

The English Debate on Taxonomy and Phylogeny, 1937-1940

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ABSTRACT – Between 1937 and 1940 the Taxonomic Principles Committee of the newly-founded Association for the Study of Systematics in Relation to General Biology (later the Systematics Association) attempted to define the relationship between evolution and taxonomy. The people who took part in the discussion were W.T. Calman, C.R.P. Diver, J.S.L. Gilmour, J.S. Huxley, W.D. Lang, J.R. Norman, R. Melville, O.W. Richards, M.A. Smith, T.A. Sprague, H. Hamshaw Thomas, W.B. Turrill, B.P. Uvarov, A.F. Watkins, E.I. White, and A.J. Wilmott. Most of the botanists asserted that taxonomy was a practical matter to be kept distinct from phylogenetic speculation, and most of the zoologists insisted that taxonomists must strive to represent evolution if they wished to be scientific. The disagreement seemed to be hardening rather than approaching compromise when World War Two stopped the committee's work.

In the 1930s many biologists were excited by the growing expectation that they were on the verge of a better understanding of evolution, but World War Two, starting in 1939, interrupted most scientific activity in Europe. When work resumed in the late 1940s, the neo-Darwinian 'modern synthesis' – so christened by Julian Huxley – was solidly in place.¹ From the vantage point of the 1930s, it looked as though systematics was poised to play several possible roles in the coming synthesis, whereas the one it actually played was the one favored by Dobzhansky and Mayr, focussing on speciation. The fact that in the late thirties several other aspects of systematics seemed equally worthy of attention is reflected in the diverse contributions to the 1940 volume *The New Systematics*. This title, as editor and contributors freely confessed, was a call to action rather than a unified vision, but when Mayr later characterized 'new systematics' as concerned with populations, its broader original meaning was forgotten.

During the 1930s there was considerable interest in the methodological foundations of systematics, particularly in Germany,² although

¹ E. Mayr and W.B. Provine, *The Evolutionary Synthesis*, Cambridge: Harvard University Press, 1980.

² M.J. Donoghue and J.W. Kadereit, 'Walter Zimmermann and the Growth of Phylogenetic Theory', *Systematic Biology*, 41 (1992), 74-85.

the most famous product of that period, Willi Hennig's book, was delayed by the war.³ At the same time a number of British botanists and zoologists, unaware of Hennig's ideas, were raising fundamental questions.⁴

Their discussions are mentioned in John Gilmour's essay for *The New Systematics*:

Another problem which has recently been discussed...is the significance of a natural classification and its relationship to phylogeny. During the past year this point has been exhaustively debated by the Taxonomic Principles Committee of the Association For the Study of Systematics in Relation to General Biology, and a certain amount of agreement has been reached. There still exist, however, two schools of thought among its members, as among biologists in general.... A resolution of these differences is surely one of the greatest needs of systematic biology.⁵

Systematists of today, wearied by decades of contention, may smile at Gilmour's innocent belief that this debate had been 'exhaustive', but they might be surprised to learn how many issues it did include. Thanks to the succession of secretaries of the Systematics Association who have preserved the files of its committees, it is possible to reconstruct much of what went on. Letters, notes, minutes, and memoranda show that the Taxonomic Principles Committee identified and articulated deep differences of opinion, but made no progress in resolving them.⁶

The New Systematics was edited by Julian Huxley and published under the auspices of the Association For the Study of Systematics in Relation to General Biology, of which he was the first chairman. Changing its name after the war, the Systematics Association is with us still, organizing conferences and publishing the proceedings of those conferences. (It is sometimes assumed, incorrectly, that Huxley's volume also originated as the proceedings of a conference.) In its early years the Association consisted of people who thought that important changes were under way in biology, modernizations which taxonomists ought to take into account. Its membership was not limited to taxonomists but included geneticists, cytologists, and ecologists. The phrase 'in Relation to General Biology' reflected the diverse motives

³ C. Dupuis, 'La "Systématique Phylogénétique" de W. Hennig', *Cahiers des Naturalistes*, 34 (1979), 1-69.

⁴ J.B. Hagen, 'Experimental Taxonomy, 1930-1960: The Impact of Cytology, Ecology, and Genetics on Ideas of Biological Classification', Dissertation, Oregon State University, 1982: 6-32.

⁵ J.S.L. Gilmour, 'Taxonomy and Philosophy'. In: J. Huxley (ed.), *The New Systematics*, Oxford: Oxford University Press, 1940: 461-474, 461-462.

⁶ Unattributed statements of fact in what follows are based upon the papers of the Systematic Association, presently located in the library of the University of Durham.

of the founders, including ecologists who wanted taxonomists to make keys that would be easier for non-taxonomists to use, senior taxonomists who sensed a lack of respect from other biologists, and junior taxonomists who thought the Linnean Society needed a ginger group to rouse it from its conservatism.

The Association was born on June 25, 1937, when more than seventy women and men assembled in the quarters of the Linnean Society near Piccadilly Circus in London and approved its name, purpose, and plan of action.⁷ This public birth had been preceded by the usual preliminaries: conception, consisting of conversations in the spring of 1936 between Gilmour, Cyril Darlington, and William B. Turrill; gestation, consisting of further meetings to which selected others were invited, including the energetic promoter of neo-Darwinism Julian Huxley; and labor, when about two dozen botanists and zoologists, calling themselves the new Association's Council, sketched out the group's purposes and committee structure. Huxley was chosen Chair of the Council, and at the June 25 open meeting his leadership was confirmed, in spite of a bit of grumbling behind the scenes that he was no systematist.

First on the list of aims of the new-born Association was 'To examine the theoretical and historical bases and the practical aims of taxonomy, and especially the relation of phylogeny to cytogenetic and taxonomic data'. This task, deriving directly from the preliminary conversations between Turrill, Darlington, and Gilmour, was assigned to the Taxonomic Principles Committee, of which Gilmour was convenor.

John Scott Lennox Gilmour was a man of great personal charm, combining physical attractiveness, perfect social ease, and organizational tact.⁸ After undergraduate studies in botany and one year as Curator of the Herbarium of Cambridge University, he had been hired in 1931 as assistant to the director of the Royal Botanic Gardens at Kew; he was regarded as someone destined to rise high.⁹ Gilmour was the youngest member of the Taxonomic Principles Committee and had yet to publish anything substantial, though he had intentions of conducting breeding experiments like those of Göte Turesson in

⁷ 'Association For the Study of Systematics in Relation to General Biology', *Nature*, 140 (1937), 163-164; 'Systematics in Relation to General Biology', *Nature*, 140 (1937), 211-212; H.W. Parker, 'The Cooperation of Corresponding Societies in the Study of Systematics in Relation to General Biology', *Report of British Association For the Advancement of Science*, 1938, 531-533.

⁸ E. Ashby, 'Address', *Plant Systematics and Evolution*, 167 (1986), 3-6.

⁹ W.T. Stearn, 'A Tribute to John Gilmour (1906-1986)', *The Garden (Journal of the Royal Horticultural Society)*, 112 (1987), 452-455.

Stockholm and James W. Gregor in Edinburgh, experiments designed to distinguish between environmental and genetical causes of morphological variation. Gilmour's Kew colleague Turrill was already collaborating with Eric Marsden-Jones on such experiments. Having adopted Turrill's view that new terminologies would have to be developed to accommodate the new findings of cytology, genetics, and ecology, Gilmour had declared, at the 1936 meeting of the British Association for the Advancement of Science in Blackpool, that conflict and confusion could be avoided if biologists would simply recognize that classification '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'. When asked to revise that talk for *Nature*, Gilmour added references to philosophical authorities which warranted this nominalist stand.¹⁰

The men meeting with Gilmour on the Taxonomic Principles Committee were a self-selected group at the top of their profession. Three of its members (William T. Calman, William D. Lang, and Hugh Hamshaw Thomas) were already Fellows of the Royal Society; Huxley became FRS in 1938, and four others (Turrill, Owain W. Richards, Boris P. Uvarov, and Errol Ivor White) would later receive that honor. Calman, just ending a term as President of the Linnean Society, was doing pathbreaking work on the morphology of Crustacea. The entomologist Richards had co-authored a book on animal variability. Uvarov had demonstrated that locusts are alternate phases of grasshoppers. Cyril R. P. Diver was doing pioneering work in both ecology and population genetics.¹¹

Counting Gilmour, the committee had fifteen members, rising to sixteen after Turrill joined it in February 1938 (Table 1). Seven were botanists, if we include the geneticist Arthur E. Watkins; three were paleontologists (Lang, Hamshaw Thomas, and White). Four of the botanists worked at Kew (Gilmour, Turrill, Thomas A. Sprague, and

¹⁰ J.S.L. Gilmour, 'Two Early Papers on Classification', *Plant Systematics and Evolution*, 167 (1989), 97-107.

¹¹ I. Gordon, 'Obituary Notice of William Thomas Calman', *Proceedings of the Linnean Society of London*, 165 (1954), 83-87; E.I. White, 'William D. Lang', *Biographical Memoirs of Fellows of the Royal Society*, 12 (1966), 367-386; T.M. Harris, 'Hugh Hamshaw Thomas', *Biographical Memoirs of Fellows of the Royal Society*, 9 (1963), 287-299; J.R. Baker, 'Julian Sorell Huxley', *Biographical Memoirs of Fellows of the Royal Society*, 22 (1976), 207-238; C.E. Hubbard, 'William Bertram Turrill', *Biographical Memoirs of Fellows of the Royal Society*, 17 (1971), 689-701; R. Southwood, 'Owain Westmacott Richards', *Biographical Memoirs of Fellows of the Royal Society*, 33 (1987), 537-571; V.B. Wigglesworth, 'Boris Petrovitch Uvarov', *Biographical Memoirs of Fellows of the Royal Society*, 17 (1971), 713-740; J. Stubblefield, 'Errol Ivor White', *Biographical Memoirs of Fellows of the Royal Society*, 31 (1985), 633-651; A.J. Cain, 'Capt. Cyril Diver', *Journal of Conchology*, 27 (1971), 273-276.

TABLE 1. Members of the Taxonomic Principles Committee of the Association for the Study of Systematics in Relation to General Biology, 1937-38.

	Age ¹	Affiliation ²	Dec 3 1937	Jan 14 1938	Feb 24 1938	Mar 25 1938	Jul 1 1938
Botanists							
J.S.L. Gilmour	31	Turrillian	+	+	+	+	o
R. Melville	35	Turrillian	+	o	+	+	+
W.B. Turrill	47	Turrillian	o ³	o ³	+ ³	+	+
H.H. Thomas	52	Turrillian	o	+	+	+	+
A.J. Wilmot	59	Turrillian	+	+	+	+	+
T.A. Sprague	70	Calmanite	+	+	o	+	o
Zoologists							
O.W. Richards	36	compromise	+	+	+	o	+
E.L. White	36	Calmanite	+	+	+	+	+
J.R. Norman	39	Calmanite	+	+	+	+	+
B.P. Uvarov	≈ 48	Calmanite	+	+	+	+	+
W.D. Lang	59	Calmanite	o	o	o	+	+
W.D. Calman	67	Calmanite	+	+	+	+	o
M.A. Smith	71	Calmanite	+	+	+	o	+
Non-taxonomists							
A.E. Watkins	39	Turrillian	o	+	+	+	+
C.R.P. Diver	40	compromise	+	+	+	+	+
J.S. Huxley	50	compromise	o	o	+	o	+

¹ Their ages are given as of January 1, 1938.² This column indicates whether the scientist agreed with Turrill that classification cannot be based upon evolution, or agreed with Calman that it must be.³ He was not yet a member of the Taxonomic Principles Committee.

Ronald Melville), one (Alfred J. Wilmott) was from the British Museum (Natural History), and two taught at Cambridge (Hamshaw Thomas and Watkins). Most of the zoologists (Calman, Lang, Uvarov, White, John R. Norman, and Malcolm A. Smith) were based in the British Museum. Of the two remaining zoologists, Richards taught at Imperial College, London; Huxley had held teaching posts at Oxford and at King's College, London, and had recently taken on the directorship of the great London zoo in Regent's Park. The only member of the committee not earning his living in biology was Diver, Clerk of Committees of the House of Commons.¹²

It ought to have been obvious to everyone that the Taxonomic Principles Committee would have to wrestle with major differences of opinion, for Calman was on record with views directly contrary to Gilmour's: 'It is certain that a Natural System does exist....It is an objective fact, not an arbitrary construction of human inventiveness.'¹³ Yet, Gilmour seemed confident that his committee could root out the causes of any differences and, by facing them with frankness, good will and clarity of definition, achieve agreement. He expected the committee to arrive at a consensus and announce its conclusions, producing a 'more or less agreed body of opinion on the principles of Taxonomy which could be embodied in a published report'. Even though he knew that differences within the committee reflected differences in the wider community, Gilmour was optimistic of making progress. 'Such a report, if it did not meet with acceptance from other biologists, would at least serve to stimulate further discussion.'

The Taxonomic Principles Committee held its first meeting on December 3, 1937. It met four times in 1938 (Jan. 14, Feb. 24, Mar. 25, July 1) and once in 1939 (June 15); then the war brought its work to a halt. In the 1950s a committee of the same name resumed work, but it did not continue this debate on foundations. The records of the pre-war committee, some still in Gilmour's Kew file folders, give evidence of his administrative skill. Having asked the members to put their views on paper, Gilmour would produce (or have a helper produce) typed stencils of what he received, which he would then circulate back to the whole committee. Although most of these statements

¹² 'Arthur Ernest Watkins', *Who Was Who*, 1961-1970, p. 1174; 'Thomas A. Sprague', *Taxon*, 1960, 93-102; 'Ronald Melville', *Directory of British Scientists*, London: Ernest Benn Ltd., 1966: 96; I.A. Williams, 'Alfred James Wilmott', *Proceedings of the Linnean Society of London*, 162 (1950), 234-236; W.P.C. Tenison, 'John Roxborough Norman', *Proceedings of the Linnean Society of London*, 156 (1945), 214-216; J.C. Battersby, 'An Appreciation of M.A. Smith', *British Journal of Herpetology*, 2 (1959), 136-148.

¹³ W.T. Calman, 'The Meaning of Biological Classification', *Proceedings of the Linnean Society of London*, 147 (1935), 145-158, 153.

are undated, cross-referencing them to other notes and letters makes the sequence of events fairly clear (Table 2).

TABLE 2. Chronology of Events Relating to the Taxonomic Principles Committee

Year	Date	Meeting
1937	June 25	Inaugural meeting of the Association for the Study of Systematics in Relation to General Biology.
	Dec 3	First meeting of the Taxonomic Principles Committee. Memos circulating on the aim of taxonomy.
1938	Jan 14	Taxonomic Principles Committee second meeting, with Calman in the Chair. Memos circulating defining phylogenetic classification.
	Feb 24	Taxonomic Principles Committee third meeting, Huxley in the Chair. Memos circulating on representing closely allied forms.
	Mar 25	Taxonomic Principles Committee fourth meeting, Calman in the Chair. Memos circulating on intraspecific categories and variation. Turrillian group statement and replies circulating.
	July 1	Taxonomic Principles Committee fifth meeting, Turrill secretary.
1939	June 15	Taxonomic Principles Committee sixth meeting.
1940	Mar 14	Discussion at the Linnean Society.

Gilmour's first step was to write to the members (some on May 31, 1937, others on July 2) asking them to consider questions such as the 'nature, purpose and principles of classification in general' (in particular, is classification of living things any different from classification of other objects?), and 'the meaning of a "natural classification" and its relationship to phylogeny'. At its first meeting, held in the Linnean Society, the members agreed to Gilmour's plan that written submissions be sent to him and distributed between meetings. Between the meeting of December 3, 1937 and January 14, 1938, he found time to send out two installments on the 'aim of taxonomy', representing the views of every member.

This first set of memoranda immediately showed that there was a vast range of opinion within the committee. At one extreme was Gilmour's insistence

(1) that, in general, classification is a human activity devised by man for the purpose of dealing with the multiplicity of phenomena and that the classes constructed in the process are subjective, and (2) that, in particular, the concept of 'species' is, in this respect, in no way different from other categories.

The other extreme was expressed by White:

The aim of Taxonomy is...to classify animals or plants...so as best to demonstrate in the opinion of the author the true relationships of the groups. The ultimate basis of Taxonomy is therefore the evolution of groups, and the idea of an artificial systematic arrangement, or pseudotaxonomy, is completely rejected.

Hamshaw Thomas had already argued in print that fossils of flowering plants contradicted, or at best failed to confirm, the supposedly evolutionary arrangement of the higher plant taxa.¹⁴ He told the committee,

A critical survey of what has happened in the history of the classification of the Angiosperms may serve as an example of the drawbacks of a consciously phylogenetic approach.

...at present we know almost nothing about the phylogeny of the Angiosperms. All that has been done during the last 75 years has been by deductive processes in which attempts have been made to fit existing groups into an imagined pre-existing scheme. The more we have learned about our plants, the more we have come to realise the impossibility of making any reasonable fit, but it is only now that we are beginning to understand that the supposed phylogenetic scheme is only a figment of the imagination and does not represent anything which has actually happened in the history of the group.

Huxley, knowing he would have to miss the January meeting, studied the first installment before sending his own long memo, which declared,

...I am sure that Gilmour's contention that the species concept is as purely subjective as other taxonomic categories would prove untenable.

But he nevertheless praised Gilmour's 'broad definitions' as generating profitable discussion. His own suggestions were pragmatic:

¹⁴ H.H. Thomas, 'The Nature and Origin of the Stigma', *New Phytologist*, 33 (1934), 173-198.

Taxonomy has both a practical and a theoretical aim. The end result must be a compromise between these two aims; the complexity of phenomena and the limitations of knowledge....

...it is desirable to divide taxonomy into 'major' and 'minor': the former concerned with higher categories, the latter concerned essentially with species, their subdivision and groupings. Major taxonomy can be and should be on a phylogenetic basis. But in minor taxonomy, phylogenetic classification may be impossible owing to (1) parallel mutation, (2) polyploidy of various kinds, (3) hybridization, with various results. On the other hand, relationship (i.e. the number of characters and genes shared by two groups) is more easily arrived at. This also implies that the concept of homology needs redefinition in regard to minor taxonomy.

But the committee failed to adopt Huxley's useful distinction of 'major' and 'minor', and whether taxonomy at any level ought to be, or can be, 'on a phylogenetic basis' turned out to be a point of permanent contention.

Gilmour, knowing Huxley would be absent from the second meeting, wrote to Calman, asked him to take the chair, and gave him precise suggestions for structuring the discussion. Terms should be clarified and definitions agreed upon, said Gilmour, and perhaps the expression 'natural classification' should be dropped altogether, or at least people should be careful to distinguish 'phylogenetically natural' (according to ancestry) from 'logically natural' (maximum number of characters in common). Experience would show that Gilmour was underestimating the emotional power adhering to the word 'natural'. He was certainly too optimistic when he told Calman, 'it should not be difficult to reach agreement on a common definition' of 'biological taxonomy'.

A dozen members were present for the second meeting of the committee, which was held at the Linnean Society in the afternoon of January 14, 1938. Gilmour later summed it up thus:

A long and interesting discussion took place, more than one member remarking that it was the best scientific discussion he had ever attended!...There was a fairly sharp divergence of opinion on the meaning of a natural classification. One group believed that a natural classification must be primarily a phylogenetic one, while the other believed that it was primarily one in which individuals were grouped into classes having the maximum number of attributes in common. The first group consisted mainly of zoologists and the second mainly of botanists - though this division was not absolute.

The memoranda circulated before and after this January meeting confirm Gilmour's report about the division between botanists and zoologists (Table 1). The zoological taxonomists all held that phylogeny is essential for natural classification, even though they recognized that

knowledge of ancestry is difficult to achieve in practice; of the botanists, all but one held the contrary: that taxonomy ought to be kept distinct from phylogenetic considerations. Sprague, the one who sided with the zoologists, was also, at age 70, the oldest botanist on the committee. Those zoologists most inclined to compromise were the ones not employed as taxonomists (Diver, Huxley, Richards).

Gilmour's minutes of the January meeting recorded that the members, having failed to agree about 'natural' classification, recognized that they lacked a common definition of 'phylogenetic classification'.

Some members asserted that there was no need to define it, as everyone knew what it was; some, however, admitted that they did not know what it was; while some suggested that it might be regarded as the same as a genealogical classification, i.e. one based on closeness of individual relationship in the sense that two brothers are more closely related than two cousins.

Consequently, another flurry of mimeographs, in two installments, swirled about London, Kew, and Cambridge before the February 24 meeting.

Fresh from the stimulation of the January meeting, several members offered substantial and thoughtful paragraphs. Diver mentioned a species of cord-grass, *Spartina townsendii*, which had been revealed to be a natural hybrid, rendered fertile and true-breeding by allopolyploidy.¹⁵ Genetic and chromosomal analysis suggested that here taxonomists were looking at a new species recently created in the wild, the result of interbreeding between a native British species and an introduced species which apparently could out-compete its parent species. The case presented a challenge to the belief that ancestry could be inferred from morphology, because in different locations populations of *S. townsendii* seemed to have arisen independently; they would thus be phylogenetically distinct but genetically and morphologically identical.

Other members also saw problems with phylogeny. Watkins wrote, '...the idea of community of descent is one that cannot in practice be defined and...its lack of precision is a handicap to taxonomy today.' Hamshaw Thomas warned,

It is useless to overlook the probability that the determination of real 'blood relationships' in many groups is impossible. In other groups we may ultimately obtain some ideas of possible lines, but our results can never have a high degree of certainty. This does not mean that the search for phylogenies is not worth-

¹⁵ C.L. Huskins, 'The Origin of *Spartina townsendii*', *Genetica*, 12 (1930), 531-538.

while, but rather that an attempt to mix the phyletic ideal with the practical task of classifying organisms on likeness is not the best method of advancing knowledge.

The difference between the practical and the ideal was alluded to also by Watkins: 'With a complete description (the unattainable ideal) the need for giving value [assigning different taxonomic weight] to different characters would disappear and numbers of differences would express relationship.'

Gilmour, who often thought his colleagues' problem was lack of clarity and precision, received Huxley's submission with irritation, writing in the margin of his copy, 'What a lot of talk. Put it concisely'. Perhaps it was Huxley's faith in phylogeny, not just his prolix language, which annoyed Gilmour. Huxley had written:

Phylogenetic relationship is usually envisaged in the form of a branching tree. When this model is correct, as it undoubtedly is for all higher taxonomic units, probably down to families, and for the majority of animals down to the smallest units, phylogenetic relationship can be safely deduced in certain cases.

Gilmour further scribbled on his copy, 'What can this sentence mean but "when this is right it is right".' Evidently, Gilmour had misunderstood what Huxley was trying to say: in some cases (like *Spartina townsendii*) genealogical connections do not form a tree-like pattern, but where such complications were absent, evolutionary relationships were probably discoverable, indeed already largely discovered.

Gilmour kept his impatience to himself, but several members of his committee were not endowed with his tactful temperament. Many years later the writer of Sprague's obituary felt compelled to mention his 'somewhat irascible exterior', charitably suggesting that 'his unflinching courage in maintaining his convictions against all opposition' and his 'masterful manner, impatience, and contempt for hesitation in others' could be excused as arising from his devotion to ideals.¹⁶ Back in 1938, Sprague probably considered his second memorandum restrained. 'If any botanist doubts that we are gradually approximating to a truly phylogenetic classification of the Angiosperms', he should study the history of botanical arrangements, or work on finding the correct position for an apparently anomalous group, Sprague advised, perhaps an allusion to Gilmour's inexperience.

¹⁶ H.S.A. Marshall, 'Thomas Archibald Sprague', *Proceedings of the Linnean Society of London*, 172 (1961), 134-135.

It is a common experience that the best way to obtain a satisfactory knowledge of a subject is to carry out original researches in it. Those who doubt that our present systems of classification of the Angiosperms...represent approximations to a phylogenetic classification have probably studied neither the groups themselves, nor their characters, but the very limited number of characters supplied for purposes of identification by various authors.

Uvarov's defense of phylogeny had an even sharper edge.

It may well be that a phylogenetic taxonomist often constructs schemes that are only temporary and far from perfection, but if a taxonomist consciously renounces every intention of trying to understand the phylogenetic relations of the organisms which he is studying, then his work tends to lose its scientific purpose and to become 'systematics without relation to general biology'.

Calman chaired the committee's third meeting, on February 24, 1938, Huxley being ill. Discussion was again steered to focus on the meaning of terms: 'community of descent', 'blood relationship', and 'monophyletic'; the only agreement reached was that common descent implied an ancestral stock, not an individual ancestor, but no decision could be reached as to how broad a category was implied by the word 'stock'. Because everyone agreed that there were special problems for categories around the species level like sub-species and varieties, members assigned themselves the task of writing about methods of studying closely-allied forms. Gilmour urged committee members to read a recent article in which the Dutch botanist H.J. Lam reviewed the history of phylogenetic trees and proposed ways to represent evolution diagrammatically.¹⁷ Several members later made explicit reference to Lam's article.

In the four weeks between February 24 and the meeting of March 25, most committee members continued to work dutifully, even energetically, but a few seemed to be growing testy. Norman, Smith, and White sent in a joint reply to the query about closely-allied forms, stating, 'As far as the methods are concerned, we feel that little of general importance can be said, since these will inevitably differ from worker to worker, and also from group to group'. Turrill's contribution was nearly as anarchic: 'Any method is valid so long as it expresses known facts and makes clear neither more nor less than the author's interpretation of those facts'. Other committee members attempted creative proposals.

¹⁷ H.J. Lam, 'Phylogenetic Symbols, Past and Present (Being an Apology For Genealogical Trees)', *Acta Biotheoretica*, Series A, 2 (1936), 153-194.

Melville mentioned polyploidy as a common cause of speciation in plants, and he said much evidence of hybridization between members of different genera of plants had been found. 'In the face of such facts I find it difficult to conceive a monophyletic origin for either families or orders among Angiosperms.' Turrill again expressed the disillusionment felt by botanists when answers to questions as basic as which flowering plants were primitive had proven elusive.

Lang described the common practice among paleontologists of collecting into one genus, various species that share a certain adaptation or grade of development, even if they probably evolved it independently. Paleontologists usually realize that such a genus is polyphyletic, he explained, but they find this practice convenient anyway.

For closely allied forms, said Uvarov, diagrams or trees require so much oversimplification that it would be better not to use them. Species could be grouped, however, by a tabulation of selected characters, once the obstacles of definition had been overcome. The alternative to such a 'statistical' approach is the 'phylogenetic' one of evaluating each character for its likely history.

Richards drew a distinction between 'the *method* by which a classification is constructed and the *significance* of the classification'. Taxonomists actually construct classifications based on numbers of common characters while stating that they are using phylogeny. Their confusing description of their procedure stems from the complex process by which they give special weight to characters they deem phylogenetically significant. Those are characters that are found correlated with a large number of other characters, since without fossil evidence the phylogeny is unknown. In the same memo Richards defined 'phylogenetic classification' as 'one in which organisms are arranged in groups which have the maximum number of *common ancestors*'. He sent Gilmour a sketch, which Gilmour rapidly redrew on each mimeograph (Fig. 1). Richards explained,

A and B, or A and C, have x ancestors in common; B and C have $x + 10$ ancestors in common. Therefore B and C are more closely related to one another than either of them is to A.

His diagram of phylogeny could represent three people who trace their family histories back twenty generations to the same patriarch derived from Adam via x parents, or it could stand for three related taxa. From our perspective, though, the measure 'maximum number of common ancestors' is a curious one. The numbers 10, 20, or x are not accumulations of character differences, but 'ancestors', irrespective of whether generations are changing or conserving their parents'

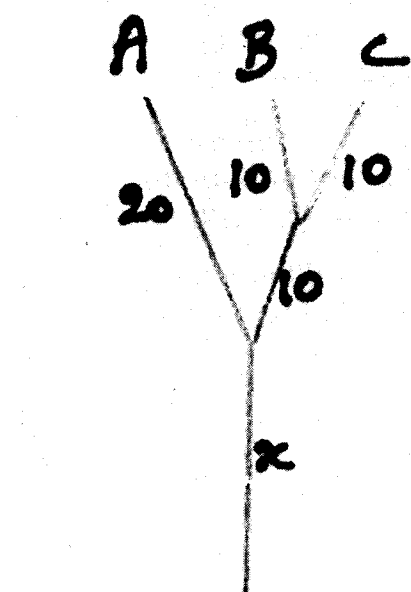


Fig. 1 Definition of phylogenetic relationship, ca. 1938, after O.W. Richards, circulated to members of the Taxonomic Principles Committee. (From Papers of the Systematics Association, University of Durham).

form. It is, however, how people define first, second, and third cousins.

This arrangement may easily (though perhaps not usually) conflict with a logical classification. The degree of resemblance between A, B and C depends on the rate of evolution along the lines A, B and C. If bigger changes have occurred along line C, A and B might be more alike one another, than either is to C.

The modern cladogram calculates degrees of relatedness by setting forth numbers of shared (and derived) character states, but Richards showed no awareness of the problems the cladogram thus avoids. In a human genealogy, distance from an ancestor can be

counted in numbers of generations, and Richards would run into fewest difficulties if his numbers were counts of generations, but Richards probably was thinking of species as his unit, so that his 10, 20, or x meant so many species, not so many generations. He did admit the basic problem with this measure of phylogenetic closeness. Far from answering the botanists' query as to which characters reveal relationship, this definition requires one to know every step in evolution. As Richards himself went on to say, 'Strictly to construct an accurate phylogenetic classification it would be necessary to have a literally complete fossil pedigree'. Cladists, by counting character states on a cladogram rather than ancestors on a genealogy, deal with the information they actually have, rather than including hypothetical forms.

Watkins proposed a distinction between three kinds of relationships: genealogical (as in human ancestry, but counting mothers as well as fathers, perhaps a polite way of exposing one of the problems in Richards's definition), genetical (number of genes in common), and phylogenetic. His definition and diagram of phylogenetic relationship

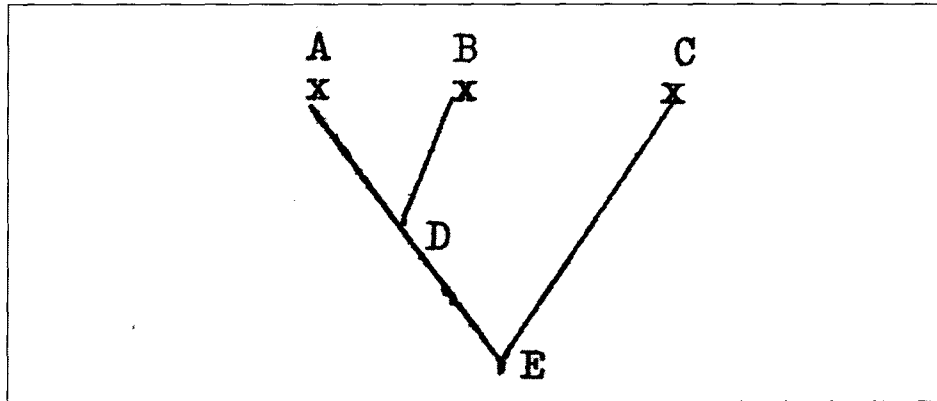


Fig. 2 Definition of phylogenetic relationship, ca. 1938, after A.E. Watkins, circulated to members of the Taxonomic Principles Committee. (From Papers of the Systematics Association, University of Durham.)

(Fig. 2), while avoiding Richards' imaginary tallying up of ancestors, also focussed on historical events rather than on characters.

Suppose the ancestors of individuals belonging to 3 species A, B and C are traced back by the parent offspring relation. Then if the ancestors of A and B form a freely interbreeding population [point D] before those of A and C or B and C, then A and B are said to be phylogenetically more closely related to each other than either is to C.

Such simple branching diagrams as this and Richards' could easily have occurred to many minds independently, but it is likely that Lam had influenced them both. His article, which Gilmour had commended to the committee members, contains a 'fundamental scheme' (Fig. 3) with similar lettering (unlike the chart in Darwin's *Origin* where the

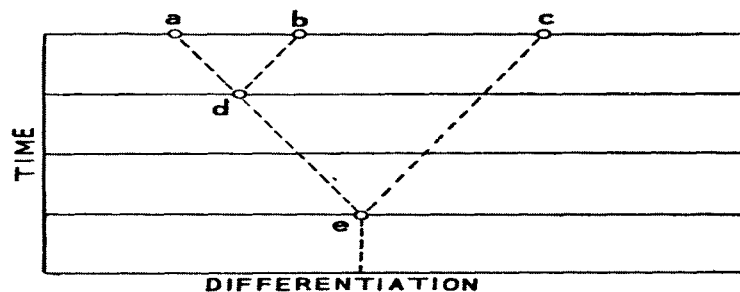


Fig. 3 H.J. Lam's 'fundamental scheme of the correlation between time and differentiation'. (H.J. Lam, 'Phylogenetic Symbols', *Acta Biotheoretica*, 2 (1936), p. 179.)

start of the alphabet belongs to the ancestors). Evidently, hoping like Gilmour, that agreement could be reached, Watkins explained,

I have had in mind here a case which, so I understand, is familiar in zoology: that in which certain groups, sometimes large, are distinguished by a common pattern or organisation which cannot be imagined to have arisen more than once, and for which there is no evidence of its having evolved more than once; such a group is said to be monophyletic.

When strict endogamy rules, and when some feature cannot have evolved more than once, phylogenetic classification is indeed possible, but when hybridization can create networks of relations (Fig. 4), and features often arise independently, then, wrote Watkins, adopting Gilmour's term, 'some form of logical classification is suggested as useful'.

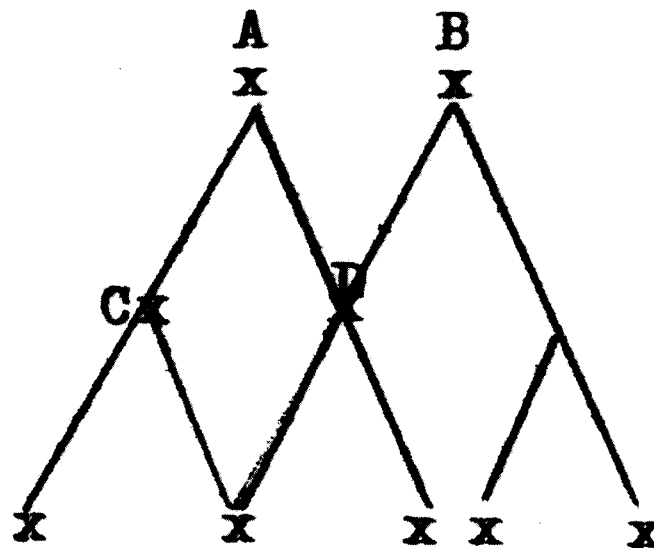


Fig. 4 Reticulated relationships caused by hybridization, ca. 1938, after A.E. Watkins, circulated to members of the Taxonomic Principles Committee. (From Papers of the Systematics Association, University of Durham.)

In a separate memo, Watkins offered as a difficult example the many strains (call them A, B, C...X) of wheat (*Triticum vulgare*), each strain an asexual line isolated from all others, plus the species *T. spbaerococcum*, a recent offshoot. The case presents two paradoxes: strain A of *T. vulgare*

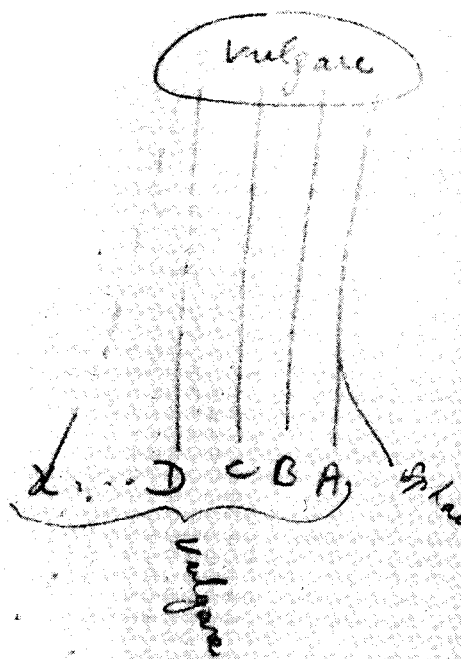


Fig. 5 Sketch of phylogeny of *Triticum*, ca. 1938, after A.E. Watkins, circulated to members of the Taxonomic Principles Committee. To the right of 'A' is a label reading 'Sphaerococcum'. (From Papers of the Systematics Association, University of Durham.)

has a more recent common ancestor with *T. sphaerococcum* than with other strains in its own species; also, strain X resembles strain A less than A resembles *T. sphaerococcum*, yet is in the same species. He sketched the situation (Fig. 5) while expressing his doubt that any diagram could substitute for words.

Lam's article had included pictures of three-dimensional evolutionary trees transected by the plane of time; taxa that are cylindrical trunks or branches become, in the present or at any chosen point in time, circles, or if viewed at an angle, ovals (Fig. 6). Diver insisted on the lack of evidence for the exact evolutionary history of any taxon and consequently argued for a diagram which 'in effect is a horizontal cross-section of the branching system at

a given time...'. Huxley endorsed the use of circles or ovals, since 'the plane is one degree nearer the facts than the tree'. The hierarchy of taxonomic groups could be represented by larger circles enclosing smaller ones, and Huxley suggested that some standard markings be adopted to indicate the cause of speciation in each instance.

Huxley also sketched a representation of speciation through polyploidy and through hybridization between polyploids (Fig. 7), a phenomenon rare in animals but common in plants. His labels are, on the left, allopolyploidy, and on the right, autopolyploidy. He shows at the bottom an ancestral genus enclosing two species, both with $2n$ chromosomes, then two descendant species which have doubled their chromosomes to $4n$, and finally, in the top oval, he shows on the left a species which owes its $6n$ chromosome count to hybridization between the original $2n$ species and its daughter $4n$ species. (The species on the top right, derived from a $4n$ parent by polyploidy, is not labelled; it would normally be $8n$ but could be $6n$.)

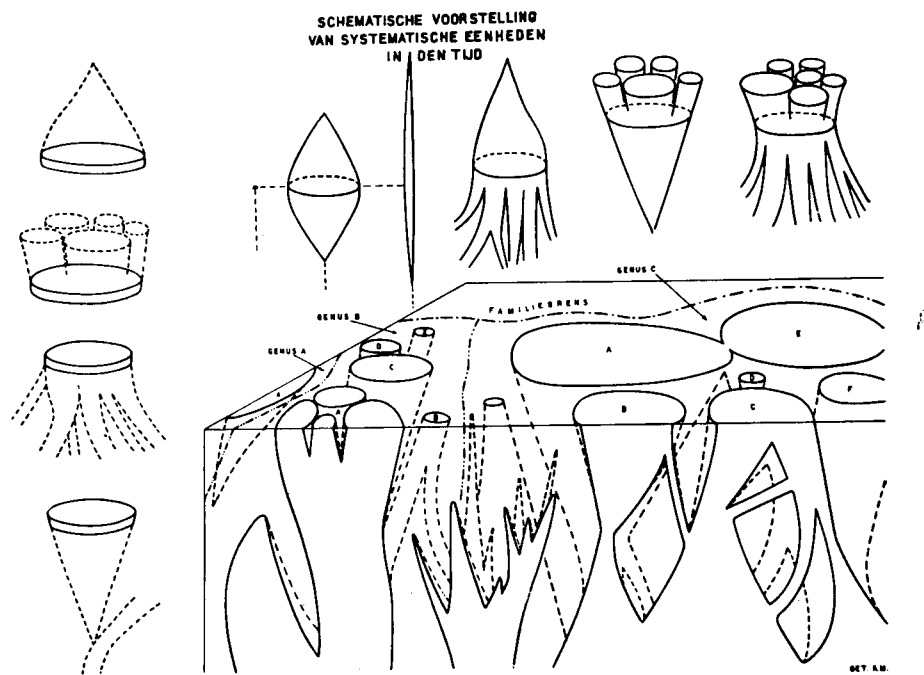


Fig. 6 H.J. Lam's generalized three-dimensional genealogical tree. (H.J. Lam, 'Phylogenetic Symbols', *Acta Biotheoretica*, 2 (1936), p. 188).

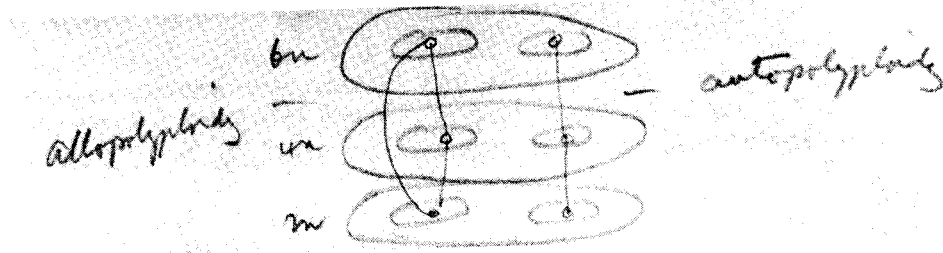


Fig. 7 Diagram of polyploidy and hybridization, ca. 1938, by J. Huxley for the Taxonomic Principles Committee. (From Papers of the Systematics Association, University of Durham.)

The effort expended on these diagrams did nothing to soften the committee members' differences over fundamentals. Turrill, in the course of his reply on methods of studying closely allied forms, pulled no punches:

It seems desirable to state somewhat dogmatically the view of one who is amazed at the gullibility of many of his zoological and some of his botanical colleagues in regard to phylogeny. They seem to swallow everything to which the 'blessed' word phylogeny is attached.

Turrill's words brought an immediate reaction. It was decided at the meeting of March 25, 1938, that a more formal statement of the skeptics' position was needed. Five botanists (Gilmour, Melville, Turrill, Watkins, and Hamshaw Thomas) agreed to formulate an exposition of their joint view. Someone, doubtless meaning to be humorous, called this group the 'Turrillian Non-Gullibles', but Calman took offence at the implication that those who disagreed were 'gullibles', so the term was suppressed. (To avoid repeating the offence, I have called the two sides 'Turrillians' and 'Calmanites'.) In writing to Huxley (absent because of illness), Gilmour called the discussion at the March meeting 'rather futile'.¹⁸ Hope of progress remained alive, though, for members agreed to produce memoranda which would give concrete examples of intraspecific variation and would list subspecific categories currently in use in different specialties.

The Turrillians challenged their opponents to specify exactly how knowledge of phylogeny is obtained. In their initial notes, Turrill and Gilmour had each suggested that chromosomal or fossil evidence was essential to assessing ancestry. The joint statement of the Turrillians declared:

That we are agreed, that in the absence of adequate palaeontological or cytogenetical evidence the only scientific classifications possible are of the 'logical' type, taking into consideration either all available attributes or only a limited number for special purposes. These may, but do not necessarily represent the phylogenetic relationships of the groups concerned.

(The implication that fossils or genes can offer privileged data was not repudiated by the Calmanites.) How, in the absence of fossil evidence, can one recognize a character as primitive or advanced, the Turrillians demanded, declaring themselves wary of the circular argument that a character is primitive because it is found in a primitive group. 'Our trouble is that we are not satisfied that this circle has been, or even that with the available evidence it can be, broken.' What criteria can one use, they ask, 'to assess closeness of phylogenetic relationship between two groups?' They concluded:

¹⁸ Papers of J.S. Huxley, Woodson Research Center, Rice University Library, Austin, Texas.

Fundamentally, what we want to discover is any criterion (apart from correlation of characters and intuitive feelings...) by which primitiveness (or advance) can be scientifically determined.... If...there is no such criterion then we say that phylogeny is...speculation, useful perhaps for certain purposes, but useless or even definitely misleading as a basis for taxonomy.

The paleontologist Lang attempted straightforward replies to specific points in the Turrillian memorandum. Sympathizing with botanists, because plants had left such a poor fossil record, he asked if nevertheless a botanist could not guess that evolution had likely proceeded in one direction rather than another - flowers of simple form, for instance, preceding composite flowers. Of course, any phylogeny 'must be conjectural, that is, a matter of opinion and not a matter of fact', but, he declared, 'After all, extreme probability, and not absolute certainty, is all that scientific research can achieve'. Lang pointed the way to escaping the trap of circular reasoning:

A character is not primarily considered primitive because it occurs in a primitive group. The criterion is its evolutionary history which, even without palaeontological evidence, may in some cases be deduced with a very strong degree of probability from comparative morphology.

The criterion for primitiveness, or otherwise, of a character is the evolutionary stage of the character in the given instance. This is not based on 'intuitive feeling', but upon the compulsion of accumulated probability. Phylogenies by their very nature are speculative;...as a basis for taxonomy they are perhaps fluid; quite likely embarrassing; but not only not useless, but provide the only basis which gives any intellectual satisfaction.

Three other zoologists (Norman, Smith, and White) who endorsed Lang's statements could not restrain their feelings of outrage at what the Turrillians seemed to be proposing.

We find the most disappointing feature of their statement is not their inability to unravel the phylogenetic history of the Angiosperms but their defeatist attitude.... May we finally be allowed to remark that in our opinion the use of the term 'scientific' in reference to a 'logical' classification is unjustifiable. 'Scientific' implies a basis of knowledge; 'logical classifications' are admittedly makeshifts based very largely upon absence of knowledge.

A few members made efforts to find a middle road. The clearest attempts at compromise came from Huxley, who was at this time hard at work on the manuscript of *Evolution: The Modern Synthesis*, although the book would not see print until 1942. Diver, whom Mayr would later praise for his contributions to the mutual under-

standing of geneticists and taxonomists, also saw the value of both viewpoints, perhaps because he, like Huxley, was not a taxonomist.¹⁹ The third man willing to compromise was O.W. Richards, an entomologist who did much field work in the company of a botanist, his brother Paul.²⁰

Agreement on a compromise resolution should have been possible, logically speaking, for the Turrillians said they 'fully acknowledge not only that there should be phylogenetic studies and schemes, but that these may well be of very great importance to the taxonomist', while the Calmanites admitted that evolutionary relationships were only the ideal at which they aimed, actual classifications being necessarily conjectural to some degree. Yet, the derisive word 'gullible' points to the human heart of the debate. The Turrillians thought the Calmanites had been hoodwinked by a false belief and were overlooking a logical flaw at the center of their methods. The Calmanites had no choice but to defend themselves by claiming that they actually understood correct scientific method better than the Turrillians. Thus, to some extent, what was at stake on both sides was pride.

Gilmour, reporting to the Council of the Association in May 1938, judged there to be such a wide divergence of opinion on the relation between taxonomy and phylogeny that he was no longer sure that consensus could be reached.

Meeting without Gilmour on July 1, the group put that grand question aside. They turned to more concrete tasks, such as compiling an index of terms which had been applied to intraspecific categories. They discussed the way words like 'subspecies' and 'variety' were used, and whether clarified definitions could be introduced.

The debate was kept at the high level now traditional for our meetings. The acting secretary [Turrill] found it very difficult to take notes as not infrequently 3, 4, or even 5, members spoke at once....

In September of 1938 Gilmour set sail for South America. His diary shows that the talk aboard the steamer centered on Neville Chamberlain's attempts to head off the European war which was so clearly looming.²¹ The next month, in Trinidad, Gilmour drafted his contribution to the *New Systematics* volume, glad to have this commitment to distract him from the ominous news coming over the air-

¹⁹ E. Mayr, *Systematics and the Origin of Species*, New York: Columbia University Press, 1942: 3.

²⁰ R.G. Davies, N. Waloff, and R. Southwood, 'O.W. Richards', *Antenna*, 9 (1985), 60-62.

²¹ Papers of J.S.L. Gilmour, Cambridge University Archives, Additional MSS 8638, box 1.

waves. The conclusion of that paper clearly arose directly out of the memoranda and discussions of the Taxonomic Principles Committee. When Gilmour wrote:

Even the most convinced phylogenetic taxonomist maintains, not that correlation of attributes is the same thing as phylogenetic relationship, but that such correlation indicates phylogenetic relationship, thereby implying that the latter is based on some other criterion.²²

he surely had in mind his recent experience learning the views of Calman, Lang and Uvarov. The eminent botanist Agnes Arber, giving Gilmour comments on his draft, said that surely he was attacking a straw man, but he told her that devotion to phylogeny was alive and well among zoologists.²³ He omitted to tell her that his Kew colleague Sprague agreed with Calman too.

The New Systematics included contributions from five other members of the Taxonomic Principles Committee besides Gilmour. Two of them side-stepped his reformist agenda: 'To discuss how far real or supposed phylogenetic data can or should be used in taxonomy would take us far beyond the realm of experimental taxonomy.'²⁴ 'We need not be concerned here whether the taxonomic hierarchy erected on these specific units [species] is a correct representation of phylogenetic relationships or not....'²⁵ Two other contributors contradicted the Turrillian view.

It is of interest to note that our botanical colleagues seem, on the whole, to be less confident than the zoologists in ascribing a phylogenetic meaning to their classification. This is no doubt due very largely to the fact that the morphology of plants is vastly simpler and less varied than that of all but the simplest animals. It may also be attributed, in some measure, to the fact that hybridization seems to have played a much greater part in the evolution of plants than it has done in that of animals, and the pattern of the phylogenetic tree, is, in many places, hopelessly obscured by interosculation of the branches.²⁶

The view has been taken, more especially by botanists without wide taxonomic experience and intimate acquaintance with many natural groups, that a natural classification in biology is not necessarily phylogenetic, but is merely a particular example of natural classification in general. The experienced taxonomic botanist usually reaches the opposite conclusion, as the result of repeated tests of the 'natural' system.²⁷

²² J.S.L. Gilmour, 'Taxonomy and Philosophy'. In: J. Huxley (footnote 5) 461-474, 469.

²³ Papers of J.S.L. Gilmour, Cambridge University Archives, Additional MSS 8638.

²⁴ W.B. Turrill, 'Taxonomic Botany, With Special Reference to the Angiosperms'. In: J. Huxley (footnote 5), 47-72, 68.

²⁵ C. Diver, 'The Problem of Closely Related Species Living in the Same Area'. In: J. Huxley (footnote 5), 303-328, 303.

²⁶ W.T. Calman, 'A Museum Zoologist's View of Taxonomy'. In: J. Huxley (footnote 5), 455-459, 458.

²⁷ T.A. Sprague, 'Taxonomic Botany, With Special Reference to the Angiosperms'. In: J. Huxley (footnote 5), 435-454, 441.

Of all the members of the Association, Julian Huxley was the best known, for he had travelled widely, was in touch with biologists on the European continent and North America, and wrote essays and books popular with a wide public. When Darlington, Gilmour, and Turrill decided, a year before the Association's birth, that a collection of articles should be published with a title like 'Modern Taxonomy' or 'The New Systematics', they agreed on the desirability of having Huxley's name on the volume. In keeping with the spirit of synthesis to which he was committed, in his introduction to *The New Systematics* Huxley strove to minimize the disagreement uncovered by the Taxonomic Principles Committee.

It would seem that these two views, apparently so dissimilar, can be reconciled. In the first place we may admit that taxonomic classification actually arrives at its results by evaluating resemblance and difference in the largest possible number of characters, and not by means of phylogeny, which can only be subsequently deduced, and is only measurable, if at all, in terms of the characters used in taxonomic evaluation. In the second place, however, it is certainly true that it can have what I may call a phylogenetic background, in that it can most often be interpreted phylogenetically; and, further, that such a phylogenetic interpretation may sometimes suggest an improved taxonomy.²⁸

The *New Systematics* was in press but not yet out when Gilmour, back from his travels, called the Taxonomic Principles Committee back to its task, in June of 1939. He later reported that

...a memorandum on Phylogeny and Classification, prepared by a section of the Committee, together with comments thereon by other members was fully discussed. It was agreed (1) that phylogeny should be defined as 'the historical sequence by which groups of organisms have come into existence', and (2) that, while one could not say that classification should be 'based on' phylogeny, classification could and should be 'interpreted phylogenetically'. A long discussion on the relationship between a 'logically natural' and a 'phylogenetic' classification produced inconclusive results. A memorandum has been prepared and will be circulated.²⁹

On September 3, 1939, Britain declared war on Germany, expecting, at first, a quick victory. The Taxonomic Principles Committee asked the Linnean Society to announce a public forum on phylogeny and taxonomy to take place on March 14, 1940. Four of the five Tur-

²⁸ J.S. Huxley, 'Introductory: Toward the New Systematics'. In: J. Huxley (footnote 5), 1-46, 19.

²⁹ J.S.L. Gilmour and H.W. Parker, 'Association For the Study of Systematics in Relation to General Biology: Annual Report II 1938-40', *Proceedings of the Linnean Society of London*, 152(4) (1941), 399-403, 400.

rillians (Gilmour, Melville, Turrill, and Hamshaw Thomas) contributed papers, as did Huxley, Richards, Sprague, and White. Their remarks show that two years of effort had not only failed to change anyone's mind, but had created some bitter feelings.

It may be objected that this attempt to clarify the aims of taxonomy is really a waste of time, that it doesn't matter what a taxonomist's aims are – the results will be much the same, anyway.³⁰

Yet, if we believe in evolution let us take it seriously.³¹

...difficulties are only to be considered as temporary and do but add zest to our studies....it came as a surprise to discover that there were workers in the field of systematics who regarded the use of phylogeny as a basis of classification as a definitely false step, not only in their own groups, but apparently in others where evidence of phylogeny may be ample.

It is not so much the practice of using non-phylogenetic taxonomy (for which there may at the time be no alternative) that is to be deplored, but the attitude of mind that accepts this position and is content to adopt a classification based on ignorance rather than consciously seek to work out one based on knowledge – for this is a policy of despair. Indeed, it is difficult to understand the aims of taxonomists who ignore phylogeny. Is their object merely to pigeon-hole material? Many at any rate seem to aim no higher.

...a taxonomic arrangement without a phylogenetic basis is only a temporary expedient due to lack of evidence. To think otherwise is to deprive systematic work of the one factor that gives it vitality and elevates it to the dignity of a science.³²

Sprague, after scorning Gilmour's growing fondness for philosophy, alluded to his own lifetime of experience.

I will not attempt to follow the first speaker [Gilmour] into the highly abstract field which he has chosen as his own, but will try instead to give the views of a practical taxonomist...the so-called natural classification in botany has been developed synthetically, by a process of trial and error, and is not based on arbitrary selection of characters....

...If the resulting natural classification in botany were merely, as has been argued, a particular example of the so-called natural classification in logic, why should characters previously unknown and unconsidered so frequently prove to be correlated in the same way? If, on the other hand, the groups previously recognized are monophyletic, there is every reason to expect such correlation.³³

³⁰ J.S.I. Gilmour, [Remarks in] 'Discussion on Phylogeny and Taxonomy', *Proceedings of the Linnean Society of London*, 153(3) (1941), 234-255, 240.

³¹ O.W. Richards, [Remarks in] 'Discussion' (footnote 30), 234-255, 242.

³² E.L. White, [Remarks in] 'Discussion' (footnote 30), 234-255, 249-250.

³³ T.A. Sprague, [Remarks in] 'Discussion' (footnote 30), 234-255, 243-246.

This public interchange was no more conclusive than the discussion at meetings of the Taxonomic Principles Committee had been. It seems clear that even without the interruption imposed by the war, Gilmour's hopes for a consensus were doomed to failure. One of his memos had concluded,

I very much hope that we may be able to reach agreement at any rate on the point that a phylogenetic classification and a logically natural one have different aims and do not necessarily coincide, and that each may be used for its own particular purpose.

Gilmour's hope did not impress Huxley, whose remarks at the Linnean Society seem to reflect some exasperation with debaters on both sides.

The believers both in a completely logical and in a completely phylogenetic taxonomy would appear to be aiming at ideas which are quite unattainable in practice; in addition, both systems are in some cases not consonant with fact....In general, however, the two concepts largely coincide.³⁴

Huxley's contribution to the Linnean Society discussion closely duplicated what he had written for *Evolution: The Modern Synthesis*.³⁵ Far from accepting Gilmour's recommendation to allow taxonomy independence from phylogenetic opinions, Huxley seems to have drawn the lesson that strict logic can be the enemy of scientific progress.

It has been customary to distinguish sharply between artificial and natural classification. But the 'natural classification' at which post-Darwinian biology has aimed is itself in certain ways artificial. For one thing it represents an unattainable ideal. And for another it assumes - what we now can perceive to be erroneous - that the only natural method of classification is one based on naïve and pre-mendelian ideas of relationship taken over from human genealogy and applied to groups instead of to individuals. Furthermore, it has unconsciously accepted certain implications of the Aristotelian method of classifying things into genus and species, implications which are of philosophical rather than scientific import and based on *a priori* logic rather than on empirical fact. The most important of such implications is a tendency to accept the discreteness and fixity of separate species (and subspecies) at more than their face value.³⁶

This debate, now more than half a century old, may give modern systematists a sense of *déjà vu*; similar issues are again mooted. On the

³⁴ J. Huxley, [Remarks in] 'Discussion' (footnote 30), 234-255, 251.

³⁵ J. Huxley, *Evolution: The Modern Synthesis*, London: Allen & Unwin, 1942: 399; the differences are as trivial as saying that the two concepts largely coincide 'in practice' rather than 'in general'.

³⁶ J. Huxley (footnote 35): 410-411.

evolutionary model of the history of scientific ideas, we may ask if the resemblance is one of homology or analogy.³⁷ For homology, we would need to evaluate the direct effect of this debate. Besides whatever power resided in the published statements in *The New Systematics*, the report of the 1940 Linnean Society discussion, and Huxley's *Evolution: The Modern Synthesis*, each participant doubtless was affected by the debate and continued to express its influence. Several of the participants repeated their opposing views at a 1951 meeting.³⁸ Nevertheless, later disagreements within systematics seem to have arisen to a large extent independently.³⁹ Possibly the pre-war debate may even have discouraged those involved (with the exception of Gilmour) from expending their energy in a direction that had proved so fruitless. If the debate influenced leaders of the neo-Darwinian synthesis to avoid the problem of phylogeny's relationship to taxonomy, this would be a phenomenon of the history of ideas hard to fit into an evolutionary model.

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³⁷ D. Hull, *Science As a Process*, Chicago: University of Chicago Press, 1988: 16-17.

³⁸ 'Phylogeny in Relation to Classification', *Nature*, 167 (1951), 503-505.

³⁹ K. Vernon, 'The Founding of Numerical Taxonomy', *British Journal For the History of Science*, 21 (1988), 143-158.