

LEMBOPHYLLACEAE (MUSCI) IN THE TROPICS

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RESUMEN

En el curso de su historia se han incluido un total de 20 géneros en las Lembophyllaceae que la hacen una familia de amplia distribución en América tropical y templada, SE Asia, Melanesia y Australasia. Sin embargo, los cambios recientes han reducido sus géneros a cinco: *Lembophyllum*, *Camptochaete* y sus segregados *Fifea* y *Fallaciella*, así como *Weymouthia*. Con su nueva definición las Lembophyllaceae son principalmente de distribución melanesiana-australasiática, con localidades en Indonesia, sur de Sudamérica y Hawái. Sus relaciones, como se entienden ahora, son Hypnaceae/ Brachytheciaceae y no con las Thamnobryaceae/Neckeraceae como se pensaba. En los trópicos, la familia está representada principalmente por *Camptochaete*, un género con 10 especies en dos secciones. En Indonesia, Melanesia y Australia tropical se conocen seis especies; en Australia subtropical existe una especie de *Lembophyllum*. La revisión reciente ha incrementado nuestro conocimiento de las Lembophyllaceae tropicales y las colecciones recientes han ampliado el área de distribución de *Camptochaete* en los trópicos.

Palabras clave: Lembophyllaceae, musgos, trópicos.

ABSTRACT

A total of 20 genera have been included in the Lembophyllaceae during its history, yielding a diverse and widespread family distributed in temperate and tropical America, South East Asia, Melanesia and Australasia. However, recent changes have reduced the genera to five: *Lembophyllum*, *Camptochaete*, and its segregates *Fifea* and *Fallaciella*, as well as *Weymouthia*. The re-defined Lembophyllaceae are mainly Melanesian-Australasian in distribution, with occurrences in Indonesia, southern South America, and Hawaii. The relationships of the family are now understood to be Hypnacean-Brachytheciacean rather than Thamnobryacean/Neckeracean as previously thought. The family is represented in the tropics chiefly by *Camptochaete*, a genus of 10 species in two sec-

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tions. Six species occur in Indonesia, Melanesia and tropical Australia. One species of *Lembophyllum* occurs in sub-tropical Australia. Recent taxonomic revision has increased our knowledge of tropical Lembophyllaceae and recent collecting has considerably extended the range of *Camptochaete* in the tropics.

Key words: Lembophyllaceae, mosses, tropics.

INTRODUCTION

From its description by Brotherus (1901-09), the family Lembophyllaceae has had a variety of generic inclusions. Fleischer (1922) and Brotherus (1924-25) laid the foundations of what came to be viewed as a "mixed bag" of genera. Andrews (1952) considered that the family was too diverse and this sentiment has been latterly echoed by a variety of authors who have recommended alternative placings for many of the genera included by Brotherus (1924-25). I have recently revised the genera included in the Lembophyllaceae, based on a species-level revision of *Camptochaete* (Tangney, 1994). This paper summarises the results of that research and outlines how changes in perception of the Lembophyllaceae affect the tropical affinities of the family, and outlines knowledge of tropical Lembophyllaceae. A summary of the history of the family is presented below.

HISTORY

Brotherus (1901-09) placed *Camptochaete*, *Lembophyllum*, *Dolichomitra*, *Tripterocladium* and *Isothecium* in the Lembophyllaceae. Subsequently, Fleischer (1922) added *Porotrichodendron*, *Porotrichopsis*, *Acrocladium* (transferred from the Amblystegiaceae) and *Rigodium* (transferred from the Brachytheciaceae), and Brotherus (1924-25) added *Elmeriobryum*, *Plasteurhynchium* and *Dolichomitriopsis*, and *Isotheciopsis* (Brotherus, 1929). Horikawa and Ando (1964) added the genus *Dixonia*.

Walther (1983) treated the family in a similar way to Brotherus (1924-25); *Porotrichodendron*, *Porotrichopsis*, *Rigodium*, *Camptochaete*, *Lembophyllum*, *Isotheciopsis*, *Dixonia*, *Dolichomitriopsis* and *Dolichomitra*, with three genera treated elsewhere, *Acrocladium* (Amblystegiaceae), *Tripterocladium* (*Hypnaceae*) and *Isothecium* (Brachytheciaceae).

In contrast, Buck (1980) restricted the family to only three genera: *Lembophyllum*, *Camptochaete* and possibly *Dixonia*, and suggested alternative familial placings for the others. Vitt (1984) also employed this restricted concept of the Lembophyllaceae. Crum (1991) included only *Fifea* (a segregate of *Camptochaete*) and *Lembophyllum* in the family. Buck (1994) has recently also included *Weymouthia*, *Pilotrichella*, *Pseudopilotrichum*, and *Squamidium* in the *Lembophyllaceae*.

With the recent changes to the generic contents of the family, there has also been a revision of the systematic position of the Lembophyllaceae. From a con-

cept which included strong affinities with tropical groups, a new concept has emerged that eschews strong tropical relations.

The Lembophyllaceae were placed by Brotherus (1901-09, 1924-25) and Fleischer (1922), in a broadly defined Neckeraceae (Isobryales), associated with the (Thamnioid) Neckeraceae, and close to the Echinodiaceae.

Many subsequent authors (*e.g.*, Dixon, 1932; Andrews, 1952; Robinson, 1971; Walther, 1983) maintained this traditional alignment of Lembophyllaceae, with both the Thamnioideae of the Neckeraceae and the Echinodiaceae in the Isobryales, with only minor changes.

Recent authors, over the last 15 years, however, have positioned the Lembophyllaceae amongst the Hypnobryalean families, *e.g.*, Crosby (1980), Buck (1980), Buck and Vitt (1986). The latter authors associated the family with the Amblystegiaceae (as sister group) in the Hypnales suborder Hypninae and the Thamnobryaceae were included in the Hypnales but in the suborder Hypnodendrineae.

A Hypnobryalean affinity for the Lembophyllaceae, Thamnobryaceae and the Echinodiaceae reflects a justifiable determination by these recent authors to give priority to peristome structure at higher levels in moss classification. The hypnoid peristomes of these three families preclude their placement in the Isobryales.

GENERIC LIMITS AND AFFINITIES OF THE LEMBOPHYLLACEAE

The results of a recent revision of the Lembophyllaceae support the proposal of a more narrowly defined family. Genera previously included in the Lembophyllaceae have been excluded on both sporophytic (*Isotheciopsis*, *Dolichomitra* and *Dolichomitriopsis*) and gametophytic grounds (*Acrocladium*, *Tripterocladium*, *Elmerobryum*, *Isothecium*, *Plasteurhynchium*, *Porotrichodendron*, *Dixonia*, and *Porotrichopsis*). (The status of the three genera recently transferred to the Lembophyllaceae by Buck (1994), *Pilotrichella*, *Pseudopilotrichella*, *Squamidium*, is uncertain and their position will be reviewed).

The family, as here understood, now includes *Lembophyllum*, *Camptochaete*, *Fifea* and *Fallaciella* (both segregates of *Camptochaete*), and *Weymouthia*.

The Lembophyllaceae, as here recognised, share a range of sporophytic and gametophytic features. They all have the same hypnoid peristome (Figs. 3-6). That of *Weymouthia mollis* has a reduced endostome, but is otherwise the same. They are pleurocarpous, weft-forming or pendent, mostly epiphytic, with ovate-oblong, concave leaves, rhombic upper laminal cells, mostly linear midlaminal cells, differentiated basal and alar cells and usually short, double costae.

The Lembophyllaceae are well placed within the suborder Hypninae and have been placed in the superfamily Brachytheciaceae within the suborder Hypninae, as a sister group to the Amblystegiaceae (Buck and Vitt, 1986). However, the Lembophyllaceae could be placed in the Hypnacaceae on the basis of its reduced costa and ovate leaves (a synapomorphy of Buck and Vitt's Hypnacaceae). The systematic position of the family is therefore not settled.

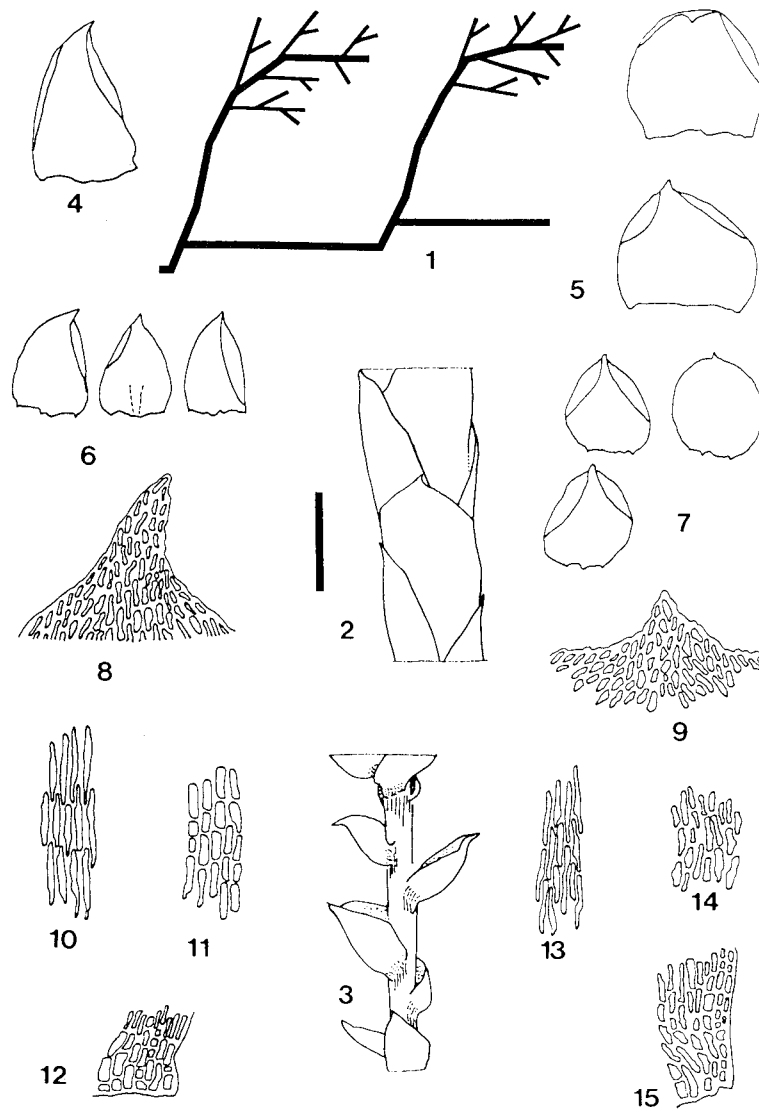


Fig. 1. Gametophytic features of *Camptochaete*. 1. Growth form. 2. Stipe leaves sect. *Camptochaete*. 3. Stipe leaves sect. *Thamniella*. 4. Frond axis leaves, *C. porotrichoides*. 5. Frond axis leaves, *C. excavata*. 6. Branch leaves, *C. porotrichoides*. 7. Branch leaves, *C. excavata*. 8. Frond axis leaf apex, *C. porotrichoides*. 9. Frond axis leaf apex, *C. excavata*. 10-12. Frond axis leaf cells, *C. porotrichoides*. 10. Midlaminal. 11. Basal. 12. Alar. 13-15. Frond axis leaf cells, *C. excavata*. 13. Midlaminal. 14. Basal. 15. Alar. Scale Bar = 0.65 mm for 2,3; 1.0 mm for 4-7; 50 μ m for 8-15.

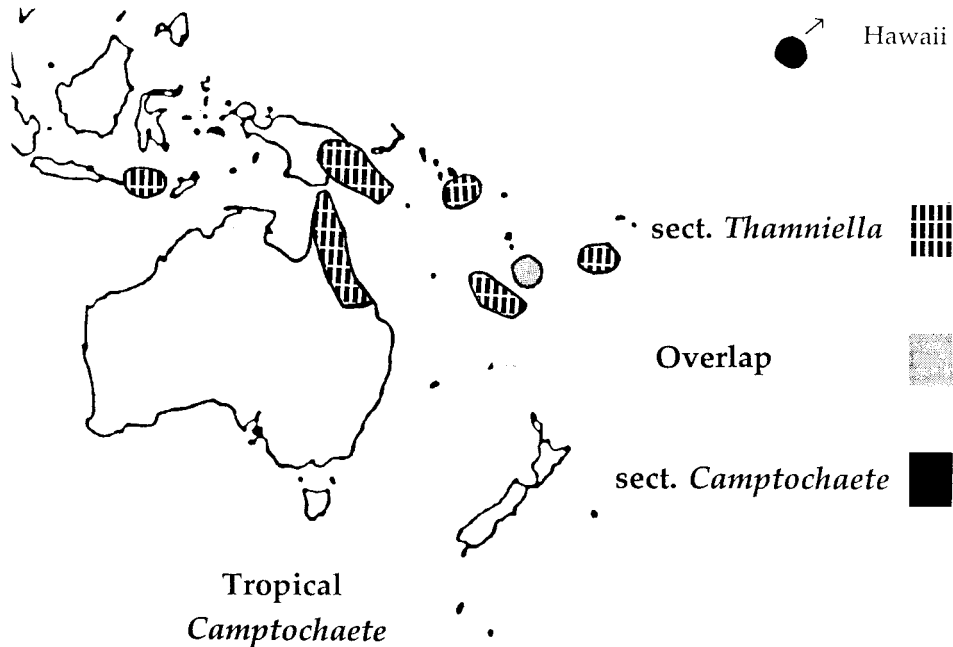


Fig. 2. Distribution of *Camptochaete* in tropical areas.

The Lembophyllaceae are distributed in southern South America (Chile and Argentina), New Zealand and its subantarctic islands, eastern Australia (Tasmania to Northern Queensland), Papua New Guinea, Indonesia (Flores), Solomon Islands, Vanuatu, Fiji, and Hawaii. Whereas the Lembophyllaceae had previously had strong tropical elements and affinities, these are now much less. The family is now most diverse in temperate areas especially in southern Australasia. For example, all five genera occur in New Zealand, four in eastern Australia and three in southern South America, compared to one in tropical areas.

LEMBOPHYLLACEAE IN THE TROPICS

The family is represented in the tropics only by *Camptochaete*, a genus of 10 species in two sections (Fig. 1). Six species occur in Indonesia, Melanesia, tropical Australia and Hawaii. Four species of Sect. *Thamniella* (*C. porotrichoides*, *C. subporotrichoides*, *C. excavata* and *C. n.sp.*), and two species of sect. *Camptochaete* (*C. leichhardtii* and *C. pulvinata*) occur in the tropics (Fig. 2).

Distribution of *Camptochaete* in the tropics

Sect. 1. *Camptochaete*

C. pulvinata. Hawaii (?). Also: New Zealand: North Island, South Island.

C. leichhardtii. Vanuatu (New Hebrides): Aneityum. Also: Eastern Australia; southern Queensland, New South Wales, Victoria.

Sect. 2. *Thammiella*

C. excavata. Papua New Guinea; Eastern Australia: northern Queensland. Also: southern Queensland, New South Wales, Victoria; Lord Howe Island.

C. porotrichoides. New Caledonia.

C. subporotrichoides. Papua New Guinea, Solomon Islands, Vanuatu, Fiji, and Indonesia (Flores).

Camptochaete n.sp. Papua New Guinea.

Problems in tropical taxa delimitation and distribution

There are taxonomic problems in *Camptochaete* associated with both within-species variation and a lack of knowledge of the genus in some areas. There is uncertainty over both the number of species and the full range of the genus.

Camptochaete exhibits within-species plasticity, and this variability is a function of plant architecture. The underlying dendroid-stipitate growth form is flexible, and plants often produce flagelliferous shoots which arch and root. Growth-form flexibility, and the resulting variability, combined with vigorous growth, give rise to elongate forms which provide taxonomic problems, as such material blurs species limits within *Camptochaete*.

Data gathered on the specific variation and variability gained from herbarium and field studies in New Zealand has allowed most of the problems in sect. *Camptochaete* to be solved. This experience was utilised in studying extra-New Zealand species, as none of the tropical species (except for *C. pulvinata* in New Zealand) have been studied in the field. As a result, some herbarium problems remain unresolved, especially for tropical taxa.

Taxa have been recognised on the basis of morphological discontinuity, but in some cases, the recognised species contain distinct forms which can occur as both separate collections and together on the same plant. This has led to the recognition of some very variable species (e.g., *C. excavata*), while others are morphologically discrete and sharply defined (*C. leichhardtii*).

In tropical Lemnophyllaceae, species plasticity is relevant in *C. subporotrichoides* where the species is both widespread and variable. There are difficulties in separating this species from *C. porotrichoides* which is both less variable and restricted to New Caledonia, where *C. subporotrichoides* does not occur. Differences between these species rest on such characters as leaf shape and arrangement, leaf orientation, and degree of imbrication, all of which are affected by architecture variation.

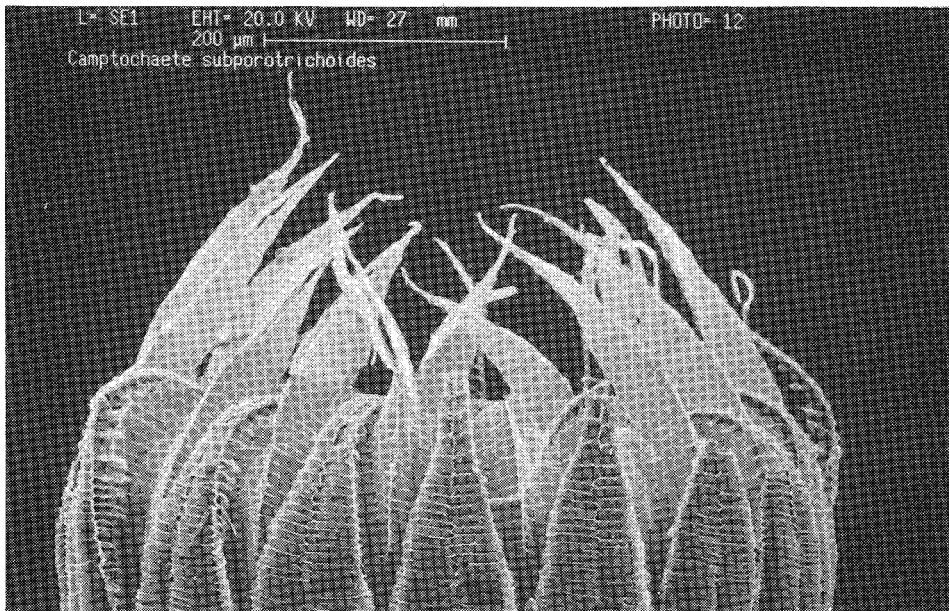
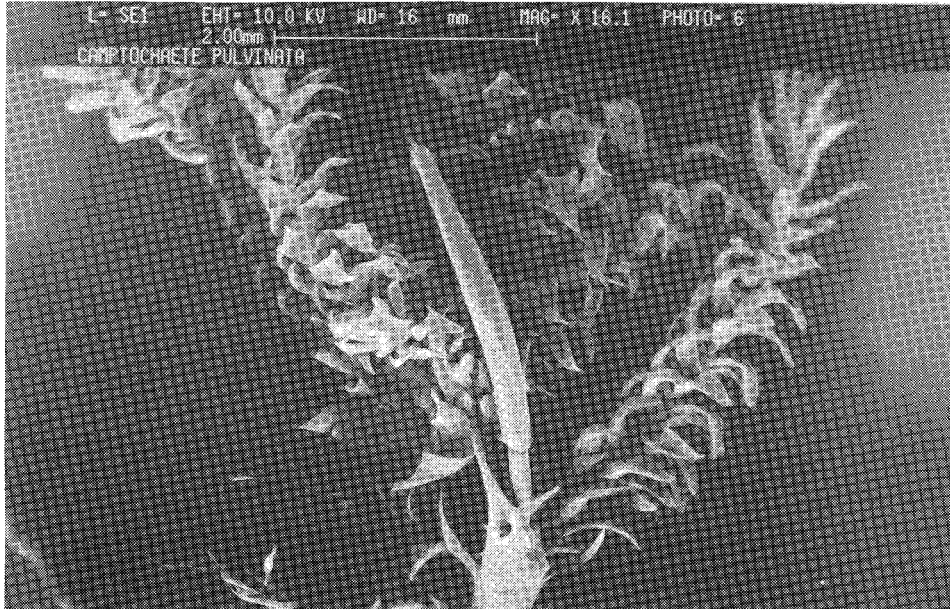
In the context of species variability, species known from only one or two specimens present difficulties, as insufficient collections may mask morphological continuity. For example, *C. pilotrichelloides* and *C. robusticaulis* are known from type specimens from New Caledonia. The status of these two *Brotherus* names is uncer-

Table 1. Generic changes in the Lembophyllaceae

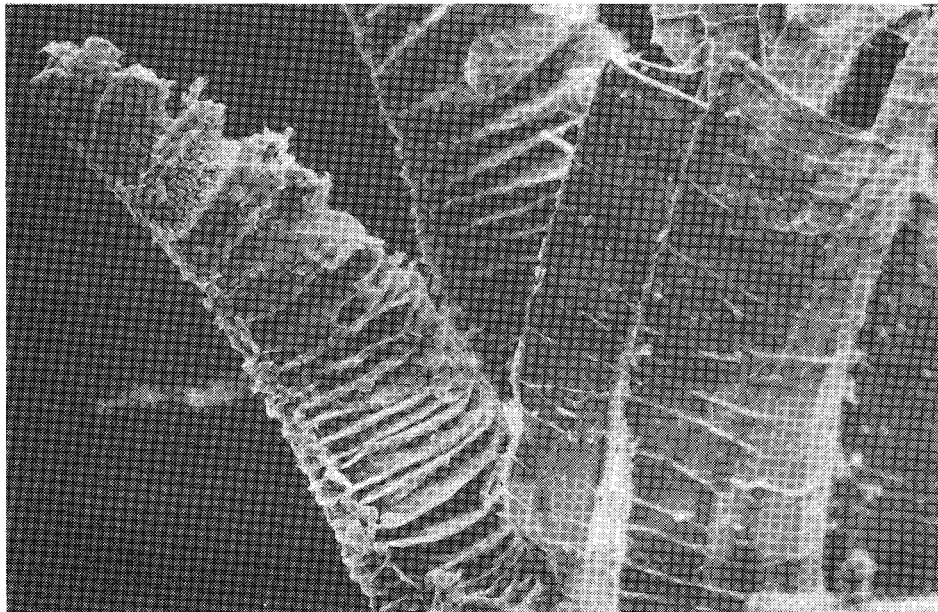
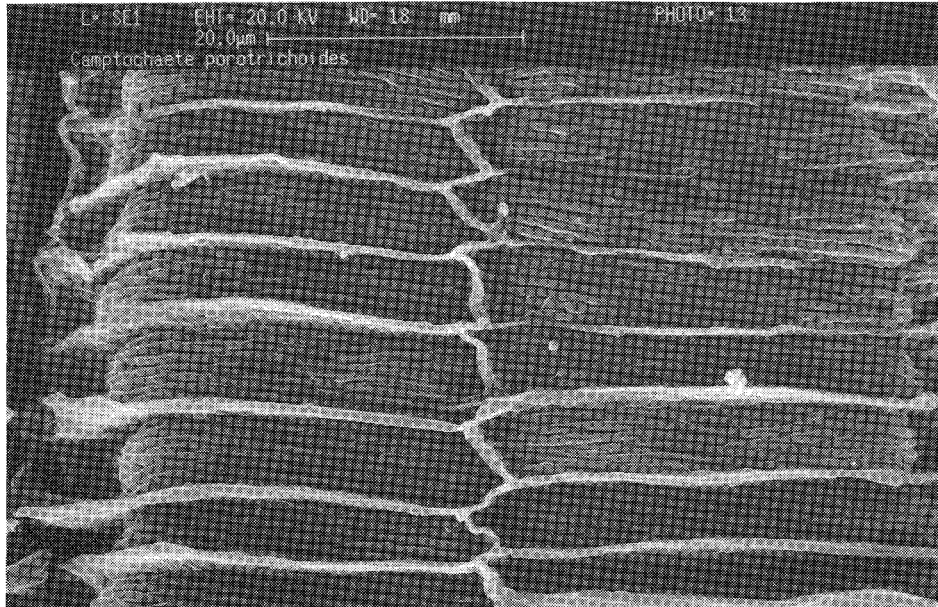
Brotherus (1901-09)	Buck (1980) Vitt (1984)	Walther (1983)	Crum (1991)	Tangney (1995)
<i>Lembophyllum</i>	<i>Lembophyllum</i>	<i>Lembophyllum</i>	<i>Lembophyllum</i>	<i>Lembophyllum</i>
<i>Camptochaete</i>	<i>Camptochaete</i>	<i>Camptochaete</i>	<i>Fifea</i>	<i>Camptochaete</i>
<i>Dolichomitra</i>	<i>Dixonia</i> (?)	<i>Dolichomitra</i>	Excluded	<i>Fifea</i>
<i>Tripterocladium</i>		<i>Porotrichodendron</i>	<i>Camptochaete</i>	<i>Fallaciella</i>
<i>Isothecium</i>	Excluded	<i>Porotrichopsis</i>	<i>Fallaciella</i>	<i>Weymouthia</i>
	<i>Dolichomitra</i>	<i>Rigodium</i>		Excluded
Fleischer (1922)	<i>Tripterocladium</i>	<i>Isotheciopsis</i>		<i>Dolichomitra</i>
<i>Porotrichodendron</i>	<i>Isothecium</i>	<i>Dolichomitriopsis</i>	<i>Dolichomitra</i>	<i>Dolichomitra</i>
<i>Porotrichopsis</i>	<i>Porotrichodendron</i>	<i>Dixonia</i>	<i>Tripterocladium</i>	<i>Tripterocladium</i>
<i>Acrocladium</i>	<i>Porotrichopsis</i>	Excluded	<i>Isothecium</i>	<i>Isothecium</i>
<i>Rigodium</i>	<i>Acrocladium</i>	<i>Tripterocladium</i>	<i>Porotrichodendron</i>	<i>Porotrichodendron</i>
	<i>Rigodium</i>	<i>Isocrocladium</i>	<i>Porotrichopsis</i>	<i>Porotrichopsis</i>
Brotherus (1924-25)	<i>Elmeriobryum</i>	<i>Elmeriobryum</i>	<i>Acrocladium</i>	<i>Acrocladium</i>
<i>Elmeriobryum</i>	<i>Plasteurhynchium</i>	<i>Plasteurhynchium</i>	<i>Rigodium</i>	<i>Rigodium</i>
<i>Plasteurhynchium</i>	<i>Dolichomitriopsis</i>		<i>Elmeriobryum</i>	<i>Elmeriobryum</i>
<i>Dolichomitriopsis</i>	<i>Isotheciopsis</i>		<i>Plasteurhynchium</i>	<i>Plasteurhynchium</i>
			<i>Dolichomitriopsis</i>	<i>Dolichomitriopsis</i>
			<i>Isotheciopsis</i>	<i>Isotheciopsis</i>
Brotherus (1929)				
<i>Isotheciopsis</i>				
Horikawa and Ando (1964)				
<i>Dixonia</i>				

tain. Morphologically they are the same species, but it is impossible to tell whether or not it is a species separate from *C. porotrichoides*, or if it is a robust form of the latter. These specimens are morphologically distinct from *C. porotrichoides*, being more concave than the latter and markedly apiculate. However, they are similar in this to robust forms of the eastern Australian *C. excavata*, which does not otherwise occur in New Caledonia. There remains the possibility that it is just a large form of *C. porotrichoides*, and that its distinct features are a function of plant size. In the absence of records of *C. excavata* for New Caledonia, and in the lack of further information, these names are treated as synonyms of *C. porotrichoides*.

Camptochaete falcifolia is known from only one specimen and is problematic in that the specimen is incomplete, not having lower portions of the stem present,



Figs. 3-4. Sporophytic and peristome features of *Campyochaete*. 3. *C. pulvinata*, young sporophyte with calyptra. 4. *C. subporotrichoides*, peristome.



Figs. 5-6. Sporophytic and peristome features of *Campyochaete* 5. *C. porotrichoides*, exostome lower outer surface. 6. *C. porotrichoides*, exostome inner surface and endostome basal membrane (right).

and therefore it is impossible to tell whether it is a *Camptochaete*, *i.e.*, whether it is stipitate or not, and, if it is, what section it belongs to, although it agrees well enough with *C. pulvinata* to be (probably) synonymous with it (Bartram, 1933; Hoe, 1974; Miller *et al.*, 1978). This specimen is important, as it is also the basis for the occurrence of the genus and (the southern) sect. *Camptochaete* in Hawaii and the northern hemisphere.

The range of the genus has recently been considerably extended in tropical areas. Touw (1992) has recorded the genus *Camptochaete* from Indonesia (Flores), a large extension westward from Papua New Guinea, and I have also recently seen specimens from the Solomon Islands, also from Touw. There remain several areas in the region peripheral to the known tropical range in Indonesia, Melanesia, Australasia and the Pacific where *Camptochaete* might occur and further collecting is needed.

This is the first revision in the history of *Camptochaete*. Its species are often characterised by extreme variability. As species recognition is based on morphological discontinuity, this treatment has been conservative. Our knowledge of the genus is uneven, both in availability of specimens and knowledge of the plants in the field. In this context, the revision of *Camptochaete* provides a foundation on which to base both more detailed collecting, particularly in tropical areas, where the species are not well known, and more detailed studies of the species, where they are better known, perhaps at the molecular level.

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