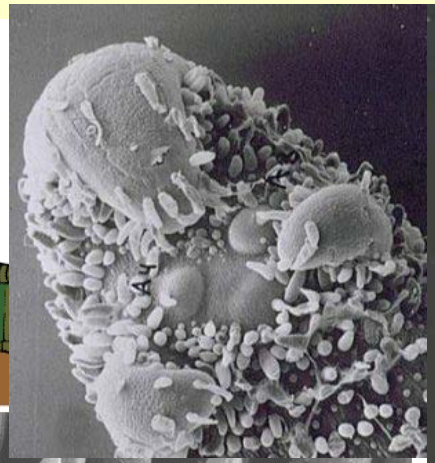
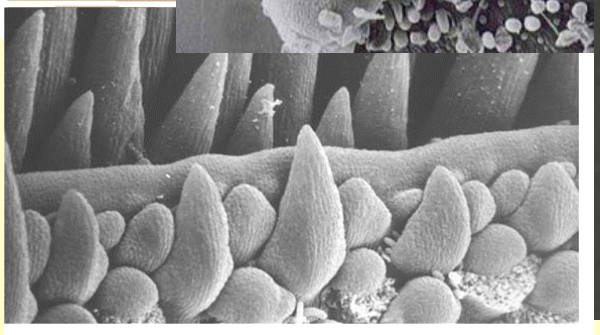
Euro Evo Devo 2012 Conference (Lisbon, 13 July, 2012)

Symposium "Morphological Misfits"

Evolution of morphological misfits in seed plants such as Podostemaceae, allowing for growth in tropical rivers

Rolf Rutishauser (Institute of Systematic Botany, University of Zürich)





- **What are morphological misfits?**
- **Agnes Arber & Rolf Sattler**
- **Podostemaceae as case study**

What are morphological misfits in plants, animals and other organisms such as fungi, bacteria?

Morphological misfits do not fit into our mind-born structural categories for describing and understanding organisms in an evo-devo context.

The german term BAUPLAN means body-plan, but captures also the idea of the architectural constraints existing in such a functional design.
Major BAUPLAN's modifications within a taxon are not tolerated.

Source: P. Cincinnati (2005) Human Bauplan Anomalies. Pediatric Research 58: 366–366.

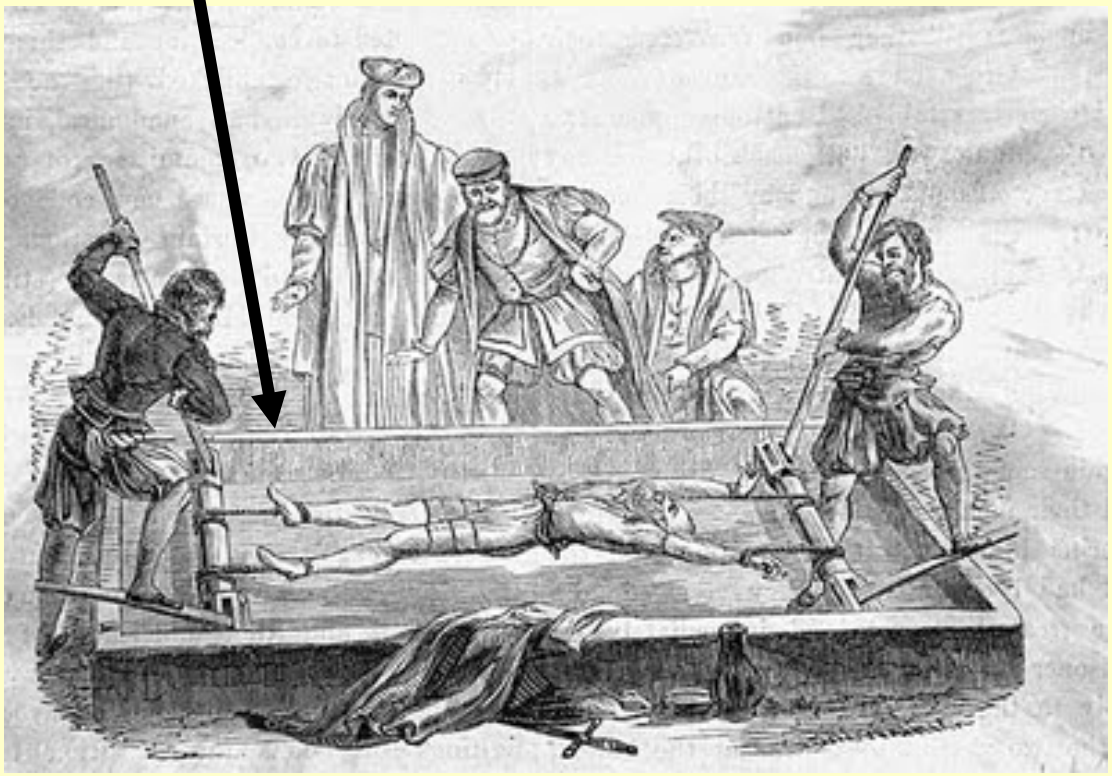
Traveller in Procrustes bed as metaphor for

MORPHOLOGICAL MISFIT

Procrustes was a son of Poseidon, a smith and a bandit. He used to lure travellers to their deaths by offering them rest on an iron bed. Once his offer had been accepted, he would make the traveller fit the bed, either by amputating his legs or stretching him out sufficiently to fit.

Bed length = bauplan

Traveller too tall or too short = morphological misfit



Source: Internet

What are morphological misfits in plants, animals and other organisms such as fungi, bacteria?

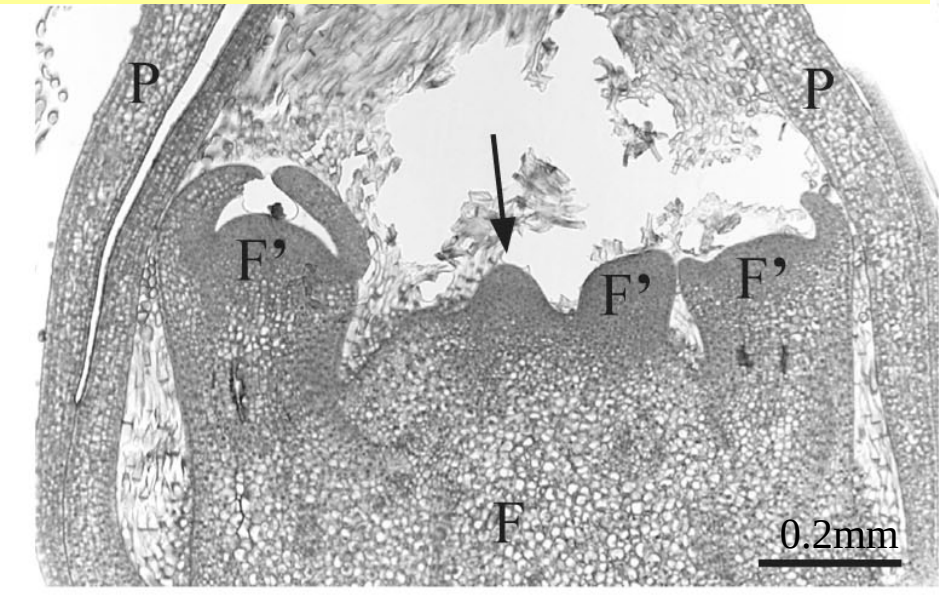
Morphological misfits are „hopeful monsters outside the geneticist‘s lab“. Inspite of their aberrant architecture (not fitting our ideas on „BAUPLANs“) morphological misfits may be well adapted to their respective habitats.

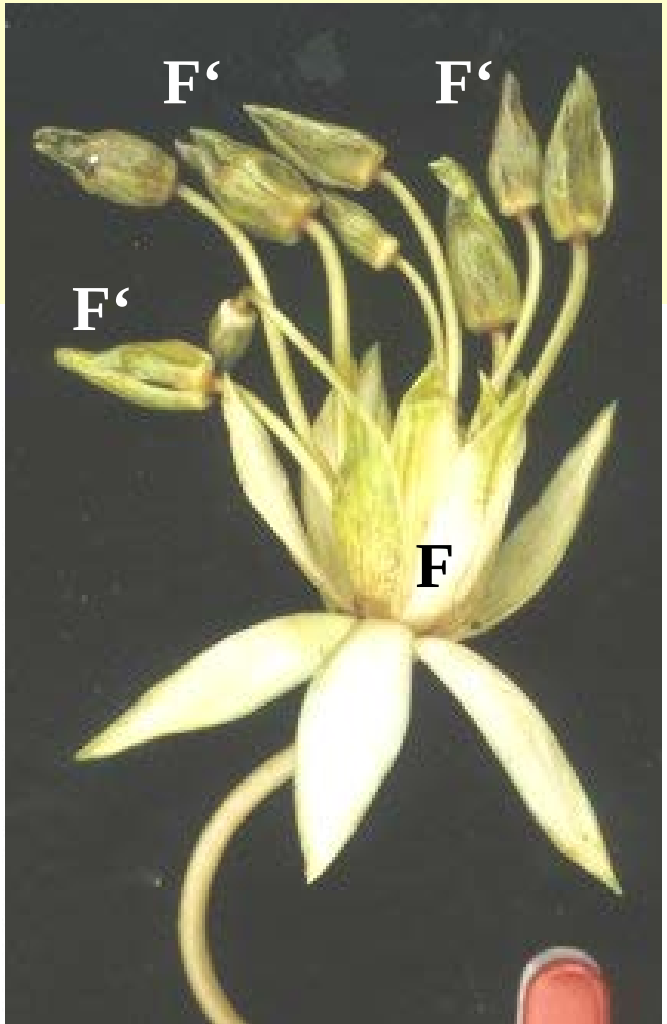
They are „morphological misfits“ to a botanical discipline, not misfits for a successful existence (cf. A. Bell 1991).

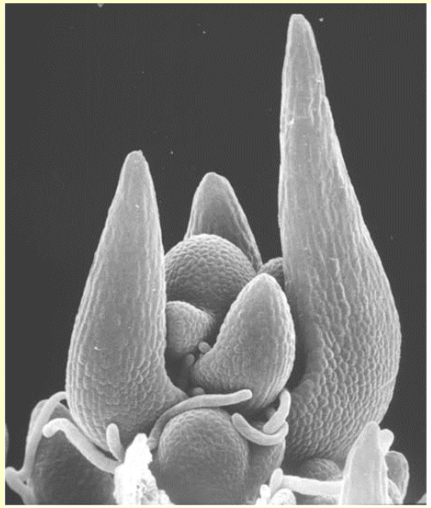
Here are three examples collected in the field…

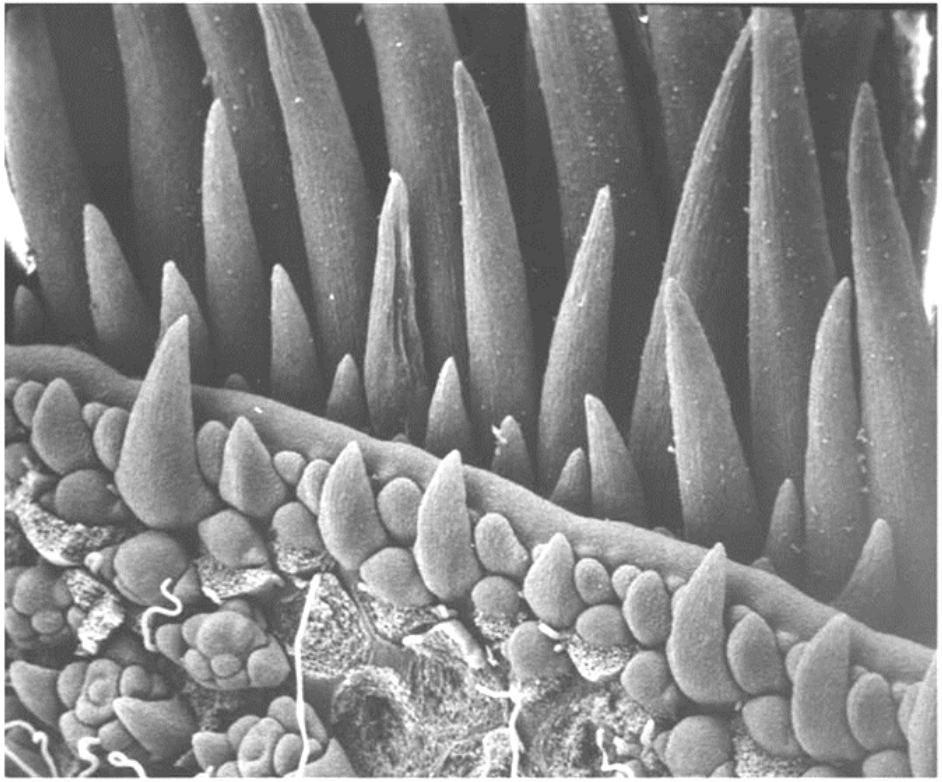
„Branching flowers“ (not allowed by definition!) in *Nymphaea prolifera* (Latin America) as hopeful monster (Grob et al. 2006 in Journal of Plant Research)

The mother flower meristem (F) switches back to shoot apical meristem (rhizome identity), resulting in several, sterile daughter flowers (F’), acting as asexual propagules.





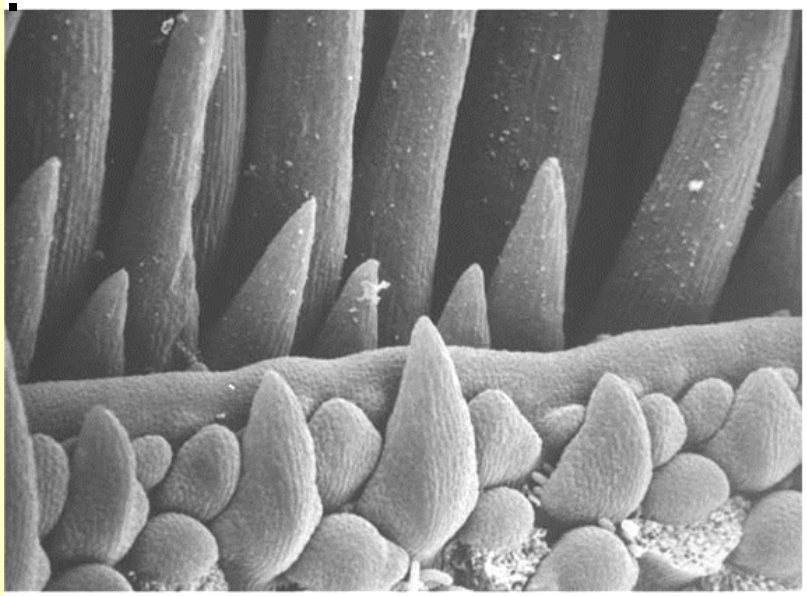


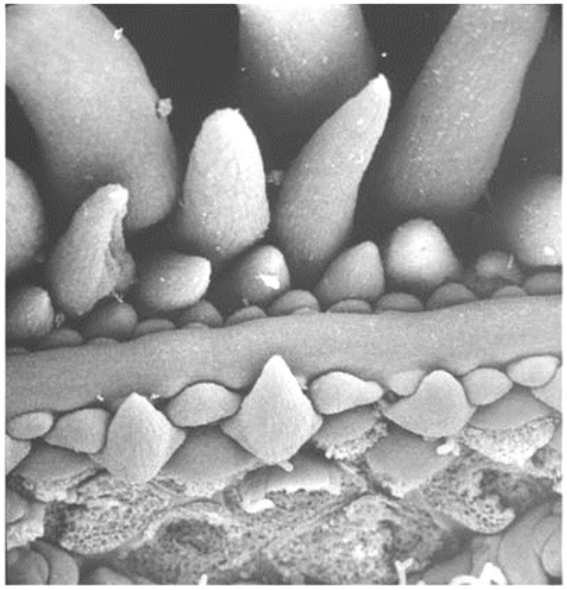


Fasciation in flowering plants (e.g. *Salsola kali*, Chenopodiaceae) as „hopeful monster outside the geneticist‘s lab“….

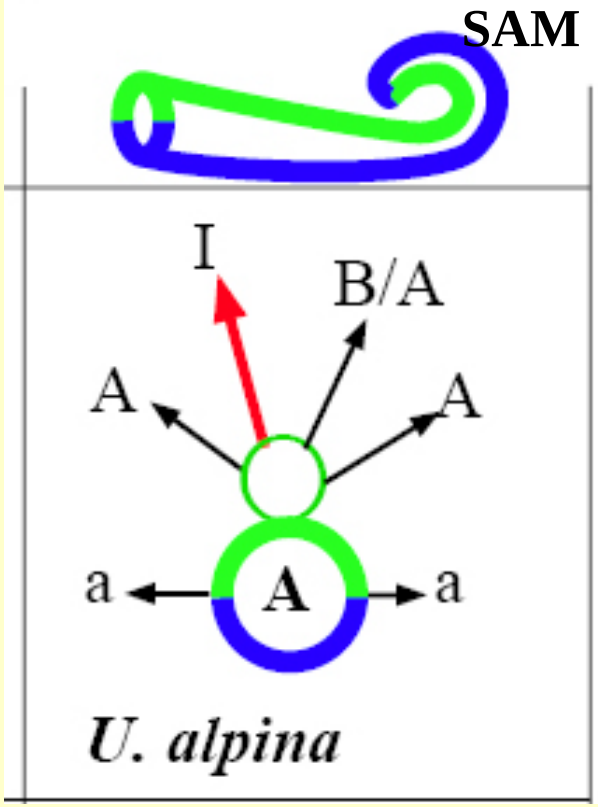
Shoot apical meristem (SAM) becomes a meristematic line….

(Rutishauser, found at North Sea coast)





Bladderworts (*Utricularia*, Lentibulariaceae) as hopeful monsters outside the geneticist‘s lab (Grob et al. 2006 in J.Plant Res.)



Lentibulariaceae e.g. *Utricularia alpina* (trop. America)

Dorsiventral stolons (A & a) arise from leaf sites (B)

Stolon tips as coiled apical meristem

I = inflorescence

Agnes Arber (1920, p. 107) **on Utricularias:** „The attempt to fit so elusive a genus into the **Procrustean bed** of rigid morphology, is doomed to failure. It is probably best… to accept that the vegetative body of the Utricularias partakes of both stem nature and leaf nature."

What are morphological misfits in plants, animals and other organisms such as fungi, bacteria?

Morphological misfits are „hopeful monsters outside the geneticist‘s lab“. Inspite of their aberrant architecture (not fitting our ideas on BAUPLANS) morphological misfits may be well adapted to their respective habitats.

The fourth example are the PODOSTEMACEAE = podostems = riverweeds = flowering plants adapted to river rapids and water-falls in the tropics. I will show them later during my talk…

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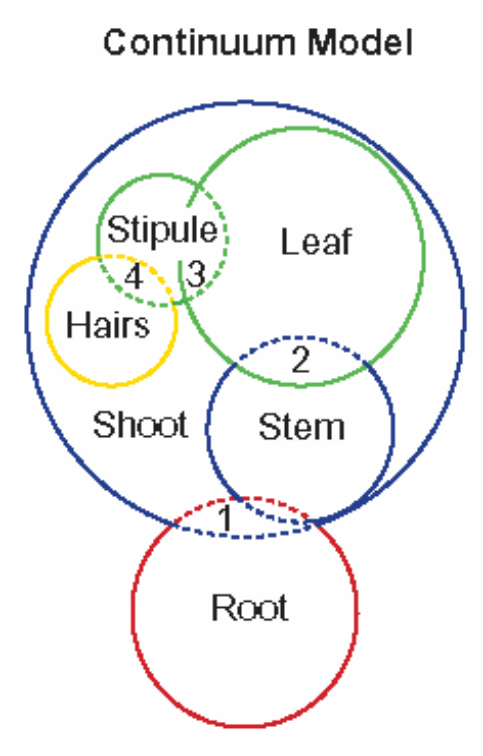
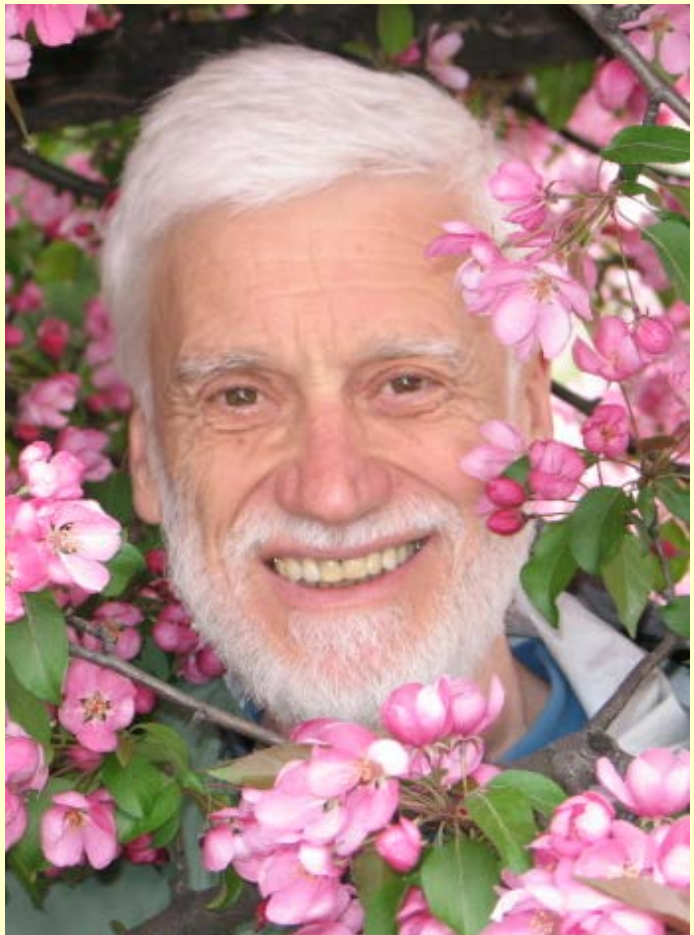


- **What are morphological misfits?**
- **Agnes Arber & Rolf Sattler**
- **Podostemaceae as case study**

Agnes Arber (1879 – 1960)
British botanist, historian, philosopher of biology, first woman to receive the Gold Medal of the Linnean Society of London.

Rolf Sattler *1936 Canadian botanist and biophilosopher, research on the development and evolution of flowering plants
www.beyondwilber.ca/about/rolf_sattler.html



Agnes Arber (1879 – 1960) and her three “late” books

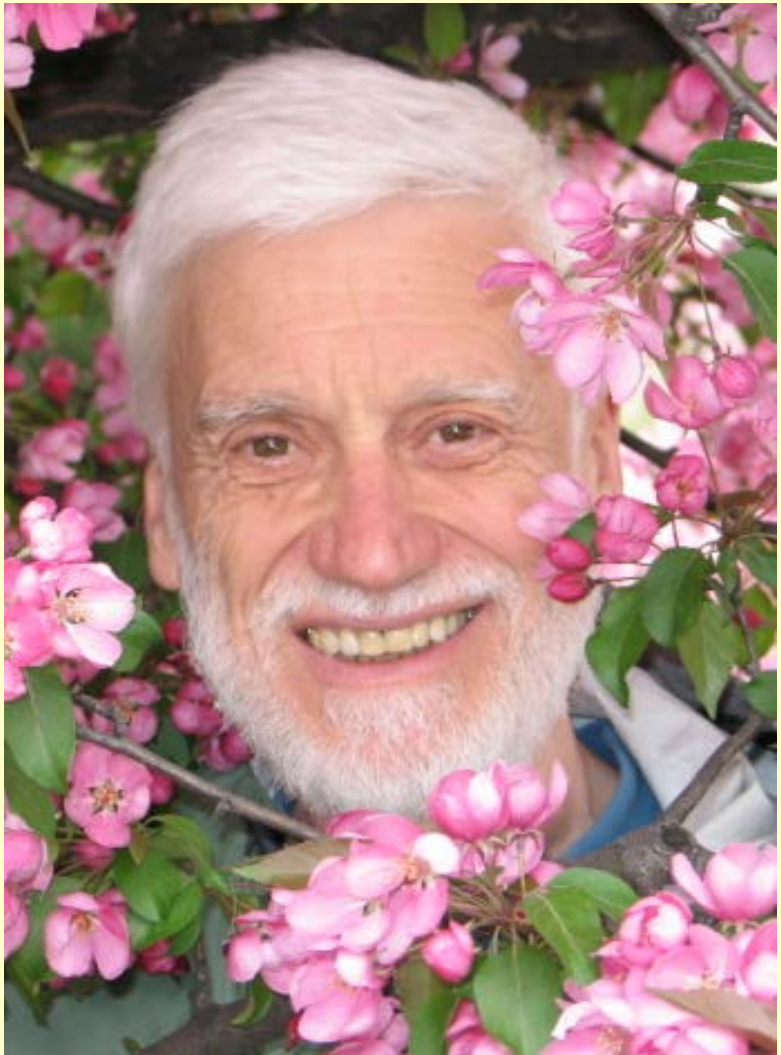
1950: The Natural Philosophy of Plant Form
1954: The Mind and the Eye
1957: The Manyfold and the One

Arber (1950) anticipated the holographic paradigm for plants: **“The whole is built up of the parts in such a way that each part bears something of the whole within it.“**

Sandro Minelli (2003) proposed similar **hypothesis of axis paramorphisms for animals**: „It may be justified, to look for correspondences between the appendages and the main body axis of the same animal, as the latter might be the source of the growth and patterning mechanisms which gave rise to the former. Int.J.Dev.Biol.47: 573-581.

Rolf Sattler (*1936)

giving emphasis on continuum and process morphology

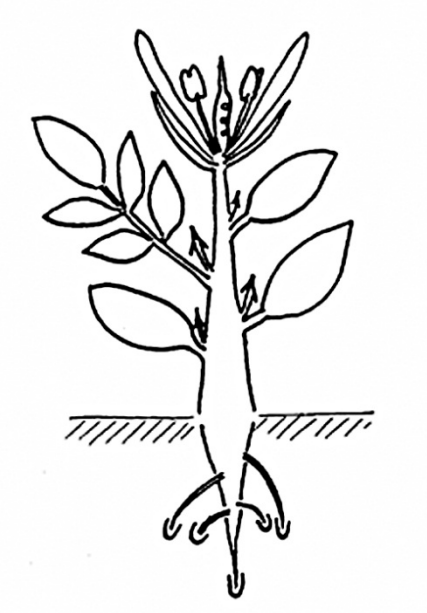


„Organisms are better viewed as a continuous flowing process of unfolding which encompasses the entire unbroken movement from fertilization to death.“

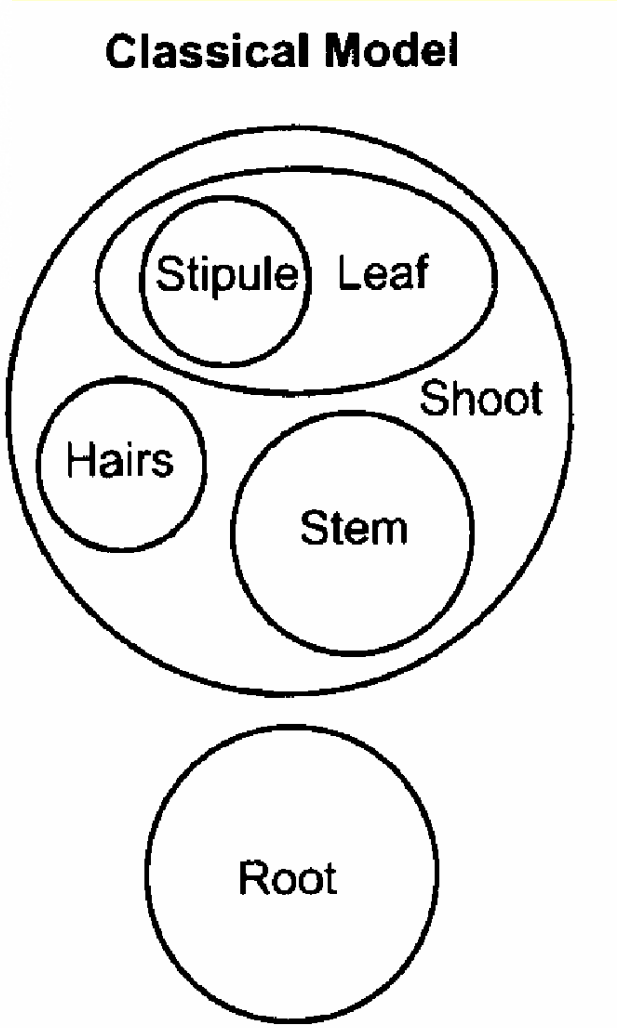
„According to process morphology, structures do not have process(es), they *are* process(es).“

www.beyondwilber.ca/about/rolf_sattler.html

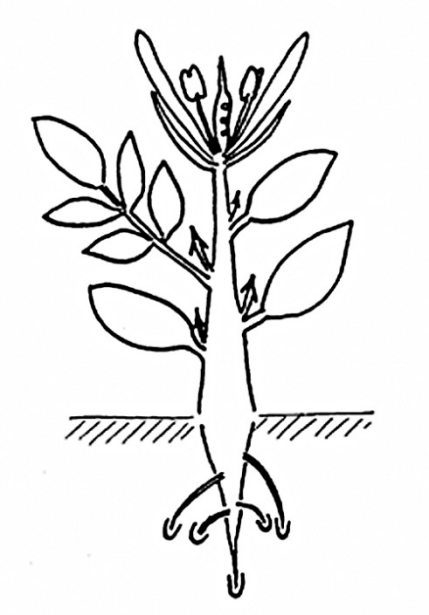
Organisms as a continuous flowing process: THE DANCE as metaphor […performed by Rolf Sattler 4 July 2012]



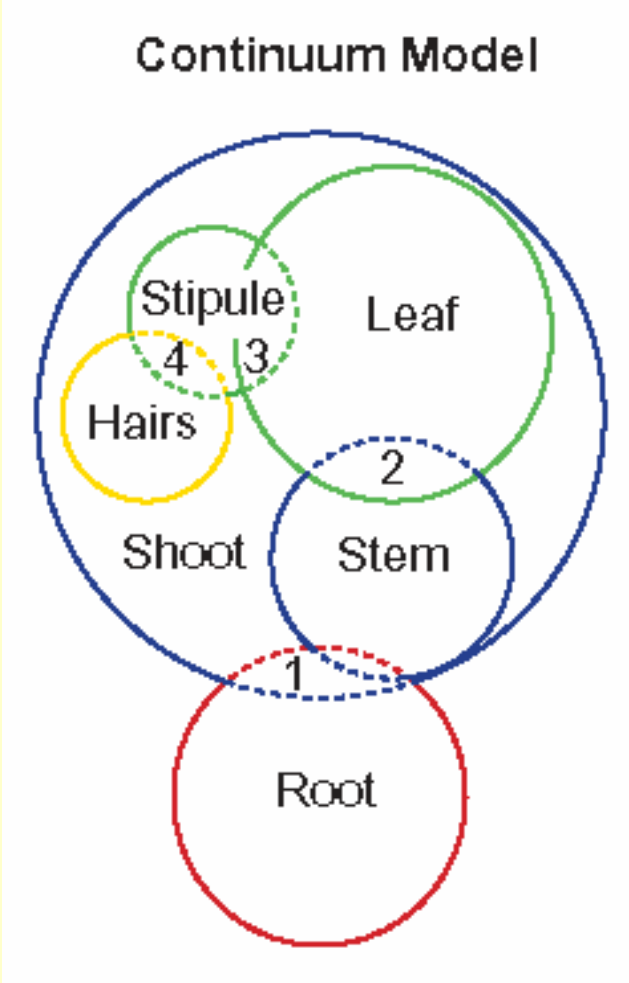
Bauplan of seed plants, viewed as CRS model: no intermediates allowed!



Typical seed plants have roots, stems and leaves, with stems and leaves forming shoots and flowers. Lateral shoots arise from axils of subtending leaves. This CLASSICAL ROOT-SHOOT MODEL (CRS) appears suitable for terrestrial habitats, but…



Bauplan of seed plants, viewed as continuum model: 1 – 4 = intermediates between structures („organs“) accepted by CRS model.



…. but some taxa lost or transcended it by switching to aquatic environments, or for other reasons.

DYNAMIC & CONTINUUM VIEWS on bauplan evolution in seed-plants were anticipated by Agnes Arber (1879 – 1960) and Rolf Sattler (*1936) and their schools of thought.

Arber (1950) proposed the PARTIAL-SHOOT THEORY OF THE LEAF in vascular plants. Leaves are partial shoots that show reduced growth capacity, „revealing an inherent urge towards becoming a whole shoot, but never actually attaining this goal, since radial symmetry and the capacity for apical growth suffer inhibition".

Recent developmental genetic evidence (e.g. KNOX genes, auxin/PIN developmental module) **has supported aspects of the evo-devo hypotheses of Arber and Sattler.**

„Perhaps the acquisition of a shoot-like identity promotes leaf dissection… Compound leaf primordia are shoot-like, and leaflets initiate in a process homologous to leaf initiation at the shoot apical meristem."

Source: D. Koenig & al. 2009. Development 136: 2997-3006.
http://en.wikipedia.org/wiki/Agnes_Arber

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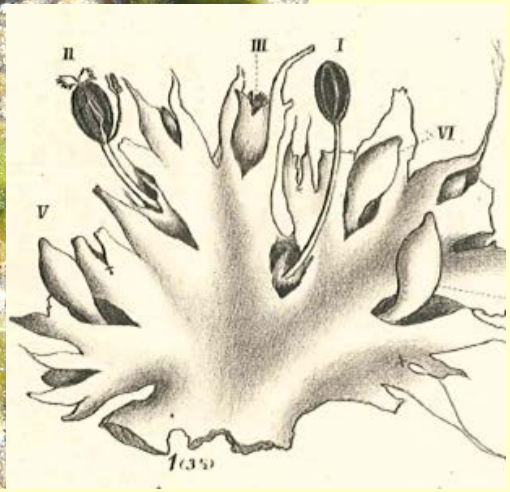

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- **Podostemaceae as case study**

What are Podostemaceae (podostems = riverweeds)?

e.g. *Podostemum ceratophyllum* (Eastern N America)

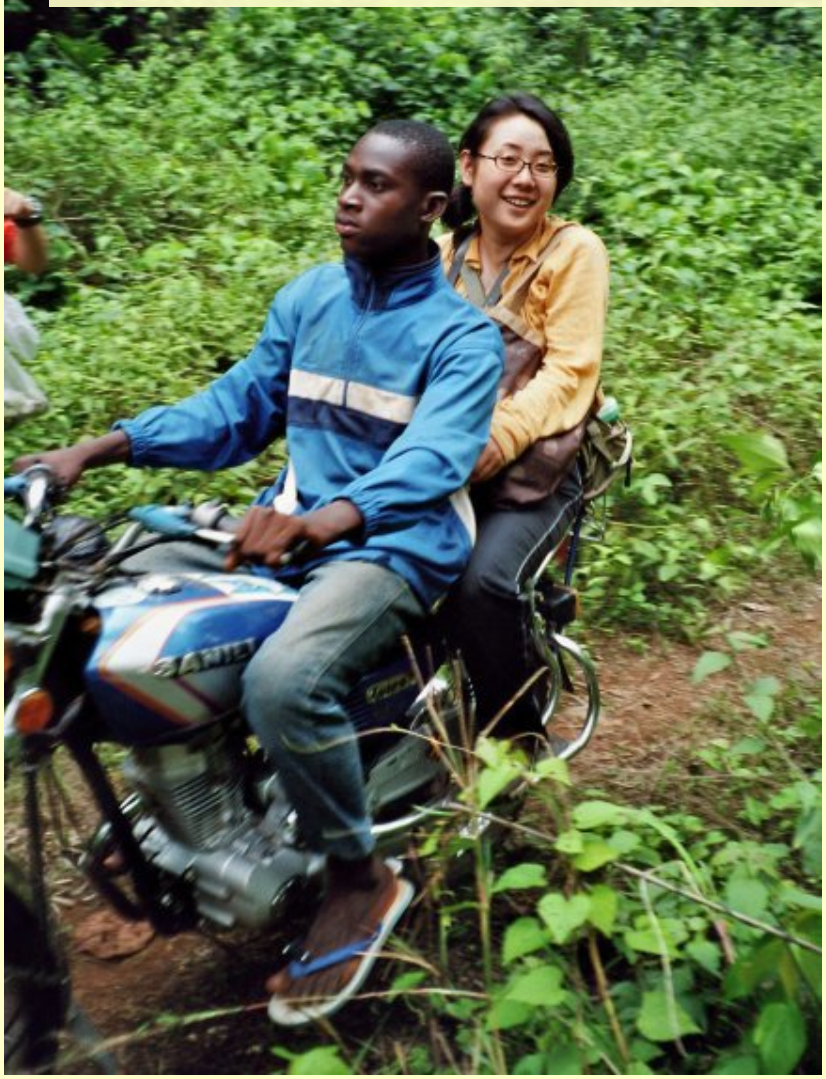
- Flowering plants – Eurosids – clusioid Malpighiales, related to St.John's worts = Hypericaceae (Gustafsson & al. 2002, Ruhfel & al. 2011)
- Podostemaceae-Hypericaceae clade appearing 76 mya (Davis et al. 2005)
- 54 genera / c.300 spp.
- Only in vitro culture
- Visit our website: www.systbot.uzh.ch/static/podostemaceae

Where to find podostems? In tropical waterfalls and river rapids!

80 km on motorcycle

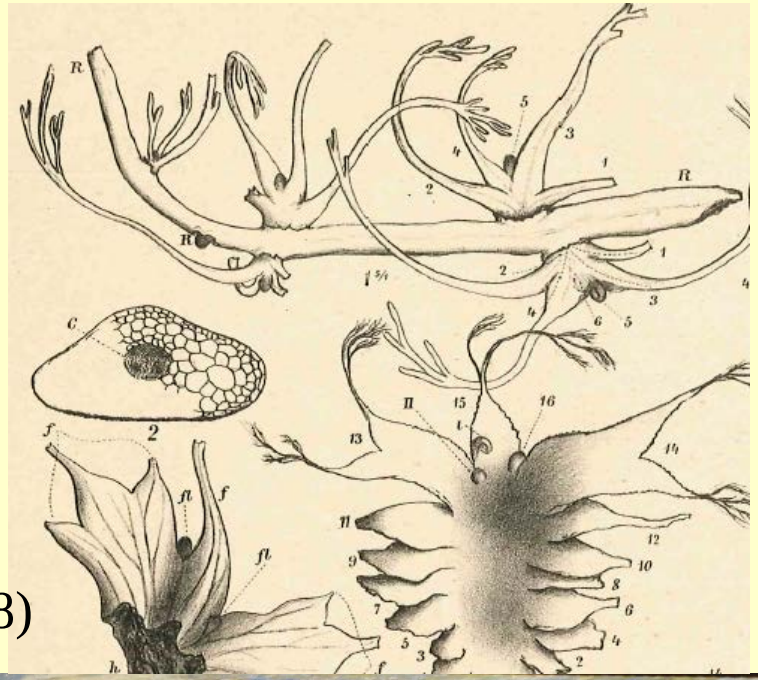
Podostemaceae Trip Febr. 07 – Mve'élé Falls in S Kamerun

with Gabriel Ameka, Jean-Paul Ghogue, **Natsu Katayama**, Satoshi Koi, Koni Huber & RR



Where to find podostems?

e.g. *Lophogyne lacunosa* in SE Brazil (August 2010)



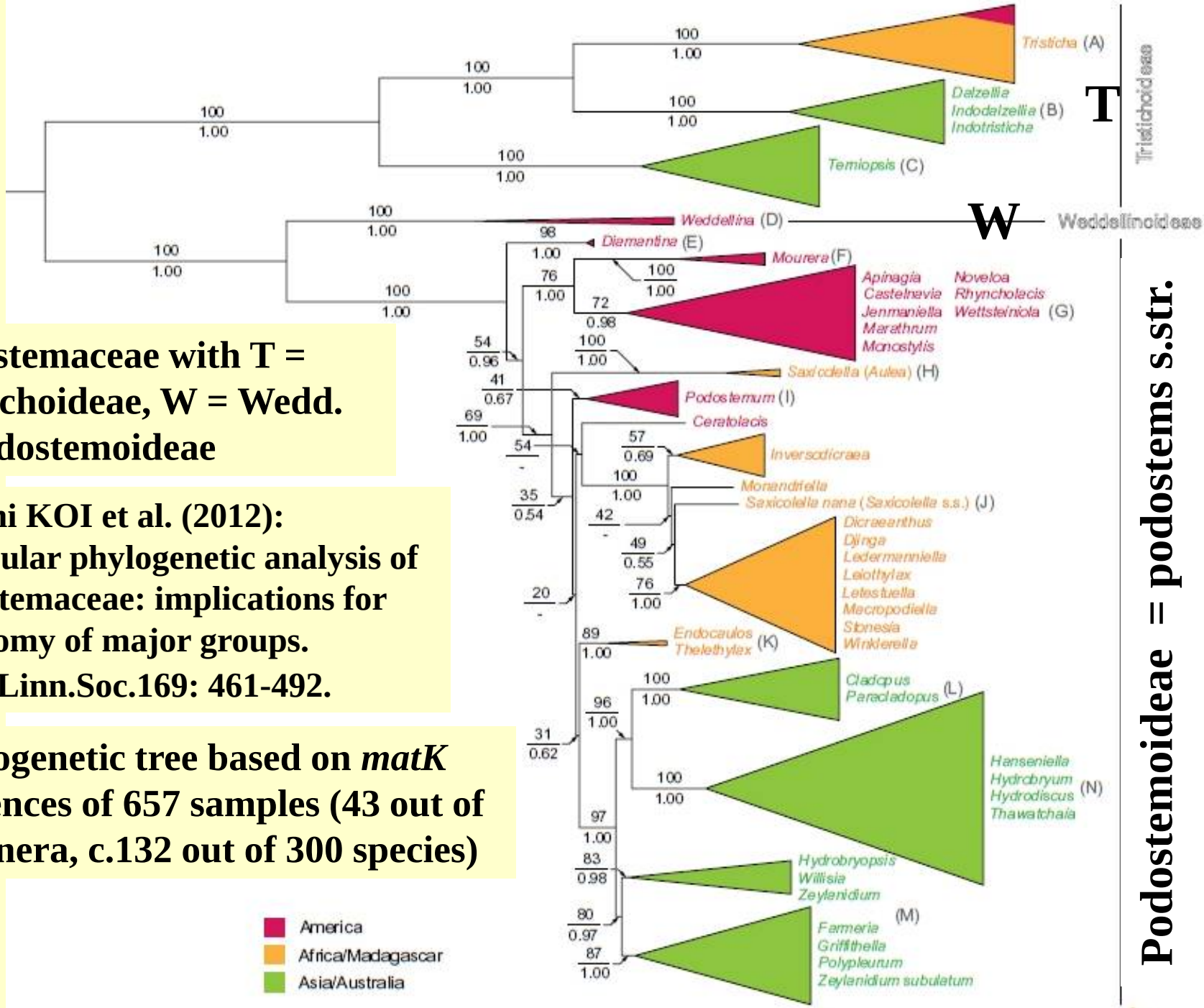
(Warming 1888)

Podostems = river-weeds specialise in living in fast-moving, temporary streams and waterfalls that become dry for part of the year, usually on rocky surfaces. Many podostem species are known for having small distributions, often restricted to a single river.

Podostemaceae with T = Tristichoideae, W = Wedd. & Podostemoideae

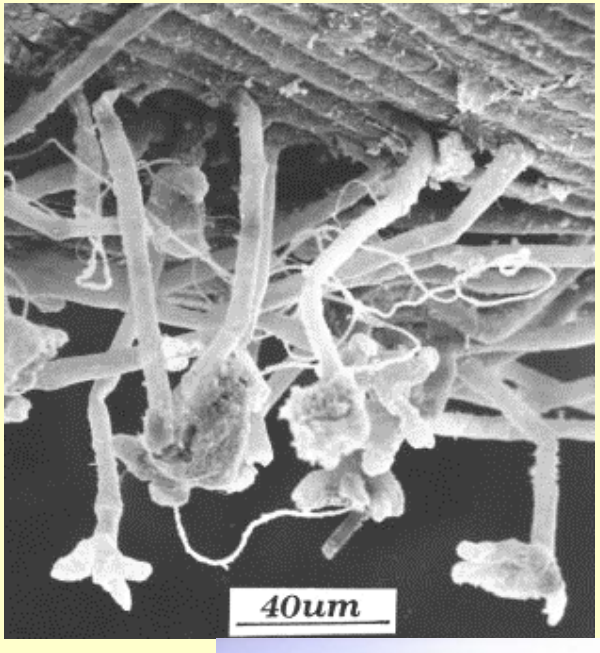
Satoshi KOI et al. (2012): Molecular phylogenetic analysis of Podostemaceae: implications for taxonomy of major groups. Bot.J.Linn.Soc.169: 461-492.

Phylogenetic tree based on *matK* sequences of 657 samples (43 out of 54 genera, c.132 out of 300 species)

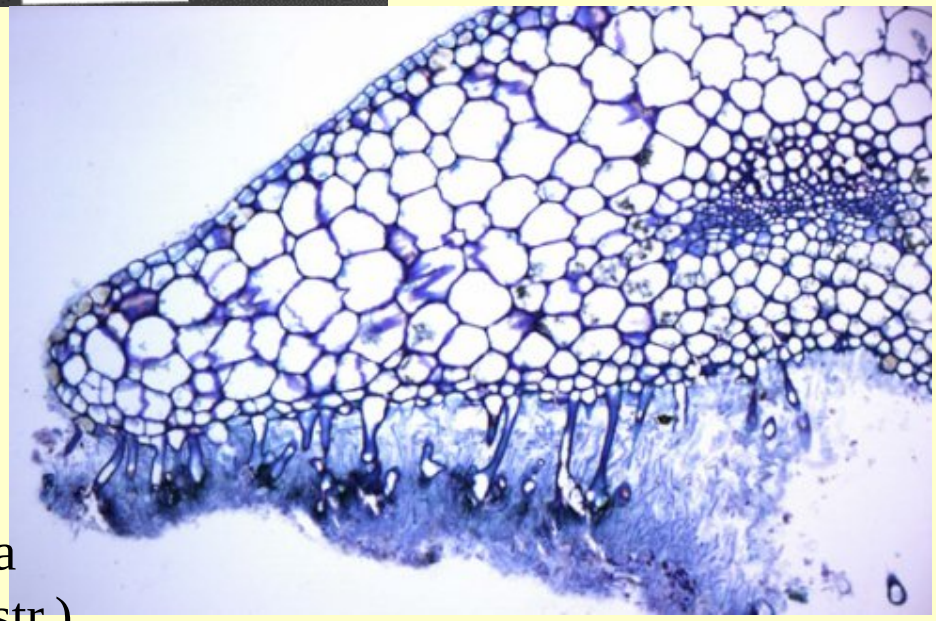


PODOSTEMS as morphological misfits

The plant attaches itself to the rock by adhesive hairs growing from the 'roots' or by disk-shaped holdfasts. The hairs secrete their own sticky mucilage a/o attach themselves in biofilms of cyanobacteria.



Indotristicha ramosissima from S India (subfamily Tristichoideae)

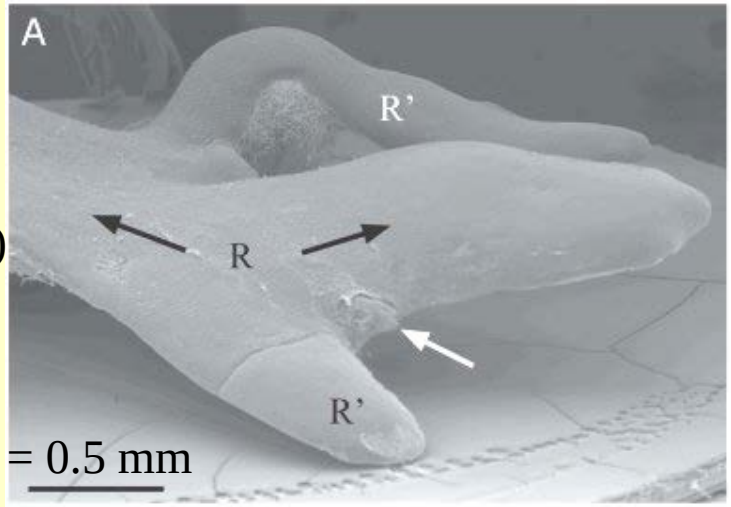


Ledermanniella bosii from tropical Africa (subfamily Podostemoideae = podostems s.str.)

PODOSTEMS as „phase-only“ morphological misfits
(cf. Minelli in EuroEvoDevo 2012 Abstract p.101)

The usually flattened 'roots' give rise to branching 'shoots' that in turn produce 'leaves'. All parts are photosynthetic and probably do not correspond directly to comparable structures in typical flowering plants.

Stonesia ghoguei (Cameroon)



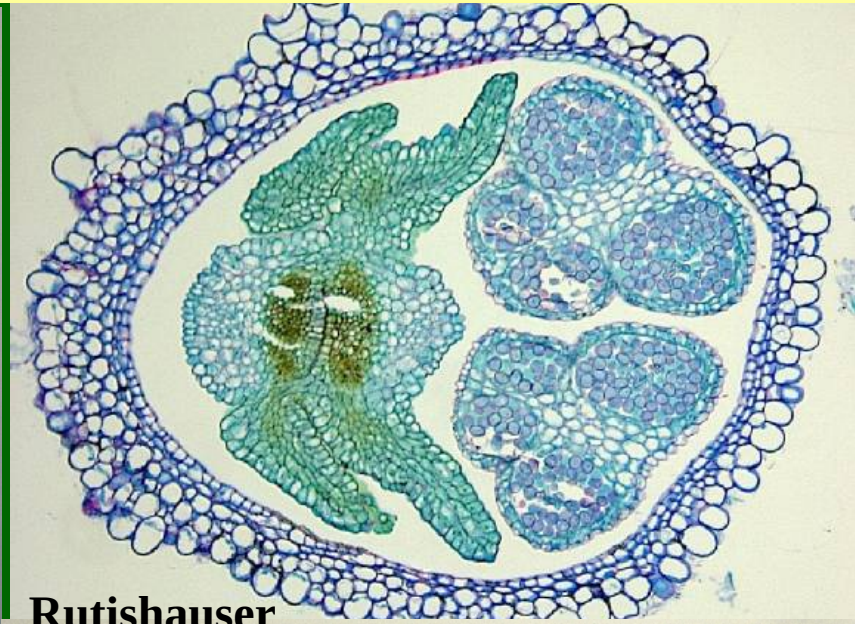
Podostemum ceratophyllum (Eastern NAmerica)

Hydrobryum japonicum (Japan)

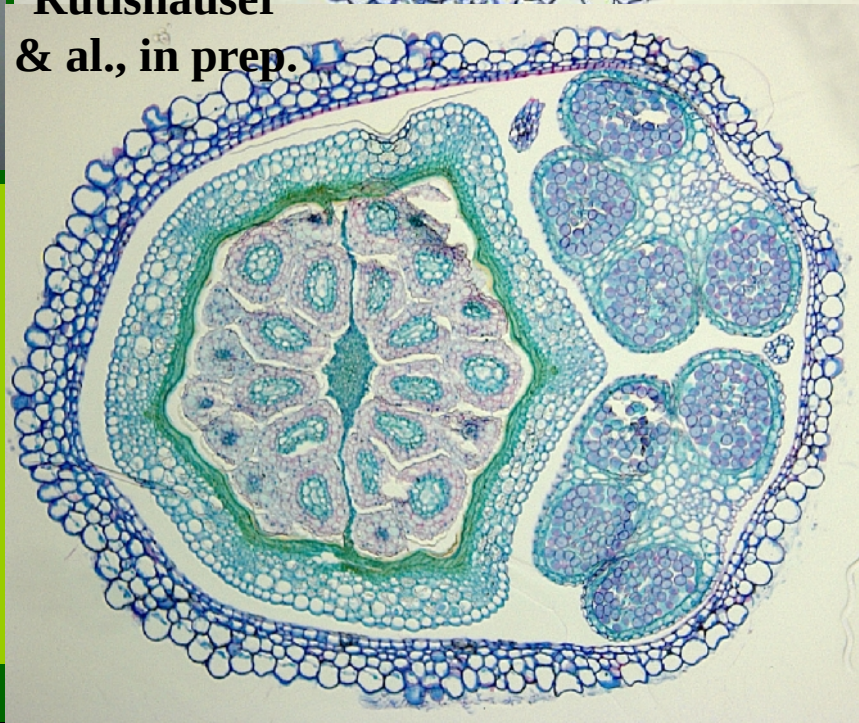
But: Podostems fit the flower bauplan of angiosperms!!!

Photographs:
C. Koschnitzke
(Rio de Janeiro)

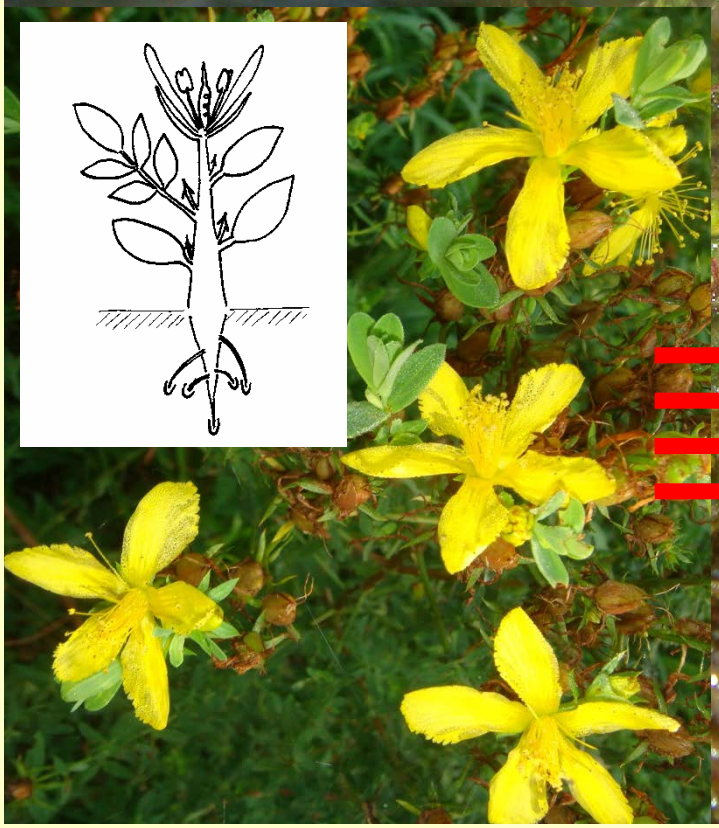
e.g. *Lophogyne lacunosa* (SE Brazil) **with A2-3, <u>G(3)</u> encased in a sac-like covering called a spathella**

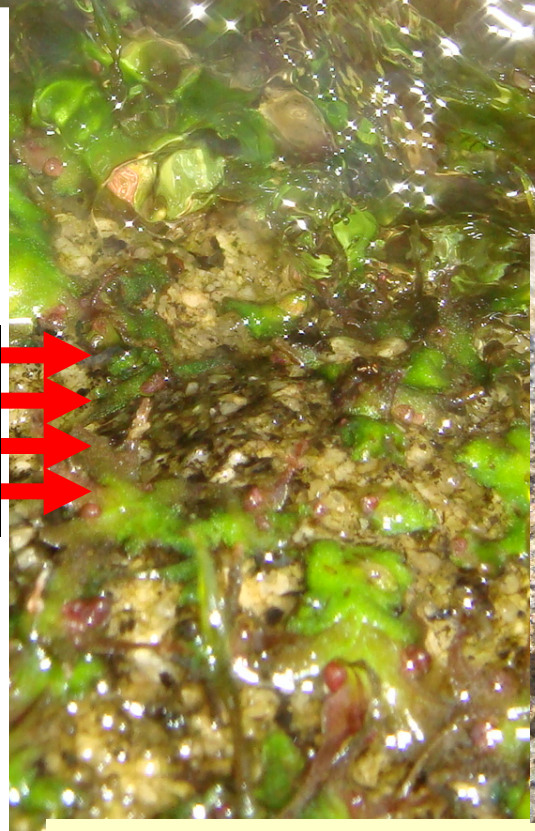


Rutishauser & al., in prep.



Podostemaceae probably arose by SALTATIONAL EVOLUTION from clusioid Malpighiales (especially Hypericaceae = St Johns worts**), which have an ordinary bauplan (Rutishauser 1997, Gustafsson & al. 2002, Katayama & al. 2008).**



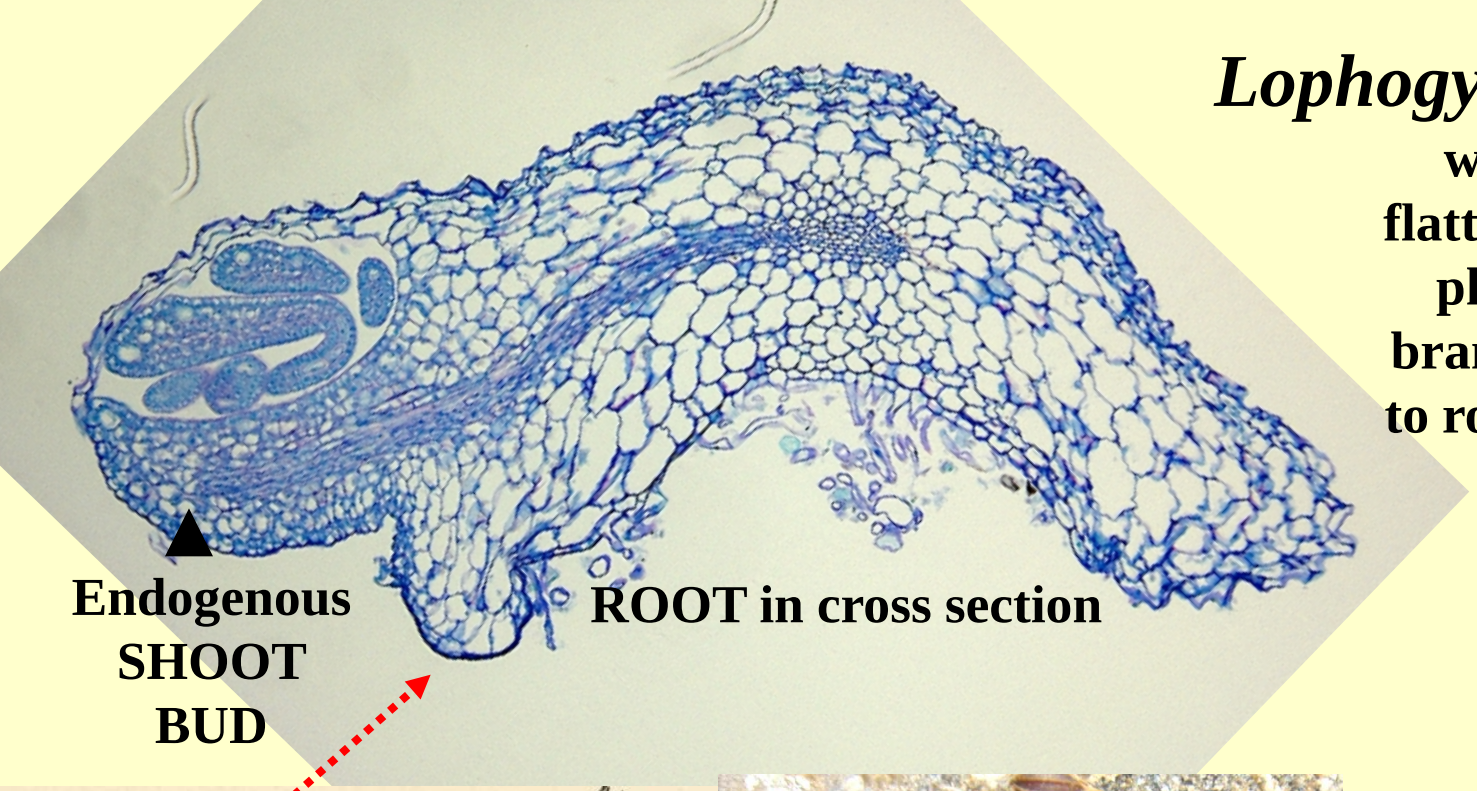


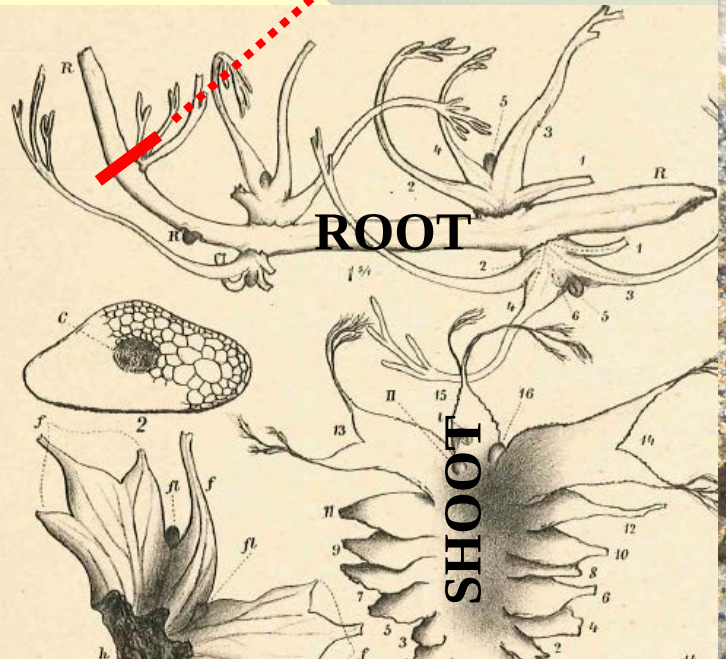
***Hypericum*-like ancestor**

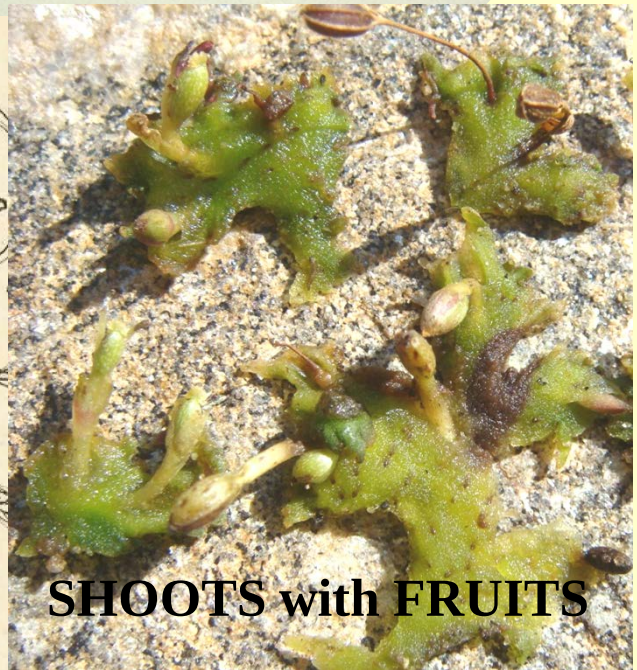
e.g. Podostem *Lophogyne lacunosa*

Lophogyne lacunosa

with 'ROOTS' flattened, green and photosynthetic, branched, attached to rock via adhesive hairs.





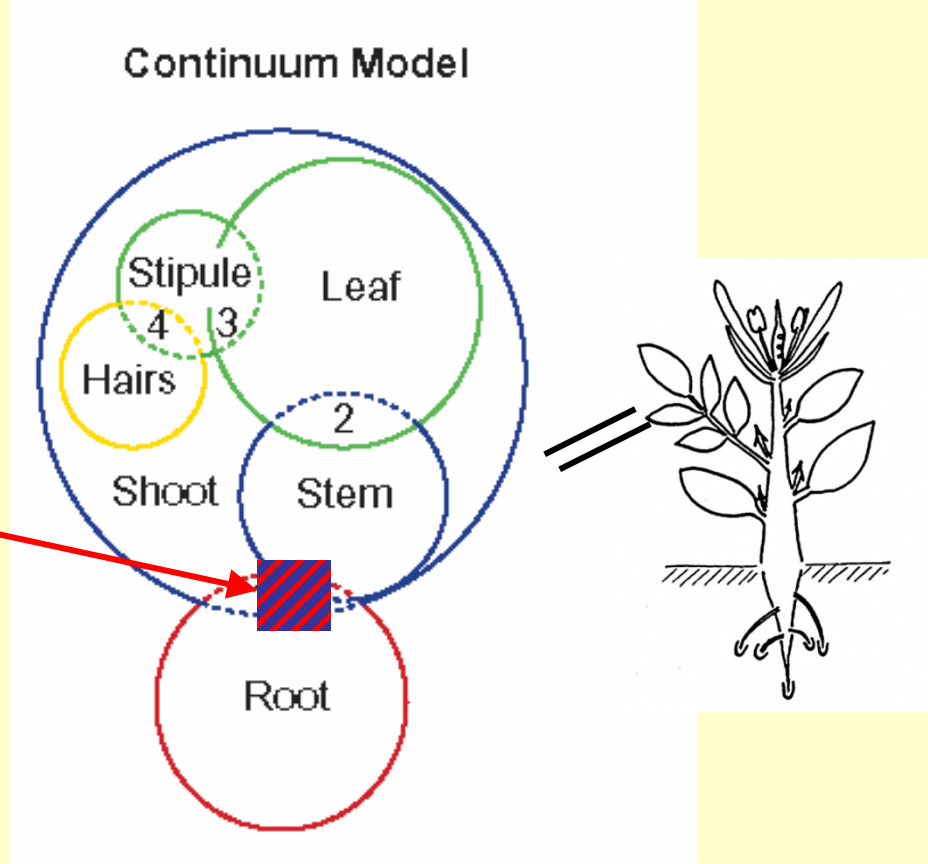


Flattened 'SHOOTS' arising along flanks of roots, prostrate with distichous leaves. Distinction between leaf base and flattened stem obscure (drawings by Warming 1888; photographs from RR lab)

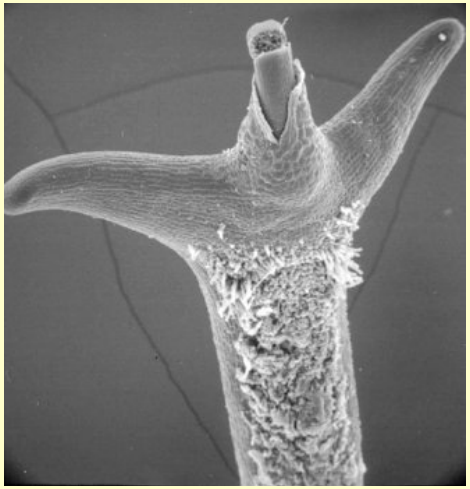
OPEN QUESTION: Is there a root identity crisis in podostems?

Are the green ribbons / crusts:

- highly modified roots? (most botanists agree)
- structural novelties transcending classical root-shoot model (Sehgal et al. 2007)
- intermediates between roots and shoots = **root-shoot fuzzy organs?**



Zeylanidium subulatum **(S India)**



Hydrobryum floribundum **(S Japan)**

Rutishauser et al. (2008): Plants are used to having identity crises. Pp.194-213. In Minelli & Fusco (eds.): Evolving pathways. CUP

Molecular developmental studies by Natsu Katayama & al. (2010) on podostems support dynamic models for BAUPLANs in seed plants: "It is now generally accepted that compound leaves express both leaf and shoot properties and that this at least partly reflects ectopic expression of genes related to *STM* in the leaf." (Eckardt & Baum 2010)

…from field work in Cameroon to the molecular lab in Japan….

Katayama & al. 2010. Expression of *SHOOT MERISTEMLESS, WUSCHEL and ASYMMETRIC LEAVES 1* homologs in the shoots of **Podostemaceae:** Implications for the evolution of novel shoot organogenesis. Plant Cell 22:2131–2140 [Introduced by Eckardt & Baum]

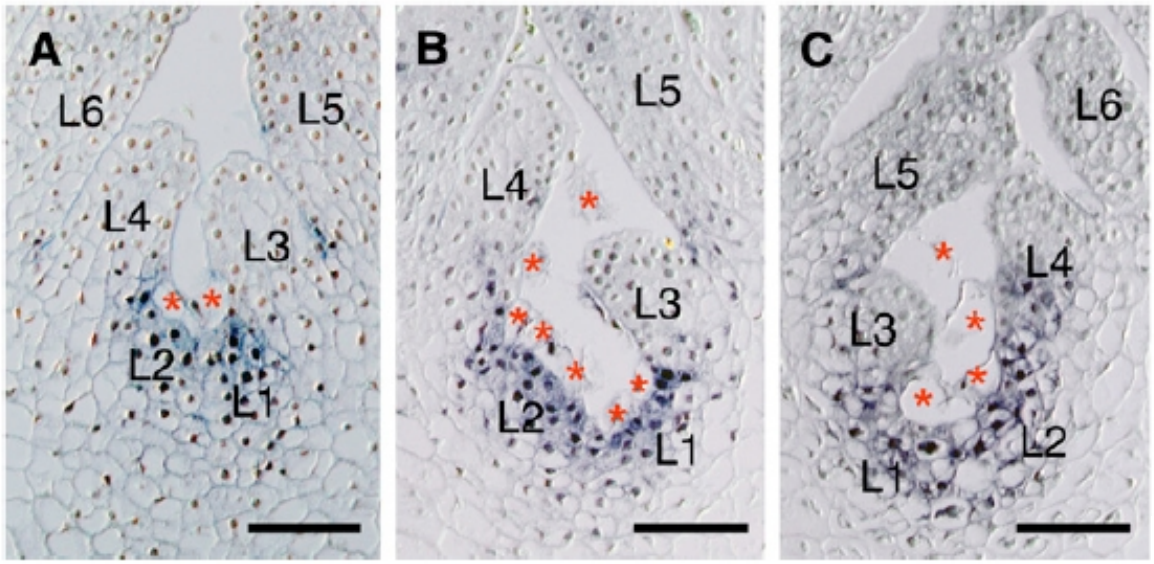
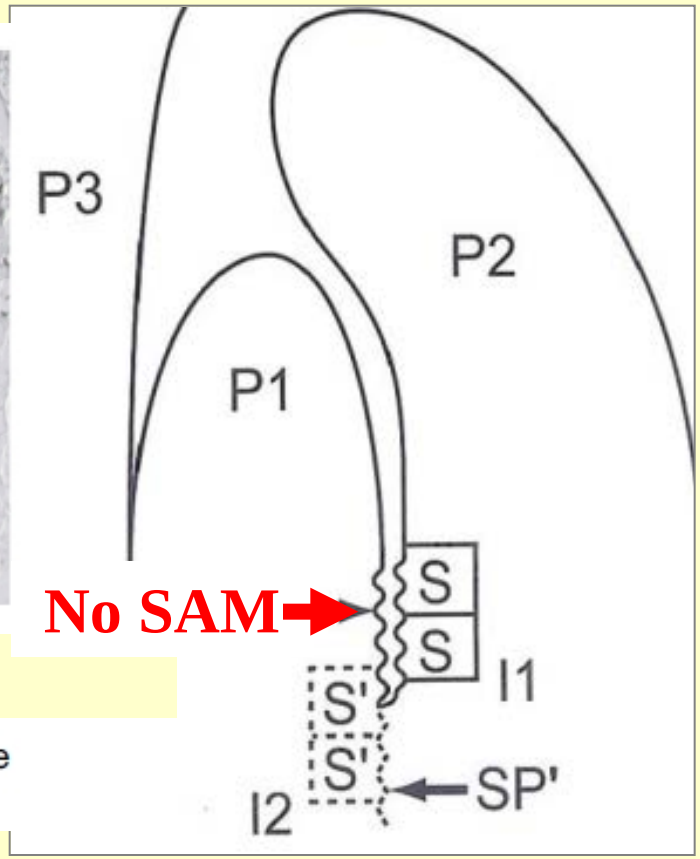


Figure 6. Expression of Cd *STM* in *Cladopus doianus* shoots

(A) to **(C)** Longitudinal sections of vegetative shoots at successive developmental stages.

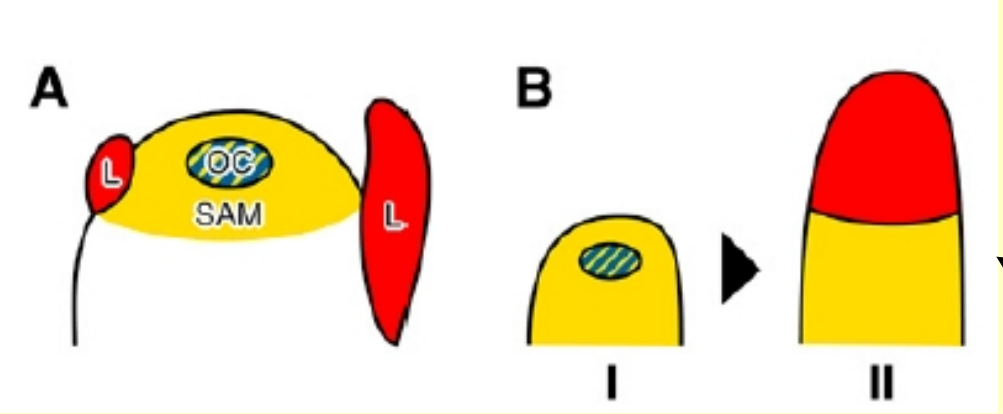
*** Vacuolated cells**



Japanese botanists (Imaichi et al. 2005, Koi et al. 2005, Koi & Kato 2007, Katayama & al. 2010) observed internal leaf initiation & cleavage between adjacent leaves.

„The apparent absence of a SAM in podostems is not due to its loss but to the transformation of the shoot to a leaf-stem fuzzy organ.“ (Katyama & al. 2010 in Plant Cell 22:2131–2140)

The shoot apex (SAM) appears to have been converted into a single, terminal leaf by losing STM/WUS expression and gaining ARP expression (Katayama & al. 2010).

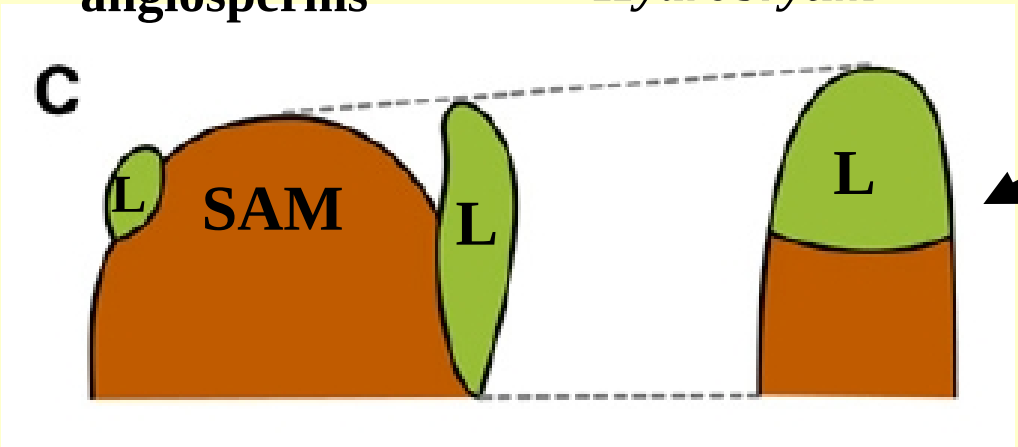


Typical angiosperms

Podostems, e.g. *Hydrobryum*

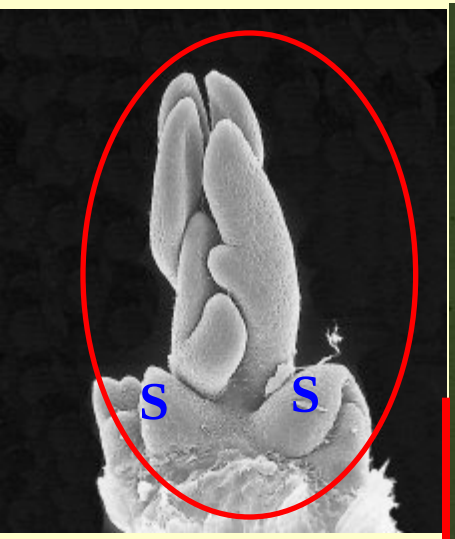
Gene expression patterns of WUS, STM and ARP

Leaf-stem fuzzy organ = sympodial module of meristematic shoot zone and apical leaf



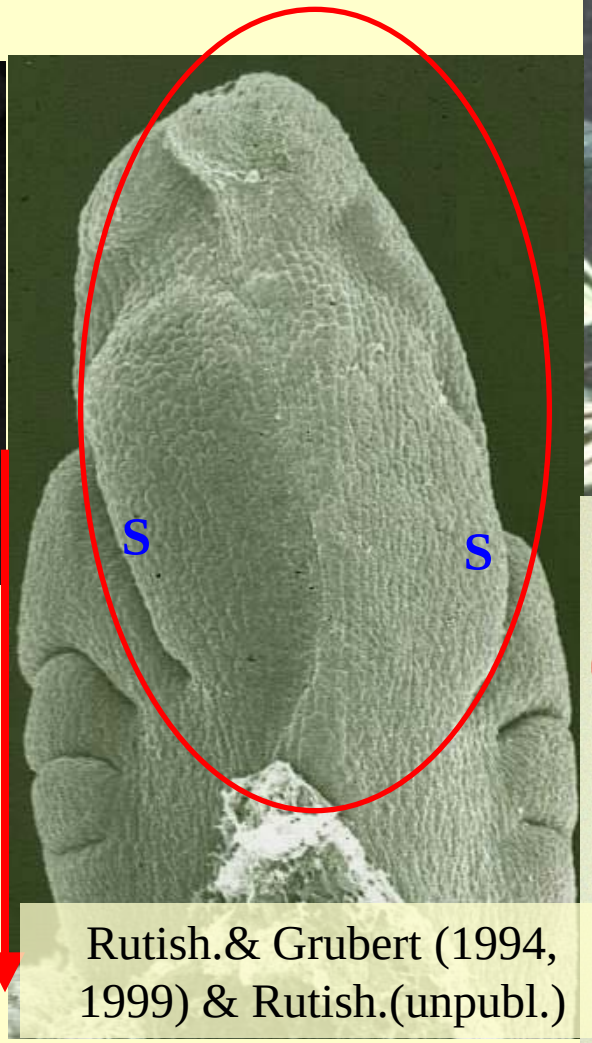
Comparison of organ identity

Leaf-stem fuzzy organ usually present as double-sheathed 'leaf' (having two sheaths S) in apical position, giving rise to novel branching patterns

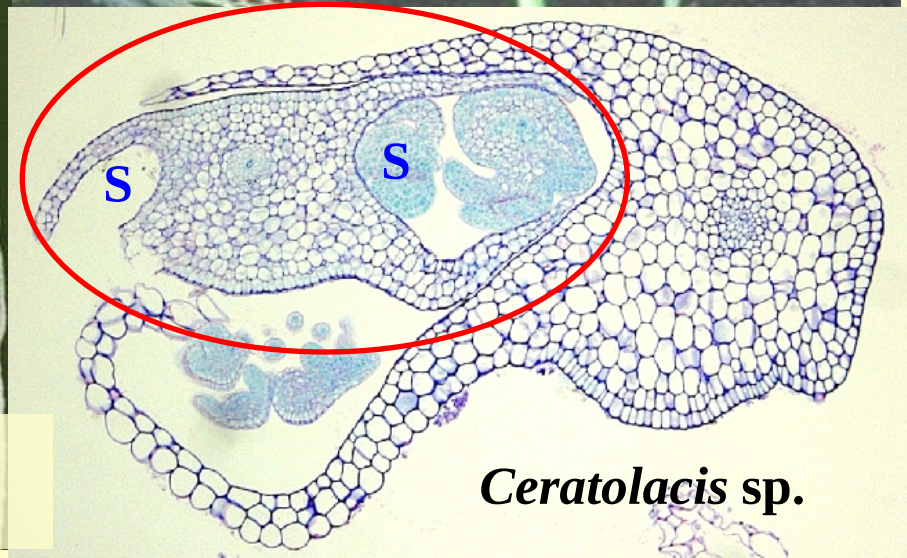


Podostemum sp.

Basipetal leaf inception in sword-like inflorescence of *Mourera* spp.



Rutish.& Grubert (1994, 1999) & Rutish.(unpubl.)



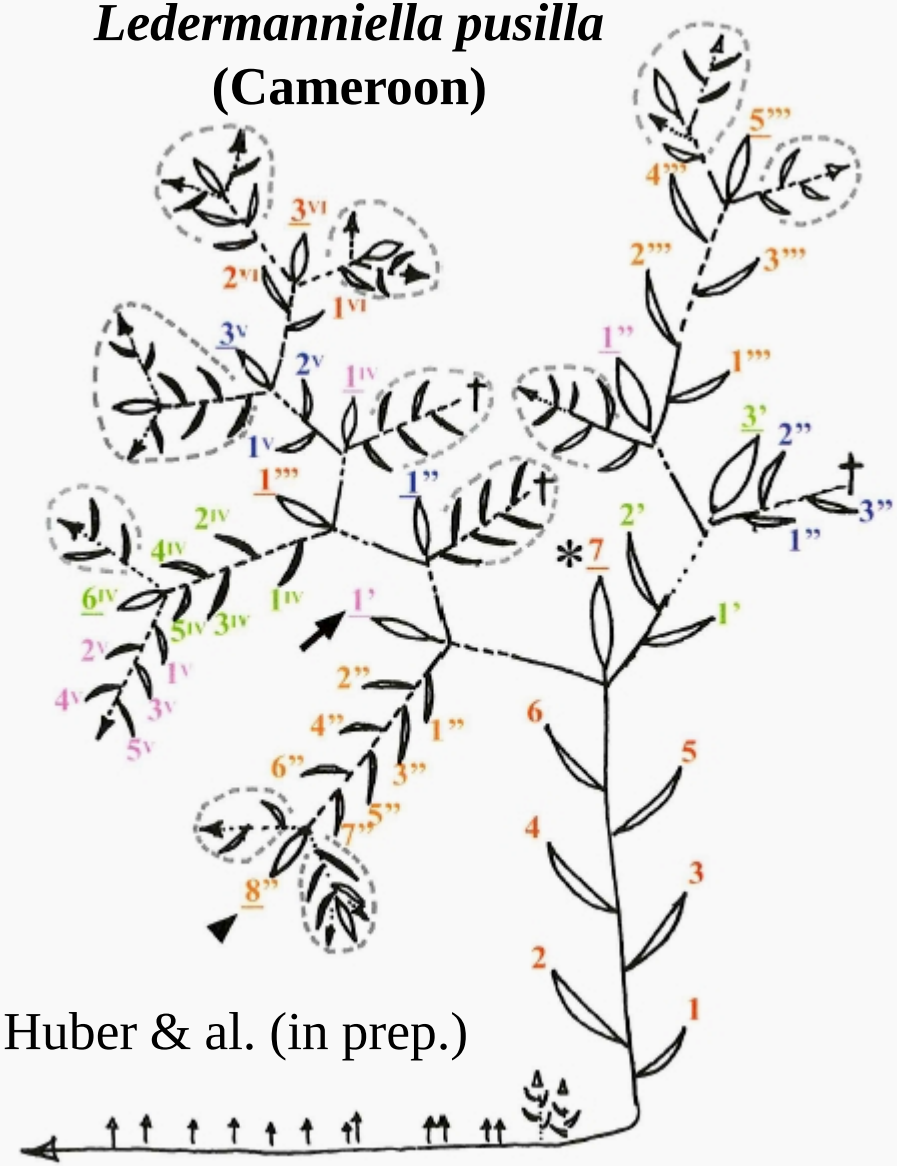
***Ceratolacis* sp.**

Leaf-stem fuzzy organ, giving rise to novel branching patterns

Modes of sympodial branching in Podostemoideae of the New World (adapted from Warming 1888 etc. and own studies)

Podostemum cerato-phyllum (N America) **Mourera fluviati-lis (North.S Am.)** **Apinagia latifolia (British Guyana)**

Ledermanniella pusilla **(Cameroon)**



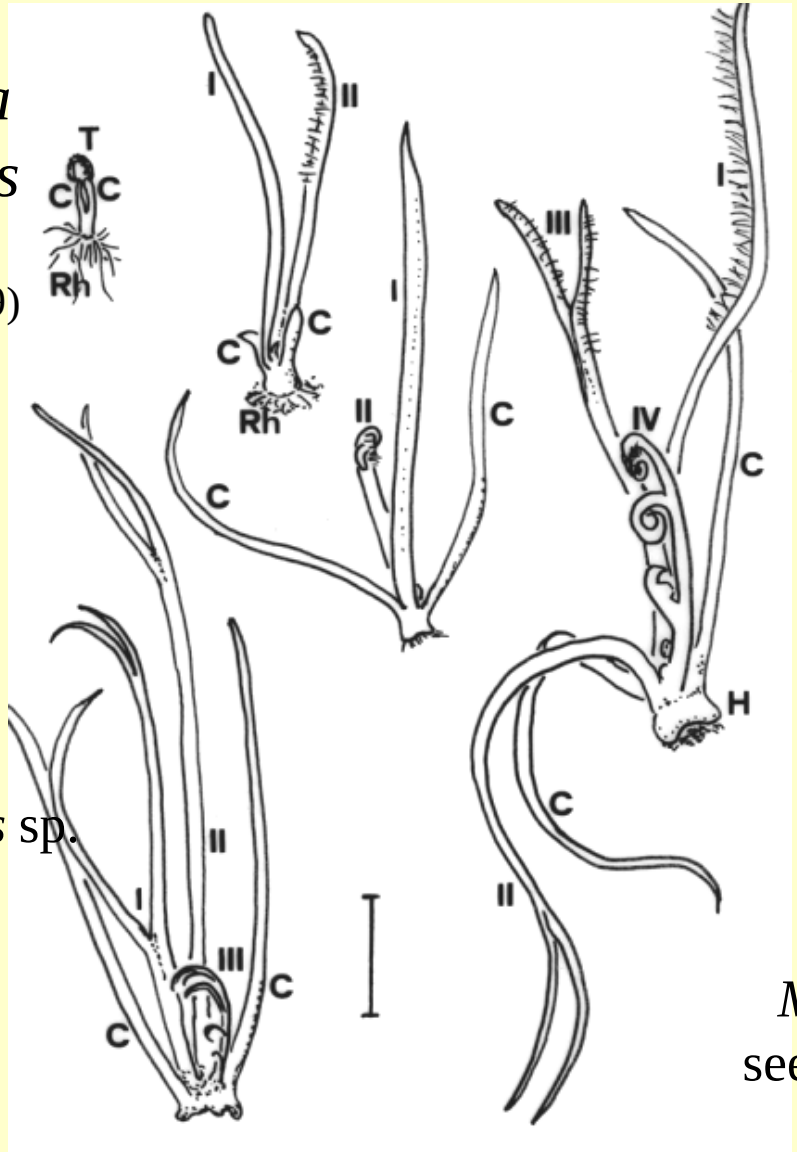
Huber & al. (in prep.)

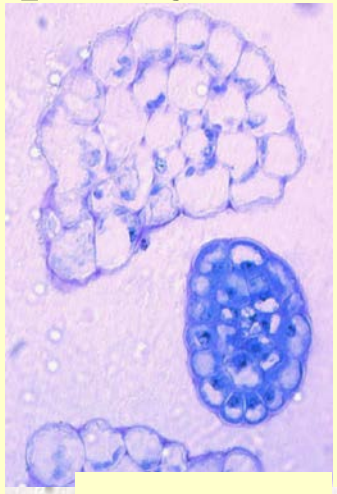
Podostem seedlings as morphological misfits: Both plumule and radicle are absent or short-lived. The plant body (with ‚roots‘ and ‚stems‘) develops as lateral outgrowth of the hypocotyl.

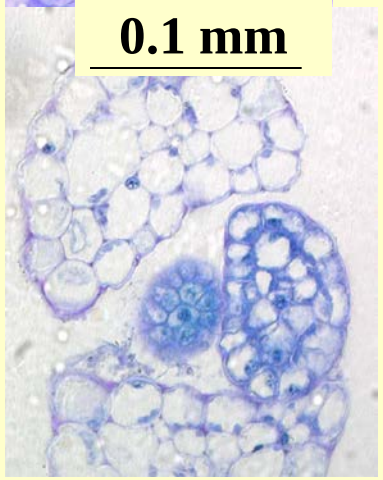
Marathrum sp.

Mourera fluviatilis

(Rutish. & Grubert 1999)

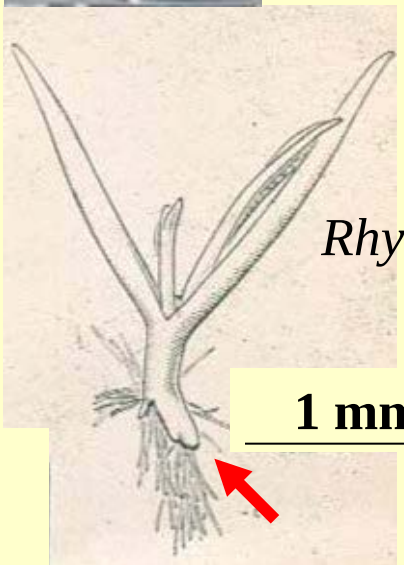






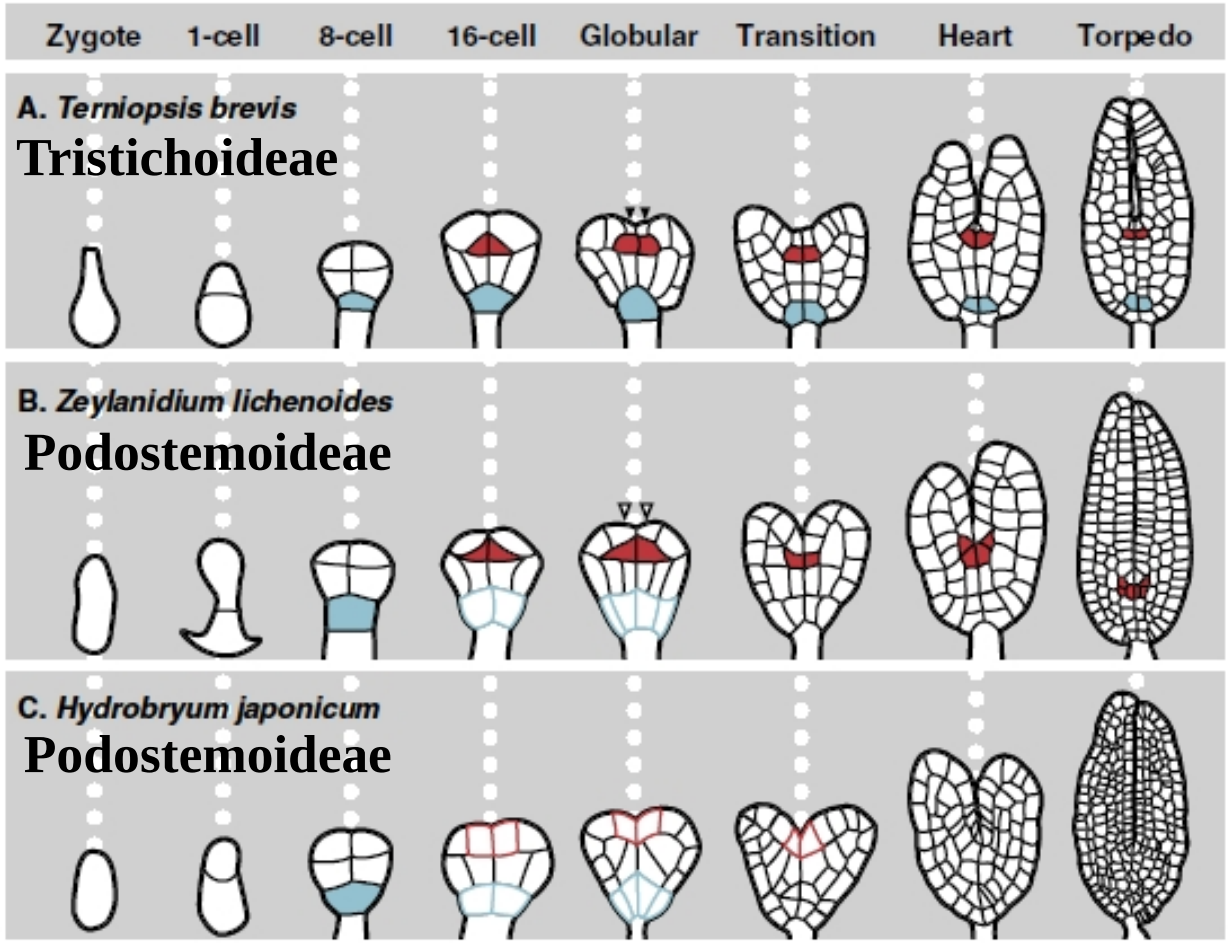
0.1 mm

Rhyncholacis sp.



1 mm

Mourera fluviatilis: seedling cross-sections (RR lab)

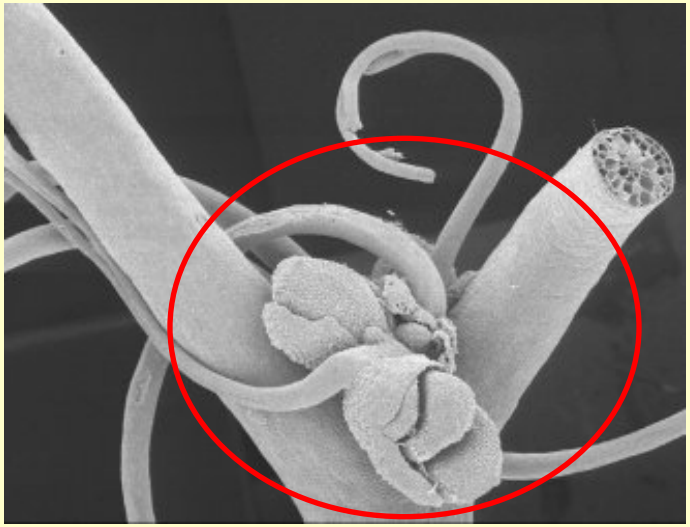


Precursor cells for SAM and RAM present

Precursor cells for SAM present but no RAM

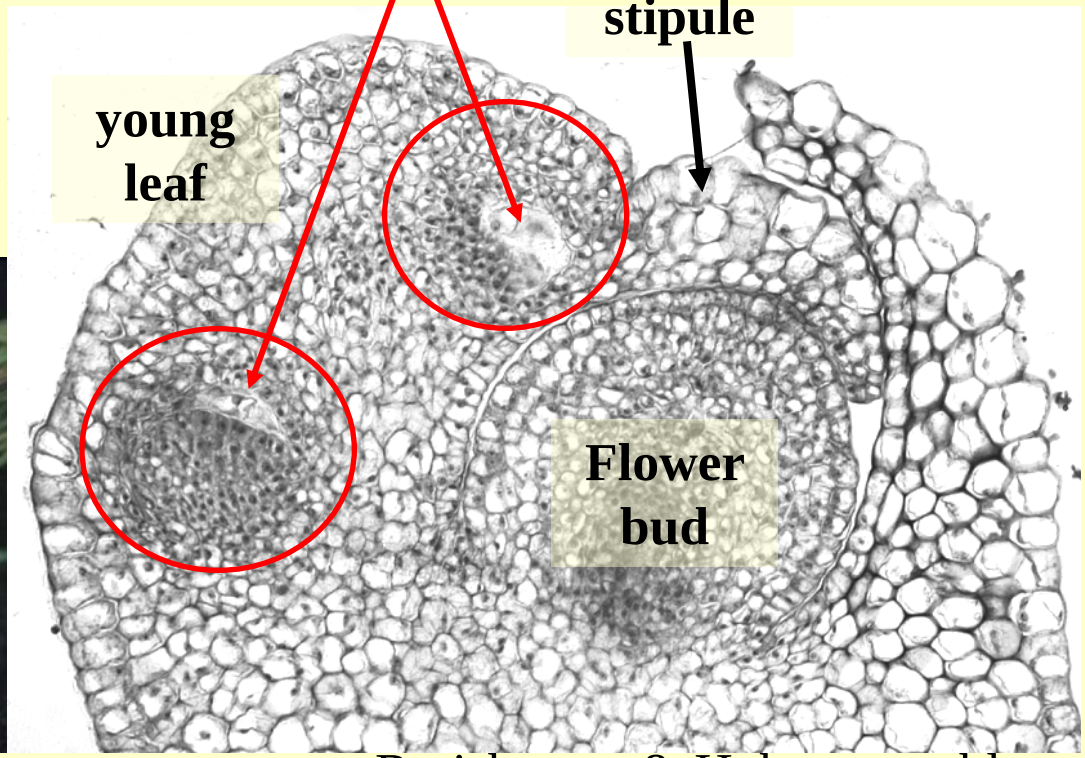
Precursor cells for both SAM and RAM lacking

Katayama & al. (2011): Comparative anatomy of embryogenesis in three species of Podostemaceae… Evolution & Development 13: 333-342.



Ledermanniella prasina

L.bowlingii

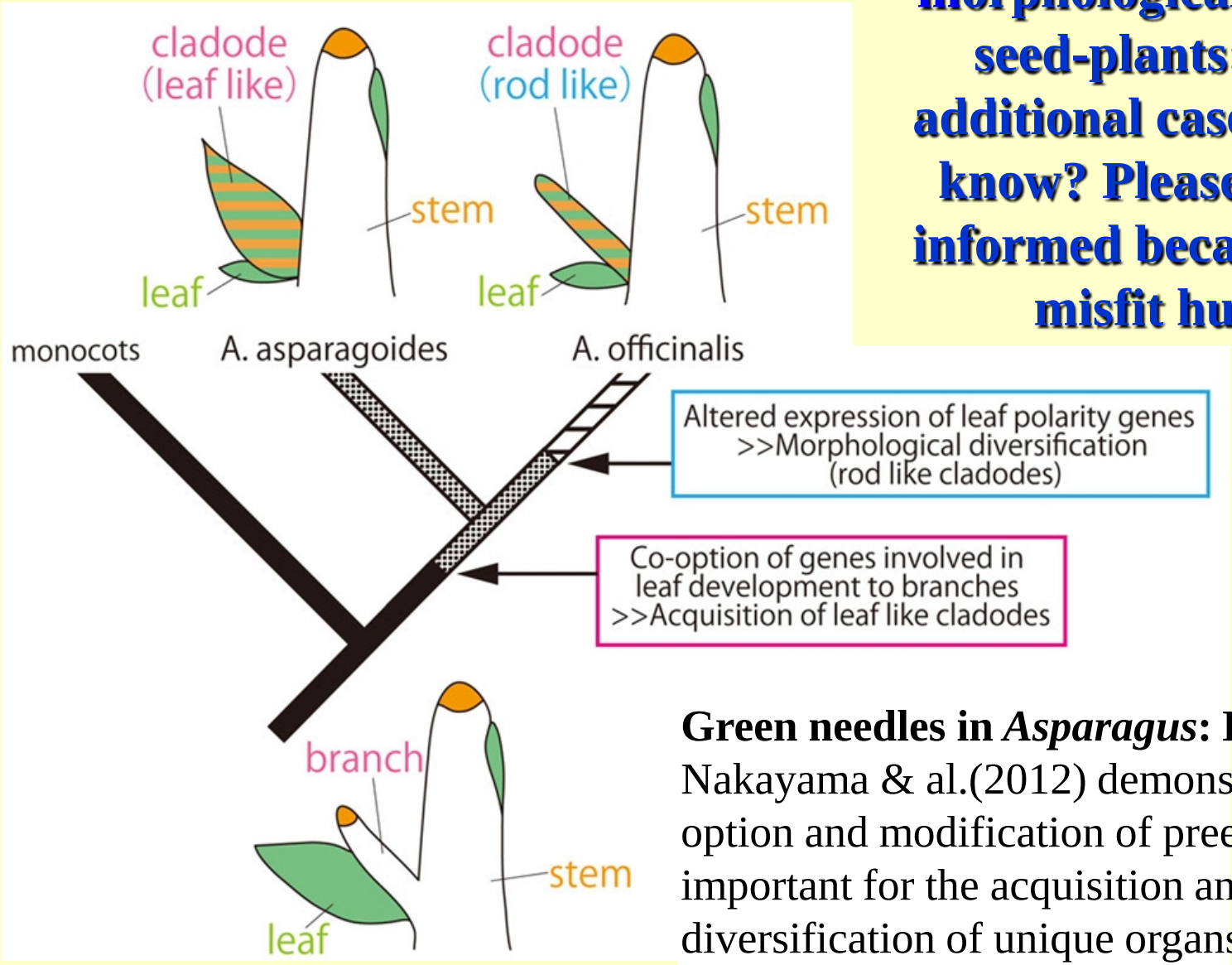


Rutishauser & Huber, unpubl.

OPEN QUESTION on epiphyllous shoots: Which genes are responsible for programmed cell death and **endogenous flower inception** in young leaves of African podostems?

… a final brand-new example!

OPEN QUESTION on morphological misfits in seed-plants: Which additional cases do YOU know? Please keep me informed because I am a misfit hunter!



BAUPLAN of typical angiosperms

Green needles in *Asparagus*: Leaf or branch?
Nakayama & al.(2012) demonstrate that the co-option and modification of preexisting genes are important for the acquisition and subsequent diversification of unique organs in plants.
Source: The Plant Cell 24: 929-940.

Evolution of morphological misfits in seed plants such as Podostemaceae, allowing for growth in tropical rivers

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