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# The *Cerastium scaposum* group (*Caryophyllaceae*): three annual taxa endemic to Crete (Greece), two of them new

# Abstract

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*Cerastium deschatresii* and *C. scaposum* subsp. *peninsularum* are described as two closely related taxa new to science. *C. scaposum* (subsp. *scaposum*) was described from the White Mountains (Lefka Ori) and was long believed to be restricted to the western segment of Crete, but it has been gathered once, in 1942, at the island's opposite end. It is a large-flowered, obviously outbreeding, locally abundant plant. *C. scaposum* subsp. *peninsularum* has smaller flowers, reduced petal size, and is a (perhaps facultative) selfer; it is known from several gatherings in the northwestern coastlands of Crete. *C. deschatresii* is more widespread, growing in scattered populations from west to east central Crete; it has minute, apetalous flowers, a distinctive capsule shape, and is a cleistogamous selfer.

## Introduction

*Cerastium scaposum* was discovered in 1845 by the French geologist Victor Raulin in the White Mountains (Lefka Ori) of western Crete, between Askifou and Aradhena in the Sfakia district. In the following year Theodor von Heldreich collected it nearby above Askifou, at 900-1200 m in altitude, and the new species was based on his material (Boissier 1849: 104). Raulin (1869: t. 10) provided a beautiful illustration with accurate details. The species has remained uncontroversial and unchallenged ever since.

Change came about in two ways. First, the distributional area of *Cerastium scaposum*, long delimited to comprise the White Mountains and their immediate surroundings, was greatly extended by Rechinger's find of indistinguishable plants near the top of Mt Afendis Kavousi in easternmost Crete (Rechinger 1944: 70). Recent publications have mapped the area to include the Psiloritis massif in central Crete (Turland & al. 1993: 219; Strid in Phitos & al. 1997: map 396). Chilton & Turland (1997, maps: 4) added further localities, and Jahn & Schönfelder (1995: 80) gave the species as present in all four of the island's provinces or nomoi. Many of these additional records we are going to challenge here.

The second uncertainty arose when, in recent years, dwarf plants were repeatedly collected

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which, while obviously akin to *Cerastium scaposum*, were hard to accommodate within the known range of variation of that species. Such a population of undersized plants was sampled in 1961 on the Akrotiri Peninsula near Hania by Greuter, who prudently preferred to leave the plants, which lack mature fruits, as an unnamed variant in *C. scaposum*. The French botanist Robert Deschatres, who collected equally dwarf plants in 1992 near the village Kambos on Crete's western edge, was unwilling to leave it at that. He raised in vitro progeny at his home at Bellerive-sur-Allier and sent his observations and photographs to Greuter. His prompting, together with new collections of similar specimens made in the subsequent years by Böhling and Jahn during their ecological field work, triggered the studies whose conclusions are presented here.

## Material and methods

The specimens studied are kept in B, M, REG, UPA, and W (see Holmgren & al. 1990 for explanation of these standard abbreviations) as well as in the personal herbaria of Böhling, Egli, Greuter, Jahn, Matthäs, Schönfelder, Strasser, and Zaffran.

Specimen enumeration follows a west to east and north to south sequence. Label texts have been translated and standardised, except for the purpose of type designation where portions of the original label text are added between quotation marks; transcription of Greek place names follows the phonetic system set out in Greuter (1977: 27). The distribution map was produced with the aid of the DMAP software (Morton 2002).

## Taxonomy

The dwarf plants mentioned before as being related to *Cerastium scaposum* eventually turned out to belong not to one as yet undescribed taxon, as we had originally thought, but to two. Along with their diagnostic descriptions we prepared one for *Cerastium scaposum* s.str. for comparison, also tabulating the main differences between the three taxa (Table 1) and mapping their distributions (Fig. 1).

*Cerastium scaposum* Boiss. & Heldr. (Boissier 1849: 104) subsp. *scaposum* – Illustrations: Fig. 2a; Raulin (1869: t. 10), Alibertis (1994: 62), Jahn & Schönfelder (1995: photo 6).

*Planta humilis*, floribus inclusis 5-15 cm alta; *pedicelli* fructiferi (15-)25-40(-70) mm longi, dense retrorse pilosi; *sepala* 4.5-6 mm longa; *petala* 5, sepalis tertia parte usque ad subduplo longiora, ambitu obovato-cuneata, lamina antice obcordato-expansa patula ad medium bifida; *stamina* 10; *ovarium* 5-merum, *stylis* 1.5-2.5 mm longis coronatum; *capsula* immatura ovoidea, operculo convexo cupuliformi vel late conico diametro capsulae ipsius minore clausa, matura 6.5-7.5(-9) mm longa; capsulae dentes 10, anguste elongato-triangulares apice truncati, 1-1.3 mm longi, latitudine subquadruplo longiores, recti, margine revoluti; *semina* diametro 0.7-0.8 mm, dorso tuberculata, tuberculis rotundatis in centro minute atro-mamillatis.

#### Specimens seen

NOMOS HANIA, EPARHIA SELINOS: Ajia Irini gorge, limestone rock, 35°19'10"N, 23°50'40"E, 460-470 m, 23.10.1997, *Böhling 6917* (B); Mt Psilafi, N slope, 35°18'N, 23°53'E, 1200 m, 26.4.1942, *Rechinger 12379* (W); Psilafi, doline No. 100, 35°19'15"N 23°53'E, 1435 m, 3.5.1985, *Egli* (herb. Egli). — EP. KIDHONIA: Ascent from Lakki to the Omalos plain, 35°22'N, 23°54'E, 900 m, 25.4.1942, *Rechinger 12314* (W); pass N of Omalos, 35°21'N, 23°54'E, 1090 m, 22.4.1988, *Seidl* (REG); limestone rocks W of Lakki, 35°22'30"N, 23°54'30"E, 13.4.1971, *Hansen 453* (herb. Greuter); between Xiloskala and the Linoseli spring, 35°18'30"N, 23°54'30"E, 1370-1600 m, 11.5.1983, *Risse 788* (B); Omalos plain, 35°20'N, 23°54'E, 1100 m,

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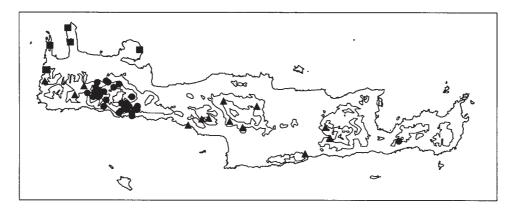


Fig. 1. The total known distribution of *Cerastium scaposum* subsp. *scaposum* (circles,  $\bullet$ ), *C. scaposum* subsp. *peninsularum* (squares,  $\blacksquare$ ) and *C. deschatresii* (triangles,  $\blacktriangle$ ), based on herbarium specimens seen by us.

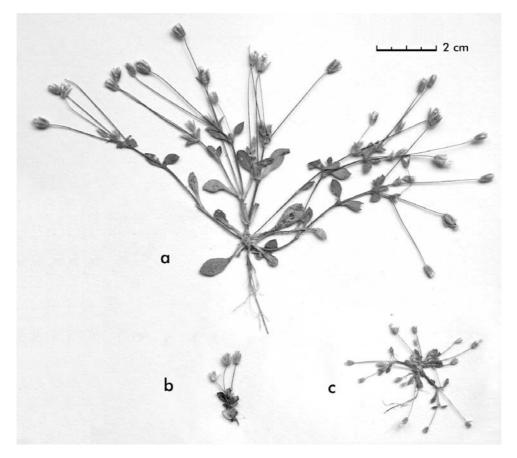


Fig. 2. Individual plants of a: Cerastium scaposum subsp. scaposum (Kallerji, Böhling 5899); b: C. scaposum subsp. peninsularum (Sarakinovigla, 24.4.1994, Jahn); c: C. deschatresii (Hondradha, 25.4.1985, Egli). – Photographs by I. Haas.

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Table 1. A comparison of morphological features diagnostic of the three taxa of the *Cerastium scaposum* group.

	C. scaposum		C. deschatresii
Features	subsp. scaposum	subsp. peninsularum	
Fruiting pedicel length	(15-)25-40(-70) mm	12-20(-30) mm	8-15(-20) mm
Sepal length	4.5-6 mm	3-4 mm	2-2.5 mm
Petal number	5	(4-)5	$0 (or 2-4 rudiments)^1$
shape	obovate-cuneate	elliptic-spathulate	_
length rel. to sepals	1.3-2	0.7-1.1	_
Stamen number	10	(8-)10	1-3
Carpel number	5	(4-)5	3-4
Shape of maturing ovary	ovoid	ovoid	cylindrical
Capsule lid shape	convex	convex	flat
relative size	< capsule diam.	< capsule diam.	= capsule diam.
Capsule teeth length	1-1.3 mm	0.8-1 mm	0.2-0.3 mm
shape	narrowly triangular	elongate-triangular	square
length : width ratio	c. 4	c. 3	$\leq 1$
Style length	1.5-2.5 mm	1.0-1.3 mm	0.5-0.7 mm
Dorsal seed tubercles	rounded, mamillate	conical, not mamillate	rounded, not mamillate

<sup>1</sup> It is not clear whether the 2-4 tiny transparent scales observed between the stamens, in *Cerastium deschatresii*, are reduced petals or rather staminodes. As the petals in *Caryophyllaceae* are staminodial in nature (Leins & al. 2001), this makes no real difference anyway.

17.4.1987, Strasser 56 (herb. Strasser); Omalos plain, SE edge, 35°19'N, 23°55'E, 1020 m, 15.4.1987, Schönfelder 87-62 (herb. Schönfelder); Omalos plain, Xiloskala, 35°18'N, 23°55'E, 1000 m, 5.6.1966, Zaffran 646 (herb. Zaffran); same place, 1200 m, Zaffran 632, 650 (herb. Zaffran); same place, 1200 m, 7.5.1982, Montmollin (UPA); Xiloskala, onset of the hiking path to the Kallerji refuge, 35°18'28"N, 23°55'07"E, 1260 m, 5.6.1993, Jahn (herb. Jahn); Xiloskala, upper entrance to the Samaria gorge, above the car park area, 35°18'30N, 23°55'30E, 1200-1220 m, 10.5.1984, Matthäs 1371 (herb. Matthäs); between Theriso and Zourba, 35°23'N, 23°58'E, 30.3.1980, Kalheber 80-480 (M); Xerakokefala, doline No. 137, 35°22'35"N 23°58'45"E, 1025 m, 5.4.1985, Egli (herb. Egli); S of Kambi, gorge from the Volikas refuge down to the Kriariko, 35°22'N, 24°03'E, 1380-1800 m, 6.6.1982, Risse 505 & 513 (B ,UPA); Pahi Ammi doline near the Volikas refuge S of Kambi, 35°22'N 24°03'E, 1600 m, 5.6.1982, Risse 490 (B, UPA). — EP. SFAKIA: Mt Volakias, 30.5.1884, 35°20'N, 23°55'E, 22.6.1884, Reverchon 225 (M); between the car park area at the entrance to the Samaria gorge (1300 m) and the Kallerji refuge (1677 m), 35°19'N, 23°55'E, 8.5.1996, *Bässler* (B); Xiloskala pass, 35°18'N, 23°55'E, 1220 m, 16.4.1962, Greuter 4158 (G, HUJ, LD, W, Z, herb. Greuter); Samaria gorge, 35°18'N, 23°55'E, 1300 m, 10.5.1975, Faber KR 44 (B); Kallerji, S-facing schistose slope, 35°19'39"N, 23°57'05"E, 1475 m, 20.5.1997, Böhling 5899 (B); near Samaria, 35°15'N, 23°57'E, 12.5.1963, *Phitos* 749 (M); Samaria valley, along the mule track to the Xiloskala pass, 35°17'N, 23°58'E, 300-1200 m, 15.4.1961, Greuter 3502 (G, LD, W, Z, herb. Greuter); Mt Mavri, 35°21'N, 24°01'E, 1760 m, 18.7.64, Zaffran 649 (herb. Zaffran); Aradhena gorge, calcareous scree, 35°13'N, 24°03'E, 350 m, 8.8.1998, Böhling 8759 (B); same place, 22.4.1996, Diewald (REG); Aradhena gorge between the old footpath and the bridge, 35°13'27"N, 24°03'42"E, 480-620 m, 19.3.1993, Bergmeier & Matthäs 2839 (B); Lakki, 35°16'N, 24°04'E, 5.7.1883 and 1.6.1884, Reverchon (M); S slopes of Mt Mavri, 35°15'N, 24°05'E, 1475 m, 22.4.1993, Jahn (herb. Jahn); Anopoli, doline No. 86, 35°15'30"N 24°05'55"E, 1395 m, 22.6.1985, Egli (herb. Egli); above

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Anopoli, 35°16'N, 24°06'E, 1650 m, 1.5.1986, Tiniakou 1442 (UPA); Anopoli, doline No. 162, 35°14'30"N 24°06'20"E, 1005 m, 27.5.1986, Egli (herb. Egli); along road N of Anopoli, W of Timios Stavros, 35°14'N, 24°06'E, 1160 m, 16.5.1998, Hörandl & Hadaček 8603 (W); above Anopoli, along the road to the Lefka Ori 8.2 km beyond its junction with the Aradhena-Anopoli road, 35°14'45"N, 24°06'25"E, 1080-1100 m, 22.5.1993, Bergmeier & Matthäs 3216 (B); road from Anopoli to the Lefka Ori, 4th fence, 35°15'N, 24°07'E, 1100 m, 28.3.1994, Jahn (B, herb. Jahn); end of the track N of the upper Niato plain, 35°18'N, 24°08'E, 1360 m, 15.5.1992, Jahn (herb. Jahn); Kavi gorge NW of Hora Sfakion, 35°13'N, 24°08'E, 100-200 m, 27.4.1960, Greuter 2778 (Z, herb. Greuter); Hora Sfakion, 35°12'N, 24°08'E, 18.4.1904, Dörfler 284 (M); near Sfakia, Anopoli, Aradhena, etc., 4.1904, Dörfler 284 (W) and in Herb. Norm. 4716 (B, W); road N of Hora Sfakion, 35°14'N, 24°09'E, 800 m, 21.4.1984, Hiepko 2753 (B); road Vrisses-Hora Sfakion, 100 m S of the signpost noting the upper end of the Imbros gorge, 35°14'40"N, 24°09'50"E, 760 m, 1.6.1984, Matthäs 1651 (herb. Matthäs); 500 m S of Imbros, slope at the entrance to the Imbros gorge, 35°15'02"N, 24°10'10"E, 720 m, 12.5.1992, Jahn (herb. Jahn); Imbros gorge above Hora Sfakion, 35°14'N, 24°10'E, 650 m, 5.4.1989, Strasser 29 (herb. Strasser).

NOMOS LASITHI, EP. IERAPETRA: Afendis Kavousi, 35°04'N, 25°52'E, 1400 m, 21.5.1942, Rechinger 13239 (W).

*Cerastium scaposum* subsp. *peninsularum* Greuter, N. Böhling & R. Jahn, **subsp. nova** – Holotype: [Crete, Nomos Hania, Eparhia Kidhonia], "H.-I. Akrotiri, NW-Grat des Hügels Sklocha", 430 m, strictly local, covering like lawn a soil pocket in the limestone rock, 17.3.1961, *Greuter 3273* (herb. Greuter; isotype: Z). – Illustration: Fig. 2b.

*Planta humilis*, floribus inclusis 1-4(-12) cm alta; *pedicelli* fructiferi 12-20(-30) mm longi, dense retrorse pilosi; *sepala* 3-4 mm longa; *petala* (4-)5, sepalis subaequilonga, ambitu elliptico-spathulata, lamina antice vix expansa erecta breviter biloba; *stamina* (8-)10; *ovarium* (4-)5-merum, *stylis* 1-1.3 mm longis coronatum; *capsula* immatura ovoidea, operculo convexo cupuliformi vel late conico diametro capsulae minore clausa, matura 4-5 mm longa; capsulae dentes (8-)10 anguste triangulares apice truncati, 0.8-1 mm longi latitudine subtriplo longiores, recti, margine revoluti; *semina* diametro 0.6-0.7 mm, dorso tuberculata, tuberculis conicis mamilla centrali carentibus.

#### Additional specimens seen

Nomos HANIA, EPARHIA KISSAMOS: Coastal plain at the N end of Sfinari bay, 100 m SE of Panajia chapel, 35°26'30"N, 23°34'20"E, 50 m, 27.4.1994, *Jahn* (herb. Jahn); W slope of Mt Profítis Ilias (Manna) above the N end of Sfinari bay, 220 m, 35°26'40"N, 23°34'50"E, 27.4.1994, *Jahn* (herb. Jahn); Gramvousa peninsula, between Ajia Irini and Valos, on calcareous scree along track, 35°34'22"N, 23°36'01"E, 190 m, 11.3.1998, *Böhling 7027* (B?, specimen missing; colour slides!); Rodhopou peninsula, NE slope of Mt Sarakinovigla, 600 m, 35°35'20"N, 23°44'00"E, 24.4.1994, *Jahn* (herb. Jahn); Titiron [Rodhopou] peninsula, Akrofarango gorge at Cape Spatha, 35°40'N, 23°43'E, 22.4.1942, *Rechinger 12255* (W).

*Cerastium deschatresii* Greuter, N. Böhling & R. Jahn, **sp. nova** – Holotype: [Crete, Nomos Iraklio, Eparhia Pedhias], "Piste Miliarades-Amalos-Hochebene, Apliki-NE-Hang 2 km SEE Miliarades", 35°04'N, 25°24'E, 860 m, 8.4.1994, *Jahn* (B; isotype: herb. Jahn). – Illustration: Fig. 2c.

*Planta nana*, floribus inclusis 1-2 cm fructifera interdum ad 4 cm alta; *pedicelli* fructiferi 8-15(-20) mm longi, modice retrorse pilosi; *sepala* 2-2.5 mm longa; *petala* nulla, *stamina* 1-3 (insuper squamulae 2-4 diaphanae ad summum 0.4 mm longae adsunt); *ovarium* 3-4-merum, *stylis* 0.5-0.7 mm longis coronatum; *capsula* jam immatura truncato-cylindrica, operculo plano

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diametrum capsulae aequante clausa, matura 2.5-4 mm longa; capsulae dentes initio nulli serius 6-8 breves quadrati, 0.2-0.3 mm longi ac lati, plani scilicet marginibus haud revolutis sed apice demum nonnusquam extus curvato; *semina* diametro 0.4-0.6 mm, dorso inconspicue rotundato-tuberculata, tuberculis haud mamilliferis.

Species domino Robert Deschatres qui eam inter primos collegit primusque agnovit dicata.

#### Additional specimens seen

Nomos HANIA, EPARHIA KISSAMOS: Kambos area,  $35^{\circ}23'N$ ,  $23^{\circ}34'E$ , 5.5.1992, *Deschatres* (herb. Deschatres); Kambos-Keramoti, schistose rock,  $35^{\circ}23'01''N$ ,  $23^{\circ}33'56''E$ , 370-380 m, 29.6.1999, *Böhling 10291* (B). — EP. SELINOS: W slope of Mt Pirgos (Angadoseli) above Vamvakades,  $35^{\circ}18'40''N$ ,  $23^{\circ}45'40''E$ , 940 m, 2.6.1993, *Jahn* (herb. Jahn); road Prases-Ajia Irini, W of the turn-off toward the Omalos plain,  $35^{\circ}21'30''N$ ,  $23^{\circ}49'20''E$ , 850 m, 23.3.1994, *Jahn* (herb. Jahn). NoMos RETHIMNO, EP. AJIOS VASILIOS: S slope of the Korifi hill 500 m W of the Ajios Ioannis chapel, 2.5 km SW of Kerames,  $35^{\circ}09'10''N$ ,  $24^{\circ}29'40''E$ , 180 m, 18.4.1994, *Jahn* (herb. Jahn). — EP. AMARI: Western Kedhros, NNW-exposed ruderal phrygana,  $35^{\circ}11'N$ ,  $24^{\circ}35'E$ , 1120 m, 12.5.1997, *Böhling* 5651 (B); Kedhros, doline No. 1,  $35^{\circ}16'45''N$ ,  $24^{\circ}37'45''E$ , 1215 m, 27.4. 1985, *Egli* (herb. Egli); Aravanes, doline No. 141,  $35^{\circ}16'45''N$ ,  $24^{\circ}43'35''E$ , 1040 m, 8.4.1985, *Egli* (herb. Egli); Hondradha, doline No. 148,  $35^{\circ}10'15''N$ ,  $24^{\circ}45'55''E$ , 1040 m, 25.4.1985, *Egli* (herb. Egli); same place, 1.11.1985, *Egli* (herb. Egli).

NOMOS IRAKLIO, EP. KENOURJIO: N slope of Mt Angavanias 1.5 km S of Vorizia,  $35^{\circ}08'20''N$ ,  $24^{\circ}51'00''E$ , 710 m, 16.6.1994, *Jahn* (herb. Jahn). — EP. MALEVIZI: Voskero, doline No. 160,  $35^{\circ}15'05''N$ ,  $24^{\circ}56'40''E$ , 1010 m, 12.6.1986, *Egli* (herb. Egli). — EP. MONOFATSI: Track Mesohorio-Tsoutsouros near the turn-off to Maridhaki,  $34^{\circ}59'50''N$ ,  $25^{\circ}15'30''E$ , 560 m, 12.4. 1993, *Jahn* (herb. Jahn). — EP. PEDIAS: Track Jeraki-Langadha, at the ascent 4 km E of Jeraki,  $35^{\circ}08'20''N$ ,  $25^{\circ}23'20''E$ , 870 m, 14.3.1994, *Jahn* (herb. Jahn); track from Miliaradhes to the Amalos plain, slope Varna NE of Mt Apliki 3 km ESE of Miliaradhes,  $35^{\circ}04'50''N$ ,  $25^{\circ}25'20''E$ , 920 m, 8.4.1994, *Jahn* (herb. Jahn).

#### Relationships

The plants discussed here belong in a fairly clear-cut East Mediterranean species assemblage that was first formally recognised by Lonsing (1939: 145) as *Cerastium* ser. *Brachiata* Lonsing, mainly on the basis of its consistently eglandular indumentum of long, patent or reflexed hairs. Apart from *C. scaposum* and its Cretan allies it comprises *C. pedunculare* Bory & Chaub. (endemic to the southern and western Peloponnese), the species group centred on *C. illyricum* Ard. (extending from the Peloponnese to Aetolo-Akarnania and the Ionian Islands), and the more widespread, autogamous *C. comatum* Desv. (ranging from Greece to Lebanon and Libya, with an isolated occurrence in Corsica). This classification within the assemblage is the one adopted in Greuter & al. (1984) and contrasts with the unnaturally synthetic views of Sell & Whitehead (1964), who treated the *C. illyricum* group plus the very distinct *C. comatum* as a single species with several subspecies.

Lonsing (1939) recognised two subgroups within his series: on the one hand *Cerastium* scaposum and *C. pedunculare*, characterised by short calyx hairs, a cylindrical capsule and the presence of a central mamilla on the seed tubercles; and on the other hand the remaining species which have long calyx hairs, a tapering capsule, and emamillate seed tubercles. Of these distinctions the hair and perhaps the capsule characters hold true (although capsule shape variation is complex), but not the third criterion: *C. deschatresii* lacks mamillae on the seed tubercles. Even so, we accept the idea that *C. pedunculare* is the closest relative of the *C. scaposum* group. It is a robust, relatively tall plant with larger flowers and remarkably long styles, easily distinguished by these and other features from its Cretan kin. The only chromosome number so far known in the group is that of *Cerastium scaposum* subsp. scaposum, which is 2n = 36 (Montmollin 1982;

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Franzén & Gustavsson 1983). This is the most frequent diploid number in the genus. The related *C. comatum*, however, has consistently 2n = 34 chromosomes (Montmollin 1982, 1986; Runemark 1996).

The three Cretan taxa treated here form a reduction series, starting from the largest, Cerastium scaposum subsp. scaposum with its showy white, consistently pentamerous flowers. This is an attractive plant - not only for humans but certainly also for pollinators - and even though no studies of floral biology have so far been conducted there can be no doubt that it is normally outbreeding. Nevertheless, selfing may frequently occur, as the elongating styles bring the receptive stigmas into close vicinity of the dehisced anthers. In contrast, C. deschatresii gives insects neither incentive nor indeed opportunity to serve as pollen vectors. Its diminutive flowers are characterised by aborted petals, much reduced stamen number and size, and gynoecial oligomery. The flowers open only to expose the tip of the maturing capsule. The few pollen grains produced in the 1-3 diminutive anthers are deposited directly on the stigmas, borne on styles that do not conspicuously elongate: a typical cleistogamy syndrome. The third member of the trio, Cerastium scaposum subsp. peninsularum, stands between the other two. Its petals are reduced in size but still develop regularly; the inner floral whorls show incipient oligomery, but fully pentamerous flowers still prevail; the styles elongate somewhat, but almost hesitantly so; and the ovary in freshly opened flowers is already fertilised and on its way to maturation. Even though there may be exceptions, selfing in this taxon appears to be the rule.

A comment on capsule shape is necessary. As is the rule in Cerastium, the capsules in our group open by a lid crowned by the styles. In both subspecies of C. scaposum the lid is smaller than capsule diameter, dome-shaped or broadly conical, crowning the maturing ovary, which has an ovoid shape. The capsule teeth, already clearly visible in immature capsules, are narrowly triangular, with a truncate tip where they meet the lid margin. At dehiscence they straighten up, falling into line with the lower portions of the capsule wall to form an overall cylindrical shape. Simultaneously their margins curve outward so that the teeth, and soon the corresponding lower sectors of the capsule wall, become channelled like a classical Greek temple column. The capsule of C. deschatresii is quite different. Already when immature it is cylindrical in shape, with a sharply truncate apex entirely formed by the wide and flat lid. When the lid is shed, which happens promptly, the capsule has a plain apical pore. The pre-formed teeth are short and split apart hesitantly. They are square in shape and remain flat but may bend outward slightly by their tip, and the capsule as a whole remains unchannelled. Incidentally, the long tapering capsules of C. comatum have the form of a truncate cone, with a similarly flat and wide apical lid, and they too have flat teeth that barely separate. The analogy between those two species, in capsule features and breeding habit alike, is striking.

By the characteristics of the capsule lid and mouth *Cerastium deschatresii* stands clearly apart from the two other taxa, which can be distinguished by quantitative characters only. Although there is no overlap in measurements nor in distributional range among the two subspecies of *C. scaposum*, this rank is appropriate in their case, whereas *C. deschatresii* is a fairly clear-cut separate species.

# Chorology

Bearing in mind that, to an extent, the chorological picture might change due to further collecting, one may recognise in it a complex vicarious pattern. *Cerastium scaposum* subsp. *scaposum* has a coherent core area where it is frequent, centred on the White Mountains of western Crete and hardly if at all spreading beyond that range, just reaching Mt Krioneritis towards the east (Chilton & Turland 1997); and in addition a single isolated, local occurrence on Mt Afendis Kavousi in eastern Crete. That pattern is reminiscent of the Cretan endemic *Verbascum spinosum* L. – a species that is frequently associated with *C. scaposum* – and of the non-endemic *Helianthemum hymettium* Boiss. & Heldr., both widespread in the White Mountains and with a single known locality in eastern Crete but apparently lacking in between – even though Rackham & Moody's (1996: 56) distribution map for *V. spinosum* includes a single unexplained, isolated dot near Kali Limenes in central Crete.

The alleged occurrence of *Cerastium scaposum* in the central part of the island, mentioned in the introduction, is not based on solid evidence so far. In one of his phytosociological tables, Zaffran (1982, 1990: table 26, column 3) lists *C. scaposum* as occurring in the Psiloritis range on Mt Timios Stavros – the basis for a corresponding dot in the distribution maps in Turland & al. (1993) and Chilton & Turland (1997) (N. Turland, pers. comm.). As no such specimen is mentioned in the floristic part of Zaffran's (1976, 1990) publication, nor did Greuter find one in Zaffran's herbarium when he revised it, the record from Timios Stavros is most likely based on some kind of error. Egli (1993) mentions *C. scaposum* from Mt Kedhros and various places in the Psiloritis massif, but in so far as they are substantiated by specimens (which is the case for four out of six), all these records refer to *C. deschatresii*.

A report of *Cerastium scaposum* from the northern coastland of western Crete, by Rechinger (1944: 70), concerns subsp. *peninsularum*, and the same is likely true for one by Strasser (1989: 15-16) from near Gouverneto on the Akrotiri Peninsula, for which no voucher specimen or photographic documentation exists (W. Strasser, pers. comm.). This subspecies is still known from rather few gatherings, all from the limestone blocks forming the large peninsulas of the Cretan Northwest and their southerly extension along the western coast, an area where subsp. *scaposum* has not so far been collected.

The area of *Cerastium deschatresii* appears to be cut into two halves. In its western portion it borders that of *C. scaposum*, with subsp. *scaposum* to the east and subsp. *peninsularum* to the north. The eastern half fills the gap left by *C. scaposum* between its main occurrence in the White Mountains and its isolated easterly outpost. The scattered distribution of *C. deschatresii*, visible on the map, may in part be due to the fact that the plants are diminutive and easily overlooked; in the future, *C. deschatresii* may well turn up in other areas as well.

# Ecology

All three taxa grow in open, slightly disturbed habitats with moderately nutrient-rich soil. In his study of Cretan doline ecology, Egli (1993) found both species on various soil types on limestone bedrock (to which dolines are by and large confined), in conditions ranging from dry (rendzina) through intermediate (cambisols) to moist (luvisols) – but not on the heavy, waterlogged planisols.

*Cerastium scaposum* shows a clear preference for hard limestone of the various geological series, only exceptionally, in the close neighbourhood of limestone areas, is it found on phyllite-quartzite or on gypsum-holding substrata. It occurs in various vegetation types such as scree communities, mountain phrygana and open *Cupressus* woodland. The altitudinal range of *C. scaposum* subsp. *scaposum* is (200-)500-1600(-1800) m, that of *C. scaposum* subsp. *penin-sularum* is more restricted (50-600 m).

Based on the available evidence, it would seem that around the White Mountains, where their areas meet to within 1 km or less (e.g. along the road west of the Omalos plain), *Cerastium deschatresii* and *C. scaposum* behave as ecological vicariants, the former being confined to phyllite-quarzite and the latter to limestone bedrock. In a general way, however, *C. deschatresii* is quite versatile in its substrate preferences, having been found on schists (flysch and of phyllite-quarzite) as well as on hard limestone. It grows in, but is not restricted to, phrygana communities of varying species composition, and has also been found in sun-exposed to partially shaded  $\pm$  ruderal situations, at altitudes between 200 and 1300 m. More than on soil acidity, it appears to depend on a relatively constant water supply during the wet season, a substrate with high potential for water retention, and/or a northerly exposed situation (see also Böhling 2000: 246) – features that are shared by most of its localities. The habitats of *C. deschatresii* are often subjected to grazing, which in a general way tends to favour the growth of small annuals as it opens up the vegetation cover and eliminates larger competitors (Bergmeier 1996).

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