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Distribution and ecology of *Cystopteris (Athyriaceae)* species within the Flora Iranica region*

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Abstract: The distribution of *Cystopteris fragilis* and *C. dickieana* in Afghanistan within the Flora Iranica region is studied. The latter species, for some ecological reason, occurs more frequently at higher altitudes. In both taxa higher polyploid levels also occur at high altitudes. The phenomenon can be correlated with the boreal-arctic distribution pattern. Polyploidism and spore-size classes are briefly mentioned as well as possible ecological adaptations. Evolutionary differentiation within both taxa are complex and still unknown.

Floristic and ecological investigations of the montane regions of the Hindu Kush range in Afghanistan (BRECKLE 1973) revealed that 46 plant families comprising approximately 160 genera and 400 species are known to occur at altitudes above 4 000 m of which only two or three are pteridophytes. Examination of herbarium material of *Cystopteris* showed that two taxa occur in Afghanistan which, however, resemble each other very closely and can be distinguished apparently only on spore morphology. The main aim is to show whether there are significant differences in the distribution and ecology of both taxa within the Flora Iranica region and whether there are distinct ecological niches for each taxon. The data presented cover mainly Afghanistan.

General remarks on the genus *Cystopteris*

Cystopteris BERNH. comprises 10–15 species in the world, these have been placed in two subgenera. The characters used to distinguish the various species are referred to by BLASDELL (1963), some are constant, others complex and variable. *C. fragilis* (L.) BERNH. as a species is especially highly polymorphic with substantial synonymy. It has been investigated in detail by several workers, e.g. VIDA (1970) analysed the genome structure which revealed polyploidy; in several other papers (VIDA 1972,

* Dedicated to Univ.-Prof. Dr K. H. RECHINGER on the occasion of his 80th birthday and in recalling historical trips to the marvellous Afghan flora and vegetation.

1974) the work of BLASDELL (1963) is refuted as there was no clear correlation between spore size and degree of ploidy. Counts by MANTON & REICHSTEIN (1965) also revealed tetraploid levels for *C. sudetica* A. BR. & MILDE although according to BLASDELL, the small-spored forms were diploid. According to MORAN (1982) hybridization is apparently of some importance with the development of allopolyploids. The relatively high base number of n = 42 points to a comparatively phylogenetically ancient genus.

C. fragilis (L.) BERNH. sensu stricto (= subsp. *fragilis*) from Europe and the Flora Iranica region is distinguished chiefly by its echinate spores. The other taxon occurring in the Flora Iranica region is *C. dickieana* SIM. This was first described from Scotland (MARREN 1983); and is characterized by rather smooth, verrucose or rugose (but never echinate) spores. HAGENAH's (1961) studies on *Cystopteris* in North America showed that the two taxa cannot be easily separated except on spore morphology (see also ALSTON 1958). Although *C. dickieana* has been characterized as possessing smaller and more overlapping pinnae and pinnules than *C. fragilis*, this is not typical as according to later descriptions by BLASDELL (1963), FIORI (1943) and ELVEN (1984), sporophyll size in both taxa is subject to variation unlike that in *C. montana* (LAM.) DESV., *C. regia* (L.) and *C. sudetica*. PROFUMO (1969) studied the gametophytes of both *C. fragilis* and *C. dickieana* but concluded that the prothalli are very similar without any diagnostic characters. PEARMAN (1976) distinguished 5 spore types in *Cystopteris* based on scanning electron microscopic studies on spore ornamentation but made no taxonomic correlations.

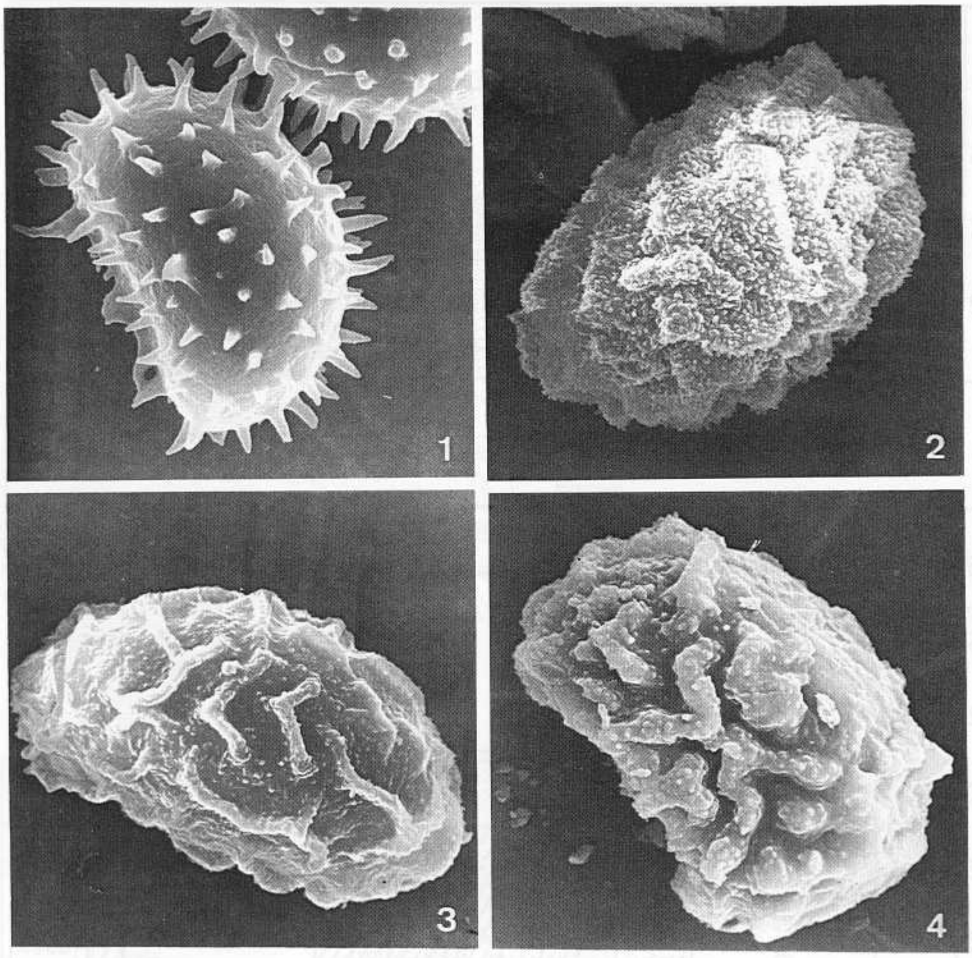
Materials and methods

Cultivated material was obtained from rootstocks with their native origin in from Afghanistan and Central Europe. Herbarium material was examined from B, E, G, GB, GOET, M (PODLECH), US, W as well as the personal herbaria of FREY (TUB, Giessen, B) and BRECKLE (BIEL). A complete list of specimens studied (ca 250 sheets) is available from the Dept. of Ecology, Faculty of Biology, University of Bielefeld. An average of 100–400, mature spores prepared in glycerol-gelatine were counted. We are grateful to the curators and owners of the above mentioned institutes for their help. Spore morphology was investigated by light microscopy and the scanning electron microscope.

We would like to thank Prof. SIEHL and Mrs HINDORF at the Dept. of Geology and Palaeontology, University of Bonn, for their kind help in SEM preparations and photography. Miss I. MEIER has helped with various technical aspects including measurement of spore size. Miss U. LETSCHERT assisted in mathematical and statistical calculations with the aid of the Rechenzentrum, University of Bonn.

Results

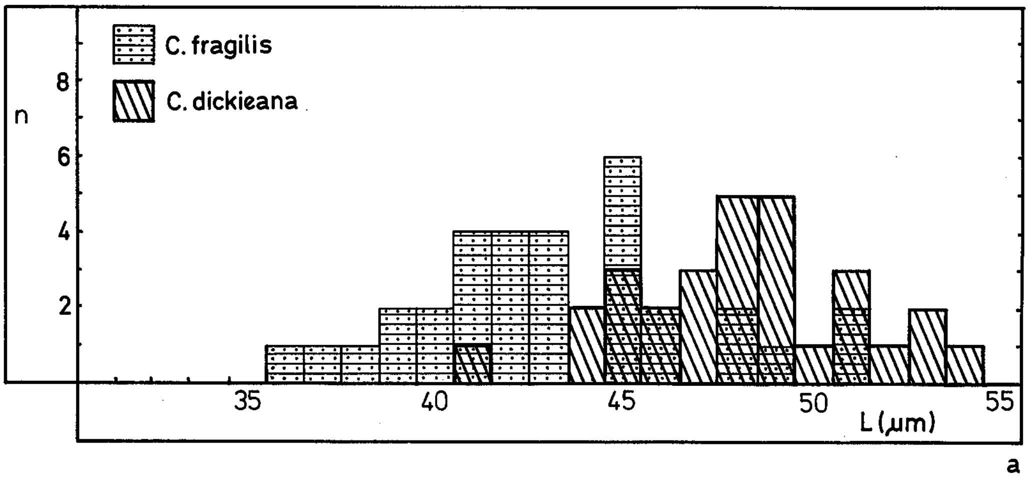
The gathered data revealed broad variation in spore size and morphology in at least one taxon. The spores in *C. dickieana* are almost smooth or warty (Fig. 2), granular, rugose, folded or thinly ridged (Fig. 3) or with thick ridges (Fig. 4). Those of *C. fragilis* are always echinate (Fig. 1) and distinctly smaller (Fig. 5*a, b*). There is some overlap in size range 42–52 µm in the samples from Afghanistan (Fig. 5*a*) and 31–52 µm in all samples from the whole Flora Iranica region (Fig. 5*b*). There is no random statistical distribution along the size gradient but discrete size groups are evident with maxima around 43, 46, and 49 µm. It is interesting to note that these



Figs. 1–4. SEM-images of *Cystopteris* spores. – Fig. 1. *Cystopteris fragilis*, with typical echinate sculpture (BRECKLE A3246: Afghanistan, Bargematol, 2150 m s. m.; herb. BRECKLE). Diam. of spore: 42 µm. – Fig. 2. *C. dickieana*, with typical warty-rugose sculpture (FREY 493: Afghanistan, Shalatal, 2900 m s. m.; herb. FREY). Diam. of spore: 51 µm. – Fig. 3. *C. dickieana*, with thinly ridged sculpture (FREY 255: Afghanistan, Jokhamtal, 2500 m s. m.; herb. FREY). Diam. of spores: 52 µm. – Fig. 4. *C. dickieana*, with strongly ridged sculpture (BRECKLE A1444: Afghanistan, Wakhan, Wazitpass, 4480 m s. m.; herb. BRECKLE). Diam. of spore: 45 µm

slight maxima occur in a similar position for the samples of both species from Afghanistan; in the Flora Iranica samples, there is a more pronounced fourth maximum at ca. 53 µm for *C. dickieana*.

The distribution of both *Cystopteris* taxa in the Flora Iranica area (within Afghanistan) is mapped in Fig. 6. It shows *C. fragilis* is more widespread than *C. dickieana*. The latter, however, occurs more commonly in areas of high altitude. Both species grow in shaded habitats, in limestone or crystalline rock fissures. There are little available data on ecological preferences and behaviour of each species. Fig. 7 demonstrates that within Afghanistan, there is a distinct separation in spore size according to altitude. Plants with abortive spores have also been observed, they may represent hybrids between different cytotypes.



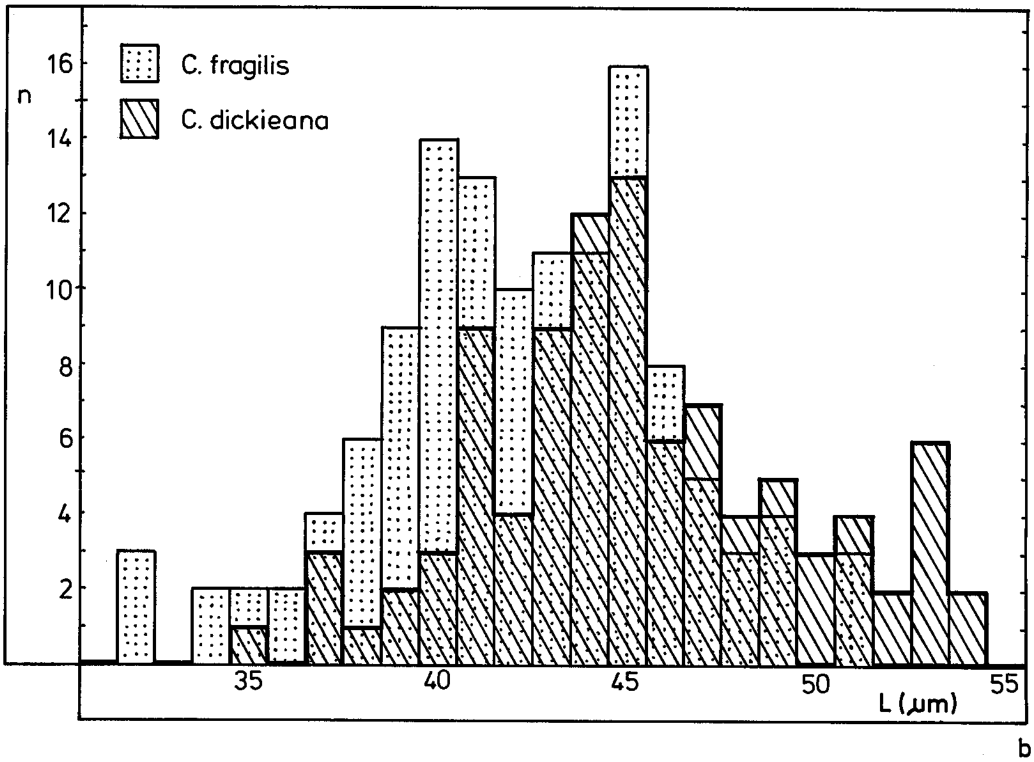


Fig. 5. The spore size classes of *Cystopteris fragilis* (stippled columns) and *C. dickieana* (hatched columns): *a* within the Afghanistan area, and *b* within the whole Flora Iranica area

Discussion

The question whether *C. dickieana* should be considered merely another smooth-spored race or whether there are real underlying differences in ecological and physiological behaviour, e.g. higher frost resistance, a more efficient photosynthetic mechanism which might explain the distinct geographical differentiation, is still unsolved. When and at which developmental levels these differences arose, whether at the gametophytic or sporophytic stage, are still unknown.

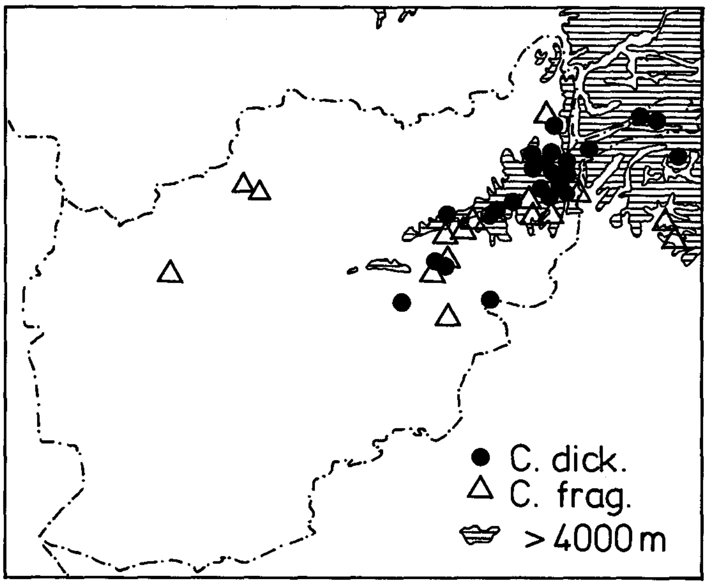


Fig. 6. Distribution of *Cystopteris fragilis* (triangles) and *C. dickieana* (dots) in Afghanistan and adjacent mountains

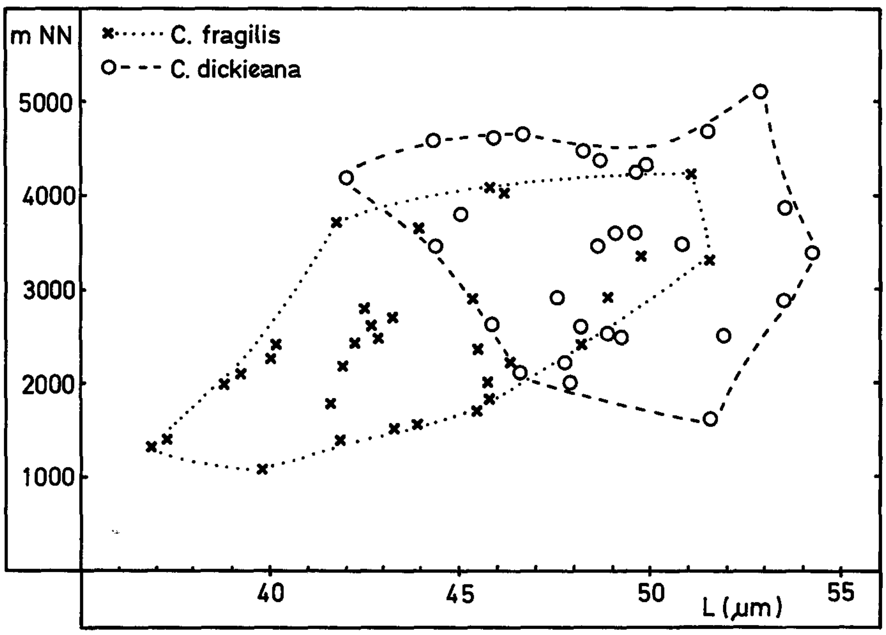


Fig. 7. Altitudinal distribution of spore size groups of *Cystopteris fragilis* (crosses) and *C. dickieana* (circles) within Afghanistan

FARRAR's (1976) studies on sporangia maturation showed much difference in various taxa. However, the differences in spore release, which might give some insight to reproduction in nature for both taxa, are unknown. HAUFLER & RANKER (1985) have investigated the antheridiogens which determine gametangial initiation in gametophyte cultures of American species of *Cystopteris*, and found marked physiological differences in morphologically similar taxa. This suggests a controlled breeding mechanism which may be associated with species delimitation.

HILL (1976) showed that bud-break, frond and sori number in several American ferns are enhanced by cold treatment and thus cold requirements may perhaps be involved in the ecological differentiation of the *C. dickieana-fragilis* group in the Arctic as well as in the Flora Iranica area. The present investigation showed that evolutionary differentiation within the two taxa is far more complex than hitherto indicated and detailed ecological and physiological studies to determine requirement and behaviour under different environmental conditions are much needed. It is obvious that *C. dickieana*, for some ecological reasons, is more adapted to the higher altitudes of the Iranian and Afghan mountains.

The limit of *C. dickieana* is also much further north than that of *C. fragilis* (LARSEN 1952). Higher ploidy levels exist in both taxa at higher altitudes, this correspond with the known distribution pattern in the boreal-arctic regions, e.g., in Greenland and Alaska. The polar limit of *C. dickieana* is much more to the North than that of *C. fragilis* s. str. (LARSEN 1952, WIGGINS 1954, GJAEREVOLL 1958, HAGENAH 1961). The same is true in the Spitzbergen region (communication by SCHWEITZER, Bonn; see also HADAČ 1944) and in Kamchatka (YAKUBOV 1983). In Europe only very few sheets of *C. dickieana* are known. DAMBOLDT (1963) mentions only 3 from the Alps. A few more are known from Italy (NARDI 1974). BIR & TRIKHA (1974) consider *C. dickieana* to be a good species, and not only a spore-form of *C. fragilis*, because of distinct overlapping pinnae (arising in proximity to each other), at least in Himalayan samples. This cannot be confirmed by our studies. The modificatory variations, e.g., by exposition to the sun, availability of water at the stand etc. are normally greater than morphological differences correlated with spore-form and -size. For the Western Himalayas BIR & TRIKHA (1976) described *C. fragilis* f. *granulosa* distinguished from the type form by granulose-warty spores, and *C. fragilis* f. *himalayensis*, distinguished by pinnules acute at the apex, the lobes acutely toothed. No ecological data are given.

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