RESEARCH ARTICLE

Taxonomy and nomenclature of *Rubus* ser. *Glandulosi* (Rosaceae) across its Eurasian range: Revised concepts and new approaches

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Abstract *Rubus* ser. *Glandulosi* is one of the most taxonomically intricate taxa of the genus, which is by itself considered a taxonomical nightmare. Around 46 species are currently recognised in the group, but most of its morphological diversity could not be classified at the species level until recently due to unclear reproductive patterns, high genotypic diversity, low morphological differentiation among genotypes, and high phenotypic plasticity. This contribution utilises the recent findings in biosystematics of this taxon and aims at a natural classification reflecting its evolution. First, we explicitly define two different species concepts for sexual and apomictic populations. Second, we utilise microsatellite genotyping to identify widely distributed apomictic genotypes, some of which can be linked with currently recognised species. To this end, we genotyped 31 nomenclatural types and 14 "topotype" specimens or specimens of the original material. For the sexual species and apomictic microspecies whose genotypic homogeneity, considerable distribution, and identity with the nomenclatural type were studied and confirmed by genotyping, we provide morphological diagnostic characters and photographic documentation. Epitypes for the names *R. flaccidifolius*, *R. guentheri*, and *R. lusaticus* are designated. Three morphologically identifiable and molecularly characterised genotypes are described as new species – *R. coronae-aureae*, *R. divulgatus*, and *R. piceeticola*. A complete annotated checklist of currently recognised species and a simplified determination key are provided. Several older names are further proposed for exclusion due to their probably low taxonomic value.

Keywords agamospecies; apomixis; microspecies; SSR genotyping; taxonomic revision; Weberian batology

Supporting Information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

The genus *Rubus* L. is undoubtedly one of the most intricate plant taxa. Particularly in Europe, West Asia, and North America, brambles form a hardly distinguishable tangle of species, which are classified into not-quite natural series, sections, and other infrageneric taxa and informal groups. It has long been known that this taxonomic complexity is caused by a combination of several evolutionary phenomena, mainly polyploidy, apomixis (asexual reproduction via seeds), and frequent hybridisation (Gustafsson, 1942), along with a complex Quaternary history of range reductions and expansions, extinctions, and local survivals (Sochor & al., 2017). In Europe and West Asia, only five species are diploid (and thus strictly sexual). Most of the distinguished species (over 750 in Europe) are polyploid with varying degrees of facultative apomixis, which appears to be influenced by both the genotype and the environment (Šarhanová & al., 2012). Only two polyploid taxa of *R.* subg. *Rubus* probably exhibit strict sexuality in Eurasia. The first one is *R. caesius* L. (Christen, 1950; Dowrick, 1961; Kasalkheh & al., 2024), although it is often reported as an obligate apomict (Lidforss, 1914; Gustafsson, 1942; Czapik, 1981). The second one belongs to *R.* ser. *Glandulosi* (Wimm. & Grab.) Focke, in which, however, both apomictic and sexual populations have been reported with a peculiar pattern of geographic parthenogenesis (Sochor & al., 2024a).

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Rubus ser. *Glandulosi* is widely distributed from Ireland and Spain in the west to Hyrcania in the east (Juzepczuk, 1941; Kurtto & al., 2010; Sochor & al., 2024a). Only one diploid species – *R. moschus* Juz., an endemic of the western Lesser Caucasus – and one pentaploid species – *R. nigricans* Danthoine – are known in the series, other taxa are tetraploid, while penta- or hexaploidy is only occasionally reported in some specimens (Krahulcová & al., 2013; Sochor & Trávníček, 2016; Sochor & al., 2024a). In total, around 46 species of *R.* ser. *Glandulosi* are currently recognised in Europe (Kurtto & al., 2010; Ferrez & Royer, 2021; Hassler, 2024) and another 4 in West Asia (Juzepczuk, 1941), most of the European species being facultatively apomictic (Sochor & al., 2024a). A special position was chosen for *R. hirtus* s.l. It is nowadays considered a group of biotypes with dark red glands in their indumentum that do not belong to any apomictically stabilised, predominantly northwestern European microspecies (Weber, 1998; Kurtto & al., 2010). Consequently, the vast majority of individuals of *R.* ser. *Glandulosi* (including *R. hirtus* s.l., other sexuals, and unclassified apomicts) across Eurasia cannot be classified at the species rank, although these brambles dominate in many vegetation types and are even diagnostic for several phytosociological syntaxa, particularly in southern and eastern Europe (e.g., Villegas, 2004; Tzonev & al., 2006; Fascetti & al., 2013) but also in western Europe, e.g., the Senecioni ovati-Rubetum iuvenis (Haveman & al., 2014) and the Rubio hirto-pedemontani (syn. Athyrio-Rubion) and its associations (Royer & Ferrez, 2018). Taxonomic diversity in West Asia is also obscured. Since only sexual reproduction and the tetraploid level (apart from *R. moschus*) have been discovered there (Sochor & Trávníček, 2016; Kasalkheh & al., 2024; Sochor & al., 2024a), the key question remains whether the two main morphological groups (with leaves felted vs. non-felted abaxially; Juzepczuk, 1941) are one or two species and whether they can be considered taxonomically identical with some European populations.

Recently, we obtained a complex insight into evolutionary history and biosystematic patterns in *Rubus* ser. *Glandulosi* by utilisation of reproductive mode assessment, genotyping, and phylogenomic and ecological analyses (Sochor & al., 2024a,b). It was discovered that the tetraploid sexuals and apomicts exhibit parapatric geographic distributions with very limited overlap, despite their large overlap in ecological niches. This pattern is probably a result of secondary contact of the two groups (forming two or more phylogeographic lineages) during the recolonisation of central and northwestern Europe and subsequent neutral microevolutionary processes (Sochor & al., 2024a). Although some genetic differentiation between and within the reproductive groups was detected, it was caused mostly by gene-flow between apomicts and sexuals, as well as genetic introgression from many other *Rubus* taxa. The most prominent differentiation from other populations was observed in eastern Caucasian and Hyrcanian sexuals, introgressed from *R. dolichocarpus* Juz., and the apomicts, exhibiting genetic signatures of *R.* subsect. *Rubus* (so called Suberecti subgenome; Sochor & al., 2024b).

Naturally, these data should be reflected in the revised taxonomy and nomenclature of the group. In this contribution, we aim to discuss the new biosystematic findings from taxonomical perspectives and characterise species concepts and conceptions that reflect natural patterns and processes. The presented treatment covers both sexual and apomictic taxa and aims at rational, pragmatic, and evolution-based taxonomy that follows the principles of Weberian batology (Weber, 1996; Holub, 1997), taking into account the classification approach in other apomictic groups, e.g., *Taraxacum* F.H.Wigg., *Sorbus* L. (s.l.). To this end, we extended the previously published genotypic data in apomicts by additional contemporary collections, as well as 31 nomenclatural types and 14 "topotype" specimens or specimens of the original material. This enabled us not only to delimit natural entities of taxonomic value but also to link the correct names to some of the observed genotypes and exclude several other names as probably valueless (i.e., belonging to singular or local genotypes). For the apomictic microspecies whose genotypic homogeneity, considerable distribution, and identity with the nomenclatural type were studied and confirmed by genotyping (wherever possible), we provide morphological diagnostic characters and photographic documentation based on the molecularly characterised material. Three morphologically identifiable and molecularly characterised genotypes are further described as new species, one of which was initially identified as widespread by genotyping and only later was distinguished by morphology.

■ MATERIALS AND METHODS

Plant material. — The complete microsatellite dataset published in Sochor & al. (2024a) was used and supplemented by 307 presumably apomictic specimens, mostly from Czechia, Germany, France, and the United Kingdom (suppl. Table S1). Thirty-one DNA samples of available type specimens (holo-, lecto-, neo- or paratypes or their duplicates) and three specimens of original material of one name were further obtained from herbaria BR, DAO, GLM, HBG, JE, KOR, LAU, M, NMW, PRC, and WRSL or from the authors of the names. Further 13 specimens were collected at the same localities as holo-, lecto- or paratypes ("topotypes") by the authors of the names or in their presence, if they were alive during the course of the study (in other cases by the authors of this study). Eighteen specimens of the pentaploid *Rubus nigricans* were also added, including one specimen from the *locus classicus*.

Microsatellite (SSR) analysis. — Microsatellite data acquisition and analysis were performed as in Sochor & al. (2024a), that is the genomic DNA was extracted using the CTAB protocol of Doyle & Doyle (1987) and quantified with Nanodrop 2000 (Thermo Scientific, Waltham, Massachusetts, U.S.A.). Microsatellite loci amplification was performed in three multiplex reactions using Multiplex PCR Kit

(Qiagen, Hilden, Germany) with 15 ng of DNA per reaction and six, three, and two fluorescently labelled primer pairs, respectively (Graham & al., 2004, 2006; Woodhead & al., 2008). PCR products were separated on ABI 3730XL capillary sequencer by Macrogen Europe (Amsterdam, Netherlands). The protocol was modified for historical specimens with strongly fragmented DNA; the DNA isolate was purified and size-selected with Mag-Bind TotalPure NGS (Omega Bio-tek, Norcross, Georgia, U.S.A.; 1.8× of the DNA volume), 2× concentrated, and used directly for PCR, which was ten cycles longer than for the contemporary specimens.

Alleles were scored manually in PeakScanner 1.0 (Applied Biosystems, Waltham, Massachusetts, U.S.A.) and coded as the corresponding DNA fragment length. Genotype/Genodive v.2.0b23 (Meirmans & Van Tienderen, 2004) was used for genotype assignment and calculating histograms of genetic distances. The optimal threshold between within-genotype and among-genotype variation was set to 3 based on the histogram of pairwise genetic distances and careful manual evaluation of raw data. Each specimen was assigned a genotype number congruently with Sochor & al. (2024a), the distribution of each genotype was mapped and its extent was measured as a distance between the remotest localities. Subsequently, we used this data to distinguish between regionally to widely distributed apomictic genotypes and local or singular genotypes (i.e., unique in our dataset; terminology after Weber, 1996; Kurtto & al., 2010), which helped us identify genotypes of taxonomic value. Genotypic identification of nomenclatural types or 'topotypes' was used to link the respective names to the molecularly delimited genotypes. The principal coordinates analysis (PCoA) was performed in GenAlEx v.6.5 (Peakall & Smouse, 2012) using genetic distance matrix without standardisation to show genetic similarities among the genotypes. The complete data matrix of the detected alleles and genotypic assignment using different threshold distances are shown in suppl. Table S2.

Taxonomy and nomenclature. — Taxonomic and nomenclatural treatment was inferred from the reproductive data of Sochor & al. (2024a), the published genomic data of Sochor & al. (2024b), and the here-presented microsatellite data. Descriptions, photos, and drawings of apomictic taxa were based on specimens that had been genotyped by microsatellites. Descriptions and diagnostic characters were inferred from herbarium specimens of moderately sun-exposed and undamaged plants, but it should be noted that plants from dry or extremely sunny situations or other extreme habitats may differ. Full descriptions of new species were based on 15 specimens per species, and quantitative traits are shown as (minimum–)lower quartile–upper quartile(–maximum).

■ RESULTS

Genotypic diversity and distributions in the apomictic complex. — Supplementing the previously published data (Sochor & al., 2024a), our new genotypic data confirmed the occurrence of tetraploid apomictic genotypes of *Rubus* ser. *Glandulosi* in most of the territory of France and Germany, as well as in the United Kingdom and the Netherlands. Two apomictic genotypes were newly discovered in north-western Lower Austria, a region almost completely surrounded by sexual populations. Many apomictic individuals were additionally detected in the Vosges and surrounding regions, although two sexual individuals were previously found there (Fig. 1). Taking into account all demonstrably or presumably apomictic tetraploid specimens (apomixis mostly confirmed by flow cytometric seed screen and/or genotyping or presumed based on the occurrence in the regions of apomicts), 217 genotypes were distinguished in the set of 586 specimens (i.e., 94 genotypes more than in Sochor & al., 2024a). Eighty of these genotypes were detected repeatedly (at two or more localities), whereas 137 genotypes were singular (detected once in our dataset). Only 12 genotypes were detected at 10 or more localities, but 4 genotypes exhibited a distribution range larger than 500 km across, 11 genotypes exhibited a range larger than 250 km, and 39 genotypes larger than 50 km (Table 1, suppl. Table S3). The PCoA did not reveal any marked patterns in genetic similarities among genotypes (suppl. Table S2).

Genotypic identity of the nomenclatural types. — We analysed 31 type specimens, 3 specimens of the original material of 1 name, and 13 "topotypes" of 10 names. These represented 37 species names and 3 varietal names. Six of these specimens (*Rubus asper*, *R. elegans*, *R. kuenicus*, *R. kuenicus* var. *guentheri*, *R. kuenicus* var. *schleicheri*, *R. serpens*) provided no or very low-quality data (absence of signal at several loci, much noise, unclear peaks, contradictory results in technical replications) due to heavily fragmented DNA. Their genotypic identification was, therefore, considered unreliable even in the direct comparison with putatively identical contemporary specimens. Further, two specimens (*R. flaccidifolius*, *R. lusaticus*) provided relatively credible data at first glance, although with some unique alleles and missing data. However, after thorough morphological examination, this data was also considered dubious (possibly influenced by contamination with a more recent DNA from other *Rubus* specimens in herbaria), and the respective "topotypes" were accepted as more credible. All of the eight specimens with unreliable data were collected prior to 1900. Eleven nomenclatural types and eleven "topotypes" (covering 18 species names) matched some of the repeatedly detected genotypes in our sample set, the oldest of which was collected in 1876 (*R. lividus*). Other specimens were assigned to unique genotypes (Table 2).

■ DISCUSSION

Two different species concepts must be applied in *Rubus* ser. *Glandulosi*. — "What is a species?" (from a philosophical point of view) and "How can a species be defined?"

(from a biological point of view) are old questions that have provoked and will likely continue to provoke many disputes, not only among biologists with varying research focuses. Since the Modern Synthesis (Huxley, 1942), around 27 species concepts (or perhaps better, *conceptions*) have been formulated. These can be reduced into seven "basic" non-exclusive species concepts: agamospecies, biospecies, ecospecies, evolutionary species, genetic species, morphospecies, and taxonomic species (Wilkins, 2011). The prevailing definition of species in current biology is the biological species concept (Mayr, 1942), which depends on the criteria of potential interbreeding and reproductive isolation and can, therefore, be used only in sexually reproducing organisms. For asexuals, some of the other species concepts can be applied. However, their applicability in taxonomy is often questionable (for detailed reviews, see Haveman, 2013; Majeský & al., 2017).

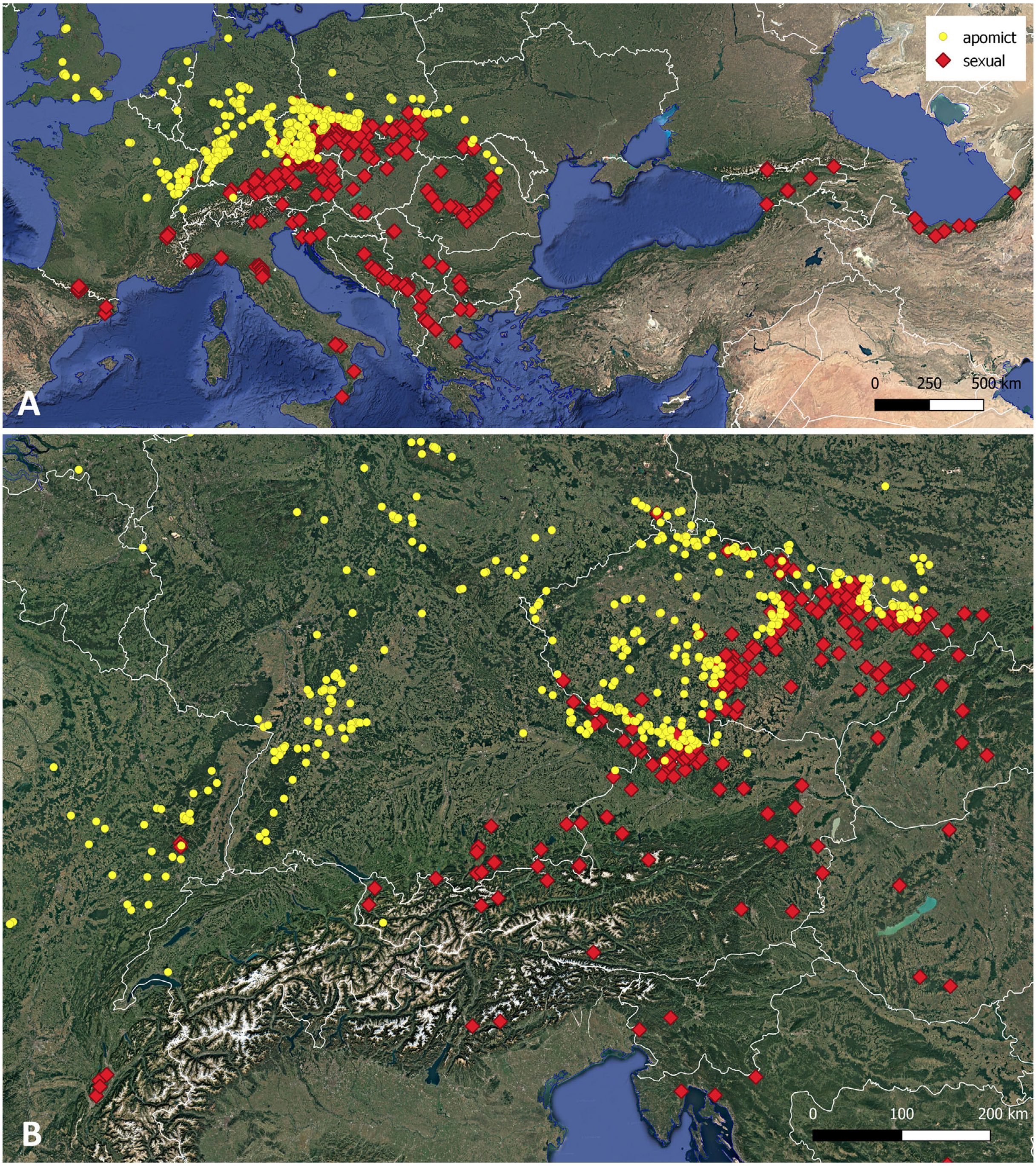

Fig. 1. Known distribution of sexual (*Rubus glandulosus*) and apomictic tetraploid populations of *R*. ser. *Glandulosi* across the total studied area (**A**) and a detailed view of the western part of Central Europe (**B**). Data was taken and updated from Sochor & al. (2024a); the background layer is from Google Earth.

The main problem is a huge diversity in evolutionary mechanisms and the resulting patterns among different genera or even within a genus. Each agamic complex, therefore, has to be approached individually, reflecting its specific nature and characteristics (Haveman, 2013). In the present authors' opinion, the primary aim of taxonomy in these taxonomically complicated groups should be to capture stable natural units that have some value for biological knowledge.

In the genus *Rubus*, a morphology-based agamospecies concept is mostly used. However, obligate sexuals (i.e., in Europe, mainly diploids such as *R. canescens* DC. and *R. ulmifolius* Schott) are treated under a biological species concept, i.e., as genetically variable units (Weber, 1996). This conceptual distinction, however, is hardly ever explicit and not always considered in *Rubus* taxonomy. Biological species exhibit much higher genetic (and thus morphological) variation than usually monoclonal apomictic microspecies. If this important difference is not considered, confusion of the two concepts frequently leads to taxonomic treatments that do not reflect biological nature of the studied system. This happens particularly in biosystematically understudied regions (cf. Van de Beek, 2021 and Sochor & al., 2022). In European brambles, the agamospecies concept has been further pragmatically adjusted to accommodate only apomictically stabilised, fertile biotypes of non-negligible age and dispersal ability, which fulfil ecological roles in local ecosystems. Such characteristics are usually reflected by the extent and density of the biotype's distribution. Consequently, the general practice, although sometimes criticised (see below), is a formal description of a species only if it has a ± continuous known distribution of at least 50 km in extent (this value is usually seen only as a guideline rather than a definite rule). This *Weberian reform* (Holub, 1997) helped to "purge" European batology considerably, making it pragmatic and usable by reducing the unmanageably high number of names, as many local biotypes of negligible importance (even if stabilised) became unclassifiable at the species level. Accidentally, it turns out that the recognised, morphologically distinguished species are monoclonal, i.e., each apomictic species is formed by a single genotype derived from a single sexual event (Nybom, 1998; Šarhanová & al., 2017; Sochor & al., 2022; this study). In rare cases, such a genotype may further diverge into morphologically distinct clonal mates via mutations, and these can be subsequently considered distinct species (Király & al., 2017). This fact means the apomictic microspecies are not only relatively easily and unambiguously identifiable by molecular methods such as traditional microsatellite analysis but are also compatible with several other species concepts, such as evolutionary (Wiley, 1978), genotypic cluster (Mallet, 1995) and phylogenetic species concept (Rosen, 1978). This makes *Rubus* microspecies relatively well-delimited natural entities.

Rubus ser. *Glandulosi*, and in particular its dominant component, "*R. hirtus*-group", has always been referred to as a conglomerate of "biotypes" (e.g., Kurtto & al., 2010; Haveman & De Ronde, 2013), implying the putative reproduction by facultative apomixis, similarly to other taxa of *Rubus* subg. *Rubus*. The apparently elevated sexuality and

Table 1. The 15 most widespread apomictic genotypes of *Rubus* ser. *Glandulosi* with the number of localities in our dataset, known geographic range (distance between the remotest genotyped samples), and taxonomic identification. For the complete table with all detected genotypes, see suppl. Table S3.

Genotype No.	Number of localities	Range [km]	Taxonomic identification
20	18	1690	*R. nigricans* Danthoine
73	18	1060	*R. angloserpens* Edees & A.Newton
16	43	1030	*R. divulgatus* Sochor
72	4	677	*R. serpens* sensu Van de Beek (2018)*
1	15	620	*R. lividus* G.Braun
3	14	485	*R. lusaticus* Rostock
263	15	464	*R. flaccidifolius* P.J.Müll.
19	2	445	Not available
142	16	423	*R. elegans* auct.*
35	11	336	*R. siemianicensis* (Sprib.) Sprib.
10	12	267	*R. exarmatus* H.E.Weber & W.Jansen
64	5	257	Not available
22	3	232	Not available
343	4	215	*R. gymnocarpus* sensu Ferrez & Royer (2021)*
17	21	192	*R. guentheri* Weihe

* Our analyses could not confirm the identity of the nomenclatural type with the respective genotype, but this name is currently used for it (see notes in Taxonomic treatment).

Table 2. List of genotyped nomenclatural types (excluding the three epitypes designated here) with their genotypic identification.

Species	Sample ID	Genotype	Type
R. angloserpens Edees & A.Newton	NMW239	73	Holotype
R. asper J.Presl & C.Presl	PRC454287	Unreliable	Lectotype
R. barberi H.E.Weber	GLM4727	5	Lectotype
R. coronae-aureae M.Lepší & P.Lepší	CB111259	69	Holotype
R. edentulus A.Beek & K.Meijer	AvdB2020.89	Unique*	"Topotype"**
R. egeniflorus Progel	M213985	Unique*	Lectotype
R. elegans P.J.Müll.	LAU0134999	Unreliable	Lectotype
R. exarmatus H.E.Weber & W.Jansen	HBG518889	10	Holotype
R. flaccidifolius P.J.Müll.	LAU0131701	Unreliable	Lectotype
R. flaccidifolius P.J.Müll.	R114/24, MS137/24	263	"Topotypes"
R. glaucinellus (Sudre) Malinv.	LAU0133995	Unique*	Isolectotype
R. hercynicus G.Braun	LD2287851	Unique	Isolectotype
R. holzfussii Sprib.	WRSL67221	Unique*	Lectotype
R. hylonomus Lefèvre & P.J.Müll.	LAU0131744	Unique	Lectotype
R. ignoratus Weber	HBG527236	Unique	Holotype
R. insidiosus Progel	M335330, M335331	Unique*	Original material
R. insidiosus Progel	M335332	Unique*	Original material
R. irroratus Progel	DAO000421712	Unique*	"Topotype"**
R. kuenicus Ant. Schott ex Utsch	LI04016601	No data	Lectotype
R. kuenicus var. *bellardii* Utsch	LI04016571	Unique*	Lectotype
R. kuenicus var. *guentheri* Utsch	LI04016588	Unreliable	Lectotype
R. kuenicus var. *schleicheri* Utsch	LI04016595	Unreliable	Lectotype
R. laetevirens Progel ex G.Braun	JE00014293	Unique*	Isotype
R. lividus G.Braun	LD2287979	1	Isolectotype
R. lucentifolius Ziel. & Kosiński	Luc_Pl10	8	"Topotype"**
R. lusaticus Rostock	GLM8796	Unreliable	Lectotype
R. lusaticus Rostock	FS5/19, FS9/19	3	"Topotypes"
R. macescens Plien.	WPl12061	274	Paratype
R. magnidentatus F.W.Sander	FS12/19, FS7/19	67	"Topotypes"**
R. melanochlamys Progel ex G.Braun	JE00014275	Unique*	Isotype
R. multisetosus Progel ex G.Braun	JE00014269	91?*	Isotype
R. nigricans Danthoine	MS267/21	20	"Topotype"
R. obscuriflorus Edees & A.Newton	NMW588	Unique	Holotype
R. ostroviensis Sprib.	WRSL67222	Unique*	Lectotype
R. perlongus H.E.Weber & W.Jansen	HBG518890	73	Holotype
R. picearum (A.Beek) A.Beek	AvdB2020.90	71	"Topotype"**
R. piceeticola M.Lepší, P.Lepší &Velebil	CB90155	82	Holotype
R. praticolor A.Beek	AvdB8/19	72	"Topotype"**
R. pseudovitis Plien.	WPl3729.n	140	Paratype
R. serpens Weihe ex Lej. & Courtois	BR5577231	Unreliable	Lectotype
R. siemianicensis (Sprib.) Sprib.	KOR29632 + KOR31414	35	Isoneotype + "topotype"

(Continues)

Table 2. Continued.

Species	Sample ID	Genotype	Type
R. urocerus Plien.	WPl6711.n	269	Paratype

Genotype numbers correspond to Sochor & al., 2024a; "unique" indicates no match with any contemporary sample; "unreliable" or "no data" indicates poor data quality due to heavily fragmented DNA. For a complete list of analysed specimens and their genotypic identifications, see suppl. Table S1.

* No other specimen identified under this name has been genotyped.

** Collected by (or in the presence of) the author of the name.

frequent hybridisation, however, did not allow for (micro)species delimitation and description except for a fraction of biotypes from northwestern Europe and adjacent parts of central Europe (Kurtto & al., 2010). Only recently, a peculiar pattern of geographic parthenogenesis has been characterised in the group (Sochor & al., 2024a). The reproductive data showed that apomixis is actually absent or rare/accidental in most populations across the series' range, whereas no strictly sexual individuals were detected approximately north and west of Bohemia (Czechia) and in Polish, Ukrainian and Romanian lowlands north and east of the Carpathians (Fig. 1). Considering the ecological and evolutionary significance of the sexual populations, it is necessary to reflect these findings in taxonomy and nomenclature, both of which have always been highly questionable. Therefore, we propose to use the biological species concept in the sexual taxon and treat it as such, whereas apomictic genotypes should be treated following agamospecies concept. A similar dual concept is already used in *R.* ser. *Discolores* (P.J.Müll.) Focke (with the diploid sexual *R. ulmifolius*) but also in *Taraxacum* (for example, with the diploid sexual *T. linearisquameum* Soest in *T.* sect. *Taraxacum* or *T. erythrospermum* Besser in *T.* sect. *Erythrosperma* (H.Lindb.) Dahlst.), or *Sorbus* subg. *Aria* Pers. (with the diploid sexual *S. aria* s.str.).

Sexual tetraploids are only one species with geographic patterns of introgression. — The extremely high morphological variability of the sexual taxon of *Rubus* ser. *Glandulosi* has resulted in the introduction of many specific and infraspecific names. Although the taxonomic value of many European "taxa" from the sexuals' range has always been considered doubtful at least (Holub, 1997), the taxonomic position of West Asian populations was far from clear and was accompanied by a lot of confusion. Above all, whitish felt on the leaf underside has always been considered a taxonomically important trait and was used to distinguish two main groups. Plants with non-felted (concolorous) leaves were treated as *R. hirtus* Waldst. & Kit., *R. serpens* Weihe and/or *R. lanuginosus* Steven ex Ser., while those with felted (discolorous) leaves as *R. caucasicus* Focke and *R. ponticus* Juz. (Juzepczuk, 1941; Gilli, 1969; Davis & Meikle, 1972). *Rubus platyphyllus* K.Koch was further treated differently in Turkish (Davis & Meikle, 1972) and Russian literature (Juzepczuk, 1925, 1941, 1952) – as the concolorous group in the former (in accordance with the holotype and protologue) and as the discolorous group in the latter. However, as the felt is often sparse and its density varies even between different leaves of the same branch, the two groups are difficult to separate unequivocally. Moreover, discolorous leaves can be observed frequently also in some regions of Europe, e.g., in Piedmont, Italy (Sochor, pers. obs.). The taxonomic value of such a trait within a genetically variable sexual taxon is, therefore, questionable.

Sochor & al. (2024b) performed a robust wide-scale analysis of evolutionary patterns using reduced representation genomic data and did not reveal any marked differentiation among geographic regions or among the morphological groups (see suppl. Fig. S1 with marked concolorous and discolorous West Asian specimens). The observed genetic variation reflected varying levels of introgression from different co-occurring diploid species but showed no differentiation expectable on the level of separate species. The introgression is presumed to be expressed in the morphology of the plants. This is probably how the white-felted plants evolved, as they occur more frequently in regions with the detected introgression from *Rubus moschus* (Western Caucasus) or *R. ulmifolius*, *R. canescens*, and *R. incanescens* Bertol. (Northern Apennines). On the other hand, the Hyrcanian population was the most prominently introgressed one (from *R. dolichocarpus* Juz., which also has whitish-felted leaves) but it mostly consisted of concolorous individuals, similarly to the Balkan population introgressed from *R. canescens*. This example shows how weakly the introgression is expressed in phenotype and thus how problematic its potential incorporation into taxonomy would be. Moreover, although the patterns of introgression are often associated with the geographical origin of the populations, they are transgressive among regions, and no clear geographic groups can be delimited. Therefore, we propose to consider the sexual across its range to be a single species with morphological and genetic variability corresponding to its sexual mode of reproduction and its complex evolutionary history. The oldest valid and legitimate name of this species known to us is *R. glandulosus* Bellardi, whose *locus classicus* in northern Italy clearly belongs to the distribution range of the sexual taxon (four individuals from its close vicinity were analysed in Sochor & al., 2024a, see suppl. Fig. S1; the lectotype itself has not been analysed for reproductive mode due to the absence of ripe fruits).

The Weberian species concept is a rational solution in the treatment of *Rubus* apomicts. — The minimal distribution area as a guideline for distinguishing between apomictic microspecies and local or singular biotypes of no taxonomic value (Weber, 1996; Holub, 1997) has been criticised by some authors as pseudoscientific and as hampering a full view of diversity in the genus. Modifications to the Weberian concept have thus emerged that advocate describing local biotypes, in extreme cases represented by only a few rametes from a single locality (Ryde, 2011; Haveman & De Ronde, 2013; Ryde & al., 2021). Such an alternative approach would be defensible in the case of evolutionarily significant narrowly endemic entities from relict localities, but hardly in partially synanthropic, evolutionarily young, and often ephemeral bramble genotypes/biotypes. Moreover, this approach is applicable only in regions with extremely low genotypic diversity, whereas in others, it would lead to a complete chaos of thousands of names. Here, we provide an example study. In our set of 586 tetraploid apomictic individuals of *Rubus* ser. *Glandulosi*, 217 genotypes were distinguished, of which 80 (forming 76.6% of the dataset) were represented by 2 or more samples but only 12 by 10 or more samples (38.5% of the dataset, but note that this proportion is likely increased by our focus on below-described new species and other morphologically well-identifiable genotypes). At the same time, the 137 singular genotypes (23.4% of the sample set) and 41 of the repeatedly detected genotypes (20.3% of the sample set) were restricted to small regions of <50 km in extent. On the other hand, 39 tetraploid genotypes from our rather limited sample set (18.0% of genotypes, forming 56.3% of the dataset) would be considered species based purely on the 50-km criterion. Although no other characteristics (such as the density of distribution) are considered in this example due to the nature of our sampling, this number is hardly manageable considering the plants' minor morphological differentiation and huge morphological plasticity. All of the individuals studied by flow cytometric seed screen (FCSS) produced viable apomictic seeds (Sochor & al., 2024a) and can be considered "stabilised", contrary to primary hybrids presumed to be mostly sexual (Gustafsson, 1943). With larger and denser sampling, the number of repeatedly detected genotypes is further expected to increase, and so is the number of unique (once detected) genotypes, particularly considering the weak yet positive correlation between relative genotypic richness and the distance from sexual populations (Sochor & al., 2024a).

A very similar situation seems to exist, e.g., in *Rubus* ser. *Pallidi* W.C.R.Watson, *R.* ser. *Hystrix* Focke and other putatively Glandulosi-derived taxa in central Europe (pers. obs.), as well as in *R.* ser. *Discolores* and its derivatives in West Asia (Kasalkheh & al., 2024). It is clear that many of such local genotypes are well stabilised by apomixis, and many may also be important in the evolution of the local/regional bramble flora and local ecosystems. However, due to the extreme difficulties in their proper morphological delimitation (caused by plasticity, high genotypic diversity and low morphological differentiation among genotypes), it seems nearly impossible to treat them as taxonomic species with any value for subsequent users of such taxonomy. The distribution range criterion, although usually accepted with certain plasticity (e.g., the 20-km minimal limit for regionally dominating types; Kurtto & al., 2010), represents an easy way of keeping the number of species at a reasonable level and, at the same time, do not neglect the natural units that are of greater importance for biological knowledge. The simplicity is both its strength and weakness. However, natural systems are not simple and all properties of each apomictic biotype should be considered before its description or non-description as a new species. This is where both the founders of Weberian batology and their opponents would probably achieve agreement. Contrary to the latter, we argue that one of the most important properties to be considered is the distribution area (not only geographical extent but also density of populations in the landscape, etc.) as it is arguably the most prominent reflection of evolutionary behaviour (especially its evolutionary age and viability) of the respective genotype.

■ TAXONOMIC TREATMENT

In the following, we provide a complete list of currently commonly accepted species of *Rubus* ser. *Glandulosi* based on Kurtto & al. (2010), Ferrez & Royer (2021), and Hassler (2024) with the revised taxonomy and nomenclature, plus several names known to us that belong to the series, but which have not been matched yet with any currently known genotype of a taxonomic value. Due to the vast number of such taxonomically unresolved names, their list can hardly ever be complete. Following the biological species concept, we recognise (A) one diploid and one tetraploid sexual species. Following the Weberian batological principles, apomictic microspecies are provisionally divided into three categories: (B) Species whose homogeneity and wide distribution are confirmed by our genotypic data; this category also includes three new species discovered during our studies. (C) Generally accepted microspecies of wide distribution, for which genotypic data is lacking or is not conclusive and which demand further analyses. As our sampling targeted mainly central Europe, this category includes mostly western European species. (D) Names relating to genotypes that we consider taxonomically valueless because of their insufficient distribution (at least until proven otherwise); in this category, we also include *R. hercynicus*, which is accepted in many literature sources and reported from central Europe (Kurtto & al., 2010), but whose isolectotype genotype did not match any contemporary specimen and whose interpretation is unclear.

Rubus ser. ***Glandulosi*** (Wimm. & Grab.) Focke in Syn. Rub. Germ.: 355. 1877 ≡ *R.* [unranked] *Glandulosi* Wimm. & Grab., Fl. Siles. 2(1): 33. 1829 – Type (designated by Weber in Abh. Westfäl. Mus. Naturk. 47(3): 356. 1985): *Rubus glandulosus* Bellardi.

Diagnostic characters. – Shrubs usually creeping to low-arching; primocane stems round, with ± dense stalked glands of different lengths and a continuous gradient from stalked glands through glandular and non-glandular acicles/pricklets to prickles; prickles thin, acicular with low widened base, mostly straight, varying in size; primocane leaves 3–5-foliolate, mostly ± dull and with scattered, ± appressed hairs adaxially; stipules thin, filiform-linear; axillar inflorescences of floricanes rather small, few-flowered, leafy, terminal inflorescences on primocanes rich, paniculate; inflorescence axis, branches and pedicels with dense long-stalked glands; petals mostly small, narrow, white; sepals spreading to erect and ± adpressed to the unripe aggregate fruit.

Distribution and ecology. – Eurasian taxon distributed from Galicia, Spain, in the west (J.A.V. Orellana, pers. comm.) to Golestan, Iran, in the east (Sochor & al., 2024a) and from Sicily, Greece and Hyrcania in the south to Denmark and southern Sweden in the north (Kurtto & al., 2010). It is associated with forest habitats (except for alluvial forests) and thus with hills and mountains, particularly in the southern part of the range. It avoids extremely dry and nutrient-poor (sandy) soils and usually also the limestone bedrock (with some exceptions, e.g., in the Balkans and some areas of the western Alps).

Notes. – Similar to other *Rubus* series, *R.* ser. *Glandulosi* is characterised primarily by morphology and has no entirely clear delimitation (Hassler, 2024). Many individuals (both apomictic and sexual) deviate more or less from the diagnostic characteristics and may be considered transient towards other series, especially *R.* ser. *Pallidi* or ser. *Hystrix*. On the other hand, due to a relatively low proportion of alleles introgressed from other ancestral *Rubus* taxa (in comparison with other series which are mixtures of ancestral genomes with no clearly prevailing one; Sochor & al., 2015, 2024b; Kasalkheh & al., 2024), it is genetically one of the most natural units in *R.* subg. *Rubus*. The relative genetic homogeneity is disrupted mainly by the Suberecti subgenome in apomicts, which is originally derived from the *R.* subsect. *Rubus* ancestor and is presumably associated with some morphological deviations. It follows that many of the untypical or transient morphotypes do not differ in their genomic composition from "typical" *Glandulosi* morphotypes. Such morphotypes may even be ancestral in the apomictic phylogeographic lineage, which only later in the Holocene evolution shifted in morphology towards the sexual taxon due to hybridisation (Sochor & al., 2024b).

A. Sexual species

1. ***Rubus moschus*** Juz. in Trudy Prikl. Bot. Selekts. 14(3): 163. 1925 – Holotype: Prope opp. Borzhom, Saliastsikhe, in silva acerosa, 15 Jul 1923, *S.V. Juzepczuk 34* (probably LE, n.v.).

Rubus moschus is illustrated in Fig. 2.

Diagnostic characters. – Usually **robust, medium- to high-arching, erect or climbing shrubs**; primocane stems **very densely covered with stellate and simple hairs, red to whitish stalked glands**, and glandular and non-glandular acicles; **prickles thin**, slender, straight and erect to slightly declinate, **mostly hidden among the glands**, stems not distinctly prickly to touch; primocane leaves almost exclusively ternate (rarely 4-foliolate), large, **glabrous and glossy above, white-felted beneath, without long simple hairs (silky to touch)**, leaflets cordate at base; **inflorescence leafy, nutant, few-flowered (c. 7–14 flowers)**; sepals long-acuminate to caudate at apex, felted and with dense long-stalked glands abaxially; petals shorter than sepals, densely short-hairy abaxially; stamens numerous, shorter than or equal to styles, with abundant pollen; stigmas and styles often pinkish to purple; aggregate fruits often large, composed of **up to 90 drupelets**.

Distribution and ecology. – *Rubus moschus* is endemic to the western Lesser Caucasus (mainly Adjara, Guria, and Samtskhe-Javakheti, probably also Imereti in Georgia and the adjacent regions of Turkey). It has not been detected in the adjacent parts of the Greater Caucasus. It occurs as a dominant shrub in *Fagus orientalis*, *Picea orientalis* and *Abies nordmanniana* forests (mainly in margins, clearings, and gaps, but also in the forest interiors), but can also be found in other forest types.

Ploidy level. – $2n = 2x = 14$ (Krahulcová & Holub, 1997; Sochor & Trávníček, 2016).

Notes. – *Rubus moschus* is one of the five extant diploid species of the Eurasian *R.* subg. *Rubus* and the only diploid in *R.* ser. *Glandulosi*. It not only participated in the Holocene evolution of polyploid brambles in the Western Caucasus (*R.* ser. *Glandulosi*, but also *R.* ser. *Discolores*), but its direct ancestor played the dominant role in the formation of the polyploid *R. glandulosus* both in Europe and West Asia (Sochor & al., 2015, 2024b; Kasalkheh & al., 2024). The preliminary observation of two morphotypes of *R. moschus* by Sochor & Trávníček (2016) was not supported by later genomic data (Sochor & al., 2024b). The variation in plant size, growth habit, and colour of glands can be ascribed to phenotypic plasticity and the environmental effects, as the two morphotypes do not differ markedly under similar conditions in cultivation (Sochor, pers. obs.).

2. ***Rubus glandulosus*** Bellardi in App. Fl. Pedem.: 24. 1792 ≡ *Rubus bellardii* Weihe in Bluff & Fingerhuth, Comp. Fl. German. 1: 688. 1825, quoad typum, non sensu auct. omn., nom. illeg. (Art. 52.1) – Lectotype (designated by Weber in Willdenowia 13: 144. 1983): [without locality and date], *Bellardi s.n.* (B barcode B -W 09894 -01 0 [image!]).

= *Rubus hirtus* Waldst. & Kit. in Descr. Icon. Pl. Hung. 2: 150. 1805 – Lectotype (designated by Weber in Feddes Repert. 109(5–6): 399. 1998): [illustration] "*Rubus hirtus*" in Waldstein & Kitaibel, Descr. Icon. Pl. Hung. 2: t. 141. 1805.

= *Rubus platyphyllus* K.Koch in Linnaea 16: 348. 1842 – **Lectotype (designated here):** Caucaus, *K. Koch s.n.* (*428*?) (B barcode B 10 0295890 [image!]).

= *Rubus caucasicus* Focke in Abh. Naturwiss. Verein Bremen 4: 183. 1874 – Lectotype (designated by Juzepczuk in

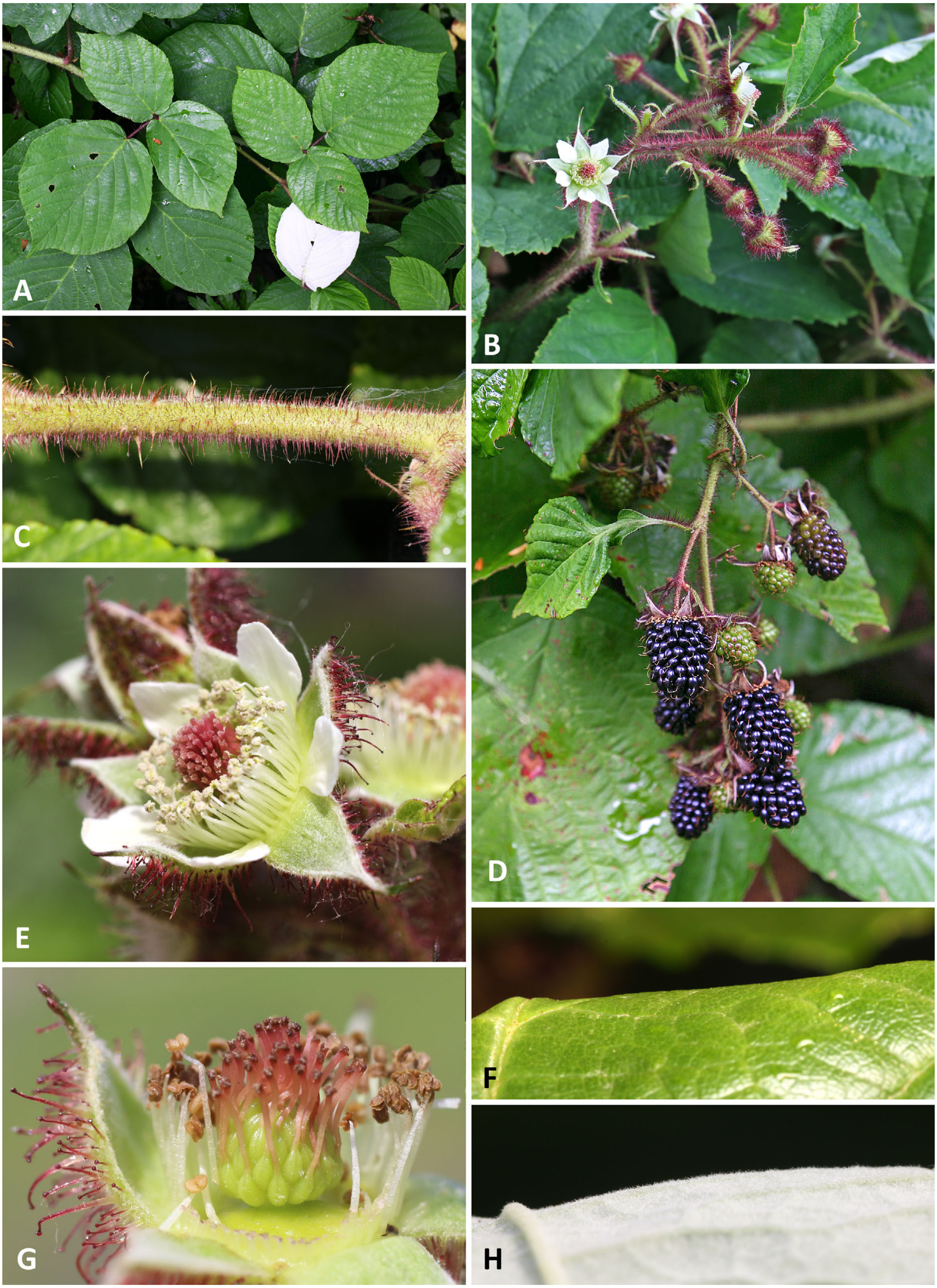

Fig. 2. *Rubus moschus*: **A**, Primocane leaves; **B**, Inflorescence; **C**, Detail of primocane stem; **D**, Infructescence with ripe fruits; **E** & **G**, Detail of flower; **F**, Detail of adaxial surface of leaf lamina; **H**, Detail of abaxial surface of leaf lamina. — From specimens *Trávníček R266/11* (B, C & E–H; origin unknown, cultivated) and *Sochor MS51/13* (A & D; Borjomi, Georgia). — Photos: M. Sochor (A–H).

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Komarov, Fl. URSS 10: 49. 1941): In regione superiori sylvaticâ Nakkerale Kachetiae, *Ruprecht s.n.* (LE?, n.v.).

= *Rubus hirtus* f. *ponticus* Focke, Sp. Rub. 3: 249. 1914 ≡ *R. ponticus* (Focke) Juz. in Komarov, Fl. URSS 10: 607. 1941 – Holotype: Caucasus, ad margines silvarum prope Alagir, 2 Jul 1899, *Markowicz, HFR No. 875* (LE?, n.v.).

Rubus glandulosus is illustrated in Fig. 3.

Diagnostic characters. – Decumbent to medium-arching shrubs; primocane stems variously covered with stellate and simple hairs, stalked glands, and glandular and non-glandular acicles; prickles usually thin, slender, straight and erect to slightly declinate; primocane leaves 3–5-foliolate, varying in size and indumentum on both adaxial and abaxial surface; inflorescence leafy, often ± nutant; sepals long-acuminate to caudate at apex, usually felted and with dense stalked glands abaxially. **Individuals within populations very variable in morphology**, with almost every individual morphologically unique; **seeds (almost) exclusively produced sexually** (reduced megagametophyte, fertilised egg cell).

Distribution and ecology. – The known distribution covers the Pyrenees, Apennines, Alps, Chartreuse Mountains, Carpathians, Bohemian Massif in Moravia, Austria, and adjacent areas of Bohemia and Bavaria (one occurrence also in Saxony), Balkans, Northern Asia Minor, Caucasus, and Hyrcania (Sochor & al., 2024a). *Rubus glandulosus* is associated predominantly with *Fagus*, *Abies*, and *Picea* forests and plantations; in higher latitudes, it can also be found in the mesophilic to thermophilic forest types (*Quercus*-, *Carpinus*-dominated forests), usually in gaps, margins and clearings and along forest roads, but also in the forest interiors in the open forest types.

Ploidy level. – $2n = 4x = 28$ (Thompson, 1995; Šarhanová & al., 2012; Kasalkheh & al., 2024; Sochor & al., 2024a).

Notes. – *Rubus glandulosus* is a very variable species (Fig. 3) due to its sexuality, introgression from many other taxa (Sochor & al., 2024b), and phenotypic plasticity. Although some individuals exhibit some characteristics of other series, most individuals within the known distribution area comply well with the diagnostic traits of *R.* ser. *Glandulosi* and can be readily determined morphologically. To determine the deviant individuals, assessing reproductive mode is usually decisive. Analysis of reproduction is also crucial for the distinction between *R. glandulosus* and most apomictic genotypes, as these two groups cannot be distinguished morphologically, apart from recognised apomictic microspecies characterised by stable combinations of characters. This fact poses a problem, particularly along the contact line between sexuals and apomicts and in regions with the lack of reproductive data (e.g., many regions of France). However, the rather distinct parapatric distribution of the two reproductive groups (Sochor & al., 2024a) makes this practical problem negligible in most regions.

The localities of the lectotypes of *Rubus glandulosus* Bellardi and *R. hirtus* Waldst. & Kit. are not known. However, their distribution as cited in the protologues, namely "Abunde nascitur in montibus vallis *Pisii* supra, & circa *Carthusiam* [the upper Pesio valley and St Mary of Pesio's Carthusian monastery]. Vidi etiam copiose nasci in monte *Bissimauda* supra *Bovisium* [Cima Besimauda above Boves]" for *R. glandulosus* and "Habitat copiosus per sylvas Croatiae, Sclavoniae, Banatus, reliquaeque Hungariae: velut in Matra Comitatus Hevesiensis, in montibus Telkebanyensibus, Ungvariensibus, Bereghiensibus, Ugotsiensibus, Bihariensibus, Baranyensibus, & in collibus humilibusque montibus Sümeghiensibus, quos sub nomine Zselitz noscunt nostrates" for *R. hirtus*, correspond with the distribution of sexual populations of *R.* ser. *Glandulosi*. Although reproductive data cannot be obtained from the lectotypes directly, their sexuality can be indirectly inferred from their geographic origin.

Nomenclatural notes. – Kováts (1992) proposed sheet XV No. 64 from the Herbarium Kitaibelianum (BP), collected by *A. Wolny 60* [without locality and date] as the lectotype of *Rubus hirtus* Waldst. & Kit. This specimen is in conflict with the protologue as already noted by Weber (1998) and this lectotypification cannot be accepted (Art. 9.19; Turland & al., 2018). Noteworthily, there is another specimen in the Kitaibel Herbarium, which fits the protologue and was probably not seen by Weber, viz. sheet XLIX. No. 11. However, because only syntype specimens have priority over illustrations for lectotype selection, the typification by Weber must be followed according to Art. 9.19.

Focke considered *Rubus glandulosus* var. *canescens* Boiss. as a synonym of *R. caucasicus* and based his description on the same two specimens as Boissier; one is probably deposited in LE, comes from Nakerala in Kakheti (probably above the upper Alazani river valley, not in Racha as was misinterpreted by Juzepczuk) and must contain primocane sections. The other specimen is deposited in G [barcode G00795305] and consists of an inflorescence, but belongs to a different taxon. Juzepczuk (1941) states about these two specimens: "Boissier included in his *R. glandulosus* var. *canescens* this species [*R. caucasicus*] and the completely different *R. ruprechtii* Juz. ined., which belongs to section *Radulae*" and apparently considered the first one to be the type. Although he did not explicitly cite any particular specimen, it is clear from the context which specimen was referred to. Therefore, we follow the interpretation of Juzepczuk and consider the specimen from Nakerala to be the lectotype.

B. Accepted and new apomictic microspecies verified by genotyping

3. ***Rubus coronae-aureae*** M.Lepší & P.Lepší, **sp. nov.** – Holotype: Bohemia meridionalis, Zlatá Koruna (dist. Český Krumlov), forest ca 690 m NNE of railway station in village, edge of *Quercus* and *Fagus* forest, 20 × 20 m, 48°51′22.8″N, 14°21′18.5″E, elev. 475 m, 8 Sep 2023, *P. Lepší SHPL/4145* (CB barcode CB/111259!, on two sheets; isotypes: LI!, PR!, PRC!, W!).

Rubus coronae-aureae is illustrated in Figs. 4 and 5; for images of the holotype, see suppl. Figs. S2 and S3.

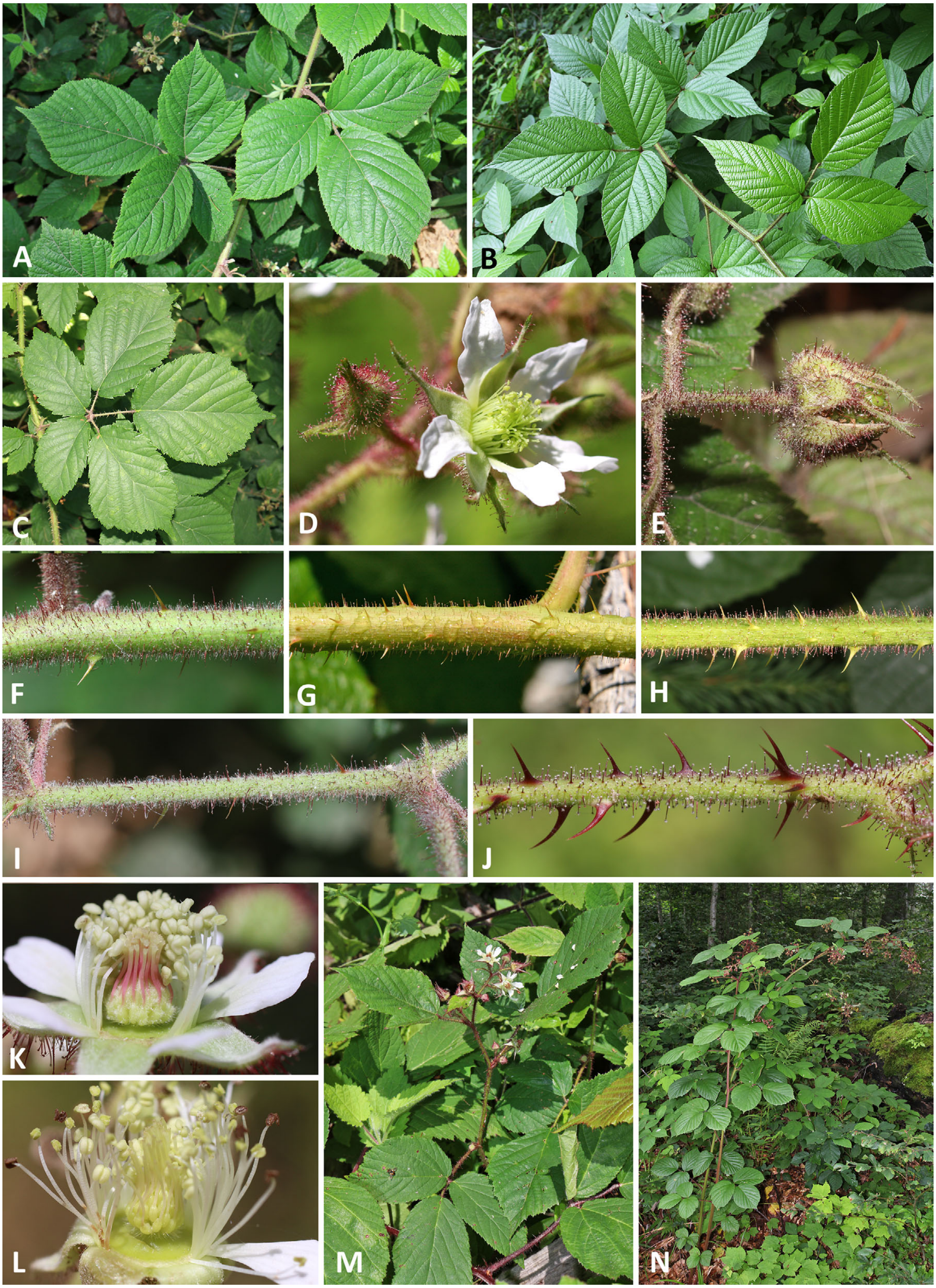

Fig. 3. *Rubus glandulosus*: **A–C**, Diversity in primocane leaf shapes; **D**, Flower; **E**, Typical pedicel and sepals adpressed to unripe fruit; **F–H**, Diversity in primocane stems; **I** & **J**, Inflorescence axis; **K** & **L**, Details of flowers with displayed carpels; **M**, Typical inflorescence; **N**, An extreme example of variability in habitus – erect stems observed in extremely wet climate in Colchis. — From populations recorded by specimens *Sochor Gla-Kop/12* (A, C, E, F, I, K & L; Olomouc, central Moravia), *Sochor MS47/14* (B & N; Chakvistavi, Adjara, Georgia), *Sochor MS450/21* (D, H & J; Těškovice, Czech Silesia), *Sochor MS46/13* (G; Mestia, Svaneti, Georgia), and an uncollected specimen from the Bílé Karpaty Mts., south-eastern Moravia (M). — Photos: M. Sochor (A–N).

Description. – Shrub up to 0.5 m tall. Primocanes mainly low-arching, rooting at apex, their stems round to bluntly angled, mostly (2.5–)3.0–4.0(–5.0) mm in diameter, grey-green, at sunny sites grey-brown-red, pruinose, densely hairy with stellate, tufted and long simple patent hairs, reaching up to the base of prickles; sessile and subsessile glands scattered; stalked glands, glandular acicles and glandular bristles abundant, unevenly long, up to (1.0–)1.3–2.0(–2.8) mm long; pricklets absent. Prickles (5–)8–11(–13) per 5 cm of stem length, ± equal, slender, straight, declining to slightly curved, (2.8–)3.1–3.7(–3.8) mm long, with flattened base (1.6–)2.1–3.4(–3.7) mm wide, yellow, at sunny sites suffused brown-red at the base, with yellowish tip. Primocane leaves ternate, convex, thin, small, dark green, matt above, hairy, with (20–)40–50(–68) hairs per 1 cm^2, green-grey beneath, pruinose, hairy to densely hairy with long patent simple hairs (indistinctly or distinctly hairy to touch). Leaflets remote from one another, the terminal one with mid-long petiolule [petiolule (28–)31–35(–40)% as long as its lamina], broadly elliptical, cordate at base, abruptly narrowing into short, (9–)11–15(–17) mm long, apex; leaflet margins flat, indentation fine, regular, crenate, with incisions (0.3–)0.6–0.8(–0.9) mm deep, teeth wider than long, apiculate, with a short and sometimes retrorse apex. Petiolules of the basal leaflets (4–)5–8(–10) mm long. Petioles usually (4.0–)4.5–6.0(–7.0) cm long, shorter than the basal leaflets, densely hairy; sessile and subsessile glands scattered; stalked glands, glandular acicles and glandular bristles abundant, unevenly long; prickles (8–)9–12(–17), straight and declining to slightly curved; stipules filiform, ca (0.5–)0.6–0.8(–0.9) mm wide, with hairs, sessile, subsessile and stalked glands. Inflorescence conical, ± rounded at apex, with erecto-patent branches, distal (3–)5–8(–12) cm long part leafless. Inflorescence leaves predominantly ternate [the uppermost 0–1(–2) leaf simple], hairy above, green-grey, slightly pruinose, sparsely to densely hairy beneath; terminal leaflets mostly broadly obovate. Inflorescence axis distinctly flexuous, felted with stellate hairs, and with abundant tufted and patent simple long hairs; sessile and subsessile glands scattered; stalked glands, glandular acicles and glandular bristles abundant, unevenly long; prickles (5–)7–10(–14) per 5 cm of axis length, ± equal, slender, straight and declining or slightly curved, (2.0–)3.1–4.3(–5.2) mm long. Pedicels (1.0–)1.3–1.7(–2.4) cm long, densely felted; stalked glands, glandular acicles and glandular bristles abundant, unevenly long, up to (0.7–)1.0–1.4(–2.1) mm long, the longest glandular acicles and glandular bristles longer than hairs; prickles (2–)5–11(–14), acicular, ± equal, slightly curved, (1.3–)1.7–2.2(–2.6) mm long. Sepals first reflexed, reflexed to erect after anthesis, (5–)6–7(–8) mm long (inclusive of the filiform appendix), abaxially green-grey with whitish felted margin, densely felted with ± stellate hairs and with scattered patent simple long hairs, with numerous stalked glands, glandular acicles and several or absent yellowish pricklets, adaxially green-grey, with green and almost glabrous base. Petals (narrowly) elliptical to (narrowly) obovate, emarginate at apex, not touching each other, (7–)9–11(–12) mm long, (4.5–)5.0–6.0 mm wide, white, glabrous above, glabrous beneath with scattered tufted hairs at base. Stamens ± as long as styles; filaments white, glabrous; anthers yellowish green, glabrous. Ovaries sparsely hairy; styles greenish yellow. Receptacle densely hairy. Aggregate fruit semiglobose. Flowering VI.

Diagnostic characters. – Primocane stems pruinose and densely hairy; primocane leaves ternate, small, hairy adaxially, pruinose, indistinctly to distinctly hairy to touch abaxially; terminal leaflet of primocane leaves broadly elliptical, abruptly narrowing into a short apex, finely and regularly crenate; inflorescences straight, conical; stamens ± as long as styles; ovaries sparsely hairy; styles greenish-yellow; receptacle densely hairy.

Etymology. – The specific name is derived from the Latin name of the village of Zlatá Koruna (*Corona Aurea*, Golden Crown), where the species was first recognised and which is in the centre of the currently known distribution of the species.

Distribution and ecology. – Currently known from ca 30 localities in southern Bohemia (Czechia) and Lower Austria (Fig. 6). The centre of distribution is in Czechia, especially in the eastern part of the Šumava foothills and the Novohradské hory foothills, but it has also been recorded in the neighbouring Třeboňská pánev basin. The distribution of the species in Czechia is delimited by the towns of Prachatice, Lišov, Nové Hrady and Vyšší Brod. In Austria, it is known only from two localities east of Gmünd. The most remote localities are 51 km distant, and the extent of occurrence (sensu IUCN, 2012) is 1214 km^2. *Rubus coronae-aureae* is a forest species which is most frequently observed at the edges of forest roads, forest fringes and clearings in conifer (*Picea abies* and *Pinus sylvestris*), broad-leaved (*Fagus sylvatica*) and mixed forest plantations.

DNA-ploidy level. – $2n = 4x$ (Sochor & al., 2024a; as Genotype 69).

Additional specimens examined (paratypes). – **AUSTRIA**. Heinrichs bei Weitra (dist. Gmünd), ca 1.1 km SW of church in village, edge of forest road in *Picea abies* plantation, medium-sized growth, 48°44′36.1″N, 14°49′26.9″E, 09 Oct 2022, *M. Lepší s.n.* (CB barcode CB/89955); Gmünd (dist. Gmünd), pagus Unterlembach, ad marginem silvae apud viam publicam, ca 1 km situ bor. a pago., 48°45′09″N, 14°53′09″E, 23 Sep 2011, *V. Žíla s.n.* (CB barcodes CB/105831, CB/105832). **CZECHIA**. Libníč (dist. České Budějovice), mezi dálnicí a asfaltovou silničkou 580 m V od sjezdu mezi obcemi Hůry a Libníč, 49°00′40″N, 14°33′05″E, 9 Oct 2021, *M. Sochor MS388/21* (OL); Libníč (dist. České Budějovice), ca 1 km SE of summit of Klauda hill, in *Quercus* and *Picea abies* mixed forest, abundant, 49°00′01″N, 14°34′54″E, 23 Oct 2022, *M. Lepší & P. Lepší s.n.* (CB barcode CB/89946); Libníč (dist. České Budějovice), ca 550 m SW of summit of Čakov hill, edge of forest road in *Picea abies* and *Quercus* forest, scattered, 49°00′52″N, 14°33′22″E, 23 Oct 2022, *M. Lepší & P. Lepší s.n.* (CB barcode CB/89944); Nové Hrady (dist. České Budějovice), Terčino údolí National Nature Monument, next to waterfall in

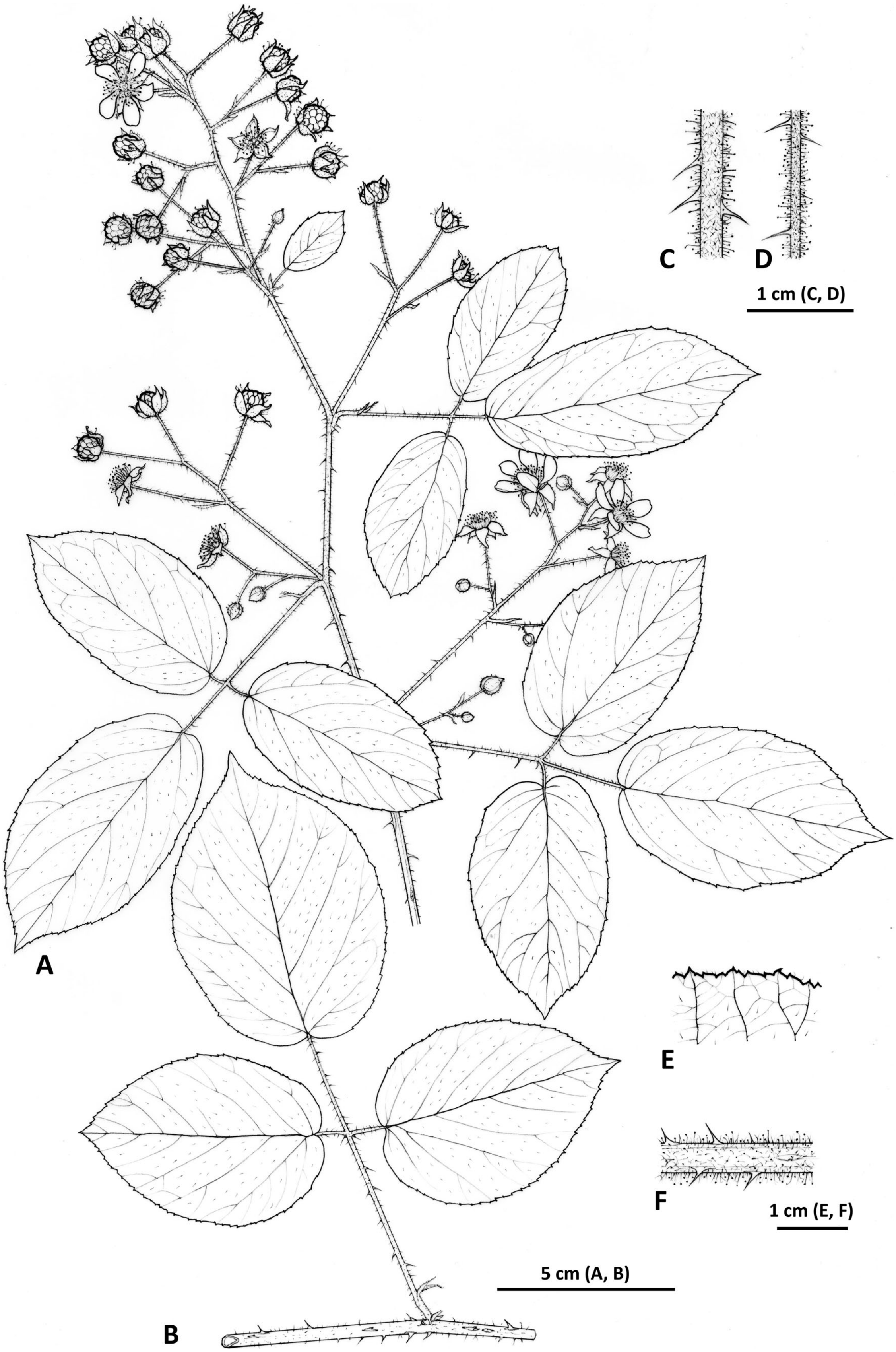

Fig. 4. *Rubus coronae-aureae*: **A**, Inflorescence; **B**, Primocane leaf; **C**, Detail of inflorescence axis; **D**, Pedicel; **E**, Margin of terminal leaflet of primocane leaf; **F**, Detail of primocane stem. — Drawn by Anna Skoumalová.

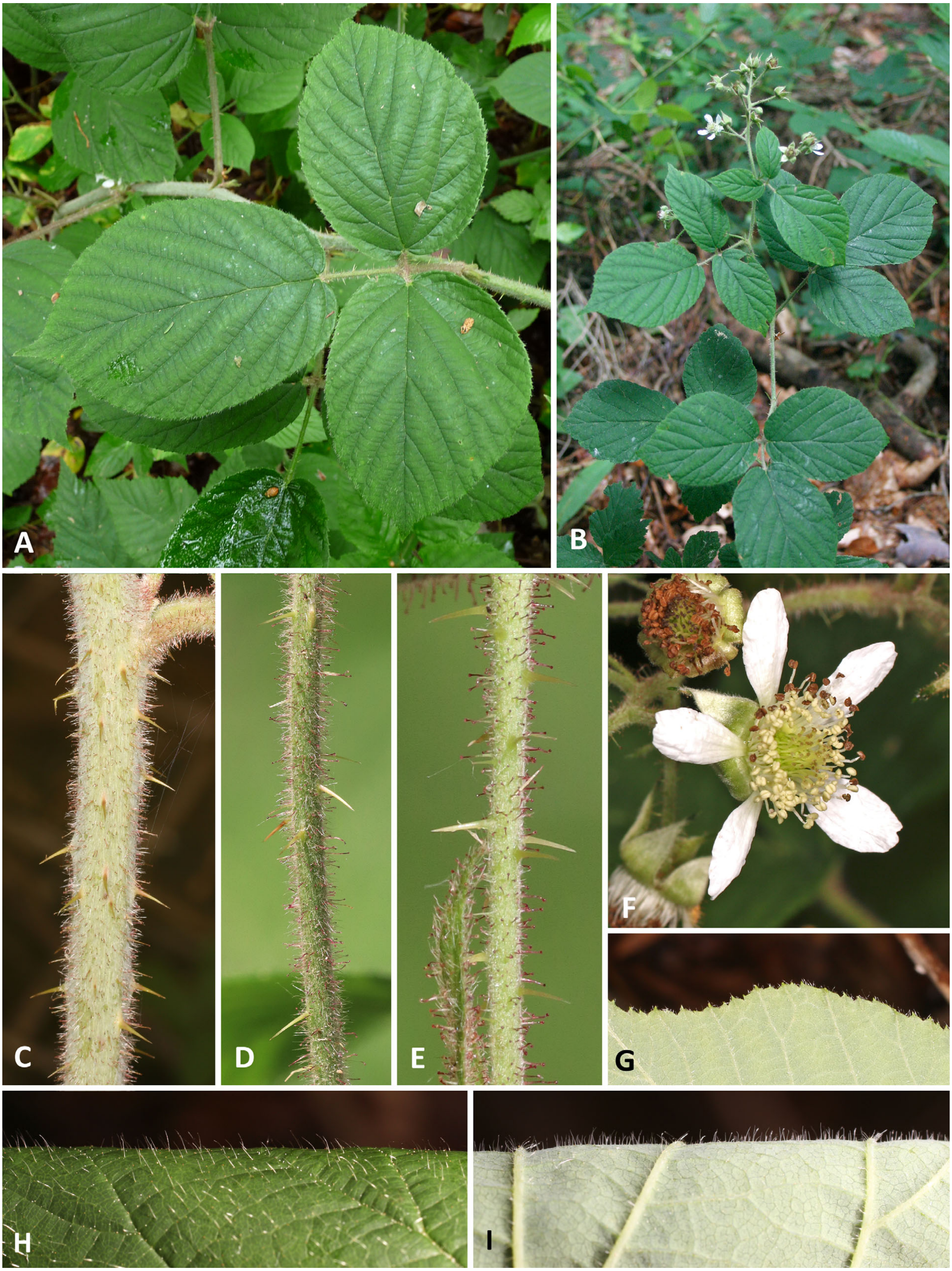

Fig. 5. *Rubus coronae-aureae*: **A**, Primocane leaf; **B**, Inflorescence; **C**, Detail of primocane stem; **D**, Inflorescence axis; **E**, Pedicel; **F**, Flower; **G**, Margin of terminal leaflet of primocane leaf; **H**, Detail of adaxial surface of terminal leaflet of primocane leaf; **I**, Detail of abaxial surface of terminal leaflet of primocane leaf. — Specimens *M. Lepší 933/20* (A, C & F–I; Zlatá Koruna, Southern Bohemia), *M. Lepší 934/20* (B, D & E; Zubčice, Southern Bohemia). — Photos: M. Lepší (A & B), M. Sochor (C & F–I), A. Lepší (D & E).

Stropnice river valley ca 510 m NNE of Cuknštejn fortress, along path in mixed forest, several ex., 48°46′47″N, 14°45′10″E, 22 Dec 2021, *P. Lepší SHPL/3993* (herb. P. Lepší); Svaryšov (dist. České Budějovice), ca 160 m NNW of summit of Výhledy hill, edge of forest clearing and *Picea abies* plantation, scattered, 48°48′12.4″N, 14°43′54.8″E, 22 Sep 2020, *M. Lepší 885/20* (CB barcode CB/87621); Svaryšov (dist. České Budějovice), paseka při cestě přes Černý les k rybníku Kartáčník, 48°47′43.7″N, 14°43′34.5″E, 14 Aug 2001, *M. Lepší 276/01* (CB barcode CB/34182); Žár (dist. České Budějovice), along road to Janovka village ca 240 m NW of summit of Výhledy hill, verge of road in forest, one small growth, 48°48′09.9″N, 14°43′45.5″E, 10 Aug 2019, *M. Lepší s.n.* (CB barcode CB/86405); Žár (dist. České Budějovice), E edge of Černý les forest ca 1.8 km SE of centre of village, along forest road, several shrubs, 48°47′43.7″N, 14°43′34.5″E, 9 Aug 2019, *M. Lepší s.n.* (CB barcode CB/86404); Český Krumlov (dist. Český Krumlov), pagus Větřní, vicus Bláha, ad marginem silvae apud viam publicam, ca 0,5 km situ occid. a vico., 48°44′44.5″N, 14°15′29.4″E, 30 Sep 2006, *V. Žíla s.n.* (CB barcodes CB/105829, CB/105830); Český Krumlov (dist. Český Krumlov), Uhlířská hájovna, při silnici vedoucí na V, 48°51′42.4″N, 14°15′46.7″E, 3 Nov 2002, *M. Lepší & K. Boublík 1329/02* (CB barcode CB/77508); Hejdlov (dist. Český Krumlov), along forest road ca 1 km NE of Kněžík hill (783 m spot height), spruce forest, small growth, 48°52′09″N, 14°15′12″E, 4 Sep 2020, *P. Lepší SHPL/3746* (CB barcode CB/104806); Hejdlov (dist. Český Krumlov), ca 1.2 km WSW of summit of U Pískovny hill, edge of forest road, large growth, 48°52′01.2″N, 14°15′13.2″E, 2 Oct 2020, *M. Lepší 932/20* (CB barcode CB/87677); Jaronín (dist. Český Krumlov), edge of forest road ca 980 m SSE of top of Vysoká Běta hill (804 m spot height), edge of road and beech forest, 2 small ex., 48°58′22″N, 14°13′06″E, 31 Aug 2022, *P. Lepší SHPL/4018* (herb. P. Lepší); Krasetín (dist. Český Krumlov), ca 1.5 km NE of summit of Kleť Mt., in *Rubus* sp. div. growth at road verge, small shrub, 48°52′23″N, 14°17′57″E, 18 Jul 2019, *M. Lepší 211/19* (CB barcode CB/86433); Lazec (dist. Český Krumlov), along forest road ca 570 m ENE of Lazecký, vrch hill (686 m spot height), edge of forest with *Betula pendula*, *Salix caprea* and *Fagus sylvatica*, one small ex., 48°50′18.8″N, 14°16′50.7″E, 12 Oct 2023, *P. Lepší SHPL/4151* (herb. P. Lepší); Lipno nad Vltavou (dist. Český Krumlov), along railway to Loučovice, ca 1 km SE of centre of dam of Lipno water reservoir, slope above railway, one shrub, 48°37′32.6″N, 14°14′44.5″E, 4 Aug 2019, *M. Lepší & P. Lepší 254/19* (CB barcode CB/86388); Loučovice (dist. Český Krumlov), ca 750 m NNE of St. Oldřich church in village, cut of railway in forest, one large growth, 48°37′32″N, 14°14′45″E, 3 Sep 2020, *M. Lepší 805/20* (CB barcode CB/87299); Nová Ves (dist. Český Krumlov), U Vacla, [ca half of the 20th century], *J. Gazda s.n.* (CB barcode CB/82197); Plešovice (dist. Český Krumlov), forest ca 430 m NW of railway stop in settlement, pine-spruce forest, several ex. on 10 × 10 m, 48°51′57″N, 14°20′45″E, 21 Oct 2021, *P. Lepší SHPL/3895* (herb. P. Lepší); Plešovice (dist. Český Krumlov), v lese při silnici do Křemže, ca 1 km SSZ kapličky, 48°52′22.9″N, 14°20′53.6″E, 5 Oct 2002, *M. Lepší 1064/02* (CB barcode CB/34132); Rychtářov (dist. Český Krumlov), ca 780 m N of summit of Albertov hill, ditch of forest road, scattered, 48°54′22.4″N, 14°12′08.5″E, 1 Jul 2021, *M. Lepší & al. 561/21* (CB barcode CB/88331); Věžovatá Pláně (dist. Český Krumlov), along forest road ca 920 m NNW of Poluška

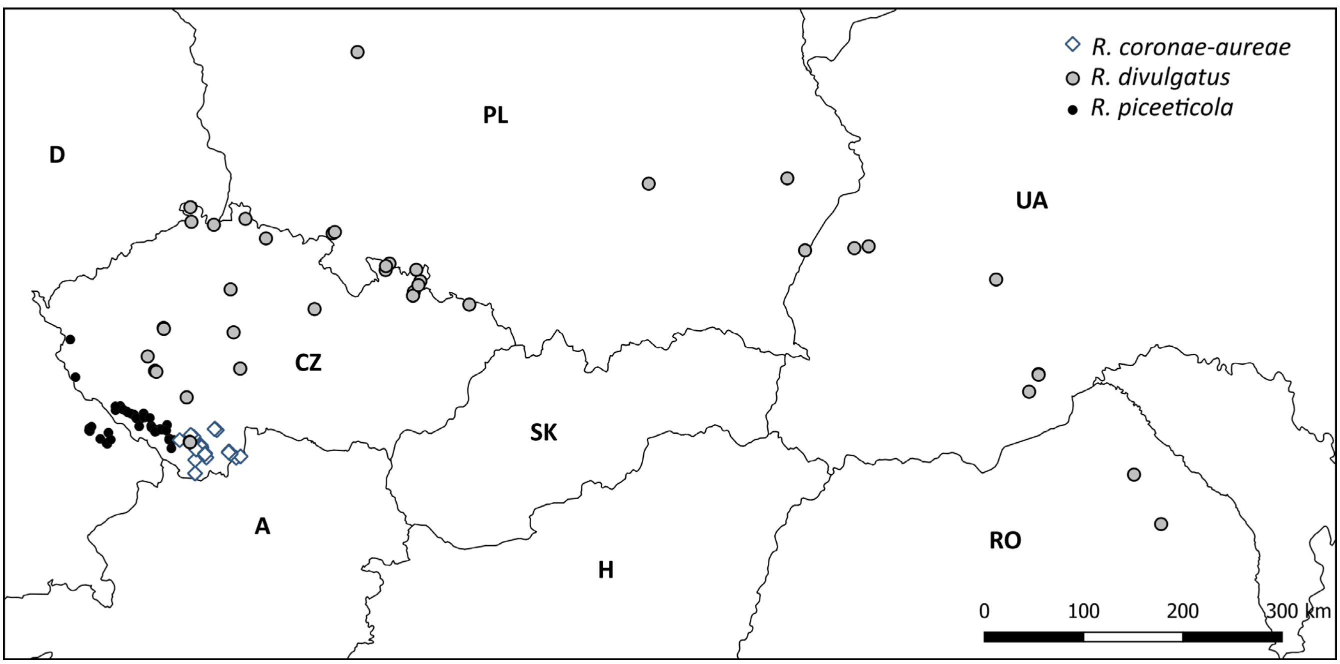

Fig. 6. Distribution of *Rubus coronae-aureae* (diamonds), *R. divulgatus* (grey circles), and *R. piceeticola* (black dots).

hill (919 m spot height), edge of road, 1 small ex., 48°45′41″ N, 14°24′52″E, 21 Oct 2023, *P. Lepší SHPL/4152* (herb. P. Lepší); Zlatá Koruna (dist. Český Krumlov), 0,3 km SZ železniční zastávky, 48°51′11.1″N, 14°20′59.5″E, 24 Oct 2002, *M. Lepší 622/02* (CB barcode CB/34129); Zlatá Koruna (dist. Český Krumlov), ca 1,7 km ZJZ železniční stanice, 48°50′ 50.9″N, 14°19′39.9″E, 24 Oct 2002, *M. Lepší 635/02* (CB barcode CB/34130); Zlatá Koruna (dist. Český Krumlov), ca 200 m NNW of train stop in village, in *Abies alba* and *Fagus sylvatica* mixed forest, several shrubs, 48°51′ 08.6″N, 14°21′02.9″E, 6 Aug 2019, *M. Lepší s.n*. (CB barcode CB/86403); Zlatá Koruna (dist. Český Krumlov), ca 200 m NNW of train stop in village, open *Pinus sylvestris* plantation, large growth, 48°51′08.8″N, 14°21′03.8″E, 2 Oct 2020, *M. Lepší 933/20* (CB barcode CB/87676); Zlatá Koruna (dist. Český Krumlov), edge of forest ca 520 m W of railway station in village, sunny edge of *Pinus* and *Picea* forest, several ex., 48°51′03.9″N, 14°20′40.6″E, 08 Sep 2023, *P. Lepší SHPL/4144* (herb. P. Lepší); Zlatá Koruna (dist. Český Krumlov), forest ca 160 m WNW of railway station in village, mixed cultural forest (*Pinus*, *Larix*, *Quercus*), abundantly, together with *R. clusii*, *R. bifrons*, *R. nessensis*, *R*. ser. *Glandulosi*, 48°51′03″N, 14°20′59″E, 08 Sep 2023, *P. Lepší SHPL/4143* (herb. P. Lepší); Zlatá Koruna (dist. Český Krumlov), forest close to parking place ca 150 m WNW of railway station in village, spruce forest, larger growth, 48°51′03″N, 14°20′58″E, 29 Jul 2022, *P. Lepší SHPL/3930* (herb. P. Lepší); Zlatá Koruna (dist. Český Krumlov), Kokotín settlement, edge of spruce forest along forest road, ca 1.42 km WNW of railway station in Zlatá Koruna village, small growth, 48°51′13″N, 14°19′59″E, 29 Jul 2022, *P. Lepší SHPL/3929* (herb. P. Lepší); Zlatá Koruna (dist. Český Krumlov), Plešovice village, forest on edge of quarry, ca 430 m NW of railway station in village, mixed forest, larger growth, 48° 51′57″N, 14°20′45″E, 29 Jul 2022, *P. Lepší SHPL/3928* (herb. P. Lepší); Zlatá Koruna (dist. Český Krumlov), při lesní cestě ca 0,3 km SSV vrchu Ohrada, 03 Nov 2002, *M. Lepší & K. Boublík 1328/02* (CB barcode CB/103825); Zlatá Koruna (dist. Český Krumlov), při lesní cestě ca 0,4 km JJV vrchu Ohrada, 03 Oct 2002, *M. Lepší & K. Boublík 1327/02* (CB barcode CB/103824); Zubčice (dist. Český Krumlov), ca 1.1 km NNE of summit of Spálený hill, in growth of pioneer woody plant at edge of forest road, scattered, 48°47′ 50.4″N, 14°23′54.6″E, 08 Oct 2020, *M. Lepší 937/20* (CB barcode CB/87672); Zubčice (dist. Český Krumlov), ca 1.4 km NNE of summit of Spálený hill, in *Pinus sylvestris* plantation, large growths, 48°47′57.5″N, 14°24′09.4″E, 08 Oct 2020, *M. Lepší 934/20* (CB barcode CB/87669); Zubčice (dist. Český Krumlov), ca 520 m NNE of summit of Spálený hill, ditch of forest road, one shrub, 48°47′29.7″N, 14°23′52.7″E, 8 Oct 2020, *M. Lepší 939/20* (CB barcode CB/87674); Chroboly (dist. Prachatice), edge of forest road ca 1.2 km SSE of railway stop Ovesné u Prachatic, edge of road in deciduous forest, small bush, 48°55′50″N, 14°03′36″ E, 17 Oct 2021, *P. Lepší & M. Lepší SHPL/3866* (CB barcode CB/105214).

4. ***Rubus divulgatus*** Sochor, **sp. nov.** – Holotype: Czechia, western Vysočina Region, Pelhřimov Dist., between Salačova Lhota and Mezilesí, at a forest road 320 m NE of the Karbanův Mlýn settlement, 49°32′07″N, 14° 57′48″E, 578 m a.s.l., 10 Jul 2024, *M. Sochor MS74/24* (OL barcode 51479!, on three sheets; isotypes: CB barcode CB/111261!, KOR No. 56274!, LI!, PR!, PRC!, W!).

Rubus divulgatus is illustrated in Figs. 7 and 8; for images of the holotype, see suppl. Figs. S4–S6.

Description. – Shrub usually up to 0.4 m tall. Primocanes creeping to low-arching, rooting at apex; stems round, (2.2–) 2.8–3.0(–4.0) mm in diameter, grey-green, at sunny sites vinaceous, whitish-pruinose, (medium to) densely hairy with stellate, tufted and long simple patent hairs (long hairs prominent to naked eye against light); sessile and subsessile glands rare; stalked glands, glandular acicles and glandular bristles abundant, unevenly long, mostly not longer than simple hairs, the longest (1.5–)2.0–2.2(–3.0) mm long, red to dark red, contrasting with pale primocane stem; pricklets scattered. Prickles (10–)11–18(–23) per 5 cm of stem length, ± equal, slender, usually straight and declining, (3.0–)3.5–4.5(–5.0) mm long, sometimes flattened at base, (1.0–)1.5–2.5(–3.5) mm wide at base, red (to yellowish-red). Primocane leaves ternate (rarely 4- to 5-foliolate), thin, dark green, matt, hairy with (28–)30–50(–84) hairs per 1 cm^2 above, greyish-green, usually thinly pruinose, sparsely hairy with long patent simple hairs on veins (roughly hairy to touch), with scattered (sub) sessile glands beneath. Leaflets remote from one another (rarely slightly overlapping); the terminal leaflet with midlong petiolule [petiolule (21–)25–31(–33)% as long as its lamina], elliptical, shallowly cordate at base, gradually to abruptly narrowing into short, ca 15 mm long apex; leaflet margins flat; indentation rough, irregular to slightly periodical, incisions 1.5–2.0(–2.5) mm deep; teeth wider than long, apiculate with a short apex; main teeth usually slightly to strongly retrorse. Petiolules of basal leaflets of ternate leaves (5–)6–9(–16) mm long. Petioles (5.0–)5.8–7.0(–8.3) cm long, shorter than basal leaflets, densely hairy, pruinose; (sub)sessile glands scattered; stalked glands, glandular acicles and glandular bristles abundant, unevenly long; prickles (4–)9–13(–23), straight and declining to slightly curved; stipules filiform, (0.2–) 0.3–0.8 mm wide, 5–8 mm from petiole base, with hairs, (sub)sessile and stalked glands. Inflorescence small, sparsely branched, mostly 5–7(–14)-flowered, with erecto-patent branches, distal (2.0–)2.5–3.5(–5.0) cm long part leafless. Inflorescence leaves predominantly ternate, uppermost 0–1(–3) leaves simple, hairy above, greyish, slightly pruinose, sparsely hairy on veins beneath, terminal leaflets narrowly elliptic to obovate. Terminal inflorescence on primocanes frequently present, rich, leafy, conical. Inflorescence axis distinctly flexuous, felted with stellate hairs, with abundant patent tufted and simple long hairs; (sub)sessile glands scattered; stalked glands, glandular acicles and glandular bristles abundant, unevenly long, mostly longer than hairs, red; prickles (4–)7–13(–22) per 5 cm of axis length, ± equal in shape,

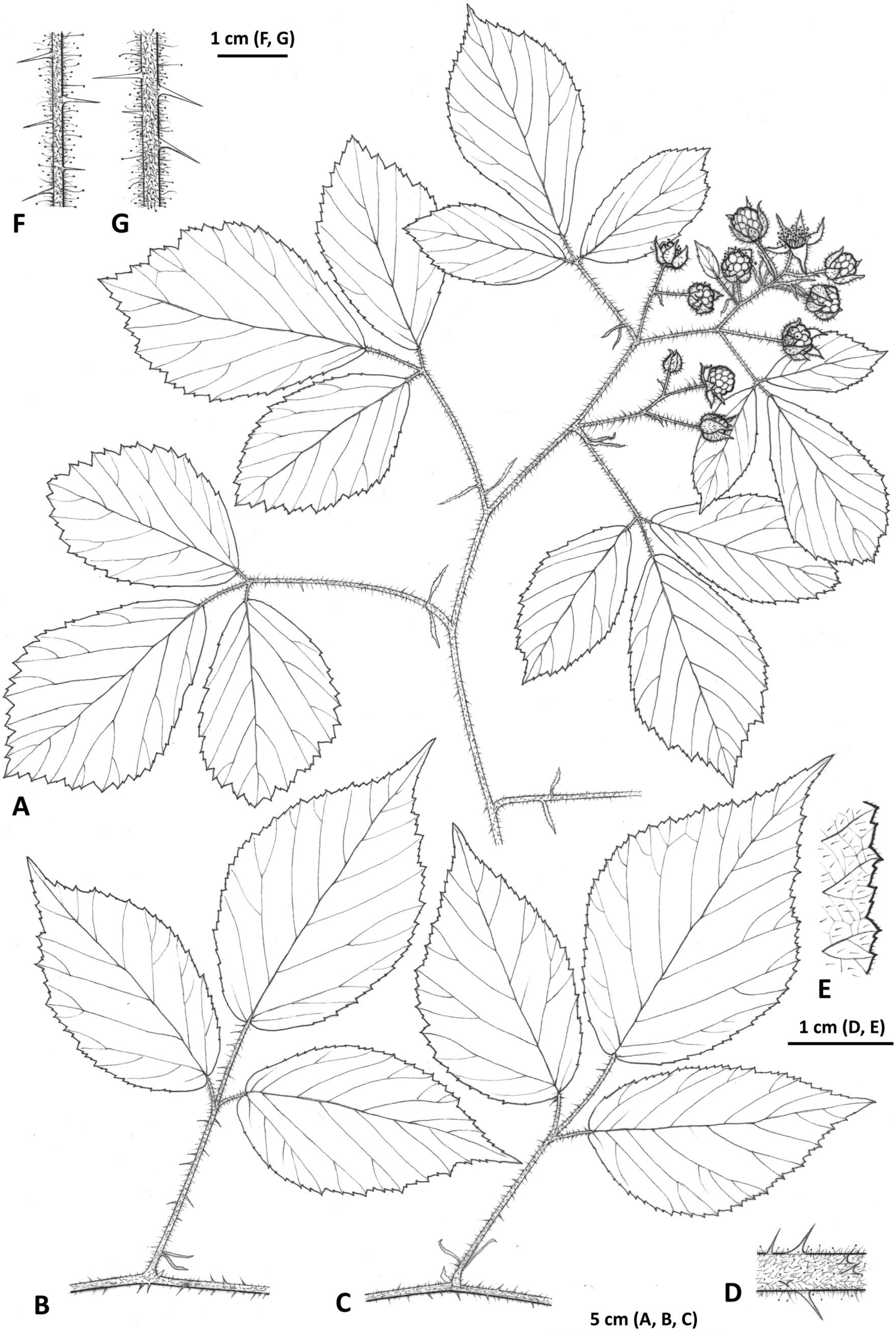

Fig. 7. *Rubus divulgatus*: **A**, Infructescence; **B** & **C**, Primocane leaves; **D**, Detail of primocane stem; **E**, Margin of terminal leaflet of primocane leaf; **F**, Detail of pedicel; **G**, Detail of inflorescence axis. — Drawn by Anna Skoumalová.

Fig. 8. *Rubus divulgatus*: **A**, Primocane leaf; **B**, Inflorescence; **C**, Detail of primocane stem; **D**, Detail of inflorescence axis; **E**, Flowers; **F**, Detail of pedicel and unripe aggregate fruit with adpressed sepals; **G**, Detail of flower with exposed carpels; **H**, Detail of adaxial side of terminal leaflet of primocane leaf; **I**, Detail of abaxial side of terminal leaflet of primocane leaf. — Specimens *Sochor MS135/22* (A, C–F, H & I) and *Sochor MS74/24* (B & G). — Photos: M. Sochor (A–I).

acicular, slender, straight and declining or slightly curved, (1.5–)2.5–3.5(–4.5) mm long, with ± gradual transition towards glandular acicles. Pedicels (0.8–)1.0–1.5(–2.0) cm long, felted with mostly short adpressed hairs; stalked glands, glandular acicles and glandular bristles abundant, unevenly long, mostly longer than hairs, the longest (1.0–) 1.8–2.1(–2.2) mm long; prickles (2–)3–6(–12), acicular, ± equal in shape, mostly straight and erect (to slightly curved), (1.5–)2.1–3.0(–3.5) mm long. Sepals reflexed or spreading during anthesis, later erect and adpressed to developing aggregate fruit, usually ± gradually tapering into the long filiform appendage, (6–)8–10(–12) mm long (including appendix), abaxially green-grey with white-felted margin, densely felted with stellate hairs and with scattered patent simple long hairs, with numerous red stalked glands, glandular acicles and several red pricklets not longer than glands, adaxially white-felted with green and (almost) glabrous base. Petals elliptical to narrowly obovate, usually irregularly shallowly notched at apex, not touching each other, (7–)8–9(–10) mm long, (2.2–)4.0(–4.5) mm wide, white, glabrous above, densely hairy beneath with short stellate hairs. Stamens shorter than styles; filaments white, glabrous; anthers cream, glabrous. Ovaries densely hairy with tufted hairs; styles deep pink to red-pink in proximal third to half; stigmas and distal part of styles yellowish. Receptacle very densely hairy with long simple hairs. Aggregate fruit semiglobose.

Diagnostic characters. – Primocane stems usually whitish-pruinose and distinctly hairy with long patent hairs; stalked glands red, contrasting with the pale stem; primocane leaves greyish-green beneath; stamens shorter than styles; styles deep pink to red-pink in the proximal third to half; sepals adpressed to unripe fruits.

Etymology. – The specific epithet *divulgatus* means (1) widespread and (2) divulged, disclosed, revealed. It reflects both the large distribution range of the species and the fact that, despite its widespread occurrence, it had remained unrecognised until molecular methods enabled its discovery.

Distribution and ecology. – Together with *Rubus anglo-serpens*, it is the most widespread tetraploid apomictic species of *R.* ser. *Glandulosi*. It is relatively common along the northern limit of *R. glandulosus* from Southern Bohemia (Czechia), through Silesia (Poland/Czechia) and Saxony to the extra-Carpathian regions of south-east Poland, western Ukraine and north-eastern Romania. A somewhat isolated locality is known near Poznań, Poland (Fig. 6). The current known range is 1030 km (measured as the distance between the remotest localities), and the extent of occurrence (sensu IUCN, 2012) is 292,239 km^2. It grows most frequently along forest roads and in clearings in broadleaf (or mixed) forests from upper lowlands and midlands (oak or hornbeam forests) to lower mountain zone (beech-fir forests).

DNA-ploidy level. – 2*n* = 4*x* (Sochor & al., 2024a; as Genotype 16).

Additional specimens examined (paratypes). – **CZECHIA**. Sázava-Sedliště (dist. Benešov), 270 m SE of the Bílý kámen hill, 49.861766°N, 14.904797°E, 25 Aug 2020, *M. Sochor MS129/20* (OL barcode 51713); between Kublov and Svatá (dist. Beroun), S of Zelený kříž junction, 49.938837°N, 13.920905°E, 09 Jul 2024, *M. Sochor MS67/24* (OL barcode 51705); Svatá (Beroun dist.), 830 m NE of Jezevčí skála, 49.930217°N, 13.923872°E, 09 Jul 2024, *M. Sochor MS69/24* (OL barcode 51704); Krasov (dist. Bruntál), 1.3 km SE of the Svoboda hill, 50.085722° N, 17.496101°E, 27 Sep 2020, *M. Sochor MS193/20* (OL barcode 51709); Brloh (dist. Český Krumlov), edge of forest road ca 560 m NE of top of Bulový hill (953 m spot height), medium-sized ex., scattered, 48°54′39.4″N, 14°11′ 48.5″E, 26 Sep 2023, *P. Lepší SHPL/4116* (herb. P. Lepší); Brloh (dist. Český Krumlov), edge of forest road ca 890 m SE of top of Bulový hill (953 m spot height), medium-sized ex., scattered, 48°54′23.1″N, 14°12′06.8″E, 05 Oct 2023, *P. Lepší SHPL/4118* (herb. P. Lepší); Brloh (dist. Český Krumlov), forest road ca 860 m ESE of Bulový hill (953 m spot height), ditch of road, large growth, 48°54′25″N, 14°12′06″E, 07 Oct 2020, *P. Lepší SHPL/3760* (herb. P. Lepší); Brloh (dist. Český Krumlov), edge of asphalt road and beech-spruce forest ca 540 m NE of top of Bulový hill (953 m spot height), growth ca 50 m long, 48°54′40.6″N, 14°11′46.1″E, 24 Jul 2024, *P. Lepší SHPL/4199* (CB; isoparatypes: BRNM, LI, M, OL barcode 52494, PR, W); Labské pískovce, Jetřichovice (dist. Děčín), 390 m SE of the Rudolfův kámen rock, 50.869727°N, 14.404356°E, 44129, *M. Sochor MS203/20* (OL barcode 51711); Kobylá nad Vidnávkou (Jeseník dist.), 350 m SW of Jahodník, 50.339936° N, 17.138234°E, 20 Jul 2024, *M. Sochor MS82/24* (OL barcode 51699); Vidnava (Jeseník dist.), E bank of the Kaolínka pond, 50.359747°N, 17.191755°E, 20 Jul 2024, *M. Sochor MS78/24* (OL barcode 51698); Jizerské hory, Hejnice (dist. Liberec), 500 m NNW of the Ořešník rock, 50.865223°N, 15.185519°E, 26 Oct 2020, *M. Sochor MS204/20* (OL barcode 51715); Písek, 100 m NW of the Jarník hill summit, 49.308817°N, 14.19048°E, 22 Aug 2020, *M. Sochor MS118/20* (OL barcode 51690); 1 km SW of top of Třemšín (Příbram dist.), 49.5598°N, 13.769137°E, 07 Jul 2024, *M. Sochor MS63/24* (OL barcode 51703); 940 m SW of top of Třemšín (Příbram dist.), 49.560801°N, 13.76849°E, 07 Jul 2024, *M. Sochor MS62/24* (OL barcode 51701); Roželov (Příbram dist.), in front of the castle, 49.551737°N, 13.786271°E, 08 Jul 2024, *M. Sochor MS64/24* (OL barcode 51700); Mirošov (Rokycany dist.), N bank of Cihelský rybník, 49.69231°N, 13.675431°E, 10 Jul 2024, *M. Sochor MS73/24* (OL barcode 51706). **GERMANY**. Saxony, Hain, 700 m NNW of the view tower on top of Hochwald, 50.831611°N, 14.724833°E, 07 Aug 2022, *M. Sochor MS135/22* (OL barcode 51707). **POLAND**. Lublin Voivodeship, Zwierzyniec, 2 km NE of Zalew Rudka, 50.625071°N, 23.004423°E, 17 Sep 2020, *M. Sochor MS169/20* (OL barcode 51714); Silesia, Trzebina, at a forest road SE of Zbylut W of the village, 50.279965°N, 17.563362°E, 23 Jun 2024, *M. Sochor MS55/24* (OL barcode 51702); Świętokrzyskie Voivodeship, Złota Woda, 1.4 km W of the village, 50.779846°N, 21.02425°E, 18 Sep 2020, *M. Sochor MS180/20* (OL barcode 51617); Wielkopolska Province, Kórnik District, 1.2 km S of Borówiec, 52.263333°N, 17.027083°E, 27 Sep 2020, *P. Kosiński s.n.* (OL barcode 51697); Województwo Podkarpackie, Korczowa, between roads 94 and A4, 1 km NW of the village centre (church), 49.964709°N, 23.071301°E, 14 Sep 2021, *M. Sochor MS317/21* (OL barcode 51696). **ROMANIA**. Judeţul Iasi, Hârlău, 200 N of Mănăstirea Sângeap - Basaraba, 47.404122°N, 26.880271°E, 17 Sep 2021, *M. Sochor MS341/21* (OL barcode 51708); Judeţul Neamţ, at DN15D just NW of Bughi, 46.916778°N, 27.080434°E, 18 Sep 2021, *M. Sochor MS343/21* (OL barcode 51691). **UKRAINE**. Cherniveska Oblast, Korostuvata, 650 m E of the church, 48.334773°N, 25.743309°E, 16 Sep 2021, *M. Sochor MS332/21* (OL barcode 51710); Cherniveska Oblast, Malyi Kuchuriv, 1.1 km E of the church, 48.465075°N, 25.919846°E, 16 Sep 2021, *M. Sochor MS330/21* (OL barcode 51712); Cherniveska Oblast, Malyi Kuchuriv, 1.2 km ENE of the church, 48.47041°N, 25.920859°E, 16 Sep 2021, *M. Sochor MS327/21* (OL barcode 51693); Cherniveska Oblast, Malyi Kuchuriv, 1.2 km ENE of the church, 48.470495°N, 25.920706°E, 16 Sep 2021, *M. Sochor MS327/21b* (OL barcode 51694); Lvivska Oblast, Briukhovychi, just S of the cemetery E of the town, 49.89589°N, 23.965583°E, 15 Sep 2021, *M. Sochor MS323/21* (OL barcode 51716); Lvivska Oblast, Stradch, at the former arboretum, 49.90379°N, 23.762523°E, 15 Sep 2021, *M. Sochor MS321/21* (OL barcode 51695); Termopilska Oblast, at the restaurant between Volia and Druzhba, 49.377524°N, 25.62768°E, 15 Sep 2021, *M. Sochor MS326/21* (OL barcode 51692).

5. ***Rubus piceeticola*** M.Lepší, P.Lepší & Velebil, **sp. nov.** – Holotype: Southern Bohemia, Volary (dist. Prachatice), ca 360 m SW of summit of Vysoký les hill, edge of forest road in spruce forest, growth of ca 150 square meters, 48° 56′16.1″N, 13°54′54.4″E, elev. 880 m, 8 Aug 2024, *M. Lepší & P. Lepší 177/24* (CB barcode CB/90155!, on two sheets; isotypes: LI!, OL barcode 52493!, PR!, PRA!, PRC!, W!).

Rubus piceeticola is illustrated in Figs. 9 and 10; for images of the holotype, see suppl. Figs. S7 and S8.

Description. – Shrub up to 0.7 m tall. Primocanes mainly low-arching, rooting at apex; their stems round to bluntly angled, mostly (3.0–)4.5–5.5(–6.0) mm in diameter, grey-brown or grey-green, at sunny sites reddish or vinaceous, slightly pruinose, densely hairy, mainly with tufted and long simple patent hairs, with rare stellate hairs, reaching up to the base of prickles; sessile and subsessile glands scattered; stalked glands, glandular acicles and glandular bristles abundant, unevenly long, up to (1.3–)1.8–2.7(–3.3) mm long; pricklets rare. Prickles (19–)22–28(–34) per 5 cm of stem length, ± equal, slender, straight and declining to slightly curved, (3.5–)4.4–5.2(–6.7) mm long, with flattened base (1.5–)2.4–3.1(–4.0) mm wide, yellow to ochre, at sunny sites suffused brown-red at the base, with yellowish tip. Primocane leaves pedate, 5-foliate, flat, thin, medium-sized, dark green, matt, and hairy with (20–)35–50(–70) simple hairs per 1 cm^2 above, green beneath, hairy with long patent simple hairs, distinctly hairy to touch. Leaflets remote from one another, the terminal one with mid-long petiolule [petiolule (21–)26–27(–33) % as long as its lamina], obovate or elliptic, cordate at base, gradually narrowing into (13–)19–24(–32) mm long apex; leaflet margins flat, indentation regularly to slightly periodically serrate, with incisions (1.0–)1.5–2.0(–3.0) mm deep, teeth wider than long, acute with a short and sometimes retrorse apex. Petiolules of the basal leaflets (2.5–)3.5–4.5(–6.0) mm long. Petioles usually (5.5–)6.5–8.0(–9.0) cm long, longer than the basal leaflets, densely hairy; sessile and subsessile glands scattered; stalked glands, glandular acicles and glandular bristles abundant, unevenly long; prickles (13–)16–23(–29), straight and declining to slightly curved; pricklets scattered; stipules filiform, ca (0.5–)0.7–1.0(–1.2) mm wide, with hairs, sessile, subsessile and stalked glands. Inflorescence straight or pendulous, conical, ± rounded at apex, with mainly patent branches, distal (4.5–)5.5–6.5(–8.5) cm long part leafless. Inflorescence leaves predominantly ternate (the uppermost 0–1 leaf simple), hairy and dark green above, distinctly hairy beneath; terminal leaflets mostly obovate to broadly obovate or broadly elliptic, distinctly coarsely dentate to shallowly lobed (particularly the lowermost leaves). Inflorescence axis distinctly flexuous, felted with stellate hairs, and with abundant tufted and patent simple long hairs; sessile and subsessile glands scattered; stalked glands, glandular acicles and glandular bristles abundant, unevenly long; pricklets scattered, prickles (11–)13–17(–32) per 5 cm of axis length, ± equal, slender, straight and declining or slightly curved, (2.4–)3.1–4.1(–4.5) mm long. Pedicels (1.0–)1.3–1.7(–1.9) cm long, densely felted, stalked glands, glandular acicles and glandular bristles abundant, unevenly long, up to (0.7–)1.2–1.5(–1.8) mm long, the longest glandular acicles and glandular bristles longer than hairs; prickles (8–)9–13(–19), acicular, ± equal, straight to slightly curved, (1.2–)1.4–2.1(–2.4) mm long. Sepals first spreading to reflexed, reflexed to erect after anthesis, (6.5–)7.5–8.5(–10.0) mm long (inclusive of the filiform appendix), abaxially green-grey, with whitish felted margin, densely felted with ± stellate hairs and with scattered patent simple long hairs, with numerous stalked glands, glandular acicles and numerous yellowish pricklets, adaxially white-grey felted. Petals narrowly elliptical to narrowly obovate, emarginate at apex, not touching each other, (6.5–)8.0–11.5(–12.0) mm long, (2.5–)3.0–5.0(–5.5) mm wide, white, with scattered hairs (± at base) above, hairy beneath. Stamens longer than styles; filaments white, glabrous; anthers yellowish, glabrous. Ovaries sparsely hairy; styles greenish yellow. Receptacle densely hairy. Aggregate fruit subglobose. Flowering VI–VII.

Diagnostic characters. – Primocane stems densely hairy; primocane leaves 5-foliolate, hairy adaxially, distinctly hairy to touch abaxially; terminal leaflet of primocane leaves

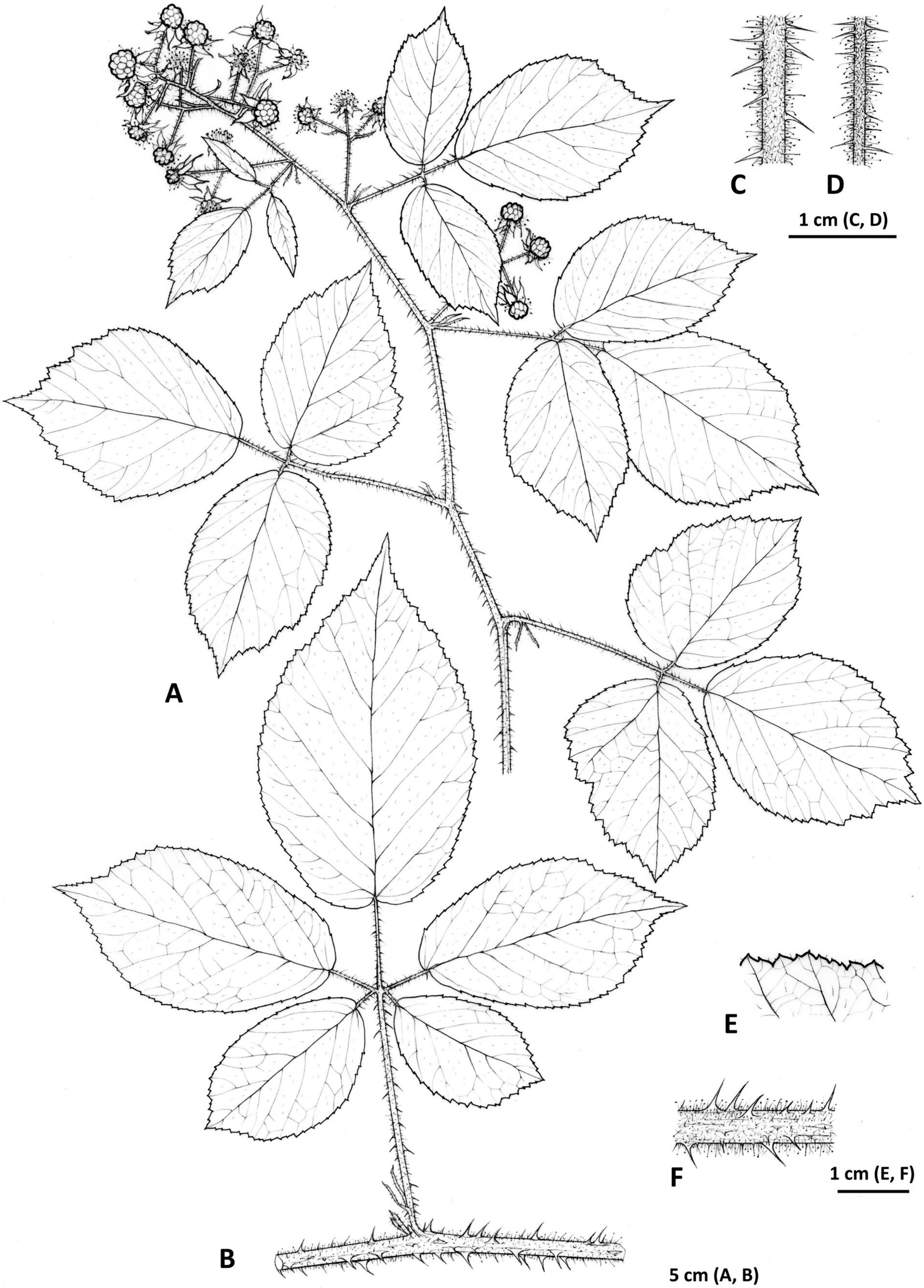

Fig. 9. *Rubus piceeticola*: **A**, Infructescence; **B**, Primocane leaf; **C**, Detail of inflorescence axis; **D**, Detail of pedicel; **E**, Margin of terminal leaflet of primocane leaf; **F**, Detail of primocane stem. — Drawn by Anna Skoumalová.

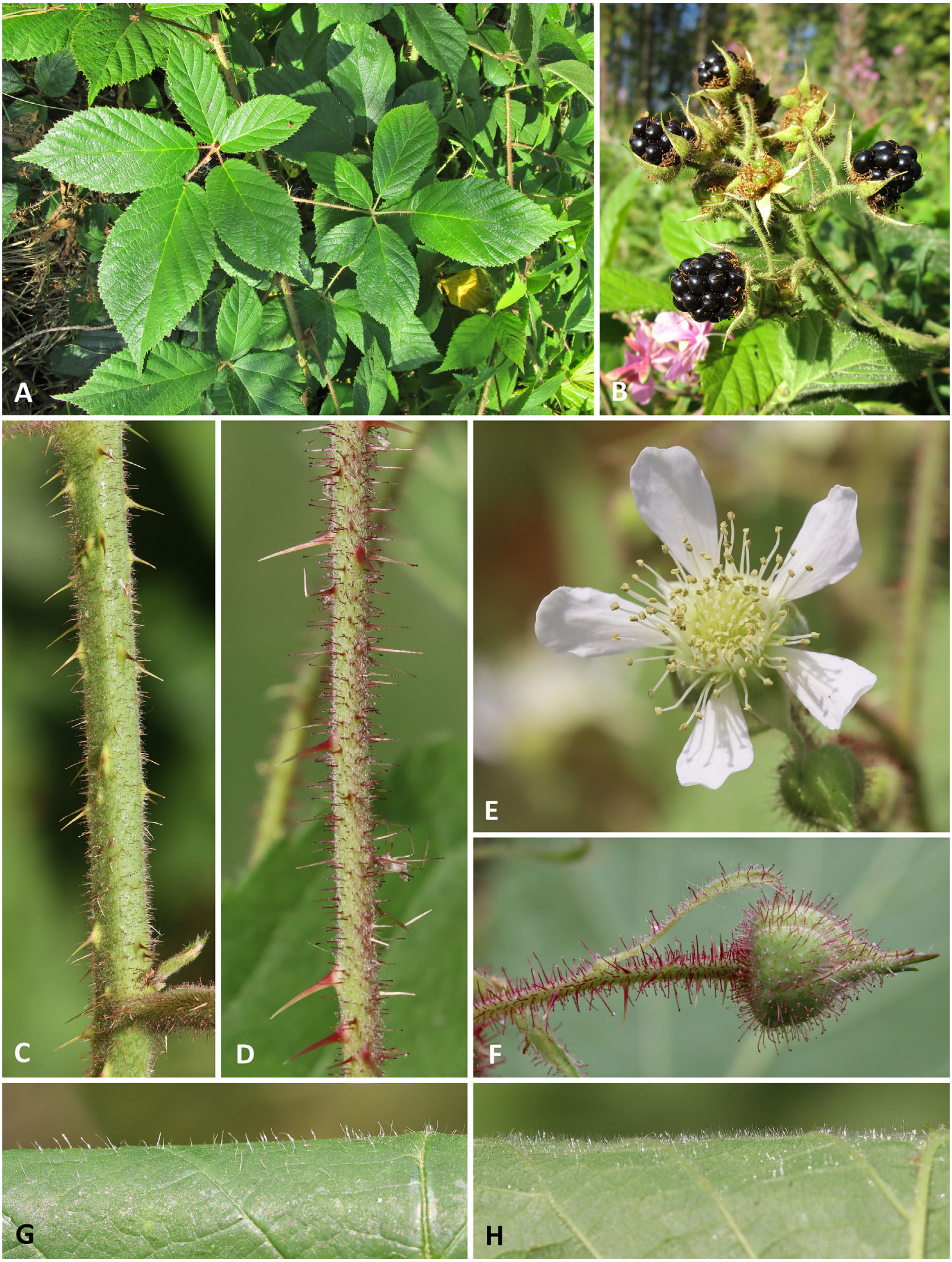

Fig. 10. *Rubus piceeticola*: **A**, Primocane leaves; **B**, Upper part of infructescence; **C**, Detail of primocane stem; **D**, Detail of inflorescence axis; **E**, Flower; **F**, Pedicel with flower bud; **G**, Detail of adaxial surface of terminal leaflet of primocane leaf; **H**, Detail of abaxial surface of terminal leaflet of primocane leaf. — Specimens *M. Lepší 816/22* (A & B; Zbytiny, Southern Bohemia), *M. Lepší 349/23* (C, G & H; Kavrlík, South-western Bohemia), *M. Lepší & Velebil 506/22* (D–F; Hartmanice, South-western Bohemia). — Photos: P. Lepší (A & B), A. Lepší (C, G & H), M. Lepší (D–F).

obovate or elliptic, gradually narrowing into the apex and regularly to slightly periodically serrate; inflorescences straight or pendulous, conical; stamens longer than styles; ovaries sparsely hairy; styles greenish yellow; receptacle densely hairy.

Etymology. – The Latin name refers to the species' most common habitat, the *Picea abies* plantations.

Distribution and ecology. – Currently known from about 40 localities in the Šumava/Bayerischer Wald Mts. and its foothills in southern and western Bohemia, Czechia, and Lower Bavaria, Germany. Two other localities are recorded from the Český les Mts. in western Bohemia (Fig. 6). The most distant localities are located near the towns of Prachatice and Mariánské Lázně and are 145 km apart. The extent of occurrence (sensu IUCN, 2012) is 5142 km^2. *Rubus piceeticola* grows most frequently along forest roads and in clearings in *Picea abies* plantations. It has also been recorded in spruce forest margins and gaps, and rarely in *Pinus sylvestris* and *Fagus sylvatica* plantations.

DNA-ploidy level. – $2n = 4x$ (Sochor & al., 2024a; as Genotype 82).

Additional specimens examined (paratypes). – **CZECHIA**. Chřepice (dist. Klatovy), Pohádka settlement, ca 1.5 km NNE of summit of Plošina hill, forest clearing, growth of several square meters, 49°15′39″N, 13°15′38″E, 19 Jul 2023, *M. Lepší 368/24* (CB barcode CB/90129); Hartmanice (dist. Klatovy), Hořejší Těšov village, along forest road ca 740 m S of summit of Na Čihadle hill (710 m spot height), edge of clearing, 1 ex., 49°10′48″N, 13°26′37″E, 11 Jul 2023, *P. Lepší & al. SHPL/4135* (herb. P. Lepší); Hojsova Stráž (dist. Klatovy), ca 2 km NNW of Neposkvrněné početí Panny Marie church in village, railway cut, rare, 49° 13′34″N, 13°11′26″E, 22 Aug 2022, *J. Velebil & M. Lepší 478/23* (CB barcode CB/83668); Hořejší Těšov (dist. Klatovy), ca 560 m WSW of centre of village, edge of forest along a road, medium-sized growth, 49°10′57″N, 13°25′26″E, 23 Aug 2022, *M. Lepší & J. Velebil 505/22* (CB barcode CB/83664); Hořejší Těšov (dist. Klatovy), ca 740 m S of summit of Na Čihadle hill, edge of forest road in *Picea abies* plantation, small growth, 49°10′48″N, 13°26′37″E, 11 Jul 2023, *P. Lepší, M. Lepší & al. 350/24* (CB barcode CB/90138); Javorná (dist. Klatovy), ca 500 m NW of summit of Hamerský vrch hill, clearing in *Picea abies* plantation, small growth, 49°13′43″N, 13°17′48″E, 19 Jul 2023, *M. Lepší 370/24* (CB barcode CB/90127); Kašperské Hory (dist. Klatovy), ca 240 m SW of summit of Šibeniční vrch hill, old forest clearing in beech forest, small growth, 49°08′31″N, 13°32′24″E, 25 Aug 2022, *J. Velebil, M. Lepší 521/23* (CB barcode CB/83710); Kavrlík (dist. Klatovy), ca 970 m S of summit of Zámecký vrch hill, edge of *Picea abies* plantation and road, one small shrub, 49°09′03″N, 13°34′33″E, 11 Jul 2023, *P. Lepší, M. Lepší & al. 349/24* (CB barcode CB/90139); Keply (dist. Klatovy), ca 550 m SSW of summit of Svinenský hill, edge of forest road in *Picea abies* plantation, small growth, 49°12′42″N, 13°20′34″E, 11 Jul 2023, *M. Lepší, P. Lepší & al. 351/24* (CB barcode CB/90137); Kochánov (dist. Klatovy), ca 1.2 km WNW of summit of Kamenáč hill, edge of forest road in young *Picea abies* plantation, growth of several square meters, 49°11′55″N, 13°22′02″E, 11 Jul 2023, *M. Lepší, P. Lepší & al. 353/24* (CB barcode CB/90135); Malý Radkov (dist. Klatovy), ca 1.4 km NW of summit of Radkovský vrch hill, edge of forest road, large growth, 49°08′44″N, 13°28′28″E, 23 Aug 2022, *M. Lepší & J. Velebil 506/22* (CB barcode CB/83707); Matějovice (dist. Klatovy), ca 560 m N of summit of Křížový vrch hill, in *Picea abies* plantation, growth of several square meters, 49°15′37″ N, 13°11′29″E, 19 Jul 2023, *M. Lepší 366/24* (CB barcode CB/90130); Mochov (dist. Klatovy): ca 620 m ESE of summit of Na Zámku hill, edge of *Picea abies* plantation, growth of several square meters, 49°11′23″N, 13°24′13″E, 19 Jul 2023, *M. Lepší 371/24* (CB barcode CB/90126); Srní (dist. Klatovy), clearing along forest path close to Klostrmannův most bridge ca 1.48 km N of road bridge over Vydra river in Antýgl settlement, one middle-size ex., 49°04′22″N, 13°30′ 31″E, 29 Oct 2023, *P. Lepší SHPL/4154* (herb. P. Lepší); Ždánov (dist. Klatovy), ca 860 m WSW of summit of Ždánov hill, under power line in *Picea abies* plantation, large growth, 49°08′58″N, 13°35′28″E, 19 Jul 2023, *M. Lepší 374/24* (CB barcode CB/90124); Žihobce (dist. Klatovy), Kakánov settlement, ca 700 m SE of summit of Sedlo hill, edge of forest road, medium-sized growth, 49°11′10″N, 13°34′44″E, 25 Aug 2022, *M. Lepší & J. Velebil 526/23* (CB barcode CB/89556); Žlíbek (dist. Klatovy), ca 250 m SSE of summit of Zámecký vrch hill, edge of forest road in *Picea abies* plantation, growth of several square meters, 49°09′27″N, 13°34′ 42″E, 19 Jul 2023, *M. Lepší 373/24* (CB barcode CB/90125); Buk (dist. Prachatice), ca 480 m ESE of summit of Výšina hill, edge of forest road in *Pinus sylvestris* forest clearing, growth of several square meters, 49°01′57″N, 13° 50′03″E, 29 Sep 2023, *M. Lepší 551/24* (CB barcode CB/90106); Javorník (dist. Prachatice), ca 850 m NE of summit of Javornik Mt., edge of forest road, scattered, 49°08′33″ N, 13°39′45″E, 25 May 2022, *J. Velebil & M. Lepší s.n*. (CB barcode CB/89578); Lipka (dist. Prachatice), ca 580 m ENE of train stop in village, open *Picea abies* forest, one small growth, 49°01′18″N, 13°44′36″E, 14 Oct 2022, *M. Lepší & P. Lepší 744/22* (CB barcode CB/89960); Lipka (dist. Prachatice), ca 820 m WSW of train stop in village, old wet forest clearing, rare, small shaded growth, 49°01′03″N, 13°43′30″E, 14 Oct 2022, *M. Lepší & P. Lepší 745/22* (CB barcode CB/89959); Mlynářovice (dist. Prachatice), ca 630 m SSW of summit of Kádrův kopec hill, edge of forest road in *Pinus sylvestris* plantation, growth of ca 50 square meters, 48°56′ 57″N, 13°54′59″E, 5 Oct 2023, *M. Lepší 583/24* (CB barcode CB/90083); Pěkná (dist. Prachatice), ca 320 m WNW of summit of Hůrka hill, edge of forest road in *Picea abies* plantation, small shrub, 48°51′43″N, 13°56′20″E, 11 Oct 2023, *M. Lepší 597/24* (CB barcode CB/90116); Pravětín (dist. Prachatice), ca 470 m SSW of summit of Na Vršcích hill, edge of forest road in *Corylus avellana* growth, growth of ca 50 square meters, 49°01′57″N, 13°49′00″E, 29 Sep 2023, *M. Lepší 550/24* (CB barcode CB/90105); Pravětín (dist. Prachatice), ca 800 m

ESE of summit of Sviní vrch hill, gap in *Picea abies* and *Larix decidua* mixed plantation, growth of ca 150 square meters, 49°02′023″N, 13°47′46″E, 29 Sep 2023, *M. Lepší 546/24* (CB barcode CB/90107); Radhostice (dist. Prachatice), lesní světlina cca 1 km J od kapličky v Libotyni (poblíž NPP U Hajnice), velký porost, 49°04′21″N, 13°53′49″E, 05 Aug 2010, *P. Lepší SHPL/2162* (CB barcode CB/101960); Včelná pod Boubínem (dist. Prachatice), ca 660 m SSW of summit of Skalní hora hill, forest clearing, one shrub, 49°01′23″N, 13°52′51″E, 14 Oct 2022, *P. Lepší & M. Lepší 762/22* (CB barcode CB/89956); Volary (dist. Prachatice), ca 360 m WSW of summit of Vysoký les hill, edge of forest road in *Picea abies* plantation, growth of ca 150 square meters, 48°56′16″N, 13°54′54″E, 05 Oct 2023, *M. Lepší 587/24* (CB barcode CB/90086); Zbytiny (dist. Prachatice), ca 820 m S of St. Vít church in village, open *Pinus sylvestris* plantation, large growth, 48°56′07″N, 13°58′40″E, 01 Nov 2022, *M. Lepší 816/22* (CB barcode CB/89941); Zdíkov (dist. Prachatice), ca 1.9 km SW of St. Ludmila church in village, verge of forest road, medium-sized growth, 49°04′18″N, 13°40′35″E, 04 Sep 2020, *P. Lepší & M. Lepší 821/20* (CB barcode CB/87308); Zdíkov (dist. Prachatice), ca 540 m E of summit of Hrb hill, edge of forest road in *Picea abies* plantation, small growth, 49°03′18″N, 13°40′49″E, 28 Sep 2023, *M. Lepší 525/24* (CB barcode CB/90097); Zdíkov (dist. Prachatice), ca 640 m SSE of summit of Kamenná hora hill, edge of forest road in *Picea abies* plantation, growth of ca 60 square meters, 49°02′45.1″N, 13°42′21.3″E, 28 Sep 2023, *M. Lepší 530/24* (CB barcode CB/90100). **GERMANY**. Achslach (dist. Regen), ca 1.8 km ENE of St. Jakobus church in village, edge of road in *Picea abies* forest, small shadowed shrub, 48°58′34″N, 12°57′43″E, 06 Sep 2022, *M. Lepší 643/23* (CB barcode CB/90052); Bischofsmais (dist. Regen), ca 2.2 km NW of St. Jakobus church in village, forest clearing, one shrub, 48°55′40″N, 13°3′22″E, 06 Sep 2022, *M. Lepší 639/23* (CB barcode CB/90048); Bischofsmais (dist. Regen), ca 3.4 km NW of St. Jakobus church in village, edge of forest road in *Picea abies* plantation, scattered, 48°56′11″N, 13°02′42″E, 06 Sep 2022, *M. Lepší 640/23* (CB barcode CB/90049); Münchshöfen (dist. Regen), ca 700 m W of summit of Kastenstein hill, open *Picea abies* plantation, small growth, 49°02′56.6″N, 12°49′16.6″E, 06 Sep 2022, *M. Lepší 651/23* (CB barcode CB/90028); Oberauerkiel (dist. Regen), ca 720 m E of church in village, edge of *Picea abies* forest and road, several growths, 49°01′40.8″N, 13°04′42″E, 07 Sep 2022, *M. Lepší 667/23* (CB barcode CB/89995); Obermühle (dist. Regen), ca 1.3 km NNW of summit of Hofberg hill, edge of forest road, large growth, 49°04′31″N, 12°49′01″E, 07 Sep 2022, *M. Lepší 654/23* (CB barcode CB/90021); Obermühle (dist. Regen), ca 1.3 km SW of summit of Hofberg hill, open Picea abies forest, scattered, 49°03′20″N, 12°48′39″E, 07 Sep 2022, *M. Lepší 653/23* (CB barcode CB/90022); Prackenbach (dist. Regen), ca 1.7 km ESE of church in village, forest clearing, large growth, 49°05′15″N, 12°50′49″E, 07 Sep 2022, *M. Lepší 655/23* (CB barcode CB/90034); Regen (dist. Regen), ca 1.7 km SW of St. Michael church in town, young *Picea abies* plantation, 48°57′54″N, 13°06′25″E, 06 Sep 2022, *M. Lepší 635/23* (CB barcode CB/90044).

6. ***Rubus angloserpens*** Edees & A.Newton in Watsonia 12: 135. 1978 – Holotype: Stanford-on-Teme, just within wood at iron gate on north-west side of road, Worcestershire, 31 Jul 1964, *Edees 18596* (NMW barcodes NMW0000239, NMW0000240, NMW0000241, on 3 sheets [images!]).

= *Rubus perlongus* H.E.Weber & W.Jansen in Osnabrück. Naturwiss. Mitt. 27: 82. 2002 – Holotype: Thuringia, Wald am SW-Hang des Großen Mühlberges bei Hämmern, 27 Jul 1993, *W. Jansen 93727.10* (HBG barcode HBG-518890 [image!]), **syn. nov.**

Rubus angloserpens is illustrated in Fig. 11.

Diagnostic characters. – Primocane stems bluntly angled or round, often grey-pruinose, **sparsely hairy with short**, mostly simple hairs; prickles straight to slightly curved, declining, 1.5–2 mm broad at base, **pinkish or reddish at base**; primocane leaves 3–4(–5)-foliolate, sparsely hairy on both sides (**not hairy to touch**), dark green above, somewhat paler beneath; terminal leaflet ovate or elliptical, shallowly cordate at base, (long-)acuminate at apex, indentation sharp, periodic, petiolule short (petiolule length 19%–25% of the lamina length); inflorescence paniculate, conical, **sparsely branched in the terminal part with ± patent branches and long patent pedicels**, inflorescence axis somewhat flexuous, with short prickles, leaves similar to those on primocanes, but more greyish beneath; **sepals with long appendix**, **spreading to suberect**, later after anthesis erect, abaxially greyish-green, with a white felted margin; **stamens longer than styles**; **ovaries pubescent at first, later glabrous**. See Velebil & al. (2016; as *R. perlongus*) for the full description and drawing.

Distribution. – Formerly reported only from the British Isles, central Germany (Kurtto & al., 2010), and westernmost Czechia (Velebil & al., 2016). By genotyping, it was also confirmed from eastern France (Dpt. Doubs) and the Netherlands. The remotest known localities are 1060 km distant, which makes *Rubus angloserpens* the most widespread tetraploid genotype of *R.* ser. *Glandulosi* (Table 1).

DNA-ploidy level. – $2n = 4x$ (based on FCSS of specimen *Sochor MS305/21*).

Notes. – The holotype specimen is unambiguously of the same genotype as 12 other specimens in our dataset, including the holotype of *Rubus perlongus* and other specimens determined as such. One specimen was collected in the Netherlands and determined by A. van de Beek as *R. ignoratus*. The genotype of the *R. ignoratus* holotype is, however, unique in our dataset. Curiously, two specimens that we obtained from the U.K. under the name *R. angloserpens*, one of them determined by A. Newton, belong to a different genotype identical to *R. serpens* sensu Van de Beek (2018; see note at that species).

7. ***Rubus barberi*** H.E.Weber in Abh. Ber. Naturkundemus. Görlitz 61(8): 35. 1987 ≡ *R. rugosus* Barber in Jahresber.

Fig. 11. *Rubus angloserpens*: **A**, Primocane leaf; **B**, Detail of primocane stem from shady situation; **C**, Detail of primocane stem from sunny situation; **D**, Flower; **E**, Pedicel; **F**, Infructescence. — Specimen *Trávníček R300/13* (Luby, Western Bohemia). — Photos: J. Velebil (A–F).

Schles. Lehrervereins Naturwiss. 1907–1908: 32. 1909, nom. illeg., non *R. rugosus* Sm. 1819 – Lectotype (designated by Weber in Abh. Ber. Naturkundemus. Görlitz 61(8): 35. 1987): Neißtal [= "rechter Talhang unterhalb Station Rosenthal", Barber 1911], 21 Jul 1906, *Barber s.n.* (GLM No. 04727 [image!]).

Rubus barberi is illustrated in Fig. 12.

Diagnostic characters. – Creeping shrubs; primocane stems round, **very densely hairy** with short stellate and longer simple hairs, **pruinose**; primocane **leaves 3-foliolate**, (light) green above, greyish beneath, distinctly hairy with long simple hairs on both sides (hairy to touch), their margins evenly **shallowly crenate**; terminal leaflet ± broadly elliptical, with cordate to rounded base and short acuminate tip; inflorescence conical; inflorescence axis somewhat flexuous, greyish-felted; **stamens longer than styles**; **young ovaries densely hairy (felted)**, with hairs persisting even on ripening fruits.

Distribution. – Local species with tendency to regional distribution currently known only from southeasternmost Saxony. Along with the lectotype, three collections were genotyped within a range of more than 30 km. Several historical specimens also provided records from the adjacent parts of Poland (Zieliński & al., 2004, citing Barber's specimens in GLM) and Czechia (Holub, 1995). A plant rediscovered at one of the cited Czech localities was not confirmed as *Rubus barberi* by genotyping.

DNA-ploidy level. – 2*n* = 4*x* (Sochor & al., 2024a [as Genotype 5]).

8. ***Rubus exarmatus*** H.E.Weber & W.Jansen in Osnabrück. Naturwiss. Mitt. 27: 78. 2002 – Holotype: Thuringia, Waldrand W Steinpöhl, 500 m, 10 Aug 1998, *W. Jansen 98810.7* (HBG barcode HBG-518889 [image!]).

Rubus exarmatus is illustrated in Fig. 13.

Diagnostic characters. – Low-arching shrubs; primocane stems round, **densely hairy** with stellate hairs and long (up to 1 mm) simple or tufted hairs and dense reddish to yellowish stalked glands mostly not exceeding hairs; **prickles ± sparse, small (up to 2.5 mm long), slender**, straight to slightly curved, declining, not distinctly differentiated from pricklets and acicles; primocane leaves mostly **ternate or 4-foliolate** (rarely up to 5-foliolate), moderately hairy above, somewhat pruinose and rather sparsely hairy on veins beneath (**not distinctly hairy to touch**); terminal leaflet shortly petiolulate (petiolule length 22%–28% of the lamina length), **wide-elliptic to obovate**, cordate to rounded at base, ± abruptly to gradually acuminate at apex, **serration ± regular with incisions around 1 mm deep**, with mucronate teeth; **stipules narrowly to widely lanceolate, 1–3 mm wide**; inflorescence cylindrical (to somewhat conical), truncate on top, distal 3–9 cm long part leafless; terminal leaflets of leaves with short, indistinctly acuminate apex; inflorescence axis densely hairy to white-felted with short adpressed and numerous long patent hairs, with rather sparse small acicular pricklets not distinctly differentiated from glandular acicles; pedicels felted, with numerous yellowish to slightly reddish stalked glands and glandular acicles of varying lengths; sepals with filiform apex, felted on both sides, abaxially with numerous yellowish (to reddish) stalked glands, (mostly) **without pricklets**; petals white, narrowly obovate, emarginate; **stamens longer than styles**, filaments white, anthers glabrous; styles yellowish-green, **ovaries glabrous**; flower **receptacle hairy**.

Distribution. – The species is known and was confirmed by genotyping from northwestern Bavaria, eastern Thuringia and adjacent parts of Saxony (see also Hassler, 2024) and was newly discovered on the basis of genotyping in northwestern Bohemia. Its currently known range is 267 km.

DNA-ploidy level. – 2*n* = 4*x* (Sochor & al., 2024a [as Genotype 10]).

9. ***Rubus flaccidifolius*** P.J.Müll. in Bonplandia (Hannover) 9: 300. 1861 – Lectotype (designated by Moret in Candollea 48: 396. 1993): Gérardmer (Vosges), Vallée des Granges, 9 Jul 1859, *Müller 3136* (LAU 2D-barcode LAU-0131701 [image!]). **Epitype (designated here):** France, Vosges, Gérardmer, 140 m NE of the confluence of La Vologne and La Jamagne, 48°05′40″N, 6°53′05″E, 5 Aug 2024, *Trávníček & Sochor R114/24* (OL barcode 51481!, on three sheets; isoepitypes: CB barcode CB/111263!, LI!, M!, PR!, W!).

Rubus flaccidifolius is illustrated in Fig. 14; for images of the epitype, see suppl. Figs. S9–S11.

Diagnostic characters. – Primocane stems round, **densely patent-hairy**, with **numerous short-stalked glands not exceeding hairs**; prickles with broad base, straight to slightly curved, declining; primocane leaves **large** (around 20 cm long), mostly **ternate**, **leaflets convex, drooping**; terminal leaflet wide-ovate or elliptical, cordate or rounded at base, acuminate at tip, indentation regular to slightly periodical with wide teeth and incisions 1.5–3 mm deep; **moderately hairy above (15–40 hairs per cm^2)**, hairy only on veins beneath (not distinctly hairy to touch); petiole much shorter than lateral leaflets; **inflorescence broadly conical, usually short, leafy (almost) to the top, flat on top**; inflorescence axis densely patent-hairy, stalked glands mostly not exceeding hairs, prickles thin, acicular; pedicels with numerous long-stalked glands, glandular bristles, acicles and pricklets; sepals with long tip, abaxially felted and patent-hairy, with numerous stalked glands and pricklets; petals not exceeding sepals; **stamens as long as or slightly longer than styles**; **styles greenish-white**; ovaries ± hairy when young, later glabrescent; receptacle hairy.

Distribution. – The currently known distribution area, whole confirmed by genotyping, extends from Baden-Württemberg, Germany, through the Vosges to the French department Oise in the north-west and Dpt. Saône-et-Loire in the south-west (see also Ferrez & Royer, 2015). The remotest known localities are 464 km distant.

Ploidy level. – 2*n* = 4*x* (Sochor & al., 2024a [as Genotype 263]).

Notes. – Although the lectotype was genotyped, its genotype did not match any other sample in our dataset. However,

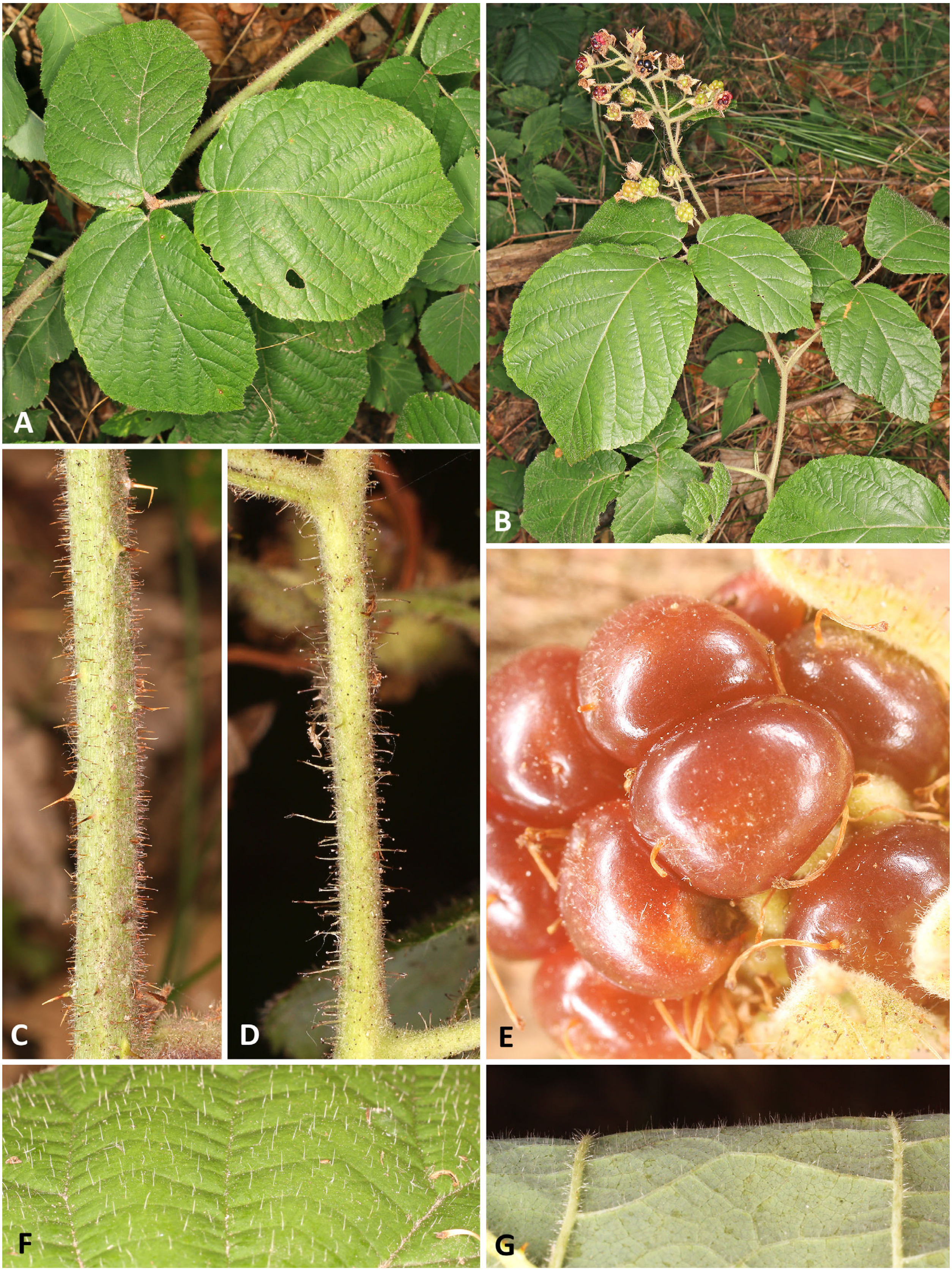

Fig. 12. *Rubus barberi*: **A**, Primocane leaf; **B**, Infructescence; **C**, Detail of primocane stem; **D**, Detail of infructescence axis; **E**, Drupelets with persisting stellate hairs; **F**, Adaxial side of terminal leaflet of primocane leaf; **G**, Abaxial side of terminal leaflet of primocane leaf. — Specimen *Sochor MS137/22* (Eichgraben, Saxony). — Photos: M. Sochor (A–G).

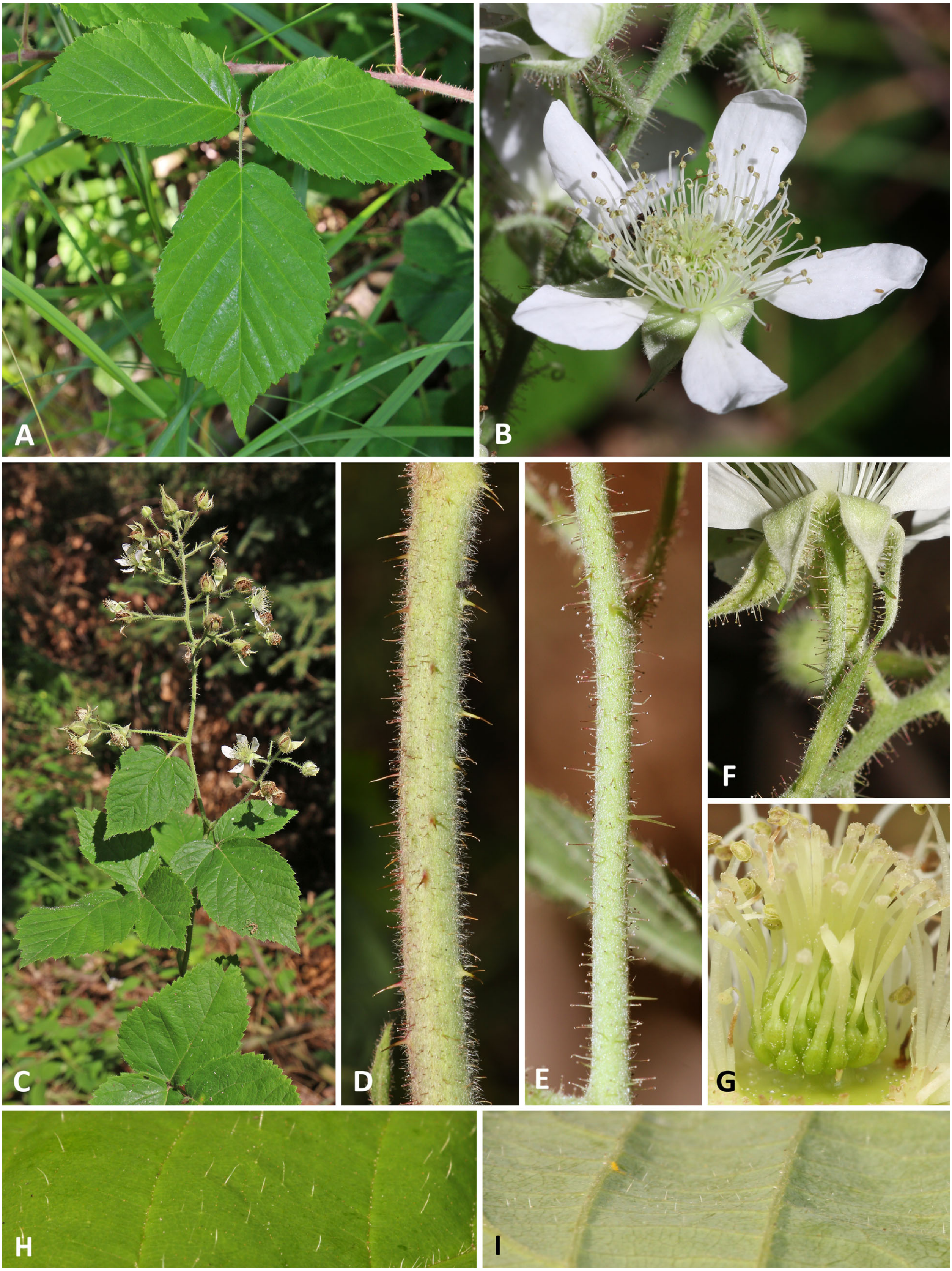

Fig. 13. *Rubus exarmatus*: **A**, Primocane leaf; **B**, Flower; **C**, Inflorescence; **D**, Detail of primocane stem; **E**, Detail of inflorescence axis; **F**, Pedicel; **G**, Detail of flower with exposed carpels; **H**, Detail of terminal leaflet of primocane leaf adaxially; **I**, Detail of terminal leaflet of primocane leaf abaxially. — Specimen *Sochor MS70/24* (Velká Černoc, northwestern Bohemia). — Photos: M. Sochor (A–I).

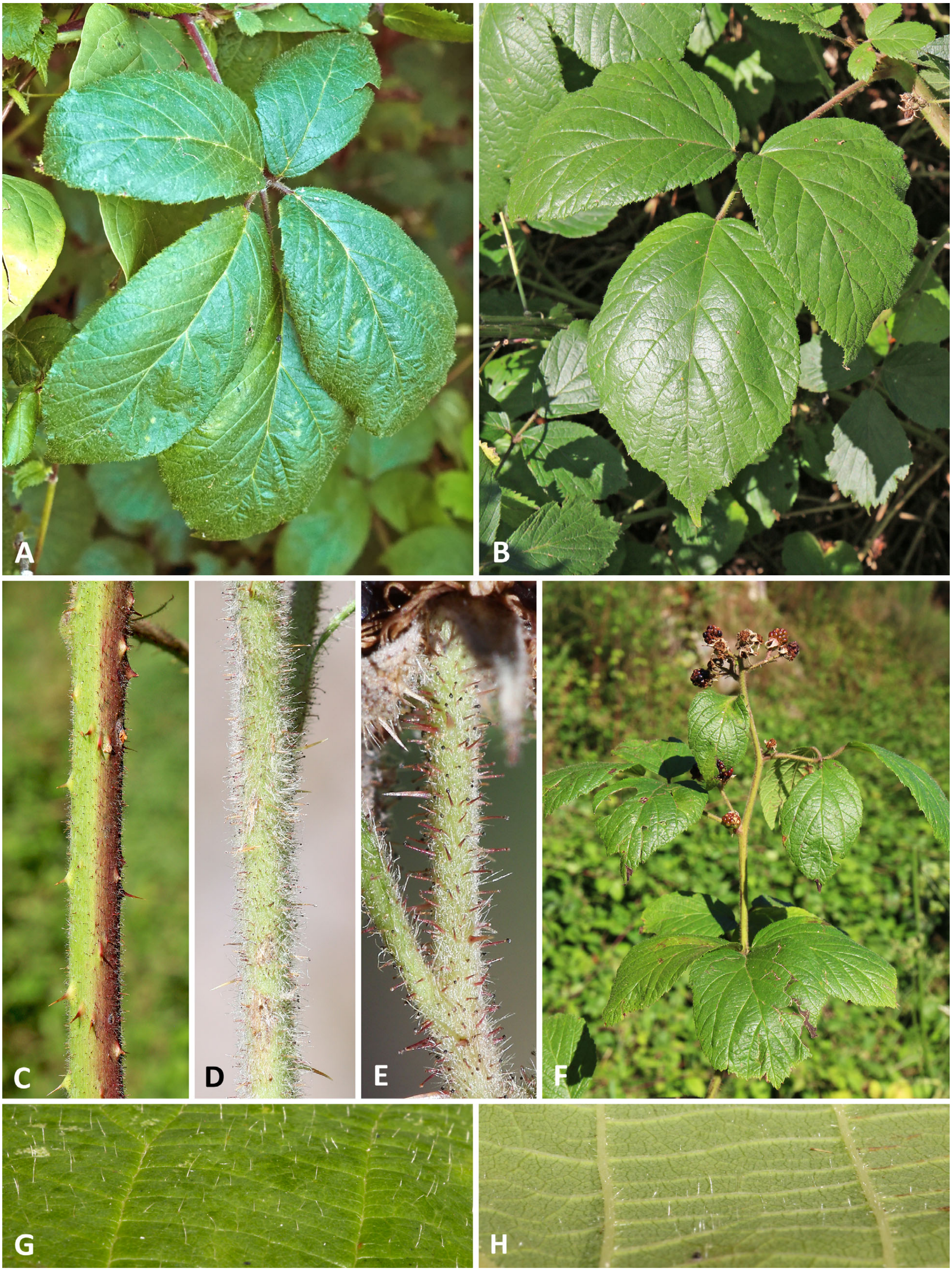

Fig. 14. *Rubus flaccidifolius*: **A** & **B**, Primocane leaves; **C**, Primocane stem; **D**, Inflorescence axis; **E**, Pedicel; **F**, Infructescence; **G**, Detail of adaxial surface of terminal leaflet of primocane leaf; **H**, Detail of abaxial surface of terminal leaflet of primocane leaf. — Specimen *Sochor MS137/24* (*locus classicus*). — Photos: B. Trávníček (A), M. Sochor (B–H).

besides an unclear signal at some loci (resulting from highly fragmented DNA), several unique alleles were observed in the lectotype DNA fingerprint, which pointed to a possible contamination of the lectotype with another, younger *Rubus* specimen, e.g., via pollen transfer. After a careful morphological evaluation of the lectotype and specimens collected at the *locus classicus*, we concluded that the SSR data, although technically seemingly correct, should be considered misleading in this case. Considering the large genotypic diversity in *R*. ser. *Glandulosi* and relatively high importance of genotyping for unambiguous species identification, the false genotyping data makes the lectotype demonstrably ambiguous. Therefore, we designate here an epitype in compliance with Art. 9.9 of the *Code* (Turland & al., 2018) for unambiguous interpretation of the name. The genotype of our topotypes (and the epitype) matches 12 specimens identified as *R. flaccidifolius* by various batologists, including seven specimens cited and shown in Ferrez & Royer (2015), so the epitype designation complies with the current use of the name.

10. ***Rubus guentheri*** Weihe in Bluff & Fingerhuth, Comp. Fl. German. 1: 679. 1825 – Lectotype (designated by Weber in Bot. Jahrb. Syst. 106: 312. 1986): Silesia [handwritten label], in montosis Sudetorum, amic. Köhler Schmiedebergae exemplaria collegit [printed label], s. dat., *Köhler s.n*. (B barcode B 10 0295787 [image!]; isolectotype: B barcode B 10 0295788 [image!]). **Epitype (designated here):** Germany, Saxony, between Hain and Lückendorf, 170 m SW of Kamloch, 50°49′43″N, 14°44′26″E, 7 Aug 2022, *M. Sochor MS136/22* (OL barcode 51480!; isoepitype: GLM barcode GLM-P-0054008!).

Rubus guentheri is illustrated in Fig. 15; for an image of the epitype, see suppl. Fig. S12.

Diagnostic characters. – Creeping to low-arching shrubs; primocane stems round, green (in shade) to dark-vinaceous (in sun), **not pruinose, subglabrous to sparsely hairy** with stellate hairs, with moderate to dense **red to dark-vinaceous stalked glands**; **prickles thin, only slightly longer than the longest glands**, with very low widened base; primocane leaves **3(–5)-foliolate**, densely hairy above, (sub)glabrous among veins beneath; terminal leaflet (broadly) elliptic to obovate, acuminate at apex, with serration rather irregular (to somewhat periodic), sharp; inflorescence narrow-conical, leafy almost to the top, the apical part rather dense; terminal primocane inflorescence often present, larger and richer than the one of floricanes; inflorescence axis densely hairy but not felted, with dense red stalked glands; sepals long-acuminate or with appendix, **spreading to reflexed at anthesis**, spreading to erect after anthesis; stamens somewhat to distinctly **shorter than styles**; **ovaries hairy** with tufted hairs; **styles (light) pinkish**.

Distribution. – By genotyping, the species was confirmed from central, northern and eastern Bohemia (Czechia) and adjacent parts of eastern Saxony (Germany) and Lower Silesia (Poland). This distribution likely extends further west to Thuringia and eastern Hesse (Germany; Hassler, 2024) and north-east to other parts of south-western Poland, but we cannot confirm the isolated localities in the Ukraine and south-eastern Poland (Kurtto & al., 2010) at this moment. The extent of occurrence (sensu IUCN, 2012) confirmed by genotyping is 17,459 km^2 and the distance between the remotest samples is 192 km.

Ploidy level. – $2n = 4x$ (Sochor & al., 2024a [as Genotype 17]). Boratyńska (1996) reported on $2n = 28 = 4x$ for three specimens and $2n = 42 = 6x$ for one specimen. Krahulcová & Holub (1998) also reported on the predominant tetraploid level, but found one plant with $2n = 35 = 5x$. Both of the sources are credible and the material was determined by leading *Rubus* experts of that time (J. Zieliński and J. Holub, respectively). Although we detected only tetraploid plants and no hexaploid embryos in the five specimens analysed by flow cytometry (50 seeds; Sochor & al., 2024a), the formation of a hexaploid via B_{III} hybridisation within a single genotype (fertilisation of an unreduced egg cell) cannot be excluded. Subsequently, reduced gametes of such a hexaploid and the prevailing tetraploids may produce pentaploid offspring without the need of participation of any other genotype. Such polyploids exhibit no or very little differences in their SSR genotypes and remain undistinguished from tetraploids by genotyping.

Notes. – The modern interpretation of the name appears unproblematic as regards its homogeneity, as several specimens independently determined morphologically by different collectors shared the same genotype. This genotype (number 17) is one of the most common in our dataset. However, the lectotype could not be easily localised. Weber (1986) considered the whole exsiccata collection of *Rubus guentheri* distributed by Günther & al. in 1824 to be the original material, except for one mixed specimen with a leaf from *R. caesius*. He selected one specimen (cited as "Sudetis, sine dat., [*Wimmer*], det. Weihe, KIEL") to be the lectotype. This specimen probably had a printed label "*R. guentheri* Weihe", as further notes in Weber (1986) indirectly imply. There is no such specimen in KIEL (D. Langel, pers. comm.). However, two specimens of the Weihe's collection are deposited in herbarium B and both of them have a label of Museum botanicum Universitatis Kiliensis (that is the KIEL herbarium) and one was labelled by Weber as lectotype on the 6 Apr 1975. Although the collector cited in Weber (1986) differs from the labels on the specimens in B (Wimmer vs. Köhler) and the locality also slightly differs ("Sudetis" vs. "Silesia" in handwriting or "In montis Sudetorum" in print), we consider this to be a transcription error and the latter specimen to be the lectotype. Since all of the exsiccata specimens of *R. guentheri* probably originated from a single collection by Köhler from Schmiedeberg (now Kowary) in Polish Silesia, all of the other specimens can be considered isolectotypes. All of them, except the one above-mentioned mixed specimen, are also morphologically homogeneous and unambiguously identical with Genotype 17. However, because of the ambiguous identification of the lectotype and low chance for obtaining good genotypic

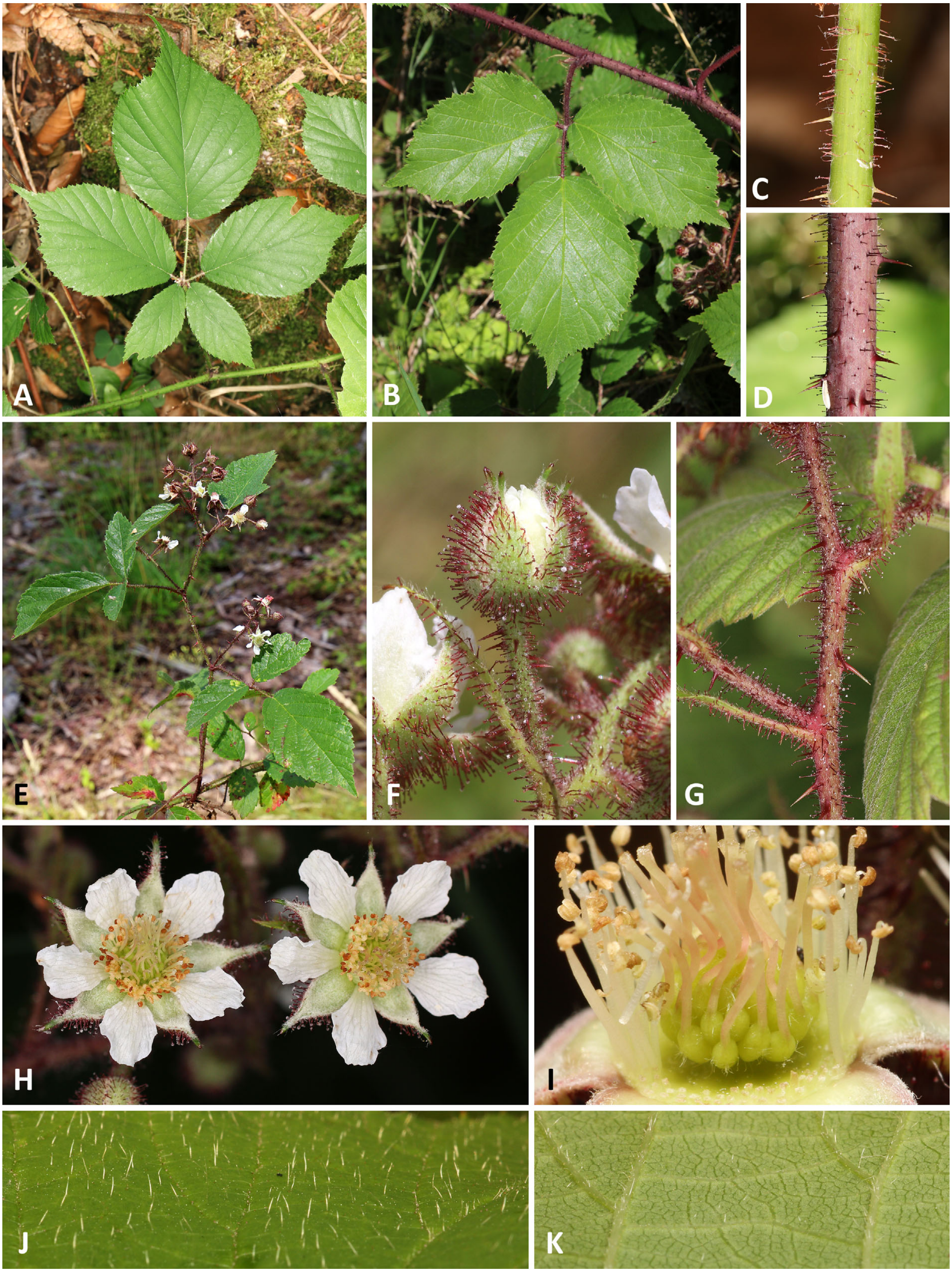

Fig. 15. *Rubus guentheri*: **A** & **B**, Diversity in primocane leaves; **C**, Primocane stem from shady situation; **D**, Primocane stem from sunny situation; **E**, Inflorescence; **F**, Pedicel with opening bud; **G**, Inflorescence axis; **H**, Flowers; **I**, Detail of flower with displayed carpels; **J**, Detail of adaxial surface of terminal leaflet of primocane leaf; **K**, Detail of abaxial surface of terminal leaflet of primocane leaf. — Specimens *Sochor MS1/21* (A & C; Malá Skála, Northern Bohemia), *Hlaváček RH1/19* (B, D, E & I–K; Kochnov, Central Bohemia), and *Sochor MS136/22* (F–H; Hain, Saxony). — Photos: M. Sochor (A–K).

data from the original material of Weihe, we select here a genotyped and precisely localised specimen as an epitype to avoid any doubts in the future.

11. ***Rubus lividus*** G.Braun, Herb. Ruborum Germ. (exs.): no. 18. 1877 – Lectotype (designated by Weber in Abh. Ber. Naturkundemus. Görlitz 61(8): 37. 1987): Harz: Zwischen Harzburg und Oker, Jul 1876, *G. Braun, Herb. Ruborum Germ. no. 18* (HAN, n.v.; isolectotypes: JE barcode JE00014390 [image!], KFTA barcode KFTA0001486 [image!], LD barcode 2287979, n.v.).

Rubus lividus is illustrated in Fig. 16.

Diagnostic characters. – Creeping to low-arching shrubs; primocane stems angular with flat or convex sides to round, light green (to slightly vinaceous when exposed to sun), often **bluish-pruinose** (bloom may be washed away easily), **(sub) glabrous or sparsely hairy** with (mostly) stellate or simple hairs, prickles up to ca twice as long as the longest glands; primocane leaves 3–5-foliolate, moderately (to densely) hairy above, sparsely hairy between veins beneath, but with dense hairs on veins (both sides distinctly hairy to touch), **abaxial side white-blueish**; terminal leaflet elliptic to obovate, cordate at base, acute to shortly acuminate at apex; serration regular to somewhat periodical, **shallow**, with teeth wide, rounded, with short tip; inflorescence loose, leafless at least in the upper half; inflorescence axis densely hairy to weakly felted; sepals abaxially whitish-felted, with pale stalked glands, **almost without pricklets, weakly reflexed at anthesis, erect after anthesis; stamens longer than styles; ovaries glabrous; styles pale green-yellowish**; receptacle long-hairy.

Distribution. – By genotyping, the species was confirmed from the Harz Mts., Hesse, Thuringia, and northern Baden-Württemberg, as well as western and central Bohemia and Czech Silesia. Although its frequency of occurrence appears to be rather low, particularly in the eastern part of the range, with a known distribution of ca 620 km in extent, *Rubus lividus* is one of the most widespread species of *R.* ser. *Glandulosi*.

Ploidy level. – $2n = 4x = 28$ (Krahulcová & Holub, 1997; Sochor & al., 2024a [as Genotype 1]).

12. ***Rubus lucentifolius*** Ziel. & Kosiński in Polish Bot. J. 49: 5. 2004 – Holotype: S Poland, Prov. Opole, CF4216, Eastern Sudety Mts., Opawskie Mts., Długota Mt., Dębowiec near Prudnik, 335 m, mixed forest, section 158, 29 Jul 1999, *Kosiński, Tomaszewski & Zieliński s.n.* (KOR No. 41471, n.v.).

Rubus lucentifolius is illustrated in Fig. 17.

Diagnostic characters. – Low-arching shrubs; primocane stems round (to angular with convex sides), with scattered to numerous long simple and stellate hairs and ± numerous sessile and stalked glands, glands red with green-yellowish stalks; prickles thin with very low widened base, distinctly longer than the longest glands (up to 3 times as long); well-developed primocane leaves **5-foliolate**, sparsely hairy above, (sub)glabrous between veins, **green and glossy beneath**; leaflets **narrow, long-acuminate**, terminal leaflet narrowly elliptic to narrowly ovate, **serration ± regular, shallow**, teeth abruptly acuminate with narrow tips; inflorescence rather loose, leafy almost to the top; inflorescence axis densely hairy with long patent hairs, slender needle-like prickles and glands mostly not longer than hairs; **sepals ± spreading** during and after anthesis, abaxially felted, densely long-hairy with glands hidden in hairs; stamens as long as styles or somewhat shorter; **ovaries densely hairy, styles green-yellowish**.

Distribution. – The species was confirmed by genotyping in the *area classica* along the Czech-Polish border in Silesia, but it was also detected as far east as Gliwice, Silesian Voivodeship, Poland. The remotest localities confirmed by genotyping are 101 km distant. In the west, it was also reported from the Kłodzko basin (southern Lower Silesia, Poland; Zieliński & al., 2004) and the Bardzkie Mountains (Lower Silesia, Poland; Kosiński, 2010).

Ploidy level. – $2n = 4x$ (Krahulcová & al., 2013; Sochor & al., 2024a [as Genotype 8]).

13. ***Rubus lusaticus*** Rostock in Mitth. Voigtl. Vereins Allg. Naturk. Reichenbach 4: 22. 1884 – Lectotype (designated by Weber in Abh. Westfäl. Mus. Naturk. 47(3): 375. 1985): Am Pichow bei Dretschen, sächsische Oberlausitz, sine dat., *Rostock s.n.* (GLM No. 8796! [image!]). **Epitype (designated here):** Czechia, Lotouš-Písek (dist. Kladno), 200 m WSW of the junction of road R7 and the road to Byseň, 50°15′09″N, 14°01′33″E, 21 Aug 2020, *Trávníček R95/20* (OL barcode 51482!, on two sheets; isoepitypes: CB barcode CB/111262!, GLM barcode GLM-P-0185525, PR!).

Rubus lusaticus is illustrated in Fig. 18; for images of the epitype, see suppl. Figs. S13 and S14.

Diagnostic characters. – Creeping to low-arching shrubs; primocane stems round, somewhat pruinose, moderately to rather densely hairy with tufted and simple patent hairs, with dense **yellow-brown stalked glands**; prickles numerous, up to 5 mm long, ca twice as long as the longest glands, thin, green-yellowish, or strong and (brown-)reddish when exposed to sun; primocane leaves 3-foliolate, ± leathery, glossy and sparsely to densely hairy above, light green and distinctly **densely hairy beneath** (veins felted with short hairs, long patent hairs between veins), at sunny sites whole abaxial surface **with whitish felt**; terminal leaflet elliptic to obovate, with cordate base, with ca 1–2 cm long acuminate tip; **serration very shallow** (ca 1 mm) and sharp, regular, teeth broad at base and with long narrow tip; **inflorescence cylindrical**, **leafless in the upper half**; inflorescence axis densely patent-hairy and with long (up to 4 mm) needle-like prickles and almost as long glandular acicles; stalked glands on pedicels dense, often red (at least in distal part); **sepals spreading** (or somewhat reflexed) during and after anthesis, abaxially felted, whitish green, with stalked glands and glandular acicles, long-acuminate with appendix; petals not distinctly longer than sepals; **stamens longer than styles**; **styles yellowish**, ovaries (sub)glabrous; receptacle hairy.

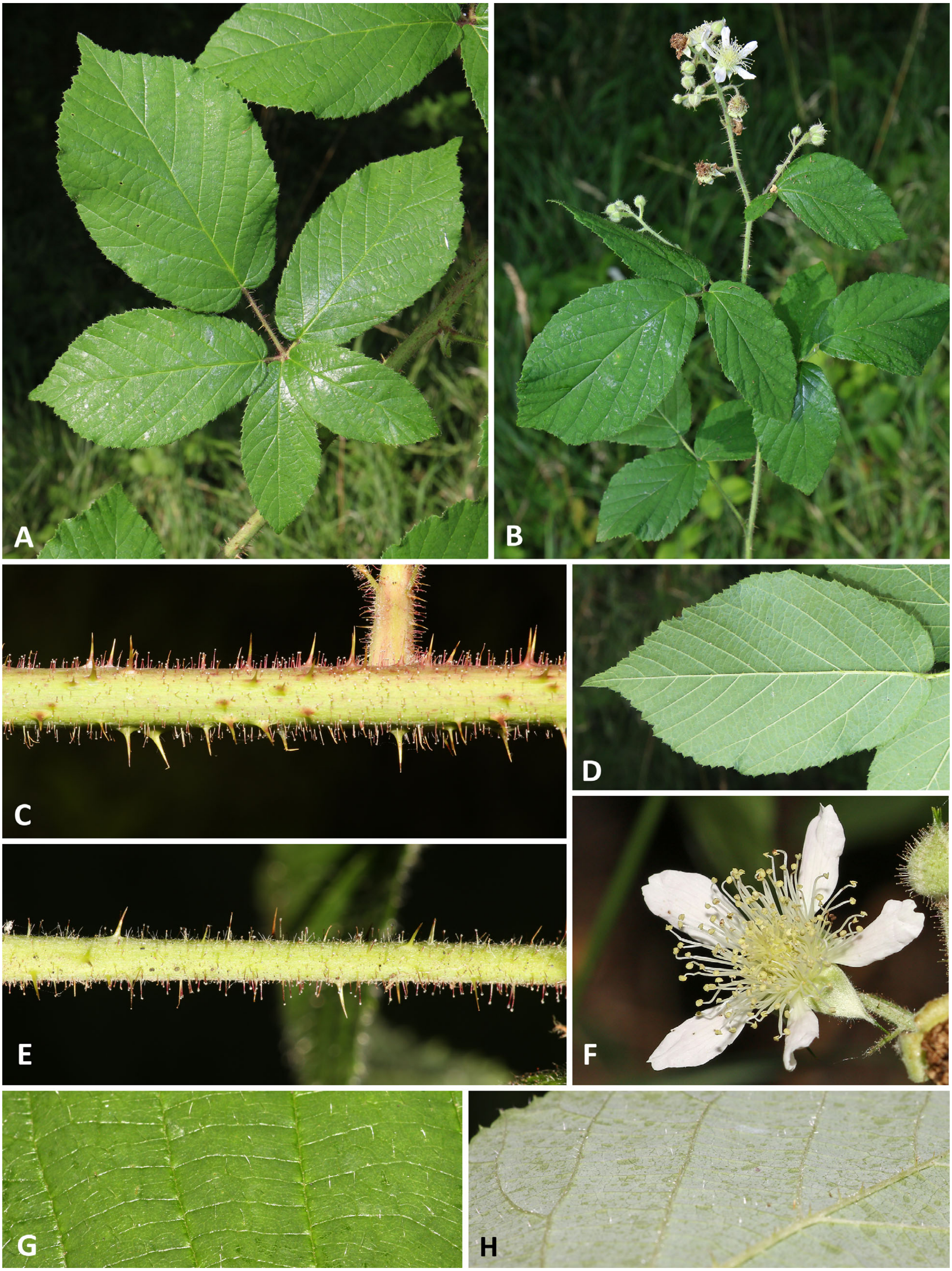

Fig. 16. *Rubus lividus*: **A**, Primocane leaf; **B**, Inflorescence; **C**, Detail of primocane stem; **D**, Abaxial surface of terminal leaflet of primocane leaf; **E**, Inflorescence axis; **F**, Flower; **G**, Detail of adaxial surface of terminal leaflet of primocane leaf; **H**, Detail of abaxial surface of terminal leaflet of primocane leaf. — Specimen *Sochor MS60/24* (Kosova Hora, Central Bohemia). — Photos: M. Sochor (A–H).

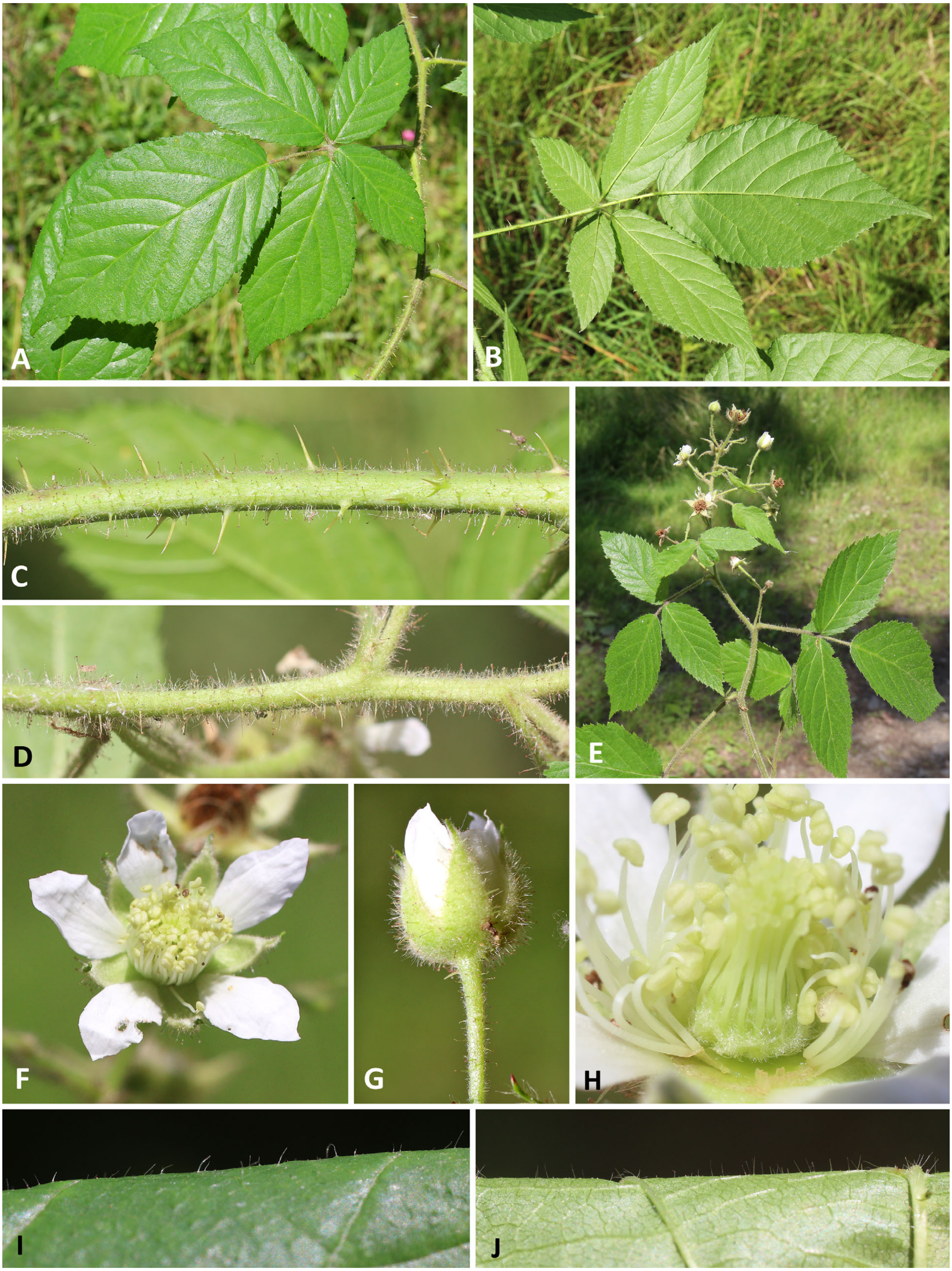

Fig. 17. *Rubus lucentifolius*: **A**, Primocane leaves in adaxial view; **B**, Primocane leaves in abaxial view; **C**, Detail of primocane stem; **D**, Inflorescence axis; **E**, Inflorescence; **F**, Flower; **G**, Pedicel with flower bud; **H**, Detail of flower with carpels displayed; **I**, Detail of adaxial surface of terminal leaflet of primocane leaf; **J**, Detail of abaxial surface of terminal leaflet of primocane leaf. — Specimen *Sochor MS56/24* (*area classica*, between Trzebina and Dębowiec, Polish Silesia). — Photos: M. Sochor (A–J).

Fig. 18. *Rubus lusaticus*: **A**, Primocane leaf; **B**, Typical shape of inflorescence; **C**, Detail of primocane stem; **D**, Inflorescence axis; **E**, Pedicel with young flower; **F**, Detail of flower with displayed carpels; **G**, Adaxial surface of terminal leaflet of primocane leaf from sunny situation; **H**, Abaxial surface of terminal leaflet of primocane leaf from sunny situation. — Specimen *Sochor MS135/20* (Mimoň, Northern Bohemia). — Photos: M. Sochor (A–H).

Distribution. – The species was confirmed by genotyping from eastern Saxony, northern and central Bohemia, and northern Baden-Württembeg, the two regions being separated by an extraordinary hiatus of ca 300 km without the known occurrence of the species (see also Hassler, 2024). The remotest localities are 485 km distant. Zieliński & al. (2004) reported it as far north-east as southern Greater Poland.

Ploidy level. – 2*n* = 4*x* = 28 (Krahulcová and Holub, 1997; Boratyńska, 1998; Sochor & al., 2024a [as Genotype 3]).

Notes. – Genotyping data from the lectotype did not match any contemporary specimen from our dataset. Although the DNA sample was taken correctly and the data were seemingly correct from the technical point of view, a few unique alleles detected in the lectotype sample pointed to its possible contamination with another, younger *Rubus* specimen, e.g., via pollen transfer. This obstacle can never be completely avoided in old specimens with highly degraded DNA. Our thorough morphological examination did not reveal any differences between the lectotype and our specimens of Genotype 3. Consequently, we consider the lectotype SSR data false and prioritise the data from topotypes collected by the local expert F.W. Sander. Since the molecular identification of the lectotype is misleading (making it demonstrably ambiguous), we designate here a molecularly characterised epitype in compliance with Art. 9.9 of the *Code* (Turland & al., 2018). This epitype corresponds with the modern conception of the species sensu Kurtto & al. (2010) and Hassler (2024) and is morphologically identical to the lectotype.

14. ***Rubus nigricans*** Danthoine in J. Sci. Utiles 2: 223. 1791 – Lectotype (designated by Van de Beek in Gorteria 41: 59. 2019): [without locality and date], *Danthoine s.n.* (P barcode P03134111 [image!]). Epitype (designated by Van de Beek in Gorteria 41: 60. 2019): France, Chartreuse de Durbon, along the road to the former monastery, 29 Jun 2018, Van de Beek *2018.45* (P, n.v.; isoepitype: L, n.v.).

= *Rubus kuenicus* Ant.Schott ex Utsch in Deutsche Bot. Monatsschr. 16: 22. 1898 – Lectotype (designated by Lepší & Lepší in Preslia 97: 282. 2025): Ebenschlag, bei Hinterhäuser bei Neuern, 2 Aug 1897, *A. Schott s.n.* (LI barcode 04016601 [image!]).

= *Rubus pedemontanus* Pinkw. in Deutsche Bot. Monatsschr. 16: 131. 1898 – Lectotype (designated by Weber in Willdenowia 13: 146. 1983): Flora Silesiaca, Bürgerberg bei Goldberg, 3 Jul, 24 Aug 1897, *Pinkwart, Baenitz, Herb. Europ. 9550* (MANCH, n.v.; isolectotypes: BREM, n.v., M, n.v.).

Rubus nigricans is illustrated in Fig. 19.

Diagnostic characters. – Creeping to low-arching shrubs; primocane stems round, **subglabrous to sparsely hairy**, often pruinose, dark vinaceous in sunny situations; prickles unequal, straight and declining, **some with very wide base**; primocane leaves almost exclusively **3-foliolate**, adpressed-hairy above, subglabrous between veins beneath (not hairy to touch); **terminal leaflet elliptic, rounded or shallowly cordate at base, with abruptly acuminate, often recurved apex**; serration shallow (1–2 mm), (almost) regular, teeth acuminate with long apex; **inflorescence few-flowered, rather broad, weakly branched, with patent branches and pedicels**; inflorescence axis with dense stellate and sparse simple hairs; sepals abaxially green, sparsely felted, gradually tapering into a long apex, somewhat reflexed during anthesis, erect and adpressed to fruits after anthesis; anthers as long as or slightly longer than styles; ovaries glabrous, styles yellowish-green.

Distribution. – The species was confirmed by genotyping from the U.K., France (*locus classicus*), Germany, Netherlands, Czechia, and Poland. Kurtto & al. (2010) reported it also from Denmark, southern Sweden, western Ukraine, Switzerland, Belgium, Luxembourg, and western Austria.

Ploidy level. – 2*n* = 35 = 5*x* (Gustafsson, 1933; Boratyńska, 1995; Krahulcová & Holub, 1997; Sochor, unpublished data).

Notes. – The name *Rubus bellardii* Weihe was widely used for this species. However, contrary to the conclusions of Van de Beek (2019), it must be considered to be an illegitimate name according to Art. 52.1, because the protologue definitely included the type of *R. glandulosus* Bellardi.

15. ***Rubus siemianicensis*** (Sprib.) Sprib. in Z. Naturwiss. Abt. Deutschen Ges. Kunst Posen 9: 124. 1902 – Neotype (designated by Zieliński in Polish Bot. Stud. 16: 206. 2014): Marianka Siemiańska, 3 km SWW of Siemianice, 7 Aug 1992, *Zieliński 102/92* (KOR No. 29632 [image!]).

Rubus siemianicensis is illustrated in Fig. 20.

Diagnostic characters. – Prostrate to low-arching shrubs; primocane stems **very densely hairy** with mostly long patent simple and stellate hairs, with **rather sparse stalked glands** and glandular pricklets **mostly hidden in hairs**, **prickles slender**, slightly curved and declinate, **with reddish base** and yellowish tip, up to 4 mm long; primocane leaves **5-foliolate**, palmate or somewhat pedate, adpressed-hairy above, densely hairy on veins beneath but sparsely hairy to subglabrous between veins; terminal leaflet elliptic to obovate, with long acuminate apex, often **convex**, **serration shallow**, up to 2 mm deep, rather irregular to somewhat periodical, main teeth often recurved; inflorescence **narrowly conical or cylindrical, sparsely branched** (sometimes racemose), **leafless apically**, usually slightly **recurved** at apex, with patent pedicels and branches; inflorescence axis very densely patent-hairy, with numerous stalked glands shorter than hairs; pedicels with short and mostly adpressed hairs, long stalked glands exceeding hairs, and numerous prominent up to 2 mm long prickles; sepals abaxially felted, with short stalked glands, without prickles, **reflexed or spreading after anthesis**; **stamens longer than styles**; **ovaries glabrous**.

Note. – The species is morphologically not a typical member of *Rubus* ser. *Glandulosi* mainly because its stems are not covered by stalked glands in the density usual in this group. Thus, it is sometimes classified as a member of *R.* ser. *Pallidi*

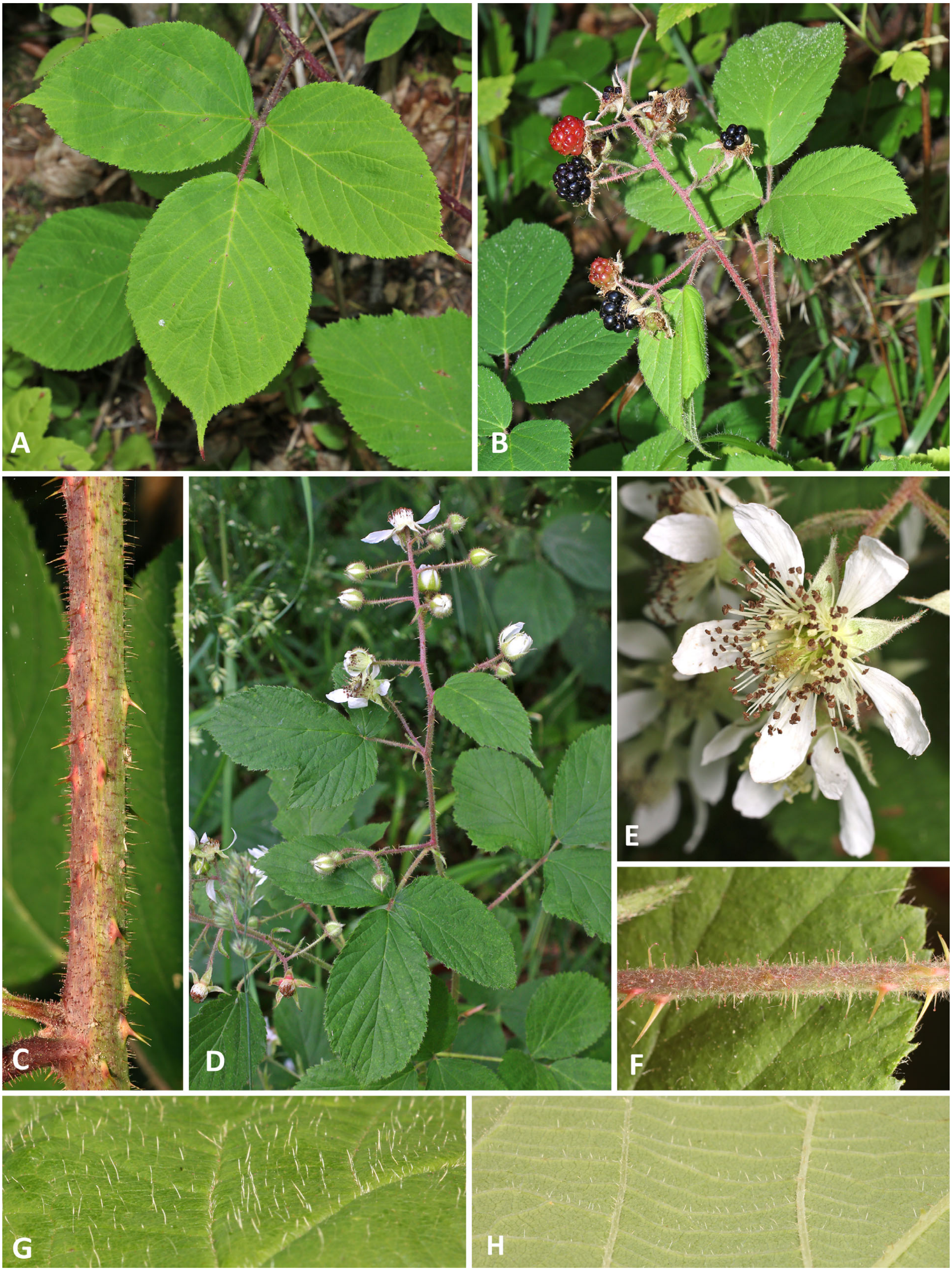

Fig. 19. *Rubus nigricans*: **A**, Primocane leaf; **B**, Infructescence; **C**, Detail of primocane stem; **D**, Inflorescence; **E**, Flower; **F**, Inflorescence axis; **G**, Adaxial surface of terminal leaflet of primocane leaf; **H**, Abaxial surface of terminal leaflet of primocane leaf. — Specimens *Sochor MS267/21* (A & B; *locus classicus*), *Sochor MS521/21* (C, G & H; Čechtice, Vysočina Region, Czechia), and an uncollected specimen from Blanský les, southern Bohemia (D–F). — Photos: M. Sochor (A–H).

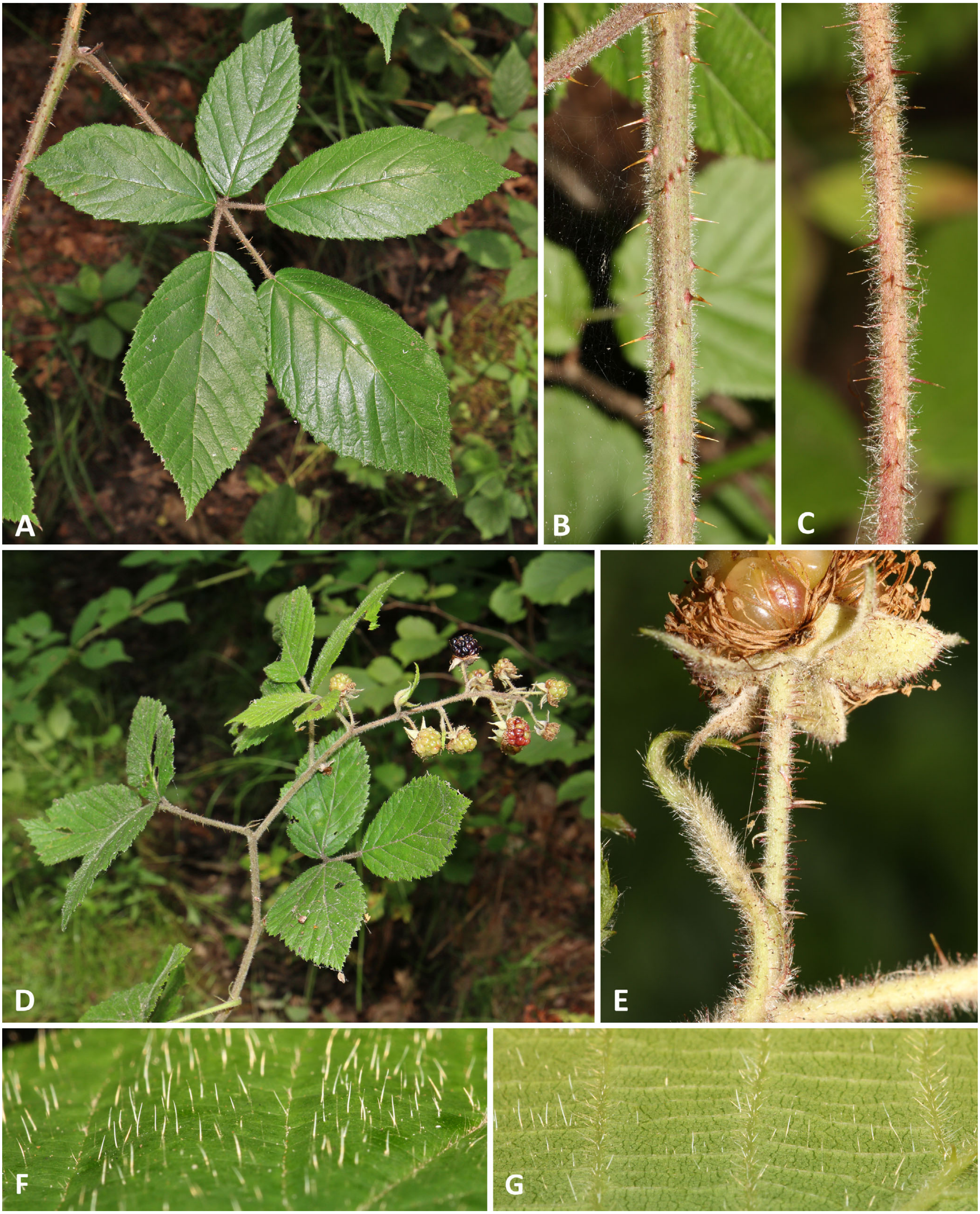

Fig. 20. *Rubus siemianicensis*: **A**, Primocane leaf; **B**, Detail of primocane stem; **C**, Inflorescence axis; **D**, Infructescence; **E**, Pedicel; **F**, Adaxial surface of terminal leaflet of primocane leaf; **G**, Abaxial surface of terminal leaflet of primocane leaf. — Specimen *Sochor MS80/24* (Vidnava, Czech Silesia). — Photos: M. Sochor (A–G).

(Kirschner, 2019). In this series, it is relatively close to two other Czech-Polish species, *R. josholubii* Weber and *R. chaerophylloides* Sprib. Similar species in appearance are also *R. holzfussii* Sprib., *R. posnaniensis* Sprib. and *R. ostroviensis* Sprib. All these species form a relatively natural group of brambles with primocanes not creeping, with primocane leaves predominantly 5-foliolate, lower density of glands on their stems, sepals often reflexed after anthesis, and also with similar geographical distribution (mainly SW Poland and NE Czechia, often in Silesia). Their inclusion in *R*. ser. *Pallidi* could, therefore, be more appropriate.

Distribution. – Confirmed by genotyping from Polish and Czech Silesia and central Bohemia (west of Beroun). Zieliński (2004) reported on occurrences also in the Greater Poland Voivodeship and rarely as far east as the Podkarpackie Voivodeship. Chytrý & al. (2021) recorded the species in several other regions of Czechia, including Northern Bohemia and Southern Moravia, the latter of which falls within the range of *Rubus glandulosus* (sexual populations of *R*. ser. *Glandulosi*); this may be another reason for inclusion of this species rather in *R*. ser. *Pallidi* (see above), because tetraploid apomicts clearly belonging to *R*. ser. *Glandulosi* usually do not occur in the range of sexuals (Sochor & al., 2024a).

Ploidy level. – $2n = 4x = 28$ (Boratyńska, 1997; Sochor & al., 2024a [Genotype 35]).

C. Accepted apomictic microspecies lacking conclusive genotypic data

Rubus atrovinosus H.E.Weber in Abh. Westfäl. Mus. Naturk. 47(3): 361. 1985 – Holotype: Westfalen, Sauerland, Südrand von Silberg, westlich vom Wasserbehälter, 475 m NN, 21 Jul 1981, *Weber 81721.15* (HBG [image!]; isotype: MSTR, n.v.).

Rubus chlorostachys P.J.Müll. in Bonplandia (Hannover) 9: 303. 1861 – Lectotype (designated by Van de Beek & al. in Gorteria 39: 15. 2017): Gérardmer (Vosges), Vallée de la Vologne, Route de St. Dié avec le *R. leucadenes*, 10 Jul 1859, *P.J. Müller 3128* (LAU, n.v.).

Note. – Two specimens collected and identified as this species by J.-M. Royer were genotyped and confirmed as belonging to the same genotype (305). Only one other specimen of this genotype was detected in our dataset. The maximum distance between these three localities is 9.3 km.

Rubus ducatuscola G.H.Loos in Florist. Rundbr. 34(2): 82. 2001 – Holotype: Germania, Westphalia, Brilon-Scharfenberg, Hang am Waldbruch-Gebiet/Horst, 29 Jul 2000, *Loos 007-223* (MSTR, n.v.; isotype: BOCH, n.v.).

Rubus echinophorus Genev. in Mém. Soc. Acad. Maine Loire 24: 32. 1868 ≡ *R. echinatus* P.J.Müll. in Flora 41: 171. 1858, nom. illeg. ≡ *R. leptadenes* Sudre in Bull. Soc. Études Sci. Angers 35: 51. 1906 – Lectotype (designated by Van de Beek & al. in Gorteria 39: 19. 2017): Heiligenbach, Vendredi, 10 Jul 1857, *Müller 3112* (LAU, n.v.).

Rubus edentulus A.Beek & Meijer in Gorteria 40: 66. 2018 – Holotype: Veenendaal, tuin Petenbos 8, overgeplant van Epen, Onderste Bos, bosrand bij eind van pad tegenover Schweibergerweg, 19 Jun 2016, *Van de Beek 2016.01* (L, n.v.).

Note. – A single specimen (topotype collected by A. van de Beek) was genotyped but did not match any other samples of the dataset. However, no other specimens identified as this species were available for analysis.

Rubus elegans P.J.Müll in Flora 41: 170. 1858 – Lectotype (designated by Matzke-Hajek in Beitr. Bot. Arbeitsgem. Südwestdeutschl. 1: 41. 2001): Au fond de la Reissbach, dans le vallon latéral, à droite, 15 Jul 1857, *Müller BE 624* (STR [herb. Stiefelhagen Nr. 2217]; isolectotype: LAU 2D-barcode LAU-0134999 [image!]).

Note. – The genotype of the lectotype has not been associated with any specimen in our dataset. However, this data should be considered highly unreliable due to much missing data, numerous unique alleles, and a lot of noise in the chromatograms. The modern conception of this name appears unambiguous since 16 specimens from our dataset identified as this species by various specialists were assigned to Genotype 142. Its total range is 423 km from eastern France to central Germany. However, since we could not collect a "topotype" and can neither confirm nor reject the identity of lectotype with the contemporary specimens identified as *Rubus elegans*, we are treating this name as lacking conclusive genotypic data for the time being.

Rubus elongatifolius Boulay & Gillot in Boulay, Assoc. Rubol. (exs.) 1: 54. 1877 – Type: not designated?

Rubus erythradenes P.J.Müll. in Bonplandia (Hannover) 9: 288. 1861 – Lectotype (designated by Moret in Candollea 48: 395. 1993): Gérardmer (Vosges), Vallée des Granges, 9 Jul 1859, *Müller 3280* (LAU, n.v.).

Note. – Five specimens, of which three were identified as this species by J.M. Royer and Y. Ferrez, were identified as belonging to Genotype 306. Its total currently known range is 144 km.

Rubus erythrocomos G.Braun, Herb. Ruborum Germ. (exs.) 6: no. 113. 1878 – Lectotype (designated by Matzke-Hajek in Willdenowia 27: 26. 1997): Bei Hackenberg unweit Derschlag in der Rheinprovinz, s. dat., *Braeucker in Braun, Herb. Ruborum Germ. no. 113*. (HAN, n.v.; isolectotype: JE, n.v.).

Rubus gymnocarpus Boulay & Pierrat in Boulay, Assoc. Rubol. (exs.) 1: 51. 1877 – Type: not designated?

Note. – Four specimens identified as this species by J.-M. Royer and Y. Ferrez were identified as belonging to Genotype 343. Its total currently known range is 215 km.

Rubus haeupleri H.E.Weber in Florist. Rundbr. 42: 84. 2009 – Holotype: Westfalen, Weg am Südost-Hang des Kahlen Asten, von der B236 Richtung Lenneplätze, nahe der Bundesstraße, 750 m s. m., E08°29′44″ N51°19′31″, 28 Jun 2007, *Weber 07.628.6* (HBG barcode HBG-506910 [image!]; isotype: MSTR, n.v.).

Rubus hilsianus H.E.Weber in Osnabrück. Naturwiss. Mitt. 20–21: 147. 1995 – Holotype: Niedersachsen, Hils, Roter Fuchs, zwischen Grünenplan und Holzen, 23 Jul 1984, *Weber & Pedersen 84.723.11* (HBG [image!]).

Rubus holzfussii Sprib. in Urban & Graebner, Festschr. Aschers.: 344. 1904 – Lectotype (designated by Zieliński in Polish Bot. Stud. 16: 199. 2014): Kreis Groß Strehlitz, Olschowaer Wald, 22 Jul 1903, *Spribille s.n.* (WRSL barcode WR SS 067221 [image!]).

Note. – The genotype of the lectotype has not been identified in any other sample from our dataset, possibly because we consider this species to be rather a member of *Rubus* ser. *Pallidi* and, therefore, we have excluded such specimens from our sampling.

Rubus hylonomus Lefèvre & P.J.Müller in Jahresber. Pollichia Naturwiss. Vereins Rheinpfalz 16–17: 224. 1859 – Lectotype (designated by Moret in Candollea 48: 401. 1993): Forêt de Retz, Jul 1896 [?], *Lefèvre 3148* (LAU 2D-barcode LAU-0131744, n.v.).

Note. – The lectotype was genotyped but did not match any other sample in our dataset. However, no other specimens identified as this species were available for analysis. Kurtto & al. (2010) reported this species from Wales to Belgium.

Rubus ignoratus H.E.Weber in Abh. Westfäl. Mus. Naturk. 47(3): 368. 1985 – Holotype: Westfalen, Straße zw. Welchen-Ernest und Littfeld, etwas westlich vom Gasthaus auf der Rohrbacher Höhe, 440 m NN, 27 Jul 1981, *Weber 81.727.10* (HBG [image!]).

Note. – The genotype of the holotype has not been associated with any other specimen from our dataset. However, only one other specimen identified as this species was available for analysis.

Rubus iuvenis A.Beek in Gorteria 12: 58. 1984 – Holotype: Ravensbosch bij Valkenburg, 24 Jun 1980, *Van de Beek A1069* (L, n.v.).

Rubus macescens Plien. in Hassler, Fl. German. 3: 255. 2024 – Holotype: Baden-Württemberg, Schwäbisch-Fränkische Waldberge, W-Rand "Kalter Berg", an Waldweg parallel (S) Straße, bis 100 m von Str., 2 Aug 2009, *Plieninger Pl 6554* (STU barcode SMNS-STU-PH-0158065-2 2 [image!]; isotype: KR, n.v.).

Note. – Two specimens collected 12 km from each other (including paratype *Plieninger Pl 12061* [STU]) were genotyped, and their identity was confirmed. No other specimen in our dataset matched their genotype. However, no other specimens identified as this species were available for analysis.

Rubus magnidentatus F.W.Sander in Ber. Naturf. Ges. Oberlausitz 27: 84. 2019 – Holotype: Sachsen, Oberlausitz: Rammenau – ca. 3,5 km NW, SW-Fuß des Hochsteins (Sibyllensteins), etwa 400 m östlich vom Forsthaus Luchsenburg am "unteren Beginn" des Burkauer Weges (14°05′57″E, 51°10′36″N, 330 m), 5 Jul 2017, *Sander 17705.5* (GLM, n.v.).

Note. – Two specimens collected by F.W. Sander from the same localities as the holotype and a paratype, 6.4 km distant from each other, were genotyped, and their identity was confirmed. They did not match any other specimen from our dataset. However, no other specimens identified as this species were available for analysis.

Rubus negatus A.Beek in Gorteria 31: 8. 2005 – Holotype: Wijster, tegenover biologisch station, 15 Jul 1998, *A. van de Beek 98199* (L, n.v.; isotype: BM, n.v.).

Note. – A sample from the *area classica* provided by the author of the name was genotyped but has not been associated with any other sample from our dataset yet. However, no other specimens identified as this species were available for analysis.

Rubus nigricatus P.J.Müll. & Lefèvre in Jahresber. Pollichia Naturwiss. Vereins Rheinpfalz 16–17: 204. 1859 – Lectotype (designated by Van de Beek in Gorteria 39: 29. 2017): Forêt de Retz et les bois des environs, 1851 and 1857, *Müller 3254* (LAU 2D-barcode LAU-0131791, n.v.).

Rubus obscuriflorus Edees & A.Newton in Watsonia 12: 135. 1978 – Holotype: Seckley Wood, Staffordshire, 26 Jul 1954, *Edees 10975* (NMW barcodes NMW0000588 [image!], NMW0000589 [image!], NMW0000590 [image!], on three sheets).

Note. – The genotype of the holotype has not yet been associated with any other specimen from our dataset. However, no other specimens identified as this species were available for analysis.

Rubus oreades P.J.Müll. & Wirtg. in Wirtgen, Herb. Ruborum Rhenan. (exs.) 1: no. 154. 1860 – Lectotype (designated by Weber in Abh. Westfäl. Mus. Naturk. 47(3): 364. 1985): Ahler Berg bei Oberlahnstein, 15 Jul 1860, *Wirtgen Herb. Rub. Rhen. 1: 154* (W, n.v.; isolectotypes: HAN, n.v., MANCH, n.v., WU, n.v.).

Rubus ostroviensis Sprib. in Verh. Bot. Vereins Prov. Brandenburg 39: 49. 1897 – Lectotype (designated by

Zieliński in Polish Bot. Stud. 16: 202. 2014): Wturker Wald, 11 Sep 1898, *Spribille s.n.* (WRSL barcode WR GS 067222 [image!]).

Note. – The lectotype genotype has not been matched with any other specimen in our dataset, possibly because we consider this species transitional or belonging to *Rubus* ser. *Pallidi*, and therefore, we have excluded such specimens from our sampling if fully developed.

Rubus pallidifolius E.H.L.Krause in Prahl, Krit. Fl. Schlesw.-Holst. 2(1): 78. 1889 – Lectotype (designated by Weber in Nordic J. Bot. 18: 40. 1998): Locis apricis et arenosis ad "Sahr" in collibus Hyttebjergene, 10 Aug 1886, *Friderichsen & Hinrichsen; Friderichsen & Gelert, Rubi Exs. Dan. Slesv. no. 45* (C, n.v.; isolectotype: KIEL, n.v.).

Rubus picearum (A.Beek) A.Beek in Gorteria 12: 58. 1984 – Holotype: Epen, Onderste Bos, 8 Aug 1967, *Van de Beek A74* (U, n.v.; isotype: L 2D-barcode L.3288058 [image!]).

Note. – A plant from the *locus classicus* cultivated by the author of the name and shown in Van de Beek (2018) was genotyped. Its genotype has not yet been associated with any other sample in our dataset. However, no other specimens identified as this species were available for analysis.

Rubus praticolor A.Beek in Gorteria 24: 26. 1998 – Holotype: Putven tussen Chaam en Alphen, aan begin van laantje naar dagrecreatieterrein/speelweide, 26 Jul 1996, *Van de Beek 9675* (L, n.v.).

Note. – A topotype collected by the author of the name proved to be identical with the plant of "*Rubus serpens*" sensu Van de Beek (2018) – Genotype 72. More data is needed to clarify these two names.

Rubus proiectus A.Beek, Brombeeren Geldrischen Dist. [Thesis]: 102. 1974 – Holotype: Amelisweert bij Utrecht, 31 Jul 1971, *Van de Beek A56a* (U barcode U 0005888 [image!]).

Note. – Although Kurtto & al. (2010) included this species in *Rubus* ser. *Glandulosi*, Van de Beek (2025) and Hassler (2024) included it in *R.* ser. *Pallidi*, which is probably more appropriate considering the strong prickles and rather sparse shortly stalked glands.

Rubus pseudolusaticus G.H.Loos in Florist. Rundbr. 34(2): 81. 2001 – Holotype: Germania, Westphalia, Höxter-Ottbergen, der Stoot, Waldweg direkt an der Höhe 322.8, 5 Sep 1999, *Loos 999-66* (MSTR, n.v.; isotype: BOCH, n.v.).

Rubus pseudovitis Plien. in Hassler, Fl. German. 3: 257. 2024 – Holotype: Baden-Württemberg, Schwäbisch-Fränkische Waldberge, "Rößwald", Waldweg von TP 515.8 nach NE, nach <100 m, 1 Aug 2011, *Plieninger Pl 7051* (STU barcode SMNS-STU-PH-0158058 [image!]; isotype: KR, n.v.).

Note. – Only two specimens identified as this species (including paratype *Plieninger Pl 3729* [STU]) were genotyped; only one other specimen of the same genotype (*Sochor MS298/21* [OL] from Warmbronn; 50 km distant) was detected in our dataset.

Rubus pulchricaulis Plien. in Carolinea 66: 54. 2008 – Holotype: Baden-Württemberg, Kraichgau (Westteil), Südteil "Hammberg", Waldweg nahe (nördlich) der Bundesstraße, 2 Jul 2006, *Plieninger Pl 5818* (KR [image!]; isotype: STU, n.v.).

Rubus rynnestiganus Schön in Kochia 18: 54. 2025 – Holotype: Deutschland, Thüringen, Landkreis Gotha, nördlich Georgenthal, ostnordöstlich Wachskopf und Schönauer Straße (K26), West-Rand Waldfahrweg in einem Laubwald, 30 Jul 2021, *Schön 1017* (JE barcode JE00028913 [image!]; isotypes: herb. Fürnrohr, n.v., herb. Jansen, n.v., herb. Matzke-Hajek, n.v., herb. Schön, n.v.).

Rubus serpens Weihe ex Lej. & Courtois, Comp. Fl. Belg. 2: 172. 1831 – Lectotype (designated by Van de Beek in Gorteria 40: 57. 2018): Malmed et prope Verviam, s. dat., *s.n.* (BR barcode BR0000005577231 [image!]).

Note. – The lectotype DNA sample turned out to be unusable for unambiguous genotype determination due to heavily fragmented DNA. For the sake of stability of nomenclature, we accept the conception of A. van de Beek (Van de Beek, 2018) for the time being, whose cultivated material from Drielandenpunt, Netherlands (accession number AvdB2020.94) was genotyped. It belongs to Genotype 72 which has so far been detected (apart from two Dutch localities) at two nearby localities in southern Lancashire, England.

Rubus speculatus Matzke-Hajek in Osnabrück. Naturwiss. Mitt. 23: 215. 1997 – Holotype: Nordrhein-Westfalen, Oberbergischer Kreis, nordwest-exponierter Waldrand 1 km südwestl. Hespert, unweit A4-Anschlußstelle Reichshof-Eckenhagen, 6 Jul 1996, *Matzke-Hajek 960706.5* (B [image!]; isotypes: HBG, n.v., MSTR, n.v., herb. Matzke-Hajek, n.v.).

Rubus urocerus Plien. in Hassler, Fl. German. 3: 241. 2024 – Holotype: Baden-Württemberg, Kraichgau, "Garnberg", Waldweg N-S, N Kreuzung bei TP 299.0, 26 Jun 2023, *Plieninger Pl 12055* (STU [image!]).

Note. – Three specimens identified under this name, including a paratype (*Plieninger Pl 6711.n* [STU]) were proved to belong to the same genotype (269).

D. Doubtful taxa and names with unclear taxonomic value

Rubus asper J.Presl & C.Presl, Delic. Prag.: 222. 1822 – **Lectotype (designated here):** In sylvaticis ad Tučap C. Tab. [circuli Taborensis], ad Haynspach cir. Lit.

[circuli Litomericensis; now Lipová near Šlunkov], Jun 1819, *s. coll., s.n.* (PRC barcodes PRC 454287 [image!], PRC 454288 [image!], PRC 454289 [image!], on three sheets).

Note. – The protologue includes only one locality (ad Tučap circuli Taborensis), but two localities are stated on the label of the type specimen. However, this specimen is morphologically homogeneous and probably originated from a single plant. Due to the age and condition of the lectotype, no genotypic data could have been obtained from its sample. Although the lectotype may appear similar to *Rubus divulgatus*, it differs from it by large straight inflorescence with long leafless apex, rather sparse stalked glands on sepals, and stamens longer than styles. The differences from other recognised species are even larger. Therefore, it must be concluded that *R. asper* is probably only a singular or local genotype.

Rubus egeniflorus Progel in Ber. Bot. Vereines Landshut 11: 136. 1889 – **Lectotype (designated here):** Waldmünchen am Böhmerwald. In der vord. Heinzlgrün, Jul 1887, *A. Progel s.n.* (M barcode M-0213985 [image!]).

Note. – No other sample in our dataset matched the genotype of the analysed lectotype. The name, therefore, probably refers to a singular or local genotype or *Rubus glandulosus*.

Rubus glaucinellus Sudre in Bull. Soc. Bot. France 52: 341. 1905 – Type: not designated.

Note. – DNA sample of a proposed isolectotype LAU-0133995 (D. Mercier, unpub.) was studied, but has not been associated with any other specimen from our dataset. This species is not accepted in modern literature (e.g., Kurtto & al., 2010).

Rubus hercynicus G.Braun, Herb. Ruborum Germ. (exs.): no. 19. 1877 – Lectotype (designated by Weber in Abh. Ber. Naturkundemus. Görlitz 61(8): 34. 1987): Harz, bei Goslar (auf Grauwacke), Jul 1876, *Braun Herb. Ruborum Germ. no. 19* (HAN, n.v.; isolectotypes: JE barcode JE00014278 [image!], KFTA barcode KFTA0000185 [image!], LD, n.v.).

Notes. – The genotype of isolectotype from LD has not been associated with any other specimen yet. Thirteen specimens from the Lausitzer Gebirge and the Fulda-Werra-Bergland region identified by F.W. Sander and W. Jansen, respectively, as *Rubus hercynicus* were of seven different genotypes, mostly singular or narrowly local. Also, in the rest of the batological community, the conception of this species is very unclear. These are the reasons for considering *R. hercynicus* doubtful (a singular or local genotype).

Rubus insidiosus Progel in Ber. Bot. Vereines Landshut 11: 137. 1889 – **Lectotype (designated here):** Waldmünchen, im Rieselwald, an der Straße vor den Himmelreichwiesen, Jul 1879, *Progel 664* (M barcode M-0214008 [image!]).

Note. – Three specimens from the original material analysed showed two genotypes unique within our dataset, so the name probably refers to a singular or local genotype or *Rubus glandulosus*.

Rubus irroratus (Progel) Sabr. in Deutsche Bot. Monatsschr. 8: 6. 1890 ≡ *R. cerchoviensis* var. *irroratus* Progel in Ber. Bot. Vereines Landshut 8: 92. 1882 (“1880–1881”) – Holotype: exs. n. 616 (untraced).

Note. – We analysed a specimen collected by A. Progel at/near the type locality (Loc. typ. cit.: W. a. B. [Waldmünchen am Böhmerwald], Rieselwald). However, this specimen was probably not a part of the original material, as it was probably collected after the species’ formal description. This can be deduced only indirectly from the label’s text and the comments in Progel (1882, 1889). Its genotype is unique in our dataset and if it is taxonomically identical to the type, the name probably refers to a singular or local genotype or to *Rubus glandulosus*.

Rubus laetevirens Progel ex G.Braun, Herb. Ruborum Germ. (exs.) 10: no. 204. 1881 – Holotype: s. locus [Waldmünchen, vom Rieselwald bis Unterhütte; Progel, 1882], s. dat., *Progel 204*. (not located; isotypes: JE barcode JE00014293 [image!], KFTA barcode KFTA0000622 [image!]).

Note. – No other sample in our data set matched the genotype of the isotype analysed. The name, therefore, probably refers to a singular or local genotype or *Rubus glandulosus*.

Rubus melanochlamys Progel ex G.Braun, Herb. Ruborum Germ. (exs.) 10: no. 202. 1881 – Holotype: Waldmünchen am Böhmerwald, in Bergwäldern, Aug 1881, *Progel 202* (untraced; isotype: JE barcode JE00014275 [image!]).

Note. – The isotype analysed showed a unique genotype within our dataset, so the name probably refers to a singular or local genotype or *Rubus glandulosus*.

Rubus melamporphyrus A.Beek in Gorteria 24: 23. 1998 – Holotype: Silesia, s. dat., *Weihe s.n.* (BR barcode BR0000005294824 [image!]).

Note. – Since the type collection is very old (with a low probability of obtaining good genotyping data), morphologically hardly interpretable, and geographically too broadly localised (Austrian Silesia of that time partly overlapped with the range of *Rubus glandulosus*), we conclude that this name has unclear interpretation (probably name for a local biotype or a later synonym of *R. glandulosus*) for the present moment.

Rubus multisetosus Progel ex G.Braun, Herb. Ruborum Germ. (exs.) 10: no. 203. 1881 – Holotype: Waldmünchen am Böhmerwald, in Bergwäldern, Aug 1881, *Progel 203* (not located; isotype: JE barcode JE00014269 [image!]).

Note. – No other sample in our dataset matched unambiguously the genotype of the analysed isotype. It was tentatively (due to poor genotypic data) assigned to Genotype 91, which was detected only once in our data set, namely in a specimen from northern Bohemia.

Rubus praetextus Sudre, Excurs. Batol.: 78. 1900 – Type: unknown.

Note. – The species is accepted in Kurtto & al. (2010) based on Edees & Newton (1988) and reported from Belgium, England, and France. The two available samples under this name identified by A. Newton and R. Randall from the U.K. belong to the same genotype. However, the type locality (Loc. typ. cit.: Saint-Lizier d'Ustou, vers Bielle) lies in the Pyrenees 30 km from the region where Sochor & al. (2024a) detected strictly sexual populations (*Rubus glandulosus*). If sexuality is confirmed on the northern side of the Pyrenees and the type agrees with the delimitation of *R.* ser. *Glandulosi*, this name should be considered a later synonym of *R. glandulosus*, while the British genotype highly probably forms a different species.

Simplified key to species of *Rubus* ser. *Glandulosi*

Note. – This key is intended for rapid identification only. Due to the extensive variability and plasticity in the group and many singular or local genotypes or genotypes taxonomically not yet recognised, a reliable determination can only be achieved by further confirmation by detailed morphological studies or genotyping.

1. Stems high-arching to suberect; prickles on primocanes mostly hidden among red long-stalked glands; leaves glabrous and glossy above, white-felted without long patent hairs, velvety to touch beneath; diploids........***R. moschus***
1. Stems usually prostrate to low-arching, rarely up to suberect; prickles on primocanes prominent, usually distinctly longer than stalked glands; leaves usually hairy and ± matt above, not felted or felted, but always with long patent hairs, more or less hairy to touch beneath; polyploids........2
2. Seeds produced almost exclusively sexually; plants forming morphologically variable populations without repeatedly occurring stable morphotypes; plants of West Asia and southern Europe up to the Carpathians, Moravia and adjacent regions of Bohemia and Silesia, Alps, and Pyrenees ....***R. glandulosus***
2. Seeds produced partly via apomixis; plants forming stable morphotypes within and among populations; plants of northwestern Europe and extra-Carpathian regions of Poland, Ukraine, and Romania........3
3. Primocane leaves mostly 3-foliolate........4
3. Primocane leaves mostly 5-foliolate........27
4. Primocane stems glabrous or subglabrous........5
4. Primocane stems sparsely to densely hairy........14
5. Styles greenish........6
5. Styles at least basally reddish or pinkish........9
6. Ovaries hairy........7
6. Ovaries glabrous........8
7. Stamens shorter than styles ....***R. edentulus***
7. Stamens longer than styles ....***R. angloserpens***
8. Stamens shorter than styles ....***R. serpens***
8. Stamens as long as or longer than styles ..... ***R. nigricans***
9. Ovaries hairy with tufted hairs ....***R. guentheri***
9. Ovaries glabrous (to slightly hairy) 10
10. Inflorescence wide, open-paniculate........11
10. Inflorescence narrow, rather dense 12
11. Serration of primocane leaves shallow, 1.0–1.5 mm deep, periodical .... ***R. picearum***
11. Serration of primocane leaves 2–3 mm deep, weakly periodical ....***R. erythradenes***
12. Inflorescence leafy (almost) to the top .... ***R. oreades***
12. Inflorescence leafless on top........13
13. Primocane stems thin, rounded to bluntly angled; leaf serration rough ....***R. hilsianus***
13. Primocane stems thicker, angled; leaf serration fine ....***R. atrovinosus***
14. Styles at least basally reddish 15
14. Styles greenish or yellowish 16
15. Leaves glossy above; ovaries glabrous ....***R. speculatus***
15. Leaves matt above; ovaries hairy ....***R. divulgatus***
16. Robust shrubs; leaflets drooping, convex ....***R. flaccidifolius***
16. Usually rather small shrubs; leaflets not drooping, ± flat........17
17. Stamens as long as or longer than styles 18
17. Stamens shorter than styles 24
18. Ovaries tomentose ....***R. barberi***
18. Ovaries glabrous or glabrescent (to sparsely hairy)......19
19. Leaf serration rough, somewhat irregular........20
19. Leaf serration very fine, regular 22
20. Leaflet margin deeply incised to lobed, incisions 3–5(–6) mm deep; ovaries at the beginning with crisped hairs, later glabrescent ....***R. pseudovitis***
20. Leaflet margin with incisions around 1.0(–2.5) mm deep; ovaries glabrous 21
21. Leaves velvety hairy beneath........ ***R. haeupleri***
21. Leaves sparsely hairy on veins beneath, not distinctly hairy to touch........***R. exarmatus***
22. Terminal leaflets of primocane leaves broadly elliptical, abruptly narrowing into the apex, pruinose beneath........***R. coronae-aureae***
22. Terminal leaflets of primocane leaves obovate or elliptical, gradually narrowing into the apex, epruinose beneath........23
23. Terminal leaflets of primocane leaves distinctly hairy to touch, with stellate hairs, at sunny sites with whitish felt beneath; pedicels with prickles up to 3 mm long ....***R. lusaticus***
23. Terminal leaflet of primocane leaves not distinctly hairy to touch, without stellate hairs, at sunny sites without whitish felt beneath; pedicels with prickles up to 2 mm long........***R. pseudolusaticus***
24. Leaves sparsely hairy above .... ***R. chlorostachys***
24. Leaves with scattered to dense hairs above........25
25. Receptacle hairy ....***R. elegantifolius***
25. Receptacle glabrous........26

26. Terminal leaflets of primocane leaves narrowly elliptical to rhombical, with very short petiolule (15%–26% of the length of the lamina)................................ ***R. macescens***
26. Terminal leaflets of primocane leaves ovate-elliptical, with petiolule 32%–38% of the length of the lamina .... ***R. urocerus***
27. Primocane stems densely hairy....................................28
27. Primocane stems glabrous to sparsely hairy 39
28. Ovaries glabrous (to sparsely hairy) 29
28. Ovaries hairy 35
29. Styles reddish; stamens as long as or shorter than styles ....***R. hylonomus***
29. Styles greenish or yellowish; stamens longer than styles 30
30. Leaves subglabrous (to sparsely hairy) above...............31
30. Leaves rather densely hairy above 32
31. Upper inflorescence leaves small, simple ....***R. praticolor***
31. Inflorescence leaves mostly very large, top leaf 8–14 cm long...***R. negatus***
32. Terminal leaflets of primocane leaves convex ....***R. siemianicensis***
32. Terminal leaflets of primocane leaves flat 33
33. Terminal leaflets of primocane leaves suborbicular ....***R. gymnocarpus***
33. Terminal leaflets of primocane leaves obovate or elliptic 34
34. Stems grey-brown or grey-green, at sunny sites reddish or vinaceous; sepals reflexed to erect, with filiform tip........ .... ***R. piceeticola***
34. Stems dull reddish-purple; sepals (patent to) erect, with leafy-tip...***R. obscuriflorus***
35. Styles reddish or pink at least at base 36
35. Styles greenish or yellowish 37
36. Stalked glands on stems mostly less than 0.5 mm long (rarely up to 1.5 mm), prickles distinctly longer than glands.. ***R. elegans***
36. Stalked glands on stems very uneven in length, the longest almost as long as prickles, up to ca 5 mm long...***R. magnidentatus***
37. Leaves glossy beneath ....***R. lucentifolius***
37. Leaves matt beneath 38
38. Prickles on primocanes 3–4 mm long .... ***R. iuvenis***
38. Prickles on primocanes 5–6 mm long ..... ***R. pallidifolius***
39. Leaves subglabrous above 40
39. Leaves hairy above 41
40. Terminal leaflets of primocane leaves ovate or elliptical, serration periodic, blunt........................***R. erythrocomos***
40. Terminal leaflets of primocane leaves elliptical or obovate, serration rather regular, sharp............ ***R. holzfussii***
41. Leaves white-blueish beneath .... ***R. lividus***
41. Leaves green beneath..42
42. Indentation of leaves roughly serrate, leaves glabrous beneath and above .... ***R. ducatuscola***
42. Indentation of leaves fine serrate, leaves sparsely to scattered hairy beneath and above 43
43. Receptacle hairy; stamens shorter than styles ....***R. ostroviensis***
43. Receptacle glabrous or subglabrous; stamens as long as or longer than styles 44
44. Indentation of leaves fine serrate, with incisions 1–2 mm deep, teeth very broad and rounded; terminal leaflet gradually narrowing into 10–20 mm long apex ......***R. ignoratus***
44. Indentation of leaves more roughly serrate, with incisions up to 3 mm deep, teeth very sharp; terminal leaflet abruptly narrowing into (10–)20–30 mm long apex........ .... ***R. pulchricaulis***

■ AUTHOR CONTRIBUTIONS

Design of the research: MS with contribution of all authors; sampling: all authors; lab work and molecular data analysis: MS; data interpretations: all authors; species descriptions: ML, PL, JV, MS; first draft of the manuscript: MS. All authors contributed to and approved the final manuscript.

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