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A critical approach to *Ophrys calypsus (Orchidaceae)* and to the records of *O. holoserica* subsp. *apulica* from Greece

Abstract

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Ophrys holoserica subsp. *apulica* was until recently considered endemic to southern Italy, but during the last few years several finds have been reported from Greece. In the present paper, a comparison is made between plants from Rhodes and Monte Gargano in Italy. It is concluded that they are not conspecific and that *O. holoserica* subsp. *apulica* must still be considered endemic to southern Italy. The Rhodean taxon is considered identical with the recently described *O. calypsus* from Leipsoi and Naxos. However, the taxonomic validity of *O. calypsus* is questioned, and it is hypothesized that it should rather be regarded as cases of hybridization and probably introgression between *O. holoserica* subsp. *holoserica* and *O. scolopax* subsp. *heldreichii*. A distance diagram of morphological *Ophrys* data from Rhodes and Crete, as well as phenological observations on the Rhodean specimens, support our hypothesis. Possible pre- and post-zygotic barriers between the supposed parental taxa are discussed. While Hirth & Spaeth (1994) recognized *O. calypsus* as a separate species, Delforge (1995) split the complex into *O. heldreichii* var. *calypsus* and *O. heldreichii* var. *pseudoapulica*. In contrast, we propose that *O. calypsus* should be treated merely as a hybrid complex with no need to be recognized as one or more independent taxa.

Introduction

Ophrys holoserica (Burm. f.) Greuter subsp. *apulica* (O. & E. Danesch) Buttler was originally described under the basionym *O. fuciflora* (F. W. Schmidt) Moench subsp. *apulica* O. & E. Danesch, cf. Danesch & Danesch (1970). For nearly a decade, it was considered endemic to southern Italy, being distributed from Sicily northwards to Molise and Monte Gargano. During the last few years, however, a few records have been made of finds in Greece. Thus Gölz & Reinhard (1978, 1981) with hesitation referred a single *Ophrys* population in Kos to *O. holoserica* subsp. *apulica*, while Peter (1989) confidently assigned 13 populations in Rhodes to the same taxon. Furthermore, he stated that three specimens depicted as *Ophrys heldreichii* Schltr. in Nelson (1962), i.e. specimens from Syros (Pl. XLIII(69)) and Naxos (Pl. XLIII(70-71)) also belong to *O. holoserica* subsp.

apulica. In all three papers, this taxon was given the rank of species, *O. apulica* (O. & E. Danesch) O. & E. Danesch. Referring to the earlier records of *O. holoserica* subsp. *apulica* from Greece, Paulus & Gack (1992) reported a number of similar populations from Naxos. Based on anthecological observations, however, Paulus & Gack doubted that the Greek populations should be referred to *O. holoserica* subsp. *apulica*, finding it more likely that they are hybrid populations or belong to an undescribed species.

Hirth & Spaeth (1994) compared the above population from Kos to a population in Leipsoi and concluded that the plants of the two populations should be considered taxonomically identical. However, Hirth & Spaeth did not agree that the populations belong to *O. holoserica* subsp. *apulica*. Instead, they described the new species *O. calypsus* M. Hirth & H. Spaeth to accommodate the two populations. They did not state whether the claimed populations of *O. holoserica* subsp. *apulica* in Rhodes, Syros, and Naxos should be considered conspecific. Lately, however, Kretschmar & Kretschmar (1996) have listed 11 populations of *O. calypsus* from Naxos without mentioning *O. holoserica* subsp. *apulica*.

Delforge (1995), in his account on the orchid flora of Paros and Antiparos, split *O. calypsus* into *O. heldreichii* var. *pseudoapulica* P. Delforge and *O. heldreichii* var. *calypsus* (M. Hirth & H. Spaeth) P. Delforge.

In the present paper, we attempt a critical approach to the taxonomic validity of *O*. *calypsus* and to the claimed occurrence of *O*. *holoserica* subsp. *apulica* in Greece. We apply the working hypothesis that *O*. *calypsus* and the Greek populations assigned to *O*. *holoserica* subsp. *apulica* are taxonomically identical and should be interpreted as cases of hybridization and probably introgression between *O*. *holoserica* subsp. *holoserica* and *O*. *scolopax* Cav. subsp. *heldreichii* (Schltr.) E. Nelson.

Methods and study sites

The characteristics of *Ophrys holoserica* subsp. *apulica* were critically observed in Monte Gargano in Italy with the aim to perform a comparison with the protologue of *O. calypsus* as well as with the published descriptions and illustrations of the claimed Greek representatives of the former taxon. A comparison was also made to specimens of *O. apulica* sensu Peter examined by ourselves in Rhodes. Neither the type of *O. calypsus* (fide Georg Zizka, in litt. 1996) nor the type of *O. holoserica* subsp. *apulica* (fide Silvia Klein, in litt. 1996) could be retrieved in the herbaria indicated in the protologues (FR and IB, respectively), so, unfortunately, we had to give up our intention to include type material in our study. In Monte Gargano *O. holoserica* subsp. *apulica* was found and examined at the following stations: Torre di M. Pucci, c. 3 km W. S. W. of Péschici (9 April 1995); S. Lorenzo, c. 2.5 km N. W. of Vieste (10 April 1995); c. 11 km N. E. of Mattinata (15 April 1995); c. 7.5 km W. of Vieste (16 April 1995).

In 1993 and 1996 field work was carried out in Rhodes at the following localities:

1. East of Hotel Filerimos, c. 5 km south of the town of Rhodes, 14 April - hills covered with phrygana. In 1993 N. Faurholdt found several specimens of *O. holoserica* subsp. *holoserica* - a taxon which could not be retrieved in 1996. Instead we discovered eight specimens of *O. apulica* sensu Peter, all of which were included in the study.

2. Gadouras River, 3.2 km north of Kalathos, 16 and 18 April - phrygana and grassland in a dry river bed. In 1993 N. Faurholdt found *O. holoserica* subsp. *holoserica*, *O.*

scolopax subsp. heldreichii, and O. apulica sensu Peter - all in numbers. In 1996 O. holoserica subsp. holoserica was retrieved in numbers, but we only found one specimen of O. scolopax subsp. heldreichii and three specimens of O. apulica sensu Peter. Twelve Ophrys specimens were included in the study.

3. Kamiros (between the coast and the monument of antiquity), 18 April - phrygana on low hills. In 1996 we found *O. holoserica* subsp. *holoserica* in numbers. Ten specimens were included in the study.

Additional material of *O. scolopax* subsp. *heldreichii* was measured in phrygana on Crete in 1997, viz.: locality 4 - east of Melambes, Nomos Rhethimnon (24 March, 3 specimens); locality 5 - along the old road between Agia Galini and Melambes, immediately west of Melambes (25 March, 2 specimens); locality 6 - 0.6 km south of Agios Pareskevi, Nomos Rhethimnon (26 March, 2 specimens).

Our hypothesis that the populations on Rhodes referred to *O. holoserica* subsp. *apulica* represent simple or introgressive cases of hybridization between *O. holoserica* subsp. *holoserica* and *O. scolopax* subsp. *heldreichii* was tested by a distance diagram, applying the method of Wells (1980). Seven morphological characters (Table 1, Fig. 1) were selected to distinguish between the two presumed parental taxa. The states of these characters were scored for 37 specimens in the study populations on Rhodes and Crete. Additionally, two reference points were constructed ("A" for *O. holoserica* subsp. *holoserica*; "B" for *O. scolopax* subsp. *heldreichii*). The reference points were based on descriptions of (I) *O. holoserica* subsp. *holoserica* and (II) *O. scolopax* subsp. *heldreichii* constructed by pooling the information from descriptions and illustrations of:

I. O. holoserica subsp. holoserica "Variante 1" and "Variante 2 ("maxima")" in Buttler (1986), O. fuciflora and O. episcopalis Poir. in Delforge (1994), and O. holosericea (sphalm.!) in Baumann & Künkele (1982);

II. O. scolopax subsp. heldreichii in Buttler (1986), O. heldreichii in Delforge (1994), and O. heldreichii in Baumann & Künkele (1982).

1.	Length of dorsal sepal (mm).
2.	Length of right petal (mm).
3.	Basal auriculations of right petal, on a scale 0-2 (0 = absent; 1 = barely recognizable; 2 = distinct).
4.	Longitudinal vaultedness of labellum, on a scale 0-4 (0 = not at all longitudinally vaulted, through to 4 = anterior part of labellum subspherical).
5.	Direction of lateral labellum margins in front, on a scale 1-3 (1 = spreading; 2 = somewhat reflexed; 3 = completely reflexed).
6.	Lobedness of labellum, on a scale 0-2 ($0 = labellum entire$; $1 = side lobes barely recognizable$; $2 = side lobes distinct$).
7.	Shape of labellum bulges, on a scale 0-4 (0 = absent; 1 = barely recognizable; 2 = breast-like; 3 = conical; 4 = horn-like).

Table 1. Survey of the morphological characters selected to distinguish between *Ophrys holoserica* subsp. *holoserica* and *O. scolopax* subsp. *heldreichii*. See Fig. 1 for comments on character no. 4.

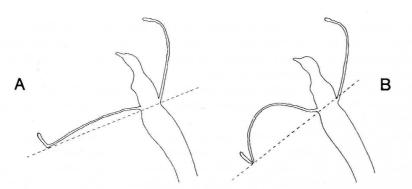


Fig. 1. Graphic representation of *Ophrys* flowers having: **A**, a flat labellum; **B**, a strongly longitudinally vaulted labellum. The labellum margins may or may not be recurved in both flowers. The character of longitudinal vaultedness is by a number of authors being confused with the direction of the labellum margins. This confusion has led to the general misunderstanding that the labellum of *O. holoserica* subsp. *apulica* is strongly vaulted. In reality it is nearly flat (Fig. 2D).

Having obtained the field data and the pooled descriptions as well as the reference points, all characters were ranged between zero and one (cf. Gower 1971) to secure equal weighting of the different scales of measurement used on the various characters.

Applying the euclidean distance equations supplied by Wells (1980) the distance between A and B was determined as well as the distances between the reference points and each of the measured specimens. Finally, the 37 specimens were plotted in a distance diagram.

Phenological data were collected from the specimens from Rhodes included in the morphological evaluation. On each specimen, the numbers of buds, fresh flowers, and withered flowers were counted.

For the specimens accommodated in each of the tentative categories (*O. holoserica* subsp. *holoserica*, *O. apulica* sensu Peter, *O. scolopax* subsp. *heldreichii*) the mean numbers of buds, fresh flowers, and withered flowers per specimen were then determined to facilitate a phenological comparison.

Table 2. Pooled descriptions of *O. holoserica* subsp. *holoserica* and *O. scolopax* subsp. *heldreichii* based on information from the literature (see the text for references). The characters are numbered in accordance with Table 1.

Character no.	<i>holoserica</i> Range Average		<i>heldreichii</i> Range	Average
1	9.0-16.0	12.50	12.5-16.0	14.25
2	2.0-7.0	4.50	3.0-7.2	5.10
3	1-2	1.50	0-1	0.50
4	0-2	1.00	3-4	3.50
5	1-2	1.50	3	3.00
6	0-1	0.50	2	2.00
7	0-3	1.50	3-4	3.50



Fig. 2. A, B, Ophrys apulica sensu Peter (= O. holoserica subsp. holoserica \times scolopax subsp. heldreichii) from Rhodes, 14 Apr 1996; C, D, O. holoserica subsp. apulica from Monte Gargano in Italy, 16 Apr 1995. — Scale-bar = 1.0 cm. - Del.: H. Ae. Pedersen.

Results

Several differences were found between the plants we examined on Monte Gargano and on Rhodes, respectively.

On Monte Gargano, the plants (Fig. 2C, D) are generally slender with the stems being floriferous in (usually!) their upper 1/3 or less. The leaves are greyish green, contrasting with the mid-green stem. The labellum margins, in a fully developed flower, are distinctly recurved and subsequently spreading to somewhat incurved (thus designating a graceful, S-like curve in transverse section). The labellum is nearly flat, never distinctly longitudinally vaulted (cf. Fig. 1), and the speculum reaches from the base to slightly over the middle of the labellum.

On Rhodes, the plants (Fig. 2A, B) are generally compact with the stems being floriferous in their upper 1/2 or more. The leaves are mid green, not contrasting with the stem. The labellum margins, in a fully developed flower, are more or less recurved, but not subsequently spreading or incurved (and consequently not designating an S-like curve in transverse section). The labellum is distinctly longitudinally vaulted (cf. Fig. 1), and the speculum reaches from the base to just behind the apex of the labellum.

The sketched dissimilarities remain consistent, also when comparisons are made to the protologue of *O. calypsus* (Hirth & Spaeth 1994) - as well as to the descriptions and illustrations produced by Nelson (1962), Gölz & Reinhard (1978), Peter (1989), and Paulus & Gack (1992) for Greek plants assigned by one or more authors to *O. holoserica* subsp. *apulica*.

Table 2 gives the pooled descriptions compiled from published descriptions and illustrations. The distance between the reference points (A and B), determined from ranged values, was found to be 0.97. The distance diagram is presented in Fig. 3.

Inflorescences of the 18 specimens of *O. holoserica* subsp. *holoserica* carried a mean of 59 % buds, 35 % fresh flowers, and 6% withered flowers, while the inflorescence of the sole specimen of *O. scolopax* subsp. *heldreichii* on Rhodes carried 0 % buds, 25 % fresh flowers, and 75 % withered flowers. Inflorescences of the 11 specimens of *O. apulica* sensu Peter were phenologically intermediate, carrying a mean of 18 % buds, 48 % fresh flowers, and 34 % withered flowers at the time of study.

Discussion

In the protologue of *Ophrys calypsus*, Hirth & Spaeth (1994) indicate a number of differences to plants of those populations on Rhodes that Peter (1989) identified as *O. holoserica* subsp. *apulica*. All of these differences, however, are concerned with characters which are often highly variable at the intraspecific level in *Ophrys*, viz. bract length, colouring of sepal veins, and details of the hairyness of the labellum. Having compared the protologue of *O. calypsus* to the description of Peter (1989) and photographs of the plants on Rhodes, as well as to our own observations from Rhodes, we have no choice but to consider the two entities conspecific. The problem now remains, whether this Greek entity, from now on generally referred to as *O. calypsus*, is synonymous with *O. holoserica* subsp. *apulica*, whether it constitutes a separate and taxonomically valid species, or whether it is best regarded as a hybrid complex.

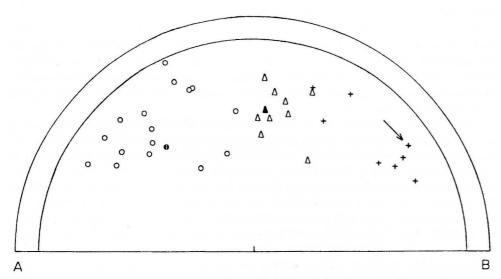


Fig. 3. Distance diagram of the *Ophrys* data from Rhodes and Crete. Circle = specimen identified as *O. holoserica* subsp. *holoserica*, triangle = specimen identified as *O. apulica* sensu Peter, cross = specimen identified as *O. scolopax* subsp. *heldreichii*. A filled circle or triangle indicates two specimens with identical coordinates. An arrow points at the sole specimen of *O. scolopax* subsp. *heldreichii* from Rhodes. A and B are the reference points of *O. holoserica* subsp. *holoserica* and *O. scolopax* subsp. *heldreichii*, respectively.

As indicated above, we have noticed several dissimilarities between *O. calypsus* and *O. holoserica* subsp. *apulica*. These dissimilarities, encompassing differences in leaf colour, inflorescence morphology, labellum morphology, and speculum size, convincingly demonstrate that we are indeed dealing with two separate taxa. Consequently, *O. holoserica* subsp. *apulica* must still be considered endemic to southern Italy.

When describing *O. calypsus*, Hirth & Spaeth (1994) compared their new species to *O. holoserica* subsp. *apulica*. In addition to most of the differences acknowledged above, they even regarded a few more features to be of diagnostic value, i.e. features relating to flower size and gynostemium morphology. We believe Hirth & Spaeth to be correct in distinguishing *O. calypsus* from *O. holoserica* subsp. *apulica*. On the other hand, we do not believe that *O. calypsus* constitutes a taxonomically valid species. If the photographs of *O. calypsus* in Hirth & Spaeth (1994: 435-436) are compared to each other, they give the impression of a heterogeneous complex rather than a homogeneous species. A series can be realized from flowers resembling *O. scolopax* subsp. *heldreichii* (p. 435 fig. a, d) through "typical" *O. calypsus* flowers (p. 435 fig. b; p. 436) to flowers approaching *O. holoserica* subsp. *holoserica* (p. 435 fig. c). Almost the same can be said of the flowers depicted in Peter (1989: 305 fig. b, c; 325 fig. a, b; 335 fig. a) and in Paulus & Gack (1992: pl. IIIa-c). Likewise, it is interesting to note that, in Naxos, Paulus & Gack (1992) repeatedly found all three kinds of flower to be present in the same inflorescence!

The lack of obviously diagnostic features and the marked heterogeneity, which was also noted by Kretschmar & Kretschmar (1996) on Naxos, suggest that *O. calypsus* should possibly be considered a hybrid complex rather than a species (see also Paulus & Gack

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1992). Specifically, we observe the intermediate position *O. calypsus* seems to assume between *O. scolopax* subsp. *heldreichii* and those large-flowered forms of *O. holoserica* subsp. *holoserica* which some authors (in our opinion, superfluously) recognize taxonomically as *O. episcopalis* or *O. holoserica* subsp. *maxima* (H. Fleischm.) Greuter. We have assumed, as a working hypothesis, that *O. calypsus* can be interpreted as a hybrid complex between the two, and we have prepared a distance diagram (Fig. 3) to assess the credibility of this hypothesis.

In the distance diagram (Fig. 3), the 18 specimens identified as *O. holoserica* subsp. *holoserica* group themselves nicely towards the reference point of that taxon. Similarly, the eight specimens identified as *O. scolopax* subsp. *heldreichii* are found at the other end of the diagram, closer to the reference point of the latter taxon. The eleven specimens identified as *O. calypsus* form a group between the two other taxa, close to the middle of the diagram. This distribution, combined with the fact that all specimens of *O. calypsus* are bounded by the hemicircle just surrounding all specimens of the parental taxa, supports our hypothesis (cf. Wells 1980). Further support is offered by the finding that *O. calypsus* is phenologically intermediate between the two supposed parental taxa. Admittedly, a single specimen on Rhodes of *O. scolopax* subsp. *heldreichii* is not much from which to estimate the mean phenological stage of that species, but the temporal distinction of the peaks of flowering in *O. holoserica* subsp. *holoserica* and *O. scolopax* subsp. *heldreichii* remains a well-established fact (Paulus & Gack 1986).

O. holoserica subsp. holoserica \times scolopax subsp. heldreichii has been found among the parental taxa in Crete (Renz 1932; Smucker 1935). Although the fertility of the F₁ hybrids remains to be demonstrated, Paulus & Gack's (1986) suggestion that a postzygotic barrier may exist between "O. heldreichii" and "O. maxima" can probably be dismissed. It is known that both O. scolopax subsp. heldreichii and the large-flowered forms of O. holoserica subsp. holoserica are most often pollinated by Tetralonia berlandi (Hymenoptera: Anthophoridae) (Paulus & Gack 1986, Paulus 1988), and thus it seems obvious to expect frequent hybridization between the two. However, hybridization is not frequent in Crete, probably because the phenological discrepancy constitutes an effective pre-zygotic barrier. The hybrid populations in, for example, Rhodes and Leipsoi, on the other hand, indicate that the phenological barrier sometimes may be less pronounced.

Hybridization in islands of the eastern Aegean probably involves cases of introgression. Indeed it is difficult to spot any entirely typical specimens of *O. scolopax* subsp. *heldreichii* on Rhodes, and Kretschmar & Kretschmar (1996) have noted the same phenomenon in Naxos. The F_1 hybrid is undoubtedly fertile, and intermediate specimens are not always limited to occur sympatrically with the parental taxa (see also the comments of Vöth & Ehrendorfer (1976) on hybridization between *O. holoserica* s. lat. and *O. scolopax* s. lat.). The occurrence of "*O. calypsus*" in certain Cycladean islands with no specimens of *O. holoserica* subsp. *holoserica* present (see, however, Raus 1996) may be explained by recent immigration and colonization by the former, originated as a hybrid elsewhere, or by hypothesizing former populations of *O. holoserica* subsp. *holoserica* which have now vanished due to introgression into *O. scolopax* subsp. *heldreichii*.

In certain areas, e.g. on Rhodes, it is often possible to recognize *O. holoserica* subsp. *holoserica*, *O. scolopax* subsp. *heldreichii* and the F_1 , F_n or variously backcrossed hybrid as three different entities. This may be due to the fact that the hybrid seems less attractive

to *Tetralonia berlandi* when compared to either of the parents (cf. Paulus & Gack 1992). Still, as long as no clearly diagnostic features have evolved in an actively backcrossing and highly variable hybrid, it is in our opinion inexpedient to recognize that hybrid as an independent species in accordance with Hirth & Spaeth (1994) or to assign varietal rank to individual components of the heterogeneous populations as practised by Delforge (1995).

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