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American cudweeds (*Gamochaeta*; *Gnaphalium* s.l., Asteraceae) in Belgium and the Netherlands

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Key words

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Abstract – In recent years several species of American cudweeds (*Gamochaeta*; *Gnaphalium* s.l.) have increasingly been recorded in Belgium and the Netherlands, especially (but not exclusively) in urban habitats. Since these species are naturalizing – at least one even on a relatively large scale – assessing their genuine identity is necessary. Three species are eventually accepted: *G. coarctata* (previously erroneously ascribed to *G. purpurea*), *G. pensylvanica* and *G. subfalcata* (surprisingly often overlooked for the native species *Gnaphalium sylvaticum*). In this paper all are copiously depicted and characters useful for their separation are discussed. A key for their identification is also presented, as are details about their distribution and habitat preferences in Belgium and the Netherlands. The naturalized populations reported in this paper are probably the northernmost known worldwide. Finally, the genome size was assessed for several accessions. It turned out that genome size does hardly allow to separate *G. pensylvanica* and *G. subfalcata*.

Samenvatting – De laatste jaren zijn er in België en Nederland verschillende soorten Amerikaanse droogbloemen (*Gamochaeta*; *Gnaphalium* s.l.) waargenomen, vooral (maar niet uitsluitend) in stedelijke milieus. Omdat deze soorten aan het inburgeren zijn – minstens één bovendien op relatief grote schaal – is het vaststellen van hun echte identiteit noodzakelijk. Drie soorten worden uiteindelijk weerhouden: *G. coarctata* (eerder ten onrechte *G. purpurea* genoemd), *G. pensylvanica* en *G. subfalcata* (merkwaardig genoeg herhaaldelijk over het hoofd gezien voor de inheemse soort *Gnaphalium sylvaticum*). In dit artikel worden alle soorten uitgebreid afgebeeld en de kenmerken die nuttig zijn voor hun onderscheiding worden besproken. Een determinatiesleutel wordt ook gepresenteerd, evenals details over hun verspreiding en habitatvoorkeur in België en Nederland. Voor deze drie soorten zijn de hier gesignaleerde ingeburgerde populaties momenteel waarschijnlijk de meest noordelijke ter wereld. Ten slotte werd ook het genoomgewicht bepaald voor meerdere accessies. Op basis van hun genoomgewicht kunnen *G. pensylvanica* en *G. subfalcata* nauwelijks onderscheiden worden.

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INTRODUCTION

In Belgium and the Netherlands only a few species of *Gnaphalium* L. s.l. (Asteraceae, Gnaphalieae) are native: *Gnaphalium luteo-album* L., *G. sylvaticum* L. and *G. uliginosum* L. (Lambinon & Verloove 2012, Duistermaat 2020). As a result of changed taxonomy, mostly based on recent molecular phylogenetic data, these species are now sometimes accommodated in segregate genera, respectively as *Laphangium luteo-album* (L.) Tzvelev, *Omalotheca sylvatica* (L.) Sch.-Bip. & F.W. Schultz and *Filaginella uliginosa* (L.) Opiz (see, e.g., Stace 2019). In addition, some further species have been recorded as aliens, e.g., *Gnaphalium undulatum* L. (*Pseudognaphalium undulatum* (L.) Hilliard & B.L.Burtt), although only in the Netherlands so far (Denters 2020, Duistermaat 2020). All these species look superficially similar.

Several representatives of yet another segregate of *Gnaphalium*, namely of the New World genus *Gamochaeta* Weddell, are weedy ('cudweeds') and have naturalized in the (warm-) temperate and (sub-) tropical regions of the world.

The genus *Gamochaeta* was segregated from *Gnaphalium* by Weddell (1855), in order to accommodate those species with spicate inflorescences and pappus hairs that are connate at base and thus fall as a unit. Since then, the genus has been moved back and forth. Many authors accepted its status as a distinct genus (Anderberg 1991, Cabrera 1961, Chen & Bayer 2011, Deble & Marchiori 2007, Freire & Iharlegui 1997, Freire et al. 2016, Holub 1976, Martínez Ortega 2019, Nesom 2006, Pignatti 2017, Rocha Afonso 1984). Others, however, for instance Wagenitz (1965) and Drury (1971), but also more recent ones, including Stace (2010), Lambinon & Verloove (2012), Tison & de Foucault (2014), and Duistermaat (2020), preferred

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considering it as part of a broadly circumscribed genus *Gnaphalium*. Recent molecular data confirm the generic status for *Gamochaeta*, unless *Gnaphalium* would be very broadly circumscribed (see phylogenetic trees presented by Acosta-Maindo & Galbany-Casals 2018, Freire et al. 2015, Urtubey et al. 2016). DNA sequences from the plastid (*trnL-F*) and nuclear (ETS and ITS) genomes further redefined the circumscription of the genus (Urtubey et al. 2016). It now includes c. 60 species that are primarily distributed in tropical and subtropical America.

Several of the more widespread species are weedy and have naturalized outside their native distribution area. They are particularly well-represented in, for instance, southwestern Europe (Rocha Afonso 1984), New Zealand (Drury 1971) and North America (Nesom 2006). However, assessing the correct identity of these species has proved to be not an easy task and, as a result, several names have been used incorrectly.

In Belgium and the Netherlands species of *Gamochaeta* have always been rare ephemerals until recently, at least in part because climatological circumstances were unfavorable for most of the species. Three species were mentioned from Belgium by Verloove (2006) (as members of *Gnaphalium*, namely *G. antillanum* Urban, *G. calviceps* Fernald and *G. pensylvanicum* Willd.) but all were seen for the last time at the end of the 19th and the beginning of the 20th century, mostly as wool aliens (compare with Nesom 2004c). In the Netherlands, a few collections were made of *Gamochaeta*, especially in the first half of the 20th century, but their identity should be critically reassessed. Most records were associated with grain mills.

In the past two decades, however, several species of *Gamochaeta* have increasingly been recorded, both in Belgium and the Netherlands. They are mostly found in urban habitats (foot of walls, sidewalks, cracks in concrete, parking lots, on gravel paths, etc.) but one species also often in (near-)natural ones, including heaths. In addition, some of these species have repeatedly been introduced as contaminants in plant containers (often olive trees and palms) and subsequently naturalized in garden centers and nurseries. Climatologically, conditions are now probably more favorable than ever before. Urban and suburban habitats are characterized by elevated temperatures, compared to the surrounding countryside. Also, global warming doubtlessly also enhanced the perseverance of these thermophilous weeds, to such an extent that at least three species can now be considered naturalized.

As said before, identifying *Gamochaeta* species is often difficult. In nearly all identification keys (e.g., Drury 1971, Nesom 2006, Rocha Afonso 1984), the first dichotomy highlights plant life and characteristics of the basal rosette but these characteristics are difficult to discern in incomplete specimens. Similarly, the shape of the apices of the phyllaries has been given a lot of taxonomic importance. Excellent illustrations of phyllary apices of various common species were provided by Drury (1971) and Nesom (2004a). However, inner and outer phyllaries often differ in shape although some authors explicitly refer to the inner (e.g., Freire & Iharlegui 1997) others to the outer (e.g., Nesom 2006). In reality, the apices of the phyllaries (inner as well as outer) appear to be variable, even within a single flower, and also seem to change in shape during anthesis. This was recently also noticed by Martínez Ortega (2019) in Flora iberica: "(…) conviene observar este carácter en capítulos ni demasiado inmaduros, ni demasiado maduros". Freire, who formerly strongly emphasized this character (Freire & Iharlegui 1997) no longer refers to it in more recent treatments of the genus (Freire et al. 2016). Interestingly, species of *Gamochaeta* are often more easily recognized as living plants in the field than dried in the herbarium. This was already noticed by Godfrey (1958).

In the present paper, three species of *Gamochaeta* are presented, characterized and depicted, and their actual distribution in the study area is outlined.

MATERIAL AND METHODS

Our study is mostly based on the examination of herbarium specimens that were recently collected by the authors and their collaborators and that now are preserved in the herbaria of Naturalis (L), Leiden, and De Bastei (NMNL), Nijmegen, both in the Netherlands, and Meise Botanic Garden (BR), Meise, Belgium. In addition, field work was undertaken in order to study characters that are best seen in fresh plant material.

In order to track and trace records of potentially interesting species and/or localities the nature observations platforms waarneming.nl and waarnemingen.be were surveyed (up to December 2020). For this purpose, all records of *Gamochaeta* pl. spec. (and their synonyms in *Gnaphalium*) were verified; in addition all observations of '*Gnaphalium sylvaticum*' (a native species reminiscent of *Gamochaeta subfalcata*) and '*Gnaphalium* spec.', substantiated by photographs, were also checked.

Numerous literature references, protologues and images of type specimens of the species relevant for our study were consulted.

Genome sizes were measured with a Partec PAS III flow cytometer equipped with a 20 mW 488 nm solid state laser. We used the commercial kit Cystain PI absolute P (Partec, Germany) for sample preparation. For each plant sample, less than a square cm of leaf was chopped with a sharp razor blade at room temperature together with an internal standard which was either *Solanum lycopersicum* L. (2C = 1.96 pg, Doležel et al. 1992) or *Glycine max* (L.) Merr. (2C = 2.50 pg, Doležel et al. 1994). The resulting nuclei suspension was filtered through a 50 µm mesh CellTric disposable filter (Partec GmbH, Münster, Germany) and stained with propidium iodide following the specifications of the kit. For each accession (n = 10) one to three replicates were incubated for at least 30 min in the dark before measuring with the flow cytometer. Genome size measurements were performed using the Flomax software (Quantum Analysis, Germany) and were replicated on at least three different days for each of the three *Gamochaeta* species. Genome size was calculated from the relative fluorescence intensities of the sample of interest and the internal standard with known genome size and was averaged across accessions to obtain the genome size for each *Gamochaeta* species in this study.

RESULTS

Morphology

Three naturalized species of *Gamochaeta* are recognized in Belgium and the Netherlands. They are distinguished in the following identification key:

1. Mature leaves strikingly bicolored, shiny green (when fresh) and glabrous or glabrate above, white pannose beneath. Plant usually biennial with distinct rosette at flowering. Flower heads glabrous at base . . . . . *Gamochaeta coarctata* (Willd.) Kerguélen
   Mature leaves concolorous or very weakly bicolored, both surfaces hairy (at least when young). Plant annual, rosette leaves readily withered at anthesis. Flower heads arachnoid at base 2

2. Inflorescence with leaf-like bracts, these hardly differing from cauline leaves. Leaves often slightly bicolored, less hairy on upper surface than on lower, the upper cauline normally more than 10 mm wide. Capitulae with phyllaries rarely purplish-tipped before flowering . . . . . *Gamochaeta pensylvanica* (Willd.) Cabrera

   Inflorescence with bracts not leaf-like, much narrower than cauline leaves, often folded and sickle-shaped. Leaves concolorous, more or less equally hairy on both surfaces, the upper cauline less than 10 mm wide. Capitulae with phyllaries conspicuously purplish-tipped before flowering . . . . . *Gamochaeta subfalcata* (Cabrera) Cabrera

Gamochaeta coarctata (Willd.) Kerguélen, Lejeunia 120: 104. 1987. — Fig. 1, 2, 3 & 10.

Gnaphalium coarctatum Willd., Sp. Pl. 3(3): 1886. 1803.

Gamochaeta spicata Cabrera, Bol. Soc. Argent. Bot. 9: 380. 1961. (nom. superfl.).

Gnaphalium spicatum Lam., Encycl. 2(2): 757. 1788. (nom. illegit.).

Gamochaeta purpurea auct. eur. (fide, e.g., Duistermaat 2020, Vivant 1980).

Gamochaeta americana auct. ital. (fide, e.g., Nepi et al. 2009).

The basal leaves of *Gamochaeta coarctata* are strongly bicolored, especially at the time of flowering when upper leaf surfaces have become (near-) glabrous. In seedlings, the difference in color between upper and lower leaf surfaces is much less obvious. Seedlings of *Gamochaeta coarctata* differ from both other *Gamochaeta* species in their color and shape: the upper leaf surface is shiny green with a distinct, sunken midvein and blades are very gradually narrowing towards base. In the other two species, the upper leaf surface is dull with a hardly discernible midvein and the blades are clearly spathulate, i.e. abruptly narrowed towards base (Fig. 10).

Known distribution — South America. Naturalized in Mexico, West Indies and North America (Nesom 2006), southwestern Europe (France, Italy, Portugal, Spain; Castro 2004, Longo 2017, Rocha Afonso 1984, Tison & de Foucault 2014, Vivant 1980), Africa (Hilliard 1986), New Zealand (Drury 1971), China and Taiwan (Chen & Bayer 2011), Japan, and Australia (Nesom 2004a).

Presence in Belgium and the Netherlands — Recently very locally naturalizing in a few localities, all located in the Netherlands. *Gamochaeta coarctata* was probably first recorded in Breda-Doornbos (Province of North Brabant) in 2012. The plants were found in the joints of the pavement tiles in front of garage boxes. The persistence of this population was confirmed in 2016 and by 2020 the species was noted to be numerous (at least one hundred individuals were counted) and the population having much extended (pers. comm. Jacques Rovers, June 2020). In 2017 the species was observed in Oost-Knollendam (Province of North Holland) by Niko Buiten (waarneming.nl). In 2018, *G. coarctata* was recorded between pavers in Rhenen (Province of Utrecht) by Erik Slootweg and its presence there was subsequently confirmed in 2020. Moreover, later in the same year scattered individuals were found by Marinus Dieleman a few blocks away, suggesting that the species is locally spreading. In the spring of 2020 the species was also spotted on a campsite in Makkum (Province of Friesland) by Hinko Talsma et al. and in the autumn of the same year a single individual was observed near Nijmegen in Malden-Heumensoord (Province of Gelderland), in a quite natural area (heath) by Erik van Dijk. The plant was found there in a place that is periodically used for camping activities, although with fixed tents.

Fig. 1. *Gamochaeta coarctata* (Willd.) Kerguélen in Breda, Province of North Brabant (the Netherlands), in June 2020. The species is a biennial with rosette leaves well-developed at flowering and upper and lower surfaces strongly contrasting in colour. Photo: J. Rovers.

Taxonomy and comparison — In the Netherlands, *Gamochaeta coarctata* was named "*Gnaphalium purpureum*" up to the present (e.g., Duistermaat 2020). The latter binomial is sometimes applied in a very broad sense as to include *Gamochaeta coarctata* and *G. pensylvanica*, or even as a collective species that includes more or less all weedy American cudweeds ("Gnaphalium purpureum Group"; e.g., Clement & Foster 1994, Greuter 2006+). However, true *Gamochaeta purpurea* (L.) Cabrera, is a quite distinct species, not only morphologically. Genetically, based on both nuclear and plastid genes, both species were shown to be only remotely related (Urtubey et al. 2016). *Gamochaeta purpurea* has a persistently pubescent upper leaf surface with trichomes with glassy basal cells ('glandular hairs'), whereas in *G. coarctata* the upper leaf surface is glabrous or glabrescent, glandular hairs always being absent. Also, the midvein of *G. coarctata* is typically paler and sunken and the inflorescence very tightly spicate (Fig. 1, 2, 3 & 10).

In fact, *Gamochaeta coarctata* is morphologically more reminiscent of *G. americana* (Mill.) Wedd. and some recent authors have considered them to be conspecific (Freire et al. 2016), the latter name having nomenclatural priority. These two species, as well as *G. ustulata* (Nutt.) Holub, all three with strongly discolorous, widely obovate basal leaves, form a clade in a recent phylogenetic study (Urtubey et al. 2016). The plants currently naturalized in the Netherlands and elsewhere in western Europe conform with typical *G. coarctata* and this name is therefore applied here as well. A record of *G. americana* from Liguria in Italy (Nepi et al. 2009) refers to *G. coarctata* (Galasso et al. 2018). The differences with genuine *G. americana* were recently emphasized by Pruski (2018): in the latter, stems are loosely woolly

Fig. 2. *Gamochaeta coarctata* (Willd.) Kerguélen in Breda, Province of North Brabant (the Netherlands), in June 2020. The phyllaries are glabrous at base. Photo: J. Rovers.

(vs. densely, appressed sericeous), basal leaves are generally withered at anthesis and leaves narrower (linear-oblanceolate to obovate-oblanceolate), with the upper surface opaque and margins usually not wavy or crenulate. *Gamochaeta americana* probably also is a more thermophilous species: claims of it from North America all turned out to be erroneous and referable to *G. coarctata* (Nesom 2004a, Pruski 2018).

Nesom (2004a) newly described two very similar species from the southern U.S.A. (one of them extending to Puerto Rico), i.e., *Gamochaeta argyrinea* Nesom and *G. chionesthes* Nesom. Especially the former is a common and widespread, weedy species. Its presence in southwestern Europe has been confirmed, at least from France and Italy (comm. G. Nesom, G. Galasso, March 2006). It has persistently arachnoid upper leaf surfaces, phyllaries that are not purplish-tinged and capitulae with more numerous (4–5 vs. 2–3) bisexual florets. However, plants found in France do never seem to combine all these features (Tison & de Foucault 2014). In a strict consensus tree from combined moleculara data (Urtubey et al. 2016) these two species were resolved in a separate clade and thus indeed distinct species.

Less often, *Gamochaeta coarctata* has also been confused with *G. pensylvanica*, for instance in northeastern Spain (Guardiola & Petit 2020).

Nomenclature — *Gamochaeta coarctata* was known for many decades as *G. spicata* (syn.: *Gnaphalium spicatum*), see, e.g., Drury (1971), Freire (1995), and Rocha Afonso (1984). Pruski & Nesom (2004), however, pointed out that *G. coarctata* is the nomenclaturally correct name for this species.

Introduction — The introduction vector of *Gamochaeta coarctata* in the Netherlands is not completely resolved. In southwestern France this species commonly occurs in campsites; two recent observations in the Netherlands (in a campsite in Makkum and a heath in Malden) seem to suggest that the species may have been introduced accidentally by campers and their equipment (compare with Verloove et al. 2020a). The other records all are from urban habitats, at least in part in front of or near to garage boxes. In such cases a similar introduction vector is not unlikely (seeds introduced unconsciously, attached to car tires, car mats, camping equipment, etc.). There are no clear indications that this species occurs as a weed in the horticultural trade, like the two others do (see below).

Specimens examined[1]

Netherlands

Province of North Brabant — Breda, Koelemei (km-square: 113-401, coordinates: 113.996-401.100), between the stones and tiles of a sidewalk

[1] Dutch labels were translated to English by the authors.

Fig. 3. *Gamochaeta coarctata* (Willd.) Kerguélen in Malden, Province of Gelderland (the Netherlands), in November 2020. Upper leaf surfaces are shiny and glabrous, with a pale mid vein, whereas lower leaf surfaces are white-pannose. Photo: N. Eimers.

and parking lot, also many seedlings – The species was first found during a FLORON Camp in 2012 and has now expanded to over 100 specimens, 14 June 2020, *J. Rovers s.n.* (BR).

Province of Gelderland — Rhenen, 51.9569, 5.5688, parking lot, between tiles, 30 May 2020, *E. Slootweg s.n.* (BR).

Gamochaeta pensylvanica (Willd.) Cabrera, Bol. Soc. Argent. Bot. 9: 375. 1961. — Fig. 4, 5, 6 & 10.

Gnaphalium pensylvanicum Willd., Enum. Pl. 2: 867. 1809.

Gnaphalium peregrinum Fernald, Rhodora 45(539): 479–480, pl. 795. 1943.

Known distribution — South America. Despite the specific epithet, this species is probably only (long-)naturalized in North America, not native (Nesom 2004b). Also naturalized in temperate and tropical areas throughout the world, including New Zealand (Drury 1971), Australasia (Chen & Bayer 2011, Ji et al. 2014), the Middle East (Kilian & Danin 1999, Shahid 2014), Africa (Hilliard 1986), southern Europe (Italy, Portugal, Spain; for which see Ardenghi 2013, Carretero & Esteras 1979, Manni 2013, Musarella et al. 2019, Rocha Afonso 1984, Soldano 2000 – claims from France are erroneous according to Tison & de Foucault 2014), the British Isles (Anonymous 2018) and Macaronesia (Azores, Madeira, and Canary Islands; Hansen 1972, Rocha Afonso 1984). *Gamochaeta pensylvanica* is steadily expanding further north and recently also established stable populations in for instance New York in North America (Atha et al. 2016).

Presence in Belgium and the Netherlands — Naturalized since the 1990s, very locally so in Belgium, more widely spread in the Netherlands. In Belgium *Gamochaeta pensylvanica* was first recorded as a weed in a greenhouse in 1891 near Liège. It was first seen in the wild in 2007 when it was found as an urban weed in Wilrijk (Antwerp). Scattered individuals were observed at the foot of a house wall and its presence in that district was subsequently confirmed on several occasions (2008, 2014, 2018, 2020); it can be considered to be locally naturalized. In 2019 a single individual was observed in a sandy roadside next to a garden in Koksijde. An apparently well-established population with several dozens of specimens was discovered in 2020 in Boom by Nico Wysmantel (base of wall in urban area). Still in 2020, a few individuals were seen as a garden weed in Hoogstraten by Bart Hoeymans. In addition, *G. pensylvanica* has repeatedly been observed in garden centers and private gardens, often as a weed in plant containers. The species is a fairly characteristic weed in imported containers with olives and palms (Hoste et al. 2009).

In the Netherlands, this species was probably first reported in 1967 when it was found as a weed in a botanic garden in Baarn (van Ooststroom 1970; as *Gnaphalium peregrinum*). Since 1996

Fig. 4. *Gamochaeta pensylvanica* (Willd.) Cabrera in Denekamp, Province of Overijssel (the Netherlands), in July 2020. All leaves are more or less similar in shape and width, including the upper cauline and leaf-like bracts. Upper surfaces become glabrescent with age. Photo: T. Denters.

it has been known uninterruptedly from Nijmegen where it has become a widespread weed (Denters 2020). In Nijmegen it is now locally abundant between pavement stones, in gutters near parking places and along sidewalks, also by walls next to sidewalks. There are also a few collections from places near Nijmegen (Beugen, Overloon). It was later furthermore observed as an urban weed in Utrecht in 2005 and subsequently noticed to have established itself there (Holverda et al. 2009). Since then *Gamochaeta pensylvanica* has been recorded in rather numerous, widely spread cities in the Netherlands, some of them in the northernmost part of the country. According to the online nature platform waarneming.nl [as on 8 December 2020] it has also been observed by now (only records confirmed by photographs) in Aalten, Alkmaar, Ammerstol, Amsterdam, Boxmeer, Den Haag, Denekamp, Deventer, Dordrecht, Eindhoven, Etten-Leur, Gouda, Groningen, Groot-Ammers, Haarlem, Helmond, Helvoirt, 's Hertogenbosch, Heusden, Huijbergen, Langbroek, Laren, Leeuwarden, Leiden, Liessel, Middelburg, Nieuwegein, Ospel, Overloon, Peel en Maas, Rijswijk, Roosendaal, Rotterdam, Sevenum, Stevensweert, Velp, Wageningen, Woudrichem, Zierikzee and Zwolle. In many of these localities the species has repeatedly been recorded and it is doubtlessly naturalized.

Taxonomy and comparison — *Gamochaeta pensylvanica* and *G. subfalcata* are usually readily separated, at least in the field. Compared with the latter, *G. pensylvanica* has much wider, obovate-spathulate, weakly bicolored upper cauline leaves and these are usually flat (not folded). The cauline leaves, including the upper, hardly differ in shape from the basal ones (Fig. 4, 5 & 10). Although usually easily assessed, these are quantitative rather than qualitative character states. Also, these two species overlap in their genome sizes (see below). However, since morphologically (and genetically; see Urtubey et al. 2016) these two species are clearly separated, they are here accepted as two distinct species. It is also worth noting that *G. subfalcata* is the only species that is also found in (semi-)natural habitats in the study area, suggesting that *G. pensylvanica* and *G. subfalcata* differ in their ecology as well.

Introduction — *Gamochaeta pensylvanica* is often associated with garden centers in the study area. It is seen in or near plant containers with trees imported from southern Europe, especially olive trees and palms (Hoste et al. 2009). In addition, it is frequently observed as a weed in plantations and gardens, which also seems to suggest a direct link with garden centers or plant nurseries. Therefore, it is very likely that this weed is dispersed through the horticultural trade, a hardly known but important vector for the introduction and spread of weeds (Hoste 2013, Hoste & Verloove 2010). Records of *G. pensylvanica* in urban habitats (foot of walls, sidewalks, joints of tiles, etc.) may result from the

Fig. 5. *Gamochaeta pensylvanica* (Willd.) Cabrera in Stevensweert, Province of Limburg (the Netherlands), in September 2019. The phyllaries are densely cobwebby-hairy. Photo: K. Paquée.

same introduction vector. Seeds may also have been introduced inadvertedly by tourists returning from southern Europe (attached to their belongings, car tires, etc.) although this is less likely than for the other two species here concerned: *G. pensylvanica* is relatively rare there and even absent from France.

Specimens examined

Belgium

Province of Antwerp — Antwerp, Wilrijk, corner of Struisbeeklaan and Galliardstraat, foot of wall, four flowering individuals, 28 October 2007, *F. Verloove 6978* (BR); Antwerp, Wilrijk, Ullenstraat, sidewalk and foot of walls, several dozens in scattered subpopulations, known in this area since 2007, 2 August 2020, *F. Verloove 13843* (BR); Boom, Parkstraat, sidewalk and foot of walls, small population with a few dozens of individuals, 2 August 2020, *F. Verloove 13840* (BR).

Netherlands

Province of North Brabant — Overloon, Bergkampweg, 193,9-397,9, as a garden weed, between low herbs [translated], August 1999, *T. Verrijdt s.n.* (BR); Sint-Oedenrode, wasteland/construction site, +/- 60 individuals, 2 August 2007, *J. Bruinsma s.n.* (BR).

Province of Gelderland — Beugen, in plant nursery, 19 November 2009, *T. Verrijdt* (NMNL 7808); Nijmegen, between tiles, in shadow, July 1996, *R. Barendse* (NMNL 624); Nijmegen, terrain Katholieke Universiteit Nijmegen, on the edge of the path to the loading and unloading area, also in adjacent plantations, 1 June 1997, *E. Brouwer s.n.* (L [L.2105508]) – Some thousands of flowering and tens of thousands non-flowering individuals in a strip of ca. 150 m, in 1996 already seen by R. Barendse. The species further expanded in 1998. In an area of a few square kilometers; the species now occurs with several ten thousands of individuals; Nijmegen, between streetstones and at foot of walls, 15 August 1998, *G.M. Dirkse* & *S.M.H. Hochstenbach* (NMNL 621, 622, 623); Nijmegen, embankment of Kapittelweg, on the verge of parking lot, 3 November 2006, *G.M. Dirkse* & *S.M.H. Hochstenbach* (NMNL 5436); Nijmegen, between streetstones, 6 July 2007, *C. van Wijck* (NMNL 5813); Nijmegen, 13 July 2007, *G.J. Haverkamp* (NMNL 6163); Nijmegen, sidewalk, 28 August 2007, *G.M. Dirkse* (NMNL 6132); Nijmegen, foot of wall in alley, on sand, 30 August 2007, *G.M. Dirkse* (NMNL 5878); Nijmegen, Universiteit Nijmegen, Tandheelkunde Radboud, 187-426, zandig walletje onder bomen, 5 October 2007, *G.M. Dirkse* (NMNL 5846, 5847, 5848; dupl. BR); Nijmegen, on street, more than 750 individuals, 30 August 2009, *M. Feenstra* (NMNL 7579); Nijmegen, sidewalk, two individuals, 24 July 2012, *M. Feenstra* (NMNL 8680); Nijmegen, in front of petting zoo, 19 November 2017, *M.-E. Dekkers-Li Shin-Yin* (NMNL 11570); Nijmegen, Beemdstraat 3, between paving stones, along sidewalk, 15 June 2020, *G.M. Dirkse & S.M.H. Hochstenbach 12407* (NMNL, dupl. BR); Nijmegen, Beemdstraat 6-12, foot of wall, 15 June 2020, *G.M. Dirkse & S.M.H. Hochstenbach 12410* (NMNL, dupl. BR); Nijmegen, Polderstraat, roadside, 30 June 2020, *G.M. Dirkse & S.M.H. Hochstenbach 12043* (NMNL, dupl. BR); Nijmegen, Veldstraat 46, alongside sidewalk, 30 June 2020, *G.M. Dirkse* & *S.M.H. Hochstenbach* 12398 (NMNL, dupl. BR); Nijmegen, Oude Haven, in plant box alongside sidewalk, 17 July 2020, *G.M. Dirkse* & *S.M.H. Hochstenbach* 12426 (NMNL, dupl. BR); Overloon, rough ground near War Museum, 3 August 2008, *A.I. Reijerse* (NMNL 7375); Wageningen, Dreijen, area N of Botanical centre, previously with greenhouses, waste ground area, 28 October 2005, *J.J. Wieringa 5721* (WAG.1409749 and WAG.1409750); Wageningen, plantation of *Prunus spinosus*, between pavement, 28 September 2012, *E.L.A.N. Simons 967* (WAG.1409748).

Province of Utrecht — Utrecht, Catharijnesingel, 136-810/454-714, foot of house wall and pavement, seven flowering and nine vegetative individuals, 4 September 2007, *W. Vuik s.n.* (BR).

Province of North Holland — Amsterdam, Staatsliedenbuurt, De Kempenaerstraat, foot of wall, gutter, pavement, 12 individuals, 23 July 2007, *T. Denters s.n.* (BR); Huizen, 19 September 2014, *P. Wetzels s.n.* (L.3974553).

Gamochaeta subfalcata (Cabrera) Cabrera, Bol. Soc. Argent. Bot. 9: 383. 1961. — Fig. 7, 8, 9 & 10.

Gnaphalium subfalcatum Cabrera, Revista Mus. La Plata, Secc. Bot. 4: 174. 1941.

Known distribution — South America. Naturalized in North America, southwestern Europe (France, Portugal, Spain) (Font et al.

Fig. 6. *Gamochaeta pensylvanica* (Willd.) Cabrera in Nijmegen, Province of Gelderland (the Netherlands), in August 2018. The plants are annuals with rosette leaves mostly withered at anthesis. The inflorescences are typically interrupted at maturity. Photo: T. Denters.

2002, Rocha Afonso 1984, Vivant 1980), Sicily (Giardina et al. 2007), Macaronesia (Padrón Mederos et al. 2007), North and South Africa (Hamel & Azzouz 2018, Hilliard 1986) and New Zealand (Drury 1971).

Presence in Belgium and the Netherlands — Recently locally naturalized in several localities, both in the Netherlands and Belgium. In Belgium, nearly all records are from the Province of East Flanders. A small population with c. 50 individuals was detected by Indra Jacobs on a gravel parking lot in Oostakker (Ghent) in the spring of 2020. A few weeks later a massive population with more than 1,000 individuals (initially erroneously identified as *Gnaphalium sylvaticum*) was discovered by David Berten on the semi-paved parking area of a supermarket in Lochristi, less than five kilometers east of the first locality. Subsequently, two individuals were observed on a construction site in Sint-Gillis-Dendermonde by Bert Biesmans. In June 2020, the first author discovered another massive population with several hundreds of individuals in an urban habitat in the city of Ghent. Google Streetview images from the same spot showed the species to be already present there in 2017, though with only a few individuals. Finally, a record of '*Gnaphalium sylvaticum*' from a military base in Tielen from May 2020 almost certainly also belongs to *G. subfalcata* (waarnemingen.be).

In the Netherlands, *Gamochaeta subfalcata* turned out to have already been present since several years, but the species was not recognized as such until 2020. All populations were initially overlooked, either as a result of confusion with the native species *Gnaphalium sylvaticum* or, less often, *Gamochaeta pensylvanica*. Based on observations from waarneming.nl, it was apparently first recorded in June 2016 in Gilze (Province of North Brabant) at the Princenbosch Golfclub by Erik-Jan Beenackers. Interestingly, only two days later it was observed in another Golfclub by Lenie van Hal, this time in Milheeze, also in the Province of North Brabant. In this locality, the species was no longer seen in 2020 (comm. L. van Hal, July 2020). It is also known from Uden, where it is plentiful as a garden weed in an urban area since 2019 (Mark Stevens). In similar circumstances, it has been observed in Rijswijk (Province of South Holland) by Peter Hegi, also since 2019. It is also known from Haringvliet in Rotterdam (Province of South Holland), where it has been confused with *G. pensylvanica*. In 2020 about 30 individuals were counted there growing in cracks of the sidewalk. Interestingly, *G. subfalcata* also appeared to occur in quite natural habitats. In the Stabrechtse Heide in Beuven (Province of North Brabant), the species occurs in a heathland near a bog. In Ulicoten, also in the Province of North Brabant, five individuals were seen in a clearing in a woodland in 2020. Finally, also in 2020 it was observed in Heibloem-Weijenhout and in the nature reserve Heidsche Peel in Venray (both Dutch Province of Limburg), on former agricultural fields from which the top soil was removed.

Fig. 7. *Gamochaeta subfalcata* (Cabrera) Cabrera in Oostakker, Province of East Flanders (Belgium), in June 2020. The plants are annuals with rosette leaves mostly withered at anthesis. The upper and lower leaf surfaces are equally hairy and concolorous. Photo: F. Verloove.

Taxonomy and comparison — In several recent accounts, *Gamochaeta subfalcata* has been synonymized with *G. antillana* (Urb.) Anderberg (e.g., Nesom 2006, Pignatti 2017, Tison & de Foucault 2014; see, on the contrary, Martínez Ortega 2019), the latter binomial indeed having nomenclatural priority if both species are considered to be conspecific. *Gamochaeta antillana* was described from the Caribbean and thought to be identical with *G. subfalcata* by Nesom (2004b). Plant material from the southern U.S.A. identified by Cabrera and Freire as *G. subfalcata* was considered to be morphologically identical with

Fig. 8. *Gamochaeta subfalcata* (Cabrera) Cabrera in Mariakerke, Province of East Flanders (Belgium), in June 2020. The upper cauline leaves are much narrower (and often folded and falcate) than the lower cauline and rosette leaves. Photo: F. Verloove.

G. antillana. Although these views were subsequently followed in Europe (see before but also, e.g., Hamel & Azzouz 2018), South American authors kept separating these two species (e.g., Deble & Marchiori 2007, Freire et al. 2016, Urtubey et al. 2016). In fact, molecular data demonstrated that *G. subfalcata* and *G. antillana* are only remotely related and thus not conspecific (Urtubey et al. 2016). In Brazil, where both species occur, *G. subfalcata* is a common and widespread species in anthropized habitats, whereas *G. antillana* is a very rare and localized species of stony and sandy fields (Deble & Marchiori 2007).

Fig. 9. *Gamochaeta subfalcata* (Cabrera) Cabrera in Mariakerke, Province of East Flanders (Belgium), in June 2020. The long and narrow unbranched inflorescences with narrow leaf-like bracts somewhat remind of those of *Gnaphalium sylvaticum* L., the native species with which *G. subfalcata* had been confused for several years. Photo: F. Verloove.

These species are similar in general habit but differ in a number of (rather subtle) characters: the upper cauline leaves are linear in *G. antillana* as can be seen in the lectotype and the protologue ("Folia… linearia"; Urban 1915), whereas they are obovate in *G. subfalcata* (Freire & Iharlegui 1997). According to Deble & Marchiori (2007), both species also differ in indumentum type (the leaves of *G. antillana* being less woolly) and the shape of the inner phyllary apices (those of *G. antillana* being more acute-acuminate). The plants actually found naturalized in Belgium and the Netherlands correspond with the description of *G. subfalcata* rather than with that of *G. antillana*. Therefore, the former name is applied in this account.

Exactly because of the (narrowly) obovate cauline leaves, some of the Belgian and Dutch plants show some resemblance to *Gamochaeta pensylvanica* and were initially, erroneously, ascribed to that species. *Gamochaeta subfalcata* has leaves that are more or less uniformly pubescent on both sides (Fig. 7, 8 & 9), whereas they are slightly but markedly paler below in *G. pensylvanica*. Also, upper cauline leaves of *G. subfalcata* are often typically folded and falcate (compare Fig. 4 with Fig. 9). The inflorescence of *G. subfalcata* is usually less interrupted and the stems are less branched (compare Fig. 6 with Fig. 7, 8 & 9). Its phyllary apices are strikingly purplish tinged, especially just before anthesis.

Morphologically, *Gamochaeta subfalcata* and the native species *Gnaphalium sylvaticum* are at least superficially similar. In fact, a

Fig. 10. Seedlings of (a) *Gamochaeta coarctata* (Willd.) Kerguélen, (b) *G. subfalcata* (Cabrera) Cabrera, and (c) *G. pensylvanica* (Willd.) Cabrera. The seedling leaves of the two latter species are spathulate (distinctly narrowed towards the base). Photos: F. Verloove (Fig. 10.a & b) & I. Hoste (Fig. 10.c).

majority of the recent records were erroneously ascribed to the latter on waarnemingen.be and waarneming.nl. Both species are, however, easily separated based on characteristics of their pappus: all pappus hairs are united at base and fall as a whole in *Gamochaeta*, whereas they are free in *Gnaphalium*. In addition, *Gnaphalium sylvaticum* is a rhizomatous perennial with a distinct rosette at anthesis, a lax and interrupted inflorescence and large, narrow (turbinate) flower heads c. 5–6.5 mm long.

Gamochaeta subfalcata, in turn, is an annual with rosette leaves mostly withered at anthesis, a denser inflorescence and much smaller, campanulate flower heads c. 2.5–3 mm long. Moreover, *G. sylvaticum* always is confined to natural habitats, mostly heaths and clearings, whereas *G. subfalcata* also and more often grows in strongly disturbed, human-mediated environments.

Introduction — The introduction vector for *Gamochaeta subfalcata* in Belgium and the Netherlands is probably twofold. This species has been observed as a weed in plant containers, though much less frequently so than *G. pensylvanica*. For instance,*G. subfalcata* was seen in 2015 in Oostham (Belgian Province of Limburg) by R. Barendse in a container with *Quercus suber* L. and a species of *Gamochaeta* found in a container, also in 2015, in Amsterdam by Ton Denters probably also belongs to this species. The other records are from various types of habitats, mostly however in urban environments. Some populations may have arisen from seeds that were unintentionally introduced by tourists returning from southwestern Europe (stuck to their car tires, car mats or other belongings). In Sint-Gillis-Dendermonde (Province of East Flanders) plants were observed on a construction site, without obvious vector of introduction (perhaps building materials, like sand or gravel?). Several records of *G. subfalcata* were made in more natural habitats, including heathlands. It is absolutely unknown how and when it was introduced there, but it is remarkable that the species occurs in the same type of habitats in southwestern Europe.

Specimens examined

Belgium

Province of East Flanders — Ghent (Oostakker), Krijtestraat (IFBL D3.13.14), gravel plot in front of house, used as parking place, +/- 50 individuals, most weeded by the end of June, 1 June 2020, *F. Verloove 13810* (BR); Ghent, Wittelinkstraat (IFBL D3.12.31), foot of wall, cracks in pavement, between cobble stones, very common, several hundreds, 20 June 2020, *F. Verloove 13853* (BR); Lochristi, Antwerpsesteenweg (IFBL C3.54.34), semi-paved parking next to Colruyt supermarket, +/- 500 individuals, very variable morphologically, 20 June 2020, *F. Verloove 13852* (BR); Sint-Gillis-Dendermonde, former maize field, now construction site, 26 June 2020, *B. Biesemans s.n.* (BR).

Netherlands

Province of Limburg — Heibloem-Weijenhout, 7July 2020, *J. Slaats s.n.* (BR); Venray, Ysselsteyn, Heidsche Peel nature reserve, former agricultural fields (top soil removed), 10 August 2020, *O. van Koutrik s.n.* (BR).

Province of North Brabant — Beuven, Stabrechtse Heide, 11 June 2020, *L. van Hal s.n.* (BR).

Province of South Holland — Rijswijk, Steenplaetsstraat, 15 June 2020, *P. Hegi s.n.* (BR); Rotterdam, Haringvliet, 7 July 2020, *R. Andeweg s.n.* (BR).

Genome size measurements

Cellular DNA content or genome size, as measured by flow cytometry, can be a key value to detect species and hybrids and determine ploidy (Zonneveld 2019). Genome size is particularly well-studied in Asteraceae (Garnatje et al. 2011, Vitales et al. 2019) and has shown to be, indeed, helpful for the separation of cryptic taxa (see, e.g., Verloove et al. 2020b). However, it has been shown that there is little variation in genome size in Gnaphalieae. For example, Russell et al. (2013) found little variation among six East Asian species of *Leontopodium* R.Br. ex Cass. Furthermore, according to Andrés-Sánchez et al. (2013) 2C-values of *Filago* L. and related genera are highly homogeneous among species. Also, flow cytometry measurements of genome size could not be used as a reliable proxy for the precise determination of higher ploidy levels across the genus *Craspedia* G.Forst. (Castelli et al. 2017).

According to the Genome Size in Asteraceae database (GSAD; online at: www.asteraceaegenomesize.com) 2C-values have only been assessed for two species of *Gamochaeta* so far, only one of them relevant for our study area (*G. coarctata*). Therefore, genome sizes were measured for accessions of the three species encountered in Belgium and the Netherlands (Table 1).

Gamochaeta coarctata was found to have a genome size that ranges between 1.53 and 1.70 pg (mean genome size = 1.62 ± 0.12 pg), which is roughly in line with a previous count for that species (1.49 pg; Garcia et al. 2013). This species is clearly separated from the two others. However, although morphologically well-demarcated, *G. pensylvanica* (mean genome size = 1.11 ± 0.02 pg) and *G. subfalcata* (mean genome size = 1.20 ± 0.04 pg) nearly overlap in their genome sizes. It has been suggested before that *G. pensylvanica*, *G. subfalcata* and a few other similar species perhaps only represent a single very variable species (Drury 1971, Godfrey 1958), although this is neither corroborated by molecular data (Urtubey et al. 2016) nor by their gross morphology.

DISCUSSION AND CONCLUSION

Three species of *Gamochaeta* have recently managed to establish self-sustaining populations in Belgium and the Netherlands, at least locally. The identity of all these species long remained unclear. *Gamochaeta coarctata* and *G. pensylvanica* have been confused with *G. purpurea* and *G. subfalcata* with *G. antillana*. Furthermore, *G. subfalcata* has been overlooked because of its superficial resemblance with native *Gnaphalium sylvaticum*. The currently established identities (*Gamochaeta coarctata*, *G. pensylvanica*, and *G. subfalcata*) are in line with those assessed in areas with comparable climatological circumstances (compare for instance with data presented by Romero Buján (2008) for Galicia in the northwestern Iberian Peninsula). These three cudweeds probably are also the most widespread naturalized species elsewhere in Europe.

The recent naturalization of these three species of *Gamochaeta* in Belgium and the Netherlands is remarkable. All are native to South America and have naturalized in warm-temperate regions of the world. Even in southwestern Europe, the genuine naturalization

Table 1. Average genome sizes (pg) of ten *Gamochaeta* accessions found in Belgium and the Netherlands belonging to three species (*Gamochaeta coarctata* (Willd.) Kerguélen, *G. pensylvanica* (Willd.) Cabrera, *G. subfalcata* (Cabrera) Cabrera) with their provenance, number of replicated genome size measurements (N), and the standard deviation (SD).

Species name	Provenance	N	Cellular DNA content (pg)	SD
G. pensylvanica	Wilrijk	3	1.10	0.03
G. pensylvanica	Boom	3	1.10	0.02
G. pensylvanica	Bellem	3	1.13	0.02
G. subfalcata	Lochristi	2	1.17	0.08
G. subfalcata	Oostakker	1	1.17	NA
G. subfalcata	Rotterdam	1	1.19	NA
G. subfalcata	Mariakerke	1	1.22	NA
G. subfalcata	Heibloem	2	1.27	0.01
G. coarctata	Breda	1	1.53	NA
G. coarctata	Rhenen	3	1.70	0.04

and spread of these three species is a relatively recent phenomenon. In Portugal — where the highest diversity of the genus in Europe is encountered (Rocha Afonso 1984) — these species have already been known since the 1940s (Almeida 1999) and have now become quite widespread. Elsewhere, however, namely in France, Italy, and Spain, these species naturalized less (often even much less) than 40 years ago and started expanding further north only recently. The fact that they now have reached Belgium and the Netherlands obviously is not a direct result of global warming. The uninterrupted secondary distribution area in France for the northernmost species (*G. subfalcata*) at present barely reaches the northern half of the country (distribution map sub *G. antillana* at siflore.fcbn.fr, consulted 18 June 2020). *Gamochaeta coarctata* is still limited to southwestern France whereas *G. pensylvanica* is not even known from France (comm. J.-M. Tison, June 2020). These three species were inadvertedly introduced by man in the study area, either as contaminants in plant containers or potting soil, as seeds carried by tourists returning from southern Europe (attached to tires, clothes, camping equipment, etc.; see Verloove et al. 2020a) or perhaps also as a result of military training activities. However, while such thermophilous species hardly would have survived in the climatologically unfavorable conditions usually encountered in Belgium and the Netherlands, they now apparently have adapted to the local climate. The urban habitats in which they have predominantly naturalized are known as so-called heat islands with average temperatures that are higher than in the surrounding countryside (Zipper et al. 2016). The specific habitats in which they are usually found (i.e., stony, gravelly or sandy, fast-heating substrates, often in direct sunlight) also enhance the survival chances of these species. Similarly, populations found in more natural environments (mainly heaths) are found on fast-heating, sandy soils. To our knowledge, for these three species, the naturalized populations here reported actually are probably the northernmost known worldwide.

Our expectation is that all or at least part of these species will naturalize on a wider scale in the next years. Moreover, it is not impossible, and even likely, that some are more widespread already: they are easily overlooked species from very ordinary habitats. Also, because of confusion with other (native) species of *Gnaphalium* s.l., some populations may have passed unnoticed. This is especially true for *Gamochaeta subfalcata*. In southwestern Europe, these *Gamochaeta* species also occur in other habitat types and the same can probably be expected to occur in Belgium and the Netherlands as well. The biennial species *G. coarctata*, for instance, frequently occurs as a weed in disturbed lawns where it easily withstands regular mowing and trampling. The same holds true for *G. pensylvanica*. *Gamochaeta subfalcata*, in turn, is often encountered in various kinds of disturbed open sandy or gravelly habitats: sand and gravel pits but also synantropically in more natural habitats like heath lands. Its wider occurrence in such habitats in the study area is not unlikely, for instance in hard-to-access military training areas.

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Postscript – The text of this manuscript was closed on 31 December 2020. Since then, all species discussed here have been found in new locations, in Belgium as well as in the Netherlands, demonstrating that these species have not only established themselves but are also spreading. Updated distribution maps for all species for the Netherlands were recently published (Denters & Verloove 2022). Moreover, in 2022 a first seemingly established population of *Pseudognaphalium undulatum* was discovered in Belgium (pers. obs. first author).

In addition, a number of papers have since been published highlighting the nomenclature and taxonomy of one of the taxa covered, *Gamochaeta coarctata*. In a new morphometric analysis, Freire et al. (2021) reaffirmed that *G. americana* and *G. coarctata* cannot be distinguished on morphological grounds. Since *G. americana* has nomenclatural priority, the plants currently found in Belgium and the Netherlands should be ascribed to that species, while *G. coarctata* becomes a (heterotypic) synonym.

Nesom (2022) confirmed the conspecificity of these two species. However, according to him the widespread and common species in the southeastern USA, which had been identified as *Gamochaeta coarctata* (Nesom 2006), differs in a number of features from the Mexican/Central American/South American species. It was therefore described as a new species, *G. impatiens* Nesom. It differs from *G. americana* (incl. *G. coarctata*) by stems decumbent-ascending to nearly prostrate from the first (vs. erect), upper leaf surface glabrous or rarely glabrate, usually shiny, the basal leaves persistent (vs. usually glabrescent, sometimes becoming shiny, the basal leaves often not persistent), involucres shorter and rose-tinged, outer phyllaries depressed-ovate, bisexual florets fewer and corolla apices reddish (Nesom 2022). *Gamochaeta impatiens* is supposedly native to South America, but probably widely naturalized elsewhere in the world: Nesom referred to its presence as an adventive in the southern U.S.A., Swaziland, New Zealand, and China. The taxonomic relevance of this species will have to be demonstrated, preferably supported by molecular phylogenetic studies. However, at least part or even a majority of the populations found in our study area seem to belong to this newly described species.

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