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Fold and shape of leaves

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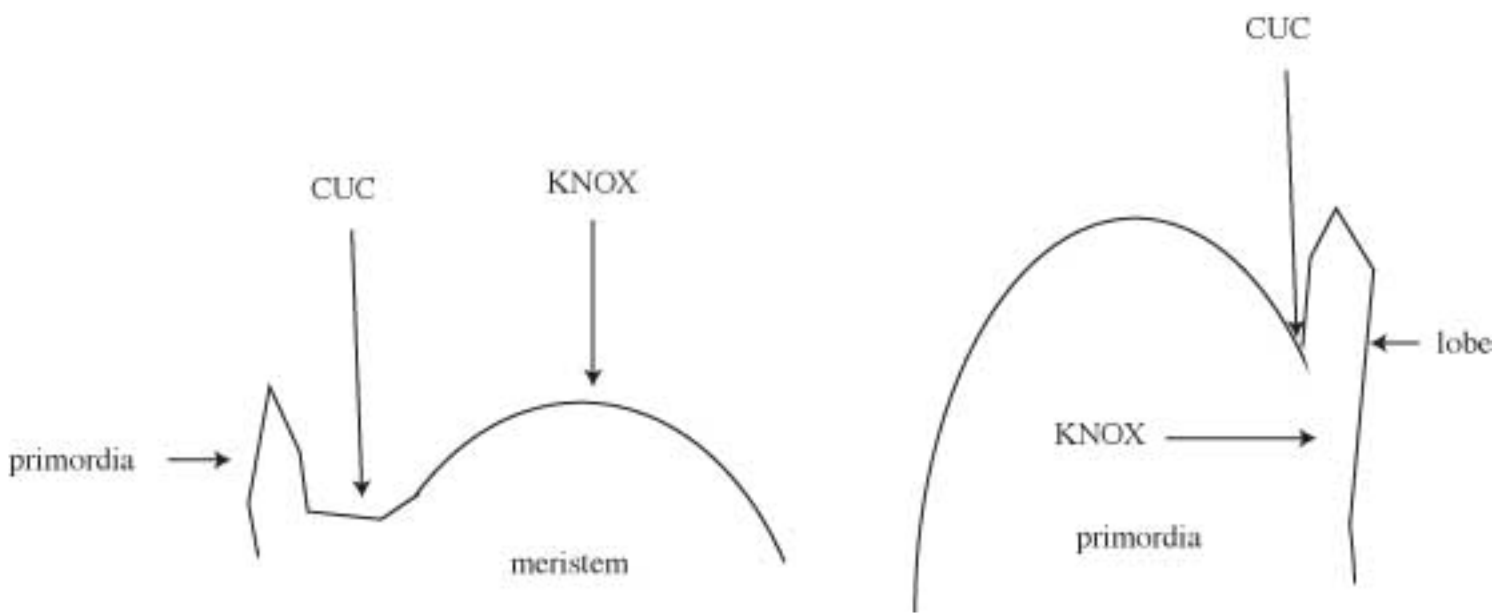
A small introduction to lobe development

From a genetic point of view, a lobe behaves as a primordium, which grows on the primordium itself.

The same genes (CUC and KNOX) are expressed in both case.



Lobe initiation begins to be understood.

What coordinates the size of different lobes to create the final leaf shape ?
Something crucial has been forgotten: a lot of leaves develop folded in the bud.
The shape of these leaves is determined at this stage.

Acer sacharinum

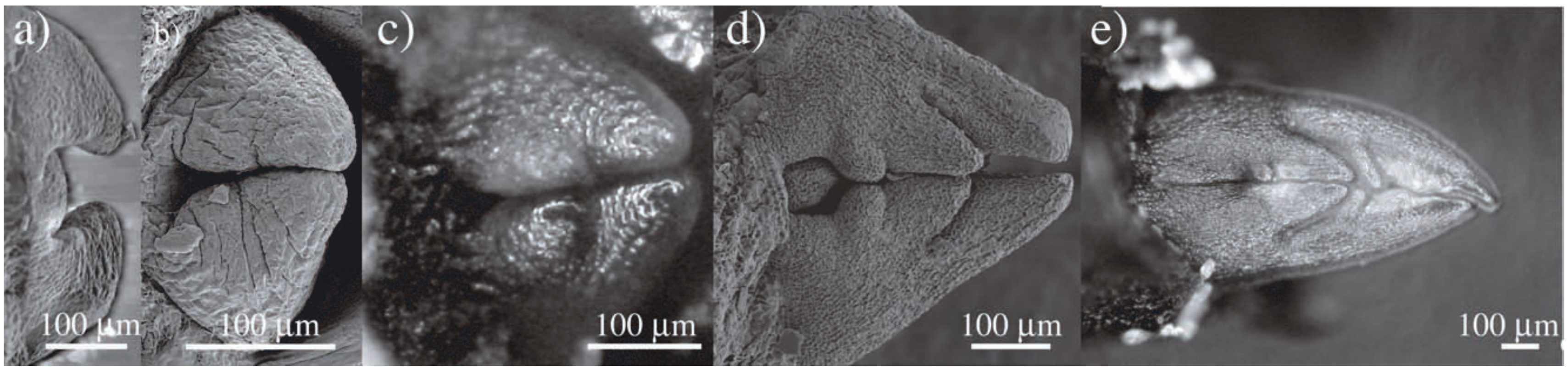
Carpinus betulus

Tetrapanax papyrifer

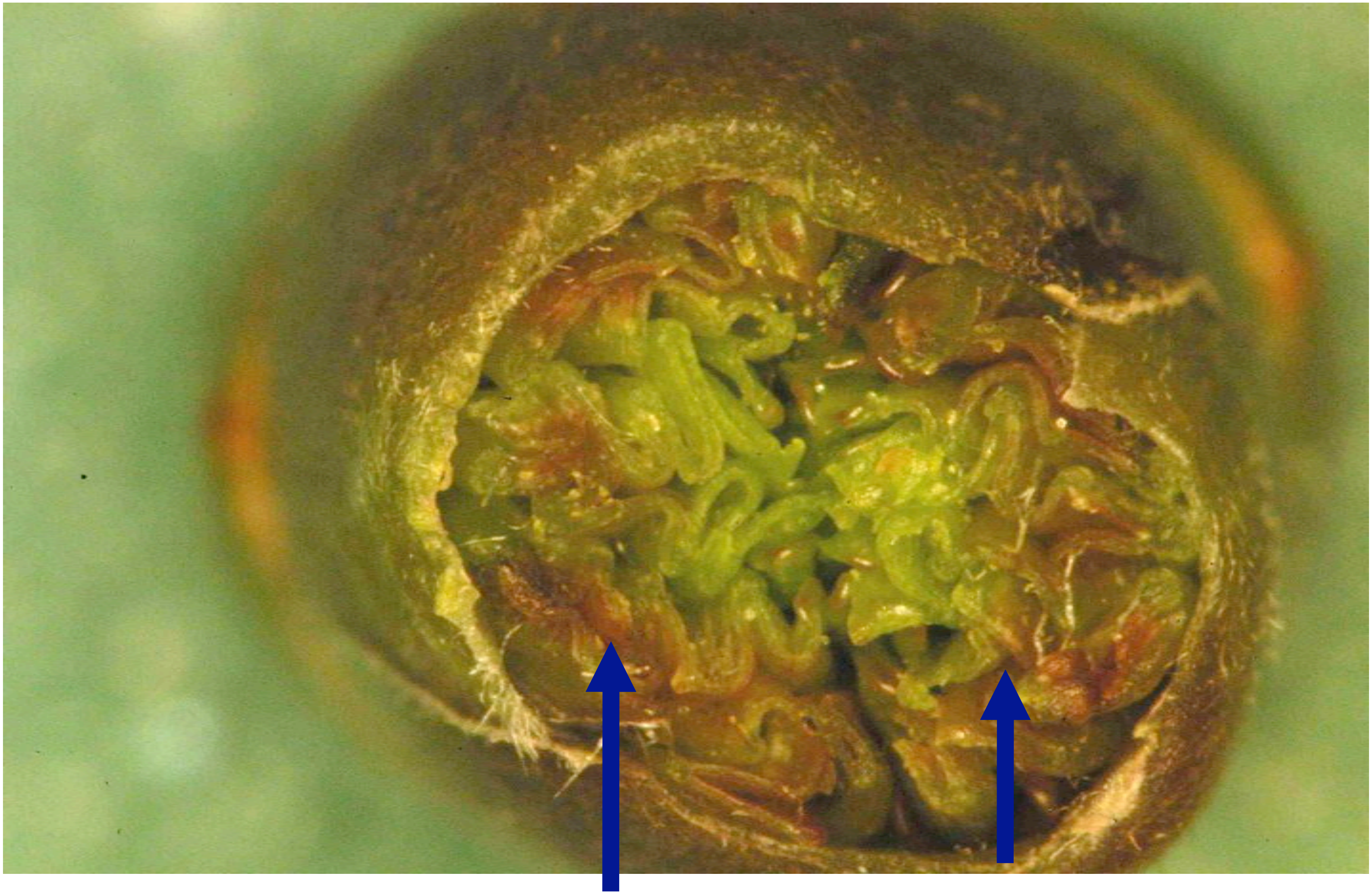
Ficus cariaca

Acer pseudoplatanus

Successive stages of the development of the *Acer Pseudoplatanus* leaf



Transversal cut of an *Acer pseudoplatanus* bud

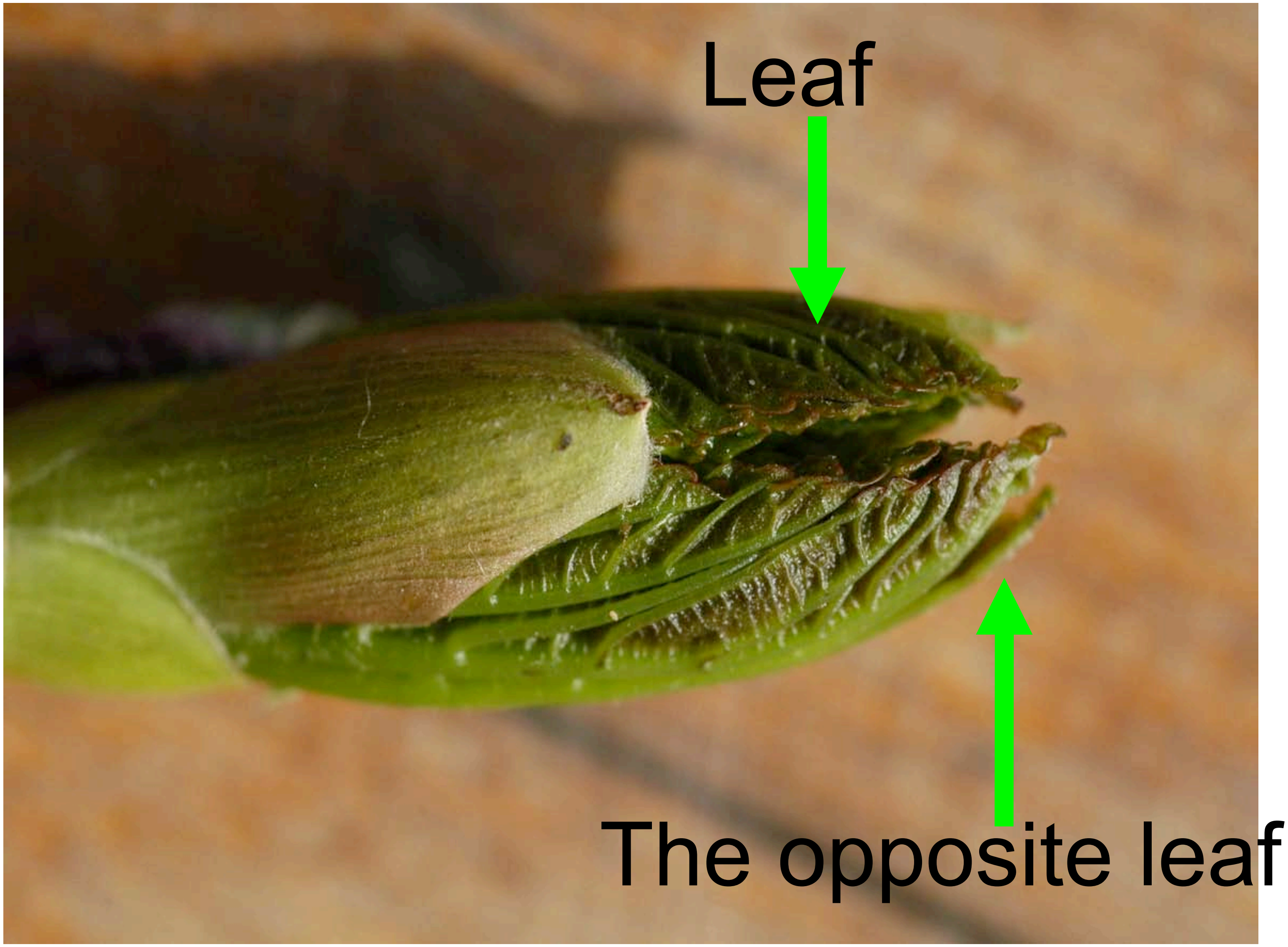


A leaf

The opposite leaf

Leaf form:
The kirigami scenario

Being folded with its edge on a plane strongly constrains leaf shape



An *Acer campestre* Leaf

Each fold corresponds either to a sinus either to a lobe.


Acer pseudoplatanus
Murus platanifolium
Pelargonium cuculatum
Ribes nigrum
Ricin

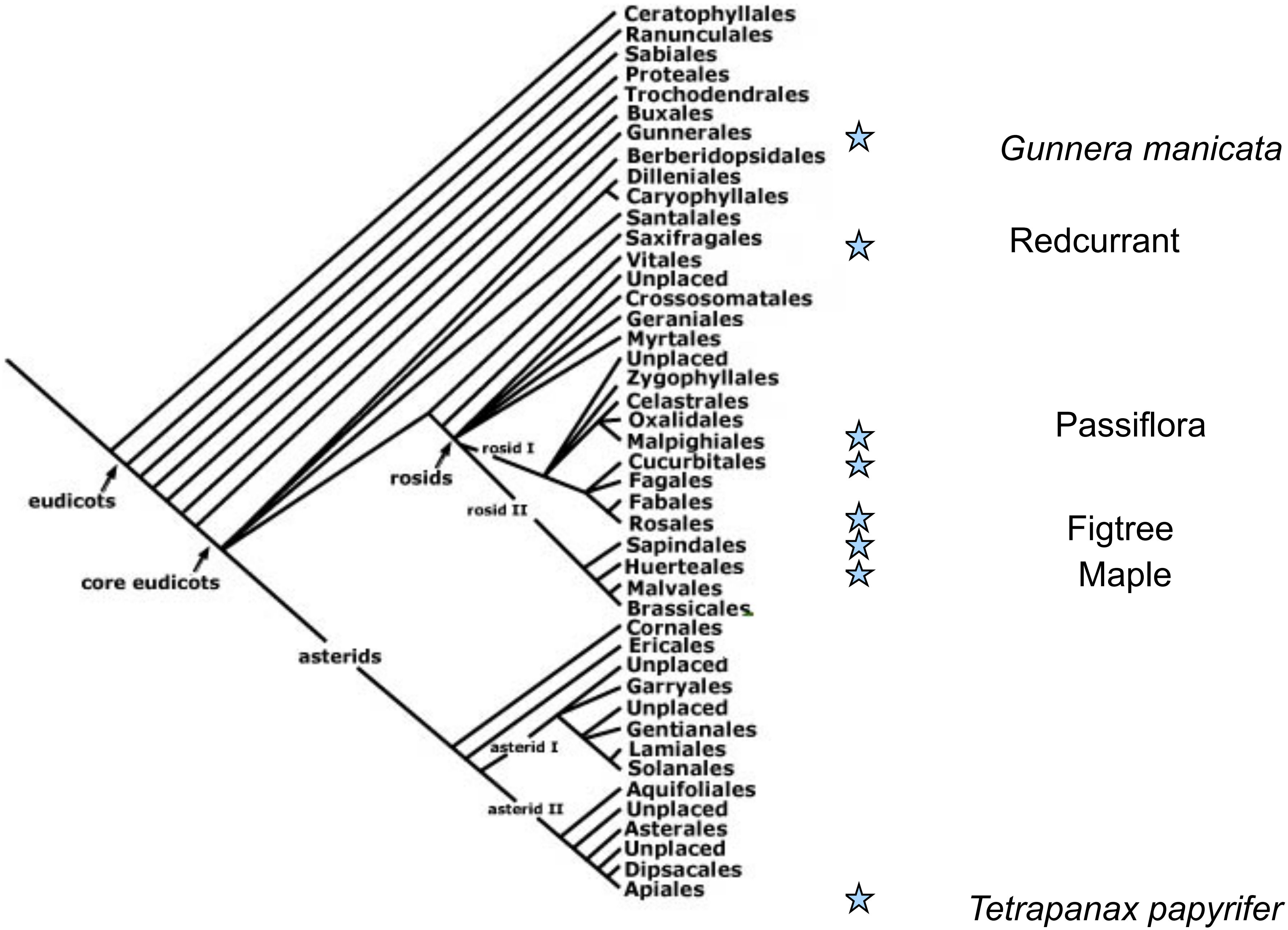
Many leaves grow folded in the bud

Pelargonium cuculatum *Malva sylvestra*

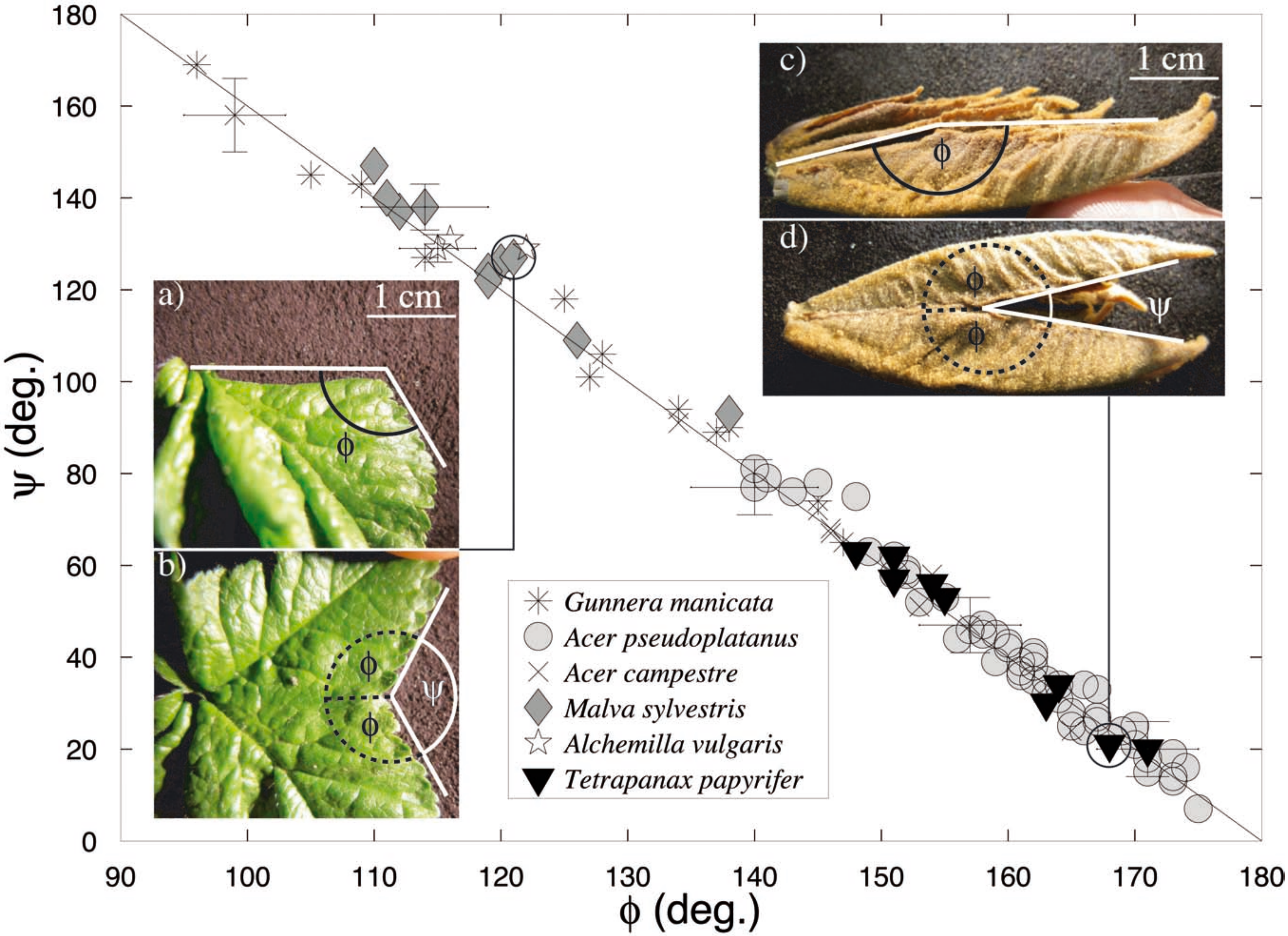
Ribes nigrum

Gunera manicata Passiflora *Tetrapanax papyrifer*

Phylogenetic tree of eudicots (APG 2003)



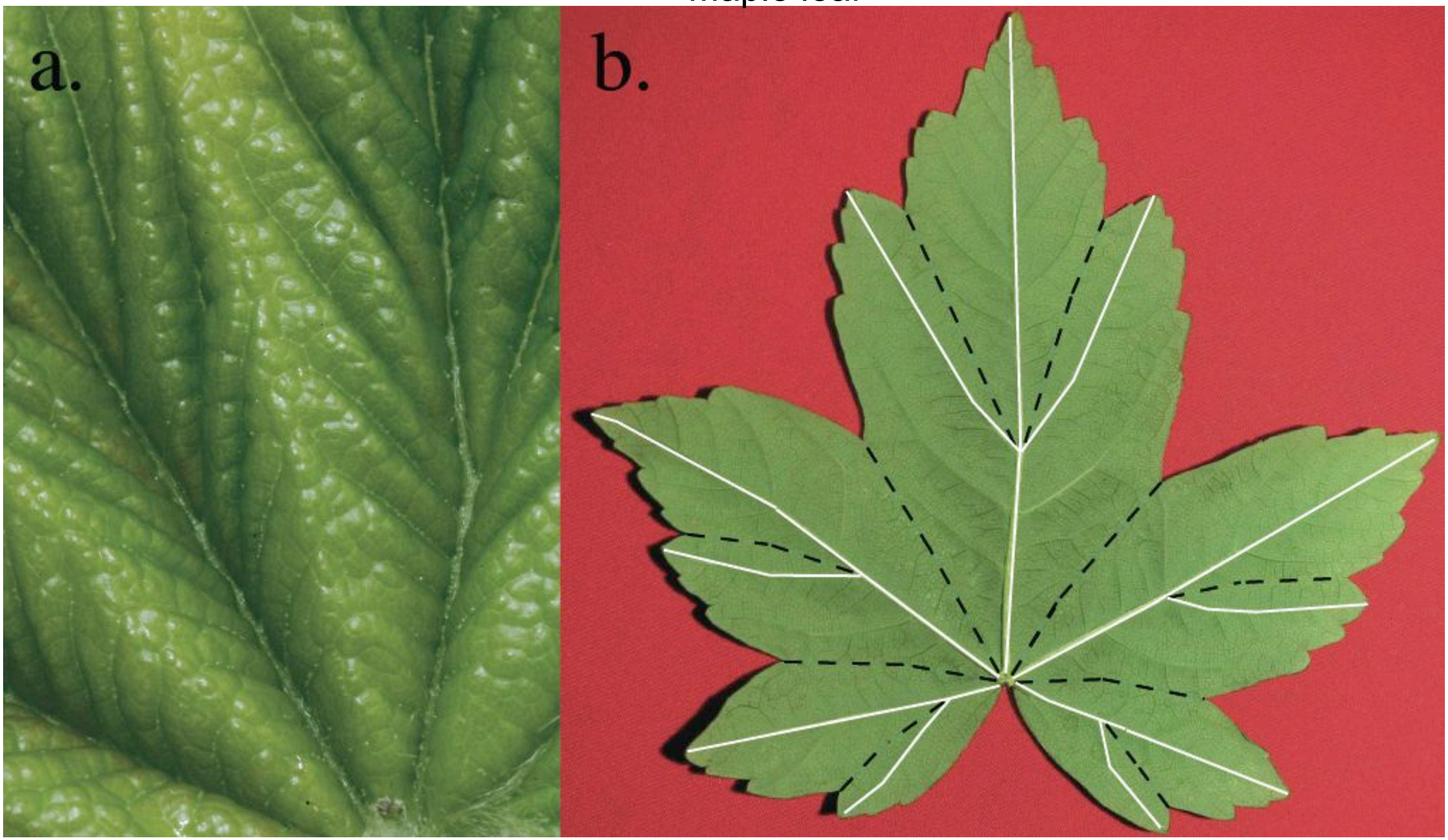
Kirigami leaves are very diverse



How can we recognise the folds on a mature leaf ?

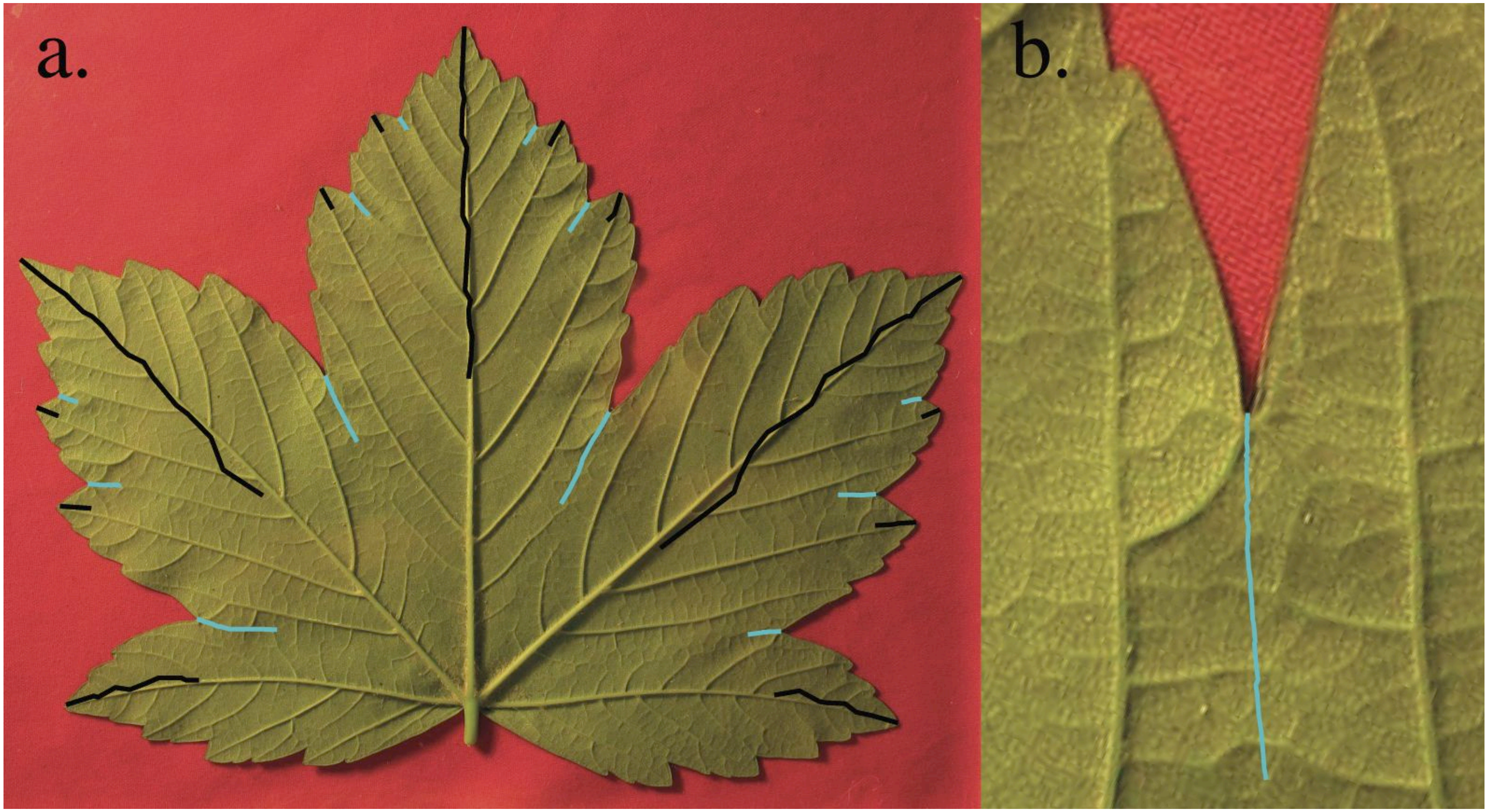
Maple antifold

Maple leaf



Secondary veins joins along the antifold. You can find the antifold even on a mature leaf.

Folds are axes of symmetry of the margin



Black line = medial axis of lobe
Blue line = medial axis of sinus

The medial axes of lobes correspond to the central veins.
The medial axes of sinuses correspond to the place where secondary veins join.

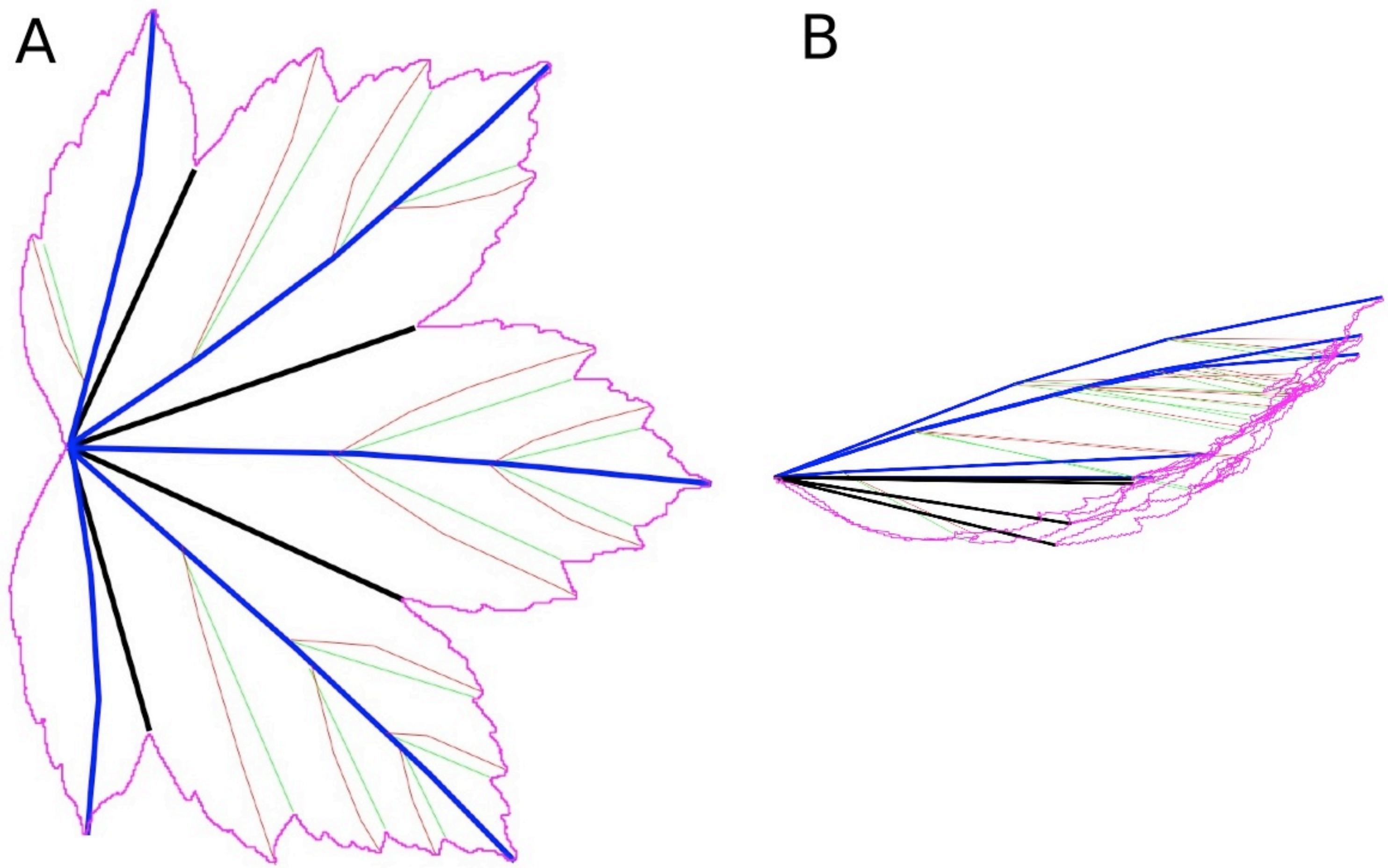
An impressive observation

Acer saccharinum

A folded leaf. The shape is very simple.

The same leaf once unfolded.
The shape is very branched.
It can still be refolded on a plane.

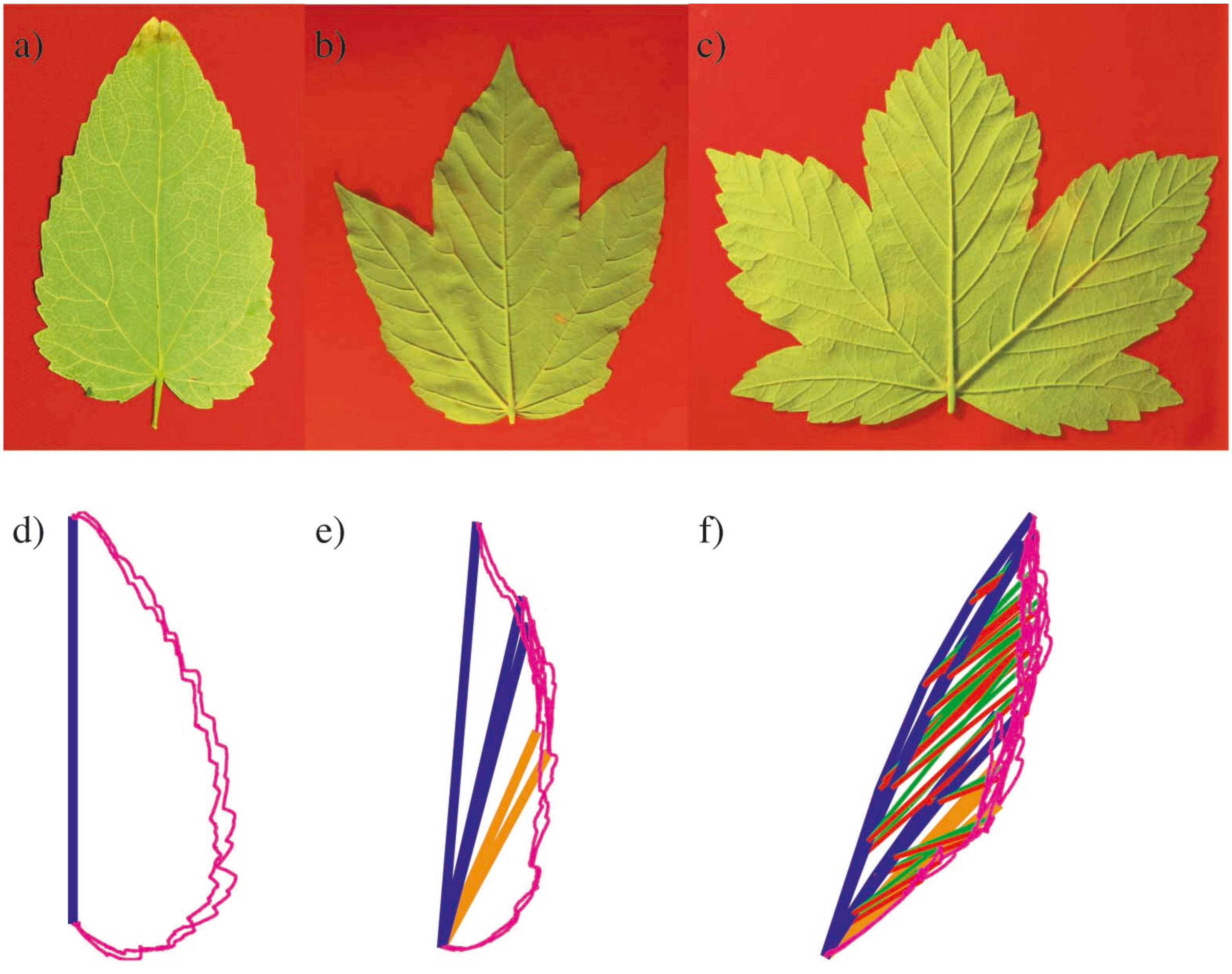
The mature leaf keeps the proportion of the folded leaf



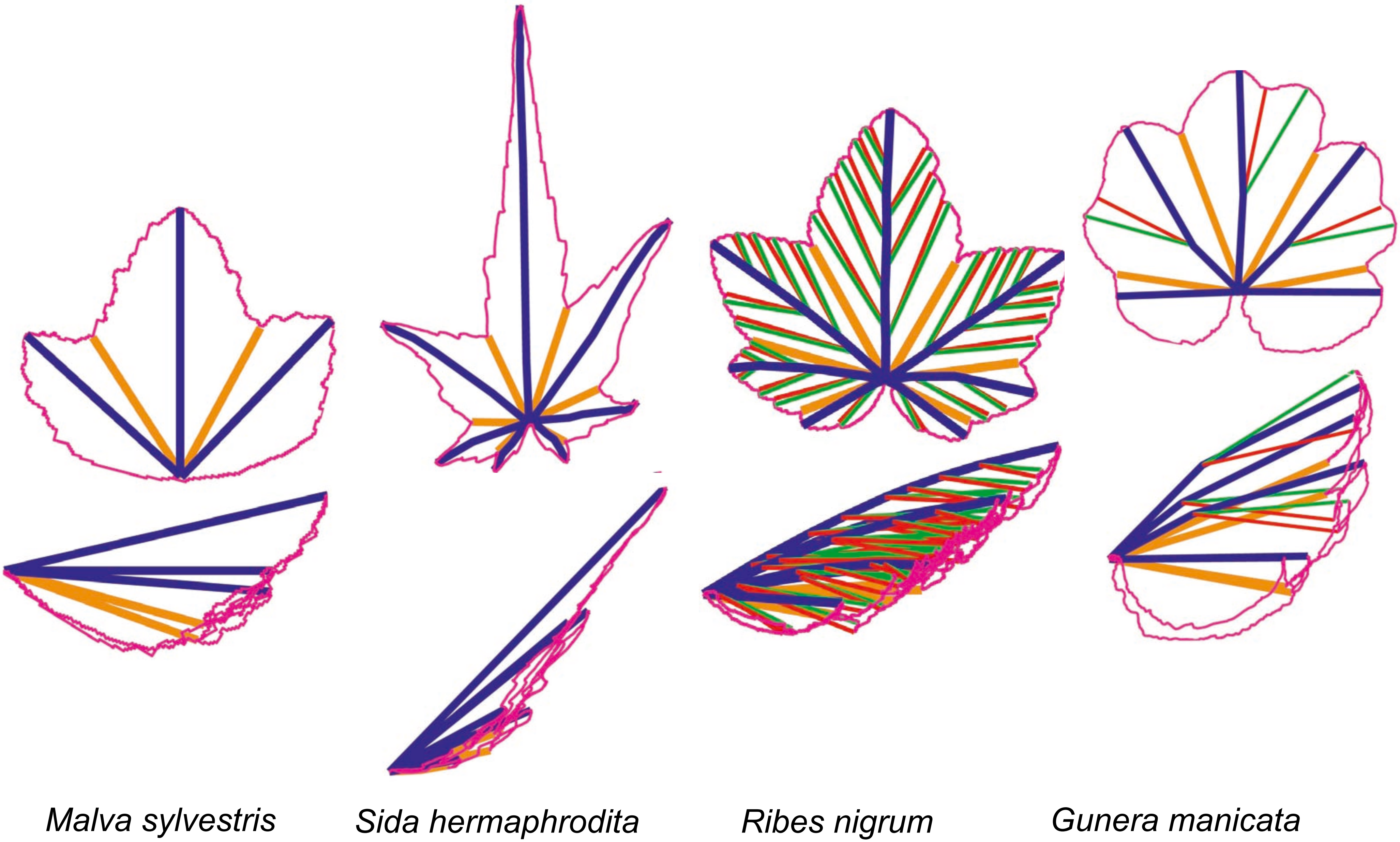
Acer pseudoplatanus leaf

The same leaf once folded

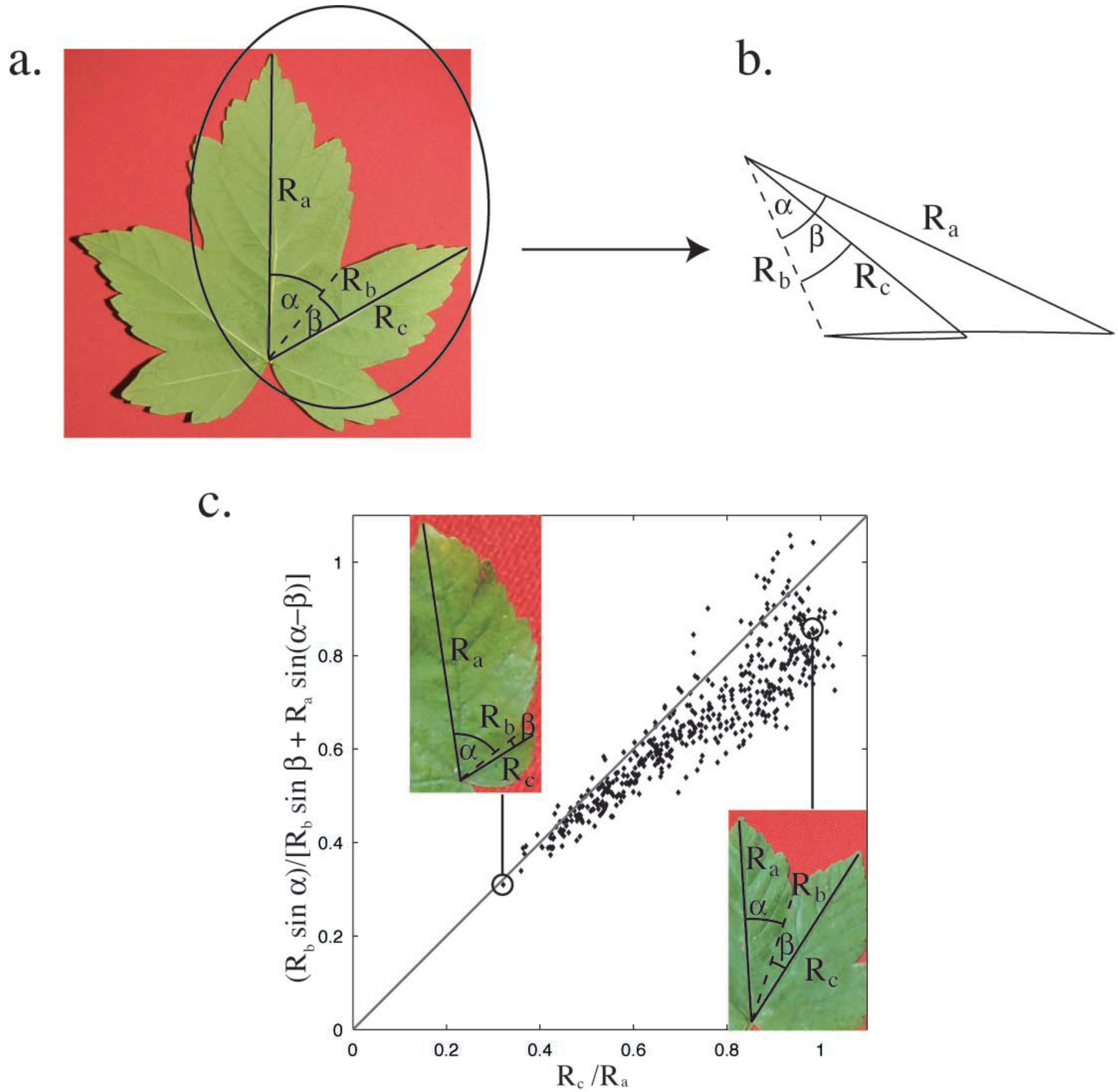
It works for all the shapes of sycamore leaves



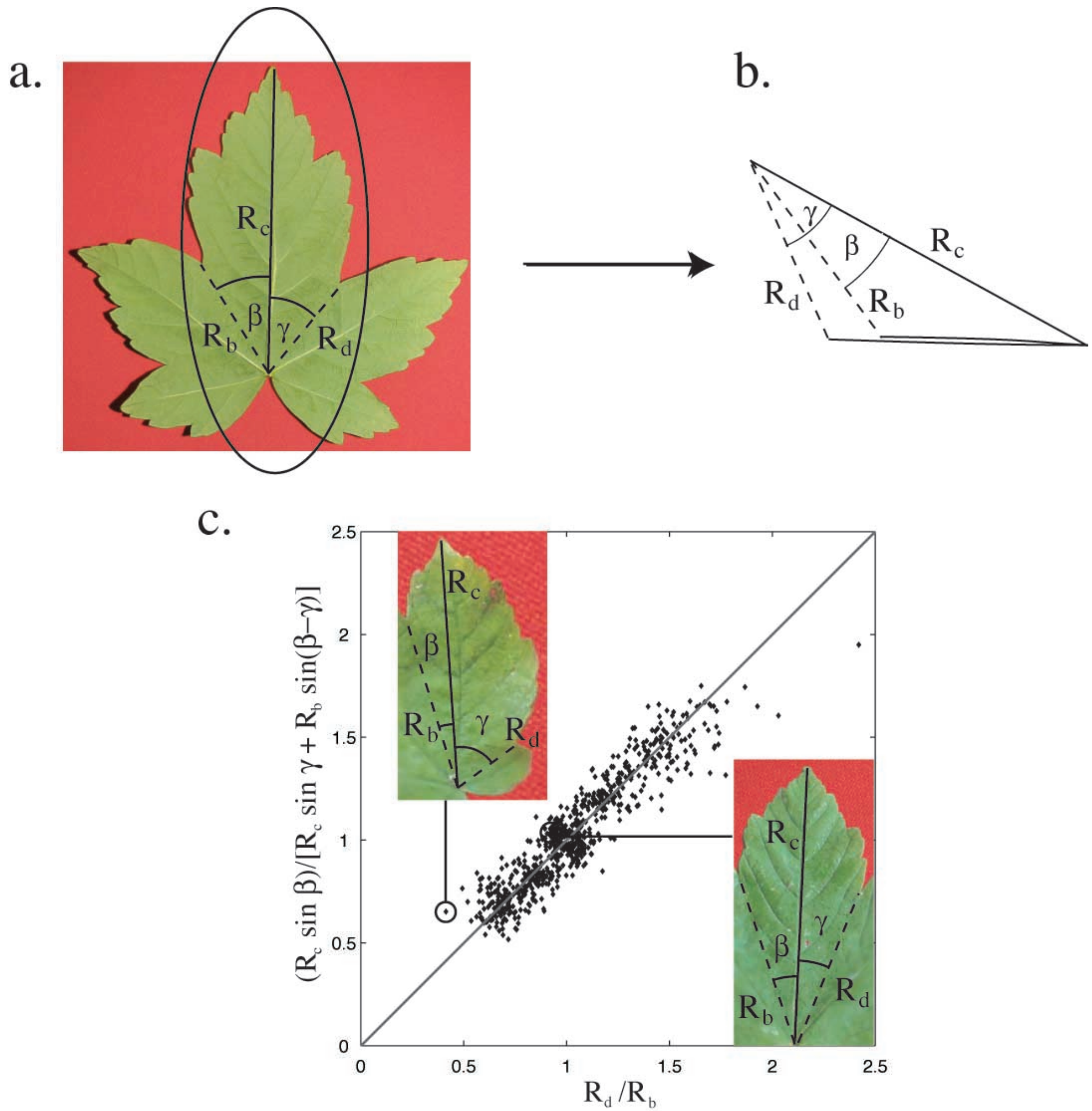
Different shapes of kirigami leaves in different species



Quantitative results : Prediction of the size of lobes

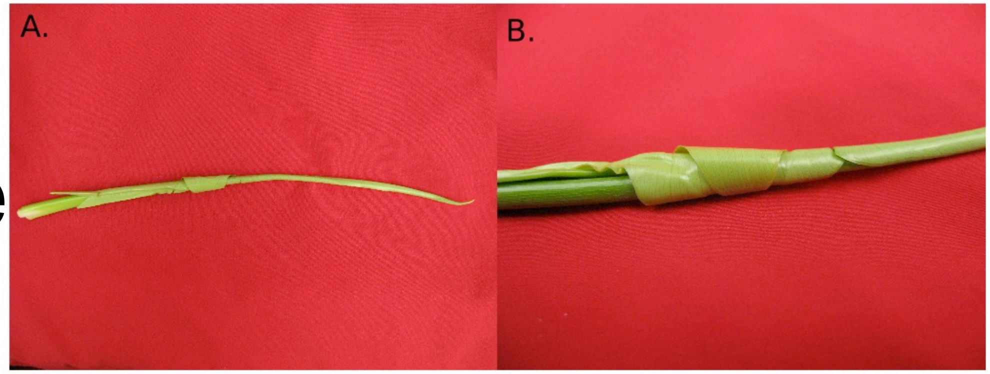


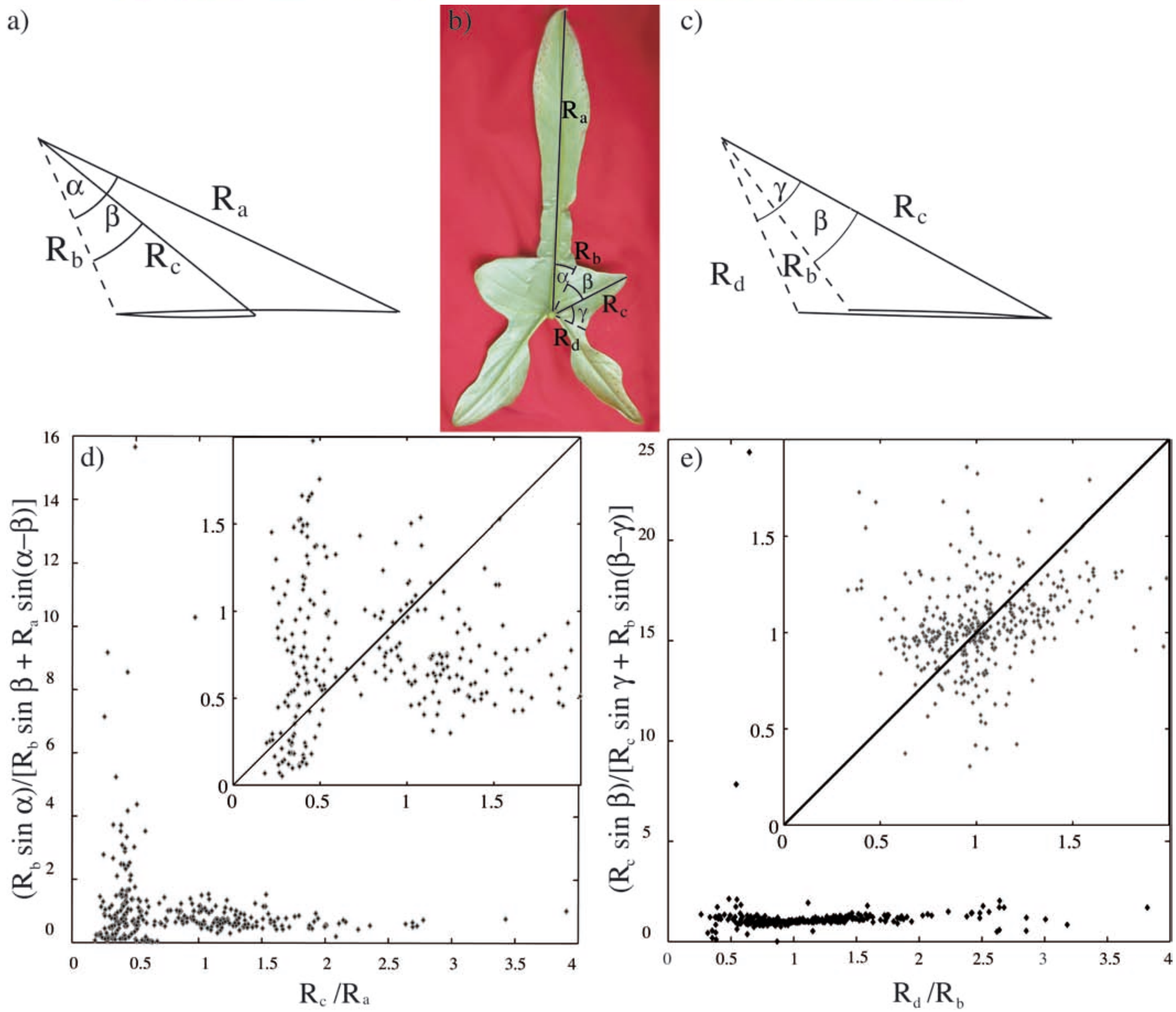
Prediction of the size of sinus



A negative control

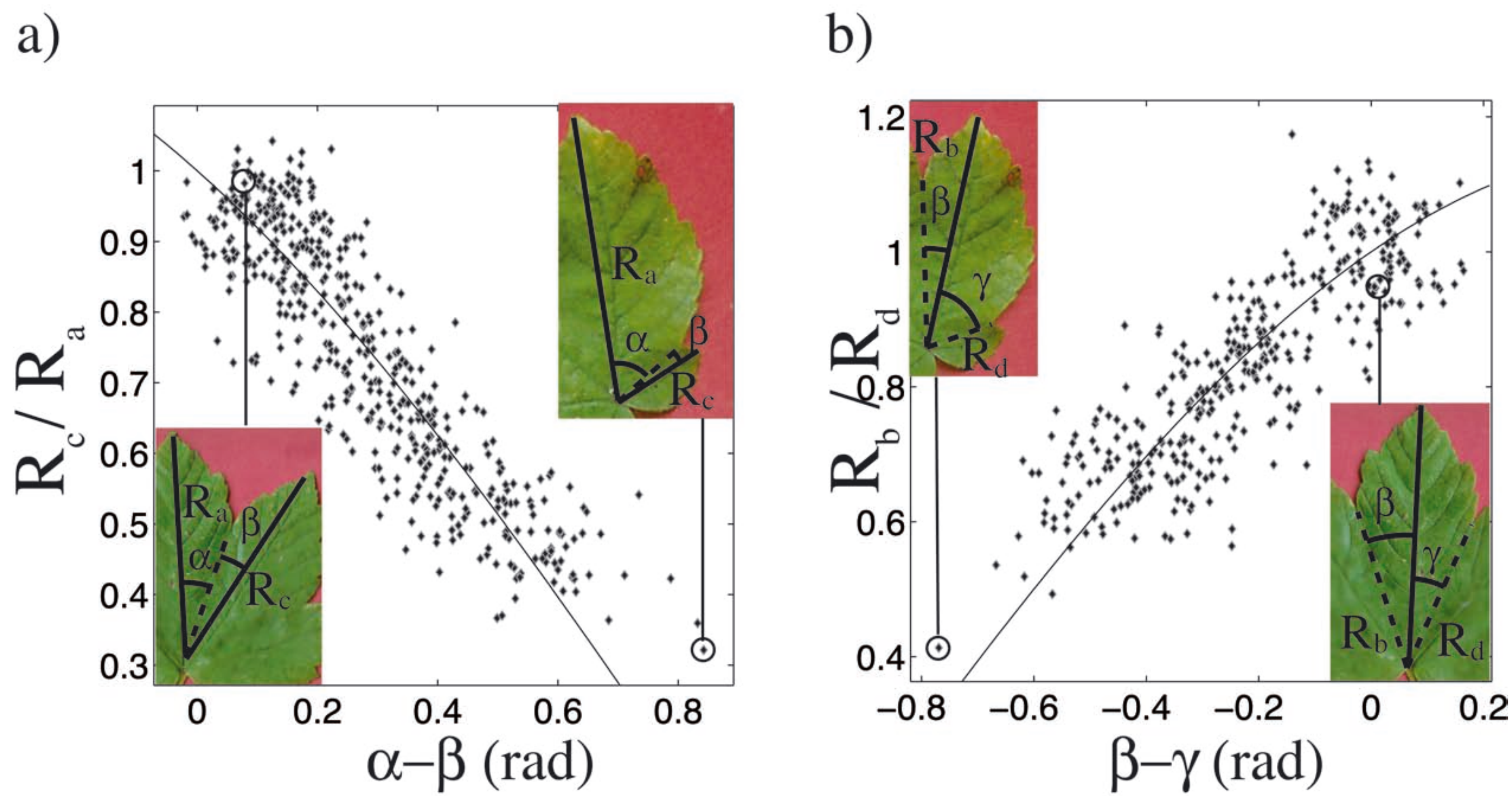
Phylodendron bipenifolium





How can you recognize kirigami leaves ?

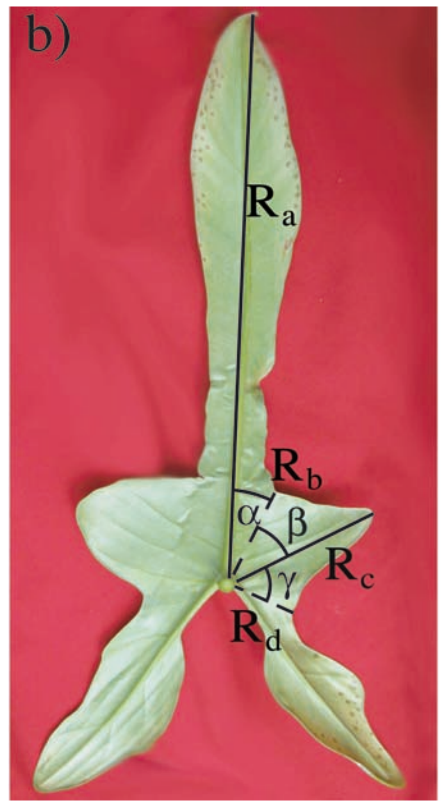
The smaller of two consecutives lobes is the one which makes the smaller angle with the sinus between them.

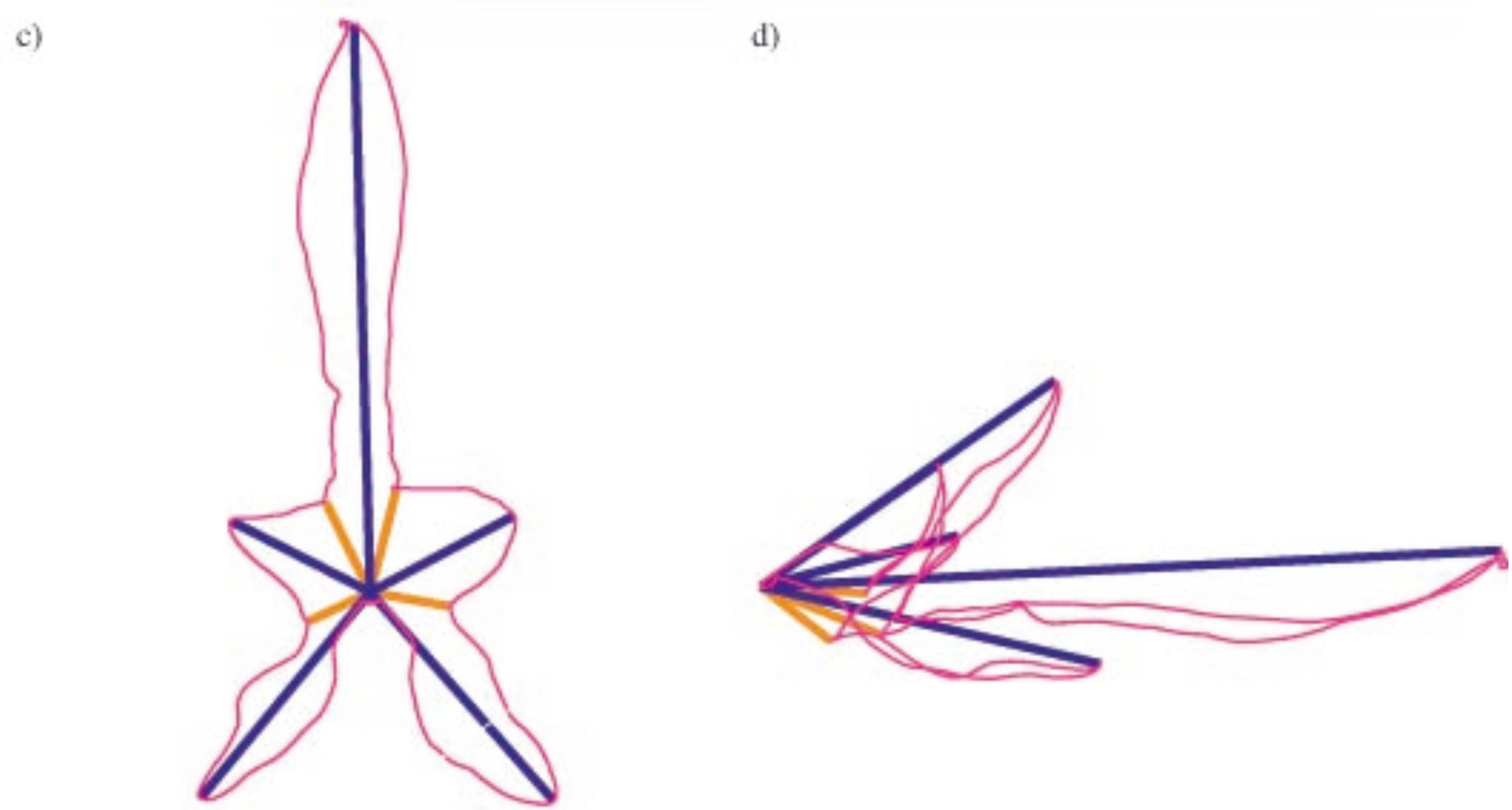


Is it a kirigami leaf?

Yes

No

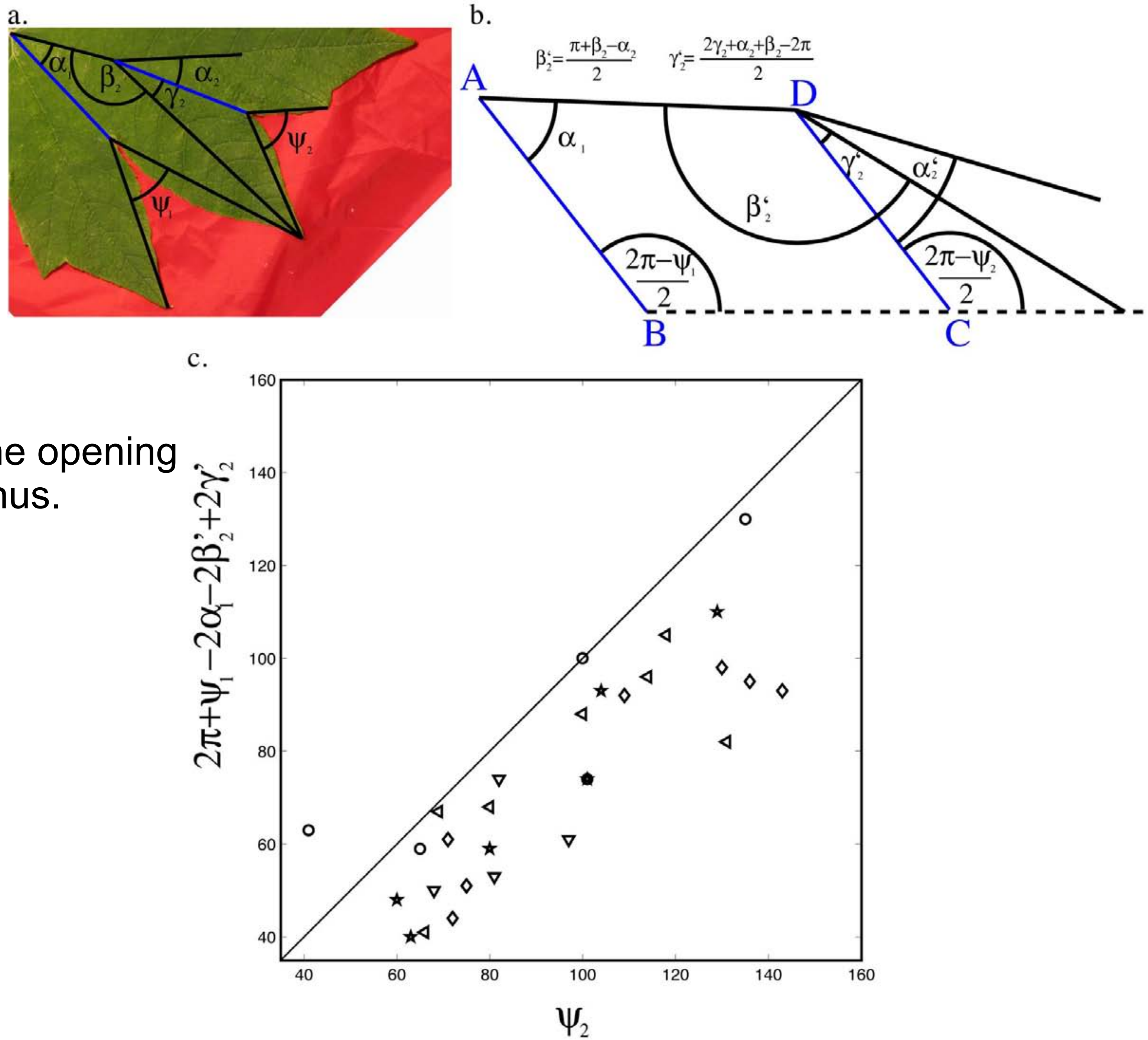




Phylodendron bipennifolium

Veins are still axes of symmetry of the edge - but not the sinus.

Effect of secondary folds on the shape

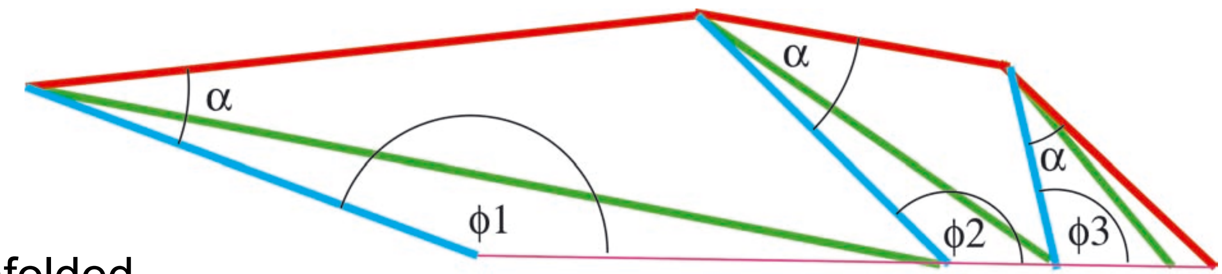


A numerical law links the opening angles of secondary sinus.

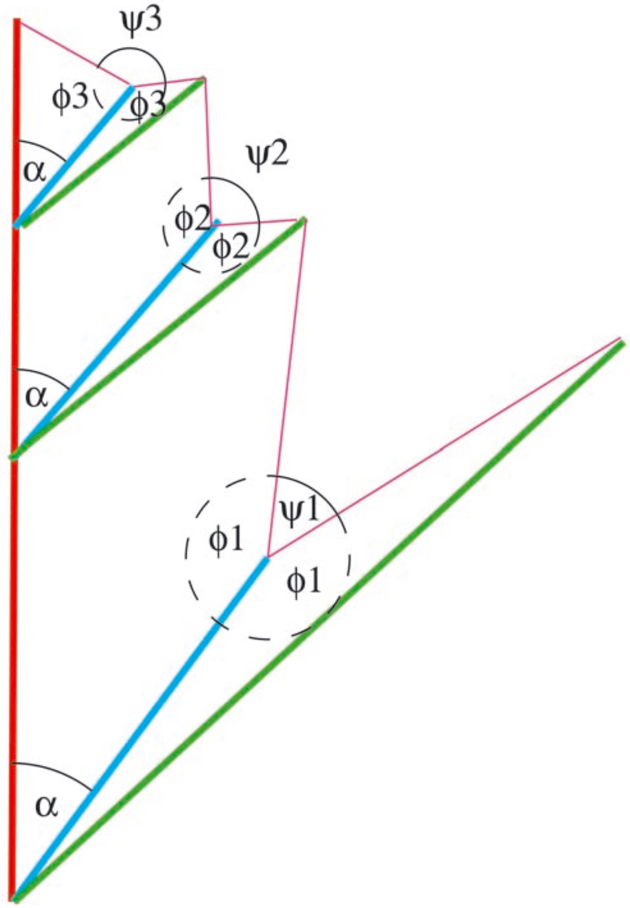
Tetrapanax papyrifer

Along a vein, the sinuses become more obtuse

Folded



Same lobe once unfolded



α=27.4 ° for the first fold along the vein mean on 20 folds.

α=27.7° for the second mean on 20 folds.

α=29° for the third one mean on 15 folds.

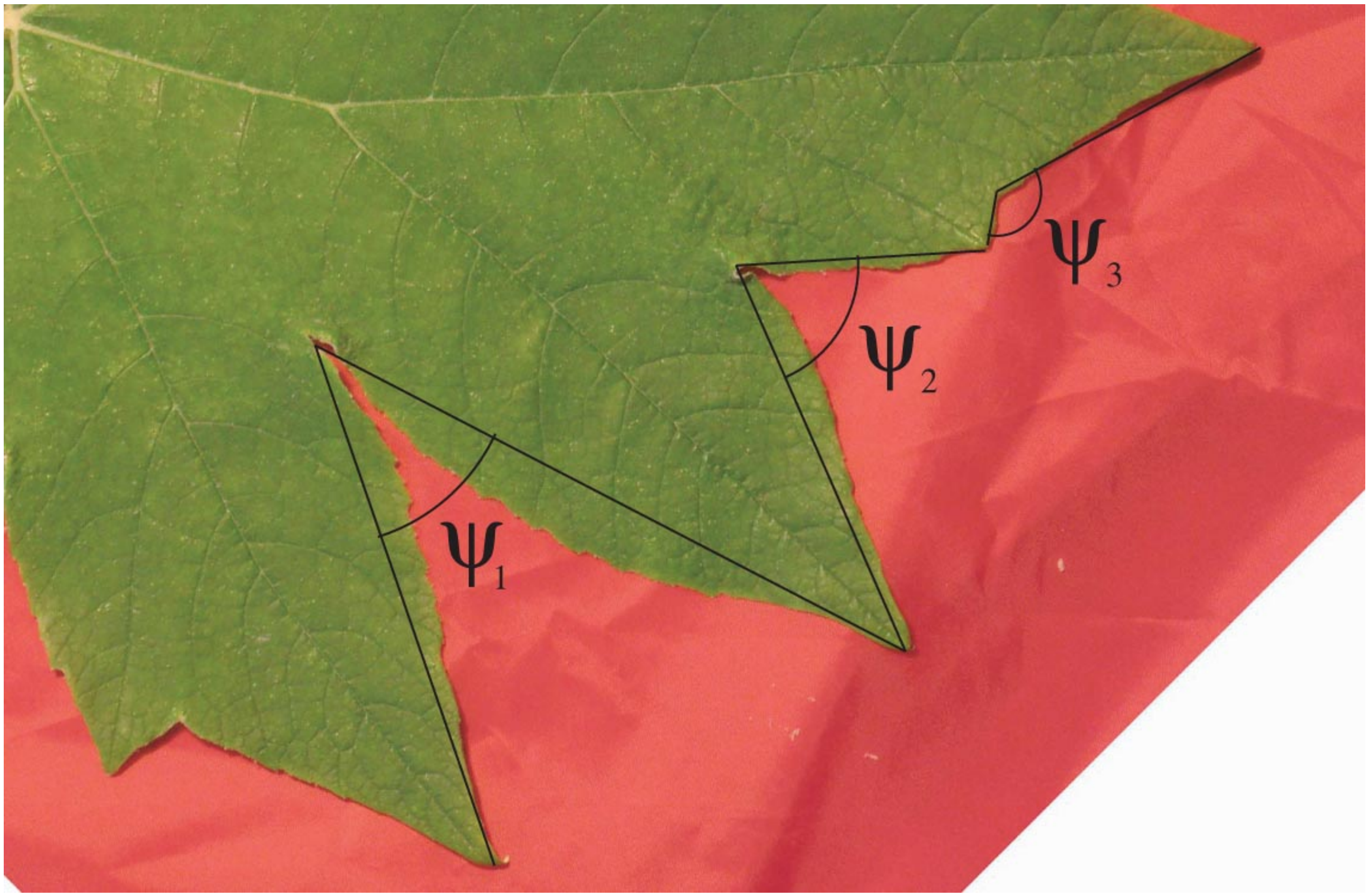
α does not change along the fold.

As at each fold the vein (red line) curves for geometric reasons, the angle between antifold (blue line) and the margin (pink line) decreases along the vein: $\phi 1>\phi 2>\phi 2$.
So the opening angle of the sinus increases along the vein $\psi 1<\psi 2<\psi 3$.

Mesurements are made on *Tetrapanax papyrifer* leaves.

Opening angles of the sinuses increase along a lobe

Tetrapanax papyrifer



The reiteration unit is the fold, not the lobe.

We have seen the simple case of kirigami:

-The main folds originate from the same point.

- The folded margin lays on a plane which corresponds to the surface of some object in the bud.
We will say that this object limitates the growth of the margin for teaching purposes.

Nature can be more tricky :

- Folds can be more complicated.

- The fold orientation relative to the limiting object can be different.

- The shape, which limits the margin, can be different from a plane.

We will see how this affects leaf shape.

Different kinds of folds exist in nature

Some leaves have folds with gaussian curvature.
You can’t obtain them from a sheet of paper.

Folds stops before the margin.
This changes the rule of symmetry of the leaf margin. Unlike in maple, veins are no more axes of symmetry of the lobe.

Murus platanifolium blackberry bush

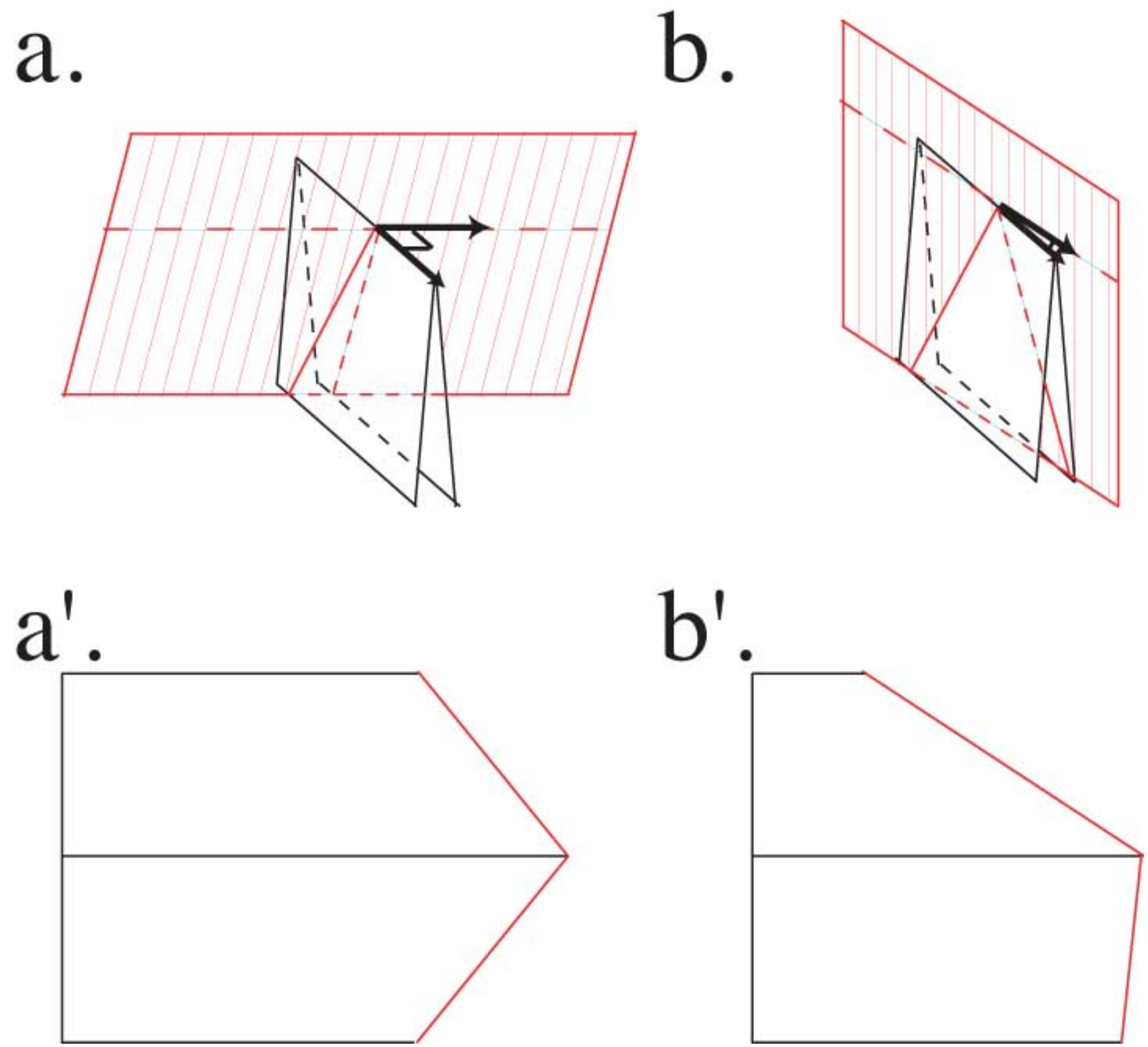
Inverted folds change the shape

Murus platanifolium

Inverted fold create this kind of vein pattern

Murus platanifolium

What happens if the cut plane is tangent to the fold ?



Fagus sylvatica

Beech

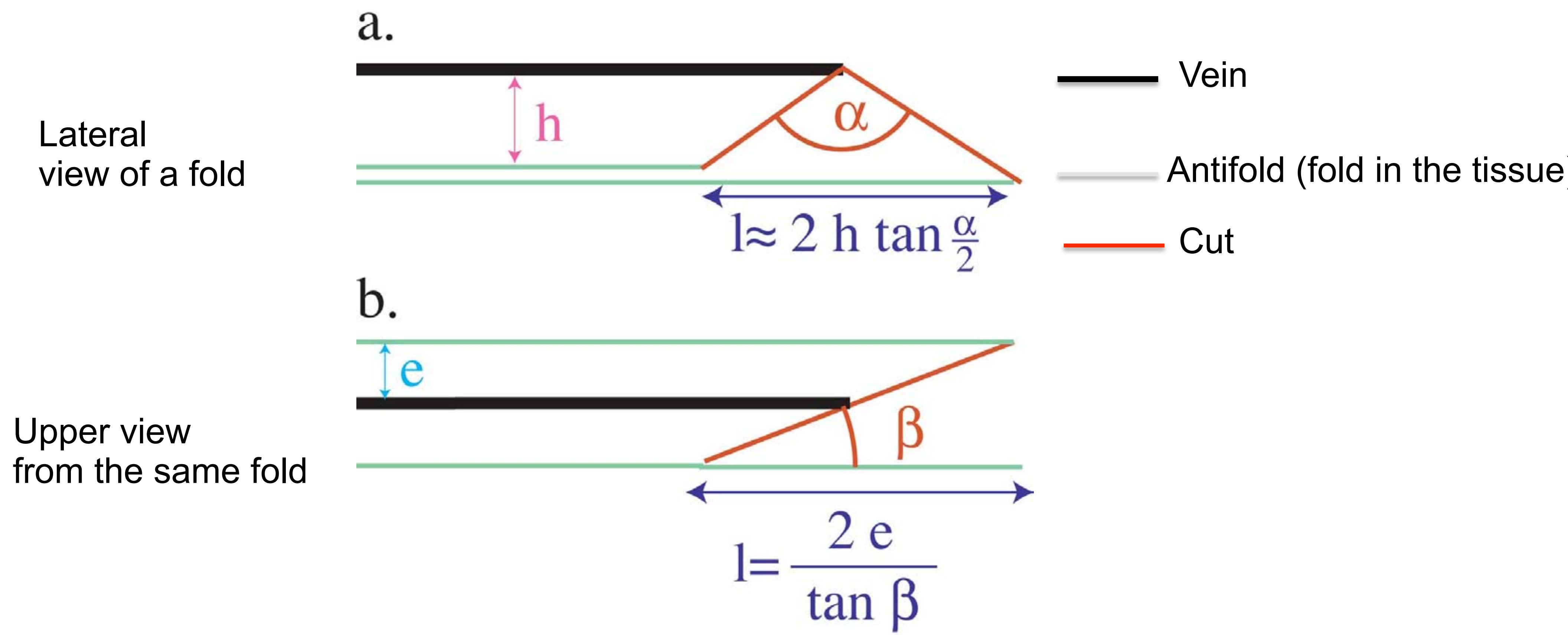
The envelope limits the growth of the leaf margin.

At the base of the bud, the envelope is tangent to the fold.
Folds are not axes of symmetry of the edge (blue array).

At the tip of the bud, the envelope is transversal to the fold.
Folds are axes of symmetry of the edge (red array).

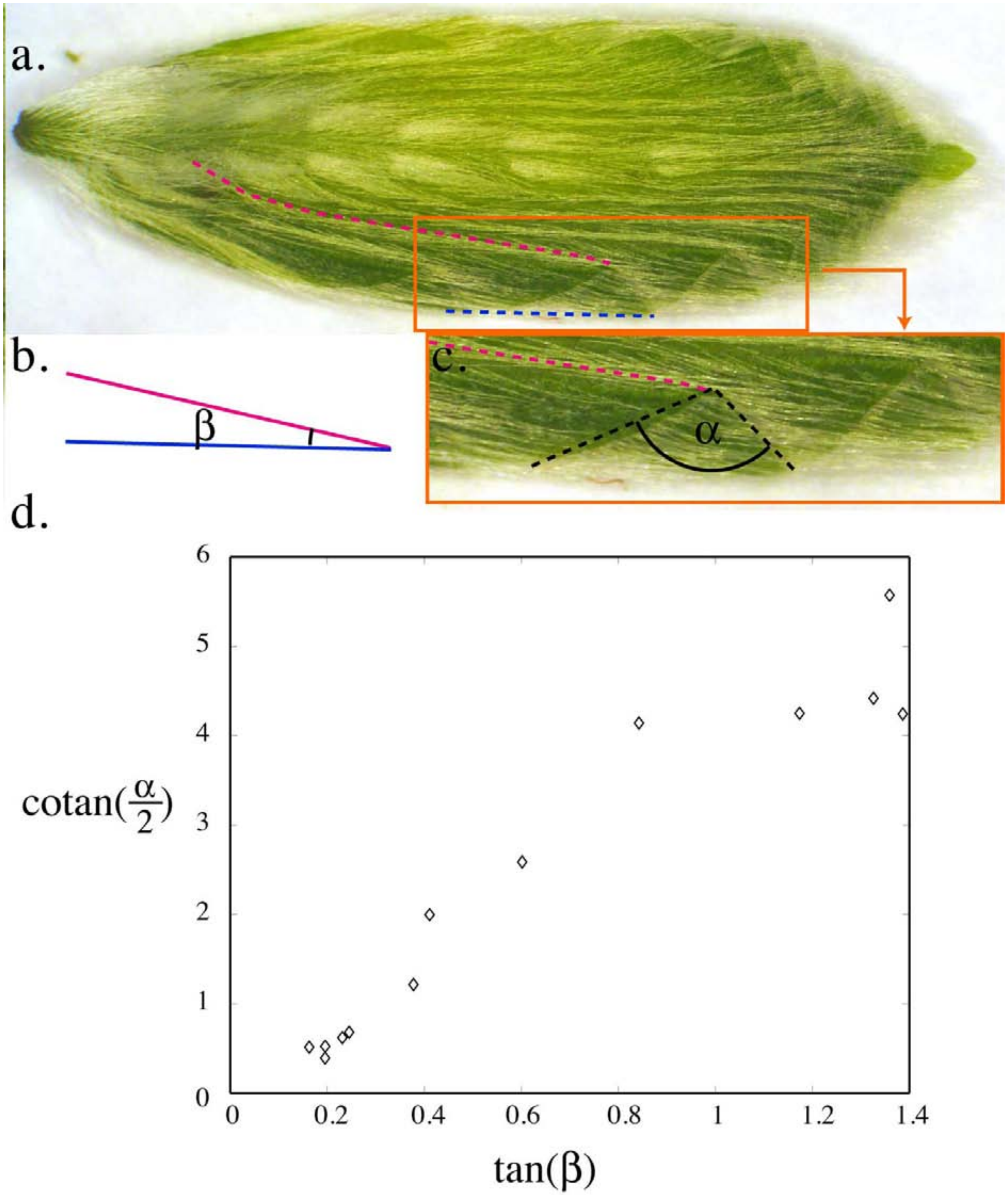
We can link β (the angle between the fold and the cut), and α (the angle which measures the asymmetry of the fold).

l = the distance between two consecutive antifold ends

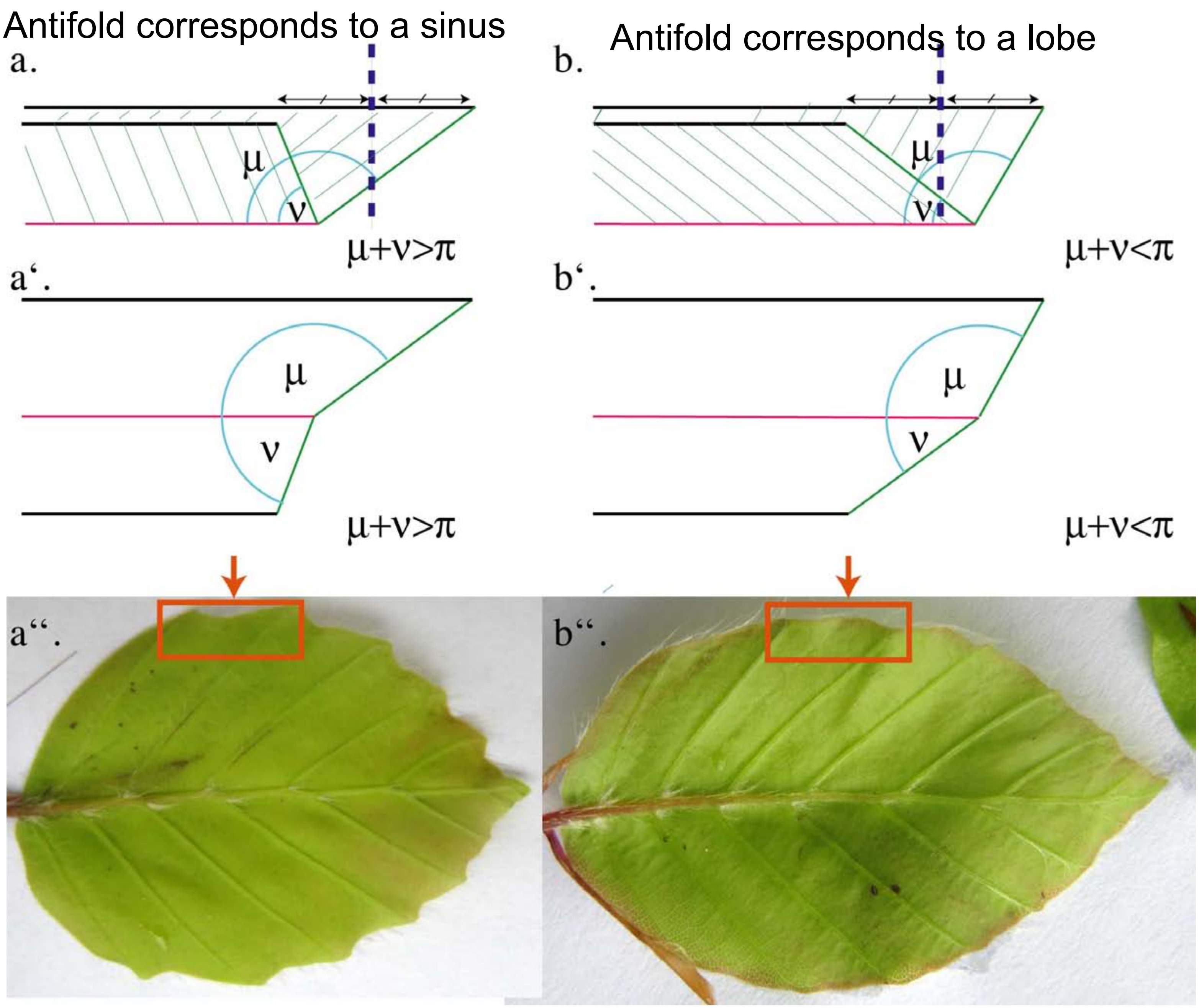


$$\mathrm{Cotan}(\alpha/2) = h \tan(\beta) / e$$

Beech leaves follow the geometrical rule



An antifold (fold in the tissue) does not always corresponds to a sinus



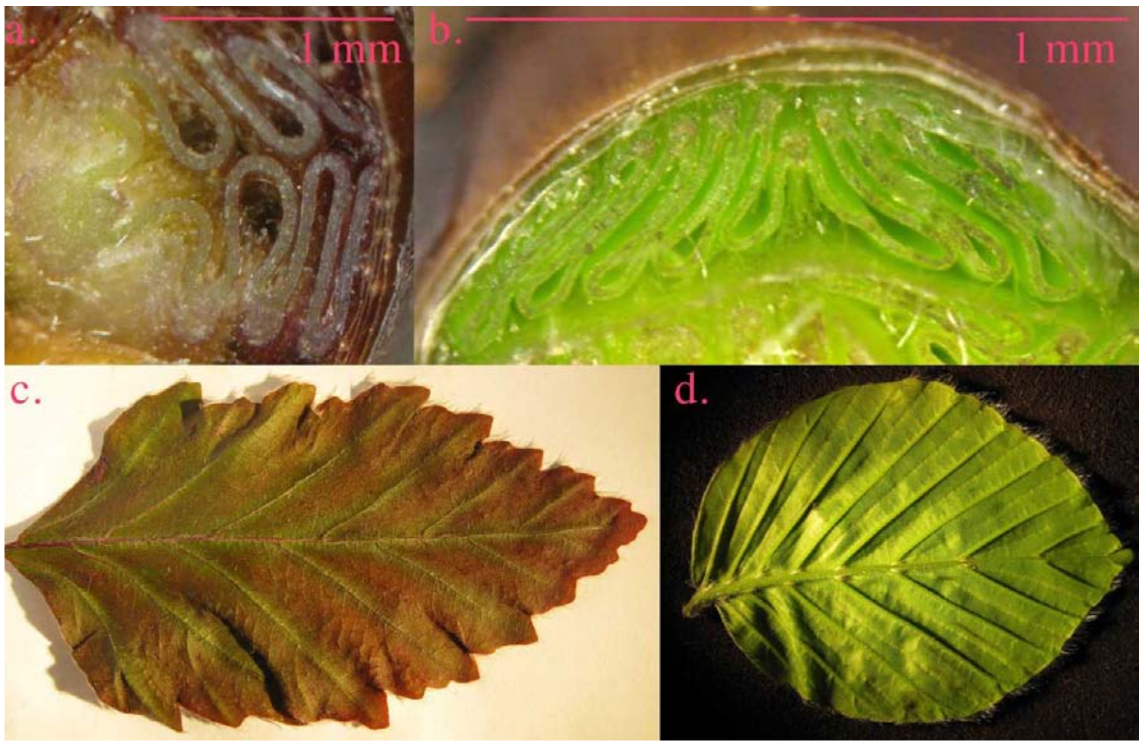
Black line = vein
Pink = antifold
Green = cut
Blue dashed line = middle of the two vein tips.

Leaf shape is more correlated to bud geometry than to genetic difference between cultivars

Fagus sylvatica
Rohan obelix

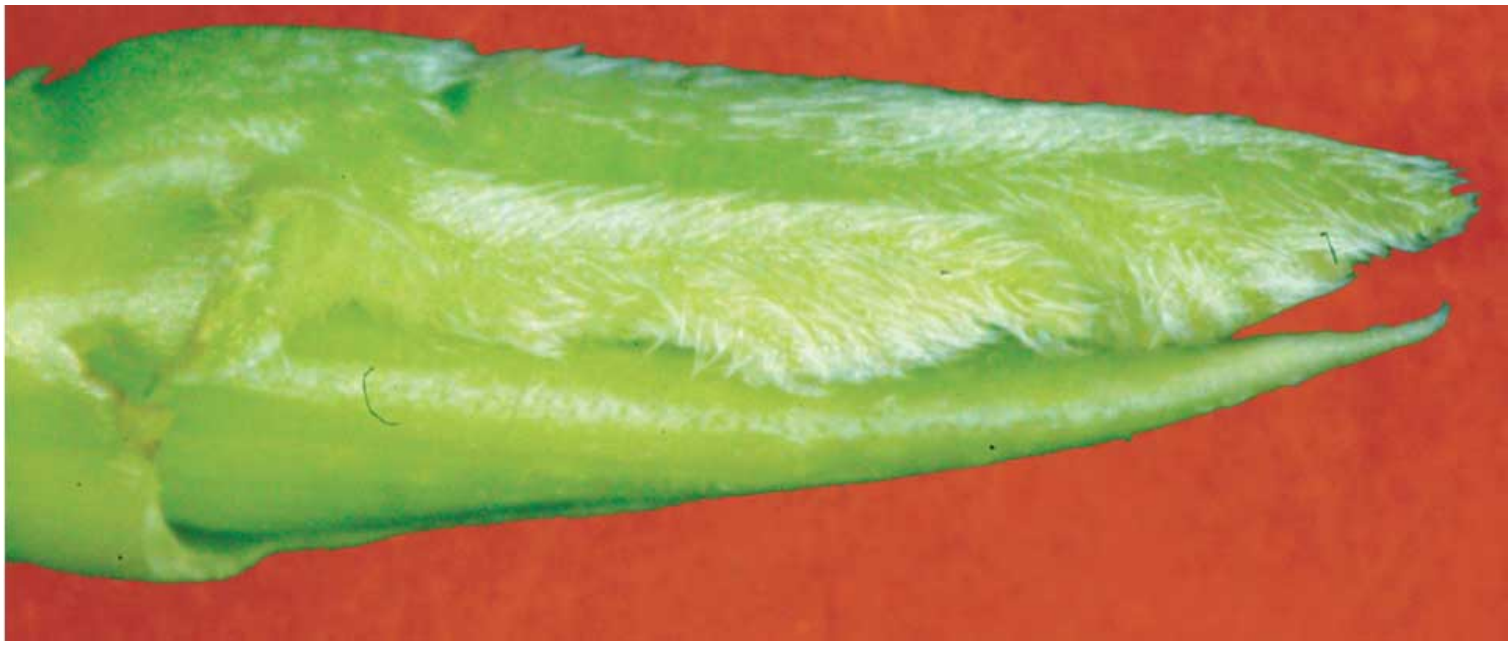
The disposition of the two leaves in the bud differs between cultivars

Fagus sylvatica
Rohan obelix



Fagus sylvatica

Ficus Cariaca buds are similar to Russian dolls:
Each bud is constituted by a leaf and a smaller bud.
Apparently the leaf margin lay on the smaller bud.



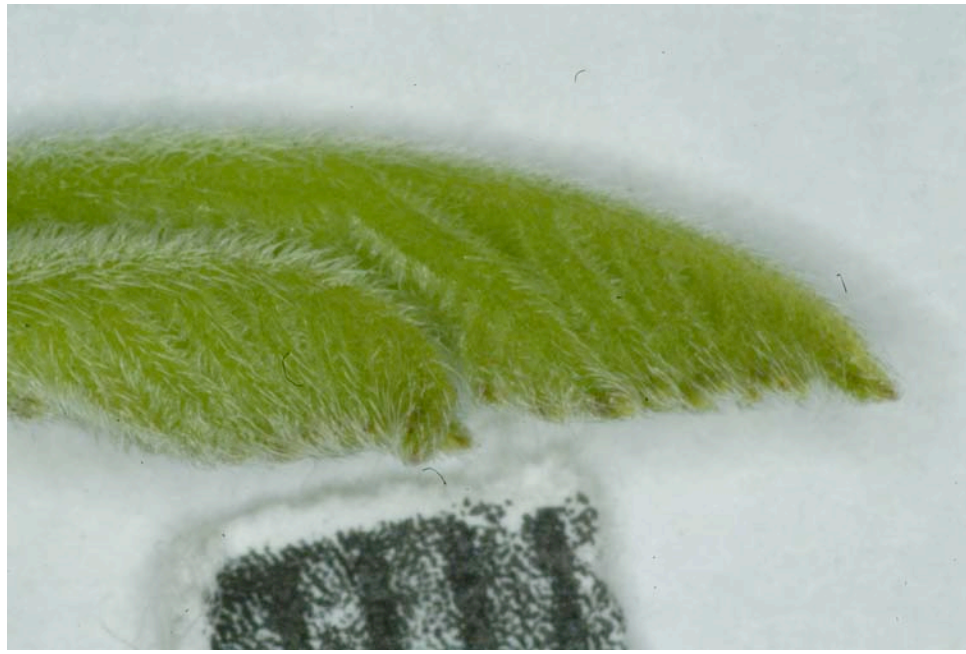
There are two kinds of limitations :

- The lobe base margin is limited by the lateral vein.
- The lobe tip margin is limited by bud surface.

Ficus cariaca

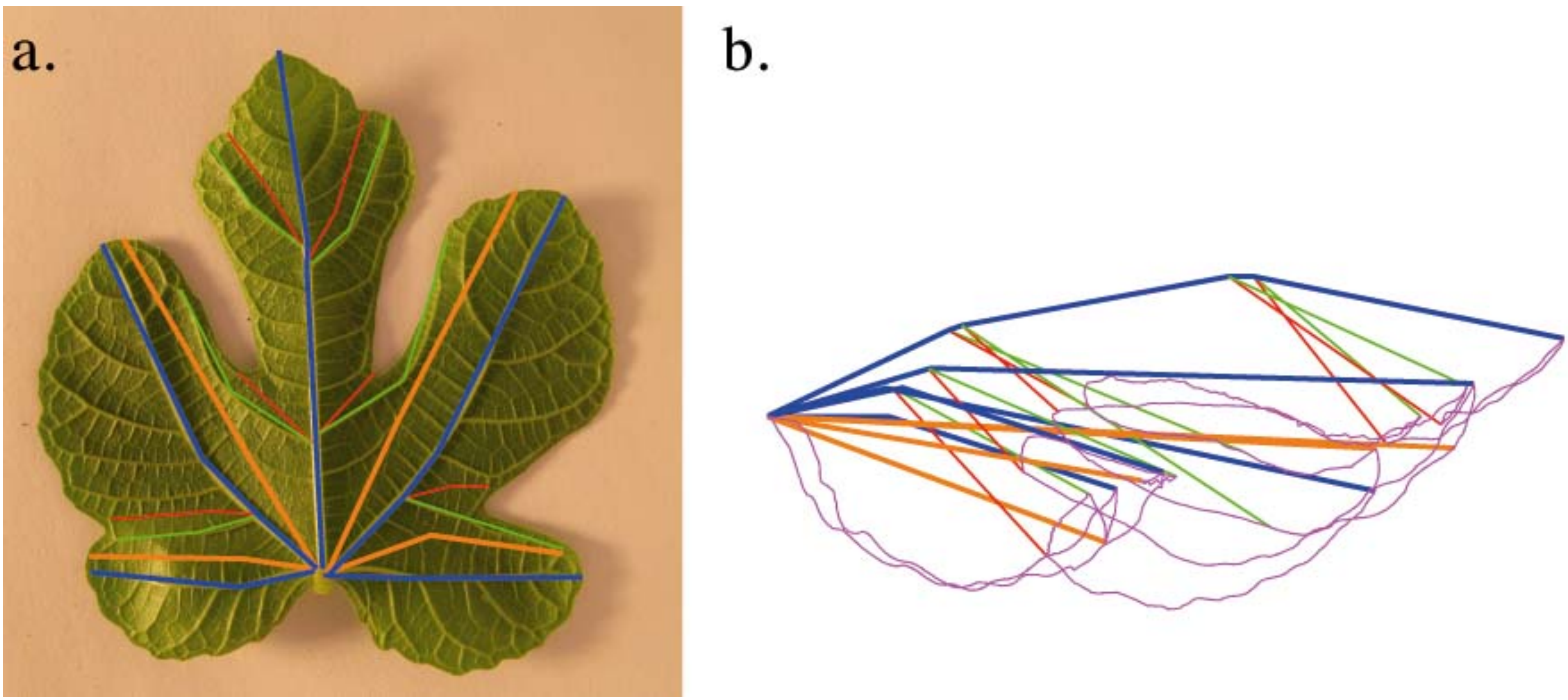
Veins of lateral lobes limit the growth of the central lobe margin. It explains the spoon shape of the figtree lobe.

Another image of the limitation of the margin by the lateral vein



Ficus cariaca

If we refold numerically the leaf, we find both limitations.



Kirigami : a unifying principle for different leaf shapes.

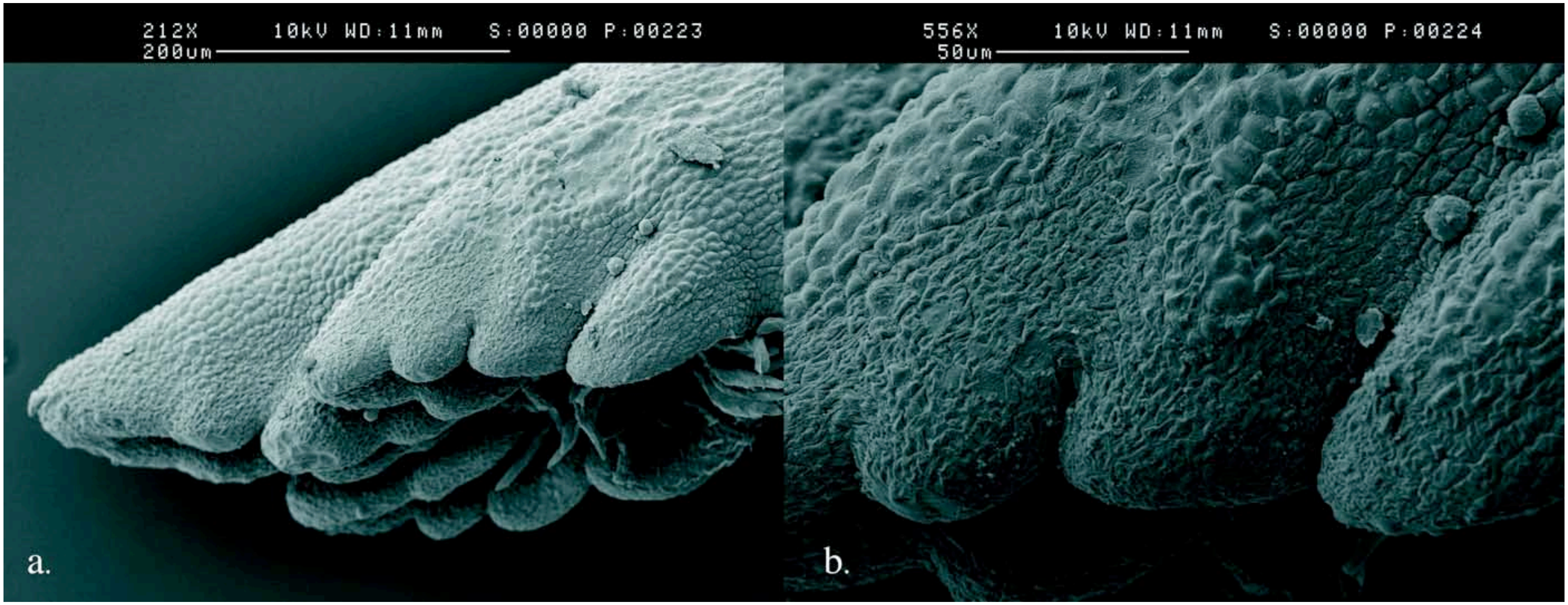
All these shapes are solutions of a geometrical problem of packing.

What are developmental mechanisms that explain this phenomenon?

- How do folds appear?

- What works as a scissor?

Small lobes appear before the folds



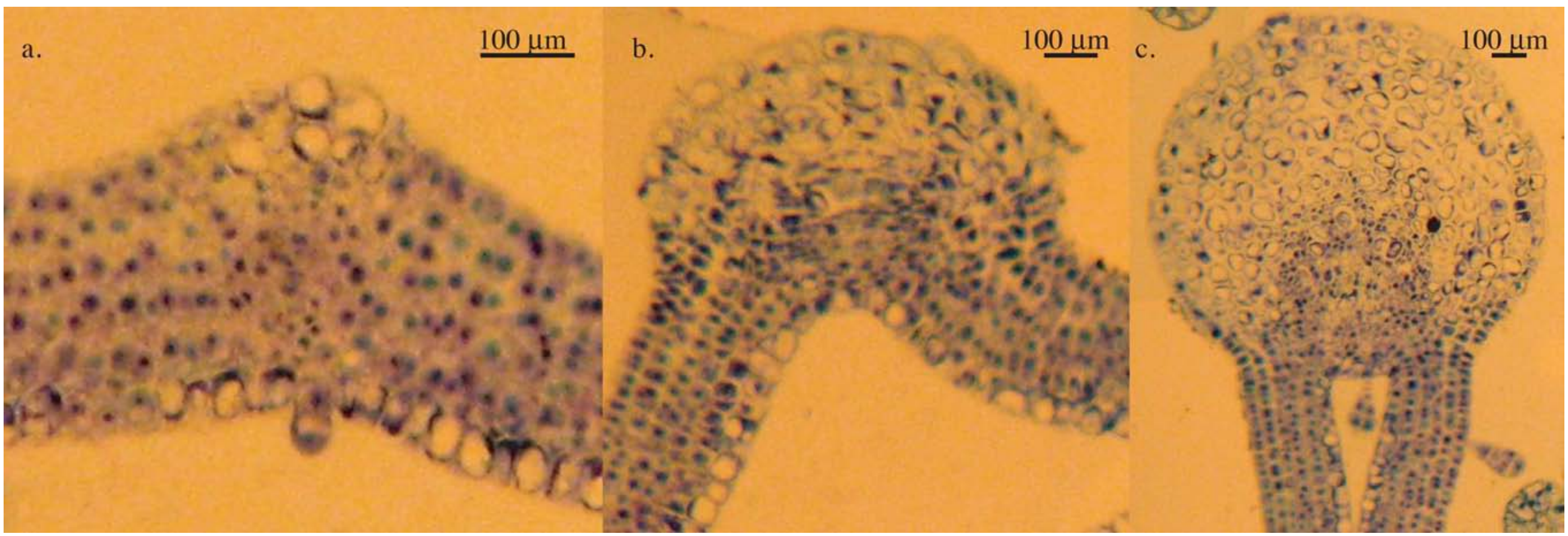
A primordium and its secondary lobes: A vein corresponds to each lobe.

Auxin accumulation ●

Auxin flux →

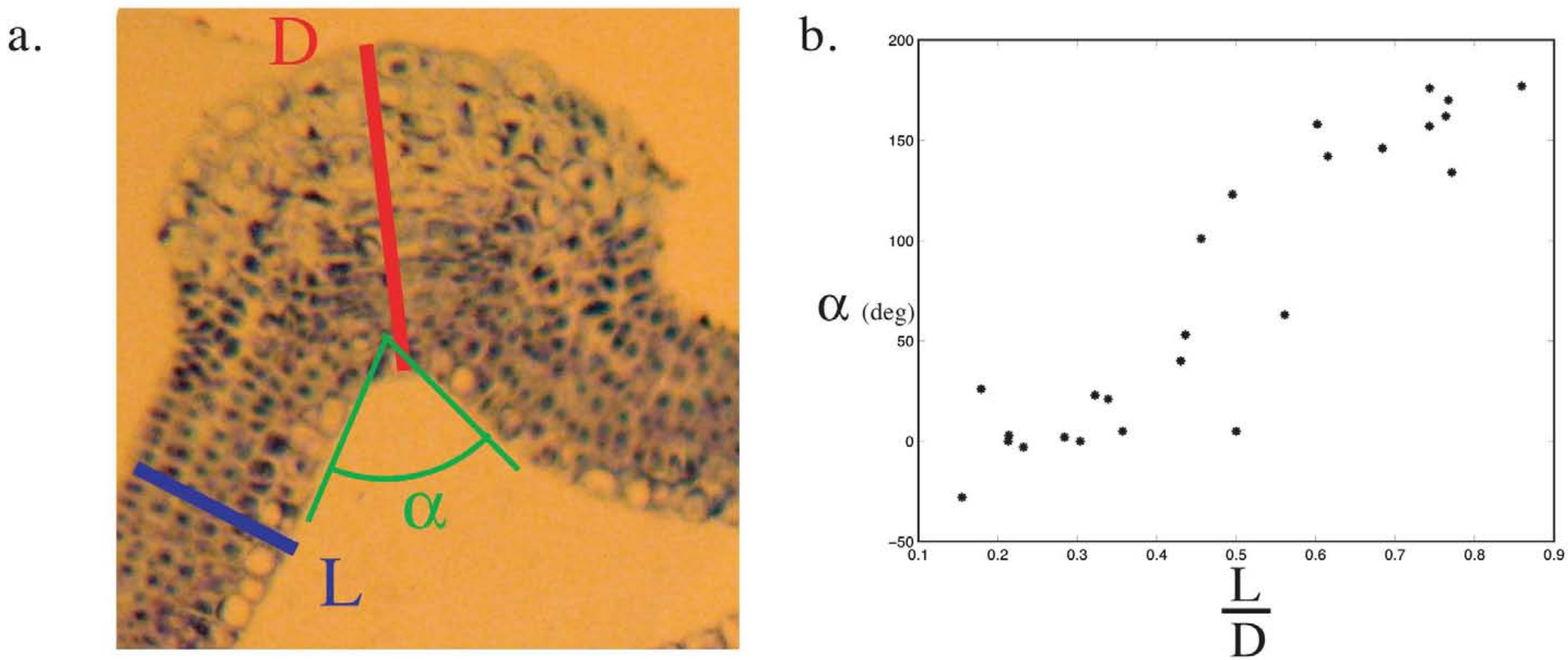
Effect of the differentiation of vein tissue

The abaxial part of the vein grows quicker than the adaxial one. It clips the neighbouring tissue.

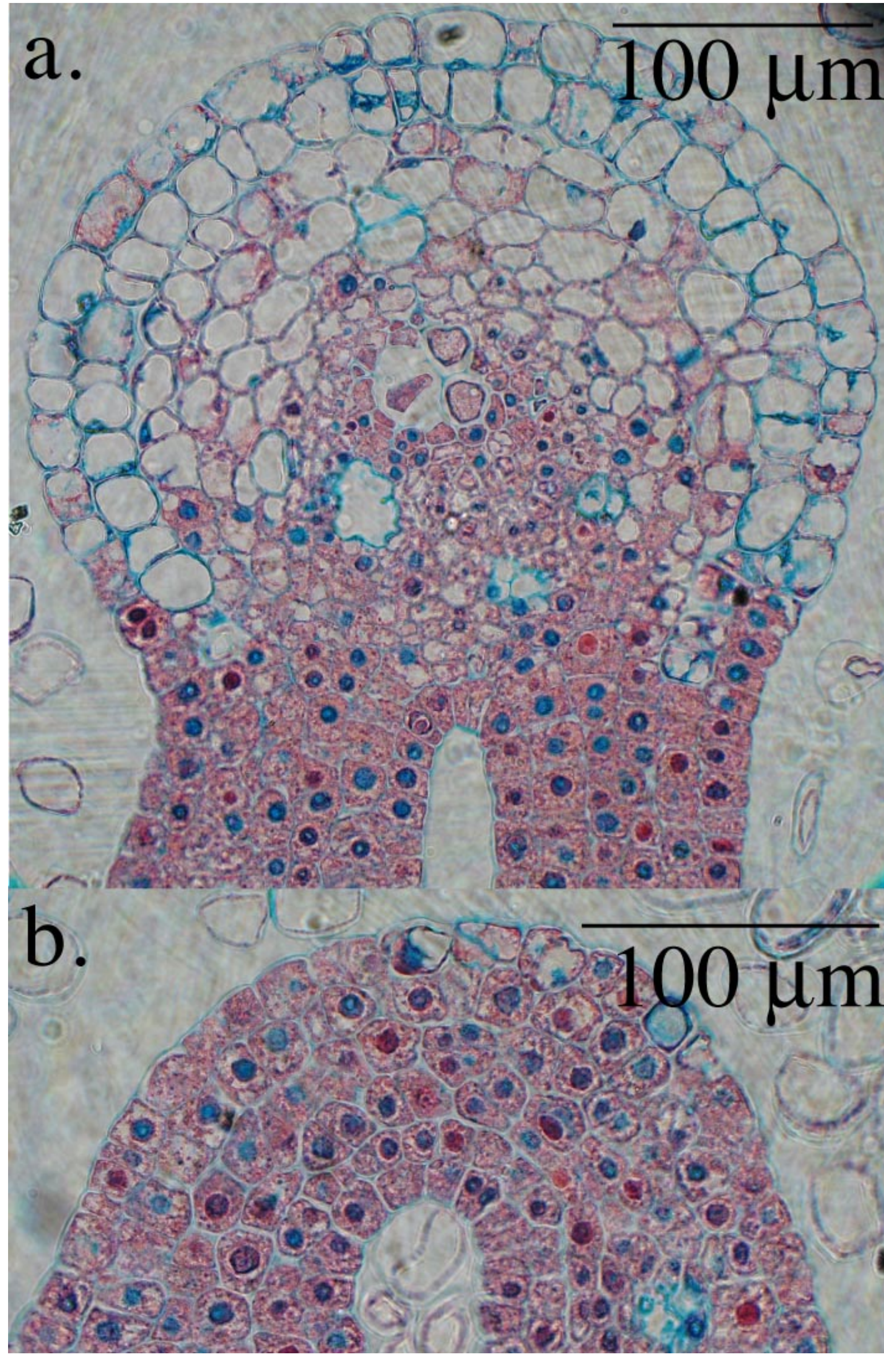


Different stages of the maple vein development

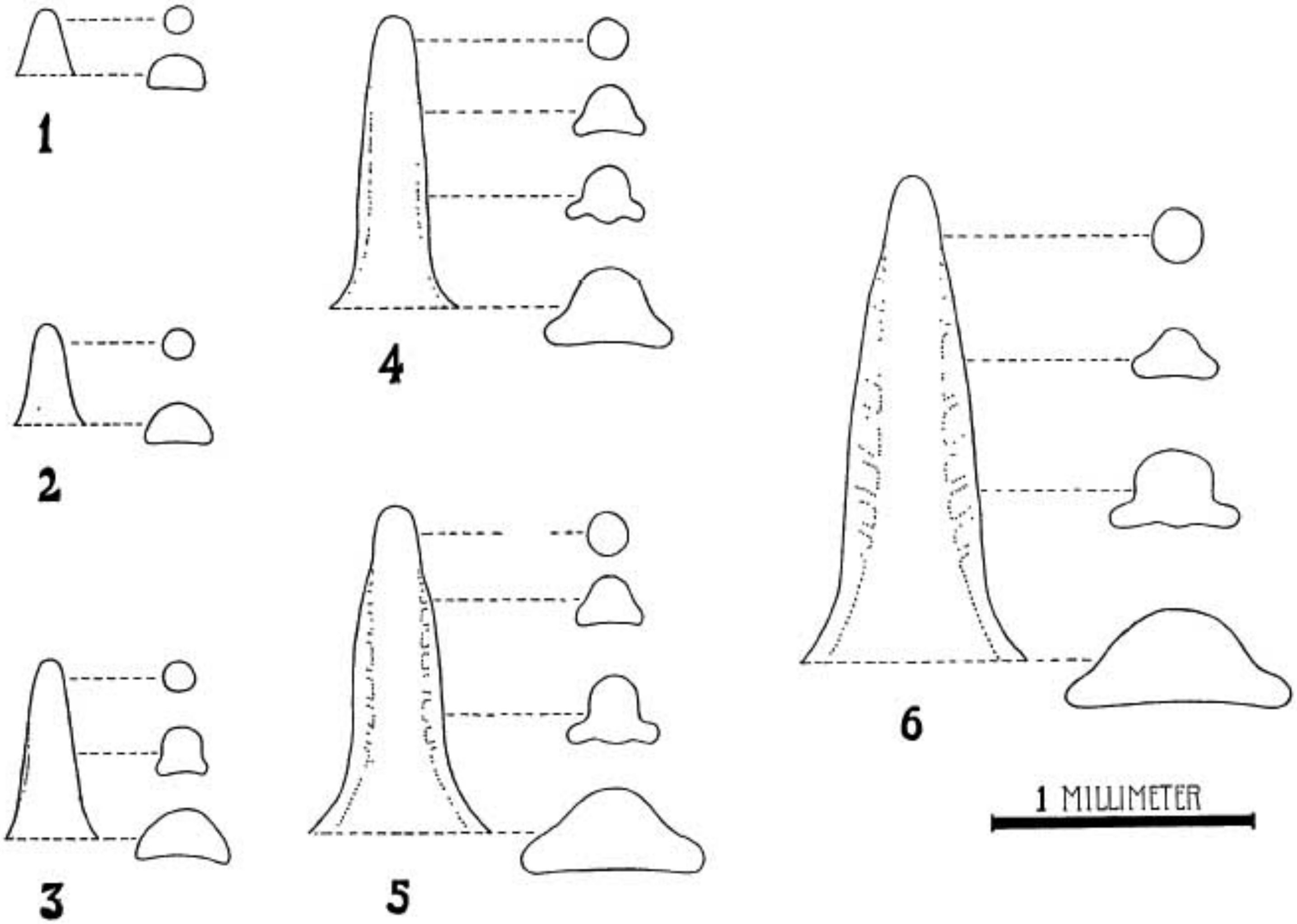
The bigger the vein compared to the tissue, the closer the fold



Veins clip the lamina.
Cells look like the cut stones of an arch.



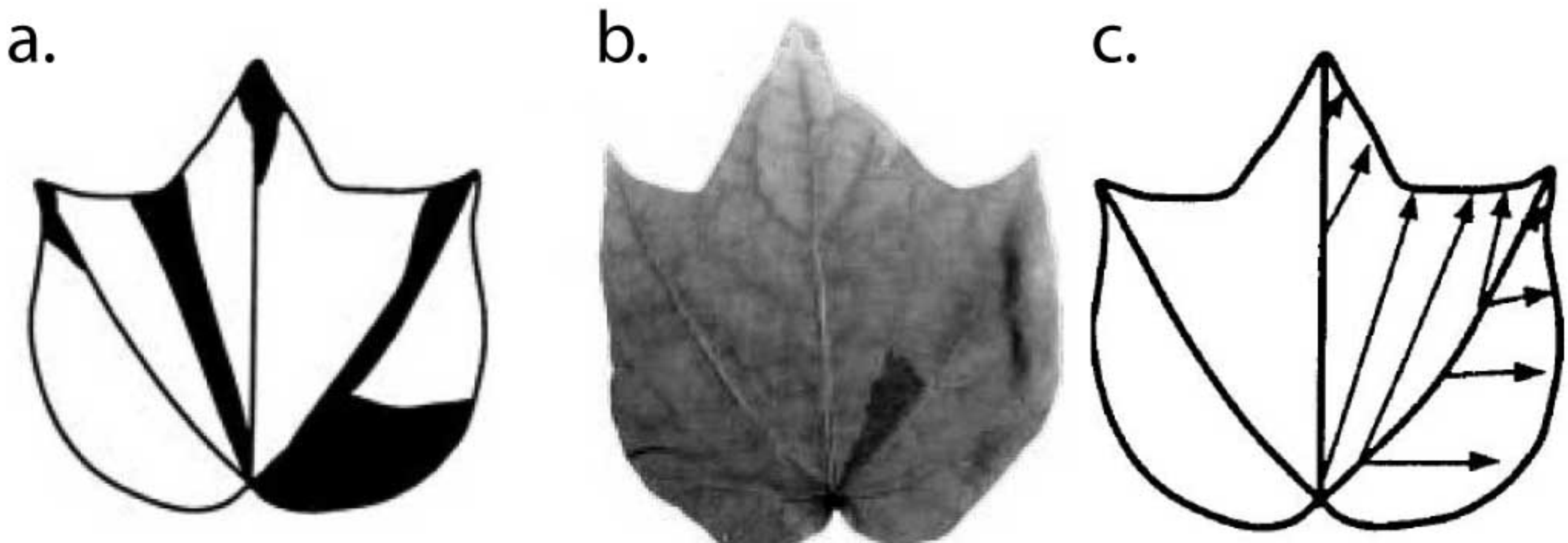
A small digression: Tobacco leaf development



Avery 1934

A second digression: the coton leaf, a kirigami leaf, which is ignored.

- Each antifold corresponds to only one antifold.
- The lineage of each vein is limited by both neighbouring antifolds.

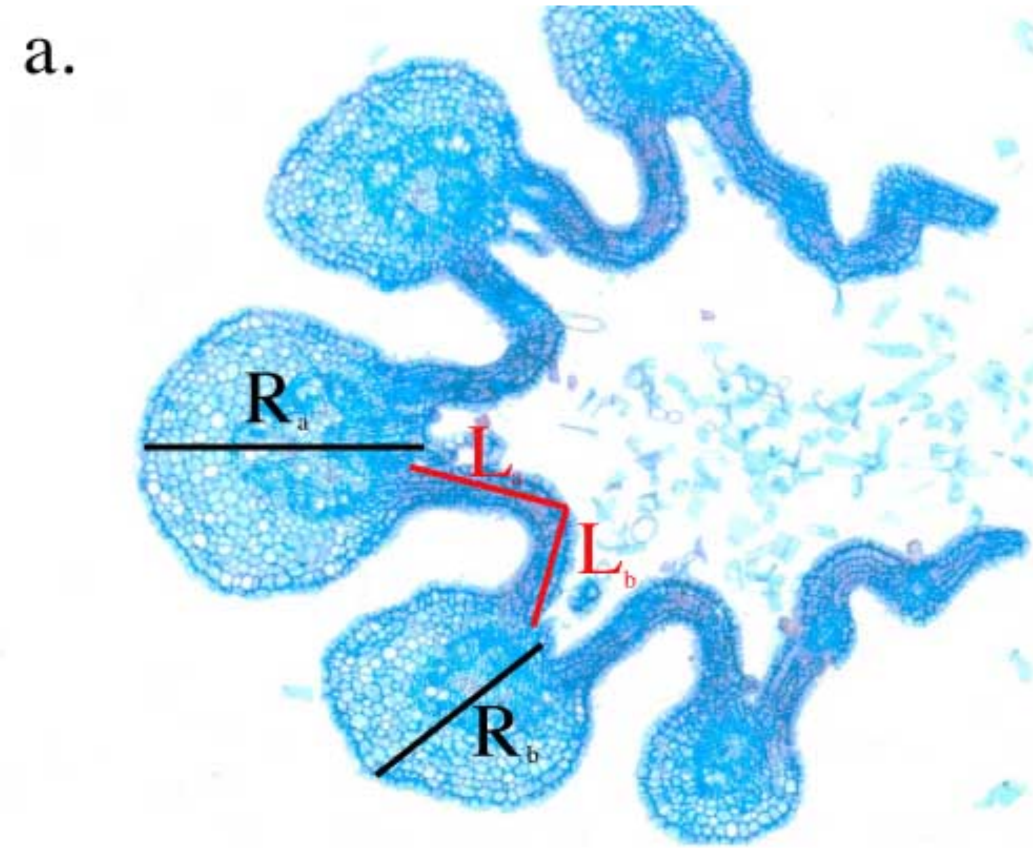


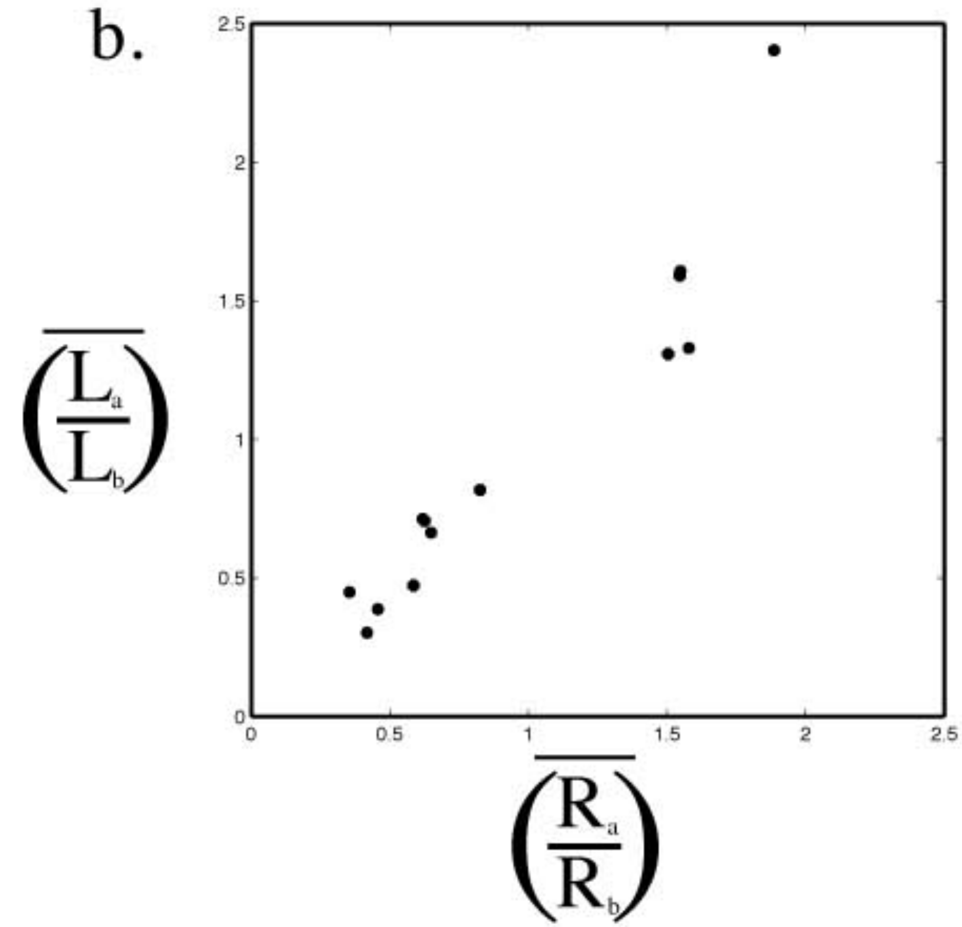
Coton leaf Dolan and Poethig 1998

Each antifold delimits the two zones irrigated by its two neighbouring veins

Veins have an egoist behaviour, it irrigates only its own lineage.

A more dynamic view of this development





The size of a fold is proportional to the size of the corresponding vein.

Each fold grows independently from others.

Fold development

- The differentiation of abaxial side of the vein plays a role in folding.

- Each unit formed by a fold and its vein corresponds to the lineage of one cell and grows independently from its neighbouring.

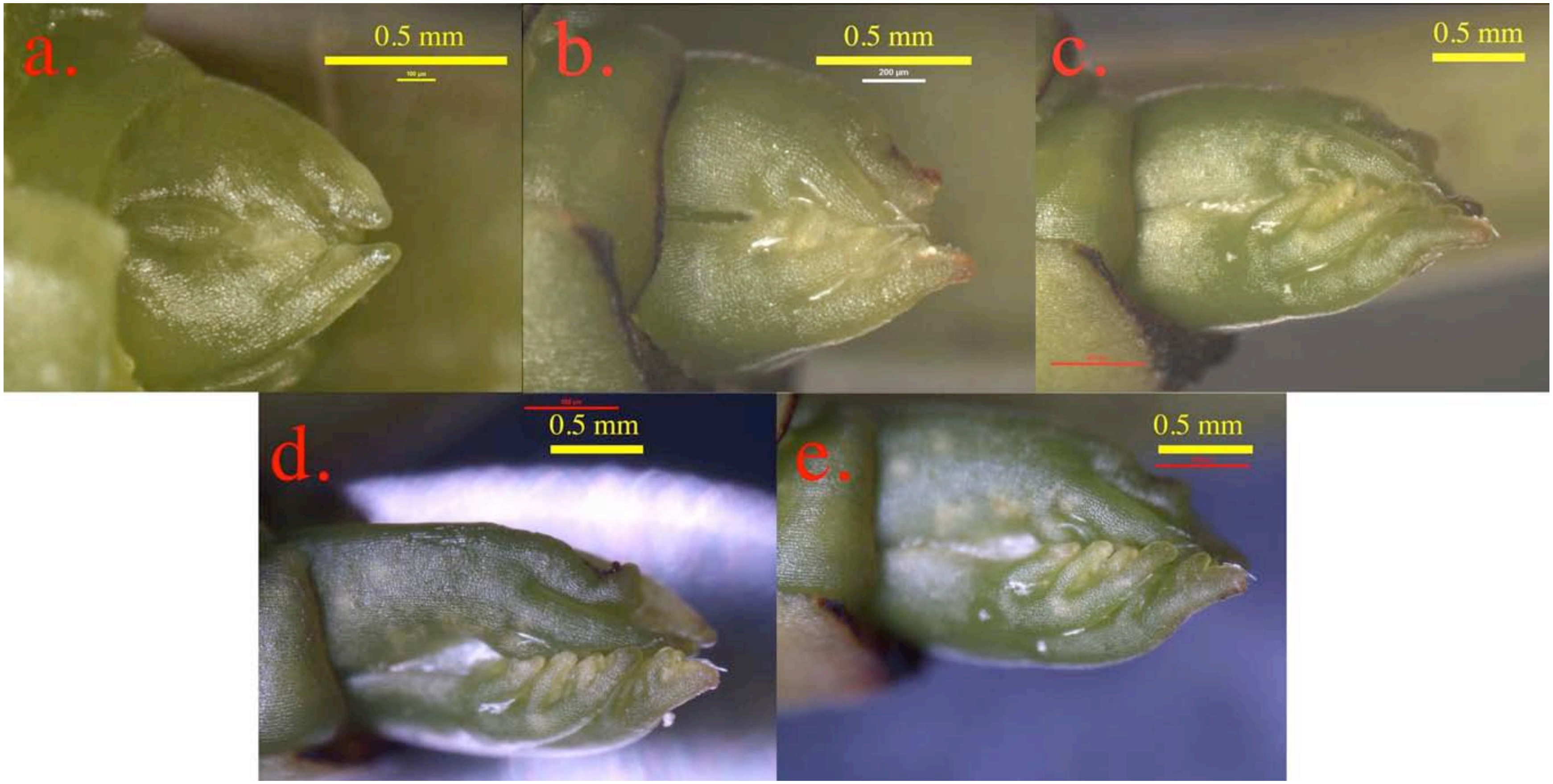
What coordinates the growth of these independent unit to fill the bud ?

A scissor candidate: contact limitation

Two maple leaves, which grow without their envelope

Day 1

Day 4



Day 14

Day 18

We remove one of the two leaves

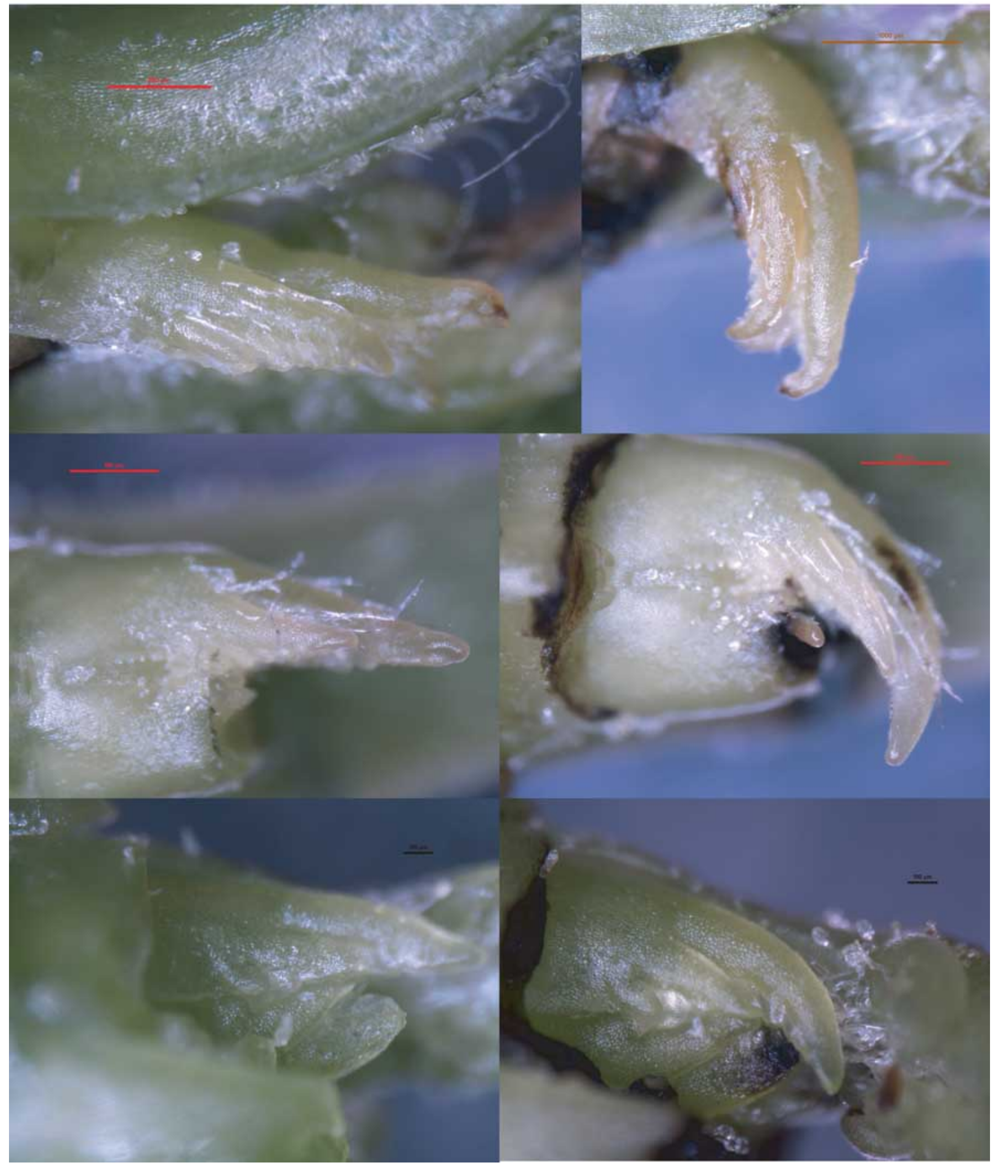
A passive and quick response (1day)

Constraints are no longer compensated.

The remaining leaf curves on itself.

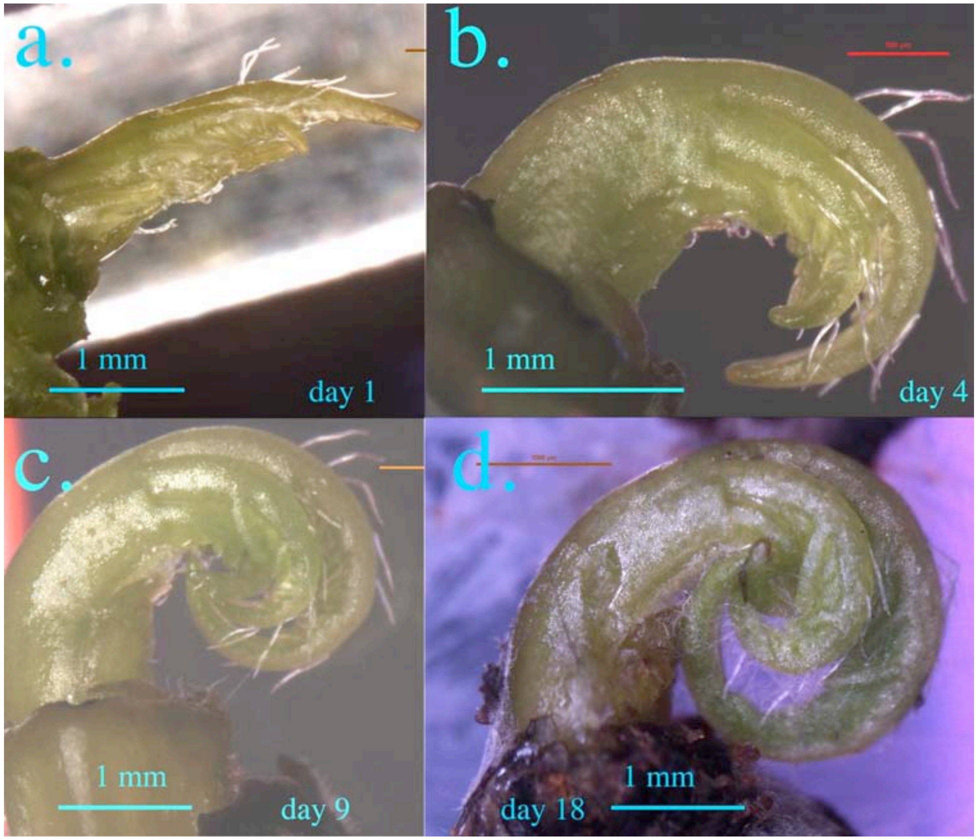
The opposite leaf had a mechanical role to sustain the remaining one.

jour 1 jour 2



Cause of the mechanical conflict

- A long time response (10 days). The leaf grows a lot.

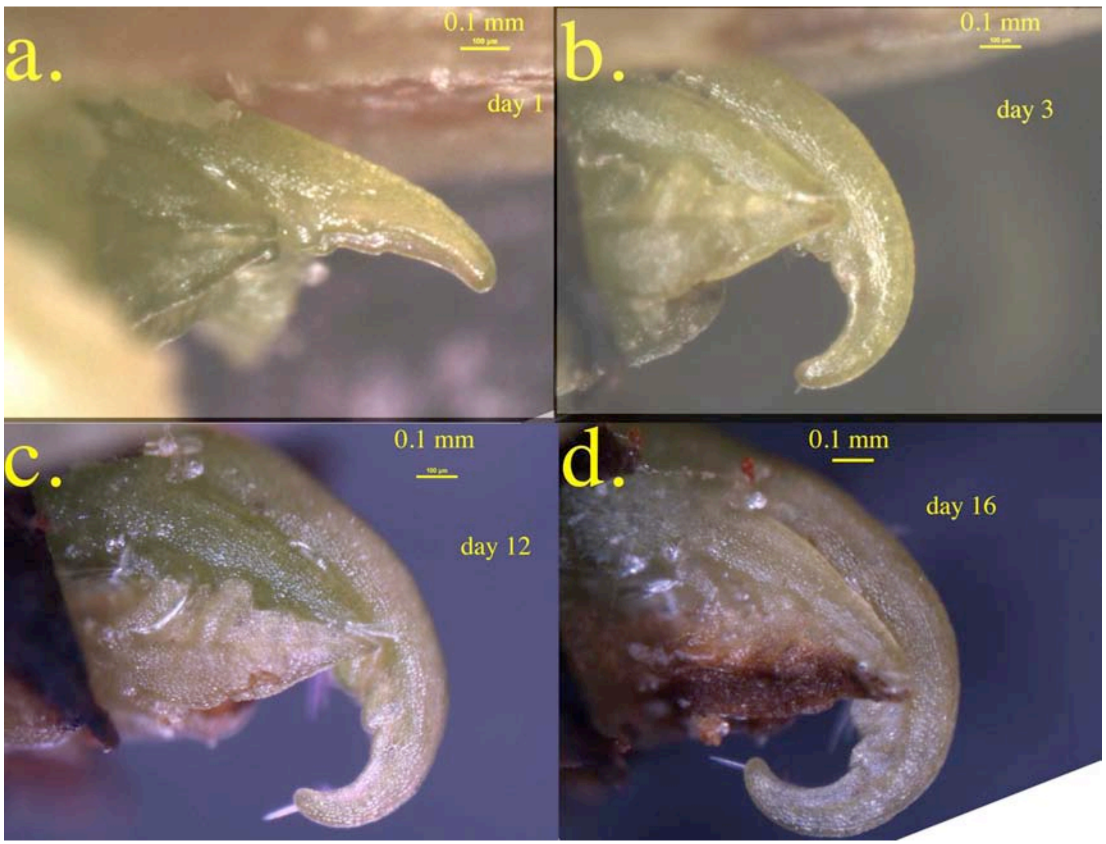


The growth response.

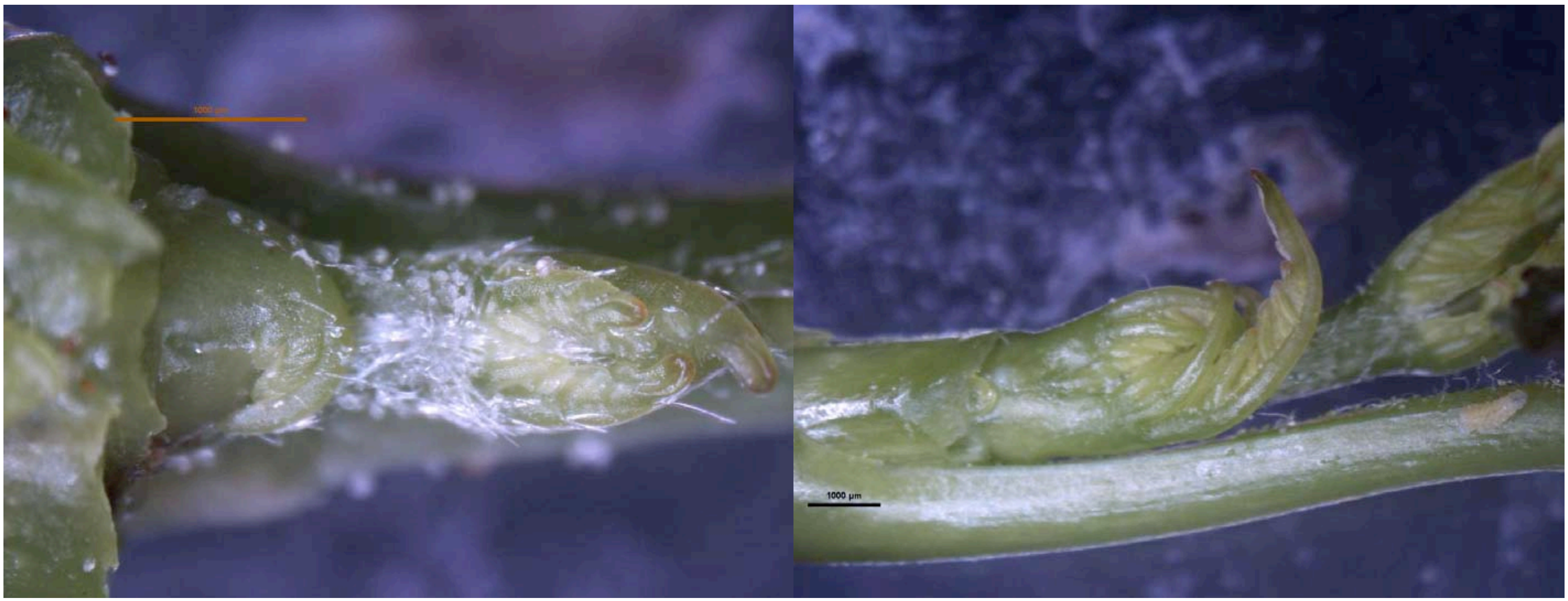
Lobes grow independantly by curving.

The abaxial part of the vein grows more than the adaxial one.

Only the central lobe of the opposite leaf is removed.
The central lobe of the remaining leaf curves, and not the lateral ones, which are still under constraint



Two other examples without surgery



The opposite leaf stabilizes the folding of the other leaf, without which the lobes of the remaining leaves grow independently and curve on themselves.

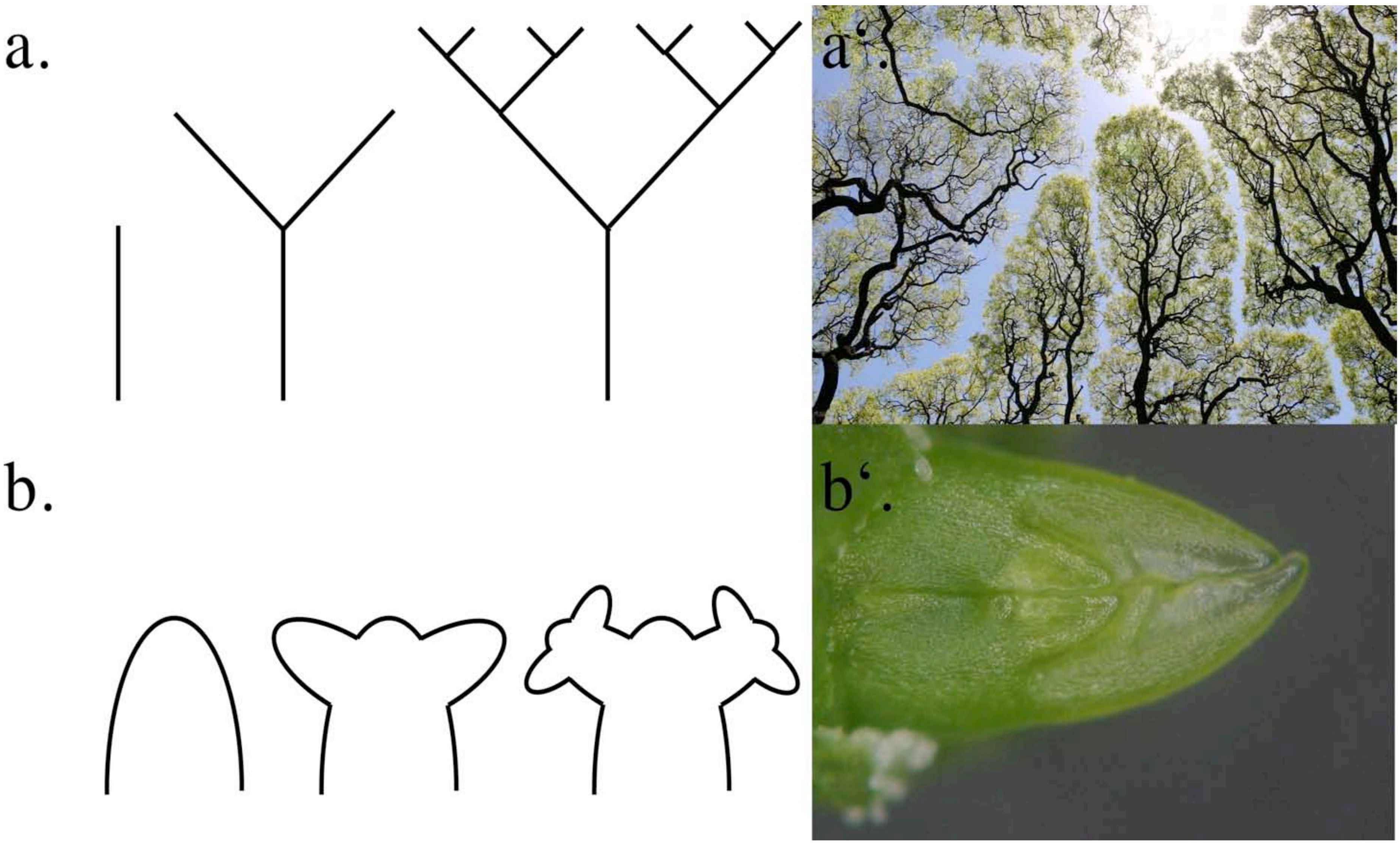
The cause of this bending of the vein might be as in folding - the vacuolization of the abaxial part of the vein.

Each leaf prevents the bending of the opposite leaf because both have the same turgescent pressure.

Conclusion

An equivalent to shyness of crown

Reiteration and limitation by the environment play a role for tree shape formation as for leaf shape formation.

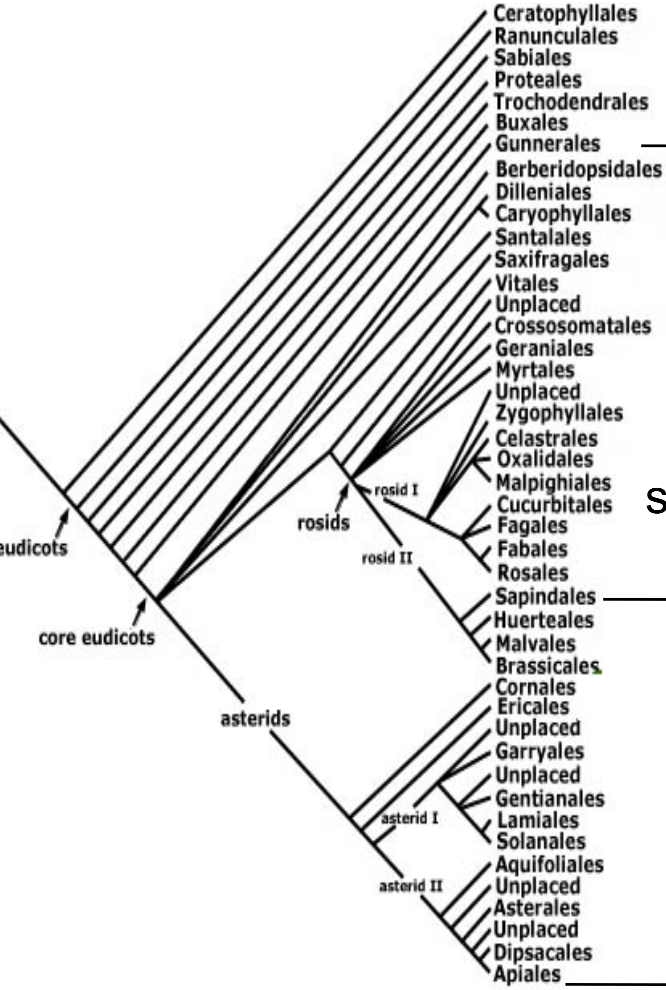


Evolutionary conclusion

What is the evolutionary interest of leaf shape ?

It is not the shape itself.
It is to fold efficiently the surface in a small volume to limit water loss during winter.

It explains the statistical observation of Bayley and Sinott which dates from 1916:
There are many more lobe leaves in temperate climate than in tropical ones.
It is a criterion used by paleontologists to rate the climate of sediment fossils.



Gunera manicata

sycomore

Tetrapanax papyrifer

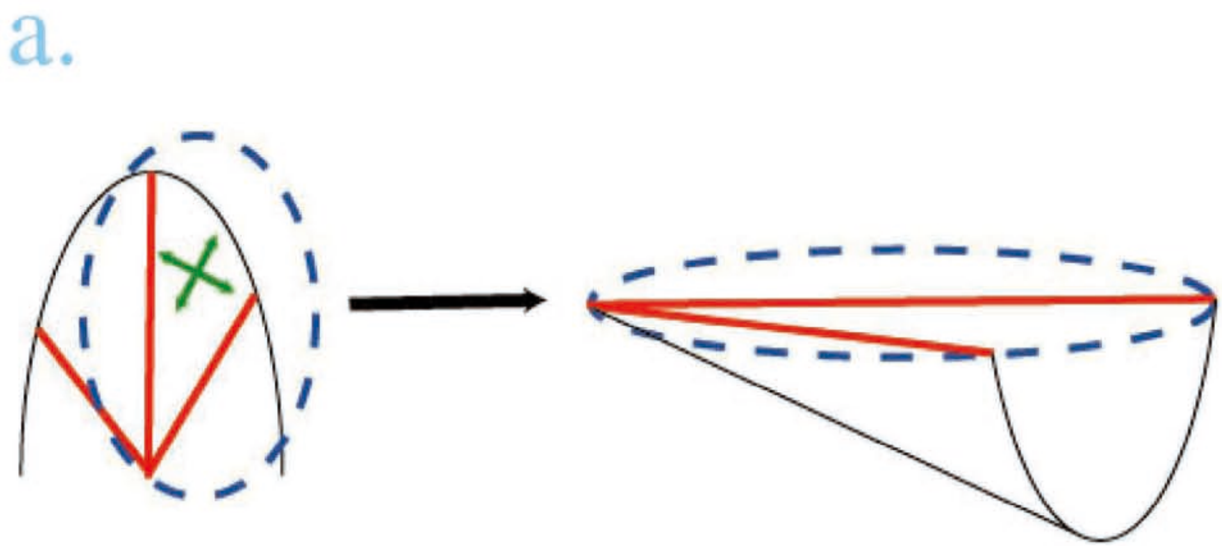
"All *science* is either physics or *stamp* collecting."
Ernest Rutherford

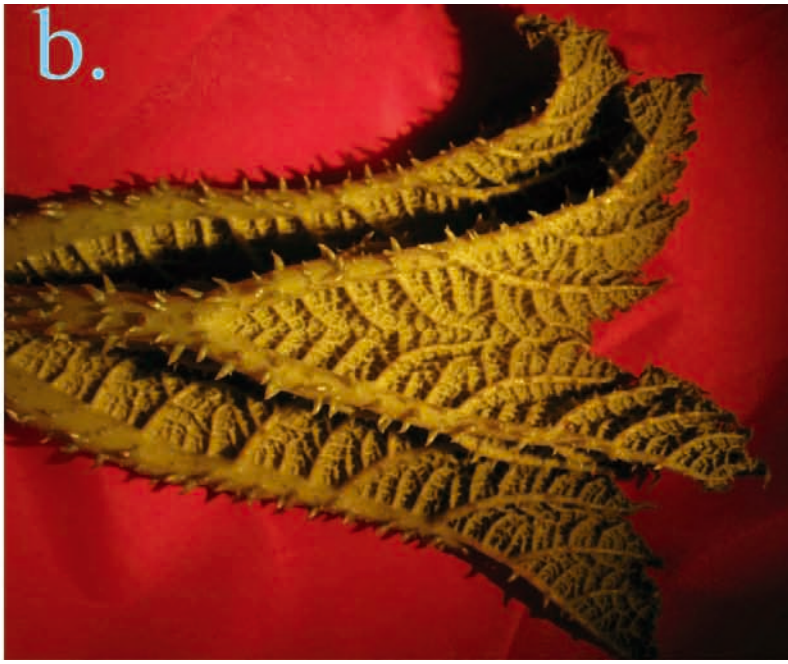
I hope you have appreciated our stamp collection

Vein do an armour around the lamina

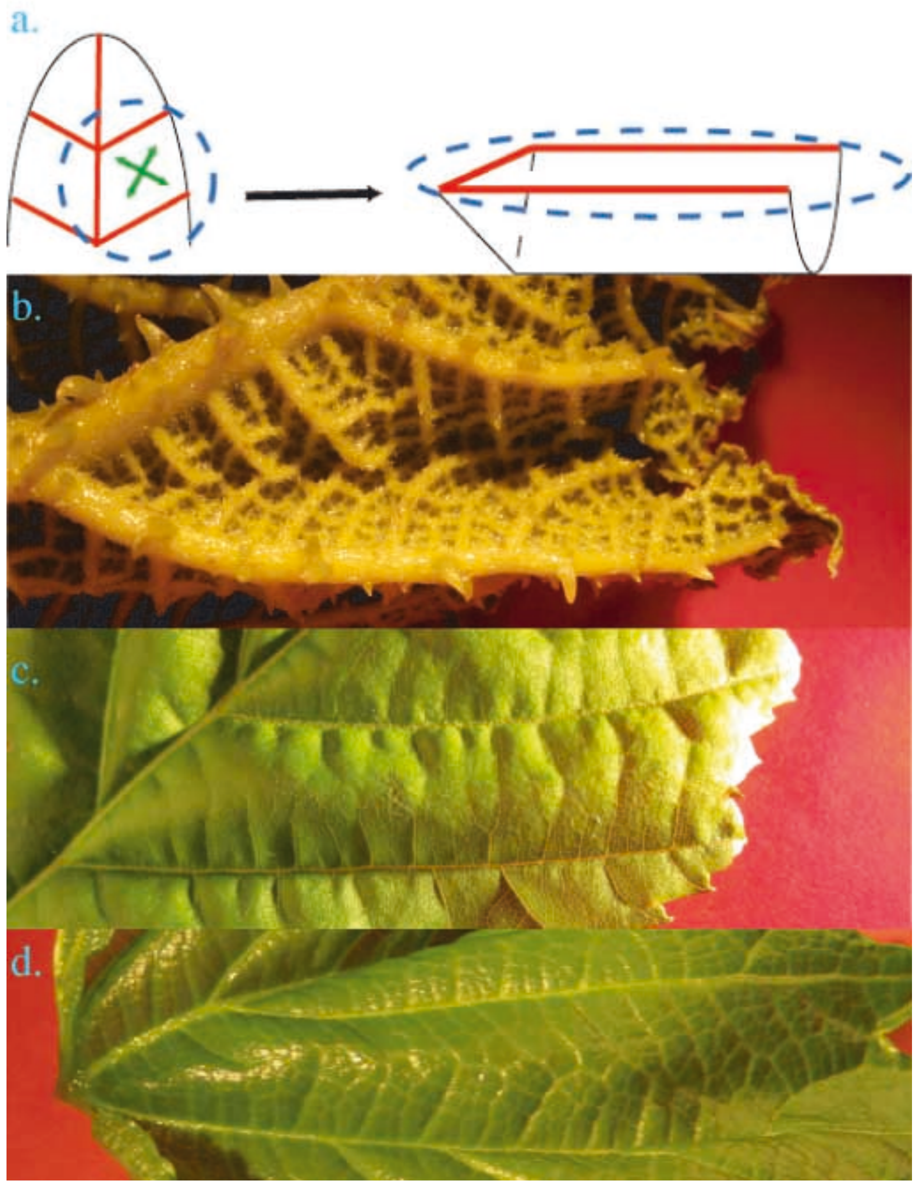
Alle the leaves are folded in the same way.
Veins do an armour around the lamina.
It implies that folds are constitutd by piece of veins bissectors in order to fold one vein the next vein.

Between two veins. Folds are along the bissectrice of the two veins

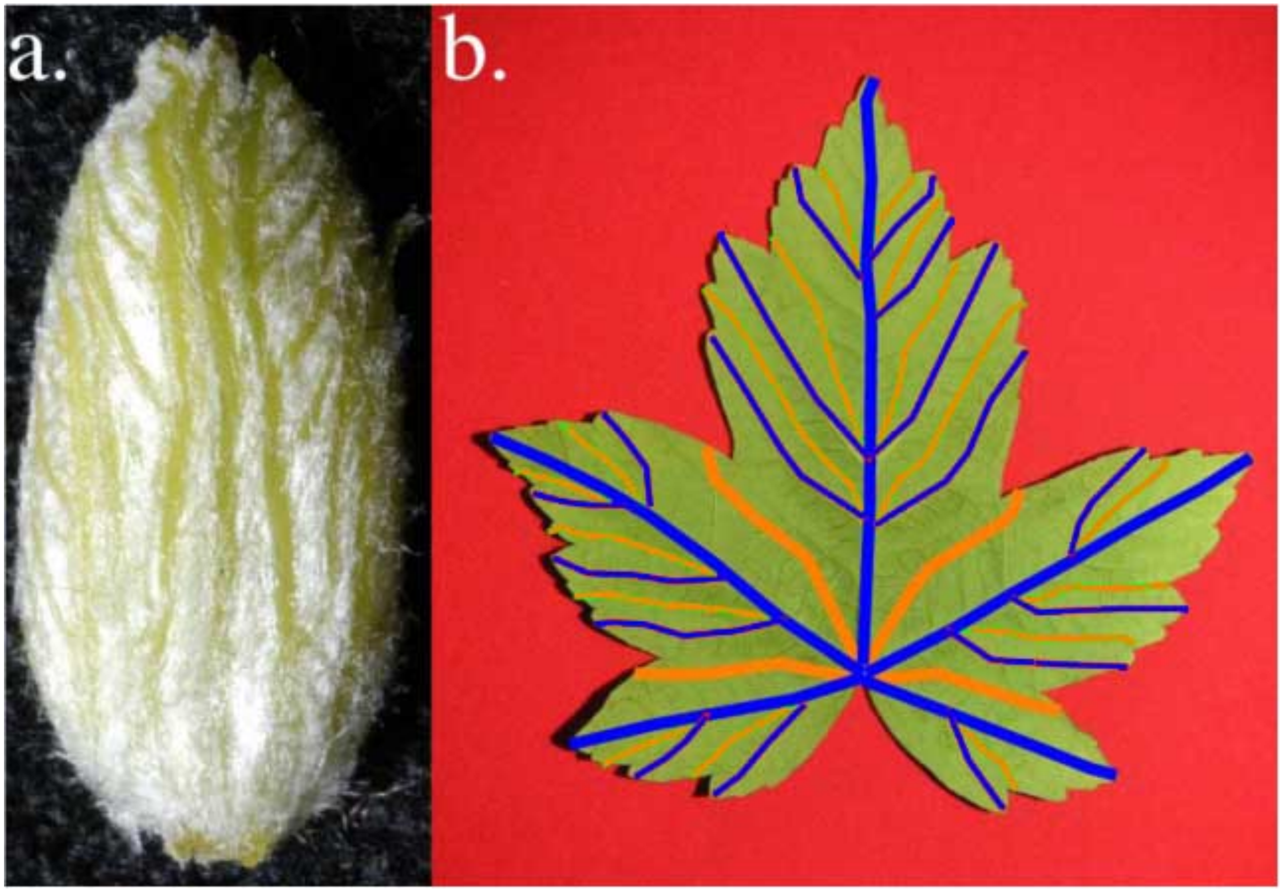




Between three veins folds are along the three bissectrice of these veins



As antifolds are axes of symetrie of the vein. There is some other constrain on leaf shape.



Maple folded leaf

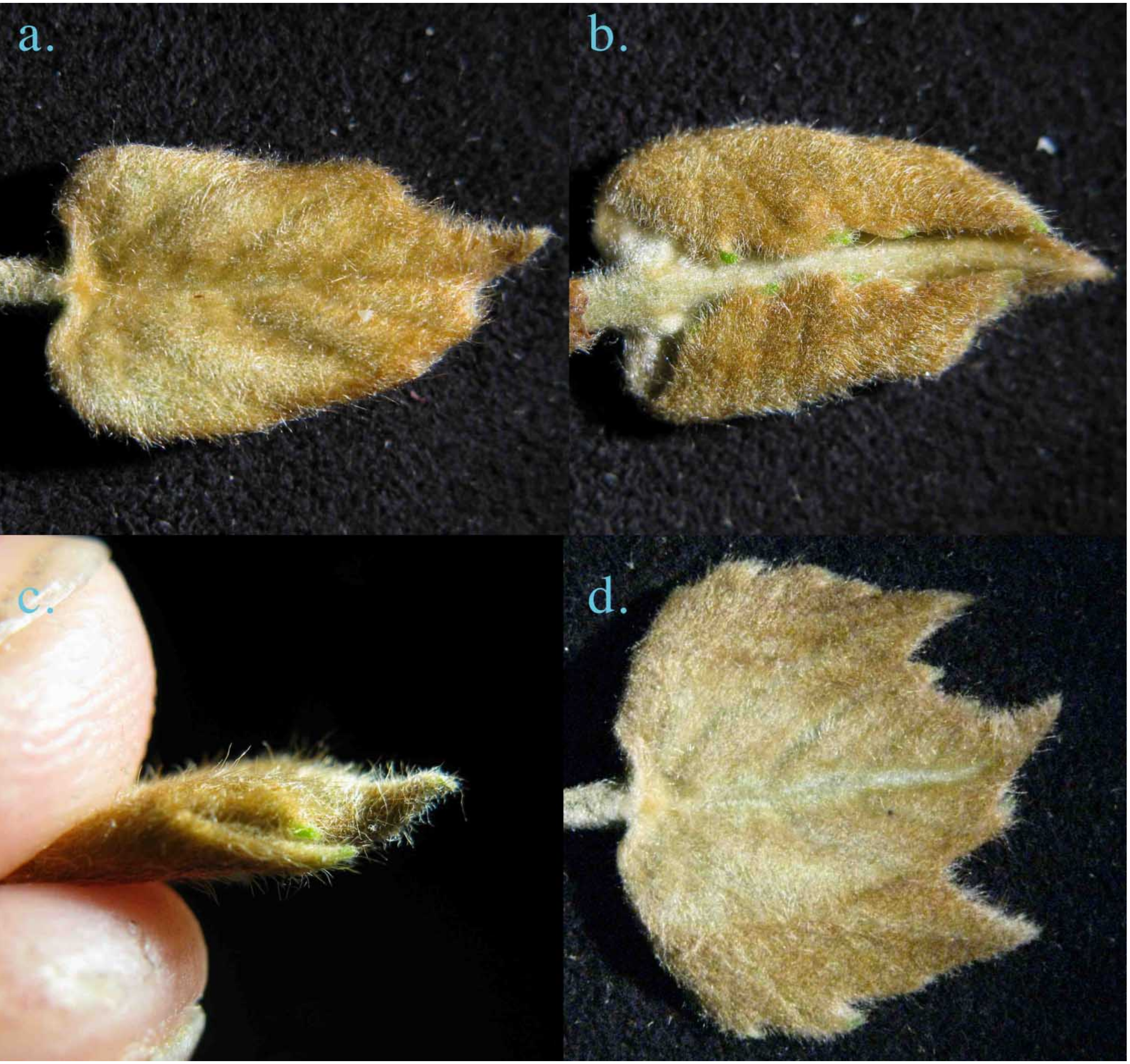
Maple leaf
Blue = Vein
Orange = Medial axes of the vein

Medial axes of the vein correspond nearly to the antifold

Difference of packing between the two first maple leaves generation implie
a difference for leaf shape.
The first generation is less constraint than second one so leaves are larger.

A cut of Acer pseudoplatanus bud

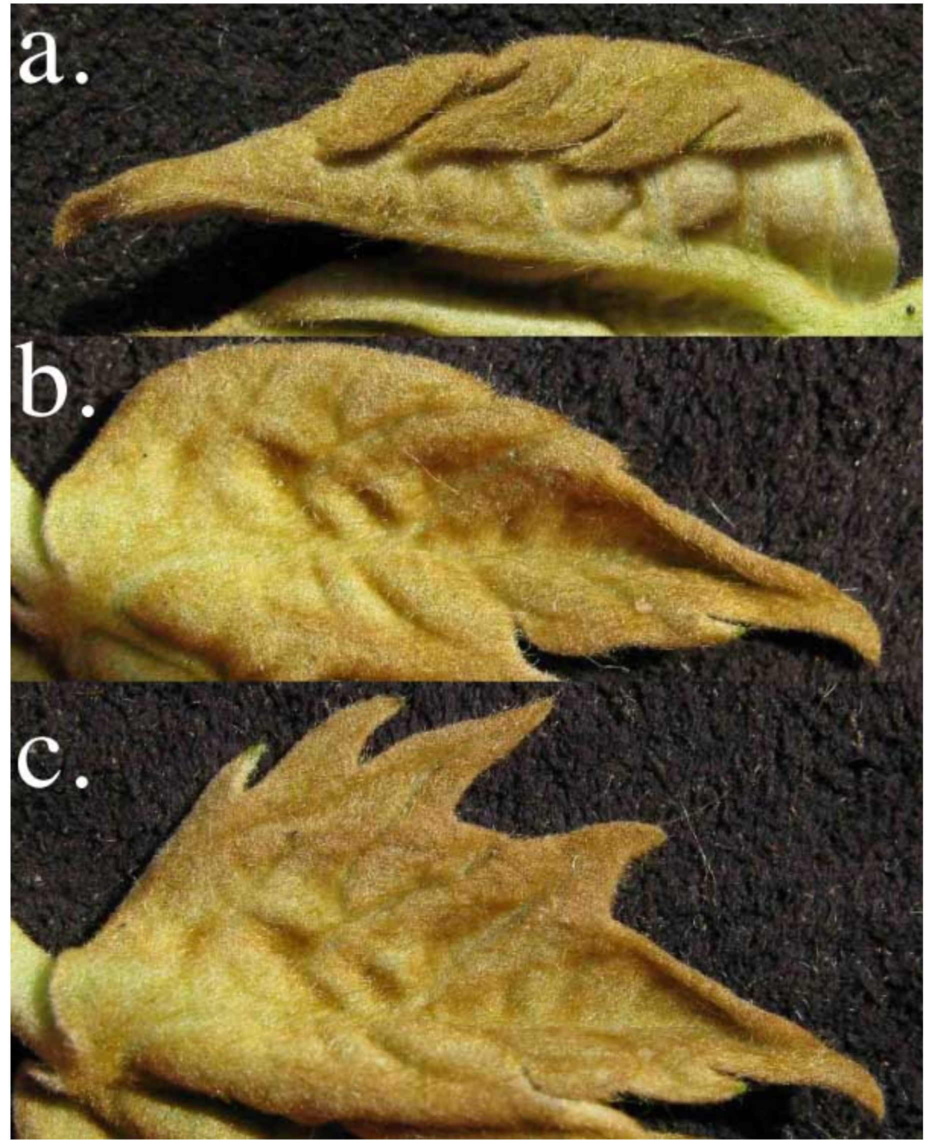
Two succesive generation of Acer pseudoplatanus Leaves .
Second generation is thiner than the first one.



Platane leaf

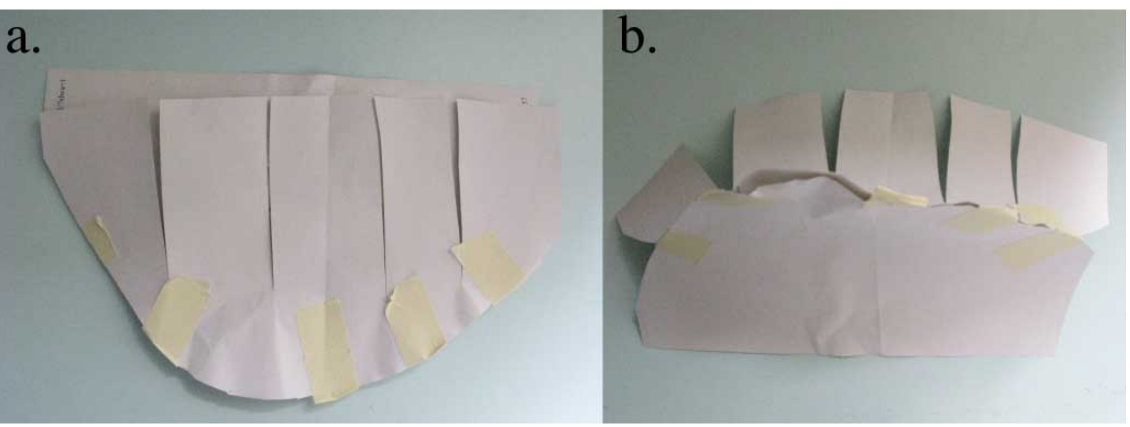
Leaf shape has a
link with folding but
not as in kirigami.
Fold are not along the
vein.
Fold are still axe of symetrie
of main sinus.

Same Platane Leaf detail
After and before unfolding



In case of platane folds are bit round not straight line.
It plays a role to create the shape of the leaf.

As in the case of the sheet of paper, the slits become lobes after unfolding. Opening the round folds enlarge the slits, which become lobes.



Pavement cell of the red cabbage. It is constituted by two half leaves, which are intricated. It is delimitated by two successive phylotactic spirale.

A case of mecanical folding the red cabage. Leaf fold because they touch veins of leaf in the precedent and next parastiche (black dashed line). It makes a repetitive cell of pavement delimitated by two successive parastiche.