

## ***Antitrichia californica* Sull. (*Leucodontaceae*) in France. Identification, distribution, habitat and communities**

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**Abstract** – Major morphological traits distinguishing *Antitrichia californica* Sull. from *A. curtispindula* (Timm ex Hedw.) Brid. are provided. New characters are included. The French distribution of *Antitrichia californica* is mapped and the worldwide distribution commented. The habitat, community structure and dynamics of *Antitrichia californica* Sull. are analysed. In France, *Antitrichia californica* appears as a typical inhabitant of semi-open woods, mostly growing over rocks in different types of bryophytic communities.

***Antitrichia californica* Sull. / *Antitrichia curtispindula* (Timm ex Hedw.) Brid. / Identification / Chorology / Taxonomy / Ecology / Sociology / Strategy**

**Résumé** – Les principales caractéristiques morphologiques permettant la distinction de *Antitrichia californica* Sull. et de *A. curtispindula* (Timm ex Hedw.) Brid. sont données. De nouveaux caractères sont apportés. Les distributions mondiale et française sont fournies, celle de France sous forme de carte. Ensuite, l'habitat, la structure et la dynamique des groupements à *Antitrichia californica* Sull. sont analysés. En France, *Antitrichia californica* croît typiquement dans des habitats boisés semi-ouverts, sur des rochers, et appartient à différentes communautés bryophytiques.

***Antitrichia californica* Sull. / *Antitrichia curtispindula* (Timm ex Hedw.) Brid. / Identification / Chorologie / Taxonomie / Ecologie / Sociologie / Stratégie**

### **INTRODUCTION**

In Europe, the family *Leucodontaceae* comprises 9 species according to Hill *et al.* (2006). Besides *Antitrichia*, *Leucodon* (6 species) and *Pterogonium* (1 species) are widely admitted as belonging to *Leucodontaceae*. Although more than 10 species have been attributed historically to the genus *Antitrichia* (Wijk *et al.*, 1959), only 2 species are today accepted: *Antitrichia curtispindula* (Timm ex Hedw.) Brid. and *A. californica* Sull. The bulk of the other combinations have been either put into synonymy with each of the two preceding taxa or with species included in related genera. For instance, Townsend (1964-65) showed that

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*Antitrichia californica* and *A. breidleriana* Schiffn. were mere synonyms. Several species or infra-specific taxa of both *A. californica* and *A. curtispindula* are in need of re-evaluation.

Unlike *Antitrichia curtispindula*, which is a widely spread species, though not very common in many parts of his known range, *A. californica* exhibits a much more restricted range. In France, *Antitrichia californica* is a poorly known taxon, and no compilation has been made with respect to its ecology and chorology. In addition, its discrimination from the supposedly related *Antitrichia curtispindula* relies mostly on vegetative characters that are notably subject to ample variation. In the first part of the following account we then try to fill this gap through a morphological study of both species and an analysis of their distribution in France.

In southern Europe and south-eastern Asia, the sociology and the strategy of the species were investigated by several authors (Walther & Leblebici, 1969; Walther, 1979; Varo, Zafra & Mateo, 1988; Frey & Kürschner, 1995; Kürschner, 1999). Numerous corticolous and saxicolous associations containing *Antitrichia californica* were cited in the literature. Its ecological profile was recently drawn by Dierssen (2001).

In France, the great rarity of the species did not facilitate ecological studies with the consequence that the local habitat and communities are poorly known. With the exception of the relevé published by Hébrard (1973), the species has never been studied from a community perspective. The mentioned habitats are rather vague as they originate from floristic notes whose aim is not ecology (Renauld, 1876; Camus, 1903; Amigo, 2002; Thouvenot *in* Aicardi, 2006). *Antitrichia californica* was never cited growing on bark, a niche that seems to be rather frequent in other parts of its European range. Hence, we provide in a second part a description and an analysis of the habitats, communities and strategy of *Antitrichia californica*.

## STUDY AREA

The study was carried out in south-eastern France, in three distinct localities: Ardèche and Gard (the Païolive site), Loire (the Malleval site) and Var (the Aigle site).

The Païolive site (WGS 84, N44°24'32"; E4°12'55") is a typical submediterranean environment with two wet seasons (spring and autumn) and a relatively dry period (summer). This is a vast karstic system which never holds water superficially, so vegetation is typically xerophytic. The geological substratum consists in massive Jurassic calcareous pavements. Wooded habitats mostly correspond to *Quercion pubescenti-sessiliflorae* Br.-Bl. 1932 and *Quercion ilicis* Br.-Bl. *ex* Molinier 1934.

The Malleval site (N45°22'52"; E4°43'34") is located in the Rhône valley (collinean belt) in a protected environment with a special richness in Mediterranean taxa. The site is mostly made of crystalline rocky outcrops with *Asplenio billotii-Umbilicion rupestris* B. Foucault 1988 in the cracks, and *Sedo albi-Veronicion dillenii* Oberd. *ex* Kornek 1974 as dry grass-land over a thin layer of soil.

The Aigle site (N43°11'46"; E5°48'44") is a vast mesomediterranean *Quercus humilis* wood over a basaltic geologic substratum.

## MATERIAL AND METHODS

The morphological study is based upon examination of herbarium specimens (from PC) and fresh collections of plants referable to *Antitrichia californica* from France and other parts of the species distribution range. Herbarium materials examined are from northern America (British Columbia, California, Idaho Montana, Oregon, and Washington), south-western Asia (Turkey), southern Europe (Portugal, Sicily, and Spain), Macaronesia (Canary Islands) and North Africa (Algeria, Morocco). French materials came from Ardèche (Païolive), Corsica, Loire (Malleval), Basses-Alpes, Loire and Var (L'Aigle). A detailed list of examined specimens can be obtained from the author upon request, but those from PC originating from France are listed in the appendix.

Sporophytes have been found to be rare in France. They have been collected in Ardèche, and were not abundant in herbarium collections.

All potential morphological characters have been reassessed in the course of our study. The taxonomic value of these features has been inferred from traditional examination of both dry and fresh plants. Dry specimens were analysed for the determination of the habit, the leaf position, the characters of the sporophytes (seta, urn). In addition the specimens were examined when wet for the habit and the leaf stance and the microscopic details (leaf form, leaf cell shape, alar cells, perichetial leaves, peristome...). The characters are illustrated by photographs from our own observations.

The ecological account is based upon field prospections in the French sites known to harbour populations of *Antitrichia californica*. Phytosociological relevés were carried out in the three localities described above. The implementation of phytosociological classic methods offers serious difficulties as far as bryophyte communities are concerned, because of the great difficulties in distinguishing genets and ramets. Bryophyte cover of the relevés was made following the combined scale of Braun-Blanquet (1964) for the abundance-dominance adapted to bryophytes in terms of clone cover. Sociability was determined considering that an individual stem is an autonomous "individual", which is, from a strictly genetic perspective, frequently not the case. The implementation of this method leads to a high coefficient (4 or 5) for pleurocarpous mosses that form large clonal colonies.

The nomenclature of taxa follows Hill *et al.* (2006) for mosses and Ros *et al.* (2006) for liverworts. For syntaxa, we refer basically to Marstaller (1993, 2007) and Bardat & Hauguel (2002). The authors of syntaxa are mentioned in the syntaxonomic scheme (Annex 1).

## IDENTIFICATION AND CHOROLOGY

### Description of French material of *Antitrichia californica* Sull.

Plants forming dense colonies of interwoven axes adhering to the surface of the substratum that may form thick layers. Colonies golden green in fresh material, dark green in herbarium material. Branching pattern made of a creeping stoloniform main shoot, provided with ascending secondary stems that are more

or less irregularly pinnately branched. Anisophyllic differentiation of branches. Rarely, secondary stems may additionally bear flagelliform branches (= microphyllous branches that grow downwards). All types of axes may potentially become stoloniferous with a strong heteroblastic differentiation. Stem with central strand. Rhizoids very prominent in stoloniferous shoots, brown, smooth, arising as robust bundles from the basal abaxial side of nerves over special areas facing the substrate. Paraphyllia absent. Pseudoparaphyllia suborbicular to broadly ovate, sometimes not clearly distinguishable from proximal branch leaves. Proximal leaves broadly ovate. Axillary hairs with 2 brown basal cells and 2-3 hyaline upper cells. Branch leaves imbricate when dry, smooth or slightly plicate, erecto-patent to spreading when wet, ovate, suddenly and shortly acuminate. Costa strong, ending in the acumen, more than 200 µm wide at base, very often with several branches at base. Margin strongly and broadly recurved almost to the apex, dentate at the apex, the teeth often recurved and spinose. Mid-leaf cells with thickened walls and often porose, 10-30 × 6-10 µm, basically ovate-rhomboidal, slightly sinuose, shortly linear-flexuose in best developed leaves. Basal cells wider, strongly incrassate and more porose than the upper ones. Alar cells in an indistinct group of quadrate or rectangular cells, ascending along the margin. Leaves of stoloniferous shoots much reduced, more longly attenuated than normal branch leaves, occasionally lacking costa, at least some of them apically recurved and hooded.

Dioicous. Male plants similar to the female ones. Perigonial leaves ovate, concave. Perigonium with numerous paraphyses. Perichaetial leaves longly attenuated. Inner perichaetial leaves erect, lanceolate, not plicate and longly acuminate. Perichaetial paraphyses numerous. Calyptra not seen. Seta twisted upwards in a clockwise spiral. Lid not seen. Urn narrowly cylindrical, 2-4 mm. Annulus of one row of rectangular vesiculose cells. Stomata restricted to the apophysis (= capsule neck), Exothecium mainly of hexagonal cells with thickened walls. Peristome double. Exostome teeth 16, whitish, papillose, slightly perforate along the middle line, often irregularly fused with other teeth at base or at the apex. Papillae obscure towards the base where a more or less indistinct cross-striolate pattern occurs. Endostome 16 subfiliform and papillose segments shorter than exostome, fragile, fugacious, without a basal membrane. Cilia lacking. Spores globose, roughly papillose, 15-25 µm across the diameter.

## Identification

The major supposed diagnostic characters based upon consulted literature (Table 1) have a more or less powerful diagnostic value, but most of them are subject to variation and overlapping. Those notably subject to variation and classically used to differentiate *Antitrichia californica* from *A. curtispindula*, are subsequently discussed.

**Habit.** The habit of the two species appears clearly distinct in the opinion of the majority of authors. *Antitrichia curtispindula* is a glossy plant for Hedenäs (1992), with not julaceous and often homomallous branches (Figs 16, 17) for Limpricht (1895), Grout (1928), Engler (1925) and Lawton (1971), in contrast with *A. californica* that is dull when dry, has julaceous branches and not homomallous leaves (Figs 1, 2). All these characters do possess a diagnostic value but none of them is sufficient for a positive determination because of overlapping polymorphism. Very robust forms of *Antitrichia californica* exhibit a tendency towards the habit of *A. curtispindula*, i.e., a more or less appreciable glossiness, not

Table 1. Morphological distinguishing characters of *Antitrichia californica* Sull. and *A. curtipendula* (Timm ex Hedw.) Brid. from the literature.

Character/author	LIMPRICHT (1895)		ENGLER (1925)		GROUT (1928)		LAWTON (1971)		HEDENÅS (1992)	
	<i>A. californica</i>	<i>A. curtipendula</i>	<i>A. californica</i>	<i>A. curtipendula</i>	<i>A. californica</i>	<i>A. curtipendula</i>	<i>A. californica</i>	<i>A. curtipendula</i>	<i>A. californica</i>	<i>A. curtipendula</i>
habitus	non homomallous leaves	more or less homomallous leaves	regularly pinnate; leaves imbricate	stem without branches or irregularly pinnate; loosely appressed, often homomallous	branches nearly or quite julaceous	leaves loosely appressed, often subsecund; non secund leaves	branches julaceous	branches not julaceous	plant dull when dry	plant glossy when dry
nervation	no secondary nerves	secondary nerves extend	single nerved		seldom branched	often divided at base	leaves without supplementary costae or the supplementary costae weak	leaves with supplementary costae often to 1/3 the length of the leaf	with several, usually short branches near base	with several branches near base, occasionally one or two branches long and extending 1/3(-1/2) way up leaf
leave	not plicate	plicate	not plicate	plicate		somewhat plicate when dry			not or hardly plicate	distinctly plicate
denticulation	not or slightly toothed	toothed			stem leave much less strongly toothed above, but branch leave as <i>curtipendula</i>	sharply dentate-serrate above with long, often reflexed teeth			less strongly denticulate; some or no teeth recurved	more strongly or spinosely denticulate or dentate, many teeth recurved
alar cells									indistinctly delimited	
areolation	shorter	cells 6-10 times longer than wide	rhombic cells with ovate lumina	narrowly rhomboidal with linear lumina			cells walls not pitted or the pits inconspicuous; cell length 18-22 µm	cells with strongly pitted walls; cell length 24-36 µm	12-28(-33) × (6-7)-10 µm	(21)-26-60 (-66) × (4)-5-9 µm

Table 1. Morphological distinguishing characters of *Antitrichia californica* Sull. and *A. curtispindula* (Timm ex Hedw.) Bröd. from the literature. (*suite*)

Character/author	LIMPRICHT (1895)		ENGLER (1925)		GROUT (1928)		LAWTON (1971)		HEDENÄS (1992)	
Taxon	<i>A. californica</i>	<i>A. curtispindula</i>	<i>A. californica</i>	<i>A. curtispindula</i>	<i>A. californica</i>	<i>A. curtispindula</i>	<i>A. californica</i>	<i>A. curtispindula</i>	<i>A. californica</i>	<i>A. curtispindula</i>
male bud	paraphysis shorter and less numerous	paraphysis numerous and longer as the antheridia								
length of seta	5-6 mm	5-12 mm								
length of capsule	longer	longer	cylindric to oblong-cylindric, 3,5 mm	oblong-ovoid 3 mm long	capsule 3-5:1; 2,5-4,5 mm long	capsule 2-2,5:1; 2,5-3 mm long				
stomates	stomata easier to see	small stomata difficult to see, restricted to apophyse								
exostome	segments at times fused in pair at the apex, roughly papillose, at the base with faint striation	the dorsal basal 2/3 with transverse and oblique striations, the apex finely papillose; dorsal middle line zig-zag; ventral trabeculae not papillose	roughly papillose	the basal 2/3 with transverse and oblique striations, transparent, only at the apex finely papillose	strongly papillose throughout	teeth strongly papillose with or without lamellae at extreme base	teeth with lamellae and horizontal striations in the lower part			
endostome	almost the same length as the exostome	fugacious and short	very short and fragile	almost the same length as exostome	nearly as long as teeth	segments short	segments nearly as long as the teeth			
spore	16-22 µm	20-35 µm	16-22 µm	20-35 µm	19-22 µm	20-30 µm				

julaceous branches and leaves slightly homomallous. *Antitrichia californica* is not always the smallest of both species, since robust forms clearly approach that of *A. curtispindula*. Highly correlated with the character “branches julaceous”, the plicateness of the leaves (theoretically smooth in *Antitrichia californica* and plicate in *A. curtispindula*) is useful to the determination but equally liable to variation: leaves of robust forms of *Antitrichia californica* may show distinct rugosity or curling. Stem leaves of *Antitrichia californica* exhibit more commonly a tendency towards those of *A. curtispindula* than do the branch leaves. Then the number of secondary and tertiary axes accounts for very distinct facies of the colony: richly branched plants appear as dense masses of interwoven julaceous and poorly branched plants as largely interspaced primary axes that are only slightly julaceous.

**Leaf-costa.** *Antitrichia curtispindula* supposedly possesses secondary nerves that are very well marked (Fig. 24), in contrast with *A. californica* that lacks them (Limpricht, 1895; Engler, 1925; Grout, 1928; Lawton, 1971; Hedenäs, 1992) (Fig. 9). This is generally true but, as Hedenäs (1992) pointed out, “the basal nerve branches in *Antitrichia curtispindula* are not always stronger or longer than in *A. californica*”. In fact, robust forms of *Antitrichia californica* may possess secondary nerves and, at times, *A. curtispindula* does not present distinct subsidiary nerves.

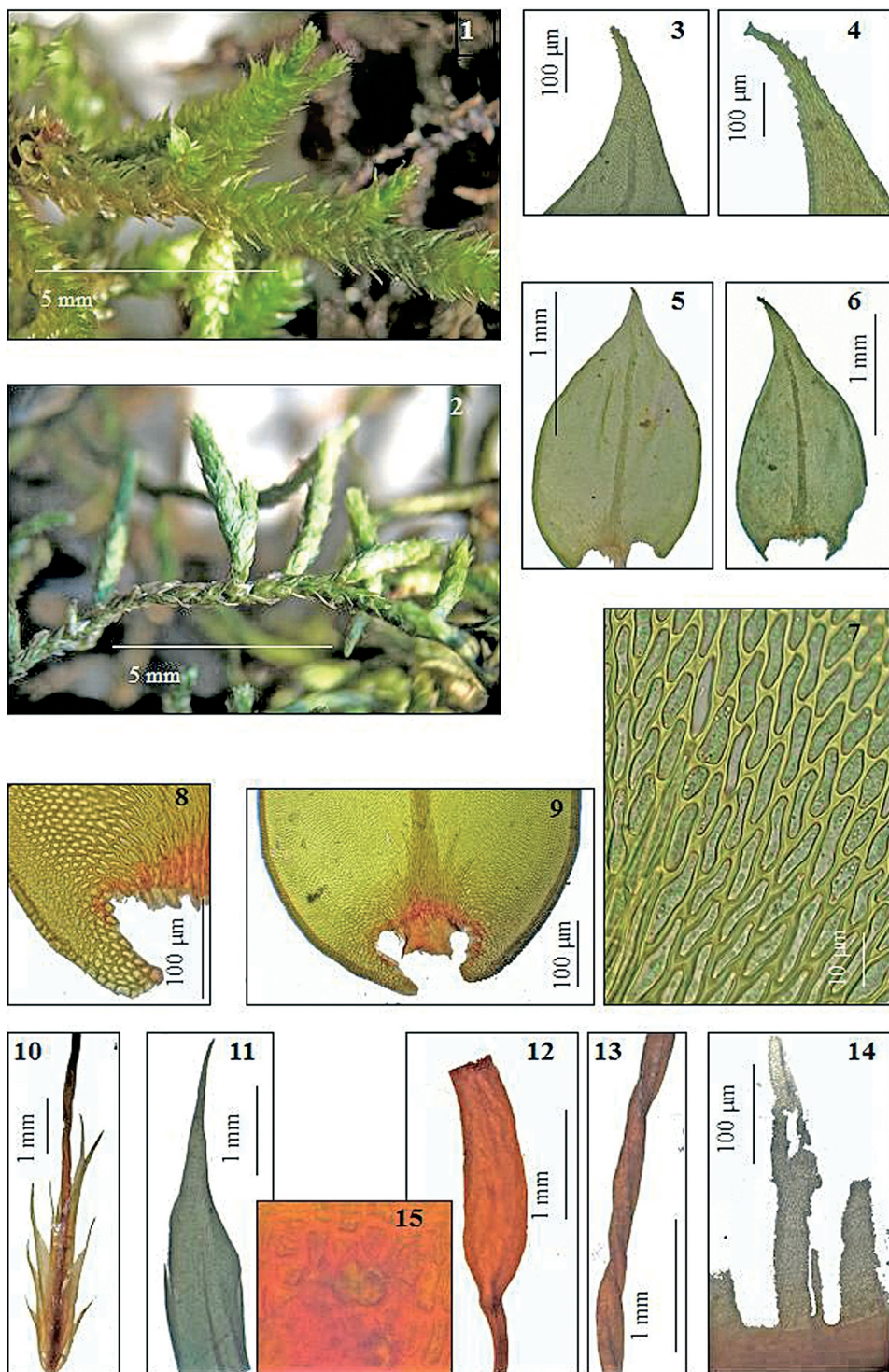
**Denticulation.** *Antitrichia curtispindula* reputedly has sharply dentate-serrate leaves at the apex (Figs 18, 19), whereas *A. californica* has much less dentate ones (Figs 3, 4). This is generally true but by no means infallible, because forms of *Antitrichia californica* may well show distinct denticulation, with recurved teeth, notably in North American specimens.

**Leaf-cells.** Areolation of *Antitrichia californica* is used as a prominent diagnostic criterion in the key of Hedenäs (1992) (Figs 7, 22). In fact in certain cases, it allows a clear delimitation of the taxa but, at times, difficult plants are found when *Antitrichia curtispindula* shows rather short cells or *A. californica* shows longer ones than is usual. The alar group (Figs 8, 23) appears more distinct when the mid leaf cells are longer. The mid leaf cells of *Antitrichia californica* are most often said to be eporose, which is in contradiction with our observations. We report here that the cells of *Antitrichia californica* are very often distinctively porose.

So far as vegetative characteristics are concerned, one can conclude that almost all criteria used for both species discrimination, are liable to much variation and character overlapping is frequent. However, the combination of the following morphological traits often helps to identify both species: areolation (short in *Antitrichia californica* and long in *A. curtispindula*), alar group (not distinct in *A. californica* and distinct in *A. curtispindula*), habit (julaceous branches in *A. californica* and not julaceous in *A. curtispindula*). A synthetical comparison of vegetative structures of both species is to be found in Renauld (1876). It is worth quoting Grout (1928): “depauperate or undeveloped plants are often difficult to place”. Again, Crundwell (1957) described a specimen of *Antitrichia curtispindula* that “shows a slight approach to *A. californica*”, because it had notably less second and more imbricate leaves, weakly toothed stem leaves and very poor development of secondary nerves. North American specimens of *Antitrichia californica* show more often a tendency towards *A. curtispindula* than do the European ones.

In the following paragraphs, we provide details of new morphological characters that in our opinion more efficiently discriminate *Antitrichia californica* from *A. curtispindula*.







**Stoloniform stem leaves.** A character that has been neglected so far is the apex of stoloniform stem leaves (i.e. the leaves of the elongated axes that tend to profusely develop rhizoids) that appears to us to be species specific. The apex of these stolon leaves in *Antitrichia californica* is frequently curved abaxially (Fig. 30) and even frequently rolled up abaxially and “hooded”, which is never the case in *A. curtispindula*, where the apex of these leaves is frequently subpiliferous and more or less flexuose (Fig. 31). In our opinion, this vegetative character is sufficient for a positive determination of much reduced material.

**Inner perichaetial leaves.** The inner perichaetial leaves of *Antitrichia californica* are longly – and gradually – attenuated (Fig. 11) whereas those of *A. curtispindula* are abruptly and rather shortly acuminate (Fig. 26).

**Seta.** The twisting of the seta provides a very good distinguishing character. *Antitrichia curtispindula* upwards seta twisting is in a counterclockwise spiral (Fig. 28) (but rather variable along the whole length), whereas *A. californica* seta twisting is mostly distally in a clockwise spiral (Fig. 13).

**Peristome.** The best distinctive criteria are to be found in the peristome (Figs 14, 29, 32, 33). In *Antitrichia curtispindula* the external side of the exostome (OPL) is marked with transverse, oblique or longitudinal lamellae at base but is epapillose (Fig. 33) above (or occasionally faintly papillose) where it exhibits a regular profile. The basal lamellae may nevertheless show some transition towards an obscurely papillose pattern. The exostomial PPL is virtually smooth. The segments of the endostome are subfiliform and slightly shorter or the same length as teeth of exostome. The endostomial PPL is epapillose (or indistinctly papillose) as is the IPL. In *Antitrichia californica*, exostome OPL is very distinctly papillose (Fig. 32) and often slightly perforate along the middle line. Neighbouring teeth are often irregularly fused at base or at the apex, which exhibit not infrequently an irregular profile. The papillae are obscured towards the base where a more or less indistinct lamellose pattern may occur. Exostomial PPL is papillose. PPL of endostome teeth is papillose too, as is the IPL. Segments are subfiliform and often much shorter than exostome teeth.

### New key proposed:

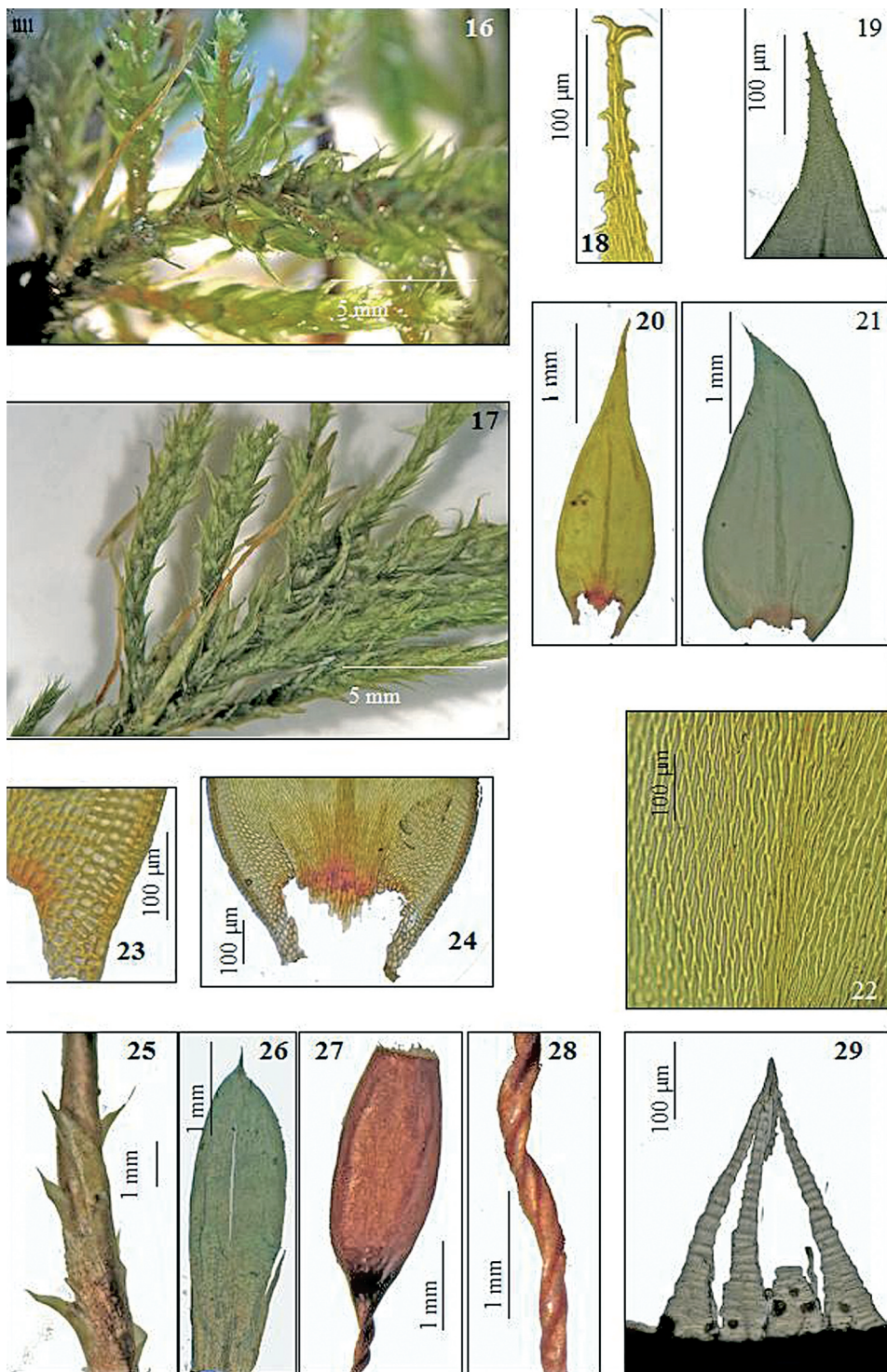
– First rank characters: Apex of the leaves of the stoloniferous shoots curved or rolled up dorsally; inner perichaetial leaves gradually and longly subulate; seta twisting distally in a clockwise spiral; exostome and endostome clearly papillose on both faces

Second rank characters: Branches julaceous; leaves commonly smooth; mid leaf cells less than 30 µm long; alar group not clearly delimited from neighbouring cells; secondary nerve often indistinct; acumen slightly (to distinctly) denticulate; spore 20-35 µm in diameter

*Antitrichia californica* Sull.

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Fig. 10. *Antitrichia californica* Sull. 1: habitus in hydrated state. 2: habitus in dry state. 3: apex of stem leaf. 4: apex of branch leaf. 5: stem leaf. 6: branch leaf. 7: areolation from middle part of stem leaf. 8: alar part of a leaf. 9: base of a leaf showing the nerves. 10: perichaetium. 11: perichaetial leaf. 12: urn. 13: upper part of seta. 14: peristome. 15: stomata from base of an urn. (Figs 1, 2, 3, 5, 7, 8 and 9 from herbarium Hugonnot L'aigle Var France ; Fig. 4 and 6 from PC0080163 ; Fig. 10, 11, 12, 13, 14 and 15 from PC0080144)



– First rank characters: Apex of the leaves of stoloniferous shoots subpiliferous; inner perichaetial leaves suddenly contracted to an acuminate apex; seta twisting distally in a counterclockwise spiral; exostome and endostome almost smooth (=devoid of papillae) on both faces

Second rank characters: Branches not julaceous; leaves plicate to rugose; mid leaf cells less than 60 µm long; alar group distinctly delimited from neighbouring cells; secondary nerve often present and distinct; acumen distinctly (to slightly) denticulate; spore 15-25 µm in diameter

*Antitrichia curtispindula* (Timm ex Hedw.) Brid.

### Distribution

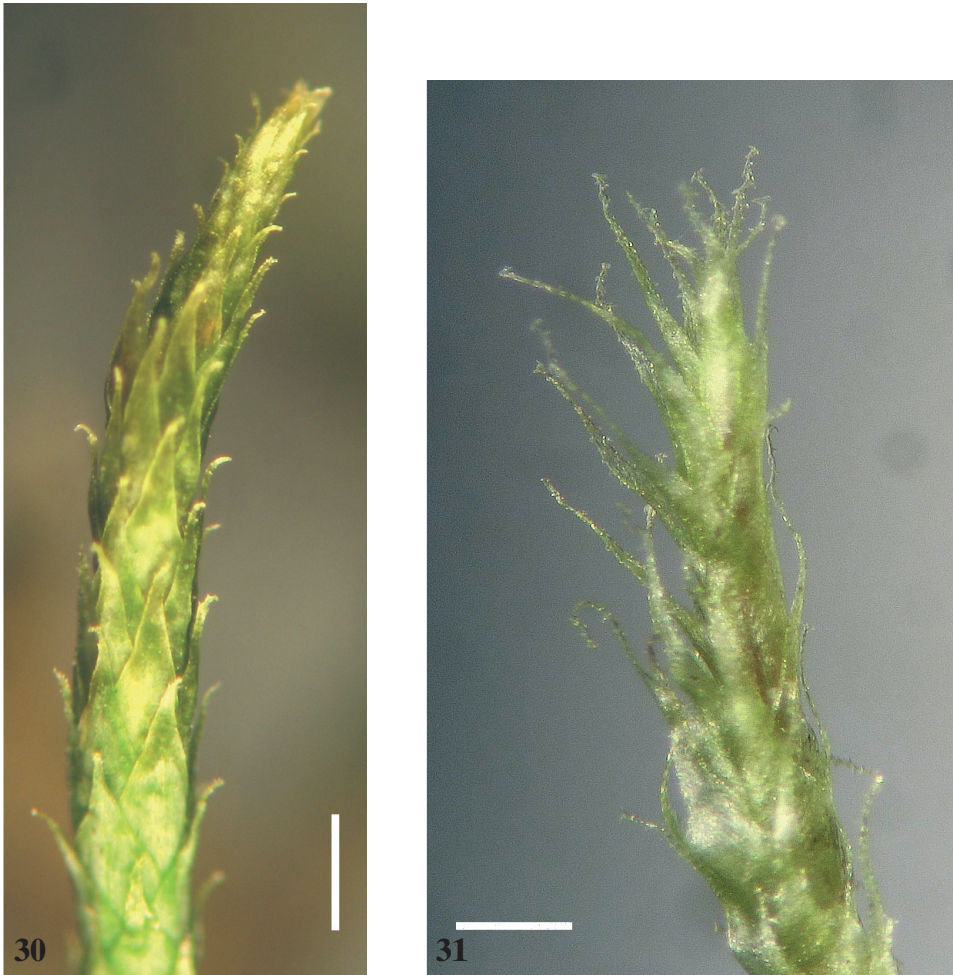
At a worldwide scale, *Antitrichia californica* shows a widely disjunct distribution as it has a largely Mediterranean range in Eurasia and a north-western American range. This taxon exemplifies the Mediterranean-Californian disjunction [“Californian disjunction” as often abbreviated] that was initially named by Allorge (1947). Herzog (1926) made only a brief mention on this striking disjunction. Düll (1985) considered *Antitrichia californica* to belong to the Mediterranean element, and Frey & Kürschner (1983, 1988) to the circum-tethyan’s one. Podpera (1954) and Düll (1985) gave an overview of the distribution of the species. European or worldwide maps of *Antitrichia californica* have been provided by Allorge (1947), Martinčič (1966), Schofield & Crum (1972) and Sérgio (1990).

In **southern Europe**, it was reported from Portugal (Sérgio & Carvalho, 2003; Sim-Sim & Sérgio, 1998), Mainland Spain and Balearic Islands (Allorge & Allorge, 1946; Podpera, 1954; Allorge, 1934; Casas *et al.*, 1985), southern France and Corsica (details given in the following section), Mainland Italy, Sicily and Sardinia (Podpera, 1954; Dia *et al.*, 1987; Cortini Pedrotti, 2001), ex-Yugoslavia (Düll *et al.*, 1999), Greece (including Crete) (Podpera, 1954 ; Düll, 1995). The mention in Switzerland is from Düll (1985) but as it is not compiled in Schnyder *et al.* (2004), it is considered as erroneous. *Antitrichia californica* is also reported in **Macaronesia**, from Madeira (Luisier, 1956; Eggers, 1982; Hedenäs, 1992) and in Canary Islands, from Gran Canary (Stormer, 1960; Eggers, 1982; Dirkse *et al.*, 1993), Tenerife and La Palma. (Dirkse *et al.*, 1993). Podpera (1954) mentions the species in **South-western Asia**. The species is known from Israel (Heyn & Herrnstadt, 2004), Syria, Lebanon and Jordan (Heyn & Herrnstadt, 2004), western Turkey (Kürschner, 1999; Kürschner & Erdag, 2005), Cyprus (Düll, 1985) and north of Iraq (Agnew & Vondracek, 1975). *Antitrichia californica* is also known from **North Africa** (Ros *et al.*, 1999): Algeria (Podpera, 1954) and Morocco (Jiménez *et al.*, 2002a and 2002b ; Draper *et al.*, 2003). The **western North American range** includes British Columbia (and Vancouver Island: Hübschmann, 1978), Washington, Oregon, Idaho, Montana, California, Nevada, south-western Alaska (Podpera, 1954; Lawton, 1971). It was erroneously mentioned in Colorado by Podpera (1954).



Figs 16-29. *Antitrichia curtispindula* (Timm ex Hedw.) Brid. **16:** habitus in hydrated state. **17:** habitus in dry state. **18:** apex of stem leaf. **19:** apex of branch leaf. **20:** branch leaf. **21:** stem leaf. **22:** areolation from middle part of stem leaf. **23:** alar part of a leaf. **24:** base of a leaf showing the nerves. **25:** perichaetium. **26:** perichaetial leaf. **27:** urn. **28:** upper part of seta. **29:** peristome. (all figures from herbarium Chavoutier 8091, Ecole-en-Bauges, Savoie, France).

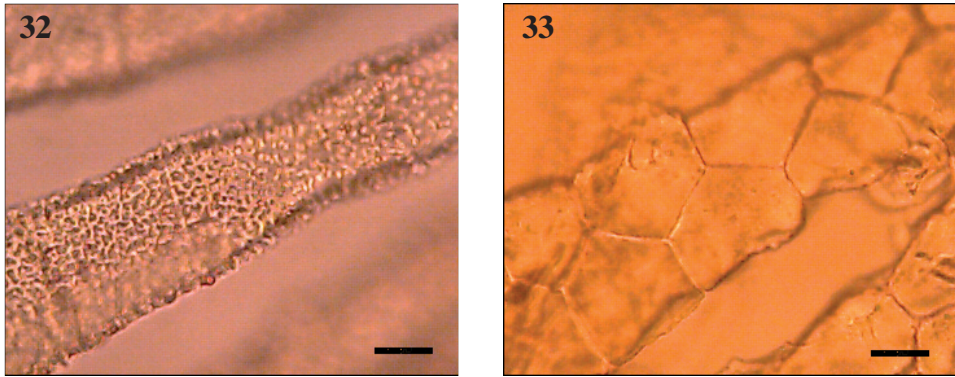




Figs 30-31. **30.** Apex of stolon of *Antitrichia californica* Sull. (from herbarium JC 11160, Berrias et Casteljalou, Ardèche, France) (scale bar: 0.78 mm). **31.** Apex of stolon of *Antitrichia curtispindula* (Timm ex Hedw.) Brid. (from herbarium JC 9154, Arvillard, Savoie, France) (scale bar : 0.77 mm).

A survey of literature (Renauld, 1876; Boulay, 1884; Husnot, 1892-94; Camus, 1903; Corbière & Jahandiez, 1921; Berner, 1948; Augier, 1966; Hébrard, 1973, 1986; Amigo, 2002; Hébrard, 2003; Aicardi, 2005; Thouvenot *in* Aicardi, 2006) and of the cryptogamic herbarium of PC shows that, in France, *Antitrichia californica* occurs in the departments of Alpes-de-Haute-Provence, Corsica, Loire, Pyrénées Orientales, Var and Vaucluse. Several new localities from Ardèche and Gard have been discovered in the course of the present work. All the aforementioned localities have been used to draw the French map on a UTM grid (Fig. 34).

In France *Antitrichia californica* is genuinely a rare moss restricted to a few localities in a small south-eastern portion of the country. This species is



Figs 32-33. **32.** Middle zone of OPL of *Antitrichia californica* Sull. (from PC0080144). **33.** Middle zone of OPL of *Antitrichia curtispindula* (Timm ex Hedw.) Brid. (from Chavoutier 8091, Ecole-en-Bauges, Savoie, France) (scale bars : 10  $\mu$ m).

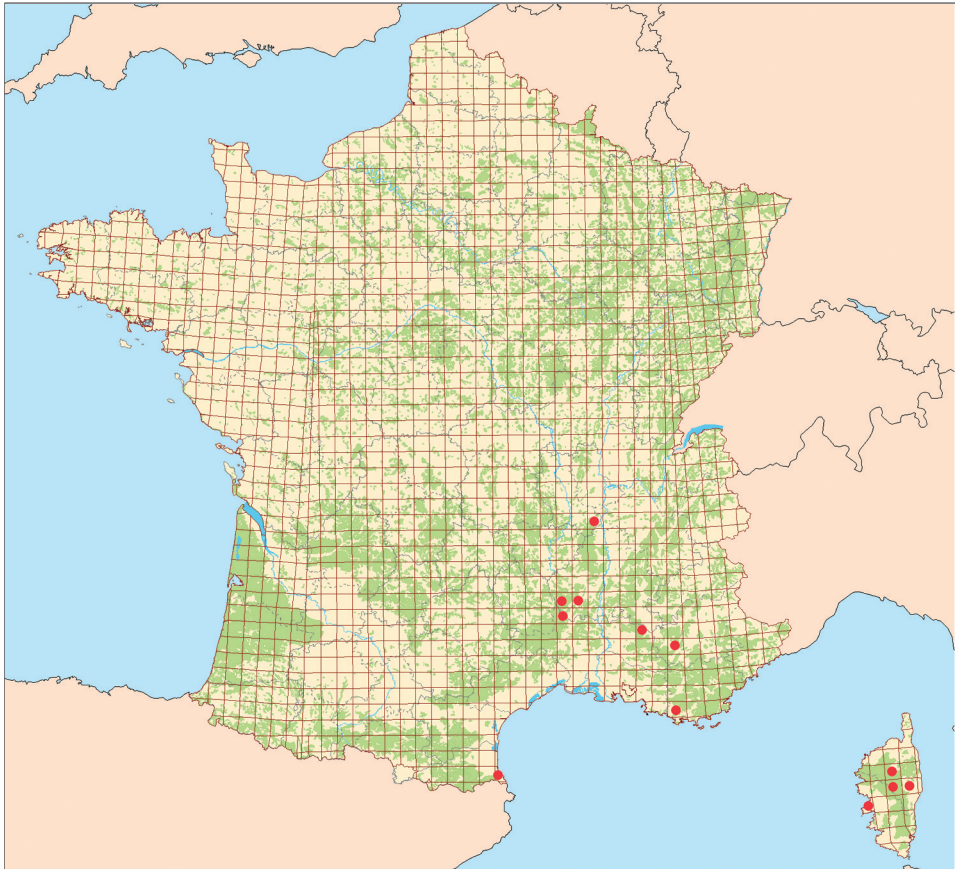


Fig. 34. Distribution of *Antitrichia californica* Sull. in France.



confined to sites exhibiting a Mediterranean climate. The northernmost national records (Loire) come from a Mediterranean enclave lying in the Rhône valley (Malleval site). The most important populations could be those of Corsica and Ardèche (notably that of the Païolive site).

*Antitrichia californica* appears a rare species in many parts of its known range and is considered as vulnerable or endangered in several countries. In our opinion, it should be added to the awaited Red Data List of French bryophytes (Deperiers-Robbe, 2000), with the IUCN category Rare.

## HABITAT AND COMMUNITIES

### Habitat of *Antitrichia californica*

*Antitrichia californica* is mostly epilithic, more rarely epiphytic. When behaving as an epiphyte, this species thrives on trunks at the base or middle parts of broad-leaved phorophytes (mostly *Quercus humilis*). Consequent populations have been observed on the facing-up part of horizontal branches. It occasionally thrives in exposed sites, as, for example, bare granitic outcrops or calcareous pavements (of Ordovician, Jurassic or Berriassian age), but mostly grows in wooded sites (oak, pine or beech woods).

As far as altitudinal affinities are concerned, it appears that the species shows wide amplitude, from localities under 200 m up to 670 m a.s.l.

In the Païolive site (Ardèche), 78 distinct populations were localized (total surface of the site: 12769 ha), of which 81% were found growing at the summit of karstic "clints". These clints mostly emerge from the shrub layer and are typically sub-horizontal. An individual colony may achieve complete dominance and extend beyond the margin of the clints, where it generally suffers the destruction of peripheral stems. The oak trees growing in the immediate vicinity may also be colonized. The surface of the colonies was investigated in Païolive: they range from 225 cm<sup>2</sup> to 113000 cm<sup>2</sup> and 50% of the colonies are above 13000 cm<sup>2</sup>. In the same site 80% of the forest stands with *A. californica* were rather open woods (total cover between 25% and 50%) or semi-open ones (total cover between 50% and 75%), with a marked bias in favour of the latter (75%). Additionally, the stands of *A. californica* were almost always (90% of the colonies) situated in the immediate vicinity of a "light source" originating from a rupture in the canopy of the tree layer.

In France, *Antitrichia californica* seems to be mostly a mesomediterranean to supramediterranean taxon. From a worldwide perspective, it is basically a Mediterranean-mountainous taxon, occurring mainly from the mesomediterranean to the supramediterranean thermotypes and more exceptionally to the oromediterranean one (Guerra, 1982; Varo, Zafra & Mateo, 1988; Varo & Zafra, 1990; Gil., 1997; García-Zamora *et al.*, 2000). The species shows a wide altitudinal amplitude, being present in localities near the sea (under 100 m a.s.l.) up to more than 2000 m in the south of the Mediterranean region.

*Antitrichia californica* favours protected environments with a rather high atmospheric humidity, due to the prevalence of fog, to the presence of a (temporary) stream running in the vicinity or to the occurrence of a

protecting canopy as exemplified by the site of Païolive. The species' link with humid air mass is largely confirmed by the literature (Gil, 1997; Jimenez *et al.*, 2002). It has even been reported from "wet rocks" (Erdağ, 2002), a biotope never observed in France. It might be hypothesized that *A. californica* exhibits a tendency to grow in exposed sites in the northernmost part of its Mediterranean range, whereas it occurs in shaded habitats in drier regions.

In France, *A. californica* is able to grow over a wide variety of geological substrata. The species thus seems to be largely indifferent as regards the nature of the subtending rocks (Walther & Leblebici, 1969; Varo, Zafra & Mateo, 1988; Varo & Zafra, 1990; García-Zamora *et al.*, 2000). It appears in fact equally capable of growing on basic rocks of wholly calcareous nature or on dolomite, or on acid rocks: schists and micaschists, granite or even quartzites, slates and basaltic rocks. We are not able to confirm the occurrences of the species on soil (Hébrard, 1973).

The occurrence of *A. californica* exclusively on *Quercus humilis* in France should not be generalized. In fact, a survey of the literature in other parts of its range yielded a remarkably wide variety of phorophytes (Table 2). Rugosity, pH, water-holding capacity of the bark do not seem to preclude the settling of the species, as the phorophytes appear most varied from these characteristics. In our opinion, *A. californica* is rather non bark-specific, but appears to be more sensitive to local ecological characteristics.

## **Bryophyte communities with *Antitrichia californica***

### **Saxicolous communities**

*Antitrichia californica* was observed on calcareous pavements in southern Ardèche (Païolive, Table 3), where it occurred as extended mats over bare calcareous pavements, or preferably over a thin layer of humus. As seen above, the community is more or less protected from direct sunlight by the oakwood trees growing in the cracks of the karstic system. *Antitrichia californica* was constantly the dominant or co-dominant species. The pioneer species of the *Grimmion tergestinae* are relictual from communities formerly established in the area, and colonize bare rocks. The erosive power of violent storms or the activity of fauna might also account for a certain opening of the dense mats that favours the occurrence of pioneer species. The accumulation of a humus layer into small cracks accounts for the occurrence of *Tortella tortuosa* (Hedw.) Limpr., a typical species of *Ctenidieta mollusci* v. Hübschmann *ex* Grgic 1980, and of *Homalothecium lutescens* (Hedw.) H. Rob. Several relevés (for example 6, 7, 8, 4) belong to *Antitrichietum breidlerianae*. Relevé 6 corresponds to *Leptodontetum smithii*, whereas relevés 1, 2, 3, 5, 9, 10 are more difficult to place satisfactorily.

*Antitrichia californica* has also been observed on siliceous outcrops in Loire (Malleval) and in Var (L'aigle, Table 4). The substrata are granite-like leptynites in Loire and basalt in Var. Siliceous rocks are exposed to direct sunlight in Loire but not so in Var, since the open *Quercus* wood provides some shade there. Several relevés (4, 6, 7 from Table 4) are part of the *Grimmion commutatae*. They could be incorporated into the *Hedwigio ciliatae-Antitrichietum californicae* as can be deduced from the comparison of our data to those of Varo & Zafra (1990).

Table 2. Species or genera supporting colonies of *Antitrichia californica* Sull. and reference.

<i>Phorophyte</i>	<i>Reference</i>
<i>Abies cephalonica</i> Loudon	Knapp, 1965
<i>Abies pinsapo</i> Boiss.	Allorge & Allorge, 1946 Guerra, 1982
<i>Acer macrophyllum</i> Pursh	v. Hübschmann, 1978
<i>Alnus orientalis</i> Decne	Kürschner, 1999
<i>Alnus rubra</i> Bong.	v. Hübschmann, 1978
<i>Castanea sativa</i> Miller	Allorge, 1934 Allorge & Allorge, 1946
<i>Crataegus monogyna</i> Jacq.	Allorge & Allorge, 1946 Varo <i>et al.</i> , 1977
<i>Fagus sylvatica</i> L.	Allorge, 1934
<i>Juglans regia</i> L.	Gil, 1997
<i>Liquidambar orientalis</i> Mill.	Kürschner, 1999
<i>Olea europea</i> L.	Gil, 1997
<i>Pinus nigra</i> subsp. <i>laricio</i> Maire	Allorge & Allorge, 1946
<i>Pinus pinaster</i> Aiton	Gil, 1997
<i>Platanus orientalis</i> L.	Walther & Leblebici, 1969 Kürschner, 1999
<i>Populus tremuloides</i> Michaux	v. Hübschmann, 1978
<i>Populus trichocarpa</i> Torrey & A.Gray <i>ex</i> Hooker	v. Hübschmann, 1978
<i>Quercus boissieri</i> Reut.	Frey & Kürschner, 1995
<i>Quercus calliprinos</i> Webb.	Frey & Kürschner, 1995
<i>Quercus humilis</i> Miller	Present work
<i>Quercus ilex</i> L.	Allorge & Allorge, 1946 Jelenc, 1953
<i>Quercus rotundifolia</i> Lam.	Guerra, 1982 Gil, 1997 Guerra <i>et al.</i> , 2002
<i>Quercus suber</i> L.	Guerra 1982
<i>Salix alba</i> L.	Walther & Leblebici, 1969 Kürschner, 1999
<i>Salix amygdalina</i> L. <i>emend.</i> Fries	Walther & Leblebici, 1969 Kürschner, 1999
<i>Sambucus</i> sp.	v. Hübschmann, 1978

### Corticolous communities

Only 4 relevés could be made on corticolous communities, owing to the rarity of that station in south-eastern France (Table 5). It was only possible to see *Antitrichia californica* on bark in Ardèche (Païolive) and in Var (L'Aigle). From a bryosociological point of view, the low number of observations prevents an

Table 3. Relevés with *Antitrichia californica* Sull. on calcareous rocks.

Locality	Païolive	Païolive	Païolive	Païolive	Païolive	Païolive	Païolive	Païolive	Païolive	Païolive
N°	1	2	3	4	5	6	7	8	9	10
Geology	Calcareous	Calcareous	Calcareous	Calcareous	Calcareous	Calcareous	Calcareous	Calcareous	Calcareous	Calcareous
Slope (°)	70	70	20	5	0	50	45	50	0	10
Direction of exposure	NW	E	NW	SE	–	SW	SW	SW	–	NW
Surface (cm <sup>2</sup> )	1500	3000	4000	1600	3600	1500	10000	1400	6000	1600
Total cover (%)	90	90	90	60	50	90	70	90	95	95
Number of taxa	6	7	8	4	5	4	3	4	3	1
<i>Antitrichia californica</i>	5.5	3.5	4.5	3.5	3.4	3.4	3.5	4.5	5.5	5.5
<b>Characteristic species of <i>Neckeretalia complanatae</i> and <i>Neckerion complanatae</i></b>										
<i>Porella platyphylla</i>	1.3	1.3		+	2.4					
<i>Anomodon viticulosus</i>				+3						
<b>Characteristic species of <i>Grimmion tergestinae</i></b>										
<i>Schistidium elegantulum</i>	+	+	+4			+	+2			
<i>Grimmia dissimulata</i>	+	+						+		
<i>Orthotrichum anomalum</i>		+								
<b>Companions</b>										
<i>Homalothecium lutescens</i>	2.3	3.5	+2	2.2	3.4	3.4	3.5	3.5	2.4	
<i>Hypnum cupressiforme</i> var. c.	+3	3.5	+3	3.5						
<i>Syntrichia montana</i>								1.2		
<i>Leptodon smithii</i>						3.4				
<i>Leucodon sciuroides</i>			1.3		2.4					
<i>Syntrichia ruralis</i>					1.2				1.1	
<i>Tortella tortuosa</i>			+3							
<i>Pleurochaete squarrosa</i>			+2							

unambiguous interpretation. Relevé 2 comprises the two characteristics of the *Orthotricho franzoniani-Antitrichietum breidleriana*, namely *Antitrichia californica* and *Orthotrichum rupestre* Schleich. ex Schwägr. Nevertheless, the attribution of this relevé to this association should be based on many more relevés. However, some of the relevés provided by Kürschner (1999) and attributed to the same association are notably close to relevé 2. The relevé 3 was made on the facing-down side of a vertical branch, in a position much protected from direct rainfall (ombrophobous). This relevé is attributable to the *Fabronietum pusillae* Ochs. 1936.

Table 4. Relevés with *Antitrichia californica* Sull. on siliceous rocks.

Locality	Malleval	Malleval	Malleval	Malleval	L'Aigle	L'Aigle	L'Aigle	L'Aigle
N°	1	2	3	4	5	6	7	8
Geology	Leptynites	Leptynites	Leptynites	Leptynites	Basalt	Basalt	Basalt	Basalt
Slope (°)	80	85	85	85	20	70	80	50
Direction of exposure	SE	SE	SE	SE	NE	E	E	E
Surface (cm <sup>2</sup> )	1600	2000	900	2000	3600	2000	800	1600
Total cover (%)	65	60	90	60	85	90	70	90
Number of taxa	7	7	3	11	5	8	7	5
<i>Antitrichia californica</i>	2.3	3.5	4.5	3.4	4.5	4.5	3.5	5.5
<i>Hedwigia ciliata</i> var. <i>leucophaea</i>	3.4	2.5	4.5	3.5	1.2	3.3	3.4	
<b>Grimmion commutatae</b>								
<i>Grimmia lisae</i>	2.4	2.4	2.2	2.3	3.5	+3	+2	+
<i>Grimmia laevigata</i>						2.3	2.2	+
<i>Grimmia ovalis</i>				+3				
<i>Hedwigia stellata</i>				+3				
<b>Companions</b>								
<i>Homalothecium sericeum</i>		1.5			2.3	1.4	+3	
<i>Pleurochaete squarrosa</i>	1.4	+4		+3				
<i>Syntrichia montana</i>	1.4					+	+4	
<i>Orthotrichum rupestre</i>						2.2	2.2	+
<i>Pterogonium gracile</i>					2.3	1.4		1.3
<i>Hypnum cupressiforme</i> var. <i>c.</i>	1.3			+2				
<i>Bryum capillare</i>	1.3			+3				
<i>Orthotrichum anomalum</i>		+3						
<i>Dialytrichia mucronata</i>		1.4						
<i>Fabronia pusilla</i>				+3				
<i>Polytrichum piliferum</i>				+3				
<i>Syntrichia ruralis</i>				+3				

### Synthesis on the communities

In south-eastern France, *Antitrichia californica* thrives in groupings that stand very close or are attributable to *Orthotricho franzoniani-Antitrichietum breidlerianae*, *Hedwigio ciliatae-Antitrichietum californicae* (an association considered as synonym of *Antitrichietum breidlerianae* by Marstaller (2006)) and *Antitrichietum breidlerianae*. These 3 associations are equally the most prominent ones for *A. californica* in Eurasia.

Nevertheless, on a worldwide scale, a survey of the relevant literature provided numerous groupings with *A. californica* (8 corticolous associations and 7 saxicolous ones are mentioned in the literature, Table 6 and Annex 1). *Antitrichia californica* stands as a characteristic, frequent or accidental species in these groupings. The cover of *A. californica* varies from dominant to very scarce. The great majority of groupings occur on bark, but a non negligible number was recorded on siliceous or calcareous rocks, which is obviously the reverse in France. Note that the *Homalothecio sericei-Leptodontetum smithii* is a synonym of *Leptodontetum smithii* (Marstaller, 2006).



Table 5. Corticolous relevés with *Antitrichia californica* Sull.

Locality	Païolive	L'Aigle	Païolive	Païolive
N°	1	2	3	4
Phorophyte	<i>Quercus humilis</i>	<i>Quercus humilis</i>	<i>Quercus humilis</i>	<i>Quercus humilis</i>
Diameter of phorophyte	35	30	40	45
Slope (°)	85	80	0	0
Direction of exposure	E	E	–	–
Surface (cm <sup>2</sup> )	1200	600	450	600
Total cover (%)	85	70	95	95
Number of taxa	4	5	4	4
<i>Antitrichia californica</i>	3.5	3.5	1.3	4.5
<i>Fabronia pusilla</i>			5.5	+
<i>Leucodon sciuroides</i>	3.5		+	3.4
<i>Syntrichia laevipila</i>	3.3			
<i>Zygodon rupestris</i>			1.4	
<i>Hypnum cupressiforme</i> var. <i>c.</i>		2.4		2.4
<i>Leptodon smithii</i>		1.3		
<i>Orthotrichum rupestre</i>		1.2		
<i>Homalothecium sericeum</i>	+3			
<i>Hedwigia ciliata</i> var. <i>leucophaea</i>		+		

### Strategy

The canopy of the main stations of *Antitrichia californica* is marked by notable gaps that favour the entrance of light. At the Païolive site, the opening of the canopy can be the result of a dissected tree layer due to massive calcareous pavements, with rare “grickes”, hence without any significant quantity of earth, or to tree fall or snapped branches. The disturbance regime of natural or semi-natural forests (wind, storm...) may explain localized opening of the canopy. In a sense, *Antitrichia californica* may then be considered as a typical inhabitant of forests exhibiting a “natural” structure and where “natural” processes operate.

*Antitrichia californica* is a typical “perennial shuttle species” (in the sense of During, 1979), which characterizes long-standing and stable biotopes that predictably end after a long period, i.e. after the canopy has recovered a continuous cover. This species does not possess any specialized vegetative diaspore and rarely produces sporophytes. Hence, it is considered as “passive” perennial shuttle species in Frey & Kürschner (1995) and Kürschner (1999).

Morphological traits are clearly linked to the space occupancy strategy of the species, notably the architecture of the stem and the branches. In optimal cases, the branching pattern is made of a creeping stoloniform main shoot, provided with upright branches that are more or less branched. The upright branches may additionally bear flagella. All types of branches may become stoloniferous (and expand above ground). Flagella are rather rare structures in *Antitrichia californica*, in contrast to the situation observed in other

Table 6. Synthesis of the known syntaxa with *Antitrichia californica* Sull. from the literature.

Substrate	Syntaxon	Status of <i>Antitrichia californica</i>	Ecology	Origin of the relevés	References	Notes
	<i>Antitrichio-Homalothecietum fulgenscens</i> v. Hübschm. 1976	Characteristic	On the smooth bark of a wide variety of the median part of deciduous trees ( <i>Populus</i> , <i>Acer</i> , <i>Alnus</i> ) in open woods near streams	Vancouver Island (British Columbia)	Hübschmann (1978)	
	<i>Orthotricho-franzoniani-Antitrichietum breidlerianae</i> Walther 1969	Characteristic	Mesoxerophil and photosciaphil, base and middle trunks of <i>Crataegus</i> , <i>Pinus</i> , <i>Quercus</i> , <i>Salix</i> and <i>Platanus</i> , sometimes in humid and shadier sites in alluvial forests; sites subject to periodic fogs and rather extended periods of drought.	Andalucía, Jaen, Malaga (Spain); Atlas (Morocco); Anatolia (Turkey)	Allorge (1934); Werner (1937); Jelenc (1953); Walther & Leblebici (1969); Varo <i>et al.</i> (1977); Walther (1979); Guerra (1982); Gil (1997); Kürschner (1999)	Marstaller (1985)
	<i>Pterogonium-Neckera cephalonica</i> Gesellschaft in Knapp (1965)	Characteristic	On <i>Abies cephalonica</i> bark	Cephalonia (Greece)	Knapp (1965)	
Bark	<i>Brachythecio olympici-Dicranoweisietum cirratae</i> Walther 1969	Accidental	Bark of <i>Pinus</i> species in open <i>Pinus</i> woodlands; support strong periododic dessication; fissured and profound barks exposed to direct humid air masses	Anatolia (Turkey)	Walther & Leblebici (1969); Walther (1979); Kürschner (1999)	Marstaller (1985)
	<i>Leptodoniolum smithii</i> Jaeggli 1933 nomen nudum	Accidental	"Oceanic" situations with a good illumination but not direct sunlight; bark of <i>Quercus calliprinos</i>	Golan Heights (Israel)	Frey & Kürschner (1995)	Marstaller (1985)
	<i>Neckeretum menziesii</i> v. Hübschm. 1976	Accidental	On the bark of <i>Populus</i> in dense and old woods	Vancouver Island (British Columbia)	Hübschmann (1978)	
	<i>Orthotrichetum striati</i> Gams 1927	Accidental	Twigs of <i>Sambucus</i> (Vancouver); open mountain <i>Quercus</i> woodlands, on the bark of <i>Quercus boissieri</i> (Golan)	Vancouver Island (British Columbia); Golan Heights (Jordan)	Hübschmann (1978); Frey & Kürschner (1995)	
	<i>Pterigynandro filiformis-Orthotrichetum speciosi</i> Guerra 1982	Accidental	Sciophilous, meso-xerophilous, feably acidophilous of the <i>Abies pinsapo</i> bark at high altitudes (1500 m and more)	South of Spain	Guerra (1982)	

Table 6. Synthesis of the known syntaxa with *Antitrichia californica* Sull. from the literature. (suite)

Substrate	Syntaxon	Status of <i>Antitrichia californica</i>	Ecology	Origin of the relevés	References	Notes
Siliceous rock	<i>Syntrichietum pulvinatae</i> Pec. 1965	Accidental	Meso-xerophilous grouping, at the base of <i>Quercus calliprinos</i>	Galilea and Golan Heights (Israel)	Frey & Kürschner, 1995	
	<i>Cryphaetum arboreae</i> Barkm. 1958	Accidental	On <i>Quercus rotundifolia</i> , meso-xerophilous and sciophilous association of deep ravines near streams	Andalucia (Spain)	Gil (1997)	
	<i>Hedwigia ciliatae-Antitrichietum californicae</i> Varo & Zafra 1990	Characteristic	Acid rocks (notably granites, quartzites...), typical of protected sites with a mesophil ambient	Spain	Varo & Zafra (1990)	
	<i>Hedwigia ciliatae-Orthotrichetum rupestris</i> Varo, Zafra & Mateo 1988	Frequent	Acidophilous, mesoxerophilous and photosciophilous association	Anatolia (Turkey); Rif (Morocco); Spain	Walther & Leblebici (1969); Varo <i>et al.</i> (1988); Varo & Zafra (1990); García Zamora <i>et al.</i> , 2000; Jimenez <i>et al.</i> (2002)	
	<i>Grimmietum decipiensis</i> Varo, Zafra & Mateo 1988	Accidental	Acidophilous, mesophilous and photophilous association; siliceous rocks of median continentality	Spain	Varo <i>et al.</i> (1988)	
	<i>Antitrichietum breidlerianae</i> Walther 1969	Characteristic	Calcareous rocks in sciophilous conditions	Anatolia (Turkey)	Walther & Leblebici (1969)	
	<i>Homalothecio sericeo-Leptodontietum smithii</i> Moya, Ros & Guerra 1994	Accidental	Calcareous rocks at northern adspsect	Rif (Morocco)	Jimenez <i>et al.</i> (2002a)	
	<i>Homalothecio sericeo-Neckeradelphetum menziesii</i> (Varo, Guerra & Gil 1977) Guerra & Varo 1981	Accidental	Pioneer association is typically well developed on calcareous and dolomite substrate in very shaded and high humidity conditions	Rif (Morocco)	Jimenez <i>et al.</i> (2002a)	
	<i>Orthotricho anomali-Grimmietum pulvinatae</i> Stod. 1937	Accidental	Basophilous pioneer association; variant with <i>Antitrichia californica</i> more inclined, more humid and shadier	Rif (Morocco)	Jimenez <i>et al.</i> (2002a)	
	Calcareous rock					

*Leucodontaceae* such as the members of the genus *Leucodon*. Rhizoids are a prominent structure in *Antitrichia californica*. They arise as very robust bundles from the basal abaxial side of nerves over special areas facing the substratum. They are predominantly located in the stoloniform parts (and flagella) of the branching system and seem to act as “studs”. The clone’s extension is prominently radial because of elongation of primary axes. The stoloniferous axes tend to arch and “root” at their tips and then anchor there firmly. The mode of extension follows a two-step pattern: first a rapid growth of above ground stolons that arch, root and allow radial increment, second a slower growth made of the reiteration and development of secondary axes that allow the colony to get thicker. These combined attributes are very efficient in making the species able to form dense colonies of interwoven axes tightly adhering to the surface of the substratum (densely intricate *tails* or *wefis* in the sense of Mägdefrau, 1982) that may form thick layers that are mostly photosynthetically active from the periphery. These make *Antitrichia californica* a competitive species that can (as a clone) achieve dominance of many supports in rather shaded and humid sites of Mediterranean environments.

Casas *et al.* (1985) showed that most recent records are sterile, whereas ancient ones are mostly fertile. In France, we lately collected the plant with sporophytes, albeit rarely, and it is unclear whether this reduction is due to an artefact or to any genuine depletion in fertility. The known populations are isolated from each other and do not seem to produce sporophytes regularly. Due to the extreme abundance of potential sites not colonized by the species (notably in southern Ardèche, Vaucluse, Alpes-de-Haute-Provence, Var...) it might be hypothesized that the taxon is limited by rather low expansion possibilities, possibly linked to the rather high diameter of the spores (more or less 30 µm).

### CONCLUDING REMARKS

The structure of the forest stands favoured by *Antitrichia californica*, the strategy of the species, its rarity and its apparent inability to colonize efficiently new sites largely suggests that it could have, at least locally, a potential value as indicator of ancient woodlands. In fact, several authors postulated that it could be an indicator of old growth forests, ancient woodlands or sites that (presumably) never (or rarely) endured human disturbance. Allorge (1947) mentions *A. californica* on the bark of beeches in old relictual forests of the Mediterranean, and Kürschner (1999) highlights the sensitivity of that taxon towards rigid forest management and human impact. Like *Antitrichia curtispindula* (Hedw.) Brid., *A. californica* is furthermore considered to be a highly toxiphobous species. The value of *Antitrichia californica* as regards ancient woodlands must nevertheless not be overemphasized, since it is possible to find the species in rather disturbed biotopes, such as tiny remnants of maquis (= scrub) enclosed in vineyards in Pyrénées-Orientales (Louis Thouvenot pers. comm.), or small stands of young oakwoods in Ardèche.

Hence, these hypotheses should be tested using experimental devices, including the measure of colony growth rates and transplants. It remains to be proved whether *A. californica* is restricted by ecological factors or by settling. Relative importance of sexual vs. asexual reproduction should equally be determined, together with the pattern of sexuality in the colonies.

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**ANNEX 1**

French specimens kept at PC and examined in the course of the present work. The writings on the herbarium labels have been transcribed in full. UTM coordinates are written in **bold face**. **Not localised** means that the UTM could not be determined.

PC0080131 ; Société d'Echanges de Muscinées ; Année 1951 N° 578 ; Corse – Corté ; gorges du Tavignano, granits secs ombragés ; Juin 1951 ; *P. Doignon* ; N° 18436 ; Herbarier Charrier ; **UTM 31NM08**

PC0080136 ; France, Corse, pentes de la Punta di Pozzo di Borgo, près d'Ajaccio ; Alt. : 200-300 m ; Troncs d'arbres ; 22/5/1901 ; *Camus F.* ; Det. : Camus F. ; **Not localised**

PC0080132 ; Corse Vallée du Fium'Orbo ; Défilé de l'Inzecca ; Rochers de serpentine ; 350 m ; 31 mars 1959 ; Herbarier *E. Bonnot* ; Herbarier *Charrier* ; N°23069 ; **UTM 32NM26**

PC0080141 ; Rochers calc. A Niozelles, Basses-Alpes ; Leg. *Renauld*, 1875 ; Hb. *F. Renauld* ; **UTM 31GJ26**

PC0011323 ; Société d'Echanges de Muscinées ; Année 1956 N° 1.355 ; **UTM 31GJ26**

PC0080142 ; Niozelles Basses Alpes ; Herbarier de *F. Renauld* acquis en 1909 ; **UTM 31GJ26**

PC0080143 ; France, Basses-Alpes, Niozelles près Forcalquier ; Blocs calcaires sous les pins ; 12/1874 ; *Renauld F.* ; Det : *Renauld F.* ; **UTM 31GJ26**

PC0080140 ; Herbarier *M. Bizot* ; Hb. *Bonnot* ; N° 15 ; Leg. *Castelli* ; 9040 ; Malleval (Loire), sur rochers de gneiss, 8 fév. 1953 ; **UTM 31FL32**

PC0080139 ; Herbarier *L. Castelli* ; Mâle ; Herbarier *M. Bizot* ; N° 15 ; Leg. *Castelli* ; 9622 ; Malleval (Loire), sur rochers de gneiss, 31 mai 1953 ; **UTM 31FL32**

PC0011323 ; Loire – Massif du Pilat ; Malleval ; rochers granitiques, exposition sud ; Altitude 200 m ; 2 décembre 1956 ; *L. Castelli* ; Herbarier *M. Bizot* 10425 ; **UTM 31FL32**

## ANNEX 2

### Syntaxonomic scheme of associations with *Antitrichia californica* Sull.

? indicates that we have not been able to place the association satisfactorily; the associations with \* are those in which *Antitrichia californica* plays a prominent role.

#### ***Frullanio dilatatae-Leucodontetea sciuroidis* Mohan 1978**

*Orthotrichetalia* Had. in Kl. & Had. 1944

*Ulotion crispae* Barkm. 1958

*Orthotrichetum striati* Gams 1927

*Syntrichion laevipilae* Ochn. 1928

*Syntrichietum pulvinatae* Pec. 1965

*Fabronion pusillae* (Barkm. 1958) Gil & Guerra 1981

*Cryphaetum arboreae* Barkm. 1958

*Pterigynandro filiformis-Orthotrichetum speciosi* Guerra 1982

*Orthotricho franzoniani-Antitrichietum breidlerianae* Walther 1969\*

*Brachythecio olympici-Dicranoweisietum cirratae* Walther 1969

*Fabronietum pusillae* Ochn. 1936

? *Antitrichio-Homalothebietum fulgescentis* v. Hübschm. 1976\*

? *Neckeretum menziesii* v. Hübschm. 1976

#### ***Grimmietea alpestris* Had. & Vondr. in Jež. & Vondr. 1962**

*Grimmietalia alpestris* Šm. 1944

***Grimmion commutatae* v. Krus. 1945**

*Grimmietum decipientis* Varo, Zafra & Mateo 1988

*Hedwigia ciliatae-Orthotrichetum rupestris* Varo, Zafra & Mateo 1988

#### ***Grtimmietea anodontis* Had. & Vondr. in Jež. & Vondr. 1962**

*Grimmietalia anodontis* Šm. & Van. ex Kl. 1948

***Grimmion tergestinae* Šm. ex Kl. 1948**

*Orthotricho anomali-Grimmietum pulvinatae* Stod. 1937

#### ***Neckeretea complanatae* Marst. 1986**

*Neckeretalia complanatae* Jež. & Vondr. 1962

***Plasteurhynchion meridionalis* Guerra & Varo 1981**

*Leptodontetum smithii* Watez ex Marst. 1992

*Homalotheccio sericei-Neckeradelphetum menziesii* (Varo, Guerra & Gil 1977) Guerra & Varo 1981

*Antitrichietum breidlerianae* Walther 1969\*