

Oil-producing flowers of *Sisyrinchium* species (Iridaceae) and their pollinators in southern South America

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Summary

The floral relationships existing between the mainly New World genus *Sisyrinchium* (Iridaceae) and oil-collecting bees were investigated in southern South America. In addition to a single species known before as producing floral oil and being pollinated by oil-dependent bees, the present paper documents 11 further species of Sections *Sisyrinchium* and *Echthronema* (including Sect. *Cephalanthum*), which share this ecological status. The oil is secreted by one-celled, headed glandular trichomes which form in many species dense carpets (elaiophors) covering the staminal column basally, rarely parts of free filaments or tepals. Based on literature, 23 additional species possessing columnar hair carpets, presumable elaiophores, are listed. The principal and in some taxa exclusive visitors of oil-bearing *S.* are species of *Lanthanomelissa* (Anthophoridae-Tapinotaspidini), a southern genus that appears to have coevolved with its oil hosts. The females bear special scrapers on the forelegs by which they disrupt the oil-filled cuticular blisters of the hairs to forage the fluid. The oil then becomes mixed with pollen passively taken up from the same flower. Species of *Tapinotaspis* and *Chalepogenus* (Tapinotaspidini) also forage oil in *S.* species. The oil-harvesting and pollinating procedure is described in detail for *S. arenarium*, *chilense*, *pachyrrhizum*, and *laxum*. Sympatric *S.* species may display divergent day-times of flower opening. – Altogether, seven flower types including taxa lacking elaiophors are discriminated in *S.* The latter – pollen flowers exploited by polylectic bees – are distributed over the genus and predominate in the related genera. The oil-based partnership of *S.* is so far only known from the southern Neotropics, the probable centre of origin of both partners. The North America members of *S.*, presumable derivatives from the Neotropical stock, bear vestigial elaiophors no longer used and are pollinated by pollen-collecting bees or are autogamous.

Key words: *Sisyrinchium*, *Lanthanomelissa*, *Chalepogenus*, oil-collecting bees, oil-flowers, elaiophores, pollination biology.

1. Introduction

Sisyrinchium is one of the several iridaceous genera known to produce flower oil as a floral reward to their bee pollinators. Iridaceae count among eight plant families of diverse phylogenetic affinities and disparate geographic provenance, members of which produce lipidic oils by special floral glands, called elaiophores (VOGEL 1988). These oils, which are not volatile, are collected by bees of only certain groups for which purpose they are equipped with special oil-collecting structures on their legs or abdomen (NEFF & SIMPSON 1981). The oils are mixed by the bees with pollen to make the larval provision or to apply it purely as lining on the inner walls of the brood cells (CANE et al. 1983).

It is an outstanding phenomenon that each floral realm has its own independent sets of oil-based flower-

bee partnerships (VOGEL 1988). These flower-bee associations are most richly developed in the Neotropics, where species of five plant families and an estimate of 54 endemic plant genera bear oil-flowers. In the Neotropics oil-collecting bees belong to eight genera, while in other parts of the World there is only one oil-collecting bee genus per realm (VOGEL 1988). Since the existence of oil flowers and oil-collecting bees was unveiled and the richness of their representatives in the Neotropics first assessed, knowledge on several plants and bees involved in the association has notably increased. However, since the first observations little progress has been achieved on the oil-bearing Iridaceae.

The primarily New World genus *Sisyrinchium* is the largest oil-bearing member of the family – ca. 80 species according to GOLDBLATT et al. (1989) or 110 according to RODRÍGUEZ (1986). However, detailed observa-

tions on flower biology are available just for one species (VOGEL 1974). In the taxonomic literature often reference is made to glandular vestiture of the staminal column or the inside of the perianth (see table 2). Here we report that these glands are involved in the association of *Sisyrinchium* with oil-collecting bees in a number of other species different in their functional morphology and pollinator species from that previously reported case. Among the new observations a certain degree of specialisation is evident in mutual adaptations not before recognised. In fact, in a general way *Sisyrinchium* and allied genera have been suspected to rely on unspecialised generalistic pollination (GOLDBLATT et al. 1998). These new data provide also insights into the diversity and evolution of flower types among genera of the *Sisyrinchium* alliance and also into historical and geographical aspects of the association as a whole. This knowledge may shed light on the systematics of the group that has recently been subject to major changes (GOLDBLATT et al. 1990). As a matter of fact, *Sisyrinchium* species of the Section *Eriphilema* have been united with *Ona*, *Phaiophleps*, and *Chamelum* under *Olsymium* (GOLDBLATT et al. 1990).

2. Material and methods

Taking into account the most recent taxonomical changes by GOLDBLATT et al. (1990) we will consider here *Sisyrinchium* s.str. (excluding Sect. *Eriphilema*). Field observations were made by the authors at different natural populations of Argentina, Brazil, Chile and Uruguay that are given in Table 1.

Fresh and FAA preserved samples were used for flower analysis. For anatomical studies of the elaiophores, stamina or tepals were peeled off and mounted in 50% glycerine.

For SEM studies, flower parts were dehydrated with formaldehyde-dimethylacetal (FDA) after GERSTBERG & LEINS (1978), dried with a critical point drier and sputter coated with gold.

For SEM studies of the oil-collecting structures the bees were cleaned with solvents under sonication and dried at room temperature after the procedure by SIMPSON & NEFF (1981), the legs were mounted and sputter coated with gold.

Patterns of daily flowering were controlled in natural populations by counting at intervals of 10, 15, 20 or 30 minutes the number of open flowers in a given plant patch.

Skewness of the patterns of daily flowering was tested with g_1 statistics (SOKAL & ROHLF 1995). A negative skewness ($g_1 < 0$) signifies that the mode (time at the maximum number of flowers are open) is shifted

to the right of the mean, while a positive ($g_1 > 0$) skewness means that the mode is shifted to the left of the mean.

Author names of the species are shown in Table 2.

3. Results

General flower features

Six tepals in 2 whorls form in *Sisyrinchium* a wheel- or bell-shaped perianth. The tepals are subequal in the wheel-shaped kind or more or less differentiated in morphology between the whorls in the flowers of the second kind. The bell shape is given by the broadened basal parts of the exotepals. The stamens are only exceptionally free (*S. galapagense*, *S. arenarium* p.p., see Figs. 4.2, 4.3) and are united in most species along one half to more of their whole length to build a column at the top of which the extrorse anthers are inserted. There is a correlation between filament fusion and anther movability: when filaments are fused along their whole length, anthers are sessile, not movable, while they are versatile when filaments are free or only basally fused. Three stylodia carrying dry stigmata are united to varying degree.

Flowers are scentless in all species studied by us and there is no reference to flower odour in the literature.

Location of the hairs on the flowers

Trichomes of the morphological type to be mentioned below are present in the flowers of several *Sisyrinchium* species, though in few it has been tested if they secrete oil (table 2).

Within the flowers the hairs maybe distributed either on the stamens or on the tepals (Table 2 and Figs. 1–4, 12A, B). On the filaments they are concentrated on the column's base, which is conical or bulging (Figs. 1.1, 7/A, E). In *S. minutiflorum* there is in addition a ring of radiating long and thin finger-like emergences each ending in a single gland (Fig. 3.3, 5.3). On the tepals they are concentrated on the basis (Figs. 2, 4.2b, 4.3.a) and in some species they also extend in each petal in a row along the middle vein (Figs. 1.2c, 1.2d, 7C). The presence of elaiophores is not always constant at the species level since they are lacking in subspecies *microspathum* of the regularly oil bearing *S. adenostemon*. Glands are also lacking in some populations of *S. arenarium* (Table 2).

In some species (*S. arenarium*, *S. azureum*, *S. chilense*, *S. graminifolium*, *S. micranthum*, *S. pachyrhizum*, and *S. laxum*; also see Fig. 5.5b), outside the flowers, the same morphological type of hair may be present

Table 1. Species studied. Provinces of Argentina: (BS AS: Buenos Aires; CBA: Córdoba; CHU: Chubut; MZA: Mendoza; NQN: Neuquén; R NGRO: Río Negro; T FGO: Tierra del Fuego; TUC: Tucumán; States of Brazil: MG: Minas Geraes; PR: Parana; RGS: Rio Grande de Sul; RIO: Rio do Janeiro; SP: São Paulo; Provinces of Chile: ACO: Aconcagua; AR: Arauco; COQ: Coquimbo; Province of the Republic of South Africa: WC: Western Cape; Departments of Uruguay; COL: Colonia. Collectors: AAC: Andrea A. Cocucci (deposited in CORD); SV: Stefan Vogel (deposited in WU).

Species	Site	Altitude (m)	Date	Voucher	Oil
<i>Bobartia rufa</i>	WC: Cedarberg, near Algeria		August, 1999	AAC et al. 1141	
<i>Diplarrhena paecock</i>	Cult. Bot. Gard. Göteborg		June, 1992		
<i>Libertia chilensis</i>	AR: Nahuel Buta	1300–1400	Jan. 9, 1998	AAC et al. 954	
<i>Olsynium junceum</i> var. <i>lainezii</i>	BS AS: Tandil	300–400	Sept. 25, 1997	AAC et al. 924	
<i>O. junceum</i>	MZA: Cristo Redentor		Dec. 10, 1994	SV 241	
<i>O. philippi</i> ssp. <i>illapelinum</i>	ACO: El Portillo	3500–4000	Dec. 9, 1994	AAC et al. 561, SV 239	
<i>Phaiophleps biflorum</i>	T FGO:	10	Dec. 23, 1993	AAC et al.	
<i>Sisyrinchium arenarium</i>	CHU: Lago Cholila	1000–2000	Jan. 7, 1994	AAC et al. 526	
<i>S. arenarium</i>	MZA: Vallecitos	3800	Jan. 4, 1984 Dec. 7, 1994	AAC et al. 63 AAC et al. 554, SV 214/2	+
	CHV: Tecka		Jan 5, 1994	AAC et al. 519	
<i>S. arenarium</i> ssp. <i>arenarium</i>	R NGRO: El Bolsón	1000–1500	Jan. 21, 1998		+
<i>S. arenarium</i> ssp. <i>adenostemon</i>	MZA: Cristo Redentor	3500–4000	Dec. 10, 1994	SV 246	+
<i>S. azureum</i>	MZA: Vallecitos	3800	Jan. 4, 1984	AAC et al. 61, 64 AAC et al. 550, SV 221	+
	S JUAN: Agua Negra	3000–4000	Dec. 6, 1988	AAC et al. 633	
<i>S. chilense</i>	BS AS: Tandil	300–400	Dec. 9, 1997		+
	CBA: Cuesta Blanca	700–800	Dec. 16, 1983 Dec. 9, 1983 Nov. 19–27, 1994 Dec. 24, 1995	AAC 47 SV 165 SV 154	
	CBA: Carlos Paz	600–700			
	CBA: Pampa de Achala	1800–2100	Dec. 1, 1987 Dec. 15, 1987 Nov. 6, 1988	AAC et al. 172	
	CBA: El Durazno	1100	Nov. 23, 27, 1984 Nov. 25, 1994 Jan. 17, 1996	AAC 41, 44	
	TUC: Quebrada de los Sosa		Dec. 10, 1994		
<i>S. fasciculatum</i>	RGS: Guaritas	200–400	Nov. 5, 1992	SV 87	+
<i>S. graminifolium</i> var. <i>graminifolium</i>	COQ: Pichidangui	0–100	Dec. 12, 1995	AAC et al. 574	+
<i>S. laxum</i>	BS AS: Tandil	300–400	Dec. 9, 1997	AAC et al. 931	+
	CBA: Cuesta Blanca	700–800	Dec. 24, 1995	AAC 45	
	CBA: El Durazno	1100	Nov. 25, 1994	AAC 43, SV 185	
	CBA: Pampa de Achala	1800–2100	Dec. 15, 1987	AAC 13, 69	
	TUC: Horco Molle	500–1000	Dec. 9, 1987	AAC nn	
	TUC: Quebrada de los Sosa		Dec. 10, 1989	SV 119	
	COL: Colonia	0–50	Nov. 17, 1997	AAC 936	

Table 1 continued

Species	Site	Altitude (m)	date	Voucher	Oil
<i>S. macranthum</i>	CBA: Pampa da Achala	1800–2100	Dec., 15, 1987 Jan. 7, 1988	AAC 189	+
<i>S. macrocarpum</i>	CHU: Paso de los Indios MZA: Vallecitos	3800	Jan. 5, 1994 Jan. 4, 1984 Dec. 6, 1994	AAC et al. 64	
<i>S. micranthum</i>	CBA: El Durazno TUC: Horco Molle TUC: Quebrada de los Sosa COL: Colonia	1100 500–100 0–50	Nov. 25, 1994 Dec. 9, 1989 Dec. 10, 1989 Nov. 14, 1997	SV 75, SV 162 AAC 934	+
<i>S. minutiflorum</i>	CBA: El Durazno CBA: Cuesta Blanca BS AS: Tandil COL: Colonia	1110 700–800 300–400 0–50	Dec. 25, 1994 Dec. 24, 1995 Nov. 10, 1997 Nov. 17, 1997	AAC et al. 932 AAC 935	+
<i>S. nanum</i>	MZA: Vallecitos	3800	Jan. 4, 1984 Dec. 7, 1994	AAC et al. 60 AAC et al. 560 SV 214/1	
<i>S. pachyrhizum</i> var. <i>pachyrhizum</i>	BS AS: Tandil CBA: Tanninga CBA: Córdoba TUC: Los Chorrillos	300–400 900–1000 300–400	Nov. 10, 1997 Dec. 3, 1983 Nov. 12, 1996 Dec. 8, 1989	AAC et al. 930 AAC et al. 23 SV 71	+
<i>S. palmifolium</i>	CBA: Cuesta Blanca CBA: El Durazno	700–800 1100	Dec. 15, 1990 Nov. 12, 17, 1994 Nov. 25, 1994	SV 143	
<i>S. patagonicum</i>	CHU: Lago Cholila Cult. Bot. Gard. München	1000–2000	Jan. 7, 1994 June 25, 1987	AAC et al. 527	+
<i>S. platense</i>	SP: Campos do Jordao	1000–2000	Nov. 9, 1992	SV 102	
<i>S. restioides</i>	RIO: Itatiaia	500–1000	May 7, 1997	SV 162a	
<i>S. setaceum</i>	RGS: Guaritas	200–400	Nov. 6, 1992	SV 78	+
<i>S. striatum</i>	Chile		June, 1992	Cult. Bot. Gard. Mainz	+
<i>S. unguiculatum</i>	CBA: Tanninga CBA: Pampa de Achala CBA: El Durazno	900–1000 1800–2100 1100	Dec. 3, 1983 Jan. 3, 1984 Dec. 1, 1987 Dec. 15, 1987 Jan. 7, 1988 April 7, 1991 Nov. 15, 1994	AAC et al. 24 AAC 55, 56, 57 AAC et al. 173 SV 142	
<i>S. vaginatum</i>	PR: Serra da Graciosa SP: Campos do Jordao RIO: Itatiaia	1000–2000 500–1000	April 24, 1996 Mar. 20, 1991 Nov. 9, 1992 May 7, 1997	AAC 648 SV 59a SV 104 SV 161	
<i>S. vaginatum</i> ssp. <i>weirii</i>	MG: Serra do Cipó	1000–2000	1987	SV 183	
<i>S. sp.</i>	RIO: Itatiaia	500–1000	May 7, 1997	SV 160	+
<i>S. sp.</i>	RGS: Guaritas	200–400	Nov. 5, 1992	SV 76–78	+
<i>S. sp.</i>	SP: Campos do Jordao	1000–2000	Nov. 9, 1992	SV 122	

Table 2. Distribution of glandular trichomes on the inside of tepals or on the filaments of South America species of *Sisyrinchium*. 0: no glands.

Species	Glands on (F) filaments (T) tepals	Range	Source
<i>S. arenarium</i> Poeppig ssp. <i>adenostemon</i>	F	W Argentina Chile	RAVENNA 1969a
<i>S. arenarium</i> Phil. ssp. <i>microsphathum</i> (Phil.) Ravenna	0	Santa Cruz	RAVENNA 1969a RAVENNA 1981
<i>S. alatum</i> Hook.	F	Brazil	CHUCR 1992
<i>S. arenarium</i> Poeppig var. <i>arenarium</i>	0, T	Argentina Chile	RAVENNA 1969a RODRÍGUEZ 1986 VOGEL 1974
<i>S. avenaceum</i> Klatt	0	E Argentina Uruguay	JOHNSTON 1938 RAVENNA 1969b
<i>S. azureum</i> Phil.	F	NW Argentina Chile Bolivia	RODRÍGUEZ 1984
<i>S. chilense</i> Hooker	F	W Argentina Chile	RAVENNA 1969a RODRÍGUEZ 1984
<i>S. claritae</i> Herter	F	Brazil Uruguay	JOHNSTON 1938
<i>S. commutatum</i> Klatt	F	Brazil	WANDERLEY & TOLEDO 1986 JOHNSTON 1938
<i>S. convalidum</i> Rav.	0	Argentina Chile	RAVENNA 1981
<i>S. cuspidatum</i> Poeppig	T	Chile	RODRÍGUEZ 1984
<i>S. eserrulatum</i> Johnston	0	Brazil	JOHNSTON 1938
<i>S. fasciculatum</i> Klatt	F	Brazil	JOHNSTON 1938
<i>S. fiebrigii</i> Johnston	F	Brazil	JOHNSTON 1938
<i>S. foliosum</i> Johnston	F	NW Argentina	JOHNSTON 1938
<i>S. galapagense</i> Ravenna	0	Galápagos Islands	RAVENNA 1979
<i>S. graminifolium</i> Lindley ssp. <i>graminifolium</i>	F	Chile	RODRÍGUEZ 1986
<i>S. graminifolium</i> ssp. <i>luteum</i> (Steudel) Rodr.	F	Chile	RODRÍGUEZ 1986
<i>S. hasslerianum</i> Baker	F	Paraguay	JOHNSTON 1938
<i>S. hirsutum</i> Baker ex Hassler spp. <i>dasyspathum</i>			
<i>S. hoehnei</i> Johnston	F	Brazil	JOHNSTON 1938
<i>S. iridiflorum</i> Kunth var. <i>voldivianum</i> (Phil.) Ravenna	F	USA to Tierra del Fuego	RAVENNA 1969b
<i>S. itabiritense</i> Rav.	0	Brazil	RAVENNA 1981
<i>S. laxum</i> Otto ex Sims	F	Argentina Brazil Paraguay Uruguay	WANDERLEY et al. 1986 JOHNSTON 1938
<i>S. luridum</i> Ravenna	0	S. Argentina	RAVENNA 1969a
<i>S. luzula</i> Klotsch ex Klatt	F	Brasil	JOHNSTON 1938
<i>S. macranthum</i>	F	Argentina	This work
<i>S. macrocarpum</i> Hier. var. <i>laetum</i> Ravenna	F	Argentina	RAVENNA 1969a

Table 2 continued

Species	Glands on (F) filaments (T) tepals	Range	Source
<i>S. macrocephalum</i> Graham	0	Brazil Paraguay Uruguay	JOHNSTON 1938
<i>S. macrocephalum</i> Graham ssp. <i>fuscoviride</i> Rav.	0	NE Argentina	RAVENNA 1981
<i>S. macrocephalum</i> Graham ssp. <i>giganteum</i> Rav.	0	Brazil	RAVENNA 1981
<i>S. megapotamicum</i> Malme	0	Argentina Brazil	JOHNSTON 1938
<i>S. micranthum</i> Cav.	F	Argentina Brazil Paraguay	JOHNSTON 1938
<i>S. minus</i> Engelm. & Gray	F	Argentina Uruguay	JOHNSTON 1938 RAVENNA 1968
<i>S. minutiflorum</i> Klatt	F	Argentina Brazil Uruguay	JOHNSTON 1938 RAVENNA 1969b
<i>S. nanum</i> Philippi (= <i>S. graminifolium</i> ssp. <i>nanum</i> (Phil.) Ravenna)	0	S Argentina	RAVENNA 1969a RODRÍGUEZ 1984
<i>S. nudicaule</i> (Hand.-Mazz.) Johnst.	0	Brazil	CHUCR 1992 JOHNSTON 1938
<i>S. obconicum</i> Rav.	0	Argentina	RAVENNA 1981
<i>S. ostenoanum</i> Beauvard	F	Uruguay	
<i>S. pachyrhizum</i> Baker	F	NE Argentina Brazil Paraguay	JOHNSTON 1938 RAVENNA 1969b
<i>S. palmifolium</i>	0	Argentina	
<i>S. patagonicum</i> Phil. (= <i>S. nudicaule</i> Phil.)	F	S Argentina Chile	RAVENNA 1969a
<i>S. pearcei</i> Phil.	0	S Argentina Chile	RODRÍGUEZ 1986
<i>S. philippi</i> Klatt ssp. <i>philippi</i>	0	Chile	RODRÍGUEZ 1984
<i>S. philippi</i> var. <i>illapelinum</i> (Phil.) Rodr.	0	Chile	RODRÍGUEZ 1984
<i>S. piliferum</i> Klatt	F	Paraguay	JOHNSTON 1938
<i>S. platense</i> Johnston	F	E Argentina Uruguay	JOHNSTON 1938 RAVENNA 1969b
<i>S. plicatum</i> Rav.	0	Brazil	RAVENNA 1981
<i>S. rosengurtii</i> Johnston	F	Brazil Uruguay	JOHNSTON 1938
<i>S. sellowianum</i> Klatt	F		JOHNSTON 1938
<i>S. setaceum</i> Klatt	F	NE Argentina Brazil	JOHNSTON 1938
<i>S. soboliferum</i> Rav.	F	Brazil	RAVENNA 1981
<i>S. striatum</i> Smith	T	Chile	RODRÍGUEZ 1984
<i>S. trinerve</i> Baker	0	Bolivia Chile	RODRÍGUEZ 1984

Table 2 continued

Species	Glands on (F) filaments (T) tepals	Range	Source
<i>S. tucumanum</i> Rav.	F	NW Argentina	RAVENNA 1981
<i>S. uliginosum</i> Rav.	F	NE Argentina Brazil	RAVENNA 1981
<i>S. unguiculatum</i> Trisz 8.	0	Argentina	RAVENNA 1981
<i>S. vaginatum</i> Spreng.	0	E Argentina Brazil	CHUCR 1992 ; JOHNSTON 1938 ; RAVENNA 1969b
<i>S. vaginatum</i> Spreng. ssp. <i>ciliolatum</i> Rav.	0	NE Argentina	RAVENNA 1981
<i>S. vaginatum</i> Spreng. ssp. <i>marchio</i> (Vell.) Rav.	0	Brazil	RAVENNA 1981
<i>S. wettsteinii</i> Hand.-Mazz.	0	Brazil	JOHNSTON 1938

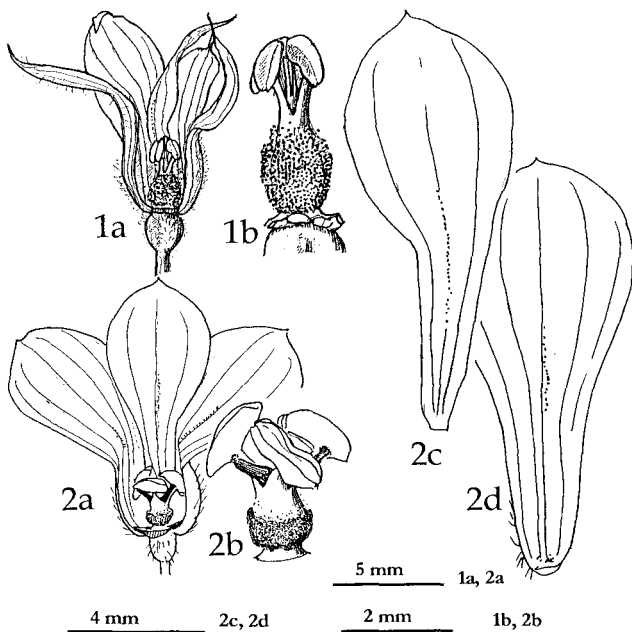


Fig. 1. Flower architecture in *Sisyrrinchium laxum*: 1. (SV 112); 2 (AAC et al. 931). a. dissection, b. column, c. endotepal, d. exotepal.

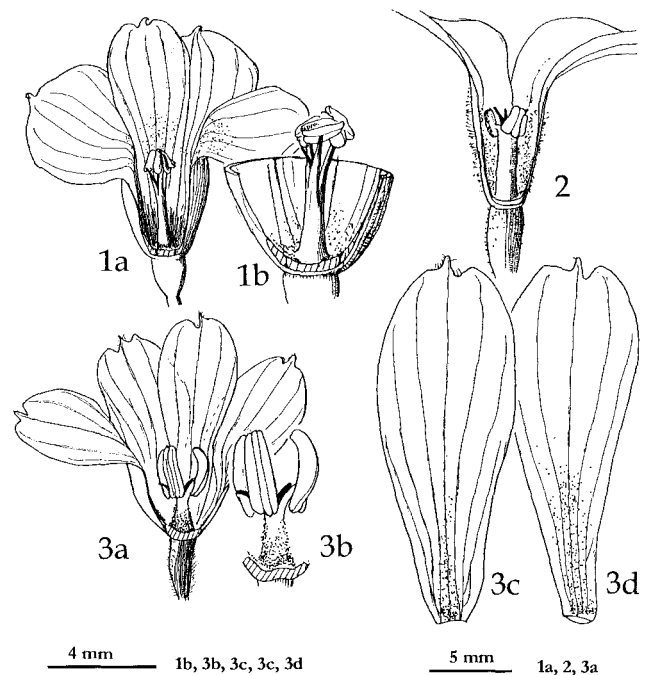


Fig. 2. Flower architecture in *Sisyrrinchium*: 1. *S. striatum* (Cult. Mainz); *S. graminifolium* var. *graminifolium* (AAC et al. 574); 3. *S. arenarium* (AAC et al. 526). a. dissection, b. column, c. exotepal, d. endotepal.

though usually longer and perhaps not secretory. The nature of their secretion if there is any has not been determined.

Elaiophore structure and oil secretion

The elaiophores of *Sisyrrinchium* are of the trichomatic type (Fig. 5). They are built by one-celled capitate trichomes that arise between, and are homologous to, the epidermal cells. A foot, a stalk and the head build up

each single cell. There may be a slight basiscopic curvature of the stalk and asymmetry of the head as in *S. minutiflorum* and *S. patagonicum* (Figs. 5.3, 5.4). In *S. arenarium* and *S. striatum* the stalk bears cell wall protuberances (Fig. 5.8). The outer walls of the trichomes are cutinized and thinner than the outer walls of the epidermal cells proper. At the foot, the inner wall thickenings form a constriction. Branched but still one-celled trichomes were observed only as rare aberrations (Fig. 5.6).

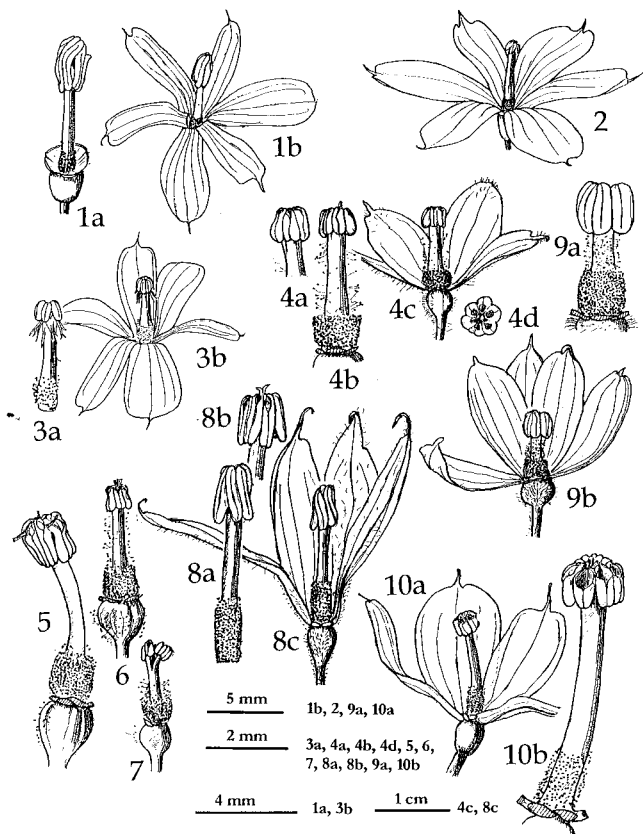


Fig. 3. Flower architecture in *Sisyrrinchium*: 1. *S. patagonicum* (AAC at al. 527), 2. *S. macranthum* (AAC 189); 3. *S. minutiflorum* (AAC et al. 932); 4. *S. sp.* (SV 76), a. partial view of the column at male phase, b. column at the female phase, c. flower dissection, d. column at males phase viewed from above; 5. *S. laxum* (SV 108); 6. *S. fasciculatum* (SV 87); 7. *S. setaceum* (SV 78); 8. *S. pachyrhizum* var. *pachyrhizum* (SV 71), a. column at male phase, b. partial view of the column at female phase, c. flower dissection; 9. *S. plantense* (SV 102), 10. *S. chilense* (SV 214).

There are differences in the manner in which the oil is secreted. In most elaiophore-bearing species studied, except for those belonging to Sec. *Echthronema*, at the trichome's head, the cuticle separates from the primary wall and builds up a subcuticular space (Fig. 5.1–5.5, 5.7, 8F). Oil is stored beneath the cuticle and forms a blister-like structure. No such blisters were found in the species of Sect. *Echthronema*. Here the oils apparently permeate the intact cuticle (Figs. 5.8, 6). The blister, when present, represents a well defined and sharply delimited portion of the trichome's head (Figs. 7D, 8G). This particular portion of the head is already well defined early in the trichome development (Fig. 7F).

When present, the oil-blister is generally placed on the head's apex but in *S. patagonicum*, it is eccentric, pointing to the base of the column (Fig. 5.4). The cuticle on the blister is relatively tough, since it does not break

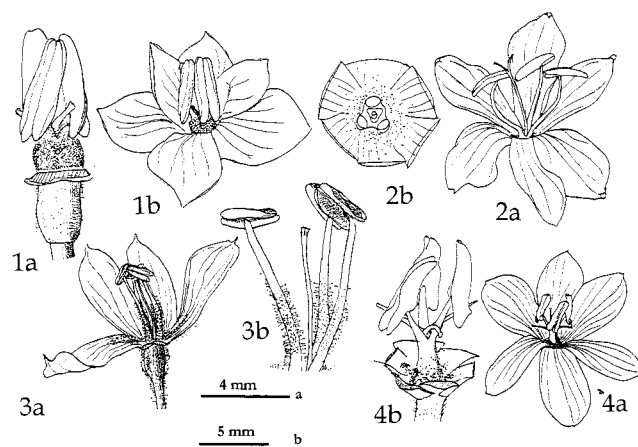


Fig. 4. Flower architecture in *Sisyrrinchium*: 1. *S. macrocarpum* (AAC Dec. 6, 1994), a. tepals removed, b. whole flower; 2. *S. arenarium* ssp. *adenostemon* (AAC et al. 63), a. whole flower, b. central part of the perianth with stamens removed; 3. *S. arenarium* ssp. *adenostemon* (SV 246), a. flower dissection, b. stamens and style; 4. *S. arenarium* ssp. *adenostemon* (AAC et al. 519), a. whole flower, b. column.

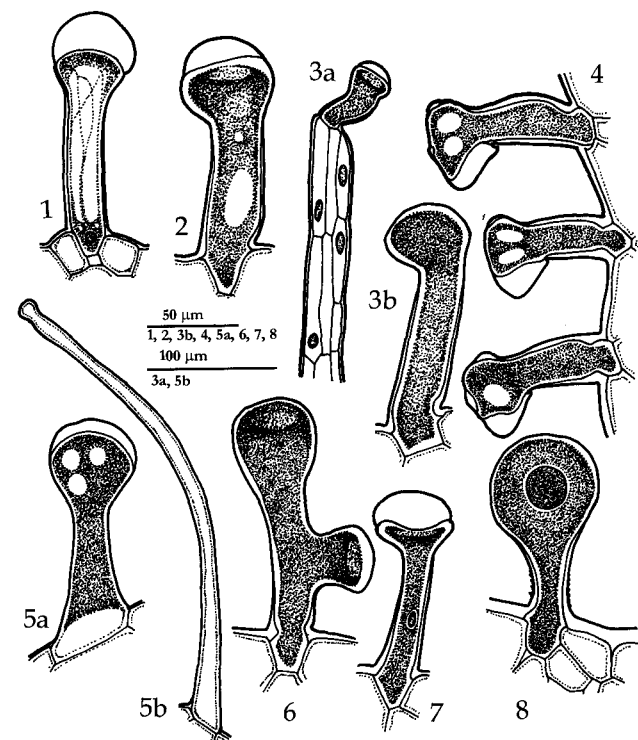


Fig. 5. Oil-producing trichomes and related trichome types in *Sisyrrinchium*: 1. *S. micranthum*; 2. *S. chilense*; 3. *S. minutiflorum*, glandular cell (a) and emergence at the base of the column. 4. *S. patagonicum*; 5. *S. laxum*, trichome on the internal (a) and the external (b) tepal face; 6. *S. arenarium* ssp. *adenostemon*; 7. *S. pachyrhizum* ssp. *pachyrhizum*; 8. *S. striatum*. 1 and 8 from fresh flowers, rest from FAA fixed flowers.

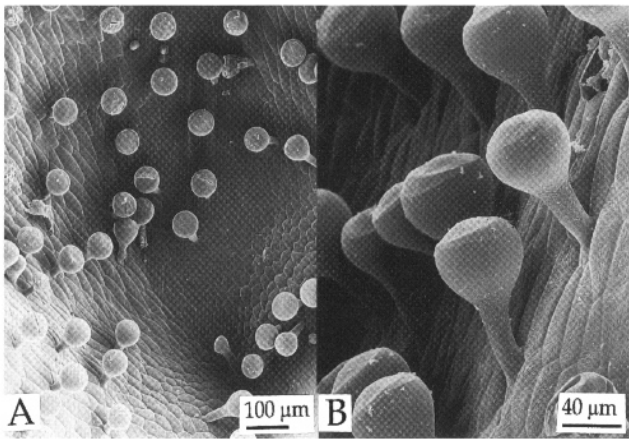


Fig. 6. Elaiophores of *S. striatum*. Views of a tepal at anthesis.

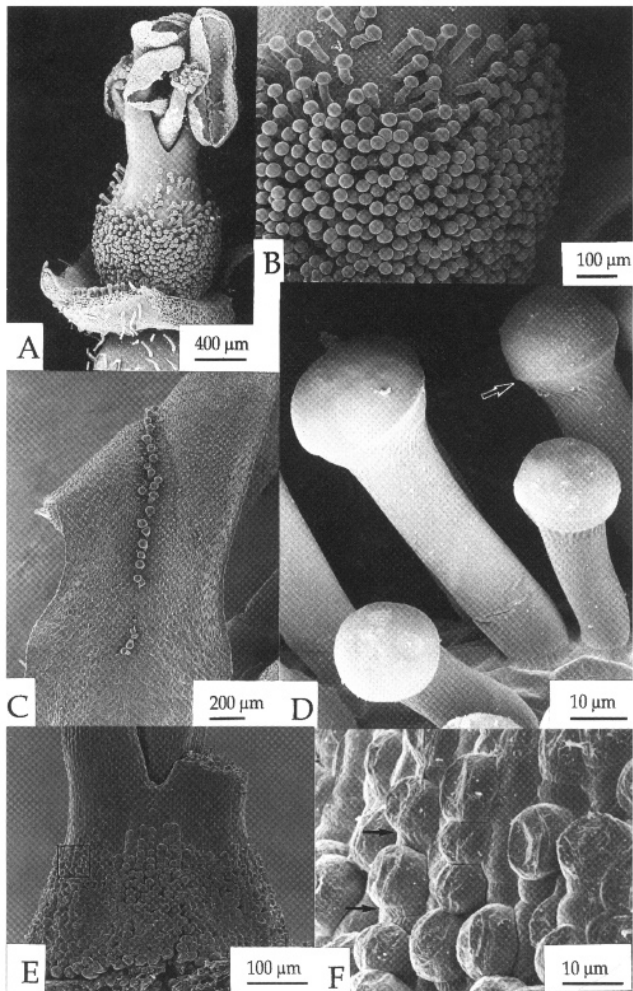


Fig. 7. Elaiophores of *S. micranthum*. A–D: Unvisited flower at anthesis. A: Column. B: Partial view of the conical part of the column. C: Trichomes of an endotepal. D: individual trichomes on the column. E, F: Column trichomes in the bud stage. E: General view of the column after anther removal. F: Detail marked in E showing the boundary of the oil-blister on the trichomes' heads (arrows).

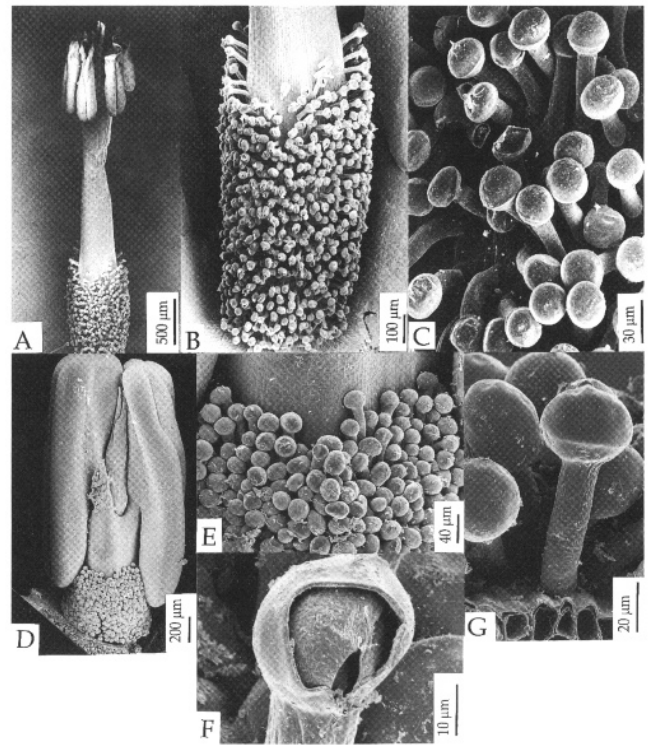


Fig. 8. Elaiophores of *S. pachyrhizum* spp. *pachyrhizum*: A–C: open flowers; D–E: young bud; F: bud prior to flowers opening, head partly sectioned during preparation has revealed the structure of the cuticular blister.

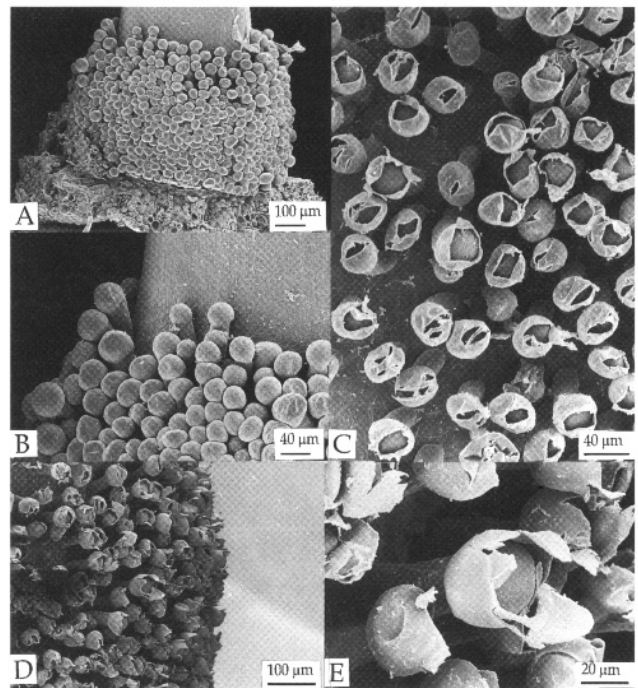


Fig. 9. Elaiophores of *S. chilense*. A, B: Basal part of the column in the bud stage; C–E: Trichomes of visited flowers, note rupture scars on the cuticles.

Table 3. Patterns of daily flowering in 4 species of *Sisyrinchium*. P is the significance level of the *t*-test for *g*1, for *** P < 0.001, for * P < 0.05, NS: non significant.

Species	range	mean	s ²	mode	n	<i>g</i> 1	P
<i>S. azureum</i>	8:50–19:40	14:22	0:14	15:00	86	-2.07	NS
<i>S. laxum</i>	9:30–15:20	12:09	0:03	11:50	154	0.09	*
<i>S. chilense</i>	12:30–19:20	16:35	0:03	16:40	147	-0.24	***
<i>S. minutiflorum</i>	8:30–15:20	11:37	0:04	11:30	168	0.34	***
<i>S. palmifolium</i>	15:40–21:10	18:32	0:02	18:40	183	-0.04	NS

when rubbed with a pin or attempted to be thrust with the sharp end of an eyelash. The blister was not seen to burst spontaneously. The trichome's cytoplasm is generally provided with vacuoles at the middle of the foot portion while the cytoplasmic stroma is richer in the foot (Fig. 5.5). In fresh trichomes strong cytoplasmic streaming can be seen between the foot's base and the head. The oil drops when mounted in tap water form myelin figures.

In *S. chilense* a rough estimate of the amount of oil secreted during anthesis was made. At 11:30, 14:00, and 16:00 the columns of 10 flowers that had been excluded from insect visitors, or nearly opening buds were pressed against cigarette paper and the oil spots viewed with transmitting light. No major differences were seen in the number and size of the spots between the sampling hours. This suggests that a maximum oil quantity is secreted before flower opening and that more doesn't accumulate during anthesis.

Anthesis

In species of the section *Sisyrinchium* flower buds remain within the spikelets until the day of flower opening. In section *Echthronema* buds are already

exposed in the bud stage. Protandry, evident as delayed elongation and unfolding of the stylodia, could be detected in *S. chilense*, *S. laxum*, *S. platense*, *S. pachyrhizum* var. *pachyrhizum* (Fig. 3.8a, 3.8b) and in an undetermined species (SV 76–78, see Figs. 3.4a, 3.4b). The same condition is also evident in *Olsynium philippi* and *O. scirpoideum*.

Dynamics of flower opening could be studied in *S. azureum*, *S. chilense*, *S. laxum*, *S. minutiflorum* and *S. palmifolium*. Flowers are lasting 2 days and open and close each day. First day flowers when closing move the tepals back to the bud position by upward turning of the tepals first of the inner and later of the outer whorl. In second-day flowers at the end of anthesis, probably by an active process, the perianth collapses and rapidly shrivels to a partially liquefied rounded mass.

Among the species studied there are marked differences in the daily blooming patterns. *S. laxum* and *S. minutiflorum* are morning blooming; their flowers start to open after 9:00 and the last one closes before 15:30 (Table 3). *S. chilense* and *S. palmifolium* are narrow afternoon blooming since their flowers start opening at 12:30 or 15:30 respectively (Table 3). *S. azureum* differs markedly, since their flowers are open throughout daytime (Table 3).

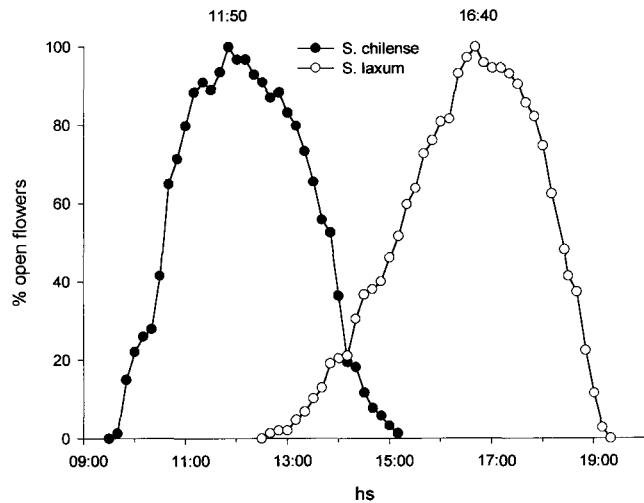


Fig. 10. Patterns of daily flowering in *S. chilense* and *S. laxum*.

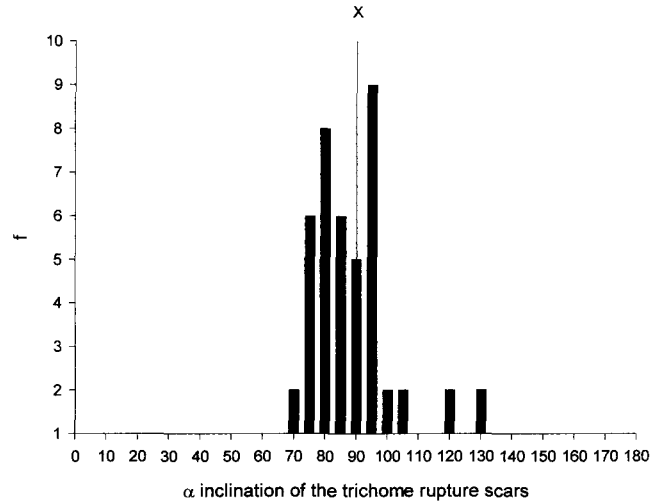


Fig. 11. Angle frequency of 53 rupture scars on the trichomes of *S. chilense*.

Table 4. Records on visitation of species of *Sisyrinchium* by oil collecting bees

Species of <i>Sisyrinchium</i>	Visitor	Region/Province : Locality	Date	Source
<i>S. arenarium</i>	<i>Chalepogenus caeruleus</i>	Neuquen: Cerro Bajo and Cerro Valverde	Jan. 8, 9, 18, 1970	VOGEL 1974
	<i>Chalepogenus caeruleus</i>	Neuquén: Fortín Chacabuco	Jan. 25, 1970	VOGEL 1974
	<i>Chalepogenus caeruleus</i>	Neuquén: Cerro Piltriquitrón	Jan., 1998	This work
	<i>Chalepogenus crassificiatus</i> Roig-Alsina	Chile Farellones	Dec. 20, 1980	ROIG-ALSINA 1999
	<i>Chalepogenus herbsti</i> (Friese)	Chile		ROIG-ALSINA 1999
<i>S. chilense</i>	<i>Lanathanomelissa discrepans</i>	Córdoba: El Durazno	Nov. 25, 1994	This work
	<i>Lanathanomelissa discrepans</i>	Córdoba: Cuesta Blanca	Dec. 24, 1995	This work
<i>S. laxum</i>	<i>Lanathanomelissa discrepans</i>	Córdoba: Copina	Dec. 1, 1987	This work
	<i>Lanathanomelissa discrepans</i>	Córdoba: Carlos Paz	Nov. 28, 1993	This work
	<i>Lanathanomelissa discrepans</i>	Córdoba: Cuesta Blanca	Nov. 22, 23, 27, 1994	This work
	<i>Chalepogenus goeldianus</i>	Buenos Aires: Tandil Cerro de las Animas	Nov. 10, 1997	This work
<i>S. micranthum</i>	<i>Lanathanomelissa discrepans</i> (as <i>L. goeldiana</i>)	Brazil: Guaritas	Oct.–Nov. 1989–1993	SCHLINDWEIN 1995
	<i>Chalepogenus muelleri</i> (as <i>Tapinotaspis sabularum</i>)			
<i>S. pachyrhizum</i>	<i>Lanathanomelissa discrepans</i>	Tucumán: Los Chorrillos	Dec. 7, 1989	This work
<i>S. plantense</i>	<i>Lanathanomelissa discrepans</i>	Buenos Aires: La Plata,	1997	ROIG-ALSINA 1997
	<i>Tapinotaspis latitarsis</i> (Friese)	Hudson		Roitman pers. com.
<i>S. setaceum</i>	<i>Lanathanomelissa discrepans</i> (as <i>L. goeldiana</i>)	Brazil: Guaritas	Oct. 1989–1993	Sch lindwein, pers. com
	<i>Lanathanomelissa mageliae</i> Urban	Brazil: Caçapava do Sul	Nov. 5, 1995	This work
<i>S. sp.</i>	<i>Lanathanomelissa betinae</i>	Brazil: Curitiba	Nov. 2–4, 1995	Bustos Singer, pers. com
<i>S. sp. 104</i>	<i>Lanathanomelissa betinae</i>	Brazil: Campos de Jordao	Nov. 11, 1994	This work
<i>S. spp.</i>	<i>Chalepogenus muelleri</i> (as <i>Lanathanomelissa completa</i>)	Brazil: Guaritas		SCHLINDWEIN 1995

Only in *S. laxum* and *S. chilense* (Carlos Paz and Pampa de Achala populations) the curves of daily blooming are skewed, *S. laxum* with a positive skewness (modes shifted to the early morning) and *S. chilense* with a negative skewness (mode shifted to the late afternoon, see Fig. 10). In the other species the daily blooming pattern is nearly symmetrical.

Observations on oil foraging

Oil harvesting has been observed in detail in *S. arenarium* when visited by *Chalepogenus caeruleus* and in *S. chilense*, *S. laxum* and *S. pachyrhizum* when visited by *Lanathanomelissa discrepans*. Other reports on visitation of *Sisyrinchium* by oil-collecting bees have not given results on the oil-foraging behaviour (see Table 4).

The behaviour of *Chalepogenus caeruleus* on *S. arenarium*

Oil foraging by *C. caeruleus* on *S. arenarium* has been described in detail by VOGEL (1974) and is confirmed in the present work with further observations made in additional populations (Table 1).

Only females visited the flowers provided there was enough sunlight and no wind. They appeared seldom but exploited all the available flowers in the focal flower patch. It took the bees 1 to 3 seconds to exploit each flower. The bees settled on the perianth and curved deep into the flower (Fig. 12D), whereby they made contact with stamens and styloids with the underside of the head and thorax. The middle and hind legs kept hold on the horizontal part of the perianth. Small scars on the tepals can be attributed to the spurs



Fig. 12. Elaiophores and oil collection on flowers of *Sisyrinchium*: A–B: Elaiophores of *S. chilense*. C: *Lanthanomelissa discrepans* collecting oils on *S. chilense*: D: *Chalepogenus caeruleus* collecting oils on *S. arenarium*. E–F: *L. discrepans* collecting oils on *S. chilense*.

on these legs when attempting to get a fixed position on the flower. Movements of the oil-collecting legs on the elaiophore-covered deep part of the perianth could not be clearly seen but enough to recognise that the filament column was worked. Since the bees did not change position while collecting oils, apparently the whole glandular surface was within reach of the fore-legs from the same position. Pollen and oil were collected during the same procedure. During collection the bees performed an audible vibration. On the scopae a deep orange mixed load of pollen and oil was always present. Exclusive foraging of oil was never observed.

Behaviour of *Lanthanomelissa discrepans* on *S. chilense* and *S. pachyrhizum*

Lanthanomelissa discrepans was seen visiting *S. chilense* at three (Table 1) and *S. pachyrhizum* at one site as exclusive oil forager. This bee was not seen visiting other synchronically blooming *Sisyrinchium* species. Always females were recorded (between 25 and 50 visitations in 5 observation days on *S. chilense* and 5 to 10 visitations in one day on *S. pachyrhizum*). *S. chilense* was visited between 14:30 and 18:00 that is between the time when about 36% of the flowers had opened and when 77% of the flowers had closed. These two species of *Sisyrinchium* have a similar flower structure, their perianth being spreading, the column slender, not enlarged at the base, filaments fused along their total length and elaiophores covering the basal 1/3 of the column (Figs. 3.5, 3.8, 3.10, 12A, B). Since the behaviour of *Lanthanomelissa discrepans* on the flowers of both species is identical, it can be treated here in a combined form.

The bees settled on the column and did not touch the perianth in any moment. The end of the column was held between the thorax and the metasoma (Fig. 12C). Mid legs and hind legs were extended and did not take hold on the column. The forelegs scraped with their ventral part the elaiophore-covered base of the column, making an active friction when they were drawn toward the body. While performing this movement the bees turned pivoting around the column.

Oil collection was interrupted by movements of ipsilateral oil transference to the hind leg scopae. Examination of the bees under the stereomicroscope revealed the presence of pollen clumps on the articulation between thorax and metasoma. Pollen loads were wetted with oils turning it to a pasty orange mass.

The examination of columns of flowers that had been visited showed that nearly all the glandular trichome heads had their cuticle ruptured (Fig. 8B, 9 C–E). The

head's apex of nearly all trichomes showed one or two scars each. When two were present on one trichome, these scars were parallel. Most scars were vertical or nearly vertically (Fig. 1) orientated. If the cuticles had ruptured spontaneously it would not be expected that there were more than one scar on each trichome and that they had a non-random orientation.

Behaviour of *Lanthanomelissa discrepans* on *S. laxum*

Always females of *Lanthanomelissa discrepans* were seen visiting *S. laxum* at the two sites. During two days observation, between 25 and 30 times bees appeared at the flower patch and normally exploited all available flowers at the focal flower patch. They visited open flowers and even buds that were nearly opening. The first appeared at 10:20, when about 28% of the flowers that would open that day were completely outspread. Visitations were more frequent between 11:00 and 12:00 that is during the blooming peak. In a focal patch in this period 140 to 160 flowers were open and the bees appeared settling on the flowers at 10 min. or shorter intervals. The last visitation was seen at 14:20 when 82% of the flowers had closed.

Flower structure is clearly different from the previous two species. The perianth is bell shaped, the column being completely included in the deep part of the bell (Fig. 1.1). The spreading part of the perianth builds a more or less horizontal surface. The column is relatively short and the filaments fused at about half their length. The fused part of the column is notably bulging and bears a dense cover of glandular trichomes (Fig. 7A–B, D). Anthers are versatile and normally resting more or less perpendicular to the filament.

The bees settled on the horizontal part of the perianth and curved into its deep part (Figs. 12E, F). To reach the column in the bell shaped perianth, the bees introduced the forelegs and part of the head into the flower. To do this the flower had to be partially opened by forcing the tepals apart. This was done with the midlegs, whereby the tepals got scared. While taking oils two tepals were held apart with the midlegs and other two by the hind legs. Down-up scraping of the column with the forelegs could be observed directly. Alternate movements were evident by the pressure rhythmically applied to the tepals. The bees were not seen to circle around in the flowers. Oil was transferred ipsilaterally just before leaving the flower.

Examination of the bees under the stereomicroscope revealed pollen clumps of *Sisyrinchium* on the hind coxa and the base of the metasoma. Pollen on the scopae was soaked with oil.

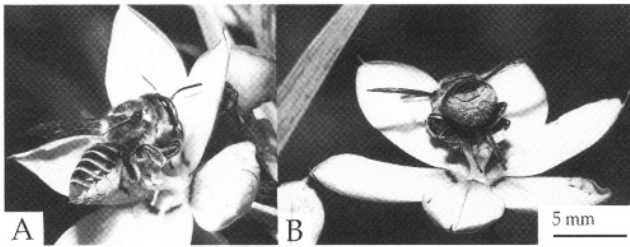


Fig. 13. *Megachile* sp. taking pollen from *Sisyriochiu palmifolium*.

Oil foraging in other species

Four other species of *Chalepogenus* and *Tapinotaspis latitarsis* have also been reported as oil-foragers of *Sisyriochium* (Table 4). *L. discrepans* is known to forage oil at least on other three species, and two other *Lanthanomelissa* species (*L. betinae* and *L. magaliae*) are known oil forager of two or three other species of *Sisyriochium*. *Chalepogenus goeldianus* was observed by us to visit a variety of *S. laxum* at Tandil (see Table 4). The bees alighted briefly on the flowers and curved deep into the flower in a manner similar to *L. discrepans*, however details on oil-foraging could not be observed. The only captured female had pollen laden scopae; the middle and forelegs including their coxae also carried pollen. Pollen loads of the scopae were not markedly oily or pasty as seen on other bees captured on oil-bearing *Sisyriochium* species. It consisted of 99.27% of *Sisyriochium* pollen and 0.73% of *Nierembergia ericoides* Miers pollen (n = 512). The latter is a co-occurring solanaceous species bearing oil-flowers. The frons of the bee carried 100% of *Nierembergia ericoides* pollen.

Structure and function of the oil collecting organs of *Lanthanomelissa*

We have studied the oil collecting structures of *L. discrepans* and *L. betinae*, which are identical in their oil-collector morphologies. Some aspects have also been treated by ROIG ALSINA (1997) and COCUCCI et al. (in press). The forelegs have an enlarged and slightly crescent-shaped basitarsus, its posterior surface being concave and covered with very few (between 60 and 65) exceedingly short, flat and hooked hairs (Fig. 14). Most of this surface is smooth and destitute of any other kind of hairs. The remaining surfaces of the forebasitarsus are densely covered by two other kinds of hairs: 1) long, unbranched, apically curved and wide hairs; 2) shorter, slender, and branched feather-like hairs. The first kind of hairs is particularly dense at the anterior border, between the ventral and dorsal basitarsus surfaces (Figs. 14 C–D).

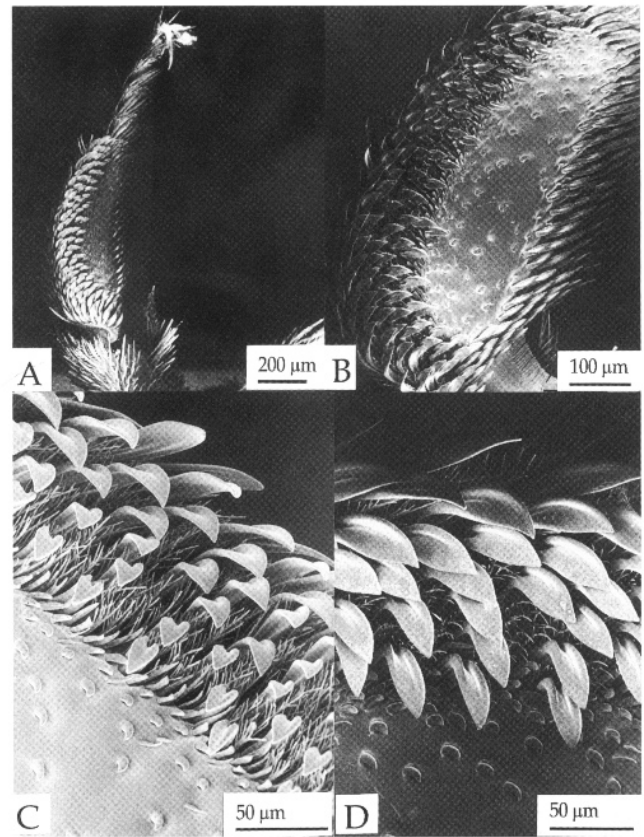


Fig. 14. Oil collecting structures of *Lanthanomelissa discrepans*. A: Front view of the right foreleg. B: basitarsus, C, D: Details of the forebasitarsus posterior border.

As it could be clearly seen when *L. discrepans* foraged oils on *S. chilense*, the posterior surface of the forebasitarsus is utilised to scrap the elaiophores. Most probably it is this surface that ruptures the cuticles of the trichome heads. The position and number of the scars left on the elaiophores suggests that the hooked hairs of the posterior surface of the basitarsus rupture the cuticle of the oil chamber. Apparently the part covered with feather-like hairs absorbs by capillarity the oil that has been let free by rupture of the trichome cuticles. Thus, one part of the basitarsus would work as a scraper, the other one as a soaker.

Structure of the oil collector of *Chalepogenus* and *Tapinotaspis* that collect oil on *Sisyriochium*.

The structure of the oil collecting structures of *Chalepogenus caeruleus* has been studied by VOGEL (1974). These are placed on the forelegs. The basitarsus has its nearly plane front face covered by a dense, velvety and well-delimited pad of one-side branched setae. The distal part of the tibia also bears a small patch of a simi-

lar kind of cover. Stiff and unbranched hairs otherwise sparsely cover basitarsus and tibia.

Other species of *Chalepogenus* such as *Ch. muelleri* have similar oil-collecting organs but not extending to the tibia: COCUCCI et al. (2000).

Tapinotaspis latitarsis has dense brushes of hairs, especially on tarsomers 2–4 of the midlegs, the front legs lack structures associated to oil-collection (ROIG-ALSINA 1997).

Pollen foraging in *Sisyrinchium* and *Olsynium*

Pollen consumption by syrphid flies or pollen collection by bees of several groups (Halictidae, Megachilidae) was observed by other authors (BERNARDT, in litt.; HENDERSON 1976). We also observed pollen collecting activities on elaiophore-bearing species of *Sisyrinchium*, by *Psaenythia* sp. (Andrenidae) and a *Plebeia* sp. (Apidae) on *S. pachyrhizum* and by *Megachile* sp. (Megachilidae) on *S. azureum* and *S. laxum*. These activities are regarded here as opportunistic since the oil-rewards are not utilised. Regular visits by pollen collecting bees to *Sisyrinchium* species with trichomeless flowers were observed by us in *S. palmifolium* and *Olsynium philippi*. Their behaviour is apparently suited to the flower structure and reward offered.

The flowers of *S. palmifolium* were heavily visited in the study site (Table 1) by bees of the family Halictidae (undetermined species of *Halictus* and *Augochloropsis*) and by two also undetermined species of *Megachile*. These bees move hastily on the flower pushing the anthers against the metasoma, which is held in upright position (Fig. 13). Also *Apis mellifera*, *Bombus morio* and *B. bellicosus* appeared regularly visiting flowers. The bumblebees, which seemed oversized for the flower dimensions, knocked the flowers down and in a pendant position bunched the anthers under their body and vibrated them.

On *Olsynium philippi* *Centris orellanai* was observed. The bees settled on the column without touching the perianth. They grasped it in such a way that their thorax came in ventral contact with the anthers or stylodia. The column was vibrated with an audible buzzing in a manner identical as in *Solanum* and flowers of the same type.

Flower types a reward systems in *Sisyrinchium* and *Olsynium*

Taking into consideration the flower form, the presence of glandular trichomes and, as far as it can be ascertained, the nature of the trichome secretion, three biotypes of three rewarding systems (oil, nectar and pollen)

can be distinguished among *Sisyrinchium* and *Olsynium*. Among those bearing oils three further categories are recognised.

Oil-flowers

A: Perianth spreading, flat and stellate, column slender, not bulging, stamens united throughout, anthers vertically fixed, and elaiophores on the basal part of the column. Species included (Fig. 3): *S. chilense*, *S. fasciculatum*, *S. macranthum*, *S. minutiflorum*, *S. pachyrhizum*, *S. patagonicum*, *S. platense*, and *S. setaceum*. These species have blue, purple, yellow or light yellow flowers.

B: Perianth deep bell-shaped or somewhat urn-shaped, that is, globose below the mouth. The bell form is given by the exotepals that are sturdier and bear a thicker triangular area near the base. Column short, included in the concave part of the perianth. Filaments fused at about half their length. Elaiophore on the basal conical half of the column. Anthers versatile and horizontally resting. Species included (Fig. 1): *S. laxum*, *S. micranthum* and *S. iridiflorum*. These species have blue, light blue, or light yellow flowers with yellow or brown markings inside.

C: Perianth bell-shaped, not urn-shaped, the exotepals being somewhat broader than the endotepals, filaments united at about half to their whole length. Elaiophore on the tepals only or when also extending to the column not on a special globose part. Species included (Fig. 2): members of Sect. *Echthronema* such as *S. arenarium* ssp. *arenarium*, *S. graminifolium* and *S. striatum*. These species have large, pale yellow flowers with brown markings inside. It must be noted that the flower architecture of *S. arenarium* is not stable at the species level, since *S. arenarium* var. *adenostemon* (Figs. 4.2–4.4) presents strong aberrations from the above mentioned more common form. The same is also true for the closely related *S. macrocarpum* (Fig. 4.1).

Nectar flowers

Flowers of *Olsynium junceum* (Fig. 16.3) and *O. uniflorum* (Fig. 16.2) have a funnel-shaped perianth and filaments fused to their whole length, the column being swelled near the base such that it builds a chamber. At least for *O. junceum* it has been determined that flowers bear nectar (see FORCONE et al. 1998 for nectar characters). Flowers of various populations we examined showed no trichomes. Only stomata were found at the base of the endotepals.

Pollen flowers

The flowers of *Olsynium philippi* (Fig. 16.1) are rotaceous and nutant, their tepals being turned to rear. Filaments completely fused in a tube and swelled near the

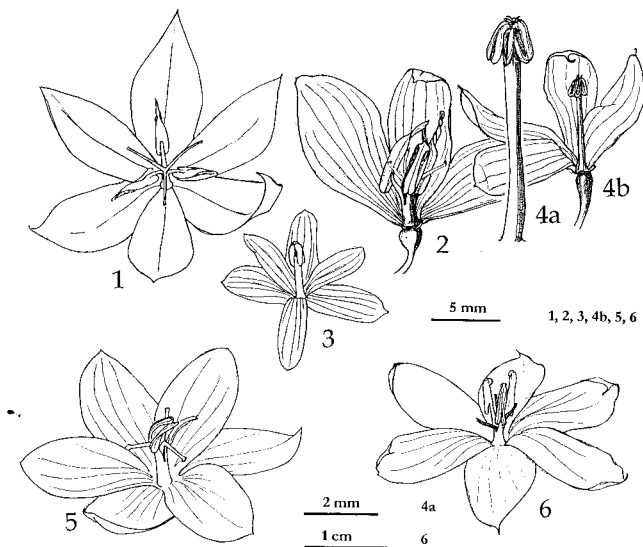


Fig. 15. Types of pollen flowers of *Sisyrrinchium* and *Olsynium*: 1–2: *S. vaginatum*: 1 (AAC 649), 2 (SV 59^a); 3: *S. nanum* (AAC et al. 560); 4: *S. unguiculatum*; 5: *Olsynium junceum* ssp. *leucanthum*; (AAC et al. 562); 6: *S. palmifolium*.

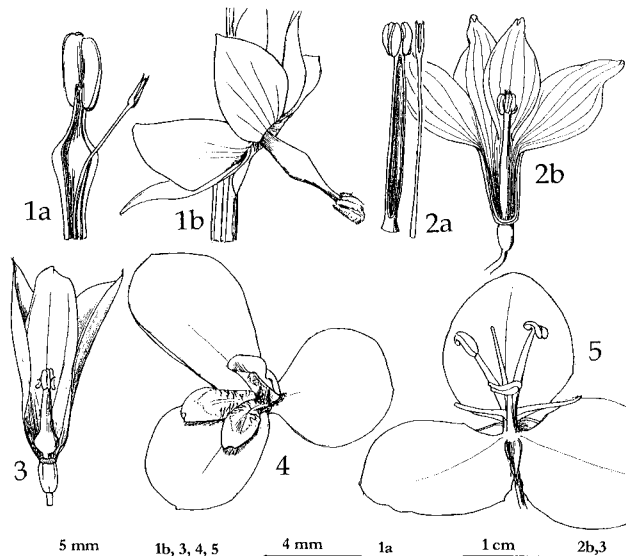


Fig. 16. Diversity of flower types in genera of the tribe *Sisyrrinchieae*: 1. *Olsynium philippii* spp. *illapelinum* (AAC et al. 561), dissection of the inflated column (a), flower side view (b); *O. uniflorum* (AAC Dec. 23, 1993), dissection of the hollow column with removed style (a), flower dissection; 3. *O. junceum* ssp. *lines* (AAC et al. 924); 4. *Diplarhena peacock* (Göteborg Botanic Garden); 5. *Libertia chilensis* (AAC et al. 954).

middle. Pollen is here the only reward. The column swelling is yellow and probably has a visual effect by mimicking an anther cone.

Flowers of *S. virgatum*, *S. palmifolium* and *Olsynium junceum* pp. (Fig. 15.1, 15.2, 15.5, 15.6) are erect and

bear a horizontally spreading perianth. Filaments are fused to about half their length and the large anthers have a specialised apical part that progressively turns or curls during anthesis. This peculiarity of anther development is also known among the Iridaceae for *Calydorea crocoides* Rav. (RAVENNA 1965). *Bobartia rufa*, the flowers of which are identical to those of *S. palmifolium*, can also be included here.

Certain yellow flowered species of *Sisyrrinchium* (*S. nanum* and *S. unguiculatum*; see Fig. 15) have flowers strongly resembling those of the above type A but lack elaiophores. Here either pollen is the only reward or seed production by autogamy is habitual.

4. Discussion

Elaiophores

The elaiophores of *Sisyrrinchium* belong to an anatomical type universal in the Iridaceae as pointed out by HUMMEL & STAESCHE (1962). The mode of secretion by which oil is stored in a subcuticular space between wall and cuticle is known for some trichome elaiophores (COCUCCI 1991) and trichomatic glands secreting essential oils (KISSER 1958).

Trichome elaiophores are known, outside the Iridaceae, in the Orchidaceae, Scrophulariaceae and Solanaceae (VOGEL 1988). Rupturing of the cuticle of the oil-glands by the oil-collecting bees has been reported for *Krameriaceae* (SIMPSON et al. 1977) and the malpighiaceae genus *Dinemandra* (COCUCCI et al. 1996) which all have epithelial elaiophores foraged by *Centris*. Cuticle rupturing of trichomes by oil-collecting bees has not been observed previously but has been suggested to occur when *Chalepogenus* forages oils on *Nierembergia* (COCUCCI 1991).

Otherwise the secretion mode in the trichome elaiophores (Cucurbitaceae, Primulaceae, Scrophulariaceae) are not known to occur by cuticle rupturing (VOGEL 1974, 1990).

Among the *Sisyrrinchieae* glandular trichomes are absent in the flowers of most genera related to *Sisyrrinchium*. However, for the relatively primitive *Libertia* trichome “nectaries”, in form of papillae are reported for inner and outer tepals in *L. formosa* Graham (DAUMANN 1970). This character is not uniform in *Libertia*, since trichomes are absent in *L. chilensis*. Perigonal nectaries – that can be epithelial or rarely trichomatic – appear to be the basic feature in the subfamily *Iridoideae* where Tribe *Sisyrrinchieae* belongs, while septal nectaries are the rule in other subfamilies, the *Ixioideae* and *Nive-noideae* (DAUMANN 1970). Among the Iridaceae, oil flowers appear only in the New World, and among the subtribe *Sisyrrinchioideae* only in *Sisyrrinchium*.

Oil-source sharing by oil-collecting bees visiting *Sisyrrinchium*

Records of oil-foraging suggest a narrow association of the oil-bearing *Sisyrrinchium* species with bees of the tribe *Tapinotaspini* (family Apidae, genera *Chalepogenus*, *Lanthanomelissa*, and *Tapinotaspis*).

Lanthanomelissa (Subgenus *Lanthanomelissa*) is oil forager of all but 2 of 11 *Sisyrrinchium* species for which oil-foraging records are available and *Sisyrrinchium* is its only known oil-source. Species of this bee genus are the main oil-foragers of *Sisyrrinchium* Sect. *Sisyrrinchium* since it appears as the dominant or the only forager in 12 of 14 localities. Oil-sources previously attributed to this bee subgenus, i.e. *Nierembergia* (COCUCCI 1991) and *Herbertia* (*Alophia*) (SCHILDWEIN 1995) were based on misidentifications (ROIG-ALSINA 1997).

Chalepogenus caeruleus has been reported for several localities as oil-forager of *Sisyrrinchium arenarium*. This bee species and other closely related ones (ROIG-ALSINA 1999) are probably the exclusive oil-collectors of this and other related species of Sect. *Echthronema* with which its ranges overlap (Fig. 17). In the same region *Lanthanomelissa* is apparently absent. *Ch. caeruleus* is reported to forage oil also on several species of the scrophulariaceous genus *Calceolaria* (SÉRSIC 1994; VOGEL 1974).

Chalepogenus goeldianus (cited as *L. completa*) is known to collect oils also from the iridaceous species *Herbertia* (*Alophia*) *lahue* and the solanaceous genus *Nierembergia* (SCHILDWEIN 1995). In this work we confirm the latter association with palynological findings.

Tapinotaspis latitarsis is known to forage oils only from *Sisyrrinchium*. Other oil sources of the genus include *Nierembergia* to which special adaptations are evident (COCUCCI 1991).

Concluding, the two sides of the association between oil-collecting bees and *Sisyrrinchium* are as follows: from the side of the bees, the relation is monoleptic only in *Lanthanomelissa*, while with other bees (*Chalepogenus* and *Tapinotaspis*) the relation is diffuse. From the side of the plant, oil-bearing species of *Sisyrrinchium* mostly depend on one or few species of oil-collecting bees, though sometimes they are visited by opportunistic pollen-collecting bees or by other oil-collecting bees. Their legitimate partners are either *Chalepogenus* on the western part of its range or *Lanthanomelissa* on the eastern part of its range.

Oil-collecting structures

Three functional types of oil collecting structures appeared associated to oil-foraging on *Sisyrrinchium*: 1. absorbing foreleg pads (*Chalepogenus*), 2. absorbing

middle leg pads (*Tapinotaspis*), and 3. abrasive-absorbing front leg pads (*Lanthanomelissa*).

The particular oil-collecting structures of *Lanthanomelissa*, which are diagnostic characters for the genus (URBAN 1995), appear to be specially suited to rupture the oil-blister of the trichomes of *Sisyrrinchium* (Sect. *Sisyrrinchium*). Types 1 and 2 are also found associated to trichome elaiophores of other plant genera (*Calceolaria* and *Nierembergia*). Cuticle rupture is only exceptional in *Calceolaria* (SÉRSIC 1994) and it occurs spontaneously in *Nierembergia* (COCUCCI 1991).

S. arenarium, the elaiophores of which do not form an oil blister, has as partners bees lacking abrasive structures on the oil collector. Bee genera without scrapers on the oil-collecting structures (*Chalepogenus* and *Tapinotaspis*) that do visit *Sisyrrinchium* species bearing oil-blisters, co-occurred with *Lanthanomelissa* in two of the four populations studied (see Table 4). In one of the two populations (*S. laxum*), where *Lanthanomelissa* was not present, the scopal loads of *Chalepogenus goeldianus* had only little oil. This evidence suggests that bees different from *Lanthanomelissa* visit flowers with blister-bearing elaiophores, either to take remnant oil of flowers whose glands had already been opened by *Lanthanomelissa* or, when this bee is absent, only to take pollen. Without suitable oil-collecting structures they would not get oil though attempting it and oil requirements should then be covered with other oil-sources.

Flowering patterns

Short-lived flowers are probably correlated at least in *S.* Sect. *Sisyrrinchium* with the modes of oil presentation in rupturable blisters, since it would be depleted during the first visit and not replenished. In addition, depletion of flowers resources during the first visits would lead to high competition among the bees to be the first to visit the flowers. It could, thus, be explained that they appeared mostly during the first period of flower opening and even foraged buds. Contrarily, in *Calceolaria*, where anthesis is prolonged over several days, oil output is maintained during anthesis by continuous secretion (SÉRSIC 1994).

Geographical distribution and evolutionary history

The phylogenies presented by GOLDBLATT (1990) and by RUDALL (1994) indicate a south-hemispheric origin of the *Sisyrrinchioideae* since the extant most basal of its members are shared between South Africa, Australasia and South America. These also include the nearest relatives of *Sisyrrinchium* and *Olsynium* (GOLDBLATT et al. 1990). Further radiation occurred only in the New World. Within *Sisyrrinchium* oil-flowers and oil-less

ones are found in two distinctive clades, Sects. *Sisyrrinchium* and *Echthronema*.

Pollen flowers, i.e. with pollen as the only reward, are reported here for the first time in *Sisyrrinchium* (*S. palmifolium* and *S. vaginatum*) and *Olsynium* (*O. philippi*). Other possible cases are according to flower characters *Libertia chilensis* (Fig. 16.5), *Bobartia* and *Tapeinia*. Nectar flowers are reported only in *Olsynium junceum* (FORCONE et al. 1998) but the nature of its nectaries remains a mystery. The presence of stomata near the base of the tepals suggests a mesenchymatic type of nectary. However, detailed studies would be needed to ascertain if this kind of nectary unusual in the Monocots is actually present. Zygomorphic flower symmetry that is suggestive of melittophilous nectar flowers is present in *Diplarhena* but again nothing is known about its nectaries (Fig. 16.4).

An attempt to overlay distribution patterns and phylogenetic groupings should help to understand the evolutionary processes in the genus in relation to its association with oil-collecting bees.

Sisyrrinchium has its main native range in the New World, from the Arctic (Alaska, Greenland, to Tierra del Fuego (Fig. 17). Exclaves of this main area are the Galapagos Islands (*S. galapagense* RAV., see RAVENNA 1979), Hawaii (*S. acre* MANN, see DEGENER 1932) and Ireland (*S. bermudina*, see INGRAM 1967). Several species are also adventive in other parts of the World such as Europe (PARENT 1980) and Australia (COOKE 1986). The taxonomical works and checklists revised (BRAKO & ZARUCCHI 1993; BROTERENBROOD 1966; CORELL & JOHNSON 1970; CUNHA DE MENDOÇA et al. 1998, FREDSKILD 1966; GLEASON & KILLIP 1939; HENRICH & GOLDBLATT 1987; HULTÉN 1999; JOHNSTON 1938; RAMBO 1954; VARESCHI 1970, and ZULOAGA & MORRONE 1996) show that species diversity is highest in South America, particularly in the Pananá river basin, an area shared by Brazil, NE Argentina, Paraguay and Uruguay.

Subgeneric groupings have either been completely disregarded (JOHNSTON 1938) or differently understood by other authors (BAKER 1876; BENTHAM & HOOKER 1883; GOLDBLATT et al. 1990; PAX 1888; RODRÍGUEZ 1986), so that systematic knowledge within the genus is still unsatisfactory. This will probably remain so until a comprehensive revision is carried out. Fortunately, considerable progress has been achieved by extensive chromosome studies (BÖCHER 1966; CHOLEWA & HENDERSON 1984; HENDERSON 1976; INGRAM 1967; INGRAM 1968; KENTON & HEYWOOD 1984; MOSQUIN 1970; OLIVER & LEWIS 1962; RODRÍGUEZ 1986; RUDALL et al. 1986) that may help overcoming this difficulty. According to the data made available by these authors, at least two groups with deviating basic chromosome numbers ($x = 8$ and $x = 9$) can be recognised. In

addition, as RODRÍGUEZ (1986) pointed out, allopolyploidy events may have given rise to some new species.

Sect. *Sisyrrinchium* is the most uniform since its species have small chromosomes and base number $x = 8$ (RUDALL et al. 1986). Morphologically the group includes oil bearing types A and B as well as the oil-less types related to A by the stamens completely united in a column and ending in sessile anthers. Species of the section are blue, bluish red or yellow flowered. Ploidy levels within the Section *Sisyrrinchium* vary widely between diploids ($2n = 16$) and dodecaploids ($2n = 96$), diploids being more frequent in South America. As a general trend, in the Northern Hemisphere ploidy levels increase with latitude, but in Greenland populations are tetraploids ($2n = 32$, see INGRAM 1968).

According to HENDERSON (1976) *S. alpestre*, *S. bermudianum*, *S. montanum*, *S. sarmentosum* bear glands on the column, but the nature of their secretion has yet to be determined. However, no oil-collecting bees have been reported visiting these plants and no oil-collecting *Tapinotaspidini* reach farther north than Peru (MICHENNER & MOURE 1957; ROIG-ALSINA 1997, 1999). The oil-bees of North America, species of the melittid genus *Macropis*, are known to forage oil only from *Lysimachia* (Primulaceae, see VOGEL 1990) but not from *Sisyrrinchium*.

Sisyrrinchium of northwestern United States are protandrous, less pronounced so in the octoploids. Diploids (*S. bellum*, *S. halophilum* and *S. septentrionale*) are self-incompatible, cross-pollination being accomplished by megachilid bees (HENDERSON 1976), while tetra- and octoploids (all species except for *S. hitchcockii*) are self-compatible.

This body of evidence supports the idea that this Section originated in South America and migrated northward. During that transit they lost their association with oil-collecting bees while switching to pollen-collecting polylectic bees or turning autogamous. The glands present in the North American species would be a vestigial condition from the earlier associations. The nature of their secretion has yet to be determined. The area of highest diversity for the group is the Paranaense region and the subandean ranges. This area corresponds to the distribution of *Lanthanomelissa* and two of the four *Chalepogonus* species associated with *Sisyrrinchium* (*Ch. goeldianus* and *Ch. muelleri*).

The generic group with $x = 9$ has chromosomes small to medium in size. Ploidy levels also range from diploids to dodecaploids, however high polyploids are less common than in Sect. *Sisyrrinchium*. It includes the sections *Echthronema* and *Cephalanthum*, the latter sometimes included in the former. Very different flower types can be found within it, i.e. oil bearing flowers of our C type and oil-less pollen-only flowers. The latter include *S. palmifolium* and species with morphologically

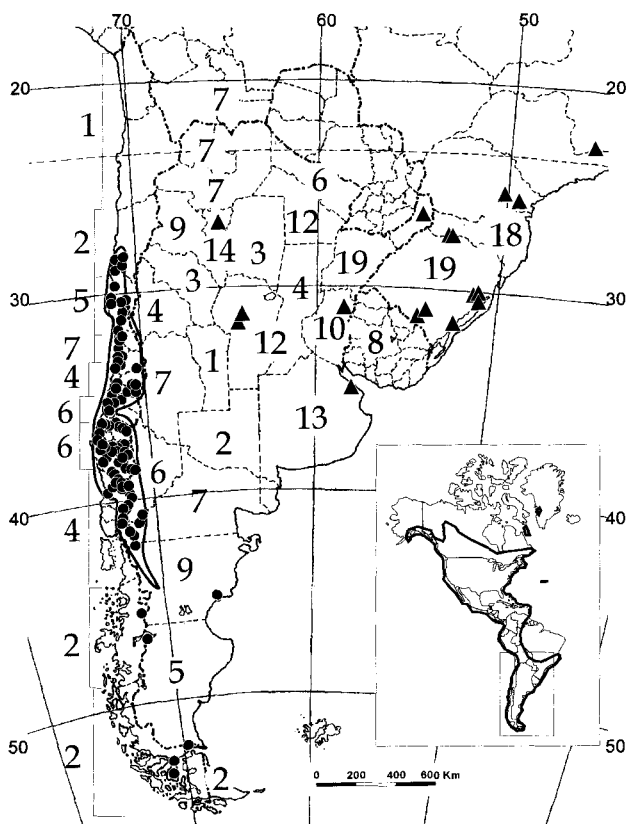


Fig. 17. Geographical distribution of *Sisyrrinchium*: map at the right: native range in the New World the rectangle indicating the area enlarged at the left. Numbers indicate the species number in Bolivia, Paraguay, Southern Brazil, and the provinces of Argentina and Chile. The black dots on the main map correspond to the distribution of the oil-bearing species of Sect. *Echthronema*, the triangles to *Lanthanomelissa* (all species), and the area bounded by the dark line to the range of the *Chalepogenus* species known to collect oil from *S. arenarium*. The distribution of *Sisyrrinchium* based on HOWARD (1979), ZULOAGA et al. (1996), and FREDSKILD (1966); bee distribution based on ROIG-ALSINA (1999), URBAN (1995), and specimens collected by the authors.

similar flowers that are widespread within the range of the genus.

The oil-bearing species can be clearly recognised by the characters given above and by the inflorescences with many lateral spikelets. It also builds a geographically restricted group from middle Chile and SW Argentina (Fig. 17). We believe these oil-bearing species of Sect. *Echthronema* represent a well-defined monophyletic group. It is primarily associated to *Chalepogenus caeruleus* and closely related species. It has eventually lost elaiophores out of the range of these bees in southernmost Patagonia. This oil-bearing species can be linked on the ground of morphological agreements with

B Type of flowers of Sect. *Sisyrrinchium* such as bell shaped perianth, differentiation between exo- and endotepals, versatile anthers, and only basely fused stamens. However the species of Sect. *Sisyrrinchium* with bell-shaped flowers are mainly distributed in NW Argentina and neighbouring Brazil, Paraguay and Uruguay.

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