A REVISION OF THE EAST-ASIAN SPECIES OF CAMPYLOPUS

JAN-PETER FRAHM

SUMMARY: A revision of all taxa of Campylopus reported for E Asia (China, Korea, Japan and Taiwan) revealed thirteen species and two subspecies. Campylopus gracilis (Mitt.) Jaeg. has proven to be synonymous with C. subulatus Schimp. in Rabenh. and is reported here as new to Japan. Campylopus gracilentus Card. described from Taiwan is synonymous with the SE-Asian C. laxitextus Lac. Campylopus fragilis ssp. goughii (Mitt.) Frahm (C. goughii (Mitt.) Jaeg.) and C. fragilis ssp. zollingerianus (C. zollingerianus (C. Müll.) Bosch & Lac.), C. crispifolius Bartr., C. boswellii (C. Müll.) Par. are reported as new to China. Campylopus involutus (C. Müll.) Jaeg. is synonymous with C. ericoïdes (Griff.) Jaeg. Campylopus yakushimensis Sak. and C. japonicus Broth. var. fuscoviridis Card. have proved to be inseparable from C. atrovirens De Not. and are regarded as synonyms of the latter. Campylopus atrovirens is reported for the first time with sporophytes. Lectotypes have been chosen for Campylopus ericoïdes, C. involutus and C. gracilentus.

The Campylopus flora of East Asia (in the sense of "As. 2" of the Index Muscorum, cf. Wijk et al. 1959, including China, Korea, Taiwan and Japan) is relatively poorly known. This is largely due to our limited knowledge of the bryofloras of China and Korea resulting from publications and herbarium labels being in Chinese and the inaccessibility of both literature and specimens. During the past few years, some basic information on the history of bryology in China has been provided by Koponen (1984) and Wu (1984). Reports on recent activities have been published for China by Wu (1986, 1989) and for Korea by Huneck et al. (1987). Several checklists of the mosses of Taiwan have been published (Wang, 1970, Lai & Wang-Yang 1976, Kuo & Chiang 1987).


For China, Chen et al. (1963) list 18 species of Campylopus. Most of these are southern in distribution, since Gao and Chang (1983) list only 5 species in their checklist for Northeast China. In the most comprehensive compilation Redfearn and Wu (1986) list 25 species (nomenclature based on Index Muscorum, Wijk et al. 1959). Of these, Campylopus richardii has to be referred to C. umbellatus, as the SE-Asian C. umbellatus has commonly be named as C. richardii, a neotropical species (Frahm 1976). Campylopus longigemmatus Gao has been recognized as a species of Dicranodontium (Frahm 1985). Campylopus alpigena Broth. and C. handelii Broth. are synonymous with C. schimperi (Frahm 1982), Campylopus caudatus (C. Müll.) Mont.

1 Universitäts-Duisburg, Fachbereich 6, Botanik, Postfach 10 15 03, D-4100 Duisburg, Germany.
with *C. comosus* Bosch & Lac. (Frahm 1984), *Campylopus irrigatus* Thér. with *C. japonicus* (Frahm 1987), *C. latinervis* (Mitt.) Jaeg. with *C. gracilis* (Frahm 1984), *C. scabridorus* Dix. with *C. serratus* Lac. (Frahm 1987), and *C. tenuinervis* Fleisch. with *C. involutus* (C. Müll.) Jaeg. (Frahm 1984a).

Wang (1970) listed 7 species from Taiwan: *Campylopus aureus* Bosch & Lac. (= *schmidii* C. Müll.), *C. gracilentus* Card., *C. japonicus* Broth., *C. nakamurae* Sak., *C. richardii* Brid. (= *C. umbellatus* (Arn.) Par.), *C. schwarzii* Schimp. and *C. taiwanensis* Sak. The status of *C. nakamurae* and *C. taiwanensis* is doubtful, since the types are not available.

For the present study, approximately 1600 specimens of *Campylopus* from the following herbaria have been examined: the Herbarium of the Academy of Science, Beijing (PE), the Herbarium of Cryptogams, Kunming Institute of Botany (HKAS), the Shanghai Museum of Natural History (SHM), the herbaria of the Southwest Missouri State University (SMS), the Missouri Botanical Garden (MO), the Botanical Museum Helsinki (H), the Hattori Botanical Laboratory (NICH), Kochi University (KOCHI), Hiroshima University (HIRO) and the herbarium of M.-J. Lai (Taipei). In addition, smaller numbers of specimens were studied from the British Museum (BM), the herbarium of V. F. Brotherus (H-BR) and the Museum National d’Histoire Naturelle, Paris (PC).

The treatment includes Japan, Korea (confined here to South Korea due to the lack of literature and herbarium specimens from North Korea), Taiwan and mainland China, which includes the province of Xizang, formerly the independent state of Tibet.

Only synonyms from E Asia are given for each species. For a complete list of synonyms see Frahm (1987).

**Key to the East Asiatic Species of Campylopus**

1 Basal laminal cells thin-walled.

2 Costa excurrent in a hyaline hairpoint. *C. schmidii*

2* Costa not excurrent in a hyaline hairpoint.

3 Costa occupying 3/4 of the leaf width. Lamina present only in the lower 1/3 of the leaf. Alar cells protruding into the costa. Transverse section of the costa without stereids. *C. schwarzii*

3* Costa narrower. Lamina longer. Alar cells not or only slightly protruding into the costa. Transverse section of the costa with or without stereids.

4 Plants comose foliate. Costa in transverse section with dorsal groups of stereids and lax ventral hyalocysts, smooth at back. *C. fragilis* s.lat.

5 Costa widened below midleaf and contracted towards leaf base. Vegetative propagation by small, hooked brood leaves at stem tips. *C. fragilis* ssp. *fragilis*

6 Upper laminal cells short, quadrate or oval.

7 Upper laminal cells quadrate. *C. fragilis* ssp. *fragilis*  
7* Upper laminal cells oval. *C. fragilis* ssp. *goughii*

6* Upper laminal cells rectangular. *C. fragilis* ssp. *zollingerianus*

5* Costa gradually contracted from leaf base to leaf tips. Upper laminal cells oblique or rectangular. Costa excurrent in a subhyaline serrate point. Vege-
J.-P. Frahm: A revision of the East-Asian species of *Campylopus*

4* Sterile plants not comose.

8 Costa in transverse section without dorsal groups of stereids. Leaves lanceolate, concave, the tip not distinctly channelled.


8* Costa in transverse section with dorsal groups of stereids. Leaves ending in a long, narrow channelled tip.

1* Basal laminal cells incrassate.

10 Basal laminal cells shortly rectangular to subquadrate.

11 Costa narrow, occupying 1/3 of the leaf width, lamellose at back in the upper part, excurrent in a distinct hyaline hairpoint. Leaves contracted at leaf base.

11* Costa wider, occupying 1/2 of the leaf width, smooth or only slightly ridged at back, excurrent in a concolorous, rarely hyaline point. Leaves not narrowed at leaf base.

12 Leaves ending in a long tip (rarely cucullate in var. *cucullatifolius*), smooth at margins. Widespread.

12* Leaves lanceolate, ending in a hyaline serrate point, serrate in the upper third. Known only from Hong Kong.

10* Basal laminal cells rectangular.

13 Upper laminal cells rectangular or slightly oblique.

14 Costa excurrent in a subhyaline, sometimes hyaline point, in transverse section with ventral hyalocysts in the lower part of the leaf and ventral stereids in the upper part. Calyptra fringed at base. Capsules erect, symmetric, scabrous at base.

14* Costa percurrent or excurrent in a concolorous point, in transverse section with ventral substereids or hyalocysts. Calyptra ciliate at base. Capsules curved, strumose, smooth at base.

15 Leaves longly pointed. Transverse section of the costa with ventral substereids. Plants without microphyllous branches.

15* Leaves shortly pointed. Transverse section of the costa with small, firm ventral hyalocysts. Plants with microphyllous branches.

13* Upper laminal cells elongate-oval.

16 Leaves ending in a hyaline hairpoint.

16* Leaves ending in a cucullate tip.

1* Basal laminal cells incrassate.

10 Basal laminal cells shortly rectangular to subquadrate.

11 Costa narrow, occupying 1/3 of the leaf width, lamellose at back in the upper part, excurrent in a distinct hyaline hairpoint. Leaves contracted at leaf base.

11* Costa wider, occupying 1/2 of the leaf width, smooth or only slightly ridged at back, excurrent in a concolorous, rarely hyaline point. Leaves not narrowed at leaf base.

12 Leaves ending in a long tip (rarely cucullate in var. *cucullatifolius*), smooth at margins. Widespread.

12* Leaves lanceolate, ending in a hyaline serrate point, serrate in the upper third. Known only from Hong Kong.

10* Basal laminal cells rectangular.

13 Upper laminal cells rectangular or slightly oblique.

14 Costa excurrent in a subhyaline, sometimes hyaline point, in transverse section with ventral hyalocysts in the lower part of the leaf and ventral stereids in the upper part. Calyptra fringed at base. Capsules erect, symmetric, scabrous at base.

14* Costa percurrent or excurrent in a concolorous point, in transverse section with ventral substereids or hyalocysts. Calyptra ciliate at base. Capsules curved, strumose, smooth at base.

15 Leaves longly pointed. Transverse section of the costa with ventral substereids. Plants without microphyllous branches.

15* Leaves shortly pointed. Transverse section of the costa with small, firm ventral hyalocysts. Plants with microphyllous branches.

13* Upper laminal cells elongate-oval.

16 Leaves ending in a hyaline hairpoint.

16* Leaves ending in a cucullate tip.

**Campylopus atrovirens** De Not., Syll. Musc. Ital. 221, 1838.


**Campylopus yakushimensis** Sak., Bot. Mag. Tokyo 47: 332, 1933. Type not available from MAK.

Often very similar in appearance to *C. japonicus* with long comal leaves and deciduous stem tips and occurring in the same habitats and often in the same localities, e.g. China, JingXi, JinXi, *Wang 119a* (*C. japonicus*) and 119 (*C. atrovirens*).

**Campylopus atrovirens** has conspicuously elongate-oval upper laminal cells. Ac-
According to the description, *C. yakushimensis* also has this type of upper laminal cell. *Campylopus yakushimensis* is described and illustrated by Takaki (1967) who states that "this species seems to be allied to *C. atrovirens*. . . ." According to Takaki, both species should be separable by the leaf shape and longer upper laminal cells. Type material was not available for study from the herbarium of Sakurai (MAK). Noguchi (1987) compares it with *C. japonicus* from which *C. yakushimensis* shall differ in its linear upper laminal cells. His view is supported by the fact that a variety of *C. japonicus*, with longer upper laminal cells, has been described by Cardot as var. *fuscoviridis*. *Campylopus yakushimensis* is apparently the same as *C. fuscoviridis*, which was originally recognized by Cardot as a variety of *C. japonicus*. I find *C. fuscoviridis* inseparable from *C. atrovirens*.

*Campylopus atrovirens* and *C. japonicus* share several characters, such as the habit with deciduous stem tips with longly pointed leaves, shortly rectangular to quadrate basal laminal cells, alar cells protruding into the costa which is ill defined at the leaf base, the presence of side nerves, and the general structure of the transverse section of the costa. Therefore it is hard to decide whether this taxon is conspecific with *C. atrovirens* or a variety of *C. japonicus* with elongate upper laminal cells. The reasons to place *C. fuscoviridis* to *C. atrovirens* are the transverse section of the costa, and identical upper laminal cells. In a transverse section of the costa, both have small ventral hyalocysts, even in the upper part of the leaf, whereas the ventral hyalocysts become stereids in *C. japonicus*. In addition, *C. atrovirens* and *C. fuscoviridis* are nearly always found with distinct hyaline hair-pointed leaves, whereas *C. japonicus* is frequently subepilose or epilose.

Takaki (1967) separated *C. yakushimensis* and *C. atrovirens* on the shape of the upper laminal cells (narrowly and longitudinally linear in *C. yakushimensis* and long-rhombooidal in *C. atrovirens*) and the shape of the leaves (triangularly linear in *C. yakushimensis* and linear-lanceolate in *C. atrovirens*), characters which are regarded as falling into the same range of variation.

The distribution of *C. atrovirens* is oceanic and accordingly most records are close to the China Sea. Specimens named as *C. atrovirens* from Yunnan proved to be *C. laxitextus*, *C. japonicus*, *C. ericoides* or *C. comosus*.

**Distribution:**


Ecology: On moist rocks and wet cliffs in humid regions, in Japan at elevations between 400 and 1500 m.


Rarely specimens with cucullate instead of hyaline-tipped leaf apices have been found. Although the stem leaves are cucullate, the perichaetial leaves, which have been found in Wang 703 (HKAS), are hyaline-tipped. Interestingly, distinctly piliferous and semicucullate leaves are produced along the same stem in Schofield 51876 (NICH). This may indicate that these cucullate forms are phenotypic modifications, and that the specimens with both types of leaf are the result of changed habitat factors. In Schofield 51876, the basal leaves are cucullate but the upper leaves are piliferous. However, these may also develop into perichaetial leaves.

Cucullate leaves are a common feature in several other species with hyaline hairpoints, but are rarely found in *C. atrovirens*. Such specimens have been found only once in Alaska and once in Britain. Plants with cucullate leaf tips seem to occur mostly in alpine habitats, whereas the hyaline-tipped forms occur at lower elevations, or in wet habitats such as swamps. Such forms are usually regarded as varieties, although it is not known whether they are genetically distinct or only habitat modifications. A few studies on these subject are contradictory. Cultivation of the hyaline-tipped (and thus more xerophytic) *C. bicolor* var. *ericeticola* in high humidity growth chambers did not produce cucullate modifications. On the other hand, both hyaline and cucullate tipped leaves along the stem have be found in *C. acuminatus* and *C. bicolor*, but so far only in
one specimen of each species.

The frequency of cucullate forms varies greatly. In *C. atrovirens*, only a few specimens are known with cucullate leaves, but in *C. bicolor* specimens with cucullate leaves are more common than those with hyaline tipped leaves.

Cucullate rather than piliferous leaf apices are not characteristic of any particular subgenus of *Campylopus*. They are found in several species of subg. *Thysanomitriion* (*C. exasperatus*, *C. praemorsus*, *C. flaccidus* var. *cucullatifolius*) as well as in subg. *Campylopus* (*C. cuspidatus* var. *dichemoides*, *C. acuminatus* var. *kirkii*, *C. bicolor*, *C. atrovirens* var. *cucullatifolius*).

**Wang 703** and **Chen 90-16** from Yunnan posses sporophytes, which were not previously known in this species. All of the many specimens from Europe and North America collected so far are sterile. One to five sporophytes are produced in one perichaetium. The seta is relatively short, 3–5 mm long and dark brown to blackish. The capsules are 1.2–1.5 mm long, erect and nearly symmetric, light to dark brown and furrowed. The lid is 0.8 mm long, oblique-rostrate and reddish brown. Calyptrae are not present. The peristome teeth are reddish at the base and pale at the tips, and narrowly lanceolate. The capsules resemble somewhat those of species of the subg. *Thysanomitriion*, but are not scabrous at the base and do not have filiform peristome teeth. The combination of an erect, +/− symmetric capsule and leaves with firm, incrassate basal laminal cells and a costal transverse section with relatively thick-walled, small ventral hyalocysts is rarely met within the genus *Campylopus*. Usually erect capsules are correlated with hyaline basal laminal cells, and curved capsules with incrassate basal laminal cells. It demonstrates that the sections *Campylopus* and *Homalocarpus* (cf. Frahm 1977) can perhaps not be distinguished by means of curved viz. erect capsules. The sporophyte as well as the elongate upper laminal cells resemble those met in the genus *Dicranodontium*, which, however, is distinguished by ventral stereids in transverse section of the costa under the present circumscription of the genus.

**Distribution:** Map 2.

Specimens examined: **CHINA. YUNNAN.** Gongshan, Dulongjiang 2400 m, Zhang 20 (HKAS); Fugong, **Wang 703 c.spor.**; Chengde, **Chen 90-16 c.spor.** (HKAS). **JAPAN.** Mie Pref., Mt. Gozaisho area, Schofield 51876 (NICH).

**Campylopus comosus** (Schwaegr.) Bosch & Lac., Bryol. Jav. 1: 75, 1858.  
*Campylopus caudatus* (C. Müll.) Mont. in Dozy & Molk., Bryol. Jav. 1: 78, 1858.  

The leaf shape, rectangular upper laminal cells, long leaf tip with excurrent serrate costa and comose foliation are all similar to *C. laxitextus*. However, the latter has hyaline basal laminal cells (the perichaetial leaves of *C. comosus* also have hyaline basal laminal cells), and a different transverse section of the costa with lax ventral hyalocysts. These are even visible without sectioning from the ventral side of the leaf. In contrast, *C. comosus* has firm incrassate basal laminal cells and a transverse section of the costa with ventral stereids.
Campylopus comosus can also be confused with C. ericoides, which has a similar areolation of the leaf. However, the latter has shorter pointed leaves with an excurrent subhyaline costa and, as in all species of the subgenus Thysanomitrion, erect symmetric capsules, scabrous at base. Campylopus comosus has very elongate leaves and curved, strumose capsules.

The appearance, leaf shape and areolation of Campylopus comosus are similar to those of Bryohumbertia subcomosa (Dix.) J.-P. Frahm (B. walkeri (Mitt.) J.-P. Frahm, Campylopus walkeri (Mitt.) Jaeg., cf. Frahm 1989). However, when well developed, B. subcomosa is interruptedly foliate, has pitted basal laminal cells, a longer seta, smooth inner surfaces of the peristome teeth, an annulus, and a lid which is as long as, or longer than, the urn. This species, widely distributed through S- and SE-Asia from Sri Lanka to Borneo, has been reported as new to Japan (Frahm & Deguchi 1987) where it had been collected several times in plantation forests in Honshu. It has not been found in any other collection from mainland Asia, e.g. Yunnan. Therefore it may be assumed that the records from Japan are not the northernmost extension of the range of this tropical species (as in C. umbellatus) but represent introductions.

Campylopus comosus is regarded as a vicariant species of Campylopus flexuosus in SE-Asia. It shares with the latter the areolation of the leaves, but has longer-pointed leaves, comal tufted stems and a transverse section of the costa with ventral stereids. Campylopus flexuosus has shorter leaves, evenly foliate stems, small, firm ventral hyalocysts in a transverse section of the costa and is, in addition, mostly characterized
by the presence of microphyllous branches.


Habitat: On humic soil, base of trees and rotten wood in elevations from 200 to 3000 m.

Specimens examined. China. Guangdong. Ding Hu Nat. Preserve, Redfearn et al. 34407 (SMS). Jiangxi. Lushan, Nanjing University 25 (PE). Yunnan. Menghai: Nannuo Mtn, Magill et al. 7985 (SMS, MO); Menghai-Mengzhe road km 32, Magill et al. 7935 (MO, SMS); Mengla, Hwy Menglun to Mengla km 109, Redfearn et al. 33810, 33816 (SMS); Nanping, km 6 road Hangla to Jiuzhaigou, Redfearn et al. 35347 (SMS); Mengla km 637 along Menglun-Mengbang road, Magill et al. 7694 (MO, SMS); Quiubei, Li 205 (HKAS); Xishuangbanna, Meng La, Li 3001a (HKAS). Zhejiang. Maoshan, Wu 341 (PE).


At indicated by the sporophyte, Campylopus ericoides belongs to the subgenus Thysanomitrion, although it does not look much like the more “advanced” species of this subgenus, such as C. umbellatus with incrassate, pitted laminal cells and wide leaves with a relatively small costa occupying only less than 1/3 of the leaf width. It has,
in contrast, narrow leaves with a broad costa and pitted laminal cells as in *C. comosus* or *C. flexuosus*. In a transverse section of the costa, it has small ventral hyaloysts or substereids in the basal part of the costa which are replaced by stereids in the upper part of the leaf, indicating a more primitive species of the subgenus. This is also expressed in the lack of the appressed foliate stalks bearing perichaetia, which are typical of other species of the subgenus. The sporophytes, however, show the characteristics of the subgenus *Thysanomitrion*: erect symmetric capsules, peristome teeth ending in filiform tips and the capsule being scabrous at the base. *Campylopus ericoides* thus shows structural affinities to *C. clavatus* from the southern hemisphere from which it could have been derived. The main difference between them concerns the basal laminal cells, which are thin-walled in *C. clavatus* as a habitat adaptation in subantarctic heathlands, and firm in *C. ericoides* as an adaptation against desiccation in tropical latitudes.

Although the type of *C. tenuinervis* is identical with *C. involutus*, all specimens named *C. tenuinervis* in Chinese herbaria must be referred to *C. umbellatus*. This might therefore be the first true record of *C. ericoides* for China.

**Distribution.** China: Redfearn & Wu (1987) sub *C. tenuinervis*. New Guinea, Java, Malaysia, Borneo, Sri Lanka, S-India. **Map 4.**

Ecology: on soil in scrubby woods, along paths, on road banks and in other open places, also on rocky road cuts, at elevations between 1000 and 2700 m.

Specimens examined. **China.** HAINAN. Changjiang Co. 19°15'N, 109°15'E, Redfearn et al. 35703 (SMS); Ledong Co., Jiangfengling Forestry Station 18°52'N, 108°42'E, Reese 17754 (LAF). GUANGDONG. Dinghushan, Lin 33 (PE); Hainandao, Chen 223, 732 (PE). GUANGXI. Longsheng, Jin & Hu 630 (PE). YUNNAN. Menghai: Mannuo Mtn., Redfearn et al. 34234 (SMS); Magill et al. 7988 (SMS, MO); Mengla, Hwy Menglun to Mengbang km 631, Redfearn et al. 33835 (SMS); Menghai, Hwy Menghai to Menghe km 32, Redfearn et al. 34171 (SMS); mengla, Menglun – Mengbang road km 637, Magill et al. 7698 (MO, SMS); Kunming Qiongzhusi Temple, 25°04'N, 102°37'E, Redfearn et al. 2137 (SMS); Jinghong, km 662 Hwy Dadugang to Mengyang, Redfearn et al. 34288 (SMS); Mengla, km 636 Menglun to Mengbang, Redfearn et al. 33898 (SMS); Songming, 59 km N of Kunming, 25°28'N, 102°46'E, Redfearn et al. 1833 (SMS); Menghai, Hwy Menghai to Menghe km 32, Redfearn et al. 34156 (SMS); Dali, vicinity of Yinglofeng, 25°42'N, 100°07'E, Redfearn et al. 1134 (SMS); Yiniang, Li 4548 (HKAS); Xishuangbanna, Menghai, Li 2470 (HKAS); Cangyuan, Li 4843 (HKAS); Luchun, Zang 417 (HKAS); Yuanyang, Zang 4843 (HKAS).

**Campylopus flexuosus** (Hedw.) Brid., Muscol. Recent. Suppl. 4: 71, 1819.

*Campylopus flexuosus* has a very uneven distribution in the northern hemisphere. Predominantly of tropical montane distribution in Central and South America and Africa, it occurs outside the tropics in the temperate regions of the northern hemisphere in North America, Europe and Asia, probably as a relic of the Tertiary. Probably due to differential survival of the Pleistocene glaciations, it is found in North America only in British Columbia and in one locality in the Appalachians, but is widespread in western Europe and the Canary Islands. In East Asia, it seems to be as rare as in North America. It has been found only in the subtropical parts of China and in Taiwan, which might be Pleistocene refugia, from which it has not extended its range during the Holocene, e.g. to Japan.

*Campylopus flexuosus* is replaced in SE Asia by the closely related *C. comosus*, which differs mainly in its longer, narrower leaves and transverse section of the costa
with ventral stereids. Interestingly, the range of the two species overlap in southern China, probably as a result of climatic fluctuations.


Habitat: on soil and tree trunks.


**Campylopus fragilis** (Brid.) B.S.G., Bryol. Eur. 1: 164, 1847.


*Campylopus fragilis* is easily recognized by the numerous boomerang-shaped brood leaves in the axils of the upper leaves. Forms without brood leaves are recognized microscopically by the leaves which are widened in the mid leaf and contracted at the base and by the hyaline, lax basal laminal cells, which are very sharply differentiated from the small, subquadrate upper laminal cells. It may be confused with *C. subulatus* which has, however, no stereids in a transverse section of the costa whereas *C. fragilis* has distinct groups of dorsal stereids.

In unfavourable conditions and at high elevations, *Campylopus fragilis* produces
small forms with minute stems and numerous propaguliferous leaves.

Habitat: On humic soil in open places, on earth-covered rocks and on decaying wood, 500-2800 m.


Map 6. Selected specimens examined: CHINA. Yunnan: Gongshan, Dulongjiang, Zhang 20d (HKAS); YiLiang, Chen 79-10 (HKAS). Taiwan. Taitung, Siangyang, Lai 9571 (NICH); Chia-yi between Mt. Ali and Tong-pu, Iwatsuki & Sharp 512 (NICH). JAPAN. Shikoku. Kochi Ml, Shiraga, Deguchi 20694 (Kochi, NICH); Ehime Pref., Mt. Higashiakaishi, Deguchi 21744, 21726 (Kochi); Saitama Pref., Chichibu-gun, Nakatsugawa valley, Kiguchi 6060 (NICH); Saitama Pref., Chichibu Mtn., Iwatsuki 44867 (NICH). Honshu. Pref. Aomori, Tashirotaib bog, Deguchi 18739 (Kochi); Yamaguchi-ken, Asahi-son, Nagano, Shiomai 29176 (HIRO). Mt. Akagi, Tannoda 300 - holotype of C. akagiensis (H-BR).


In Campylopous goughii, microphyllous branches, which were not previously known in this species have been found once (Pang 8a, HKAS). However, species of Campylopous can have all kinds of vegetative propagation, such as broken leaf tips, broken stem tips, caducous leaves or microphyllous branches, although only one kind is common and characteristic of a species. Similar microphyllous branches have been found (again only once) in C. fragilis ssp. fragilis from Germany.

Habitat: on soil at 1900–2400 m elevation.
Specimens examined: CHINA. YUNNAN. Lijiang, Wang 81-177 (HKAS); Cangyuan, Zeng 80-1660 (HKAS); Teng Chong, Pang 8a (HKAS); Kunming, Songming, Yu s.n. (HKAS); Kunming, Xu 111 (PE); Yangbi Co., 25°43'N, 100°03'E, Redfearn et al. 513 (SMS).

Campylopus boswellii (C. Müll.) Par., Ind. Bryol. Suppl. 89, 1900.

This taxon was known from SE Asia as C. crispifolius (Frahm & Mohamed 1987). Later, this species was recorded from Hawaii, from where it had been described earlier as C. boswellii (Frahm 1991a). A revision of the type specimen of C. zollingerianus revealed that this species is again identical with both species mentioned before and that this name has priority (Frahm 1991b). Since this species differs from C. fragilis s.str. only in the shape of the upper laminal cells and its range is vicariant with the latter, it has been placed as a subspecies to C. fragilis (Frahm 1991b).

Habitat: humic soil on ridge, 1260 m elevation.
Specimens examined: CHINA. HAINAN. Changjiang Co., Bawanglin Forestry Station, 19°15'N, 109°15'E, Reese 17567 (LAF).

The subspecies of C. fragilis form a complex of closely related taxa with vicariant ranges, which do, however, partly overlap in S China. All three subspecies are
J.-P. Frahm: A revision of the East-Asian species of *Campylopus*

**Map 7.** Distribution of *Campylopus fragilis* ssp. goughii.

**Map 8.** Distribution of *Campylopus fragilis* ssp. zollingerianus.
characterized by hyaline basal laminal cells, lax ventral hyalocysts in both transverse section and surface view of the costa, and the costa widened at midleaf and narrowed towards leaf-base. Small, hooked brood leaves in the axils of the comal leaves at the shoot tips can be found in all three subspecies, although they are found frequently, and are thus characteristic, only in *C. fragilis* ssp. *fragilis* and ssp. *zollingerianus* and less often in ssp. *goughii*.

All three subspecies are mainly differentiated by the shape of the upper laminal cells (quadrate in ssp. *fragilis*, oval in ssp. *goughii* and rectangular in ssp. *zollingerianus*). Beside, the leaf shape is slightly different, being ovate-lanceolate with relatively short tips in *C. fragilis* ssp. *fragilis* but longer and narrower in the other subspecies.

*Campylopus fragilis* s.str. is distributed in the mountains of tropical Africa and America and also in the northern hemisphere in oceanic parts of North America, Europe and East Asia. In SE Asia, it is replaced by the subsps. *goughii* and *zollingerianus* ranging from India to China and from Indonesia to Hawaii respectively.

*Campylopus laxitextus* resembles the subspecies of *C. fragilis* in the structure of the costa with wide and lax ventral hyalocysts and, when well developed, the appearence with appressed foliate stems and comal tufts at stem tips, but has leaves and costae which are not widened and gradually contracted, upper laminal cells which are rectangular, oblique or oval, 1:2–4, and very long acuminate leaves with slender tips formed by the (often subhyaline) excurrent, serrate costa.

*Campylopus japonicus* Broth., *Hedwigia* 38: 207, 1899.


When typically developed, the plants are several cm high, growing in loose, brownish tufts with yellowish-green tips. The uppermost leaves are longer and somewhat spreading with subhyaline tips. This species can be confused with *C. atrovirens*, which has a similar appearance, a similar leaf shape with very longly pointed leaf tips, and similar short, thick-walled basal laminal cells. In *C. japonicus*, however, the upper laminal cells are shortly rectangular and the transverse section of the costa shows ventral stereids in the upper part of the leaf instead of small ventral hyalocysts.

Herbarium specimens of *C. japonicus* have often been misidentified as *C. umbellatus* (or “richardii”). However, the latter has a different leaf shape with broadly lanceolate to ovate leaves, widened below midleaf and contracted at the leaf base (not narrowly lanceolate leaves gradually contracted to the leaf tips), a distinct hyaline, serrate hairpoint, and a costa lamellose on the back, but has no elongate leaves at the shoot tips.

Rarely, forms with slightly homomallous leaves are found, a modification which is often found in other species of the genus.

Dwarf forms are light green with stems only a few mm high, and show the
conspicuous deciduous stem tips with long comal leaves that are found in larger forms of the species.

In Japan, *Campylopus japonicus* is known only in sterile condition. Sporophytes are produced only in the tropical part of its range, showing the tropical origin of the species (as in nearly all other species of the subg. *Thysanomitrion*). The type material of *C. irrigatus* has sporophytes, which shows clearly that this species belongs to the subgenus *Thysanomitrion*. Due to the lack of knowledge about sporophytes, this species was not included in the monograph of *Campylopus* subg. *Thysanomitrion* by Frahm (1984a). The species propagates vegetatively by means of deciduous stem tips and broken leaf tips.

*Campylopus japonicus* has an oceanic distribution. Half of the Japanese specimens have been collected on Yakushima Island. It is one of the amphi-pacific elements ranging from E Asia to western North America. In North America, however, the distribution is very scattered, the species being known only from British Columbia (unpublished record based on an unidentified specimen from Queen Charlotte Islands, leg. Vitt, ALTA), and Mexico, where it had been described as *C. saint-pierrei* Thér. (Frahm 1991). Phytogeographically, these records from Chiapas and Michoacan resemble those from Taiwan and southern China. In E Asia, *C. japonicus* is found only in oceanic areas. Herbarium specimens from Yunnan belong to *C. involutus* or *C. laxitextus*.

Many specimens from China named *C. atrovirens* have proved to be *C. japonicus*. The species are separable by the shape of the upper laminal cells, which are elongate-oval to vermicular in *C. atrovirens* but rectangular in *C. japonicus*.

Habitat: on humic soil, wet rocks and cliffs from 120 to 2400 m elevation.


*Campylopus laxitextus* is a very variable species. It can be recognized by the lax, hyaline basal laminal cells, which are very distinct from the short, rectangular upper laminal cells, and by the excurrent, subhyaline slightly serrate or smooth costa. The leaves are contracted at the base and wider above. The alar cells may be hyaline and well developed, or lacking, and the basal laminal cells may be rectangular and also
subquadrate. When well developed, this species is easily recognized by the comal-tufted, often radiculose shoots with long-tipped comal leaves. As in other tropical species, the plants are smaller and less developed at the northern border of its range, e.g. in Yunnan. These specimens resemble those from the southern border of its range in Queensland, Australia (Frahm 1990).

Small forms of *Campylopus laxitextus* can be confused with *C. subulatus*. However, the latter has a ridged back of the costa, which is not subhyaline and excurrent.


Habitat: on humus in forests, and on rotten stumps, 1000–2600 m.

Selected specimens examined: CHINA. HAINAN. Changjiang Co., Bawangling Forestry Station, 19°15'N, 109°15'E, Reese 17577 (LAF). YUNNAN. Anning: East of Anning Keteeleria forest, Redfearn et al. 34346 (SMS); Mengla: road Menglin–Mengbang km 637, Magill et al. 7704, 19861222 SMS (MO); Menghai: road Menghai–Mengzhe km 32, Magill et al. 7923 (SMS, MO); Jinghong: road Menglin–Xiaomengy km 15, Magill et al. 7802 (MO, SMS); Yangbi: road from Xieshanhe to Dapingzi, 25°43'N, 100°02'E Redfearn et al. 468 (SMS); Kunming 43 km N of Kunming, 25°22'N, 102°45'E Redfearn et al. 1949 (SMS); Xintian, Zang s. n. (HKAS); Cangyuan, Zeng 80-1257 (HKAS); Songming, Wang 81-8694c (HKAS); Luchun, Zang 210 (HKAS); Gongshan, Wang 11243 (HKAS); Tengchong, Li 80-632 (HKAS); Qiaojia, Zhang 6078 (HKAS); LuXi, Li 80-773 (HKAS). TAIWAN. Yangmingshan Nat. Park, Lai YM 3, 4 (hb. Frahm); Taitum, Faurie 35 – holotype of *C. gracilentus* (PC).

*Campylopus pyriformis* (Schultz) Brid., Bryol. Univ. 1: 469, 1826.
MAP 10. Distribution of *Campylopus laxitextus*.


The specimens *Handel-Mazzetti 684* (NY) belong to *C. subulatus* (Frahm & Corley 1981).


This species has been reported from China by Gao (1977) and Gao and Chang (1983). It was described from Europe and known only from western Europe for 180 years until Corley and Frahm (1981) found that it was widely distributed through the southern hemisphere in temperate (sometimes subtropical) to subantarctic regions. This range and the habitats of *C. pyriformis* in Europe (on open sandy or peaty soil) led to the hypothesis that the species had been introduced into Europe, like *C. intraflexus*. The latter has a almost identical range in the southern hemisphere and has spread in western Europe since its introduction 50 years ago. For this reason records of *C. pyriformis* from China have been doubted, especially since there are several species such as *C. subulatus* (*C. gracilis*), *C. goughii* or *laxitextus* with which *C. pyriformis* can be easily confused. Recently, *C. pyriformis* was found in herbarium specimens from Louisiana (Arts & Frahm 1990) and Florida (unpubl.). In the course of examination of *Campylopus* specimens from Chinese herbaria, no specimens named as *C. pyriformis* were found. However, several specimens named as *C. albecens* from the herbarium PE proved to be *C. pyriformis*. As in the case of specimens from North America, the
identity of at least two of these could be confirmed by Th. Arts by the presence of rhizoidal tubers characteristic for this species (Arts 1986).

According to these recent studies, *Campylopus pyriformis* has a holarctic range in the northern hemisphere and a circumsubantarctic range in the southern hemisphere and thus has a bicentric distribution pattern. This kind of distribution has not been previously known in the genus *Campylopus* (except for the recent introduction of *C. introflexus* in the northern hemisphere). The uneven distribution of *C. pyriformis* in the northern hemisphere is, however, striking. Whereas this species is weedy in the oceanic parts of western Europe, only three records are so far known from North America and six from China (plus the specimens on which the records of Gao and Chang are based, which were not seen). Any attempt to explain this phenomenon must be highly hypothetical. One explanation could be that the few records from Asia and North America are relics of a formerly more widespread range. Reduction in its range could have been caused by Pleistocene climatic changes. In North America this is supported by its occurrence in subtropical regions which were not glaciated during the Pleistocene and served as refugial areas for many bryophyte species. *Campylopus pyriformis* might have lost the ability to spread in the Holocene. Another explanation could be that *C. pyriformis* was originally present in the northern hemisphere only in Europe, either introduced by man 200–400 years ago or native, and has spread to North America and China by means of spores. This would have been facilitated by its relatively frequent spore production. Small spore size (13 µm) and its frequent occurrence in Europe.
Whereas *C. pyriformis* is found only in temperate regions of Europe and subtropical parts of North America, it has been found in both in China, in Jilin and Heilongjiang as well as in Yunnan. This wide geographical amplitude is also met in the southern hemisphere, where *C. pyriformis* occurs from the subantarctic islands to southern Brazil and from Tasmania to Queensland.

Although specimens of *C. pyriformis* seen from China were sterile, Gao (1977) illustrates this species with capsules. It propagates vegetatively by means of small, ovate brood leaves (not seen in Chinese material), and deciduous leaves.

*Campylopus pyriformis* shares its areolation (thin-walled basal laminal cells and shortly rectangular upper laminal cells) with similar species such as *C. subulatus* or *C. laxitextus* but differs from these in its very narrow and long leaves ending in a long and narrow tip which is characteristically canaliculate.

Specimens examined: CHINA. YUNNAN. Kunming, Xu 75a, 117a, 121a, 132a, 128a with tubers, teste Th. Arts (PE); Xiongdang, Zang 4214 with tubers, teste Th. Arts (PE). JILIN. Mt. Chang Area, 41°40' N, 128°10'E, Vitt 34818 (ALTA).

Habitat: Insufficiently known. The Vitt specimen is from peat at 1250 m elevation in a temperate region. The Yunnan specimens are (according to the contents of the packages) from sandy soil.


*Campylopus alpigena* var. lamellatus Broth., Symb. Sin. 4: 17, 1929.


*Campylopus handelii* Broth. var. setschwanicus Broth., Symb. Sin. 4: 18, 1929.

*Campylopus schimperi* has often been considered to be a variety under *C. subulatus*. It differs in having more elongate upper laminal cells (1: 4 in contrast to 1: 1, 5–2 in *C. subulatus*) and a nearly smooth back of the costa (which is ridged in *C. subulatus*, cf. Frahm & Vitt 1978). These differences, as well as the different ecological preferences of the species, indicate that they should be regarded as separate species.

Habitat: On soil, humus and peat, preferably over basic rocks in the subalpine and alpine belt at (2300–) 3200–4400 m elevation.


Specimens examined: CHINA. YUNNAN. Dali: Diancang Mtn., 25°42'N, 100°05'E, Redfearn et al. 1398a (SMS); Yinglofeng above Dali, 25°42'N, 100°07'E, Redfearn et al. 136784 (SMS); Luquan: Zang 7292 (HKAS); Deqin: Li 81-2071 (HKAS); Type. China, Yunnan, Handel-Mazetti 3078 – holotype of *C. alpigena* (H-BR). XIZANG: Ximalayashan, Wang 57 (PE); Mangeqou: Li 76023 (PE); supra vicum Anangu, Handel-Mazetti 3078 (H-BR); in montium Daliang-schan, Handel-Mazetti 3079 (H-BR). SICHUAN. XiangCheng: Zhibei Dui 4382 (PE); in montium Daliang-schan, Handel-Mazetti 3079 – type of *C. handelii* var. setschwanicus (H-BR).


*Campylopus aureus* Bosch. & Lac., Bryol. Jav. 1: 80, 1858.

*Campylopus schmidii* is regarded as the vicariant species of *C. pilifer* Brid. in SE
Asia, and differs from it only in the lack of costal lamellae. *Campylopus schmidii* is thus related to *C. pilifer* in the same way as *C. serratus* (see under this species) is related to *C. savannarum*. *Campylopus savannarum* and *C. pilifer* have nearly identical ranges in Central and South America, Africa and Sri Lanka (with the difference that *C. pilifer* extends to northern temperate regions), indicating an gondwanalandic origin for both species with subsequent new speciation in SE Asia.

**Distribution.** China: Redfearn & Wu (1986) sub *C. aureus*; Taiwan: Wang (1970), Kuo & Chiang (1987) and Lai & Wang-Yang (1976) sub *C. aureus*; Japan: reported by Sakurai (1954), but according to Takaki (1967) no material could be found for confirmation. Widely distributed in SE Asia, south to northern Australia, and east to Hawaii and California. **Map 13.**

**Habitat:** on mineral soil between 2000 and 3000 m elevation.

**Specimens examined:** CHINA. YUNNAN. Kunming: Mt. Twan, 25°04'N, 102°41'E, Koponen 37568 (H-BR); Dali: Diancang Mtn., 25°42'N, 100°05'E, Redfearn et al. 1398a (SMS); Yinglofeng above Dali, 25°42'N, 100°07'E, Redfearn et al. 136784 (SMS); Luquan: Zang 7292 (HKAS); Deqin: Li 81-2071 (HKAS); XIZANG: Ximalayashan, Wang 57 (PE); Mangcuo: Li 76023 (PE). SICHUAN. XiangCheng: Zhibei Dui 4382 (PE).


*Campylopus schwarziiz* is the most confused species of this genus in E Asia. Many herbarium specimens named *C. schwarziiz* proved to be *C. umbellatus*, *C. japonicus* or *C. subulatus*, and it is therefore less frequent than the literature would suggest.

*Campylopus schwarziiz* is nevertheless easily recognized by its large, inflated alar...
cells which protrude conspicuously into the costa, very broad costa (3/4 of the leaf width), and very small short-rectangular upper laminal cells. These characters are not found in any other species of Campylopus in E Asia. The plants are usually very robust, several cm tall, with very long leaves.

Campylopus schwarzii is a laurasian species which also occurs in North America and Europe. In SE Asia there are two related species which resemble C. schwarzii in the very long-tipped leaves, the lax ventral hyalocysts of the costa, the transverse section of the costa and the alar cells which protrude into the costa. These are C. sericeoides Dix., known only from a few hectares on Mt. Kinabalu, Borneo, and C. subluteus (Mitt.) Jaeg. which is known only from the type from Birma. Campylopus sericeoides is found in the same habitats as C. schwarzii, on wet or periodically flooded rocks. The habitat of C. subluteus is not known. It may be assumed that these species are systematically related but any interpretation seems to be difficult due to their limited distribution. Campylopus sericeoides differs in its oval upper laminal cells, a character which is also met with in C. atrovirens, a species of similar appearance and habitats.


Habitat. On wet soil and soil covered rocks, and on wet cliffs, at relatively low elevations in oceanic regions, higher elsewhere, 800-3300 m alt.

Specimens examined: CHINA. SHANXI. QinLing, Huang 1531 (PE). YUNNAN. Weixi, Wang 378 (HKAS); Cang Shan, Fang 80-5 (HKAS); Lijiang, Zang 1605 (HKAS); Weixi, Zhang 746 (HKAS); Fugong, Wang 465 (HKAS); Lushui, Sun 8 (HKAS); Qiaojia, Zhang 6105 (HKAS); Weixi, Wang 82-14 (HKAS); Lijiang,

Campylopus scabridorsus Dix. Hong Kong Naturalist Suppl. 2: 5, 1933.

Reported from China (Redfearn & Wu 1987) as Campylopus scabridorsus. Specimens named as C. scabridorus are not present in Chinese herbaria and this record is probably based on the type of this species from Hong Kong which belongs to C. serratus, a species hitherto known from Thailand, peninsular Malaysia and Borneo (Frahm & Mohamed 1987), with its northernmost occurrence in Hong Kong.

Campylopus serratus is closely related to C. savannarum (C. Müll.) Mitt. of Central and South America, Africa and Sri Lanka (and thus of gondwanalandic range) and is regarded as a vicariant species of C. savannarum in SE-Asia.

Campylopus subulatus Schimp. in Rabenh., Bryothec. Eur. 9 no. 451, 1861.


Campylopus subulatus was regarded as a Europe endemic species for more than 100 years. It was first reported outside Europe from California (Frahm 1980). From

MAP 14. Distribution of Campylopus schwarzii.
Asia it has been reported so far only from the NW-Himalaya (Mussoorie distr.) by Frahm (1982) who recognised it as identical with *Campylopus barbuloides* Broth. nom. nud., and from Yunnan (Frahm 1984b) based on a specimen collected by Handel-Mazzetti and named by Brotherus as *C. pyriformis*. Therefore, a map of the world range of this species (Frahm 1984b) showed a wider range in western Europe and scattered occurrences in SW Iceland, California, India and S China. It has recently been recorded for Turkey (Cetin 1988). Specimens from Mexico (*Sharp 59178c*, **TENN**), which were named *C. subulatus* by the author, belong to *C. albidovirens* Herz. The record by Bowers et al. (1973) from Mexico, as well as record of *C. subulatus* from Venezuela (Robinson 1965, 1967), may belong to the same species. The species is reported here as new to Japan.

The discovery that the SE Asian *C. gracilis* is identical with *C. subulatus* together with the new record of this species from Japan, has resulted in a different view of the range of this species. It now turns out to be a holarctic species widely distributed in Asia and Europe but, less frequent in North America. This is principally the same type of distribution as in *C. schwarzi*, *C. schimperi* and *C. atrovirens*. Considering the records for *C. gracilis* and its synonyms (Frahm 1984c), the range of *C. subulatus* in Asia includes India, Sri Lanka, Sikkim, Nepal and China. Specimens from Burma and Thailand have not seen.

*Campylopus subulatus* is primarily recognized by the transverse section of its costa which lacks stereids. The ventral hyalocysts are relatively small (see Frahm 1984c fig. 7 sub *C. gracilis*) compared with those in species with a similar transverse section of the costa. The reverse side of the costa is distinctly ridged or possesses even low lamellae as seen in transverse section (cf. Frahm & Vitt 1978) and also in a side view of the leaf tip. The ridges are slightly serrate. A conspicuous feature is that parts of the stem cortex are pulled off when the leaves are stripped off the stem, and remain attached to the base of the costa. The alar cells are lax, hyaline and often inflated, sometimes protruding a little into the costa. The basal laminal cells are hyaline and thin-walled, and narrower at the margins. The upper laminal cells are short-rectangular, c. 1, 5 times longer than broad.

*Campylopus subulatus* has some similarity to small forms of *C. laxitextus*. The areolation of the leaf is particularly similar. However, the latter has, however, a transverse section of the costa with dorsal stereids, and a subhyaline, usually smooth leaf tip. The areolation of the leaves also resembles that of *C. pyriformis* (probably for that reason Brotherus named specimens of *C. subulatus* from Yunnan as *C. pyriformis*), but the upper laminal cells are longer in *C. pyriformis*, the back of the costa is not ridged and serrate, and the transverse section of the costa has dorsal stereids.

At higher elevations, the plants are smaller and have shorter leaves with inflexed leaf margins. Vegetative propagation occurs by means of microphyllous branches.

Takaki (1967) gave a detailed account of the differences between *C. subulatus* and *C. schimperi* and seemed to know the species quite well but did not record *C. subulatus* for Japan. Therefore this species is reported here for the first time for Japan.

Many specimens labelled *C. latinervis* in Chinese herbaria belong to *Paraleuco-
bryum enerve (Thed.) Loeske.


Habitat. On soil, rarely on stumps, in China in pine forests, subalpine forests and bamboo thickets, 1750–3000 m. In Japan on soil and soil-covered rocks between 100 and 1900 m.

Specimens examined: CHINA. GUANGDONG. Ding Hu Shan Nat. Preserve, 23°08′N, 112°35′E, Redfearn et al. 34410 (SAMS). SICHUAN. Nanchuan: Jinfu Shan, Hu 47 (PE). YUNNAN. Dali: Vic of Huadian by Herbal Farm, 25°53′N, 101°01′E, Redfearn et al. 1464b (SAMS); Bijiang, Zang 5775 (HKAS); Tengchong, Wang 83-82 (HKAS); Kunming, Xu 84 (PE); Yunnanfu: v. Handel-Mazzetti 684, 1914 (NY) sub C. pyriformis; Schöndusula 3600–3950 m, Handel-Mazzetti 3077 (NY, s) sub C. gracilis; Pe Yen Tsin, Ten 23 (s); Song Ming Co.: Xio-xio 96 km NE of Kunming, Koponen 37742b (H-BR) sub C. gracilis; An Ning 30 km SW of Kunming, Koponen 37979, 38009 (H-BR) sub C. gracilis and C. gracilentus; Jin Dian 25°04′N, 102°41′E, Koponen 37624, 37657 (H) sub C. gracilentus; Schöndusula 28°04′E, Handel-Mazzetti 3077 (H-BR).

TAIWAN, Yangmingshan National Park, Lai YM-5 (hb. Frahm). JAPAN. HONSHU. Aomori Pref.: Asasumi, Higuchi 11391 (NICH); Shiga Pref.: Mt. Ryou, Deguchi 23906; SHIKOKU. Tokushima Pref.: Kawanaru, Deguchi 11498; between Koboke and Ooboke, Deguchi 4392; Mt. Tsugurugi, Deguchi 20136, 17092; Ehime Pref.: Mt. Higashikataishi, Deguchi 21674; Gongengoe pass, Deguchi 11498; Akita-ken, Mt. Tsubai, Deguchi 30788 (KCH).

Campylopus umbellatus (Arn.) Par., Ind. Bryol. 264, 1894.
Campylopus blumii (Dozy & Molk.) Bosch & Lac., Bryol. Jav. 1: 81, 1858.

Map 15. Distribution of Campylopus subulatus.
Campylopus coreensis var. amoyensis Dix. & Thér., Hong Kong Naturalist Suppl. 2: 5, 1933.
Campylopus ferriei Broth. in Par., Index Bryol. Suppl. 92, 1900.
Campylopus leptoneuron Broth. ex Ihs., Cat. Moss Japan 32, 1929.
Campylopus nagasakinus Broth. in Par., Index Bryol. Suppl. 94, 1900.
Campylopus scabripilus Warnst., Hedwigia 57: 80, 1915.
Campylopus richardii auct. non Brid.

Dixon (1922) erroneously synonymized C. umbellatus with C. richardii, a decision which was followed by the authors of the Index Muscorum (Wijk et al. 1959). Therefore many records in the literature and herbarium specimens of C. umbellatus have been named C. richardii. For the differences between the two taxa see Frahm (1976). C. richardii is a species strictly confined to the neotropics, whereas C. umbellatus has a wide distribution in SE- and E-Asia ranging from Sri Lanka to Hawaii and Korea to Queensland, Australia. There is a considerable variation in this species concerning the presence or absence of hyaline hairpoints, the length of the hairpoints, the length of the stems, and the ratio between lamina width and costa width.

A few specimens are epilose (e.g. Higuchi 14631, Chuang 182, HIRO). These plants are conspicuously greenish, never blackish as is usual in this species. It can be concluded that these are modifications growing in shady habitats, and lacking the blackish colour as a filter against insolation.

In pilose forms the length of the hyaline hairpoint varies from a short hyaline mucro to 1/2 the length of the lamina (e.g. in Higuchi 10077, HIRO).

Forms with relatively narrow leaves and long excurrent hairpoints, which are nearly half as long as the lamina, have been collected in Yunnan and named C. tenuinervis Fleisch.

The size of the plants varies, but there seems to be a gradient in size from the tropical interior parts of its range to the margins of its range. Specimens from SE Asia to southern China reach several centimeters in length, whereas specimens from northern parts of its range reach only 1 cm. This can be explained by the different ecological conditions over its enormous range, which are suboptimal in the northern part. The N–S extension of its range from Korea to Queensland is comparable to a range in the Americas from New York to Rio de Janeiro. Typical expressions in the tropical part of its range are several cm high, and blackish with lighter tips. In the northern part of its range, the plants are smaller and not blackish but olive-green (e.g. as C. viridulus Card.). However, apart from small forms, real dwarf forms also exist. Such forms were described as C. coreensis. These plants are only 4–5 mm high, with leaves only 2 mm long and a hairpoint of 1 mm (e.g. Deguchi 17579, HIRO, Liu 30034, Li 326, 552, 5656c, 17474, Gao 7646, SHM). They are very densely and evenly foliate, and resemble C. pilifer in appearance. Such forms are encountered in extratropical parts of the range of C. umbellatus. They are found frequently in the Chinese provinces of Hunan, Quzhou and Jinaxi. Interestingly, Cardot (1907) differentiated both, the
The costa usually occupies 1/3 of the leaf width but can be much narrower, occupying only 1/5 of the width (the name _C. leptoneuron_ refers to this feature). In the latter case, the costa is not actually narrower and is of about the same size as in other expressions, but the lamina is broader. Such broad-leaved forms also occur in _C. exasperatus_ (in forms described as _C. archboldii_), in _C. richardii_ (in forms described as _C. atratus_) and in _C. flaccidus_, all species of the subg. _Thysanomitrion_. The taxonomic value of these broad-leaved forms is not known.

Rarely, specimens of _C. umbellatus_ with reflexed hairpoints have been found. Such hairpoints are a characteristic feature of _C. introflexus_ (Hedw.) Brid. These forms have already been observed in material from Papua New Guinea (Frahm et al. 1985) and in specimens of _C. pilifer_ Brid. from Mexico and South Africa.

Sporophytes are produced frequently in the tropical part of its range but only rarely in the northern part e.g. in Japan (cf. Deguchi 24592). They are found only in well- and typically developed plants, not in the small forms cited above.


Habitat: on rocks and soil, rarely concrete walls. In Taiwan at elevations of 700–1000 m, in China at 700–2000 m and in Japan (Honshu) at 100 m.


FUJIAN. Mt. Wu-yi, Li 1872, Gao 7424, Li & Gao 9144, 11492, 11540, 9110 (SHM); Manping City, Gao 25545 (hb. Shenyang); Yongcun County, Li 326 (SHM). GUANGDONG. Lofu Mts., Magill et al. 8120 (MO).

HAINAN. Mt. Jiangfunching, Gao 25538 (hb. Shenyang); Ledong Co., 18°52'N, 108°42'E, Redfearn et al. 35992 (SMS).


PHYTOGEOGRAPHICAL EVALUATION

The East Asiatic species of Campylopus can be grouped into the following phytogeographical elements:

4. Tropical montane with extension to the holarctic: C. flexuosus, fragilis ssp. fragilis.
5. Bicentric in the northern and southern hemispheres: C. pyriformis.

Campylopus ericoides, japonicus and umbellatus belong to the subgenus Thysanomitrion, all other species to the subgenus Campylopus.

Most species of Campylopus are tropical in distribution. For these, a subantarctic origin has been postulated (Frahm 1988, 1990). Many tropical species can be derived from:

<table>
<thead>
<tr>
<th>North America</th>
<th>East Asia</th>
<th>Europe</th>
</tr>
</thead>
<tbody>
<tr>
<td>atrovirens</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>schimperi</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>schwarzii</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>fragilis ssp. fragilis</td>
<td>(x)</td>
<td>x</td>
</tr>
<tr>
<td>flexuosus</td>
<td>(x)</td>
<td>(x)</td>
</tr>
<tr>
<td>subulatus</td>
<td>(x)</td>
<td>x</td>
</tr>
<tr>
<td>pyriformis</td>
<td>(x)</td>
<td>(x)</td>
</tr>
<tr>
<td>japonicus</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>comosus</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>ericoides</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>umbellatus</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>laxitextus</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>schmidii</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>serratus</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>fragilis ssp. goughii</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>fragilis ssp. zollingerianus</td>
<td>x</td>
<td></td>
</tr>
</tbody>
</table>
from subantarctic ones, e.g. *C. schmidii* from *C. introflexus*, *C. umbellatus* and *C. japonicus* from *C. clavatus*.

Of the SE Asian species of *Campylopus*, the highest number occur in southern India and Sri Lanka. Therefore a gondwanalandic origin of these species has been postulated (Frahm, in press). The origin of those species which are confined to the holarctic is a problem (group 1). In the case of *C. subulatus*, there are no closely related species in the tropics except for *C. flindersii* Catcheside & J.-P. Frahm in Australia. The latter differs only in its subquadrate upper laminal cells. Since parts of northern Australia have drifted towards and been connected to Laurasia, this might have been a pathway for the migration of *C. flindersii* to Laurasia, with subsequent new speciation. This pathway has been previously postulated for the genus *Desmotheca* (Vitt & Frahm 1990).

Compared with North America and Europe, East Asia has the highest number of tropical species of *Campylopus*. This is probably a result of the fact that East Asia was not affected by glaciations during the Pleistocene but only by worldwide climatic fluctuations. Only North America also has a tropical element in its Campylopus-flora, in the coastal plains of the SE, where such species as *c. surinamensis*, *C. gracilicaulis* and *C. carolinae* have apparently been introduced or spread from Brazil, as there has never been a land connection between the south east of North America and South America. All of the temperate species found in East Asia also occur in North America and Europe. This supports the hypothesis that southern hemispheric ancestors entered Laurasia via “Noah’s arcs” such as India (Frahm, in press).

**EXCLUDED SPECIES**


This species has been tentatively synonymized with a species of *Dicranodontium* (Frahm 1985).

In Chinese herbaria there were many specimens identified as *C. longigemmatus* which are identical with the type of this species. These specimens resemble *Campylopodiella himalayana* (Broth.) J.-P. Frahm, a species which was known only from India, Nepal, Sikkim (Müller & Frahm 1988) and Bhutan (unpubl. record). *Campylopodiella himalayana* is characterized by a transverse section of the costa with median groups of stereids, ventral and dorsal hyalocysts and a small narrow band of ventral stereids in the midleaf. This band of stereids is even visible, without sectioning, in a surface view of the ventral side of the costa, as a darker band. *Campylopodiella himalayana* closely resembles *Brothera leana* in its gametophyte and can easily be confused with the latter when the characteristic brood leaves are not present. In this case, the transverse section of the costa of *Campylopodiella himalayana*, as described above, is the only distinguishing character between the two.

All of the Chinese plants show this kind of transverse section of the costa, but are generally larger (1–2 cm) than the specimens of *Campylopodiella himalayana* known so far, and have their leaves very distantly arranged along the stem and easily falling off. The naked stems show the...
places where the leaves were attached, as in the branches of Picea sp. (see Li 1985 fig. 13). Without detailed studies, it cannot be decided at present whether such a type of transverse section also occurs in the genus Dicranodontium, and whether these specimens are a species of Dicranodontium or represent tall expressions of Campylopodiella himalayana.

Some specimens (Hu 137, 635) are interruptedly-comes foliate and resemble Bryohumbertia subcomosa in appearance; while another specimen (Hu 191) has homomallous leaves.

Specimens examined: CHINA. YUNNAN. WeiXi, Zhang 203, 208a; Lijiang, Li 80-141, Xu s.n. (PE); Kunming, Xu 114a (PE); Biijiang, Zang 5412, 5941; Deqin, Zang 8430a, Wang 81-2361; Jingdong, Xuan 81-17; Jizushan, Xu 53 (PE); Zhong Tian, Li 81-1097; Gongshan, Zang 744 (HKAS). XIZANG. Mangkang, Li 76009, XimaLayashan, Wang 31 (PE). Helongjiang, Xichun, Shandang Agriculture College s.n. (PE); Yangbi Co., 25°43'N, 100°03'E, Redfearn et al. 201, 509b (SMS).

DOUBTFUL SPECIES
Campylopus hakonae C. Müll., Gen. Musc. Fr. 266, 1900, nom. nud.
Campylopus kiusiuensis Broth. in Ihs., Nihon-Senrui Bunrui 137, 1932.

DOUBTFUL RECORDS
Campylopus setifolius Wils.
China: Redfearn and Wu (1987). This species, known from Scotland and Ireland, has been reported from Yunnan by Chen et al. (1963). Herbarium specimens from PE consist of species of Dicranodontium or other species of Campylopus.

Material not available from the herbarium of Sakurai (MAK). It is reported from China (Redfearn & Wu 1987) and Taiwan (Wang 1970, Lai & Wang-Yang 1976, Kuo & Chiang 1987).

ACKNOWLEDGMENTS
I wish to thank Dr. Z. Iwatsuki (Hiroshima University, HIRO), Dr. M.-L. Lai (Taipei), Dr. Lin (Shanghai Museum of Natural History, SHM), Dr. A. J. Harrington (British Museum, BM), Dr. H. Deguchi (Kochi University, KOCHI), Dr. Gao Chien (Institute of Applied Ecology, Shenyang, China), Dr. P. Redfearn jr. (Missouri State University), Dr. W. D. Reese (University of Southwestern Louisiana, LAF), Dr. Wu, Pan-Cheng (Academia Sinica, Beijing, PE), Dr. Zeng, Shu-ying (Kunming Institute of Botany, HKAS) and Dr. P. Isoviita (Botanical Museum, Helsinki) for the loan of specimens. Material from North Korea was not available from the Korean Academy of Science, and there seems to be no bryophyte herbarium in South Korea. Dr. R. E. Magill (Missouri Botanical Garden) provided the results of a search in the TROPICOS database. The records from China and the references to the Chinese bryological literature were obtained from the compilation by Dr. Redfearn on the IAB Software Library diskettes 68–70, for which Dr. Redfearn kindly provided additions and corrections. Mr. Yi Lin (University of Duisburg) kindly transliterated some hundred Chinese herbarium labels. Th. Arts (Belgium) studied herbarium specimens for the presence of rhizoidal gemmae. Dr. A. J. Harrington (London) kindly corrected the English text.
LITERATURE CITED


J.-P. Frahm: A revision of the East-Asian species of Campylopus


APPENDIX

Index to scientific names of Campylopus reported from E-Asia, accepted names in italics, * = type-material of this species was not available, ? = doubtful record, specimens were not available, (1) occurrence in As. 2 indicated by Index Muscorum, but neither a reference in the literature nor a herbarium specimen could be traced.

akagiensis Broth. & Yas. = fragilis ssp. fragilis
alkigena Broth. = schimperi
- var. lamellatus Broth. = schimperi
atrovirens De Not.
aureus Bosch & Lac. = schmidii
blumii (Dozy & Molk.) Bosch & Lac. = umbellatus
boswellii (C. Müll.) Par. = C. fragilis ssp. zollingerianus
caudatus (C. Müll.) Mont. in Dozy & Molk. = comosus
comosus (Schwaegr.) Bosch & Lac.
corensis Card. = umbellatus
- var. amoensis Dix. & Thér. = ?umbellatus
crispinolius Bartr. = fragilis ssp. zollingerianus
dozyanus (C. Müll.) Jaeg. = umbellatus
dozyi C. Müll. ex Kindb. = umbellatus
ericoides (Griff.) Jaeg.
ferrei Broth. in Par. = umbellatus
flexuosus (Hedw.) Brid.
- ssp. pyriformis (K. Schultz) Dix. = pyriformis
fragilis (Brid.) B.S.G.
- var. pyriformis (K. Schultz) Agst. = pyriformis
- ssp. goughii (Mitt.) J.-P. Frahm
- ssp. zollingerianus (C. Müll.) J.-P. Frahm
fuscoviridis (Card.) Dix. & Thér. ex Hong & Ando = japonicus var.
goughii (Mitt.) Jaeg. = C. fragilis ssp. goughii
gracilentus Card. = laxitextus
- var. brevifolius Card.

gracilis (Mitt.) Jaeg. = subulatus
* hakoniae C. Müll. nom. nud.

handelli Broth. = schimperi
- var. setschwanicus = schimperi

involutus (C. Müll.) Jaeg. = ericoidea

irrigatus Thér. = japonicus

japonicus Broth.
* kiuisiensis Broth. in Ihs.

latinervis (Mitt.) Jaeg. = gracilis

laxitextus Lac.

leptoneuron Broth. = umbellatus

longigematus Gao = Dicranodontium sp.

nagasakinus Broth. in Par. = umbellatus

nakamurae Sak. = japonicus

* pinfaensis Thér.

?pseudogracilis Card. & Dix. = fragilis ssp. goughii (1)

pseudomuelleri Card. = japonicus

pyriformis (K. Schultz) Brid.

richardii Brid. = erroneously for umbellatus

? roellii Ren. & Card. = flexuosus (1)

scabridorsus Dix. = serratus

scabripilus Warnst. = umbellatus

schimperi Milde

schimidii C. Müll.

schwarztii Schimp.

? setifolius Wils.

subulatus Schimp. in Rabenh.
- var. schimperi = schimperi

* taiwanensis Sak.

tenuinervis Fleisch. = involutus

torfaceus Bruch & Schimp. in B.S.G. = pyriformis

turfaceus Schimp. = pyriformis

uii Broth. = japonicus

umbellatus (Arn.) Par.

viridulus Card. = umbellatus

yakushimensis Sak. = japonicus

zollingerianus (C. Müll.) Bosch & Lac. = C. fragilis ssp. zollingerianus