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The genus *Dionysia* (*Primulaceae*), a synopsis and five new species

Abstract

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Five new species of *Dionysia* are described (*D. viva*, *D. zschummelii*, *D. crista-galli*, *D. zetterlundii* and *D. tacamahaca*) from the Zagros mountains of W Iran. One subspecies (*D. sarvestanica* subsp. *spatulata*), one variety (*D. gaubae* var. *macrantha*) and two sections (*D. sect. Zoroasteranthos* and *D. sect. Mucida*) are also described as new. A revised classification of the genus is suggested and a complete list of species is provided, in which some emendations to previously published data are given. A dichotomous key to the species is presented.

Key words: Iran, Zagros Mts, *Primula*, cushion primroses, taxonomy.

Introduction

The genus *Dionysia* Fenzl, belonging in *Primula* sensu lato, is a typically Irano-Turanian genus almost restricted to the rather dry mountains of the Flora Iranica area, from SE Anatolia and W Iran to Tadjikistan and Afghanistan. Most species are cushion forming chasmophytes – in spring completely smothered in yellow, purple, violet or pink flowers – but some are more lax and “*Primula* looking”. Some species are very choosy about their habitat and only grow below overhangs, whereas other species can be found also on slightly sloping rocks. In spite of being difficult to grow, a large number of species are cultivated by devoted specialists or in botanical gardens.

When Per Wendelbo (1961a) revised the genus *Dionysia*, he recognised 28 species, but added several more in later publications. 41 species were known to science when Christopher Grey-Wilson (1989) published his semi-popular account “The genus *Dionysia*”, in which all species are described and illustrations (including several colour photographs) and distribution maps are provided. The number of recognised species in the present paper is 49 and there is every reason to suspect that there are even more species waiting to be discovered, as several are known from a single locality and/or based on very recent finds.

The number of species in cultivation has also increased dramatically in recent years, from a handful in the 1960s, to an estimated 21 in 1989, when Grey-Wilson wrote his book. Today 44

species are grown, representing 90 % of the known taxa. As live plants are indispensable for a proper understanding of morphology and biology, plants in cultivation have contributed considerably to current progress in our knowledge of the “cushion primroses”.

Molecular investigations by Ida Trift & al. (2004) have given us a far better understanding of evolution and biogeography of *Dionysia*. Recent field expeditions have brought us important observations on their habitat and many informative photographs of flowering individuals in the wild.

Several species are considered threatened by nature conservation authorities in Iran, mainly due to their restricted distributions, but some populations are also subjected to collection for medicine. Because of their beauty, rarity and dramatic stations, *Dionysias* are among the few plants referred to in Iranian tourist information.

Material and methods

This paper is based on experience from field studies in Iran (Zagros), plants cultivated in greenhouses at Göteborg Botanic Garden and herbarium studies. It takes as a starting point the monograph by Per Wendelbo (1961, with emendations up to 1980), which is accepted as to species level taxonomy. Types (at least isotypes) and other cited herbarium specimens have been seen unless otherwise indicated.

Since Wendelbo’s monograph, rich herbarium material has accumulated in the herbarium of the Institute of Forests and Rangelands (TARI) in Tehran. During the same period, hardly anything has reached other major herbaria. In addition, some recent expeditions to Iran, notably SLIZE (Swedish-Latvian-Iranian-Zagros-Expedition, with Assadi, Mozaffarian, Popp, Seisums & Lidén) in 1998 and T4Z (Tjerdema, Zetterlund, Zschummel & Zschummel to Zagros) in 2002, have brought more than 60 accessions of 31 taxa into cultivation. This means that I have had the opportunity to study a far richer material from Zagros than Wendelbo, Grey-Wilson or even Jamzad had available. Of the Iranian species *D. bornmuelleri*, *D. tacamahaca* and *D. sawyeri* has not been studied in cultivation.

The following herbaria were consulted, directly or indirectly: A, B, BASBG, BG, BR, C, DBN, E, GB, K, LD, LE, MB, NY, P, PE, PR, PRC, S, Shiraz University, TARI, W (abbreviations according to Holmgren & Holmgren 1998-).

Unless otherwise indicated, single measurements of leaves, calyx, etc. always refer to length.

Taxonomic history

Dionysia was first recognised as a genus by Fenzl (1843), based on material of *D. odora* collected by Kotschy in Kurdistan. This, however, was not the first *Dionysia* known to science. Already in 1817 Lehmann had described *Primula aretioides* on material collected in N Iran in 1770, but only in 1846 Boissier formally transferred it to *Dionysia*, at the same time describing three new species. In the meantime Duby (1844) had treated the *Primulaceae* for Candolle’s Prodrômus, in which he included the *Dionysia* species in *Gregoria*, a synonym of *Douglasia*, a rather remotely related genus. To complicate matters, Duby later the same year erected the genus *Macrosyphonia*, to which he transferred his *Gregoria caespitosa*.

Bunge (1871) published an account of *Dionysia*, recognising it as a genus separate from *Primula*, as did Boissier (1879). Kuntze (1891) merged *Dionysia* into *Primula* as a section. Knuth (1905) treated *Dionysia* for Engler’s Pflanzenreich, recognising 20 species. Bornmüller (1899, 1903, 1904, 1905, 1910, 1937; for references, see the List of species, below) was ambiguous concerning generic status; although he accepted *Dionysia* as a genus, he was careful to ensure that his new names should remain valid also in *Primula*, and even provided the alternative combinations, in one case a nomen novum.

Melchior (1943) discussed the evolution and subdivision of *Dionysia*. His thoughts were largely followed by Wendelbo (1961), whose exhaustive monograph has been the basis for subsequent revisions, of which the most important are Grey-Wilson (1989), with a forerunner (1970),

and an account of Iranian taxa by Jamzad (1996). All in all, Grey-Wilson contributed three and Jamzad four new species.

An evolutionary approach to the classification of *Dionysia* has now been made possible by the recent molecular studies by Mast & al. (2001) and Trift & al. (2004). These authors present a phylogeny, which in parts differs drastically from the speculative schemes of Melchior (1943) and Wendelbo (1961a), which involved now obsolete concepts like “advancement level”.

Morphology and relationships

That *Dionysia*, though surely a natural group in itself, can not be demarcated from *Primula* has been obvious from the start. Both Wendelbo (1961a) and Grey-Wilson (1989) realised that *Dionysia* belongs in *Primula* in a genealogical classification, but as both accepted a polyphyletic *Primula*, they saw no problems in recognising *Dionysia* as a genus, following the tradition of Bornmüller and Melchior.

Dionysia differs from most *Primula* in the base chromosome number 10, the suffruticose habit, long corolla tube and a capsule that splits to the base into 5 valves. Further, several species are characterised by woolly farina, which is very rare in *Primula* (Wendelbo 1961a) but present in *P. qinghaiensis* (Trift & al. 2002). Efarinose species and species with powdery farina are also known in *Dionysia*. All characters distinguishing *Dionysia* can be found in other groups of *Primula*, though never in combination, and accordingly *Dionysia* can be quite easily circumscribed and its naturalness has been strongly confirmed by molecular evidence, including large unique deletions in two of the sequenced regions (Trift & al. 2004). Recognising *Dionysia* as a genus, however, makes *Primula* polyphyletic, since the sister group of *Dionysia* is not *Primula*, but only a part of *Primula*: the subgenus *Sphondylia* (Mast & al. 2001, Trift & al. 2004, Wendelbo 1961a-c).

The species of *Primula* subg. *Sphondylia* are similar to some species of *Dionysia* sect. *Dionysiopsis* Pax (e.g., *D. mira* and *D. bornmuelleri*), although the *Sphondylia* species differ in involute young leaves, 3-furrowed pollen grains and a capsule that splits apically into ten teeth. The pollen in *Dionysia* usually has 6-8 furrows. Both pollen types are known from *Primula* s.str. (Wendelbo 1961c). Wendelbo (1961b) considered the subgenus *Sphondylia* “primitive” in *Primula*, but it seems as if at least the peculiar type of conduplicate-involute leaf vernation (Mast & al. 2001) is a derived character (synapomorphy) for the subgenus *Sphondylia*.

Towards a natural classification of *Dionysia*

It can be concluded from character optimization on phylogenetic trees (Mast & al. 2001, Trift & al. 2002, 2004) that the ancestral *Dionysia* had a lax habit with large dentate revolute leaves, flowers in a stalked umbel (or in superposed verticils) subtended by foliaceous bracts and a yellow, externally hairy corolla with a long tube – conclusions reached already by Melchior (1943). Consequently, there is nothing that suggests that the species with these characteristics (1-5, 15-18 in the list below) assembled in *D.* subsect. *Scaposae* by Wendelbo form a natural group, as the traits used to circumscribe subsect. *Scaposae* are all ancestral in *Dionysia*.

Indeed, the molecular results suggest that two “*Scaposae*” species, *Dionysia hissarica* and *D. balsamea*, together form a sister group to the other *Dionysia*. The union of these two species is surprising, as it seems to be in conflict with morphological evidence, *D. balsamea* being superficially more similar to *D. paradoxa*. However, the molecular evidence is very clear and there are some morphological characters that distinguish the two from *D. paradoxa*: comparatively few-seeded capsules, blunt teeth on the leaves and long eglandular hairs.

The western species (15-18) of subsection *Scaposae* sensu Wendelbo are better put together with the similarly western species of subsection *Revolutae* Wendelbo, with which they share many characters. Although here is no molecular support for this grouping, there is nothing that contradicts it. The valid name for this taxon is *D.* sect. *Dionysiopsis*.

The second important deviation from previous classifications (Wendelbo 1961, Grey-Wilson 1989) is the reshuffling of the species of section *Dionysia* sensu Wendelbo. It is obvious that un-

Table 1. Revised classification of the genus *Dionysia*.

A. Eastern species	
I. Probably polyphyletic group not placed to section <i>D. hissarica</i> , <i>balsamea</i> , <i>paradoxa</i> , <i>lacei</i> , <i>saponacea</i>	Large leaves (> 10 mm) with revolute margin
II. <i>D.</i> sect. <i>Dionysiastrum</i> Smoljan.	Flat leaves up to 10 mm
a. <i>D.</i> subsect. <i>Tapetodes</i> Wendelbo <i>D. denticulata</i> , <i>tapetodes</i> [<i>kossinskyi</i>]	Leaf veins raised, farina woolly; corolla yellow, glabrous
b. <i>D.</i> subsect. <i>Involucratae</i> Wendelbo <i>D. involucrata</i> [<i>gandzhinae</i>], <i>hedgei</i> , <i>freitagii</i> , <i>viscidula</i> [<i>wendelboi</i>], <i>microphylla</i>	Leaf veins raised, farina powdery (if present); corolla violet, glandular-hairy
c. <i>D.</i> subsect. <i>Aghanicae</i> Grey-Wilson <i>D. afghanica</i>	Leaves entire, truncate, with obscure veins, covered with short glandular hairs; corolla violet, glandular-hairy
d. <i>D.</i> subsect. <i>Heterotrichae</i> Wendelbo <i>D. lindbergii</i>	Leaves entire, truncate, with obscure veins, covered with short glandular hairs and long dense eglandular hairs towards the apex; corolla violet, glabrous
B. Western species	
III. <i>D.</i> sect. <i>Dionysiopsis</i> Pax <i>D. mira</i> , <i>viva</i> (nov.), <i>bormmuelleri</i> , <i>teucroides</i> , <i>aretio-</i> <i>ides</i> , <i>leucotricha</i> , <i>revoluta</i> , <i>archibaldii</i> , <i>zschummelii</i> (nov.), <i>esfandiarii</i> , <i>rhaptodes</i> , <i>oreodoxa</i>	Leaf margin revolute, farina usually present
IV. <i>D.</i> sect. <i>Zoroasteranthos</i> Lidén (nov.) <i>D. curviflora</i> , <i>janthina</i> , <i>khatamii</i>	Leaves flat, eglandular with long articulate hairs, no farina; corolla violet with yellow eye and deeply emarginate lobes; seeds few
V. <i>D.</i> sect. <i>Mucida</i> Lidén (nov.) <i>D. lurorum</i>	Leaves flat, strongly farinose; flowers yellow; seeds numerous
VI. <i>D.</i> sect. <i>Dionysia</i> <i>D. sawyeri</i> (incertae sedis), <i>iransharii</i> , <i>caespitosa</i> , <i>gaubae</i> , <i>odora</i> , <i>haussknechtii</i> , <i>crista-galli</i> (nov.), <i>zetterlundii</i> (nov.), <i>tacamahaca</i> (nov.), <i>lamingtonii</i> , <i>mozaffarianii</i> , <i>iranica</i> , <i>zagrica</i> , <i>khuzistanica</i> , <i>terme-</i> <i>ana</i> , <i>michauxii</i> , <i>bryoides</i> , <i>diapensiifolia</i> , <i>sarvestanica</i>	Leaves flat without farina; flowers yellow, or – if violet – plant with abundant glandular hairs or corolla lobes not emarginate; seeds few

related elements were brought together here. It is not surprising that the subsections *Tapetodes* and *Heterotrichae* are shown to be more related to the eastern species of sect. *Dionysiastrum* as they share similarities in leaf shape and leaf anatomy (Bokhari & Wendelbo 1976, Trift & Anderberg 2006). Also geographically they come closer.

More perplexing it is that the densely pulvinate species *Dionysia curviflora* and *D. janthina* from the Schir Kuh area SW of Yazd (included in *D.* sect. *Dionysia* subsect. *Bryomorphae* by Wendelbo) are not related to superficially similar species from the Zagros chain such as *D. lamingtonii*. Instead they group with strong support with the third Schir Kuh endemic, the recently described rather lush *D. khatamii*. If analysed more in detail, this grouping is less surprising; all the Schir Kuh species have pubescent violet corollas with a yellow eye and deeply emarginate corolla lobes, entire leaves equipped with long coarse articulate hairs and lack glands on the leaf lamina. These three species are here recognised as a new section *Zoroasteranthos*.

Wendelbo divided the remaining Iranian species with small flat leaves (all from Zagros) between the subsections *Bryomorphae* (i.e. together with the Schir Kuh species) and *Caespitosae*, based on cushion compactness and degree of exertion of style in pin-eyed flowers. However,

e.g., *Dionysia sarvestanica* and *D. zagrica*, agreeing with subsect. *Bryomorphae* in their compact habit, nevertheless have exerted styles, which is a *Caespitosae* character. It is also clear in the molecular phylogeny that the two groups are completely intermingled.

Three conclusions that can be drawn from the molecular study by Trift & al (2004): (1) geographically neighbouring species or higher clades are usually each others closest relatives; (2) very tight cushions have evolved four times in dry areas from ancestors with less condensed growth; and (3) *Dionysia* presumably originated in the eastern part of the current distribution area. For a fuller discussion of these patterns the reader is referred to that paper.

Based on the discussion above, I suggest a classification (Table 1), which recognises morphologically distinguishable entities that are either well supported in the molecular tree of Trift & al (2004), or (in the case of *Dionysia* sect. *Dionysiopsis*) is not in conflict with well supported nodes in that tree.

Note that the *Dionysia* subsect. *Tapetodes* and *Heterotrichae* have been transferred from *D.* sect. *Dionysia* to sect. *Dionysiastrum*.

Key to the species of *Dionysia*

1. Leaf margin revolute or all leaves more than 10 mm. 2
 - Leaves flat or slightly involute, 2-10 mm (bracts and leaves of new “vegetative” shoots occasionally longer) 18
2. Flowers purple, violet or pink 3
 - Flowers yellow 5
3. Leaf indumentum very dense, apically retrorse; corolla hairy; cushions very dense 26. *D. esfandiarii*
 - Leaf indumentum sparse to moderately dense, not retrorse apically; corolla glabrous or almost so 4
4. Cushions very dense; hairs few and short; leaf margin entire, strongly inrolled 23. *D. zschummelii*
 - Cushions lush; leaves distinctly hairy, crenate-dentate 22. *D. archibaldii*
5. Inflorescence consisting of an umbel or of superposed verticils of flowers 6
 - Flowers sessile, 1-2 per inflorescence; bracts linear 13
6. Inflorescence sessile 4. *D. lacei*
 - Inflorescence stalked, bracts foliaceous 7
7. Leaves 25-80 mm, inflorescence usually with 2 or more whorls of flowers, one above the other 8
 - Leaves 10-20 mm, inflorescence a single umbel with 2-3 flowers 12
8. Leaves with short-stalked glands only 3. *D. paradoxa*
 - Leaves with both long hairs and short-stalked glands 9
9. Capsule with 5-10 seeds; corolla limb 10-18 mm broad, with broad obovate lobes (Afghanistan) 2. *D. balsamea*
 - Capsule with 40-70 seeds; corolla limb 7-10 mm broad, lobes broadest towards the base, rectangular to oblong-triangular 10
10. Leaves 5 times as long as broad, with 10-15 regular teeth on each side 15. *D. mira*
 - Leaves 3 times as long as broad, with 4-5 irregular teeth or lobes 11
11. Corolla tube 20-30 mm; calyx split to $\frac{3}{4}$ or more 16. *D. bornmuelleri*
 - Corolla tube 13-15 mm; calyx split to $\frac{2}{3}$ 17. *D. viva*
12. Leaves clearly revolute 18. *D. teucroides*
 - Leaves almost flat 1. *D. hissarica*
13. Leaves 15-30 × 6-20 mm, flat at maturity 5. *D. saponacea*
 - Leaves much shorter and narrower, strongly revolute 14
14. Corolla lobes emarginate 15
 - Corolla lobes entire 17

15. Calyx lobes with broad blunt erose-dentate apices 20. *D. leucotricha*
 – Calyx lobes entire, acute 16
16. Leaves densely glandular with 5-8 crenations 21. *D. revoluta*
 – Leaves sparsely glandular with 4-5 crenations 19. *D. aretioides*
17. Cushions very dense; leaves bluish green with densely set short, acute hairs above (rarely glabrous) and stalked glands marginally and below; leaf margin usually strongly inrolled, not or only very slightly crenate-dentate 24. *D. rhaptodes*
 – Cushions soft; leaves bright green, glabrous or with a few scattered hairs, with subsessile glands marginally and below, usually farinose; leaf margin clearly crenate-dentate 25. *D. oreodoxa*
18. Flowers in a stalked umbel (rarely with a single flower); bracts foliaceous, usually larger than leaves 19
 – Flowers sessile, single or rarely in pairs; bracts shorter and much narrower than leaves 24
19. Flowers purple, violet or pink 20
 – Flowers yellow 22
20. Leaves 1.5-2.5 mm, with few veins 13. *D. microphylla*
 – Leaves 5-12 mm, with conspicuous flabellate venation 21
21. Leaves and bracts dentate; corolla lobes emarginate; homostylous 12. *D. involucrata*
 – Leaves and bracts entire; corolla lobes acute, entire; heterostylous 11. *D. hedgei*
22. Plant not farinose or only on corolla; leaves in a tight rosette 33. *D. caespitosa*
 – Plant farinose (especially in axils); leaves not in a tight rosette 23
23. Corolla hairy; leaves crenate-lobed 1. *D. hissarica*
 – Corolla glabrous; leaves entire to serrate 30. *D. lurorum*
24. Strongly anisophyllous with “vegetative” leaves 3-4 times longer than overwintering leaves; corolla glabrous, lobes deeply emarginate; ovules 15-25 (corolla limb possibly violet/purple) 31. *D. sawyeri*
 – Not strongly anisophyllous; corolla usually hairy; ovules 3-10 25
25. Flowers purple, violet or pink 26
 – Flowers yellow 35
26. Leaves with strongly raised veins 27
 – Leaf veins not conspicuous 28
27. Calyx 5 mm, divided to $\frac{1}{2}$; corolla tube c. 15 mm 10. *D. freitagii*
 – Calyx 3-4 mm, divided to $\frac{3}{4}$; corolla tube 10 mm 9. *D. viscidula*
28. Leaves apically divided into 3-5 lobes 41. *mozaffarianii*
 – Leaves entire 29
29. Leaves with long eglandular hairs (0.5 mm), with or without short glandular hairs 30
 – Leaves without eglandular hairs but densely set with sessile or short-stalked glands 34
30. Leaves with short-stalked glands; calyx split to base 14. *D. lindbergii*
 – Leaves without glands; calyx divided $\frac{1}{2}$ - $\frac{2}{3}$ 31
31. Leaves obovate, glabrous below 27. *D. curviflora*
 – Most leaves hairy on both surfaces 32
32. Corolla glabrous 32. *D. iranshahrii*
 – Corolla hairy 33
33. Leaves c. 5-8 mm, cushions loose 29. *D. khatamii*
 – Leaves 3 mm, cushions dense 28. *D. janthina*
34. Calyx split to base, leaves narrowly elliptic 47. *D. bryoides*
 – Calyx split to $\frac{2}{3}$, leaves rounded-obtriangular 6. *D. afghanica*
35. Leaves without glands or glandular hairs 36
 – Leaves glandular hairy or with sessile glands 37
36. Leaves with long (0.5 mm) curly articulate hairs; corolla glandular hairy 40. *D. lamingtonii*

- Leaves with short straight retrorse hairs; corolla with eglandular hairs . . . 46. *D. michauxii*
- 37. Corolla glabrous, very rarely with short eglandular hairs (NE Iran to Afghanistan) . . . 38
- Corolla glandular hairy (Zagros mountains) 39
- 38. Calyx lobes mucronate 7. *D. denticulata*
- Calyx lobes not mucronate 8. *D. tapetodes*
- 39. Leaves of adult plants up to 3 mm, entire or rarely slightly tridentate at apex 40
- Leaves longer, at least some with a few lateral teeth or lobes 46
- 40. Leaves with a uniform indumentum of sessile or short-stalked glandular hairs (up to 0.1 mm) 41
- Leaves with some longer hairs, especially adaxially 43
- 41. Glands sessile (leaves obovate, calyx lobes broadest at the middle) 43. *D. zagrica*
- Glands shortly stalked 42
- 42. Leaves oblong to obovate, rounded obtuse at apex; calyx lobes usually broadest at the middle 49. *D. sarvestanica*
- Leaves ovate, often tridentate at apex; calyx lobes broadest at the base 44. *D. khuzistanica*
- 43. Calyx divided to about halfway; leaves acute, densely glandular hairy on both sides 39. *D. tacamahaca*
- Calyx divided almost to the base; leaves obtuse 44
- 44. Leaves with an apical whitish fimbriate crest 37. *D. crista-galli*
- Apical marginal hairs not confluent to a whitish crest 45
- 45. Leaves with ciliate margin; most hairs gland-tipped 36. *D. haussknechtii*
- Leaf margin not distinctly ciliate; leaves adaxially with long straight eglandular hairs in addition to shorter glandular hairs 38. *D. zetterlundii*
- 46. Leaves with eglandular hairs more than 0.5 mm 47
- All hairs gland-tipped, less than 0.2 mm 48
- 47. Calyx 5-6 mm; marcescent leaves not spirally reflexed 35. *D. odora*
- Calyx 7.5-9 mm; marcescent leaves spirally reflexed 34. *D. gaubae* v. *megalantha*
- 48. Glands all sessile 42. *D. iranica*
- Most glands clearly stalked 49
- 49. Calyx divided to $\frac{3}{4}$; marcescent leaves strongly reflexed so as to become more or less coiled 34. *D. gaubae*
- Calyx divided almost to the base; marcescent leaves not reflexed 50
- 50. Style of long-styled flowers long exerted; calyx accrescent to 10 mm in fruit 48. *D. diapensifolia*
- Style in long-styled flowers not or only slightly exerted; calyx c. 5 mm in fruit 45. *D. termeana*

List of taxa

Synonyms are listed in chronological order, except that homotypic synonyms are kept together.

The list is (hopefully) nomenclaturally complete, although the emphasis is on Iranian species. Descriptions are restricted to new taxa plus a few corrections and emendations to the previous treatments by Wendelbo (1961), Grey-Wilson (1989) and Jamzad (1996). Three eastern species, for which taxonomic status has not been ascertained as the types have not been seen, are included in the list under a closely similar species.

Dionysia Fenzl in Flora 26: 389. 1843 \equiv *Primula* sect. *Dionysia* (Fenzl) Kuntze in Post & Kuntze, Lex. Gen. Phan.: 406. 1903. – Type: *D. odora* Fenzl
 \equiv *Macrosyphonia* Duby in Mem. Soc. Phys. Hist. Nat. 10: 426. 1844. – Type: *Dionysia caespitosa* (Duby) Boiss. [\equiv *Gregoria caespitosa* Duby \equiv *Macrosyphonia caespitosa* (Duby) Duby].

A. Eastern species

I. Species not placed to section

1. *Dionysia hissarica* Lipsky in Trudy Imp. St.-Petersburgsk. Bot. Sada 18: 83. 1900 ≡ *Primula hissarica* (Lipsky) Bornm. in Bull. Herb. Boissier, ser. 2, 3: 592. 1903. – Holotype: USSR, Pamir-Alai, above Den-Surkh, near river Surkhan, *Lipsky* (LE; isotypes: A, B, E, G)

Morphologically, the most aberrant species in the genus. A possibly unique feature not noted before is the finely papillose spherical seeds. *Dionysia balsamea* (its putative sister species, Trift & al. 2004) has, however, not been studied in this respect. If they share this character, it would constitute a strong corroboration of the molecular tree.

2. *Dionysia balsamea* Wendelbo & Rech. f. in Aarbok Univ. Bergen Mat.-Naturvitensk. Ser. 19(4): 7, fig. 2, 3e-f. 1964. – Holotype: Afghanistan, Ghorat, Kuh-Tscheling-Safed-Daraq (Pirestan), 7.-8.1962, *Rechinger 19094* (W; isotype: BG).

3. *Dionysia paradoxa* Wendelbo in Bot. Not. 112: 497. 1959. – Holotype: Afghanistan, Kabul river, Sarobi, *Volk 2411* (BG; isotype: BASBG).

4. *Dionysia lacei* (Hemsley & Watt) Clay, Present-Day Rock Gard.: 195. 1937 ≡ *Primula lacei* Hemsley & Watt in J. Linn. Soc. Bot. 28: 298, 325, t. 41. 1891. – Holotype: Pakistan, Baluchistan, Torkhan, *Lace 3648* (K; isotypes: BM, E).

5. *Dionysia saponacea* Wendelbo & Rech. f. in Aarbok Univ. Bergen Mat.-Naturvitensk. Ser. 19(4): 10, fig. 3a-b. 1964. – Holotype: Afghanistan, Ghorat, Kuch-Tscheling-Safed-Daraq (Pirestan), 7.-8.1962, *Rechinger 19092* (W; isotype BG).

II. *Dionysia* sect. *Dionysiastrum* Smoljan. in Šiškin & Bobrov, Fl. SSSR 18: 718. 1952. – Type: *D. involucrata* Zaprjag.

a. *Dionysia* subsect. *Afghanicae* Grey-Wilson, Gen. *Dionysia*: 168. 1989. – Type: *D. afghanica* Grey-Wilson

6. *Dionysia afghanica* Grey-Wilson in Kew Bull. 29: 57. 1974. – Holotype: Afghanistan, Darreh Zang, S of Belcheragh, 7.1971, *Grey-Wilson & Hewer 1308* (K; isotypes: E, GB, W).

b. *Dionysia* subsect. *Tapetodes* Wendelbo in Aarbok Univ. Bergen Mat.-Naturvitensk. Ser. 19(4): 10. 1964 [–*D. sect. Bryonanthe* Smoljan., nom. nud.]. – Type: *Dionysia tapetodes* Bunge

7. *Dionysia denticulata* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 19(4): 11, fig. 4. 1964. – Holotype: Afghanistan, Bamian, between Shahtu and Panjao, 6.1962, *Hedge & Wendelbo W 4876* (BG; isotype: E).

8. *Dionysia tapetodes* Bunge in Bull. Acad. Imp. Sci. Saint-Pétersbourg 16: 562. 1871 ≡ *Primula tapetodes* (Bunge) Kuntze, Rev. Gen. Pl. 2: 400. 1891. – Holotype: NE Iran, above Derrud, between Nishapur and Meshed (Masshad), *Bunge* (LE; isotypes: G, P).

= *Dionysia trinervia* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 19(4): 14. 1964. – Holotype: Afghanistan, Orozgan, Kotal-Tachakmak, 3100 m, 6.1960, *K. Lindberg 938* (BG).

8b. *Dionysia kossinskyi* Czerniak. in Izv. Glavn. Bot. Sada SSSR 26: 116. 1927. – Holotype: Iran: Khorrasan, Mt. Kisil-Chisht, above Khorkei, *Czerniakovska 375* (LE).

The type (and *Czerniakovska 96*, LE, from the same area) differs from “typical” *Dionysia tapetodes* in having a corolla with short eglandular hairs, and leaves with slightly longer glands. Possibly, it can also be recognised by longer leaves and pink or violet corolla, but this is as yet uncertain.

c. *Dionysia* subsect. *Involucratae* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 78. 1961. – Type: *D. involucrata* Zaprjag.
= *Dionysia* subsect. *Microphyllae* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 78. 1961. – Type: *D. microphylla* Wendelbo

9. *Dionysia viscidula* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 19: 20, fig. 11, 16. 1964. – Holotype: Afghanistan, Darrah Zang, near Belcheragh, 5.1962, *Hedge & Wendelbo W 3722* (BG; isotype: E).

9b. *Dionysia wendelboi* Podlech in Mitt. Bot. Staatssamml. München 17: 481. 1981.

“Differt a *Dionysia viscidula* foliis minoribus farinosis minutissime tantum glandulosi-puberulis floribus minoribus”. I have not seen the type of this name. The species is said to differ from *D. viscidula* in smaller leaves and flowers.

10. *Dionysia Freitagii* Wendelbo in Bot. Not. 123: 303, fig. 2A-F. 1970. – Holotype: Afghanistan, Balkh, Ali Kuh, 5.1969, *Hedge, Wendelbo & Ekberg W 8497* (GB; isotype: E).

11. *Dionysia hedgeri* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 19: 18, fig. 9, 10-16. 1964. – Holotype: Afghanistan, Mazar-i-Sharif, Koh-i-Elburz, *Hedge & Wendelbo W 3888* (BG; isotype: E).

12. *Dionysia involucrata* Zaprjag. in Trudy Tadzhiksk Bazy, Bot. 2: 153, fig. 3. 1936. – Holotype: USSR, Pamir-Alai, Hissar (LE).

12b. *Dionysia gandzhinae* Kamelin in Bot. Zhurn. 69(10): 1403. 1984. – Holotype: S Tadjikistan, jugum Gasimailik, declivum orientale, prope pagum Gandzhina et supra locum Gusabulak, in fissuris rupium 3.5.1983, *R. Kamelin, A. Borodina, A. Geldychanov, I. Mochova, E. Nikolaev, T. Schevljakova, V. Solovjov & I. Tagaev N 1437* (LE?, TAD, not seen).

Although the type of *Dionysia gandzhinae* has not been seen (it could not be recovered in LE), it must, judging from the description, be very similar to *D. involucrata*. Alleged points of difference are the shorter peduncles (“1 cm” instead of 1.2-1.8) and smaller flowers (“15-18 × 7-8 mm” instead of 20-29 × 9-14 mm).

13. *Dionysia microphylla* Wendelbo in [Köie & Rech. f., Symb. Afghan. 4] Biol. Skr. 10(3): 68, fig. 26. 1958. – Holotype: Afghanistan, around 35°N, 65°E, *Edelberg 2313* (C; isotype: BG).

Contrary to the descriptions by Wendelbo and Grey-Wilson, the leaves usually have short hairs towards the base, not only sessile glands.

d. *Dionysia* subsect. *Heterotrichae* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 78. 1961. – Type: *D. lindbergii* Wendelbo

14. *Dionysia lindbergii* Wendelbo in Bot. Not. 112: 495, fig. 1. 1959. – Holotype: Afghanistan, Darreh Zang, *Lindberg 454* (BG; isotype: LD).

B. Western species

III. *Dionysia* sect. *Dionysiopsis* (Pax) Melchior in Mitt. Thüring. Bot. Vereins 50: 159. 1943 ≡ *Primula* sect. *Dionysiopsis* Pax in Jahresber. Schles. Ges. Vaterl. Cult. 87: 20. 1909 ≡ *Dionysia* sect. *Ariadna* Wendelbo in Bot. Not. 112: 496. 1959, nomen superfl. ≡ *Dionysia* sect. *Anacamptophyllum* subsect. *Scaposae* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 77. 1961. – Type: *D. bornmuelleri* Pax
= *Dionysia* sect. *Anacamptophyllum* Melchior in Mitt. Thüring. Bot. Vereins 50: 167. 1943. – Type: *D. aretioides* Lehm.
= *Dionysia* sect. *Anacamptophyllum* subsect. *Mirae* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 77. 1961. – Type: *D. mira* Wendelbo
= *Dionysia* sect. *Anacamptophyllum* subsect. *Revolutae* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 77. 1961. – Type: *D. revoluta* Boiss.

15. *Dionysia mira* Wendelbo in Bot. Not. 112: 500. 1959 \equiv *Primula aucheri* Jaub. & Spach, III. Pl. Orient. 1: 97, t. 49. 1842. – Holotype: Oman, Djebel Akdar, *Aucher-Eloy 5236* (P; isotypes: BM, G, K, UPS) – non *Dionysia aucheri* (Duby) Boiss., q.e. *D. odora*.

Grey-Wilson (1989) gives the calyx division as halfways. However, usually it is divided to at least $\frac{3}{4}$. Although this species is similar in detail to *Dionysia bornmuelleri*, it has a rather different habit.

16. *Dionysia bornmuelleri* (Pax) Clay, Present-Day Rock Gard.: 194. 1937 \equiv *Primula bornmuelleri* Pax in Jahresber. Schles. Ges. Vaterl. Cult. 87: 21. 1909. – Holotype: Iran, Kermanshah, Noah Kuh near Kerind, *Strauss 601* (B; isotypes: E, K, W).

In Grey-Wilson (1989) this species is said to have a smaller petal limb than *Dionysia mira*. At least as often the opposite relation holds.

17. *Dionysia viva* Lidén & Zetterlund, **sp. nov.**

Holotype: Iran, Fars, Vallyabad (29.47.19; 53.12.56), 1700 m, 22.4.2002, *Zschummel, Zschummel, Zetterlund & Tjerdsmas T4Z 035* (GB; isotypes: TARI, UPS) – Fig. 1.

Caespites laxi. *Folia* (petiolo incluso) 25-50 \times 7-13 mm, lamina obovata apice rotundata, in petiolum anguste alatum attenuata, margine plus minusve profunde sinuato-dentata vel duplo-dentata, subtus lanato-farinoso, pilis glandulosis et eglandulosis obsita. *Inflorescentia* e verticillis superpositis 1-2(-3)-nis approximatis 2-4-floris, scapo (2-)5-8 cm longo. *Bracteae* ovatae 12-18 \times 4-9 mm, grosse serratae. *Calyx* 9-10 mm longus, ad $\frac{2}{3}$ in segmenta late lanceolata divisus. *Corolla* (longistylis) 14 mm longa, flava, pilis crispatis glandulosis obsita, limbo 5-6 mm diametro lobis 2-2.5 mm longis subrectangularibus. *Capsula* c. 70-sperma, seminibus atrobrownis 0.5 mm longis subquadrangularibus.

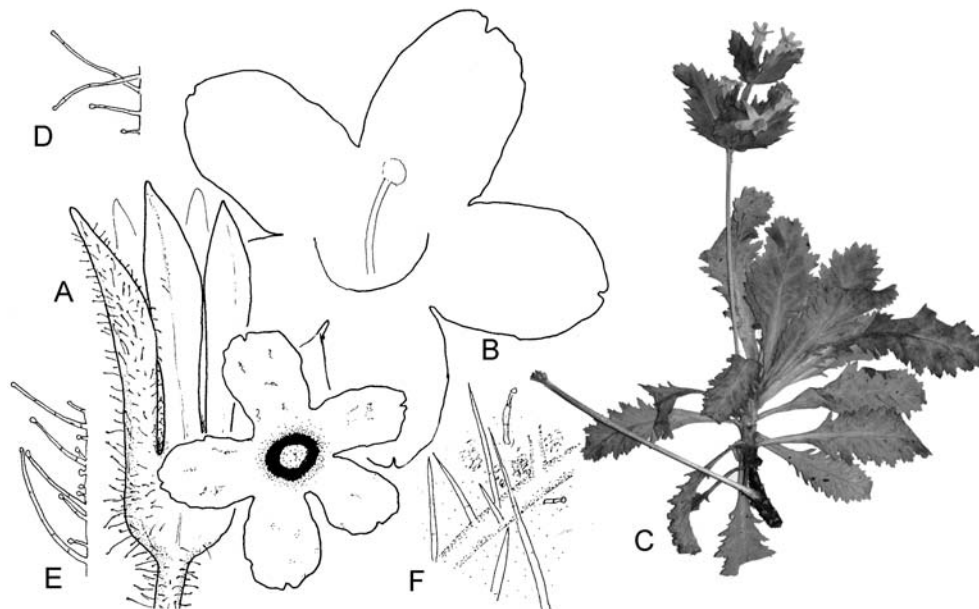


Fig. 1. *Dionysia viva* – A: calyx; B: corolla, showing size extremes in cultivation; C: whole plant; D-F: hair details, corolla (D), calyx (E), underside of leaf (F). – From the holotype (C) and flower details (A, D-F) from plants cultivated in the Göteborg Botanic Garden from seeds of the holotype.

Dionysia bornmuelleri Pax calyce fere ad basim diviso lobis angustioribus, tubo corollae profunde longiore, a *D. viva* differt.

Etymology. – Swedish “viva” means any species of the genus *Primula*.

Lax chasmophytic subshrub with leaves crowded at branch tips; each terminal rosette with 1-2 sparsely leafy “vegetative” axillary shoots, 2-6 cm long, eventually producing new terminal rosettes towards the end of the season, and with one flowering scape (rarely with second scape); defoliated stem segments with a reddish brown lustre; the leaf (remnants) crowded towards the end of the branches (stem segments) clearly discernible also in older parts; the amount of secondary growth modest, thickest stems 3-4 mm in diameter. *Indumentum* of green plant parts of (a) scattered sessile glands, (b) rather dense many-celled articulated glandular hairs 0.2-1 mm long, and especially on veins on the underside of leaves, (c) scattered coarse and straight, acute glandular hairs up to 1.5 mm. *Farina* woolly and mainly on the underside of leaves, at petiole bases and inside of calyx. *Leaves* (including petiole) 25-50 × 7-13 mm, narrowed into a long narrowly winged petiole, lamina obovate, with raised veins below, flat or (especially when young) with slightly revolute margin, coarsely dentate with obtuse to subacute primary teeth, each usually with 1-3 minute secondary teeth. *Scapes* (2-)5-8 cm long with 1-3 closely set whorls of flowers, each with 2-4 flowers. *Bracts* ovate, sessile, coarsely serrate, 9-17 × 4-9 mm (or the uppermost smaller). *Calyx* 9-10 mm, divided to $\frac{2}{3}$ into broadly oblanceolate lobes. *Corolla* (long-styled) yellow, sparsely crispate-glandular hairy in lower half, more densely so in upper half and on the underside of lobes; tube 14 mm long, limb 5-6 mm broad with lobes 2 mm long, obtusely sub-rectangular in shape, sometimes with a minute notch at apex; style in long-styled flowers exerted. *Capsule* rounded with up to 70 dark brown small angular seeds, 0.5 mm long.

Dionysia viva is vegetatively very similar to *D. bornmuelleri*, only somewhat less hairy and a bit smaller in all parts. It is, however, well separated on floral characters. In *D. bornmuelleri* the calyx is split almost to the base and the calyx lobes are narrow, the corolla tube is much longer (20-30 mm; in *D. viva* 14 mm) and the corolla lobes are differently shaped, being bluntly triangular. *D. bornmuelleri* is distributed far to the NW of *D. viva*.

The plants of *Dionysia viva* in cultivation are, as can be expected, larger in most vegetative parts, and the floral whorls are more distant. They show a surprising variation in floral width; one plant had flowers twice as broad as those of the type.

18. *Dionysia teucroides* P. H. Davis & Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 76. 1961. – Holotype: Turkey, Hakkari, Cilo Dag, in Diz derezi, 6.8.1954, P. H. Davis & Polunin 23884 (K; isotype: E).

19. *Dionysia aretioides* (Lehm.) Boiss., Diagn. Pl. Orient., ser. 1, 7: 68. 1846 ≡ *Primula aretioides* Lehm., Monogr. Primul.: 90, t. 9. 1817 ≡ *Gregoria aretioides* (Lehm.) Duby in Candolle, Prodr. 8: 46. 1844. – Holotype: N Iran, Ghilan, *Hablitz* (LE?; isotypes: B, BN, C, G, W). = *Dionysia demawendica* Bornm. in Beih. Bot. Centralbl., Abt. 2, 33: 301, t. 2 fig. 1. 1915. – Holotype: N Iran, foot of Mt Demawand, Abigerm, *Bruns* (B; not seen, teste Wendelbo).

20. *Dionysia leucotricha* Bornm. in Beih. Bot. Centralbl., Abt. 2, 28: 460. 1911 ≡ *Dionysia aretioides* var. *adenophora* Bornm. in Bull. Herb. Boissier, ser. 2, 3: 593, t. 6 fig. 5. 1903. – Holotype: Iran, Mt Elvend by Hamadan, *Strauss* (B; isotype: JE).

Superficially similar to *Dionysia aretioides* and *D. revoluta*, but immediately distinguished by the peculiar calyx with long hairs at base and broad dentate lobe-apices.

21. *Dionysia revoluta* Boiss., Diagn. Pl. Orient., ser. 1, 7: 65. 1846 ≡ *Primula revoluta* (Boiss.) Bornm. in Bull. Herb. Boissier 7: 73. 1899. – Holotype: Iran, Fars, Kuh-e-Sabzpuhon, *Kotschy* 426 (G; isotypes: B, BM, K, W).

= *Dionysia revoluta* var. *canescens* Boiss., Fl. Orient. 4: 18. 1879 ≡ *Dionysia revoluta* subsp. *canescens* (Boiss.) Wendelbo in Aarbok Univ. Bergen Mat.-Naturvitensk. Ser. 3: 48. 1961. –

Lectotype (designated by Wendelbo, id.): Iran, Luristan, Kuh Eschker, *Hausknecht* (G [not seen]).

This is the most common and widespread of the *Dionysia* species in Zagros. Although it is variable, it is questionable whether subsp. *canescens* can be upheld despite geographical trends. In the type locality, however, there are plants with dense long hairs occurring together with bright green individuals with only glandular hairs. Long glandular hairs are frequently found also on the corolla.

22. *Dionysia archibaldii* Wendelbo in Bot. Not. 120: 144. 1967. – Holotype: Iran, Bakhtiari, Tang-i-Sirdan, 4000 m, 8.1966, *Archibald 3053* (GB).
= *Dionysia bazoftica* Jamzad in Iran. J. Bot. 7: 20. 1996. – Holotype: Bakhtiari, Bazoft, Chebd, N slope of Kuh-e-Taraz, 1700-2300 m, *Mozaffarian 57824* (TARI).

The seedlings raised from the original Archibald collection gave rise to a very heterogeneous offspring (Grey-Wilson 1989: 90), as is indeed very common with *Dionysia*. The type material (GB, collected in the field) has broad, crenate-dentate leaves with long hairs and rather lush growth. The single Archibald clone still surviving in cultivation, however, is of a denser type with less hairy and strongly revolute almost entire leaves. It should be noted that at least part of Archibald's original introduction was collected at very high altitude late in the year.

After having seen a good number of individuals in the field, in cultivation, in herbaria and on photographs I have come to the conclusion that this and the following taxon are clearly separate species. In leaf morphology, they afford a striking parallel to the species pair *D. rhapsodes/oreodoxa* (24-25). Unlike these two they seem to have non-overlapping, though contiguous, distribution areas.

Jamzad (1996) described a new species, *Dionysia bazoftica*, said to differ from *D. archibaldii* i.a. in the possession of long hairs (she also lists differences in leaf arrangement, and a few other minor details). However, the type specimen of *D. archibaldii* indeed has long hairs, lush growth, rather broad, strongly crenate leaves, etc., and is in every respect similar to the type of *D. bazoftica*, which must accordingly be sunk in synonymy.

A population from the upper Kuhrang river was studied more closely by myself in 1998. The plants here vary a lot in indumentum: most have long hairs, but there are also some without. Presence of farina also varies within populations. General habit is partly depending on exposure, age and time of the year, but there is a very strong genetic component. In seed offspring from a single plant of this population (*SLIZE 115*, cult. Göteborg Botanic Garden) one is struck by the immense variation shown (much surpassing that of adult plants in the wild), both in vegetative and floral characters, clearly showing the high degree of heterozygosity in individuals of these populations, as indeed in many other species, such as *Dionysia aretioides*, *D. termeana* and *D. diapensiifolia*. Considerable variation in populations of *D. archibaldii* was noted by the T4Z expedition.

According to Grey-Wilson (1989) the corolla is sometimes slightly glandular-pubescent. The number of ovules are 4-8, but often only 3-4 seeds develop.

23. *Dionysia zschummelii* Lidén, **sp. nov.**

Holotype: Iran, Lorestan, between Aligoudarz and Shoulabad, Ghadee Kuh (33.06.42; 49.25.25), 2600-2700 m, 5.5.2002, *T4Z 166* (UPS; isotypes: GB, TARI) – Fig. 2.

A *Dionysia archibaldii* habitu densissimo, foliis minutis crassiusculis fere glabris differt.

Caespites densissimi non farinosi. *Folia* parva, sessilia, lamina oblona obtusa margine non crenato-dentata, profunde et abrupte revoluta, fere glabra. *Bractae* lineares. *Calyx* 3.5-4 mm longus, usque ad basin in lobis linearibus divisus. *Corolla* 10-14 mm longa, purpureo-lilacina vel lavandulacea, glabra, limbo 9-14 mm diametro lobis late ovatis vel obovatis profunde emarginatis stylo parce exserto. *Capsula* c. 4-sperma, seminibus atrobrunneis 0.9 mm longis.

Eponymy. – Named after Dieter Zschummel, who discovered this species and brought it into cultivation.

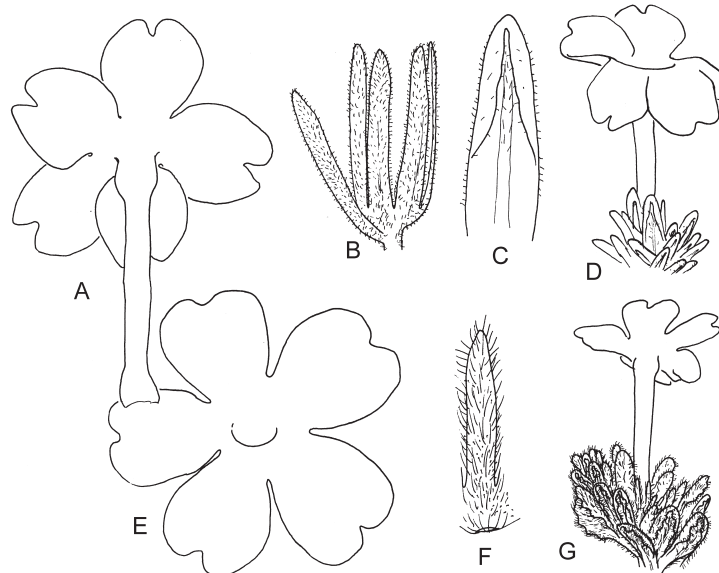


Fig 2. A-D: *Dionysia zschummelii* – corolla (A); calyx with bract (B); leaf, abaxial view (C); flowering branch (D); from plants cultivated in the Göteborg Botanic Garden from seeds of the type collection. – E-G: *D. archibaldii* – corolla (E); calyx segment (F); flowering branch (G); upper Kuhrang valley, SLIZE 115, UPS.

Very dense non-farinose cushions. *Leaves* 5-6 × 1.5 mm, bluish green, sparsely and shortly hairy; slightly longer hairs on the under side, but due to the sharply reflexed leaf margin these not visible. *Bracts* 2, 3.5-4 mm long, linear, shortly hairy abaxially, glabrous adaxially. *Calyx* 4(-4.5) mm, divided to the base into linear obtuse erect lobes, shortly hairy outside, glabrous inside. *Corolla* glabrous, pale lilac to lavender; tube 10-11 mm long; limb 10-12 mm across, divided into ovate rather deeply emarginate lobes. *Style* of long-styled flowers slightly exserted.

Dionysia zschummelii is a northern vicariant of *D. archibaldii* with extremely dense habit. It has small entire leaves with strongly inrolled leaf margins, so as to render the leaf subtrigonal-semicircular in cross-section. The few hairs are mainly confined to the edges where the pale greyish green thickish central plain of the upper leaf surface is more or less sharply reflexed into a darker more bluish green lateral side. The flowers are very similar to those of *D. archibaldii*. Plants in cultivation differ but little from those of wild populations.

Additional record. – Type locality: 7.5.2001, *Dionysia zschummel* 01-17 (UPS).

24. *Dionysia raptodes* Bunge in Bull. Acad. Imp. Sci. Saint-Petersbourg 16: 562. 1871. – Holotype: Iran, Kerman, between Chabbis and Kerman, 30.3.1859, *Bunge* (E; isotypes: G, K, P). = *Dionysia heterochroa* Bornm. in Bull. Herb. Boissier 7: 72, t. 2 fig. 3. 1899 ≡ *Primula heterochroa* (Bornm.) Bornm. in Bull. Herb. Boissier 7: 73. 1899. – Holotype: Kuh-i-Jupar, *Bornmüller* 3872 (B; isotypes: G, JE).

25. *Dionysia oreodoxa* Bornm. [*Primula oreodoxa* (non Franchet) Bornm. in nota] in Bull. Herb. Boissier 7: 68, t. 2 fig. 1. 1899 ≡ *Primula kermanensis* Bornm. in Bull. Herb. Boissier, ser. 2, 3: 592. 1903 – Holotype: Iran, Kerman, Kuh-i-Jupar, *Bornmüller* 3873b (B).

26. *Dionysia esfandiarii* Wendelbo in Bot. Not. 123: 302, fig. 2m-n. 1970. – Holotype: Iran, Abadeh, Bacanat, Kuh Khataban, 6.1969, *Termé* 8128E (GB; isotype: TARI).

This species is well described by Grey-Wilson (1989) although he complained that the material was immature. Material from the SLIZE expedition is now in cultivation in several places. It

lacks glandular hairs and is covered in long articulate hairs that are retrorse towards the apex of the leaf. The reflexed leaf margin is often slightly crenate-dentate, indicating relation with the other species in the section despite its widely divergent habitus, like a tight hairy ball.

IV. *Dionysia* sect. *Zoroasteranthos* Lidén, sect. nov.

Type: *Dionysia curviflora* Bunge

Plantae plus minusve caespitosae. *Folia* parva integra pilis articulatis longis non glanduliferis. *Bracteeae* parvae. *Flores* singulares sessiles. *Corolla* lilacina plerumque flavoannulata lobis emarginatis stylo incluso. *Semina* pauca sat magna.

Etymology. – *Zoroaster*, Farsi *Zarathushtra*, the founder of mazdaism, a very old belief system which in Iran has (had) a strong foothold in the Yazd area; Greek: *anthos* = flower.

27. *Dionysia curviflora* Bunge in Bull. Acad. Imp. Sci. Saint-Pétersbourg 16: 562. 1871 ≡ *Primula curviflora* (Bunge) Kuntze, Rev. Gen. Pl. 2: 400. 1891. – Holotype: Iran, Yazd, Schir Kuh, *Buhse 1352* (G; isotypes: B, P).

The corolla tube usually has a mixture of tiny eglandular and glandular hairs, rarely glabrous.

28. *Dionysia janthina* Bornm. & Winkl. in Bull. Herb. Boissier 7: 70, t. 2 fig. 2. 1899 ≡ *Primula janthina* (Bornm. & Winkl.) Bornm. in Bull. Herb. Boissier 7: 73. 1899. – Holotype: Iran, Yazd, [S of] Schir Kuh [proper], *Bornmüller 3869* (B; isotypes: BM, E, JE, K).

29. *Dionysia khatamii* Mozaff. in Pakistan J. Bot. 34: 391. 2002. – Holotype: Yazd, Mehriz, Darre Damgahan, in deep granitic stone wall, 2400-2550 m, *V. Mozaffarian 79250* (TARI; isotype: UPS).

This species was recently found and described by Valiollah Mozaffarian, and is in cultivation in a few gardens. It is similar to *Dionysia iranshahrii* in its narrow, densely pubescent leaves and violet flowers. It differs, however, in its less dense growth, much larger flowers with deeply divided calyx and narrower deeply emarginate petal lobes, and the presence of glands on the stem. It is not restricted to granitic rocks, but occurs on limestone as well.

V. *Dionysia* sect. *Mucida* Lidén, sect. nov.

Type: *Dionysia lurorum* Wendelbo

Herba perennis non pulvinaris dense farinosa. *Folia* late oblanceolata serrata vel integra. Inflorescentia scaposa 2-4-flori. *Bracteeae* grandes, saepe profunde serrato-dentatae. *Flores* lutei. *Semina* minuta numerosa (ad 100!).

Etymology. – From Latin *mucidus* = mouldy, referring to the woolly farina that usually covers much of the plant.

30. *Dionysia lurorum* Wendelbo in Notes Roy. Bot. Gard. Edinburgh 38: 105. 1980. – Holotype: Iran, Luristan, 61 km on road from Aligoudarz to Shoulabad (valley after the pass), 2400 m, 29.6.1977, *Runemark & Lazari 26216* (G; isotypes: E, TARI).

= *Dionysia aubretioides* Z. Jamzad & Mozaff. in Iran. J. Bot. 7: 19. 1996. – Holotype: Bakhtiari, Bazoft valley, Mavaraz, Talkhdan, Kuh-e-Mafaron (Kuh-e-Sefid) 2700 m, *Mozaffarian 74002* (TARI).

A homogenous and easily recognised species, very different from all other *Dionysia*. *D. aubretioides* was based on a shade-grown rather luxurious individual, but is in all details indistinguishable, and cultivated plants from the type locality do not differ from those from type locality of *D. lurorum*.

This species is sometimes completely covered in farina. Shade-grown plants are notable for their long and thin internodes, whereas plants from more exposed sites can be rather tight.

The rather isolated position of this species is emphasized by its combination of flat leaves, stalked inflorescences and numerous seeds. In the molecular tree (Trift & al. 2004) it appears as sister group to *Dionysia* sect. *Dionysia* with moderate support, but except for the flat leaves there are no obvious morphological synapomorphies.

VI. *Dionysia* sect. *Dionysia*

= *Dionysia* subsect. *Bryomorphae* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 78. 1961. – Type: *D. bryoides* Boiss.

[– *Dionysia* sect. *Epicamptophyllum* Melchior in Mitt. Thüring. Bot. Vereins 50: 167. 1943], nom. inval. (Art. 22.2 ICBN, McNeill & al. 2006) as this name is based on the type of the generic name.

[– *Dionysia* subsect. *Caespitosae* Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 77. 1961], nom. inval. (Art. 22.2 ICBN, McNeill & al. 2006) as this taxon explicitly includes *D. odorata*, the type of the generic name.

31. *Dionysia sawyeri* (Watt) Wendelbo in Aarbok Univ. Mat.-Naturvitensk. Ser. 3: 64. 1961 ≡ *Primula sawyeri* Watt, Report Bot. Coll. SW Persia H. A. Sawyer: 94. 1891. – Holotype: W Iran, Kar Kanun, Kuhrang, Sawyer (not found by Wendelbo or me, probably lost).

= *Dionysia bachtiarica* Bornm. & Alexeenko in Bull. Herb. Boissier, ser. 2, 4: 515, t. 2 fig. 3. 1905 ≡ *Primula bachtiarica* Bornm. in Bull. Herb. Boissier, ser. 2, 4: 515. 1905. – Holotype: Iran, Kellar, Alexeenko 2722 (B, not seen, teste Wendelbo).

The application of the epithet *sawyeri* is not absolutely certain, as the type is lost, but *Dionysia bachtiarica* from the same area, was considered synonymous by Wendelbo, based on the presence of stout marginal hairs on the leaves. I will accept this opinion. The type of *D. bachtiarica* is in B (Alexeenko 2722), but there are two more specimens in LE (Fig. 3) under different numbers (“ad rupes N jugi Kellar”, 8.9.1903 [cal. jul.], Alexeenko 821; “Vallis Lebze (?) in declivibus ad jugi Kellar ad rupes N”, 4.1902 [cal. jul.], Alexeenko 827).

The colour of the corolla was given as yellowish with pale purple limb in the original description, which can be variously interpreted. The tube is often very pale in purple flowered species, but hardly yellowish. There are some purple flowered species with a yellow “eye”, and hybrids between yellow and purple species may show more yellow. Further, it is not uncommon for yellow corollas of *Dionysia* to turn brown, green or even greenish blue in herbarium specimens. The flower colour of this species is thus doubtful, although purple is perhaps the most probable.

Dionysia sawyeri is only tentatively placed in the section *Dionysia* and was not included in the molecular study by Trift & al. (2004). It deviates in its glabrous corolla with deeply emarginate lobes and the high number of seeds per capsule. 24 ovules can be found in one ovary, compared to 3-5 in the other species. It differs also in the pronounced foliar heteromorphism. The early summer leaves (of “vegetative” shoots) are up to five times as long as subsequent (over-wintering) leaves, and much thinner and greener. The leaves are always completely glabrous abaxially, but have a varying amount of long hairs on the adaxial side (Fig. 3).

The type of *Dionysia sawyeri* was collected by Sawyer in “Kar Kanun, Kuhrang”, whereas Alexeenko's collections are from “Kellar”. Kellar is, according to Wendelbo (1965), the same as Kuh-e Kukalar (= Kuh-e Kallar). Mozaffarian collected rich *Dionysia* material on Kuh-e Kallar S of Sibak, 4.7.1986, M 57420, 57399 (TARI). These plants, however, belong to *D. lamingtonii*. Zschummel looked for this species on the N side of Kuh-e Kallar in 2001, but found only *D. caespitosa* (Zschummel 01-12, UPS). Possibly, *D. sawyeri* does not grow in the same kind of habitats as most other species of *Dionysia*.

32. *Dionysia iranshahrii* Wendelbo in Iran. J. Bot. 1: 72. 1976. – Holotype: W Iran, Bakhtiari, Kuh Pashmaku W Semirom, 6.1974, M. *Iranshar* (Ministry of Agriculture, Evin, Tehran; isotypes: GB, TARI).

Like the previous species, this occupies a somewhat isolated position in the section, both in morphology and according to the molecular tree (Trift & al. 2004) where it is the sister species to

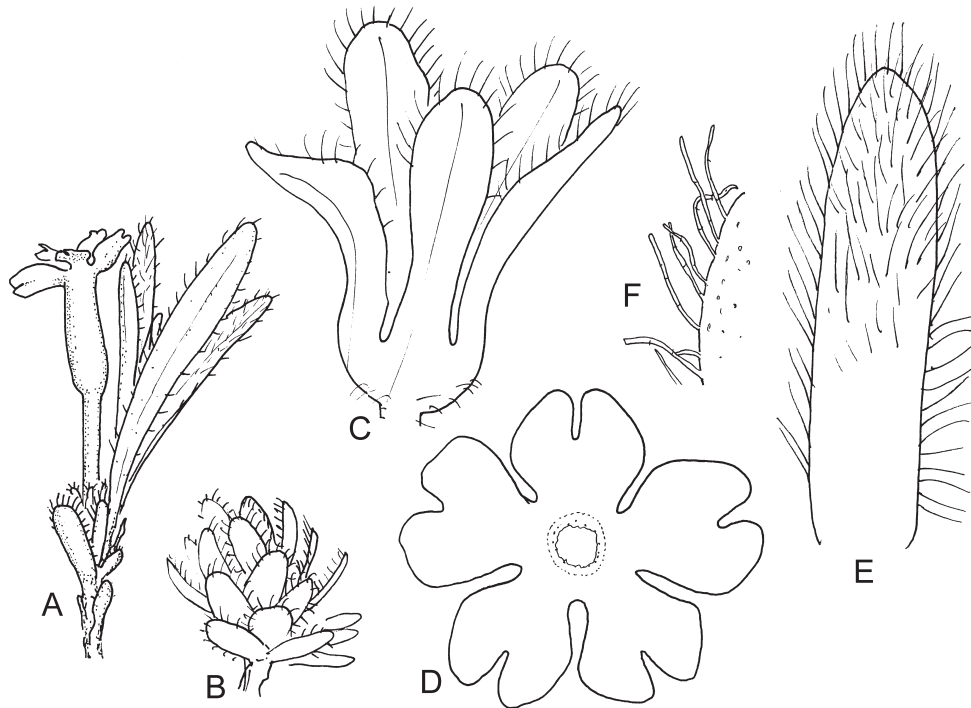


Fig. 3. *Dionysia sawyeri* – A: flowering branch with fresh axillary shoot; B: old shoot (overwintering); C: calyx; D: corolla; E: small leaf from above; F: marginal hairs of leaf. – From Alexeenko 821, LE.

the rest of the section (*Dionysia sawyeri* not included). It has a glabrous corolla in common with *D. sawyeri*, but is otherwise not similar.

In Grey-Wilson (1989) it is depicted with deeply divided calyx, but usually this is divided to only $\frac{1}{2}$ or at most to $\frac{2}{3}$. In the cliffs of the Kuh Pashmaku it is often found growing in places well protected from overhead water. It has proven rather difficult to keep in cultivation.

33. *Dionysia caespitosa* (Duby) Boiss., *Diagn. Pl. Orient. ser. 1, 7: 67. 1846* \equiv *Gregoria caespitosa* Duby in Candolle, *Prodr. 8: 46. 1844* \equiv *Macrosiphonia caespitosa* (Duby) Duby in *Mem. Soc. Phys. Genève 1844: 427. 1844* \equiv *Primula macrosiphonia* Kuntze, *Rev. Gen. Pl. 2: 400. 1891*. – Lectotype (designated by Grey-Wilson 1989): Iran, Elwend Kuh, near Esfahan, *Aucher-Eloy 2609* (K; isolectotypes: BM, P).

= *Dionysia peduncularis* Bornm. in *Bull. Herb. Boissier, ser. 2, 5: 261. 1905*. – Holotype: W Iran, Kohrud, 4.1904, *Strauss* (B, not seen, teste Wendelbo).

= *Dionysia bolivari* Pau in *Trab. Mus. Ci. Nat., Ser. Bot. 14: 27. 1918* \equiv *Dionysia caespitosa* subsp. *bolivarii* (Pau) Grey-Wilson, *Gen. Dionysia: 99. 1989*. – Holotype: W Iran, Bazoft valley, *Escalera 1899* (MA, not seen, teste Wendelbo).

According to Jamzad (1996) *Dionysia bolivari* is not distinct enough to be recognised as separate taxon.

The corolla is glandular pubescent (illustrated with glabrous corolla in Grey-Wilson 1989) and sometimes has dense farina. Farina is rare in the section *Dionysia*, and is in *D. caespitosa* confined to the (upper part of the) exterior of the corolla and the interior of calyx. For the only other occasion of farina in this section, see discussion under *D. diapensifolia*.

34. *Dionysia gaubae* Bornm. in Feddes Repert. Spec. Nov. Regni Veg. 41: 179. 1937. – Holotype: Iran, Luristan, Khorramabad, Pole-Kalhor, 4.1936, *Gaubae* (B).

This rare species was recently refound (Lorestan: Peesh Kuh [32.58.26; 49.37.21], 2450 m. 6.5 2002, *T4Z 190*, UPS). Its closest relative appears to be *Dionysia odora*, which differs in crispate-hairy leaves, more discrete leaf whorls and not strongly reflexed marcescent leaves.

Dionysia gaubae var. *megalantha* Lidén, var. nov.

Holotype: Iran, Lorestan: Peesh Kuh, *T4Z 1028* (UPS) – Fig. 4.

Caespites densiusculi efarinosi, caulis foliatus ramosus foliis marcescentibus valde revolutis obsitus. *Folia* viridia, obovata vel oblanceolata, hirsuta obsita, pilis longitudine varia glanduliferis praeter pilis longissimis eglandulosis. *Flos* plerumque solitarius, sessilis. *Bractee* anguste oblanceolatae non vel parce dentatae, dense glanduloso-hirsutae. *Calyx* 8-10 mm longus, ad $\frac{4}{5}$ in lobis anguste oblongis fissus, extus et intus dense glanduloso-hirsutus. *Corolla* laete flava, 20-28 mm longa, saepe leviter curvata, extus dense glanduloso-hirsuta limbo 13-16 mm lato lobis ellipticis vel obovatis integris. In flore longistylis stylus ex corolla manifeste excertus. *Ovarium* 5-ovulatum. *Capsula* ignota.

Etymology. – From Greek *megalos* = very big and *anthos* = flower.

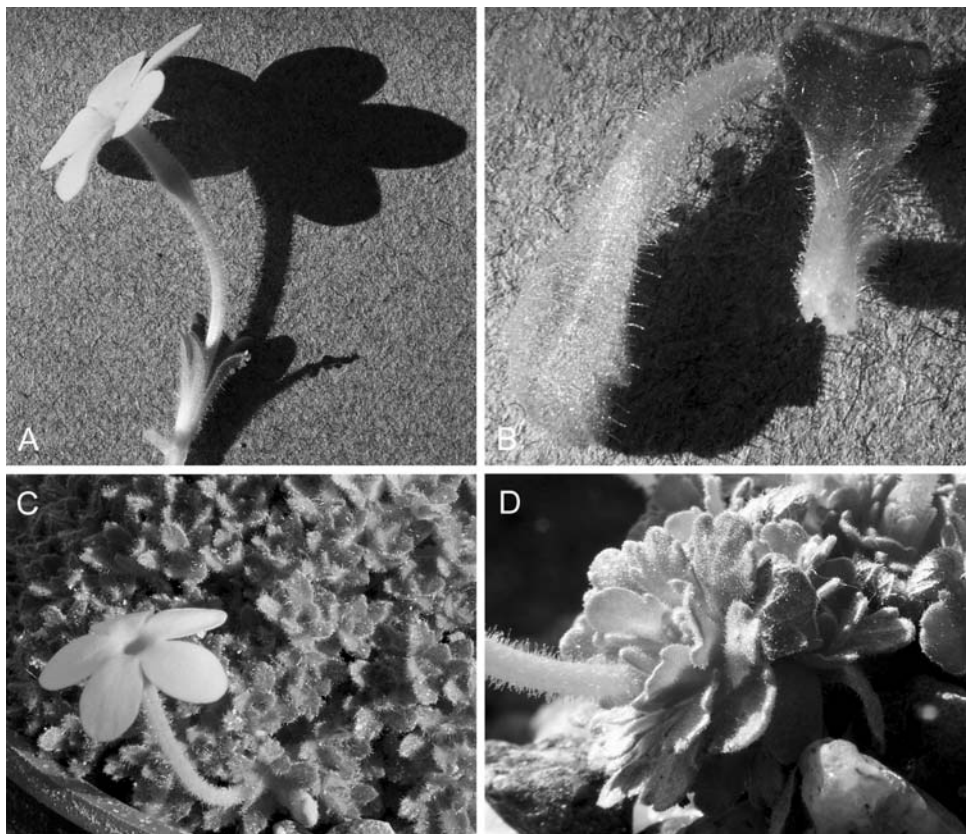


Fig. 4. A-B: *Dionysia gaubae* var. *megalantha* – flower (A); leaf, left adaxial view, right abaxial view (B); cutting from holotype cultivated in the Göteborg Botanic Garden. – C: *D. odora* – flowering plant; Prov. Kermanshah, Kuh-e-Parou, KMZ 9511, cultivated Göteborg Botanic Garden. – D: *D. gaubae* var. *gaubae* – flowering plant; *T4Z 190*, cultivated Göteborg Botanic Garden.

Suffruticose efarinose perennial forming rather lax cushions. *Stems* leafy and branched, densely glandular hairy when young, becoming pale reddish brown; new growth with more distant leaves at first, eventually very densely leafy towards the apex; dead (marcescent) leaves remaining on the stem for up to 4 years, usually rolled backwards, often as much as to form a little coil. *Leaves* green, 6-17 × 2.5-4 mm, gradually attenuate into a pale petiole again becoming slightly wider at the point of attachment, covered all over with glandular hairs, from very short or subsessile to at least 0.5 mm, and more sparsely with longer articulate hairs (up to 1.1 mm) that usually lack a gland; *lamina* obovate in outline, with 4-6 large blunt teeth; on each branch, the lower, first formed, sparsely set leaves are much longer than the ones in the apical overwintering flowering leaf rosette. *Inflorescence* sessile, 1(-2)-flowered. *Bracts* 1-2, 7-10 mm long, narrowly oblanceolate, entire or with a few teeth, densely glandular hairy on both sides. *Calyx* 8-10 mm long, cleft to $\frac{4}{5}$ into narrowly oblong lobes, glandular hairy on both sides. *Corolla* (long-styled) bright yellow (paler beneath), 20-28 mm long, often slightly curved, densely hairy with long and short glandular hairs; limb 13-16 mm broad, divided into elliptic to obovate slightly overlapping lobes. *Style* exerted 1-4 mm, eventually even up to 7 mm. *Stamens* situated very high up, $\frac{1}{4}$ to $\frac{1}{3}$ from the throat of the corolla. *Capsule* and seeds not known; number of ovules 5.

This variety is similar to *Dionysia gaubae* sensu stricto in general habit and in the strongly back-rolled marcescent leaves, but differs in the much longer indumentum, the much larger calyx and the longer and comparatively narrower leaves. "Typical" *D. gaubae* has only glandular hairs, rarely longer than 0.2 mm. Our plant differs from *D. odora* in the much larger calyx, the much longer "vegetative" leaves that roll back when withering and in the large corolla with longer hairs on the tube.

It grows in close proximity to the *Dionysia gaubae* population mentioned above (T4Z 190), and the specimen was selected for its large flowers. To emphasise its very deviating morphology I have chosen to give it a formal recognition but lack information on the variation pattern in the population.

35. *Dionysia odora* Fenzl in Flora 26: 390. 1843 ≡ *Primula odora* (Fenzl) Kuntze, Revis. Gen. Pl. 2: 400. 1891. – Holotype: Iraq, Kurdistan, Mt Gara, *Kotschy* 386 (W; isotypes: B, BM, G, K). = *Gregoria aucheri* Duby in Candolle, Prodr. 8: 46. 1844 ≡ *Dionysia aucheri* (Duby) Boiss., Fl. Orient. 4: 19. 1879. – Holotype: Iran/Iraq, Nal Kuh, *Aucher-Eloy* 2832 (G; isotypes: BM, K). = *Dionysia straussii* Bornm. & Hausskn. in Bull. Herb. Boissier, ser 2, 3: 591, t. 6 fig. 1. 1903 ≡ *Dionysia odora* subsp. *straussii* (Bornm. & Hausskn.) Bornm. in Beih. Bot. Centralbl., Abt. 2, 28: 462. 1911 ≡ *Dionysia odora* var. *straussii* (Bornm. & Hausskn.) Bornm. in Beih. Bot. Centralbl., Abt. 2, 33: 167. 1915. – Holotype: Iran, Kuh Gerru, near Burudjerd, 6.1902, *T. Strauss* (J(?); isotype: S). ?= *Dionysia odora* var. *integrifolia* Bornm. in Beih. Bot. Centralbl., Abt. 2, 33: 167. 1915. – Holotype: not seen. = *Dionysia sintenisii* Bornm. in Bull. Herb. Boissier, ser. 2, 3: 592, t. 6 fig. 3. 1903. – Holotype: Turkey, Mardin, Bakahri, *Sintenis* 1282 (B; isotypes: G, K).

36. *Dionysia haussknechtii* Bornm. & Strauss in Bull. Herb. Boissier, ser. 2, 4: 514, t. 2 fig. 2. 1904 ≡ *Primula haussknechtii* (Bornm. & Strauss) Bornm. in Bull. Herb. Boissier, ser. 2, 4: 516. 1904. – Holotype: Iran, Luristan, Shuturun Kuh, *T. Strauss* 1903 (B).

37. *Dionysia cristagalli* Lidén, **sp. nov.**

Holotype: Iran, Lorestan, 61 km from Aligodarz to Shoulabad, 2 400 m, lime cliffs, 29.6.1971. *Runemark & Lazaro* 26215 (TARI) – Fig. 5.

Caespites densissimi grisei efarinosi, caulis numerosis foliis dense imbricatis. *Folia* anguste elliptica, subtus sparse et breviter glandulosa, supra et margine pilis glandulosis et eglandulosis obsita. *Pili* eglandulosi apicales basin confluentes cristam membranaceam albida formantes. *Bracteae* 1-2 lineare-oblongae foliis similes. *Calyx* usque ad basin in lobis anguste oblanceolatis fissus. *Corolla* flava, extus pubescens, lobis obcordatis. *Ovarium* 3-5-ovulatum.

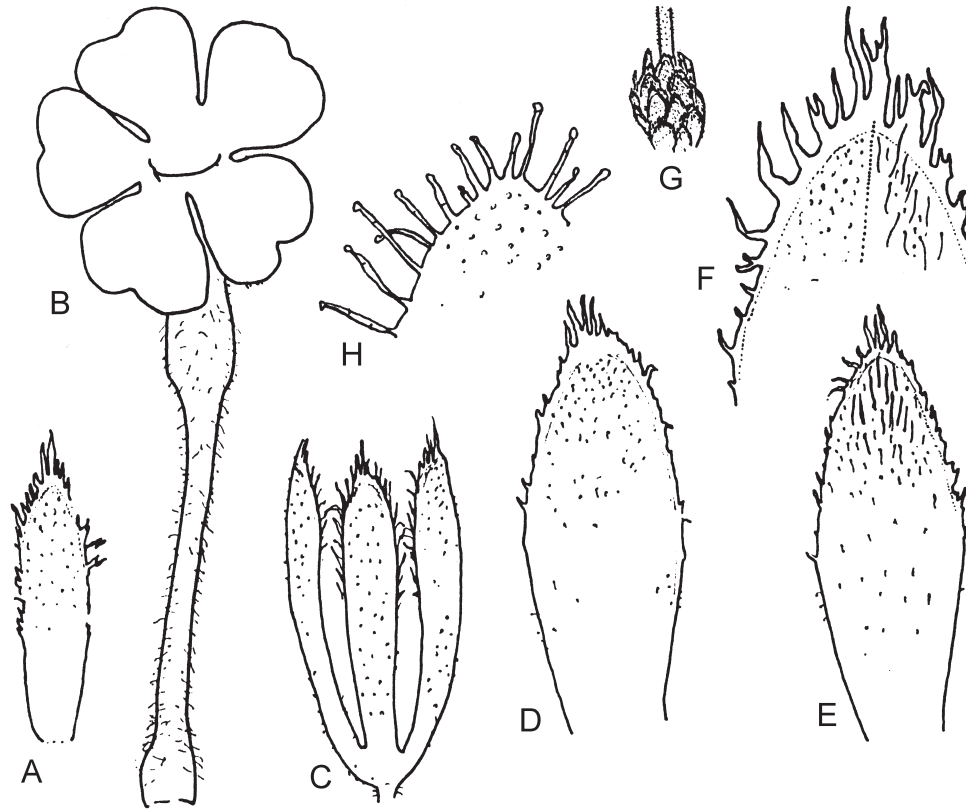


Fig. 5. A-G: *Dionysia crista gallii* – bract (A); corolla (B); calyx (C); leaf, lower side (D); leaf, upper side (E); apex of leaf (F); flowering branch (G); from the type. – H: *Dionysia haussknechtii* – apex of leaf; from the type.

Etymology. – From Latin *crista* = crest and *gallus* = cock.

Dense cushions, rather similar to *Dionysia haussknechtii*, but more grey in appearance. *Branches* eventually becoming bare below, but densely clad with closely imbricate marcescent leaves for at least one cm, and more straight and “columnar” than those of *haussknechtii*; the difference between early and late leaves not pronounced, but the young overwintering shoots produced in autumn being quite discrete, ovate, with closely packed leaves. *Leaves* narrowly obovate-elliptic, 3-4 × 1-1.5 mm, often slightly involute, at apex with a conspicuous crest of whitish basally confluent hairs; both sides of leaf beset with short-stalked capitate glands, longer hairs (both glandular and eglandular) confined to the distal part of the adaxial side (as is common in *Dionysia*). *Flowers* sessile. *Bracts* 1-2, like the leaves, but shorter and narrower, 2-2.5 × 0.5-0.7 mm. *Calyx* almost 3 mm long, divided to the base into narrowly oblanceolate lobes, similar to the bracts, and (like the leaves) equipped with an apical crest of basally confluent hairs. *Corolla* yellow, externally glandular-pubescent, (7-)9-12 mm; limb 5-6 mm broad, divided into obcordate emarginate lobes. *Capsule* narrower than in most other species of the genus, containing 3-5 seeds.

The whitish membranous lacerate fringe that ornates the apices of leaves, bracts and calyx lobes, immediately set this species apart from all other *Dionysia* species.

Additional records. – Lorestan, between Aligouzarz and Shoulabad, Ghadee Kuh (33.06.51; 49.24.53), 2500 m, 5.5.2002, T4Z 175 (UPS); id., 7.5.2001, Zschummel 01-18 (UPS).

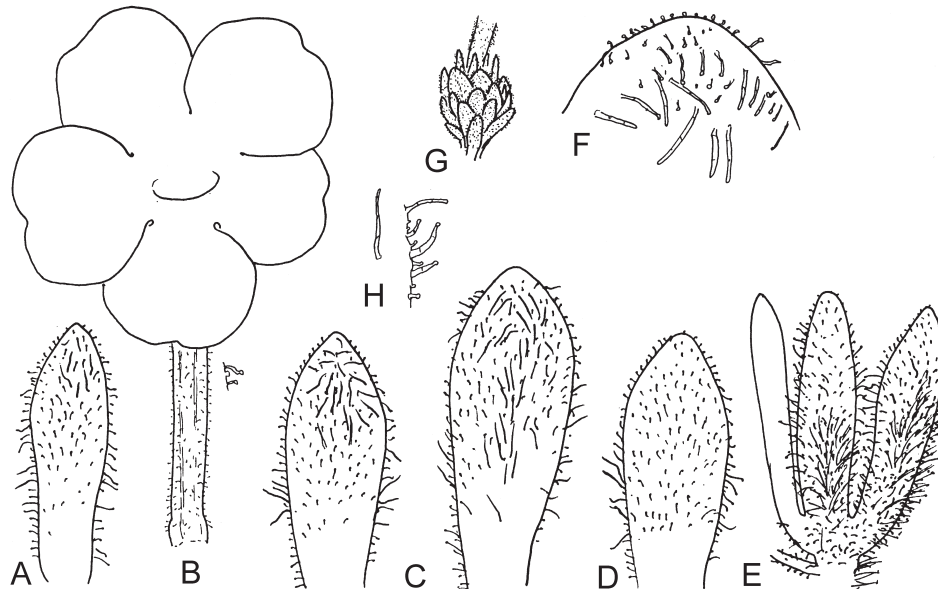


Fig. 6. *Dionysia zetterlundii* – A: bract; B: corolla; C: leaf, upper side; D: leaf, lower side; E: calyx; F: apex of leaf from above; G: flowering branch; H: hair details, left corolla, right leaf margin. – From plants cultivated in the Göteborg Botanic Garden from seeds of the type collection.

38. *Dionysia zetterlundii* Lidén, sp. nov.

Holotype: Bachtari Charee pass to Bazoft valley (32.11.26; 50.11.58), 2700 m, 30.4.2002, T4Z 125 (GB; isotypes: UPS, TARI) – Fig. 6.

Caespites densissimi efarinosi, ramulis numerosis foliis dense imbricatis. *Folia* obovata obtusa glanduloso-hirsuta, superne cum pilis eglandulosis longis immixtis. *Bractee* 1-2, foliis similes. *Calyx* ad $\frac{5}{6}$ in lobis oblongis fissus. *Corolla* flava, extus pubescens, lobi late obcordati. *Ovarium* 4-5-ovulatum.

Dense cushions, efarinose, with stems clad with marcescent leaves, eventually becoming bare in the older parts; most parts of the plant rather densely equipped with short to rather long glandular hairs. *Leaves* entire, obovate, obtuse to subobtuse, slightly involute, 3-4.5 × 1.3-1.7 mm; in seedlings broad leaves with a couple of apical teeth may form, but soon succeeded by entire leaves; lamina densely set with glandular hairs of varying length, and on the adaxial side (especially in the distal part) with long eglandular straight hairs perpendicular to the leaf surface or (towards the upper margin) retrorse; rarely, long eglandular hairs occur also on the abaxial side of the leaves. *Bracts* 1-2, like the leaves, 3-3.5 × 1 mm. *Calyx* 3-3.5 mm, split to $\frac{5}{6}$ in oblong to oblong-elliptic obtuse lobes, glandular pubescent like the leaves. *Corolla* yellow, with 10-14 mm long tube, externally densely pubescent with short-stalked glands; limb 9-10 mm broad with broadly obcordate overlapping slightly emarginate lobes. *Ovary* with 4-5 ovules.

Hardly to be confused with other species. *Dionysia haussknechtii* is superficially similar, but differs clearly in long marginal glandular hairs and absence of eglandular hairs, and in smaller calyx divided to the base.

Growing on limestone, mostly on vertical and overhanging cliffs, in the Charee (Cheri) pass between the Kuhrang and Bazoft river valleys in West-Central Zagros.

Eponymy. – Named after Henrik Zetterlund, a member of the T4Z team who found this species and brought it into cultivation. Henrik has – since the time of Per Wendelbo – maintained the

worlds largest living collection of *Dionysia* in the Göteborg Botanic Garden, a collection that has been and is of prime importance for research on taxonomy, phylogeny, anatomy and chemistry of the genus.

Additional record. – Charee pass (32.09.44; 50.10.44), 3.5.2002, T4Z 140 (UPS).

Note. – This species was provisionally called *Dionysia heterotricha* in cultivation in Gothenburg Botanic Garden, a name which – although never published – may have diffused into *Dionysia* circles. Due to the presence of the unrelated subsection *Heterotrichae*, this name would, however, cause confusion, and has therefore been abandoned.

39. *Dionysia tacamahaca* Lidén, sp. nov.

Holotype: Iran, Kermanshah, Bimar Mt., near Hukani Vill., South Kerend, 1500 m, *Wendelbo & Assadi 16761* (TARI) – Fig. 7.

Caespites densissimi, grisei, efarinosi, ramulis numerosis foliis marcescentibus tectis. Folia anguste obovata subacuta, dense glanduloso-hirsuta. Bracteae 2, lineares. Calyx ad 1/2 usque ad 3/5 in lobis late ovato-lanceolatis subacutis fissus. Corolla flava, extus pubescens, lobis ovatis non emarginatis. Ovarium 3-5-ovulatum.

Etymology. – Spanish *tacamahaca* (from Nahuatl: *tecamaca*) = balsam, with aromatic resin (cfr. *Populus tecamaca* = *P. balsamifera*).

Dense aromatic greyish green cushions with stems in the upper part covered with marcescent leaves. No pronounced difference between early and late leaves. *Leaves* 3-4.5 × 1.3-1.6 mm, slightly bent outwards, narrowly obovate, subacute, densely covered on both surfaces with both short and rather long glandular hairs; the marginal hairs are longer in the lower half of the leaf; the longest hairs sometimes lack an apical gland. *Flowers* sessile. *Bracts* 1-2, linear, shorter than calyx. *Calyx* campanulate, 3.5-4.5 mm long, split about halfway into broadly ovate-lanceolate

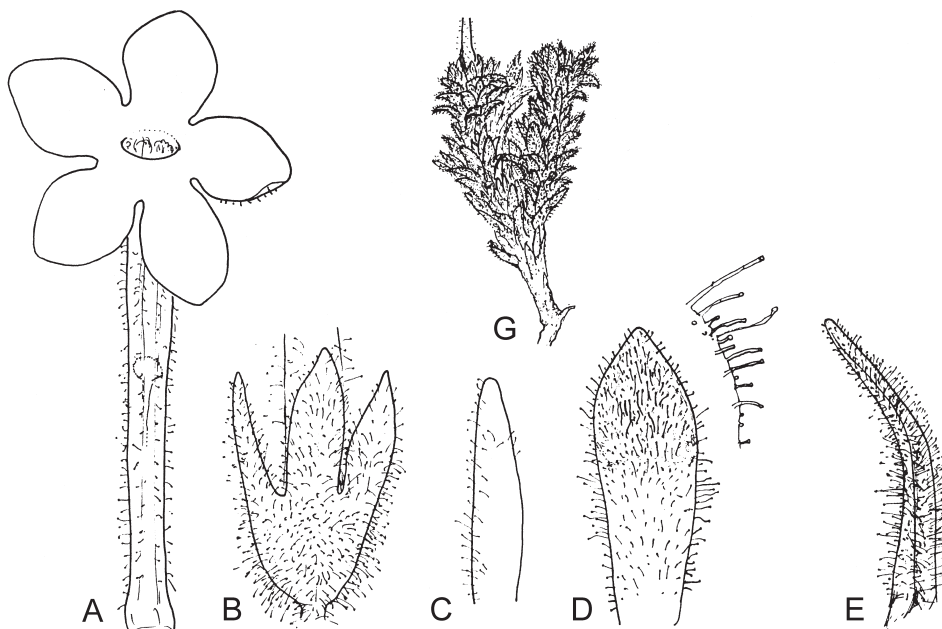


Fig. 7. *Dionysia tacamahaca* – A: corolla; B: calyx; C: bract; D: leaf from above; E: leaf in profile; F: hairs on leaf margin; G: flowering branch. – From the type.

acute lobes. *Corolla* yellow, externally glandular-pubescent; tube c. 10 mm long; limb 7-8 mm broad, lobes ovate-subacute. *Ovary* with 3 to 5 ovules.

Dionysia tacamahaca cannot be easily confused with other species. It is slightly similar to *D. zetterlundii*, but differs in several characters, such as the rather homogenous indumentum, acute leaves, and the large calyx that is cleft only to half or at most up to two thirds. *Tarakli & al. 2385* differs from the type in larger calyx (4.5-5 mm) divided to two thirds into oblong lobes, but is similar in indumentum and leaf form (flowers are lacking). Possibly, the calyx lobes enlarge after flowering.

Additional record. – *Tarakli & al. 2835* (TARI). I have at present no locality information for this specimen.

40. *Dionysia lamingtonii* Stapf in Bull. Misc. Inform. Kew 1913: 43. 1913. – Holotype: Iran, Bakhtiari, 7.1912, *Lamington* (K).

This species has been collected several times in recent years by V. Mozaffarian (e.g., Kuh-e Kallar, Chebd, Chelgerd Kuh, Zardlich, all TARI). The small thickish blue-green eglandular leaves with distinct venation and long soft crispate hairs makes the species unmistakable. In earlier descriptions (Wendelbo 1961, Grey-Wilson 1989) the leaves are said to be glabrous above and hairy below. On the contrary, the long coarse hairs so typical of this species are more prominent on the adaxial side of the leaf. They may even be absent from the abaxial side, but never from the adaxial side. Pubescence varies a lot, even between successive leaves on the same stem. A segment with leaves glabrous on the outside can be followed by one with rather densely hairy leaves.

41. *Dionysia mozaffarianii* Lidén in Iran. J. Bot. 8: 304. 2000. – Holotype: Chaharmahale Bakhtiari, Semrom, at the entrance into the city from the Shahreza road (3°26'N, 51°35'E), West-facing lime cliffs, 17.5.1998, *Lidén, Mozaffarian, Popp & Seisums SLIZE 232* (TARI; isotype: UPS).

42. *Dionysia iranica* Z. Jamzad in Iran. J. Bot. 7: 23. 1996. – Holotype: Bakhtiari, Lordegan, Monj, Badamestan Kuh, N of Bon-e-Gerd, 1500-2350 m, *Mozaffarian 54700* (TARI).

Recent material (*T4Z 118*, UPS) of this fine species, from more exposed sites at the type locality, deviates slightly from the type in that the plants are much more compact and the marcescent leaves not or only very slightly reflexed.

43. *Dionysia zagrica* Grey-Wilson in Kew Bull. 29: 691. 1974. – Holotype: W Iran, Kuh-i-Sehquata, 58 km N Pataveh (= Patureh), *Hewer 2023* (K; isotypes: GB, W).

This species has recently been recollected (Zhelgerd tunnel), probably close to the type locality. For a comparison with *Dionysia khuzistanica*, see that species.

44. *Dionysia khuzistanica* Z. Jamzad in Iran. J. Bot. 7: 25. 1996. – Holotype: Khuzestan, Dehdez, Kuh-e-Sefid opposite Sar Sahra village and Bazoft valley, *Mozaffarian 74001* (TARI).

Very similar to *Dionysia zagrica*, and evidently closely related, but with considerably harder cushions and with shorter leaves. They both have rather stiff and thick flat leaves with the sclereid reinforcements clearly visible externally as more or less longitudinal striae, and yellow flowers with small narrowly elliptic usually entire lobes. The style in longistylous flowers is slightly exerted. The characters given by Jamzad (1996) to differentiate the two species do not hold (Table 2.). She gave the corolla of *D. khuzistanica* as glabrous, in contrast to that of *D. zagrica*; actually both have hairy corollas, *D. zagrica* rather less so than *D. khuzistanica*. A similar situation obtains with the calyx. That of *D. zagrica* is if anything more deeply divided than that of *D. khuzistanica*, contrary to Jamzad.

45. *Dionysia termeana* Wendelbo in Bot. Not. 123: 306, fig. 2g-i. 1970. – Holotype: Iran, Kuh-i-Dena, Sisakht to Gadaneh-Bidjan, 6.1969, *Termé 8131E* (GB; isotype: TARI).

Table 2. Comparison between *Dionysia zagrica* and *D. khuzistanica*.

	<i>D. zagrica</i>	<i>D. khuzistanica</i>
Leaves	obovate, subobtusate	broadly ovate, acute, sometimes trifid
Glandular hairs	sessile	very shortly stalked
Calyx	divided $4/5$ - $5/6$	divided $3/4$ - $4/5$
Calyx lobes	oblanceolate with narrow base	narrowly triangular, broadest at the base

Dionysia termeana is extremely variable in habit; plants growing in more shady situations are generally broad-leaved and lush, whereas plants from drier and more exposed stations are pulvinate with small leaves. It is thus understandable that it has been attributed to both “*Bryomorphae*” and “*Caespitosae*” by different authors. Experience from cultivation shows that this variation is to a large extent genetically based. It is erroneously illustrated by Grey-Wilson (1989) as having glabrous corolla.

46. *Dionysia michauxii* (Duby) Boiss., Diagn. Pl. Orient., ser. 1, 7: 67. 1846 ≡ *Gregoria michauxii* Duby in Candolle, Prodr. 8: 46. 1844 ≡ *Primula michauxii* (Duby) Kuntze, Revis. Gen. Pl. 2: 400. 1891. – Holotype: “Persia”, 1783-84, *Michaux* (G; isotypes: K, P).

This species grows very abundantly on the mountain behind the university library in Shiraz, where it was collected by Wendelbo and Bokhari and later (1998) by the SLIZE expedition. As Michaux gave only “Persia” on his label, there is no reason to consider the other known locality “Bamu” to be the type locality, as stated by Grey-Wilson (1989: 124). The species has a peculiar dense pubescence of rather short retrorse acute eglandular hairs. It is not confined to vertical cliffs, but also grows on gentle slopes.

47. *Dionysia bryoides* Boiss., Diagn. Pl. Orient., ser. 1, 7: 66. 1846 ≡ *Dionysia kotschyi* Bunge in Bull. Acad. Imp. Sci. Saint-Pétersbourg 16: 560. 1871, nom. illeg. ≡ *Primula bryoides* (Boiss.) Kuntze, Rev. Gen. Pl. 2: 400. 1891 [as *bryodes*] ≡ *Primula kotschyi* (Bunge) Kuntze, Rev. Gen. Pl. 2: 400. 1891, nom. illeg. – Holotype: Iran, Fars, Kuh Ayub, *Kotschy* G([?]; isotypes: BM, K, UPS, W); probably same as *Kotschy 406b*: B, LE, P).

One of the more widespread of the Zagros *Dionysias*, occurring as far north as the vicinity of Semirom (Gardane-e Shir, *Nowroozi* 2139, TARI). In general, the northern colonies seem to have slightly longer glandular hairs than those from Fars.

48. *Dionysia diapensiifolia* Boiss., Diagn. Pl. Orient., ser. 1, 7: 65. 1846 ≡ *Dionysia drabaefolia* Bunge in Bull. Acad. Imp. Sci. Saint-Pétersbourg 16: 558. 1871, nom. illeg. ≡ *Primula drabifolia* (Bunge) Kuntze, Rev. Gen. Pl. 2: 400. 1891 ≡ *Primula diapensiifolia* (Boiss.) Kuntze, Rev. Gen. Pl. 2: 400. 1891, nom. illeg. – Holotype: Iran, Fars, near Persepolis, *Kotschy* 236 (G; isotypes: BG, BM, K, LE, PO, W).

Dionysia drabaefolia was described from what appears to be an isotype of *D. diapensiifolia* in LE, distributed to P.

This species may rarely have a peduncle up to 20 mm, and with 2 flowers. Some populations included here by Wendelbo, have entire leaves and corollas that may have farina on the apical outside, like is sometimes seen in *Dionysia caespitosa*. More research is needed. Possibly this represents an undescribed species.

49. *Dionysia sarvestanica* Z. Jamzad & Grey-Wilson in Kew Bull. 44: 124. 1989. – Holotype: Iran, Fars, Post-i-Chenab SE Sarvestan, 6.1983, *Mozaffarian 46754* (TARI; isotypes: K).

A species not unlike *Dionysia bryoides* vegetatively, but the columnar stems are slightly broader, the glandular hairs on the leaves are slightly longer (i.e. still short, but never sessile) and more dense, and the corolla is yellow with entire lobes and the style usually distinctly exerted in long-styled flowers. It is not impossible that some of the early records of *D. bryoides* from the mountains S of Shiraz could refer to this species, which grows on rather gently sloping rocks, as well as on more vertical sites.

a. subsp. *sarvestanica*

b. *Dionysia sarvestanica* subsp. *spathulata* Lidén, **subsp. nov.**

Holotype: Firozabad: Kuh-e- Sefida e-Meaymand, 24.3.1971, *Dehgani 5466* (TARI).

A subspecies *sarvestanica* foliis spatulatis valde latioribus facile distinguenda.

Very dense cushions of closely packed cylindrical columns; leaves much broader and more rounded at apex than those of subsp. *sarvestanica*.

Additional specimens examined. – Locus classicus: *T4Z 1044* (UPS).

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