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Dedicated to my Friend Univ.-Doz. Dr. Franz SPETA (Linz) on the Occasion
of his 70th Birthday

[For a biography see Verh. zool.-bot. Ges. Österr. 148-149: 397–417 (2012)]

Notes on Morphology and Karyology of *Onosma fruticosa* (Boraginaceae-Lithospermeae) from Cyprus

By

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With 25 Figures

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Summary

TEPPNER H. 2012. Notes on morphology and karyology of *Onosma fruticosa* (*Boraginaceae-Lithospermeae*) from Cyprus. – *Phyton* (Horn, Austria) 52 (2): 301–320, with 25 figures.

Onosma fruticosa is an *Onosma* species with very peculiar, shrubby growth habit and – contrary to the literature – with an asterotrichous indumentum. The variability of the latter is demonstrated. The chromosome number of $2n = 20$ is interpreted as a derived one originating from the tetraploid level. The transition from $2n = 14$ to $2n = 20$ as well as between the haplotrichous and asterotrichous condition of the indumentum occurred within a group of species traditionally united as group *Suffruticosa*. Most probably, *O. fruticosa* can be regarded as a palaeoendemic of Cyprus.

Zusammenfassung

TEPPNER H. 2012. Notes on morphology and karyology of *Onosma fruticosa* (*Boraginaceae-Lithospermeae*) from Cyprus. [Notizen zu Morphologie und Karyologie von *Onosma fruticosa* (*Boraginaceae-Lithospermeae*) von Cypern]. – *Phyton* (Horn, Austria) 52(2): 301–320, mit 25 Abbildungen.

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Onosma fruticosum ist eine *Onosma*-Art mit eigenartiger, strauchiger Wuchsform und – entgegen den Angaben in der Literatur – mit einem asterotrichen Indumentum. Dessen Variabilität wird dargestellt. Die Chromosomenzahl von $2n = 20$ wird als abgeleitet, vom tetraploiden Niveau hergeleitet, interpretiert. Der Übergang von $2n = 14$ zu $2n = 20$ und zwischen haplotrichem und asterotrichem Indumentum erfolgte offensichtlich innerhalb einer Gruppe von Arten, die üblicherweise als Gruppe *Suffruticosum* bezeichnet wird. *O. fruticosum* kann am ehesten als Paläoendemit Cyperns angesehen werden.

1. Introduction

Onosma fruticosum LABILLARDIÈRE 1809: 10, Tab. 6, is an endemic of Cyprus (GREUTER & al. 1984: 107) and seems to be an isolated, very peculiar species. The interest in this species was apparently high, so a number of excellent photos can be found in the internet.

POPOV 1953: 195 mentioned *O. fruticosum* within his group *Suffruticosum* beside of *O. polyphyllum* LEDEB., endemic in the mountains of Crimea and in the Markotkh Range (Krasnodarskiy Krai, near Noworossiysk, north-westernmost Transcaucasus) and *O. simplicissimum* L. from W. Russian and E. Ukrainian steppes. In the first sight this is surprising by the very different habits of *O. polyphyllum*, a large, high cushions forming subshrub with many-flowered, terminal, doubled cymes and very densely foliated sterile shoots and *O. simplicissimum*, a loose, procumbent subshrub, also with doubled cymes terminal on the this year's shoots.

Furthermore, some characteristics mentioned for the group *Suffruticosum* are not appropriate for *O. fruticosum* (e. g., elongated leaves, pure yellow corolla of 18 mm and more, stamens not exerted, filaments as long as anthers). The group *Suffruticosum* is placed in the subsect. *Haplotricha*, that means only simple hairs should be present; MEIKLE 1985: 1158 explicitly describes "Indumentum simple, not stellate-pilose" and the long setae as "arising from a glabrous, sulcate base". POPOVA & ZEMSKOVA 1990 write that the small hairs between the tubercles are sometimes grouped around the tubercles. All this is apparently not true. Today it is clear, that the distinction between *Haplotricha*, *Heterotricha* and *Asterotricha* within *Onosma* is an artificial one (TEPPNER, unpubl.). Nevertheless, the indumentum is an important character of species and species groups and therefore, should be correctly described. So, further investigations of the mentioned species are provoked.

2. Material and Methods

Herbarium material from few localities, field fixations from three stations and root tips from two cultivated populations were available. Vouchers are deposited in GZU.

Descriptions of the indumentum refer always to the upper side of the leaf blade of leaves on sterile shoots (= basal leaves in the next year flowering shoots), if not otherwise indicated.

The material for the karyological investigations (flower buds, root tips) was gained in the field and from plants cultivated in the Botanic Garden at the Institut fuer Pflanzenwissenschaften der Universitaet Graz, and in a private garden, respectively. Fixations were made in ethanol : chloroform : glacial acetic acid 5 : 3 : 1 and the material was stained in acetic acid carmine in the usual way for squash preparations; root tips were pre-treated with an 8-hydroxyquinoline solution (e. g., DARLINGTON & LA COUR 1963, SHARMA & SHARMA 1965).

LM investigations were made with a Zeiss Photomikroskop III (with a camera lucida) and for herbarium material a Wild M38 stereomicroscope was used.

For the SEM images air dried herbarium material was mounted on aluminium stubs using C-impregnated double sided tape and sputtered with gold. An SEM XL 30 was used (E. STABENTHEINER). The probes are kept in the collection of the Institute of Plant Sciences in Graz.

3. Morphology

Most distinct characteristics seem to be the habit of small, erect or suberect shrubs (few parts drying back annually, usually the short inflorescence shoots only) or subshrubs with small, narrow leaves, reminding somewhat of *Lavandula* leaves and the terminal one- or two-flowered (very rarely three-flowered) inflorescences (Fig. 1–4), as well as the indumentum of stellate and small simple hairs.

Stem: Indumentum of long setae and short hairs \pm appressed to patent, tubercles bulged, without or with few rays on the periphery.

On full grown plants in nature the leaves are narrow obovate or lanceolate, usually c. $(0.4-1.0-1.5(-1.8) \times (0.1-0.15-0.3(-0.4))$ cm, strongly enrolled at the margin, and appear fascicled on the young shoots in the leaf axils. On seedlings grown in the garden, the leaves reach $2.3-2.5 \times 0.5-0.7$ cm, are lanceolate with a short petiole-like part and only a bit enrolled at the margin. The structure of the indumentum can easily be seen, for e. g., on such seedling leaves (Fig. 8–9): around the \pm patent, long setae, the large, flat tubercles bear 1–3 rows (circles) of glabrous cells and many short rays [c. (10–)25–40] on the periphery. Between the large tubercles smaller ones occur with (0–)1–10(–15) rays, so there are transitions to true, short, simple hairs between the tubercles (Fig. 9). In adult plants the indumentum is slightly patent (Fig. 10) or usually strongly appressed and often so dense, that its exact character is difficult to discern (Fig. 5, 19). The number of rays reaches up to 45–50 and more per tubercle. Toward the short petiole-like base of the leaves the number of rays becomes progressively reduced and the number of small glandular hairs increases (Fig. 16–18).

Sepals $6.0-7.5 \times 0.6-1.2$ mm, narrow lanceolate to narrow triangular, free up to the base, little enlarged in fruit, up to 9.0×1.5 mm, indumentum outside appressed to patent, tubercles of long setae with or without rays, short hairs in-between, whitish-bearded at the margin in the lower $1/2-2/3$, inside with short hairs up to the base, longer hairs in the upper $2/3$, dense toward the tips.

The corolla [(10–)12–15 mm] is dark yellow, becoming orange or red-brown at the mouth during anthesis, fading bluish when wilting and drying up (Fig. 1–4), papillose outside, hairy on the tips and along the back of the lobes, sparsely hairy along the dorsal veins of the tube for c. 1–6 mm, inside smooth, except for the slightly papillose tips. The annulus (basal scales) is 0.5–0.6 mm wide, slightly ten-lobed and glabrous. The corolla-filament-tube is nearly of the same length (ca. 5–6.5 mm) as the free parts of the filaments (c. 5.5–6.5 mm). The winged part of the adnate filaments is only c. 1.5–2 mm long. The basal part of the anther below the filament insertion is short (ca. 1.6–3.2 mm) and much shorter than the free part of the filaments (c. 5.5–6.5 mm).

The anthers are c. (7–)8.0–8.5(–9.8) mm long, strongly connected side by side at the very base, more or less stucked loosely together laterally (connective tips excepted) at least at the begin of anthesis, from c. 4 mm above the base on, gradually narrowed to the tip. Anthers exert for c. 2.2–4.0(–5.0) mm (1.5–2.2 mm from this are the connective tips, also gradually narrowed, slightly emarginate to truncate or acute at the very tip, margin not papillose).

Nutlets (Fig. 6) 1–2 per calyx, c. (1.9–)2.3–3.4 × 1.6–2.1 mm, ovoid, often one half a bit smaller, widest near the middle or little below, no shoulders, apex strongly rounded, ventral edge a little protruding, rounded, not sharp, areole with scar of the vascular bundle excentric near the ventral edge, light grey or light ochre, marbled with dark brown.

Seedlings: cotyledons after germination (3.5–)3.8–4.5 × (3.0–)3.5–4.0 mm, fully grown c. 8–9 × 6–7 mm, roundish-ovate, basally abruptly contracted in a c. 1.0–2.0 mm long petiole-like part, upper side of the blade moderate-densely covered with stiff hairs, 0.1–0.3 mm long, obliquely patent towards the leaf tip, hairs on lower side more dense, c. 0.1–0.2 mm long, thinner and erect-patent (Fig. 7). Seedlings at the end of the first season erect, 8.0–11.5 cm high, internodes of the primary stem approximately of even length, leaves all similar, the uppermost ones diminished, not crowded on the top, leaves up to 2.3–2.5 × 0.5–0.7 cm, indumentum see Fig. 8–9, short axillary shoots (tufts of leaves) in the axils of c. the lower $\frac{2}{3}$ of the stem.

4. Karyology

4.1. Material and Chromosome Numbers

- N-Zypern, W Koruçam, N 35° 19.454' / E 33° 00.430', 158 m, Kalk; 21. 3. 2011; leg. F. SPETA NZ 11–11. – Herb. (GZU) & field fixation n = 10
- N-Zypern, zwischen Akdeniz und Yayla, N 35° 17.232' / E 33° 01.500', 195 m, sandig auf Kalkstein; 29. 3. 2011; leg. F. SPETA NZ 11–40. – Herb. (GZU), field fixation, live plants grown as BOR 1257 in a Garden in Graz and BOR 1264 in the Bot. Garden in Graz n=10, 2n = 20
- [Cyprus] On Kafkalla, near Nicosia International Airport, 21. May 1978, leg. B. F. OSORIO-TAFALL. – Cult. no BOR 380 (GZU)..... 2n = c. 20 (± 2)



Fig. 1–2. *Onosma fruticosa*, between Akdeniz and Yayla. – Fig. 1. Habit of shrubs. – Fig. 2. Details of another individual. – Tufts of leaves in previous year's leaf axils produce a terminal flowering shoot. – Phot. Elise SPETA.



Fig. 3–4. *Onosma fruticosa*, between Akdeniz and Yayla. – Fig. 3. A flowering shoot system with one flower at the start of anthesis and a dry, fruiting shoot of the previous year. – Fig. 4. A two flowered partial inflorescence, the open flower after the start of anthesis, the other withered with dry corolla. – Phot. Elise SPETA.

Cyprn, Distr. Larnaka, Trockenhänge an der Straße von Khirokitia nach Vavla S Lefkara, ca. 1 km NW Khirokitia, ca. 200 m, 17. 4. 1987, mit *Sarcopoterium spinosum*, *Cistus creticus*, *Pistacia lentiscus* und *Helichrysum stoechas* s. l., leg. M. & H. MAYRHOFER. – Herb. (GZU), field fixation $2n = c. 20 (\pm 2)$

Hitherto unpublished chromosome numbers mentioned in the discussion:

Onosma limitanea I. M. JOHNSTON:

Persia: E: Khorasan: In montibus serpentinis 17–21 km E Sabzevar versus Soltanabad, 1150–1400 m, 17.6.1975, leg. K. H. RECHINGER 48928 (W). – Cult. no BOR 501 $2n = 20$

Onosma tanaitica KLOKOV:

[Ukraine] Donetsk, environ de Bogorodichnoye [Bogoroditskoe], the Artem mts. [nutlets received from W. GUTERMANN]. – Cult. No BOR 496 $2n = 14$

4.2. Nuclei and Chromosomes

The interphase nuclei (Fig. 21) contain little heterochromatin, approximately four distinct particles, which most probably correspond to the satellites. Few small particles are additionally present (up to the size of



Fig. 5. *Onosma fruticosa*, axillary tuft of leaves, live plant grown in a garden in Graz. Origin: between Akdeniz and Yayla. – Phot. H. TEPPNER.

euchromomeres and thus not distinguishable from these). The euchromatin shows a pattern of small chromomeres. Because of the few heterochromatin and not fully adequacy of the fixations the fate of the euchromatin was difficult to observe, apparently (as concluded from the best sites in the preparation) it is condensing late (Fig. 21, 22) as usual in many asterotrichous *Onosma* species.



Fig. 6. *Onosma fruticosa*, nutlets in different positions. Origin: between Akdeniz and Yayla. – Phot. H. TEPPNER. – Scale bar equals 1 cm.

The chromosome number is $2n = 20$ and $n = 10$, respectively (Fig. 23, 25). The chromosomes at mitotic metaphase are somewhat heteromorphic and can be grouped as follows (Fig. 24): three chromosomes (three pairs in the diploid set) possess centromeres in the median region (for the terminology see LEVAN & al. 1964 and TEPPNER 1980b), five are distinctly heterobrachial (in the sense of SOROKIN 1929: 408; with centromeres in the submedian and subterminal regions) and two heterobrachials bear SAT-zones and satellites, respectively, with short segments between centromere and NOR (nucleolus organizer region).

Meiotic divisions were not available in our material, but must be highly regular because of the very low number of degenerated pollen grains of c. 2%. Nevertheless, the number of large grains (Fig. 25 d, e) with unreduced chromosome number was relatively high (c. 2.4%). First pollen grain mitosis (Fig. 25a) and the second pollen grain mitosis (Fig. 25c) show regularly $n = 10$ chromosomes.

5. Discussion

According to MEIKLE 1985: 1158–1159 *Onosma fruticosum* occurs in all eight divisions of Cyprus and is locally common.

Before entering a discussion of the indumentum details, a recapitulation of definitions of hair types on the leaf blade could be useful. BOISSIER 1875: 179–180 defined haplotrichous as „Foliorum setae tuberculis glabris insidentes“. This includes an indumentum with a gradual sequence from long to short hairs as well as a dimorphic cover of long setae with short or very short simple hairs in-between. Asterotrichous is defined as „Foliorum setae tuberculis stellatim pilosis insidentes“. This means that on a tubercle the long seta is surrounded by variable numbers of short hairs (rays) in a radial or slightly bilateral manner. Sporadic short, scattered, simple hairs may be present only along the mid-vein or on the petiole-like base of the leaf. If tubercles of very different size occur on the same leaf, beside of the smallest ones with one to few rays also few simple hairs without rays may be possible. On the petiole-like part rays may also be reduced. Very vague is the definition for heterotrichous. It seems the best to applicate this term if long setae without and with rays occur on the same leaf or when between stellate hairs (with long setae and rays) a very different indumentum of short simple hairs is present (also a dimorphic indumentum; TEPPNER 1971: 197, a similar definition could be found in JÁVORKA 1906: 425).

From these three morphological traits heterotrichous is the most difficult one to delimit because of the existence of taxa intermediate between asterotrichous and heterotrichous as well as between heterotrichous and haplotrichous. In *O. fruticosum* we have all gradual transitions from large stellate hairs over hairs of middle and smaller size with few rays to



Fig. 7. *Onosma fruticosum*. Seedling, BOR 1264/1, c. three weeks old. – Largest leaf c. 2.8 mm wide. – Phot. H. TEPPNER.

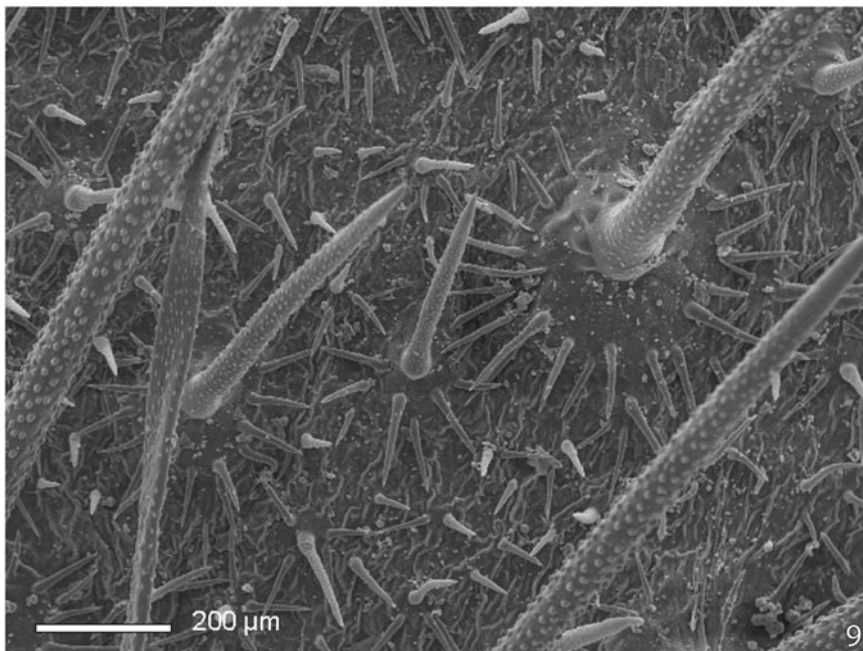
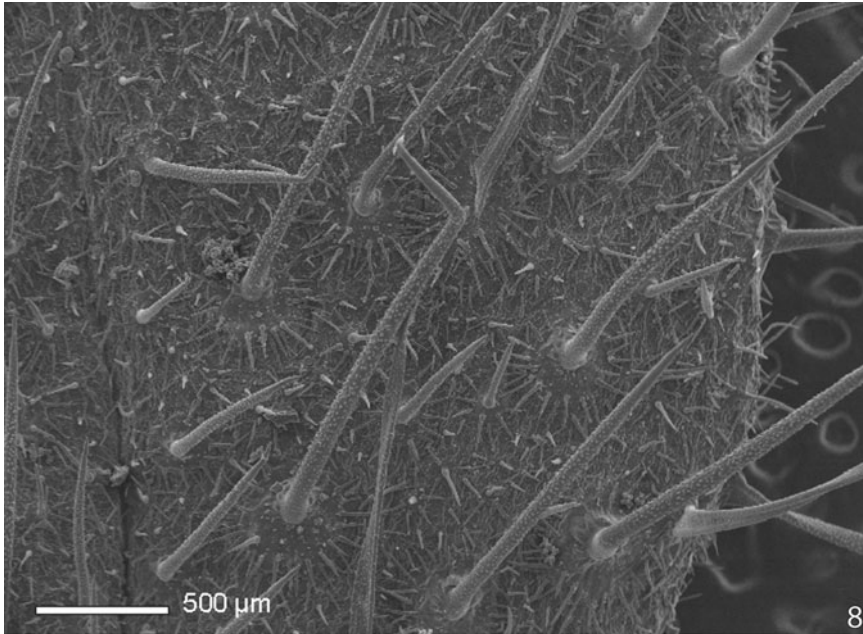


Fig. 8–9. *Onosma fruticosa*. BOR 380/1, seedling, upper side of a leaf of the primary axis. Indumentum loose and patent. – Phot. E. STABENTHEINER.

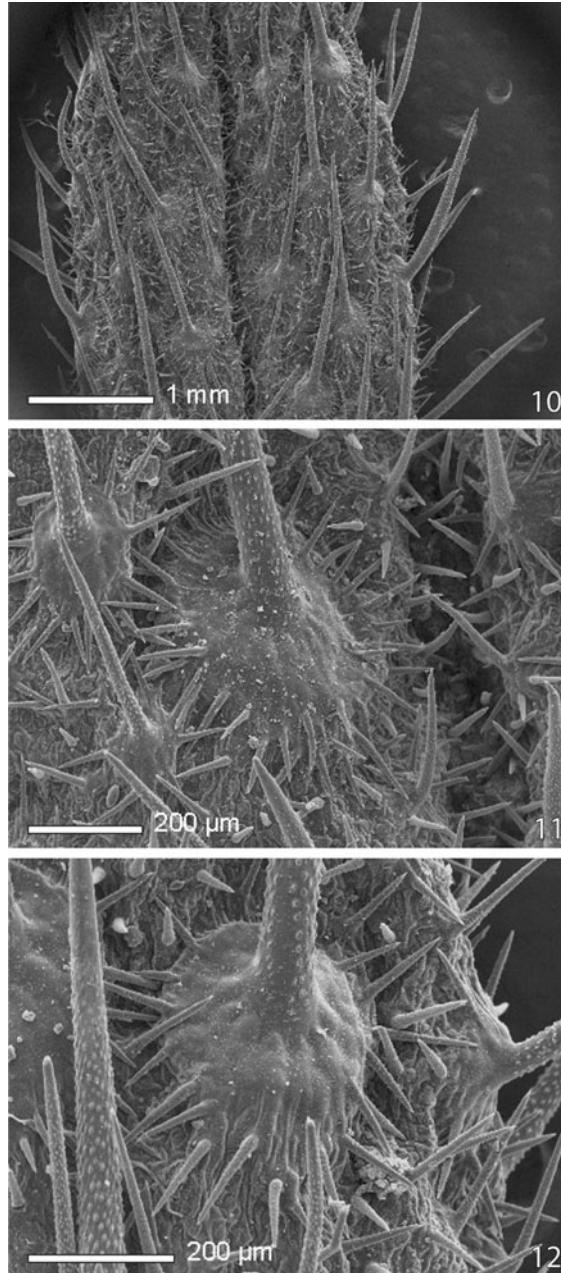


Fig. 10–12. *Onosma fruticosum*. Adult plant with an indumentum of mainly obliquely patent setae and rays. Origin: Evlenja, 1. 4. 1974, leg. G. JOSCHT 7101 (GZU). – Phot. E. STABENTHEINER.

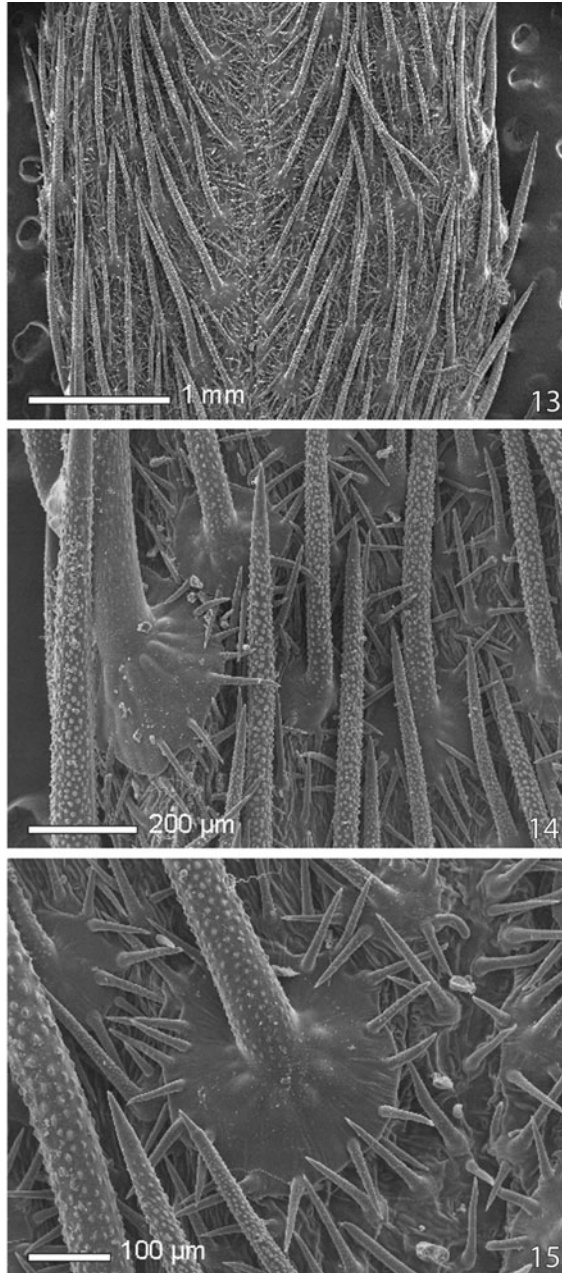


Fig. 13–15. *Onosma fruticosa*. Adult plant with an indumentum of predominantly appressed setae and medium numbers of rays. Origin: S Lefkara. – Phot. E. STABENTHEINER.

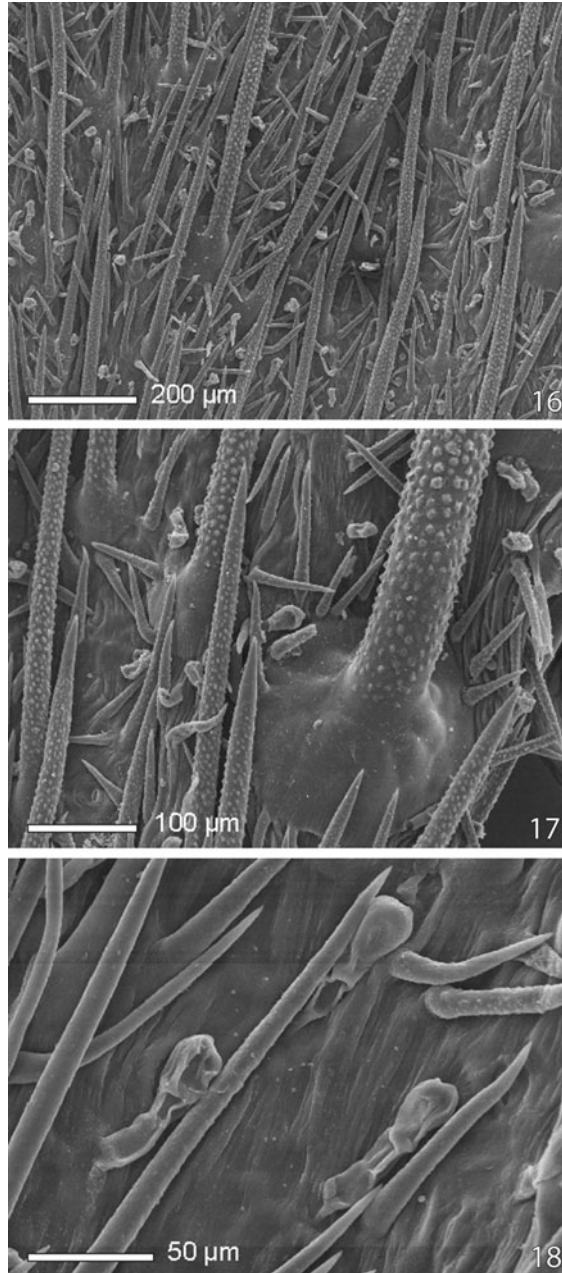


Fig. 16–18. *Onosma fruticosa*. Same leaf as in Fig. 13–15, but basal, petiole-like part with progressive reduction of the number of rays and increasing number of short glandular hairs. – Phot. E. STABENTHEINER.

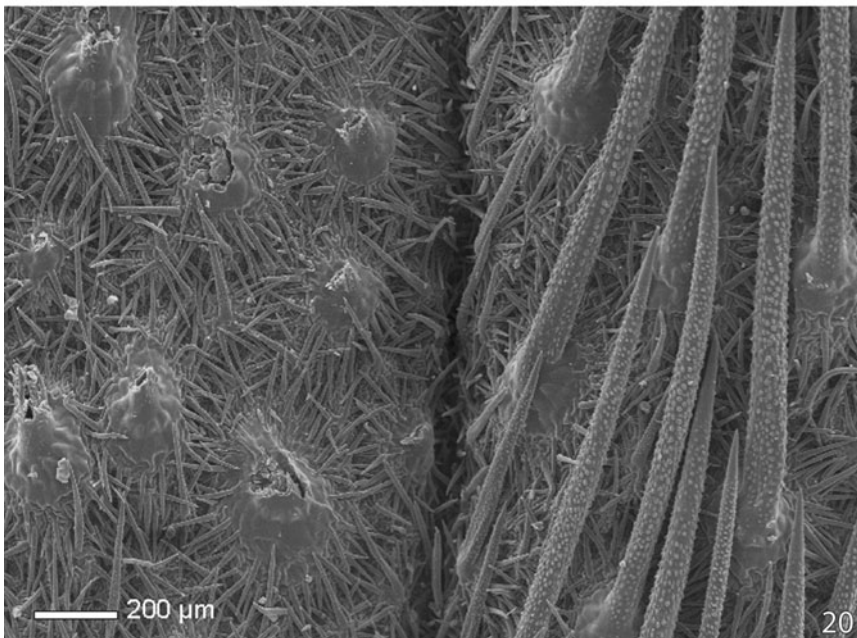
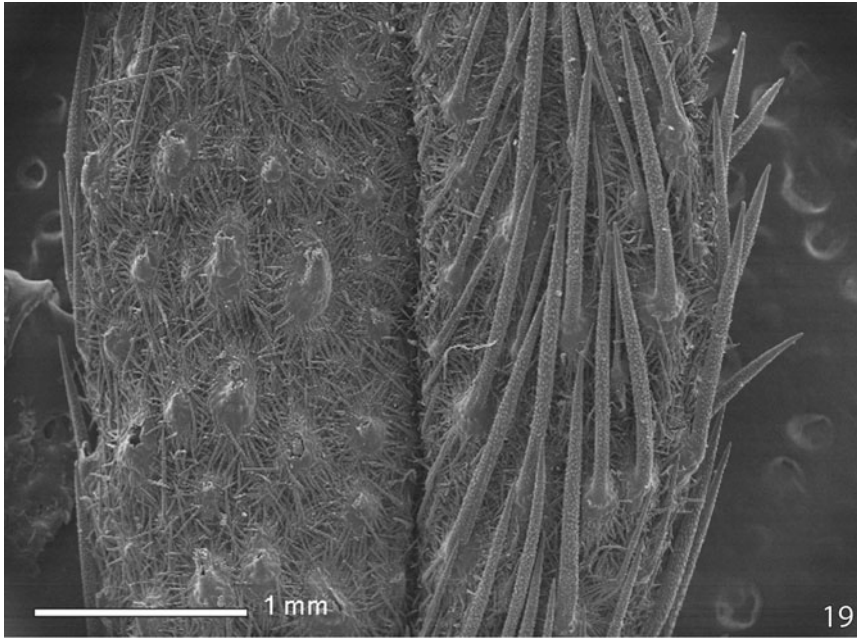


Fig. 19–20. *Onosma fruticosum*. Adult plant with an indumentum of strongly appressed setae and high numbers of rays. In the left part of the leaf the setae are removed for a better view onto the rays. Origin: between Akdeniz and Yayla. – Phot. E. STABENTHEINER.

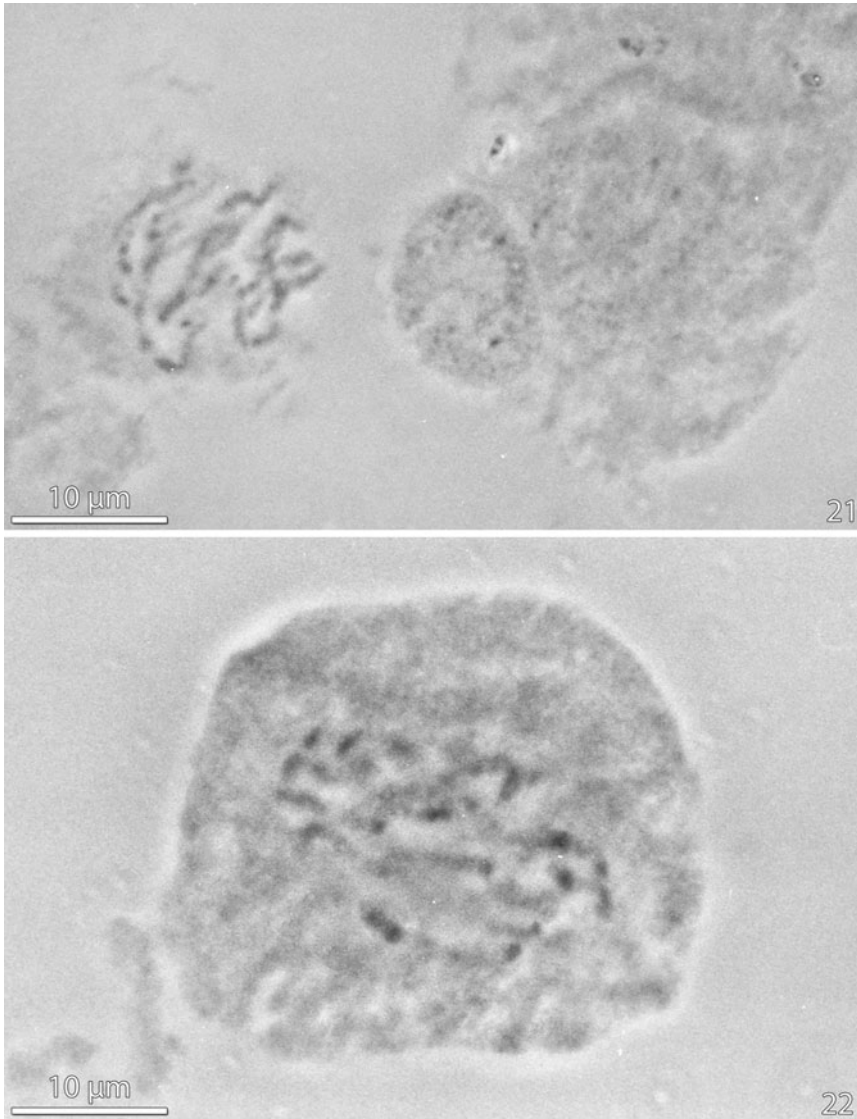


Fig. 21–22. *Onosma fruticosa*. Mitotic nuclear cycle, BOR 1264/1. – Fig. 21. Middle prophase, interphase nucleus and very early prophase (from the left). – Fig. 22. Late prophase nucleus. – Phot. H. TEPPNER.

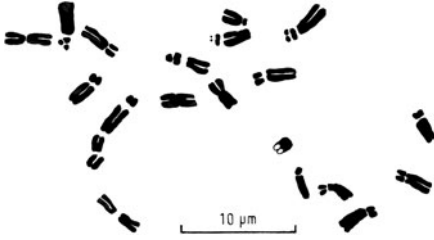


Fig. 23. *Onosma fruticosa*. Mitotic metaphase plate with $2n = 20$ chromosomes, BOR 1257/1.

one ray only and finally short simple hairs. Long and middle-sized setae are always surrounded by rays, there are not two distinct classes of hairs (as in heterotrichous species) and thus *O. fruticosa* is treated as asterotrichous.

It appears very surprising that (to my knowledge) the asterotrichous character of the indumentum was not described till now. The character that the inner

circles of tubercle-cells are glabrous is found in the minority of asterotrichous *Onosma* species, in the majority inner cells – at least of the second circle – bear rays, too. If the delimitation of the group *Suffruticosa* is correct, then we have asterotrichous and haplotrichous species in the same affinity group. The author hopes to discuss the phylogenetically interesting fact in a forthcoming paper.

Furthermore, *O. fruticosa* is used here as an example for describing the possible variability of the indumentum (Fig. 8–20). The principal character of the indumentum is a very important species-characteristic in *Onosma* but there is a certain variability between individuals and within individuals. Leaves of different seasons may show great differences, as well

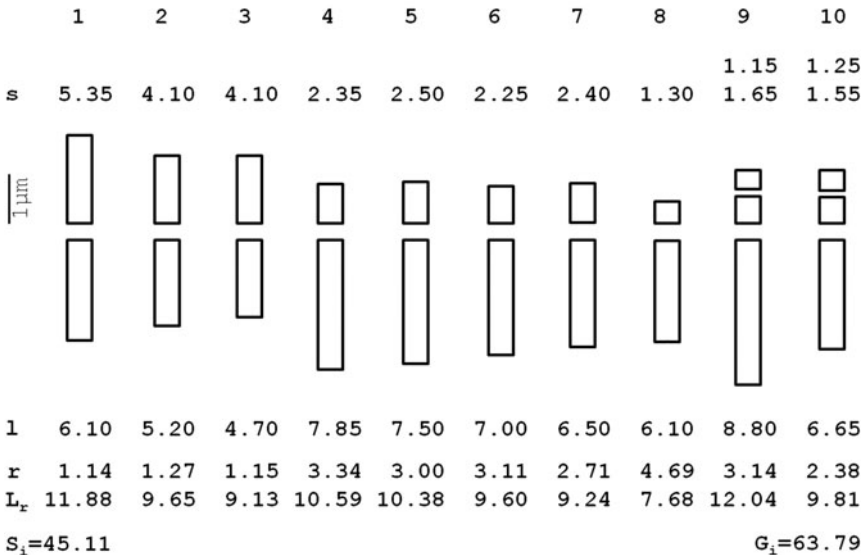


Fig. 24. *Onosma fruticosa*. Idiogram of the haploid chromosome set. – For the idiogram method see, for e. g., TEPNER 1974 or TEPNER & WETSCHNIG 1980.

as leaves of different positions on the plant (e. g., sterile shoots and flowering stems), different parts of the leaves (blade, midrib, petiole-like part) and of course the upper and the lower side.

From some literature one can get the impression, that by consideration of few hairs or the investigation of only one leaf the indumentum of an *Onosma* species can be sufficiently characterised. This is absolutely not true.

A highly remarkable point is the orientation of the short hairs in the simple haired species *O. simplicissima* and *O. tanaitica* with the primitive chromosome number (see below) of $2n = 14$. Long and intermediate setae are oriented toward the leaf tip. In

the majority of short hairs this is also true but to a more or less high percentage their tips look toward the base and fewer short hairs are irregularly oriented. In asterotrichous species the rays in the base-oriented half of a tubercle always point to the base. In *O. polyphylla* a low percentage of short hairs is oriented toward the base of the leaf and sometimes the one or another of the short hairs originates on the margin of a tubercle. If these conditions are the prerequisite for the origin of an asterotrichous indumentum or are – in contrary – a relic because of the deviation from an asterotrichous situation, needs further investigations.

The only other species in the *Suffruticosa* group known till now to possess also the chromosome number of $2n = 20$ is *Onosma polyphylla* (TEPPNER 1971: 198), already mentioned in the introduction. The value of the characteristic “same chromosome number” is diminished by remarkable morphological differences: The set of *O. polyphylla* is somewhat bimodal: the six larger chromosomes of the haploid set measure c. 2.0–3.4 μm in length whereas the four smaller chromosomes are only 1.3–1.7 μm long (TEPPNER unpubl.). On the other hand both species possess the same type of transformation during the mitotic nuclear cycle with late condensing euchromatin [*O. echiodides* type (TEPPNER 1971, 1972) very characteristic for many asterotrichous *Onosma* species with the basic chromosome number $x = 7$ or a closely related type]. So, however, affinities are not excluded.

The only other *Onosma* species with a comparable number of $2n = 20$ chromosomes which I ever counted is *O. limitanea* I. M. JOHNSTON (TEPPNER

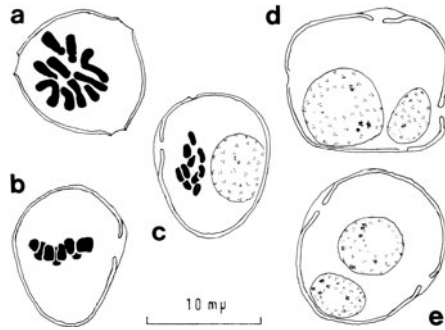


Fig. 25. *Onosma fruticosa*. Pollen grains. – a First pollen grain mitosis with $n = 10$ chromosomes, polar view of the metaphase plate. – b First pollen grain mitosis, lateral view. – c Second pollen grain mitosis with $n = 10$ chromosomes, polar view of the metaphase plate. – d-e Unreduced pollen grains, approximately in polar view (d) and in lateral view (e). – c: W Koruçam, a, b, d, e: between Akdeniz and Yayla, field fixations.

unpubl.): It belongs in a group of species usually named *O. stenosiphon* group. The plant architecture is very different, all parts above soil are herbaceous and the inflorescences with few stem leaves originate below the actual leaf rosette. The basal scales of the corolla are hairy in the majority of species in this group. Thus, at the present stage of knowledge, I sympathize with convergent evolution rather than direct relationship. On the other hand, investigation of chromosome morphology shows in the haploid set of *O. limitanea* no bimodality in size but five chromosomes with centromeres \pm in the median region and five strongly heterobrachial chromosomes: some similarity to *O. polyphylla* – due to an accident? Further, detailed investigations will be exciting.

The $2n = 20$ chromosomes of the not related, permanently anorthoploid *Onosma arenaria* W. K. are not discussed in connection with *O. fruticosa* and *O. polyphylla* because they have a very different origin. The set of the hybridogenous *O. arenaria* is well understood and consists of 12 large chromosomes of the *O. setosa*-type, 7 small chromosomes of the *O. echioides*-type and one B-chromosome (TEPPNER 1971, 1972).

Two other species of the group *Suffruticosa* possesses $2n = 14$ chromosomes and also transformation of the *O. echioides*-type: *O. simplicissima* (POPOVA & ZEMESKOVA 1990: 837–838) and *O. tanaïtica* KLOKOV (TEPPNER, unpubl.). If the circumscription of the group *Suffruticosa* is true, then a transition from $2n = 14$ to $2n = 20$ occurred within this group and doubtless with $2n = 14$ as the primitive character state. It is apparent that $2n = 20$ is a derived, most probably palaeopolyploid condition. Probably the tetraploid level with $2n = 28$ or 26 was the starting point. The heteromorphic and asymmetric set of *O. fruticosa* and the bimodal set of *O. polyphylla* also speak for chromosomal rearrangements.

The most apparent morphological characters of *O. fruticosa*, such as the strict shrubby habit, the one- or few flowered inflorescences, the glabrous basal scales of the corolla, and the indumentum with simple hairs between the tubercles, all can be interpreted at present as plesiomorphic or derived because of lack of sufficient knowledge in the group.

The only DNA study with inclusion of *O. fruticosa* (CECCHI & al. 2011) is not very conclusive because only short sequences were investigated and the selection of species was not adequate; only an affinity to true asterotrichous species can be concluded. In these latter species small simple hairs – if any – occur only sporadically along the midvein and on the petiole-like part. The karyology (prophasic transformation of chromosomes) also speaks for a closer relationship of group *Suffruticosa* to asterotrichous species than to the typical halpotrichous ones as *O. setosa*, *O. fastigiata*, *O. visianii* etc. Because of the clearly derived condition of the chromosome set I tend to interpret the above mentioned characteristics as derived as well. Thus I consider *O. fruticosa* as an old segregate from *Suffruticosa*-progenitors which survived as a palaeoendemic in Cyprus.

Four to five other species are included by POPOV 1951 and POPOVA & ZEMSKOVA 1990 in the group *Suffruticosa*. Here is not the place to discuss all these relationships. It should only be said 1) that *O. caerulescens* BOISS. from the Anti-Lebanon (excluded from the *O. alborosea* group by TEPPNER 1980a: 153) must be included in the affinity of *O. fruticosa* and *O. polyphylla* for morphological reasons, 2) *O. aksoyi* AYTAÇ & TÜRKMEN 2011 from Konya according to the description and the figure has good chance to be close to *O. polyphylla* and 3) *O. sintensisii* HAUSSKN. ex BORNH. from Turkey doubtless must be excluded from this group, it belongs to the affinity of *O. sericea* WILLD.

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