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Autor: Reichstein, Tadeus / Viane, Ronald / Rasbach, Helga

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Asplenium adiantum-nigrum L. subsp. *yuanum* (Ching) Viane, Rasbach, Reichstein & Schneller stat. nov., and the status of *A. woronowii* Christ (Aspleniaceae, Pteridophyta).

Studies in *Asplenium* for "Flora Iranica": 6

For the fifth article in this series see A. Sleep & T. Reichstein, *Candollea* 39: 675-691 (1984).

TADEUS REICHSTEIN
RONALD VIANE
HELGA RASBACH
&
JAKOB SCHNELLER

RÉSUMÉ

REICHSTEIN, T., R. VIANE, H. RASBACH & J. SCHNELLER (1994). *Asplenium adiantum-nigrum* L. subsp. *yuanum* (Ching) Viane, Rasbach, Reichstein & Schneller stat. nov., et le status de *A. woronowii* Christ (Aspleniaceae, Pteridophyta). *Candollea* 49: 281-328. En anglais, résumés français et anglais.

Nous décrivons la nouvelle position d'*Asplenium yuanum* comme sous-espèce d'*Asplenium adiantum-nigrum*. Elle est rare en Chine, mais plus abondante en Abchasié (Géorgie, ancienne U.R.S.S.), Artvin (Turquie) et la côte Caspienne de l'Iran, mais elle se trouve aussi en Turkménistan, Afghanistan, Pakistan, au N. de l'Inde, en Ethiopie, La Réunion et peut-être en d'autres parties d'Asie et d'Afrique. C'est un taxon tétraploïde sexuel d'une morphologie qui suggère qu'il s'agit d'une plante allo-tétraploïde (OnOnWoWo) formée par doublement des chromosomes dans un hybride diploïde (OnWo) entre l'*A. onopteris* (OnOn) et l'*A. woronowii* (WoWo). Dans les endroits où la sous-espèce *yuanum* et l'*A. woronowii* croissent ensemble, les deux produisent un hybride que nous décrivons comme *A. × centovallense* D. E. Meyer nothosubsp. *demirizii* nothosubsp. nov., et que nous avons aussi obtenu par hybridation expérimentale. La méiose dans cet hybride est irrégulière avec formation de ca. 36 bivalents (WoWo) et 36 chromosomes univalents (On), ce qui est en accord avec la formule génétique (OnWoWo). Un fait remarquable et inattendu produisant des difficultés taxinomiques et autres est la capacité de la subsp. *yuanum* (OnOnWoWo) de former des hybrides complètement fertiles avec la subsp. *adiantum-nigrum* (CuCuOnOn) avec introgression mutuelle. La seule conclusion simple pour expliquer ce fait est d'accepter que le génome de l'*A. cuneifolium* (CuCu), un des ancêtres de l'allo-tétraploïde subsp. *adiantum-nigrum*, est complètement homologue avec celui de l'*A. woronowii* (WoWo). Pour prouver cette parenté supposée nous avons produit sous conditions expérimentales l'hybride (TR-5490) de la subsp. *adiantum-nigrum* (CuCuOnOn) avec l'*A. woronowii* (WoWo). Cet hybride était triploïde (CuOnWo) produisant ca. 36^{II} et 36^I en méiose, en accord parfait avec notre hypothèse. Dans ce cas particulier les 36 paires doivent représenter les deux génomes (Cu) et (Wo) et les 36 chromosomes univalents le génome (On). Par conséquence de cette parenté très proche, il est indiqué d'abaisser le status de l'*Asplenium woronowii*: *Asplenium cuneifolium* Viv. subsp. *woronowii* (Christ) Viane, Rasbach, Reichstein & Schneller, comb. et stat. nov.

ABSTRACT

REICHSTEIN, T., R. VIANE, H. RASBACH & J. SCHNELLER (1994). *Asplenium adiantum-nigrum* L. subsp. *yuanum* (Ching) Viane, Rasbach, Reichstein & Schneller stat. nov., and the status of *A. woronowii* Christ (Aspleniaceae, Pteridophyta). *Candollea* 49: 281-328. In English, French and English abstracts.

A new status as subspecies of *Asplenium adiantum-nigrum* L. is proposed for *A. yuanum* Ching. This taxon is rare in China but more abundant in Abkhazia (Georgia, former U.S.S.R.), Artvin (Turkey), the region of the Caspian coast in Iran and it also grows in Turkmenistan, Afghanistan, Pakistan,

N. India, La Réunion, and Ethiopia. We obtained living material and raised progeny and hybrids which allowed us to emend the description and to propose a parentage. In gross morphology tetraploid subsp. *yuanum* looks similar to diploid *A. woronowii* Christ (1906). The examination of microcharacters (exospore length, stomata length, scales of rhizome and petiole bases and structure of epidermis cells) usually allows a reliable identification, but counting of chromosomes provides the final proof. Cytotaxonomical experiments with precise analysis of pairing behaviour of chromosomes in wild and experimentally produced hybrids showed that it is an allo-tetraploid subspecies of *A. adiantum-nigrum*. Its morphology suggests that it originated by chromosome doubling in a diploid hybrid (OnWo) of *A. onopteris* (OnOn) with *A. woronowii* (WoWo). The genome formula (OnOnWoWo) can thus be attributed to *A. adiantum-nigrum* subsp. *yuanum*. From places where both *A. adiantum-nigrum* subsp. *yuanum* and *A. woronowii* grow together we received the wild triploid hybrid and describe it as *A. × centovallense* D. E. Meyer nothosubsp. *demirizii* nothosubsp. nov. We also obtained this hybrid under experimental conditions; it showed irregular meiosis with ca. 36 pairs and 36 univalent chromosomes which is in agreement with the genome formula: OnWoWo. *A. adiantum-nigrum* subsp. *adiantum-nigrum* (CuCuOnOn) and *A. adiantum-nigrum* subsp. *yuanum* (OnOnWoWo) must have homologous genomes because in places where they grow together they produce fully fertile hybrids (CuOnOnWo) with introgression in both directions. Based on micromorphology, we assumed that *A. cuneifolium* (CuCu), one ancestor of subsp. *adiantum-nigrum*, and *A. woronowii* (WoWo), one ancestor of subsp. *yuanum*, most probably have fully homologous chromosomes. To prove this we made the hybrid (TR-5490) of *A. adiantum-nigrum* subsp. *adiantum-nigrum* (CuCuOnOn) with *A. woronowii* (WoWo), and of *A. adiantum-nigrum* subsp. *yuanum* (OnOnWoWo) with *A. cuneifolium* (CuCu). Both are triploid with ca. 36^{II} and 36^I in meiosis which is in agreement with the formula (CuOnWo), and in this particular case shows that the Cu- and Wo-genome are homologous. As a consequence we reduce the status of *A. woronowii* to: *Asplenium cuneifolium* Viv. subsp. *woronowii* (Christ) Viane, Rasbach, Reichstein & Schneller, comb. et stat. nov.

KEY-WORDS: *Asplenium adiantum-nigrum* — *Asplenium cuneifolium* — *Asplenium onopteris* — *Asplenium sajanense* — *Asplenium woronowii* — *Asplenium yuanum* — Cytotaxonomy — Hybridization — Introgression — Micromorphology — Homology of chromosomes in taxa with different morphology.

1. Introduction and nomenclature

SHIVAS (1969) first showed that *Asplenium adiantum-nigrum* L. s.s. (typification based on DODOENS, 1616; see FERNANDES, 1983) is an allotetraploid species which originated by chromosome doubling from a diploid hybrid between *A. cuneifolium* Viv. and *A. onopteris* L. (Fig. 22). Her conclusion based on cytological research was recently also confirmed by an analysis of the polyphenolic C-glycosylxanthones in this complex (RICHARDSON & LORENZ-LIBURNAU, 1982). *A. adiantum-nigrum* is very widely distributed today, and found in continents and on islands where one or both of its ancestors are not present. Next to this wide distribution the species shows considerable morphological variation, but SHIVAS (1969) found no differences in the chromosomal pairing behaviour between European plants and those of Kenya, S. Africa (Transvaal) or the U.S.A. Minor (micro)morphological differences do not warrant that a special status is given, e.g., to the slightly aberrant *A. adiantum-nigrum* from La Réunion and from Hawaii (raised from spores, Fig. 11).

Two European forms which in extreme cases can completely imitate one of their diploid ancestors are treated as varieties. The first, growing on serpentinite or other ultrabasic rocks, is a form of *A. adiantum-nigrum* which mimics and becomes almost indistinguishable from the diploid *A. cuneifolium* in gross morphology. It is, however, tetraploid and can be identified by a chromosome count or by careful examination of microcharacters (length of exospore and guard cells, rhizome scales, rachis structure, etc.), see SLEEP & al. (1978); SLEEP (1980; 1983; 1985); RASBACH & al. (1986); VIANE & REICHSTEIN (1994). It breeds true from spores and has occasionally been referred to as *A. lamotteanum* HÉRIBAUD (1880) ≡ *A. adiantum-nigrum* var. *lamotteanum* (Héribaud) DE REY-PAILHADE (1893: 20) ≡ *A. serpentini* Tausch β var. *lamotteanum* ROUY (1913: 449). A valid name based on Héribaud's material has not been used recently (see SLEEP, 1985: 333; RASBACH & al., 1986: 222) as no typematerial could be found among Héribaud's plants purchased by the BM in 1954, nor in CFS (pers. comm. Mr. M. Boudrie). The name *A. adiantum-*

nigrum var. *corunnense* CHRIST (1904) was used in “Flora Iberica” (NOGUEIRA & ORMONDE, 1986: 102), but according to one of us (RV), who studied the holotype (Merino s.n.) in Paris (P), this material seems to represent another more compact ecotype but not the true “serpentine form” of *A. adiantum-nigrum*.

We also prefer to treat the true “serpentine form” as a variety and, as we found an earlier epithet, we now propose to call it:

A. adiantum-nigrum subsp. **adiantum-nigrum** var. **silesiacum** (Milde) Viane & Reichstein, **comb. nov.**

Basionym: *Asplenium adiantum-nigrum* L. subsp. *silesiacum* Milde, Jahresb. Schles. Ges. Vaterl. Cult. 33: 92 (1855); see also MILDE, 1858 (p. 605-609), 1865 (p. 28). = *Asplenium adiantum-nigrum* L. subsp. *onopteris* L. var. *silesiacum* Milde (MILDE, 1867: 88; see also LUERSSEN, 1889: 279).

Icon.: MILDE (1858: Tab. 45, Fig. 114-115), LUERSSEN (1889: Fig. 127-g). Our Fig. 12-14. Milde’s type is from Poland: Weinberg bei Zobten, *Milde s.n.* (B!, 2 sheets, lectotype: sheet 1: see Fig. 12).

A second form, occasionally found in the Insubrian region (around the large lakes in N. Italy and S. Switzerland), will be described as var. *onopterioides* VIANE & al. (1994). This taxon is often indistinguishable in gross morphology from diploid *A. onopteris* and is sometimes found in herbaria under this name. It can again be identified by the counting of chromosomes or by the examination of microcharacters. It does, however, not breed true from spores. Sowing gave \pm normal *A. adiantum-nigrum* var. *adiantum-nigrum*.

Within the *A. adiantum-nigrum* complex *A. chihuahuense* BAKER (1891) from Mexico (see also DAVENPORT, 1896: 264-265) is the only hexaploid taxon (RASBACH & al., 1994); although some authors have reduced its name to a synonym of *A. adiantum-nigrum* (e.g., KNOBLOCH & CORRELL, 1962; WINDHAM, 1983) it also deserves to be treated as a distinct species.

SHIVAS (1969) had no Asiatic material at her disposal. Thus, when working on the Aspleniaceae for “Flora Iranica”, we carefully examined many Asian specimens a.o. from Afghanistan, Azerbaidzhan, the Caucasus and Transcaucasus, China, India, Iran, Pakistan, Turkey, and Turkmenistan. Many of which we consider to be *A. adiantum-nigrum* sensu stricto. Among these collections and in material from Ethiopia we also found specimens with a distinct gross morphology that are identified as subspecies *yuanum* (see below under 3).

2. Material and methods

2.1. — The origin of the plants used for raising progeny and for hybridization experiments is given in appendix 7.3.

2.2. — The collecting of living plants and their cultivation in pots with lime free soil was done as described by RASBACH & al. (1983: 44).

2.3. — The collecting of pure spores. Clean mature fronds or fragments are washed quickly under running water to clear them from any trace of soil, they are pressed in clean white paper (or “flimsies”) folded so that no spores can be lost. Specimens are dried and pressed without heating by changing the pressing paper. The spores (fine black powder) are collected and packed in a small thin pergamin paper (not plastic), which is folded and put in a labeled, small plastic bag, preferably mounted on the same sheet. Spores should never touch plastic nor scotch tape. Also any other sticky plastic should be avoided to close the folded pergamin paper. For examination, a small heap of spores is embedded in balsam (e.g., DePeX) on a slide, and kept as a permanent preparation.

2.4. — Procedures for making fixings and their examination were followed as reviewed in DEMIRIZ & al. (1990).

2.5. — Measuring microcharacters was done by H.R. and T.R. as given in DEMIRIZ & al. (1990), while RV used the quicker and statistically more precise method (DEMIRIZ & al., 1990) described in VIANE (1990). The micromorphological data presented are based on a continuously updated database; from the ca. 150 different specimens presently studied within this complex, 75 belong to *A. adiantum-nigrum* subsp. *adiantum-nigrum*, 15 to subsp. *yuanum*, 20 to *A. cuneifolium*, 15 to *A. woronowii*, and 30 to *A. onopteris*.

2.6. — Preparing flasks with agar-medium. T.R. uses Erlenmeyer-flasks ca. 5.5 cm diameter and the medium recommended by DYER (1979: 282), but slightly modified as described by RASBACH & REICHSTEIN (1990: 344). The empty flasks are washed with hot tap-water and a few drops of detergent, rinsed with clean water and dried. Hot liquid Agar medium is filled in until it forms a layer of ca. 1-1.5 cm high; afterwards the opening is covered with Aluminum-foil. Flasks are sterilized for 20 minutes in steam, as higher temperature (pressure) is detrimental. After cooling, the Aluminum foil is taken off, but the opening is immediately tightly covered with adhesive plastic foil ("Parafilm M", Amer. Can. Comp. Greenwich CT. 06830). These flasks, ready for use, are kept in boxes and can be stored for 2-3 years. Occasional fungal infections are easily visible, and can be removed with a spatula before these flasks are re-sterilized.

2.7. — Sowing. Between 50-300 mature spores are spread on a glass slide. The plastic foil of one flask is lifted, and the spores are allowed to fall on the Agar medium by reversing and gently knocking the slide. The opening is closed again tightly with adhesive plastic foil, and the flask is placed on a south exposed window ledge at ca. 8-28°C in full sun (even in summer). The formation of water droplets on the inner wall of the flask shows that the atmosphere is saturated with water. Depending on the species, small green prothalli become visible after 2 to 20 weeks.

2.8. — Planting of prothalli. To raise progeny ca. 20 to 50 small green prothalli of ± 2 mm length are planted in a pot with lime free soil, watered carefully, and covered with a plastic cup. The pots are placed in a temperate greenhouse (or living-room) at ca. 8 to 28°C in half shade, so that they get some sun in the morning or afternoon but are shaded from 10-17 h. When the prothalli are firmly fixed by their rhizoids (after ca. 2-4 weeks) they get their first "bath" to promote fertilization, and are further treated as given in RASBACH & al. (1994) for *A. chihuahuense*.

2.9. — Experimental hybridization. J.Sch. used Manton's classical method (LOVIS, 1968), slightly modified as described under 7.4. T.R. used the simpler method mentioned in BENNERT & al. (1988: 384), and extensively described by RASBACH & al. (1994) for *A. chihuahuense* (see also Appendix and Fig. 12 in RASBACH & al., 1994). This method is quite successful, but does not allow to say which species functioned as the male and which as the female partner.

3. The new status of *A. yuanum* Ching

3.1. Nomenclature and emended description

***Asplenium adiantum-nigrum* L. subsp. *yuanum* (Ching) Reichstein, Viane, Rasbach & Schneller, stat. nov.**

Basionym: *Asplenium yuanum* Ching, Bull. Fan. Mem. Inst. Biol. 10: 174 (1940). \equiv *A. adiantum-nigrum* L. var. *yuanum* (Ching) Ching in ANONYMOUS, Flora Tsinlingensis II, Pteridophyta (1974: 125 and figs. 12-14 p. 119).

The type is from China, Yunnan: Tehching, (Atuntze) Kaa-ker-pu, 2800 m alt., in ravine, June 4, 1937, T. T. Yü 8461 (PE!). Judging from the type specimen's (Fig. 1) label CHING (1940) wrongly cited the type locality as: "*Sikang prov.: Muli, on the border of NW Yunnan.*"

Icon.: ANONYMUS (1974: figs. 12-14 p. 119) and our Fig. 1-8.

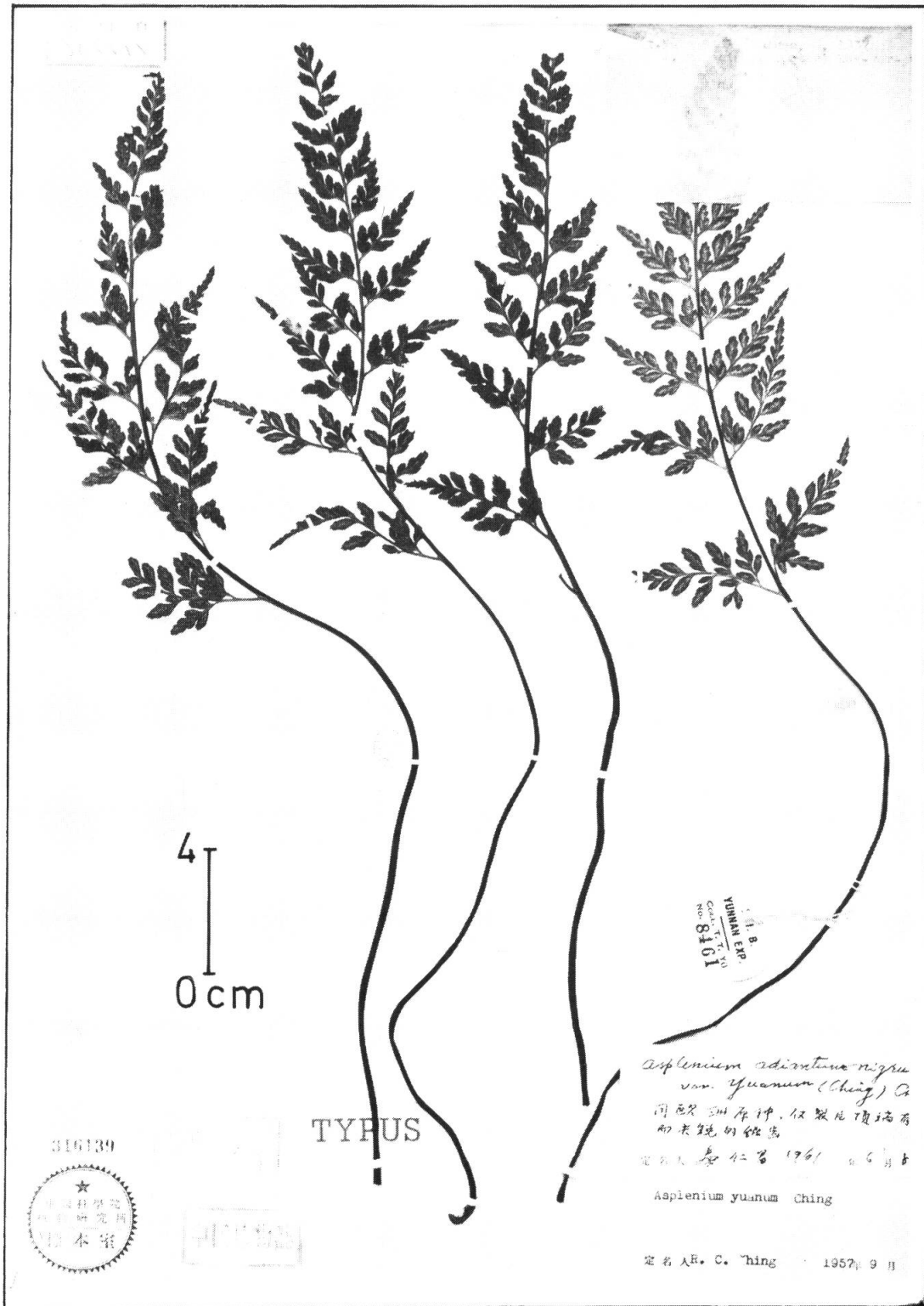


Fig. 1. — *Asplenium adiantum-nigrum* subsp. *yuanum*. Silhouette of holotype from China, Yunnan: Yü 8461 (PE). (Photo: R.V.).

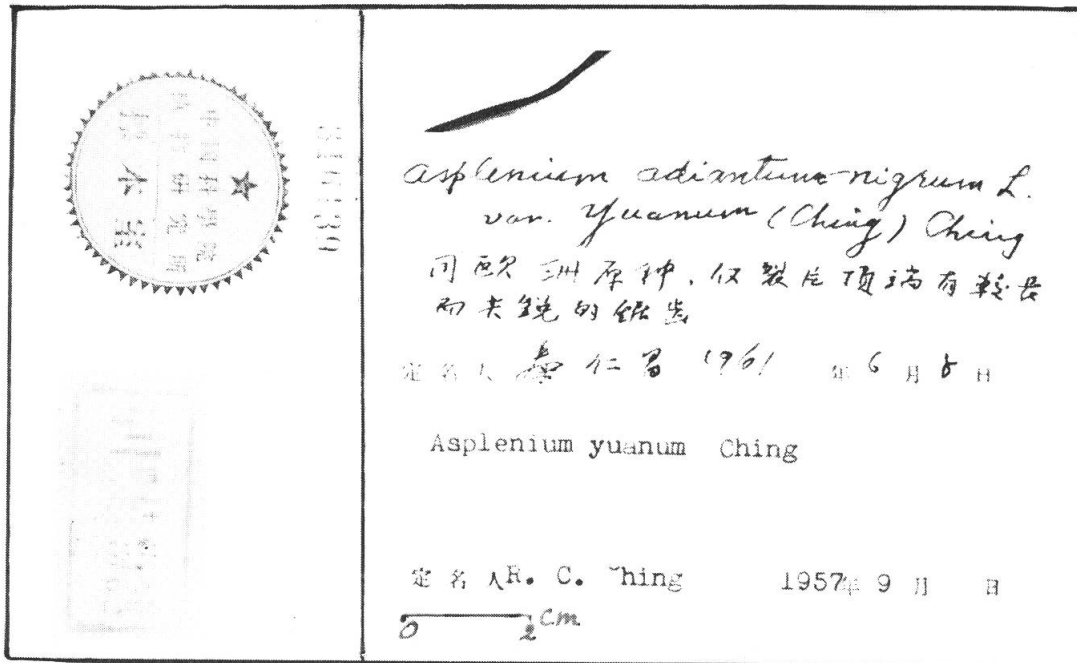


Fig. 2. — *Asplenium adiantum-nigrum* subsp. *yuanum*. Labels and stamps of type specimen. The following additional data are almost illegibly typed on the thin paper in the upper right corner (Fig. 1): June 4, 1937, Yunnan, Tehching, (Atuntze) Kaa-ker-pu, 2800 m alt., in ravine.

Emended description. This subspecies differs from subsp. *adiantum-nigrum* in its usually narrower, lanceolate fronds; in each plant at least one leaf can usually be found in which the lowest pair of pinnae is not distinctly larger than the next. The apexes of the larger pinnules are usually somewhat rounded (not acute as in subsp. *adiantum-nigrum*).

Subsp. *yuanum* can easily be confused in gross morphology with the diploid *A. cuneifolium* Viv. subsp. *woronowii* (Christ) Viane & al. (see below). It is, however, tetraploid (Fig. 29) and can be distinguished unequivocally by its chromosome number and usually also by the examination of microcharacters, particularly by the length of the exospore (Table 1), the stomata (Table 1) and the scales at the stipe base (Table 3), which all agree with those of subsp. *adiantum-nigrum*.

In gross morphology subsp. *yuanum* is also very similar to *A. sajanense* GUDOSCHNIKOV & KRASNOBOROV (1967) described (holotypus in TK) from the western Sajan mountains (Siberia, Russia). As this publication is usually absent in west European libraries the name *A. sajanense* is hardly known to any botanist outside the former U.S.S.R., and is not quoted in JARRETT & al. (1985). The taxon is cited by CZEREPANOV (1973: 466) and also by KRASNOBOROV (1988: 69). Apart from the type material (holo-: TK, para-: NS!) only few specimens exist. The only paratype (Krasnoborov & Sukojan s.n. — 10.V.1964), is immature so that spores could not be measured. However, immature sporangia containing well formed spores (exospore without perispore) could be studied in an epidermis preparation, showing that the specimen is not a hybrid. From measurements of other microcharacters (length of stomata and scales at the stipe base) and the form of the indusial cell walls in epidermis preparations it became evident that *A. sajanense* is the same taxon as *A. cuneifolium* subsp. *woronowii*.

We must also point out that the chromosomes of subsp. *yuanum* are most probably homologous with those of subsp. *adiantum-nigrum* (see 5), and that a swarm of fertile hybrids with intermediate morphology forms wherever the two grow together. Thus introgression probably occurs in both directions, blurring differences within the species. Such intermediate forms do not merit a special status and are listed under subsp. *adiantum-nigrum* versus subsp. *yuanum* (see Appendix 7.2).

Judging from its morphology we may conclude that subsp. *yuanum* arose by chromosome doubling in a diploid hybrid between *A. cuneifolium* subsp. *woronowii* and *A. onopteris*. Cytological

examination of the hybrid *A. × centovallense* nothosubsp. *demirizii* Viane & al. (see below) = *A. adiantum-nigrum* subsp. *yuanum* × *A. cuneifolium* subsp. *woronowii* is in agreement with this conclusion. It is however impossible to prove this by cytotaxonomical methods as *A. cuneifolium* subsp. *cuneifolium* (one putative ancestor of subsp. *adiantum-nigrum*) and *A. cuneifolium* subsp. *woronowii* (one putative ancestor of subsp. *yuanum*) also have homologous genomes (see below). These taxa are usually well separated ecologically as *A. cuneifolium* subsp. *cuneifolium* grows nearly exclusively on serpentinite, magnesite or other ultrabasic rocks, while *A. cuneifolium* subsp. *woronowii* is reported from limestone or from siliceous formations, though it (as “*A. sajanense*”) was also found on serpentinite containing rocks (KRASNOBOROV, 1988: 69). We have studied typical specimens of subsp. *yuanum*, listed as “unnamed tetraploid taxon” in DEMIRIZ & al. (1981), from Turkey (Artvin), where the diploid *A. cuneifolium* subsp. *woronowii* also grows (DEMIRIZ & al., 1981).

3.2. Distribution

We have seen specimens of subsp. *yuanum* from the former U.S.S.R. (Caucasus, Transcaucasus), Turkey, Iran, Afghanistan, Pakistan, China and from Ethiopia (where no subsp. *adiantum-nigrum* seems to grow) and La Réunion. Most are listed in Appendix 7.1.

4. A new nothosubspecies of *A. × centovallense*

4.1. Nomenclature and description

Asplenium × centovallense D. E. Meyer nothosubsp. **demirizii** Viane, Rasbach, Schneller & Reichstein, nothosubsp. nov. (= *A. adiantum-nigrum* subsp. *yuanum* × *A. cuneifolium* subsp. *woronowii*).

Diagnosis: *A. centovallense* subsp. *centovallense* simile, sed folia angustiora, magis elongata, jugo infimo pinnarum secundum quasi aequante, interdum eo paulo longiore vel brevior; segmentis terminalibus laminae pinnarumque majorum interdum elongatis (caudatis) apicibus rotundatis. Sporae abortivae. Numerus chromosomatum sicut in subsp. *centovallense*: $2n = 108$, triploideus, meiosi 36^{II} et 36^I .

Description. Fronds up to 28 cm long and ca. 8 cm wide. Usually distinctly more elongate than nothosubsp. *centovallense*; large fronds often prominently tapering to their apex and becoming caudate, the same is shown by the larger pinnae; apex of the frond and the larger pinnae is nevertheless usually roundish with small teeth. The spores are abortive. The original plant of nothosubsp. *demirizii* was collected living, brought to Basel and cultivated as TR-3636, it was triploid with $n = 36^{II}$ and 36^I in meiosis (G. Vida, in litt. 24 May 1975).

Typus: TR-3636-C (cultivated in Basel, pressed 29 Aug. 1973); holotype (3 fronds) in Z, isotype (2 fronds) in BM, G.

Original type locality: Turkey, Trabzon, Soganli Dağ, above Çaykara, N of Bayburt, 1500 m alt., among the parents and the following other ferns: *Dryopteris oreades*, *D. expansa*, *Polystichum lonchitis*, *Asplenium ruta-muraria*, *A. septentrionale* subsp. *caucasicum*, and its diploid hybrid with *A. trichomanes* subsp. *trichomanes*, *Cystopteris fragilis*, 29 Aug. 1973, C. R. Fraser-Jenkins 4067.

Paratypes: Turkey, Trabzon, Khabakhor valley, Rize, 1000 m alt., growing with *A. adiantum-nigrum* subsp. *yuanum*, 28 Aug. 1973, C. R. Fraser-Jenkins 4050 (= TR-3642, stomata: 53 ± 4 µm long, Fig. 19). Type locality, 29 Aug. 1973, C. R. Fraser-Jenkins 4066a p.p., (= TR-3643, plant F & K, 2 leaves of each).

Derivatio: Dedicated to H. Demiriz who showed us the first specimen of *A. cuneifolium* subsp. *woronowii* from Turkey (DEMIRIZ & al., 1981).

This hybrid seems to form easily, both in nature and under experimental conditions, as shown independently by J. Schneller and by T. Reichstein (see Table 4).

5. Putative origin of *A. adiantum-nigrum* subsp. *yuanum*

5.1. Cytological results

As tetraploid subsp. *yuanum* is very similar to diploid *A. cuneifolium* subsp. *woronowii* in gross morphology, we suspected that this last taxon might be a direct ancestor of *A. adiantum-nigrum* subsp. *yuanum*. In some places both taxa were found growing together, producing the triploid hybrid nothosubsp. *demirizii*. The pairing behaviour of the chromosomes in this hybrid ($36^{II} + 36^I$, see above) is in agreement with the attributed genome formula (OnWoWo) and with our assumption that the tetraploid *A. adiantum-nigrum* subsp. *yuanum* has the formula (OnOnWoWo). It also shows that subsp. *yuanum* most probably originated by chromosome doubling in a hypothetical diploid hybrid (OnWo) between *A. onopteris* (OnOn) and *A. cuneifolium* subsp. *woronowii* (WoWo) (see Fig. 22). In order to explain our cytological results and the morphological variation between subsp. *adiantum-nigrum* (CuCuOnOn) and subsp. *yuanum* (OnOnWoWo) we assume that the genomes of *A. cuneifolium* s.s. (CuCu) are homologous with those of *A. woronowii* (WoWo), giving full chromosome pairing during meiosis in the tetraploid hybrid (CuOnOnWo), representing the "intermediate form" between subsp. *adiantum-nigrum* and subsp. *yuanum*. They nevertheless express themselves in different morphology (see Figs. 3-8) and distinct ecological requirements.

5.2. The experimental hybrid of *A. adiantum-nigrum* subsp. *adiantum-nigrum* with *A. woronowii*

T.R. was only able to perform one decisive experiment confirming that *A. cuneifolium* and *A. woronowii* must have homologous chromosomes. He made the cross between *A. adiantum-nigrum* from Europe (TR-4421), with genome formula CuCuOnOn (SHIVAS, 1969), and the diploid *A. woronowii* (WoWo) from the Transcaucasus (TR-4639). Hybridization occurred easily (ca. 40% yield, see Table 4) which is already indicative of a homologous genome in both parents. He obtained 12 well growing young hybrids (TR-5490, see Fig. 21), morphologically intermediate between nothosubsp. *centovallense* and nothosubsp. *demirizii*. Fixings of sporangia from plant 3 were examined by H.R. (26 May 1982). Three good preparations of meiosis, showing 36 bivalents and 36 univalents, were unfortunately lost during the preparation of permanent slides. One less perfect permanent slide showed ca. $35^{II} (\pm 2)$ and ca. $34^I (\pm 5)$. In spite of lacking the highest precision this result shows that ca. equal amounts of pairs and univalents are present. This can easily be understood if the chromosomes in the genomes (Cu) and (Wo) are homologous.

The only other rational possibility would be that the genomes of *A. onopteris* (On) and *A. woronowii* (Wo) are homologous. This is very unlikely since the gross morphological differences between *A. onopteris* (Fig. 17) and *A. woronowii* are too large for such a putative close relationship, while *A. cuneifolium* (Fig. 15) and *A. woronowii* (Fig. 16, 18) are more similar both in gross morphology and in their microcharacters (see below).

Taxon	2n	Investigator	N	Exospore length in μm	N	Stomata length in μm
<i>A. adiantum-nigrum</i> subsp. <i>adiantum-nigrum</i>	144	RV TR	2340	(21-)31-34-37(-44) (30-)33-36-39(-45)	1404	(32-)51-57-62(-74)
<i>A. adiantum-nigrum</i> subsp. <i>yuanum</i>	144	RV TR	540	(26-)31-34-36(-45) (30-)33-36-39(-45)	750	(37-)51-57-63(-75)
<i>A. cuneifolium</i> subsp. <i>cuneifolium</i>	72	RV TR	620	(23-)28-31-34(-44) (27-)30-32-34(-36)	1320	(27-)44-49-53(-66)
<i>A. cuneifolium</i> subsp. <i>woronowii</i>	72	RV TR	470	(25-)28-31-33(-39) (27-)30-31-33(-36)	760	(27-)44-49-53(-64)
<i>A. × centovallense</i> nothosubsp. <i>centovallense</i>	108	RV		—	200	(33-)49-54-59(-64)
<i>A. × centovallense</i> nothosubsp. <i>demirizii</i>	108	RV		—	120	(41-)49-53-57(-64)
<i>A. onopteris</i>	72	RV TR	1120	(21-)26-28-31(-38) (25-)28-30-32(-33)	680	(33-)45-50-54(-64)

Table 1. — Microcharacters in different members of the *A. adiantum-nigrum* group: length of the exospore and guard cells. Some specimens of subsp. *yuanum* from Pakistan (TR-5975; 5978) had distinctly smaller spores (exospore: $31 \pm 2 \mu\text{m}$) but a stomatal length in the normal range ($57 \pm 6 \mu\text{m}$), while some specimens from Ethiopia (TR-5968 & TR-5969) with smaller stomata ($50 \pm 5 \mu\text{m}$) but “normal” spore size ($35 \pm 2 \mu\text{m}$) were found to be tetraploid ($n = 72^{II}$). *N* is the sample size.

5.3. Micromorphology

5.3.1. — *Spores*. Apart from the significant size differences between the exospore length of diploids and tetraploids (Table 1), light microscopical study (Fig. 23) already shows that the prominently lophate (= set with ridges) and relatively dark brown perispores of *A. cuneifolium*, *A. woronowii*, and *A. adiantum-nigrum* s.l. are more similar to each other than to those of *A. onopteris* (usually more translucent and paler brown). Important morphological differences of the perispore are illustrated on Fig. 24, showing SEM photographs of spores in equatorial view. In *A. onopteris* the typical euperforate perispore has usually less crests (yielding wider areolae) and distinctly more perforations than in the other taxa. Perispores in *A. cuneifolium* and *A. woronowii* are almost imperforate, show very few sculptural elements in the areola (region in between the ridges), and indicate a closer relationship between these taxa than to *A. onopteris*. The perispore of *A. adiantum-nigrum* is variable but generally intermediate between that of *A. onopteris* and the *A. cuneifolium-woronowii* set. The form of the ridges varies slightly with maturity (Fig. 24b, e, and f may represent less ripe spores) and cannot be used as the sole diagnostic character in this complex.

Taxon	Dorsal epidermis					Ventral epidermis	
	subsidiary cell		epidermal cell			epidermal cell	
	length	width	length	width	lobes	length	width
<i>A. onopteris</i>	58 ± 4	47 ± 3	175 ± 34	30 ± 3	6 ± 1	236 ± 39	20 ± 2
<i>A. cuneifolium</i>	75 ± 16	62 ± 5	152 ± 19	50 ± 6	16 ± 3	149 ± 19	31 ± 8
<i>A. woronowii</i>	69 ± 10	62 ± 5	135 ± 28	51 ± 8	16 ± 4	141 ± 26	30 ± 4
<i>A. adiantum-nigrum</i> s.l.	86 ± 22	65 ± 9	210 ± 51	48 ± 6	14 ± 3	213 ± 64	27 ± 4
subsp. <i>adiantum-nigrum</i>	90 ± 23	67 ± 9	230 ± 52	49 ± 6	14 ± 3	213 ± 44	29 ± 3
subsp. <i>yuanum</i>	79 ± 21	52 ± 9	169 ± 17	49 ± 9	10 ± 2	212 ± 90	25 ± 4

Table 2. — Leaf epidermal cell characters: mean values \pm 1st. dev. (in μm).

5.3.2. — *Leaf epidermis*. An extensively illustrated study of epidermal cell patterns will be published elsewhere (VIANE & REICHSTEIN, 1994). Apart from size (see Table 1) the following morphological differences are visible on Figs. 25-26.

In *A. onopteris* the stomata are restricted to narrow bands parallel to, but not overlying, the veins. The dorsal epidermis is distinctly heteromorphous, i.e. with the supra-vascular cells different (more elongated, and less deeply lobed) from the others. Stomata are predominantly polocytic to copolocytic; the subsidiary cell (i.e., the cell at the proximal side of the guard cells) is typically shorter and narrower (Table 2) than in the other taxa. Both the ventral and the dorsal epidermal cells are (typically) longer and narrower than in the other diploid taxa of this complex. R.V. could not find any significant morphological difference in the leaf epidermis of *A. cuneifolium* and *A. woronowii* (Table 2). In these taxa the dorsal epidermis is usually isomorphous, the stomata are not restricted to a particular zone, and are predominantly polocytic. The subsidiary cell is larger than in *A. onopteris*, and the dorsal epidermal cells are more deeply lobed. No significant morphological difference was found in the epidermis of both the subspecies of *A. adiantum-nigrum*, nor of the nothosubspecies of *A. × centovallense* (Table 2; Fig. 26).

5.3.3. — *Indusia*. In *A. onopteris* the edge of the indusium is generally even with the marginal cells mostly uniform but morphologically different from those below (Fig. 27: A). These marginals are more narrow with their longitudinal axis typically tilted to one side and their anticlinal cell walls usually less lobed.

The indusia of *A. cuneifolium* and *A. woronowii* are very similar and have distinctly lobed margins composed of cells generally undifferentiated from those below. Though the form of the indusial cells is variable in *A. adiantum-nigrum* (both in subsp. *adiantum-nigrum* and in subsp. *yuanum*), the indusia are mostly intermediate between those of *A. onopteris* and *A. cuneifolium* s.l. In both taxa the expression of the *A. onopteris* genome in the marginal cells can be more or less pronounced (Fig. 27: E-F). R.V. could find no significant difference between the indusia of the two subspecies of *A. adiantum-nigrum*, nor between those of the nothosubspecies of *A. × centovallense* (Fig. 27: G-H).

All taxa studied also possess uniseriate multicellular laminar hairs too similar to be used for identification.

<i>Taxon</i>	<i>Mean scale length in mm</i>	<i>Mean scale width in mm</i>
<i>A. adiantum-nigrum</i> s.l.	5.0 ± 1.14	0.6 ± 0.17
subsp. <i>adiantum-nigrum</i>	5.0 ± 0.85	0.6 ± 0.21
subsp. <i>yuanum</i> s.l.	6.5 ± 0.71	0.6 ± 0.07
subsp. <i>yuanum</i> (type)	5.2 ± 0.61	0.5 ± 0.14
<i>A. cuneifolium</i>	2.6 ± 0.38	0.3 ± 0.02
<i>A. woronowii</i>	2.5 ± 0.42	0.4 ± 0.11
<i>A. onopteris</i>	5.0 ± 1.58	0.6 ± 0.09

Table 3. — Mean length and mean width (± 1 st. dev.) of stipe base scales.

5.3.4. — *Scales*. Apart from size differences (Table 3) the paleae of *A. cuneifolium* s.l. are generally distinct from those of *A. adiantum-nigrum* and *A. onopteris* (Fig. 28) by lacking prominent basal appendages (= fimbriae, two cells wide at their base but terminating in an uniseriate apex). R.V. has been unable to confirm the colour and cell-size differences between the scales of *A. adiantum-nigrum* (both subspecies) and those of *A. onopteris* as reported in the literature (FERNANDES & FERNANDES, 1983; FERNANDES, 1984). Though subsp. *yuanum* has larger scales (Table 3), the morphology and the structure of the paleae are similar within the two subspecies of *A. adiantum-nigrum* (Fig. 28: E & F). The scales of both nothosubspecies of *A. × centovallense*

(Fig. 28: D & H) are also similar and usually lack the basal fimbriae (possibly by the influence of two “Cu” or “Wo” genomes against one “On” genome).

5.3.5. *Conclusion.* R.V. has not found any significant micromorphological difference between *A. cuneifolium* and *A. woronowii* and thus, among the diploid ancestors, only *A. onopteris* can be distinguished by its perispore, epidermis (including indusium) and paleae.

Micromorphology does not allow to discriminate the subspecies of *A. adiantum-nigrum* nor the nothosubspecies of *A. × centovallense*. Consequently, micromorphology clearly supports the proposed genome homology between CuCu and WoWo and also sustains the putative genome formulae given to *A. adiantum-nigrum* subsp. *yuanum* (OnOnWoWo) and to *A. × centovallense* nothosubsp. *demirizii* (OnWoWo).

The combination of the preceding cytological and micromorphological results led us to reduce the status of *A. woronowii* to a subspecies of *A. cuneifolium* (see below).

6. The new status of *A. woronowii* as a subspecies of *A. cuneifolium*

6.1. Nomenclature and description

Asplenium cuneifolium Viv. subsp. **woronowii** (Christ) Viane, Rasbach, Reichstein & Schneller, **comb. et stat. nov.**

Basionym: *Asplenium woronowii* Christ, Vestn. Tiflisk. Bot. Sada 6: 25 (1906).

The type (see CHRIST, 1906) is from Georgia (former U.S.S.R.): “Hab. in Caucasi prov. Abchasia. In convalle ad pedem S. montis Arbika in rupestribus calcareis. 7500’ ca. 11 VIII 1905. n° 16. leg. G. Woronow.” (holo-: P!, photograph: TR-5174; iso-: BR!, TGM).

Synonyms: *A. pseudolanceolatum* FOMIN (1912). *A. sajanense* GUDOSCHNIKOV & KRASNOBOROV (1967).

Icon.: FOMIN, 1908: Tab. I, figs. IIIa, b (opposite p.10); GUDOSCHNIKOV & KRASNOBOROV, 1967: 2; DEMIRIZ & al., 1981: Figs. 1-6. Our Fig. 16 & 18.

6.2. Similar variation in other species

The case of subsp. *cuneifolium* and subsp. *woronowii* is not unique in ferns. A most remarkable example is the *Pteris quadriaurita* complex examined by T. G. WALKER (1958), who showed that the monopinnate *Pteris multiaurita* Ag. and the morphologically very different bipinnate *P. quadriaurita* Retz. (both diploid, sexual species) produce swarms of fertile hybrids with all grades of intermediate morphology, wherever the parents grow together. Progeny of the hybrids showed segregation.

Similar cases were reported for some *Dryopteris* species. *D. intermedia* (Muhl. ex Willd.) Gray, from N America (diploid) and *D. azorica* (Christ) Alston endemic to the Azores (diploid) can easily be distinguished on gross morphology but have nevertheless homologous genomes (GIBBY, 1977, 1983, 1985; GIBBY & WALKER, 1977; GIBBY & al., 1978). Even more pronounced is the morphological difference between the tetraploid *D. crispifolia* Rasbach & Reichstein (in GIBBY & al., 1977: 270-274) and the tetraploid *D. guanchica* Gibby & Jermy (in GIBBY & al., 1977: 256-262). The experimentally produced hybrid between them gave mostly full pairing in meiosis with a few univalents in some cells (GIBBY, 1985: 254-255). The pairing behaviour of chromosomes in meiosis is obviously a very conservative character and changed little during millions of years while morphological diversification slowly took place. Furthermore, singular morphological differences are sometimes based on one or a few mutations that do not affect chromosome pairing. Notwithstanding several new methods (gel electrophoresis, chloroplast DNA research), the pairing behaviour during meiosis seems to be the most reliable tool to decide upon genetical relationships in the modern ferns (Filicopsida).



Fig. 3. — *Asplenium adiantum-nigrum* subsp. *yuanum*. Silhouette of whole plant (reduced) from Turkey (Prov. Çoruh): A. Nieschalk s.n., 9-VI-1973 (= TR-3591-B), sexual tetraploid (det.: G. Vida). (Photo: P. Eglin, Basel).

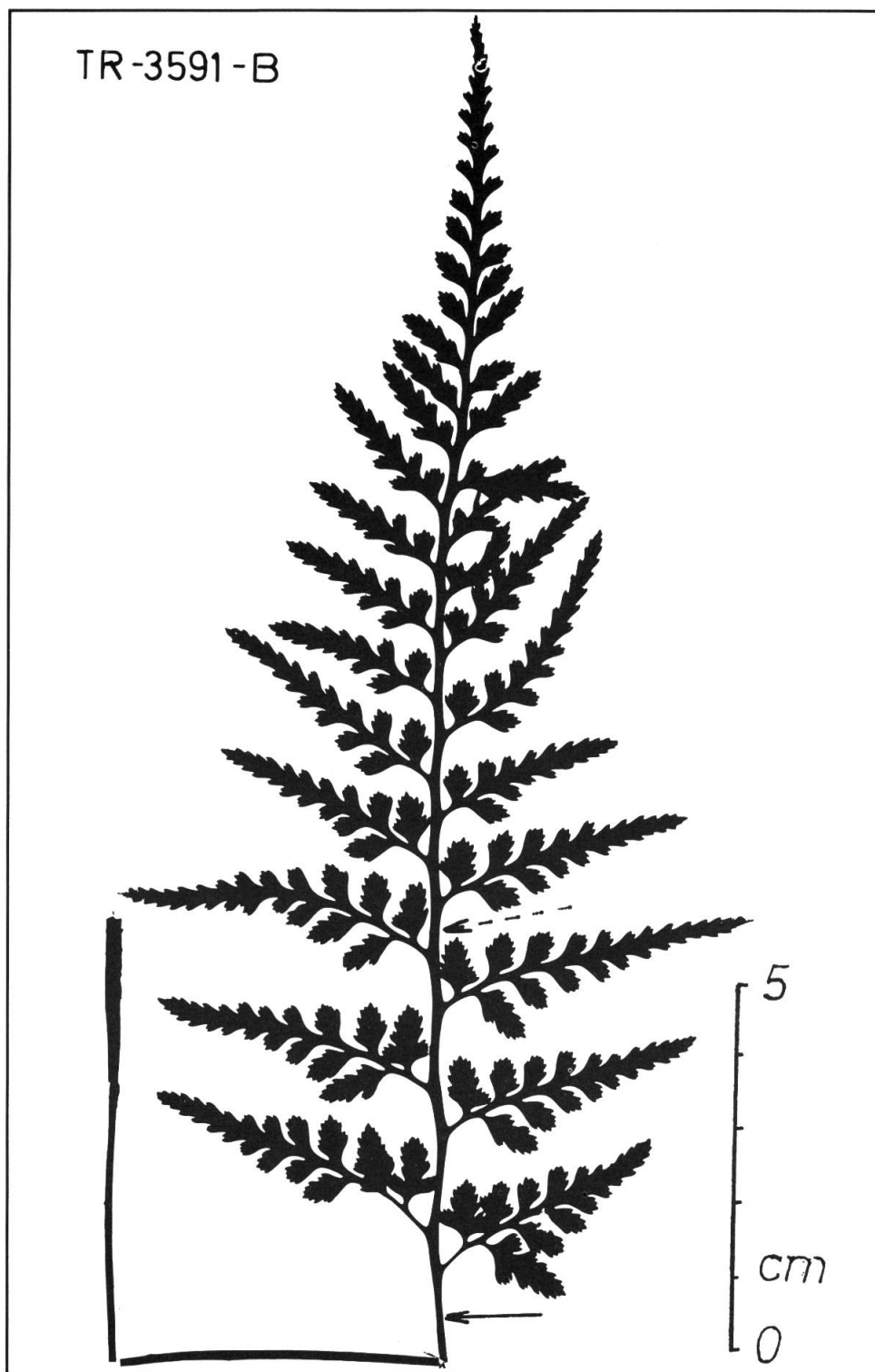


Fig. 4. — *Asplenium adiantum-nigrum* subsp. *yuanum*. Silhouette of one leaf in natural size, same origin as in Fig. 3. Pressed 1-VII-1978. (Photo: P. Eglin, Basel). Arrows show where the brown colour of the basal part of the petiole or rachis changes into green. A full arrow is used for the dorsal (under)side, an interrupted arrow for the ventral (upper) side.

7. Appendix

7.1. *Asplenium adiantum-nigrum* subsp. *yuanum*

List of specimens examined, including microcharacters and cytology, arranged by country (from west to east, north to south).

Turkey: Çoruh (= Artvin): 10 km E of Hopa along rd. to Borka, at 600 m (TR-3591, TR-3597) and 800 m (TR-3592), 9 June 1973, *A. & Ch. Nieschalk s.n.*, (three plants cult.: tetraploid, $n = \text{ca. } 72^{\text{II}}$, G. Vida in litt. 17 April 1974 and 24 May 1975). — Trabzon: Soganli Dağ Pass, above Çaykara, N of Bayburt, 1500 m alt., 29 Aug. 1973, *C.R. Fraser-Jenkins 4066-b* (a mixed collection separated in Basel into 8 specimens *TR-3692 a-h*. Two of them (g, h) were *A. cuneifolium* subsp. *woronowii* (good, small spores etc.), three others (a, b, c) were *A. adiantum-nigrum* subsp. *yuanum* (good, large spores). Progeny of TR-3692b was raised for counting chromosomes and found tetraploid ($n = \text{ca. } 72^{\text{II}}$, det. G. Vida in litt. 24 May 1975). The remaining 3 specimens (d, e, f) could not be identified properly. In the immediate vicinity of these plants a hybrid (*C. R. Fraser-Jenkins 4067*) was collected living, brought to Basel and cultivated as TR-3636 (see 3.2. and below). — Rize, Khabakhor valley, above İkizdere, ca. 1000 m alt., 28 Aug. 1973, *C. R. Fraser-Jenkins 4047* (progeny raised from spores under *TR-3698* was tetraploid, $n = 72^{\text{II}}$ (det. G. Vida in litt. 24 May 1974). — From the same locality, *C. R. Fraser-Jenkins 4049a* (with large spores, living progeny (= *TR-3908*) raised in Basel was tetraploid; det. J. Schneller, in litt. 26 May 1978). — From the same locality, *C. R. Fraser-Jenkins 4049b*, again a mixed collection, was separated in Basel into four specimens: *TR-3699a, b, c, d*. Specimen TR-3699d was *A. cuneifolium* subsp. *woronowii* (small, good spores) while a, b and c were *A. adiantum-nigrum* subsp. *yuanum*. Living progeny (TR-3699a) was raised from specimen a) and found tetraploid ($n = 72^{\text{II}}$, G. Vida in litt. 3 May 1975).



Fig. 5. — *Asplenium adiantum-nigrum* subsp. *yuanum*. Silhouette of one leaf from Ethiopia: R. Cholmondali-Tapper No. 7 (= TR-3319). (Photo: P. Eglin, Basel).



Fig. 6. — *Asplenium adiantum-nigrum* subsp. *yuanum*. Silhouette of one leaf from Ethiopia: R. Cholmondali-Tapper No. 703 (= TR-3323), original collection. (Photo: P. Eglin, Basel).



Fig. 7. — *Asplenium adiantum-nigrum* subsp. *yuanum*. Silhouette of one plant from Ethiopia: I. Kukkonen 12603A, H (= TR-5968). (P. E.) (Photo: P. Eglin, Basel).



Fig. 8. — *Asplenium adiantum-nigrum* subsp. *yuanum*. Silhouette of one leaf from the Caucasus: C. R. Fraser-Jenkins 5700 (= TR-5183-B). (Photo: P. Eglin, Basel).

Georgia: Transcaucasus: Sataplia, NW side of Kutaisi, N of Tbilisi, 450 m alt., *Quercus* on calc., together with *A. ruta-muraria*, *Dryopteris affinis* subsp. *borreri* (labeled as *A. onopteris*), 24 Aug. 1976, C. R. Fraser-Jenkins 5597 (BM), (TR-3760: one frond: exospore ca. 33-36 μm long). — Abkhasia, shale just above Lake Ritsa, N of Bzib, Lashipse-Bzib valley, Sukhumi-Sochi, 1100 m alt., 28 Aug. 1976, C. R. Fraser-Jenkins 5700 (BM), (= TR-5183, Fig. 8, exospore $34 \pm 2 \mu\text{m}$ long: RV).

We have seen several other herbarium specimens from Abkhasia, Armenia, Azerbaidzhan and Turkmenistan which most probably represent subsp. *yuanum* but were not able to examine microcharacters.

Iran: Gorgan: Loveh ($37^{\circ}24'N$, $55^{\circ}45'E$), in silvis frondosis, 400 m alt, 19 April 1967, K. H. Rechinger 33104 (W 08678) (stomata $54 \pm 6 \mu\text{m}$ long). — Parrotio-Carpinetum, 14 Nov. 1966, Tregubov 12 (RAW). — Inter Gorgan et Ziarat, 27 April 1935, E. Gauba s.n. (= TR-5979; stomata $56 \pm 6 \mu\text{m}$ long) (W 08718). — Mazandaran: Harar valley, Karehsang, in dense deciduous forest, ca. 100 m alt., $38^{\circ}18'N$, $52^{\circ}20'E$., 19 April 1959, P. Wendelbo 268 (W 15219). — 6 km SE of Shahpasand, *Carpinus-Quercus* forest, ca. 200 m alt, 27 March 1965, M. L. Grant 17334 (W 17402). — Harar valley, near Karehsang, 400 m alt., in dark forest; 26 Sept. 1974, Hedge, Wendelbo, Assadi, Ali 14712 (Ariamehr). — SE of Banderpey, above microwave station, 780 m alt., in forest with outcrops of limestone rocks, 30 Aug. 1974, P. Wendelbo, M. Assadi 14582 (Ariamehr). — ca. 27 km S of Amol on the road to Tehran, deciduous forest on the steep E facing slope, shallow hollow, 320 m alt., 9 Aug. 1972, P. Uotila 19310 (H; G). — near Veysar, N. facing steep slope covered with *Fagus orientalis*, 1500 m alt., 24 May 1974, Wendelbo & Shirdelpur 11726 (Ariamehr). — in forest on cliff, 15 July 1940, W. Koelz 16249 (W 12956). — Kelerd in Harar valley, in saxosis calc., 17 April 1967, K. H. Rechinger 33044 (W 08670). — Gilan: woodland 15 km from Astara on road to Bandar-e Pahlavi ($48^{\circ}51'E$, $38^{\circ}18'N$), 18 Aug. 1963, N. Jardine 918 (E). — Bandar-e Pahlavi to Astara, between Rizwand and Navrud (Asalem), 50 m alt., *Parrotia-Carpinus* woodland, 15 May 1971, J. Lamond 2951 (E). — Hashtpar to Astara, ca. 65 km from Astara, ca. 23 km from Hashtpar 50-120 m alt., 16 Aug. 1971, J. Lamond 3013 (E). — Astara to Ardabil before Heyran, roadside slopes on steep pass, 125-500 m alt., 17 May 1971, J. Lamond 3031 (E). — Elburz Mts., Nezva Kuh area: between Orim and Taru, in forest, $31^{\circ}59'N$, $53^{\circ}11'E$., 6 July 1959, Wendelbo 1128 (Ariamehr). — Astara in collibus litori Caspio finitimis, 10-100 m alt., 17 May 1971, K. H. Rechinger 39853 (G). — S. de Racht, boisement dégradé, 100 m alt., 9 June 1960, H. Pabot 3600 (G). — road from Assalem to Khalkhal, near Assalem, on stone near brooklet in forest, 200 m alt., 22 Oct. 1974, Wendelbo & Shirdelpur 14895 (E). — Foumen to Masullah, in forest, 200-300 m alt., 18 June 1975, P. Wendelbo & M. Assadi 18577 (Ariamehr). — Entre Ramsar et Tchalous, bord de la route (reste de boisement), 21 Aug. 1960, H. Pabot 4944 (G). — Dimalu, in forest in shade. 9000 ft alt., 23 July 1940, W. Koelz 16537 (= TR-5981; exospore 37 ± 2 , stomata $58 \pm 6 \mu\text{m}$ long) (W 10958). — In collibus 10-20 km W of Astara ad viam versus Heyran ducentem, 500 m alt., 17 May 1971, K. H. Rechinger 39890 (W 08704). — Talesh Mts., Ardabil-Astara, limestone rocks, 1490 m alt., 14 Aug. 1973, C. R. Fraser-Jenkins 3930 (BM) (Sowing in Basel gave progeny: TR-3714). — Talesh Mts., 30 km up Nav valley above Assalem, S of Siadun, Astara to Bandar-e Pahlevi, 1400 m alt., 1 July 1977, C. R. Fraser-Jenkins 6019 to 6023 (obtained living and cult. in Basel as TR-4256) (Herb. T. Reichstein). — Talesh Mts., 32 km up Nav valley, 1500 m alt., 1 July 1977, C. R. Fraser-Jenkins 6024-6025 (obtained living and cult. in Basel as TR-4261 and 4262) (Herb. T. Reichstein). — Talesh Mts., 11 km up Nav valley, Assalam, on calc. rocks in side gorge, 250 m alt., 2 July 1977, C. R. Fraser-Jenkins 6047 (obtained living and cult. in Basel as TR-4263). — Qazvin: in valle fluvii Keredj prope Azadbar, no date, *Esfandiari* s.n. (W 11257: ex Herb. Fak. Agron. Keredj 1808 = TR-5980, stomata $54 \pm 4 \mu\text{m}$ long).

Afghanistan: C. Nuristan: am Seitenbach des Petsch-Flusses bei Wama, sehr feucht, 1380 m alt., 7 June 1935, G. Kerstan 791 (W 11110). This may be an intermediate form, very close to subsp. *yuanum*.

Pakistan: Dir: "Chitral", N.W.F.P., Lowari top to Dir, 6 Aug. 1954, M. A. Siddiqi & A. Rahman s.n. (RAW). — Swat: Bahrein, ca. 5000 (ft) alt., 17 Aug. 1952, R. R. Stewart 24467 (RAW; spore

prep.: *TR-5982*, with exospore length $33 \pm 2 \mu\text{m}$). — Lower Swat, 3-4000 (ft) alt., 4-8 April 1956, *R. R. Stewart 27504* (RAW; spore prep.: *TR-5978*, with small exospore $31 \pm 2 \mu\text{m}$, but stomata $58 \pm \mu\text{m}$ long).

India: Kashmir: Poonch, 1.2 miles above Bafftiiaz, E of Swanhot, 1700-1900 m alt., 7 Dec. 1990, *C. R. Fraser-Jenkins sheet 161* (= *TR-7541*, exospore $33 \pm 2 \mu\text{m}$ long).

China: Yunnan: Tehching, Atuntze, Kaa-ker-pu, in ravine, 2800 m alt., 4 June 1937, *T. T. Yü 8461* (PE; very few spores available, exospore small: $30 \pm 2 \mu\text{m}$ long, but stomata $58 \pm 6 \mu\text{m}$ and stipe base scales 5.6 mm long). — 2500 to 2700 m alt., 22 July 1940, *K. M. Feng 5686* (PE; exospore 35 ± 2 , stomata $61 \pm 6 \mu\text{m}$, and stipe base scales 4.7 mm long).

Ethiopia: Simien: Djinn Barr, in rock crevices within 2 yards of river, 3300 m alt., 20 May 1971, *R. Cholmondely-Tapper 7* (Herb. Fraser-Jenkins). A frond with ripe spores obtained as *C. R. Fraser-Jenkins 3546* (in litt. 14 Dec. 1971; *TR-3319*, Fig. 5). Sowing in Basel (11 Jan. 1972) gave good progeny which was tetraploid ($n = 72^{\text{II}}$ and $2n = 144$ det. G. Vida 1974). — Balé (Diushu): among mosses and rocks near scrub forest, 3400 m alt., Dec. 1971, *R. Cholmondely-Tapper 703* (Herb. Fraser-Jenkins). A frond with mature spores (*TR-3323*, Fig. 6) obtained as *C. R. Fraser-Jenkins 3547* in litt. 14 Dec. 1971. Sowing made in Basel (24 Jan. 1972) gave living progeny. — Sanati plateau and Mt. Batu, $06^{\circ}55'N$, $39^{\circ}40'E$, in alpine belt dominated by *Festuca schefflerii*, *Euryops prostrata*, *Anthemis tigrensis*. On foot of the highest point of Mt. Batu, in rock crevices, ca. 4100 m alt., 8 Nov. 1982, *I. Kukkonen 12603A*, two sheets (= *TR-5968* and *5969*) each with two plants (Fig. 7). Sowing of spores in Basel on 24 Febr. 1984, gave living tetraploid progeny (*TR-5968*) with $n = 72^{\text{II}}$ (det. H.R. in litt. 6 May 1986). Exospore length: $35 \pm 2 \mu\text{m}$; stomata relatively small: $50 \pm 5 \mu\text{m}$ long. — Abyss. merid.: Entotto, Dec. 1886, *Dr. Traversi s.n.* (Photogr. *TR-5597*) (P); this was first assumed to represent the diploid *A. cuneifolium* subsp. *woronowii*, but the exospore length ($33 \pm 2 \mu\text{m}$), the long guard cells ($65 \pm 6 \mu\text{m}$) and the epidermis structure are indicative for the tetraploid *A. adiantum-nigrum* subsp. *yuanum*.

La Réunion: Cirque de Cilaos, Forêt de Grande Matorum, ca. 3 km above Cilaos, ca. 1700 m alt., 27 July 1986, *C. R. Fraser-Jenkins 12326* (BM; a mutilated frond: *TR-6616*, with exospore length: $32 \pm 2 \mu\text{m}$).

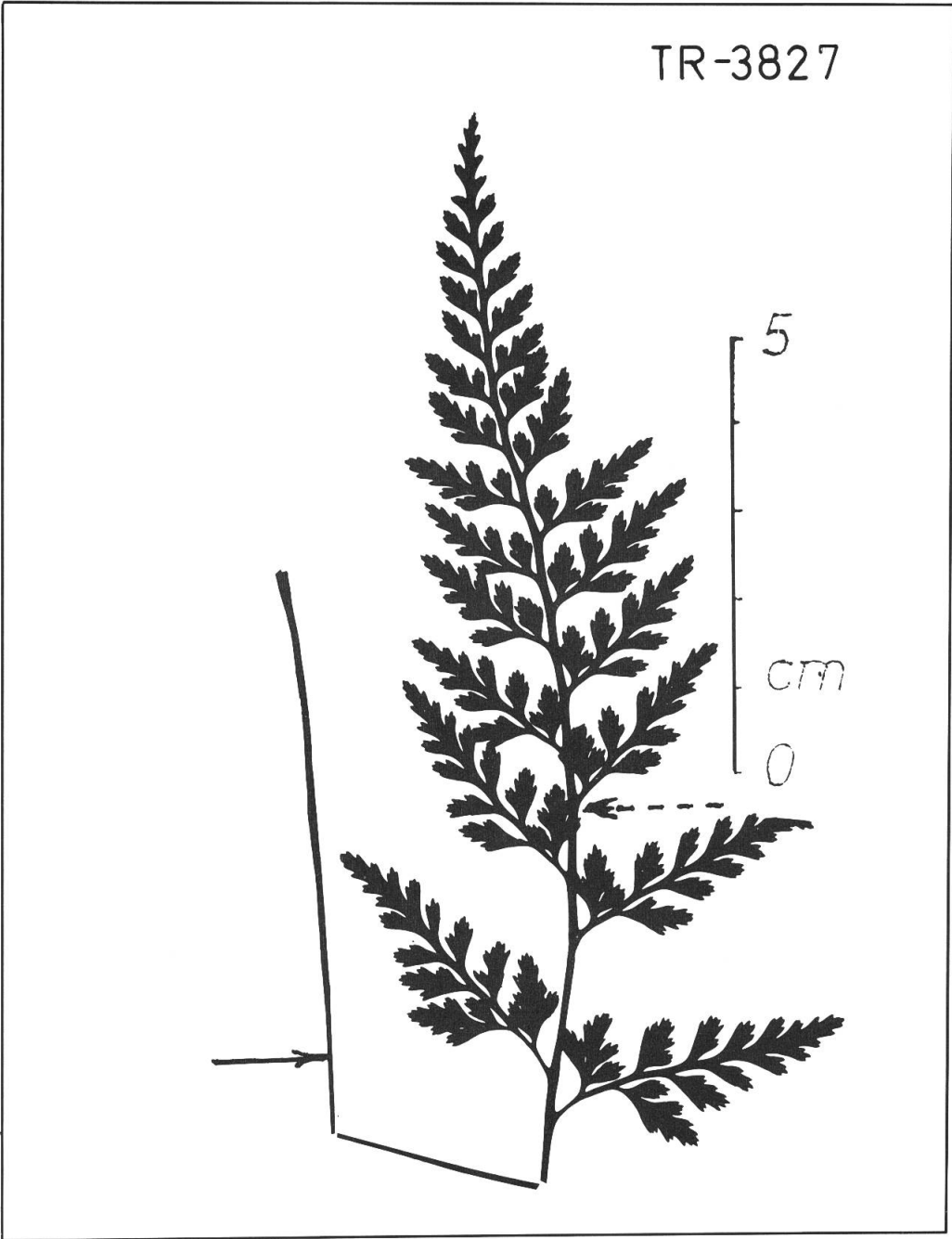


Fig. 9. — *Asplenium adiantum-nigrum* subsp. *adiantum-nigrum*. Silhouette of TR-3827, cult. ex spores: Switzerland, Ticino. Pressed 1-VII-1978. (Photo: P. Eglin, Basel).

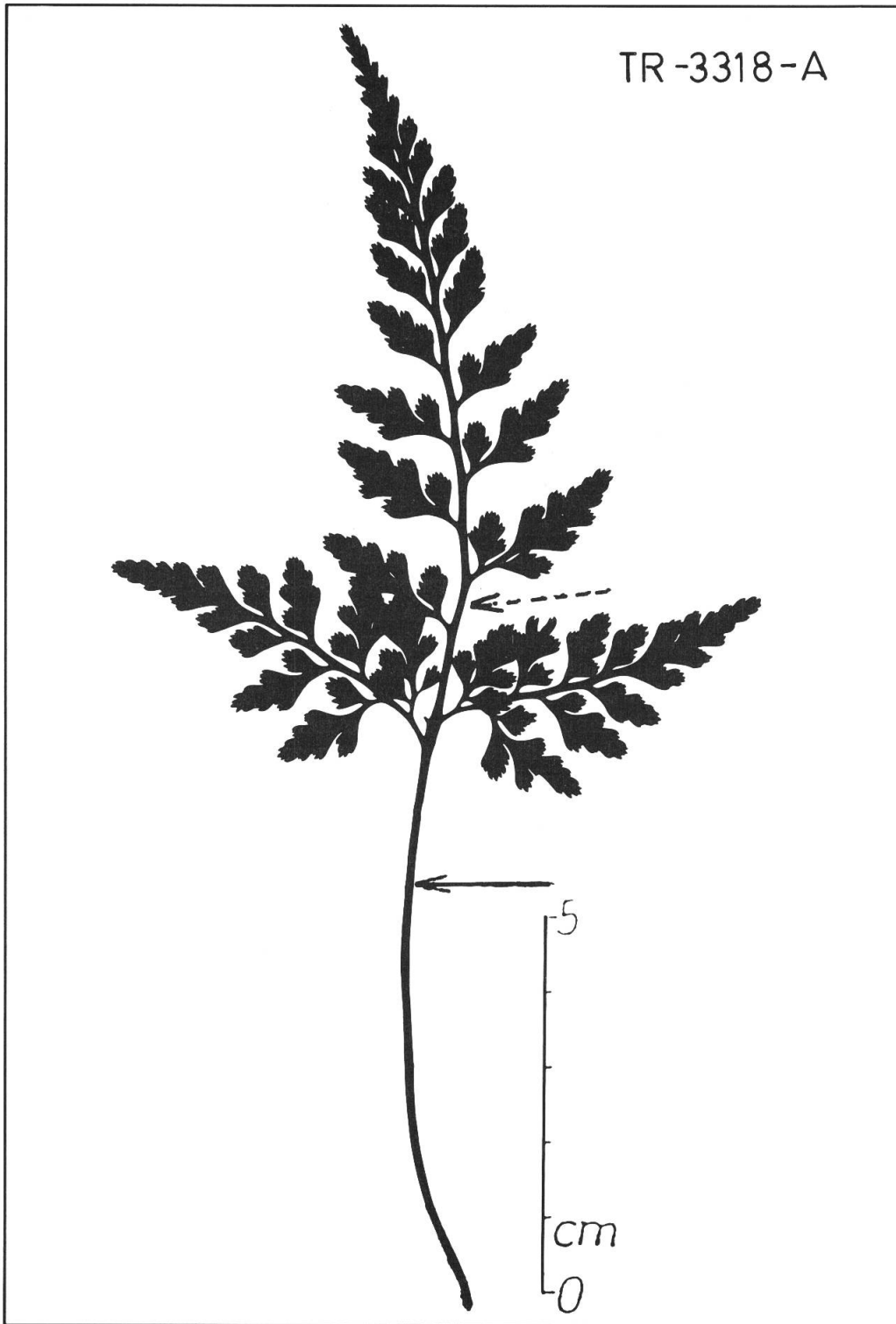


Fig. 10. — *Asplenium adiantum-nigrum* subsp. *adiantum-nigrum*. Silhouette of TR-3318, cult. ex spores of C. R. Fraser-Jenkins 2752 from Georgia (former U.S.S.R.), tetraploid (G. Vida). Pressed I-VII-1978. (Photo: P. Eglin, Basel).

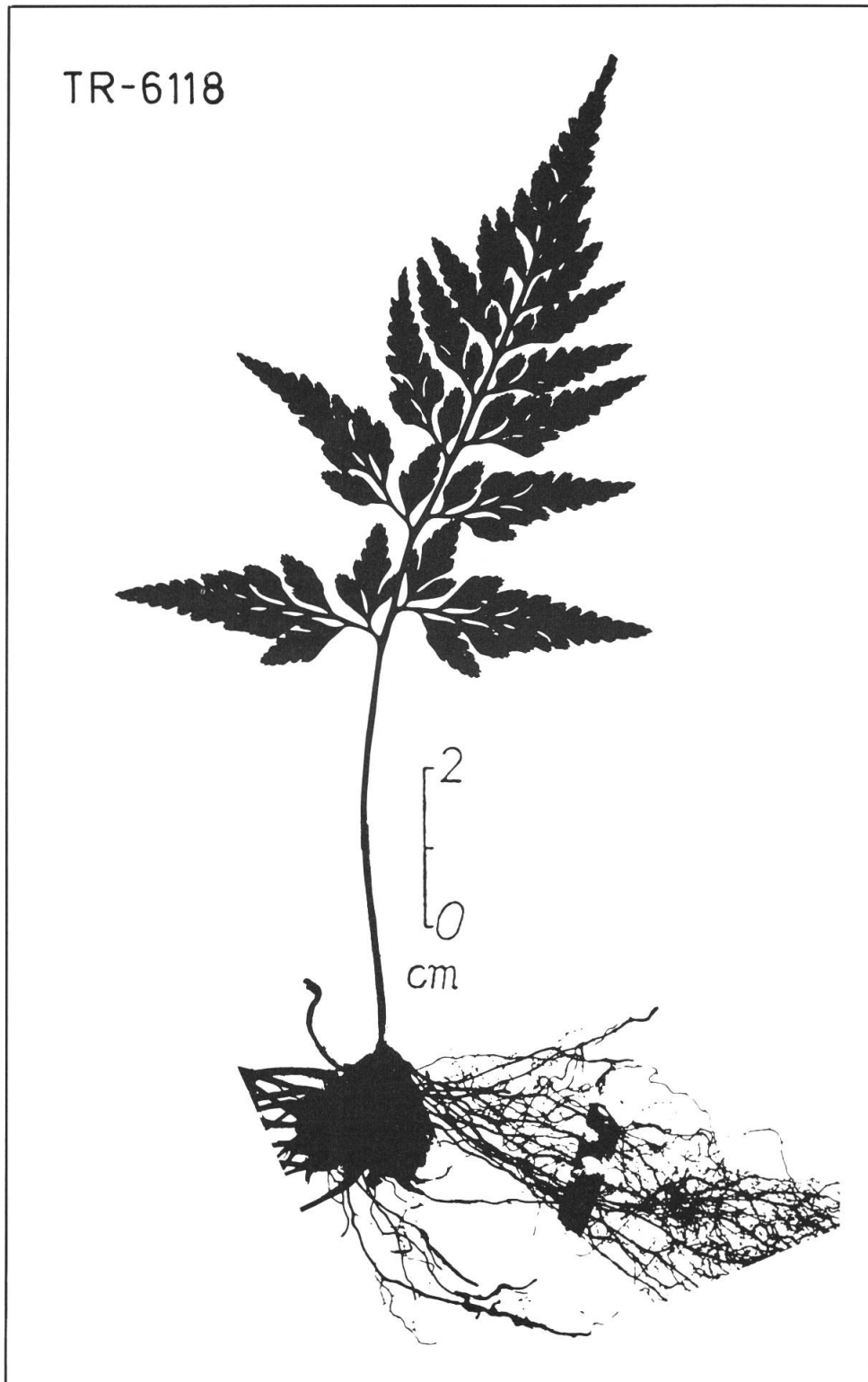


Fig. 11. — *Asplenium adiantum-nigrum* subsp. *adiantum-nigrum*. Silhouette of one leaf with part of rhizome of TR-6118, cult. ex spores of A. G. Piggott 3222 from Hawaii (USA), tetraploid (det.: H.R.). (Photo: P. Eglin, Basel).



Fig. 12. — *Asplenium adiantum-nigrum* subsp. *adiantum-nigrum* var. *silesiacum*. Silhouette of the holotype (B) from “Weinberg bei Zobt:n” (Silesia, now in Poland). (Photo: R.V.).

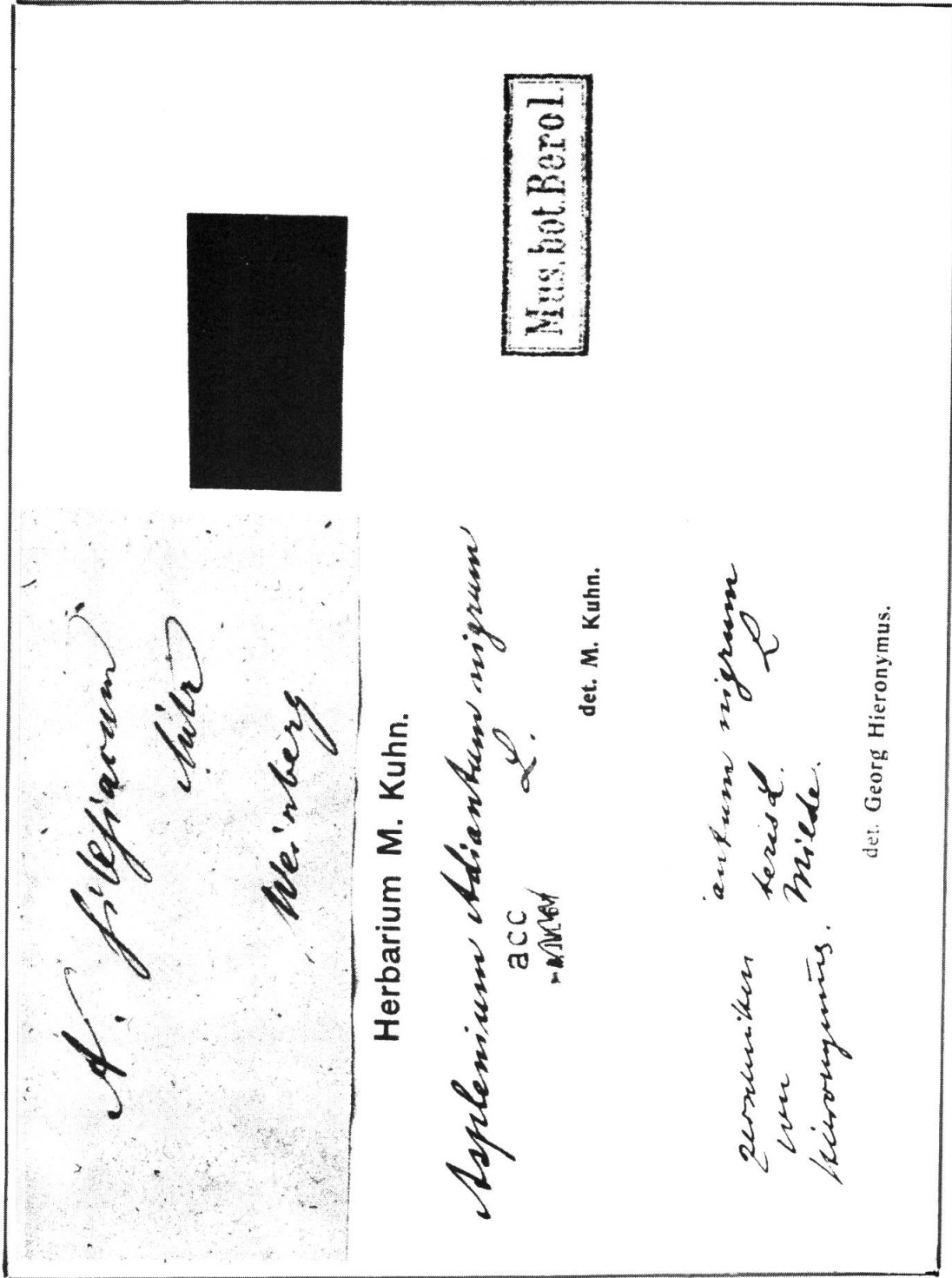


Fig. 13. — *Asplenium adiantum-nigrum* subsp. *adiantum-nigrum* var. *silesiacum* Milde. Labels of the holotype in B.



Fig. 14. — *Asplenium adiantum-nigrum* subsp. *adiantum-nigrum* var. *silesiacum*. Silhouette of one leaf of the extreme form (TR-4700) from Mt. Ramazzo, Italy (from RASBACH & al., 1986: Fig. 7). Progeny was tetraploid.

7.2. List of some intermediate forms of *A. adiantum-nigrum* subsp. *adiantum-nigrum* versus subsp. *yuanum* (putative products of introgression)

Iran: Gilan: Astara, shaded rocks along little water courses running into the Caspian Sea, close to the Russian border, ca. 30 m below the sea level, together with *Dryopteris pallida* subsp. *raddeana*, *Daffinis* subsp. *borreri*, *Polystichum aculeatum* and *A. trichomanes* subsp. *quadrivalens*, July 1965, E. Hauser s.n. (= TR-1551) obtained living in Basel, one frond pressed 6 Aug. 1965. — In declivibus montium 23 km N. Hashtpa, ad viam versus Astara ducentum 20-150 m, 16 May 1971, K. H. Rechinger 39781 (W 08700). — Astara, in collibus litori Caspio finitimis, 10-100 m alt. spores large, 17 May 1971, K. H. Rechinger 39853 (W 08698). — Gorgan: Bandar Gaz, May 1948, Sharif 86 (W 11213). — Mohamed Reza Shah National Park forest, SE side of Abshar, N exp. slope, 800 m alt., 29 July 1974, Wendelbo & Cobham 14276 (Ariamehr, W 12668). — Mazandaran: ca. 200 m alt., 6 Aug. 1937, K. H. Rechinger 2068 (W; spores large).

Pakistan: Gilgit: Gullapur, 21 Oct. 1956, S. Ali s.n. (RAW). — Swat, Mt. Ilam, ca. 8000 (ft), 12 Aug. 1952, R. R. Stewart 24336 (RAW).

India: Kashmir, Kishtwar, 5000 ft, July 1980, S. P. Khullar 325 (exospore (27)36-39(42) μm long; = TR-5700). Close to subsp. *yuanum*.

7.3. List of specimens used for figures, for comparison, for micromorphology, or for hybridization experiments

7.3.1. *Asplenium adiantum-nigrum* L. subsp. *adiantum-nigrum*

Switzerland: Ticino: Agarone, above Cugnasco, Gneiss wall, ca. 350 m alt. 23 Aug. 1977, TR-4421 (a plant from the same clump, TR-3827, was tetraploid, Fig. 9).

Germany: Baden-Württemberg: Black Forest, Glottertal, gneiss rocks partly under trees, 13 Jan. 1988, ca. 330m alt., H. Rasbach s.n. (= TR-6966, sowing on Agar-medium on 20 Feb. 1988 in Basel. A plant from the same population was tetraploid: det. H.R.). — S. exposed hillside, 3 Sept. 1980, R. Viane 1839 (stipe base scales: 5.4 ± 0.42 mm, stomata: 52 ± 5.1 , and exospore: 34 ± 2.3 μm long).

Georgia: Abkhasia: Sochi to Sukhumi, E of Bzib, walls of the village Kholdakvara, at bottom of Bzib valley, ca. 150 m, C. R. Fraser-Jenkins 2752 (= TR-3318). Sowing 19-I-1972 gave good progeny, tetraploid, $n = \text{ca. } 72^{\text{II}}$ (G. Vida, 22-V-1973). Frond pressed 1-VII-1976, see Fig. 10.

U.S.A.: Hawaii: Maui, Haleakala crater, terrestrial in cinder cone, ca. 3000 m, 5-VI-1984, A. G. Piggott 3222 (= TR-6118; obtained from CRFJ in litt. Dec. 1984). Sowing on 5-I-1985 gave 5 sporophytes (6-XII-1985), cytological fixation on 27-III-1986, tetraploid $n = 72^{\text{II}}$ (H.R., 25-V-1986), exospore length: 37 ± 2 μm (RV). Frond pressed on 17-VII-1987, see Fig. 11.

Pakistan: Dir: N facing rock between Pankote and Orlandi, N of Dir, 1750 m, 8 Oct. 1990, C. R. Fraser-Jenkins sheets 140 to 142 (= TR-7520 to TR-7522, spores good, large; det. T.R.). — Chitral: Rocks on W side of river, 1 mile N of Ziarat, N of Lowari Pass, 2100 m alt., 8 Oct. 1990, C. R. Fraser-Jenkins sheet 139 (= TR-7519). — Swat: W side of Mt. Ilam, above Karakar Pass, SW of Saidu Sharif 1750 m, 12 Oct. 1990, C. R. Fraser-Jenkins sheet 146 (= TR-7526, with exospore relatively small: 32 ± 2 μm , but stomata 58 ± 5 μm long; det.: R.V.).



Fig. 15. — *Asplenium cuneifolium* Viv. subsp. *cuneifolium*. Silhouette of one leaf of TR-4690 from Mt. Ramazzo (locus classicus), Italy (from RASBACH & al., 1986: Fig. 6). Progeny was diploid. (Photo: P. Eglin, Basel).

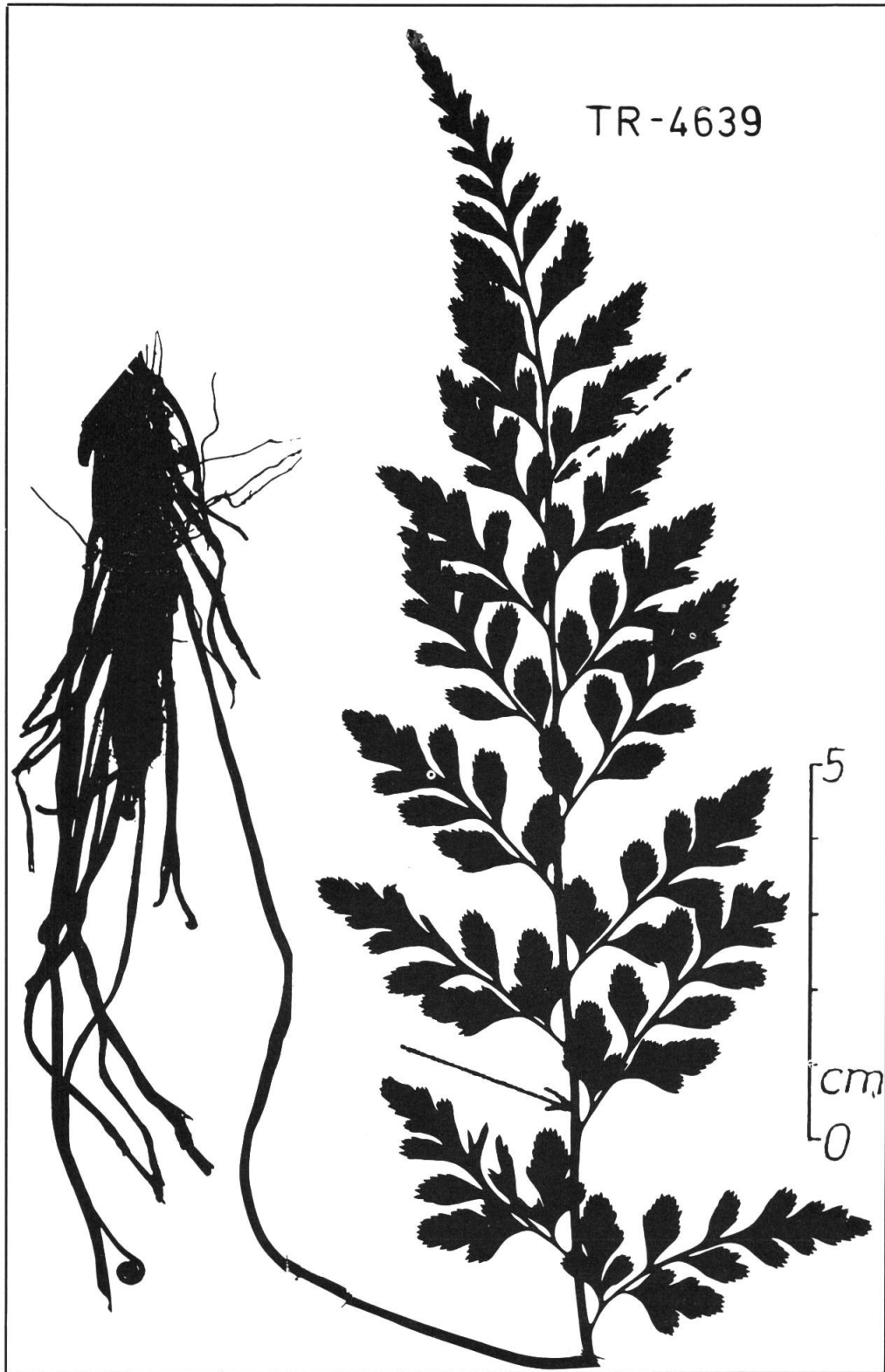


Fig. 16. — *Asplenium cuneifolium* Viv. subsp. *woronowii*. Silhouette of part of the whole plant with one leaf of C. R. Fraser-Jenkins 5560, from the locus classicus of *A. pseudolanceolatum* Fomin in Georgia (former U.S.S.R.). Progeny (= TR-4639) was diploid (Det.: J.Sch.). (Photo: P. Eglin, Basel).

7.3.2. *A. adiantum-nigrum* L. subsp. *yuanum*

Turkey: see under 7.1.

Iran: Mazandaran: Galandrud, *Probst VO-971* (stomata: $58 \pm 5 \mu\text{m}$, exospore: $32 \pm 2 \mu\text{m}$ long) (BSB). — Gilan: Talesh, 32 km up Nav valley, above Assalem, S of Siadun, Astara to Bandar-e Pahlevi, ca. 1500 m, 1 July 1977, *C. R. Fraser-Jenkins 6024* (coll. living, cult. as *TR-4261*, spores good).

Ethiopia: see under 7.1.

7.3.3. *A. cuneifolium* subsp. *cuneifolium*

Austria: Burgenland: Kienberg near Bernstein, ca. 790m, serpentine rocks, 22 July 1975, *J. Schneller Sch-II*. A plant from the same population (*Sch-9*) was diploid, $n = 36^{\text{II}}$ (J.Sch., April 1976).

Italy: Liguria: Monte Ramazzo retro Sestri di Ponente, 1803, *Bertoloni & Viviani s.n.* (p.p.) (lectotype, BOLO) — Mt. Ramazzo, Miniera above Sestri Ponente (W of Genova), ca. 520 m alt., on serpentinitic rocks and scree (locus classicus), 23-VII-1978, *TR-4690*. Diploid with $2n = 72$ (H.R., 30-X-1984), exospore length: $32 \pm 2 \mu\text{m}$, stomata: $49 \pm 4 \mu\text{m}$ long (RV); see RASBACH & al. (1986), and Fig. 15.

Switzerland: Graubünden: Laret near Davos, 1520 m, serpentinitic rocks and scree, 13 July 1987, *H. & K. Rasbach 599*. This well known population is diploid (*R. Viane 2035*, from the same population, has an exospore $31 \pm 2 \mu\text{m}$, and stomata $51 \pm 5 \mu\text{m}$ long). Sowing on Agar-medium 20-II-1988.

7.3.4. *A. cuneifolium* subsp. *woronowii*

Turkey: Çoruh (= Artvin): Arhavi, Dikyamaç Köyü Yaylası, Küçük-çamlık yaylası, 3 Sept. 1967, *A. Kuru s.n.* (cult. ex spores as *TR-2344*, diploid, see DEMIRIZ & al., 1981). Exospore $33 \pm 2 \mu\text{m}$, stomata $46 \pm 3 \mu\text{m}$ long (RV). — Trabzon: Soganli Dağ, 1500 m, 29 Aug. 1973, *C. R. Fraser-Jenkins 4066a* (coll. living, cult. as *TR-3643*; diploid: $n = 36^{\text{II}}$, det: J. Schneller 27-V-1975; exospore $31 \pm 2 \mu\text{m}$, stomata $53 \pm 4 \mu\text{m}$ long (RV); sowing 6-VII-1975).

Georgia: Transcaucasus: above Borzhomi, on Bakuriani road, W of Tbilisi, 1200 m, shale, 23 Aug. 1976, *C. R. Fraser-Jenkins 5560* (progeny ex spores = *TR-4639*; sowing on Agar-medium 26-III-1978, diploid $2n = 72$, det.: J. Sch. 18-IV-1980); exospore $29 \pm 2 \mu\text{m}$, stomata $49 \pm 4 \mu\text{m}$ long (det.: R.V.), Fig. 16, 18.



Fig. 17. — Silhouette of *Asplenium onopteris*. One (typical) leaf from Italy, E. Liguria: D. Marchetti s.n. (= TR-6942). (Photo: P. Eglin, Basel).

7.3.5 *A. onopteris*

Algeria: SSE of Alger, Atlas de Blida, 950m, 1982, *R. Bosmans 82/67* (stipe base scales: ca. 4.7 mm, stomata: 50 ± 5 , and exospore: $31 \pm 2 \mu\text{m}$ long) (GENT).

France: Var: St. Tropez, Baie des Canébières, 24 Febr. 1982, *R. Viane 2071* (stipe base scales: 4.1 ± 0.71 mm, stomata: 49 ± 4.6 , and exospore: $28 \pm 2.7 \mu\text{m}$ long).

Italy: Liguria: sul colle di Panano, sopra Deiva Marina, ca. 900 m, su serpentino, 18 March 1982, *D. Marchetti s.n.* (= *TR-6942*), Fig. 17. Exospore $27 \pm 2 \mu\text{m}$ long (RV), sowing on Agar-medium 11-I-1986.

Portugal: Algarve: along N124 near Barranco do Velho, in dry rivulet bed under *Quercus suber*, 2 July 1979, *R. Viane 745* (stipe base scales: 4.9 ± 1.12 mm, stomata: 48 ± 5.6 , and exospore: $28 \pm 2.1 \mu\text{m}$ long).

7.3.6.A. \times *centovallense* nothosubsp. *centovallense*

Switzerland: Ticino: Centovalli, Borgnone, NE of Tries, Serpentine, 550m alt., 26 Sept. 1969, *A. Becherer s.n.* (Herb. T. Reichstein). Stomata $54 \pm 5 \mu\text{m}$ long.



Fig. 18. — *Asplenium cuneifolium* Viv. subsp. *woronowii*. Silhouette of C. R. Fraser-Jenkins 5560 from Georgia.



Fig. 19. — Silhouette of *Asplenium* × *centovallense* nothosubsp. *demirizii*. Paratype, TR-3642 (= progeny of Fraser-Jenkins 4050). (Photo: R. V.).

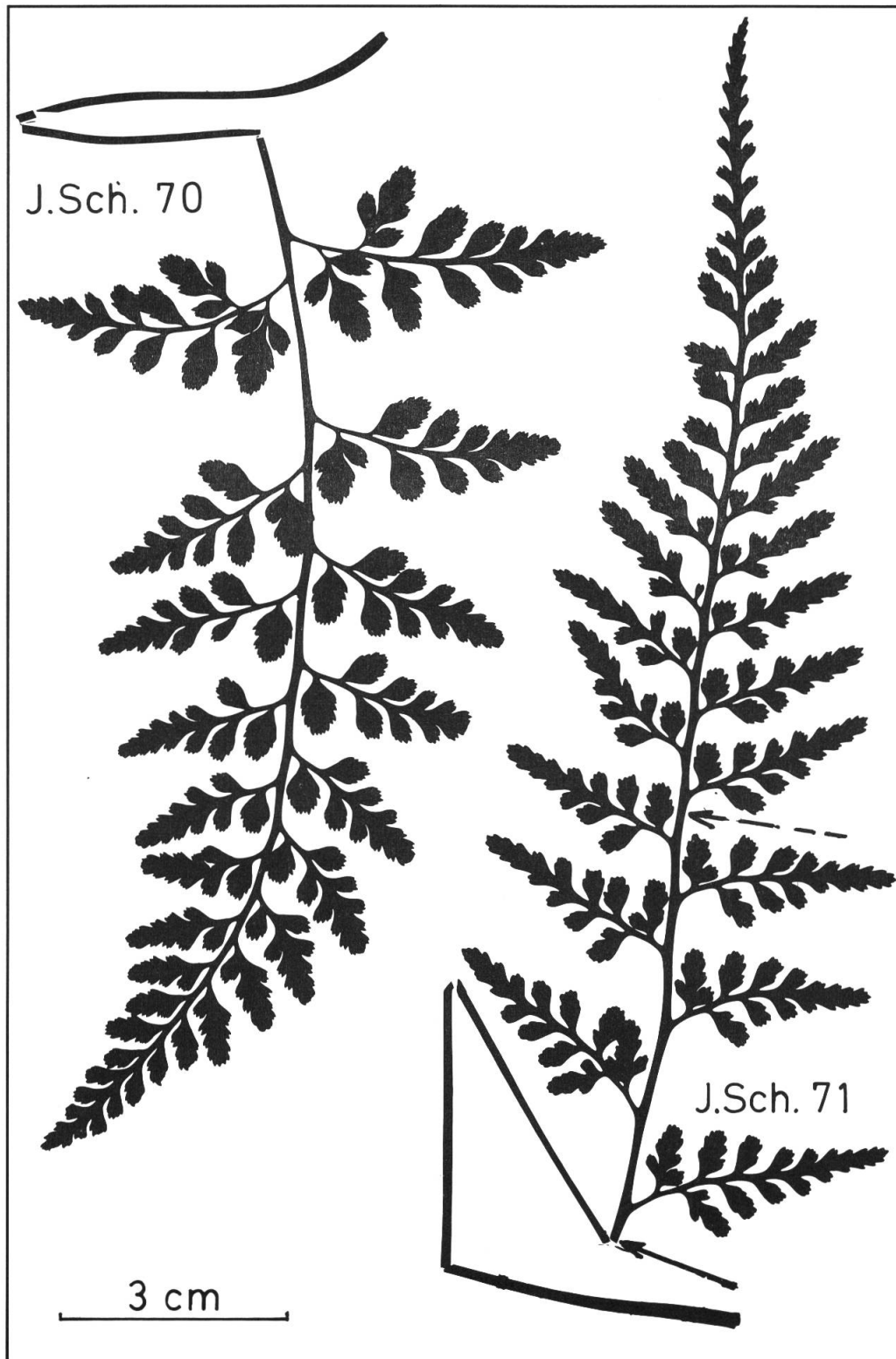


Fig. 20. — Silhouette of two experimentally produced *Asplenium* × *centovallense* nothosubsp. *demirizii* hybrids. J.Sch. 70 after cult. in Basel (= TR-4071-A), with *A. adiantum-nigrum* subsp. *yuanum* as female parent. Pressed 28-VI-1977. J.Sch. 71 (= TR-4071-B), the reverse hybrid with *A. cuneifolium* subsp. *woronowii* as female parent. (Photo: P. Eglin, Basel).

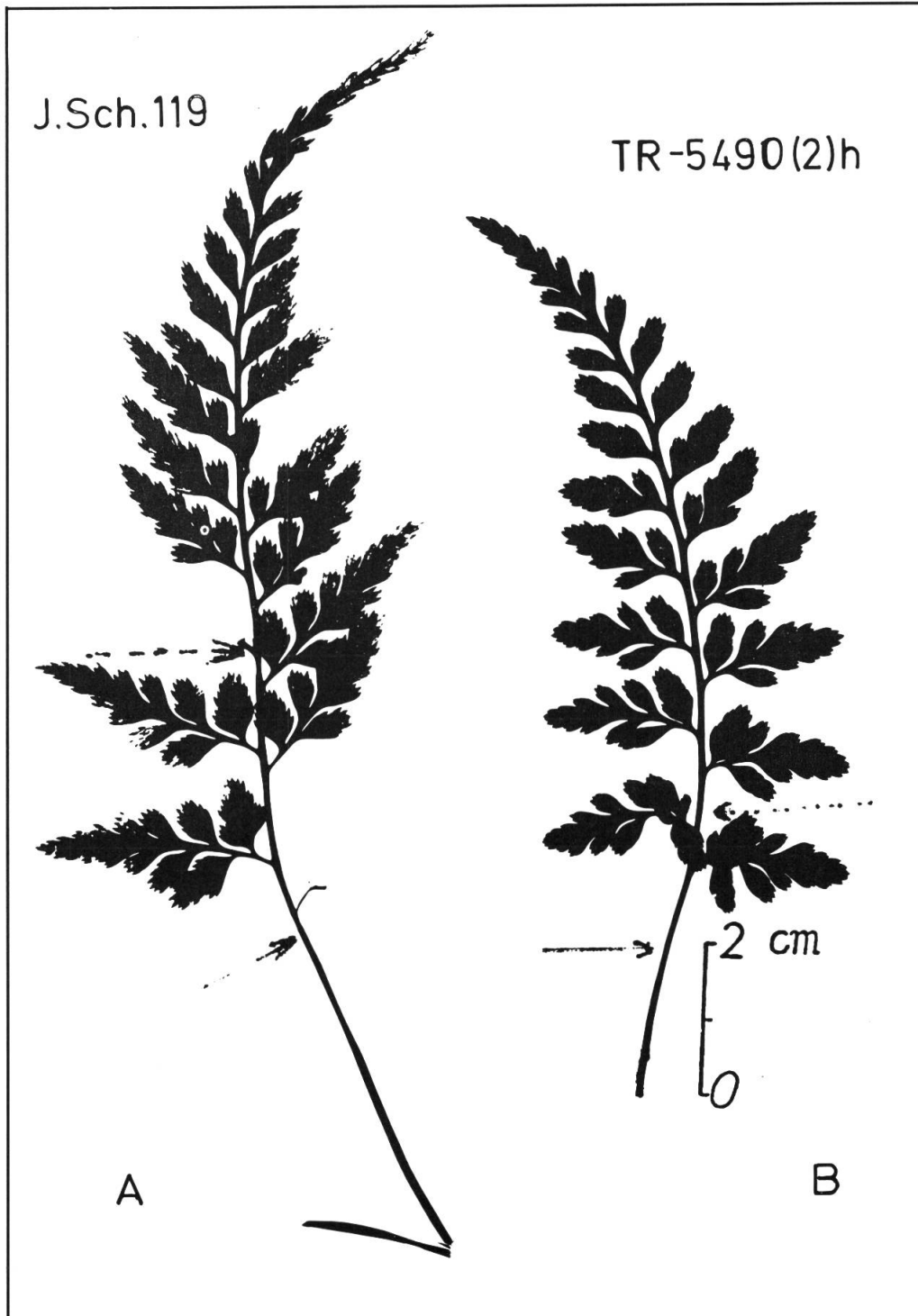


Fig. 21. — Silhouettes of two experimentally produced triploid hybrids.

A: J.Sch. 119 = Female *Asplenium cuneifolium* subsp. *cuneifolium* (J.Sch. 11) × male *A. adiantum-nigrum* subsp. *yuanum* (TR-3591), pressed 10-VIII-1977.

B: TR-5490 (2)h = *A. adiantum-nigrum* subsp. *adiantum-nigrum* (TR-4421) × *A.cuneifolium* subsp. *woronowii* (TR-4639), pressed 12-IX-1982. Both hybrids have the genome formula (CuOnWo) in "A" derived from (Cu) plus (OnWo), in "B" from (CuOn) plus (Wo). (Photo: P. Eglin, Basel).

7.4. Hybridization experiments

Four experiments were performed involving *A. adiantum-nigrum* subsp. *yuanum* and a fifth with subsp. *adiantum-nigrum*. The second partner was *A. cuneifolium* subsp. *woronowii*, except in the last one mentioned in Table 4. As mentioned in paragraph 2.9, two different methods were used. J. Schneller applied a modification of Manton's classical method by

- 1) using a single female prothallium per glass cup, and
- 2) by limiting the experiment to ca. one hour.

T. Reichstein used the method of planting prothalli of both parents in a square arrangement (RASBACH & al., 1994). The results are summarized in Table 4, and the details are given below.

There was no morphological difference (see Fig. 20) between the plants of experiment 7.4.1. (J.Sch. 70) and the reverse hybrid 7.4.2. (J.Sch. 71). Both compared well in shape with natural *A. × centovallense* nothosubsp. *demirizii* (TR-3636-C, see Fig. 19).

Experiment number, initials and number of worker (see text for details)	Prothalli (female) used Number	Sporo- phytes Number	Selves Number	Hybrids	
				Number	Yield
7.4.1. <i>A. adiantum-nigrum</i> subsp. <i>yuanum</i> × <i>A. cuneifolium</i> subsp. <i>woronowii</i> — J.Sch. 70	3	2	1	1	33%
7.4.2. <i>A. cuneifolium</i> subsp. <i>woronowii</i> × <i>A. adiantum-nigrum</i> subsp. <i>yuanum</i> — J.Sch. 71	7	7	2	5	70%
7.4.3. <i>A. adiantum-nigrum</i> subsp. <i>yuanum</i> × <i>A. cuneifolium</i> subsp. <i>woronowii</i> — TR-3643-Z	12 + 9	10	8	2	20%
7.4.4. <i>A. adiantum-nigrum</i> subsp. <i>adiantum-nigrum</i> × <i>A. cuneifolium</i> subsp. <i>woronowii</i> — TR-5490	12 + 18	30	18	12	40%
7.4.5. <i>A. cuneifolium</i> subsp. <i>cuneifolium</i> × <i>A. adiantum-nigrum</i> subsp. <i>yuanum</i> — J.Sch. 119	4	4	3	1	25%

Table 4. — Scheme of results of hybridization experiments 7.4.1. - 7.4.5.

Hybridization experiments performed by J. Schneller and T. Reichstein. Experiments 7.4.1. to 7.4.3. produced the triploid hybrid *A. × centovallense* nothosubsp. *demirizii*; no subspecific names are given to the hybrids produced in experiments 7.4.4. and 7.4.5. as they have never been found in the wild.

Explication of the hybridisation experiments.

7.4.1: J.Sch. 70 = TR-4071-A. Female *A. adiantum-nigrum* subsp. *yuanum* (TR-3591) × male *A. cuneifolium* subsp. *woronowii* (TR-3643). Three isolated female prothalli in 3 separated glass cups were used (20 Oct. 1977). Two sporophytes resulted, one self and one hybrid (33% yield). The hybrid was triploid and was sent to Basel on 21 July 1977, where it was cultivated as TR-4071-A (Fig. 30-C).

7.4.2: J.Sch. 71 = TR-4071-B. Female *A. cuneifolium* subsp. *woronowii* (TR-3643) × male *A. adiantum-nigrum* subsp. *yuanum* (TR-3591). 7 isolated female prothalli in 7 glass cups were used (20-X-1977). Seven sporophytes resulted, two of them were selves and five were hybrids (70% yield). One of the hybrids was sent to Basel and cultivated as TR-4071-B (Fig. 20). It was triploid with ca. 36^{II} and 36^I in meiosis (Fig. 30-D).

7.4.3: TR-3643-Z. Nine prothalli of *A. adiantum-nigrum* subsp. *yuanum* (TR-3643a) and twelve prothalli of *A. cuneifolium* subsp. *woronowii* (TR-2344) were used (6-IX-1975). Ten sporophytes (TR-3643 A-K) were raised to maturity. Of these 8 were selves and two (plants F and K) were triploid hybrids (20% yield). They matched the natural and above mentioned experimental hybrids J.Sch. 70 and 71 well.

7.4.4: TR-5490. Twelve prothalli of *A. adiantum-nigrum* subsp. *adiantum-nigrum* (TR-4421) and eighteen prothalli of *A. cuneifolium* subsp. *woronowii* (TR-4639) were used (13-VIII-1980). Thirty sporophytes were raised to maturity (Aug. 1981), eighteen were selves and 12 were hybrids (Fig. 21-B shows a pressed frond). Fortunately good sporangia could be fixed (Nov. 1981) before all plants were lost during the following winter (see under 5.2.).

7.4.5: J. Sch. 119. Female *A. cuneifolium* subsp. *cuneifolium* (Sch-11) × male *A. adiantum-nigrum* subsp. *yuanum* (TR-3591). Four isolated female prothalli in 4 glass cups were used (27-X-1975). Four sporophytes resulted (Fig. 21-A shows a pressed frond). Three of them were selves, one was a triploid hybrid with 36^{II} and 36^I in meiosis (J.Sch.).

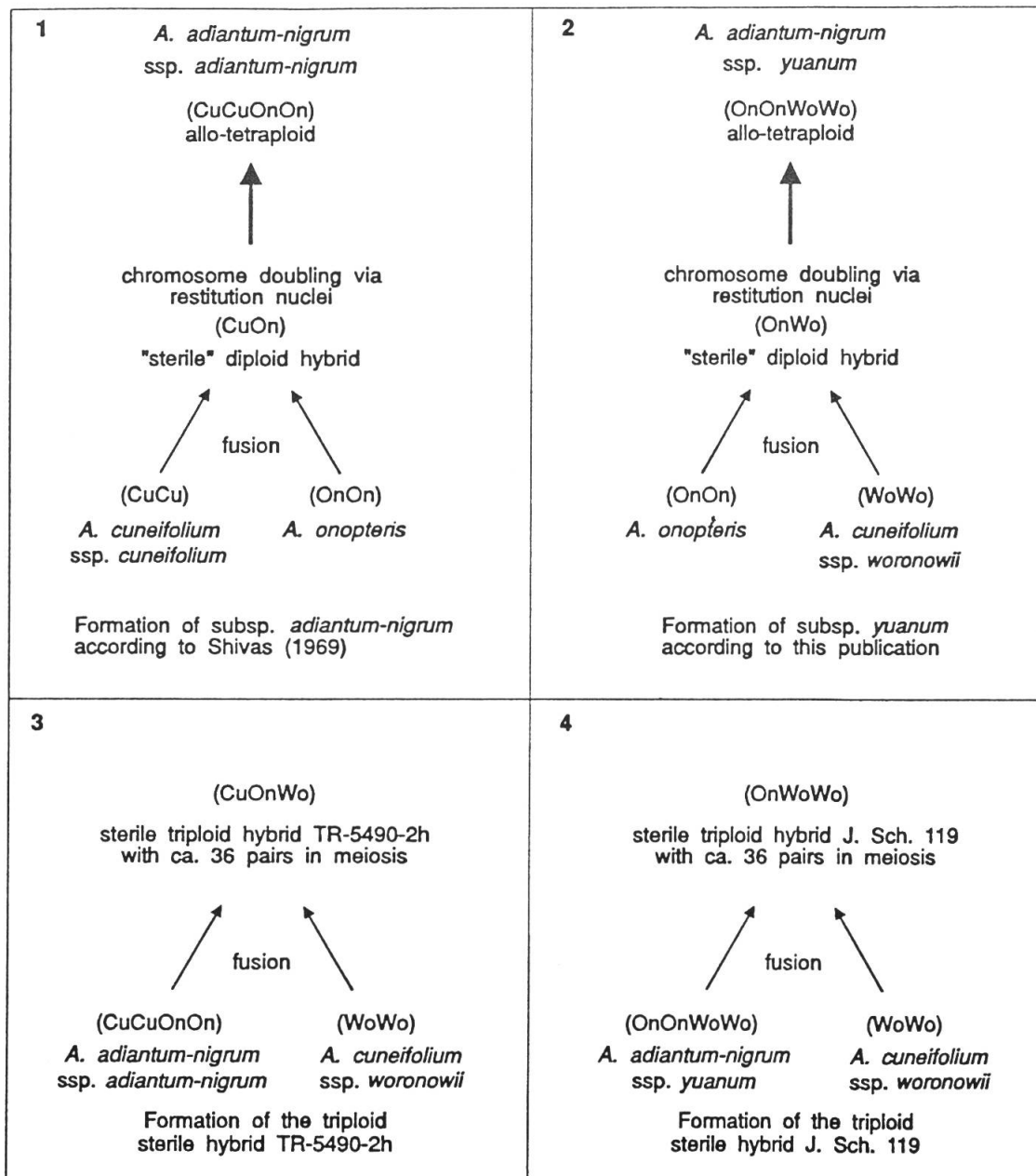


Fig. 22. — Scheme of the putative formation of *A. adiantum-nigrum* subsp. *adiantum-nigrum* (after Shivas 1969) and of subsp. *yuanum* (this article). Cu, On and Wo each stand for one genome of the following diploid ancestors: *A. cuneifolium* subsp. *cuneifolium*, *A. onopteris*, and *A. cuneifolium* subsp. *woronowii*.

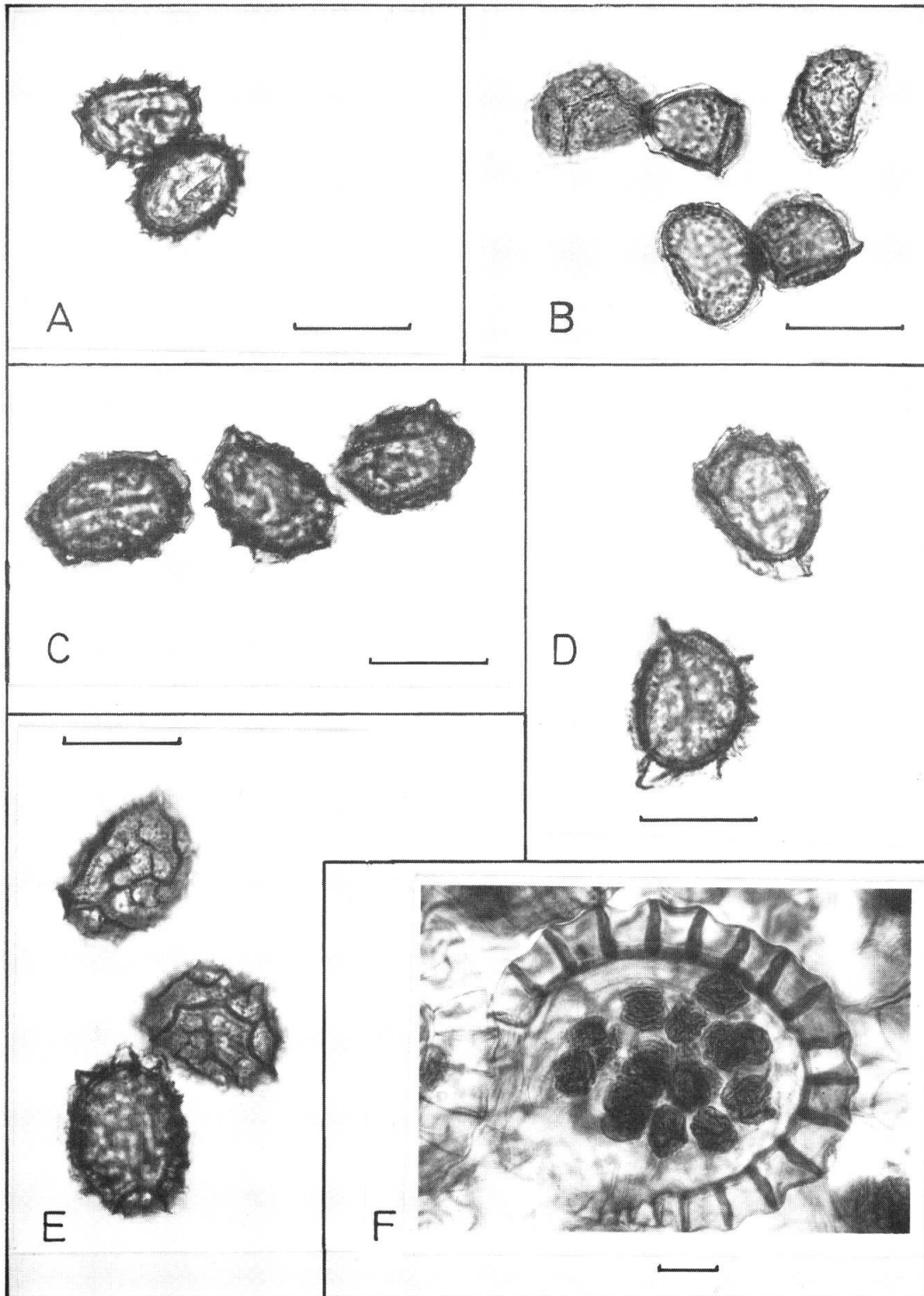


Fig. 23. — Spores and sporangia content. **A** = *A. cuneifolium* subsp. *woronowii*: Woronow 16 (isotype), good spores; **B** = *A. onopteris*: R. Viane 745, good spores; **C** = *A. cuneifolium* subsp. *cuneifolium*: TR-4960, good spores; **D** = *A. adiantum-nigrum* subsp. *adiantum-nigrum*: R. Viane 1839 (good spores); **E** = *A. adiantum-nigrum* subsp. *yuanum*: Kukkonen 12603A (= TR-5969-B), good spores; **F** = *A. × centovallense* subsp. *demirizii*: Fraser-Jenkins 4050, aborted spore material inside an immature sporangium of an epidermis preparation. Bar = 30 μ m. (Photo: R.V.).

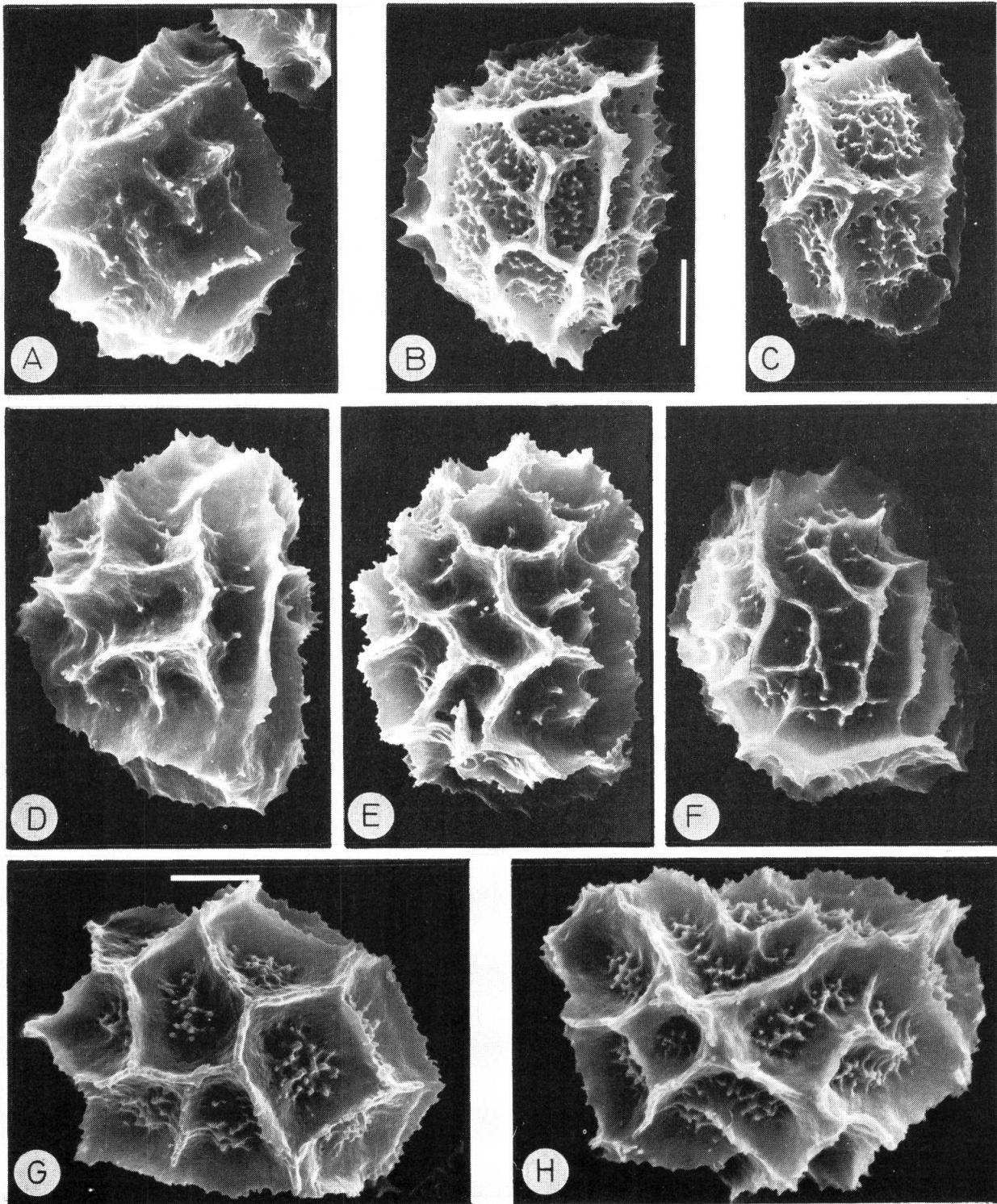


Fig. 24. — SEM photographs of spores: **A** = *A. cuneifolium* subsp. *cuneifolium*: TR-4690; **B-C** = *A. onopteris*, **B**: Bosmans 82/67, **C**: R. Viane 745; **D-E** = *A. cuneifolium* subsp. *woronowii*, **D**: TR-4028, **E**: Woronow 16; **F-G** = *A. adiantum-nigrum* subsp. *yuanum*, **F**: Kukkonen 12603A, plant b (= TR-5969), **G**: Probst VO-971; **H** = *A. adiantum-nigrum* subsp. *adiantum-nigrum*: R. Viane 2942. Bar = 10 μ m. (Prep.: R.V., photo: R.V. & K. Rasbach).

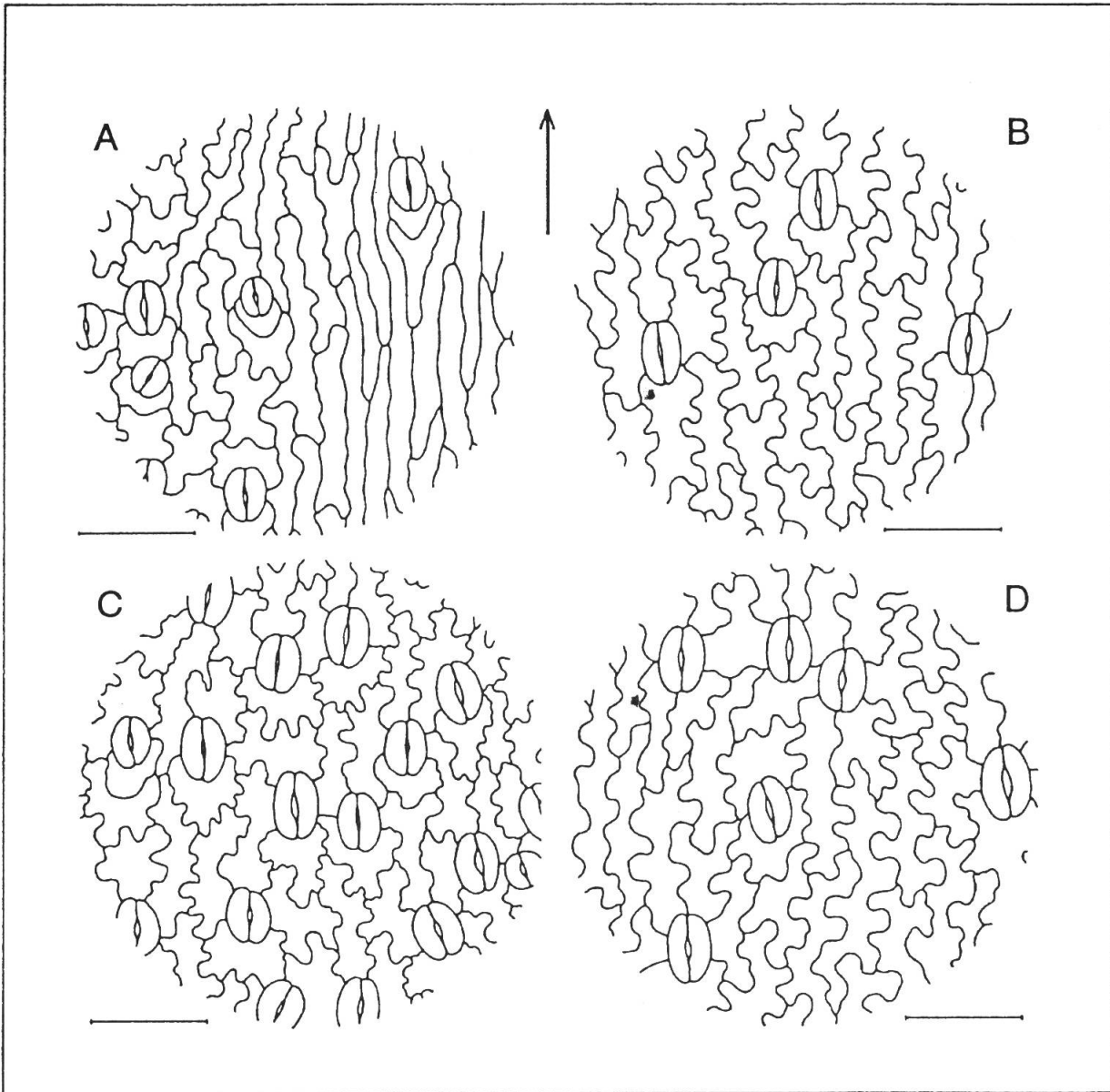


Fig. 25. — Cell pattern of the dorsal leaf epidermis. **A** = *A. onopteris* (R. Viane 745); **B** = *A. cuneifolium* subsp. *cuneifolium* (TR-4690); **C, D** = *A. cuneifolium* subsp. *woronowii* (**C**: Woronow 16, P!; **D**: TR-4639a). Bar = 100 μ m, arrow indicates the direction of the veins towards the leaf margin. (Prep. and drawing: R.V.).

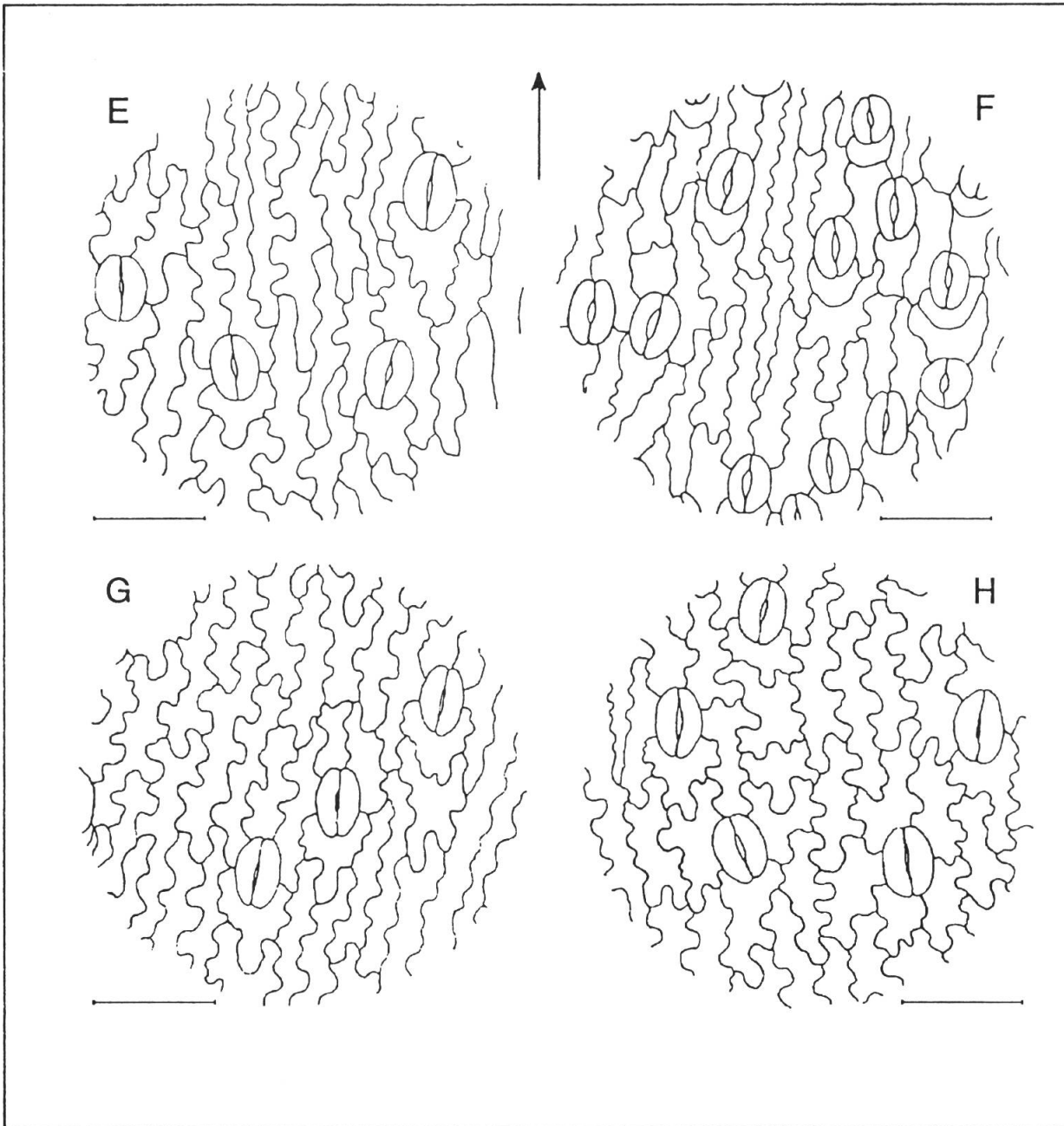


Fig. 26. — Cell pattern of the dorsal leaf epidermis (continuation). **E** = *A. adiantum-nigrum* subsp. *adiantum-nigrum* (R. Viane 1839); **F** = *A. adiantum-nigrum* subsp. *yuanum* (I. Kukkonen 12603A = TR-5969); **G** = *A. × centovallense* nothosubsp. *centovallense* (Becherer s.n.); **H** = *A. × centovallense* nothosubsp. *demirizii* (Fraser-Jenkins 4050 = TR-3642). Bar = 100 μ m; arrow indicates the direction of the veins towards the leaf margin. (Prep. and drawing: R.V.).

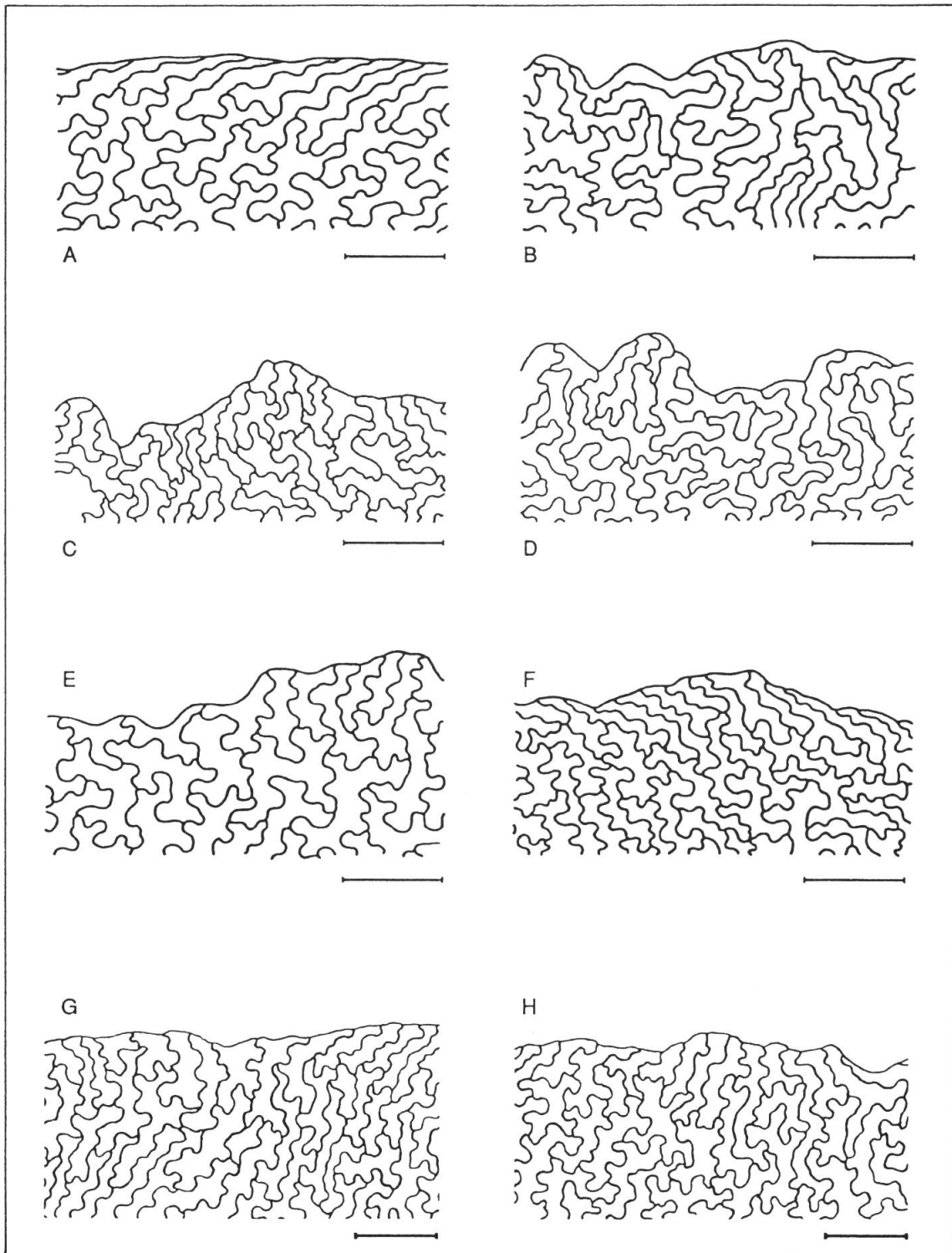


Fig. 27. — Margin and cell outline in the indusia. **A** = *A. onopteris* (R. Viane 2071); **B** = *A. cuneifolium* subsp. *cuneifolium* (TR-4690); **C, D** = *A. cuneifolium* subsp. *woronowii* (**C**: Woronow 16, P; **D**: TR-4639e); **E** = *A. adiantum-nigrum* subsp. *adiantum-nigrum* (R. Viane 1839); **F** = *A. adiantum-nigrum* subsp. *yuanum* (I. Kukkonen 12603A = TR-5969); **G** = *A. × centovallense* nothosubsp. *centovallense* (Becherer s.n.); **H** = *A. × centovallense* nothosubsp. *demirizii* (Fraser-Jenkins 4050 = TR-3642). Bar = 100 μ m. (Prep. and drawing: R.V.).

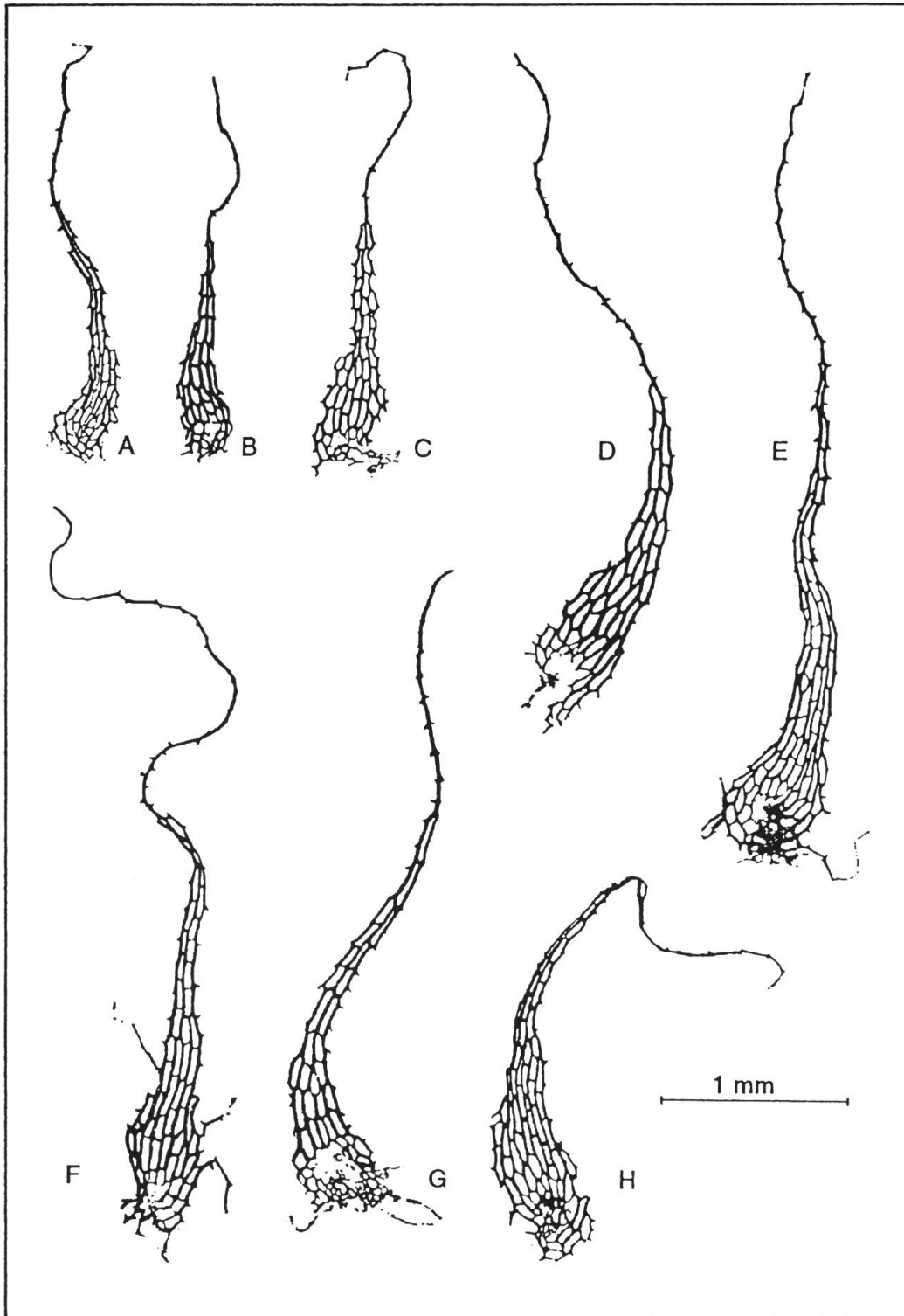


Fig. 28. — Stipe base scales. **A-B** = *A. cuneifolium* subsp. *cuneifolium*, **A**: TR-4713, **B**: Bertoloni & Viviani s.n. (1803, lectotype: small plant); **C** = *A. cuneifolium* subsp. *woronowii*: Woronow 16 (isotype); **D** = *A. × centovallense* nothosubsp. *demirizii*: C. R. Fraser-Jenkins 4050 (paratype); **E** = *A. adiantum-nigrum* subsp. *yuanum*: Kukkonen 12603A; **F** = *A. adiantum-nigrum* subsp. *adiantum-nigrum*: R. Viane 1839; **G** = *A. onopteris*: R. Viane 745; **H** = *A. × centovallense* nothosubsp. *centovallense*: Becherer s.n. Bar = 1 mm. (Prep. & photo: R.V.).

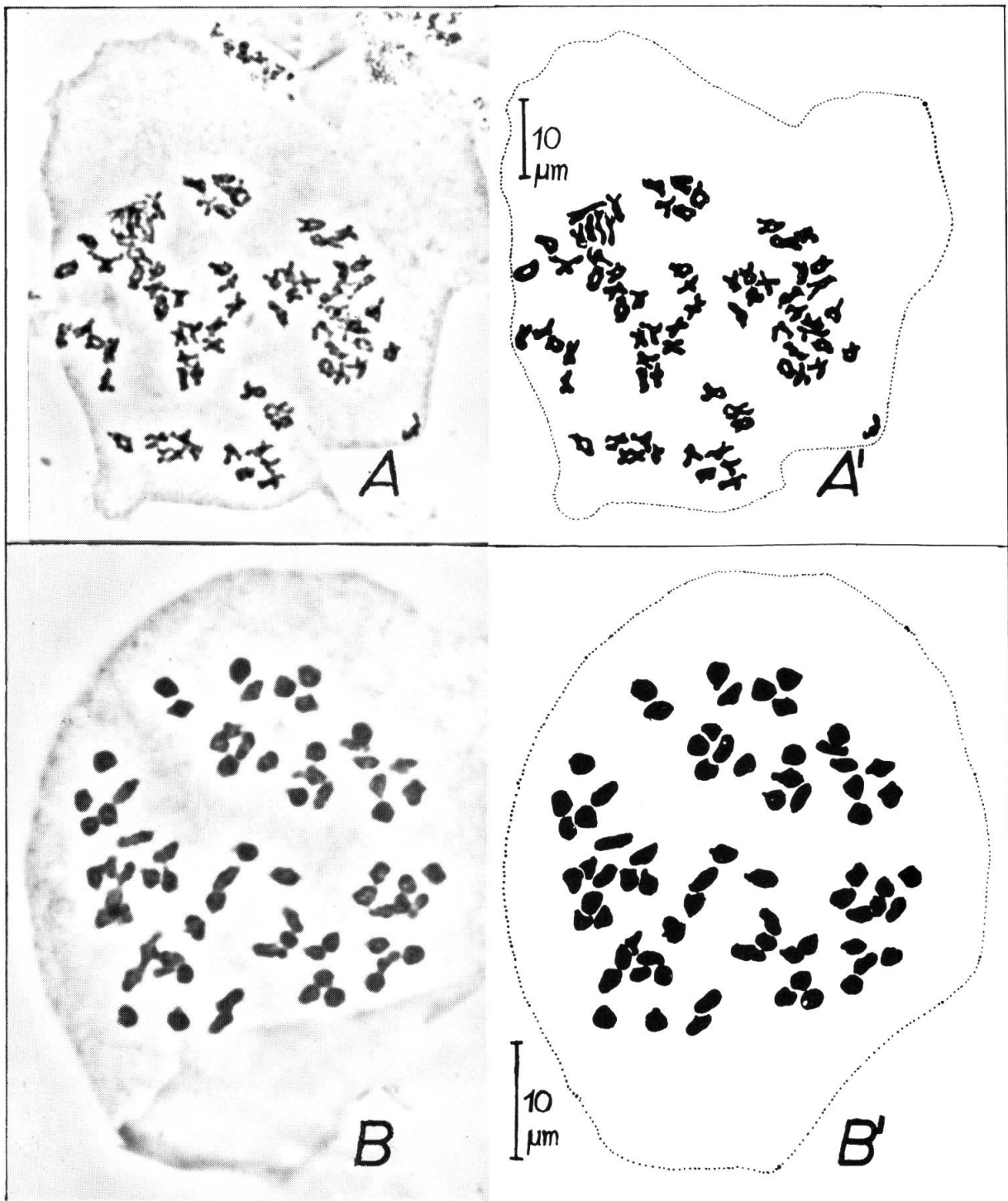


Fig. 29. — Cytology: **A-B** photographs, **A'-B'** explanatory diagrams. Pairs given in black, univalent chromosomes in outline. **A, A'**: *A. adiantum-nigrum* subsp. *adiantum-nigrum* from Hawaii (TR-6118), spore mother cell in meiosis (diakinesis) showing 72^{II} (H. R., 25-V-1986). **B, B'**: *A. adiantum-nigrum* subsp. *yuanum* from Ethiopia (TR-5968), spore mother cell in meiosis (metaphase I) showing 72^{II} (Det.: H. R., 6-V-1986). (Prep. & photo: H. R.).

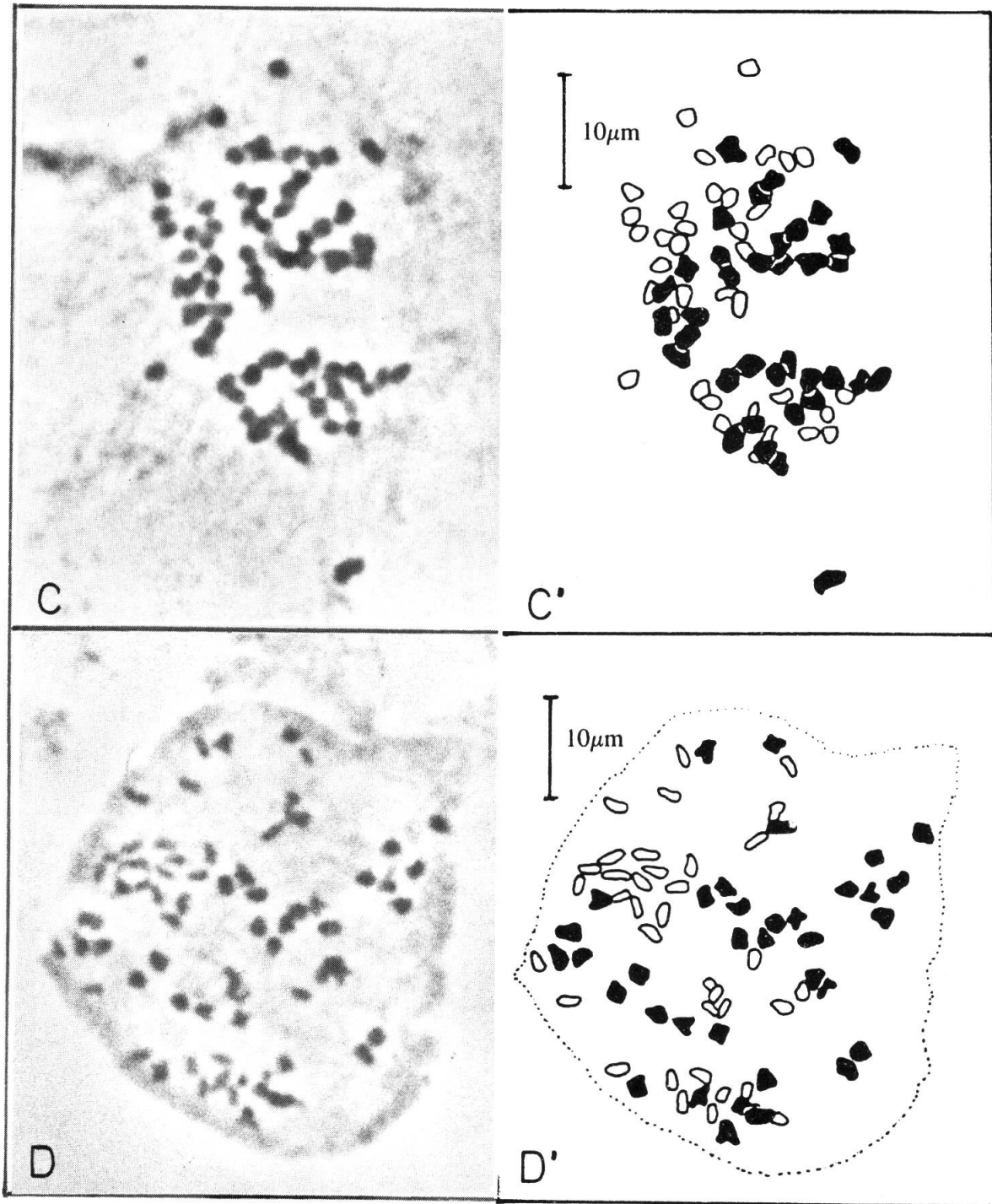


Fig. 30. — Cytology (continuation): **C-D** photographs, **C'-D'** explanatory diagrams, presentation as in Fig. 22. **C, C'**: *A. × centovallense* nothosubsp. *demirizii* experimentally produced, J. Sch. 70 (= TR-4071-A), with *A. adiantum-nigrum* as female parent. Spore mother cell in meiosis (metaphase I) showing ca. $36^{II} + 36^I$ (J. Sch. 23-XII-1976). **D, D'**: experimentally produced reverse hybrid with *A. cuneifolium* subsp. *woronowii* as female parent, J. Sch. 71 (= TR-4071-B); spore mother cell in meiosis (metaphase I) showing ca. $36^{II} + 36^I$ (Det.: J. Sch. 23-XII-1976). (Prep. & photo: J. Sch.).

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Addresses of the authors:

T. R.: Institut für Organische Chemie der Universität Basel, St. Johannis-Ring 19, CH-4056 Basel (Switzerland).

R. V.: Lab. Plantsystematics, Ledeganckstr. 35, B-9000 Gent (Belgium).

H. R.: Dätscherstrasse 23, D-79286 Glottental (Germany).

J. S.: Institut für Systematische Botanik, Zollikerstrasse 107, CH-8008 Zürich (Switzerland).