A TANGLEGRAM KURATOWSKI THEOREM

ÉVA CZABARKA, LÁSZLÓ A. SZÉKELY AND STEPHAN WAGNER

ABSTRACT. A tanglegram consists of two rooted binary plane trees with the same number of leaves and a perfect matching between the two leaf sets. Tanglegrams are drawn with the leaves on two parallel lines, the trees on either side of the strip created by these lines, and the perfect matching inside the strip. If this can be done without any edges crossing, a tanglegram is called planar. We show that every non-planar tanglegram contains one of two non-planar 4-leaf tanglegrams as induced subtanglegram, which parallels Kuratowski's Theorem.

1. Introduction

Kuratowski's Theorem [8], a cornerstone of graph theory, asserts that a graph is non-planar if and only if it contains a subdivision of $K_{3,3}$ or K_5 . This is not the only characterization of planarity: Wagner's Theorem [13] asserts that a graph is non-planar if and only if $K_{3,3}$ or K_5 is a minor of the graph. Tanglegrams are a special kind of graph, consisting of two binary trees of the same size and a perfect matching joining the leaves, with restrictions on how they can be drawn. Tanglegrams are well studied objects in phylogenetics and computer science. Planarity of tanglegrams is directly characterized by Kuratowski's Theorem in terms of subgraphs, if the tanglegram is augmented by a certain edge (Lemma 1). In this paper we provide a characterization of planarity of tanglegrams not in terms of its subgraphs, but in terms of other tanglegrams (Theorem 4). As tanglegrams are not widely known objects, we immediately turn to the technical definitions.

2. Tanglegrams

A plane binary tree has a root vertex assumed to be a common ancestor of all other vertices, and each vertex either has two children (left and right) or no children. A vertex with no children is a leaf, and a vertex with two children is an internal vertex. Note that this definition allows a single-vertex tree that is considered as both root and leaf to be a rooted binary tree. A plane binary tree is easy to draw on one side of a line, without edge crossings, such that only the leaves of the tree are on the line.

A tanglegram layout (L, R, σ) consists of a left plane binary tree L with root r drawn in the halfplane $x \leq 0$, having its leaves on the x = 0 line, a right plane binary tree R with root ρ , drawn in the halfplane $x \geq 1$, having its leaves on the x = 1 line, each with n leaves,

²⁰¹⁰ Mathematics Subject Classification. Primary 05C10; secondary 05C05, 05C62, 92B10.

Key words and phrases. trees, subtrees, tanglegram, graph drawing, planarity, crossing number.

The second author was supported in part by the NSF DMS, grant numbers 1300547 and 1600811, the third author was supported by the National Research Foundation of South Africa, grant number 96236.

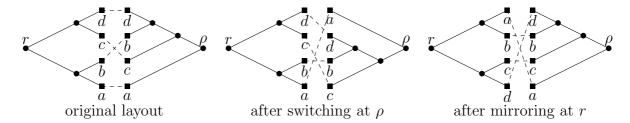


FIGURE 1. Results of a switch and a mirror operation.

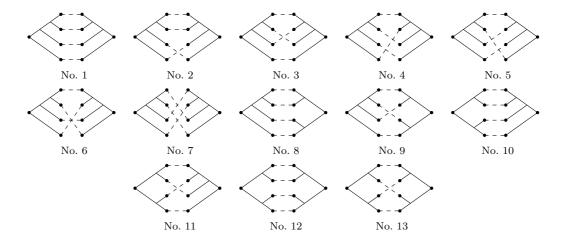


FIGURE 2. The 13 tanglegrams of size 4 from [7].

and a perfect matching σ between their leaves drawn in straight line segments. We treat tanglegram layouts combinatorially, and understand them as ordered triplets (L, R, σ) . A switch on the tanglegram layout (L, R, σ) is the following operation: select an internal vertex v of one of the two trees L and R. Vertex v in L has an up-subtree L_u and a down-subtree L_d , with leaf sets $L(L_u)$ and $L(L_d)$ (or vertex v in R has an up-subtree R_u and a down-subtree R_d , with leaf sets $L(R_u)$ and $L(R_d)$). In the first case interchange L_u and L_d such that on the line x = 0 the order of two leaves changes precisely when one is in $L(L_u)$ and the other is in $L(L_d)$. In the second case interchange R_u and R_d such that on the line x = 1 the order of two leaves changes precisely when one is in $L(R_u)$ and the other is in $L(R_d)$. The edges of the matching move with the leaves that they connect during the switch. This is also illustrated in Figure 1.

Two layouts represent the same tanglegram if a sequence of switches moves one layout into the other. For an internal vertex v, one may also take the *mirror image* of the subtree rooted at v. This is called the *mirror operation* at vertex v, which is illustrated in Figure 1. Matching edges still connect the corresponding leaves. As the mirror operation can be obtained by doing a sequence of switch operations from v down towards the leaves, mirror operations do not change the tanglegram. Tanglegrams partition the set of tanglegram layouts, or equivalently a tanglegram can be seen as an equivalence class of tanglegram

layouts. Note that interchanging L and R is not allowed and may result in a different tanglegram.

The *size* of a tanglegram is the number of leaves in L (or R) in any of its layouts. Billey, Konvalinka, and Matsen [1] considered the enumeration problem for tanglegrams: they obtained an explicit formula for the number t_n of tanglegrams with n leaves on each side. The counting sequence starts

$$1, 1, 2, 13, 114, 1509, 25595, 535753, 13305590, 382728552, \ldots$$

Figure 2 illustrates the fourth term in this sequence. The asymptotic formula

$$t_n \sim n! \cdot \frac{e^{1/8} 4^{n-1}}{\pi n^3}$$

was derived in [1] as well, and a number of questions on the shape of random tanglegrams were asked. Those were answered in [7] by means of a strong structure theorem.

3. Tanglegram crossing number and planarity of tanglegrams

The crossing number of a tanglegram layout is the number of crossing pairs of matching edges. The crossing number of a tanglegram layout does not depend on details of the drawing, such as the exact positions of leaves on the vertical lines, just on the rankings of the matched leaves in the linear orders of leaves on the lines x = 0 and x = 1. This fact justifies the combinatorial treatment of tanglegram layouts for studying crossings.

It is desirable to draw a tanglegram with the least possible number of crossings, which is known as the Tanglegram Layout Problem [14]. This problem is NP-hard [4]. The (tanglegram) crossing number crt(T) of a tanglegram T is defined as the minimum number of crossings among its layouts.

Tanglegrams play a major role in phylogenetics, especially in the theory of cospeciation. The first binary tree is the phylogenetic tree of hosts, while the second binary tree is the phylogenetic tree of their parasites, e.g. gopher and louse [5]. The matching connects the host with its parasite. The tanglegram crossing number has been related to the number of times parasites switched hosts [5], or, working with gene trees instead of phylogenetic trees, to the number of horizontal gene transfers ([2], pp. 204–206).

A tanglegram is planar if it has zero tanglegram crossing number; in other words, if it has a layout without crossing matching edges. Otherwise it is called non-planar. In an earlier paper [3] we showed that the tanglegram crossing number of a randomly and uniformly selected tanglegram of size n is $\Theta(n^2)$ with high probability, i.e. as large as it can be within a constant multiplicative factor. As one would therefore expect, the number of planar tanglegrams of size n grows much more slowly than the total number of tanglegrams. The counting sequence p_n starts

$$1, 1, 2, 11, 76, 649, 6173, 63429, 688898, 7808246, \ldots$$

and an asymptotic formula of the form

$$p_n \sim A \cdot n^{-3} \cdot B^n,$$

where A and B are constants, holds [10].

Recall [12] that a drawing of a graph G in the plane places the vertices of G on distinct points in the plane and then, for every edge uv in G, draws a continuous simple curve in the plane connecting the two points corresponding to u and v, in such a way that no curve has a vertex point as an internal point. The crossing number cr(G) of a graph G is the minimum number of intersection points among the interiors of the curves representing edges, over all possible drawings of the graph, where no three edges may have a common interior point.

Note that the (graph) crossing number cr(T) of a tanglegram T is less or equal to the (tanglegram) crossing number crt(T) of T, since the tanglegram layout is more restrictive than the graph drawing. The following lemma is essentially taken from [3]:

Lemma 1. Assume that a tanglegram T is represented by the layout (L, R, σ) , and let the roots of L and R be r and ρ . Let T^* denote the graph in which the underlying graph of T (consisting of the two binary trees and the matching edges) is augmented by the edge $r\rho$. Then the following facts are equivalent:

- (1) $crt(T) \ge 1$,
- (2) $cr(T^*) \ge 1$,
- (3) T^* contains a subdivision of $K_{3,3}$.

Proof. (1) \Rightarrow (2). This is equivalent with $\operatorname{cr}(T^*) = 0 \Rightarrow \operatorname{crt}(T) = 0$. If $\operatorname{cr}(T^*) = 0$ then T^* can be drawn in the plane with straight lines. This means both the left and right trees are drawn with straight lines, and we can draw a curve in the plane that goes through each matching edge once and no other edges of T^* (the latter can be easily proven e.g. by induction on the number of leaves). Using the order of the leaves on this curve, one can easily obtain the desired planar layout of T.

- $(2)\Rightarrow(3)$ follows from Kuratowski's Theorem, as T^* cannot contain a subdivision of K_5 . This is because none of its vertices has degree greater than 3.
- $(3)\Rightarrow(1)$ is proved by the contrapositive: if T was to admit a planar tanglegram layout, then we could add the additional edge between r and ρ , creating a planar drawing of the graph T^* .

Note that a subdivision of a $K_{3,3}$ in the tanglegram T^* may be such that the six vertices of $K_{3,3}$ are all in L or all in R.

Now consider the tanglegrams T_1 and T_2 below, No. 6 and 13 in Figure 2, each augmented with the extra edge connecting the roots. Figure 3 shows a layout with one crossing for the tanglegrams T_1 and T_2 , and a subdivision of $K_{3,3}$ in the graphs T_1^* and T_2^* , showing $\operatorname{crt}(T_1) = \operatorname{crt}(T_2) = 1$ in view of Lemma 1.

As it turns out, these two are the only non-planar tanglegrams of size 4 (cf. Corollary 5). All others that have crossings in Figure 2, can in fact be drawn without crossings. For example, Figure 4 shows a crossing-free drawing of tanglegram No. 2.

In the following, we will show that the two non-planar tanglegrams of size 4 are in fact sufficient to characterize non-planarity of tanglegrams in the same way that K_5 and $K_{3,3}$ characterize non-planarity of graphs: every non-planar tanglegram has to contain at least one of the two.

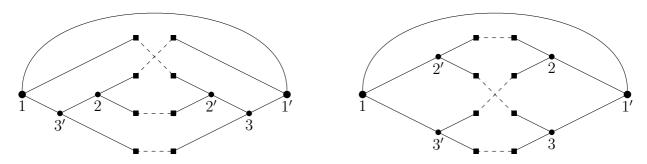


FIGURE 3. Finding copies of $K_{3,3}$ in tanglegrams No. 6 and No. 13 after adding edges between the roots [3].

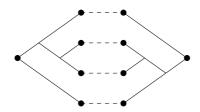


FIGURE 4. A drawing of tanglegram No.2 without crossings.

4. Induced subtanglegrams

In a rooted plane binary tree B with root r, a choice \mathcal{L} of a set of leaves induces another rooted binary tree by taking the smallest subtree containing these leaves and designating as new root (which we will denote by $r_{\mathcal{L}}$) the vertex of the subtree closest to the old root, and suppressing all vertices of degree 2 other than the root, see Figure 5. The study of induced binary subtrees of (rooted or unrooted) leaf-labeled binary trees is topical in the phylogenetic literature [11]. It is immediate that for any $v \in \mathcal{L}$ the vertex $r_{\mathcal{L}}$ lies on the unique path between r and v. For brevity, we use the notation r_{xy} instead of $r_{\{x,y\}}$.

Given a layout of the tanglegram T with left binary tree L with root r and right binary tree R with root ρ and a set E of matching edges between the leaf sets of the left and right binary plane trees, E identifies a subset of leaves on both sides. These leaf sets induce respectively a left and right induced binary plane tree, which define a layout of a tanglegram T' when we put back the edges of E between the corresponding leaves. We say that E induces this sublayout of the original layout of tanglegram T, and we call T' the subtanglegram of tanglegram T induced by the matching edge set E. As the sublayout and switch operators commute, this definition does not depend on the particular layout of T, it just depends on the tanglegram. We will use r_E and ρ_E for the vertices in T corresponding to the roots of the left and right subtrees of this induced subtanglegram. There is a natural partial order by inclusion on the set of induced subtanglegrams of a given tanglegram.

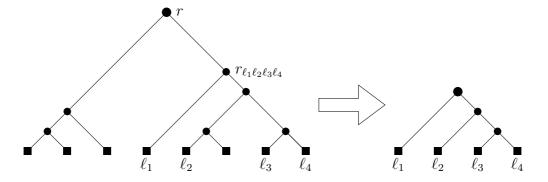


FIGURE 5. A rooted binary tree with root r, four leaves $\ell_1, \ell_2, \ell_3, \ell_4$ selected, the vertex $r_{\ell_1 \ell_2 \ell_3 \ell_4}$ and the tree induced by the selected leaves.

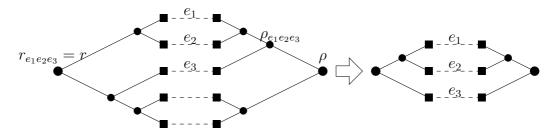


FIGURE 6. A tanglegram T with matching edges e_1, e_2, e_3 selected, the vertices $r_{e_1e_2e_3}$ and ρ_{e_1,e_2,e_3} , and the subtanglegram induced by the selected edges.

Sometimes we put scars on the edges of induced subtanglegrams to remember where the eliminated matching edges were connected to the surviving part. Let $e \in \sigma \setminus E$ be a matching edge in a layout of the tanglegram T. When we consider L_E and R_E , the smallest subtrees of L and R that contain the leaf set corresponding to E, the unique path connecting e to r in L either enters L_E at a vertex of degree 2 or does not enter L_E at all, and similarly, the unique path connecting e to ρ in R either enters R_E at a vertex of degree 2 or does not enter R_E at all. We refer to these degree 2 vertices (when they exist) as the hosts of e in L_E and R_E . A single vertex can host several other matching edges not in E. Hosts in L_E (respectively in R_E) are in a natural partial order by separation from r (respectively ρ).

Scars are markings on the edges of the induced subtanglegram, corresponding to the host vertices and following the natural partial order above, such that every scar marks the names of all edges hosted. Note that the partial order of the scars and the corresponding marks do not depend on the layout, they only depend on the tanglegram. Figure 7 illustrates a scar.

The following lemmata will be used to prove our main result:

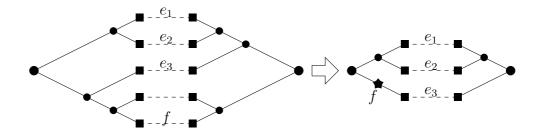


FIGURE 7. The scar of edge f in the example of Figure 6. Notice that the right tree does not have a scar for f.

Lemma 2. If F is a planar tanglegram with a distinguished marked non-matching edge, such that in every planar layout of F, the marked edge does not lie on the boundary of the infinite face, then F has a set of three edges E that induces the following subtanglegram S, where the marked edge lies on one of the paths of F corresponding to the bold edges.

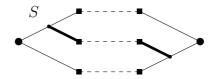


FIGURE 8. The subtanglegram S.

Proof. Let the left and right tree of F be L and R with roots r and ρ respectively, and σ denote the set of matching edges. We denote the marked edge by m and assume without loss of generality that m is an edge of R (the argument is the same otherwise with the roles of L and R exchanged). Consider the unique path P in R that starts from ρ and whose last edge is m. Let m^* be the edge of P closest to ρ that does not lie on the boundary of any planar layout of F (potentially $m^* = m$).



FIGURE 9. The possible subtanglegrams of F induced by e_1, e_2, e_3 . The edge containing m^* is bold.

Consider a planar layout of F where one endpoint of m^* (which we will denote by ρ^*) lies on the boundary of the infinite face; by the definition of m^* such a layout exists. Without loss of generality it is the lower of the two r- ρ paths on the boundary. Let E^* be the set of matching edges on the leaves of the subtree of R rooted at ρ^* . By our assumptions

 $\rho \neq \rho^*, |E^*| \geq 2, E^* \neq \sigma, \text{ and all edges of } E^* \text{ lie below all edges of } M \setminus E^* \text{ in the layout.}$ Let $e_1 \in E^*$ and $e_3 \in \sigma \setminus E^*$ be the matching edges of F that are on the boundary of the infinite face of the layout and let $e_2 \in E^*$ be the edge that lies above all other edges of E^* in the layout; so we have $\rho = \rho_{e_1e_3}, r = r_{e_1e_3}$ and $\rho^* = \rho_{e_1e_2}$ (See Figure 9). We must have $r \in \{r_{e_1e_2}, r_{e_2e_3}\}$. If $r = r_{e_2e_3}$, then $r_{e_1e_2}$ lies on the unique r- e_1 path in L, and performing a mirror operation on $r_{e_1e_2}$ and ρ^* results in a planar layout of F where m^* lies on the boundary of the infinite face, which is a contradiction. Therefore we must have $r = r_{e_1e_2}$, and $r_{e_2e_3}$ lies on the unique r- e_3 path in L.

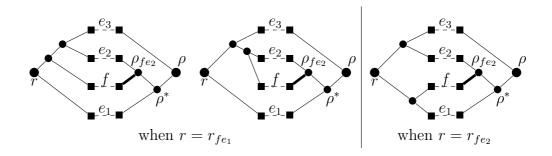


FIGURE 10. The possible subtanglegrams of F induced by e_1, e_2, e_3, f . The edge containing m is bold.

If m lies on the unique ρ^*-e_2 path in R (including the case that $m=m^*$), then the subtanglegram induced by e_1, e_2, e_3 satisfies the conclusion of our lemma and we are done. Otherwise let f be any matching edge such that m lies on the unique ρ^*-f path in R. By our assumptions, $f \notin \{e_1, e_2\}$, f lies between e_1 and e_2 in our planar layout and ρ_{fe_2} lies on the unique ρ^*-e_2 path in R (Figure 10). We have $r \in \{r_{e_1f}, r_{e_2f}\}$. If $r = r_{e_1f}$, then the subtanglegram of F induced by e_1, e_3, f satisfies the conclusion of our lemma. If $r = r_{e_2f}$, then the subtanglegram induced by e_1, e_2, f satisfies the conclusion. Either way, we are done.

Lemma 3. Let F be a tanglegram with two sets of matching edges, E_1, E_2 , such that $E_1 \cap E_2 = \{f\}$ and $E_1 \cup E_2$ contains all matching edges of F. For $i \in \{1,2\}$, let F_i be the subtanglegram induced by E_i , and assume that the scars of the edges of E_1 in F_2 as well as the scars of the edges of E_2 in F_1 are on a unique root-to-root path containing f but no other matching edge. If F_1 and F_2 each have planar layouts in which the two matching edges on the boundary of the infinite face are f and g and g and g the infinite face are g and g and g and g are g and g and g and g and g are g and g and g and g and g are g and g and g and g are g and g and g and g and g are g and g and g and g and g are g and g and g and g are g and g are g and g and g are g and g are g and g and g are g and g and g are g are g

Proof. Let the left and right roots of F be r and ρ respectively, and let P be the unique r- ρ path in F containing f but no other matching edges, and let r^1 , ρ^1 and r^2 , ρ^2 be the left and right roots of F_1 and F_2 respectively. From the assumptions on f we get that r^1 , r^2 , ρ^2 , ρ^2 lie on P.

The conditions on F_1 and F_2 imply that F_1 has a planar layout such that the r^1 - ρ^1 path P_1 containing f lies on a straight line, all other edges of F_1 lie above this line and e_1 is on the boundary of the infinite face; also, F_2 has a planar layout such that the r^2 - ρ^2 path P_2 containing f lies on a straight line, all other edges of F_2 lie below this line and e_2 is on the boundary of the infinite face. Since the order of vertices on P is independent of the drawings, P_1 and P_2 can be obtained from subpaths of P by suppressing some vertices, so these two layouts can be merged into the required planar layout of F; see Figure 11 for an illustration of this lemma.

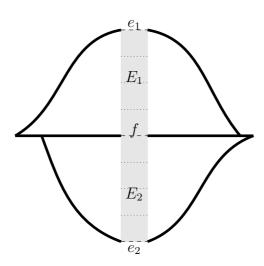


FIGURE 11. Illustration of Lemma 3.

5. Crossing-critical tanglegrams

Another key concept in this paper is that of a *crossing-critical tanglegram*. A tanglegram is crossing-critical if it is non-planar, but every proper induced subtanglegram of it is planar. For example, tanglegrams No. 6 and No. 13 are crossing-critical. Clearly any non-planar tanglegram contains a crossing-critical induced subtanglegram.

Theorem 4. The only crossing-critical tanglegrams are No. 6 and No. 13. Therefore, every non-planar tanglegram contains No. 6 or No. 13. as an induced subtanglegram.

Corollary 5. The remaining eleven tanglegrams of size 4 in Figure 2 are planar.

Corollary 6. For every non-planar tanglegram T, the augmented graph T^* contains a subdivision of $K_{3,3}$, where three of the original vertices of the $K_{3,3}$ are located in L and the other three in R.

It would be interesting to see if a more general theorem holds for tanglegrams exhibiting an even higher degree of non-planarity:

Question 1. For an integer $k \geq 3$, is there a characterization of tanglegrams that have k pairwise crossing matching edges in every layout, in terms of a finite list of tanglegrams that they must have as induced subtanglegrams, analogous to Theorem 4?

Proof of Theorem 4. Assume that T is a crossing-critical tanglegram, with left subtree L rooted at r and right subtree R rooted at ρ . Let L_u , L_d be the rooted subtrees of L rooted at the neighbors r^u and r^d of r and R_u , R_d be the rooted subtrees of R rooted at the neighbors ρ^u and ρ^d of ρ . Since the leaves of both L_u and L_d are matched to the leaves of at least one of R_u and R_d , and vice versa, we may assume without loss of generality that there are matching edges between L_u and R_u , and between L_d and R_d . (If this is not the case, we can achieve this situation using switch operations.)

Denote the non-empty set of matching edges between L_u and R_u by E_u , and between L_d and R_d by E_d , and let E_m be the (potentially empty) set of matching edges not in $E_u \cup E_d$. Let T_u and T_d be the subtanglegrams of T induced by the matching edges E_u and E_d , respectively. Since T is crossing-critical, both T_u and T_d are planar tanglegrams.

If $E_m = \emptyset$ (part (a) in Figure 12) then T has a planar layout (just put the planar layouts of T_u and T_d above each other, and connect the vertex r to the left roots of T_u and T_d , and ρ to the right roots of T_u and T_d , which is a contradiction. Therefore $E_m \neq \emptyset$.

If E_m contains a matching edge g between L_u and R_d and a matching edge f between L_d and R_u (part (b) in Figure 12), then let $e \in E_u$ and $h \in E_d$. The subtanglegram induced by the edges e, f, g, h in T is No. 13, and we are done. So we are left to consider the case when only one of the pairs L_u, R_d and L_d, R_u has matching edges between them, in this case without loss of generality (using the mirror image operation at r and ρ , if needed) E_m is the non-empty set of matching edges between L_u and R_d (part (c) in Figure 12).

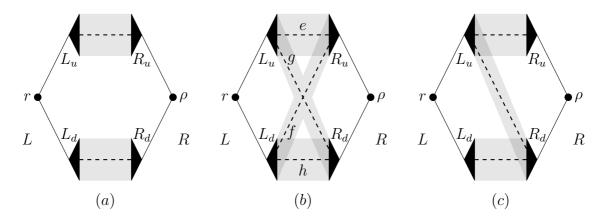


FIGURE 12. Case analysis on the qualitative distribution of matching edges between subtrees of L and R. Dashed lines mark the existence of matching edges between the subtrees.

We will consider two cases:

Case (A): $\min(|E_u|, |E_d|) \ge 2$. We are going to show that this does not happen in a crossing-critical tanglegram T.

Let $e \in E_d$ and consider the subtanglegram T' induced by all matching edges except e with left tree L' and right tree R'. T' is planar, contains T_u as a subtanglegram, and contains the vertices ρ^u and ρ^d . As the unique path from the root to a matching edge in R' passes through ρ^u for every matching edge in E_u and passes through ρ^d for every matching edge in $E_d \cup E_m$, in any planar layout of T' the edges of E_u appear contiguously, and the edges of E_m appear on only one side of them. Consequently, any planar layout of T' gives a planar sublayout of T_u where all scars from E_m lie on the same root-to-root path bordering the infinite face; denote the matching edge which this path travels through by f_u . Similar logic gives that T_d has a planar layout in which all scars lie on the same root-to-root path bordering the infinite face, denote the matching edge which this path travels through by f_d . Let T'' be the tanglegram induced by $E_m \cup \{f_u, f_d\}$. Consider a planar layout of T''(as T is crossing-critical, such a layout exists), without loss of generality (up to a mirror operation) f_u lies above f_d in this layout. Let P_u be the unique shortest path leading from r to f_u and P_d be the unique shortest path leading from ρ to f_d , and let $g \in E_m$ be arbitrary. Consider the vertical strip between the two vertical lines going though r and ρ - this is the region where T'' is drawn. The r- ρ paths containing f_u and f_d and no other matching edge cut this strip into three subregions, and g must lie in the unique subregion that borders both P_u and P_d . That means g lies between f_u and f_d in this planar layout of T'', and consequently in any planar layout of T'', f_u and f_d are on the boundary of the infinite face. Two applications of Lemma 3 (first on T'' and T_u using the common edge f_u , then on the resulting tanglegram and T_d using the common edge f_d) show that T itself has a planar layout, which is a contradiction.

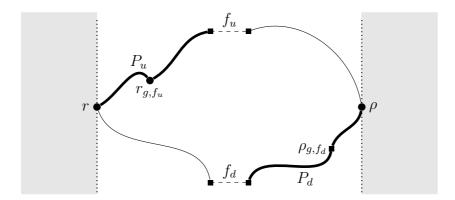


FIGURE 13. Analysis of a planar drawing of the subtanglegram T''. The white region between the dotted vertical lines is where T'' is drawn.

Case (B): $\min(|E_u|, |E_d|) = 1$. We are going to exhibit No. 6 as an induced subtangle-gram in T.

Assume first that $|E_d| = 1$, and let e be the single matching edge between L_d and R_d . This means in particular that L_d consists of a single leaf vertex r^d that is matched by the edge e. Now, by the crossing-criticality of T, the subtanglegram induced by all matching edges but e, denoted by \hat{T} , is planar, and a non-matching edge of its right subtree, \hat{R} , has a scar

marking e (this scar exists, as R_d has leaves matched by E_m and therefore $\rho_{\sigma\backslash\{e\}} = \rho$). If \hat{T} has a planar layout in which the marked edge is on the boundary of the infinite face, then T has a planar layout, contradicting the crossing-criticality of T. Therefore in all planar layouts of \hat{T} , the marked edge is not on the boundary of the infinite face. Lemma 2 shows that \hat{T} contains the subtanglegram S with the mark m positioned as in Figure 14, and, using the fact that r is connected to one of the endpoints of e, we find that the subtanglegram induced by the edges a, b, c, e is No. 6, so we are done. If $|E_u| = 1$, the argument is essentially the same after exchanging the roles of L and R.

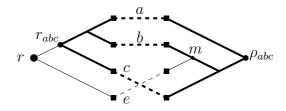


FIGURE 14. Finding subtanglegram No. 6 in T starting from a copy of S drawn in bold.

References

- [1] S. C. Billey, M. Konvalinka, and F. A. Matsen. On the enumeration of tanglegrams and tangled chains. *Journal of Combinatorial Theory Series A*, 146:239–263, 2017.
- [2] A. Burt and R. Trivers. Genes in Conflict. Belknap Harvard Press, 2006.
- [3] É. Czabarka, L. A. Székely, S. Wagner. Inducibility in binary trees and crossings in tanglegrams. to appear in SIAM J. Discrete Math. arXiv:1601.07149.
- [4] H. Fernau, M. Kaufmann, and M. Poths. Comparing trees via crossing minimization. In *Proc. 25th Intern. Conf. Found. Softw. Techn. Theoret. Comput. Sci. (FSTTCS'05)*, Lecture Notes in Computer Science 3821:457–469, Springer-Verlag, 2005.
- [5] M. S. Hafner and S. A. Nadler. Phylogenetic trees support the coevolution of parasites and their hosts. Nature, 332:258–259, 1988.
- [6] M. R. Henzinger, V. King and T. Warnow. Constructing a tree from homeomorphic subtrees, with applications to computational evolutionary biology. *Algorithmica* 24(1):1–13, 1999.
- [7] M. Konvalinka and S. Wagner. The shape of random tanglegrams. Advances in Applied Mathematics 78:76–93, 2016.
- [8] K. Kuratowski, Kazimierz. Sur le problème des courbes gauches en topologie. Fund. Math. 15:271–283, 1930.
- [9] F. A. Matsen, S. C. Billey, A. Kas, and M. Konvalinka. Tanglegrams: a reduction tool for mathematical phylogenetics. *IEEE/ACM Transactions on Computational Biology and Bioinformatics*, to appear.
- [10] D. Ralaivaosaona, J. B. Ravelomanana, and S. Wagner. Enumeration of planar tanglegrams. In preparation.
- [11] C. Semple, M. A. Steel. *Phylogenetics*. Oxford University Press, 2003.
- [12] L. A. Székely. A successful concept for measuring non-planarity of graphs: the crossing number. Discrete Math. 276(1–3): 331–352, 2004.
- [13] K. Wagner. Uber eine Eigenschaft der ebenen Komplexe. Math. Ann. 114:570–590, 1937.

[14] B. Venkatachalam, J. Apple, K. St. John, and D. Gusfield. Untangling tanglegrams: Comparing trees by their drawings. *IEEE/ACM Transactions on Computational Biology and Bioinformatics*, 7(4):588–597, 2010.

ÉVA CZABARKA AND LÁSZLÓ A. SZÉKELY, DEPARTMENT OF MATHEMATICS, UNIVERSITY OF SOUTH CAROLINA, COLUMBIA, SC 29208, USA

E-mail address: {czabarka,szekely}@math.sc.edu

STEPHAN WAGNER, DEPARTMENT OF MATHEMATICAL SCIENCES, STELLENBOSCH UNIVERSITY, PRIVATE BAG X1, MATIELAND 7602, SOUTH AFRICA

E-mail address: swagner@sun.ac.za