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Research Article

Anthemis sect. Hiorthia (Asteraceae) on Kriti Island, Greece: high ploidy levels and a new species

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Abstract

A morphological and karyological investigation of the *Anthemis* sect. *Hiorthia* representatives of Kriti (Greece) revealed that three different species are found on the island, all endemic, and each characterised by a different ploidy level based on the haploid series of x = 9. *Anthemis abrotanifolia*, the species with the widest distribution, is tetraploid with 2n = 4x = 36. *A. samariensis*, a local endemic of the Lefka Ori, was found being decaploid, with 2n = 10x = 90, the highest number ever recorded in *Anthemis*. The recently discovered population on Mt. Kedros (south-central Kriti) is morphologically distinct from all the *Anthemis* entities growing on Kriti; it also differs from the variable and widespread *A. cretica* group. It is here described as a new species, *A. pasiphaes* Goula & Constantinidis. It is a hexaploid, with 2n = 6x = 54. All chromosome numbers are reported for the first time. Polyploidy might have acted as a reproductive barrier among these perennial species, complementing isolation by spatial distance and evolutionary divergence. Further, it might have contributed adaptation advantages to these three predominately mountain species.

Key words: Anthemideae, chromosomes, Greek endemic, karyology, Mediterranean area, taxonomy

Introduction

Among the biodiversity hotspots in the Mediterranean Basin, Kriti or Crete (Greece) has a prominent position (Médail 2017). No fewer than 2240 plant taxa have been recorded on this large continental island (Kougioumoutzis et al. 2020), where the percentage of endemism is the highest known in Greece (Dimopoulos et al. 2013). The island's geographical isolation, permanent since the early Pliocene (Greuter 1972; Sakellariou and Galanidou 2016), combined with mountain isolation due to Kriti's uplifting and rugged topography, have played a significant role in plant endemism (Legakis and Kypriotakis 1994). The mountains of Kriti, in particular, have served both as refugia for old montane species and as cradles for plant diversification (Greuter 1972; Trigas et al. 2013).

One of the richest families in endemics on the island is Asteraceae, with at least 29 taxa endemic to Kriti, 13 of them restricted to mountainous areas (see Strid 2016b). With respect to the genus *Anthemis*, there are 14 taxa on the island (Strid 2016b; Goula and Constantinidis 2021); five of them, i.e., *A. abrotanifolia* (Willd.) Guss., *A. filicaulis* (Boiss. & Heldr.) Greuter, *A. glaberrima* (Rech.f.)



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Copyright: © K. Goula & T. Constantinidis. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). Greuter, A. samariensis Turland, and A. tomentella Greuter, being regional endemics confined to Kriti and the nearby islets (Strid 2016b). Anthemis sect. Hiorthia (DC.) R.Fernandes, formed mainly by perennial species of high altitude (Oberprieler 1998), was represented up to now by two endemic species in Kriti: A. abrotanifolia and A. samariensis. The latter is the Anthemis species that was most recently described on the island (Turland 2008). This chasmophyte was initially found in only two adjacent but distinct localities in the Lefka Ori, the richest area of Kriti in numbers of local endemic taxa (Montmollin and latrou 1995). The two subpopulations seem to face no threats by human activities or grazing. However, the species was assessed as "Vulnerable" according to the IUCN Red List criteria, due to its very restricted distribution area (Turland 2009). Five years after the description of A. samariensis, another population of a perennial Anthemis was discovered by Vangelis Papiomytoglou on Mt. Kedros, approximately 58 km as the crow flies ESE of the type locality of A. samariensis in the Lefka Ori. It was reported by Strid and Tan (2017) as conspecific with A. samariensis. Mt. Kedros is located in the central-southern part of Kriti, reaching 1776 m a.s.l., and is closer to Mt. Psiloritis (2456 m, the highest mountain of Kriti) than to the Lefka Ori.

In 2018, during field work focused on the taxonomic diversity of Greek *Anthemis*, the first author visited Mt. Kedros to collect material from this particular population. When this material was compared to *A. samariensis* from the *locus classicus*, the extent of the noticed morphological divergence led us to a more thorough examination of the samples. In addition, a karyological survey of the Mt. Kedros population, as well as those of *A. abrotanifolia* and *A. samariensis*, was carried out in order to explore and understand chromosome diversity and ploidy levels of all *A.* sect. *Hiorthia* members found in Kriti. The results are presented in this study.

Materials and methods

Plant material, which included flowering and fruiting samples, was collected during two field trips on Mt. Kedros, in spring and summer of 2018. Dried specimens prepared from these samples were deposited in ATHU (the acronym follows Thiers 2022, continuously updated) and were examined thoroughly, in comparison with specimens of Anthemis samariensis from its locus classicus preserved at the herbarium of the Mediterranean Agronomic Institute of Chania (MAIC). The morphological diversity within the A. sect. Hiorthia members was also studied based on specimens collected between 2017 and 2021 (Goula, unpublished material), as well as specimens and digital specimen images provided by the herbaria ATH, ATHU, B, BM, BR, E, GOET, JE, K, MNHN, MO, NHMC, P, TAU, TAUF, UPA, W, WAG, and WU. The concept of the A. cretica entities and the protologues of subspecific taxa attributed to this name, together with descriptions and nomenclatural comments, were studied in historic and recent literature (Linnaeus 1737, 1753, 1763; Bieberstein 1808; Boissier 1875; Eig 1938; Fernandes 1975; Grierson and Yavin 1975; Fernandes 1976; Franzén 1986; Franzén 1991; Greuter et al. 2003; Greuter 2006+; Turland 2008; Strid 2016a, b).

In order to investigate the chromosome numbers of *Anthemis* sect. *Hiorthia* of Kriti, mature achenes originating from populations of *A. abrotanifolia* on Mt. Psiloritis, *A. samariensis* on the Lefka Ori and plants of Mt. Kedros were cultivated in pots at the facilities of the Department of Biology, National and Kapodistrian University of Athens. Root tips from the seedlings were treated with a combined

cycloheximide 0.0009% and 8-hydroxyquinoline 0.0006% solution for three hours, fixed in Carnoy's solution for at least 24 hours and stored in ethanol 70% at -20 °C. To obtain photographs of metaphase plates, root tips were hydrolyzed in HCl 1N at 60 °C for 12 minutes, placed in Feulgen stain for up to two-and-a-half hours and squashed over microscope slides with a few drops of acetic acid 45%. Idiograms were constructed from photographs of at least three different metaphase plates (Goula and Constantinidis 2021). Construction of the idiograms was conducted using the KaryoType software, ver. 2.0 (Altinordu et al. 2016).

Results

Morphology

The morphological characters of the population on Mt. Kedros made it stand out as different from all known taxa of *Anthemis* sect. *Hiorthia* from Kriti. Its closest relative, regarding morphology, seems to be *A. samariensis*, although it also appears to share common features with taxa of the variable *A. cretica* group from the Greek mainland and Anatolia. The morphological differences among members of *A.* sect. *Hiorthia* of Kriti are summarised in Table 1. *Anthemis cretica* subsp. *cretica*, the member of the *A. cretica* group morphologically and geographically nearest to the Mt. Kedros population, has also been added for comparison reasons.

 Table 1. Morphological differences between the Anthemis sect. Hiorthia members of Kriti Island and A. cretica subsp.

 cretica from Peloponnisos (Greece). All measurements in mm.

		Anthemis abrotanifolia	Anthemis samariensis	Mt. Kedros population	Anthemis cretica subsp. cretica
Stem indumentum		sericeous	usually glabrous to subglabrous	woolly	sericeous
Leaf indumentum		sericeous	villous	woolly	sericeous
Lobed leaves alon	g stem	present	usually absent	present	present
Leaf dimensions	Outline	15-40 × 10-20	20-45 × 15-20	20-30 × 14-16	15-40 × 8-15
	Petiole width	0.3-0.6	1.5-2	0.5-1	0.3-0.6
	Ultimate lobes width	0.3-0.8	1-1.8	0.7-1.5	0.3-0.6
Number of primary leaf segments		5-7	usually 7	usually 7	(7–)9–15
Involucral bracts dimensions	Length	3-5	4-6	3.5-5	2-5
	Width	0.8-1.4	2-2.5	1.2-1.5	1.3-2
	Margin width	ca. 0.1	0.3-0.5	0.1-0.3	ca. 0.1
Receptacular scales	Length	3-3.5	6.5-7	4-6	3.5-4
	Width	0.9-1.3	ca. 1	0.7-1	ca. 1
	Apex	trucate to cuneate	emarginate	usually cuneate	cuneate
	Arista	0.1-0.2	ca. 1	1.5-2	0.5
Number of ligulate florets		0-8	8-14	14-20	14-16(-20)
Ligulate florets	Tube length	1.6-2	1.5-2	2-2.5	1.8-2
dimensions	Tube width	0.5-0.7	0.5-0.7	ca. 1	0.5-0.7
	Ligule width	1-2.5	5-6.5	3-5	3-4
Achene dimensions	Length	1.3-2	(2.1-)2.3-2.5(-2.8)	1.8-2.6	1.4-2
	Width	0.5-0.8	0.8-1	0.5-0.8	0.8-1
Pappus	Corona	0.1	0.2	0.2-0.4	0.3-0.6
dimensions	Auricle	absent	1.5	0.5-1	0.3-0.6
Pappus on achenes of ligulate florets		acute, dentate rim with 2–3 larger teeth	3-lobed auricle	denticulate auricle	denticulate to lobed oblique corona

In addition to the morphological differences of Table 1, the Mt. Kedros Anthemis and the variable A. cretica group also exhibit two noteworthy qualitative dissimilarities, as follows: a) the stem leaves of the Mt. Kedros population are clearly petiolate, whereas the stem leaves of A. cretica have a pair of lobes at or near their rachis base, thus appearing as almost sessile, and b) the receptacular scales of the Mt. Kedros population are aristate, in contrast to the acute to acuminate scales of the A. cretica group. A comparison of the Mt. Kedros population with the morphologically most relevant A. cretica subspecies, i.e., A. cretica subsp. cretica, and also A. cretica subsp. carpatica (Willd.) Grierson and A. cretica subsp. cassia (Boiss.) Grierson, reveals additional qualitative and quantitative differences. Anthemis cretica subsp. cretica, particularly those populations from the mountain areas of Peloponnisos that are geographically closest to Kriti, differ further in that they bear a large number of primary leaf segments (up to 15 vs. usually 7 in the Mt. Kedros Anthemis) with much narrower ultimate lobes (0.3-0.6 mm vs. 0.7-1.5 mm in the Mt. Kedros Anthemis), narrower involucres (7-11 mm vs. 10-12 mm in the Mt. Kedros Anthemis), a conical, acute receptacle, smaller outer and inner achenes (1.4-2 mm with a pappus up to 0.6 mm vs. 1.8-2.6 mm with a pappus up to 1 mm in the Mt. Kedros Anthemis), and in the shape of the corona on the achenes of the ligulate florets (see Fig. 4, F1 & F3). Anthemis cretica subsp. carpatica differs from the Kedros population in its indumentum, varying from totally glabrous to slightly sericeous, and the completely different pappus shape, consisting of an acute rim or a very small, ca. 0.2 mm corona, with no auricle. Anthemis cretica subsp. cassia from E and S Anatolia, Syria and Lebanon (Grierson and Yavin 1975; Greuter 2006+) has wider ultimate leaf lobes (usually 2-3.5 mm vs. 0.7–1.5 mm in the Mt. Kedros Anthemis), shorter pappus on the achenes (0.5 mm vs. up to 1 mm in the Mt. Kedros Anthemis), whereas its involucral bracts margin may be pale, in contrast to the Mt. Kedros population with its always dark bract margin.

Karyology

The examination of metaphase plates of the three Anthemis sect. Hiorthia members of Kriti revealed three distinct ploidy levels. Anthemis abrotanifolia from Mt. Psiloritis was found to be tetraploid with 2n = 4x = 36 (Fig. 1a). The Mt. Kedros population was found to be hexaploid with 2n = 6x = 54 (Fig. 1b). All the cultivated plants of A. samariensis from the Lefka Ori were found to be decaploid with the surprising number of 2n = 10x = 90 (Fig. 1c). The chromosome numbers of all taxa are reported here for the first time. The decaploid chromosome level was unknown up to now in Anthemis and is therefore reported here as new. The large chromosome number of A. samariensis complicated its idiogram construction and the detailed study of chromosome morphology. The idiograms of A. abrotanifolia and the Mt. Kedros population are shown in Fig. 1 (1d and 1e, respectively). The karyotype of A. abrotanifolia consists of 22 metacentric, ten submetacentric and four subtelocentric chromosomes that bear satellites (karyotype formula: 2n = 4x = 22m + 10sm+ 4st^{4sat}). The karyotype of the Mt. Kedros population consists of 24 metacentric, 18 submetacentric and 12 subtelocentric chromosomes. Six of the latter bear satellites (karyotype formula: $2n = 6x = 24m + 18sm + 12st^{6sat}$). In



Figure 1. Metaphase plates and idiograms of *Anthemis* sect. *Hiorthia* members in Kriti **A** *A. abrotanifolia* from Mt. Psiloritis **B** *Anthemis* population from Mt. Kedros **C** *A. samariensis* from Lefka Ori **D** idiogram of *A. abrotanifolia* **E** idiogram of Mt. Kedros population. Scale bars: 10 µm.

Greek representatives of *A*. sect. *Hiorthia*, tetraploids are more common. The karyotypes of the Greek tetraploid (2n = 4x = 36) *A*. *cretica* populations (various subspecies) also consist of 24 metacentric chromosomes, but usually with four submetacentric and eight subtelocentric chromosomes that bear four to six satellites (Goula, unpublished data). The only hexaploid *A*. *cretica* subspecies in Greece (*A*. *cretica* subsp. *carpatica*) has a different karyotype structure from that of the Mt. Kedros population, formulated as $2n = 6x = 28m + 14sm + 10st^{2sat} + 2t^{2sat}$. *Anthemis cretica* subsp. *cretica* from Peloponnisos is tetraploid with a karyotype formula of $2n = 4x = 24m + 6sm + 6st^{6sat}$ (Goula, unpublished data).

Discussion

The morphological distinction of the Mt. Kedros *Anthemis* population from the other two members of *A*. sect. *Hiorthia* of Kriti and the related *A*. *cretica* group, coupled with the different ploidy levels revealed in our study, allow the recognition of a new species described here as *Anthemis pasiphaes* Goula & Constantinidis (see below). According to current knowledge, this new species is endemic to Mt. Kedros (Fig. 2) and adds a new narrow endemic to the flora of Kriti. As a rule, local and regional Greek endemics are more common in the southern

parts of the country, particularly Kriti and Peloponnisos, following an increase of the endemism rate observed in a north to south direction (e.g., Georghiou and Delipetrou 2010). The center of *Anthemis* diversity is in SW Asia (Lo Presti et al. 2010) and that of the heterogenous *A. cretica* group, to which both *A. samariensis* and *A. pasiphaes* presumably link, is apparently in Anatolia (Franzén 1991).

In order to decide on the taxonomic position of *Anthemis pasiphaes* we considered the discussion provided by Turland (2008) in the case of *A. samariensis* and the arguments presented below. We concluded that *A. pasiphaes* would better be kept as a separate species and not fall under the variability of the *A. cretica* group for the reasons explained below.

- a. Geological evidence indicates that Kriti has been permanently isolated from continental Greece and SW Asia since the early Pliocene, about 4 mya. By that time, it appears that the *Anthemis cretica* clade had already been separated from the rest of *Anthemis*, although diversification within its clade began about 2 mya (Lo Presti and Oberprieler 2009). It is plausible that the speciation of the *A. sect. Hiorthia* members on Kriti (*A. abrotanifolia*, *A. pasiphaes*, *A. samariensis*) was the result of geographical vicariance events of a local clade. Allopatric speciation due to isolation in mountain ranges drove diversification in other groups of Asteraceae rich in endemic species as well (e.g. *Centaurea*, López-Vinyallonga et al. 2015).
- b. The Anthemis cretica assemblage is a diverse group of taxa with a complicated phylogenetic, taxonomic, and nomenclatural history. Concepts related to the group have changed over the decades. Most of the nowadays accepted subspecific entities classified under A. cretica appeared as new combinations in Grierson (1975). Grierson (1974) delved into the labyrinth of the historic literature on A. cretica and elucidated several species names, which, as he characteristically mentioned "had suffered a history of misapplication". However, the origin and taxonomic category of the A. cretica lectotype specimen (Herb. Clifford: 415, Anthemis 2, BM000647187!) remains unresolved. Linnaeus (1763), cited "Habitat in Italia Helvetia" as the origin area of the species (under A. montana L., an illegitimate replacement name for A. cretica), whereas Franzén (1986), after examining material from the entire A. cretica distribution area, considered the East Aegean Islands as a more probable origin area. Furthermore, it is not yet clarified whether the Linnaean lectotype specimen was collected from a wild population or belongs to a cultivated specimen, i.e., it possesses possible distorted characters. According to the points presented above, the concept of the A. cretica needs further elucidation and is rather built on a shaky foundation. As of today, the number and rank of taxa within the A. cretica collective species are not yet fully resolved and large databases are not in full accordance. Euro+Med Plantbase (Greuter 2006+), for example, accepts 25 subspecies within A. cretica, compared to the World Flora Online (WFO 2022), which accepts 23 subspecies. Morphological differences between infraspecific A. cretica entities and certain corresponding species of A. sect. Hiorthia may be guite vague. For example, our field experience with some Anthemis populations of N Greece, particularly those of high mountains, makes distinguishing



Figure 2. Distribution of Anthemis sect. Hiorthia on Kriti Island. Pink dot: A. samariensis, red dot: A. pasiphaes, yellow dots: A. abrotanifolia. Based on Strid (2016b) and additional specimens in ATHU, MAIC and NHMC. Background map data: Google, SIO, NOAA, U.S. Navy, NGA, GEBCO.

between *A. cretica* subsp. *carpatica* and *A. pindicola* Halácsy problematic. Grierson (1975) himself characterised his *A. cretica* group classification as "possibly oversimplified" and "tentative" and underlined the necessity of a biosystematic study within the group. The inclusion of new taxa within an even broader *A. cretica* complex would add intricacy to the whole structure. Cutting-edge molecular tools, when used, would presumably help in elucidating phylogeny and would offer a classification scheme in compliance with evolutionary patterns.

c. Polyploidy is one of the reproductive barriers responsible for isolating plant populations, and at the same time a driving force of speciation (Rieseberg and Willis 2007). Within the Mediterranean Basin in particular, polyploidy has played a major role in the diversification of several plant genera (e.g., Tomasello and Oberprieler 2022). In Anthemis, polyploidy has been recorded almost exclusively in A. sect. Hiorthia, where it is evolutionarily important (Kuzmanov et al. 1981). Hexaploids (2n = 6x = 54) and octoploids (2n = 8x = 72) have been recorded in only one representative of this section: A. cretica subsp. carpatica (Küpfer 1974; Baltisberger 1993). In Greece, tetraploid cytotypes (2n = 4x = 36), along with the typical diploid number (2n = 2x = 18), are more common, but hexaploid cytotypes also occur within the A. cretica complex (Goula and Constantinidis 2019). In our case, the three different, high ploidy levels of the Anthemis on Kriti (A. abrotanifolia, A. pasiphaes, A. samariensis) corroborate their morphological differentiation forming reproductive barriers and thus supporting their specific rank.

Incidence of polyploidy in plants depends on various factors, among them the climate and the life form (Rice et al. 2019). High chromosome numbers are more common within certain families, e.g., Asteraceae (Semple and Wata-nabe 2009). Within tribe Anthemideae, in particular, several genera have been reported to form extensive polyploid complexes as, e.g., *Leucanthemum* with ploidy levels varying from 2x to 22x (see Oberprieler et al. 2009). The higher genetic diversity provided through polyploidy improves environmental adaptation and tolerance, resulting in the ability of plants to colonise and be successful in harsh environmental contexts (Meudt et al. 2021). Polyploidy in the three *Anthemis* sect. *Hiorthia* representatives of Kriti, restricted to calcareous stony slopes (*A. abrotanifolia*) or cliffs in mountain regions (*A. pasiphaes* and *A. samariensis*), seems to offer an advantage in adapting to and surviving in hostile habitats.

Taxonomic treatment

Anthemis pasiphaes Goula & Constantinidis, sp. nov. urn:lsid:ipni.org:names:77323168-1

Diagnosis. Member of *Anthemis* sect. *Hiorthia* related to *A. samariensis*, but differing in its woolly indumentum, presence of lobed leaves on flowering stems, longer aristae (1.5–2 mm) on receptacular scales, and presence of denticulate auricle on achenes of ligulate florets.

Type. GREECE. Kriti: Nomos Rethimnou, Eparchia Amariou. Mt. Kedros, ca. 2 km linear distance S of Gerakari village, vertical limestone rocks facing N, on the northern slopes of the mountain, 1265 m a.s.l., 35°11'N, 24°36'E, 29 April 2018, Goula, Kofinas, Papanikolaou & Papiomytoglou 2379 (holotype, ATHU). Figs 3–5.

Description. Perennial herb with stock covered in last year's leaf sheaths. Indumentum woolly, ± appressed, hairs medifixed. Glands present in most parts of plant. Stems simple or branched; leafy non-flowering shoots present at anthesis. Flowering stems decumbent to erect, simple, 10-25 cm tall, angled, woolly, greyish-green, with successively smaller and less dissected leaves up to middle, and entire, scale-like leaves up to almost below capitulum. Leaves somewhat aromatic with golden stalked glands on leaf surface, greyish-green, up to 6 cm long, with both surfaces woolly; petiole up to 3 cm long and 0.5-1 mm wide; leaf blade 2-pinnatisect, ovate in outline, 2-3 cm × ca. 1.5 cm; primary segments usually 7, each one divided into 2-5 ultimate lobes; ultimate lobes narrowly oblanceolate to obovate, 0.7-1.5 mm wide, apex subacute with minute cartilaginous cusp, usually hidden below the dense trichomes. Capitulum solitary, radiate. Involucre hemispherical, 10-12 mm wide. Involucral bracts imbricate, greyish-green, lanceolate, 3.5-5 × 1.2-1.5 mm, outer surface villous with dark green or dark brown midvein; margin dark brown, 0.1-0.3 mm wide, membranous, densely and minutely lacerate, apex dark brown to black, acute to acuminate. Receptacle hemispherical becoming hemispherical-conical, apex obtuse. Receptacular scales narrowly oblanceolate, navicular, $4-6 \times 0.7-1$ mm, scarious, apex usually cuneate or emarginate, midvein straw coloured, prominent, leading to arista (1-)1.5-2 mm long. Ligulate florets 14-20; tube green, cylindrical, 2–2.5 mm × ca. 1 mm; ligules patent at anthesis, later reflexed, white, oblong to oblong-obovate, $10-15 \times 3-5$ mm, spotted with sessile glands. Disk florets yellow, spotted with sessile glands; tube cylindric, 3–3.5 mm long (including the lobes), 0.5–0.8 mm wide; lobes 5, triangular, 0.5–0.7 mm long; lower part of disk florets swollen and spongy at maturity. Achenes straw-co-loured, narrowly obconic-oblong. Achenes of disk florets weakly 4-angled, slightly curved, 1.8–2.5 mm long, excluding pappus, 0.5–0.8 mm wide, more or less longitudinally ribbed; pappus oblique, forming short lacerate corona 0.2–0.4 mm wide and lacerate auricle adaxially; auricle scarious, 0.5–0.8 mm long, densely and finely longitudinally veined. Achenes of ligulate florets more curved and more prominently ribbed, 2.3–2.6 mm long excluding pappus, surface characters as in achenes of disk florets, but additionally sessile glands present; pappus as in achenes of disk florets, but auricle entire, 0.8–1 mm long, with lacerate apex. 2n = 6x = 54.

Distribution and habitat. Anthemis pasiphaes is apparently endemic to Mt. Kedros, restricted to its northern part (Fig. 2). It grows on steep, calcareous cliffs, mostly inaccessible even to the numerous goats that graze the area. Currently known only from the type locality, at 1265 m a.s.l., but presumably also occurring higher up, on the same slope. It grows together with other endemics of Kriti, like *Crepis auriculifolia* Spreng., *Dianthus juniperinus* subsp. *pulviniform-is* (Greuter) Turland, *Erysimum raulinii* Boiss., *Lomelosia albocincta* (Greuter) Greuter & Burdet, *Sesleria doerfleri* Hayek, and *Staehelina petiolata* (L.) Hilliard & B.L.Burtt.

Etymology. The specific epithet derives from the female name Pasiphaë and consists of the Greek words $\pi \dot{\alpha} \sigma \iota$ (= all) and $\varphi \dot{\alpha} \sigma \varsigma / \varphi \tilde{\omega} \varsigma$ (= light), i.e., "she who illuminates everyone". Pasiphaë was daughter of Helios (god of the Sun), wife of King Minos, Queen of Kriti and immortal, according to Greek mythology.

Phenology. Flowering from late April to early June; fruiting from June to July.

Conservation status. Anthemis pasiphaes is currently known from the type locality only. This single population is considerably small, with no more than 50 individuals counted, and restricted to practically inaccessible cliffs. The species has not been recorded elsewhere, although there are several similar habitats around in Kriti, which is botanically one of the best explored regions of Greece (Strid and Tan 2017). Potentially suitable localities on Mt. Kedros have not revealed any additional populations so far. The presence of grazing animals in the area is very apparent, limiting the small population to very steep cliffs. Neither mature individuals nor leaf rosettes were observed in localities accessible to goats. A rock-climbing area on the southern slopes of Mt. Kedros is not a threat to A. pasiphaes at present; however, the northern part of the mountain is also suitable for rock-climbing activities that would potentially destroy the only known population. Although we counted a very small number of mature plants, it is possible that more plants are present, very locally, on cliffs surrounding the locus classicus, given that they are not accessible to goats and retain enough moisture and some shade to permit uninterrupted growth of A. pasiphaes. If distribution and frequency of mature plants follow the same patterns we observed during field work, we may then estimate with some certainty that the total population of the species is fewer than 250 mature individuals. Therefore, the species meets the Criterion D



Figure 3. Holotype of Anthemis pasiphaes Goula & Constantinidis (ATHU).



Figure 4. Anthemis pasiphaes Goula & Constantinidis and comparison with A. samariensis and A. cretica subsp. cretica **A** capitulum **B** leaf **C** receptacular scales **D** flowering stems **E** achenes of disk florets **F** achenes of ligulate florets $C_1 - F_1$ A. pasiphaes $C_2 - F_2 A$. samariensis $C_3 - F_3 A$. cretica subsp. cretica. Scale bars: 5 mm (**A**); 1 cm (**B**); 2 mm (**C**, **F**); 3 cm (**D**); 1 mm (**E**). Drawn by N.A. Katsaros. A. pasiphaes was drawn from the holotype (Goula et al. 2379) and Goula & Katsaros (2644), both in ATHU, A. samariensis from material collected from the type locality (Ap. Kal. 9685, MAIC) and A. cretica subsp. cretica from material collected on Mt. Parnonas (Goula & Katsaros 2610, ATHU).

(number of mature individuals <250) following the IUCN Guidelines for the assessment of taxa known only from the type locality (IUCN Standards and Petitions Committee 2022). The IUCN Red List category of Endangered seems suitable (EN D).



Figure 5. Anthemis pasiphaes at its locus classicus **A** plant growing on a vertical rock **B** capitulum. Photo taken on 29.04.2018 by K. Goula. Scale bars: 5 cm (**A**); 5 mm (**B**).

A revised key to genus *Anthemis* and the related genus *Cota* from Kriti (including surrounding islets)

1	Achenes compressed, rhombic in transverse section; leaf segments pecti-
	nate2
-	Achenes not compressed, orbicular or sub-quadrangular in transverse
	section; leaf segments usually not pectinate3
2	Receptacular scales straw colour at maturity; plant usually erect
-	Receptacular scales purplish-brown to almost black at maturity; plant usu-
	ally procumbent C. melanolepis
3	Plant annual, non-flowering shoots absent at anthesis4
-	Plant perennial, non-flowering shoots present at anthesis13
4	Receptacle without scales5
-	Receptacle with scales present at least on upper part6
5	Leaves somewhat fleshy, lobes obtuse; ligules absent; achenes caducous,
	with a ca. 0.5 mm long corona A. ammanthus subsp. ammanthus
-	Leaves not fleshy, lobes acute; ligules occasionally present; achenes with a ca.
	1 mm long corona, outer achenes persistent, inner caducous A. filicaulis
6	Receptacle without scales in lower part; achenes cylindrical to turbinate,
	tuberculate, pappus absentA. cotula
-	Receptacle with scales all over, at least when young; achenes with a differ-
	ent combination of characters7

7	Receptacular scales hairy A. ammanthus subsp. paleacea
-	Receptacular scales glabrous8
8	Peduncles not or slightly clavate in fruit; at least inner achenes not firmly attached to receptacle
-	Peduncles clavate in fruit; achenes firmly attached to receptacle or involu- cre indurate at maturity11
9	Plants slender; ligules not more than 5 mm or absent; margin of involucral bracts pale; achenes not or obscurely ribbed 10
-	Ligules always present, longer than 7 mm; involucral bracts usually with dark margin; achenes with $7-10$ distinct ribs
10	Ligules always present, pinkish at least beneath; receptacular scales lin- ear-lanceolate; achenes with a fimbriate corona
-	Ligules absent or, if present, white; receptacular scales linear-setaceous; achenes with an entire to lacerate corona
11	Stems erect; receptacle conical, elongated; achenes with a thickened mar-
	ginal rim nannua abaant A aruanaia auban inaraasata
	ginal rim, pappus absent A. arvensis subsp. incrassata
-	ginal rim, pappus absent A. arvensis subsp. incrassata Stems prostrate to ascending; receptacle shortly conical; achenes with acute rim and a corona at least 0.3 mm long12
- 12	ginal rim, pappus absent
- 12 -	ginal rim, pappus absent A. arvensis subsp. incrassata Stems prostrate to ascending; receptacle shortly conical; achenes with acute rim and a corona at least 0.3 mm long 12 Ligules absent; capitula discoid A. rigida subsp. rigida Ligule present, white; capitula radiate A. rigida subsp. ammanthiformis
- 12 - 13	ginal rim, pappus absent A. arvensis subsp. incrassata Stems prostrate to ascending; receptacle shortly conical; achenes with acute rim and a corona at least 0.3 mm long 12 Ligules absent; capitula discoid A. rigida subsp. rigida Ligule present, white; capitula radiate A. rigida subsp. ammanthiformis Involucre 4–7 mm long, ligules usually absent; disk florets yellow or pink;
- 12 - 13	ginal rim, pappus absent A. arvensis subsp. incrassata Stems prostrate to ascending; receptacle shortly conical; achenes with acute rim and a corona at least 0.3 mm long 12 Ligules absent; capitula discoid A. rigida subsp. rigida Ligule present, white; capitula radiate A. rigida subsp. ammanthiformis Involucre 4–7 mm long, ligules usually absent; disk florets yellow or pink; achenes without pappus or with a very short acute rim A. abrotanifolia
- 12 - 13 -	ginal rim, pappus absent A. arvensis subsp. incrassata Stems prostrate to ascending; receptacle shortly conical; achenes with acute rim and a corona at least 0.3 mm long 12 Ligules absent; capitula discoid A. rigida subsp. rigida Ligule present, white; capitula radiate A. rigida subsp. ammanthiformis Involucre 4–7 mm long, ligules usually absent; disk florets yellow or pink; achenes without pappus or with a very short acute rim A. abrotanifolia Involucre 8–12 mm long, ligules present, large; disk florets yellow; achenes with a 0.5–1.5 mm long auricle 14
- 12 - 13 - 14	ginal rim, pappus absent A. arvensis subsp. incrassata Stems prostrate to ascending; receptacle shortly conical; achenes with acute rim and a corona at least 0.3 mm long 12 Ligules absent; capitula discoid A. rigida subsp. rigida Ligule present, white; capitula radiate A. rigida subsp. ammanthiformis Involucre 4–7 mm long, ligules usually absent; disk florets yellow or pink; achenes without pappus or with a very short acute rim A. abrotanifolia Involucre 8–12 mm long, ligules present, large; disk florets yellow; achenes with a 0.5–1.5 mm long auricle 14 Flowering stems glabrous at least at middle part, leafless except for small, scale-like leaves; receptacular scales with an arista ca. 1 mm long;
- 12 - 13 - 14	ginal rim, pappus absent A. arvensis subsp. incrassata Stems prostrate to ascending; receptacle shortly conical; achenes with acute rim and a corona at least 0.3 mm long 12 Ligules absent; capitula discoid A. rigida subsp. rigida Ligule present, white; capitula radiate A. rigida subsp. ammanthiformis Involucre 4–7 mm long, ligules usually absent; disk florets yellow or pink; achenes without pappus or with a very short acute rim A. abrotanifolia Involucre 8–12 mm long, ligules present, large; disk florets yellow; achenes with a 0.5–1.5 mm long auricle 14 Flowering stems glabrous at least at middle part, leafless except for small, scale-like leaves; receptacular scales with an arista ca. 1 mm long; achenes of ligulate florets with a 3-lobed auricle A. samariensis
- 12 - 13 - 14	ginal rim, pappus absent A. arvensis subsp. incrassata Stems prostrate to ascending; receptacle shortly conical; achenes with acute rim and a corona at least 0.3 mm long 12 Ligules absent; capitula discoid A. rigida subsp. rigida Ligule present, white; capitula radiate A. rigida subsp. ammanthiformis Involucre 4–7 mm long, ligules usually absent; disk florets yellow or pink; achenes without pappus or with a very short acute rim A. abrotanifolia Involucre 8–12 mm long, ligules present, large; disk florets yellow; achenes with a 0.5–1.5 mm long auricle 14 Flowering stems glabrous at least at middle part, leafless except for small, scale-like leaves; receptacular scales with an arista ca. 1 mm long; achenes of ligulate florets with a 3-lobed auricle A. samariensis Flowering stems woolly, bearing dissected leaves usually up to middle; receptacular scales with an arista 1.5–2 mm; achenes of ligulate florets

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Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

Conceptualization: KG. Data curation: KG. Formal analysis: KG. Methodology: TC. Supervision: TC. Writing - original draft: KG. Writing - review and editing: TC.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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