

The origin and distribution of Neotropical species of *Campylopus*

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Summary: Of the 65 species of *Campylopus* known from tropical America, 33 are andine in distribution, 16 are found only in SE Brazil, 8 have wide ranges through Central and South America, 3 species are disjunct in SE-North America and Brazil, 3 are confined to the Caribbean and one species belongs to the circum-pacific and one to the tethyan element. For different parts of the Neotropics, the composition of phytogeographical elements is calculated. For the first time, bryophyte distributions are compared to the Pleistocene forest refuges proposed by zoologist and phanerogamists. The distribution of several rainforest species of *Campylopus* coincides with the major part of the montane refugia. Using an interpretation of the present-day ranges, a hypothetical survey is given of the origin and evolution of this genus in tropical South and Central America. The ranges of part of the species can be explained only by long distance dispersal, while the ranges of other species seem to be relictual.

1. Introduction

A phytogeographical analysis of a single genus may be of limited value and not be useful for any generalized conclusions. However, this may be different for the genus *Campylopus* because of the following reasons:

1. *Campylopus* is one of the largest genera of mosses, with approximately 180 species worldwide, 65 of them in the Neotropics.
2. Taxa of this genus have an enormously wide ecological range, occupying habitats all over the world from the subantarctic to the subarctic and from sealevel to more than 4500 m.
3. It is supposedly an relatively old genus (Frahm 1988), with relatively recent diversification.
4. It occurs in virtually all parts of the Neotropics and in all types of habitats from savannahs to rainforests, and coastal deserts to the alpine.

The only limitations are the restriction of all species to acidic substrates and the lack of species in the interior of lowland rainforests. The restriction to acidic substrates (which also concerns related genera such as *Dicranum*, *Chorisodontium*, *Dicranodontium*, *Atractylo-carpus*, *Pilopogon* and others) may indicate an origin of these groups in a geological period,

when only acidic substrates were available.

The preparation of a taxonomic treatment of Campylopodioideae and Paraleucobryoideae for the Flora Neotropica series (Frahm in press) allowed for the first time an examination of the distribution of the neotropical species of *Campylopus*, based on a revision of about 320 binomina reported from Central and South America. 65 species are recognized in the Neotropics, offering a solid base for a phytogeographic evaluation.

These 65 neotropical species of *Campylopus* can be grouped into the following distribution patterns (Fig. 1):

1. Andine species: 33 (approx. 50%) (3 disjunct in SE-Brazil)
2. SE-Brazilian species: 16 (25%)
3. Neotropical and wide tropical species: 8 (12%)
4. Species disjunct in Brazil and SE North America: 3 (4.6%)
5. Caribbean species: 3 (4.6%) (one species also in Europe)
6. Circum-pacific species: 1 (1.5%)
7. Tethyan species: 1 (1.5%)

For a general geological and floristic background

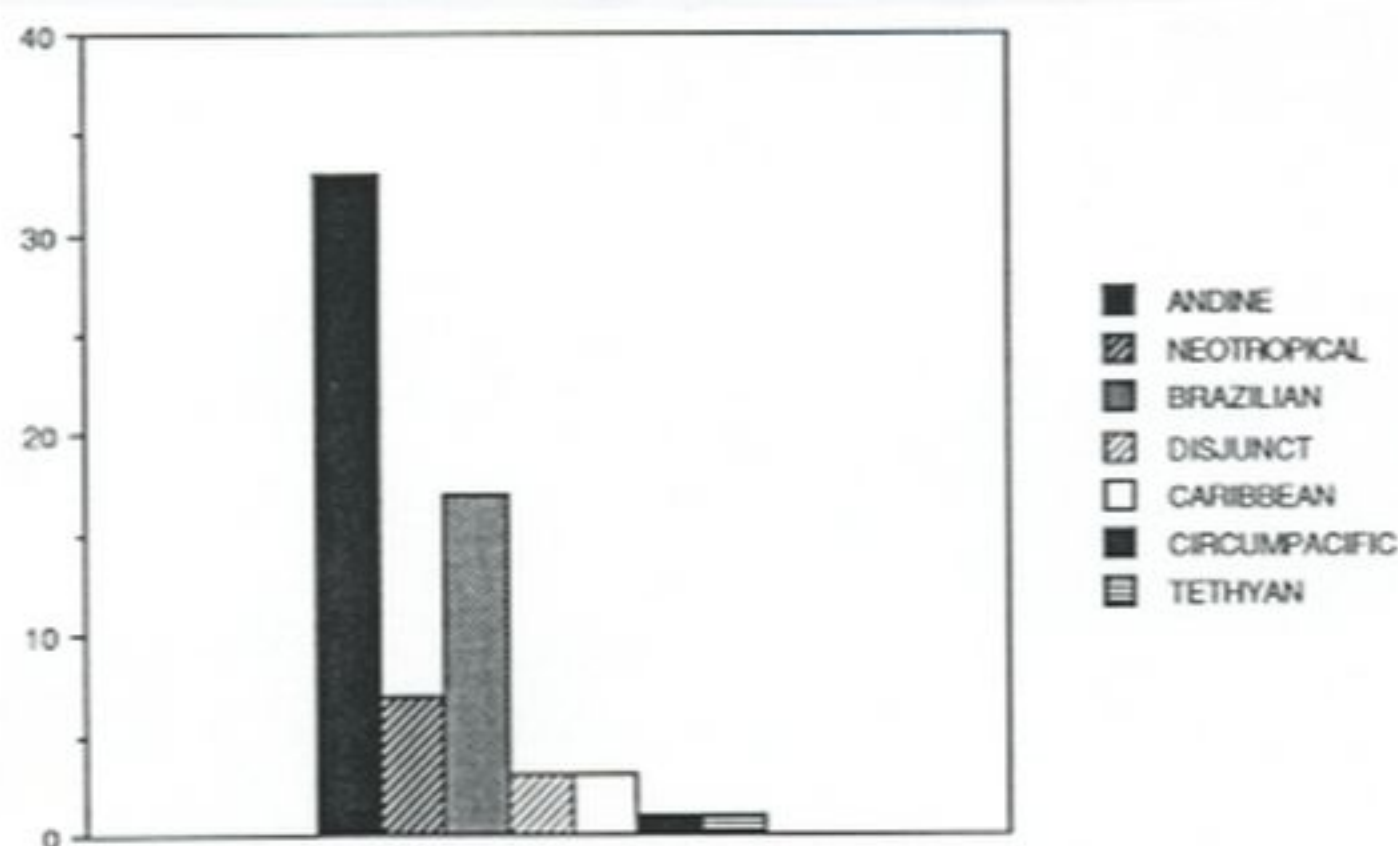


Fig. 1: Number of species of Neotropical *Campylopus* referred to different phytogeographic elements.

7. Tethyan species: 1 (1.5%)

For a general geological and floristic background (based on phanerogams) for the Neotropical flora see Gentry (1982).

2. Phytogeographic elements

2.1. Andine Species (fig. 2)

Most of the species of *Campylopus* in tropical Central and South America belong to the andine element, mostly confined to the montane and the alpine belts of the Central and South American Cordillera, partly disjunct in SE-Brazil. The Andes stretch through the whole continent and provide an ideal pathway for migration and a broad variety of habitats. In contrast, there are only a few montane to alpine species in tropical Africa and therefore the higher richness of species of *Campylopus* of South America (65 species) as compared with Africa (50 species) goes back on the more numerous andine species.

The uplift of the Andes took place during Pliocene and the present day elevation was attained about 3 Mio years ago (van der Hammen 1982).

Three of the andine taxa (*C. jamesonii* (Hook.) Jaeg., *C. reflexisetus* (C. Muell.) Broth., *C. cuspidatus* (Hornsch.) Mitt. var. *dicnemioides* (C. Muell.) J.-P. Frahm) also occur in the Sierra do Itatiaia in SE-Brazil, where they are found in comparable habitats as in the Andes in the

(sub)alpine belt confined to a small (less than one squarekilometer) range. Another andine species (*C. heterostachys* (Hampe) Jaeg.) has been found only once in the coastal mountain range of Brazil. It remains an open question whether these species came to SE-Brazil by long distance dispersal or by a connection of the now disjunct range during a cooler (pleistocene) climatic period.

The N-S extension of the ranges of the andine species vary considerably. Part of them extend from Central or Southern Mexico to Bolivia or even Northern Argentina. (*C. albidovirens* Herz., *cuspidatus* (Hornsch.) Mitt., *heterostachys* (Hampe) Jaeg., *jamesonii* (Hook.) Jaeg., *nivalis* Brid., *oblongus* Ther., *pauper* (Hampe) Mitt., *pittieri* Williams, *reflexisetus* (C. Muell.) Broth., *zygodontocarpus* (C. Muell.) Par.) or have slightly smaller ranges from Guatemala to Bolivia (*C. anderssonii* (C. Muell.) Jaeg., *concolor* (Hook.) Brid.) or Mexico to Peru (*C. sharpii* J.-P. Frahm, Horton & Vitt, *tallulensis* Sull. & Lesq.). These include species from the alpine as well as from the subalpine and high montane belt (for altitudinal limits see Frahm & Gradstein in prep.). Since there is a gradient in the humidity of these habitats from the equator to the North and South, it might be supposed that these species are drought resistant species. This might be true for widespread species with a broad ecological range such as *C. nivalis* Brid. occurring from wet paramos to dry punas, but

	only in SAM	also in CentralAm
alpine	14	2
high montane	4	12

Tab. 1: Number of tropical-alpine and high montane species of *Campylopus* confined to South America or occurring in South and Central America.

not for hygrophytic species such as *C. pittieri* Williams.

Other groups of species are confined to ranges between Costa Rica and Bolivia (*C. asperifolius* Mitt., *cavifolius* Mitt., *densicoma* (C. Muell.) Par., *huallagensis* Broth., *trivialis* C. Muell. ex Britt.) or to the continent of South America, ranging from Venezuela to Bolivia (*C. ambo-roensis* Ther., *areodictyon* (C. Muell.) Mitt., *argyrocaulon* (C. Muell.) Broth., *capitulatus* Bartr., *edithae* Broth., *jugorum* Herz., *luteus* (C. Muell.) Par., *perexilis* (C. Muell.) Par., *subjugorum* Broth., *trichophylloides* Ther.). Even smaller ranges (according to the present state of knowledge) are found in *C. bryotropii* J.-P. Frahm and *C. incertus* Ther. (found between Venezuela and Peru), or in *C. cleefii* J.-P. Frahm and *C. longicellularis* J.-P. Frahm, hitherto found only in Colombia.

The main reason for the different extensions of ranges may be the fluctuation of vegetation belts in the Pleistocene. For the Northern Andes, about 20 colder periods alternating with warmer periods have been identified by palynological analysis, resulting in changes of the altitudinal forest limit between 3300-3600 m and less than 2000 m (van der Hammen 1982). In this way, the paramos expanded in glacial times and fused to larger areas.

The species stretching from South America into Central America could have reached the northern parts of their ranges first in the late Tertiary after the fusion of North and South America. At first, a comparison of species confined to South America and those extending to Central America gives no explanation for this successful invasion of Central America. Species of these both groups belong to different morphological groups and are rarely or

often found with sporophytes. However, most of the andine species occurring in Central America are high montane and not tropical alpine species (Tab. 1).

The two alpine species (*C. nivalis* Brid., *C. pittieri* Williams) were presumably able to spread by spores or fragments attached to birds from South to Central America, because direct migration of paramo species was possible only in elevations above 2500 (the lower limit of Paramos in glacial times, cf. van der Hammen 1974). Since there is no land connection in elevations above 2500 m between South and Central America, a direct migration to Central America was not possible and long distance dispersal must be accepted as a possible means of dispersal. This seems to be easy in *C. nivalis*, which is a weedy species producing sporophytes frequently and which is also found once in the Caribbean (and in Africa), testifying its ability for long distance dispersal. In contrast, the occurrence of *C. pittieri* in Central America (found only once in Chiapas close to the Guatemalan border) seems to be the result of occasional dispersal. It seems also to indicate that most montane species came from South to Central America by stepwise migration and that long distance dispersal has not been the common method of range extension, otherwise the number of alpine species in Central America (with no chance for stepwise migration) would be higher.

A comparison of the forest species (confined to the Andes as well as species with a wide neotropical range) of *Campylopus* on the Eastern and Western slope of the Andes (especially in Ecuador and Northern Peru) shows considerable differences. Some species are found only on the E-side of the Andes (*C. anderssonii* (C.

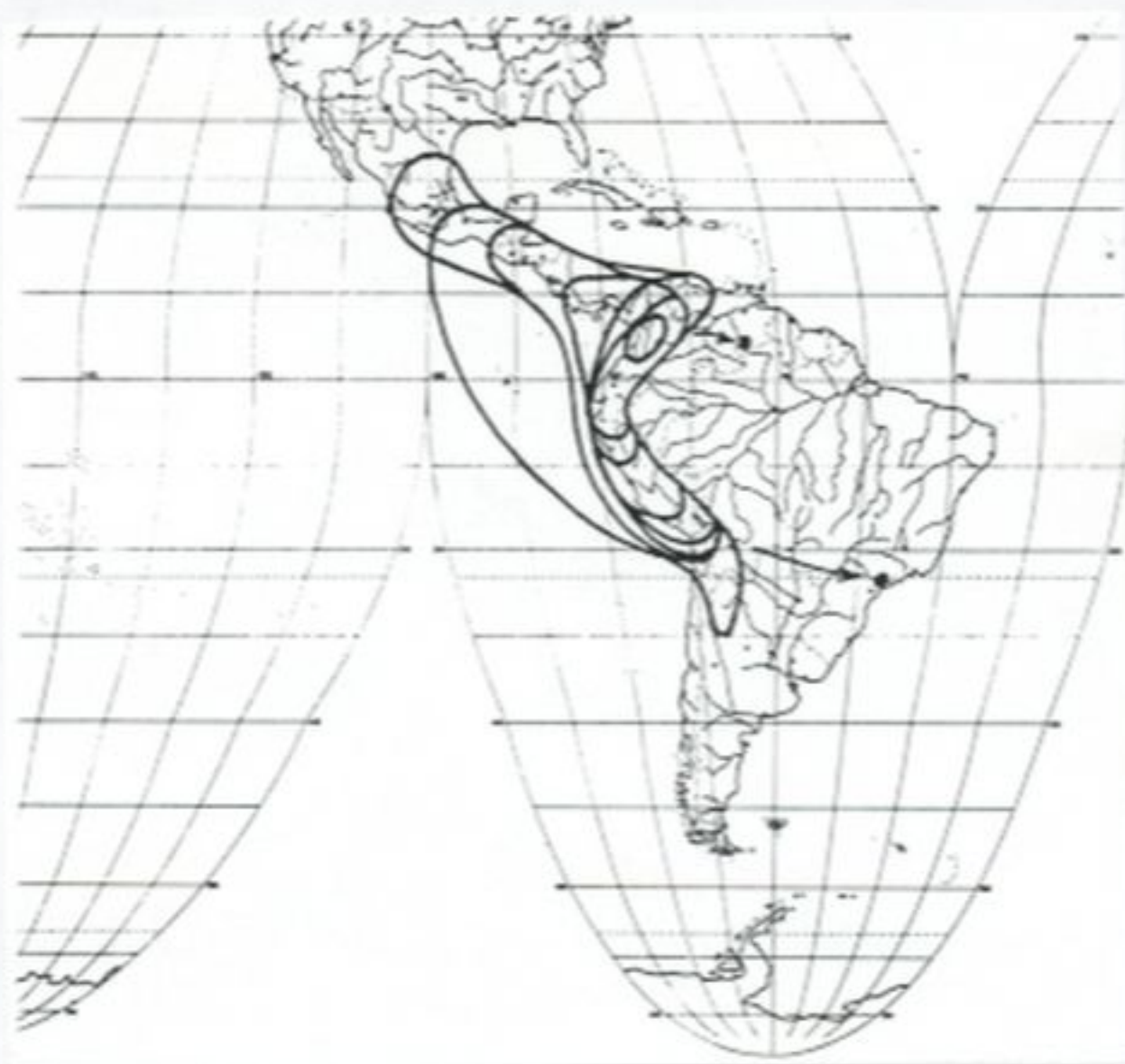


Fig. 2: Ranges of andine species of *Campylopus*.

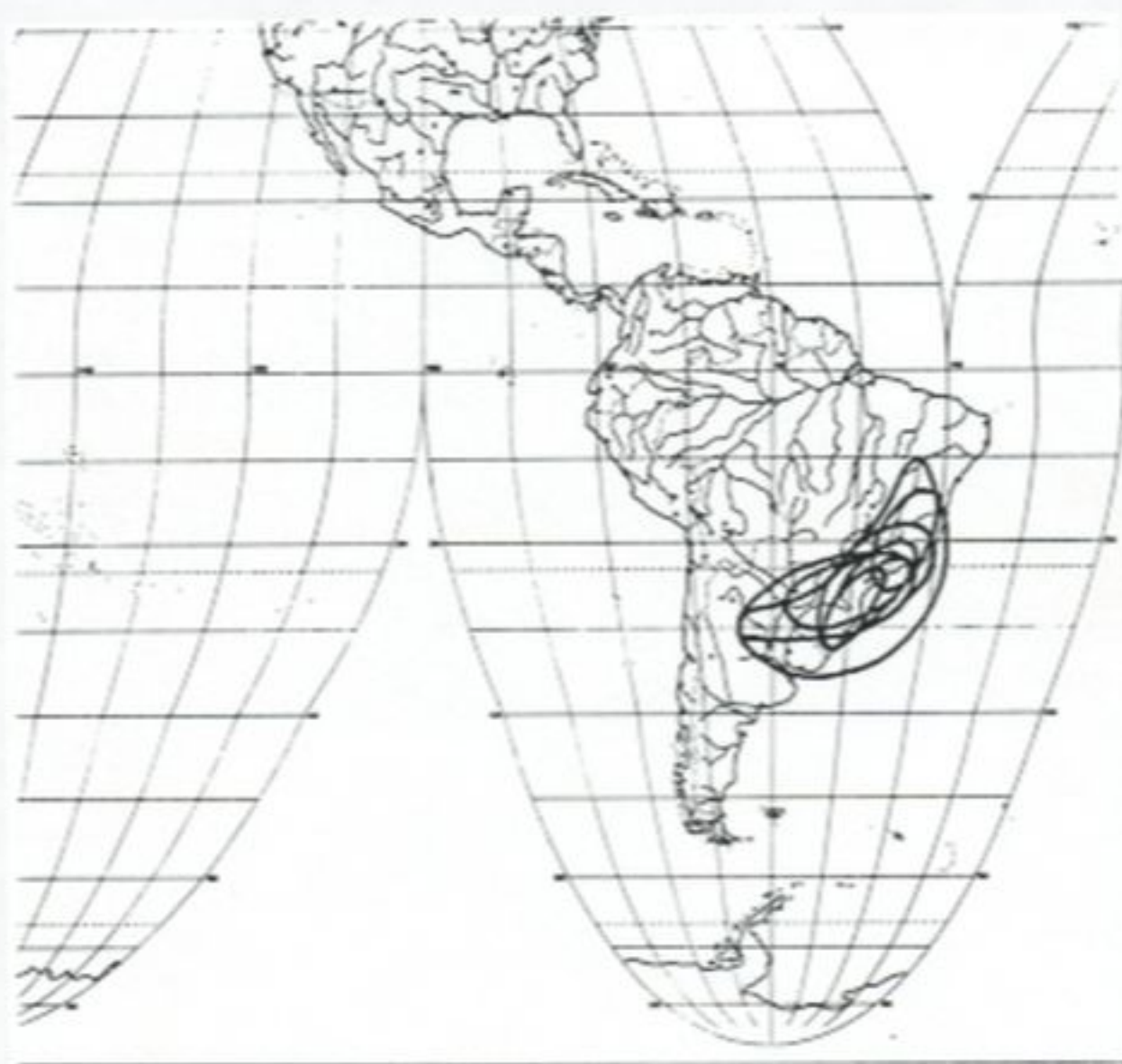


Fig. 3: Ranges of species of *Campylopus* confined to SE-Brazil

Jaeg., *jamesonii* (Hook.) Jaeg., *reflexisetus* (C. Muell.) Broth.). There are no *Campylopus* species confined to the W-side of the Andes. Conspicuously, the species occurring on both sides are species which also occur at higher elevations in the Polylepis forests. This seems to indicate that the forest species of the E-side have survived the glaciation periods in refugia on the humid East slope. Part of these species were not able to spread to the West side because of the lack of ability for spore dispersal over longer distances, since a direct path for migration from one side of the Andes is prohibited by dry inner andine valleys.

A few andine species are also found in the mountains of Africa (Frahm 1982, 1985): *Campylopus nivalis* Brid., *C. flexuosus* (Hedw.) Brid. var. *incacorrallis* (Herz.) J.-P. Frahm, *C. jamesonii* (Hook.) Jaeg. For these species long distance dispersal should be considered. However, according to van Zanten (1983), the trade winds go from East to West and origin of these species in the scattered mountains of tropical Africa seems unlikely.

The highest percentage of andine species belongs to the section Homalocarpus with erect capsules and ventral hyalocysts in transverse sections of the costa. This section is represented most frequently in the subantarctic, where 11 of 14 species belong to this section (Frahm 1988). Thus a subantarctic origin of most of the andine species of *Campylopus* can be proposed, as it is the fact in many well documented examples of bryophytes and angiosperms found in the Andes (Cleef 1978, Griffin et al. 1982).

2.2. SE-Brazilian species (fig. 3)

The SE-Brazil phytogeographic element is (with 16 species) the second largest element in the genus *Campylopus* in the Neotropics. It includes *C. aemulans* (Hampe) Jaeg., *controversus* (Hampe) Jaeg., *cryptopodioides* Broth., *dichrostis* (C. Muell.) Par., *gardneri* (C. Muell.) Mitt. *gastro-alaris* (C. Muell.) Par., *gemmatus* (C. Muell.) Par., *griseus* (Hornsch.) Jaeg., *julaceus* Jaeg., *julicaulis* Broth., *occultus* Mitt., *sehnmii* Bartr., *trachyblepharon* (C. Muell.) Mitt., *uleanus* (C. Muell.) Broth., *viridatus* (C. Muell.) Broth. and

widgrenii (C. Muell.) Mitt. Of these species, *C. dichrostis*, *gardneri* and *gastro-alaris* are elements of the Caatinga (*C. gastro-alaris* being a species of gallery forests) and are not found in the coastal areas. The others show more or less concentric ranges around the coastal range, and most of them are montane species confined to the humid mountain chains along the coast or rarely with some refugia on cloud covered mountaintops in drier regions ('brejos') in Espirito Santo or Bahia. Lowland species with a wider range into the interior of Brazil include *C. julaceus*, *C. aemulans*, and *C. griseus*, which even extend all three to the eastern slopes of the Andes in southern Bolivia and northern Argentina. This seems to indicate a former closed range from SE-Brazil to the Andes in cooler climatic periods of the Pleistocene, when the vegetation belts were lower than today. So species ranging today in Brazil between 600 and 1000 m elevation have ranged between 100 and 500 m elevation in the Quaternary when the temperatures were 5°C lower worldwide, and thus may have reached the foothills of the Andes through the lowlands of the Paraguay river basin. These species are not found in the intermediate lowlands of Paraguay today. The fact that these species do not occur in Paraguay nowadays does not preclude their occurrence there during the Pleistocene.

Two species occur disjunct in E-Africa, where they are replaced by vicariant subspecies. So *Campylopus trachyblepharon* ssp. *trachyblepharon* is replaced in E-Africa by ssp. *comatus* (Ren. & Card.) J.-P. Frahm and *C. julaceus* ssp. *julaceus* by ssp. *arbogastii* (Ren. & Card.) J.-P. Frahm. Both subspecies differ only in the length of the dorsal lamellae of the costa. These species are found in both parts of their range in the same habitat: on sandy soil close to the seashore. This disjunction presumably dates back to the end of the Mesozoic when the South Atlantic Ocean opened and there was a continuous range along the coasts of South America and Africa.

Campylopus fragilis (Brid.) B.S.G., which is common through the Neotropics and tropical Africa, is replaced in SE-Brazil (high elevations of the Serra dos Orgaos and Serra do Itatiaia) by a vicariant subspecies, ssp. *fragiliformis* (J.-P. Frahm) J.-P. Frahm. This is one of the few cases of narrow endemic taxa in *Campylopus* (the other



Fig. 3a: Ranges of species of *Campylopus* confined to the Cerrado regions of Brazil.

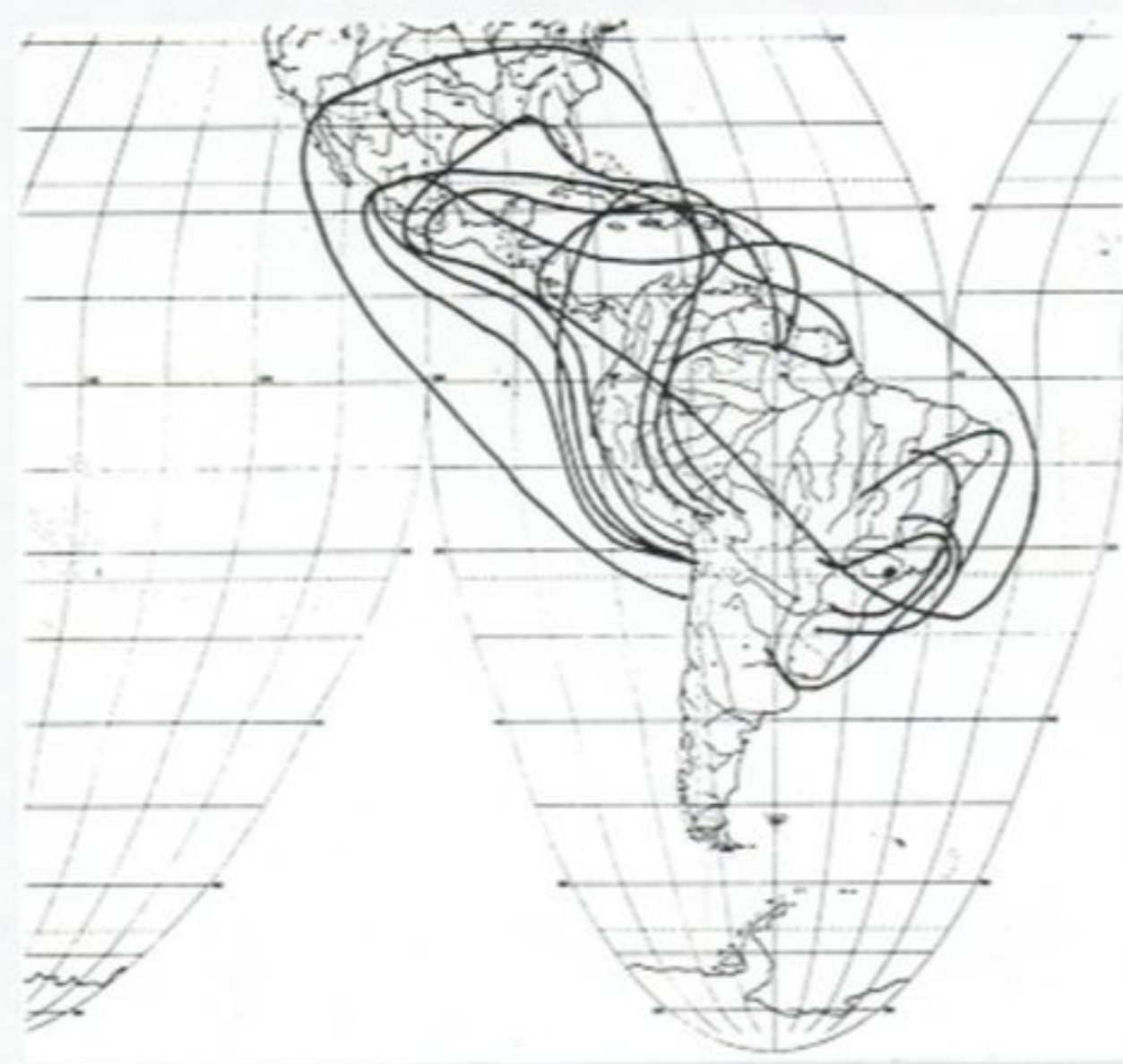


Fig. 4: Ranges of species of *Campylopus* widely distributed in the Neotropics.

being *Campylopus pilifer* Brid. ssp. *galapagensis* (J.-P. Frahm & Sipman) J.-P. Frahm on the Galapagos Islands). Although *Campylopus fragilis* ssp. *fragilis* is common in Central America and the Andes, it does not occur in SE-Brazil, but is replaced by a vicariant subspecies. This demonstrates that parts of a possible range is not occupied by this species and therefore long distance dispersal is not as much frequent as one might consider. The subspecies might have reached SE-Brazil by a connection of the now disjunct range during a cooler (pleistocene) climatic period.

The richness of the *Campylopus* flora of SE-Brazil (and probably of the bryoflora of SE-Brazil in general) may be due to a continuous humid climate through the Tertiary and Quaternary. Especially during glacial times, many parts of Brazil had arid climates because of displaced climate belts (Damuth & Fairbridge 1970; for palaeoecological climate maps see Nacib Ab'Saber 1982). Only a few species could stand the climatic change in the present cerrado region (*C. dichrostis*, *C. gardneri*) or survived in gallery forests (*C. dichrostis*). Thus the persistence of a uniform climate could have led to the persistence of the *Campylopus* flora since the end of the Triassic (180 Mio years ago). This may have occurred along the south coast of Gondwanaland, which is situated now between the arid areas of E-Patagonia and the Cerrado region of Brazil. In addition, long isolation combined with geological and ecological changes such as the uplift of the SE-Brazilian mountains could have led to the evolution of new taxa. Of the 13 species of *Campylopus* endemic to the humid parts of SE-Brazil (thus excluding the three Brazilian Cerrado species), the following can easily be recognized as derived from present subantarctic species:

- from either *C. introflexus* or *C. incrassatus*: *C. aemulanus*, *C. julaceus*, *C. julicaulis*, *C. sehne-mii*. All these species are characterized by leaves with hyaline hairpoints and hyaline basal laminal cells and differ by the shape of the upper laminal cells and appearance (for example appressed or distant leaves).

- from *C. aureonitens*: *C. griseus* differing by firm basal laminal cells.

- from *C. pyriformis*: *C. occultus* differing by comal tufted perichaetia and quadrate upper

laminal cells;

- from *C. acuminatus*: *C. uleanus*;

- from *C. purpureocaulis*: *C. controversus*.

In addition, *Campylopus surinamensis* (extending to Amazonia and SE-North America) has strong affinities to the subantarctic *C. vesticaulis* and seems to be one of the more successful descendents which remained not confined to SE-Brazil but extended northwards into drier habitats. Five species (*C. cryptopodioides*, *C. viridatus*, *C. widgrenii*, *C. trachylepharon* and *C. gemmatus*) cannot be directly related to present day subantarctic species. *C. gemmatus* has a strong relationship to the andine *C. asperifolius*. This species and *C. cryptopodioides* are some of the few epiphytic species of *Campylopus*. The range of *C. trachylepharon* (with a vicariant subspecies in E-Africa) reflects a previously larger range.

Some of the SE-Brazilian species are quite common throughout their range (for example *C. occultus*, *C. griseus*) but others have been found so far only in a very few localities (*C. uleanus* in 2, *C. viridatus* in three, *C. widgrenii* in 4), which demonstrates the relictual status of these species.

2.3. Neotropical and wide-tropical species (fig. 4)

Eight species (*C. arctocarpus* (Hornsch.) Mitt., *subcuspidatus* (Hampe) Jaeg., *fragilis* (Brid.) B.S.G., *flexuosus* (Hedw.) Brid., *lamellinervis* (C. Muell.) Mitt., *pilifer* Brid., *richardii* Brid., *savannarum* (C. Muell.) Mitt.) are distributed throughout the neotropics; all occur in montane regions with the exception of *C. savannarum*. The latter species, together with *C. surinamensis* C. Muell., is the only one of the 65 neotropical species found in the Amazon lowland, where it is confined to open, savannah-like-habitats ('Pseudo-Caatinga', 'Campina'). *Campylopus* species are entirely lacking in the equatorial lowland rainforest, which indicates an extratropical origin of the genus.

Half of the neotropical species are also found outside the Neotropics: in Africa (*C. pilifer*, *fragilis*, *flexuosus*, *savannarum*) or even extending to southern India and Sri Lanka (*C. pilifer*, *C. savannarum*). *Campylopus arctocarpus* is replaced in tropical Africa by a vicariant race (ssp. *madegassus* (Besch.) J.-P. Frahm). This type of range may be regarded as Gondwanalandic, and

in fact most of the species of *Campylopus* with such wide tropical ranges may be considered of Mesozoic origin. It seems especially be true for drought adapted species such as *C. pilifer* and *C. savannarum*, which may have evolved as a response to the dry Mesozoic climate in the interior of Gondwanaland. *Campylopus pilifer*, *C. fragilis* and *C. flexuosus* have an even wider distribution, ranging into the oceanic parts of Europe and North America. This range should extend to at least to the Late Mesozoic or Early Tertiary, when the northern continents were still connected.

Whereas most of these species with a neotropical type of range have a very wide distribution through Central and South America, usually including the Caribbean, *C. subcuspidatus* is the only example of a montane species occurring in Costa Rica, Venezuela (outside the Andes), Puerto Rico, the Guyanas and SE Brazil but not in the Andes. It indicates perhaps an old montane range in SE-Brazil and the highlands of Guyana with a recent extension to Puerto Rico and Costa Rica. It might indicate a species which originally occupied a wider range and has become extinct in parts of its former range, for example during the vegetation fluctuations and climatic changes during the Quaternary.

2.4. Caribbean species (fig. 5)

Three species are more or less confined within the Neotropics to the Caribbean: *Campylopus cubensis* Sull., *C. cygneus* (Hedw.) Brid. and *C. shawii* Wils. *Campylopus cubensis* is apparently the nearest relative of *C. arctocarpus* and can be considered as a vicariant species of the latter (for discussion of differentiating characters see Frahm & Gradstein 1988). Although *C. arctocarpus* is found in the Caribbean islands, it is less frequent, which probably indicates a later invasion in this region after *C. cubensis* had become well separated and ecologically established.

Campylopus cygneus is also found on the young volcanic islands of the Acores, which may be interpreted as an introduction (for example with flowering plants) or a long distance dispersal event. A relationship to or derivation from any other species is not apparent.

Campylopus shawii is related to and has probably derived from *C. subcuspidatus*. This species

is also found on the Acores and in the British Isles (Frahm 1985a). Although a disjunction between tropical America and the oceanic parts of Europe is also found in other bryophytes (e.g. *Cyclodictyon laetevirens* (Hook. & Tayl.) Mitt., *Adelanthus decipiens* (Hook.) Mitt., *Leptoscyphus cuneifolius* (Hook.) Mitt.), such a distribution pattern seems to be difficult to explain, since the Caribbean islands are of relatively young age (late Mesozoic), and there was no landbridge to North America and no longer a land bridge between North America to Europe.

According to Coney (cited in Brown & Gibson 1983) the Caribbean Islands originated as part of the Caribbean plate which developed from a series of volcanic islands between the isthmus of Tehuantepec and Colombia and was pushed eastwards, becoming the Greater Antilles. Since the Greater Antilles achieved their present position in Eocene time, the Caribbean Islands and their flora are relatively young. This is well documented by a relatively poor *Campylopus* flora represented by some common neotropical species, a few later occasional extensions from Central or South America by species with a limited range and the few number of species endemic to the Caribbean Islands, which have evolved from common neotropical species.

2.5. Brazil - North America disjunct species (fig. 6)

Three species of *Campylopus* occur in the arid parts of SE-Brazil and disjunct in SE-North America (*C. carolinae* Grout), scattered in the Caribbean and also in SE-North America and Brazil (*C. angustiretis* (Aust.) Lesq. & Jam.) or widespread from Brazil through the Amazon lowlands to the Guianas, and also in the Caribbean (rare) and SE-North America (*C. surinamensis* C. Muell.). The stations in North America are confined to the coastal plain. All of these species are characteristic of open white sand. During the Cretaceous, North and South America were continuously separated, even wider than today (Raven & Axelrod 1974), and the present coastal plain in North America was submerged during Cretaceous and most of the Tertiary times. Coney (cited in Brown & Gibson 1983) considers it unlikely that a landbridge has ever existed



Fig. 5: Caribbean ranges of species of *Campylopus*.



Fig. 6: Ranges of species of *Campylopus* disjunct in South America and SE-North America.

between Florida and South America via the Caribbean Islands or the Greater Antilles. Therefore, the disjunct stations were never connected (or only if a Pangaeian age of these species is considered). Long distance dispersal must be taken into account. Spore dispersal, however, is unlikely in present times for *C. angustiretis*, of which no sporophytes are known, or *C. carolinae*, of which sporophytes are extremely rare and have been found only a few times in Brazil, but not in the North American part of its range. In addition, *C. carolinae* has extremely short setae with capsules buried in the perichaetial leaves (Vital 1984, Frahm 1986). Dispersal of gametophyte fragments by hurricanes or birds may perhaps be taken into account for these species. The latter seems to be unlikely on the first view, but is the most probable explanation for the occurrence of *C. trachyblepharon* on the Bermudas during a few years at the begin of this century. This species is found along the seashores of SE-Brazil and rarely also in the Guianas. The latter localities may also be a result of dispersal by birds along a coastal migration route. Therefore the occurrence of these three species on the coastal plain of SE-North America may be regarded as extensions of the South American ranges at a time when suitable and very similar habitats to those in South America were established along the coast of Alabama, Florida, Georgia and the Carolinas.

2.6. Circum Pacific species

This type of range has been well documented by Sharp (1972) and Sharp & Iwatsuki (1965) for disjunctions between Japan and Mexico. The only example in the *Campylopus* flora of the Neotropics is *C. japonicus* Broth., described and reported from a few localities in Mexico as *C. saint-pierrei* Ther. The range in Australasia extends from Queensland to Japan. The limited occurrence in Mexico is due to the lack of sporophytes in this part of its range, where this species probably survives as a relict of a wider range in Tertiary times.

2.7. Circum-Tethyan species

Only one species of *Campylopus*, *C. oerstedianus*,

can be referred to this type of distribution, which is more common in Marchantiaceae, Pottiaceae, and pleurocarpous mosses. This species is known only sterile and from a few localities in Costa Rica, Jamaica, Georgia, France, Spain and Italy. If these records are plotted on a map showing the extension of the Tethyan sea (fig. 7), they are all situated along the north coast of the mesozoic ocean. The closest affinities of this species are to *C. pilifer*, a presumably Gondwanalandic species with a wide tropical distribution. *Campylopus oerstedianus* was probably derived from the latter as a vicariant species separated along the northern coast of the Tethyan Sea, by reduction of the dorsal lamellae of the costa under a more humid climate. It, however, remained unsuccessful in the following geological times and it seems to be a left over of the Mesozoic. In contrast, *C. pilifer* extended its range northwards to Laurasia.

3. Composition of phytogeographical elements in different regions

Percentage diagrams are given showing the composition of phytogeographical elements in different regions of the Neotropics including Mexico, Costa Rica, Venezuela, Guianas, Caribbean, Bolivia, and Brazil. (fig. 8).

In the andine regions, the total number of species increases from Mexico (19) to Costa in Bolivia, 2 Brazilian species are found in the foothills of the Andes. Thus the composition of phytogeographical elements within the Andes is very homogenous.

The highest mixture of phytogeographic elements is found in the Caribbean, with 42% neotropical species, 21% endemics and 14% each for andine species and Brazil - North American disjuncts, reflecting the young geological age of these islands and limited access. The latter is expressed by the generally low total number of species, with 14 one of the poorest *Campylopus* floras in tropical South and Central America. This is insofar surprising since the extension of the Caribbean islands was much larger during Pleistocene caused by lowering of the sealevel and thus the distances to the surrounding continents were smaller.

A similar heterogenous flora of *Campylopus*

species is found in the Guiana region. Whereas the *Campylopus* floras of other regions are often dominated by one element (andine in the Andes, SE-Brazilian in SE-Brazil), the *Campylopus* flora of the Guianas consists of widely distributed species as well as of a mixture of each one of all the other main phytogeographic elements. Of the 9 species recorded from there (Frahm & Gradstein 1987), 5 belong to the widely distributed neotropical species (*C. pilifer*, *arctocarpus*, *savannarum*, *richardii*, *subcuspidatus*), one is andine (*C. luteus*), one is caribbean (*C. cubensis*), one is a Brazil - North America disjunct element (*C. surinamensis*) and one is a coastal element of SE-Brazil (*C. trachylepharon*). Together with the high geological age of this region it suggests that the Guiana region belongs to the oldest phytogeographical units in South America with the oldest stock (the widely distributed neotropical species). *Campylopus surinamensis* as a drought adapted savannah species must probably be included in this old group. The other species (caribbean, andine) are apparently younger and/or a result of occasional dispersal. The only recognisable speciality in the *Campylopus* flora of Mt. Roraima is the presence of 'giant forms' in *Campylopus richardii* (described as *C. roraimae* Broth.) and *C. subcuspidatus*, which may be either a modification caused by the humid climate or a genotypic difference.

In SE-Brazil, the total number of species of *Campylopus* (31) is comparable to andine regions. It has also the highest number of endemics outside the Andes (with 55%), the rest consisting of a mixture of andine, neotropical or disjunct species.

4. *Campylopus* and the refuge theory

The refuge theory was developed by the ornithologist Haffer (1969) who demonstrated the existence of several centers of endemism in tropical South America. The theory was supported by plant distributional data of Simpson (1975, 1976) and Prance (1973, 1982) on a large scale and by Toledo (1976) and Steyermark (1979) for small areas in Mexico and Venezuela. The theory suggests that certain areas were forest refuges during arid climatic periods in the Pleistocene. The theory has also been applied to tropical

regions in Africa and Australia, and is supported by palynological and pedological data (Prance 1982). An evaluation of this theory has not yet been undertaken for bryophytes. However, during floristic and taxonomic studies on Neotropical Dicranaceae (Frahm 1983, 1984, Frahm in press) it became evident that there were some regions which were much richer in species than others. Examples are the Sierra Juarez in Mexico, where half the number of the species of *Campylopus* of Mexico are found (some of them confined to this or a few other localities), the eastern slopes of the Andes in Peru and Ecuador, and some mountain areas in southern Venezuela. An evaluation of the distribution maps of the genus *Campylopus* prepared for the Flora Neotropica treatment showed that the records of several montane rainforest species (fig. 9) are predominantly from the areas indicated as montane forest refugia by Prance (l.c.). These include mainly species in which sporophytes are not known or found only rarely, and therefore species lack the ability to spread. The many lowland refugia recognised by Prance cannot be supported by species of *Campylopus*, since there are only two species occurring in the Amazon lowland (*C. savannarum*, *surinamensis*), which are savannah relicts. Three of the six species (*C. huallagensis*, *C. luteus*, *C. sharpii*) have been yet found only in the refugia and may be endemic to these regions. The other species (*C. arctocarpus*, *C. lamellinervis*, *C. subcuspidatus*) are more widespread but have been found so far in South America in refuge areas only. Other refugia are not supported by bryophytes because there are no collections, for example in the Choco region of Colombia. In addition, bryophytes probably have more, but smaller refugia as indicated for forest trees and may thus be better indicators for small refugia, which must not be forests but cliffs or tops of mountains.

Of the eight refugia listed by Toledo (1976, 1982) for Mexico, most of them are not explored bryologically. Only Los Tuxtlas and Sierra Juarez are known to keep the richest *Campylopus* flora in Mexico, with many species confined to these regions (Table 2).

With the exception of *C. richardii*, which has a wider range, all of these species are of andine distribution and occur in the high montane belt. There seems to be another refugium at least for

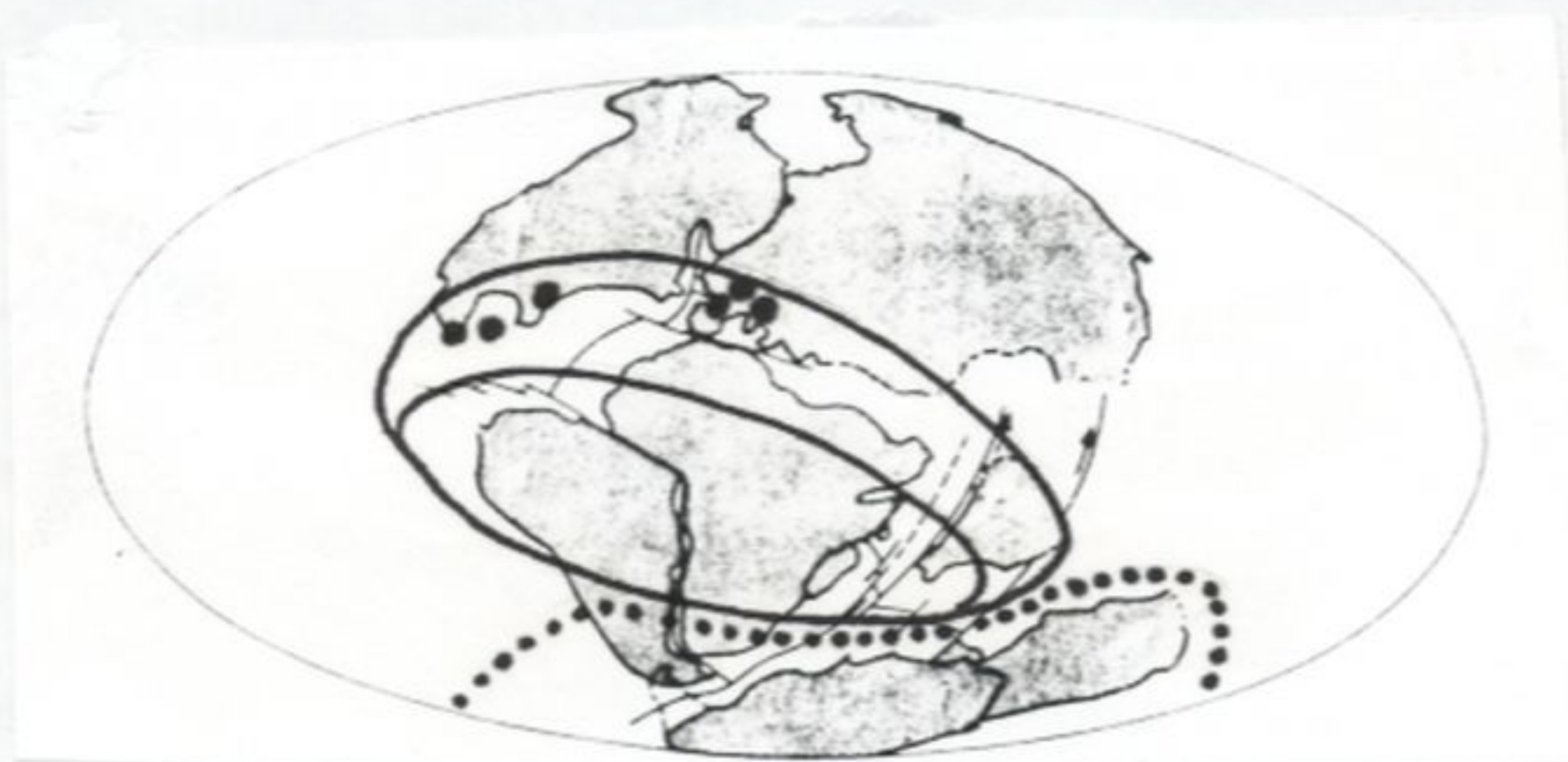


Fig. 7: Present records of *Campylopus oerstedianus* plotted on a map showing the continents at the end of the Jurassic, 135 my BP, and distribution of species with a Gondwanalandic range such as *C. flexuosus*, *C. fragilis* and *C. pilifer* (extending to Europe) or *C. savannarum*. Dotted line: range of *C. introflexus*, the probable ancestor of *C. pilifer* (Map after Dietz & Holden in Stott, 1981).



Fig. 7a: Ranges of taxa disjunct between SE-Brazil and E-Africa such as *C. trachblepharon* ssp. *trachblepharon* and ssp. *comatus* and *C. julaceus* ssp. *julaceus* and ssp. *arbogastii*, shown on a map of the location of continents at the end of the Triassic (180 my BP), indicating an originally closed range along the south coast of Gondwanaland (Map after Dietz & Holden in Stott, 1981).

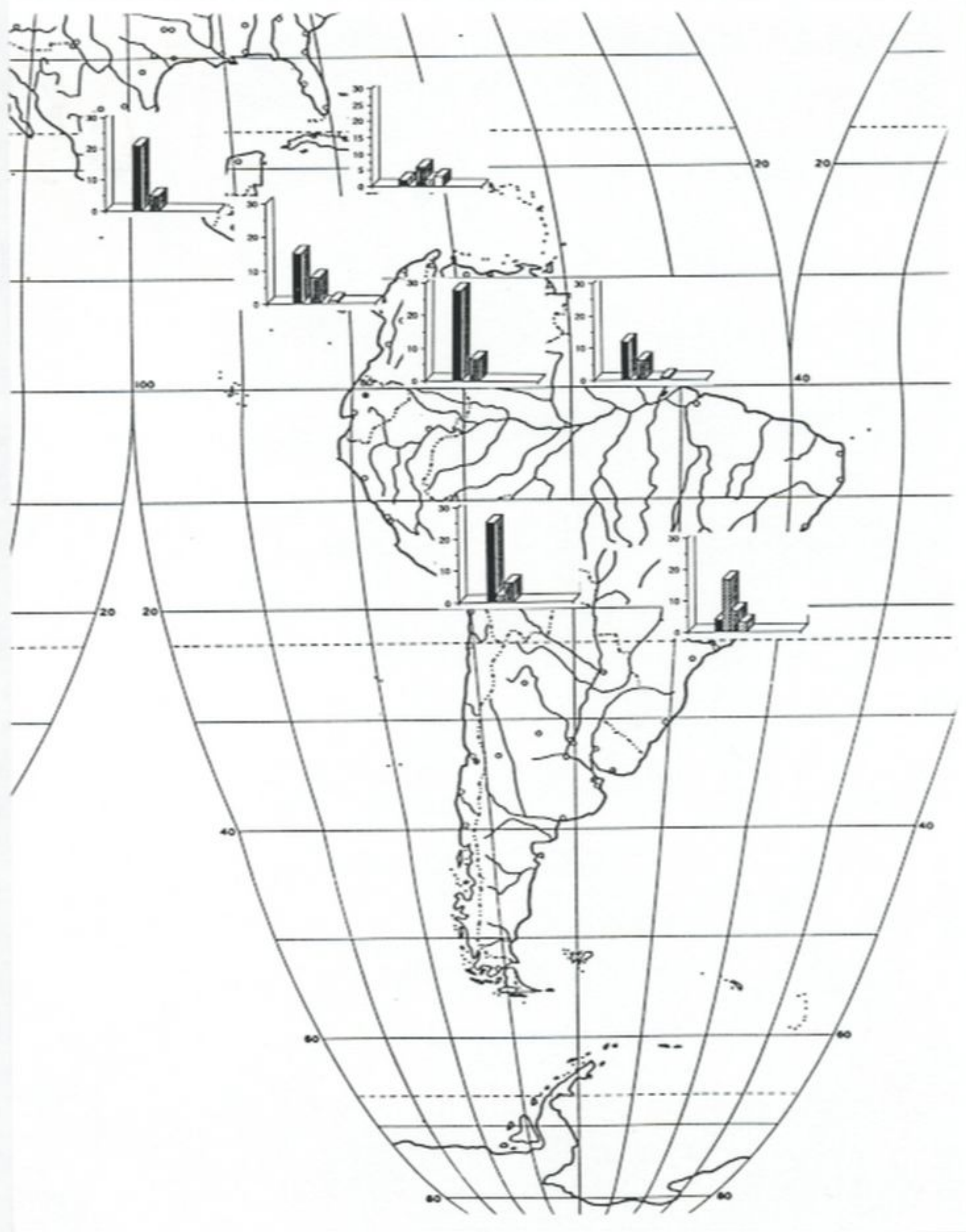


Fig. 8: Percentage diagram for the phytogeographical elements of species of *Campylopus* in different parts of the Neotropics.

<i>Campylopus</i>	L.T.	S.J.	
<i>andersonii</i>		x	also in Chiapas
<i>zygodontocarpus</i>	x		Guatemala to Bolivia
<i>tallulensis</i>	x	x	
<i>sharpii</i>		x	Venezuela to Peru
<i>richardii</i>	x		next in Costa Rica
<i>reflexisetus</i>		x	
<i>pauper</i>	x	x	Costa Rica to Bolivia
<i>oblongus</i>		x	Costa Rica to Bolivia
<i>jamesonii</i>		x	Costa Rica to Bolivia

Table 2: Occurrence of species of *Campylopus* in two of the refugia indicated by Toledo (1976, 1982) for Mexico. L.T. = Los Tuxtlas, S.J. = Sierra Juarez.

have been yet found only in the refugia and may be endemic to these regions. The other species (*C. arctocarpus*, *C. lamellinervis*, *C. subcuspidatus*) are more widespread but have been found so far in South America in refuge areas only. Other refugia are not supported by bryophytes because there are no collections, for example in the Choco region of Colombia. In addition, bryophytes probably have more, but smaller refugia as indicated for forest trees and may thus be better indicators for small refugia, which must not be forests but cliffs or tops of mountains.

Of the eight refugia listed by Toledo (1976, 1982) for Mexico, most of them are not explored bryologically. Only Los Tuxtlas and Sierra Juarez are known to keep the richest *Campylopus* flora in Mexico, with many species confined to these regions (Table 2).

With the exception of *C. richardii*, which has a wider range, all of these species are of andine distribution and occur in the high montane belt. There seems to be another refugium at least for bryophytes in Cerro Tres Picos, Chiapas, close to the Guatemalan border, where *C. andersonii* and *C. oblongus* are found for a second time in Mexico (here cited for Sierra Juarez) and in addition containing the only records of *C. cuspidatus* and *C. pittieri* in Mexico.

5. Disjunctions with tropical Africa.

Six species of *Campylopus* found in the Neo-

tropics also occur in Africa (Frahm 1982, 1985). They are either lowland species (*C. savannarum*), montane species (*C. fragilis*, *C. flexuosus*, *C. piilifer*), subalpine (*C. jamesonii*, *C. flexuosus* ssp. *incacorralis*) or alpine species (*C. nivalis*). Some other neotropical taxa are replaced in tropical Africa by vicariant taxa, which are distinguished at a subspecies rank (*C. arctocarpus* ssp. *madegassus*, *C. trachyblepharon* ssp. *comatus*, *C. julaceus* ssp. *arbogastii*).

6. Evaluation of possible long distance dispersal

It is still an open question of how effective long distance dispersal is in mosses and what influence it has on the present-day ranges. Although the ability for long distance dispersal in mosses has been shown by the experiments of van Zanten (1983), long distance dispersal may not necessarily occur. In the Neotropics, the ranges of *Campylopus* allow or even require the assumption of long distance dispersal events in the following cases:

- colonization of the Caribbean Islands from South or Central America,
- migration of alpine species from South to Central America,
- extension of ranges into SE-North America,
- dispersal of caribbean species to the coasts of the continent,
- occasional occurrences of andine species in the Caribbean (*C. nivalis* and *C. albidovirens*)



Fig. 9: Records of montane rainforest species *Campylopus huallagensis*, *C. sharpii*, *C. luteus*, *C. lamellinervis*, *C. arctocarpus* and *C. subcuspidatus* plotted on a map showing the forest refugia proposed by Prance (1973, 1979). Hatched: probable additional refugia indicated by these bryophyte species.

7. Hypothetical survey of the evolution of *Campylopus* in tropical South and Central America.

For the genus *Campylopus*, an origin at the south coast of the Gondwanaland continent is proposed here based on the following interpretations of recent ranges:

(1) The wide distribution of some species such as *C. fragilis*, *flexuosus*, *pilifer* or *savannarum* ranging from the Neotropics through tropical Africa to India is that of Gondwanalandic species and seems to indicate a Gondwanalandic origin of these taxa. Since some of them (*C. pilifer*, *C. savannarum*) are dry adapted species, they seem to have evolved from ancestors under wetter conditions along the south coast of the Gondwana continent.

(2) The origin of the genus at the south coast of the Gondwanaland continent is furthermore supported by circum-subantarctic ranges of species with primitive characters (Frahm 1988).

(3) The asymmetric distribution of *Campylopus* over the world with 14 species in the Subantarctic but only one in the Subarctic and the fact that nearly all northern hemisphere temperate species are tropical montane species and thus probably relicts from the Tertiary clearly supports the theory of a Gondwanalandic origin. In contrast to *Campylopus*, *Dicranodontium* has the opposite distribution, confined mainly to the Holarctic. This is the genus most closely related to *Campylopus*. Species of *Dicranodontium* can only be distinguished from certain species of *Campylopus* with ventral stereids in the costa by elongate upper laminal cells. Thus, *Dicranodontium* was probably a vicariant genus to *Campylopus* in Laurasia and both genera may have had a common ancestor.

Speciation in *Campylopus* may have begun in the Mesozoic, probably in acidic habitats, on which the species still depend on, and probably also in a cool temperate climate.

During Triassic there were still coal forming swamp remaining in Antarctica, Australia, Southern Africa and Southern South America (Seyfert & Sirkin 1973) and therefore hygrophytic species could still persist. Coal deposits in this area are found from the Palaeozoic to the Tertiary and therefore there seemed to be a conspicuous consistency of ecological conditions for hygrophytic plants for more than 200 Mio years until present. Since most

of the present subantarctic species of *Campylopus* inhabit swamps and show large ventral hyalocysts in transverse section of the costa, these species may form the oldest stock of species in the genus. However, the major upper part of Gondwanaland was arid and provided habitats for dry adapted species, which could extend their ranges north to the Tethyan sea.

During late Cretaceous, Gondwanaland started to split up. The common gondwanalandic species became disjunct and remained either unchanged, perhaps by gene exchange through spore dispersal, or developed vicariant species or races which are now recognised at the subspecies rank. Examples for species pairs developed after the separation of South America and Africa are the dry adapted, savannah inhabiting *C. carolinae* in South America and *C. perpusillus* in Africa (both members of subg. *Campylopidulum* and probably derived from a common gondwanalandic ancestor), and the subtropical rainforest species *C. controversus* in SE-Brazil and *C. stenopelma* in Transvaal. Examples of the evolution of subspecies are taxa disjunct between the coastal areas of SE-Brazil and E-Africa (*Campylopus trachyblepharon* ssp. *trachyblepharon* and ssp. *comatus*, *C. julaceus* ssp. *julaceus* and ssp. *arbogastii*).

In Tertiary, the continental drift continued with the uplift of mountain systems and increasingly humid conditions. Towards the end of the Tertiary cool temperatures caused renewed diversification by

(a) Invasion of subantarctic species into the high elevations, especially in the Andes. This was the richest diversification of species, for 50% of the present species in the Neotropics belong to this element. Part of the species may have colonized the afro-alpine mountains by long distance dispersal, since the Andes provided a better pathway for migration of subantarctic species as compared with Africa, where only mountain hopping was possible. This would also explain the lower number of afro-alpine species as compared with the andine ones.

(b) Invasion of subantarctic species into tropical and subtropical forests, sometimes from one ancestor independently in South America, Africa and Australia as shown for the subantarctic *Campylopus incrassatus*, from which *C. sehne-*

mii evolved in S-Brazil, and *C. cataractilis* in Africa and Australia (Frahm 1988).

(c) Evolution of endemic taxa in mountains (*C. amboroensis* derived from *C. pilifer*, *C. fragilis* ssp. *fragiliformis* in SE-Brazil) or on islands (the caribbean species evolved from spore dispersal of continental species with subsequent isolation and differentiation in the Early Tertiary, *C. pilifer* ssp. *galapagensis* in the Late Tertiary).

The Quaternary was a period with intensive vegetational fluctuation caused by expansions of savannahs, separation of forest regions and isolation of populations, lowering and raising of vegetation belts in the mountains, worldwide lowering of temperatures of about 5°C, and shifting of climatic belts to lower latitudes. These all may be reasons for extinctions of species. There is no evidence that species of *Campylopus* have evolved in the Quaternary.

Based on this hypothetical interpretation of present day ranges the percentage of species of *Campylopus* that evolved in the different geological periods can be calculated:

Quaternary: 0%

Tertiary: ca. 60% (all andine, caribbean and ciumapacific species)

Cretaceous: ca. 32% (all SE-Brazilian species and species disjunct between Brazil and SE-North America as well as species with a wide range in the neotropics but not occurring in Africa).

Jurassic: ca. 8% (all drought adapted Gondwanalandic and Tethyan species).

These data suggest that most of the species evolved in the Tertiary, and also a considerable number in the Cretaceous.

Consideration of the evolution of species of *Campylopus* would give the wrong impression that the number of species has steadily increased through the past time. This seems to be unlikely, since the total number of bryophyte species may have been higher in past geological periods and probable extinctions of numerous species may have happened.

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