The genesis of IOPB: A personal memoir

Vernon H. Heywood

School of Biological Sciences, University of Reading, Reading RG6 6AS, U.K.; v.h.heywood@reading.ac.uk

Abstract An account is given of the circumstances that led to the decision to create the International Organization of Plant Biosystematics. The pioneer work of biologists on both sides of the Atlantic in biosystematics and experimental taxonomy is outlined, especially that of the San Francisco Bay group in the U.S.A. and that of J.S.L. Gilmour, G. Turesson, and J.W. Gregor on genecology and the deme terminology in Europe. The continuing need for a biosystematics perspective in our understanding of taxonomy at the species level and below is stressed.

Keywords biosystematics; deme terminology; experimental taxonomy; genecology

■ INTRODUCTION

In the post-war years, the taxonomic world, like the rest of botanical science, was beginning to go through a period of reassessment and development. The focus of mainstream taxonomy was still on writing Floras and monographs and in some countries this was largely confined to the national institutions while taxonomic teaching and research had fallen out of favour in many universities. A major development was the publication of a series of outstanding texts that revolutionized evolutionary and phylogenetic studies that began in the 1940s with such classics as J.S. Huxley's The New Systematics (1940) and Evolution: The Modern Synthesis (1942), T. Dobzhansky's Genetics and the Origin of Species (1941), E. Mayr's Systematics and the Origin of Species (1942), S.A. Cain's Foundations of Plant Geography (1944), E. Anderson's Introgressive Hybridization (1949) and continued in the 1950s with G.L. Stebbins's landmark Variation and Evolution in Plants (1950), J. Clausen's Stages in the Evolution of Plant Species (1951), J. Heslop-Harrison's New Concepts in Flowering Plant Taxonomy (1953) and A.J. Cain's Animal Species and Evolution (1954). Other seminal works included E.B. Babcock's The Genus Crepis (1947), especially Part I on the taxonomy, phylogeny and evolution of the genus (Babcock, 1947), and the landmark studies of J. Clausen, D.D. Keck and W.M. Hiesey (1940, 1945, 1948) Experimental Studies on the Nature of Species.

I still remember the eagerness with which these works were devoured: they opened up a new world of exciting ideas and dynamism and introduced one to the research that had been going on, especially in the United States, in biosystematics and evolutionary and genetic mechanisms (for a detailed analysis see Kleinman, 2009), that contrasted so strongly with the material then being taught in most university courses. Although there had been major developments in Europe, especially in genecology and experimental taxonomy and the deme terminology, as discussed below, with figures such as Danser, Du Rietz, Turesson, Turrill, Gregor, Gilmour, Böcher, Heslop-Harrison and Valentine, the literature was scattered in journals and few works of synthesis were published. In general, as I have noted elsewhere (Heywood, 2002), few taxonomic text books were available and those that did exist were out of date or scarcely stimulating: they focused largely on classification at the family level and above and on constructing so-called phylogenetic systems based on supposed trends in character evolution while largely ignoring how to undertake taxonomy at the genus and species level and below. It was largely for this reason that Peter Davis and I decided to prepare *Principles of Angiosperm Taxonomy* (Davis & Heywood, 1963), the first major textbook on plant taxonomy that had as its object "to seek out the principles and methodology of plant classification".

ATTEMPTS TO CATEGORIZE BIOSYSTEMATIC INFORMATION

Camp and Gilly's extensive 1943 paper "The structure and origin of species with a discussion of intraspecific variability and related nomenclatural problems" had been discussed before publication with, as Kleinman (2009) put it "a virtual Who's Who of the founders of experimental taxonomy or biosystematics": E. Anderson, E.B. Babcock, J. Clausen, R.E. Cleland, L. Constance, Th. Dobzhansky, N.C. Fassett, W.M. Hiesey, D.D. Keck, H.L. Mason, G.L. Stebbins, Jr., W.C. Steere, and I.L. Wiggins. In fact it was a group of botanists, zoologists, palaeontologists and others, in the San Francisco Bay area of the United States, including Stebbins, Babcock, Clausen, Keck, Hiesey, and Constance, that met weekly from 1936 to discuss the impacts of genetics, cytology and evolution on taxonomy and systematics that first proposed the term "Biosystematists" to describe themselves (Keck, 1963). From this the term "Biosystematics" (or Biosystematy sensu Camp & Gilly, 1943; Camp, 1951) derives and subsequently became widely adopted. The term "experimental taxonomy" apparently derives from the ecologist F.E. Clements (1905) and was later used by Clausen & al. (1932) and Gregor & al. (1936).

A somewhat parallel development to the San Francisco group was the creation of the Association for the Study of Systematics in Relation to General Biology in the U.K. which held its first meeting in the rooms of the Linnean Society of London on 25 June 1937 under the presidency of Dr. Julian Huxley (see Nature 140: 163–164. 24 July 1937; Winsor, 1995; Forey, 2000). It had its origins in informal meetings between members of the staff of the Royal Botanic Gardens, Kew—J.S.L. Gilmour, then Assistant Director, and W.B. Turrill, Keeper of the Herbarium—and some members of the John Innes Horticultural Institution which led to the formation of a joint botanical and zoological committee that was later renamed the Association. The members of the first council of the Association included Huxley (chairman), H.W. Parker, J.S.L. Gilmour, W.T. Calman, C.D. Darlington, E.B. Ford, R. Ruggles, H. Godwin, J.W. Gregor, E.B. Worthington and W. Wright-Smith. The ambitious aims of the Association included:

(1) to examine the theoretical and historical bases and the practical aims of taxonomy, and especially the relation of phylogeny to cytogenetic and taxonomic data;

(2) to examine the criteria employed in defining species and other systematic categories in different groups and the possibility of obtaining greater uniformity in their usage;

(3) to consider how far in the light of cytogenetic, ecological, physiological, embryological, and palaeontological data, existing classification might require to be modified and new subsidiary terminology to be introduced; further, to investigate the relation of any such subsidiary terminology to the International Rules of Nomenclature;

(4) to investigate the data and material already available, either taxonomic or bearing on taxonomy, with the view of correlating them with general biological principles and of establishing generalizations in comparative systematics.

One of the first publications from the committee was a series of essays edited by Huxley, *The New Systematics* (1940). Subsequently, the name of the group was changed to The Systematics Association which subsequently played a major role in the international development of taxonomy and systematics.

Another important strand in the history of biosystematics was the work of the Swedish Göte Turesson on genecology (Turesson, 1922a,b, 1923), although with a somewhat different focus. Turesson's pioneering transplant experiments, bringing together under controlled garden conditions plants from diverse habitats so as to elucidate which modifications were phenotypic only and which had an underlying genetic basis led to the widespread adoption of the ecotype concept. The ecotype was, however, not only an adaptational product of environmental selection (ecological race) but was also the basic unit in his genecological hierarchy-ecotype, ecospecies, coenospecies—which, although later criticized as being too typological, remains in use today by plant breeders in the gene pool concept of Harlan & de Wet (1971) to define the degree of relatedness of crop wild relatives to the crop. The narrowing of Turesson's genecological concepts by other workers such as Gregor (1939) and Clausen & al. (1939, 1945) so as to change the emphasis from the ecological side to the genetical aspects, had both advantages and disadvantages as discussed in a review of the taxonomic treatment of ecotypic variation that I wrote around the time of the founding of IOPB (Heywood,

1959).¹ A detailed assessment of Turesson's work and his contribution to the development of plant taxonomy is given by Chambers (1995; see also Heslop-Harrison, 1953, 1964).

My mentor in genecology was J.W. Gregor, a leading member (and director 1950-1965) of the Scottish Plant Breeding Station at East Craigs and later Pentlandfield, outside Edinburgh, and I spent many an afternoon there in the war time Nissen hut where he had his laboratory, learning from him. Gregor was a key figure in the development of biosystematics although often underappreciated: as early as 1927 he started a series of publications with F.W. Sansome on the genetics of wild populations and in the 1930s Gregor and his co-workers undertook a series of studies under the title of "Experimental Taxonomy", the principles of which were set out by Gregor & al. (1936). His 1931 paper on the experimental delimitation of species in some ways anticipates the kind of discussions initiated by the Bay group in the U.S.A. He also published a series of papers discussing the concepts of genecology, the ecotype and ecotypic differentiation (e.g., Gregor, 1942, 1946).

It was there at the Scottish Plant Breeding Station that I also met that charismatic figure Erna Bennett. Gregor and Bennett applied the genecological approach to plant breeding and introduction and Gregor also introduced the term agroecotype, the latter largely equivalent to the concept of landrace. Bennett later became one of the pioneers of the plant genetic resources movement. Her papers on historical perspectives in genecology (1964) and plant introduction and genetic conservation (1965), a term she introduced, are classics although not as well known as they should be having been published in the *Record of the Scottish Plant Breeding Station* which is not readily accessible.

The "deme" terminology was introduced by Gilmour & Gregor (1939) to meet the need "for a term that could be applied to any specified assemblage of taxonomically closely related individuals". The term deme was proposed, with appropriate prefixes to denote particular kinds of demes such as gamodeme, topodeme and ecodeme. The term was widely misused without a qualifying prefix, especially by zoologists, including Huxley, usually in the sense of a local interbreeding population (gamodeme) and by 1954 when Gilmour and Heslop-Harrison published their definitive paper on the deme terminology, and insisted on the need always to use it with a prefix, it was too late as Walters (1989) notes in his history of this innovative but ill-fated system. One of the aims of the deme terminology was to try and bridge the gulf between traditional taxonomists and those engaged in evolutionary and experimental approaches as Winsor (2000) notes in her account of Gilmour and The New Systematics.

By the 1950s, the focal point of the biosystematics debate had to a large extent moved from the United States back to Europe and I remember taking part in numerous discussions, often lasting long into the night, on these issues with many of the protagonists.

¹ Based on a paper I gave at the Systematics Association symposium on Function and Taxonomic Importance where I found myself the sole botanical speaker on the programme! It was also the first time I had met Julian Huxley.

■ THE CREATION OF IOPB

In his review of the development of experimental methods in plant taxonomy in the period 1920–1950, Hagen (1983) concludes:

Despite the optimistic predictions of some early experimental taxonomists ..., experimental taxonomy did not constitute a revolutionary revision of general taxonomic theory or practice. By the end of the 1940s most taxonomists viewed experimental taxonomy as a limited, though important, area of research situated on the borderline between taxonomy and other biological disciplines. Experimental taxonomy for a number of reasons. Most importantly, the methods used by experimental taxonomists during the period 1920–1950 were largely restricted to studying the lowest taxonomic categories.

What then led some of us to propose the creation of a new organization for plant biosystematics? I cannot endorse Hagen's assessment. On the contrary, the conditions during the wartime and postwar 1940s scarcely allowed any definitive agreement to be reached on the role or potential of experimental taxonomy/biosystematics. Communication and contact between those taxonomists still in post was restricted and moreover, as I have outlined above, several significant developments took place in the 1950s (and continued into the 1960s). Indeed, it was partly the renewal of contact between systematists on both sides of the Atlantic in the 1950s and the gradual availability of hitherto inaccessible literature that created the intellectual stimulus that created the circumstances in which the International Organization of Biosystematists (IOB) had its origins. On the one hand, there was a strongly growing interest, especially amongst younger workers, in applying these new ideas and thereby revitalizing plant taxonomy. On the other hand, there was a growing sense of frustration that much of the taxonomic "establishment" as reflected in IAPT and its journal Taxon did not adequately reflect these developments. And at the same time, all kinds of problems were being debated about the ways in which the new information from cytogenetics, population genetics, should be handled and how if at all it should be systematised and related to formal classification, with much discussion centred around the proposals for new categories such as those of Camp and Gilly, Turesson and the deme terminology already noted. While traditional taxonomic data were brought together and synthesised in Floras and monographs, no such mechanisms existed for the gathering, coordination and synthesis of biosystematic data nor was there a means of publishing synopses of the processed data in a systematic manner (Heywood, 1962; Heywood & al., 1984).

These concerns were voiced at a joint meeting of Sections 2 and 6 of the IX International Botanical Congress held in Montreal in August 1959 and subsequently, as related by Heywood & Löve (1961), an International Committee on Biosystematic Terminology for which I acted as secretary was set up by the Council of IAPT and it held its first meeting in Copenhagen in September 1960. A point worth emphasizing is that many of those involved in the development of IOB were engaged in field and herbarium taxonomy as well as "experimental" approaches, a point also noted by Hagen (1983) in his valuable account of the early days of experimental taxonomy. We were not intent on setting up a parallel organization to IAPT as David Keck shrewdly noted in his presidential address at the first IOB symposium on biosystematics (Keck, 1963). Rather, IOB was established in agreement with the Council and Executive of IAPT of which it constituted the Committee on Biosystematics.

The first symposium on biosystematics organized by IOB (as it then was) was held in Montreal in the first week of October 1962 (Heywood & Löve, 1961). It had a stellar cast of speakers—D.D. Keck, T.W. Böcher, W. Gajewski, J.W. Gregor, H. Lewis, A. Löve, B. Lövkist, H. Merxmüller, W.H. Wagner and the proceedings were published as volume 27 of *Regnum Vegetabile* (Heywood & Löve, 1963).

RETROSPECT AND PROSPECT

I had the privilege of knowing most of the key figures involved in the development of biosystematics and am alas the only survivor of the original group that founded IOPB. Since the early days of IOPB, I have witnessed and often participated in the major and even more dramatic changes that taxonomy has subsequently undergone, most notably the revolutionary impacts of the use of DNA sequence data and their interpretation using cladistics, phyletic and other analytic procedures. It is ironic, however, that today we need reminding that plant species are not just phyletic lineages that deserve taxonomic recognition but consist of dynamic evolving populations whose reactions and relationships can only be fully understood by applying the lessons we have learnt from biosystematics and experimental taxonomy. There is an echo here of the circumstances that led to the development of biosystematics. Furthermore, the need for handling and synthesising the data of biosystematics, which was one of the reasons behind the establishment of IOB/IOPB, remains a challenge that has yet to be resolved, even in these days of proliferating computerized databases and information systems. IOPB still has an important role to play.

LITERATURE CITED

- Babcock, E.B. 1947. The genus *Crepis*. Part 1. The taxonomy, phylogeny, distribution, and evolution of *Crepis*. Part 2. Systematic treatment. *Univ. Calif. Publ. Bot.* 21–22: 1–1013.
- Bennett, A. 1964. Historical perspectives in genecology. *Rec. Scott. Pl. Breed. Sta.*, 1964: 49–115.
- Bennett, A. 1965. Plant introduction and genetic conservation: Genecological aspects of an urgent world problem. *Rec. Scott. Pl. Breed. Sta.*, 1965: 17–113.
- Camp, W.H. 1951. Biosystematy. Brittonia 7: 113-127.
- Camp, W.H. & Gilly. C.L. 1943. The structure and origin of species with a discussion of intraspecific variability and related nomenclatural problems. *Brittonia* 4: 323–385.
- Chambers, K.L. 1995. The contributions of Göte Turesson to plant taxonomy. Pp. 37–55 in: Kukeberg, A.R., Walker, R.B. & Leviton,

A. (eds.), Genecology and ecogeographic races: Papers in the biological sciences presented at the 73rd Annual Meeting of the Pacific Division AAAS on the occasion of the 100th anniversary of the birth of Göte Turesson. San Francisco: Pacific Division AAAS.

- Clausen, J., Keck, D.D & Hiesey, W.M. 1932. Experimental taxonomy. Yearb. Carnegie Inst. Washington 31: 201–205.
- Clausen, J., Keck, D.D. & Hiesey, W.M. 1939. The concept of species based on experiment. *Amer. J. Bot.* 26: 103–106.
- Clausen, J., Keck, D.D & Hiesey, W.M. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. *Publ. Carnegie Inst. Washington* 520: 1–452.
- Clausen, J., Keck, D.D & Hiesey, W.M. 1945. Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autopolyploidy, with examples from the Madiinae. *Publ. Carnegie Inst. Washington* 564: i–vi, 1–174.
- Clausen, J., Keck, D.D & Hiesey, W.M. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. *Publ. Carnegie Inst. Washington* 581: 1–129.
- Clements, F.E. 1905. *Research methods in ecology*. Lincoln, Nebraska: University Publishing Company.
- Davis, P.H. & Heywood, V.H. 1963. Principles of angiosperm taxonomy. Edinburgh & London: Oliver & Boyd.
- Forey, P. 2000. How we were born. Syst. Assoc. Newslett. 15: 3-4.
- Gilmour, J.S.L. & Gregor, J.W. 1939. Demes: A suggested new terminology. *Nature* 144: 333.
- Gilmour, J.S.L. & Heslop-Harrison, J.W. 1954. The deme terminology and the units of micro-evolutionary change. <u>Genetica 27</u>: 147–161.
- Gregor, J.W. 1931. Experimental delimitation of species. New Phytol. 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 Phytol.* 38: 291–322.
- Gregor, J.W. 1942. The units of experimental taxonomy. *Chron. Bot.* 7: 193–196.
- Gregor, J.W. 1946. Ecotypic differentiation. New Phytol. 45: 254-270.
- Gregor, J.W., Davey, V. McM. & Lang, J.M.S. 1936. Experimental taxonomy. I. Experimental garden technique in relation to the recognition of the small taxonomic units. *New Phytol.* 35: 323–350.
- Hagen, J.B. 1983. The development of experimental methods in plant taxonomy, 1920–1950. *Taxon* 32: 406–416.
- Harlan, J.R. & de Wet, J.M.J. 1971. Towards a rational classification of cultivated plants. *Taxon* 20: 509–517.
- **Heslop-Harrison, J.** 1953. *New concepts inflowering-plant taxonomy*. London: Heinemann.

- Heslop-Harrison, J.W. 1964. Forty years of genecology. Pp. 159–247 in: Cragg, J.B. (ed.), *Advances in ecological research*. London: Academic Press.
- Heywood, V.H. 1959. The taxonomic treatment of ecotypic variation. Pp. 87–112 in: Cain, A.J. (ed.), *Function and taxonomic importance*. Systematics Association Publication 3. London: Systematics Association.
- Heywood, V.H. 1962. The information problem in biosystematics. *Nature* 193: 935–936.
- Heywood, V. 2002. Desarollo de la botánica en los últimos años y su contribución a las ciencias ambientales y la conservación de los recursos naturales. Pp. 69–81 in: Hernández Tristan, R., Corral Mora, L. & Infante García-Pantaleón, F. (eds.), 50 Años de Biología en España. Conferencia Española de Decanos de Biología. Córdoba: Ed. Publicaciones Cajasur.
- Heywood, V.H., Moore, D.M., Derrick, L.N., Mitchell, K.A. & Van Scheepen, J. 1984. The European taxonomic, floristic and biosystematic documentation system – an introduction. Pp. 79–89 in: Allkin, R. & Bisby, F.A. (eds.), *Databases in systematics*. London: Academic Press.
- Heywood, V.H. & Löve, A. 1961. International Organization of Biosystematists. *Taxon* 10: 257–262.
- Heywood, V.H. & Löve, A. (eds.). 1963. *Symposium on biosystematics*. Regnum Vegetabile 27. Utrecht: International Bureau for Plant Taxonomy and Nomenclature.
- Huxley, J.S. (ed.). 1949. The New Systematics. Oxford: Clarendon Press.
- Keck, D.D. 1963. President's address. Pp. 7–10 in: Heywood, V.H. & Löve, A. (eds.), *Symposium on Biosystematics*. Regnum Vegetabile 27. Utrecht: International Bureau for Plant Taxonomy and Nomenclature.
- Kleinman, K. 2009. Biosystematics and the origin of species: Edgar Anderson, W.H. Camp, and the evolutionary synthesis Pp. 73–91 in: Cain, J. & Ruse, M. (eds.), *Descended from Darwin: Insights into the history of evolutionary studies, 1900–1970.* Philadelphia: American Philosophical Society.
- Turesson, G. 1922a. The species and variety as ecological units. *Hereditas* 3: 100–113.
- **Turesson, G.** 1922b. The genotypical response of the plant species to the habitat. *Hereditas* 3: 211–347.
- **Turesson, G.** 1923. The scope and import of genecology. *Hereditas* 4: 171–176.
- Walters, S.M. 1989. Experimental and orthodox taxonomic categories and the deme terminology. *Pl. Syst. Evol.* 167: 35–41.
- Winsor, M.P. 1995. The English debate on taxonomy and phylogeny, 1937–1940. *Hist. Philos. Life Sci.* 17: 227–52.
- Winsor, M.P. 2000. Species, demes, and the omega taxonomy: Gilmour and The New Systematics. *Biol. & Philos.* 15: 349–388.