Article

Fl. Medit. 30: 273-291
https://doi.org/10.7320/FlMedit30.273
Version of Record published online on 17 December 2020

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Inventorying and mapping the orchids of the island of Antikythera (Greece), including a new taxon: *Ophrys aegilica* (*Orchidaceae*)

Abstract

Engelen, D.: Inventorying and mapping the orchids of the island of Antikythera (Greece), including a new taxon: *Ophrys aegilica* (*Orchidaceae*). — Fl. Medit. 30: 273-291. 2020. — ISSN: 1120-4052 printed, 2240-4538 online.

The Mediterranean Basin with all its islands encompasses a high diversity of plant species. Nonetheless, floristic overviews of these islands are often incomplete or lacking entirely and as a result they have an increased chance of harboring undescribed taxa. In 2014, I stumbled on such a likely new taxon belonging to the mammosa-complex of the genus *Ophrys* (*Orchidaceae*) on Antikythera, Greece. Therefore, in March 2018, I organized a 3 week orchid survey on the island during which 14226 specimens of 12 species were recorded, including the new taxon *Ophrys aegilica*. It mostly resembles *O. taigetica*, but differs from this species in habitat preference and flowering time, as well as a few morphological features (e.g. size of the petals). Furthermore, I report on the local status of other orchid species on Antikythera, including 4 which have not previously been observed on the island: *Anacamptis papilionacea* subsp. *aegaea*, *Neotinea maculata*, *Ophrys bombyliflora*, and *O. attica*. For at least three species their occurrence on Antikythera marks the border of their distributional range in Greece. These results underline the importance of botanical surveys on Mediterranean islands during winter and early spring in order to get a complete picture of the occurrence and distribution of plant species. For the future conservation of orchids on Antikythera it is important that the vegetation keeps its open character, especially on former agricultural terraces, and that currently unknown pollinators are identified.

Key words: Mediterranean Basin, Greek flora, plant distribution, island endemics.

Introduction

The Mediterranean Basin is a global plant biodiversity hotspot with more than 25.000 vascular species (about 10% of the world's total) on just 1.6% of the earth's land surface (Médail & Quezel 1997; Comes 2004). More than half of these plant species are endemic to the region, many of which have a narrow distributional range, particularly on islands and in high mountain areas (Médail & Quezel 1997; Greuter 2001; Georghiou & Delipetrou 2010). Although the number of studies documenting this spectacular diversity is growing (e. g. Strid & Tan 2017), many islands remain

understudied and either lack proper species' distributions data or a flora inventory altogether (Greuter 2001). The following study aims to make a small contribution to this knowledge gap by focusing on orchids of the island of Antikythera. Despite its location between Crete and the Peloponnese, the two areas with the highest levels of endemism in Greece (Médail & Quezel 1997; Georghiou & Delipetrou 2010), this Greek island has been scantly visited by botanists or (amateur) orchid enthusiasts.

Antikythera is a small (20.8 km^2, maximum altitude 379, coastline 24 km), rather remote Greek island in the southwestern Aegean Sea. It is situated 38 km southeast of Kythira and 35 km northwest of western Crete (Fig. 1a & 1b). The climate is typically Mediterranean and is characterized by warm winters without much frost or snow, and a relatively dry period of up to 6 months between April and September. There are around 30 permanent inhabitants, who share the island with a large population of roughly 3000 feral goats (Palmer & al. 2010).

The oldest signs of human presence on Antikythera date back to the 5th millennium BC and these were probably people that visited the island seasonally (Bevan & al. 2007). Small settlements and the construction of agricultural terraces first appeared in the 2nd millennium BC. Since then, Antikythera has had a history of periods with (re)colonization alternated with (long) periods of complete abandonment (Bevan & al.

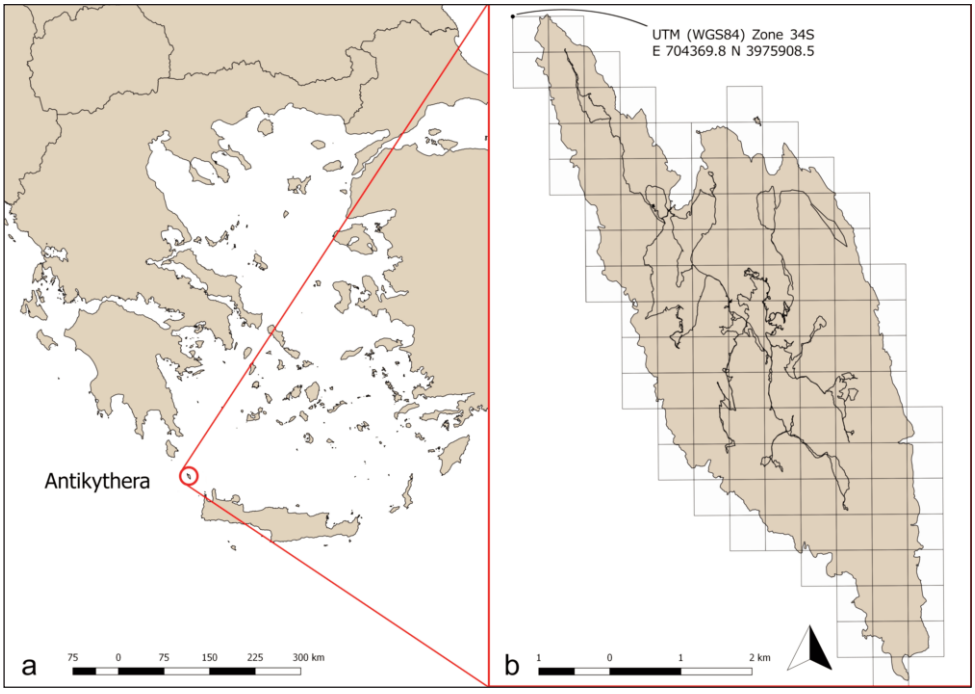

Fig. 1. a) Map of Greece with geographic location of Antikythera. b) Overview map of Antikythera, showing the routes surveyed for orchids in March 2018. The coordinates in the top left corner correspond to the Greek coordinate system GRS87 EPSG: 2100 E 433500, N 3973500.

2007). During the early 19th century, the island supported close to 1000 inhabitants, but this number started declining throughout the 20th century and especially after World War II (Bevan & al. 2007).

Over time around 30 percent of Antikythera's surface was converted into agricultural terraces, while the rest of the island was grazed by goats. At present nearly all these terraces are abandoned and contain secondary plant communities of different structure and species diversity (Palmer & al. 2010). Due to the geographical location of Antikythera and the fact that the island was formerly part of a land-bridge connecting Crete to the Peloponnese (Georghiou & Delipetrou 2010), the vegetation on Antikythera is a mix of plant species belonging to the Kythira-Peloponnese communities, as well as those part of the Crete-Karpathos communities (Tzanoudakis & al. 2006). For a long time, the only plant list available for the island was the floristic catalogue of Greuter & Rechinger (1967) which mentions a total of 226 plant taxa, but this was largely based on botanical surveys done in May. More recently, Tzanoudakis & al. (2006) visited the island in April and during autumn and documented an additional 120 taxa. Antikythera is home to 25 Greek endemic taxa (Tzanoudakis & al. 2006), including the autumn-flowering *Allium aegilicum*, which is exclusively found on the island (Tzanoudakis 2000).

The total of 346 plant taxa includes only three orchid species, namely *Spiranthes spiralis*, *Anacamptis pyramidalis* and *Ophrys sicula* (Tzanoudakis & al. 2006). However, on many other Mediterranean islands the flowering season of orchids starts well ahead of April and can even be as early as mid-December (Antonopoulos & al. 2010). In the Atlas of the Greek orchids, Antonopoulos & Tsiftsis (2017) mention 5 more species for Antikythera, namely *O. omegaifera*, *O. tenthredinifera*, *O. ceto*, *Serapias parviflora* and *S. orientalis* subsp. *orientalis*, but this is largely based on observations of Nikos Tsiopelas and myself.

Material and Methods

The first time I visited Antikythera was at the end of March 2014 when I joined the bird ringing camp of the Hellenic Ornithological Society at the Antikytheran Bird Observatory. I stayed until the middle of April and then returned for nearly four weeks in May. During this period of two months, I observed several species of orchids, namely *Ophrys omegaifera*, *O. sicula*, *O. ceto* and *Anacamptis pyramidalis.* On the 31st of March I also came across some plants clearly belonging to the *Ophrys mammosa*-complex, but without the typical mammosities (Fig. 2). Unfortunately, only few withering plants were left during this time and so I could not study them any further. In March 2015 I wanted to have a closer look at the orchid, but last-minute alterations in the boat schedule put an end to those plans. Finally, in March 2018, I managed to visit the island for a proper three weeks, giving me enough time to study this species and the orchids of Antikythera in general.

Together with a friend, Diego Jansen, I walked along all the existing paths of the island, but also randomly through different kinds of habitats while on the way documenting our track (Fig. 1b) and every (group of) orchid(s) we encountered. The different routes did not overlap. During our first survey from March 10 to March 18 we walked a total of 70 kilometers and we only registered orchids that were in full flower or at the end of flowering.

Fig. 2. First plant of *Ophrys aegilica* found on Antikythera in March 2014 – photo taken on 31.03.2014.

We walked the same routes again after a twelve-day interval in order to spread our sampling efforts as much as possible during our stay on the island. In the second survey (from March 22 to March 30) we registered only the flowering plants and those that were still in the budding stage. We left out the plants at the end of flowering in order to prevent double counting the same individuals. Orchids were identified based on personal experience gained during previous visits to Greece and with the help of species guides (Delforge 2016; Antonopoulos & Tsiftsis 2017) and two websites (www.ophrys-genus.be; www.orchidsofbritainandeurope.co.uk). All observations were recorded on a smartphone using the ObsMapp application and each taxon has been photographed in order to strengthen the credibility of the records. The results can be seen in Table 1 and distribution maps based on the observations can be seen in Fig. 3.

Furthermore, plant and flower measurements were taken of 35 individuals of *Ophrys aegilica* from seven locations on the island, covering its entire distributional range on Antikythera. The values presented in the results section are the arithmetic means -/ + the standard deviation with the smallest and highest measured values between brackets.

Results

A total of 14226 individual orchids, belonging to 12 different species, were counted during the three week period on Antikythera (Table 1): 6440 during the first survey and 7786 during the second round. All eight species known from the island were observed, except *Serapias orientalis* (Greuter) H. Baumann & Künkele subsp. *orientalis* (Fig. 4). Furthermore, five species were observed for the first time on Antikythera (indicated with *), of which one is a new taxon altogether (Figs. 5 & 6).

Serapias parviflora Parl.: This autogamous species has a large distribution range in southern Europe. In Greece it mainly grows in the western and southern regions and flowers during April and May (Antonopoulos & Tsiftsis 2017). On Antikythera the species was observed in two locations, but almost all of the 52 plants were seen close to the village of Katsaneviana. The plants were only observed during the second survey when the first individuals just started flowering.

Serapias orientalis (Greuter) H. Baumann & Künkele subsp. ***orientalis***: While being a fairly common species in southern Greece and around the Aegean Sea (Antonopoulos & Tsiftsis 2017), only a single record is known from Antikythera. Nikos Tsiopelas found a single plant in the center of the island in April 2015 (Fig. 4). Although the flowering time of the species ranges from middle March to middle May, no individuals were found during our survey.

Anacamptis pyramidalis (L.) Rich.: In most of Europe and Greece this is a very widespread and common orchid species and on Antikythera this is no different. With 7262 individuals counted, it was by far the most numerous orchids on the island. It can form large colonies, especially on the calcareous soils like marl. The first plants started to flower at the end of March, but the vast majority of the plants still had closed flower buds at this point. The flowering peak of *A. pyramidalis* on Antikythera is during April (pers. obs. 2014).

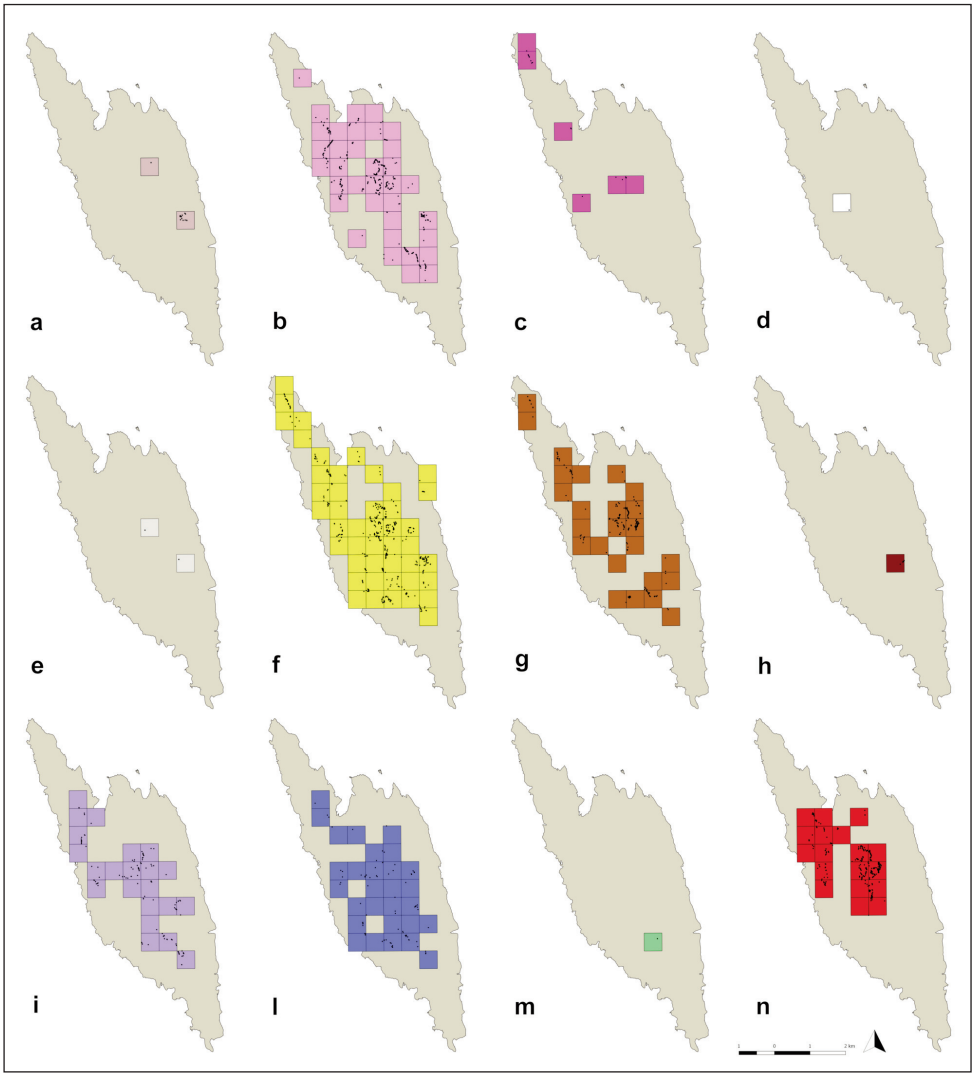

Fig. 3. Distribution maps of 12 orchid species on Antikythera based on 14226 individuals (as listed in Table 1) observed in March 2018. The black dots within the 500 × 500 m squares mark the actual locations of observations. a) *Serapias parviflora*; b) *Anacamptis pyramidalis*; c) *Anacamptis papilionacea* subsp. *aegaea*; d) *Neotinea maculata*; e) *Spiranthes spiralis*; f) *Ophrys sicula*; g) *O. omegaifera*; h) *O. bombyliflora*; i) *O. tenthredinifera* s. l.; l) *O. ceto*; m) *O. attica*; n) *O. aegilica*.

* ***Anacamptis papilionacea*** subsp. ***aegaea*** (P. Delforge) L. Lewis & Kreutz: It is the first time this early flowering subspecies, or any *A. papilionacea* for that matter, has been observed on Antikythera. It was formerly known as *A. papilionacea* subsp. *heroica* (E. D. Clarke) H. Baumann (see Lewis & Kreutz 2013) and its distribution range includes south-

Table 1. Updated list of orchid species known to occur on Antikythera, including the numbers of individuals found per species during the two surveys in March 2018.

Species	**# of ind. survey 1 10 - 18 March**	**# of ind. survey 2 22 - 30 March**	**Total**
Serapias parviflora Parl.	0	52	52
Serapias orientalis (Greuter) H. Baumann & Künkele subsp. *orientalis*	0	0	0
Anacamptis pyramidalis (L.) Rich.	0	7262	7262
Anacamptis papilionacaea subsp. *aegaea* (P. Delforge) L. Lewis & Kreutz	484	0	484
Neotinea maculata (Desf.) Stearn	1	0	1
Spiranthes spiralis (L.) Chevall.	0	7	7
Ophrys sicula Tineo	2191	200	2391
Ophrys omegaifera H. Fleischmann	1399	27	1426
Ophrys bombyliflora Link	116	0	116
Ophrys tenthredinifera Willd. s. l.	462	2	464
Ophrys ceto P. Devillers, J. Devillers-Terschuren & P. Delforge	0	186	186
Ophrys attica (Boiss. & Orphanides) B. D. Jackson	2	0	2
Ophrys aegilica D. Engelen	1785	50	1835

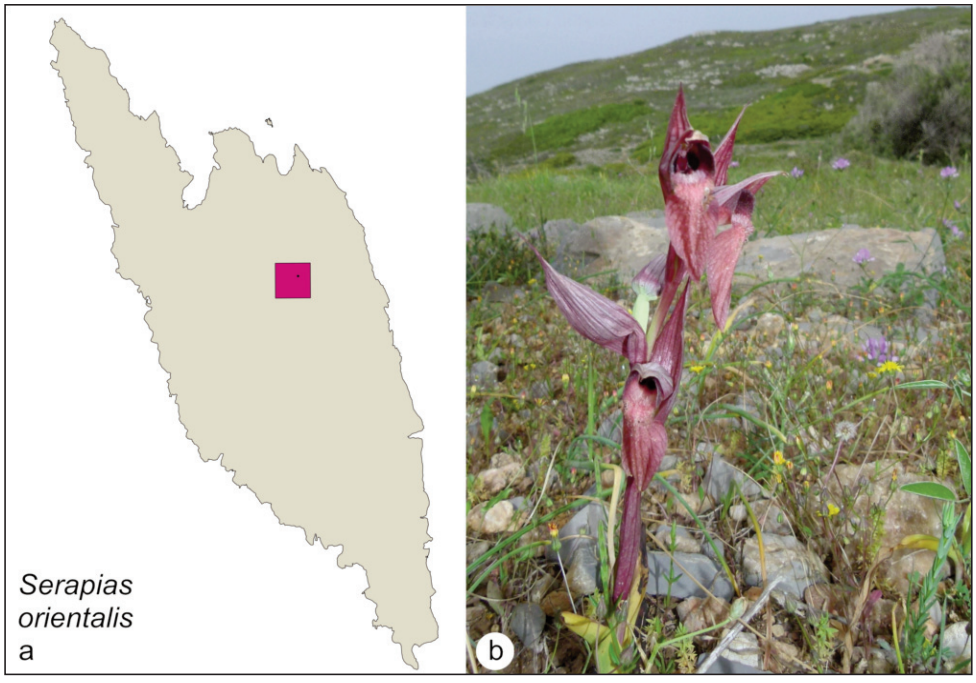

Fig. 4. Location (a) and photo (b) of the only individual of *Serapias orientalis* subsp. *orientalis* ever recorded on Antikythera – photo taken on 19.04.2015 by Nikos Tsiopelas.

ern and insular Greece, as well as western Turkey (Antonopoulos & Tsiftsis 2017). Several small populations were found across the island and a total of 484 individuals were counted. Most plants had started to wither already by the first survey round in the middle of March.

* ***Neotinea maculata*** (Desf.) Stearn: This autogamous species has a wide distribution, ranging from the Canary Islands, across Europe and into the Levant. In Greece it is more common in the southern areas and the islands (Antonopoulos & Tsiftsis 2017), but for Antikythera it is the first time this species is observed. Only a single individual was found on the road to Plagara, the highest peak of Antikythera (379 m). This individual was found during the first survey and had already started to wither by that time.

Spiranthes spiralis (L.) Chevall.: This autumn-flowering orchid is widespread in Europe and Greece. During spring the rosettes are visible, but they wither away before the flowering spike appears, which is an adaptation to hot and dry summers (Waller 2016). Seven rosettes were found in two places on the island, but it is likely this species has been overlooked at times during this study.

Ophrys sicula Tineo: This is one of the most common *Ophrys* species in Greece (Antonopoulos & Tsiftsis 2017) and with 2192 individuals counted, it is the second most numerous species on Antikythera. Flowering individuals were observed during both survey rounds, but they were clearly more abundant during the first one (Table 1). It is the most widespread orchid species on the island and grows in all kinds of habitats; sometimes with just a few plants, but other times in large colonies.

Ophrys omegaifera H. Fleishmann: Like *O. sicula* this species was observed during both survey rounds. It mostly flowers during March, but few individuals are still found in April as well (pers. observ. 2014). With 1399 individuals counted, it was the fourth most numerous species in this study and prefers abandoned terraces dominated by *Sarcopoterium spinosum* (L.) Spach and *Erica manipuliflora* Salisb. Currently Antikythera seems to be the most western point of the distribution range of *Ophrys omegaifera* in Greece, as the records known from Kythira and the Peloponesse are from before 1985 (Antonopoulos & Tsiftsis 2017).

* ***Ophrys bombyliflora*** Link: This widespread Mediterranean species is quite common in coastal Greece (Antonopoulos & Tsiftsis 2017), but it is the first time this species is observed on Antikythera. During the first survey a colony of 116 individuals was found near the village of Katsaneviana, but all these plants had completely disappeared by the time of the second visit.

Ophrys tenthredinifera Willd. s. l.: This taxon is widespread in southern Europe and plants growing in the eastern Mediterranean were previously known as *O. villosa* Desf. (see Paulus & Hirth 2012). However, in recent years Greek plants belonging to the *tenthredinifera*-complex have been split into a number of new (sub)species, such as *O. leochroma* P. Delforge, *O. ulyssea* P. Delforge, *O. dictynnae* P. Delforge, *O. korae* M. Hirth & Paulus and *O. lycomedis* P. Delforge (Paulus & Hirth 2012; Delforge 2005, 2013). Both Crete and Kythira are home to several species from this complex, but on

Antikythera there seems to be only one species form. The 464 individuals found in this study were almost exclusively seen during the first survey and the species is largely gone after the middle of March. It is difficult to say, however, whether this species is the widespread *O. tenthredinifera* s. s. or the Cretan endemic *O. dictynnae* P. Delforge. The species are difficult to separate morphologically and both species could still be flowering during the first half of March (Antonopoulos & Tsiftsis 2017). Furthermore, an insect study on the island during the spring of 2014 (Petanidou & al. unpublished data) did not find *Eucera nigrilabris* (the pollinator of *Ophrys tenthredinifera*), but did come across *Eucera albofasciata* (the pollinator of *Ophrys dictynnae*). Further pollination studies in the *tenthredinifera*-complex are needed on Antikythera specifically to shed light on this issue, but also generally to better understand how reproductive isolation between the different species is achieved (Cuervo & al. 2017).

Ophrys ceto Devillers, Devillers-Tersch. & P. Delforge: The distribution of this species in Greece is centered around the Cyclades islands, ranging from Kythira to Samos, and its flowering season runs from mid-April to mid-May (Antonopoulos & Tsiftsis 2017). Antikythera is the most southern point of its distribution and the first flowering plants were found during the second survey at the end of March. However, the vast majority of the 186 counted plants had closed flower buds that will open during April and May. Individuals in full flower have been observed as late as 15th of May (pers. observ. 2014), suggesting quite a long flowering period for *O. ceto* on Antikythera.

* ***Ophrys attica*** (Boiss. & Orph.) Soó: It is the first time this or any species of the *Ophrys umbicilata*-complex has been observed on Antikythera. For *O. attica* the island seems to be the most southern point of its distribution range in Greece (Antonopoulos & Tsiftsis 2017). During the first survey two flowering individuals were found several meters from each other on the southern plateau of the island. A revisit to this location during the second survey showed that both plants had been eaten by goats.

* ***Ophrys aegilica*** D. Engelen: This is a new taxon and the first time any species belonging to the *Ophrys mammosa*-complex has been observed on Antikythera. Even widespread species of this complex in Greece, such as *O. mammosa* Desf. (with its characteristic mammosities) and *O. spruneri* Nyman (with its purple sepals and trilobed lip) have never been found on the island. *O. aegilica* was the third most counted species during the surveys with a total of 1835 plants. Among the observed plants was also an individual with a hypochromic inflorescence (Fig. 6). Its distribution is focused around the terraces found in the centre of the island. Flowering starts in March and the very last plants wither during the first days of April.

Ophrys aegilica D. Engelen ***spec. nov.***

Holotype – About 700 m. southwest of Skariana area, in the central north part of Antikythera island, Greece; UTM (WGS84) Zone 34S: E 707821.1, N 3971649.8 (35°52'1.40"N, 23°18'6.48"E); roadside with phrygana; 143 m a.s.l.; 22.03.2018, Leg. Dries Engelen (NHMC 43-12785) (Fig. 7).

Description – Plant 10 - 35 cm, inflorescence usually 2 – 7 flowers (maximum 12). Sepals triangular with rounded tops, greenish, occasionally with reddish tinge, lateral sepa-

Fig. 5. Four orchid species found for the first time on Antikythera: a) *Anacamptis papilionacea* subsp. *aegaea* – photo taken on 12.03.2018; b) *Neotinea maculata* – photo taken on 18.03.2018; c) *Ophrys bombyliflora* – photo taken on 14.03.2018; d) *O. attica* – photo taken on 13.03.2018.

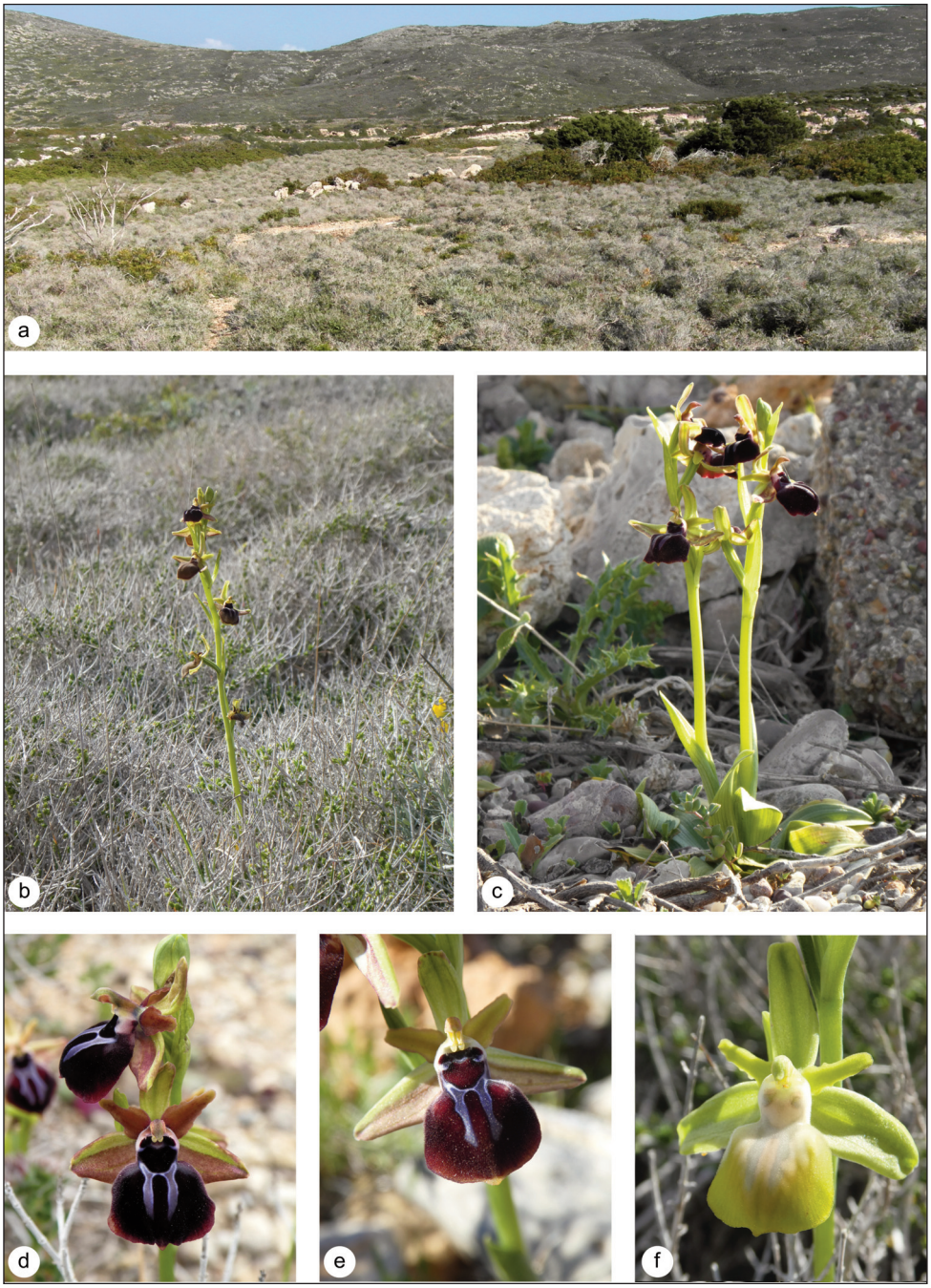

Fig. 6. *Ophrys aegilica*: a) Habitat with *Coridothymus capitatus* and *Sarcopoterium spinosum* – photo taken on 14.03.2015; b, c) Entire plant – photos taken on 11.03.2018; d, e) Close-ups of flower – photos taken on 10.03.2018; f) Hypochromic individual – photo taken on 11.03.2018.

Fig. 7. Holotype of *Ophrys aegilica,* Antikythera, 22.03.2018; Herbarium of the Natural history Museum of Crete, University of Crete.

ls bicoloured, basal half weakly to strongly reddish, length x width (9)10.9 – 14.1(16.5) × (5)5.4 – 6.8(7) mm. Petals triangular, broadened at base and rounded tops, yellow-green, sometimes with reddish tinge, lightly undulated with an irregular margin, length × width (7)7.2 – 9.5(12) × (2.5)2.9 – 4.0 (4.4) mm. Labellum oval to rounded-trapezoid shape, entire margin occasionally obscurely three lobed, burgundy colour (dark reddish purple tending towards brown-black) rarely with a very thin yellow border, length (10)11.4 – 13.4 (15) mm, center of lip bulged, mammosities absent or very weakly apparent, small hairs along (half of) the lip margin, same colour as the lip with a whitish shimmer. Appendage small, triangular elongation of the lip, yellow-orange to light red, always lighter than lip colour, rarely completely lacking. Speculum H-shaped, occasionally missing horizontal line, covering three quarters of the lip, bright metallic blue, sometimes with (partial) white border. Basal field reaching half of the gynostemium, same colour as the lip. Pseudo-eyes same blueish colour as the speculum, sometimes also connected to it. Stigmatic cavity constricted at base, outer upper side white or whitish-reddish. Stigmatic hole dark with a large whitish specular stage, which sometimes has a hint of blue similar to the colour of the speculum, and is occasionally connected to the pseudo-eyes by a white line. Gynostemium greenish in center and reddish on sides, sometimes entirely reddish or entirely greenish.

Diagnosis – *O. aegilica* clearly belongs to the *mammosa*-complex as it has the characteristic dark-blue to black pseudo-eyes, the dark basal area of the lip, the green and red bicolored lateral sepals, the velutinate petals and the small appendix prolongating the labellum (Delforge 2016; Antonopoulos & Tsiftsis 2017). The near absence of mammosities in *O. aegilica* is a characteristic also found in *O. hansreinhardii* M. Hirth, a species which also flowers at the same time (Hirth 2007). However, *O. hansreinhardii* is distributed from southern Albania to northwestern Greece, is often found at higher altitudes (~600 m a.s.l.) and is clearly distinguished by several morphological characteristics (Table 2). Flowers of *O. aegilica* have a larger lip size; smaller lateral pilosity; rarely backwards folded sepals; and overall appear to be less dull with stronger contrast between the blue-grey speculum and the dark red lip. Furthermore, the pollinator of *O. hansreinhardii* (*Andrena assimilis*) has not been found on Antikythera (Petanidou & al. unpublished data).

Another species of the *mammosa*-complex which usually lacks mammosities is *Ophrys taigetica* Presser & S. Hertel, found in the Peloponnese (Presser & Hertel 2010). Although this is geographically closer to Antikythera, *O. taigetica* is found in *Abies cephalonica* Loudon and *Pinus nigra* J. F. Arnold mountain forests (950 – 1560 m a.s.l.) and flowers from mid-May to early June. Apart from these ecological distinctions, *Ophrys aegilica* also differs morphologically from *O. taigetica* in the size of its petals, the stronger red-purple tinge of the lateral sepals and the more pronounced blue colour of the speculum, pseudo-eyes and specular stage (Table 2).

Etymology – As *O. aegilica* is the first orchid species described from Antikythera, its name is derived from Aegila (Αἰγιλα), which was the name of Antikythera during the Hellenistic and Roman times. This classical name probably meant ‘goat island’ (Bevan & Conolly 2013).

Pollinator – Currently unknown.

Habitat – *O. aegilica* can be found in stony wastelands and road sides, but it predominantly grows on relatively recently abandoned terraces with a loose and open phrygana vegetation dominated by *Coridothymus capitatus* (L.) Rchb. and *Sarcopoterium spinosum*

(Fig. 6). It prefers dry, calcareous soil. Antikythera is an almost wholly limestone island with comparatively high pH levels and magnesium content and low levels of zinc and phosphorus (Bevan & al. 2013).

Flowering time – The species starts flowering in early March and only very few flowering individuals will be left during the beginning of April. Other orchids flowering at the same time are *Ophrys omegaifera*, *O. sicula* and *O. tenthredinifera* s. l. In the same habitat *Anacamptis pyramidalis* starts flowering when *Ophrys aegilica* is nearly finished.

Altitudinal distribution – From sea level until 200 m.

Distribution – *O. aegilica* seems to be endemic to Antikythera. Its distribution is focused around the terraces found in the centre of the island (Fig. 3) where it can form large groups in places with suitable habitat conditions.

Discussion

Plant communities of Mediterranean islands are often understudied. A short but intense orchid survey on the island of Antikythera in March 2018 revealed 5 taxa not known to occur on the island, including a previously undescribed endemic: *Ophrys aegilica*. This new species belongs to the *mammosa*-complex, a group that currently contains over 30 species of which the distribution is centered around the Northeastern Mediterranean (Delforge 2016). While *O. mammosa* is the most widespread species of this complex in Greece (Antonopoulos & Tsiftsis 2017), it seems to be absent from Antikythera and instead replaced by *O. aegilica*. It is therefore not surprising that the pollinator of *O. mammosa,* the mining bee *Andrena morio*, was not found on the island during an insect survey between late March and late April 2014 (Petanidou & al. unpublished data). A similar situation occurs on nearby Crete where *Ophrys mammosa* and its pollinator are lacking, and replaced by the Cretan endemic *O. doerfleri* Fleischmann and its pollinator *Andrena fuscosa* (see Paulus & Hirth 2017). Pollinator specificity is one of the main factors resulting in reproductive isolation between taxa and speciation events in the genus *Ophrys* (Ayasse & al. 2010; Breitkopf & al. 2014; Cuervo & al. 2017; Paulus & Hirth 2017). Particularly *Eucera* or *Andrena*-pollinated *Ophrys* species have had recent episodes of diversification (Breitkopf & al. 2014) and emphasize the importance of studies on Antikythera to identify the pollinator of *O. aegilica* and to clarify the aforementioned *O. tenthredinifera* s. s./ *O. dictynnae* issue (see result section). Also, as the reproductive success of orchids is often limited by pollinator access (Vereecken & al 2010), identifying the pollinator and ensuring its wellbeing will ultimately benefit the conservation of *O. aegilica*.

The new orchids found on Antikythera during this study, combined with those mentioned for the island in the new "Atlas of the Greek orchids" (Antonopoulos & Tsiftsis 2017) add a total of 10 taxa to the existing plant list of Antikythera (Greuter & Rechinger 1967; Tzanoudakis & al. 2006), making for a total of 356 species. For *O. omegaifera*, *O. ceto* and *O. attica* (and possibly *O. dictynnae*) Antikythera even marks a new border of the distributional ranges of these species in Greece. Also, the fact that species such as *Neotinea maculata* and *Anacamptis papilionacea* subsp. *aegaea* were already at the end of flowering during the first half of March, underlines the importance of botanical surveys on Antikythera and other Mediterranean islands during the winter months in order to obtain

Table 2. Ecological and morphological characteristics of *Ophrys aegilica* compared to other closely related taxa from the *mammosa*-complex.

	Ophrys mammosa	*Ophrys spruneri*	*Ophrys doerfleri*	*Ophrys hansreinhardii*	*Ophrys taigetica*	*Ophrys aegilica*
Source	Delforge (2016: 554)	Delforge (2016: 549)	www.cretanflora.com	Hirth (2007: 509-513)	Presser & Hertel (2010: 160-167)	Own observations
Pollinator	*Andrena morio*	*Xylocopa iris*	*Andrena fuscosa*	*Andrena assimilis*	Unknown	Unknown
Distribution	North-eastern Medit.	Greece	Crete	Albania and Northwestern Greece	Peloponnese	Antikythera
Habitat	Short grassland, phryganae, scrub, open woodland;	Short grassland, phryganae, scrub, open woodland;	Phryganae, terraces, scrub, thin forests;	Chalk soil; phryganae with *Erica arborea*;	Mountain forests with *Abies cephalonica* and *Pinus nigra*	Phryganae with *Coridothymus capitatus* and *Sarcopoterium spinosum*;
Altitude	To 1400 m	To 900 m	To 1200 m	~ 600 m	950–1560 m	To 200 m
Flowering time	Mar – early May	Late Feb – early May	Mar – Apr	March – April	Mid May – early June	March – early April
Sepals	10 – 17 mm; 4 – 8 mm; olive green, lateral sepals bicoloured, tinted violet in lower half	10 – 16.5 mm; 5 – 6,5 mm; lateral sepals bicoloured whitish and dark violet-pink	Green-white to pink (like *O. spruneri*)	10.1 – 11.8 mm; 3.5 – 5 mm; green, lateral sepals lightly red tinted	12 – 14 mm; 3 - 6 mm; lateral sepals mostly green, sometimes light reddish in lower half	10.9 – 14 mm; 5.4 – 6.8 mm; greenish, lateral sepals bicoloured, basal half weakly to strongly reddish
Petals	7 – 12 mm; 2 – 4.5 mm; yellowish-green or purplish; little curvy; small or no hairs	7 – 12 mm; 2 – 4 mm; pink-purple or yellow-brownish; curvy	Often Pinkish-red; smooth or velvety; little curvy	7 – 8.6 mm; 2.3 – 5.1 mm; greenish, red-brown; little curves and small hairs	9 – 14 mm; 2 mm width, yellower or browner than sepals; little curvy and without hairs	7.2 – 9.5 mm; 2.9 – 4.0 mm; Yellow-green with reddish tinge; little curvy
Lip	12 × 17 mm; Entire; Reddish-brown to blackish-purple	12 × 17 mm; Tri-lobed; Blackish-purple	Smaller than *O. mammosa*; Entire, Convex (beak-like); Dark reddish to brown-black with paler red (rarely yellow) border	9.4 – 11 mm; Entire, Rounded-trapezoid; Blackish-purple	11 – 13 mm; Entire, Oval to rounded; Reddish Black-brown; sometimes with light red or yellow border	11.4 – 13.4 mm; Entire, Oval to rounded-trapezoid; Dark reddish-purple to brown-black, sometimes with light red (rarely yellow) border

Table 2. continued.

Mammosities	Yes	Usually absent	Yes	Small or absent	Usually absent	Usually absent
Peripheral Pilosity	Short, more at shoulder	Short, more at shoulder	Short, more at shoulder	Strong pilosity along entire lip margin	Short, more at shoulder	Short, more at shoulder
Appendage	Short or absent; greenish-yellow to crimson-brown	Short or absent; greenish to crimson-brown	Small to absent; yellow-greenish or red-brown	Short; yellowish-pink	Small; yellowish (rarely red)	Small; yellow-orange to light red
Speculum	H-shaped; glossy bluish-grey or lilac, sometimes with white border	H-shaped; glossy azure-blue with white border	H-shaped; glossy bluish-grey or lilac, usually with white border	Dissolved H-shape; bluish-purplish, rarely with white border	Dissolved H-shape; a bit blueish; sometimes with white border	H-shaped; bright metallic blue, sometimes with white border
Pseudo-eyes	Whitish-pale blue with grey central spot	Blackish-pale blue with grey central spot	Whitish to blue with grey central spot	Black	Black, sometimes with white border	Pale blueish
Stigmatic cavity colour	Blackish with blue specular stage	Blackish whit pale blue specular stage	Blackish, with bluish specular stage	Darker than lip, white or lila-ish specular stage	Coloured like lip with lighter specular stage	Blackish with white-blueish specular stage

complete floristics overviews of these places. Alike observations have been made on other, similar-sized Greek islands where some species are known to flower as early as late December (Antonopoulos & al. 2010). Especially when climatic conditions are as such that plants tend to wither and visually disappear altogether in the timespan of just a few weeks. Most of the flowering orchids encountered on Antikythera during the first half of March had completely vanished by the time of the second survey at the end of March, as was the case for instance for all individuals of *Oprhys bombyliflora*.

On Antikythera, orchids predominantly grow on abandoned agricultural terraces (Fig. 8; compare with Bevan & al. 2013: 258, Fig. 3c). As this habitat was created by humans, who have now largely left the island, the future presence of the orchids will mainly depend on the speed and type of vegetation succession (Kranjčev 2001). Directly after abandonment terraces hold a rich herbaceous flora with many annual species, but this is quickly followed by the establishment of the first woody perennials, such as *Coridothymus capitatus* and *Sarcopoterium spinosum*, but later also *Genista acanthoclada* DC., *Erica manipuliflora* and *Calicotome villosa* (Poir.) Link. (Tzanoudakis & al 2006; Palmer & al 2010). These phryganic communities are rich in orchids, but 20 – 60 years after cultivation has ceased, this habitat develops into low maquis with evergreen, sclerophyllous shrubs such as *Pistacia lentiscus* L., *Juniperus phoenicea* L. and *Quercus coccifera* L. (Palmer & al 2010). Over time the maquis grows taller and becomes nearly impenetrable and orchids are more restricted to the edges of the habitat or road sides. However, as Antikythera holds a large population of feral goats that browse the

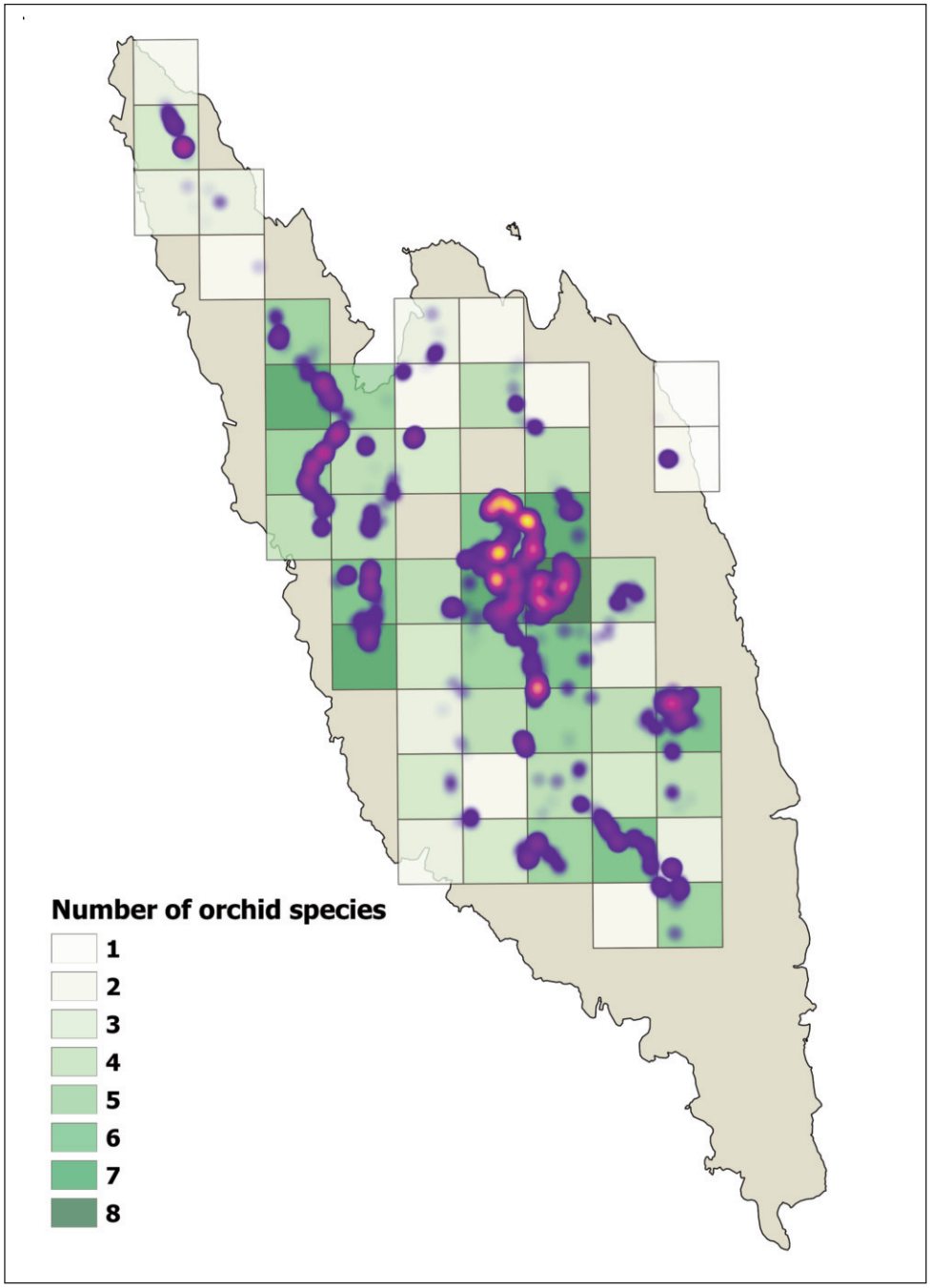

Fig. 8. Orchid richness of Antikythera, both in terms of number of species present within a 500 × 500 m square (the higher the diversity, the darker the shade of green) and overall abundance (heatmap based on all 14226 individuals, as listed in Table 1, in which brighter colours indicate higher abundance).

island, the succession of the vegetation is slowed down (Palmer & al. 2010). While grazing may benefit orchid populations on a larger scale by keeping the habitat more open and delaying succession, it can still have severe impacts on individual plants and species with small populations (Georghiou & Delipetrou 2010). During this study several orchids were observed that had been grazed and for *Ophrys attica* it even meant that the only two individuals found on the island were both eaten. Also, in the case of Antikythera it should be pointed out that the majority of orchids was found on abandoned agricultural terraces (Fig. 8); places from which goats were formerly excluded. Thus, for the maintenance of orchid populations on Antikythera, and the endemic *O. aegilica* in particular, it is important that the vegetation on some of the abandoned terraces keeps its open phryganic character, but preferably by other means than grazing.

Acknowledgments

I would like to thank Diego Jansen (Rotterdam, The Netherlands) for assisting me with the fieldwork and the creation of the species distribution maps; Nikos Tsiopelas and Christos Barboutis from the Hellenic Ornithological Society (Athens, Greece) for helping out with the logistics on Antikythera; Laurens Krol (Berlin, Germany) and Biljana Ječmenica (Zagreb, Croatia) for help with the figures; Zissis Antonopoulos (Thessaloniki, Greece) and Karel Kreutz (Landgraaf, The Netherlands) for their expert opinions on orchids and valuable comments at various stages of this study. This is contribution n. 28 from the Antikythira Bird Observatory – Hellenic Ornithological Society. The Antikythira Bird Observatory is funded from the A.G. and A.P. Leventis Foundation.

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