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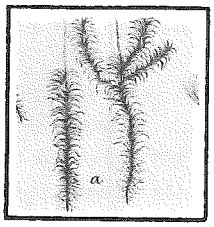

FRIENDS OF THE FARLOW

Number 13 October 1988 Robert Edgar, Editor

SPECIES

Brent D. Mishler

"Species" play a major role in systematic and evolutionary biology. Herbaria are organized using species names. Monographers and flora writers base their work on categorizing diversity at the specific level. Community ecologists use species as quanta in comparing different sites. Conservationists are especially concerned with preserving diversity at the species level. Population biologists regard speciation as a critical focus for study. Macroevolutionary theorists consider species as potential units of natural selection.

But, what are species? It is remarkable that a biological level of organization as apparently important as the species level can remain so controversial, for so long. Why is there such a chasm between theoretically-oriented biologists (who remain deeply concerned about the nature of species) and practically-oriented biologists (who proceed with their uses of species as if nothing could be more obvious)?

There are three different types of ontological questions to keep in mind when discussing species. (1) Are species real? That is, do they exist independently of the taxonomist who describes them? (2) If real, are species real in some special way that taxa at other levels (e.g., populations, genera, or phyla) are not. (3) If real, are species real in the same sense in all groups of organisms? Are the same causal factors responsible for the reality of all species such that a universal concept is possible, or do species concepts need to be group-specific?

Many different positions have been held on these fundamental questions. My own answers to them are: yes, no, and maybe, respectively. To justify these answers, some historical background is needed.

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Notions of basic "kinds" or "types" in the natural world trace back in western thought to the ancient Greeks. Like other fundamental themes in our intellectual heritage, we take the existence of such kinds for granted, so much so that it is even difficult for us to conceive of a world in which basic kinds could not be recognized in nature. Thus, it is dangerous to take the unanimous recognition of species by modern biologists as prima facie evidence that species really exist.

However, it is not just modern biologists in the western tradition that recognize basic taxonomic groups. Native tribes in several regions of the world employ folk taxonomies that tend to name the same basic taxa of birds and plants as are recognized by western taxonomists. Hosts of careful biological studies of geographical, morphological, and genetic

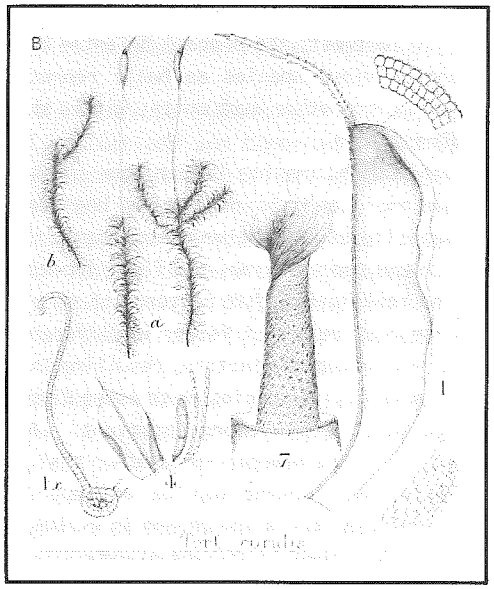

Fig. 1. Tortula ruralis

variation among organisms leave little doubt that diversity of the natural world is not continuous. At least the majority of living things are organized into discrete clusters, which are often structured hierarchically into progressively more inclusive clusters.

This observation may explain why it seems so straightforward and natural to recognize species taxa, without worrying about theoretical aspects of species concepts. Most species (at least of macroscopic organisms) recognized by pre-evolutionary taxonomists are supported (with perhaps minor adjustments) by modern evolutionary taxonomists with much more sophisticated data.

The evident existence of discontinuous groups at the traditional species level is what has allowed taxonomic practice to go forward despite disagreement on exactly how to define this level. The patterns of variation may be clear, but the processes responsible for producing the patterns remain unclear and constitute what, in my opinion, is one of the most important open questions in evolutionary biology. What processes are responsible for the production and maintenance of the units we call species?

In arriving at a satisfactory definition of species, the interplay and balance between pattern and process in our thinking are historically and logically paramount. Most thinkers have tended to emphasize either pattern or process in their definitions of species. Those who emphasize pattern are biased by their views on how to recognize taxa in general; those who emphasize process are of course biased by their views on which processes are important.

In simplified form, this dichotomy in debates over species concepts has been described as between typological or morphological concepts (pattern) versus populational or biological concepts (process). The predominant morphological species concept has been that species are basic clusters of phenotypically similar organisms. In contrast, the process-oriented biological species concept views species as basic reproductive units, isolated from other such units, within which interbreeding occurs.

This classic dichotomy has broken down in the last couple of decades, and the debate has been enlivened by the splintering of both halves into competing concepts. On the process side, the first important break was the realization that patterns of gene flow may not be the most important factor in differentiating species and that ecological factors, resulting in selection either to stabilize species or to cause divergence between them, were really more important. A second break has arisen in the general realization that the conservatism of development can be an important causal force in both stasis and change in evolution. Groups defined from these different standpoints (i.e., phenotypic similarity, gene flow, and ecology) may not correspond. Different processes may well be "most

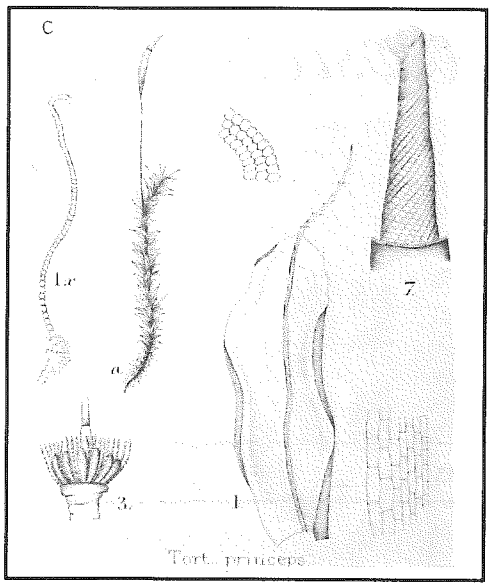

Fig. 2. Tortula princeps

important" in different cases.

On the pattern side, the argument between those who would use patterns of interbreeding to define species versus those who would use patterns of phenotypic variation has also diversified. On the one hand, defining patterns of interbreeding is fraught with problems. Do you use actual, observed interbreeding, or potential interbreeding as determined in experimental tests? How is "potential" to be defined? How are asexual organisms to be handled? Various solutions to these sorts of questions have been proposed, including those that emphasize either actual or potential interbreeding and those that deny that asexual organisms form species at all! On the other hand, due to arguments advanced by systematists who emphasize the branching aspects of phylogenetic history (i.e., cladists), the determination of phenotypically similar groups of organisms has been seen to be more problematic than was first thought. Not all morphological species concepts are the same: the classic phenetic species concept attempts to group organisms on overall similarity; a cladistic species concept would group only on the basis of "special" similarity, i.e., that based on derived, rather than ancestral, characters shared among groups.

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Recently with Robert Brandon, I proposed a "phylogenetic species concept" (PSC). It was developed to take both pattern and process considerations seriously. The key link between these two considerations derives from the realization that sound studies of evolutionary process depend on independent, rigorously established phylogenies or evolutionary histories. The discovery and naming of lineages (the products of evolutionary processes) is the primary business of sys-

tematics, and these can be recognized by patterns of derived characters shared among taxa.

Our PSC is a two-part concept, reflecting both pattern and process concerns. Its first part (the grouping or pattern component) states that species should be monophyletic in a cladisitic sense, that is, they should contain all and only descendants from an ancestral individual or population, as evidenced by the shared possession of derived characters. But since monophyletic groups are found at all levels of inclusiveness, a ranking component is needed. This second part states that species are the least inclusive monophyletic groups deemed to be worthy of recognition in a formal classification. The criteria to be used in the latter part of the definition are purposefully not specified, since it is argued that a universal specification is impossible. Ideally, these criteria should involve those processes that are involved in producing and maintaining lineages in the group of organisms in question (e.g., breeding barriers, selective constraints, or developmental canalization). In cases (such as in many cryptogamic plants!) where little is known about such processes, practical and pragmatic ranking criteria are recommended, including size of morphological gaps (i.e., number of derived characters along any particular internode of a cladogram - a tree reflecting the branching history of a group).

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The use of the phylogenetic species concept can be illustrated by its application to the Tortula ruralis species complex. This small group of mosses (Figs. 1 & 2) in the diverse genus Tortula can be clearly recognized as a monophyletic group because of several shared, derived characters, most notably a unique ultrastructural ornamentation on the basal membrane of the peristome. Species distinctions in this complex have long been controversial. In a series of comparative growth experiments, field transplant studies, and biometric studies of natural populations, I have evaluated characters previously considered to be of taxonomic importance at the species level.

These studies resulted in a list of heritable character states that vary among, but not within, six tentatively recognized species in North America (see Fig. 3). T. intermedia and T. ruraliformis as delimited by North American authors are lumped within T. ruralis, since both appear to be non-monophyletic assemblages defined by phenotypically plastic characters, thus not meeting the grouping requirement of the PSC. Other local, distinct, and arguably monophyletic variants nested within these species are judged to be too minor for formal Linnaean recognition (i.e., ranking as species under the PSC).

Two of the species remain problematic in that shared, derived characters defining them as monophyletic taxa have not yet been found. These species occur at different levels within the complex, T. princeps at the "base" of the complex, and T. ruralis in an unresolved trichotomy with T. papillosissima and T. norvegica. Such groups (which may be common if species originate by peripheral isolation) have an uncertain status, but can be recognized under the PSC using a nomenclatorial convention to clearly distinguish them from monophyletic species. We have suggested the convention of an asterisk to mark such "metaspecies".

This highly consistent cladogram demonstrates that clear patterns of cladistic relationships can be found at the species level in mosses, and that the PSC can be used to define theoretically justifiable "morphological" species taxa even when little is known of the important causal processes referred to above.

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Figures 1 and 2 are from R. Braithwaite, The British Moss Flora, 1887.

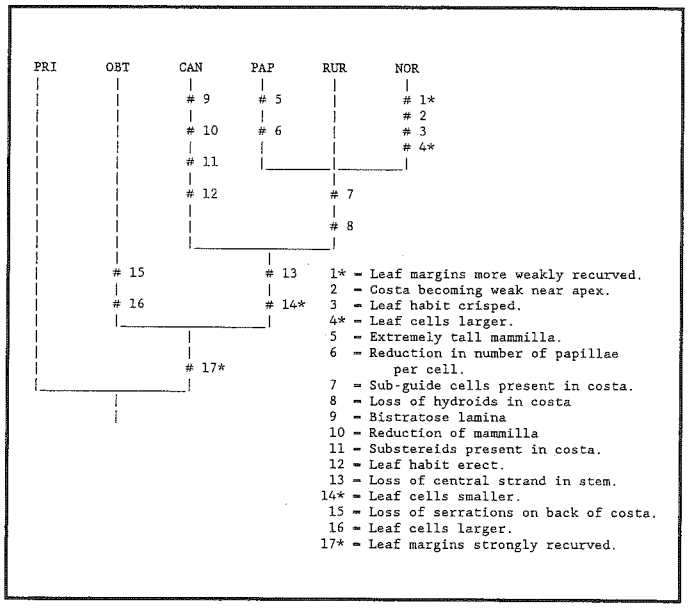

Fig . 3. A preliminary cladogram of North American species recognized by the author in the Tortula ruralis complex. Species shown, in order, are T. princeps, T. obtusissima, T. caninervis, T. papillosissima, T. ruralis, and T. norvegica. Character transformations are numbered and keyed. Homoplastic changes are indicated with an asterisk (i.e., parallelisms or losses).

Introductory references to the literature on topics covered in this article are available upon request from the author.

ABOUT THE AUTHOR

The author of this newsletter's article on "Species", Brent Mishler, has been an assistant professor of biology at Duke University since 1984. Brent worked at the Farlow on bryophytes from 1978 to 1984 as a student of Norton G. Miller. His research has focussed on a bryophyte systematics, particularly the genus Tortula, and the broad range of morphological, developmental and phylogenetic studies fundamental to it.

READING ROOM

The Farlow Library reading room's ceiling and skylight have undergone a major renovation. After extensive repairs were completed to the Farlow exterior roof last year, sights were set on repairing the water damage to the interior. For a week the library was up to its arches in scaffolding as workers plastered and painted the ceiling and repaired and cleaned the skylight glass. Illumination in the Farlow takes various forms: the contemplation of past works, the FOF table lamps installed last year and now, in addition, greater reflection and perfusion from above.

FOF FINANCES

6/30/87 Balance	$ 11,768.95
Income	
Memberships	$ 3 808.00
Book Sales	2 392.17
	$ 6 200.17
Expenses	
Purchase of Books	$ 1 511.28
Printing	672.00
Library Lamps	552.00
Binding	380.00
Miscellaneous	344.26
Copying	337.50
Postage	323.84
Travel	320.77
Services	55.00
Stationery	21.32
	$ 4 517.97
6/30/88 Balance	$ 13,451.15

Data as tabulated by Harvey Pofcher, FOF Treasurer.

FARLOW VISITORS

(April - October 1988)

H. P. Baldwin (Thorton, NH), O. Brunin (Königsfeld, FRG), W. Burk (Chapel Hill, NC), S. Campbell (Cambridge), J. L. Crane (Urbana, IL), Y. Dalte (Ottawa), D. Everleigh (New Brunswick, NJ), R. A. Fralich (Plymouth, NH), L. Hillis-Colinvaux (Columbus, OH), J. & P. Hinds (Orono), R. Hoay (Chelmsford), S. R. Huilil (Boston), C. Klotz (Arlington, MA), R. Lipman (Cambridge), R. Lowen (New York), W. Mechaber (Boston), R. T. Moore (Coleraine, Northern Ireland), M. B. Nagarkos (Pune, India), M. C. Nash (Watertown, MA), R. Price (Berkeley, CA), C. Shearer (Urbana, IL), R. Shoemaker (Ottawa), D. R. Smith (Watertown, MA), T. Smith (Fort Knox, KY), C. Sun Lee (Cambridge), M. Tishman (Genetics Institute), G. Tucker (Albany, NY), R. Tulloss (Roosevelt, NJ), and E. Urbach (Cambridge).

LIBRARY PHOTOCOPYING

Limited free photocopying is available at the Farlow Library to FOF members between now and June, 1989. No charge will be made for copies of a maximum of five titles of twenty or fewer pages each. Inquiries and orders can be made by contacting Jean Boise, Farlow Library, by phone (617-495-2369), by mail or in person.

FOF FELLOWSHIPS

Rosalind Lowen, a graduate student at City University of New York with Clark Rogerson (New York Botanical Garden) spent four days at the Farlow in May supported by an FOF Fellowship. Her work involved a study of the genus Nectriella (Ascomycetes, Hypocreaceae). She examined many slides made from type collections by von Höhnel and Weese in the early 1900's and which were preserved well enough to make observations and drawings of asci, ascospores and perithecia. Also, she elicited sufficient information from the Farlow in some cases to resolve the status of questionable species, or at least to clarify the fate of type material important to her study.

In the past few weeks a special solicitation has been made for FOF graduate fellows among students of cryptogamic botany in Central and South American institutions. Over fifty universities and other research centers were mailed packages introducing them to the Farlow and the fellowship supported by its Friends.

Howard Elson Bigelow
(1923-1987)

We are saddened by the death of Howard E. Bigelow at his home in Conway, Massachusetts, November 1987. Professor Bigelow was a patient and amiable friend to New England's mushroom fanciers and a mycologist of international repute for his studies in the Tricholomataceae (Agaricales). During thirty years at the Botany Department of the University of Massachusetts at Amherst, Professor Bigelow was mentor to the countless undergraduate and graduate students who sought his advice in designing their programs of study. Furthermore, Professor Bigelow gave stalwart support to his professional societies including the Mycological Society of America for which he served as President (1975-76) and Charter Membership in the Friends of the Farlow.

Jean Boise

Carroll William Dodge
(1895-1988)

It is with regret that we note the death in late July of Carroll William Dodge. Professor Dodge was born in Vermont in 1895 and attended Middlebury College, where mycologist E. A. Burt was then teaching. He received his Ph.D. at Washington University in St. Louis in 1918. He taught at Brown University in 1919-1921. From 1921 to 1931 he was instructor, assistant professor and curator at the Farlow. From 1931 to 1963 he was a professor at the Shaw School of Botany at Washington University and mycologist at the Missouri Botanical Garden. In retirement he was a research professor at the University of Vermont. His Farlow years marked the development of the Farlow collections as we now know them. He largely oversaw the move of the collections and the library to 22 Divinity Avenue, and he oversaw the vast expansion of the Farlow collections in the 1920's. His research was on hypogeous fungi, medical mycology and lichenology. Much of his retirement was spent continuing his work in lichenology. His work in medical mycology was begun during his time at Harvard and led to the landmark publication of his medical mycology text -- the first of its kind.

Don Pfister

Edwin Theodore Moul
(1903-1988)

Phycology and many phycologists lost a dear friend in April with the death of Edwin T. Moul of Falmouth, Massachusetts. Professor Moul hailed from York, Pennsylvania and was graduated from Franklin and Marshall College. After teaching high school for twenty years, he went on to receive a masters degree from Cornell (entomology) and a doctorate from the University of Pennsylvania (botany). His dissertation work on the bryophyte flora of central and eastern Pennsylvania was published in Farlowia in 1952. From 1948 to 1969 Professor Moul taught at Rutgers University, but spent his summers teaching in the marine algae course at the Marine Biological Laboratory in Woods Hole. After retirement from Rutgers he continued lecturing at Farleigh Dickinson University and in the summers at the University of Delaware Marine Laboratory. He was a president and founder of the Phycological Society of America and a charter member of FOF. An avid botanical collector, both above and below the shoreline, a complete naturalist, and a delightfully entertaining student of classical opera and dance, he engaged his students as a consummate mentor and a trusted friend.

Robert Edgar

FOF ANNUAL MEETING

The sixth annual meeting of the Friends of the Farlow will be held on Saturday, November 5th at the Farlow. At this meeting the FOF will host a convening of New England Mycologists, who were responsible for inspiring and organizing the scheduled roundtable. The afternoon's agenda will be:

3:00 pm A brief FOF business meeting.

3:30 pm A lecture by Dr. James Anderson of Erindale College, University of Toronto on "The Impact of Molecular Techniques on Fungal Species Concepts."

4:30 pm A roundtable discussing ''Systematics, Classical Collections and Contemporary Biology.'' The roundtable participants will include Jim Anderson (University of Toronto), John Haines (New York State Museum), Walter Litten (College of the Atlantic), Currie Marr (State University College of New York at Oneonta), Greg Mueller (Field Museum of Natural History) and Don Pfister (Harvard University).

5:30 pm Reception in the Farlow Library for Friends of the Farlow, New England mycologists and their guests hosted by the Friends of the Farlow.

Parking will be available in the Andover Lot behind the Farlow (enter from Oxford Street opposite Everett Street).

FIRST CLASS

20 Divinity Avenue • Cambridge • Massachusetts 02138 • U.S.A.

FRIENDS of the FARLOW

FARLOW REFERENCE LIBRARY OF CRYPTOGAMIC BOTANY • HARVARD UNIVERSITY

M U G S

Friends of the Farlow coffee mugs are scheduled to arrive at the Farlow in late October. We plan to distribute them at the FOF annual meeting on Saturday, November 5th, to members who are able to attend and thus save ourselves unnecessary expenses in mailing. For those unable to attend the annual meeting, mugs will be posted during the week of November 7th.

FARLOW GRADUATE STUDENT

The Farlow has a new resident graduate student. Sam Hammer has joined the crew to engage in systematic studies on the lichen genus Cladonia, primarily on its species from western North America, under the direction of Don Pfister. Sam did undergraduate work at Grinnell College in Iowa and later recieved his master's degree from Harry Thiers at San Francisco State University. The Friends welcomes him on board.

Friends of the Farlow is an international group of amateur and professional botanists concerned with supporting the programs and resources of the Farlow Reference Library and Herbarium of Cryptogamic Botany of Harvard University. Membership categories are: Associate member, $5-$15; Full member, $25; Sponsor, $50-$1000; Benefactor, over $1000. (To join please make your check payable to the Friends of the Farlow and send to the address below.) Members receive a discount on Farlow publications and services, participate in book sales, annual meetings and other events, and receive a special welcome at the Farlow. This newsletter is published twice a year, in April and October. For more information please contact the Farlow Reference Library, 20 Divinity Avenue, Cambridge MA 02138, USA (tel. 617-495-2369).