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A new red alga *Herposiphonia japonica* (Rhodomelaceae, Ceramiales) from the north-western Pacific

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Abstract — The red alga *Herposiphonia japonica* Masuda *et* Shimada, sp. nov. (Rhodomelaceae, Ceramiales) is described from the Pacific coast of central Japan. It is characterized by the following combination of features: 1) a relatively broad (150-200 µm) prostrate axis bearing either a determinate branch or an indeterminate branch (or branch primordium) from every segment, commonly in a sequence of three determinate branches followed by one indeterminate branch; 2) determinate branches that are terete and relatively long (to 2.5 mm long and consisting of 15-32 segments) and slender (75-80 µm in diameter); 3) central axial cells in mature segments of determinate branches that are cask-shaped and 30-50 µm in diameter (2-3 times broader than surrounding pericentral cells); 4) proximal positions of tetrasporangia, procarpial trichoblasts, and spermatangial branches on fertile determinate branches; 5) a secund arrangement of 4-12 spermatangial branches in two rows along the concave or convex side (or the lateral and either the concave or convex side) of fertile branches and sometimes in three rows along the lateral and either the concave or convex side or along these three sides; and 6) a slight thickening of the proximal segments of cystocarp-bearing branches.

Ceramiales / *Herposiphonia japonica* / morphology / Rhodomelaceae / Rhodophyta / taxonomy

Résumé — Une nouvelle algue rouge de la région nord-ouest du Pacifique, *Herposiphonia japonica* (Rhodomelaceae, Ceramiales). L'algue rouge *Herposiphonia japonica* Masuda *et* Shimada, sp. nov. (Rhodomelaceae, Ceramiales) est décrite dans les côtes Pacifique du Japon central. Elle est caractérisée par l'ensemble des particularités suivantes : 1) un axe prostré relativement large (150-200 µm) portant, soit une ramification à croissance limitée, soit une ramification à croissance illimitée (ou ramification primaire) sur chaque segment, ordinairement en série de trois ramifications à croissance limitée suivie d'une ramification à croissance illimitée ; 2) les ramifications à croissance limitée ont une section circulaire et sont relativement longues (jusqu'à 2,5 mm de longueur, et comportant de 15 à 32 segments) et fines (75-80 µm de diamètre) ; 3) les cellules axiales des segments âgés des ramifications à croissance limitée ont une forme de tonneau et mesurent de 30-50 µm de diamètre (2-3 fois plus larges que les cellules péricentrales qui les entourent) ; 4) les tétrasporocystes, les trichoblastes procarpiques et les rameaux mâles des ramifications fertiles à croissance

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limitée sont en position proximale ; 5) une disposition de 4-12 rameaux mâles sur deux rangs du côté concave ou convexe (ou latéralement, et alors soit du côté concave, soit du côté convexe) du rameau fertile et quelquefois sur trois rangées latérales, ou du côté concave ou du côté convexe, soit le long de ces trois côtés ; et 6) un léger épaississement des segments proximaux des rameaux portant les cystocarpes. (Traduit par la Rédaction.)

Ceramiales / *Herposiphonia japonica* / morphologie / Rhodomelaceae / Rhodophyta / taxinomie

INTRODUCTION

The red algal genus *Herposiphonia* (Ceramiales, Rhodomelaceae) currently includes approximately 56 species that are distributed in the tropical to warm-temperate regions of the world (Masuda & Kogame, 2000). The taxonomic characters (about 25 of them) that are useful in distinguishing these species were reviewed by Masuda & Shimada (2002). The following characters are especially important as they show no variability: 1) the presence or absence of distichous branching; 2) the shape of determinate branches (terete, clavate or compressed); 3) the presence or absence of branching in determinate branches; 4) the presence or absence of conspicuously elongated suprabasal segment of determinate branches; 5) the frequency of vegetative trichoblasts; 6) the position of tetrasporangia (distal, middle or proximal); 7) the number of tetrasporangia per segment (one or two); 8) the position of cystocarps (terminal, distal or proximal); 9) the shape and size of cystocarps; 10) the presence or absence of thickened growth of cystocarp-bearing branches concurrently with development of the cystocarp; 11) the arrangement of spermatangial branches (spiral or secund); and 12) the position of spermatangial branches (distal or proximal). Several other features, however, 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. It is, therefore sometimes difficult to find clear-cut vegetative differences between species with terete determinate branches, such as *H. parca* Setchell, *H. secunda* (C. Agardh) Ambronn and *H. tenella* (C. Agardh) Ambronn [Hollenberg, 1968; Wynne, 1984, as *H. secunda* f. *tenella* (C. Agardh) Wynne; Masuda & Kogame, 2000]. In such cases reproductive features, especially the position of sexual reproductive structures, can provide critical taxonomic characters (Hollenberg, 1968; Masuda & Kogame, 2000; Masuda & Shimada, 2002).

In the north-western Pacific the following 19 species have been reported: 1) *H. caespitosa* Tseng (1944); 2) *H. crassa* Hollenberg (Silva *et al.*, 1987); 3) *H. delicatula* Hollenberg (1968); 4) *H. dendroidea* Hollenberg (Silva *et al.*, 1987); 5) *H. elongata* Masuda *et* Kogame (2000); 6) *H. fissidentoides* (Holmes) Okamura (1899); 7) *H. insidiosa* (Greville *ex* J. Agardh) Falkenberg (Okamura, 1930; Tseng, 1944); 8) *H. nuda* Hollenberg (Silva *et al.*, 1987); 9) *H. obscura* Hollenberg (Silva *et al.*, 1987); 10) *H. pacifica* Hollenberg (1968; Masuda *et al.*, 2000); 11) *H. parca* (Yoshida, 1998), including as a synonym *H. terminalis* Segi (1954); 12) *H. pecten-veneris* (Harvey) Falkenberg (Tseng, 1944); 13) *H. plumula* (J. Agardh) Falkenberg (Silva *et al.*, 1987); 14) *H. ramosa* Tseng (1944); 15) *H. secunda* (Phang, 1994);

16) *H. subdisticha* Okamura (1899); 17) *H. tenella* (Masuda & Kogame, 2000); 18) *H. trichia* Hollenberg (Silva *et al.*, 1987); and 19) *H. vietnamica* Pham (1969; Masuda *et al.*, 2000; Masuda & Shimada, 2002). Records of several species, however, such as *H. plumula* and *H. secunda*, need verification because adequate descriptions are not given.

In this paper we describe a new species of *Herposiphonia* that is characterized by a particular combination of morphological features, including a secund arrangement and proximal position of spermatangial branches.

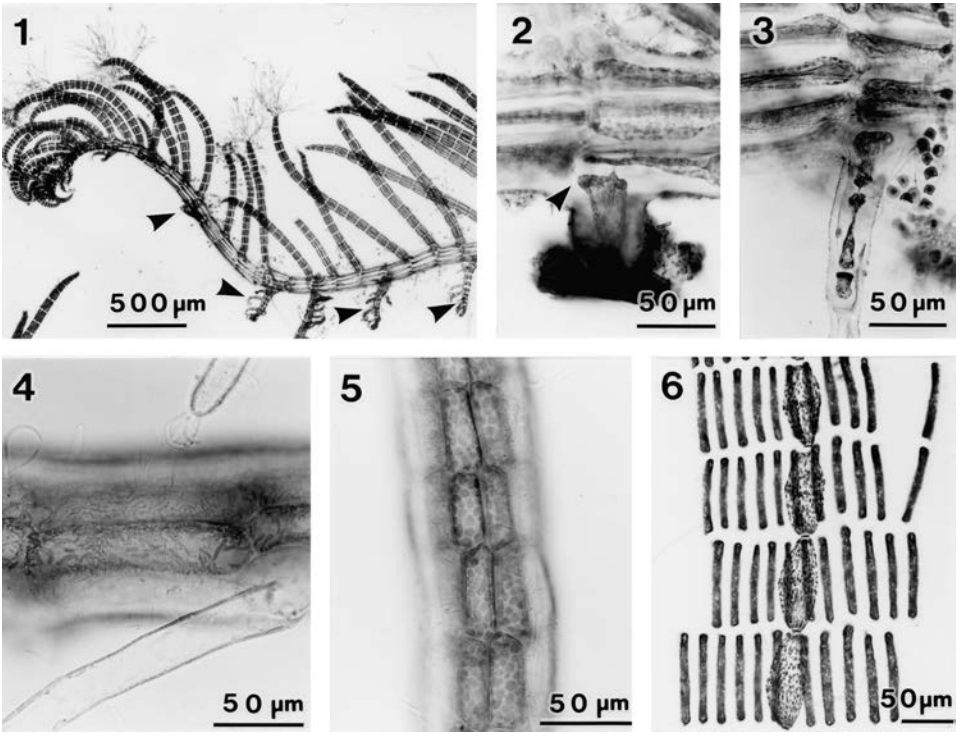
MATERIALS AND METHODS

Specimens were collected at Irago-misaki (Aichi Prefecture) on the Pacific coast of central Japan. Voucher specimens were mounted in 30 % Karo® on microscope slides or dried on herbarium sheets and are deposited in the Herbarium of the Graduate School of Science, Hokkaido University, Sapporo (SAP): (1) 9 Sept. 1999, vegetative (089201-089203), procarpic/cystocarpic (089204-089206), spermatangial (089207, 089208), *leg.* S. Shimada; and (2) 13 Nov. 2000, vegetative (089209), tetrasporangial (089210-089213), procarpic/cystocarpic (089214, 089215), spermatangial (089216-089219), *leg.* M. Masuda. Specimens were fixed in 10 % formalin in seawater and later the majority were mounted in 30 % Karo® on microscope slides after staining with 0.5 % (w/v) cotton blue in a lactic acid/phenol/glycerol/water [1:1:1:1 (v/v)] solution. The number of pericentral cells was determined in squash preparations.

RESULTS

***Herposiphonia japonica* Masuda *et* Shimada, sp. nov.**

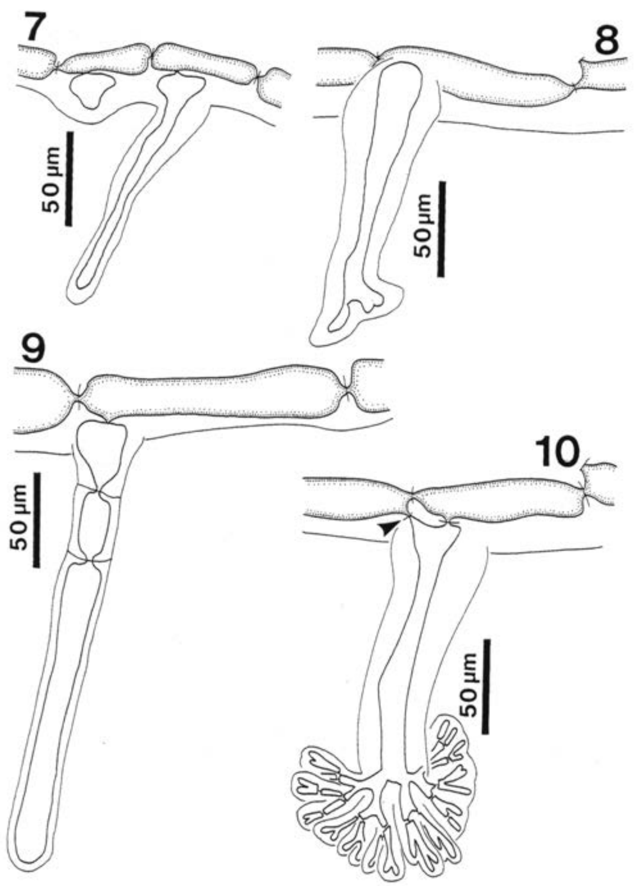
Axes prostrati, epiphytici in algis aliis, 12-28 mm in longitudine, 150-200 µm diametro, 10 vel 11 cellulis pericentralibus in quoque segmento, e omni segment ramum determinatum vel ramum indeterminatum ferentes, vulgo in serie e 3 ramis determinatis deinde uno ramo indeterminato; rami determinati teres, 0.8-2.5 mm in altitudine, 75-80 µm diametro, ex 15-32 segmentis constantes, 4 cellulis pericentralibus in segmento basali, 8 or 9 cellulis pericentralibus in segmento suprabasali, 9-11 cellulis pericentralibus in segmentis ceteris; cellulae axiales centrales in segmentis maturis ramorum determinatorum doliiformes, 30-50 µm diametro; trichoblasti vegetativi in segmentis successivis 4-8(-12) distalibus ramorum determinatorum in serie spirali facti, 300-450 µm longi, decidui. Tetrasporangia in ramis determinatis fertilibus 7-15 segmentorum praeter proximales 2 vel 3(-4) et distales (6-)8-12(-20) segmentorum in serie recta (vel partim spirali); tetrasporangia matura prominentia, 60-75 µm diametro. Trichoblasti procarpiferi in segmento tertio vel quarto (interdum secundo vel quinto) e basi rami determinati fertilis facti; cystocarpia matura late ovoidea vel fere globosa, 600-800 µm in altitudine et 480-650 µm diametro. Rami spermatangiis e segmento tertio (raro secundo vel quarto) e basi rami fertili versus 3-11 segmenta distalia successiva formati, plerumque biseriales secus laterem concavum vel convexum (seu laterem laterale et unumquidque



Figs 1-6. *Herposiphonia japonica*. Formalin/seawater-preserved material, unless otherwise indicated. Fig. 1. 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)]. Fig. 2. Rhizoid secondarily pit-connected (arrowhead) with the closest pericentral cell of the foregoing segment. Fig. 3. Septate rhizoid. Fig. 4. Portion of a prostrate axis, showing ribbon-like chloroplasts (living material). Fig. 5. Portion of a young determinate branch, showing discoid chloroplasts (living material). Fig. 6. Squash preparation of a mature determinate branch; note each segment consisting of a cask-shaped central axial cell and 11 slender pericentral cells.

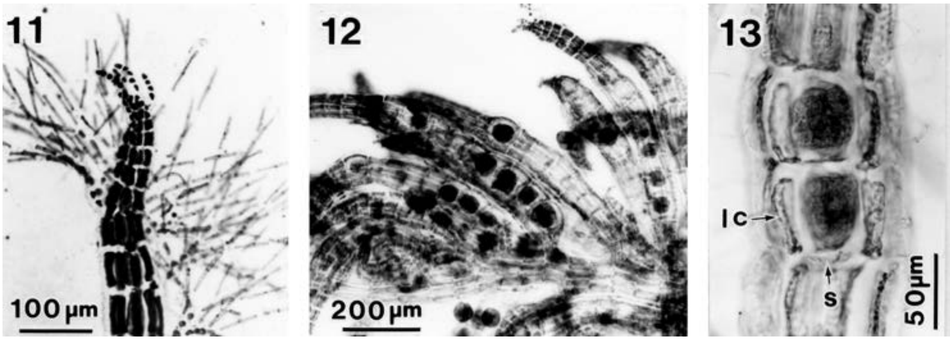
laterum concavorum et convexorum) ramorum fertilium, nonnunquam triseriales secus laterem laterale et unumquidque laterum concavorum et convexorum (vel latera tria horum); apex sterilis ex 1-6 segmentis unicellularibus constans, 15-65 µm in longitudine; pars fertilis ramorum spermatangiis conica, ex 8-14 segmentis constans, 150-380 µm in longitudine, 45-75 µm diametro.

Prostrate axes epiphytic on other algae, 12-28 mm in length, 150-200 µm in diameter, with 10 or 11 pericentral cells in each segment, bearing a determinate branch or an indeterminate branch from every segment, commonly in a sequence of three determinate branches followed by one indeterminate branch; determinate branches terete, 0.8-2.5 mm in height, 75-80 µm in diameter, consisting of 15-32 segments, with four pericentral cells in the basal segment, eight or nine pericentral cells in the suprabasal segment, with 9-11 pericentral cells in the other segments; central axial cells in mature segments of determinate branches cask-shaped, 30-50 µm in diameter; vegetative trichoblasts formed on the distal 4-8(-12) successive segments of determinate branches in a spiral series, 300-450 µm long,



Figs 7-10. *Herposiphonia japonica*. Formalin/seawater-preserved material. Fig. 7. Two young unicellular rhizoids. Fig. 8. Forked unicellular rhizoid. Fig. 9. Septate rhizoid. Fig. 10. Rhizoid with a digitate multicellular pad; note a secondary pit-connection (arrowhead) between the rhizoid and the closest pericentral cell of the foregoing segment.

deciduous. Tetrasporangia formed on fertile determinate branches of 7-15 segments except for the proximal 2 or 3(-4) and distal (6-)8-12(-20) segments in a straight (or partially spiral) series; mature tetrasporangia prominent, 60-75 µm in diameter. Procarpial trichoblasts produced on the third or fourth (sometimes second or fifth) segment from the base of a fertile determinate branch; mature cystocarps broadly ovoid or nearly globose, 600-800 µm in height and 480-650 µm in diameter. Spermatangial branches produced from the third (rarely second or fourth) segment from the base of a fertile branch towards 3-11 successive distal segments, usually in two rows along the concave or convex side (or the lateral and either the concave or convex side) of fertile branches, sometimes in three rows along the lateral and either the concave or convex side or along these three sides; sterile tip consisting of 1-6 unicellular segments, 15-65 µm in length; fertile portion of spermatangial branches conical, consisting of 8-14 segments, 150-380 µm in length and 45-75 µm in diameter.



Figs 11-13. *Herposiphonia japonica*. Formalin/seawater-preserved material. Fig. 11. Tip of a young determinate branch bearing vegetative trichoblasts. Fig. 12. Tetrasporangial branches. Fig. 13. Tetrasporangia without a basal cover cell: lc, lateral cover cell (another lateral cover cell is out of focus); s, stalk cell.

Holotypus: Spermatangial specimen deposited in SAP (089219), Irago-misaki, Aichi Prefecture, central Japan, 13 Nov. 2000, *leg*. M. Masuda.

Etymology: The specific epithet, *japonica*, alludes to the geographical range of the species.

Plants are gregariously attached to other algae, such as *Amphiroa misakiensis* Yendo, *Chondracanthus intermedius* (Suringar) Hommersand and *Laurencia cartilaginea* Yamada, which grow on bedrock or rocks in the mid- to lower intertidal zone on an exposed, high-energy coast. Plants are dark red in colour. Primary axes are 12-28 mm in length, prostrate (Fig. 1) and are attached to the basiphyte by numerous rhizoids that are cut off from the distal ends of ventral pericentral cells (Figs 2, 3, 7-10). The rhizoids grow to 75-800 µm in length by 25-50 µm in diameter and generally have a multicellular, digitate attachment pad (Fig. 10), but are also sometimes simple (Figs 7, 9) or forked (Fig. 8). Mature rhizoids are often secondarily pit-connected with the closest pericentral cell of the foregoing segment (Figs 2, 10). Monosiphonous portions of rhizoids are often divided into two to four parts by transverse septa (Figs 3, 9). Prostrate axes are uncorticated and 150-200 µm in diameter, with segments 0.7-2.0 diameters long, and consisting of a central axial and 10 or 11 pericentral cells.

The axes bear either a determinate branch or an indeterminate branch (or branch primordium) from every segment in a sequence of three determinate branches (d) followed by one indeterminate branch (i), i.e., in a repetitive pattern of d/d/d/i (from base to apex) (Fig. 1). A d/i pattern and intermediate patterns (d/d/i, d/d/i/i, d/d/d/i/i/i) between the d/d/d/i and d/i patterns are rarely present in some portions of the same or different individuals along with the d/d/d/i pattern. Occasionally a naked (unbranched) node interrupts the above-mentioned patterns. In dorsal view, branches are displaced to the left (l) and right (r) sides of the parental indeterminate axis. The most frequent pattern found in *H. japonica* is a repeat of ld/rd/ld/li/rd/ld/rd/ri (from base to apex). Some indeterminate branches grow like the parental axis, and function as secondary axes; others, however, remain short or rudimentary (these are potential indeterminate branches or secondary axes).

All determinate branches are curved towards the apex of the parental axis when young but become straight and erect as they mature. Mature determinate branches are terete, 0.8-2.5 mm in height by 75-80 µm in diameter and con-

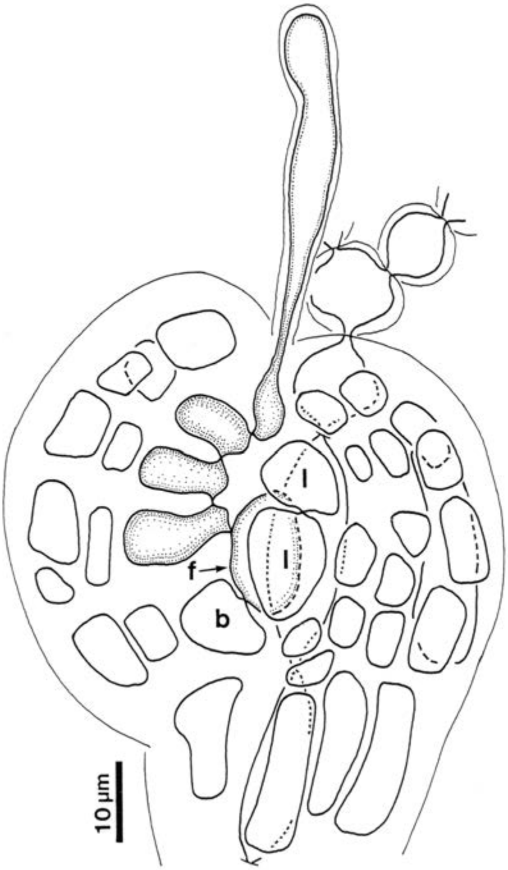


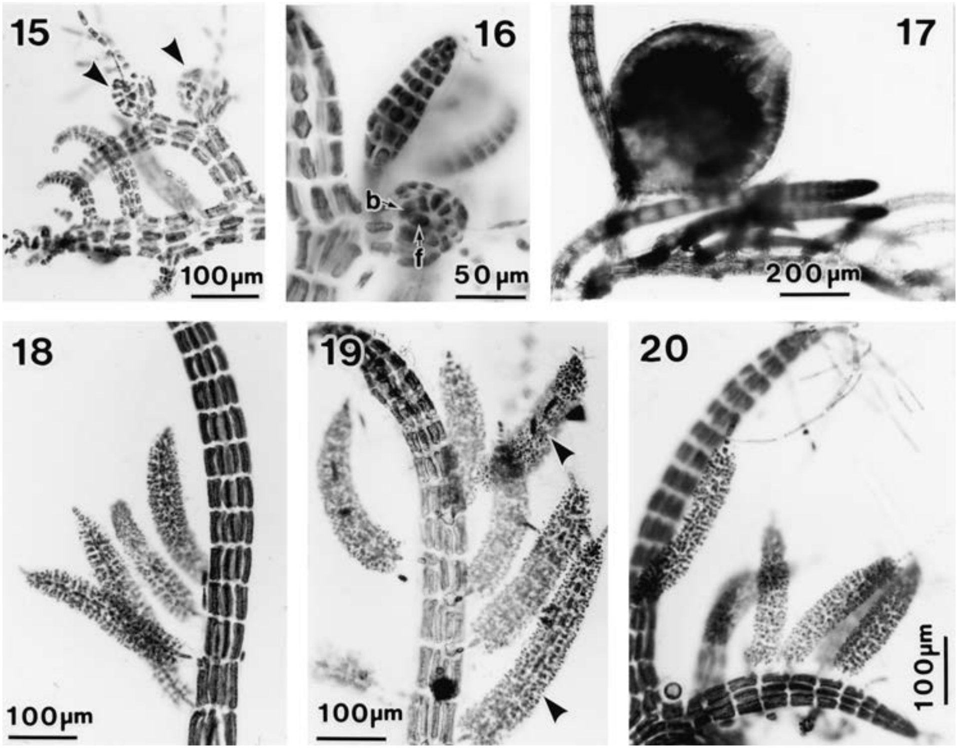
Fig. 14. Mature procarp of *Herposiphonia japonica*. Formalin/seawater-preserved material. b, initial of the basal sterile-cell group; f, fertile pericentral cell bearing a four-celled carpogonial branch (dotted); l, initial of the lateral sterile-cell group. Cells of the pericarp above the carpogonial branch and the upper portion of the procarpial trichoblast are not depicted.

sist of 15-32 ecorticate segments that are 0.8-1.4 diameters long in the lower to middle portions. Basal segments are exceptionally short and mostly less than 0.6 diameters long. The basal segments of determinate branches have four pericentral cells, the suprabasal segments eight or nine pericentral cells, and other segments 9-11 pericentral cells. Chloroplasts are irregularly ribbon-like (Fig. 4) in cells of mature segments, although they are discoidal (Fig. 5) in those of young segments. Central axial cells in mature segments of determinate branches are cask-shaped (Fig. 6), 30-50 µm in diameter, and 2-3 times broader than the surrounding pericentral cells, which are 10-18 µm in diameter.

Vegetative trichoblasts arise in a spiral pattern on the distal 4-8(-12) successive segments of determinate branches (Fig. 11), including fertile branches. They are deciduous and leave scar cells. Fully-grown trichoblasts are 300-450 µm long and are divided pseudodichotomously three or four times. Scar cells are 7-15 µm in height by 10-18 µm in diameter.

Tetrasporangia are formed on fertile determinate branches, which are 400-1200 (up to 1800) μm in height, in a straight (or partially spiral) series of 7-15, one per segment, except for the proximal two or three (rarely four) and distal (6-)8-12(-20) segments (Fig. 12). Tetrasporangia are associated with two lateral cover cells and lack a basal cover cell (Fig. 13). Mature tetrasporangia are 60-75 μm in diameter and have tetrahedrally arranged spores.

A single procarpial trichoblast is produced on the convex, concave or lateral side of the third or fourth (sometimes second or fifth) segment from the base of each fertile determinate branch (Fig. 14); an additional procarpial trichoblast is rarely formed on the fifth (or sixth or eighth) segment of the fertile branch (Fig. 15). Each procarp is formed on the suprabasal segment of a procarpial trichoblast and consists of a fertile pericentral cell bearing a four-celled carpogonial branch and two sterile-cell groups: one two-celled and lateral, the other one-celled and basal (Figs 14, 16). The procarp is covered prior to fertilization by a pericarp. The apical cell of the fertile branch continues to grow as the cystocarp develops



Figs 15-20. *Herposiphonia japonica*. Formalin/seawater-preserved material. Fig. 15. Tip of a female gametophyte; note two procarps (arrowheads) formed on a fertile branch. Fig. 16. Procarp: b, initial of the basal sterile-cell group (initial of the lateral sterile-cell group is out of focus); f, fertile pericentral cell bearing a four-celled carpogonial branch. Fig. 17. Mature cystocarp. Fig. 18. Spermatangial branches arranged in two rows along the concave side of a fertile branch. Fig. 19. Spermatangial branches arranged in three rows along the concave, lateral and convex (arrowheads) sides of a fertile branch (portion of the holotype specimen). Fig. 20. Spermatangial branches arranged in two rows along the convex side of a fertile branch.

and eventually forms 18-30 sterile segments, resulting in the cystocarp being located on the proximal region of the branch (Fig. 17).

Mature cystocarps are ovoid (Fig. 17) and 600-800 µm in height by 480-650 µm in diameter. The proximal two to five segments (i.e., the cystocarp-bearing one and those below) of the fertile branches become slightly thickened as the cystocarp develops; those with mature or nearly mature cystocarps are 90-120 µm in diameter, whereas corresponding segments of neighbouring branches (sterile, with abortive cystocarps or with non-fertilized procarps) are 65-80 µm in diameter.

Spermatangial trichoblasts (Figs 18-20) are formed initially on the third (rarely second or fourth) segment from the base of fertile branches and then progressively on 3-11 successive distal segments (rarely one or two segments do not bear spermatangial trichoblasts). More distal portions of these fertile branches (consisting of 10-25 segments) are completely sterile and bear three to six vegetative trichoblasts spirally on the apical successive segments after the production of the spermatangial trichoblasts (Fig. 20). Spermatangial trichoblasts are converted entirely into spermatangial branches and are secundly arranged, usually in two rows along the concave (Fig. 18) or convex side (Fig. 20) (or the lateral and either the concave or convex side) of fertile branches and sometimes in three rows along the lateral and either the concave or convex side or along these three sides (Fig. 19). They are straight or slightly curved and form numerous spermatangia, with the exception of the proximal two (sometimes three) segments (30-65 µm in length) and distal one to six segments (15-65 µm in length). The fertile portion of spermatangial branches is conical, 150-380 µm in length by 45-75 µm in diameter, and consists of 8-14 segments.

DISCUSSION

In *Herposiphonia*, the arrangement and position of cystocarps and spermatangial branches are regarded as the most important criteria for species discrimination (Morrill, 1976; Masuda & Kogame, 2000), but unfortunately such reproductive structures are known for relatively few species of the genus. Three variations in cystocarp position can occur: 1) When a procarpial trichoblast is produced on the subterminal segment of a fertile determinate branch, the fertile branch ceases apical growth as the cystocarp develops, which is therefore positioned terminally on the branch, 2) When several procarpial trichoblasts are produced spirally on the distal several segments of a fertile determinate branch, the apex of the fertile branch grows upwards as the cystocarp develops and forms many segments distally. In this case, the cystocarp is positioned on the distal or median region of the bearing branch, or 3) When several procarpial trichoblasts are formed secundly on a fertile determinate branch and a first-formed procarp is fertilized, the cystocarp is positioned on the proximal region of the parental branch. With regard to spermatangial branches, they can be spiraled at the apex of a fertile determinate branch, or secund on the proximal or median (occasionally distal) region of the bearing branch.

Many combinations of the positions of cystocarps and spermatangial branches have been recognized. Some species bear terminal cystocarps and spiraled spermatangial branches, e.g., *H. caespitosa* Tseng (1944), *H. elongata* Masuda *et* Kogame (2000), *H. filifera* Hollenberg (1968) and *H. parca* Setchell (Hollenberg, 1968). Other species have median (sometimes distal) cystocarps and spiraled spermatangial branches, e.g., *H. arcuata* Hollenberg (1968), *H. tenella* (Børgesen, 1920; Morrill, 1976; Masuda & Kogame, 2000) and *H. vietnamica* (Masuda & Shimada, 2002). The following species have median or proximal cystocarps and secundly arranged spermatangial branches that are similar to *H. japonica*: *H. ceratoclada* (Montagne) Reinbold (Falkenberg, 1901), *H. delicatula* (Morrill, 1976; Schneider & Searles, 1991), *H. falcata* (Kützing) De Toni [Wynne, 1984, as *H. prorepens* (Harvey) F. Schmitz; Stegenga *et al.*, 1997], *H. nuda* (Hollenberg, 1968), *H. paniculata* Baardseth (1941) and *H. verticillata* (Harvey) Kylin (Dawson, 1963; Morrill, 1976). Proximal segments (including the suprabasal segment) of fertile determinate branches in these species may have reproductive activity, which is entirely different from other species of the genus that produce reproductive structures exclusively on the distal segments. Of these, *H. ceratoclada* is excluded from further discussion, because the type specimen of *H. ceratoclada* is not a *Herposiphonia* (Wynne, 1984, p. 168).

In many species of *Herposiphonia*, the angle between the left and right branches is very narrow, as in the case of *H. japonica*, whereas it is 180° or nearly so in some other species. In the latter, the branches appear to be distichous, as in *H. paniculata* (Baardseth, 1941) and *H. verticillata* (Dawson, 1963; Morrill, 1976), so that these species are clearly distinguished from *H. japonica*. An Australian species, *H. calva* Millar (1990) is known to have proximal cystocarps, although its spermatangial branches are unknown. This Australian species is also distinguished from *H. japonica* by its distichously arranged branches (Millar, 1990).

Only three species require further consideration, *H. delicatula, H. falcata*, and *H. nuda* (Tab. 1). *Herposiphonia delicatula* is widely distributed in tropical regions of the Pacific Ocean (Hollenberg, 1968; Abbott, 1999), Indian Ocean (Hollenberg, 1968; Wynne, 1995) and the Atlantic Ocean (Hollenberg, 1968; Morrill, 1976; Schneider & Searles, 1991) [type locality: Falas Island (Truk group), Caroline Islands in the western Pacific (Hollenberg, 1968)]. There are some discrepancies between the Indo-Pacific and Atlantic specimens of *H. delicatula* (Tab. 1), although these specimens all possess extremely slender primary axes, a small number (seven or eight in primary axes and six to eight in determinate branches) of pericentral cells per segment, and three or four vegetative trichoblasts, all of which distinguish *H. delicatula* from *H. japonica*. The different position of sexual reproductive structures, on the proximal half of bearing branches in the Indo-Pacific specimens vs. distal in the Atlantic specimens, is a serious discrepancy, as it is the most critical feature in defining species of this genus (Morrill, 1976; Masuda & Kogame, 2000). Further study is needed to elucidate the taxonomic relationships of the Indo-Pacific and Atlantic specimens.

Herposiphonia falcata, which is endemic to South Africa (Stegenga *et al.*, 1997), is similar to *H. japonica*, but some critical differences are apparent (Tab. 1), including the number of pericentral cells in basal segments, the frequency of vegetative trichoblasts, cystocarp shape, and the presence or absence of thickened growth of the proximal segments of cystocarp-bearing branches.

Basal segments of determinate branches in all species of *Herposiphonia* have fewer pericentral cells than other segments. In many species the basal segments have four pericentral cells (as does *H. japonica*), including *H. clavata* Wynne (1984), *H. elongata* (Masuda & Kogame, 2000), *H. pacifica* (Masuda *et al.*, 2000), *H. prorepens* (Norris, 1992, as *H. akidoglossa* R. Norris; Stegenga *et al.*, 1997), *H. tenella* (Stegenga *et al.*, 1997; Masuda & Kogame, 2000), and *H. vietnamica* (Masuda *et al.*, 2000; Masuda & Shimada, 2002). However, the basal segments of some other species have a greater number of pericentral cells: five or six in *H. falcata*, six in *H. didymosporangia* Stegenga *et* Kemperman, and seven in *H. heringii*

(Harvey) Falkenberg (Stegenga *et al.*, 1997). Thus, the number of pericentral cells in basal segments of determinate branches is constant and a significant taxonomic feature, although that of other segments is variable depending on species, such as *H. parca* (Hollenberg, 1968) and *H. tenella* (Wynne, 1984, as *H. secunda* f. *tenella*).

The frequency of vegetative trichoblasts is a specific feature in the genus *Herposiphonia*; in some species vegetative trichoblasts are frequent to abundant, but in others they are rare or absent (Hollenberg, 1968). The frequency of vegetative trichoblasts in *H. japonica* and *H. falcata* is markedly different (Tab. 1).

The shape (and size) of cystocarps may be significant species-specific feature (Masuda & Shimada, 2002). Cystocarps of *H. falcata* are urceolate (Wynne, 1984, as *H. prorepens*; Stegenga *et al.*, 1997), whereas those of *H. japonica* are broadly ovoid or nearly globose [compare our Fig. 17 with Wynne's fig. 10 (1984)].

Lower segments of cystocarp-bearing branches in *H. japonica* become slightly broader as the cystocarp develops. Such growth is regarded as a distinctive feature of some species of *Herposiphonia*, such as *H. caespitosa*, *H. elongata*, *H. pecten-veneris* and *H. tenella* (Masuda & Kogame, 2000). Although less conspicuous in *H. japonica* than in those species (Masuda & Kogame, 2000), it should be regarded as a diagnostic feature of the new species. Wynne (1984) and Stegenga *et al.* (1997) did not describe such growth for their South African specimens of *H. falcata*.

Herposiphonia nuda, which was established on the basis of specimens from Ilio Point, Molokai, Hawaiian Islands (Hollenberg, 1968) and is known in tropical regions of the Pacific and Indian Oceans (Tab. 1), is distinguished from *H. japonica* by a smaller number of pericentral cells per segment, the presence of occasional branching of determinate branches, the absence of vegetative trichoblasts, and fewer spermatangial branches (Tab. 1). Furthermore, *H. nuda* may be distinguished from *H. japonica* by the diameter of central axial cells. Hollenberg (1968) described *H. nuda* as having: "determinate branches very slender, ... with 4-5 pericentral cells slightly flattened periclinally and a much more slender central cell", whereas *H. japonica* possesses cask-shaped central axial cells that are 2-3 times broader than surrounding pericentral cells.

The larger dimension of central axial cells has been used by Hollenberg (1968) as a diagnostic feature of some species, such as *H. dendroidea*, *H. dubia* Hollenberg, *H. filifera*, *H. pacifica* and *H. variablis* Hollenberg. Morrill (1976) recognized two distinct shapes of mature central axial cells, each of which characterizes individual species: (1) long, slender and cylindrical; and (2) plump, rounded and cask-shaped. *Herposiphonia japonica* is another species with central axial cells that are cask-shaped and conspicuously larger than their surrounding pericentral cells. Wynne (1984) illustrated cask-shaped central axial cells for his South African specimens of *H. falcata* (as *H. prorepens*).

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Tab. 1. Comparison of four closely related species of Herposiphonia among those with secundly arranged spermatangial trichoblasts.

	H. delicatula (Indo-Pacific)[1]	*H. delicatula* (Atlantic)[2]	*H. falcata*[3]	*H. nuda*[4]	*H. japonica*
Diameter of primary axes	35-40 µm	30-45 µm	Unknown	80-105 µm	150-200 µm
Number of pericentral cells per segment in primary axes	7 or 8	7 or 8	10-12	7 or 8	10 or 11
Rhizoids	With multicellular tips	With multicellular tips	With digitate tips[5]	Unicellular	With multicellular tips or septate filaments
Height (number of segments) and diameter of determinate branches	(12-30)[6] and 50-75 µm	(12-53)[6] and 30-40 µm	1.2(-2) mm (15-30) and 80-120 µm	2-3.5 mm (25-44) and 40-80 µm	0.5-2.5 mm (15-32) and 75-80 µm
Branching of determinate branches	Absent	Absent	Absent	Occasional	AbsentNumber of
Number of pericentral cells in the basal segment of determinate branches`	Unknown	Unknown	5 or 6	Unknown	4
Number of pericentral cells in segments other than the basal segment of determinate branches	6-8	6-8	10-14 (often 12)	4 or 5	8-11
Chloroplasts	Zonate	[Discoid]	Unknown	Not zonate	Discoid in young segments and ribbon-like in mature segments
Number of vegetative trichoblasts	3 or 4	3 or 4	Rare[7]	Absent	4-12
Position of tetrasporangia from the base of fertile branches	Proximal to middle[8]	Various positions[8]	3rd to 14th segments	Unknown	3rd to 18th
Arrangement of tetrasporangia	Unknown	Straight	Straight	Unknown	Straight or partially spiral
Number of tetrasporangia per branch	5-8	5-32	Up to 12	Unknown	7-15
Position of procarpial trichoblasts from the base of fertile branches	4th to 6th	[Distal portion[8]]	[4th or 5th]	Well above median point[8]	2nd to 5th
Shape and size of cystocarps	Unknown	Ovoid and 200 µm diam.	Urceolate and 500-600 µm diam.	Unknown	Broadly ovoid or nearly globose and 600-800 µm in height by 480-650 µm diam.

Thickened growth of the proximal segments of cystocarp-bearing branches	Unknown	Unknown	Absent	Unknown	Present (slightly)
Position of spermatangial trichoblasts from the base	Convex side of 3rd to 5th segments	Singly or in a series on concave side of branches below apex[8]	[Concave side] of 3rd to 9th segments	Concave side of 2 or 3 segments of branches well above	Concave or convex side lateral and either concave or convex side) of 3rd to 14th segments
Sterile tip of spermatangial trichoblasts	Absent	1- to 4-celled	Unknown	2- or 3-celled	1- to 6-celled, 15-60 μm long
Number of sterile segments of spermatangial trichoblast-bearing branches	Proximal 2-4 segments[9]	Unknown	Proximal 2 segments[9]	Unknown	Proximal 2 (rarely 1) and distal 10-25
Geographical range	Hawaii, Marshall Islands, Caroline Islands, Philippines, Mariana Islands, Malaysia, Maldives, Seychelles*	North Carolina	South Africa	Hawaii, Marshall Islands, Maldives	Japan
Reference	Hollenberg, 1968; Wynne, 1995	Morrill, 1976; Schneider & Searles, 1991	Wynne, 1984 (as *H. prorepens*) Stegenga *et al.*, 1997	Hollenberg, 1968	Present paper

1. Data are cited from Hollenberg (1968) except for that with an asterisk (Wynne, 1995)
2. Data are cited from Schneider & Searles (1991) except for those in brackets (Morrill, 1976).
3. Data are cited from Stegenga *et al*. (1997) except for those in brackets (Wynne, 1984).
4 Data are cited from Hollenberg (1968).
5 The authors did not describe whether rhizoids are multicellular or unicellular.
6. Height was not given by the authors.
7. The number was not given by the authors.
8. The position from the basal segment was not given by the authors.
9 The number of distal sterile segments was not given by the authors.

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