

Limit Cycles in a Model of Olfactory Sensory Neurons

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We propose an approach to study small limit cycle bifurcations on a center manifold in analytic or smooth systems depending on parameters. We then apply it to the investigation of limit cycle bifurcations in a model of calcium oscillations in the cilia of olfactory sensory neurons and show that it can have two limit cycles: a stable cycle appearing after a Bautin (generalized Hopf) bifurcation and an unstable cycle appearing after a subcritical Hopf bifurcation.

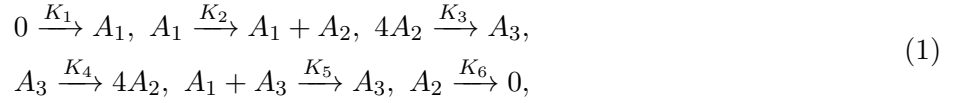
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1. Introduction

In this paper, we consider the mathematical model for calcium oscillations in the cilia of olfactory sensory neurons proposed in [Reidl et al., 2006].

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The model involves three species, a cyclic-nucleotide-gated (CNG^o) channel, calcium Ca^{2+} , and calmodulin $CaM4$, which we denote by A_1 , A_2 and A_3 , respectively, and six reactions:



where K_1, \dots, K_6 are the reaction rates. As is usual in such schemes, zero on the left-hand side means that the reaction is a source, where certain substances are introduced into the system. Zero on the right-hand side means that the reaction is a sink, where certain substances are removed from the system. Let us denote the concentrations of A_1 , A_2 and A_3 by X , Y and Z , respectively.

In [Reidl et al., 2006] by using the mass action kinetics (see e.g. [Feinberg, 1987]) and the generalized mass action kinetics, the three-dimensional system of differential equations

$$\begin{aligned} \dot{X} &= K_1 - K_5 X Z, \\ \dot{Y} &= K_2 X - 4K_3 Y^2 + 4K_4 Z - K_6 Y^\epsilon \\ \dot{Z} &= K_3 Y^2 - K_4 Z, \end{aligned} \quad (2)$$

associated with the network (1) is derived. Since the generalized mass action kinetics were used for the last reaction, the corresponding term in the second equation is not $-K_6 Y$, but $-K_6 Y^\epsilon$, where the effective exponent ϵ corresponds to the extrusion of Ca^{2+} from cilium by pumps and exchangers.

In practice, the rate constants K_i are not usually known, so one of the main tasks in the investigation of chemical reaction networks is to ask whether the resulting differential system has the capacity to admit certain kinds of qualitative behavior, among them, the most important are the behavior near steady states and the oscillatory behavior. That is, it is important to know whether rate constant values such that the differential system resulting from a presumed chemistry admits behavior of a specified kind can even exist. In this way, one can determine whether a postulated chemistry taken with mass action kinetics can be observed (see [Feinberg, 1987] for more details).

Since biochemical reaction models derived using the mass action law are represented by polynomial or analytical differential equations involving many parameters (reaction rates), even the determination of stationary states and their stability analysis become extremely difficult problems, which are usually unfeasible for general values of parameters, even in the case of polynomial models. The search for limit cycles, which describe auto-oscillatory regimes, is a much more difficult problem than the investigation of singular points. Because of the complexity of the biochemical reaction models, the study of limit cycles in such models seldom goes beyond the determination of possible Hopf bifurcations (even without verifying the transversality, or crossing, condition) and mostly such bifurcations are found numerically for heuristically chosen values of parameters, although in recent years some symbolic computation algorithms for detection of Hopf bifurcations have been developed (see e.g. [Errami et al., 2013, 2015; Niu & Wang, 2008, 2012; Sturm et al., 2009]).

If a smooth system of autonomous differential equations admits a two-dimensional center manifold, then it is possible to study not only Hopf bifurcations, but also the so-called Bautin bifurcations, or degenerated Hopf bifurcations on the center manifolds, see e.g. [Kuznetsov, 1995; Farr et al., 1989]. To perform the study of such bifurcations one can use one of the following six methods known in the literature: The method of Poincaré-Birkhoff normal forms, the method of Lyapunov quantities (constants), the method of the succession function, the method of averaging, the method of intrinsic harmonic balancing, and the Lyapunov-Schmidt method (see e.g. [Farr et al., 1989] for a nice review of the methods). Although from a theoretical point of view all of them allow performing a complete bifurcation analysis, in practice, they require extremely laborious computations, so the computational efficiency becomes an important issue. It appears that the most efficient method from the computational point of view is the method of Lyapunov quantities, used in [Bonin & Legault, 1988; Songling, 1980], since it involves only collection of similar terms in polynomial expressions and solving systems of linear algebraic equations.

However, the method of Lyapunov quantities used in [Songling, 1980] and other works involves the search for positively defined Lyapunov functions. In this paper, we propose a generalization of the method

for the case when the Lyapunov function is semi-positively defined, that is, the quadratic form defined by the lowest part of the Lyapunov function has one zero eigenvalue and the other eigenvalues are positive. We then apply the method to study the degenerate Hopf bifurcations in the system (2) and show that the system can have two limit cycles as the result of such bifurcations.

The paper is organized as follows. In Section 2, we describe an approach to study limit cycle bifurcations using a Lyapunov function on the center manifold. In Section 3, we study singular points of system (2). In the last section, we use the approach proposed in Section 2 to study limit cycles of system (2). In particular, it is shown there that the system can have two limit cycles bifurcating from a singular point, and numerical examples are provided confirming the existence of two limit cycles.

2. Limit cycle bifurcations on the center manifold

Consider a three-dimensional system of the form

$$\dot{\mathbf{x}} = A\mathbf{x} + F(\mathbf{x}) = G(\mathbf{x}), \quad (3)$$

where $\mathbf{x} = (x, y, z)$, the matrix A has the eigenvalues $\lambda_1, \lambda_2, \lambda_3$ and $\lambda_1 < 0$, $\lambda_2 = i\omega$, $\lambda_3 = -i\omega$, F is a vector-function, which is analytic in a neighborhood of the origin, and such that its series expansion starts from quadratic or higher terms, and $G(\mathbf{x}) = (G_1(\mathbf{x}), G_2(\mathbf{x}), G_3(\mathbf{x}))^T$.

Since two eigenvalues of system (3) are purely imaginary and the third one has the real part different from zero, according to the Center Manifold Theorem [Chicone, 1999], the system has a center manifold defined by a function $x = f(y, z)$. After a linear transformation and rescaling of time, system (3) can be written in the form

$$\begin{aligned} \dot{u} &= -v + P(u, v, w) = \tilde{P}(u, v, w) \\ \dot{v} &= u + Q(u, v, w) = \tilde{Q}(u, v, w) \\ \dot{w} &= -\lambda w + R(u, v, w) = \tilde{R}(u, v, w), \end{aligned} \quad (4)$$

where λ is a positive real number and P, Q, R , are power series without constant and linear terms which are convergent in a neighborhood of the origin.

Since system (4) is analytic, for every $r \in \mathbb{N}$ there exists in a sufficiently small neighborhood of the origin a C^r invariant manifold W^c , the local center manifold, that is tangent to the (u, v) -plane at the origin, and which contains all the recurrent behavior of system (4) in a neighborhood of the origin in \mathbb{R}^3 ([Chicone, 1999, §4.1], [Sijbrand, 1985]). For system (4), the phase portrait in a neighborhood of the origin on W^c can be, depending on the nonlinear terms P, Q and R , either a center, in which case every trajectory (other than the origin itself) is an oval surrounding the origin, or a focus, in which case, every trajectory spirals towards the origin or every trajectory spirals away from the origin as the time increases.

According to the Lyapunov theorem, for system (4) with the corresponding vector field

$$\mathfrak{X} = \tilde{P} \frac{\partial}{\partial u} + \tilde{Q} \frac{\partial}{\partial v} + \tilde{R} \frac{\partial}{\partial w}$$

the origin is a center for $\mathfrak{X}|_{W^c}$ if and only if \mathfrak{X} admits a real analytic local first integral of the form

$$\Phi(u, v, w) = u^2 + v^2 + \sum_{j+k+\ell=3}^{\infty} \phi_{jkl} u^j v^k w^\ell \quad (5)$$

in a neighborhood of the origin in \mathbb{R}^3 . Moreover, when a center exists, the local center manifold W^c is unique and analytic (see [Bibikov, 1979, §13]).

For system (4), one can look for a function $\Phi(u, v, w)$ of the form (5) such that

$$\mathfrak{X}\Phi = \sum_{i=1}^{\infty} g_i (u^2 + v^2)^{i+1}. \quad (6)$$

In the case of the two-dimensional system (when in (4) $\tilde{R} \equiv 0$) it is well-known that it is possible to find functions Φ and g_i satisfying (6). If the right hand-sides of (4) are functions depending on parameters,

then ϕ_{jkl} and g_i also depend on the parameters of the system. If, for some values of parameters, all g_i vanish, then the corresponding system (4) has a center at the origin, but if, for some values of parameters, not all g_i vanish, then by the Lyapunov stability theorem (see e.g. [Bibikov, 1979; Romanovski & Shafer, 2009]), the singular point at the origin is a stable focus if the first non-zero g_i is negative, and it is an unstable focus if the first non-zero g_i is positive (since Φ is a positively defined Lyapunov function with negatively and positively defined derivatives, respectively). If the first non-zero coefficient in (6) is g_i , then perturbing the system in such way that $|g_{k-1}| \ll |g_k|$ and the signs of g_s alternate we obtain $i - 1$ limit cycles bifurcated from the origin of the system [Songling, 1980].

In the following theorem, we show that a similar approach can be applied to study bifurcations of limit cycles on the center manifold of three-dimensional systems (3). Although it is possible to transform system (3) to a system of the form (4), in the case when the matrix A in system (3) depends on parameters, such transformation usually involves expressions containing radicals, so then the radicals will also appear in the coefficients of system (4). It will slow down computations of function (5) and focus quantities g_i in (6) sharply. For this reason, we do not transform system (3) to system (4), but work with system (3), for which we assume that the function G depends on parameters α , $\alpha = (\alpha_1, \dots, \alpha_m)$.

Theorem 1. *Suppose that for system (3) there exists a polynomial*

$$\Psi(\mathbf{x}) = \sum_{j+l+m=2}^s a_{jlm} x^j y^l z^m \quad (7)$$

such that

$$\mathfrak{X}(\Psi) := \frac{\partial \Psi(\mathbf{x})}{\partial x} G_1(\mathbf{x}) + \frac{\partial \Psi(\mathbf{x})}{\partial y} G_2(\mathbf{x}) + \frac{\partial \Psi(\mathbf{x})}{\partial z} G_3 = g_1(y^2 + z^2)^2 + g_2(y^2 + z^2)^3 + \dots + g_{n-1}(y^2 + z^2)^n + O(\|\mathbf{x}\|^{2n+1}). \quad (8)$$

Let

$$x = f(y, z, \alpha^*) \quad (9)$$

be the center manifold of system (3) corresponding to the value α^* of parameters of the system and

$$q(\mathbf{x}, \alpha^*) = \sum_{j+l+m=2} a_{jlm} x^j y^l z^m \quad (10)$$

be the quadratic part of (7). Let $q_1(y, z, \alpha^*)$ be $q(\mathbf{x}, \alpha^*)$ evaluated on (9). Assume that $q_1(y, z, \alpha^*)$ is a positively defined quadratic form and

$$g_1(\alpha^*) = g_2(\alpha^*) = \dots = g_k(\alpha^*) = 0, \quad g_{k+1}(\alpha^*) \neq 0, \quad (11)$$

where $k < n - 1$. Then,

1) If $g_{k+1}(\alpha^*) < 0$, the corresponding system (3) has a stable focus at the origin on the center manifold, and if $g_{k+1}(\alpha^*) > 0$, then the focus is unstable.

2) If it is possible to choose perturbations of the parameters α in the system (3), such that

$$|g_1(\alpha_k)| \ll |g_2(\alpha_{k-1})| \ll \dots \ll |g_k(\alpha_1)| \ll |g_{k+1}(\alpha^*)|, \quad (12)$$

α_{j+1} is arbitrarily close to α_j and the signs of $g_s(\alpha_m)$ in (12) alternate, then system (3) corresponding to the parameter α_k has at least k limit cycles on the center manifold.

Proof. 1) Since q_1 is positively defined, the function Ψ restricted to the center manifold is positively defined in a small neighborhood of the origin. The derivative of Ψ with respect to the vector field on the center manifold has the same sign as $g_{k+1}(\alpha^*)$. Thus, by the Lyapunov theorem, the origin is a stable focus on the center manifold if $g_{k+1}(\alpha^*) < 0$, and an unstable focus if $g_{k+1}(\alpha^*) > 0$.

2) Assume for determinacy that $g_{k+1}(\alpha^*) < 0$. Under the condition of the theorem, the equality $\Psi(\mathbf{x}, \alpha^*) = c$ ($c \in (0, c_1]$) defines, in a small neighborhood of the origin near the center manifold (9), a family of cylinders which are transversal to the center manifold. Let C_1 be the curve formed by the

intersection of the cylinder $\Psi(\mathbf{x}, \alpha^*) = c_1$ and the center manifold $M(\alpha^*)$ of system (3), defined by (9). If c_1 is sufficiently small, then C_1 is an oval on $M(\alpha^*)$ and the vector field is directed inside C_1 , since

$$\mathfrak{X}(\Psi(\mathbf{x}, \alpha^*)) = g_{k+1}(\alpha^*)(y^2 + z^2)^{k+2} + h.o.t$$

and $g_{k+1}(\alpha^*) < 0$. By the assumption of the theorem, there is an α_1 arbitrarily close to α^* and such that $g_k(\alpha_1) > 0$. Then, for some $c_2 < c_1$ the intersection of the cylinder $\Phi(\mathbf{x}, \alpha_1) = c_2$ ($c_2 \in (0, c_1]$) defines a curve C_2 on the center manifold $x = f(y, z, \alpha_1)$, such that the vector field of system (3) is directed outside of C_2 (since $g_k(\alpha_1) > 0$). Since the perturbation is arbitrarily small, the curve C_1 is transformed to a curve $C_1^{(1)}$, such that the vector field on $C_1^{(1)}$ is still directed inside the curve. Then, according to the Poincaré-Bendixson theorem, there is a limit cycle on the center manifold $x = f(y, z, \alpha_1)$ in the ring bounded by C_2 and $C_1^{(1)}$. Continuing the procedure on the center manifold corresponding to a parameter α_k we obtain k curves $C_1^{(k)}, C_2^{(k-1)}, \dots, C_k$, such that the vector field on $C_1^{(k)}$ is directed inside the curve, the vector field on $C_2^{(k-1)}$ is directed outside of the curve, the vector field on $C_3^{(k-2)}$ is directed inside the curve, and so on. Then, in each ring bounded by the curves $C_i^{(j)}$, system (3) corresponding to the parameter α_k has at least one limit cycle on the center manifold $x = f(y, z, \alpha_k)$. ■

Corollary 2.1. *If condition (11) holds, then the origin of system (15) is asymptotically stable if $g_{k+1}(\alpha^*) < 0$, and it is unstable if $g_{k+1}(\alpha^*) > 0$.*

Proof. By the Reduction Principle [Pliss, 1964; Guckenheimer & Holmes, 1990], the stability of the origin of a system (15) is the same as the stability of the singular point at the origin on the center manifold. ■

3. Singular points of system (2)

To simplify the study of singular points and limit cycles of system (2), we introduce dimensionless variables performing the substitution

$$X_1 = K_2 X, \quad Y_1 = Y, \quad Z_1 = K_5 Z,$$

which transforms (2) into the system

$$\begin{aligned} \dot{X}_1 &= k_1 - X_1 Z_1, \\ \dot{Y}_1 &= X_1 - 4k_3 Y_1^2 + \frac{4k_4}{k_5} Z_1 - k_2 Y_1^\epsilon \\ \dot{Z}_1 &= k_3 k_5 Y_1^2 - k_4 Z_1, \end{aligned} \tag{13}$$

where $k_1 = K_1 K_2$, $k_2 = K_6$, $k_3 = K_3$, $k_4 = K_4$ and $k_5 = K_5$.

Thus, without loss of generality, instead of system (2) we will study system (13). Since X, Y, Z in (2) are concentrations of the species and K_i are reaction rates, all parameters k_i in (13) are positive, and we are interested in the behavior of trajectories of (13) in the domain $X_1 > 0, Y_1 > 0, Z_1 > 0$.

In order to simplify computations, we assume that system (13) has a stationary point in the plane $y = 1$. It happens when

$$k_1 = \frac{k_2 k_3 k_5}{k_4}, \tag{14}$$

and then the unique stationary point of system (13) is the point $P(X_1^{(0)}, Y_1^{(0)}, Z_1^{(0)})$ with the coordinates $X_1^{(0)} = k_2$, $Y_1^{(0)} = 1$, $Z_1^{(0)} = \frac{k_3 k_5}{k_4}$. Moving the origin to the point P using the substitution $x =$

$X_1 - X_1^{(0)}, y = Y_1 - Y_1^{(0)}, z = Z_1 - Z_1^{(0)}$ we obtain the system

$$\begin{aligned}\dot{x} &= -\frac{k_3 k_5}{k_4} x - k_2 z - xz, \\ \dot{y} &= k_2 + x - 8k_3 y - 4k_3 y^2 - k_2(1+y)^\epsilon + \frac{4k_4}{k_5} z, \\ \dot{z} &= 2k_3 k_5 y - k_4 z + k_3 k_5 y^2.\end{aligned}\tag{15}$$

The Jacobian of the matrix of the linear approximation of system (15) at the origin is

$$A = \begin{pmatrix} -\frac{k_3 k_5}{k_4} & 0 & -k_2 \\ 1 & -\epsilon k_2 - 8k_3 & \frac{4k_4}{k_5} \\ 0 & 2k_3 k_5 & -k_4 \end{pmatrix}.$$

The eigenvalues of A are roots of a cubic polynomial and have rather complicated expression. To simplify calculations, we impose the condition that one of the eigenvalues is -1 . To find this condition, we calculate the characteristic polynomial of A obtaining

$$p = -\frac{1}{k_4} (2k_2 k_3 k_4 k_5 + \epsilon k_2 k_3 k_4 k_5 + \epsilon k_2 k_4^2 u + \epsilon k_2 k_3 k_5 u + 8k_3^2 k_5 u + k_3 k_4 k_5 u + \epsilon k_2 k_4 u^2 + 8k_3 k_4 u^2 + k_4^2 u^2 + k_3 k_5 u^2 + k_4 u^3).$$

Then, the condition $p|_{u=-1} = 0$ gives

$$k_2 = \frac{(-1 + 8k_3 + k_4)(-k_4 + k_3 k_5)}{2k_3 k_4 k_5 - \epsilon(-1 + k_4)(k_4 - k_3 k_5)}.\tag{16}$$

Proposition 1. *Assume that for system (15) $\epsilon > 0$ and condition (16) is fulfilled. Then, the system has a center manifold passing through the origin O , with the stationary point O being a center or a focus at the center manifold if and only if*

$$k_3 > 0 \wedge k_4 > 0 \wedge k_5 > 0 \wedge 8k_3 < 1 \wedge 8k_3 + k_4 < 1 \wedge 8k_3 k_4 + k_3 k_5 + k_4^2 < k_4.\tag{17}$$

Proof. Computing the eigenvalues of matrix A we find that they are $\lambda_1 = -1$, $\lambda_{2,3} = \alpha \pm \beta$, where

$$\alpha = -\frac{a}{2k_4(-\epsilon k_4 + \epsilon k_4^2 + \epsilon k_3 k_5 - 2k_3 k_4 k_5 - \epsilon k_3 k_4 k_5)},\tag{18}$$

$$\beta = \frac{\sqrt{b}}{2k_4 k_5(-\epsilon k_4 + \epsilon k_4^2 + \epsilon k_3 k_5 - 2k_3 k_4 k_5 - \epsilon k_3 k_4 k_5)}\tag{19}$$

with

$$a = -\epsilon k_4^3 + 8\epsilon k_3 k_4^3 + \epsilon k_4^4 - \epsilon k_3 k_4 k_5 + 2k_3 k_4^2 k_5 + 2\epsilon k_3 k_4^2 k_5 - 16k_3^2 k_4^2 k_5 - 8\epsilon k_3^2 k_4^2 k_5 - 2k_3 k_4^3 k_5 - \epsilon k_3 k_4^3 k_5 + \epsilon k_3^2 k_5^2 - 2k_3^2 k_4 k_5^2 - \epsilon k_3^2 k_4 k_5^2$$

and

$$\begin{aligned}b &= k_5^2(4k_3^2 k_4^2 k_5^2(2(1 + 8k_3)k_4^3 + k_4^4 + k_4^2(-3 + 64k_3^2 - 2k_3(-8 + k_5)) + \\ &\quad 2(1 - 8k_3)k_3 k_4 k_5 + k_3^2 k_5^2) + \epsilon^2(k_4^4 - k_4^3(1 + k_3(-8 + k_5)) - 8k_3^2 k_4^2 k_5 - \\ &\quad k_3^2 k_5^2 + k_3 k_4 k_5(1 + k_3 k_5))^2 + 4\epsilon k_3 k_4 k_5(-k_4^6 + k_3 k_4^5(-16 + k_5) - k_3^3 k_5^3 + \\ &\quad k_3^3 k_4 k_5^2(8 + k_5) - k_3(-1 + 8k_3)k_4^2 k_5(3 + 2k_3 k_5) + k_4^4(3 + 16k_3^2(-4 + k_5) + \\ &\quad 2k_3 k_5) + 2k_4^3(-1 + k_3(8 - 3k_5) + 32k_3^3 k_5 - k_3^2(-8 + k_5)k_5))).\end{aligned}$$

Thus, the matrix A can have a pair of purely imaginary eigenvalues if and only if $\alpha = 0$. Solving the latter equation for ϵ we obtain

$$\epsilon = -\frac{2k_3 k_4 k_5(-k_4 + 8k_3 k_4 + k_4^2 + k_3 k_5)}{(-k_4 + k_3 k_5)(-k_4^2 + 8k_3 k_4^2 + k_4^3 - k_3 k_5 + k_3 k_4 k_5)}.\tag{20}$$

Now, solving the semialgebraic system

$$k_1 > 0 \wedge k_2 > 0 \wedge k_3 > 0 \wedge k_4 > 0 \wedge k_5 > 0 \wedge b < 0 \wedge \epsilon > 0$$

with `Reduce` of `MATHEMATICA`, we obtain that the solution is given by inequalities (17). ■

4. Limit cycles of system (2)

In this section we study the limit cycle bifurcations of system (15). The system (15) is not a polynomial system, so we expand the function on the right-hand side of the second equation of (15) into a power series up to the third order, obtaining the system

$$\begin{aligned} \dot{x} &= -\frac{k_3 k_5}{k_4} x - k_2 z - xz, \\ \dot{y} &= x - (\epsilon k_2 + 8k_3)y + \left(\frac{\epsilon k_2}{2} - \frac{\epsilon^2 k_2}{2} - 4k_3\right) y^2 \\ &\quad + \left(-\frac{\epsilon k_2}{3} + \frac{\epsilon^2 k_2}{2} - \frac{\epsilon^3 k_2}{6}\right) y^3 + \frac{4k_4 z}{k_5} + \dots, \\ \dot{z} &= 2k_3 k_5 y - k_4 z + k_3 k_5 y^2, \end{aligned} \tag{21}$$

where the dots stand for terms of the order higher than three.

Using a linear transformation, it is possible to transform system (13) to a system of the form (4) (with $\lambda = -1$) and then study its limit cycle bifurcations using the normal form theory. However, then the coefficients of the obtained system will contain radical expressions, which will essentially slow down symbolic computations with `MATHEMATICA` (or another computer algebra system). So, instead of transforming (15) to a system of the form (4) and then applying the normal form theory, we use the way provided by Theorem 1. Using this approach, we look for function (7) satisfying (8), where now G_1, G_2, G_3 are the right-hand sides of (21).

The computational procedure to find the first m polynomials g_i is as follows.

1. Write down the initial string of (7) up to order $2m$, $\Psi_{2m}(x, y, z) = q(\mathbf{x}) + \sum_{j+k+l=3}^{2m} a_{jkl} x^j y^k z^l$.
2. For each $i = 3, \dots, 2m$ equate coefficients of terms of order i in the expression

$$F_{2m} = \frac{\partial \Psi_{2m}}{\partial x} G_1 + \frac{\partial \Psi_{2m}}{\partial y} G_2 + \frac{\partial \Psi_{2m}}{\partial z} G_3 - g_1(y^2 + z^2)^2 - \dots - g_{2m}(y^2 + z^2)^{2m} \tag{22}$$

to zero, obtaining $2m - 1$ systems of linear variables in unknown variables a_{jkl} , and g_1, \dots, g_m .

3. Look for solutions of the obtained linear systems consequently, starting from systems that correspond to $i = 2$. Each linear system that corresponds to odd $i = 2i_0 - 1$ has a unique solution with respect to unknown a_{jkl} . After solving the system (for instance, with the command `Solve` in `MATHEMATICA`), substitute the obtained values of a_{jkl} to the linear systems that correspond to $i > 2i_0 - 1$. For systems that correspond to even $i = 2i_0$, consider the linear system as a system in unknowns a_{jkl} and g_{i_0} . In this case, one of a_{jkl} can be chosen arbitrarily. After solving the system, assign the value 1 to the undefined a_{jkl} if $i_0 = 2$, or assign the value 0 for the undefined a_{jkl} if $i_0 > 2$, then substitute the obtained values of a_{jkl} to the linear systems that correspond to $i > 2i_0$. In this step the quantity g_{i_0-1} is computed.

The calculations using the procedure described above (we did them with `MATHEMATICA`) yield the polynomial g_1 given in Appendix 1.

Let us denote $k = (k_3, k_4, k_5)$.

Theorem 2. *If for system (15) conditions (16) and (20) are fulfilled, and for some fixed values $k^* = (k_3^*, k_4^*, k_5^*)$ satisfying (17) $g_1(k^*) < 0$, then the system has a stable focus at the origin on the center manifold, and if $g_1(k^*) > 0$, then the focus is unstable. Moreover, if at least one of the functions $\frac{\partial g_1(k)}{\partial k_3}, \frac{\partial g_1(k)}{\partial k_4}, \frac{\partial g_1(k)}{\partial k_5}$ is different from zero for $k = k^*$, then the system undergoes a subcritical Hopf bifurcation if $g_1(k^*) < 0$, and a supercritical Hopf bifurcation if $g_1(k^*) > 0$.*

Proof. Calculations using the procedure described above yield that, for system (21), the quadratic part of function (7) is

$$\begin{aligned}
 q(x, y, z) = & -\frac{k_4}{(-1 + 8k_3)k_4^2 + k_4^3 - k_3k_5 + k_3k_4k_5}x^2 - \\
 & \frac{2k_3k_5}{(-1 + 8k_3)k_4^2 + k_4^3 - k_3k_5 + k_3k_4k_5}xy + y^2 - \\
 & \frac{k_4^2(-1 + 8k_3 + k_4)}{k_3k_5((-1 + 8k_3)k_4^2 + k_4^3 - k_3k_5 + k_3k_4k_5)}xz - \\
 & \frac{-k_4 + k_4^2 + k_3k_5}{k_3k_4k_5}yz + \frac{k_4 - (1 + 8k_3)k_4^2 - k_3k_5 + k_3k_4k_5}{4k_3^2k_4k_5^2}z^2.
 \end{aligned} \tag{23}$$

We look for the center manifold in the form

$$x = h(y, z) \tag{24}$$

Then the function h is computed from the equation

$$\dot{x} - \dot{y}\frac{\partial h}{\partial y} - \dot{z}\frac{\partial h}{\partial z} = 0,$$

where the left-hand side is evaluated for x , defined by (24).

Computing the first two terms of the series expansion of the center manifold we find

$$x = \frac{k_4 - k_3k_5}{k_4}y - \frac{(k_4 - k_3k_5)(k_4^2 + k_3k_5)}{2k_3k_4^2k_5}z + h.o.t.$$

We substitute the obtained expression into (23), and using the Sylvester criterion with **Reduce** of Mathematica, verify that, if condition (17) holds, then the quadratic approximation of the obtained expression is a positively defined quadratic form. Thus, from the Hopf theorem (see e.g. Theorem 3.4.2 in [Guckenheimer & Holmes, 1990]) and Theorem 1 we obtain that the conclusion of the theorem holds. ■

Since we were unable to compute the quantity g_2 for general parameters k_3 and k_4 at our computational facilities, in order to simplify the further analysis we set

$$k_3 = k_4 = \frac{1}{10}. \tag{25}$$

Then, from (17), we obtain that $0 < k_5 < 0.1$. The only root of the polynomial g_1 in this interval is $\bar{k}_5 \approx 0.05147292$, and g_1 is strictly increasing on this interval. The plot of g_1 on this interval is given in Fig. 1.

The quantity g_2 computed for the values of parameters given by (25) is given in Appendix 2.

Theorem 3. *There are systems (15) with two limit cycles in a neighborhood of the singular point at the origin.*

Proof. Since $g_1(k_5)$ is an increasing function on $(0, 0.1)$, if $0 < k_5 < \bar{k}_5$, then the singular point at the center manifold is a stable focus, and if $\bar{k}_5 < k_5 < 0.1$, then it is an unstable focus. If $k_5 = \bar{k}_5$ then $g_2(\bar{k}_5) \approx -0.554882 < 0$ and, therefore, the singular point is a stable focus. Thus, according to Theorem 1, after the perturbation of k_5 in a neighborhood of $k_5 = \bar{k}_5$ in such a way that g_1 becomes positive, a stable limit cycle is born at the center manifold.

Since, after such perturbation, the real part of the eigenvalue is still zero and the transversality condition for α defined by (18) is satisfied, one more limit cycle is born as the result of the Hopf bifurcation. ■

Example 1. The existence of a stable limit cycle of system (13) for the values of parameters

$$k^* = (k_1, k_2, k_3, k_4, k_5, \epsilon) = (0.320238, 4.92673, 0.1, 0.1, 0.065, 0.0071041) \tag{26}$$

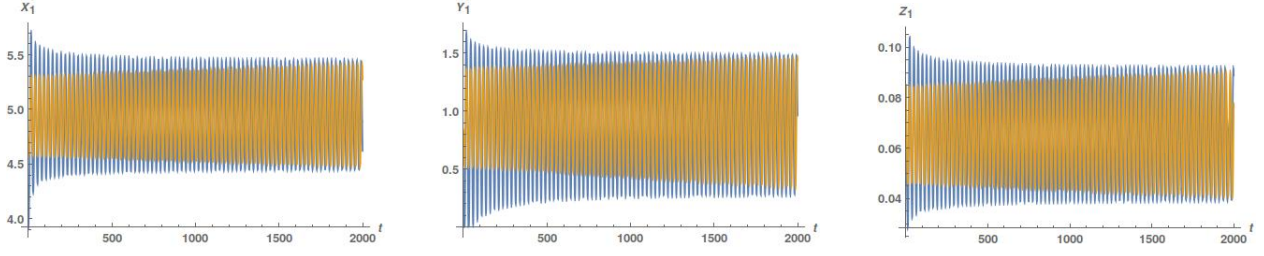


Fig. 1. Solutions $X_1(t)$, $Y_1(t)$ and $Z_1(t)$ of the initial problems $X_1(0) = 3.9267, Y_1(0) = 0.5, Z_1(0) = 0.085$ and $X_1(0) = 4.7267, Y_1(0) = 0.8, Z_1(0) = 0.085$ of the system (13) for parameters k^* given in (26) converge to a stable limit cycle when $t \rightarrow \infty$.

is evident from Figure 1. Since for these values of parameters the real part of the eigenvalues of the singular point at the origin of system (15) is zero and

$$\frac{\partial \alpha}{\partial k_4} \Big|_{k^*} \neq 0,$$

where α is defined by (18), an unstable limit cycle can appear from the singular points after the Hopf bifurcation.

Example 2. In Figure 2 we observe 2 limit cycles in system (13) for the values of parameters

$$k^* = \{k_1, k_2, k_3, k_4, k_5, \epsilon\} = \{0.320238, 4.92673, 0.1, 0.1, 0.065, 0.0072041\}. \quad (27)$$

The outer stable limit cycle is clearly visible. Since for these values of parameters α defined by (18) is negative, the singular point is stable. Thus, the trajectories corresponding to the smallest ring in Figure 2 tend to zero when time increases. It means that there is an unstable limit cycle in the area between the smallest and middle rings in Figure 2.

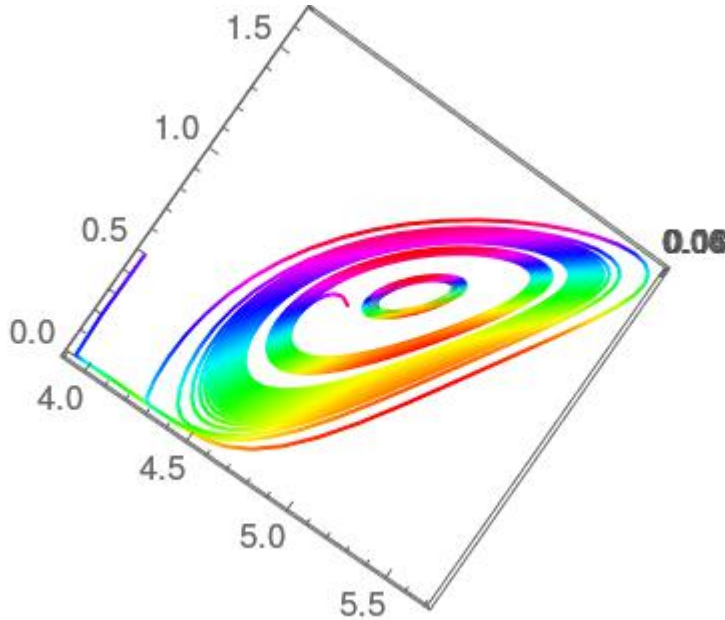


Fig. 2. Two limit cycles in system (13) with parameters (27) and the initial conditions $(X_1, Y_1, Z_1) = (, ,), (, ,)$ and $(, ,)$.

To conclude, we have shown that for some values of parameters in system (2) not only a Hopf bifurcation occurs, but also degenerate Hopf bifurcations occur, so there are systems in the family with two limit cycles.

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Appendix 1

$$\begin{aligned}
g_1 = & -((-k_4^3 + 8k_3k_4^3 + k_4^4 - k_3k_4k_5 + k_3k_4^2k_5 + k_3^2k_5^2)(-3k_4^{14} + 288k_3k_4^{14} - 8320k_3^2k_4^{14} + 112640k_3^3k_4^{14} - \\
& 798720k_3^4k_4^{14} + 2883584k_3^5k_4^{14} - 4194304k_3^6k_4^{14} + 68k_4^{15} - 3448k_3k_4^{15} + 67904k_3^2k_4^{15} - 670208k_3^3k_4^{15} + \\
& 3485696k_3^4k_4^{15} - 8912896k_3^5k_4^{15} + 8388608k_3^6k_4^{15} - 258k_4^{16} + 9992k_3k_4^{16} - 149248k_3^2k_4^{16} + 1073664k_3^3k_4^{16} - \\
& 3702784k_3^4k_4^{16} + 4849664k_3^5k_4^{16} + 416k_4^{17} - 12424k_3k_4^{17} + 136000k_3^2k_4^{17} - 645120k_3^3k_4^{17} + 1114112k_3^4k_4^{17} - \\
& 335k_4^{18} + 7384k_3k_4^{18} - 53504k_3^2k_4^{18} + 126976k_3^3k_4^{18} + 132k_4^{19} - 1952k_3k_4^{19} + 7168k_3^2k_4^{19} - 20k_4^{20} + 160k_3k_4^{20} - \\
& 12k_3k_4^{12}k_5 + 1056k_3^2k_4^{12}k_5 - 25344k_3^3k_4^{12}k_5 + 264192k_3^4k_4^{12}k_5 - 1277952k_3^5k_4^{12}k_5 + 2359296k_3^6k_4^{12}k_5 + 342k_3k_4^{13}k_5 - \\
& 15640k_3^2k_4^{13}k_5 + 270592k_3^3k_4^{13}k_5 - 2287104k_3^4k_4^{13}k_5 + 9928704k_3^5k_4^{13}k_5 - 20840448k_3^6k_4^{13}k_5 + 16777216k_3^7k_4^{13}k_5 - \\
& 1679k_3k_4^{14}k_5 + 61408k_3^2k_4^{14}k_5 - 872704k_3^3k_4^{14}k_5 + 6153216k_3^4k_4^{14}k_5 - 22704128k_3^5k_4^{14}k_5 + 42336256k_3^6k_4^{14}k_5 - \\
& 33554432k_3^7k_4^{14}k_5 + 3618k_3k_4^{15}k_5 - 108416k_3^2k_4^{15}k_5 + 1242752k_3^3k_4^{15}k_5 - 6830592k_3^4k_4^{15}k_5 + 18251776k_3^5k_4^{15}k_5 - \\
& 19791872k_3^6k_4^{15}k_5 - 4135k_3k_4^{16}k_5 + 98864k_3^2k_4^{16}k_5 - 860736k_3^3k_4^{16}k_5 + 3260416k_3^4k_4^{16}k_5 - 4653056k_3^5k_4^{16}k_5 + \\
& 2606k_3k_4^{17}k_5 - 46936k_3^2k_4^{17}k_5 + 276992k_3^3k_4^{17}k_5 - 544768k_3^4k_4^{17}k_5 - 852k_3k_4^{18}k_5 + 10400k_3^2k_4^{18}k_5 - 31744k_3^3k_4^{18}k_5 + \\
& 112k_3k_4^{19}k_5 - 736k_3^2k_4^{19}k_5 - 18k_3^2k_4^{10}k_5^2 + 1440k_3^3k_4^{10}k_5^2 - 27264k_3^4k_4^{10}k_5^2 + 196608k_3^5k_4^{10}k_5^2 - 491520k_3^6k_4^{10}k_5^2 + \\
& 690k_3^2k_4^{11}k_5^2 - 27624k_3^3k_4^{11}k_5^2 + 400064k_3^4k_4^{11}k_5^2 - 2664448k_3^5k_4^{11}k_5^2 + 8208384k_3^6k_4^{11}k_5^2 - 9437184k_3^7k_4^{11}k_5^2 - \\
& 4370k_3^2k_4^{12}k_5^2 + 144784k_3^3k_4^{12}k_5^2 - 1830336k_3^4k_4^{12}k_5^2 + 11218432k_3^5k_4^{12}k_5^2 - 34574336k_3^6k_4^{12}k_5^2 + 48234496k_3^7k_4^{12}k_5^2 - \\
& 16777216k_3^8k_4^{12}k_5^2 + 12134k_3^2k_4^{13}k_5^2 - 342592k_3^3k_4^{13}k_5^2 + 3705152k_3^4k_4^{13}k_5^2 - 19392000k_3^5k_4^{13}k_5^2 + 50798592k_3^6k_4^{13}k_5^2 - \\
& 61997056k_3^7k_4^{13}k_5^2 + 33554432k_3^8k_4^{13}k_5^2 - 18133k_3^2k_4^{14}k_5^2 + 426432k_3^3k_4^{14}k_5^2 - 3743232k_3^4k_4^{14}k_5^2 + 15162368k_3^5k_4^{14}k_5^2 - \\
& 28049408k_3^6k_4^{14}k_5^2 + 19922944k_3^7k_4^{14}k_5^2 + 15526k_3^2k_4^{15}k_5^2 - 290456k_3^3k_4^{15}k_5^2 + 1907840k_3^4k_4^{15}k_5^2 - 5130240k_3^5k_4^{15}k_5^2 + \\
& 4718592k_3^6k_4^{15}k_5^2 - 7541k_3^2k_4^{16}k_5^2 + 104208k_3^3k_4^{16}k_5^2 - 443648k_3^4k_4^{16}k_5^2 + 557056k_3^5k_4^{16}k_5^2 + 1900k_3^2k_4^{17}k_5^2 - \\
& 16960k_3^3k_4^{17}k_5^2 + 32768k_3^4k_4^{17}k_5^2 - 188k_3^2k_4^{18}k_5^2 + 768k_3^3k_4^{18}k_5^2 - 12k_3^3k_4^8k_5^3 + 864k_3^4k_4^8k_5^3 - 11776k_3^5k_4^8k_5^3 + \\
& 45056k_3^6k_4^8k_5^3 + 694k_3^3k_4^9k_5^3 - 23400k_3^4k_4^9k_5^3 + 264960k_3^5k_4^9k_5^3 - 1218560k_3^6k_4^9k_5^3 + 1933312k_3^7k_4^9k_5^3 - 5874k_3^3k_4^{10}k_5^3 + \\
& 169888k_3^4k_4^{10}k_5^3 - 1800832k_3^5k_4^{10}k_5^3 + 8670208k_3^6k_4^{10}k_5^3 - 18333696k_3^7k_4^{10}k_5^3 + 11534336k_3^8k_4^{10}k_5^3 + 21136k_3^3k_4^{11}k_5^3 - \\
& 539104k_3^4k_4^{11}k_5^3 + 5157888k_3^5k_4^{11}k_5^3 - 23117824k_3^6k_4^{11}k_5^3 + 48726016k_3^7k_4^{11}k_5^3 - 40370176k_3^8k_4^{11}k_5^3 - 40377k_3^3k_4^{12}k_5^3 + \\
& 885440k_3^4k_4^{12}k_5^3 - 7203712k_3^5k_4^{12}k_5^3 + 26811392k_3^6k_4^{12}k_5^3 - 44810240k_3^7k_4^{12}k_5^3 + 26214400k_3^8k_4^{12}k_5^3 + 44336k_3^3k_4^{13}k_5^3 - \\
& 798872k_3^4k_4^{13}k_5^3 + 5100160k_3^5k_4^{13}k_5^3 - 13600768k_3^6k_4^{13}k_5^3 + 12976128k_3^7k_4^{13}k_5^3 - 28329k_3^3k_4^{14}k_5^3 + 391376k_3^4k_4^{14}k_5^3 - \\
& 1725440k_3^5k_4^{14}k_5^3 + 2457600k_3^6k_4^{14}k_5^3 + 10054k_3^3k_4^{15}k_5^3 - 94624k_3^4k_4^{15}k_5^3 + 217088k_3^5k_4^{15}k_5^3 - 1724k_3^3k_4^{16}k_5^3 + \\
& 8448k_3^4k_4^{16}k_5^3 + 96k_3^3k_4^{17}k_5^3 - 3k_4^3k_6k_5^4 + 192k_3^5k_6k_5^4 - 1536k_3^6k_6k_5^4 + 346k_3^4k_4^7k_5^4 - 9312k_3^5k_4^7k_5^4 + 73472k_3^6k_4^7k_5^4 - \\
& 172032k_3^7k_4^7k_5^4 - 4322k_3^4k_4^8k_5^4 + 104136k_3^5k_4^8k_5^4 - 853440k_3^6k_4^8k_5^4 + 2750464k_3^7k_4^8k_5^4 - 2621440k_3^8k_4^8k_5^4 + \\
& 20944k_3^4k_4^9k_5^4 - 463160k_3^5k_4^9k_5^4 + 3682688k_3^6k_4^9k_5^4 - 12698624k_3^7k_4^9k_5^4 + 17268736k_3^8k_4^9k_5^4 - 4194304k_3^9k_4^9k_5^4 - \\
& 51788k_3^4k_4^{10}k_5^4 + 1019000k_3^5k_4^{10}k_5^4 - 7254080k_3^6k_4^{10}k_5^4 + 22577152k_3^7k_4^{10}k_5^4 - 28655616k_3^8k_4^{10}k_5^4 + 8388608k_3^9k_4^{10}k_5^4 + \\
& 72244k_3^4k_4^{11}k_5^4 - 1201240k_3^5k_4^{11}k_5^4 + 6972160k_3^6k_4^{11}k_5^4 - 16416768k_3^7k_4^{11}k_5^4 + 12451840k_3^8k_4^{11}k_5^4 - 58443k_3^4k_4^{12}k_5^4 + \\
& 763216k_3^5k_4^{12}k_5^4 - 3156992k_3^6k_4^{12}k_5^4 + 4063232k_3^7k_4^{12}k_5^4 + 26670k_3^4k_4^{13}k_5^4 - 242592k_3^5k_4^{13}k_5^4 + 532480k_3^6k_4^{13}k_5^4 - \\
& 6192k_3^4k_4^{14}k_5^4 + 29696k_3^5k_4^{14}k_5^4 + 544k_3^4k_4^{15}k_5^4 + 68k_3^5k_4^{15}k_5^4 - 1344k_3^6k_4^{15}k_5^4 + 5632k_3^7k_4^{15}k_5^4 - 1655k_3^5k_4^{16}k_5^4 + \\
& 30784k_3^6k_4^{16}k_5^4 - 168192k_3^7k_4^{16}k_5^4 + 241664k_3^8k_4^{16}k_5^4 + 11838k_3^5k_4^{17}k_5^4 - 215104k_3^6k_4^{17}k_5^4 + 1296256k_3^7k_4^{17}k_5^4 - \\
& 2836480k_3^8k_4^{17}k_5^4 + 1441792k_3^9k_4^{17}k_5^4 - 39681k_3^8k_4^{18}k_5^4 + 671152k_3^6k_4^{18}k_5^4 - 3906240k_3^7k_4^{18}k_5^4 + 9007104k_3^8k_4^{18}k_5^4 - \\
& 6291456k_3^9k_4^{18}k_5^4 + 71812k_3^5k_4^{19}k_5^4 - 1062240k_3^6k_4^{19}k_5^4 + 5312896k_3^7k_4^{19}k_5^4 - 10094592k_3^8k_4^{19}k_5^4 + 5505024k_3^9k_4^{19}k_5^4 - \\
& 73618k_3^5k_4^{20}k_5^4 + 878128k_3^6k_4^{20}k_5^4 - 3235072k_3^7k_4^{20}k_5^4 + 3538944k_3^8k_4^{20}k_5^4 + 42216k_3^5k_4^{21}k_5^4 - 356768k_3^6k_4^{21}k_5^4 - \\
& 708608k_3^7k_4^{21}k_5^4 - 12388k_3^5k_4^{22}k_5^4 + 55296k_3^6k_4^{22}k_5^4 + 1408k_3^5k_4^{13}k_5^5 - 258k_3^6k_4^{13}k_5^5 + 3168k_3^7k_4^{13}k_5^5 - 7680k_3^8k_4^{13}k_5^5 + \\
& 3514k_3^5k_4^{14}k_5^5 - 47840k_3^6k_4^{14}k_5^5 + 179456k_3^7k_4^{14}k_5^5 - 147456k_3^8k_4^{14}k_5^5 - 17641k_3^6k_4^{15}k_5^5 + 239952k_3^7k_4^{15}k_5^5 - 1016896k_3^8k_4^{15}k_5^5 + \\
& 1327104k_3^9k_4^{15}k_5^5 - 262144k_3^{10}k_4^{15}k_5^5 + 43696k_3^6k_4^{16}k_5^5 - 548304k_3^7k_4^{16}k_5^5 + 2182528k_3^8k_4^{16}k_5^5 - 2856960k_3^9k_4^{16}k_5^5 + \\
& 524288k_3^{10}k_4^{16}k_5^5 - 58519k_3^6k_4^{17}k_5^5 + 614848k_3^7k_4^{17}k_5^5 - 1908736k_3^8k_4^{17}k_5^5 + 1622016k_3^9k_4^{17}k_5^5 + 42672k_3^6k_4^{18}k_5^5 - \\
& 325824k_3^7k_4^{18}k_5^5 + 569344k_3^8k_4^{18}k_5^5 - 15704k_3^6k_4^{19}k_5^5 + 64512k_3^7k_4^{19}k_5^5 + 2240k_3^6k_4^{20}k_5^5 + 416k_3^7k_4^{20}k_5^5 - 3392k_3^8k_4^{20}k_5^5 +
\end{aligned}$$

$$\begin{aligned}
& 4608k_3^9k_4^3k_5^7 - 4039k_3^7k_4^4k_5^7 + 39008k_3^8k_4^4k_5^7 - 89856k_3^9k_4^4k_5^7 + 32768k_3^{10}k_4^4k_5^7 + 15354k_3^7k_4^5k_5^7 - 149840k_3^8k_4^5k_5^7 + \\
& 397568k_3^9k_4^5k_5^7 - 221184k_3^{10}k_4^5k_5^7 - 28653k_3^7k_4^6k_5^7 + 249568k_3^8k_4^6k_5^7 - 588544k_3^9k_4^6k_5^7 + 278528k_3^{10}k_4^6k_5^7 + \\
& 27662k_3^7k_4^7k_5^7 - 183712k_3^8k_4^7k_5^7 + 260096k_3^9k_4^7k_5^7 - 13108k_3^7k_4^8k_5^7 + 48128k_3^8k_4^8k_5^7 + 2368k_3^7k_4^9k_5^7 - 335k_3^8k_4^9k_5^7 + \\
& 1696k_3^9k_4^9k_5^7 - 1024k_3^{10}k_4^9k_5^7 + 2642k_3^8k_4^3k_5^8 - 16256k_3^9k_4^3k_5^8 + 16896k_3^{10}k_4^3k_5^8 - 7849k_3^8k_4^4k_5^8 + 49792k_3^9k_4^4k_5^8 - \\
& 61184k_3^{10}k_4^4k_5^8 + 10886k_3^8k_4^5k_5^8 - 57440k_3^9k_4^5k_5^8 + 55296k_3^{10}k_4^5k_5^8 - 7008k_3^8k_4^6k_5^8 + 21760k_3^9k_4^6k_5^8 + 1664k_3^8k_4^7k_5^8 + \\
& 132k_3^9k_4^7k_5^8 - 320k_3^{10}k_4^7k_5^8 - 940k_3^9k_4^2k_5^9 + 2752k_3^{10}k_4^2k_5^9 + 2228k_3^9k_4^3k_5^9 - 6976k_3^{10}k_4^3k_5^9 - 2156k_3^9k_4^4k_5^9 + 4864k_3^{10}k_4^4k_5^9 + \\
& 736k_3^9k_4^5k_5^9 - 20k_3^{10}k_4^5k_5^9 + 144k_3^{10}k_4k_5^{10} - 284k_3^{10}k_4^2k_5^{10} + 160k_3^{10}k_4^3k_5^{10})) / (k_4^2(-k_4 + k_3k_5)(-k_4^2 + 8k_3k_4^2 + k_4^3 - \\
& k_3k_5 + k_3k_4k_5)^3(-k_4^2 - 4k_4^3 + 32k_3k_4^3 + 4k_4^4 - 4k_3k_4k_5 + 4k_3k_4^2k_5 + 4k_3^2k_5^2)(3k_4^6 - 48k_3k_4^6 + 192k_3^2k_4^6 + 6k_3k_4^4k_5 - \\
& 48k_3^2k_4^4k_5 - 6k_3k_4^5k_5 + 48k_3^2k_4^5k_5 + 3k_3^2k_4^2k_5^2 - 12k_3^2k_4^3k_5^2 + 48k_3^3k_4^3k_5^2 + 3k_3^2k_4^4k_5^2 + 8k_3^2k_4^5k_5^2 - 64k_3^3k_4^5k_5^2 + 16k_3^2k_4^6k_5^2 - \\
& 6k_3^3k_4^3k_5^3 + 6k_3^3k_4^2k_5^3 + 8k_3^3k_4^3k_5^3 - 8k_3^3k_4^4k_5^3 + 3k_3^4k_5^4 - 8k_3^4k_4^2k_5^4 + 48k_3^4k_4^4k_5^4))
\end{aligned}$$

Appendix 2

$$\begin{aligned}
g_2 = & - (2936684087935203 + 1903329794381968962k_5 + 526356269068940036058k_5^2 + \\
& 79212661161468359120682k_5^3 + 6624774681223327162056312k_5^4 + \\
& 226210368780713535116189198k_5^5 - 11069401291544927561200467090k_5^6 - \\
& 1681061474736283778980266837290k_5^7 - 88270101979612138277063002374075k_5^8 - \\
& 2477699412162830370947947313822600k_5^9 - 36765039251191521107996938881205000k_5^{10} - \\
& 225936898431835263136354705676085000k_5^{11} + 1355580393385771642526807674775000000k_5^{12} + \\
& 4225634014554480900089535196731000000k_5^{13} - 7447510173322764423476685804685000000k_5^{14} - \\
& 55286614599318489486752585449650000000k_5^{15} + 251173978392196043283302794468500000000k_5^{16} - \\
& 3078962879351248032859287900000000000k_5^{17} - 2169631665992185188025531440150000000000k_5^{18} + \\
& 5262165240502910370909490745000000000000k_5^{19} - 212358888489564564273413665000000000000k_5^{20} - \\
& 13651336452235596514164796000000000000000k_5^{21} + 3540730840932428085069046600000000000000k_5^{22} - \\
& 47646890714938134580571205000000000000000k_5^{23} + 4390145224310429991855340000000000000000k_5^{24} - \\
& 31151597239468216641843000000000000000000k_5^{25} + 18249194021574604996285000000000000000000k_5^{26} - \\
& 8792944539548463715050000000000000000000k_5^{27} + 3137409734404532590500000000000000000000k_5^{28} - \\
& 6219252088637741600000000000000000000000k_5^{29} - 4084082501899995000000000000000000000000k_5^{30} + \\
& 6468224839928100000000000000000000000000k_5^{31} - 1774924054002000000000000000000000000000k_5^{32} + \\
& 2159429746500000000000000000000000000000k_5^{33} - 9443174400000000000000000000000000000000k_5^{34}) / \\
& (36000(-1 + k_5)^3(1 + 90k_5)^5(-13 - 45k_5 + 50k_5^2)^2(-401 - 90k_5 + 100k_5^2) \\
& (98209 + 739620k_5 - 748900k_5^2 - 162000k_5^3 + 90000k_5^4) \\
& (-5 - 675k_5 - 29643k_5^2 - 389205k_5^3 + 1470264k_5^4 - 1661040k_5^5 + 610560k_5^6) \\
& (3 + 540k_5 + 30683k_5^2 + 561150k_5^3 - 34888k_5^4 - 2005920k_5^5 + 1462400k_5^6))
\end{aligned}$$

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