Groupe de travail APR, LIP6
Paris – 18/11/2011

Structure and enumeration of level-k phylogenetic networks

Philippe Gambette

Université Paris-Est Marne-la-Vallée
Gaspard-Monge Institut

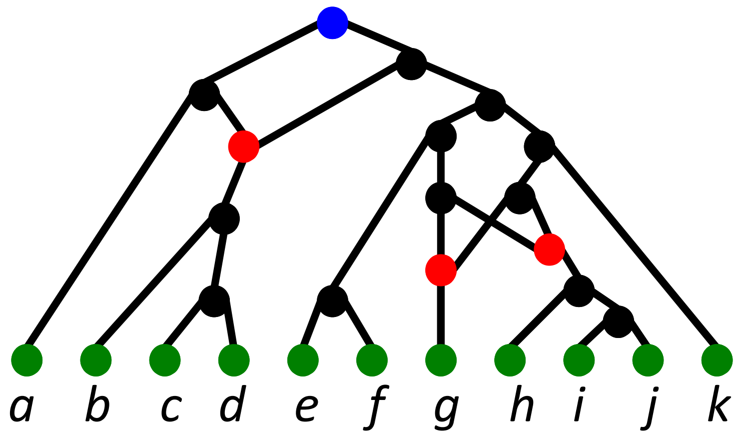
Outline

- 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

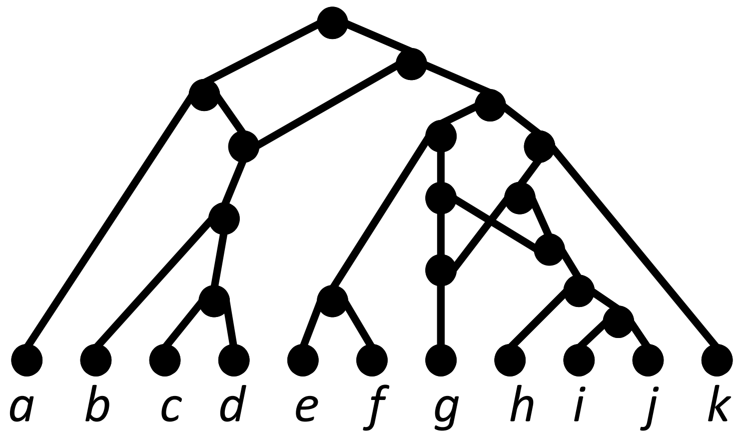
Rooted binary phylogenetic networks



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

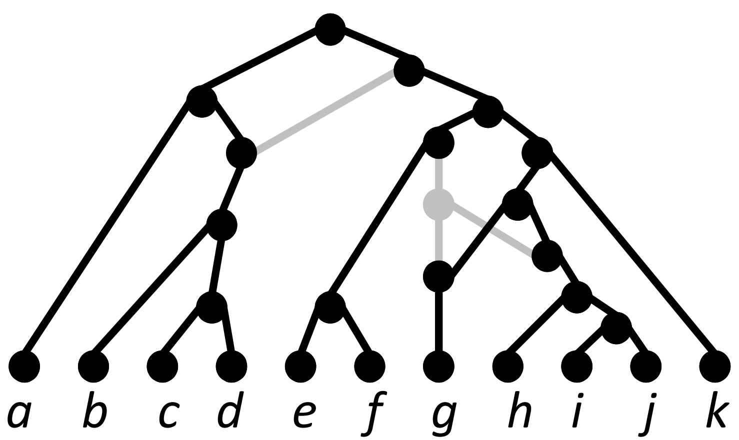
- **root**
- **split vertices** (speciation)
- **hybrid vertices** (hybridization, horizontal gene transfer)

Rooted binary phylogenetic networks

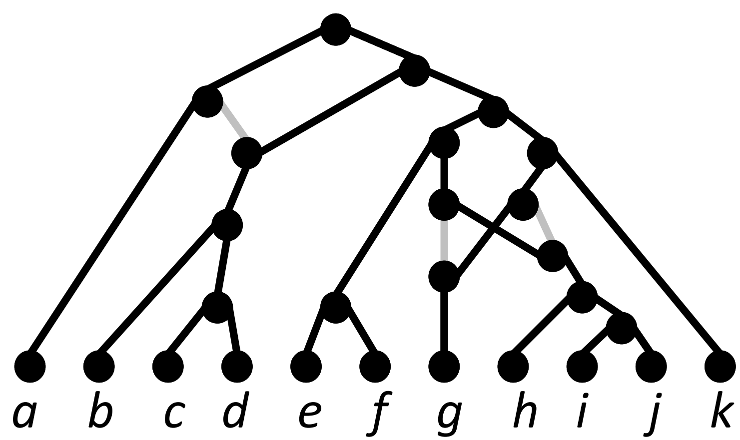


Model: each gene comes from one parent:

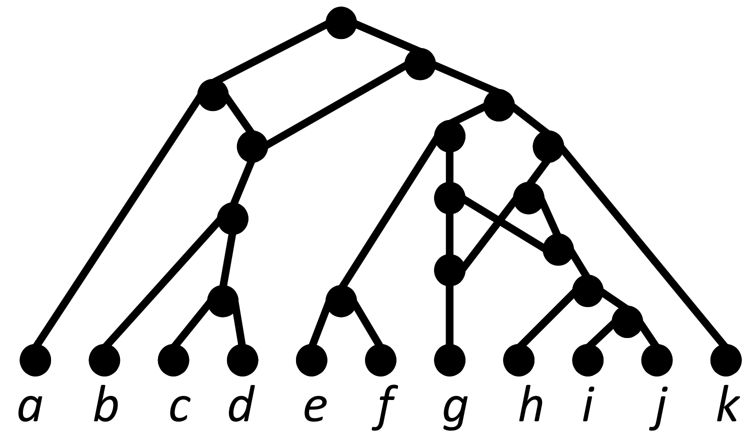
Gene 1



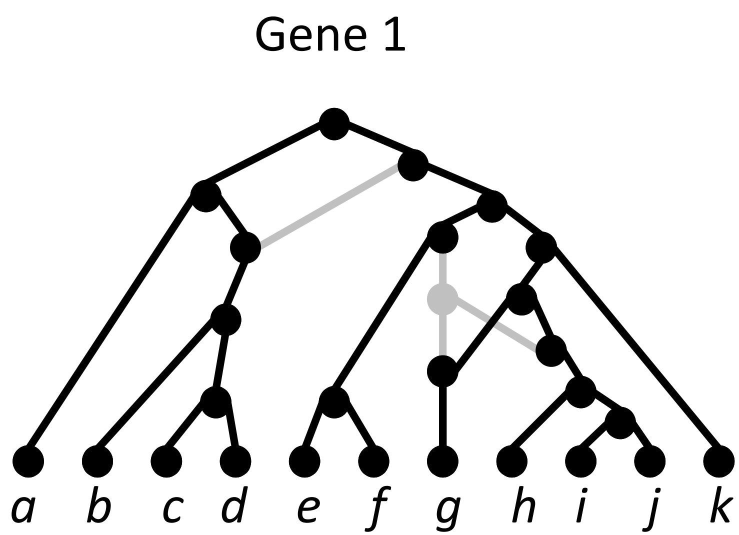
Gene 2

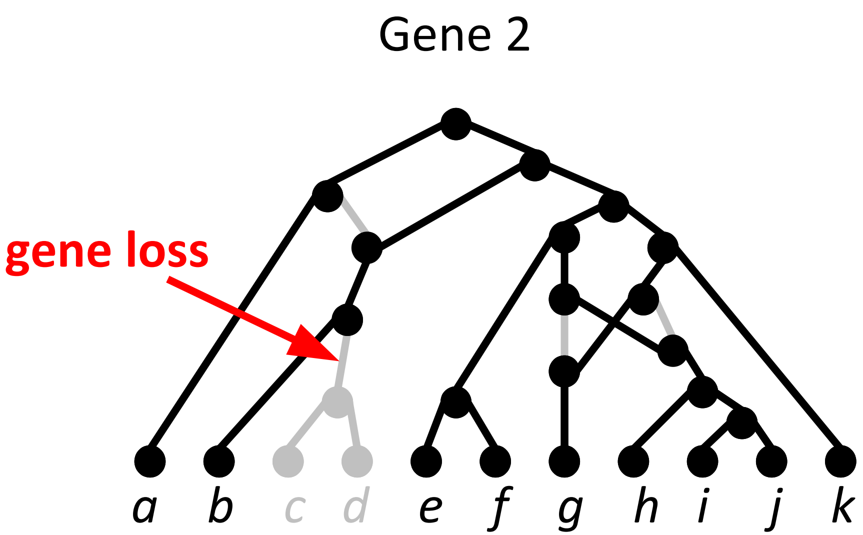


Rooted binary phylogenetic networks



Model: each gene comes from one parent:





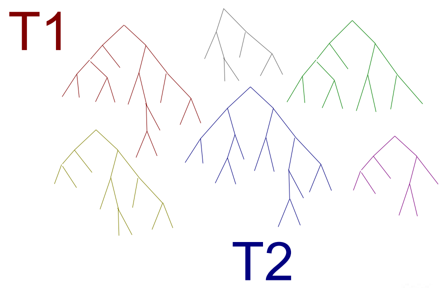
Combinatorial phylogenetic network reconstruction

```
species 1 : AATTGCAG TAGCCCAAAAT
species 2 : ACCTGCAG TAGACCAAT
species 3 : GCTTGCCG TAGACAAGAAT
species 4 : ATTTGCAG AAGACCAAAT
species 5 :          TAGACAAGAAT
species 6 : ACTTGCAG TAGCACAAAAT
species 7 : ACCTGGTG TAAAAT
            G1       G2
```

{gene sequences}

↓

{trees}



HOGENOM database
Dufayard, Duret, Penel, Gouy, Rechenmann & Perrière, *BioInf*, 2005

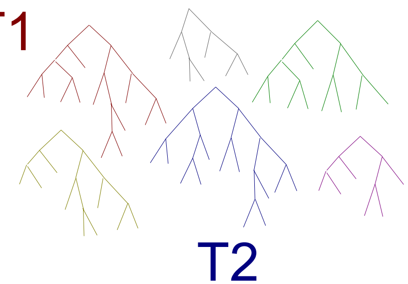
Combinatorial phylogenetic network reconstruction

```
species 1 : AATTGCAG TAGCCCAAAAT
species 2 : ACCTGCAG TAGACCAAT
species 3 : GCTTGCCG TAGACAAGAAT
species 4 : ATTTGCAG AAGACCAAAT
species 5 :          TAGACAAGAAT
species 6 : ACTTGCAG TAGCACAAAAT
species 7 : ACCTGGTG TAAAAT
```

G1 G2

{gene sequences}

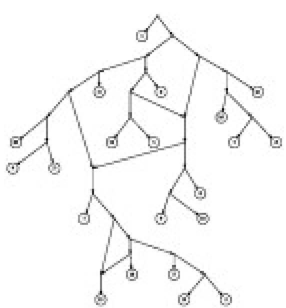
{trees}



HOGENOM database
Dufayard, Duret, Penel, Gouy, Rechenmann & Perrière, *BioInf*, 2005

Phyl-ARIANE

ANR



network

contains the trees
+ “optimal”

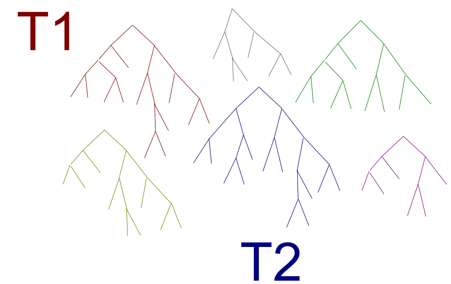
Combinatorial phylogenetic network reconstruction

```
species 1 : AATTGCAG TAGCCCAAAAT
species 2 : ACCTGCAG TAGACCAAT
species 3 : GCTTGCCG TAGACAAGAAT
species 4 : ATTTGCAG AAGACCAAAT
species 5 :          TAGACAAGAAT
species 6 : ACTTGCAG TAGCACAAAAT
species 7 : ACCTGGTG TAAAAT
```

G1 G2

{gene sequences}

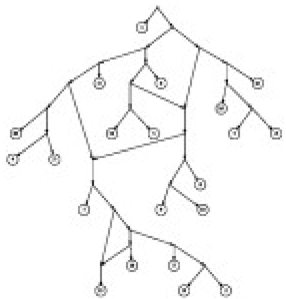
{trees}



HOGENOM database
Dufayard, Duret, Penel, Gouy, Rechenmann & Perrière, *BioInf*, 2005

Phyl-ARIANE

ANR



network

contains the trees
+ “optimal”

NP-complete for 2 rooted trees

Bordewich & Semple, *DAM*, 2007

Combinatorial phylogenetic network reconstruction

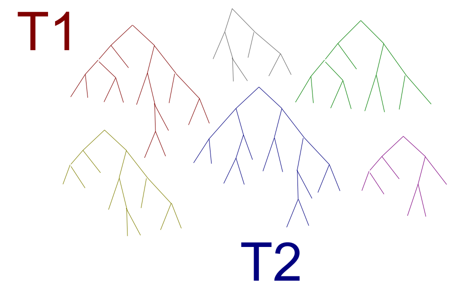
```
species 1 : AATTGCAG TAGCCCAAAAT
species 2 : ACCTGCAG TAGACCAAT
species 3 : GCTTGCCG TAGACAAGAAT
species 4 : ATTTGCAG AAGACCAAAT
species 5 :          TAGACAAGAAT
species 6 : ACTTGCAG TAGCACAAAAT
species 7 : ACCTGGTG TAAAAT
```

G1 G2

{gene sequences}

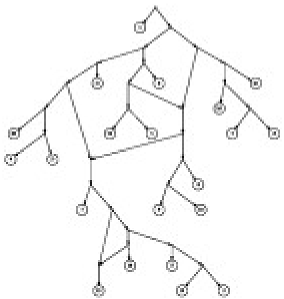
↓

{trees}



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

↓



network

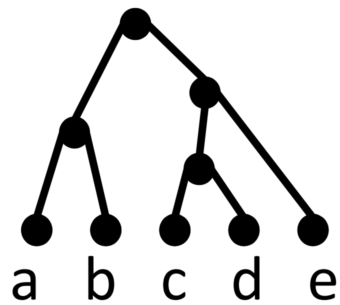
contains the trees
+ “optimal”
NP-complete for 2 rooted trees

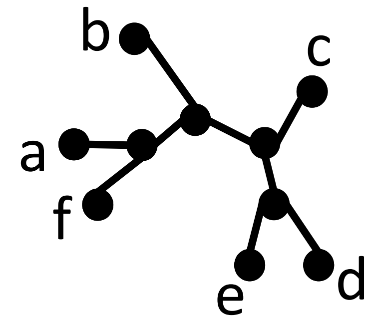
Bordewich & Semple, *DAM*, 2007

Reconstruction from triplets / quartets

{gene sequences}

{trees}



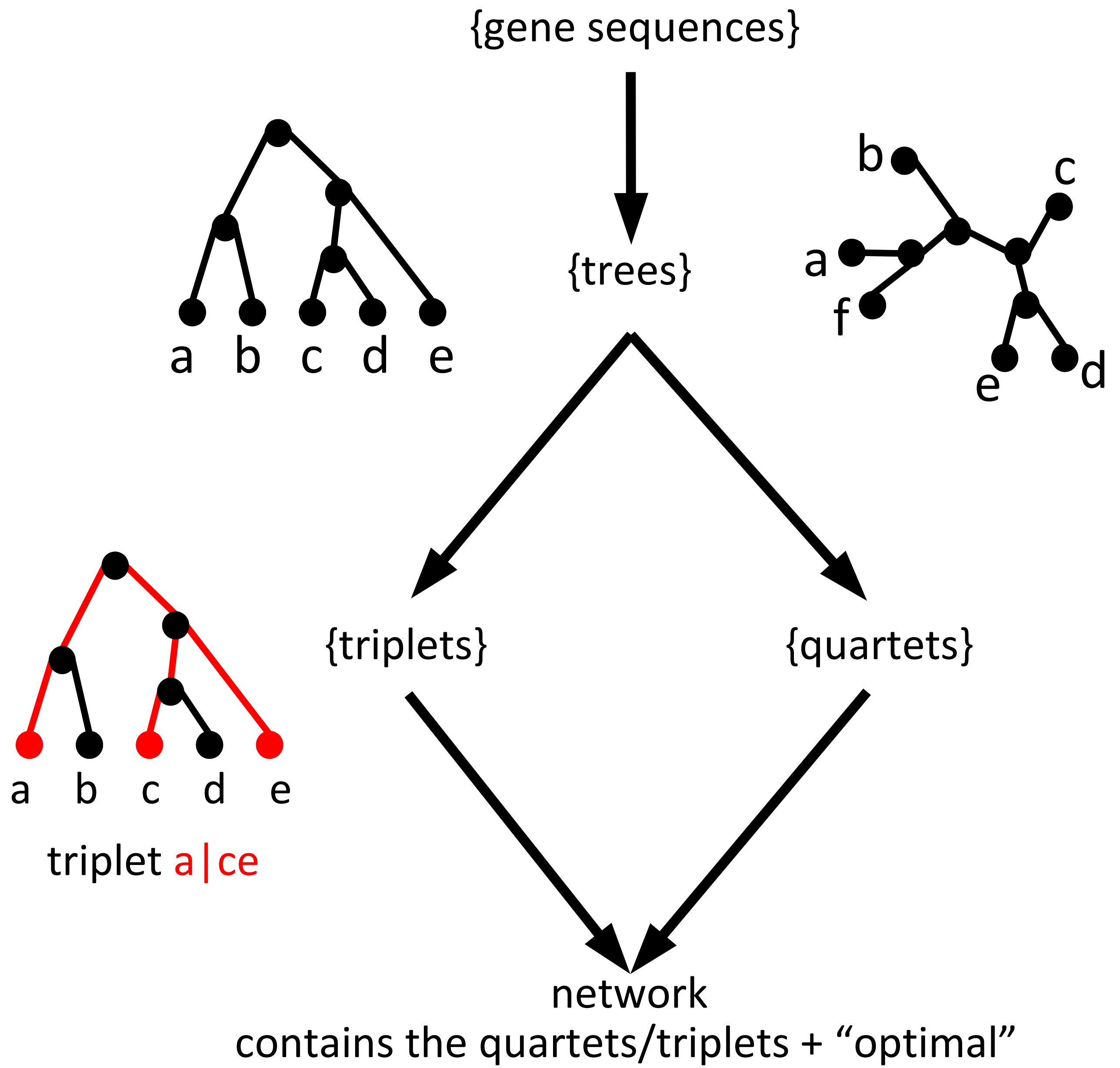


{triplets}

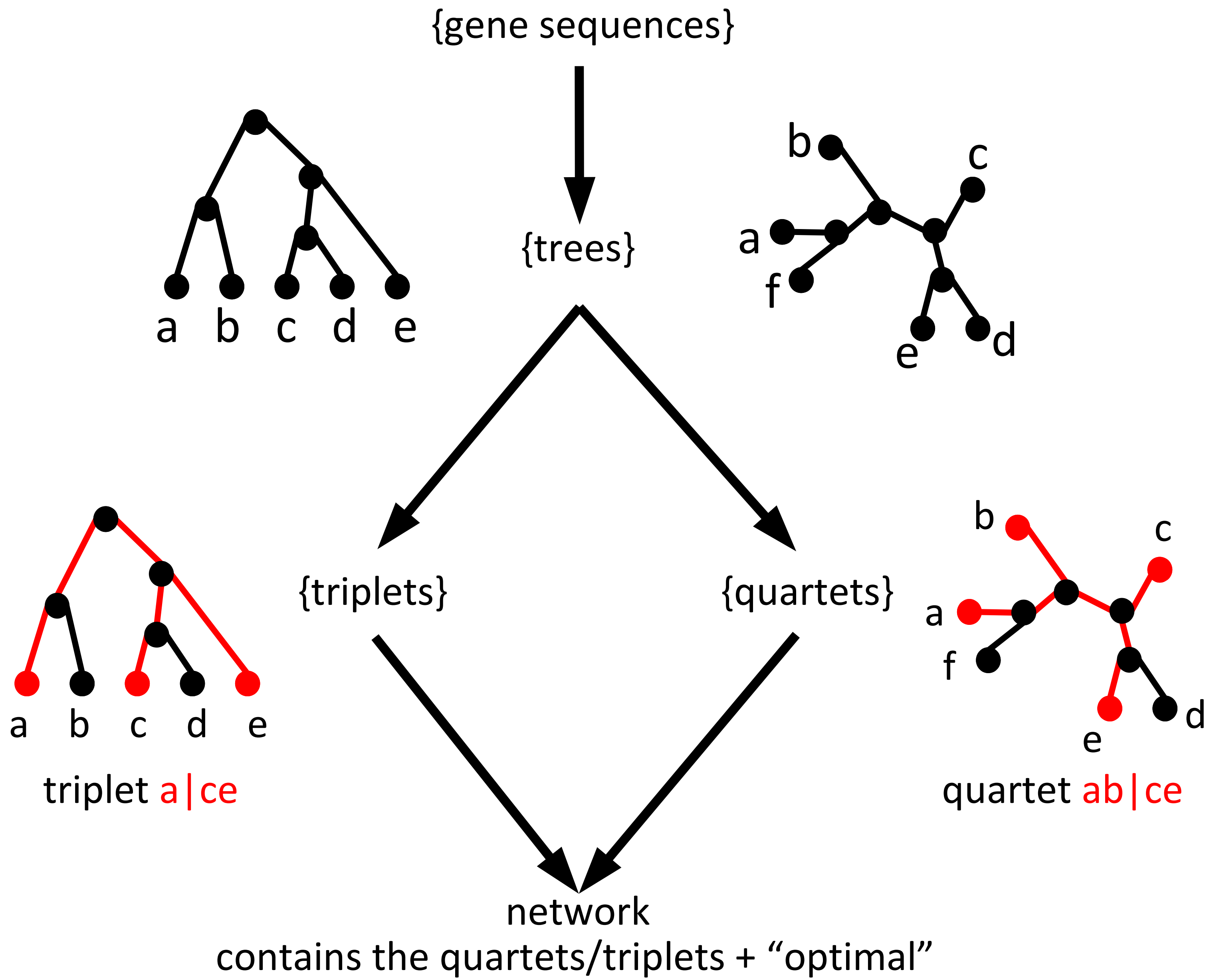
{quartets}

network
contains the quartets/triplets + "optimal"

Reconstruction from triplets / quartets



Reconstruction from triplets / quartets



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

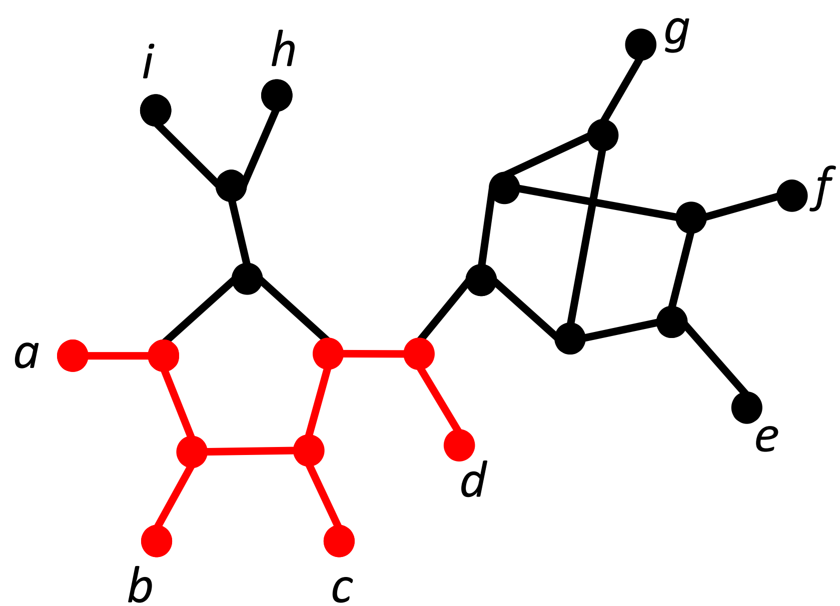
Checking the solution:

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: $O(n^3)$

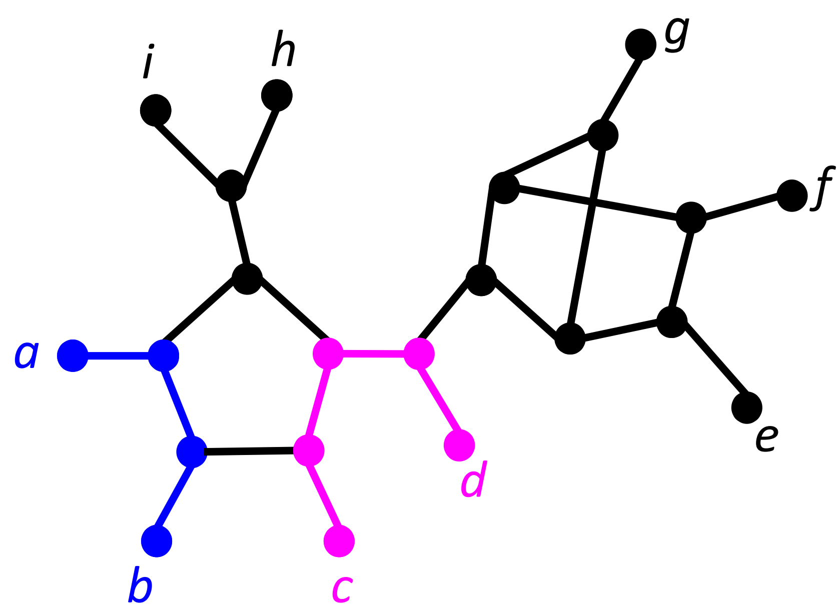
Byrka, Gawrychowski, Huber & Kelk, *JDA*, 2010

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

quartet *ab*|*cd*

⬍

2-disjoint paths
a-b,*c-d*



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 ≤3: $O(n(1+\alpha(n,n)))$

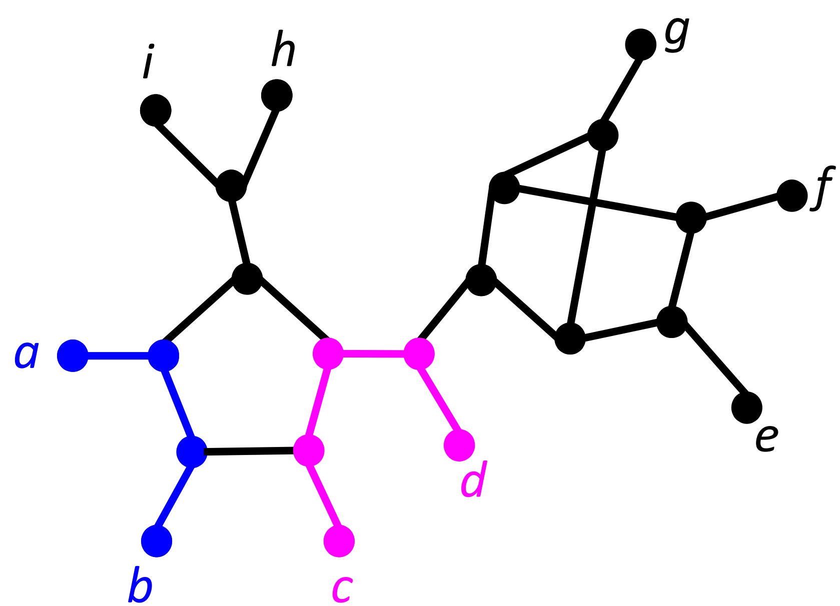
Tholey, *SOFSEM'09*, 2009

quartet *ab*|*cd*

⬍

2-disjoint paths

a-b,*c-d*

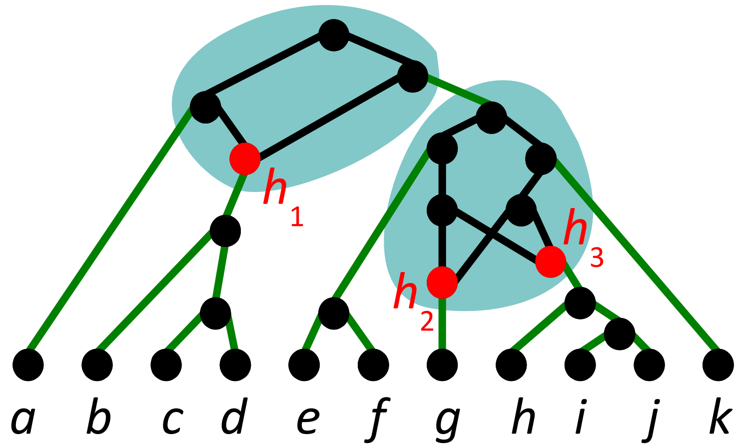


Plan

- 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 ➡ tree structure ➡ fast algorithms



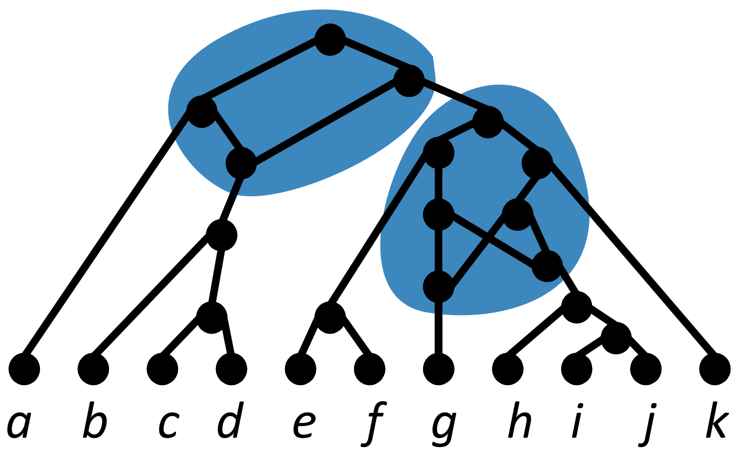
level-2 network

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

Choy, Jansson, Sadakane & Sung, *TCS*, 2005

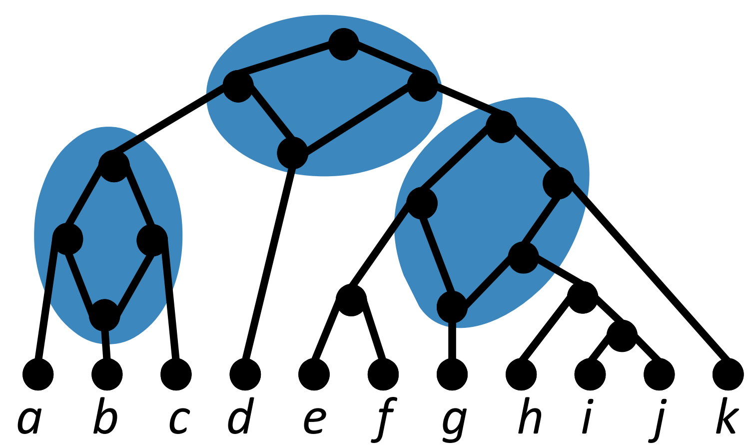
Level-*k* networks

level: how "far" is the network from a tree ?
small level ➡ tree structure ➡ fast algorithms



level-2 network

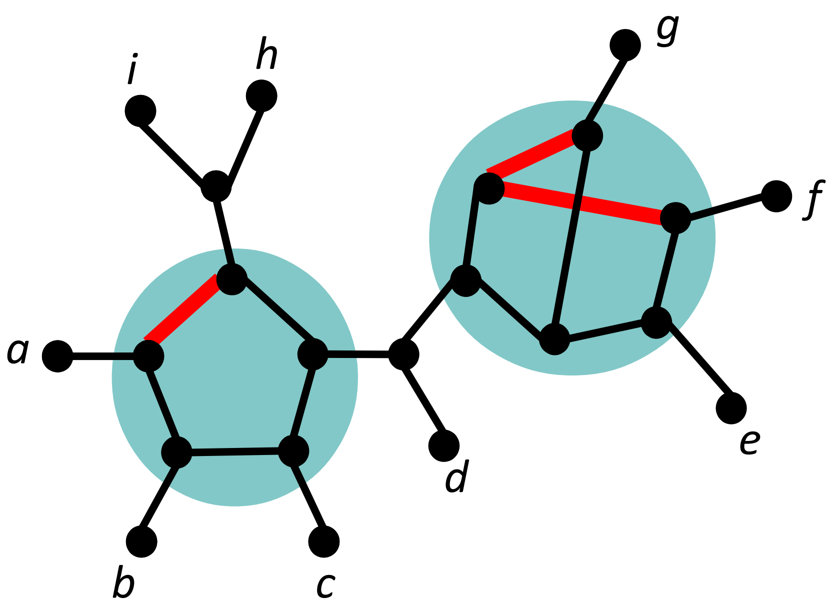
level =
maximum number of hybrid vertices
by *blob*.



level-1 network
("*galled tree*")

Unrooted level-*k* networks

level: how "far" is the network from an unrooted tree ?
small level ➡ tree structure ➡ fast algorithms



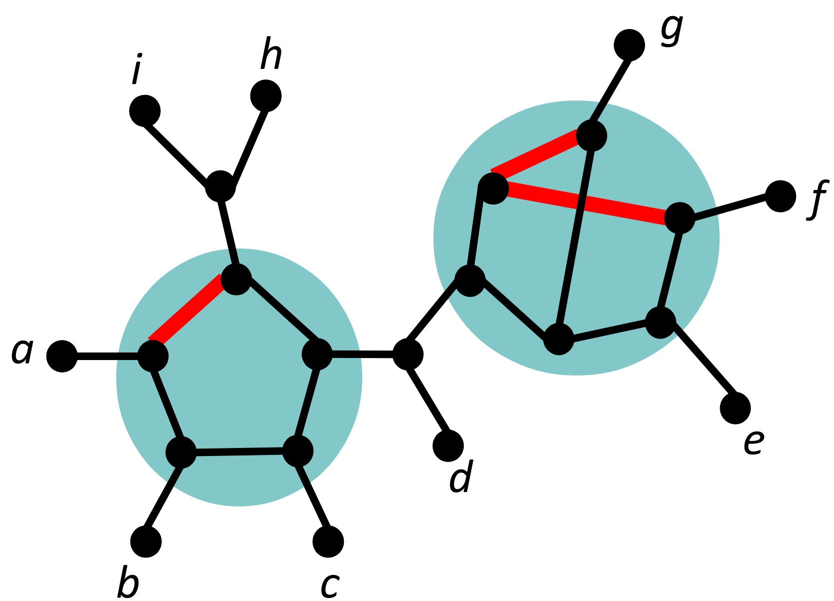
unrooted level-2 network

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

Gambette, Berry & Paul, manuscript, 2011

Unrooted level-*k* networks

level: how "far" is the network from an unrooted tree ?
small level ➡ tree structure ➡ fast algorithms

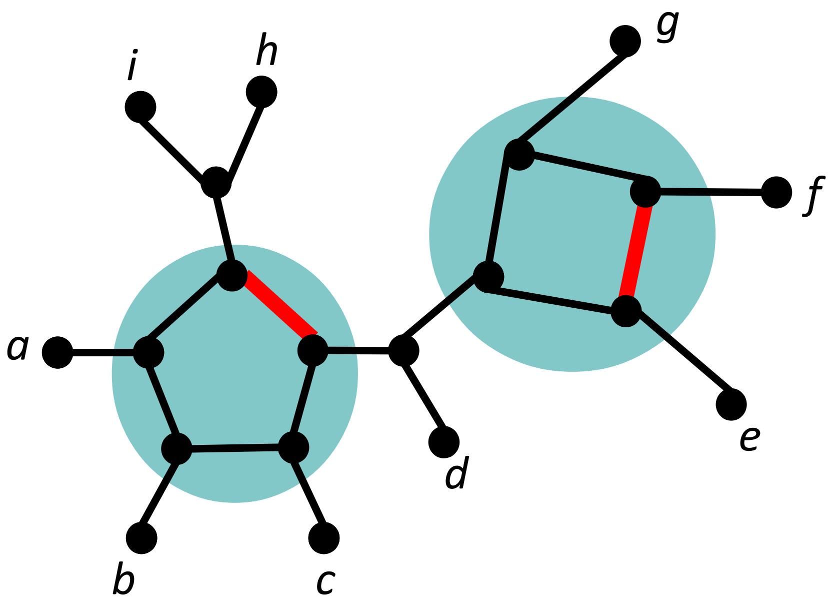


level =
maximum number of edges to remove, by *blob*, to obtain a tree.
= maximum ***cyclomatic number*** of the blobs

unrooted level-2 network

Unrooted level-*k* networks

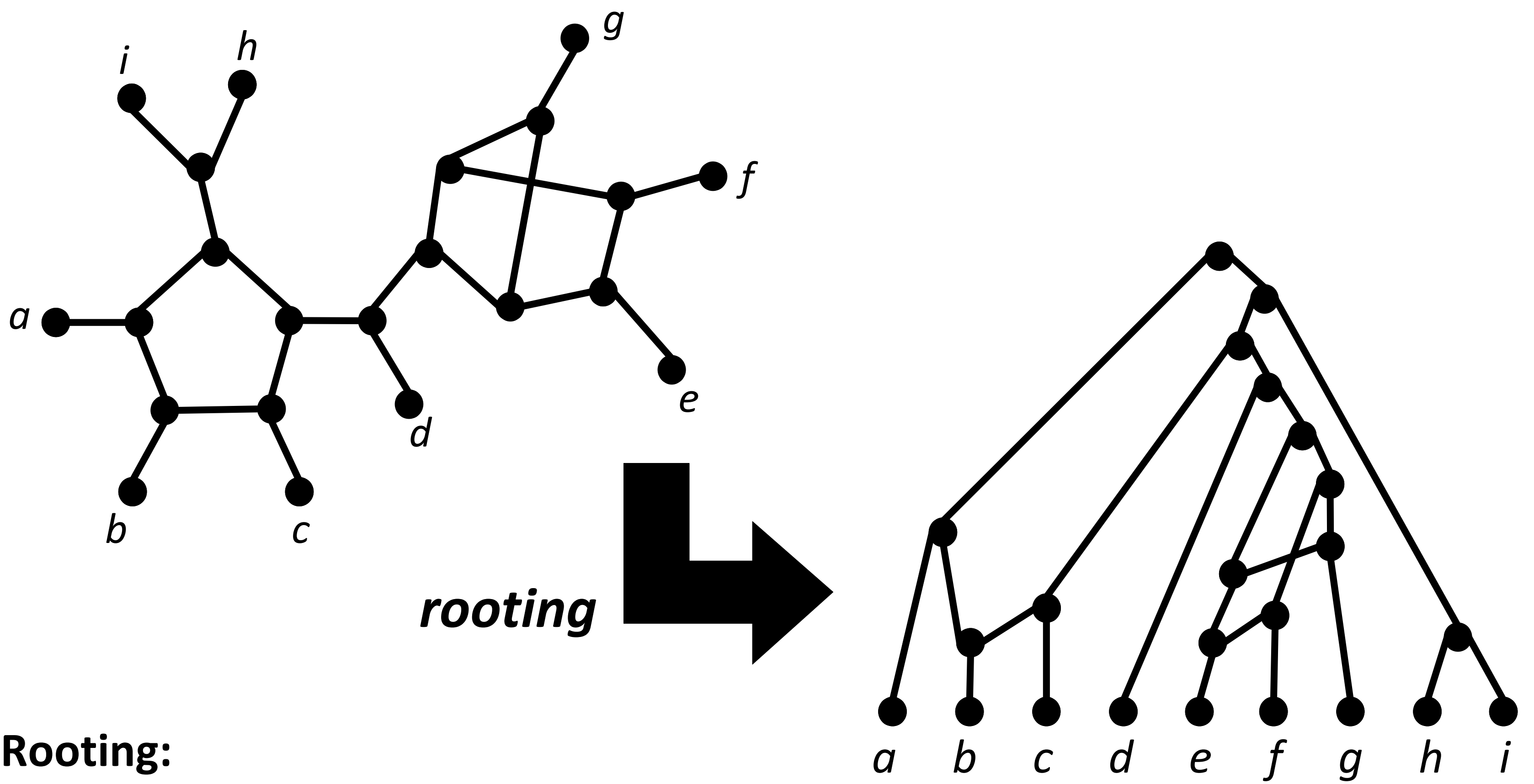
level: how "far" is the network from an unrooted tree ?
small level ➡ tree structure ➡ fast algorithms



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

unrooted level-1 network ➡ tree of cycles
(unrooted galled tree)

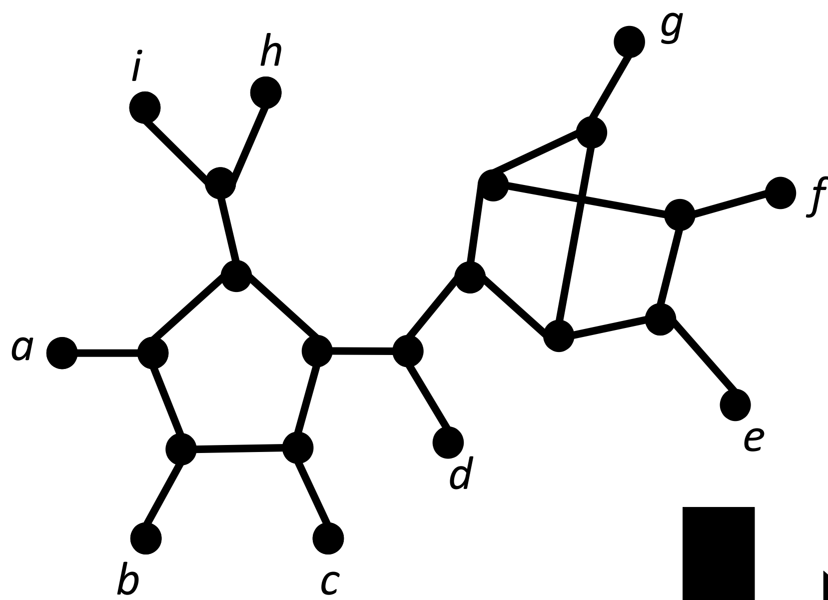
Equivalence between rooted and unrooted level

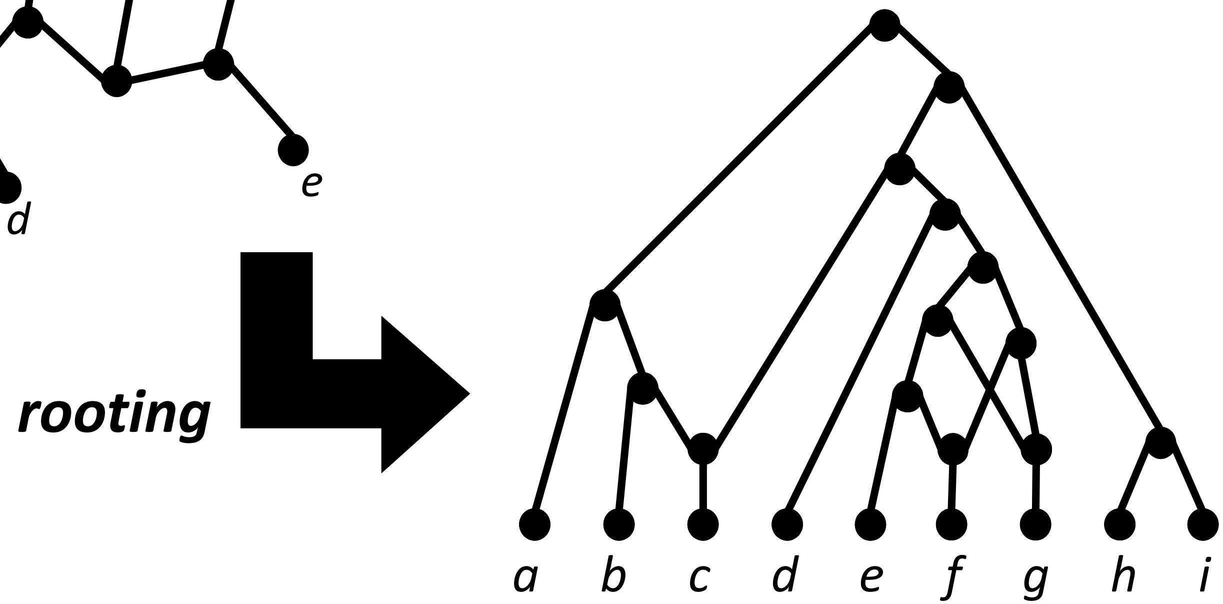


Rooting:
- choosing a root
- choosing an orientation for the edges

Gambette, Berry & Paul, manuscript, 2011

Equivalence between rooted and unrooted level

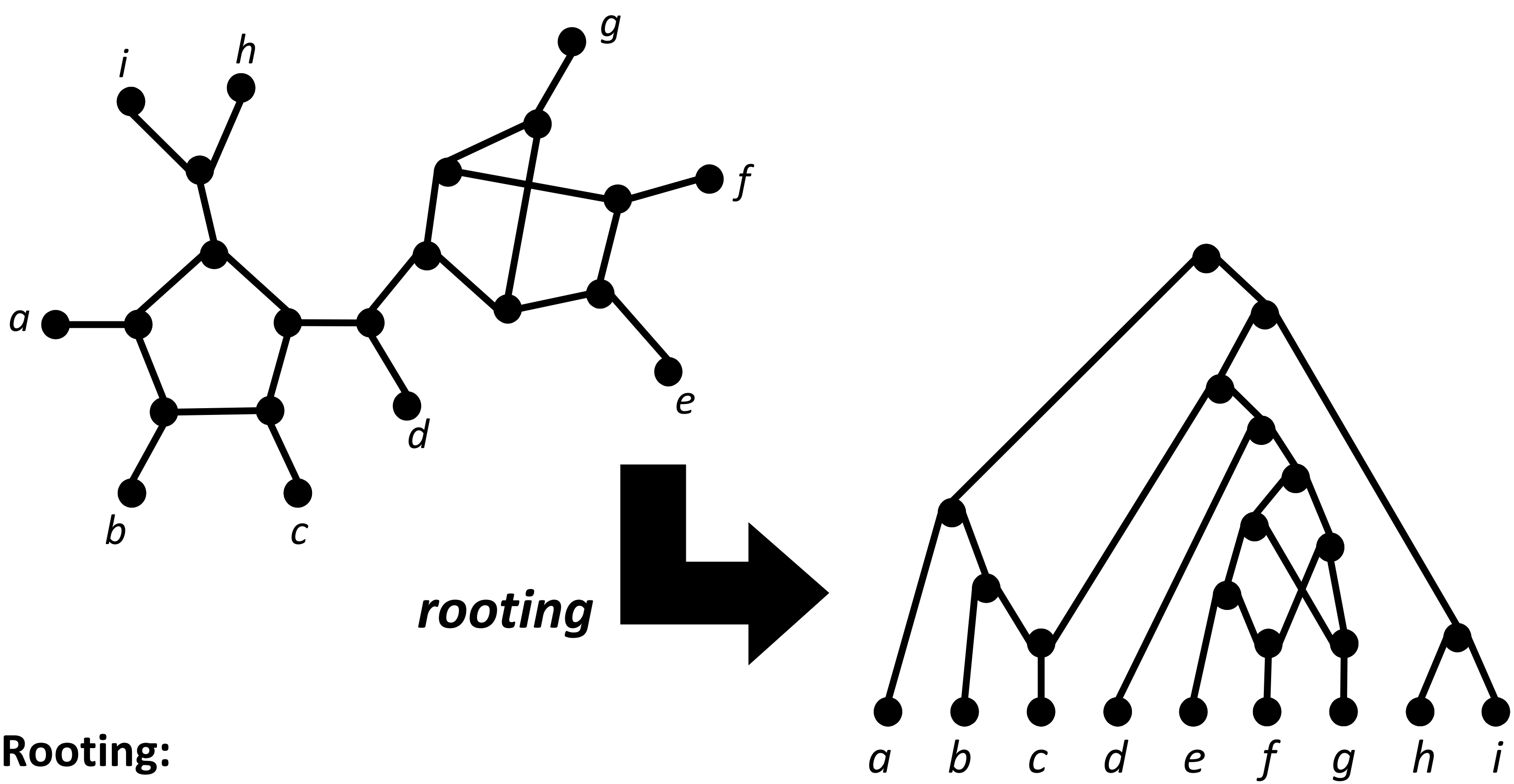




Rooting:
- choosing a root
- choosing an orientation for the edges

Gambette, Berry & Paul, manuscript, 2011

Equivalence between rooted and unrooted level

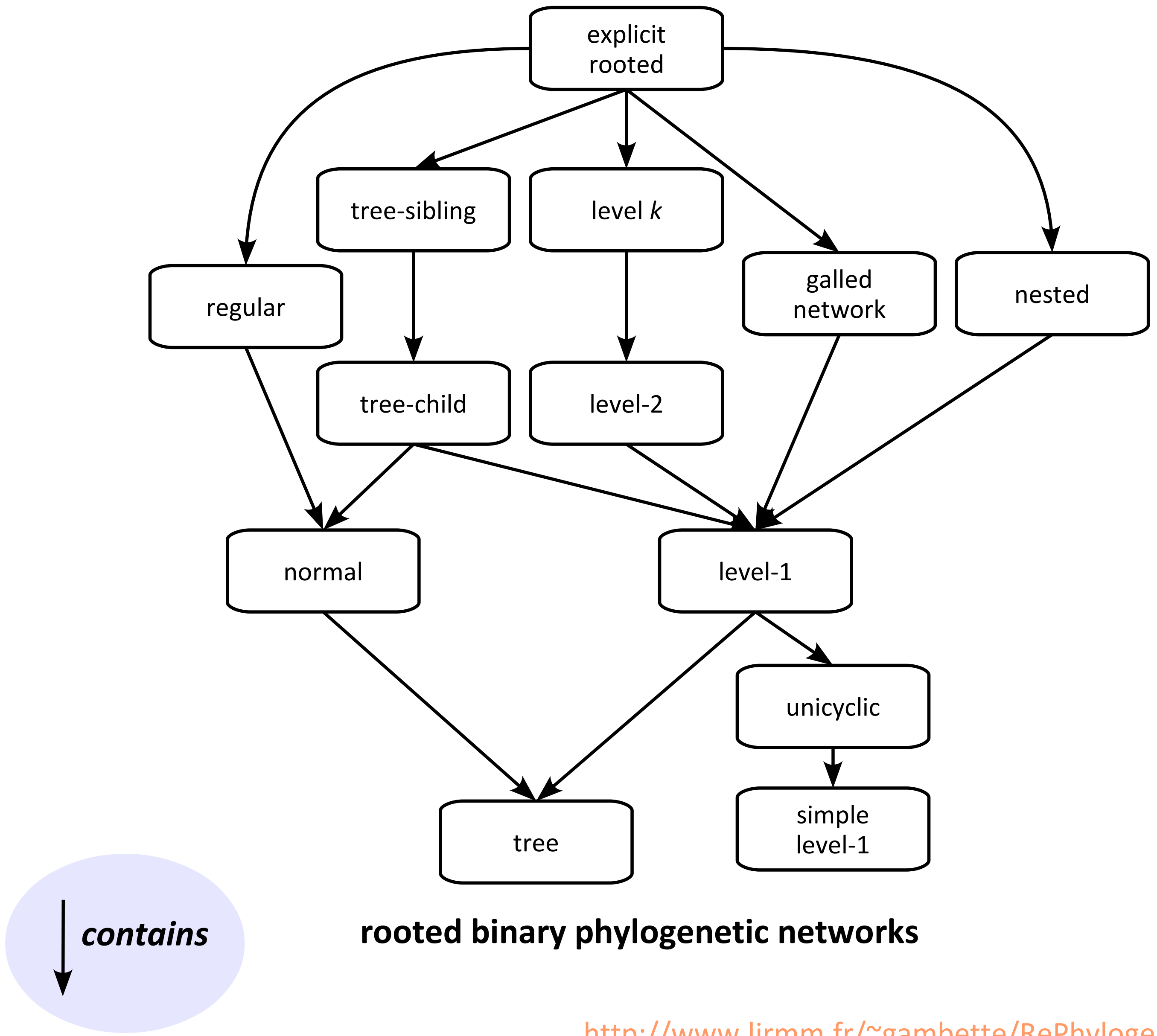


Rooting:
- choosing a root
- choosing an orientation for the edges

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

Gambette, Berry & Paul, manuscript, 2011

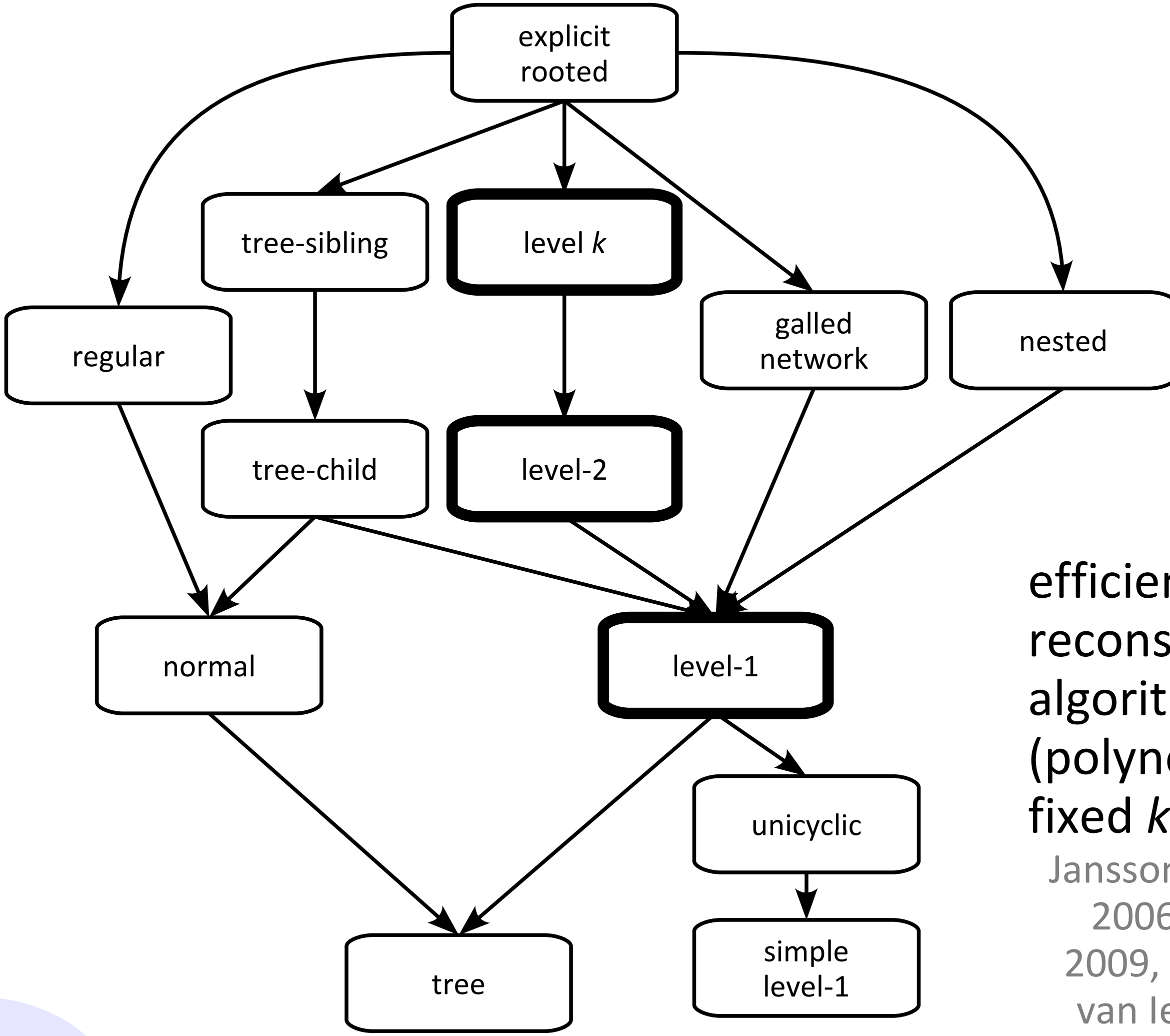
Phylogenetic network subclass hierarchy

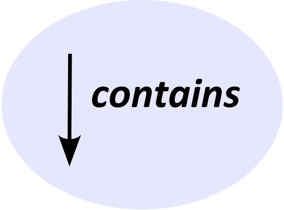


rooted binary phylogenetic networks

http://www.lirmm.fr/~gambette/RePhylogeneticNetworks.php

Phylogenetic network subclass hierarchy





rooted binary phylogenetic networks

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

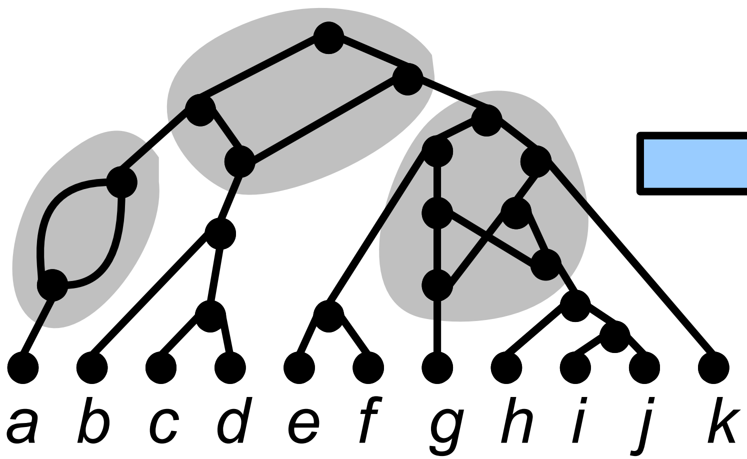
http://www.lirmm.fr/~gambette/RePhylogeneticNetworks.php

Plan

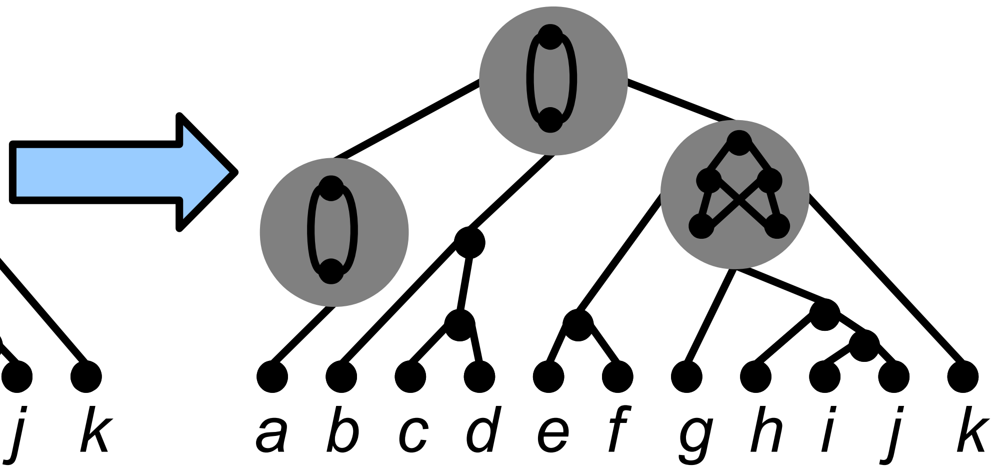
- Phylogenetic motivations
- Level-*k* network reconstruction
- Structure of level-*k* networks
- Counting level-1 and 2 networks

Decomposition of level-*k* networks

We formalize the decomposition into blobs:



N, level-*k* network.

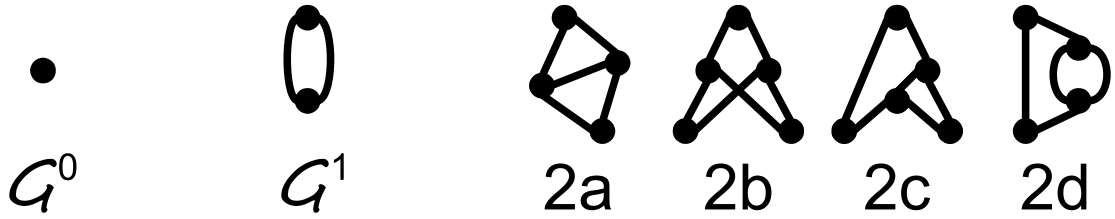


N decomposed as a **tree** of simple graph patterns: **generators**.

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

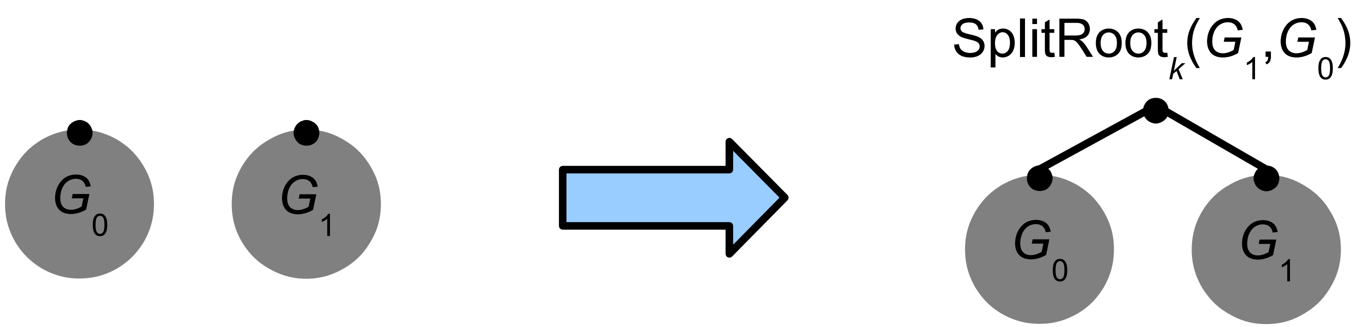
there exists a sequence $(l_j)_{j\in[1,r]}$ of r locations
(arcs or reticulation vertices of outdegree 0)
and a sequence $(G_j)_{j\in[0,r]}$ of generators of level at most k, such that:
- $N = \text{Attach}_k(l_r, G_r, \text{Attach}_k(\ldots \text{Attach}_k(l_2, G_2, \text{Attach}_k(l_1, G_1, G_0))\ldots))$,
- or $N = \text{Attach}_k(l_r, G_r, \text{Attach}_k(\ldots \text{Attach}_k(l_2, G_2, \text{SplitRoot}_k(G_1, G_0))\ldots))$.

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



Decomposition theorem of level-k networks

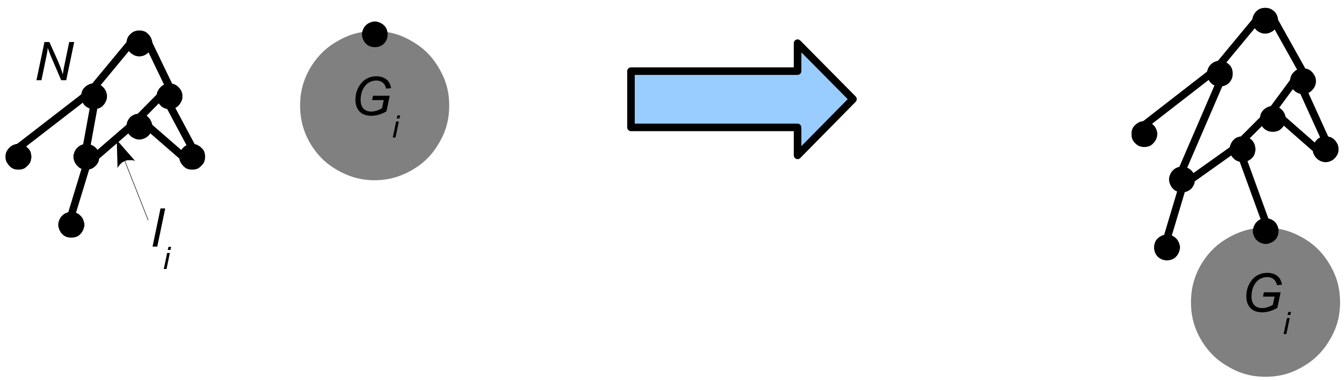
N is a level-*k* network

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:

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

l_i is an arc of *N* $\mathrm{Attach}_k(l_i, G_i, N)$



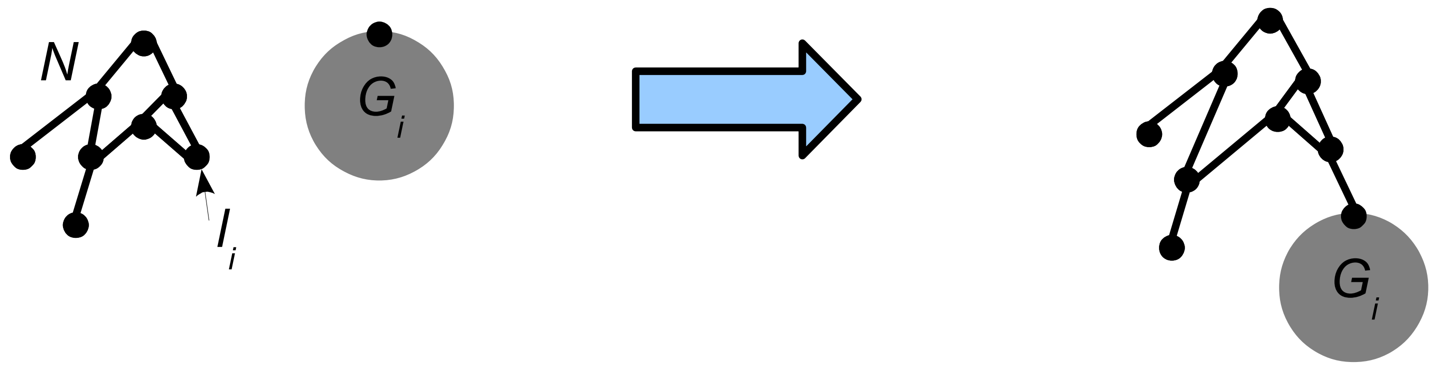
Decomposition theorem of level-*k* networks

N is a level-*k* network

iff

there exists a sequence $(l_j)_{j\in[1,r]}$ of *r* locations
(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:
- $N = Attach_k(l_r,G_r,Attach_k(\ldots\ Attach_k(l_2,G_2,Attach_k(l_1,G_1,G_0))\ldots))$,
- or $N = Attach_k(l_r,G_r,Attach_k(\ldots\ Attach_k(l_2,G_2,SplitRoot_k(G_1,G_0))\ldots))$.

l_i is a reticulation vertex of *N* $\qquad$ $Attach_k(l_i,G_i,N)$



Decomposition theorem of level-*k* networks

N is a level-*k* network

iff

there exists a sequence $(l_j)_{j\epsilon[1,r]}$ of *r* locations
(arcs or reticulation vertices of outdegree 0)
and a sequence $(G_j)_{j\epsilon[0,r]}$ of generators of level at most *k*, such that:
- N = $\text{Attach}_k(l_r, G_r, \text{Attach}_k(\ldots\ \text{Attach}_k(l_2, G_2, \text{Attach}_k(l_1, G_1, G_0))\ldots))$,
- or N = $\text{Attach}_k(l_r, G_r, \text{Attach}_k(\ldots\ \text{Attach}_k(l_2, G_2, \text{SplitRoot}_k(G_1, G_0))\ldots))$.

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.

Integer Sequences

Greetings from The On-Line Encyclopedia of Integer Sequences!

1,4,65 Search 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)

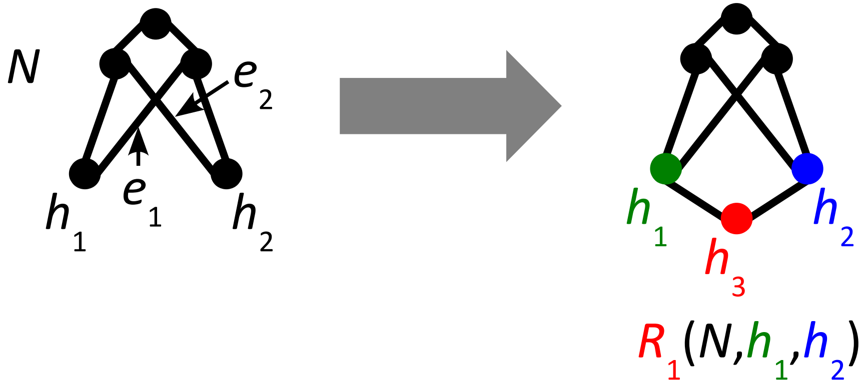
OFFSET 0,3

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

CROSSREFS Sequence in context: A119601 A058438 A041119 this_sequence A025585 A048828

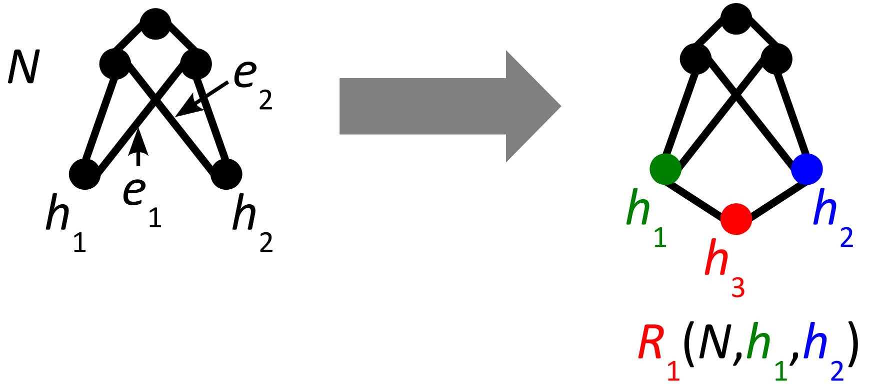
Construction of level-*k* generators

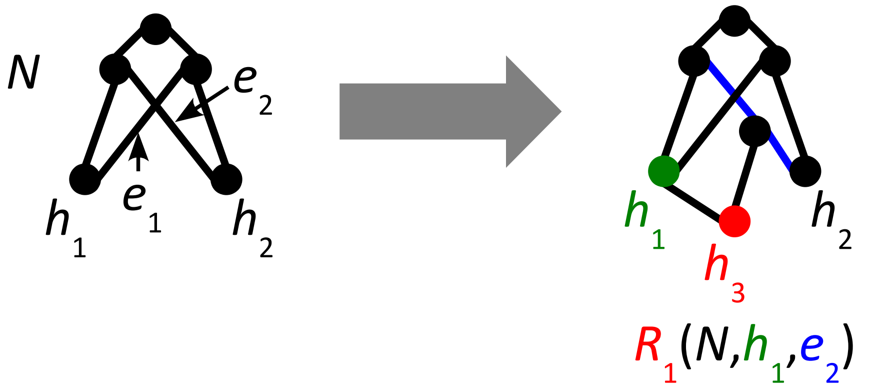
Construction rules of level-(k+1) generators from level-k generators



Construction of level-*k* generators

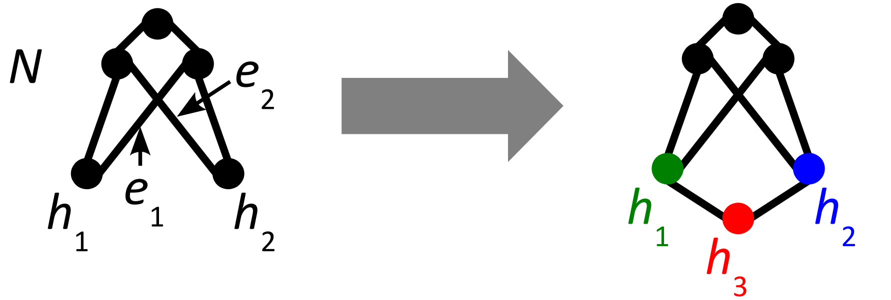
Construction rules of level-(k+1) generators from level-k generators



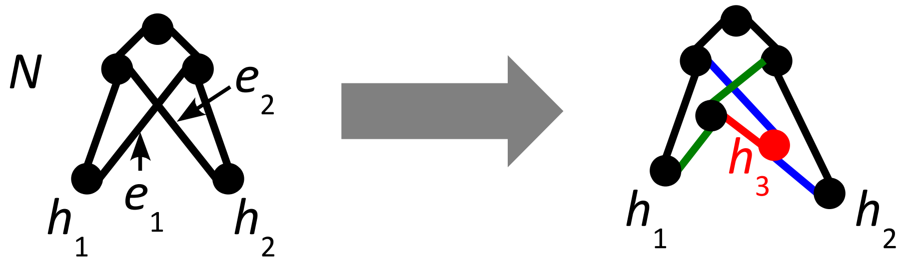


Construction of level-*k* generators

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



$R_1(N,h_1,h_2)$



$R_2(N,e_1,e_2)$

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

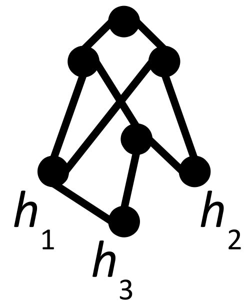
Practical corollary:

$$g_4 < 28350$$

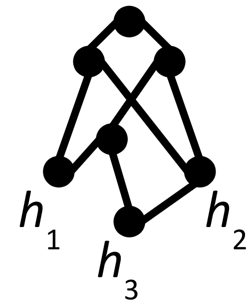
→ it is possible to enumerate all level-4 generators.

Construction of level-*k* generators

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



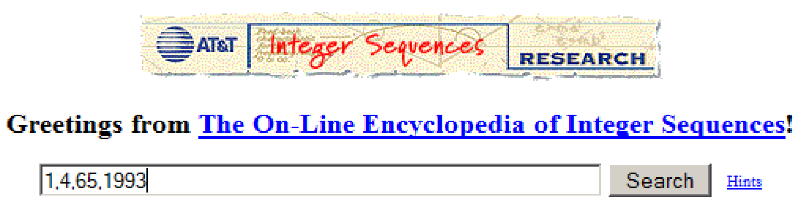
$R_1(N,h_1,e_2)$



$R_1(N,h_2,e_1)$

→ difficult to count

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



Search: **1, 4, 65, 1993**

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

Lower bound on the number of level-k generators

Lower bound:

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

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

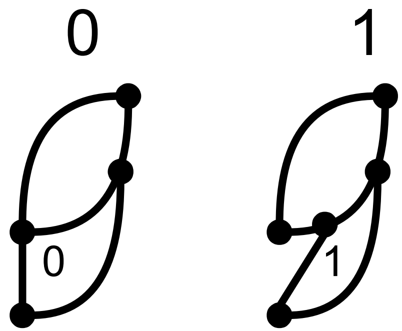
Lower bound:

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

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

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

$k = 1$



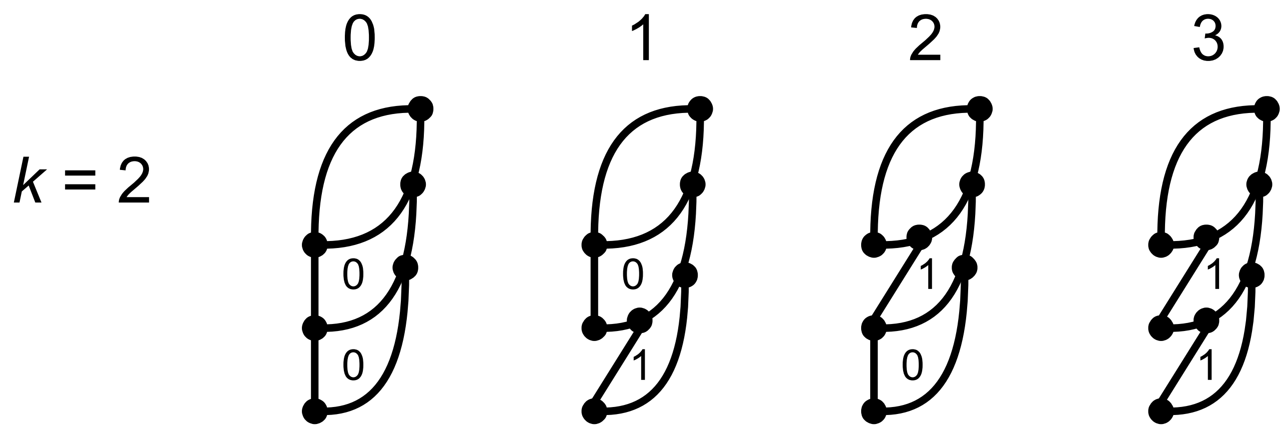
Lower bound on the number of level-*k* generators

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

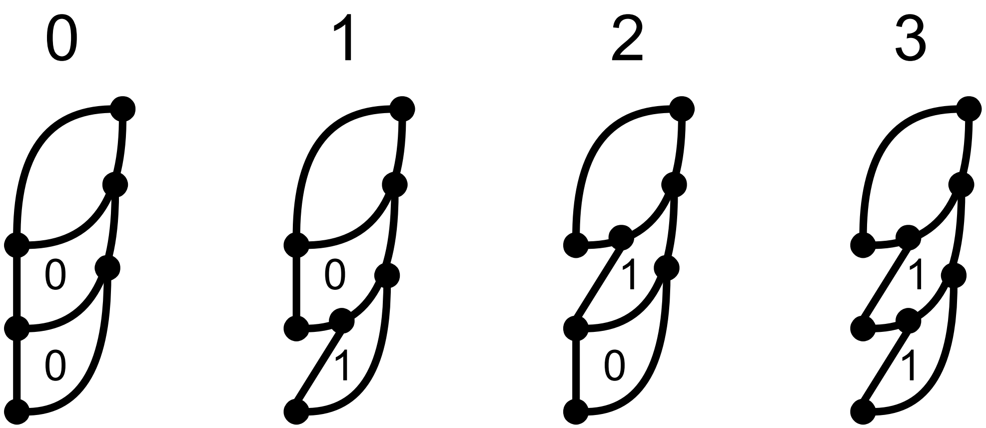
Lower bound:

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

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

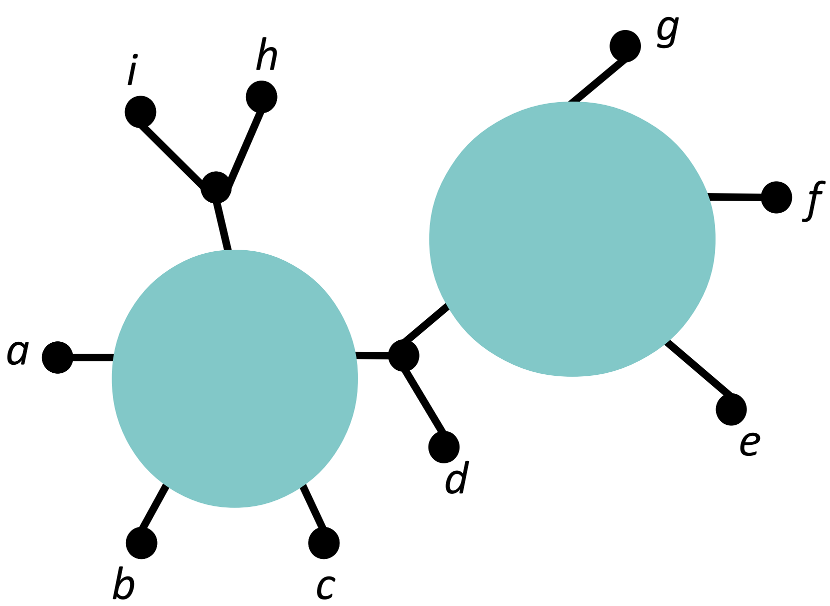
Idea:
Code every number between 0 and 2^{k-1}-1 by a level-*k* generator.

$k = 2$



Practical corollary:
Phylogenetic reconstruction algorithms based on generators are not practical.

Unrooted level-*k* networks

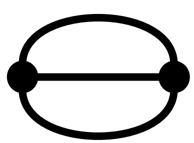


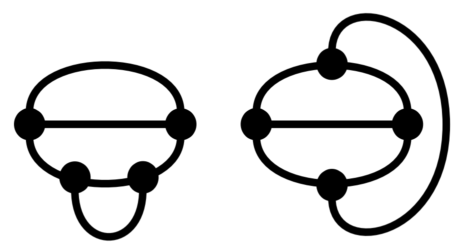
level =
maximum number of edges to remove, by *blob*, to obtain a tree.

unrooted level-*k* network ➡ tree of blobs

➡ tree of **generators** of level ≤*k*

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

level-2 generator 

 level-3 generators

Berry, Bouvel, Gambette & Paul, manuscript, 2011

Plan

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

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

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.

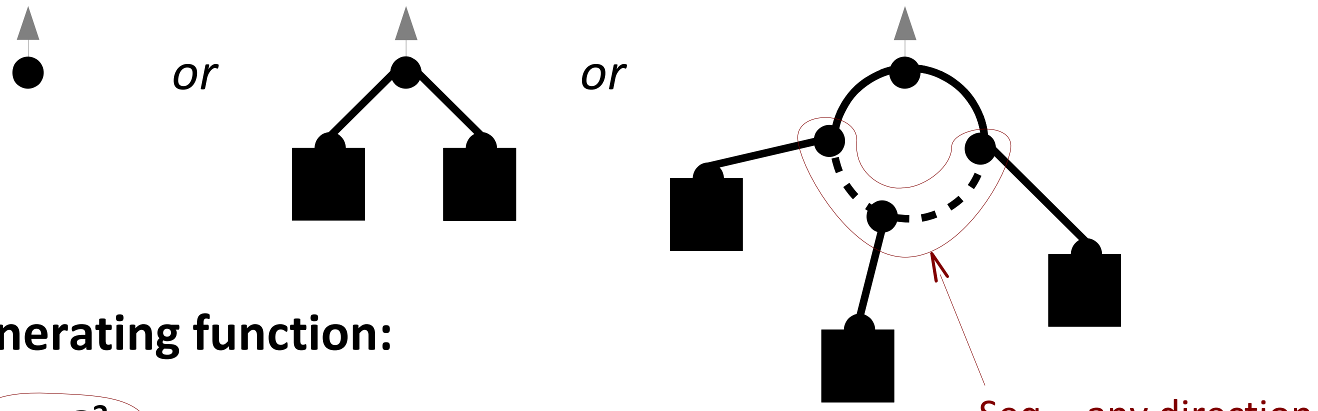
Semple & Steel, *TCBB*, 2006

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.

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



Exponential generating function:

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

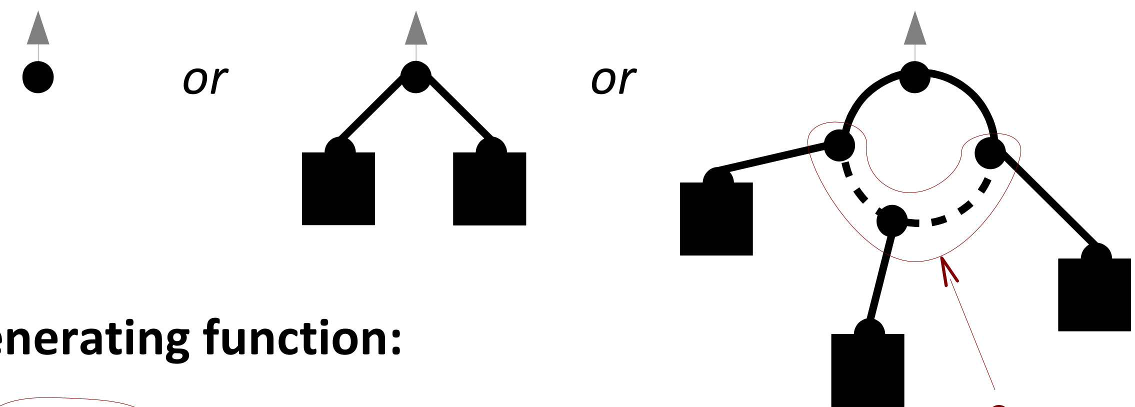
Semple & Steel, *TCBB*, 2006

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.

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



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

Exponential generating function:

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

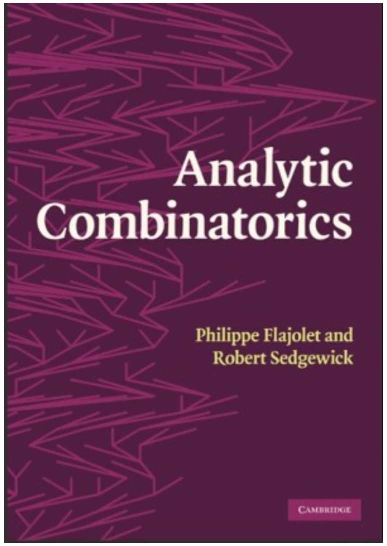
Semple & Steel, *TCBB*, 2006

Counting labeled unrooted level-1 networks

Exponential generating function:

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

Using the Singular Inversion Theorem (Theorem VI.6 of



):

$$\frac{y(n)}{n!} \approx 0,1467\frac{5,1376^n}{\sqrt{\pi n^3}} \approx 0,0827\frac{5,1376^n}{\sqrt{n^3}}$$

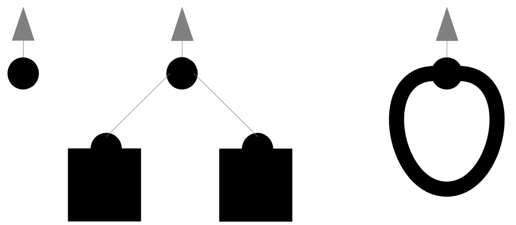
so $y(n) \approx 0,2074\frac{n^{n-1}}{1,8904^n}$

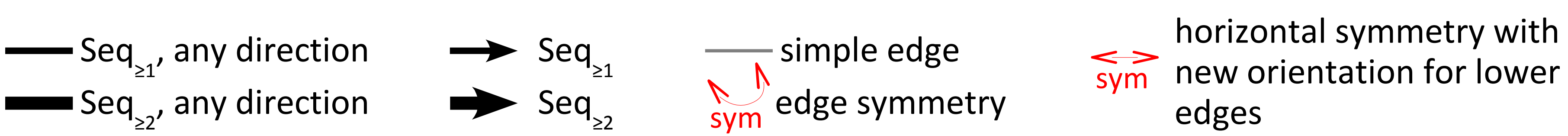
Berry, Bouvel, Gambette & Paul, manuscript, 2011

Counting labeled unrooted level-2 networks

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

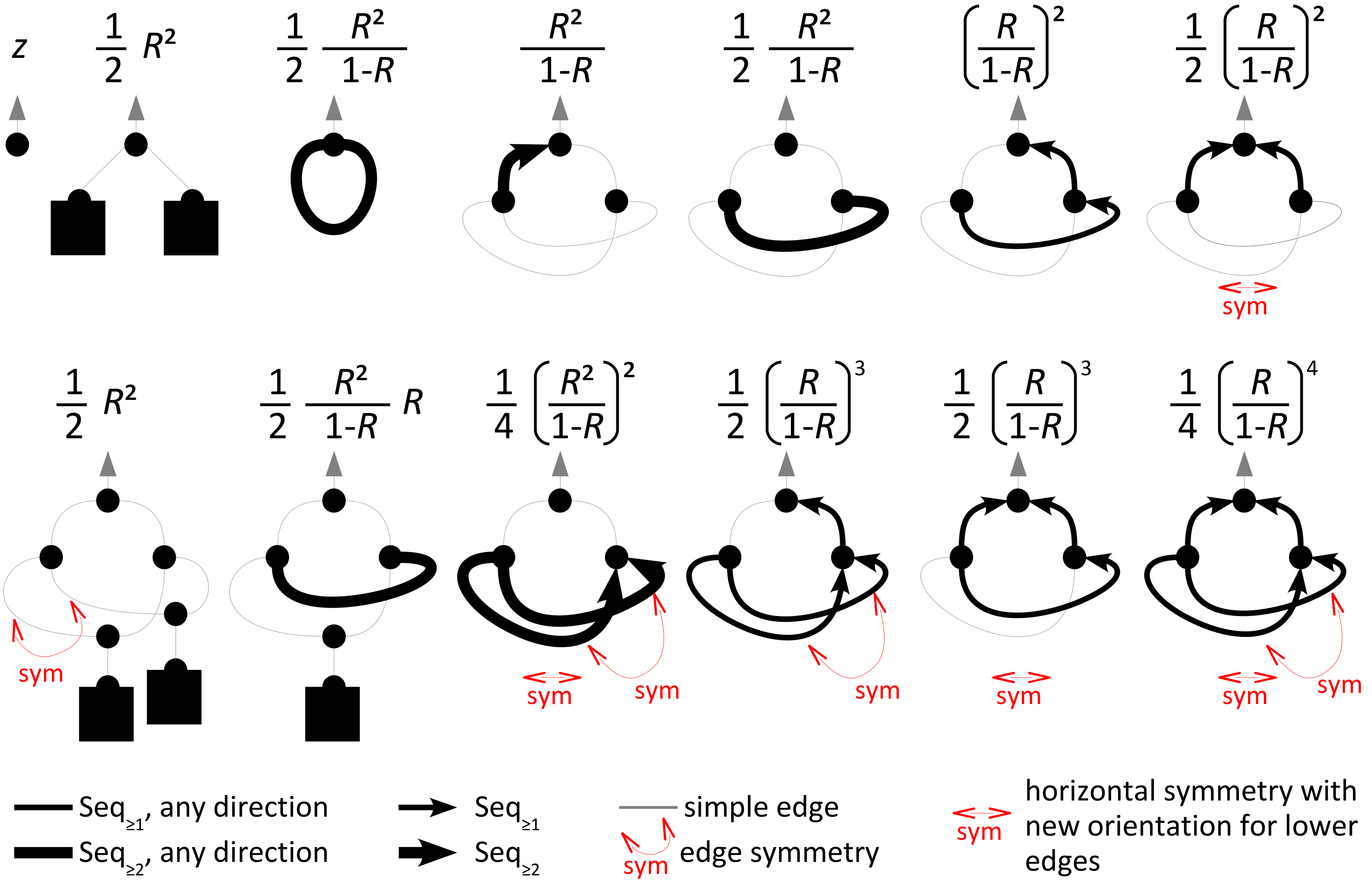
z $\qquad \frac{1}{2} R^2 \qquad \frac{1}{2} \frac{R^2}{1-R}$ $\qquad$ *or...*





Counting labeled unrooted level-2 networks

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



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:

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

Berry, Bouvel, Gambette & Paul, manuscript, 2011

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:

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

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

Berry, Bouvel, Gambette & Paul, manuscript, 2011

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:

$$R = z\phi(R) \text{ where } \phi(R) = \frac{1}{1 - \frac{4r^5 - 21r^4 + 46r^3 - 46r^2 + 18r}{4(r-1)^4}}.$$

Lagrange inversion:

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

Taylor expansions + Newton formula:

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

Berry, Bouvel, Gambette & Paul, manuscript, 2011

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: $\approx 0.207 \dfrac{n^{n-1}}{1.890^n}$

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

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	1 071 720	100 461 195

Berry, Bouvel, Gambette & Paul, manuscript, 2011

Thank you for your attention!

Co-authors of these results

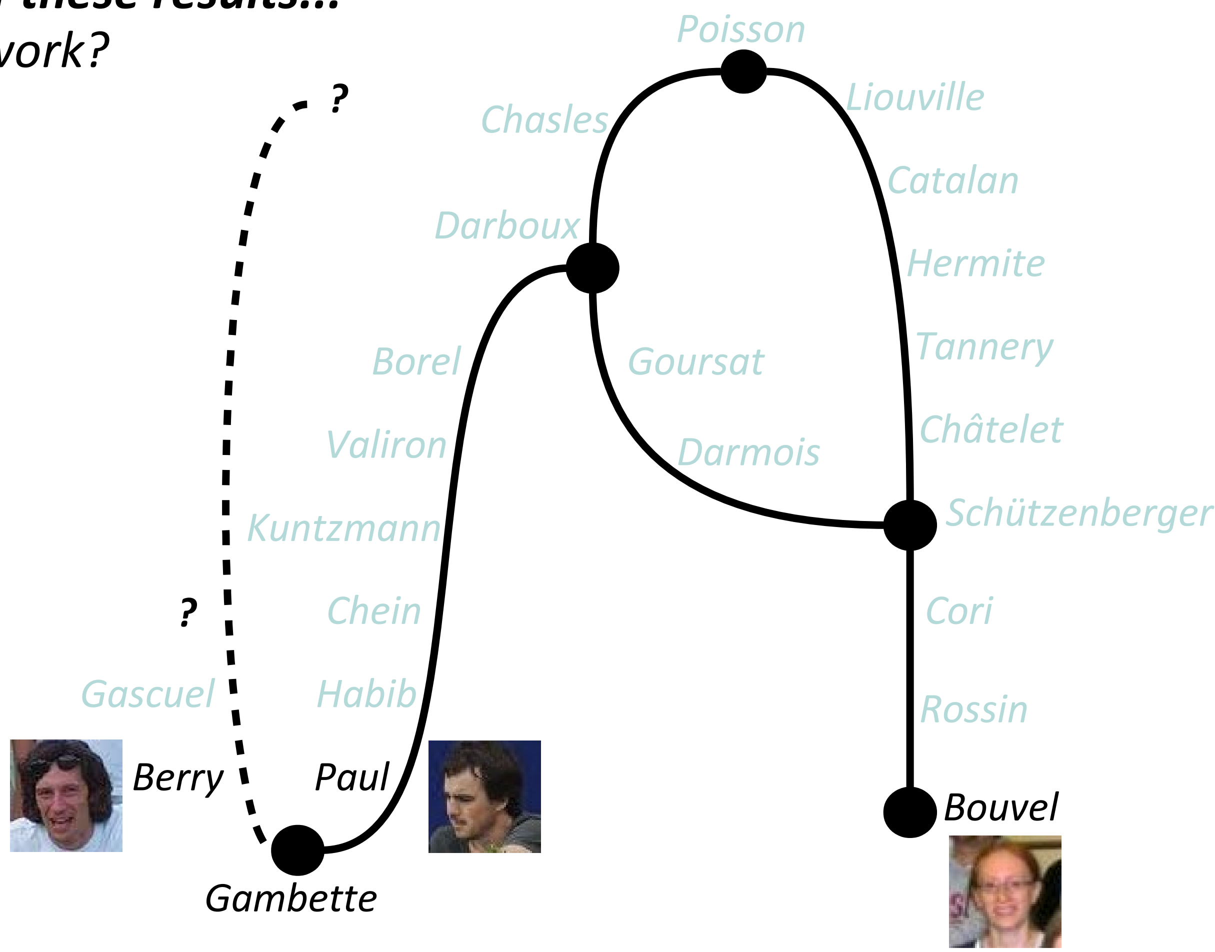
Vincent Berry & Christophe Paul (LIRMM, Montpellier)
Mathilde Bouvel (LABRI, Bordeaux)

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?

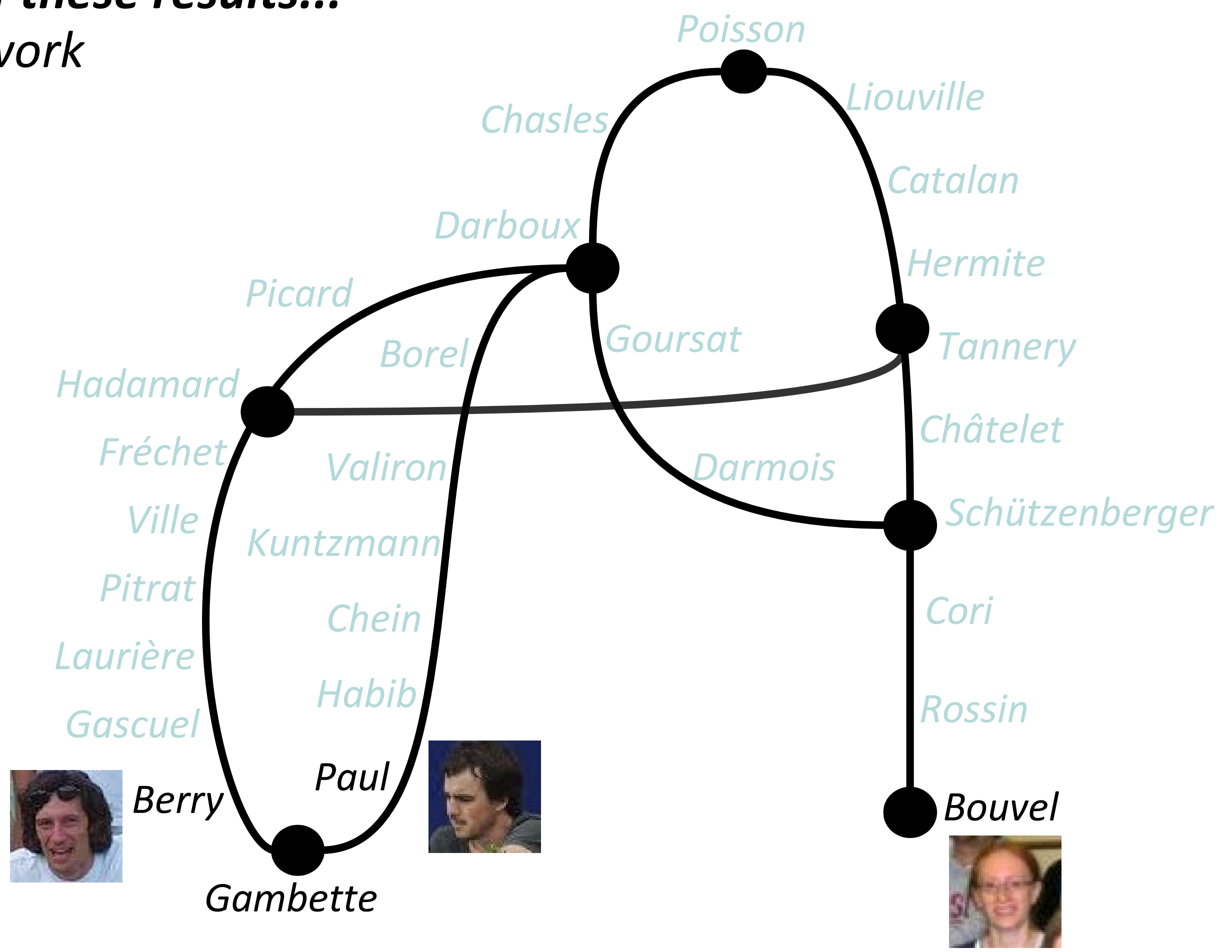


The Mathematics Genealogy

Thank you for your attention!

Co-authors of these results...

A level-3 network



The Mathematics Genealogy