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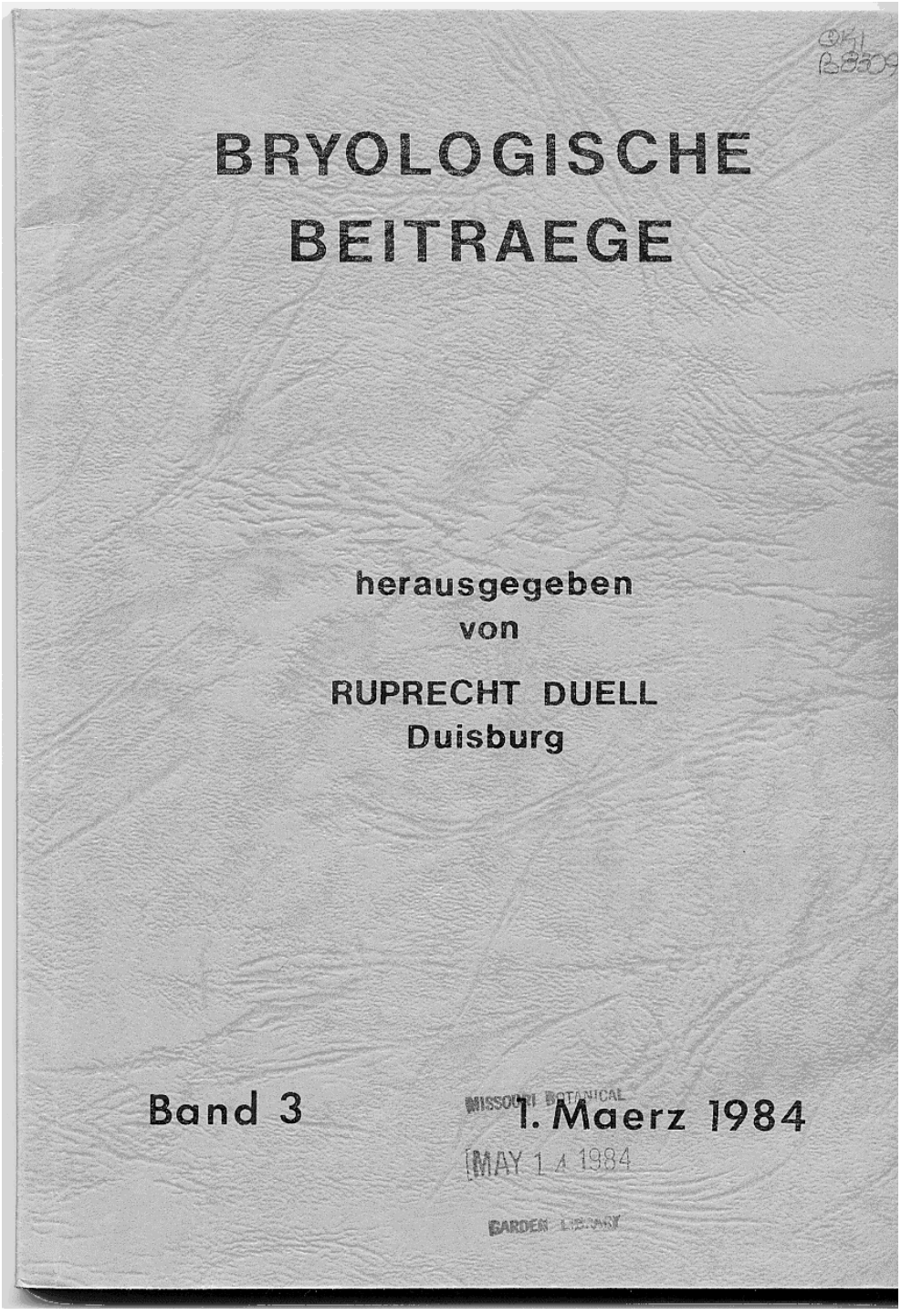

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BRYOPHYTE SEXUAL SYSTEMS : -OICOUS VERSUS -OECIOUS

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Zusammenfassung :

Unterschiede in den Schreibweisen der Endungen -oizisch und oezisch (engl. -oicy bzw. -oecy) sind historisch gesehen eine Frage des Stils. Die Endung -oizisch (engl. -oicy) wird aber nur bei Termina verwendet, die Sexualvorgänge im Gametophytenstadium beschreiben, die Endung -oezisch (engl. -oecy) dagegen für solche im Sporophytenstadium. Daher erscheinen einige wichtige Unterscheidungen für die Populationsbiologie notwendig.

Summary :

Differences in the literary use of the endings -oicy and -oecy , and their variants, are historically usually a matter of style; however, using -oicy endings only for terms describing gametophyte sexuality and -oecy for those regarding sporophyte sexuality emphasizes some distinctions of importance in population biology.

The use of the ending -oicous rather than -oecious for such terms as dioicous, monoicous, heteroicous, etc. is common among English-speaking bryologists but is by no means universal. There is a tacit understanding among many bryologists that the oicous ending in some way refers to the fact that the sexual organs in bryophytes are disposed on the gametophytes rather than on the sporophytes as is the case in seed plants. Other bryologists continue to use -oecious endings for the same terms, considering -oicous a mere orthographic variant. Most biological and botanical dictionaries I have consulted consider the endings essentially equivalent, and prefer -oecious. Both usages can, in fact, be defended.

I have urged (ZANDER 1979) the use of oicous endings for bryophyte sexual terms to emphasize that bryophytes have reproductive systems that are not directly comparable to those of seed plants. Terminology in discussions of

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reproductive biology of populations should reflect this fact. Briefly, bryophytes have sexual differentiation of gametophyte tissue while seed plants have sexual differentiation of sporophyte tissue. Sporophytes of bryophytes are always sexless, but the gametophytes may be "dioecious" or "monoecious". Sporophytes of seed plants may be monoecious or dioecious but the gametophytes are always "dioecious". Dioicy (= gametophyte dioecy) and monoicy (= gametophyte monoecy) are associated with homospory and the production of hermaphrodite gametophytes or of sexually differentiated gametophytes from the same sporangium, while dioecy and monoecy of sporophytes are associated with heterospory and the production of sexually different gametophytes in different sporangia. Maleness and femaleness are also attributes whose significance in discussions of reproductive biology depends on the particular tissue, haplontic or diplontic, affected. The terms "andro-" and "gynogametophyte" and "gynandrogametophyte" are suggested for use when exactness is required.

The historical origin of -oicous endings for bryophyte sexual terms in English was, however, not by an attempt to devise different terms for analogous sexual morphologies. According to NYBAKKEN (1959), Greek words used in scientific terminology are usually translitterated into Latin before use in English words. Thus, the Greek diphthong οι becomes oe in Latin and then oe or just e in English. Some English scientific terms, however, have been taken directly from the Greek without first Latinizing them. This, apparently, has been the case in early English-language literature for terms for bryophyte sexual arrangements. HOOKER (1838) did not mention disposition of sexual organs of bryophytes. WILSON (1855) used the terms dioicous, monoicous and synoicous, as did HOBKIRK (1884). BERKELEY (1857) used monoecious and dioecious. He discussed differences between homologous and analogous organs of bryophytes and seed plants but not with respect to arrangement of sexual organs. BERKELEY (1863) later used the terms dioicous, monoicous and pseudomonoicous. He had none of these words in his glossary but did include in it the term synoecious. BRAITHWAITE (1884) introduced the modern system of bryophyte sexual nomenclature into the English language by adopting LINDBERG's (1878) terminology. Braithwaite used the terms monoicous, synoicous, paroicous, autoicous, heteroicous (= synoicous + autoicous), dioicous and polyoicous (= synoicous + dioicous, or autoicous + dioicous, or heteroicous + dioicous). He, too, made no distinction between the use of -oicous and -oecious in respect to the different reproductive systems of bryophytes and seed plants.

Authors of English-language bryophyte identification manuals have used either -oicous or -oecious endings for sexual terms largely as a matter of style. British-educated authors generally use -oicous and American authors usually use -oicous. In their glossary, the American authors CRUM and ANDERSON (1980) simply indicated that -oicous endings are used for gametophytes of bryophytes while -oecious endings are used for higher plants, but they gave no further explanation. Major papers on the genetics of bryophytes have used various endings for sexual terms. ALLEN (1935) used -oecious endings. In a modern review of bryophyte genetics, LEWIS (1972) used the -oecious endings but discussed at length the differences between haploid and diploid dioecism, and haploid and diploid selfing.

RICHARDS (1978) has stated that in "dioecious bryophytes where two kinds of sex organs are on separate plants, outcrossing is obligatory and the heterozygosity of the species will generally be greater than in monoecious species....". This is correct in that the term "outcrossing" refers to relative heterozygosity of sporophytes of two bryophyte reproductive systems. The term "outcrossing", however, should be used with care in bryophyte literature. for instance, haploid selfing produces completely homozygous sporophytes, but haploid "outcrossing" between two separate gametophytes grown from spores from a single capsule is genetically equivalent to diploid selfing, whether the gametophytes are monoicous or dioicous.

The gametophytes of a population of a dioicous bryophyte species that was established by sexually different spores from the same capsule may be considered "obligatorily outcrossing" but their sporophytes may not be genetically more diverse than those of gametophytes of a population of a monoicous bryophyte species that was derived from two spores from genetically different sporangia. The former population may be quite inbred, even if dioicous. A monoicous species having abundant long-distance gene flow between populations by spore dispersal may have inherently far more potential for genetic variability than a dioicous species with little gene flow between populations. "Outcrossing" in a monoicous bryophyte species is not different from haploid selfing if the individual gametophytes interacting sexually are genetically identical. Clones or clonal equivalents may be derived (1) asexually, (2) from different spores of a homozygous capsule, or (3) from spores of more than one capsule if the capsules are genetically identical, being themselves derived by haploid selfing - perhaps through several generations - from a single spore

(a homozygous spore in the case of polyploid gametophytes).
Moss haploid-diploid species pairs are probably not very different in degree of heterozygosity in that half the spores of an allodiploid "haploid selfer" would be homozygous for particular allelic traits, and this proportion would increase over sucessive generations, assuming no crossing between genetically different gametophytes. In addition to mechanism favoring outcrossing in monoicous mosses reviewed by LONGTON (1976), such as possible self-sterility and high perichaetia-perigonia number ratio, genetic control of synoicy, paroicy and autoicy (including distance of autoicous buds on the stem relative to the perichaetia) in a population of a monoicous species would be a possible regulator of degree of outcrossing and therefore of heterozygosity of sporophytic traits. However, "outcrossing" takes place only within rather short (ANDERSON & LEMMON 1974) sperm flow distances between sexually mature gametophytes no matter how far spores or propagula are dispersed. Therefore, different alleles (determining gametophytic traits) in an heterozygous sporophyte must have been able to exist within much the same habitat previously as sexually mature gametophytes. Outcrossing of haploid gametophytes is therefore probably important (in maintaining relative heterozygosity of gametophytic allelic traits in sporophytes) only when it takes place between different habitats or microenvironments or between phenotypically plastic genotypes.
The degree of heterozygosity in polyploid gametophytes would also be controlled by mechanism favoring outcrossing, since recessives would not be selected against when gametophytes are heterozygous even when both gametophytic "parents" are growing together within sperm gene flow distance. It must be kept in mind, however, that the spores of monoicous diploid gametophytes are probably, in large proportion, either functionally haploid (LONGTON 1976) or homozygous, and selection on "outcrossing" gametophytes growing together within sperm gene flow distances - and therefore mainly in the same habitat - would act to eliminate all but the most recent sheltered mutations enhancing survival in other environmental conditions, just as is the case with haploid gametophytes. The known and theoretical population biology of monoicous mosses has been discussed more fully by LONGTON (1974, 1976) and ANDERSON & LEMMON (1974).
In view of the rather different significance of the relative positions of the sexual organs in bryophytes and seed plants, there is a need for a distinctive

terminology for bryophyte sexual conditions. In English, the -oicous ending is convenient and avoids the coining of yet another new set of terms. An alternative to the -oicous endings is to append "haplo-" to terms ending in "-oecious" (pers. comm. H.L.K. WHITEHOUSE). Both French and Spanish have alternate endings using oi and oe diphtongs for sexual terms for bryophytes based on the Greek οἶκος. German, however, apparently uses only ö.

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