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The distinction between *Sagina apetala* and *S. micropetala* (Caryophyllaceae: Sagineae), their phylogenetic relationships, and a note on the coastal origin of some widespread ruderals

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Abstract: The distinction of the annual *Sagina apetala* and *S. micropetala* (= *S. apetala* subsp. *erecta*, *S. filicaulis*) is based mainly on the position of sepals in fruit and shape and colour of the sepals, but identification of the two species is difficult. A molecular phylogeny of material identified as *S. apetala* and *S. micropetala* as well as other species of the genus using two nuclear and two plastid markers showed that there exist two lineages that are sister to each other and can be unambiguously distinguished molecularly. Although many of the morphological characters used in the literature proved useful in distinguishing these two lineages, sepal indumentum is the most reliable character to discriminate between them in Germany. Whereas *S. micropetala* usually has glabrous sepals, the sepals of *S. apetala* usually are glandular-pubescent. The chromosome number of $2n = 12$ for *S. micropetala*, here determined for the first time, is identical to that of *S. apetala*, supporting the close relationship between the two species. *Sagina apetala* and *S. micropetala* are sister to *S. maritima*, an annual species from European coasts, which may imply a coastal origin of the two species. A brief review of the possible origin of other European ruderals from coastal relatives is provided.

Keywords: Caryophyllaceae, chromosome count, phylogeny, *Sagina*, *Sagina apetala*, *Sagina filicaulis*, *Sagina maritima*, *Sagina micropetala*, *Sagineae*

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Introduction

Sagina L. of tribe Sagineae (Caryophyllaceae) is a predominantly northern hemisphere genus of c. 33 species (Bittrich 1993; Alban & al. 2022). The genus occurs on all continents except Antarctica, and has its centre of diversity in Europe. The closest relative of *Sagina* is *Colobanthus* Bartl. (Harbaugh & al. 2010; Greenberg & Donoghue 2011), and the monophyly of these two genera was recently confirmed in a comprehensively sampled molecular phylogeny (Alban & al. 2022). Species of *Sagina* are small, erect or procumbent, sometimes caespitose or cushion-forming herbs. Most species have white petals while some are apetalous (Clapham & Jardine 1993; Jonsell 2001; Crow 2005). In Germany, seven species and one hybrid are currently recognized (Jäger 2011). Of these seven species, three have pentamerous flowers with white petals, and the other four have tetramerous flowers and often lack petals. The only perennial species among the tetramerous taxa is *S. procumbens* L., the type species of the genus. This species is a common weed typically growing in pave-

ment cracks and has been introduced to different parts of the world (e.g. the Americas; Crow 2005). Apart from being perennial, *S. procumbens* can be distinguished from other tetramerous species by the presence of a persistent basal leaf rosette, its procumbent growth, and pedicels curved downward after anthesis (Jäger 2011). Petals are often present and, when the flowers open, the anthers are still closed (pers. obs.). In contrast, the remaining tetramerous species, i.e. *S. apetala* Ard., *S. maritima* Don and *S. micropetala* Rauschert, are erect, have basal leaf rosettes that wither quickly, pedicels that remain erect after anthesis (Jäger 2011), petals present only rarely, and anthers open when flowers open (pers. obs.).

Sagina maritima is a coastal species of Europe occurring from the North Sea to the Mediterranean Sea (Clapham & Jardine 1993) in open sandy to clayey salt marshes (Jäger 2011). It has slightly succulent leaves that are shortly mucronate, and its sepals are obtuse. *Sagina apetala* and *S. micropetala* are never succulent and do not grow in coastal habitats. Their leaves have a long mucro, and at least the outer sepals (i.e. the two sepals

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overlapping the other two sepals) have been described as cucullate, mucronate or acute (Jonsell 2001; Jäger 2011; Duistermaat 2020).

The distinction between *Sagina apetala* and *S. micropetala* is more difficult to characterize. Both species occur in human-influenced habitats such as pavement cracks, open and disturbed habitats along roads and sandy dry grassland or sandy farmland (Jäger 2011). *Sagina apetala* has been reported to occur in more natural habitats such as sandy dry grasslands of Europe, western Asia and northern Africa (POWO 2021), whereas *S. micropetala* has mostly been reported from more strongly human-influenced habitats such as pavement cracks of Europe (POWO 2021). Both species seem to be more vulnerable to trampling than *S. procumbens* and avoid central parts of sidewalks (pers. obs.).

While some floras do not distinguish the two species (e.g. Crow 2005), other floras give different characters to discriminate between them. Parolly & Rohwer (2019) used only the position of sepals in fruit in most flowers, which are appressed to the capsule in *Sagina apetala* vs horizontally spreading in *S. micropetala*. This trait has also been used by Clapham & Jardine (1993), Duistermaat (2020) and Jäger (2011). All of these authors also stated that the outer sepals are (sub)acute and more or less flat in *S. apetala* vs (sub)obtuse, hooded or cucullate with a mucro in *S. micropetala*. Furthermore, Duistermaat (2020) described *S. micropetala* as having reddish sepal margins; these are white in *S. apetala*. Duistermaat (2020) and Jäger (2011) also stated that the sepals are much shorter than the capsules in *S. micropetala* but almost equal the capsule length in *S. apetala*.

In contrast to the above treatments, Jonsell (2001) gave different frequencies for the above traits. According to Jonsell (2001), *Sagina micropetala* has at least some flowers with spreading sepals (not necessarily spreading in most), the reddish margin of the sepals has been described for at least the bud stage, and the outer sepals are obtuse or cucullate. In contrast, *S. apetala* was distinguished by having acuminate to acute sepals with a white margin appressed to the fruit (Jonsell 2001).

In conclusion, position and shape of the (outer) sepals are the most commonly used traits to distinguish *Sagina apetala* and *S. micropetala*, sometimes complemented by other characters. Unfortunately, some of these characters are difficult to observe for various reasons. For example, sepal position depends on the developmental state of flowers and can be assessed correctly only at complete fruit maturity. Another example is the shape of sepals. While distinction between (sub)acute vs (sub)obtuse sounds fairly straightforward, this distinction refers only to the outer sepals, and the observation of white or hyaline margins and tiny mucros is very difficult in dry sepals at fruiting stage. For both species a large number of varieties have been described (e.g. 13 synonyms at varietal level for *S. apetala* incl. *S. micropetala* are given in Montserrat Martí & Montserrat Martí 1990) and are

still used for both species by some authors (e.g. Sell & Murrell 2018), indicating substantial morphological variation. All this raises the question whether distinction of *S. apetala* and *S. micropetala* at whatever rank is meaningful at all.

We use here the names *Sagina apetala* and *S. micropetala* according to Jäger (2011), although the name *S. micropetala* has some taxonomic problems, which we will discuss below. Although some of the floras cited above treat these two taxa at subspecific rank (i.e. *S. apetala* subsp. *apetala* and subsp. *erecta* (Hornem.) F. Herm.; e.g. Clapham & Jardine 1964, 1993; Parolly & Rohwer 2019), they use the same set of characters to distinguish between them.

In this study we will investigate the following questions: (1) Are there, among material provisionally identified as *Sagina apetala* and *S. micropetala*, two clades that can be distinguished with standard molecular markers? (2) If there are two clades, can these be unambiguously characterized morphologically? (3) Which names should be used for these clades? We will investigate these questions using a broad sample of *S. apetala* and *S. micropetala* from Germany and elsewhere in Europe for the observation of morphological characters and for phylogenetic reconstruction using standard DNA markers, i.e. the Internal and External Transcribed Spacers (ITS/ETS) and the two plastid spacers *atpB-rbcL* and *trnQ-rps16*. As we found that *S. apetala* and *S. micropetala* are closest relatives of the coastal *S. maritima*, we will briefly discuss the possibly coastal origin of *S. apetala* and *S. micropetala* as well as of other widespread European ruderals.

Material and methods

We used 76 samples of *Sagina* (Table 1), including *S. apetala* and *S. micropetala* (48 samples), *S. maritima* (14 samples) and *S. procumbens* (8 samples). We sampled all tetramerous species from Germany, but did not sample other tetramerous species of the genus because either these are perennials and of extra-European distribution, or they were sampled by Alban & al. (2022) and were found not to be closely related to the species of interest in this study. The sampling was complemented by the closest relatives of *S. apetala*, *S. micropetala* and *S. maritima* (i.e. *S. hookeri* Timaná, *S. japonica* (Sw. ex Steud.) Ohwi and *S. maxima* A. Gray) identified in a recent phylogenetic analysis (Alban & al. 2022). Samples were collected and dried on silica-gel, or herbarium specimens were used. The sampling was focused on Germany for the species of interest, but also included samples from other European countries and one introduced population from New Zealand.

DNA extraction and amplification of the nuclear ribosomal Internal Transcribed Spacer (ITS) and the two plastid spacers *atpB-rbcL* and *trnQ-rps16* were carried out as described in Alban & al. (2022). Primer design for

the External Transcribed Spacer (ETS) was performed for three samples of *Sagina*, i.e. Min209, Min319 and Sab141 (Table 1). The whole Intergenic Spacer region (IGS) was amplified using primer 18S-2L (Linder & al. 2000) and 26S-II (Ochsmann 2000). Amplified fragments were sequenced unidirectionally with primer 18S-2L. Based on these sequences, two reverse primers in conserved regions were designed: Sam1 5'-GGT AGT TCG CTG CCG GTA C-3' and Sam2 5'-AAG GAT GCT CGC GGT GTC A-3'. Most samples were amplified with primers 18S-2L and Sam2, which produced better results in the PCR. Sam1 was only used for some *S. maritima* samples where Sam2 did not result in any amplification. The PCR was carried out in 25 µL reactions containing 1× reaction buffer, 3.2 mM MgCl₂, 0.2 mM dNTPs, 80 µg/mL bovine serum albumin, 0.8 µM of each primer, and 0.04 U/µL NEB-Taq-polymerase. PCR cycles consisted of 94 °C for 1 min, followed by 35 cycles of 94 °C for 20 s, 62 °C for 30 s and 72 °C for 1 min, and finished by 94 °C for 20 s, 62 °C for 1 min 20 s, and 72 °C for 8 min. PCR products were sequenced with both primers used in the PCRs by StarSeq (Mainz, Germany). Sequences were checked, edited and aligned manually and were made available on GenBank (Table 1).

Phylogenetic reconstructions using maximum likelihood were carried out using RAXML v.8.2.12 (Stamatakis 2014). Each of the four DNA regions was run individually under the GTRGAMMA model and bootstrapping was stopped automatically. To combine datasets, phylogenies of individual markers were checked manually for supported conflicts (bootstrap support in both phylogenies ≥70). The phylogenies of the nuclear ribosomal spacers ITS and ETS were congruent, except for the position of *Sagina maxima*. In the ITS dataset, *S. maxima* was sister to *S. hookeri*, while it was sister to *S. procumbens* in the ETS dataset. To combine the ITS and ETS dataset, *S. maxima* was removed from both datasets. The phylogenies of the plastid spacers *atpB-rbcL* and *trnQ-rps16* were found to be congruent and the datasets were combined into the plastid dataset. Phylogenetic reconstructions were carried out for both combined datasets as described above. The resulting phylogenies were again checked for supported conflict. There was no supported conflict between the plastid and the nuclear phylogenies, but *S. maxima* was removed from the plastid dataset before combination with the nuclear dataset. Phylogenetic reconstruction with RAXML was carried out for the complete dataset including all markers as described for all other datasets.

Morphology was investigated using specimens from MJG (Table 1; herbarium codes according to Index herbariorum <http://sweetgum.nybg.org/science/ih/>). We observed the following morphological characters based on descriptions in different floras and other publications (Arduino 1764; Jordan 1849; Gremler 1878; Koch 1878; Hermann 1912; Clapham & Jardine 1993; Jäger 2011; Jonsell 2001; Stace 2010; Tison & Foucault 2014;

Pignatti 2017; Sell & Murrell 2018; Parolly & Rohwer 2019; Duistermaat 2020): position of sepals at fruiting time, comparative size of sepals and capsule, shape of sepal tips, presence of glandular hairs on sepals, sepal margin colour, indumentum of leaves, indumentum of axis, and shape of capsule. Characters were observed, when available, in five individuals per herbarium sheet and five flowers, leaves and axes per individual.

For chromosome counts of *Sagina apetala* and *S. micropetala*, seeds obtained from herbarium specimens and silica dried samples were treated with 0.2% gibberellic acid on filter paper in petri dishes for 24 h in a refrigerator. Gibberellic acid was then replaced by water and seeds were kept in the refrigerator and checked for germination every three days. Germination usually occurred within 2–4 weeks. Seedlings were either transferred into pots with standard substrate and kept in the greenhouse, or root tips were taken directly from the seedlings. Root tips were taken in the morning and treated with 2 mM 8-hydroxyquinoline for 3 h at room temperature, and then transferred to ethanol/acetic acid (volume ratio 3:1) for 24–48 h at room temperature. Afterward, root tips were transferred to 70% ethanol and stored in the refrigerator until further treatment. Hydrolysis was carried out for 10 min at 60 °C in 1N HCl. The root tips were transferred to H₂O to stop hydrolysis and stained in propionic orcein. Chromosomes were observed with an Olympus CX31 microscope.

For lectotypification of names we identified herbaria with type collections of the respective author(s) based on Taxonomic Literature, ed. 2 (TL-2; Stafleu & Cowan 1976–1988; Stafleu & Mennega 1992–2000; Dorr & Nicolson 2008–2009) and searched for type material in the digital collections of these herbaria (i.e. COI – <https://coicatalogue.uc.pt/>; E – <https://data.rbge.org.uk/search/herbarium/>; G – <https://www.ville-ge.ch/musinfo/bd/cjb/chg/>; LY – <https://explore.recolnat.org/search/botanique/type=index>; P – <https://science.mnhn.fr/institution/mnhn/collection/p/item/search/>) and in major indices (Tropicos – <https://www.tropicos.org/>; JSTOR Global Plants – <https://plants.jstor.org/>; JACQ Virtual herbaria – <https://www.jacq.org/>; SEINet – <https://swbiodiversity.org/seinet/collections/>; Sweden's Virtual Herbarium – <http://herbarium.emg.umu.se/>; GBIF – <https://www.gbif.org/>). For type identification at C, E, LD and LY, we contacted herbarium staff. Specimens were seen as digital images, and specimens not seen were indicated as “n.v.”.

Results

All phylogenetic reconstructions using the individual markers were congruent, except for the position of *Sagina maxima*. While *S. maxima* was sister to *S. hookeri* in the ITS phylogeny, it was sister to *S. procumbens* in all other individual phylogenies (not shown). Therefore, *S. maxima* was removed from the complete dataset. The

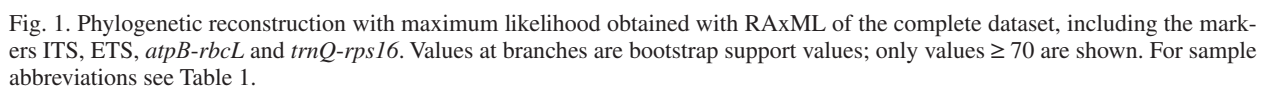
Table 1. List of specimens used for phylogenetic analyses, including lab abbreviations (Abbr.), locations, vouchers and GenBank accession numbers (n.a. = not amplified/available).

Abbr.	Locality	Coordinates	Voucher	ITS	ETS	<i>atp B-rbc L</i>	<i>trnQ-rps 16</i>
<i>Sagina apetala</i> Ard.							
Sab163	Germany, Hessen, Leun-Biskirchen	50°31'58.0"N, 08°18'48.4"E	<i>M. S. Dillenberger 20018</i> (MJG 028562)	OK446566	OK505919	OK505858	OK505796
Sab167	Germany, Hessen, Frankfurt-Schwanheim	50°05'26.2"N, 08°33'50.6"E	<i>M. S. Dillenberger 20012</i> (MJG 028399)	OK446567	OK505920	OK505859	OK505797
Sab178	Germany, Hamburg, Hoheluftchaussee		<i>J. W. Kadereit 1</i> (MJG 028391)	OK446568	OK505921	OK505860	OK505798
Sab186	Germany, Hessen, Hochheim-Massenheim	50°02'16.9"N, 08°23'24.7"E	<i>M. S. Dillenberger 20011</i> (MJG 028396)	OK446569	OK505922	OK505861	OK505799
Sab192	Germany, Hessen, Frankfurt-Schwanheim	50°05'26.2"N, 08°33'50.6"E	<i>M. S. Dillenberger 20012</i> (MJG 028399)	OK446570	OK505923	OK505862	OK505800
Sab195	Germany, Hessen, Leun-Biskirchen	50°31'58.0"N, 08°18'48.4"E	<i>M. S. Dillenberger 20018</i> (MJG 028562)	OK446571	OK505924	OK505863	OK505801
Sab205	Cyprus, Dhiorios		<i>R. F. Meikle 2424</i> (C s.n.)	OK446572	OK505925	OK505864	OK505802
Sab206	New Zealand, Canterbury Land District, Leeston	43°49'S, 172°15'E	<i>H. Nielsen 10077</i> (C s.n.; CHR 512186)	OK446573	OK505926	OK505865	OK505803
Sab209	Greece, Mitikas	38°41'N, 20°56'E	<i>A. Strid & al. 33344</i> (C s.n.)	OK446574	OK505927	OK505866	OK505804
Sab211	Greece, Mistras	37°04'N, 22°22'E	<i>A. Strid & al. 39232</i> (C s.n.)	OK446575	OK505928	OK505867	OK505805
Sab213	Greece, Island of Lesbos, Megalochorion	39°01'N, 26°22'E	<i>A. Strid & al. 26149</i> (C s.n.)	OK446576	OK505929	OK505868	OK505806
Sab217	Greece, Island of Samothraki, Loutra (Therma)	40°28'N, 25°40'E	<i>A. Strid & al. 43233</i> (C s.n.)	OK446577	OK505930	OK505869	OK505807
Sab218	Greece, Island of Samothraki, Akr. Kipos	40°25'N, 25°41'E	<i>A. Strid & al. 43160</i> (C s.n.)	OK446578	OK505931	OK505870	OK505808
<i>Sagina hookeri</i> Timaná							
Sab128	France, TAAF, Île Amsterdam	37°50'24.1"S, 77°31'54.3"E	<i>J.-C. Jolinon 962</i> (P 04937020)	MT415638	OK505932	MT534486	MT671701
Sab151	France, TAAF, Île Amsterdam		<i>P. Noel s.n.</i> (P 00915539)	MT415639	OK505933	MT534487	OK505809
<i>Sagina japonica</i> (Sw. ex Steud.) Ohwi							
Sab25	China, Anhui, Qimen		<i>not readable 93201</i> (OSC 177365)	MT415640	OK505934	MT534488	MT671702
<i>Sagina maritima</i> Don							
Sab63	Spain, Mallorca, Porto Cristo	39°32'N, 03°21'E	<i>Excursion</i> (C 3094)	MT415642	OK505947	MT534490	MT671704
Sab78	United Kingdom, East Sussex, Seaford		<i>A. Hansen s.n.</i> (C s.n.)	MT415643	OK505948	MT671787	MT671705
Sab141	Germany, Schleswig-Holstein, Hallig Langeneß	54°36'N, 08°30'E	<i>J. W. Kadereit, T. Messerschmid s.n.</i> (MJG 027604)	MT415641	OK505935	MT534489	MT671703

Sab176	United Kingdom, Cardiganshire, Aberystwyth	<i>A. O. Chater s.n.</i> (MJG 028669)	OK446579	OK446579	OK505936	OK505871
Sab183	United Kingdom, Cardiganshire, Aberystwyth	<i>A. O. Chater s.n.</i> (MJG 028669)	OK446580	OK446580	OK505937	OK505872
Sab194	United Kingdom, Cambridge	<i>C. D. Preston s.n.</i> (MJG 028557)	OK446581	OK446581	OK505938	OK505873
Sab204	Portugal, Azores, Ilha do Faial, Horta	<i>A. Hansen 28</i> (C s.n.)	OK446582	OK446582	OK505939	OK505874
Sab212	Spain, A Coruña, Praia do Testal	<i>F. Gómez Vigide s.n.</i> (C 263)	OK446583	OK446583	OK505940	OK505875
Sab215	Greece, Keramoti, Salines	<i>A. Strid & al.</i> 42288 (C s.n.)	OK446584	OK446584	OK505941	OK505876
Sab216	Greece, Anaxiatiko	<i>A. Strid 34428</i> (C s.n.)	OK446585	OK446585	OK505942	OK505877
Sab219	Greece, Anaxiatiko	<i>A. Strid 34421</i> (C s.n.)	OK446586	OK446586	OK505943	OK505878
Sab220	Greece, Island of Lesbos, Parakila	<i>A. Strid & al.</i> 26026 (C s.n.)	OK446587	OK446587	OK505944	OK505879
Sab221	Greece, Island of Lesbos, Skala Kalloni	<i>A. Hansen & H. Nielsen 8488</i> (C s.n.)	OK446588	OK446588	OK505945	OK505880
Sab222	Greece, Island of Lesbos, Plomari	<i>A. Hansen & H. Nielsen 3814</i> (C s.n.)	OK446589	OK446589	OK505946	OK505881
<i>Sagina maxima</i> subsp. <i>crassicaulis</i> (S. Watson) G. E. Crow						
Sab18	U.S.A., Oregon, Yachats	<i>R. R. Halse 4693</i> (OSC 179610)	MT415644	n.a.	MT534491	MT671706
Sab75	Canada, British Columbia, Moresby Island	<i>Calder & Taylor 23785</i> (C s.n.)	MT415645	OK505949	MT534492	MT671707
<i>Sagina micropetala</i> Rauschert						
Min209	Germany, Rheinland-Pfalz, Mainz	<i>M. S. Dillenberger 20121</i> (MJG 007678)	KF737496	OK505950	MT534495	KY700825
Sab162	Germany, Rheinland-Pfalz, Herrstein	<i>R. Hand 9365</i> (MJG 028519; B)	OK446590	OK505951	OK505882	OK505821
Sab164	Germany, Niedersachsen, Northeim	<i>P. Ciongwa PC 329</i> (MJG 028663)	OK446591	OK505952	OK505883	OK505822
Sab165	Germany, Hessen, Hattersheim am Main	<i>M. S. Dillenberger 20017</i> (MJG 028518)	OK446592	OK505953	OK505884	OK505823
Sab166	Germany, Hessen, Nentershausen	<i>M. S. & S. Dillenberger 20014</i> (MJG 028388)	OK446593	OK505954	OK505885	OK505824
Sab168	Germany, Rheinland-Pfalz, Schloßböckelheim	<i>T. Gregor 19147</i> (MJG 028384; FR)	OK446594	OK505955	OK505886	OK505825
Sab169	Germany, Rheinland-Pfalz, Boppard	<i>T. Gregor 19146 & C. Schmitt</i> (MJG 028385; FR)	OK446595	OK505956	OK505887	OK505826
Sab170	Germany, Niedersachsen, Northeim	<i>P. Ciongwa PC 329</i> (MJG 028663)	OK446596	OK505957	OK505888	OK505827
Sab171	Germany, Rheinland-Pfalz, Mainz-Gonsenheim	<i>J. W. Kadereit 3</i> (MJG 028390)	OK446597	OK505958	OK505889	OK505828

Abbr.	Locality	Coordinates	Voucher	ITS	ETS	<i>atpB-rbcL</i>	<i>trnQ-ps16</i>
Sab172	Germany, Rheinland-Pfalz, Mainz-Gonsenheim		<i>J. W. Kadereit</i> 3 (MJG 028390)	OK446598	OK505959	OK505890	OK505829
Sab173	Germany, Hamburg, Landungsbrücken		<i>J. W. Kadereit</i> 2 (MJG 028392)	OK446599	OK505960	OK505891	OK505830
Sab174	Germany, Niedersachsen, Northheim	51°43'33.6"N, 09°58'08.4"E	<i>P. Ciongwa PC 327</i> (MJG 028664)	OK446600	OK505961	OK505892	OK505831
Sab175	United Kingdom, Cambridge		<i>C. D. Preston s.n.</i> (MJG 028558)	OK446601	OK505962	OK505893	OK505832
Sab177	Germany, Hamburg, Hoheluftchaussee		<i>J. W. Kadereit</i> 1 (MJG 028391)	OK446602	OK505963	OK505894	OK505833
Sab179	Germany, Schleswig-Holstein, Großenbrode	54°22'30.3"N, 11°05'05.0"E	<i>J. Timmermann-Trosiener ITT-1</i> (MJG 028395)	OK446603	OK505964	OK505895	OK505834
Sab180	Germany, Niedersachsen, Northheim	51°42'05.4"N, 10°01'32.9"E	<i>P. Ciongwa PC 330</i> (MJG 028666)	OK446604	OK505965	OK505896	OK505835
Sab181	Germany, Niedersachsen, Northheim	51°42'28.8"N, 10°00'28.8"E	<i>P. Ciongwa PC 328</i> (MJG 028665)	OK446605	OK505966	OK505897	OK505836
Sab182	Germany, Schleswig-Holstein, Bad Schwartau	53°55'34.4"N, 10°41'07.7"E	<i>J. Timmermann-Trosiener ITT-2</i> (MJG 028394)	OK446606	OK505967	OK505898	OK505837
Sab184	Germany, Schleswig-Holstein, Lauenburg	53°42'16.1"N, 10°33'35.6"E	<i>J. Timmermann-Trosiener ITT-3</i> (MJG 028393)	OK446607	OK505968	OK505899	OK505838
Sab185	Germany, Hessen, Weißenhasel	51°01'36.2"N, 09°56'06.8"E	<i>M. S. & S. Dillenberger 20010</i> (MJG 028397)	OK446608	OK505969	OK505900	OK505839
Sab187	Germany, Hessen, Schlitz-Frauombach	50°40'29.3"N, 09°36'43.2"E	<i>T. Gregor & C. Latka s.n.</i> (MJG 028401)	OK446609	OK505970	OK505901	OK505840
Sab188	Germany, Hessen, Schlitz-Frauombach	50°40'29.3"N, 09°36'43.2"E	<i>T. Gregor & C. Latka s.n.</i> (MJG 028401)	OK446610	OK505971	OK505902	OK505841
Sab189	Germany, Rheinland-Pfalz, Herrstein	49°46'52.0"N, 07°20'08.0"E	<i>R. Hand 9365</i> (MJG 028519; B)	OK446611	OK505972	OK505903	OK505842
Sab190	United Kingdom, Cambridge		<i>C. D. Preston s.n.</i> (MJG 028560)	OK446612	OK505973	OK505904	OK505843
Sab191	United Kingdom, Cambridge		<i>C. D. Preston s.n.</i> (MJG 028561)	OK446613	OK505974	OK505905	OK505844
Sab193	Germany, Hessen, Hochheim-Massenheim	50°02'21.5"N, 08°23'16.8"E	<i>M. S. Dillenberger 20013</i> (MJG 028400)	OK446614	OK505975	OK505906	OK505845
Sab196	Germany, Hessen, Nentershausen	51°00'50.8"N, 09°55'59.3"E	<i>M. S. & S. Dillenberger 20015</i> (MJG 028387)	OK446615	OK505976	OK505907	OK505846
Sab197	United Kingdom, Cambridge		<i>C. D. Preston s.n.</i> (MJG 028559)	OK446616	OK505977	OK505908	OK505847
Sab198	Germany, Hessen, Hofheim-Diedenberg	50°03'42.3"N, 08°25'04.2"E	<i>M. S. Dillenberger 20005</i> (MJG 028312)	OK446617	OK505978	OK505909	OK505848
Sab199	Germany, Hessen, Hofheim-Diedenberg	50°03'42.3"N, 08°25'04.2"E	<i>M. S. Dillenberger 20005</i> (MJG 028312)	OK446618	OK505979	OK505910	OK505849
Sab200	Germany, Hessen, Schlitz		<i>T. Gregor 19189</i> (FR 38361684)	OK446619	OK505980	OK505911	OK505850

Sab207	United Kingdom, Westmoreland, Gatebeck		<i>G. Halliday 9/76 (C s.n.)</i>	OK446621	OK505982	OK505912	OK505851
Sab223	Belgium, Gent, Koopvaardijlaan		<i>P. Goetghebeur 5219 (C 11192)</i>	OK446622	OK505983	OK505913	OK505852
Sab224	Germany, Hessen, Wetzlar	50°33'19.6"N, 08°30'54.6"E	<i>M. S. Dillenberger & C. Dinges 20008 (MJG 028398)</i>	OK446623	OK505984	OK505914	OK505853
Sab225	Germany, Rheinland-Pfalz, Reitzenhain	50°09'26.7"N, 07°47'12.5"E	<i>M. S. Dillenberger 20016 (MJG 028386)</i>	OK446624	OK505985	OK505915	OK505854
<i>Sagina procumbens</i> L.							
Min183	Bulgaria, Kjustendil, Rila	42°07'48"N, 23°10'48"E	<i>J. Klein & S. Gencheva 29.8.7.2 (MJG 004137)</i>	KF737444	OK505986	MT534506	KY700826
Min208	Germany, Rheinland-Pfalz, Mainz	49°59'24"N, 08°14'24"E	<i>M. S. Dillenberger 20127 (MJG 009791)</i>	KF737495	OK505987	MT534507	KY817729
Min319	Germany, Hessen, Hofheim-Diedenbergen	50°03'36"N, 08°25'12"E	<i>M. S. Dillenberger 15002 (MJG 016484)</i>	KY817666	OK505988	MT534508	KY817731
Sab72	Greece, Pieria, Skotina	40°12'00"N, 22°10'48"E	<i>Andersen 11368 (C s.n.)</i>	MT415659	OK505991	MT534509	MT671714
Sab99	Germany, Rheinland-Pfalz, Mainz	49°59'24"N, 08°14'24"E	<i>M. S. Dillenberger 14047 (MJG 014940)</i>	MT415660	OK505992	MT534510	MT671715
Sab201	Germany, Schleswig-Holstein, Hallig Langeneß	54°36'N, 08°30'E	<i>J. W. Kadereit, T. Messerschmid s.n.</i>	OK446625	OK505989	OK505916	OK505855
Sab208	United Kingdom, Middlesex, Ruislip		<i>G. A. Matthews s.n. (C s.n.)</i>	OK446626	OK505990	OK505917	OK505856
Sab226	Germany, Nordrhein-Westfalen, Borken	51°50'37"N, 06°51'40"E	<i>M. S. Dillenberger 15022 (MJG 017807)</i>	OK446627	n.a.	OK505918	OK505857



results of the phylogenetic reconstruction of the complete dataset of all DNA markers is shown in Fig. 1. Based on Alban & al. (2022), *S. procumbens* was used as root. *Sagina japonica* and *S. hookeri* were sister to each other and together were sister to the group containing *S. maritima*, *S. apetala* and *S. micropetala*. The latter group was supported with bootstrap support (BS) of 99. The existence of a well-supported clade containing *S. maritima*, *S. micropetala* (as *S. apetala* subsp. *erecta*) and *S. apetala* had already been shown by Alban & al. (2022) in their phylogenetic analysis of *Sagina* including 25 species of the genus. We consider it unlikely that any of the species not sampled by Alban & al. (2022) fall into the clade of *S. maritima*, *S. apetala* and *S. micropetala* identified here. Of the six species not sampled by Alban & al. (2022) only one is tetramerous but is found only on a southern Indian Ocean island. Of the five pentamerous species, three are from New Guinea and one is from South America. The only unsampled species that occurs geographically close to Europe is *S. libanotica* Rech. f., from Lebanon, which is a perennial with pentamerous flowers and morphologically most similar to *S. saginoides* (L.) H. Karst. (Rechinger 1952).

Sagina maritima (BS 100) and the clade comprising *S. apetala* and *S. micropetala* (BS 92) were both monophyletic. The samples containing the two species of interest clearly fell into two clades. The larger clade contained 35 samples (clade I; BS 97), the smaller clade 13 samples (clade II; BS 100). Within clade II, one subclade (BS 98) contained six samples from Germany, and the other subclade (BS 79) contained seven samples from Greece, Cyprus and the introduced sample from New Zealand. Within clade I, no supported groups (BS ≥ 70) could be found.

For clades I and II, we obtained the following morphological results (Table 2). Unless indicated otherwise, percentage values refer to the percentage of flowers, leaves and axes with the relevant trait. In specimens of clade I, sepals were horizontally spreading in 56% of the flowers. While 87% of the individuals had at least some flowers at fruiting time showing this trait, 13% of the individuals had only flowers with sepals appressed to the capsule. Flowers had sepals equalling the capsule length in 87% (sepal length $> 4/5$ of capsule length). The capsule was more often broadly ovoid (capsule almost as wide as long; 60%) than narrowly ovoid (capsule width $\leq 4/5$ of capsule length; 40%). Sepal tips were usually obtuse (93%) and cucullate (62%), and a sepal mucro was visible in only 9% of the flowers. Mostly (97%) there were no glandular hairs on the sepals. The 3% of flowers with glandular-pubescent sepals represented 6% of the individuals investigated (94% of individuals had only glabrous sepals). Of these, three individuals were from the United Kingdom (all specimens from the United Kingdom investigated) and only two from Germany. The sepal margin was more often red (69%) than white (31%). Most individuals (87%) had at least some flow-

ers with a red sepal margin. The leaf margin was ciliate (84%), and half of the leaves had cilia extending to the upper half of the leaf (46%), while 38% were ciliate only at the base of the leaves. The axes were often glabrous (65%), non-glandular-pubescent in 31% of the individuals, and glandular-pubescent in 4%. Highest density of hairs, when present, could be found at the base of plants and decreased toward the inflorescence.

In clade II, sepals were appressed to the capsule in 91% of the flowers. Plants had sepals that were equaling the capsule length in 88%. The capsules were more often narrowly (65%) than broadly ovoid (35%). The sepal tip was acute in 61% of the flowers and usually flat (78%), and a sepal mucro was visible in only 11% of the flowers. The sepals were glandular-pubescent in 91% of the flowers, and all individuals had at least a few sepals with glandular hairs, especially in young flowers. The sepal margin was almost always white (96%). Half of the leaves were not ciliate (54%), while 45% were ciliate at the base. Only 1% of the leaves showed cilia on the upper half of the leaf. The axes were often glabrous (85%), never eglandular-pubescent, and glandular-pubescent in 15%. Indumentum density decreased strongly toward the base of plants where the axis was usually glabrous.

Chromosome counts are summarized in Table 3. For *Sagina micropetala*, a chromosome number of $2n = 12$ was counted for six populations from Germany. *Sagina apetala* was counted with $2n = 12$ for one population from Germany.

Discussion

Phylogeny of annual European *Sagina* species

Our phylogeny clearly shows that there exist three different clades among the tetramerous annual species from Germany. *Sagina maritima*, from across its distribution range from the North Sea to the Mediterranean Sea including a sample from the Azores, was found to be monophyletic. It is sister to all samples that were assigned to *S. apetala* and *S. micropetala*. These samples form two well-supported clades which, given the taxonomic history of the samples, can be recognized as two taxa (Fig. 1). We will treat these two taxa here as species because they are clearly separated molecularly, they occur sympatrically and even next to each other in pavement cracks (e.g. Sab177/178 from Hamburg, Germany; Table 1), and because we found no evidence for hybridization between them, even when growing in a mixed population.

Morphological characterization of *Sagina apetala* and *S. micropetala*

Recent floras (Clapham & Jardine 1993; Jäger 2011; Jonsell 2001; Stace 2010; Tison & Foucault 2014; Pignatti 2017; Sell & Murrell 2018; Parolly & Rohwer 2019; Duistermaat 2020) have used a common set of

Table 2. Morphological characters investigated in specimens of *Sagina apetala* and *S. micropetala*.

Character	Percentage of flowers/leaves/ axes		Percentage of individuals with only this character state	
	Clade II (<i>Sagina apetala</i>)	Clade I (<i>Sagina micropetala</i>)	Clade II (<i>Sagina apetala</i>)	Clade I (<i>Sagina micropetala</i>)
Sepals appressed to capsule	91.25	44.15	62.5	12.94
Sepals horizontally spreading	8.75	55.85	0	21.18
Sepals equalling capsule length	87.5	86.76	50.0	62.35
Sepals distinctly shorter than capsule (sepal length $\leq$ 4/5 capsule length)	12.5	13.24	0	1.18
Outer sepals acute	61.25	6.86	31.25	0
Outer sepals obtuse	38.75	93.14	6.25	72.94
Outer sepals flat	78.25	37.83	50.0	4.71
Outer sepals cucullate	21.25	62.17	0	16.47
Outer sepals mucronate	11.25	8.51	0	0
Outer sepals not mucronate	88.75	91.49	56.25	68.24
Sepals glandular-pubescent	91.25	2.84	75.0	1.18
Sepals glabrous	8.75	97.16	0	94.12
Sepal margins red	3.75	68.87	0	49.41
Sepal margins white-hyaline	96.25	31.13	87.5	12.94
Leaves not ciliate	53.75	16.04	31.25	9.41
Leaves ciliate only at base	45.0	37.5	25.0	21.18
Leaves ciliate beyond their middle	1.25	46.46	0	31.76
Axis glabrous	85.0	65.09	75.0	55.29
Axis eglandular-pubescent	0	31.17	0	22.35
Axis glandular-pubescent	15.0	3.54	0	2.35
Capsule narrowly ovoid (capsule width $\leq$ 4/5 capsule length)	65.0	39.62	25.0	9.41
Capsule broadly ovoid	35.0	60.38	6.25	23.53

traits to distinguish *Sagina apetala* and *S. micropetala*. All characters except two appear to be suitable for this distinction based on our observations. Plants of clade I typically showed at least some of the following characters: sepals horizontally spreading in fruit, capsules broadly ovoid, sepal tips obtuse and cucullate, sepals not glandular-pubescent, sepal margins red, and leaf margins ciliate. Therefore, clade I can be identified as *S. micropetala*. We did not observe that the capsule was much longer than the sepals. Sepal tip mucros were observed in only very few flowers. This could be related to the fact that mucros are curved inward in *S. micropetala* and are hidden when sepals are withered.

Plants of clade II usually had sepals appressed to the capsule, and the capsules were narrowly ovoid. Sepals were usually acute and flat, but some had a small erect mucro at the tip. The plants always had at least some flowers with glandular-pubescent sepals and the sepal margin was white. Leaves were ciliate at the base or without cilia. Therefore, clade II can be identified as *Sagina apetala*.

As is evident from our detailed results (Table 2), none of these characters is unambiguous, and we saw plants of one species that showed several of the character states typical for the other species. The most reliable character to distinguish the two species is the presence of glandular hairs on the sepals, a character that has not been used before in *Sagina* but has been found useful in other genera of the *Caryophyllaceae* (e.g. *Cerastium* L.; Rabeler & Hartman 2006, 2020). Whereas *S. apetala* had glandular hairs in 91% of the flowers, and at least some flowers of all individuals had glandular hairs, *S. micropetala* had no glandular hairs in 97% of the flowers and in 94% of the individuals examined. Red sepal margins were similarly reliable for *S. micropetala*. Whereas 69% of *S. micropetala* flowers (and 87% of individuals) showed this character, only 4% of *S. apetala* flowers had red sepal margins. In contrast, white sepal margins were not a reliable character for *S. apetala*. Although most flowers of *S. apetala* showed white margins (96%), white margins were also found in 31% of *S. micropetala* flowers,

Table 3. Chromosome counts for *Sagina apetala* and *S. micropetala* from Germany obtained from mitotic root cells. Specimen information for all populations (Pop.) can be found in Table 1.

Clade	Pop.	Species	Locality	Coordinates	Chromosome count
II	Sab186	<i>Sagina apetala</i>	Hessen, Hochheim-Massenheim	50°02'16.9"N, 08°23'24.7"E	2n = 12
I	Sab170	<i>Sagina micropetala</i>	Niedersachsen, Northeim	51°42'25.2"N, 10°00'39.6"E	2n = 12
I	Sab181	<i>Sagina micropetala</i>	Niedersachsen, Northeim	51°42'28.8"N, 10°00'28.8"E	2n = 12
I	Sab198/9	<i>Sagina micropetala</i>	Hessen, Hofheim-Diedenberg	50°03'42.3"N, 08°25'04.2"E	2n = 12
I	Sab224	<i>Sagina micropetala</i>	Hessen, Wetzlar	50°33'19.6"N, 08°30'54.6"E	2n = 12
I	Sab196	<i>Sagina micropetala</i>	Hessen, Nentershausen	51°00'50.8"N, 09°55'59.3"E	2n = 12
I	Sab225	<i>Sagina micropetala</i>	Rheinland-Pfalz, Reitzenhain	50°09'26.7"N, 07°47'12.5"E	2n = 12

and 13% of individuals had only flowers with white sepal margins. In combination, sepal pubescence and sepal margin colour are highly (but not completely) reliable in distinguishing *S. apetala* and *S. micropetala*. All other characters discussed can further support identification based on these two characters.

Some of the characters discussed appear to be influenced by the environment. For example, plants of *Sagina micropetala* collected at shady localities had a smaller percentage of red sepal margins, and some did not have a single flower with red sepal margins. Similar variation of red bands at the base of the calyx has been observed in *Stellaria pallida* (Dumort.) Piré by Rabeler (1988).

Our findings are mostly based on German material and will have to be carefully tested in other parts of their native distribution ranges as well as in introduced populations around the world. For example, in contrast to the German material, all material of *Sagina micropetala* from the United Kingdom had glandular-pubescent sepals.

Taxonomy and nomenclature of *Sagina apetala* and *S. micropetala*

The taxonomy of *Sagina apetala* and *S. micropetala* as used in several floras (e.g. Jäger 2011) harbours some problems. *Sagina apetala* was described by Arduino (1764: 22) and is clearly the first validly published name for clade II. A supposed later homonym attributed to Linnaeus (1771: 559) is not a new name because Linnaeus clearly cited Arduino (1764) as the author. The name was lectotypified by Crow (1978: 73) with a Linnaean specimen (Herb. Linn. No. 177.2 in LINN; <http://linnean-online.org/2016/>).

For the material falling into clade I, three names are currently used: *Sagina micropetala* Rauschert (e.g. Jäger 2011; Duistermaat 2020), *S. apetala* subsp. *erecta* (Hornem.) F. Herm. (e.g. Clapham & Jardine 1993; Parolly & Rohwer 2019) and *S. filicaulis* Jord. (e.g. Tison & Foucault 2014; Sell & Murrell 2018).

Sagina micropetala was described by Rauschert (1969: 413) as a replacement name at species rank for *S. apetala* subsp. *erecta* (Hornem.) F. Herm. because *S. erecta* L. (= *Moenchia erecta* (L.) G. Gaertn. & al.) is blocking the epithet. Therefore, *S. micropetala* is a ho-

motypic synonym of *S. apetala* subsp. *erecta*. Unfortunately, the combination for subsp. *erecta* by Hermann (1912: 182) was made in an identification key and lacks further information about the basionym except for giving “*erecta* Lam.”, which does not fit with the basionym author (Hornemann) that is usually given. The study of all available publications of Lamarck in the Biodiversity Heritage Library (<https://www.biodiversitylibrary.org/>) offers a possible explanation for this incorrect authorship. Lamarck used the name “*Sagina erecta*. Lin. Sp. 185 [...] β. *Sagina apetala*. Lin. mant. 559” (Lamarck 1778: 9), best interpreted as *S. erecta* var. *apetala*. This implies the existence of a var. *erecta*, which consequently is a synonym of *Moenchia erecta* (= *S. erecta*). Later, Lamarck cited his own work as “*S. apetala*. Linn. Mant. 559. – *S. erecta*, β. Lam. Fl. fr. 3. p. 9” (Lamarck & Candolle 1815: 769). The second part might incorrectly imply a var. *erecta* published by Lamarck. Considering all of this, there is no validly published name by Lamarck in the entire *Caryophyllaceae* at species rank or below called “*erecta*”, so that the authorship of Lamarck for this name seems to be incorrect. The first traceable valid publication of the name *S. apetala* “var. α *erecta*” can be found in Hornemann (1834), who illustrated this variety in comparison to “var. β *decumbens*”. The growth form of var. *decumbens* clearly excludes it from *S. apetala* and *S. micropetala* so that var. *decumbens* most likely represents *S. procumbens*. Hermann (1912) stated that subsp. *erecta* has spreading sepals at fruit maturity, and in the illustration of var. *erecta* by Hornemann (1834) one of more than 20 flowers shows this trait. The lectotype has obtuse sepals spreading horizontally without glandular hairs (Olof Ryding, Copenhagen, pers. comm.), confirming its identification as *S. micropetala*.

For the third name, *Sagina filicaulis*, Jordan (1849) stated “Elle est très-rapprochée des *Sagina apetala* L. [...] mais elle se distingue de la première par ses sépales toujours appliqués sur le fruit et non étalés en croix [It is very close to *S. apetala* L. [...] but it is distinct from the former by its sepals always appressed to the fruit and not spread in a cross]”. This trait can clearly be attributed to *S. apetala*. In the Jordan collection at LY two specimens of *S. filicaulis* can be found. Only specimen LY 0826452

was possibly collected before the publication date (date missing on sheet), and this specimen fits the protologue information. It also fits the description by Jordan (1849) of a filiform plant with sepals appressed to the capsule, but does not have any glandular hairs on the sepals. The sepal margin appears to be white-hyaline, and the leaves are ciliate not only at the base but have cilia beyond their middle. Although typical glandular hairs are missing, several characters imply that the specimen belongs to *S. apetala*. As shown for British material of *S. micropetala*, indumentum of sepals can vary, and the most important character used in its description to distinguish *S. filicaulis* (sepals appressed to the capsule, Jordan 1849) is a character that is most common in *S. apetala*. Our data show that appressed sepals also occur in *S. micropetala*, but only 9% of individuals had appressed sepals in all flowers, and not a single population (with more than two individuals on the specimen) showed that character for all individuals. The type specimen together with all other specimens cited by Jordan (1849) indicates that this character is common in his material, supporting our decision to consider *S. filicaulis* a synonym of *S. apetala*. In the future, DNA sequencing of material with similar morphology from the type locality might further support our treatment.

Chromosome number variation in *Sagina*

Chromosome numbers reported for *Sagina* are highly variable. Although only available for about half of the species, chromosome numbers include $2n = 12, 18\text{--}22, 20, 22, 28, 36, 46, 56, c. 60, 64, 66, 84$ and $c. 88$ (Crow 1978; Goldblatt & Johnson 1979–2021). For *S. apetala*, $2n = 12$ has been counted (Petrova 1995; Runemark 1996; Lövkvist & Hultgård 1999) in material from the Mediterranean region and from Sweden. Our chromosome count of $2n = 12$ for *S. apetala* confirms previous findings from other regions and provides the first count of this taxon from Germany/Central Europe. No chromosome counts have been published until now for material that can be assigned to *S. micropetala*. Our count of $2n = 12$ from mitotic root tip cells of *S. micropetala* confirms the close relationship of this species to *S. apetala*. It clearly sets both apart from their closest relative *S. maritima* with $2n = 24/28$. The chromosome number of *S. maritima* is not entirely clear because Wulff (1937) counted $n = 11\text{--}12$ (“annäherungsweise”, i.e. approximately) for material from Schleswig-Holstein (Germany) and Runemark (1996) counted $2n = 28$ for material from the Mediterranean region.

A note on the coastal origin of some widespread ruderals

As shown above, *Sagina apetala* and *S. micropetala* are the closest relatives of *S. maritima*. This may imply, irrespective of chromosome number variation, that the ancestral habitat of these two species might have been coastal sites, i.e. thin soil on cliff tops, the spray zone,

open places in salt marshes, damp sandy places behind beaches, dune slacks and pavement cracks on seaside promenades, where *S. maritima* occurs. Interestingly, an origin from coastal habitats such as salt marshes, dunes and particularly tidal drift vegetation has been suggested for a number of important ruderals (Nordhagen 1939/1940; Baker 1974; Willerding 1986; Sukopp & Scholz 1997; Ellenberg & Leuschner 2010). Of those species commonly found in tidal drift vegetation, ruderal *Senecio vulgaris* L. var. *vulgaris* (Kadereit 1984a, 1984b; Ellenberg & Leuschner 2010), *Tripleurospermum maritimum* subsp. *inodorum* (L.) Appleg. (Ellenberg & Leuschner 2010) and ruderal forms of *Atriplex prostrata* DC. (Taschereau 1985; Grime & al. 1988) have been suggested to probably have originated from tidal drift populations. For *T. maritimum* subsp. *inodorum*, however, Kay (1972) did not discuss this possibility and later (Kay 1994) hypothesized that the type of natural habitat of the taxon before colonization of man-made habitats may no longer exist (in the British Isles). In *Beta vulgaris* L., ruderal beets in SW France (Desplanque & al. 1999; Fénart & al. 2008) and Morocco (Leys & al. 2014), to be distinguished from weedy beets, which are probably the result of hybridization between ruderal and coastal beets, have been postulated to be most closely related to the coastal *B. maritima* L. subsp. *maritima*. Other ruderal species commonly found in tidal drift habitats and partly on primary and white dunes include *Polygonum aviculare* L., *Rumex crispus* L. and *Sonchus arvensis* L. Interestingly, among the species sampled by Kim & al. (2007) and Mejías & al. (2018), *S. arvensis*, with subsp. *uliginosus* (M. Bieb.) Nyman in coastal and other habitats, is most closely related to *S. crassifolius* Willd. and *S. maritimus* L., which are species of damp saline and calcareous soils. Such relationship may imply that a coastal or at least saline habitat is ancestral in *S. arvensis*, which would support the idea of an origin of ruderal populations of the species from the coast, as already speculated by Hegi (1929). *Rumex crispus* commonly grows in tidal drift vegetation when left undisturbed (Tüxen 1950), and also in dunes. Populations from such habitats have been referred to as *R. crispus* subsp. *littoreus* (J. Hardy) Akeroyd. Although no explicit suggestion has been made that inland ruderal populations originated from coastal forms, Cavers & Harper (1964) and Akeroyd & Briggs (1983), in cultivation experiments, found that whereas inland plants often flower in their first year, this can never be observed in coastal plants, which flower in their second or later years. This observation may imply evolutionary directionality from the coast to inland habitats. However, different from the findings for *Senecio vulgaris*, where the coastal subsp. *denticulatus* (O. F. Müll.) P. D. Sell shows substantial seed dormancy, which is absent from ruderal var. *vulgaris* (Kadereit 1984a), *R. crispus* subsp. *littoreus* lacks seed dormancy, which is present in ruderal populations (Cavers & Harper 1966). Finally, ruderal *Polygonum aviculare* may also be of coastal origin, although this possibility has never been

discussed (e.g. Styles 1962). Coastal forms have been referred to as, e.g., *P. aviculare* var. *littorale* (Link) Mert. & W. D. J. Koch (Rechinger 1958), *P. neglectum* Besser (Scholz 1959) or *P. aviculare* subsp. *rurivagum* (Boreau) Berher (Jäger 2011).

In each case discussed, the direction of habitat shift – either from coastal to ruderal sites or *vice versa* – is not unambiguously clear. However, the ecological similarity between particularly tidal drift and ruderal sites, i.e. irregular disturbance, low competition and high nutrient contents, make tidal drift a probable starting point for the evolution of the above ruderals, and indeed all of them (except *Sagina apetala*, *S. micropetala* and *Senecio vulgaris*) are known as subfossils from glacial times in the British Isles (Godwin 1975). Interestingly, the oldest finds (Iron age) of *Tripleurospermum maritimum* associated with human activity appear to belong to subsp. *maritimum* and have been recorded from sites near the North Sea coast (Willerding 1986).

Taxonomic treatment

The taxonomic treatment is focused on the *Sagina apetala*–*S. micropetala* group. Numerous synonyms exist that have usually been assigned to *S. apetala*. We did not check all of these names in detail but only compared descriptions with the characters we observed. Some synonyms (e.g. *S. patula* Jord.) clearly fit our circumscription of *S. apetala*, while others are less clear. Only one younger name can clearly be assigned to the synonymy of *S. micropetala*, but further investigation especially of type material might lead to a different result. If any other existing name belongs to *S. micropetala*, it would have priority because all of these names are older than *S. micropetala*. We did not consider further intraspecific synonyms.

Identification key to annual *Sagina*-species of Germany

1. Leaves (at least slightly) succulent, upper leaves with a short mucro < 0.18 mm long; sepals obtuse; plants in coastal habitats (e.g. salt marshes) **2. *S. maritima***
- Leaves never succulent, upper leaves with a longer mucro > 0.2 mm long; outer sepals obtuse, mucronate, acuminate or acute; plants not in coastal habitats **2**
2. Sepals usually glabrous, often with red margin; other traits: sepals often spreading horizontally at fruiting time at least in some flowers, outer sepals usually obtuse or cucullate, sometimes with an incurved mucro; leaves usually ciliate, often beyond their middle; capsule more often broadly ovoid (width > 4/5 of length) than not **3. *S. micropetala***
- Sepals usually glandular-pubescent (at least at base), usually with white-hyaline margin; other traits: sepals

usually appressed to mature capsule, outer sepals often acute and flat, sometimes with an erect mucro; leaves ciliate at base or without cilia; capsule more often narrowly ovoid (width ≤ 4/5 of length) than not

..... **1. *S. apetala***

1. *Sagina apetala* Ard., Animadv. Bot. Spec. Alt.: 22. 1764 ≡ *Sagina inconspicua* Rossmann in Ber. Oberhess. Ges. Natur- Heilk. 8: 24. 1860, nom. illeg. superfl. ≡ *Sagina quaternella* Schloss. in Schlosser & Vukotinović, Fl. Croat.: 343. 1869, nom. illeg. superfl. – Lectotype (designated by Crow 1978: 73): Herb. Linn. No. 177.2 (LINN). – Note: Linnaeus (1771) did not publish a new name but cited Arduino's name. Nevertheless, Linnaeus is often incorrectly cited as author of the name. Rossmann (1860) considered the epithet "*apetala*" as meaningless for a plant with (minute) petals and provided a nomenclaturally superfluous (and hence illegitimate) replacement name for *S. apetala*. Schlosser & Vukotinović (1869) cited "*Moenchia quaternella* Alsch." as a synonym of *S. quaternella*. However, they were not citing a basionym but rather what they evidently regarded as a misapplied name – *M. quaternella* sensu Alschinger, non Ehrh. – because on p. 356 "*Moenchia quaternella* Ehrh." was cited as a synonym of *M. erecta* (L.) G. Gaertn. & al. *Sagina quaternella* was nomenclaturally superfluous when published, and is an illegitimate replacement name for *S. apetala*, because the latter name was also cited in its synonymy.

= *Sagina ciliata* Fr., Utkast Sv. Fl., ed. 3: 713. 1816 ≡ *Sagina apetala* subsp. *ciliata* (Fr.) Hook. f., Student Fl. Brit. Isl.: 61. 1870. – Type: not designated. – Protologue: "V. på åkerfält vid Nebelöf nära Ystad".

= *Sagina depressa* Schultz, Prodr. Fl. Starg. Suppl. 1: 10. 1819. – Type: not designated. – Protologue: "prope Neobrandenb. auf dem Broda'schen Felde gegen Belvedere, Jun. Jul.".

= *Sagina patula* Jord., Observ. Pl. Nouv. 1: 23. 1846 ≡ *Sagina apetala* var. *patula* (Jord.) P. D. Sell, Fl. Gr. Brit. Ireland 1: 686. 2018. – **Lectotype (designated here):** [France], dans les terres argileuses à Quincieux (Rhône), 2 Jun 1845, A. Jordan s.n. (LY 0826462). – Protologue: "Je l'ai récoltée dans les champs cultivés, à sol argileux, à Quincieux (Rhône)".

= *Sagina filicaulis* Jord., Observ. Pl. Nouv. 7: 16. 1849 ≡ *Sagina apetala* subsp. *filicaulis* (Jord.) Sennen & Mauricio, Cat. Fl. Rif Orient.: 21. 1933. – **Lectotype (designated here):** [France], Toulouse à Blagnac, s.d., Timbal-Lagrave s.n. (LY 0826452). – Protologue: "Je l'ai récoltée à Bedous, dans la vallée d'Àspe, en juillet 1838, et l'ai recue depuis de Toulouse de M. Timbal-Lagrave, d'Angers de M. Boreau, etc.".

= *Sagina lamyi* F. W. Schultz in Jahresber. Pollichia 8: 30. 1850 ≡ *Sagina apetala* subsp. *lamyi* (F. W. Schultz) Rouy & Foucaud in Rouy, Fl. France 3: 288. 1896. – **Lectotype (designated here):** [France], (Cher) Bois du Loire près Saint Florent, May 1848, s.coll. s.n. (P 05052247). – Protologue: "Cher, Saint-

- Florent, sable du Cher (*Tourangin*). — Haute-Vien. Magnc-Bourg, roches de Serpentine (*Lamy*). — Note: Schultz based *S. lamyi* on *S. depressa* sensu Boreau (1849), non Schultz. The lectotype was originally in the herbarium of Alfred Déséglise, who was a student of Gustave Tourangin (Briquet 1940: 206–209). The lectotype is now in P.
- = *Sagina ambigua* J. Lloyd, Fl. Ouest France: 74. 1854. — Type: not designated. — Protologue: "c. golfe du Morbihan, murs, lieux secs; je l'ai revu à Cadeuil (char.-Inf.), sur les côteaux du Gouessant près Lamballe (C.-Nord), et M. Pontarlier me l'a donné de Challans (Vend.) localités qui sont supposer que cette espece croît sur plusieurs points intermédiaires".
 - = *Sagina reuteri* Boiss., Diagn. Pl. Orient., ser. 2, 1: 82. 1854 ≡ *Sagina apetala* subsp. *reuteri* (Boiss.) P. Fourn., Quatre Fl. France: 311. 1936. — **Lectotype (designated here)**: [Spain], circa Matritum, 1841, *Reuter s.n.* (G 00226953; isolectotype: G 00226954). — Protologue: "Hab. circà Matritum ubi legit vere 1841 amic. Reuter".
 - = *Sagina urbica* Phil. in Linnaea 28: 613. 1857 ≡ *Sagina apetala* var. *urbica* (Phil.) Reiche, Fl. Chile 1: 186. 1896. — **Lectotype (designated here)**: [Chile], Curacasi, Sep 1853, *Philippi s.n.* (SGO 000001986). — Protologue: "In plateis urbis Santiago frequens, ad Quillota, Curacasi etc.". — Note: Other original material from Santiago is available at HAL (HAL 0117866).
 - = *Sagina valdiviana* Phil. in Linnaea 33: 22. 1864 ≡ *Sagina apetala* var. *valdiviana* (Phil.) Reiche, Fl. Chile 1: 186. 1896. — **Lectotype (designated here)**: Chile, Corral, s.d., *H. Krause s.n.* (SGO 000001988). — Protologue: "Propo Corral legit orn. Krause".
 - = *Sagina apetala* [unranked or forma] *capillaris* Lange in Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn, ser. 2, 7: 104. 1865 ≡ *Sagina capillaris* (Lange) Vayr. in Anales Soc. Esp. Hist. Nat. 30: 508. 1902. — Type: not designated. — Protologue: "In muris Urbis Santiago de Compostela, Aug. c. fl. et fr.".
 - = *Sagina melitensis* Gulia ex Duthie in J. Bot. 13: 37. 1875. — Lectotype (designated by Crow 1978: 73): [Malta], Insula Melita, Corradino, 13 Mar 1874, *Duthie s.n.* (K 000723212).
 - = *Alsinella ciliata* Greene, Fl. Fran. 126. 1891 ≡ *Sagina ciliata* (Greene) A. Heller in Muhlenbergia 1: 50. 1904, nom. illeg. [non *Sagina ciliata* Fr., Utkast Sv. Fl., ed. 3: 713. 1816] ≡ *Sagina ciliata* (Greene) Piper in Contr. U.S. Natl. Herb. 11: 259. 1906, isonym ≡ *Sagina apetala* subsp. *ciliata* (Greene) A. E. Murray in Kalmia 12: 24. 1982. — **Lectotype (designated here)**: U.S.A., California (Amador Co.), near Ione, Jun 1889, *E. L. Greene s.n.* (NDG 16653). — Protologue: "Vicinity of Ione".
 - = *Sagina pachyrrhiza* Phil. in Anales Univ. Chile 81: 773. 1892. — **Lectotype (designated here)**: Chile, Santiago, 1888, *J. Philippi s.n.* (SGO 000001984; isolectotype: SGO 000001985). — Protologue: "In plateis urbis Santiago a nepote Julio vere 1888 reperta".
 - = *Sagina brevipedicellata* Sennen in Bol. Soc. Iber. Ci. Nat. 25(9–10): 216. 1927 ≡ *Sagina apetala* var. *brevipedicellata* (Sennen) O. Bolòs & Vigo, Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 86. 1974. — **Lectotype (designated here)**: Spain, Baléares: Pont d'Inca, lieux sablonneux, 9 Apr 1919, *F. Bianor s.n.* (BC 11053; isolectotype: P 05398131). — Protologue: "Hab. Baléares: Pont d'Inca, lieux sablonneux. Leg. F. Bianor".
 - = *Sagina rodriguezii* var. *condensata* Sennen. Diagn. Nouv.: 144. 1936. — **Lectotype (designated here)**: Spain, Barcelona: Premia, bords de la Méditerranée, 29 Mar 1932, *F. Sennen 8213* (BC 75090). — Protologue: "Hab.—Barcelona: Premia de Mar, étroite bande entre la voire ferrée et la mer". — Note: "*Sagina condensata*" was cited by Sennen in the synonymy of *S. rodriguezii* var. *condensata* (l.c.) and is therefore not validly published.
 - = *Sagina vasconica* Sennen, Diagn. Nouv.: 145. 1936. — **Lectotype (designated here)**: Spain, Alava: Pipahon, montagne, 800 m, 1932, *M. Losa s.n.* (BC 75091; isolectotype: MPU 021876). — Protologue: "Hab.—Alava: Pipahon, montagne, 800 m. Leg. Dr. M. Losa".
- 2. *Sagina maritima*** Don, Herb. Brit., Fasc. 7, no. 155. 1806. — **Lectotype (designated here)**: Herbarium Britannicum, Fasc. 7, no. 155 (E 00455340; isolectotype: PH 00022257). — Protologue: "On the sea coast not unfrequent, in Angus-shire, Isle of Sky, near Aberdeen, Queensferry and Edinburgh".
- = *Sagina stricta* Fr., Novit. Fl. Suec. 1(3): 47. 1817. — **Lectotype (designated here)**: [Sweden], in litore maris petroso ad Cimbritshamn [Simrishamn], s.d. [early 19th century], *s.coll. s.n.* (LD 1078922A; isolectotype: LD 1769712). — Protologue: "In litore maris petroso ad Cimbritshamn". — Note: The lectotype was chosen based on the locality, its deposition in a Swedish herbarium and its assumed age based on the collection it belongs to (C. A. Agardh).
 - = *Sagina urceolata* Viv., Fl. Libyc. Spec.: 67. 1824; Fl. Cors. Prodr.: 3. 1824. — Type: not designated. — Protologue: "H. in Corsicae montibus"; "H. in Corsicae australis montibus".
 - = *Sagina densa* Jord., Observ. Pl. Nouv. 3: 49. 1846. — **Lectotype (designated here)**: [France], Hyères (Var), 1843, *s.coll. s.n.* (LY 0027692). — Protologue: "J'ai récolté cette espèce à Hyères (Var), tout près de la mer, au Ceinturon, dans les sables humides sur lesquels l'eau a séjourné pendant l'hiver". — Note: The lectotype is part of the Herbar Alexis Jordan at LY.
 - = *Sagina debilis* Jord., Observ. Pl. Nouv. 3: 50. 1846. — Type: not designated. — Protologue: "J'ai récolté cette espèce dans les lieux maritimes, à Collioure (Pyrénées orientales), et l'ai reçu de Bayonne".
 - = *Sagina setigera* Bisch. in Ann. Sci. Nat., Bot., sér. 3, 19: 357. 1853. — Type: not designated. — Protologue:



- “Patria ignota. Semina ex horto Gottingensi nomine *Sagina saxatilis* a° 1849 et 1851 accepimus”.
- = *Sagina rodriguezii* Willk. in Oesterr. Bot. Z. 25: 113. 1875. – **Lectotype (designated here):** [Spain], Menorca: in arenosis ditionis littoralis la Canasia, 3 Apr 1873, *H. M. Willkomm* 156 (COI 00057387). – Protologue: “Menorca: in arenosis littoralibus, v. c. in ditione la Canasia, d. 3. April”.
 - = *Sagina thiebautii* Gand. ex C. Thiébaud in Bull. Soc. Dauphin. Échange Pl.: 71. 1876. – **Lectotype (designated here):** [France], Brest (Finistère): vases marines desséchées, May-Jun 1875, *C. Thiébaud* 719 (P 05052250; isolectotypes: DAO 000000068, JE 00011381, LECB 0000563 n.v., KFTA 0001138 n.v., P 05052317). – Protologue: “H b. Vases marines desséchées de la France boréale-occidentale près Brest (Finistère)”.
 - = *Sagina carnosula* Norman in Forh. Vidensk.-Selsk. Kristiania 16: 21. 1893. – **Lectotype (designated here):** [Norway], Nordland., s.d., *J. M. Norman s.n.* (LD 1852993). – Protologue: “Hab. in Nordlandia arctica ad litora maris sub fluxu inundata”. – Note: The lectotype was chosen based on the locality and the collector.
 - = *Sagina emporitana* Sennen in Treb. Inst. Catalana Hist. Nat. 3: 84. 1917. – Type: not designated. – Protologue: “champs sablonneux entre Port de Molins et Figueres”. – Note: Sennen (1917: 84) wrote: “Nous ne devons pas omettre une forme probablement ampourdanaise des champs sablonneux entre Pont de Molins et Figueres, que nous croyons avoir distribuée comme variété *emporitana* du *S. maritima* Don. et qui serait plutôt une race *S. emporitana* Sennen, forme du *S. Rodriguezii* Willk.” [We must not omit a probably ampourdanaise form from the sandy fields between Pont de Molins and Figueres that we believe we have distributed as a variety *emporitana* of *S. maritima* Don. and which would seem to be rather a race of *S. emporitana* Sennen, a form of *S. Rodriguezii* Willk.; translated from French by Ellen Lévy/Toulouse]. It is not clear if the terms “race” and “forme” indicate Sennen’s intention to designate a taxonomic rank. If yes, this would be in conflict with the species rank indicated by the name used by him, i.e. *S. emporitana*.
 - = *Sagina mariana* Sennen, Pl. Espagne 1925 n. 5612 (1925–1926), in sched. – **Lectotype (designated here):** Spain, Sierra Morena: Trespuentes, 20 May 1920, *C. Pau s.n.* (MA 35175). – Protologue: “Sierra Morena: Trespuentes, 1920-20-V, Leg. Dr. C. Pau”.
- 3. *Sagina micropetala*** Rauschert in Feddes Repert. 79: 413. 1969 ≡ *Sagina apetala* var. *erecta* Hornem., Fl. Danica [Hornem.] 12: 3, tab. MCII. 1834 ≡ *Sagina apetala* subsp. *erecta* (Hornem.) F. Herm., Fl. Deutschl. Fennoskand.: 182. 1912. – **Lectotype (designated here):** [Germany], Heiligenhafen, Aug 1825, *Nolte s.n.* (C 10024083 specimen no. 3 on sheet; Fig. 2). – Protologue: “Inter segetes solo pingui ad Heiligenhafen, Blankenese, Altonam et Buchholz Lauenburgise legit celeberr. Professor Nolte”. – Note: The protologue does not provide separate information for var. *erecta* and var. *decumbens*. Specimen no. 3 on the sheet consists of three large plants all belonging to *S. micropetala* and has the correct location, collector and date. Specimen no. 1 seems to include var. *decumbens*, no. 2 lacks a date, and label information of no. 4 does not fit the protologue.
- = *Sagina schiraevskii* Tzvelev in Bot. Zhurn. (Moscow & Leningrad) 87(3): 122. 2002. – Holotype: Ukraine, prope opp. Starobeljsk, in arena humida, Aug 1904, *J. Schiraevski s.n.* (LE n.v.; isotype: LE n.v.). – Note: Tzvelev (2002) gave as main differences to *S. apetala* and *S. micropetala* the indumentum of the plant and the shorter apex of the leaves. Considering the morphological variability of the group, we treat this name as a synonym of *S. micropetala*, based on its obtuse, cucullate and mucronate (mucro incurved) sepals, which are spreading horizontally in fruit.

Conclusions

Our phylogenetic analysis of material provisionally identified as *Sagina apetala* and *S. micropetala* revealed the existence of two distinct and well-supported lineages that are sister to each other and closest relatives of the morphologically similar *S. maritima*. Morphological investigation of mainly German material showed that the two lineages correspond to the morphological species *S. apetala* and *S. micropetala* and helped in identifying characters useful for their discrimination. Although our results highlight that no morphological character is unambiguous in discriminating the two species, indumentum of sepals and colour of the sepal margin are most reliable. Several other characters should be considered for their correct identification. The close relationship of *S. apetala* and *S. micropetala* is further supported by their shared chromosome number of $2n = 12$, first reported in this study for *S. micropetala*. Future studies will have to show whether the characters identified by us are useful in other parts of the distribution range of the two species.

Author contributions

MSD and JWK designed the study. MSD generated the datasets and analysed the data. MSD and JWK wrote the manuscript.

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See <https://doi.org/10.3372/wi.52.52101>

Annotated alignments in Nexus format for ITS, ETS, *atpB-rbcL* and *trnQ-rps16*.

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