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Taxonomic notes on *Herposiphonia vietnamica* (Rhodophyta, Ceramiales)

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Abstract — Taxonomic features of the red alga *Herposiphonia vietnamica* Pham (Ceramiales, Rhodomelaceae) are described on the basis of material collected from its type locality, Phu Quoc Island, Vietnam. This species is characterised by relatively slender (50-120 µm wide) prostrate axes with a small number of pericentral cells (eight to 10 per segment), short (300-700 µm high and consisting of seven to 11 segments), slender (50-100 µm wide) and terete determinate branches, tetrasporangia arranged in a straight series of two to five, an ovoid cystocarp (380-420 µm high and 280-320 µm wide) that is lateral on a determinate branch and relatively large in comparison with the thallus size, and three to five, spiralled spermatangial branches that lack a sterile tip.

Ceramiales / *Herposiphonia vietnamica* / marine algae / morphology / Rhodomelaceae / Rhodophyta / taxonomy

Résumé — Note taxinomique sur *Herposiphonia vietnamica* (Rhodophyta, Ceramiales). Les caractères taxinomiques de l'algue rouge *Herposiphonia vietnamica* Pham (Ceramiales, Rhodomelaceae) sont décrits à partir du matériel récolté dans la localité type, l'île Phu Quoc, au Vietnam. Cette espèce se caractérise par des axes prostrés relativement fins (50-120 µm de largeur) avec un petit nombre de cellules péricentrales (huit à 10 par segment), courts (300-700 µm de hauteur et comportant sept à 11 segments), des rameaux définis fins (50-100 µm de largeur) cylindriques, deux à cinq tétrasporocystes disposés en une série rectiligne, un cystocarpe ovoïde (380-420 µm de hauteur et 280-320 µm de largeur) placé latéralement sur un rameau défini et relativement grand par rapport à la taille du thalle, et trois à cinq rameaux mâles spiralés ne présentant pas de sommet stérile. (Traduit par la rédaction)

Algues marines / Ceramiales / *Herposiphonia vietnamica* / morphologie / Rhodomelaceae / Rhodophyta / taxinomie

INTRODUCTION

The red algal genus *Herposiphonia* (Ceramiales, Rhodomelaceae) currently includes 56 species that are distributed in the tropical to warm-temperate

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regions of the world (Masuda & Kogame, 2000). Species discrimination in this genus, especially that in species with terete determinate branches, is difficult due to a high degree of morphological variation of some vegetative features within individual species. In such cases, reproductive features are essential in defining species (Hollenberg, 1968; Morrill, 1976; Masuda & Kogame, 2000). However, sexual reproductive structures are known for relatively few species.

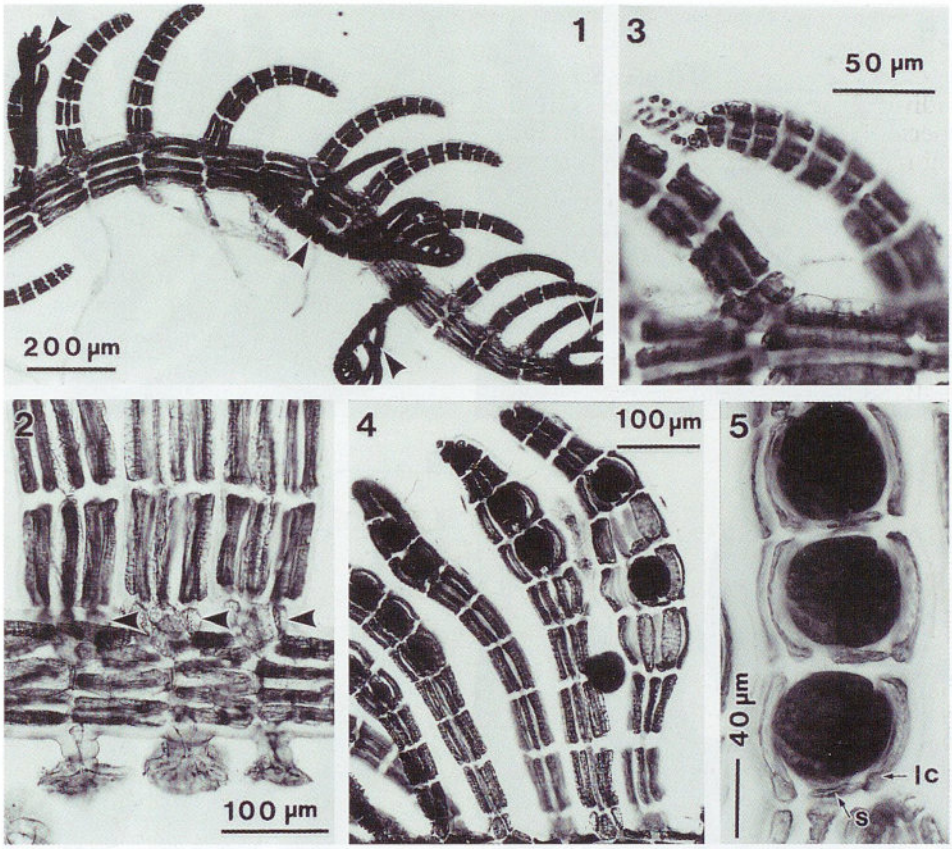
Herposiphonia vietnamica Pham was originally described on the basis of material collected from Phu Quoc Island, Kien Giang Province, Vietnam, by Pham (1969), and recently reported from Sandakan and Kota Kinabalu, Sabah (Borneo Island), Malaysia (Masuda *et al.*, 2000). The original description of this species (Pham, 1969) lacks details of many taxonomic features including reproductive structures now considered to be necessary for comparison of species of *Herposiphonia*. In this paper, we report such features of the alga on the basis of material collected from its type locality.

MATERIALS AND METHODS

Specimens of *Herposiphonia vietnamica* were collected at Duong Dong, Phu Quoc Island, Kien Giang Province, Vietnam, on 9 February 1993 by M. Masuda. Material was fixed in 10 % formalin in seawater and later mounted in 30 % Karo® on microscope slides and stained with 0.5 % (w/v) cotton blue in a lactic acid/phenol/glycerol/water (1:1:1:1) solution. The number of pericentral cells was determined in squash preparations. Voucher specimens mounted in 30 % Karo® on microscope slides are deposited in the Herbarium of the Graduate School of Science, Hokkaido University, Sapporo (SAP 087662-087667).

RESULTS

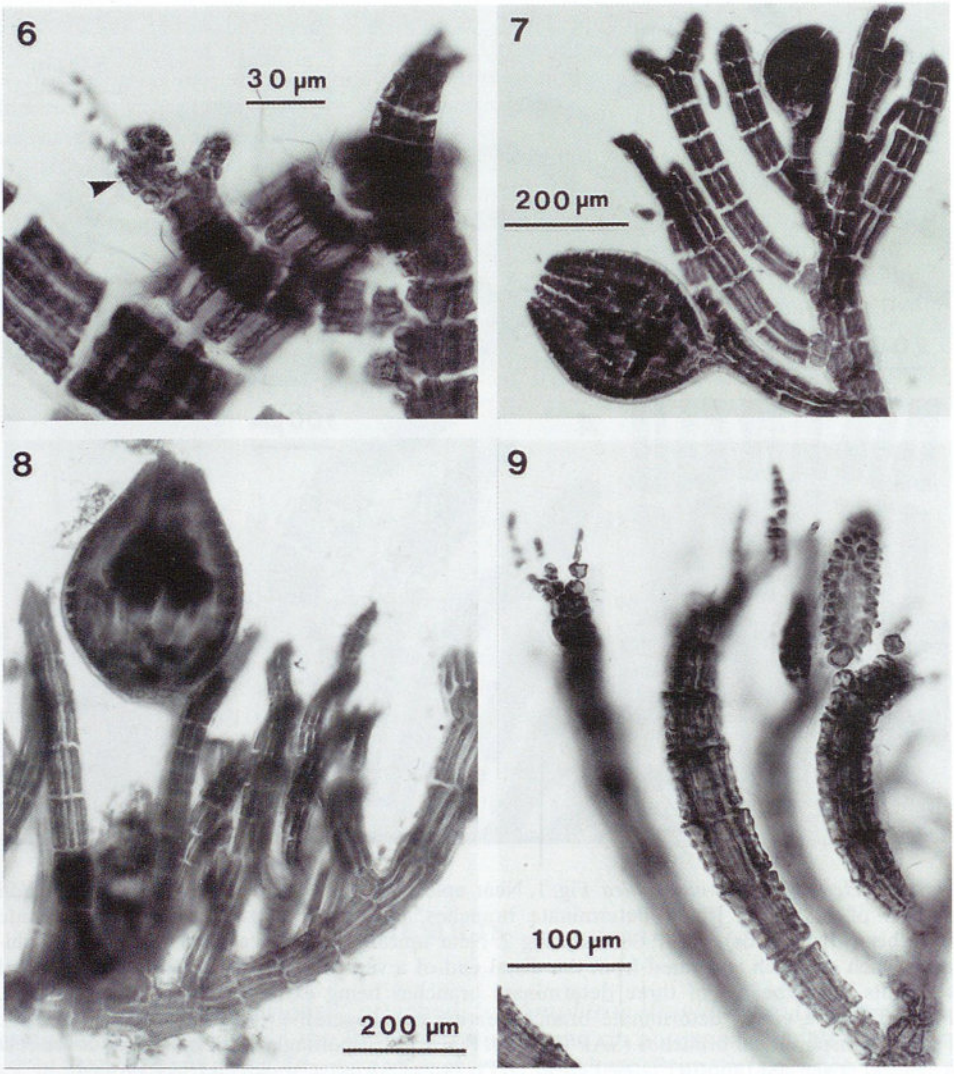
Plants are gregariously attached to *Amphiroa fragilissima* (Linnaeus) Lamouroux, which grows in the lower intertidal zone on an exposed, high-energy coast of Phu Quoc Island. Plants are dark red in colour. Primary axes are prostrate (Fig. 1) and 5-12 mm long and are attached to the basiphyte by numerous unicellular rhizoids (Figs 2, 10-14), which are cut off from the distal end of ventral pericentral cells (Fig. 2). The rhizoids are 25-850 µm long by 20-40 µm wide and possess a digitate (Figs 2, 10-12) or forked (Fig. 13) attachment pad, but are sometimes simple (Fig. 14). The prostrate axes are 50-120 µm wide and possess segments 0.7-2.0 diameters long, each of which consists of eight to 10 pericentral cells and lacks cortical cells. The axes bear either a determinate branch or an indeterminate branch (or branch primodium) from every segment in a sequence of three determinate branches followed by one indeterminate branch (d/d/d/i pattern) (Fig. 1); however, a d/i pattern and intermediate patterns (d/d/i/i, d/d/d/d/i) between the d/d/d/i and d/i patterns are rarely present on the same or different individuals. Some indeterminate branches grow like the parental axis, but others remain short or rudimentary. All determinate branches are dorsally arranged and incurved towards the apex of the parental axis when young, but become erect with



Figs. 1-5. *Herposiphonia vietnamica*. Fig. 1. Near apical portion of a main axis, showing a d/d/d/i pattern of branching [three determinate branches are formed between two indeterminate branches (arrowheads)] (SAP 087662). Fig 2. Near apical portion of a main axis, showing rhizoids, each of which is formed from the distal end of a ventral pericentral cell; notes the basal segments (arrowheads) of three determinate branches being extremely short (SAP 087662). Fig. 3. Tip of a young determinate branch bearing two vegetative trichoblasts (SAP 087662). Fig. 4. Tetrasporangial branches (SAP 087663). Fig. 5. Tetrasporangia without a basal cover cell: lc, lateral cover cell (another lateral cover cell is out of focus); s, stalk cell (SAP 087664).

age. Mature determinate branches are terete, 300-700 µm high by 50-100 µm wide and consist of seven to 11 ecorticate segments that are 0.7-1.8 diameters long in the lower to middle portions except for the basal segments (Fig. 2), all of which are exceptionally short (less than 0.5 diameters long). The basal segments of the determinate branches possess four pericentral cells, the suprabasal segments having six or seven pericentral cells, and other segments having six to nine pericentral cells. Chloroplasts are discoid or ribbon-like. Axial cells in mature segments of determinate branches are cask-shaped, 25-35 µm wide, and thicker than pericentral cells that are 12-20 µm in diameter.

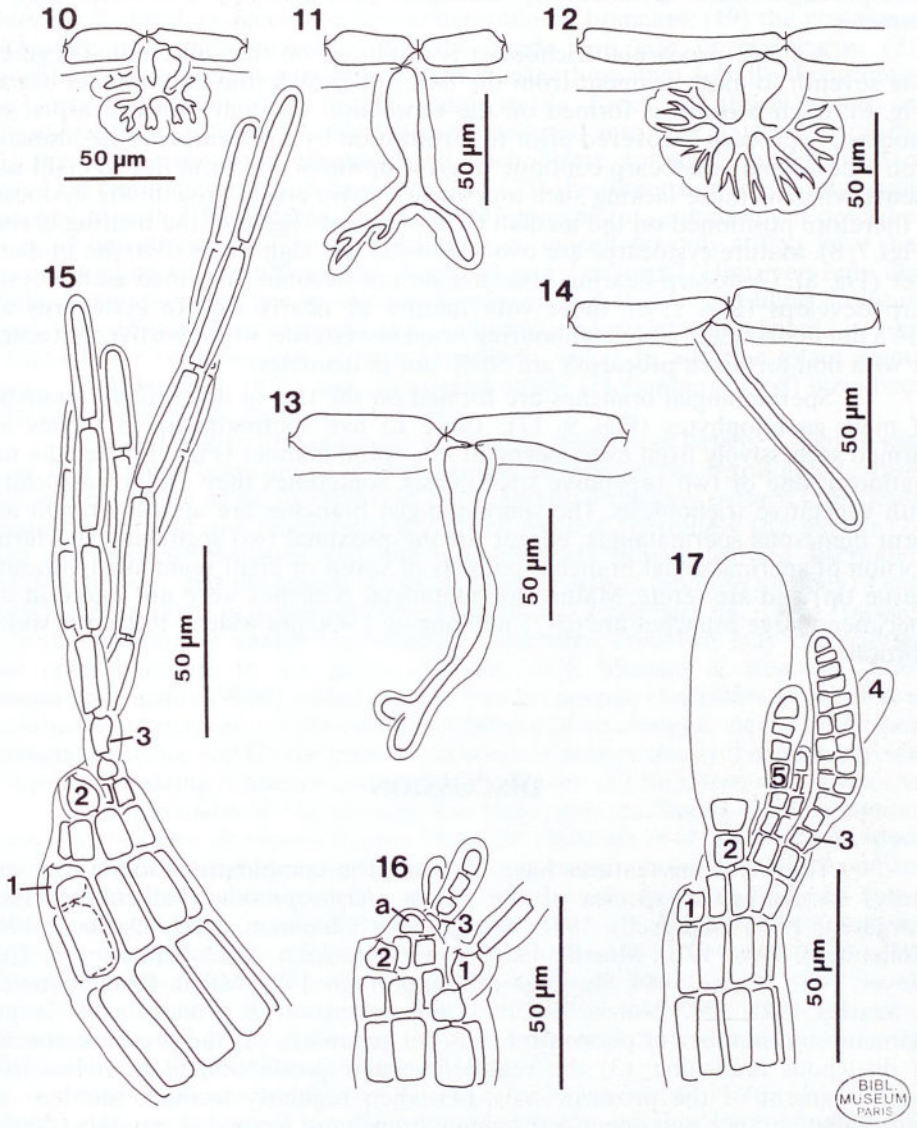
Vegetative trichoblasts are formed on apices of young determinate branches (Figs 3, 15, 16). They are formed on the distal two successive segments (Fig. 3) of each branch; sometimes three successive segments in a spiral manner



Figs. 6-9. *Herposiphonia vietnamica*. Fig. 6. Procarpial trichoblast (arrowhead) formed on the subterminal segment of a procarp-bearing branch (SAP 087665). Fig. 7. Two developing cystocarps lateral on the cystocarp-bearing branches; note no size difference between the cystocarp-bearing branches and other branches (SAP 087666). Fig. 8. Mature cystocarp (SAP 087667). Fig. 9. Spermatangial branches formed at the distal end of fertile branches (SAP 087665).

(Figs 15, 16). The trichoblasts are quickly shed, leaving scar cells (Figs 15, 16). Fully-grown trichoblasts were not found in our specimens: young trichoblasts reach 200 µm long and are divided pseudodichotomously up to four times. The scar cells are 8-15 µm high by 10-18 µm wide.

Tetrasporangia are formed on fertile determinate branches, which are 400-700 µm high, in a straight series of two to five, one per segment, except for the proximal two to four and distal two to four segments (Fig. 4). Tetrasporangia are



Figs. 10-17. *Herposiphonia vietnamica*. Figs 10-14. Various shapes of rhizoids, all of which are unicellular (Fig. 10, female plant of SAP 087665; Fig. 11, tetrasporangial plant of SAP 087664; Fig. 12, female plant of SAP 087666; Fig. 13; vegetative plant of SAP 087662; Fig. 14; male plant of SAP 087665). Figs 15, 16. Apices of determinate branches of female plants, with spirally arranged vegetative trichoblasts or their scar cells (Fig. 15, SAP 087666; Fig. 16, 087665). a, apical cell (apical cell in Fig. 15 that is behind the last-formed trichoblast and is not depicted); numerals, sequence of formation of vegetative trichoblasts. Fig. 17. Spirally arranged spermatangial branches at the distal end of a fertile branch (SAP 087665). numerals, sequence of formation of spermatangial branches (the first-formed lateral, which leaves its scar cell, is probably a vegetative trichoblast).

associated with two lateral cover cells, lacking a basal cover cell (Fig. 5). Mature tetrasporangia have tetrahedrally arranged prominent spores, 60-75 μm in diameter.

A single procarpial trichoblast is produced on the subterminal segment (the seventh to ninth segment from the base) of each fertile determinate branch (Fig. 6). Each procarp is formed on the suprabasal segment of a procarpial trichoblast. A procarp is covered prior to fertilization by a pericarp. Fertile branches with a developing cystocarp continue to grow upwards and form five to eight segments, whereas those lacking such a cystocarp cease apical growth: the cystocarp is therefore positioned on the median to upper third region of the bearing branch (Figs 7, 8). Mature cystocarps are ovoid, 380-420 μm high by 280-320 μm in diameter (Fig. 8). Cystocarp-bearing branches do not become thickened as the cystocarp develops (Figs 7, 8): those with mature or nearly mature cystocarps are 50-75 μm in diameter and neighbouring branches (sterile, with abortive cystocarps or with non-fertilized procarps) are 50-80 μm in diameter.

Spermatangial branches are formed on the tips of determinate branches of male gametophytes (Figs 9, 17). Three to five spermatangial branches are formed successively from every segment in a spiral manner (Fig. 17) after the formation of one or two vegetative trichoblasts; sometimes they are not associated with vegetative trichoblasts. The spermatangial branches are almost straight and form numerous spermatangia, except for the proximal two segments. The fertile portion of spermatangial branches consists of seven or eight segments (without a sterile tip) and are terete. Mature spermatangial branches were not found in our specimens: large branches are 65-75 μm long by 25-30 μm wide at the lower widest portion.

DISCUSSION

The following features have been used in combination (sometimes solitarily) to distinguish species of the genus *Herposiphonia* (Falkenberg, 1901; Børgesen, 1920; Baardseth, 1941; Tseng, 1944; Chapman, 1963; Dawson, 1963; Hollenberg, 1968, 1970; Morrill, 1976; Lawson & John, 1982; Schnetter & Bula Meyer, 1982; Wynne, 1984; Stegenga & Kemperman, 1987; Millar, 1990; Schneider & Searles, 1991, 1997; Norris, 1992): (1) the dimension of primary axes (length, diameter and number of pericentral cells per segment); (2) the presence/absence of distichous branching; (3) the regular/irregular production of branches from every segment of the prostrate axis; (4) when regularly formed, whether one determinate branch and one indeterminate branch are formed alternately (d/i pattern), or three determinate branches and one indeterminate branch alternately (d/d/d/i pattern); (5) uni-/multicellular rhizoids; (6) the shape of determinate branches, terete, clavate, or compressed (ligulate); (7) the dimension of determinate branches (length, number of segments and diameter); (8) the presence/absence of branching in determinate branches; (9) the presence/absence of conspicuously elongated suprabasal segment of determinate branches; (10) the length/diameter ratio in segments of determinate branches; (11) the frequency of vegetative trichoblasts; (12) the length of vegetative trichoblasts and number of pseudodichotomy; (13) the position of tetrasporangia, distal, middle or proximal; (14) the number of tetrasporangia per branch; (15) the number of tetrasporangia

per segment, one or two; (16) the arrangement of tetrasporangia, spiral or straight; (17) the size of tetrasporangia; (18) the arrangement of procarpial trichoblasts, subterminal, distal, or secund on fertile determinate branches; (19) the position of cystocarps, terminal or lateral; (20) the shape and size of cystocarps; (21) branched/unbranched spermatangial trichoblasts, those that basally dichotomise into fertile (spermatangial branch) and sterile forks, or those which are unbranched (the entire trichoblast being converted into spermatangial branch); (22) the arrangement of spermatangial trichoblasts, spiralled, terminalized or secund on fertile determinate branches; and (23) the dimension of spermatangial branches. Morrill (1976) stated as follows: "*Herposiphonia* commonly is described as having unicellular rhizoids; in reality they are unicellular only at first, later they become digitate then multicellular, dendroid and disciform". However, only unicellular rhizoids, which are in various developmental stages (including a mature stage), were found in our material of *H. vietnamica*. More attention should be paid to rhizoids for reassessment of their taxonomic value. In addition, plant colour (Tseng, 1944; Jaasund, 1977) and chloroplast shape (Hollenberg, 1968) have been given taxonomic value by some workers.

It is difficult to find clear-cut vegetative differences between species with terete determinate branches in *Herposiphonia*, as some of the taxonomic features such as the number of pericentral cells per segment, branching pattern [one determinate branch and one indeterminate branch formed alternately (d/i pattern) or three determinate branches and one indeterminate branch formed alternately (d/d/d/i pattern)], and the length of determinate branches (and the number of segments) are variable in some species (Hollenberg, 1968; Morrill, 1976). In such cases the position of sexual reproductive structures, however, may provide the most critical feature in the genus (Morrill, 1976; Masuda & Kogame, 2000). Masuda & Kogame (2000) added further two taxonomic characters in relation to reproductive structures: (1) the presence/absence of an elongate sterile tip of spermatangial branches and (2) the presence/absence of conspicuously thickening growth of cystocarp-bearing branches concurrently with the development of a cystocarp.

A comparison of Vietnamese and Malaysian specimens of *H. vietnamica* shows a low degree of morphological variation (Masuda *et al.* 2000). These specimens are characterised by relatively slender prostrate axes with a small number of pericentral cells, short, slender, terete determinate branches, straight short-chained tetrasporangia, a relatively large, ovoid cystocarp that is positioned on the median to the upper third region of the parental determinate branch, and spiralled spermatangial branches without a sterile tip. Although Pham (1969) and Masuda *et al.* (2000) described the cystocarp shape of this species as urceolate, it is more appropriate to call it ovoid because mature cystocarps lack a conspicuous neck (Pham, 1969, fig. 2.197; Masuda *et al.*, 2000, fig. 23).

Herposiphonia tenella (C. Agardh) Ambronn seems to be most closely related to *H. vietnamica*. It is widely distributed in tropical regions of the Pacific (Dawson, 1963; Hollenberg, 1968; Masuda & Kogame, 2000), Indian Ocean [Hollenberg, 1968; Wynne, 1995, as *H. secunda* (C. Agardh) Ambronn f. *tenella* (C. Agardh) Wynne], the Atlantic (Børgesen, 1920; Joly *et al.*, 1963; Morrill, 1976; Schneider & Searles, 1991) and the Mediterranean (Agardh, 1828, as *Hutchinsia tenella* C. Agardh; Falkenberg, 1901; Coppejans, 1983) [type locality: Sicily (Agardh, 1828)] and is known as a variable species in vegetative and reproductive features (Tab. 1). Several species may be involved in the above-cited reports of *H. tenella*. However, each of variously circumscribed populations of *H. tenella* is distinguished from *H. vietnamica* by the combination of the following features: 1) longer determinate branches; 2) the presence of multicellular rhizoids; 3) the

Tab. 1. Comparison of *Herposiphonia vietnamica* and related species.

	H. delicatula (*Indo-Pacific*)[1]	*H. delicatula* (*Atlantic*)[2]	*H. tenella* (*Indo-Pacific*)[3]	*H. tenella* (*Atlantic*)[4]	*H. vietnamica* (*Vietnam*)
Diameter of primary axes	35-40 µm [36-44 µm]	30-45 µm	80-100 µm [80-90 µm]	50-100 µm [50-90 µm]	50-120 µm
Number of pericentral	7 or 8 [6-8]	7 or 8	8-10 [8]	7-10	8-10
Branching pattern	d/d/d/i pattern	d/d/d/i pattern	d/d/d/i pattern	d/d/d/i pattern	d/d/d/i pattern
Rhizoids	With multicellular tips	With multicellular tips	Unicellular	Unicellular or few-celled	Unicellular
Height (number of segments) and diameter of determinate branches	(12-30)[5] and 50-75 µm [780-950 µm (10 or 11)[6]]	(12-53)[5] and 30-40 µm	600-1200 µm (10-18) and 50-75 µm [up to 1500 µm (16-18) and 50-60 µm]	1000-8000 µm (11-45) and 30-70 µm	300-700 µm (7-11) and 50-100 µm
Length/diameter ratio in segments of determinate branches	1.0-1.5	1.0-2.0	0.9-1.7 [1.5]	1.0-5.0	0.7-1.8
Chloroplasts	Zonate	[Discoid]	Discoid [zonate]	Unknown	Discoid or ribbon-like
Number of vegetative trichoblasts	3 or 4 [2 or 3]	3 or 4	2 or 3 [2-5]	Unknown	2 or 3
Length of vegetative trichoblasts	Up to 700 µm	Unknown	Up to 1000 µm [1500 µm] cell	Unknown	200 µm long[7]
Height of tetrasporangial branches	Unknown	Unknown	600-1100 µm	Unknown	400-700 µm
Position of tetrasporangia on fertile branches	Proximal to middle	Various portions	Middle	Various portions	Middle
Number of tetrasporangia/branch	5-8 [5-7]	5-32	2-6	10-30 [10-40]	2-5
Diameter of tetrasporangia	Unknown	60 µm	55-60 µm	35-60 µm	60-75 µm

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Tab. 1. (continued)

	H. delicatula (Indo-Pacific)[1]	*H. delicatula* (Atlantic)[2]	*H. tenella* (Indo-Pacific)[3]	*H. tenella* (Atlantic)[4]	*H. vietnamica* (Vietnam)
Position of procarpial trichoblasts on fertile branches	Basal half	[Distal portion]	Distal portion	Distal portion	Distal portion
Cystocarp-bearing segment from the base	4th to 6th segment	Unknown	8th to 15th segment	Unknown	7th to 9th segment
Number of sterile segments above cystocarp-bearing segment	Unknown	Unknown	7-12	Unknown	5-8
Shape and dimension of cystocarps	Unknown	Ovoid, 200 µm wide	Urceolate, 400-700 µm high by 250-500 µm wide	Urceolate[8], 300-500 µm wide	Ovoid, 380-420 µm high by 280-320 µm wide
Thickening growth of cystocarp-bearing branches	Unknown	Unknown	Present	Unknown	Absent
Spermatangial branches	Arising on convex side of branches 3-5 segments from the base	Secundly arranged along concave side of branch apex	Spiralled in distal successive 4 to 6 segments	[Spiralled in distal successive (up to 10) segments]	Spiralled in distal successive 3 to 5 segments
Number of fertile segments of spermatangial branches	Unknown	Unknown	7-9	4 or 5 [10 to 12]	7 or 8
Sterile tip of spermatangial branches	Absent	1- to 4-celled	1 or 2-celled	1 or 2-celled [2-5]	Absent
Reference	Hollenberg, 1968; Wynne, 1995	Morrill, 1976; Schneider & Searles, 1991	Hollenberg, 1968; Masuda & Kogame, 2000	Børgesen, 1920; Morrill, 1976; Schneider & Searles, 1991	Present paper

1. Data are cited from Hollenberg (1968) except for those in brackets (Wynne, 1995).
2. Data are cited from Schneider & Searles (1991) except for those in brackets (Morrill, 1976).
3. Data are cited from Masuda & Kogame (2000) except for those in brackets (Hollenberg, 1968).
4. Data are cited from Schneider & Searles (1991) except for those in brackets (Børgesen, 1920) and in braces (Morrill, 1976).
5. Length was not given by the author.
6. Diameter was not given by the author.
7. Mature trichoblasts were not measured.
8. Schneider & Searles (1991) stated: "cystocarps ovoid when immature, becoming globular, with obvious necks and ostioles". This means that the overall shape of each cystocarp is urceolate.

BIBL. MUSEUM PARIS

presence of conspicuously thickening growth of cystocarp-bearing branches concurrently with the development of a cystocarp (see Masuda & Kogame, 2000, figs 18, 19), 4) the shape of cystocarps; and 5) the presence of a sterile tip on spermatangial branches (Tab. 1).

Hollenberg (1968) reported zonate chloroplasts (as chromatophores) for some *Herposiphonia* species including *H. tenella* and *H. delicatula* Hollenberg. However, Morrill (1976) mentioned as follows: "I have never found any zonate chloroplasts (as chromoplasts) in any member of this genus examined thus far. They all seem to have small, discrete, scattered, discoid chromoplasts or, less often, discoid ones joined into occasional reticulations. Where incised walls intrude, the protoplast is thinner, and where teeth obtrude, the protoplast is thicker, hence a darker color; this appears to account for the false impression of zonate chromoplasts. In senescent plants, chromoplasts sometimes coalesce into irregular ribbons or patches that might be construed as bands, but they are not necessarily zonate". Hollenberg's (1968) zonate chloroplasts could correspond to pectinately arranged chloroplasts described by Abbott (1999, as plastids). More attention should be paid to chloroplasts.

A further species that requires comparison with *H. vietnamica* is *H. delicatula*, which is closest to *H. tenella*, according to Hollenberg (1968). *Herposiphonia delicatula* is also widely distributed in tropical regions of the Pacific (Hollenberg, 1968; Abbott, 1999), Indian Ocean (Hollenberg, 1968; Wynne, 1995) and the Atlantic (Hollenberg, 1968; Morrill, 1976; Schneider & Searles, 1991) [type locality: Falas Island (Truck group), Caroline Islands in the western Pacific (Hollenberg, 1968)]. *Herposiphonia delicatula* is distinguished from *H. vietnamica* by extremely slender primary axes and rhizoids with multicellular tips, although there are some discrepancies between the Indo-Pacific and Atlantic specimens of *H. delicatula* besides the above-mentioned chloroplast type (Tab. 1). The position of sexual reproductive structures is different, basal half in the Indo-Pacific specimens *versus* distal in the Atlantic specimens, although it is one of the most critical features in defining species of this genus (Morrill, 1976; Masuda & Kogame, 2000). A further study is needed to elucidate their taxonomic relationship. In spite of this problem, the Indo-Pacific *H. delicatula* is clearly distinguished from *H. vietnamica* by the position of female and male reproductive structures, and the Atlantic *H. delicatula* is distinguished from *H. vietnamica* by the secundly arranged spermatangial branches (Tab. 1).

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