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The Mackey-Glass models, 40 years later

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Abstract

In 1977, Michael Mackey and Leon Glass published a short paper that presented and analyzed three delay-differential physiological models, one of which, now known as the Mackey-Glass equation, was shown to generate chaotic behavior. This paper also introduced the concept of a dynamical disease. In this perspective article, I attempt to place the Mackey-Glass paper and a 1979 followup in historical context, and thereby to gain some understanding of the very significant influence it has had across the sciences. This influence is mapped through a citation analysis, revealing both the timelessness of the themes broached in the Glass-Mackey papers, and of the broad influence of these papers, far transcending the specific scientific problems originally tackled.

Keywords: mathematical physiology, delay-differential equations, dynamical disease, chaos

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1 Introduction

Some coincidences are too good to pass up. This Year of Mathematical Biology coincides with the 75th birthdays of Leon Glass and Michael Mackey (Fig. 1), two key figures in the development of mathematical biology as we know it today. And it is just a bit over 40 years since the 1977 publication of their classic article "Oscillation and chaos in physiological control systems" [1]. The moment therefore seems appropriate to revisit this paper and to consider its impact.

2 Historical context

Before we delve into the Mackey-Glass paper [1] and its more detailed companion paper [2], it is useful to consider the historical context. With apologies to our colleagues in other parts of the world, I will focus on the situation in the West, and particularly in North America, since that was the context in which Glass and Mackey evolved.

The organization of mathematical biology as a distinct discipline is relatively modern, and much was happening around the time of the Glass-Mackey papers. The Society for Mathematical Biology, of which both Glass (1997–1999) and Mackey (2009–2011) would go on to serve as President, was founded in 1973 and held its first meeting in 1975 [3]. The Gordon Research Conference on Theoretical Biology and Biomathematics started about a decade earlier, in 1964. Although there were some forerunners, several key journals in the field were founded in the decade preceding the Mackey-Glass paper (Table 1).

Regarding the scientific context of the time, Edward Lorenz's classic paper "Deterministic nonperiodic flow", which introduced many of the key ideas later to be associated with chaotic dynamics, had been published more than a decade earlier [4] but had yet to have an enormous impact. By the end of 1977, it had been cited just 65 times (Web of Science search), with only a handful of citations in an explicitly biological context [5, 6, 7, 8]. The term "chaos" was itself first used with its modern dynamical-systems meaning in 1975 [9].

Delay-differential equations (DDEs) were not yet in wide use in

Figure 1: Michael Mackey (left) and Leon Glass at the *Leon Glass and Michael C. Mackey Diamond Symposium*, which was held at McGill University on June 14th and 15th, 2018. Photo courtesy of Tomas Gedeon.

Table 1: First publication dates of some key journals in mathematical biology.

Journal	**Start date**
Acta Biotheoretica	1935
Bulletin of Mathematical Biophysics[a]	1939
Journal of Theoretical Biology	1961
BioSystems	1967
Mathematical Biosciences	1967
Theoretical Population Biology	1970
Journal of Mathematical Biology	1974

[a] Renamed *Bulletin of Mathematical Biology* in 1973

biological modeling. To get a sense of the change, I conducted a search of MathSciNet for papers whose database entries contain the terms “delay” or “lag”, and whose primary subject classification was “Biology and other natural sciences”. There were just 18 such papers in the database published in 1977. For 2017, the same search yielded 372 papers. I need not explain to the readers of this article the ways in which this search is flawed. Nevertheless, it speaks to a tremendous growth in interest in delay systems in the biological context since 1977, and to the relatively small literature on the topic at the time the Mackey-Glass paper was written.

The modern theory of delay-differential equations was not yet well known, despite some early work by Krasovskiĭ [10] and Hale [11]. The main theoretical tools in use at that time consisted of linear stability analysis [12, 13, 14] and of transformation to chains of linear ordinary differential equations [15, 16, 17, 18]. Numerical simulations were of course also used, but were carried out on computers that were much less capable than today’s.

3 The 1977 Mackey-Glass paper

The 1977 Mackey-Glass paper [1] is under three pages long, but a lot is accomplished in those three pages.[1] Although one model from this paper became known as "*the* Mackey-Glass equation" [19], there are actually three models discussed there, one for respiratory control, and two variants for the control of hematopoiesis (production of blood cells). These models have a few features in common. They are explicitly cast as members of the class of production-destruction models, a concept that an der Heiden and Mackey would formalize a few years later [20]. Each model consists of a single delay-differential equation with a single delay and a nonlinearity from the family of generalized Hill functions. The space of equations of this family is explored by looking at models with the delayed Hill function in the production or destruction term, and by considering both conventional (monotone) Hill functions, and a unimodal "hilly" function, i.e. a function of a generalized Hill form with a single maximum on the positive semi-axis. Let us briefly examine each of these models.

3.1 Respiratory control

Ventilation is largely controlled by the arterial carbon dioxide concentration detected in the brainstem, denoted x. The dependence of the ventilation on the CO_2 concentration is known to be sigmoidal. Increased ventilation leads to an increased rate of removal of CO_2 from the blood in the lungs, but there is a delay τ before the blood from the lungs reaches the brainstem. Thus, the ventilation at any time t depends on the delayed concentration of CO_2, $x_\tau = x(t - \tau)$. If the metabolic rate is constant, then CO_2 is produced at some fixed rate

[1] A modern reader might expect that a three-page paper would be supplemented by many more pages of online supplementary materials. Of course, the web did not exist in 1977, never mind online supplementary materials. Writing concise, self-contained papers was an art form.

λ. These assumptions lead to the model

$$\frac{dx}{dt} = \lambda - x\frac{a(x_\tau/\theta)^n}{1+(x_\tau/\theta)^n}. \tag{1}$$

The constant a depends on the maximum ventilation, and on the efficiency with which CO_2 is removed from the bloodstream in the lungs, while θ determines the concentration of CO_2 at which half-maximal ventilation is achieved.

Using linear stability analysis and numerical simulations, Mackey and Glass found that this model could have a stable equilibrium point, or an oscillatory regime. Using parameters either found in or estimated from the experimental literature, Mackey and Glass showed that their model predicted a stable steady state for normal subjects. However, sufferers of Cheyne-Stokes breathing, in which periods of high ventilation alternate with apneic phases, have an increased delay between gas exchange in the lungs and brainstem detection, as well as an increased sensitivity to CO_2 [21]. Putting the parameters for a Cheyne-Stokes patient into the model resulted in high-amplitude oscillations with a relatively long latent period between pulses, the latter corresponding to apneas. A very simple model with parameters estimated from the literature was therefore able to reproduce both healthy and pathological behaviors.

3.2 Hematopoiesis

In hematopoiesis, the production of new blood cells is controlled by circulating blood cell counts. Proliferation and maturation of blood cells takes time, so there is a delay, τ, between the detection of a deficiency in a circulating population, P, and the appearance in the bloodstream of cells to replenish this population. At the time the Mackey-Glass paper was written, the form of the dependence of the production term on the population was not known, so two models were investigated:

$$\frac{dP}{dt} = \frac{\beta_0}{1+(P_\tau/\theta)^n} - \gamma P, \tag{2}$$

and

$$\frac{dP}{dt} = \frac{\beta_0 P_\tau}{1 + (P_\tau/\theta)^n} - \gamma P. \tag{3}$$

In these equations, γ is the specific rate of loss of blood cells from circulation, and θ is a scale factor for the population. In particular, in variant (2), θ is the population at which the production term, which is monotonically decreasing, falls to half its maximal value from a maximum of β_0. In variant (3), the production term is unimodal on the positive semi-axis, with a maximum at $P_\tau = \theta(n-1)^{-1/n}$.

Model (2) was shown, by numerical simulation, to have a regime with a stable equilibrium point, and an oscillatory regime at larger values of the delay τ. Model (3) has these types of solutions as well, but Mackey and Glass found that the initial Andronov-Hopf bifurcation was followed by a sequence of period-doubling bifurcations leading to chaos as τ is increased (Fig. 2). The oscillatory solutions were related to periodic hematological diseases, specifically to cyclical neutropenia and to one particular clinical presentation of chronic granulocytic leukemia. In the latter ailment, the cell maturation time is significantly increased, which would correspond to an increase in τ. This correlates well with the oscillatory and chaotic solutions found at larger τ. Because of its interesting dynamics, equation (3) has been studied by many authors, and quickly became known as "the Mackey-Glass equation" [19].

In discussing the bifurcations of equation (3), Mackey and Glass specifically mention bifurcations in maps, especially the work of May [6] as well as the famous Li and Yorke "Period three implies chaos" paper [9]. Interestingly, they did not mention the chaotic solutions in ordinary differential equations discovered by Lorenz [4], which might seem odd to a modern reader. Mackey (and probably Glass) did know about Lorenz's work, but were more strongly influenced by contemporary work demonstrating chaos in unimodal maps, particularly May's work [6, 22] (Glass, personal communication; Mackey, personal communication). Beyond simple analogy, Mackey and Glass were aware that it was possible to derive a map from their DDE by a singular

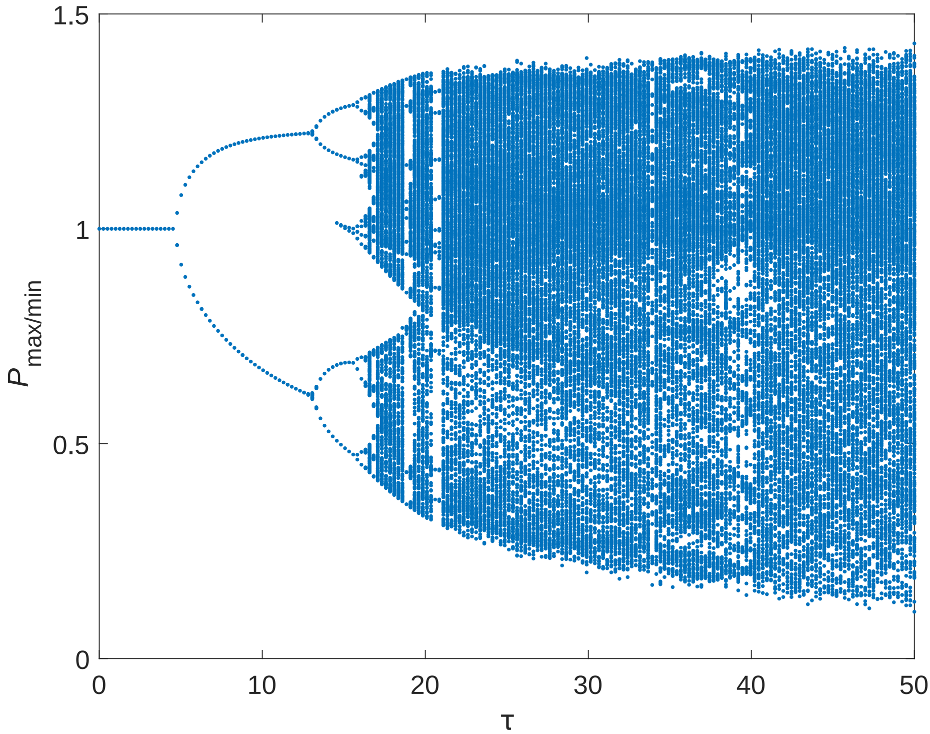

Figure 2: Bifurcation diagram as a function of the delay τ for the model (3), showing minima and maxima along trajectories after discarding a transient of 2000 time units. Parameters: $\beta_0 = 0.2$, $\gamma = 0.1$, $n = 10$, $\theta = 1$.

perturbation argument (not presented in their paper): Consider the scaling

$$\xi = t/\tau, \qquad \varpi = P/\theta,$$
$$\epsilon = (\gamma\tau)^{-1}, \qquad \beta = \beta_0/\gamma,$$

which transforms (3) to

$$\epsilon \frac{d\varpi}{d\xi} = \frac{\beta\varpi_\tau}{1+\varpi_\tau^n} - \varpi, \tag{4}$$

keeping the subscript τ as a graphical convenience to denote a delayed quantity, albeit now $\varpi_\tau = \varpi(\xi - 1)$. By a standard argument of singular perturbation theory extended to DDEs [23], in the limit $\epsilon \to 0$ (i.e. the case of a large delay $\tau \gg \gamma^{-1}$), equation (4) reduces to the map

$$\varpi_{i+1} = \frac{\beta \varpi_i}{1 + \varpi_i^n}, \tag{5}$$

where now the continuous time argument has been replaced by a discrete iteration index i. Given that unimodal maps generically display fixed points, periodic solutions and chaos in appropriate parameter regimes [22], Mackey and Glass expected that their DDE would also display these behaviors at larger values of the delay τ, as indeed proved to be the case.

3.3 Dynamical diseases introduced

In the very last paragraph of this paper, Mackey and Glass introduced a concept that would become highly influential, namely that of a dynamical disease. A dynamical disease is characterized by an intact control system operating in an aberrant parameter range, resulting in pathological behavior. Thus note that, in the Mackey-Glass study, oscillations or chaos are obtained by varying the value of a delay, not by setting a parameter to zero (corresponding to a broken component of a control system) or by modifying the control function in any way.

3.4 Great minds thinking alike

When the time is right, it is not unusual for an idea to be enunciated at more-or-less the same time by multiple authors, each unaware of the others' work. So it was with the Mackey-Glass equation, similar equations having been studied around the same time by Lasota [24, 25] and by Perez, Malta and Countinho [26], the latter focusing on population models for insects. Specifically, these papers discuss models with a unimodal delayed nonlinearity, in each case finding chaotic solutions.

Lasota's work is particularly worthy of discussion, given that it shares deep connections with that of Glass and Mackey, and in many ways anticipated it. Lasota's work also focused on hematopoiesis, specifically in his case on the control of the circulating red blood cell population. Although Lasota's first publication on the topic was in 1976 [24], a 1974 paper by Chow analyzes an even earlier, unpublished model of Lasota and Wazenska with an exponentially decaying delayed term [27]. This early model displayed regimes with a stable fixed point and with oscillatory solutions. In Lasota's work of the period, the link to the dynamics of maps is much more explicit than in the Mackey-Glass papers, where this link is mentioned but not developed. Even more striking is the discussion of diseased states arising as the parameters of Lasota's model are varied [25], which implicitly contains the idea of a dynamical disease. Lasota and Mackey eventually became acquainted, and went on to become friends and collaborators, a story told by Mackey elsewhere [28].

4 The 1979 Glass-Mackey paper

The 1977 paper [1] was followed up in 1979 with a more detailed study of these models [2]. In addition, the 1979 paper discussed a number of additional disorders that might be described as dynamical diseases: cardiac arrhythmias, psychological disorders and cancer were particularly discussed, but a number of others were mentioned. The section discussing potential dynamical diseases lays out an ambitious research program for those interested in the intersection of dynamical systems and human health, which many researchers were more than happy to take up [29]. Glass and Mackey's book, *From Clocks to Chaos* [30], which emphasized the concept of a dynamical disease, no doubt also played a role in popularizing this concept.

For those of us familiar with the mathematical biology literature of the era, another striking feature of the 1979 paper was the use of realistic parameters extracted from the literature. This is also true of the 1977 paper, but because of space limitations and because much of the discussion of parameters appears in footnotes, it is less obvious there. A large subset of the mathematical biology literature of the time studied models in the absence of any parameter estimates. This was an unavoidable state of affairs given the paucity of quantitative data across many fields of biology, with a few exceptions, notably population biology. It is fortunate that Glass and Mackey were studying problems in physiology, a field that had long emphasized rigorous, quantitative measurements. The parameters needed for their modeling work were therefore either directly available, or could be estimated from published measurements.

5 Long-term impact

Clearly, the concept of a dynamical disease was an important new idea to most researchers in the field at the time, and giving this concept a name increased its impact. It was, and remains, an important organizing idea for much research in mathematical biology, and is likely the most important contribution of these papers. It also immediately attracted the attention of clinicians. The first reference to dynamical diseases in the (non-mathematical) medical literature appeared in 1979, in a comment in which Mali argues that psoriasis is a dynamical disease [31]. By 1994, the idea of a dynamical disease had become so important that a NATO Advanced Research Workshop was dedicated to this topic, with a special issue of *Chaos* publishing papers from the workshop [29].

The Mackey-Glass equation very quickly captured the imaginations of researchers as a key paradigmatic chaotic system [32, 33, 34, 35], finding a place alongside the logistic map and Lorenz equations, specifically in the study of chaos in infinite-dimensional systems. Among early citations, the Mackey-Glass equation was used by Farmer in this vein to study the development of high-dimensional chaos [36], which is related to classical ideas of turbulence in fluids.

Citation analyses can be abused, but they still do give us some information on the influence of a paper. By October 11th of this year, the two papers discussed here [1, 2] had been cited in 2438 distinct sources indexed in the Web of Science (WoS). The vast majority of these cited at least the 1977 paper (2356 citations).

One of the more striking features of the citation data is the enduring appeal of these papers (Fig. 3). In fact, the number of citations has, on the whole, been trending up since the publication of the *Science* paper more than 40 years ago, reaching a plateau since 2009 of 119 ± 5 citations per year. (Note that the data for 2018 are incomplete.)

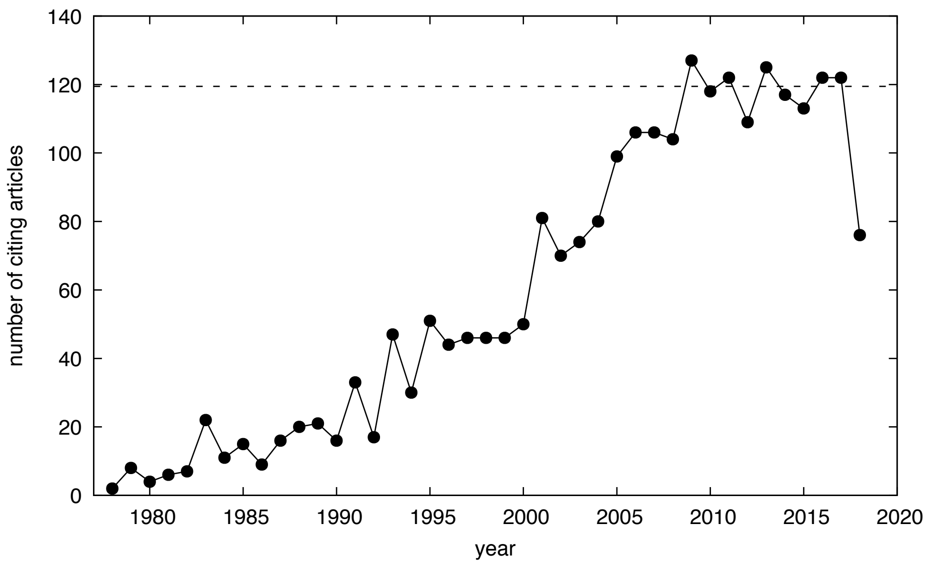

Figure 3: Number of sources citing one or both of the Glass-Mackey papers [1, 2] by year. Search performed in the Web of Science on October 11, 2018. The dashed line shows the average number of citations in the period 2009–2017.

We can dig into the areas influenced by the Mackey-Glass papers in a couple of different ways using the Web of Science. First, we can use the WoS subject areas. The results of this analysis are presented in Fig. 4. The broad impact of these papers across virtually all areas of science is obvious at a glance. Given the biomedical topics at the heart of these papers, I also calculated a total citation count for all medical subject areas combined, shown as the right-most bar in the graph. The 357 citations in this combined category represent a significant citation count for purely theoretical papers, demonstrating that the topics discussed by Glass and Mackey resonated with medical scientists. Whether this is due to the specific systems studied, respiratory control and hematopoiesis, or to the concept of dynamical diseases is difficult to assess. However, it seems likely that some combination of both is responsible for the popularity of these papers in the medical literature.

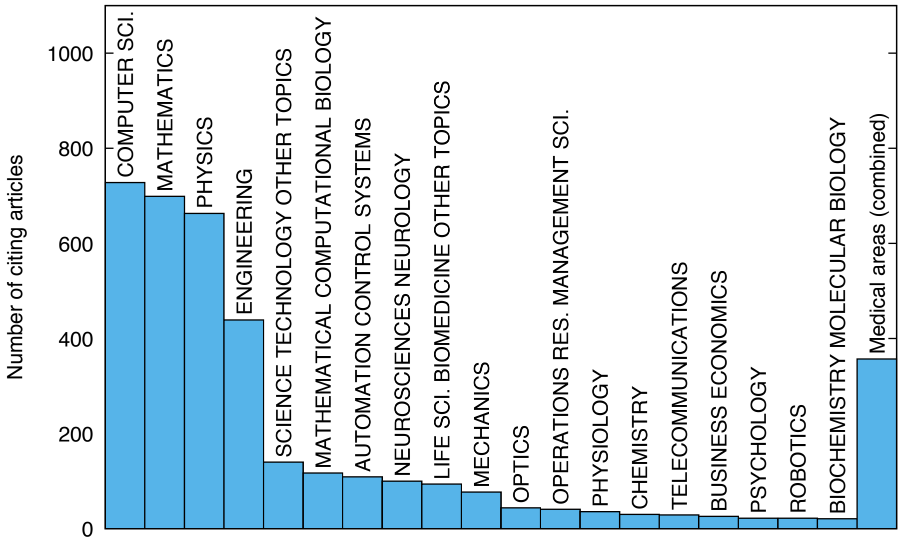

Figure 4: Number of sources citing one or both of the Glass-Mackey papers [1, 2] by WoS subject areas. Search performed in the Web of Science on October 11, 2018. Only subject areas generating 20 or more citations are shown here. The final bar represents combined citations in all medical subject areas.

Another way to gauge where these papers have had an impact is to look at the citing articles themselves. To do this, I carried out a series of keyword searches on the downloaded citation data from WoS. As necessary, keywords were combined to account for different ways to express the same concept. The searches were guided in part by the issues directly raised in the Mackey-Glass papers, and in part by an examination of the titles of at least some of the papers in the search results. Such searches will necessarily underestimate the number of papers in a particular area that cited Mackey and Glass since they are dependent on the appropriate keywords appearing in article titles. This strategy is also somewhat limited by the appearance of reliable keywords in the titles of papers. For example, while there seem to be quite a few papers on gene expression in the output, I failed to find keywords that extracted these papers specifically and with reasonable reliability. Nevertheless, the results are informative, and are presented in Table 2. Some of the topics in this table reflect those discussed by Glass and Mackey in their two papers: hematopoiesis, cardiovascular function, and respiratory control. Similarly, as seen above, studies of singularly perturbed equations flow naturally from a study of the Mackey-Glass equation. Others may seem surprising at first glance, but are typically connected to the status of the Mackey-Glass equation as a paradigmatic chaotic system, which moreover has an attractor of variable dimension, depending on the value of the delay [36]. This is clearly the case for the development of time-series analysis methods, as well as for studies on the control of chaotic systems. At first glance, the appearance of neural networks as one of the top research topics citing Glass and Mackey might be surprising, except that predicting a chaotic system's evolution in time given a part of its time series is a frequent challenge tackled in the field. As for synchronization, this relates to the search for secure communication methods using synchronized chaotic systems [37]. ODEs with low-dimensional attractors may not be up to the job [38], so a system with a high-dimensional attractor like the Mackey-Glass equation is an attractive chaos generator in this area of research.

6 Closing comments

Great papers don't have to be long. One short paper can present an equation that is in itself a fertile object for study, or define a new concept around which entire research programs can be built. A short paper can inspire young scientists, as we repeatedly heard at the Leon

Table 2: Partial classification of the citations to the Glass-Mackey papers [1, 2] based on keyword searches in the downloaded results from the Web of Science (Oct. 11, 2018 search).

Research topic	**Citing sources**
Neural networks	353
Time-series analysis	322
Synchronization	165
Control of chaotic systems	110
Hematopoiesis	69
Cardiology and circulation	62
Respiratory control	59
Singularly perturbed equations	54

Glass and Michael C. Mackey Diamond Symposium earlier this year. The 1977 Mackey-Glass paper [1] did all of those things. This Year of Mathematical Biology is the perfect time to recognize a paper that is not only an important part of the history of our field, but also a vibrant part of its present.

Acknowledgments

This paper was stimulated in part by a conversation with Harvey Brown (University of Oxford Department of Philosophy) at the Leon Glass and Michael C. Mackey Diamond Symposium in June of this year. Special thanks to Michael and Leon for answering my questions, and my apologies for not fully disclosing my motive at the time. Happy birthday, gentlemen. I hope this paper is a pleasant surprise for both of you. I would also like to thank Tomas Gedeon (Montana State University Department of Mathematical Sciences) for sharing his photo of Michael and Leon.

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