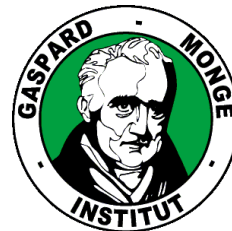


UEA Spring Phylogenetics  
Norwich – 17/04/2012

***Structure and enumeration  
of level-k phylogenetic networks***

Philippe Gambette



# Outline

---

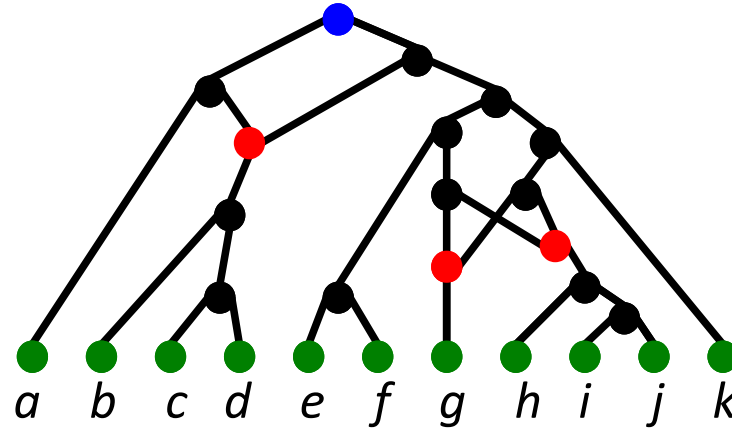
- Phylogenetic motivations
- Level- $k$  network reconstruction
- Structure of level- $k$  networks
- Counting level-1 and 2 networks

# Outline

---

- Phylogenetic motivations
- Level- $k$  network reconstruction
- Structure of level- $k$  networks
- Counting level-1 and 2 networks

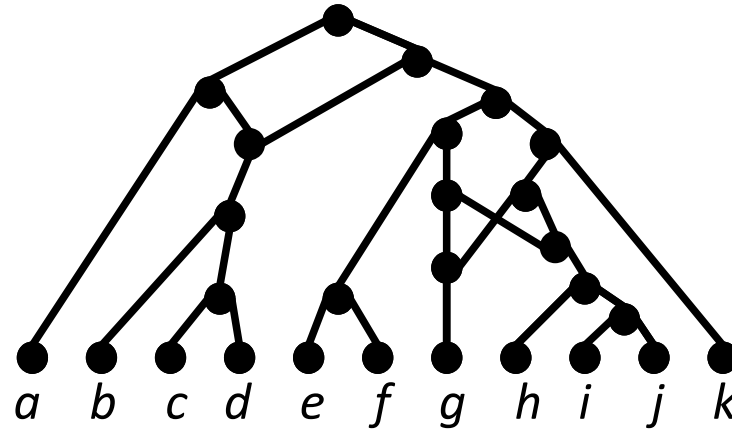
# Rooted binary phylogenetic networks



**leaves** bijectively labeled by current species  
+ internal vertices (extinct species) :

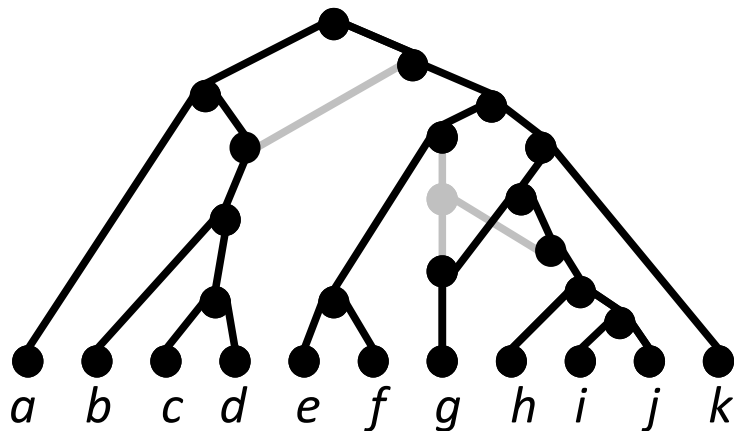
- **root**
- **split vertices** (speciation)
- **hybrid vertices** (hybridization, horizontal gene transfer)

# Rooted binary phylogenetic networks

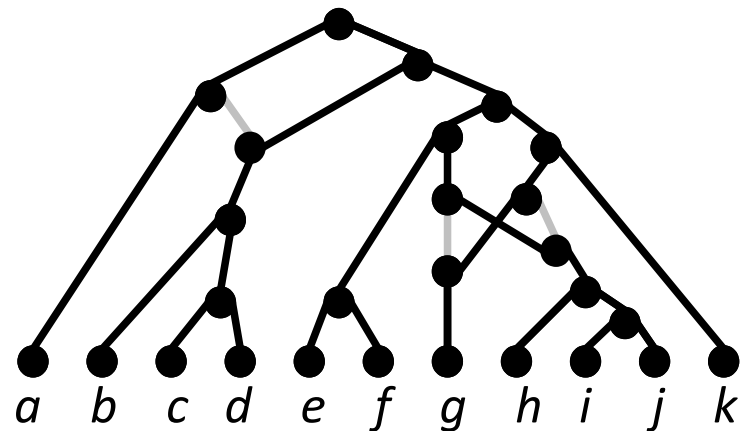


Model: each gene comes from one parent:

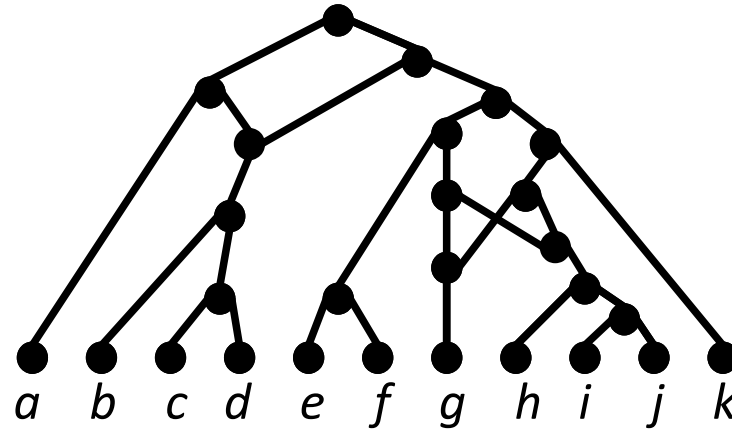
Gene 1



Gene 2

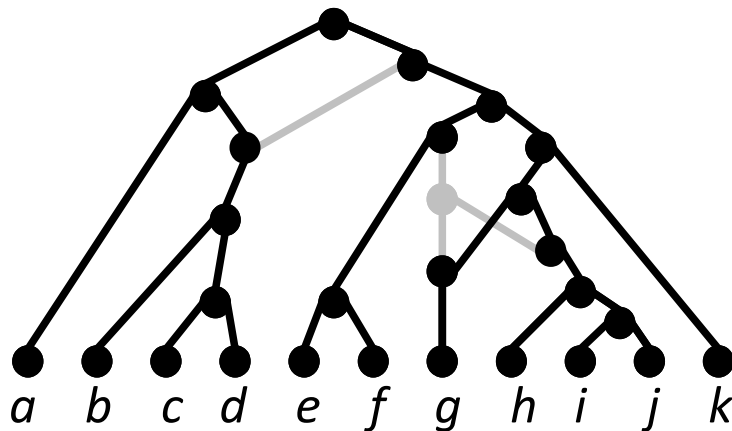


# Rooted binary phylogenetic networks



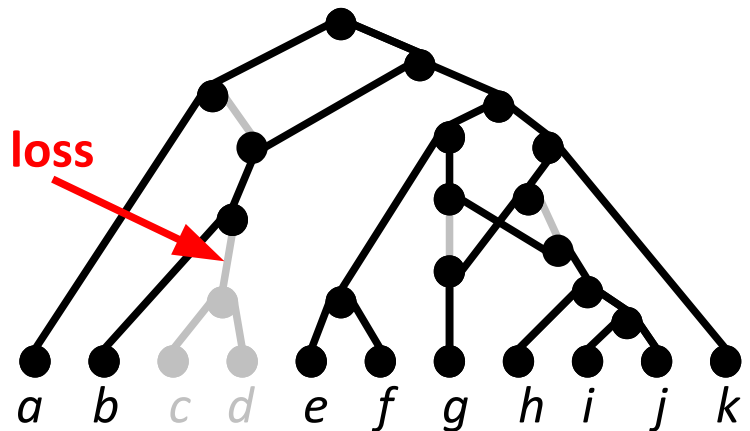
Model: each gene comes from one parent:

Gene 1



Gene 2

gene loss

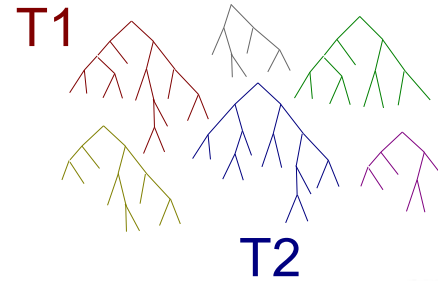
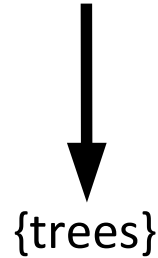




# Combinatorial phylogenetic network reconstruction

species 1 : AATTGCAG TAGCCCCAAAAT  
species 2 : ACCTGCAG TAGACCAAT  
species 3 : GCTTGCCG TAGACAAGAAT  
species 4 : ATTTGCAG AAGACCAAAT  
species 5 : TAGACAAGAAT  
species 6 : ACTTGCAG TAGCACAAAAT  
species 7 : ACCTGGTG TAAAAAT

G1 G2

{gene sequences}



HOGENOM database  Phyl-ARIANE  
Dufayard, Duret, Penel, Gouy,  ANR  
Rechenmann & Perrière, *BioInf*, 2005

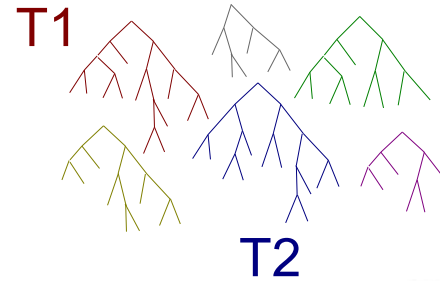
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G1 G2

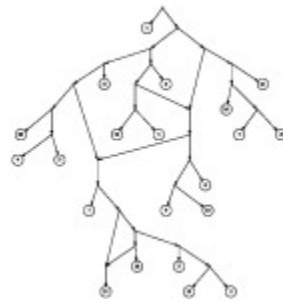
{gene sequences}

{trees}



HOGENOM database  Phyl-ARIANE  
Dufayard, Duret, Penel, Gouy,  ANR  
Rechenmann & Perrière, *BioInf*, 2005

network



contains the trees  
+ "optimal"



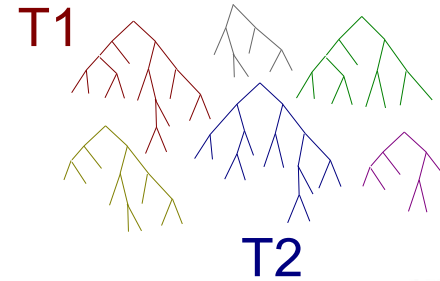
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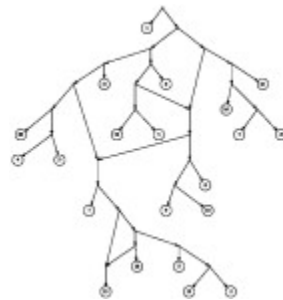
G1 G2

{gene sequences}

{trees}



HOGENOM database  Phyl-ARIANE  
Dufayard, Duret, Penel, Gouy,  ANR  
Rechenmann & Perrière, *BioInf*, 2005



network

contains the trees  
+ “optimal”

NP-complete for 2 rooted trees

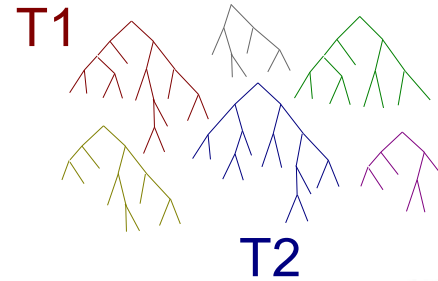
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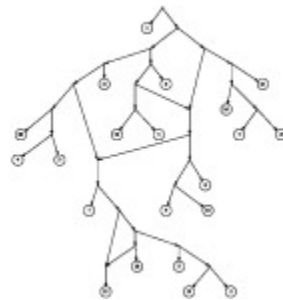
G1 G2

{gene sequences}

{trees}



HOGENOM database  Phyl-ARIANE  
Dufayard, Duret, Penel, Gouy,  ANR  
Rechenmann & Perrière, *BioInf*, 2005  
> 500 species, >70 000 trees

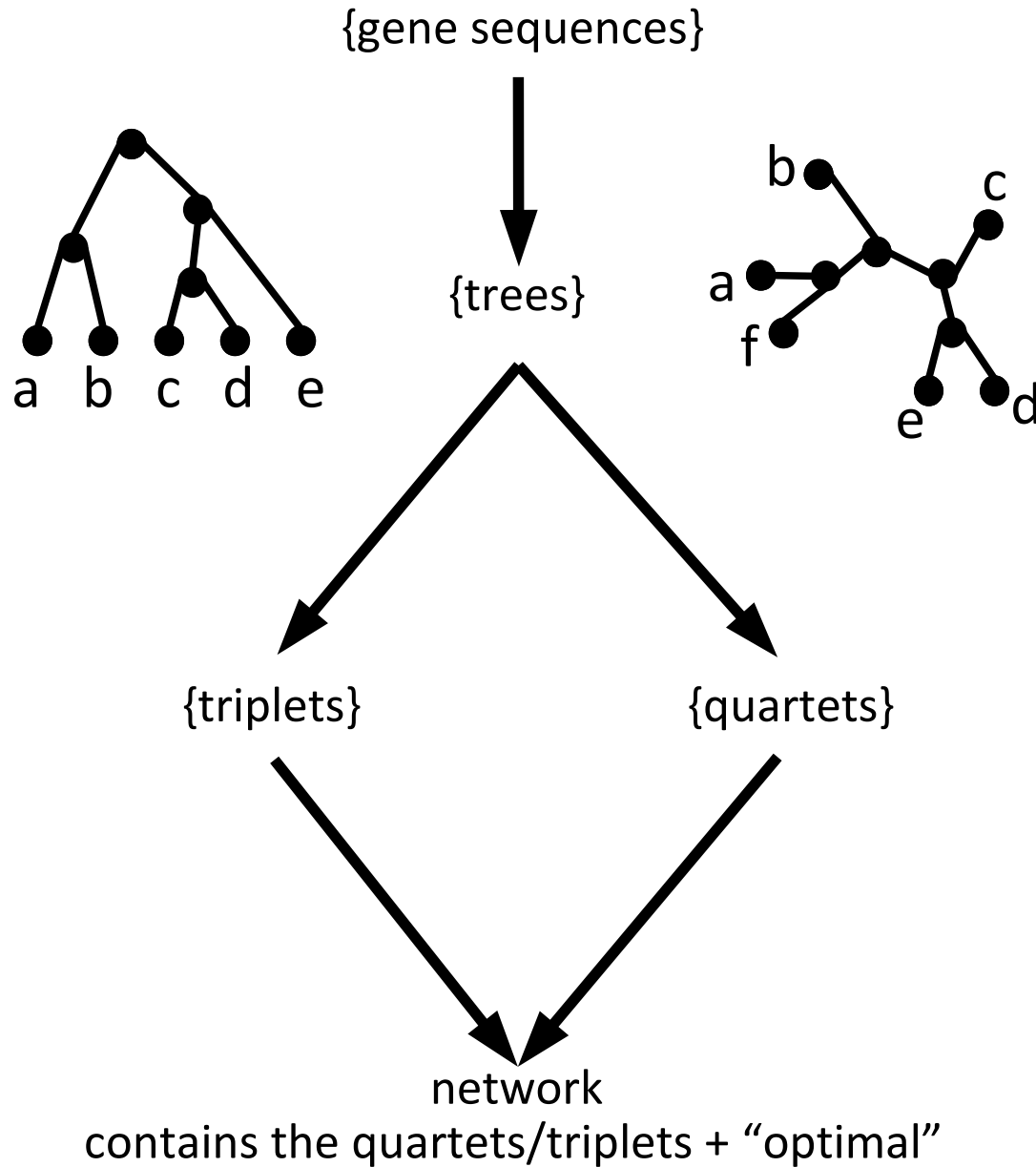


network

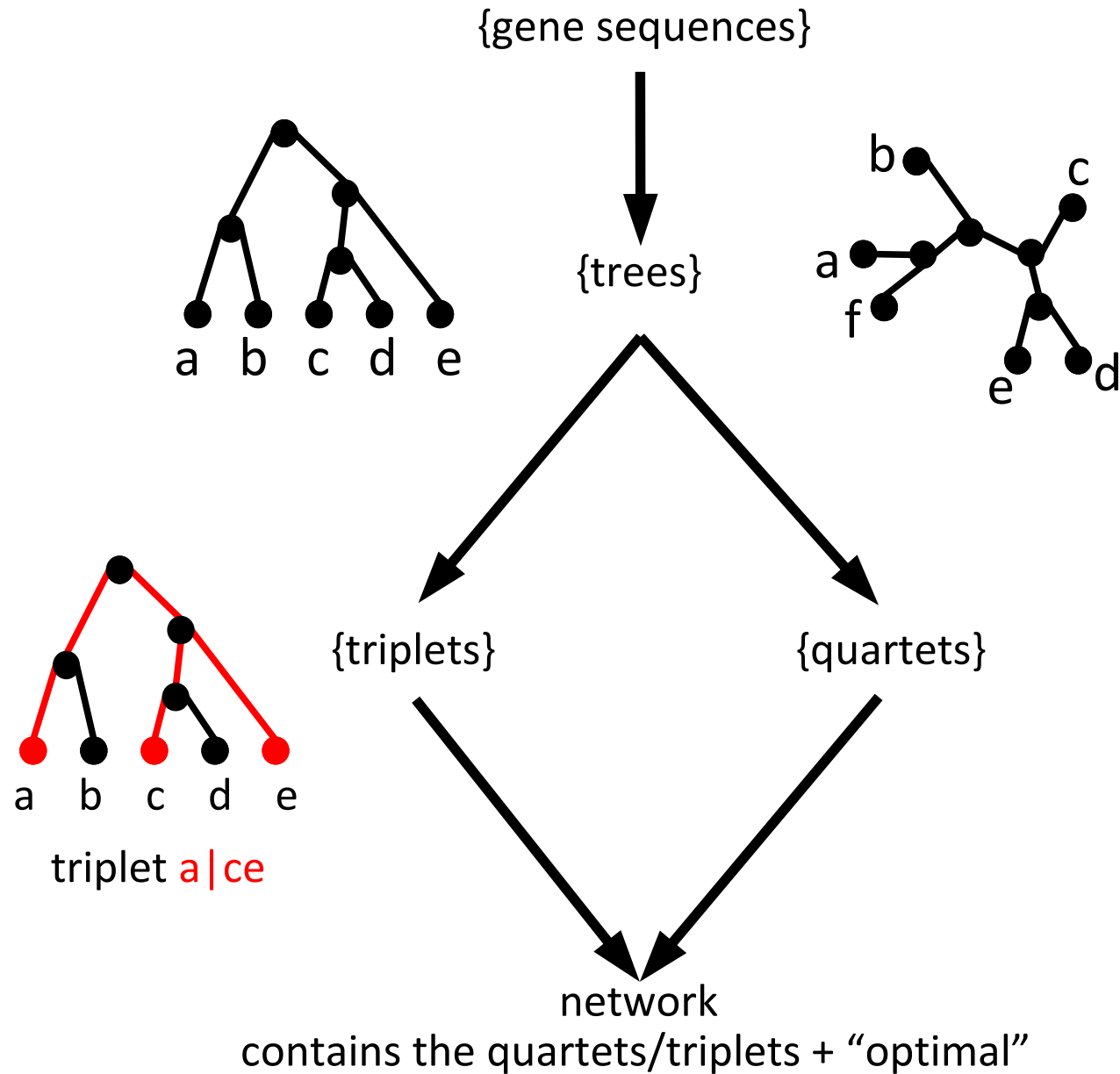
contains the trees  
+ “optimal”

NP-complete for 2 rooted trees

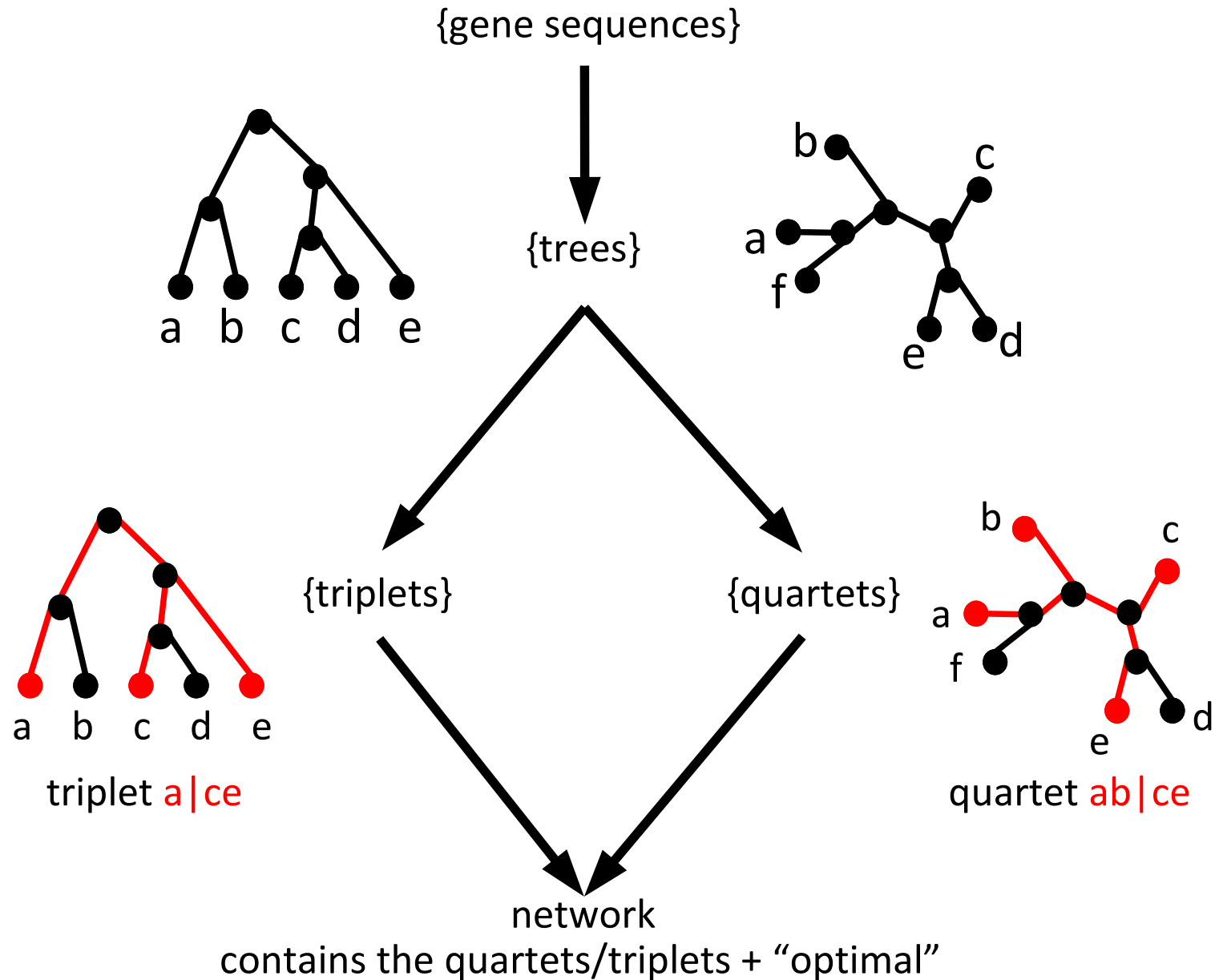
# Reconstruction from triplets / quartets



# Reconstruction from triplets / quartets



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# Reconstruction from triplets / quartets

Checking the solution:

Finding **all triplets** of a rooted network:  $O(n^3)$

Byrka, Gawrychowski, Huber & Kelk, *JDA*, 2010

# Reconstruction from triplets / quartets

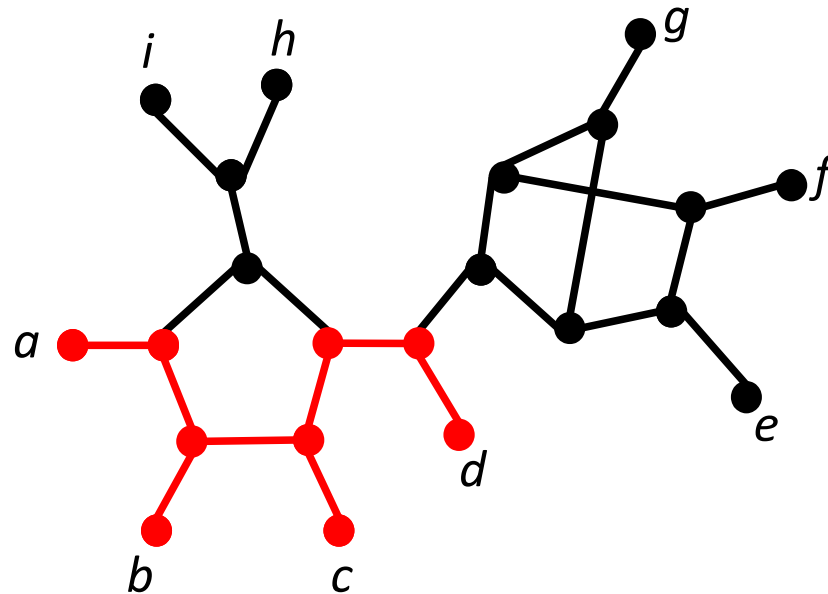
Checking the solution:

Finding **all triplets** of a rooted network:  $O(n^3)$

Byrka, Gawrychowski, Huber & Kelk, *JDA*, 2010

Finding **all quartets** of an unrooted network?

quartet *ab|cd*



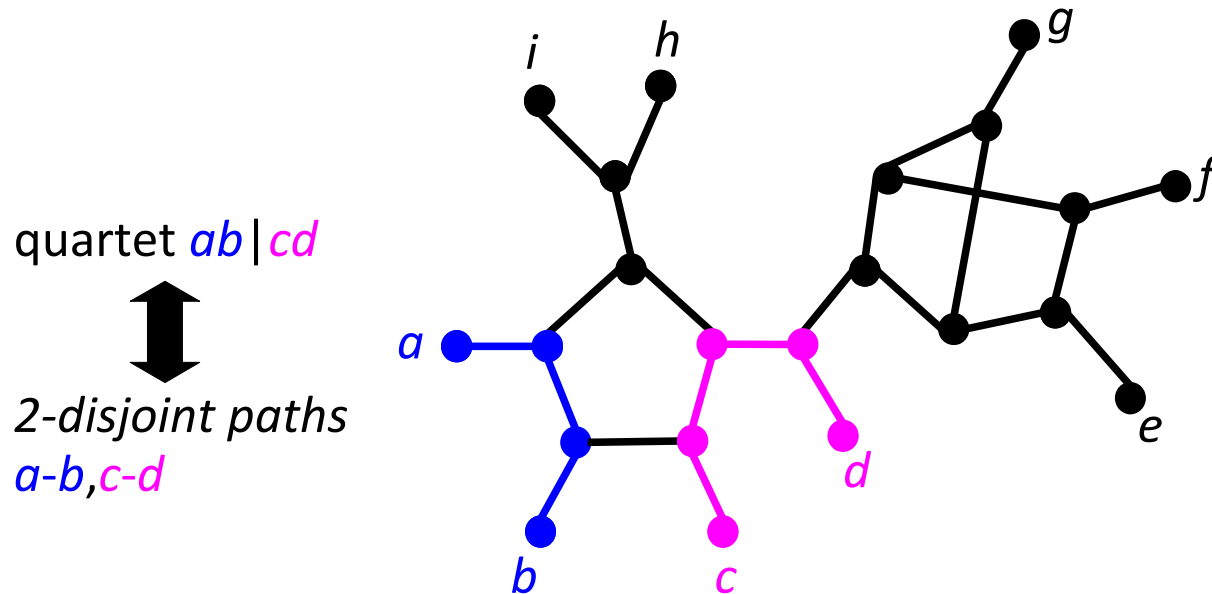
# Reconstruction from triplets / quartets

Checking the solution:

Finding **all triplets** of a rooted network:  $O(n^3)$

Byrka, Gawrychowski, Huber & Kelk, *JDA*, 2010

Finding **all quartets** of an unrooted network?





# Reconstruction from triplets / quartets

Checking the solution:

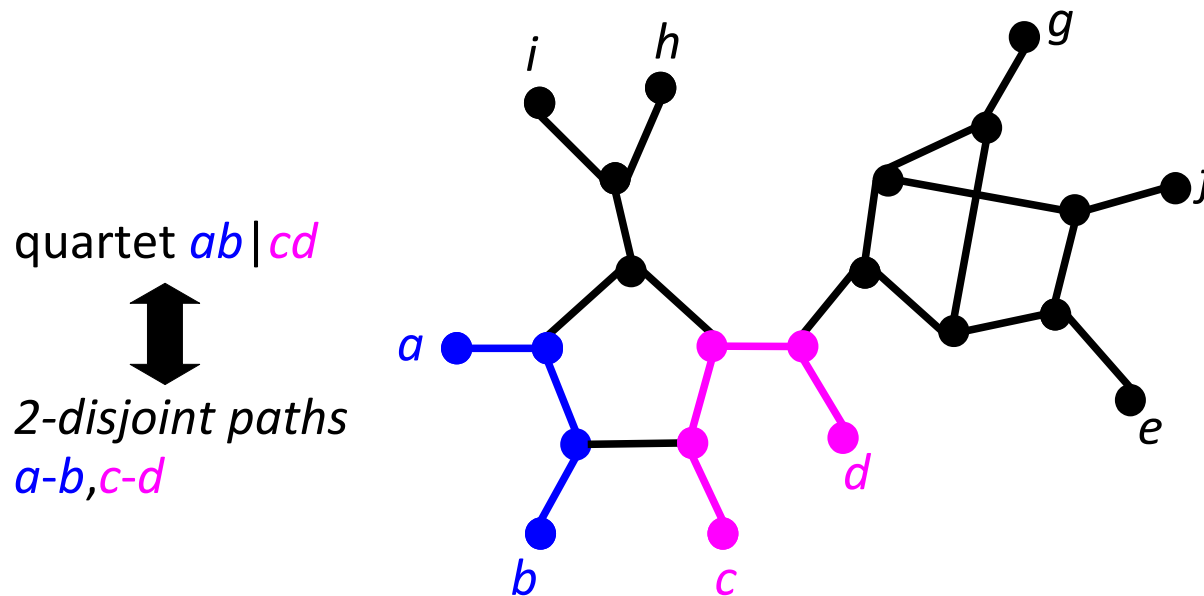
Finding **all triplets** of a rooted network:  $O(n^3)$

Byrka, Gawrychowski, Huber & Kelk, *JDA*, 2010

Finding **all quartets** of an unrooted network:  $O(n^6)$

2-Disjoint Paths in a graph of degree  $\leq 3$ :  $O(n(1+\alpha(n,n)))$

Tholey, *SOFSEM'09*, 2009



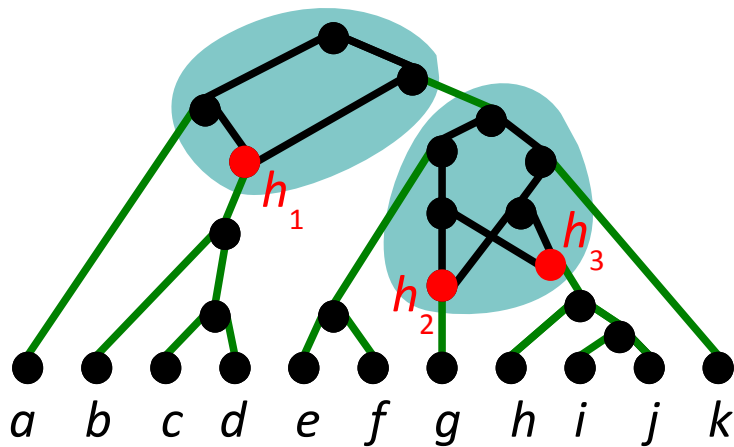
# Plan

---

- Phylogenetic motivations
- **Level- $k$  network reconstruction**
- Structure of level- $k$  networks
- Counting level-1 and 2 networks

# Level- $k$ networks

level: how “far” is the network from a tree ?  
small level  $\Rightarrow$  tree structure  $\Rightarrow$  fast algorithms

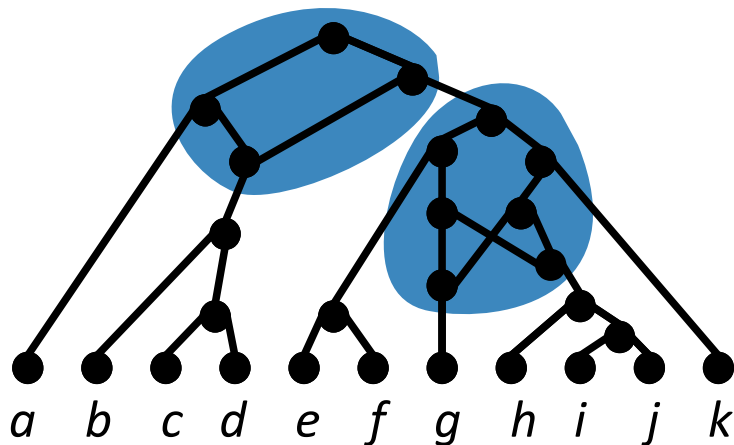


level-2 network

**level =**  
maximum number of **hybrid vertices**  
by **bridgeless component (blob)** of  
the underlying undirected graph.

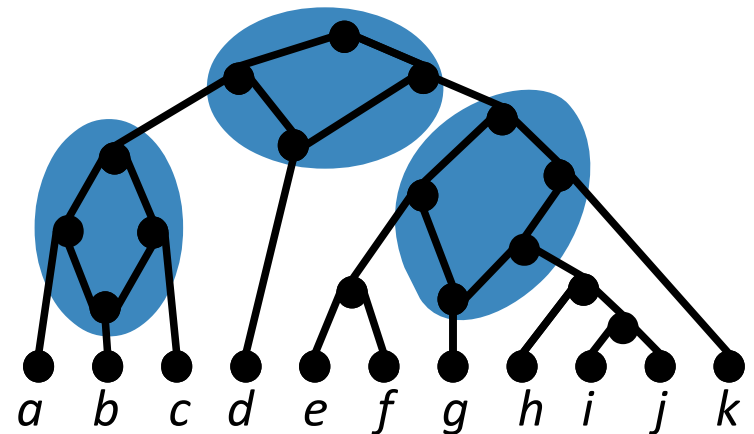
# Level- $k$ networks

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level-2 network

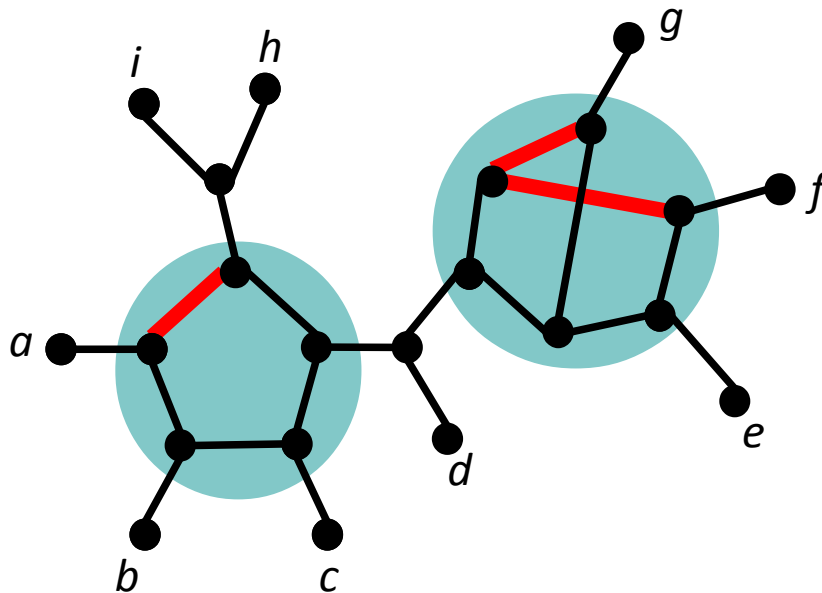
level-1 network  
("galled tree")



level =  
maximum number of **hybrid vertices**  
by *blob*.

# Unrooted level- $k$ networks

level: how “far” is the network from an unrooted tree ?  
small level  $\Rightarrow$  tree structure  $\Rightarrow$  fast algorithms

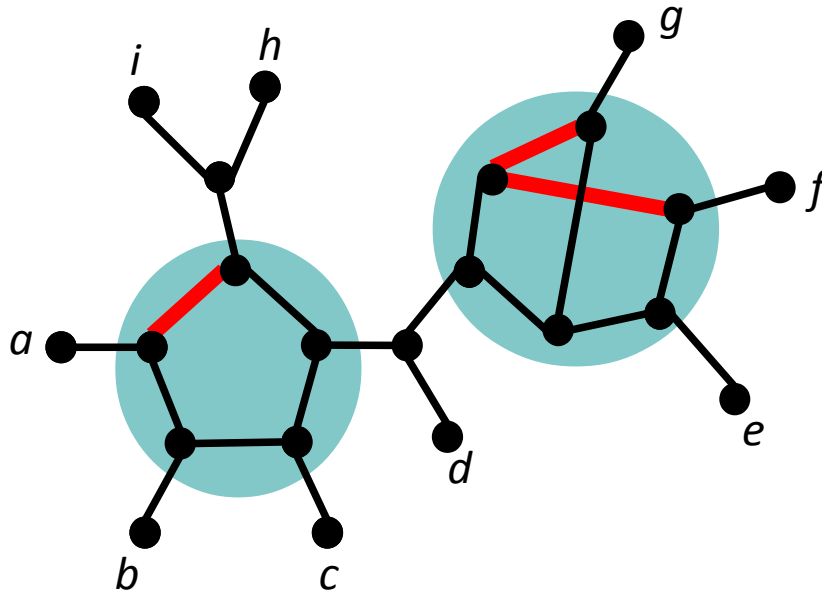


**level =**  
maximum number of **edges to remove**, by *blob*, to obtain a tree.

unrooted level-2 network

# Unrooted level- $k$ networks

level: how “far” is the network from an unrooted tree ?  
small level  $\Rightarrow$  tree structure  $\Rightarrow$  fast algorithms

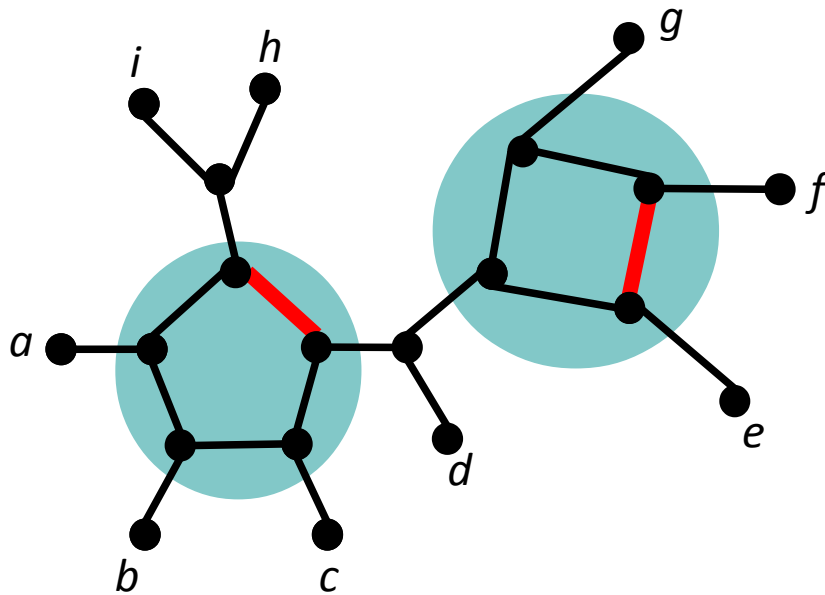


**level =**  
maximum number of **edges to remove**, by **blob**, to obtain a tree.  
= maximum ***cyclomatic number*** of the blobs

unrooted level-2 network

# Unrooted level- $k$ networks

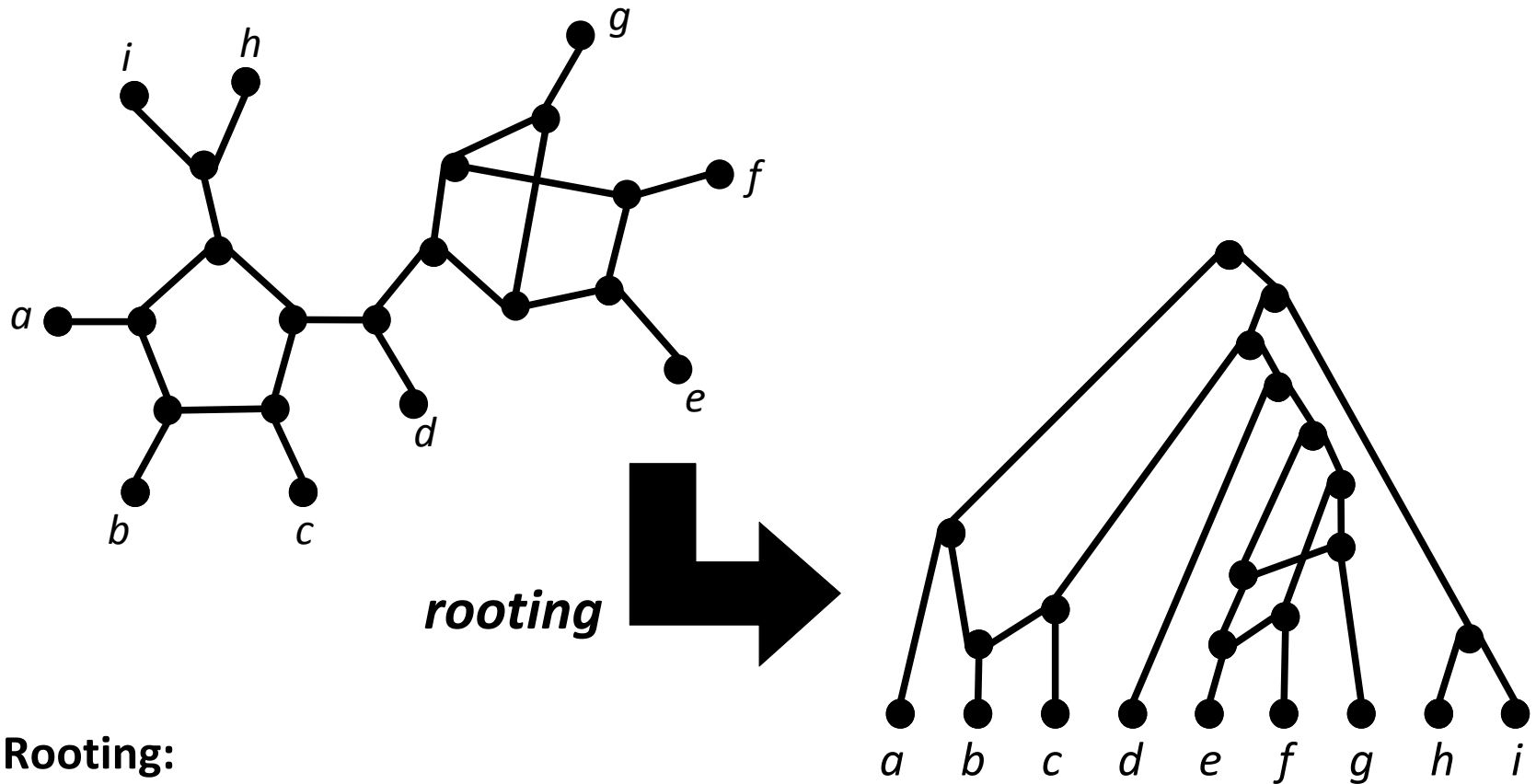
level: how “far” is the network from an unrooted tree ?  
small level  $\Rightarrow$  tree structure  $\Rightarrow$  fast algorithms



**level =**  
maximum number of **edges to remove**, by *blob*, to obtain a tree.

unrooted level-1 network  $\Rightarrow$  tree of cycles  
(unrooted galled tree)

# Equivalence between rooted and unrooted level

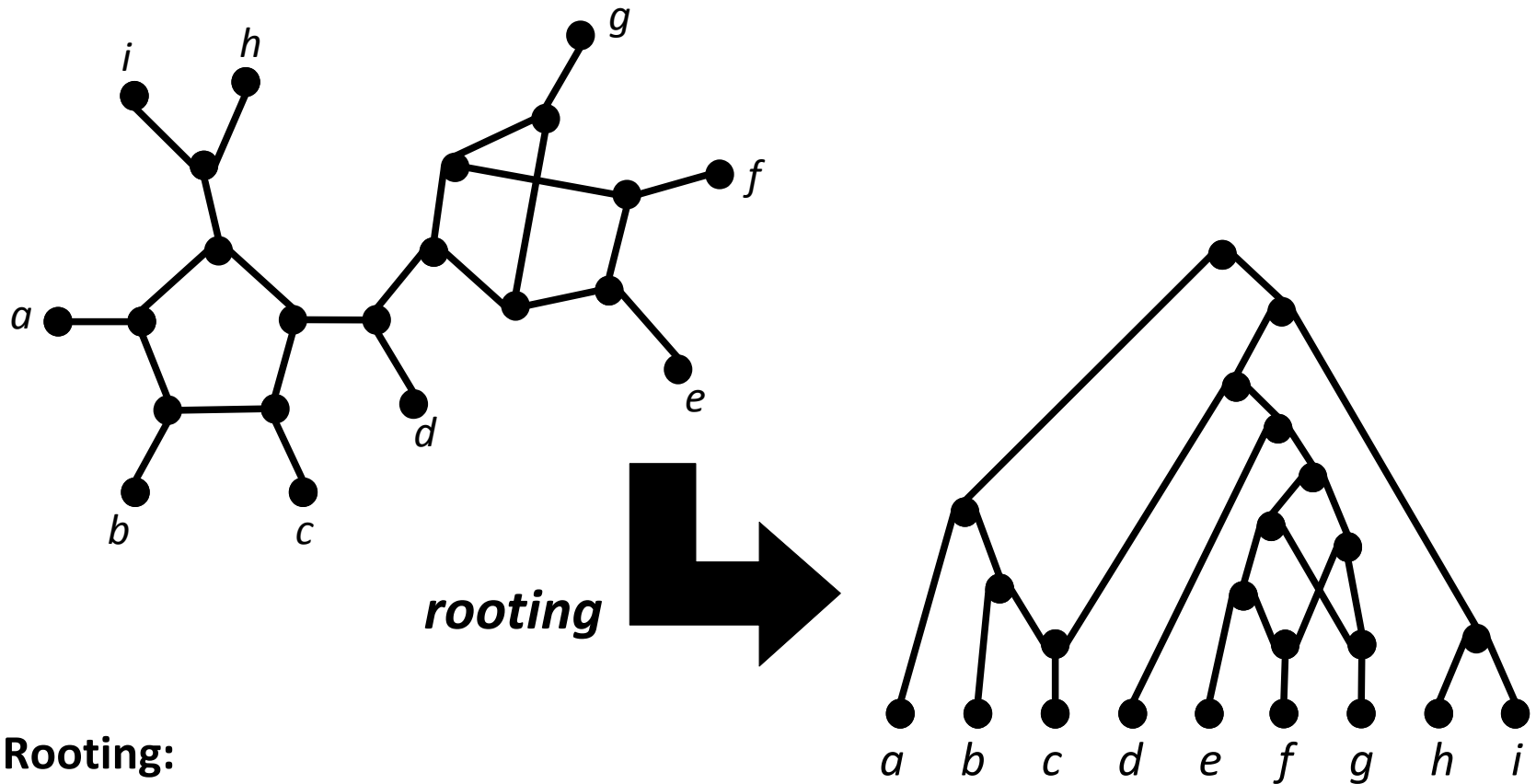


## Rooting:

- choosing a root
- choosing an orientation for the edges



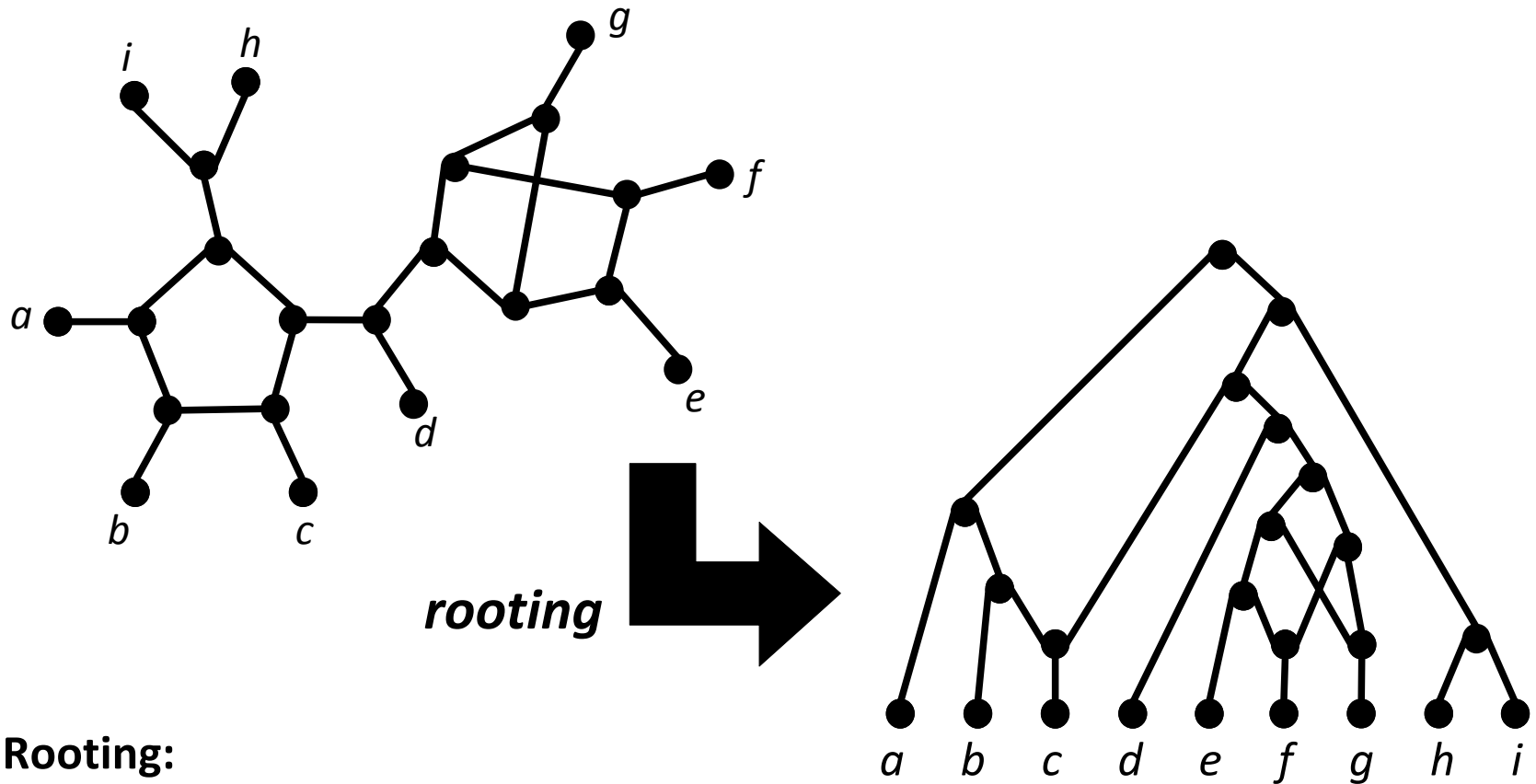
# Equivalence between rooted and unrooted level



## Rooting:

- choosing a root
- choosing an orientation for the edges

# Equivalence between rooted and unrooted level



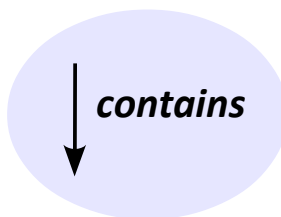
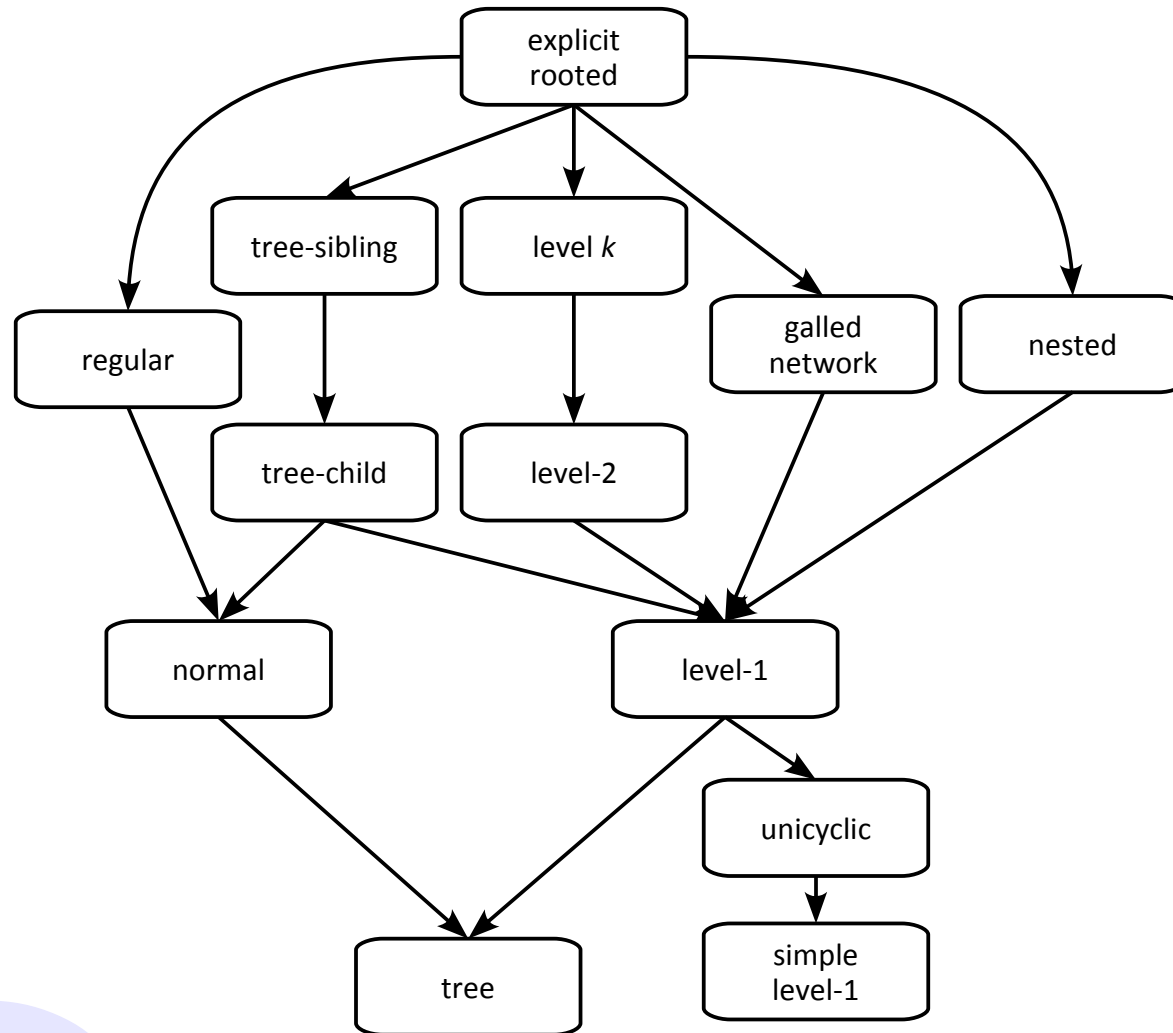
## Rooting:

- choosing a root
- choosing an orientation for the edges



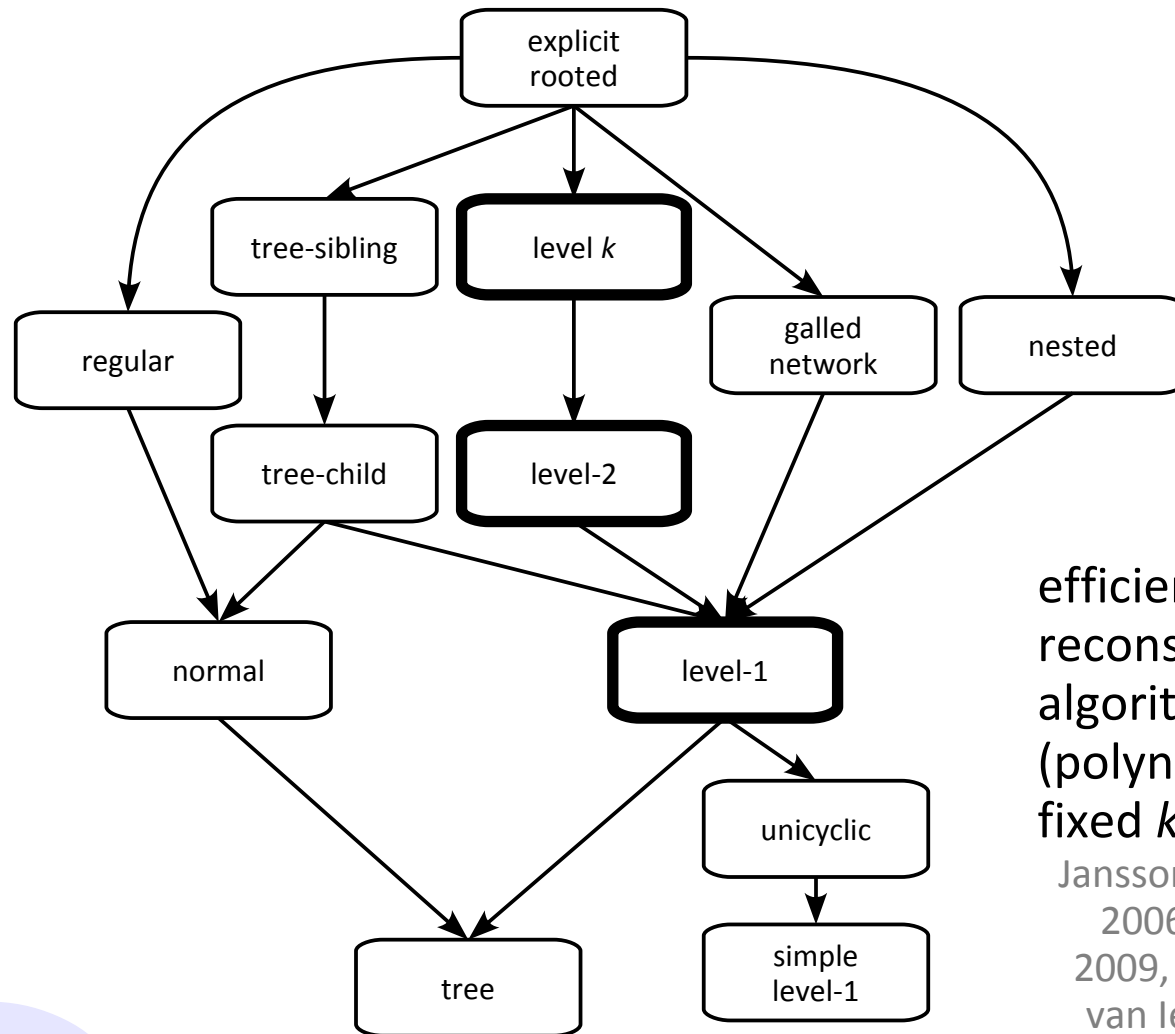
- **many** possible rootings (possibly exponential in the level)
- **same level** (invariant)

# Phylogenetic network subclass hierarchy



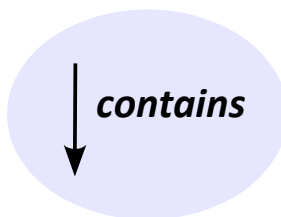
rooted binary phylogenetic networks

# Phylogenetic network subclass hierarchy



efficient  
reconstruction  
algorithms  
(polynomial for  
fixed  $k$ )

Jansson, Nguyen & Sung  
2006, van Iersel *et al.*  
2009, To & Habib 2009,  
van Iersel & Kelk 2010,  
van Iersel *et al.* 2010



rooted binary phylogenetic networks

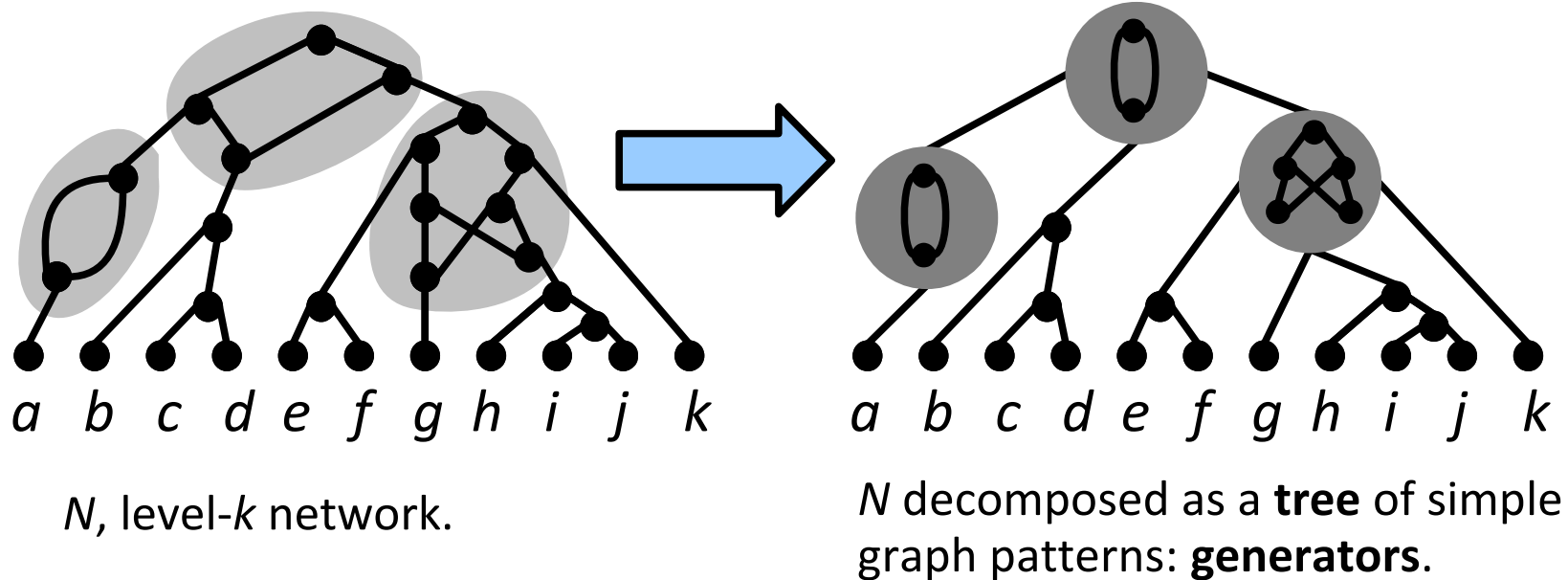
# Plan

---

- Phylogenetic motivations
- Level- $k$  network reconstruction
- **Structure of level- $k$  networks**
- Counting level-1 and 2 networks

# Decomposition of level- $k$ networks

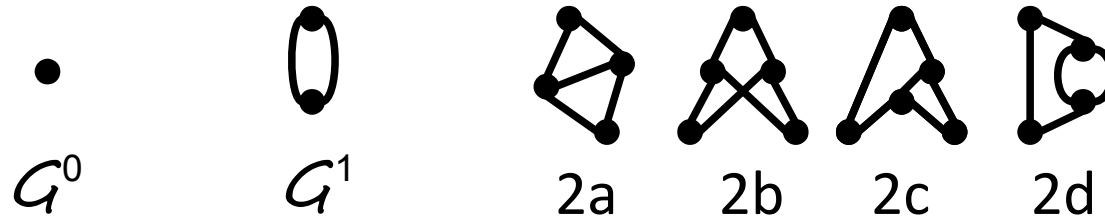
We formalize the decomposition into blobs:



Generators introduced by van Iersel & al (Recomb 2008) for the restricted class of simple level- $k$  networks.

# Level- $k$ generators

A **level- $k$  generator** is a level- $k$  network with no cut arc.



The **sides** of the generator are:

- its arcs
- its reticulation vertices of outdegree 0

# Decomposition theorem of level- $k$ networks

$N$  is a level- $k$  network

iff

there exists a sequence  $(l_j)_{j \in [1,r]}$  of  $r$  locations

(arcs or reticulation vertices of outdegree 0)

and a sequence  $(G_j)_{j \in [0,r]}$  of generators of level at most  $k$ , such that:

- $N = \text{Attach}_k(l_r, G_r, \text{Attach}_k(\dots \text{Attach}_k(l_2, G_2, \text{Attach}_k(l_1, G_1, G_0)) \dots))$ ,
- or  $N = \text{Attach}_k(l_r, G_r, \text{Attach}_k(\dots \text{Attach}_k(l_2, G_2, \text{SplitRoot}_k(G_1, G_0)) \dots))$ .



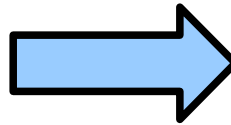
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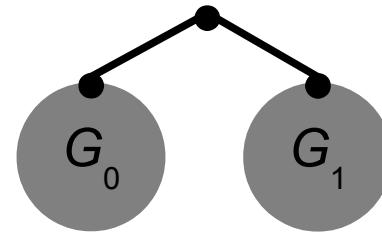
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$\text{SplitRoot}_k(G_1, G_0)$



# Decomposition theorem of level- $k$ networks

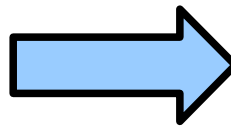
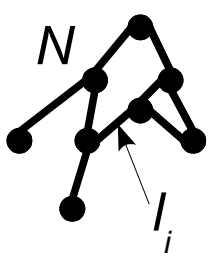
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iff

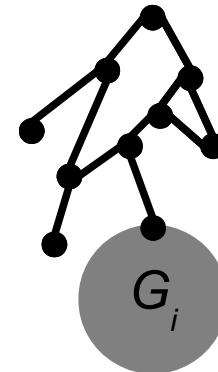
there exists a sequence  $(l_j)_{j \in [1,r]}$  of  $r$  locations  
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$l_i$  is an arc of  $N$



$\text{Attach}_k(l_i, G_i, N)$



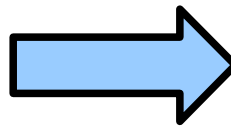
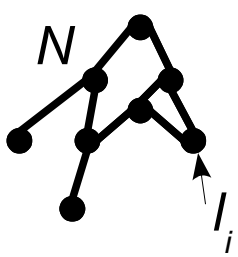
# Decomposition theorem of level- $k$ networks

$N$  is a level- $k$  network

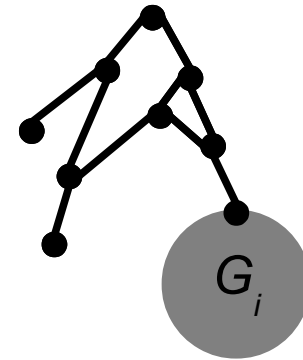
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there exists a sequence  $(l_j)_{j \in [1,r]}$  of  $r$  locations  
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$l_i$  is a reticulation vertex of  $N$



$\text{Attach}_k(l_i, G_i, N)$



# Decomposition theorem of level- $k$ networks

$N$  is a level- $k$  network

iff

there exists a sequence  $(l_j)_{j \in [1,r]}$  of  $r$  locations

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This decomposition is **not unique!**

*recursive decomposition later, for level-1...*

# Construction of level- $k$ generators

Case analysis by van Iersel & al to find the 4 level-2 generators  
Exponential algorithm by Steven Kelk to find the 65 level-3 generators.



Greetings from [The On-Line Encyclopedia of Integer Sequences!](#)

[Hints](#)

Search: 1, 4, 65

Displaying 1-2 of 2 results found.

page 1

Format: long | [short](#) | [internal](#) | [text](#)    Sort: relevance | [references](#) | [number](#)    Highlight: on | [off](#)

[A041119](#)    Denominators of continued fraction convergents to  $\sqrt{68}$ . +20  
2

1, 4, 65, 264, 4289, 17420, 283009, 1149456, 18674305, 75846676, 1232221121, 5004731160, 81307919681, 330236409884, 5365090477825, 21790598321184, 354014663616769, 1437849252788260, 23359602708228929 ([list](#); [graph](#); [listen](#))

OFFSET            0, 2

CROSSREFS        Cf. [A041118](#).  
Sequence in context: [A138835](#) [A119601](#) [A058438](#) this\_sequence [A015475](#) [A025585](#)  
[A048828](#)  
Adjacent sequences: [A041116](#) [A041117](#) [A041118](#) this\_sequence [A041120](#) [A041121](#)  
[A041122](#)

KEYWORD           nonn, cofr, easy

AUTHOR            njas

[A015475](#)     $q$ -Fibonacci numbers for  $q=4$ . +20  
1

0, 1, 4, 65, 4164, 1066049, 1091638340, 4471351706689, 73258627454030916, 4801077413298721817665, 1258573637505038759624004676, 1319710110525284599824799048959041 ([list](#); [graph](#); [listen](#))

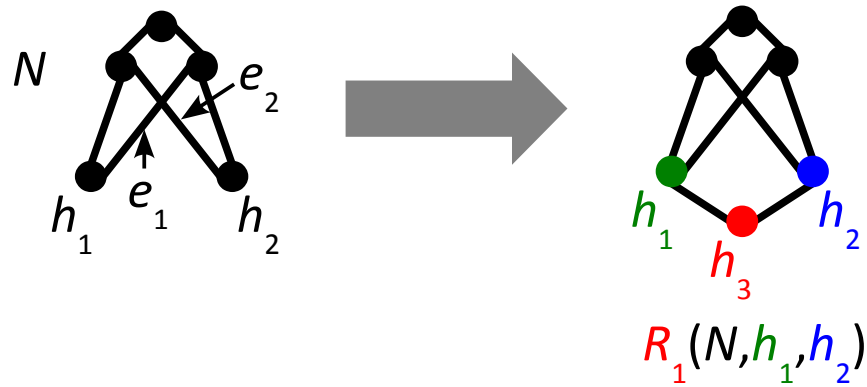
OFFSET            0, 3

FORMULA            $a(n) = 4^{(n-1)} a(n-1) + a(n-2)$ .

CROSSREFS        Sequence in context: [A119601](#) [A058438](#) [A041119](#) this\_sequence [A025585](#) [A048828](#)

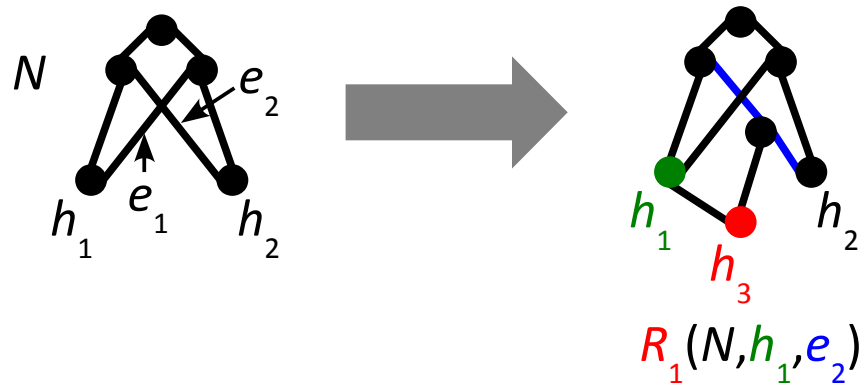
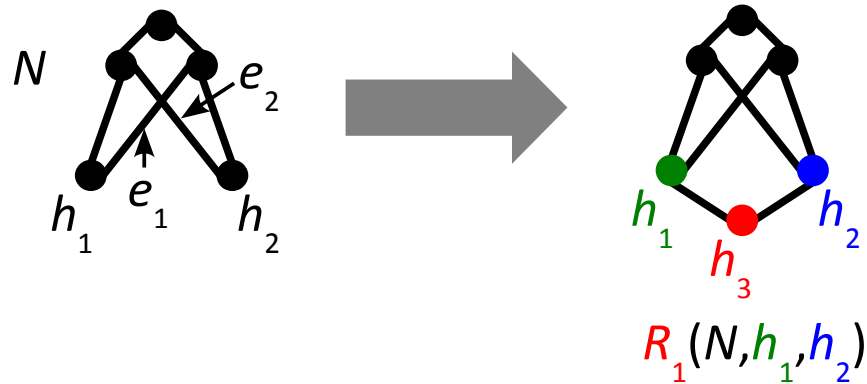
# Construction of level- $k$ generators

Construction rules of level- $(k+1)$  generators from level- $k$  generators



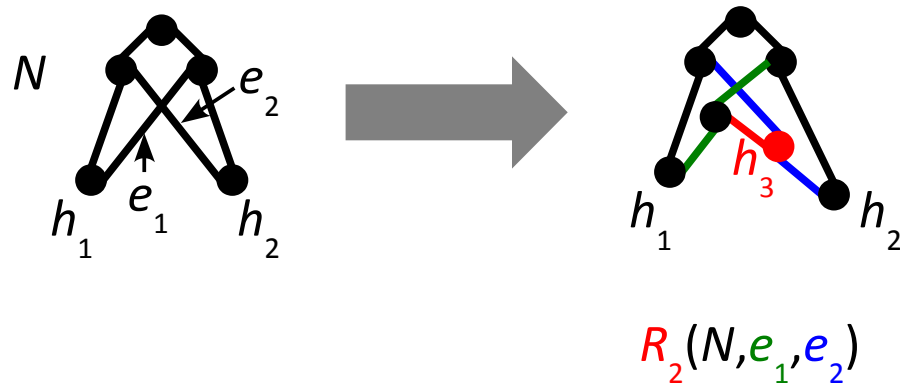
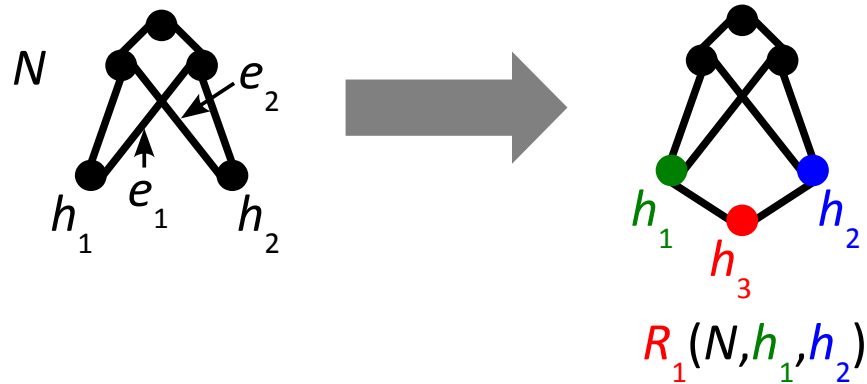
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# Construction of level- $k$ generators

Construction rules of level- $(k+1)$  generators from level- $k$  generators





# Upper bound on the number of level- $k$ generators

$R_1$  and  $R_2$  can be applied at most on all pairs of sides

A level- $k$  generator has at most  $5k$  slides:

$$g_{k+1} < 50 k^2 g_k$$

**Upper bound:**

$$g_k < k!^2 50^k$$

**Theoretical corollary:**

There is a polynomial algorithm to build the set of level- $(k+1)$  generators from the set of level- $k$  generators.

→ polynomial time algorithms to reconstruct level- $k$  networks with fixed  $k$

Kelk, Scornavacca & van Iersel, *TCBB*, 2011

**Practical corollary:**

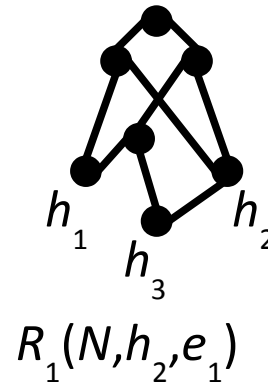
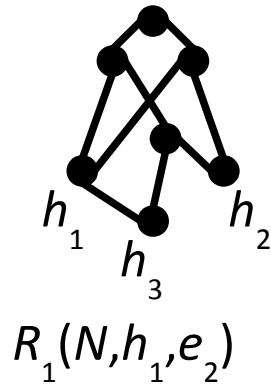
$$g_4 < 28350$$

→ it is possible to enumerate all level-4 generators.

# Construction of level- $k$ generators

## Problem:

Some of the level- $(k+1)$  generators obtained from level- $k$  generators are isomorphic!



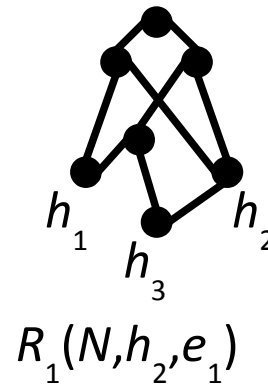
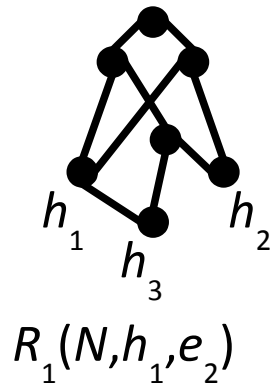
→ difficult to count

→ possible generation up to level 5 :  
1, 4, 65, 1993, 91454

# Construction of level- $k$ generators

## Problem:

Some of the level- $(k+1)$  generators obtained from level- $k$  generators are isomorphic!



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Greetings from [The On-Line Encyclopedia of Integer Sequences!](http://www.oeis.org/)

[Hints](#)

Search: 1, 4, 65, 1993

I am sorry, but the terms do not match anything in the table.

Gambette, Berry & Paul, CPM 2009

<http://www.lirmm.fr/~gambette/ProgGenerators.php>

# Lower bound on the number of level- $k$ generators

***Lower bound:***

$$g_k \geq 2^{k-1}$$

There is an **exponential number** of generators!

***Idea:***

Code every number between 0 and  $2^{k-1}-1$  by a level- $k$  generator.

# Lower bound on the number of level- $k$ generators

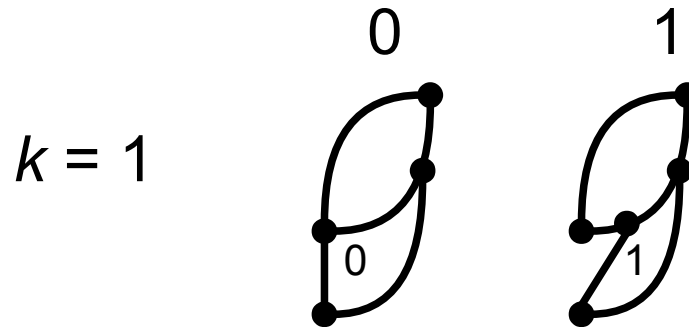
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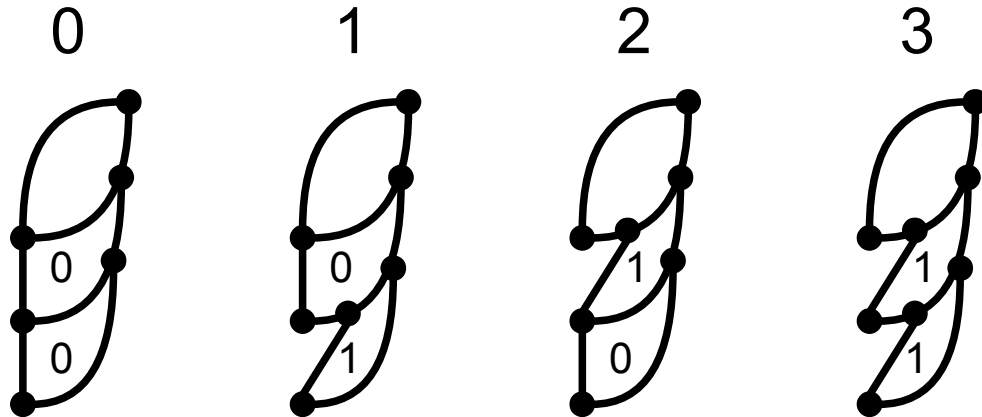
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Code every number between 0 and  $2^{k-1}-1$  by a level- $k$  generator.

$k = 2$



# Lower bound on the number of level- $k$ generators

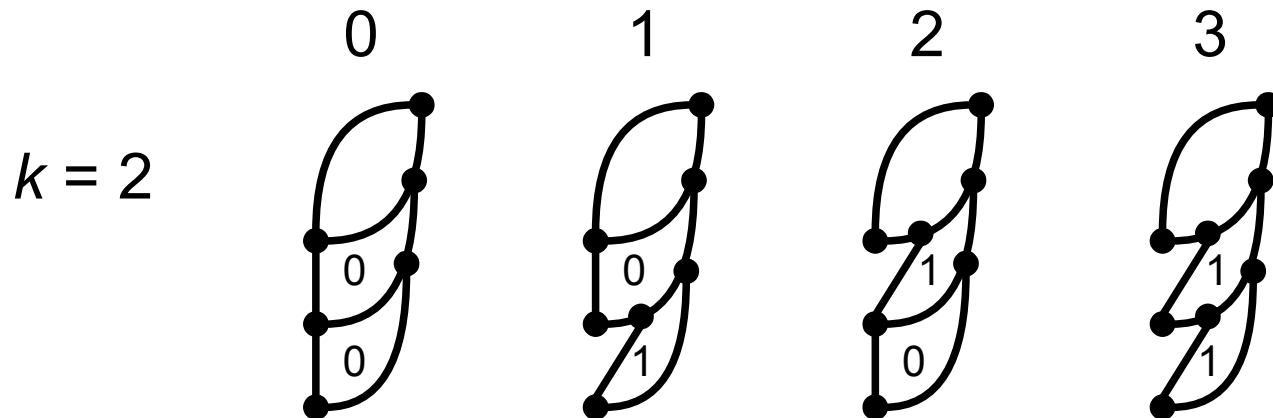
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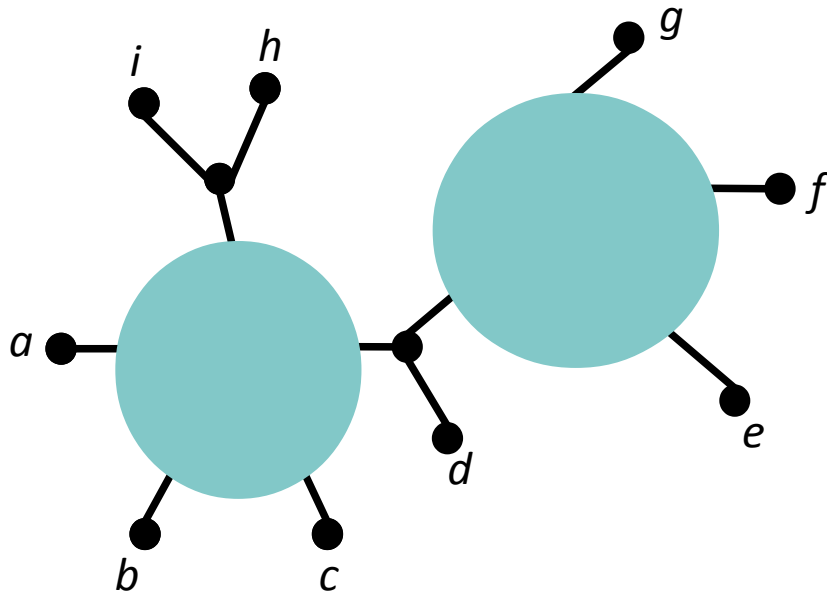
Code every number between 0 and  $2^{k-1}-1$  by a level- $k$  generator.



**Practical corollary:**

Phylogenetic reconstruction algorithms based on generators are not practical.

# Unrooted level- $k$ networks

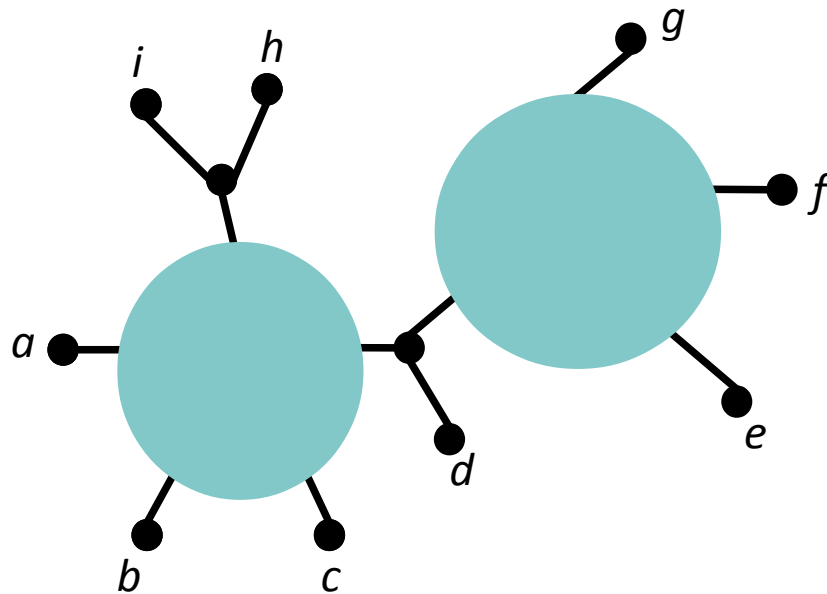


**level =**  
maximum number of **edges to remove**, by **blob**, to obtain a tree.

unrooted level- $k$  network  $\Rightarrow$  tree of **blobs**  
 $\Rightarrow$  tree of **generators** of level  $\leq k$



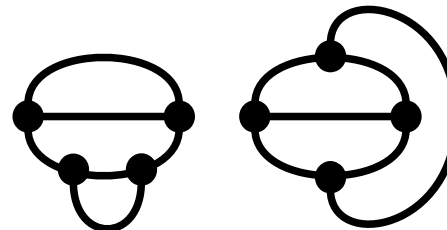
# Unrooted level- $k$ networks



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**Unrooted level- $k$  generators:** bridgeless loopless 3-regular multigraphs with  $2k-2$  vertices



level-3 generators

# Plan

---

- Phylogenetic motivations
- Level- $k$  network reconstruction
- Structure of level- $k$  networks
- Counting level-1 and 2 networks

# Counting labeled unrooted level-1 networks

## Unrooted level-1 networks:

explicit formula for  $n$  leaves,  $c$  cycles,  $m$  edges involved in the cycles.

Semple & Steel, *TCBB*, 2006

# Counting labeled unrooted level-1 networks

## **Unrooted level-1 networks:**

explicit formula for  $n$  leaves,  $c$  cycles,  $m$  edges involved in the cycles.

## **Pointing + bijection:**

Bijection between labeled unrooted level-1 networks with  $n+1$  leaves and labeled pointed level-1 networks with  $n$  leaves.

# Counting labeled unrooted level-1 networks

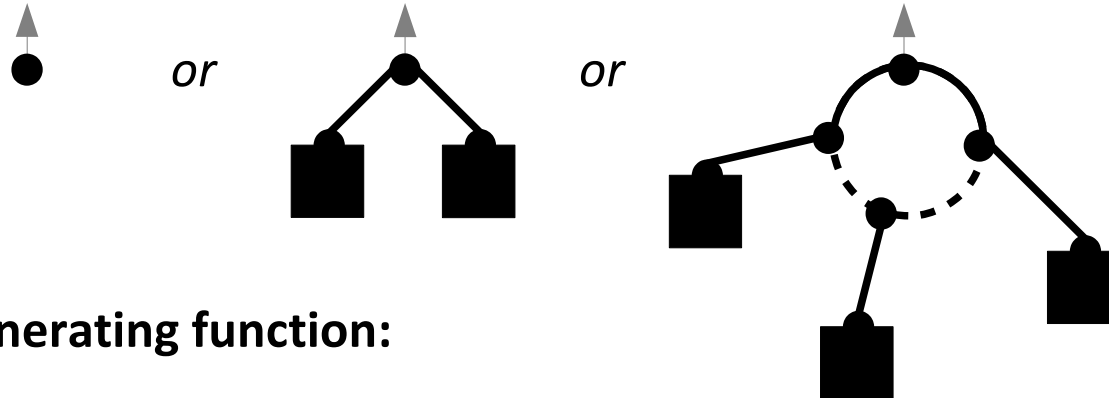
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## Recursive decomposition of pointed level-1 networks with $n$ leaves:



## Exponential generating function:

$$G = z + \frac{1}{2}G^2 + \frac{1}{2} \frac{G^2}{(1-G)}$$

# Counting labeled unrooted level-1 networks

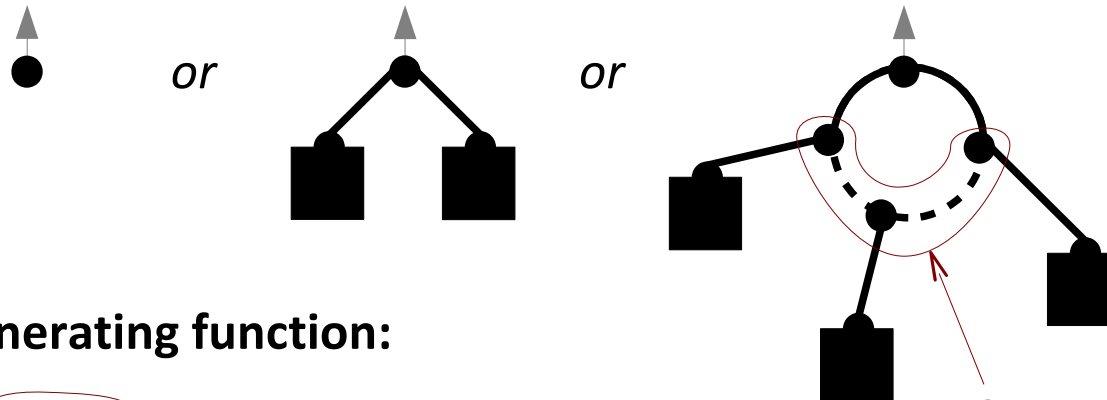
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$$G = z + \frac{1}{2}G^2 + \frac{1}{2} \frac{G^2}{(1-G)}$$

$\text{Seq}_{\geq 2}$ , any direction

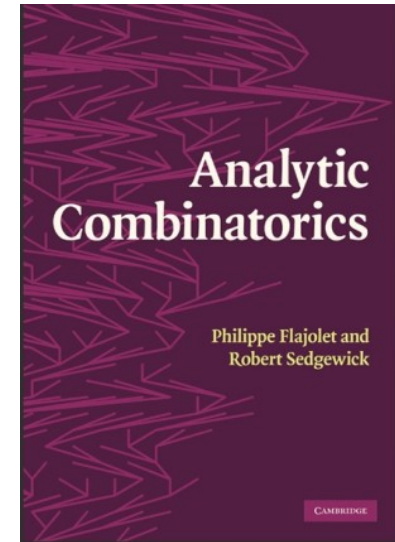
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Using the Singular Inversion Theorem (Theorem VI.6 of

$$g_n \approx 0.2074 (1.8904)^n n^{n-1}$$



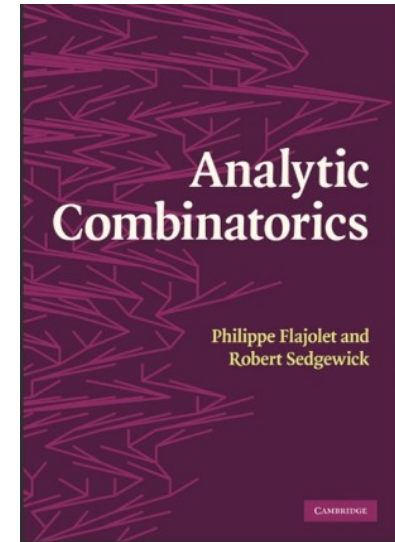
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**Proof :**

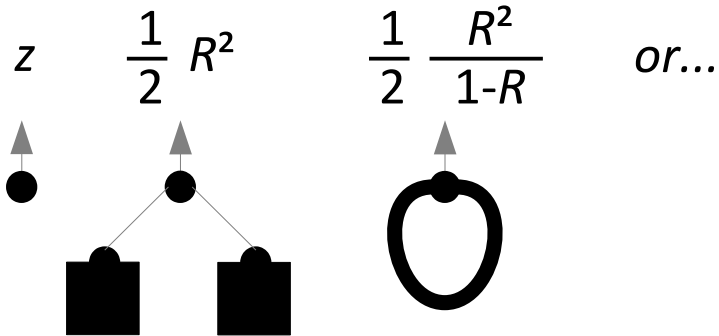
We write  $G = z \varphi(G)$ , with  $\varphi(z) = \frac{1}{1 - \frac{1}{2} z (1 + 1/(1-z))}$

Then  $g_n \approx n! \sqrt{\frac{\varphi(\tau)}{2\varphi''(\tau)}} \frac{\rho^{-n}}{\sqrt{\pi n^3}}$ , with  $\rho = \tau / \varphi(\tau)$   
and  $\tau$  is the solution of  $\varphi(z) - z\varphi'(z) = 0$



# Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with  $n$  leaves:




—  $\text{Seq}_{\geq 1}$ , any direction


■  $\text{Seq}_{\geq 2}$ , any direction

→  $\text{Seq}_{\geq 1}$

➔  $\text{Seq}_{\geq 2}$

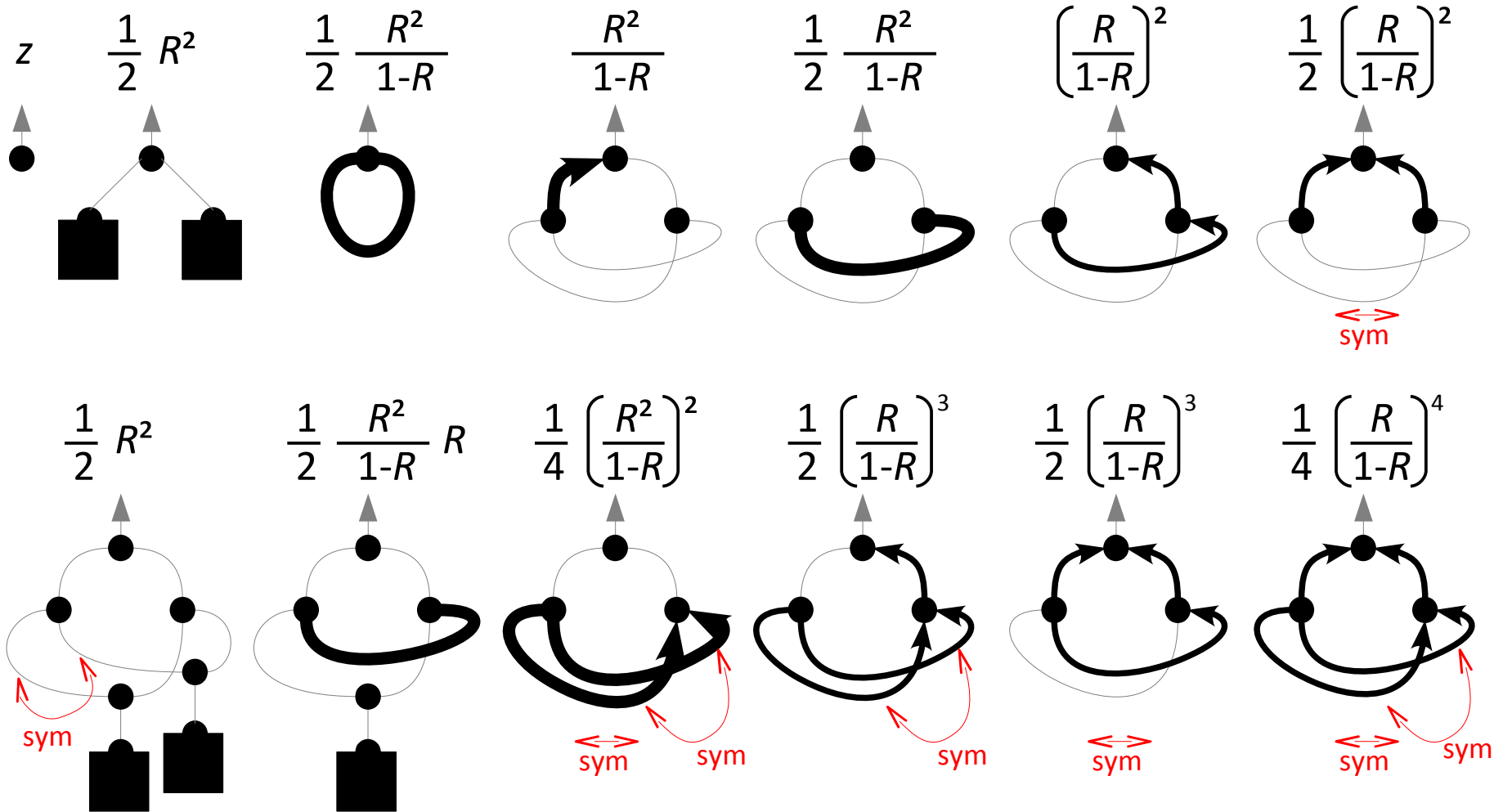
— simple edge

 edge symmetry

 horizontal symmetry with new orientation for lower edges

# Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with  $n$  leaves:



—  $\text{Seq}_{\geq 1}$ , any direction  
 —  $\text{Seq}_{\geq 2}$ , any direction

→  $\text{Seq}_{\geq 1}$   
 →  $\text{Seq}_{\geq 2}$

— simple edge  
 ↻ edge symmetry

↔  $\text{sym}$  horizontal symmetry with new orientation for lower edges

# Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with  $n$  leaves:

$$R = z + \frac{R^2}{2} + \frac{R^2}{2(1-R)} + \frac{R^2}{1-R} + \frac{R^2}{2(1-R)} + \frac{R^2}{(1-R)^2} + \frac{R^2}{2(1-R)^2} \\ + \frac{R^2}{2} + \frac{R^3}{2(1-R)} + \frac{R^4}{4(1-R)^2} + \frac{R^3}{2(1-R)^3} + \frac{R^3}{2(1-R)^3} + \frac{R^4}{4(1-R)^4}$$

Rewrite:

$$R = z\phi(R) \text{ where } \phi(R) = \frac{1}{1 - \frac{3r^5 - 20r^4 + 46r^3 - 46r^2 + 18r}{4(r-1)^4}}$$

# Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with  $n$  leaves:

$$R = z + \frac{R^2}{2} + \frac{R^2}{2(1-R)} + \frac{R^2}{1-R} + \frac{R^2}{2(1-R)} + \frac{R^2}{(1-R)^2} + \frac{R^2}{2(1-R)^2} \\ + \frac{R^2}{2} + \frac{R^3}{2(1-R)} + \frac{R^4}{4(1-R)^2} + \frac{R^3}{2(1-R)^3} + \frac{R^3}{2(1-R)^3} + \frac{R^4}{4(1-R)^4}$$

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Lagrange inversion:

$$r(n) = n![z^n]R(z) = \frac{n!}{n}[\lambda^{n-1}]\phi^n(\lambda),$$

Taylor expansions of  $\varphi^n(\lambda)$ :

number of leaves	2	3	4	5	6	7
unrooted level-2	-	9	282	14 697	1 071 750	100 467 405

# Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with  $n$  leaves:

$$R = z + \frac{R^2}{2} + \frac{R^2}{2(1-R)} + \frac{R^2}{1-R} + \frac{R^2}{2(1-R)} + \frac{R^2}{(1-R)^2} + \frac{R^2}{2(1-R)^2} \\ + \frac{R^2}{2} + \frac{R^3}{2(1-R)} + \frac{R^4}{4(1-R)^2} + \frac{R^3}{2(1-R)^3} + \frac{R^3}{2(1-R)^3} + \frac{R^4}{4(1-R)^4}$$

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Taylor expansions + Newton formula:

$$r(n) = (n-1)! \sum_{\substack{0 \leq s \leq q \leq p \leq k \leq i \leq n-1 \\ j = n-1-i-k-p-q-s \geq 0 \\ i \neq 0}} \binom{n+i-1}{i} \binom{4i+j-1}{j} \binom{i}{k} \binom{k}{p} \binom{p}{q} \binom{q}{s} \\ \times \left(\frac{-4}{21}\right)^s \left(\frac{9}{2}\right)^i \left(\frac{23}{9}\right)^k (-1)^p \left(\frac{-21}{46}\right)^q.$$

# Counting labeled level- $k$ networks

## Unrooted level-1 networks:

explicit formula for  $n$  leaves,  $c$  cycles,  $m$  edges involved in the cycles

Semple & Steel, *TCBB*, 2006

+ asymptotic evaluation for  $n$  leaves:  $\approx 0.207 (1.890)^n n^{n-1}$

## Rooted level-1 networks :

Explicit formula for  $n$  leaves,  $c$  cycles,  $m$  edges across cycles

+ asymptotic evaluation for  $n$  leaves:  $\approx 0.134 (2.943)^n n^{n-1}$

## Unrooted level-2 networks :

Explicit formula for  $n$  leaves :  $(n-1)! \sum_{\substack{0 \leq s \leq q \leq p \leq k \leq i \leq n-1 \\ j = n-1-i-k-p-q-s \geq 0 \\ i \neq 0}} \binom{n+i-1}{i} \binom{4i+j-1}{j} \binom{i}{k} \binom{k}{p} \binom{p}{q} \binom{q}{s} \left(\frac{-3}{20}\right)^s \left(\frac{9}{2}\right)^i \left(\frac{-23}{9}\right)^k (-1)^p \left(\frac{-10}{23}\right)^q$

+ asymptotic evaluation for  $n$  leaves:  $\approx 0.059 (7.662)^n n^{n-1}$

number of leaves	2	3	4	5	6	7
unrooted level-1	-	2	15	192	3 450	79 740
rooted level-1	3	36	723	20 280	730 755	32 171 580
unrooted level-2	-	9	282	14 697	1 071 750	100 467 405

# Thank you for your attention!

## *Co-authors of these results*

Vincent Berry & Christophe Paul (LIRMM, Montpellier)

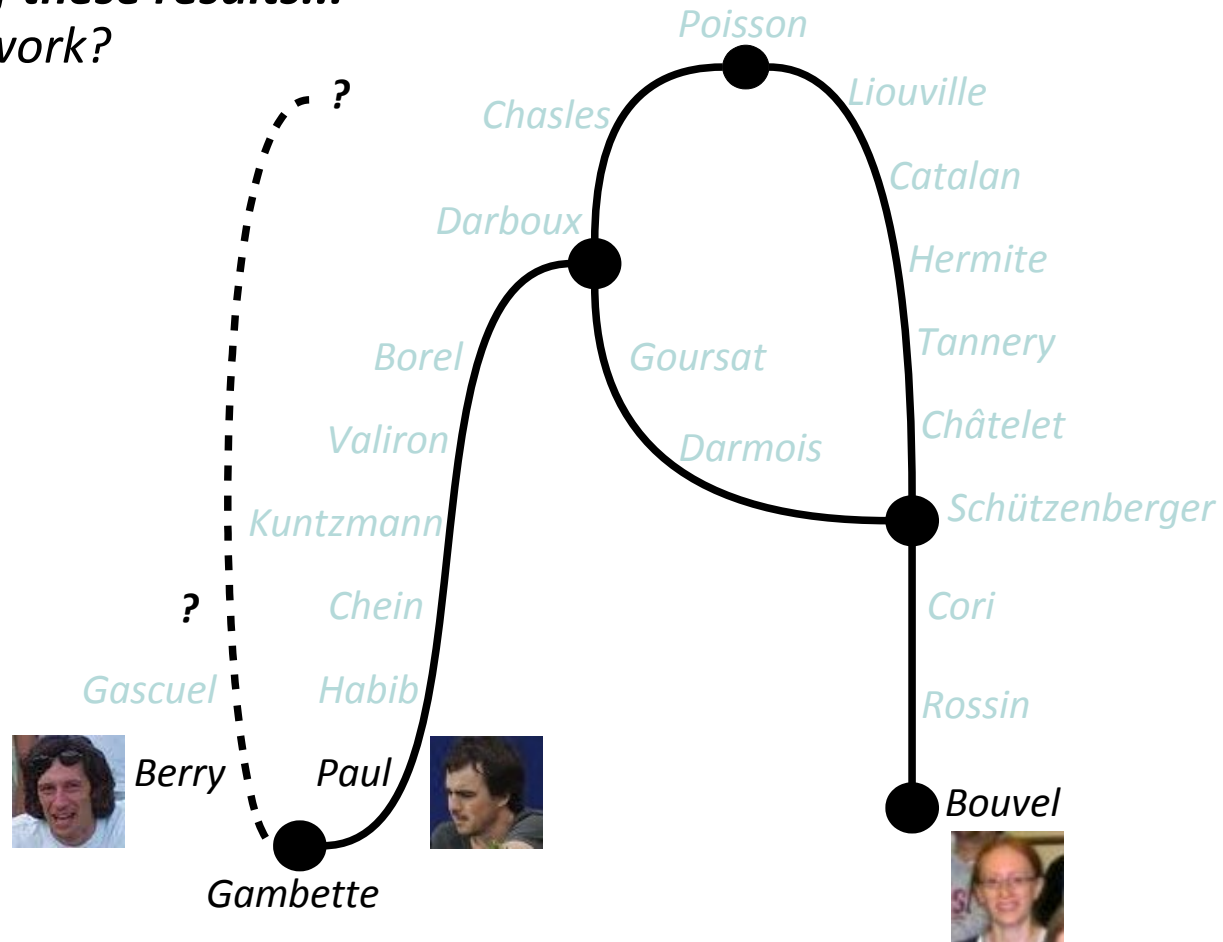
Mathilde Bouvel (LABRI, Bordeaux)

Thanks to the LABRI for their *Junior Guest* grant in April 2011!



# Thank you for your attention!

*Co-authors of these results...  
A level-2 network?*





# Thank you for your attention!

*Co-authors of these results...*  
*A level-3 network*

