Research Article

Turk J Bot
34 (2010) 367-377
© TÜBİTAK
doi:10.3906/bot-0907-98

An account on the floral dimorphism and ecology of the genus *Moltkiopsis* I.M.Johnst. (Boraginaceae) in Saudi Arabia

Turki Ali. AL-TURKI[1], Jacob THOMAS[2,*]

[1]Herbarium (MUZ), Natural Resources and Environmental Research Institute, King Abdulaziz City for Science and Technology, PO Box 6086, Riyadh 11442, SAUDI ARABIA

[2]Herbarium (KSU), Dept. of Botany and Microbiology, College of Science, King Saud University, P.O. Box 2455, Riyadh-11451, SAUDI ARABIA

Received: 18.07.2009
Accepted: 05.05.2010

Abstract: A brief account on the morphology and ecology of the monotypic genus *Moltkiopsis* I.M.Johnst. (Boraginaceae) is given. An overview of the genus with notes on heterostyly, communities, soil, regeneration, vernacular names, etc. is presented. Variations present in some of the populations of *Moltkiopsis ciliata* (Forssk.) I.M.Johnst., particularly in the floral parts, are also explained in detail.

Key words: *Moltkiopsis ciliata*, Boraginaceae, Saudi Arabia, floral dimorphism, ecology

Introduction

The Boraginacean genus *Lithospermum* L. was originally established by Tournefort and later adopted and maintained by Linnaeus (1753). The generic circumscription as outlined by Tournefort and Linneaus was followed by Vahl (1790), Poiret (1811), De Candolle (1846), Boissier (1879), Ascherson and Schweinfurth (1887), Johnston (1953), and Riedl (1967). Johnston (1953) segregated 3 species from *Lithospermum* as 3 monotypic genera. He regarded these as being remotely related to the rest of the species of *Lithospermum*. The morphological separation between these genera may be either the outcome of a long period of disjunction or the result of fast morphological evolution triggered by the split of a common ancestor. These 3 genera, *Moltkiopsis* I.M.Johnst., *Mairetis* I.M.Johnst., and *Neatostema* I.M.Johnst., differ from *Lithospermum* by their nutlets having a relatively thin pericarp, obliquely basal nutlet attachment, and the presence of a ventral keel at the base of the nutlets. As per the recent findings by Cecchi and Selvi (2009), Internal Transcribed Spacer (ITS) sequences have provided a better resolution of relationships, which showed the similarities and dissimilarities of some of the genera included under *Lithospermum* with *Moltkiopsis* and *Mairetis*. *Moltkiopsis ciliata* may be the taxon closer to such a progenitor and this would be confirmed by the possibly plesiomorphic feature of the 3-aperturate pollen (Johnston, 1953). Occurring continuously from Morocco in the West to Iran in the East, *Moltkiopsis ciliata* is the more widely distributed taxon in this clade and provides a partial chorological link between *Mairetis* and other genera. Johnston (1953)

* E-mail: jacobthomas1959@yahoo.com

erroneously placed these genera in the tribe Eritrichieae while Riedl (1967) grouped *Moltkiopsis* and *Neatostema* into the subtribe Moltkiopsidinae in the *Flora Iranica* treatment. Nevertheless, the placement of Moltkiopsidinae in the tribe Trigonotideae by Riedl (1967) does not find support in the recent ITS findings, since all these genera are firmly nested within Lithospermeae (Cecchi & Selvi, 2009).

Moltkiopsis closely resembles the genera *Mairetis* and *Neatostema*, in the presence of the ventral keel of the nutlet, but differs in its perennial life form, circumscissile calyx (at maturity), the nectary at the base of the corolla tube being annular, stamens inserted high in the corolla tube at different levels, and the pollen being ellipsoid and triporate. *Moltkiopsis* comprises only a single species, *M. ciliata*. Locally, this species is called "Crapsi" (Al-Dahna), "Halam" (southern tribes in "Al-Murrah", Bani Hajir and Al-Rashid tribes; Mandaville, 1990), and "Hamat" (northern Saudi Arabia, used by the Bani Hajir tribe only to refer to the dry state where it is not palatable to the livestock; also in Iraq around Al-Ghazlani). *Moltkiopsis*, characterised by the herbaceous habit, squarrose hairy leaves, helical cymes, and stony nutlets, is a coloniser of deserts and sand dunes in the New World and particularly in the Saharo-Sindian belt of the Old World. Seedlings are scarcely observed; heavy browsing scarcely permits producing seeds perhaps. Vegetative propagation by means of stoloniferous runner roots, as seen with some species of *Heliotropium* (Chaudhary, 1985), is not known in *Moltkiopsis*.

Moltkiopsis ciliata belongs to the Saharo-Sindian phytochorion extending from North Africa to Iran from 0 to 900 m a.s.l. It is known from Morocco, Tunisia, Algeria, Libya, Egypt, Palestine, Jordan, Israel, Syria, Kuwait, Saudi Arabia, Yemen, Oman, Iraq, and Iran (Feinbrun-Dothan, 1978; Mandaville, 1990). In Saudi Arabia, it is reported mainly from the central, eastern, and southern parts. On the basis of field explorations and herbarium specimens deposited both inside and outside the Kingdom (MUZ, KSU, RIY, E, K), a map has also been provided to show the distribution range of the species (Figure 1). Flowering of this species is generally from February to June. A

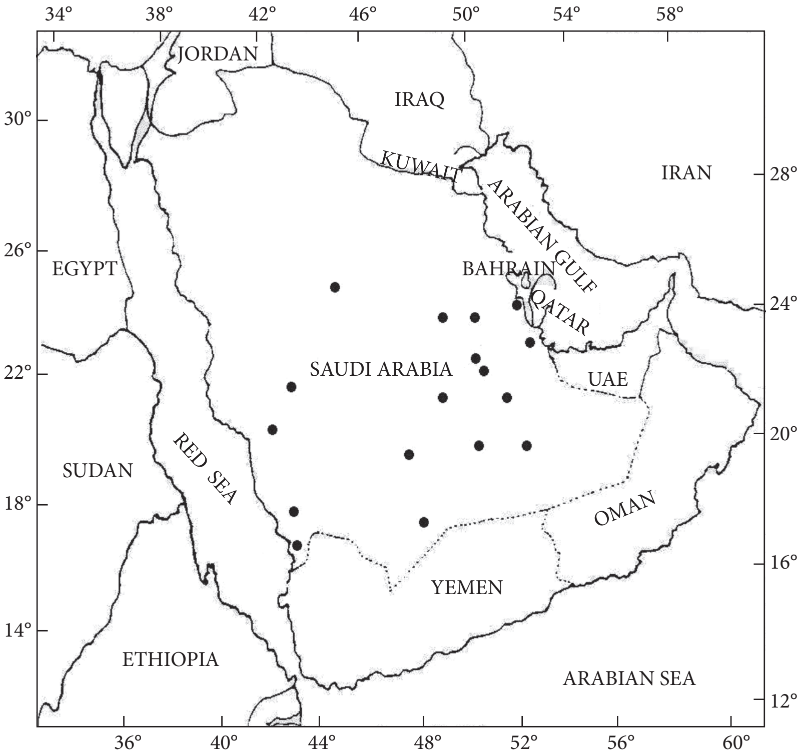

Figure 1. Distribution of *Moltkiopsis ciliata* in Saudi Arabia.

second flowering period has also been observed in populations from Egypt and Iraq, when the plants flower between September and December and very rarely late in August. The observed bi-seasonal flowering perhaps results from the unpredictable rains in the deserts.

Heterostyly is a floral polymorphism characterised by the reciprocal positioning of stigmas and anthers between morphs. Floral dimorphism is widely prevalent in Boraginaceae (Ganders, 1975a, 1975b, 1976, 1979). Three types generally occur (1). Reciprocal herkogamy in which the stamen heights and style lengths differ reciprocally (Barrett, 1992), e.g. *Arnebia* Forssk. (18 spp.) and *Lithospermum* (11 spp.) (Bessey, 1880; Johnston, 1953). (2). Style length is constant, but anther heights vary, e.g. *Stenosolenium saxatile.* (3). Style length varies independent of anther height, e.g. *Ulugbekia tschimganica*. The objective of the present paper was to give an outline of the floral structure prevailing in various populations and their ecology by means of soil analysis.

Materials and methods

The taxonomic studies were based on collections deposited in various herbaria in Saudi Arabia such as King Abdulaziz City for Science and Technology (MUZ), King Saud University (KSU), and the National Herbarium, Ministry of Agriculture (RIY). Specimens available at the herbaria of the Royal Botanic Gardens, Edinburgh (E) and Kew (K) were also studied to ascertain the variation present in the various populations. Over 200 specimens from various parts of the Middle East were investigated in this study. A consolidated list of voucher specimens is presented in Appendix. The description of soil is based on soil profiles studied by the authors from the Dahna region of Saudi Arabia. Three replicates of soil samples from various depths (5-60 cm) were collected, from a pure *Moltkiopsis* community and *Panicum turgidum-Moltkiopsis* communities located in areas between 200 and 350 km east of Riyadh city. Soil samples were collected from the "root zones" of the plants growing in the area and transported to the laboratory. These were later dried at room temperature with the help of an exhaust fan to remove moisture-laden air. Samples were crushed with a mechanical grinder equipped with a porcelain mortar and stainless steel auger and subsequently passed through a stainless steel 10-mesh sieve to remove larger clods and unwanted debris. Soil mechanical analysis was carried out by the pipette method (Black, 1968) and total water soluble salts were determined by the procedure described by Richards (1954).

Results

Moltkiopsis ciliata is common in both sandy as well as stony deserts. Its presence in the deserts of Rub-al-Khali (Saudi Arabia) and Sahara (Africa) shows its extreme drought resistance abilities. The plant is very common in the Dahnas. It also grows on dune tops, slopes and wadis, often seen as small caespitose clumps. The maximum height seen in most of the populations is 30 cm, yet bushy plants as large as 75 × 100 cm have been noticed along the Riyadh-Dammam road in Saudi Arabia (Figures 2A & B). The rootstock is actually the apical region of the buried stem, which is also branched, and the tap root system branches off further down beneath the rootstock (Figure 2 C).

Floral dimorphism was present in the specimens from the Central province of Saudi Arabia. The observed floral dimorphism concerns 2 different flower sizes: long flowered, where the flower is 10-15 mm long, and short flowered (Figures 3 & 4), where it is only 4-7 mm long. Long flowers have anthers and stigma at the same level, while in short flowers, the stigma is always above the anthers and exserted. These differences are reported in Table 1. Populations of these 2 categories are distinct in a few localities in the Central and Eastern provinces. However, these populations are not consistent in a few other localities and are often seen side by side.

Flower colour varies considerably. Blue-violet, red, bluish limb with red tube, and white have been observed in various populations seen in different geographical locations not far away from each other. Blue-violet and red flowers are seen on the same plant. Plants with white flowers are extremely rare. However, one small population with both violet and red flowers is observed in the Eastern province. Plants with white or pure yellow flowers are also occasionally seen in the Central province of Saudi Arabia.

Figure 2. *Moltkiopsis ciliata*. A. General habit, B. Flowering branch, C. Root system.

Moltkiopsis grows on deep to moderately deep sand masses, sometimes colonising thin sand upon a shallow rocky substratum. The species is common especially where the sand is particularly reddish due to a coating of iron oxide. Along the Riyadh-Dammam road transect (Saudi Arabia), the plant populations are sparse about 100 km before Dammam, where the soil becomes whitish. Details of layering of the soil profiles of 2 different communities from the Dahna area of Central Saudi Arabia in which *Moltkiopsis* is found are illustrated in Figure 5 and the properties described in Table 2. In both communities the soil is invariably reddish sand.

In the pure *Moltkiopsis* community (consociation; Figure 5a, b), the profile is homogeneous, or sparingly stratified, within 60 cm in depth. In the *P. turgidum*-*Moltkiopsis* seral community (Figure 5c, d), the soil profile is distinctly stratified, 4-5 layered with 2 layers of pure reddish sand alternating with 1 or 2 layers of small gravel or pebbles mixed with sand. The alternating layers of sand are interspaced with layers of a mixture of pebbles and sand; this is indicative of long-term periodic sand movements. The buried root-stock and deep seated root system perhaps owes its origin to the drifting sand. Compared to the layered soil, the non-stratified soil of the pure

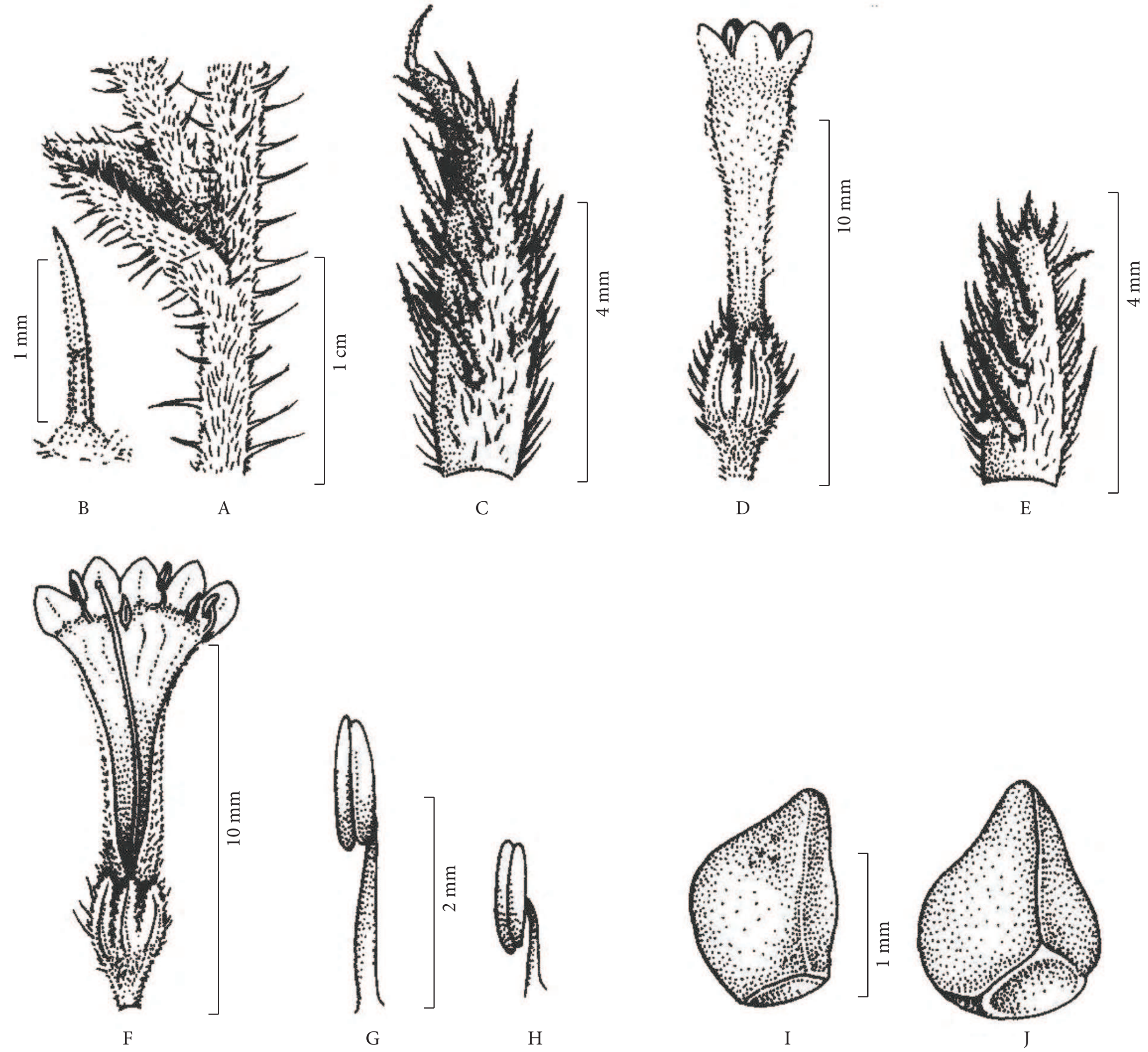

Figure 3. Morphological features of flower with long corolla tube. A. Enlarged portion of a branched stem, B. Trichome, C. Leaf, D. Flower, E. Bract, F. Flower with open corolla tube, G. Long stamen, H. Short stamen, I and J. Two views of a nutlet.

Moltkiopsis community (consociation) is more recent, and in this sense *Moltkiopsis* seems to be a pioneer species in the desert.

Physico-chemical properties of the different layers of soil in the 2 communities, viz *Moltkiopsis* community (consociation) and *P. turgidum*-*Moltkiopsis* community are given in Tables 3 and 4. The soil is composed of 92%-96% sand and 2%-4% silt and clay each, and near neutral values of pH ranging between 6.9 and 7.2. The soil is deficient in the macronutrients N, P, and K (Table 5). Calcium, magnesium, and sulphate ions also do not show higher values. Comparative details of the soil in the top layer across the 2 communities are given in Table 5.

Discussion

The red and blue flowered plants are either long- or short-flowered whereas the white ones are always short-flowered and the yellow ones long-flowered. Generally, white flowers are indicative of pollination by nocturnal insects (Young, 2002). The difference in

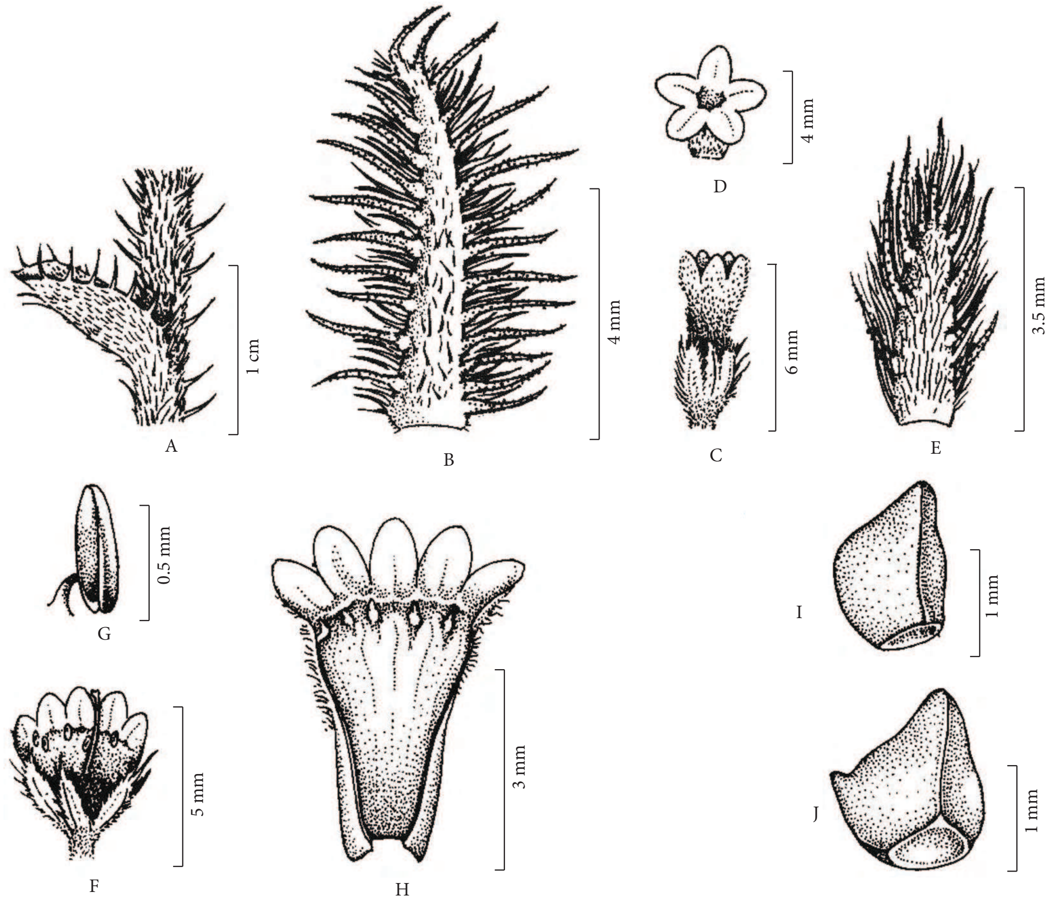

Figure 4. Morphological features of a flower with short corolla tube. A. Enlarged portion of the stem, B. Leaf, C. Flower, D. View of the flower from above, E. Bract, F. Open flower, G. Stamen, H. Open corolla, I and J. Two views of a nutlet.

Table 1. Comparison of character states in the 2 ecotypes of *Moltkiopsis ciliata*.

No.	Character states	Ecotype-I	Ecotype-II
1	Stem	Fine hairs interspersed with a few bossed strigose hairs	Greater number of bossed strigose hairs present
2	Bracts	With a few thick strigose hairs on the outer surface, pubescent within	Devoid of thicker strigose hairs except along the margins, glabrescent within
3	Sepals	Long ciliate, with 1-3 strigose bossed hairs on the outer surface, fine hairs on the margins short	Long ciliate along the margins and the outer surface, devoid of thick strigose hairs on the outer surface, fine hairs on the margins very long, c. twice as long as that of var. *ciliata*
4	Corolla tube	8-10(-15) mm long	4(-7) mm long
5	Corolla lobes	2-2.5 mm long	1.5 mm long
6	Stamens	3 long + 2 short	5, all of same length
7	Style	Slightly shorter than the longer stamens, as tall as the shorter stamens, as tall as the longer stamens, or longer than the stamens	Almost always exceeding the stamens
8	Nutlets	2 × 1.2 mm, devoid of a cusp on its margin	1.5 × 1 mm, with a cusp on one margin, or the cusp absent.

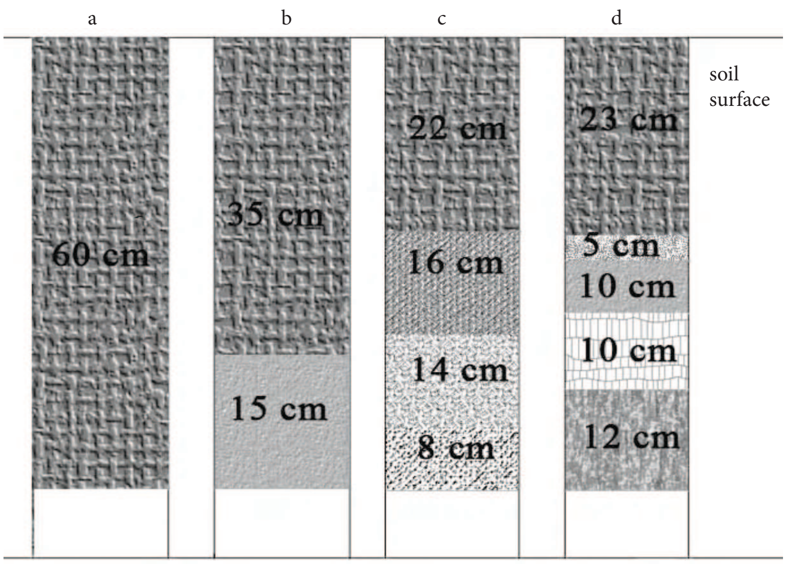

Figure 5. Stratification of the soil profiles of the communities in which *Moltkiopsis* grows. A and B. Pure *Moltkiopsis* community; C and D. *Panicum turgidum*-*Moltkiopsis* community.

Table 2. Stratigraphy of soil profiles of communities in which *Moltkiopsis* grows.

Comm.	Profiles	Pit depth	Horizons	Depth (horizon)	Colour	Texture
MC	1*	60 cm	0	60 cm	R	Sandy
MC	2*	60 cm	0	35 cm	R	Sandy, interspersed with granules
			1	15 cm	R	Sandy
PM	3**	60 cm	0	22 cm	R	Sandy
			1	16 cm	R	Sandy, interspersed smaller and larger gravel
			2	14 cm	R	Sandy, very few pebbles
			3	8 cm	R	Sandy, compact
PM	4**	60 cm	0	23 cm	R	Sandy
			1	5 cm	R	Sandy, mixed with white pebbles, sand coarse
			2	10 cm	R	Sandy, interspersed with white grains
			3	10 cm	R	Sandy, compact, interspersed with granules
			4	12 cm	—	Boulder stones

Abbreviation: Comm. – Community; MC – Pure *Moltkiopsis* community; PM – *Panicum turgidum* – *Moltkiopsis* community; R – Reddish.
*Locality of profiles 1-2: *c*. 70 km on the Riyadh-Dammam Road, Saudi Arabia, 25°6.816′N, 47°39.590′E, + 565 m, motorway embankment.
**Locality of profiles 3-4: Same as for profiles 1 and 2, but on a hill slope near a bridge.

Table 3. Soil properties of profile no. 2 [pure *Moltkiopsis* community].

Layer	Depth	pH	EC	ESP	SAR	Cations				Anions				Texture			
						Ca^{2+} (me/L)	Mg^{2+} (me/L)	Na^{+} (me/L)	K^{+} (me/L)	N (%)	PO_4^{3-} (me/L)	Cl^{-} (me/L)	SO_4^{2-} (me/L)	Sand (%)	Silt (%)	Clay (%)	Texture class
1	35 cm	7.0	0.21	-1.026	0..27	0.68	0.47	0.94	0.09	0.011	0.06	0.90	0.40	94	4	2	Sandy
2	15 cm	7.1	0.20	-0.903	0.42	0.68	0.40	0.80	0.13	0.006	0.06	0.51	1.08	94	2	4	Sandy

Abbreviation: EC – Electrical conductivity; ESP – Exchangeable sodium percentage; SAR – Sodium absorption rate

Table 4. Soil properties of profile no. 4 [*Panicum turgidum* – *Moltkiopsis* community].

Layer	Depth	pH	EC	ESP	SAR	Cations				Anions				Texture			
						Ca^{2+} (me/L)	Mg^{2+} (me/L)	Na^{+} (me/L)	K^{+} (me/L)	N (%)	PO_4^{3-} (me/L)	Cl^{-} (me/L)	SO_4^{2-} (me/L)	Sand (%)	Silt (%)	Clay (%)	Texture class
1	23 cm	7.2	0.30	-0.993	0.24	1.22	1.34	0.31	0.11	0.014	0.06	0.60	1.84	94	4	2	Sandy
2	5 cm	7.2	0.24	-1.036	0.25	0.68	1.08	0.22	0.12	0.013	0.12	0.70	1.26	94	2	4	Sandy
3	10 cm	6.9	0.38	-0.72	0.52	0.82	1.18	0.52	0.17	0.015	0.06	1.00	1.42	96	2	2	Sandy
4	10 cm	7.2	0.24	-0.935	0.35	0.68	1.08	0.31	0.11	0.008	0.06	0.60	1..34	92	4	4	Sandy

Abbreviation: EC – Electrical conductivity; ESP – Exchangeable sodium percentage; SAR – Sodium absorption rate

Table 5. Comparison of the properties of the upper layer of soil in the pure *Moltikopsis* community and *Panicum turgidum* – *Moltkiopsis* community.

Comm	Profile	Depth	pH	EC	ESP	SAR	Cations				Anions				Texture			
							Ca^{2+} (me/L)	Mg^{2+} (me/L)	Na^{+} (me/L)	K^{+} (me/L)	N (%)	PO_4^{3-} (me/L)	Cl^{-} (me/L)	SO_4^{2-} (me/L)	Sand (%)	Silt (%)	Clay (%)	Texture class
MC	1	25 cm	7.20	0.37	-0.87	0.27	1.76	1.38	0.43	0.13	0.011	0.09	0.70	2.08	96	2	2	Sandy
MC	2	35 cm	7.00	0.21	-1.026	0.27	0.68	0.94	0.22	0.09	0.011	0.06	0.90	0.40	94	4	2	Sandy
PM	3	22 cm	7.10	0.27	-1.015	0.22	0.82	1.22	0.22	0.11	0.015	0.06	0.60	1.34	94	4	2	Sandy
PM	4	23 cm	7.20	0.30	-0.993	0.24	1.22	1.34	0.31	0.11	0.014	0.06	0.60	1.84	94	4	2	Sandy

Abbreviation: MC – Pure *Moltkiopsis* community; PM – *Panicum turgidum* – *Moltkiopsis* community.

the height of the anther and the stigma situated much above in short flowers indicates bee and insect pollination, whereas in the long flowers a high percentage of self-pollination might take place. Plants with purely long flowers are the general rule. Plants with purely short flowers, where the corolla tube is only slightly longer than the calyx lobes, are rare. Sometimes, in many plants where the flowers at the base of the inflorescence were all long, the length of flowers gradually decreased towards the tip, and approached the 'short flower' state, although dimorphy of the stamens was still persistent.

Johnston (1953) suspected the short flowers to be functionally male with a non-functional stigma, perhaps due to viral infection. Fertile nutlets have been collected from short flowered plants in the Central province of Saudi Arabia, although not from all plants with short flowers. In most short-flowered plants we observed that the stamens are highly reduced and apparently sterile (as opposed to functionally male as suspected by Johnston in 1953). Plants with short flowers may compensate for their loss of male fitness by reassigning possessions from male function, such as pollen production and pollinator attraction, to female function (seeds and fruits), thus increasing seed production (Charles et al., 2000). Floral dimorphism may permit females to assign more resources to seed production than hermaphrodites. Although females, in general, produce more seeds per flower than hermaphrodites, long-term studies are required to better elucidate fecundity differences in this species. Floral dimorphism is also linked with 2 other procedures of reproductive success, namely pollinator attraction and pollen receipt. Plants with 'female flowers' will have fewer pollinator visits and less pollen on their stigmas than hermaphrodites (Charles et al., 2000).

Physiologically *Moltkiopsis* is a C_3 plant (Ganders, 1979). *Moltkiopsis* inhabits 4 geographic regions in Saudi Arabia: (1) Southern wadis, (2) The Great Nafud, (3) The Dahna, and (4) The Southern Empty Quarter. It is very rare along the western coastal plains (the Tihama) and the mountain escarpments of the west. Chaudhary and Al-Jowaid (1999) document *Moltkiopsis* in 8 communities spread over the 4 regions. In addition, it occurs in the *Rhanterium epapposum* Oliv. – *Rhazya stricta* Decne – *Deverra tortuosa* (Desf.) DC. community in the central province. This community is under severe grazing pressure, particularly *Moltkiopsis*, which is highly grazed by camels. Shaltout et al. (1997) reported the species in the *Plantago boissieri* Hausskn. et Bomm. – *Savignya parviflora* (Delile) Webb. – *Panicum turgidum* Forssk. – *M. ciliata* community (subsequently referred to as the *P. turgidum* – *Moltkiopsis* comm.) in the lowlands of Eastern Saudi Arabia, which is probably a seral variation of the much extensive *Rhanterium epapposum* – *Rhazya stricta* – *Deverra tortuosa* community. In the Central province, the seral community forms smaller patches on the lower reaches of gentle slopes, where the soil moisture regime is slightly better. Very often *Moltkiopsis* forms pure communities especially along motorway embankments on reddish sand, which presumably has been deposited as a result of motorway works. Its distribution in Saudi Arabia is given in Figure 1.

Organic carbon in the soil, soil salinity, and the water holding capacity of the soil appear to have substantial influence on determining the density, abundance, and vegetation composition. Similar studies (Abd El-Ghani, 2000; Al-Fredan, 2008) in the same phytogeographical region showed that there is a correlation between soil moisture content, organic matter, and soil electrical conductivity (EC) and between soil moisture content and fine soil fraction. Except for some minor differences in the values for nitrogen and chlorine no significant differences are observed between the 2 communities. The higher species number and the large size of *Moltkiopsis* in the *P. turgidum* – *Moltkiopsis* community is presumably a matter of topography. This community always inhabits lower levels of hill slopes; therefore, the moisture regime could be slightly better than that in the upper reaches. Species richness and elevated community biomass may also be due to the slightly higher nitrogenous resources, another indication of a higher moisture regime (Table 5).

The present study is in agreement with the views reported by Forsskal (1775), Vahl (1790), and De Candolle (1846) that the variability in the leaves and the presence/absence of strigose hairs are not useful in differentiating the ecotypes. However, the long and short flowered forms of the species exhibit certain differences, especially in their floral bracts, calyx lobes, corolla, and stamens. The variation present in these 2 ecotypes should be studied in detail in order to find out whether these differences are sufficient to allow segregation into 2 separate taxa.

Acknowledgements

The authors are grateful to the Director, Natural Resources and Environmental Research Institute (NRERI) for encouragement and appreciation of the work being reported. The keepers of the herbaria of the King Abdulaziz City for Science and Technology (MUZ), King Saud University, Riyadh (KSU), National Herbarium (RIY), Royal Botanic Garden, Edinburgh (E), and Royal Botanic Gardens, Kew (K) kindly provided materials of the species for our study. Help received from Mr. I.C. Hedge in the Edinburgh herbarium (E), and Dr. B.L. Stannarad, Dr. D.J. Goyder, and Dr. Owlson in the Kew Herbarium is gratefully acknowledged. We are grateful to Dr. R.R. Mill (Edinburgh) for the very helpful discussions on heterostyly in Boraginaceae and some pertinent references. The support extended by Dr. K. Swaupanandan and Mr. Abdul Ghafoor (NRERI) is also thankfully acknowledged. The authors also wish to express their gratitude to the authorities of the Centre of Excellence in Biodiversity Research, King Saud University for moral support. The cooperation offered by Mr. Sheikh Karimulla, NRERI for carrying out the analysis of the soil samples and Dr. A.J. Davy, University of East Anglia, for extending his expertise in the interpretation of the results of soil analysis. Mrs. Jane Hutcheon and Miss Ruth Hourston, Royal Botanic Garden, Edinburgh, traced some very important literature for the study. We are also thankful to Mr. Mohammad Rafiquddin for the illustrations.

References

Abd El-Ghani MM (2000). Vegetation composition of Egyptian inland saltmarshes. *Bot Bull Acad Sin* 41: 305-314.

Ascherson P & Schweinfurth G (1887). *Illustration De La Flore D'Egypte*. p. 260. Cairo: Memoires de l'institut Egyptien.

Al-Fredan MA (2008). Sand dune and sabkha vetations of eastern Saudi Arabia. *Int J Bot* 4: 196-204.

Barrett SCH (ed.) (1992). *Evolution and Function of Heterostyly.* p. 290. Berlin: Springer-Verlag.

Bessey CE (1880). The supposed dimorphism of *Lithospermum longiflorum. Am Nat* 7: 417-419.

Black CA (1968). *Soil-Plant relationships*. John Wiley & Sons, New York.

Boissier E (1879), *Lithospermum* and *Moltkia*, *Flora Orientalis,* Vol. 5. pp. 216-222 Geneva: H. Georg.

Cecchi L & Selvi F (2009). Phylogenetic relationships of the monotypic genera *Halacsya* and *Paramoltkia* and the origins of serpentine adaptation in circum-mediterranean Lithospermeae (Boraginaceae): insights from ITS and *matK* DNA sequences. *Taxon* 58: 700-714.

Charles FW, Margaret AK & Allison D (2000). Floral dimorphism, pollination, and self-fertilization in gynodioecious *Geranium richardsonii* (Geraniaceae). *Am J Bot* 87: 661-669

Chaudhary SA (1985). Studies on *Heliotropium* in Saudi Arabia. *Arab Gulf J Sci Res* 3: 33-53

Chaudhary SA & Al-Jowaid AA (1999). *Vegetation of the Kingdom of Saudi Arabia.* Riyadh: Ministry of Agriculture and Water.

De Candolle AP (1846). *Prodromus systemaitis naturae vegetabilis,* Vol. 10. Paris: Masson.

FÖrsskal P (1775). *Flora Aegyptiaco-Arabica*. pp. 38-40. Copenhagen: Tabula Arabiae Felicis Geographic-Botanica.

Feinbrun-Dothan N (1978). *Flora Palaestina,* pt. 3. Text. p. 59. Jerusalem: Academy of Sciences and Humanities.

Ganders FR (1975a). Mating patterns in self-compatible distylous populations of *Amsinckia* (Boraginaceae). *Can J Bot* 53: 773-779.

Ganders FR (1975b). Heterostyly, homostyly and fecundity in *Amsinckia spectabilis* (Boraginaceae). *Madrono* 23: 56-62.

Ganders FR (1976). Pollen flow in distylous populations of *Amsinckia* (Boraginaceae). *Canad J Bot* 54: 2530-2535.

Ganders FR (1979). Heterostyly in *Lithospermum cobrense. Am J Bot* 66: 746-748.

Johnston IM (1953). Studies in the Boraginaceae. XXIV. A. Three genera segregated from *Lithospermum*. *J Arnold Arbor* 35: 1-16.

Linnaeus C (1753). *Species Plantarum, ed. 1*. Holmiae.

Mandaville JP (1990). *Flora of Eastern Saudi Arabia.* pp. 254-255. London: Kegan Paul International.

Poiret JLM (1811). *Lamarck's Encyclopedie Methodique, Suppl. 2*. Paris: Agasse.

Richards LA (1954). *Diagnosis and improvement of saline and alkaline soils.* pp. 102-104. Agric. Handbook 60. USDA, U.S. Government Printing Office, Washington D.C.

Riedl H (1967). Boraginaceae. pp. 1-281 in: Rechinger KH (ed.), *Flora Iranica*, vol. 48. Akademische Druck-u. Verlagsanstalt, Graz.

Shaltout KH, El-Halwany EF & El-Garawany MM (1997). Coastal lowland vegetation of eastern Saudi Arabia. *Biodi and Cons* 6: 1027-1040.

Vahl M (1790). *Symbolae Botanicae.* Vol. 1. Hauniae: Moller & Sons.

Young HJ (2002). Diurnal and nocturnal pollination of *Silene alba* (Caryophyllaceae) *Am J Bot* 89: 433-440

Appendix. Voucher specimens.

SAUDI ARABIA: Khurais, Abdulaziz, *A.Jalil & Sait s.n.* (KSU); Riyadh, *A.Al-Haji s.n.* (KSU); Abha, 15.iv.1980, fl. *A.Sheikh s.n.* (KSU); iv.1983, fl. *Ahmed Ali* 14 (KSU); Kuraish, fl. *A.N.Idris s.n.* (KSU); Near Jabal, msl, 30.iii.1985, fl. *A.M.Alder* (E); Raudhat Khuraim, 11.iii.1996, fl. *Al-Farhan & J. Thomas s.n.* (KSU 10196); south of Asir, 18.xii.1393, AH. fl. *Al-Henthi s.n.* (KSU); 1 km from exit to Khurais, c. 250 km before Dammam on Riyadh-Dammam road, 17.x.1994, *Al-Turki & A.Ghafoor* 141 (MUZ); Exit 8, near Dagla, c. 100 km from Riyadh on road to Qassim, 6.iv.1995, *Al-Turki & A.Ghafoor* 728 (MUZ); Exit 8, near Dagla, c. 100 km from Riyadh on road to Qassim, 7.iv.1995, *Al-Turki & Ghafoor* 756 (MUZ); 90 km on Riyadh-Dammam road, red sand, 6.iii.1999, *Al-Turki, Swarupanandan & Mehmood*, 3883 (MUZ); North Midian, ix.1928?, *Barton s.n.* (K); Khurais, Nafud, 8.iv.1980, *S.Chaudhary* 535 (E, ex RIY); Between Riyadh al-Khabra and Qassim, 15.ii.1980, *I.S.Collenette* 1869 (E, K); Jabal Qutn, 15 km NE of Uqlat As-Suqur off the Medina-Qassim road, 3000 ft, 18.iv.1981, *I.S.Collenette* 2433 (E); Dawadimi Camp, 24°33′N, 44°13′E, 2900 ft, 3.iii.1983, *I.S.Collenette* JS 4073 (E, K); Wadi Huraymla NW, Ar-Riyadh, 600 m, Acacien Bestande, 26.iii.1981, *W.Frey, H.Kurschner & A.M.Migahid* 6351 (KSU); Riyadh, 1983, *Hassan-Kabban s.n.* (KSU); 15 km N of Taif, 1720 m, military base, 12.iii.1978, *Jack Humbles* 10114 (E); Al-Jawb, 23°06′N, 49°58′E, 25.iii.1982, J.P. Mandaville Jr 7669 (E); Rub Al-Khali, 18°N, 47°E, 17.ii.1952, 2200 ft. upper fls. shorter, *J.Popov & Guilliland* 4197 (K); Al-Kharj, 1983, *M.Ali-Amni s.n.* (KSU); Al-Dahna, 23.iii.1973, *Migahid s.n.* (KSU); *W.Al-Hafi,* 23.iii.1973, *Migahid s.n.* (KSU); Riyadh-Qassim Road, ii.1968, *Migahid s.n.* (KSU); Eastern Region, 17.iii.1971, *Migahid & Hammouda s.n.* (KSU); Khurais Road, 1.iv.1976, *Migahid & M.S.Awad* 183-A (KSU); Wadi Huraymla, 4.iii.1973, *Migahid & M.S.Awad* 270-M (KSU); Huraymla Valley, 4.iii.1973, *Migahid & M.S.Awad* 323-M (KSU); Al-Hama Thaiyat, 20.ii.1981, *Migahid & Shaikh* 15 (KSU); Al-Hafji, 25.ii.1981, *Migahid & Sheikh s.n.* (KSU); Dammam-Safaniya Road, 24.ii.1981, *Migahid & Shaikh s.n.* (KSU); 17 km NW of Al-Hafika, 18.iii.1982, *Migahid & Sheikh s.n.* (KSU); Salbukh, 1.iv.1976, *Migahid & Sheikh*, 331-A (KSU); Shakra, 5.ii.1388 H., *M.Hhudaie s.n.* (KSU); Wadi Horaimila, 13.v.1975, *M.S.S.Aud* 250-E (KSU); Ad-Dahna, 2.iv.1981, *S.al-Din M.Nur s.n.* (KSU); 17 km NW of Al-Hakika, 18.iii.1982, *Sheikh & Migahid s.n.* (KSU).