

## Systematics of *Udotea* species (Bryopsidales, Chlorophyta) in the tropical western Atlantic

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D.S. LITTLER AND M.M. LITTLER. 1990. Systematics of *Udotea* species (Bryopsidales, Chlorophyta) in the tropical western Atlantic. *Phycologia* 29: 206–252.

Twenty-one taxa of the genus *Udotea* from the tropical western Atlantic are treated. Ten new species (*U. abbottiorum*, *U. caribaea*, *U. dixonii*, *U. dotyi*, *U. fibrosa*, *U. goreau*, *U. loensis*, *U. luna*, *U. norrisii*, *U. unistratea*) and one new variety (*U. cyathiformis* var. *flabellifolia*) are described. *Udotea sublittoralis* W.R. Taylor and *U. infundibulum* J. Agardh are reduced to *formae* of *U. cyathiformis* Decaisne. Distinguishing features of the eight pre-existing taxa are clarified, and all 21 taxa are illustrated.

A cladistic analysis, with all 47 characters weighted equally, of the *Udotea* species from the tropical western Atlantic indicates that, although 11 of the 12 phylogenetic trees produced represent a gradation without formally recognizable groups and no major evolutionary breaks, the twelfth tree depicts four monophyletic groups and one paraphyletic group. The group possessing the most derived characters (Flabellum group) consists of the fully corticated species with blunt-tipped lateral appendages (*U. dixonii*, *U. dotyi*, *U. flabellum*, *U. norrisii*, *U. occidentalis*). *Udotea goreau* and *U. wilsonii* comprise the second group (Wilsonii group) of partially corticated species with blunt appendage apices. A third group (Verticillosa group) contains those uncorticated and partially corticated species in which the lateral appendages of the stipe or blade terminate in long tapering points (*U. loensis*, *U. luna*, *U. spinulosa*, *U. verticillosa*). The uncorticated species in which appendages of the stipe end in blunt or swollen tips (*U. abbottiorum*, *U. caribaea*, *U. conglutinata*, *U. cyathiformis*, *U. fibrosa*) comprise a fourth group (Conglutinata group). The fifth entity (Unistratea group) consists of *U. unistratea*, which has a simple, unistratose, uncorticated blade and blunt stipe appendages. Although our phylogenetic analysis suggests that *Udotea* in the tropical western Atlantic comprises five evolutionary groups, the differences are not substantial enough to warrant formal subdivision into segregate genera. The fact that eleven of the 12 trees in the analysis were variations of a gradation (species branching off a single line extending from simple to derived) supports this interpretation. We conclude that *Udotea*, as currently defined, is a coherent, monophyletic unit that should be maintained as a single genus.

### INTRODUCTION

The genus *Udotea* Lamouroux 1812 [Udoteaceae, Bryopsidales (= Caulerpales, see Silva 1982)] is characterized by calcified erect thalli composed of three parts: (1) an uncalcified, basal, rhizoidal mass anchored to rock or, more often, found in soft substrata such as sand, mud or peat; (2) an upright corticated stalk (= stipe); and (3) a funnel- or fan-shaped terminal blade (= flabellum). The blades are composed of dichotomously branched siphons that, in some cases, bear simple to variously compound lateral appendages. Each stalk consists of central, longitudinal siphons (= 'filaments') surrounded by lateral appendages that form a distinct, cortical layer.

The term filament, used by previous workers when referring to these siphons, is generally defined as a chain of cells attached end to end and is, strictly speaking, incorrectly applied to completely siphonous algae such as *Udotea*.

The first recorded plant that can be assigned definitely to *Udotea* is found in Sloane (1707), where a variety of what we now know as *Padina pavonica* (L.) Lamouroux was described as having 'thicker and whiter leaves'. According to our own observations and those of Gepp & Gepp (1911), the documentary specimen of this variety in the Sloane Herbarium (BM) is representative of *U. flabellum*. When Lamouroux (1812) established the genus *Udotea*, he mentioned as a single example '*Corallina flabellum* Ellis', without

making the combination. Lamouroux (1816, p. 311) subsequently changed the specific epithet, adopting the superfluous name *U. flabellata*. The proper epithet was not restored until 1904, by Howe.

At the time of Lamouroux, calcified algae were regarded as animals, and it was not until 30 years later (Chauvin 1842; Decaisne 1842) that the genus, with four species, was placed within the plant kingdom as then understood. J.G. Agardh (1887) divided *Udotea* into four groups containing seven species, which formed the basis for the treatment by De Toni (1889) in which eight species, six regarded as questionable by Gepp & Gepp (1911), were added. De Toni's treatment is not particularly significant, but for accuracy it should be noted that he definitely included in the genus two species (*U. amadelpa* Montagne and *U. argentea* Zanardini) that J. Agardh had listed only by name, not having seen specimens. The genus has not been treated monographically since the careful and detailed work of A. Gepp & E.S. Gepp (1911), to whom only limited Caribbean material was available.

In this paper, we deal taxonomically and phylogenetically with only the western Atlantic species of *Udotea*. We feel that the treatment of this biogeographical group from an evolutionary/monographic perspective is justified, since the Indo-Pacific and tropical western Atlantic have been isolated for a period of 3 million to 20 million years (Adey 1976). Corals, a rapidly evolving group, exemplify this evolutionary separation, with only 6% of the hermatypic scleractinian genera (and no species) common to both oceans (Adey 1976). Therefore we consider tropical western Atlantic populations of *Udotea* to be genetically isolated, although many taxa have similar 'parallel' species (comprising 'species pairs') present in the Indo-Pacific region.

We became acutely aware of the need for a tropical western Atlantic monograph of *Udotea* while attempting to use existing treatments for the identification of our extensive collections. So many unidentifiable entities were present, particularly in the deep-water collections, that it became apparent that the genus *Udotea* had been inadequately collected and described in western Atlantic waters. This prompted an intensive examination of all available material, including Pacific and Indian Ocean type specimens, in the following herbaria (abbreviations derived from Holmgren *et al.* 1981): Laboratoire d'Algologie Fondamentale et Appliquée, Caen (CN); Botan-

ical Museum and Herbarium, Copenhagen (C); Rijksherbarium, Leiden (L); British Museum (Natural History), London (BM); Botanical Museum, Lund (LD); New York Botanical Garden, New York (NY); Harbor Branch Oceanographic Institution, Fort Pierce, Florida (HBFH); Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris (PC); United States National Herbarium, Washington, D.C. (US). A total of approximately 800 specimens, including both historical and recently collected material, forms the basis for the present treatment.

## MATERIALS AND METHODS

Extensive field collections were made in many regions of the tropical western Atlantic from 1980 to 1989, and all material was fixed in 4% formalin in seawater prior to being pressed and dried. Although this treatment focuses on the Caribbean region, the ranges of some taxa extend variously to all waters of the tropical western Atlantic (i.e. Bermuda and North Carolina through Florida and the Windward Islands to Panama and Brazil). Observations of gametangial and vegetative reproduction were recorded at the time of collection, together with environmental data.

Specimens were examined macroscopically and portions prepared for anatomical study on microscope slides from dried herbarium mounts and living material. Entire lengths of siphons were worked free, as fragments can give an incomplete or misleading representation. Material was decalcified and stained with a mixture of 5% hydrochloric acid and 1% aniline blue, and 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 ensure accuracy, while internal measurements were made using a calibrated ocular micrometer. For purposes of designating *varietas* (var.) and *forma* (f.), we distinguish between the two as follows: a *varietas* is a category immediately subordinate to a species whose evolutionary development has not progressed to the extent of being markedly different from the parent species, while a *forma* is a relatively minor variant, usually distinguished by a single character that often lacks constancy. Because all *Udotea* plants show erect growth, overall length measurements (also given as height or tallness) refer to the vertical distance

**Table 1.** List of characters used in matrix (Table 2)

- 
- 1—Stipe siphon diameter small <100  $\mu\text{m}$  (0), large >100  $\mu\text{m}$  (1).
  - 2—Blade siphon diameter small <100  $\mu\text{m}$  (0), large >100  $\mu\text{m}$  (1).
  - 3—Stipe constrictions equal (0), other than equal (1).
  - 4—Stipe constrictions unequal (0), other than unequal (1).
  - 5—Blade constrictions equal (0), other than equal (1).
  - 6—Blade constrictions unequal (0), other than unequal (1).
  - 7—Blade appendages lobed (0), not lobed (1).
  - 8—Blade appendages tapering and not highly branched (0), not tapering and highly branched (1).
  - 9—Blade appendages blunt and not highly branched (0), not blunt and highly branched (1).
  - 10—Blade appendages blunt and highly branched (0), highly branched and without blunt tips (1).
  - 11—Blade appendages highly branched with flat tips (0), not highly branched and without flat tips (1).
  - 12—Stipe appendages with tapering tips (0), without tapering tips (1).
  - 13—Stipe appendages with blunt swollen tips (0), without blunt swollen tips (1).
  - 14—Complete cortex present (0), other than complete (1).
  - 15—Incomplete cortex present (0), other than incomplete (1).
  - 16—No cortex present (0), cortications present (1).
  - 17—Flabellum cup-shaped (0), other than cup-shaped (1).
  - 18—Flabellum fan-shaped (0), other than fan-shaped (1).
  - 19—Flabellum much lobed (0), not lobed (1).
  - 20—Blades radiating from central axis (0), blades in one plane (1).
  - 21—Blade highly divided (0), other than highly divided (1).
  - 22—Stipe/blade junction sharp (0), not sharp (1).
  - 23—Blade appendages occurring in ranks of two (0), other than ranks of two (1).
  - 24—Blade siphons free at base (0), conglutinate (1).
  - 25—Single thalli arise from a single holdfast (0), multiple thalli (1).
  - 26—Reduced rhizoid/rhizome system (0), other anchoring system (1).
  - 27—Rhizoid large and bulbous (0), other anchoring system (1).
  - 28—Small holdfast (0), other anchoring system (1).
  - 29—Blade appendages occurring in two ranks often paired or opposite and numerous (0), sparse and scattered, not in ranks (1).
  - 30—Blade appendage tips very short on non-dichotomous lobes (0), tips on branched appendages (1).
  - 31—Many blades along stipe (0), terminal blade or blades present (1).
  - 32—90% or more of the blade unistratose (0), less than 90% of the blade unistratose (1).
  - 33—Growing tips always unistratose (0), growing tips not unistratose (1).
  - 34—Blade siphons branching in ranks (0), not branching in ranks (1).
  - 35—Blade siphons not torulose or moniliform (0), blade siphons torulose or moniliform (1).
- 

**Table 1.** Continued

- 
- 36—Short dichotomous tips on stipe lateral branches (0), digitate tips (1).
  - 37—Blade siphons parallel or subparallel (0), not parallel (1).
  - 38—Blade siphons have narrow dichotomies (0), wide dichotomies (1).
  - 39—Stipe constrictions absent (0), present (1).
  - 40—Blade constrictions absent (0), present (1).
  - 41—Growing tips always multistratose (0), tips not always multistratose (1).
  - 42—Tips of blade siphons parallel to subparallel (0), haphazard (1).
  - 43—Supra-dichotomous swellings may be present (0), always absent (1).
  - 44—Blade appendages occurring in ranks of four (0), other than ranks of four (1).
  - 45—Pseudocortex resulting in upturned tips of blade siphons (0), no pseudocortex (1).
  - 46—Calcareous sheath porous (0), not porous (1).
  - 47—Blade appendages pedicillate (0), not pedicillate (1).
- 

from the surface of the substratum to the distal tip of the blade (flabellum), the rhizoidal mass not being included. Of the ~800 specimens examined, examples for each taxon were selected that represent the range of morphological variation and biogeographical regions, and they are cited with the descriptive analyses.

Samples for examination with a scanning electron microscope (SEM) were treated as follows: four small (2 mm<sup>2</sup>) sections were removed from pressed and dried specimens of *Udotea*. Sections were taken from the blade at the growing tip, mid-portion and just above the stipe transition, as well as from the stipe. The sections were mounted vertically on glass coverslips and then attached to scanning electron-microscopy stubs using Electrodag glue, coated with a 400 nm thick layer of gold-palladium in a Technics Hummer I sputter-coater, and scanned in a Novascan scanning electron microscope at 15 kV beam voltage.

The final data matrix, including 17 species of *Udotea* and 47 characters, was analysed phylogenetically by the PAUP 2.4.0 computer program (Swofford 1985) to test a priori intuitive hypotheses concerning evolutionary lineages within the genus. The characters were treated independently, and were not ranked within character groups, in order to avoid the need for speculation regarding primitive vs. derived states. If a given character state was not applicable to a given species, a code of 9 was used (see Tables 1 and 2 for a complete list of characters and

details of matrix). Several other characters were considered at various times during the analysis. However, these characters were ultimately rejected because they were too highly variable within the taxon to enhance the cladistic interpretation.

In phylogenetic systematics, one of the most useful tools for the introduction of elements of objectivity in cladistic analysis is character polarity. This is best determined by outgroup comparison (Wiley 1981), where one or more sister taxa are postulated to be most closely related and are chosen to serve as outgroups. We have selected as the sister taxon a morphologically sim-

ilar genus in the Bryopsidales, *Rhipocephalus*, since the plants have corticated stipes and blades composed of constricted, dichotomously divided siphons and are calcified, all characters shared with *Udotea*. *Rhipocephalus phoenix* (Ellis et Solander) Kützing was used as the outgroup taxon following the rule of parsimony (Swofford 1985), since this species possesses the simplest similar characters (i.e. unistratose blades of laterally consolidated siphons).

Holotypes of newly described species and other voucher materials are deposited in the Algal Collection, United States National Herbarium (US) unless otherwise indicated.

**KEY TO THE CARIBBEAN SPECIES OF *UDOTEA***

- (1) Blade unistratose (single-layered) throughout ..... *U. unistratea*
- (1) Blade at least proximally multistratose ..... 2
  - (2) Blade siphons smooth, lacking lateral appendages and a cortical layer ..... 3
  - (2) Blade siphons completely or incompletely corticated by lateral appendages ..... 9
- (3) Lateral appendages on stipes with acute tips ..... 4
- (3) Lateral appendages on stipes with blunt or swollen tips ..... 5
  - (4) Blade thin and delicate, outer margin unistratose ..... *U. looensis*
  - (4) Blade thick and leathery, outer margin multistratose ..... *U. luna*
- (5) Blade cup-like or funnel-shaped, rarely flabellate or peltate ..... *U. cyathiformis*
- (5) Blade flabellate or fan-shaped, never cup-shaped or peltate ..... 6
  - (6) Blade siphons <70 μm diam., not fibrous, tightly adherent (conglutinate) ..... 7
  - (6) Blade siphons >85 μm diam., fibrous, laxly adherent (not conglutinate) ..... 8
- (7) Blade siphons terminating in numerous dichotomies, tips tortuous (contorted), not parallel or subparallel, distinct concentric bands ..... *U. conglutinata*
- (7) Blade siphons terminating in few dichotomies, tips straight and parallel to subparallel, faint concentric bands ..... *U. caribaea*
- (8) Filaments lightly calcified, exposed blade siphons 85–110 μm diam., blade surface having a finely fibrous appearance; blade siphons with narrow-angled dichotomies ..... *U. abbottiorum*
- (8) Filaments heavily calcified; exposed blade siphons 100–150 μm diam., blade surface having a stiff and coarsely fibrous appearance; blade siphons with wide-angled dichotomies ..... *U. fibrosa*
- (9) Lateral appendages on blade siphons not forming a continuous cortex ..... 10
- (9) Lateral appendages on blade siphons closely packed forming a continuous outer cortex .. 13
  - (10) Lateral appendages on blade and stipe siphons acute ..... 11
  - (10) Lateral appendages on blade and stipe siphons bluntly rounded or truncate ..... 12
- (11) Lateral appendages on the exposed blade siphons arranged unilaterally throughout ..... *U. spinulosa*
- (11) Lateral appendages on blade siphons arranged in whorls at the siphon tips, irregularly arranged proximally ..... *U. verticillosa*
- (12) Length of lateral appendages (25–120 μm) on the blade as great or greater than the width of the blade siphons (40–80 μm) ..... *U. wilsonii*
- (12) Length of lateral appendages (<55 μm) shorter than the width of the blade siphon (100–150 μm) ..... *U. goreauii*

**Table 2.** Matrix from which the cladograms (Figs 24, 25) were derived; RPH, *Rhipocephalus phoenix*; UAB, *Udotea abbotiorum*; UCA, *U. caribaea*; UCO, *U. conglutinata*; UCY, *U. cyathiformis*; UDI, *U. dixonii*; UDO, *U. dotyi*; UFI, *U. fibrosa*; UFL, *U. flabellum*; UGO, *U. goreauii*; ULO, *U. loensis*; ULU, *U. luna*; UNO, *U. norrisii*; UOC, *U. occidentalis*; USP, *U. spinulosa*; UUN, *U. unistratea*; UVE, *U. verticillosa*; UWI, *U. wilsonii*

	Characters																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
RPH	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	0
UCO	0	0	1	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1
UCY	0	0	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	1	1	1	0
UFL	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	1	1	0	0	1	1	1
UOC	0	0	1	0	1	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1
USP	0	0	0	1	0	1	1	0	1	1	1	0	1	1	0	1	1	0	1	1	1	1
UVE	1	0	1	1	1	1	1	0	1	1	1	0	1	1	0	1	1	0	1	1	1	1
UWI	0	0	1	0	1	0	1	1	0	1	1	1	0	1	0	1	1	0	1	0	1	1
UUN	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	0
UNO	0	0	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	1	1	1	0	1
UAB	0	0	0	1	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1
ULO	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1
UGO	1	1	1	0	1	0	1	1	0	1	1	1	0	1	0	1	1	0	1	1	1	1
UDO	0	0	1	0	1	0	1	1	1	1	0	1	0	0	1	1	1	0	1	1	1	1
UFI	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1
UDI	0	0	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	0	0	1	1	1
ULU	1	1	0	1	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1
UCA	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1

- (13) Frond having numerous narrow branch-like divisions, stipe often branched . . . . . *U. norrisii*  
 (13) Frond consisting of a single large flat blade, often repeatedly lobed, stipe never branched . . . . 14  
 (14) Lateral appendages on blade siphons randomly and sparsely scattered . . . . . *U. flabellum*  
 (14) Lateral appendages on blade siphons often opposite and abundant, closely aligned . . 15  
 (15) Lateral appendages on blade siphons not branched but terminating in swollen lobes each with 6–12 small knobs . . . . . *U. occidentalis*  
 (15) Lateral appendages on blade siphons widely branched, not terminating in swollen lobes . . 16  
 (16) Lateral appendages on blade siphons terminating in closely packed, truncate (flattened) projections . . . . . *U. dotyi*  
 (16) Lateral appendages on blade siphons terminating in dichotomously branched, rounded tips . . . . . *U. dixonii*

## SPECIES TREATMENTS

### *Udotea abbotiorum* sp. nov.

Fig. 1

**DESCRIPTION:** Lamina anguste flabellata multistratosa non corticata longior quam latior, siphonis libris intertextis laevibus leniter calciferis diametro 70–100  $\mu\text{m}$  supra dichotomas omnia aequaliter constrictis; stipes corticatus siphonis diametro 70–100  $\mu\text{m}$  supra dichotomas constrictis; pars superior stipitis plana 6–15 mm longa et 4–11 mm lata, appendicibus lateralibus apice dichotome divisus tumidis; pars inferior stipitis cylindrica 47 mm longa et diametro 2–3 mm, appendicibus lateralibus apice saepe truncatis.

**HOLOTYPE:** US-30596, Content Keys, Monroe County, Florida, 5 m deep, anchored in deep

sand or attached to hard substrata beneath a thin layer of sediment on the north-west side of the westernmost Key, 15 December 1987, leg. *D.S. Littler, M.M. Littler, S. A. Reed, W.D. Lee.*

**ETYMOLOGY:** This species is named in honour of Isabella A. Abbott and the late Donald P. Abbott, both of whose systematic research and patient teaching over the years have shaped the careers of many biologists.

**DISTRIBUTION:** Bermuda, Florida, Puerto Rico, Belize, Panama, Colombia.

**REPRESENTATIVE SPECIMENS EXAMINED:** Belize: Tobacco Range, north-west side of the mangrove island complex, 3 m deep on decomposed mangrove peat, 10 February 1988, US-30614. Bermuda: Horn's Bay, tidepool, January 1913, NY, *Hervey-1913*. Florida: Content Keys, Monroe County (HOLOTYPE).

Table 2. Continued

Characters																								
23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1	0	0	1	1	0	1
1	1	1	0	1	1	1	1	1	1	1	1	0	1	0	0	1	1	0	1	0	1	0	0	1
1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	1
1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	9	0	0	0	0	1	1	1	1	1
1	1	1	1	0	1	0	0	1	1	1	1	1	0	0	9	1	1	0	0	1	1	1	1	1
0	1	1	0	1	1	1	1	1	1	1	1	1	9	0	1	1	1	0	0	0	1	1	1	0
1	1	1	1	0	1	1	1	1	1	1	1	1	9	0	1	0	0	0	0	1	1	1	1	1
1	1	1	0	1	1	1	1	1	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	1
1	0	1	0	1	1	1	1	1	0	0	0	1	0	0	1	1	1	1	0	0	1	1	0	1
1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	9	1	0	1	0	1	1	1	1	1
1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0	1
1	1	1	1	1	0	1	1	1	1	1	1	1	9	0	1	1	1	0	0	0	1	1	0	1
1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1	1	1
1	1	1	1	0	1	0	0	1	1	1	1	1	0	0	9	1	1	0	0	1	1	1	1	1
1	1	1	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1
1	1	0	1	0	1	0	0	1	1	1	1	1	0	0	9	0	1	0	0	1	1	1	1	1
1	1	1	1	1	0	1	1	1	1	1	1	9	0	1	1	1	1	1	0	1	1	1	0	1
1	1	1	0	1	1	1	1	1	1	1	1	0	1	0	0	1	1	0	0	0	1	1	0	1

Puerto Rico: Santurce, 0.3 m deep on sand covered rock, 23 May 1903, NY, *Howe-2064*.

**HABIT:** Frond (= stipe + blade) to 15 cm tall (= frond length = height), yellow-green, outer growing margin often a darker green. Blade narrowly fan-shaped, ecorticate (= uncorticated), multistratose, rather thick (1–2 mm) and spongy (Fig. 1a, 1b, 1c), usually much longer (up to 8 cm) than wide (up to 5 cm), younger plants lightly zonate, zonation becoming obscure with age. Stipe cylindrical in lower half (4–7 mm long, 2–3 mm in diameter), the upper half (6–15 mm long) flattened (4–11 mm wide), forming the transition into the blade (Fig. 1a, 1b, 1c), distinction between the upper and lower stipe not always apparent. Anchored in soft substrata by a bulbous mass of entangled rhizoidal siphons (Fig. 1a, 1b, 1c).

**ANATOMY:** Blade siphons lacking appendages, subparallel, 90–110  $\mu\text{m}$  in diameter, with symmetrical constrictions above each wide angled dichotomous division (Fig. 1d), calcareous sheath with open pores (small scattered holes). Stipe siphons 70–100  $\mu\text{m}$  in diameter, tendency toward equal constrictions above each dichotomy (Fig. 1g); stipe frequently divided into two visibly different sections—the upper flattened portion has appendages with swollen tips (Fig. 1e), whereas the lower cylindrical section has appendages with abruptly truncated tips (Fig. 1f).

**REMARKS:** Previously, *Udotea abbottiorum* has been recorded or identified as *U. conglutinata*; however, its blade siphons are about twice the diameter of those in *U. conglutinata* and are easily visible to the unaided eye. Terminal projections of the stipe appendages also differ, those in *U. abbottiorum* being short and dichotomously divided, with blunt, swollen or flattened apices (Fig. 1e, 1f), compared to the more digitate tips (Fig. 2d) of *U. conglutinata*. *Udotea abbottiorum* is commonly found in shallow waters (1–10 m) on mangrove peat or sand.

*Udotea caribaea* sp. nov.

Fig. 2

**DIAGNOSIS:** In filamentis laminae laevibus conglutinatis et in appendicibus lateralibus stipitis apice obtusis et digitatis *Udotea conglutinata* similis sed in filamentis laminae parallelis vel subparallelis anguste et paucis dichotomis differt.

**HOLOTYPE:** US-30615, Belize, Central America, northwest side of the mangrove island complex of Tobacco Range, 1–3 m deep on sand, 18 February 1988, leg. D.S. Littler, M.M. Littler, B.L. Brooks, P.R. Taylor.

**DISTRIBUTION:** Cuba, Belize.

**REPRESENTATIVE SPECIMENS EXAMINED:** Belize: Tobacco Range (HOLOTYPE). Cuba: Cayo San Felipe, 7 m deep, dredged, 10 April 1937, US-54725.

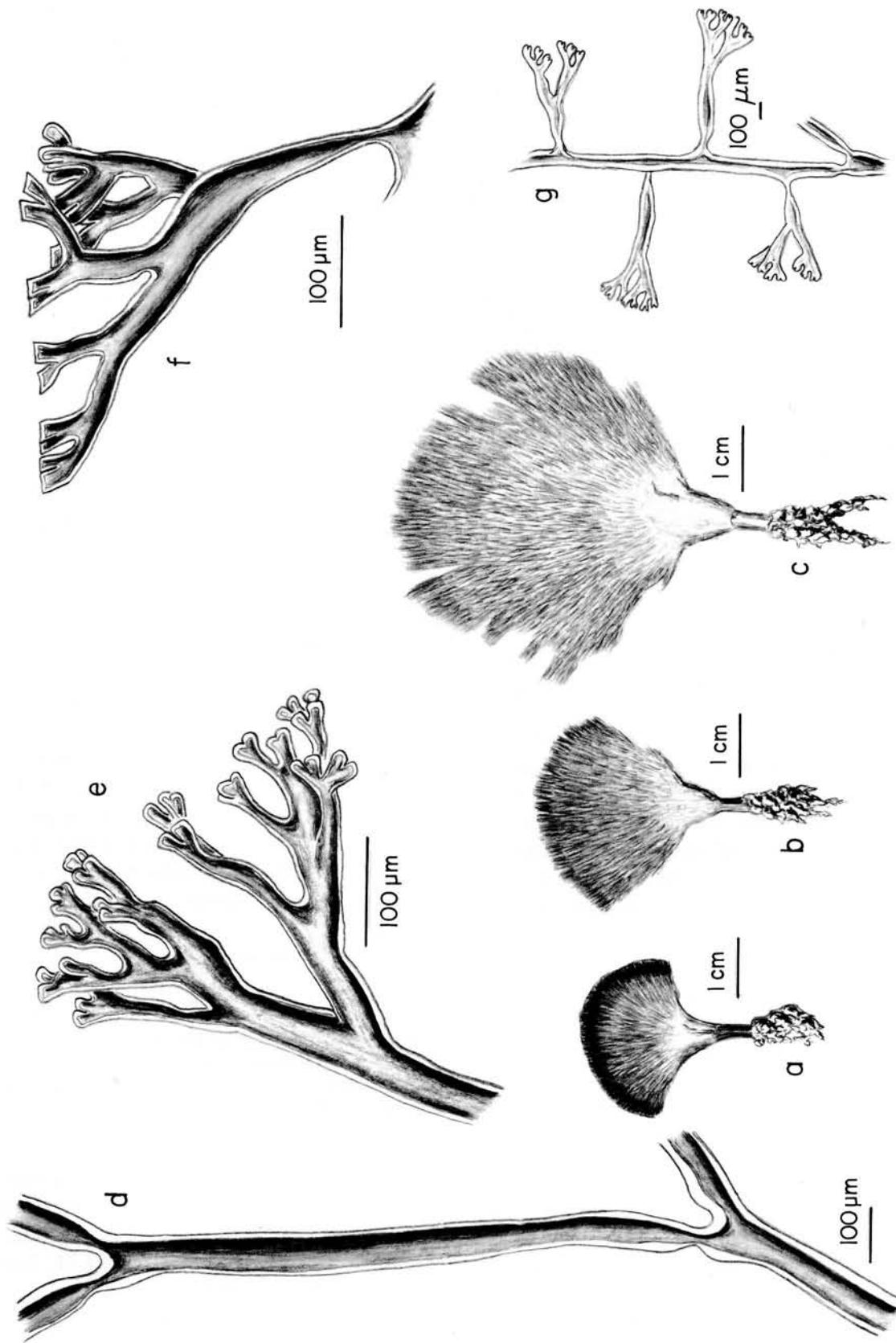


Fig. 1. *Udotea abbottiorum* sp. nov. a, b and c, habit showing development of the blade; a, juvenile thallus; b, intermediate; c, mature plant; d, blade siphon; e, lateral appendage from upper stipe; f, lateral appendage from lower stipe; g, stipe siphon.

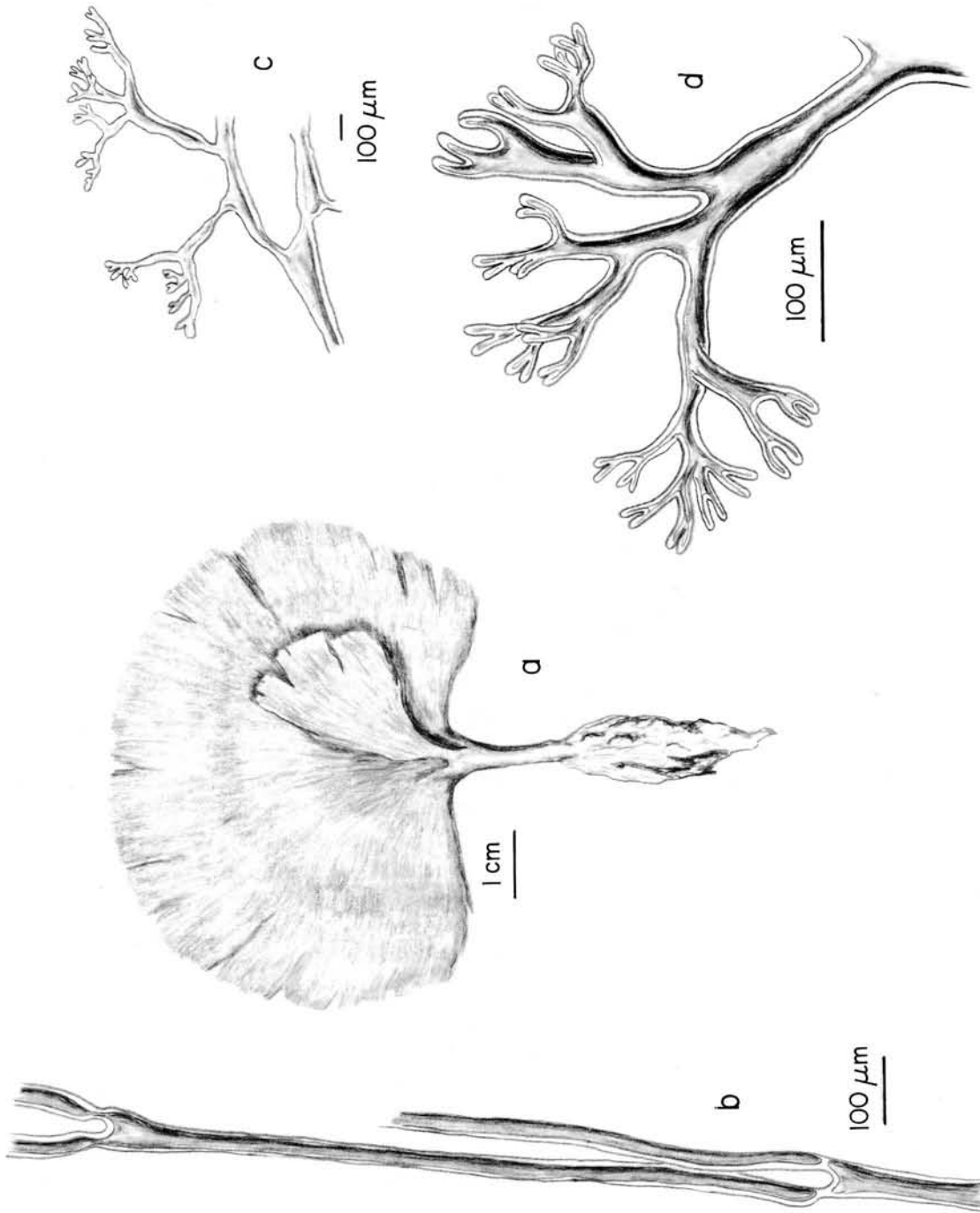


Fig. 2. *Udotea caribaea* sp. nov. a, habit of plant; b, smooth (lacking appendages) blade siphon; c, stipe siphon; d, lateral appendage of stipe showing digitate apices.



**HABIT:** Frond 4–9 cm tall, yellow or whitish-green when living, ash-white when dried. Blade fan-shaped, occasionally with one or two additional wide lobes (Fig. 2a) attached near the central axis, 0.5–1.0 mm thick; siphons tightly compacted, subparallel, conglutinated or cemented together by heavy calcium carbonate (aragonite) deposits. Stipe 2–5 mm in diameter, up to 2.5 cm long, no clear distinction or demarcation between the blade and stipe surface texture, one gradually merging with the other. Anchored in soft substrata by entangled, fibrous rhizoids forming a bulbous to elongated mass (Fig. 2a).

**ANATOMY:** Blade siphons 30–50  $\mu\text{m}$  in diameter, smooth and lacking lateral appendages, distinctly constricted equidistant and immediately above each narrowly angled dichotomous division (Fig. 2b), calcareous sheath possesses pores. Stipe siphons 60–80  $\mu\text{m}$  in diameter, generally asymmetrical constrictions above the dichotomous divisions (Fig. 2c), cortex formed by stubby, digitate tips of the lateral appendages (Fig. 2d).

**REMARKS:** The closest ally of *Udotea caribaea* is *U. conglutinata*. The two differ in that *U. caribaea* has parallel to subparallel siphons in the blade with few dichotomies, whereas *U. conglutinata* has blade siphons that are generally interwoven, with many dichotomies and random branching near the apices. The short ultimate branchlets in the latter are also contorted or tortuous. The lateral appendages of the stipes in *U. caribaea* tend to have shorter digitate apices than those in *U. conglutinata*, and the siphons generally have unequal constrictions (75% unequal) above the dichotomies, in contrast to the consistently equal constrictions of the latter. *Udotea caribaea* is occasionally found growing in organic-rich sand or on mangrove peat in shallow waters (to 7 m deep).

***Udotea conglutinata* (Ellis et Solander) Lamouroux 1816: 312.**

Fig. 3

**BASIONYM:** *Corallina conglutinata* Ellis et Solander 1786: 125, pl. 25, fig. 7.

**LECTOTYPE:** The type specimen has been lost (Howe 1909; Gepp & Gepp 1911; Dixon 1960). In the absence of a known holotype, we follow Dixon (1960) in selecting Ellis & Solander's illustration (1786, pl. 2, fig. 7) as the LECTOTYPE [Arts. 42.2 and 44.2, International Code of Botanical Nomenclature (ICBN), Greuter *et al.*

1988]. Locality: Bahamas (precise locality not specified).

**DISTRIBUTION:** Bahamas, Puerto Rico.

**REPRESENTATIVE SPECIMENS EXAMINED:** Bahamas: Bimini Harbor, 0.1–0.8 m deep on sand, 16 April 1904, NY, *Howe-3240a*; Fort George Cay, Caicos Islands, 0.3–0.6 m deep on sand, 18 December 1907, NY, *Howe-5628*; San Salvador Island at the mouth of Pidgeon Creek, 16 October 1983, US-30618. Puerto Rico: Monito Island, 40 m deep on sand, 14 May 1989, US-96581.

**HABIT:** Plants to 14 cm tall, green to ash-white. Mature blades to 12 cm tall, 9 cm wide (Fig. 3a), 1–2 mm thick; siphons heavily calcified, nap-like (tomentulose) surface. Stipe 5 mm in diameter, to 2.5 cm long, cylindrical below, flattened above, gradual transition into blade. Anchored in soft substrata by a fibrous rhizoidal mass.

**ANATOMY:** Blade siphons 40–60  $\mu\text{m}$  in diameter, smooth, lacking lateral appendages, symmetrical constrictions immediately above dichotomous divisions (Fig. 3b, 3c), many repeated divisions at the apices, ultimate branchlets tortuous and contorted (Fig. 3d), calcareous sheath with pores. Stipe siphons 50–70  $\mu\text{m}$  in diameter, equal constrictions above the dichotomies, cortex formed by digitate tips of the lateral appendages (Fig. 3d, 3e), rhizoids consisting of elongated hyaline lateral branches (Fig. 3f).

**REMARKS:** In the past, all forms of *Udotea* bearing fan-shaped blades composed of siphons lacking lateral appendages were referred to *U. conglutinata*. However, on close examination, several segregate species are shown to be involved (see also *U. abbottiorum*, *U. caribaea*, *U. fibrosa*, *U. looensis* and *U. luna*). *Udotea conglutinata* superficially resembles *U. caribaea*, but the blade is thicker (1–2 mm) than that of *U. caribaea*. The taller form of *U. conglutinata* (Fig. 3a) grows to 14 cm in height and 7 cm in width, whereas the shorter form is much wider than long (one individual blade being 9 cm wide and only 5 cm long). Little difference in surface texture between the blade and stipe is apparent to the unaided eye. Characteristically, the apical portions of the blade siphons terminate in at least one short dichotomy or several branches (Fig. 3b, 3c), often with each independently protruding toward the surface of the blade to produce a tomentulose surface unique to this species. Concentric lines are formed on the surface of the blade by the alternation of areas of much repeated terminal divisions of the siphons with zones where few siphons terminate or divide. *Udotea conglutinata*

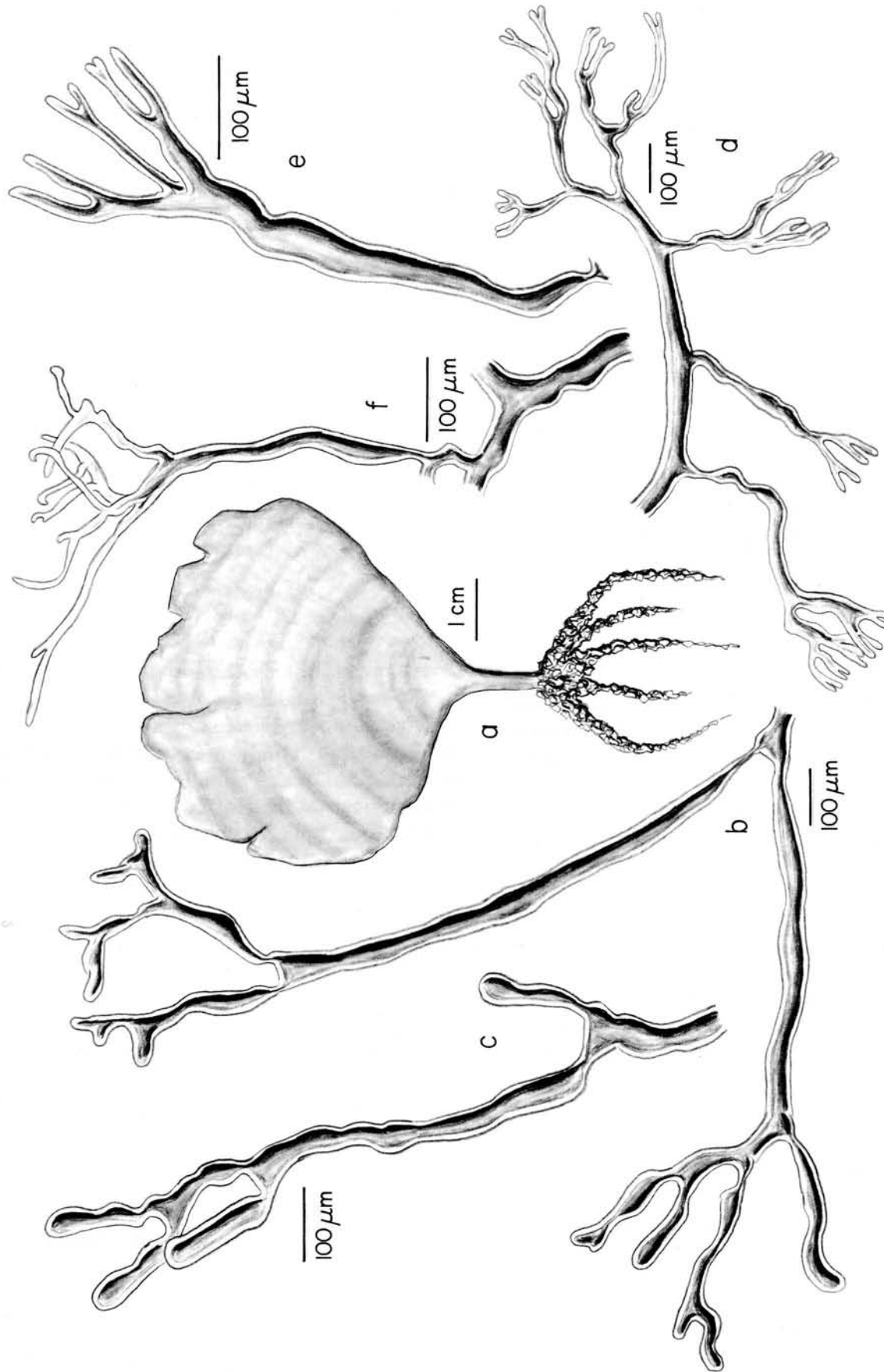


Fig. 3. *Udotea conglutinata* (Ellis et Solander) Lamouroux. a, habit; b and c, smooth siphons of blade showing wide dichotomies and highly branched apices; d, stipe siphon; e, lateral appendage of stipe showing digitate apices; f, lateral appendage of basal stipe at point where appendages gradually elongate to eventually form rhizoids.

has sinuous or wavy margins of the siphon walls at or near the apex, while *U. caribaea*, its closest ally, has extremely straight walls. In addition, the lateral appendages of the stipe in *U. conglutinata* tend to be thinner and are usually less branched (Figs 3d, 3e) than in *U. caribaea*. Until our recent Puerto Rican collections from a depth of 40 m, this plant was only known from shallow waters.

***Udotea cyathiformis* Decaisne 1842: 106**

var. *cyathiformis* f. *cyathiformis*

Fig. 4

HOLOTYPE: Specimen labelled '*Udotea acetabulum* Decaisne MS.', PC. Iles des Saintes, Guadeloupe, Lesser Antilles, 1842, leg. *d'Avrainville*.

DISTRIBUTION: Common throughout the tropical western Atlantic.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Mangrove Cay, Andros Island, 13.3 m deep on sand, 15 August 1986, US-30616. Belize: Carrie Bow Cay, 43 m deep, in sand pockets on a vertical reef wall, 7 February 1988, US-30617. Haiti: Caracol Reef, Caracol Bay, 28 m deep on a sand plain, 14 May 1981, US-14055. Lesser Antilles: Iles de Saintes, Guadeloupe (HOLOTYPE). Puerto Rico: Mayagüez, south of La Chalpa, 20 m deep on a sand plain, 26 December 1972, US-50213.

HABIT: Frond to 8 cm tall, green. Blade cup-shaped (Fig. 4a), 0.5–1.0 mm thick, multistratose, lightly zoned, ecorticate, fibrous to papery, occasionally asymmetrical, porous calcareous sheath. Stipe 0.3–2.0 cm long, 1–4 mm in diameter, cylindrical, a sharp junction occurring where the blade meets the stipe. Anchored in sand by a mass of fibrous rhizoids.

ANATOMY: Blade siphons 30–70  $\mu\text{m}$  in diameter, lacking appendages, subparallel to interwoven, equally constricted above dichotomies (Fig. 4e). Stipe siphons 50–120  $\mu\text{m}$  in diameter, constrictions usually unequal above dichotomies (about 25% show equal constrictions; Fig. 4b), divisions occasionally trichotomous (Fig. 4c); lateral appendages irregularly branched, often terminating in asymmetrical dichotomies, with swollen or flattened apices (Fig. 4d).

REMARKS: *Udotea cyathiformis* var. *cyathiformis* f. *cyathiformis* is intermediate between f. *sublittoralis* and f. *infundibulum* in all anatomical dimensions. *Udotea cyathiformis* var. *cyathiformis* differs from var. *flabellifolia* in that the former is cup-shaped, whereas the latter has a flattened or fan-shaped blade. *Udotea cyathiformis* var. *cyathiformis* is a ubiquitous species

commonly occurring in many habitats from shallow mangrove peat areas to deeper (30 m) sand plains.

***Udotea cyathiformis* Decaisne var. *cyathiformis***

f. *infundibulum* (J. Agardh) comb. nov.

Fig. 5

BASIONYM: *Udotea infundibulum* J.G. Agardh 1887: 71.

HOLOTYPE: LD-15733, West Indies. The TYPE specimen labelled 'W. India'. J.G. Agardh (1887) initially interpreted this as the East Indies, but later stated that the locality is doubtful, while Gepp & Gepp (1911) correctly presumed the locality to be the West Indies.

DISTRIBUTION: Florida, West Indies, Belize, Honduras.

REPRESENTATIVE SPECIMENS EXAMINED: Florida: Singer Island, Palm Beach County, 25 m deep on sand, 1 April 1980, HBFH-4867; HBFH-4866. West Indies (HOLOTYPE). Belize: Curlew Cay, on the outer ridge drop off, 14–37 m deep attached to rock or in sand pockets on the vertical reef wall, 15 February 1988, US-30619. Honduras: Media Luna Cay, Media Luna Bay, 10–20 m deep, attached to rock or in sand, 24 May 1981, US-14056.

REMARKS: On close examination, *Udotea cyathiformis* f. *infundibulum* reveals several distinctive features. The frond is papery (Fig. 5a) and is unistratose at the margins (Fig. 5b), whereas both f. *sublittoralis* and f. *cyathiformis* are multistratose throughout. In f. *infundibulum*, the siphons are parallel at the apices, parallel to subparallel below (Fig. 5c) and tightly cemented together by calcium carbonate, rather than lying laterally free. The blade siphons of f. *infundibulum* are generally smaller (20–40  $\mu\text{m}$  vs. 30–70  $\mu\text{m}$  in f. *cyathiformis* or 60–80  $\mu\text{m}$  in f. *sublittoralis*). The stipe siphons are similar (Fig. 5f); however, the stipe appendages of f. *infundibulum* branch widely (Fig. 7d, 7e) and the appendage tips resemble short, stubby 'fingers', whereas the stipe appendage tips of f. *sublittoralis* are quite blunt, often swollen and asymmetrical (Fig. 5c, 5d). This form generally occurs in deep-water habitats (20 m or deeper).

***Udotea cyathiformis* Decaisne var. *cyathiformis***

f. *sublittoralis* (W.R. Taylor) comb. nov.

Fig. 6

BASIONYM: *Udotea sublittoralis* W.R. Taylor 1928: 91, pl. 8, fig. 16, pl. 9, figs 8–9.

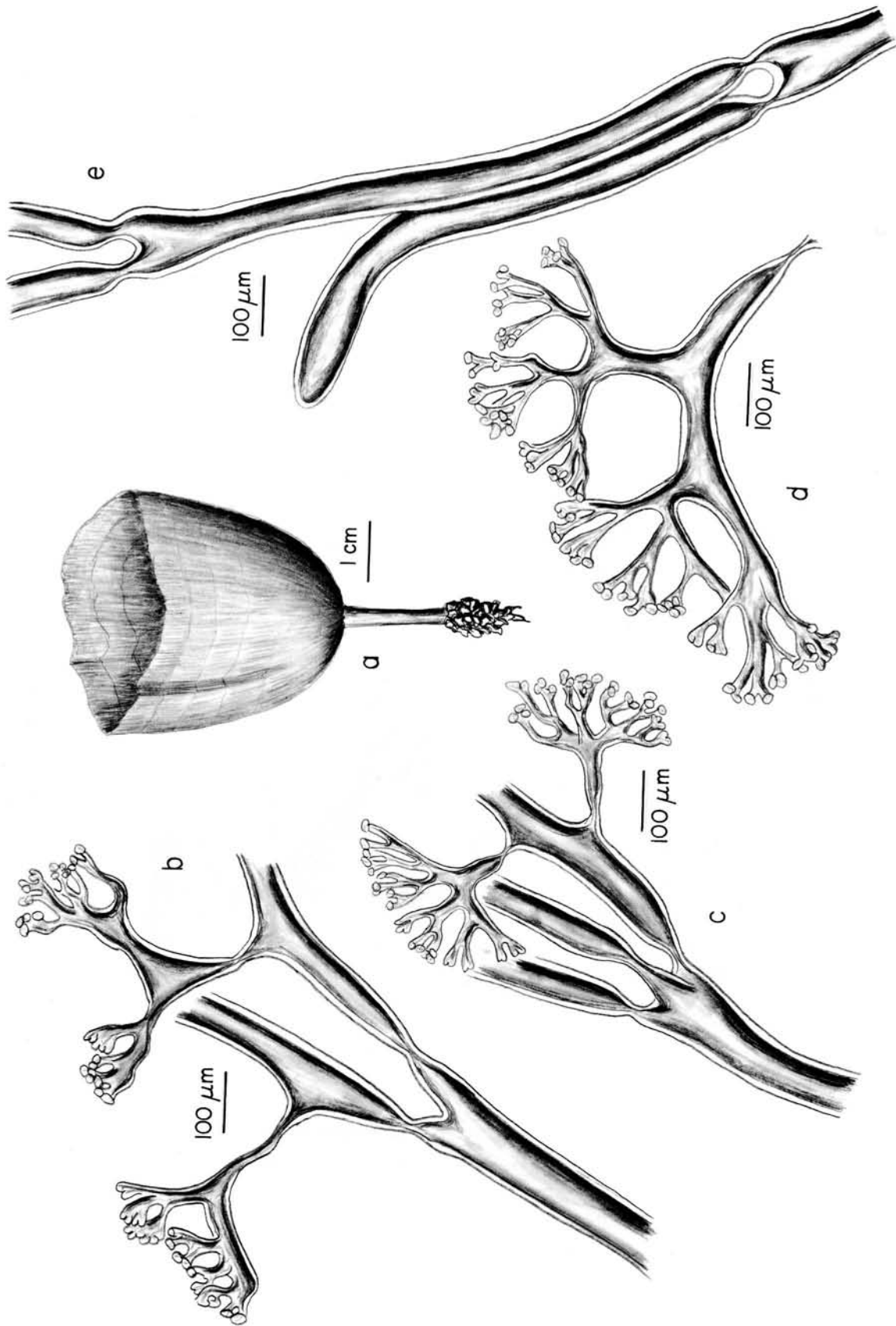


Fig. 4. *Udotea cyathiformis* Decaisne var. *cyathiformis* f. *cyathiformis*. a, habit; b, dichotomous division of stipe siphon; c, trichotomous division of stipe siphon; d, stipe lateral appendage; e, blade siphon.

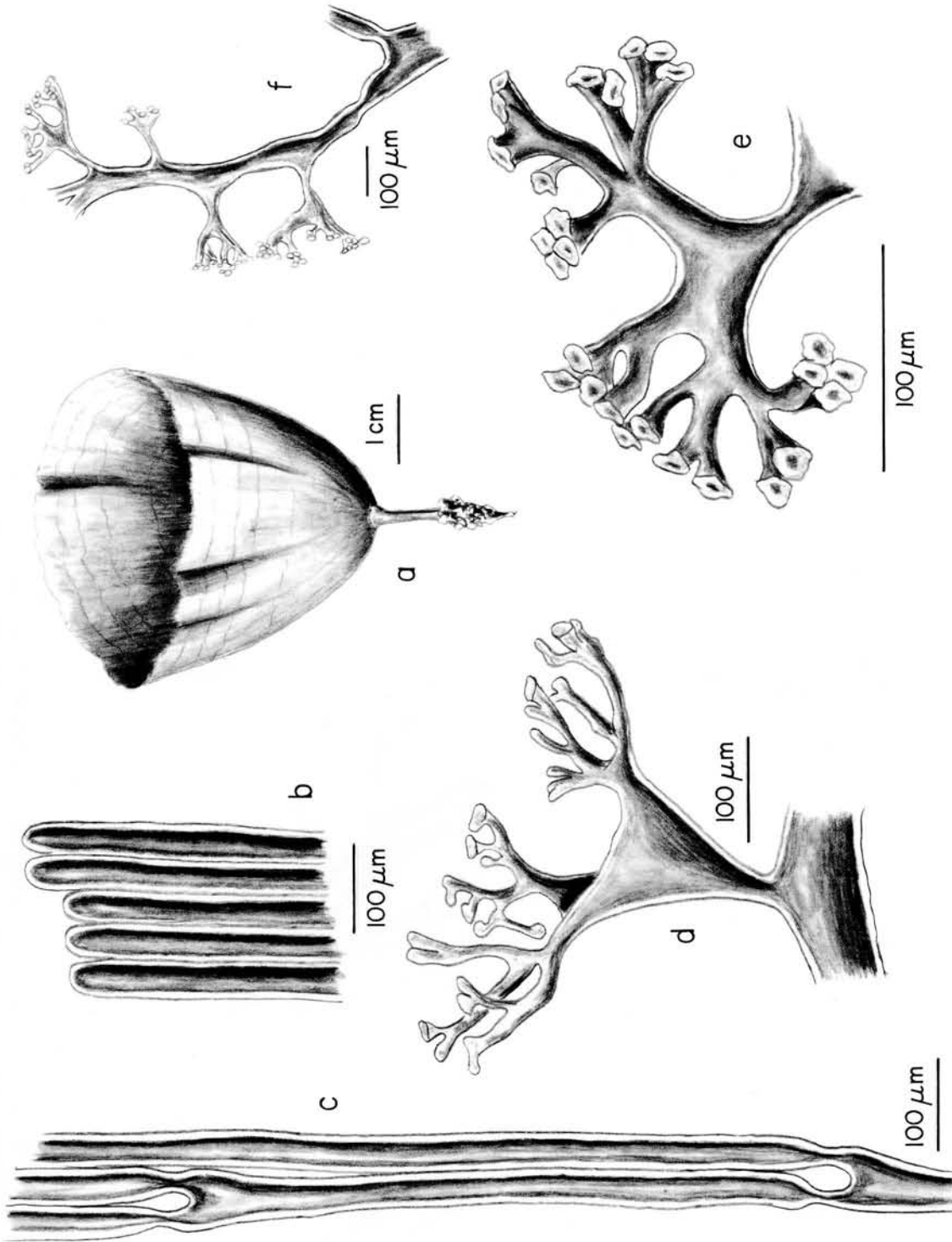


Fig. 5. *Udotea cyathiformis* f. *infundibulum* (J. Agardh) comb. nov. a, habit; b, outer margin of blade showing unistratose, parallel siphons; c, blade siphons with narrow dichotomies; d and e, lateral appendages of stipe; f, stipe siphon.

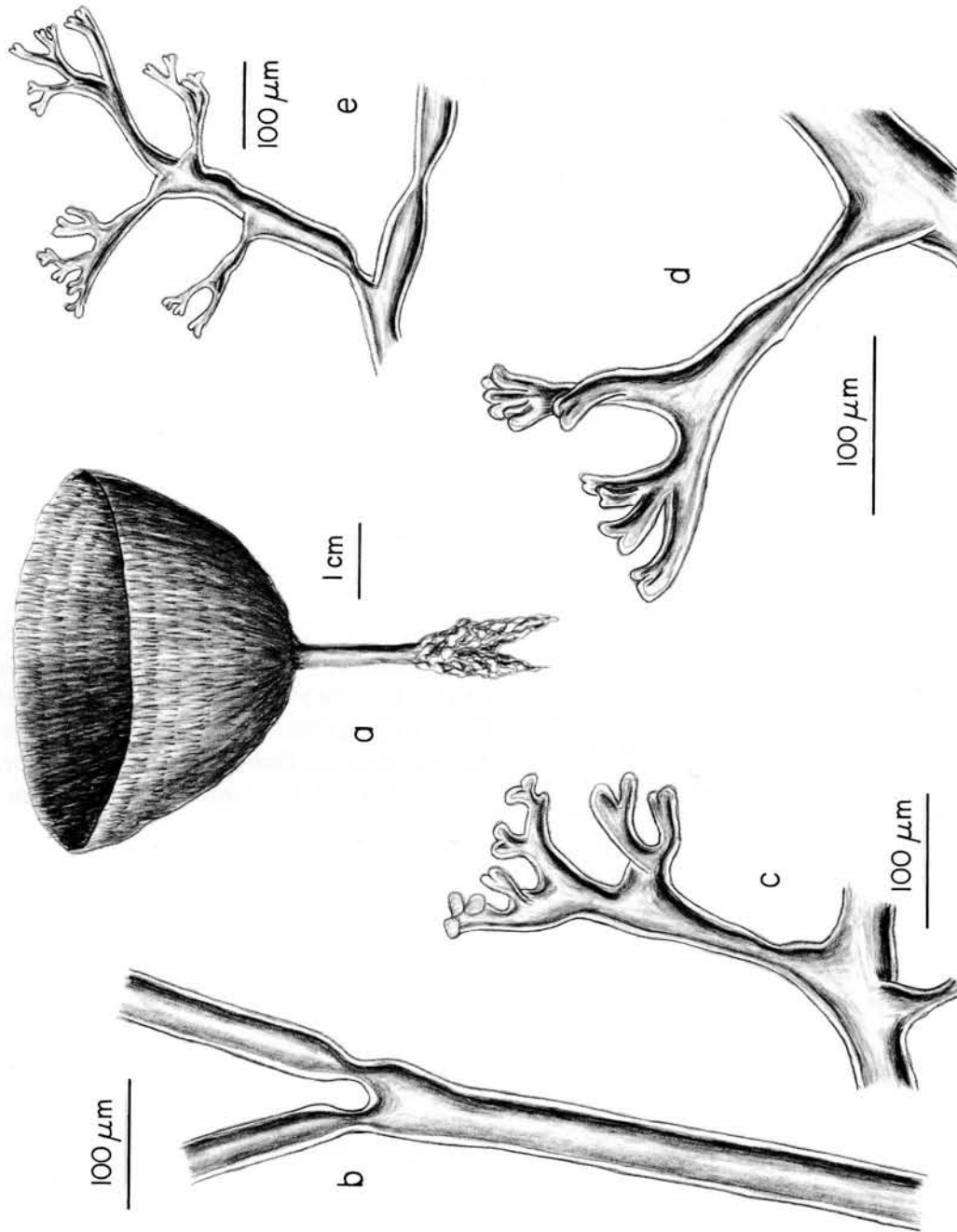


Fig. 6. *Udotea cyathiformis* f. *sublittoralis* (W.R. Taylor) comb. nov. a, habit; b, blade siphon showing wide dichotomy; c and d, lateral appendages of stipe; e, stipe siphon.

HOLOTYPE: MICH-8845, Garden Key, Dry Tortugas, Florida, 12 m deep, 1 July 1924, leg. W.R. Taylor (designated as HOLOTYPE by annotation of the author).

DISTRIBUTION: Bahamas, Florida, Puerto Rico, Lesser Antilles.

REPRESENTATIVE SPECIMENS EXAMINED: Florida: Garden Key, Dry Tortugas (HOLOTYPE); Bush Key, Dry Tortugas, 13 June 1924, US-33723. Bahamas: Cave Cays, Exuma Chain, 1 m deep on silty sand, 19 February 1905, NY, *Howe-3976*. Lesser Antilles: Mayreau, Tobago Cays, Grenadines, 2 m deep on sand, 22 July 1986, US-30620. Puerto Rico: Playa Tortuguero, Manati, 1–2 m deep, 3 August 1962, NY-(FP-DB)3022.

REMARKS: Taylor (1928) described the fibrous-appearing, cup-shaped form of *Udotea cyathiformis* as a new species, *U. sublittoralis*. However, after examining numerous specimens ranging in texture from papery and thin (with unistratose outer margins) to fibrous (multistratose), we find a continuum of variation. In this paper, we synonymize *U. sublittoralis* W. R. Taylor with *U. cyathiformis* Decaisne and reduce it to the status of a forma as *U. cyathiformis* f. *sublittoralis*. This form is characterized by the relatively large thickness of the blade (2–3 mm) compared with f. *cyathiformis* (1–2 mm), and the larger diameter of the smooth, lightly calcified, blade siphons (60–80  $\mu\text{m}$  compared with 30–70  $\mu\text{m}$  in f. *cyathiformis*). The dichotomies are wider (Fig. 6b) than those of f. *infundibulum* and not laterally adhering, thus creating an interwoven, fibrous texture (Fig. 4a). Blade margins are always multistratose as opposed to the unistratose margins of f. *infundibulum*, and the cup-shaped blade is usually wider (up to 4 cm) than long (to 3.5 cm). The stipe siphons are similar in all forms (Figs 4e, 5f, 6e), while the stipe appendages of f. *sublittoralis* are not so widely spreading (Fig. 6c, 6d) as those of the others. *Udotea cyathiformis* f. *sublittoralis* could be confused with *U. fibrosa*, as both are fibrous in texture. However, the blade siphons of the former are considerably smaller (60–80  $\mu\text{m}$  vs. 100–150  $\mu\text{m}$ ) than those of *U. fibrosa*, and it generally has faint concentric zones (Fig. 6a) on the blade, whereas the latter lacks any form of zonation (Fig. 11). Also, the cup or scoop-shaped blade of *U. cyathiformis* f. *sublittoralis* is considerably thinner (2–3 mm vs. 3–5 mm) than the flat or lobed blade of *U. fibrosa*. *Udotea fibrosa* is generally found in shallow water habitats.

### *Udotea cyathiformis* Decaisne

var. *flabellifolia* var. nov.

Fig. 7

DIAGNOSIS: *Udotea cyathiformis* var. *cyathiformis* anatomicaliter eadem atque sed in laminis planis et flabellatis non cyathiformis et non cochleariformis differt.

HOLOTYPE: US-96439, San Blas Islands, Republic of Panama, 20 m deep on a sand plain at Pigsty Reef, 8 November 1978, leg. M.E. Hay.

DISTRIBUTION: Found throughout the tropical western Atlantic.

REPRESENTATIVE SPECIMENS EXAMINED: Belize: Carrie Bow Cay, 42 m deep on sandy carbonate mud, 19 March 1982, US-96440. North Carolina: Carteret County, Onslow Bay, 29 m deep, 3 July 1984, US-14321. Panama: San Blas Islands (HOLOTYPE).

REMARKS: This variety differs from *Udotea cyathiformis* var. *cyathiformis* only in having a fan-shaped blade (Fig. 7a) rather than a cup-shaped or scoop-shaped blade (Fig. 4a). The blade siphons have the same diameters and arrangements (Figs 4e, 7e), while the stipe siphons (Figs 4b, 7b) and their lateral appendages (Figs 4d, 7c, 7d) are also similar. *Udotea explanata* A. Gepp & E.S. Gepp from the Celebes is much like this form (especially those specimens found in Panama) in both habit and anatomy, but the absence of cyathiform plants in the Indian Ocean suggests that the taxa are distinct. Therefore we prefer to separate the two taxa until further collections can be examined.

### *Udotea dixonii* sp. nov.

Fig. 8

DESCRIPTION: Thalli e systematis rhizoideorum fibroso interdum plures ad 21 cm alti; lamina lobata corticata flavo-viridis, siphonis laminae diametro 20–35  $\mu\text{m}$  cylindricis vel leniter moniliformibus supra dichotomas inaequaliter constrictis in appendicibus lateralibus in seriebus verticalibus binatis obsitis appendicibus in ramis numerosis tumidis terminatis; stipes 2–6 cm longus, siphonis diametro 30–60  $\mu\text{m}$  supra dichotomas non constrictis, appendicibus lateralibus in ramis brevibus obtusis dichotome digitatis terminatis.

HOLOTYPE: US-30598, Belize, Central America, on the east side of Curlew Cay, attached to sand-covered rock, with several thalli arising from the same holdfast, 46 m deep, 10 February 1988, leg. D.S. Littler, M.M. Littler, B.L. Brooks, B.E. Lapointe.

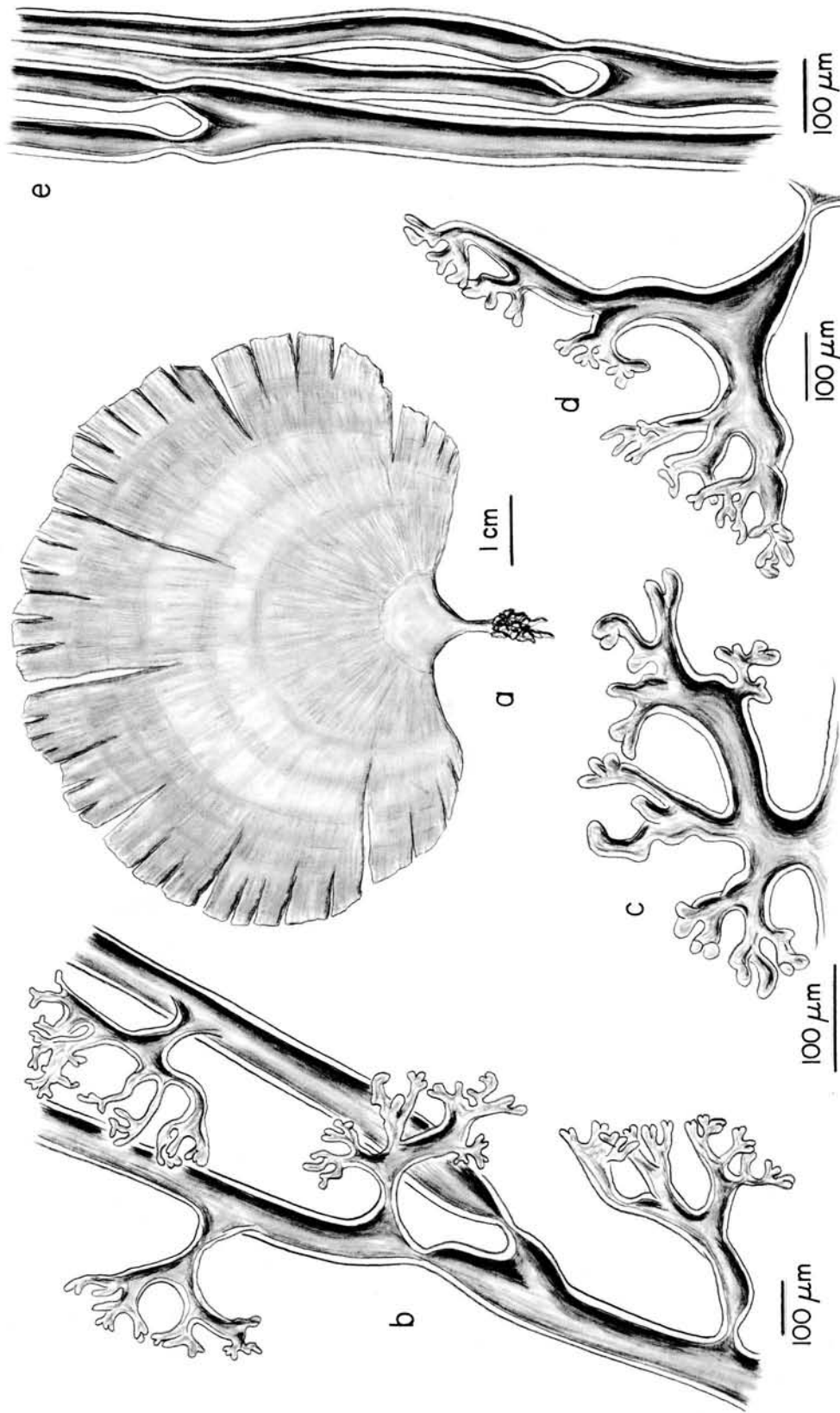


Fig. 7. *Udotea cyathiformis* var. *flabellifolia* var. nov. a, habit showing characteristic terminal flattened blade; b, smooth siphons of blade showing typical elongated constrictions above dichotomies; c and d, lateral appendages of stipe showing distorted digitate apices; e, unequal constrictions of stipe siphon (present in approximately 2.5% of dichotomies).



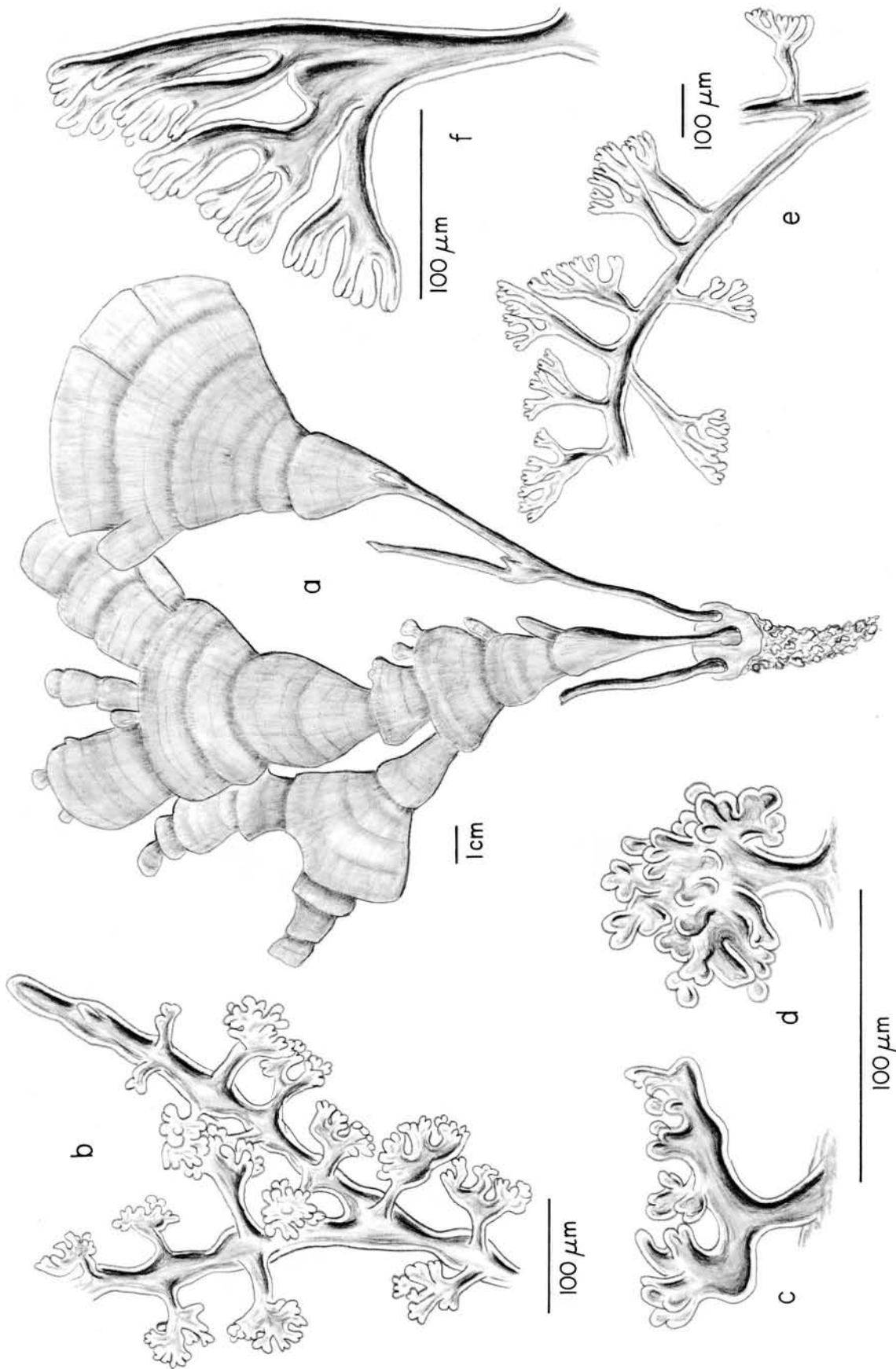


Fig. 8. *Udotea dixonii* sp. nov. a, habit; b, blade siphon showing abundance of lateral appendages; c and d, lateral appendages of blade; e, stipe siphon; f, lateral appendage of stipe.

**ETYMOLOGY:** This species is named in honour of Peter S. Dixon, whose generous support and guidance through our initial years of research are gratefully acknowledged.

**DISTRIBUTION:** Florida, Haiti, Puerto Rico, East Flower Garden Banks in the Gulf of Mexico, Belize, Nicaragua, Panama.

**REPRESENTATIVE SPECIMENS EXAMINED:** Belize: Curlew Cay (HOLOTYPE). Florida: Palm Beach County, 2.2 km east of Lake Worth Inlet, 38 m deep on a sand and rubble bottom, 10 March 1976, HBFH-783. Haiti: Caracol Reef, Caracol Bay, on the fore-reef slope, 20 m deep, 14 May 1981, US-14069. Panama: Galeta Island, 17 m deep, 9 February 1978, US, MEH-32.

**HABIT:** Plants to 21 cm tall, yellow-green, occur as individuals or in groups of two to five arising from the same rhizoidal mass. Blade long (6–12 cm), usually narrow (4–10 cm), 0.2–0.8 mm thick, flat, lobed, corticate, distinct concentric zones, distriatose at the outer margin, proximally multistratose. Stipe 2–3 mm in diameter, 2–6 cm long. Anchored by a mass of fibrous rhizoids (Fig. 8a).

**ANATOMY:** Blade siphons 20–35  $\mu\text{m}$  in diameter, unequal constrictions above the dichotomies (Fig. 8b), cylindrical or slightly moniliform (regularly swollen at close intervals), densely covered with two vertical rows (often paired) of lateral appendages oriented toward the surface of the blade; siphon appendages interlock with the adjacent appendages to form blade cortex, appendages widely spreading (Fig. 8c) or clustered (Fig. 8d), terminating in multiple, swollen knobs or short projections (Fig. 8c, 8d). Stipe siphons 30–60  $\mu\text{m}$  in diameter, no constrictions at the dichotomies (Fig. 8e); bearing numerous branched, lateral appendages that terminate in dichotomously divided, stubby, digitate projections (Fig. 8f), appendages intertwined and in such close proximity that it is difficult to separate components of the stipe cortex, even after prolonged decalcification.

**REMARKS:** The internal structure of *Udotea dixonii* most closely resembles that of *U. dotyi*, which also possesses numerous blade appendages. However, whereas the blade appendages of *U. dotyi* terminate in a cluster of flattened tips (Figs 9d, 9e, 10c, 10d), those of *U. dixonii* terminate in a dense array of short, swollen tips (Fig. 9a, 9b, 9c). In habit, *U. dixonii* resembles *U. flabellum*, although its blades are thinner and more delicate. *Udotea dixonii* often occurs in groups of two to five arising from the same rhi-

zoidal mat, whilst *U. flabellum* has a tougher, more leathery blade and usually occurs as a single individual. The two species are sometimes found sympatrically at the lower depth range of *U. flabellum* and the upper limit for *U. dixonii* (i.e. about 15 m deep). Apparently a plant of fairly deep waters (15–54 m, rarely to 10 m in shaded habitats), growing in sandy pockets on vertical walls or on deep sand plains.

*Udotea dotyi* sp. nov.

Fig. 10

**DESCRIPTION:** Thallus magnus ad 23 cm altus et 16 cm latus; lamina paucelobata cinerio-iridis obovatis multistratosis corticatis base profunde cordatis, siphonis subcylindricis diametro 40–80  $\mu\text{m}$  in seriebus verticalibus duplicibus appendicum dense obstitis, appendicibus in ramis multis congestis truncatis terminatis; stipes corticatis teretibus ad 2 cm longis et diametro 4 mm, siphonis diametro 70–100  $\mu\text{m}$  in dichotomis inaequaliter constrictis, appendicibus longe stipitis in apicis numerosis rotundatis terminatis.

**HOLOTYPE:** US-30600, Tobago Cays, Grenadines, Lesser Antilles, on sand-covered, dead coral at a depth of 12 m, 18 July 1986, leg. M.E. Hay.

**ETYMOLOGY:** This species is named in honour of Maxwell S. Doty, an inspirational, resolute, broad-thinking scientist.

**DISTRIBUTION:** Haiti, Puerto Rico, Lesser Antilles, Honduras.

**REPRESENTATIVE SPECIMENS EXAMINED:** Haiti: Caracol Reef, Caracol Bay, on the fore-reef slope, 3–20 m deep, 14 May 1981, US-14068. Honduras: Media Luna Bay, 23 m deep on a sand plain, 28 May 1981, US-14065. Lesser Antilles: Tobago Cays, Grenadines (HOLOTYPE).

**HABIT:** Plants to 23 cm tall, dark grey-green when living, light grey-green when dried. Blade corticate, large, often wider (up to 13 cm) than long (8 cm), 0.5–1.0 mm thick, unlobed or sparingly lobed, flat, paddle-shaped, lower margin deeply cordate in mature plants, multistratose throughout, faint concentric zonation. Stipe to 4 mm in diameter, 2 cm long, no differentiation between the stipe and blade surface texture. Anchored by a mass of fibrous rhizoids (Fig. 10a).

**ANATOMY:** Blade siphons oval, 60–80  $\mu\text{m}$  wide on the flattened side and 40–50  $\mu\text{m}$  wide when observed from the edge, unequal supradichotomal constrictions (Fig. 10b), densely covered along the margins (two subopposite rows) by short (up to 200  $\mu\text{m}$  long) stipe appendages (Fig. 10b)

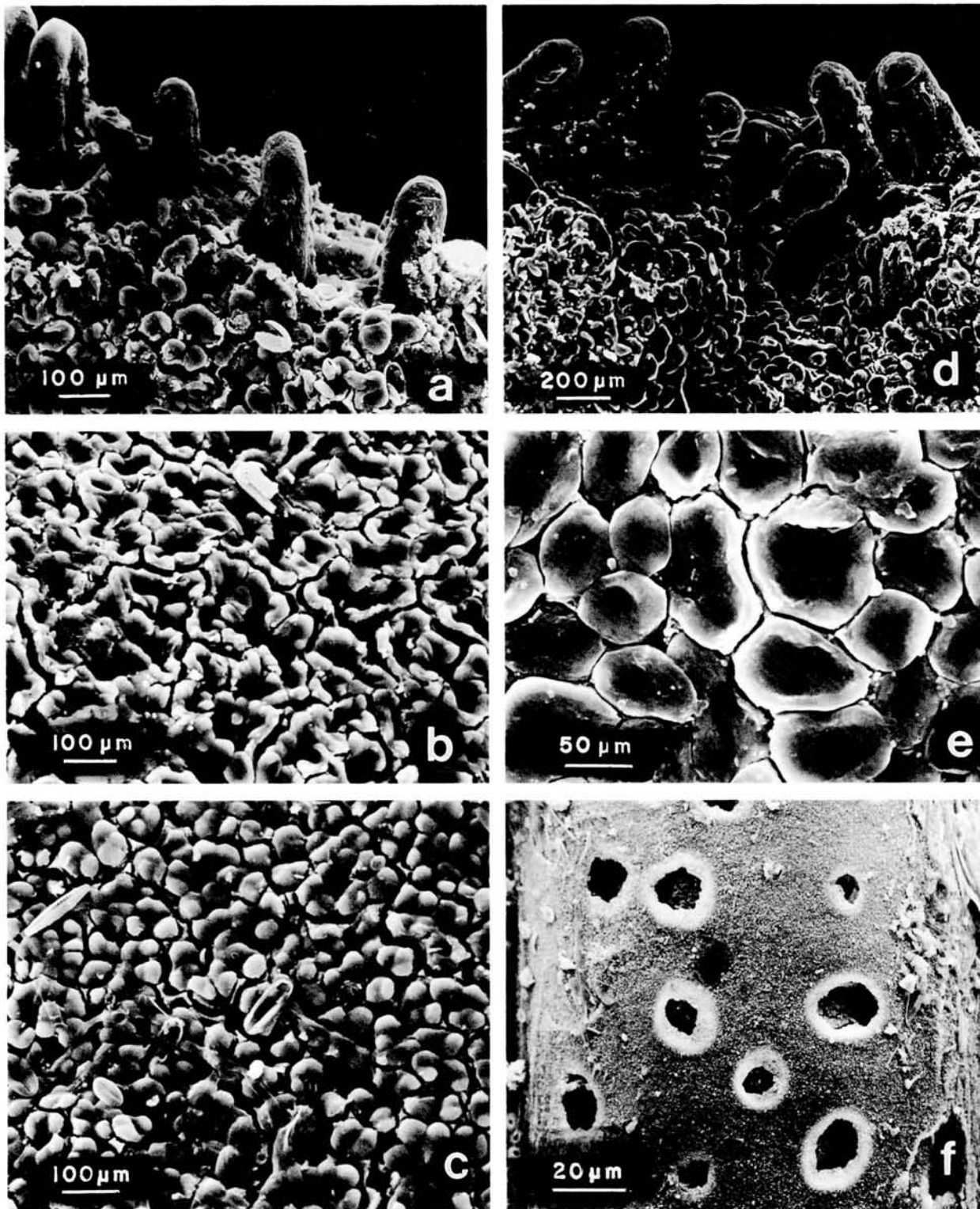


Fig. 9. Scanning electron micrographs. a, growing tip of blade in *Udotea dixonii*; b, *U. dixonii* blade surface showing shrunken tips and slight calcification; c, surface near mid-section of *U. dixonii* blade with well-calcified rounded, lateral appendage tips forming cortex; d, growing tip of *U. dotyi* blade; e, *U. dotyi* blade surface showing flat, lateral appendage tip; f, *U. unistratea* blade siphons with pores in calcareous sheaths.

that terminate in densely packed, flat-topped projections (Fig. 10c, 10d). Stipe siphons 70–100  $\mu\text{m}$  in diameter, unequal constrictions above dichotomies (Fig. 10f); lateral appendages long-stalked, branching dichotomously above,

terminating in numerous blunt rounded tips (Fig. 10e).

REMARKS: *Udotea dotyi* is closely allied with *U. argentea* Zanardini from the Pacific and Indian Oceans (see Gepp & Gepp 1911), *U. occidentalis*

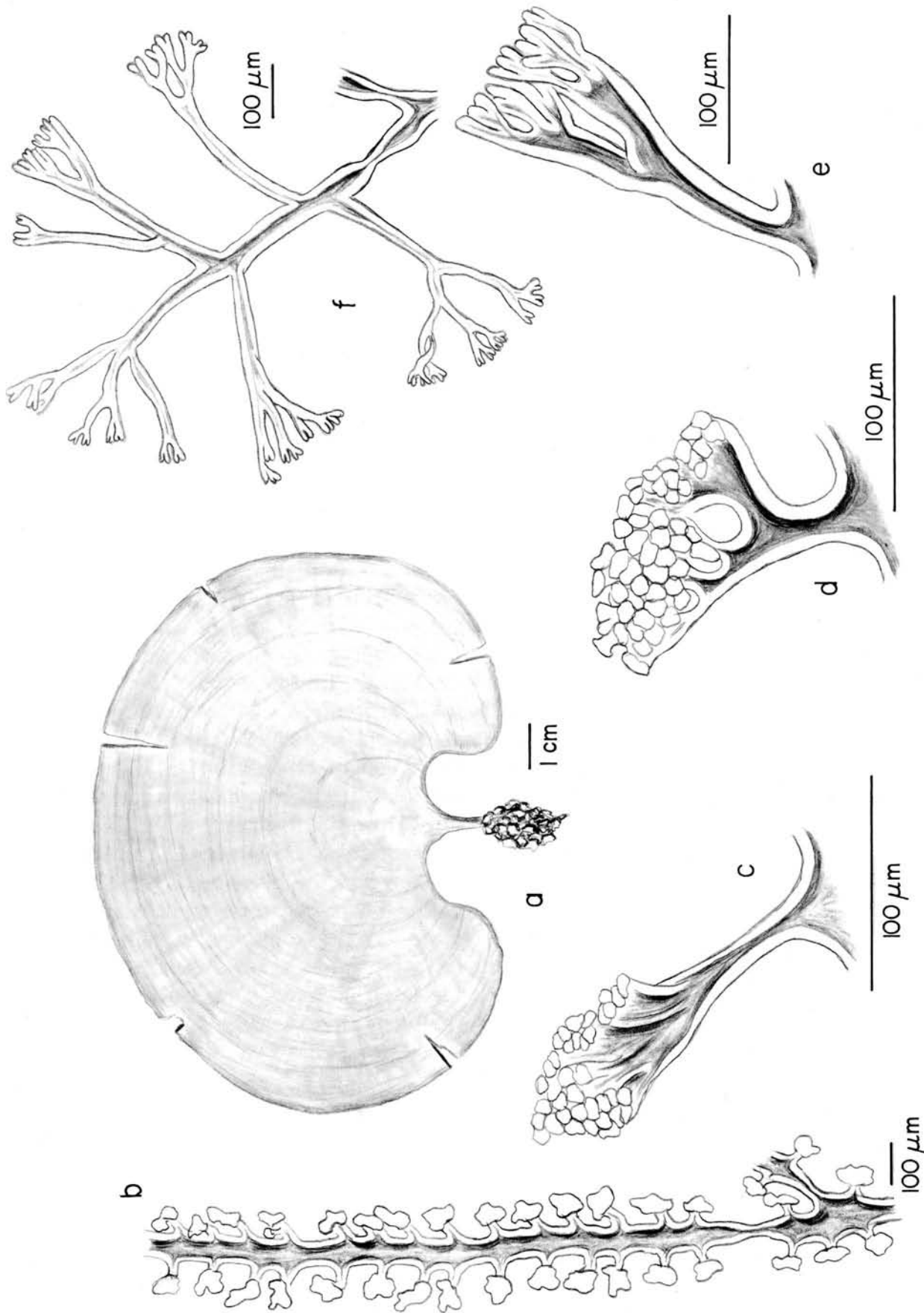


Fig. 10. *Udotea dotyi* sp. nov. a, habit; b, blade siphon illustrating abundant lateral appendage arrangement; c and d, lateral appendages of blade with markedly flattened tips; e, lateral appendage of stipe; f, stipe siphon.

and *U. dixonii*, all of which have blade siphons that are densely covered with lateral appendages. The blade appendages of *U. argentea* are simple, expanded and flattened or lobed at the apices, whereas those of *U. occidentalis* are rather more complex, terminating in broad lobes with low, rounded knobs. *Udotea dixonii*, in contrast, has lateral appendages that are widely branched and terminate in a dense array of blunt but rounded tips. Conversely, the lateral appendages of *U. dotyi* terminate in several wide branches that are almost obscured by the dense covering of flat-topped projections. The cordate blade is distinctive among corticated species. Plants are most often collected from moderately deep (15–25 m) sand plains.

***Udotea fibrosa* sp. nov.**

Fig. 11

DESCRIPTION: Lamina incrassata fibrosa sordido-viridis anguste flabellata ad 5 cm alta, siphonis intertextis laevibus magnis diametro 100–150  $\mu\text{m}$  multo late dichotomis supra dichotomas aequaliter constrictis distaliter saepe seriete constrictis et moniliformibus; stipes 1 cm longus et 5 mm latus corticatus, siphonis primariis diametro 120–180  $\mu\text{m}$  in dichotomis inaequaliter constrictis, ramis lateralibus in divisibus dichotomis tumidis terminatis.

HOLOTYPE: US-30602, Belize, Central America on the shallow reef flat off the east side of Carrie Bow Cay approximately 50 m from shore, 0.5 m deep on sand, 17 March 1987, leg. D.S. Littler, M.M. Littler, B.L. Brooks.

ETYMOLOGY: This species is named after the visibly fibrous texture of the blade.

DISTRIBUTION: Jamaica, Haiti, Belize.

REPRESENTATIVE SPECIMENS EXAMINED: Belize: Carrie Bow Cay (HOLOTYPE); Curlew Cay, 0.1–0.5 m deep on sand or attached to sand-covered beach rock, 5 February 1988, US-30621; Gallows Point, 3 m deep on sand, 30 July 1962, NY, *Goreau-22a*.

HABIT: Plants to 6 cm tall, dull dark green, light green when dried, heavily calcified. Blade typically longer than wide, fan-shaped but often lobed or convoluted (Fig. 11a), multistratose, 3–5 mm thick, lacking zonal bands, fibrous, intertwined siphons distinctly visible to the unaided eye. Stipe stout, heavily calcified, flattened above, 1 cm long to 5 mm wide. Anchored to substratum by a deep, broad, fibrous mass of relatively large rhizoids, main rhizoids covered with fine branchlets (Fig. 11a).

ANATOMY: Blade siphons lacking appendages,

large (100–150  $\mu\text{m}$  in diameter), slightly moniliform, deep supradichotomal constrictions (sometimes absent in younger divisions), many widely spreading dichotomies (Fig. 10b) resulting in non-parallel siphons and a thick, fibrous blade; basal siphons (lower 2–5 mm) covered by short appendages (fibulae), increasing in density toward the stipe, fairly sharp distinction between the surface of the blade and stipe, calcareous sheath with pores. Stipe central siphons large (120–180  $\mu\text{m}$  in diameter), unequally constricted at the dichotomies (Fig. 11c); lateral branchlets terminate in short, dichotomously divided, rounded or slightly bulbous tips (Fig. 11d).

REMARKS: *Udotea fibrosa* differs from *U. conglutinata* in that the siphons are much larger (mean dimensions of 122  $\mu\text{m}$  vs. 40  $\mu\text{m}$  in diameter for *U. conglutinata*) and not conglutinate, siphons are randomly oriented and do not radiate in a subparallel manner from the stipe. *Udotea fibrosa* is also superficially similar to *U. abbotiorum*, but again the blade siphons are consistently larger (122  $\mu\text{m}$  in diameter in the former vs. 90  $\mu\text{m}$  in diameter in the latter). *Udotea fibrosa* tends to be asymmetrical without a consistent external shape, in contrast to *U. abbotiorum* and *U. conglutinata*, and the blade is the thickest within the genus (3–5 mm vs. 2–3 mm in *U. cyathiformis* f. *sublittoralis* and 1 mm in *U. abbotiorum* and *U. conglutinata*). *Udotea fibrosa* can be confused with *U. cyathiformis* f. *sublittoralis*, since both have a coarse fibrous texture. However, the blade siphons of *U. fibrosa*, as mentioned, are larger (122 vs. 70  $\mu\text{m}$  in diameter) and the blade lacks the alternating zonal bands characteristically exhibited by *U. cyathiformis* f. *sublittoralis*, aside from the typically symmetrical cup or scoop-shaped blade of the latter. *Udotea fibrosa* occurs in extremely shallow waters (usually <1.0 m).

***Udotea flabellum* (Ellis et Solander) Howe 1904: 94.**

Fig. 12

BASIONYM: *Corallina flabellum* Ellis et Solander 1786: 124, pl. 24.

LECTOTYPE: *Udotea flabellum* was described by Ellis & Solander (1786) at the same time as *U. conglutinata*. After searching unsuccessfully, we presume the type of *U. flabellum*, like that of *U. conglutinata*, to be lost. In the absence of a known holotype or isotype, we follow Dixon (1960) in

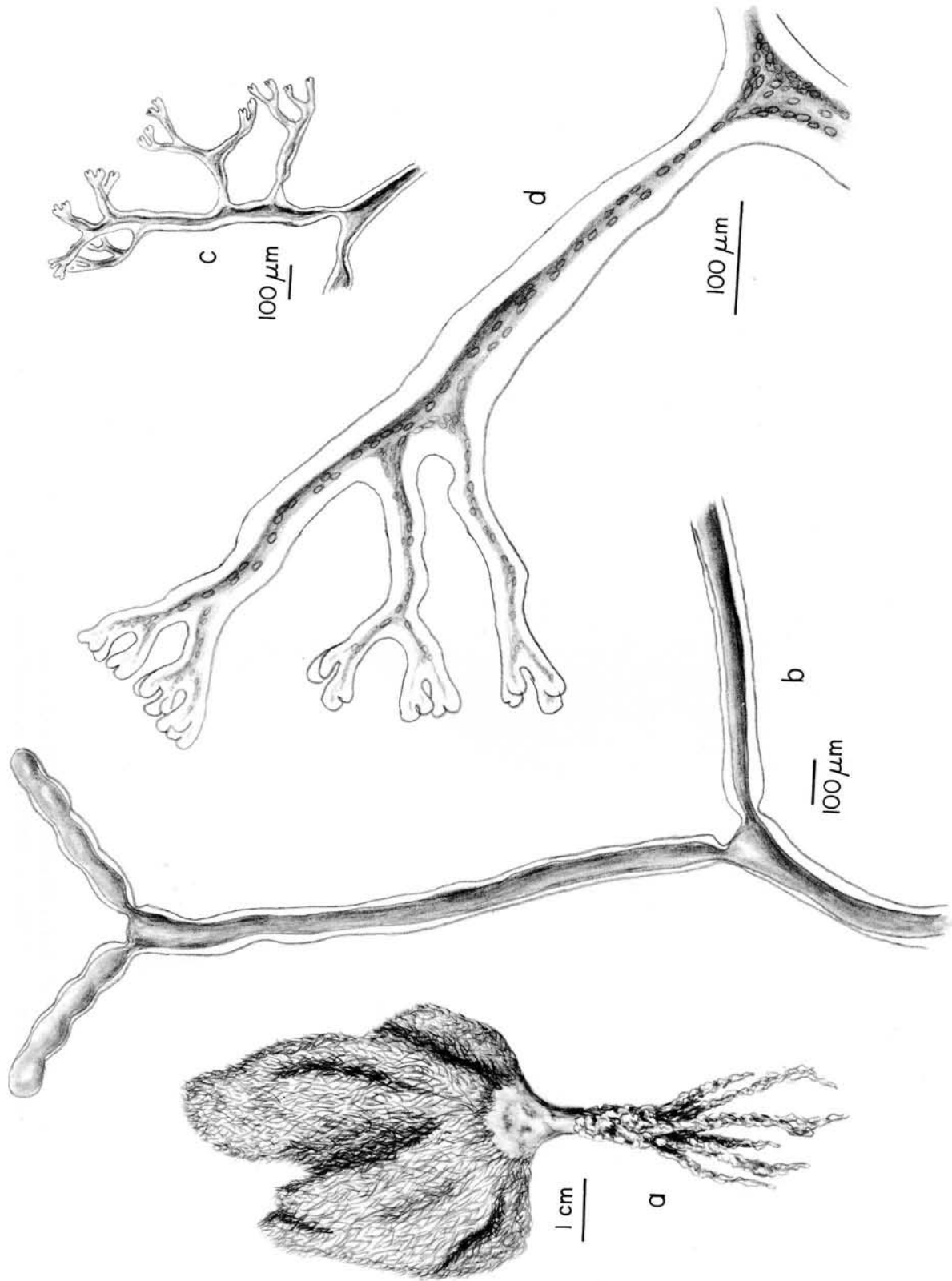


Fig. 11. *Udotea fibrosa* sp. nov. a, habit; b, blade siphon showing wide dichotomies; c, stipe siphon; d, lateral appendage of stipe.

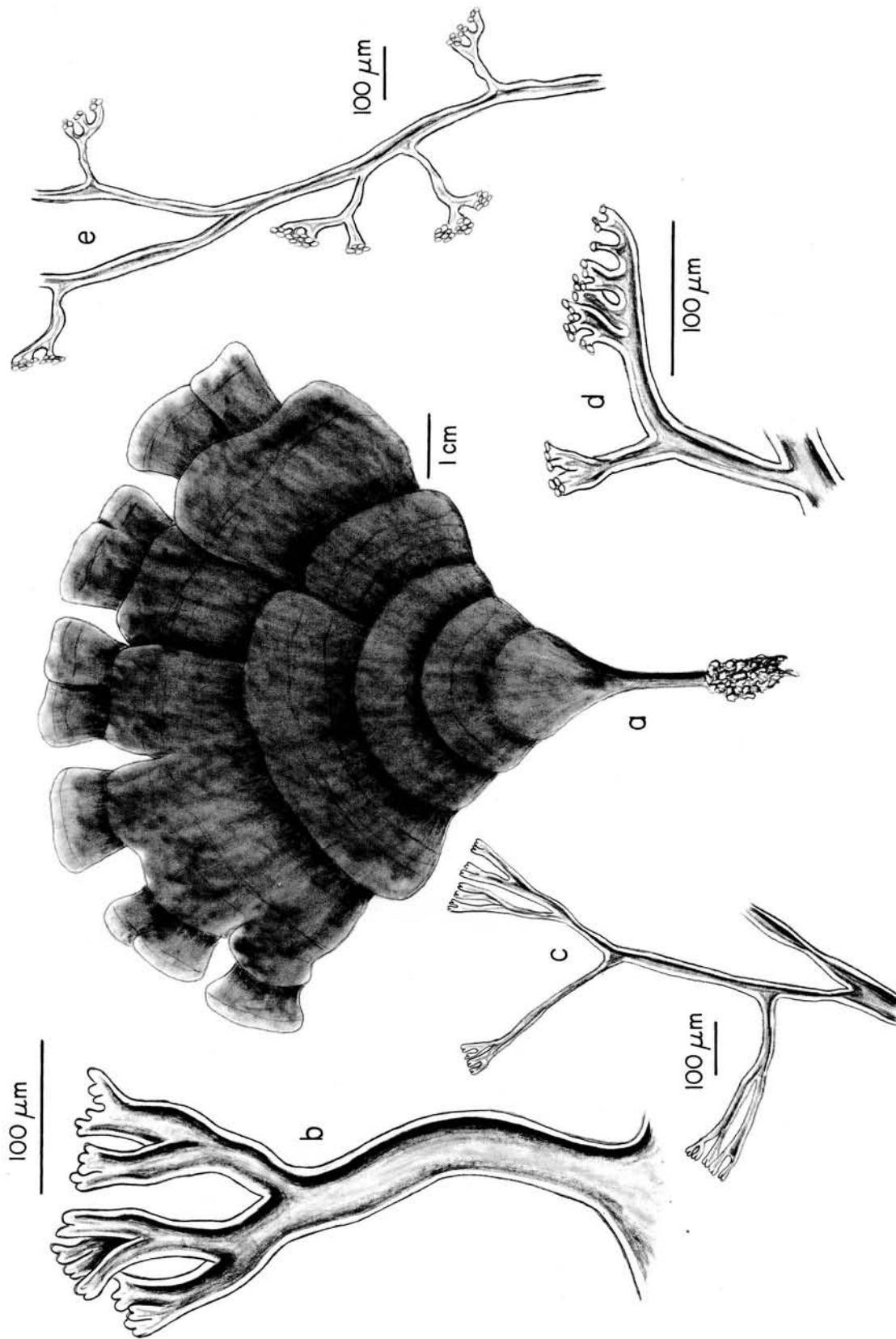


Fig. 12. *Udotea flabellum* (Ellis et Solander) Howe. a, habit of typical plant (external morphology is highly variable); b, lateral appendage of stipe; c, stipe siphon; d, lateral appendage of blade; e, blade siphon.

designating Ellis & Solander's illustration (1786, pl. 24) as the LECTOTYPE [Arts. 42.2 and 44.2 (ICBN), Greuter *et al.* 1988]. Type locality: West Indies (precise locality not specified).

**DISTRIBUTION:** The most abundant and widely distributed species of the genus, found throughout the tropical western Atlantic.

**REPRESENTATIVE SPECIMENS EXAMINED:** Belize: Lighthouse Reef, 1 m deep on sand, 30 May 1987, US-30623. Florida: Looe Key, Monroe County, 3 m deep on a sand and rubble habitat shoreward of the reef crest, 19 June 1984, US-30622. Lesser Antilles: near Mayreau, Tobago Cays, Grenadines, 2 m deep on sand, 22 July 1986, US-30624.

**HABIT:** Plants to 30 cm tall, deep dark green to pale green, heavily calcified, highly variable in habit. Blades multistratose throughout, corticate, 0.8–1.5 mm thick, leathery and moderately calcified, generally marked by distinct, somewhat concentric zonation lines, initially composed of a single, broad, undivided, fan-shaped blade, which may later become highly divided with many overlapping lobes (Fig. 12a). Stipe stout, simple, 5–7 mm in diameter to 2 cm long, cylindrical below, flattened above, no surface differentiation or demarcation where the stipe gradually joins the blade. Anchored in soft substrata by a bulbous to elongated mass of fibrous rhizoids.

**ANATOMY:** Blade siphons 30–50  $\mu\text{m}$  in diameter, without constrictions, or showing a slight tendency toward unequal constrictions above the infrequent dichotomies (Fig. 12e), siphons possess widely and irregularly spaced long-stemmed lateral appendages (in contrast to the densely crowded appendages of *Udotea dixonii*, *U. dotyi* and *U. occidentalis*), blade appendages terminate in numerous, often crowded, short, dichotomously branched projections, apices rounded, often shrunken and flat when dried (Figs 12d, 13a, 13b). Stipe siphons 20–80  $\mu\text{m}$  in diameter, no constrictions above the dichotomies (Fig. 12c); stipe appendages irregular, long-stemmed (dichotomous branches occur only in the outer portions), stipe appendages terminate in small rounded tips (Fig. 12b), similar to the blade appendages but more compact.

**REMARKS:** A morphologically variable species, *Udotea flabellum* tends to be tallest (to 30 cm) in shaded areas, whereas thalli in sunny, shallow waters are usually shorter (to 20 cm) and often develop more compact blades. This species is readily distinguished from all but the highly branched *U. norrisii* by its internal structure,

which remains relatively constant irrespective of the external form. It is the most widespread species of *Udotea*, commonly occurring in sandy areas to a depth of 10 m.

***Udotea goreau* sp. nov.**

Fig. 14

**DESCRIPTION:** Thallus ad 12 cm altus; lamina flabellata delicata unistratosa, siphonis diametro 100–150  $\mu\text{m}$  parallelis lateraliter conglutinatis supra dichotomas inaequaliter constricta; stipes longus tenuis, siphonis diametro 150–180  $\mu\text{m}$  supra dichotomas inaequaliter constricta, appendicibus lateralibus in divisibus dichotomis congestis obtusis terminatis.

**HOLOTYPE:** NY, *Goreau-23a*, West Runaway Bay, Jamaica, in sand on the fore-reef slope at 40 m deep, 7 January 1962, leg. T. Goreau, E. Graham.

**ETYMOLOGY:** This species is named after the collector, Thomas Goreau Sr, a pioneer in the field of tropical reef research.

**DISTRIBUTION:** Jamaica, Puerto Rico.

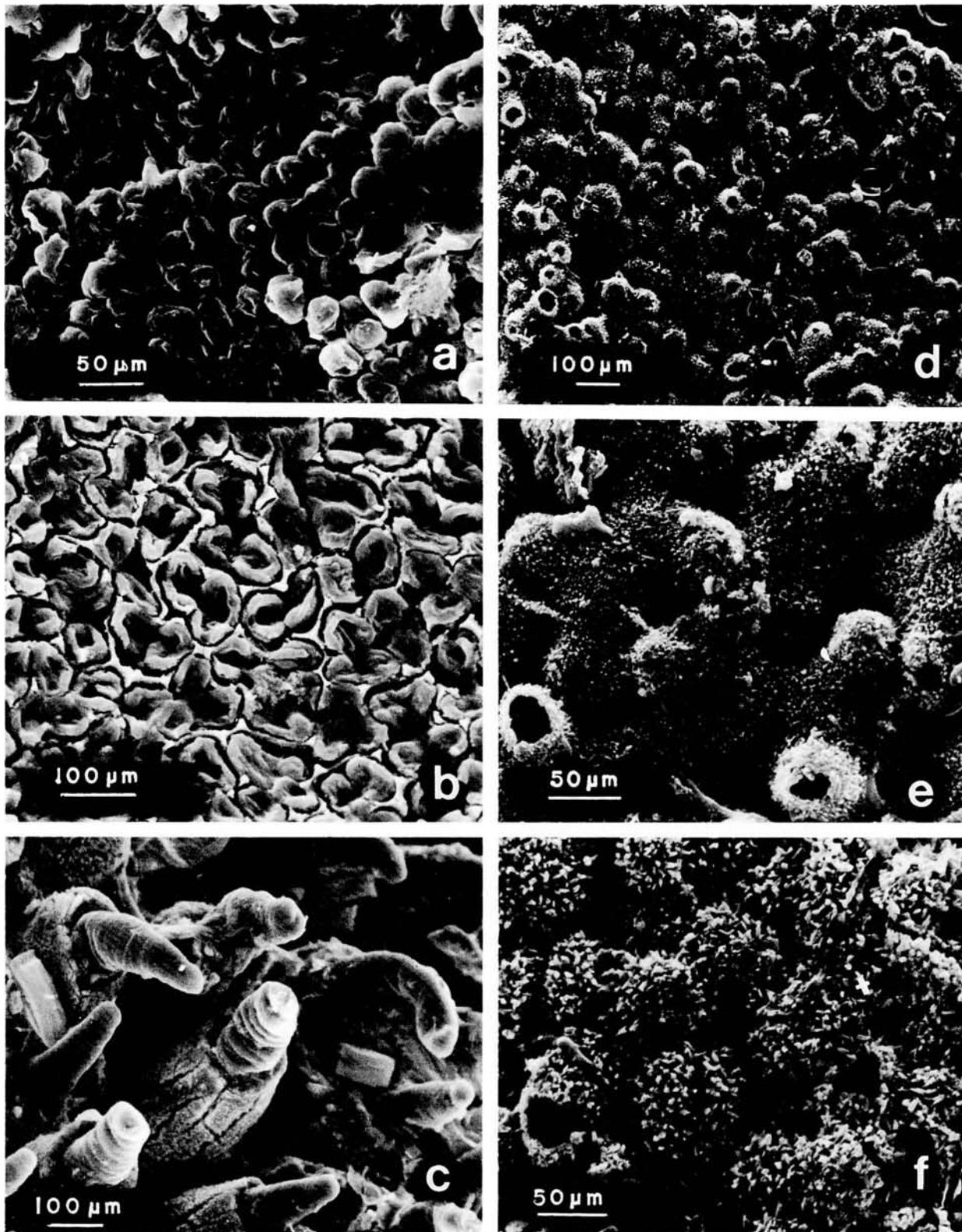
**REPRESENTATIVE SPECIMENS EXAMINED:** Jamaica: West Runaway Bay (HOLOTYPE); South Cay, Port Royal Cays, 10–13 m deep, 24 August 1962, NY, *Goreau-23*. Puerto Rico: 1.5 km seaward of Media Luna Reef, 17 m deep, 6 February 1980, US-091656; Salinas, from the edge of the insular shelf, 18 m deep, 9 February 1980, *Ballantine-667*; seaward of Margarita Reef, 24 m deep, 2 January 1980, *Ballantine-530*.

**HABIT:** Plants to 12 cm tall, greyish-green when dried, heavily calcified. Blade thin, fan-shaped, slightly wider than long, shape often obscured by portions being torn away, distal two-thirds unistratose (0.1–0.2 mm thick), proximally (lower third) multistratose (to 1 mm thick), lightly zoned. Stipe slender, 1 mm in diameter, to 1.5 cm long, gradual transition between blade and stipe. Anchored by a fine, fibrous, rhizoidal mass (Fig. 14a).

**ANATOMY:** Blade siphons 100–150  $\mu\text{m}$  in diameter, deep unequal constrictions appear just above the dichotomies (Fig. 14b), consistently parallel, bound together laterally by heavy deposits of calcium carbonate and by interlocking papillae, generally covered by four vertically aligned rows (Fig. 14c) of simple or sparingly branched papillae (Fig. 14d, 14e, 14f). Stipe siphons 150–180  $\mu\text{m}$  in diameter, unequal constrictions above the dichotomies; stipe appendages branched, generally unilateral, terminating in dichotomously divided blunt tips (Fig. 14g).

**REMARKS:** *Udotea goreau* is similar to *U.*





**Fig. 13.** Scanning electron micrographs. a, blade surface of *Udotea flabellum* in mid-section of blade; b, *U. norrisii* blade surface showing calcareous matrix between siphon tips; c, *U. luna* stipe surface depicting the heavily calcified sheath terminating well below the acute apex; d, *U. occidentalis* blade surface showing numerous pores that form on knobs of lateral appendages; e, *U. occidentalis* spiny blade surface and pores; f, *U. occidentalis* stipe surface.

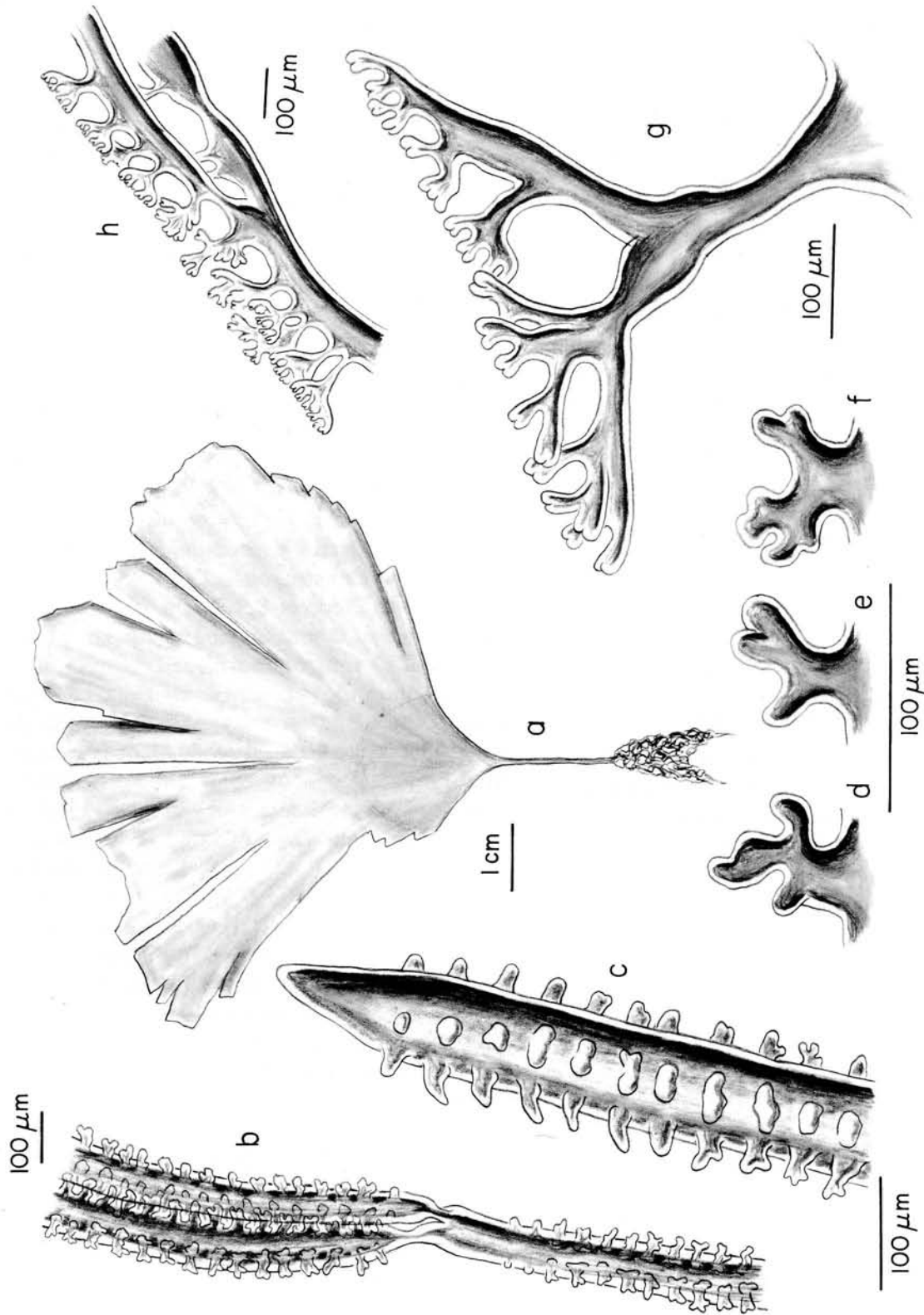


Fig. 14. *Udotea goreauai* sp. nov. a, habit; b, blade siphon; c, tip of blade siphon showing vertical rows of paired, lateral appendages; d, e and f, lateral appendages of blade; g, lateral appendage of stipe; h, stipe siphon.

*papillosa* A. Gepp et E.S. Gepp of the Pacific, although the latter is much shorter (only 2 cm tall vs. 12 cm tall) with smaller siphons (30–45  $\mu\text{m}$  in diameter), produces shorter knob-like papillae and has an incompletely corticated stipe. *Udotea goreau* is also anatomically similar to *U. wilsonii*, but the lateral appendages of the blade in the former seldom exceed 55  $\mu\text{m}$  in length and are much shorter than the width of the larger siphons, while those of *U. wilsonii* are normally as long or longer than the width of the bearing siphon (25–120  $\mu\text{m}$ ). In contrast to the radial symmetry typical of the numerous blades found on *U. wilsonii*, the single fan-shaped blade of *U. goreau* is bilaterally symmetrical and the majority (distal two-thirds) of the blade is unistratose. Generally found growing on deep (below 17 m) sand plains.

***Udotea looensis* sp. nov.**

Fig. 15

**DESCRIPTION:** Thallus ad 7 cm altus; lamina zonata simplex flabellata in marginis distalibus unistratosa base truncata vel leniter cordata, siphonis laevibus parallelis vel subparallelis diametro 50–70  $\mu\text{m}$ , siphonis laminae et stipitis supra dichotomas omnia aequaliter constrictis, siphonis stipitis in appendicibus lateralibus apice longe attenuatis.

**HOLOTYPE:** US-30604, Looe Key, Monroe County, Florida, on the intermediate reef, 12–30 m deep, attached to carbonate rock or to larger pebbles in sand pockets, 12 March 1988, leg. D.S. Littler, W.D. Lee.

**ETYMOLOGY:** This species is named after the type locality, the Looe Key National Marine Sanctuary, where it occurs in exceptional abundance.

**DISTRIBUTION:** Bahamas, Florida, Belize, Honduras, Panama.

**REPRESENTATIVE SPECIMENS EXAMINED:** Bahamas: Fernandez Bay, San Salvador Island, 7 m deep, 25 July 1974, HBFH-456. Belize: Twin Cays, along the east and west banks of the north end of the main channel, 1 m deep on silt, 7 March 1983, US-30626; Glovers Reef, 23 m deep, 19 November 1985, US-30625. Florida: Looe Key (HOLOTYPE); Molasses Reef, Key Largo, 5 m deep, 6 June 1979, HBFH-3397; HBFH-3398.

**HABIT:** Plants to 7 cm tall, dark green when young, lighter green with age. Blades simple, ecorticate, unistratose at the outer margins (Fig. 15e), multistratose proximally, fan-shaped (Fig. 15a), to 1 mm thick, generally broader (5–7 cm) than long (3–4 cm), lower margin truncate to

slightly cordate, distinctive banding. Stipe 2 mm in diameter, to 8 mm in length, with a gradual transition at the blade juncture. Anchored to rock or larger pebbles in sand by a small rhizoidal mass forming the holdfast.

**ANATOMY:** Blade siphons 50–80  $\mu\text{m}$  in diameter, lacking appendages, equal constrictions above each dichotomous division (Fig. 15e), dichotomies more frequent proximally, infrequent in the parallel unistratose outer margin, calcareous sheath with pores. Stipe siphons 45–90  $\mu\text{m}$  in diameter, constricted equally above the dichotomies (Fig. 15c); lateral branchlets dichotomously divided, apices characteristically long and tapering (Fig. 15b).

**REMARKS:** *Udotea looensis* is similar to *U. spinulosa*; however, none of the upper siphons of the blade in the former have lateral appendages. The transitional area between the stipe (bearing acute apices on the lateral appendages) and the lower blade (composed of smooth siphons) possesses reduced lateral appendages (Fig. 14d). Gepp & Gepp (1911) distinguished *U. spinulosa* f. *palmettoidea* A. Gepp et E.S. Gepp on the basis of the absence of lateral appendages from the uppermost 2–3 mm of the blade siphons. In *U. looensis*, the stipe appendages continue on to the base of the blade for only 2–3 mm, while the remainder (up to 60 mm) of the blade is smooth. In addition, *U. looensis* has terete (cylindrical) blade siphons, not flattened as in *U. spinulosa*. *Udotea luna* is also closely related, having smooth blade siphons and acute-tipped lateral appendages on the stipe siphons. *Udotea looensis* differs in having parallel, unistratose siphons at the margins of the blade, whereas multistratose, subparallel siphons reach the blade margins in *U. luna*. The latter two species also grow in different habitats—*U. looensis* is generally found attached to rock in moderately deep waters (10–20 m) or shaded areas, while *U. luna* is most often found in shallow waters (1–3 m), often in great abundance, on peat substrata near mangrove islands.

***Udotea luna* sp. nov.**

Fig. 16

**DIAGNOSIS:** In siphonis laminae laevibus et in appendicibus lateralibus stipitis apice attenuatis *Udotea looensis* similis sed in thallo ad 5 cm alto non 7 cm alto et in margine laminarum distaliter multistratose non unistratose et non delicato differt.

**HOLOTYPE:** US-30606, Content Keys, Monroe County, Florida, 5 m deep, attached to hard,

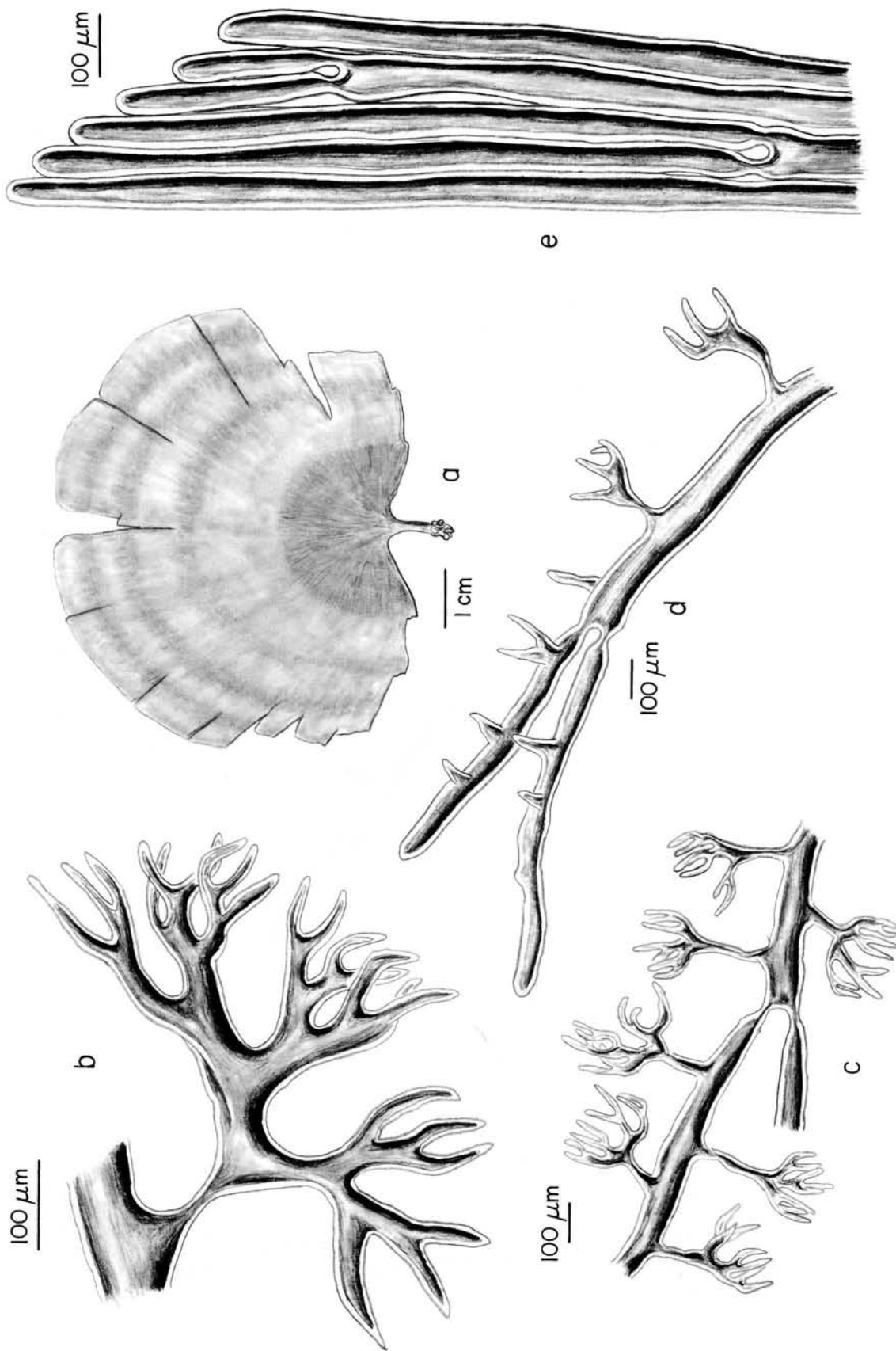
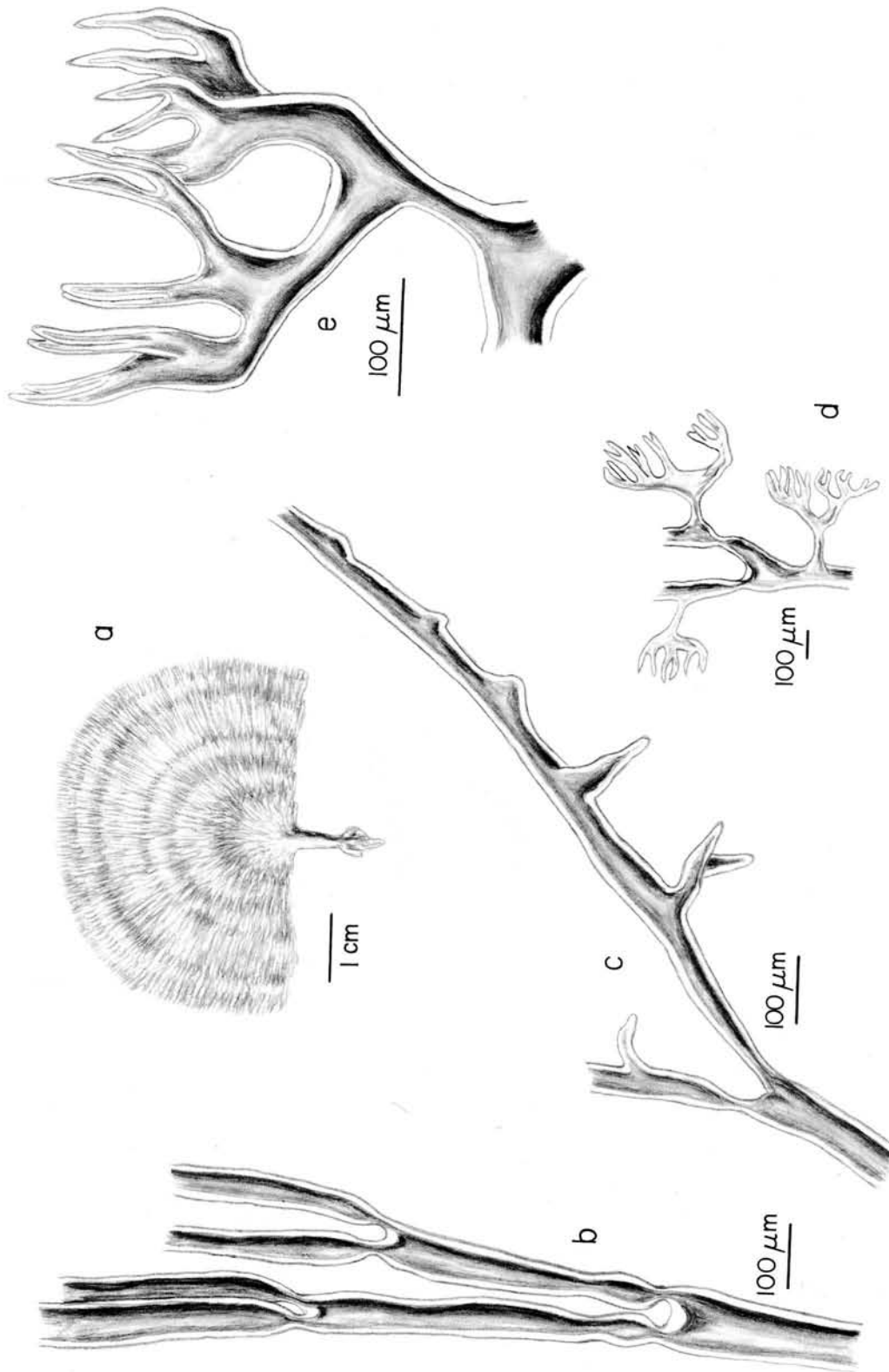


Fig. 15. *Udotea loeensis* sp. nov. a, habit; b, lateral appendage of stipe; c, stipe siphon; d, basal siphon of blade in transition area joining stipe; e, blade siphons.



**Fig. 16.** *Udotea luna* sp. nov. a, habit; b, blade siphon; c, basal siphon of blade in transition area joining stipe; d, stipe siphon; e, lateral appendage of stipe.

sand-covered, carbonate substrata on the north-northwest side of the largest and westernmost Key, 13 December 1987, leg. *D.S. Littler, M.M. Littler, S. A. Reed, W.D. Lee*.

ETYMOLOGY: The epithet of this species refers to the blade, which is often half-moon shaped.

DISTRIBUTION: Bahamas, Florida, Belize.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: North Cat Cay, 15 April 1904, NY, *Howe-3213*. Belize: Tobacco Range, on the north-west side of the mangrove island complex, 3 m deep on mangrove peat, 18 February 1988, US-30627; Lighthouse Reef, Half-Moon Cay, 22–23 m deep on vertical wall, 21 November 1985, US-96441. Florida: Content Keys (HOLOTYPE); Southernmost Beach, Key West, 2 m deep on sand, 5 June 1979, HBFH-3396.

HABIT: Plants to 7 cm tall, dark green when young (lightly calcified), turning lighter green when older (due to more calcification and many epiphytes, especially small crustose corallines). Blade ecorticate, fan-shaped to half-moon shaped (Fig. 16a), usually broader (6 cm) than long (4 cm), margins ragged and often torn, truncate to subcuneate base, multistratose throughout, to 1 mm thick, lightly zoned, with velvety texture when young. Stipe 1–2 mm in diameter, to 5 mm tall, with a gradual transition where it joins the blade. Anchored in mud, sand or to firmer substrata by a tangled, rhizoidal mass.

ANATOMY: Blade siphons 50–80  $\mu\text{m}$  in diameter, smooth, equal and deep constrictions above each dichotomous division, occasionally double constrictions occur above the dichotomies on one or both branches (Fig. 16b); basal siphons possess abbreviated appendages having acute apices (Fig. 16c), appendages increasing in density toward the stipe, calcareous sheath porous. Stipe siphons 60–90  $\mu\text{m}$  in diameter, constrictions slightly uneven above the dichotomies (Fig. 16d); lateral appendages terminate in acute tips (Fig. 16e).

REMARKS: This species is anatomically similar to *Udotea looensis*, the major differences being the multistratose outer margin and the shallower habitats of *U. luna*. The two species also differ in habit: *U. looensis* is larger, thin and delicate, whereas *U. luna* is smaller and thicker. *Udotea luna* resembles the basal multistratose portion of *U. looensis* and does not develop the upper unistratose section.

Occasionally, specimens or populations may be found where the outer margins are highly divided and the keel-like narrow segments turn 90° from the original plane of the blade, giving the

distal portion of the plants a fluted appearance. A common species found in shallow waters around mangrove islands but also present in many habitats to depths of 23 m.

*Udotea norrisii* sp. nov.

Fig. 17

DESCRIPTION: Thallus ad 11 cm altus cinereo-viridis ex ramis numerosis complanatis constans, siphonis laminae diametro 40–80  $\mu\text{m}$  in dichotomis inaequaliter constrictis, appendicibus lateralibus ramulis dichotomis apice obtusis tumidis terminatis; stipes 1–2 cm longus saepe ramosis diametro 2–3 mm, siphonis primariis diametro 80–120  $\mu\text{m}$  supra dichotomis non constrictis, siphonis secundariis diametro 40–50  $\mu\text{m}$ , appendicibus lateralibus in apicibus bulbosis vel truncatis terminatis.

HOLOTYPE: US-30609, Chub Cay, Andros Reef, Bahamas, exceptionally abundant on carbonate sand among tall pinnacle formations that arise in great numbers from the sandy bottom, 10 m deep, 21 August 1986, leg. *D.S. Littler, M.M. Littler, B.L. Brooks*.

ETYMOLOGY: This species is named after our colleague and frequent collaborator James N. Norris.

DISTRIBUTION: Bahamas.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Chub Cay, Andros Reef (HOLOTYPE); Freeport, Grand Bahama Island, 3 m deep on sand, 1 September 1981, US-82871; Cross Harbor, Great Abaco Island, Little Bahamas Bank, 30 m deep on sand, 17 June 1989, US-156538.

HABIT: Plants to 11 cm tall, heavily calcified, grey-green. Blades corticate, highly and irregularly dissected into long linear segments, 1–3 mm wide (Fig. 17a), coarse but bushy in appearance; when examined closely, deeply zoned, almost cross-segmented (although sectioning shows no non-calcified genicula). Stipe cylindrical, simple or branched, 1–2 cm long, 2–3 mm in diameter, cortex continuous and unmodified between the stipe and frond. Anchored in sand by a bulbous mass of rhizoids.

ANATOMY: Blade siphons 40–80  $\mu\text{m}$  in diameter, unequal or offset constrictions above the dichotomies (Fig. 17b), siphons possess wide and irregularly spaced long-stemmed lateral appendages, tightly adherent at the tips (Fig. 17d). Outer siphons of stipe 40–50  $\mu\text{m}$  in diameter, main siphons 80–120  $\mu\text{m}$ , no constrictions or slightly unequal constrictions above the dichotomies (Fig. 17c); stipe appendages densely compacted forming a thick cortex, appendages terminate in

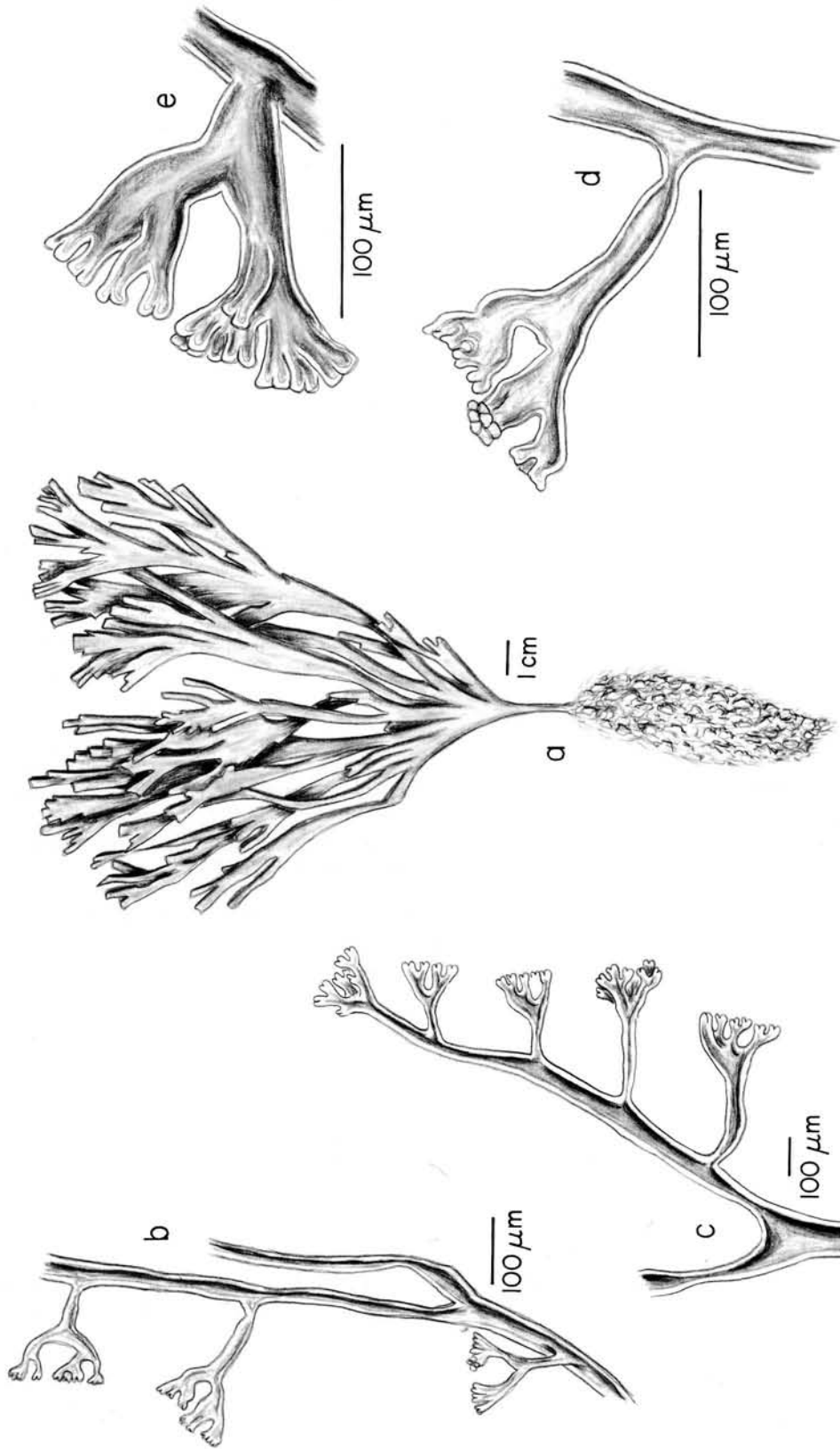


Fig. 17. *Udotea norrisii* sp. nov. a, habit, capitulum often fuller than represented here and, most frequently, a branched stipe; b, blade siphon (note characteristic offset constrictions); c, stipe siphon; d, lateral appendage of blade; e, lateral appendage of stipe.

various shapes—bulbous to flattened to dichotomously branched with blunt ends (Fig. 17e).

REMARKS: The internal anatomy of *Udotea norrisii* is similar to that of *U. flabellum* (Fig. 12), with the exception of more frequent unequal (offset) constrictions above the dichotomies of the blade siphons. The external features readily distinguish the two species (cf. Figs 12a and 17a). *Udotea flabellum* is a morphologically variable species, and some dissected forms may superficially resemble *U. norrisii*; however, these consistently lack the characteristically branched stipe and concomitant three-dimensional bushiness. Generally found at depths of 3–30 m on sand plains or in sandy patches around coral pinnacles.

***Udotea occidentalis* A. Gepp et E.S. Gepp 1911: 127, pl. II: figs 18, 22a, 22b, pl. VII: 63–65.**

Fig. 18

HOLOTYPE: BM, XIII-12, St. Thomas, U.S. Virgin Islands, 2–5 m deep, collected on the 'Challenger' Expedition, 1884, leg. *H. Moseley*.

DISTRIBUTION: Bahamas, Florida, Puerto Rico, Virgin Islands, Belize, Brazil.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Chub Cay, Andros Reef, 10 m deep on sand, 16 August 1986, US-30628. Belize: Long Cay, Glover's Reef, 500 m west of Long Cay, 1–2 m deep on sand, 2 November 1971, US-48063. Puerto Rico: Isla Caja de Muertos, 2 m deep, 16 October 1979, US-091657. U.S. Virgin Islands: St. Thomas (HOLOTYPE); St. Thomas, 36 m deep, dredged, 11 August 1986, US, *Ballantine-2987*.

HABIT: Plants to 10 cm high, light grey-green below and greener toward the margins, heavily calcified. Blade corticate, obovate, fan-shaped, about as wide as it is long (8 cm), thin (less than 1 mm), papery, concentrically zoned, lower margin cuneate to deeply cordate, blades tending to proliferate from their distal margins and basal surfaces (Fig. 18a). Stipe simple, cylindrical, 2 mm in diameter, 1 cm long, surface texture unmodified in transition to the blade. Anchored in soft substrata by a small mass of fibrous rhizoids (Fig. 18a).

ANATOMY: Blade siphons 20–50  $\mu\text{m}$  in diameter, sparingly dichotomous, unequal constrictions above the dichotomies (Fig. 18b); numerous lateral branchlets terminate in lobes (Fig. 18c), the latter possessing 6–20 low rounded knobs that form windows in the surface encrustation, lobed blade appendages fit together

intricately to give a unique 'jigsaw puzzle' appearance (Fig. 12d, 12e), all surfaces covered by minute spines (visible under SEM). Stipe siphons 40–70  $\mu\text{m}$  in diameter, unequal constrictions above the dichotomies (Fig. 18e); long-stalked stipe appendages appear at irregular intervals, appendages are dichotomously branched above and terminate in numerous stubby, rounded (Fig. 18d) projections.

REMARKS: *Udotea flabellum* is often confused with this species because both possess a corticated blade, but upon close inspection *U. occidentalis* is easily distinguishable. The latter tends to be much smaller and has thinner blades with a cuneate lower margin. *Udotea occidentalis* has uniquely lobed blade appendages, and is the only Caribbean species of *Udotea* in which both the blade and the stipe are covered by minute spines, larger on the surface of the stipe (Fig. 13f) than on the blade (Fig. 13d, 13e). *Udotea occidentalis* closely resembles *U. argentea* of the Pacific and Indian Oceans, but the blade siphons of the former are generally smaller (20–50  $\mu\text{m}$ ), while the blade appendages are shorter, more lobed and consistently contain knobs. *Udotea occidentalis* is rarely encountered, but is often mistaken for its common relative *U. flabellum*.

***Udotea spinulosa* Howe 1909: 97, pl. 4, fig. 2; pl. 8, figs 1–7.**

f. *spinulosa*

Fig. 19

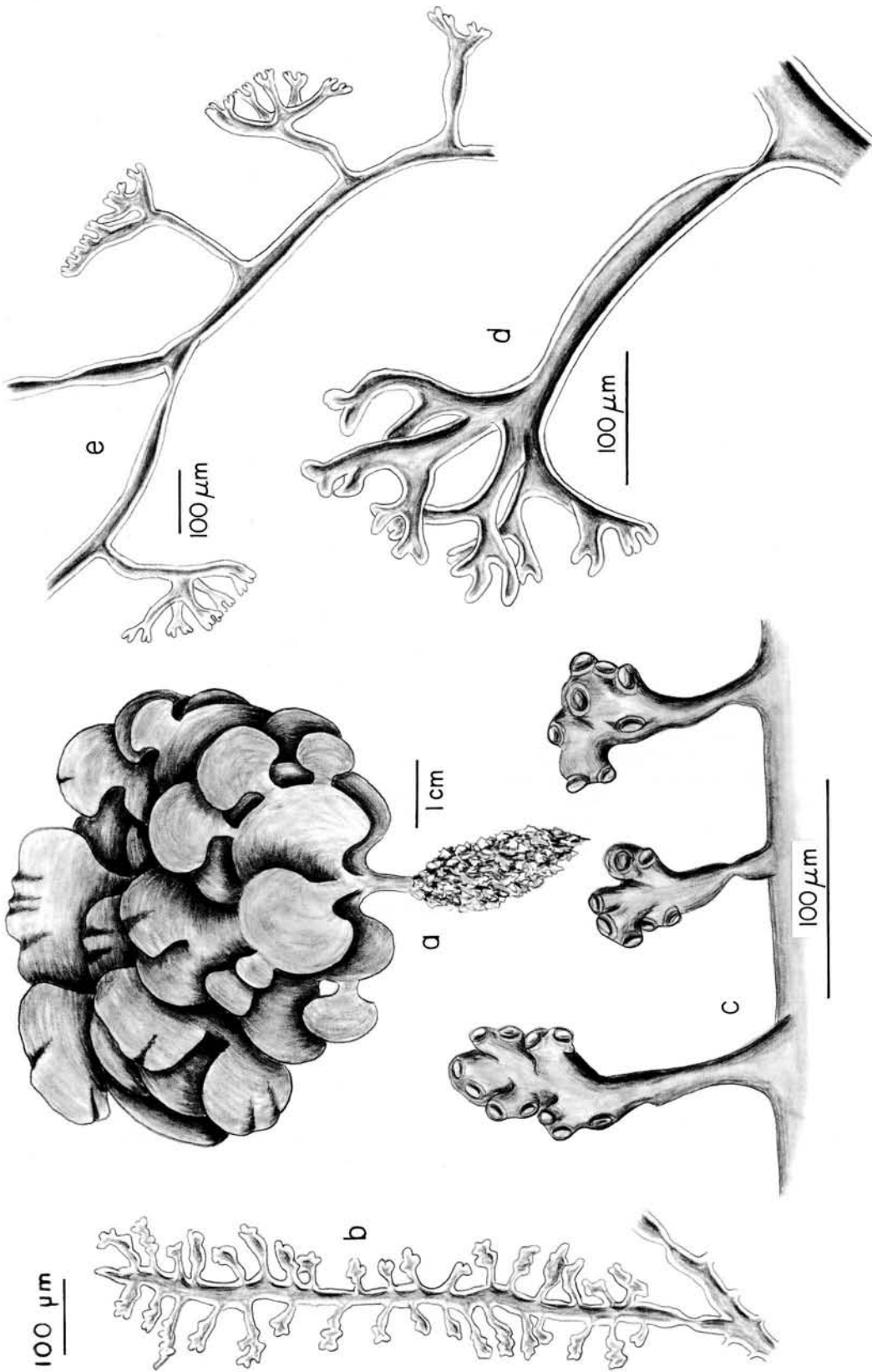
HOLOTYPE: NY, Howe-3272, Bimini Harbor, Bahamas, on a sandy bottom near the low-water mark, 17 April 1904, leg. *M.A. Howe*.

DISTRIBUTION: Bahamas, Florida, Cuba, Puerto Rico, U.S. Virgin Islands, eastern Mexico.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Bimini Harbor (HOLOTYPE); Eleuthera, 2–6 m deep on patch reef, 6 May 1981, US-4071. Jamaica: Cow Bay, St Thomas Parish, 10–13 m deep on muddy sand, June 1967, BM, SP-19. Mexico: Puerto Moretos, Quintana Roo, in front of the Pesca Laboratory, 27 m deep on sand, 11 April 1983, US-14389. Puerto Rico: La Parguera, off Margarita Reef, 20–33 m deep, dredged from a sandy-rock bottom, 10 April 1967, US-45056.

HABIT: Plants to 8 cm tall, heavily calcified, white, brittle and thin when dried. Blades variable in shape, 5–6 cm long, 4–6 cm broad, less than 0.8 mm thick, incomplete or partial cortex, faint concentric zonation, mature plants striate (narrow dark and light markings radiating from





**Fig. 18.** *Udotea occidentalis* A. Gepp et E.S. Gepp. a, habit; b, blade siphon; c, lateral appendages of blade showing unique knobs; d, lateral appendage of stipe; e, stipe siphon.

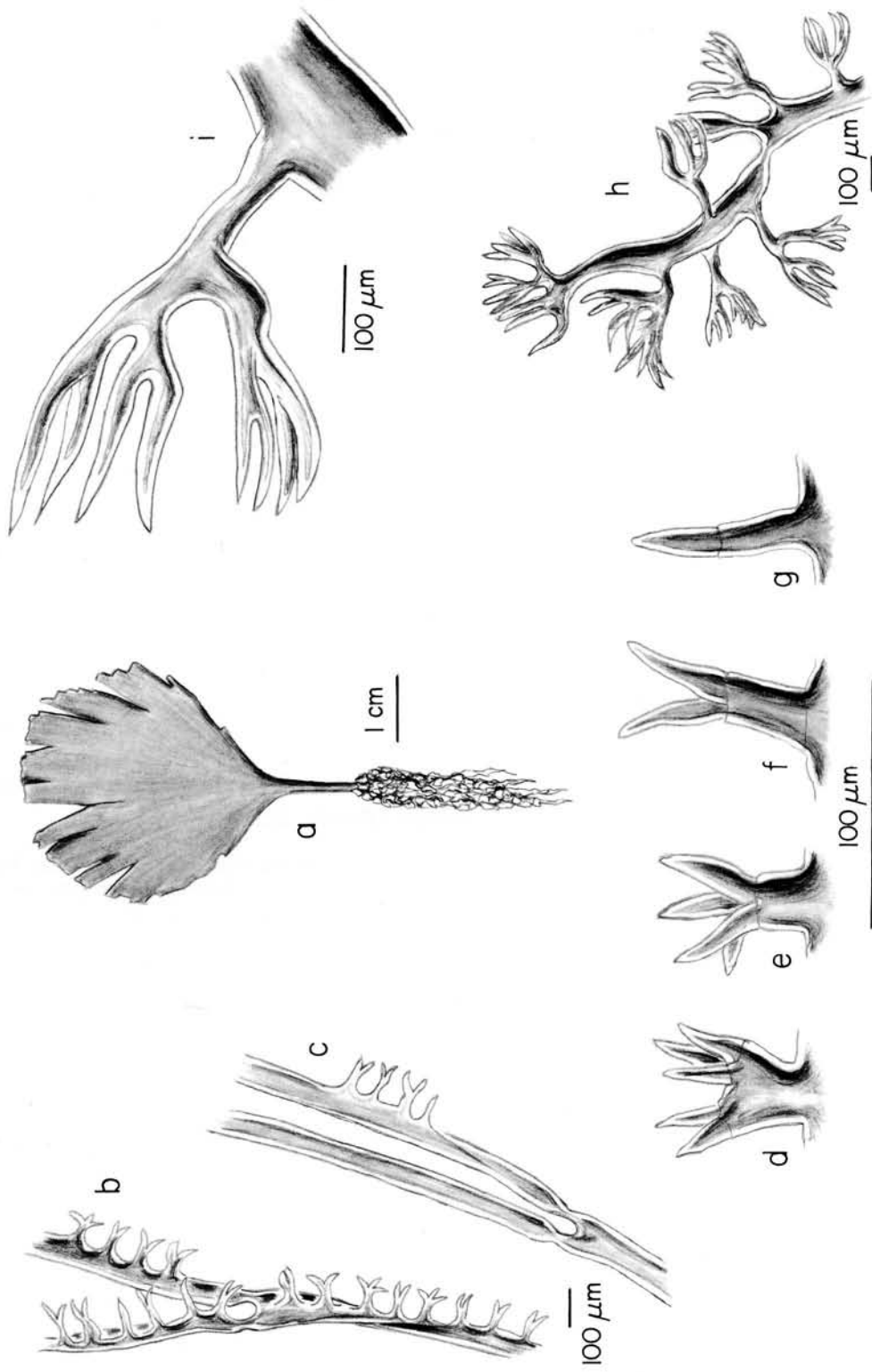


Fig. 19. *Udotea spinulosa* Howe f. *spinulosa*. a, habit; b, blade siphon; c, interior blade siphon showing spiked lateral appendages where a section has become exposed to the surface; d, e, f and g, unique pedicellate lateral appendages of blade; h, stipe siphon; i, lateral appendage of stipe.

the stipe toward the margins) on drying. Stipe 1–2 cm long, 1–2 mm in diameter, cylindrical below and flattened above, gradually tapering into the blade. Anchored in soft substrata by a siphonous, rhizoidal system (Fig. 19a).

**ANATOMY:** Blade unistratose at the growing margin, multistratose below, siphons somewhat flattened, 60–90  $\mu\text{m}$  in diameter, equally constricted above at the dichotomies; blade appendages present only on the exposed surface (Fig. 19b), absent on internal siphons and where one siphon crosses over another (Fig. 19c), blade appendages have a unique small (50–150  $\mu\text{m}$  long), cylindrical ‘trunk’ (pedicel) crowned with one to eight prongs or spines (Fig. 19d, 19e, 19f, 19g). Stipe siphons 80–120  $\mu\text{m}$  in diameter, equal constrictions above the numerous dichotomies (Fig. 19h); stipe appendages terminating in long, pointed, digitate projections (Fig. 19i).

**REMARKS:** *Udotea spinulosa* is distinctive because of the unilateral appendages on the blade siphons, and it cannot be confused with any other Atlantic species. *Udotea palmetta* Decaisne, from the Indian Ocean, is similar in shape and morphology, but its blade siphons are smaller (approximately 30  $\mu\text{m}$  in diameter) and the constrictions above the dichotomies are unequal. *Udotea spinulosa* is most often encountered on moderately deep (10–20 m) sand plains.

### *Udotea spinulosa* Howe

f. *palmettoidea* A. Gepp et E.S. Gepp 1911: 125, 143, pl. VI, fig. 56.

Fig. 20

**HOLOTYPE:** BM, St. Thomas, U.S. Virgin Islands, 5–15 fathoms, ‘Challenger’ Expedition.

**DISTRIBUTION:** Bahamas, U.S. Virgin Islands.

**REPRESENTATIVE SPECIMENS EXAMINED:** Bahamas: Stanyard Key, Andros Island, 3 m deep on calcium carbonate rock, 14 August 1986, US-30645. U.S. Virgin Islands: St. Thomas (HOLOTYPE).

**REMARKS:** This form differs from *Udotea spinulosa* f. *spinulosa* in the weakly developed lateral appendages of the blade siphons. The surface siphons have scattered, characteristically pedicellate, acute, poorly developed lateral appendages (Fig. 20b) to within 2–3 mm of the blade margin, thus forming a sparse incomplete cortex proximally, while completely lacking a cortex at the distal margin. Conversely, *U. spinulosa* f. *spinulosa* has highly developed, pedicellate, acute, lateral appendages on all blade surface siphons

as well as on those immediately below the surface, thus giving a dense, although incomplete, cortex. In other respects the two forms are very similar—in blade shape (Figs 20a, 19a), stipe siphons (Figs 20f, 19h) and siphon appendages (Figs 20c, 20d, 20e, 19i).

### *Udotea unistratea* sp. nov.

Fig. 21

**DESCRIPTION:** Lamina parva 6 cm alta olivaceo-viridis non corticata leniter unistratosa plana vel leniter (conica), siphonis laevibus magnis inferne diametro ultra 200  $\mu\text{m}$  lateraliter adhaerentibus supra dichotomas aequaliter constrictis, dichotomis in parte inferiore laminarum in seriebus e basis aequidistantibus dispositis; stipes parvus 1.5 cm longus diametro 1 mm, siphonis centralibus supra dichotomas inaequaliter constrictis, appendicibus lateralibus corticem tenuem formantibus in ramulis brevibus simplicibus vel dichotome lobatis apice obtusis terminatis.

**HOLOTYPE:** US-30610, Belize, Central America on the east side of Carrie Bow Cay, seaward of the outer ridge in deep water, attached to hard substrata by small fibrous rhizoids, 46 m deep, 15 February 1988, leg. D.S. Littler, M.M. Littler, B.L. Brooks, P.R. Taylor.

**ETYMOLOGY:** This species is named after the unistratose nature of the blade.

**DISTRIBUTION:** Florida, Bahamas, Jamaica, U.S. Virgin Islands, Belize.

**REPRESENTATIVE SPECIMENS EXAMINED:** Bahamas: Hogsty Reef, Royal Island, Eleuthera, 46 m deep under a dark ledge, 10 May 1981, US, Hay-1467; Cay Sal Banks (north bank), 24 m deep on sand, May 1967, US-30118. Belize: Carrie Bow Cay (HOLOTYPE). Jamaica: US-70133; South Cay, Port Royal Cay, 22 August 1962, NY, *Goreau-269*.

**HABIT:** Plants to 7 cm tall, olive green. Blade unistratose, ecorticate, 0.1–0.4 mm thick, scoop-shaped or flat (Fig. 21a), faint concentric lines present. Stipe 1 mm in diameter, 1.5 cm long. Anchored in the sand by fine fibrous rhizoids.

**ANATOMY:** Blade siphons large (100–240  $\mu\text{m}$  in diameter), lacking appendages, strictly aligned or parallel to one another (Fig. 21b), adhering laterally by heavy deposits of calcium carbonate, dichotomies generally occur equidistant from the stipe, forming distinct rows or ranks (Fig. 21b) that result in faint concentric lines, calcareous sheath with pores; base of blade fibrous (340  $\mu\text{m}$  in diameter) and not conglutinate, parallel arrangement becoming lost. Stipe siphons 80–130  $\mu\text{m}$  in diameter, unequally constricted above the

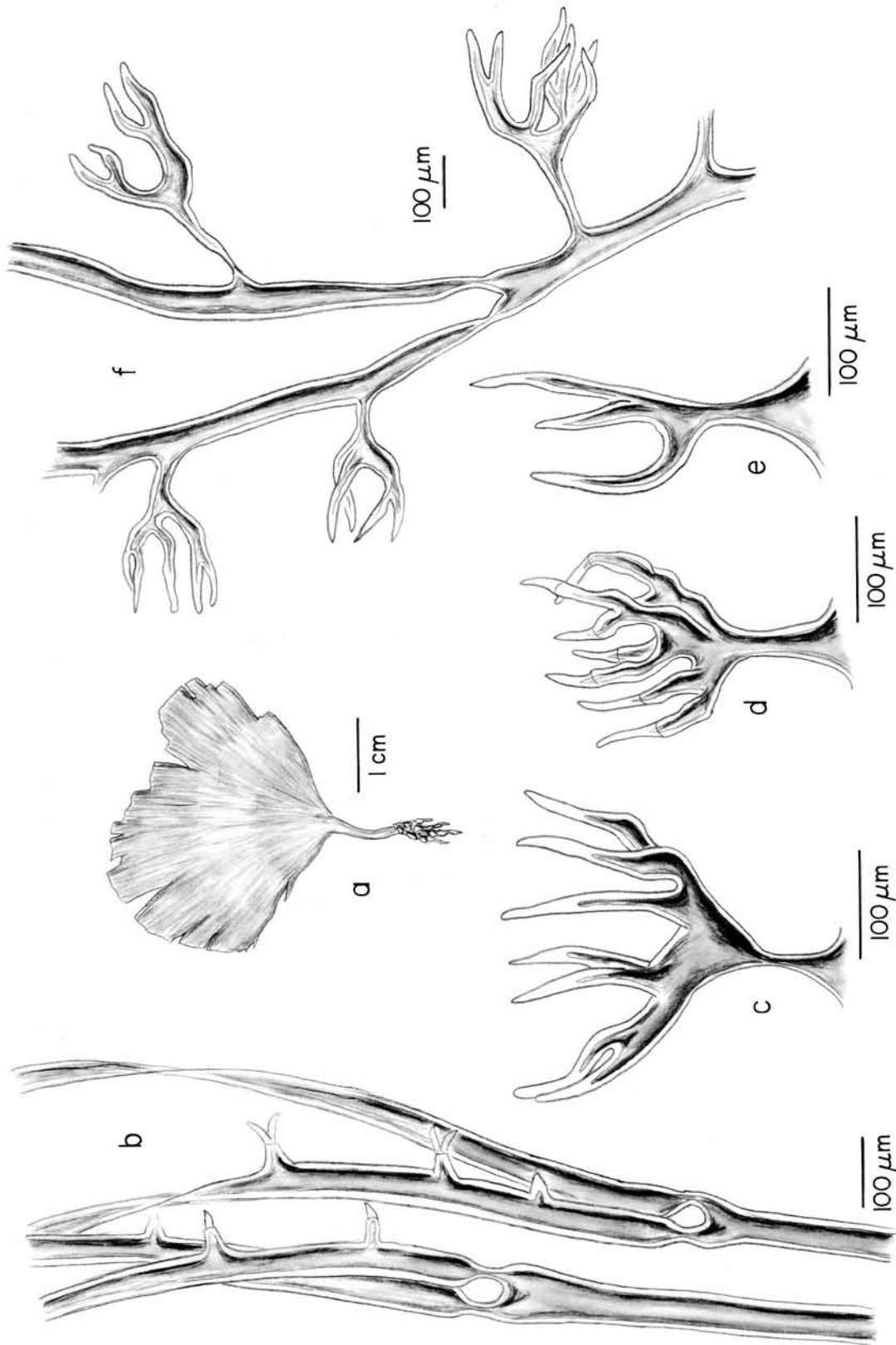


Fig. 20. *Udotea spinulosa* f. *palmettoidea* A. Gepp et E.S. Gepp. a, habit; b, stipe siphon; c, d and e, lateral appendages of stipe showing acute apices; f, blade siphons with sparse, simple or spiked, uniquely pedicellate, lateral appendages.

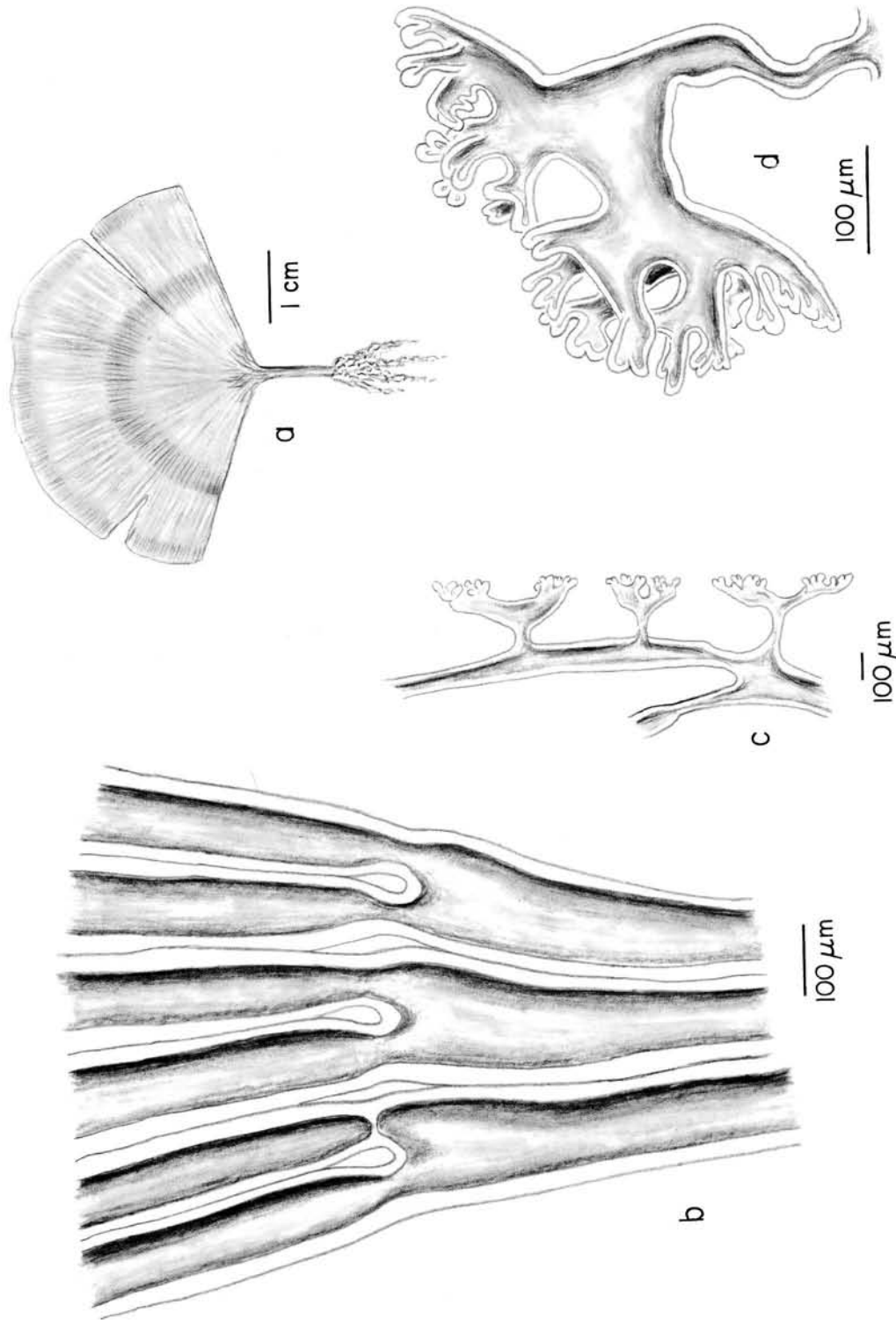


Fig. 21. *Udotea unistrirata* sp. nov. a, habit; b, unistratose siphons of blade with dichotomies generally occurring at equal distances from point of stipe attachment in lower part of blade; c, stipe siphon; d, lateral appendage of stipe.

dichotomies, stipe appendages dichotomously branched (Fig. 21c), terminating in short, simple or dichotomously lobed, blunt tips (Fig. 21d), stipe occasionally absent.

**REMARKS:** *Udotea unistratea* closely resembles *U. glaucescens* Harvey ex J. Agardh found in the Indian Ocean and the tropical Pacific. However, in *U. glaucescens*, the blade constrictions above the dichotomies are unequal (typical of most Pacific and Indian Ocean *Udotea* species), the blade siphons are smaller in diameter (65–105  $\mu\text{m}$ ) and the stipe has an irregular cortex with no conspicuous demarcation where it joins the blade. The blade of *U. unistratea* is superficially similar in structure to the individual bladelets of *Rhipocephalus phoenix*; but differs in the non-parallel lower siphons of the blade and the presence of a single blade produced apically, whereas in *R. phoenix* all siphons of each bladelet are parallel, and new bladelets form continuously along the growing rachis. *Udotea unistratea* can closely resemble the habit of *U. cyathiformis* f. *infundibulum* growing in deep water, but is clearly distinguished by the larger siphon size (to 340  $\mu\text{m}$ ) at the base of the blades, and by the dichotomies being equidistant from the stipe (particularly pronounced in the lower portion of the blade). We predict that this species is widely distributed, but that it has seldom been collected owing to its deep-water habitats (depths of 24–46 m).

***Udotea verticillosa* A. Gepp et E.S. Gepp 1909: 269**

Fig. 22

**HOLOTYPE:** BM, XIII-13, St. Thomas, West Indies (U.S. Virgin Islands), leg. *H. Moseley* on the 'Challenger' Expedition, 1884.

**DISTRIBUTION:** Bahamas, U.S. Virgin Islands.

**REPRESENTATIVE SPECIMENS EXAMINED:** Bahamas: Great Bahama Bank, 20 m deep on sand, 22 June 1967, US-30119. U.S. Virgin Islands: St. Thomas (HOLOTYPE); Cruz Bay, St. Jan (St. John), 3 m deep on sand, 8 March 1906, NY, *Børgesen-1895a*; 9 March 1906, NY, *Børgesen-1915a*; St. Thomas, 36 m deep, dredged, 11 August 1987, US-18357.

**HABIT:** Plants to 10 cm tall, greyish-green when dried. Blades generally broader (6–10 cm) than long (4–7 cm), to 1 mm thick, with a faint concentric zonation. Stipe 0.5–1.5 cm long, 1 mm in diameter, cortex gradually merging with that

of the blade. Anchored in sand by a small, fibrous, rhizoidal system (Fig. 22a).

**ANATOMY:** Blade siphons 60–90  $\mu\text{m}$  in diameter, unistratose and parallel at the outer margins, subparallel and multistratose below, lacking constrictions above the dichotomies (Fig. 22f); lateral appendages 60–90  $\mu\text{m}$  long in the distal portion of the blade, to 180  $\mu\text{m}$  proximally where the blade interfaces with the stipe; blade appendages abundant, variously arranged from distinctly opposite to alternate to haphazard, verticillate at the margins (Fig. 22e), simple or short-stalked appendage projections terminating in two to four short, acute prongs (Fig. 22d). Stipe siphons 80–120  $\mu\text{m}$  in diameter, lacking constrictions above the dichotomies (Fig. 22c); stipe appendages terminate in dichotomously divided, tapered tips (Fig. 22b).

**REMARKS:** *Udotea verticillosa* resembles *U. spinulosa* anatomically with regard to its pointed, tapered, blade appendages. However, *U. spinulosa* has unilateral appendages on each flattened siphon, as well as equal constrictions above the dichotomies, whereas *U. verticillosa* has a verticillate to haphazard arrangement of blade appendages on terete siphons and no visible constrictions. *Udotea wilsonii* may be closely related as there are few anatomical differences apart from its blunt, rather than acutely tapered, blade appendage apices.

*Udotea verticillosa* may be a deep-water species (most specimens are from depths of 20–40 m) and hence would seldom be encountered by collectors.

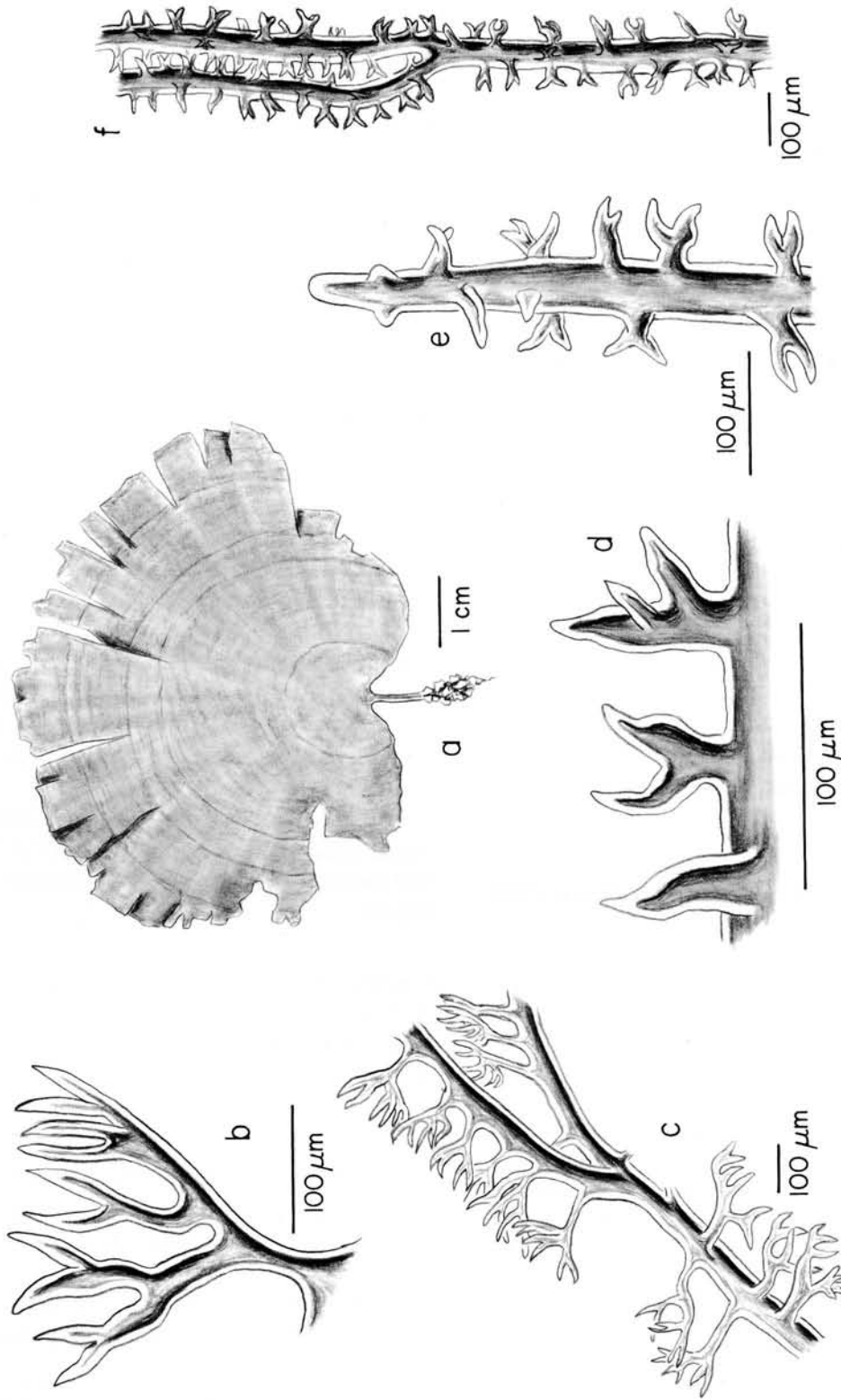
***Udotea wilsonii* A. Gepp, E.S. Gepp et Howe in A. Gepp & E.S. Gepp 1911: 130–131, 144, pl. VII, fig. 66, pl. VIII, figs 67, 67a, 68, 68a. [as '*U. wilsoni*']**

Fig. 23

**HOLOTYPE:** NY, *Howe-7968*, North End, Salt Key Bank, Anguilla Isles, Bahamas, collected at depths of <1 m on sand, 15–18 May 1909, leg. *P. Wilson*.

**DISTRIBUTION:** Bermuda, Florida, Bahamas, Cay Sal Banks, Cuba, Belize, Panama.

**REPRESENTATIVE SPECIMENS EXAMINED:** Bahamas: Salt Key Bank, Anguilla Isles (HOLOTYPE); Jews Bay, Little Sound, West Bermuda, 2 m deep on a sandy bottom, 25 July 1953, US-38252. Belize: Tobacco Range, 7 m deep on muddy mangrove peat, 23 February 1988, US-30629. Cuba: Esperanga, 4 m deep, 2 June 1914, US-54743.



**Fig. 22.** *Udotea verticillosa* A. Gepp et E.S. Gepp. a, habit; b, lateral appendage of stipe; c, stipe siphon; d, lateral appendages of blade; e, tip of blade siphon; f, blade siphon.

**HABIT:** Plants 4–13 cm tall, dark grey-green, lightly calcified. Blades fan-shaped, radiating from the upright central axis (Fig. 23a), to 10 cm diameter, 8 cm tall, occasionally consisting of a single, flat blade; outer edge entire when young, often lobed when old. Stipe 1–2 mm in diameter, 1–4 cm long (typically 1–2 cm), lower portion cylindrical and flaring to 3.5 mm wide above. Anchored by entangled, fine, fibrous rhizoids producing a bulbous mass.

**ANATOMY:** Blade siphons 40–80  $\mu\text{m}$  in diameter, unistratose near the margin, multistratose below, generally lacking constrictions above the dichotomies but unequal constrictions sometimes present (this feature is often masked by the numerous lateral appendages, Fig. 23b); blade appendages short, knobby and blunt (Fig. 23d), simple or forked, 25–90  $\mu\text{m}$  long (occasionally to 120  $\mu\text{m}$ , in two to four somewhat vertical rows (apparent only at the growing tip, soon becoming obscured, Fig. 23c). Stipe siphons 50–100  $\mu\text{m}$  in diameter, equal constrictions above the dichotomies (Fig. 23f); stipe appendages terminate in short dichotomous branchlets, often expanded at the apex (Fig. 23e).

**REMARKS:** *Udotea wilsonii* can usually be distinguished from other members of the genus by its gross morphology because of the many radiating blades extending from a central axis; when viewed from directly above, the upper blade edges resemble the spokes of a wheel (Fig. 23a). Infrequently, individuals may consist of a single blade, but can always be recognized by the numerous blunt blade appendage projections, their length being approximately equal to the width of the bearing siphons. The length of the lateral appendages increases with increased depth.

Other *Udotea* species sometimes have blade proliferations forming at the stipe or on the lower portion of the central axis (Fig. 2a), although these proliferations are few in number compared to typical *U. wilsonii*. Anatomically, *U. wilsonii* could be confused with the deep-water species *U. goreau*, where the blade siphons also have short knobby appendages arranged in double vertical rows on the exposed surface. However, in *U. goreau*, the lateral appendages are proportionately much shorter (<55  $\mu\text{m}$ ) and the siphons are much larger (100–150  $\mu\text{m}$ ), with the siphons being cemented tightly together in a parallel, unistratose fashion and bearing distinct, unequal constrictions above the dichotomies. *Udotea wilsonii* is generally found growing in

organically rich silt or sand plains in moderately shallow waters (2–10 m) and most often with many thalli appearing in the area due to rhizomatous vegetative reproduction.

## PHYLOGENETIC ANALYSIS

Several works, including the present treatment, have divided the genus *Udotea* into groups. J.G. Agardh (1887) divided the genus into four sections: Fibuliferae, which has now been segregated to include the genera *Flabellia* and *Rhipiliopsis*; Palmettae, containing the simpler forms with uncorticated or partially corticated stipes (e.g. the Pacific species *U. glaucescens*); Incrustatae, with smooth siphons and corticated stipes (includes *U. conglutinata*) and Corticatae, comprising the completely corticated species. Gepp & Gepp (1911) subdivided the genus further, concentrating on the characteristics of the blade siphons, but they did not propose formal names for their groupings. These authors also produced a phenetic tree of affinities, in which they grouped those species with non-unilateral blade appendages (i.e. verticillate, random, and opposite), including *U. argentea*, *U. flabellum*, *U. occidentalis*, *U. verticillosa* and *U. wilsonii*. As might be predicted, this complex group arose from *U. subpapillata* A. Gepp et E.S. Gepp and *U. papillosa* A. Gepp et E.S. Gepp as more primitive forms, with these stemming in turn from a precursor similar to *U. javensis* A. Gepp et E.S. Gepp. Another major branch of their tree suggested a *U. glaucescens*-like ancestor giving rise to *U. orientalis* A. Gepp et E.S. Gepp (smooth blade siphons), *U. palmetta* and *U. indica* A. Gepp et E.S. Gepp (simple or sparingly branched, unilateral appendages only present on the exposed, outer, blade siphons). A side branch of this set contained those species that possess smooth siphons and completely corticated stipes (*U. cyathiformis*, *U. explanata* A. Gepp et E.S. Gepp and *U. conglutinata*), whereas a *U. conglutinata*-like precursor gave rise to *U. spinulosa* with its pedicellate, highly branched, unilateral appendages on the exposed siphons of the blade.

Farghaly (1980) divided the genus *Udotea* into five genera; however, this was reported in an unpublished dissertation that lacked Latin diagnoses, so that the generic names are invalid. Farghaly's generic arrangement appears to be reasonable: (1) species with uncorticated blades;



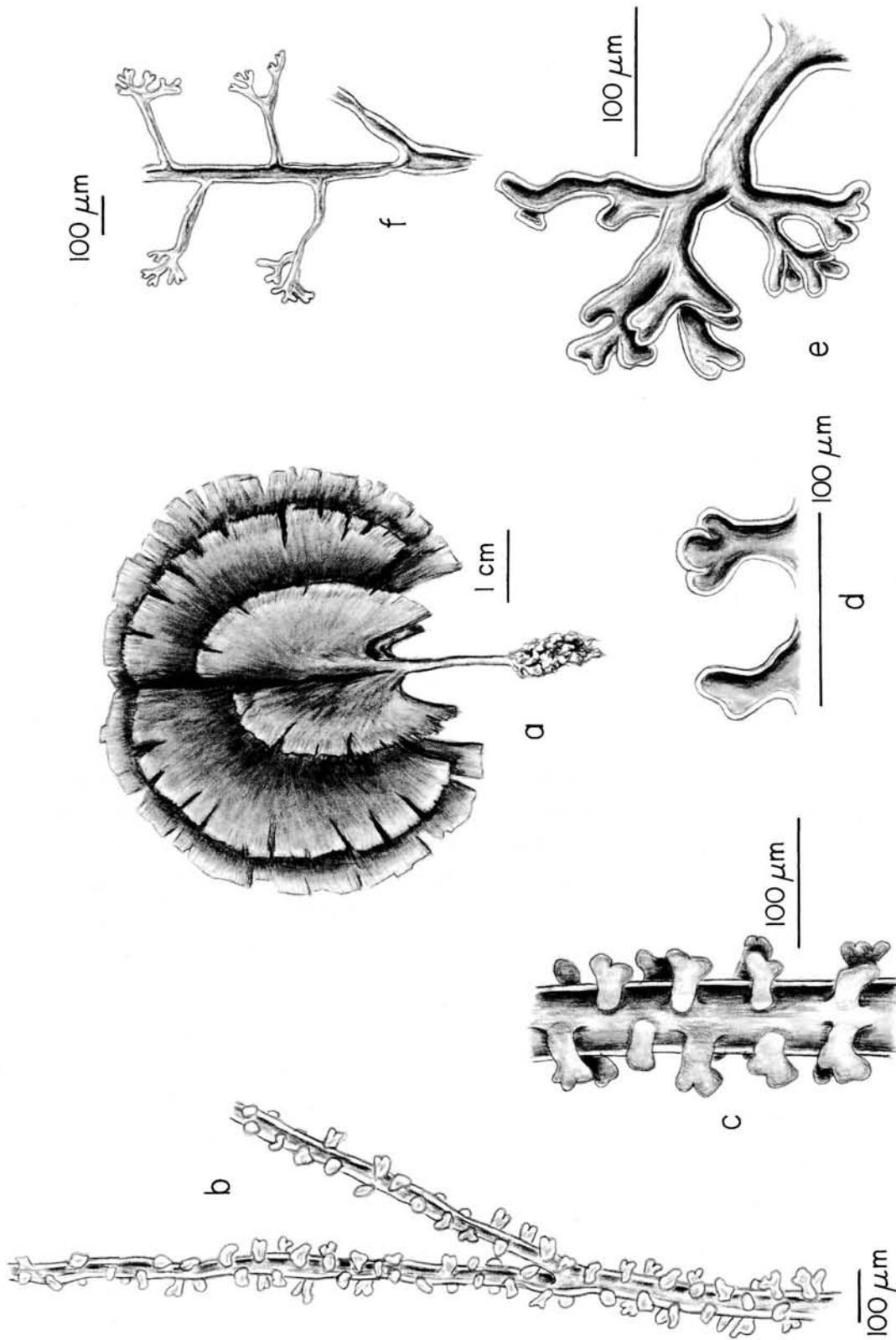


Fig. 23. *Udotea wilsonii* A. Gepp, E.S. Gepp et Howe. a, habit; b, blade siphon; c, blade siphon with lateral appendages; d, lateral appendages of blade; e, lateral appendage of blade; f, stipe siphon with lateral appendages.

(2) species with a partial cortex consisting of simple or sparingly branched papillae; (3) species with blades partially corticated by acute apices of the appendages; (4) species with a complete cortex; (5) species with numerous blades radiating from a central axis.

The a priori evolutionary hypothesis we propose for Caribbean species of *Udotea* is that *U. unistratea*, with its unistratose blades, represents the primitive condition within the assemblage. The blade structure closely resembles that of *U. glaucescens* from the Pacific, which has a partially corticated stipe and unistratose blade, both of which are presumed to be primitive characters. Hypothetically, the species next in line on an evolutionary basis should be those with smooth, ecorticate, blade siphons (*U. abbotiorum*, *U. caribaea*, *U. conglutinata*, *U. cyathiformis*, *U. fibrosa*, *U. looensis* and *U. luna*), followed by those with partially corticated siphons (i.e. *U. goreau*, *U. spinulosa*, *U. verticillata* and *U. wilsonii*) and finally those with a complete cortex (i.e. *U. dixonii*, *U. dotyi*, *U. flabellum*, *U. norrisii* and *U. occidentalis*).

Our cladistic analysis of Caribbean *Udotea* suggests two alternatives. The first (Fig. 24) represents a gradation showing mostly uniform branching off a single main axis with no group dominating and all taxa separate except for four pairs; this series is in agreement with all other trees in placing *U. unistratea* at the base of the genus, while the corticated species have the highest number of derived characters and are near the apex. The second alternative (Fig. 24) postulates four monophyletic assemblages and one paraphyletic assemblage based on the degree of cortication in conjunction with appendage anatomy. Eleven trees were depicted (e.g. Fig. 24), differing only in minor character changes and in the paraphyletic assemblage containing those species with ecorticate blade siphons and blunt apices on lateral appendages of the stipe, which did not group together and were inconsistently placed. This inconsistency could be caused by the plesiomorphic (primitive) character of the group. The lack of resolution in the lower plesiomorphic levels of a cladogram is not uncommon (Cairns 1984—stylasterid corals) in marine systems. The other alternative (Fig. 25) depicts five groups, with the largest monophyletic group (Flabellum group) having the most derived characters and consisting of the five fully corticated species (*U. dixonii*, *U. dotyi*, *U. flabellum*, *U. norrisii* and *U. occidentalis*), all of which have

blunt apices on the lateral appendages of the stipe. The two partially corticated species (*U. goreau* and *U. wilsonii*), with the unifying character of blunt tips on the lateral appendages of both the blade and stipe, comprise the Wilsonii group. The Verticillosa group is composed of species with tapered or pointed apices on the lateral appendages of the stipe (*U. looensis*, *U. luna*, *U. spinulosa* and *U. verticillosa*), whereas the presence or absence of a partial cortex was not a factor in determining this group. The Conglutinata group consists of species that have blunt apices on the lateral appendages of the stipe and lack a cortex or partial cortex (*U. abbotiorum*, *U. caribaea*, *U. conglutinata*, *U. cyathiformis* and *U. fibrosa*); here the apical features of the lateral appendages are also key factors, since *U. looensis* and *U. luna* (with pointed stipe appendages and also with smooth blade siphons) cluster with the Verticillosa group. *Udotea unistratea* stands alone (Unistratea group) with its simple, unistratose blade.

As predicted, *Udotea unistratea* ranks as the species with the most primitive characters, whereas the completely corticated forms displayed the most highly derived characters (Figs 24, 25). The uncorticated and partially corticated species did not group as expected on the basis of the degree of cortical development. Instead, the terminal arrangement of the lateral appendages of the stipes and, when present, the lateral appendages of the blades were more important phylogenetically than the presence or absence of a blade cortex alone.

In retrospect, these findings differ markedly from Gepp & Gepp's (1911) intuitive phenetic tree, but to a limited extent approximate to Farghaly's (1980) divisions. Our Conglutinata group (ecorticate, blunt apices on the lateral appendages of the stipe) is in agreement with Farghaly's (1980) uncorticated group. There are no Caribbean species with simple papillae comparable to his second group; however, *Udotea palmetta*, which he includes in this group, has pointed apices on the lateral appendages of its stipe and therefore would be placed in our Verticillosa group. The cluster with pointed lateral appendages on the blade siphons is similar to those species placed by Farghaly in his third group, which contains *U. verticillosa* and *U. spinulosa*. As previously mentioned, those species with smooth blade siphons in conjunction with acute points on the lateral appendages of the stipe are also included in our Verticillosa group. The

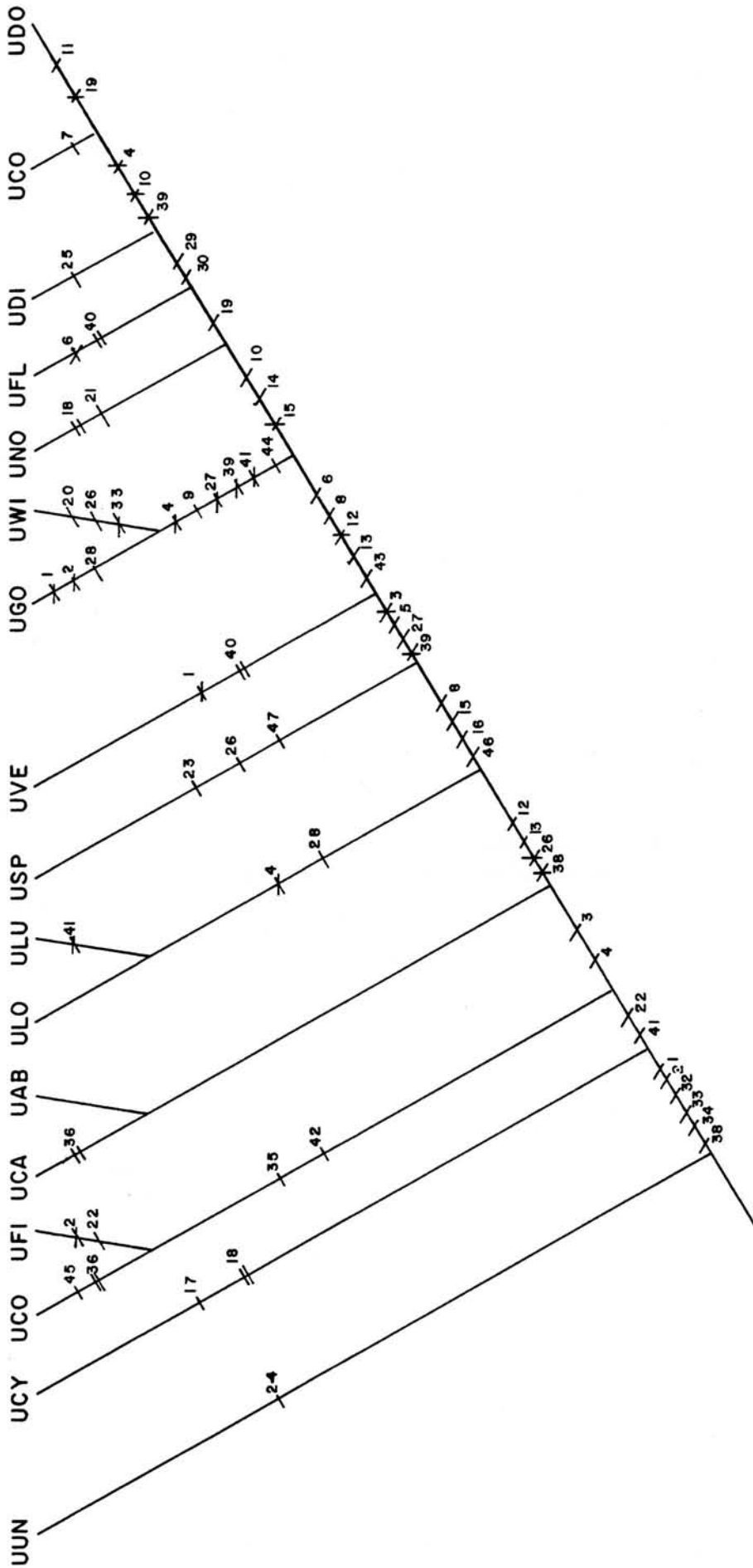


Fig. 24. The first phylogenetic grade produced by the PAUP cladistics program. *Rhipocephalus phoenix* is the designated outgroup. Note that there are no substantial groupings present on the diagram, only a continual gradation from *U. unistratea*, the species with the most primitive characters, to the most complex or corticated species. Numbers on the cladogram correspond to characters in Table 1; taxa abbreviations are shown in Table 2. Slashes represent character advances, crosses indicate character reversals or losses, and double lines depict areas of parallel or convergent evolution.

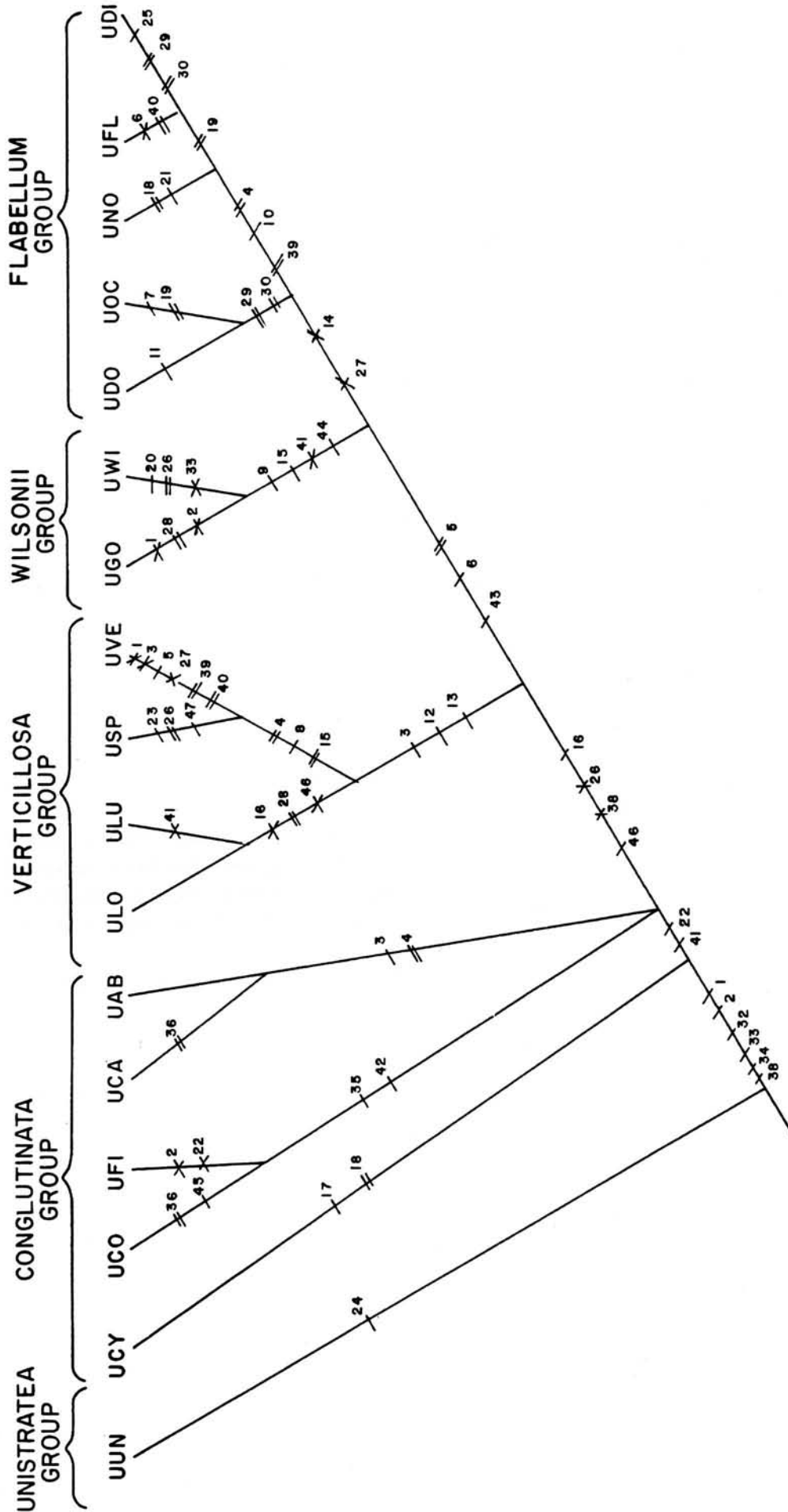


Fig. 25. Cladogram of phylogenetic relationships among Caribbean species of *Udotea*. *Rhipocephalus phoenix* is the designated outgroup. Numbers on the cladogram correspond to characters in Table 1; taxa abbreviations are in Table 2. Symbols as in Fig. 24.

completely corticated group (Flabellum) agrees with that of Farghaly (1980); furthermore, he considers *U. wilsonii* to be a separate group on the basis of the external feature of multiple blades radiating from a central axis. Our phylogenetic analysis (Fig. 25) also separates this species (with *U. goreauii*), but on the basis of the blunt tips of the lateral appendages, and not of gross morphology.

The phylogenetic results of the cladistic analysis (Figs 24, 25), in conjunction with the work of Gepp & Gepp (1911), support the view that the genus is a coherent monophyletic unit as presently defined, and we consider that no information would be gained by its subdivision.

### ECOLOGICAL ADAPTATIONS

We now have sufficient material, representing a broad spectrum of anatomical forms and habitats, to enable limited correlations concerning ecological adaptations. For example, species of *Udotea* appear to be vulnerable to herbivory from large fish, and bite marks are often present on the blade margins. In particular, the deep-water forms (e.g. *U. dixonii*) typically show extensive grazing damage at their shallowest (~30 m) depth ranges. Of the six *Udotea* species examined for secondary chemicals related to herbivore deterrence (Hay & Fenical 1988), only four, including *U. cyathiformis* and *U. flabellum* from the Caribbean, have been found to contain active compounds (see Paul & Fenical 1986). In accordance, the above Caribbean species are the two most frequently found in reef habitats with a relatively high incidence of fish herbivory, and they appear to contain fewer bite marks, on average, than other species of *Udotea*. Hypothetically, the presence of aragonite throughout the genus strengthens the thallus and siphon structure against losses due to physical forces, as well as making the plants less palatable to herbivores, particularly the smaller invertebrate grazers. The species of *Udotea* that lack blade lateral appendages all have pores in their CaCO<sub>3</sub> sheaths (i.e. *U. looensis*, *U. luna*, *U. cyathiformis*, *U. conglutinata*, *U. caribaea*, *U. abbottiorum* and *U. fibrosa*). Pores could represent an adaptation to increase the efficiency of nutrient uptake relative to the remaining species that lack pores; however, this possibility has yet to be examined.

There is a general tendency for thalli to become

longer and thinner with increasing depth, as well as in other habitats where light is reduced. In addition, the lengths of lateral appendages tend to increase with increasing depth within a given species (e.g. *Udotea wilsonii*). These phenomena indicate the operation of processes analogous to etiolation in vascular plants. Raven *et al.* (1979) correlated algal cell size with environmental light intensity, predicting that large cells are adaptive for low-light habitats and indicative of shade plants. Exceptionally large siphons, which in the case of coenocytic plants are equivalent to large cells, would therefore be expected to be adaptive for low-light environments because there is less structural material to shade the light received. In accordance with this view, the two deep-water (below 35 m) uncorticated or partially corticated species (*Udotea unistratea* and *U. goreauii*) have relatively large siphon diameters in both stipe and blade, and blades that are single-layered. *Udotea fibrosa* also has comparatively large siphons, but grows in shallow waters in full sunlight, and therefore represents an exception, although it is thickly multistratose. The fact that *U. unistratea* is moderately calcified appears inconsistent with the light-adaptation hypothesis. However, the deepest growing plants in the ocean (Littler *et al.* 1985, 1986) are extensively calcified red algae.

Horn's (1971) model for the adaptive geometry of forest trees has been applied to marine algae (Hay 1986) in order to interpret the manner in which thallus shape and layering might affect growth in seaweeds as a function of light energy. This model predicts that self-shading should be minimized at low-light levels, yielding a single-layered thallus oriented perpendicular to the incoming light. The unistratose morphology and orientation of some of the deep-water species such as *U. unistratea* is consistent with this prediction and, as mentioned, should be more efficient for the harvesting of energy in low-light environments. However, *U. dixonii* is also a deep-water species growing in the same microhabitat as *U. unistratea* but, conversely, it possesses among the narrowest siphons in the genus, and the siphons are corticated with lateral appendages. Further, the blade apex is distratose for only a few mm, and then becomes multistratose, thus contradicting the above predictions of large cell size and single-layering for deep-water, low-light species. Therefore, at the present time, caution must be exercised when speculating on the adaptive significance of the unistratose, large siphons

found in *U. goreaui*, *U. unistratea* and other deep-water species.

## REPRODUCTION

Because several taxa were observed in the fertile state for the first time, we take this opportunity to review the limited knowledge of reproduction in *Udotea*. Little is known about reproduction in *Udotea* from the western Atlantic, although limited data are available for Pacific and Indian Ocean species (see Hillis-Colinvaux 1984). Interestingly, we have observed living *U. caribaea* in the field to extend its outer margin some 2–3 cm by the development of specialized, elongate, terminal, reproductive siphons (presumably gametangia). These siphons are usually larger than normal (100–200  $\mu\text{m}$  in diameter), and often clump together in small clusters consisting of 3–30 or more siphons that conglutinate just below the tips. The cytoplasmic contents, including chloroplasts, migrate from the thallus to the new extensions of the siphons, leaving the thallus white (= holocarpic reproduction). The high concentration of dense, green material eventually forms round or oblong, non-flagellate spheres (100–200  $\mu\text{m}$  in diameter) that occur in single, linear series down the length of each extended siphon. The release of these non-motile structures occurs when the apex breaks open and the contents slowly flow out within a gelatinous matrix, eventually falling free. We have also observed these extended, terminal, reproductive siphons on herbarium specimens of *U. caribaea* and *U. cyathiformis*. Meinesz (1969, 1972) has made an extensive study of the reproduction and life history of a Mediterranean species, named *Udotea petiolata* (Turra) Børgesen. However, Nizamuddin (1987) correctly transferred this non-calcareous species back to the genus *Flabellia*, and as a result reproductive information about *Udotea* remains scanty (see Hillis-Colinvaux 1984).

Vegetative reproduction is also important but virtually unstudied [see Colinvaux (1968) for a single observation of *Udotea* sp. in culture]. Some species of *Udotea* spread vegetatively from a delicate, translucent, subterranean, rhizoidal or rhizomatous system that extends from the rhizoidal holdfast. If certain *Udotea* populations are carefully separated from the sedimentary substratum, and the rhizomatous system is followed laterally, individual rhizomes (usually larger than holdfast rhizoids) are often found to lead to other

nearby, mature *Udotea* thalli, or multiple juvenile plants may be seen sprouting from such lateral rhizomes a considerable distance from the parent plant. We have observed this clonal system of vegetative propagation for the first time in *U. cyathiformis*, *U. fibrosa*, *U. wilsonii* and *U. unistratea*. *Udotea dixonii* appears to be unique, since new fronds occur in close proximity to the parent thallus, arising from the same rhizoidal holdfast system. Clumps of *U. dixonii* often consist of relatively young plants perennating from a single holdfast that may also contain a series of older stipes which have completely lost their blades. Detailed field observations and controlled culture studies of *Udotea* life histories are needed to determine the significance of reproductive phenomena in relation to the systematics and biology of this diverse and widespread tropical genus.

## ACKNOWLEDGEMENTS

We are grateful to Barrett L. Brooks for valuable field and laboratory assistance throughout this project, and to J.B. Piraino, W.D. Lee and S.A. Reed for field and SEM assistance. We thank V. A. Funk for expert assistance with the cladistic analysis, W.J. Fenical and B.E. Lapointe for inviting us to participate in their 1986, NSF-sponsored cruises to the Lesser Antilles and the Bahamas, respectively, and H.E. Robinson for the Latin translations. Distinguished Visiting Scientist Awards initiated by D. Ballantine allowed us to observe important living Puerto Rican material. Special thanks to P.S. Dixon, G.T. Kraft, J.N. Norris and P.C. Silva, whose thorough and helpful reviews greatly improved this monograph. Field work was supported by grants from the Smithsonian Marine Station at Link Port, Florida (SMS Contribution No. 232), Caribbean Coral Reef Ecosystem Program of the National Museum of Natural History (CCRE Contribution No. 268) and the Research Opportunities Fund of the Smithsonian Institution.

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