

## ***Rhipidosiphon lewmanomontiae* sp. nov. (Bryopsidales, Chlorophyta), a calcified udoteacean alga from the central Indo-Pacific based on morphological and molecular investigations**

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A new species of the green algal genus *Rhipidosiphon*, *Rhipidosiphon lewmanomontiae* sp. nov., is described after material from the Mu Ko Tha Lae Tai area (SE Thailand) and Okinawa (Japan) on the basis of morphology and molecular analyses. The new species grows epilithically, just under the low water mark and is occasionally exposed at spring low tide. It differs mainly from the other known species, the Indo-Pacific *Rhipidosiphon javensis* and the western Atlantic *Rhipidosiphon floridensis*, by the presence of a rhizoidal pseudocortex surrounding the monosiphonous stipe and the presence of intercalary siphon constrictions. A similar pseudocortex has been described in juvenile stages of some *Udotea* species, but in this genus, the stipe is polysiphonous and possesses a cortex of lateral appendages in the adult phase.

KEY WORDS: Bryopsidales, Green algae, Molecular phylogeny, Okinawa, *Rhipidosiphon lewmanomontiae*, Thailand, Ulvophyceae

### INTRODUCTION

*Rhipidosiphon* Montagne (1842: 15) is a green algal genus belonging to the family Udoteaceae (Bryopsidales). This genus was previously studied by Gepp & Gepp (1904), Littler & Littler (1990a) and Vroom *et al.* (2001). Until now, two species have been described: *Rhipidosiphon javensis* Montagne, occurring in the Indo-Pacific, and *Rhipidosiphon floridensis* D.S. Littler & Littler, which is only known from the Caribbean Sea.

Both species have a well-marked monosiphonous and uncorticated stipe supporting a monostromatic flabellum composed of dichotomously branched, straight siphons contiguously arranged in a single plane. The plants are lightly calcified. In all these characters *Rhipidosiphon* is very similar to unistratose representatives of the genus *Udotea*, but the latter is corticated, at least on the stipe.

During recent fieldwork in Thailand and Japan, specimens of unclear affinity were collected. They were reminiscent of *Rhipidosiphon* in having a uniaxial stipe and unistratose blade yet also similar to *Udotea* in blade size and the presence of a rudimentary pseudocortex enveloping the stipe. The aim of this paper is to document the morphological and phylogenetic characteristics of these specimens in detail.

### MATERIAL AND METHODS

Morphological observations were made on specimens collected in the Mu Ko Tha Lae Tai area (vicinity of Ko Samui, SE Thailand) and in Miyagi (Okinawa, Japan). Herbarium specimens are deposited in the Ghent University herbarium (GENT) in Belgium and at Prince of Songkla University in Thailand. Photographs were taken with a ColorView (Olympus) digital camera mounted on a Leitz Diaplan compound microscope or Leica Wild M10 stereomicroscope. Cells were examined for crystalline inclusions, as the presence and morphologies of these structures have been found to be species specific in siphonous and siphonocladalean green algae (e.g. Ducker 1967; Leliaert & Coppejans 2004). Measurements of siphons are presented as the 95% range of our observations, with absolute minimum and maximum values given in parentheses. Figs 2–28 are based on specimens of HEC 16223A preserved in a 5% formalin–seawater solution.

DNA was extracted from four specimens belonging to the genus *Rhipidosiphon* and *Udotea unistratosa* D.S. Littler & Littler with a DNA extraction followed by a cetyltrimethylammonium bromide protocol modified from Doyle & Doyle (1987). Sequences of the large subunit of the ribulose-1,5-bisphosphate carboxylase/oxygenase gene (*rbcL*) were generated following previously described protocols (Verbruggen *et al.* 2009) and submitted to GenBank. The newly generated data were added to an alignment of Udoteaceae *rbcL* sequences downloaded from

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**Table 1.** List of species used in the phylogenetic analyses, with voucher numbers and GenBank accession numbers of the *rbcL* sequences. Newly generated sequences are in bold.

Species	Voucher	GenBank
Udoteaceae		
<i>Chlorodesmis fastigiata</i> (C.Agardh) S.C.Ducker	HV102 (GENT)	FJ432639
<i>Flabellia petiolata</i> (Turra) Nizamuddin	HV1202 (GENT)	FJ432640
<i>Penicillus capitatus</i> Lamarck	HV338 (GENT)	FJ432641
<i>Penicillus dumetosus</i> (J.V.Lamouroux) Blainville		AY942175
<i>Penicillus lamourouxii</i> Decaisne		DQ469333
<i>Penicillus pyriformis</i> A.Gepp & E.S.Gepp		AY942162
<i>Rhipidosiphon javensis</i> Montagne	DML40128 (US)	<b>HQ871691</b>
<i>Rhipidosiphon javensis</i>	DML40134 (US)	FJ432644
<i>Rhipidosiphon lewmanomontiae</i> Coppejans <i>et al.</i>	HEC16223 (GENT)	<b>HQ871689</b>
<i>Rhipidosiphon lewmanomontiae</i>	JAP080 (GENT)	<b>HQ871690</b>
<i>Rhipocephalus oblongus</i> (Decaisne) Kützing		DQ469319
<i>Rhipocephalus phoenix</i> (J.Ellis & Solander) Kützing		AY942172
<i>Tydemania expeditionis</i> Weber-van Bosse		AY942161
<i>Udotea conglutinata</i> (J.Ellis & Solander) J.V.Lamouroux		AY942168
<i>Udotea flabellum</i> (J.Ellis & Solander) M.A.Howe		AY942166
<i>Udotea glaucescens</i> Harvey ex J.Agardh	H.0862 (GENT)	FJ432650
<i>Udotea spinulosa</i> M.A.Howe		AY942160
<i>Udotea unistratea</i> D.S.Littler & Littler	HV405 (GENT)	<b>HQ871692</b>
Outgroup taxa		
<i>Halimeda discoidea</i> Decaisne		AB038488
<i>Halimeda incrassata</i> (J.Ellis) J.V.Lamouroux		AY942167
<i>Halimeda opuntia</i> (Linnaeus) Lamouroux		AY942174
<i>Halimeda tuna</i> (J.Ellis & Solander) Lamouroux		AY942177
<i>Pseudocodium floridanum</i> Dawes & Mathieson		AM909692
<i>Pseudocodium natalense</i> De Clerck <i>et al.</i>	KZNb2241	AM909693
<i>Rhipilia crassa</i> A.J.K. Millar & G.T. Kraft	H.0748	FJ432645
<i>Rhipilia nigrescens</i> Coppejans & W.F. Prud'homme van Reine	H.0847	FJ432646
<i>Rhipilia tomentosa</i> Kützing		AY942164
<i>Rhipiliopsis profunda</i> (N.J. Eiseman & S.A. Earle) J.N. Norris & S.M. Blair	DML51973	FJ432647

GenBank (Hanyuda *et al.* 2000; Lam & Zechman 2006; Curtis *et al.* 2008; Verbruggen *et al.* 2009). Rhipiliaceae, Pseudocodiaceae and Halimedaceae sequences were used as outgroups to root the phylogenetic trees (Verbruggen *et al.* 2009). An overview of all sequences used is given in Table 1. A suitable model for phylogenetic inference was determined using the Bayesian information criterion as implemented in MrAIC 1.4.4 (Nylander 2004). Maximum likelihood (ML) phylogenetic trees were inferred with PhyML 3.0 using the GTR+I+G model of sequence evolution suggested by MrAIC, a BioNJ starting tree and subtree pruning–regrafting/nearest-neighbor interchange (NNI) branch swapping (Guindon *et al.* 2010). Maximum parsimony (MP) phylogenetic trees were inferred with Mega 5.0 (Kumar *et al.* 2008), using closest-neighbor interchange branch swapping on 10 random addition start trees. Nonparametric bootstrapping (500 replicates for ML with NNI swapping, 1000 for MP) was used to assess branch support for both ML and MP (Felsenstein 1985).

## RESULTS

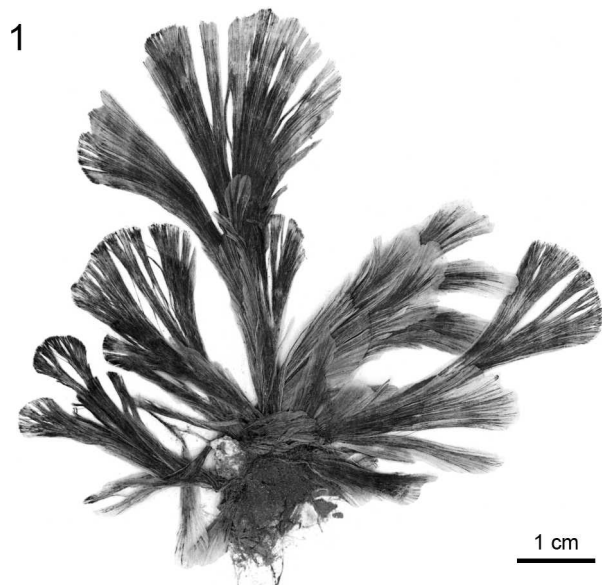
### *Rhipidosiphon lewmanomontiae* Coppejans, Leliaert, Verbruggen, Prathep & De Clerck *sp. nov.*

Figs 1–28

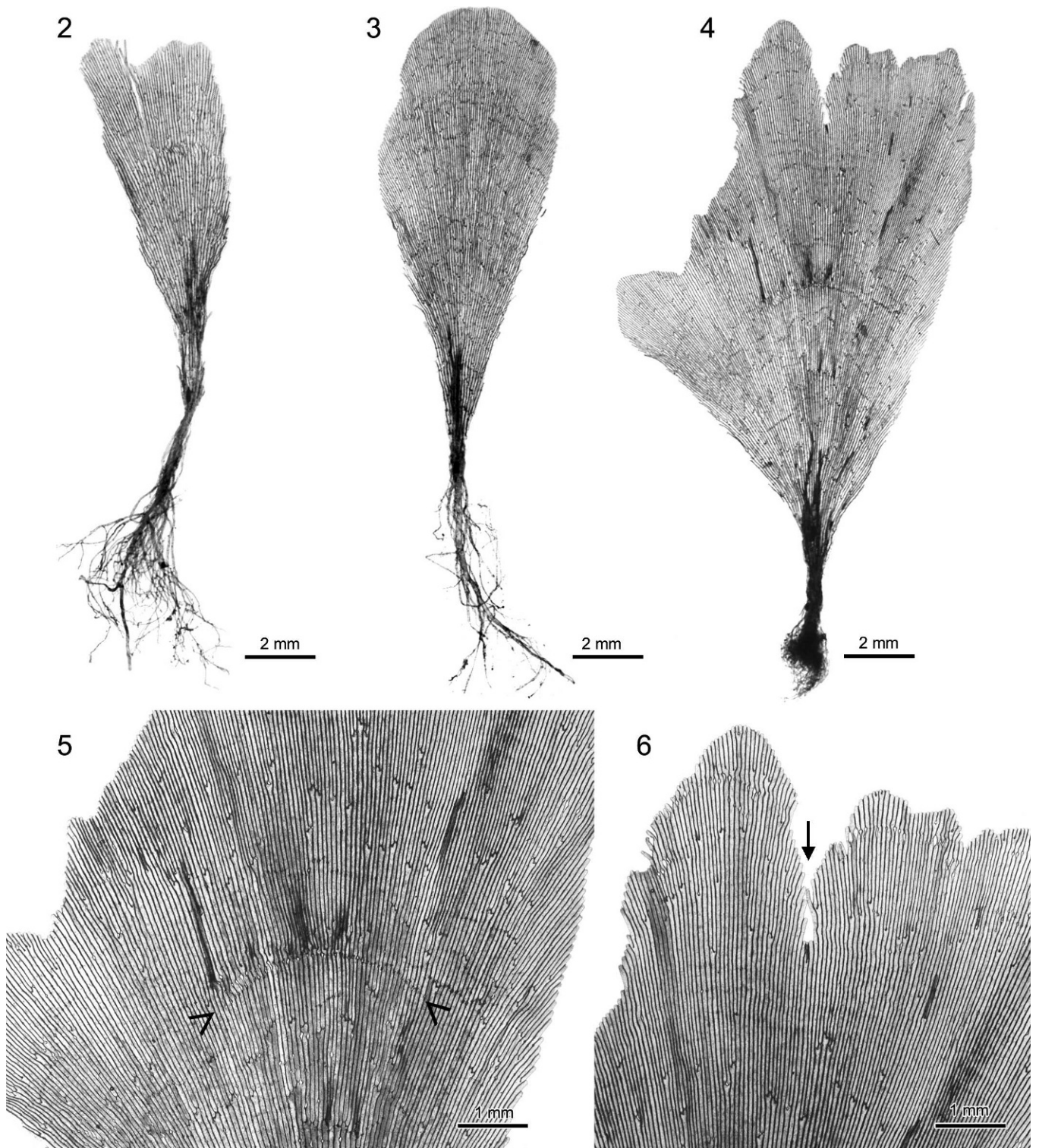
*A Rhipidosiphon floridensis* differt *constrictionibus supra-dichotomibus asymmetricis*; *a R. floridensis et R. javensis* differt *stipes cum pseudocortex rhizoidibus circum stipes*

*monosiphonibus et presentia constrictionibus intercalares siphonibus flabellum.*

Differs from *R. floridensis* by the asymmetrical supra-dichotomous constrictions; differs from *R. floridensis* and *R. javensis* by the presence of a rhizoidal pseudocortex



**Fig. 1.** *Rhipidosiphon lewmanomontiae*. Holotype (part of herbarium specimen HEC 16223A).

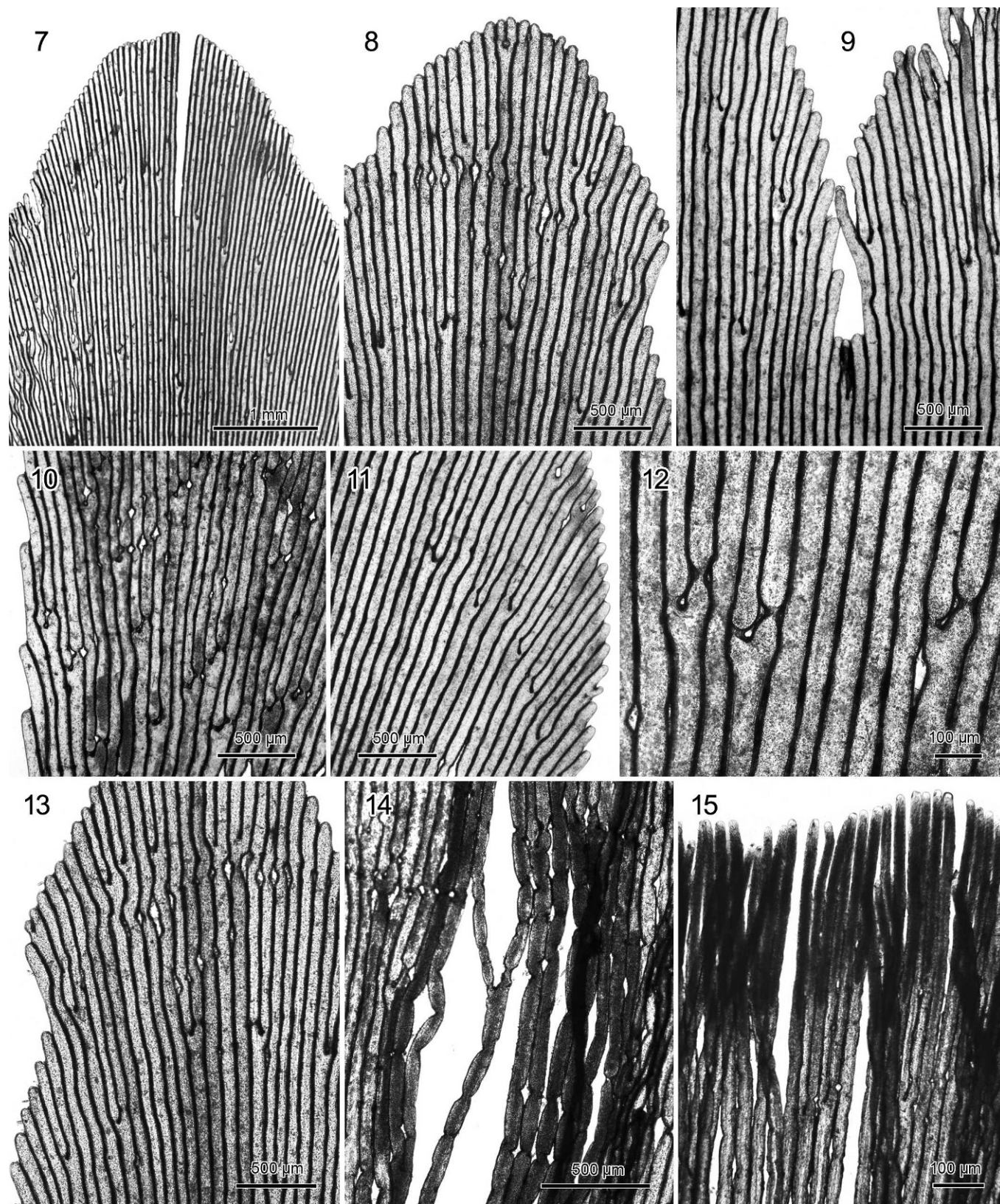


**Figs 2–6.** *Rhipidosiphon lewmanomontiae*. General morphology (HEC 16223A).

**Figs 2, 3.** Juvenile plants.

**Fig. 4.** Mature plant.

**Figs 5, 6.** Details of the blade. Arrowheads indicating a concentric row of constrictions and dichotomies. Arrow indicating an incision of the blade margin.



**Figs 7–15.** *Rhipidosiphon lewmanomontiae*. Details of blade siphons (HEC 16223A).

**Figs 7, 9.** With blade incision.

**Figs 8–11, 13.** Calcification limited to the ridges between the siphons.

**Figs 11, 12.** Details of dichotomies with unilaterally directed, asymmetrical constrictions.

**Fig. 13.** The lowermost of each constriction frequently directed to the same side of the blade in the left half of the blade and to the other side in the other half.

**Fig. 14.** Intercalary constrictions.

**Fig. 15.** Ciliate blade margin (possibly gametangia formation).

around the monosiphonous stipe and the presence of intercalary constrictions in the flabellum siphons.

**HOLOTYPE:** HEC 16223A, coll. E. Coppejans, just under low water mark, Thailand, Suratthani Province, Mu Ko Tha Lae Tai area, Wang Nai (small island vic. Ko Samui; 9.312°N, 99.893°E), 19.iv.2007. See Coppejans *et al.* (2010: figs 91A & 64G as *Rhipidosiphon* sp.) for an *in situ* and herbarium sheet colour photograph of the type collection. Deposited in GENT. GenBank accession number of the *rbcL* sequence of the holotype: HQ871689.

**ISOTYPES:** HEC 16223B and SP 99, deposited in Princess Maha Chakri Sirindhorn Natural History Museum, Thailand.

**OTHER SPECIMENS EXAMINED:** **Thailand:** Suratthani Province, Mu Ko Tha Lae Tai area, Ko Taen (island vic. Ko Samui; 9.383°N, 99.952°E; E. Coppejans, 18 April 2007, HEC 16193Aa) (HEC 16193Ab is *R. javensis* from the same locality); **Japan:** Miyagi, Okinawa (26.329°N, 127.743°E; K. Pauly, 24 July 2009, JAP 080).

**ETYMOLOGY:** This species is named in honour of Professor Dr Khanjanapaj Lewmanomont, a pioneer and present leading figure in Thai phycology.

### Morphology

Plants erect, mostly in dense tufts of supple, cuneate, flat blades, (1.5–) 4–6 (–8) cm long; the numerous fronds originating from a felted mat of rhizoids from where the blades gradually broaden in fan-shaped structures (Figs 1–4). Young specimens still with a gradually tapering, unbranched, monosiphonous basis (stipe), 1–2 mm long that in a very early stage becomes surrounded by thin, branched, smooth (i.e. without lateral appendages) rhizoids. Rhizoids arising all along the stipe (Figs 16–19), originating perpendicularly to the mother siphon and showing a marked, thick-walled constriction at their basis, after which they bend downward (Figs 20–22) and become narrower after each branching. Stipe monosiphonous, covered by an intricate rhizoidal mass in older plants (Figs 4, 24). In fully grown plants, downwardly growing rhizoids are also produced (diameter 52–67 µm) from the basal part of the flabellum (up to the third or fourth dichotomy of the blade siphons) (Figs 16, 17, 23, 24). A real cortex (as found in *Udotea*) is never formed. Blades thin, cuneate to narrowly flabellate, frequently spatulate, (1.5–) 4–6 (–8) cm long, 2.5–4 cm wide in the subapical, widest part, with a rounded or lobed apical margin, unistratose, except for the extreme basis, where it is covered by downwardly growing rhizoids in adult plants. Fully grown blades markedly and deeply longitudinally lacerate, greyish dark green, composed of radially arranged, parallel, straight and smooth siphons (Figs 5–13) of about 60–67 µm diameter at the blade basis, 58 µm at the margin. Blade siphons devoid of papillae or appendages (including the basal part) and with rounded apices. Siphons branching dichotomously, with asymmetrical constrictions above the dichotomies (Fig. 12). Intercalary constrictions also present, locally numerous and pronounced, especially in the upper marginal parts of the blade (Fig. 14). In some specimens, constrictions or dichotomies are arranged in

concentric rows (Fig. 5, arrowheads). Blade siphons loosely attached to each other by a thin layer of calcification that remains limited to the ridges between the siphons (Figs 8–11). Apical and outer walls of growing siphons devoid of calcification. In old blades, the upper marginal filaments are loose and uncalcified, resulting in a ciliate blade margin (Fig. 15). Refrangent quadrangular crystals with two opposite concave sides (Figs 26, 27) and stacks of refrangent needle-shaped crystals (Fig. 28) are frequent in the siphons. Gametangia have not been observed.

### Distribution and habitat

*Rhipidosiphon lewmanomontiae* is presently only known from the Mu Ko Tha Lae Tai area (Thailand) and Miyagi (Japan). In the former locality it is abundant from low tide level (exposed at spring low tide, see Coppejans *et al.* 2010: fig. 30G as *Rhipidosiphon* sp.) down to 2 m depth, growing epilithic on horizontal to vertical walls.

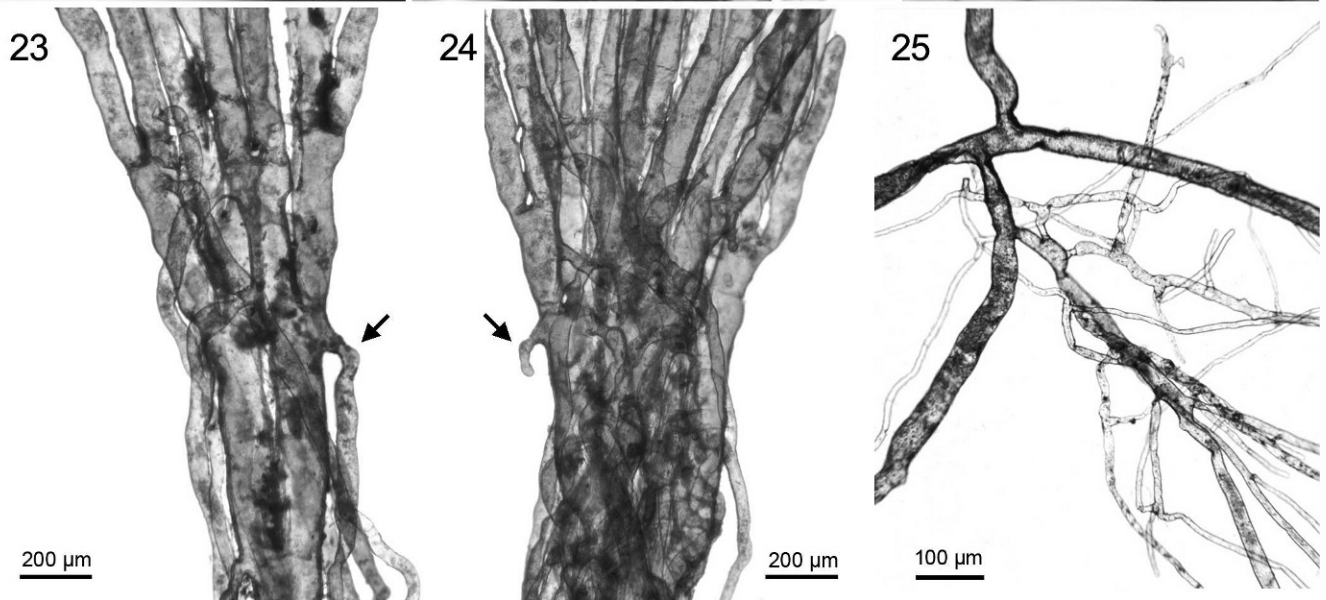
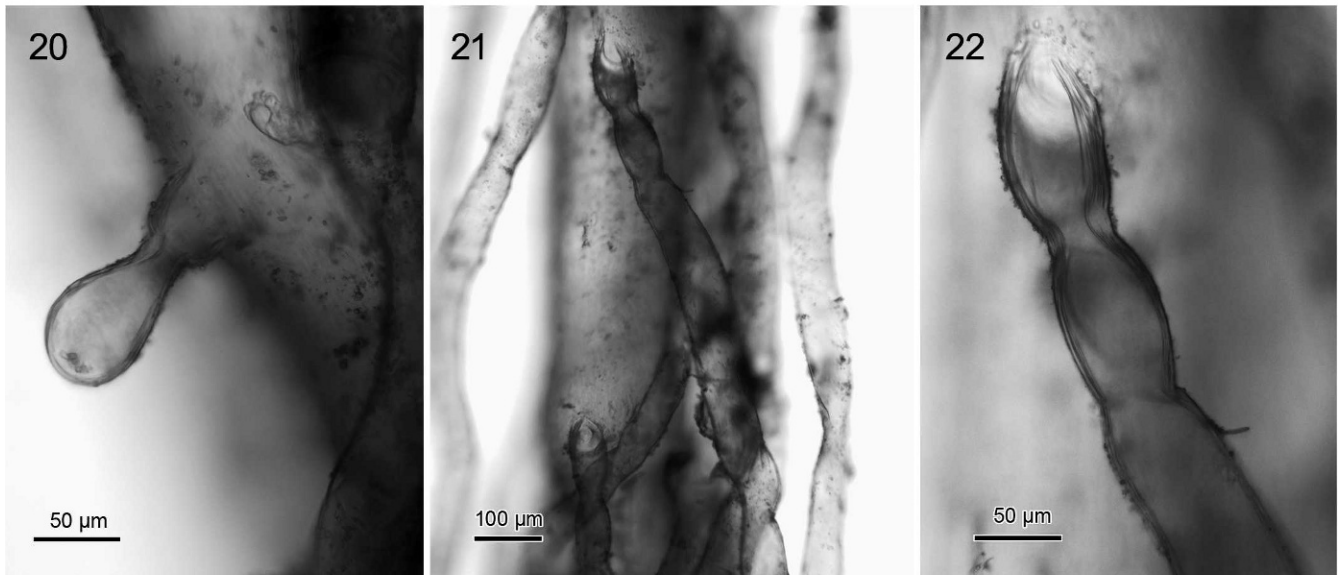
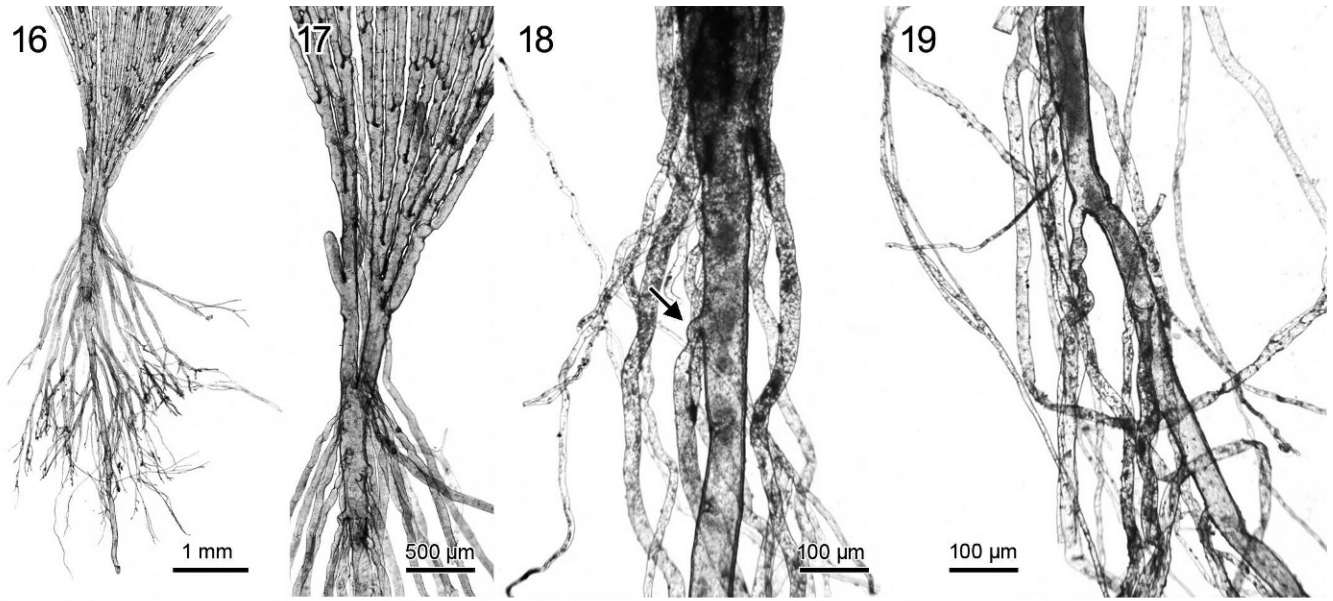
### Molecular phylogenetics

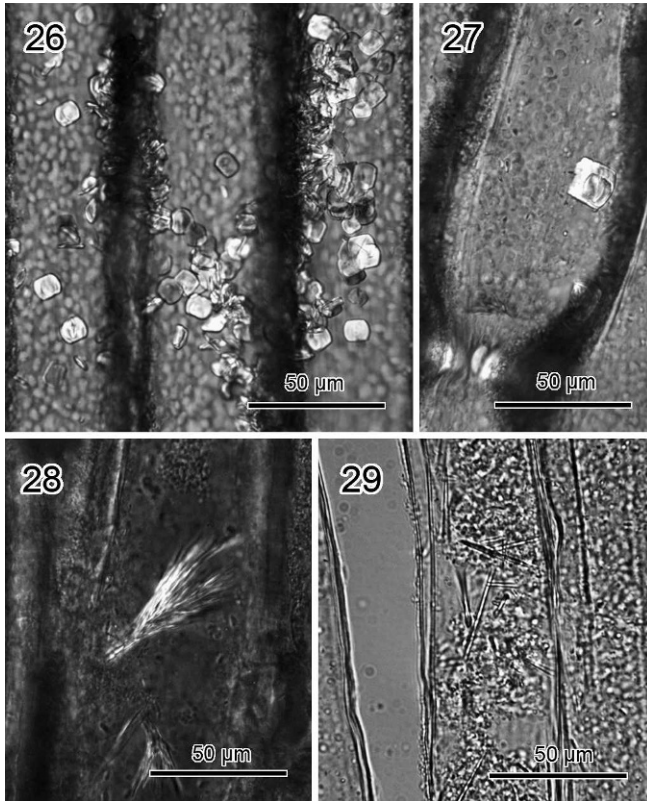
The inferred trees (ML and both MP trees) differ only in poorly supported relationships. They clearly show that *R. javensis* and *R. lewmanomontiae* are distinct species, both being on relatively long and strongly supported branches (Fig. 30). The *rbcL* sequences of the two *Rhipidosiphon* species differ by 3.8–4.3% (uncorrected p-distance). In our tree, the genus *Rhipidosiphon* is sister to *Chlorodesmis fastigiata* (C. Agardh) S.C. Ducker in a cluster nested within the poorly resolved Udoteaceae. *Udotea unistratea* is not closely related to the *Rhipidosiphon* clade; instead, it clusters with *Penicillus capitatus* Lamarck. Congruent with previous studies (Kooistra 2002; Lam & Zechman 2006; Verbruggen *et al.* 2009), several genera of the Udoteaceae are non-monophyletic in our tree (e.g. *Udotea*, *Penicillus*).

### DISCUSSION

The well-supported sister relationship between *R. lewmanomontiae* and the type species *R. javensis* in the phylogeny supports the placement of the new species in the genus *Rhipidosiphon*. This is confirmed by the total absence of a real cortex formed by lateral appendages of the siphons, characteristic for the genus *Udotea*. Our molecular results clearly support the distinctness of *R. lewmanomontiae* and *R. javensis*, the specimens of each species clustering closely together on a relatively long and strongly supported branch of the phylogenetic tree (Verbruggen *et al.* 2007; Leliaert *et al.* 2009). Morphologically, *R. lewmanomontiae* differs from *R. javensis* in being taller, less strongly calcified and having a stipe covered by a rhizoidal pseudocortex.

In the Mu Ko Tha Lae Tai area, both *R. javensis* and *R. lewmanomontiae* occur, locally rather close to each other. In the field they can be distinguished by their colour, the former being greyish blue-green (as a result of higher calcification), the latter being greyish dark green. They also differ in size, *R. javensis* only reaching 0.5–1.0 cm (rarely up to 4 cm) in height, as opposed to (1.5–) 4–6 (–8) cm for *R. lewmanomontiae*. Moreover, *R. javensis* generally grows as





**Figs 26–29.** Intracellular crystals (differential interference contrast).  
**Figs 26–27.** Quadrangular crystals in *Rhipidosiphon lewmanomontiae* (HEC 16223A).  
**Fig. 28.** Stacks of refringent needle-shaped crystals in *Rhipidosiphon lewmanomontiae* (HEC 16223A).  
**Fig. 29.** Isolated, nonrefringent needle-shaped crystals in *Rhipidosiphon javensis* (HEC 16193Ab).

individual plants but sometimes is grouped in open populations (Coppejans *et al.* 2009, fig. 102; 2010, fig. 30F), mostly on vertical walls, whereas *R. lewmanomontiae* mostly grows in dense clusters where the individual specimens are difficult to separate because of the intricate felt of rhizoids from which they arise, on horizontal to vertical rock substratum.

Both *R. javensis* and *R. floridensis* have an uncalcified, monosiphonous, unbranched, smooth, naked and clearly visible stipe, even in fully grown specimens, with basal, rather short rhizoids (e.g. Littler & Littler 1990a: figs 2&3, 7&8; Coppejans *et al.* 2001: figs 32, 33; Wysor & Kooistra 2003: fig. 24; Abbott & Huisman 2004: figs 52C,D; Kraft 2007: figs 83B,C; Lewmanomont *et al.* 2007: fig. p. 40). In *R. javensis*, rhizoids rarely originate from the upper parts of the stipe and never from the flabellum (Gepp & Gepp 1911,

fig. 36c). In *R. lewmanomontiae*, the naked stipe siphon is only visible in juvenile specimens (Figs 2, 3, 16–19). Soon afterward, downwardly growing branched rhizoids slightly thinner than the stipe siphon are being formed all along the stipe (Figs 16–19), covering it in a woolly mass. At a later stage, rhizoids are also formed from the basal part of the flabellum (up to the third or fourth dichotomy of the blade siphons). These rhizoids are more closely appressed to the stipe (Figs 23, 24), completely hiding it. We interpret this structure as a pseudocortex. A similar development of the stipe has been described and illustrated by Gepp & Gepp (1911: 111–114, figs 40, 43) in *Udotea papillosa* A. Gepp & E. Gepp and *Udotea glaucescens* Harvey ex J. Agardh. In *R. lewmanomontiae* the rhizoids remain smooth (without appendages) even in adult plants as opposed to *Udotea*, where a cortex is formed by the contiguous, frequently intricate siphon appendages; in *R. lewmanomontiae* the rhizoids continue to grow over the rocky substratum or in the algal turf, resulting in a well-attached felted mass that sprouts numerous, densely packed cuneate blades. Some of the downwardly growing rhizoids continue their growth horizontally upon reaching the substratum. They also show constrictions and form tufts of thin, branched rhizoids (Fig. 25) as well as new uprights.

In all three species of *Rhipidosiphon* the blade is unistratose, composed of radially arranged, parallel, straight and smooth, dichotomously branching siphons without papillae or appendages (even in the basal part), with rounded apices, but in *R. lewmanomontiae*, the basal part of adult blades can be partly covered by downwardly growing rhizoids. The constrictions above the dichotomies are symmetrical in *R. floridensis*, whereas they are asymmetrical in *R. javensis* and *R. lewmanomontiae*. The observation of Littler & Littler (1990b: 243) that in *Udotea* the supradichotomous constrictions are unequal in most Pacific and Indian Ocean representatives and equal in Atlantic species is also valid for *Rhipidosiphon*. Sometimes, the supradichotomous constrictions are more or less placed on concentric lines. The diameter of the blade siphons is similar in all three species (Table 2). In both *R. javensis* and *R. lewmanomontiae*, the lowermost of each supradichotomous constriction is mostly more pronounced and frequently directed to the same side of the blade (Figs 10–12) in the left half of the blade and to the other side in the other half (Figs 7, 13). In *R. lewmanomontiae*, intercalary constrictions are also present, sometimes locally numerous and pronounced (Fig. 14) as opposed to both other species where they are absent. In all three species, the blade siphons are loosely attached to each other by a thin layer of calcification. In *R. javensis*, calcification is also present on the blade surfaces, whereas in both other species

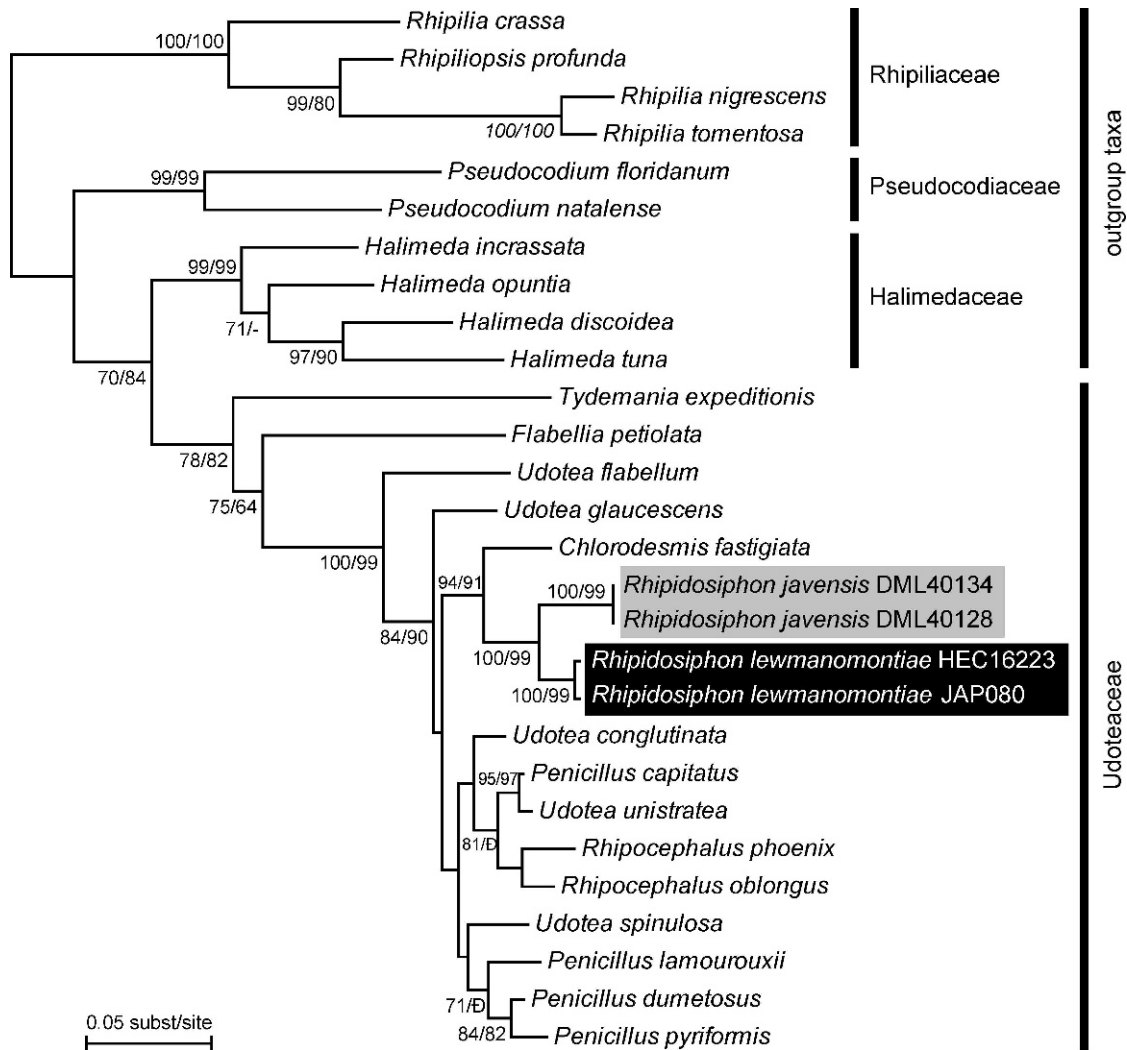
**Figs 16–25.** *Rhipidosiphon lewmanomontiae*. Rhizoid formation (HEC 16223A).

**Figs 16–18.** Basal parts of young plants with visible stipe siphon and initial rhizoid formation. Arrow indicates rhizoid, which originated perpendicularly to the mother siphon, after which it bends downward.

**Figs 19–22.** Rhizoids produced by the stipe siphon (Fig. 20 perpendicular rhizoid initiation, Figs 21, 22 downwardly bending rhizoids with thick-walled constriction).

**Figs 23, 24.** Rhizoid formation by the basal blade siphons resulting in a pseudocortex. Arrows indicate rhizoids originating perpendicularly to the mother siphon after which they bend downward.

**Fig. 25.** Details of the prostrate rhizoids from the felt.



**Fig. 30.** Phylogenetic relationships of the Udoteaceae inferred from an *rbcL* alignment and rooted with three other families of the Halimedineae. The tree highlights two distinct species of *Rhipidosiphon*, *R. javensis* and the new species *R. lewmanomontiae*. Branch support is given as ML bootstrap values before and MP bootstrap values after the slash. Values lower than 70 are not shown.

calcification remains limited to the grooves between the siphons. In *R. javensis* and *R. lewmanomontiae*, the blade often becomes cleaved (lacerated), in the latter generally at the level where one or a few siphons appear to stop growing, resulting in an incision of the blade margin (Figs 6, 7, 9). The fact that in old blades the marginal filaments are loose and uncalcified, resulting in a ciliate blade margin, could be a precursor of gametangia formation (Fig. 15), but mature gametangia have not been observed. Reproduction in *R. lewmanomontiae* might be mainly vegetative, new blades arising from the felted rhizoidal mass (Fig. 1) as in other Bryopsidales (e.g. *Udotea* spp. as described by Littler & Littler 1990a: 35, 1990b: 251).

Quadrangular crystals are abundant in the siphons of *R. lewmanomontiae* (Figs 26, 27) from Thailand but were apparently absent from Japanese specimens, possibly indicating intraspecific variation in this trait. This is in contrast with other bryopsidalean species where the presence of particular crystalline inclusions has been found

to be species specific (e.g. *Chlorodesmis*: Ducker 1967). Stacks of strongly refringent needle-shaped crystals are more rare and present in specimens from both localities (Fig. 28). The siphons of *R. javensis* only contain isolated, nonrefringent needle-shaped crystals (Fig. 29), indicating that they might have a different composition from those of *R. lewmanomontiae*.

*Rhipidosiphon lewmanomontiae* closely resembles *U. unistratea* from the Atlantic and *U. glaucescens* Harvey ex J. Agardh from the Indo-Pacific. These *Udotea* species also have a unistrate flabellum composed of smooth siphons, but in both species the stipe of adult plants is polysiphonous, the siphons bearing appendages forming a cortex. Our phylogenetic analysis shows that *U. unistratea* and *U. glaucescens* are not closely related to *Rhipidosiphon*. *Udotea unistratea* clusters with *P. capitatus*, whereas *U. glaucescens* forms a separate lineage within the Udoteaceae. *Udotea papillosa* is also similar, but the blade siphons bear papillose appendages. No sequence data are currently available for this species.



**Table 2.** Comparison of morphological features between *Rhipidosiphon floridensis*, *R. javensis* and *R. lewmanomontiae*.

	<i>R. floridensis</i>		<i>R. javensis</i>		<i>R. lewmanomontiae</i>
	Littler & Littler (1990a)	Wysor & Kooistra (2003)	Littler & Littler (1990a)	This study (Mu Ko Tha Lae Tai area)	This study (Thailand and Japan)
Total size	1 cm	3 cm	0.2–3 cm	1–4 cm	(1.5–) 3–6 (–8) cm
Diameter of blade siphons (µm)	45–116	45–150	40–110	36–115	41–125
Blade basis					
Under dichotomy	95–116	105–115	85–110	60–115	77–115
Above dichotomy		50–75		40–55	52–77
Middle of blade					
Under dichotomy	not mentioned	80–150	not mentioned	50–65	72–125
Above dichotomy		50–70		36–55	45–67
Blade margin					
Under dichotomy	45–60	75–90	40–50	62–90	67–110
Above dichotomy		45–50		40–58	41–67
Supradichotomous constrictions	symmetrical, both constrictions similar		asymmetrical, lowermost constriction more pronounced		asymmetrical, lowermost constriction more pronounced
Intercalary constrictions		absent		absent	present
Stipe		naked		naked	with rhizoidal pseudocortex
Stipe siphon diameter (µm)	130–220	115	120–175	165–185 tapering downward to 120–130	60–70 tapering downward to 10–46
Diameter of rhizoids (µm) <sup>1</sup>		not mentioned	not mentioned	88 proximally 15–21 distally	52–67 proximally 10–21 distally
Crystals		not mentioned	not mentioned	isolated, needle-like in blade siphons	quadrangular frequent and stacks of needle-shaped more rare, both in blade and rhizoids

<sup>1</sup> In *R. lewmanomontiae* rhizoids originating from the blade and stipe have a similar diameter.

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