Suleyman Cenk Sahinalp
S. Muthukrishnan
Ugur Dogrusoz (Eds.)

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Combinatorial Pattern Matching

15th Annual Symposium, CPM 2004
Istanbul, Turkey, July 2004
Proceedings

Springer

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Volume Editors

Suleyman Cenk Sahinalp
Simon Fraser University, School of Computing Science
Burnaby BC, V5A 1S6 Canada
E-mail: cenk@cs.sfu.ca

S. Muthukrishnan
Rutgers University, Department of Computer and Information Sciences
319 Core Bldg, 110 Frelinghuysen Rd, Piscataway, NJ 08854, USA
E-mail: muthu@cs.rutgers.edu

Ugur Dogrusoz
Bilkent University, Computer Engineering Department
06800 Ankara, Turkey
E-mail: ugur@cs.bilkent.edu.tr

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Preface

The 15th Annual Symposium on Combinatorial Pattern Matching was held in Ciragan Palace Hotel, Istanbul, Turkey during July 5–7, 2004. CPM 2004 repeated the success of its predecessors; it even surpassed them in terms of the number of invited speakers, the number of submissions, and the number of papers accepted and presented at the conference.

In response to the call for papers, CPM 2004 received a record number of 79 high-quality submissions. Each submission was reviewed by at least three program committee members and the comments were returned to the authors. Following an extensive electronic discussion period, the Program Committee accepted 36 of the submissions to be presented at the conference. They constitute original research contributions in combinatorial pattern matching algorithms and data structures, molecular sequence analysis, phylogenetic tree construction, and RNA and protein structure analysis and prediction.

CPM 2004 had five invited speakers. In alphabetical order they were: Evan Eichler from the University of Washington, USA, Martin Farach-Colton from Rutgers University, USA, Paolo Ferragina from the University of Pisa, Italy, Piotr Indyk from MIT, USA, and Gene Myers from the University of California, Berkeley, USA.

It is impossible to organize such a successful program without the help of many individuals. We would like to express our appreciation to the authors of the submitted papers and to the program committee members and external referees, who provided timely and significant reviews.

July 2004

S.C. Sahinalp,
S. Muthukrishnan,
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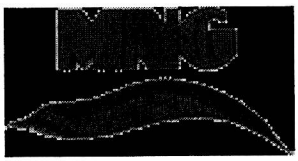

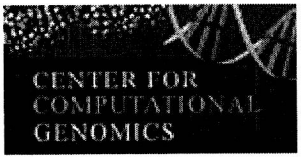

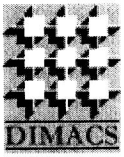

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Sorting by Reversals in Subquadratic Time*

Eric Tannier[1] and Marie-France Sagot[1,2]

[1] INRIA Rhône-Alpes, Laboratoire de Biométrie et Biologie Évolutive
Université Claude Bernard, 69622 Villeurbanne cedex, France
{Eric.Tannier,Marie-France.Sagot}@inrialpes.fr
[2] King's College, London, UK

Abstract. The problem of sorting a signed permutation by reversals is inspired by genome rearrangements in computational molecular biology. Given two genomes represented as two signed permutations of the same elements (*e.g. orthologous genes*), the problem consists in finding a most parsimonious scenario of reversals that transforms one genome into the other. We propose a method for sorting a signed permutation by reversals in time $O(n\sqrt{n \log n})$. The best known algorithms run in time $O(n^2)$, the main obstacle to an improvement being a costly operation of detection of so-called "safe" reversals. We bypass this detection and, using the same data structure as a previous random approximation algorithm, we achieve the same subquadratic complexity for finding an *exact* optimal solution. This answers an open question by Ozery-Flato and Shamir whether a subquadratic complexity could ever be achieved for solving the problem.

1 Introduction

The problem of sorting a signed permutation by reversals is inspired by a problem of genome rearrangement in computational biology. Genome rearrangements such as reversals may change the order of the genes (or of other markers) in a genome, and also the direction of transcription. We identify the genes with the numbers $1, \ldots, n$, with a plus or minus sign to indicate such direction. Their order will be represented by a *signed permutation* of $\{\pm 1, \ldots, \pm n\}$, that is a permutation π of $\{\pm 1, \ldots, \pm n\}$ such that $\pi[-i] = -\pi[i]$, where $\pi[i]$ denotes the i^{th} element in π. In the following, we indicate the sign of an element in a permutation only when it is minus.

The *reversal* of the interval $[i, j] \subseteq [1, n]$ $(i < j)$ is the signed permutation $\rho = 1, \ldots, i, -j, \ldots, -(i+1), j+1, \ldots, n$. Note that $\pi\rho$ is the permutation obtained from π by reversing the order and flipping the signs of the elements in the interval. If $\rho_1, \ldots, \rho_k$ is a sequence of reversals, we say that it sorts a permutation π if $\pi\rho_1 \cdots \rho_k = Id$ (Id is the all positive identity permutation $1, \ldots, n$). We denote by $d(\pi)$ the number of reversals in a minimum size sequence sorting π.

* Work supported by the French program bioinformatique Inter-EPST 2002 "Algorithms for Modelling and Inference Problems in Molecular Biology".

S.C. Sahinalp et al. (Eds.): CPM 2004, LNCS 3109, pp. 1–13, 2004.

The problem of sorting by reversals has been the subject of an extensive literature. For a complete survey, see [2]. The first polynomial algorithm was given by Hannenhalli and Pevzner [4], and ran in $O(n^4)$. After many subsequent improvements, the currently fastest algorithms are those of Kaplan, Shamir and Tarjan [5] running in $O(n^2)$, a linear algorithm for computing $d(\pi)$ only (it does not give the sequence of reversals) by Bader, Moret and Yan [1], and an $O(n\sqrt{n \log n})$ random algorithm by Kaplan and Verbin [6] which gives most of the time an optimal sequence of reversals, but fails on some permutations with very high probability. A reversal ρ is said to be *safe* for a permutation π if $d(\pi\rho) = d(\pi) - 1$. The bottleneck for all existing exact algorithms is the detection of safe reversals. Many techniques were invented to address this problem, but none has a better time complexity than linear, immediately implying a quadratic complexity for the whole method. In a recent paper [7], Ozery-Flato and Shamir compiled and compared the best algorithms, and wrote that: "A central question in the study of genome rearrangements is whether one can obtain a subquadratic algorithm for sorting by reversals".

In this paper, we give a positive answer to Ozery-Flato and Shamir's question. A good knowledge of the Hannenhalli-Pevzner theory and of the data structure used by Kaplan-Verbin is assumed.

In the next section, we briefly describe the usual tools (in particular the omnipresent breakpoint graph) for dealing with permutations and reversals. We mention some operations for sorting by reversals without giving any details (concerning, for instance, hurdle detection and clearing for which linear methods exist). The aim of this paper is to deal only with the most costly part of the method, that is sorting a permutation without hurdles. We introduce a new and elegant way of transforming the breakpoint graph of a permutation π by applying reversals either on π *or on its inverse permutation* π^{-1}. In section 3, we describe the method to optimally sort by reversals. With any classical data structure, the time complexity of this algorithm is $O(n^2)$, but even in this case it presents a special interest because it bypasses the detection of safe reversals which is considered as the most costly operation. Then in the last section, we indicate the data structure used to achieve subquadratic time complexity.

2 Mathematical Tools

To simplify exposition, we require that the first and last elements of a permutation remain unchanged. We therefore adopt the usual transformation which consists in adding the elements 0 and $n+1$ to $\{1, \ldots, n\}$, with $\pi[0] = 0$, and $\pi[n+1] = n+1$. The obtained permutation is called an *augmented permutation.* In this paper, all permutations are augmented, and we omit to mention it from now on. The inverse permutation π^{-1} of π is the (signed) permutation such that $\pi\pi^{-1} = Id$.

2.1 Breakpoint Graphs for a Permutation and Its Inverse

The *breakpoint graph* $BG(\pi)$ of a permutation π is a graph with vertex set V defined as follows: for each integer i in $\{1, \ldots, n\}$, let i^a (the *arrival*) and i^d

(the *departure*) be two vertices in V; add to V the two vertices 0^d and $(n+1)^a$. Observe that all vertex labels are non negative numbers. For simplicity and to avoid having to use absolute values, we may later refer to vertex $(-i)^x$ (for $x = a$ or d). This will be the same as vertex i^x. The edge set E of $BG(\pi)$ is the union of two perfect matchings denoted by R, the *reality edges* and D, the *dream edges* (in the literature, reality and dream edges are sometimes called reality and desire edges, or, in a more prosaic way, black and gray edges):

- R contains the edges $(\pi[i])^d(\pi[i+1])^a$ for all $i \in \{0, \ldots, n\}$;
- D contains an edge for all $i \in \{0, \ldots, n\}$, from i^d if $\pi^{-1}[i]$ is positive, from i^a if $\pi^{-1}[i]$ is negative, to $(i+1)^a$ if $\pi^{-1}[i+1]$ is positive, and to $(i+1)^d$ if $\pi^{-1}[i+1]$ is negative.

The reality edges define the permutation π (what you have), and the dream edges define Id (what you want to have). Reality edges always go from a departure to an arrival, but in dreams, everything can happen. An example of a breakpoint graph for a permutation is given in Figure 1.

To avoid case checking, in the notation of an edge, the mention of departures and arrivals may be omitted. For instance, $i(i+1)$ is a dream edge, indicating nothing as concerns the signs of $\pi^{-1}[i]$ and $\pi^{-1}[i+1]$.

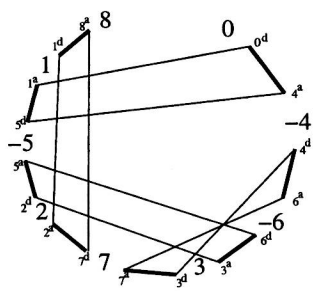

Fig. 1. The breakpoint graph of the permutation $0\ -4\ -6\ 3\ 7\ 2\ -5\ 1\ 8$. The bold edges are reality edges, and the thin ones are dream edges. The permutation should be read clockwise from 0 to $n+1$. This circular representation makes the cycles in the graph more visible. The edges that cross in the drawing correspond to crossing edges according to the definition.

A reality edge $(\pi[i])^d(\pi[i+1])^a$ is *oriented* if $\pi[i]$ and $\pi[i+1]$ have opposite signs, and *unoriented* otherwise. A dream edge $i(i+1)$ is *oriented* if $\pi^{-1}[i]$ and $\pi^{-1}[i+1]$ have opposite signs (that is, if the edge joins two departures or two arrivals), and *unoriented* otherwise. In the example of Figure 1, $(0,4)$, $(6,3)$, $(2,5)$ and $(5,1)$ are oriented reality edges, while $(3,4)$, $(6,7)$ are oriented dream edges.

To every dream edge $i(i+1)$, we associate the interval $[|\pi^{-1}[i]|, |\pi^{-1}[i+1]|]$ (or $[|\pi^{-1}[i+1]|, |\pi^{-1}[i]|]$ if $|\pi^{-1}[i]| > |\pi^{-1}[i+1]|$). Two dream edges are said to

cross if their associated intervals intersect but one is not contained in the other. Only dream edges may cross in a breakpoint graph.

Dream and reality edges are trivially and uniquely decomposed into cycles (the sets of both types of edges are perfect matchings of the vertices). By the cycles of a permutation π, we mean the cycles of $R \cup D$ in $BG(\pi)$. We call the *size* of a cycle the number of dream edges it contains (it is half the usual length of a cycle). Two cycles are said to *cross* if two of their edges cross.

A *component* $\mathcal{C}$ of $BG(\pi)$ is an inclusionwise minimal subset of its cycles, such that no cycle of $\mathcal{C}$ crosses a cycle outside $\mathcal{C}$. A component is said to be *oriented* if it contains a cycle with an oriented edge, and *unoriented* otherwise. A *hurdle* is a special type of unoriented component. We do not define it more precisely, since we deal only with permutations without unoriented components, therefore without hurdles. See for example [5] for a complete description of what a hurdle is, and how to cope with hurdles when there are some. In the example of Figure 1, there is a single oriented component.

The following operation establishes the correspondence between dream and reality in $BG(\pi)$ and $BG(\pi^{-1})$. Let $(BG(\pi))^{-1}$ be the graph resulting from applying the following transformations to $BG(\pi)$:

- change each vertex label i^a into i^d and i^d into i^a whenever $\pi^{-1}[i]$ is negative;
- change each vertex label $(\pi[i])^a$ into i^a, and $(\pi[i])^d$ into i^d;
- change dream into reality and reality into dream.

The result of such a transformation applied to the example of Figure 1 is given in Figure 2.

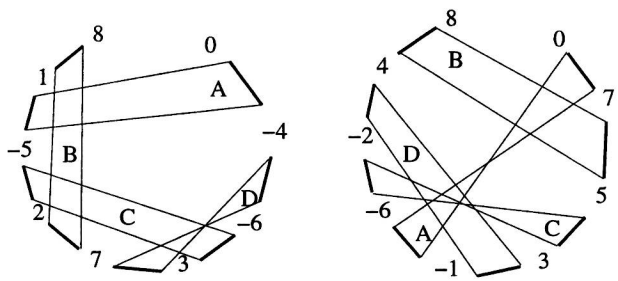

Fig. 2. A breakpoint graph and its inverse. The correspondence of the cycles in shown.

Lemma 1. $(BG(\pi))^{-1} = BG(\pi^{-1})$.

Proof. By definition, $(BG(\pi))^{-1}$ and $BG(\pi^{-1})$ have the same vertex set. There is a reality edge $(\pi[i])^d(\pi[i+1])^a$ in $BG(\pi)$ for all $i \in \{0, \ldots, n\}$. In $(BG(\pi))^{-1}$, it becomes a dream edge from i^d if $\pi[i]$ is positive or from i^a if $\pi[i]$ is negative, to $(i+1)^d$ if $\pi[i+1]$ is positive or to $(i+1)^a$ if $\pi[i+1]$ is negative. This corresponds