A taxonomic re-assessment of *Ammocharis herrei* and *Cybistetes longifolia* (Amaryllideae : Amaryllidaceae)

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ABSTRACT

The infructescence of the poorly known Ammocharis herrei F.M. Leight, is similar to that which is diagnostic for Cybistetes tongifolia (L.) Milne-Redh. & Schweick. In the absence of distinct morphological differences A. herrei is placed into synonymy under C. longifolia. Plants of the amplified C. longifolia have fewer, large seeds in Namaqualand and the Richtersveld and smaller, more numerous seeds in the Western Cape. This pattern is postulated to reflect divergent strategies of resource allocation in different habitats. It is suggested that the infructescence of C. longifolia, a highly derived structure suited to tumbling, evolved from the unspecialised condition in Ammocharis as an adaptation to the high winds of southwestern Africa.

UITTREKSEL

Die vrugstadiumbloeiwyse van die betreklik onbekende Ammocharis herrei F.M. Leight, is soortgelyk aan dié wat diagnosties is vir Cybistetes longifolia (L.) Milne-Redh. & Schweick. In die afwesigheid van duidelike morfologiese verskille, word A. herrei in sinonimie onder C. longifolia geplaas. Plante van die vergrote C. longifolia het minder, groot sade in Namakwaland en die Richtersveld en kleiner, meer sade in die Wes-Kaap. Die veronderstelling word gemaak dat hierdie patroon uiteenlopende strategieë van hulpbrontoewysing in verskillende habitats weerspieël. Daar word voorgestel dat die vrugstadiumbloeiwyse van C. longifolia, 'n hoogs afgeleide struktuur wat kan rol, van die ongespesialiseerde toestand by Ammocharis as 'n aanpassing by die sterk winde van suidwestelike Afrika ontwikkel het.

INTRODUCTION

The monotypic *Cybistetes* Milne-Redh. & Schweick. is a Western Cape representative of Amaryllidaceae tribe Amaryllideae with a specialised infructescence in which the pedicels elongate, spread apart, stiffen and ultimately radiate equally in all directions. Its separation from the widely distributed sub-Saharan *Ammocharis* Herb. was based on the interpretation of Milne-Redhead & Schweickerdt (1939) that the pedicels of the infructescence and the dry, strongly ribbed capsules constitute a substantially distinct set of characters from the basic infructescence structure of *Ammocharis* in which the pedicels neither reflex nor elongate and the fruits remain submembranous and subglobose. This treatment, however, rendered uncertain the taxonomic position of *A. herrei* F.M. Leight. whose fruits have remained unknown until now.

Even in the absence of fruiting material, Milne-Redhead & Schweickerdt (1939) commented on the close resemblance of the type of *A. herrei* to the Western Cape species, *C. longifolia* (L.) Milne-Redh. & Schweick. They noted differences, however, in inflorescence characters and ovule numbers.

Several recent collections of Amaryllidaceae from the Richtersveld in the Northern Cape Province match the type of *A. herrei*, which consists of leaves and an inflorescence from a bulb originally collected by H. Herre south of Kommaggas, Namaqualand in the Northern Cape Province and later cultivated at the Stellenbosch University Garden. The position and status of this taxon are re-assessed and the current data on the fruits and seeds of *Cybistetes* are discussed.

INFRUCTESCENCE, INFLORESCENCE AND OVULE NUMBER

The new infructescence data given here were taken from three recent collections of Amaryllidaceae from the Richtersveld [Van Jaarsveld et al. 3511 (NBG, PRE), G. & F. Williamson 4626 (K, MO, NBG, PRE) and G. & F. Williamson 4637 (NBG, PRE)]. They augment the previously collected flowering data of A. herrei from the same area [Hall 592 (NBG), Williamson 2943, 2944 and Williamson & Gassner 2925 (BOL)]. This new material has roughly spherical, stiff, infructescences with long pedicels and dry indehiscent capsules (Figure 1B, C). These characters fully match those diagnostic for Cybistetes and clearly align the material with this genus.

Milne-Redhead & Schweickerdt (1939) had noted that in *A. herrei* the number of flowers per umbel is greater, the pedicels are longer and the number of ovules (2–4) per locule is smaller than is usual for *C. longifolia* (8–19). These differences are reduced, however, by the subsequent collections of *Hall 1081* and *Snijman 435, 1314* at NBG & PRE, from near Vanrhynsdorp. Observations based on all the available material at BOL, NBG, PRE and STE show that plants of *C. longifolia* from the south have 13–40flowered umbels and pedicels up to 100–210 mm long; those from further north near Vanrhynsdorp have 35–47-

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FIGURE 1.—Cybistetes longifolia on the alluvial plains of the Orange River, Richtersveld. A, solitary bulb with two inflorescences; B, developing infructescence showing damage by a snout beetle (*Brachycerus* sp.); C, dispersed infructescence having released its seeds through tumbling; D, leaves withering back after a short growth flush in February.

flowered umbels and pedicels up to 125-175 mm long; whereas the Richtersveld plants from yet further north, have 37-90 flowers per umbel and pedicels up to 100-150 mm long. Data on variation in ovule number in plants from throughout the range are lacking but differences in the abundance of seed per capsule from plants within the Western Cape, near Vanrhynsdorp and the Northern Cape in the Richtersveld support the observations of Milne-Redhead & Schweickerdt (1939) on divergent ovule numbers from plants (Table 1). Infructescences collected near Vanrhynsdorp and Namaqualand have a greater maximum number of seeds per capsule than the fruiting material collected in the Richtersveld. The capsules from the south also tend to be longer and narrower than those in the north (Figure 2). The differences, however, are not discrete and the increase in seed number per capsule from the north

to the south appears to be continuous. There is also an inverse relationship between seed size and seed number per capsule within the species' distribution range (Table 1). Thus plants in the Richtersveld and Namaqualand tend to have especially large seeds (up to 29 mm across) whereas the seeds of those in the south are smaller (7–19 mm across) (Figure 2). Seed size within a capsule is nevertheless variable throughout the distribution range.

DISCUSSION

In the absence of any vegetative, floral or clearly discontinuous fruiting characters to distinguish *A. herrei* from the variable *C. longifolia*, we propose that *A. herrei* is conspecific with *C. longifolia* (L.) Milne-Redh. & Schweick. but that plants of *C. longifolia* produce few, large seeds in

TABLE 1.—Seed number and seed size in individual plants of Cybistetes longifolia throughout the distribution range

Locality Gordon's Bay	Grid 3418 BB	Collector		Maximum no. of seeds per capsule	Range in seed size (mm)
		Duncan s.n.	(a) (b) (c)	14 12 7	9–15 7–15 10–19
Near Vanrhynsdorp	3118 DA	Snijman 1314	(a) (b)	16 8	5–29 10–25
Annisrivier	2816 BD	Williamson 4639		6	9–27
Beauvallon	2816 DA	Williamson 4637		6	10-20
Beauvallon	2816 DA	Williamson 4702		3	10-20



FIGURE 2.—Variation in size of capsules and seeds of *Cybistetes longifolia*. A, disintegrating capsule revealing many seeds from Gordon's Bay, Western Cape (*Duncan s.n.*); B, seed from Gordon's Bay (*Duncan s.n.*); C, capsules and seed from Beauvallon, Richtersveld (*Williamson 4637*); D, large seed from Annisrivier, Richtersveld (*Williamson 4639*). Scale bars: 10 mm.

the semi-arid environments of the Richtersveld and Namaqualand, and many, relatively small seeds in the more equable south. Accordingly *A. herrei* is treated here as a synonym of *C. longifolia*.

As regards the comparative biology of individuals within the amplified C. longifolia, the most noteworthy variables are seed size and seed number. According to Harper et. al. (1970) and Stebbins (1974) seed size and seed number represent alternative strategies in the disposition of reproductive resources. However, due to divergent and often conflicting advantages and disadvantages of seed size versus seed number, most plant species have evolved compromise strategies which depend on various conditions of their habitat as well as their evolutionary ancestry (Stebbins 1974). In the Richtersveld the annual vegetative growth period of C. longifolia is often more variable and shorter than that of plants in the Western Cape whose foliage leaves are green for five to six months throughout the winter rainfall season. The fleshy seeds of C. longifolia, which germinate immediately after being shed in autumn, are potentially susceptible to desiccation injury before the onset of winter rain. Thus within the constraints of the restricted and unpredictable growing season for C. longifolia in the semi-arid Richtersveld and Namaqualand the selection of large seeds, which have optimal reserves for their initial growth, appears to have been favoured at the expense of seed numbers. In contrast, the more reliable growing season of the Western Cape may have promoted the selection of large seed numbers over seed size to increase the probability that some seeds lodge in suitably open habitats amongst the otherwise densely vegetated communities of this region.

In several evolutionary lines Stebbins (1970) observed the transference of function of a particular structure. A notable example is the functional shift in the fruit wall from that of providing protection for developing ovules to one of effecting the dispersal of mature seeds. This pattern is paralleled in *Ammocharis* and *Cybistetes* whose indehiscent fruit walls initially protect the fleshy seeds during development, but thereafter effect divergent dispersal strategies.

The lax infructescences of Ammocharis, which favours seasonally moist habitats, initially elongate then flop to the ground, releasing their seeds close to the parent plants. In contrast, the indehiscent fruits of Cybistetes, which inhabits open, dry situations, become dry, rigid capsules, that radiate outward to form a sphere which then tumbles in the wind (Markötter 1936; Martley 1938; Milne-Redhead & Schweickerdt 1939) (Figure 1C). Following the concept of transference of function (Stebbins 1974), it is postulated that the basic protective function of the fruits has shifted to include a derived dispersive function in Cybistetes, where the entire infructescence serves as the unit of dispersal. Clearly, the specialised infructescence characters defined by Milne-Redhead & Schweickerdt (1939) as separating Cybistetes from Ammocharis are highly integrated and functionally interrelated to effect dispersal by tumbling (anemogeochory of Van der Pijl 1982). It does not seem unlikely that this syndrome of characters evolved from a most recent common ancestor within Ammocharis as an adaptation to the high winds of the Western Cape which probably date from the inception of its Mediterranean-type climate in the Late Pliocene (Deacon et al. 1992; Tankard & Rogers 1978). This interpretation suggests that Ammocharis sensu Milne-Redhead & Schweickerdt (1939) is paraphyletic and that the current classification of Cybistetes and Ammocharis warrants re-examination. Evidence of this, however, awaits a phylogenetic analysis of all the species in the generic complex and a character analysis of the closely related and variable genus Crinum L.

In Amaryllideae anemogeochory is also known in *Boophane* Herb. and *Brunsvigia* Heist. In most taxa the infructescences detach at ground level and roll away in the wind with the scape intact. The scape, which approximates the length of the radiating pedicels in most species, appears to confer symmetry on the infructescence, a configuration which Maddox & Carlquist (1985) have shown ranks highly in tumbling ability. *Boophane disticha* (L. f.) Herb. and *Boophane haemanthoides* F.M. Leight. are exceptional in having infructescences which detach from the scape distally. The resultant dispersal unit lacks symmetry and appears to lose its integrity rapidly. These observations suggest that *Cybistetes, Boophane* and *Brunsvigia* offer interesting possibilities for experimental studies in wind dispersal.

Cybistetes longifolia (*L.*) *Milne-Redh. & Schweick.* in Botanical Journal of the Linnean Society 52: 192 (1939); Adamson & T.M. Salter: 211 (1950). Type: figure in P. Herm., Paradisus batavus: t. 195 (1698), lecto.!, here designated.

Amaryllis longifolia L.: 293 (1753). *Crinum longifolium* (L.) Thunb.: 59 (1794) pro parte, excl. descr. *Ammocharis longifolia* (L.) M. Roem.: 62 (1847).

Crinumfalcatum Jacq.: 34,t. 60(1776). Amaryllisfalcata (Jacq.) L'Hér.: 13 (*1788*, 1789). Haemanthus falcatus (Jacq.) Thunb.: 58 (1794). Brunsvigia falcata (Jacq.) Ker Gawl.: t. 1443 (1812). Ammocharis falcata (Jacq.) Herb.: 17 (1821); Baker: 96 (1888); Baker: 204 (1896) pro parte (excluding Ammocharis coranica Herb. & Amaryllis coranica Burchell). Type: figure in Jacq., Hortus botanicus vindobonensis 3: t. 60 (1776), lecto.!, designated here.

Amaryllis coranica var. pallida Lindl. (sphalm. Burchell) sec. Markötter: 13 (1936), non Lindl.: t. 1219 (1829).

Ammocharis herrei F.M. Leight.: 110 (1932), syn. nov. Type: South Africa, Namaqualand, 60 miles S of Kommaggas, fl. ex hort. Stellenbosch, April 1931, *Herre sub SUG 3072* (BOL, holo.!).

Bulb solitary, ovoid to globose, 100-150 mm across, extended into a neck up to 60 mm long, entirely subterranean; outer tunics dark brown, tough and leathery; inner tunics fleshy, cream-coloured. Leaves present or absent at anthesis, 9-14, biflabellately arranged, spreading, strapshaped, more or less falcate, variable in length and width, with the inner narrower and shorter than the outer, 6-270 \times 13–55 mm, glaucous, smooth; margins scarious, obscurely toothed or entire; apex truncate in mature leaves, obtuse in young leaves. Inflorescence 13-90flowered, ranging from somewhat clustered to widely spreading, 150-340 mm across; scape erect, up to 200 mm long, compressed, about 10×22 mm, fleshy, smooth, detaching from the bulb at ground level when dry; spathe valves 2, reflexed, broadly lanceolate, $20-30 \times 40-75$ mm, thinly coriaceous; bracteoles filiform; pedicels 50-110 mm long at anthesis, somewhat triangular in cross section, radiating outward, stiffening and lengthening to 100-210 mm in fruit. Perigone widely trumpet-shaped, slightly zygomorphic due to the declinate style, ivory to pink, turning deeper pink with age, dark reddish when collapsed,

sweetly scented; tube subcylindrical, widening slightly towards the mouth, 8-15 mm long, firm and fleshy; lobes oblanceolate, 40–65 \times 8–15 mm, spreading and slightly recurved distally, with a raised midrib on the abaxial surface; stamens spreading, very slightly declinate, fused to the perigone tube just below the throat, otherwise free; filaments filiform, more or less equalling the perigone lobes; anthers dorsifixed, about 12 mm long and creamcoloured before opening; pollen cream-coloured. Ovary about 10 mm long, narrowly fusiform, obscurely triangular in cross section, placentation axile, 1–19 ovules per locule; style slender, slightly longer than the perigone lobes, declinate; stigma truncate, penicillate. Capsule indehiscent, pyriform, ovoid, ellipsoid to subfusiform, 25-100 \times 10–35 mm, somewhat triquetrous, strongly 6-ribbed, bluntly beaked distally. Seeds subglobose or somewhat bluntly angled by pressure, 5-29 mm wide, fleshy, greenish; outer covering corky, pale; embryo green. Chromosome number 2n = 22 (Gouws 1949). Figure 1.

Flowering phenology

Bulbs usually produce a single inflorescence between December and March or occasionally in early April. Dissections of mature bulbs from the wild retain evidence of many aborted inflorescences which indicates that flowering is sporadic. Despite this irregular flowering pattern, inflorescence buds arise consistently in mature bulbs at four-leaf intervals. Each vegetative shoot consists of a non-amplexicaul bladeless prophyll, two amplexicaul foliage leaves and a non-amplexicaul foliage leaf. This leaf series is also known in Ammocharis heterostyla (Bullock) Milne-Redh. & Schweick. and several species of Crinum but, unlike Cybistetes, two inflorescences often develop from each bulb within a few weeks of each other (Hannibal 1955). Only rarely does the bulb of C. longifolia produce two inflorescences simultaneously (Figure 1A). The infructescences of C. longifolia usually mature and detach within four weeks of flowering but during rare wet autumn seasons the period from flowering to fruit dispersal may last three months.

Vegetative phenology

Foliage leaves are present only when conditions are favourable. Usually two growth flushes occur in response to alternating wet and dry sequences throughout the year. Thus leaves often appear briefly after late summer or autumn rains when the bulbs may flower, but may soon die back with the onset of a warm, dry period when the infructescences are released (Figure 1D). Thereafter successive winter showers initiate rapid regrowth of the withered leaves. The leaves may persist up to six months in the wetter Western Cape (Markötter 1936), unlike the more variable pattern of growth in the semi-arid Richtersveld, where the leaf blades may elongate and die a further two times during the year (G. Williamson pers. obs.). This growth sequence gives the leaves the truncate apices which are also found in A. coranica. Morphological studies of A. coranica have shown that the regrowth of mature leaves is due to a well-developed intercalary meristem (Troll 1954).

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Pollination

Markötter (1936) reports that wild plants of *C. longifolia* from Stellenbosch in the Western Cape are pollinated by night-flying moths. Other visitors to flowers of *C. longifolia* in the Richtersveld are moths during the early morning and two common butterflies, the painted lady and green-yellow lucerne butterfly during the day (G. Williamson pers. obs.). Snout beetles (*Brachycerus* sp.) have been observed eating all parts of *C. longifolia* (Figure 1B).

Distribution and habitat

Cybistetes longifolia is widely distributed in southwestern Africa from the Orange River to the Cape Peninsula (Figure 3). The bulbs favour open, flat terrain either in light sandy soil or hard gravelly clay.

DISTRIBUTION RECORDS

NORTHERN CAPE.—2816 (Oranjemund): Annisrivier, (-BD), G. Williamson 2943 (BOL); Richtersveld, Grootderm, (-DA), Hall 592 (NBG, PRE); Arrisdrif, about 40 km E of Oranjemund, (-DA), G. & F. Williamson 4626 (K, MO, NBG, PRE); Beauvallon, (-DA), Williamson 4637 (NBG, PRE); Williamson & Gassner 2925 (BOL); Beesbank, (-DA), Williamson 2944 (BOL). 2817 (Vioolsdrif): Richtersveld,



FIGURE 3.—Known distribution of Cybistetes longifolia.

Sandberg, (-AA), Van Jaarsveld, Forrester & Jacobs 8511 (NBG, PRE). 3017 (Hondeklipbaai): 60 miles S of Kommaggas, (-DA), Herre sub SUG 3072 (BOL).

WESTERN CAPE.—3118 (Vanrhynsdorp): 1 mile S of Widows River, (-DA), *Hall 1081* (NBG, PRE); flats between Wiedouw River and Klaver, (-DA), *Snijman 435* (NBG, PRE); 2.2 km S of Wiedouw River towards Klawer, (-DA), *Snijman 1314* (NBG, PRE); Farm Sandkraal, Vanrhynsdorp Dist., (-DB), *Van Breda 4377* (PRE). 3218 (Clanwilliam): Farm Vondeling Op De Nardouwsberg, (-BB), *Snijman 1315* (NBG); Eendekuil, (-DB), *Peers s.n.* (BOL 16389). 3317 (Saldanha): Saldanha, (-BB), *Duncan 304* (NBG). 3318 (Cape Town): Darling Flora Reserve, (-AD), *Marais 10* (NBG); Lion's Head, (-CD), *Compton 21950* (NBG); Rietvalley, (-DC), *Zeyher 4115* (SAM); near Paarl, (-DB), *Barker 5329* (NBG); Stellenbosch, (-DD), *Duthie sub NBG 1353/26* (NBG). 3319 (Worcester): Breederivier, Worcester Dist., (-CB), *Walters 2443* (NBG). 3418 (Simonstown): Sandy Bay, (-AB), *Snijman 1017* (NBG); between Faure and Lynedoch, (-BA), *Esterhuysen 10113* (BOL, NBG, PRE); flats between Gordon's Bay and Strand, (-BB), *Goldblatt 6463* (PRE). 3320 (Montagu): near Bonnievale, (-CC), *Smith* (BOL 21376).

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