Species, Demes, and the Omega Taxonomy: Gilmour and *The New Systematics*

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Abstract. The word "deme" was coined by the botanists J.S.L. Gilmour and J.W. Gregor in 1939, following the pattern of J.S. Huxley's "cline". Its purpose was not only to rationalize the plethora of terms describing chromosomal and genetic variation, but also to reduce hostility between traditional taxonomists and researchers on evolution, who sometimes scorned each other's understanding of species. A multi-layered system of compound terms based on deme was published by Gilmour and J. Heslop-Harrison in 1954 but not widely used. Deme was adopted with a modified meaning by zoologists leading the evolutionary synthesis – Huxley, Simpson, Wright, and Mayr. Connections are shown between Gilmour's ideas around defining the deme, his role in founding the Systematics Association, and his chapter "Taxonomy and Philosophy" in the book *The New Systematics*. This historical episode raises questions about the role of carefully-defined words in scientific practice.

Key words: cline, definition, deme, evolutionary synthesis, experimental taxonomy, J. Heslop-Harrison, J.S. Huxley, J.S.L. Gilmour, nominalism, systematics, Systematics Association, taxonomy

Introduction

"When I use a word," Humpty Dumpty said, in rather a scornful tone, "it means just what I choose it to mean – neither more nor less."

"The question is," said Alice, "whether you *can* make words mean so many different things."

"The question is," said Humpty Dumpty, "which is to be master – that's all." Lewis Carroll, *Through the Looking Glass*, 1872.

In science, words obey their master's bidding, at least, this is what students are led to believe; scientific terms have precise definitions, and the resulting clarity of language is supposed to be a distinguishing feature of science

(Keller and Lloyd 1992). The English botanist John Gilmour held the ideal of clear language in high regard all his life, but putting this ideal into practice turned out to be a surprisingly frustrating experience for him. The tale of his ideals and disappointments may perhaps hold some lessons about the function of definitions in science.

The simplified history

In 1939, Gilmour, with J. W. Gregor, coined the word "deme" plus three compounds built on it - "gamodeme", topodeme", and "ecodeme". "Deme" was to denote any set of similar individuals, while "gamodeme" meant "a more or less isolated local intrabreeding community". Individuals from the same locality were to be called a "topodeme", while "ecodeme" were those in a given habitat. Several zoologists, overlooking the intention of the proposal, used "deme" where they were supposed to use "gamodeme". In 1954 Gilmour appealed to his fellow botanists to support a revised elaboration of his terminology, but his effort to recapture his word was not a success. "Deme" in the sense of "local interbreeding population" took hold and spread in the evolutionary literature, while its compounds were rarely used. In the 1950s, Gilmour, "depressed by what he interpreted as the misunderstanding of the purpose of the terminology" by zoologists, was "much more disappointed ... with the failure of ... botanists" to adopt his proposed words (Walters 1989, pp. 39-40). In 1969, Max Walters gave prominence to the Gilmourean deme and its compounds in a botany textbook, but when the time came for a second edition, Walters had to admit defeat, for a survey of the literature showed that the "incorrect" usage had become the norm (Briggs and Walters 1969, 1984; Briggs and Block 1981).

Misunderstandings

Of course, to those who were content with the modified "deme", its history looked rather different. Ernst Mayr said in 1978,

The term was rather vaguely defined at the occasion of its original proposal, essentially as a new term for population with all the heterogeneity and ambiguity of that word. Several zoologists, for instance Simpson (1953) and Wright (1955), gave the term a more specific meaning by restricting it to the "local population", the representatives of a local gene pool (= the community of potentially interbreeding individuals at a given locality). In spite of the acknowledged impossibility of delimiting a given

local population against others, the term deme is now quite widely used in this sense, at least by zoologists and geneticists (Mayr 1978, p. 84).

As a matter of fact the American zoologists George Gaylord Simpson and Sewall Wright were not the ones responsible for shifting the meaning of "deme", although they certainly did much to entrench the word, in its modified sense, in the evolutionary literature. The honor, or blame, of altering its use clearly belongs to the British zoologist Julian Huxley, who stated in his 1942 book *Evolution: The Modern Synthesis*:

Gilmour and Gregor (1939) have recently proposed the term *deme* for "any specified assemblage of taxonomically closely related individuals". This should be useful to replace such cumbersome phrases as "local intrabreeding populations". The ultimate natural unit in sexually reproducing species is then the deme, and analysis is needed to show to what extent demes are isolated from each other ... (Huxley 1942, p. 203).

Probably Huxley, with whom Gilmour was on friendly terms, had not meant to change his definition but had simply misunderstood Gilmour's intent.

Botanists confront a different world than zoologists do, because the simple laws of life followed by all birds, mammals, and many other animals – reproduce sexually, grow up to resemble your parents – are commonly scorned by plants. In the 1930s the young science of genetics was revealing that many plants familiar in hedgerow or garden do not actually interbreed, even though they flower and set seed; each individual plant reproduces itself asexually. All the hawkweed in a valley makes a topodeme but is not a gamodeme. Also, with plants the local environment can have dramatic effects on appearance. Some of the green things growing low and flat on sand dunes would have grown tall if germinated elsewhere. As if that were not confusing enough, it can be shown, by transplanting individuals and cultivating their offspring, that such differences of form are in some cases entirely genetic, in other cases entirely environmental, in still others due to both kinds of cause. Gregor had been investigating exactly this phenomenon in the sea plantain, Plantago maritima, since 1930 (Gregor 1930, 1939). Zoologists concentrating on guinea pigs or fruit flies faced no such complications.

It is clear that the botanists Gilmour and Gregor, when they wrote "any specified assemblage", had in mind a set of specimens assembled on a herbarium table or in someone's imagination, not organisms actually "assembled" in nature, for they mentioned as exemplars of one ecodeme dune-adapted plants from Devon and Scotland. Yet a zoologist could very easily miss this key point, and would imagine instead that an assemblage consisted of individuals not only living cheek-by-jowl but naturally interbreeding. Gilmour and Gregor's opening sentences did not do much to prevent such a misunderstanding. They wrote,

In the course of work on the experimental delimitation of botanical groups, the need has arisen for a term which can be applied to any specified assemblage of taxonomically closely related individuals. Such phrases as 'local intrabreeding populations' or 'populations occupying a specific ecological habitat' are cumbersome, and it is felt that a more concise terminology would be useful and, further, would focus attention on certain concepts undoubtedly of great importance in the study of intragroup variation. We propose the term deme (from the Greek $\delta \hat{\eta} \mu o \zeta$) for this purpose, with appropriate prefixes to denote particular kinds of demes. For example, in a taxonomic group consisting of a number of potentially interfertile individuals all the individuals do not have an equal chance of interbreeding in nature. The tendency is for individuals in close proximity to interbreed more frequently with each other than with individuals at a distance, and thus small, more or less isolated intrabreeding colonies are set up. The distinctive features so commonly exhibited by local communities, for example of sea plantain, provide evidence of this. These 'breeding communities' are likely to become increasingly important in the intensive study of evolutionary problems ...(Gilmour and Gregor 1939, p. 333).

The Greek "demos" and the Latin root of "population" both denote a group of people bound together both by region and by ties of blood. Thus we may allow that Huxley could carelessly have missed the point of the ending of the sentence: "These 'breeding communities' are likely to become increasingly important in the intensive study of evolutionary problems and we propose to name them *gamodemes*".

Gilmour would later look back and explain, without naming Huxley, that to use "deme" instead of the full "gamodeme"

cuts across the whole idea underlying the deme terminology, as it is essential to keep the suffix -deme completely 'neutral', otherwise the connotation of "breeding population" becomes injected into all the compound terms, thus destroying the intended use of many of them (Gilmour 1960, p. 103).

The problem became clear, however, only with the benefit of hindsight. In 1939 Gilmour and Gregor had not made this explicit, and their short article did not explicitly forbid the use of "deme" with no modifying prefix (Walters 1989, p. 37).

After the hiatus caused by the Second World War, a second zoologist followed Huxley's reading. George Stuart Carter was acquainted with Gilmour as well as Huxley, for all three were on the founding council of the new Association for the Study of Systematics in relation to General Biology (Winsor 1995). Along with other advocates of the neoDarwinian

"modern synthesis", Carter saw local populations of interbreeding individuals as entities crucial for Darwinian selection. In his 1951 textbook *Animal Evolution*, Carter declared,

Without doubt this organisation into communal populations [ones which "live and breed together" (p. 119)] is a general and fundamental fact of natural history. For these populations the name *deme* has been proposed and is convenient (Carter 1951, p. 121).

Like Huxley, Carter credited Gilmour and Gregor with coining the word; unlike Huxley, Carter used the word prominently throughout his book. Two years later, G. G. Simpson adopted "deme" in *The Major Features of Evolution*, without bothering to cite a source for it. Nor did Wright name a source for "deme" when he adopted it for what he had been calling "groups", a step he took at the Cold Spring Harbor Symposium of 1955 (which Mayr attended) (Wright 1955).² Yet Simpson and Wright certainly learned the meaning of "deme" from Carter's textbook. In his own 1953 text Simpson had named, in his list of outstanding recent surveys, Carter's *Animal Evolution* along with Huxley's *Evolution: the Modern Synthesis*, and he singled out Carter's as "remarkably fine" (Simpson 1953, p. x). Wright too quoted Carter, including Carter's citation of Gilmour and Gregor, in 1956 (p. 16).

In 1954 Gilmour, with a botanical co-author from a younger generation, John Heslop-Harrison, published an explanation and elaboration of the deme terminology. In contrast to the 1939 proposal, which had covered less than a page, this one filled 14 pages; where the pre-war paper defined 3 compounds (gamodeme, topodeme, ecodeme), the post-war revival defined 12 "first order derivatives" (phenodeme, genodeme, plastodeme, clinodeme, chronodeme, and so on) plus 24 "second order derivatives" (phenoecodeme, plastogamodeme, topoautodeme, monoendodeme and so on). The only third order derivative offered was "coenogamo-agamodeme", but the authors noted, apparently with all seriousness, that more terms of the sort "could, of course, be constructed if need was felt for them" (Gilmour and Heslop-Harrison 1954, p. 160). In this paper the word "assemblage" was replaced with "group" "so as to indicate even more unequivocally that no idea of 'population' enters into the definition of the root" (Gilmour and Heslop-Harrison 1954, p. 152n).

In a footnote to this 1954 article, the zoologists' misuse was mentioned, with the great tact characteristic of Gilmour.

Since the original publication, Huxley (1942) and Carter (1951) have used the word 'deme' in a sense corresponding *more or less* with "gamodeme" as defined originally and in this paper, but, for the scheme here outlined, it is basic that "deme" should connote nothing beyond, simply, a group of individuals of a specified taxon (emphasis added; Gilmour and Heslop-Harrison 1954, p. 152n).

Gilmour and Heslop-Harrison state (pp. 147–148) that their paper, submitted in November 1953, was based on meetings held in 1952 and 1953. These dates tempt us to believe that Carter's 1951 text had roused Gilmour to take action. Yet Gilmour and Heslop-Harrison take pains, in a long note on the article's first page, to situate their proposal in a longer history.

The proposals put forward in this paper have arisen out of discussions between botanists and zoologists at meetings of the Taxonomic Principles Committee of the Systematic Association extending, with interruptions, over a period of nearly 16 years.... About two years ago some of the botanists connected with that Committee felt that further progress in discussions of the terminology of the units of micro-evolutionary change might be best attained if a group of botanists could reach agreement on certain definite proposals which could then be considered by their fellow botanists and by their zoological colleagues ... We are authorised to say that the following botanists who took part in the discussions are in general agreement to test the scheme now advanced: - Dr J [sic - misprint for H]. G. Baker (Botany Department, Leeds); Mr B.L. Burtt (Royal Botanic Garden, Edinburgh); Dr. J.W. Gregor (Scottish Plant Breeding Station, Corstorphine, Edinburgh); Dr Y. Heslop-Harrison (Department of Botany, University College, London); Dr W.B. Turrill (Royal Botanic Gardens, Kew); Professor D.H. Valentine (Botany Department, Durham); Dr S.M. Walters (The Botany School, Cambridge); Dr E.R. Warburg (Botany Department Oxford) (Gilmour and Heslop-Harrison 1954, pp. 147–148).

While this historical footnote was evidently designed to add credibility to the revised proposal, it has the effect, for us who know the proposal's fate, of making its failure more surprising. The puzzle is cleared up when we look back through those "nearly 16 years" of background. There we discover that the story of the term "deme" is inextricably bound up in the upheavals affecting the concept and definition of the term "species" that were at the center of the modern evolutionary synthesis.

Gilmour's botanical background

When John Scott Lennox Gilmour was studying botany in Clare College, Cambridge, from 1925 to 1930, his teachers and fellow students were aflame with a spirit of reform, as newer disciplines including ecology and genetics supplemented and challenged morphological systematics (Godwin 1985, pp. 149–150). The work of Göte Turesson in particular was creating enormous excitement (Dean 1979, 1980; Stebbins 1980; Hagen 1982, 1984). Collecting plants from diverse habitats in Sweden, he grew them and propagated them

in standardized environments, a technique that allowed him to distinguish between genetic and environmental causes of variability. Turesson called his work "genecology" to suggest that it combined genetics and ecology; it was also known as "experimental taxonomy". In the spring of 1930, Gilmour, having earned his bachelor's degree, stayed on as curator of the Cambridge University Herbarium and began a correspondence with Turesson. (Gilmour Papers, Turesson to Gilmour, 16 June 1930). In August of that year the International Botanical Congress took place in Cambridge, and the twenty-three-year-old Gilmour, with the cordial spirit that endeared him to so many friends, invited Turesson to stay with him and offered to meet him at the train (Gilmour Papers, Gilmour to Turesson, 11 August 1930).

Dr. James Wyllie Gregor of the Scottish Plant Breeding Station, five years older than Gilmour, also attended the 1930 congress (Foister 1981, pp. 21–22; Gregor 1930). Shortly afterwards, Gilmour travelled to Edinburgh to visit him, and in Gregor's next letter in October 1930, he congratulated Gilmour on having obtained a plot of garden to undertake genecological work. Rambling on with suggestions and comments, Gregor said, "I am afraid I am becoming like Turesson who talked botany when sipping his Crawford's [whiskey]" (Gilmour Papers, Gregor to Gilmour, 28 August, 12 September, and 7 October 1930). One of the recurrent and lively topics of debate at the 1930 congress was what terminology should be used for subsets of species. The eminent ecologist Arthur G. Tansley declared that no committee could solve the problem,

partly because of the extreme complexity and mutability of vegetation and still more because of the widely different and probably irreconcilable points of view and lines of approach of different workers. He was convinced that they should leave the matter to the survival of the fittest concepts and terms (Brooks and Chipp 1931, p. 83).

How the fittest terms were created and selected was surely one of the subjects Gilmour, Gregor, and Turesson talked about over their drinks.

The following year, 1931, fortune dealt Gilmour a high card. The Assistant to the Director of the Royal Botanic Gardens in Kew, Thomas Ford Chipp, a man in his prime, died suddenly, and Gilmour was hired in his place. As one of Gilmour's contemporaries explains,

Such appointments of promising young men to responsible positions were not so uncommon then as later, because the dreadful slaughter of the First World War had so tragically deprived Britain of those who would rightfully have taken such positions (Stearn 1987, pp. 453–454).

Moving to Kew (a suburb of London), Gilmour became a colleague of William Bertram Turrill, a highly productive herbarium taxonomist and plant

geographer who had also been inspired by Turesson's experiments (Hubbard 1971; Turrill 1929). Failing to persuade his superiors to allow space and manpower for genetic investigations, Turrill teamed up with a dedicated amateur near Bath, Eric Marsden-Jones, who had enough land for an experimental garden (Marsden-Jones and Turrill 1928a, 1930; Turrill 1960).³ This made Turrill one of a tiny minority of botanists, one of the few who understood from first-hand experience both traditional and modern methods. Most taxonomists only knew about genetics, ecology, and cytology from their reading, if the jargon of these new disciplines did not bar outsiders entirely. For their part, the devotees of these intense new specialties consulted taxonomists or their literature when they needed a name for the plants they were manipulating, sometimes coming away with a low opinion of old-style botany.

Conflict around the species

Throughout the 1920s and 1930s botanists were looking across disciplinary boundaries at their fellow botanists with increasing distrust and even hostility. Jealousies flared at the point where expertise overlapped, the species. That it was the job of the traditional taxonomist to christen new species and identify specimens was confirmed by an international congress in 1910 that promulgated rules for making names of new species, but the species itself was left undefined. Hugo DeVries, whose theory of mutation attracted much attention between 1901 and 1920s, declared that the species of taxonomists were a fiction, that the only real, objective entities in nature were his "elementary species" of identical forms that bred true. Likewise J. P. Lotsy in 1916 declared traditional concepts arbitrary and meaningless. "He who ventures to write on the origin of species, ought to define what a species is", he mocked. Lotsy dubbed the Linnaean species the "Linneon", and honored one of the pioneers of plant transplant experiments, Alexis Jordan, by calling sections of the Linnaean species "Jordanons". Lotsy reserved the word "species" for his own true-breeding unit (Dean 1980, pp. 63-74). It was as if a physicist should try to shift the word "atom" down to the proton and then on to the quark. Even though Lotsy's theory of evolution soon lost its credibility as knowledge of genetics progressed, his new words were commonly used for another decade or two. There was a fundamental tension between geneticists, who followed the presence, absence, and combinations of striking characters, versus herbarium taxonomists, who looked for suites of ordinary characters that stayed constant.

Another direction of attack on the taxonomists' authority over the species came from the Dutch botanist Benedictus Hubertus Danser, who summarized

the increasing level of knowledge of degrees of sterility in cross-breeding, which undermined the longstanding assumption (already attacked by Darwin in Chapter 8 of the *Origin of Species*) that there was an automatic correlation between natural barriers to crossing and observable differences of form. Danser insisted that there were different kinds of populations in nature, too complex to be adequately represented by the term "species". He invented the term "comparium" for all individuals which could produce offspring, however infertile those hybrids might be, "commiscuum" for all individuals whose offspring were fertile, and "convivium" for those which normally interbreed and look the same (Hagen 1984, pp. 161–163).

Turesson too claimed that his experiments and theories exposed the weakness of the traditional notion of species. His discovery of "ecotypes" (genetically adapted races) showed that the ill-defined species of taxonomists took no account of what he called the real "ecospecies" in nature, nor of the "coenospecies" of all possible breeding combinations (Turesson 1922a, b). He made it clear that in future the unscientific approach of herbarium taxonomists would have to be superseded by work like his. In 1930 his countryman Gustaf Einar du Rietz rejected these claims in an exhaustive and influential review titled "The Fundamental Units of Biological Taxonomy". He declared that Turesson's terms were "dispensable" synonyms of existing words like "subspecies" and that Turesson's claim "to have replaced the old 'descriptive taxonomy' with a new 'experimental taxonomy' must therefore be firmly disputed" (Du Rietz 1930, pp. 358, 361, 389). Turesson published a brief but vigorous retort (Müntzing et al. 1931).

Gregor's research enabled him to come to Turesson's defense. He had supplemented analysis by the transplant method of the grasses *Phleum pratense* and *P. alpinum* with chromosome counts, done by the cytologist F. W. Sansome, who was a doctoral student at the time (Dean 1980, p. 145; Gregor 1931, p. 207n). They found a wonderfully complex range of forms, for the taxonomists' species *P. pratense* consisted of two races, one with 14 chromosomes and another with 42 chromosomes, while *P. alpinum* included a 14-chromosome race and a 28-chromosome race. There were sterility barriers within the old named species as well as between them; also, fertile hybrids could be produced which seemed not to occur naturally. Gregor argued that Turesson's concepts of a great coenospecies consisting of various ecospecies and ecotypes described reality better than could orthodox taxonomy based on morphology, which "cannot do much more than supply to its smaller units an appellation of little or no evolutionary significance" (Gregor 1931, p. 204). Gregor entitled his article "The Experimental Delimitation of Species".

To those whose profession consisted of the delimitation of species, such an announcement from a young man at a northern agricultural station bordered

on the insolent. Alfred James Wilmott, Deputy Keeper at the British Museum, wrote sneeringly in 1932,

Of the paper one may say that, although it is a pity that some taxonomists have an insufficient knowledge of modern genetics and cytology, it is at least equally to be regretted that some geneticists have no knowledge of taxonomy. The author's statement ... will seem absurd to the really capable taxonomist.... The author needs to think in terms of the realities behind words. The Scotch universities generally supply a philosophic basis, which seems to be lacking in this theoretical paper (Wilmott 1932a, pp. 49–50).

Furthermore, Wilmott later added, Gregor "appears to think that he can attack taxonomists without getting a reply and I have been thanked for doing a necessary deed, and even told that it was too restrained" (Wilmott 1932b, p. 155). Gilmour, who was just then collaborating with Wilmott, (Wilmott and Gilmour 1934), must have known about this quarrel.

Because everyone personally acquainted with Gilmour testify to his kind-hearted nature, we may assume that he felt real distress to see his colleagues so at odds. Congruent with temperament was his deeply held moral sense. Soon after moving to Kew he had experienced a personal epiphany that left him convinced that an atheistic humanism that replaced religion with rationality could improve the wellbeing of mankind (Gilmour, personal communication; Walters 1987 and personal communication).

Yet Gilmour, unlike Gregor, was not generating new botanical data. His administrative duties at Kew were occupying his full attention, and his plans to do experimental botany faded away, nor would he ever manage to become a productive researcher (Stearn 1989). Yet he continued to care about the issues, and he found other ways to contribute to the debate. He helped organize a symposium on "The Species Problem in Phanerogams [flowering plants]" which was held at the Linnean Society in London on the 4th of April, 1935 (Botany Archives, Gilmour to Wilmott, 10 January 1935). There he opened the discussion with the statement,

The species problem, in its broadest aspect, is that of devising a system of terminology that will adequately express the constantly developing concepts of modern taxonomy (Gilmour 1935, p. 103).

For those who believed then, as well as those who now believe, that the broadest aspect of the species problem is the complexity of the object under investigation, which is a natural phenomenon in space and time that behaves more like a fluid than a solid, Gilmour's claim that the key issue was terminology would have been, and still is, startling. Evidently he was taking for granted that biologists all shared a common understanding of what

nature's complexities were. In that case, any disagreements could only be mere confusions of language. He continued,

...In all progressive sciences it is found necessary to create a new terminology as the increasing complexity of the observed phenomena is revealed, and this must inevitably be done in the case of the new intensive taxonomy. Several attempts on these lines (notably Du Rietz's comprehensive scheme ...) have already been made, but there is no agreement among botanists as to how far old terms should be used or new ones coined (Gilmour 1935, p. 103).

Later in the day, Wilmott pointed out that the word "species" was used for many different concepts, while another participant insisted that the word's meaning had been so vitiated it should be abandoned.

Turrill's contribution to the discussion was deeply pragmatic.

The term species has been used for such groups or general populations of plants as are united by common morphological characteristics, are separated from other groups by constant morphological characteristics, which inbreed in nature and are isolated from other such groups. In using this or a similar definition one soon realizes how few are the trustworthy data available regarding even our common British Plants for such criteria as inbreeding and isolation. It also becomes evident that the above criteria sometimes break down and that the limitation of species is then a matter of scientific convenience. Thus there can be no *a priori* objection to considering a given group for one purpose as a species, for another purpose as a subspecies or a variety of a larger group which is then considered as the species, so long as the facts and reasons are clearly stated (p. 104).

The kind of experience that contributed to Turrill's firmly flexible attitude was what he and Marsden-Jones had been discovering about two familiar British species: the bladder campion, *Silene vulgaris*, tall and common on roadsides, and *S. maritima*, the sea campion, low-growing, with larger flowers, found on beaches. These turned out to be perfectly interfertile in the experimental garden, yet the hybrid was hardly ever found in nature. Far from finding this situation a problem, Turrill and Marsden-Jones understood that such unruly facts were to be expected according to Darwin's theory, and that it was a purely arbitrary decision whether to call them two species or two varieties within one species (Turrill 1946, pp. 41–43; Marsden-Jones and Turrill 1957; Walters 1993).

Turrill's omega taxonomy

For more than ten years Turrill had already been urging upon his fellow botanists an integrated approach. "More actual field-observations should be made and collecting done by the trained taxonomist. An experimental garden and laboratory should be attached to every herbarium" (Turrill 1925, p. 365). Now, at the Linnean Society in 1935, he wrapped his plea in new rhetorical dress.

... the time has come when the student of floras should attempt to investigate species by much more complete analyses of a wider range of characters than is now the rule. There is thus distinguished an alpha taxonomy and an omega taxonomy, the latter being an ideal which will probably never be completely realized.... The aim of the alpha taxonomist must be to complete the preliminary and mainly morphological survey of plantlife....

Those who, having been trained to an appreciation of modern discoveries in ecology, cytology, genetics, etcetera, are trying to widen the basis of taxonomy, have undertaken a long, slow and perhaps thankless task. They have, however, a vision of a revivified taxonomy in which an important place is found for all observational and experimental data ... Some of the criteria which those who aim at an omega taxonomy are already using ... [are] ecological, genetical, cytological, and biometrical (pp. 104–105).⁴

Turrill repeated his message (without the Greek alphabet) at the International Botanical Congress which met that autumn in Amsterdam. A great deal of work of the traditional kind remains to be done "by the older methods", he declared, "the usefulness of which will probably never be exhausted". However, the sciences of genetics and experimental ecology have much to offer to taxonomy, and so does taxonomy to them. "The importance of studying living material is often forgotten by herbarium workers, just as the importance of herbarium material is often ignored by experimentalists", Turrill warned (1936, p. 563). For practical and financial reasons, breeding work is most often done on domestic species, but the taxonomist needs the experimentalist's help with wild forms that are problematical. For nightmare cases like the British brambles, probably "the usual taxonomic recording is really impracticable" Turrill says, so that

a totally different scheme from that of species and varieties will have to be evolved before stability of expression is reached. Before such can be elaborated, the taxonomist requires data concerning genetical stability, hybridisation, heterozygosity and so on, which can only be obtained by genetical experiment (Turrill 1936, p. 565).

If those with the opportunity would use modern methods to study some group of related species "with a taxonomic ideal", they would be contributing to "the unity of botanical science", according to Turrill (p. 566).

Gilmour and Turrill were not just mouthing pious hopes; they were willing to labor for the reconciliation of botanists. At some point in the summer of 1936 they met with Cyril Darlington, a cytologist from the John Innes Horticultural Institution in Merton (a London suburb). Darlington was a leading figure in the study of chromosome morphology, a lively new field which was uncovering surprises daily on how plants can make new species overnight by doubling their chromosome count. They agreed that further private meetings, with a few more botanists invited, should be held.

Gilmour turns to philosophy

That same summer, 1936, the editor of *Nature*, Richard A. Gregory, encouraged Gilmour to develop his ideas for publication, and Gilmour also proposed to read a paper at the upcoming meeting of the British Association for the Advancement of Science.⁵ He sent in an abstract in which he promised to argue that the old and new styles of taxonomy "should be much more clearly separated than at present if they are not to interfere with each other to their mutual disadvantage....[There should be] full recognition of the different concepts and terminology involved in the two taxonomies ..." (Gilmour 1936, p. 417). He speaks of "two streams" of taxonomy, the morphological, which he also calls "alpha", and the ecological, cytological, and genetic, which he calls "omega". In this he seems to have somewhat misunderstood Turrill, for whom "omega" was a distant ideal, but Gilmour also referred to "omega" progress", which is to be expected when all botanists are working together. His short abstract gave no hint that he intended to base his argument on first principles.

Gilmour sent a draft of his paper to the distinguished morphologist Agnes Arber, and she wrote him encouragingly, "I think you are really helping things forward by insisting on the separation of the two types of taxonomy – (at least at our present level of ignorance), and making people face up to it" (Gilmour Papers, 4 August 1936). Her parenthetical qualification, however, signalled a greater difference between her views and Gilmour's than either of them chose to explore, for she, like Turrill with his "omega", was expressing belief in progress toward a unified understanding.

In the autumn of 1936, British scientists attending the BAAS meeting assembled in the seaside resort town of Blackpool. Molly Gilmour, newly married, remembered ever afterwards the holiday atmosphere, including Jim Gregor's delight in the amusement park (Molly Gilmour, personal communi-

cation 1 February 1986). Gilmour's twenty-minute talk "Whither taxonomy?" was scheduled for September 11, in a session of miscellaneous botanical topics. The typescript of his talk ends thus:

The standpoints of morphological taxonomy and of evolutionary taxonomy respectively are so different that it is essential that they should employ distinct and separate classifications. Morphological taxonomy may be said to be static and to deal with the results of evolution, while evolutionary taxonomy is dynamic and deals with the methods of evolution. Any attempt to use the terminology of one for the purpose of the other must lead to confusion. The morphological classification should be retained for the purpose for which it was devised, while a new evolutionary classification should gradually be constructed step by step with the development of our knowledge of the mechanism of evolutionary processes (Gilmour 1976, p. 9; Gilmour 1989, p. 103).

The implication was that combatants like Wilmott and Gregor, or Turesson and DuRietz, should cease their quarrels and agree to work in parallel. Traditional and modern methods could coexist in peace if each worker would keep to his own domain.

The value of peace, and the hope that reason could resolve conflict, was on everyone's mind because of Germany's rearmament and withdrawal from the League of Nations; Hitler invaded the Rhineland in March of 1936.

Unlike his abstract, the typescript of Gilmour's Blackpool talk makes no reference to "two streams" nor to "alpha" and "omega". What it does contain are strong claims about the ontological foundations of classification. He states that

all classification is primarily utilitarian. It is a tool by the aid of which the human mind can deal effectively with the almost infinite variety of the universe. It is not something inherent in the universe, but is, as it were, a conceptual order imposed on it by man for his own purposes (Gilmour 1976, p. 3; Gilmour 1989, p. 98).

Consequently

there cannot be one ideal and perfect classification of living things..... Biologists who urge the possibility of an ideal and all-embracing classification often claim that it should be based on "the natural relations" of plants and animals

but they need to realize, he says, that "natural" and "artificial" are "purely relative terms" expressing that members of a group have more or less characteristics in common (Gilmour 1976, pp. 4–5; Gilmour 1989, pp. 99–100). Although we recognize such claims as philosophical, in 1936 he did not

allude to any philosopher nor use the word "philosophy". His few citations are to botanical papers.⁶

An argument which asks the reader to begin by considering first principles naturally leads us to assume that the author arrived at his conclusions in the same way he is asking his audience to do, the logical sequence corresponding at least roughly to chronology. In fact, however, the ordered steps of an argument have no necessary relation to biographical events. In this case circumstantial evidence suggests that only after Gilmour had decided that the terminology of the old and new taxonomies should be kept separate, did he then look to philosophy to lend a rational justification to his view.

In his undergraduate studies, Gilmour had concentrated in biology, and was much admired as a junior member of the Botany School (Godwin 1985, pp. 149–150; Gilmour Papers, Seward to Gilmour 24 June 1929, 9 April 1930, 11 August and 20 November 1931). There is no record of his enrollment in any philosophy course, nor is his name found in the records of the Moral Sciences Club. In the *Nature* paper, written after Blackpool, Gilmour states that the principles of classification are discussed in "the standard works on logical and scientific method", of which he lists thirteen in a footnote.⁷ That ill-digested list includes several books not particularly pertinent to Gilmour's claims. Of course Gilmour may have read some philosophy before 1936, but all the evidence suggests that his serious reading of the literature of philosophy was only just beginning when he went to Blackpool.

Pre-history of the Systematics Association

After the Blackpool meeting, Turrill and Gilmour followed up their consultation with Darlington by organizing a series of two or three small meetings at Kew in November of 1936, involving about a dozen botanists: some taxonomists from Kew, some cytologists from Merton, Gilmour's Cambridge botany teacher Harry Godwin (who was editor of the journal *The New Phytologist*), and Turrill's collaborator Marsden-Jones. At least one of these meetings ended with tea in the Gilmours' home. The announced topic of the meetings was "The Impact of Cytology, Ecology, Genetics and Physiology on Taxonomy", and Gilmour's notes show that the issue of developing an acceptable terminology was the main item on the agenda. The assembled men and women agreed that further meetings would be useful, they planned to send out a questionnaire to other botanists, and they contemplated expanding their meetings to include zoologists. To this end, it was decided to approach Julian Huxley (Systematics Association Archives).

It may seem odd for the botanists to have turned to Huxley, the recently appointed head of the London Zoo, since none of his research had much

to do with taxonomy, but Huxley was known to be keenly interested in the dynamics of species. He had co-authored a popular introduction to biology in 1922, *The Science of Life*, which gave prominence to Darwinian evolution, and at the Blackpool meeting had delivered a presidential address dealing with the species problem (Baker 1976; Huxley et al. 1931; Huxley 1936). In connection with a survey he was writing, to be called *Evolution: The Modern Synthesis*, Huxley was reading widely and pressing experts for useful examples. In January 1937 he was approached and agreed to help expand the meetings Turrill and Gilmour had begun.

Gilmour develops his 1937 paper

Huxley also agreed to read the draft of the paper Gilmour was working on for *Nature*. In February he wrote to Gilmour,

- 1. The Meeting of the Zoological Sub-Committee has been fixed for March 4th at 4.30 in Hogben's department at the London School of Economics, Houghton Street, Aldwych, W. C. 2. I think it desirable that one or preferably both of you and Turrill should be present, and have written to ask him to come. Do come too if you can. Hogben, myself, Ford, a zoologist from the Museum, Worthington, and possibly Diver, will be present. I am delighted that we are making progress.
- [E.B. Ford, E.B. Worthington, and Cyril Diver were ecologists rather than taxonomists, and Lancelot Hogben was working on the mathematics of human population genetics; all would contribute articles to *The New Systematics* the following year. The zoologist from the British Museum was relatively junior, the ornithologist James D. Macdonald (Gilmour Papers, Turrill and Gilmour to Hill, 6 March 1937)].
 - 2. With reference to your MS., I was much interested. The only major criticism I would like to make is on page 9, where I think you ought to amplify the first paragraph, bringing out the ways in which the two schemes [presumably morphological versus experimental taxonomy] would differ. Personally I do not think they would differ at all at any rate in essentials as regards large groups, but would differ radically in regard to small groups since modern genetics and cytology has largely destroyed the meaning of phylogenetic homology in closely related forms.

[By "large groups" and "small groups" Huxley must have meant higher taxonomic categories (like order) and lower categories (like species). Plant species that can arise more than once, through hybridism or polyploidy, do undermine definitions of homology strictly based on ancestry.]

Page 12: I disagree with you when you say that species is equally artificial with genus. One may not be able to draw a line, but very often there are assemblages which you can give a biological meaning to as species, whereas genus is a matter of pure convenience always (Gilmour Papers 23 February 1937).

"Pure convenience" was of course hyperbole, because no one thought species should be assembled into genera according to the first letters of their names, or their average weight, or whether they flew or swam. Huxley doubtless meant that whether a hundred closely similar species are lumped into one genus, or split into five genera of twenty species each, involves nothing but convenience. Gilmour extended this same "pure convenience" to all levels of classification, including species.

Huxley's objection pointed to an aspect of the species concept central to the modern evolutionary synthesis. Its leaders insisted that species, for all their subtleties, really exist. Historians, following the lead of Ernst Mayr, have focussed on the shift from typological to populational definitions of species, with little attention to the nominalist (conventionalist) view; an exception is found in T. H. Morgan's biography (Allen 1978). In the *Nature* article, without admitting that the species category required special treatment, Gilmour conceded only this much:

Owing to the method of reproduction and evolution of living things, involving the inheritance of parental characteristics, and to the preeminent influence that these factors exert on the attributes of plants and animals, the possibility exists of constructing a series of classifications which are more natural than any others, namely, those based on inherited characters (Gilmour 1937, p. 1041).

Nevertheless, Gilmour insisted that "more natural" meant only that more statements could be made about all the members of a group. In this he was parting company with his colleague Turrill, who in 1925 had cited with approval John Stuart Mill's notion of "natural kinds".

Kinds differ one from another in an indefinite number, 'an unknown multitude,' of properties and characters. We select a set of characters to discriminate each Kind from all other Kinds. Our selection of these characters is arbitrary and matter of convenience, but separate Kinds really exist (Turrill 1925, p. 362).

Turrill was as keenly aware of the dynamics of plant form as any botanist of his day, so his feeling that "there does seem to be some qualitative basis for many species" (Turrill 1925, p. 361) did not bode well for Gilmour. Nor did the appearance in 1937 of Theodosius Dobzhansky's influential book

Genetics and the Origin of Species, which concluded with a chapter titled "Species as Natural Units".

Drafting his manuscript for *Nature*, Gilmour tried to strengthen his position by adding a classical problem of formal logic he had found in the textbooks.⁸

The categories, genus, species, etc., are of the same nature as such categories as herd or heap, individual characters taking the place of individual animals or stones. A well-known trick in logic known as the "sorites" illustrates this point. The question is put "Does one stone form a heap?" If the respondent answer "No", it is asked, "Do two stones form a heap?" and so on.

His meaning was that if two goats cannot be called a herd but some larger number can, the concept "herd" must be admitted to have arbitrary limits, and likewise since naturalists could not specify what number of characters two plants must have in common to be members of the same species, that category too cannot be defined exactly. Turrill, "overwhelmed with work" and hurriedly reacting to Gilmour's draft, told him "I dislike this analogy" (Gilmour Papers, 24 February 1937). Arber's reaction was,

I cannot myself believe that you are right in thinking that "genus and species" have no more defin[i]te content than the concepts of "herd" and "crowd"; indeed I can hardly believe that you really think so yourself! But no doubt it is a good thing to wake poeple [sic] up by a little paradox[.] You will make them consider the grounds of their beliefs! (Gilmour Papers, 10 March 1937).

Gilmour kept the example, but made explicit that the goats or stones were analogous to characters rather than to individual organisms.

A book on the new systematics

Meanwhile it had become clear that the idea of discussing the future of taxonomy had tapped into a great reservoir of discontent and eagerness for reform. Consumers of taxonomy, that is, people like ecologists who needed organisms identified, were exasperated by inadequacies in the taxonomic literature. Junior taxonomists were frustrated by the conservatism of their elders, including those who ran the Linnean Society of London as a staid and expensive club. In April 1937 Huxley and Diver paid calls on seven or eight staff members of the British Museum, all of whom were "most friendly". That same month, Darlington suggested to Turrill that Huxley should be asked to edit a volume. In May a group of fifteen botanists and zoologists

met in the rooms of the Linnean Society, calling itself the "Committee on Systematics in Relation to General Biology", with Huxley as Chairman and Gilmour as Botanical Secretary. As the number of people involved increased, so did the list of things the group thought it might accomplish, such as encouraging improvements in British floral and faunal handbooks and pressing for more jobs for taxonomists. Subcommittees began work, with the idea of demonstrating, at the first open meeting in June, that achievement and not just talk was possible. The projected edited volume was described in June 1937 as "a book under some such title as 'The New Systematics' or 'Modern Taxonomy', to be written by a group of, say, 20 biologists on various aspects of the relationship between taxonomy and other branches of biology ...". By July the book idea was well along, Gilmour and Darlington drafting lists of contributors and letters for Huxley to send out (Systematics Association Archives).

Gilmour versus Turrill on philosophy

Gilmour sent the final draft of his *Nature* article to Huxley, asking him to forward it to the editor if he thought its meaning clear. Huxley informed him,

I altered the draft of the leader a little: e.g., after careful consideration, I deleted the terms "alpha" and "omega", as I thought they were not only rather odd but really misleading, since they are not usually used in the sense of earlier and later, or less perfect and more perfect (Gilmour Correspondence, 3 July 1937).

Published with the modest title "A Taxonomic Problem", Gilmour's 1937 paper in *Nature* explicitly appealed, unlike his Blackpool talk, to the authority of philosophy; he asserted that well-known principles of logic and scientific method could clear up the current disagreements between taxonomy on the one hand and genetics, cytology, and ecology on the other.

Any given collection of objects can, of course, be classified in a great number of different ways, depending on the particular attributes chosen....Further, the choice of particular attributes depends on the *purpose* in view in making the classification...logically any grouping of plants and animals should be considered a taxonomic process....It is usually stated in logic that a system of classification is the more natural the more propositions there are that can be made regarding its constituent classes.... Thus a natural classification is one founded on attributes which have a number of other attributes correlated with them ... a natural classification can be used for a great variety of purposes, while an artificial one

serves only the limited purpose for which it was constructed (Gilmour 1937, p. 1040).

The philosophy books Gilmour cited did indeed contain all these ideas, but most of them also treated biological taxonomy as a perfect example of what Mill meant by natural kinds. This Gilmour alluded to only indirectly, mentioning that some attributes have "a number of other attributes correlated with them", and he omitted the consequence philosophers drew, which was that classifications are of two fundamentally different sorts, rather than, as Gilmour asserted, that classifications differ only in degree.

For example, a traditional taxonomist may divide a genus into a certain number of species on morphological characters, the result being a good natural grouping. A cytologist may then investigate the same genus and find that, say, sterility barriers in some cases cut right across the taxonomist's groups....[The sterility classification] should be retained as a distinct classification for the purpose of establishing the relationship between sterility and other attributes....This principle of 'multiple classification' is fundamental....Additional classifications necessary for special investigations ...[should have categories with] different terminology from that of traditional taxonomy. A good example of such a system is Danser's classification into commiscuum, comparium and convivium, which is based purely on interfertility criteria (Gilmour 1937, p. 1042).

In other words, where morphology would tell the traditional taxonomist to call the English campions two species of one genus, Turesson would say there are two ecotypes of one coenospecies and Danser would say there are two convivia within one commiscuum. The taxonomist should not be threatened by this, Gilmour implied, for all such groupings are legitimate and may coexist.

The call to meeting that the Committee on Systematics in Relation to General Biology had published in *Nature* was being favorably received. On June 25, 1937, approximately seventy men and women, representing botany and zoology about equally, gathered in a lecture-room at the Linnean Society where they endorsed the terms of reference of the new society and ratified the membership of the self-appointed council. Thus began what would become, after the war, the Systematics Association.

Turrill, deeply involved in the developing association and keenly interested in its goals, in the fall of 1937 wrote down his own vision of the future, published in 1938 as "The Expansion of Taxonomy". Although he refers respectfully to Gilmour, thanking him "for valuable constructive criticism", Turrill directly challenges Gilmour's assumption that biologists must bow to the authority of philosophy.

Fortunately for his peace of mind, the biologist rarely worries about either logic or philosophy. It may, indeed, be argued that the biologist has a scientific right to use any philosophy he likes, as he likes, temporarily or permanently....[L]ogic and philosophy are not themselves absolute; they are continually being modified and the biologist can point to many imperfections in any given system of philosophy (pp. 345–346).

The image he had proposed in 1935 he repeats more fully, of the older, mostly morphological, taxonomy developing over time by making use of information drawn from other specialties. He says that

while accepting the older invaluable taxonomy, based on structure, and conveniently designated "alpha", it is possible to glimpse a fardistant taxonomy, and one in which [quoting himself] "place is found for all observational and experimental data relating ...to the constitution, subdivision, origin and behaviour of species and other taxonomic groups". Ideals can, it may be said, never be completely realized. They have, however, the great value of acting as permanent stimulants, and if we have some, even vague, ideal of an "omega" taxonomy we may progress a little way down the Greek alphabet. Some of us please ourselves by thinking we are now groping in a "beta" taxonomy (pp. 346-347)....Before attempting to see the dim outlines of a full general classification, a far distant, if not visionary and unreachable goal of the most optimistic taxonomist, it will be well to attend to the possible contributions which other branches of biology, and especially those of considerable recent development, may be expected to make, or even have already made, to taxonomy (Turrill 1938, p. 350).

Turrill does more than discuss what these other branches might contribute, however. He begins by noting that they must in the first place begin by depending upon alpha taxonomy to identify their subject organisms. He notes with satisfaction that Turesson lists his ecotypes "under taxonomic ('Linnean') species". Thus Turrill introduces a sense of progress through time; taxonomy is present before other biology can begin, it persists and improves, moving "towards far off omega perfection of the classification of all (biological) knowledge" (p. 370). Like a soft ameoba engulfing a nugget of food, Turrill's taxonomy can incorporate whatever is of value in Danser's "very hypothetical" scheme and in Turesson's deservedly-famous research.

Turrill and Gilmour, colleagues at Kew, were also meeting frequently in London on business of the new Association for the Study of Systematics. Gilmour was convenor of the Taxonomic Principles Committee in which Turrill was active. Gilmour had explained to the embryonic council on 31 May 1937 that one task of his committee would be to consider

the impact of the recent data of genetics, cytology, ecolo[g]y etc. on the principles and methods of 'traditional' taxonomy. Should the basis of traditional taxonomy be expanded to include these data, or should subsidiary terminologies be employed to express them.

Gilmour's committee postponed consideration of that task, however, tackling first the question of the relationship of phylogeny to taxonomy. In that context any differences between Turrill's view and Gilmour's appeared trivial in comparison with their common stand against the zoologists, who saw the distinction between "natural" and "phylogenetic" as an attack on the scientific justification of taxonomy (Winsor 1995).

Huxley's "cline"

Also serving on Gilmour's Taxonomic Principles Committee was Julian Huxley. Gilmour in turn was a member of the committee of which Huxley was convenor, the Committee on Comparative Systematics. Its mandate, which was Huxley's idea, was to develop ways for taxonomists specializing in different taxa, such as ornithologists, cryptogamic botanists, or carcinologists, to compare phenomena such as patterns of variability. Faithfully attending its meetings (11 October 1937, 18 March 1938, 29 June 1938), Gilmour had a fine opportunity to watch the dynamic Huxley at work. Although the members decided at the outset that any thought of publication should be deferred until they had had a chance to do some work, the convenor asked them at the next meeting to look over a paper he had written.

Dr. Huxley's article on 'Phenogrades': an auxiliary method of taxonomic description was then considered, and it was agreed that this matter should be put before biologists for their consideration. Dr. Huxley agreed to re-draft the article in view of a number of suggestions and criticisms received, and to submit this for publication in his own name. Dr. [John] Ramsbottom [mycologist, Keeper of Botany, BM(NH)] suggested the substitution of "phenocline" for "phenograde["], and this was accepted unanimously (Committee 1937–1938, pp. 12–13).

At the next meeting, "Dr. Huxley suggested the substitution of the term 'cline' for 'phenocline,' and this was approved" (Committee 1937–1938, p. 16). Not long thereafter Huxley's "Clines: an Auxiliary Taxonomic Principle" appeared in the July 30 issue of *Nature*, with due thanks to Ramsbottom and the other members of his Committee on Comparative Systematics (Huxley 1938a).

Huxley's idea was to call attention to a phenomenon common to many species of plants and animals, that features can vary gradually as one collects specimens across its geographic range. There may be a gradient running east to west as red feathers become orange and then yellow, and average size may shift considerably from north to south, yet if specimens reaching the museum came from only a few localities, which is often the case, the taxonomist does not see the intermediates and, if he thinks in terms of subspecies, he is tempted to name them. By proposing a label for the phenomenon, Huxley hoped to reduce the number of meaningless taxonomic names and increase the study of variation. "Prefixes can be used to denote clines of different types, for example, ecocline, genocline (gradient in genes), geocline (geographical cline), chronocline (paleontological trend), etc" (Huxley 1938a, p. 219). He followed up his *Nature* proposal with a long article packed with examples (Huxley 1938b), and soon the newly-coined "cline" took firm hold, doing exactly the job he had intended.

Meanwhile Gilmour's Taxonomic Principles Committee was finding itself hopelessly divided on the epistemological issues it had begun with, and had turned its attention to a more practical job. Gilmour reported to the council in May, 1938,

it was finally decided that, before progress could be made, each member should put down in detail a concrete example of intraspecific variation which presented difficulties of classification and terminology. It was further decided that the committee should draw up a list of the categories below the rank of species actually in use in the different groups of animals and plants.

Gilmour was unable to attend the next meeting of his committee, on July 1, 1938, but Turrill took careful minutes. One member, A. J. Wilmott, the British Museum botanist who had scolded Gregor, agreed to standardize information about category names on $4" \times 6"$ cards. The committee members agreed that their aim was to "come to an agreement for our own general usage, with the hope that such usage, if found to be satisfactory, would become general". Turrill's minutes record several comments that Gilmour must have been interested to read.

Huxley referred to his paper on clines which is to appear in "Nature". The committee as such did not wish to be committed. It was desirable to find some term that was non-committal except that it should mean "differing from the type in any measurable or definable manner" ... It was generally agreed (with some at least temporary objection) that it was best to use words of Greek or Latin origin.... Huxley considered there were probably three main categories of terms which might be considered useful: (1) loose terms; (2) technical terms to be applied to individuals and to individual variation; (3) technical terms to be applied to groups. Uvarov showed that variation is different in different groups and Huxley

asked "Must a term always mean the same thing?" It was agreed that one might try using a general term (subspecies) and prefixes (geo-, eco-, etc.)....

Turrill pointed out that on this definition [subspecies being forms so closely allied "that it is undesirable to separate them as species"] subspecies have to be defined and accepted very largely as a matter of scientific convenience. Huxley said that the complexity of nature is too great for any simple scheme and one must do the practical thing and separate species and subspecies on a practical basis.

'Taxonomy and philosophy' in The New Systematics

In May, 1938, Huxley had told the council of the association that "the contributions for the book 'The New Systematics' were coming in well and that it was hoped that all would be in before the end of the summer" (Systematics Association Archives, Council Minutes, 31 May 1938). But at summer's end, Gilmour's promised chapter was still unfinished. In September his notes and draft travelled with him to Rio de Janiero, where he was an official delegate to a botanical conference. Hitler's aggressions in Austria and Czechoslovakia so clearly threatened wider war that Molly Gilmour recalls fearing for her husband's safe return. Aboard ship, John Gilmour noted in his diary, "Everyones reaction to the situation (my own included) convinces me more and more that a scientific approach to human affairs is the only hope of peace in the future. Everyone deals in out of date and emotional slogans, when a scientific weighing of evidence & facts is essential" (Gilmour 1938). He carried his unfinished paper on the airplane to Trinidad, where he spent two weeks enjoying the hospitality of the Imperial College of Tropical Agriculture. There Gilmour burned the midnight oil and on November 2, 1938, completed his draft of "Taxonomy and Philosophy". He was back at Kew on December 2 (Kew Review 1939, pp. 479–480; Gilmour 1938).

The citations to Gilmour's *New Systematics* contribution show that he had been reading up on the latest philosophy. Whereas in *Nature* he had cited nothing more recent than a 1930 textbook, now the only philosophy textbook mentioned is one published in 1937, and he makes reference to several items published in 1938.

Certainly what was most impressive about Gilmour's *New Systematics* article was its appeal to formal philosophy.

In this chapter the view is put forward that no satisfactory solution to these problems is possible without first examining the fundamental principles which underlie the process of classification, and, further, that these principles cannot be adequately formulated without basing them on some epistemological theory of how scientists obtain their knowledge of the external world. Recent developments in experimental physics have induced physicists to examine the philosophical foundations of their work. [In June of 1937 readers of *Nature* had been treated to a special supplement containing a heated debate on metaphysics by physicists.] It is suggested that biologists, and especially taxonomists, must follow their [physicists'] lead if the theoretical problems of taxonomy are to find solutions which will stand the test of time. In recent years scientific epistemology, or 'the philosophy of science', has received a great deal of attention from philosophers, especially ... 'logical positivists' (Gilmour 1940, p. 462).

Yet the essence of his argument, which had been sketched out in 1936 with no reference to logical positivism, was unchanged.¹⁰

Scientific epistemology requires us to understand, Gilmour patiently explained, that "the object which we call a chair consists partly of a number of experienced sense-data such as colours, shapes, and other qualities, and partly of the concept chair which reason has constructed to 'clip' these data together". Sense-data, he said, are "given once and for all, and cannot be altered", whereas ideas are like clips to join bits of data together, and they "can be created and abolished at will" (Gilmour 1940, p. 464). These ideas, including the "clip" metaphor, were simply a summary of Dingle (1938), the physicist whose conventionalism started the debate in *Nature* in mid 1937; Dingle was trying to cope with an electron being "a wave on Mondays and a particle on Tuesdays" (p. 153).

Gilmour concedes that phylogeny, so far as it is known, can be the basis of a very useful taxonomy, but he still considers this to be one of many subsidiary classifications used for a special purpose, with no special status. A natural classification he defines as

that grouping which endeavours to utilize *all* the attributes of the individuals under consideration, and is hence useful for a very wide range of purposes. This, in practice, is the procedure followed in what is sometimes called 'orthodox' taxonomy, and it would seem best to confine the use of the ordinary taxonomic categories of species, genus, family etcetera, to a natural classification of this type. In so far as it is theoretically possible to envisage a classification on these lines, which does in fact embody all the attributes of the individuals being classified, it can be said that one final and ideal classification is a goal to be aimed at. In practice, however, this aim would never be attained, owing both to the limitations of our knowledge and to the differences of opinion between taxonomists (p. 472).¹¹

Although seemingly so close to Turrill, Gilmour does not use the term "omega", and the qualifying "insofar as it is theoretically possible" seems to leave open the question whether the unattainable final classification is really a coherent idea. He concludes by mentioning Du Rietz and Turesson and urging that the terminology of orthodox taxonomy should be kept separate from the data of genetics, cytology, and ecology.

Gilmour's Taxonomic Principles Committee, frustrated by its attempts at philosophy, took very seriously the challenge of terminology for parts of species. Late in 1938 or early in 1939 they sent to Gilmour long memoranda packed with examples of how experts working on different organisms used words like "variety", "subspecies", "race", and "form", along with definitions of these and scores of other terms like "biotype", "clone", "ecophene", and "linneon". In return he sent them mimeographed copies of each other's memos, creating files some of them would return to after the war.

Gregor and Gilmour coin "deme"

While Gilmour was reading philosophy and chairing committees, his friend Gregor was facing decisions as to how to describe the plants in his experimental plots outside Edinburgh. In spite of the stimulus he had felt from Turesson's results and polemic, Gregor found that "ecotype" was a hard word to use if one cared about precision, because it included the claim that a particular form was genetically determined, which was a matter of fact that only a season of careful breeding experiments would reveal. When the very dynamics of species was the subject being investigated, all the nomenclatures around the species level were too burdened with interpretation to describe day-to-day experimental taxonomy. Exactly how Gilmour collaborated with Gregor to solve this problem - by letter, telephone, or meetings - is not recorded, but their brief proposal "Demes: a Suggested New Terminology" appeared in the August 19, 1939, number of Nature. They distanced themselves from those like Lotsy, Turesson, and Danser whose new terms were coined in a spirit of criticism of taxonomists. This new scheme would in no way interfere with orthodox naming.

Whether the deme concept may entail a system of nomenclature for naming individual demes is a matter for future experience; but we would emphasize that any such system should be kept quite separate, both in form and in function from systems of taxonomic nomenclature.

Encouraged no doubt by the example of Huxley's "cline", they suggested that a fresh, short word would not only prove convenient but would focus

attention on phenomena of species dynamics. Their timing, however, was unlucky; only two weeks later, Britain declared war on Germany.

The volume *The New Systematics* finally appeared in 1940 (though its contributors, writing in 1938, had all optimistically cited each other's chapters expecting a 1939 publication date). Huxley explained in his introduction the usefulness of "cline", and Gilmour managed to add a mention of "deme" to his own chapter. Cline was quickly taken up by several zoologists and botanists, including Gregor (1939), but none picked up deme.

During the years of war Gilmour, seconded to the Ministry of Fuel and Power, continued to live in Kew, but Turrill supervised the removal of an important part of the herbarium to Oxford for safekeeping and stayed there for the duration. He and Gilmour found time, however, to respond to a leading Dutch botanist who had written.

For the moment the attitude of the taxonomist towards the progress of genetic investigation should be that of an interested spectator, not more. If he engages himself in hybridization experiments, he should know that he leaves the domain of taxonomy (Bremekamp 1939, p. 403).

In their reply, called "The Aim and Scope of Taxonomy", Gilmour accepts Turrill's view that "the word natural has become so confused in meaning" that taxonomy, the biological classification of maximum usefulness because based on all possible attributes, should be called "general" rather than "natural" (Gilmour and Turrill 1941, p. 218). Turrill accommodates to Gilmour's view by omitting talk of unreachable ideals and foregoing the terms alpha and omega. Classifications based on limited features, including ecological, genetic, and phylogenetic, they call "special classifications for restricted purposes". When ordinary taxonomists use only morphological characters, it may seem that they are doing a "special" classification, but Turrill and Gilmour suggest instead that

such classifications have to be considered as stages towards a general classification which will become possible when more information is available.... The special classifications A-D etc., exist in their own right for special purposes, and, by utilizing all the separate types of attribute on which they are based, the general or taxonomic classification is constructed. It can be seen, then, that a classification based on a limited number of attributes may either be a special classification or it may be a stage towards a general classification, necessarily restricted owing to lack of information (Gilmour and Turrill 1941, p. 219).

Turrill and Gilmour confidently designated this article "Contributions to the Technique and Philosophy of Plant Taxonomy and Geography, No. 1", but in fact it was their only collaboration.

After Germany's surrender and Japan's loss of Okinawa, Gregor wrote a letter to Gilmour, expressing hope that after the war the Association for the Study of Systematics in Relation to General Biology would do something to get terms of experimental taxonomy under control (Gilmour Correspondence, 7 July 1945). The Association was slow to resume its activities, however, and explored the idea of merging with the Linnean Society. Gilmour himself was swamped with pressing duties; in 1946 he left Kew to become director of the gardens of the Royal Horticultural Society at Wisley. This was a move from the world's pre-eminent center of scientific botany to a provincial gardening club; he resigned as botanical secretary of the Systematics Association in the same year and turned his diplomatic skills to committees concerned with rules for naming horticultural varieties. To the relief of the friends concerned about Gilmour's career, in 1951 Cambridge University invited him to direct its historic Botanic Garden (Stearn 1987; Walters 1987).

Gilmour had, however, been keeping up his interest in experimental taxonomy, its connections with orthodox taxonomy, and the relevance of philosophy to curing the tensions that persisted between those communities. Tensions certainly still ran high. For example, in a review of a catalogue of chromosome counts for thousands of European species of plants, Darlington noted that arranging them under existing Linnaean names was nonsense, for it "conceals the essential value of the chromosome counts, which depends on the fact that they destroy the classical notion of species ... [That notion] is now going to pieces ... " (Darlington 1951, pp. 662–663). In August of 1951 Gilmour spoke at the British Association for the Advancement of Science meeting in Edinburgh, where he repeated the views he had outlined in 1936.

The post-war revival

In 1952 the Taxonomic Principle Committee was reborn, convened by Peter Colley Sylvester-Bradley, a paleontologist from the University of Sheffield. The committee picked up where it had left off, circulating for discussion a long list of categories applied to parts of species. Carter, whose 1951 text-book featured the word "deme" in the sense of "gamodeme", was on the committee, but Gilmour looked forward to setting that confusion straight; in fact he had not himself read Carter's text (Gilmour Correspondence, Gilmour to Heslop-Harrison, 24 August 1953) and had no way of knowing that leading American zoologists would soon follow Carter's example. More significant than Carter's usage was the persisting confusion of terminology among botanists. Attempts at uniformity or even cataloguing the proliferation of terms only illustrated the problem (Camp and Gilly 1943). "Red" Camp, as president of the American Society of Plant Taxonomists, at the close of 1949

had declaimed against the subjectivity of classical taxonomists' identification of species in contrast to the enlighted view of Dobzhansky (1937) and Mayr (1942) (Camp 1951). Gilmour's memoranda to the committee, circulated before the March 11 meeting, suggested that because of "the modern background of evolutionary change" the term "species" could not be rigorously defined, so its use should be limited to "what might be called 'general purpose' classification, i.e. when there is no wish, or insufficient knowledge, to classify the group concerned into units of evolutionary significance". Citing Camp's address, Gilmour urged that people doing genetics, cytology, or experimental taxonomy should use a separate set of terms to represent the complexity they were discovering – "perhaps a non-committal word such as 'deme' with suitable prefixes".

Jack and Yolande Heslop-Harrison

Gilmour, now in his mid-40s, won the support of two promising younger botanists, John ("Jack") Heslop-Harrison of University College, London, and Max Walters of the Botany School, Cambridge, both men in their early 30s. During cordial weekend visits, Gilmour enthusiastically described his ideas on philosophy and taxonomy, in thoughtful conversations without dogmatism, while Molly Gilmour developed close friendships with their wives. (Walters 1981, p. xii) After the Taxonomic Principles Committee meetings, Gilmour, with the agreement of Walters and Heslop-Harrison, wrote a letter to selected botanists explaining that

the gulf between the botanists and zoologists [on the Taxonomic Principles Committee] is, at the moment, so deep that we shall not get very much further until the botanists have reached some fairly well agreed conclusions which they can present to the zoologists. With this in mind (and also with the aim of setting our own house in order, irrespective of the zoologists!) we feel that it would be very useful to have an informal discussion between five or six botanists who have thought a good deal about these problems and had experience both of experimental work and of orthodox taxonomy (Gilmour Correspondence, Gilmour to Gregor, 18 November 1952).

The job of getting agreement among the botanists would not be easy, though. Herbert George Baker (then at Leeds, later of Berkeley, California) was reading Gilmour's memoranda in light of his own transplant experiments and did not like Gilmour's insistence that the word "species" should only be used when issues of evolutionary significance are laid aside. Baker had already written an article envisioning the progressive union of experimental

results with classical taxonomy, leading "towards the 'omega' taxonomy which Turrill has visualized as the taxonomists' Holy Grail" (Baker 1952, p. 66). Baker wrote to Gilmour explaining his view that

If we relegate 'species-containing classifications' to the position of mere historical relics from pre-evolutionary days, we are denying the possibility of refining our 'alpha' classification, of removing its out-of-date features and making it representative of the present state of our beliefs. For all that 'species' were thought of in the days when Special Creation was accepted by most biologists, they do seem (in most sexual cases) to have a solidity and worth that are not easily wished away. The early workers had hit on something fairly natural even though they hadn't understood the mechanisms involved. If I may draw a parallel: We still recognise atoms in chemistry even though nuclear physics has shown them not to be of the billiard-ball kind, has shown that they are somewhat tenuous, that they sometimes lose their separate existences (as in the solid state) and that they may be transmuted (cf. evolution!) ... (Gilmour Correspondence, Baker to Gilmour, 24 November 1952).

The difficulty of defining the word "species" did not worry Baker; he approved of the recent statement of the American botanist Herbert L. Mason, "I am not searching for definitions: I am interpreting usage, oftentimes over and above, or in spite of definition, for it is usage and the history of usage that ultimately molds the meanings of our words and terms" (Mason 1950, p. 193).

Responding to Baker, Gilmour warned him, "I am gradually coming to the conclusion that the former ["an 'omega' classification, which would incorporate all data"] is neither possible nor desirable ...", to which Baker replied, "I shall be very interested to hear why the omega classification may not be desirable after all. I feel a little bit like a Roman Catholic priest who has heard the existence of God doubted by the Pope!" (Gilmour Correspondence, 26 November and 4 December 1952).

The informal discussion to set the botanists' own house in order, arranged by Gilmour and Heslop-Harrison, took place in London, on the 8th of January, 1953, in the Ecology Room in the Department of Botany of University College. Heslop-Harrison had produced a memorandum to structure the discussion, in which he described the distinction between old-fashioned Linnaean nomenclature and research on variation as "the two 'taxonomies'". Yolande Heslop-Harrison, a botanist herself, took careful notes. As a result of the meeting, Heslop-Harrison and Gilmour drafted a paper setting forth an elaboration of the deme terminology, which they circulated to the other botanists for suggestions, and then submitted to the rest of the Taxonomic Principles Committee.

Not surprisingly, the most negative response was a memorandum from Carter, who insisted that there had been nothing wrong with his own use of "deme", and that "it is always unwise to attempt a redefinition of a term already in use". If an elaborate terminology on a neutral root is needed, he suggested the Greek for "assembly", *-plethe*. In response to Gilmour's earlier memo urging that the word "species" be reserved for old-fashioned taxonomists, Carter declared,

On grounds of convenience that seems to me an impossible situation. I hold strongly that one important function of nomenclature is to assist the general progress of biology, and that in its ability to do so its convenience plays almost as large a part as its logical accuracy. Apart from this I think it most unlikely that zoologists would follow Mr. Gilmour's suggestion if it were made.

Yet when the committee gathered to discuss the deme paper on October 28, 1953, the zoologists were much less contentious than Gilmour had feared. Afterwards he asked Heslop-Harrison "Did they really form an acquiescodeme or was it a flabbergastodeme?" (Gilmour Correspondence, Gilmour to Heslop-Harrison, 30 October 1953). Still, the committee merely encouraged the botanists to publish, without recommending that the Systematics Association formally endorse the paper. In November Heslop-Harrison sent the "Deme Terminology and the Units of Micro-Evolutionary Change" to *Genetica*, where it was printed in 1954.

Factors in the failure

After so much careful thought and consultation – memoranda circulated and feedback compiled, meetings of rump groups and committees, drafts and revisions – why did this rationally-constructed set of words fail in the market-place of biologists' use? Walters, in continual contact and friendship with Gilmour in Cambridge, did his utmost to pump life into the system, even requiring his students to employ the terminology in their dissertations. He finally concluded (Walters, personal communication) that contrary to what scientists say, they do not actually want a "logically satisfactory set of terms" (Walters 1989, p. 40).

What seemed logical to Gilmour was keeping the observational data of science distinct from the ideas which clip those data together into meaningful concepts. In a fundamental sense, then, it was never the case that Gilmour's "deme" was independent of any theory. The theory behind "deme" was that words in science can be divorced from all theory. This notion seems as disingenuous as the grocery brand "No Name", which of course

had to be registered as a trade mark. Linguists and psychologists as well as psychologists no longer think that words acquire meaning by stipulation.

It was certainly Gilmour's experience that keeping "deme" limited to an assemblage with no attributes was not so easy. In the summer of 1953 Gregor published a study of local strains of ryegrass, ending his discussion with an endorsement of the article just then being worked on by Heslop-Harrison and Gilmour. Calling for an improved terminology Gregor wrote:

It would be helpful if all the terms used were to have a common suffix and preferably a suffix with some biological meaning on its own account, e.g. a term such as *deme* (Gilmour and Gregor 1939) signifying a population. If this were done then informative prefixes denoting the various kinds of population could be added . . . (Gregor and Watson 1954, pp. 299–300).

Notwithstanding his participation in the discussion in University College London the previous January, to say nothing of his 1939 joint authorship with Gilmour, Gregor still wanted "deme" to be "a suffix with some biological meaning on its own account". Gilmour remonstrated in a letter, with his neverfailing courtesy,

There is just one small point about demes which I hope you won't mind my mentioning. On p. 299 you say that *deme* signifies "a population". You may remember that this was a point of controversy with the zoologists ... the suffix deme alone should be a purely neutral term with no spatial connotation of population, so as to be quite free to add prefixes to signify any kind of deme that we desire. The zoologists have been using deme in the sense of gamodeme, i.e. an intrabreeding population, and we want to try to persuade them to get back to our original neutral definition of deme in our *Nature* letter. It is not perhaps a very vital point, but I thought I would mention it in the hope that you will agree, and will do battle on our side on behalf of the original definition in the future (Gilmour Correspondence, 21 September 1954).

But Gilmour may as well have tried to sweep back the tide. Yolande Heslop-Harrison's minutes show that at the January 8 meeting Gilmour several times stated the definition of "deme" as "any assemblage of taxonomically related individuals", illustrating the idea with the ecodeme, which he defined as "any assemblage of taxonomically related individuals growing in the same ecological habitat". Later in the meeting he repeated the idea "that ecodeme might be useful as a neutral term meaning, for example 'all the plants *Bellis perennis* growing in sand dunes all over the world.' In the experimental sense, however, for plants growing in one place only, the word should be ecogamodeme". Although no one in the room contradicted him, everyone else continued to speak of demes as populations, and Jack Heslop-Harrison even suggested that

the word "population" should be in all the definitions. In a book he finished that summer, Heslop-Harrison defined "deme" as "population" (1953, pp. 105, 123). It is true that by the time their joint paper went to press two years later, Gilmour had brought him to see that "no idea of 'population' enters into the root, 'deme' " (Gilmour and Heslop-Harrison 1954, p. 152 fn. 1). Yet it is telling that what was to Gilmour, in spite of his gentle style, really a vital point, was so far from obvious to his joint authors and fellow botanists. Gilmour's ideals of linguistic correctness contradicted his colleagues' interest in naming natural rather than hypothetical entities.

Other details of the January 8 meeting and subsequent exchanges suggest that the botanists did not agree with Gilmour in another important respect. He had been insisting, like a parent sending ill-tempered children to separate rooms, that classical taxonomy be kept strictly apart from evolutionary research; the resulting need for separate languages was what the deme was designed to fill. But early in the meeting Turrill said that "he wished to avoid the divergence between orthodox and experimental taxonomy: his whole aim was towards a *synthetic* taxonomy". So it was time for the papal confession Baker had jokingly feared to hear.

Gilmour pointed out the divergence of his point of view with that of Turrill's: Gilmour believed that the omega taxonomy was not a possible aim: it was a chimera. He said the desire of an omega taxonomy arose because the human mind loves the absolute: we should ultimately have to have *separate* classifications for *separate* purposes. The omega taxonomy was neither philosophically desirable nor practically possible.

Here Gilmour's point resembles, it seems to me, those colleagues of mine who warn that historical truth is not attainable. "History does not exist until we write it", I am told, and since even eye-witnesses will differ in the reality they simultaneously experience, historians are foolish to set their sights on uncovering what really happened. In reply to such relativists I say, what the other botanists told Gilmour, that the ideal is still the right thing at which to aim.

That the botanists' exchange of views finally resulted in the 1954 publication is evidence, not of botanists' support for his philosophy, but of Gilmour's great negotiating skill. At the eleventh hour Baker allowed himself to be named as a supporter only when part of the statement "the following botanists who took part in the discussions are in general agreement *with* the scheme" was altered to "general agreement *to test* the scheme" [italics mine]. All participants knew very well that they had no powers to legislate, that "gamodeme" and its ilk would live or die according to whatever mysterious forces determine usage.

The 1954 publication did not constitute a neat experiment to test any philosophical question about scientific terminology, because the zoological use of "deme" in place of "gamodeme" was already widespread. Emotional attachment to the 1939 proposal made Gilmour and his friends ignore Carter's practical suggestion that "-plethe" could have served as a neutral syllable free of the meaning "deme" had already acquired. If only Gilmour's acquaint-ance with Huxley had been closer, so that *Evolution: The Modern Synthesis* had promoted "gamodeme" instead of "deme", if only Carter, Simpson, and Wright had understood the distinction and respected it, would the 1954 enlarged family of terms have been adopted? The scenario is unrealistic, for the zoologists did not care about the botanists' many kinds of populations. The focus of the modern synthesis was the local interbreeding population; that was the natural entity for which the zoologists wanted a name. If Huxley had offered "gamodeme", then Carter, Simpson and Wright might well have shortened it to the four-letter root themselves.

Huxley's "cline" with its derivatives did become well established terms, first in zoology and botany, and then in anthropology (Birdsell 1972, p. 146). There are several variables in comparing the fates of these coinages, including cline's one-year headstart before the interruption of war, and Huxley's vastly greater visibility among scientists than Gilmour. Another significant difference was Huxley's pointing to a large number of examples; his first announcement in *Nature* named eighteen different species which demonstrated what he meant, in contrast to only one species mentioned in Gilmour and Gregor's paper, and then Huxley immediately supplemented his initial announcement with a long paper in which he set forth dozens more examples with their possible causes (Huxley 1938b), repeating the exercise in twenty pages of his book (1942, pp. 206–227). Instead of coining the term and waiting to see if anyone used it, he demonstrated its use at length himself.

History does not support Gilmour's conviction that science would work better if it used "neutral" words. T. H. Morgan at first avoided using the recently-coined "gene" because W. Johannsen had specified its lack of material reference; the word lived on when geneticists ignored its creator and linked it to the chromosome theory (Allen 1978, pp. 209–210). As pope of a church sceptical of natural kinds, Gilmour had few converts, not enough certainly to sustain a language, though his influential sympathizers would later include, in addition to Walters and Heslop-Harrison, Arthur Cain, Robert Sokal, Peter Sneath, and Colin Patterson. The idea of ridding science of confusion and contention by sharpening the link between words and facts remains attractive.

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Notes

- ¹ Unlike the clear difference between "intracellular" (within a cell) and "intercellular" (between cells), the distinction between "intrabreeding" and "interbreeding" can be subtle and is no longer much used. Those who used "intrabreeding" evidently meant to focus on sexual exchange within a small group of related individuals.
- ² Wright also coined (1956, p. 16) "intrademic" and "interdemic" selection for what he had been calling internal and external selection.
- ³ Although John Dean (1979, p. 218) calls Marsden-Jones a cytologist, this may be inaccurate, for when they wanted chromosomes counted, they called in outside help (Marsden-Jones and Turrill 1928b).
- ⁴ The use of "alpha to omega" (first to last letters of Greek alphabet) to mean all aspects of a topic was a common idiom, but any church-goer also knew that the biblical Book of Revelation opens with the divine pronouncement, "I am Alpha and Omega, who is and who was and who is to come ...", and again at its close "I am Alpha and Omega, the beginning and the end, the first and the last" (Rev. 1:8 and 22:13). Thus this idiom may have brought a tinge of the ineffable which "A to Z" lacks. Systematists who use the designations alpha, beta, and gamma taxonomy to describe descriptions of species, genera and families, following Mayr et al. (1953, p. 19) will notice that Turrill's alpha includes all taxonomic levels, described by morphological characters, while the beta stage uses other information such as fertility. Mayr's usage makes no mention of Turrill's idea of progress toward an ideal omega.
- ⁵ John and Molly Gilmour both recalled that it was Gregory who initiated the idea of an article in *Nature*, but they assumed, as did I, that Gregor's invitation came after the BASS meeting. The fact that the *Nature* article was agreed upon before Blackpool is proven by a letter from Agnes Arber (Gilmour Papers, 4 August 1936).

- ⁶ The bibliography of his typescript has not been found, but the names he mentions leads us to these sources, of which all but Singer are botanists: Cockayne and Allan 1927; Du Rietz 1930; Hayata 1920; Shull 1929; Turrill 1925, 1935, 1936; Raunkiaer 1934; Singer 1931, p. 539; Stojanoff 1936; Watson 1847, pp. 65–66.
- ⁷ He lists them in chronological order: Mill 1843, Bain 1870 [Gilmour says 1878], Jevons 1883, Read 1898, Stephen 1900, Sidgwick 1901, Fowler 1904, Schiller 1912, Mercier 1912, Johnstone 1914, Ritchie 1923, Woodger 1929, and Stebbing 1930.
- ⁸ Although he gives no citation to this point, among the philosophy works he lists, the one with wording closest to his on this standard problem is Schiller (1912, pp. 370–371).
- ⁹ Gilmour's footnote to Danser's 1929 article erroneously gives its year as 1920.
- He mentions the fourth International Congress for the Unity of Science, held in Cambridge in July 1938, but it is not known whether he attended it.
- Defining "natural" classification thus, rather than as an arrangement reflecting phylogeny, was of course not original to Gilmour, harking back to the usage that was standard before 1859, but systematists now refer to it as "Gilmour-naturalness" (Farris 1977).
- 12 Dean misread Camp, however, as Gilmour too had done, in thinking that Camp advocated dropping the word "species" in favor of his "binom" (Dean 1980, p. 144). Instead what Camp meant was that a description based only on classical herbarium techniques constitutes a binom, since "species do not exist in the filing cabinets of museums, but consist of populations of living organisms" (Camp 1951, p. 120). Camp and Gilly had "toyed with the idea of throwing out the category 'species'" but then backed down (Camp to Gilmour, 16 June 1954, Gilmour Correspondence). Field and garden observations could elevate a binom to a species.
- Attending this meeting were Baker, Gilmour, Gregor, John Heslop-Harrison, Yolande Heslop-Harrison, Turrill, D. H. Valentine, Walters, and Edmund F. Warburg. Although absent from this meeting, B. L. Burtt did receive and reply to memoranda as a member of the group. A. R. Clapham had also been invited but seems not to have taken part.

References

Allen, G.E.: 1978, *Thomas Hunt Morgan: The Man and his Science*, Princeton University Press, Princeton.

Bain, A.: 1870, Logic, Longman's, Green, Reader and Dyer, London.

Baker, H.G.: 1952, 'The Ecospecies - Prelude to Discussion', Evolution 6, 61-68.

Baker, J.R.: 1976, 'Julian Sorell Huxley', Biographical Memoirs of Fellows of the Royal Society of London 22, 207–238.

Birdsell, J.B.: 1972, 'The Problem of the Evolution of Human Races: Classification or Clines?', *Social Biology* **19**, 136–162.

Botany Archives: Botany Library, British Natural History Museum, London.

Bremekamp, C.E.B.: 1939, 'Phylogenetic Interpretations and Genetic Concepts in Taxonomy', *Chronica Botanica* **5**, 398–403.

Briggs, D. and Walters, S.M.: 1969, Plant Variation and Evolution, Weidenfeld & Nicholson, London.

Briggs, D. and Walters, S.M.: 1984, *Plant Variation and Evolution*, 2nd edn., Cambridge University Press, Cambridge.

Briggs, D. and Block, M.: 1981, 'An Investigation into the Use of the "Deme" Terminology', New Phytologist 89, 729–735.

Camp, W.H. and Gilly, C.L.: 1943, 'The Structure and Origin of Species', *Brittonia* 4, 323–385.

- Carter, G.S.: 1951, Animal Evolution: A Study of Recent Views of its Causes, Sidgwick and Jackson, London.
- Cockayne, L. and Allan, H.H.: 1927, 'The Bearing of Ecological Studies in New Zealand on Botanical Taxonomic Conceptions and Procedure', *Journal of Ecology* **15**: 234–277.
- Committee on Comparative Systematics of the Association for the Study of Systematics in Relation to General Biology, Minutes [1937–1938] (manuscript volume), Library of the British Natural History Museum, Z.89oA.
- Danser, H.B.: 1929, 'Über die Begriffe Komparium, Kommiskuum und Konvivien und über die Entstehungsweise der Konvivien', *Genetica* 11, 399–450.
- Darlington, C.D.: 1951, 'Do the Chromosomes Fit the Species?' Nature 167, 662-663.
- Dean, J.P.: 1979, 'Controversy over Classification: A Case Study from the History of Botany', in B. Barnes and S. Shapin (eds.), *Natural Order: Historical Studies in Scientific Culture*, Sage, London, pp. 211–230.
- Dean, J.P.: 1980, A Naturalistic Model of Classification and Its Relevance to Some Controversies in Botanical Systematics, 1900–1950, dissertation, University of Edinburgh.
- Dickinson, T.A. and Phipps, J.B.: 1985, 'Studies in Crataegus L. (Rosaceae: Maloideae). XIII.
 Degree and Pattern of Phenotypic Variation in Crataegus sect. Crus-galli in Ontario',
 Systematic Botany 10, 322–337.
- Dingle, H.: 1938, 'The Rational and Empirical Elements in Physics', *Philosophy (The Journal of the British Institute of Philosophy)* **13**, 148–165.
- Du Rietz, G.E.: 1930, 'The Fundamental Units of Biological Taxonomy', *Svensk Botanisk Tidskrift* **24**, 333–428.
- Farris, J.M.: 1977, 'On the Phenetic Approach to Vertebrate Classification', in M.K. Hecht, P.C. Goody and B.M. Hecht (eds.), *Major Patterns of Vertebrate Evolution*, Plenum Press, New York, pp. 823–850.
- Fositer, C.E.: 1981, 'James Wyllie Gregor', *Royal Society of Edinburgh Yearbook*, pp. 21–22. Fowler, T.: 1904, *Elements of Inductive Logic*, 6th edn., Clarendon Press, Oxford.
- Gilmour Correspondence, Archives of Directors of the Cambridge Botanical Garden (most items have been transferred to Cambridge University Library).
- Gilmour Papers, Cambridge University Library.
- Gilmour, J.S.L.: 1935, 'The General Problem', *Proceedings of the Linnean Society of London* **147**, 103.
- Gilmour, J.S.L.: 1936, 'Whither Taxonomy?' [abstract], Report of the British Association for the Advancement of Science, p. 417.
- Gilmour, J.S.L.: 1937, 'A Taxonomic Problem', Nature 139, 1040–1042 [reprinted in 1976 and 1989].
- Gilmour, J.S.L.: 1938, Diary (two bound manuscript volumes) Gilmour Papers (Additional MSS 8638, Box 1), Cambridge University Archives.
- Gilmour, J.S.L.: 1940, 'Taxonomy and Philosophy', in J.S. Huxley (ed.), *The New Systematics*, Clarendon Press, Oxford, pp. 461–474.
- Gilmour, J.S.L.: 1951, 'The Development of Taxonomic Theory Since 1851', *Nature* **168**, 400–402.
- Gilmour, J.S.L.: 1960, 'The Deme Terminology', Scottish Plant Breeding Station Report, 99– 105.
- Gilmour, J.S.L.: 1976, 'Two Early Papers on Classification', *Classification Society Bulletin* 3, 2–15.
- Gilmour, J.S.L.: 1989, 'Two Early Papers on Classification' [reprint of Gilmour 1976], *Plant Systematics and Evolution* **167**, 97–107.

- Gilmour, J.S.L. and Gregor, J.W.: 1939, 'Demes: A Suggested New Terminology', *Nature* **144**. 333.
- Gilmour, J.S.L. and Heslop-Harrison, J.: 1954, 'The Deme Terminology and the Units of Micro-evolutionary Change', *Genetica* 27, 147–161.
- Gilmour, J.S.L. and Turrill, W.B.: 1941, 'The Aim and Scope of Taxonomy', *Chronica Botanica* **6**, 217–219.
- Godwin, H.: 1985, Cambridge and Clare, Cambridge University Press, Cambridge.
- Gregor, J.W.: 1930, 'Experiments on the Genetics of Wild Populations. I. Plantago maritima L.', Journal of Genetics 2, 19–27.
- Gregor, J.W.: 1931, 'The Experimental Delimitation of Species', New Phytologist 30, 204– 217
- Gregor, J.W.: 1939, 'Experimental Taxonomy IV. Population Differentiation in North American and European Sea Plantains Allied to *Plantago maritima* L.', *New Phytologist* 38, 293–322.
- Gregor, J.W. and Watson, P.J.: 1954, 'Some Observations and Reflexions Concerning the Patterns of Intraspecific Differentiation', *New Phytologist* **53**, 291–300.
- Hagen, J.B.: 1982, Experimental Taxonomy, 1930–1950: The Impact of Cytology, Ecology, and Genetics on Ideas of Biological Classification, dissertation, Oregon State University.
- Hagen, J.B.: 1984, 'Experimental Taxonomy 1920–1950', *Journal of the History of Biology* 17, 249–270.
- Hayata, B.: 1920, *Icones Plantarum Formosanarum nec non et contributiones ad Floram Formosanum: or, Icones of the Plants of Formosa*, Bureau of Productive Industries, Government of Formosa, Taihoku, vol. 10.
- Heslop-Harrison, J.: 1953, New Concepts in Flowering Plant Taxonomy, Heinemann, London. Hubbard, C.E.: 1971, 'William Bertram Turrill', Biographical Memoirs of Fellows of the Royal Society 17, 689–701.
- Huxley, J.S.: 1936, 'Natural Selection and Evolutionary Progress', Report of the British Association for the Advancement of Science 106, 81–100.
- Huxley, J.S.: 1938a, 'Clines: An Auxiliary Taxonomic Principle', Nature 142, 219-220.
- Huxley, J.S.: 1938b, 'Clines: An Auxiliary Method in Taxonomy', *Bijdragen tot de Dierkunde* **27**, 491–520.
- Huxley, J.S.: 1942, *Evolution: The Modern Synthesis*, G. Allen & Unwin, London (also Harper & Brothers, New York, 1943).
- Huxley, J.S., Wells, H.G. and Wells, G.P.: 1931, The Science of Life, Cassell, London.
- Jevons, W.S.: 1883, The Principles of Science: A Treatise on Logic and Scientific Method, Macmillan, London.
- Johnstone, J.: 1914, The Philosophy of Biology, Cambridge University Press, Cambridge.
- Keller, E.F. and Lloyd, E.A.: 1992, 'Introduction', in E.F. Keller and E.A. Lloyd (eds.), *Keywords in Evolutionary Biology*, Harvard University Press, Cambridge, pp. 1–6.
- Kew Review: 1939, 'Review of the Work of the Royal Botanic Gardens, Kew, During 1938', Bulletin of Miscellaneous Information of Royal Botanic Gardens 1938, Appendix I.
- Marsden-Jones, E.M. and Turrill, W.B.: 1928a, 'Researchers on *Silene maritima* and *S. vulgaris*: I.', *Kew Bulletin*, 1–17.
- Marsden-Jones, E.M. and Turrill, W.B.: 1928b, 'A Tetraploid *Saxifraga* of Known Origin', *Nature* **122**, 58.
- Marsden-Jones, E.M. and Turrill, W.B.: 1930, 'Report on the Transplant Experiments of the British Ecological Society at Potterne, Wilts.', *Journal of Ecology* **18**, 352–387.
- Marsden-Jones, E.M. and Turrill, W.B.: 1957, The Bladder Campions, Ray Society, London.

Mason, H.L.: 1950, 'Taxonomy, Systematic Botany and Biosystematics', *Madroño (Journal of the California Botanical Society)* **10**, 193–208.

Mayr, E.: 1978, 'Origin and History of Some Terms', Systematic Zoology 27, 83-88.

Mayr, E., Linsley, E.G. and Usinger, R.L.: 1953, *Methods and Principles of Systematic Zoology*, McGraw-Hill, New York.

Mercier, C.A.: 1912, A New Logic, Heinemann, London.

Mill, J.S.: 1843, A System of Logic, J.W. Parker, London.

Müntzing, A., Tedin, O. and Turesson, G.: 1931, 'Field Studies and Experimental Methods in Taxonomy', *Hereditas* **15**, 1–12.

Raunkiaer, C.: 1934, *The Life Forms of Plants and Statistical Plant Geography*, Clarendon Press, Oxford.

Read, C.: 1898, Logic, Deductive and Inductive, G. Richards, London.

Ritchie, A.D.: 1923, Scientific Method, Harcourt, Brace, New York.

Schiller, F.C.S.: 1912, Formal Logic: A Scientific and Social Problem, Macmillan and Co., London.

Shull, G.H.: 1929, 'Species Hybridizations Among Old and New Species of Shepherd's Purse', in B.M. Duggar (ed.), *Proceedings of the International Congress of Plant Sciences*, Ithaca, New York, August 16–23, 1926, **1**, 832–888.

Sidgwick, A.: 1901, The Use of Words in Reasoning, Black, London.

Simpson, G.G.: 1953, *The Major Features of Evolution*, Columbia University Press, New York.

Singer, C.: 1931, A Short History of Biology, Clarendon Press, Oxford.

Stearn, W.T.: 1987, 'A Tribute to John Gilmour (1906–1986)', *The Garden (Journal of the Royal Horticultural Society)* **112**, 452–455.

Stearn, W.T.: 1989, 'List of Publications of John S.L. Gilmour', *Plant Systematics and Evolution* **167**, 109–112.

Stebbing, L.S.: 1930, A Modern Introduction to Logic, T.Y. Crowell, New York.

Stebbins, G.L.: 1980, 'Botany and the Synthetic Theory of Evolution', in E. Mayr and W. Provine (eds.), *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, Harvard University Press, Cambridge, MA.

Stephen, L.: 1900, The English Utilitarians, Duckworth, London.

Stojanoff, N.: 1936, 'Über den Artbegriff und die Aussichten der modernen Systematik', *Zesde Internationaal Botanisch Congres Amsterdam*, 2–7 *September*, 1935: *Proceedings* 1, 185–188, E.J. Brill, Leiden.

Systematics Association Archives, Library, University of Durham.

Turesson, G.: 1922a, 'The Species and the Variety as Ecological Units', *Hereditas* 3, 100–113.

Turesson, G.: 1922b, 'The Genotypical Response of the Plant Species to the Habitat', *Hereditas* 3, 211–350.

Turrill, W.B.: 1925, 'Species', Journal of Botany 63, 359-366.

Turrill, W.B.: 1929, The Plant-Life of the Balkan Peninsula: A Phytogeographical Study, Clarendon Press, Oxford.

Turrill, W.B.: 1929, 'Modern Methods in Taxonomic Botany', *Bulletin de la Société Botanique de Bulgarie* **3**, 119–124.

Turrill, W.B.: 1935, 'The Investigation of Plant Species', *Proceedings of the Linnean Society of London* **147**, 104–105.

Turrill, W.B.: 1936, 'Contacts between Plant Classification and Experimental Botany', *Nature* **137**, 563–566.

Turrill, W.B.: 1938, 'The Expansion of Taxonomy with Special Reference to Spermatophyta', *Biological Reviews* **13**, 342–373.

- Turrill, W.B.: 1946, 'The Ecotype Concept: A Consideration with Appreciation and Criticism, Especially of Recent Trends', *New Phyologist* **45**, 34–43.
- Turrill, W.B.: 1960, 'Obituary of Eric Marsden Marsden-Jones', *Proceedings of the Linnean Society* **172**, 132–133.
- Walters, S.M.: 1987, 'Obituary of John Scott Lennox Gilmour', The Linnaean 3, 35-36.
- Walters, S.M.: 1989, 'Experimental and Orthodox Taxonomic Categories and the Deme Terminology', *Plant Systematics and Evolution* **167**, 35–41.
- Walters, S.M.: 1993, Wild and Garden Plants, Harper Collins, London.
- Watson, H.C.: 1847, Cybele Britannica: Or British Plants and Their Geographical Relations, Vol. 1. Longman, London.
- Wilmott, A.J.: 1932a, 'Experimental Delimitation of Species', Journal of Botany 70, 49-50.
- Wilmott, A.J.: 1932b, 'Correspondence', Journal of Botany 70, 155.
- Wilmott, A.J. and Gilmour, J.S.L.: 1936, 'Abstracts of Papers Bearing on the Study of the British Flora', *Report of the Botanical Society and Exchange Club of the British Isles* 10, 497–507.
- Winsor, M.P.: 1995, 'The English Debate on Taxonomy and Phylogeny, 1937–1940', *History and Philosophy of the Life Sciences* **17**, 227–252.
- Woodger, J.H.: 1929, Biological Principles, Paul, Trench, Trubner, London.
- Wright, S.: 1955, 'Classification of the Factors of Evolution', *Cold Spring Harbor Symposium on Quantitative Biology* **20**, 16–24.
- Wright, S.: 1956, 'Modes of Selection', American Naturalist 90, 5-24.