Campylopus, a modern and successful genus !?

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Abstract. *Campylopus* with nearly 200 revised species is one of the largest genera of mosses in the world and has extremely broad geographical, altitudinal and ecological ranges. Factors to be considered for the rich speciation are 1) the enormous anatomical plasticity of the structure of the costa, 2) the ability for vegetative propagation utilizing different methods, and 3) the special twist mechanism of the cygneous setae. Phytogeographical interpretations of present ranges of species of *Campylopus* lead to the conclusion that this genus is of Gondwanalandic origin. Most of the species seem to be cool temperate in origin. They have adapted to dry habitats in the Mesozoic and invaded the tropical mountains during the Tertiary, accompanied by rich speciation. This is supported by the physiology of these species. According to preliminary gas exchange measurements, tropical montane species do not differ from temperate species, and are not able to stand climatic conditions of the tropical lowland rainforests; a relatively young habitat for bryophytes. A cladistic analysis of the infrageneric categories of *Campylopus* using phytogeographical evaluations of apomorphic character states shows that the section *Homalocarpus* seems to be the most primitive and the subgenera *Campylopidulum* and *Thysanomitrion* the most derived.

1. Introduction

The somewhat provocative title goes back to Schuster (1984), who (as a hepaticologist) interpreted some distribution maps of *Campylopus* and called this genus 'modern and successful'. So it would be interesting to prove whether a moss genus such as *Campylopus* is really modern and successful.

In total, more than 1000 species of *Campylopus* have been described. Twenty years ago, Index Muscorum (Wijk et al. 1959) listed more than 700 legitimate species. Since that time, the number has been reduced by worldwide revisions to less than 200. This is a common effect in bryophytes, especially in tropical ones, where rates of reduction owing to worldwide revisions, are about 60-70%. This indicates that there are not 25.000 species of bryophytes in the world as given in textbooks, but probably no more than 10.000 (4.000 species of hepatics and 6.000 species of mosses). There are only a few genera of mosses with numbers of species comparable to *Campylopus*, but these have not yet been revised critically on a worldwide basis, and therefore *Campylopus* may be one of the largest genera of mosses in the world. Based on an estimated total of about 6000 species of mosses, i of every 30. mosses (or 3.3% of all mosses) belong to the genus *Campylopus*.

The genus *Campylopus* has a wide latitudinal range between 65^0N (Alaska) and and 65^0S (South Sandwich Islands) and an enormous altitudinal range between sealevel and more than 4500 m elevation. The species occur on a variety of different substrates such as nutrient poor sand, humic soil, peat, rocks, rotten and living wood,
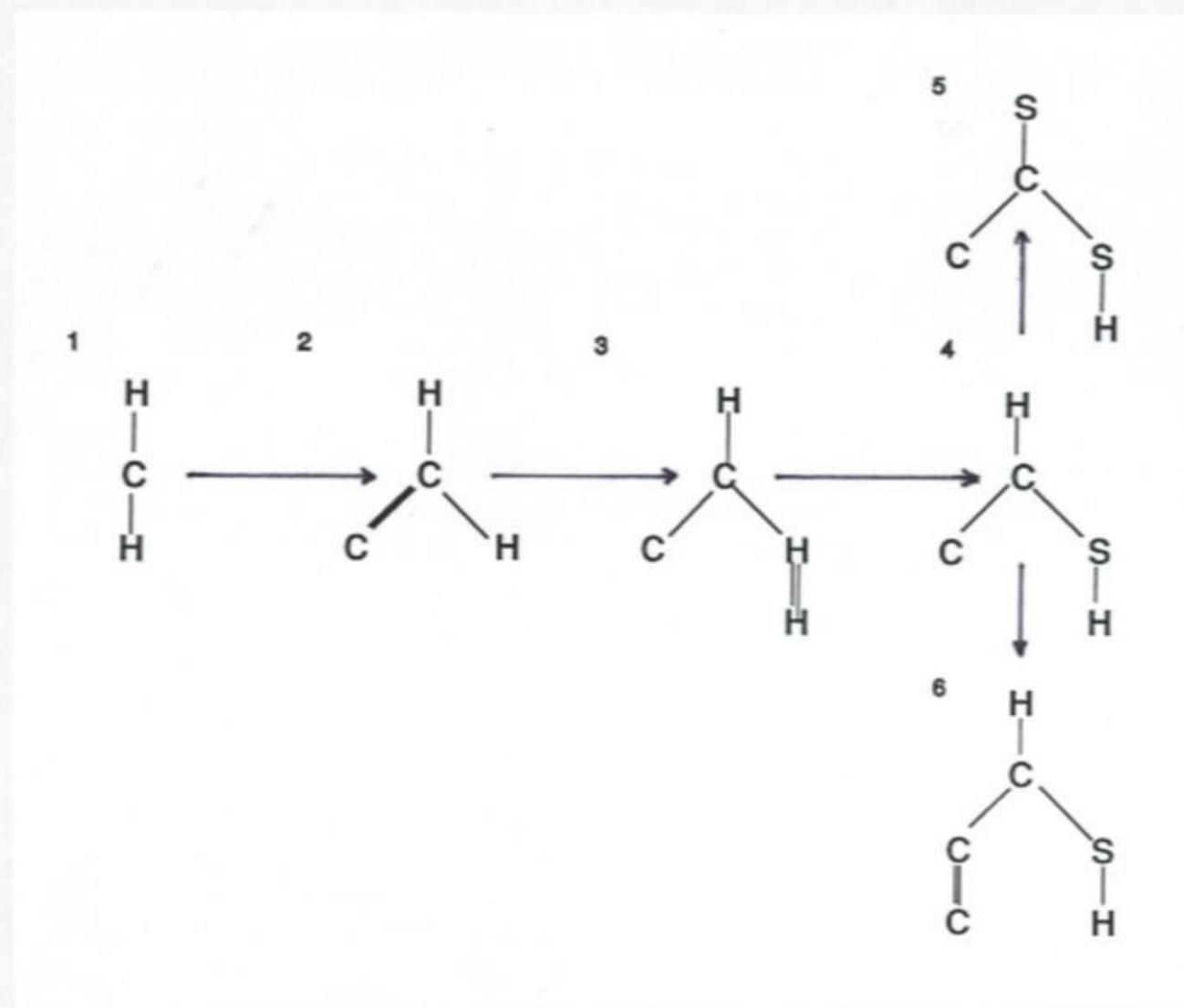
Fig. 1: Formulas explaining the different morphological types of costae in the genus *Campylopus* by stepwise cell division. H = hyalocysts, C = chlorocysts, S = stereid cell.

period, when mostly acidic substrates were present. Accordingly, the morphology varies from a few millimeters to 15 cm tall plants, and from small, *Dicranella*-like species to large *Dicranum*-like species.

The question now is, which factors made this genus successful

to occupy this large horizontal and vertical geographical range,

to occupy such a broad variety of habitats,

to produce such a broad variety of morphological expressions, and to have such a high number of species.

How has this genus evolved? Which are the earliest representatives of this genus; which are the most advanced ones? Is the genus a modern one as suggested by Schuster?

To answer these questions, different approaches shall be applied by examining the morphology, the phytogeography, the physiology and the evolution of this genus.

2. Morphological and anatomical specialities
2.1 Gametophyte
2.1.1 Costa

The most conspicuous vegetative character of the genus *Campylopus* is the broad costa with extreme diversity of internal differentiation. There is no comparable range of variation in the structure of the costa in any other moss genus. All the different expressions between

2.1 Gametophyte
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The most conspicuous vegetative character of the genus *Campylopus* is the broad costa with extreme diversity of internal differentiation. There is no comparable range of variation in the structure of the costa in any other moss genus. All the different expressions between types with two stereid bands and a median deuter band (as commonly found in the Dicranaceae and also other families) and costae with no stereids at all can be explained by a few cell divisions (fig. 1). Thus the mechanism behind this broad variety of structures is relatively simple.

What are the advantages of these different costal structures?

a. mechanical stability. Stereids with firm thickened walls, provide mechanical support either in layers on the adaxial surface or in bundles in the abaxial part of the costa. They are supposed to be good protection against shrinking caused by desiccation and are therefore are found frequently in dry adapted species. In species pairs (often sympatric species differing mainly in one character of the costa and the habitat), the species of the wetter habitat has ventral hyalocysts, whereas that of the drier habitat has ventral stereids. One of many examples is *Campylopus comosus* (Reinw. & Hornsch.) Bosch & Lac. growing on soil, with small ventral hyalocysts and *C. flagelliferus* (C. Müll.) Jaeg. growing in the same range but epiphytic with ventral stereids (Frahm 1985, Frahm et al. 1985)

b. Photosynthesis. Assimilation is carried out by a median band (the so called deuter cells) and a dorsal band of chlorocysts. Since the width of the costa is usually more than half of the leaf width, and the basal laminal cells are often nonchlorophyllose, the costa is the main source for photosynthesis.

c. Water uptake and storage. Water is easily taken up and stored by hyalocysts, especially the large ventral ones. This seems to function only in wet habitats, since the cell walls of large hyalocysts are very delicate and can probably not stand desiccation. In species pairs the species of wet habitats have larger hyalocysts than species in drier habitats, as exemplified by *Campylopus shawii* Wils. growing in swamps and *C. setifolius* Wils. growing on wet cliffs (Frahm 1985). It seems, however, to be paradox that species of wet habitats should depend on storing water, where there is no dry daily or annual season. Thus it may be that the function of the hyalocysts (as well in the Leucobryaceae) have been misinterpretated. As Robinson (1985) has observed, the hyalocysts in the Leucobryaceae often show air bubbles, and the major function may not be water storage but gas exchange. This hypothesis is supported by the location of the chlorocysts, which are situated in the middle of the leaf without any direct contact to the atmosphere.

Another method of water storage is between the dorsal lamellae of the costa. In species pairs, the species of drier habitats have the longer lamellae, for example *Campylopus pilifer* Brid. and *C. introflexus* (Hedw.) Brid. (Frahm 1985).

d. Water conducting is probably possible not only from cell to cell or through the pectine lamellae of the walls but also more efficiently through bundles of stereids. In some species the alar cells (functioning for water uptake from the water conducted along the stem) bulge into the costa, indicating a conducting pathway from the alar cells to the costa.

e. Gas exchange combined with photosynthesis. Effective gas exchange requires a large surface. Lamellae (being chlorocysts) seem to function not only for water storage but also for gas exchange as shown by *Campylopus pilifer* Brid. var. *lamellatus* (Mont.) Gradstein & Sipman, which is not found in arid environments like *C. pilifer* s.str. but in rainforests. In this kind of habitat, water storage is not required, but gas exchange in high humidity may be a problem.

Thus the plasticity of different structures of the costa allows adaptations to a broad variety of habitats. The facility to modify such structures has promoted the broad ecological and geographical ranges and enhanced the high number of species.

2.1.2 Vegetative propagation

Compared with other genera of mosses, vegetative propagation is relatively important in *Campylopus*. In this genus, all different kinds of vegetative propagation from microphyllous branches and deciduous leaves to special brood leaves, broken leaves and stem tips are found. If 40% of all species are known only sterile, the importance of vegetative propagation is evident. The vegetative propagation allows a species to survive in a habitat as a unisexual clone. It also allows clones to survive long unfavourate climatic conditions with no sexual reproduction. At least it allows propagation over short distances until clones of different sexes meet and allow fertilization. Apparently most of the species (if not all) are able to vegetative propagate by more than one kind of vegetative propagation.

2.1.3 Perichaetia

Differentiated bud-like perichaetia function for splash cup dispersal of spermatozoids and also as protection for the young sporophyte during the stage of development when the seta is curved into the perichaetial leaves. Such perichaetia are found in all infrageneric categories of *Campylopus.*

2.2 Sporophyte

The major characteristic of this genus is the seta which is curved sigmoid in the middle and twisted in the upper and lower part and uncoils when moistened. This character which is also present in genera such as *Microcampylopus, Campylopodium, Dicranodontium* or *Campylopodiella* (but not in other closely related genera such as *Atractylocarpus* or *Pilopogon*).

The sigmoid curve in the seta is caused by its development (Frey & Frahm 1987 figs. 1-7). When the seta has reached half of its final length, it curves down, the capsule developes, often leaves the calyptra between the perichaetial leaves and curves up again.

In this way the young sporophyte developes protected in the perichaetial leaves which is an advantage, especially in exposed or dry habitats.

The twist mechanism of the seta causes wide movements of the capsule in a moistened state at the same time as when the peristome is open. The function of these circular movements of the capsule is not clear. It may enhance spore dispersal to all directions, but this is a relatively small advantage compared with the anatomical structures necessary for these movements. Spore dispersal in wet weather conditions also prohibits long distance dispersal. However, since *Campylopus* as many other genera of Dicranaceae are dioicous, male and female spores need to land near to one another in order to establish new male and female clones which are situated close enough to allow fertilisation. The mechanism for these uncoiling movements have not been known yet but could be explained by a study of the ultrastructure of the setae (Frey & Frahm 1987). The epidermal cell layer of the setae possesses a three layered wall with asymmetric lumens. SEM and TEM studies revealed a distinct lamination in the second layer and small pores in the outer, asymmetrically thickened epidermal cell layer of the seta, and a firm inner teriary cell wall. In dry state the setae are coiled by spirally arranged microfibrils in the secondary cell wall. Water (or water vapour) is taken up through the outer cell wall, stored between the microfibrils of the secondary wall, causing elongation of the setae and uncoiling movements. Opposite twist directions in the upper and

lower part of the setae prevent the setae from being twisted off.

3. Distribution and Speciation

Campylopus is an ideal genus for phytogeographic interpretations because of its wide distribution, broad ecological range, wide altitudinal range and high number of species. Insofar it is equivalent to several other genera or even one or more smaller families.

The worldwide distribution of the genus is uneven on both sides of the equator. There are 14 species in the subantarctic but only 1 species in the subarctic (Frahm 1988). In the tropics, the species of *Campylopus* are mostly confined to the montane belt. There are only a few species occurring in the lowlands, mainly in savannahs and not in lowland rainforests. The species in the temperate belt of the northern hemisphere are (1) either mainly tropical montane species occurring as remnants of the Tropical Tertiary flora in oceanic regions (cf. many species of North America and Europe, Frahm 1980, 1984), or (2) are of subantarctic origin and probably introduced into the northern hemisphere (cf. *Campylopus introflexus* (Hedw.) Brid. in North America and Europe, Frahm 1980, or *C. pyriformis* (Schultz) Brid. in Europe, cf. Corley & Frahm 1982), or (3) are endemics related to sister species of tropical areas (cf. *Campylopus setifolius* Wils. derived from *C. shawii* Wils., Frahm 1985a). This leads to the suspicion that the genus may have its origin on the southern coast of Gondwanaland and has spread to the tropics. This pathway is illustrated by several subantarctic species, which have closely related species in the tropics, sometimes 3 such species derived from the same (still present) ancestor in South America, Africa and Australia (Frahm 1988), representing a species group with a species mosaic of several small, mostly allopatric but also sympatric species.

There are apparently several ways of speciation:

1. adaptations to dry habitats. For example, *Campylopus introflexus* (Hedw.) Brid. can be regarded as the ancestor of *C. pilifer* Brid., adapting to dry habitats by longer costal lamellae for storing water. Both species show a gondwanalandic range: *C. introflexus* along the south coast (today circumsubantarctic), *C. pilifer* in the interior (today from South America to India). By the same way, *C. julaceus* Jaeg. (with one subspecies in SE-Brazil and one in E-Africa) and *C. aemulans* (Hampe) Jaeg. (in SE-Brazil) can be derived. *Campylopus surinamensis* C. Muell., a neotropic savannah species, is derived from the subantarctic *C. vesticaulis* Mitt.

2. Adaptations to alpine habitats. There seem to be two pathways to alpine habitats, one from the subantarctic, especially through the Andes, which is well known for many other tropical alpine bryophytes, and another one from montane species. There are several pairs of species or subspecies, one of them confined to montane, the other to alpine habitats. Examples are *C. albidovirens* Herz. in subalpine forests of the Andes and *C. pittieri* Wils. in the Paramos; *C. flexuosus* (Hedw.) Brid. ssp. *flexuosus* in the montane regions and ssp. incacorralis (Herz.) J.-P. Frahm in the subalpine regions of the Neotropics and Africa, *C. cuspidatus* (Hornsch.) Mitt. var. *cuspidatus* in montane rainforests of the Neotropics and var. *dicnemioides* (C. Müll.) J.-P. Frahm in the alpine. Other examples are *C. amboroensis* Thér. in the high Andes and *C. johannis-meyeri* (C. Müll.) Kindb. in the afroalpine mountains, both derived from *C. pilifer* Brid. The origin of the alpine taxa may be explained as ecological adaptations, which may have been supported by extensions of the alpine belt during the fluctuations of vegetation belts in the Quaternary.

Interestingly, one new habitat like the páramo has been colonized by different taxa from different relationships within the genus, resulting in very similar

adaptations. For instance, *Campylopus pittieri* Williams and *C. cavifolius* Mitt. both grow often intermixed and can hardly be distinguished in the field. Only transverse sections of the costa show that these two species belong to different systematic groups. There are similar analogous developments in *Dicranum.* Species adapted to alpine habitats show the same growth form (compact cushions, orthophyllous appressed leaves, subtubular leaf apices). They show, however, significant differences in the structure of the costa and the shape of the capsules (for example *D. groenlandicum* Brid. with erect capsules and two stereid bands, *D. brevifolium* (Lindb.) Lindb. with curved capsules and two stereid bands, and *D. muehlenbeckii* B.S.G. with curved capsules and two stereid bands and two epidermal layers). This demonstrates that species from different evolutionary lines have adapted to similar habitats.

The only species of *Campylopus* occurring in the subarctic and alpine regions of the northern hemisphere, *C. schimperi* Milde, surprisingly shows the closest affinities to subantarctic species. It is, however, not found in the Andes of South America or the African mountains. This may be an example for a species which has drifted from the southern hemisphere to Asia via the Indian subcontinent and has spread through the northern hemisphere. This pathway has been pointed out by Schuster (1972, 1976) for hepatics, Smith (1972) for Polytrichaceae, and Raven & Axelrod (1974) for Angiosperms.

3. Adaptations to different habitats: This concerns sympatric species which occur in different habitats, especially epiphytic species, that are derived from terrestrial ones. Examples are *C. comosus* (Reinw. & Hornsch.) Bosch & Lac. and *C. flagelliferus* (C. Müll.) Jaeg. in SE-Asia, or *C. lamellinervis* (C.Müll.) Mitt. and *C. huallagensis* Broth. in South America, the latter species being epiphytes. By the same differentiation, *Campylopus setifolius* Wils. seems to have split from *C. shawii* Wils. in the British Isles by changing habitats from swamps to wet rocks.

4. Physiology

The cool-temperate origin of the species of *Campylopus* as that of many bryophytes (Schuster 1984) and probably most tropical montane mosses is supported by their physiology. These species lack the ability to descend to the tropical lowlands, as measurements of the gas exchange have shown (Frahm 1987, 1987a), due to high rates of respiration. Physiologically seen tropical montane bryophytes react as do cool-temperate species. Only a few species were able to adapt to the humid tropical lowlands, probably the youngest in evolution. In *Campylopus,* there are no lowland rainforest species, and only a few lowland savannah ones. The majority are montane in distribution. Tests in climate chambers show that species such as *Campylopus flexuosus* cannot stand the ecological conditions of tropical lowland forests characterized by high temperatures and low light intensities.

5. Cladistics

A cladistic analysis could give an idea, which species posses the most primitive characters and which have the most advanced features in this genus. This could also provide a hypothetical background of the origin of this genus. It requires, however, the evaluation of primitive and derived characters. This is a major problem in this genus because of the enormous variation of characters. For example, the capsules may be asymmetric or symmetric, the calyptras ciliate or nonciliate, the basal laminal cells hyaline and thin-walled or incrassate and pitted.

There is some support for the evaluation of morphological character states by the interpretation of ecological, phytogeographical phytochemical, developmental and palaeobotanical facts.

Fig. 2: Transverse section of the leaf tips of the youngest leaves in the stem tips of a. *Campylopus flexuosus* (Hedw.) Brid., b. *Dicranum spadiceum* Zett.
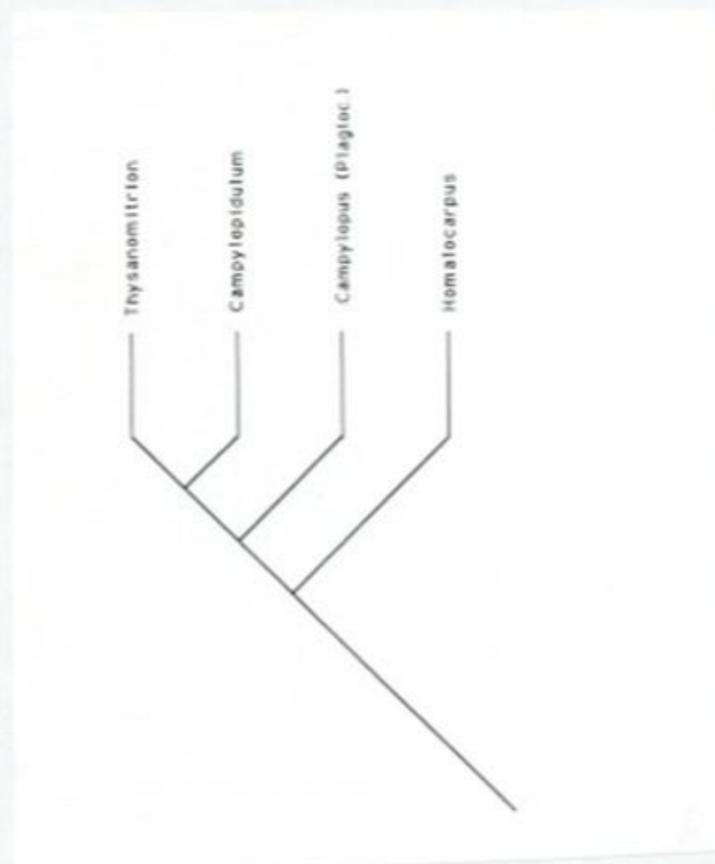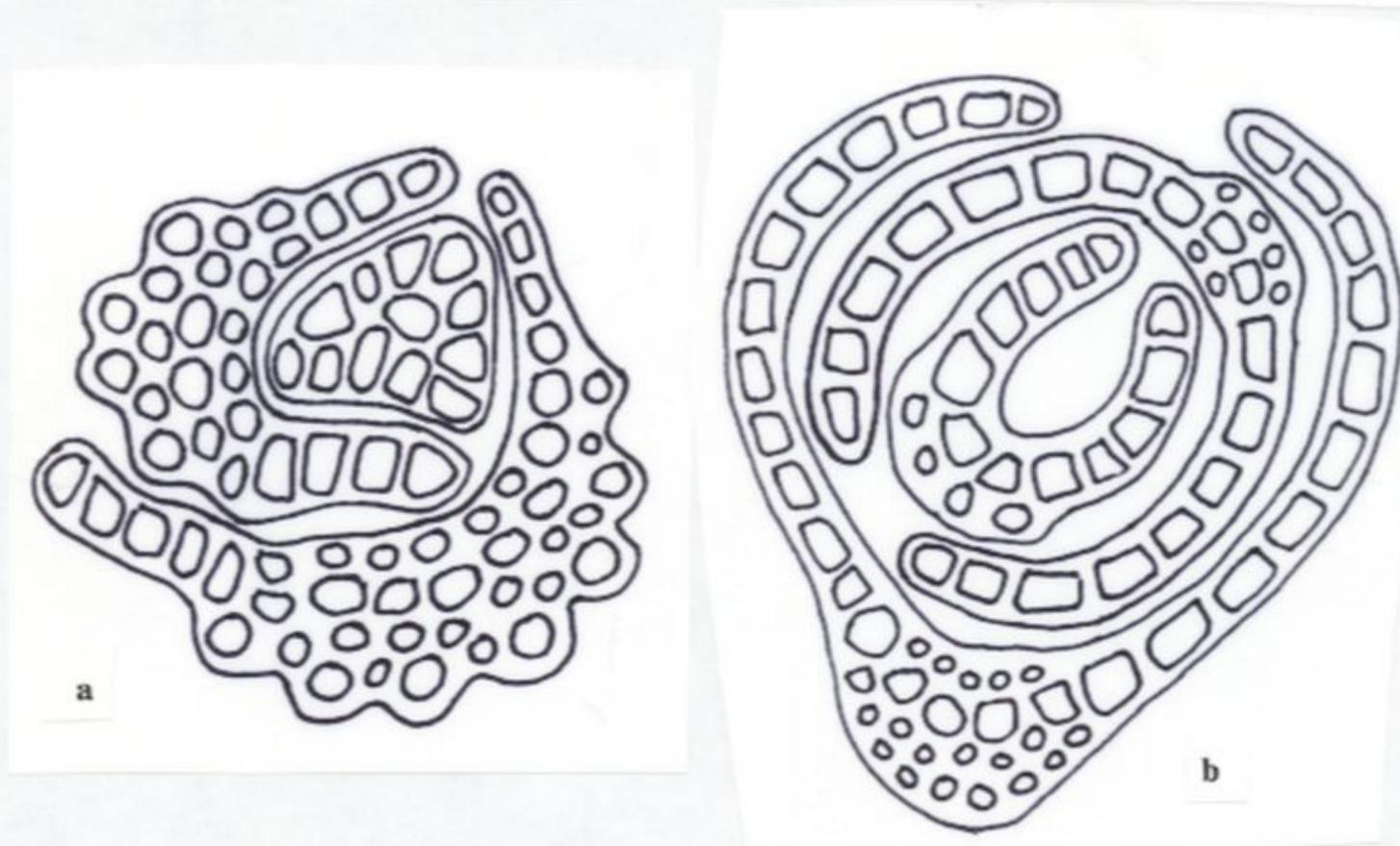

Fig. 3: Cladogram of the infrageneric categories of the genus *Campylopus*.

It is in ecological evidence that epiphytic species (found only rarely in this genus) show apomorphous character states such as incrassate laminal cells and stereids in transverse section of the costa. These are the same adaptions as found in dry adapted soil species.

There is phytogeographical evidence that the subgenus *Thysanomitrion* has most of its representatives in SE Asia but only one in the subantarctic, which is the probable ancestor and its character states can be regarded as plesiomorphous.

There are only a few phytochemical data present for this genus (Frahm 1983). These data show that certain species in the section *Homalocarpus* have no flavonoids whereas the highest diversity is found in the subgenus *Thysanomitrion*.

A major problem is in the interpretation of the costal anatomy. Are transverse sections without stereids and large hyalocysts or those with ventral and dorsal stereids pleisiomorphe? Within the Dicranaceae, the most common type of costa is that with ventral and dorsal stereid bands. Therefore for genera such as *Dicranum,* species with tendencies to larger cells instead of stereids are regarded as derived (Peterson 1979). However, this seems not to be the fact in *Campylopus.* As shown for the epiphytic species and species of the subgenus *Thysanomitrion,* these supposed young species have bands of stereids. So the genus *Campylopus* may be derived from a dicranoid ancestor by evolving hyalocysts (as it might have been the same with the genera of Paraleucobryaceae), but within *Campylopus* there seems to be support for the opposite evolution, that is reducing the hyalocysts.

Transverse sections of the leaf tips of the youngest leaves in *Campylopus flexuosus* show that the apical cell developes into the median chlorophyllose deuter band. The deuter cells produce abaxial and adaxial hyalocysts (fig. 2a). By this way the transverse section in an early stage of development of a *Campylopus* leaf resembles that of a mature leaf of *Paraleucobryum enerve.* Stereids are produced in later stages of development by cell divisions of hyalocysts. In contrast, in young leaves of *Dicranum spadiceum* Zett., the median deuter cells produce abaxial and adaxial stereids (fig. 2b). The ontogenesis of stereids in *Campylopus* seems therefore to be different from that in *Dicranum.*

There might also be palaeontological evidence for the fact that hyalocysts in the costae are a plesiomorphous character state. Smoot & Taylor (1986) described a moss from silicified peat of the late Permian of the Antarctic that possessed a multilayered costa. The areolation (figs. 11-13) is quite similar to present species of *Dicranum.* One transverse section (fig. 2) resembles much the structure of a species of *Campylopus* with a median row of deuter cells, ventral hyalocysts and smaller dorsal, nonstereidal cells. The other transverse section (fig.5), which I would not refer to the same species, shows ventral and dorsal hyalocysts with two median clusters of stereids similar to costa in present species of *Brothera* or *Campylopodiella.* Therefore multilayered costae with hyalocysts were already present in the Late Palaeozoic.

In conclusion, costae with hyalocysts, erect capsules, a dicranoid peristome with elongate triangular striate teeth split halfway are regarded as plesiomorphic. To the contrary, costae with double stereid bands, asymmetric capsules or filiform peristome teeth are regarded as apomorphic.

For the cladistic analysis, the infrageneric categories (subgenus *Thysanomitrion*, subg. *Campylopus* with sections *Campylopus* and *Homalocarpus*) as proposed by Frahm (1983) have been used along with the subgenus *Campylopidulum* described later by Vital (1984).

The analysis using Henningian cladistics (fig. 3) shows that the subgenera *Campylopidulum* and *Thysanomitrion* have the highest number of apomorphous character states, whereas the subgenus

Campylopus is the most primitive one in which the sect. *Homalocarpus* turns out to have the most plesiomorphic characters. This does not automatically include any conclusion about the age of these categories. As explained by its rich speciation in SE—Asia, the subgenus *Thysanomitrion* seems to be the youngest branch, indeed. However, the two representatives of subgenus *Campylopidulum* each with one species in the dry savannah regions of the Neotropics and Africa (Frahm 1986) seem to go back on an origin in the dry climatic periods of the Mesozoic and seem to have developed from the same Gondwanalandic ancestor. At least there was considerable speciation in subg. *Campylopus* sect. *Homalocarpus* in the Andes, probably by a spreading of subantarctic ancestors in this mountain chain in Tertiary, although this group is considered here as the most primitive and probably also oldest group.

6. Origin and evolution of the genus

It would be worth to speculate about the age of the genus and species and the probable time of its origin. Since there are no species in *Campylopus* with a pangaean distribution, the genus itself should be younger than 200 Mio years.

An indication of the presumed origin of the genus may be a region with the most primitive forms, with a maximum of continuity of the climate through the past geological periods and a continuity of habitats. The most primitive forms according to the cladistic analysis are species of the section *Homalocarpus* with a center in the subantarctic, where 12 of 14 species belong to this group.

A reconstruction of the palaeoclimate allows conclusions whether the climate at any time was humid, either cool or tropical, or arid, and thus less favourable for bryophytes in general or only for adapted species. Furthermore it is important to know to which extent humid climates were present and whether they were continous (allowing migration) or separated by arid regions. An interpretation of geological sediments allows such conclusions in the way that coal deposits indicate humid forests, coral reefs tropical climates, and sandstones, evaporites and Red Beds desert climates. Maps of the coal deposits from different geological periods by Seyfert & Sirkin (1973) show that there must have been a continuous humid climate in the present subantarctic since the late Palaeozoic, which may indicate (together with the high percentage of primitive taxa) an origin of *Campylopus* along the south coast of Gondwanaland. The next diversification is indicated by dry adapted species with a present wide (gondwanalandic) range from South and Central America to Africa and India. This type of range may go back to the Jurassic period about 150 Mio years ago, when the continents where still connected. Examples are *Campylopus pilifer* Brid., *C. savannarum* (C. Müll.) Mitt., or ancestor of species pairs occurring in savannahs such as *C. carolinae* Grout in Brazil and *C. perpusillus* Mitt. in Africa. It could be that also mesic forest species such as *C. fragilis* (Brid.) B.S.G. or *C. flexuosus* (Hedw.) Brid. were derived in this period by invading the drier interior of Gondwanaland. A reason for this migration and adaptation to drier habitats could be the drainage of swamp forest pressing the species into new habitats (probably combined with a considerable number of extinctions). It could be argued that these widespread ranges are based on relatively recent long distance dispersal. However, this would not explain why *Campylopus fragilis*, for instance, does not occur in the mountains of SE-Brazil (which should be easily accessible for long distance dispersal) but is replaced there by a local, morphologically different subspecies. It would also not explain why *Campylopus flexuosus* is not present in SE-Brazil, allthough it has a wide, nearly pantropical range. Therefore these wide ranges seem

not to be the result of long distance dispersal but of previously continuous ranges at a time when the continents where still partially connnected.

There are some examples for disjunctions of species between SE-Brazil and E-Africa, where they occur in vicariant subspecies or species. Examples are *Campylopus trachyblepharon* (C. Müll.) Mitt. ssp. *trachyblepharon* in SE-Brazil and ssp. *comatus* (Ren. & Card.) J.-P. Frahm in E-Africa, *C. julaceus* Jaeg. ssp. *julaceus* and ssp. *arbogastii* (Ren. & Card.) J.-P. Frahm, *C. controversus* (Hampe) Jaeg. and *C. stenopelma* (C. Müll.) Rehm. ex Par. These species must have been present when the South Atlantic had just opened and there was a continuous shore-line stretching from SE-Brazil to Malagasy, about 135 Mio years ago. Separation of the continents lead to isolation and to geographical races.

Relicts of the former *Campylopus* flora of the coastal areas of South America just after the split of Gondwanaland are preserved in SE-Brazil. This region is characterized by 13 endemic species, of which 8 can easily be derived from species with present subantarctic ranges (Frahm in prep.). SE-Brazil had also a continuous humid climate through the past geological periods (Nacib Ab'Saber 1982) and thus species could survive here (at least in part) since the Mesozoic.

Old species with an age of 100 Mio years or less may be those which are confined to the Neotropics or tropical Africa, where they have a wide range. Examples are *Campylopus subcuspidatus* (Hampe) Jaeg., *C. richardii* Brid. and *C. lamellinervis* (C. Müll.) Mitt. in the Neo-tropics.

Younger species (with an age of 70 Mio years or less) are presumambly those of young Mesozoic islands such as the Caribbean Islands or of mountain massifs of Teriary age. 50% of all neotropical species belong to the andine element and therefore the richest speciation took place during Tertiary.

The most recent speciation probably took place at the subspecies level on isolated mountain massifs such as the Serra do Itatiaia in SE-Brazil (*Campylopus fragilis* (Brid.) B.S.G. ssp. *fragiliformis* (J.-P. Frahm) J.-P. Frahm) or young volcanic islands such as the Galapagos Islands (*C. pilifer* Brid. ssp. *galapagensis* (J.-P. Frahm & Sipman) J.-P. Frahm).

There is no convincing indication for spe-ciation during the Quaternary, in spite of strong climatic changes and fluctuation of vegetation belts. It could be that a local endemic like *Campylopus cleefii* from the colombian páramo and apparently derived from the montane *C. arctocarpus* (Hornsch.) Mitt. has evolved only in one paramo system, which extended to lower elevations in cold phases of the Pleistoce-ne. However, these fluctuations have pro-bbaly only had an influence on the expansion of present ranges.

Based on this distribution-based estimation of the age of the 65 neotropical species of *Campylopus,* 60% have been evolved in the Tertiary, 30% in Cretaceous, 2% in Jurassic and 8% in the Triassic, demonstrating that the Tertiary speciation was the most important (Frahm, in prep). This should not, however, lead to the conclusion that the number of species of *Campylopus* has raised through the past 180 Mio years. There were almost certainly numerous extinctions, for example in the Quaternary by lowering or raising of sealevels, lowering and raising of temperatures causing splitting of continuous vegetation belts (like rainforests), and expansion of alpine belts. There are indications of species showing scattered distributions, which probably are extinct in parts of their ranges, like *C. subcuspidatus* in South America. Other species are confined to extremely small ranges like *C. uleanus* (C. Müll.) Broth., *C. viridatus* (C. Müll.) Broth. and *C. widgrenii* (C. Müll.) Mitt. in SE-Brazil, each known from only 2-4 localities, or have a wide range but with only a few records of small, sterile populations, like

C. oerstedianus (C. Müll.) Mitt. a relic tethyan range from central America to Europe, or the Mexican population of *C. japonicus* Broth. trapped in Mexico as a relict of a previous circum-pacific range. These are the really endangered species and may be the next candidates for extinction.

6. Conclusion

Coming back to the statement by Schuster (1984), who called *Campylopus* a modern and successful genus. Apparently it is successful. This is expressed by the high number of species, and the broad geographical and ecological amplitude. This success is due to anatomical and morphological features, of which the structural plasticity of the costa probably plays the most important role. The genus itself, however, cannot be called a modern genus. The interpretation of the worldwide distribution shows that it probably evolved on the Gondwana continent and therefore has probably been already present in Mesozoic ages. The main speciation, however, may be of Tertiary origin, caused by the uplift of mountain systems and continental drift, and thus diversification is relatively modern. Insofar *Campylopus* might be called one of the most successful genera of mosses with relatively recent diversification.

Literature cited:

Corley, M.F.V. & J.-P. Frahm 1982. Taxonomy and world distribution of Campylopus pyriformis (Schultz) Brid. Journal of Bryology 12: 187-190.

Frahm, J.-P. 1980. Synopsis of the genus Campylopus in North America North of Mexico. The Bryologist 83: 570-588.

—————— **1983.** A new infrageneric classification in the genus Campylopus Brid. Journal of the Hattori Botanical Laboratory 54: 207-225.

—————— **1984.** Phytogeography of European Campylopus species. Proceeding of the Third Meeting of Bryologists from Central and Eastern Europe, Praha, pp. 191-212.

—————— **1985.** The ecological significance of the costal anatomy in the genus Campylopus. Abstracta Botanica 9, Suppl. 2: 159-169.

—————— **1985a.** The worldwide range of Campylopus shawii Wils. Journal of Bryology 13: 329-332.

—————— **1986.** Campylopus Brid. 2. Subg. Campylopidulum Vital. Nova Hedwigia 43: 221-227.

—————— **1987.** Which factors control the growth of epiphytic bryophytes in tropical rainforests? Symposia Biologica Hungarica 35: 639-648.

—————— **1987a.** Oekologische Studien ueber die epiphytische Moosvegetation in Regenwaeldern NO-Perus. Beih. Nova Hedwigia 88: 143-158.

—————— **1988.** The subantarctic and southern hemispheric species of Campylopus (Dicranaceae), with contributions to the origin and speciation of the genus. Journal Hattori Botanical Laboratory 64: 367-388.

—————— **in prep.** Origin and distribution of Neotropical species of Campylopus.

Frahm, J.-P., M. Giese, M. Padberg, T. Koponen and D.H. Norris 1985. Bryophyte flora of the Huon Peninsula, Papua New Guinea. IX. Atractylocarpus, Bryohumbertia, Campylopodium and Campylopus (Dicranaceae, Musci). Acta Botanica Fennica 131: 63-88.

Frey, W. & J.-P. Frahm 1987. The twist mechanism in the cygneous setae of the genus Campylopus. Morphology, structure and function. Nova Hedwigia 44: 291-304.

Nacib Ab'Saber, A. 1982. The Paleoclimate and Paleoecology of Brazilian Amazonia. In: G.T. Prance (ed.) Biological Diversification in the Tropics. Proceedings of the Fifth International Symposium of the Association for Tropical Biology held at Macuto Beach, Caracas, Venezuela, 1979, pp. 41-59.

Peterson, W. 1979. A revision of the genera Dicranum and Orthodicranum (Musci) in North America north of Mexico. Ph.D. Thesis Univ. of Alberta.

Raven, P.H. & D.I. Axelrod 1974. Angiosperm Biogeography and Past Continental Movements. Annals of the Missouri Botanical Garden 61: 539-673.

Robinson, H. 1985. The structure and significance of the leucobryaceous leaf. Monographs in Systematic Botany from the Missouri Botanical Garden 11: 111-120.

Schuster, R.M. 1972. Continental Movements, "Wallace's Line" and Indomalayan-Australasian dispersal of Landplants: Some eclectic concepts. Bot. Rev. 38: 3-86.