2 HISTORY AND BIOGRAPHY

4 Remembering Joan (Jan) Mary Anderson (1932-2015)

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26 **Abstract**

Joan Mary Anderson, known to most people as Jan, was born on May 12, 1932 in Dunedin, New Zealand. She died on August 28, 2015 in Canberra, Australia. To celebrate her life, we present here a brief biography, some comments on her discoveries in photosynthesis during a career spanning more than half a century, and reminiscences from family and friends. We remember this wonderful person who had an unflagging curiosity, creative ability to think laterally, enthusiasm, passion, generosity and love of color and culture.

34 **Key words** Bertil Andersson • Keith Boardman • Lateral heterogeneity • Molecular organization of thylakoids • Photosystems • Stoichiometry of photosystems

36 **Early Years**

38 Jan Anderson was born in Dunedin in New Zealand and grew up in her mother's hometown, Queenstown. Her father had immigrated to New Zealand from Kent in England when he was 18 years old. After a long period of hospitalization as a result of having been thrown from a horse, he was determined to become a doctor. In fact, he became the sole doctor in the region, and hoped that his daughter would follow in his footsteps. Jan's mother suffered a long illness and died of cancer when Jan was only eight years old, but not before having inculcated in Jan a love of books, music and painting. At school, Jan did not think of becoming a scientist, but instead wanted to be a teacher, partly because some of her high-school teachers were mediocre, and she thought she could do better. She was good at English, language and abstract thought, and had an excellent memory. Jan recalled growing up in a loving family and a small caring community. Until she started school, each morning her father took her to the cottage hospital and on visits to see patients in their homes. He taught her to work hard, strive for good health, enjoy life and help as many others as possible.

Place Figure 1 (a,b, c and d) here.

After completing her schooling, Jan accepted a New Zealand Department of Education Scholarship to attend the University of Otago in Dunedin where she reveled in chemistry, physics, mathematics, psychology and philosophy (Fig. 1 (a, b, c and d) shows 4 photographs of Jan in early days of her life). She did not study biology then, and only attended an introductory medical biochemistry course. After graduating with a BSc and an MSc, in organic chemistry, Jan was offered a national PhD scholarship, but was not permitted to accept the offer because she had been supported by the Department of Education. On the other hand, she was informed that an overseas scholarship might be acceptable. Thus, she won an English-Speaking Union scholarship to study anywhere in the USA for one year, with the blessing of the Head of the New Zealand Department of Education, Dr. Beeby. However, Jan was faced with a dilemma: whether to accept the scholarship to study in the USA or gamble on getting a scholarship to attend Cambridge University in England. Dr. Beeby strongly advised Jan to “go to the New World”, advice which she took. Jan then needed to decide which university in the US to attend, and whether to continue with chemistry or move into biology. By chance, Nobel Laureate Dr. Harold Urey arrived at Otago University to give a series of lectures on the origin of the biological processes of life, two of which were about photosynthesis. He instantly became Jan’s mentor. More importantly, he recommended his friend Melvin Calvin at the University of California (UC) Berkeley as a possible supervisor.

When Jan arrived at Berkeley in 1956, she found that the University of California did not recognize her New Zealand degrees. To do research and use the library, her only option was to enroll as a PhD student, fully funded by the university as long as she obtained “good grades”. Coming from a remote place in New Zealand to the marvelous Old Radiation Laboratory (ORL), Jan felt like Alice in Wonderland. Back in the late 1930s, Samuel (Sam) Ruben and Martin Kamen at the ORL had discovered the long-lived ^{14}C isotope, which was used by Calvin, Andrew (Andy) Benson, James Al Bassham and others to trace the path of the conversion of CO_2 to carbohydrates in

photosynthesis (for this work Calvin received the Nobel Prize in Chemistry in 1961). [For a
76 glimpse of this period, see e.g., Benson (2010), Gest (2004), Govindjee et al. (2016), Kamen (1989),
Lichtenthaler et al. (2016) and Nonomura et al. (2016).] Calvin attracted a diverse stream of both
78 eminent old and upcoming young scientists from many disciplines. The atmosphere at the
workplace was electric. Calvin had little time to supervise his students, and when Jan had decided
80 on her own research project, she had to ‘sink or swim’ on her own, but this was the best way of
supporting Jan, by allowing her to pursue independent research of her choice. Of course, Jan also
82 had support from the group of outstanding visitors and students in Calvin’s lab, including Ning Gin
Pon. (For an oral history transcript of the Calvin Lab, see
84 <https://archive.org/stream/thecalvinlaboral01moserich/thecalvinlaboral01moserich_djvu.txt>.) In
her research, Jan used ¹⁴C-labeled compounds to work on the later steps in the biosynthesis of
86 chlorophyll (Chl) *a* and Chl *b* in *Scenedesmus* (Anderson et al. 1959). She completed her PhD in
three years and wrote her thesis beside a swimming pool! Dr. Beeby had given Jan five years to
88 obtain her PhD before being required to fulfill her obligations to the New Zealand Department of
Education. Thus, Jan had two “free” years before having to return to New Zealand.

90 Jan declined numerous job offers and decided instead to travel around Europe and the
Middle East, sometimes visiting major photosynthesis labs and sometimes museums and art galleries,
92 at one time even living in a kibbutz in Israel. Throughout that time, she tried to decide whether to
remain in research or take up high-school teaching. She decided against teaching when a telegram
94 summoned her to Wellington Girls’ College as Senior Science Mistress. Instead, she telephoned
John Falk, Chief of the Commonwealth Scientific and Industrial Research Organization (CSIRO)
96 Division of Plant Industry in Canberra, to ask him whether he had a position for her. Jan had
introduced herself to John Falk after he had given a seminar at UC Berkeley. With a job offer from
98 Canberra, she paid off her bond to the New Zealand Department of Education, and came to join
Keith Boardman’s laboratory in Canberra.

100 **Discoveries on the organization and composition of thylakoid membranes**

Keith and Jan worked during a time of great excitement arising from the proposal by Hill & Bendall
102 (1960) and Duysens & Ames (1962) that photosynthesis involved two separate pigment systems
performing two different light reactions, rather than just one [see Anderson (2005) and Govindjee et
104 al. (2012)]. What was missing was the experimental evidence that the two light reactions occurred
in two separate physical entities (photochemical systems). Keith Boardman and Jan Anderson (Fig.
106 2a) together obtained such evidence. Keith wrote that he incubated spinach thylakoid membranes
with a solution containing digitonin and separated the mixture by centrifugation, and that Jan was his
108 key collaborator in characterizing the composition and properties of the particles. Keith and Jan
isolated and characterized lighter particles that contained photosystem I (PS I), and heavier particles
110 that were enriched in photosystem II (PS II) (Boardman and Anderson 1964; Boardman et al. 1966).
Characterization of the particles was aided by recently acquired advanced instrumentation: an
112 Aminco-Chance dual wavelength spectrophotometer; a state-of-the-art spectrofluorometer
constructed by John Thorne (an electronics engineer); and a Cary spectrophotometer equipped with
114 an accessory for low temperature measurements, constructed in the CSIRO Divisional Workshop.
From the spectra of chloroplasts and the PS I and PS II particles at liquid nitrogen temperature Jan
116 and Keith established the presence of cytochrome *b559* in PS II (Boardman and Anderson 1967).

Place Figure 2 (a, b and c) here

118 Subsequently, Jan made a number of sabbatical visits to research groups overseas in order to
further characterize the digitonin-fractionated particles. The first visit in 1966 took her to the
120 Carnegie Institution of Washington (now, Carnegie Institution of Science) on the Stanford University
campus, where she worked with C. Stacey French (Fig. 2b) and David Fork. It was during one of
122 these visits that she began a lifelong friendship with Shirley Jeffrey, who was on a sabbatical visit,
from CSIRO Fisheries, to Mary Belle Allen's laboratory at Berkeley and where Shirley discovered
124 Chl *c₁* and Chl *c₂*. At the Carnegie, Jan also met Olle Björkman who joined the Carnegie shortly

before Jan left. Olle subsequently visited Australia for ten months in 1971 to collaborate with
126 scientists in CSIRO and the ANU on an integrated study of acclimation of the composition, function
and structure of chloroplasts of sun and shade plants in contrasting light environments. One
128 important outcome of this landmark collaboration with Olle was the demonstration that the extent of
granal stacking, the composition and the function of the chloroplasts depended on the light regime
130 (Björkman et al. 1972).

Another sabbatical visit in 1973 took Jan to Paul Levine's laboratory at Harvard University,
132 where she separated and characterized a number of photosynthetic membrane proteins from green
algae. Finally, during 1973-1974, Jan achieved her dream and visited the University of Cambridge
134 to work with Derek Bendall, with the aim of separating proteins from developing chloroplasts.
Power-cuts due to a coalminers' strike and a refrigerator explosion meant that the laboratory was
136 closed for several months. Unable to do any experiments, Jan had unlimited time to think in a
'perfect ivory tower' – her attic room at Newnham College, newly equipped with heating by North
138 Sea gas. The result was her ground-breaking 1975 review (Anderson 1975) in which she was the
first to discuss plant photosynthetic membranes in terms of the S.J. Singer and G.L. Nicholson fluid
140 mosaic model for cell membranes, pointing out that the elucidation of the organization of
photosynthetic membranes was crucial for understanding their composition, structure and function.
142 The organization of chlorophylls that facilitates efficient energy capture was seen to be particularly
intriguing, and important. Many people had believed that the pigments were not bound to proteins,
144 but free in the lipid phase of the membrane. However, in 1965, Philip Thornber demonstrated the
existence of two chlorophyll-carotenoid-protein complexes and by 1975, he had obtained three
146 complexes containing 60-75% of all the chlorophyll (see Camm and Green 2004). Later, with
laboratory technician John Waldron, Jan used her improved "green gel" method to demonstrate that
148 90-94% of the chlorophylls were bound to six different pigment-protein complexes.

The next exciting phase in Jan's research career came in 1979 when Bertil Andersson (Fig.

150 2c) arrived from Sweden on an EMBO Postdoctoral Fellowship. Bertil brought with him the
two-phase aqueous polymer partition technique developed in Per-Åke Albertsson's laboratory, which
152 allowed the separation of stacked and unstacked membrane fractions, which Jan analyzed with her
'green gel' method. Together, they obtained evidence for an extreme lateral heterogeneity in the
154 distribution of the two photosystems, in which PS I is exclusively restricted to unstacked membrane
domains (Andersson and Anderson 1980). At the 5th International Congress on Photosynthesis in
156 1980, this 'heresy' was given a rather cool reception; the bi-partite and tri-partite models for the
organization of the photosystems depicting PSI and PSII in close proximity were still favored by
158 most researchers, although James (Jim) Barber was beginning to also think in terms of lateral
heterogeneity of the two photosystems (Barber 1979).

160 With the consecutive hiring of Ta-Yan Leong from the Carnegie Institution, USA (1981)
and Wah Soon (Fred) Chow from the Glasshouse Crops Research Institute, England (1985) and the
162 return of John Evans from Cambridge (1985), all as postdoctoral fellows, Jan's attention returned to
the acclimation of the composition, structure and function of photosynthetic membranes to the
164 irradiance and spectral quality of the light environment (Anderson 1986). One notable controversy
at the time was the exact stoichiometry of the two photosystems, and whether this is fixed or variable.
166 Jan reasoned that there was no reason to expect a 1:1 ratio of the two photosystems since they are
located in different membrane domains. Indeed, it was discovered that the ratio of PS II to PS I is
168 not only considerably greater than 1.0 in higher plant photosynthetic membranes, but it varies
according to the light environment (Chow et al. 1988; Fan et al. 2007). Anastasios (Tasso) Melis at
170 UC Berkeley was also making measurements of the photosystem stoichiometry, and it was natural
that Jan went to visit his laboratory and Tasso to visit Jan's laboratory. In collaboration with Tasso,
172 it was demonstrated that growth in light that favored one photosystem over the other tended to
induce an increase in the content of the reaction centers of the other photosystem, and that the
174 quantum yield of photosynthetic oxygen evolution in limiting light was only optimal when measured

in light that resembled the growth light in spectral quality, prompting the conclusion that adjustment
of the stoichiometry of the two photosystems was a way of improving the quantum efficiency of
photosynthesis (Chow et al. 1990).

Place Figure 3 (a) and (b) here

Jan continued to attract international visitors to her laboratory (see Figure 3a, which
includes Gunnar Öquist and Bob Porra, and Figure 3b, which includes Jim Barber and Govindjee).
The visitors included: Wolfgang Haehnel from Germany; Gunnar Öquist, Cecilia Sundby and Åke
Strid from Sweden; Eva-Mari Aro from Finland; Philip van Hasselt from Holland; Brian Jordan from
England; Yun-Kang Shen, Lu-Ping Qian, Jie He and Lixia Liu from China; Youn-Il Park from South
Korea; and John Sinclair from Canada. With the skillful assistance of Jan's technician, Stephanie
McCaffery, these visitors kept Jan's lab vibrant amidst the gradual tightening of financial strings
during the 1990s.

In 1994, CSIRO decided to phase out photosynthesis research by mid-1997, when Jan was
due to retire and when MD (Hal) Hatch would have retired a year earlier. Thus, Jan moved to
Barry Osmond's "Photobioenergetics Group" in the Australian National University (ANU) in May
1996. Fred Chow also joined this group, in July 1996.

As Adjunct Professor at the ANU, Jan continued her research. Partly to stay outside of
Jan's umbrella, Fred Chow set up a lab at Weston, about 10 km from the main campus where space
was abundant. Nonetheless, the collaboration between them continued – at a distance, until Fred's
lab was burnt in the Canberra fire of 2003. A topic of mutual interest was grana stacking. Indeed,
Barry Osmond, with the help of his wife Cornelia, organized a conference at Arnsberg, Germany, in
1998 following the 11th International Congress on Photosynthesis in Budapest, with the title "Why
Grana?" to honor Jan. On the question of "How Grana?", the collaboration between Jan, Fred,
Fred's student (Eun-Ha Kim) and Peter Horton at Sheffield University led to the conclusion that the

main attractive force that overcomes the electrostatic repulsion between thylakoid membranes is
probably not van der Waals attraction (as previously thought) but has its origin in the maximization
of the entropy of the system (Kim et al. 2005).

In more recent years, Jan's attention turned from the relatively static view of the structural
organization of plant thylakoid membranes during long-term acclimation to the dynamic changes
following rapid transitions in irradiance. In 2012, Jim Barber and Peter Horton organized a meeting
on "The plant thylakoid membrane: structure, organization, assembly and dynamic response to the
environment". This meeting, held at Chicheley Hall on May 3 and 4, honored Jan and her research
achievements, and celebrated her 80th birthday. (See volume 367 of the *Philosophical Transactions
of the Royal Society of London, section B.*) In this issue are Jan's last two publications (Anderson
2012; Anderson et al. 2012): "Lateral heterogeneity of plant thylakoid protein complexes: early
reminiscences", and "Towards elucidation of dynamic structural changes of plant thylakoid
architecture."

Place Figure 4 (a, b c and d) here

Since joining the ANU, Jan's role broadened to include mentoring of students, postdocs and
early-career researchers, as well as interaction with established researchers (Fig. 4a, b, c, d; see e.g.,
Warwick Hillier and Tom Wydrzynski in 4 (a); Min Chen in 4(b); one of the authors, Fred Chow, in
4(c) and Roberto Bassi in 4(d)). In particular, she was a role model for female researchers, a role
she was still passionately fulfilling until just before her untimely death. Jan was one of the most
internationally recognized Australian plant scientists. She was elected to the Australian Academy
of Science in 1987 and to the Royal Society of London in 1996. Jan received an Honorary
Doctorate from the University of Umeå in 1998 and the Lifetime Achievement Award from the
International Society of Photosynthesis Research (ISPR) in 2007. Other awards include the Marie
Cabbot Fellowship at Harvard University (1973), the Ann Horton Research Fellowship at Cambridge

University (1974), the Lemberg Medal awarded by the Australian Biochemical Society (1983), Life
224 Membership, and the R. N. Robertson Medal of the Australian Society of Plant Scientists (1998), the
Centenary Medal (2001) that commemorated 100 years of Federation in Australia, and Thomson ISI
226 Australian Citation Laureate in the category of Plant & Animal Science (2004). With great
dedication, Jan served on various committees of the Australian Academy of Science, as a member of
228 the International Photosynthesis Committee (1978-86), President of the Australian Society for
Biophysics (1984-85), President of the Australian Society of Plant Scientists (1992-94) and
230 Vice-President of the Australian Academy of Science, and on editorial boards of prestigious
scientific journals.

232 **Personal life**

Without biological children of her own, Jan was keenly interested in, and kind-hearted towards, her
234 friends, colleagues and their families. The most important friend was Jack Barrett, who worked in
Jan's lab from the mid-1970s to the early 1980s, following the closure of a medical research institute
236 in Sydney. When Jack suffered ill health from the mid-1980s, Jan looked after him until his death
in 1998. Jack's children became Jan's adopted children and Jan was particularly devoted to Jack's
238 grandchildren. This aspect of Jan's life is sensitively documented below by Martin Barrett and
Chris Barrett (Jack's sons). In a similar vein, when Fred Chow joined the Boardman laboratory as a
240 postdoc in 1977, Jan orchestrated the arrangements for his wedding ceremony at Commonwealth
Park, on the shores of Lake Burley Griffin in the National Capital. In 1985 Fred left a job in
242 England to return to Australia as Jan's postdoc. Thus, for the past 30 years, Jan has been Fred's
boss, colleague and mentor, and a close family friend. Not only was Jan a passionate and creative
244 scientist, but she was also a warm-hearted human being. She is greatly missed but will be long
remembered by her friends.

246

Comments by others, arranged alphabetically by last name

248 **Bertil Andersson (Singapore)**

Excerpt from a speech given on October 6, 2015, at the memorial celebration of Jan's life and
250 *legacy, National Arboretum, Canberra*

It is still hard for me to comprehend that Jan is gone. Only in July we spent many days together in
252 London during a scientific meeting at Royal Society and Imperial College London as well as at a
private function with Jim Barber in West Sussex. Jan stayed with me and my family at a nice
254 countryside hotel and when we said goodbye on the 19th of July after some very nice days together in
the beautiful Sussex ambiance, no one had a feeling that this was saying goodbye forever. Life
256 is unpredictable. Jan invited me to come here to Canberra in the following November, and as
always she had last minute reminders to me on urgent things I had to do in the weeks to come,
258 contact several persons and collect x amount of information that I needed to send to her; it was just
the same as it had been when I was her post doc.

260 During those nice days in the English garden landscape also my daughter Matilda and her
family joined Jan, myself and my wife Susana. As some of you may remember my oldest daughter
262 was born here in Canberra so she is a real Aussie (hence the name) and she was always close to Jan
and regarded her sort of the Godmother. On this occasion Jan for the first time met Matilda's 2
264 year old daughter Elsie, which was very nice and also meaningful to us all.

I meet Jan for the first time in 1977 but before that I had extensively studied her scientific
266 papers. In 1972 I started my PhD work in Sweden at Umeå University in the Swedish Siberia far up
north. My task was to sub-fractionate chloroplast membranes with a special separation method
268 developed by my supervisor, Professor Per-Åke Albertsson. I then came across several papers from
the late 1960s authored by Jan Anderson and Keith Boardman. The papers from the Canberra
270 scientists gave me crucial directions in my thesis work. In 1975 Jan Anderson published a review
on the molecular architecture of the photosynthetic membranes or the thylakoid membranes which
272 is the correct term. For me as a PhD student that paper was dynamite with a high wow factor.

It put Nature's solar cells for energy conversion into the terms of modern membrane biology. This
274 seminal paper described the lateral and transverse asymmetry as well as the dynamics of the
thylakoid membranes. This paper is a citation classic and for me personally it gave me the idea to
276 try and isolate inside-out thylakoid membranes so you really could look into the various
heterogeneities of the thylakoid membranes. Jan gave me the original idea and I together with one
278 of my PhD colleagues actually succeeded to do that using our new separation technique. That opened
up a new door to look at photosynthesis and that became the basis for my thesis which I defended in
280 1978.

But already the year before in 1977 there was the 4th International Congress on
282 Photosynthesis in Reading UK. When I finally pinned her down during the conference and I
presented my plans she was actually a little bit hesitant because she said she had absolutely no
284 money for another post doc and of course the administration of CSIRO had starved her badly. I
was actually not taken too much aback by this financial detail but said that I would fix that myself.
286 And so I did. On August 27, 1979 my first wife Elisabeth and I arrived at Canberra airport and
my post-doctoral dream had become true. Jan and I combined our methods and we had some
288 significant progress in getting exciting results that suggested a quite radically different view of how
the photosynthetic machinery is built and how it operates. In 1980 we published our results of what
290 was to be called the Anderson and Andersson (1980) lateral heterogeneity model. It created a lot of
discussions and also resistance. One scientist from the UK made a firm statement that the A and
292 A model should be thrown into the waste bin. That never happened but instead our model became
quite accepted and introduced into most text books in biochemistry and plant physiology. We
294 published a lot of papers together in the years to come and we maintained close scientific and
personal contact up to now. And I am extremely grateful for this in many, many ways.

296 On the private side Jan was a very kind and caring person, but also quite demanding. As I
said, I benefitted from her mentorship but many others have had the same privilege as I have had. I

298 should also add that she had a lot of collaborations with Scandinavia and in particular with Swedes.
It started with Olle Björkman and myself but I am sure about 10 people if not more from Scandinavia
300 have spent time in her laboratory. If I should mention a few it would be Gunnar Öquist and
Eva-Mari Aro. Jan also spent sabbaticals in Sweden at various universities, and she received an
302 honorary doctorate from Umeå University.

Jan sent many letters to her collaborators. I have tried to say a lot of nice things about Jan
304 but her handwriting was not the most easy to read. I was probably the one that got most letters
(and of course this was the old snail mode of sending letters) so I acquired a certain skill to decipher
306 her messages. And actually it happened that other Swedish colleagues sent copies of her letters to
me for interpretation. Of course Jan was saved when the emails became the state of the art.

308 Jan, you were my teacher, advisor, colleague and friend and a little bit as a family member.
And I am very grateful for that. On behalf of my daughters, my wife Susana and many
310 Scandinavian colleagues I am just saying we will miss you immensely. Thank you, Jan.

Eva-Mari Aro (Finland)

312 Dear Jan,

I remember your long hair and hasty steps from the Halkidiki International Photosynthesis Congress
314 in Greece 1980. You were unreachable for me, no way of daring to talk to you. Yet, I felt like
knowing you very well – so many years I had been reading your publications. Secretly I dreamed
316 of being you, in the middle of the most hectic photosynthesis research. Producing terrific scientific
results and developing hypotheses on how the thylakoid membrane works in harvesting solar energy
318 and changing it into chemical energy to support all life forms on Earth. You were living a real and
exciting life as a scientist, and above all as a female scientist. It indeed was possible. Those were
320 the times of lateral heterogeneity of the thylakoid membrane, which also became one of the deepest
interests in my own work..... and still continues with your memory inspiring us here in Turku to

322 gain further understanding on how the thylakoid membrane is regulated.

When I started photosynthesis research in Finland together with my supervisor Niina
324 Valanne in 1975, her dream already at that time was to work with you in Canberra. Times were not
easy in those days and she never succeeded to live her dream through. For so many reasons, I felt
326 extremely happy when you accepted me to work in your lab some ten years after the Halkidiki
meeting.

328 Finally I learned to know you personally – you were so fair and straight, also demanding but
always giving your full support and credits when they were deserved – yes, you also gave criticism
330 when appropriate. Those characters I try to keep in my mind when educating my own students. In
my mind you remain as a dear and always a supporting friend and mentor.

332 Many members of the photosynthesis society had a privilege to enjoy your enthusiasm and
never-ending encouragement. I know that many of us, after publishing a paper, received a
334 delightful letter from you congratulating us on the progress we had made in photosynthesis research.
This was particularly important for the female scientists, who were close to your heart. As an
336 appreciation of your wonderful research and all your efforts in helping us, we named you a *Queen of*
Photosynthesis and crowned you with a green leaf in the pendant. This took place at the 2012
338 Royal Society Meeting, held in Chicheley Hall on “Structure and dynamics of the thylakoid
membrane”, and this is how we always remember you.

340 ***James (Jim) Barber (UK)***

In 1967 I wrote to Professor L.N.M. Duysens at the State University of Leiden asking if I could join
342 his laboratory as post-doc. He replied back enthusiastically (Note that I did have my own
fellowship!) and in describing his facilities he made mention of their capability to make “Boardman
344 and Anderson” particles. I had absolutely no idea what he meant. However I was aware that there
was evidence that PS II and PS I could be partially separated into two distinct biochemical entities

346 which was hard to believe in the context of the Z-scheme at that time. How then could the two
photosystems be tightly redox coupled? I asked myself. Of course it was Jan Anderson working
348 with Keith Boardman who made this ground making discovery and it was the beginning of our
understanding of how the Z-scheme was a transmembrane system.

350 While I was in Leiden I worked a great deal on purple photosynthetic bacteria and I never
had a reason to isolate B&A particles but on taking up a lectureship at Imperial College London a
352 year later, I did start to work on higher plant thylakoid membranes, looking at prompt and delayed
chlorophyll fluorescence and the effect of ion gradients and membrane potentials. Although I was
354 aware of the excellent biochemical work of Jan Anderson, it was not until 1975 that she wrote to me
from Cambridge where she was on sabbatical. She had heard that I was organizing and editing
356 the first volume of Topics in Photosynthesis entitled "The Intact Chloroplast" published by Elsevier
in 1976. She offered me a manuscript for including in the book entitled "The molecular
358 organization of chloroplast thylakoids." It was truly an excellent and very thoughtful overview of
how the photosynthetic electron chain could be integrated into the fluid-mosaic membrane model
360 of Singer and Nicolson. I would have been more than happy to have included it in the book but she
later informed me that she had also sent it to *Biochimica et Biophysica Acta* and they had accepted
362 it (Anderson 1975). In my opinion this was one of her very best contributions and I have drawn the
attentions to others emphasizing its ground breaking nature at a critical time when membrane biology,
364 protein biochemistry and molecular biology were starting to emerge as tools to unravel the molecular
details of the light reactions of photosynthesis.

366 **Place Figure 5 here**

In 1979 the CIBA Foundation in London asked Professor Sir George Porter and myself to
368 organize a meeting on photosynthesis. We decided to focus on Chlorophyll Organization and
Energy Transfer in Photosynthesis, specifically energy transfer that occurred between discrete
370 pigment-protein membrane complexes rather than a tightly coupled system envisaged in the tripartite

model of Warren Butler. Thus we invited not only Warren Butler, but Jan Anderson and Andrew
372 Staehelin to put the fluid-mosaic model of membrane structure into the discussions. [Figure 5 shows
Jan with Warren Butler and Pierre Joliot at that meeting.] I guess this was the beginning of
374 recognizing the importance of protein biochemistry and structure in understanding the biophysics of
energy and electron transfer in photosynthesis and Jan Anderson deserves the credit for this
376 important development.

Because of this I developed a close friendship with Jan Anderson which involved several
378 trips to see her at CSIRO/ANU in Canberra and when she came to the UK I would meet her in
London. In 2012, Peter Horton and I organized a Royal Society Discussion meeting to celebrate
380 Jan's 80th birthday, and in July 2015 she came to the UK to attend my 75th birthday party at
Imperial College and my 50th wedding anniversary garden party at our Cottage in West Sussex.
382 Just before these social events I organized a meeting at The Royal Society entitled "Solar Fuels:
From Materials to Devices" as it relates to artificial photosynthesis. Jan attended along with Fred
384 Chow, and I was amazed to see Jan at every talk despite most of them being non-biological. At 83
years she was still hungry to learn new things. At that time it was impossible to imagine that a
386 couple of months later she would die. Jan Anderson was an outstanding scientist and special
human being who became a great friend. I will miss her and her regular emails, her scholarship and
388 her close friendship.

Chris Barrett (Australia)

390 *Excerpt from a speech given on October 6, 2015, at the memorial celebration of Jan's life and
legacy, National Arboretum, Canberra*

392 I am deeply honored today to speak on behalf of Jan's family and friends. My first reflection is the
relationship between Jan and my father, Jack Barrett, another scientist and explorer of life. Jan first
394 met my father in about 1965 when they were both in the San Francisco Bay area – he at Berkeley,
she at Stanford. Jan and Jack became emotionally engaged in 1977, when my father moved to

396 Canberra to work at CSIRO. [Fig. 6a shows Jan and Jack on an excursion in the mountains.]

Place Figure 6 (a, b) here

398 Jan quickly became part of the family network, although I won't pretend it was always plain
sailing, either with my father or the broader family. How could it be otherwise, when my father
400 was such an enigma, and the pains of the breakdown of his marriage endured for so long? Jan's
place in our life was cemented by the birth and nurturing of another generation. Jan had enormous
402 affection for Jack's grandchildren and for us Jan was a constant fixture at family events like
Christmas and birthdays and other big occasions for over 30 years. Not only was she there, but she
404 gave practical support and made us realize how lucky we were to have a family.

As Jan became more and more wrapped up in our lives, and as Jack gradually faded away,
406 we learnt more about Jan in her own right, about her upbringing and early career, about what gave
her joy and about what gave her inspiration. That said, I'm still not sure that I know all I should
408 know about Jan, or understand how the myriad facets of her life intertwined. Why, for example, I
used to ask myself, should she continue to be so loyal to her step mother Mollie, when it seemed
410 from what she told us that their relationship had provided little but angst for Jan. It was obvious
that Jan led a life of obligations, from which she could sometimes but not always break away. This
412 to me is the clue as to why she seemed at times so agonizingly to procrastinate when to others the
way forward seemed so simple. Yes, she was a dutiful daughter, and superego gripped her fiercely
414 but, as I said, she could break out of the mold at times. My theory is, it's more likely she simply
ended up someplace she never dreamed of, a world renowned scientist by accident not design.

416 Let me share a couple more points about Jan. Jan was immensely gregarious. Sociability
was her mainspring. I'm sure that's the only way she put up with me. My way of doing things
418 and approaching life on occasions drove her to frustration. But one thing she always loved was a
vigorous debate, so we always had something in common. And from what I can tell, this is how she
420 lived her scientific life, and it propelled her to keep going, even when she experienced heated

resistance from scientific colleagues and competitors.

422 Something else mattered even more. Jan was permanently, fundamentally, furiously
curious. Her eyes lit up at the sight of new people or new ideas, and she never tired of testing her
424 discoveries. What did they think? What did they do? Jan was possessed of a remarkably
energetic and creative mind.

426 In life and in science, Jan was prone to accidents, literally and figuratively. The physical
accidents we all know about and frankly it's a wonder they didn't hold her back. But Jan's
428 accidents also thoroughly enriched her career and life. By accident, Jan heard a leading
photosynthesis researcher speak at Otago University, so learnt of Berkeley as a leading American
430 research center. By accident, Jan buttonholed the NZ Minister for Education, who advised her to
seek out the New World to pursue further studies. By accident, Jan ended up saving enough while
432 in the New World to back pack around Europe at the end of the 1950s and in the process to make
lifelong friends. By accident, Jan's path crossed my father's when they were both researching in
434 the Bay Area in 1965 and, by accident, they ended up working in the same lab in Canberra in 1977.
Jan was a scientist by accident; Jan came into my family by accident. Thank goodness for accidents!

436 On behalf of family and friends, we will miss you, Jan, but we will not forget you.

Martin Barrett (one of the authors of this paper, Australia)

438 *Eulogy given at Jan's funeral*

Family, friends and colleagues of Jan, our champion has gone. Joan Mary Anderson, who we know
440 as Jan, is no more. I have said so many goodbyes to her in the past several weeks and shed many
tears. Today is our final goodbye. Soon enough her ashes will start their journey to her mother
442 Mary's grave in Queenstown, New Zealand.

Jan's stellar intellectual career was a journey, one which she gave in a full blooded and
444 generous way to the world of science and the world of humanity. It was a journey of intellectual

curiosity that took her to California and to the door of Nobel Laureate Melvin Calvin, and afterwards
446 principally to Australia, to the UK and to Sweden, to conferences and to meetings throughout the
world. New Zealand was generally somewhere on her itinerary each year.

448 It was through my dad that I met Jan. Somewhere in the mid-1970s he came to Canberra,
a refugee from the closure of Dr Rudi Lemberg's laboratory in Sydney and a protracted marriage
450 break up. One of Jan's great attributes was to see the positive in a person and to draw it out and
champion it. Despite some imbalance in their relationship they benefited tremendously from each
452 other's companionship. In 1984 Jack's scientific career ended abruptly. He returned from a year at
Rockefeller University in a wheelchair, to a triple bypass operation and 15 years of struggle with
454 Parkinson's disease, which Jan nursed him through.

Dad enlarged Jan's world enormously; he had a genuine feeling for and knowledge of a
456 wider culture than science that she greatly appreciated. He had an eclectic knowledge of the world
that touched on so many areas – art, archaeology, ceramics, poetry, languages, theatre, literature,
458 film and history. There is something of my dad in all of his four children and Jan could see and relate
to it in each of us: in myself – art, music and European culture; in brother Roger, architecture,
460 American culture and financial investment; in sister Marion, something imaginative, something
spiritual, and the world of Nature, yet also a talent for languages; in brother Chris, just about
462 everything – he is a Renaissance man as my dad was.

Jan's knowledge of art often surprised me. Her house is full of lovely ceramics and
464 pictures, in particular watercolors. We quite often would sit by her pool and watch cloud-scapes,
sunsets or approaching storms; sometimes it was the early morning spectacle of hot-air balloons.
466 She had an immediate and acute eye, which as a scientist must have been of great benefit. I
frequently visited the National Gallery of Australia with Jan; our most recent visit was to the James
468 Turrell exhibition where we had one of our familiar animated discussions comparing our different
responses to his work. The intensity and freshness of Jan's interest and perception has always

470 impressed me. I was puzzled at how she could respond with such a practiced eye, until in one of
her many anecdotes Jan told me how, after she wrote up her PhD thesis in California, she went off
472 to Europe using saved funds from her scholarships. Somehow her passport was stolen in Florence.
She sensibly entertained herself for the next six weeks while waiting for its replacement by
474 saturating herself in the contents of Florence's art museums.

Jan was an intrepid explorer, forever bold, undaunted and confident; an independent,
476 energetic and willful traveler in the worlds of ideas and places. She had the kind of free spirit that
is untamed by modern large cities, that responds so immediately to Nature and feels so confident
478 amongst it. Jan often used to describe the freedom of her youth, where she would roam freely while
her country doctor father worked. How much she hated the petty controls of boarding school.
480 How much she always backed herself against the system to get to where she wanted to go – how she
defied the University of California to get the PhD supervisor who didn't supervise PhD students;
482 how she roamed illegally behind the communist controls of Czechoslovakia. Something of the
latter experience gave her a bond with her great friends Lou and Tanya.

484 Jan and I have been friends for 40 years; she has known many details of my family life and
helped a great deal with a particular medical challenge some years ago. Whether agony aunt, friend
486 or step-mother she helped my siblings also. I am glad that I was able in recent weeks to return just
a little of the steadfast love and care that she gave my dad for so many years.

488 To me Jan has been a wonderful, stimulating, dedicated and generous friend. Never
precious, never pompous, not always understanding, but consistently loyal deep down.

490 Jan was delighted to see in the past year how happy I had become in my changed personal
circumstance. Jan took a shine to Caroline who helped her through several medical and
492 administrative emergencies. Caroline persuaded Jan to have the photo taken on Tuesday, August 4
at an Academy of Science reception and lecture. There is Jan, beaming smile, strong jaw and bright
494 eyes (Fig. 6b). The next evening she fell from her stool in her kitchen while talking on the phone,

compounding an earlier sequence of blows to her head. After three weeks of surgeries and
496 intensive care in hospital we were forced to admit defeat and to let her pass peacefully from the
embrace of our small group – my sister Marion, my partner Caroline, my nephew Alexander, and me.
498 And so her spirit passed.

So farewell Jan, larger than life, indomitable spirit, faithful friend. It has been a
500 remarkable friendship through my Dad, and my life has been the richer for it. A little of you is in
each of us, and a very large love for you, in me.

502 ***Keith Boardman (Australia)***

My contribution to this celebration of the life and science of Jan Anderson mainly relates from the
504 time she joined my laboratory at the CSIRO Division of Plant Industry in 1961 until about 1977
when I left Plant Industry to join the governing body of CSIRO. In 1960, a new research scientist
506 position was made available to me for research on the state of chlorophyll in plants and I was indeed
fortunate to be joined by a colleague of the caliber and potential of Jan Anderson.

508 I had developed a procedure for the separation and purification of haem proteins by
ion-exchange chromatography during my PhD at Cambridge. John Falk, the head of the
510 biochemistry section at Plant Industry was a porphyrin biochemist and it was appropriate that I
should attempt to isolate chlorophyll protein complexes. Unlike hemoglobin and myoglobin,
512 chlorophyll is not soluble in aqueous solvents. A number of ionic and non-ionic detergents were
used for the extraction of chlorophyll but the solubilized chlorophyll did not exhibit the
514 photochemical properties of chlorophyll *in vivo*. Fred Collins, a lipid biochemist at the ANU told
me that digitonin, a non-ionic natural detergent had been used to solubilize an active retinene
516 complex from the rods of the eye. I incubated spinach chloroplasts with a solution containing
digitonin and separated the mixture by centrifugation. A surprising result was obtained. It
518 appeared that a separation of the two photochemical systems of photosynthesis had been achieved.

The light particles contained PS I and the heavy particles were enriched in PS II. Jan was my key
520 collaborator in characterizing the composition and properties of the particles.

We developed a method for measuring the cytochromes of chloroplasts and the particles
522 from the digitonin treatment without the need to extract the chlorophyll. It involved the use of a
Cary spectrometer with a scatter transmission attachment and cuvette assembly designed by Cyril
524 Appleby and constructed in the divisional workshop. We showed that cytochrome *f* and
cytochrome *b6* were in the PS I fraction and we found a new cytochrome (cytochrome *b559*) located
526 in PS II. We also elucidated the role of the cytochromes from light-induced absorbance changes.
For fluorescence measurements we collaborated with John Thorne, an electronics engineer in the
528 laboratory who designed and built a spectrofluorometer suitable for the accurate measurement of
chlorophyll fluorescence spectra. Fluorescence measurements of the particles produced by
530 digitonin confirmed that the fluorescence emitted at 735 nm originates mainly from PS I and that
emitted at 683 nm and 693 nm arises primarily from PS II.

532 Jan and I also enjoyed a successful collaboration in several other research projects. These
included the formation of chloroplasts and the development of photochemical activity during the
534 greening of dark grown bean plants and the photochemical properties of the mesophyll and bundle
sheath chloroplasts of plants with the C4 pathway of photosynthesis. We also had a successful
536 collaboration with Olle Björkman, a visitor to the ANU from the Carnegie Institution at Stanford and
with Barry Osmond on the comparative photosynthesis of sun and shade plants.

538 Jan and I shared the same laboratory over some 16 years. She was a great companion, so
enthusiastic about the research and cheerful even if the result of an experiment was disappointing.
540 Jan was a well organized person not only in the laboratory but in her life that included a love and
appreciation of the visual arts and classical music. Her friendly and cooperative attitude made her
542 popular with the members of the Biochemistry Section. She loved being a research scientist
although she thought there was prejudice against women.

544 Jan and I maintained regular contact and she kept me up to date on the latest research on the
structure of the thylakoid membrane and the photochemical systems of photosynthesis. She phoned
546 me just before her last trip to London in July to inform me about the meeting at the Royal Society
on artificial photosynthesis. I shall indeed miss her.

548 ***John Evans (Australia)***

Excerpt from a speech given on October 6, 2015, at the memorial celebration of Jan's life and
550 *legacy, National Arboretum, Canberra*

During my PhD, I became aware of the exciting concepts that Jan Anderson was proposing for the
552 "light reactions" of photosynthesis. Unlike the argumentative scientific reviewers, I naively
accepted her concepts and was drawn to the experimental evidence she produced. There were two
554 main ideas. Firstly, together with Bertil Andersson, Jan proposed lateral heterogeneity in the
thylakoid membranes with appressed grana regions lacking PS I (Andersson and Anderson 1980).
556 That meant that the two photosystems did not simply slosh around together interacting alongside
each other in the membrane. How did light get divided between the two photosystems and how did
558 electrons pass between them? Their proposal was heretical and contrary to the dogma at the time.
Secondly, plants adapted to their light environment by altering the relative amounts of the major
560 protein complexes in the thylakoid membranes. While some could accept that relative pigment
contents varied, there was strong opposition to the notion of flexibility in the ratio between the two
562 photosystems. Together with Ta-Yan Leong, Jan published a series of papers in the early 1980s
demonstrating the effects of growth light and spectral composition on thylakoid proteins and
564 pigments. As I reviewed literature to construct the first chapter of my thesis, I was wondering if
there was a possibility that it provided a way to investigate the relationship between photosynthesis
566 and the biochemistry of light capture, electron flow and ATP synthesis. So, I applied for a CSIRO
post-doctoral fellowship proposing to work in Jan's lab. In those days, the fellowship paid for a
568 period of study overseas followed by a period back in Australia. I had begun experiments looking

at the effect of growth light on photosynthesis while I was in the UK and returned to Jan's lab in
570 CSIRO Division of Plant Industry, Canberra in July 1985.

At that time, Jan's lab consisted of Ta-Yan Leong who was in the process of moving up to
572 CSIRO administration, Fred Chow who had just arrived from the UK and Stephanie McCaffery. In
the next lab was Robert (Bob) Porra working on chlorophyll chemistry and David Goodchild and
574 Celia Miller contributed their microscopy expertise. Ronald (Ron) Pace also used to come in
regularly to discuss the oxygen evolving complex. Jan gave me free reign to do what I liked and
576 Fred and Steph taught me many techniques. It was a happy and busy lab and we celebrated
successes with drinks leaning against the lab benches and shelves filled with various chemicals.

578 Jan identified three main attributes required for a successful researcher: an unflagging
curiosity, enthusiasm/passion, and a creative ability to think laterally.

580 Clearly, Jan exemplified the first attribute of unflagging curiosity. In 2004, 7 years after
'retiring', the Institute of Scientific Information identified Jan as a citation laureate. Her continued
582 prolific publishing was having an impact. This year she had travelled to the UK to attend scientific
meetings in London and Cambridge and on the day before she fell at home, she had been at a lecture
584 at the Australian Academy of Science. She avidly read the literature and often drew my attention to
papers that she had just come across. Although she suffered from an arthritic knee that constrained
586 her mobility, her mind was remarkably sharp.

Jan's enthusiasm for the "light reactions" of photosynthesis was infectious. The process of
588 changing accepted dogma is fraught with difficulty and from stories Jan recounted, this was not
made easier by her being a woman. While some barriers towards women in science have been
590 lowered, there is still much to be done.

Creative thought. Jan demonstrated independence throughout her life. She was forever
592 dreaming up new ideas. While on sabbatical leave in Cambridge during 1973, a coal miner's strike

prevented her from doing experimental work. Instead she dreamt about how the two photosystems
594 were arranged within the thylakoid membranes. The result was a seminal article (Anderson 1975),
filled with speculations, but translating the Z scheme into the concept of molecular complexes
596 distributed within photosynthetic membranes. As Jan said "*Perhaps my most celebrated and
initially heretical concept together with Bertil Andersson was to demonstrate that the plant
598 photosystems are actually separated from one another and occur in different membrane domains.*"
While the lateral heterogeneity model eventually displaced the colocation model, there remain many
600 aspects that are still uncertain such as how much light is absorbed by PS I versus PS II.

While Jan was an ideas person, she also generated experimental evidence using the latest
602 available instruments and developing new techniques. She used gel electrophoresis to separate
different intact pigment protein complexes. She utilized electron microscopy and immunology to
604 localize proteins and their orientation in membranes. She quantified the components of the
thylakoid membrane and demonstrated that their relative abundance varied in response to the
606 environment or in mutants.

Perhaps it was her love of color that reflected her passion for the light reactions of
608 photosynthesis. She wore colorful clothes that expressed her vibrant personality, created colorful
diagrams that were memorable and impactful and she has left a colorful scientific legacy.

610 ***Govindjee (USA)***

I have fond memories of Jan Anderson. She was always very kind and friendly to me. And, I had
612 great fun whenever we met at conferences. My last interaction with Jan, before she passed away,
was when I was preparing a Tribute, with Winslow Briggs, for Jan Brown (of the Carnegie Institute
614 of Sciences at Stanford). She wrote wonderfully well about her interactions with Jan B. in the
article. Unfortunately, right after sending me her draft, she was not well, and then passed away
616 while the paper was at the typesetters. My e-mails remained un-replied; it was a very sad time for

me.

618 I remember two totally different things related to Jan. The *first* was in Europe, when we were
all together at a conference and we were going to another conference by train. It was during 1972, I
620 believe I noticed Jan and Keith Boardman were going to be on the same train – but I was literally
shocked to see Keith transporting two suitcases, one a normal one and another a huge steel case!
622 Then, he had another one that he left for me to look after until he returned to take that also. I asked
Keith why he was carrying so much on this trip. He gently responded that this heavy one belonged
624 to Jan! I quietly moved away fearing being volunteered to take care of Jan's suitcase.

Obviously, she carried a household, it seems, when she travelled! The *second*, a more serious one,
626 has to do with my first academic encounter with her research. In 1960, we had discovered two light
effects in chlorophyll *a* fluorescence (Govindjee et al. 1960), and during 1963-1964, I had found an
628 emission band at 696 nm (F696) at 77 K, as well as a band at 693 nm (F693) at room temperature
when photosynthesis was blocked. We were struggling to understand which band came from which
630 photosystem: I or II; antenna or reaction center? We suspected and suggested that these new bands
arose not from the major antenna, but from some “energy trap” in PSII. One day, I went to the
632 Biology Library and discovered to my surprise and delight a paper in *Nature*, published by Keith
Boardman and Jan Anderson (1964). Excitedly, I rushed back to the lab and told Carl Cederstrand
634 about it and we began to prepare the heavy (presumably PS II) and light (presumably PS I) particles
as in Jan's work with Keith to understand the origin of the various fluorescence bands at room
636 temperature as well as at 77K. Cederstrand and Govindjee (1966) published a *Short
Communication* showing that the Photosystem II fraction, which had a lower degree of polarized
638 fluorescence, a lower Chl *a*/Chl *b* ratio, and a higher ratio of F696/ F735. This was published in
May 1966. To my surprise, I discovered a thorough paper by Boardman, Thorne and Anderson
640 (1966) published in August 1966, on this very topic. Although I was somewhat happy that Jan and
Keith did cite our earlier attempt to understand the nature of F693 nm, I said to myself “*Well*

642 *Govindjee, accept defeat, but since they are nice people, you may have to carry Jan's suit case next*
time you meet her." That opportunity never came and now I miss her. She was such a great
644 person and such a great scientist that the photosynthesis community will miss her.

Peter Horton (one of the authors of this paper)

646 Jan Anderson was a beacon, shining throughout my research career, from when I was a PhD student
in the 1970s until the present day. Over several decades she carried out ground-breaking research
648 on the structure and function of thylakoid membranes, pioneering the methodology for isolation of
the protein complexes present and for analyzing their composition, discovering how they are
650 organized in the thylakoid membrane and how this composition and organization responds to the
external environment of the whole plant. Jan's review articles had great impact; three stand out for
652 me: her 1975 review "Molecular organization of chloroplast thylakoids" was a bible, a source of
information and inspiration during my early years; her outstanding Trends in Biochemical Science
654 article written in 1982 with Bertil Andersson has stayed in my mind ever since as a beautiful
depiction of the organization of thylakoid membranes and as a model in science communication; and
656 finally the article written in 1995 co-authored by Fred Chow and brilliantly entitled "The grand
design of photosynthesis". This article was, and still is, the most complete statement of the
658 dynamic acclimation of the photosynthetic apparatus to environmental cues; it guided all my work
on this topic and was compulsory reading for all incoming members of my research group.

660 Her scientific contributions are immense and lasting of course, but Jan gave much more
than that. Most notable was her support for her colleagues, especially young scientists and her
662 boundless enthusiasm for photosynthesis and for life in general. Jan helped me through the
difficult times we all face in our lives and our careers, through many kind and supportive emails.
664 *How I will miss those emails, usually chaotic, but so full of ideas, and so human!*

I first met Jan in the early 1980s at a photosynthesis workshop in Japan and I still remember

666 how thrilled I was when she came up to complement me after my presentation. Now, thirty years
later, it is a great privilege for me to be able say that Jan was a friend, a trusted colleague and a great
668 collaborator, and to have co-authored three papers with her. I am particularly proud to have been
invited by Jan to contribute to one of her last papers published a couple of years ago, “Towards
670 elucidation of dynamic structural changes of plant thylakoid architecture” (Anderson et al. 2012),
which demonstrated her unstoppable passion, insight and creativity, in the field of research which
672 will forever be associated with her name. How pleased I am that I was able to assist Jim Barber in
giving Jan such a great 80th birthday event at the Royal Society Meeting at Chicheley Hall in 2012
674 and to have co-edited with Jim the volume of *Philosophical Transactions* dedicated to her work. I
will miss her greatly.

676 ***Anthony (Tony) Larkum (Australia)***

I first met Jan Anderson in 1970, when I came from the Johnson Foundation in Philadelphia, and I
678 went on a pilgrimage to Canberra, as already this seemed like haloed territory. Keith Boardman
and Jan had done the seemingly impossible, of separating PS I and PS II. Roger Hiller and I had
680 both come to Australia in recent times and we together made further pilgrimages to Canberra and
CSIRO Plant Industry where the equipment existed to carry on those necessary investigations to
682 extend this work.

It was a great place to work but Jan worked in an atmosphere of intense engagement and *woe*
684 *betide* those who tried to stand in her way. We all learned strategies to mollify Jan and get her back
on track, some better than others. But it is fair to say that we all had an endearing affection for Jan.

686 Roger Hiller and I related this work to algae to see whether membrane fractions could be
obtained there too. At just that time, Jack Barrett moved to CSIRO Plant Industry from Sydney and
688 joined forces with Jan. In no time at all he was isolating interesting fractions from brown algae.
Something we all thought was impossible. But which he went on to publish with Jan.

690 Soon that led to Jack and myself writing a review of photosynthesis at the molecular level in
algae and this led to spirited debate and a mammoth compilation of the literature on the physical
692 separation of pigments, pigment-proteins and thylakoid membranes in algae.

 Then Jack's health deteriorated and Jan became more and more Jack's caregiver, while she
694 stayed as my scientific mentor and colleague. These were not easy times, especially for Jan. Her
fights with the local health service became legendary. In the end she took Jack out of the system
696 and cared for him with her private means. Jack died in 1998 and few of us realized what a deep
laceration this made in Jan's psyche. For those of us in contact with Jan at this time, we found a
698 gentler, more caring friend.

 During these later years Jan devoted herself to her adopted family, to her colleagues and
700 friends and to journal reviewing. She was faithfully in her office every day except when she was
attending business elsewhere or attending overseas conferences. And gracing conferences with her
702 presence was something she did right up to the end.

 Jan stands out as a luminary in the field of photosynthesis, respected by her peers and
704 mourned by colleagues and admirers around the world. Jan, you were a trusted friend, a mentor, a
colleague, a co-author and much more - and the world will not be the same without you.

706 *Anastasios (Tasso) Melis (USA)*

 Our research efforts converged to an apparent shared concept around 1980, when Jan and Bertil
708 Andersson showed localization of the two different photosystems (PSII and PSI) in separate domains
of the thylakoid membrane (grana and stroma-exposed lamellae, respectively), whereas, at about the
710 same time, I showed that photosystem stoichiometry in sub-thylakoid fractions and in thylakoid
membranes from different photosynthetic systems varied, often substantially, from the 1:1
712 ratio hitherto depicted in textbooks (Melis and Brown 1980). Both of these experimental
observations flew in the face of the accepted dogma in the field at the time, which stipulated that the

714 two photosystems formed a 1:1 super-complex surrounded by the auxiliary light-harvesting antenna.
Our seminal findings caused a stir in the field, and forced revision of textbooks on the organization
716 of the photosystems in the thylakoid membrane of photosynthesis. Jan came to Berkeley in 1982
for a 3-month fruitful sabbatical resulting in several collaborative publications (e.g. Anderson and
718 Melis 1983), and I visited Canberra in 1989 for a visit of equal import (Chow et al. 1990). From
thence onward, we shared a commonality of opinion on matters of photosynthesis. It was a
720 pleasure to know Jan and I immensely enjoyed interacting and chatting with her about our mutual
interests. Sadly, she will be missed.

722 ***Gunnar Öquist (Sweden)***

Jan was inspiring, passionate, creative, talented, positive, caring, and a great mentor. She was
724 simply a wonderful lady, friend and colleague. This is how we remember Jan and why we all felt
great sadness when the message that Jan had left reached us.

726 When the message reached me, I and my wife Gunvor were staying in our mountain cottage.
Lots of memories came to our mind. We remembered when Jan had stayed with us in Umeå, but
728 first of all we remembered the wonderful time we spent in Canberra in 1990. How Jan with great
enthusiasm and energy helped us to settle in, and how she made our stay so pleasant and memorable.
730 One weekend we went with Jan and Jack to the coast close to Pebble Beach. We had a good time
together, talking, cooking, strolling around, looking at plants, birds and kangaroos and when the
732 night came we looked at the stars and Jack pointed out the Southern Cross to us. It is the kind of
night you remember of the simple reason that we were together with friends whose company we
734 enjoyed and appreciated.

We went there in Jan's car. Jan drove, Jack sat beside her, and Gunvor and I were in the
736 back seat. We were talking and having a good time, but I noticed that Jan did not care very much
about changing to a lower gear when we went uphill or when slowing down. She kept on

738 complaining about the performance of the car. After short break, I offered to drive and she gladly
handed over the key to me. I drove, changing gear when needed, and Jan was impressed saying
740 “the car behaves much better when you drive than when I drive”. I think that this small episode
also says something about Jan. She did not care very much about trivial things like shifting gear,
742 especially not when more interesting thoughts occupied her mind.

I do not remember exactly when I met Jan for the first time, but it was in the early 1970s at
744 a meeting and I remember that I was very impressed, not only by the novelty of her work but also by
the way she presented her data. It was about the isolation of thylakoid particles enriched in PSI and
746 PSII. She showed how Chl *a* and Chl *b* were differently distributed in the two fractions and she
showed it very pedagogically by presenting the absorption spectra of the two chlorophylls in their
748 respective color, deep green for Chl *a* and more yellowish green for Chl *b*. At that time I was still
working on my PhD, and I remember very clearly what came to my mind at that moment: one day I
750 want to work in her lab.

It had to wait until 1990. Together with Jan and Fred, I showed that the phenomenon of
752 photoinhibition of photosynthesis was not just a damage to PS II, but it was a physiological response
of plants for the long-term adjustment of photosynthesis to match the capacity of downstream
754 processes. Jan appreciated new ideas and brave hypotheses even if they later turned out to be wrong.
I think that she just liked the intellectual challenge, to try to look at things from different perspectives,
756 and in doing so she could really excel with her associative mind. I think that we all grew as
scientists in her presence.

758 ***Robert (Bob) Porra (Australia)***

Excerpt from a speech given at the memorial celebration of Jan's life and legacy, National
760 *Arboretum, Canberra, 6 October 2015*

It was, of course, with great sadness that my wife and I learnt of Jan's death while holidaying in

762 Switzerland, and it was even more distressing that we learnt of her death a week after it occurred.
But we are both indebted to Fred Chow and Hugo Scheer's sleuthing that we were found and
764 informed. Fred's news also explained why we could not contact Jan by phone at her laboratory or
home before we departed for Europe: Jan was already in hospital. I also thank Fred for delaying
766 this ceremony so that I could participate. As we only returned to Canberra this morning, I have
been unable to refer to notes and papers, so my tribute to Jan will be brief but, nevertheless, sincerely
768 heartfelt; and, as Jan's scientific achievements have been so expertly described by Bertil
Anderssen and John Evans, my comments will be of a more personal nature.

770 I first met Jan in 1961 when she Joined CSIRO before the new Plant-Biochemistry
Laboratories had been built. Before she joined Keith Boardman in his laboratory, she moved into a
772 lab occupied by Phil Trudinger, Cyril Appleby and myself, and occasionally visited by John Falk.
After working in Melvin Calvin's laboratory in Berkeley, she must have been underwhelmed by our
774 dark, modest laboratory in the original CSIRO White Central Building. But the most distressing
event for Jan at this time was the breakage, in transit to Canberra, of much of her beloved collection
776 of Long-Playing vinyl records and, if I remember correctly, she had a long-running dispute with
her insurer who probably learnt very quickly that Jan could be very persistent.

778 Jan then went on to work with Keith Boardman and great things were achieved. But Jan
then went on in her own right and showed that she was very creative with great intuition tempered by
780 her vast knowledge of her field. When visiting Cambridge in 1973/1974, work in the lab was
curtailed by a miner's strike and power cuts, but she used this time to think about problems and
782 anomalies in studies of Photosystems I and II. Her career was now on the rise and many
international researchers were to visit her lab. In due course, her brilliance was rewarded with
784 many Awards and with Fellowships to the Australian Academy of Science and the Royal Society.

Jan always maintained that women in science were discriminated against. In her case,
786 however, her contributions to her field were so significant that they could not be ignored as, indeed,

her Awards and Fellowships showed. So! As David Goodchild once declared, although I have
788 forgotten his exact words, the gist was: *Jan got to the top in her own right and in spite of the*
discrimination and impediments, (whether real or imagined). As we all know, from then on her
790 Star shone brightly.

Jan was always prepared to help and advise her colleagues, and her advice was always
792 worth noting. For instance, when two colleagues from CSIRO-Forestry, Bill Thompson and Paul
Kriedemann, found that the assays for Chls *a* and *b* were probably faulty and asked for my help to
794 correct them, Jan was immediately interested: she was aware that Structural Biologists, using
electron microscopy and later X-ray crystallography, were having problems matching the 14 Chls
796 observed in their X-ray-diffraction-derived structure of Light Harvesting Complex II (LHC II) with
the Chl content of their crystals, as measured by the then available assay, which was 15 Chls . She
798 could see that the extra Chl may be due to a faulty assay. When our corrected assay procedure
(Porra et al. 1989) was used, the 15th Chl was eliminated: it did not exist. This result delighted Jan
800 and also Werner Kühlbrandt and his X-ray crystallographers.

Not everything that Jan did was necessarily superb as anybody who has received a postcard
802 or e-mail from her can attest. Her handwriting could take hours to decipher and her e-mails or first
drafts of papers were unpunctuated and typos were abundant: Hugo Scheer suggested that her
804 active mind was always far ahead of her pen. Jan could be very blunt with people she thought were
being unfair to her. She could also be very impatient, bordering on rudeness, when progress was
806 slower than she anticipated. I observed this when Jack Barrett, her friend and partner, was
sharing a lab with me. Jack and Jan were working together on the photosynthetic pigments of a
808 seaweed. Jack was a slow and careful writer and, obviously, too slow for Jan and she made life
very hard for Jack and others in the lab: we would all wince each time she swept into the lab
810 demanding that Jack finish his draft quickly. However, years later when Jack was terminally ill,
Jan cared for him lovingly and patiently. Right through to the very end, she fought to have Jack

812 receive every possible medical and nursing advantage. They were a devoted couple and, with a
shared interest in nature, science, art and music, they truly were *Lebensgefährten* – partners for life.

814 Finally, however, it would be wrong to leave the impression that Jan was always impatient
or impolite with her colleagues. Jan liked a happy, productive laboratory and she was always a
816 jolly hostess at parties in her lab at CSIRO. When welcoming or farewelling international
researchers or celebrating some achievement, somebody would be sent to the O'Connor shops to
818 procure several bottles of sparkling wine, cheese and biscuits: these parties were spontaneous, happy
affairs with lots of stories about previous visitors, achievements, current problems and reminiscences
820 of interesting incidents at international conferences. Unfortunately, that lively voice and smiling
countenance is no longer with us.

822 I shall miss Jan. Indeed, her untimely death leaves a great void in the lives of all her close
friends and colleagues.

824

Additional material on Jan Anderson may be found at: <http://biology.anu.edu.au/people/jan-anderson>

826 **Acknowledgments**

We are very grateful to all of Jan's friends (in alphabetical order: Bertil Andersson; Eva-Mari Aro;
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830 particularly want to thank Martin Barrett for providing scans of photos of Jan, some of which had
never been seen by us. We also thank Cornelia Büchen-Osmond, Duncan Fitzpartick, Govindjee and
832 Geoff Wilson for taking some of the photographs included here.

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906

Figure legends

908 **Fig. 1.** Photos of Jan Anderson during her school days. **(a)** In primary school uniform; **(b)** in high
school uniform with badges and ribbon; **(c)** in a smart casual dress, perhaps in her early twenties;
910 **(d)** in a formal dress, perhaps for an official appointment. Jan Anderson Archives; custodian:
Martin Barrett

912 **Fig. 2.** **(a)** A photo of Jan Anderson and Keith Boardman, with whom she shared a lab in CSIRO
Division of Plant Industry for some 16 years. This photo was taken outside the Biological

914 Laboratories of Harvard in 1973 while Jan was on sabbatical with Paul Levine and Keith was
visiting Lawrence Bogorad. From Jan Anderson Archives. (b) Jan Anderson as Carnegie
916 Institution Research Fellow (1965-1966) with C. Stacy French. From Jan Anderson Archives. (c)
Jan Anderson and Bertil Andersson at the Symposium “*Why Grana?*” in Jan’s honor, Arnberg,
918 Germany, 1998. Photo by Fred Chow

Fig. 3. (a) Jan’s lab group, CSIRO lab, 1990. *Front:* Fred Chow, Lin-Ke Huang and Stephanie
920 McCaffery; *back:* Gunnar Öquist, Brian Jordan, Jan, a visiting student, Bob Porra, and Jie He.
From Jan Anderson Archives. (b) *Left to right:* Govindjee, Jim Barber, Jan and Alexander Hope.
922 at the R.N. Robertson Symposium on *Chlorophyll Fluorescence: Origins, Measurements,*
Interpretations and Applications, ANU, 1994. Photo by Fred Chow

924 **Fig. 4.** (a) Jan as mentor to the ANU Photobioenergetics Group, 2002. *Front row:* Iain
McConnell. *Second row:* Riichi Oguchi, Lydia (Honors student), Husen Jia, Adele Williamson
926 and Fred Chow. *Back row:* Jan, Hossein Fallahi, Brendon Conlon, Warwick Hillier and Thomas
(Tom) J. Wydrzynski. Photo by Geoff Wilson; (b) Min Chen with her mentor, Jan, 2007. Photo
928 by Govindjee; (c) Fred Chow with his supervisor, colleague, and mentor for 30 years, in the
ANU lab, 2013. Photo by Duncan Fitzpatrick; (d) Jan in animated conversation with Roberto
930 Bassi at PS2007 Glasgow. Photo by Cornelia Büchen-Osmond

Fig. 5. Jan in discussion with Pierre Joliot (left) and Warren Butler (middle) at the Symposium on
932 *Chlorophyll Organization and Energy Transfer in Photosynthesis*, Ciba Foundation, London,
1978. From Jan Anderson Archives

934 **Fig. 6.** (a) Jan and Jack Barrett on an excursion in the mountains. From Jan Anderson Archives.
(b) Jan and Caroline Mordaunt at an Australian Academy of Science gathering a day before Jan
936 fell and soon passed away. Photo by Martin Barrett