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Hybrids in European Aspleniaceae (Pteridophyta)

Significance, recognition, genome analysis, and fertility; checklist of species and hybrids.
Description of some new hybrids and cytology of several already known hybrids

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Dedicated to Prof. Irene Manton who first emphasized the importance of hybrids in understanding many relations in ferns (in her book 1950).

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Zusammenfassung

Farnhybriden haben seit je das Interesse der Pteridologen gefunden; trotzdem wurde sogar ihre Existenz noch bis in unser Jahrhundert angezweifelt. Experimentelle Methoden, besonders Cytologie und experimentelle Hybridisierung (Manton 1950; Vida 1976; Lovis 1977; Walker 1973, 1979) lassen heute eindeutige Schlußfolgerungen zu. Zur Erkennung von Hybriden ist neben der Beobachtung im Feld die mikroskopische Prüfung des Sporangieninhalts unumgänglich; ein praktisches Beispiel wird gegeben. Die Untersuchung von Farnhybriden hat maßgeblich zum besseren Verständnis der Verwandtschaft von reinen Arten beigetragen, insbesondere der Abstammung allopolyploider Arten, die oft große taxonomische Probleme stellen.

Über Sterilität und Fertilität von Farnhybriden wurde viel spekuliert; gesicherte Aussagen lassen sich mit experimentellen Methoden erbringen. Von wenigen Ausnahmen abgesehen (wie Hybridschwärme bei zwei asiatischen Arten von *Pteris*, vgl. T. G. Walker 1958, sowie Abkömmlingen gewisser Apomikten) sind die Hybriden der europäischen Farne völlig oder nahezu steril, jede (oder fast jede) natürliche Hybride entsteht *de novo* an dem Ort, wo sie wächst. Jeder Fall kann sich aber anders verhalten und muß für sich untersucht werden. Es gibt trotzdem gewisse Gruppen, die gemeinsame Züge tragen. Dazu gehören folgende: Einige der seltenen diploiden Hybriden (nicht alle) vermögen nach Chromosomenverdoppelung (vermutlich meistens durch Restitutionskernbildung) einige Diplosporen zu erzeugen, die keimfähig sind und allotetraploide, voll fertile Nachkommen liefern. Dieser Vorgang hat vermutlich bei der Entstehung allotetraploider Arten eine große Rolle gespielt und in gewissen (wenigen) Fällen kann er heute noch stattfinden. Triploide interspezifische Hybriden sind bei den europäischen Aspleniaceae-Arten, soweit untersucht, ganz steril. In der Gattung *Polystichum* wurde aber gelegentlich (vermutlich durch einen apomiktischen Vorgang) eine geringe Fertilität beobachtet.

Einen besonderen Fall stellt die «verzögerte Allopolyploidie» dar. Wenn eine autotetraploide Art, wie *Asplenium ruta-muraria* (RuRuRu'Ru'), sich mit einer zweiten autotetraploiden Art, wie *A. trichomanes* ssp. *quadri-valens* (TrTrTr'Tr'), kreuzt, so entsteht das *A.* × *clermontae* (RuRu'TrTr'), das in der Meiose eine sehr hohe Zahl von Bivalenten bildet und dementsprechend eine geringe Zahl guter keimfähiger Sporen produziert, aus denen sich in Kultur einige Sporophyten von richtigem *A.* × *clermontae* erhalten ließen. Ganz gleich verhielt sich *A.* × *murbeckii* (RuRu'SpSp'), die natürliche Kreuzung von *A. ruta-muraria* mit tetraploidem *A. septentrionale*. Diese besonderen Hybriden zeigen somit zwar sehr geringe, aber doch eindeutige Fertilität, und es gelang bei *A.* × *murbeckii* auch experimentell, Rückkreuzungen zu erzeugen. Es ist von erheblichem Interesse, daß es Fraser-Jenkins und Vida gelang, eine solche Rückkreuzung von *A.* × *murbeckii* × *septentrionale* auch in der Natur (in Ungarn) zu finden. Sie wird hier (vgl. Appendix I) beschrieben. In der Literatur wurden viele solcher Kreuzungen beschrieben, sie beruhen aber alle auf Fehlbestimmungen. Die genannte Hybride aus Ungarn ist der erste Fall einer solchen gesicherten natürlichen Rückkreuzung.

Es werden Listen der europäischen Aspleniaceae-Arten und -Hybriden gegeben und einige neue Hybriden beschrieben (Appendix I) sowie über die Zytologie bekannter Hybriden berichtet (Appendix II), wobei die Abstammung gesichert und eine teilweise neue Interpretation gegeben werden konnte.

1. Introduction

When revising the chapter on Aspleniaceae for the 3rd ed. of Hegi: «Illustrierte Flora von Mitteleuropa» Vol. I (in press), the author had to include both new hybrids and new cytological data on some already known ones. The present paper was originally intended to provide the necessary diagnoses and other details about the hybrids which could not be included in Hegi. But, at the suggestion of friends, it was expanded into an annotated checklist of all known species and hybrids in Europe, with some general remarks on these plants, including cytology and possible fertility of hybrids, if any. New hybrids are described in Appendix I and new cytological data in Appendix II. The author is most grateful to the discoverers and to the workers on cytology for their agreement to this proce-

ture. Documentation for the cytological results (established partly by J. D. Lovis when still in Leeds and partly by G. Vida when still at the research Institute of Botany of the Hungar. Acad. of Science, Budapest) can unfortunately not be provided. During heavily disorganized periods (when professor Lovis had to move to New Zealand and professor Vida to the Dept. of Genetics at the Eötvös Lorand University), the cytological slides had to be packed and were displaced, so that the photographs could not be produced in time. Fortunately, however, most data had been recorded and were available. The cytological results are based on these records and on the authority of these two well-known workers.

2. What is a hybrid?

For a general discussion see Stace (1975: 2-6). The term is used here in the strict sense of an F₁ cross between two different species or subspecies. In the pteridophyta such hybrids are usually (with few exceptions, see below sub. 9.) sterile or nearly so and therefore are formed *de novo* where they occur. Allopolyploids, although sometimes of known hybrid origin, like *Asplenium adiantum-nigrum* L. (Shivas 1969), are accepted here as good species, not as hybrids. About 50 % of the known fern species are probably of allopolyploid origin, but their status and their ancestors are often unknown.

3. Significance of hybrids

Fern hybrids have always attracted the attention of pteridologists. One may even say that an expert knows the species only when he is able to recognize the hybrids. Study of natural and experimentally produced hybrids is also essential for evaluating the relationship between species and particularly for understanding the formation of allopolyploids which often pose difficult taxonomic problems (Manton 1950; Vida 1976; Lovis 1977; Walker 1973, 1979).

4. Recognition of hybrids

Intermediate morphology of a particular plant in a mixed population of two or more species is usually the first indication of possible hybridity; but this should always be checked by examination of the contents of the sporangia and, if possible, the cytology.

4.1. Checking sporangial content.— This is an indispensable and simple means for recognizing hybrids. To be reliable, it is essential that the material is collected with care, if possible as follows. The best time for collecting fronds is when the sporangia are just beginning to open and are still black, but in many species overripe fronds with brown sporangia are sometimes still usable. Detach carefully 1-3 whole, clean ripe fronds (*without* rhizome and *without* soil!); put them on a *clean* piece of paper (which has never been used for pressing any plants before; the best is thin white paper, but clean newspaper is also acceptable); fold this paper so that no spores can get lost, label it and dry this «envelope» in the press. After 1-2 days the sporangial content will be visible as yellow, green, brown or black powder which, as long as it remains in the closed envelope, will be still available

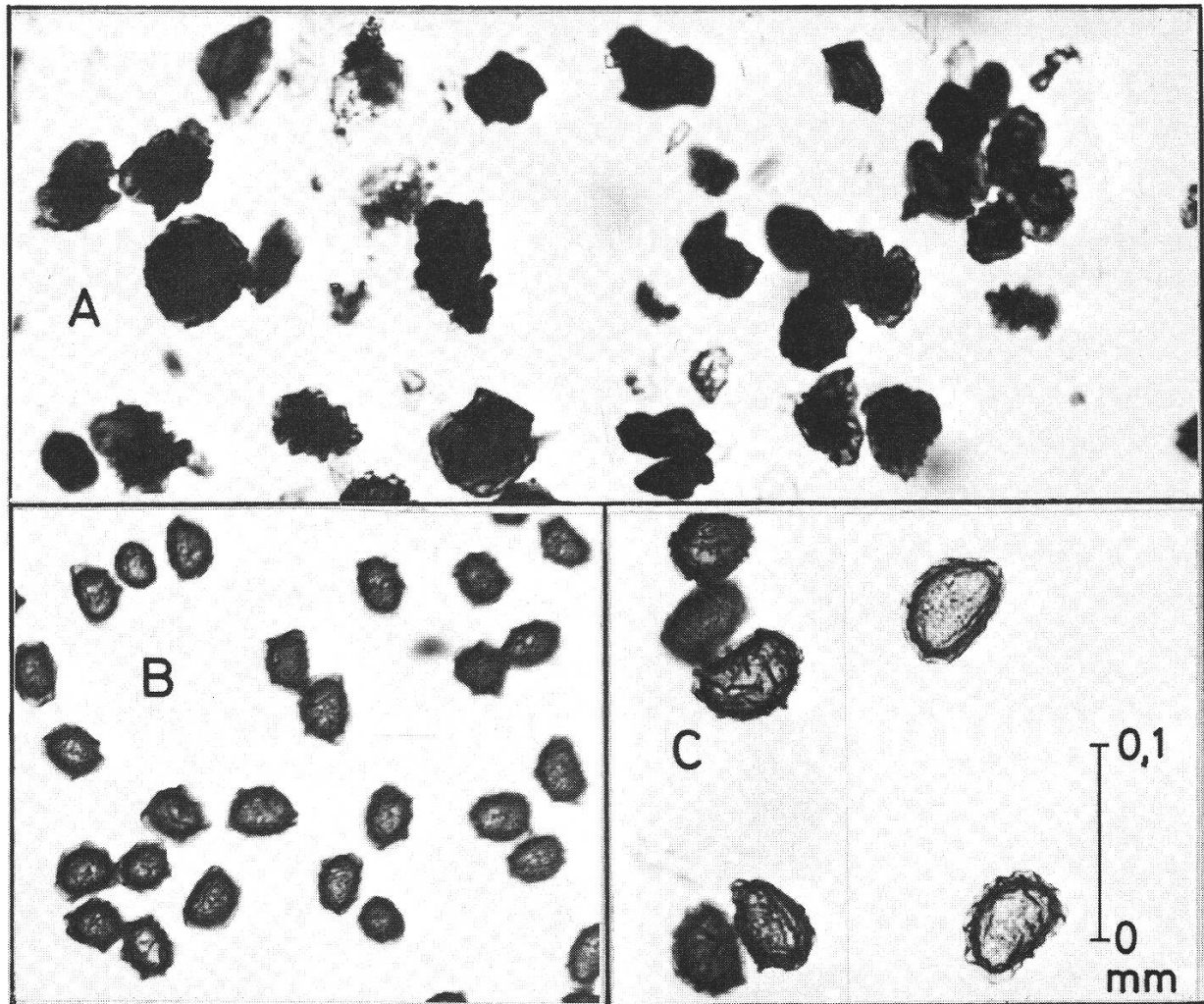


Fig. 1. Sporangial content of a typical hybrid and its parent species

A = *A. × alternifolium* (TrSpSp), Switzerland, Ct. Ticino, gneiss wall without mortar above Agarone (between Bellinzona and Locarno), c. 400 m alt. 26.7.1978. TR-4723A.

B = *A. trichomanes* (2x) (TrTr), from the same locality, 22.8.1977. TR-4415.

C = *A. septentrionale* (4x) (SpSpSpSp), Switzerland, Ct. Ticino, gneiss wall without mortar, at Convento Bigorio, above Tesserete.

for study for many years after. It can, of course, be transferred to a small piece of «pergamine» paper which should be folded and put in a small plastic bag. After labelling, it is best mounted on the same sheet as the pressed fronds. Never keep sporangial content directly in plastic bags. For microscopic inspection a small amount of the powder is mounted in a drop of balsam, lightly pressed with a cover glass, labelled, and best kept as a permanent preparation for reference purposes. Fig. 1 shows the sporangial content of *A. × alternifolium* and its parents.

Spores can often be checked even in very old herbarium specimens, if these have neither been handled too often nor the sporangia attached to the sheet with paste. Such samples may also be contaminated with foreign spores and then no reliable conclusions are possible.

5. Genome formulae as an abbreviation for explaining behaviour at meiosis

In the nucleus of each cell of its sporophyte a diploid *Asplenium* species contains 72 chromosomes: these consist of two homologous (essentially equal) sets (genomes). The 36 chromosomes within each set are different from one another (or nearly so). If, for example, we designate one genome of the diploid *A. cuneifolium* Viv. as (Cu), the sporophyte will have the formula (CuCu). During meiosis each of the 36 chromosomes of one genome finds its partner (homologue) of the other genome to form a pair (or bivalent), giving 36 regular pairs (formulated as 36^{II}), which is the picture of a good diploid species. After chromosome separation two haploid nuclei are formed which after a further mitotic division yield four haploid spores. Each of these contains one genome only and may be designated (Cu). After germination these yield haploid gametophytes (also Cu), which produce haploid gametes (Cu). Fusion of two gametes (Cu)+(Cu) yields the diploid zygote (CuCu) and from this the new diploid sporophyte (CuCu) arises.

Similar genome formulae can be attributed to tetraploid species which contain in their sporophytes four genomes, at least two pairs of equal ones, in the case of *Asplenium* (of 36 chromosomes each). *A. adiantum-nigrum* L. (an allotetraploid) will be given the genome formula (CuCuOnOn) in which (Cu) is again one genome of *A. cuneifolium* (one of the two ancestors of *A. adiantum-nigrum*) and (On) one genome of *A. onopteris* L. (the other ancestor of this species, see Shivas 1969). The spores, gametophytes and gametes of *A. adiantum-nigrum* will have the formula (CuOn). Fusion of two of these gametes will give rise to a zygote (CuCuOnOn) from which a sporophyte of similar constitution arises.

6. Diploid hybrids and formation of allopolyploids

As an example, let us take the diploid hybrid of *A. cuneifolium* (CuCu) and *A. onopteris* (OnOn). It will be formed by fusion of one gamete (Cu) with one gamete (On) and the sporophyte of the hybrid *A. cuneifolium* × *onopteris* will therefore have the genome formula (CuOn). During meiosis in this hybrid none (or hardly any) of the 36 chromosomes of the (Cu) genome will find a homologue within the 36 chromosomes of the (On) genome and up to the maximum of 72 univalents will be observed, with no (or very few) pairs. This is the typical picture in such hybrids. Normal further division is not possible; instead of four good spores, only abortive material is produced. This is what happens in the majority of cases and, if no other process takes place, such hybrids are completely sterile.

6.1. Formation of allopolyploids by chromosome doubling.— Chromosome doubling can in principle occur at different stages, in the sporophyte or in the gametophyte. A process which seems to be relatively important is the formation of restitution nuclei during meiosis. In the case of *A. cuneifolium* × *onopteris* the chromosomes (CuOn) in a few mother cells of the hybrid may not separate, but may stay together, forming a restitution nucleus (CuOn); after a mitotic division this produces two diplospores (occasionally visible among much abortive material under the microscope). Such diplospores after germination can give rise to diploid gametophytes (CuOn), gametes (CuOn) and after normal fertilization (CuOn) + (CuOn), to an allotetraploid zygote and sporophyte (CuCuOnOn). According to Shivas (1969), this is the genome formula of allotetraploid *A. adi-*

antum-nigrum and this species must once have been formed from the diploid hybrid in this way or by some equivalent process, although it has not yet been obtained under experimental conditions.

Like all allopolyploids, *A. adiantum-nigrum* (CuCuOnOn), although of hybrid origin, is again fully fertile, because two sets of homologous genomes (CuCuOnOn) capable of pairing regularly at meiosis are now present. Good spores with the constitution (CuOn) can be produced and such an allotetraploid behaves as a normal species.

7. Proof for allopolyploid status and recognition of ancestors

The proof that a fern is allo- (not auto-) polyploid, and recognition of its ancestors, in principle require three steps. Again hybrids are essential for such work. Let us again take *A. adiantum-nigrum* as an example.

7.1. *Crossing with an unrelated species.*— When *A. adiantum-nigrum* (CuCuOnOn) is crossed with diploid *Phyllitis scolopendrium* (ScSc), fusion of one gamete (CuOn) with one gamete (Sc) yields the triploid hybrid (CuOnSc). At meiosis this produces only univalents (Lovis & Vida 1969) showing that no homologous genomes are present. Instead of the diploid *Phyllitis*, a cross with an unrelated allotetraploid of known ancestry could be examined, e.g. *A. forsiense* (FoFoObOb) in which (Fo) stands for one genome of *A. fontanum* and (Ob) for one genome of *A. obovatum* (Sleep 1966, c. 1982). The tetraploid cross has the genome formula (CuOnFoOb) and again produces only univalents at meiosis, thus confirming that the two species crossed do not contain any homologous genomes.

7.2. *Backcrossing with ancestors.*— The triploid hybrids *A. adiantum-nigrum* × *cuneifolium* (CuCuOn) and *A. adiantum-nigrum* × *onopteris* (CuOnOn) have both been produced by Shivas (1969) under experimental conditions and are also known to occur in nature. Both produce c. 36^{II} and 36^I at meiosis, showing that each contains two homologous genomes (CuCuOn) and (CuOnOn.) *A. cuneifolium* and *A. onopteris* must therefore be the ancestors of the allotetraploid *A. adiantum-nigrum*.

In similar ways the allopolyploid status and the ancestors of many other European *Asplenium* species have been established following the pioneering work of Manton (1950) and her students.

8. Autopolyploids

Autopolyploidy is relatively common in European Aspleniaceae (Lovis 1964; Vida 1965 etc.). The following species have been found to possess this status: *A. billotii* F.W. Schultz (Sleep 1966; c. 1982; Girard & Lovis 1968; Lovis & Vida 1969; Lovis, Brownsey, Sleep & Shivas 1972), *A. petrarchae* (Guérin) DC. (Meyer 1964a; Sleep 1966; c. 1982; Lovis, Sleep & Reichstein 1969), *A. ruta-muraria* L. (Lovis 1964; Vida 1970; Bouharmont 1972a, 1977a, b), *A. trichomanes* (Manton 1950; Meyer 1962; Lovis 1964), *A. septentrionale* (Lovis 1964; Vida 1970; Bouharmont 1973), *Ceterach officinarum* DC. (Vida 1963; Meyer 1964a).

8.1. *Recognition of autotetraploids.*— If diploid and tetraploid representatives of a fern are morphologically hardly distinguishable, the tetraploid can be suspected to be

of autotetraploid origin. This was first observed in *A. trichomanes* by Manton (1950: 105-107). The cytological proof for the fact that both *A. ruta-muraria* (4×) and *A. septentrionale* (4×) are of essentially autopolyploid origin was first demonstrated by Lovis (1964a) when examining the tetraploid hybrid *A. × murbeckii* Dörfler = *A. ruta-muraria* × *septentrionale*. He found that this hybrid produces mainly pairs in meiosis, in some cells up to the theoretically possible maximum of 72 pairs (when all 144 chromosomes have paired). This is only possible if both parents are essentially autotetraploids and the hybrid has the formula (RuRuSeSe). A similar example was discovered by Sleep (1966) when she found experimentally produced tetraploid hybrids of *A. billotii* × *petrarchae* to behave in a similar way (with very many pairs in meiosis). She concluded that both parents must be autotetraploid and thus the hybrid must be given the formula (BiBiPePe).

A more general method is to cross the tetraploid with an unrelated species. Taking the tetraploid *A. septentrionale* as an example, we may attribute it the genome formula (SpSp SpSp) or perhaps more correctly (SpSpSp'Sp') in which Sp and Sp' are predominantly but not always completely homologous. This is based on the assumption that it is an autotetraploid species, once arisen by chromosome doubling from the diploid *A. septentrionale* ssp. *caucasicum* Fraser-Jenkins & Lovis, which is morphologically very close to the tetraploid. If we cross this tetraploid *A. septentrionale* with diploid *A. trichomanes* ssp. *trichomanes* (TrTr) which, for morphological reasons, may be assumed to be unrelated (i.e. not representing one ancestor of tetraploid *A. septentrionale*), we arrive, by fusion of one gamete (SpSp) with one gamete (Tr), at the well known triploid hybrid *A. × alternifolium* Wulfen (Manton 1950; Meyer 1952) which shows c. 36^{II} + 36^I at meiosis (Manton 1950: 104; Lovis & Shivas 1954; Bouharmont 1966, fig. 31-A). The 36 pairs (or sometimes a few less) are explained as a result of chromosome pairing between the two Sp genomes (autosyndesis). The fact that the total number of pairs (it is not always possible to determine them precisely) is often a little less than 36, is taken as evidence that not all Sp genomes of *A. septentrionale* are fully homologous and that there is a small difference between Sp and Sp', probably produced by divergence during the long period since the tetraploid *A. septentrionale* arose by chromosome doubling from its diploid ancestor.

The great morphological difference between *A. trichomanes* and *A. septentrionale* alone is not a complete proof that the two species are really genomically unrelated (i.e. have no common ancestor). To make the proof quite conclusive, it would be necessary to cross the tetraploid *A. septentrionale* with two more species and obtain three different hybrids showing c. 36^{II}, because an allotetraploid cannot have more than two ancestors. This meets with practical difficulties as such crosses are often hard to obtain. In the particular case of *A. septentrionale*, the natural hybrids with *A. adiantum-nigrum* and with *A. forisiense* Le Grand (Callé et al. 1975) provided such proof, as both species were known to be allotetraploids of established parentage and neither having *A. septentrionale* as an ancestor.

8.2. *Induced apogamy*.— Proof for allo- versus autopolyploidy can sometimes be obtained by experimental haploidization through induced apogamy (Lang 1898; Manton 1950: 196; Manton & Walker 1954). When prothallia are kept growing for a long time and fertilization is prevented by the exclusion of liquid water, apogamously produced sporophytes may result. If derived from an allotetraploid parent, they will show practically no pairing at meiosis, while some or many pairs will result in plants («dihaploids», TrTr', RuRu' and SpSp') obtained in this way from autotetraploid *A. trichomanes* (TrTrTr'Tr'), *A. ruta-muraria* (RuRuRu'Ru') and *A. septentrionale* (SpSpSp'Sp') (Bouharmont 1968, 1972a, 1973).

8.3. *Formation of tri- and tetravalents at meiosis.*— In some cases, autotetraploids can be recognized when they are crossed with their corresponding diploid cytotypes or with allotetraploids containing a pair of homologous genomes. Such crosses possess in their nuclei three homologous genomes and often show formation of trivalents (sometimes even a few tetravalents) at meiosis, detectable by careful analysis.

Formation of trivalents is particularly pronounced in hybrids containing three genomes of *A. ruta-muraria* but is also observed in \pm decreasing order in analogous derivatives of *A. petrarchae*, *A. septentrionale* and the *A. billotii*-*A. obovatum* complex (*A. billotii* may be an essentially autotetraploid *A. obovatum*). This is illustrated in the following examples.

The triploid *A. × baldensis* (= *A. ruta-muraria* ssp. *ruta-muraria* \times ssp. *dolomiticum*) (RuRuRu') produces a very high number of trivalents at meiosis (Vida 1965, 1970; Lovis unpubl.; see also Appendix I) and occasionally some tetravalents may be detected. The same was observed in the tetraploid hybrid *A. × javorkae* (= *A. lepidum* \times *ruta-muraria* ssp. *ruta-muraria*) (AeRuRuRu'). Irregular meiosis with formation of tri- and tetravalents has even been observed in *some*, otherwise normal, plants of tetraploid *A. ruta-muraria* (Vida 1970). Such behaviour is, however, a remarkable exception in autotetraploid ferns.

A significant number of trivalents was found in the experimentally produced triploid *A. petrarchae* ssp. *bivalens* \times ssp. *petrarchae* (PePePe') (Lovis unpubl.) and a range of c. 12-15 trivalents was reported for the tetraploid *A. × sollerense* (= *A. majoricum* \times *petrarchae* ssp. *petrarchae*) (FoPePePe') (Lovis, Sleep & Reichstein 1969). About 8-10 trivalents were found in the experimentally produced triploid *A. septentrionale* ssp. *caucasica* \times ssp. *septentrionale* (SpSpSp') and a similar order in the experimentally produced tetraploid hybrid of *A. × murbeckii* \times *septentrionale* (RuSpSpSp') (Lovis unpubl. see 10.5.) and in the corresponding natural *A. × hungaricum* (see Appendix I). A few trivalents were observed in the triploid *A. × cyrnosardoum* (= *A. billotii* \times *obovatum*) (BiBiOb or ObObOb', if *A. billotii* is an autotetraploid *A. obovatum*) (see Appendix I) and a range of c. 12-15 trivalents was reported for the experimentally produced hybrid of *A. billotii* \times *forisiense* (BiBiFoOb or FoObObOb', if *A. billotii* is an autotetraploid *A. obovatum*) (Sleep c. 1982).

Formation of trivalents in hybrids with three homologous genomes is, however, not a general rule in *Asplenium*. The triploid *A. trichomanes* *A. × lusaticum* (TrTrTr') produces c. 36^{II} and 36^I at meiosis (Bouharmont 1968) and *A. × praetermissum* the tetraploid hybrid of *A. adulterinum* \times *trichomanes* ssp. *quadrivalens* (TrTrTr'Vi) gives c. 36^{II} and 72^I (see Appendix I). A similar behaviour is observed in hybrids with three homologous genomes of other species, showing that a mechanism is at work which prevents the formation of tri- or tetravalent chromosomes at meiosis.

The status of most European *Asplenium* species is known today, see list (12.2.).

9. Nomenclature of hybrids

Most workers prefer to assign binomials to fern hybrids and cite the putative (or established) parents as additional interpretation; others prefer to name only the parents. The first method is followed here. The advantage of a binomial is that the name can remain unchanged even if later the attribution of putative parents turns out to be wrong. We give the following hybrid as an example with its status corresponding to present-day knowledge.

Asplenium × *alternifolium* Wulfen (in Jacquin 1781) = *A. septentrionale* (L.) Hoffm. ssp. *septentrionale* × *A. trichomanes* L. ssp. *trichomanes* = (SpSpTr). Old synonyms: *A. × germanicum* Weiss (nom. inval.); *A. × breynii* Retz., and some others.

Much has been written about this plant (Luerssen 1889: 238-250; Guétrot 1926; Becherer 1929; Manton 1950: 100-106, and others). It is one of the most conspicuous and most common *Asplenium* hybrids. Collected for the first time in 1664 and described, with figure, by Jacob Breyn (1678), it has for a long time been taken for a species. Bory de Saint-Vincent (1821, 1837) was probably the first to suspect that it might be a hybrid, and he assumed it to be *A. ruta-muraria* × *septentrionale*. This interpretation was accepted by some workers including Heufler (1856: 287-300), who gave extensive comments, but Milde (1867: 82-83) rejected the idea of its hybrid origin. The correct interpretation as *A. trichomanes* × *septentrionale* (without further details) was given by Ascherson (1864: 916) and independently by Abbé Chaboisson in Loret (1866). But even Christ (1900: 93-97) assumed it to be a species of hybrid origin, which is able to reproduce by spores and to produce backcrosses with *A. trichomanes* and *A. septentrionale*, and this was also accepted by Rouy (1913: 450). The last detail about parentage (participation of the diploid cytotype of *A. trichomanes*) was contributed by Manton (1950: 100-106) by means of cytological methods and confirmed by Meyer (1952), who also synthesized the hybrid under experimental conditions. Synthesis had already been claimed by Kestner (1935, but no voucher exists) and was reported, including results at meiosis, by Lovis & Shivas (1954).

10. Fertility of fern hybrids

There has been much speculation about sterility and fertility of fern hybrids, and wrong interpretations of observations in the field have since been put right by the use of experimental methods.

In flowering plants F_1 hybrids between two species are sometimes fertile, i.e., able to produce viable seeds and progeny, which may show segregation of characters (see Stace 1975: 38-53 and other chapters). Such behaviour has rarely been observed in ferns but T. G. Walker (1958, see also 1960, 1962) reported a most remarkable case for *Pteris multiaurita* Ag. and *P. quadriaurita* Retz. These two morphologically rather distinct diploid species form fully fertile hybrid swarms, including backcrosses, with an uninterrupted range of forms with intermediate morphology. Analogous behaviour may be expected in hybrids between closely related species where introgression has been suspected as, for example, in the appropriate cytotypes of *Cystopteris fragilis* (L.) Bernh. and *C. diaphana* (Bory) Blasdell (1963: 47-48); also according to Brownsey (1976a, b) in *Asplenium haussknechtii* Godet et Reuter and *A. lepidum* Presl. Most of the other European fern hybrids are either completely sterile (as far as has actually been checked) or possess very low fertility. An exception are some hybrids that include one apomictic ancestor (see below). Each case may behave in a different way and has to be specially examined, but some groups show particular behaviour, as will be reported in the following chapters.

10.1. Hybrids between sexually reproducing fern species.— Most of the known natural or experimentally produced hybrids of this type are highly or completely sterile. An irregular meiosis and a high proportion of abortive spores may be found even in some hybrids between two subspecies of the same complex, provided they have the same ploidy,

e.g. *A. trichomanes* ssp. *pachyrachis* Lovis & Reichstein \times *quadrivalens*. But this hybrid probably produces some progeny (proof lacking as yet).

As an example for a fern hybrid which is probably completely sterile we quote again the triploid *A. \times alternifolium* (SpSpTr). As mentioned (sub 9), this plant had for a long time been assumed to multiply by means of spores and to produce backcrosses with its parents. Claims that it could be found growing in places where either one or both its parents were missing could not be confirmed (Meyer 1952 and others). Repeated experiments by the present author with sowings of sporangial content resulted either in no growth at all or in a few prothallia which afterwards invariably turned out to be weeds (*Dryopteris*, *Cystopteris*, *A. adiantum-nigrum*, etc.) arising from contamination with foreign spores. This is nearly impossible to avoid completely in fronds collected in the field, even under careful conditions. We cannot exclude completely that *A. \times alternifolium* is able to produce a few viable spores by some as yet unknown process, but we may safely assume that under natural conditions each plant represents an F₁ generation and was formed *de novo* where it grows.

10.2. Diploid hybrids, formation of diplospores and allotetraploids.— As mentioned above (unter 6), diploid hybrids may be able to produce some diplospores, which can germinate to give rise to fully fertile allotetraploids. This is obviously one mode of chromosome doubling occurring in nature. Under experimental conditions it was first observed by Wagner & Whitmire (1957), then by Lovis & Reichstein (1968), Lovis (1968, 1970); it is also known in other cases (TR unpubl.). There is great variation in the ability of particular diploid species to form hybrids and in the potential of such hybrids for subsequent chromosome doubling. The diploid hybrid *Asplenium \times woynarianum* Ascherson & Graebner = *A. cuneifolium* \times *viride* (CuVi), which can occasionally be found in Austria, seems to produce only abortive spore material. No diplospores could be detected in the sporangia, and repeated sowings of such material gave no progeny (TR unpubl.). *A. \times protoadulterium* Lovis & Reichstein (1968) = *A. trichomanes* ssp. *trichomanes* \times *viride* (TrVi), a diploid hybrid which obviously forms with great difficulty, and found so far only twice in nature, produces abundant diplospores (up to 10 per sporangium, doubling proceeds with great ease), and sowing has always yielded a considerable quantity of tetraploid progeny which was indistinguishable from natural *A. adulterinum* Milde. The diploid hybrid *A. fontanum* (L.) Bernh. \times *A. petrarchae* ssp. *bivalens* (Meyer) Lovis & Reichstein (FoPe) has so far only been synthesized under experimental conditions (Lovis unpubl.); it spontaneously produced some diplospores which yielded the allotetraploid *A. majoricum* Litard. (FoFoPePe) (Lovis unpubl.). Another diploid hybrid, *A. gastonii-gautieri* Litard. = *A. fontanum* \times *viride* (FoVi), is known in the wild, and was experimentally synthesized by Lovis (1970). This doubled its chromosomes, producing fertile allotetraploid progeny (FoFoViVi), which, although growing well in cultivation, have so far never been found in nature. A similar case is *A. \times lessinense* Vida & Reichstein = *A. fissum* \times *viride* (FiVi) which occurs in nature and which, under experimental conditions, also produced some fertile allotetraploid progeny (FiFiViVi) growing vigorously in cultivation. But again this allotetraploid has never been encountered in nature. The other extreme was observed in European *Polystichum*. The rare diploid *P. \times lonchitiforme* (Halácsy) Becherer = *P. lonchitis* (L.) Roth \times *P. setiferum* (Forskål) Woynar (LoSe) can be obtained under experimental conditions with great ease (Sleep 1966), but it doubles its chromosomes with much difficulty. Repeated sowings of sporangial content always gave some prothallia, but these grew rather slowly and produced only a few sporophytes. They were tetraploid (LoLoSeSe) and indistinguishable from *P. aculeatum* (L.) Roth

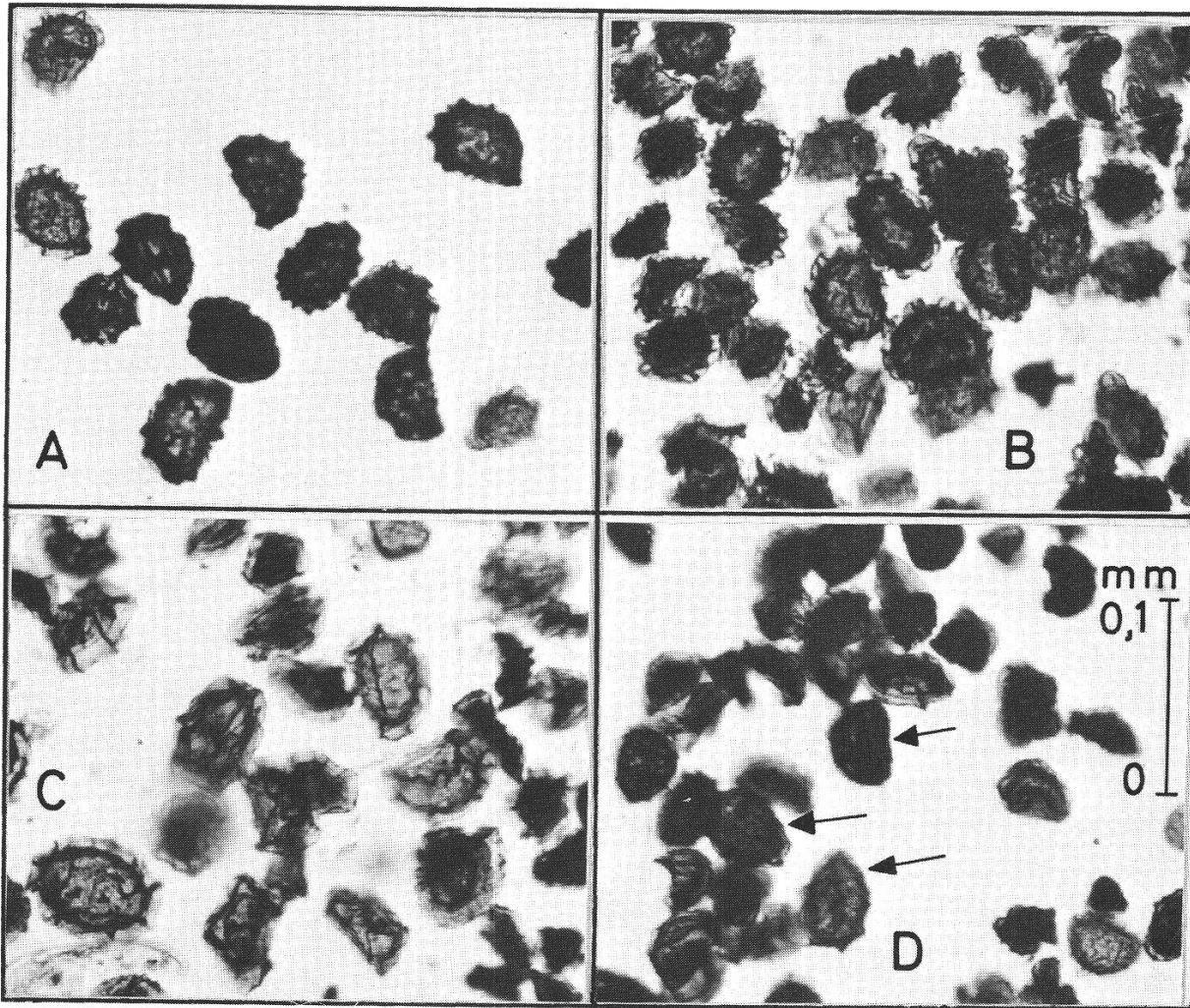


Fig. 2. Sporangial content of four delayed allotetraploids showing some good viable spores. For comparison see fig. 3 of *A. × dolosum* (triploid hybrid, sterile).

A = *A. × murbeckii* (RuRu'SpSp'), Switzerland, Ct. Ticino, gneiss wall at Convento Bigorio above Tesserete, c. 720m alt., 19.8.1960, leg. H.L. and T. Reichstein. TR-263. Showing many good spores.

B = *A. × clermontae* (RuRu'TrTr'). Austria, leg. Melzer, 1.3.1964. TR-1073, see Appendix II.

C = *A. × souchei* (BiBi'SpSp'). From *locus classicus*. TR-2248, see Callé et al. (1975).

D = *A. × heufleri* (TrTr'SpSp'). Northern Italy. TR-594, see Appendix II.

(TR unpubl.). The more vigorous natural hybrid from Scotland gave a slightly higher yield (Sleep, unpubl.).

10.3. *Triploid hybrids of sexually reproducing species.*— In *Asplenium* such hybrids as *A. × alternifolium* (see 9 and 10.1.) are probably all sterile, but so far only a few have been checked by experimental methods. In other genera different conditions may prevail. In *Polystichum* the case of *P. × illyricum* (Borbás) Hahne = *P. aculeatum* × *lonchitis* has been reported (Vida & Reichstein 1975). This triploid hybrid, as mentioned above (10.2.), is a backcross of the allotetraploid *P. aculeatum* (LoLoSeSe) with one of its ancestors. It is formed by fusion of one gamete (LoSe) with one gamete (Lo) and can be assigned the formula (LoLoSe). The sporangia of this hybrid contain mainly abortive material, but some good spores, probably diplospores (LoLoSe), are always present.

Sowing of such material always gave a considerable number of prothallia (probably triploid LoLoSe) and, after sufficient time, a number of sporophytes. Some were hexaploid (probably by sexual reproduction, i.e. fusion of LoLoSe + LoLoSe) and some (more vigorous ones) triploid (LoLoSe), probably produced apomictically without fertilization. Most of these triploid plants agreed well with *P. × illyricum* in morphology, but there was segregation. Some were hardly distinguishable from *P. × aculeatum*, but were nevertheless triploid and produced abortive spores. Some other triploid *Polystichum* hybrids are able to reproduce in a similar way, again to a very limited degree (TR unpubl. and also T. Pintér et G. Vida unpubl., personal communication). In Europe this process can hardly be expected to be successful in wild plants and triploid *Polystichum* hybrids are probably always (or nearly always) formed *de novo* at the place where they grow. No wild hexaploid progeny has so far been observed in Europe. But such hexaploid plants behaving like a species and assigned to *P. setigerum* (C. Presl) C. Presl have been reported from North America by D. Wagner (1979: 27, 53).

No analogous case has hitherto been observed in *Asplenium* for interspecific triploid hybrids, but intraspecific *Asplenium* hybrids obviously do sometimes produce fertile hexaploid progeny. As reported by Bouharmont (1968), the triploid hybrid *A. trichomanes* ssp. *trichomaes* × ssp. *quadrivalens*, to which we can attribute the formula (TrTrTr), may produce a few fertile hexaploid plants (TrTrTrTrTrTr). Such hexaploids have been found in the wild first in New Zealand (Brownlie 1954), and Australia (Lovis 1977: 369), but have since been located also in Belgium and France (Bouharmont 1968). The hexaploid taxon from Madeira (Lovis 1977: 369) is probably of different parentage.

10.4. Apomicts and their hybrids.— Some ferns reproducing from spores by an apomictic process (i.e., without fertilization) usually do not produce any archegonia on their gametophytes, although they bear functional antheridia. The spermatozoids, although of no significance in reproduction of the species, are capable of hybridization with sexual species. This is best known in some hybrids of *Dryopteris*, viz. *D. × tavelii* Rothmaler = ♀ *D. filix-mas* (L.) Schott × ♂ *D. affinis* (Lowe) Fraser-Jenkins (Döpp 1939, 1950), 1955, 1967; Manton 1950: 55-61, 185-195; Lovis 1977: 387). Tetraploid and pentaploid cytotypes of *D. × tavelii* are known, formed respectively from diploid or triploid *D. affinis*. These hybrids have inherited the apomictic way of reproduction from their male parent and can in cultivation be readily propagated from spores. Nevertheless, the production of good spores is relatively low (only c. 5-10% of the total output). In the field *D. × tavelii* has little chance to reproduce, and most wild plants are F₁ crosses. Reports of wild populations of *D. × tavelii* in places without both their parents are, as far as could be checked, based on misidentifications (confusion with triploid *D. affinis*).

Apomicts are also known in *Asplenium* but only one species, *A. monanthes* L., occurs in Europa (Azores). No hybrids of this species are known.

10.5. Delayed allopolyploidy (Lovis 1977: 365-371).— Hybrids between two autotetraploid species, like *Asplenium × murbeckii* Dörfler = *A. ruta-muraria* ssp. *ruta-muraria* × *A. septentrionale* ssp. *septentrionale*, show a remarkable peculiarity and can sometimes actually multiply from spores. The genome formula of *A. × murbeckii* is (RuRu SpSp), or more precisely (RuRu'SpSp') where Ru and Ru' as well as Sp and Sp' are predominantly, but not completely, homologous. This is very similar to the formula of an allotetraploid in the strict sense. Such a true allotetraploid would result from chromosome doubling of a diploid hybrid (RuSp) formed from *A. ruta-muraria* ssp. *dolomiticum* (RuRu) and *A. septentrionale* ssp. *caucasicum* (SpSp), which is, however, not known. The

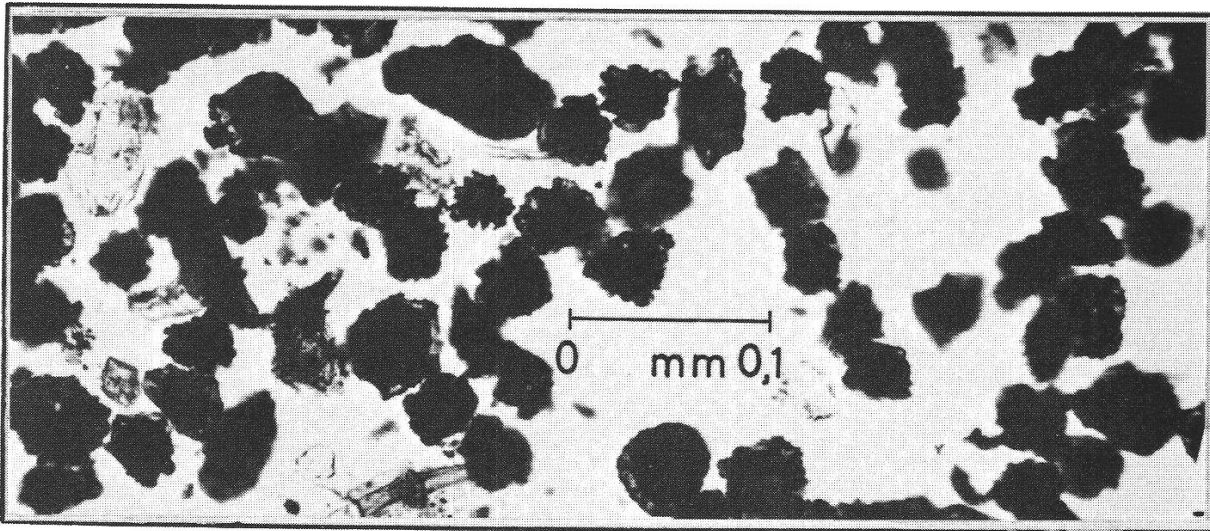


Fig. 3. Sporangial content of *A. × dolosum* (CuOnTr). TR-3324 (see Appendix II). Only abortive material.

true allotetraploid (RuRuSpSp) of this origin would be expected to produce good spores and show full pairing at meiosis. Both natural and experimentally produced plants of *A. × murbeckii* only partly approach this condition. Some cells actually show full pairing at meiosis, while others produce some univalents (Lovis 1963, 1964a; Bouharmont 1972), the sporangia normally contain much abortive material, but some good spores are usually visible and sowing resulted in some sporophytes (Lovis & Reichstein unpubl., see Lovis 1977: 363). The resulting plants corresponded well to the parent *A. × murbeckii* in general morphology, but showed some segregation, some plants being more similar to *A. ruta-muraria*, others to *A. septentrionale*. The entire F₂ generation showed a similar picture at meiosis with very many, sometimes all, the chromosomes paired. There can therefore be no question that *A. × murbeckii* is a hybrid which is able to multiply from spores but, as far as could be observed, this happens only in exceptional cases in nature. Most specimens of this rare hybrid are found as single plants, always among the parents. A rare exception are the 4 or 5 colonies found by the Nieschalks (1961) in Hessen (Germany) where they showed us groups of 5-20 hybrids in relative proximity to each other.

Lovis (unpubl.) was also able to produce backcrosses of *A. × murbeckii* with both parents that showed the expected morphology. The hybrid with *A. septentrionale*, with the formula (RuSpSpSp) gave some trivalents in meiosis, two cells showed in first analysis $10^{III} + 27^{II} + 59^I$ and $8^{III} + 32^{II} + 54^I$, whereas in the hybrid with *A. ruta-muraria* with the genome formula (RuRuRuSp) the number of trivalents was still higher. This is in agreement with other hybrids containing three Ru genomes. It is of great interest that Fraser-Jenkins & Vida found a wild backcross, *A. × murbeckii × septentrionale*, in Hungary that showed the correct morphology and also c. 6–13 trivalents at meiosis (see description sub *A. × hungaricum* in Appendix I). This is the first case of a natural backcross in a fern hybrid, with the exception of the *Pteris* examined by T. G. Walker 1958 and perhaps the hybrids between some very closely related species which show introgression (see above sub 10). All other such backcrosses involving *Asplenium* hybrids reported in older literature must be regarded as non-existent.

Another natural hybrid behaving as a delayed allotetraploid is the very rare *A. × clermontae* Syme = *A. ruta-muraria* ssp. *ruta-muraria* × *A. trichomanes* ssp. *quadrivalens*, to which we may assign the genome formula (RuRu'TrTr'). It again shows very high, in some cells complete, pairing at meiosis; the sporangia contain much abortive material but also some well-formed viable spores which yielded fertile progeny with the correct morphology and cytology (Lovis & Reichstein unpubl.) No attempts to produce further crosses of this hybrid were undertaken.

Further natural hybrids with an analogous genomic constitution are *A. × heufleri* Reichardt = *A. trichomanes* ssp. *quadrivalens* × *A. septentrionale* ssp. *septentrionale* with the formula (TrTr'SpSp'), *A. × nieschalkii* D.E. Meyer = *A. petrarchae* (Guérin) DC. × *A. trichomanes* ssp. *quadrivalens* with the formula (PePe'TrTr'), *A. × souchei* Lit. = *A. billotii* F. W. Schultz × *A. septentrionale* ssp. *septentrionale* with the formula (BiBi'SpSp'), and × *Asplenoceterach badense* D.E. Meyer = *A. ruta-muraria* ssp. *ruta-muraria* × *Ceterach officinarum* DC. ssp. *officinarum* with the formula (RuRu'CeCe'). All four hybrids produced some apparently good spores, and two of them (× *Asplenoceterach* was not studied) gave a very high number of bivalents at meiosis. Experimental raising of progeny has been done only for *A. × heufleri* and one sporophyte was obtained (Lovis unpubl.) But the experimentally produced hybrid *A. billotii* × *A. petrarchae* ssp. *petrarchae* (Sleep 1966), with the genome formula (BiBi'PePe'), showed a very high number of bivalents at meiosis (Sleep 1966, c. 1982) and its spores after sowing produced some sporophytes with the correct morphology and cytology (unpubl.).

Summarizing one may say that hybrids between two autotetraploid *Asplenium* species (= products of delayed allopolyploidy) often show a low degree of real fertility, but that, contrary to true allotetraploids, this will allow them only in a few extreme cases to spread in the field.

11. Checklist of European species of Aspleniaceae

With brief indication of type, distribution, ploidy, and genome formula (as far as known). For the distribution in Europe see Jalas & Suominen (1972). «Serpentines» is used in the wide sense, i.e. including other ultrabasic rocks. For abbreviations of the genomes see under the diploid species. Diploid: $n = 36$, $2n = 72$; tetraploid: $n = 72$, $2n = 144$.

11.1. Remark on nomenclature.— *Asplenium*, *Ceterach*, *Phyllitis* and *Pleurosorus* are treated here as separate genera. Within each genus the species are arranged in alphabetical order. As far as possible the names given by Crabbe, Jermy & Lovis (1964) in *Flora Europaea* are used.

Cytotypes of aggregate species containing both diploid and polyploid representatives of essentially autopolyploid origin (like *Asplenium petrarchae*, *A. ruta-muraria*, *A. septentrionale*, *A. trichomanes*, *Ceterach officinarum*) are, for practical reasons, treated here as subspecies of the complex (see Vida 1972: 54). This allows the worker in the field to give them a valid name. Other experts (Rothmaler 1963; Löve et al. 1977) prefer to treat them as different species. I agree with Vida (1965: 166) that neither of these methods is adequate. Such cytotypes correspond neither to real species nor to subspecies in their original sense. They are genetically separated from each other in the manner of species (i.e. exchange of genes is not, or only rarely possible), but they can hardly (often not at all) be distinguished from each other in their gross morphology (characters other-

wise used for distinguishing subspecies). It is hoped that in future a decision can be taken on a new category for naming such cytotypes. The present state creates difficulties, not only for naming them correctly, but particularly in the naming of hybrids in which such cytotypes are involved (see section 12.).

11.2. *Asplenium* L.

1. *A. adiantum-nigrum* L., Sp. Pl. 1081 (1753). Descr. from southern Europe. Typification not settled. Distr. North America, Macaronesia, southern Africa, Europe, western Asia. Prefers silicate rocks. Tetrapl. Manton (1950). Allotetrapl. (CuCuOnOn), Shivas (1969). Lovis & Vida (1969).

2. *A. adulterinum* Milde, Die höheren Sporenpfl. Deutschl. u.d. Schweiz 40 (1865). Descr. from northern Bohemia. Endemic to Europe. Serpentine. Tetrapl., Meyer (1952). Allotetrapl. (TrTr ViVi), Lovis (1955, 1968); Lovis & Reichstein (1968a).

3. *A. aegaeum* Lovis, Reichst. & Greuter, Ann. Mus. Goulandris 1: 141-144 (1973). Descr. from Crete, Type: BM. Also reported from Greece and Turkey. Limestone. Diploid (AeAe), Reichstein et al. (1973).

4. *A. anceps* Lowe ex Hooker et Grev., Icon. Fil. 2: t. 195 (1830-31) see Lovis et al. (1977). Descr. from Madeira, Type: BM. Endemic to Macaronesia Volcanic and silicate rocks. Diploid (AnAn), Lovis et al. (1977).

5. *A. azoricum* Lovis, Rasb., Rasb. & Reichst., Amer. Fern J. 67: 88(1977). Descr. from São Miguel. Type: BM; isotypes: G, K, P, US. Endemic to the Azores, volcanic rocks and walls. Allotetrapl. Lovis et al. (1977). (AnAn??), Reichst. & Schneller (in prep.).

6. *A. balearicum* Shivas, Brit. Fern Gaz. 10: 75(1969). Descr. from Balearic Islands (precise locality unknown). Type: BM. Known only from Type and cult. progeny. Allotetrapl. Lovis et al. (1972), (ObObOnOn), Shivas (1969); Sleep (c. 1982).

7. *A. billotii* F. W. Schultz, Fl. Pfalz 568 (1845); Flora (Regensb.) 28: 738(1845). Descr. from sandstone rocks near Steinbach, Vosges. Type not located. Distr.: Macaronesia, Atlantic to western Mediterranean Europe and northern Africa. Silicate rocks and walls. Tetrapl. Manton (1950). Autotetrapl. (BiBiBi'Bi), Sleep (1966); Lovis & Vida (1969); or (ObObOb'Ob) if *A. billotii* arose by chromosome doubling in *A. obovatum*, Sleep (c. 1982).

8. *A. bourgaei* Boiss. ex Milde, Bot. Zeitung 24: 384(1866); Fil. Eur. et Atl. 61-62(1867). Descr. from Amanus Mts., S. of Iskenderun (formerly Alexandrette), since 1939 southern Turkey, Vilayet Hatay, (formerly Syria). Type: K. Fig. see Meyer (1962). Aegaeon Islands (Rhodos, Chalki), southern Turkey, Lebanon. Outside area of Flora Europaea (1964). Limestone rocks. Diploid Lovis (unpubl.).

9. *A. creticum* Lovis, Reichst. & Zaffran, Ann. Mus. Goulandris 1: 145-148(1973). Descr. from Crete. Type: BM; isotypes: G, K, P, Z, T. Perhaps also occurring (rarely) in Turkey. Limestone. Allotetrapl. Reichstein et al. (1973), (AeAeViVi), Brownsey (1976b).

10. *A. cuneifolium* Viv., Fl. Ital. Fragm. 16 t. 18 (1808). Descr. from Mt. Ramazzo, W. of Genova. Isotype: BOLO (herb. Bertoloni), Pichi Sermolli, Webbia 33: 39-41 with fig. Europe and Turkey. Serpentine. Diploid Meyer (1952, 1957). (CuCu) Shivas (1969).

11. *A. eberlei* D.E. Meyer, Ber. Deutsch. Bot. Ges. 75: 29(1962); 80: 28-32(1967). Descr. from the Dolomites (northern Italy). Type: B. Known only from type locality. Dolomitic rock. Tetrapl. Meyer (1967). Assumed allotetrapl. (RuRuSeSe).

12. *A. fissum* Kit. ex Willd., Linné Spec. Pl. (ed. 4.) 5(1): 348(1810). Descr. from the Velebit Mts., Croatia. Types: BP, B. Endemic to s.e. Europe. Limestone. Diploid Meyer (1958a). (FiFi).

13. *A. fontanum* (L.) Bernh. in Schrader, Journ. für die Bot. 314(1799). Descr. i.a. from southern France. Type based on C. Bauhin's «*Filicula fontana minor*» (1671) in Burser's «*Hortus siccus*» XX: 38(UPS). Endemic to s.w. and central Europe. Limestone. Diploid Manton (1950); Sleep (1966). (FoFo). According to H.P. Fuchs the correct name for this taxon is *A. halleri* A. W. Roth, Tent. Fl. Germ. III: 60(1799).

14. *A. forsiense* Le Grand, Statist. Botan. Forez: 252(1873). Descr. from the vicinity of Montbrison (Dép. Loire, France). Distr. s.w. Europe. Silicates. Tetrapl. Meyer (1960b, 1961). Allotetrapl. (FoFoObOb) Sleep (1966). Synon.: *A. foresiense* Le Grand ex Sudre, Rev. Bot. XII: 29 (1894); *A. foresiacum* (Le Grand) Christ, Beitr. Kryptogamenfl. Schweiz 1(2): 84(1900).

15. *A. haussknechtii* God. et Reut. in Milde, Fil. Eur. et Atl. 78(1867). Descr. from Turkey

(near Malatya). Type: K. = *A. lepidum* C. Presl. ssp. *haussknechtii* (God. et Reut.) Brownsey (1976a: 261). Distr. e. Crete, Middle East, w. Asia. Limestone. Allotetrapl. Reichstein et al. 1973. (AeAeRuRu) Brownsey (1976a, b). Genetically very close to *A. lepidum*, with genomes almost completely homologous with those of this species.

16. *A. hemionitis* L. Sp. Pl. 1078(1753). Descr. erroneously from Italy and Spain. Type: LINN. Distr.: Macaronesia, Portugal, northern Africa. Silicates. Diploid (Lovis, unpubl.) for plant from Portugal.

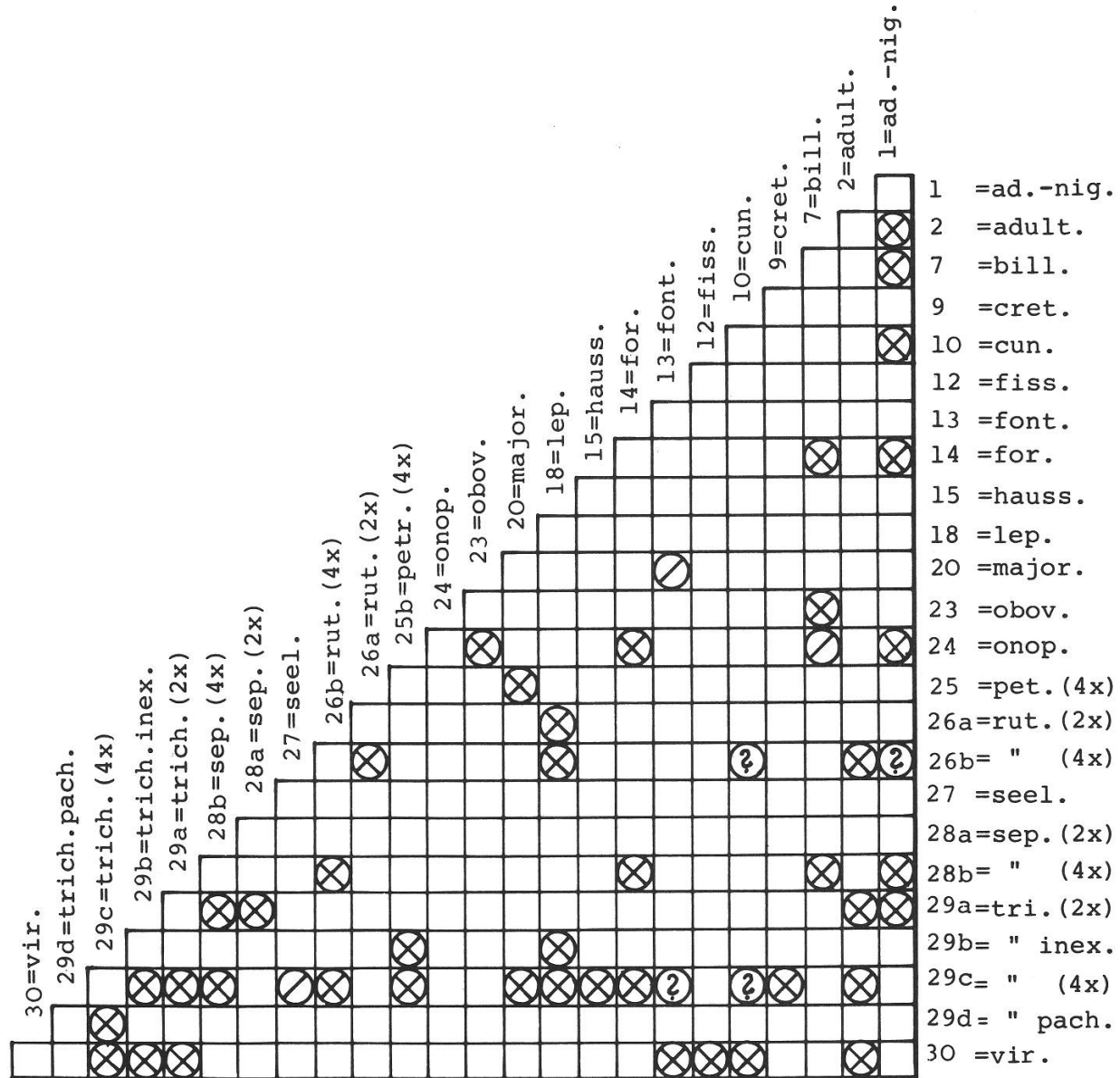


Fig. 4. *Asplenium* hybrids. The $24 \cdot (24-1) : 2$ theoretically possible crosses between 24 taxa arranged in a triangular scheme according to Meyer (1960a). The following species are not included because no natural hybrids of them are known as yet: 3 = *A. aegaeum*, 4 = *A. anceps*, 5 = *A. azoricum*, 6 = *A. balearicum*, 8 = *A. bourgaei*, 11 = *A. eberlei*, 16 = *A. hemionitis*, 17 = *A. jahandiezii*, 18 = *A. macedonicum*, 21 = *A. marinum*, 22 = *A. monanthes*, 25a = *A. petrarchae* (2x), 27b = *A. seelosii* ssp. *glabrum*.

- ⊗ = natural hybrid with checked cytology, total 43.
- ⊘ = putative natural hybrid, cytology not checked, total 3.
- ⊙ = doubtful reports, total 4.

17. *A. jahandiezii* (Litard.) Rouy, Fl. Fr. 14: 437(1913). Descr. from Gorge du Verdon, France (Dép. Basses-Alpes). Endemic to this region. Limestone. Diploid Meyer (1960b, 1961).
18. *A. lepidum* C. Presl, Verh. Ges. Vaterl. Mus. Böhm. 1836: 63. Descr. erroneously from Bohemia (origin probably southern Italy). Type: PR. Distr. France (rare), s.e. Europe. Limestone and dolomitic rocks. Tetrapl. Meyer (1969). Allotetrapl. Lovis, Melzer & Reichstein (1966); Vida (1969), (AeAeRuRu) Brownsey (1976a, b). Its genomes are highly homologous to those of *A. haussknechtii*.
19. *A. macedonicum* Kümmerle, Bot., Közl. 15: 145(1916) = *A. bornmülleri* Kümmerle, Bot. Közl. 19: 81(1921). Descr. from surroundings of Prilep, Macedonia (southern Yugoslavia). Endemic to this region. (Type originally in BP, disappeared during the war (1939-1945). Allotetrapl. Emmott (1964); (FoFoObOb). Sleep (1966, 1967). Its genomes are homologous with those of *A. forisiense*, Sleep (1966).
20. *A. majoricum* Litard., Bull. Géogr. Bot. (Le Mans) 21: 28(1911). Descr. from Mallorca (Balearic Islands, Spain). Endemic to this island. Tetrapl. Jermy & Lovis (1964). Allotetrapl. (FoFoPePe), Sleep (1966, 1977); Lovis & Reichstein (1969).
21. *A. marinum* L., Sp. Pl. 1081(1753). Descr. from Great Britain. Type: LINN. Distr.: Macaronesia, Atlantic and Mediterranean coastal regions. Silicates. Diploid (MaMa), Manton (1950).
22. *A. monanthes* L., Mantissa 130(1767). Descr. from southern Africa. Type: LINN. Distr.: America, Africa, Macaronesia. Generally triploid and apogamous Manton (1950); Manton & Vida (1968); Wagner et al. (1970); Lovis et al. (1973). But Smith & Mickel (1977) have reported a sexual tetraploid form Mexico.
23. *A. obovatum* Viv., Fl. Lib. Spec. 68(1824). Descr. from Monte La Trinité, Corsica. Isotype in BOLO (herb. Bertoloni), see fig. in Pichi Sermolli (1976: 36-39). Mediterranean area to Turkey. Silicate rocks. Diploid Manton & Reichstein (1962), (ObOb).
24. *A. onopteris* L., Sp. Pl. 1081(1753). Descr. from Italy and France. Dr. H. P. Fuchs (in litt. 16.4.81) recommends to accept No. 12 in Burser's «Hortus siccus» XX(UPS) as lectotype. Distr.: Macaronesia, Mediterranean area to w. Asia. Mainly silicates. Diploid Manton (1950); Shivas (1955, 1969); Meyer (1960b, 1961); Sleep (1967).
25. *A. petrarchae* (Guérin) DC. in Lam. et DC. Fl. Fr. ed. 3.5: 238(1915). Descr. from Grottes de Vaucluse (France). Type: AV.
- 25a. *A. petrarchae* (Guérin) DC. ssp. *bivalens* (Meyer) Lovis & Reichst., Ber. Schweiz. Bot. Ges. 79: 336 footnote (1969). Descr. from s. Spain. Type: B. Known only from s. Spain. Limestone. Diploid Meyer (1964), (PePe). Synon.: *A. glandulosoides* Löve & Löve, Taxon 26: 323 (1977).
- 25b. *A. petrarchae* (Guérin) DC. ssp. *petrarchae*. Mediterranean area, absent from Anatolia. Limestone. Tetrapl. Manton (1950); Meyer (1964). Autotetrapl. (PePePe'Pe), Sleep (1966, c. 1982); Lovis, Sleep & Reichst. (1969).
26. *A. ruta-muraria* L. Sp. Pl. 1081(1753). Descr. from Europe. Type: LINN.
- 26a. *A. ruta-muraria* L. ssp. *dolomiticum* Lovis & Reichst., Brit. Fern Gaz. 9: 141-146(1964). Descr. from n. Italy (Trentino Alto Adige). Type: BM. So far reported from s. France, n. Italy, Yugoslavia. Diploid (RuRu) Lovis & Reichst. (1964). Synon.: *A. dolomiticum* (Lovis & Reichst.) Löve & Löve, Preslia 46: 125(1974).
- 26b. *A. ruta-muraria* L. ssp. *ruta-muraria*. N. hemisphere, on limestone and dolomitic rocks and walls. Tetrapl. Manton (1950); Meyer (1952); Wagner (1955). Autotetrapl. (RRR'R'), Lovis (1964); Vida (1970); Bouharmont (1972a, 1977a, b), sometimes forming tri- and multivalents at meiosis and producing bad spores.
- 26c. *A. ruta-muraria* L. hexaploid cytotype. Not yet named, found in Japan (Kikuchū Prov., limestone cliffs by side of Akkagawa River, leg. A. Sleep 15.8.1968, cult. TR-2292), Sleep et al. (publ. in prep.). Could occur in Europe.
27. *A. seelosii* Leybold, Flora (Regensb.) 38: 348(1855). Descr. from n. Italy (Schlern). Type: W.
- 27a. *A. seelosii* Leybold, ssp. *seelosii*. Endemic to s.e. Europe (Italy, Germany, Austria, Yugoslavia). Dolomitic rocks. Diploid Meyer (1957, 1964), (SeSe).
- 27b. *A. seelosii* Leybold, ssp. *glabrum* (Litard. & Maire) Rothm. in Cadevall & Font Quer Fl. Catalunya 6: 339(1937). Endemic to the w. Mediterranean area (s. Spain, s.w. France, North Africa). Limestones. Diploid Meyer (1967), (Se'Se'). Genetically very close to ssp. *seelosii* producing fertile hybrids (Lovis unpubl.). Synon.: *A. celtibericum* Rivas Martinez, Bull. Jard. Bot. Bruxelles 37: 329(1967).

28. *A. septentrionale* (L.) Hoffm., *Deutschl. Fl.* 2: 12(1795). Descr. from Europe. Typification not settled.

28a. *A. septentrionale* (L.) Hoffm. ssp. *caucasicum* Fraser-Jenkins & Lovis in Parris & Fraser-Jenkins, Checklist of Turkish Pteridophyta, *Notes Roy Bot. Gard. Edinburgh* 38: 281(1980). Descr. from the Caucasus (USSR). Type: BM, isotypes BM, E, G. Also found in Turkey and further East. Not in Europe; listed here as ancestor of 28b. Diploid (SpSp), Lovis (unpubl.); Gibby (unpubl.).

28b. *A. septentrionale* (L.) Hoffm. ssp. *septentrionale*. Circumboreal with gaps. Silicate rocks. Tetrapl. Manton (1960); Meyer (1952) and others, see Löve et al. (1977). Autotetrapl. (SpSpSp' Sp'), Lovis (1964); Vida (1970); Bouharmont (1972c).

29. *A. trichomanes* L., *Sp. Pl.* 1080(1753). Descr. from Europe. Type material: LINN and BM. Typification see Lovis (1964b). *Synon.*: *A. melanocaulon* Willd.

29a. *A. trichomanes* L. ssp. *trichomanes* sensu Lovis (1964b). Distr. World-wide, with gaps. Silicate rocks and walls, including serpentines. Diploid Manton (1950); Meyer (1952); Lovis (1964b) and others, see Löve et al. *Cytotax. Atlas* (1977), (TrTr).

29b. *A. trichomanes* L. ssp. *inexpectans* Lovis, *Brit. Fern Gaz.* 9: 155(1964). Descr. from Austria. Type: BM. Known from Mallorca, s. France, Austria, Yugoslavia, Greece, Crete. Limestone rocks. Diploid Lovis, Melzer & Reichst. (1966). (Tr'Tr'). Genetically very close to ssp. *trichomanes*, producing fertile hybrids Lovis (unpubl.), ecologically separated.

29c. *A. trichomanes* L. ssp. *quadrivalens* D.E. Meyer, *Ber. Deutsch. Bot. Ges.* 74: 456(1962). Descr. from Bavaria (Germany). Type: B. Distr. World-wide, on various kinds of rocks and walls (limestone and silicates). Tetrapl. Manton (1950); Meyer (1952, 1962a); Lovis (1964b, 1977: 363) and others, see Löve et al. (1977). Autotetrapl. (TrTrTr'Tr'), Bouharmont (1968, 1972b, 1977a, b); Lovis (1977:368). Good evidence for autopolyploidy is provided by the tetraploid *A. × clermontae* = *A. ruta-muraria* × *trichomanes* which produces a very high number of bivalents at meiosis and some good spores (Lovis & Reichst. unpubl., see Lovis 1977: 367).

29d. *A. trichomanes* L. ssp. *pachyrachis* (Christ) Lovis & Reichst., *Willdenowia* 10: 18(1980). Descr. from St. Maurice (Ct. Valais, Switzerland). Type: P. Known from southern and central Europe. Limestones. Tetrapl. Genetically at least partly distinct from 28c, the hybrid producing many abortive spores.

29e. *A. trichomanes* L. hexaploid cytotype. Not named, not mentioned in Löve, Löve & Pichi Sermolli (1977). First reported in New Zealand by Brownlie (1954) it being the prevalent cytotype there (Lovis 1977: 369). Subsequently reported from Australia (rare there, see Lovis 1977: 369), and also found in Belgium and France (Bouharmont 1968). The hexaploid plants are fertile, but probably not very vigorous and are rare in Europe. They may often be formed *de novo* by chromosome doubling from the relatively common triploid hybrid ssp. *trichomanes* × ssp. *quadrivalens* (Bouharmont 1968). A hexaploid found by Lovis in Madeira (Lovis 1977: 369) may be a derivative of *A. anceps* × *trichomanes* ssp. *quadrivalens* (Lovis pers. communication).

30. *A. viride* Hudson, *Fl. Angl.* 385(1762). Descr. from Great Britain. Type: BM and perhaps B. Circumboreal. On limestones and serpentines. Diploid Manton (1950) and many others, see Löve et al., *Cytotax. Atl.* (1977). (ViVi).

11.3. *Ceterach* DC.

31. *C. officinarum* DC. in Lam. & DC., *Fl. Franç. ed. 3.* 2: 566(1805) Descr. from France. Type: G. *Syn. Asplenium ceterach* L.

31a. *C. officinarum* DC. ssp. *bivalens* D. E. Meyer, *Ber. Deutsch. Bot. Ges.* 77: 8(1964). Descr. from Greece. Type: B. Distr.: Italy, Yugoslavia, Greece, Turkey, mainly on limestone, but also on silicates. Diploid Vida (1963); Váróczy & Vida (1963); Meyer (1964). (CeCe). *Synon.*: *Asplenium javorkeanum* Vida, *Acta Bot. Acad. Sci. Hung.* 9: 202(1963); *Ceterach javorkeanum* (Vida) Soó, *Acta Bot. Acad. Sci. Hung.* 9: 419(1963); *Asplenium ceterach* L. ssp. *bivalens* (D.E. Meyer) Greuter & Burdet, *Willendowia* 10: 17(1980).

31b. *C. officinarum* DC. ssp. *officinarum*. Distr.: southern and central Europe, North Africa and w. Asia, mainly on limestone, dolomitic rocks and walls. Tetrapl. Manton (1950), for others see Löve et al., *Cytotax. Atl.* (1977). Autotetrapl. (CeCeCe'Ce') Vida (1965), but final proof still missing (Lovis 1977: 363). *Syn. Asplenium ceterach* ssp. *ceterach*.

11.4. *Phyllitis* Hill

32. *Ph. sagittata* (DC.) Guineá & Heyw., Collect. Bot. (Barcelona) 4:(2): 246(1954). Descr. from vicinity of Marseille (France). Mediterranean area. Limestones. Map in Fenaroli (1967). Diploid (SaSa) Manton (1950); Emmott (1964). Synon.: *Ph. hemionitis* (Sw.) O. Kuntze; *Scolopendrium sagittatum* DC. in Lam. & DC., Fl. Franç. ed. 3. 5: 28(1815) (Basion.); *Asplenium sagittatum* (DC.) A.J. Bange, Bull. Mens. Soc. Bot. Lyon 21: 84(1952).

33. *Ph. scolopendrium* (L.) Newman, Hist. Brit. Fern ed. 2 10(1844). Descr. from Europe. Type: LINN. Distr. North America, Macaronesia, Europe, Mediterranean area, Asia to Japan. Limestones. Synon.: *Asplenium scolopendrium* L., Sp. Pl. 1079(1753) (Basion.).

33a. *Ph. scolopendrium* ssp. *scolopendrium*. Distr. from Macaronesia throughout the range to western Asia. Diploid Manton (1950), Emmott (1964), for others see Löve et al., Cytotax. Atl. (1977). (ScSc). Synon. *Asplenium scolopendrium* L. ssp. *scolopendrium*.

33b. *Ph. scolopendrium* ssp. *antri-jovis* (Kümmerle) Dostál comb. nova [Basion.: *Biropteris antri-jovis* Kümmerle, Magyar Botan. Lapok 19: 2(1922)]. Descr. from Crete. Type: Originally in BP, disappeared during the war (1939-1945). Otherwise in Turkey (rare), but similar plants reported from England (fig. 6 in Brownsey & Jermy 1973: 342). Diploid. Genetically very close to ssp. *scolopendrium* (Vida 1972). Synon.: *Asplenium scolopendrium* ssp. *antri-jovis* (Kümmerle) Brownsey & Jermy (1973); *Phyllitis antri-jovis* (Kümm.) Seitz, Jahrb. Ver. z. Schutze d. Bergwelt 43: 200 (1978, München).

33c. Tetraploid cytotypes replace the diploid in N. America (Britton 1953; Emmott 1964) and Japan (Emmott 1964; Mitui 1977 and others, see Löve et al. 1977). They have been given names: *Phyllitis scolopendrium* var. *americana* Fernald, Rhodora 37: 200(1935), *Ph. fernaldiana* Löve, Svensk Bot. Tidskr. 48: 214(1954) = *Ph. japonica* Kom. ssp. *americana* (Fern.) Löve & Löve and *Ph. japonica* Kom. (quoted from Löve et al., Cytotax. Atl. 1977). Both are difficult to cultivate and are probably essentially autotetraploid (ScScSc'Sc), Emmott (1964).

11.5. *Phyllitopsis* Reichst., genus novum

Diagnosis: Inter genera *Phyllitis* et *Ceterach* interjecta. Lamina simplex, circumscriptione lanceolata, irregulariter lobata et sinuata, solum statu juvenili paleacea. Sori pro parte singuli, pro parte bini, scilicet ad venas adjacentes alter ad alterum spectans (ut in *Phyllitide*); indusia praestantia sed angusta. Venae furcatae, ad marginem laminae anastomosis sat numerosis.

Type: *Phyllitopsis hybrida* (Milde) Reichstein, comb. nova. Basion.: *Scolopendrium hybridum* Milde, Verh. zool.-bot. Ges. Wien 14: 235 + t. 18(1864).

A monotypic genus. Its sole representative is usually treated as *Phyllitis hybrida* (Milde) C. Chr., Ind. Fil. 492(1906). This is not correct, because it contains 50% genetic material of *Phyllitis* and 50% of *Ceterach* (see below sub 34). Milde described it from a single specimen and suspected it to be a hybrid of *Phyllitis scolopendrium* and *Ceterach officinarum* but noticed that it had good spores. Luerssen (1889: 125-129) pointed out that it is nearer to *Ph. sagittata* and that its hybrid nature is doubtful. The correct interpretation as an allotetraploid species is by Vida (see below under 34.)

34. *Phyllitopsis hybrida* (Milde) Reichstein (see above). Synon.: *Scolopendrium hybridum* Milde, Verh. zool.-bot. Ges. Wien 14: 235(1864). Basion.: *Phyllitis hybrida* (Milde) C. Chr., Ind. Fil. 492(1906); *Asplenium hybridum* (Milde), A.J. Bange, Bull. Mens. Bot. Lyon 21: 84(1952). Descr. from Dalmatia (Yugoslavia). Endemic to this region. Limestone rocks. Tetraploid Manton (1950), for others see Löve et al. (1977). Allotetraploid (CeCeSaSa), Vida (1963a, 1965); Emmott (1964) and resynthesized under experimental conditions by spontaneous chromosome doubling in the experimentally produced hybrid of diploid *Ceterach* (31a) and *Phyllitis sagittata* (32), Vida (1965, 1973).

11.6. *Pleurosorus* Fée

35. *P. hispanicus* (Cosson) C.V. Morton, Bull. Soc. Bot. Fr. 106: 233(1959). Descr. from southern Spain, Type:P. Distr.: north-western and southern Spain, North Africa. Limestone. Diploid Meyer (1964). Synon.: *Asplenium hispanicum* (Cosson) Greuter & Burdet, Willdenowia 10: 17(1980).

36. *P. nevadensis* Salso, Lazaroa 1: 147(1979). Descr. from Spain. Type: MGC. Known only from Type locality. Cytology not established.

12. Hybrids in European Aspleniaceae

12.1. *Remark on nomenclature.*— As mentioned in section 9, I prefer to use binomials for each hybrid as most experts have done for more than 100 years. This leads to difficulties when cytotypes of an aggregate species containing autoploid taxa are involved (reasons see section 11.1.). The case of *A. alternifolium* Wulfen (SpSpTr) and *A. × heufleri* Reichardt (SpSpTrTr) may be quoted as example. These two hybrids have one parent (*A. septentrionale* = SpSpSpSp) in common and two different cytotypes of an aggregate species, as the second parent (*A. trichomanes* ssp. *trichomanes* in *A. × alternifolium* and ssp. *quadrivalents* in *A. × heufleri*). The simple binomial *A. × heufleri* is only in agreement with the International Code of Nomenclature as long as the two cytotypes of the aggregate species (*A. trichomanes*) are treated taxonomically as different species (as Rothmaler 1963; Löve et al. 1977 and some others have done). However, for reasons given in section 11.1. and as long as a more appropriate category is not available, I prefer to treat such cytotypes as subspecies. In the example given here, the correct name for *A. × heufleri* would be *A. × alternifolium* nothom. *heufleri*. It is my opinion that the category of nothomorphs has neither been created, nor is it suitable for naming this particular type of hybrid ferns, and I prefer not to use it here and follow the conservative (historical) way. As pointed out by Reichardt (1859), the two hybrids mentioned above are quite distinct morphologically (see also fig. 15). No intermediates exist. This is easily understandable, as they have different genomic constitution. Treatment of *A. × heufleri* under *A. × alternifolium* creates confusion and obscures facts.

12.2. *Hybrids within the genus Asplenium.*— A total of 50 such hybrids has been reported, 43 of them with checked cytology, i.e. with well-established parentage (see fig. 4).

12.3. *Checklist of Asplenium hybrids found in Europe.*— With types (as far as known) and genome formulae (as far as established). For denotation of genomes see checklist of species (11.1.).

1 × 2 = *A. × bechereri* D. E. Meyer, Ber. Deutsch. Bot. Ges. 81: 101-102(1968) = *A. adiantum-nigrum* × *adulterinum*. Descr. from Verdasio, Switzerland (Ct. Ticino). Type: B, isotype: Herb. Becherer (now in Lugano). New interpretation and cytology (CuOnTrVi) see Appendix II.

1 × 7 = *A. × sarniense* A. Sleep, Brit. Fern Gaz. 10(4): 209-211(1971) = *A. adiantum-nigrum* × *billotii*. Descr. from Guernsey. Type: BM, isotypes: B, K, LDS, STP. (CuOnBiBi) Sleep (1971); Sleep & Ryan (1972) or (CuOnObOb) if *A. billotii* is an autotetraploid of *A. obovatum*, see A. Sleep (c. 1982).

Note: Perhaps the same as *A. trojanii* R. de Litardière, Ann. Soc. Linn. Lyon 1923, 70: 121-133 (1924), sp. (vel hybr.?), Type P. Descr. from Vallée d'Ascò, Corsica. The morphology of this specimen is correct, spores abortive (det. TR), sporangia abortive (det. A. Sleep). But it could not yet even be established that the putative parents occur at the *locus classicus*. As there is no possibility for establishing the parentage of this specimen beyond doubt, it is preferred to retain the name *A. × sarniense* for the specimens of this hybrid with checked cytology.

1 × 10 = *A. × centovallense* D.E. Meyer, Ber. Deutsch. Bot. Ges. 81: 102-104(1968) = *A. adiantum-nigrum* × *cuneifolium*. Descr. from Verdasio, Switzerland (Ct. Ticino). Type: B. (CuCuOn) see Appendix II. This hybrid has also been synthesized experimentally by Shivas (1969). It forms with great ease.

1 × 14 = *A. × brissaginense* D.E. Meyer, Ber. Deutsch. Bot. Ges. 73: 389-391(1960, publ. 1961) = *A. adiantum-nigrum* × *forisiense*. Descr. from above Brissago, Switzerland (Ct. Ticino). Type: B. (CuOnFoOb) D.E. Meyer (1968). Meiosis with virtually only univalents (c. 144¹), confirmed by J. Schneller for plant coll. 27.3.1972 by W. & C. Bennert, near Lamastre (W. of Valence, France) cult. by TR (No. 4448A).

1 × 24 = *A. × ticinense* D.E. Meyer, Ber. Deutsch. Bot. Ges. 73: 391-392 (1960, appeared 1961) = *A. adiantum-nigrum* × *onopteris*. Descr. from near Brissago, Switzerland (Ct. Ticino). Type: B. (CuOnOn) see Appendix II. This hybrid has also been produced under experimental conditions by Shivas (1961).

1 × 26b = *A. × perardi* R. de Litard., Bull. Soc. Bot. Deux-Sèvres 21: 109(1910) (nomen) type not seen. Putative *A. adiantum-nigrum* × *ruta-muraria*. See also A. Pérard, Bull. Soc. Bot. Fr. 16: 262-263(1869); H. Christ (1900: 74-75) with fig. It was also described as *A. × lingelsheimii* W. Seymann, Österr. Bot. Zeitschr. 60: 278-280(1910) with fig. The cytology could, of course, not have been checked at those times, but no reports on sporangial content were given either. The existence of this hybrid is doubtful. The specimen coll. 4.10.1961 near Enkhuizen (Holland) and described by S. Segal, Gorteria 1962: 56-59 with fig. and lit. could be examined; it bore good spores and was identified as *A. adiantum-nigrum* (TR).

1 × 28b = *A. × contrei* Callé, Lovis & Reichst., Candollea 30: 194(1975) = *A. adiantum-nigrum* × *septentrionale*. Descr. from Col d'Aspin, France (Dép. Hautes-Pyr.) Type: BM, isotypes: G, K, P. (CuOnSpSp). A very rare hybrid but already found in Wales (Great Britain) about 1870 see Lovis & Reichst. (1968b).

1 × 29a = *A. × dolosum* Milde, Verh. zool-bot. Ges. Wien 14: 165(1864) with fig. = *A. adiantum-nigrum* L. × *trichomanes* ssp. *trichomanes* (see Appendix II). Descr. from Küchelberg near Meran, Italy (S. Tirol). Type: (MB) see fig. 4 in D.E. Meyer, Willdenowia 2: 529(1960). (CuOnTr).

2 × 26b = *A. × lobmingense* Melzer, Lovis & Reichstein, Ber. Schweiz. Bot. Ges. 91: 114 (1981) = *A. adulterinum* × *ruta-muraria* ssp. *ruta-muraria* (see Appendix I). Descr. from serpentinite rocks above Lobming, Austria (Steiermark, above St. Stefan a.d. Mur). Type: G. (RuRuTrVi). Known only from the specimen, but the hybrid has been also made under experimental conditions (Lovis, unpubl.).

2 × 29a = *A. × trichomaniforme* Woyнар, Mitt. Naturw. Ver. Steiermark 49: 153(1913) = *A. adulterinum* × *trichomanes* ssp. *trichomanes* (see Appendix II), the relatively rare triploid hybrid. Descr. from serpentinite rocks near Trafös, Austria (Steiermark). Type: (GJO) see fig. in D.E. Meyer, Willdenowia 2: 521(1960). (TrTrVi). Synthesized by Lovis (1955a).

2 × 29c = *A. × praetermissum* Lovis, Melzer & Reichst., Ber. Schweiz. Bot. Ges. 91: 114 (1981) = *A. adulterinum* × *trichomanes* ssp. *quadri-valens* (see Appendix I), the relatively common tetraploid hybrid. Descr. from Austria, Steiermark. Type: G. (TrTrTrVi). It has also been synthesized under experimental conditions by Lovis (1958).

2 × 30 = *A. × poscharskyanum* (Hoffm.) Preissmann, Mitt. Naturwiss. Ver. Steiermark 33: 179(1896) = *A. adulterinum* × *viride*. Descr. from Austria. Known also from other countries where the parents grow together. (TrViVi) Lovis (1955a), also synthesized under experimental conditions.

7 × 14 = *A. billotii* × *forisiense* discovered by F. Badré in herbarium material (P), meanwhile found living and cytology checked by Badré et al. (c. 1982). (BiBiFoOb), but might be (FoObObOb), if *A. billotii* is essentially autotetraploid *A. obovatum*. Pairing behaviour in this hybrid (c. 32-35^{II} + c. 72^I and perhaps some trivalents) would fit both possibilities. The hybrid was also produced by A. Sleep (1966; c. 1982) under experimental conditions. The synthetic plants showed the same morphology but gave c. 12-15 trivalents in meiosis. The reason for the slightly discordant results is not clear. Formation of trivalents shows that at least some of the chromosomes of *A. obovatum* and *A. billotii* are homologous. Will be described as *A. × sleepei* by Badré et al., c. 1982.

7 × 23 = *A. × cyrnosardoum* Rasbach, Vida & Reichst., Ber. Schweiz. Bot. Ges. 91: 114 (1981) = *A. billotii* × *obovatum*, see Appendix I, described from Corsica. Type in G. and herb. TR (BiBiOb) or (ObOb'Ob'), if *A. billotii* is an essentially autotetraploid *A. obovatum*.

7 × 24 = *A. × joncheerei* D. E. Meyer, Willdenowia 2: 332-336(1960) = putative *A. billotii* × *onopteris*. This would be (BiBiOn) but no cytological data available. Described from Madeira, Type: B. This hybrid has also been synthesized by Sleep (1966) but it died before yielding cytological results.

7 × 28b = *A. souchei* Litard., Bull. Soc. Bot. Deux-Sèvres 21: 100-101(1910) with good fig. (as *A. adiantum-nigrum* × *septentrionale*) = *A. billotii* × *septentrionale*, see Callé et al. (1975). Described from Tines de Chobert, Vallon de Magnerolles, commune de Nanteuil, France (Dép. Deux-Sèvres). Type not seen (probably in herb. Litardière, inaccess.) but isotype in herb. J. Callé (Paris) and one frond in herb. TR (Basel) and original plant seen, still living in 1975. (BiBiSpSp) with very many (66-69) pairs at meiosis and behaving as a «delayed allotetraploid» (det. J.D. Lovis). This

hybrid is very rare but has been found already on 24.7.1874 by Giraudias, near Aspières, France (Dép. Aveyron), herb. J. Callé.

9 × 29c = *A. × khaniense* Brownsey & Jermy, *Candollea* 30: 22(1975) with fig. = *A. creticum* × *trichomanes* ssp. *quadrivalens*. Descr. from Crete. Type: BM. (AeTrTrVi). This hybrid has also been obtained under experimental conditions (TR-2093), showing c. 36^{II} + 72^I, as in the natural plant, Reichstein et al. (1973 tab. 23, 28, 29).

10 × 26b = *A. × murariaeforme* Waisbecker, *Öster. Bot. Zeitschr.* 49: 63(1899); presumed to be *A. ruta-muraria* × *Forsteri* (?) in *Magyar Bot. Lap.* 1: 175(1902), i.e. putative *A. cuneifolium* × *ruta-muraria*. Described from Saxony (Germany) and from Hungary, see also Christ (1903: 29-30). No cytological data available. Considering the great variability of both presumed parents some ± abnormal forms of one of them may have been taken for a hybrid. The existence of this hybrid is doubtful. Both H. Melzer and the author (TR), have searched in vain for it.

10 × 29 = *A. × wachaviense* Ascherson & Graebner, *Syn. Mitteleur. Fl.* ed. 2, 1: 125(1913, publ. 1912) = *A. cuneifolium* × *trichomanes*. Descr. from Gurhofgraben near Aggsbach (Austria). A doubtful hybrid. If it exists, it could only be derived from the diploid *A. trichomanes*, because the influence of *A. cuneifolium* is rather pronounced. In this case a morphology similar to that of *A. × bechereri* would be expected. A triploid hybrid derived from ssp. *quadrivalens* should be closer to *A. trichomanes*.

10 × 30 = *A. woynarianum* Ascherson & Graebner, *Syn. Mitteleur. Fl.* ed. 2, 1: 126 (1913, publ. 1912) = *A. cuneifolium* × *viride*. Described from Austria, Steiermark. Type: GZU, see Meyer (1961). The variation in the shape of the fronds given by Meyer is due only to growing conditions. Diploid (CuVi) showing mainly only univalents at meiosis but occasionally one or a few bivalents (Lovis, unpublished). In spite of several sowings, this hybrid has never yielded progeny (TR, unpubl.).

12 × 30 = *A. × lessinense* Vida & Reichst., *Candollea* 26: 192(1971) = *A. fissum* × *viride*. Described from Mt. Lessini, n. Italy. Type: BM, isotypes BP, G, K, ZT. Dolomitic or limestone rocks and scree. Also found in Bavaria (Germany), see Rasbach et al. (1979). (FiVi). One of the rare diploid hybrids which is able to double its chromosomes spontaneously and to produce fertile allotetraploid progeny in cultivation. But no such plants have so far been found in nature.

13 × 20 = *A. fontanum* × *majoricum* Jaquotot & Orell, *Collectanea Bot.* (Barcelona) 29: 564 and fig. 4(1968). Described from Mallorca but *A. fontanum* has become extremely rare in Mallorca. In spite of the (?) given in the publication, I agree that the assignment is most probably correct. The hybrid has been synthesized under experimental conditions by Sleep (1967, c. 1982) and forms easily; it showed c. 36^{II} + 36^I at meiosis, in agreement with the genome formula (FoFoPe).

13 × 29 = *A. × corbariense* Rouy *Fl. Fr.* 14: 453(1913) = *A. fontanum* × *trichomanes* ssp. (?), see *Bull. Soc. Bot. France* 35: CXI (1888). Descr. from France (Dép. Aude) près Quillan (Rouy & Gautier). Should be regarded as very doubtful.

13 × 30 = *A. × gastonii-gautieri* Litard., *Bull. Geogr.-Bot.* (Le Mans) 21: 274(1911) = *A. fontanum* × *viride*. Descr. from France, fig. in Christ (1900:88), found also in Switzerland D. E. Meyer (1957). A rare hybrid. Diploid (FoVi), also obtained under experimental conditions by Lovis (1970). The synthetic plant doubled its chromosomes in cultivation to produce fertile allotetraploid progeny. Such plants have, however, not yet been found in the wild.

14 × 24 = *A. × ruscinonense* Nieschalk, Lovis & Reichst., *Ber. Schweiz. Bot. Ges.* 91: 115 (1981), = *A. forsiense* × *onopteris*, see Appendix I. Described from France (Dép. Pyr. Or.). Type: G. So far not found elsewhere. Triploid (FoObOn). This hybrid has been synthesized experimentally by Sleep (1966, c. 1982).

14 × 28b = *A. × costei* Litard. *Notes ptéridologiques*, *Bull. Acad. Int. Géogr. Bot.* (Le Mans) 21: 150(1911) = *A. forsiense* × *septentrionale*. Descr. from France. Found several times since. Tetraploid Meyer (1967). (FoObSpSp'), see Callé et al. (1975).

14 × 29c = *pagesii* Litard., *Bull. Géogr.-Bot.* (Le Mans) 20: 204(1910) = *A. forsiense* × *trichomanes* ssp. *quadrivalens*. Descr. from France. Found also in Spain and in s. Switzerland. Tetraploid (det. Lovis, mentioned in Meyer 1967). (FoObTrTr'), see Appendix II. Synon.: *A. × guichardii* Litard., *Bull. Géogr. Bot.* (Le Mans) 21: 75-77(1911); *A. × verbanense* v. Tavel, *Ber. Schweiz. Bot. Ges.* 26/29: 165(1920), see F. W. Stansfield *Brit. Fern Gaz* 6: 307(1934) with fig., and P. Kestner, *Brit. Fern Gaz.* 7: 19(1935) with fig.

15 × 28c = *A. × reuteri* Milde, Bot. Zeitung 25: 148(1867) (pro sp.) Descr. from Gülek Pass, s. Turkey. Type in G. = *A. haussknechtii × trichomanes* ssp. *quadrivalens*, see T. Reichstein (1969). (AeRuTrTr'). Very close to *A. × aprutianum* Lovis, Melzer & Reichst. (= 18 × 28c). Also reported from Crete (Reichstein et al. 1973: 151), but Brownsey & Jermy (1975) did not accept this determination. *A. × reuteri* has also been obtained under experimental conditions (TR-3762), which gave 26-31^{II} and 89-83^I at meiosis (Reichstein et al. 1973, tab. 28, 29) in good agreement with the suggested formula.

18 × 26a = *A. × eglüi* Lovis & Reichst., Ber. Schweiz. Bot. Ges. 91: 116 (1981) = *A. lepidum × ruta-muraria* ssp. *dolomiticum*, see Appendix I. Descr. from Buco di Vela, Trentino, Italy. Type: G. Triploid (AeRuRu), see Brownsey (1976a) mentioned in Reichstein et al. 1973: 157. This hybrid forms easily and has also been produced under experimental conditions by Brownsey (1976a).

18 × 26b = *A. × javorkae* Kümmerle, Magyar Bot. Lapok 21: 1-3(1923) = *A. lepidum × ruta-muraria* ssp. *ruta-muraria*. Descr. from Albania. Found also in France, Italy, Austria and Yugoslavia, nearly everywhere where the parents grow together, i.e. in most places where *A. lepidum* grows, because *A. ruta-muraria* is usually also present there. Tetraploid (2n = 144) with irregular meiosis, difficult to analyse correctly, with many bivalents, trivalents, and perhaps even some quadrivalents present, the remainder of the chromosomes being univalents (AeRuRuRu'). Reichstein et al. (1973 tav. 28, 29), also Vida (unpubl.).

18 × 29b = *A. stiriicum* D. E. Meyer, Ber. Deutsch. Bot. Ges. 75: 29(1962) = *A. lepidum × trichomanes* ssp. *inexpectans*, see Lovis et al. (1966). Descr. from Bärenschützklamm near Mixnitz, Steiermark, Austria. type: GZU. Triploid (AeRuTr) Lovis, Melzer & Reichstein (1966). So far not found outside Austria (rare). On limestone and dolomitic rocks.

18 × 29c = *A. × aprutianum* Lovis, Melzer & Reichstein, Bauhinia (Basel) 3(1): 89(1966) × *A. lepidum × trichomanes* ssp. *quadrivalens*. Descr. from Abruzzi, Italy. Type: BM. Known also from Austria and Hungary (rare). On limestone and dolomitic rocks. Tetrapl. (AeRuTrTr).

20 × 25b = *A. × sollerense* Lovis, Sleep & Reichst., Ber. Schweiz. Bot. Ges. 79: 370(1969) = *A. majoricum × petrarchae* ssp. *petrarchae*. Descr. from Mallorca. Type: BM. Not found elsewhere. (FoPePePe').

20 × 29c = *A. × orellii* Lovis & Reichst., Ber. Schweiz. Bot. Ges. 79: 339(1969) = *A. majoricum × trichomanes* ssp. *quadrivalens*. Descr. from Mallorca. Type: BM. Not found elsewhere. (FoPeTrTr).

23 × 24 = *A. obovatum × onopteris*, found by R. Prelli No. 1163 in s. France. Cytology correct. Will be described by Badré et al. (c. 1982) as *A. × bouharmontii*.

25b × 29b = *A. × litardierei* Bennert & Meyer, Ber. Deutsch. Bot. Ges. 87: 22(1973) = *A. petrarchae* ssp. *petrarchae × trichomanes* ssp. *inexpectans*. Descr. from Mallorca. Type: B. Not found elsewhere. Triploid (PePeTr).

25b × 29c = *A. × nieschalkii* D.E. Meyer, Ber. Deutsch. Bot. Ges. 76: 18(1963) = *A. petrarchae* ssp. *petrarchae × trichomanes* ssp. *quadrivalens*. Descr. from s. France. Type: B. Known also from Spain. On limestone rocks (rare). Tetrapl. (PePe'TrTr'), but not behaving like a delayed allotetraploid, see Appendix II.

26a × 26b = *A. × baldense* Sleep, Vida & Reichst., Ber. Schweiz. Bot. Ges. 91: 116 (1981) = *A. ruta-muraria* ssp. *dolomiticum × ssp. ruta-muraria*. Descr. from Mt. Baldo, Italy. Type: G., see Appendix I. Found also in other places in Italy and Yugoslavia where the parents grow together. (RRR'). Also synthesized by Vida (1970: 541-543); Bouharmont (1972: 378).

26b × 28b = *A. × murbeckii* Dörfner, Österr. Bot. Zeitschr. 45: 223(1875) = *A. ruta-muraria* ssp. *ruta-muraria × septentrionale* ssp. *septentrionale*. Descr. from eastern Sweden. Type: UPS. Synon.: *A. × suevicum* K. Bertsch ex Meyer (1959: 40).

Known from many countries in Europe and also from the Caucasus, but except for some places in Hessen (Germany), see Nieschalk (1961), rare everywhere. (RuRu'SpSp'). It shows well the phenomenon of delayed allopolyploidy, with often almost complete or complete pairing at meiosis (Lovis 1963, 1964; Vida 1970; Bouharmont 1972a), together with production of some good spores (see fig. 2) which yield some progeny. It has also been obtained experimentally (Vida 1970; Bouharmont 1972).

26b × 29c = *A. × clermontae* Syme, Engl. Bot. ed. 3, 12: 132(1886) = *A. ruta-muraria* ssp. *ruta-muraria × trichomanes* ssp. *quadrivalens*. Descr. from Ireland. Type: BM (teste Alston 1940:

137). *Synon.*: *A. × preissmannii* Ascherson & Luerssen (1895); Ascherson & Graebner (1913); *A. × reicheliae* Ascherson & Dörfler (1896); *A. × hauchecornei* Ascherson & Graebner (1896). Known also from n. Italy, Austria, Czechoslovakia and N. America (Wagner 1963: 14; Wagner & Wagner 1976) but everywhere very rare. (RuRu'TrTr'), see Appendix II and Lovis (1977 : 367). Sporangia contain mostly abortive material, but a few good, viable spores are also present (fig. 2.).

27a × 29c = *A. × valgannense* Attinger, Ber. Schweiz. Bot. Ges. 75: 92-95 (1965) = *A. seelosii* × *trichomanes* ssp. *quadrivalens*. Descr. from N. Italy. Type: ZT.

28a × 29a = *A. septentrionale* ssp. *caucasicum* × *trichomanes* ssp. *trichomanes*. Found by C.R. Fraser-Jenkins in the Caucasus. Diploid (SeTr).

28b × 29a = *A. × alternifolium* Wulfen in Jacquin, Misc. Austr. Bot. 2: 51, t. 5, f. 2(1781) = *A. septentrionale* ssp. *septentrionale* × *trichomanes* ssp. *trichomanes*. Descr. from Austria. Type: W. *Synon.*: *A. × breynii* Retz. (nom. illegit); *A. × germanicum* Weiss (nom. inval.). The commonest *Asplenium* hybrid. This is remarkable considering the widely distinct morphology of the parents. Known from nearly all of Europe and from Western Asia to the Himalayas. On silicate rocks and walls. Triploid (Manton 1950; Meyer 1952). (SpSpTr). Has been obtained under experimental conditions by several workers. Claimed first by Kestner, Brit. Fern Gaz. 7: 19-24(1935), but no voucher available. With proof: Meyer (1952); Lovis & Shivas (1954); Bouharmont (1966).

28b × 29c = *A. × heufleri* Reichardt, Verh. zool.-botan. Ges. Wien 9: 95(1859) = *A. septentrionale* ssp. *septentrionale* × *trichomanes* ssp. *quadrivalens*. Descr. from S. Tirol (n. Italy). Type: ? *Synon.*: *A. × baumgartneri* Dörfler, Österr. Bot. Zeitschr. 45: 169-171; 221-224 + Tab. 9(1895). Originally assumed to be a cross of *A. × alternifolium* with *A. trichomanes*. Known from many countries in Europe, but rare everywhere. On silicate rocks and walls. Correct interpretation Meyer (1958). Tetraploid. (SpSp'TrTr'), see Appendix II.

29a × 29c = *A. × lusaticum* D.E. Meyer, Ber. Deutsch. Bot. Ges. 71: 16(1958) = *A. trichomanes* ssp. *trichomanes* × ssp. *quadrivalens*. Descr. from Landeskrona, Oberlausitz (Poland). Type: B. *Synon.*: *A. lovisii* × *trichomanes* = *A. × saxonicum* Rothm. Exkurs.-Fl. Ergänzt. Bd. IV: 5(1963) nom. nud. In many countries, not rare. It occurs commonly on silicates. Triploid. (TTT'). See also Meyer (1959: 45). Giving c. 36^{II} + 36^I at meiosis (Lovis 1977).

29a × 30 = *A. × protoadulterinum* Lovis & Reichst., Naturwiss. 55: 118(1968) = *A. trichomanes* ssp. *trichomanes* × *viride*. Descr. from Switzerland, Ct. St. Gallen, above Quarten. Type: BM. Only one additional finding from Austria (TR). Produces a relatively high number of good diplospores which, after sowing, yield tetrapl. *A. adulterinum*. Also produced under experimental conditions (Lovis 1968). *Synon.*: *A. × mendelianum* D.E. Meyer (1968). Diploid TV).

29b × 29c = *A. trichomanes* ssp. *inexpectans* × *quadrivalens*. This triploid hybrid is similar to *A. × lusaticum* D.E. Meyer, but more prostrate; not rare in places where ssp. *inexpectans* grows, as usually the tetraploid is present also there. Has not been given a name.

29b × 30 = *A. × adulteriniforme* Lovis, Melzer & Reichst., Bauhinia 2: 233(1965) = *A. trichomanes* ssp. *inexpectans* × *viride*. Descr. from Austria. On limestone, among the parents, occasional. Diploid (T'V).

29c × 29d = *A. trichomanes* ssp. *pachyrachis* × *quadrivalens* Lovis & Reichst. in Greuter Med-Checklist Notulae, 1. Willdenowia 10: 18(1980).

29c × 30 = *A. × bavaricum* D.E. Meyer, Ber. Deutsch. Bot. Ges. 76: 16(1958) = *A. trichomanes* ssp. *quadrivalens* × *viride*. Descr. from Bavaria, Germany. Type: B. Found also in n. Italy and Austria on limestone among the parents, rare. Tripl. (TT'V). This hybrid therefore has the same genome formula as *A. × trichomaniforme* (2 × 29a). It is indeed impossible to distinguish these two hybrids, either by morphological or cytological means. They differ only in a historical way, as one is formed from (T) + (TV) and the other from (TT) + (V). Examination of the habitat will usually show soon which parents are involved.

(26b × 28b) × 28b = *A. × hungaricum* Fraser-Jenkins & Vida, Ber. Schweiz. Bot. Ges. (1981) = *A. × murbeckii* × *septentrionale* ssp. *septentrionale*. Descr. from Hungary. Type: BM. Known only from the type collection. tetraploid (RSSS'). Sterile. This is the first real backcross of an *Asplenium* hybrid found in nature. Many other have been postulated, but all incorrectly. See Appendix I.

12.4. Remark on nomenclature

According to the code, this hybrid should become a nothomorph of *A. × murbeckii*. In our opinion, the category of nothomorphs is useful for naming hybrid swarms, but not appropriate for

this unique fern hybrid, which also needs the new concept of delayed allopolyploidy to properly understand its formation.

12.5. Hybrid within the genus *Ceterach*

31a × 31b = *C. × mantoniae* (Váróczy & Vida) Soó, Acta Bot. Acad. Sci. Hungaricae 9 (3-4): 419(1963 = *C. officinarum* ssp. *bivalens* × ssp. *officinarum*. Descr. from Hungary. Tripl. (CeCeCe') with c. 36^{II} + 36^I at meiosis. Will probably be found in other places where the parents grow together. A specimen (TR-1599) coll. by E. Hauser in Turkey, limestone rocks, above Gülek Pass, c. 1000 m, Aug. 1965, cult. in Basel, showed 2^{III}, 34^{II} and 34^I at meiosis (det. G. Vida).

12.6. Intergeneric hybrids

12.6.1 × *Asplenoceterach* D.E. Meyer (1957)

26b × 31b = × *Asplenoceterach badense* D.E. Meyer, Ber. Deutsch. Bot. Ges. 70: 61(1957) = *Asplenium ruta-muraria* × *Ceterach officinarum*. Descr. from Kaiserstuhl, s.w. Germany. Type: B. Found once in Switzerland also, but not yet elsewhere. Assumed (CeCe' RuRu') D.E. Meyer (1959: 46). This corresponds to a delayed allotetraploid. The plant had mainly abortive, but probably also some good spores.

20 × 31b = × *Asplenoceterach barrancense* W. Bennert & D.E. Meyer, Willdenowia 6: 463 (1972) = *Asplenium majoricum* Litard. × *Ceterach officinarum* DC. in Lam. et DC. Descr. from Mallorca. Type: B. Not found elsewhere. Cytology not examined (the plant died).

12.6.2. × *Asplenophyllitis* Alston (1940)

29c × 33a = × *Asplenophyllitis confluens* (T. Moore) Alston, Proc. Linn. Soc. London 152 (2): 139(1940) = *Asplenium trichomanes* × *Phyllitis scolopendrium*. Descr. from England (Cumberland). Type: K, Herb. Moore (teste Alston). Alston gave two more records from England and Ireland. It has since been found in Yugoslavia (Mayer 1963) on limestone. Cytology not examined. The present author could see the plant from Yugoslavia and also the place where it had been collected. Masses of *A. trichomanes* ssp. *quadrivalens* and *Phyllitis* were growing there. This very rare hybrid is the triploid cross derived from ssp. *quadrivalens*, it was resynthesized by Lovis (see Stace 1975: 105).

1 × 33a = *Asplenophyllitis jacksonii* Alston, Proc. Linn. Soc. London 152(2): 142(1940) = *Asplenium adiantum-nigrum* × *Phyllitis scolopendrium*. Descr. from England (Devon). Lectotype: Herb. Moore (K), see Lovis & Vida (1969: 57 and fig. 17). Reported also from the Channel Islands (Guernsey & Jersey). Produced under experimental conditions by Lovis & Vida (1969). Triploid (CuOnPh).

7 × 33a = *Asplenophyllitis microdon* (T. Moore) Alston, Proc. Linn. Soc. London 152(2): 140 (1940) = *Asplenium billotii* × *Phyllitis scolopendrium*. Descr. from Guernsey. Lectotype: Herb. Moore (K), see Lovis & Vida (1969: 57 and fig. 14). Recorded several times from Guernsey, also from Cornwall. Cytology see Girard & Lovis (1968) and resynthesis Lovis & Vida (1969). Tripl. (BiBiPh).

1b × 33a = × *Asplenophyllitis kummerlei* G. Vida, Acta Bot. Acad. Sci. Hung. 6: 431(1960) = *Asplenium lepidum* × *Phyllitis scolopendrium*, see Vida (1963, 1964, 1970). Descr. from s. Hungary, near Pécs. Habitat now destroyed by construction of a factory, but plant kept in cultivation in Budapest and Basel and propagated by division. Tripl. with c. 108^I at meiosis (Vida 1963) corresponding to (AeRuPh). Also resynthesized by Vida (1965) and by Brownsey (unpubl.). Sterile.

Appendix I. New hybrids

$2 \times 26b = \textit{Asplenium} \times \textit{lobmingense}$ Lovis, Melzer & Reichst. *hybr. nova* = *A. adulterinum* Milde \times *ruta-muraria* L. ssp. *ruta-muraria*.

Diagnosis. Planta hybrida, *A. \times clermontae* simillima, ab eo recedens: rhachide tota viridi, petiolo solum ad basim fusco; sporis omnibus abortivis, bene efformatis nullis; chromosomatibus meiosi ca. 30-36 bivalentibus et 72-84 univalentibus.

Type: Austria, Steiermark, Mur valley, steep serpentine rocks at c. 800m alt., c. 1.7 km NNW of the church of Lobming (S.E. and above St. Stephan), leg. H. Melzer, 20.6.1974. One frond preserved will be deposited at BM. Living plant taken into cultivation as TR-1236. General appearance very similar to *A. \times clermontae* Syme, but even in mature fronds only the base of the stipe is brown, the upper part and rachis being green. Spores completely abortive. Tetraploid like *A. \times clermontae*, but at meiosis showing only c. 30-36 pairs, the other 72-84 chromosomes as univalents. This is in agreement with the genome formula (RuRu'TrVi). Fig. 8 E.

The hybrid has been synthesized by Lovis (unpublished). The experimentally produced plants had the same morphology and showed the same pairing behaviour at meiosis.

$2 \times 28c = \textit{Asplenium} \times \textit{praetermissum}$ Lovis, Melzer & Reichst. *hybr. nova* = *A. adulterinum* Milde \times *A. trichomanes* L. ssp. *quadrivalens* D. E. Meyer. This tetraploid is relatively common among the parents and has already been collected many times, but has never been described.

Diagnosis. *Asplenio trichomanes* ssp. *quadrivalens* proximum, sed apex rhachidis per 2-6 mm viridis; sporis abortivis; chromosomatibus 144, meiosi circiter 36 binis, circiter 72 univalentibus.

Type: Austria, Steiermark, serpentine rocks above Trafös, c. 1000m alt., 6.9.1964, leg. H. Melzer, J.D. Lovis, A. Sleep & T. Reichstein. Cult. in Basel TR-1341. Plant preserved 1.7.1968(G). Fig. 9 C.

Similar to *A. trichomanes* ssp. *quadrivalens*, but even in the mature state the tip of the rachis is green for c. 2-6 mm of its length; spores abortive; tetraploid with c. 34-36 pairs and c. 72-76 univalents at meiosis, compatible with the formula (TTT'Vi). Synthesized in Leeds by Lovis (unpubl). In the triploid *A \times trichomaniforme* the green tip at the rachis is usually slightly longer (3-8 mm), the end pinna a little narrower (more pointed), and the larger pinnae more roundish (less long).

$7 \times 23 = \textit{Asplenium} \times \textit{cyrnosardoum}$ Rasbach, Vida & Reichst. *hybr. nova* = *A. billotii* F. W. Schultz \times *obovatum* Viv.

Diagnosis. Planta hybrida, forma foliorum *Asplenio billotii* similis, sed dentibus paulo minus distinctis; sporis abortivis; chromosomatum numerus somaticus 108, meiosi circiter 36 binis, 36 univalentibus.

Type: Corsica, La Trinité (W of Bonifacio), near the monastery, between the parents. 26.4.1971, leg. H. & K. Rasbach. Fronds preserved (G). Plant collected in living state for cytological examination. Fig. 10 A.

Similar to *A. billotii*, but teeth slightly less pronounced, mature sori orange-brown spores abortive; triploid with 0-3 trivalents, 31-36 bivalents and 35-37 univalents at meiosis (G. Vida in litt. 29.11.1971). This would be compatible with (ObObOb') and (BiBi'Ob), i.e. assuming *A. billotii* to be an autotetraploid derived from chromosome doubling in either *A. obovatum* or in another related, diploid species. The hybrid has been synthesized experimentally by Sleep (1966, mentioned c. 1982) but the cytology not examined.

14 × 24 = *Asplenium* × *rusciniense* Nieschalk, Lovis & Reichst. *hybr. nova* = *A. forisiense* Le Grand × *A. onopteris* L.

Diagnosis. Planta hybrida, *A. forisiense* sat similis, sed ab eo recedens; lamina circumscripta elongato-deltaoidea, id est, pinnis basalibus sequentibus aequilongis vel iis longioribus, ad apicem longe acuminatis; sporis abortivis; numero chromosomico somatico $2n = 108$, meiosi chromosomatibus fere omnibus univalentibus.

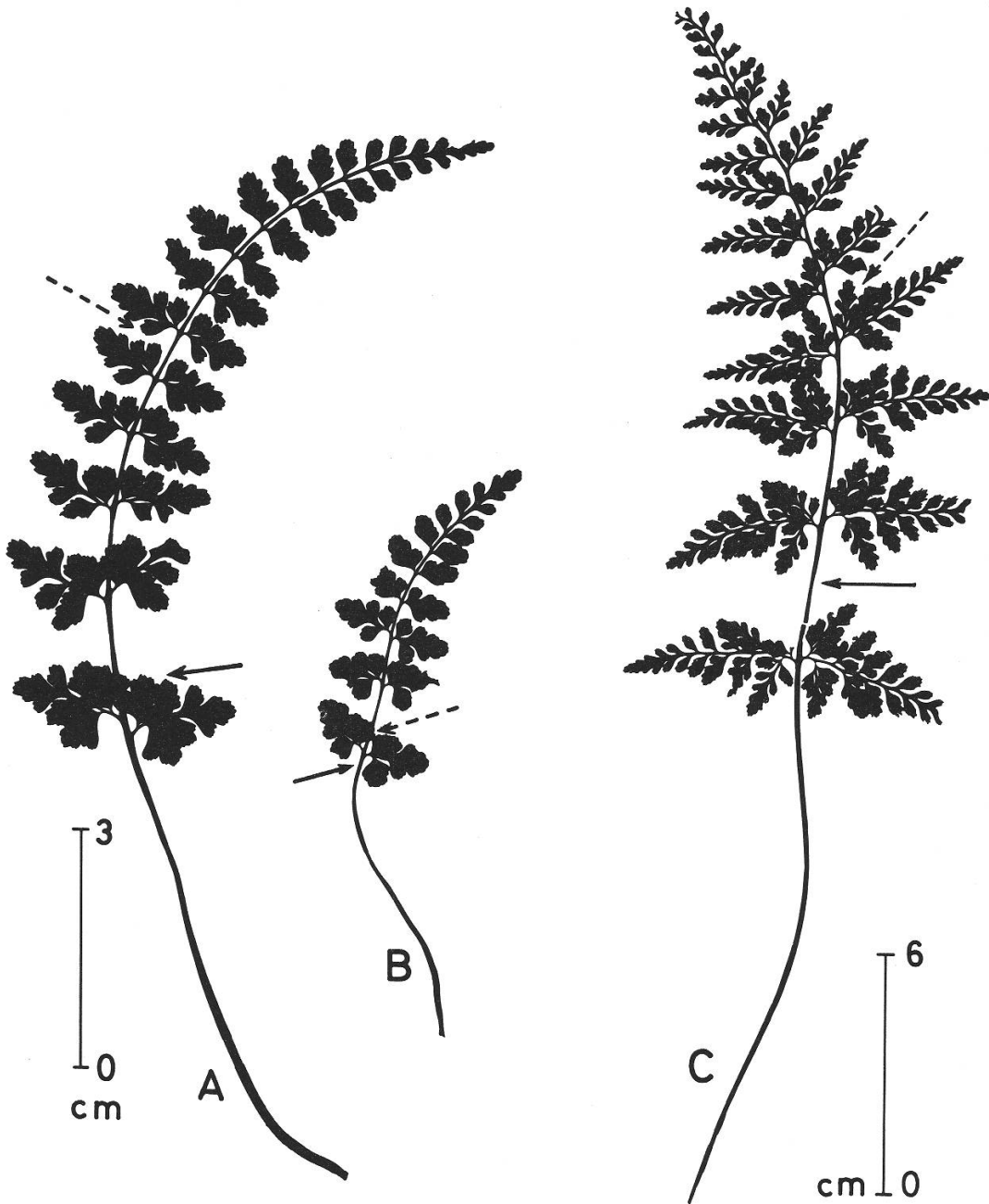


Fig. 5. A, B = *A. × bechereri*, (CuOnTrVi), A = TR-2337, B = 2357, see Appendix II. C = *A. × sarniense*, (CuOnBiBi), AS-1104, Guernsey, paratype.

The arrows in this and the following figures give the upper limit of brown colour on the upper (adaxial) side (solid line) and on the lower (abaxial) side (broken line).

Type: France, Roussillon (Dép. Pyr. or.), silicate-schist rocks, near Cerbère, c. 150 m alt., among the parents. 15.6.1968, leg. A. & Ch. Nieschalk. The living plant was brought to Basel and kept in cultivation for cytological examination as TR-2198. Preserved fronds deposited in G. Fig. 11 A.

This hybrid is not conspicuous and not easy to detect. It differs from *A. forisiense* mainly in the distinctly elongated tip and the lowest pair of pinnae being at least as long as, usually slightly longer than, the next. Spores abortive. Triploid with most or often all the chromosomes as univalents at meiosis, compatible with (FoObOn). Several plants of this hybrid have been synthesized by Sleep (1966, c. 1982) in both possible ways. They showed similar morphology and the same behaviour: complete failure of chromosome pairing at meiosis.

$18 \times 26a = \textit{Asplenium} \times \textit{eglii}$ Lovis & Reichst. *hybr. nova* = *A. lepidum* C. Presl \times *A. ruta-muraria* L. ssp. *dolomiticum* Lovis & Reichst. [= *A. dolomiticum* (Lovis et Reichst.) Löve & Löve].

Diagnosis. *Asplenio lepidum* simillimum, ab eo recedens pilis glanduligeris nullis vel paucissimis, sporis abortivis et numero chromosomico somatico $2n = 108$, meiosi chromosomatibus fere circa 36 bivalentibus et 36 univalentibus.

Type: N. Italy, Buco di Vela, W. of Trento, dolomitic rocks, c. 410 m alt., among the parents. Collected living (as assumed *A. lepidum*) by E. Hauser & Th. Egli, in May 1960, cult. first in Egli's greenhouse. Obtained 24.10.1962 and cult. in Basel as TR-786. Fronds preserved 19.11.1966. G, isotypes BM, FI. Fig. 13 A.

Shape of fronds and colour (yellowish-green) similar to *A. lepidum*, but less glandular or nearly glabrous; sori also in basal position, but spores abortive. Triploid, $2n = 108$ with c. 36 pairs and c. 36 univalents at meiosis, in agreement with the genome formula (AeRu Ru). The place was revisited by Lovis, Hauser and Reichstein on 11.9.1963, when two more hybrids were detected, photographed and another plant (TR-945) collected. This gave the same cytological results. The hybrid will probably occur in other places where the parents grow together.

Theodor Egli (1912-1975) established a private botanical garden, first at Schönau (above Hütten, Ct. Zürich), then at Ennetbühl (Ct. St. Gallen), raising rare alpine plants and exchanging seeds. His *Asplenium* hybrid gave us the clue to search for diploid *A. ruta-muraria*.

$26 \times 26b = \textit{Asplenium} \times \textit{baldense}$ Sleep, Vida & Reichst., *hybr. nova* = *A. ruta-muraria* L. ssp. *dolomiticum* Lovis et Reichst. [= *A. dolomiticum* (Lovis et Reichst.) Löve & Löve] \times ssp. *ruta-muraria* [*A. ruta-muraria* sensu Löve et Löve].

Diagnosis. Planta hybrida, ex *A. ruta-muraria* ssp. *dolomiticum* et ssp. *ruta-muraria* orta; facie *A. ruta-murariae*, sed ab eo recedens: sporis abortivis, numeroque chromosomico somatico $2n = 108$, chromosomatibus meiosi trivalentibus pluribus.

Type: E. side of Mt. Baldo, n. Italy, dolomitic rocks near path from S. Zeno to Costabella, c. 1500 m alt., among the parents. 13.9.1970, leg. E. Hauser, A. Sleep and T. Reichstein TR, 3157. Plant and parents taken into cultivation at Basel for cytological examination. Fronds preserved 4.6.1972 as type G, isotype BM, Z.

More plants of the hybrid were found in the vicinity between c. 1400 and 1700 m alt. Some were distinctly glandular. The same was observed for both cytotypes of *A. ruta-muraria* growing there as well as in some other localities in n. Italy. This triploid hybrid ($2n = 108$) had already been found by Meyer (1958: 19) at a time when the diploid *A. ruta-muraria* was not yet known; he assumed it to be *A. ruta-muraria* \times *viride*. It was

called *A. × meyeri* Rothm., *Exkursionsfl. v. Deutsch. IV: 5*(1963), *nom. nudum* (Rothmaler's premature death did not permit him to validate this and some other names).

The hybrid is indistinguishable in gross morphology from both diploid and tetraploid *A. ruta-muraria*, but can be recognized by the abortive spores (sporangia often red-brown) and by cytological examination. It is triploid (RuRuRu) and at meiosis the

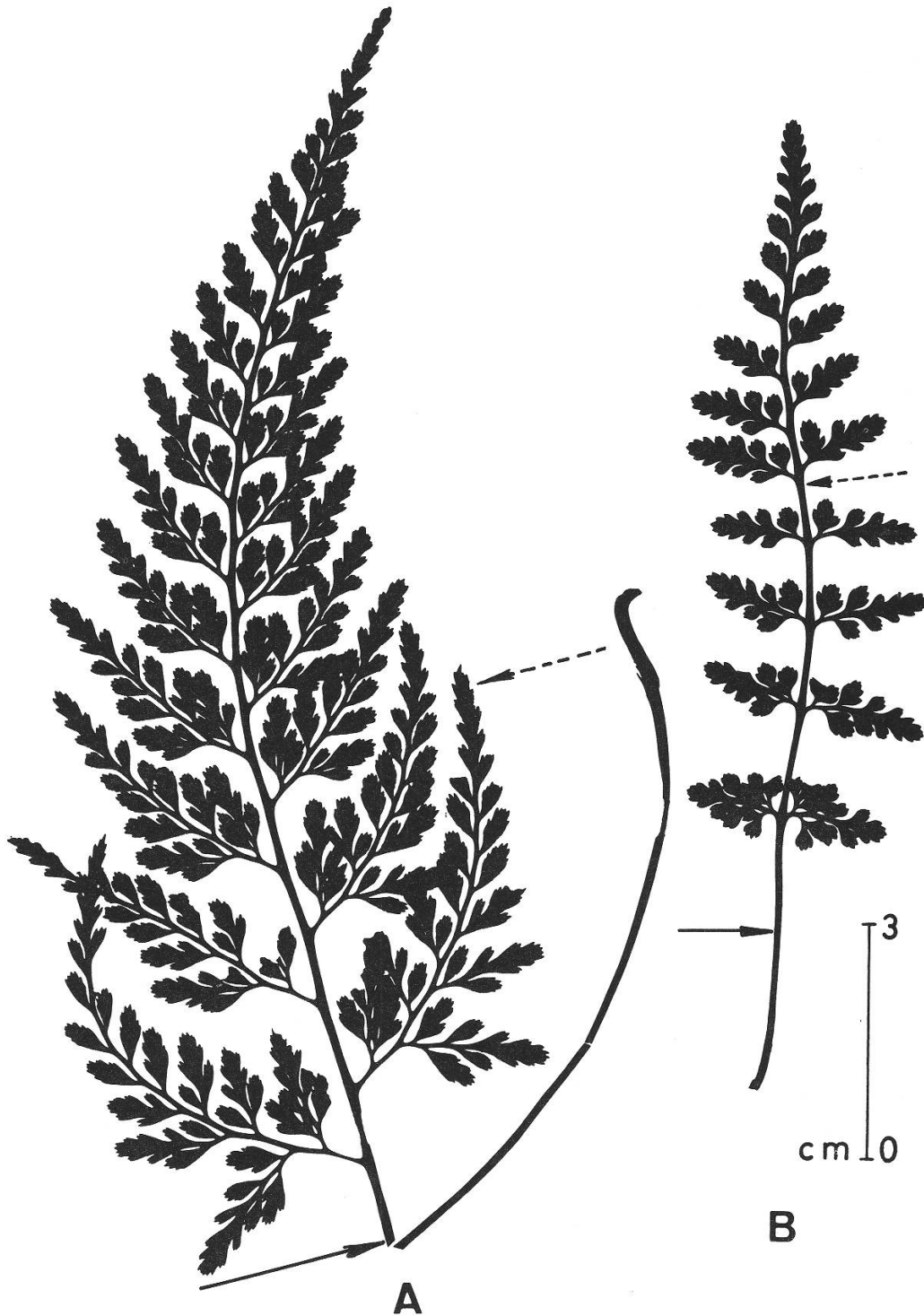


Fig. 6. A = *A. × centovallense* (CuCuOn) TR-2397; B = *A. × brissaginense* (FoObCuOn) TR-4448-A, from France, Lamastre (W. of Valence), W. & C. Bennert, 20. w. 1972, since 10.10.1977 cult. in Basel.

majority of the chromosomes form trivalents (Vida in litt. 10.3. and 4.9.1971). It forms easily and has been synthesized under experimental conditions several times, showing the same behaviour at meiosis (Vida 1970: 541-543); Bouharmont 1972: 378).

$(26b \times 28b) \times 28b = \textit{Asplenium} \times \textit{hungaricum}$ Fraser-Jenkings & Vida *hybr. nova* = *A. \times murbeckii* Dörfler \times *A. septentrionale* (L.) Hoffm.

Diagnosis. Planta hybrida tetraploidea, structura inter *A. \times murbeckii* et *A. septentrionale* interjecta; differt ab *A. \times murbeckii* segmentis plerumque angustioribus, sporis perfecte abortivis, meiosi chromosomatibus trivalentibus circ. 6–13, atque paribus minus et univalentibus plus quam in *A. \times murbeckii*.

Type: N. Hungary, on gabbro rocks, near Bator (vicinity of Eger), among the parents and *A. ruta-muraria*, September 1969, leg. C.R. Fraser-Jenkins and G. Vida. Coll. living, cult. in Budapest, since 6.9.1971 in Basel. Preserved fronds deposited in BM, isotypes BP, G. Fig. 16 D.

Plant similar to *A. \times murbeckii*, but segments of the fronds narrower, more pointed and less spatulate. Spores completely abortive, no good spores visible. Tetraploid, but with c. 6–13 trivalents, c. 23–30 pairs and c. 59–66 univalents at meiosis. This is compatible with the genome formula (RuSpSpSp') and corresponds well with the experimentally produced backcross (Lovis 1977: 365), which had similar gross morphology.

This plant is unique, representing the first really true natural backcross of an *Asplenium* hybrid.

Appendix II. New cytological results

$1 \times 2 = \textit{A. \times bechereri}$ D.E. Meyer. New interpretation by J.D. Lovis, H. & K. Rasbach & T. Reichstein. Dr. Meyer obtained the herbarium specimen collected by Becherer and Mokry with the indication that it had been growing on serpentine between *A. adulterinum* and *A. cuneifolium*. Examination showed that it was a hybrid and the morphology seemed to fit a cross between these two species.

On 28.9.1968 R. Gumprecht, on an excursion with H. & K. Rasbach and O. Wilmanns to the upper Valle Cannobina (s.e. of Malesco, E. of Domodossola), n. Italy, found an excellent specimen of the hybrid on serpentine containing rocks, c. 1.3 km E. of Finero, at c. 850 m (Rasbach et al. 1969: 135). It was turned over to us for cultivation (TR-2337). To our great surprise it proved to be tetraploid, a very good cell showing 3^{II} and 138^I at meiosis (J.D. Lovis in litt. 8.6.1969).

The area was revisited on 19.10.1968 by H. & K. Rasbach & T. Reichstein, when Mrs. Rasbach found another specimen of the rare hybrid, c. 1.75 km E. of Finero. It was left in situ, but a frond was preserved and fixings were made (TR-2357); it was again seen by Lovis & Reichstein on 15.9.1969, but it had disappeared in 1980 (TR). This second plant was also tetraploid, showing only univalents (det. Lovis in litt. 26.10.1969). Careful search revealed that beside *A. adulterinum* and *A. cuneifolium* a small plant of *A. adiantum-nigrum* (TR-2829, tetraploid, det. J.D. Lovis) was growing only 20 cm from *A. \times bechereri* and also a plant of the triploid hybrid *A. \times centovallense* (TR-2356) within a distance of less than 2 m.

In both specimens of our *A. \times bechereri* the fronds matched very well those of \pm equal size of the isotype (loan from Dr. A. Becherer). We are therefore forced to conclude that it represents the cross *A. adiantum-nigrum* \times *adulterinum* with the genome formula (CuOnTrVi), in agreement with the cytology.

This makes it understandable why *A. × bechereri* has never been recorded from the large and well searched serpentine areas in Austria (near Kraubath and elsewhere), where *A. adulterinum* and *A. cuneifolium* grow together in abundance. There is no *A. adiantum-nigrum* present (perhaps for climatic reasons), and *A. × centovallense* is therefore also absent (it is common in s. Switzerland and n. Italy).

1 × 10 = *A. × centovallense* D. E. Meyer. Cytology of the wild hybrid by J. D. Lovis, H. & K. Rasbach & T. Reichstein. Again Meyer had only the preserved specimen for his description and quoted the cytological results of Manton (1961) obtained by Shivas from the experimentally produced hybrids *A. adiantum-nigrum* × *cuneifolium*.



Fig. 7. *A. × ticinense* (CuOnOn), TR-3444. Switzerland, Ct. Ticino, c. 100m W. of Arogno, C. 600m alt., leg. E. Attinger, 22.11.1972.

We give here the result for the natural hybrid TR-2356 growing near *A. × bechereri* (see above), among many plants of *A. cuneifolium*, some of *A. adiantum-nigrum* and some other ferns, northern Italy, Valle Cannobino, c. 1.75 km e. of Finero, mixed serpentine containing rocks, leg. H. & K. Rasbach & T. Reichstein 19.10.1968. Spores abortive. Taken living into cultivation. Fixings to Leeds, were triploid with c. $36^{II} + 36^I$ (J. D. Lovis in litt. 29.10.1968). Other plants gave similar results.

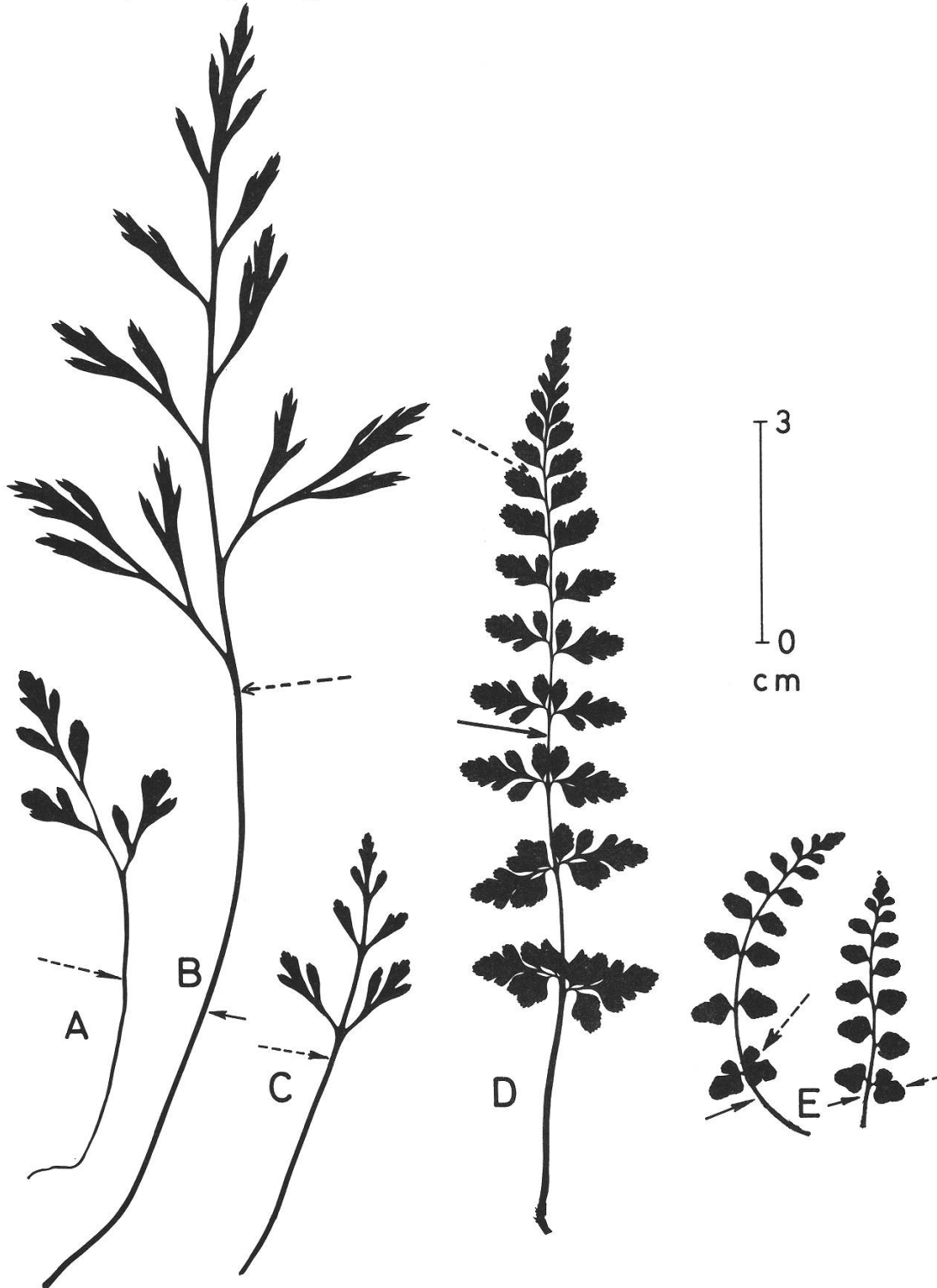


Fig. 8. A, B, C = *A. × contrei* (CuOnSpSp); A, C = TR-456; B = TR-459, both from *locus classicus*. D = *A. × dolosum* (CuOnTr), TR-3324, see Appendix II; E = *A. × lobmingense* (RuRu'TrVi), type specimen, TR-1236, see Appendix I.

The hybrid is very common in places where both parents grow together. In particular situations it may become more frequent than *A. cuneifolium*, because it is more resistant to drought etc. and longer lived. Small specimens are \pm similar to *A. adiantum-nigrum*, larger ones with fronds up to 50 cm long may be rather similar to *A. × ticinense*. An exceptionally large plant (TR-2376), with fronds up to 60 cm long, first suspected to be *A. onopteris*, was found 20.10.1968 on serpentine scree c. 50m above the ski-escalator

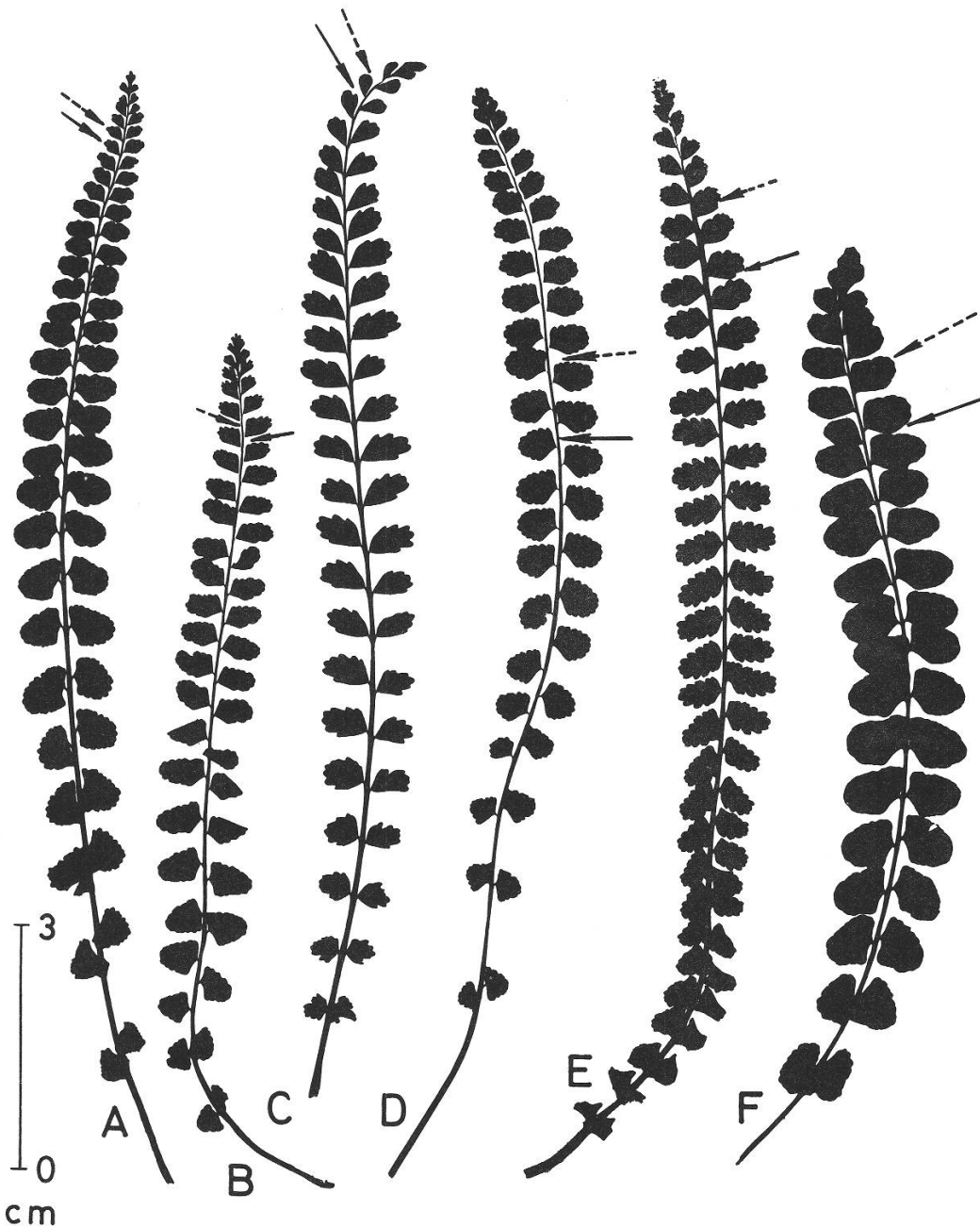


Fig. 9. A = *A. × trichomaniforme* (TrTrVi), TR-1589, Kienberg near Bernstein, Austria; B = *A. × bavaricum* (TrTrVi), TR-2774, n. Italy, limestone-dolomitic rocks, along small road to Andreis (E. of Belluno), c. 400m alt., H. Kunz, H. Melzer & T. Reichstein, 4.8.1969; C = Tetraploid hybrid *A. adulterinum* × *trichomanes* 4x, (TrTrTrVi), TR-1342, see Appendix I; D = *A. × poscharskyanum* (TrViVi), TR-921, Kraubath, Austria, 5.9.1969; E = *A. × protoadulterinum* (TrVi), WG-70. Type specimen, cult.; F = *A. × adulteriniforme* (Tr'Vi), TR-823, Type specimen, cult.

station S. of Druogno, Valle Vigezzo (E. of Domodossola, n. Italy), leg. H. & K. Rasbach & T. Reichstein. But it had bad spores and was triploid (det. J.D. Lovis). No true *A. onopteris* was growing in the vicinity, but much *A. cuneifolium*, *A. adiantum-nigrum* and other fern species (Rasbach et al. 1969). It was taken into cultivation at Agarone (s. Switzerland) out of doors in limefree soil. After two years it produced normal fronds. c. 40 cm long, matching well typical *A. × centovallense*.

Synthesis and cytology of the experimental hybrid was described by Shivas (1969).

$1 \times 24 = A. \times \text{ticinense}$ D. E. Meyer. Cytological investigation by Reichstein & Vida.

A plant collected in Corsica, Gorge de la Restonica, c. 1000-1050 m alt., 21.9.1971, leg. A. Sleep & T. Reichstein, cult. in Basel as TR-3270 was triploid with $n = c. 36^{II} + 36^I$ at meiosis (G. Vida in litt. 14.10.1974). Several plants of this hybrid were growing in this place among many of both parents. The cytological result corresponds to the report of Shivas (1969) for the synthetic hybrid.

$1 \times 29a = A. \times \text{dolosum}$ Milde. Cytological investigation by Reichstein & Vida.

Material: The plant (TR-3324) was found in Switzerland, Ct. Ticino, gneiss wall (without mortar), near the road from Cugnasco to Medoscio at c. 420 m, among the parents. Leg. H. L. & T. Reichstein, 8.2.1972, since then cult. in Basel. It grew well and the shape of the fronds matched very well the figures of Milde (1864: 165 tab. 4) and Luerksen (1889: 258), with the stipe and the greater part of the rachis blackish-brown. Fixings sent to Vida were found to be triploid with 108 univalents at meiosis; this is completely compatible with the genome formula (CuOnTr).

Theoretically a tetraploid hybrid of *A. adiantum-nigrum* with *A. trichomanes* ssp. *quadrivalens* should also be possible, but would be expected to be closer to *A. trichomanes*. We therefore are confident that Milde's material did indeed also represent the triploid hybrid.

$2 \times 29a = A. \times \text{trichomaniforme}$ Woynar, investigated by Lovis, Melzer & Reichstein. Identification of the type: During a visit to Graz J.D. Lovis could examine the specimen in GJO. After careful comparison with both experimentally produced and cytologically checked hybrids: *A. adulterinum* \times *trichomanes* ssp. *trichomanes* (triploid hybrid) and *A. adulterinum* \times *trichomanes* ssp. *quadrivalens* (tetraploid hybrid) he was able to conclude that Woynar's type is the rare triploid.

On 6.9.1964 the *locus classicus* (serpentine rocks above Trafös) was visited by H. Melzer, J.D. Lovis, Anne Sleep & T. Reichstein. In a small, shady ravine at c. 750 m *A. adulterinum* was growing together with much *A. trichomanes* ssp. *trichomanes* (teste Lovis) (TR-1346) and without any ssp. *quadrivalens*. In spite of two hours' search, no hybrid was found.

Much higher up, at c. 1000 m, on more exposed rocks, ssp. *quadrivalens* was growing, and soon the tetraploid hybrid could be detected (TR-1341, 1342).

The true triploid hybrid (two plants) was found by Melzer on the Kienberg near Bernstein (Austria) among the parents on 12.10.1965 and sent living to Basel, cult. as TR-1588 and 1589. The first gave good fixings and was found to be triploid with $c. 36^{II} + 36^I$ at meiosis (Lovis in litt. 3.7.1967). This is the same result as for the synthetic hybrid (Lovis 1954).

Two other plants (TR-2361 and 2362) of the triploid hybrid were found in a wall of serpentine rock c. 1.6 km E. of Finero (Valle Cannobino, n. Italy), at c. 830 m among the parents, leg. H. & K. Rasbach & T. Reichstein 19.10.1968.

14 × 29c = *Asplenium* × *pagesii* Litard. Examined by J. D. Lovis and T. Reichstein. The following three plants were studied cytologically TR-862. Switzerland, Ct. Ticino, old vineyard, gneiss wall without mortar, between Brissago and Piodina at c. 300 m alt., 1.6.1963, leg. T. Reichstein, since then cult. in Basel (cool greenhouse during winter) and propagated by division, still in good state (1981). Fronds of plant originally very small (4-6 cm long), unipinnate, in appearance ± like those of an *A. adulterinum* with long



Fig. 10 A = *A. × cyrnosardoum* (BiBiOb) or (ObObOb), TR-3219, see Appendix I; B, C = *A. × woynarianum* (CuVi). B = TR-920, Kraubath, Austria, H. Melzer, J.D. Lovis & T. Reichstein, 5.9.1963. C = TR-1045, Tanzmeistergraben, above Leoben, Austria, leg. H. Melzer, 21.10.1963, cult. in Basel (72¹, det. J.D. Lovis).

green tips, after increasing in size becoming bipinnate like fig. in F. W. Stansfield, Brit. Fern Gaz. 6: 307(1934).

TR-1802. Switzerland, from the same area at c. 320 m alt., was discovered on 17.6. 1966 and only collected living on 14.10.1966, just a day before the place was destroyed by house building. The morphology of this plant also changed with size.

TR-3105. Spain, Prov. Gerona, c. 2 km S. of Port Bou (Fraile) on silicate rocks, c. 200 m alt., 22.5.1970, leg. J. Koch. Cultivated in Basel since 1.7.1970, still growing well (1981). This originally had also small unipinnate fronds, \pm like *A. adulterinum*, became large and bipinnatifid like fig. in Kestner, Brit. Fern Gaz. 7: 19(1935), i.e. less divided than the Swiss plant (TR-862 and TR-1802). All these specimens were tetraploid (reported for the first time by Meyer 1967: 34) with c. $33^{II} + 78^I$ at meiosis (Lovis in litt. 5.5.

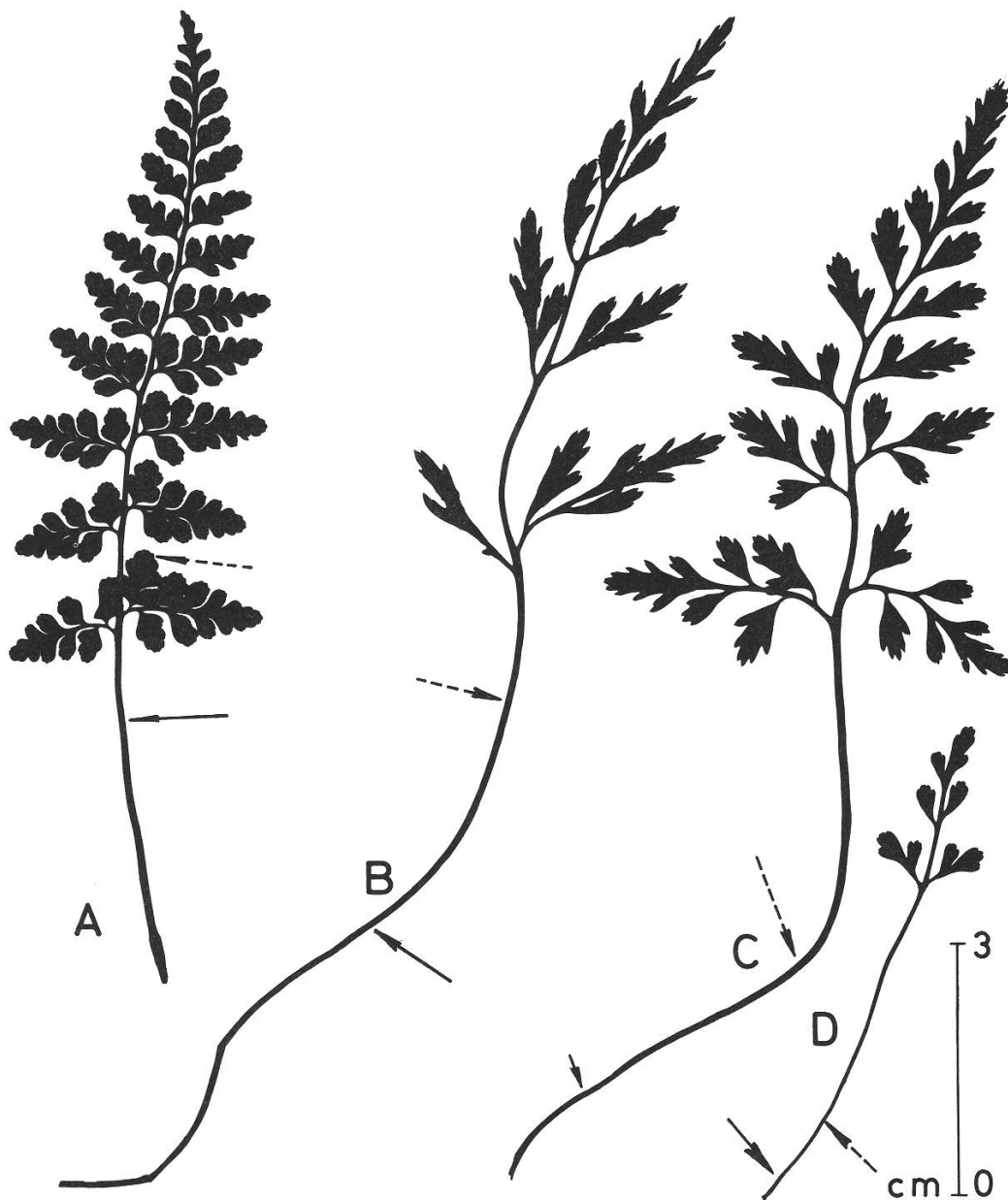


Fig. 11. A = *A. × ruscionense* (FoObOn), TR-2195, type (App. I.); B = *A. × souchei* (BiBi'SpSp'), isotype ex herb. J. Callé; C, D = *A. × costei* (FoObSpSp'). B = TR-1519, France, Val Vizézy near Montbrison, leg. A. & Ch. Nieschalk, 17.6.1965, since then cult. at Basel. C = TR-1210 from same locality, wild coll. TR. 6.6.1964.

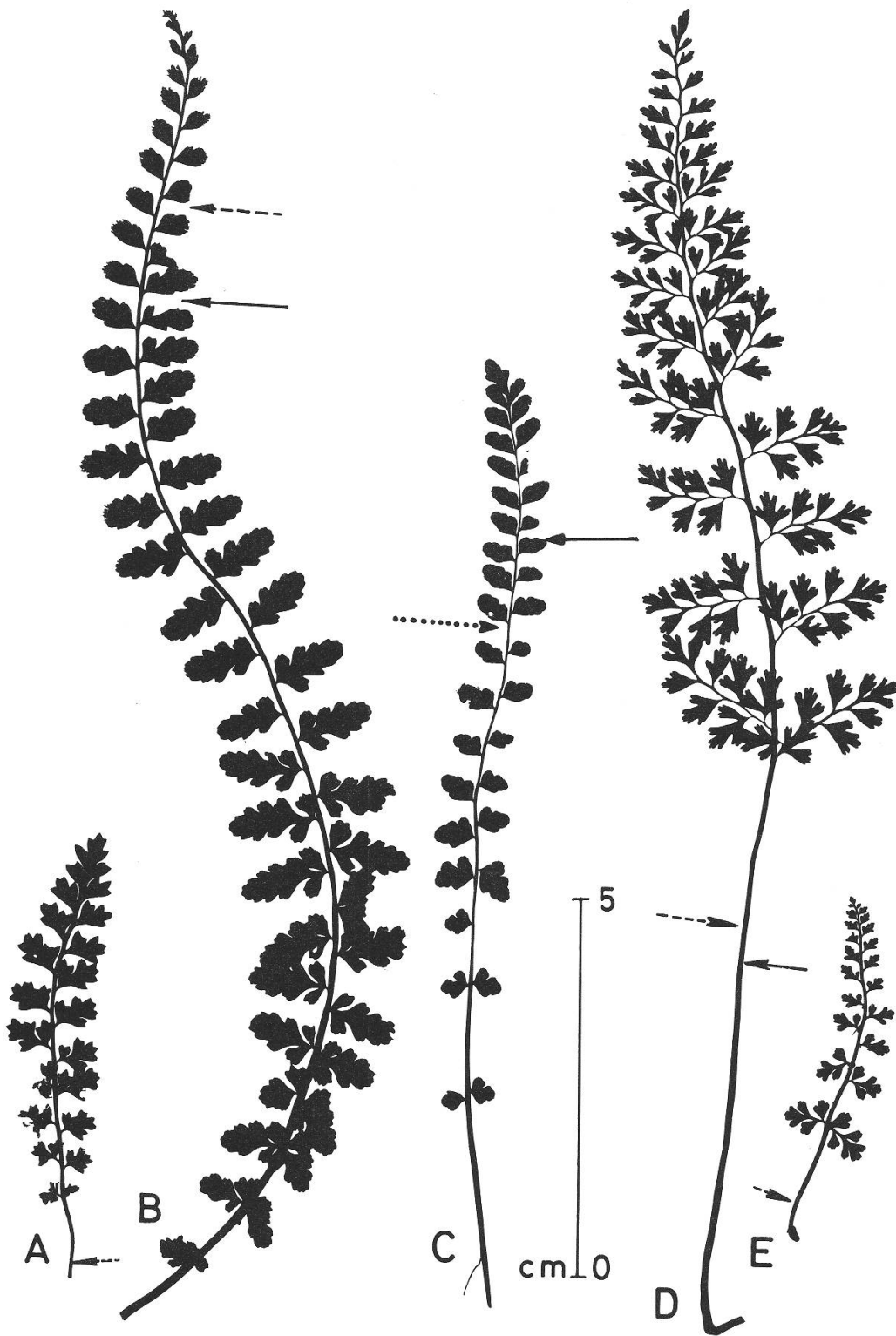


Fig. 12. A = *A. × gastonii-gautieri* (FoVi) D.E. Meyer-1822 from Switzerland; B, C = *A. × pagesii* (FoObTrTr), both after cultivation. B = TR-862 from Switzerland; C = TR-3165 from Spain (see App. II). D, E = *A. × lessinense* (FiVi) from *locus classicus*, TR-4734 from large plant, TR-2748 from small plant.

1966; 23.8.1971). Theoretically a triploid hybrid *A. forisiense* × *A. trichomanes* ssp. *trichomanes* should also be possible. In morphology it can be expected to be closer to *A. forisiense* than the tetraploid. Litardière has described a hybrid as *A. × guichardii* (= *A. perforasiacum* × *trichomanes*) Litard., Bull. Géogr.-Bot. (Le Mans) 21: 75-77 (1911), but at best this corresponds to the more developed form of *A. × pagesii*.

25b × 29c = *A. × nieschalkii* D.E. Meyer. Investigated by A. Nieschalk, J.D. Lovis, T. Reichstein and G. Vida. This hybrid was found to be tetraploid ($2n = 144$) by Meyer (1963), but he did not analyse its meiosis. We could check the following plant: Spain, Prov. Málaga, limestone rocks near Beñaojan, W. of Ronda, 8.6.1971, leg. A. & Ch. Nieschalk, brought to Basel for cultivation as TR-3229. Fixings sent to Leeds on 29.7.1971 showed that the plant was indeed tetraploid, but its meiosis gave an unexpected result. In the only two analysable cells obtained at that time Lovis found $29^{II} + 86^I$ and $30^{II} + 84^I$ (in litt. 12.5.1972). Vida (in Budapest) agreed to count another fixing independently, sent to him 28.4.1975. Without knowing Lovis' former results, he reported (in litt. 8.5.1975): «tetraploid hybrid, but showing surprisingly low number of bivalents! $n = c. 30^{II} + 84^I$, in many cells.» It is therefore unquestionable that despite the genome formula (PePe'TrTr') which must be attributed to it this plant did not behave like a delayed allotetraploid.

Should another specimen of this rare hybrid become available, it should be checked again together with the parent species from the immediate vicinity. It may be that a special strain of one or other of the parents is responsible for the unexpected behaviour.

26b × 29c = *A. × clermontae* Syme. Investigated by J.D. Lovis, H. Melzer and T. Reichstein (see Lovis 1977: 367).

Material: Living fragments of two plants collected in May 1964 by H. Melzer in Austria (precise locality not disclosed for reasons of protection) were sent to Basel, cultivated and propagated by division as TR-1073 and TR-1075. Still growing well in pots out of doors (1981). H. Melzer found another small plant in Austria, Steiermark, dolomitic and sandstone rocks of the Admonterkogel near Graz-St. Gotthard (the so-called «Klettergarten»). It was also propagated as TR-1427 in Basel, and is still growing well (1981). Fixings and plants were sent to Leeds. A fourth plant was collected in the gorge of Valganna, n. Italy, Prov. Varese, 1969 by R. Schweizer, given to T. Reichstein on 3.6.1970 and cultivated in Basel. Morphologically this plant was slightly different, the stipes being a little longer and the lowest pair of pinnae distinctly larger than the next. It was less vigorous.

All four plants turned out to be tetraploid and produced a high number of bivalents at meiosis. In some cells all the chromosomes were paired, giving 72 bivalents. Their sporangia contained abortive material, but quite a number of good spores were visible (see fig. 2.B).

Sowing of sporangial content of TR-1075 gave many prothallia, and c. 20 sporophytes were raised in Basel. All showed correct morphology, but about 12 were very poor growers, some died, six surviving remained crippled even after four years; the eight plants which had grown well from the beginning after two years reached almost the same size as the original stock. No segregation of characters was visible. Even so, the plants obtained by division were more vigorous. The sporangial content in the progeny was also similar. There is no question that *A. × clermontae* is able to multiply to a very limited extent by means of spores, but under natural conditions it will hardly have the chance to do so.

28b × 29c = *A. × heufleri* Reichstein. Investigated by J. D. Lovis and T. Reichstein.

Material: TR-476. Living fragment of plant coll. in Switzerland, Ct. Graubünden, Poschiavo, gneiss wall without mortar, near Ginetto, N. of Brusio, c. 890 m, 19.8.1961, leg. H. Kunz, E. Oberholzer & T. Reichstein (det. by G. Eberle). Cult. in Basel and propagated by division. Grows well but needs cool greenhouse during winter.



Fig. 13. A = *A. × eglia* (AeRuRu), TR-786, type, see App. I; B = *A. × javorkae* (AeRuRuRu), TR-932, Bärenschützklamm near Mixnitz, Austria, 7.9.1963, H. Melzer, J.D. Lovis & T. Reichstein; C, D = *A. × stiriacum* (AeRuTr'). C = TR-930, Hohe Wand, Austria, c. 700m, 6.9.1963; D = TR-1260, Drachenhöhle near Mixnitz, Austria, c. 900m, 8.6.1964; E, F = *A. × aprutianum* (AeRuTrTr'). E = TR-700, type specimen (Abruzzo), cult.; F = TR-789, Austria, Gahnsleiter near Payerbach, H. Melzer, 30.10.1962, cult. in Basel.

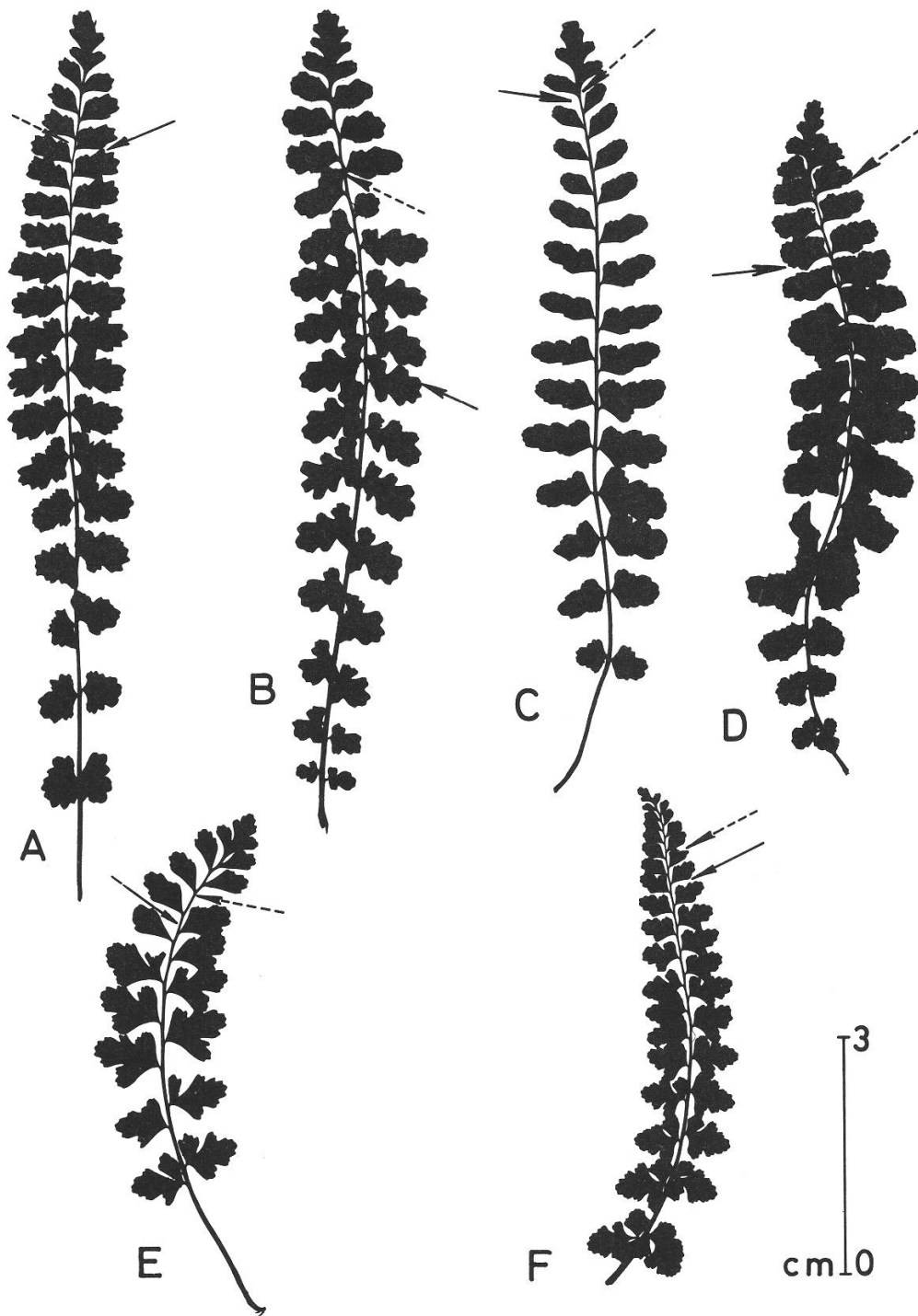


Fig. 14. A. \times *orellii* (FoPeTrTr), TR-1652, Mallorca, near Biniaraix, 16.3.1966, leg. H.R. & T. Reichstein, cult. frond preserved 11.2.1967. B = A. \times *sollerense* (FoPePePe'), TR-1675, Mallorca, same place, 18.3.1966, leg. H.L. & T. Reichstein, cult. frond preserved 19.5.1968. C = A. \times *nieschalkii* (PePeTrTr), TR-3226, Spain, Prov. Málaga, limestone rocks near Beñaajan (w. of Ronda), leg. A. & Ch. Nieschalk, 8.6.1971, cult. in Basel, frond preserved 6.7.1972. D = A. \times *litardierei* (PePe'Tr), Mallorca, near Biniaraix, leg. H. Bennert, 10.4.1971, obtained living in Basel 13.2.1973, frond preserved 17.12.1973. E = A. \times *reuteri* (HaHaTrTr), exper. produced in Basel, TR-3262, frond preserved 19.6.1973. F = A. \times *khanienese* (AeViTrTr), P. J. Brownsey No. C-55, Crete, leg. A.C. Jermy & P. J. Brownsey, 19.8.1971, cult. in Leeds, frond preserved summer 1972 (exper. produced plant see Reichstein et al. 1973, fig. 21.b.).

TR-594. Coll. living by Dr. K. Tenius near Meran (northern Italy), 30.5.1956, given to Dr. D.E. Meyer for cult. in B. Obtained in Basel 1.5.1962 and propagated by division under same conditions as 476; grew very well.

TR-803. Germany, Black Forest, Wittelsbachertal, W. of Oberried (S. E. of Freiburg). In granitic wall c. 650 m, W. Wimmenauer & T. Reichstein, 17.11.1962. Plant left and for many years observed occasionally, but c. 1976 no longer visible. A frond pressed and a fixing taken in good state 8.7.1963.



Fig. 15. A, B = *A. x clermontae* (RuRu'TrTr'), both TR-1427, Admonterkogel near Graz, St. Gotthard (Austria), leg. H. Melzer, see App. II. A from large plant after cult. in Basel, B from smaller plant; C = *A. x alternifolium* (TrTr'Sp), TR-804, s. Black Forest (Germany), granitic wall near Oberriedertal, 650m, 17.9.1962; D, E = *A. x heufleri* (TrTr'SpSp'), both TR-476; E = original collection; D = after two years of cultivation in Basel.

TR-1538. N. Italy, Venosta (= Vintschgau) near Solda (= Ausser-Sulden), N.E. of Ortler Mts., leg. Dr. J. Koch, 13.7.1964, obtained living and cult. in Basel 28.7.1965.

TR-1539. Germany, Harz, Oker valley, Rabenklippen above Oker, c. 300 m alt., 1.10.1961, leg. Dr. J. Koch, first cult. in his house in Haina-Kloster, sent to Basel 22.7.1965.

TR-2408. N. Italy, silicate rocks, c. 2.2 km E. of Finero, Valle Cannobino (S.E. of Malesco in Valle Vigizzo, E. of Domodossola), c. 800 m alt., 9.11.1968, leg. H. & K. Rasbach & T. Reichstein. Small plant cult. in Basel.

TR-3035. Switzerland, Ct. Ticino, small old gneiss wall with mortar near Mt. Verità, above Ascona, with *A. septentrionale*, *A. trichomanes* ssp. *quadri-valens*, *A. ruta-muraria* and *Ceterach officinarum*, 23.3.1970. Minute plant, only c. 1.5 cm high, taken living,

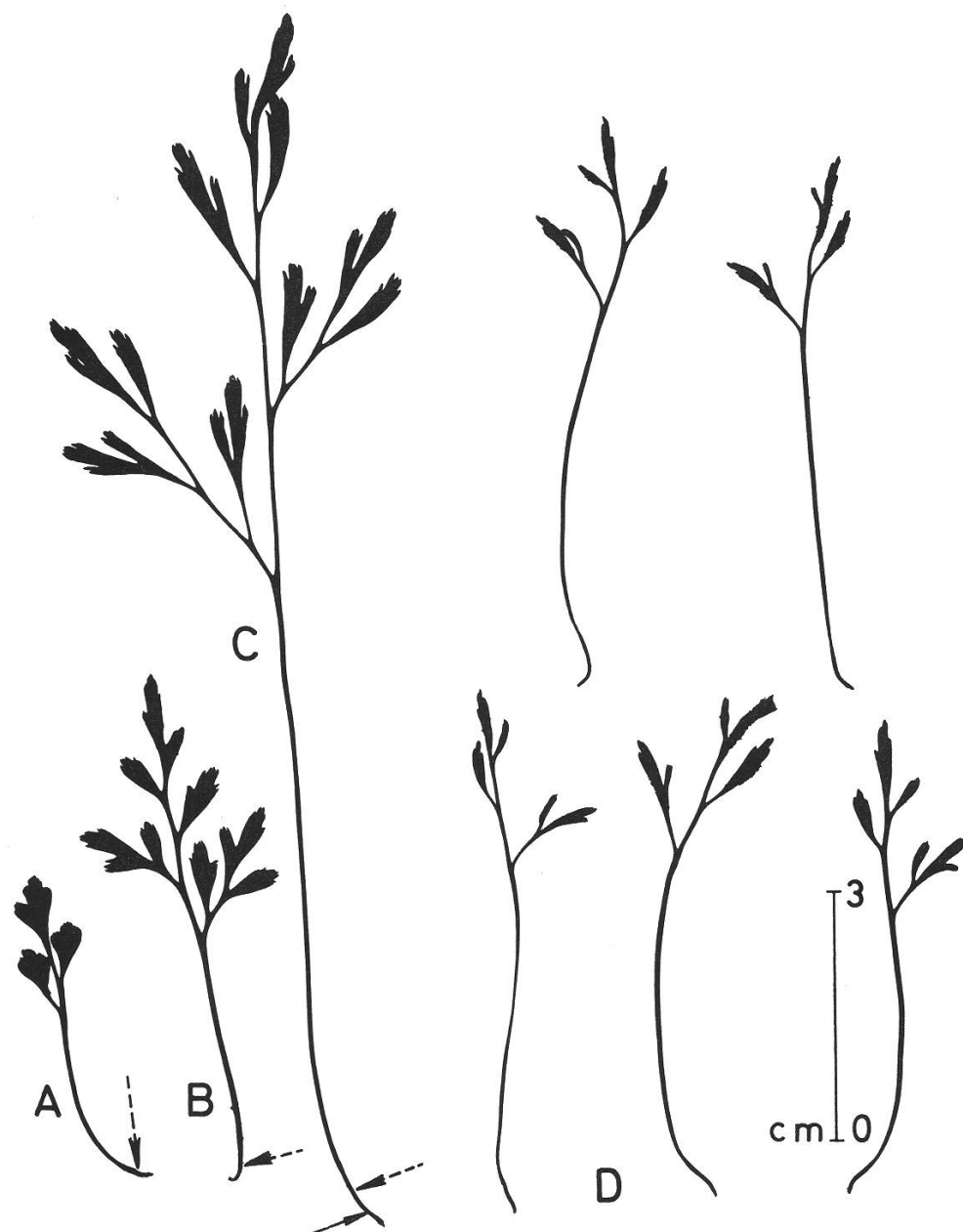


Fig. 16. A, B, C = *A. x murbeckii* (RuRu'SpSp'); A = from Bilstein near Bad Wildungen (s.w. of Kassel), Germany, A. & Ch. Nieschalk, original coll.; B = after cult. in Basel; C = TR-263, Switzerland, Ct. Ticino, Convento Bigorio near Tesserete, c. 720m (det. by G. Eberle), frond of large plant, 19.7.1960; D = *A. x hungaricum* (RuSpSpSp'), five fronds of type specimen, see App. I.

cult. in Basel, then in gneiss wall out of doors in the garden of TR. in Agarone (s. Switzerland). Is still in good state with fronds up to 18 cm long (1981).

Fixings of all plants sent to Leeds. All were tetraploid with irregular meiosis, producing many bivalents, and difficult to analyse precisely, with a mean range of about 50-70 bivalents, in rare cases reaching the theoretical maximum of 72 with all chromosomes pairing.

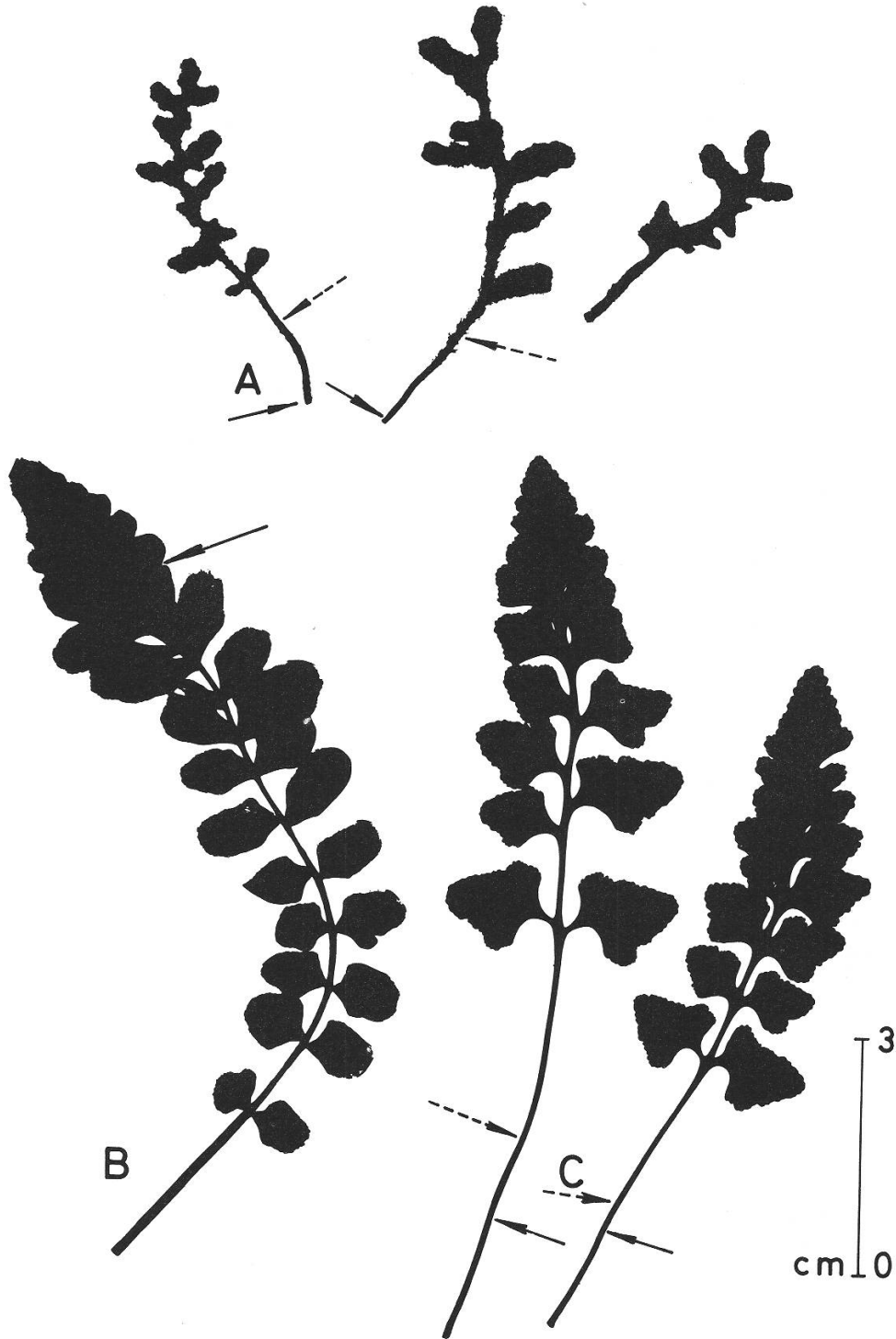


Fig. 17. A = \times *Asplenoceterach badense* (CeCe'RuRu'), three fronds of type specimen, court. Dr. D. E. Meyer; B = \times *Asplenophyllitis confluens* (ScTrTr') from Yugoslavia, court. Prof. E. Mayer; C = \times *Asplenophyllitis kummerlei* (ScAeRu), two fronds from piece of type specimen, cult. in Basel as TR-1047.

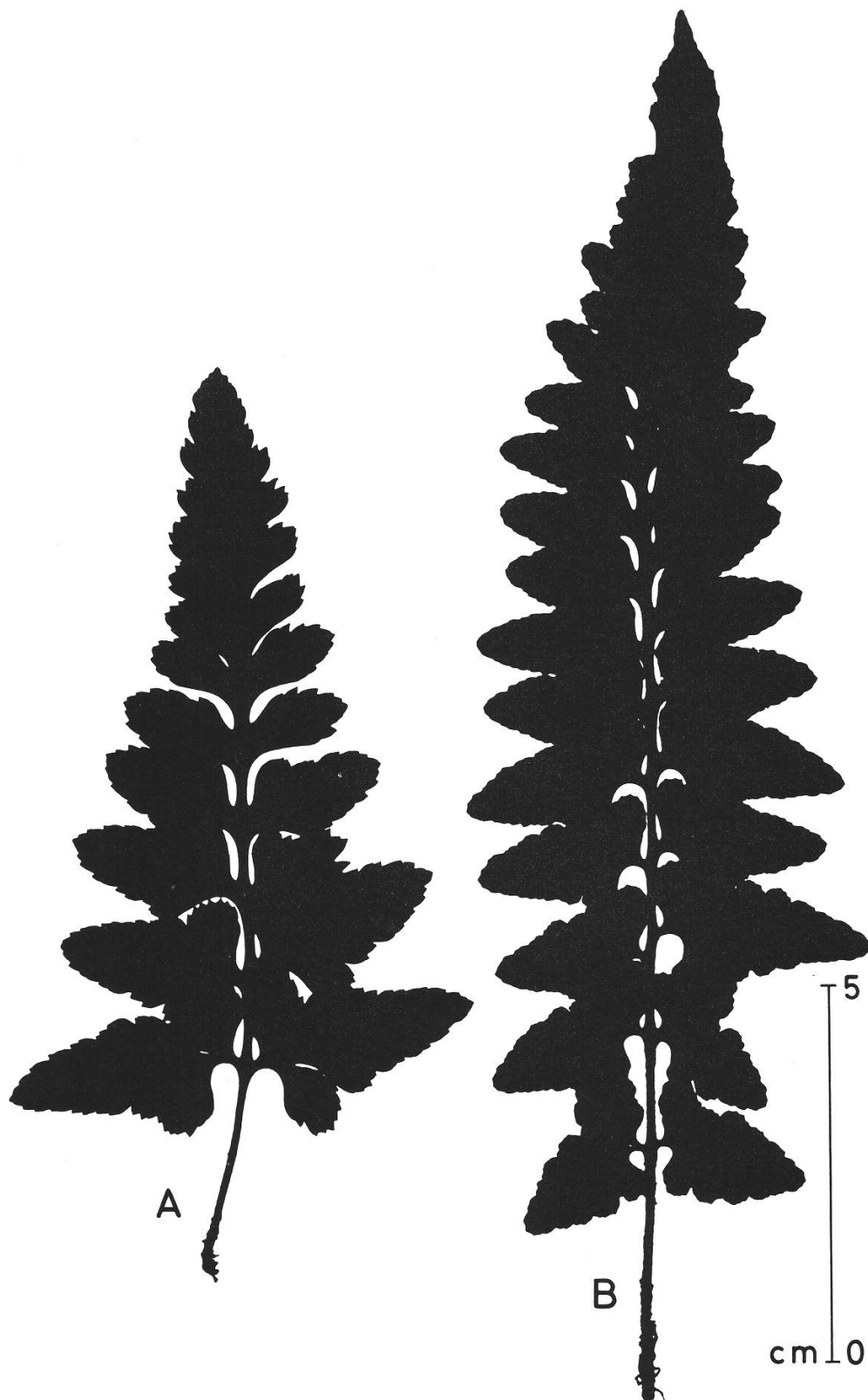


Fig. 18. A = \times *Asplenophyllitis jacksonii* (ScCuOn); B = \times *Asplenophyllitis microdon* (ScBiBi). Both from experimentally produced plants (Lovis & Vida 1969).

Sporangia contained mainly abortive material with a few obviously good spores (fig. 2 D). Repeated sowings of such material in Basel gave no progeny, but Lovis was able to raise a sporophyte with the correct morphology and the same meiotic behaviour as the original hybrid. The effect of delayed allopolyploidy is therefore expressed to a small extent, but is much less pronounced than in *A. × clermontae* and *A. murbeckii*.

TR-476 and TR-3035, originally corresponding to «*A. × heufleri* sensu stricto» in morphology (as figured by Reichardt) became bigger and more divided during cultivation and finally produced fronds of virtually the same shape as TR-594 which originally had been identified as *A. × baumgartneri* (corresponding to fig. in Dörfler). Contrary to our former view, we therefore accept this name as a synonym of *A. × heufleri*; *A. × baumgartneri* represents only a more developed form of *A. × heufleri*. Like all fern hybrids it shows, however, some variation in its morphology.

A. × heufleri has been produced by Lovis under experimental conditions. From ♀ *A. septentrionale* (ex Borrowdale, Gr. Britain) and ♂ *A. trichomanes* ssp. *quadrivalens* (ex Honshu, Japan) some plants with correct morphology resulted; one was obtained in Basel and cult. as TR-856. Also synthesized by Vida (1965).

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- Asplenium × aprutianum* = 18 × 29c = *A. lepidum* × *trichomanes* subsp. *quadrivalens*, p. 111.
- Asplenium × baldense* Sleep, Vida et Reichstein = 26a × 26b = *A. ruta-muraria* subsp. *dolomiticum* × subsp. *ruta-muraria*, p. 111.
- Asplenium × bavaricum* D.E. Meyer = 29c × 30 = *A. trichomanes* subsp. *quadrivalens* × *viride*, p. 112.
- Asplenium × bechereri* D.E. Meyer = 1 × 2 = *A. adiantum-nigrum* × *adulterinum*, p. 108.
- Asplenium × bouharmontii* Badré, Boudrie, Prelli & Schneller = 23 × 24 = *A. obovatum* × *onopteris*, p. 111.
- Asplenium × brissaginense* D.E. Meyer = 1 × 14 = *A. adiantum-nigrum* × *forisense*, p. 108.
- Asplenium × centovallense* D.E. Meyer = 1 × 10 = *A. adiantum-nigrum* × *cuneifolium*, p. 108.
- Asplenium × clermontae* Syme = 26b × 29c = *A. ruta-muraria* subsp. *ruta-muraria* × *trichomanes* subsp. *quadrivalens*, p. 111.
- Asplenium × contrei* Callé, Lovis & Reichstein = 1 × 28b = *A. adiantum-nigrum* × *septentrionale* subsp. *septentrionale*, p. 109.
- Asplenium × corbariense* Rouy = 13 × 29c = *A. fontanum* × *trichomanes* (?), p. 110.
- Asplenium × costei* Litard. = 14 × 28b = *A. forisense* × *septentrionale* subsp. *septentrionale*, p. 110.
- Asplenium × cyrnosardoum* Rasbach, Vida & Reichstein = 7 × 23 = *A. billotii* × *obovatum*, p. 109.
- Asplenium × dolosum* Milde = 1 × 29a = *A. adiantum-nigrum* × *trichomanes* subsp. *trichomanes*, p. 109.
- Asplenium × egliei* Lovis & Reichstein = 18 × 26a = *A. lepidum* × *ruta-muraria* subsp. *dolomiticum*, p. 111.
- Asplenium fontanum* × *majoricum* Jaquotot & Orell = 13 × 20, p. 110.
- Asplenium × gastonii-gautieri* Litard. = 13 × 30 = *A. fontanum* × *viride*, p. 110.
- Asplenium × heufleri* Reichstein = 28b × 29c = *A. septentrionale* subsp. *septentrionale* × *trichomanes* subsp. *quadrivalens*, p. 112.
- Asplenium × hungaricum* Fraser-Jenkins & Vida = (26b × 28b) × 28b = *A. × murbeckii* × *septentrionale* subsp. *septentrionale*, p. 112.
- Asplenium × javorkae* Kümm. = 18 × 26b = *A. lepidum* × *ruta-muraria* subsp. *ruta-muraria*, p. 111.
- Asplenium × joncheerei* D.E. Meyer = 7 × 24 = *A. billotii* × *onopteris* (?), p. 109.
- Asplenium × khaniense* Brownsey & Jermy = 9 × 29c = *Asplenium creticum* × *trichomanes* subsp. *quadrivalens*, p. 110.

- Asplenium* × *litardieri* Bennert & Meyer = 25b × 29b = *A. petrarchae* subsp. *petrarchae* × *trichomanes* subsp. *inexpectans*, p. 111.
- Asplenium* × *lessinense* Vida & Reichstein = 12 × 30 = *A. fissum* × *viride*, p. 110.
- Asplenium* × *lobmingense* Melzer, Lovis & Reichstein = 2 × 26b = *A. adulterinum* × *ruta-muraria* subsp. *ruta-muraria*, p. 109.
- Asplenium* × *lusaticum* D.E. Meyer = 29a × 29c = *Asplenium trichomanes* subsp. *trichomanes* × subsp. *quadrivalens*, p. 112.
- Asplenium* × *murariaeforme* Waisbecker = 10 × 26b = *A. cuneifolium* × *ruta-muraria*, p. 110.
- Asplenium* × *murbeckii* Dörfler = 26b × 28b = *A. ruta-muraria* subsp. *ruta-muraria* × *septentrionale* subsp. *septentrionale*, p. 111.
- Asplenium* × *nieschalkii* D.E. Meyer = 25b × 29c = *Asplenium petrarchae* subsp. *petrarchae* × *trichomanes* subsp. *quadrivalens*, p. 111.
- Asplenium* × *orellii* Lovis & Reichstein = 20 × 29c = *A. majoricum* × *trichomanes* subsp. *quadrivalens*, p. 111.
- Asplenium* × *pagesii* Litard. = 14 × 29c = *A. forisiense* × *trichomanes* subsp. *quadrivalens*, p. 110.
- Asplenium* × *perardii* Litard. = 1 × 26b = *A. adiantum-nigrum* × *ruta-muraria* (?), p. 109.
- Asplenium* × *poschkarskyanum* (Hoffm.) Preissm. = 2 × 30 = *A. adulterinum* × *viride*, p. 109.
- Asplenium* × *praetermissum* Lovis, Melzer & Reichstein = 2 × 29c = *A. adulterinum* × *trichomanes* subsp. *quadrivalens*, p. 109.
- Asplenium* × *protoadulterinum* Lovis & Reichstein = 29a × 30 = *A. trichomanes* subsp. *trichomanes* × *viride*, p. 112.
- Asplenium* × *reuteri* Milde = 15 × 28c = *A. haussknechtii* × *trichomanes* subsp. *quadrivalens*, p. 111.
- Asplenium rusciniensis* Nieschalk, Lovis & Reichst. = 14 × 24 = *A. forisiense* × *onopteris*, p. 110.
- Asplenium* × *sarniense* Sleep = 1 × 7 = *A. adiantum-nigrum* × *billotii*, p. 108.
- Asplenium septentrionale* subsp. *caucasicum* × *trichomanes* subsp. *trichomanes* Fraser-Jenkins = 28a × 29a, p. 112.
- Asplenium* × *sleepei* Badré, Boudrie, Prelli & Schneller = 7 × 14 = *A. billotii* × *forisiense*, p. 109.
- Asplenium* × *sollerense* Lovis, Sleep & Reichstein = 20 × 25b = *A. majoricum* × *petrarchae* subsp. *petrarchae* p. 111.
- Asplenium* × *souchei* Litard. = 7 × 28b = *A. billotii* × *septentrionale* subsp. *septentrionale*, p. 109.
- Asplenium* × *striciacum* D.E. Meyer = 18 × 29b = *A. lepidum* × *trichomanes* subsp. *inexpectans*, p. 111.
- Asplenium* × *ticinense* D.E. Meyer = 1 × 24 = *A. adiantum-nigrum* × *onopteris*, p. 109.
- Asplenium trichomanes* subsp. *inexpectans* × *quadrivalens* = 29b × 29c, p. 112.
- Asplenium* × *trichomanes* subsp. *paehyrachis* × *quadrivalens* = 29c × 29d, p. 112.
- Asplenium* × *trichomaniforme* Woynar = 2 × 29a = *A. adulterinum* × *trichomanes* subsp. *trichomanes*, p. 109.
- Asplenium* × *valgannense* Attinger = 27a × 29c = *A. seelosii* × *trichomanes* subsp. *quadrivalens*, p. 112.
- Asplenium* × *wachaviense* Aschers. & Graebner = 10 × 29 = *A. cuneifolium* × *trichomanes* (?), p. 110.
- Asplenium* × *woynarianum* Aschers. & Graebner = 10 × 30 = *A. cuneifolium* × *viride*, p. 110.
- X *Asplenoceterach badense* D.E. Meyer = 26b × 31b = *Asplenium ruta-muraria* subsp. *ruta-muraria* × *Ceterach officinarum* subsp. *officinarum*, p. 113.
- X *Asplenoceterach barrancense* W. Bennert & D.E. Meyer = 20 × 31b = *Asplenium majoricum* × *Ceterach officinarum* subsp. *officinarum*, p. 113.
- X *Asplenophyllitis confluens* (T. Moore) Alston = 29c × 33a = *Asplenium trichomanes* subsp. *trichomanes* × *Phyllitis scolopendrium*, p. 113.
- X *Asplenophyllitis jacksonii* Alston = 1 × 33a = *Asplenium adiantum-nigrum* × *Phyllitis scolopendrium*, p. 113.
- X *Asplenophyllitis kummerlei* G. Vida = 18 × 33a = *Asplenium lepidum* × *Phyllitis scolopendrium*, p. 113.
- X *Asplenophyllitis microdon* (T. Moore) Alston = 7 × 33a = *Asplenium billotii* × *Phyllitis scolopendrium*, p. 113.
- Ceterach* × *mantoniae* (Váróczy & Vida) Soó = 31a × 31b = *Ceterach officinarum* subsp. *bivalens* × *officinarum*, p. 113.

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