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The genus *Rhanterium* (Asteraceae: Inuleae)

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WIKLUND, A., 1986. **The genus *Rhanterium* (Asteraceae: Inuleae).** This revision of the genus *Rhanterium* Desf. of the *Inula*-group in the Asteraceae: Inuleae, subtribe Inulinae, is based on studies of herbarium material. The genus is distributed over western North Africa, the Arabian peninsula, Iraq and Iran. Three species are recognized: *R. adpressum* Coss. & Durieu, *R. epapposum* Oliver and *R. suaveolens* Desf. A fourth previously accepted species, *R. intermedium* Coss. & Durieu ex Pomel, is here considered to be composed of hybrids between *R. adpressum and R. suaveolens*. A taxonomical recognition of these hybrids is not found to be justified. The morphology, phylogeny and phytogeography of the species are discussed and a cladogram of the genus is proposed.

ADDITIONAL KEY WORDS:—Cladistics – hybridization – *Inula*-group – taxonomic revision.

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INTRODUCTION

This paper revises *Rhanterium*, a genus belonging to the *Inula*-group of the Asteraceae: Inuleae (Merxmüller, Leins & Roessler, 1977). The study is based exclusively on herbarium specimens. Material was obtained from the following herbaria (for key to abbreviations see Holmgren, Keuken & Schofield, 1981): BM, C, G, K, MPU, P, S, UPS and W. The methods used were those previously outlined by Wiklund (1985). A list of all examined collections is kept at the Swedish Museum of Natural History, Section for Phanerogamic Botany, in Stockholm (S).

MORPHOLOGY

All three *Rhanterium* species are somewhat spiny subshrubs. Their stems and branches are covered by a thick indumentum of white, matted hairs (Fig. 1A).

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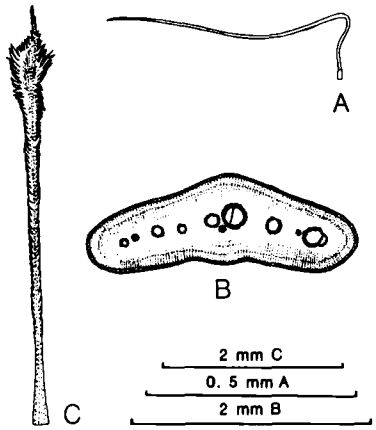

Figure 1. A. *Rhanterium adpressum*, leaf hair. B. *Rhanterium suaveolens*, leaf cross-section. C. *R. adpressum*, pappus bristle. A. S Oran, surroundings of Ain Sefra, 1934 *Faure* (S). B. Arak, Hoggar Mts, central Sahara, Meinertzhagen. (BM). C. Baniou (Hodna), v. 1882 *Letourneux*, (UPS).

The leaves are always sessile. In *R. adpressum* they are obovate-oblong to broadly lanceolate, whereas in *R. epapposum* and *R. suaveolens* they are narrowly oblong to linear. In all three species they usually have a very weak indumentum of the same type as found on the stems and branches.

The capitula are small and deciduous in *R. epapposum* and *R. suaveolens*. The involucres in these two species are squarrose, with the involucral bracts bent outwards and apically pointed, features which are the most pronounced in *R. suaveolens*. In *R. adpressum* the capitula are larger and firmly attached to the scapes. The involucral bracts are appressed and not as narrowly pointed as in the other *Rhanterium* species.

The involucral bracts in *Rhanterium* are coriaceous. The margins are thin and have a particularly broad scarious rim in *R. adpressum*. A similar, but narrower, rim may also be observed in *R. epapposum* and *R. suaveolens* at least along the basal parts of the margins. In *R. adpressum* the bracts are covered with a weak indumentum, whereas they are glabrous in *R. epapposum* and *R. suaveolens*. The bracts in the innermost row of the involucre (alternatively the outermost row of the paleae), i.e. those that mainly subtend the ray-florets, are three- to four-sided and completely enclose the florets. In *R. adpressum* and *R. suaveolens* they frequently have a few irregular dorsal ridges, whereas they are alway smooth in *R. epapposum*.

The receptacle is flat and paleate in all three *Rhanterium* species. However, in *R. adpressum* and *R. suaveolens* paleae are lacking centrally. The paleae are uniformly flat and narrowly oblong to linear in *Rhanterium*. The ray-florets are bright yellow in *R. adpressum* and *R. suaveolens* (*fide coll.*) and pale yellow in *R. epapposum*. In all three species they are glabrous and eglandular. The cells of the adaxial epidermis of the ray-florets in *Rhanterium* appear to belong to the 'Senecionoid-type' which is common in the Inuleae (Baagøe, 1977).

The styles of the ray-florets have branches which are often slightly tapering and apically more or less rounded. In *R. adpressum* the style-branches have minute dorsal sweeping-hairs whereas in *R. epapposum* and *R. suaveolens* the style-branches appear dorsally smooth in the light-microscope. The disc-florets in

Rhanterium are glabrous and eglandular, except for *R. epapposum*, where a few minute glands were occasionally found dorsally on the corolla lobes. The style-branches of the disc-floret styles are apically acute and dorsally covered with sweeping hairs.

The achenes of all three species are glabrous and eglandular. They have many (10–20) sclerenchymatic ribs underneath the epidermis except for the disc-floret achenes of *R. epapposum*. In this species the disc-floret achenes do not seem to mature and develop sclerenchyma and no embryos were found. The ray-floret achenes are always epappose in *Rhanterium* as are the disc-floret achenes of *R. epapposum*. The disc-floret achenes of *R. adpressum* and *R. suaveolens* have a pappus consisting of broad, dorsiventrally flattened and apically plumose bristles (Fig. 1C). In *R. adpressum* they are widened basally and additional very small scale-like protrusions may also often be observed. The bristles are entire along the lower half but towards the apex they become increasingly serrate along the margins and finally they terminate in an apical tuft of long pointed cells. An additional row of teeth perpendicular to the margins may also occur.

In all three *Rhanterium* species secretory canals are common. They were found in the leaves (Fig. 1B), the involucral bracts and the paleae. Crystals are also frequent. They occur in the epidermal cells of the achenes, in the corollas of the ray-florets and the disc-florets, in the filaments of the stamens, and in the styles.

Pollen grains of *R. adpressum* and *R. epapposum* have been investigated by Leins (1971). They were found to be of the type generally found in the *Inula*-group. The chromosome number is known only in *R. adpressum*, for which Reese (1957) has reported $n = 12$. This chromosome number is as yet unique in the *Inula*-group where most genera are based on $x = 10$ or 9 (Merxmüller *et al.*, 1977).

PHYLOGENY AND NOTES ON THE PHYTOGEOGRAPHY

I consider the genus *Rhanterium* to be monophyletic and defined by the presence of inner involucral bracts that completely enclose the florets (character 2 in Tables 1 & 2 and Fig. 2). This character is unique within the *Inula*-group (Merxmüller *et al.*, 1977) of the Inuleae: Inulinae.

The sister-group of *Rhanterium* is here assumed to be the genus *Rhanteriopsis* (= *Postia*) with which it shares the presence of very broad pappus bristles. These were not found in any other genera of the *Inula*-group. *Rhanteriopsis*, which is characterized by a distinct kind of leaf venation, has paleae which are very similar to those of *Rhanterium*, but lacks the characteristic inner involucral bracts found in *Rhanterium*.

Within the genus *R. suaveolens* shares a single character (no. 3, absence of paleae centrally in the capitulum) with *R. adpressum* whereas it shares five other characters (5, 6, 7, 8, 9; Table 1) with *R. epapposum*. For the single character 3, a parallel origin in *R. adpressum* and *R. suaveolens* would normally be hypothesized due to the much higher number of characters uniting *R. suaveolens* with *R. epapposum*. However, if introgression between *R. adpressum* and *R. suaveolens* is indeed found to occur (see discussion p. 242), character 3 can equally well be considered to be introduced into *R. suaveolens* from *R. adpressum* (or vice versa). This supposition would also be supported by the fact that a few completely paleate collections of *R. suaveolens* were found in the easternmost part of its distribution, which is situated furthest away from *R. adpressum*.

Table 1. Apomorphic and plesiomorphic characters in *Rhanterium* and its sister-group *Rhanteriopsis*. Numbers correspond to numbers in Table 2 and in the cladogram (Fig. 2)

	Plesiomorphy (−)	Apomorphy (+)
1	Pappus bristles basally narrow (<0.08 mm)	Pappus bristles basally broad (>0.09 mm)
2	Inner bracts not enclosing florets	Inner bracts enclosing florets
3	Receptacle centrally paleate	Receptacle centrally epaleate
4	Involucral bracts not densely appressed	Involucral bracts densely appressed
5	Habit not straggling	Habit straggling
6	Leaves ± lanceolate	Leaves linear
7	Capitula persistent	Capitula deciduous
8	Involucre not squarrose	Involucre squarrose
9	Involucral bracts pubescent	Involucral bracts glabrous
10	Involucral bracts slightly reflexed	Involucral bracts revolute
11	Achenes of disc-florets pappose	Achenes of disc-florets epappose
12	Leaves not deeply alveolate	Leaves deeply alveolate

The distribution of the three *Rhanterium* species is shown in Fig. 4. Their sister-group *Rhanteriopsis* occurs north of the distribution of *R. epapposum*, in Lebanon, Syria and Iran. The overlapping distributions of *R. adpressum* and *R. suaveolens* are, under an allopatric model of speciation, considered to be the result of secondary dispersal into once fully separated areas of distribution. Distributions similar to that of *Rhanterium* are found in *Anvillea* and *Iphiona* (Anderberg, 1982, 1985), in *Cuminum* (Davis & Hedge, 1971) and in *Zilla* of the Brassicaceae.

Table 2. Character distribution in *Rhanterium* and its sister-group *Rhanteriopsis*. Numbers correspond to numbers in Table 1 and in the cladogram (Fig. 2)

	Rhanteriopsis	*R. adpressum*	*R. suaveolens*	*R. epapposum*
1	+	+	+	+
2	−	+	+	+
3	−	+	+	−
4	−	+	−	−
5	−	−	+	+
6	−	−	+	+
7	−	−	+	+
8	−	−	+	+
9	−	−	+	+
10	−	−	+	−
11	−	−	−	+
12	+	−	−	−

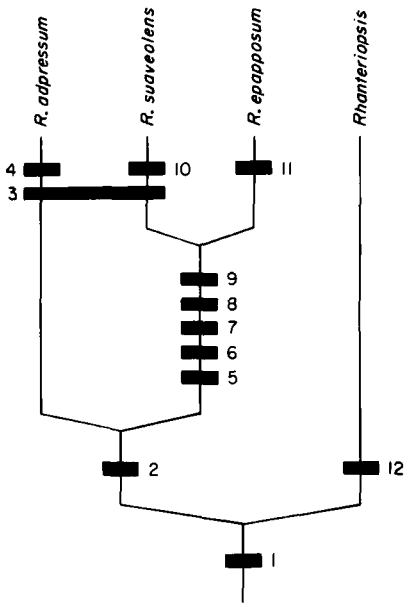

Figure 2. Cladogram of the genus *Rhanterium* with out-group *Rhanteriopsis*. Numbers correspond to apomorphic characters in Tables 1 & 2.

TAXONOMY

Rhanterium Desf.

Rhanterium Desfontaines, *Flora Atlantica, 1:* 291 (1798).

TYPE: *R. suaveolens* Desf.

SYNONYMS: *Musilia* Velenovsky, Plantae arabicae ex ultimo itinere A. Musili a. 1915. *Mémoires de la Société Royale des Sciences de Bohême; Classe des Sciences, 6:* 6 (1923).

TYPE: *R. epapposum* Oliver.

NOMENCLATURAL NOTE: In connection with his studies of Musil's Arabian collections kept at PRC (Vegter, 1976) in Prague, Velenovsky (1911) described the new species *Asteriscus arabicus*. Later (1923) he placed this species in the new genus *Musilia*. No collections made by Musil have been found at PRC of this species, but according to Velenovsky's description it seems very probable that his species is identical to *Rhanterium epapposum* (see also Burtt in Merxmüller *et al.*, 1977).

Erect, richly branched subshrubs. BRANCHES erecto-patent to ascending, ±spiny, striate, densely and appressedly white-woolly, eglandular, becoming glabrous and pale brown. LEAVES sparsely set, alternate, sessile, with an obvious midrib, flat to somewhat canaliculate, broadly lanceolate to obovate-oblong to narrowly oblong to linear, basally narrow, entire to remotely serrate-dentate to remotely narrow-lobed, apically acute to rounded, minutely mucronate, woolly to glabrous, eglandular to minutely glandular with clavate biserial glands, with

longitudinal secretory canals. CAPITULA solitary, terminal, heterogamous, deciduous or persistent. Involucre subspherical or cyathiform to broadly cyathiform. Involucral bracts imbricate in *c.* four layers, appressed or squarrose, increasing in size towards centre of capitulum, coriaceous with thin and often scarious lateral margins, glabrous or slightly pubescent, slightly glandular to eglandular, dorsally with a ±obvious central secretory canal; outer ±narrowly oblong to ovate, entire to slightly fimbriate, apically acute to rounded, glandular to eglandular; inner ovate to oblong, apically acute to rounded, irregularly fimbriate to entire. Innermost involucral bracts clasping ray-florets and sometimes outer disc-florets completely, slightly curved, bluntly three- to four-edged, ±oblong in outline, fimbriate to entire, apically acute to acuminate, dorsally smooth or with a few irregular longitudinal ridges, glandular, with an obvious central secretory canal and sometimes also with additional lateral ones. RECEPTACLE flat, paleate, with or without an epaleate centre. Paleae narrowly oblong to linear, entire to serrate to fimbriate, glandular. RAY-FLORETS female, uniseriate, pale yellow to bright yellow, spreading or with a patent lamina, glabrous, eglandular. Tube ±triquetrous. Lamina generally three-lobed and three- to eight-veined, oblong to narrowly oblong, sometimes containing small crystals. Staminodia sometimes present. Style terete, bifid, sometimes containing crystals; style-branches ±semiterete, narrowly oblong to linear, apically rounded to subacute, dorsally entirely covered with sweeping-hairs or smooth. ACHENES brown, straight to slightly curved, three-edged to subcylindrical, sometimes laterally compressed, narrowly oblong to narrowly obovate in outline, basally truncate to rounded, glabrous, eglandular, with many narrow longitudinal sclerenchymatic ribs, with single oxalate crystals in the epidermal cells, epappose. DISC-FLORETS protruding well above the involucre, bisexual, yellow, glabrous, containing small crystals; tube subcylindrical to funnel-shaped; limb narrowly cyathiform to funnel-shaped, corolla lobes usually eglandular. Anthers tailed, apically acute; tails long and narrow, fimbriate; filaments sometimes containing crystals; filament collar with smaller basal cells; endothecial tissue polarized. Style terete, bifid, generally with crystals; style-branches ±semiterete, narrowly oblong, apically acute, dorsally entirely covered with sweeping-hairs. ACHENES brown, four- to five-edged to subcylindrical, sometimes compressed, narrowly oblong to narrowly obovate in outline, basally truncate to rounded, glabrous, eglandular with or without many longitudinal sclerenchymatic ribs, with single oxalate crystals in the epidermal cells, with or without pappus; pappus consisting of up to seven broad, dorsiventrally flattened, apically plumose bristles.

Key to the species

1 Capitula persistent; involucral bracts densely appressed; lamina of ray-florets 8–15 mm long . . . . . *R. adpressum*

1′ Capitula deciduous; involucral bracts squarrose; lamina of ray-florets 4–6 mm long 2

2 Involucral bracts apically slightly reflexed (<90°); achenes of disc-florets without pappus . . . . *R. epapposum*

2′ Involucral bracts apically revolute (>90°); achenes of disc-florets with pappus . . . . . *R. suaveolens*

Rhanterium adpressum Cosson & Durieu de Maisonneuve in Cosson, Rapport sur un voyage botanique en Algerie. *Annales des Sciences Naturelles; Botanique, 4(4):* 252 (1855).

SYNONYM: *Rhanterium suaveolens* Desf. ssp. *adpressum* (Cosson & Durieu) Quezel & Santa, *Nouvelle Flore de l'Algerie et des régions désertiques méridionales, II.* Paris: 948 (1963).

LECTOTYPE selected here: *Jamin 270,* pl. d'Algerie, Montagne de sable prés Biskra, 3 Juin 1852 (P lectotype, G, MPU isolectotypes).

ILLUSTRATION: Figure 3.

A robust, up to 0.5 m high, richly branched subshrub. BRANCHES ascending (to erecto-patent) apically, thick and hollow. LEAVES flat, obovate-oblong to broadly lanceolate, remotely serrate-dentate to entire, apically acute to rounded, 8–22 × 2–8 mm, very slightly woolly. CAPITULA firmly attached. Involucre subspherical, 5–12 mm wide. Involucral bracts 14–40, densely appressed, straw-coloured with central area initially greenish, with scarious margins, sometimes with a dorsally faintly visible secretory canal, sometimes marginally glandular; outer ovate to oblong, entire apically rounded to subacute, 1.7–4.1 × 0.5–2.2 mm, very slightly woolly; inner obovate-oblong to oblong, sometimes with cracked margins, entire to fimbriate, apically rounded to acute, 2.7–7.4 × 1.7–3.0 mm, with a few hairs to glabrous. Bracts subtending ray-florets subcylindrical to bluntly three-edged, fimbriate (to entire), apically acute, dorsally with a few longitudinal ridges, 4.6–6.8 mm long, glandular along margins and sometimes dorsally. RECEPTACLE paleate with epaleate centre. Paleae narrowly oblong, irregularly serrate, 5.7–9.2 × 0.5–1.6 mm, glandular along margins and sometimes dorsally. RAY-FLORETS 5–35, bright yellow; lamina patent, two- or three-lobed, 3–6(–8)-veined, narrowly oblong, 9–18 × 1.3–2.3 mm. Staminodia absent. Style-branches slightly tapering towards the rounded apex, dorsally covered with appressed and apically rounded sweeping-hairs. ACHENES generally slightly curved and laterally compressed, narrowly oblong (to oblong) in outline, with 10–20 ribs, 2.5–4.3 × 0.5–1.0 mm. DISC-FLORETS 20–100, 4.7–10 × 0.8–1.4 mm, eglandular. ACHENES easily separated from corolla, four- to five-edged to subcylindrical, narrowly oblong in outline, basally truncate, with *c.* 15 ribs, 2.3–5.1 × 0.2–0.8 mm; pappus consisting of usually two to seven, 4.2–5.8 mm long, basally broad bristles (the number varies even within a single capitulum and individual achenes may lack bristles altogether).

FLOWERING PERIOD: mainly March to June.

NOTES: *R. adpressum* is easily recognized by its broad, densely appressed involucral bracts. Apart from being grazed by animals this species has also been used by the local population in the production of cheese (*fide coll.*).

GEOGRAPHICAL DISTRIBUTION AND HABITAT: Figs 4, 6. *R. adpressum* has been found in the northern half of Algeria and the bordering areas of eastern Morocco. Almost all specimens studied have been collected in the semi-desert region classified by White (1983) as "sub-Mediterranean semi-desert grassland and

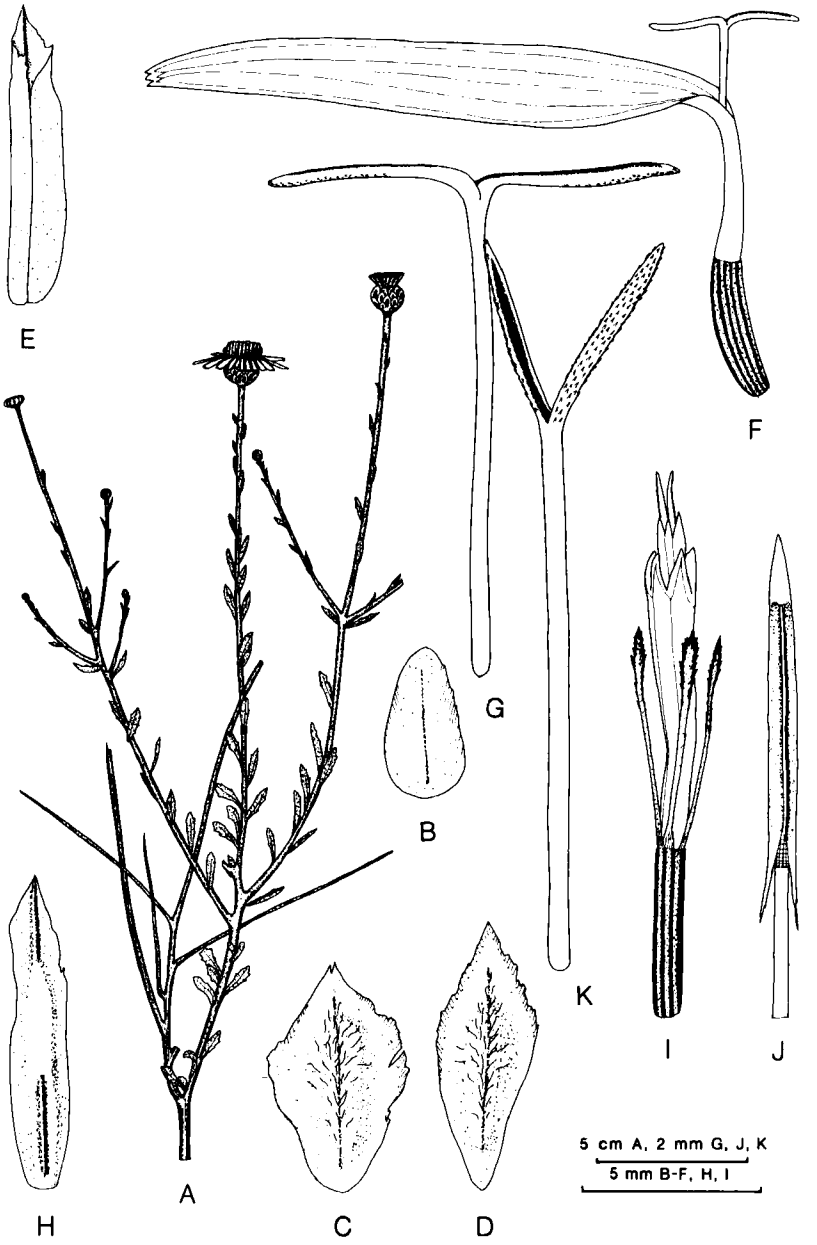

Figure 3. *Rhanterium adpressum*. A. Habit. B–D. Involucral bracts. E. Innermost involucral bract. F. Ray-floret. G. Style of ray-floret. H. Palea. I. Disc-floret. J. Stamen. K. Style of disc-floret. A–K. *Pitard 3417* (P).

shrubland", although a few specimens are from pure desert regions. The species has been found at altitudes up to 1150 m and it has been collected mainly on sand-dunes, in sandy and silty riverbeds and on sandy and clayey plains, where it forms large tufts. More rarely it has been found on rocks and on rocky plains.

REPRESENTATIVE COLLECTIONS (69 collections examined): MOROCCO: El Aradja, iii 1913, *Pitard 3417* (K). ALGERIA: SW Oran Province, in Ain Sefra, 1856, *Kralik*

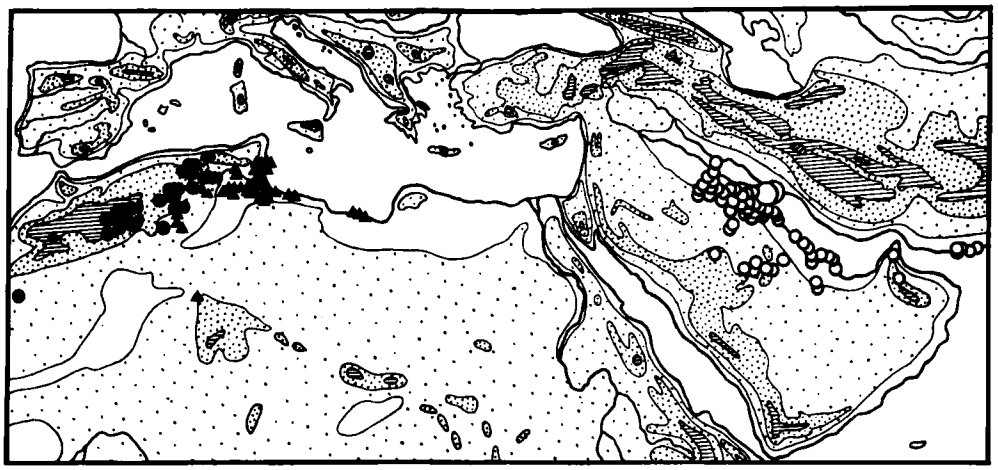

Figure 4. Known distribution of *Rhanterium adpressum* (●), *R. suaveolens* (▲) and *R. epapposum* (○). Large dots, triangles and circles indicate 10 collections.

(G, K, MPU); S Oran, near Colomb-Bechar, 1934, *Weiller* (S); Mzab region, River-bed of Oued-en-Nsa near El Farch, 1858, *Kralik 48* (C, G, K, MPU, UPS, W).

Rhanterium suaveolens Desfontaines, *Flora Atlantica, 1.* Paris: 291 (1798).

SYNONYMS: *Rhanterium suaveolens* Desf. ssp. *suaveolens*. Quezel & Santa, *Nouvelle Flore de l'Algerie et des régions désertiques méridionales, II.* Paris: 949 (1963).

LECTOTYPE selected here: *Desfontaines,* Herbier de la Flore Atlantique ("in arenis ad maris littora prope Sfax in regno Tunetano" *fide* Desfontaines, *loc. cit.*) (P lectotype, G isolectotype).

NOMENCLATURAL NOTE: Desfontaines' *Flora atlantica* herbarium is now kept separately at P and a second series of *Flora atlantica* plants are found at G (Stafleu & Cowan, 1976). Because the P collection carries the original manuscript slips for the *Flora atlantica* and because Desfontaines worked at P, I choose the P collection in the *Flora atlantica* herbarium as lectotype. Other collections of *R. suaveolens* by Desfontaines were found at C, G, MPU and P. As these do not carry any annotations showing that they belong to the *Flora atlantica* herbarium, they were not included among the types.

ILLUSTRATION: Figure 5.

An up to 0.5 m high, richly branched subshrub. BRANCHES erecto-patent (to ascending), apically slender and usually compact. LEAVES flat to somewhat canaliculate, narrowly oblong to linear, remotely serrate-dentate to entire, apically acute, 7–25 × 1–3 mm, slightly to moderately woolly, eglandular. CAPITULA deciduous. Involucre cyathiform to broadly cyathiform, 3–6 mm wide. Involucral bracts 20–40, straw-coloured, with a dorsally faintly visible central secretory canal, entire to slightly fimbriate, apically acute, glabrous, marginally glandular; outer reclining to revolute, narrowly ovate, 2.0–4.0 × 0.5–1.2 mm; inner revolute, ovate to oblong to narrowly oblong,

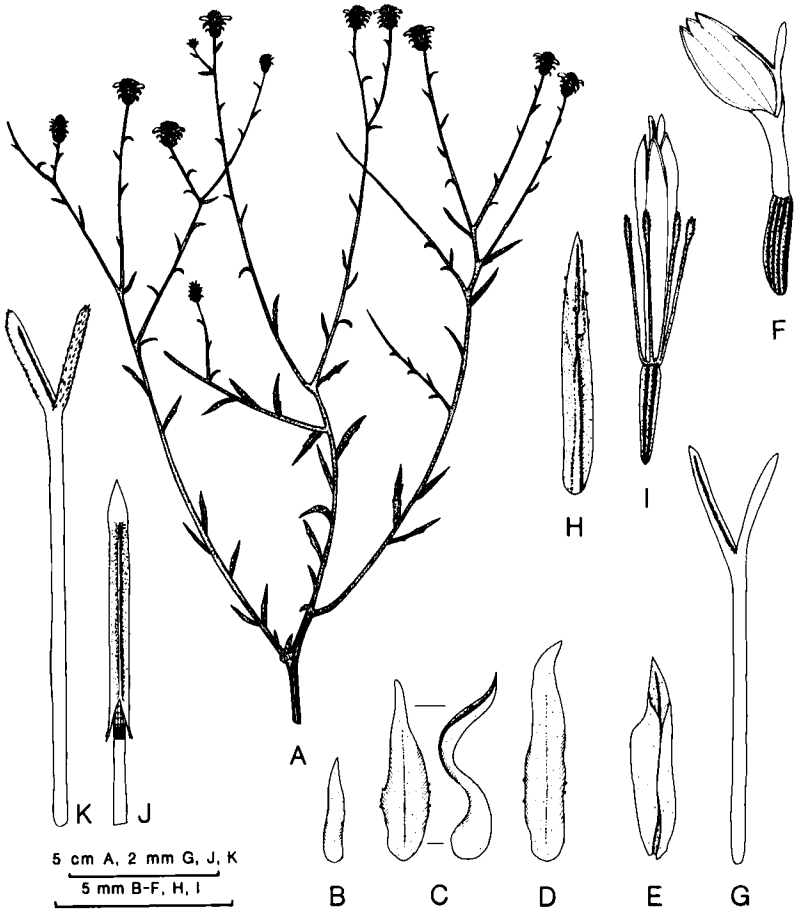

Figure 5. *Rhanterium suaveolens*. A. Habit. B–D. Involucral bracts. E. Innermost involucral bract. F. Ray-floret. G. Style of ray-floret. H. Palea. I. Disc-floret. J. Stamen. K. Style of disc-floret. A–K. 10 vii 1884, on plain between Oued Methlaghiou?, Ain Kebirita and Ain Kebiriti, *Letourneux* (P).

3.8–6.9 × 0.8–1.6 mm, marginally narrowly subscarious. Bracts subtending ray-florets bluntly three- to four-edged, entire, apically acute to acuminate, dorsally with a few longitudinal folds, 3.6–5.6 mm long, sometimes glandular dorsally and along margins. RECEPTACLE paleate with an epaleate center. Paleae narrowly oblong to linear, entire to slightly serrate, 3.8–7.2 × 0.3–0.9 mm, glandular dorsally and along margins. RAY-FLORETS 4–16, bright yellow (*fide coll.*); lamina patent, three-lobed, 4–5(–8)-veined, oblong, 4.0–5.8 × 1.1–1.8 mm. Staminodia sometimes present. Style-branches apically slightly tapering into a rounded to subacute apex, dorsally smooth. ACHENES straight (to slightly curved), three-edged, sometimes laterally compressed, narrowly oblong to narrowly obovate in outline, with *c.* 15 ribs, 2.4–3.1 × 0.5–0.9 mm. DISC-FLORETS (9–)15–35, 4.2–6.3 × 0.9–1.5 mm, eglandular. *Achenes* easily separated from corolla, subcylindrical to compressed, narrowly oblong to narrowly obovate in outline, basally truncate, with *c.* 20 ribs, 1.3–3.1 × 0.2–0.6 mm. Pappus consisting of up to seven bristles, 3.1–4.5 mm long.

FLOWERING PERIOD: February to June.

NOTES: This species is generally easily recognized by the narrow, pointed and, when mature, revolute involucral bracts. Young specimens may be confused with *R. epapposum*, the bracts of which, however, become slightly reflexed but never revolute.

GEOGRAPHICAL DISTRIBUTION AND HABITAT: Figs 4, 6. *R. suaveolens* occurs in northeastern Algeria, in the southern part of Tunisia and in coastal Tripolitania (Libya). It has been found mainly in semi-deserts in sub-Mediterranean, semi-desert grassland and shrubland (White, 1983) but also in the desert. It has been collected on sand and in dry and sandy pastures, often by the sea or near river-beds.

REPRESENTATIVE COLLECTIONS (59 collections examined): ALGERIA: Near Nadour tower, 1854, *Kralik 246* (BM, G, K, P, S, UPS, W); Tozzer, 1884, *Doumet* (P); Matmata, Bordj Toual, 1910, *Pitard 844* (G, MPU, S, W). *Libya*: Near Tripoli, 1952, *Guichard KG/Lib/387* (BM).

Morphological intermediates between *Rhanterium adpressum* and *R. suaveolens*.

Rhanterium adpressum and *R. suaveolens* are to a large extent geographically separated and each generally displays only limited morphological variation.

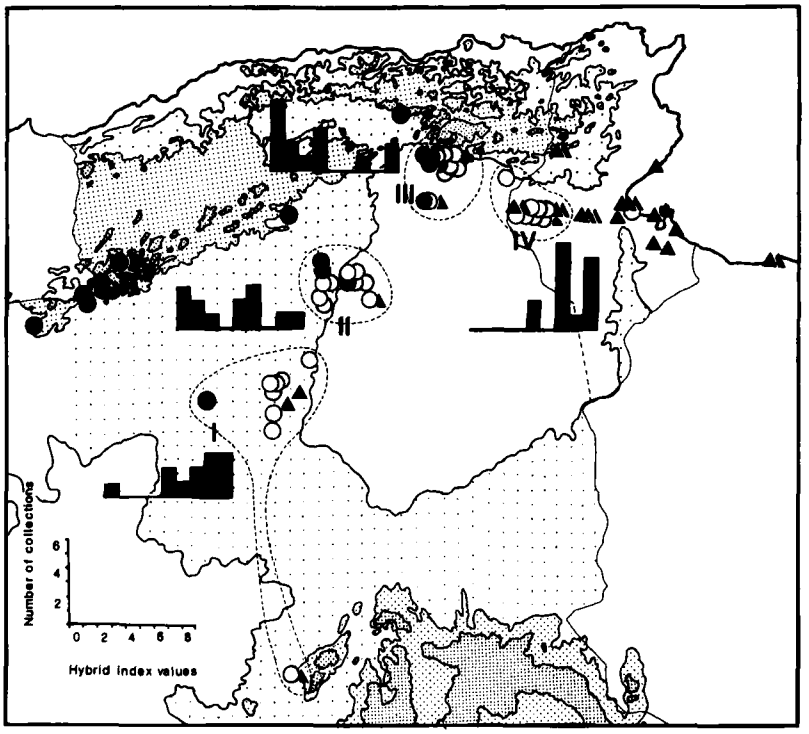

Figure 6. Map of distribution and hybrid index histograms representing collections of *Rhanterium* from the meeting zone between *R. adpressum* (●) and *R. suaveolens* (▲) in northeastern Algeria and in western Tunisia. Intermediate collections are indicated by a circle (○). The four demarcated areas are: El Golea and Arak (I), Ghardaia (II), Biskra (III) and Tozeur (IV). For characters employed in constructing indices, see Table 3.

Their distributions meet in the northeastern part of Algeria (Fig. 6). In this meeting zone and in an area adjacent to it in western Tunisia many specimens appeared to be intermediate between the two species or to approach one or the other in morphology.

To study this morphological variation the hybrid index method (Anderson, 1949) was employed (Fig. 6). Collections of *R. adpressum* and *R. suaveolens* from the areas outside the meeting zone between the two species were selected to represent 'typical' *R. adpressum* and 'typical' *R. suaveolens*. In the area thus demarcated for 'typical' *R. adpressum* no obvious intermediate collections were found but in the case of *R. suaveolens* there is a clearly intermediate collection (*Pitard*, Gabès (Nefzaoua) 1909 (BM, P)) from eastern coastal Tunisia. This collection was excluded from the analysis.

A morphological comparison between 'typical' *R. adpressum* and 'typical' *R. suaveolens* revealed that four of the characters in which they differed were readily adjustable to the hybrid index method, viz. scape width, degree of outward-bending of involucral bracts, shape of inner involucral bracts and length of ray-floret laminas (Table 3). Measurements falling within the range of variation of 'typical' *R. adpressum* were then given a score of 0 whereas measurements falling within the range of variation of 'typical' *R. suaveolens* obtained a score of 2. Measurements falling between these values were given a score of 1 (Table 3). In this way any collection of 'typical' *R. adpressum* obtained a total score of 0 whereas collections of 'typical' *R. suaveolens* each scored 8. Collections intermediate between the two above mentioned species could obtain scores in the range 1–7. The collections from the areas where great morphological variability occurred were then divided roughly into four geographical groups and a hybrid index was constructed for each group with the aid of the above-mentioned characters (Fig. 6).

One result of the analysis was that several collections that had earlier been considered to belong to the 'typical' *R. suaveolens* morph, and that should as such have scored 8, were found to be slightly deviating from this standard, scoring only 6 or 7. Similarly some specimens previously assigned to 'typical' *R. adpressum* scored higher than the expected 0.

As can be seen in Figure 6 'typical' *R. adpressum* and 'typical' *R. suaveolens* were found to occur in the vicinity of more or less intermediate morphs in three of the four areas demarcated. In the fourth area (no. IV) which is situated closest to the 'typical' *R. suaveolens* region, 'typical' *R. adpressum* was found to be

Table 3. Characters (scored 1–3) used in construction of the hybrid index (Fig. 7)

Character	*R. adpressum*	*R. suaveolens*	
	0	1	2
1 Scape width (mm)	1.3–3.4	1.0–1.2	0.5–0.9
2 Degree of outward-bending of involucral bracts	0°	45°	90°
3 Shape of inner involucral bract (1/b)	1.8–3.4	3.5–3.9	4.0–7.3
4 Lamina length (mm)	9.0–18.0	5.9–8.9	4.0–5.8

lacking and the intermediate collections were found often to approach 'typical' *R. suaveolens* in morphology. In area III (although not in area II), where *R. adpressum* dominated over *R. suaveolens* the intermediate collections similarly approached 'typical' *R. adpressum.*

The hybrid index can, in this case, give only a very crude picture of the actual morphological variation in the region because of the few characters used, the rather arbitrarily demarcated areas and the sometimes poor herbarium material. Potentially valuable information from cytology, or from the production of artificial hybrids, is also lacking. Seed production in *Rhanterium*, including the intermediate morphs, appears to be low as embryos were found only rarely. This possibly excludes any important role of selfing or apomixis.

Despite these limitations I suggest that the occurrence of hybridization gives the most likely explanation of the observed morphological variation and geographical pattern of distribution of the species. A circumstance that points in this direction is that *R. adpressum* and *R. suaveolens* are morphologically relatively homogeneous throughout most of their areas of distribution, and that intermediate morphs occur almost exclusively where the two species meet (areas I–III). Sometimes the intermediates were found to occur in close vicinity of 'typical' *R. adpressum* or 'typical' *R. suaveolens* and in one instance a collection (*Zickel 23,* Zaouiet-el-Arab?, Oued Rir, 1864 (MPU, P)) was found to be composed of a mixture of the two above-mentioned species and an intermediate morph. This suggests that the intermediate morphs are hybrids which have resulted from crosses between *R. adpressum* and *R. suaveolens.*

Heiser (1973) points out that a similar pattern of variation could arise without hybridization in regions of great ecological change. Then it is thought that an initially smoothly intergrading belt of populations could be broken up and become very variable. In this way it would resemble a zone of secondary intergradation where highly variable populations are thought to occur (Heiser, 1973). However, from the information available I have not found any indications that the intermediate morphs should occur in particularly disturbed areas so that this explanation appears to be less probable.

Highly variable populations are also suggested to arise through chromosomal segregation in polyploids descended from hybrids (Heiser, 1973). This possibility is not dealt with here because of insufficient chromosomal information. The above-discussed more frequent occurrence of *R. suaveolens*-like morphs in area IV, which is closest to the area of 'typical' *R. suaveolens*, and the similarly more frequent occurrence of *R. adpressum*-like morphs in area III (although not in area II), where *R. adpressum* was found to be most frequent, may be an indication of the occurrence of introgression.

I do not find a taxonomic recognition of the intermediate morphs justifiable, due to the fact that they are extremely variable and apparently merge gradually into *R. adpressum* and *R. suaveolens.* The name *R. intermedium* Cosson & Durieu ex Pomel (1874: 432) with the synonym *R. suaveolens* Desf. ssp. *intermedium* (Pomel) Quezel & Santa (1963: 948) is therefore not retained here.

A consequence of the above-discussed pattern of variability is that the species delimitations of *R. adpressum* and *R. suaveolens* are obscured and in practice to some extent become subjective. The descriptions provided here are based on specimens from the areas where the two species were found not to be in immediate contact with each other.

REPRESENTATIVE INTERMEDIATE COLLECTIONS (39 collections examined): ALGERIA: Sahara, Biskra, right side of oued, above the village, towards the mountain, 1896, *Chevalier P.S.A. 140* (P); In river-bed of Oued Segrir near Guerrara, towards Mzab, 1858, *Kralik 48bis* (C, G, K, MPU, P, UPS, W). TUNISIA: Tozeur, 1934, *Cuenod* (G).

Rhanterium epapposum Oliver in Hooker, *Icones Plantarum*. London & Edinburgh: 50 (1881).

LECTOTYPE selected here: *Pierce 11/80*, coast of Belouchistan, Ispeldar (K).

SYNONYMS: *Asteriscus arabicus* Velenovsky, Plantae arabicae Musilianae. *Sitzungsberichte der königlichen böhmischen Gesellschaft der Wissenschaften. Matematisch-naturwissenschaftliche Classe, 11:* 11 (1911).

Musilia arabica (Velen.) Velenovsky, Plantae arabicae ex ultimo itinere A. Musili a. 1915. *Mémoires de la Société Royale des Sciences de Bohême; Classe des Sciences, 6:* 6 (1923).

TYPE: not seen.

ILLUSTRATION: Figure 7.

An up to 0.5(–0.9) m high, very richly branched subshrub. BRANCHES erecto-patent (to ascending), apically slender and generally hollow. LEAVES flat to somewhat canaliculate, (narrowly obovate-oblong to) narrowly oblong to linear, entire to remotely serrate-dentate to remotely narrow-lobed, apically acute to rounded, 5–45 × 1–3 mm, woolly to glabrous, slightly and minutely glandular. CAPITULA deciduous. Involucre subsquarrose, subspherical, 4–11 mm wide. Involucral bracts 25–60, yellowish, with thin lateral margins, apically acute, ventrally and marginally slightly glandular, with dorsally clearly visible central secretory canal; outer slightly concave, oblong to narrowly oblong to narrowly ovate, entire, 1.8–4.2 × 0.4–1.2 mm, with a few hairs dorsally; inner apically slightly reflexed, narrowly ovate to ovate, irregularly fimbriate to entire, 3.3–7.0 × 1.6–2.2 mm. Bracts subtending ray-florets bluntly three-edged, fimbriate, apically acuminate, dorsally smooth, 5.5–7.4 mm long, apically glandular. RECEPTACLE paleate. Paleae narrowly oblong, fimbriate, 5.0–7.0 × 0.5–1.3 mm, marginally glandular on apical part. RAY-FLORETS 5–14, pale yellow (*fide coll.*); lamina ±patent, (2–)3(–4)-lobed, 4–6 veined, oblong, 3.9–5.8 × 1.6–2.4 mm. Staminodia present. Style-branches apically rounded to subacute, dorsally smooth. ACHENES somewhat curved, subcylindrical, (oblong to) narrowly oblong to narrowly obovate in outline, with *c.* 15–20 ribs, 2.3–3.6 × 0.8–1.3 mm. DISC-FLORETS 6–60, 4.5–6.8 × 0.8–1.7 mm; corolla lobes sometimes with minute glands. ACHENES firmly attached to corolla, subcylindrical, obovate to narrowly obovate to narrowly oblong to oblong in outline, basally rounded to truncate, 1.1–2.8 × 0.3–0.7 mm, epappose.

FLOWERING PERIOD: Mainly March and April, although flowering specimens have been found between December and May.

NOTES: This species may be identified by its subsquarrose involucres and epappose disc-floret achenes. It is used as firewood by the bedouins and it is grazed by camels and sheep (*fide coll.*).

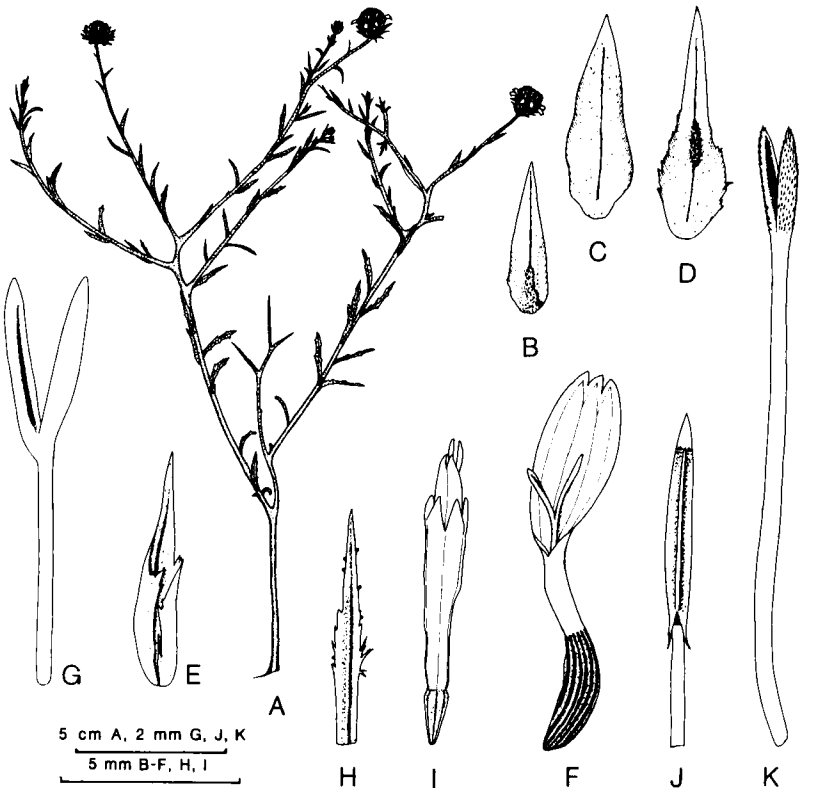

Figure 7. *Rhanterium epapposum*. A. Habit. B–D. Involucral bracts. E. Innermost involucral bract. F. Ray-floret. G. Style of ray-floret. H. Palea. I. Disc-floret. J. Stamen. K. Style of disc-floret. A. *Mandaville 2709* (BM). B–K. *Mandaville 1756* (BM).

GEOGRAPHICAL DISTRIBUTION AND HABITAT: Figure 4. *R. epapposum* is distributed in the central and eastern parts of the Arabian peninsula, in southern Iraq and along the eastern coast of Iran, reaching into Pakistan. It has been collected at usually low altitudes ranging from sea-level up to 900 m in desert to semi-desert areas (*fide coll.*). It has often been found on sandy substrates such as sandy deserts and sandy patches in gravel deserts but it has also been found on gravel and rocks.

REPRESENTATIVE COLLECTIONS (84 collections examined): IRAQ: Diwaniya district, Southern Desert, 15 km SE Ashuriya, 50 km WNW Shabicha, 1957, *Rechinger 9465* (G, K, W); Umm Quasr, 1967, *Alizzi & Omar 35018* (K). SAUDI ARABIA: Great Nefud, SW of Linah, 1966, *Hemming 2424* (BM); Abu Hadriyah, 1968, *Mandaville 1756* (BM).

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