sommerfeltia supplement

3

G. Hestmark

To sex, or not to sex... Structures and strategies of reproduction in the family Umbilicariaceae (Lecanorales, Ascomycetes)

1991

sommerfeltia

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G. Hestmark

To sex, or not to sex...
Structures and strategies of reproduction in the family Umbilicariaceae (Lecanorales, Ascomycetes)

1991

Doctoral dissertation publicly defended at the University of Oslo, June 1991, for the degree Doctor of Science (Doctor scientiarium).

"Quo minoris et vulgatiores sunt creaturæ,
eo pluribus seminum sortibus et propagationis
modis abundant." [!]

L.-R. & C. Tulasne 1861

"We do not even in the least know the final cause
of sexuality; why new beings should be produced
by the union of two sexual elements, instead of
by a process of parthenogenesis....The whole subject
is as yet hidden in darkness."

C. R. Darwin 1862

"Die Umbilicarien bilden jedenfalls eine
der natürlichsten Familien im System.
Die Zwei Gattungen, aus welchen dieselbe
besteht, sind schon durch ihren eigenthümlichen
Habitus vor den übrigen Lichenen in hohem
Grade ausgezeichnet; sie erscheinen gleichsam
als fremdartige Gebilde in die Reihe derselben
eingeschoben...."

S. Schwendener 1863.

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This is a study of the evolution and ecology of reproduction in the family of lichen-forming fungi Umbilicariaceae comprising the two genera *Umbilicaria* and *Lasallia*. Members of this family exhibit a variety of reproductive structures and strategies. The fungal partner of the symbiosis may reproduce by sexually generated ascospores, asexual thalloconidia, or both. Propagules reproducing the intact symbiosis include asexual isidia, soredia, thallyls, phyllidia and schizidia. The algal partner - unicellular *Pseudotrebouxia* (Chlorophyceae) - reproduces by asexual autospores when in symbiosis, and in addition zoospores and aplanospores in pure culture.

In about half of the species in Umbilicariaceae the fungal partner can only reproduce sexually - it is exclusively teleomorphic. In these species, apparently, the option of asexual reproduction has not been presented by evolution. In the taxa where this option *has* been presented, the forces of ecology and evolution seem to favour this option. Although no taxon with asexual reproduction appears to have dispensed with sexuality altogether, the allocation to sexual reproduction tends to decrease and the resources are translocated to asexual reproduction. Different taxa represent progressive stages in this de-evolution of sex. In some of these cases sex is correlated with geographical distribution patterns or ecological factors such as high humidity or high population density and sib-competition. The latter observation supports the 'Tangled Bank' hypothesis for the maintenance of sex, as well as ESS models for reproductive allocations in heterocarpic plants. In some cases exclusively teleomorphic taxa co-exist with morphologically virtually identical but mainly asexual (anamorphic) taxa, suggesting that a difference in reproductive mode may have led to speciation.

Associated with different propagule types are a number of other traits with consequences for the ecological performance of the species. These sets of correlated traits constitute strategies of reproduction, the core sets of specific life-history strategies. Three 'pure' reproductive strategies are tentatively distinguished in the Umbilicariaceae, depending on whether the propagule is sexually or asexually generated and whether it is symbiotic or not. The asexual propagules are close-dispersed while sexual propagules are more far-dispersed. A comparative study of the performance of representatives of the three strategy types in two glacier forelands shows that the sexually reproducing species are the fastest colonizers. The need to re-establish symbiosis at target site appears to be no great obstacle to sexual reproduction by ascospores.

Keywords: Asexual reproduction, ESS, Evolutionary ecology, *Lasallia*, Lichen-forming fungi, Reproduction, Sex, Tangled Bank, Thalloconidia, *Umbilicaria*.

Geir Hestmark, Botanical Garden and Museum, University of Oslo, Trondheimsveien 23B, N-0562 Oslo 5, Norway.

PREFACE

Except for the obligatory *Xanthoria* craze and a few side-glances at *Cladonias* and *Cetrarias*, the first lichens to catch my attention were members of the family Umbilicariaceae. Sailing down the south coast of Norway in the summer of 1979 I once went ashore in a small sound between two islands. On a slightly dipping gneiss slope facing a small lagune I stumbled upon thousands of large, light grey lichen shields. Their sheer abundance impressed me, and I remember wanting to know their name there and then. In the same locality was another lichen, shields grey to brown-olive in colour and with a pustulate surface. Later I recognized that what I had seen was a typical lichen community on the rocky south coast of Norway, populations of *Umbilicaria spodochroa* and *Lasallia pustulata*, both members of the family Umbilicariaceae. Despite, or perhaps exactly because of their overlapping ecological niche and their gross morphological similarity, the two species have very different structures and strategies of reproduction.

When professor Hildur Krog during her work with the African members of the family Umbilicariaceae in the fall of 1984 suggested I take a closer look at the 'Brutkörner' that had been reported on these lichens, I soon found myself involved with the task of describing and interpreting these structures. The result was my *cand. scient.* thesis *Thalloconidia in the genus Umbilicaria*, submitted in May 1987.

The present thesis, that was submitted for the degree of *doctor scientiarium* at the University of Oslo April 30, 1991, is a continuation of my earlier work. The subject matter has been expanded to the family Umbilicariaceae, and a number of special studies have been undertaken to elucidate structures and strategies of reproduction in this family.

Still, this work does not tell you 'all you ever wanted to know about - - - (but were afraid to ask)'. I clearly recognize that the work presented here is only the first small steps on a long road to a more thorough understanding of the structures and strategies involved. During the progress of this work hundreds of new questions suggested themselves for further exploration, and I hope to have the opportunity to continue working in this field in the years to come.

The work presented in this thesis attempt to integrate the study of the lichen-forming fungi into general mycological research. I also connect my studies with current theorizing in ecology and evolutionary biology. The evolutionary ecology of lichens is, to say it mildly, a little developed subject. In Grime's widely applied CSR classification of life histories (1977, 1979) all lichens are lumped in the triangle corner of 75-100% 'stress' and 0-25% competition; which to me indicates that Grime has hardly seen a lichen in its natural habitat. (Except, perhaps, an *Umbilicaria* sitting alone on a rock in a glacier foreland in the alpine zone during a snow-storm!).

Fungi are in many ways very different from animals and plants, and because most of what passes as 'general theory' in ecology and evolutionary biology has been developed by zoologists who usually use birds, mammals, Daphnias or Drosophilas as their research organisms, it is to be expected that studies of ecology and evolution in the fungi will add new and complementary dimensions to current general theories.

CONTENTS

DISSERTATION CONTENTS

This thesis is based on the following papers:

I Hestmark, G. 1990. Thalloconidia in the genus Umbilicaria. - Nord. J. Bot. 9: 547-574.

II Hestmark, G. 1991. Thalloconidiogenesis in five species of Umbilicaria. - (submitted).

III Hestmark, G. 1991. Teleomorph-anamorph relationships in Umbilicaria. I. Making the connections. - Lichenologist 23: 343-359.

IV Hestmark, G. 1991. Teleomorph-anamorph relationships in Umbilicaria. II. Patterns in propagative morph production. - Lichenologist 23: 361-380.

V Hestmark, G. 1991. To sex, or not to sex. Strategies of reproduction and dispersal in Lasallia pustulata (L.) Hoffm. (Umbilicariaceae, Ascomycetes). - (submitted).

VI Hestmark, G. 1991. Sexy lichens run faster. Primary colonization by sexually and asexually reproducing species of Umbilicaria (Lecanorales, Ascomycetes) in two glacier forelands. - (submitted).

The papers will be referred to by roman numerals, e.g., [IV, VI].

INTRODUCTION

THE MOST GENERAL SETTING

> "Reproduction is the fundamental process of all living things. The other so-called characteristic properties, irritability, metabolism and so on, may be absent; but if an individual reproduces, it must be alive." (Cohen 1977: 1).
>
> "And as Natural Selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection." (Darwin 1859: 489)

Reproduction or Destruction

If love and death are the ultimate human themes, reproduction and destruction is the run of life more generally.

The great ecologist Carl von Linné in his *Oeconomia Naturæ* (1749) described the life of the individual as a brief, dreamlike moment of *conservatio* between the beginning and end of *propagatio* and *destructio.*

Given the state of the world with its eternal flux in environmental conditions, it seems guaranteed with 100% probability that any spatially distinct, single biological organism will - eventually - die. An organism may be hit by sudden death by external forces (e.g. a predator, an episode of climatic extreme, an atomic bomb), it may languish and then die at a certain critical minimum point because it looses out in a competition for resources (e.g. water, mineral nutritients); in some organisms the cellular molecular machinery may also start to malfunction progressively as the organism becomes older - the phenomenon of aging or senescence (Comfort 1979). There appear to be no 'safe sites' in the universe, and no eternal life for any structure more complex than an elementary particle. Even the elementary particles and - paradoxically - even time itself may have a beginning and an end (Weinberg 1977, Hawking 1988).

Thus all spatially distinct individuals are also temporally distinct, and unless the individual reproduces and multiplies, it will soon be in the past tense.

One of the very first events in this history of life on Earth must have been the 'invention' of reproduction. The origin of life is traced to an accidental assembly of certain simple organic molecules under prebiotic conditions (Ferris & Usher 1988). These amino acids and nucleotides joined to form linear polymers: polypeptides and polynucleotids. The complementary templating mechanisms of polynucleotides may be considered the first attempts in biological reproduction. Such molecules are capable of directing their own synthesis, their own multiplication. In particular the polynucleotide RNA has recently been shown to be able to act both as template and catalyst in the process of templated polymerization (Eigen et al. 1981, Cech 1986). By multiplying, the first molecules of life outrun death and destruction. This game continues... for a while. - Molecules replicate, organisms reproduce. The effect is largely the same: mechanisms of heredity produce a new individual molecule or organism which is identical or near identical to the 'original' - they are re-plicas and re-productions. Organisms leaving no copies or 'back-ups' are erazed from the great chain of being. Contemporary eukaryotic protists are separated from their common ancestor by more than 10^{10} successive re-productive events (Bell 1988). To be, or not to be, then, is a question of reproduction.

Or Sex

There *could* in fact be an alternative to reproduction or death: protection, defense and repair. If a molecule or organism can protect, defend or repair itself from potentially lethal impacts, it will survive. Current evidence suggests that the phenomenon of sex - defined as genetic recombination - originally evolved as part of repair mechanisms for DNA-molecules exposed to destructive UV-radiation in 'the primeval soup' on Earth which in those days 3 billion years ago had no protecting atmospheric ozone screen (Dougherty 1955, Bernstein 1983, Bernstein et al. 1985, Bernstein et al. 1987, Margulis & Sagan 1990).

But although sex may have originated as an aspect of a molecular repair mechanism (double-strand repair), and this perhaps continues to be its main function in procaryotes, it is open to discussion whether this is its main function in eucaryotes (cf. contributions in Michod & Levin 1988). Indeed, to many it seems a puzzle why sex is maintained at all (Ghiselin 1974, Williams 1975, Maynard-Smith 1978, Bell 1982, Shields 1982, Halvorson & Monroy 1985, Stearns 1987, Michod & Levin 1988). Because, although sex obviously ought to be maintained for hedonistic reasons in humans, for most other organisms it seems such a lot of fuzz compared with the alternative - not to sex. Even among humans some militant woman liberationists would wellcome parthenogenesis as a great step forward - for womankind. Dictators, egalitarians and other orderly people may wellcome parthenogenesis as the ultimate solution to the problem of creating conformity or equality (cf. Huxley's *Brave New World*).

Sex should not be confused with *reproduction*. This point, so well caught by the contraseptives industry and so little understood by the Vatican (despite a very famous instance of parthenogenesis in the year 0 AD (which, incidentally, may have been the product of a translation error from Hebrew to Greek rather than a holy spirit, cf. Templeton 1982)), cannot be emphasized enough. Although sex and reproduction are often *associated* in multicellular organisms, there is no necessary connection between the two processes. In bacteria, for instance, sex usually occurs without reproduction (Levin 1988), and in a host of organisms - including the fungi - reproduction often occurs without sex (Cole & Kendrick 1981, Bell 1982, Hughes 1989, [I-VI]). Failure to separate sex from sexual reproduction is responsible for much confusion in the discussion of sex. The following aspects should be distinguished: (1) the essence of sex, (2) the immediate consequences of sex, and (3) the circumstances of sex

(1) *The essence of sex* - or simply: sex - is *genetic recombination*, the exchange of DNA segments between two DNA molecules (Devoret 1988), alternatively RNA segments between RNA molecules (e.g. Bujarski and Kaesberg 1986). Some (classical geneticists) will also include independent assortment of whole chromosomes (Crow 1988). Much of our current information of how recombination proceeds in natural systems is derived from studies of the fungi (Orr-Weaver & Szostak 1985, Low 1988).

(2) *The immediate consequences or effects of sex* are: (i) the creation of a new arrangement, a new combination of genes. This represents a *change* in genotype, a change in gene frequencies, the creation of new *genetic variation*. Because most cell functions are

regulated by genes, the change in genotype will affect phenotype expression, including those circumstantial aspects of sex that are parts of the anatomy, morphology, physiology and behaviour of the organism, and (ii) break up of linkage disequilibrium.

In addition sex may result in (iii) a reduction of heterozygosity (in diploid or polyploid organisms), (iv) gametes/propagules that have passed through the meiotic process and are thus chromosomally fairly 'normal' (the 'meiotic sieve'), (v) zygotes free from virus (plant viruses seem unable in most cases to survive the sexual process in their hosts, cf. Richards (1986: 402)), and (vi) the spread of parasitic DNA (Hickey 1982, Rose 1983, Hickey & Rose 1988).

(3) *The circumstances of sex* are all those molecular, physiological, anatomico-morphological, behavioural, environmental aspects that in biological systems may - in one way or another - be connected with the process of genetic recombination. Some of these circumstances - notably the molecular structure and function of DNA and associated enzymes - constitute necessary preconditions for sex. Others are only contingently connected with sex. Indeed, most of the features that people tend to associate with sex - anisogamy, sexual organs, mating behaviour, pleasure - are only contingently connected with the essence of sex. (I realize that to some this may come as a disappointment ....)

Reproduction is a common circumstance of sex. A somewhat special circumstance since reproduction is quite independent of sex and connected with it only by evolutionary contingency. One interesting question is why this linkage between reproduction and sex exists. A second what the consequences of this linkage are [IV-VI]. A third what may be the consequences if the linkage is severed [IV-VI].

The evolutionary ecology of sex - costs and benefits

The organisms living today, with their tremendous variation in traits - including the circumstances of sex and reproduction - are presumed to be the product of an evolutionary process where natural selection has worked to optimize fitness. This, in essence, is the 'adaptationist programme', delineated by Darwin (1859), inspired by 17th to 19th century natural theology, criticized by Gould & Lewontin (1979), and again defended by Ernst Mayr (1983) and a host of other evolutionary biologists. Few traits, if any, are thought to be neutral to this selection pressure, and thus it should be possible to explain why a particular trait - for instance sex - is maintained, that is, how the trait contributes to the fitness of the organisms exhibiting it.

If sex is a necessary consequence or prerequisite of double-strand DNA-repair, this obviously explains part of the fitness-contribution of this process, *especially* in organisms which during most of their life cycle are haploid, such as the majority of fungi. But because sex has other effects than repair, it is of interest to study how these other effects may influence the fitness of the organism. Similarly it is of interest to understand how the *circumstances* of sex may influence fitness [V-VI].

Fitness is defined in relation to a particular environment, and thus any trait is supposed to have an ecological correlate. The environment is the selector. There is genotype x environment interaction (Bell 1988). The question then becomes: how do the effects and circumstances of sex work in the environment (Ghiselin 1974, Williams 1975, Maynard-Smith 1978, Bell 1982, [IV-VI])? What may be the effects of eliminating sex and its circumstances (Jackson et al. 1985, Hughes 1989, [IV-VI]) ?

The problem with sex is that it seems costly, and in combination with reproduction it is both inefficient and risky (Williams 1975, Maynard Smith 1978, Lloyd 1980, Lewis 1987):

(1) Recombination and segregation breaks up exceptionally fit genotypes (recombinational and segregational load, Crow & Kimura 1970). As noted by Wright (1931): "a successful combination of characteristics is attained in individuals only to be broken up in the next generation by the mechanism of meiosis itself".

(2) Meiosis, syngamy and karyogamy are time-consuming processes in comparison with mitosis (Lewis 1983).

(3) Fertilization incurs mating costs - it may expose the individual to increased vulnerability to predation, or desease or parasite transmission, or waste of energy and effort through waste of gametes.

(4) In species with separate sexes or in obligately outcrossing hermaphrodites fertilization also requires a minimum density of individuals to assure successful mating (Gerritsen 1980). The fertilization of animal- and wind-pollinated plants is often limited by the availability of pollinating agents (R. Williams 1970, Lloyd 1980).

(5) In the large book reporting his experiments on *The Effects of Cross and Self Fertilization in the Vegetable Kingdom* (1876, 2nd ed. 1878), Charles Darwin wrote that in dioeceus plants "Half the individuals, moreover, namely, the males, produce no seed, and this might possibly be a disadvantage" (Darwin 1878: 416-417). John Maynard Smith (1971, 1978) - without reference to Darwin's observation - has argued that this does indeed constitute a twofold disadvantage of sex - 'the cost of males' - in comparison with asexually reproducing and notably parthenogenetic individuals. Half the reproductive effort (if sex ratios are 50/50 - which they often are) is 'wasted' by producing males, and half the available, suitable habitats are filled with 'unreproductive' males. This argument is not aimed at sex as such, but rather at the special situation of dioecy with unisexual individuals, thus it is not unconditionally valid for e.g. the majority of higher plants (>95%) which are hermaphrodites (Richards 1986).

(6) A somewhat different two-fold cost of sex was described by Williams (1971) who noted that a sexual female passes only half of her genes to each offspring, while an asexual 'female' passes all her genes to each offspring. "Other things being equal, the parthenogenetic female would be twice as well represented in the next generation as the normal [sexual] one" (Williams 1971).

(7) With sexual reproduction selection acts on the genic or additive component of the genetic variance (Fisher 1930), whereas selection among asexuals acts on the genotypic or total genetic variance. If the genetic variances are the same, an asexual species can respond more rapidly to selection (Crow 1988).

It is seen that in several of these arguments sex in combination with reproduction is contrasted with reproduction without sex. The disadvantages of sex are particularly highlighted when thus compared with the option not to sex. The benefits of cloning are numerous and in part obvious (Lloyd 1980, Hughes 1989):

(1) By avoiding recombination and segregation, cloning enables exceptionally fit genomes to be inherited intact. This facilitates evolutionary response to directional selection and allows selection to act upon epistatic genetic traits.

(2) By avoiding the need for mating, cloning enables isolated individuals to breed, so facilitating their colonizing abilities.

(3) By avoiding the production of males, cloning enables resources to be allocated entirely to parous individuals, potentially doubling the reproductive rate.

(4) By generating somatic replicas from undifferentiated somatic cells, cloning delays or circumvents senescence.

(5) By spreading the risk of localized mortality among scattered individuals, cloning increases the survivorship of the genome.

(6) The high reproductive potential of clones enables them to quickly replace losses.

(7) Cloning avoids the allometry between metabolic rate and body mass. By remaining small, clonal individuals maintain a high metabolic turnover rate, which itself promotes rapid development and reproduction, yet their collective biomass can increase by orders of magnitude without affecting metabolic rate.

(8) Cloning circumwents the declining surface area to volume ratio that otherwise accompanies increasing body size. By remaining small, individuals preserve optimal morphological dimensions, while leaving the clonal biomass free to accumulate without constraint.

(9) The genetic identity among clonal individuals enables selection at the level of the genome to generate advanced polymorphisms.

Considering these massive lists of *pros & cons*, sex seems a lost case indeed. And yet it persists to a remarkable degree in the kingdoms fungi, plantae and animalia. With few exceptions, asexual forms occur as small taxomically isolated groups whose nearest relatives are sexual (Bell 1982, Bierzychudek 1985, Hebert 1987, Hughes 1989). This observation also appears to be valid for Deuteromycetes (Fungi Imperfecti) which in most cases are presumed to be derived secondarily from sexual Ascomycetes (Cole & Kendrick 1981, Hawksworth et al. 1983). In protists and procaryotes the pattern breaks down, sex often being absent in large groups. The received interpretation of this taxonomic distribution is that asexual multi-cellular organisms are the short-lived offshoots of sexual lineages, doomed to early extinction. In addition to this taxonomic correlate, the option not to sex also appears to have ecological correlates. Asexually reproducing organisms tend to dominate in novel, disturbed habitats where biotic interactions are few. Many of the 'pioneer species' in plant successions have amictic reproduction (Stebbins 1950, Baker & Stebbins 1965), and there is a significant correlation between the geographical distribution of parthenogenesis and formerly glaciated areas (Suomalainen 1950, Bierzychudek 1985). Furthermore, asexually reproducing forms or taxa often have larger ranges and are more common in islands or island-like habitats than their nearest sexual relatives (Vandel 1931, Suomalainen 1950, Stebbins 1950, 1971, Cuellar 1977, White 1973, 1978, Glesener & Tilman 1978, Bell 1982, Bierzychudek 1985, Hughes 1989). Such geographical distribution patterns have also been described in the lichen-forming fungi (Hale 1965, Poelt 1970, Bowler & Rundel 1975, Lawrey 1980, [IV]).

How can we explain the prevalence of sex and the taxonomic and ecological correlates of those organisms that do not sex? Several possible mechanisms have been suggested to balance the disadvantages of sex:

(1) One of the direct consequences of recombination is, as noted above, the generation of genetic variation, and H. J. Muller (1932) gave the answer that the advantage of sex(ual reproduction) is "the providing of an opportunity for continual shifting and readjustment of the relative abundance of different [geno]types as external conditions vary". Sewall Wright (1932) similarly spoke of "an almost infinite field of possible variations through which the species may work its way under natural selection". Thus, according to Muller and Wright (and Weismann, Guenther, and Fisher) flexible response in a variable (heterogeneous) environment and also evolutionary potential are consequences and advantages of sex.

(2) Another possible advantage of recombination is the possibility of combining beneficial mutations from different lineages/individuals (Fisher 1930, Muller 1932, 1958, Crow & Kimura 1965). Thus the probability of creating an optimal genotype is high.

(3) Getting rid of deleterious mutations. The majority of mutations are deleterious and thus have a negative effect on fitness (Haldane 1937), the mutations constitute a 'genetic load'. In diploid organisms the creation of homozygotes exposes recessive, deleterious alleles to natural selection. More generally recombination creates some new 'clean' genotypes that do not incorporate the mutations in the parent genomes, as well as some 'double dirty' genotypes that incorporate deleterious mutations from both parent genomes. The latter are soon eliminated by natural selection. Thus recombination + selection works as an 'exogeneous DNA-repair' or cleaning mechanism (Muller 1932, 1964, Kondrashov 1982, 1984). In contrast, in an asexual organism with a finite population the class of non-mutant (unloaded) individuals will, due to the rarity of back mutation as well as stochastic processes influencing population size, eventually approach zero in number (Muller 1964, Bell 1988). The same fate will after a while strike the class of 'next-best-fit' individuals, those having a single deleterious mutation, and so on with the next classes. This process, termed "Muller's ratchet" (by Felsenstein 1974) leads to an increased genetic load in asexual lineages and a progressive reduction of fitness.

The above arguments seem to attribute the benefits of sex to populations or species rather than individuals and are thus liable to the critique levelled against group selection theories (Maynard-Smith 1964, Williams 1966). That weak evolutionary forces work on the differential survival of populations is, however, plausible. Some of the genetical premisses underlying some of the above hypotheses may, however, also be used to derive quite contrary conclusions, e.g. that sex slows down evolution rather than accellerate it (cf. Bell 1982: 98-100).

New models based on individual short time benefit and selection, and genotype-environment interaction have been developed in recent years.

(4) According to the 'Tangled Bank' or 'Elbow Room' theory (Ghiselin 1974, Young 1981, Bell 1982, Price & Waser 1982, Koella 1988), sex - by creating genetic variation - enables an organism to exploit a 'spatially' heterogeneous environment more fully, thus reducing intraspecific competition (e.g. sib-competition) and raising environmental carrying capacity by increasing the number of niches. The name of the model is derived from a passage in Charles Darwin's *On the Origin of Species* (1859: 489): "It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us."

(5) According to the 'Red Queen' theory (e.g. Van Valen 1973, Levin 1975, Glesener & Tilman 1978, Bremerman 1980, Hamilton 1980), (the variation created by) sex is necessary because the (antagonistic) biotic environment of an organism evolves all the time, and the organism must co-evolve to keep up with it (e.g. maintaining the balance in host-parasite or host-pathogen relationships). This evolutionary arms race got its name from the Red Queen in Lewis Carrol's *Through the Looking Glass* who had to keep running to stay in the same place. The analogy was initially used by Van Valen (1973) to explain the strange fact that the probability that a family of marine invertebrates will go extinct has not changed appreciably during the last 600 million years, despite the assumption of optimizing (adaptive) evolution.

Although a large amount of experimental work on the environmental significance of sex is currently in progress all over the world (Antonovics & Ellstrand 1984, 1985, Ellstrand and Antonovics 1985, Schmitt & Antonovics 1986, Kelley et al. 1988, Bierzychudek 1987, Vrijenhoek 1989), support for the environmental hypothesis is still mostly circumstantial and often based on the geographical distribution patterns of *asexual* taxa described above. One problem with the interpretation of these geographical patterns is that they may also be correlated with other traits than the sexual-asexual dichotomy, e.g. ploidy levels (Bierzychudek 1985), sexuals tend to be diploid (haploid in haploid organisms), asexuals polyploid.

Law & Lewis (1983), in a paper reviewing the reproductive modes in symbiotic partners, found that sexuality tended to dominate in the exhabitants, that is, the outside partners facing the environment. The inhabitants (endosymbionts, partners living inside the exhabitants) had generally lost sexuality. Law and Lewis explained this result by claiming that endosymbionts are not subject to variable environments and accordingly do not need the genetic variation produced by recombination. The exhabitants, in contrast, maintain sexuality as their mechanism for the generation of genetic variation face to face with the rigors of a changing environment. Although the authors themselves noted a number of exceptions to their general thesis, it certainly adds to the evidence for the 'environmental' point of view.

PLEOMORPHIC FUNGI

Except for the yeasts, which have supplied data supporting the DNA-repair hypothesis (cf. Bernstein 1983, Bernstein et al. 1987), and evidence for genotype-environment interaction in *Schizophyllum commune* and *Aspergillus nidulans* (Fripp & Caten 1971, Butcher et al. 1972) used to support the 'Tangled Bank' (Bell 1985), and Law & Lewis's (1983) symbiosis theory, the fungi have been notably absent in the discussion of the differential advantages of the options to sex or not to sex. This is remarkable considering the following facts:

(1) The fungi include a whole class of organisms which are not known to reproduce sexually - the Fungi Imperfecti or Deuteromycetes (Ellis 1971, 1976, Kendrick 1971, Sutton 1980, Cole & Kendrick 1981), comprising between 20 and 30% of all known fungi. Some of the groups in this class are considered to be at the taxonomic level of order. The majority of Deuteromycetes are considered to be derived from sexual ancestors, notably in the Ascomycetes. The propagules of the Deuteromycetes are often highly specialized, and (genetically) independent of the sexual apparatus of their presumed ancestors (Weber & Hess 1976, Cole & Samson 1979, Fincham et al. 1979, Turian & Hohl 1981).

(2) Several orders within the major groups of fungi (e.g. Ascomycetes, Basiodiomycetes) exhibit step-wise, progressive reduction in the *circumstances* of sexuality - the apparatus of sex - (Kniep 1928, Gaümann 1964, Raper 1966), 'terminating' in the complete elimination of sex (Gaümann 1964).

(3) Few other groups of organisms have such an abundance of individual species with both sexual and asexual modes of reproduction - the *pleomorphic* fungi (Tulasne and Tulasne 1861-1865, Kendrick 1979, Sugiyama 1987, [III-VI]).

(4) The different reproductive stages or phases in pleomorphic fungi often show pronounced differences in ecology, and this may be related to different selection pressures that have worked through evolutionary history (Savile 1976, Pirozynski & Weresub 1979).

(5) The fungi exhibit a vast variety of complex breeding systems associated with *homo-* and *heterothallism,* sometimes with within-species incompatibility of over a thousand strains (Esser & Kuenen 1967, Fincham et al. 1979).

(6) Most fungi are *haploid* during most of their life cycle (Raper 1966), and thus the

question of the functional benefits of sex or not sex is not obscured by the effects of 'mere' diploidy (for this important distinction, see Maynard Smith 1988).

(7) Many fungi have developed alternatives to creating genetic variation through sex: *heterokaryosis* and *parasexuality* (Jinks 1952, Pontecorvo 1956, Hastie 1981). *Extrachromosomal (extranuclear) inheritance* may also be a more important factor in the genetics of fungi than in many other organisms (Jinks 1966, Hastie 1981).

These features should make fungi the perfect organisms, the perfect biological system for studying and identifying the biological effects of the consequences and circumstances of sex, and sexual versus asexual modes of reproduction.

With regard to the question concerning the maintenance of sex it would seem that the best organisms to study this problem on is organisms actually featuring both a sexual and an asexual mode of reproduction, or members of a group of closely related organisms that have adopted either a sexual or an asexual mode of reproduction. This simply because one may suspect that the option 'to sex or not to sex' has only been offered to a limited number of living organisms through their evolutionary history (Williams 1975), and also because the existence of both modes presumably may put in relief the function of both modes in the life of the organism. (cf. Williams & Mitton 1973).The pleomorphic fungi represent a large group of such organisms.

STRUCTURES OF REPRODUCTION IN THE FAMILY UMBILICARIACEAE

The family Umbilicariaceae (Lecanorales, Ascomycetes), consisting of the genera *Umbilicaria* and *Lasallia* (Frey 1933, Llano 1950, 1965, Poelt 1977a, 1977b, Krog & Swinscow 1986) is a group of lichen-forming pleomorphic fungi [I-VI].

Few families of organisms can match the family Umbilicariaceae in its variety of reproductive structures and strategies (e.g. Micheli 1729, Schaerer 1823, Minks 1900, Frey 1929, Scholander 1934, Hasenhüttl & Poelt 1978, [I-VI]).

In the following I make a review of reproductive structures in the family Umbilicariaceae, their taxonomic distribution and frequency.

The mycobiont

Mycobiont sex

The essential sexual processes in members of the family Umbilicariaceae are as in most other organisms, those processes requisite to and including the juxtaposition and fusion of compatible nuclei and the subsequent sorting out of genetic factors in meiosis. These processes impose a cyclic progression during which plasmogamy, karyogamy, and meiosis are the irreducible cardinal events (Raper 1966).

The gameto-phase is characterized by the production of separate 'male' and 'female' gametangia. The male gametangia are immersed, flask-shaped, ostiolate organs termed *spermogonia* (sing.: *spermogonium*; Fig. 1: 11, 17-18), in which the male gametes - the *spermatia* (non-motile, single, cylindrical to fusiform, non-septate, thin-walled and hyaline cells, Fig. 1: 12, 18, 20) - are developed and seceded from specialized, hyphal structures termed *spermatiophores* (Fig. 1: 12, 18-19) lining the inner cavity. Select Umbilicariaceae spermogonia have been described in some detail by Tulasne (1852; Fig. 1: 17-20), Lindsay (1859), Glück (1899) and Vobis (1980); ontogenetic aspects have been described by Janex-Favre (1977). Some variation in anatomy seem to exist, but no full systematic study is available. As observed already by Tulasne (1852: 205), many Umbilicariaceae produce spermogonia and spermatia very abundantly. Vobis (1977) attempted to germinate spermatia from *Umbilicaria virginis* with negative result.

The female gametangium consists of an *ascogonium*, a bundle of ascogonial cells (cf. Letrouit-Galinou 1973). Attached to the ascogonium are sterile receptive hyphae - *trichogynes*, and supporting the ascogonium is sometimes a group of sterile cells.

Although the sexual process has not been documented cytologically in Umbilicariaceae, it is presumably similar to the one first described in some detail for *Collema microphyllum* by Stahl (1877) and later in many non-lichenized fungi (Fincham et al. 1979). The copulation is of the gamete-gametangial type (Raper 1966). A released spermatium fuses (plasmogamy) with a trichogyne which acts as a mediator of the male nucleus towards the ascogonium. Through a temporarily opened porus (establishing a second plasmogamy) the male nucleus wanders from the trichogyne into the ascogonium, forming a *heterokaryon* with the female nucleus. This phase is followed by the conjugation (karyogamy) of the two (sexual) nuclei, and the subsequent genetic recombination by meiosis in the *ascus* (the sporangium) prior to mitotic divisions giving rise by so-called free-cell formation to *ascospores*.

Associated with the development of asci is the development on the upper side of the thallus of elaborate, cup-shaped fruit bodies - *apothecia* - in which the asci and interspersed sterile cells - *paraphyses* - form a *hymenium* (Fig. 1: 5-9, 13-15, [III: Fig. 1]). Anatomical and morphological aspects of the apothecia have notably been investigated by Tulasne (1852), Lindau (1899), Frey (1929, 1936) and Scholander (1934). Ontogenesis was studied by Krabbe (1882), Lindau (1899), Scholander (1934) and Henssen (1970). Scholander (1934) distinguished four apothecium morphologies (cf. [III: Fig. 2]), subsequently termed 'leiodisc', 'omphalodisc', 'gyrodisc' and 'actinodisc' by Llano (1950). Scholander (1934), Llano (1950) and others have used these morphologies as diagnostic at the generic level. The functional significance of the different apothecium morphologies remains obscure, and Henssen's (1970) study indicate that they only represent small modifications of a common *Bauplane* (cf. discussion in [III]).

The ascospores, the propagules produced by the sexual apparatus can be divided into three groups on criteria of septation and pigmentation: (1) non-septate and hyaline, (2) non-septate and pigmented, (3) multi-septate (muriform) and pigmented (Fig. 1: 10, 16; Frey 1929, 1931, 1933, 1936, 1949, Llano 1950, [III, V-VI]). In a few instances 1-septate ascospores have been reported. Detailed studies of ascospore morphology, anatomy and ontogeny in Umbilicariaceae are not available. The size of ascospores is usually within the range 5-50 µm.

Breeding systems

Essentially nothing is known about the breeding systems in Umbilicariaceae. Individual thalli are hermaphroditic, producing both male and female gametangia (own observations), but it is not known whether myciobionts are homothallic (self-compatible) or heterothallic (obligately out-crossing). Chromosome-numbers are unknown, and thus possible occurrence of polyploidy

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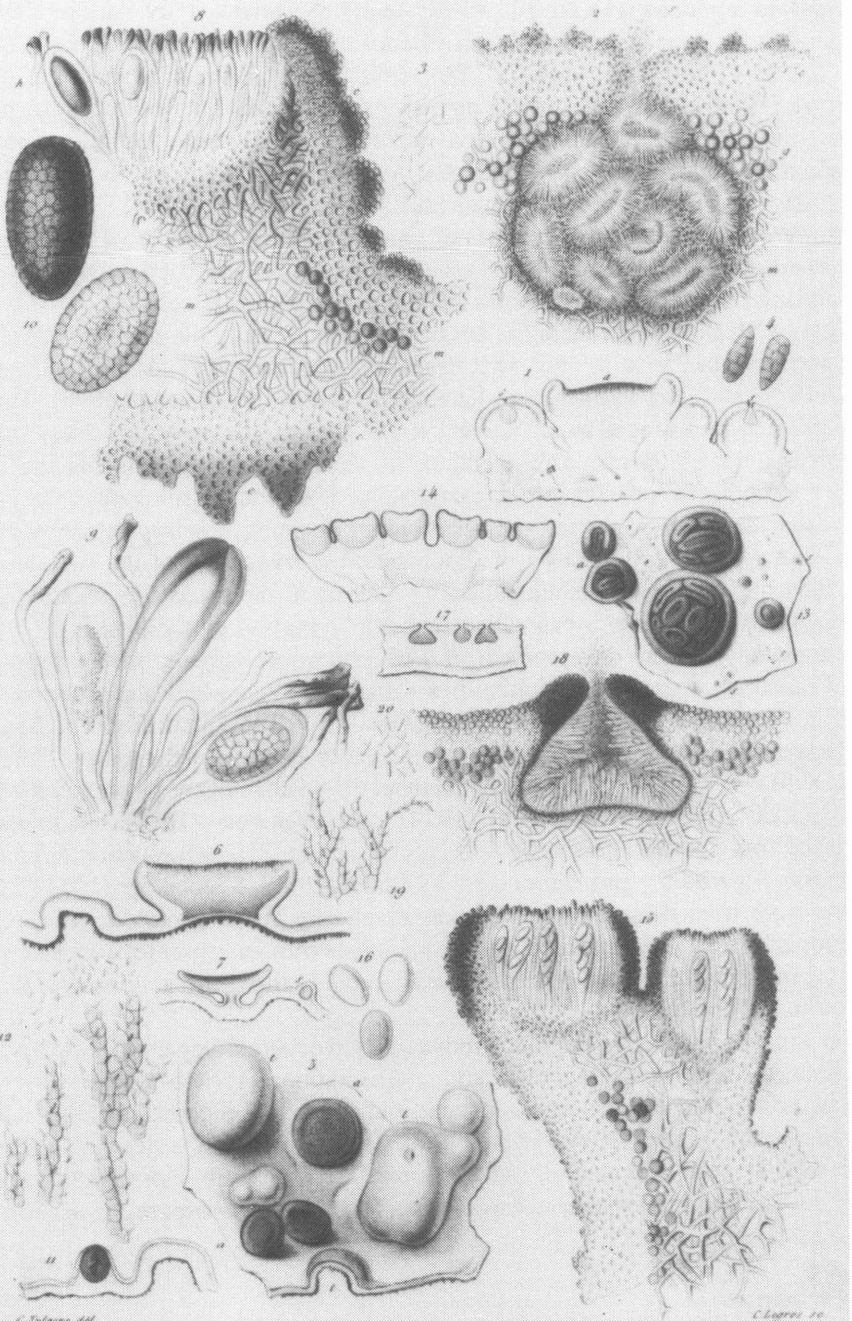

C. Tulasne del.

C. Legros sc.

1-4. Lecanora Villarsii Ach. 5-12. Umbilicaria pustulata Hoffm. 13-20. Gyrophora proboscidea Ach.

N. Rémond imp. r. des Noyers, 63. Paris

is not known. Staining with aceto-orcein of growing hyphae reveal very small, intertwined chromosomes which are virtually impossible to count (Hestmark, unpubl. obs.).

Asexual mycobiont propagules

(1) *Thalloconidia.* The thalloconidia in the genus *Umbilicaria* were early noted by taxonomists (see historical review in I), but only in recent years it has become increasingly accepted that these structures should be considered a type of fungal conidia primarily acting as propagules (Poelt 1977, Hasenhüttl & Poelt 1978, Hestmark 1987, [I-II]). The thalloconidia are brown to dark brown, single- to multi-cellular (up to 2500 cells), spherical to irregular, smooth to rugged; their walls two- or three-layered. The thalloconidia are produced and seceded directly from the cortex and/or the rhizinomorphs on the lower side of the thallus. Detailed studies and illustrations of structure and ontogenesis are provided in [I] and [II]. The size of thalloconidia is mostly within the range 5-100 µm.

(2) *Rhizinomorphs* (?). Many members of the genus *Umbilicaria* feature rhizine-like, multicellular structures on the lower cortex, termed rhizinomorphs by Hannemann (1973). Presumably these structures mainly serve purposes of water balance (Larson 1981) and possibly temperature regulation, but it cannot be excluded that a rhizinomorph broken off from the lower cortex may be able to disperse and establish a new individual in a suitable site. The rhizinomorphs do, however, in most cases seem rather well attached to the lower cortex, and it seems unlikely to me that they constitute a propagule type of any significance. It should also be noted that in many instances the rhizinomorphs are used for the production of thalloconidia, this an indication that the rhizinomorphs themselves are probably not very effective as propagules. A special case, where modified rhizinomorphs clearly fullfill a propagative function, are the symbiotic *thallyls* described below.

(3) *'Marginal isidia'* (?). Frey (1949) described 'isidia' without photobiont developing marginally on thalli in a number of *Lasalliae*. Although these structures may possibly occasionally break off, be dispersed and give rise to new individuals, they do not seem particularly brittle, and their significance as propagules remains highly conjectural.

The photobiont

Lichens are symbiotic organisms. Successful reproduction requires the successful reproduction of both the mycobiont and the photobiont. The photobiont of Umbilicariaceae lichens belong in the genus *Pseudotrebouxia* (Chlorellales, Chlorophyceae), single-celled, green algae (cf. Tschermak-Woess 1988). When in symbiosis the algae reproduce by autospores. Isolated in pure culture they may also reproduce by zoospores, aplanospores or autospores (cf. Tschermak-Woess 1988). Sexual reproduction have not been reliably reported. It is not known whether *Pseudotrebouxia* disperse independently in nature.

Fig. 1. Tulasne's (1852) illustrations of sexual organs in Umbilicariaceae. 5-12. *Lasallia pustulata.* 13-20. *Umbilicaria proboscidea.* See text for further explanation.

Symbiotic propagules

A number of reproductive structures propagate the intact symbiosis:

(1) *Soredia* are loosely interwoven bundles of algae and fungal hyphae produced and seceded from the upper cortex and the algal layer of lichens (Du Rietz 1924). Minks' (1900: 15) contention that soredia are absent in the genus *Umbilicaria* is certainly wrong. Soredia are present in a small group of *Umbilicaria* species which from a number of basic similarities in morphology, anatomy, secondary substance chemistry and ecology may be suspected to be closely related (by Frey 1933 distinguished as Sektion Velleae of Subgenus Gyrophoropsis); occasionally they may even be difficult to separate (e.g. *U. hirsuta* vs. *U. grisea*). The anatomical features facilitating the genesis of soredia in *U. hirsuta* was studied by Frey (1929: 231) who also noted that particularly abundant production of soredia was found in shadow-growing individuals where presumably the algae multiplied to compensate for the reduction in light. The soredia of *U. hirsuta* develop by desintegration of the often pallisade-plectenchymatous upper cortex and algal layer, while the compact lower cortex remains as the base. Hirsuta has according to the classification of DuRietz (1924: 377) a *soredium diffusum*. In *U. hirsuta* the soredia develop from margin to center of thallus; in *U. grisea* more patchy, no distinct pattern of development. The size of individual soredial propagules are usually within the range 0.05-0.5 mm.

(2) *Isidia* - cylindrical or branched to corralloid outgrowths from the upper cortex that contain algae sheltered by a fungal cortex. The anatomy of isidia in *U. deusta* were studied by Schade (1955) and by Larson & Scott (1984). The corralloid isidia of *Lasallia pustulata* are described and depicted in V, Fig.2. The size of isidia is very variable but usually within a range of 0.1-1.0 mm.

(3) *Phyllidia* - leaf-formed isidia, size occasionally up to 5 mm.

(4) *Schizidia* - small patches of the upper cortex + algal layer (0.5-2 mm in diam.) which become detached along fissures in the upper cortex. Suggested by Minks (1900: 42) who claimed that patches of the upper cortex and algal layer of *U. vellea* could secede from the thallus, disperse and develop into new thalli. Well developed schizidia in *U. thamnodes* were described by Poelt (1977).

(5) *Thallyls* - small thalli developing from the tip of rhizinomorphs - were originally described and depicted by Schaerer (1823). Frey (1929) thought the algae originated from the outside and were 'picked up' by the rhizinomorphs, but anatomical studies by Krog & Swinscow (1986) revealed that algae wander from the algal layer close to the upper cortex and down towards the lower cortex where they become integrated into tissues growing out of the lower cortex as rhizinomorphs. Beautiful thallyls on *U. umbilicarioides* are depicted in Krog & Swinscow (1986). Size up to 1 cm in diam. The thallyls are evidently detached from the mother thallus by the breaking of the rhizinomorphs.

The soredia, isidia, phyllidia, schizidia and thallyls appear to be more or less specialized structures or anatomical modifications of the thalli which clearly serve a propagative function in addition to the photosynthetic production of organic compounds (as long as they remain attached to the thallus). The following structures or anatomical modifications appear less specialized and their reproductive function is highly conjectural.

(6) *Squamules* (?) - small folds, ridge- or wing-like structures produced by abnormal growth of the upper cortex.

(7) *Bridges* (?) - similar to the stolons of many plants. Described and depicted in *U. indica* var. *nana* by Frey in Poelt (1977). Dubious. May simply be several thalli growing

together.

(8) *Splitting* - described as 'dilaceratio' by Minks (1900) and by him considered perhaps the major mode of reproduction in *Umbilicaria.* True, the margins of *Umbilicaria* thalli are often lacerate, and it cannot be excluded that parts of the margins occasionally break off, disperse and establish new individuals. It should however be noted that the lacerate margins often have an eroded or necrotic appearance (due to ice-blasting and other environmental forces), something which makes it less probable that they may generate viable propagules. Splitting would also seem to constitute a constant threat to the integrity, survival and fitness of the thallus, and thus seems unlikely to have been selected as an evolutionary stable or optimal strategy. The irregular laceration of *Umbilicaria* thalli contrasts with the controlled fission or budding of a number of clonally reproducing animals and plants (Hughes 1989, Richards 1986).

(9) *Fragmentation* - a dry thallus will fragment into hundreds of pieces if you step on it. Given their usual habitat preferences for more or less vertical rock and cliff outcrops, the probability of an Umbilicariaceae being jumped on does however seem rather small (although this factor was invoked by Hakulinen (1962) for the spread of *Umbilicaria* lichens along Finnish lakes). Du Rietz (1931) who harvested a rich material of different lichens in snow drifts on the Tron mountain in Norway found only very sparse fragments he identified as *U. proboscidea.* This in contrast to e.g. *Cetraria nivalis* which amounted to 13.7 gr in his samples. From snow fields in Torne Lappmark, Sweden, Du Rietz reported sparse fragments of *Umbilicaria cylindrica, U. torrefacta* and *U. vellea* (alt. 1050 m), and *U. proboscidea* (with apothecia) and *U. rigida* (with apothecia) (alt. 1650-1700 m). The ability of such fragments to establish new individuals should be investigated further.

(10) *Whole thallus.* This is a mode of dispersal rather than reproduction. Dahl (1957: 360) reports whole thalli of *U. viriginis* on snow in Rondane mountains in Norway. I have myself observed large thalli of *U. rigida, U. cinereorufescens, U. havaasii* on many occasions on glaciers and snow fields in the Norwegian mountains. It seems highly improbable to me that these thalli - usually large and aging - should be able to fasten themselves on a new rock surface and reproduce.

Taxonomic distribution

A world monograph of the family Umbilicariaceae is not yet available (though an ambition by the present author), but several regional studies and monographs have established quite a number of what seems to be 'good' species (Du Rietz 1925, Frey 1929, 1931, 1933, 1936, 1949, Llano 1950, 1965, Krog 1973, Poelt 1977a, 1977b, Krog & Swinscow 1986, Filson 1987, Sancho & Crespo 1989). The following list of the taxonomic distribution of the different types of propagules is based on own observations.

Apothecia with *ascospores* have been observed in all members of the Umbilicariaceae. In the following species no other specialized propagules have been observed:

Umbilicaria angulata Tuck.
Umbilicaria arctica (Ach.) Nyl.
Umbilicaria badia Frey
Umbilicaria bigleri Frey
Umbilicaria bolusiana Frey

Umbilicaria calvescens Nyl.
Umbilicaria caroliniana Tuck.
Umbilicaria crustulosa (Ach.) Frey
Umbilicaria corsicae Frey
Umbilicaria cylindrica (L.) Delise ex Duby
Umbilicaria dichroa Nyl.
Umbilicaria durietzii Frey
Umbilicaria haplocarpa Nyl.
Umbilicaria hyperborea (Ach.) Hoffm.
Umbilicaria indica Frey
Umbilicaria intermedia Frey
Umbilicaria josiae Frey
Umbilicaria krascheninnikovii (Savicz) Zahlbr.
Umbilicaria krempelhuberi Müll.-Arg.
Umbilicaria laevis (Schaerer) Frey
Umbilicaria microphylla (Laur.) Massal.
Umbilicaria mühlenbergii (Ach.) Tuck.
Umbilicaria nanella Frey & Poelt
Umbilicaria nepalensis Poelt
Umbilicaria peruviana Llano
Umbilicaria phaea Tuck.
Umbilicaria polaris (Schol.) Zahlbruckner
Umbilicaria proboscidea (L.) Schrader
Umbilicaria rigida (DuRietz) Frey
Umbilicaria ruebeliana (DuRietz & Frey) Frey
Umbilicaria spodochroa (Hoffm.) DC in Lam. & DC
Umbilicaria subaprina Frey
Umbilicaria torrefacta (Lightfoot) Schrader
Umbilicaria virginis Schaerer
Umbilicaria yunnana (Nyl.) Hue
Umbilicaria zahlbruckneri Frey
Lasallia brigantium (Zschacke) Llano
Lasallia papulosa (Ach.) Llano
Lasallia pensylvanica (Hoffm.) Llano
Lasallia glauca (Stiz.) Llano
Lasallia rubiginosa (Pers.) Llano
Lasallia membranacea (Laur.) Llano

Thalloconidia have been observed in the following taxa:

Umbilicaria africana (Jatta) Krog & Swinscow
Umbilicaria antarctica Frey & M. Lamb
Umbilicaria aprina Nyl.
Umbilicaria cinerascens (Arnold) Frey
Umbilicaria cinereorufescens (Schaerer) Frey
Umbilicaria decussata (Vill.) Zahlbr.

Umbilicaria dendrophora (Poelt) Hestmark
Umbilicaria esculenta (Miyoshi) Minks
Umbilicaria havaasii Llano
Umbilicaria leiocarpa DC
Umbilicaria lyngei Schol.
Umbilicaria mammulata (Ach.) Llano
Umbilicaria nylanderiana (Zahlbr.) Magnusson
Umbilicaria polyphylla (L.) Baumg.
Umbilicaria polyrrhiza (L.) Fr.
Umbilicaria subglabra (Nyl.) Frey
Umbilicaria umbilicarioides (B. Stein) Krog & Swinscow
Umbilicaria vellea (L.) Hoffm.
Umbilicaria viperina Llano ?
Umbilicaria cristata Dodge & Baker ?

Thalloconidia have recently been discovered by the author in several new *Umbilicaria* species from Tenerife and South America (unpubl.). Thalloconidia have not been reported from the genus Lasallia (cf. [I]).

Soredia have been observed in:

Umbilicaria grisea Hoffm.
Umbilicaria hirsuta (Sw. ex Westr.) Hoffm
Umbilicaria pacifica Magnusson
Umbilicaria soralifera (Frey) Krog & Swinscow
Umbilicaria vellea f. *leprosa* Frey (1933)
Umbilicaria haplocarpa Nyl. var. *subhirsuta* Frey (1949)
Umbilicaria freyi Poelt

Isidia have been observed in:

Umbilicaria deusta (L.) Baumg.
Lasallia asiae-orientalis Asah.
Lasallia daliensis Wei
Lasallia chiriquiensis Llano
Lasallia pertusa (Rassad.) Llano (isidiate soralia?)
Lasallia pustulata (L.) Mérat

Phyllidia have been observed in *Umbilicaria deusta* (L.) Baumg.
Schizidia have been observed in *Umbilicaria thamnodes* Hue.
Thallyls have been observed in:

Umbilicaria indica
Umbilicaria umbilicarioides
Umbilicaria vellea
Lasallia pustulata

Tab. 1. Number of taxa displaying different structures of reproduction in Umbilicariaceae.

Structure	*Umbilicaria*	*Lasallia*
Ascospores	36	6
Thalloconidia	18	
Soredia	6	
Schizidia	2	
Isidia	1	5
Phyllidia	1	
Thallyls	3	1

From Tab. 1 it is seen that in *Umbilicaria* the dominant structures are ascospores and thalloconidia, while in the genus *Lasallia* the dominant structures are ascospores and isidia. In contrast to many other lichen genera (cf. Bowler & Rundel 1975), symbiotic propagules are not very common in Umbilicariaceae. Furthermore, the sorediate habit is confined to a small group of anatomically and morphologically similar taxa which may be closely related. Similarly the isidial habit is almost exclusively confined to the genus *Lasallia* which show much less interspecific variation than *Umbilicaria*.

STRATEGIES OF REPRODUCTION IN THE FAMILY UMBILICARIACEAE

> "The main work of providing a workable theoretical structure for understanding the enormous diversity of life cycles remains to be done" (Williams 1975: 119)

Life-history strategies

Science without generalization easily degenerates into a catalogue of disconnected facts. Among the more fruitful attempts in recent years to arrive at generalizations in evolutionary ecology are the attempts to classify *life histories* (Stearns 1976, 1977, 1980, Caswell 1989). The apparent tendency for plants and animals to express sets of correlated life history characters has led some authors (*e.g.* MacArthur & Wilson 1967, MacArthur 1972, Blondel 1976, Grime 1977, 1979, Southwood 1977, Barbault et al. 1980, Caswell 1989) to describe these sets as strategies - *life history strategies* or ecological strategies. The concept has also been applied to the fungi (Pugh 1980, Cooke & Rayner 1984). A number of particular strategies have been described, the most famous being the r-, K-, C-, R-, and S-strategies (cf. MacArthur & Wilson 1967, Pianka 1970, Gadgil & Solbrig 1972, Grime 1979, Parry 1981, Boyce 1984).

The ultimate aim of life history theory is to compare the fitness of phenotypes which differ in their development rates or age-(or size-) specific fecundity- or survivorship-schedules under specified ecological circumstances (Crawley 1986, Partridge 1989). Although life history theorizing so far has failed to establish a single, general, solid and confirmed theory, it has served heuristically to focus attention and research on how certain traits may affect fitness and population dynamics. The tremendous variation in life-histories revealed by empirical studies over the past 20-25 years suggests that current theoretical models, presuppositions and predictions are too simplistic and that further progress in our understanding will mainly depend on further empirical case studies. The studies reported in [IV-VI] represent new contributions to this empirical data base.

Life history theory is based on a number of assumptions:

(1) *Fitness-maximizing evolution*: evolution leads to specializations ('adaptations') that maximize fitness (cf. Darwin 1859, Cohen 1966, Gadgil & Bossert 1970, Schaffer & Gadgil 1975). The life history leading to the greatest fitness is the one maximizing the 'Malthusian parameter' r, the intrinsic rate of population increase of the genotype specifying the trait (phenotype) in a given environment. This is usually considered an adequate measure of fitness in constant, density independent environments, but also holds for density dependent populations where maximizing r is equivalent to maximizing the carrying capacity of the environment, K (Charlesworth 1980).

(2) *Environmental determination*: species growing in similar spatio-temporal microhabitats will exhibit similar life history patterns (Murphy 1968, Partridge & Harvey 1988, Southwood 1977, 1988).

(3) *Finite economy and principle of allocation*: organisms allocate resources to several different, necessary life functions from a limited pool of resources (Cody 1966, Harper & Ogden 1970, Harper 1977, Lloyd 1985). Every function has a cost on the total budget; allocation takes place between competing demands.

(4) *Complementarity of traits*: the traits in a strategy set are integrated and represent an equilibrium situation where the change of one trait will entail the correlated change of one or several of the other traits to maintain equilibrium. This may be linked up with the concept of evolutionary stable strategies (ESS; Maynard-Smith & Price 1973, Maynard-Smith 1982).

(5) *Trade-off between traits/variables*: the principle of complementarity entails the possibility of trade-offs between some life history traits/variables, e.g. one may be increased (e.g. seed size) and another decreased (e.g. seed number) and the fitness remain the same (cf. list of typical trade-offs in plants in Crawley 1986). The optimum trade-off will be the one maximizing fitness.

Although all these assumptions may be questioned or rediculed it should be realized that they constitute much of the theoretical foundation of contemporary biological science, notably the disciplines of ecology and evolutionary biology. Still it is important to remember that: (1) evolution produces practical, temporary solutions based on available, historically given, genetically and developmentally constrained material, not the theoretical, mathematical optimum, (2) the intrinsic rate of increase *r* is arbitrarely defined with regard to a specific laboratory situation (Andrewartha & Birch 1954: 33), (3) the carrying capacity *K* is not defined by life history traits, (4) intraspecific variation blurr the distinctiveness of traits, (5) it is difficult to ascertain stable age distribution, although this is assumed in the equation determining *r*, (6) several stable equilibrium situations may be possible, (7) real biological systems are - as every field biologist knows - so complex that it is easy to overlook important factors influencing fitness (e.g. a biotic factor), and (8) several alternative explanations which are not necessarily mutually exclusive are often possible for any trait (several of these points are made by Stearns 1977).

Strategy of reproduction - the core set of life history

Certainly the greatest amount of variation in life histories relates to aspects of reproduction, and thus it seems valid to assert that the central sub-set of a life history is *the strategy of reproduction.* Harper & Ogden (1970) equated 'strategy of reproduction' with the resource/energy allocation associated particularly with reproduction. A rather special sub-set of this concept would be strategies of sex allocation (Charnov 1982, Lloyd 1985). Bowler & Rundel (1975) in a paper on 'reproductive strategies in lichens' did not define 'reproductive strategy', but seem to include a mixture of propagule characteristics and life history traits in this concept. Ott's (1987a, 1987b) papers on 'reproductive strategies in the lichens' mainly focus on what may be termed 'the strategy of resynthesis (licheniziation)' and initial development. Reproductive strategies are not included in the ecological 'strategies of lichens' outlined by Kershaw (1985: 256-260), despite the fact that they are inspired by Grime (1977, 1979) where life history traits of reproduction are integrated parts of the CSR-scheme.

Cohen (1977) has emphasized that the term 'reproduction' should be taken to imply a full generation cycle, the production of a new *reproducing* individual. This could lead to the conclusion that life is *nothing but* reproduction. In contrast Harper (1977) states that the essential tension in life histories is the one between growth and reproduction. The disagreement may be more apparent than real. It seems to me that the concept of a 'strategy of reproduction' should include all aspects of *structures* and *events* of reproduction (cf. also contributions in Doust & Doust 1988).

The concept of strategy is *comparative* - it implies the existence of variation, two or more 'options'. Most of the variation in reproductive strategies relates to numerical (quantitative) aspects of structures and events, the questions being: how many? how big? and how often? Important aspects include time to first breeding, time between subsequent breeding attempts, fecundity at each breeding attempt, survival from propagule to first reproduction, survival between successive breeding attempts, sex or not sex, mating (breeding) system, propagule characteristics, mode of propagule dispersal, kind and degree of propagule dormancy; environmental factors include biotic interactions (predation, parasitism), availability of dispersal vectors and availability (average frequency) of germination microsites in the environment.

The attempts to integrate the qualitative option to sex or not to sex into life history theory has only recently begun, and few if any of the available models integrate recombination

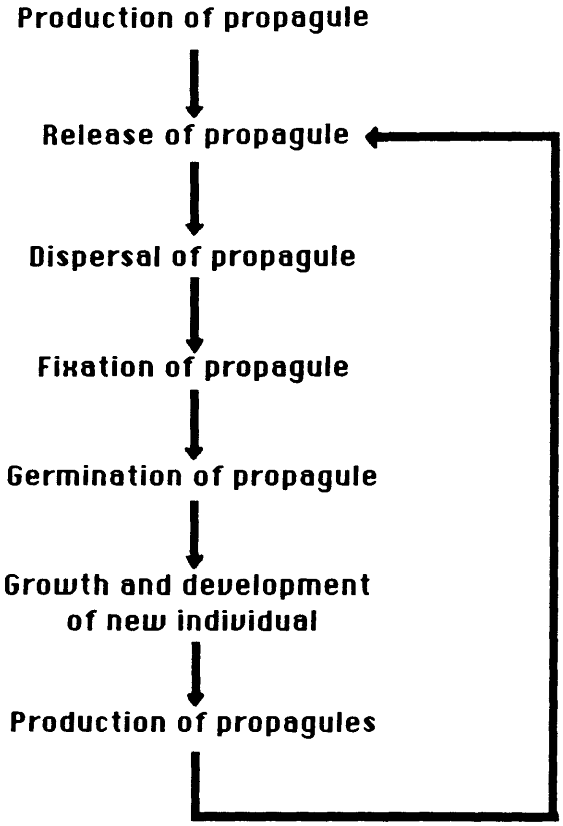

Fig. 2. The cycle of life in Umbilicariaceae.

as such (what was termed 'the essence of sex' above). Models by Sibly & Calow (1982, 1985, 1986), Calow & Sibly (1987), Caswell (1982, 1983, 1985), Sackville Hamilton et al. (1987) predict circumstances under which gametic or agametic reproduction yields the faster population growth, but due to some of the assumptions of these models - which really relate to particular *circumstances* of sex/asex rather than the essence or immediate consequences - these models are not universally applicable.

Umbilicariaceae strategies

Turning our attention to the family Umbilicariaceae: On the face of it the life of these lichens do not seem overly exciting or eventful - sitting on the rocks, watching life go by. But precisely because of this simplicity it is possible to use these organisms as 'model systems'

Tab. 2. Characteristics of the three major reproductive strategies in the family Umbilicariaceae.

	AS	TC	SY
Gametophase (spermogonia and ascogonia)	yes	no	no
Fertilization	yes	no	no
Propagule			
meiotic	yes	no	no
symbiotic	no	no	yes
size	small	small	large
form	ellipsoid	ell. to irreg.	irregular
no. of cells	1 to many	1 to many	many
pigmented	±	+	±
robustness	small	great	medium
Allocation of:			
total resource to reproduction	medium	small	medium
resources per propagule	large	small	medium
Total number of propagules	medium	medium/large	medium
Supporting tissue	much	none	none/some
Age/size of reproductive maturity	late	early	early
Iteroparous	yes	yes	yes
Seasonality of production	yes	yes ?	no?
Secession	active	passive	passive
Site of production on thallus	upper side	lower side	upper or lower
Main dispersal vector	wind	water	water/wind
Dispersal	good	poor	poor
Resynthesis	yes	yes	no

on which to test, extend and complement biological theories. In particular their individual, sessile and perennial habit make them suitable for population studies.

Fig. 2 gives a generalised life cycle or life history for members of the family Umbilicariaceae. The cycle is equivalent to the life cycle of any organism reproducing by propagules, thus all fungi, most plants and protists, and many invertebrates. Each stage in this cycle may be considered a task to be 'solved' by the organism (Harper & White 1971, Harper 1977), and the successful completion of each stage depends on a number of environmental conditions being satisfied.

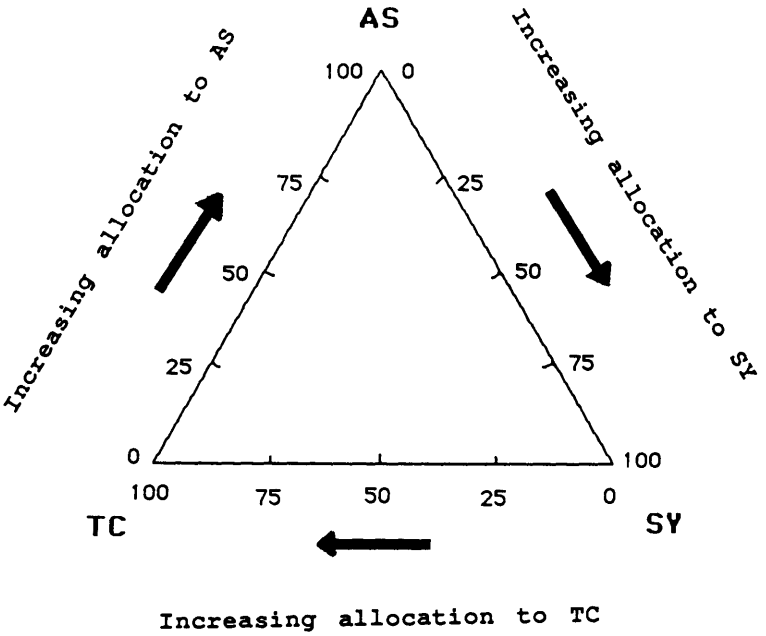

Fig. 3. Triangle of Umbilicariaceae strategies.

I will tentatively distinguish three reproductive strategies in the Umbilicariaceae that we may term 'pure' strategies. Pure because they represent extreme cases, idealizations, and are probably not realized 100% in any species. In most cases they occur mixed, but one of them will usually will tend to predominate.

(1) Sexual reproduction by ascospores
(2) Asexual reproduction by thalloconidia
(3) Asexual reproduction by symbiotic propagules

These strategies will be denoted *AS*, *TC*, and *SY* for short. The main criteria for distingushing these three strategies is seen to be whether they involve sex or not, and whether they involve symbiosis or not. What makes them into strategies is however the fact that associated with these propagules or groups of propagules is a number of other distinguishing traits (Tab. 2). These associated sets of traits have consequences for the ecological performance of the species [IV-VI].

As in most other strategy tables (e.g. Grime 1977, 1979) some of the data are qualitative rather than quantitative. This is mainly because precise quantitative data are lacking. Some of the traits are also highly conjectural and need verification.

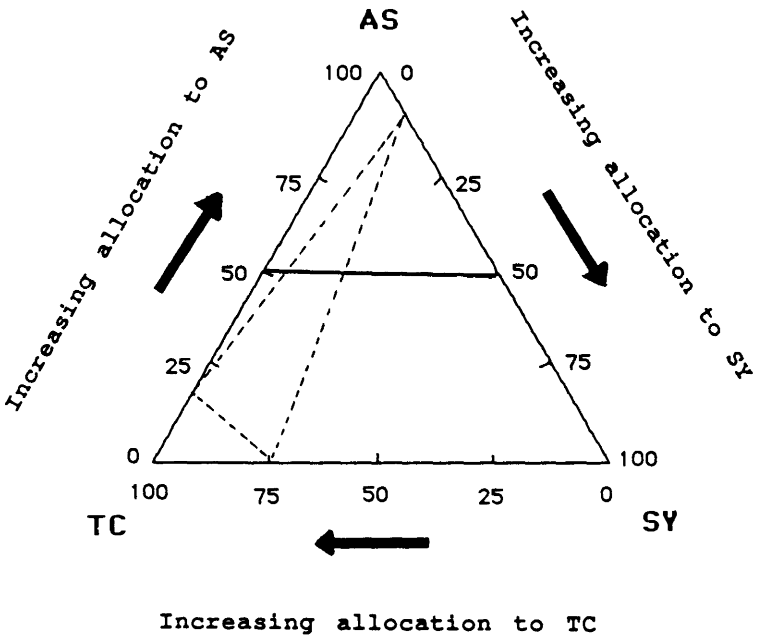

Fig. 4. Examples of individual allocations. The solid bar represents an allocation strategy of 50% AS and 50% SY (e.g. a thallus of *Lasallia pustulata* in the middle growth phase, cf. [V]). The stippled triangle represents a strategy of 75% TC, 10% SY and 15% AS (e.g. a thallus of *Umbilicaria umbilicarioides*, cf. [IV]).

The allocation of a given individual, population or species to these strategies may be represented in an allocation triangle (Figs 3-4) where the percentages may indicate amount of energy allocation, number of propagules, or number of individuals in a population [cf. IV-V].

The majority of the taxa listed above will group around one of the corners in the triangle. An individual may perhaps be a pure AS, TC or SY strategist throughout its life but populations or species are likely to exhibit mixed strategies [IV-V] (e.g. we cannot entirely exclude the possibility that in a predominantly sexually reproducing species without special asexual propagules a piece of the thallus may occasionally be torn off, disperse and establish a new individual in a new habitat). In some cases the allocation to different strategies may change over time as the individual passes through developmental stages. This is documented for *Lasallia pustulata* in [V]. In many cases the allocation may also seem to have changed in the course of evolutionary history [IV].

The de-evolution of sex - ecology and evolution

A number of traits seem to suggest that in the family Umbilicariaceae the organs of sexual reproduction are phylogenetically older than the asexual ones, that is, sexual reproduction with ascospores preceeded asexual with thalloconidia or isidia, soredia etc. Pointing in this direction is the similarity of the teleomorphs (ascocarp structure) and also the spermogonia with a large number of apparently non-anamorphic members in the Lecanorales (see Henssen 1970, 1981, Vobis 1980: 22-24, 85-86, Glück 1899: 148-153). This suggests a common, non-anamorphic ancestry, though neither convergence in ascocarp structure nor secondary loss of anamorphs (in other Lecanorean genera) may be entirely excluded. This phylogenetic presedence of sex is presumed for other pleomorphic Ascomycetes (Pirozynski & Weresub 1979), as it is for apomictic higher plants (Gustafsson 1946, 1947a, 1947b) and many asexual animals (Bell 1982, Hughes 1989).

In the species primarily reproducing sexually by ascospores, the number of apothecia produced vary from individual to individual, and some individuals for some reason or other do not apparently reach the sporophytic (teleomorphic) stage (Hestmark, unpublished). The great majority of individuals in these species do however eventually produce an abundance of apothecia and ascospores (Hestmark, unpublished), this an indication that the ascospores really function as the main propagules in these taxa.

In the species possessing asexual propagules [cf. I-VI], in contrast, the frequency of individuals producing ascospores tend to be very low [IV-V]). In these species there appears to be a pronounced 'de-evolution' of sex. Thus, where the option not to sex has been presented, evolutionary and ecological forces seem to have favoured this option and sexuality is greatly reduced or postphoned [IV-V].

The first major challenge in the study of the reproductive strategies in the family Umbilicariaceae is to identify these evolutionary and ecological forces - the forces switching reproductive allocations from the AS-strategy to the TC- and SY-strategies. The second challenge is to establish whether current allocation patterns represent evolutionary stable strategies, or whether they represent stages in a continuing evolutionary process that will eventually lead to the complete elimination of sex.

The answer to the first challenge will in part be found in the list of functional benefits of asexual reproduction listed above (e.g. no requirement for fertilization etc.). In part it will also be found in the table contrasting the three pure strategies (Tab. 2). The asexual modes are obviously more efficient in cost-benefit terms because of the absence of a gametophase and supporting tissues of propagules. Although large symbiotic propagules represent a substantial energy-allocation, these propagules have the unique feature that they produce their own energy. Thus there is only a minor if any re-allocation of resources from vegetative growth. The thalloconidia develop protected within lower cortex or rhizinomorph tissues [II] and under the shelter of the shield-formed thallus [I] and may thus evade predators and deleterious UV radition [IV]. The robustness of the asexual propagules also contrast favourably with most ascospores. The close-dispersal habit of the asexual propagules increases the probability of propagule success in heterogeneous environments [V-VI]. The symbiotic propagules in addition have the advantage of not needing to resynthesize.

One explanation for the short term selection of asexual reproduction - superior colonizing ability - seems fairly definitively refuted in the case of Umbilicariaceae [VI]. The first stages of primary colonization is exclusively the arena of sexually reproducing *Umbilicaria* species [VI]. Thus the asexual Umbilicariaceae cannot be considered so-called 'fugitive' or 'r-selected' species (cf. MacArthur & Wilson 1967, Armstrong 1976, Parry 1981). The essential distinction to make is between within-habitat colonization (close-dispersal) and between-habitat colonization ('long-distance' dispersal). The asexual propagules are superior within-habitat colonizers but the ascospores are better between-habitat colonizers. Both the sexual and asexually reproducing Umbilicariaceae species appear to pursue mixed life-history strategies which incorporate typical r-strategy elements as well as K-strategy elements (e.g the ascospore is a small propagule (r) but the proportion of reproductive resource invested in the propagule is large (K)). The perennial and iteroparous habit of the Umbilicariaceae as well as their often density-dependent population dynamics [V] do, however, suggest that they incline to the K-side of the spectrum.

In part the answer to the first challenge may also be found in particular local ecological circumstances [IV, VI]. In at least one species - *Umbilicaria africana* - the production of sexual and asexual propagules appear to be phenotypically plastic traits the expression of which is correlated with climatic factors, radiation and drought favouring asexual reproduction by thalloconidia. The absence of predominantly sexually reproducing *Umbilicaria* species in the extreme environments of Africa and Antarctica (cf. Hestmark 1987) also indicates the significance of ecological conditions. In the interesting case where a taxon have split or is on the verge of splitting into one sexual and one predominantly asexual species, there are pronounced differences in geographical distribution of the members of the pair [IV].

The second challenge is more difficult to answer and seem to require different answers depending on the species. *Umbilicaria havaasii* appear to be on the brink of eliminating sex completely [IV]. Similarly *Umbilicaria cinerascens* [IV]. The extremely low frequency of sexual reproduction in these species makes it unlikely that sexual reproduction have any significance for the genetic structure of the populations or for life-history strategy. In contrast *Lasallia pustulata* may appear to pursue a consistent ESS of early asexual reproduction and late sexual reproduction [V].

The evolutionary consequences of a complete elimination of sex will depend on the stability of the environment and on the ability of the organism to generate genetic variation by other means than sexual recombination. The 'environmental' theories for the maintenance of sex all view the creation of genetic variation as the key issue. If an asexually reproducing species have only a single genotype, it will be extremely vulnerable to environmental change which may wipe it off its 'adaptive peak' and drive it to extinction.

The genetic structure of the Umbilicariaceae have been studied notably by Cecilia Hagemann and Dianne Fahselt using enzyme polymorphism as a measure of variation. Fahselt (1989) examined thalli from three stands of the sexually reproducing *Umbilicaria virginis*, two of the asexual *U. decussata*, one of the 'sterile' *U. hyperborea* and one of an unidentified non-sexual taxon in the Canadian High Arctic, and found a somewhat higher degree of enzyme polymorphism in the sexual *U. virginis*, suggesting that regular sexual reproduction result in greater genetic variation. This result must be interpreted with some caution, however, since the difference in dispersal mode of species reproducing by thalloconidia vs. ascospores will cause differences in the geographical distribution of genetic variation. A stand of sexually reproducing species is likely to be more heterogeneous not only because there is genetic recombination at site, but because due to the more or less random dispersal of ascospores the stand is likely to have been parented by many individuals from many sites, whereas a stand of an asexually reproducing spacies may be the progeny of a single locally established individual, thus a clone. In a recent study of the sexually reproducing *U. muhlenbergii*, *Lasallia papulosa*, the isidiate-phyllidiate *U. deusta*, the sorediate *U. hirsuta*, and the thalloconidial *U. vellea* and *U. mammulata*, Hagemann and Fahselt (1990a) conclude that the enzyme electromorph variation is in general not higher in sexually reproducing Umbilicariaceae species, although thalli of *U. vellea* with apothecia have a slightly higher degree of variation in some enzymes than thalli of the same species without apothecia (Hagemann & Fahselt 1990b). This confirms earlier reports of considerable variation in the enzymes and secondary products in asexually reproducing *Umbilicaria* species (Hagemann & Fahselt 1984, Larson & Carey 1986, Feige et al. 1987, Fahselt 1989), perhaps suggesting somatic mutation to be a significant cause of variation in this genus. The sun-exposed habitats and long life of Umbilicariaceae lichens (100+ ?) years make such mutations probable. There is an increasing recognition that somatic mutation may be an important mode of creating genetic variation (Suomalainen et al. 1976, Silander 1985, Ellstrand & Roose 1987, Mischler 1988). The absence of distinct germ lines in the fungi means that any somatic mutation may at some instance be integrated into propagules. As indicated above, however, most mutations will be deleterious, and there are also uncertainties connected with the interpretation of isoenzyme data in terms of variation and significance for evolution. A common presupposition of the technique is that isozyme variation is more or less selectively neutral.

In an evolutionary and ecological context the question will be whether the presumed advantage gained by the sexual generation of variation is big enough to combat the invasion of a clone svarm and reach an equilibrium situation between sexually and asexually reproducing individuals (Bell 1982). If there is any cost to sex, an invasion by asexuals can only be combated by evasion. The genetic variation of the sexuals have to be greater than that of the asexuals, and the sexuals have to retreat into the part of their niche that lies outside the niche of the invading clone. Unless the genetic variation in the clone is increased (by mutation) or reduced (e.g. by sampling error), or the environment changes, a steady state equilibrium will be reached between the sexual and asexual parts of the 'population' (Bell 1982). The virtual elimination of sex in some *Umbilicaria* species [IV] may indicate that these taxa consist of a large number of clones with a variety of genotypes, and thus have been able to outcompete the sexual mother strain in most or all niches. The morphological and chemical variation in some of these species support this conjecture [cf. IV]. Thus these taxa may not any longer be functioning as species in the sense that they constitute an interbreeding unit.

SUMMARY OF PAPERS

PAPER I

This paper is a descriptive study of the *thalloconidia* of 18 species in the genus *Umbilicaria*, and provides detailed data on septation, shape, size, colour, surface ornamentation, wall structure, and site of production on thallus. The main methods used are transmission electron microscopy (TEM), scanning electron microscopy (SEM) and light microscopy (LM). Protocols for the fixation and preparation of thalloconidia for these microscopic techniques are provided.

The thalloconidia are asexual propagules, brown to dark brown, single- to multi-cellular (up to 2500 cells), spherical to irregular, smooth to rugged; their walls two- or three-layered. The thalloconidia are produced and seceded directly from the cortex and/or the rhizinomorphs on the lower side of the thallus. Conidiomata and conidiophores are absent. The thalloconidia show distinct patterns of distribution on the lower cortex and/or the rhizinomorphs. A tentative division into eleven basic patterns is made. The anamorphs of *Umbilicaria antarctica* and *U. esculenta* are described for the first time.

The characteristics of the thalloconidia prove to be of substantial value for taxonomical work at the specific level. For instance, *U. nylanderiana* is distinguished from *U. polyphylla* by having non-septate thalloconidia versus multi-septate. A similar distinction exists between *U. aprina* and *U. africana*. The anamorphs of Asian *U. esculenta* are shown to be similar to those of the American species *U. mammulata*, and this is further evidence of the suspected close phylogenetic relationship between these two taxa, constituting an Amphi-Beringian connection.

Thalloconidia are also reported from ten other *Umbilicaria* taxa which are probably in most cases synonymous with one or another of the 18 studied in detail. Thirty-five taxa from the genus *Umbilicaria* and 10 from the genus *Lasallia* were screened for the occurrence of thalloconidia with negative result. The absence of thalloconidia in the genus *Lasallia* supplies one more diagnostic feature separating this genus from *Umbilicaria*.

The paper extends and corrects the previous work of a number of earlier researchers (see historical introduction in the paper). Perhaps the main force of the paper is to document beyond reasonable doubt that the thalloconidia are specialized propagules of the conidial type. Many lichenologists who were not convinced by the previous studies, have now been convinced (e.g. Ewich 1985 vs. Posner 1990). The term 'thalloconidia' has also been adopted by many lichenologists, to the degree that some do not think it necessary to cite its origin (e.g. Hageman & Fahselt 1990a, 1990b).

PAPER II

In this paper the study of the thalloconidia is extended to anatomical and cytological aspects of their genesis. Five species - *Umbilicaria aprina*, *U. decussata*, *U. havaasii*, *U. polyphylla* and *U. vellea* - are examined with TEM, SEM and LM. The five species represent four types of thalloconidia [cf. I]. The objective was descriptive and comparative. One central question concerned the degree to which thalloconidiogenesis could throw light on the hypothesis put forward in [III] that thalloconidia have evolved several times in the genus *Umbilicaria*. If this hypothesis is correct, we should expect significant differences in thalloconidiogenesis from species to species.

The thalloconidia of the five species differ in size, septation and cytology, but their genesis is seen to be fairly similar with regard to the differentiation of wall-layers and pigmentation. Free vegetative hyphae in the medulla and fused hyphae in the lower cortex have three distinct wall layers; the thalloconidia emerge from the lower cortex with two wall-layers usually having shed the outermost, amorphous third wall-layer. Thalloconidium formation is accompanied by a number of changes in cytology and cell wall features. The basic determinant on size and number of cells appears to be the architectural constraints associated with the site of production and the degree of sharp differentiation between the second and third wall layers. With the exception of *U. havaasii* much of the differentiation process takes place while the conidium initials are still an integrated part of the tissues of the lower cortex or the rhizinomorphs. The two species with unicellular thalloconidia - *U. aprina* and *U. decussata* - are shown to have virtually identical conidiogenesis. Thus the data cannot be used to support an hypothesis of multiple origin of unicellular thalloconidia. Thalloconidiogenesis in *U. polyphylla* is seen to represent a slight modification of the process observed in the species with unicellular thalloconidia. Thalloconidiogenesis in *U. havaasii* and *U. vellea* differ markedly from the unicellular mode. Several more-or-less independent hyphal rows may contribute to a single conidium. This substantiates the hypothesis put forward in [III] that the multicellular thalloconidia of these species have evolved independently of the unicellular mode.

PAPER III

The paper connects 17 of the 18 thalloconidial anamorphs described in [I] with specific teleomorphs through what is termed the *thallic* connection. The teleomorphs of *Umbilicaria aprina* and *U. cinerascens* are described for the first time.

A comparison of the teleomorphs and anamorphs reveal that there is no general similarity between the propagules. However, there is a fairly strong positive correlation between non-septate thalloconidia and leiodisc or omphalodisc apothecia, and multi-septate thalloconidia and gyrodisc or actinodisc apothecia. Suggestive of a correlated evolutionary trend, this relationship between anamorphs and teleomorphs is discussed in relation to

Scholander's (1934) hypothesis concerning the phylogenetic relationship of the species with different teleomorph morphologies. A number of problems connected with such a simplistic hypothesis leads to the conclusion that the thalloconidial trait probably originated several times in the genus *Umbilicaria*. The multi-septate trait is also shown to be correlated with production of thalloconidia from rhizinomorphs where the conidia are free to expand in several directions during their development. This indicates that architectural constraints may be the most important factor regulating the number of cells per propagule. This view receives support from the study of thalloconidiogenesis reported in [II].

PAPER IV

Frequencies of anamorph and teleomorph production in 18 species of Umbilicaria were calculated from field samples and herbarium collections together constituting c. 26000 individuals.

In one group of species teleomorphs production (with sexually generated ascospores) is almost entirely suppressed and compensated by an abundant production of anamorphs (asexual thalloconidia).

A second group of species exhibits a continuum from exclusively anamorphic through ana-teleomorphic to exclusively teleomorphic individuals. In this group there are distinct biogeographic patterns in the distribution of the teleomorphic individuals. Ecological and historical factors that may be responsible for the patterns are discussed.

A third group consists of pairs of apparently closely related taxa where one taxon is richly anamorphic and rarely produces teleomorphs, while the other taxon is richly and exclusively teleomorphic. In this case we speak of a phylogenetic teleomorph-anamorph relation. The members of these taxon pairs commonly have different geographical distributions.

PAPER V

A study of 14 Norwegian and Corsican populations (6163 individuals) of *Lasallia pustulata* shows that individuals of this species pursue a mixed strategy where they start to reproduce with large, asexual, symbiotic propagules - isidia - at an early stage when the thalli are small. Sexual reproduction by ascospores first commences when the thalli have grown larger and then increases steadily in frequency with increasing thallus size. Populations growing in comparatively harsh conditions (high altitudes or dry climate) do not reproduce sexually at all but show an increased frequency of asexual reproduction in small individuals. The sexually generate propagules appear to be specialized for long-distance dispersal by wind, and the asexual propagules for close-dispersal by water.

The observations are consistent with ESS models of dispersal allocations in heterocarpic plants according to which the production of far-dispersed propagules should increase as clutch size and sib-competition in the local habitat increases. The observations are also consistent with the 'Tangled Bank'/'Elbow Room' hypothesis for the maintenance of sexuality, according to which sex by generating genetic variation, represents an escape from competition in biologically saturated environments. Thus the advantage of sex is density dependent. There is significant correlation between frequency of sex in a population and the mean size of the individuals. Due to the clumped distribution pattern in the populations increasing mean size may be interpreted as indicative of increased competition.

PAPER VI

The frequency patterns in propagative morph production described in [IV] suggest that when the option not to sex has been offered, evolutionary and ecological forces tend to favour this option to the detriment of sexual reproduction. Similar patterns exist in species having the option to reproduce asexually by symbiotic propagules such as isidia, phyllidia, soredia [V]. The question is why. What is the advantage of reproducing asexually by thalloconidia or symbiotic propagules? One possible explanation is that asexual reproduction is more effective in dispersal and colonization, and thus the asexuals outcompete the sexuals by being faster and more successful in establishment. Paper [VI] aims to test this hypothesis by observing the colonization success of asexually and sexually reproducing *Umbilicaria* species in two glacier forelands.

In relation to the intial hypothesis the results are surprising but uniform: four species reproducing sexually by ascospores are the most successful colonizers in both forelands. In particular the two species *Umbilicaria cylindrica* and *U. hyperborea* are dominant. Species reproducing asexually by thalloconidia or symbiotic propagules are slow colonizers and have only invaded the margins of the forelands. The pattern is explained by differences between the sexual and asexual species in

(1) mode of propagule release - thalloconidia are passively seceded from the lower side of the thallus and onto the substrate rock, and thus appear most effective in close dispersal; ascospores, in contrast, are actively discharged from apothecia on the upper surface of the thallus and into the turbulent air above, and thus appear to be more effective in 'long-distance dispersal'; symbiotic propagules are produced on the upper surface, but are passively seceded;

(2) dispersal vectors - thalloconidia appear to have their most effective dispersal vector in rain water running down the rock beneath the thalli; this vector is a close-dispersal, within-habvitat disperser; ascospores are carried away long distances by wind.

(3) size and number of propagules - the sexually generated ascospores are smaller and lighter than most asexual propagules, and are thus more likely to travel longer with the wind than asexual propagules; the number of ascospores produced per individual is however probably smaller than the number of thalloconidia produced by asexual species;

(4) habitat requirements - the asexual species have more narrow ecological niches than the sexual fast colonizers; the distribution of suitable habitats for the asexuals is more patchy than that for the sexual fast colonizers; this creates a difference in

(5) the population size of the source-communities - the wide ecological amplitude of the fast colonizing sexuals make the sizes of their populations outside the forelands much bigger than the populations of asexual species; thus the number of sexual propagules produced by the source community in all probability exceeds that of asexual propagules.

The study demonstrates the difficulty of isolating and studying the effects of sex as such in real biological systems. The traits of recombinational and non-recombinational reproduction are linked up with a number of other traits in complete 'strategy sets', and the effect of sex cannot be directly observed or assessed.

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