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Asplenium trichomanes L. nothosubsp. *melzeri* nothosubsp. nov.
The triploid hybrid between *A. trichomanes* subsp. *inexpectans* and
subsp. *quadrivalens*

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ABSTRACT

LOVIS, J. D., H. RASBACH & T. REICHSTEIN (1989). *Asplenium trichomanes* L. nothosubsp. *melzeri* nothosubsp. nov. The triploid hybrid between *A. trichomanes* subsp. *inexpectans* and subsp. *quadrivalens*. *Candollea* 44: 543-553. In English, English and German abstracts.

The new triploid hybrid *A. trichomanes* nothosubsp. *melzeri* is described from Austria, where it was found in three localities, it was also found in southern Spain. So far it was always observed growing on limestone rocks or walls among the parents (*A. trichomanes* subsp. *inexpectans* and subsp. *quadrivalens*). It can therefore be used as a marker for searching the rare subsp. *inexpectans*. In morphology it is similar to the triploid *A. trichomanes* nothosubsp. *lusaticum* (= *A. trichomanes* subsp. *trichomanes* × subsp. *quadrivalens*) which, however, was always found on siliceous rocks. Results on pairing behaviour of the chromosomes in meiosis (inclusive formation of a few trivalents) in this hybrid (containing 3 homologous *A. trichomanes* genomes) is given and discussed.

ZUSAMMENFASSUNG

LOVIS, J. D., H. RASBACH & T. REICHSTEIN (1989). *Asplenium trichomanes* L. nothosubsp. *melzeri* nothosubsp. nov. Die triploide Hybride von *A. trichomanes* subsp. *inexpectans* und subsp. *quadrivalens*. *Candollea* 44: 543-553. In English, englische und deutsche Zusammenfassungen.

Die neue Hybride *A. trichomanes* nothosubsp. *melzeri* wird aus Österreich beschrieben, wo wir sie an drei Lokalitäten fanden, wir fanden sie auch in Süd-Spanien. Bisher sahen wir sie nur auf Kalkfelsen und Mauern in der Nähe der Eltern (*A. trichomanes* subsp. *inexpectans* und subsp. *quadrivalens*). Sie kann daher als "Zeiger" bei der Suche der seltenen subsp. *inexpectans* dienen. Morphologisch ist sie dem triploiden *A. trichomanes* nothosubsp. *lusaticum* (= *A. trichomanes* subsp. *trichomanes* × subsp. *quadrivalens*) sehr ähnlich, das aber bisher nur auf Silikatgestein gefunden wurde. Das Paarungsverhalten der Chromosomen in der Meiose (inklusive Bildung von einigen wenigen Trivalenten) bei dieser Hybride (die 3 homologe *A. trichomanes* Genome enthält) wird beschrieben und diskutiert.

Abbreviations for Herbaria follow HOLMGREN & al., *Ind. Herb.* I, 7th ed., Utrecht 1981.
— Ras means herbarium H. & K. Rasbach; TR stands for herbarium T. Reichstein.

1. Introduction

Asplenium trichomanes L. is an aggregate species (LOVIS, 1964, 1977; LOVIS & REICHSTEIN, 1984). The following subspecies have been described: subsp. *trichomanes* (sensu LOVIS, 1964), diploid; subsp. *inexpectans* (LOVIS, 1964), diploid; subsp. *quadrivalens* D. E. Meyer (1962), tetraploid; subsp. *pachyrachis* (Christ) Lovis & Reichstein (1984), tetraploid. At least three different

hexaploids have been reported. One discovered in New Zealand by BROWNLIE (1954) is the dominant cytotype there (BROWNSEY, 1977; LOVIS, 1956, 1958, 1959). A hexaploid detected from a single locality in Australia (BROWNSEY, 1977; LOVIS, 1977) may not be identical. A hexaploid met with in Europe, but very rare, was reported by BOUHARMONT (1968) from siliceous rocks in Belgium and France (as stated in litt. 1. Aug. 1989). It may have arisen by chromosome doubling in nothosubsp. *lusaticum* (D. E. Meyer) Lawalrée. Another hexaploid was recently found by Bennert & al. (1989a; 1989b) on limestone rocks in southern Spain. A further hexaploid, known only from Madeira (MANTON & al., 1986) though treated taxonomically as a subspecies of *Asplenium trichomanes* (GIBBY & LOVIS, 1989), is probably of a very different genetic constitution, since it is believed that it has arisen by allopolyploidy from *A. trichomanes* subsp. *quadrivalens* and *A. anceps*. All other hexaploids mentioned above are believed to be of intraspecific origin.

The following two intraspecific hybrids have been described: nothosubsp. *lusaticum* (D. E. Meyer) Lawalrée in DE LANGHE & al. (1983: 24), the triploid hybrid between subsp. *quadrivalens* and subsp. *trichomanes*; nothosubsp. *staufferi* Lovis et Reichstein (1985), the tetraploid hybrid between subsp. *pachyrachis* and subsp. *quadrivalens*. We describe here a second triploid intraspecific hybrid between subsp. *inexpectans* and subsp. *quadrivalens*, already mentioned by REICHSTEIN (1984 in HEGI: 218 under 3).

2. The new triploid intraspecific hybrid

***Asplenium trichomanes* L. nothosubsp. *melzeri* Lovis, Rasbach & Reichstein, nothosubsp. nov. (= *A. trichomanes* subsp. *inexpectans* × *A. trichomanes* subsp. *quadrivalens*).**

Typus: TR-1371, 12 Sept. 1964, leg. H. Melzer, J. D. Lovis, Anne Sleep & T. Reichstein among the parents. Fixed in the field, plant collected living, cultivated at Basel, multiplied by division and pressed 11 July 1968 (Fig. 1). **Holotypus** (B), **Isotypi** (G, Z).

Locus. — Steiermark (Austria), steep limestone rocks above road No. 23, 1 km N. of Mürzsteg at ca. 800 m alt., just S. of the bridge over the river Mürz.

Derivatio. — Named after Helmut Melzer, our friend and, very active field botanist who found many new plants mainly in Austria and northern Italy, including most specimens of this hybrid.

Diagnosis. — Recedit a nothosubsp. *lusaticum* pinnis terminalibus paucè latioribus, frondibus minus erectis, potius cernuis, et substrato calcareo vel dolomitico nec silicioso.

Description. — This hybrid has the usual aspect of most forms of *A. trichomanes*. It is particularly similar to subsp. *quadrivalens* and to nothosubsp. *lusaticum*, and like the latter often shows hybrid vigour.

Rhizome short, erect or ascending, branching in old plants, clad at its apex with up to 3(-3.5) mm long clathrate scales with a blackish middle stripe (Fig. 4). Fronds up to ca. 100(-200) mm, tufted, with black or dark red-brown, short stipes, up to ca. 5 cm long, ca. 1 mm thick, bearing at their bases a tuft of scales like those of the rhizome and glabrous or sparingly beset with ca. 0.9-1.5 mm long, whitish bi- or tricellular, glandular hairs higher up. Blades up to 15 cm long and ca. 2 cm wide, pinnate, with 6-20 pairs of subopposite or alternate pinnae, sublinear in outline, tapering to the apex (Fig. 2). Rachis black or dark red-brown like the stipe and also glabrous or sparingly beset with whitish, appressed, bi- or tricellular glandular hairs (Fig. 5) similar to those of subsp. *inexpectans* and subsp. *quadrivalens*, winged on upper (adaxial) side (see cross section Fig. 6). Pinnae up to 8(-10) mm long with short (up to 1 mm) petiolules, ± entire, ± oval-ovate, often dentate (teeth up to 0.5 mm long), not or only slightly auriculate at their bases; the apical pinnae similar in shape but more symmetrical. Sori up to 6 on both sides of the costa, up to 2 mm long, diverging from the costa at an angle of ca. 20°. Spores completely abortive (Fig. 3). Chromosome number $2n = 108$, usually with a few trivalents, ca. 31-36 pairs and 44-31 univalents at meiosis. One cell with 4^{III} , 32^{II} , 32^I is shown in Fig. 7.

This hybrid grows as single plants on calcareous or dolomitic rocks among the parents. This means that it can often be found in the vicinity of the rare diploid *A. trichomanes* subsp. *inexpectans*, as the common subsp. *quadrivalens* nearly always grows nearby.

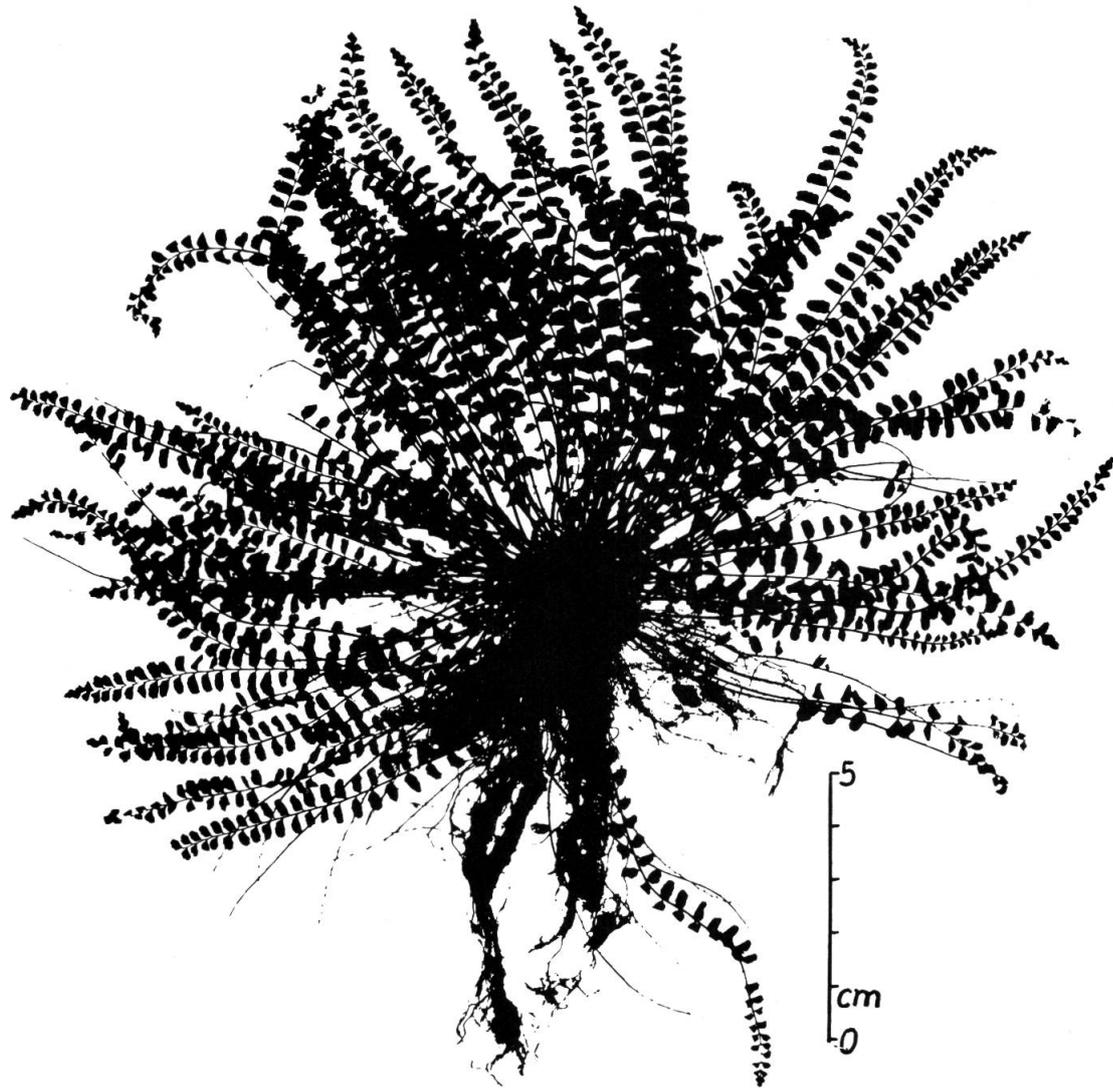


Fig. 1. — *Asplenium trichomanes* nothosubsp. *melzeri*. Type specimen TR-1371 after cultivation, (B). Photogr. (silhouette) H.R.

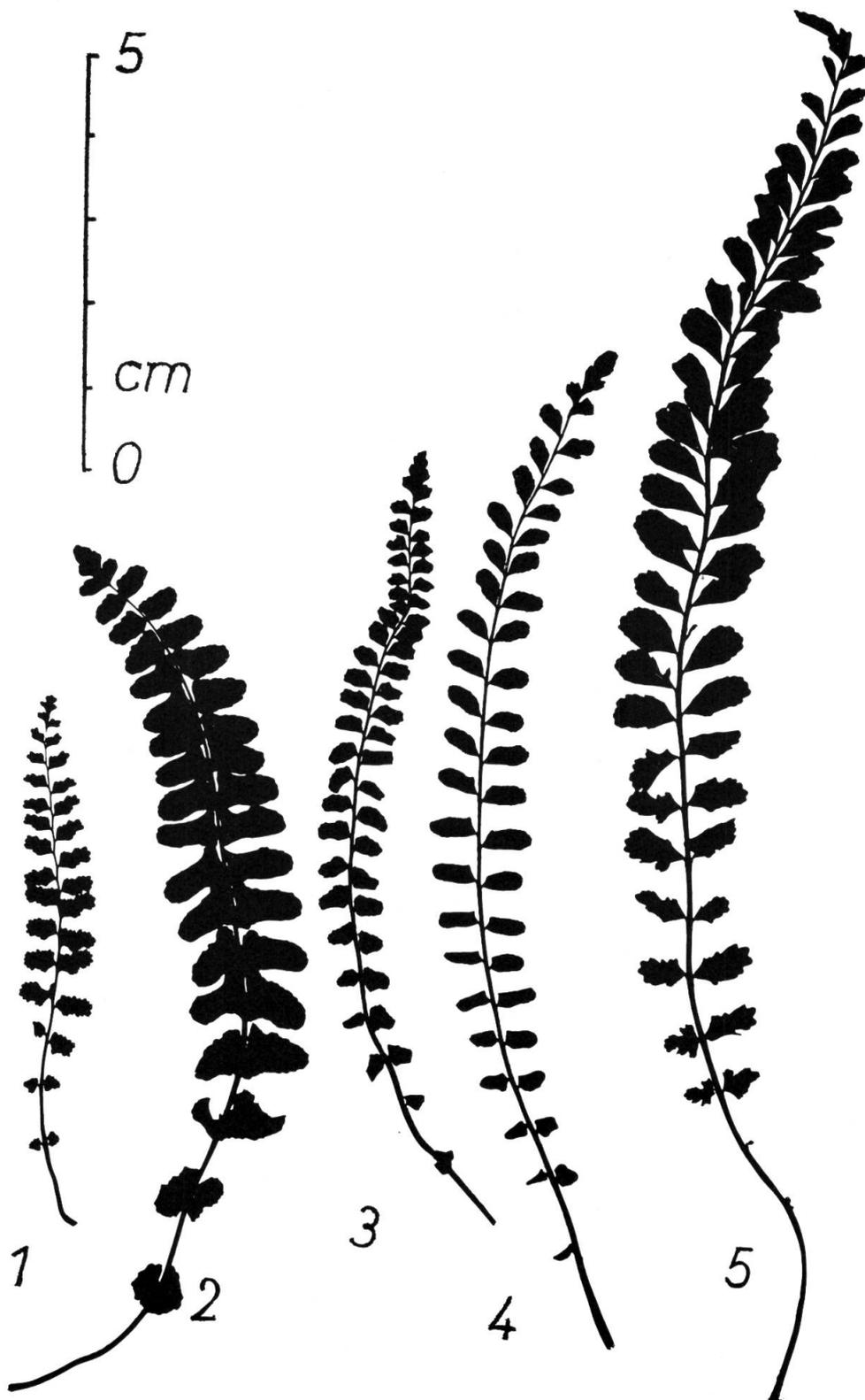


Fig. 2. — Silhouettes of pressed fronds: 1, *A. trichomanes* subsp. *inexpectans* (Ras-629 A = TR-7004 a) from Spain; 2, subsp. *inexpectans* (Ras-405 = TR-6033) from France; 3, nothosubsp. *melzeri* (TR-1371) from Austria; 4, nothosubsp. *melzeri* (SJ-1770/1 = TR-6698) from Austria; 5, subsp. *quadrivalens* (WB-32/86) from Mallorca. Photogr. H. & K. R.

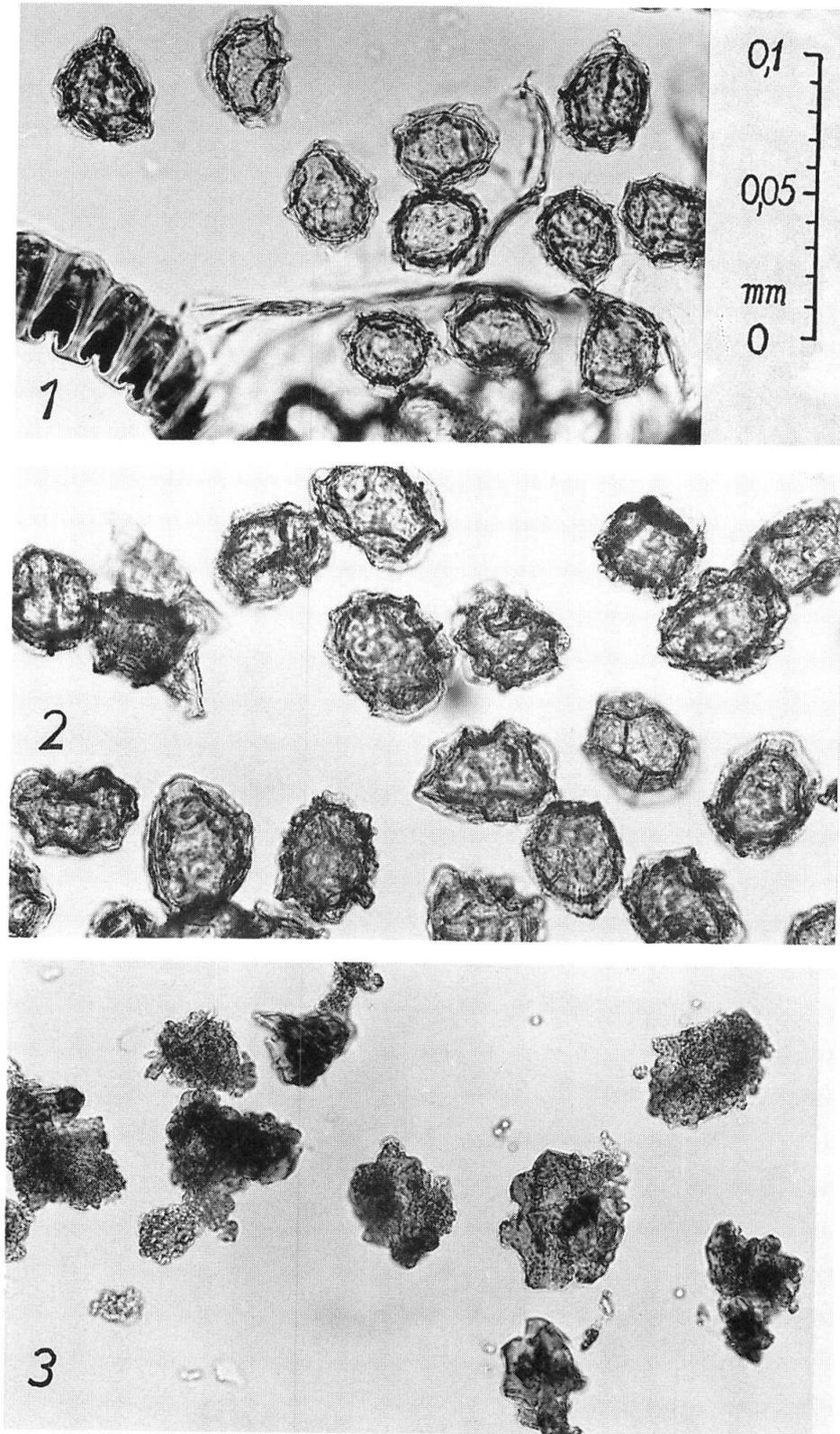


Fig. 3. — Spores under the light microscope: 1, *A. trichomanes* subsp. *inexpectans* (Ras-629 A = TR-7004 a) from Spain; 2, subsp. *quadrivalens* (Ras-561) from Mallorca; 3, sporangial content of *A. trichomanes* nothosubsp. *melzeri* (TR-1371 = Ty-pus). Photogr. H. & K. R.



Fig. 4. — Rhizome scales: 1, *A. trichomanes* subsp. *inexpectans* (Ras-405 = TR-6033) from France; 2, *A. trichomanes* notho-subsp. *melzeri* (TR-1371) from Austria; 3, *A. trichomanes* subsp. *quadrivalens* (TR-1651) from Mallorca. Prep. and drawing H. R.

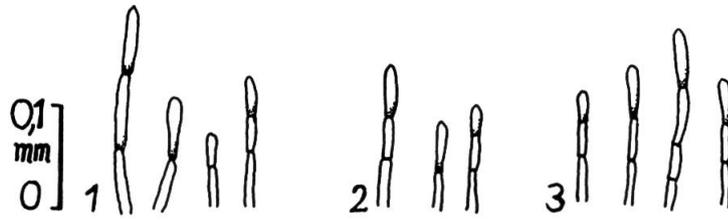
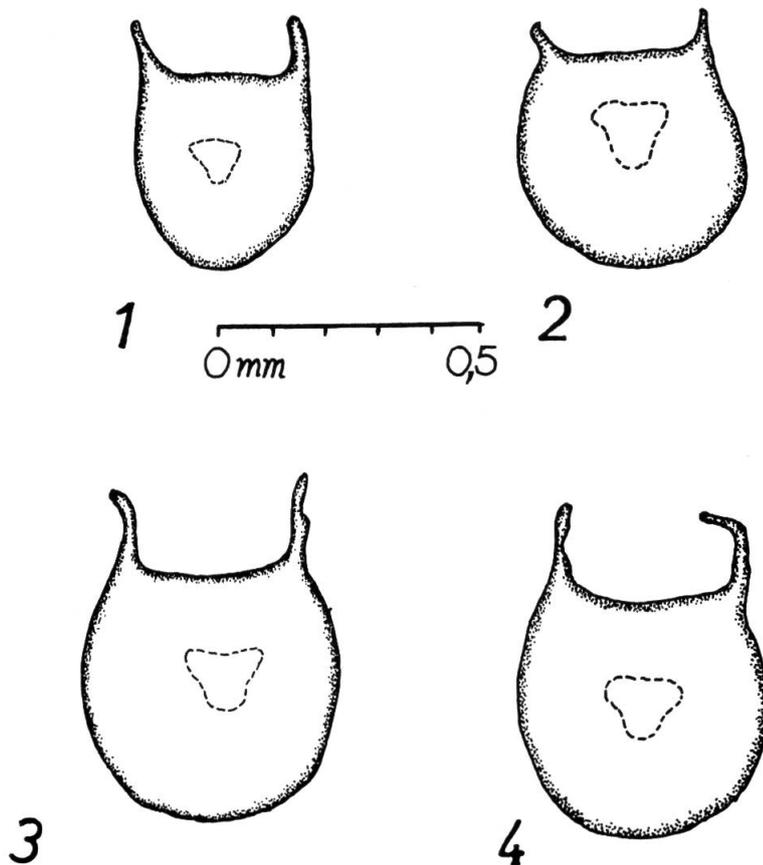


Fig. 5. — Glandular hairs from the middle part of the rachis: 1, *A. trichomanes* subsp. *inexpectans* (Ras-405 = TR-6033) from France; 2, *A. trichomanes* nothosubsp. *melzeri* (SJ-1770/1 = TR-6698) from Austria; 3, *A. trichomanes* subsp. *quadrivalens* (TR-1177) from Mallorca. Drawings H. R.

Fig. 6. — Cross sections of the middle part of the rachis (the length of the corresponding frond is given in brackets): 1, *A. trichomanes* subsp. *trichomanes* (RV-3274) from Turkey (7 cm); 2, *A. trichomanes* subsp. *inexpectans* (Ras-405 = TR-6033) from France (16 cm); 3, *A. trichomanes* nothosubsp. *melzeri* (TR-1371 = Typus) from Austria (12 cm); 4, *A. trichomanes* subsp. *quadrivalens* (Ras-481) from Germany (18 cm). Prep. and drawings H. R.



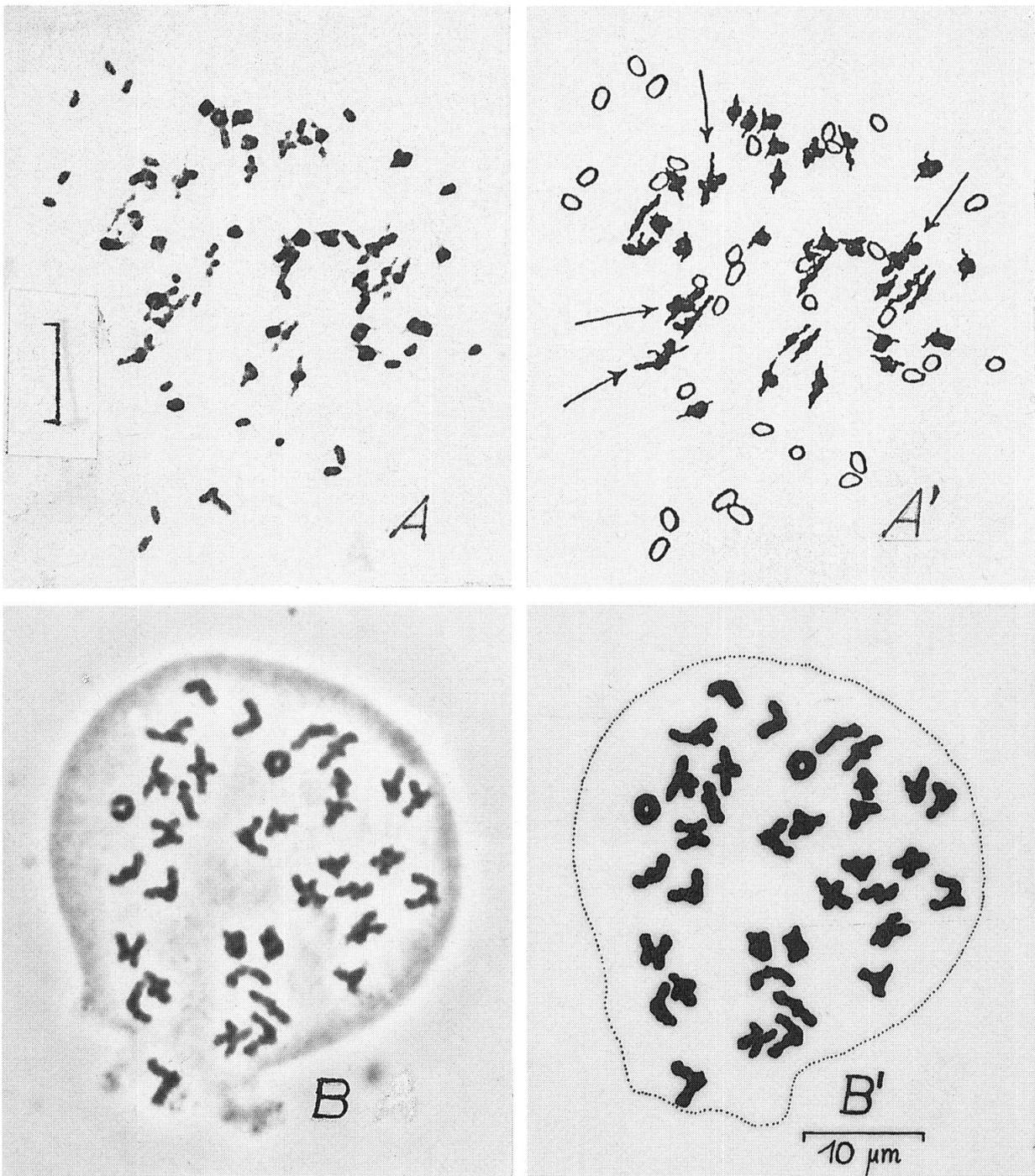


Fig. 7. — Cytology, showing spore mother cells in meiosis: **A** and **B** = photographs, **A'** and **B'** = explanatory diagrams. **A**, **A'** = *A. trichomanes* nothosubsp. *melzeri* (type specimen TR-1371), fixed in the field by J. D. L. on 12th Sept. 1964, squashed and roughly analysed on 23rd Sept. 1964 at Leeds. The old slide (still in good state) was reanalysed carefully in May 1989 at Christchurch. Showing 4^{III} , 32^{II} and 32^I , trivalents indicated by arrows (J. D. L.). **B**, **B'** = *A. trichomanes* subsp. *inexpectans* (W. Bennert & U. Peters SP 35/86) Mallorca, diakinesis showing 36^{II} . Prep. and photogr. H. R.

This hybrid may, by chromosome doubling be able to produce a hexaploid fertile cytotype of *A. trichomanes* that grows on limestone. So far we have not seen such a plant. The rare hexaploid, reported by BOUHARMONT (1968) for Belgium and France, was found on siliceous rocks. The hexaploid from limestone rocks in S. Spain (BENNERT & al., 1989a; 1989b) is different in morphology (see RASBACH & al., 1989). Another hexaploid cytotype is the dominant form of *A. trichomanes* in New Zealand (BROWNLIE, 1954; LOVIS, 1956 quoted by BROWNSEY, 1977). It will be described by Lovis in the near future. As in similar cases, the length of the guard cells in the stomata of the triploid hybrid is intermediate between that of the parent species (see Table 1).

Taxon	Ploidy level	Guard cells
subsp. <i>trichomanes</i>	2	(32-)35-40(-45) μm
subsp. <i>inexpectans</i>	2	(31-)37-40(-43) μm
nothosubsp. <i>lusaticum</i>	3	(35-)41-45(-48) μm
nothosubsp. <i>melzeri</i>	3	(32-)40-43(-46) μm
subsp. <i>quadri-valens</i>	4	(37-)45-47(-55) μm

Table 1. — Length of guard cells in stomata (method see BENNERT & al., 1989b). The values for subsp. *trichomanes* and nothosubsp. *lusaticum* are given for comparison.

Paratypes

Austria. TR-1254, Ost-Tirol, border to Kärnten, under N-exposed, overhanging dolomitic rocks at ca. 700 m alt. above (S. of) Nikolsdorf, together with the parents and with *Asplenium seelosii*, *Anemone trifolia*, *Rhodothamnus chamaecistus*, *Rhododendron hirsutum*, etc., partly under trees, 22 June 1964, H. Melzer, H. L. and T. Reichstein. Two fronds pressed, cytology not checked, spores abortive.

TR-1357, Steiermark, dolomitic and limestone rocks near the "Drachenhöhle" above Mixnitz (N. of Graz) at ca. 900 m alt., among the parents, and with *Asplenium lepidum*, *A. ruta-muraria*, *A. x. stiriaticum*, and *A. trichomanes* subsp. *pachyrachis*, 12 Sept. 1964. H. Melzer, J. D. Lovis, Anne Sleep and T. Reichstein. Fixed in the field 15 Sept. 1964 by JDL, collected living and cultivated at Basel by TR. This plant was finally pressed 20 Sept. 1969.

TR-1371e, Steiermark, same locality as the type locality (see above), collected living, cultivated at Basel and pressed 4 July 1972.

TR-6698, Steiermark, steep limestone rocks, N. facing, behind the ruin of Liechtensteinberg Castle near Judenburg, 15 Sept. 1987. S. Jessen, H. Melzer and H. Wagner (= SJ-1770/1). Plant collected living and cultivated in Karl-Marx-Stadt. Fixing sent to H. R. gave countable but not really good cells. The best cell showed ca. 3^{III}, 33^{II}, 33^I (total 108 chromosomes) at meiosis. Plant pressed 30 July 1988.

Continental Spain. — WB, HR, & KR SP. 52/89. Prov. Málaga, carstic limestone rocks with cracks and holes near Benaoján, ca. 700 m alt., 18 Apr. 1988, W. Bennert, H. & K. Rasbach (see BENNERT & al. 1989a, 1989b). Plant coll. living, cult. in Bochum, immature sporangia fixed in Aug. 1989. The poor quality of these fixings did not allow searching for trivalents but an approximate meiotic count was possible. HR found ca. 32-36^{II}, 44-36^I (total 108 chromosomes).

WB, HR & KR Sp. 56/89. Spain, Prov. Cadiz, limestone rocks and walls above road from Grazalema to Ubrique, WSW of Villaluenga del Rosario at road km 12, ca. 800 m alt. 29th Apr. 1989. Plant coll. living, cult. at Bochum and from 25th Aug. on at Basel (as TR-7262). Immature sporangia fixings were sent to HR (on 12th Aug. 1989); they again did not allow searching for trivalents but an approximate count of bivalents was possible. It showed ca. 36^{II} + 36^I.

Mallorca (Balears, Spain). Slope above the Torrent d'es Barranc, SE of Biniraix, in old walls of limestone rocks, 17th Apr. 1986 leg. W. Bennert & U. Peters. This is the place where Reichstein (see GREUTER, 1980: 18) first found subsp. *inexpectans* in Mallorca. Bennert and Peters found

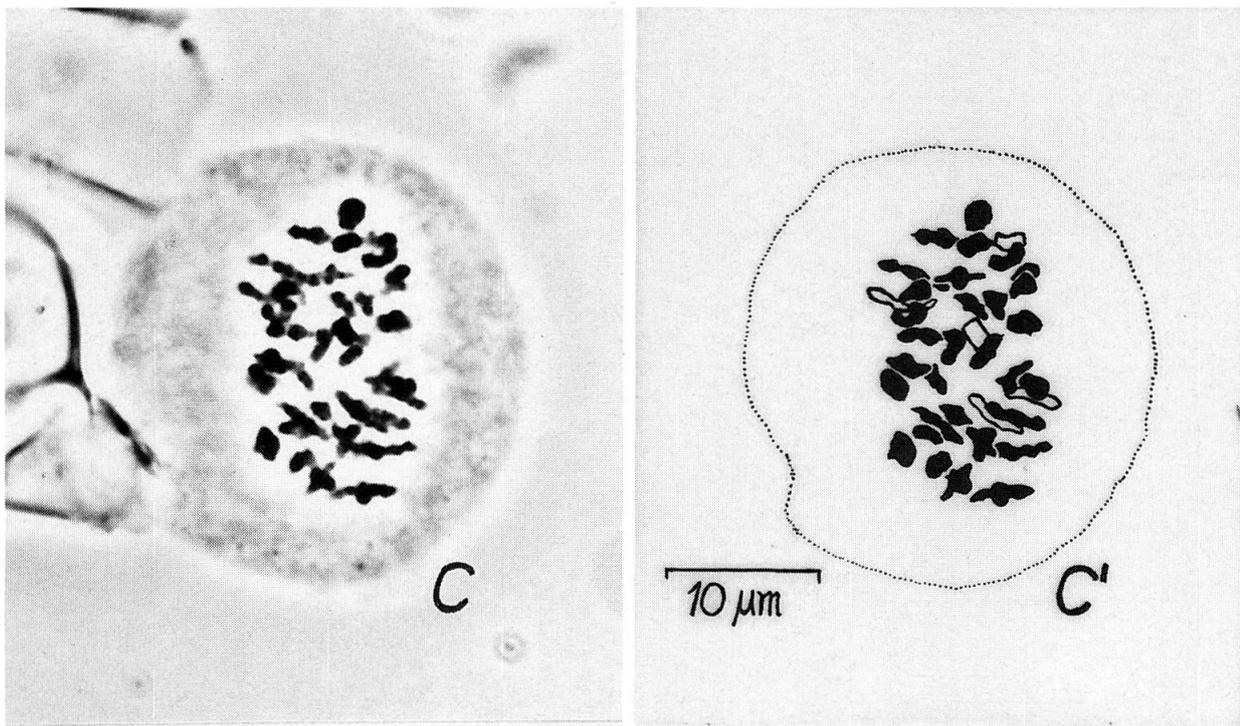


Fig. 8. — Cytology (continuation). C, C' = *A. trichomanes* subsp. *inexpectans* (TR-7207 A = RV 4202 after cult.), Menorca. Metaphase I showing $n = 36^{II}$. Chromosomes not all in the same plane, the five pairs in a lower plane given in C' in outline. Prep. and photogr. H. R.

one plant of subsp. *inexpectans* SP 35/86 and one of the triploid hybrid SP 34/86. Other ferns in the vicinity were *A. majoricum* Litard. (rare), *A. trichomanes* subsp. *quadrivalens* (common), *A. petrarchae* (Guérin) DC. (rare), \times *Asplenoceterach barrancense* W. Bennert & D. E. Meyer (rare), *Ceterach officinarum* Willd. (common), *Polypodium australe* Fée (a dwarf form, common). Both the hybrid SP 34/86 and subsp. *inexpectans* were collected living, cultivated in Bochum in the greenhouse of the Inst. of Botany. — Fixing of immature sporangia were sent to H. R. Subsp. *inexpectans* gave a clear count of 36^{II} (Fig. 7). Meiotic counts of 8 cells of the hybrid showed a range of ca. $0-2^{III}$, $34-36^{II}$ and $34-36^I$ (total 108 chromosomes).

Menorca (Spain). Subsp. *inexpectans* has meanwhile also been found on Menorca (diploid forms of *A. trichomanes* were reported for this island by SALVO, 1988: 6). The hybrid may therefore well be present there, too. We give here the precise locality of subsp. *inexpectans*. R. Viane 4202, Menorca, N-facing, dolomitic (Jura) rocks at ca. 340 m alt. just (50 m) below the top of Es Toro, common in rock fissures, 24th Oct. 1988, coll. A. C. Jermy and R. Viane. Brought living to Basel and cult. as TR-7207 A. Fixed 3rd Apr. 1989, $n = 36^{II}$, see Fig. 8.

3. Discussion

The hybrid is formed relatively often wherever *A. trichomanes* subsp. *inexpectans* is present. It can actually be used as a marker to help finding the rare subsp. *inexpectans* (see BENNERT & al., 1989b). Its behaviour in meiosis is another welcome example of the fact that *A. trichomanes* hybrids, containing three homologous genomes, usually do produce some trivalents. As pointed out by RASBACH & al. (1989 and further literature quoted by them), the formation of trivalents is one of the most important tools for proving the presence of three homologous genomes in a hybrid and thus for establishing the *auto*-tetraploid status of its parents. When *A. petrarchae*, *A. rutamuraria*, *A. septentrionale*, and others are involved as autotetraploids, the number of trivalents in the corresponding hybrids can be quite high. — When 3 genomes of *A. trichomanes* are present

in such hybrids, usually only few trivalents are formed (0-5, in rare cases up to 7). The technical difficulties in establishing the precise number of trivalents in such hybrids are great. — Reliable and most significant results can, however, be obtained if an expert with long experience can devote sufficient time for producing well-spread squashes and careful analysis.

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