 03' E. *L. H. J. Williams 719* (NY). Jaljale Pokhari (4000 m)—27° 28' N 87° 27' E. *J. F. Dobremez 1657* (as *C. atrata*) (NY). Environs of Kambachen (4060 m)—27° 44' N 87° 59' E. *S. Crawford et al. 494* (K). Between Sinion La and Mirgin La (4470 m)—27° 33' N 87° 57' E. *S. Crawford et al. 716* (as *C. cf. pseudobicolor*) (E, K).—**PAKISTAN.**

KHYBER PAKHTUNKHWA: Sindh Valley, Kashmir (3658–3962 m)—*C. J. Ward 17825* (as *C. nigerrima*) (K). Swat, to Bichigrane lake (3050–3350 m)—*R. R. Stewart & A. Rahman 24968* (as *C. nigerrima*) (K).—**10b. *Carex duthiei* subsp. *longistolonifera* (Kük.) S. Gebauer & Jim. Mejías:—CHINA. GANSU:** Gannan Zhou, Zhuoni Xian, Guanggai Shan (3467 m)—34° 20.770' N 102° 57.095' E. *X. Yin et al. LiuJQ-CN-2011-145* (as *C. kansuensis*) (HNWP, two sheets).—**QINGHAI:** Qilian Shan, Datong Xian, Baoku (3780 m)—*Z.-M. Zhang 4615* (as *C. kansuensis*) (HNWP). Makehe Linchang Shaochai Gou (3300 m)—*W.-Y. Wang 27517, 27530, 27568* (as *C. atrata* subsp. *pullata*) (HNWP, six sheets). Huz[h]u Xian, Beishan Linchang Zhalong Gou (2600 m)—*W.-Y. Wang 2821* (as *C. kansuensis*; mixed with *C. hancockiana*) (HNWP).—**SICHUAN:** Mt. Mitzunga, W of Muli Gomba (3050–4875 m)—*J. F. Rock 16562* (as *C. atrata* var. *pullata*) (E). Hongyuan Xian, Shuajingshi to Kangle Xiang (3400 m)—*s. coll. 9134* (HNWP). Tien-chuan-hsien (3500 m)—*K. L. Chu 2786* (as *C. atrata*) (E). NW Sichuan, Upper Yalong basin, Chola Shan, Dege–Garze, Manigango (4480 m)—31° 52' N 99° 07' E. *G. Miehe et al. 94-433-17* (as *C. schneideri*) (MR). Ganzi (Garze) Xian, S of Ganzi on road (Gan-Bai Lu) to Baiyu, near first pass after Ganzi (4200 m)—31° 27' 30" N 99° 58' 40" E. *D. E. Boufford et al. 34025* (as *C. schneideri*) (A). N Sichuan, N of Amuxiang (c. 3490 m)—32° 58.465' N 102° 37.683' E. *K.-S. Chung & R. Li 24-1* (as *C. schneideri*) (MOR). Mounixiang, Songpan Xian, W of Songpan (3450 m)—32° 39' 47.2" N 103° 30' 43.1" E. *S. Gebauer et al., SG-CN-053* (as *C. schneideri*) (HAL, KUN, Herb. Gebauer, three sheets). Ma'erkang [Barkam], Aba Xian, Mengbi Shan, SW of pass (4212 m)—31° 41' 57.0" N 102° 17' 59.5" E. *S. Gebauer et al., SG-CN-056* (as *C. schneideri*) (HAL, KUN, Herb. Gebauer, three sheets). NW of Balang Shan La (pass on road S303), 12 km SE of Rilong (4506 m)—30° 54' 35.4" N 102° 53' 21.6" E. *S. Gebauer et al., SG-CN-063* (as *C. schneideri*) (dwarfed form, identical with *C. atrata* subsp. *pullata* var. *subgracilentia*; somewhat transitional to *C. duthiei* subsp. *duthiei*) (HAL, KUN, Herb. Gebauer, three sheets). NW of Balang Shan La (pass on road S303), 12 km SE of Rilong (4467 m)—30° 54' 44.3" N 102° 53' 17.4" E. *S. Gebauer et al., SG-CN-066* (as *C. schneideri*) (HAL, KUN, Herb. Gebauer, three sheets). NW of Balang Shan La (below pass on road S303), 12 km SE of Rilong (4290 m)—30° 55' 03.7" N 102° 53' 28.7" E. *S. Gebauer et al., SG-CN-067* (as *C. schneideri*) (HAL, KUN, Herb. Gebauer, three sheets). Daxue Shan, Garzê Xian, Tagong, NE of Mt. Yala [Zhara Lhatse], Yarıcuò Lake (4173 m)—30° 25' 01.7" N 101° 43' 02.3" E. *S. Gebauer et al., SG-CN-080* (as *C. schneideri*) (HAL, KUN, Herb. Gebauer, three sheets). Daxue Shan, Garzê Xian, Garzê [Kangding], pass between Laoyulin and Xiaoyingpan, SW of Tian-hai-zi-shan (4050 m)—29° 54' 28.2" N 102° 00' 20.6" E. *S. Gebauer et al., SG-CN-085* (as *C. schneideri*) (HAL, KUN, Herb. Gebauer, three sheets).—**YUNNAN:** Lichiang [Lijiang] range (3960 m)—*G. Forrest 6027* (as *C. atrata* subsp. *pullata*) (E). Yangbi Xian, W side of Diancang Shan Mt. range, vicinity of Shimenguang (3300–3600 m)—25° 46' N 100° 01' E. *B. Bartholomew et al. 430* (as *C. schneideri*) (E). Zhongdian, valley north of Napa Hai (3370 m)—27° 54' 14" N 99° 38' 15" E. *Alpine Garden Society Expedition to China (1994) ACE 462* (as *C. schneideri*) (K). Zhongdian, Geza to Wengsui (3561 m)—28° 21' 03" N 99° 46' 62" E. *Alpine Garden Society Expedition to China (1994) ACE 537* (as *C. schneideri*) (E). Dali, Cangshan Mt. (3521 m)—25° 40' N 100° 45' E. *Alpine Garden Society Expedition to China (1994) ACE 931* (as *C. duthiei*) (E, K).

11. *Carex gmelinii* Hook. & Arn.:—JAPAN. NOT LOCALIZED: Japan [in Japanese handwriting]—*J. Ohwi, s.n.* (NY).—**HOKKAIDO:** Akkeshi distr., Akkeshi coast—*U. J. Faurie 5000* (K, digital image!). Kushiro plain—*U. J. Faurie 10816* (K, digital image!). Tomakomai—*S. Akiyama, s.n.* (NY). Kitami, between

Sarukotsu and Hamasarufutsu (sea level)—*T. Koyama 11074* (NY, two sheets). Nemuro, 700 m W of Tomoshiri—*T. Koyama 11095* (NY).—**RUSSIA. KHABAROVSK:** Gichiga, Okhotsk Sea—*N. G. Buxton, s.n.* (as *C. buxbaumii*) (NY). Nikolaevsky distr., Amur river—*V. Czekanj, s.n.* (A, JE, LE, NY).—**KAMCHATKA KRAI:** Kamchatka Pen., Petropavlovsk—1853–1856. *C. Wright, s.n.* (NY). Kamchatka Pen., S region, Petropavlovsk—*E. Hultén 189* (NY). Kamchatka Pen., Choetor (Hutor)—*W. Eyerdam, s.n.* (NY). Kamchatka region, Olyourtorskiy distr., island Vyerchotourov—*S. Kharkevich & T. Buch, s.n.* (NY). Kamchatka region, Olyourtorskiy distr., vicinity of village Tilichyki, sandy sea-shore of Korf Bay—*S. Kharkevich & T. Buch, s.n.* (NY, two sheets). Kuril Archipelago, Kharimkotan, Severgina Bay (c. 3 m)—49° 09' 49" N 154° 28' 27" E. *S. Gage SG2026* (NY). Kuril Archipelago, Chirinkotan, NE corner of island, small inlet just E of Cape Ptichy—48° 59' 24" N 153° 28' 08" E. *S. Gage SG2169* (NY). Kuril Archipelago, Raikoke—48° 17' 52" N 153° 15' 38" E. *B. Semsrott BS0321* (NY). Kuril Archipelago, Ushishir, Yankicha Island, inland environs of Kraternaya Bay (1 m)—47° 30' 29" N 152° 49' 02" E. *S. Gage SG1373* (NY). Kuril Archipelago, Iturup—45° 19' 53" N 147° 59' 41" E. *S. Gage SG4047* (as *C. atrata* var. *japonalpina*) (NY). Kuril Archipelago, Ushishir Group, Yankicha Island, inland environs of Kraternaya Bay—47° 30' 33" N 152° 49' 05" E. *S. Gage SG4052* (NY). Kuril Archipelago, Paramushir, NE corner of island, environs of unnamed lake fed by Savushkina river, near Putyatino (15–30 m)—50° 44' 19" N 156° 08' 59" E. *S. Gage SG4141* (NY). Kuril Archipelago, alaid, inland from Alaidskaya Bay—*B. Semsrott BS1341* (NY). Kuril Archipelago, Makanrushi Island, inland from Zakat Bay (30 m)—49° 44' 16" N 154° 24' 52" E. *S. Gage SG4608* (NY).—**SAKHALIN:** Kuril Archipelago, Sakhalin region, Urup, inland coastal margin of Otktyti Bay (150–200 m)—45° 51' 32" N 149° 47' 03" E. *S. Gage SG1125* (NY). Sakhalin region, N end of Simushir Island, S end of Broutona Bay (56 m)—47° 06.692' N 152° 13.432' E. *S. Gage SG6213* (NY). Sakhalin, Taliki river—54° 16.483' N 142° 49.111' E. *K. Stiles 2001-263* (NY). Sakhalin, along W coast, c. 8 km N of Krasnogorsk, W side of lake Baklan'ye (5 m)—48° 28' 12" N 142° 04' 36" E. *B. Legler 809* (NY). Sakhalin, W side of island along Hwy 495, 4 km SSW of Lesogorsk and just N of Tel'novskiy (3 m)—*B. Legler 844* (NY). Severo-Kuril'skiy urban distr., Kuril Islands, Paramushir Isl.—50° 34' 57.5" N 156° 09' 14.5" E. *P. Volkova et al., s.n.* (HAL, MW, UPOS, three sheets).

12. *Carex gracilenta* Boott ex Boeckeler:—BHUTAN. GASA: Rodophu (4330 m)—28° 02' N 89° 47' E. *G. & S. Miehe 00-290-08* (MR).—**CHINA. SICHUAN:** Ya'an—Hanyuan (Fulin), SW of Chengdu, Yingjin–Hanyuan pass, top (2360 m)—29° 40' N 102° 37' E. *B. Dickoré 8060* (MSB). Ma'erkang [Barkam], Aba Xian, Mengbi Shan, SW of pass (4211 m)—31° 41' 51.6" N 102° 17' 48.6" E. *S. Gebauer et al., SG-CN-057* (HAL, KUN, Herb. Gebauer, three sheets). Ma'erkang [Barkam], Aba Xian, Mengbi Shan, NE below pass (3991 m)—31° 42' 36.0" N 102° 18' 43.9" E. *S. Gebauer et al., SG-CN-058* (HAL, KUN, Herb. Gebauer, three sheets).—**XIZANG:** E Tibet, Mekong–Salween divide, Salween tributary, Bamda–Nujiang, NE of pass (Camp 3) (4480 m)—30° 10' N 97° 17' E. *B. Dickoré 8916* (MSB). S Tibet, Tibetan Himalaya N of Bhutan, Kuru Chu, Hill SW of Lhozak valley junction (4330 m)—28° 18' N 90° 51' E. *B. Dickoré 9784* (MSB).—**YUNNAN:** Diqing Pref., Zhongdian Co., Sitone tributary valley NE of Xiaozhongdian (3320 m)—27° 36' N 99° 48' E. *B. Aldén et al. 222* (E). Zhongdian, Little Zhongdian to Tianchi lake (3549 m)—27° 37' 38" N 99° 39' 95" E. *Alpine Garden Society Expedition to China (1994) ACE 111* (E, K). Zhongdian, Beta Hai–Haba Shan junction (3476 m)—27° 48' 19" N 99° 54' 31" E. *Alpine Garden Society Expedition to China (1994) ACE 405* (E). Zhongdian, valley north of Napa Hai (3370 m)—27° 54' 14" N 99° 38' 15" E. *Alpine Garden*

Society Expedition to China (1994) ACE 443 (E). Zhongdian, Geza to Wengsui (3561 m)—28° 21' 03" N 99° 46' 62" E. *Alpine Garden Society Expedition to China (1994) ACE 538* (K).—**INDIA. SIKKIM:** Sikkim, East distr., Tsomgo Chho (3720 m)—27° 22' 14" N 88° 45' 52" E. *D. G. Long & H. J. Noltie 55* (E). Sikkim, West distr., Bikbari, Choktsering Chhu valley (3950 m)—27° 30' 53" N 88° 08' 28" E. *D. G. Long et al. (ESIK) 274* (as *C. pseudobicolor*) (E). N Sikkim, North distr., S of Thanggu (3760 m)—27° 52' 28" N 88° 32' 31" E. *D. G. Long & H. J. Noltie 279* (E).—**NEPAL. GANDAKI:** Gorkha distr., Lho to Sama Gaon (3480 m)—28° 34' 25" N 84° 40' 03" E. *H. Ikeda et al. 20814073b* (*C. infusata* × *C. gracilentia?*) (E).—**MECHI:** Shiar Khola, Ganesh Himal. (3960 m)—*P. C. Gardner 1305* (as *C. obscura* var. *brachycarpa*) (NY). Kambachen (4100 m)—27° 44' N 87° 59' E. *S. Crawford et al. 605* (E, K).—**SETI:** Bajhang distr., around Dhahidunga Kharka (3281 m)—29° 36' 08" N 80° 59' 58" E. *H. Ikeda et al. 20911125* (*C. infusata* × *C. gracilentia?*) (E).

13. *Carex hancockiana* Maxim.:—CHINA. HEBEI: Berg Siao Wu Tai shan [Mt. Siao-Wutai-shan], Aufstieg v. Kloster [ascent from monastery] Tieh lin sze (c. 1097–1524 m)—*O. von Moellendorf 89* (K, digital image!). Prov. Chili, Hsiao-wu-tai-shan, Yang-kia-p'ing, in prato subalpino (1900 m)—*H. Smith 545* (UPS, digital image!). Xiaowutai Shan (1900 m)—*s. coll. 5027* (HNWP). Meixian, Xiaowutai Shan Xitai (1425 m)—*s. coll. 431* (HNWP). Laiyuan Xian, Dianzi Liang—*s. coll. 2330* (HNWP). Laiyuan Xian, Dianzi Liang (1740 m)—*s. coll. 2455* (HNWP). Wutaishan Zhangliang Gou (1570 m)—*s. coll. 1970* (HNWP). Hopei, near eastern tombs—*K. M. Liou 392* (NY). Huairou Xian, Labagoumen Xiang Maoer Shan Lujia Gou (950 m)—*s. coll. 414* (HNWP).—**JILIN:** Chang Bai Shan Nature Protection Reserve, along road to Mt. top (1450 m)—*W. Herrmann, s.n.* (M).—**NINGXIA:** Jingyuan Xian, Jingheyuan Gongshe, Longtan Dadui (1850–2000 m)—*D. Qing 76-0369* (HNWP).—**QINGHAI:** Datong Xian, Baoku Gongshe Linchang—*B.-W. Li 72-159* (HNWP). Menyuan Xian, DatongHe—*G.-Q. Luo 1329* (HNWP). Huzu Xian, Beishan Linchang (2400 m)—*T.-N. He 1753* (HNWP). Huz[h]u Xian, Beishan Linchang Zhalong Gou (2600 m)—*W.-Y. Wang 2821* (as *C. kansuensis*; mixed with *C. duthiei* subsp. *longistolonifera*) (HNWP). Huzhu Xian, Beishan Datong He (2400 m)—*R.-F. Huang 2088* (HNWP). Huzhu Tu Aut. Co., Zhalonggou village, Zhalonggou valley (2340 m)—36° 51' 18" N 102° 34' 03" E. *D. G. Long et al. 1163* (as *C. montis-wutaii*) (E). Haidong, Huzhu, Zhalonggou valley, above Gake (2430 m)—36° 51' 08.5" N 102° 33' 45.3" E. *S. Gebauer et al., SG-CN-041* (HAL, HNWP, Herb. Gebauer, three sheets). Datong Xian, Baoku (2700 m)—*Z.-H. Zhang 4603* (HNWP). Xunhua Xian, Muchangdi (2500 m)—*H.-Z. Zhang 233* (HNWP).—**SHANXI:** Prov. Shansi, Chieh-hsiu [Jiexiu] distr., Mien-shan-yeh [Mianshan], in silva subalpina (2200 m)—*H. Smith 5924* (UPS, digital image!). Taihuai Xiang, Nanshan Shi—*s. coll. 1510* (HNWP). Guan di Shan Batong Gou (1800 m)—*S.-Y. Liu 21474* (HNWP). Ningwu Dingjiawan Gou—*s. coll. 15099* (HNWP). Fenxiujian Shan Dayan Gou—*s. coll. 5165* (HNWP, two sheets). Hongtong Xian, Qilishan Gu Zhangbo Gou—*s. coll. 568* (HNWP). Lvliang Xina, Shi kou tou Dong'er Shan—*s. coll. 360* (HNWP). Yomgji Xian, Taiyukou Shujiaopantou (1470 m)—*T.-J. Liu 101* (HNWP).—**SICHUAN:** Laohegou Nature Reserve, Pingwu Co., in valley by hillside under forest (1920–1923 m)—*S. R. Zhang et al. 2032* (as *C. psychrophila*) (PE, digital image!).—**KOREA, N. NORTH HAMGYONG:** Cham-gion, flum. Tumin-gan—*V. Komarov 278* (NY; P, digital image!).—**MONGOLIA. DORNOD:** East aimak, N macroslope of Mt. Chandagat-uul (1100–1200 m)—46° 40' N 119° 15' E. *R. V. Kamelin et al. 1177* (MW, two sheets, digital images!).—**ULAANBAATAR:** Bogd-uul, Zajsan valley—*W. Hilbig 13/86* (HAL).—**RUSSIA. ALTAI REPUBLIC:** Altai Reserve, S part of lake Teletskoye, bank of river

Kygy—*N. Shvedchikova, s.n.* (MW, digital image!). Altai Mts., c. 10 km E of Chemal (462 m)—51° 22' 31.1" N 86° 05' 31.5" E. *M. H. Hoffmann M02/218* (Herb. Hoffmann).—**BURYATIA REPUBLIC:** N macroslope of Khamar-Daban, lower reaches of river Peremnoy (503 m)—51.4935° N 105.2238° E. *N. Gamova BR-0482* (MW, digital image!).—**IRKUTSK:** S Siberia, Lake Baikal region, Khamar-Daban range, Slyudyanka River valley, 10–14 km SSW of Slyudyanka (SW end of Lake Baikal) (900–1850 m)—51° 33'–35' N 103° 36'–38' E. *H. H. Iltis 912* (NY).—**TRANSBAIKAL:** Czyta (Tschita) region, between the rivers Nerchy and Kuey, Gorbitsa—*V. Sukaczew, s.n.* (LE; MW, digital image!; NY).

14. *Carex hartmaniorum* A. Cajander:—**AUSTRIA. UPPER AUSTRIA:** Eidenberg, 1 km SSE (730 m)—48° 23' 10" N 14° 14' 22" E. *G. Kleesadl 1153* (BR, digital image!).—**ESTONIA. LÄÄNE:** Near Haapsalu, village Ridala—*H. Aasamaa 17699* (MW, digital image!). Haapsalu, near Espre—*H. Aasamaa 17712* (MW, digital image!).—**FRANCE. GRAND EST:** Prairies humides et lieux marécageux à l'est a'Altenstaat près de Wissembourg—*R. Engel 2349* (BR, digital image!).—**GERMANY. HESSE:** In pratis circa Offenbach—*Baker, s.n.* (as *C. buxbaumii*) (BR, digital image!).—**MECKLENBURG-WESTERN POMERANIA:** Rosental NE of Greifswald, 0.6 km WSW of Klein-Ladebow village—*H. Krisch, s.n.* (HAL).—**SAXONY:** Rothstein bei Reichenbach—*C. Baenitz, s.n.* (GLM, digital image!). Meissen, Nassau—*Hübner, s.n.* (HAL). Upper Lusatia depression, NE of Caßlau village—*W. Hilbig, s.n.* (HAL). Ore Mts., SW of Lengefeld village (560 m)—*S. Biedermann, s.n.* (HAL). Kr. Bautzen, Rachlau—*T. Schütze, s.n.* (GLM, digital image!). Hochkirch S, Sumpfwiesen (277 m)—*T. Schütze, s.n.* (GLM, digital image!). NW of Löbau, marshy meadow between the villages of Plotzen and Lehn—*G. Zirnstein, s.n.* (HAL, three sheets). Zittau 6 km W: Hainewalde, OT Charlottenruh, Sumpfwiese and der Str. nach Hörnitz—*M. Reimann, s.n.* (GLM, digital image!). Central Saxony, NW of Dresden (195 m)—51° 08' 11.8" N 13° 38' 31.1" E. *S. Gebauer 1206/17-1* (HAL), *1206/17-2* (Herb. Gebauer). Central Saxony, NW of Dresden (184 m)—51° 08' 28.4" N 13° 36' 46.5" E. *S. Gebauer 120625* (Herb. Gebauer). Central Saxony, NW of Dresden (184 m)—51° 08' 48.5" N 13° 37' 34.3" E. *S. Gebauer 140514* (Herb. Gebauer).—**SAXONY-ANHALT:** In pratis versus Dörlau—*D. F. L. von Schlechtendal, s.n.* (HAL). Dörlau near Halle (Saale)—*A. Garcke, s.n.* (HAL). Badetz, between Zerbst and Tochheim (c. 60 m)—*M. H. Hoffmann 1432* (Herb. Hoffmann).—**THURINGIA:** Gehrenberg, Hüttensteinach—*L. Meinunger, s.n.* (HAL). Ilmenau, Gräfinau-Angstedt—*L. Meinunger, s.n.* (HAL).—**ITALY. TRENTO-ALTO ADIGE:** In pratis subalpinis montis Ritten—*Hausmann 677* (as *C. buxbaumii*) (BR, digital image!). Oberbozen—*Haynald, s.n.* (as *C. buxbaumii*) (BR, digital image!).—**LATVIA. AIZPUTE:** Liepaja distr., 2 km S of Apriki—*N. Shvedchikova, s.n.* (MW, digital image!).—**VECPIEBALGA:** Cesis distr., 2 km SE of Taurene—*N. Shvedchikova, s.n.* (MW, digital image!).—**NETHERLANDS. FRIESLAND:** Terschelling, Boschplaat—*R. D'hose, s.n.* (BR, digital image!). NW van Boschplaat, Terschelling—*H. G. Rabyns 314* (BR, digital image!).—**NORWAY. ØSTFOLD:** Onsøy Enghauberget, Slevik—*Ø. Johansen, L. '70* (BR, two sheets, digital images!).—**POLAND. LESSER POLAND VOIVODESHIP:** Libiąż-Szyjki (200 m)—*T. Kowalczyk, s.n.* (BR, digital image!).—**ROMANIA. BACĂU:** Transsilvania, Harghita distr., between Mădăraş and Racu (as *C. buxbaumii*) (c. 700 m)—*F. Raftiu & I. Gergeley, s.n.* (JE; BR, digital image!).—**RUSSIA. KALININGRAD OBLAST:** Fl. Prussica orient. Königsberg [Kaliningrad]: Westlich vom Militär-Schießstande in der Fritzener Forst—*C. Baenitz, s.n.* (as *C. buxbaumii*) (BR, digital image!). Tilsit: in pratis silvae praedii Schilleningren—*Heidenreich, s.n.* (as *C. buxbaumii*) (BR, digital image!).—**KALUGA OBLAST:** Peremyshl distr., 0.5 km E of Bukreevo—54° 13.5' N 36° 15' E. *N. M. Reshetnikova et al., s.n.* (MW, two sheets, digital images!).—

LIPETSK OBLAST: Dobrovskiy distr., Osokovoi swamp—*V. N. Tikhomirov & V. V. Nikitin, s.n.* (MW, digital image!).—**MORDOVIA REPUBLIC:** Bol'shebereznykoskiy distr., surroundings of Simkino—*S. Mayorov et al., s.n.* (MW, digital image!).—**MOSCOW OBLAST:** Taldomskiy distr., Moscow-Volga canal—*M. S. Ignatov, s.n.* (MW, digital image!).—**PSKOV OBLAST:** Prov. et distr. Pskov, in fructicetis pr. p. Saputje—*V. D. Andreev, s.n.* (LE; MW, digital image!).—**RYAZAN OBLAST:** Spasskiy distr., Oka State Reserve, road to Lipovaya Gora—*V. N. Tikhomirov & E. S. Babaeva, s.n.* (MW, digital image!).—**SMOLENSK OBLAST:** Smolenskiy distr., SE of Kuprino, NE shore of lake Kuprinsky— $54^{\circ} 48' N 31^{\circ} 42.5' E$. *N. M. Reshetnikova, s.n.* (MW, digital image!).—**TAMBOV OBLAST:** Pervomaiskiy distr., Brigadirsky forestry—*A. Sukhorukov & G. S. Usova, s.n.* (MW, digital image!).—**SWEDEN. VÄSTMANLAND:** Västmanland, Arboga, Koberg—*G. Kjellmert, s.n.* (BR, digital image!).—**SWITZERLAND. SCHAFFHAUSEN:** Kloten, Klotener Riet—*K. Isler-Hübscher 470* (ZT, digital image!).—**ZÜRICH:** Peterli Oberglatt (418 m)—*R. Hangartner 115* (Z, digital image!). Kolzensee E-Ufer (440 m)—*R. Hangartner 850* (Z, digital image!). S von Altstetten—*E. Sulger Büel, s.n.* (as *C. buxbaumii*) (ZT, digital image!).

15. *Carex heterostachya* Bunge:—CHINA. BEIJING: Beijing, near water—*H. W. Kung 1372* (NY). Beijing, Prince Park—*T. P. Wang 48* (NY). Beijing, Temple of Heaven—*H. Hertel 23290* (M).—**SHANXI:** Shanxi, Shuimo—*s. coll. 975* (HNWP). Yuanqu Xian, Tongshan Xiang—*s. coll. 34* (HNWP).

16. *Carex holostoma* Drejer:—FINLAND. LAPLAND: Lapponia Inarensis, in monte Kalkuoiivi juxta flum. Pasvik älv.—*C. W. Fontell, s.n.* (P, digital image!). Kilpisjaura in palate alpino montis Laaua—*I. Montell, s.n.* (B).—**NORWAY. TROMS:** Reisen [Reisdalen], in monte Boatkavasse [Boatkavárri] (c. 500 m)—*E. Jørgensen, s.n.* (P, L, four sheets, digital images!).—**RUSSIA. CHUKOTKA:** Anadyr distr., upper Tanyur river, Ktep-nayvaam—*A. A. Korobkov & N. A. Sekretareva, s.n.* (LE, NY).—**KRASNOYARSK:** S Putorani, lake Nyakshynda, 0.5 km SW of Agata (275 m)—*V. Kuvaev 159-12* (MW, digital image!). SE Taimyr, NW Anabar plateau, watershed area of rivers Fomich and Zriiechka, Afanasyevskie lakes— $71.4309^{\circ} N 106.248^{\circ} E$. *E. B. Pospelova 06-599* (MW, digital image!). SE Taimyr, NW of Anabar plateau, area of the confluence of rivers Mzrkju and Kotuykan— $70.5331^{\circ} N 105.96^{\circ} E$. *E. B. Pospelova 07-0103* (MW, digital image!). W Taimyr, Putorana plateau, near W part of lake Gloubokoïe, W of the mouth of river Gudke-Daptu— $69^{\circ} 15' 15.5'' N 90^{\circ} 06' 57.4'' E$. *E. B. Pospelova 15-0107, 15-0198* (MW, two sheets, digital images!).—**MURMANSK OBLAST:** Kovdorskiy distr., SE of Rikolatva, Kamenistaya Mt. (c. 400–450 m)— $67^{\circ} 27' 38'' N 31^{\circ} 25' 41'' E$. *A. V. Kravchenko 25909* (MW, digital image!).—**SWEDEN. LAPPLAND:** Torne Lappmark, Riksgränsen, Katteråive (700 m)—*C. G. Alm & A. Nygren, s.n.* (B; P, digital image!). Paroecia Jukkasjärvi, in alpe Katteråive prope stationem viae ferrae Riksgränsen (650–700 m)—*C. G. Alm, s.n.* (L, digital image!). Lapland, Vassijaure—[*Herb. Groningen*], *s.n.* (L, digital image!).

17. *Carex infuscata* Nees:—AFGHANISTAN. BAGHLAN: E lateral valley of Darya-e Khenjan (2800 m)—*O. Anders 4742* (MSB).—**KABUL:** Paghman, valley above village, streamside meadow (c. 2700 m)—*I. Hedge & P. Wendelbo 4372* (E).—**KUNAR:** Bashgal Valley (Darrah-e Katigal), above Barge Matal (2150 m)— $35^{\circ} 41' N 71^{\circ} 20' E$. *O. Anders 5136* (MSB).—**LAGHMAN:** Alishang, upper part of Darrah Rastyon [Darah-ye Rastyon] (c. 2800 m)—*P. Wendelbo & L. Ekberg W9641* (E).—**NURISTAN:** Central Nuristan (c. 2500 m)—*G. Kerstan 948a, 948b* (HAL, two sheets).—**INDIA. HIMACHAL PRADESH:** Lahul, Udaipur

(2850 m)—*R. McBeath* 2269 (E). Lahul, Udaipur, Karpat (3150 m)—*R. McBeath* 2327 (E).—**JAMMU & KASHMIR**: Upper Liddar valley (3657 m)—*R. R. Stewart* 9443a (NY). Khilanmarg (3048 m)—*R. R. Stewart* 13432 (NY). Ferozepur Nullah (2134–2438 m)—*R. R. Stewart* 14770 (NY). Shokh Daran, c. 9 km NW of Sonamarg (c. 3070 m)—*C. C. Townsend* 89/249 (K).—**PAKISTAN. ASAD KASHMIR**: Shankargarh, upper Astor valley (3048 m)—*R. R. Stewart* 18756 (NY). Above Rattu, Astor valley (2896 m)—*R. R. & I. D. Stewart* 18769 (NY). Rupal Nullah, near Nanga Parbat (2743 m)—*R. R. Stewart* 18875a (NY). Burzil Chowki, Gilgit Rd. (3353 m)—*R. R. Stewart* 19784 (NY).—**GILGIT-BALTISTAN**: Darkot, SW side, in moist alpine pasture on steep slope (3505 m)—*S. Bowes Lyon* 8138 (K). Northern Areas, Fary, Buldar Valley (2860 m)—*M. Nüsser* 1029 (B). Northern Areas, Astor–Nanga Parbat, Mushkin Forest, SE above Mushkin Rest House (2720 m)—35° 29' N 74° 44' E. *B. Dickoré* 12775 (MSB).

18. *Carex japonalpina* (T.Koyama) T.Koyama:—CHINA. JILIN: Changbaishan Nature Protection Reserve, upper *Betula ermanii* forest belt, close to timberline (c. 1900 m)—*W. Herrmann*, s.n. (as *C. atrata*) (M). Mt. Baekdusan, Jilin-sheng (2100 m)—*J. Y. Kwon & J. H. Lee*, s.n. (KH). Autu Co., Mt. Changbai—*Z.-Y. Cao et al.* 215 (as *C. atrata*) (TAIF, digital image!).—**JAPAN. HONSHU**: Mt. Senjodake, Shinano—*G. Koidzumi*, s.n. (NY). Mt. Senjō in Shinano—*J. Ohwi*, s.n. (as *C. atrata*) (NY). Pref. Nagano, Prov. Shinano, Mt. Shirouma-dake (2800 m)—*M. Furuse* 22646 (K). Pref. Toyama, Prov. Yotchuu, Shirouma-yari, Mt. Shirouma, Shimo-niikawa-gun (c. 2600 m)—*M. Furuse* 34355 (PE, digital image!). Pref. Yamanashi, near summit Mt. Kita-dake, Ashi-yasu-son, Naka-koma-gun (3100 m)—*M. Furuse* 47902, 47903 (K, two sheets). Pref. Yamanashi, Prov. Kai, Mt. Kita-dake, Ashiyasu-mura, Naka-koma-gun (2700–2800 m)—*M. Furuse* 13787 (PE, digital image!). Pref. Nagano, Prov. Shinano, Mt. Senjoo-dake, Hase-mura, Kami-ina-gun (c. 3000 m)—*M. Furuse* 13968 (PE, digital image!). Nagano Pref., Kami-ina-gun, Hase-mura, Mt. Senjogatake—*Y. Hayashi*, s.n. (OKAY, digital image!). Nagano Pref., Ina-shi, Hase, Mt. Senjogatake (2850 m)—35° 43' 24.4" N 138° 11' 04.8" E. *T. Katsuyama*, s.n. (OKAY, digital image!).—**KOREA, N. NORTH HAMGYONG**: Kwanmo-Bong [Gwanmobong]—*Anonymous*, s.n. (as *C. atrata*) (KH).—**SOUTH HWANGHAE**: Kannan ('Kannan-do'), Mt. Nambootaishan (2430 m)—*T. Mori*, s.n. (DAO, digital image!).—**RUSSIA. KHABAROVSK**: Nanayskiy distr., basin of Anyouj, Tardoki-Yani (2077 m)—*S. Kharkevich et al.* 939a, 939b (as *C. aterrima*) (MW, two sheets, digital images!; NY, two sheets).

19. *Carex jisaburo-ohwiana* T.Koyama:—TAIWAN. TAICHUNG: Formosa—*S. Sasaki*, s.n. (mixed with *C. apodostachya*) (NY). Taichung Hsien, Wuling, en route from 369 Lodge to Hsuehshan peak (c. 3600 m)—*D. S. Hsu* 744 (A). Hoping Hsiang, Hsuehshan (3600–3884 m)—*S.-P. Li* 176 (as *C. atrata* subsp. *apodostachya*) (TAIF, digital image!). Mt. Hsueh (3200–3700 m)—*S.-W. Chung* 10363 (as *C. atrata* subsp. *apodostachya*) (TAIF, digital image!).

20. *Carex kangchengyaoensis* S.Gebauer, Jim .Mejías & Noltie:—BHUTAN. THIMPHU: Bhutan-Tibetan boundary (probably on Tibetan side!), E of Phari (4572 m)—*B. J. Gould* 1495 (as *C. atrata* var. *glacialis*) (K).—**INDIA. SIKKIM**: N Sikkim, North distr., W side of Sebu La (4920 m)—27° 55' 56" N 88° 39' 01" E. *D. G. Long & H. J. Noltie* 388 (as *C. atrata* var. *glacialis*) (E).—**NEPAL. MECI ZONE**: Kambachen to Lhonak (4320 m)—27° 44' N 88° 01' E. *Kew-Edinburgh-Kathmandu/Kanchenjunga Expedition to N.E. Nepal* (1989) KEKE 531 (as *C. atrata* var. *glacialis*) (E, K).

21. *Carex kansuensis* Nelmes:—CHINA. GANSU: Tianzhu Xian, Jinqiang He (3000–3400 m)—*T.-N. He 2126* (HNWP). Tianzhu Xian, Jinqiang He Maya Shan (3200 m)—*R.-F. Huang 2457* (HNWP).—**QINGHAI:** Ledu Xian, Shangbeishan Linchang (2600 m)—*Y.-H. Wu 2283* (HNWP). Ledu Xian, Yinsheng Gou to Xiaoxi Gou—*Q. Dui 1480* (HNWP). Huangzhong Xian, Qunjia Linchang (3800–3900 m)—*S.-W. Liu 3165* (HNWP). Menyuan Xian, Qingshizui beishan (3700 m)—*B.-Z. Guo & W.-Y. Wang 12226* (HNWP). Jiangxigou xialaxiu (4000 m)—*Z.-D. Wei 22072* (HNWP, two sheets). Henan Xian, Ningmute Gongshe Zhuomao Shan (4000 m)—*L. Zhou & L.-N. Sun 2204* (HNWP, two sheets). Henan Xian, Waisi Xiang A'mi Shan—*B.-Z. Guo 9869* (HNWP, two sheets). Jiuzhi Xian, Xiemucuo Hu—*s. coll. 455* (HNWP). Baoku—*s. coll. 26* (HNWP). Datong Xian, Baoku Hongyatai (3600 m)—*Z.-M. Zhang 4808* (HNWP). Datong Xian, Baoku Bayanzhang (3300 m)—*Z.-M. Zhang 5350* (HNWP). Datong Xian, Dongxia Lanque Shan (3800 m)—*H.-C. Zhang 768* (HNWP). Huzu Xian, Jiading Gongshe Zha long tang Yun ping zhang—*B.-Z. Guo & T.-N. He 9453* (HNWP). Zhaduo Xian, Jieduo Xiang Ganwayong (4600 m)—*S.-W. Liu 319* (HNWP). Yushu, Gelong nan da Shan (4300 m)—*s. coll. 288* (HNWP). Menyuan Xian, Haibei Zhan (3250 m)— $37^{\circ} 37' 0.97''$ N $101^{\circ} 19' 0.02''$ E. *Y.-H. Wu Lio-WLS-2008-0146* (HNWP). Maqin (Maqên) Xian, Ehema, Dawu Xiang, along the Gequ He, S of Maqin (3870 m)— $34^{\circ} 21' 27''$ N $100^{\circ} 15' 20''$ E. *T. N. Ho et al. 551* (MO, digital image!). Maqin (Maqên) Xian, Dawu Xiang, along the Deleni He, S of Maqin (3870 m)— $34^{\circ} 22' 06''$ N $100^{\circ} 13' 18''$ E. *T. N. Ho et al. 858* (E). Golog Zang Aut. Pref., Maqên Co., Chihedana, S of Dawu (3830 m)— $34^{\circ} 22' 00''$ N $100^{\circ} 13' 00''$ E. *D. G. Long et al. 327* (E). Golog Zang Aut. Pref., Maqên Co., Jungun Naichong (3600 m)— $34^{\circ} 38' 50''$ N $100^{\circ} 36' 41''$ E. *D. G. Long et al. 482* (E). Laji Shan, Huangzhong Xian, along road NW of Lajishan Tunnel, 2 km W of Sancha village (3293 m)— $36^{\circ} 21' 53.7''$ N $101^{\circ} 30' 01.6''$ E. *S. Gebauer et al., SG-CN-005B* (Herb. Gebauer). E Qiajajima Shan, Yushu Xian, above road G214 between Borongcun village and Zangzuzizhizhou Pass (4200 m)— $32^{\circ} 48' 11.8''$ N $96^{\circ} 38' 53.6''$ E. *S. Gebauer et al., SG-CN-022* (HAL, HNWP, Herb. Gebauer, three sheets). E Anyi Machen, Maqên Xian, along Gequ He and adjoining valley to the W, S of Maqên [Golog] (3885–3930 m)— $34^{\circ} 21' 52.4''$ N $100^{\circ} 13' 08.7''$ E to $34^{\circ} 21' 55.0''$ N $100^{\circ} 10' 33.9''$ E. *S. Gebauer et al., SG-CN-028* (HAL, HNWP, Herb. Gebauer, three sheets). E Anyi Machen, Maqên Xian, valley W of Gequ He, S of Maqên [Golog] (3975 m)— $34^{\circ} 22' 31.9''$ N $100^{\circ} 09' 45.3''$ E. *S. Gebauer et al., SG-CN-032* (HAL, HNWP, Herb. Gebauer, three sheets).—**SHAANXI:** P'ingansze, T'aipaishan (2700 m)—*T. P. Wang 1857* (PE, digital image!).—**SICHUAN:** Yiguo Xian, DongShan (4200 m)—*s. coll. 2573* (HNWP). Sichuan [without detailed location]—*S.-W. Xishi 8854* (HNWP). Yiguo Xian, DongShan (4200 m)—*s. coll. 2573* (HNWP). Upper Yalong basin, Chola Shan, Dege–Garze, Manigango (4050 m)— $31^{\circ} 52' 00''$ N $99^{\circ} 07' 00''$ E. *G. Miehe et al. 94-408-18* (MR). Daxue Shan, Garzê Xian, Tagong, N of Mt. Yala [Zhara Lhatse], Youcuò Lake (4070 m)— $30^{\circ} 24' 50.4''$ N $101^{\circ} 41' 50.9''$ E. *S. Gebauer et al., SG-CN-078* (HAL, KUN, Herb. Gebauer, three sheets).—**XIZANG:** S Tibet, Upper Yiong Zhangbo, E of Lhari (4820 m)— $30^{\circ} 37' 00''$ N $93^{\circ} 18' 00''$ E. *G. Miehe et al. 04-045-12* (MR). SE Tibet, Upper Yiong Zhangbo, near Lhari, above Tschamä Yumco (4650 m)— $30^{\circ} 38' 00''$ N $93^{\circ} 12' 00''$ E. *G. & S. Miehe 95-017-07* (MR). SE Tibet, pass between Rawu and Zayü (4730 m)— $29^{\circ} 19' 00''$ N $97^{\circ} 01' 00''$ E. *G. Miehe et al. 04-165-08* (MR).

22. *Carex lehmannii* Drejer:—BHUTAN. GASA: Rodophu (4330 m)— $28^{\circ} 02' 00''$ N $89^{\circ} 47' 00''$ E. *G. & S. Miehe* (MR).—**CHINA. SICHUAN:** Kangding Xian, Mugecho lake (3700–3800 m)— $30^{\circ} 08' 49''$ N $101^{\circ} 51' 37''$ E. *D. E. Boufford et al. 27606* (A). Aba Xian, SE of Aba on highway 301 (road to Maerkang) on Aba side of

Ayila Shan (3830 m)—32° 43' 57" N 102° 05' 54" E. *D. E. Boufford et al. 39446* (A, MSB). Mounixiang, Songpan Xian, W of Songpan (3345 m)—32° 39' 54.0" N 103° 30' 46.5" E. *S. Gebauer et al., SG-CN-052* (HAL, KUN, Herb. Gebauer, three sheets). Daxue Shan, Garzê Xian, Tagong, N of Mt. Yala [Zhara Lhatse], Youcuò Lake (4067 m)—30° 24' 42.4" N 101° 41' 53.9" E. *S. Gebauer et al., SG-CN-079* (HAL, KUN, Herb. Gebauer, three sheets).—**XIZANG:** E Tibet, Upper Mekong basin, Dengqen–Qamdo (4150–4250 m)—31° 13' N 96° 29' E. *U. Wündisch 94-602-08* (MR). S Tibet, Tibetan Himalaya, N of Bhutan, Kuru Chu, Hill SW of Lhozak Valley junction (4130 m)—28° 18' N 90° 51' E. *B. Dickoré 9725* (MSB). SE Tibet, Tsangpo Valley, Nangxian–Mainling, valley 10 km W of Gyemdong (High Camp 13) (3700 m)—28° 56' N 93° 13' E. *B. Dickoré 10600* (MSB). SE Tibet, Gyamda Chu, NE tributary, Pasum Tso SW shore (below Camp 17) (3550 m)—30° 00' N 93° 54' E. *B. Dickoré 11904* (MSB). SE Tibet, Dong-zhang waterfall, Cou-Na Co. (3680 m)—27° 46.7089' N 91° 58.6713' E. *M. Deng DM05363* (MOR).—**YUNNAN:** Dali Xian, E side of Diancang Shan Mts. range, vicinity of Yinglofeng (3100 m)—25° 42' N 100° 07' E. *D. E. Boufford et al. 855* (A). Diqing Pref., between Xia Geza and Geza, 45 km N of Zhongdian (3095 m)—28° 07' 24" N 99° 45' 11" E. *B. Aldén et al. 300* (E). Zhongdian, Geza to Wengsui (3561 m)—28° 31' 03" N 99° 46' 62" E. *Alpine Garden Society Expedition to China (1994) ACE 536* (K). Gongshan, Cikai, vicinity of Cekeluo Qiao near Km 41 on the road from Gongshan to Kongdang, E side of Gaoligong Shan (3030 m)—27° 47' 53.2" N 98° 30' 11.8" E. *L. Heng et al. 33831* (A).—**NEPAL. BAGMATI:** Langtang (3658 m)—*O. Polunin 572* (NY). 5 mi E of Timure (4115 m)—*O. Polunin 799* (NY). Kyanging, Langtang, Khola (3600–3900 m)—*H. Kanai & P. R. Shakya 672559* (as *C. infuscata*) (NY). Rasuwa distr., Langtang Valley, Kyangjin (4000 m)—28° 13' N 85° 34' E. *K. Reiter 697* (MSB).—**KARNALI:** Jumla distr., Thakurji Lekh, S of Jumla (c. 3505 m)—*O. Polunin et al. 4751* (NY). Chankheli, Lagna, Humla distr. (3450 m)—*K. R. Rajbhandari & B. Roy 3903* (NY).—**MECHI:** Taplejung distr., above Tseram (3810 m)—27° 32' N 87° 57' E. *S. Crawford et al. 737* (E, K).

23. *Carex media* R.Br.:—**MONGOLIA. ARKHANGAI:** Upper reaches of river Bugustin gol—*B. M. Mirkin, s.n.* (as *C. norvegica*) (HAL). Changai, S of Terchijn-cagaan-nuur—*W. Hilbig 82-83/83* (as *C. norvegica*) (HAL).—**BULGAN:** Namnan-uul—*W. Hilbig 259/83* (as *C. angarae*) (HAL).—**DORNOD:** Kerulen river, to the N of Boskho-daban—*N. & V. Ikonnikov-Galitzky 354* (as *C. brachylepis*) (NY).—**KHENTII:** Khentii Mts., on summit of mountain, on the way from Azan-ipsuduk river to Ubur-ipsuduk—*N. & V. Ikonnikov-Galitzky 2430* (as *C. brachylepis*) (NY). Khentii Mts.—*N. & V. Ikonnikov-Galitzky 2672* (as *C. alpina*) (NY).—**KHÖVSGÖL:** Alag-Erdene, E Egijn-gol—*W. Hilbig 171/83* (HAL).—**TÖV:** Bornuur distr., middle reaches of Shavart-gol (1200 m)—*K. Kloss 65* (GFW, digital image!). Möngönmort, E of Kerulen, Zorgol—*W. Hilbig 341/83* (HAL). Terelzh, Tolan river flood plain (1630 m)—48° 00' N 107° 20' E. *E. Jäger, s.n.* (HAL).—**ULAANBAATAR:** S Khentii Mts., Gorkhi—*W. Hilbig 312/81* (HAL). S Khentii Mts., Gorkhi—*W. Hilbig 330/81* (HAL). Bogd-uul, Churchreegijn—*W. Hilbig 309a/83* (HAL). Bogd-uul, S of Ulaanbaatar, above Manzsir monastery (c. 1700 m)—47° 45' N 107° 00' E. *E. Jäger, s.n.* (HAL). Bogd-uul, S of Ulaanbaatar, bog at ridge of Cecee-gun Mt. (c. 2150 m)—47° 50' N 107° 00' E. *E. Jäger, s.n.* (HAL). Bogd-uul, Tör-church valley, 17 km SW of Ulaanbaatar (1670 m)—47° 45' N 107° 06' E. *W. Hilbig & E. Jäger H138* (HAL).—**Uvs:** Charchiraa near Ulaangom, valley of Little Charchiraa Mt. to Bodj nuur—*Z. Schamsran et al., s.n.* (as *C. norvegica*) (HAL). Charchiraa near Ulaangom, NE slope of Little Charchiraa Mt. (2000 m)—*H. Ansorge, s.n.* (as *C. norvegica*) (HAL). Depression WSW of Ulaangom—*H. Ansorge, s.n.*

(HAL).—**NORWAY. HEDMARK:** Hedmark, 3 km NW of Alvdal (500 m)—62° 10.058' N 10° 31.323' E. *M. H. Hoffmann a221* (Herb. Hoffmann).—**RUSSIA. ALTAI REPUBLIC:** S Siberia, Altai region, valley of river Uliat—*B. Schischkin, s.n.* (as *C. alpina*) (NY). Ajgulakskij plateau, N of Aktasch, close to Ozero Uzukjol lake (1950–2000 m)—50° 28' N 87° 37' E. *B. Heuchert B53* (HAL). Kurajskaja opening to Chujskaja Step', c. 10 km ESE of Kuraj (1617 m)—50.157196° N 88.296077° E. *M. H. Hoffmann j40, j42* (Herb. Hoffmann, two sheets).—**AMUR REPUBLIC:** Zeysky distr., Zeysky reserve, Tukuringra stream (649 m)—54.123498° N 126.800933° E. *S. V. Dudov & K. V. Kotelnikova 2013-S-284* (MW, digital image!).—**BURYATIA REPUBLIC:** N macroslope of Khamar-Daban, valley of river Mishikha, middle course (580 m)—51.54345° N 105.543267° E. *N. Gamova BR-1090* (MW, digital image!). Mukhorshibirsky distr., 2 km S of Ehzh-Nur, steppe slope along river Altash—*L. Abramova et al., s.n.* (MW, digital image!).—**IRKUTSK:** Prov. Irkutsk, distr. Balagansk (Siberia), in abiegnis humidis ad p. Bashejewsky—*N. Maltsev, s.n.* (LE; MW, digital image!; NY).—**JEWISH AUTONOMOUS OBLAST:** Khingan Mts.—*D. Litvinov, s.n.* (NY).—**KAMCHATKA:** Kamchatka Pen., Olyoutorskiy distr., vicinity of village Tilichyki—*S. Kharkevich & T. Buch 968a* (MW, digital image!; NY).—**KHABAROVSK:** Verkhnebureinsky distr., Dusse-Alin ridge (740 m)—51° 53' N 134° 30' E. *M. V. Berzina & B. A. Sharov 88-201* (MW, digital image!).—**KRASNOYARSK:** Enisseyskaya gubernia, Turukhansk, river bank of Chopko—*N. I. Kusnezow & W. W. Reverdatto 1309* (NY). Taseevskiy rayon, drainage divide of rivers Murma and Telkun [Tel'kun]—*M. Molokoedova & S. Kryukovskaya, s.n.* (NY). S Taimyr, middle course of river Maimecha—70° 41' 29.7" N 101° 22' 4.78" E. *I. N. Pospelov 09-0265* (MW, digital image!).—**OMSK OBLAST:** Tarsky distr., Martyushevo—57° 05' 33" N 72° 22' 57" E. *A. N. Efremov et al., s.n.* (MW, digital image!).—**TUVA REPUBLIC:** Ulug-Khemsy distr., Bayan-Kol, along stream—*M. Lomonosova & E. Korotkova 49* (as *C. angarae*) (MW, digital image!). Mongun-Taiginsky distr., 5 km NE of lake Ak-Khol (2126 m)—50.293879° N 89.649971° E. *M. H. Hoffmann j109* (Herb. Hoffmann).—**VOLOGDA OBLAST:** Prov. Wologda, distr. Ust-Sysolsk, In pratis pr. p. Ub-Schor—*V. D. Andreev, s.n.* (as *C. halleri*) (LE; MW, digital image!).—**SWEDEN. LAPPLAND:** Abisko—*H. Meusel, s.n.* (as *C. alpina*) (HAL).

24. *Carex melanantha* C. A. Mey.:—**AFGHANISTAN. BADAKHSHAN:** Darrah Mulaw, E of Murjan River (4500 m)—*I. Rowe & W. Sproul 50* (E). Badakhshan-Wakhan, Deliz pass, E of Sarhad (1250 m)—*C. Grey-Wilson & T. F. Hewer 1617* (K).—**NURISTAN:** Hindukush, Mingan Pass (3658 m)—*W. Koelz 12662* (E).—**PANJSHIR:** Hindukush, Lochan, NE of Base Camp, Mir Samir region (4570 m)—*W. B. Gibson 16* (E).—**AZERBAIJAN. QUBA-XAÇMAZ:** Near border with Dagestan, marshy meadow in shale mountain part opposite to Mt. Shahdagh—*Anonymous, s.n.* (as *C. melananthiformis*) (MW).—**INDIA. HIMACHAL PRADESH:** Miyah Nullah, Lahul (4150 m)—*R. McBeath 1611* (*C. melanantha* × *C. moorcroftii?*) (E). Lahul, Udaipur, Khanjar (3850 m)—*R. McBeath 2405* (*C. melanantha* × *C. moorcroftii?*) (E).—**JAMMU & KASHMIR:** Sonamarg (3050 m)—*R. R. Stewart 6666* (NY). Sonamarg, Kashmir (3962 m)—*R. R. Stewart 7321* (NY). Sonamarg, Kashmir—*R. R. Stewart 9777* (NY). Kashmir, Sonamarg (3350 m)—*R. R. Stewart 9868a* (mixed with *C. obscura*) (NY). Near Kangi La [Kanji-la pass], Ladakh (4720 m)—*W. Koelz 2839b* (*C. melanantha* × *C. moorcroftii?*) (NY). Below Pensi La to Rangdum, Zaskar (3353 m)—*W. Koelz 2937, 2939* (NY). Pensi La, Zaskar (c. 5030 m)—*W. Koelz 5837* (*C. melanantha* × *C. moorcroftii?*) (NY). Mergandob-Gadsar (3658 m)—*R. R. Stewart & I. D. Stewart 18272* (NY). Himalaya range, Tso Kar to Runtse, S of Shingbuk La Pass (5008 m)—33.44231° N 77.95442° E. *M. H. Hoffmann j297* (*C. melanantha*

× *C. moorcroftii?*) (Herb. Hoffmann).—**KAZAKHSTAN. ALMATY:** Zailiyskiy Alatau, Shen Turgen N (3250 m)—*M. Richter T30* (M). Tian Shan, Trans-Ili Alatau, S of Talgar pass (3200–3400 m)—43° 06' 20" N 77° 06' 23" E. *A. Hilpold & P. Schönswetter, s.n.* (BOZ). Tian Shan, Trans-Ili Alatau, peak SW third Kolsay lake, northeastern slope (3200–3450 m)—42° 53' 30" N 78° 19' 42" E. *A. Hilpold et al., s.n.* (BOZ).—**KYRGYZSTAN. OSH:** Fergana, Alai Mts., tributary valley of the Gadschir valley, c. 20 km SW of Schachimardan (Chamsaabad) (c. 2700 m)—*K.-F. Günther et al. 305* (JE).—**TALAS:** Talas rayon, NW of Otmök pass (3550 m)—42° 17' 28" N 73° 06' E. *J. Osborne 517* (K).—**MONGOLIA. ARKHANGAI:** NW Central Mongolia, Tariat, Changai, S of Terchijn-cagaan-nuur—*W. Hilbig 85/83* (HAL).—**KHÖVSGÖL:** N Mongolia, Alag-Erdene, E of Egijn-Gol—*W. Hilbig 171/83* (HAL).—**ULAANBAATAR:** Central Mongolia, Bogd-uul, S slope close to Manzsir monastery, N of Zuunmod—*W. Hilbig 372/81* (HAL). Central Mongolia, Töv Aimag, Bogd-uul S of Ulaanbaatar, Manzsir monastery (c. 1650 m)—*E. Jäger, s.n.* (HAL).—**Uvs:** W Mongolia, Ulaangom, Charchiraa Mts. near Ulaangom, route from Chadat to Chowin Chotgor—*W. Hilbig & D. Bumschaa 67/77* (HAL). W Mongolia, Charchiraa Mts., S of Turgen-sum Summer Camp (2550 m)—*E. Jäger & W. Hilbig J123a/H124* (HAL).—**PAKISTAN. ASAD KASHMIR:** Minimarg, Gilgit Rd. (2743–3048 m)—*R. R. Stewart 19180* (NY). Burzil pass (3962 m)—*R. R. Stewart 22050a* (NY).—**GILGIT-BALTISTAN:** Deosai Plain (3658 m)—*W. Koelz 9483* (NY). Burzil Pass (3962–4267 m)—*R. R. Stewart 19033* (NY). Burzil Chowki, Gilgit Rd. (3353–3658 m)—*R. R. Stewart 19114* (NY). Burzil Chowki, Gilgit Rd. (3353 m)—*R. R. Stewart 19874A* (NY). Burzil Chowki, Gilgit Rd. (3353 m)—*R. R. Stewart 19874* (NY). Chota Deosai (3962–4267 m)—*R. R. Stewart 19916* (NY). Burzil Pass to Deosai plains (3962 m)—*R. R. Stewart 19916A, 19916B* (NY, two sheets). Deosai plains (3962–4267 m)—*R. R. Stewart 19923* (NY). Deosai plains (3962 m)—*R. R. Stewart 20102* (NY). Thalle la, Baltistan (4572–4877 m)—*R. R. Stewart 20748* (NY). Thalle la, Baltistan (4572–4877 m)—*R. R. Stewart 20758A* (NY). Marko La, Deosai region (3960 m)—*R. R. Stewart 22291B* (*C. melanantha* × *C. moorcroftii?*) (NY).—**RUSSIA. ALTAI REPUBLIC:** Altajskij kraj, Kosh-Agachskij Rayon, dolina r. Ak-Kol—*E. A. Mungalov, s.n.* (ALTB). Altai Mts., Kosh-Agach, river Irbistu valley—*D. Karkhanin, s.n.* (ALTB). Altai Mts., Ajgulakskij Plateau, N of Aktasch, close to Ozero Uzukjol lake (2000–2150 m)—*B. Heuchert B43* (HAL). Kosh-Agach distr., Juzhno Chujskij Khrebet, valley of Elangazh (2466 m)—49.833870° N 88.054922° E. *M. H. Hoffmann j69* (Herb. Hoffmann). Kosh-Agach distr., Juzhno Chujskij Khrebet, tributary valley of Elangazh (2516 m)—49.825571° N 88.059824° E. *M. H. Hoffmann j83* (as *C. norvegica*) (Herb. Hoffmann). Kosh-Agach distr., Sajljugem (2304 m)—50.013693° N 89.247574° E. *M. H. Hoffmann j144* (Herb. Hoffmann). Kosh-Agach distr., Sajljugem (2433 m)—50.006927° N 89.262485° E. *M. H. Hoffmann j155* (as *C. norvegica*) (Herb. Hoffmann).—**DAGESTAN:** Caucasus, alpine belt, near glacier Ullu-Chyran—*Anonymous, s.n.* (as *C. melananthiformis*) (MW).—**KABARDINO-BALKAR:** near Elbrus (Mt.)—*Makhova, s.n.* (as *C. melananthiformis*) (MW).—**NORTH OSSETIA-ALANIA:** Basin of Ardon river, crest of Tsey range—*N. Shvedchikova, s.n.* (as *C. melananthiformis*; mixed with *C. aterrima* subsp. *medwedewii*) (MW).—**TUVA:** S Siberia, Tes-Khemskiy rayon, mountain ridge of V. Tannu-Ola, surroundings of Kara-Khol lake (1740 m)—*V. Khanminchun & N. Idt 4226* (as *C. melananthiformis*) (LE).—**TAJIKISTAN. SUGHD:** Hissar range, N of Dushanbe, E side of Yuzhny Gaznok pass (3700 m)—39.042 N 68.573 E. *M. H. Hoffmann T/466* (Herb. Hoffmann). Hissar range, W side of Yuzhny Gaznok pass (3805 m)—39.043061 N 68.545311 E. *M. H. Hoffmann T/472* (Herb. Hoffmann). Hissar range, N of Dushanbe, upper valley of Obiborik river (3600 m)—39.039265 N 68.536142 E. *M. H. Hoffmann T/488* (Herb. Hoffmann). Hissar range, N of Dushanbe, Angisht valley (3356 m)—38.9894 N

68.430326 E. *M. H. Hoffmann T/519* (Herb. Hoffmann).—**UZBEKISTAN. SURKHONDARYO:** N Hissar range, systema fl. Tupalang, in fauce Czormasgo (3100 m)—*I. Vassilczenko & L. Vassiljeva, s.n.* (E, digital image!; LE, M; P, digital image!).

25. *Carex melananthiformis* Litv.:—**KAZAKHSTAN. ALMATY:** Djungarski Alatau, Lepsinsk, NE slope of the ravine Say-Tentyak—*L. E. Rodin 601* (NY).—**EAST KAZAKHSTAN:** Zaysan, Narvinskiy range, Djaidak Mts.—*N. Goncharov & A. Borissova 1421* (NY).—**MONGOLIA. ARKHANGAI:** NW Central Mongolia, Chuluut, valley of Chulutyn-Gol, c. 40 km N of Chulut—*H.-D. Knapp 442/78* (HAL). Tüvshrüülekh, 32 km NNE of Chöch sumein am—*B. M. Mirkin, s.n.* (HAL).—**BULGAN-ORKHON:** N Mongolia and Khangai, meadow on the bank of Orkhon [Orchon] river—*N. Ikonnikov-Galitzky 789* (as *C. melanantha*) (NY).—**KHÖVSGÖL:** Summit of Khalzan daava pass, near Zain-gegen—*N. Pavlov 43* (NY).—**SÜKHBAATAR:** S macroslope of Mt. Dzhergalant-ula, 65 km S of Erdene-Tsagan [Erdenetsagaan]—45° 10' N 115° 05' E. *Sh. Dariymaa et al. 783, 790* (MW, two sheets, digital images!).—**RUSSIA. ALTAI REPUBLIC:** Ak-Alakhi valley, between Kara-Alakha and Karabulak—*B. Schischkin et al., s.n.* (as *C. sabulosa*) (NY). Kosh-Agach distr., Tarhata valley (2150 m)—*M. Lomonosov & N. Timukina, s.n.* (MW, two sheets, digital images!). Kosh-Agach distr., N foothills of Severo-Chuysky range—*A. Seregin & I. Seregina S389* (MW, digital image!). Kosh-Agach distr., Juzhno Chujskij Khrebet, valley of Elangazh (2455 m)—49.834872° N 88.051176° E. *M. H. Hoffmann j47, j52* (Herb. Hoffmann, two sheets). Kosh-Agach distr., Juzhno Chujskij Khrebet (2379 m)—49.860154° N 88.103670° E. *M. H. Hoffmann j91* (Herb. Hoffmann). Kosh-Agach distr., Juzhno Chujskij Khrebet (2351 m)—49.908547° N 88.173784° E. *M. H. Hoffmann j96* (Herb. Hoffmann).—**KHAKASSIA:** S Siberia, Ust-Abakanskiy Rayon, surroundings of Moskva, Khutor Prilutskogo—*I. Neyfeld & G. Dereka, s.n.* (JE).—**TUVA:** Mongun-Taiginsky distr., 5 km NE of Ak-Khol lake, along river Mogun-Buren (2126 m)—50.293879° N 89.649971° E. *M. H. Hoffmann j103* (Herb. Hoffmann). Mongun-Taiginsky distr., 5 km E of Ak-Khol lake (2091 m)—50.243638° N 89.689476° E. *M. H. Hoffmann j126* (Herb. Hoffmann).

26. *Carex melanocephala* Turcz.:—**KAZAKHSTAN. EAST KAZAKHSTAN:** Altai Mts., Ust-Kameno-gorsk, Saryschsakty Mt. (Sarışsaktı)—*V. & A. Rezniczenko, s.n.* (LE; MW, digital image!; NY; P, digital image!).—**MONGOLIA. ARKHANGAI:** NW Central Mongolia, Tariat, Tarbagataj Mts., N of Tariat (c. 2240 m)—*H.-D. Knapp 389/78* (HAL).—**BAYAN-ÖLGII:** Mongolian Altai, Sagsay, Hulagash-Nuur near Dayan-Nuur—*O. V. Zhurba 1272* (MW, digital image!).—**BULGAN-ORKHON:** C Bayan-Dzurh, Hantay, Yudugin-Gol—*O. V. Zhurba 176* (MW, digital image!). Mongolian Altai, pass Elt-Daba (2700–2750 m)—*I. A. Gubanov et al. 1954* (MW, digital image!).—**ZAVKHAN:** Somon: Tosontsengel (2500 m)—48° 16' N 98° 58' E. *D. Bajasgalan 240* (MW, digital image!).—**RUSSIA. ALTAI KRAI:** Ust-Koksinskiy distr., Katunsky, Multinsky Lake (2020 m)—50° 00' N 85° 50' E. *I. Krasnoborov & D. Shaulo, s.n.* (MW, digital image!).—**ALTAI REPUBLIC:** Altai Mts., between Ak-kem and Kair—*B. Schischkin et al., s.n.* (NY). Altai Mts., upper reaches of left tributary of river Chebdar—*M. Silantyeva, s.n.* (ALTB). Altai Mts., marshy place in the snow-lies—*M. Silantyeva, s.n.* (ALTB). Altai Mts., Kosh-Agach range, Saydigen pass between rivers Zhasator and Zhumada—49° 28' N 88° 09' E. *R. V. Kamelin et al., s.n.* (ALTB). Upper reaches of river Chebdar, mountain lake shore—*M. Silantyeva, s.n.* (ALTB). Ajgulakskij Plateau, N of Aktasch, close to Ozero Uzukjol Lake (2000–2150 m)—50° 28' N 87° 37' E. *B. Heuchert B32* (HAL). Kosh-Agachskij Rayon,

Khrebet Sajljugem, E side of Zhumaly Valley on road to pereval Tyoplyy Klych, 75 km SW of Kosh-Agach (2400 m)—49° 27' N 88° 03' E. *E. v. Raab-Straube 020288* (B). Juzhno Chujskij Khrebet, valley of Elangazh (2455 m)—49.834872° N 88.051176° E. *M. H. Hoffmann j46* (Herb. Hoffmann).—**TUVA REPUBLIC:** C Sayan, Hor Taiga, upper Aldy-Kargal (2200 m)—*I. Krasnoborov & Z. Dubrovin 6451* (MW, digital image!). Mongun-Taiginsky distr., Chikhacheva, middle course of river Jety-Tei—*A. Krasnikov et al., s.n.* (MW, digital image!). Mongun-Taiginsky distr., Pereval Buguzun (2585 m)—50.184895° N 89.411116° E. *M. H. Hoffmann j136* (Herb. Hoffmann).

27. *Carex moorcroftii* Falc. ex Boott:—CHINA. GANSU: Tianzhu Xian, Jinqiang He Maya Shan (3400 m)—*R.-F. Huang 2472* (HNWP, two sheets).—**QINGHAI:** Dulan Xian, Qu'rigang (3826 m)—36° 00' 55.32" N 98° 11' 37.74" E. *J.-B. Pan LiuJQ-2011CDM-189* (HNWP). Maqin Xian, Jungong Xiang Heitu Shan (3340 m)—*H. B. G. 214* (HNWP). Tangula Shan N, upper Yangtse basin, Gar Qu valley. Mt. Geladandong—Yanshiping (4900 m)—33° 36' N 91° 40' E. *B. Dickoré 4608* (MSB). Golog Zang Aut. Pref. Maqên Co. Chihedana. S of Dawu (4000 m)—34° 22' N 100° 13' E. *D. G. Long et al. 357* (as *C. minxianensis*) (E). Qilian Shan, 50 km NW Menyuan (3260 m)—37° 38.2' N 101° 20.3' E. *H. Kürschner & M. Sonnentag 01-372b* (B). Luanhaizi Lake, 40 km NW Menyuan (3190 m)—37° 36.2' N 101° 20.9' E. *H. Kürschner & M. Sonnentag 01-405* (B). Hainan Zang Aut. Pref. Gonghe Co. Heimahe. S side of Qinghai Lake (3130 m)—36° 38' 19" N 100° 04' 33" E. *D. G. Long et al. 82* (E). Golog Zang Aut. Pref. Maqên Co. Jiang ran valley N of Dawu (3720 m)—34° 31' 17" N 100° 13' 06" E. *D. G. Long et al. 221* (E). Golog Zang Aut. Pref. Maqên Co. Jiang ran valley N of Dawu (3675 m)—34° 30' 58" N 100° 13' 14" E. *D. G. Long et al. 234* (E). Huangnan Zang Aut. Pref. Zêkog Co. Between Tongde Xian and Zêkog Xian (3390 m)—35° 19' 20" N 100° 55' 05" E. *D. G. Long et al. 591* (E). Huangnan Zang Aut. Pref. Henan Mongol. Aut. Co. N of Henan Xian, Zequ River (3560 m)—34° 45' 59" N 100° 39' 41" E. *D. G. Long et al. 626* (E). Yushu Xian, E edge of Longbao National Nature Reserve (4170 m)—33° 09' 24" N 96° 38' 54" E. *D. E. Boufford et al. 26737* (A, NY). Lake basin, gravel and sand (4250 m)—34° 55' N 98° 31' E. *G. Miehe et al. 02-017-04* (MR). Laji Shan, Huangzhong Xian, valley below road NW of Lajishan Tunnel, 2 km W of Sancha village (3300 m)—36° 21' 55.4" N 101° 29' 57.2" E. *S. Gebauer et al., SG-CN-007* (HAL, HNWP, Herb. Gebauer, three sheets). Xinghai Xian, c. 20 km N of Hainan Zangzuzhizhou [Huangzhong], along road G214 (4300 m)—35° 31' 44.5" N 99° 30' 42.4" E. *S. Gebauer et al., SG-CN-014B* (HAL, HNWP, Herb. Gebauer, three sheets). E Anyi Machen, Maqên Xian, valley W of Gequ He, S of Maqên [Golog] (3970 m)—34° 22' 30.3" N 100° 09' 46.0" E. *S. Gebauer et al., SG-CN-031* (HAL, HNWP, Herb. Gebauer, three sheets).—**SICHUAN:** Baiyu Xian, Gan-Bai Lu (4510 m)—31° 14' 32" N 99° 51' 41" E. *D. E. Boufford et al. 36895* (A). Along streams (3490 m)—32.785778 N 102.463111 E. *K.-S. Chung & R. Li 25-3* (as *C. cf. minxianensis*) (MOR).—**XIZANG:** Tangula Shan S interior drainage basin, Taoer Jiu Yakou—Tangula P. (5020 m)—32° 38' N 91° 50' E. *B. Dickoré 4661* (MSB). Pass between Raka Tsangpo and Yarlung Tsangpo, near Tengkar (5290 m)—29° 21' N 85° 50' E. *G. & S. Miehe 03-052-09* (MR). Changthang, upper Targo Tsangpo, Tarou Shang (5060 m)—30° 05' N 86° 56' E. *G. & S. Miehe 03-102-01* (MR).—**INDIA. HIMACHAL PRADESH:** Kyung Tso, Rupshu (5030 m)—*W. Koelz 2246* (NY). Above Tsakzhun Tso, Ladakh (4877 m)—*W. Koelz 2388, 2417* (NY). Digar Polu, E Ladakh—*H. de Terra, s.n.* (NY). Serchu, Lahul, Kangra (3962 m)—*W. Koelz 5351* (NY).—**JAMMU & KASHMIR:** Tsokar lake, Rupshu (4572 m)—*R. R. Stewart 450a* (NY). Kiangchu, Rupshu (4724 m)—*W. Koelz 2124* (NY). Kargia [Kargil], Zanskar (c. 4115 m)—*W. Koelz 5536* (NY; W). Shakar,

Rangdum, Zaskar (3658 m)—*W. Koelz* 5950 (*C. melanantha* × *C. moorcroftii?*) (NY). Debring, Rupshu (4572 m)—*W. Koelz* 6555 (*C. melanantha* × *C. moorcroftii?*) (NY). Tso Kar, Rupshu (4276 m)—*W. Koelz* 6573 (NY, two sheets). Tsokar, Rupshu, Longma (4276 m)—*W. Koelz* 9863 (NY). Zaskar distr. 14 km W of Zuildo, near Rungdum (3800 m)—34° 03' N 76° 11' E. *Chadwell et al.* 166 (K). Zaskar distr. Pense-La (4176 m)—*M. Grace et al.* 159 (K). Zaskar distr. Pense-La (4115 m)—*M. Grace et al.* 174 (K). Ladakh range, Hunder to Phyang, above Hunder Dok settlement, N of Lasirmou La Pass (4923 m)—34.35818° N 77.47262° E. *M. H. Hoffmann* j259 (Herb. Hoffmann). Ladakh range, Hunder to Phyang, below S of Lasirmou La Pass (4647 m)—34.27120° N 77.52304° E. *M. H. Hoffmann* j288 (Herb. Hoffmann). Himalaya range, Tso Kar to Rumtse, S of Shingbuk La Pass (5008 m)—33.44231° N 77.95442° E. *M. H. Hoffmann* j301 (Herb. Hoffmann). Himalaya range, Tso Kar to Rumtse, S of Shingbuk La Pass (5008 m)—33.44231° N 77.95442° E. *M. H. Hoffmann* j302 (*C. melanantha* × *C. moorcroftii?*) (Herb. Hoffmann). Himalaya range, Tso Kar to Rumtse, N below Shingbuk La Pass (5033 m)—33.49109° N 77.93004° E. *M. H. Hoffmann* j312 (*C. melanantha* × *C. moorcroftii?*) (Herb. Hoffmann). Himalaya range, Tso Kar to Rumtse, pass between Shingbuk La and Kiamera La Pass (Mandalchan La) (5217 m)—33.49787° N 77.92566° E. *M. H. Hoffmann* j313 (Herb. Hoffmann). Himalaya range, Tso Kar to Rumtse, on Kiamera La Pass (5124 m)—33.53033° N 77.89625° E. *M. H. Hoffmann* j322 (*C. melanantha* × *C. moorcroftii?*) (Herb. Hoffmann). Himalaya range, Tso Kar to Rumtse, on Kiamera La Pass (5124 m)—33.53033° N 77.89625° E. *M. H. Hoffmann* j324 (Herb. Hoffmann).—**NEPAL. KARNALI:** Tingjegaon (5060 m)—*O. Polunin et al.* 1170 (NY).—**MECHI:** Taplejung distr., Kambachen to Lhonak (4690 m)—27° 44' N 88° 01' E. *S. Crawford et al.* 534 (E, K).

28. *Carex norvegica* Retz.:—**AUSTRIA. STYRIA:** In graminosis humidis ad pedem montis Kreiskogel ad Judenburg (1900 m)—*B. Przybylski, s.n.* (as *C. angarae* subsp. *pusteriana*) (GZU). Oberwölz, Halser Alpe unterhalb Plettentaler Joch (c. 1900 m)—*P. Conrath, s.n.* (as *C. angarae* subsp. *pusteriana*) (GZU). Oberwölz, Feistritz-Alm unter dem Schießbeck (c. 1950 m)—*P. Conrath, s.n.* (as *C. angarae* subsp. *pusteriana*) (GZU, two sheets). Im obersten Winterleitentale, Seetaler Alpen bei Judenburg (c. 2100 m)—*K. Pilhatsch, s.n.* (as *C. angarae* subsp. *pusteriana*) (GZU, two sheets). Seetaler Alpen: Felstriften oberhalb dem Lavantsee (2100 m)—*J. F. Widder, s.n.* (as *C. angarae* subsp. *pusteriana*) (GZU). Zirbitzkogel, Lavantseekar—*J. F. Widder, s.n.* (as *C. angarae* subsp. *pusteriana*) (GZU). Wölzer Tauern: Greimspitze bei St. Peter am Kammersberg (c. 2000 m)—*H. Melzer, s.n.* (as *C. angarae* subsp. *pusteriana*) (GZU). Seetaler Alpen: östl. des Lindersees, Rotheide (c. 1950 m)—*H. Melzer, s.n.* (as *C. norvegica* subsp. *pusteriana*) (GZU). Wölzer Tauern: westl. Umgebung der Neunkirchnerhütte, NW-Abhänge der Rettelkirchspitze (1600–2100 m)—*C. Scheuer, s.n.* (as *C. norvegica* subsp. *pusteriana*) (GZU, two sheets). Seetaler Alpen: SW oberhalb Großer Winterleitensee (c. 1900 m)—*H. Melzer, s.n.* (as *C. norvegica* subsp. *pusteriana*) (GZU). Seetaler Alps, 1.5 km NNW of Zirbitzkogel Mt. (2050–2100 m)—*B. Wallnöfer* 6900 (HAL, WU). Seetaler Alpen: am Nordfuß der Rothaide (c. 1900 m)—*H. Melzer, s.n.* (as *C. norvegica* subsp. *pusteriana*) (GZU). Seetaler Alpen: im Kar des Fuchskogels (c. 2100 m)—*H. Melzer, s.n.* (GZU).—**TYROL:** Sillian, Winnebacher Alp—*Anonymous, s.n.* (as *C. angarae* subsp. *pusteriana*) (GZU). N Tyrol, upper Inn river valley, SW slope of Serneskopf Mt. (2190–2300 m)—*B. Wallnöfer* 2658 (HAL, WU).—**ICELAND. NORÐURLAND EYSTRÁ:** E of Mývatn lake, Geiteyjarströnd SE, Dimmuborgir, Hallarflöt (c. 295 m)—65° 35' 20" N 16° 54' 30" W. *A. Buhl* 27230 (HAL, two sheets). S of Mývatn lake, Skútustaðir, southernmost pseudo-volcano NE of Verslun (c. 287 m)—65° 34' 05" N 17° 02' 20" W. *A. Buhl* 27251 (HAL).—**ITALY.**

LOMBARDIA: Sondrio, Livigno Alps (2550 m)—*A. Tribsch, s.n.* (WU).—**TRENTINO-ALTO ADIGE:** S Tyrol, Untervinschgau (2150–2200 m)—*B. Wallnöfer 7344* (HAL, WU). S Tyrol, Puster valley (2360 m)—*B. Wallnöfer 12549* (HAL, WU).—**NORWAY. NORD-TRØNDELAG:** Kongsvold (Dovrefjell) (900 m)—62° N. *C. Baenitz 5966* (as *C. alpina*) (HAL).—**OPPLAND:** Dovrefjell, Jotunheimen, below Juvasshytta (1557 m)—61° 41.836' N 08° 23.132' E. *M. H. Hoffmann a258* (Herb. Hoffmann).—**SØR-TRØNDELAG:** Dovrefjell, Knutshø, between Hjerskinn and Kongsvoll/ Drivdalen (1056 m)—62° 17.080' N 09° 37.729' E. *M. H. Hoffmann a235* (Herb. Hoffmann). Dovrefjell, Knutshø, between Hjerskinn and Kongsvoll/Drivdalen (1191 m)—62° 17.807' N 09° 38.217' E. *M. H. Hoffmann a243* (Herb. Hoffmann). Dovrefjell, between Hjerskinn and Kongsvoll/Drivdalen (925 m)—62° 16.737' N 09° 35.854' E. *M. H. Hoffmann a247* (Herb. Hoffmann).—**RUSSIA. CHUKOTKA:** W Chukotka, Anyuyskoye Nagorye, Pogyndeno—*T. M. Koroleva & V. V. Petrovsky, s.n.* (as *C. norvegica* subsp. *conicorostrata*) (M).—**MURMANSK OBLAST:** Terski distr., White Sea, Porya Guba, Bol'shoj Pedun Isl. (E part)—66.71112° N 33.64016° E. *M. N. Kozhin M-2292* (MW, digital image!). Kovdorskiy distr., SE of Rikolatva settl., Kamenistaya Mt. (c. 400–450 m)—67° 27' 38" N 31° 25' 41" E. *A. V. Kravchenko 25908* (MW, digital image!). Lovozerskiy distr., E coast of Kola Pen., N side of Ponoj River Vy (15 m)—67.09138° N 41.10995° E. *M. N. Kozhin et al. M-3464* (MW, digital image!). Lovozerskiy distr., E coast of Kola Pen., Rusinga River Vy., downstream of Levij shupash Brook (80 m)—67.13852° N 41.20895° E. *M. N. Kozhin & N. Mikhail M-3507* (MW, digital image!).—**SWITZERLAND. GRISONS:** Upper Engadine, NE of Pontresina, between Alp Languard and Piz Languard (2525 m)—46° 29.220' N 09° 56.102' E. *S. Gebauer 14085* (Herb. Gebauer). Upper Engadine, NE of Pontresina, between Alp Languard and Piz Languard (2652 m)—46° 29.183' N 09° 56.485' E. *S. Gebauer 14089* (Herb. Gebauer). Upper Engadine, NE of Pontresina, NE of Pontresina, between Alp Languard and Piz Languard (2622 m)—46° 28' 33.85" N 09° 57' 05.41" E. *S. Gebauer 140821* (Herb. Gebauer). Upper Engadine, NE of Pontresina, Piz Bernina pass (2233 m)—46° 25.198' N 10° 0.177' E. *S. Gebauer 140830* (Herb. Gebauer).

29. *Carex obscura* Nees:—BHUTAN. BUMTHANG: W side of Ura La, SE of Byakar (3500 m)—27° 27' N 90° 51' E. *A. J. C. Grierson & D. G. Long 1867* (A, K).—**CHINA. SICHUAN:** Mounixiang, Songpan Xian, W of Songpan (3345 m)—32° 39' 50.8" N 103° 30' 49.4" E. *S. Gebauer et al., SG-CN-054* (Herb. Gebauer). Ma'erkang [Barkam], Aba Xian, Mengbi Shan (3670 m)—31° 43' 11.4" N 102° 18' 01.5" E. *S. Gebauer et al., SG-CN-059* (HAL, KUN, Herb. Gebauer, three sheets).—**XIZANG:** Yache A Sang Qiao (2680 m)—*B. Qingzang 750194* (as *C. hancockiana*) (HNWP). SE Tibet, Tsangpo Vy., Nangxian–Mainling, Vy. 10 km W of Gyemdong (3580 m)—28° 57' N 93° 13' E. *B. Dickoré 10649* (MSB). SE Tibet, Tsangpo tributary, Nangxian–Mainling, Lilung Chu E branch (3900 m)—29° 01' N 93° 57' E. *B. Dickoré 10982* (MSB). SE Tibet, Gyala Peri W, Upper Bong Chu, E of pass Nyingchi–Dongjuk (4380 m)—29° 37' N 94° 41' E. *B. Dickoré 11799* (MSB). SE Tibet, India-China trading site on the border, Down Ya-Dong, Ya-Dong Co. (2700 m)—27° 22.5822' N 88° 58.5519' E. *M. Deng DM05602, DM05606* (MOR, two sheets).—**YUNNAN:** Zhongdian, valley N of Napa Hai (3370 m)—27° 54' 14" N 99° 38' 15" E. *Alpine Garden Society Expedition to China (1994) ACE 459* (E, K). Zhongdian, Geza, summit pass of Little Snow Mt. (3830 m)—28° 19' 24" N 99° 45' 80" E. *Alpine Garden Society Expedition to China (1994) ACE 518* (E, K). Gongshan, Cikai, vicinity of Cikelu Qiao, E side of Gaoligong Shan (3030 m)—27° 47' 53.2" N 98° 30' 11.8" E. *L. Heng et al. 33831* (A).—**INDIA. HIMACHAL PRADESH:** Silrundi, Sach Pass, Chamba State (3350 m)—*R. R. Stewart & I. D. Stewart 2530* (NY). Kulu, Chandarkhani (3960 m)—*W. Koelz 101* (NY), *109* (NY). Sisu [Sissu, Lahaul]

(3350 m)—*W. Koelz 633* (as *C. infusata*) (NY).—**JAMMU & KASHMIR:** Kashmir, Pahlgam (c. 3050 m)—*R. Stewart & I. D. Stewart 5603* (NY). Kashmir, Pahlgam—*R. R. Stewart & I. D. Stewart 5939* (NY). Kashmir, Pahlgam—*R. R. Stewart & I. D. Stewart 5953* (NY). Kashmir, Sonamarg (3050m)—*R. R. Stewart 7294* (NY). Kashmir, Sonamarg—*R. R. Stewart 9668a* (NY). Kashmir, Sonamarg (3350 m)—*R. R. Stewart 9868a* (mixed with *C. melanantha*) (NY). Kashmir, Khilanmarg (3200 m)—*R. R. Stewart 10500* (NY).—**NEPAL. BAGMATI:** Langtang (3658 m)—*O. Polunin 565* (NY). Oo Kharka–Mul Kharka, Chilime and Langtang Valleys (3400–3800 m)—*H. Kanai & P. R. Shakya 672183* (NY). Beding to Demdem, Dolakha distr. (3500 m)—*K. R. Rajbhandari & B. Roy 1977* (NY).—**KARNALI:** Maharigaon (4267 m)—*O. Polunin et al. 279* (NY). Sialgarhi (3050 m)—*O. Polunin et al. 997* (NY, two sheets). Ghurchi-Chuchamara, Jumla distr. (3500 m)—*K. R. Rajbhandari & B. Roy 3567* (NY).—**MECHI:** Tamur valley, Mewa Khola, Topke Gola (3810 m)—*J. D. A. Stainton 931* (NY).

30. *Carex oligantha* Steud.:—**ARMENIA. SYUNIK:** Kafansky distr., E of Kapujuh village (3200 m)—*A. L. Takhtajan & S. K. Cherepanov, s.n.* (ERE, two sheets, digital image!). Kafansky distr., Kapuzhikh village—*E. Gabrielian, s.n.* (ERE, digital image!). Kafansky distr., Kajaran, Kaputjugh Mt.—*S. Kharkevich, s.n.* (ERE, digital image!).—**RUSSIA. KABARDINO-BALKAR:** Khyzny, Khyzny-su-chirak (2600 m)—*E. & N. Bysh, s.n.* (TBI). Sukan, Sukan-bashi-ullu-chirak (2500 m)—*E. & N. Bysh, s.n.* (TBI).—**KARACHAY-CHERKESS REPUBLIC:** Rzywashka river valley, right tributary on middle reaches of river Cherek—*I. & A. Shchukin, s.n.* (MW). Karachaevskiy distr., Teberdinsky N.P., Nazalykol ravine (2600 m)—*G. A. Pokarzhevskaya, s.n.* (MW). Malokarachaevskiy distr., left basin of Tyukhan river (2520 m)—43° 29' 00" N 42° 25' 22" E. *A. S. Zernov & D. K. Tekeev 6880* (MW).—**NORTH OSSETIA-ALANIA:** N slopes of Kalperski range (2200 m)—*V. V. Shcherbakov & N. D. Filonov, s.n.* (MW).

31. *Carex parviflora* Host:—**AUSTRIA. STYRIA:** Schladminger Tauern Mts., Preunegg valley SW of Schladming (1600–1960 m)—*W. Lippert 19906* (M).—**TYROL:** Stubai Alps, N slope of Kirchdach Mt., above Trins at Gschnitz valley (c. 2600 m)—*D. Podlech 8624* (MSB). E Tyrol, St. Jakob/Defereggen, summit of Gösleswand Mt. (2912 m)—*I. Haesler 323* (M).—**BULGARIA. BLAGOEVRAD:** Pirin Mts., on the ridge of Kamenishka Kukla [Камењшкж Дял] (2650 m)—*D. Yordanov & J. Kitanov, s.n.* (as *C. pirinensis*) (SOM).—**FRANCE. AUVERGNE-RHÔNE-ALPES:** Dept. Savoyen, Col du Petit, St. Bernard (2100 m)—*G. Didier 41* (M). Dept. Savoyen, Mont Cenis area E of the reservoir lake (2400–2800 m)—*M. Röser 6481* (Herb. Röser).—**OCCITANIA:** Pyrenees, Dept. Haute-Pyrénées, Gèdre, Pic Blanc (2700 m)—*Bordère 3177* (M). Pyrenees, Dept. Haute-Pyrénées, Gèdre, Pic Blanc (2800 m)—*Bordère, s.n.* (M). Pyrenees, Dept. Haute-Pyrénées, Pic Blanc—*Bordère, s.n.* (M). Pyrenees, Dept. Haute-Pyrénées, S of Bagnères-du-Luchon, Hospice de France, below Col Venasque (2270 m)—42° 41.877' N 00° 38.454' E. *M. H. Hoffmann a120* (Herb. Hoffmann). Pyrenees, Dept. Haute-Garonne, Piau-Engaly, c. 14 km W of St. Lary-Soulan (2416 m)—42° 45.578' N 00° 7.812' E. *M. H. Hoffmann a141* (Herb. Hoffmann).—**PROVENCE-ALPES-CÔTE D'AZUR:** Dept. Hautes-Alpes, NNW of Briançon between Col de Granon and Grand Aréa (c. 2300 m)—*U. & D. Müller-Doblies 7* (B). Dept. Alpes Maritimes, Col de la Bonette between St.-Etienne-de-Tinée and Barcelonnette (2650 m)—*Th. Schauer, s.n.* (M).—**GERMANY. BAVARIA:** Steinernes Meer, close to Funtensee Alp—*A. Buhl 4467* (HAL). Berchtesgaden Alps, Totes Weib Mt.—*A. Mayer 42* (M). Berchtesgaden, plateau below Graskopf Mt., NE of Hundstod massif (c. 2000 m)—*H. Förther 4932* (M).

Hagen Mts., between Priesberg Mt.–Stiergraben–Seelein (c. 1700 m)—*F. Eberlein, s.n.* (M). Hoher Göll Mt., Hohe Brett, on summit (2300–2340 m)—*F. Eberlein, s.n.* (M). Hochkalter Mt., Steintalhörndl Mt. W side (1850 m)—*F. Eberlein, s.n.* (M). Steinernes Meer, Neuhütten Alp-W (1880 m)—*F. Eberlein, s.n.* (M). Steinernes Meer, Laubwand Mt. (c. 2300 m)—*F. Eberlein, s.n.* (M). Reiter Alp, path to Edelweißlahner Mt. (1740 m)—*W. Kortenhaus [05/1]167* (M). Reiter Alp, path to Edelweißlahner Mt. (1920 m)—*W. Kortenhaus [05/1]173* (M). Karwendel Mts., W of Karwendel pit (2200 m)—*R. Urban 4* (M). Wetterstein Mts., Höllental to Zugspitze Mt.—*R. Urban 33* (M).—**ITALY. TRENTO-ALTO ADIGE:** Ortler Mt. group, Martell valley, rock ledge at Zufall lodge (2200 m)—*J. Höller, s.n.* (M). Sextener Dolomites, Three Peaks (2400 m)—*G. Langer, s.n.* (M). Dolomites, Falzarego pass (2100 m)—*G. Langer, s.n.* (M). Pfitsch valley, Hochfinsterstern Mt.—*O. Angerer, s.n.* (M). Pfitsch valley, Großberg valley to Pfunders ridge (c. 2200 m)—*O. Angerer, s.n.* (M). Gossensaß, below Weißspitze Mt. (c. 2500 m)—*O. Angerer, s.n.* (M).—**SPAIN. HUESCA:** Benasque, subida al Posets, sendero sobre el refugio Ángel Orús (2200 m)—*P. Jiménez-Mejías et al. 412PJM05* (UPOS). Panticosa, Los Lagos—*P. Jiménez-Mejías et al. 343PJM05* (UPOS).—**SWITZERLAND. GRISONS:** Engadine, Piz Schlattain Mt.—*H. Zöttl, s.n.* (M). Ospizio Bernina, c. 0.15 km W of Alp di Lagh (2280 m)—*A. Buhl 34326* (HAL, three sheets).—**VALAIS:** Furka pass (c. 2500 m)—*J. Albrecht, s.n.* (M). Lac de Dix, S of Sion—*J. Sellmair, s.n.* (M). N of Leukerbad, SE of Daubensee lake (c. 2210 m)—*A. Buhl 41030* (HAL). NE Pontresina, Piz Languard, below Lej Languard (2622 m)—46.476069° N 09.951504° E. *S. Gebauer 140817* (Herb. Gebauer). W Poschavio, below Pass d'Ur (2495 m)—46.30052° N 09.99887° E. *S. Gebauer 140864* (Herb. Gebauer). SE Pontresina, Bernina pass, above Lago Bianco (2257 m)—46.404707° N 10.004041° E. *S. Gebauer 140870* (Herb. Gebauer).

32. *Carex peiktusani* Kom.:—CHINA. HEBEI: Eastern Tomb, Liu-li-ping-tze Shan—*H. T. Tsai 50326* (B). Eastern Tomb, Wu-ling Shan (1400 m)—*T. Tang 2062* (B).—**JAPAN. NOT LOCALIZED:** Japan [in Japanese handwriting]—25 Jul 1930. *J. Ohwi 2701, 2702* (NY, two sheets).—**HONSHU:** Shizuoka Pref., Hamamatsushi, Mizukubo-cho, Mt. Nakanone-zan (2050 m)—*T. Katsuyama, s.n.* (OKAY).—**KOREA, S. GANGWON-DO:** Pyeongchang-gun, Jinbu-myeon, Suhang-ri, Mt. Bakji (936 m)—37° 34' 21.74" N 128° 35' 56.49" E. *L. C. Shook et al. 20110622* (KB). Yeongwol-gun, Suju-myeon, Beopheung-ri, Baekdeoksan (1044 m)—37° 23' 49.8" N 128° 17' 06.1" E. *C. Mijeong et al. YR06A2006* (KB).—**GWANGJU:** Buk-gu, Geumgok-dong, Mt. Mudeung (1122 m)—35° 07' 32.63" N 127° 00' 35.07" E. *Y. Cho & H. Na WR-20130626-003* (KB).—**JEOLLABUK-DO:** Muju-gun, Seolcheon-myeon, Mt. Deogyu, Hyang Jeokbong (1580 m)—35° 51' 19.57" N 127° 44' 49.42" E. *J. H. Kim 204* (KB).

33. *Carex polymascula* P.C.Li:—CHINA. SICHUAN: Taofu (Dawo) distr., Mt. Yara [Yala], in silva Laricina (4000 m)—*H. Smith 11616* (as *C. atrata* subsp. *longistolonifera*) (UPS, digital image!). Litang-Batang, Jinsha (Yangtze) tributary E of Yidun/Yarwa, Camp 1 (3660 m)—30° 15' N 99° 25' E. *B. Dickoré 8366* (as *C. duthiei*) (MSB). Daocheng Xian, Bowa pass on road from Daocheng to Gongling (4460–4650 m)—28° 53' 57" N 100° 17' 08" E. *D. E. Boufford et al. 28285* (A). Xiangcheng Xian, between the towns of Xiangcheng and Sandui on W side of Wuming Shan (3800–4050 m)—29° 07' 40" N 99° 58' 31" E. *D. E. Boufford et al. 28634* (as *C. moorcroftii*) (A, E). Xiangcheng Xian, between the towns of Xiangcheng and Sandui on W side of Wuming Shan (3800–4050 m)—29° 07' 40" N 99° 58' 31" E. *D. E. Boufford et al. 28656* (as *C. atrata* subsp. *pullata*) (A, E). Daxue Shan, Garzê Xian, Tagong, N of Mt. Yala [Zhara Lhatse]

(4060 m)—30° 24' 59.4" N 101° 41' 48.4" E. *S. Gebauer et al.*, SG-CN-077 (HAL, KUN, Herb. Gebauer, three sheets). Daxue Shan, Garzê Xian, Tagong, NE of Mt. Yala [Zhara Lhatse], Yarıcuò Lake (4177 m)—30° 25' 00.3" N 101° 43' 01.7" E. *S. Gebauer et al.*, SG-CN-081 (HAL, KUN, Herb. Gebauer, three sheets). Daxue Shan, Garzê Xian, Garzê [Kangding], pass between Laoyulin and Xiaoyingpan, SW of Tian-hai-zhi-shan (4000 m)—29° 54' 17.9" N 102° 00' 05.3" E. *S. Gebauer et al.*, SG-CN-084 (HAL, KUN, Herb. Gebauer, three sheets).

34. *Carex popovii* V.I.Krecz.:—34a. *Carex popovii* subsp. *popovii*:—AFGHANISTAN. BADAKHSHAN: Hindukush, Panjshir valley, Darrah Rastagal, above Mukeni (2750 m)—*I. Hedge & P. Wendelbo*, W5266 (as *C. caucasica*) (E).—**IRAN. RAZAVI KHORASAN:** NE Iran, Mashhad, N slope of Binaloud, above Zoshk village (2100–3000 m)—*V. Mozaffarian*, s.n. (TARI).—**KAZAKHSTAN. SOUTH KAZAKHSTAN:** Alatau, Dzhebagly-su, lower course of Kshi-Koyanda—*M. V. Kultiasov 99* (as *C. decaulescens*) (MW, digital image!). Talaskiy-Alatau, middle reaches of Dzhebagly-su (2400 m)—*N. V. Pavlov 1049* (as *C. decaulescens*) (MW, two sheets, digital images!). Bostandyk, lower course of Maydantal, Ugam [Ugamskiy] Range, Kay-nazar-say gorge—*V. N. Pavlov 308* (as *C. decaulescens*) (MW, digital image!).—**ZHAMBYL:** Talaskiy-Alatau, Topchak-su—*N. V. Pavlov 689* (as *C. decaulescens*) (MW, digital image!).—**KYRGYZSTAN. JALAL-ABAD:** W Tian Shan, Pskemskiy Range, Sandalash (2900 m)—*V. N. Pavlov 151* (as *C. decaulescens*) (MW).—**PAKISTAN. GILGIT-BALTISTAN:** Darkot, in moist soil (3109 m)—*S. Bowes Lyon 8108B* (as *C. alsia*) (K).—**TAJIKISTAN. SUGHD:** Hissar range, N of Dushanbe, E of Pereval Anzhon Pass (3154 m)—39° 4.406' N 68° 53.276' E. *M. H. Hoffmann T/546* (Herb. Hoffmann). Hissar range, N of Dushanbe, E of Pereval Anzhon Pass (2983 m)—39° 4.226' N 68° 53.159' E. *M. H. Hoffmann T/547* (Herb. Hoffmann).—**UZBEKISTAN. TASHKENT:** Bostanliq distr., Oygaining River Vy., 7 km above Beshtor gorge—*V. N. Pavlov 37* (as *C. decaulescens*) (MW, two sheets).—**34b. *Carex popovii* subsp. *brunneola* (Kukkonen) Amini Rad:**—**IRAN. TEHRAN:** Elburz Mts., Tochal Mt. (2500–2600 m)—*M. Amini Rad & A. Torabi*, s.n. (IRAN).

35. *Carex praeclara* Nelmes:—CHINA. XIZANG: Tibet [without detailed location]—*Y. Zhang & K. Lang 2346* (KUN, digital image!). Hills S of Lhasa (4877 m)—*F. Ludlow & G. Sherriff 8797, 8797bis* (MT, two sheets, digital images!). Hills S of Lhasa (4572 m)—*F. Ludlow & G. Sherriff 9768* (MT, digital image!). Reting, 60mi N of Lhasa (4420 m)—*F. Ludlow & G. Sherriff 11135* (MT, digital image!). Dangxiong Xian, Baluotang, Nyainqentanglha Shan (5300 m)—*R.-F. Huang LG-89-160* (HNWP, two sheets). Nyainqentanglha Shan, Yangbajain–Damxung, NW of Lhasa, valley SE of Nyainqentanglha Feng (5080 m)—30° 19' N 90° 35' E. *B. Dickoré 3831* (MSB). Nyainqentanglha Shan, Yangbajain–Damxung, NW of Lhasa, valley SE of Nyainqentanglha Feng (5060 m)—30° 19' N 90° 35' E. *B. Dickoré 3853* (MSB; K, two sheets). Nyainqentanglha Shan, Yangbajain–Damxung, NW of Lhasa, S slope of Nyainqentanglha Feng (5390 m)—30° 20' N 90° 34' E. *B. Dickoré 3936* (MSB). Nagarze–Lhozak, Hill SE of Pomo Co (5240 m)—28° 28' N 90° 35' E. *B. Dickoré 9329* (MSB). Nedong–Lhünze, Upper Subansiri, Tsangpo–Subansiri pass (5020 m)—28° 38' N 92° 13'. *B. Dickoré 10398* (MSB). Nedong–Lhünze, Upper Subansiri, Tsangpo–Subansiri pass (5000 m)—28° 28' N 92° 14'. *G. Miehe & U. Wündisch 94-101-02* (MR).

36. *Carex pseudobicolor* Boeckeler:—INDIA. HIMACHAL PRADESH: Kunawur [Kinnaur], Lipa—*J. F. Royle 61* (K, digital image!). Kulu, Chandarkhani (3658 m)—*W. Koelz 252* (NY). Lahul—*W. Koelz 551, 553, 1209* (NY, three sheets). Lahul, Bara Lacha La (5029 m)—*W. Koelz 6813* (NY). Lahul, Udaipur, Gangpu Valley (3500 m)—*R. McBeath 2344A* (E).—**JAMMU & KASHMIR:** Sonamarg—*R. R. Stewart 6611* (NY). Upper end of Hushe Valley, Ghondakoro Glacier basin at the foot of the Masherbrum (c. 3960 m)—*G. L. Webster & E. Nasir 6121* (K). Rasbal, Kasturgand Mt. (c. 3600 m)—*C. C. Townsend 89/285* (K).—**PAKISTAN. ASAD KASHMIR:** Kamni pass (4115 m)—*R. R. Stewart 22661* (NY).—**GILGIT-BALTISTAN:** Burji La above Skardu (4572 m)—*R. R. Stewart 20127* (NY). Northern Areas, Bagrot Valley (3780 m)—*M. Nüsser 1228* (B). Northern Areas, middle Pattaro Valley (3950 m)—*M. Nüsser 1355* (B). Northern Areas, SW Karakoram, Gilgit, Gilgit range, upper Jutial Nala, SW of Gilgit (3700 m)—35° 51' N 74° 20' E. *B. Dickoré 12405* (MSB).

37. *Carex psychrophila* Nees:—CHINA. SICHUAN: Su-tchuen oriental., Distr. de Tchen-keou-tin [Chengkou]—*P. G. Farges, s.n.* (P, two sheets, digital images!).—**XIZANG:** Jilong Xian, Rucheng Lamamiao Shan (3700 m)—*s. coll. 317* (as and mixed with *C. duthiei* subsp. *duthiei*) (HNWP).—**INDIA. NOT LOCALIZED:** India—*J. F. Royle 111* (K, digital image!). India—Herb. of the late East Indian Company 1165, distrib. at the Royal Gardens, Kew, 1869. *Herb. H. Falconer* (M; L, digital image!). Bauhijhal (Kashmir) (1950 m)—*H. Singh & J. L. van Soest 362* (L, digital image!).—**HIMACHAL PRADESH:** Manali, Kothi (3000 m)—*G. Kirkpatrick & R. McBeath 1812* (E). Chandarkhan pass (Kulu) (3500 m)—*H. Singh & J. L. van Soest 509* (L, digital image!).—**JAMMU & KASHMIR:** Inde, Cachemyr [India, Kashmir]—Herb. E. Cosson. *V. Jacquemont 706* (P, three sheets, digital images!). Hab. Himal. Bor. Occid. Regio temp. [?Zanskar] (2438–3050 m)—Herb. Ind. Or. Hook. fil. T. Thomson. *T. Thomson, s.n.* (M; L, P, three sheets, digital images!).—**WEST BENGAL:** Phalut, Darjeeling (3000–3500 m)—*H. Hara et al. 664* (NY, two sheets; L, digital image!).—**NEPAL. GANDAKI:** Modi Khola valley from Hinko to Annapurna (3414 m)—*C. Barclay & P. M. Synge 2400* (as *C. duthiei*) (K).—**SETI:** Surmasarawar, Bajhang (2700 m)—29° 40' N 81° 02' E. *J. F. Dobremez 2133* (NY). Dhuli, Kanda (3000 m)—29° 46' N 81° 15' E. *J. F. Dobremez 2219* (E, NY).

38. *Carex sabulosa* Turcz. ex Kunth:—MONGOLIA. ARKhangai: Khangai, meadow on the slope of Egin daba [Egiyn davaa] pass, in the upper course of Chulute river—*N. Pavlov 41* (*C. melananthiformis* × *C. sabulosa*?) (NY).—**KHÖVSGÖL:** Hubsugul, Rhinchin Lhumbu, SE coast of lake Dod-Nuur—*O. V. Zhurba 849* (as *C. melanantha*) (MW, two sheets, digital images!). Hubsugul [Khövsgöl] lake, E coast against Dalayn-Kuys [Dalayn Hüy] island, sand dunes—*A. Chepurnov, s.n.* (MW, digital image!).—**ZAVKHAN:** E edge of Ubsunur depression, S Altan-Els sand, 70 km NE of Barun-Turun [Baruunturuun]—*R. V. Kamelin et al. 860* (MW, digital image!).—**RUSSIA. BURYATIA:** Lake Baikal, NE shore, Cape Turash—*M. Popov, s.n.* (LE; MW, digital image!; NY). Pribaikalsky distr., Lake Baikal, E coast, Goryachinsk, E of Cape Thin—*V. S. Sun-den-ho, s.n.* (MW, two sheets, digital images!). Mukhorshibirsky distr., 0.5 km S of the village Tsolga—*L. Abramova et al., s.n.* (MW, digital image!).—**IRKUTSK:** Balagansk distr., Baiganskoy, in sabulosis ad fl. Angara—*N. Maltsev, s.n.* (LE; MW, digital image!; NY). Lake Baikal, Aya Bay (460–650 m)—52° 47' N 106° 37' E. *H. H. Iltis et al. 240* (NY).—**KRASNOYARSK:** Prov. Jenisejsk, in sabulosis pr. urb. Minussinsk—*N. Martyanov, s.n.* (MW, digital image!).—**SAKHA (YAKUTIA):** Bulunsky distr., Czekurovka, dunes of Lena River—*V. V. Petrovsky, s. n.* (E, digital image!; JE, LE; MO, digital image!;

MW, digital image!; P, digital image!). Yakutsk, shore of river Lena, near the village Sangar-Khaya—A. B. Nikolaev, *s. n.* (MW, two sheets, digital images!).

39. *Carex serreana* Hand.-Mazz.:—CHINA. NOT LOCALIZED: [in Chinese handwriting]—X. Liu 15099 (MO, digital image!).—**GANSU:** Xi Cheng (3200 m)—38° 02' N 101° 35' E. G. Miehe 11-070-07 (MR).—**HEBEI:** Small Wutai Mts.—Anonymous 34327 (PEY, digital image!). Xiaowutai Shan Xitaigan Gou (2400 m)—*s. coll.* 763 (as *C. hancockiana*) (HNWP).—**QINGHAI:** Qilian Shan, Datong Xian, Baoku Bayanzhang (3400 m)—Z.-H. Zhang 5347 (as *C. hancockiana*) (HNWP). Qilian Shan, Daban Shan, NW of Xining (2880–3000 m)—36° 55' N 101° 19' E. G. & S. Miehe 9220/07 (MR). Huzhu Tu Aut. Co. Baishuxia (Juniper) Pass (3530 m)—37° 00' 23" N 102° 10' 40" E. D. G. Long *et al.* 1045 (as *C. gracilentia*) (E). Qilian Shan, Daban Shan, Huzhu Tu Aut. Co., N & NE-facing slopes above Baishuxia Pass (3476 m)—37° 00' 28.1" N 102° 10' 43.5" E. S. Gebauer *et al.*, SG-CN-039 (HAL, HNWP, Herb. Gebauer, three sheets).—**SHANXI:** Wutai Mts.—Anonymous 36898, 36902 (PEY, two sheets, digital images!). Ningwu Xian, Guancen Shan Shima Gou (2000 m)—*s. coll.* 15218 (as *C. hancockiana*) (HNWP).

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Scientific contributions

Publications

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Gebauer, S., Röser, M. & Hoffmann, M. H. (2015). Molecular phylogeny of the species-rich *Carex* sect. *Racemosae* (Cyperaceae) based on a combined set of four nuclear and chloroplast markers. *Systematic Botany* 40: 433–447.

Global *Carex* Group¹ (2015). Making *Carex* monophyletic (Cyperaceae, tribe Cariceae): a new broader circumscription. *Botanical Journal of the Linnean Society* 179: 1–42.

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Global *Carex* Group² (2016a). Megaphylogenetic specimen-level approaches to the *Carex* (Cyperaceae) phylogeny using barcode regions ITS, ETS, and *matK* sequences: implications for classification. *Systematic Botany* 41: 500–518.

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Global *Carex* Group³ (2016b). Specimens at the center: an informatics workflow and toolkit for specimen-level analysis of public DNA database data. *Systematic Botany* 41: 529–539.

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Chung, K.-S., Derieg, N. J., Escudero, M., Ford, B. A., **Gebauer, S.**, Gehrke, B., Hoffmann, M. H., Hoshino, T., Jiménez-Mejías, P., Jung, J., Kim, S., Luceño, M., Maguilla, E., Martín-Bravo, S., Naczi, R. F. C., Reznicek, A. A., Roalson, E. H., Simpson, D. A., Starr, J. R., Villaverde, T., Waterway, M. J., Wilson, K. L., Yano, O., Zhang, S. & Hipp, A. L.

Hoffmann, M. H., **Gebauer, S.** & von Rozycki, T. (2017). Assembly of the Arctic flora: Highly parallel and recurrent pattern in sedges (*Carex*, Cyperaceae). *American Journal of Botany* 104: 1334–1343.

Jiménez-Mejías, P., Strong, M., **Gebauer, S.**, Hilpold, A., Martín-Bravo, S. & Reznicek, A. A. (2018). Taxonomic, nomenclatural and chorological reports on *Carex* (Cyperaceae) in the Neotropics. *Willdenowia* 48: 117–124.

Conference contributions

Talks

- Gebauer, S.**, Röser, M., Starr, J. R. & Hoffmann, M. H. (2012). Why are there so few high mountain species in a highly diverse and speciose sedge group? Symposium „Evolution of Mountain Floras“, 21st International Symposium „Biodiversity and Evolutionary Biology“ of the German Botanical Society (DBG). Mainz, Germany, 16.–19.09.2012. *Abstracts*: 36 (talk MHH, SG attended).
- Hoffmann, M. H. & **Gebauer, S.** (2013). Species Recruitment and Evolution of Arctic *Carex* (Cyperaceae). Monocots V, 5th International Conference on Comparative Biology of Monocotyledons. New York, U.S.A, 07.–13.07.2013 *Abstracts*: 56-57 (talk MHH).
- Gebauer, S.**, Röser, M. & Hoffmann, M. H. (2014). Molecular phylogeny of the species-rich *Carex* L. sect. *Racemosae* G. Don (Cyperaceae). BioDivEvo 2014, Joint conference, 15th Annual Meeting of the Society of Biological Systematics (GfBS) and 22nd International Symposium „Biodiversity and Evolutionary Biology“ of the German Botanical Society (DBG). Dresden, Germany, 24.–27.03.2014. *Abstracts*: 20 (talk SG).
- Hoffmann, M. H., **Gebauer, S.**, Röser, M. & Tkach, N. (2014). Evolution of the Arctic Flora. BioDivEvo 2014, Joint conference, 15th Annual Meeting of the Society of Biological Systematics (GfBS) and 22nd International Symposium „Biodiversity and Evolutionary Biology“ of the German Botanical Society (DBG). Dresden, Germany, 24.–27.03.2014. *Abstracts*: 51-52 (talk MHH; SG attended).
- Hoffmann, M. H. & **Gebauer, S.** (2015). Convergence in sedges of the high Arctic. Botany 2015, Symposium „Ecological diversification and niche evolution in the temperate zone’s largest genus: *Carex*“. Edmonton, Canada, 24.–30.07.2015. *Abstracts* (talk MHH).

Poster presentations

- Benítez-Benítez, C., Luceño, M., **Gebauer, S.**, Hoffmann, M. H., Hipp, A. L., Masaki, T., Reznicek, A. A., Roalson, E. H., Volkova, P., Yano, O., Martín-Bravo, S. & Jiménez-Mejías, P. (2018). A black sheep in the sedges: insights on the systematics and biogeography of *Carex* sect. *Phacocystis* (Cyperaceae). Monocots VI, 6th International Conference on Comparative Biology of Monocotyledons. Natal, Brazil, 07.–12.10.2018 (presentation PJM).

Jiménez-Mejías, P., Benítez-Benítez, C., Beltrán, H., Cano, A., Donadío, S., Escudero, M., **Gebauer, S.**, Hipp, A. L., Míguez, M., Naczi, R. F. C., Reznicek, A. A., Roalson, E. H., Márquez-Corro, J. I., Villaverde, T., Dorr, L., Martín-Bravo, S. & Luceño, M. (2018). *Carex* (Cyperaceae) in South America: diversity, phylogenetics and biogeography of a Boreotemperate element in the Neotropics. Monocots VI, 6th International Conference on Comparative Biology of Monocotyledons. Natal, Brazil, 07.–12.10.2018 (presentation PJM).

Collaboration meetings

Talks

Hoffmann, M. H., **Gebauer, S.** & von Rozycki, T. (2017). Using the Global *Carex* Group megaphylogeny: the evolution and recruitment of arctic *Carex* species. Global *Carex* Group synthesis meeting 2017, The Morton Arboretum, Lisle, U.S.A, 26.–27.01.2017 (talk MHH, discussion MHH & SG).

Gebauer, S., Röser, M. & Hoffmann, M. H. (2018). Taxonomy and phylogeny of *Carex* L. sect. *Racemosae* G.Don (Cyperaceae). Institute conference “Study on the biology and sustainable development of the Qinghai-Tibetan Plateau”, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, China, 25.07.2018 (talk SG).

Curriculum vitae

Name	Sebastian Gebauer
Date, place of birth	22.06.1979, Meissen
Marital status	married
Nationality	German

School education

2005 – 2008	Secondary Education (Abendgymnasium), Dresden.
1990 – 1996	Secondary (Middle) School, Coswig.
1986 – 1990	Primary School, Coswig.

Vocational training

1996 – 1998	Assistant for Environmental Protection Technology (state certified; UTA), Technical School Pirna (BSZ für Technik), subjects: Nature conservation, Landscape management, and Environmental analyses.
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University studies

10/2008 – 09/2011	<p>Studies in Biology (BSc), Martin Luther University Halle-Wittenberg Subjects: Plant systematics, and General zoology.</p> <p>BSc thesis, Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden Supervisor: PD Dr. Matthias H. Hoffmann.</p> <p>Title: “Phylogenie von <i>Carex</i> sect. <i>Vesicariae</i> (Cyperaceae)”.</p>
10/2011 – 02/2014	<p>Studies in Biology (MSc), Martin Luther University Halle-Wittenberg Subjects: Plant systematics, Conservation biology, Plant sociology, and Agricultural biology.</p> <p>(the last two subjects, within the university network of Middle Germany, at the Friedrich Schiller University Jena, Institute of Ecology and Evolution, Professorship for Systematic Botany, Prof. Dr. Frank Hellwig, Jena).</p> <p>MSc thesis, Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden Supervisor: PD Dr. Matthias H. Hoffmann.</p>

Title: “Systematik und Evolution der *Carex* sect. *Racemosae* G.Don (Cyperaceae)”.

04/2014 – today

PhD student, Institute of Biology, Geobotany and Botanical Garden
Supervisor: PD Dr. Matthias H. Hoffmann.

Title: “Systematics, taxonomy and biogeography of species-rich groups of the genus *Carex* (Cyperaceae)”.

Scientific work experience

01/2011 – 03/2011

Research assistant (undergraduate), Martin Luther University Halle-Wittenberg Institute of Biology, Geobotany and Botanical Garden, chorology group.

06/2011 – 12/2013

Research assistant (graduate), Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden, funded by the DFG: “Taxon recruitment of the Arctic flora” (HO2213/3-1).

04/2014 – 12/2017

Research associate, Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden, funded by the DFG: “Taxon recruitment of the Arctic flora” (HO2213/3-2).

05/2018 – today

Research associate, Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden.

Grants

04/2017 – 04/2018

Graduate fellowship (State of Saxony-Anhalt).

Teaching experience

(Martin Luther University Halle-Wittenberg)

SS 2013

Co-supervision and support of a diploma thesis, title: “Phylogenetische Untersuchungen von *Carex* L. (Cyperaceae), sect. *Chlorostachyae* Meinsh., sect. *Limosae* Meinsh., sect. *Scitae* Kük.” (R. Eickner),

Co-supervision and support of a BSc thesis, title: “Morphologische Untersuchungen an *Carex acutiformis* und *Carex riparia* (Cyperaceae)” (I. Wittstock),

Co-supervision and support of a BSc thesis, title: “Phylogenie von *Carex* sect. *Foetidae*” (S. Löffler).

SS – WS 2015

Co-supervision and support of a MSc thesis, title: “Biodiversity and distribution patterns of arctic lichens and lichenicolous fungi” (E. Schröter).

SS 2013 – today

Botanical excursions (BSc students).

WS 2014 – today	Practical on methods of systematic botany (phylogenetics, comparative methods) (MSc students).
SS 2016 – today	Plant determination courses (BSc students), Practical on dissemination biology, seeds and fruits (BSc students).
<u>Non-scientific work experience</u>	
01/1996	Practical training, municipality, environment agency, Coswig (Stadtverwaltung Coswig, Umweltamt).
06/1997	Practical training, reserve administration (Reservatsverwaltung), Biosphere Reserve Oberlausitzer Heide- und Teichlandschaft, Mücka.
06/1998 – 07/1998	Practical training, municipality, environment agency, Coswig (Stadtverwaltung Coswig, Umweltamt).
11/1998 – 11/1999	Alternative service (Zivildienst), lower nature conservation authority (UNB), Meissen.
05/2000	Nursery, Gartenbaumschule & Pflanzengarten Siegfried Stübler, Steinbach (temporary).
08/2000 – 11/2001	ABS Coswig, ecological building (Ökologisches Bauen), Coswig (temporary).
10/2002 – 10/2003	Advanced training in media design, TÜV-Akademie Sachsen, Dresden; with a 3-month practical training at Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Fotoabteilung & Bildarchiv, Dresden.
08/2004 – 01/2005	Photography shop, FOTOWERKSTATT NAGEL, Friedrich-Rudolf Nagel, Torgau.
2001 – 2008	Ecological consultant, B.L.A.U., Büro für Landschaftsplanung, Artenschutz und Umweltbildung, Dipl.-Ing. Jan Blau, Dresden (part- & full-time, with interruptions).

Halle (Saale), den 19.02.2019

Sebastian Gebauer

Eigenständigkeitserklärung

Hiermit erkläre ich an Eides statt, dass die vorliegende Arbeit bisher weder der Naturwissenschaftlichen Fakultät I der Martin-Luther-Universität Halle-Wittenberg noch einer anderen Hochschule bzw. wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt worden ist. Ich erkläre, dass ich mich bisher noch nie um den Doktorgrad beworben habe. Ich erkläre weiterhin, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst habe. Ich versichere, dass ich keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen auch als solche kenntlich gemacht habe.

Halle (Saale), den 19.02.2019

Sebastian Gebauer