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Autor: Cubas, P. / Rosselló, J.A. / Pangua, E.

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A new triploid hybrid in the *Asplenium trichomanes* complex: *Asplenium trichomanes* nothosubsp. *lucanum* (*A. trichomanes* subsp. *inexpectans* × *A. trichomanes* subsp. *quadrivalens*) nothosubsp. *nova*

P. CUBAS
J. A. ROSSELLÓ
&
E. PANGUA

ABSTRACT

CUBAS, P., J. A. ROSSELLÓ & E. PANGUA (1989). A new triploid hybrid in the *Asplenium trichomanes* complex: *Asplenium trichomanes* nothosubsp. *lucanum* (*A. trichomanes* subsp. *inexpectans* × *A. trichomanes* subsp. *quadrivalens*) nothosubsp. *nova*. *Candollea* 44: 181-190. In English, English and Spanish abstracts.

Diploid, triploid and tetraploid plants of *Asplenium trichomanes* growing together on carbonate rocks were found at Caimari (Mallorca, Spain). Based on their morphology and ecology the diploids have been identified as subsp. *inexpectans*, and the tetraploids as subsp. *quadrivalens*. The triploid plants show an intermediate morphology between the above mentioned subspecies, and form trivalent chromosome associations at meiosis, indicating homology of their three genomes. The triploids are here described as *A. trichomanes* nothosubsp. *lucanum*, a hybrid of *A. trichomanes* subsp. *inexpectans* with subsp. *quadrivalens*.

RESUMEN

CUBAS, P., J. A. ROSSELLÓ & E. PANGUA (1989). Un nuevo híbrido triploide en el complejo *Asplenium trichomanes*: *Asplenium trichomanes* nothosubsp. *lucanum* (*A. trichomanes* subsp. *inexpectans* × *A. trichomanes* subsp. *quadrivalens*) nothosubsp. *nova*. *Candollea* 44: 181-190. En inglés, resúmenes en inglés y en español.

En la localidad de Caimari (Mallorca, España) se han encontrado creciendo juntas sobre sustrato calcáreo plantas de *Asplenium trichomanes* diploides, triploides y tetraploides. En base a su morfología y ecología las plantas diploides han sido identificadas como subsp. *inexpectans* y las tetraploides como subsp. *quadrivalens*. Las plantas triploides muestran una morfología intermedia entre las subspecies anteriormente mencionadas, formando en meiosis asociaciones trivalentes de cromosomas, lo que indica la homología de sus tres genomas. En este trabajo las plantas triploides se describen como *A. trichomanes* nothosubsp. *lucanum*, híbrido de *A. trichomanes* subsp. *inexpectans* y subsp. *quadrivalens*.

Introduction

In February 1987 the authors visited the locality of Caimari while collecting ferns from different places of the island of Mallorca (Balearic Islands). Although adverse weather conditions prevented a detailed survey of the Caimari area, three *Asplenium* species were found there: *A. petrarchae* subsp. *petrarchae*, *A. ceterach* and *A. trichomanes*. Different plants bearing fronds with immature sporangia were fixed in the field, and one plant of *A. trichomanes* (number PEP 45) was potted. The presence of abortive spores and the cytological behaviour of this plant revealed that we were dealing with a triploid hybrid with an irregular meiosis.

Since the plant did not display any morphological features of the other *Asplenium* species growing in the area but only those of *A. trichomanes*, we inferred that this hybrid was most likely to be the result of an intraspecific cross between two plants of *A. trichomanes* with different levels of ploidy, i.e. a diploid and a tetraploid. In order to check this, a new survey of the area was carried out during February 1988. This time more plants were fixed and/or collected, and diploid, triploid and tetraploid specimens of *A. trichomanes* were detected, thus supporting our earlier hypothesis concerning the origin of the hybrid plants.

A description of the morphology and cytology of this new hybrid named *A. trichomanes* nothosubsp. *lucanum* as well as a discussion on its cytological behaviour follows.

Material and methods

All the plants studied were collected near the town of Caimari. Herbarium specimens are kept in the private collections of the authors and will be deposited in MAF. Fronds with unripe sporangia were fixed in the field and meiosis was investigated using the classical acetocarmine squash method (MANTON, 1950). Spores were mounted in glycerojelly for L.M. measurements, and gold-coated for SEM studies of the perispore morphology. Thirty spores per sample were measured. Macromorphological details were drawn by means of stereoscopic microscope equipped with a camera lucida, using fronds collected in the field as well as from plants kept in cultivation at the Botanical Department of the Faculty of Pharmacy, Madrid.

Description of the new hybrid

Asplenium trichomanes* nothosubsp. *lucanum Cubas, Rosselló & Pangua = Intraspecific hybrid of *A. trichomanes* L. subsp. *inexpectans* Lovis × *A. trichomanes* subsp. *quadrivalens* D. E. Meyer, **hybr. nov.**

Diagnosis. — Planta hybrida triploidea, media inter parentes. Frondes usque ad 10 cm × 1.5 cm. Pinna terminalis manifesta, lata, triangularis. Sporae plerumque abortivae. Meiosi chromosomatibus trivalentibus 0-5, bivalentibus 30-35 atque univalentibus 31-38.

Holotypus: Spain, Balearic Islands, Mallorca, near Caimari (Cami dels Horts), 30 Jan. 1987, 230 m alt., on limestone rocks, leg. P. Cubas, E. Pangua, J. A. Rosselló & J. Vicens (PEP 45), MAF 129333.

Derivatio. — Named after the Monastery of Lluc, which is near Caimari.

Morphology

Fronds linear-lanceolate, abruptly terminated, 6.5-10 cm × 0.9-1.5 cm; 14-25 pairs of pinnae (Fig. 1, G-J). Terminal pinna conspicuous, broad, triangular with obtuse apex, two-three lobed (Fig. 2, H-L). Middle pinnae 0.3-0.7 cm × 0.2-0.5 cm, oblong or square, base cuneiform; (2-)4-6 sori per pinna.

The morphology of the two hybrid plants studied (PEP 45, PRP 179) are intermediate between their two proposed parents. Both plants show heterosis, and PEP 45 shows a prostrate growth habit both in the field and in the laboratory. The frond outline of the hybrid shows more similarity to that of *A. trichomanes* subsp. *inexpectans* (whose fronds also end abruptly, Fig. 1, A-C) than to subsp. *quadrivalens* (with gradually tapering fronds, Fig. 1, D-F). The apical pinna of the hybrid is triangular and conspicuous but less deeply divided than in subsp. *inexpectans* (Fig. 2, A-C). The subsp. *quadrivalens* displays (Fig. 2, E-F) a narrower terminal pinna than the hybrid. However, as indicated by LOVIS (1964), morphological differences between subsp. *inexpectans* and subsp. *quadrivalens* are not always obvious (e.g. Fig. 2, D), and consequently the hybrid is also difficult to differentiate solely on morphological grounds.

Mean spore size in the studied plants seems to be a reliable criterion to distinguish both subspecies: mean values of exospore length range from 28.0 to 31.2 µm in subsp. *inexpectans*, and from 36.0 to 37.3 µm in subsp. *quadrivalens*. Perispore pattern also helps to differentiate both subspecies:

subsp. *inexpectans* shows shorter and more abundant folds than subsp. *quadri-valens* (Fig. 3, A-B). The sporangia of the hybrid contain mainly abortive material with dark, misshapen spores of variable size, although some of them look larger and better developed (Fig. 3, C-G). Whether the latter are viable or not is something that should be tested experimentally.

Cytology

Both hybrid plants (PEP 45 and PRP 179) are triploid with a complicated meiosis which makes the pairing behaviour of their chromosomes difficult to analyse precisely. However, five cells from PEP 45 were good enough to obtain fairly accurate analyses: trivalents (five at the least), bivalents and univalents were observed (Fig. 4, E-F; Fig. 5, E-F; Table 1). In PRP 179 ca. 36 pairs and 36 unpaired chromosomes were counted.

III	II	I
5	31	31
4	30	36
3	32	36
0	35	38
0	35	38

Table 1. — Analyses of chromosome pairing in five cells of *A. trichomanes* nothosubsp. *lucanum* (plant number PEP 45).

The fertile plants growing in the vicinity of the hybrid proved, as expected, to be either diploid or tetraploid. The plants thought to be *A. trichomanes* subsp. *inexpectans* on morphological grounds (PRP 165, 169 and 175) are diploid with 36 bivalents at metaphase I (Fig. 4, A-B; fig. 5, A-B) and a regular meiosis; some lagging chromosome were observed in two cells of plant 165 at telophase I and II. The plants identified as *A. trichomanes* subsp. *quadri-valens* (PRP 168, 170, 174) proved to be tetraploid with 72 bivalents in meiosis; it was interesting to note that some unpaired chromosomes were often observed at metaphase I (Fig. 4, C-D; Fig. 5, C-D) as well as at diakinesis.

Discussion

Of the four European subspecies belonging to the *A. trichomanes* complex (LOVIS, 1964; LOVIS & REICHSTEIN in GREUTER, 1960; LOVIS & REICHSTEIN, 1985) only two, subsp. *quadri-valens* and *inexpectans*, have been recorded from the Balearic Islands (NOGUEIRA & ORMONDE, 1986).

The subsp. *inexpectans* (diploid) is restricted to the calcareous northern mountains of Mallorca and information concerning its abundance and ecology has previously been extremely limited; its occurrence in Mallorca was first suggested by BENNERT & MEYER (1974) who found a new triploid hybrid, *A. × litardierei* ($\equiv A. \times nieschalkii$ nothosubsp. *litardierei*), in Biniaraix. This hybrid was considered to be a cross between *A. petrarchae* subsp. *petrarchae* and *A. trichomanes* subsp. *inexpectans*. However, the authors did not find plants of subsp. *inexpectans* either in the vicinity of the hybrid or in other localities of Mallorca, and hence the presence of subsp. *inexpectans* was inferred from the morphological characteristics of the wild hybrid. Subsequently, the diploid taxon (subsp. *inexpectans*) was recorded near Soller by Reichstein (GREUTER, 1980) from cytologically checked material (Reichstein in litt. to Salvo, 1985). Our findings confirm the presence of the calcicole diploid in Mallorca. Besides, it seems that subsp. *inexpectans* is by no means a rarity on the island but have a wider distribution than was initially thought. In the small locality of Cai-mari four plants were found, three of them having been cytologically confirmed.

The subsp. *quadri-valens* (tetraploid) has a wide ecological distribution and seems to be the most abundant (ROSSELLÓ & al., 1986). This taxon is considered to have arisen by autopolyploidy, i.e. through intraspecific hybridization of partially differentiated diploids followed by chromosome doubling (BOUHARMONT, 1977; LOVIS, 1977). This hypothesis is supported by the meiotic

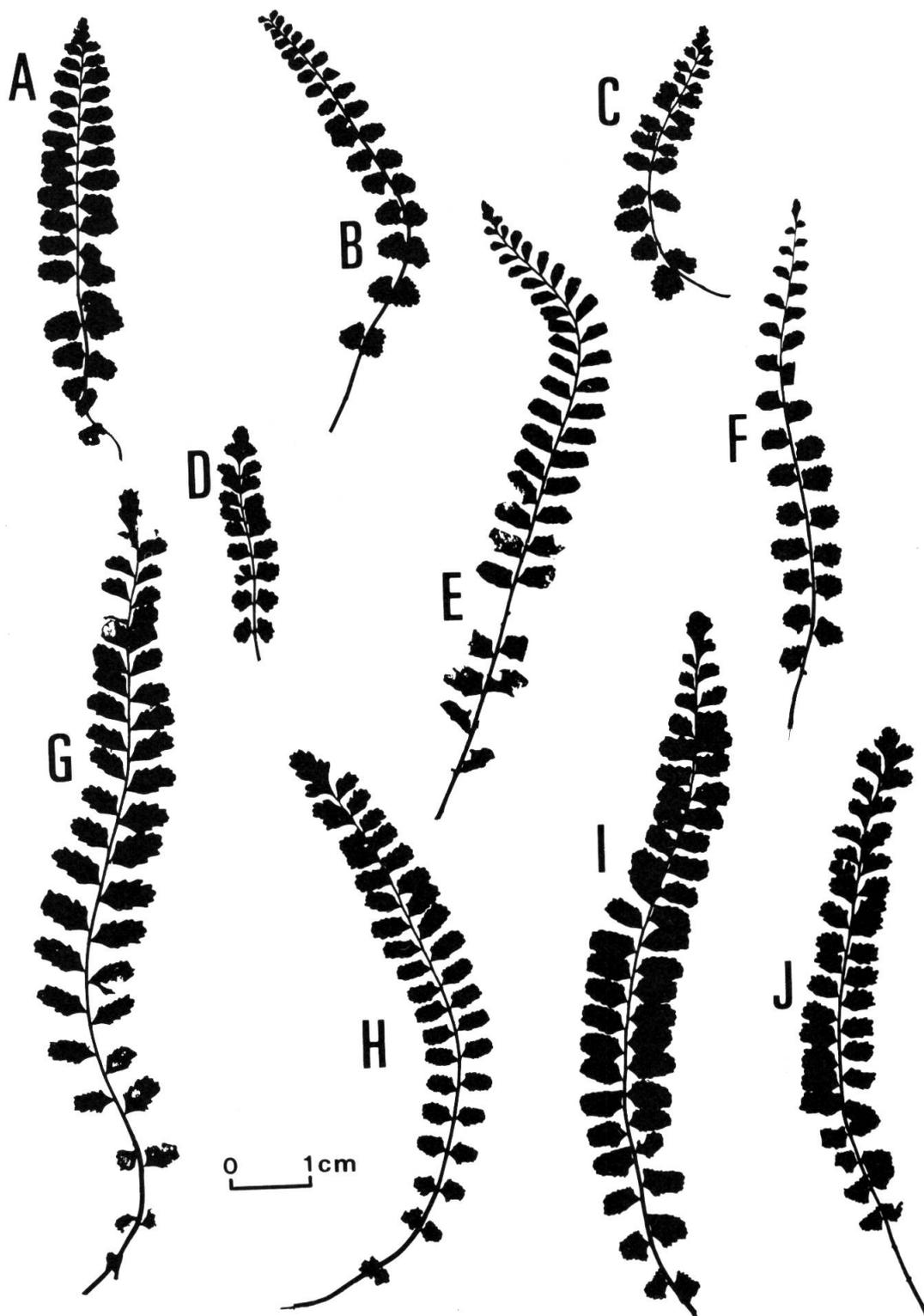


Fig. 1. — *Asplenium trichomanes* nothosubsp. *lucanum* and its parents, silhouettes of fronds. **A-C:** *A. trichomanes* subsp. *inexpectans*; **A**, PRP 165; **B**, PRP 169; **C**, PRP 175; pressed 19.2.1988. **D-F:** *A. trichomanes* subsp. *quadrivalens*; **D**, PRP 168; **E**, PRP 170; **F**, PRP 174; pressed 19.2.1988. **G-J:** *A. trichomanes* nothosubsp. *lucanum*, fronds from plant PEP 45 (in cultivation); pressed 10.3.1987 (**G**), 19.5.1987 (**H**), 5.6.1987 (**I**), 15.10.1987 (**J**).

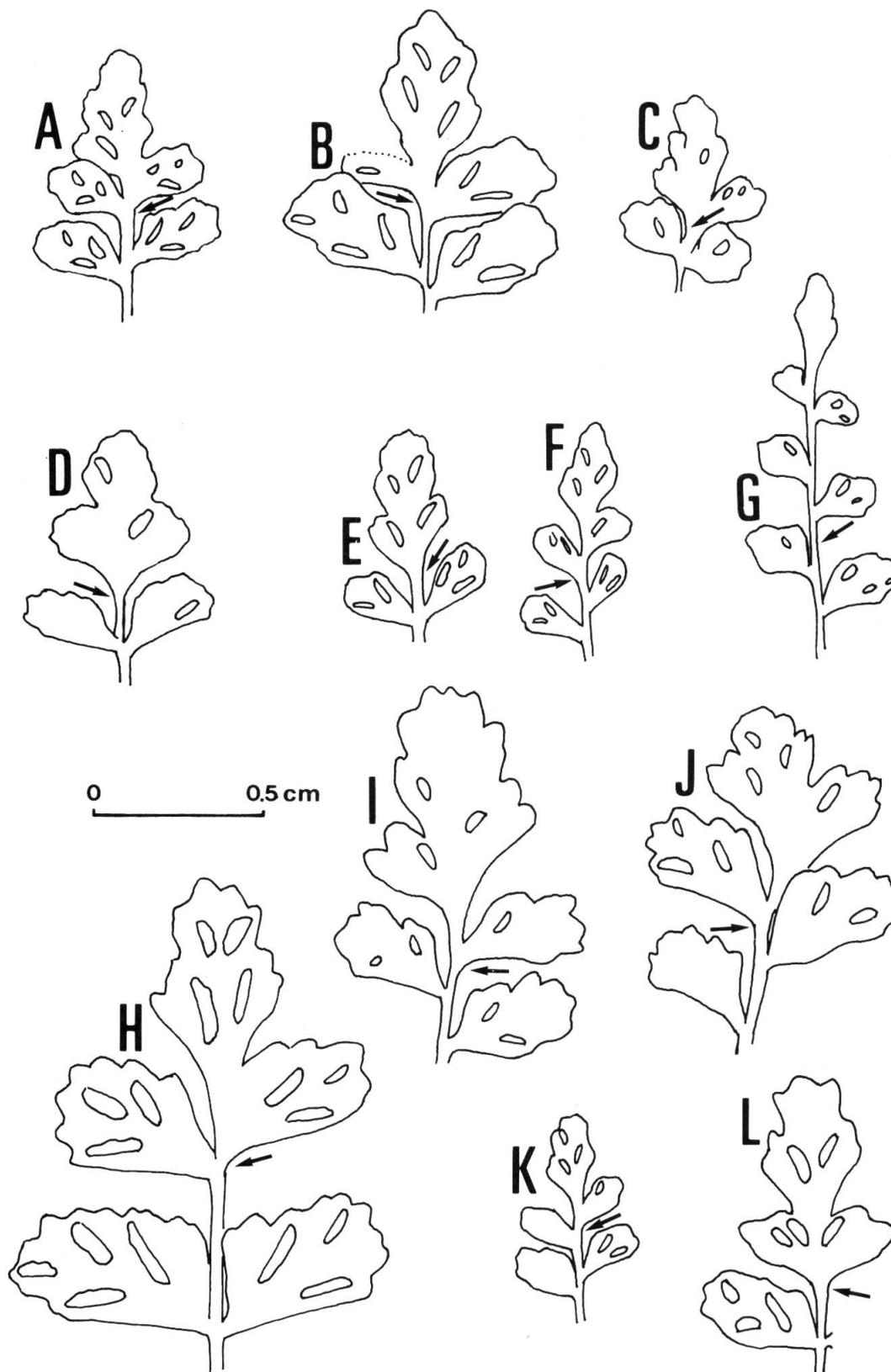


Fig. 2. — Drawings of apical pinnae of fronds
A-C: *A. trichomanes* subsp. *inexpectans*; **A**, PRP 165; **B**, PRP 166; **C**, PRP 175. **D-G:** *A. trichomanes* subsp. *quadrivalens*; **D**, PRP 168; **E** and **F**, PRP 170; **G**, PRP 174 (unripened frond). **H-L:** *A. trichomanes* nothosubsp. *lucanum*; **H-J**, PEP 45; **K** and **L**, PRP 179. The arrows mark the upper limit of the dark colour on the abaxial side of the rachis.

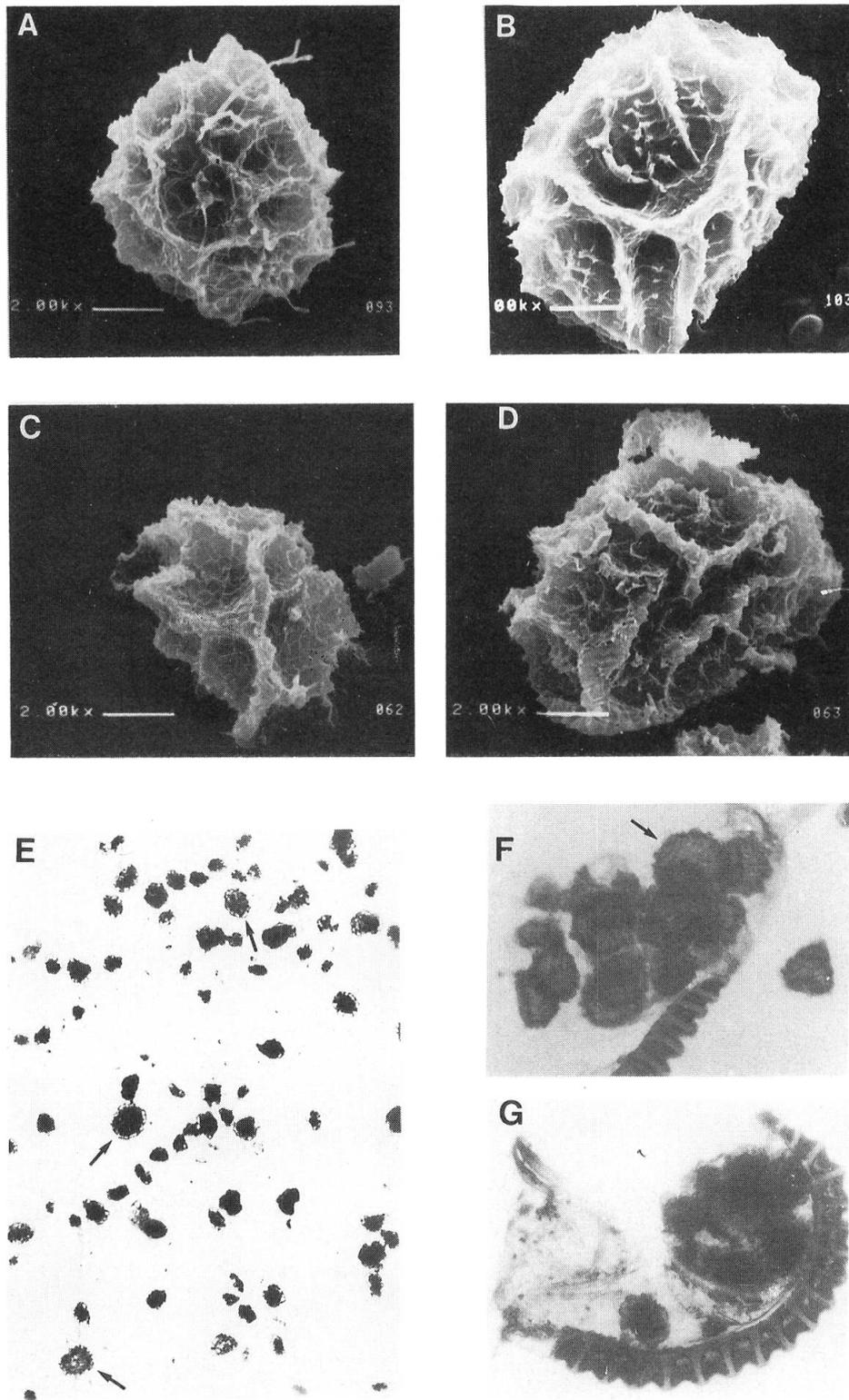


Fig. 3. — Spores of *Asplenium trichomanes* nothosubsp. *lucanum* and its parents. **A**, *A. trichomanes* subsp. *inexpectans*, PRP 165. **B**, *A. trichomanes* subsp. *quadrivalens*, PRP 170. **C-G**: *A. trichomanes* nothosubsp. *lucanum*, PEP 45; **C**, small spore partially shrunken; **D**, big spore; **E-G**, content of ripe sporangia showing mainly dark and misshapen spores (very variable in size), note the big spores (arrows).

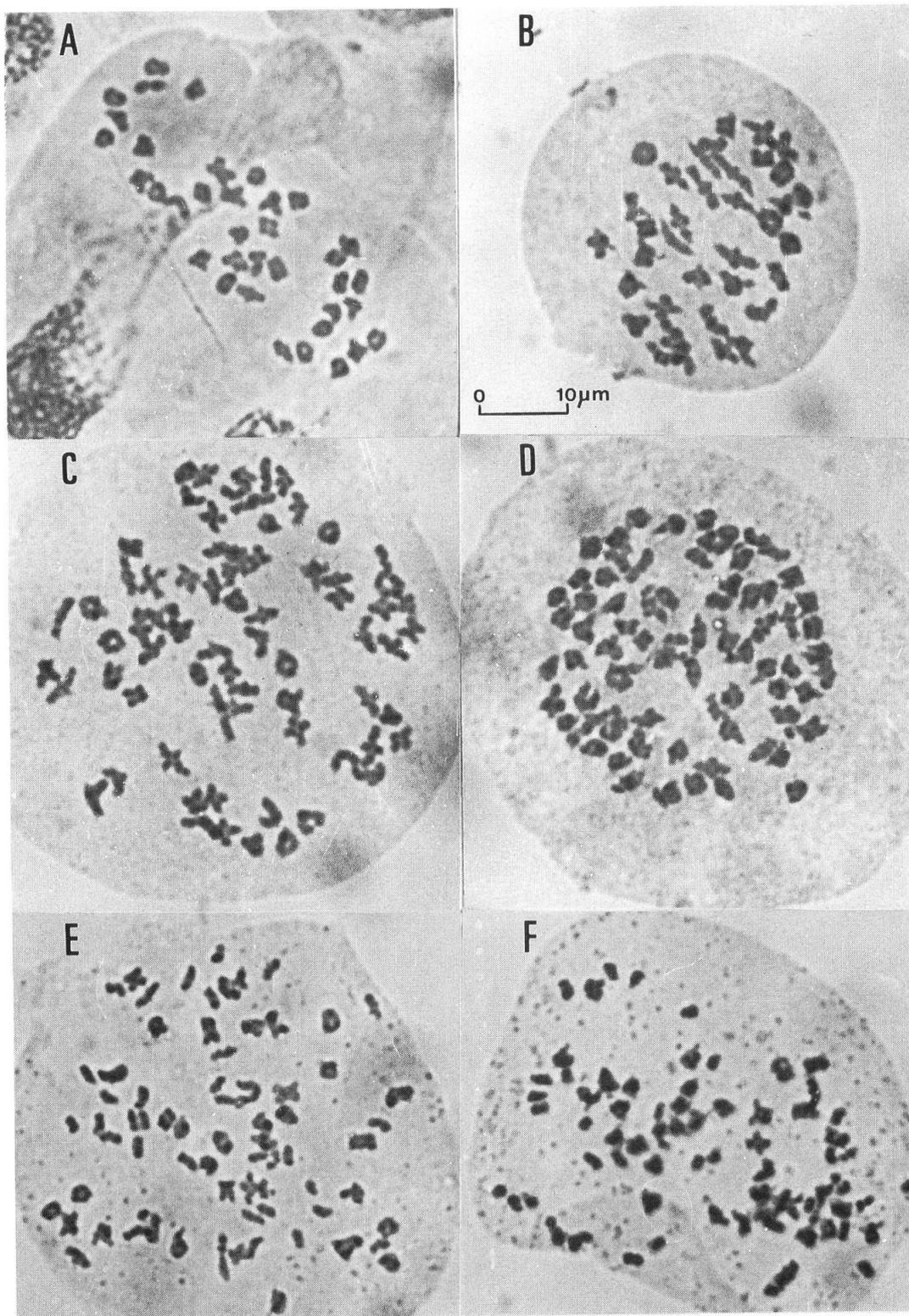


Fig. 4. — Photomicrographs of spore mother cells in first meiotic division.
A-B: *A. trichomanes* subsp. *inexpectans*; **A**, PRP 165, 36 bivalents; **B**, PRP 169, 36 bivalents. **C-D**, *A. trichomanes* subsp. *quadrivalens*; **C**, PRP 168, 71 bivalents and 2 univalents; **D**, PRP 170, 72 bivalents. **E-F**, *A. trichomanes* nothosubsp. *lucanum*, PEP 45; **E**, 5 trivalents, 31 bivalents and 31 univalents; **F**, 4 trivalents, 30 bivalents and 36 univalents.

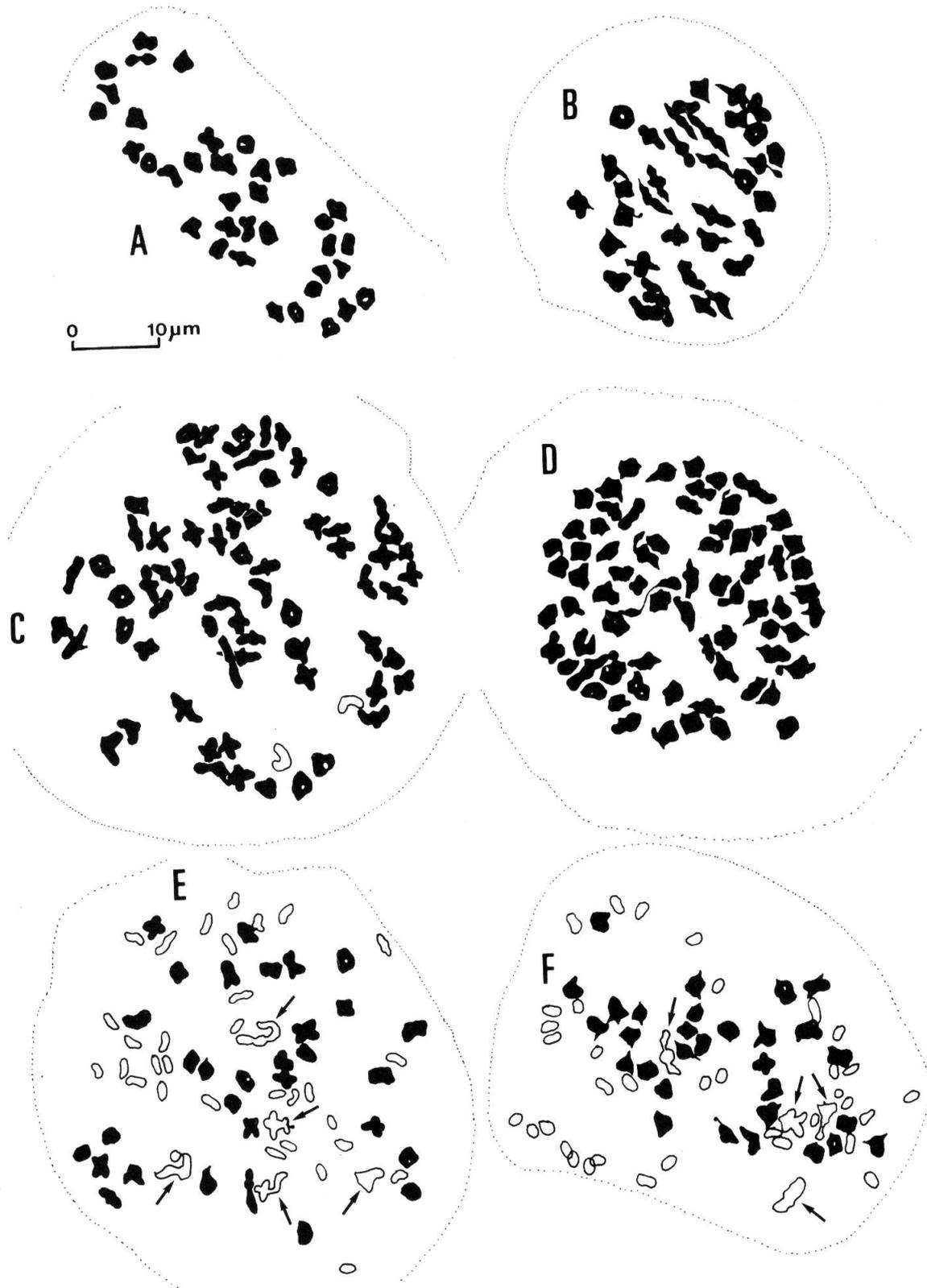


Fig. 5. — Explanatory diagrams for photomicrographs of figure 4.

A-B: *A. trichomanes* subsp. *inexpectans*: **A**, PRP 165, 36^{II}; **B**, PRP 169, 36^{II}. **C-D**, *A. trichomanes* subsp. *quadriavalens*: **C**, PRP 168, 71^I and 2^I; **D**, PRP 170, 72^{II}. **E-F**, *A. trichomanes* nothosubsp. *lucanum*, PEP 45; **E**, 5^{III}, 31^{II} and 31^I; **F**, 4^{III}, 30^{II} and 36^I. Bivalents in black, univalents in outline and trivalents in outline with an arrow.

behaviour observed in numerous hybrids between this subspecies and unrelated allotetraploid species (e.g. *A. × orelli* = *A. majoricum* × *A. trichomanes* subsp. *quadrivalens*; LOVIS & REICHSTEIN, 1969). These interspecific hybrids show in meiosis a high number of paired chromosomes (up to the maximum expected figure of 36; cf. REICHSTEIN, 1981) which is interpreted as the result of autosyndetic pairing of the two sets of homologous chromosomes supplied by *A. trichomanes* subsp. *quadrivalens*, while the chromosomes contributed by the other parent remain unpaired. In addition, the results obtained from artificially induced dihaploid plants from subsp. *quadrivalens* indicate that at diakinesis most of the chromosomes are paired, thus reflecting the homology between the two genomes present in this subspecies (BOUHARMONT, 1972a).

However, the cytological behaviour reported so far from intraspecific hybrids of *A. trichomanes* subsp. *quadrivalens* deviates from what has been observed in other autotetraploid species. The triploid intraspecific hybrids resulting from the cross between the diploid and tetraploid cytotypes (subspecies) of *A. ruta-muraria*, *A. petrarchae*, and *A. septentrionale* show a high number of trivalents in meiosis (VIDA, 1970; BOUHARMONT, 1972b; LOVIS, 1977; SLEEP & al. in REICHSTEIN, 1981: 116). Trivalent formation in intraspecific hybrids of *A. trichomanes* seems to be a rare process, this phenomenon having been cited, to the best of our belief, only once (LOVIS, 1955) in a wild triploid hybrid plant. Thus, with this sole exception, no multivalent formation has hitherto been reported for the following intraspecific hybrids: *A. trichomanes* nothosubsp. *lusaticum* (*A. trichomanes* subsp. *trichomanes* × subsp. *quadrivalens*; ca. 36^{II} and 36^I; BOUHARMONT, 1968, 1977; REICHSTEIN, 1981), *A. trichomanes* nothosubsp. *staufferi* (*A. trichomanes* subsp. *pachyrachis* × subsp. *quadrivalens*; 55-60^{II}; LOVIS, 1977; LOVIS & REICHSTEIN, 1985), and the unnamed hybrid *A. trichomanes* subsp. *inexpectans* × subsp. *quadrivalens*. The latter has been reported in Europe (BADRÉ & PRELLI, 1979; REICHSTEIN, 1981; TIGERSCHIOLD, 1981) but neither a formal description nor detailed cytology has so far been published.

The presence of trivalents in one of the two plants now named as *A. trichomanes* nothosubsp. *lucanum* supports the basically autoploidy origin of subsp. *quadrivalens* and the, at least partial, homology between the genomes present in the subspecies *inexpectans* and *quadrivalens*. With such a limited amount of material it would be unwise to speculate too far on the implications of the cytological behaviour of this hybrid. However, two possible suggestions (or a combination of both) can be put forward to explain its behaviour: *a*) a local higher degree of homology between the genomes of subsp. *inexpectans* and subsp. *quadrivalens*; and/or *b*) a relative reduction in the influence of genetically controlled factors (e.g. premeiotic chromosome orientations and structural differences; JACKSON & CASEY, 1980) which prevent the formation of multivalent associations between homologous chromosomes.

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Address of the authors: P. C., Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense, E-28040 Madrid, Spain.

J. A. R., Departamento de Botánica, Facultad de Ciencias, Universidad de las Islas Baleares, E-07071 Palma de Mallorca, Spain.

E. P., Departamento de Biología Vegetal I, Facultad de C. C. Biológicas, Universidad Complutense, E-28040 Madrid, Spain.