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STUDIES ON THE GENUS *ARUM* (ARACEAE)*MARIJA BEDALOV¹ & PHILIPPE KÜPFER²¹ Department of Botany, Faculty of Sciences, University of Zagreb, Croatia² Laboratory of Evolutionary Botany, University of Neuchâtel, Switzerland*Key-words:* Araceae, *Arum*, taxonomy, palynology, phytogeography, karyology, bibliography*Mots-clés:* Araceae, *Arum*, taxinomie, palynologie, phytogéographie, caryologie, bibliographie**Abstract**

On the basis of literature, field investigations, studies of herbarium collections and plants in cultivation, we summarize the taxonomical, phytogeographical, karyological and palynological knowledge of the genus *Arum*. Special attention is addressed to *Arum cylindraceum* s.l., including *A. alpinum*, *A. lucanum*, *A. intermedium* and *A. maculatum* subsp. *danicum*. Some comments are also made about *A. apulum* and *A. idaeum*. The misinterpretation of many species were mostly caused by old and incomplete first diagnoses, lack of type specimens and type localities, complicated by a large variability linked partly with hybridization.

Résumé

Malgré le vif intérêt suscité par les gouets (*Arum*) parmi les botanistes tant professionnels qu'amateurs, l'étude du genre *Arum* souffre encore de nombreuses lacunes. Preuves en sont les modifications incessantes, et encore récentes, de nomenclature affectant beaucoup d'espèces en Europe centrale et méridionale. Les auteurs proposent ici une analyse critique des données bibliographiques. Ils fondent leurs propres points de vue sur de nombreuses recherches originales sur le terrain et sur des analyses d'ordres taxonomiques, phytogéographiques, caryologiques et palynologiques.

Les principales difficultés qui ont retardé les progrès de la systématique des Arums tiennent à trois facteurs principaux. Plusieurs échantillons types conservés dans des herbiers d'Europe centrale, à Berlin en particulier, ont été détruits pendant la deuxième guerre mondiale. D'autre part, peu d'espèces se prêtent aussi mal à la conservation en herbier; au cours du séchage, les inflorescences sont déformées et perdent leurs couleurs. De surcroît, les organes les plus précieux pour l'identification des espèces, les tubercules, ne sont généralement pas conservés.

Dans le présent travail, une attention particulière est portée à *A. cylindraceum*, considéré à l'origine comme un endémique de Sicile. Dans son acception au sens large proposée ici, *A. cylindraceum* regroupe des populations disséminées de Sicile au Danemark et du Portugal à la Roumanie. Il n'est pas connu de Suisse.

Les données chorologiques et caryologiques pour l'ensemble des espèces reconnues à ce jour sont mentionnées dans les tableaux IA et IB. Il apparaît que le concept d'espèces retenu ici exclut le polymorphisme caryologique intraspécifique. Toutes les espèces offrent une seule valence chromosomique. Ceci laisse penser que la polyploïdisation pourrait relever de l'allopolyplôïdie; les taxons polyplôïdes dériveraient de deux parents, situation que les règles de la nomenclature ne permettent pas de traduire, d'où le rang spécifique privilégié dans la nomenclature retenue ici. Toutefois, si l'origine de la polyplôïdie reste incertaine, il

* Part of these results was presented at the VIII International Aroid Conference, Missouri Botanical Garden, St.-Louis, USA, 9-11 August 1999.

ne fait aucun doute que les hybridations jouent un rôle non négligeable dans les difficultés taxonomiques du genre *Arum*. Les données caryologiques à valence chromosomique impaire (par exemple triploïde, $2n = 3x = 42$, sont rapportées de populations naturelles. Le programme d'hybridations conduit par les auteurs démontre que des espèces mêmes éloignées du point de vue taxonomique ou offrant des valences chromosomiques très différentes peuvent être croisées. Tout laisse penser que là où deux espèces cohabitent, les hybrides doivent être nombreux. Une partie du polymorphisme intraspécifique et des difficultés taxonomiques présentes pourrait ressortir d'une large introgression entre taxons isoploïdes là où ils sont sympatriques.

INTRODUCTION

Despite several taxonomic and karyological studies published during the last 70 years, a group of species of *Arum* made up of *A. cylindraceum* Gasp., *A. lucanum* Cavara & Grande, *A. alpinum* Schott & Kotschy, *A. gracile* Unverr., *A. intermedium* Schur ex Schott, *A. besserianum* Schott and *A. orientale* M. Bieb., and their relation with *A. maculatum*, are still current subjects of discussion from taxonomic and phytogeographical points of view. With the exception of the recent monograph by BOYCE (1993), all studies are of a mostly regional nature, adopting either synthetic or analytical species concepts that do not permit an overall view of the polymorphism within the species. These studies include those of VISJULINA, 1936, 1950; PRIME, 1960, 1961, 1980; RIEDL, 1967, 1979; DIHORU, 1970; BEURET, 1971, 1972, 1977; TERPÓ, 1971, 1973; BEDALOV, 1973A, 1975A, 1976, 1977, 1978, 1981, 1983; LÖVE & KJELLQUIST, 1973; KONONOV & MOLJKOVA, 1974; MAJOVSKY *et al.*, 1974, 1978; HOLUB, 1977; SHELJAG-SOSENKO & DIDUKH, 1978; TKACHIK, 1979, 1991, 1993, 1998; DUBOVYK, 1981, 1991, 1994, 1996; BEDALOV & GUTERMANN, 1982; MILL, 1984; ALPINAR, 1985, 1986, 1987; BEDALOV & BRONIĆ, 1989; BOYCE, 1989, 1993; PETERSEN, 1989; BEDALOV *et al.*, 1993a, 1993b; POPPENDIECK & KASPRIK, 1993; FISCHER, 1994; SACHL, 1994; BEDALOV & FISCHER, 1995; BEDALOV & DRENKOVSKI, 1997; DRAPER & ROSSELÓ-GRAELL, 1997; DUBOVYK *et al.*, 1999; FRIDLENDER, 1999, 2000.

Several reasons may be invoked to explain the present taxonomic difficul-

ties, for example the similar habit of many species, large intraspecific variability, and large amounts of heteroblasty. Many species of *Arum* were first described many years ago, and their diagnoses were based on small differences concerning a few poorly delineated taxonomic characters. They are based mostly on herbarium specimens without consideration given to the large polymorphism expressed in the genus, which can be observed only in the field when the plants are in full development with leaves and inflorescences.

The annual growth cycle of *Arum* is relatively short. The first leaves appear very early in the season or even in the fall (*A. hygrophilum* Boiss., *A. italicum* Mill., *A. creticum* Boiss. & Heldr.) or winter. Production time of the inflorescence is short and explosive, with all maturing more or less at the same time. At the beginning of the summer, the time when most botanical excursions are concentrated, *Arum* become very subdued, except for their bright red fruits which do not reveal evident taxonomic characters. Herbarium specimens are often incomplete because the spathe is fragile and can easily lose its initial shape and coloration. The thick spadices are often deformed and the tubers are often not collected at all. Therefore, the most distinguishing characteristics are often not preserved in the exsiccatae.

Another obstacle is that the holotypes are infrequently found, having been destroyed or are incomplete (*A. orientale*, *A. maculatum* var. *caucasicum* Willd., *A. alpinum*, *A. cylindraceum*, *A. lucanum*, *A. maculatum* var. *immaculatum* Rchb.), and in many cases there is no precise type locality.

It is therefore not astonishing that the number of recognized species within the genus differs notably from one work to another. Schott (1860) mentions 42 species, Hruby (1912) considers 15 species and Engler (1920) only 12 species. Recently, in his monograph of the genus *Arum*, Boyce accepted 25 respectively species (1993), and 26 species (1994). He mentions six species where the status remains controversial: *A. cylindraceum* Gasp., *A. besserianum* Schott, *A. guellekense* Kotschy, *A. kasrunicum* Stapf, *A. melanopus* Boiss., and *A. neumayeri* Vis. ex Beck.

MORPHOLOGICAL CRITERIA

The taxonomic problems aren't limited only to the small number of herbarium specimens and their poor condition. In large part, they result also from the intraspecific variability observed by many authors (LEDEBOUR, 1853; RIEDL, 1967, 1985; KONONOV & MOLJKOVA, 1974; BEDALOV, 1975a, 1976, 1977; BOYCE, 1993; POPPENDIECK & KASPRIK, 1993).

The difficulty in circumscribing the taxa by discrete morphological characters has been well documented by HOLUB (1977). Due to notable heteroblasty and important differences between individuals of varying age and phenology, the morphology of the leaves provides few useful characters. Our work has demonstrated, however, that some characters appear relatively constant in side-by-side cultivation and are therefore more interesting. This is true of the consistency of the limb of leaves, and its brilliant or dull appearance that can not be examined on dry material. Other diagnostic characters, such as the leaf coloration, show large variation. For example, the epithet *maculatum* evokes the presence of spots on the leaves. However, the variation of this character is not only regional, but often also within a population. The same can be said of most of the characters of color. In living plants under comparative cultivation in the bota-

nical gardens of Zagreb (Croatia), Vienna (Austria) and Neuchâtel (Switzerland), the color of the spathe, peduncles, and petioles present important nuances from one individual to another. Another difficulty is the proportion of fertile to sterile (staminodes or pistillodes) flowers which may not be observed without destroying the living or dried inflorescences.

The importance of field investigations was emphasized by many authors because some characters depend closely on the phenological state. Thus, in some species, the peduncle is markedly accrescent during the maturation of the inflorescence. So the relative length between peduncle and petiole should be observed at the same phenological stage, during anthesis for example, and in the field if possible, taking into consideration the above ground parts of the peduncle and petiole.

Lastly, one of the best diagnostic characters, the form of the tuber, has not been seriously taken into consideration in the original diagnosis given by older authors (e.g. LINNAEUS, 1753; MARSCHALL VON BIEBERSTEIN, 1808; GASPARRINI IN GUSSONE, 1844), and in his first paper, SCHOTT (1856) did not mention the form of tuber. Four years later he cited for *A. orientale* a horizontal elongated tuber ("tuber oblongum horizontale?") with a question mark (SCHOTT, 1860), while for *A. intermedium* and *A. alpinum*, *A. maculatum* and *A. immaculatum*, he quoted a rounded, depressed ("*rotundatum, depressum*") form of tuber.

ENGLER (1920) differed in his description. For *A. orientale* he cited a discoid tuber, while for *A. maculatum* s.l. (in which he included also *A. alpinum*, *A. gracile*, *A. intermedium* and *A. cylindraceum*) he mentioned an ovoid or cylindrical, rarely, in stony places, discoid form of tuber ("*tuber plerumque ovoideum vel cylindroideum, rarius, locis petrosis, discoideum*"). He considered the shape of tuber most useful in distinguishing two varieties of *A. maculatum*, recognizing var. *vulgare* with a cylin-

drical tuber and var. *angustatum*, with a discoid tuber. In the latter, he distinguished 3 subvarieties that include plants otherwise known as *A. alpinum*, *A. gracile*, *A. intermedium*, *A. transsilvanicum* and *A. cylindraceum*.

However, for many other authors, *A. maculatum* is characterized by its horizontal rhizomatous tuber (DIHORU, 1970a; TERPÓ, 1973; BEDALOV, 1973a, 1977; KONONOV & MOLJKOVA, 1974; MAJOVSKY *et al.*, 1978; BEDALOV & GUTERMANN, 1982; MILL, 1984; ALPINAR, 1985, 1986; DOSTÁL, 1989; BOYCE, 1993; FISCHER, 1994; SACHL, 1994; BEDALOV & FISCHER, 1995; BEDALOV & DRENKOVSKI, 1997). In many floras this character is well represented (OEDER, 1770; STURM, 1825; BONNIER & DOUIN, 1931; HESS, LANDOLT & HIRZEL, 1967; WEIHE, 1972; RIEDL, 1979; ROTHMALER *et al.*, 1991).

Arum maculatum clearly differs from *A. orientale* and from *A. alpinum* which have a discoid tuber (DIHORU, 1970; TERPÓ, 1973; BEDALOV, 1973a, 1976, 1978, 1981); BEDALOV & GUTERMANN, 1982; MILL, 1984; ALPINAR, 1985, 1986; BEDALOV & BRONIĆ, 1989; BOYCE, 1993; FISCHER, 1994; SACHL, 1994; BEDALOV & FISCHER, 1995; BEDALOV & DRENKOVSKI, 1997, FRIDLINDER 2000).

For HRUBY (1912), the form of tuber manifests a polymorphism depending on the edaphic conditions and has no taxonomic value, but many other authors discuss the form of tuber, its taxonomic significance and the distribution of the species in question (DUBOVYK, 1981; 1991; 1994; 1996; DUBOVYK *et al.*, 1999; KONONOV & MOLJKOVA, 1974; SHELJAG-SOSENKO & DIDUKH, 1978; TKACHIK, 1979, 1991; 1993; 1998; VISJULINA, 1936, 1950).

The rare characters that may be observed in some credible way on most herbarium specimens are perhaps the length of the peduncles and petioles, and the form and dimensions of the spathe (the ratio of the length of the spathe-limb to the length of the spathe-tube). These criteria were used to distinguish *A. alpinum* s.l. and *A. macu-*

latum (BEDALOV, 1973a; 1976; 1977; 1981; BEDALOV & DRENKOVSKI, 1997; BEDALOV & FISCHER, 1995; BEDALOV & GUTERMANN, 1982; FISCHER, 1994; SACHL, 1994; TERPÓ, 1971; 1973).

Among the micromorphological criteria, palynological research has shown that the *Arum* species investigated have mainly spinulose pollen grains (BEDALOV, 1985; BEDALOV & HESSE, 1989; GRAYUM, 1986; 1990). The shape, size and distribution of the spinules help in a few cases to distinguish species such *A. apulum* and *A. nigrum* (BEDALOV *et al.*, 1991). Most of the species show encircled spinules separated by psilate surfaces. In *A. hygrophilum* the base of the spinules are quite contiguous (without psilate regions). Until now only one species, *A. korolkowii*, has been found which differs from the others by its pollen with a slightly verrucate surface without spinules.

EXAMPLES OF THE TAXONOMIC COMPLEXITY OF THIS GROUP

1. *Arum cylindraceum* Gasp. in Gussone

Arum cylindraceum Gasp. was described from Sicily (Italy, Madonie, al Piano della Battaglia di Petralia) (GASPARRINI in GUSSONE, 1844), and although one of the earliest published species, its actual species limits were very confused until recently. At first, Engler treated it as a separate species, very similar to *A. maculatum* (ENGLER, 1879), but later he regarded it as a variety *angustatum* of *A. maculatum*, including in this variety not only *A. cylindraceum* but plants that had been known as *A. alpinum*, *A. intermedium*, *A. gracile* and *A. transsilvanicum* (ENGLER 1920).

Arum cylindraceum was included in *A. italicum* (NYMAN, 1882; GANDOGGER, 1910; Hruby, 1912), or in *A. orientale* (ZANGHERI, 1976; PRIME, 1980), or considered as a suspect species (RICHTER, 1890). Recently it was also treated as a poorly known species (PIGNATTI, 1982; BOYCE, 1993). Only

PAGLIA (1905) noticed that *A. cylindraceum* appeared closer to *A. alpinum*, a taxon that was still subordinated to *A. maculatum*.

Another species, *A. lucanum* Cavara & Grande was described from Lucania (Italy, Monte Pollino) (CAVARA & GRANDE, 1911). It was treated as a poorly known species by ZANGHERI (1976), while PIGNATTI (1982) and BOYCE (1993) recognized it as distinct. According to our field experience, *A. lucanum* has much the same morphology and ecology as *A. cylindraceum* and also the same variability.

Based mainly on the mentioned morphological characters, Bedalov combined *A. cylindraceum*, *A. alpinum* s.l., and *A. lucanum* under the earliest binomial, *A. cylindraceum* (BEDALOV, 1980, 1982; BEDALOV et al., 1993b). On the same time, in Flora Europaea, PRIME (1980) defended another position, including *A. cylindraceum* (s.str.), *A. alpinum*, and *A. lucanum* in *A. orientale*, in which he recognized three subspecies: subsp. *orientale*, including *A. besserianum* with *A. alpinum* as a synonym, subsp. *lucanum* with *A. cylindraceum* as a synonym, and subsp. *danicum*. Because of these different taxonomic opinions, *A. cylindraceum* has been confused in many works with *A. maculatum* or *A. orientale*, and even with *A. italicum*.

Arum cylindraceum s.l. is a very variable taxon especially in Central Europe where *A. intermedium* (Schott, 1860) and *A. alpinum* var. *pannonicum* (Terpó, 1973) are growing. For *A. intermedium*, both Schott (1860) and Terpó (1973) mention a “*clava...incrassata, subconoidea, obtusa*”. Plants with such spadix have been treated variously in the literature, as *A. maculatum* (JÁVORKA, 1925; JÁVORKA & CSAPODY, 1934), Soó & KÁRPÁTI, 1968), as *A. maculatum* var. *intermedium* (Soó & JÁVORKA, 1951; JOVANOVIĆ, 1965; OBRADOVIĆ, 1966), as *A. maculatum* subsp. *intermedium* (Schur) Soó (Soó, 1964), as *A. alpinum* var. *intermedium* and var. *pannonicum* (TERPÓ, 1973; DOSTÁL & KOLLÁR, 1976; MÁJOVSKY (ed.), 1978). Several

other authors retained only the binomial *A. alpinum* (Bedalov, 1973a, 1976; DIKLIĆ 1977, PARABUČSKI et al., 1980, BEDALOV & GUTERMANN, 1982; BOYCE, 1993; FISCHER, 1994; BEDALOV & FISCHER, 1995; BEDALOV & DRENKOVSKI, 1997; (DAJDOK & KACKI, 2001; ZAJAŠ & ZAJAŠ, 2001). Finally, as stated above, based on morphological characters, all these combinations (Table II) have been put in synonymy under the name *A. cylindraceum* s.l. In this conception, *A. cylindraceum* is recognized as a largely distributed species from Portugal to Rumania, and from Sicily to Denmark (BEDALOV et al., 1993b; AEDO et al., 1994; DRAPER & ROSSELÓ-GRAELL, 1997; WISSKIRCHEN & HAEUPLER, 1998; FRIDLENDER, 1999, 2000).

Today, a real difficulty still persists in distinguishing *A. cylindraceum*, *A. orientale*, and *A. besserianum*. For example, *A. orientale* was also often confused not only with the preceding species, but also with *A. elongatum*, *A. nigrum*, and even with *A. albispalum*. We are working presently to solve the problem of the eastern limit of *A. cylindraceum*, and of the relationship with both *A. besserianum* and *A. orientale*.

2. *Arum apulum* (Carano) Bedalov

Recently, *A. apulum* from southern Italy, described as *A. nigrum* Schott var. *apulum* Carano (1934), treated in the same way also by PRIME (1980, page 408), was separated as distinct species under the name *A. apulum* (Carano) Bedalov (BEDALOV in PIGNATTI, 1982, BEDALOV et al. 1991). It was established that the two species differ not only in the base of their floral morphology such shape and color of the spathe and different form of sterile flowers, but also in different chromosome numbers (*A. nigrum* $2n=28$, *A. apulum* $2n = 56$) and different geographical distribution (*A. nigrum* in Dinaric regions and Greece while *A. apulum* only in Apulia, southern Italy) (BEDALOV 1973a, 1973b, 1975c, 1980, 1981, 1982, BIANCO et al. 1994). The two species differ also on the

basis of their palynological characters. The pollen grains in both species are spinulose like in other *Arum* species (BEDALOV, 1985; GRAYUM, 1986; BEDALOV & HESSE, 1989), but the dimension of the spinules and their respective distribution on the surface differ in two species.

In *A. nigrum* the spinules are evidently broader rather large, distinctly encircled on the base, pointed and not as densely arranged on the pollen surface as in *A. apulum*. In this last species, the spinules are not as large and not as pointed as in *A. nigrum*. Their bases are indistinctly encircled and they are almost twice as numerous as in *A. nigrum* (BEDALOV, 1985; BEDALOV & HESSE 1989). Finally, *A. apulum* (Carano) Bedalov was recognized as a single separate species and the new name was validated by PIGNATTI (1982). Important differences between the two species are presented in Bedalov *et al.* (1991). Later on, BOYCE (1993) in his monograph adopted the same treatment but with incorrect citation of the authority.

3. *Arum idaeum* Coust. & Gandoger

Another problem, the species limits of *A. idaeum* has received a recent solution. PRIME (1980) in *Flora Europaea* placed *A. idaeum* in synonymy with *A. maculatum*, probably following Riedl's opinion reported by Greuter (1973, 1974). In a revision of the arums of Crete, Greuter (GREUTER, 1984) recognized *A. idaeum* as a species distinct from *A. maculatum* and *A. creticum*, respectively. In his monograph Boyce correctly adopted the same treatment for the Cretan *Arum* (BOYCE, 1993, 1994).

IMPACT OF THIS COMPLEXITY ON INTERPRETATION OF OTHER DATA

1. Geographical distribution

The distribution of some previously mentioned species are still poorly defined, in particular in southeastern Europe and

southwestern Asia (Table IA and IB). The greatest confusion encompasses the eastern limit of *A. maculatum* and the northwestern limit of *A. orientale*, in great part because the shape of the tuber in *A. orientale* and *A. maculatum* was confused (SCHOTT, 1860; ENGLER, 1879, 1920; HRUBY, 1912; DUBOVYK, 1981, 1991, 1994, 1996) but also because the relationship between *A. orientale* and *A. alpinum* are treated differently by different authors. *Arum orientale* was considered as a separate species, while *A. alpinum* (together with *A. gracile*, *A. intermedium*, *A. transsilvanicum* and *A. cylindraceum* was included in *A. maculatum* s.l. as subordinated taxa (ENGLER, 1879, 1920; RICHTER, 1890; BECK VON MANNAGETTA, 1903; ASCHERSON & GRAEBNER, 1904; HAYEK & MARKGRAF, 1933; RIEDL, 1967). After considering the shape of the tuber as a taxonomically important character, DIHORU (1970), RIEDL (1979), HOLUB (1977), PRIME, (1980) included *A. alpinum* in *A. orientale*. As observed by DUBOVYK (1981) it seems that KONONOV & MOLJKOVA (1974) also placed *A. alpinum* under the name *A. orientale*. On the other hand, many authors considered *A. alpinum* as a separate species (TERPÓ, 1971, 1973; BEDALOV, 1973a, 1976, 1981; MAJOVSKY *et al.*, 1974, 1978, BEDALOV & GUTERMANN, 1982; DOSTÁL, 1989; RANDYSKA *et al.* 1990; BOYCE, 1993; FISCHER, 1994; SACHL, 1994, BEDALOV & FISCHER, 1995; MIREK *et al.*, 1995; BEDALOV & DRENKOVSKI, 1997; DAJDOK & KACKI, 2004; ZAJAŚ & ZAJAŚ, 2001). Finally, as mentioned above, *A. alpinum*, *A. cylindraceum* and *A. lucanum* were separated in a single species under the name *A. cylindraceum* (BEDALOV *et al.*, 1993b). All these different taxonomic opinions are necessarily reflected in the geographical distributions.

According to ENGLER (1920), MEUSEL, JAEGER & WEINERT (1965), RIEDL (1967, 1979), TERPÓ (1973), PRIME (1980), MILL (1984), FISCHER (1994), *A. maculatum* is an Atlantic-sub Mediterranean species distributed in western, central and southern

Table 1B. Chorological and karyological data for the eastern Europe and Middle Eastern *Arum* species. In both tables 1A and 1B, the species are mentioned in function of their distribution, from the West to the East.
Tableau 1B. Données chorologiques et Caryologiques relatives aux espèces d'Europe orientale et du Proche-Orient, les régions méditerranéennes incluses. Dans les deux tableaux 1A et 1B, les espèces sont mentionnées en fonction de leur distribution, de l'ouest vers l'est.

	Croatia	Bosnia-Herzegovina	Serbia	Moldavia	Romania	Macedonia	Albania	Bulgaria	Greece	Crete and SE Aegean sea	Ukraine	Russia	Rhodes	Turkey	Cyprus	Caucasus	Syria	Lebanon	Israel	Jordan	Libya	Iraq	Iran	NW Central Asia	S Central Asia	
<i>A. maculatum</i>	56	56	56	?	56	?	56	?	?		?			56	?											
<i>A. italicum</i>	84	84	84		84	+	84	84	84		+	84		84	84											
<i>A. cylindraceum</i>	28	+	28	?	28	?	?	?	28	28	28			?												
<i>A. pictum</i>																										
<i>A. apulum</i>																										
<i>A. nigrum</i>	28	28	28					+																		
<i>A. orientale</i> subsp. <i>longispatum</i>	28	28	28					28	28		+	28		28	28	+										
<i>A. orientale</i> subsp. <i>orientale</i>			28	28	28	28		+	+	+	28	+		84	28	+	+	+	+	+			28			
<i>A. elongatum</i>																										
<i>A. concinnatum</i>																										
<i>A. rupicola</i>																										
<i>A. purpureospatum</i>										56																
<i>A. idaeum</i>										28																
<i>A. creticum</i>										28																
<i>A. dioscoridis</i>										28																
<i>A. byzantinum</i>										28					28	28	+	+	+							
<i>A. gratum</i>														28	28	28	+	+	+							
<i>A. balansanum</i>														+	+											
<i>A. euxinum</i>														28												
<i>A. sintenisii</i>															28											
<i>A. hygrophilum</i>															28											
<i>A. palaestinum</i>															28											
<i>A. korolkowii</i>															28									28	+	
<i>A. hainesii</i>																										
<i>A. cyrenaicum</i>										+																
<i>A. jacquemontii</i>																										

+ : chorological observations without chromosome counts 28, 56, 84... : species present and chromosome counts in this country ? : no precise information

Europe. According to PRIME (1980) and MILL (1984), it extends eastward to western Ukraine. Finally, for BOYCE (1993) it is distributed throughout Europe, from northwestern Spain to the Caucasus, and from southern Sweden to northern Greece. The southeastern geographical border remains confused because of misidentification with *A. cylindraceum* s.l. (*A. alpinum* s.l.), *A. besserianum*, *A. orientale*, and *A. italicum*. However, LEDEBOUR (1853), KUZENJEVA (1935), KONONOV & MOLJKOVA (1974), IKONNIKOV, 1979) cited *A. maculatum* for the Flora of the SSSR, and VISJULINA (1936, 1950), SHE LJAG-SOSENKO & DIDUKH (1978), and TKACHIK (1991, 1993) for Ukraine.

Meanwhile, DUBOVİK (1981, 1991, 1994, 1996) refutes all these citations and argues that *A. maculatum* is a western European species not growing in Ukraine, Crimea and Caucasus. Following TERPÓ (1973), MAJOVSKY (1978), Sachl (1994), and our own experience, the eastern border of *A. maculatum* in Central Europe ranges from western Poland, Czech Republic, eastern Austria, central Hungary, northeastern Croatia, northeastern Serbia, southwestern Romania, Bulgaria and northwestern Turkey (CZUBINSKI, 1950; KUZMANOV, 1964; BEDALOV, 1973a, 1977; BEDALOV & GUTERMANN, 1982; MILL, 1984; FISCHER, 1994; MIREK *et al.*, 1995; BEDALOV *et al.* 1998a; BEDALOV & HODALOVA, 1998; BEDALOV & TERPÓ, 1998).

KONONOV & MOLJKOVA (1974) cited *A. maculatum*, with horizontal tuber and dark spots, for Crimea and Caucasus, but with $2n=42$ chromosomes. In our opinion, this material should be considered as a hybrid; however *A. maculatum* may be partially sympatric with *A. orientale*. In the same manner, it should be noted that the cases of sympatry on the regional scale and at the same locality are frequent, which adds to the confusion (see below under natural hybrids).

The confusion that persists around the diagnostic characters directly influences the chorological knowledge. For example,

according to Kuzmanov (1964), DIHORU (1970a), BEDALOV (1973a, 1981), TERPÓ (1973), MILL (1984), ALPINAR (1985), BEDALOV & BRONIĆ (1989), BOYCE (1993), and BEDALOV & DRENKOVSKI (1997), *A. orientale* has a discoid tuber, while DUBOVİK (1996) gives a drawing of *A. orientale* with cylindrical, rhizomatous tuber. As consequence of this, SHE LJAG-SOSENKO & DIDUKH (1978) give a map where *A. maculatum* is distributed in a large part of Ukraine, while DUBOVYK *et al.* (1999) did not mention *A. maculatum* in their nomenclatural checklist of vascular plants of Ukraine.

As mentioned earlier, following Marshall von BIEBERSTEIN (1808), *A. orientale* is distributed in Crimea and Caucasus, but based on our present knowledge, it is also in the eastern Balkans (southeastern Romania, southeastern Serbia, eastern Macedonia, Bulgaria, northeastern Greece and northern Turkey (KUZMANOV, 1964; MEUSEL *et al.*, 1965; DIHORU, 1970, BEDALOV, 1973a, 1981; TERPÓ, 1973; KONONOV & MOLJKOVA, 1974; MILL, 1984; ALPINAR, 1985, 1986, 1987; BEDALOV & DRENKOVSKI, 1997; BEDALOV *et al.*, 1998a).

Arum alpinum was considered as a central European species (TERPÓ, 1973), but later it was cited for southern Yugoslavia, Serbia, Macedonia (BEDALOV, 1973a, 1976, 1981; BEDALOV & DRENKOVSKI, 1997), Greece and Crete (GREUTER, 1984; BOYCE, 1994; BEDALOV & FISCHER, 1995), Denmark (BEDALOV, 1973a; 1976; NIELSEN & UGELVIG, 1986), southern Italy (BEDALOV *et al.*, 1993a), southern France, Corsica and Spain (BEDALOV, 1983; LÖVE & KJELLQUIST, 1973), and northern Germany (POPPENDIECK & KASPRIK, 1993). Recently, BEDALOV *et al.* (1993b) merged *A. alpinum*, *A. cylindraceum* and *A. lucanum* into a single species under the name *A. cylindraceum*. BOYCE (1993) gave the same large distribution for *A. alpinum*, but he mentioned a large part of central and southern France where until now *A. cylindraceum* has been discovered only in the southeast. Because his interpretation

of *A. alpinum* doesn't encompass *A. cylindraceum*, he gave an incomplete map for *A. alpinum* in Italy. The binomial *A. cylindraceum* has been recently used for plants from Spain and Portugal (AEDO *et al.*, 1994; DRAPER & ROSSELÓ-GRAELL, 1997), Corsica (FRIDLINDER, 1999, 2000), and Germany (WISSKIRCHEN & HAEUPLER, 1998). From its Sicilian endemic status, *A. cylindraceum* became a species largely spread throughout a major part of the south and central parts of Europe.

2. Interpretation of karyological variability

One character that has taken on importance in the course of the last few decades is chromosome number. The data corresponding to the genus *Arum* are summarized in Tables IA, IB and III. The taxa where the profile appears sufficiently certain are indexed in Column I where they are placed as a function of their distribution. The first mentioned taxa occupy the northwesternmost territory (*A. maculatum*), whereas the last two reach central Asia (*A. korolkowii* and *A. jacquemontii*).

Three principal chromosome valences have been observed: diploid of $2n=28$ (16 species), tetraploid of $2n=56$ (4 species), and hexaploid of $2n=84$ (2 species). We agree to recognize all the unpaired valences of $x=14$ ($3x=42$, $5x=70$) as the result of hybridization (see below). Four species (*A. gratum*, *A. balansanum*, *A. hainesii*, *A. jacquemontii*) do not yet have an established chromosome number.

In our interpretation of the chromosomal and morphological data, each species possesses only one euploid chromosome number, for example $2n=56$ for *A. maculatum*. Consequently, adding to the taxonomic confusion, different chromosome numbers have been published under the same name. For example, the following numbers have been cited in different flora as a part of the intraspecific diversity of *A. maculatum*: $2n=28$, 56, 84 (HESS *et al.*, 1967; ROTHMALER *et al.*,

1966; WEIHE, 1972). This misinterpretation of the karyological data provides for incorrect or incomplete taxonomic identification. For example, the chromosome number $2n=28$ published under *A. maculatum* from Italy (BEURET, 1971) and *A. immaculatum* from Denmark (HAGERUP, 1944; LÖVE & LÖVE, 1942), and Poland (WCISLO, 1970), really belong to *A. cylindraceum* (= *A. alpinum*).

The same conclusion is also valid about the diploid valence reported for *A. italicum* from Mallorca (DAHLGREN *et al.*, 1971; NILSSON & LASSEN, 1971). To our knowledge, *A. italicum* is always hexaploid, from the Iberian Peninsula to Caucasus (under *A. albipathum*). Consequently, the chromosome number published by the Scandinavian authors should correspond either to *A. pictum*, another diploid species, or to *A. cylindraceum* although this last species has never been mentioned in the Balearic Islands (DRAPER & ROSSELÓ-GRAELL, 1999). Therefore, confusion between *A. pictum* and *A. italicum* seems quite impossible because of their differing morphology and phenology.

To our knowledge, until now, almost no study of meiosis has been published, without a doubt due to the inherent difficulties of the material. Meiosis occurs much earlier than flowering while the inflorescence is still included in the foliar petiole sheath which is still underground. The images of diakinesis that we have obtained for *A. maculatum* show in an incontestable manner several multivalents. The constancy of the multivalents among all studied tetraploid individuals attests to the parentage of four genomes of *A. maculatum* and speaks in favor of autopolyploidy, as observed also by PRIME (1955).

The cases of aneuploidy in the literature are rare. Few data have been published in *A. italicum* s.l. (*A. neglectum* incl.): $2n=83$, 85 (Marchi, 1971), $2n=83$ (PRIME, 1954; PRIME *et al.* 1955). For *A. maculatum*, all our chromosomal counts reveal the same euploid valence: $2n=56$. The multivalents we have

Table II. Synonymy of *Arum cylindraceum* s.l.

Tableau II. La synonymie actuelle d'*Arum cylindraceum*, une illustration des tribulations nomenclaturales et taxonomiques de cette espèce

Arum cylindraceum Gasp. – in Guss., Fl. Sicula. Syn. 2 (2): 597 (1844)

<i>A. alpinum</i> Schott & Kotschy	Bot. Zeitung (Berlin) 9: 285 (1851)
<i>A. gracile</i> Unverr.	Verh. Mitth. Siebenbürg. Ver. Naturwiss. Hermannstadt 5: 173 (1854)
<i>A. intermedium</i> Schur ex Schott	Prodr. Syst. Aroid.: 91 (1860)
<i>A. transsilvanicum</i> Czetz	Erdély Muz.-Egyl. Evk. 6: 11 (1872)
<i>A. maculatum</i> var. <i>alpinum</i> (Schott & Kotschy) Engl.	in A. DC. & C. DC., Monogr. Phan. 2: 595 (1879)
<i>A. creticum</i> Boiss. & Heldr. var. <i>lanceolatum</i> Reverchon	nom. nud., in sched.: Reverchon (1884), n. 278;
<i>A. maculatum</i> subsp. <i>alpinum</i> (Schott & Kotschy) K. Richt.	Pl. Europ. 1: 173 (1890)
<i>A. lucanum</i> Cavara & Grande	Bull. Orto Bot. Regia Univ. Napoli 3: 409 (1911)
<i>A. maculatum</i> var. <i>angustatum</i> Engl. subvar. <i>alpinum</i> (Schott & Kotschy) Engl.	Pflanzenreich IV, Heft 73: 92 (1920)
<i>A. maculatum</i> var. <i>angustatum</i> Engl. subvar. <i>cylindraceum</i> [under the name <i>cylindricum</i> (Gasp.) Engl.]	Pflanzenreich IV, Heft 73:92 (1920)
<i>A. maculatum</i> var. <i>angustatum</i> Engl. subvar. <i>gracile</i> (Unverr.) Engl	Pflanzenreich IV, Heft 73: 92 (1920)
<i>A. italicum</i> var. <i>lanceolatum</i> (Boiss. & Heldr.) Engl.	Pflanzenreich IV, Heft 73:86 (1920)
<i>A. maculatum</i> var. <i>intermedium</i> (Schur ex Schott) Soó & Jávorka	A magyar növényvilág kézikönyve II, Budapest : 974 (1951)
<i>A. maculatum</i> subsp. <i>danicum</i> Prime	Watsonia 5: 108 (1961)
<i>A. maculatum</i> subsp. <i>intermedium</i> (Schur) Soó	Acta Bot. Acad. Sci. Hung. 10: 376 (1964)
<i>A. alpinum</i> subsp. <i>danicum</i> (Prime) Terpó	Acta Bot. Acad. Sci. Hung. 18(1-2): 238; (1973)
<i>A. alpinum</i> subsp. <i>gracile</i> (Unverr.) Terpó	Acta Bot. Acad. Sci. Hung. 18(1-2): 238 (1973)
<i>A. alpinum</i> subsp. <i>alpinum</i> var. <i>intermedium</i> (Schur ex Schott) Terpó	Acta Bot. Acad. Sci. Hung. 18(1-2): 235 (1973)
<i>A. alpinum</i> subsp. <i>alpinum</i> var. <i>pannonicum</i> Terpó	Acta Bot. Acad. Sci. Hung. 18(1-2): 234 (1973)
<i>A. orientale</i> subsp. <i>alpinum</i> (Schott & Kotschy) Riedl	in Hegi, Ill. Fl. Mitt.-Eur. 2(1): 333 (1979)
<i>A. orientale</i> subsp. <i>danicum</i> (Prime) Prime	in TUTIN <i>et al.</i> , Fl. Eur. 5: 270 (1980)
<i>A. orientale</i> subsp. <i>lucanum</i> (Cavara & Grande) Prime	in TUTIN <i>et al.</i> , Fl. Eur. 5: 270 (1980)
<i>A. italicum</i> auct. non Miller s.str.	
<i>A. maculatum</i> auct. non L. s.str.;	
<i>A. orientale</i> auct. non Bieb. s.str.	

observed for this species don't seem to interfere, notably on the symmetry of chromosome segregation in Anaphase I and on the stability of chromosome numbers. It is also possible that *Arum* is sensitive to a genetic equilibrium and that the aneuploid gametophytes born with meiotic irregularities are eliminated. For our part, all our chromosome counts supported by the comparison of several mitotic divisions give an euploid number based on $x=14$ no matter whether at the species or hybrid F1 rank. Alone, the results of back-crossing give an euploid number.

From a cytogeographical point of view, two lessons are shown in Table I (A and B). The two most widespread species, *A. italicum* and *A. maculatum* are polyploids, and the center of their distributions is also the northernmost within *Arum*. Conforming to the observations achieved in other genera and brought to light by FAVARGER (1971), the Mediterranean area appears to be the center of conservation of the primitive (diploid) species. Yet, paradoxically, the diploid *A. cylindraceum* s.l. (including *A. alpinum*, *A. lucanum* and *A. orientale* subsp. *danicum*, see above), which was described from Sicily (GASPARRINI IN GUSSONE, 1844) and occupies a large part of the northern Mediterranean basin, reaches not only eastern Europe, but also to Denmark and extreme southwest Sweden.

Until now no direct relation between a diploid taxon and its derived polyploid has been found. This would speak in favor of ancient polyploidy. On the other hand, this appears to contradict the high rate of multivalents in meiosis of *A. italicum* and *A. maculatum*, which argues for a recent polyploid event. The genus *Arum* presents an uncommon model and more molecular studies may help to solve these contradictions.

NATURAL HYBRIDS AND ARTIFICIAL CROSSES

The taxonomic difficulties in certain geographic areas could arise from a large

introgression between some species offering the same chromosomal valence. This hypothesis has to be confirmed by detailed work, but it is valuable in light of the high degree of allogamy observed in the genus *Arum*. If it was confirmed this would explain taxonomic difficulties in some areas, for example in central southeastern Europe where the distinction between some individuals of *A. cylindraceum*, *A. besserianum*, and *A. orientale* seems very difficult. The same situation could arise in Crete where GREUTER (1984) mentions both *A. creticum* and *A. idaeum* growing side by side, while Boyce mentions some plants are intermediate in color for the spadix appendix (BOYCE, 1993).

Hybridization is easier to recognize when the parents belong to different chromosomal valences. Hybrids then show an uneven valence such as 3x or 5x. Thus, the numbers $2n=42$ (KONONOV & MOLJKOVA, 1974; BEURET, 1977; BEDALOV & HODALOVA, 1998), and $2n=70$ (BEDALOV, 1984) have been observed in regions where one might expect the presence of several species, for example, diploid *A. alpinum* at $2n=28$, and tetraploid *A. maculatum* at $2n=56$ in Romania (BEURET, 1977), or diploid *A. alpinum* and tetraploid *A. maculatum* in Hungary (BEDALOV & HODALOVA, 1998). The number $2n=70$ has been interpreted as the result of crosses between *A. italicum* subsp. *neglectum* and *A. maculatum* (LOVIS, 1954; PRIME *et al.*, 1955) or *A. italicum* and *A. maculatum* (BEURET, 1977), or *A. italicum* and *A. apulum* (BEDALOV, 1984; BEDALOV *et al.*, 1998b).

The question of the identity of the *Arum* with $2n=42$, with black spots and rhizomatous tuber cited by KONONOV & MOLJKOVA (1974) under the name *A. maculatum* and by MRINSKIJ (1987) under the name *A. orientale* from Crimea and Caucasus, remains open. But in our experience, this plant should be a hybrid between two taxa, one diploid and one tetraploid. The parents should be still identified.

Table III. Annotated list of chromosome numbers for the genus *Arum*

Tableau III. Liste critique des données caryologiques relatives au genre *Arum*.

Dans la liste suivante, les données qui nous paraissent erronées ne sont pas mentionnées ; dans la colonne « 2n », les nombres figurant entre parenthèses [] concernent sans doute une autre espèce.

In the following list we suppressed the unconfirmed, probably erroneous, chromosomal counts; in the column “2n” we put in brackets [] the numbers we consider to belong to another species.

Taxa	2n	References
<i>Arum apulum</i> (Carano) Bedalov	56	GORI (1958) as <i>A. nigrum</i> Schott var. <i>apulum</i> Carano; BEDALOV <i>et al.</i> (1991, 1998b, 2002c); BIANCO <i>et al.</i> (1994)
<i>A. apulum</i> x <i>A. italicum</i>	70	BEDALOV (1984); BEDALOV <i>et al.</i> (1998b, 2002c)
<i>A. (apulum x italicum) x apulum</i>	63	BEDALOV <i>et al.</i> (1998b)
<i>A. byzantinum</i> Blume	28	ALPINAR (1986, 1987)
<i>A. concinatum</i> Schott	84	ALPINAR (1986, 1987) as <i>A. nickelii</i> Schott
<i>A. creticum</i> Boiss. & Heldr.	28	MARCHANT (1972); BEDALOV (1981, 2002c); BAYTOP (1982); MILL (1984); ALPINAR (1986, 1987)
<i>A. cylindraceum</i> Gasp.	28	HAGERUP in LÖVE & LÖVE (1942) as <i>A. maculatum</i> ; HAGERUP (1944) as <i>A. maculatum</i> ; PRIME (1961) as <i>A. maculatum</i> subsp. <i>danicum</i> ; WCISLO (1970) as <i>A. maculatum</i> ; BEURET (1971) as <i>A. maculatum</i> s.l.; BEURET (1972) as <i>A. maculatum</i> s.l.; TERPÓ (1973) as <i>A. alpinum</i> ; LÖVE & KJELLQUIST (1973) as <i>A. alpinum</i> subsp. <i>danicum</i> ; BEDALOV (1973b) as <i>A. alpinum</i> ; HINDAKOVA in MAJOVSKY <i>et al.</i> (1974) as <i>A. alpinum</i> ; MARCHI <i>et al.</i> (1974); BEDALOV (1976) as <i>A. alpinum</i> ; BEURET (1977) as <i>A. alpinum</i> ; HINDAKOVA in MAJOVSKY <i>et al.</i> (1978) as <i>A. alpinum</i> ; MURIN in MAJOVSKY <i>et al.</i> (1978) as <i>A. alpinum</i> ; MURIN <i>et al.</i> (1978) as <i>A. alpinum</i> ; BEDALOV (1981) as <i>A. alpinum</i> ; ZIMMER in GREUTER (1984) as <i>A. alpinum</i> ; MESÍCEK & JAVURKOVÁ-JAROLÍMOVÁ (1992) as <i>A. alpinum</i> ; BEDALOV <i>et al.</i> (1993a) as <i>A. alpinum</i> ; D'EMERICO <i>et al.</i> (1993) as <i>A. alpinum</i> ; BEDALOV <i>et al.</i> (1998a) as <i>A. alpinum</i> ; BEDALOV & HODALOVA (1998); BEDALOV & TERPÒ (1998) as <i>A. alpinum</i> ; BEDALOV <i>et al.</i> (1998c); BEDALOV & BIANCO (2002); BEDALOV <i>et al.</i> (2002a, 2002b, 2002d, 2002f)
<i>A. cylindraceum</i> x <i>A. maculatum</i>	42	BEURET (1971) as <i>A. maculatum</i> s.l.; BEURET (1977) with the mention “possibly <i>A. alpinum</i> x <i>A. maculatum</i> ”; BEDALOV & HODALOVA (1998) as <i>A. alpinum</i> x <i>A. maculatum</i>

<i>A. cyrenaicum</i> Hruby	56	MARCHANT (1973), BEDALOV, unpublished
<i>A. dioscoridis</i> Sibth. & Smith	28	BEDALOV (1978, 1981); ALPINAR (1986, 1987); BEDALOV <i>et al.</i> (2002c)
<i>A. elongatum</i> Steven	28	MOLJKOVA (1966) <i>in</i> AGAPOVA (1990); MOLJKOVA & ZAVTUR (1967) <i>in</i> AGAPOVA (1990); KONONOV & MOLJKOVA (1974); MOLJKOVA (1975) <i>in</i> AGAPOVA (1990); ALPINAR (1986, 1987)
<i>A. euxinum</i> R. Mill	28	ALPINAR (1986, 1987); BEDALOV <i>et al.</i> (2002c)
<i>A. hygrophilum</i> Boiss.	28	BEDALOV (1978); BEDALOV <i>et al.</i> (2002c)
<i>A. idaeum</i> Coust. & Gandoger	28	BEDALOV, unpublished
<i>A. italicum</i> Miller	84	MAUDE (1939, 1940); PRIME (1955); JONES (1957); BEURET (1971, 1972, 1977); BEDALOV (1973A, 1975A, 1981); SUŠNIK & LOVKA (1973); NATARAJAN (1977); NATARAJAN (1978); ALPINAR (1986); BEDALOV & BIANCO (2002); BEDALOV <i>et al.</i> (2002a, 2002b, 2002d, 2002f)
	84 (83,85)	MARCHI (1971)
	c. 84	MARCHANT (1972)
sub nom. <i>A. italicum</i>	[28]	DAHLGREN <i>et al.</i> (1971); NILSSON & LASSEN (1971) possibly <i>A. cylindraceum</i> or <i>A. pictum</i> , also diploid, but as <i>A. pictum</i> clearly differs morphologically and phenologically from <i>A. italicum</i> it is difficult to confuse them. Note that Draper and ROSELLÓ-GRAELL (1999) underlie “the absence of <i>A. cylindraceum</i> in Balearic Islands”.
	[70]	ALPINAR (1987), without doubt coming from hybridization
<i>A. italicum</i> subsp. <i>albispalum</i> (Steven ex Ledeb.) Prime	56	ZAKHARYEVA & ASTANOVA (1968), as <i>A. albispalum</i> ; ZAKHARYEVA & MAKUSHENKO (1969), as <i>A. albispalum</i>
	84	BEDALOV & TERPÒ (1998); BEDALOV <i>et al.</i> (2002c)
<i>A. italicum</i> subsp. <i>neglectum</i> (Townsend.) Prime	84	LOVIS (1954), as <i>A. neglectum</i> (Townsend.) Ridley); PRIME (1955), as <i>A. neglectum</i> ; PRIME, BUCKLE & LOVIS (1960), as <i>A. neglectum</i>
	83,84	PRIME (1954); PRIME <i>et al.</i> (1955), as <i>A. neglectum</i>
<i>A. italicum</i> x <i>A. maculatum</i>	70	BEURET (1977)
<i>A. italicum</i> subsp. <i>neglectum</i> x <i>A. maculatum</i>	69,70	LOVIS (1954), as <i>A. neglectum</i> x <i>A. maculatum</i>
	70	PRIME <i>et al.</i> (1955), as <i>A. neglectum</i> x <i>A. maculatum</i>

<i>A. korolkowii</i> Regel	28	MOLJKOVA & ZAVTUR (1967); ZAKHARYEVA & ASTANOVA (1968); ZAKHARYEVA & MAKUSHENKO (1969); MOLJKOVA (1975) in AGAPOVA (1990)
<i>A. maculatum</i> L.	56 [c. 84]	MAUDE (1939)
	56 [84]	MAUDE (1940)
	56	SOWTER (1949); LOVIS (1954); PRIME (1954, 1955); GADELLA & KLIPHUIS (1963); TARNAVSCHI & LUNGEANU (1970A, 1970B); BEURET (1971, 1977); LOVKA <i>et al.</i> (1971); DAMBOLDT (1971); MARCHANT (1972); BEDALOV (1973B, 1977, 1981, 1982); TERPÓ (1971, 1973); BAKER <i>in</i> ALPINAR (1986); NIELSEN & UGELVIG (1986); ALPINAR (1987); HOLLINGSWORTH <i>et al.</i> (1992); D'EMERICO <i>et al.</i> (1993); ILLUMINATI <i>et al.</i> (1995); BEDALOV <i>et al.</i> (1998a, 2000a, 2002d, 2002e); BEDALOV & TERPÓ (1998)
	[42]	MOLJKOVA (1966) <i>in</i> AGAPOVA (1990); MOLJKOVA & ZAVTUR (1967); KONONOV & MOLJKOVA (1974). No doubts, these chromosomal numbers concern some hybrids.
	[30]	ŠOPOVA (1989)
<i>A. nigrum</i> Schott	28	BEDALOV (1973b), as <i>A. petteri</i> Schott; BEDALOV (1975c, 1981); BEDALOV <i>et al.</i> (1991); D'EMERICO <i>et al.</i> (1993)
<i>A. orientale</i> M.B.	28	ZAKHARYEVA & ASTANOVA (1968); ZAKHARYEVA & MAKUSHENKO (1969); KONONOV & MOLJKOVA (1974); LOON & OUDEMANS (1976); ALPINAR (1987); D'EMERICO <i>et al.</i> (1993); BEDALOV <i>et al.</i> (1998a); TARNAVSCHI & LUNGEANU (1970a)
<i>A. orientale</i> subsp. <i>orientale</i>	28	BEDALOV (1973B, 1981)
<i>A. orientale</i> subsp. <i>longispathum</i> (Rchb.) Engler	28	BEDALOV (1973B, 1975B, 1981); BEDALOV & BRONIĆ (1989), BEDALOV <i>et al.</i> (2002a)
<i>A. palaestinum</i> Boiss.	28	JONES (1957); BEDALOV (1978)
<i>A. pictum</i> L. f.	28	CONTANDRIOPOULOS (1962); ERBRICH (1965); BEDALOV (1978); MONTI <i>et al.</i> (1978); D'EMERICO <i>et al.</i> (1993); BEDALOV <i>et al.</i> (2002c, 2002f)
<i>A. purpureospathum</i> Boyce	56	BEDALOV, unpublished
<i>A. rupicola</i>	28	ALPINAR (1986), as <i>A. detruncatum</i> ; Bedalov, unpublished
<i>A. sintenisii</i> (Engler) Boyce	28	BEDALOV <i>et al.</i> (2002c)

Artificial crosses between different *Arum* species have been done by one of the present authors (Bedalov) in 1973 in the Experimental Botanical Garden of Copenhagen (in collaboration with Prof. Dr. T.W. Böcher, Institute for Plant Anatomy and Cytology), and in 1990 in Kew Garden, London. As informed by Boyce at Kew Garden, some artificial hybrids are still in cultivation.

To estimate the potential importance of hybridization, Bedalov, in 1998 and 1999, attempted a series of artificial crosses among the species cultivated in Botanical Garden Neuchâtel between species where the phenology permits such trials. In a general manner, it appears that all the crosses produce seeds, even between non-close allied species, for example, belonging to different chromosome valences [such *A. italicum* ($2n = 84$) x *A. cylindraceum* ($2n=28$)].

Table IV presents the crosses attempted between species that differ by chromosome valences, and gives the first results of our trials. To prevent self-pollination (even if most *Arum* are strictly or partly allogamous), the entirety of the male flowers were taken away along with the spadix. To reach the stigmas, to verify their receptiveness and to conduct pollination, it was necessary to cut open the tube of the spathe. In spite of this trauma, the ovaries go on with their development and produce fruits.

Contrary to the observations seen in other genera, the reciprocal crosses are possible between different valences, and we haven't observed any notable differences in using as a female parent an individual with the higher valence or a lower one (for example ♀*A. italicum* x ♂*A. maculatum* and ♀*A. maculatum* x ♂*A. italicum*). Until now, among our hybrids we have been able to verify (cf. tab. IV), only one appears to have probably failed: *A. apulum* $2n=56$ (♀) x *A. italicum* $2n=84$ (♂). The tetraploid valence of the offspring is identical to that of the mother plant (*A. apulum*). We can assume either an autofecondation due to a too late emasculation or a hypothetical apomixis case in *A. apulum*! All other crosses

give the expected or at least understandable karyological results, the chromosome numbers adding the gamete numbers of the parents or resulting in the fusion of one reduced and one unreduced gametes. Until now, our controls were only supported by a dozen individuals.

As we have already mentioned (BEDALOV *et al.*, 1998b), spontaneous hybrids of $2n=70$ (from southern Italy) have been observed in comparative cultures in both botanical gardens of the Faculty of Sciences of Zagreb and of Neuchâtel. Among these hybrids, certain individuals are sterile while others are fertile. The fertility also expresses itself well on the level of the male organs (pollen) as well as those of the female (ovary). The first karyological verifications on seedlings formed from backcrosses suggest that the gametes produced by individuals of $2n=70$ are aneuploid, assuming $x=14$ as base number (see below). Although we don't yet have karyological results, it is interesting to note that the hybrids attempted between the results of the backcross (*A. apulum* x *A. italicum*, $2n=70$) x *A. apulum* ($2n=56$) to $2n=63$ have produced fruits. Remaining to be seen is the fertility of their seeds.

It should also be noted that no proof has been brought forth of an actual correlation between hybridization and polyploidization. Hybrids offer an intermediary valence when the parents differ by their chromosome valence, and in their descendants we haven't observed signs of polyploidy that would restore complete fertility.

The taxonomic difficulties posed by the genus *Arum* also stand out from the karyological data brought forward by KONONOV & MOLJKOVA, 1974). These two authors attribute the number $2n=42$ to *A. maculatum*. According to our experience, this number must be considered as a hybrid where one of the parents is undoubtedly *A. maculatum* or a very close taxon with $2n=56$, while the identity of the second, assuredly a diploid at $2n=28$, must still be determined.

Table IV. Artificial hybridization**Tableau IV.** Résultats des expériences de croisements.

Les nombres entre parenthèses correspondent au nombre d'individus observés. Les valences somatiques « $2n=$ » n'ont pas encore été vérifiées.

The numbers in parentheses are the number of studied individuals. The somatic valences noted by “ $2n=$ ” have not yet been verified.

♀ \ ♂	<i>A. apulum</i> $2n=56$	<i>A. maculatum</i> $2n=56$	<i>A. italicum</i> $2n=84$	<i>A. italicum</i> x <i>A. apulum</i> $2n=70$
<i>A. apulum</i> $2n=56$		$2n=$	$2n=70$	$2n=56$ (probably uncontrolled fertilisation !)
<i>A. maculatum</i> $2n=56$	$2n=$		$2n=$	$2n=$
<i>A. italicum</i> $2n=84$	$2n=$	$2n=70(1)$		$2n=75(2), 75-76$
<i>A. italicum</i> x <i>A. apulum</i> $2n=70$	$2n=67(1)$	$2n=60(2)$ $62(2), 63(1)$	$2n=79(3),$ $78-80 (1)$	

THE BASE NUMBER

Spontaneous hybrids at $2n=63$ observed in our collection, left in free pollination have been interpreted as the result of a backcross (*A. apulum* x *A. italicum*, $2n=70$) x *A. apulum* ($2n=56$). The somatic number 63, a multiple of 7, may be interpreted as being a fortuitous value, aneuploid in regard to $x=14$, being on the contrary as the reminiscence of an ancestral base number $x=7$ (BEDALOV *et al.*, 1998b). As we have recently found, the gametic valences vary little in the pentaploid $2n=70$. The precise counts finished on the offspring of the backcrosses of the hybrids at $2n=70$ with a parent at $2n=56$ or $2n=84$ (see table IV), show that the parent at $2n=70$ has produced gametes where the number is composed of

between $n=32-37$, being $n=28+4-9$. Even if our sampling is still insufficient, (more than one hundred young plants F2 must still be studied), these first results already permit to respond to questions raised in the preceding work. Today, we are able to confirm that the zygotic number $2n=63$ is the result of the fusion between a gamete of $n=28$ with an aneuploid gamete of $n=35$, fortuitously counting the chromosome number $70/2$.

The F1 hybrids of $2n=70$ possess 5 genomes of $x=14$. In function of their somewhat elevated fertility, at least in certain individuals, we suppose that they have four homologous or homeologous genomes where the degree of homologies two to two are sufficient to permit a regular syndese. The segregation of 28 formed bivalents would

produce the base of the genotype of the gametes (28 chromosomes) to which would come to be joined to some of 14 chromosomes of the last genome (for example 4 to 8). The aneuploidy appears well tolerated since the backcross individuals with $2n=63$ are robust and maintain themselves in cultivation without apparent difficulties. It is possible that the statute polyploid (hyper-tetraploid) ($4x+7$) of plants of $2n=63$ stops in some manner the unfavorable effect of aneuploidy.

THE CONCEPT OF ADOPTED SPECIES

Until now, morphological intraspecific variability appears independent of the chromosome valence. Thus, all taxa that we have checked possess a single valence that signifies that polyploidy is relatively ancient. So the phyletic links between diploid and polyploid species could be escape us today because either genetic drift and speciation of every cytodems or the disappearing of the correspondent diploids. An other explanation about the taxonomical difficulties could also be linked to the polyploidy origin. As hybridization frequency is high, several polyploids could have a hybrid origin and be allopolyploid. So polyploids could have not only one but two parents. The reticulate evolution could be the real taxonomical difficulty in the genus *Arum*. For example, polyploids as *A. maculatum* ($4x$), *A. italicum* ($6x$) and *A. purpureospathum* ($4x$) have a horizontal-rhizomatous tuber, but among checked diploids all of them present a discoid tuber, except *A. byzantinum*, which was described with rhizomatous tubers and was found to be diploid (Alpinar, 1985, 1987). On the other hand, among polyploids *Arums*, only 3 tetraploid species have discoid tubers (*A. apulum*, *A. cyrenaicum*, *A. purpureospathum*). If this result are confirmed, *A. byzantinum* could be an ancestor of polyploid *Arums* with rhizomatous tubers. Therefore, before understanding the phylogeny of the genus *Arum*,

an important gap of data for southeastern Europe and southwestern Asia still must be filled. Molecular studies and morphological observations have to be implemented before understanding the evolutionary biogeography of the genus *Arum*.

CONCLUSION

The major center of differentiation of the genus *Arum* (about 80% of the taxa examined) is located in the eastern Mediterranean and the Balkans to the Near East (see Table I). The majority of species in this area are diploid, several of them occupy very narrow areas that translate either into an allopatric origin by gradual speciation, or possibly also a misunderstanding of the parental links between poorly known species. Undoubtedly, both explanations are partly true. For example, *A. idaeum* and *A. purpureospathum* are endemic to a small territory, Crete. Alternatively, *A. cylindraceum* described from Sicily was considered first as an endemic species of the Madonie range (Sicily), but now it is well recognized in a large part of Europe.

The recognized species are based on a combination of characters comprising the form of the tuber, the relationship of the length of the spathe-limb to the length of the spathe tube, the form of the spadix, and the chromosome number. Their ecology plays only a weak part in their definition. Most of the species need shade and relatively deep and humiferous soil. The altitudinal range can be very large for some species. *Arum cylindraceum* can grow near sea level to 1500 m. Contrary to the situation in other genera; our species concept doesn't have a place for intraspecific karyological polymorphism (see Table III). Every binomial checked shows only one chromosome number. The question is perhaps more of an admission of the failure to recognize than that of a demonstrated taxonomic position. In effect, the parental links between species are not yet established.

The evolution of the species concept for arums may be illustrated with the examples of *A. cylindraceum* and *A. alpinum*. For two centuries the taxonomic status of these species has been uncertain. The first one was just considered as a local poorly known species. The taxonomic history of the second one was more debated. The initial confusion came from the geographical information given in the diagnosis by Schott: «*habitat in alpibus Transsylvaniae australis, in regione Pini pumilionis*». At this altitude and in such a locality, all the attempts to find *A. alpinum* again have been in vain (see SCHUR, 1866). In return, identical plants to the figure given by Schott have been observed at lower altitudes in Transylvania and in different regions of Europe. Progressively, the acceptance of *A. alpinum* is widened in associating this name with more precise characters: the diploid chromosome number ($2n=28$), the discoid tuber, vertical or oblique, and the relationship of the length of spathe limb to the length of the spathe tube. Alternatively, another character, the shape of the spadix, appears more polymorphic, with a dilated appendix in club in most populations in central Europe, described under different names, but also narrowly cylindrical as shown on the Schott's illustrations (SCHOTT, 1857). Poorly understood since the beginning, due to confusion with a species supposedly endemic to the Alps of Transylvania, *A. alpinum* has become a species largely widespread in southern Europe. More recently, it was recognized to be identical to *A. danicum* (BEDALOV, 1973a, 1976; TERPÓ, 1973). Since the taxonomic identity of *A. alpinum*, *A. lucanum*, and *A. cylindraceum* were observed (BEDALOV *et al.*, 1993b), numerous other data have been published. Thus, today *A. cylindraceum* (including *A. lucanum* and *A. alpinum* s.l.) covers a large geographic area.

In the near future, the history of some other species, such as *A. orientale*, *A. besserianum* or *A. longispathum* will be reconsidered. Even the type of the genus, *A. maculatum*, is poorly known at its southeastern

limit. Therefore, in spite of some recent taxonomic efforts, the genus *Arum* will need many new investigations at both taxonomic and chorological levels before the knowledge of this genus could be considered sufficient.

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