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Asplenium obovatum subsp. *obovatum* var. *protobillotii* and its hybrid with *Asplenium obovatum* subsp. *lanceolatum* in Spain (Aspleniaceae, Pteridophyta)

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Abstract

Rasbach H., Rasbach K., Reichstein T., Viane R. L. L. and Bennert H. W. 1990. *Asplenium obovatum* subsp. *obovatum* var. *protobillotii* and its hybrid with *Asplenium obovatum* subsp. *lanceolatum* in Spain (Aspleniaceae, Pteridophyta). Bot. Helv. 100: 3–16.

Asplenium obovatum Viv. subsp. *obovatum* var. *protobillotii* Demiriz et al. (1990) and its hybrid with *A. obovatum* subsp. *lanceolatum* Pinto da Silva (= *A. billotii*) were found in southern Spain, both in luxuriant size. The hybrid is described as *A. obovatum* Viv. nothosubsp. *cyrnosardoum* (Rasb. et al.) Rasb. et al. nothovar. *ibericum* Rasbach et al. nothovar. nova. In the pairing behaviour of its chromosomes at meiosis it is very similar to nothovar. *cyrnosardoum,* with formation of a few, well documented trivalents, thus indicating the presence of three homologous genomes. This result, together with the fact that the diploid subsp. *obovatum* var. *protobillotii* (in contrast to var. *obovatum*) with the naked eye is indistinguishable from the tetraploid subsp. *lanceolatum,* supports the conclusion that *A. obovatum* subsp. *lanceolatum* once arose by spontaneous doubling of chromosomes from *A. obovatum* subsp. *obovatum* var. *protobillotii.* This process must be a very rare event in *A. obovatum,* as otherwise the only partly overlapping areas of subsp. *obovatum* and of subsp. *lanceolatum* would be difficult to understand.

Key words: Asplenium obovatum group, cytology (Pteridophyta).

1. Introduction

The hybrid from the Miel Valley

During the "Reunión Internacional de Pteridología" from 11–14th Oct. 1980 in Algeciras (Spain) the committee organized excursions, one of these to the Miel Valley (c. 5 km W. of Algeciras) where a specimen of the rare *Culcita macrocarpa* was visited on

12th Oct. 1980. During this excursion one of us (H. R.) found an *Asplenium* hybrid (spores abortive, prep. TR-5297) growing among *A. onopteris* L. and *A. obovatum* Viv. subsp. *lanceolatum* Pinto da Silva (= *A. billotii* F. W. Schultz, see Demiriz et al. 1990).

We assumed this to be the true hybrid between these two taxa. – A plant collected by G. J. de Joncheere in Madeira with different morphology was described as *A.* × *joncheerei* D. E. Meyer (Meyer 1960) and supposed to be *A. billotii* × *A. onopteris*. – We have examined the holotype of this taxon (in B)[1]. The sporangia are empty, so there was little evidence for proving or disproving its hybrid nature. In its morphology we could not find any influence of *A. onopteris,* and we have the impression that it is only a form of *A. billotii* from a very shady habitat. We therefore decided that the "hybrid from the Miel Valley" deserved further study (Fig. 1).

The place was revisited by Betty Allen, H. R. and K. R. on 20th April 1981; two hybrid plants were collected living and brought into cultivation, first to Basel in pots, later to Agarone (S. Switzerland) for outdoor cultivation, as TR-5314 and 5315 B respectively, (= Ras-192 and 193). Sporangia were fixed in the field and investigated cytologically by J. J. Schneller, the plants were triploid with n = c.36^{II} and 36^{I} at meiosis (J. J. Schneller 18th June 1981 and 30th March 1989). The hybrid plants grew well in natural, non-calcareous soil near a watercourse and were still living in May 1985, but were always so heavily damaged by slugs that they finally succumbed. – The locality in the Miel Valley was again visited on 26th April 1981 by three of us (H. R., K. R. and T. R.); only clean fronds (free of soil) with spores were pressed directly in the field: TR-5342, TR-5350 (= Ras-199) were hybrids with abortive spores. – The following were collected as "*A. billotii* with *small* spores and small guard cells" (exospore c. (26)28–32(35) µm long, guard cells of stomata (33)38–46(50) µm long: TR-5343, 5344, 5345, 5347; all at c. 110 m alt. – A little lower (at c. 100 m alt.), below the small trail or close to the old mill, some fronds of "true *A. billotii*" with large spores, TR-5348, 5352, were collected. – Fronds of the following 4 plants of *A. onopteris* with small spores and typical perispore architecture were also collected: TR-5349 (at c. 100 m alt., below the small trail), 5351 (close to the hybrid, but also below the trail), 5353 and 5354 near the lowest houses, c. 65 m alt.

Examination of these collections showed that the "hybrid from the Miel Valley", of which at least 6 individuals were growing in a relatively small area, can hardly be a cross between *A. obovatum* subsp. *lanceolatum* and *A. onopteris*. – In Corsica, Sardinia, and France we visited many places where these two species were growing together without finding a single hybrid. – We therefore believe that in nature it is rarely, if ever, formed. – *A. onopteris,* growing in the vicinity of the hybrid, is obviously not involved in the local hybridogenesis. – Neither the presence nor the absence of tetraploid *A. adiantum-nigrum* in the area could be firmly established.

On the other hand, we concluded that the plants of "*A. billotii* with small spores" needed careful examination. Of TR-5343 and 5347 sowings made in Basel yielded numerous prothalli and healthy, juvenile sporophytes, but all these succumbed before cytological counts could be made. – For this reason four of us (H. R., K. R., R. V. and W. B.) visited the place again from 14th to 19th April 1988. They made spore measurements, pressed numerous fronds, took fixings in the field, and took living plants some of which were cultivated in Basel, others in Gent and Bochum (see Fig. 2).

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[1] Abbreviations for herbaria follow Holmgren et al. (1981).

Fig. 1. *Asplenium obovatum* nothosubsp. *cyrnosardoum* nothovar. *ibericum*, Ras-193 (=TR-5314), the first "hybrid from the Miel Valley". Plant at the original habitat, 20th Apr. 1981. Photo: K. Rasbach.

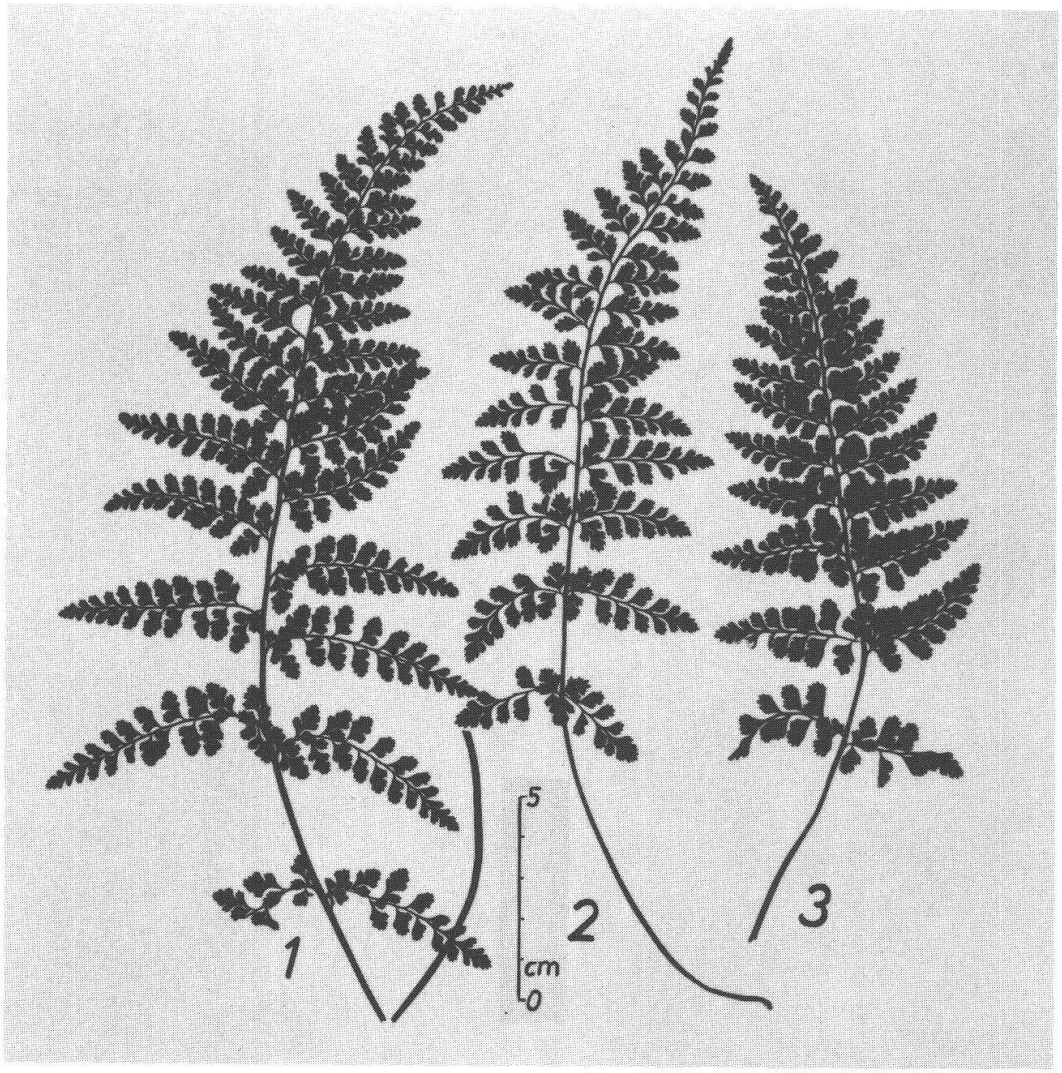

Fig. 2. Silhouettes of pressed fronds. 1 = *Asplenium obovatum* subsp. *obovatum* var. *protobillotii*, Ras-612 (= TR-7015); 2 = *A. obovatum* subsp. *obovatum* var. *protobillotii*, Ras-610; 3 = *A. obovatum* subsp. *lanceolatum*, Ras-605 (= TR-7012).

2. Material and methods

In the search for hybrids and for distinguishing diploid from tetraploid plants in the field a small microscope with calibrated eye-piece was used as described by Bennert et al. (1990). For measuring the exospore a mature sorus was scratched off, placed on a slide with a small drop of water and slightly squashed with the cover glass. 10–20 spores at random were normally measured. Collecting of living plants and their cultivation in pots in lime-free soil was done as described by Rasbach et al. (1983: 44). Fixing of immature sporangia was done either in the field or in the greenhouse as reported by Rasbach et al. (1983). All cytological work (method following Manton, 1950), the results of which are illustrated in the present paper, was done by H. R. using an Olympus microscope with oil immersion and attachment for phase contrast and drawing tube. Methods for micromorphological (epidermis, spores) and S.E.M. (spores) studies by R. V. are given in Bennert et al. (1989) and Demiriz et al. (1990).

For comparing spore sizes (Table 1), the precise mean length of the exospore was measured at home for spores embedded in balsam (Caedax/Merck or Euparal/Chroma Ges.). For measuring

Tab. 1. Microcharacters differentiating diploid subsp. *obovatum* (both varieties) from tetraploid subsp. *lanceolatum* and triploid hybrids. For conditions see under 2. Material and methods. – Co = Corsica, Sa = Sardinia, Si = Sicily, Ep = Spain. – The triploid hybrid plants produce a relatively large amount (8–32% per sample per taxon) of "good", well-formed (exo)spores with irregular perispore.

Taxon and ploidy level	Origin	Worker	Exospore length in µm	Guard cells length in in µm	Rhizome scales length up to
A. obovatum subsp. *obovatum*	Co, Sa	T. R.	(27) *30–33* (36)		
var. *obovatum* 2×	Co	H. R.		(34) *38–50* (52)	
	Co, Si	R.V.	30±2	45±5	6 mm
A. obovatum subsp. *obovatum*	Ep	T. R.	(25) *28–32* (37)		
var. *protobillotii* 2×	Ep	H. R.		(33) *38–46* (52)	
	Ep	R. V.	30±2	45±4	7 mm
A. obovatum subsp. *lanceolatum*	Co, Ep	T. R.	(30) *33–40* (45)		
(= *A. billotii*) 4×	Ep	H. R.		(50) *54–64* (68)	
	Ep	R. V.	36±2	59±5	10 mm
A. obovatum nothosubsp.	Co	H. R.	Abortive	(49) *52–55* (58)	
cyrnosardoum nothovar.	Co	R. V.	most abort.		
cyrnosardoum 3×			+31±2		7.5 mm
A. obovatum nothosubsp.	Ep	H. R.	Abortive	(47) *52–55* (58)	
cyrnosardoum nothovar.	Ep	R. V.	most abort.	49±5	8 mm
ibericum 3×			+32±2		

guard cells (of stomata) several pinnules were cleared in chloral hydrate as described by Bennert et al. (1989). Rhizome scales used for preparing figures or for measuring were also mounted in Euparal (see Table 1).

3. Habitat

Most hybrids investigated grew in a small area at c. 110 alt., in rich humus in the shade of trees. (A few hybrid plants were collected at c. 100 and at c. 180 m alt., respectively.) – The diploid *A. obovatum* subsp. *obovatum* var. *protobillotii* was growing nearby, whereas one or two tetraploid plants of subsp. *lanceolatum* were found in close proximity to the hybrids, the others having been found a few meters below or on old sandstone walls c. 100 m further down and up the valley. – *A. onopteris* was present in single plants close to the hybrids and further away. Both *A. onopteris* and *A. obovatum* subsp. *lanceolatum* occur elsewhere, i.a., in the Sierra de Ojén and Sierra de la Luna.

A. obovatum and the hybrid plants grow in the Miel Valley in a narrow streamside zone whose tree canopy consists almost entirely of *Alnus glutinosa*. *Rhododendron ponticum* subsp. *baeticum* occurs sparsely in the undergrowth. Further accessory species noted in the spring included *Osmunda regalis, Pteridium aquilinum, Athyrium filix-femina, Polypodium australe, Ruscus hypophyllum, Allium triquetrum, Tamus communis, Arum italicum, Sibthorpia europaea,* and others. – The loose humose soil and relatively

high humidity combine to provide local conditions apparently particularly favourable for the growth of *A. obovatum*. Steep rocky slopes occur on both sides of the streamside, and here the alder stand gives way to a scrub vegetation containing *Quercus suber, Erica arborea, Cistus* spp., *Halimium* spp., etc.

The outcropping rock consists of light brown to colourless sandstone containing small intergranular pores which are all unfilled. The study of the Tertiary sandstone included optical determination using thin sections and a petrographic microscope. (Investigation made by N. Widemann, Dec. 1989.)

Quartz (SiO_2) is the most common detrital component of the sandstone. This mineral shows two main grain-sizes including coarse sand and fine sand (cement). Some of the coarse grains are well rounded, others are anhedral and have slightly interdigitating boundaries. Most of the coarse grains incorporate abundant tiny mineral and/or fluid inclusions as well as numerous cracks. The extinction of this detrital quartz is undulous. Smaller grains are usually very angular and grain contacts are sometimes wavy. The whole rock is well-cemented by secondary (authigenic) quartz which can be observed in the form of irregular overgrowths on the detrital grains. Sometimes the surface of these original grains is picked out by thin red-brown rims of iron oxides.

Zircon ($ZrSiO_4$) is an abundant accessory mineral. It occurs in the whole rock as extremely fine, single grains with high relief. Most of them are rounded; translucent idiomorphic prisms seem to be very rare.

Tiny flakes and clusters of clay minerals (silicates) between the quartz grains are rather frequent and show first order grey interference colours. Usually techniques such as X-ray diffraction are needed to determine the exact identity of these minerals. – Accessory iron oxides can be divided into two groups: common amorphous pigments (yellow-brown to red-brown hydroxides, FeOOH) coating quartz grains or filling small intergranular pores, and fine single grains of some opaque to translucent ores (e.g., hematite, Fe_2O_3). – No carbonate mineral (e.g., calcite, $CaCO_3$) could be detected.

4. Results and conclusions

Examination of our material led to the conclusion that "*A. billotii* with small spores", found growing in the immediate vicinity of "the hybrid from the Miel Valley", was not *A. obovatum* subsp. *lanceolatum* (= *A. billotii*) but an extreme form of diploid *A. obovatum* subsp. *obovatum* var. *protobillotii* Demiriz et al. (Demiriz et al. 1990) with particularly pronounced teeth of the ultimate segments. This diploid, var. *protobillotii,* cannot be distinguished with the naked eye from tetraploid subsp. *lanceolatum*. For correct identification it is required either to count its chromosomes or to examine its microcharacters carefully (see Table 1 and Fig. 4).

4.1 Asplenium obovatum subsp. obovatum var. protobillotii Demiriz et al. from the Miel Valley

The plants are larger (fronds up to 45 cm long) and are more pronouncedly toothed on the ultimate segments (with teeth up to 1.6 mm) than the type from Turkey. – The more luxurious growth may be caused by the very rich edaphic conditions (see paragraph 3), whereas the pronounced dentation is probably due to genetic factors. – The plants may deserve a special name as a "forma" but we prefer to treat them under var. *protobillotii*

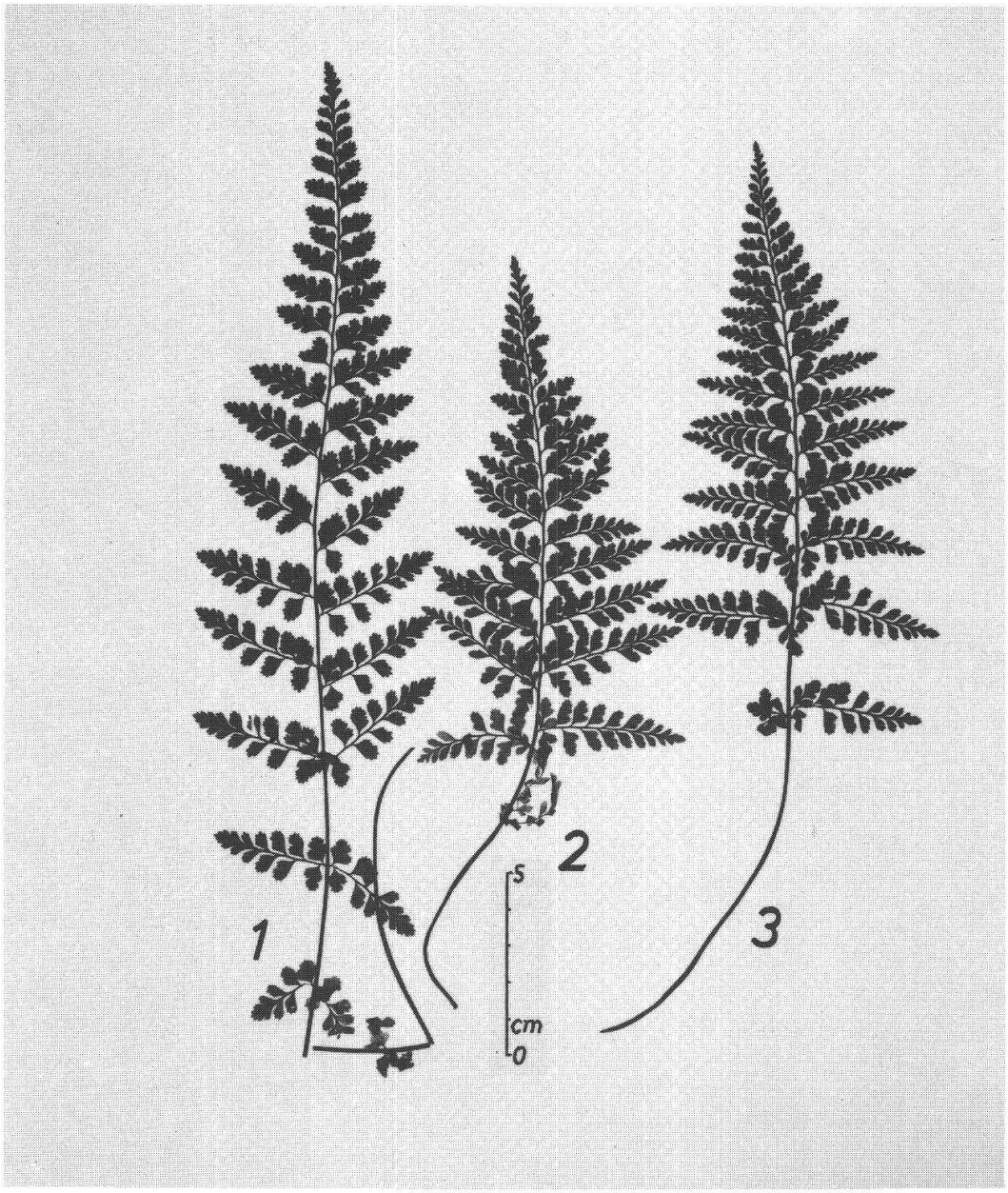

Fig. 3. Silhouettes of pressed fronds. 1 = *Asplenium obovatum* nothosubsp. *cyrnosardoum* nothovar. *ibericum*, Ras-604 (paratype); 2 and 3 = *A. obovatum* nothosubsp. *cyrnosardoum* nothovar. *ibericum*, Ras-601 (holotype).

because intermediate forms exist. We found no significant differences in microcharacters (see Table 1) between the plants from Turkey and from Spain; nor between these and var. *obovatum* (from Corsica, Ischia, and Sardinia). The plants are diploid (see Table 2 and Fig. 2 and 5).

The microcharacters listed in Table 1 are necessary to distinguish all the forms of diploid *A. obovatum* subsp. *obovatum* from tetraploid subsp. *lanceolatum* (= *A. billotii*) and triploid hybrids. (For further details see Table 2; Demiriz et al. 1990, and Viane 1990.)

Tab. 2. Collections of diploid *Asplenium obovatum* subsp. *obovatum* var. *protobillotii* and tetraploid *A. obovatum* subsp. *lanceolatum* from the Miel Valley (all from 1988). – Ras = herbarium Rasbach; TR = herbarium T. Reichstein; RV = herbarium R. Viane; WB = herbarium H.W. Bennert.

Collection no.	Spores	Ploidy level destinated by direct	Meiosis counting
Ras-Miel 12 = WB-Sp5/88 = RV-3808	Small		
Ras-Miel 13 = WB-Sp6/88	Small		
Ras-Miel 14 = TR-7021 = RV-3809	Small	2×	$n = 36^{II}$
Ras-Miel 15 = TR-7022 = RV-3810	Small	2×	$n = 36^{II}$
Ras-Miel 16 = WB-7/88	Small		
Ras-Miel 20 = WB-8/88	Small		
Ras-602 = TR-7009	Small	2×	$n = 36^{II}$
Ras-603 = TR-7010	Small	2×	$n = 36^{II}$
Ras-610	Small	2×	$n = 36^{II}$
Ras-611 = TR-7014	Small	2×	$n = 36^{II}$
Ras-612 = TR-7015	Small	2×	$n = 36^{II}$
RV-3802	Small	2×	$n = 36^{II}$
RV-3812	Small	2×	$n = 36^{II}$
Ras-Miel 1 = TR-7016	Large	4×	$n = 72^{II}$
Ras-Miel 2 = TR-7017	Large	4×	$n = 72^{II}$
Ras-Miel 3 = TR-7018	Large	4×	$n = 72^{II}$
Ras-Miel 4 = TR-7019	Large	4×	$n = 72^{II}$
Ras-Miel 5 = TR-7020 A	Large	4×	$n = 72^{II}$
= TR-7020 B	Large		
Ras-Miel 6 = WB-Sp9/88	Large		
Ras-Miel 7 = WB-Sp10/88	Large		
Ras-Miel 22 = WB-Sp11/88	Large		
Ras-Miel 23 = WB-Sp12/88	Large		
Ras-Miel 24 = WB-Sp13/88	Large		
Ras-605 = TR-7012	Large	4×	$n = 72^{II}$
Ras-606	Large	4×	$n = 72^{II}$

4.2 The hybrids between A. obovatum subsp. lanceolatum and A. obovatum subsp. obovatum

"The hybrid from the Miel Valley" is a cross of the diploid *A. obovatum* subsp. *obovatum* var. *protobillotii* with the tetraploid *A. obovatum* subsp. *lanceolatum* and thus is a new variety (see 4.2.1) of *A.* × *cyrnosardoum* (= *A. billotii* × *A. obovatum*) Rasb. et al. (1981). However, since tetraploid *A. billotii* F. W. Schultz is better treated as a subspecies of *A. obovatum* Viv. for which *A. obovatum* Viv. subsp. *lanceolatum* Pinto da Silva is the correct name (Demiriz et al. 1990; and this paper, paragraph 5), we must publish the following new combination under *Asplenium obovatum* for the hybrid between subsp. *obovatum* and subsp. *lanceolatum* (ICBN 1988, Articles H. 5 and H. 10, Greuter et al. 1988):

Asplenium obovatum Viv. nothosubsp. *cyrnosardoum* (Rasbach, Vida et Reichstein) Rasbach, Rasbach, Reichstein, Viane et Bennert comb. et stat. nov. Basionym: *Asple-*

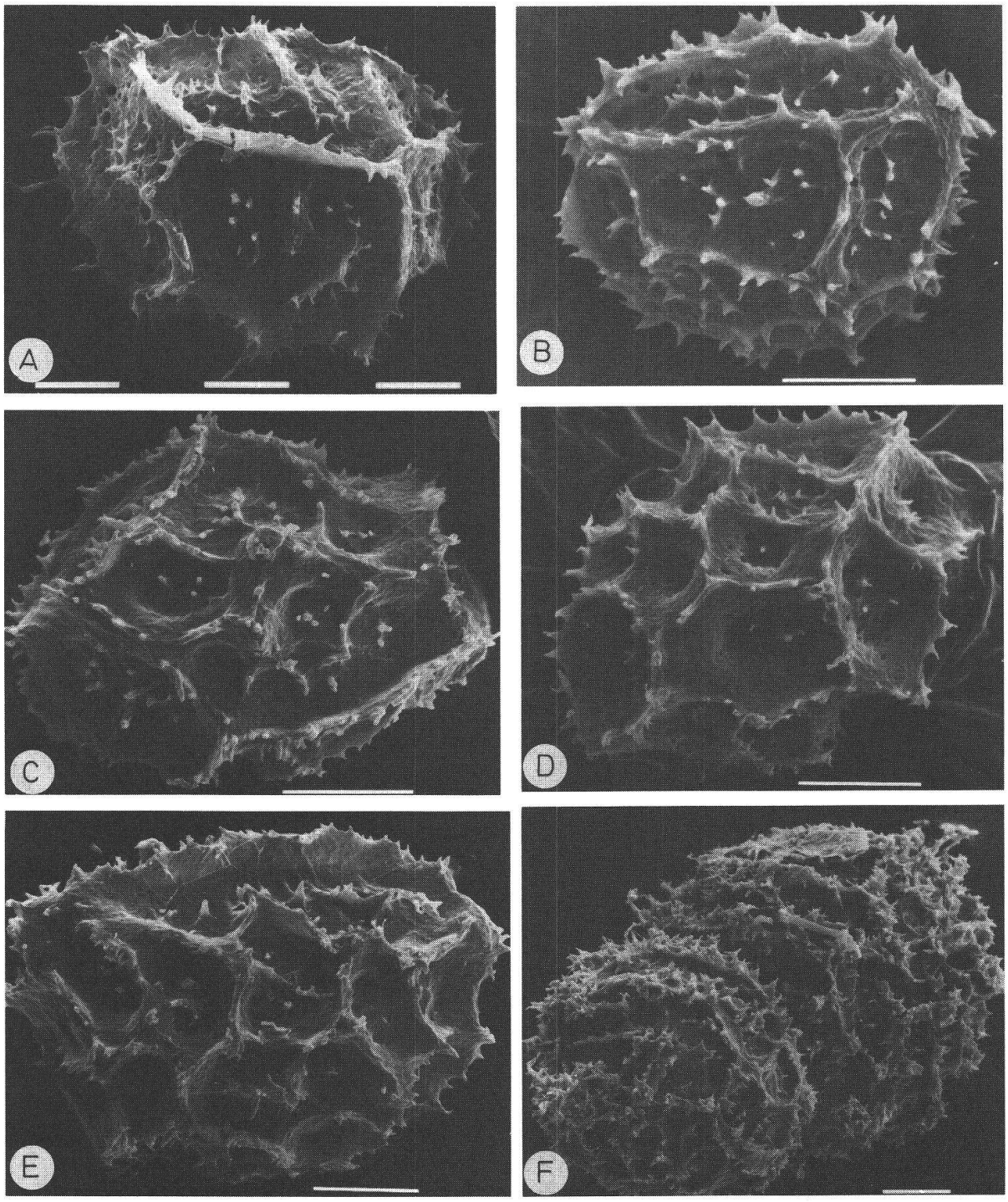

Fig. 4. Scanning electron microscopical surface of *Asplenium obovatum* spores. A = *A. obovatum* subsp. *obovatum* var. *obovatum,* TR-1785a (Ischia/Italy); c. proximal view, cristate supralaesural fold with venulate and echinulate surface and pores. B = *A. obovatum* subsp. *obovatum* var. *deltoideum,* RV-3886 (Dragos/Turkey); c. equatorial view, costate to costate-cristate perispore with venulate and echinulate surface and pores. C = *A. obovatum* subsp. *obovatum* var. *protobillotii,* TR-5343/1 (Miel Valley); c. equatorial view, costate-cristate crests with venulate and echinulate surface and few pores. D = *A. obovatum* subsp. *obovatum* var. *protobillotii,* RV-3887 (Yakacik/Turkey); distal view, costate-cristate folds with venulate and echinulate surface and pores. E = *A. obovatum* subsp. *lanceolatum,* TR-5352 (Miel Valley); equatorial view, cristate folds with scabrate-venulate surface and few pores. F = *A. obovatum* nothosubsp. *cyrnosardoum* nothovar. *ibericum,* TR-5350/2 (Miel Valley); "good" spore and diplospore or tetrad with one common perispore in background, irregularly cristate with many irregularly deposited spinules. (Perispore characters concord with other microcharacters, they stress the coherence within this group of taxa and support the presently proposed relationships). All SEM photos: R. V.; bar equals 10 μm.

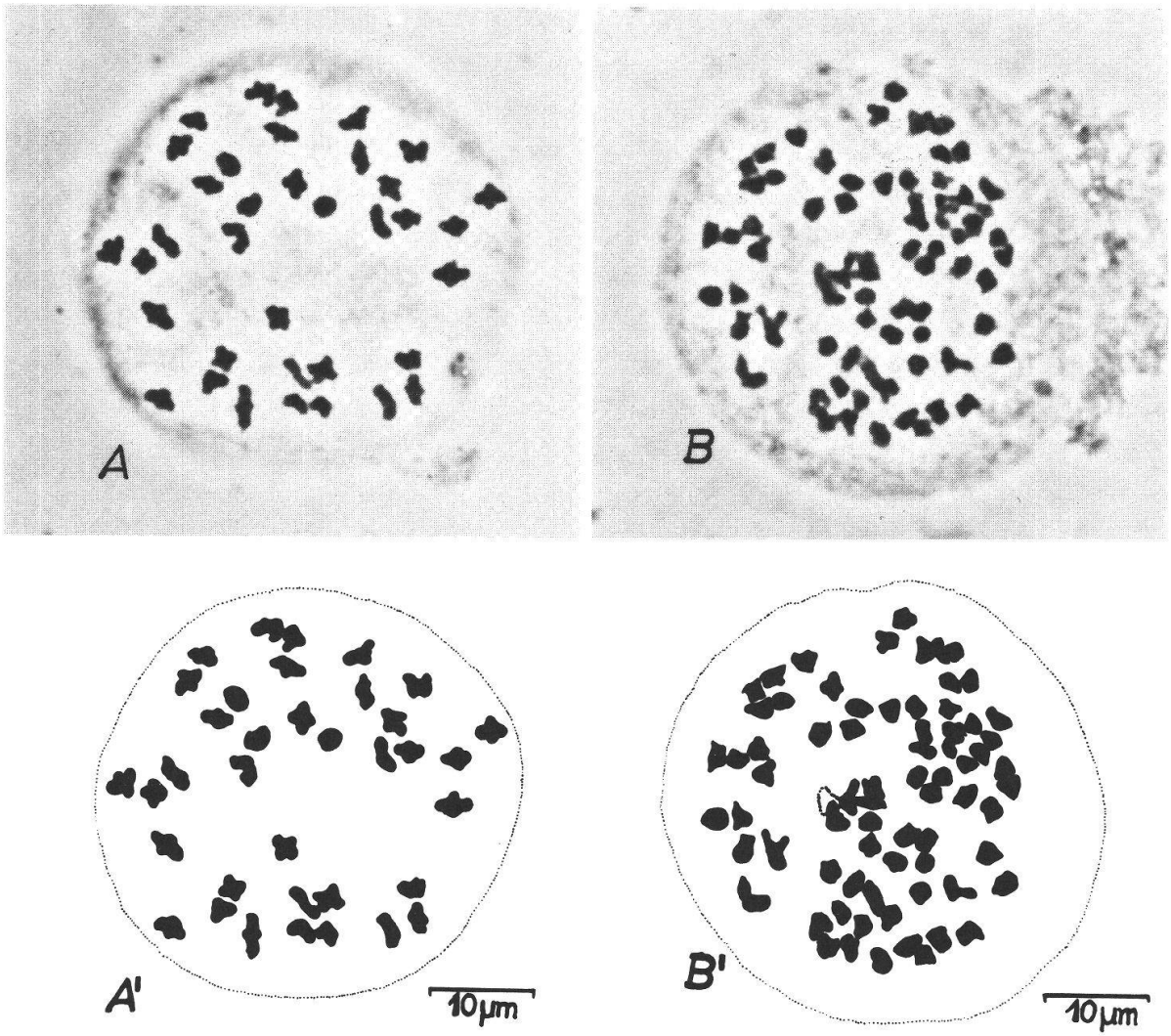

Fig. 5. Cytology: A, B = photographs, A′, B′ = explanatory diagrams. A, A′ = *Asplenium obovatum* subsp. *obovatum* var. *protobillotii* (Ras-603 = TR-7010), spore mother cell in meiosis, showing $n = 36^{II}$.
B, B′ = *Asplenium obovatum* subsp. *lanceolatum* (Ras-Miel 3 = TR-7018), spore mother cell in meiosis, showing $n = 72^{II}$. (Prep. and photo: H. R.)

nium × *cyrnosardoum* Rasbach, Vida et Reichstein (= *A. billotii* × *A. obovatum*), in: Reichstein, 1981. Bot. Helv. 91: 114. The type is from Corsica. This hybrid represents the cross between *A. obovatum* subsp. *obovatum* var. *obovatum* and *A. obovatum* subsp. *lanceolatum*. In order to differentiate it from the hybrid occurring in the Miel Valley (see chapter 4.2.1), it can be designated as *A. obovatum* nothosubsp. *cyrnosardoum* nothovar. *cyrnosardoum*.

4.2.1. The hybrid from the Miel Valley requires a new name at nothovarietal level.

Asplenium obovatum Viv. nothosubsp. *cyrnosardoum* (Rasbach et al.) Rasbach et al. nothovar. *ibericum* Rasbach, Rasbach, Reichstein, Viane et Bennert nothovar. nov. (= *A. obovatum* subspec. *lanceolatum* × *A. obovatum* subsp. *obovatum* var. *protobillotii*) (Fig. 3).

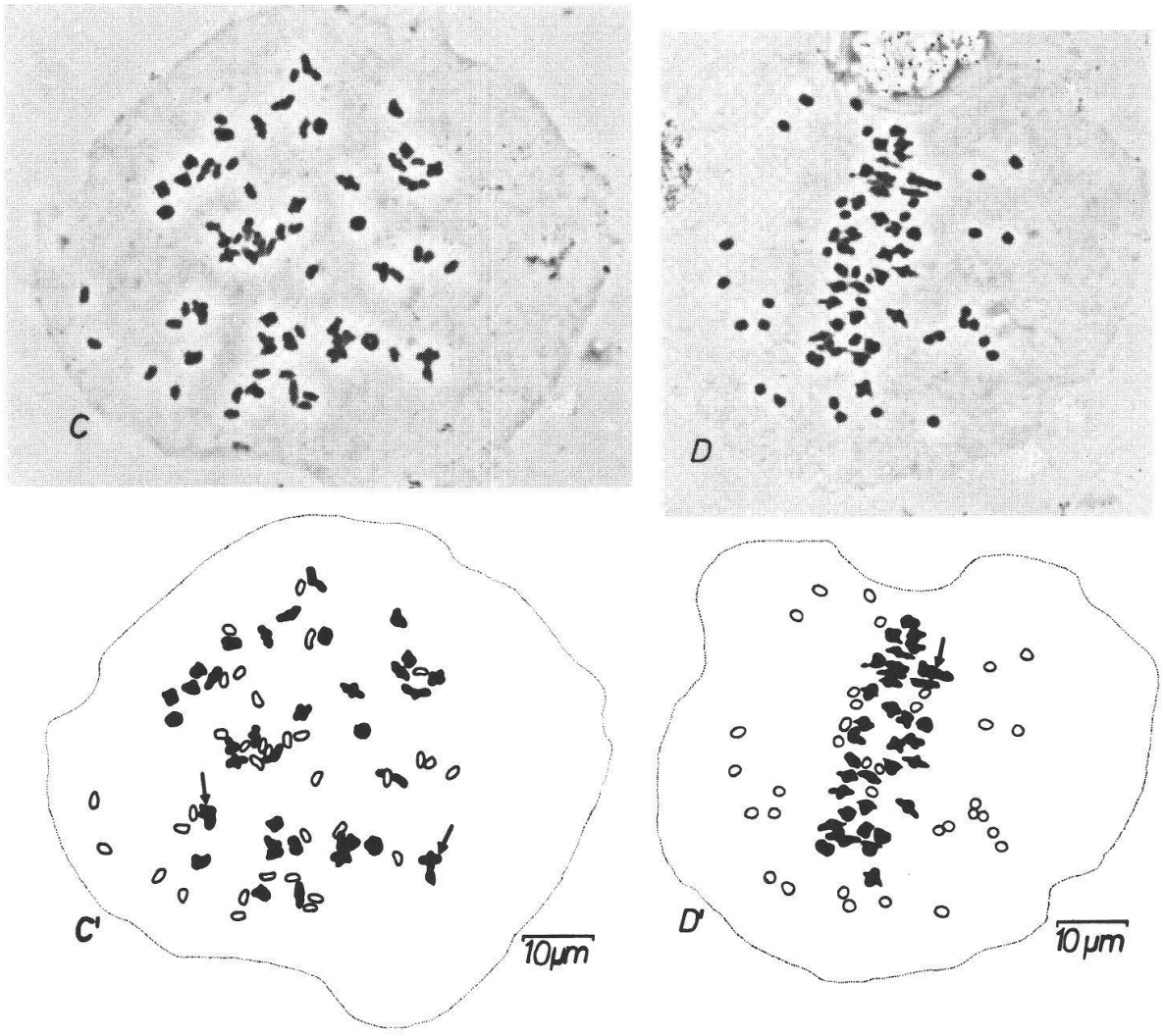

Fig. 6. Cytology: C, D = photographs, C', D' = explanatory diagrams. C, C' = *Asplenium obovatum* nothosubsp. *cyrnosardoum* nothovar. *ibericum* (Ras-601, holotype), spore mother cells in meiosis, showing $n = 2^{III}, 34^{II}, 34^{I}$.
D, D' = *Asplenium obovatum* nothosubsp. *cyrnosardoum* nothovar. *ibericum* (Ras-600 = TR-7007), spore mother cell in meiosis, showing $n = 1^{III}, 35^{II}, 35^{I}$. Trivalents and bivalents black, univalents outlined (trivalents marked by arrows). (Prep. and photo: H. R.)

Typus. Ras-601 (= TR-7008) 14th April 1988, leg. H. Rasbach, K. Rasbach & H. W. Bennert. Holotype, 4 fronds of original collection (B), (Fig. 3). Plant afterwards cultivated, used for cytological examination, divided into 5 parts and pressed as *isotype* (BM, G, MA).

Locus. Spain, Prov. Cádiz, Miel Valley, c. 5 km W. of Algeciras at c. 110 m alt.

Derivatio. Denoting the Iberian Peninsula as origin.

Diagnosis. Nothovar. cyrnosardoo simillimum sed divisiones laminae paulo magis perspicue dentatae, dentibus usque ad 1.6 mm longis.

Description. At the type locality the hybrid was growing in rich siliceous humus and produced fronds up to 43 cm long with stipes about as long as the blade. The outline of the blade is lanceolate to ovate-lanceolate, the ultimate segments are ± pointed and dentate with teeth of c. 1.6 mm. – Like nothovar. *cyrnosardoum* the hybrid is triploid and shows the same behaviour at meiosis, producing c. 1–4 trivalents, c. 32–36 bivalents and the remainder (c. 32) univalents (Fig. 6).

Isotype. TR-7008, 14th April 1988, pressed after cultivation (see above).

Paratypes. Ras-604, 14th April 1988, fixed in the field, n = c. 2^{III}, 32^{II}, 38^{I}; 4 fronds pressed in the field (Z) (Fig. 3).
Ras-Miel 17 = TR-7023, 19th 1988, fixed in the field, n = $0-4^{III}$, $39-36^{II}$, $31-35^{I}$, cultivated at Basel, divided into 6 parts and pressed 6th Sept. 1988.
Ras-Miel 18 = WB-Sp 2/88, 19th April 1988, since then cultivated at Bochum.
Ras-Miel 19 = WB-Sp 3a/88, 19th April 1988, since then cultivated at Bochum.
Ras-Miel 21 = WB-Sp 4/88, 19th April 1988, since then cultivated at Bochum.
Ras-600 = TR-7007, 19th April 1988, fixed in the field, n = $0-2^{III}$, $34-36^{II}$, $34-35^{I}$, cultivated at Basel, divided into two parts and pressed 6th Sept. 1988 (Fig. 6).
Ras-609 = WB-Sp 1/88, 19th April 1988, fixed in the field, n = c. 1^{III}, 35^{II}, 35^{I}, 3 fronds pressed in the field, plant since then cultivated at Bochum.
Ras-613, 15th April 1988, fixed in the field, n = $0-2^{III}$, $31-36^{II}$, $33-37^{I}$, 3 fronds pressed in the field.
Ras-614 = WB-14/88, 15th April 1988, fixed in the field, n = $1-3^{III}$, $32-34^{II}$, $33-36^{I}$, two fronds pressed in the field.
RV-3792, 19th April 1988, at c. 180 m alt.
RV-3799, 19th April 1988, at c. 100 m alt.
RV-3800, 19th April 1988, at c. 100 m alt.

5. Discussion

As reviewed recently by Demiriz et al. (1990), Sleep (1966 and 1983) has shown that *A. obovatum* subsp. *lanceolatum* (= *A. billotii*) is an autotetraploid species most probably arisen by chromosome doubling from the diploid *A. obovatum*. – The finding of (a few) trivalents in the meiosis of *A.* × *cyrnosardoum* = *A. obovatum* subsp. *lanceolatum* × *A. obovatum* subsp. *obovatum* very strongly supported this assumption. The importance of trivalents (even in low number), provided they can be shown to be present with confidence, is discussed in Rasbach et al. (1990), appendix. Some small differences in gross morphology between *A. obovatum* subsp. *lanceolatum* (tetraploid) and *A. obovatum* subsp. *obovatum* (diploid) were considered by Manton & Reichstein (1962), and most authors to date, as sufficient reason to separate these two taxa at the specific level. In contrast, all other autotetraploid *Aspleniums* known are almost indistinguishable with the naked eye from their diploid ancestors. The fact that *A. obovatum* subsp. *lanceolatum* can be distinguished from *A. obovatum* subsp. *obovatum* by its dentation led Sleep (1983: 18) to conclude "although they do look rather different, *A. billotii* may nevertheless have arisen by chromosome doubling from *A. obovatum* or a form with chromosomes homologous to it." As pointed out by Demiriz et al. (1990), *A. obovatum* subsp. *obovatum* var. *protobillotii* is not only such a form, but its finding in southern Spain is in optimal agreement with the assumption that *A. obovatum* subsp. *lanceolatum* has once arisen by

chromosome doubling from *A. obovatum* var. *protobillotii*. The Atlantic Islands, Atlantic Europe, and the western Mediterranean Region are the present area of *A. obovatum* subsp. *lanceolatum*. The finding of a few trivalents in "the hybrid from the Miel Valley" strongly supports the assumption that *A. obovatum* (both var. *obovatum* and var. *protobillotii*) has chromosomes homologous to those of *A. obovatum* subsp. *lanceolatum* (= *A. billotii*). For this reason it is advisable to treat *A. billotii* again as a subspecies of *A. obovatum* (see Demiriz et al. 1990).

6. Zusammenfassung

Asplenium obovatum subsp. *obovatum* var. *protobillotii* Demiriz et al. und die Hybride mit *Asplenium obovatum* subsp. *lanceolatum* Pinto da Silva (= *A. billotii*) wurden in Süd-Spanien, in einer Bachschlucht bei Algeciras (Prov. Cádiz), gefunden. Das diploide *A. obovatum* subsp. *obovatum* var. *protobillotii* und die triploide Hybride erreichen an der Fundstelle einen ungewöhnlich üppigen Wuchs und sind mit bloßem Auge nicht von der dort ebenfalls vorkommenden tetraploiden Sippe, dem *A. obovatum* subsp. *lanceolatum*, zu unterscheiden. Durch Untersuchung mikromorphologischer Merkmale und durch cytologische Untersuchungen konnten auf relativ engem Raum eine größere Anzahl von diploiden, triploiden und tetraploiden Pflanzen nachgewiesen werden. – Die triploide Hybride wird hier als *A. obovatum* nothosubsp. *cyrnosardoum* nothovar. *ibericum* beschrieben. Sie zeigt ein ähnliches Paarungsverhalten der Chromosomen in der Meiose wie nothovar. *cyrnosardoum*, deren Typus von Korsika stammt. In der Meiose beider Hybriden bilden sich einige Trivalente, die als Beweis dafür angesehen werden können, daß die Eltern homologe Genome besitzen. Dieses Resultat, zusammen mit der Tatsache, daß das diploide *A. obovatum* subsp. *obovatum* var. *protobillotii* (im Gegensatz zu var. *obovatum*) mit bloßem Auge nicht vom tetraploiden *A. obovatum* subsp. *lanceolatum* (= *A. billotii*) zu unterscheiden ist, erlaubt den Schluß, daß die tetraploide Sippe subsp. *lanceolatum* durch Chromosomenverdoppelung aus der diploiden Sippe subsp. *obovatum* var. *protobillotii* hervorgegangen ist. Der Vorgang der Chromosomenverdoppelung muß ein seltenes Ereignis bei *A. obovatum* subsp. *obovatum* sein; anders wären die sich nur teilweise überschneidenden Areale von subsp. *obovatum* und subsp. *lanceolatum* nur schwer zu verstehen.

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