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The taxonomic status of intermediate forms of *Campylopus introflexus* (Hedw.) Brid. and *C. pilifer* Brid. (Dicranaceae, Bryopsida) newly discovered in Europe

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Abstract – Recently mixed stands of *Campylopus introflexus* (Hedw.) Brid. and another piliferous *Campylopus* taxon were found in Brittany, France. The latter resembles *C. pilifer* Brid. by its straight hairpoints, but the lamellae on the dorsal costa surface are only 1-2 cells high, as typical for *C. introflexus*, instead of 3-4 cells high as characteristic for *C. pilifer*. Similar plants were recorded before from northern Argentina and the East African islands. Phylogenetic analyses based on sequences of the nuclear ribosomal DNA ITS1 and ITS2 and the chloroplast DNA *atp*B-*rbc*L spacer indicate a close relationship of intermediate plants from Brittany and Réunion with *C. pilifer* accessions from the Old World (Macaronesia, Continental Europe, Arabia). *Campylopus introflexus* from the same locality in Brittany is part of a well-supported clade of *C. introflexus* accessions from the subantarctic region, North America and Europe. For practical reasons, the intermediate specimens are distinguished on varietal level, as *Campylopus pilifer* var. *brevirameus* (Dix.) J.-P. Frahm & Stech, comb. nov. *Campylopus pilifer* subsp. *pilifer* now comprises three varieties with different types of lamellae, var. *lamellatus* (Mont.) Gradstein & Sipman with six, var. *pilifer* with three to four, and var. *brevirameus* with lamellae two cells high. If these expressions represent genotypes or modifications remains to be tested.

***Campylopus introflexus* / *Campylopus pilifer* / *Campylopus brevirameus* / taxonomy / ITS1 / ITS2 / *atp*B-*rbc*L spacer**

INTRODUCTION

Campylopus pilifer is widely distributed through the Neotropics, tropical Africa and India (distribution map in Frahm, 1988). Range extensions into the Holarctic include few occurrences in North America (Frahm, 1980) and South-western Europe. Except for these secondary extensions, the range matches a Gondwanalandic distribution pattern indicating an old phylogenetic age (Frahm, 1988). Molecular analyses based on sequences of the ITS1 and ITS2 of the nuclear ribosomal (nr) DNA and the *atp*B-*rbc*L spacer of the chloroplast (cp) DNA

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revealed *C. pilifer* as polyphyletic and differentiated into Old World and New World lineages (Stech & Dohrmann, 2004). These phenotypically indistinguishable lineages probably reflect divergent evolution after separation of the landmasses of the former Gondwana supercontinent.

Closely related with *C. pilifer* is *C. introflexus* (Hedw.) Brid., a vicariant species in the austral region (introduced into North America and Europe, cf. distribution map in Frahm, 2001). Typical plants of *C. pilifer* and *C. introflexus* are gametophytically distinguished by the height of the lamellae on the dorsal costa surface (2 to 7 *vs* 1 to 2 cells) and the hyaline hairpoints at the leaf tips (erect *vs* reflexed about 90° in dry condition). At the molecular level, a close relationship between *C. introflexus* and the Old World lineage of *C. pilifer* is indicated especially by a different sequence type of the ITS1 region compared with the New World *C. pilifer* and other *Campylopus* species (Stech & Dohrmann, 2004).

Interestingly, specimens recently collected in Brittany (France) could not directly be attributed to either *C. introflexus* or *C. pilifer*. They showed straight hairpoints as in *C. pilifer*, but the costal lamellae were only two cells high. Such specimens were earlier found in northern Argentina and described as *C. introflexus* var. *cordobaensis* Thér. (Thériot, 1934) or in the Seychelles and described as *C. brevirameus* Dix. (Dixon, 1929). Similar specimens were also mentioned from southern Africa, the Marion Islands (Frahm, 1985), and recently collected by T. Pfeiffer (Berlin) in Réunion.

Several explanations for the occurrence of such intermediate forms are conceivable:

1. The specimens belong to *C. introflexus* but have straight hairpoints, and should therefore be regarded as a variety of *C. introflexus*, as Thériot (1934) did describing such plants as *C. introflexus* var. *cordobaensis*. This hypothesis could be supported by the observation that species with straight hairpoints can have reflexed ones or vice versa. For example, few collections of *C. pilifer* with reflexed hairpoints are known, e.g. from Mexico. Similarly, forms of *C. umbellatus* (Arn.) Par. with reflexed hairpoints have been collected in SE-Asia, whereas the species normally has straight ones. Presumably, these species have genes for both expressions, but usually the character state of reflexed hairpoints is expressed in *C. introflexus*, while that of straight hairpoints is expressed in *C. pilifer*.

2. The specimens belong to *C. pilifer*, but have lower lamellae. In this case, they could be treated as a variety of *C. pilifer*, which would be more convenient for field identification than attributing them to *C. introflexus* var. *cordobaensis*, since they macroscopically resemble *C. pilifer* by their straight hairpoints. A variety of *C. pilifer* with lamellae six cells high already exists, *C. pilifer* var. *lamellatus* (Mont.) Gradstein & Sipman (Gradstein & Sipman, 1978).

3. The specimens are hybrids between *C. pilifer* and *C. introflexus*, since all these records (except those from Marion Islands) originate from areas where the distribution ranges of both species overlap. This hypothesis has been applied to the specimens described as *C. introflexus* var. *cordobaensis* (Frahm, 1987) or *C. brevirameus* (Frahm, 1985). It is also conspicuous that such intermediate forms are found around the world and are not confined to a smaller region, indicating that hybrids were produced several times independently. On the other hand, there are no observations or indications of the new possible hybrids growing together with the parental species.

4. The specimens belong to a separate species, as Dixon (1929) supposed, who described them as *C. brevirameus*.

The recent collections of plants intermediate between *C. introflexus* and *C. pilifer* from Continental Europe and the East African island of Réunion drew the attention again on this problem because of the necessity to name such specimens. Two molecular studies, one concerning the circumscription of *Campylopus* (Stech, 2004), and the second concerning relationships between *C. introflexus* and *C. pilifer* based on a world-wide sampling (Stech & Dohrmann, 2004), provide a basis for a molecular identification. Therefore, in the present study we aim to evaluate the relationships and taxonomic status of the intermediate plants from Brittany and Réunion, based on sequences of the nrDNA ITS1 and ITS2 and the cpDNA *atp*B-*rbc*L spacer regions.

MATERIALS AND METHODS

Large quantities of two morphologically distinct *Campylopus* taxa were found by the first author in France, Dépt. Finistère, Plomodiern, on open granitic rocks at the bay of Tréfeuntec, shortly above sea level, on Oct. 2, 2003, accompanied by *Hedwigia ciliata* (Hedw.) P. Beauv., *Bryum alpinum* Huds. ex With., *Campylopus fragilis* (Brid.) Bruch & Schimp., *Grimmia* spp., *Pleurochaete squarrosa* (Brid.) Lindb., *Pterogonium gracile* (Hedw.) Sm. and *Trichostomum brachydontium* Bruch. One had straight hairpoints and was attributed to *Campylopus pilifer* in the field, but in transverse section of the costa the costal lamellae were only 1-2 cells high, instead of 3-4 cells high as typical for this species. The other had reflexed hairpoints and was identified as *C. introflexus*. Both taxa were found also in mixed tufts (Fig. 1), both were present in again morphologically different

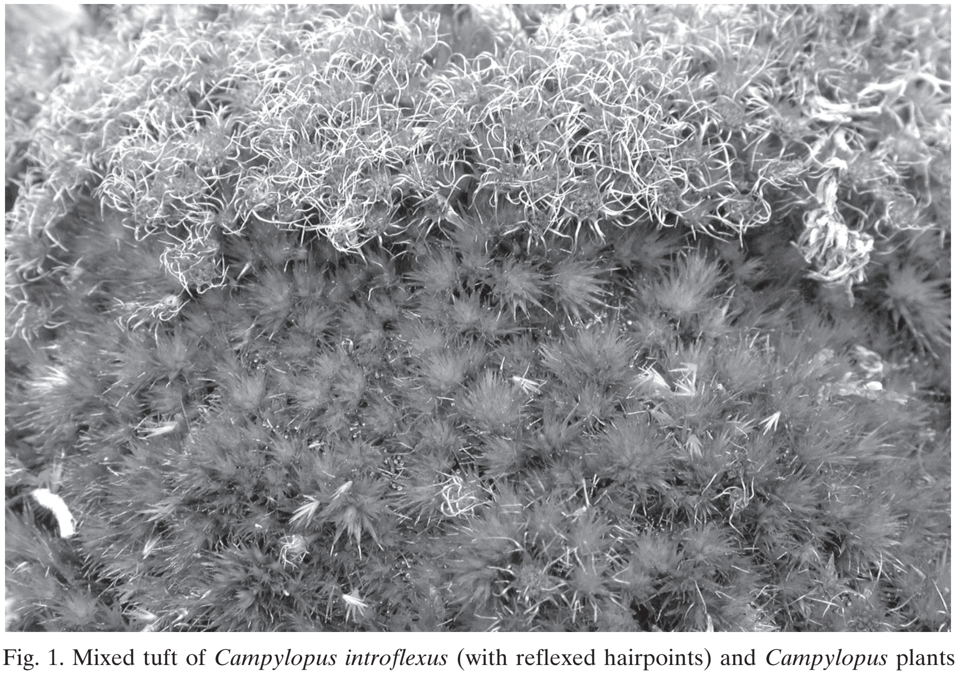

Fig. 1. Mixed tuft of *Campylopus introflexus* (with reflexed hairpoints) and *Campylopus* plants resembling *C. pilifer*, but with costal lamellae only 1-2 cells high (Plomodiern, Brittany, France, Oct. 2, 2003).

Table 1. Voucher information and GenBank accession numbers for the sequences used in this study. Asterisks indicate accessions not previously analysed in Stech (2004) and Stech & Dohrmann (2004). All herbarium vouchers are deposited at BONN .

Taxon	*Origin*	*Voucher*	*acc. n° ITS1/5.8S/ITS2*	*acc. n° atpB-rbcL spacer*
C. anderssonii (Müll. Hal.) A. Jaeger	Bolivia	*Lewis 88-305*	AF444138	AY159923
C. australis Catchs. & J.-P. Frahm	Australia 1	*Streimann 56175*	AF444129	AY159925
C. australis	Australia 2	*Blackwell 38.92*	AY540854	AY159924
C. crateris Besch.	Réunion	*Müller R638*	AF444137	AY159939
C. cryptopodioides Broth.	Brazil	*Schäfer-Verwimp & Verwimp 12018*	AF444120	AY159915
C. dichrostris (Müll. Hal.) Paris	Brazil	*Schäfer-Verwimp 6807*	AF444124	AY159910
C. exasperatus var. *lorentzii* (M. Fleisch.) J.-P. Frahm	Philippines	*Schwarz 3820*	AF444131	AY159929
C. flexuosus (Hedw.) Brid.	Germany	*Stech B960905.2*	AF444117	AY159919
C. fragilis (Brid.) Bruch & Schimp.	Australia	*Streimann 51759*	AF444122	AY159917
C. gracilis (Mitt.) A. Jaeger	Sri Lanka	*Schäfer-Verwimp 5430/I*	AY540859	AY159938
C. hensii Renault & Cardot	Equatorial Guinea	*Heras* 25.7.94, dupl. ex VIT443/94	AF444126	AY159911
C. introflexus (Hedw.) Brid.	Australia	*Coveny & P.D. Hind 15865*	AY375229	AY551363
C. introflexus	Chile	*Frahm 12-1*	AY375224	AY551365
C. introflexus	Paraguay	*Zardini & Velásquez 26060*	AY375222	AY576441
C. introflexus	USA, Oregon	*Raeymaekers 5143*	AY375227	AY551366
C. introflexus	Germany	*Stech B890407.1*	AY375225	AY551367
**C. introflexus*	France	02. Oct. 2003, *Frahm* s.n.	AY925208	AY925205
C. julicaulis Broth.	Paraguay	*Zardini 6652*	AF444119	AY159914
C. pilifer Brid.	Réunion 1	*Pfeiffer 2002-32*	AY375219	AY925203
C. pilifer	Réunion 2	*Pfeiffer 2002-30b*	AY375217	AY925202
C. pilifer	Socotra	*Kürschner 02-213*	AY372475	AY551372
C. pilifer	Azores	*Schwab SN116*	AY372483	AY551371
C. pilifer	Italy	23 Aug. 2000, *Frahm* s.n.	AY372478	AY576440
C. pilifer	Argentina	*Churchill & Schiavone 20076*	AY372470	AY576438
C. pilifer	USA, Texas	*Merrill 13328*	AY372474	AY551368
C. pilifer	Costa Rica	*Arts CR 21/12*	AF444135	AY159930

Table 1. Voucher information and GenBank accession numbers for the sequences used in this study. Asterisks indicate accessions not previously analysed in Stech (2004) and Stech & Dohrmann (2004). All herbarium vouchers are deposited at BONN *(suite)*.

C. pilifer var. *lamellatus* (Mont.) Gradst. & Sipman	Peru	*Frahm 1-3589*	AY375212	AY159927
**C. ?pilifer*	France	02. Oct. 2003, *Frahm* s.n.	AY925207	AY925201
**C. ?pilifer*	Réunion	*Pfeiffer 2002-54*	AY925206	AY925204
C. pyriformis (Schultz) Brid.	New Zealand	*Frahm X14-4*	AF444121	AY159916
C. savannarum (Müll. Hal.) Mitt.	Equatorial Guinea	*Heras* 25.7.94, dupl. ex VIT449/94	AF444125	AY159909
C. tallulensis Sull. & Lesq.	Colombia	*Lineares C. & Churchill 3820*	AF444118	AY159913
C. thwaitesii (Mitt.) A. Jaeger	South Africa	*Arts RSA 104/25*	AF444115	AY159906
C. thwaitesii	Brazil	*Vital & Buck 19682*	AF444116	AY159907
C. umbellatus (Schwägr. & Gaudich. ex Arn.) Paris	Indonesia	*Schäfer-Verwimp 20642*	AF444130	AY159928
Pilopogon africanus Broth.		*Frahm 8079*	AF444139	AY159903
P. guadalupensis (Brid.) J.-P. Frahm		*Arts CR03/07*	AF444112	AY159904

male and female plants, and both produced sporophytes. In addition, a specimen intermediate between *C. pilifer* and *C. introflexus* from Réunion, collected by T. Pfeiffer (Berlin) in 2002, was analysed. Voucher information is given in Tab. 1, vouchers of all specimens are deposited at BONN.

DNA extraction, PCR, and sequencing reactions were performed as described in Stech (2004) and Stech & Dohrmann (2004). Sequences were deposited in GenBank under the accession numbers listed in Tab. 1.

Alignments of the sequences were made manually in the Alignment Editor Align32 (Hepperle, 1997). Maximum parsimony and maximum likelihood trees of combined data sets (comprising ITS1, ITS2, *atp*B-*rbc*L spacer, and 61 bp of the 3' end of the *atp*B gene) were evaluated with *win*PAUP 4.0b10 (Swofford, 2002). To allow for more thorough searches, only a selection of specimens included in Stech & Dohrmann (2004) were analysed together with the three newly generated sequences, while most of the identical sequences of *C. pilifer* and *C. introflexus* were excluded. Heuristic parsimony searches were performed with the following options: all characters unweighted and unordered, multistate characters interpreted as uncertainties, gaps coded as missing data, performing TBR branch swapping, collapse zero length branches, MulTrees option in effect, random addition sequence with 1,000 replicates, maxtrees = 100,000. *Pilopogon africanus* Broth. and *P. guadalupensis* (Brid.) J.-P. Frahm were chosen as outgroup representatives based on the sister group relationship of *Campylopus* and *Pilopogon* inferred by Stech (2004). Heuristic bootstrap searches were performed with 1,000 replicates with 10 addition sequence replicates per bootstrap replicate. Further measurement of support for individual clades was obtained using AutoDecay 4.0 (Eriksson, 1999) with 100 random addition cycles. Maximum likelihood calculations were executed assuming a GTR+G+I model and a rate variation among sites following a gamma distribution (four categories each represented by a mean average rate). GTR+G+I was chosen as the model that best fit the data under the AIC criterion as evaluated by Modeltest v.4b (Posada & Crandall, 1998) employing the Windows® front-end (Patti, 2002). The settings proposed by Modeltest were: Basefreq = (0.3477 0.1810 0.1742), Nst = 6, Rmat = (1.6992 3.8436 0.6966 4.3523 7.9401), Shape = 0.5723, Pinvar = 0.4553. Likelihood bootstrap searches were performed with 100 replicates using the "fast bootstrap" option (bootstrapping without branch-swapping) of PAUP (Swofford, 2002). Fast bootstrapping was shown to provide estimates of support similar to, although generally less than, bootstrapping with branch-swapping, and allows to achieve a reasonable computation time (Mort *et al.*, 2000).

RESULTS

The ITS1, ITS2, and *atp*B-*rbc*L spacer regions were already characterised in detail in *Campylopus* by Stech (2004) and Stech & Dohrmann (2004). The present ITS alignment of a subset of specimens analysed in these studies comprised 1609 positions (ITS1 positions 1-1051, ITS2 1052-1609). Parts of the alignment were ambiguous due to (hyper-)variable segments in both internal transcribed spacers, especially in the ITS1, and consequently, 600 positions were excluded from phylogenetic analyses. The chloroplast DNA alignment comprised 61 positions of the 3'end of the *atp*B gene and 591 positions belonging to the *atp*B-*rbc*L spacer, which were all used for tree construction. Altogether, the combined analyses were based on 1661 included positions; 263 (15.8%) of them are variable, and 177 of the variable characters (67.3%, or 10.7% of the total number of characters) are parsimony-informative.

Separate analyses of the nrDNA and cpDNA markers did not reveal incongruencies among well-supported clades (trees not shown). Trees based on the *atp*B-*rbc*L spacer alone generally showed lower resolution than ITS trees due to lower sequence variation. The maximum parsimony calculation of the combined data set resulted in 648 trees (lengths 379, CI [excluding uninformative characters] = 0.7083, RI = 0.8849, RC = 0.6888), of which the strict consensus tree is shown in Fig. 2. In this tree, *Campylopus introflexus* is monophyletic with 100% bootstrap support (BS) and a decay index (DI) of 11. *Campylopus pilifer* is paraphyletic, with a well-supported clade of the Old World specimens (except two specimens from Réunion; 93% BS, DI = 2) being sister to *C. introflexus*. This clade also includes the intermediate specimens from Brittany and Réunion. Close relationships are also indicated for both included specimens of *C. pilifer* from South America (100% BS, DI = 7), and for both Central and North American samples (92% BS, DI = 3), whereas relationships between these clades remain ambiguous. In a maximum likelihood analysis of the same data set, two trees with identical topologies and only marginal differences in some branch lengths were recovered (lnL = – 4515.54669), of which one tree is shown in Fig. 3. Relationships of *C. pilifer* and *C. introflexus* are the same as in the parsimony tree, with equally or almost equally high bootstrap support for the branches of *C. introflexus* and *C. pilifer* from the Americas, but lower bootstrap support (72%) for the Old World *C. pilifer* samples and the intermediate specimens.

DISCUSSION

Piliferous *Campylopus* specimens with almost straight hairpoints, but with two-celled lamellae, were already reported from the Netherlands (Barkman & Mabelis, 1968) and illustrated in Landwehr (1966) as *C. polytrichoides* De Not. (= *C. pilifer*). However, this illustration shows indications of the recurved hairpoints typical for *C. introflexus* (Fig. 88d in Landwehr, 1966). Such forms are occasionally found, but can be attributed to *C. introflexus*, being either juvenile plants or plants from shady habitats. The first records of *C. introflexus* from Central Europe in the 1960s also consisted of these untypical forms (Frahm, 1970; Neu, 1968).

The specimens discovered at the locality in Brittany mentioned above, however, grew in large masses in an open habitat and in mixed tufts with typical *C. introflexus* plants. Therefore, they cannot be attributed to modifications in shady habitats or to juvenile plants, and other data, such as DNA sequence data, must be evaluated to clarify their taxonomic status.

The molecular data presented here clearly show that the specimens from Brittany and Réunion, which are anatomically and morphologically intermediate between *C. pilifer* and *C. introflexus*, belong to *C. pilifer* (Figs 2, 3). Precisely, they are part of the Old World *C. pilifer* lineage that comprises specimens from Africa, Arabia, Macaronesia, and Continental Europe (cf. Stech & Dohrmann, 2004). In contrast, the typical *C. introflexus* growing together with the intermediate form at the locality in Brittany is part of the well-supported clade of *C. introflexus* specimens from around the world. Its identity is therefore beyond doubt, which further supports the existence of two different piliferous taxa at that locality. Both species are known from this region. Finistère was the first place where *C. introflexus* was found in Continental Europe by P. Størmer in 1954 (Størmer, 1958), some years after the species had been detected on the British Isles in the 1940s (Richards, 1963). For *Campylopus pilifer*, this region belongs to the extension of its natural range in Europe, reaching from the Mediterranean to the coast of southern Belgium.

Investigation of the intermediate specimen from Réunion revealed that on this island also two different piliferous taxa occur, both attributed to *C. pilifer* on morphological grounds. Until now it seemed that the Old World lineage of *C. pilifer* did not occur on Réunion, as the specimens analysed so far were more similar to the American ones, or somewhat molecularly intermediate between the lineages (cf. Figs 2, 3; Stech & Dohrmann, 2004). The supposition of Stech & Dohrmann (2004) that the island was colonised *via* long distance dispersal may still be true for these specimens, but with the Old World lineage now found on the island, a derivation from this lineage might also be taken into account.

Because of the closer relationship of *C. pilifer* var. *lamellatus* to South American specimens of *C. pilifer* var. *pilifer* than between the *C. pilifer* var. *pilifer* specimens from the whole distribution range, Stech & Dohrmann (2004) argued that the number of lamellae on the dorsal surface of the costa might not be a useful character to distinguish infraspecific taxa. In fact, it is not known whether higher or lower lamellae represent different genotypes or are modifications. The most obvious explanation of the variation of lamellae height as an adaptation to different levels of humidity is not that plausible on closer inspection. In Southwestern Europe, *C. pilifer* is characteristic for dry exposed habitats such as rocky outcrops or garigue vegetation. Insofar, its four-celled lamellae could be regarded as an adaptation for storing water, whereas the lower lamellae of the specimens

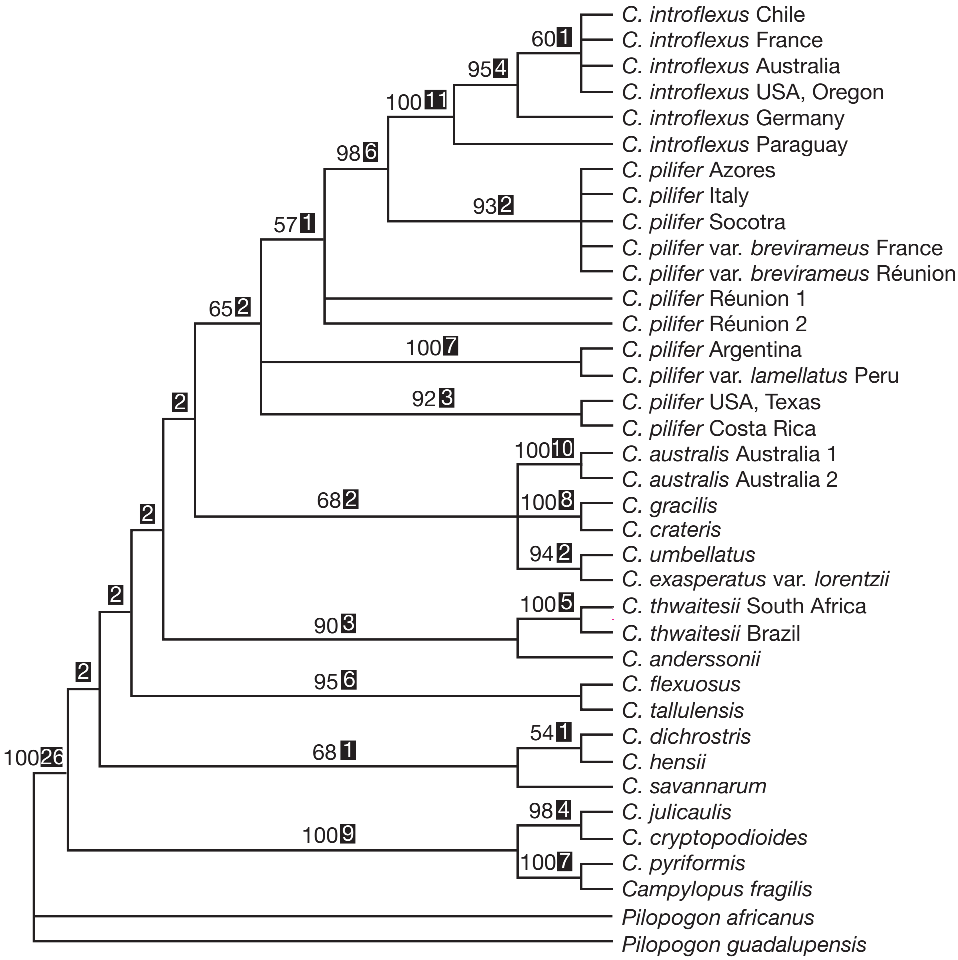

Fig. 2. Strict consensus tree of 648 most parsimonious trees inferred from a heuristic search of combined ITS1, ITS2, and *atp*B-*rbc*L spacer sequences of *Campylopus*, with *Pilopogon* as outgroup representative. Bootstrap values > 50% and decay indices (on a black background) are depicted above the branches

discovered in Brittany could be an adaptation to a more humid habitat, *i.e.*, coastal rocks. However, according to this argumentation the var. *lamellatus* specimens from extremely humid rain forest habitats should have lower, but not higher lamellae than specimens from drier habitats. The higher lamellae might instead be interpreted as a mechanism for better gas exchange.

The division of *C. pilifer* into molecular lineages, which might represent cryptic species, indicates that a completely new circumscription of *C. pilifer* is needed, which also applies to other widespread *Campylopus* species recently analysed at the molecular level (Stech & Wagner, 2005). Unfortunately, newly circumscribed taxa would only be distinguishable by molecular techniques, but not in the field. In addition, specimens of *C. pilifer* subsp. *galapagensis* (J.-P. Frahm & Sipman) J.-P. Frahm (Frahm, 1987) and subsp. *vaporarius* (De Not.) Brullo, Privitera

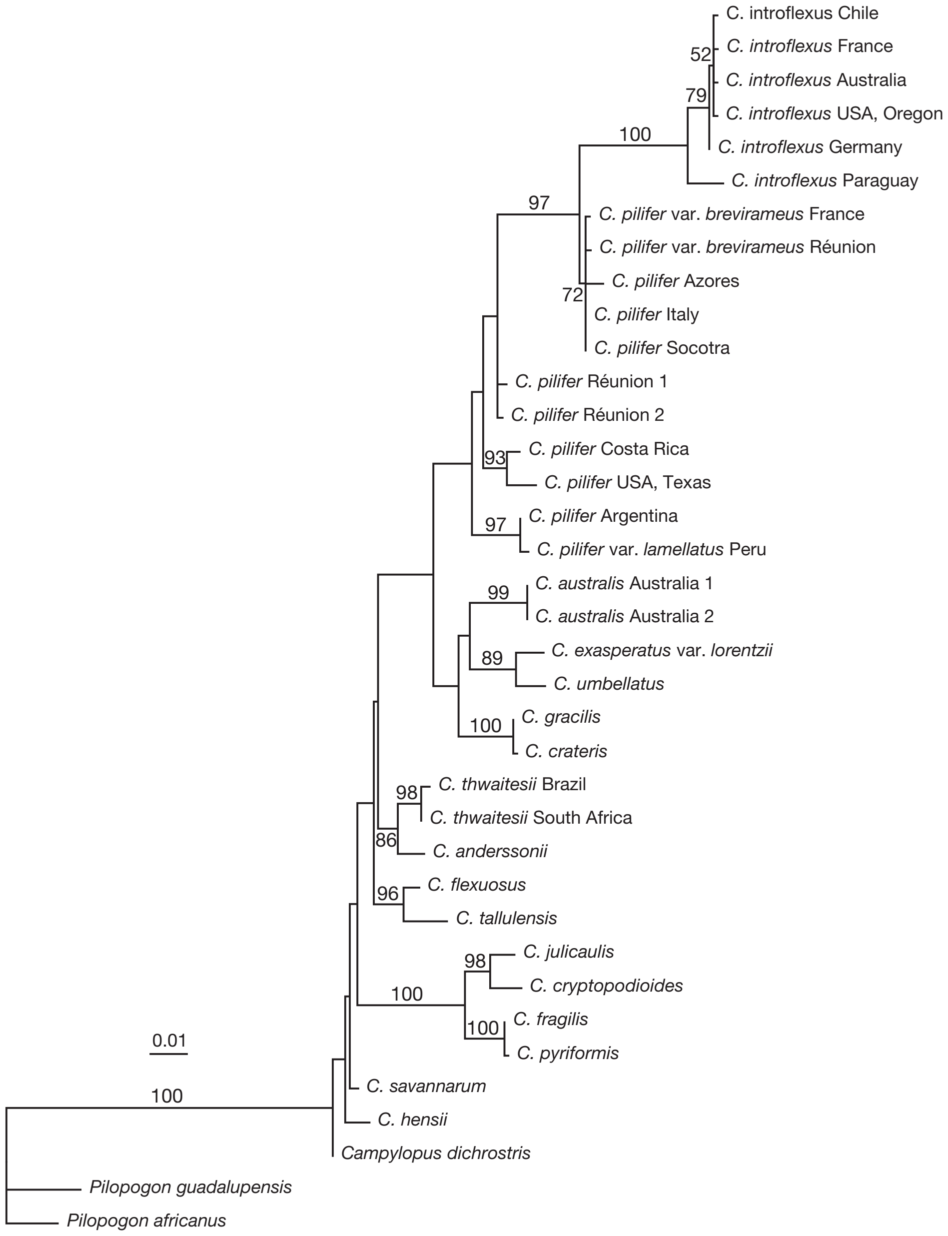

Fig. 3. One of two trees obtained by a maximum likelihood analysis (GTR+G+I model) of combined ITS1, ITS2, and *atp*B-*rbc*L spacer sequences of *Campylopus*, with *Pilopogon* as outgroup representative. Bootstrap values > 50% are depicted above the branches.

& M. Puglisi (Brullo *et al.*, 2001), as well as further specimens of subsp. *pilifer*, especially from the Indian subcontinent, should be sequenced before such extensive changes are made. Therefore, we propose a more conservative taxonomic consequence of this study, that is, the distinction of the specimens intermediate between *C. pilifer* and *C. introflexus* on an infraspecific level. The molecular results demonstrate that the specimens from Brittany and Réunion do not belong to a variety of *C. introflexus* with straight hairpoints, but to a variety of *C. pilifer* with low lamellae. For a taxonomic distinction, two epithets are available, *C. brevirameus* Dix. and *C. introflexus* var. *cordobaensis* Thér., of which *C. brevirameus* has the priority. Besides, the epithet *brevirameus* nicely illustrates the distinguishing character (short branches = lamellae). Therefore, the new combination can be made:

Campylopus pilifer* var. *brevirameus* (Dix.) J.-P. Frahm & Stech *comb. nov.
Basionym: *Campylopus brevirameus* Dix., Ann. Bryol. 2: 6, 1929.
Synonym: *Campylopus introflexus* var. *cordobaensis* Thér. ***syn. nov.***
Type: Argentina, Cordoba: El Duranzo, *Hosseus 149*, Musci Eur. & Amer. Exsicc. 45: 2204
Campylopus pilifer subsp. *pilifer* now comprises three varieties with different types of lamellae, var. *lamellatus* with six, var. *pilifer* with three to four, and var. *brevirameus* with lamellae two cells high. The scattered distribution of var. *brevirameus* in regions where both *C. introflexus* and *C. pilifer s.str.* occur could indicate a hybridogenous origin, which can presently neither be confirmed nor excluded. A brief survey of the herbarium of the first author revealed that specimens attributable to var. *brevirameus* have already been found several times in Western Europe, in regions where also typical specimens of *C. pilifer* occur: France, Caen, auf Felsen im Heidegebiet bei Huelport, leg. *Rieger* 26.8.1961; Fontainebleau, leg. *A. Braun* (Dupl. ex MO, the George Engelmann Herbarium); Ireland, West Cork, Adsigole, on rocks by the shore, leg. *E. Wallace* 31.8.1979; England, Alderney, S-coast between Les Couriaux and Val du Sud, leg. *H. Sipman* 7.4.1975. Outside Europe, such specimens are known from: South Africa, rock on summit of Table Mountain, leg. *P. Odd* 24.12.1954; *Magill 4415* (PRET); Seychelles, type of *C. brevirameus* (Dixon, 1929), a second time reported by Bartram (1950), a third time collected by Mulsow (Frahm, 1985), and quite frequently by O'Shea *et al.* (1996); Réunion, Cirque de Mafate, leg. *T. Pfeiffer* 4.4.2002; Argentina**,** Cordoba, type of *C. introflexus* var. *cordobaensis* Thér. Specimens form Marion Islands (van Zanten, 1971) have to be checked since the Marion Islands are much out of the range of *C. pilifer*.

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