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ORIGINAL ARTICLE

Unique features of the 'photo-energetics' of purple bacteria: a critical survey by the late Aleksandr Yuryevich Borisov (1930–2019)

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Abstract
We provide here an edited version of the "Farewell discussion" by the late Aleksandr (Alex) Yuryevich (Yu) Borisov (1930–2019) on several aspects related to the excitation energy transfer in photosynthetic bacteria. It is preceded by a prolog giving the events that led to our decision to publish it. Further, we include here a few photographs to give a personal glimpse of this unique biophysicist of our time. In addition, we provide here a *reminiscence*, by Andrei B. Rubin, on the scientific beginnings of Borisov. This article follows a Tribute to Borisov by Semenov et al. (2019, *Photosynthesis Research*, this issue).

Keywords Singlet electronic excitation · Rhodospirillum rubrum · Förster theory · Reaction center · Antenna · Bacteriochlorophyll · Primary photochemistry

> **"***If there is any primary rule of science… it is…… acceptance of the obligation to acknowledge and describe all of reality, all that exists, everything that is the case—It must accept within its jurisdiction even that which it cannot understand, explain, that for which no theory exists, that which cannot be measured, predicted, controlled, or ordered..It includes all levels or stages of knowledge, including inchoate…. knowledge of low reliability,– and [even] subjective experience."*—**Abraham Maslow (b. 1908—d.1970),** *an American psychologist, known for creating Maslow's hierarchy of needs.*

Prolog

On December 13, 2017, Aleksandr (Alex) Yuryevich (Yu) *Borisov wrote, in an e-mail, to Govindjee "Dear Gov: My son Andrey helped me with some of my home material. [Thus,] I could make my last effort in editing this piece of text. Unfortunately, I am strongly "uncoupled" from my papers in the University now. I hope you would have some possibility to attract one more coauthor for this (our) initial text.* ***If published, it would be my last contribution, with you my dear!—Yours very truly—Alex****"* Alex asked about it several times, but Govindjee (Gov) did not feel he was qualified to coauthor it, but since Alex is no more, and he really wanted it published, Gov decided to edit it in a way that the main message remains intact; he added additional references to help the reader find his/her way; he, then, invited Andrei P. Razjivin and Vladimir S. Kozlowsky to join him in publishing this historical perspective (now a "farewell paper" of Borisov) so that the thoughts of Borisov will become available to all. When appropriate, we have mentioned his name in the text (also see footnote). We are fully aware of the accepted views on the topic of this paper (see e.g., Scholes et al. 2011), but we provide here the views and the arguments that Alex Borisov presented in his "farewell" paper to all of us. Although the authors of this perspective did not and do not share many of the statements of Yu. Borisov on the process of transfer and capture of excitation energy, yet, we (and many others) always valued (and still value) his scholarship and always had (and have)

Although Govindjee continues to publish under one name, his formal name since 2019 is "Govindjee Govindjee"

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deep respect for his presentations at seminars, conferences as well as his outstanding publications. After Alex Borisov's death, we decided to bring his "farewell" article to publication, according to his will. Further, our decision is supported by our respect for "history", "openness", and belief that even the most established ideas may have to be modified with newer theories and experiments, as has happened many times in the past.

It is important to quote upfront **James (Jim) Barber** (of UK): "I knew Alex Borisov very well. He was not just a colleague but also a friend to my family. I am very sorry to hear the sad news about his death. He was indeed an exceptional scientist. I, whole-heartedly, approve the publication of this paper".

This manuscript was read by two anonymous readers before its publication; some of their key comments have been incorporated in the paper. However, in spite of some critical comments by our distinguished anonymous readers, and some of the arguments here, being highly qualitative, this article is being published, as is, with the hope that it will help in reaching the "final truth" after due examination of all the experiments and available theories (also see Abraham Maslow's quote below the Abstract).

Introduction

We begin our presentation by showing two photographs of Alex Borisov (b. June 29, 1930—d. June 1, 2019). For information on Borisov's life and contributions, see a Tribute in this issue of the journal (Semenov et al. 2019).

Figure 1 shows a 1984 photograph of Alex Borisov lecturing, at the invitation of Karel Vacek, in Prague, The Czech Republic, and Fig. 2 is a 2009 photograph of Borisov, sitting in his office in Moscow, Russia.

What follows is the summary by Borisov of his ideas on the features of the photo-(bio) energetics of purple bacteria.

Summary of Borisov's farewell paper

In (anoxygenic) bacterial photosynthesis, the "bottleneck" of photoinduced electronic excitation transfer and/or migration is located between the light absorbing bacteriochlorophyll (BChl) "antenna" complexes and the acceptor of electronic excitation, the special BChl pair, i.e., the P870, which is the photochemical reaction center (RC), the heart of photosynthesis (see e.g., Clayton 1980). In Alex Borisov's view, the distance between different BChl groups, in the antenna, is "large", and the efficiency of excitation energy migration must depend on the distance between them. The *critical distance*, for excitation energy migration between these groups, must play an important role in energy funneling to the RCs and hence in the net efficiency of all subsequent photosynthesis processes. In this "farewell" paper, Borisov discussed, rather briefly, the dependence of these processes on Light Harvesting (LH)-1 structure, specific parameters of BChl molecules, and those of their environment. He described eight factors, which ensure high yield of the useful photochemical conversion in the unique symmetrical LH1 structure of purple bacteria.

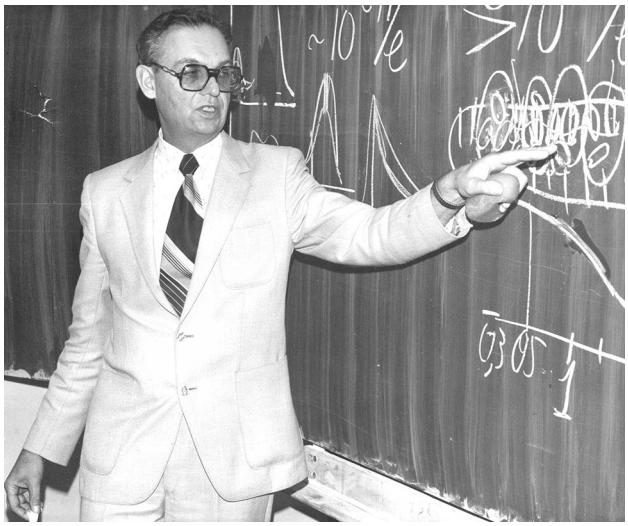

Fig. 1 Alexander (Alex) Yuryevich (Yu.) Borisov lecturing, in 1984, in the Department of Theoretical Physics, at the Charles University in Prague (The Czech Republic). *Source* Borisov's family archives

Fig. 2 A 2009 photograph of Alex Borisov in his office in the Department of Photosynthesis, A.N. Belozersky Research Institute of Physico-Chemical Biology, Lomonosov Moscow State University. This photo was taken on Borisov's 79th birthday by one of the authors (A P R)

Introduction of Borisov's thoughts

Light absorption occurs under conditions, when the wavelengths (λ) of 'active' photons are about thousand times longer than the transition dipole moments (hereafter dipoles) of dye molecules (Agranovich and Galanin 1982). Even under sunny days, we could say that we have really low light intensity (*a paradoxical statement*) since we have only one or two quanta absorbed by one dye molecule per second and this becomes about 10 times smaller under cloudy weather (see https://en.wikipedia.org/wiki/Daylight). Therefore, each energy transforming RC is associated with dozens to hundreds of "antenna" chlorophyll (Chl) molecules in plants, algae & cyanobacteria, and BChl in photosynthetic purple bacteria (cf. Yang et al. 2001). To Borisov, it seemed obvious that most antenna pigment molecules cannot be directly coupled to the energy accepting RC BChl pair. This problem must have been solved in the course of evolution of photosynthesis by the invention of a mechanism for ultrafast migration of light-induced **singlet electronic excitation** (often referred simply as *excitation* or *excitations*)from the large number of antenna BChl (or Chl) molecules to their corresponding (energy) accepting pairs in the RCs (Yang et al. 2001).

Singlet electronic excitations are known to deactivate during 100–300 ps in mildly coupled dye dimers (Khairutdinov and Serpone 1997; cf. Minami et al. 2013). Therefore, realization of high performance requires the delivery of these excitations from the antenna BChls to RC pairs in less than 100 ps. Basic bacterial "blocks", LH1 BChl-protein complexes, had been isolated long ago, e.g., by Parkes-Loach et al. (1988) from the membranes of purple bacterium *Rhodospirillum (Rsp.) rubrum.* Similar RC-LH1 particles were isolated from other purple bacteria (Brunisholz and Zuber 1992). For X-ray structure of RC-LH1 from *Rhodopseudomonas (Rps.) palustris*, see Roznak et al. (2003). Here, in the transmembrane α- and β-polypeptides, BChl molecules are organized in circles of 16 pairs with a radius of about 45 Å (see van Grondelle et al. 1994; Fleming and van Grondelle 1997; Roznak et al. 2003; Cogdell et al. 2006). RC "special pairs" (P870 s) are located in the centers of these "circles". The circle-type structure of LH1 is rather advantageous since BChl interchromophore distances are relatively small in it and excitation migration between the neighboring molecules can proceed, in Borisov's opinion, in sub-picosecond time region. Therefore, excitation energy from BChl molecules, even with "unfavorably" oriented dipoles, would rapidly reach BChls, having dipoles optimally oriented relative to those of RC acceptor pairs, the P870s.

Energy migration and capture in purple bacteria à la Borisov

Obviously, actual distances between the BChl molecules play an important role in excitation energy transfer from the many "antenna" BChls to P870 RC pairs. BChl molecules are embedded in vivo in the inner plane of thin protein-lipid membranes (van Grondelle et al. 1994; Fleming and van Grondelle 1997; Cogdell et al. 2006). Many theoretical approximations (Novoderezhkin and Razjivin 1994, 1996; Novoderezhkin et al. 1999; Jordan et al. 2001; Kodis et al. 2006; van Grondelle and Novoderezhkin 2006; Khan et al. 2008; Yaser et al. 2008) have already been developed, which describe excitation migration in RC-LH1 complexes of purple bacteria. According to Borisov, distances (> 40 Å) between antenna BChls and P870 pairs in LH1 structures favor the use of the classical inductive-resonance theory (Förster 1948, 1960) in this migration "bottleneck". The following equation describes the relationship involved (Knox and van Amerongen 2002; Knox 2012; cf. Blankenship 2014):

$$k_{DA} = \frac{\varphi_{fD}}{\tau_D} \cdot \frac{R_0^6}{R_{DA}^6} = C \cdot \frac{\varphi_{fD}}{\tau_D} \cdot \frac{1}{R_{DA}^6} \cdot \left\{ \frac{k^2}{n^4} \cdot \frac{\int_0^\infty \varepsilon_A(\lambda) \cdot F_D(\lambda) \cdot \lambda^4 \cdot d\lambda}{\int_0^\infty F_D(\lambda) \cdot d\lambda} \right\}^6 \quad (1)$$

The symbols in Eq. (1) are as follows: λ—wavelength of light; k_{DA}—rate constant of excitation migration from the excited donor molecule (D^*) to the acceptor molecule (A); C—constant, responsible for matching the dimensions of both sides in Eq. (1); R_{DA}—the distance between donor and acceptor chromophore centers; τ_D—natural lifetime of excited donor molecule; φ_{fD}—quantum yield of donor fluorescence; R_0 –the mean interchromophore distance between (D^*) and (A) in *chaotic* dye ensembles, when the probabilities of fluorescence emission from D^* and excitation migration to A are equal; n—the refractive index of the surrounding medium in the vicinity of donor and acceptor chromophores; $\varepsilon_A(\lambda)$—molar absorptivity; $F_D(\lambda)$—donor emission. Further, k^2 is the orientation factor, which is dependent on the angle between the donor and acceptor transition dipoles Θ_T, and Θ_D and Θ_A are the angles between transition dipoles and R_{DA} is a vector quantity (van der Meer 1999); and t = the orientation factor $k^2 = \left(\cos\Theta_T - 3 \cdot \cos\Theta_D \cdot \cos\Theta_A\right)$, which is equal to 2/3 in *chaotic* dye ensembles. For RC-LH1 complex, the distance between donor (D) and acceptor (A) chromophores is about 43.2–43.5 Å due to the shift of both D and A chromophores from the LH1 center, as obtained from the crystal structure (see protein

data bank: https://doi.org/10.2210/pdb1pyh/pdb; and https://doi.org/10.1126/science.1088892).

Borisov then considered the migration of excitation in random dye molecules with the mean inter-dipole distances close to those in purple bacteria. The value he used (43.3 Å) was not much different from the critical distance(s) of excitation migration in dyes such as fluorescein (54 Å) and rhodamine (47 Å) (Birks and Munro 1967). The portion $\left(p_{\mathrm{m}}\right)$ of migrated excitations in these dyes may be roughly estimated with the aid of the following simple equation:

$$p_{\mathrm{m}} = \left[1 + \left(R_{\mathrm{DA}}/R_0\right)^6\right]^{-1} \tag{2}$$

The p_{m} (see above) has a value of about 0.62 and 0.81 in random ensembles of rhodamine and fluorescein. But it has a very low value, which is less than 0.05 in the system, discussed here, provided the portion of useful excitation energy acceptors is only 1 out of 16, as is the case in LH1s of most purple bacteria. This led Borisov to ask an important question: How do BChls function in purple bacteria in such unfavorable conditions, which has such low number of energy acceptors to antenna molecules?

It seems, according to Borisov, evolution "invented" several physico-chemical and structural factors which dramatically increased the efficiency of excitation energy transfer from the many BChl antenna molecules to the RC P870 pairs. The answer to the question, raised above, was obtained in a series of fundamental studies (*as described below, under the following eight statements, by Alex Borisov;* many of these are difficult to understand, but we (Govindjee, Razjivin and Kozlovsky) hope that other authorities will examine them fully, and provide a clear understanding of these ideas followed by pros and cons of the concepts of Alex Borisov. The concept of "coherence" wherever pertinent, needs to be brought in (see e.g., Lee et al. 2007).

Borisov's eight statements (with added references, and minor changes, by Govindjee, Razjivin, and Kozlovsky)

They are:

1. BChls are the most IR-shifted of all the natural dyes known; their long-wavelength absorbing peaks are shifted from 790 nm (in solution) to about 900 nm (in vivo). Borisov noted that the dipole strength of a molecular dye is proportional to $\int \varepsilon(\lambda)\frac{\mathrm{d}\lambda}{\lambda^2}$: the further the absorption spectrum extends to the long-wavelength side, the greater the value of the integral would be. According to Borisov, this gives BChls noticeable advantage, as compared to other dye molecules that have their "red" absorption edges in the visible region. Besides, such spectra allow BChls to use photons from more than half of the incident solar spectrum; it is 1.8–2.9-times more than those of natural dye molecules that have red edges at 550–650 nm (Kiang et al. 2007).
2. After being in the singlet excited state, dye molecules may go down into the triplet state (Terenin 1967; Klan and Wirz 2009). This quenching of singlet excitation is greatly enhanced in systems in which the interchromophore spacing is close to 9–10 Å, such as in bacterial LH1s. After conversion into the triplet state (which is long-lived), energy may be dissipated by being transferred to the neighboring carotenoids or the molecules may be oxidized by oxygen in the air. But, according to Borisov, evolution has "*fixed*" the neighboring antenna BChls in the structure of LH1s in such mutual positions that "*harmful*" quenching of singlet excitation energy, by triplet formation, is strongly suppressed!
3. In bacterial photosynthesis, reaction centers trap excitations delivered from antenna BChls within 2–3 ps (Martin et al. 1986; Woodbury et al. 1986; also see Mamedov et al. 2015; and Mirkovic et al. 2017). Such short time (i.e., fast) process decrease the yield of conversion of singlet excitation energy into triplet state in LH1s by more than one order of magnitude.
4. The structure of BChl lipid tail and its flat π-electronic ring favor embedding of the ring into a thin plane inside the interior of the protein-lipid membrane. According to Borisov, two-dimensional packing in this plane must prevent BChl rings from harmful direct contacts despite their local concentration being quite high, ~ 0.5 M.
5. A complex of N interacting molecules may be considered as one molecule with its transition dipole correspondingly increased and split into N components (Davydov 1971). The dipole–dipole interaction induces absorption band splitting in P870 RC pairs into two, the dominant one, with a peak at ~ 870 nm, accounting for ~ 84% of the integral extinction of RC pairs (Mikhailjuk et al. 2006; van Grondelle and Novoderezhkin 2006). Therefore, the term of these P870-pairs in Eq. (1) requires additional factor of $2 \times 0.84 = 1.68$—due to higher dipole strength of the lower excited level of RC BChl dimer (Borisov 2014).
6. Each pair of α- and β-polypeptides in LH1 antenna carries two BChl molecules, and they rotate sequentially relative to the BChl pairs in the α- and β-polypeptides (Novoderezhkin et al. 1999; van Grondelle and Novoderezhkin 2006). BChls in such pairs interact with each other and with those in the neighboring pairs. Many split absorption bands, thus created, fall under forbidden symmetry; however, the complex long-wavelength (about 880 nm) absorbing chromophore dominates; the absorption strength of this chromophore is approximately 4–5 times of that in BChl monomers (Novo-

derezhkin and Razjivin 1995; van Grondelle and Novoderezhkin 2006). This factor of 4–5 must apparently be included in Eq. (1).

7. The migration of excitation to the RCs mostly proceeds from the antenna BChl pairs, whose long-wavelength dipoles are nearly collinear to those of P870s. The mean magnitude of their mutual orientation coefficients is at least 0.90–0.92, which exceeds the mean (~0.67) in random dye ensembles.
8. The coefficient n (See Eq. 1) has "no sense" in thin (~40 Å) membranes of photosynthetic organisms, since light refraction may proceed only at optical paths considerably exceeding the wavelength of "acting" photons. Therefore, in photosynthesis, n must be replaced in Eq. (1) by micro-coefficient of dielectric permeability (ε) around D and A molecules, according to the formula for nonmagnetic media, $\varepsilon \sim n^2$. The inner membrane volume mostly consists of highly hydrophobic lipid tails and inner parts of BChl phytol tails. Their matter is known to be very hydrophobic (Knox and van Amerongen 2002; Chamorovsky et al. 2007; Borisov 2013, 2014); hence, $\varepsilon' s$ tend to have minimal possible values. According to Borisov, this thesis has been reliably confirmed by others (see e.g., Chamorovsky et al. 2007).

The above-mentioned eight factors made it clear to Alex Borisov as to why the yield $\left(\varphi_{\mathrm{fD}}\right)$ of useful singlet excitation energy conversion is very high in purple bacteria (cf. Borisov 2010). Indeed, numerous experiments have proved that BChl lifetimes, in vivo, are within 50–80 ps (van Grondelle and Novoderezhkin 2006), while they increase to 600–800 ps or more in their RC-depleted LH1 particles (van Grondelle et al. 1994).

According to Alex Borisov, quantum losses in foregoing transfers must be small. A comparison of these lifetimes allowed Borisov to estimate the yield of useful conversion of singlet excitation energy in purple bacteria in vivo, to be

$$p_{\mathrm{m}} > (550 - 70\mathrm{ps})/550\mathrm{ps} > 0.87 \tag{3}$$

$$p_{\mathrm{m}} < (700 - 50\mathrm{ps})/700\mathrm{ps} < 0.93 \tag{4}$$

Further, according to Borisov, this high quantum yield (~90%) is the greatest achievement of evolution which enabled life to appear on our unique Earth. The energy yield of such systems is proportional to the portion of photosynthesis-active photons in the useful part of solar spectrum multiplied by the potential they generate in RCs minus its inevitable losses in the course of electron stabilization in the course of its transport via bacterial transmembrane chain. These principal losses are associated with the stabilization of 'excited electrons' to the level appropriate for the slow biochemical energy-consuming complexes. Borisov stated that really, they are much greater! The synthesis of ATPs takes place in bio-membranes at the expense of electrochemical potential (see Blankenship 2014). Unfortunately, the sum of its two components cannot exceed 200 meV, otherwise some local electron leakage and even harmful "punctures" may appear which would greatly reduce the efficiency of energy conversion in bacterial RCs (Skulachev et al. 2013).

We note that the initial singlet excitation energy in the RC equals 1400 meV, and, thus, purple bacteria can ensure that the energy yield will be no more than

$$\varphi_{\mathrm{energ}} < \left[(100 - 120)\mathrm{meV}/1400\mathrm{meV}\right] \cdot p_m < 0.07 - 0.09 \tag{5}$$

where, φ_{energ} is energy quantum yield, and p_{m} is the portion of excitation energy, which is migrated and trapped in the system.

We end this historical perspective, by Alex Borisov, by noting that, in purple bacteria, the red edge of active solar light is at about 910 nm. It is close to the optimal (1050–1100 nm) for land-based photoelectric solar systems (Rabek 1982). And, one of the last important "breakthroughs" in "building" of photosynthesis in purple bacteria was laid down by Vladimir Shuvalov and his coworkers, who measured the time of reduction of the primary electron acceptor in RCs of purple bacteria which trap excitations in about one picosecond (Shuvalov et al. 1979; Yakovlev and Shuvalov 2016). A great number of papers (mostly theoretical ones) have appeared since then, where numerous quantum–mechanical approaches for interaction and conversion of singlet excitation energy, in LH1 "circles", have been discussed (Novoderezhkin and Razjivin 1996; Hu et al. 2002; Law et al. 2004; van Grondelle and Novoderezhkin 2006; Cogdell et al. 2006; Blankenship 2014). The "biological matter" has been absent in many of these papers; these authors often looked only at purely the "physical analysis" of the dynamics of excitation energy in unique symmetrical BChl complexes. The most important feature in photosynthesis is the efficiency and the yield of solar energy photoelectrochemical conversion—which was not seriously touched in many of these papers. Thus, the field remains open for further research.

Epilog

As noted above, we are fully aware of the current opinion on the topic of this paper (see Scholes et al. 2011), but we would like the future to be the judge of how this complex process really proceeds under different experimental conditions and in different photosynthetic organisms. Obviously, there is much more to do to understand the energy conversion process even in the simplest of anoxygenic photosynthetic bacteria. We do not take any position on the content of the above perspective by Alex Borisov. However, we do believe in the words of Abraham Maslow (see his quote at the beginning of

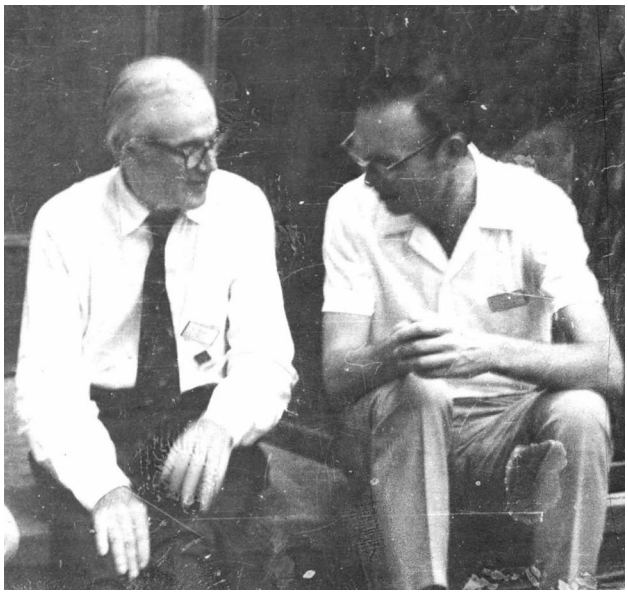

Fig. 3 Left to right: Britton Chance and Alex Borisov, 1961. *Source* Borisov Family Archives

this historical perspective). We encourage others to examine, to expand, and to provide their perspective on the topic—that is in this "farewell discussion", by Borisov.

We end our presentation by showing several photographs, provided to us by Andrei Borisov—as a way to remember Alex, one of the pioneer biophysicists of our time (also see Semenov et al. 2019). Alex Borisov had interacted extensively with many biophysicists around the World including James Barber (see Semenov et al. 2019), Roderick Clayton (Wraight 2014), and Britton Chance (Dutton 2016). Figure 3 shows Borisov and Chance (USA) in deep discussion at a meeting in Russia (1961).

The above photograph brings a special remembrance of Borisov of his early days by Andrei Borisovich (B.) Rubin (of the Department of Biophysics, Moscow State University), who wrote:

"I have known Borisov since 1957 when I entered the Physical Institute as a student in the laboratory of Lev Tumerman where Borisov worked as an electronic engineer. He was involved in constructing a phase fluorimeter to measure the lifetime of Chl *a* fluorescence. We worked together and he helped me a lot in my diploma work as a very careful and strict supervisor. He was very much impressed by the perspective of photosynthetic research and after defending his own Ph D in '*Electronics*' he decided to start his research in the area of primary processes in photosynthesis (topic of his "farewell" presentation, see above). Being a very insistent and goal-oriented researcher, he developed himself very soon into an independent and talented scientist (see Semenov et al. 2019). But he did not forget his experience as an electronic engineer and designed his own version of a *Difference Spectrophotometer* which originally had been constructed in Britton Chance's laboratory. In 1961 Britton Chance had attended the International Biochemical Congress in Moscow and visited Tumerman's laboratory together with Eugene Rabinowitch (for Rabinowitch, see Govindjee et al. 2019). Both Rabinowitch and Chance were very much impressed by the original setups, constructed mainly by Borisov, for photosynthetic research. The example of Britton Chance' career firstly as an electronic specialist and then as an outstanding scientist inspired Borisov and strongly confirmed his intention to continue his studies of excitation energy migration in photosynthesis (the topic of his "farewell" notes; see above). His scientific outstanding achievements in this area are well known."

We all know that Borisov was very active in his research group. Figure 4 shows him in a 1970 photograph with members of his department, and Fig. 5 shows him in a 2011

Fig. 4 Members of the Department of Photosynthesis, Moscow University, late 1970s. Left to right: Vitaliy Samuilov; Zoya Fetisova; Valentina Godik; Marina Il'ina; Dmitriy Domninsky and Aleksander Borisov. *Source* Borisov Family Archives

Fig. 5 Left to right: V.Z. Pashchenko, A.Yu Borisov, and V.A. Shuvalov in the Department of Biophysics, Faculty of Biology, Moscow State University, 2011. Photo by A. Razjivin (one of the authors). *Source* Borisov Family Archives

photograph with Vlad Shuvalov and V.Z. Paschenko (both well-known authorities from Russia).

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