

Reestablishment of the Green Algal Genus *Rhipidosiphon* Montagne (Udoteaceae, Bryopsidales) with a Description of *Rhipidosiphon floridensis* sp. nov.

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The genus *Rhipidosiphon* is reestablished and characterized by an upright, monosiphonous, uncorticated stipe; fine hyaline rhizoids; and a fan-shaped, unistratose, calcified, terminal blade composed of dichotomously branched siphons. *Udotea javensis*, commonly found in the Indian and Pacific Oceans, is herein transferred to *Rhipidosiphon*, with *R. javensis* as the type of the genus. *Rhipidosiphon floridensis* sp. nov., known only from the Florida Keys and Puerto Rico, is described as one of a "pair" species anatomically similar in every respect to *R. javensis* except for the presence of equal constrictions above the dichotomies; *R. javensis* has distinctly unequal constrictions.

While examining historical and type material for a monograph of Caribbean *Udotea*, we found undescribed specimens of a small related genus filed in the *Udotea* collections of the British Museum (Natural History). A thorough search of other herbaria turned up a rich collection of additional material of the same species at the Harbor Branch Oceanographic Institution Herbarium. That material, and our own collection of living specimens of *Rhipidosiphon javensis* Montagne from the Republic of the Seychelles, provided compelling evidence as to the distinct nature of the genus, which could be representative of a common ancestral taxon for the more derived genera *Udotea*, *Rhipocephalus*, *Tydemania* and *Penicillus*.

Herein, we resurrect the genus *Rhipidosiphon* from Montagne (1842), who described *Rhipidosiphon javensis* as the type for the genus. Montagne (1842) characterized the genus as having a monosiphonous stipe and fan-shaped frond with a cuneate base consisting of dichotomously divided, encrusted siphons (= filaments) that are anastomosed. The report of anastomosing

siphons is incorrect as Gepp & Gepp (1904) demonstrated. What Montagne observed was a fusion of the surrounding calcium-carbonate sheaths and not of the siphons. This anastomosing of calcium-carbonate sheaths also is occasionally observed in *Rhipocephalus* (personal observations). Gepp & Gepp (1904) point out that the monosiphonous stipe of *Rhipidosiphon* is not calcified, but our observations show that the upper portion near the blade is often calcified. Montagne's description of the genus, aside from the report of anastomosing siphons, is accurate and *Rhipidosiphon* differs from the closely related genus *Udotea* by its uniquely monosiphonous, partly uncalcified stipe.

Gepp & Gepp (1904) placed *Rhipidosiphon javensis* in the genus *Udotea* and stated that *R. javensis* is "clearly nothing but a very simple *Udotea*". This statement is misleading because *Rhipidosiphon* lacks sufficient derived characters to place it in the genus *Udotea*, since a *Rhipidosiphon*-like ancestor could have given rise to not only *Udotea* but also *Rhipocephalus*, *Tydemania* or *Penicillus*. For example, the individual unistratose

blades of *Rhypocephalus phoenix* (Ellis & Solander) Kützing closely resemble the upright portion of *Rhipidosiphon floridensis* even in regard to the gradual tapering in siphon diameter; i.e., from the larger initial siphon at the point of attachment that decreases in size with each dichotomy to the thinner siphons at the outer margin. Therefore, we reject the inclusion of *Rhipidosiphon* within *Udotea* and redefine both genera to enable *Rhipidosiphon* to stand as a separate monophyletic genus.

The genus *Rhipidosiphon* herein is characterized by an upright, monosiphonous, partially calcified, uncorticated stipe, fine hyaline rhizoids and a fan-shaped, calcified, unistratose, terminal blade. The blades are composed of dichotomously branched siphons which do not anastomose, but their calcified sheaths are frequently fused so that no demarcations are shown. *Udotea*, conversely, has distinctly corticated, completely calcified stipes made up of multiple, central, longitudinal siphons (multisiphonous), usually surrounded by lateral appendages (Littler & Littler, in press).

MATERIALS AND METHODS

Specimens from dried herbarium mounts were examined macroscopically and portions prepared for anatomical study on microscope slides. Material was decalcified and stained with a mixture of 5% hydrochloric acid and 1% aniline blue, then mounted using a 20% glucose syrup (Karo Syrup, Corn Products, Inc.) solution in distilled water containing a trace of phenol (Tsuda & Abbott, 1985). All anatomical drawings were made with a camera lucida on a Zeiss Universal Microscope to assure accuracy, while internal measurements were made with a calibrated, ocular micrometer.

OBSERVATIONS

Rhipidosiphon floridensis, sp. nov.

Description. Laminae parvae 8 mm longae et 6 mm latae calcareae unistratosae non corticatae, siphonibus parallelibus lateraliter adhaerentibus supra dichotomiae aequaliter constrictis; stipes parvi 1 mm longi non

calcarei vel in partibus superioribus calcarei unisiphonii, rhizoideis basilaribus tenuibus hyalinis ad substratum solidum affixis.

Holotype. BM, GT-1095, northwest of Loggerhead Key, Dry Tortugas, Monroe County, Florida, growing among silted sand on dead coral sticks, 17 Jun 1931. coll: G. Tandy.

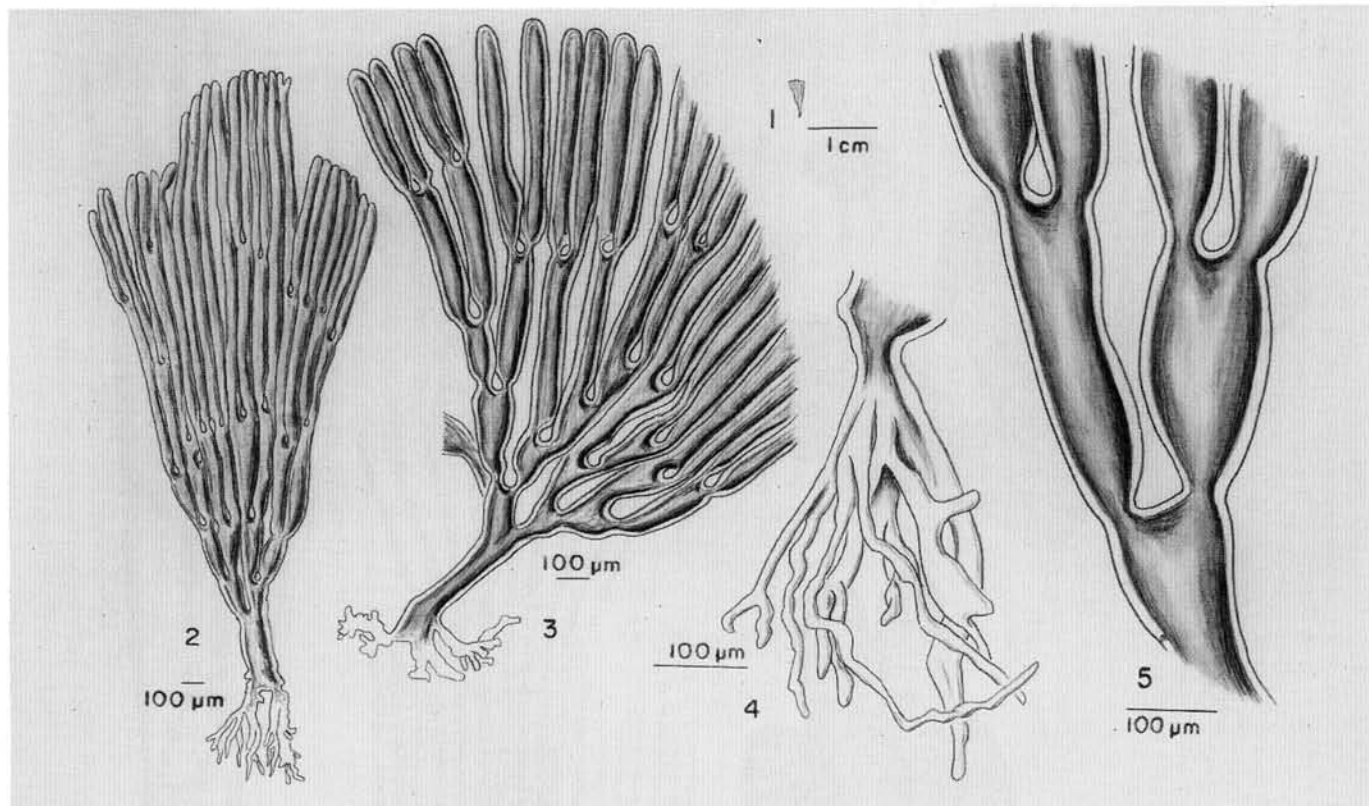
Distribution. Florida Keys, Puerto Rico.

Representative specimens examined. Florida—Loggerhead Key, Dry Tortugas (Holotype); Key Largo, Molasses Reef, 12 Sept 1985, HBFH-85-9-12; 10 Sept 1986, HBFH-86-9-10-169-1; 12 Dec 1986, HBFH-86-12-12-361; Puerto Rico—1.5 km seaward of Media Luna Reef, La Paguera, 11 May 1989, D&ML-17320.

Habit. Plants small (to 10 mm tall) consisting of a calcified, unistratose, uncorticated, fan-shaped blade (8 mm long, 6 mm wide, Fig. 1) that is generally cuneate at the base, rotund (rounded) on the outer margins but often lacerate or torn because of its delicate nature. The stipe is 1 mm long, simple, erect and smooth (Figs 2, 3); epilithic and anchored by numerous fine hyaline (transparent) rhizoids (Fig. 4).

Anatomy. The blade is composed of a single layer (unistratose) of smooth siphons that lie absolutely parallel to one another adhering laterally by deposits of calcium carbonate; siphons divide dichotomously with equal constrictions above the dichotomies (Fig. 5); siphons are larger at the base of the blade (95–116 μ m diam.) and gradually decrease in diameter toward the margin (45–60 μ m diam.). The stipe consists of a large, single, partly calcified (nearest the blade), monosiphonous and uncorticated siphon (130–220 μ m diam.).

Remarks. The minute, inconspicuous nature of this plant, we presume, is the cause for the paucity of collections. To date, the type collection, the Puerto Rican collection and additional material collected from Molasses Reef (in conjunction with a detailed ecological study directed by M. D. Hanisak of



FIGS 1-5. *Rhipidosiphon floridensis*. Fig. 1. Habit of plant. Figs 2 & 3. Enlargements of two entire thalli showing the shorter and wider branching at the base of the blade. Fig. 4. Translucent hyaline rhizoidal system. Fig. 5. Smooth blade filaments with equal constrictions at the dichotomies.

Harbor Branch Oceanographic Institution) are the only specimens in herbaria.

One specimen (HBFH-86-9-10-169-1) from Molasses Reef, Key Largo, Florida is unique in having three separate uprights arising from the same hyaline rhizoidal system, presumably demonstrating vegetative reproduction. All other specimens examined are single thalli, each with individual rhizoidal systems.

Rhipidosiphon javensis Montagne

Basionym. *Rhipidosiphon javensis* Montagne, 1842, pp. 14-15.

Holotype. PC, Java, Leyden Batavia, coll: Hombron.

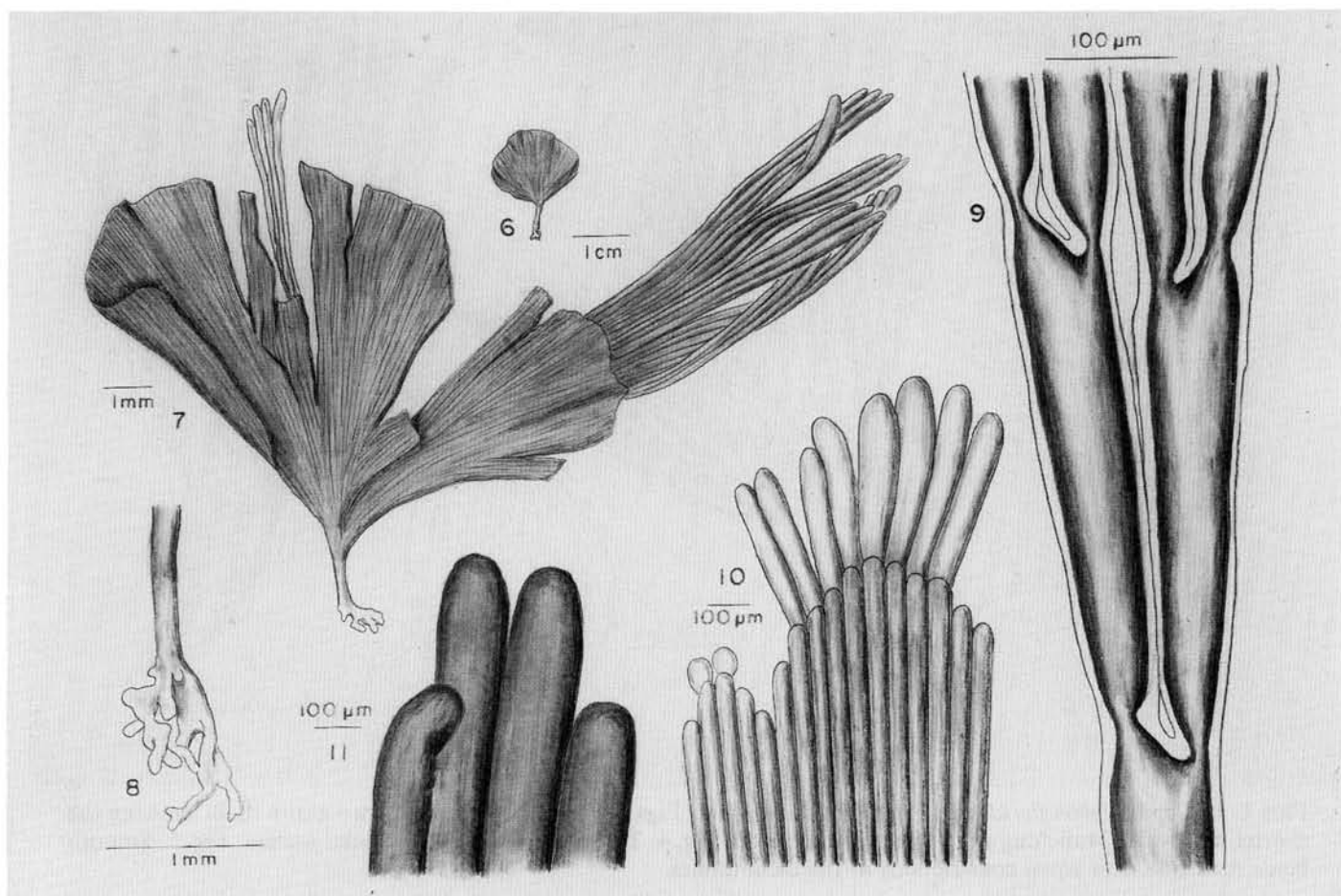
Distribution. Indian Ocean: Maldives Islands, Ceylon (Sri Lanka), Seychelles, Indonesia. Pacific: China, Japan, Vietnam, Hawaii.

Representative specimens examined. Java—Leyden Batavia, PC (Holotype). Philippines—Bamilad, Dumaguete, 3 June 1987, US-

88326; Cuyo Island, 21 May 1978, US-13720. Maldives Islands—North Malosmadula Atoll, 21 Apr 1964; South Nilander Atoll, 24 Apr 1964, US-51468. Hawaii—Kauai, Kekaha, 30 Apr 1959, US-37135; Oahu, Hanauma Bay, 19 Mar 1959, US-37147. China—Shisha chwendau, 10 Mar 1979, US-88791. Vietnam—24 Feb 1953, US-54736. Seychelles—8 Mar 1989, D&ML-18164.

Habit. Plants vary in size from 2 to 30 mm in height (Fig. 6) consisting of a calcified, unistratose, uncorticated, fan-shaped blade (Fig. 7) that is rounded at the outer margins and cuneate at the base. The stipe is simple, erect, smooth and anchored to hard substrata by fine hyaline rhizoids (Fig. 8).

Anatomy. The blade consists of a single layer of strictly parallel filaments (40–50 μ m diam. at the outer margin, 85–110 μ m at the base) with unequal constrictions (Fig. 9) above each dichotomous division. The stipe is an uncorticated, mostly uncalcified and monosiphonous filament (120–175 μ m diam.).



FIGS 6–11. *Rhipidosiphon javensis*. Fig. 6. Habit of the plant. Fig. 7. Enlargement of entire fertile thallus, the enlarged and elongated filaments extending from the old margin are the reproductive structures. Fig. 8. Translucent hyaline rhizoidal system. Fig. 9. Blade filaments with distinctly unequal constrictions at the dichotomies. Fig. 10. Initial extensions of the blade filaments during formation of the reproductive siphons. Fig. 11. Terminal portions of reproductive siphons.

Remarks. Although described in 1842 by Montagne, no further specimens of this species were obtained until the extensive collections of the Siboga Expedition during 1899–1900. Almost as small and inconspicuous as *Rhipidosiphon floridensis*, *R. javensis* has been frequently collected in recent years throughout the Pacific and Indian Oceans.

DISCUSSION

During a taxonomic and phylogenetic study of the genus *Udotea* from the Caribbean region, a small, inconspicuous, undescribed species was discovered in the *Udotea* folder at the British Museum of Natural History. This species consists of a calcified, unistratose blade arising from a monosiphonous, partly calcified stipe. When cladistic

analysis of the Caribbean *Udotea* (Littler & Littler, in press) was performed with various calcareous species of Bryopsidales as the outgroups, this simple plant always contained so few derived characters (relative to any other species) that if retained in *Udotea* would result in a polyphyletic genus. Therefore, we place this simple species into the resurrected, monophyletic genus *Rhipidosiphon* Montagne 1842.

The closely related species, known as *Udotea javensis* A. Gepp & E. S. Gepp, is herein transferred back to *Rhipidosiphon* as the type of the genus. *Rhipidosiphon javensis* is commonly found in the Indian and Pacific Oceans. The two “pair” species of the genus appear similar in every respect, except *R. javensis* has distinctly unequal constrictions above the dichotomies (Fig. 9) while *R. flori-*

densis has equal constrictions (Fig. 5). The known specimens of *R. floridensis* tend to fall within the smaller size range of *R. javensis*; conversely, the siphon diameters of *R. floridensis* tend to lie near the larger size range of *R. javensis*. However, since so few specimens of the former have been examined, these may not be consistent differences.

The closest ally to *Rhipidosiphon* is *Udotea papillosa* A. Gepp & E. S. Gepp from the Pacific, which is also small and inconspicuous with a unistratose blade. However, in mature plants of the latter, the stipe is composed of numerous, loosely consolidated, completely calcified filaments ascending to form the blade. *Udotea papillosa* also possesses single or double rows of papillae along the front and back margins of the blade filaments. From an evolutionary perspective, *U. papillosa* appears to be midway between *Rhipidosiphon* and *Udotea* in not having the monosiphonous stipe of *Rhipidosiphon*, while lacking the corticated stipe that is present in all other *Udotea* species. *Rhipidosiphon* is also closely allied to *U. glaucescens* Harvey, both possessing a unistratose blade with smooth filaments, the calcified stipe of *U. glaucescens* can be monosiphonous in extremely young plants, but soon becomes multisiphonous and eventually corticated.

We examined the possibility that *Rhipidosiphon javensis* and *R. floridensis* may represent morphologically diminutive forms of more complex species and conclude that this is not the case. Morphologically reduced forms do occur in various Bryopsidales including *Flabellia minima* (Ernst) Nizamuddin (Ernst, 1904), *Caulerpa racemosa* (Forsk.) Agardh (Lipkin & Friedmann, 1967) and *Caulerpa sertularioides* (S. G. Gmelin) Howe (personal observation). Also the *Espera* state of *Penicillus* is an exceptionally reduced form (Friedmann & Roth, 1977). However, even extremely young stipes of *Udotea* always show some form of lateral siphon branching or a slight degree of cortication. The above-mentioned reduced forms are generally thought to occur as a stress response to suboptimal conditions (Fried-

mann & Roth, 1977). In contrast, collections of *Rhipidosiphon* have not come from particularly stressful habitats and no plants examined thus far have shown any trace of cortication. To reiterate, *Rhipidosiphon* cannot be considered a diminutive form of *Udotea*, since juveniles of the latter consistently show either multisiphonous and/or corticated, completely calcified stipes early in their development, while *Rhipidosiphon* is characterized by a permanently monosiphonous, partially calcified stipe.

Reproduction in *Rhipidosiphon floridensis* has not been observed, however, we found one preserved specimen of *R. javensis* that was fertile (Fig. 7, US-51467). Reproduction appears similar to *Udotea conglutinata* (Ellis & Solander) Lamouroux (Littler & Littler, in press) and *U. indica* A. Gepp & E. S. Gepp (Nizamuddin, 1963) as shown by the presence of specialized, elongated, terminal, reproductive siphons (presumably gametangia). These siphons are generally larger than normal, from 250 to 300 μm in diameter (Fig. 10) at the expanded region approximately 400 μm from the siphon apex and 120 to 150 μm (Fig. 11) in the area immediately next to the normal blade siphons, whereas siphon diameters generally range from 40 to 50 μm at the outer blade margins. These reproductive siphons are either uncalcified (especially at the fast growing apices) or very lightly calcified with exceedingly thin walls, thus differing from those described for *U. orientalis* (Montagne) A. Gepp & E. S. Gepp (Moorjani, 1969) and *U. cyathiformis* Decaisne (Phillips, 1957) where single ovoid bodies containing a wall thicker than that of the filaments have been observed at the apex of single filaments. In the specimen observed, the majority of the chloroplasts had migrated from the thallus to the new extensions of the siphons; however, spheres had not yet developed. We assume, since the filament extensions are so similar to those of *U. conglutinata*, that the rest of the developmental sequence and release is also the same (Littler & Littler, in press).

From our detailed study of Caribbean *Udotea* (Littler & Littler, in press) and our

continuing work with the closely related genera *Rhipocephalus* and *Penicillus*, as well as additional information obtained by cladistic analysis (Littler & Littler, in press), separation of *Rhipidosiphon* from the larger and more complex genus *Udotea* is mandatory to provide independent, monophyletic genera.

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REFERENCES

ERNST, A. (1904). Siphonien-Studien. II. Beiträge zur Kenntnis der Codiaceen. *Beih. bot. zbl.*, **16**: 199–236.

- FRIEDMANN, E. I. & ROTH, W. C. (1977). Development of the siphonous green alga *Penicillus* and the *Espera* state. *Bot. J. Linn. Soc.*, **74**: 189–214.
- GEPP, A. & GEPP, E. S. (1904). *Rhipidosiphon* and *Callipsygma*. *J. Bot.*, **62**: 363–366.
- LIPKIN, Y. & FRIEDMANN, I. (1967). Persistent juvenile stage of *Caulerpa racemosa* (Forsk.) Agardh in the eastern Mediterranean. *Pubbl. Staz. zool. Napoli*, **35**: 243–249.
- LITTLER, D. S. & LITTLER, M. M. (1990). Systematics of *Udotea* species (Bryopsidales, Chlorophyta) in the tropical western Atlantic. *Phycologia*, in press.
- MONTAGNE, C. (1842). *Prodromus generum specierumque phycearum novarum, in itinere ad Polum Antarcticum*. Apud Gide, Parisiis.
- MOORJANI, S. A. (1969). A note on the possible reproductive structures in Kenyan *Udotea orientalis* A. & E. S. Gepp, (Chlorophyta). *Jl. E. Africa Nat. Hist. Soc.*, **27**: 227–229.
- NIZAMUDDIN, M. (1963). Studies on the green alga, *Udotea indica* A. & E. S. Gepp, 1911. *Pac. Sci.*, **17**: 243–245.
- PHILLIPS, R. C. (1957). Notes on gametangia in *Udotea*. *Quarterly Jl. Florida Acad. Sci.*, **20**: 253–254.
- TSUDA, R. T. & ABBOTT, I. A. (1985). Collection, handling, preservation, and logistics. In *Handbook of Phycological Methods. Ecological Field Methods: Macroalgae* (Littler, M. M. & Littler, D. S., editors), 67–86. Cambridge University Press, Cambridge.

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