

**Taxonomy and World Distribution of *Campylopus*
introflexus and *C. pilifer* (= *C. polytrichoides*):
a New Synthesis¹**

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Abstract. *Campylopus introflexus* (Hedw.) Brid. *sensu lato* comprises two widespread, closely related species: tropical and warm-temperate *C. pilifer* Brid. (= *C. polytrichoides* DeNot.) and temperate southern hemispheric *C. introflexus* (Hedw.) Brid., which was recently introduced in Europe. Main differences are in the height of the dorsal lamellae of the leaves, in spore size and in seta length. In *C. pilifer* lamellae are more pronounced in tropical mountains than in lowland areas. An extreme form with lamellae up to seven cells high is *C. pilifer* var. *lamellatus* (Mont.) comb. nov. from Bolivia.

The recent invasion of *Campylopus introflexus* (Hedw.) Brid. in Europe (Frahm, 1972) has renewed interest in the taxonomy of this species. Traditionally it was considered an almost cosmopolitan species until Giacomini (1955) showed that two species are at hand: *C. introflexus* s.str., occurring in temperate regions of the southern hemisphere, large parts of America and (at that time!) one locality in Europe (Bretagne), and *C. polytrichoides* DeNot., occurring in southwestern Europe, Africa and southern Asia. The characteristics used to distinguish the two species, particularly those of the gametophyte, have been questioned by several authors, e.g. Richards (1963), Barkman and Mabelis (1968) and Jacques and Lambinon (1968). Therefore a renewed investigation of the taxonomy of the species was undertaken, simultaneously, by J.-P. Frahm (Duisburg) and the present authors. Frahm's studies were confined to characteristics of the gametophyte, whereas ours also included characteristics of the sporophyte.

As a result of his investigations, Frahm (1974, 1975) showed that: 1. The only reliable differences in the gametophyte between the two species are found in the nerve—the height of the dorsal lamellae, the number of stereids in each group and the width of their lumen. These characteristics are best studied in transverse sections of the upper part of the leaf, near the center of the nerve. Leaves should be taken from just below the comal heads of the stems, since comal leaves ("Hochblätter") of *C. polytrichoides* may resemble leaves of *C. introflexus*. 2. The distribution of the two species as given by Giacomini is incorrect since *C. polytrichoides* also occurs in the

¹ This paper is dedicated to the memory of the late Dr. P. A. Florschütz (†1976), whose guidance and expert knowledge of *Campylopus* systematics has been of great help. We thank the curators of the herbaria cited in the text for the loan of specimens. For valuable information we express our gratitude to Dr. J. J. Barkman (Wijster), Dr. G. C. S. Clarke (London), Dr. A. C. Crundwell (Glasgow), Dr. E. Hegewald (Dortmund) and especially to Dr. J. -P. Frahm (Duisburg) in close cooperation with whom the work was carried out.

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TABLE 1. Measurements of significant characteristics of *Campylopus introflexus* and *C. pilifer*, showing geographical variation.

	temperate				
	W Europe	S Hemisphere	Tropical Africa	Tropical America	SW Europe
	<i>C. introflexus</i>				
Leaf Length (without hairpoint) ^a	(2.2-3.3(-4.8)	(1.8-3.3(-4.8)	(2.4-3.7(-5.2)	(1.8-3.3(-5.6)	(2.5-4.1(-5.2)
Hyaline Base (% of leaf length)	(20-35(-55)	(30-35(-60)	(23-35(-45)	(10-35(-50)	(15-30(-45)
Nerve (% of leaf width)	(40-55(-75)	(40-55(-75)	(35-55(-68)	(30-50(-65)	(50-60(-70)
Stereids (average number per group)	(2.4-3.6(-5.4)	(2.6-3.5(-5.2)	(2.6-4.0(-5.2)	(2.0-4.1(-6.8)	(3.0-4.5(-6.6)
Dorsal Lamellae, height (number of cells)	1(-2)	1(-2)	(1-2(-4)	(2-3(-7)	(2-3(-4)
Seta Length ^a	(5-7(-10)	(5-6-7(-9)	(4-5(-9)	(3-4(-5.5)	(3-4(-5)
Spore Diameter ^b	(10-12(-14)	(10-12(-15)	(11-15(-17)	(10-13(-16)	(14-17(-19)
Specimens Examined (number with sporophytes in brackets)	22(7)	17(10)	16(10)	38(11)	19(5)
	<i>C. pilifer</i>				

^a in mm.

^b in μ m.

U.S.A. and Central and South America, whereas *C. introflexus* is restricted to the temperate zone of the southern hemisphere and West and Central Europe. The two species overlap in distribution in Brazil, Uruguay, Argentina, South Africa and, since recent times, in western Europe.

Our studies, based on examination of over 150 collections from all over the world, confirm Frahm's conclusions on the distribution of the two taxa. We also recognize the two taxa as species, although we find fewer gametophytic differences. Measurements of significant characteristics are given in Table 1. Some "classical" characteristics, e.g. reflexion of hairpoints, leaf auricles, width of stereid lumina and length of the convoluted part of the leaf, are omitted because they proved to be less significant, as was also shown by Frahm (1974).

Table 1 shows that material assigned to *C. introflexus* (Hedw.) Brid.—from the temperate southern hemisphere and from western Europe—is morphologically rather uniform. The remaining material, assigned to *C. pilifer* Brid. (= *C. polytrichoides* DeNot.) is morphologically less uniform, but differs significantly from *C. introflexus* by the height of the dorsal lamellae, the length of the seta and the diameter of the spores. The differences are summarized in the key given below. Contrary to Frahm (1974) we cannot accept characteristics derived from the stereids as diagnostic, since a considerable overlap among all populations is present.

Nerve in transverse section with dorsal lamellae composed of 2–4 cell rows (5–7 cell rows in var. *lamellatus* (Mont.) comb. nov.); seta 3–5.5 mm (–9 mm in tropical East Africa!); spores 12–19 μ m in diam. Tropical and warm-temperate: North and South America, Europe, Africa, India.....
----- *C. pilifer* Brid.

Nerve in transverse section with dorsal lamellae composed of 1(–2) cell rows; seta 5–8(–10) mm long (only 4 mm in var. *brachycarpa* Giac.); spores 10–15 μ m in diam. Temperate southern hemisphere, neophytic in West and Central Europe*C. introflexus* (Hedw.) Brid.

Campylopus pilifer Brid.

Lectotype: Italy, "In Insula Ischia ad rupes, Auguste 1806" (B). Syntype: France, "In Sylva prope Fontainebleau, Octobre 1807" (B).

Synonyms (see Frahm, 1975, for complete listing):

Dicranum capitiflorum P. Beauv., Prodr. 53. 1805.

Type: "Bourbon" (Réunion), *Bory St. Vincent* (PC, in herb. L. C. Richard); *non Campylopus capitiflorum* Mont., Syll. 42. 1856.

Campylopus longipilus Brid., Bryol. Univ. 1: 447. 1826 *nom. illeg.*

Campylopus polytrichoides DeNot., Syll. Musc. 222. 1838.

Campylopus introflexus (Hedw.) Brid. var. *cordobaensis* Thér., in Bauer, Musci Eur. Am. exsicc. ser. 45, nr. 2204. 1934 *syn. nov.* Type: Argentina, Cordoba, El Durazno, *Hossaeus* 149 (isotypes in BM, herb. Frahm).

Description and illustrations: See Grout (1937: 93–94), Giacomini (1955: 55, fig. 1–6), Gangulee (1971: 301–303, fig. 141), Frahm (1974: fig. 6).

Distribution (Fig. 2) and Ecology.—*Campylopus pilifer* is widespread between 40°N and 35°S in North and South America, Africa, India and in Europe, where the species has a western-Mediterranean-Atlantic distribution and reaches north to 57°N. Presumed occurrence in Indomalaysia (cf. Gangulee, 1971, map LXXXVI) could not be confirmed. Records from the Netherlands proved to belong to *C. introflexus* (Hedw.) Brid. (Sipman, 1977). In warm-temperate regions the species occurs at low elevations, whereas in tropical regions it is mainly found at higher altitudes, reaching to 3500 m in the mountains of Central Africa and the Andes of northern South America.

The species occurs in regions with an, at least periodically, humid climate, on dry, acid, poor mineral soil. It often grows on thin soil covering granite or schistose rock, or in rock crevices, in open woods, heath-islands, etc.; rarely on bases of trees or rotten

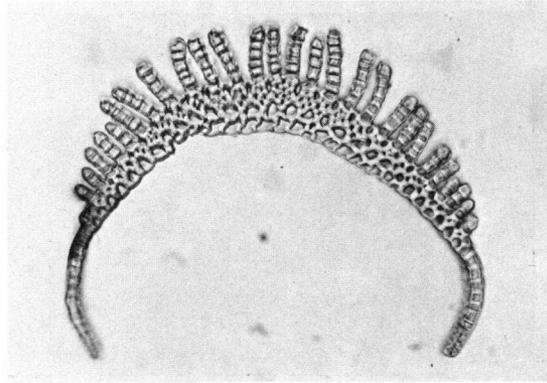


FIGURE 1. *Campylopus pilifer* var. *lamellatus* (Mont.) comb. nov. Transverse section from upper region of leaf, ca. 200 \times (from the type collection).

wood. According to Richards (1963) *C. pilifer* has a narrower ecological tolerance than *C. introflexus* in Britain and is more thermophytic.

Nomenclature.—When reestablishing *Campylopus polytrichoides* as a species, Giacomini (1955) placed three older species names in its synonymy without paying attention to priority: *Dicranum capitiflorum* P.Beauv. 1805 from La Réunion and *Campylopus pilifer* Brid. 1819 and *C. longipilus* Brid. 1826 from Europe. We have examined type material of these binomials and found them to fit Giacomini's concept of *C. polytrichoides*.

Type material of *Dicranum capitiflorum* was found in the herbarium of L. C. Richard (PC-Gén.), where it was erroneously inserted under *Campylopus capitiflorum* Mont. The plants are fairly robust, and fruiting stems have distinct comal heads with long, slightly decurved hairpoints, resembling those of *C. introflexus*. However, the 2–3 cell high lamellae, the 5–5.5 mm setae and, particularly, the spores (16–17 μ m) indicate typical "*C. polytrichoides*."

Campylopus pilifer was described by Bridel (1819) on the basis of two collections, one from Italy and the other from France: "In insulâ Ischiâ 1806, et in saxosis sylvae prope Fontainebleau 1807 caespitibus densis pulchre variegatis crescentem sed sine theca inveni" (Mant. Musc., p. 72). He recognized a close relationship of his new species to *Dicranum flexuosum* var. *piliferum* Turn. 1804, from Great Britain, based on piliferous specimens from Wales and Ireland (probably *C. atrovirens*?) and a non-piliferous plant (*C. fragilis*?) from the Dillenius herbarium (Turner, 1804: p. 74). In his *Bryologia Universa*, Bridel (1826) combined *C. pilifer* with Turner's piliferous specimens from Great Britain into *Campylopus longipilus* Brid. nom. nov. This name is superfluous since it includes the older binomial *C. pilifer*, which has priority.

Due to the courtesy of the curator of the Bridel herbarium, Dr. W. Schultze-Motel, we were able to study the original material of *C. pilifer* Brid. The two syntypes, both sterile, fit *Campylopus polytrichoides* DeNot.; the leaves have short hairpoints, short cells, very wide nerves, involuted upper margins and dorsal lamellae of 2–3 cells high. The steroids could not be studied adequately in this old material.

Thus the name *Campylopus pilifer* Brid. should now be accepted as the correct name for *Campylopus polytrichoides* DeNot. We have chosen the Ischia collection as the lectotype of *C. pilifer* Brid. because it is the oldest of the two syntype collections.

Variation (Table 1).—The morphological variation of the gametophyte was dis-

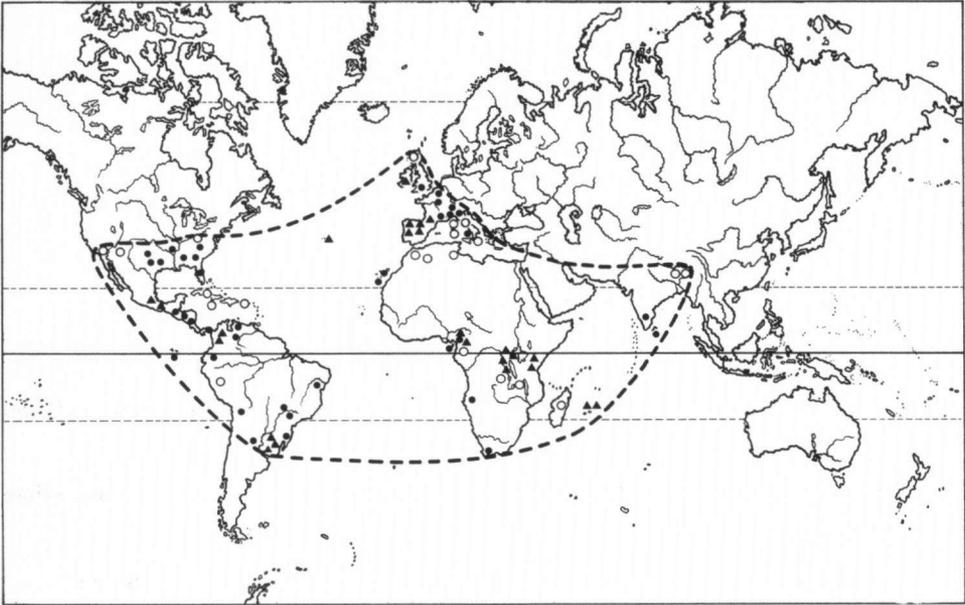


FIGURE 2. Distribution of *Campylopus pilifer* Brid. Triangle: Specimens with sporophytes. Solid circle: Non-fruiting specimens. Open circle: Literature record.

cussed by Frahm (1974) and, at length, by Giacomini (1955), who distinguished several intraspecific taxa. From our study of variation it appears that it is virtually impossible to demonstrate clear-cut discontinuities; therefore we have not paid much attention to intraspecific taxa distinguished by earlier authors.

Disagreement among authors exists on the taxonomic position of specimens with high lamellae but relatively wide stereid lumina ("substereids"). Examples are *C. introflexus* var. *cordobaensis* Thér. from Argentina (Frahm, 1975: fig. 13), *C. polytrichoides* subsp. *daldanianus* (DeNot.) Giac. from Italy (Giacomini, 1955: fig. 6), specimens from Central America reckoned with question mark to *C. polytrichoides* by Frahm (1974: fig. 6C–D) and a specimen from Brazil, Porto Alegre (Giacomini, 1955: fig. 11), which was reduced to *C. introflexus* by Giacomini but to *C. polytrichoides* by Hegewald (1973). In our opinion all these specimens belong to *C. pilifer*. Contrary to Frahm (1974), we do not find the width of the lumina of the stereids or, in other words, the thickness of their walls, a reliable characteristic to distinguish between *C. pilifer* and *C. introflexus*. In *Campylopus* species from Colombia, Florschütz & Florschütz-de Waard (1974) found striking variation in the thickness of the walls of the stereids, even within a single specimen! One would assume ecological conditions to cause this variation, but culture experiments did not substantiate this assumption (Florschütz & Florschütz-de Waard, 1974).

Dorsal lamellae tend to become four cells high in collections from tropical mountain areas between 2000 and 3500 m (cf. Frahm, 1974: fig. 6D; Bizot, 1973). These collections probably fit *C. introflexus* var. *altecristatus* Ren. & Card. from Madagascar. An extreme is a plant from the Bolivian Andes described by Montagne as *Campylopus lamellatus* (holotype—PC; isotype—K in BM), which has 5–7 cell high lamellae (Fig. 1). The specimens have very slender shoots without distinct comal heads, but other-

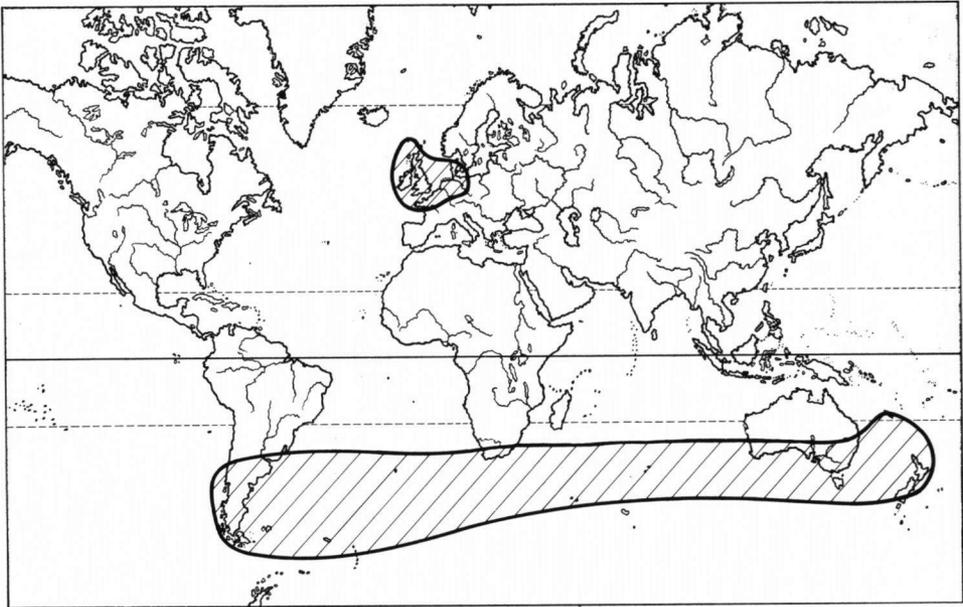


FIGURE 3. Distribution of *Campylopus introflexus* (Hedw.) Brid.

wise they fit *C. pilifer*. Therefore *C. lamellatus* is reduced to varietal rank under *C. pilifer*: *C. pilifer* Brid. var. *lamellatus* (Mont.) Gradstein & Sipman comb. nov. (basonym: *Campylopus lamellatus* Mont., Ann. Sci. Nat. Bot. ser. 2(9): 52. 1838).

Sporophyte.—*Campylopus pilifer* rarely produces sporophytes, contrary to *C. introflexus*. Up to the present time sporophytes were known only from a few localities in southwestern Europe (Venturi, 1881; Luisier, 1908; Dismier, 1909; Hegewald, 1973). We have located additional collections with sporophytes from Africa, Mexico and South America and have found that seta length varies from 3–5(–5.5) mm, whereas spore size ranges from 10–19 μm ; we cannot confirm sizes of over 20 μm given by previous authors (Dismier 1909; Casares-Gil, 1932). A geographic differentiation was found in the spore size, the African and American collections having spores of 10–17 μm , the European and Macaronesian collections 14–19 μm . Because of the small number of collections available, we consider these differences not significant enough to distinguish geographical races.

It should be noted that in European and African material at least 75% of the spores, in unopened capsules, are aborted—in the Irish collection recorded by Hegewald (1973) they are totally lacking—whereas in American collections we never saw abnormalities in spore formation. Since abortion of spores is characteristic of hybrid sporophytes, the question rises whether sporophytes in European and African *C. pilifer* are of hybrid origin. Before anything more can be said about this, data should become available on the distribution of the sexes in the field (most *Campylopus* species, including *C. pilifer*, are dioicous) and the association with other *Campylopus* species capable to hybridize with *C. pilifer*. According to Hegewald (1973) *C. pilifer* (with sporophytes) from Ireland was growing associated with *C. introflexus* (c. sp.) and *C. brevopilus* (ster.). A closer investigation of this Irish locality might prove worthwhile.

Specimens with sporophytes examined: IRELAND. CORK: Beara peninsula, *Hegewald s.n.* (Herb. Hegewald, U). FRANCE. St. Etienne de Baigony, *Dismier* (BM, PC). SPAIN. Pontevedra, *Allorge, Bryoth. Iber. 25b* (L); St. Jacques de Compostelle, *without collector* (PC). PORTUGAL. Tamalicao, Moledo do Minho, *Machado in Bauer*, Musc. Eur. Am. exs. 1905a (L); Beira Alta, Ribeiradio, *Sergio 653* (LISU). AZORES. SANTA MARIA: Pico Alto, *Monod 15112* (PC); Meio molho, *Allorge 61* (PC). CAMEROUN. Mt. Cameroon, *Mann* (BM, 2 specimens). KENYA. Mt. Kenya, *Schelte 2570* (PC). TANZANIA. Mt. Kilimanjaro, *Hedberg 1147* (PC). RUANDA. Préfecture de Cyangugu, forêt de Rugege, *De Sloover 18942* (NAM, U). ZAIRE. Massif du Kahuzi, *De Sloover 12544, 12545, 12561* (NAM, U). KIVU, entre Goma et Sake, *De Sloover 13388* (NAM, U); Mont Biega, *De Sloover 12966* (NAM, U). RÉUNION. *Bory St. Vincent* (PC); Piton Mare-à-Boue, *De Sloover 17285* (NAM, U).

MEXICO. MICHOACAN: Morelia, *Arsène 7862* (PC); MORELOS: N. of Guernavaca, *Hermann 20939* (TENN, U); OAXACA: Ixtlan, *Delgadillo 132a* (TENN, U); 112 km from Tuxtepec towards Oaxaca, *Manuel 644* (LAF, U); VERACRUZ: La Joya near Jalapa, *Sharp et al.* (TENN, U); Sierra de San Esteban, near Guadajara, *Pringle 10568* (L). COLOMBIA. CUNDINAMARCA: Torca, *Cleef 29* (U); Páramo Cruz Verde, *Cleef 3015* (U). BRAZIL. RIO GRANDE DO SUL: Tapes, *Vital 2034* (SP). URUGUAY. Arroyo Piedras, *Herter 1437* (GOET, U); Florida, La Palma, *Herter 99434* (B). PERU. URUBAMBA: Machu Picchu, *Hegewald 5585* (Herb. Hegewald, U).

Campylopus introflexus (Hedw.) Brid.

Basionym: *Dicranum introflexum* Hedw., Sp. Musc. 147. 1801.

Type: Australia, "Nova Hollandia" (G, sheet 1 "A", *vide* Richards, 1963).

Synonyms: See Frahm (1975).

Description and illustrations: See Giacomini (1955: 70, fig. 7-10), Sainsbury (1955: 112-115), Frahm (1974, fig. 2-3).

Distribution (Fig. 3) and Ecology.—*C. introflexus* is common in temperate and subantarctic regions of the southern hemisphere, between 22° and 60°S, from southern South America (South Brazil, Uruguay, Chile, Argentina) eastwards to New Caledonia and New Zealand. Since 1941 the species is found as a neophyte in West and Central Europe (Richards, 1963; Frahm, 1972).

It occurs mainly at low elevations, and prefers temporarily dry to humid, non-calcareous, poor, humous or mineral soil or peat in fairly open situations; it is also found on bases of trees or rotten wood. In Europe the species grows in disturbed habitats where competition is low (Richards, 1963; Frahm, 1972).

Variation (Table 1).—The morphological variation of the gametophyte was adequately described by Giacomini (1955) and Frahm (1974). With respect to sporophyte characteristics, considerable variation is seen in seta length (5-10 mm). Extremes were found in a collection from New Caledonia (*Robbins 3784*, L), which in one tuft had setae of 4-5 mm and 9-10 mm! Capsule size was studied by Giacomini (1955), who found that capsules are usually over 1.1 mm long and 1.6-2.5 times longer than wide. A deviating plant from Uruguay, which has shorter capsules (0.9-1 mm long, ca. 1.3 times longer than wide), was described as *C. introflexus* var. *brachycarpus* Giac. (Montevideo, *Felippone 1490*, isotype in PC). We found that it differs also in the seta, which is only 4 mm long, as in *C. pilifer*. The gametophyte, however, fits *C. introflexus*.

Spores in *C. introflexus* were never found to be aborted, as opposed to *C. pilifer*.

EPILOGUE

Although the number of differentiating characteristics has been reduced in this study, as compared with Giacomini and later authors, a slight overlap is still seen in the remaining key characteristics. We encountered no difficulties in identifying fertile specimens, but a few sterile specimens with lamellae only two cells high were difficult to place. The American, and especially the tropical African, populations of *C. pilifer* resemble *C. introflexus* much more than do the European ones. This raises the ques-

tion whether or not the two taxa deserve species rank or should be treated as subspecies (geographic races). Since they have both attained morphological individuality in the gametophyte and the sporophyte, and a pluriregional area of distribution, species rank seems justified. Moreover, the southern hemispheric *C. introflexus* has proved capable of successful invasion into the European area of *C. pilifer* with maintenance of its individuality. Presumed intergradation of the species in the overlap areas in South America and South Africa is a subject for further investigation.

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