Phycologia (2007) Volume 46 (6), 709–725 Published 1 November 2007

Systematics of the green macroalgal genus *Chamaedoris* Montagne (Siphonocladales), with an emended description of the genus *Struvea* Sonder

Frederik Leliaert[1]*, Alan J.K. Millar[2], Caroline Vlaeminck[1] and Eric Coppejans[1]

[1]*Phycology Research Group and Centre for Molecular Phylogenetics and Evolution, Biology Department, Ghent University, Krijgslaan 281 S8, 9000 Ghent, Belgium*
[2]*Royal Botanic Gardens Sydney, Mrs Macquaries Rd, Sydney, NSW 2000 Australia*

F. Leliaert, A.J.K. Millar, C. Vlaeminck and E. Coppejans. 2007. Systematics of the green macroalgal genus *Chamaedoris* Montagne (Siphonocladales), with an emended description of the genus *Struvea* Sonder. *Phycologia* 46: 709–725. DOI: 10.2216/07–51.1

Critical reinvestigation of the four presently recognised species of the green macroalgal genus *Chamaedoris* (*C. auriculata*, *C. delphinii*, *C. peniculum* and *C. orientalis*) based on morphological and molecular data reveals that at least one species, *C. orientalis*, is actually a member of the genus *Struvea* and is herein transferred to that genus as *S. okamurae nom. nov*. This has also necessitated a revised circumscription of the genus *Struvea*. Morphological features traditionally used to delimit the three other species of *Chamaedoris* (shape of capitulum and number of cells split off from the distal pole of the stipe) are not diagnostic, and the traditional species delineations need to be reassessed. Detailed morphological and morphometric analyses reveal that more subtle differences exist among the three species, including cell dimensions and crystalline cell inclusions. Observations and molecular phylogenetic analyses of new collections over the past 27 years allow us to update knowledge of their biogeographic distributions and determine their relationships with species of the closely related genera *Apjohnia*, *Boodlea*, *Cladophoropsis*, *Phyllodictyon* and *Struvea*.

Key Words: *Chamaedoris*, Cladophorales, Cladophorophyceae, Molecular phylogeny, Morphology, *Struvea*, Segregative cell division

INTRODUCTION

The green macroalga *Chamaedoris* is distributed in the tropical to subtropical waters of the Atlantic, Indian and Pacific Oceans, where it is found in intertidal to deep subtidal regions (Okamura 1931; Børgesen 1933; Littler & Littler 2000). The genus was described by Montagne (1842, p. 261) to accommodate the Caribbean species *Penicillus annulatus* Lamarck. The original genus delineation describes plants consisting of clustered, annulated stipes, each producing an apical capitulum that is composed of branched and entangled filaments. Since its discovery, two additional species, *Chamaedoris auriculata* Børgesen and *Chamaedoris orientalis* Okamura & Higashi, have been described, and another, *Chamaedoris delphinii* (Hariot) Feldmann & Børgesen, has been transferred to it from *Siphonocladus*. The type of the genus, *Chamaedoris annulata*, has been the subject of nomenclatural confusion, and its correct name should be *Chamaedoris peniculum* (Index Nominum Algarum). Most of our taxonomic knowledge of this genus has been obtained by Børgesen (1912, 1913, 1933, 1940) and Okamura (1931).

The systematic position of *Chamaedoris*, based on morphological data, is not entirely clear. While the annulated stipe cells resemble those found in the genus *Struvea*, the branching pattern of the capitulum filaments is very similar to *Cladophoropsis* species. Børgesen (1912) observed that cell division in the distal pole of the stipe cell takes place by segregative cell division, a process in which multinucleate aggregates of cytoplasm spontaneously form walled spheres that remain in the parent cell, expand and form new cells. In the capitulum filaments, the main mode of cell division is by centripetal invagination of the cell walls, although segregative cell division might occur occasionally (Børgesen 1912). Recently, two types of crystalline cell inclusions have been observed in *Chamaedoris*: prismatic calcium oxalate crystals, also found in some *Cladophoropsis*, *Phyllodictyon* and *Struvea* species, and protein crystalloids, similar to the ones present in *Valonia* (Leliaert & Coppejans 2004). Immunological studies (Olsen-Stojkovich *et al*. 1986) and molecular phylogenetic analyses based on sequences of the nuclear ribosomal internal transcribed spacers (ITS1 and ITS2) (Kooistra *et al*. 1993), nuclear small subunit ribosomal DNA (Bakker *et al*. 1994) and nuclear large subunit ribosomal DNA (Leliaert *et al*. 2003) have demonstrated a close relationship of *Chamaedoris* with the genera *Boodlea*, *Cladophoropsis*, *Phyllodictyon*, *Struvea* and *Struveopsis*.

The four *Chamaedoris* species are clearly delineated, based on differences in the shape of the capitulum (flat in *C. auriculata* and *C. peniculum*, globose in *C. delphinii* or elongate in *C. orientalis*) and by the number of cells that are formed on the distal pole of the stipe cell from which the capitulum cells develop (none in *C. delphinii*, one to three in *C. auriculata* and *C. peniculum*, and up to 28 in *C. orientalis*) (Okamura 1931; Børgesen 1933, 1940; Littler & Littler 2000; Coppejans *et al*. 2005). A clear picture of the phylogenetic affinities of these species based on molecular evidence has been lacking and is part of the research presented here. In addition, the individual species are

* Corresponding author (frederik.leliaert@ugent.be).

assessed as to their generic placement, and it is clear that *C. orientalis* does not belong in the genus *Chamaedoris* on both morphological and molecular grounds.

Therefore, this study aims to evaluate the validity of the four recognized morphospecies, update knowledge of their biogeographic distributions and determine their interrelationships and relationships with species of the closely related genera *Boodlea*, *Cladophoropsis*, *Phyllodictyon* and *Struvea* based on molecular phylogenetic evidence.

MATERIAL AND METHODS

Sample collection

This study is based on type material, historical collections and more recently collected specimens. In total, 102 specimens of *Chamaedoris* were examined morphologically (Appendix 1). Collections were made in various regions of the (sub)tropical Indo-Pacific and Atlantic Oceans, with an additional collection by the second author from the Coral Sea in the Pacific Ocean. These are deposited in GENT and NSW. Other specimens were studied from BR, C, L, NY, PC and S (herbarium abbreviations follow Holmgren *et al.* 1990). Liquid-preserved material and rehydrated herbarium specimens were examined with a light microscope, after portions were prepared on glass microscopic slides and stained with 1% methylene blue. Drawings were made with a camera lucida on a Leitz-Diaplan (Leitz, Wetzlar, Germany) bright-field light microscope. Photographs were taken with an Olympus-DP50 digital camera (Olympus, Tokyo, Japan) mounted on the microscope. Calcium oxalate crystals were examined using differential interference (Nomarski) contrast. Initial species identifications (i.e. prior to the molecular phylogenetic and morphometric analyses) were based primarily on the shape of the capitulum and the number of cells that are formed in the distal pole of the stipe cell.

DNA sequence analyses

We analyzed partial large-subunit (LSU) rDNA sequences and/or rDNA internal transcribed spacer (ITS) sequences from 15 specimens belonging to the four *Chamaedoris* species and several other species from related genera (Table 1).

The DNA was extracted from silica gel-dried specimens or from herbarium material. Total genomic DNA was extracted and the partial LSU rDNA gene (first *c.* 570 nucleotides) was amplified as described in Leliaert *et al.* (2007). The rDNA ITS1-5.8S-ITS2 region was amplified using forward primer ITS1FL (5′-CCTGCGGAGG-GATCCATAGC-3′) and reverse primer Pana5FL (5′-GGGTGTCCCTGCCTGAAC-3′). In a number of samples, only the ITS1 could be successfully amplified, using the same forward primer and reverse primer ITS2FL (5′-GCTGCGTTCTTCATCGATGTGG-3′). PCR conditions of the LSU and ITS primer combinations consisted of an initial denaturation step of 94°C for 3 min, followed by 35 cycles of 94°C for 1 min, 55°C for 1 min, 72°C for 1 min 30 s, followed by a final extension of 3 min at 72°C. Sequencing was performed as described in Leliaert *et al.* (2007).

Two data sets were considered for phylogenetic analysis. The first one was assembled to assess the phylogenetic relationship of *Chamaedoris* with closely related genera of Siphonocladales. This data set consisted of a concatenated alignment of partial LSU rDNA and rDNA ITS1-5.8S-ITS2 sequences of the four *Chamaedoris* species, along with 13 closely related species and *Dictyosphaeria cavernosa* (Forssk.) Børgesen and *Valoniopsis pachynema* (G. Martens) Børgesen as outgroup taxa based on Leliaert *et al.* (2007). This data set will further be referred to as the LSU-ITS alignment. An incongruence length difference test (Farris *et al.* 1995), implemented in PAUP* 4.0b10 (Swofford 2002), indicated that the LSU and ITS data were not significantly heterogeneous ($P = 0.41$), justifying a combined data approach. The alignment of the LSU sequences (all 566 bases in length) was unambiguous. On the other hand, the alignment of the ITS1-5.8S-ITS2 sequences, which ranged between 832 and 998 bases in length, was notoriously difficult. This alignment was checked for unstable hence unreliable alignment blocks with SOAP v1.2a4 (Löytynoja & Milinkovitch 2001) with opening/extension penalty parameters from 14/6 to 16/8. Regions of instability were deleted by computing the 50% consensus among the nine different alignments, leaving an ITS1-5.8S-ITS2 alignment of 588 positions. The second data set consisted of rDNA ITS1 sequences of 12 specimens of *C. auriculata*, *C. delphinii* and *C. peniculum*. The alignment of these sequences, with length ranging between 309 and 339 bases, was straightforward and included a limited number of gaps. This data set will further be referred to as the ITS1 alignment.

Bayesian inference (BI) was performed with MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003). For the analyses of the LSU-ITS alignment, the data set was partitioned into LSU+5.8S and ITS1+ITS2 regions because of marked differences in substitution rates between these two regions. Different substitution models were estimated for the two partitions using the Akaike Information Criterion (AIC) with PAUP/MrModeltest 1.0b (Nylander 2004): for the LSU+5.8S region a HKY+I model was selected, and for the ITS1+ITS2 region a GTR+I+Γ model was selected. For the analyses of the ITS1 alignment, a HKY+I model was estimated and selected. For all analyses, two independent, simultaneous analyses were run for 3 million generations. Summary statistics and trees were generated using the last 2 million generations, well beyond the point of convergence between the two runs.

Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed using PAUP. ML analyses consisted of heuristic searches with 1000 random sequence addition replicates and Tree Bisection Reconnection with the option Multrees. The optimal models of nucleotide substitution for ML were determined with PAUP/Modeltest 3.6 according to the AIC (Posada & Crandall 1998): a GTR+I+Γ model for the LSU-ITS alignment and a K80 model for the ITS1 alignment. The likelihood of alternative topologies was tested against the optimal ML topology using Shimodaira–Hasegawa (SH) tests as implemented in PAUP using RELL optimization and 1000 bootstrap

Table 1. Specimens used in the phylogenetic analyses with collecting data (location, collector, date of collection and voucher information) and EMBL accession numbers. Newly generated sequences are in bold.

Species	Collecting data	Partial LSU	ITS
Apjohnia laetevirens Harvey	Australia: Melbourne, Baron Heads (van Oppen, 1991, ApLB/Apj1/F273)[1]	AM503416[6]	**AM779624**
Boodlea composita (Harvey) F. Brand	Tanzania: Zanzibar, Matemwe (Leliaert, 16.vii.2001, FL950/F016)[2]	AJ544731[7]	**AM779625**
Boodlea siamensis Reinbold	Philippines: Mactan Island (Verbruggen, 16.ii.2004, HV870/F349)[2]	AM503422[6]	**AM779626**
Chamaedoris auriculata Børgesen	Socotra: Nogid (Leliaert, 14.iii.1999, SOC395/F010)[2]	AJ544739[7]	**AM779627**
C. auriculata	Socotra: Nogid (Leliaert, SOC396)[2]	—	**AM779628**
C. auriculata (‘*C. delphinii*’)	Socotra: Nogid (Schils, sMM415/F316), globose capitulum[2]	—	**AM779629**
C. auriculata	Socotra: Nogid (Schils, sMM476/F317)[2]	—	**AM779630**
C. delphinii (Hariot) Feldmann & Børgesen	South Africa: Durban, The Bluff, Treasure Beach (Coppejans *et al.*, 3.viii.1999, KZN83)[2]	—	**AM779631**
C. delphinii	South Africa: KwaZulu-Natal, Sodwana Bay (Coppejans *et al.*, 8.viii.1999, KZN215/F468)[2]	—	**AM779632**
C. delphinii (‘*C. auriculata*’)	South Africa: KwaZulu-Natal, Linkia Reef (Coppejans *et al.*, 15.viii.1999, KZN694/F321), auriculate capitulum[2]	AM503425[6]	**AM779633**
C. delphinii (‘*C. auriculata*’)	South Africa: KwaZulu-Natal, Linkia Reef (Coppejans *et al.*, 15.viii.1999, KZN710/F187), auriculate capitulum[2]	**AM779619**	**AM779634**
C. delphinii	South Africa: KwaZulu-Natal, Sodwana Bay (Coppejans *et al.*, 10.ii.2001, KZN2110.1/F011)[2]	AJ544740[7]	**AM779635**
C. delphinii	South Africa: Eastern Cape, Mzamba (Stegenga & De Clerck, 21.viii.2005, D53/F359)[3]	AM503426[6]	—
C. delphinii	South Africa: KwaZulu-Natal, Palm Beach (Boedeker, 22.viii.2005, D56/F360)[3]	AM503427[6]	—
C. peniculum (J. Ellis & Solander) Kuntze	Bahamas: Long Island (Coppejans, viii.1982, HEC5032)[2]	—	**AM779636**
C. peniculum	Dominican Republic: Puerto Plata (Dargent, 8.ii.2002, HODRD2-02-20/F333)[2]	AM503432[6]	**AM779637**
C. peniculum	Dominican Republic: Puerto Plata (Dargent, ii-2002, HODRD2-02-45/F125)[2]	—	**AM779638**
Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen	Syria: Latakia (1991, CloMT/Csmem5/CmMed SL/F295)[2]	AM503486[6]	AY055880/ AY055947[8]
C. philippinensis W.R. Taylor	Philippines: Panglao Island (Verbruggen, 1.ii.2004, HV710/F176)[2]	AM503490[6]	**AM779639**
C. sundanensis Reinbold	Tanzania: Mnazi Bay (Coppejans et al, 29.vii.2000, HEC12976/F189)[2]	AM503495[6]	**AM779640**
Phyllodictyon anastomosans (Harvey) Kraft & M.J. Wynne	St Croix: Malta Baths (Kooistra, 1988, SaMB/Sana1/F236, F413)[1]	AM503520[6]	**AM779641**
P. anastomosans	Tanzania: Zanzibar, Chwaka Bay (Leliaert, 17.vii.2001, FL966/F401)[2]	AJ544725[7]	**AM779642**
P. orientale (A. Gepp & E. Gepp) Kraft & M.J. Wynne	Comoros: Grande Comoro I. (Earle, 1977, West1631/Struv1/F414)[4]	AM503521[6]	**AM779643**
Struvea elegans Børgesen	Bahamas (West, SE1572/Sele1/F237)[4]	AM503526[6]	**AM779644**
S. gardineri A. Gepp & E. Gepp	Seychelles: Plate Island (Coppejans & Kooistra, 7.i.1993, SEY771a/F199)[2]	AM072287[6]	**AM779645**
S. okamurae Leliaert (*Chamaedoris orientalis* Okamura & Higashi)	The Philippines: Bulusan (Coppejans, 22.iv.1998, HEC12301A/F104)[2]	AM503428[6]	**AM779646**
S. okamurae (*C. orientalis*)	The Philippines: Bulusan (Coppejans, 22.iv.1998, HEC12301B/F332)[2]	AM503429[6]	—
S. plumosa Sonder	Western Australia (Schils, WA221/F287)[2]	AM503527[6]	**AM779647**
S. thoracica Kraft & A. Millar	New Caledonia: Ile aux Canards (Millar *et al.*, 13.ix.2002, NSW 610014)[5]	**AM779623**	**AM779648**
Outgroup taxa			
Dictyosphaeria cavernosa (Forsskål) Børgesen	Seychelles: Poivre Atoll (Kooistra, 1993, DISSey486/Dcav7/F285)[1]	AM503502[6]	—
Valoniopsis pachynema (G. Martens) Børgesen	Australia: Queensland, Alma Bay (4.vi.1987, West 2827/Vopsis7/F420)[1, 4]	AM503540[6]	—

[1] Culture isolate from the algal culture collection of the University of Groningen (Netherlands), now maintained in the University of Ghent (Belgium).
[2] Voucher specimen deposited in the herbarium of the University of Ghent (Belgium) (GENT).
[3] Voucher specimen deposited in the National Herbarium of the Netherlands (Leiden University Branch) (L).
[4] Culture isolate from the algal culture collection of John West (University of Melbourne, Australia), culture duplicate in the University of Ghent (Belgium).
[5] Voucher specimen deposited in the National Herbarium of New South Wales (Australia) (NSW).
[6] Sequence from Leliaert *et al.* (2007).
[7] Sequence from Leliaert *et al.* (2003).
[8] Sequence from van der Strate *et al.* (2002).

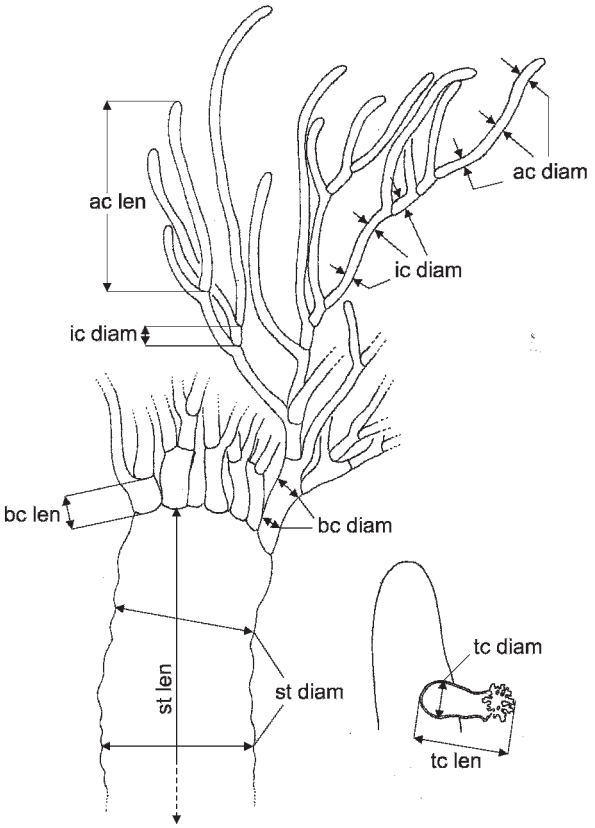


Fig. 1. *Chamaedoris*. Measurements made on the stipe cells, capitulum filaments and tenacular cells. ac len, length of the apical cells; ac diam, diameter of the apical cells; bc len, length of the basal cells; bc diam, diameter of the basal cells; st len, length of the stipe cell; ic len, length of the intermediate filaments; ic diam, diameter of the intermediate filaments; st diam, diameter of the stipe cell; tc len, length of the tenacular cells; tc diam, diameter of the tenacular cells.

replicates (Shimodaira & Hasegawa 1999). MP analyses were performed under the same heuristic search settings as ML. Bootstrap analyses consisted of 1000 replications of full heuristic searches.

The root of the LSU-ITS tree was determined both by outgroup rooting and by molecular clock rooting (where the root of the tree is placed along its oldest branch, at exactly the same distance from each terminal taxon). The ITS1 tree was left unrooted.

Morphometrics

Twelve specimens of *C. auriculata*, *C. peniculum* and *C. delphinii*, from which ITS rDNA sequences were obtained, were used in the morphometric analysis. Eleven types of measurements were taken, including diameter of the capitulum (cap diam); length and diameter of the stipe cell (st len; st diam); length and diameters of the capitulum filaments, including the most basal cell (bc len; bc diam), the intermediate filaments (i.e. any filament that is not a basal nor an apical cell) (ic len; ic diam) and the apical cells (ac len; ac diam); and length and diameter of the tenacular cells (tc len; tc diam) (Fig. 1). For each type, 10 measurements were taken per specimen, from which the average value was used for statistical analyses.

Statistical analyses were performed using Statistica 6.0 (Statsoft, Tulsa, OK, USA). ITS rDNA clades found in the molecular phylogenies were used as *a priori* groups (ITS groups). A multivariate analysis of variance (MANOVA), followed by a post hoc Tukey's honest significant difference (HSD) test, was used to test the overall significance between means of the ITS groups. A series of one-way analyses of variance (ANOVA) and the *post hoc* Tukey–HSD test were applied to identify characters showing significant between-ITS-clade variation. In all analyses, $P < 0.01$ was considered significant.

RESULTS AND OBSERVATIONS

Morphological species identification

Based on morphological characters, most of the examined *Chamaedoris* specimens could be readily assigned to one of the four, traditionally circumscribed species: *C. auriculata*, characterized by flat, auriculate capitula and one to three superimposed cells on the stipe; *C. delphinii* with globose capitula without superimposed cells on the stipe; *C. peniculum* with flat, peltate capitula and up to three superimposed cells on the stipe; and *C. orientalis* characterized by oblong capitula developing from a central axis of up to 28 cells. However, a number of specimens showed intermediate character states between the typical *C. auriculata* and *C. delphinii* morphologies. Some specimens with globose capitula (typical *C. delphinii*) contained one or two superimposed cells on the stipe, while in other specimens with a flat, auriculata capitulum (typical *C. auriculata*), superimposed cells were absent.

Various morphological types of crystalline cell inclusions were observed and found to differ consistently between the four species. Tetrahedral protein crystals were abundant and scattered among the chloroplasts of the stipe cell of *C. auriculata* and *C. delphinii* (Figs 20–22) but absent in *C. peniculum* and *C. orientalis*. Calcium oxalate crystals were found only in the latter two and were diamond-shaped in *C. peniculum* (Figs 44, 45) or elongate prismatic to needle-shaped in *C. orientalis* (Figs 58, 59).

Phylogenetic analyses

The concatenated LSU-ITS alignment of the four *Chamaedoris* species with 13 related sequences (including species of *Apjohnia*, *Boodlea*, *Cladophoropsis*, *Phyllodictyon* and *Struvea*) and *Dictyosphaeria cavernosa* and *Valoniopsis pachynema* as outgroups was 1166 sites in total (1154 when excluding the outgroup), with 578 sites of the LSU rDNA (566 sites when only including the ingroup) and 588 sites of the rDNA ITS1-5.8S-ITS2 region; 395 characters were variable, of which 287 parsimony informative (respectively, 348 and 258 in ingroup analyses). Phylogenetic trees constructed with BI, ML and MP methods gave almost identical topologies with comparable internal node resolution. Although inclusion of the outgroup sequences in the phylogenetic analyses did not affect ingroup topology, the resolution of the tree was considerably improved when only ingroup sequences were considered in the analyses. The

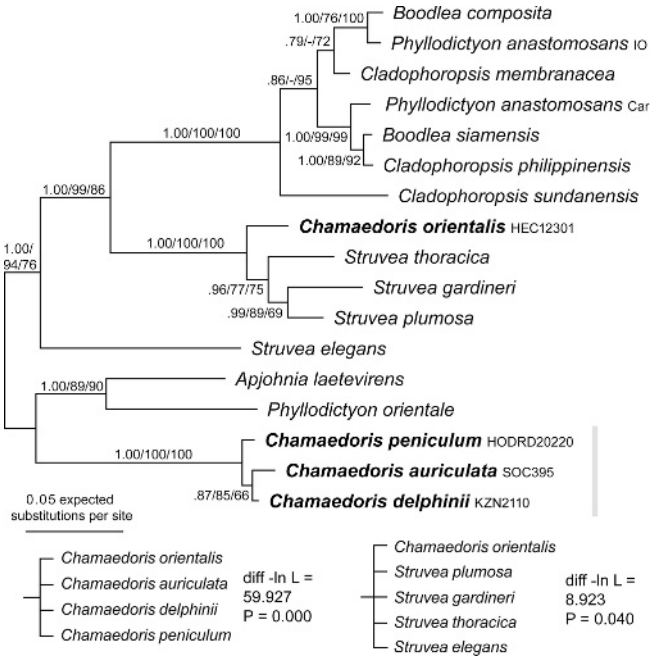


Fig. 2. BI tree of *Chamaedoris* and allied genera inferred from concatenated LSU rDNA and rDNA ITS sequences. BI posterior probabilities and ML/MP bootstrap values are indicated at branches. The likelihood of two alternative topologies, tested against the optimal ML topology (−ln L = 5085.869) using Shimodaira-Hasegawa tests are presented.

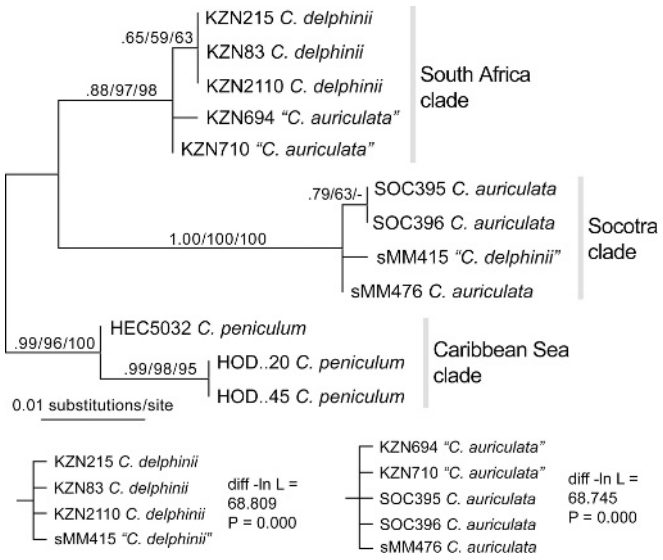


Fig. 3. Unrooted ML tree of 12 specimens belonging to *Chamaedoris auriculata*, *C. delphinii* and *C. peniculum*, inferred from ITS1 sequences. Taxon names are based on identifications according to the traditional species circumscriptions. BI posterior probabilities and ML/MP bootstrap values are indicated at branches. The likelihood of two alternative topologies, tested against the optimal ML topology (−ln L = 561.922) using Shimodaira-Hasegawa tests are presented.

phylogram obtained from the BI analysis of ingroup sequences, manually rooted along the branch as determined by outgroup and molecular clock rooting, is shown in Fig. 2. Three of the four *Chamaedoris* species, including *C. auriculata*, *C. delphinii* and *C. peniculum*, form a clade of closely related sequences, sister to *Phyllodictyon orientale* and *Apjohnia laetevirens*. *Chamaedoris orientalis* is more closely related to *Struvea gardineri* A. Gepp & E. Gepp, *S. plumosa* Sonder and *S. thoracica* Kraft & A. Millar than to the other three congeneric taxa. Nonmonophyly is furthermore noticeably shown in *Phyllodictyon*, while *Struvea* appears as a paraphyletic assemblage. SH tests (Fig. 2) showed that monophyly of the four *Chamaedoris* taxa resulted in a tree that was significantly less likely than the unconstrained ML tree. Monophyly of the three *Struvea* taxa and *Chamaedoris orientalis*, together with *S. elegans*, resulted in only a marginally significant less likely tree.

The ITS1 alignment of 12 sequences of *C. auriculata*, *C. delphinii* and *C. peniculum* was 496 sites in total, including 53 variable characters, of which 52 were parsimony informative. Phylogenies inferred with BI, ML and MP methods gave identical topologies. The unrooted ML tree (−ln L = 561.922) is shown in Fig. 3. Three strongly supported clades were recovered in the analyses, corresponding to three geographical regions: South Africa, Socotra (Arabian Sea; Fig. 60, arrow) and Caribbean Sea. The specimens in the Caribbean clade were all referable to *C. peniculum*, but the two other clades both included plants determined as *C. auriculata* and *C. delphinii*. SH tests rejected monophyly of either *C. auriculata* or *C. delphinii* as traditionally circumscribed (Fig. 3).

Morphometric analysis

All 12 specimens used in the ITS1 phylogeny were used in the morphometric analysis. Eleven measurements (Fig. 1) were obtained from all specimens, except for the measurements of the tenacular cells, which were absent or scarce in two of the three *C. peniculum* specimens. MANOVA, followed by a *post hoc* Tukey's HSD test, showed that there was no overall significant difference between means of the three ITS groups ($P = 0.027$). One-way ANOVAs and *post hoc* Tukey's HSD tests indicated that out of the 11 types of measurements, only two were significantly different between the South Africa and Socotra ITS-clades: diameter of the intermediate and apical cells (Table 2, Fig. 4).

Reexamination of the type specimen of *C. auriculata* (from India) and specimens collected from Socotra, Sri Lanka and the tropical East African coast (Kenya, Tanzania and northern Mozambique) showed that the average diameters of the intermediate and apical cells fell within the limits of those from the Socotra ITS-clade. One specimen, collected from Herald Cay (northeast coast of Australia) and tentatively identified as *C. auriculata*, was characterized by a flat capitulum and much narrower apical cells (average 55 μm in diameter). Specimens collected from Madagascar (including the type of *C. delphinii*), southern Mozambique, South Africa, Mauritius and Rodrigues had cell diameters comparable to the ones found in the South Africa ITS-clade. We therefore feel confident to assign the three ITS-clades to the three *Chamaedoris* species, two of which (*C. auriculata* and *C. delphinii*) with emended morphological circumscriptions.

Table 2. Univariate ANOVAs and Tukey HSD tests for morphometric trait variation by ITS-clade (Fig. 3). Soc-clade, Socotra clade; SA-clade, South Africa clade; Car-clade, Caribbean Sea clade; NS, not significant.

	Soc-clade	SA-clade	Car-clade	ANOVA	Probabilities for Tukey HSD tests		
	$\bar{X}$ (*s*)	$\bar{X}$ (*s*)	$\bar{X}$ (*s*)	*P* value	Between Soc- and SA-clade	Between Soc- and Car-clade	Between Car- and SA-clade
Capitulum diam. (cm)	3.9 (2.4)	1.1 (0.4)	3.3 (1.4)	NS	NS	NS	NS
Stipe length (cm)	3.7 (0.5)	3.8 (1.1)	2.1 (0.5)	NS	NS	NS	NS
Stipe diam. (mm)	1.2 (0.2)	1.4 (0.1)	1 (0)	NS	NS	NS	NS
Basal cell length (μm)	1195.3 (936.6)	843 (204)	716.7 (155.9)	NS	NS	NS	NS
Basal cell diam. (μm)	247.8 (58.1)	285.6 (62.3)	250.7 (24.6)	NS	NS	NS	NS
Interm. cell length (μm)	1435 (563)	1315.9 (772)	1321.7 (540.2)	NS	NS	NS	NS
Interm. cell diam. (μm)	90.9 (8.2)	125.1 (15.4)	130 (12.1)	0.003	0.008	0.008	NS
Apical cell length (μm)	2718.6 (1414.5)	2708.4 (961.6)	1910.7 (543.2)	NS	NS	NS	NS
Apical cell diam. (μm)	81.6 (7.4)	107.6 (9.2)	115.7 (9.4)	0.001	0.004	0.002	NS
Tenacular cell length (μm)	159.2 (95.9)	96.3 (57.3)	—	NS	NS	—	—
Tenacular cell diam. (μm)	49.1 (10.1)	46.8 (28.3)	—	NS	NS	—	—

Species accounts

Chamaedoris auriculata Børgesen
(1933, pp. 5–9, text-figs 3–5)

Figs 5–20

LECTOTYPE: Dwarka, Gujarat, India, leg. Børgesen 5447, C!. Four herbarium specimens, all from the same locality with number Børgesen 5447, are present in C; the largest specimen (Fig. 6) is here indicated as lectotype; the others becoming isolectotypes.

REFERENCE: Sartoni (1992, pp. 308–311, figs 8, 9A, B, including description and illustrations of '*C. delphinii*').

DESCRIPTION: Thallus forming erect, stipitate capitula, 4–12 cm high, attached to the substratum by branching rhizoids developing from the base of the stipe. Stipes single to densely clustered (a few to 10 or more), single-celled, with annular constrictions over the entire length, unbranched or occasionally branched. Capitulum generally flat, or occasionally ball-shaped; flat capitula, growing eccentrically to one side, penicillate to spatulate when young, later becoming auriculate to peltate (Figs 5–8), to 12 cm in diameter, about 2–4 mm thick; globose capitula up to 14 mm in diameter. Capitulum filaments arising in whorls from the swollen apex of the stipe cell and generally from one or two small cells formed at the top of the stipe (Fig. 15), sometimes these superimposed cells are lacking. Growth of the capitulum by apical and intercalary cell divisions, followed by cell elongation and formation of branches. Cells of the capitulum filaments initially producing a single lateral branch; older cells occasionally producing a second branch. Filaments of small capitula often fastigiate, those of larger capitula generally curved or sinuous. Cross wall formation at the base of the laterals markedly delayed. Branching of the capitulum filaments up to the fourth order (Figs 9, 10). Structural reinforcement of the capitulum by entanglement of the filaments (filaments often sinuous, facilitating entanglement) and by anastomosis of adjacent cells by means of laterally inserted, tenacular cells, which are often elongated and rhizoidal (Figs 16–19). Filaments from adjacent capitula may also intertwine and attach themselves by tenacular cells (Fig. 7). Apical cells of the capitulum filaments (45–) 60–110 (–125) μm in diameter (mean diameter per specimen: 70–86 μm), up to 11 mm long; cells of the intermediate capitulum filaments (60–) 70–120 (–150) μm in diameter (mean diameter per specimen: 84–105 μm), up to 11 mm long; basal capitulum cells 120–250 μm in diameter, 300–2250 μm long. Diameter of stipe cell 500–1100 μm in the middle part, slightly tapering towards both extremities, 2–7.5 cm long. Tenacular cells 32–75 μm in diameter, 50–400 μm long. Cell wall thickness of the capitulum filaments increasing from 2–8 μm in the terminal branch systems to 25–40 μm in the basal filaments. Cell walls of the stipe cell markedly stratified, up to 75 μm thick. Chloroplasts rounded, 2.6-4 μm in diameter, forming an open to relatively closed parietal network. Most chloroplasts containing a single pyrenoid, *c.* 1.3 μm in diameter. Tetrahedral protein crystals abundant and scattered among the chloroplasts of the stipe cell (Fig. 20), less frequent in the capitulum filaments; up to 45 μm in diameter. Star-shaped clusters of fine needle-shaped crystals (possibly silica) present in the capitulum filaments, *c.* 40 μm in diameter. Calcium oxalate crystals absent.

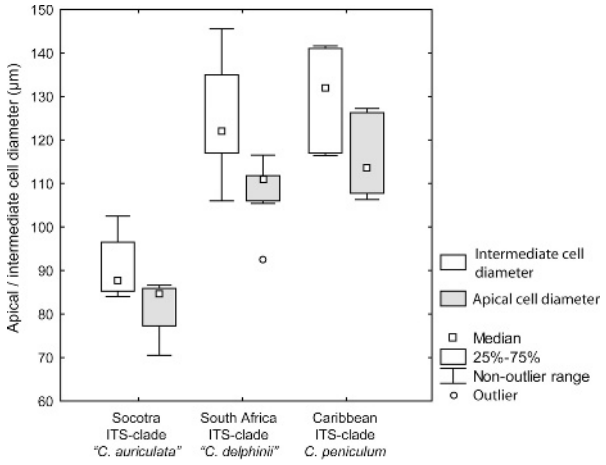
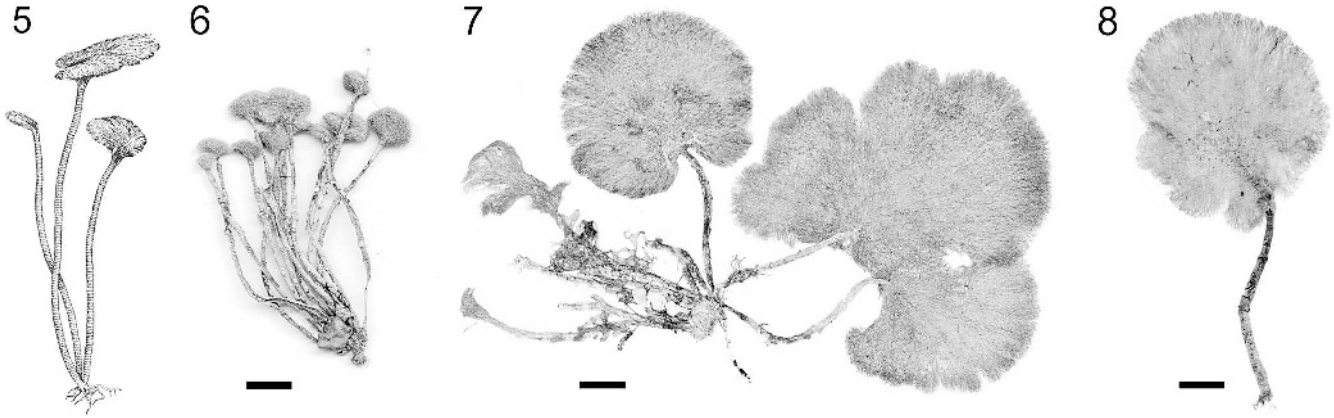
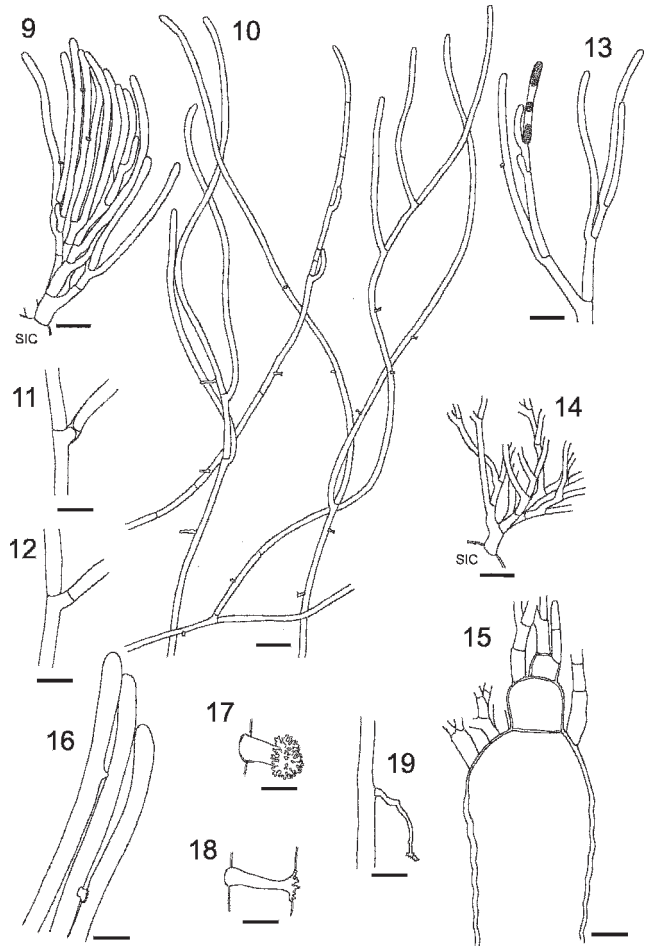


Fig. 4. Comparison of the mean apical cell diameters (white boxes) and intermediate cell diameters (grey boxes) between specimens of the three ITS-clades in Fig. 3.



Figs 5–8. *Chamaedoris auriculata.*
Fig. 5. Original drawing of the type material (Børgesen 1933).
Fig. 6. Clustered stipes forming small, auriculate capitula (C, lectotype). Scale = 1 cm.
Fig. 7. Plant from deep waters of Socotra forming large, often intricated capitula (GENT, SOC 370). Scale = 1 cm.
Fig. 8. Stipitate capitulum from Coral Sea, Australia (NSW 415041). Scale = 1 cm.



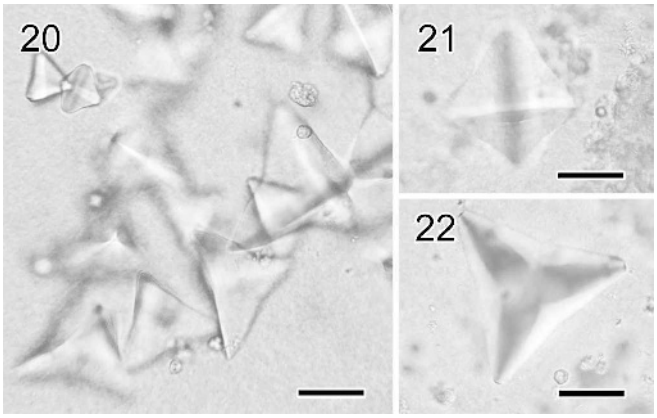
Figs 9–19. *Chamaedoris auriculata* (GENT, SOC 396).
Fig. 9. Unilaterally branched filaments of a small capitulum. SIC = superimposed cell. Scale = 500 μm.
Fig. 10. Filaments of a large capitulum with numerous, laterally formed tenacular cells. Scale = 500 μm.
Figs 11, 12. Cross wall at the base of a lateral, formed by segregative cell division. Scale = 200 μm.
Fig. 13. Apical cell undergoing segregative cell division. Scale = 500 μm.
Fig. 14. Basal branches of the capitulum. Scale = 500 μm.

HABITAT AND GEOGRAPHIC DISTRIBUTION: *Chamaedoris auriculata* grows in low intertidal to subtidal habitats, to 18 m depth, epilithic on vertical or horizontal substrata, or epiphytic (e.g. on stems of the seagrass *Thalassodendron*). The stipes are often completely epiphytized by crustose coralline rhodophytes. *Chamaedoris auriculata* occurs in India, Sri Lanka, Socotra and along the tropical East African coast, where it has been found in Somalia (Sartoni 1992), Kenya (Isaac 1967; Coppejans *et al*. 2000), Tanzania (including Zanzibar and Mafia Island) (Coppejans *et al*. 2000) and northern Mozambique (Appendix 1, Fig. 60). The single record of the species for the Pacific Ocean is that of Millar (1999, as *Chamaedoris peniculum*) from the Herald Cays in the Coral Sea, which has since been shown to be referable to *C. auriculata* based on the auriculate capitula and small apical cell diameter (45–65 μm).

REMARKS: According to Børgesen (1933), the main difference between *C. auriculata* and *C. peniculum* is the shape of the capitulum. In *C. auriculata,* the capitulum filaments are formed in whorls on the apical part of the stipe and on the small, superimposed cell(s). They grow out to one side, resulting in an eccentric capitulum. Older capitula are auriculate (Fig. 7) and sometimes become secondarily peltate by closure and anastomosis of the auriculate ends (Fig. 8). In *C. peniculum,* the capitulum filaments are also formed in whorls on the apical part of the stipe and on the superimposed cells, but in this species the filaments do not grow unilaterally, resulting in a flat, peltate or cup-shaped capitulum. *Chamaedoris auriculata* further differs from *C. peniculum* by the presence of tetrahedral protein crystals in the stipe and by the absence

←

Fig. 15. Distal end of annulated stipe and two superimposed cells, producing whorls of capitulum filaments. Scale = 500 μm.
Fig. 16. Fastigiate filaments attaching by tenacular cells; the upper tenacular cell not fully developed. Scale = 200 μm.
Figs 17–18. Tenacular cells. Scale = 50 μm.
Fig. 19. Extremely elongated (rhizoidal) tenacular cell. Scale = 200 μm.



Figs 20–22. Tetrahedral protein crystalline cell inclusions in *Chamaedoris auriculata* and *Chamaedoris delphinii.*
Fig. 20. *Chamaedoris auriculata* (GENT, SOC 344). Scale = 25 μm.
Fig. 21–22. *Chamaedoris delphinii* (GENT, KZN 215). Scale = 25 μm.

of calcium oxalate crystals in the capitulum filaments. Traditionally, *C. delphinii* has been distinguished from *C. auriculata* by the ball-shaped capitula, the absence of superimposed cells on the stipe and the slightly thicker capitulum filaments (Børgesen 1940). Morphometric analysis combined with molecular evidence demonstrates that *C. delphinii* and *C. auriculata* differ mainly in filament diameter (Fig. 4, Table 3).

Chamaedoris delphinii (Hariot) J. Feldmann & Børgesen, *in* Børgesen (1940, pp. 16–20, 21, footnote, fig. 5, pl. 1)

Figs 21–31

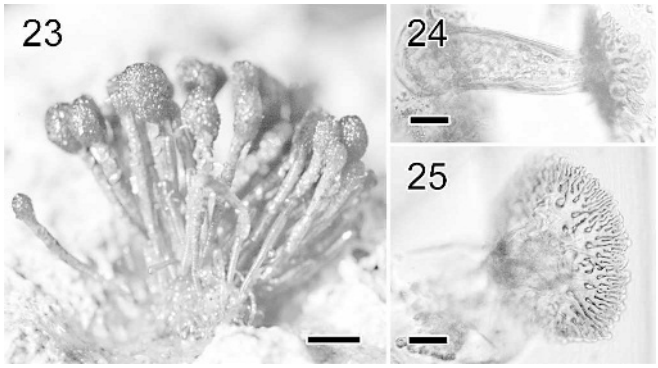
BASIONYM: *Siphonocladus delphinii* Hariot (1902, p. 470, '*delphini*').

HOLOTYPE: Fort-Dauphin, Madagascar, leg. M. Ferlus, herbier général, case 69, PC!. The holotype consists of a single capitulum lacking a stipe. One microscopic slide, made from the holotype material by Børgesen and consisting of capitulum filaments only, is present in C!.

DESCRIPTION: Thallus forming erect stipitate capitula, 4–7 (–8) cm high (Fig. 23), attached to the substratum by branched rhizoids arising from the lower pole of the stipes. Stipes single to densely clustered (a few to over 100), single-celled, with annular constrictions over the entire length. Young capitula penicillate, generally becoming ball-shaped when older, 5–15 (–18) mm in diameter, 2–15 (–23) mm high, or occasionally flat and auriculate. Capitulum filaments generally formed at the apex of the stipe (Fig. 28), or sometimes arising in whorls from the swollen apex of the stipe cell and from one or two small, superimposed cells on the stipe. Growth of the capitulum mainly by apical cell divisions, followed by cell-elongation. After being cut off from the apical cell, each new cell producing one lateral at its apical pole; the basal cells of the capitulum possibly forming a second lateral. Cross wall formation at the base of branches delayed. Branching of the capitulum filaments to 3 orders (Fig. 26). Structural reinforcement of the capitulum mainly by entanglement

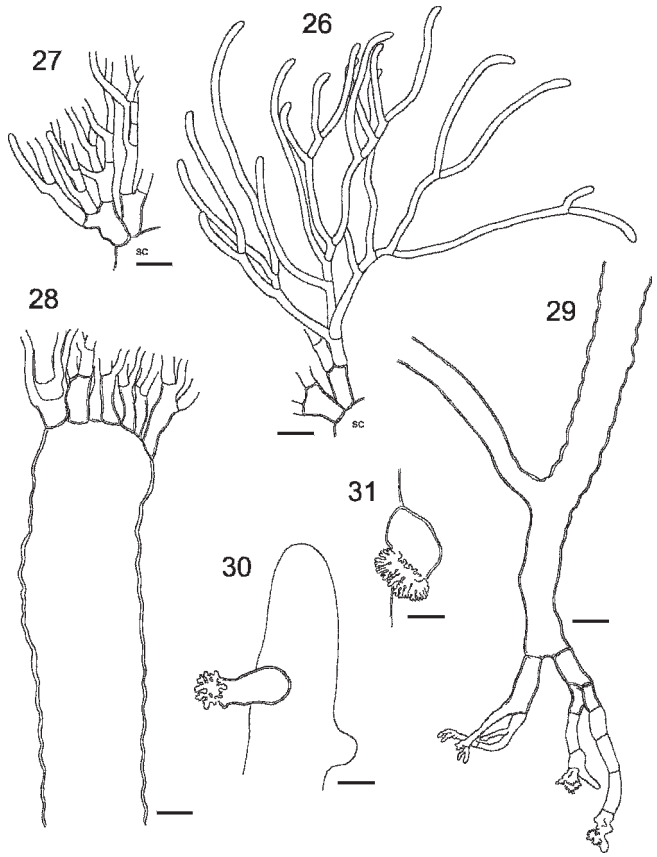
Table 3. Comparative table of features of the newly circumscribed *Chamaedoris auriculata, C. delphinii, C. peniculum and Struvea okamurae (Chamaedoris orientalis).*

	C. auriculata	*C. delphinii*	*C. peniculum*	*S. okamurae*
Thallus height	4–12 cm	4–8 cm	2–10 cm	5–20 cm
Number of superimposed cells on the stipe cell	0–2	0–1	0–3	13–28
Capitulum shape and dimensions	Generally flat, auriculate, 20–120 mm in diam. Sometimes globose, up to 20 mm in diam.	Generally globose, up to 2–20 (–30) mm in diam. Sometimes flat, auriculate, up to 35 μm in diam.	Cup-shaped to subglobose, 30–100 mm in diam.	Oblong to globose, up to 25–100 mm long, 20–40 mm in diam.
Diameter apical cells of the capitulum filaments: range and mean per specimen	50–140 μm $\bar{X}$: 70–86 μm	70–200 μm $\bar{X}$: 105–125 μm	80–175 μm $\bar{X}$: 107–126 μm	320–480 μm $\bar{X}$: 345–450 μm
Prismatic calcium oxalate crystals	Absent	Absent	Diamond-shaped	Elongate prismatic to needle-shaped
Tetrahedral protein crystals	Present	Present	Absent	Absent
Habitat	Low intertidal to subtidal (–18 m)	Mid-intertidal rock pools to subtidal (–15 m)	Shallow to deep subtidal (–50 m)	Shallow subtidal (–6 m)
Type locality* and geographical distribution	India*, Arabian Sea, Sri Lanka, tropical East Africa, NE Australia	Madagascar*, subtropical SE Africa, Mauritius	Florida*, Caribbean, tropical W Atlantic Ocean	Taiwan*, tropical West Pacific Ocean

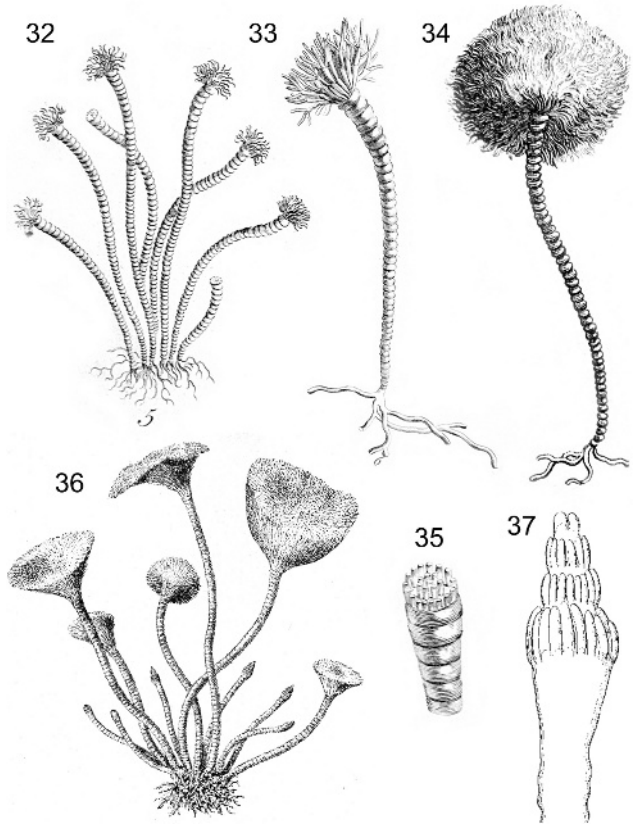


Figs 23–25. *Chamaedoris delphinii*.
Fig. 23. Habit (GENT, KZN 769). Scale = 1 cm.
Figs 24–25. Tenacular cells (GENT, KZN 694). Scale = 20 μm.

of the filaments (facilitated by the curved or sinuous filaments), occasionally also by anastomosis of capitulum filaments by means of laterally inserted tenacular cells (Figs 24, 25, 30, 31). Apical capitulum cells 80-165 μm in diameter (mean diameter per specimen: 105–125 μm), up to



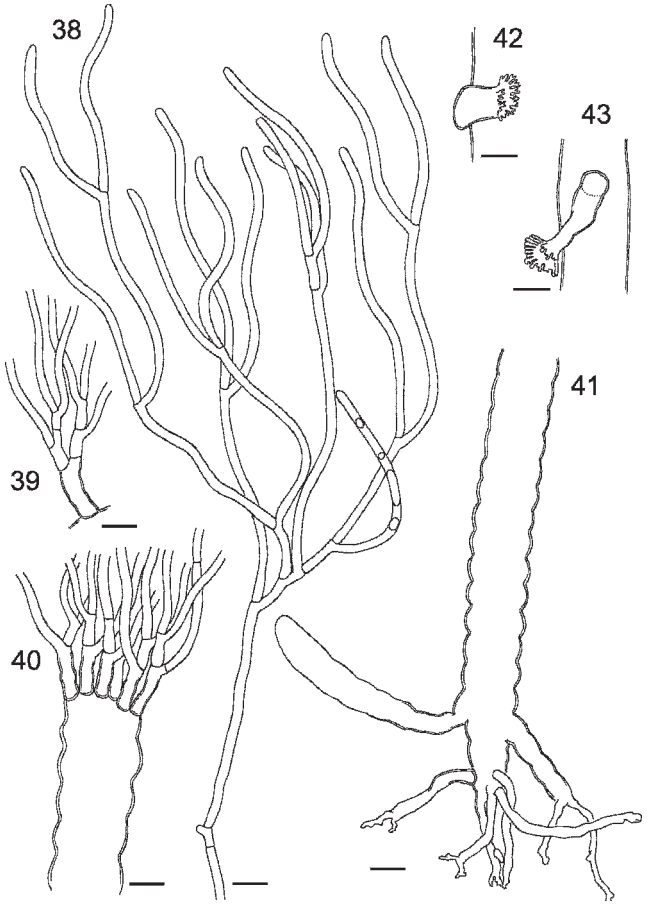
Figs 26–31. *Chamaedoris delphinii* (GENT, KZN 763).
Fig. 26. Unilaterally branched capitulum filaments, SC = stipe cell. Scale = 500 μm.
Fig. 27. Basal branches of the capitulum. Scale = 500 μm.
Fig. 28. Distal end of annulated stipe producing the capitulum filaments. Scale = 500 μm.
Fig. 29. Proximal pole of branched, annulated stipe with branched, septate rhizoids developing from the base. Scale = 500 μm.
Figs 30, 31. Tenacular cells. Scale = 50 μm.



Figs 32–37. *Chamaedoris peniculum*.
Figs 32–35. Original illustrations from Ellis & Solander (1786), here designated as the nomenclatural type of *Chamaedoris peniculum*.
Fig. 36. Habit. Reproduced from Børgesen (1913).
Fig. 37. Distal end of annulated stipe with three superimposed cells, producing whorls of capitulum filaments. Reproduced from Børgesen (1913).

7500 μm long; cells of the main capitulum filaments 90–200 μm in diameter (mean diameter per specimen: 106–147 μm), up to 7500 μm long; basal capitulum cells 160–400 μm in diameter, 250–1250 μm long. Diameter of the stipe cell 1100–1650 μm at the apex, tapering to 400–950 μm at the base, 2–7 cm long. Tenacular cells 40–70 μm in diameter, 70–400 μm long. Cell wall thickness of the capitulum filaments increasing from 2–6 μm in the terminal branch systems to 8–35 μm in the basal filaments. Cell walls of the stipe markedly stratified, up to 55 μm thick. Chloroplasts polygonal to rounded, 4–7 μm in diameter, forming an open parietal reticulum. Most chloroplasts containing a single pyrenoid, 1.5–2.8 μm in diameter. Protein crystals abundant and scattered among the chloroplasts of the stipe cell, less frequent in the capitulum filaments, tetrahedral when small, growing into 3-armed structures, up to 85 μm in diameter (Figs 21, 22). Star-shaped clusters of fine needle-shaped crystals (possibly silica) present in the capitulum filaments, *c.* 40 μm in diameter. Calcium oxalate crystals absent.

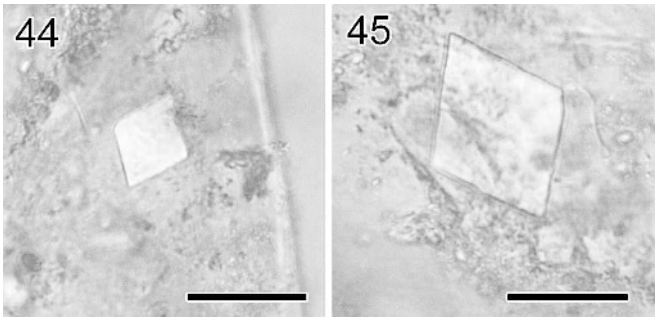
HABITAT AND GEOGRAPHIC DISTRIBUTION: *Chamaedoris delphinii* grows epilithically in mid- to low intertidal rock pools or subtidal (to 15 m depth), on vertical or horizontal substrata. The stipes are often completely covered by the



Figs 38–43. *Chamaedoris peniculum* (GENT, HOD RD2-02-45).
Fig. 38. Unilaterally branching capitulum filaments. Scale = 500 μm.
Fig. 39. Basal branches of capitulum. Scale = 500 μm.
Fig. 40. Distal pole of stipe producing capitulum filaments. Scale = 500 μm.
Fig. 41. Proximal pole of annulated stipe, producing a new stipe and rhizoids at the base. Scale = 500 μm.
Figs 42, 43. Tenacular cells. Scales = 50 μm.

crustose coralline red algal epiphyte *Pneophyllum amplexifrons* (Harvey) Chamberlain & Norris (Chamberlain & Norris 1994, p. 10, fig. 4). *Chamaedoris delphinii* is a common species along the (sub)tropical southern East African coast (southern Mozambique [Isaac 1956] and South Africa [Papenfuss 1952]), Madagascar (type locality) and Mauritius (Børgesen 1940) (Appendix 1, Fig. 60). The records from the tropical East African coast (Somalia [Sartoni 1992], Kenya [Gerloff 1960] and Tanzania [Jaasund, 1976]) are most probably referable to *C. auriculata*.

REMARKS: Although Hariot (1902, p. 470) provided a fairly detailed original description of *Siphonocladus delphinii*, it was only after Børgesen's (1940) publication that this species became better known as *C. delphinii*. Traditionally, *C. delphinii* was thought to differ from other species in the genus primarily in lacking the simultaneously produced whorls of capitulum filaments arising from the distal ends of the distal stalk-cells beautifully illustrated by Børgesen (1912, fig. 17). Based on this feature, the generic placement of *C. delphinii* was questioned by Millar (1999).



Figs 44–45. Diamond-shaped calcium oxalate crystalline cell inclusions in *Chamaedoris peniculum* (L 937 183 180). Scales = 20 μm.

Here we have shown that neither the globose shape of the capitulum nor the absence of superimposed cells are diagnostic for *C. delphinii* and that this species also includes plants with a flat capitulum and one or two superimposed cells. Morphometric analysis combined with molecular evidence demonstrates that *C. delphinii* and *C. auriculata* mainly differ in filament diameter (Fig. 4, Table 3).

Chamaedoris peniculum
(Ellis & Solander) Kuntze (1898, p. 400)

Figs 32–45

BASIONYM: *Corallina peniculum* Ellis & Solander (1786, p. 127, pl. 7, figs 5–8, pl. 25, fig. 1).

LECTOTYPE: 'American seas, particularly near the Bahama Islands', leg. Ellis. The collections of Ellis are considered lost according to Dixon (1960, pp. 28–31). Since the figures, given with the original description, are of good quality, it is proposed to designate these as the nomenclatural type of *C. peniculum* (Figs 32–35).

NOMENCLATURAL SYNONYMS: *Penicillus annulatus* Lamarck (1813, p. 299), *nom. illeg*. This name is based on the original description and illustrations of *Corallina peniculum*. It is unclear why Lamarck changed the species epithet, possibly to avoid the formation of what he perceived to be a tautonym. The change was illegitimate, however, since the eschewed binomial does not fit the definition of a tautonym given in Article 23 (International Code of Botanical Nomenclature 2006).

Nesaea annulata (Lamarck) Lamouroux (1816, p. 256, '*Nesea*'), *nom. illeg*.

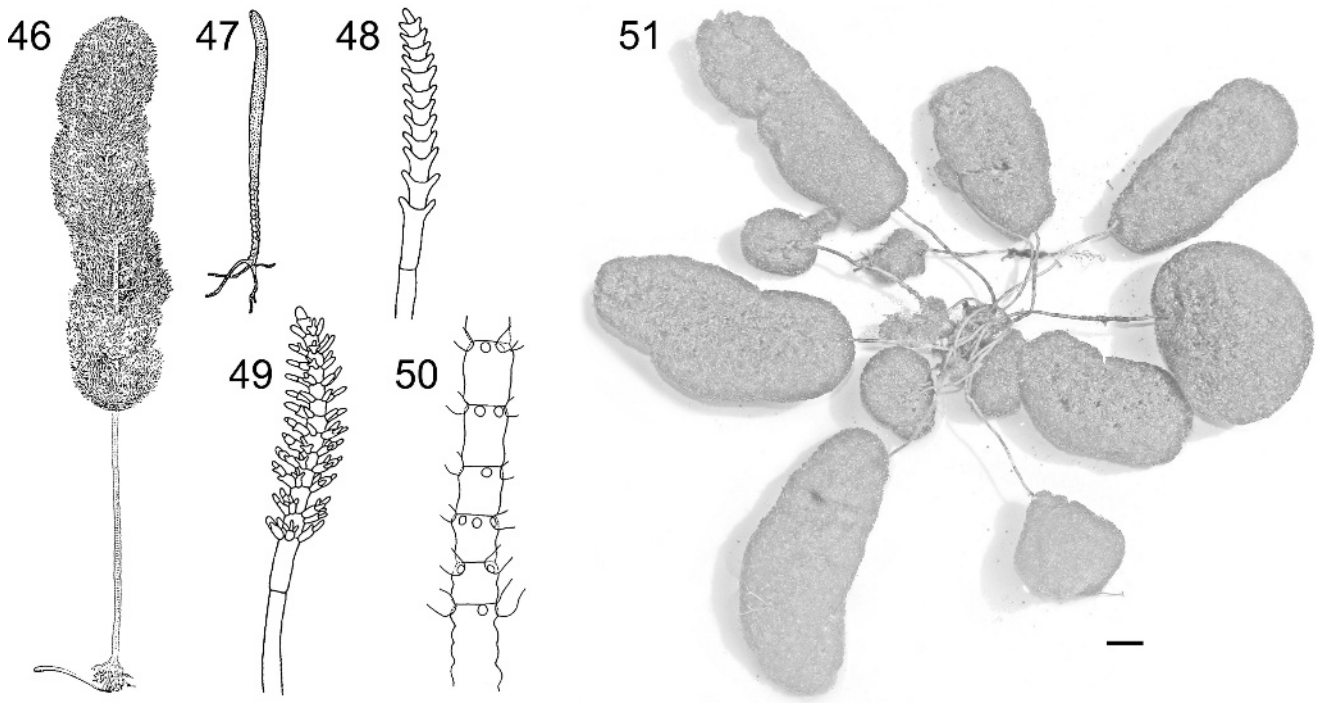
Scopularia annulata (Lamarck) Chauvin (1842, p. 122), *nom. illeg*.

Chamaedoris annulata (Lamarck) Montagne (1842, p. 261), *nom. illeg*.

Corallocephalus peniculum (Ellis & Solander) Kützing (1843, p. 311).

REFERENCES: Børgesen (1912, pp. 270–273, figs 16, 17; 1913, pp. 56–60, figs 40–43; 1940, pp. 16–20, footnote on pp. 20–21, fig. 5); Taylor (1960, p. 115, pl. 5, fig. 2); Littler & Littler (2000, p. 330, fig. on pp. 25, 331).

DESCRIPTION: Thallus forming erect, stipitate capitula, 2–10 (–14) cm high, attached to the substratum by rhizoids arising from the lower pole of the stipes. Stipes unbranched,

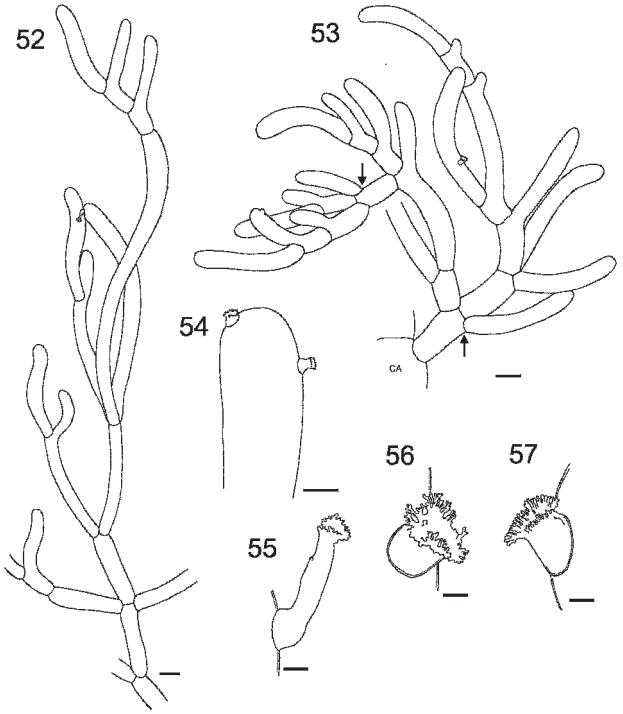


Figs 46–51. *Struvea okamurae* (*Chamaedoris orientalis*).
Fig. 46. Habit; some capitulum filaments removed, displaying the central axis. Reproduced from Yamada (1934).
Fig. 47–49. Early stages of thallus development: young cylindrical stipe with basal annular constrictions; apical division of the stipe cell into a large number of cells; each cell initially producing an opposite pair of laterals; later up to six laterals are formed per cell. Reproduced from Hori (1994).
Fig. 50. Distal end of annulated stipe cell and cells of the central axis, producing whorls of capitulum filaments. Reproduced from Okamura (1932).
Fig. 51. Habit of a plant from deep waters (25–30 m) of Guam (GUAM 00102). Photograph by T. Schils. Scale = 1 cm.

single-celled, with annular constrictions over the entire length, single or densely clustered. Capitulum oval, cup-shaped to flattened, or nearly ball-shaped, 1–10 cm across, 4–8 mm thick (Figs 34, 36). Capitulum filaments arising in whorls from the swollen apex of the stipe cell and generally from one or two small cells formed at the top of the stipe (Fig. 37); sometimes, these superimposed cells are lacking (Figs 35, 40). Growth of the capitulum mainly by division of the apical cells, followed by cell-elongation. Each new cell, after being divided from the apical cell, producing one lateral branch at its apical pole. Basal cells of the capitulum occasionally forming a second branch. Cross wall formation at the base of the laterals delayed. Branching of the capitulum filaments up to the fifth order (Fig. 38). Structural reinforcement of the capitulum mainly achieved by entanglement of the filaments (facilitated by the curved or sinuous filaments), also by anastomosis of capitulum filaments by tenacular cells (Figs 42, 43). Apical cells (80–) 100–170 μm in diameter (mean diameter per specimen: 107–126 μm), 600–7500 μm long; intermediate filaments 90–175 μm in diameter (mean diameter per specimen: 110–140 μm), 200–5000 μm long; basal cells 180–250 μm in diameter, 220–850 μm long. Stipe cells up to 1.5 mm in diameter, up to 5 (–11) cm long. Tenacular cells 45–55 μm in diameter, 80–90 μm in length. Cell wall thickness of the capitulum filaments increasing from 2–10 μm in the terminal branch systems to 15 μm in the basal filaments. Cell walls of the stipe cell markedly stratified, up to 65 μm thick. Chloroplasts rounded, 2.4–3.8 μm in diameter, forming an open to relatively closed parietal network. Most chloroplasts containing a single pyrenoid, *c.* 1.2 μm in diameter. Prismatic calcium oxalate crystals present (but rare) in the capitulum filaments, diamond-shaped, 15–30 μm in diameter (Figs 44, 45). Protein crystals absent.

HABITAT AND GEOGRAPHIC DISTRIBUTION: *Chamaedoris peniculum* grows epilithically in the subtidal, to 50 m depth, with deepwater forms possessing a large flat capitula. Stipes are often epiphytized by crustose coralline rhodophytes such as *Fosliella chamaedoris* (Foslie & M. Howe) M. Howe (Taylor 1960; Littler & Littler 2000). *Chamaedoris peniculum* is widespread in the Caribbean Sea (Florida, Bahamas, Greater Antilles, Lesser Antilles, southern Caribbean) (Littler & Littler 2000) and also occurs in Brazil (Appendix 1, Fig. 60). The Pacific record from the Coral Sea by Millar (1999) is now known to be a misidentification of *C. auriculata* (see above). Records from South Africa are misapplied names for *C. delphinii*, as already pointed out by Børgesen (1940) and Papenfuss (1952).

REMARKS: The nomenclatural history of this species is somewhat confusing, mainly because Lamarck (1813) changed the species epithet without an obvious reason. This results in the impression that *Chamaedoris annulata* and *Chamaedoris peniculum* are heterotypic. It is clear from Lamarck's (1813) diagnosis that *Penicillus annulatus* is based on the original description of *Corallina peniculum*, and that both species should be regarded as homotypic



Figs 52–57. *Struvea okamurae* (*Chamaedoris orientalis*) (GENT, HEC 12301).
Figs 52, 53. Capitulum filaments; ultimate branchlets unilateral, older cells producing a second, opposite lateral. Arrows showing cross walls at the base of single-celled laterals, indicating that these cells divided by centripetal invagination of the cell wall, rather than by segregative cell division. CA = central axis. Scale = 500 μm.
Fig. 54. Tenacular cells formed terminally and laterally on an apical cell. Scale = 200 μm.
Figs 55–57. Details of tenacular cells. Scale = 50 μm.

synonyms. Consequently the monospecific genus *Scopularia*, based on *Penicillus annulatus* (= *Corallina peniculum*), is to be regarded as a synonym of *Chamaedoris*. The species has also been placed in the obscure genera *Nesaea* and *Corallocephalus* by Lamouroux (1816) and Kützing (1843), respectively. Both taxa are synonyms of the bryopsidalean genus *Penicillus* Lamarck, which has a habit that somewhat resembles that of *Chamaedoris*.

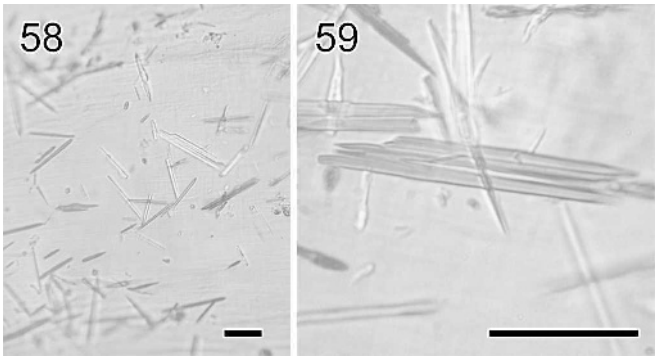
Chamaedoris orientalis Okamura & Higashi, *in* Okamura (1931, p. 98, pl. 10).

Figs 46–59

HOLOTYPE: Island of Kôtôsho (Botel Tobago Island), east of southern extremity of Taiwan, leg. Segawa (Okamura herbarium, SAP).

REFERENCES: Okamura (1932, p. 68, pl. 284, figs 8–15); Yamada (1934, pp. 48–50, fig. 11); Itono & Tsuda (1980, pp. 21, 23, fig. 1).

DESCRIPTION: Thallus forming erect, stipitate capitula, 5–20 cm high, attached to the substratum by branched, multicellular rhizoids arising from the lower pole of the stipe cells (Figs 46, 51). Stipes single to densely clustered (up to 20), single-celled, subcylindrical, generally unbranched, with annular constrictions over the entire length.



Figs 58–59. Needle-shaped calcium oxalate crystalline cell inclusions in *Struvea okamurae* (*Chamaedoris orientalis*) (GENT, HEC 12289). Scales = 20 μm.

Capitulum globose to oblong, 2–4 cm in diameter, 2.5–10 cm high. Young stipes gradually becoming annularly constricted from the base upwards. When fully grown, the distal end of the stipe cell divides (probably by segregative cell division) into a series of cells (Fig. 48), which will become the central axis of the capitulum (Figs 49, 50); later the apical cell of the central axis may redivide by segregative cell division into *c.* 14 cells. Each cell of the central axis initially produces a pair of equally developing opposite laterals (Fig. 48); later secondary lateral branches are formed, resulting in whorls of 3–6 branches (Figs 49, 50). Growth of the capitulum mainly by division of these branches, followed by cell elongation. Each new capitulum cell, after division, producing one lateral branch at its apical pole; older cells generally producing a second, opposite branch (Figs 52, 53). Cell division in the capitulum filaments presumably by centripetal invagination of the cross walls, as evidenced by the presence of basally septate single celled laterals (Fig 53, arrows). Cross wall formation of the branches delayed, with laterals in open connection with the mother cell with a length/width ratio of up to 8. In older cells, cross walls are steeply inclined to the parent cell. Branching of the capitulum filaments up to 4 orders. Structural reinforcement of the capitulum by loosely entanglement of the filaments and by occasional anastomosis of adjacent filaments by tenacular cells, which are laterally or (sub)terminally placed on apical cells (Figs 54–57). Apical cells of the capitulum filaments 320–480 μm in diameter, 2500–8800 μm long; cells of the main capitulum filaments 330–490 μm in diameter, 2000–4500 μm long; basal capitulum cells 520–680 μm in diameter, 900–

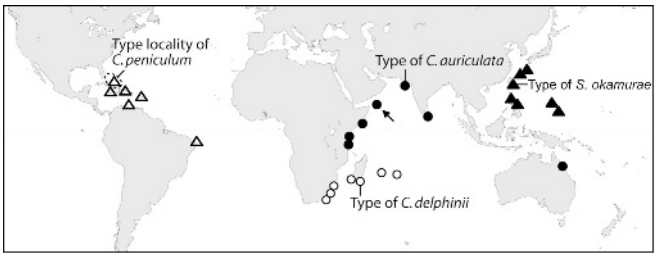


Fig. 60. Geographical distribution of *Chamaedoris auriculata*, *C. delphinii*, *C. peniculum* and *Struvea okamurae* (*Chamaedoris orientalis*) based on the investigated specimens, and verifiable literature data. Arrow indicates Socotra Island.

1300 μm long. Cells of the central axis 600–800 μm in diameter, 650–1900 μm long. Stipe cells 900–1500 μm in diameter in the middle part, slightly tapering towards both extremities, 4–7 cm long. Tenacular cells 80–100 μm in diameter, 150–250 μm long. Cell wall thickness of the capitulum filaments increasing from 2–7 μm in the terminal branch systems to 6–40 μm in the basal filaments. Cell walls of the stipe markedly stratified, up to 60 μm thick. Chloroplasts not well preserved in the herbarium material, and therefore their morphology could not be examined adequately. Prismatic calcium oxalate crystals abundant in the capitulum filaments (over 200 per cell) but absent in the stipe cell, elongate prismatic to needle-shaped, 10–30 μm long, *c.* 0.5–1.5 μm wide (Figs 58, 59). Protein crystals absent.

HABITAT AND GEOGRAPHIC DISTRIBUTION: *Chamaedoris orientalis* generally grows in the shallow subtidal (down to 6 m depth), epilithic on horizontal rock substrata. In the Island of Guam, large specimens were found in deeper subtidal regions (25–30 m depth) (Fig. 51), while in the shallow subtidal (to 4 m depth), plants were distinctly smaller (Schils, personal observations). The species seems to be restricted to the tropical West Pacific Ocean with records from near Taiwan (type locality), Ryukyu, Japan (Yamada 1934), Micronesia (Itono & Tsuda 1980), Guam (Schils, personal observations) and the Philippines (Gilbert & Doty 1969; Cordero 1977) (Appendix 1, Fig. 60).

REMARKS: The present molecular phylogeny (Fig. 2) strongly supports the evidence that *Chamaedoris orientalis* is more closely related to *Struvea plumosa*, *S. gardineri* and *S. thoracica* than to the other *Chamaedoris* species. In support of this relationship is morphological evidence where the mode of development of the capitulum is very similar to the blade formation in *Struvea* (see Discussion).

Chamaedoris orientalis differs from most *Struvea* species by the formation of a three-dimensional blade-like capitulum. We argue that this obvious difference in habit is merely a result of small differences in the number and position of branches formed by the cells of the central axis (see Discussion).

The diplohaplontic and isomorphic sexual life cycle of *C. orientalis* has been studied and illustrated by Enomoto (*in* Hori 1994).

DISCUSSION

Systematic reassessment of *Chamaedoris*

Phylogenetic studies have previously demonstrated that *Chamaedoris* is part of a clade of genera that includes *Boodlea*, *Cladophoropsis*, *Phyllodictyon*, *Struvea* and *Struveopsis* that have vague morphological boundaries (Kooistra *et al*. 1993; Leliaert *et al*. 2003). Within this genus complex, only *Chamaedoris* is morphologically easily distinguishable by the stipitate capitula, which is a unique feature in the Siphonocladales (Egerod 1952). Nevertheless, here we show that the genus is not monophyletic; *Chamaedoris orientalis* is more closely related to *Struvea* species than to the other *Chamaedoris* species, which, with the exclusion of *C. orientalis*, do form a clade of closely related species. *Chamaedoris orientalis* differs fundamentally from the other species in the genus in the development of the capitulum. In *C. auriculata*, *C. delphinii* and *C. peniculum*, either the mature stipe cell generates a small number of small cells at the distal pole by segregative cell division, from which the capitulum filaments are produced in whorls (Børgesen 1913, p. 59, fig. 41), or the capitulum filaments are formed directly from the apical pole of the stipe, without prior formation of the small superimposed cells. In *C. orientalis*, the distal end of the stipe is divided simultaneously into a series of *c.* 14 cells by segregative cell division, which will later become the central axis of the capitulum. The apical cell of the central axis may later redivide, resulting in a row of *c.* 28 cells. The cells of the central axis initially produce opposite branches in a single plane and later form secondary branches perpendicular to the initial branching plane, resulting in secondarily formed whorls of laterals. These branches will further grow, redivide and form the typical oblong capitulum (Figs 46–51). This mode of development is very similar to the blade formation in *Struvea*, which only differs in the strictly opposite branching pattern, resulting in a flat, 'unistratose' blade (Womerlsey 1984; Kraft & Wynne 1996; Leliaert & Coppejans 2007a). A three-dimensional blade-like capitulum is also not without precedent in the genus *Struvea*. Recently, Kraft & Millar (2005) described a new species, *S. thoracica*, and distinguished it from all other *Struvea* species based on a similar capitulum. In that species, however, branching of blade cells remains strictly opposite, and the 'three-dimensional' blade in mature plants is formed by the irregular filling in of spaces between the branched filaments, whereas in *C. orientalis*, the three-dimensional capitulum is formed by whorled branching of the main axes (Figs 47–49). Thus, the presence of secondary branches developing from the main axis in *C. orientalis* results in an apparent difference in thallus architecture (formation of a three-dimensional capitulum). Similarly, it has been shown that the apparent differences in thallus architecture between *Phyllodictyon* (stipitate blades) and *Boodlea* (cushion-like thalli) are mainly a result of small variations in branching pattern (Leliaert & Coppejans 2007b). In a phylogenetic study of the Udoteaceae, Kooistra (2002) revealed an analogous situation in which relatively simple anatomical changes result in diverse thallus architectures, on which the generic circumscriptions are largely based. The common taxonomic outcome of these examples is the presence of nonmonophyletic genera. In our opinion, the present molecular and developmental-morphological data provide enough evidence to warrant the transfer of *Chamaedoris orientalis* to *Struvea*. In doing so, a new epithet must be chosen because of the existence of *Struvea orientalis* A. Gepp & E. Gepp (1908), which, incidentally, has since been transferred to the genus *Phyllodictyon* as *P. orientale* Kraft & Wynne (1996):

Struvea okamurae Leliaert, *nom. nov.*

REPLACED NAME: *Chamaedoris orientalis* Okamura & Higashi, *in* Okamura (1931, p. 98, pl. 10).

ETYMOLOGY: The epithet honours Kintaro Okamura (1867–1935), who first described this species and who also devoted his scientific career to the study of Japanese seaweeds.

With the inclusion of *S. okamurae* in the genus *Struvea*, the generic character traits require a revision, and we thus offer the following emended generic circumscription:

Struvea Sonder, 1845: 49, *emend.* Leliaert

TYPE SPECIES: *Struvea plumosa* Sonder, 1845, p. 50.

DESCRIPTION: Thallus forming erect stipitate blades or capitula, composed of densely branched filaments, attached to the substratum by branching rhizoids developing from the base of the stipe. Stipes generally unbranched with annular constrictions. Young thalli consisting of an unbranched stipe composed of a single cell. When reaching its full size, the distal end of the stipe is divided simultaneously into a series of 6–22 cells (later becoming the cells of the central axis of the blade or capitulum). Each cell of the central axis initially producing a pair of equally developing opposite laterals which elongate and form the primary laterals. Cell division in the blade or capitulum filaments segregative or by centripetal invagination of the cross walls. Branching pattern in young thalli very regular and in a single plane, in some species becoming irregular or three-dimensional in older plants. Structural reinforcement of the blade or capitulum by tenacular cells connecting adjacent filaments.

SPECIES INCLUDED: *S. elegans* Børgesen, *S. gardineri* A. Gepp & E. Gepp, *S. okamurae* Leliaert, *S. plumosa* Sonder and *S. thoracica* Kraft & A. Millar.

In their reassessment of the genera *Struvea* and *Phyllodictyon*, Kraft & Wynne (1996) distinguished the two genera on the basis of the different modes of cell division: *Struvea* includes those species in which cells divide exclusively by a process of segregative cell division, and *Phyllodictyon* encompasses taxa in which cells only divide by centripetal invagination (CI) of the cell wall. However, it has been recently documented that in *S. gardineri* the mode of cell division is segregative in the initial stages of thallus development, whereas in older blades, cells divide exclusively by CI (Leliaert & Coppejans 2007a). Similarly in *S. okamurae*, cell division in the stipe is most probably segregative (as evidenced by the simultaneous formation of a series of new cells), while the cell division of the capitulum filaments are presumably by centripetal invagination of the cell wall, indicated by the presence of basally septate single-celled laterals.

Based on the present phylogeny (Fig. 2) we could hypothesise that the common ancestor of *Chamaedoris* and allied genera had a *Struvea*-like thallus architecture, characterized by stipitate, reticulate blades composed of filaments with a regular opposite branching pattern. Variations on this type of thallus architecture have been maintained in the *Struvea*-clade, in *Struvea elegans*, *Phyllodictyon orientale* and the clade containing *P. anastomosans*. In *Chamaedoris*, this stipitate, reticulate blade then evolved to a stipitate three-dimensional capitulum, composed of unilaterally branching and entangling filaments. The loss of a regular opposite branching pattern also occurred independently in the *Cladophoropsis* species and to some extent in *Struvea okamurae*.

Delineation of *Chamaedoris auriculata, C. delphinii* and *C. peniculum*

Although the *Chamaedoris* species *C. auriculata*, *C. delphinii* and *C. peniculum* appear to be clearly delineated, based on differences in the shape of the capitulum and number of superimposed cells on the stipe (Børgesen 1933, 1940; Littler & Littler 2000; Coppejans *et al.* 2005), the identification of some specimens from the Indian Ocean has proven to be problematic because of intermediate character states. Moreover, the original circumscriptions of the three taxa are in disagreement with the present molecular phylogeny based on rDNA ITS1 sequences. Although the ITS tree reveals three distinct clades (Caribbean Sea, South Africa and Socotra clade), the two Indian Ocean clades consist of a mixture of specimens belonging to *C. auriculata* (characterized by a flat capitulum and 1–3 superimposed cells on the stipe) and *C. delphinii* (characterized by a globose capitulum and without superimposed cells) (Fig. 3). This indicates that the morphological features used to delimit the species within *Chamaedoris* until now are not diagnostic and that the traditional species delineations of especially *C. auriculata* and *C. delphinii* need to be reassessed. Morphometric analyses reveal that more subtle differences exist between the two Indian Ocean clades. The width of the capitulum filaments (more precisely the mean diameter of the intermediate and apical cells) is significantly larger in specimens of the South Africa clade than in those in the Socotra clade. Morphological examination of a large number of specimens from the western Indian Ocean shows that this discontinuity in cell dimensions equally holds between specimens from India (type of *C. auriculata*), Sri Lanka, Socotra, the African East coast from Somalia to northern Mozambique and specimens from Madagascar (type of *C. delphinii*), South Africa, southern Mozambique, Mauritius and Rodrigues. We therefore feel confident in considering cell diameter as a more reliable diagnostic character to distinguish *C. auriculata* from *C. delphinii*. The newly circumscribed species moreover seem to be restricted to well-defined, geographical regions, without overlap (Fig. 60). Although the cell dimensions of *C. peniculum* fall within the limits of *C. delphinii*, this Caribbean species can be distinguished by a flat, peltate capitulum and additionally by the presence of diamond-shaped calcium oxalate crystals in the capitulum filaments and the absence of tetrahedral protein crystals in the stipe cell.

The separation of Indian Ocean species (*C. auriculata* and *C. delphinii*) from the Atlantic *C. peniculum* in our phylogenetic trees (Figs 2, 3, 60) suggests a vicariance event, possibly coinciding with the closure of the Tethys Sea. The subsequent split between the two Indian Ocean species might have originated from an ecological differentiation leading to a tropical (*C. auriculata*) and subtropical (*C. delphinii*) lineage. It should be noted, however, that the establishment a credible hypothesis of historical biogeography of *Chamaedoris* is hampered by the unknown age of the genus.

ACKNOWLEDGEMENTS

We sincerely thank Tom Schils, Olivier De Clerck, Heroen Verbruggen, Christian Boedeker, Olivier Dargent and Herre Stegenga for collecting specimens. John West, Jeanine Olsen and Wytze Stam are gratefully acknowledged for providing cultures of *Apjohnia laetevirens*, *Phyllodictyon orientale* and *Struvea elegans*. We are grateful to Ruth Nielsen (C), Willem Prud'homme van Reine (L), Ellen Bloch (NY), Bruno de Reviers (PC), Marianne Hamnede (S) and Michio Masuda (SAP) for loans and information on collections. The authors greatly appreciate the editorial efforts of David Ballantine and two anonymous reviewers. This research was funded by FWO-Flanders (grants G.0136.01 and G.0142.05) and the Flemish Government (bilateral research grant 01/46). FL is indebted to BOF (Ghent University) for a postdoctoral fellowship grant.

REFERENCES

Bakker F.T., Olsen J.L., Stam W.T. & van den Hoek C. 1994. The Cladophora complex (Chlorophyta): new views based on 18S rRNA gene sequences. *Molecular Phylogenetics and Evolution* 3: 365–382.

Børgesen F. 1912. Some Chlorophyceae from the Danish West Indies. II. *Botanisk Tidsskrift* 32: 241–273.

Børgesen F. 1913. The marine algae of the Danish West Indies. Part 1. Chlorophyceae. *Dansk Botanisk Arkiv* 1(4): 158.

Børgesen F. 1933. Some Indian green and brown algae especially from the shores of the Presidency of Bombay. III. *Journal of the Indian Botanical Society* 12: 1–16.

Børgesen F. 1940. Some marine algae from Mauritius. I. Chlorophyceae. *Kongelige Danske Videnskabernes Selskab, Biologiske Meddelelser* 15(4): 81.

Chamberlain Y.M. & Norris R.E. 1994. *Pneophyllum amplexifrons* (Harvey) comb. nov., a mastophoroid crustose coralline red algal epiphyte from Natal, South Africa. *Phycologia* 33: 8–18.

Chauvin J.F. 1842. Essai d'une répartition des polypiers calcifères de Lamouroux. In: *Recherches sur l'organisation, la fructification et la clasification de plusieurs genres d'algues* (Ed. by J.F. Chauvin), 132 pp. A Hardel, Caen.

Coppejans E., Leliaert F. & De Clerck O. 2000. Annotated list of new records of marine macroalgae for Kenya and Tanzania, since Isaac's and Jaasund's publications. *Biologisch Jaarboek Dodonaea* 67: 31–93.

Coppejans E., Leliaert F. & Verbruggen H. 2005. Green algae. In: *Guide to the seaweeds of KwaZulu-Natal* (Ed. by O. De Clerck, J.J. Bolton, R.J. Anderson & E. Coppejans), pp. 39–93. *Scripta Botanica Belgica* 33.

Cordero P.A. Jr. 1977. The marine algae of Batan Island, Northern Philippines, II: Chlorophyceae. *Fisheries Research Journal of the Philippines* 2: 19–55.

Dixon P.S. 1960. Notes on important algal herbaria, II. The herbarium of John Ellis (?1710–1776). *British Phycological Bulletin* 2: 28–31.

Egerod L.E. 1952. An analysis of the siphonous Chlorophycophyta with special reference to the Siphonocladales, Siphonales, and Dasycladales of Hawaii. *University of California Publications in Botany* 25: 327–367.

Ellis J. & Solander D. 1786. *The natural history of many curious and uncommon zoophytes, collected from various parts of the globe by the late John Ellis. Systematically arranged and described by the late Daniel Solander*. London. 208 pp.

Farris J.S., Källersjö M., Kluge A.G. & Bult C. 1995. Constructing a significance test for incongruence. *Systematic Biology* 44: 570–572.

Gepp A. & Gepp E.S. 1908. Marine algae (Chlorophyceae and Phaeophyceae) and marine phanerogams of the "Sealark" Expedition, collected by J. Stanley Gardiner, M.A., F.R.S., F.L.S. *Transactions of the Linnean Society of London, Second Series, Botany* 7: 163–188.

Gerloff J. 1960. Meeresalgen aus Kenya. I. Cyanophyta und Chlorophyta. *Willdenowia* 2: 604–627.

Gilbert W.J. & Doty M.S. 1969. Some additional records of Philippine marine Chlorophyta. *Micronesica* 5: 121–130.

Hariot P. 1902. Quelques algues de Madagascar. *Bulletin du Muséum d'Histoire Naturelle (Paris)* 8: 470–472.

Holmgren P.K., Holmgren N.H. & Barnett L.C. 1990. *Index herbariorum. Part I: The herbaria of the world,* ed. 8 New York Botanical Garden, New York. 693 pp.

Hori T. 1994. *An illustrated atlas of the life history of algae. Volume 1. Green algae* Uchida Rokakuho Publishing Co., Ltd, Tokyo. 367 pp.

Index Nominum Algarum. University Herbarium, University of California, Berkeley, Compiled by Paul SilvaAvailable at: http://ucjeps.berkeley.edu/INA.html (7 September 2007).

International Code of Botanical Nomenclature (Vienna Code, 2006). *Regnum Vegetabile* 146. Ruggell: A.R.G. Gantner Verlag KG.

Isaac W.E. 1956. Marine algae of Inhaca Island and of the Inhaca Peninsula. I. *Journal of South African Botany* 22: 161–193.

Isaac W.E. 1967. Marine botany of the Kenya coast 1: a first list of Kenya marine algae. *Journal of East Africa Natural History Society* 26: 75–83.

Itono H. & Tsuda R.T. 1980. New algal genera and species records from Micronesia: *Chamaedoris orientalis* (Chlorophyta) and *Rhodopeltis gracilis* (Rhodophyta). *Micronesica* 16: 21–27.

Jaasund E. 1976. *Intertidal seaweeds in Tanzania* University of Tromsø, Tromsø. 159 pp.

Kooistra W.H.C.F. 2002. Molecular phylogenies of Udoteaceae (Bryopsidales, Chlorophyta) reveal nonmonophyly for *Udotea*, *Penicillus* and *Chlorodesmis*. *Phycologia* 41: 453–462.

Kooistra W.H.C.F., Olsen J.L., Stam W.T. & van den Hoek C. 1993. Problems relating to species sampling in phylogenetic studies: an example of non-monophyly in *Cladophoropsis* and *Struvea* (Siphonocladales, Chlorophyta). *Phycologia* 32: 419–428.

Kraft G.T. & Millar A.J.K. 2005. *Struvea thoracica* sp. nov. (Cladophorophyceae), a new deep-water chlorophyte from the Great Barrier Reef and New Caledonia. *Phycologia* 44: 305–311.

Kraft G.T. & Wynne M.J. 1996. Delineation of the genera *Struvea* Sonder and *Phyllodictyon* J.E. Gray (Cladophorales, Chlorophyta). *Phycological Research* 44: 129–143.

Kuntze O. 1898. *Revisio generum plantarum.* Part 3. Leipzig. 576 pp.

Kützing F.T. 1843. *Phycologia generalis*. Leipzig. 458 pp.

Lamarck J.B. de. 1813. Sur les polypiers empâtés. *Annales du Muséum d'Histoire Naturelle (Paris)* 20: 294–312, 370–386, 432–458.

Lamouroux J.V.F. 1816. *Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes*. Caen. 559 pp.

Leliaert F. & Coppejans E. 2004. Crystalline cell inclusions: a new diagnostic character in the Cladophorophyceae (Chlorophyta). *Phycologia* 43: 189–203.

Leliaert F. & Coppejans E. 2007a. Systematics of two deep-water species from the Indo-West Pacific: *Struvea gardineri* A.Gepp & E.Gepp and *Phyllodictyon orientale* (A.Gepp & E.Gepp) Kraft & M.J.Wynne (Siphonocladales, Chlorophyta). *Botanical Journal of the Linnean Society* 153: 115–132.

Leliaert F. & Coppejans E. 2007b. Morphological re-assessment of the *Boodlea composita-Phyllodictyon anastomosans* species complex (Siphonocladales: Chlorophyta). *Australian Systematic Botany* 20: 161–185.

Leliaert F., Rousseau F., de Reviers B. & Coppejans E. 2003. Phylogeny of the Cladophorophyceae (Chlorophyta) inferred from partial LSU rRNA gene sequences: is the recognition of a separate order Siphonocladales justified? *European Journal of Phycology* 38: 233–246.

Leliaert F., De Clerck O., Verbruggen H., Boedeker , C. & Coppejans E. 2007. Molecular phylogeny of the Siphonocladales (Chlorophyta: Cladophorophyceae). *Molecular Phylogenetics and Evolution.* 44: 1237–1256.

LITTLER D.S. & LITTLER M.M. 2000. *Caribbean reef plants: an identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico.* Offshore Graphics, Washington. 542 pp.

LÖYTYNOJA A. & MILINKOVITCH M.C. 2001. SOAP, cleaning multiple alignments from unstable blocks. *Bioinformatics* 17: 573–574.

MILLAR A.J.K. 1999. Marine benthic algae of North East Herald Cay, Coral Sea, South Pacific. *Proceedings of the International Seaweed Symposium* 16: 65–74.

MONTAGNE C. 1842. *Prodromus generum specierumque phycearum novarum, in itinere ad polum antarcticum collectarum.* Parisiis (Paris). 16 pp.

NYLANDER J.A.A. 2004. MrModeltest v2., Evolutionary Biology Centre, Uppsala University, Available at: http://www.abc.se/~nylander/ (7 September 2007).

OKAMURA K. 1931. On the marine algae from Kôtôsho (Botel Tobago). *Bulletin of the Biogeographical Society of Japan* 2: 95–122.

OKAMURA K. 1932. *Icones of Japanese algae Vol. VI, Fasc. VII.* Tokyo. pp. 63–101 (English), 61–96 (Japanese), pls. CCLXXXI–CCC.

OLSEN-STOJKOVICH J., WEST J.A. & LOWENSTEIN J.M. 1986. Phylogenetics and biogeography in the Cladophorales complex (Chlorophyta): some insights from immunological distance data. *Botanica Marina* 29: 239–249.

PAPENFUSS G.F. 1952. Notes on South African marine algae. III. *Journal of South African Botany* 17: 167–188.

POSADA D. & CRANDALL K.A. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

RONQUIST F. & HUELSENBECK J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

SARTONI G. 1992. Research on the marine algae of South-central Somalia. 3. The Siphonocladales-Cladophorales complex. *Webbia* 46: 291–326.

SHIMODAIRA H. & HASEGAWA M. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* 16: 1114–1116.

SONDER O.G. 1845. Nova algarum genera et species, quas in itinere ad oras occidentales Novae Hollandiae, collegit L. Preiss, Ph. Dr. *Botanische Zeitung* 3: 49–57.

SWOFFORD D.L. 2002. *PAUP*: phylogenetic analysis using parsimony (*and other methods). Version 4* Sinauer Associates, Sunderland, Massachusetts.

TAYLOR W.R. 1960. *Marine algae of the eastern tropical and subtropical coasts of the Americas.* The University of Michigan Press, Ann Arbor. 870 pp.

VAN DER STRATE H.J., BOELE-BOS S.A., OLSEN J.L., VAN DE ZANDE L. & STAM W.T. 2002. Phylogeographic studies in the tropical seaweed *Cladophoropsis membranacea* (Chlorophyta, Ulvophyceae) reveal a cryptic species complex. *Journal of Phycology* 38: 572–582.

WOMERSLEY H.B.S. 1984. The marine benthic flora of southern Australia. Part I. Government Printer, South Australia, Adelaide. 329 pp.

YAMADA Y. 1934. The marine Chlorophyceae from Ryukyu, especially from the vicinity of Nawa. *Journal of the Faculty of Science, Hokkaido Imperial University, Series V, Botany* 3: 33–88.

Received 2 July 2007; accepted 14 August 2007
Associate editor: David Ballantine

APPENDIX 1.
SPECIMENS EXAMINED MORPHOLOGICALLY.

Chamaedoris auriculata Børgesen – **Indian Ocean: India.** Dwarka (leg. Børgesen 5447, 1927–1928, C: holotype *Chamaedoris auriculata*); **Kenya.** Kanamai, shallow subtidal, 1 m deep, outer side of the reef (leg. Coppejans, 13.ix.1991, HEC 8760); Nyali Reef, Mombasa, subtidal, wave exposed seaward side of the reef, epilithic (leg. Coppejans, 26.ix.1991, HEC 8877); Kanamai (leg. Coppejans, 29.vii.1987, HEC 7032); Mambrui, 10 km N of Malindi (leg. Coppejans, 27.xii.1988, HEC 8169); **Mozambique.** Praia Chokas, N of Lumbo (leg. Papenfuss & Scagel PR-28-6, 15.xi.1962, L 385004); **Sri Lanka.** unknown locality (leg. Pike, 1861, NY); **Tanzania.** Chole Bay, Mafia Island, infralittoral fringe, horizontal coral substratum (leg. Coppejans & De Clerck, 9.i.1996, HEC 11155); Ras Fumba, Zanzibar, shallow subtidal, 1 m deep, epilithic on vertical coral walls (leg. Coppejans & De Clerck, 25.viii.1994, HEC 10635); Nungwi, Zanzibar, shallow subtidal, 5 m deep, seaward side of the reef (leg. Coppejans & De Clerck, 23.viii.1994, HEC 10556); in front of Bahari Beach Hotel, Kunduchi, N of Dar es Salaam, shallow subtidal, 2 m deep, epilithic on rock covered with *Jania*, in *Thalassodendron* bed (leg. Coppejans & De Clerck, 3.i.1996, HEC 11046); in front of Sea Safari Lodge, Ruvula beach, Mnazi Bay, Mtwara area, subtidal, 18 m deep, on coral fragments (leg. Coppejans *et al.*, 24.vii.2000, HEC 12880; 9.viii.2000, HEC 14201); Ruvula beach, Mnazi Bay, shallow subtidal, 3 m deep, epiphytic on a *Thalassodendron* stem (leg. Coppejans *et al.*, 13.viii.2000, HEC 14241); S coast of Mbutya Island, shallow subtidal, 4 m deep, epiphytic on *Thalassodendron* stem (leg. Leliaert, 11.vii.2001, FL 906); Kunduchi, N of Dar es Salaam, shallow subtidal, wave exposed, epilithic (leg. Dargent, 5.viii.1997, HEC 12178); **Yemen.** W of Rhiy di-Diblih, Nogid, S coast of Socotra, subtidal, 6 m deep, epilithic on sand covered rock, between dense seaweed vegetation (leg. Leliaert, 15.iii.1999, SOC 344, SOC 398); Mahfirhin, Socotra, subtidal, 10 m deep, epilithic on sand covered rock (leg. Leliaert, 16.iii.1999, SOC 438); Steroh, Nogid, S coast of Socotra, subtidal, 15 m deep, epilithic (leg. Leliaert, 14.iii.1999, SOC 370); 3 km W of Bidholih, Nogid, S coast of Socotra, subtidal, 15 m deep, epilithic on horizontal rock (leg. Leliaert, 14.iii.1999, SOC 395, SOC 396); Ghubbah di-Net, SW coast of Socotra, subtidal, 6 m deep, epilithic on vertical rock wall (leg. Leliaert, 3.iii.1999, SOC 273); Nogid, S coast of Socotra (leg. Schils, sMM476); Quray, East of Qatanhin, Socotra (leg. Schils, 9.iv.2000, sMM 226, sMM 239); East of Bedolah, Socotra (leg. Schils, 1.v.2000, sMM 476); Bay of Mahfirin, Socotra, subtidal (leg. Schils, 22.iv.2000, sMM 349, sMM 394); West of Bedolah, Socotra (leg. Schils, 30.iv.2000, sMM 466). **Pacific Ocean: Australia.** North East Herald Cay, Coral Sea (Millar & Christian, 26.vi.1997, NSW 415041).

Chamaedoris delphinii (Hariot) J. Feldmann & Børgesen – **Indian Ocean: Madagascar.** Balise, N of Tuléar, subtidal, 15 m deep, on horizontal rock substratum (leg. Coppejans *et al.*, 20.viii.2002, HEC 15087); Fort-Dauphin (leg. Ferlus s.n., PC: holotype *Chamaedoris delphinii*); Plage de Monseigneur, Fort Dauphin, low intertidal rock pools, epilithic on horizontal rock substratum (leg. Coppejans *et al.*, 31.viii.2002, HEC 15236); unknown locality (leg. Børgesen s.n., C); **Mauritius.** Unknown locality (unknown collector, NY); **Mozambique.** Ponta Abril, Inhaca Peninsula (leg. Isaac 699, 22.vii.1956, L 095901); Santa Maria, near Inhaca Island (leg. Isaac 146, 19.vi.1954, L 095898); **Rodrigues.** Cotton Bay, mid intertidal rock pools, epilithic on vertical

walls (leg. Coppejans, 18.ix.2001, HEC 14617); **South Africa.** Bluff, Durban, KwaZulu-Natal (leg. Weber-van Bosse s.n., 1894, L 936 73 446); Durban (unknown collector, S); Durban, KwaZulu-Natal (leg. Krauss 326.1, BR); Durban, KwaZulu-Natal (leg. Weber-van Bosse s.n., 1894, BR); Isipingo, KwaZulu-Natal (leg. Weber-van Bosse s.n., 1894, L 936 73 463; 1894, NY; xi.1894, BR); Isipingo, KwaZulu-Natal, mid- to low intertidal pools, epilithic on vertical walls (leg. Coppejans, 21.i.1995, HEC 10945); Linkia Reef, subtidal, 15 m deep, epilithic, as '*C. auriculata*' (leg. Coppejans *et al.*, 15.viii.1999, KZN 0694); Kosi Bay, KwaZulu-Natal, intertidal rock pools, as '*C. auriculata*' (leg. Coppejans *et al.*, 16.viii.1999, KZN 0765); Bhanga Nek, KwaZulu-Natal, intertidal, as '*C. auriculata*' (leg. Coppejans *et al.*, 15.viii.1999, KZN 0710); Treasure Beach, Bluff, Durban, KwaZulu-Natal, infralittoral fringe rock pools, epilithic on vertical & overhanging walls, as '*C. auriculata*' (leg. Coppejans *et al.*, 3.viii.1999, KZN 0083); Island Rock, KwaZulu-Natal, intertidal rock pools (leg. De Clerck & Cocquyt, 14.viii.2000, KZN 1704); Kosi Bay, KwaZulu-Natal, intertidal rock pools (leg. Coppejans *et al.*, 16.viii.1999, KZN 0763); Mabibi, KwaZulu-Natal, infralittoral fringe rock pools (leg. Coppejans *et al.*, 9.viii.1999, KZN 0372; leg. De Clerck & Cocquyt, 13.viii.2000, KZN 1652); Mission rocks, KwaZulu-Natal, intertidal rock pools (leg. De Clerck & Cocquyt, 17.viii.2000, KZN 1765); Mission Rocks, KwaZulu-Natal, mid- to low intertidal pools, epilithic on vertical walls (leg. Coppejans, 23.xi.1995, HEC 11028.1); Mission Rocks, KwaZulu-Natal, shallow subtidal (leg. Bolton, 8.vii.1998, KZN 1047); Palm Beach, KwaZulu-Natal, intertidal rock pools (leg. Coppejans *et al.*, 19.viii.1999, KZN 0853); Palm Beach, KwaZulu-Natal, intertidal rock pools (leg. Coppejans *et al.*, 19.viii.1999, KZN 0839); Rabbit Rock, intertidal (leg. Coppejans *et al.*, 13.viii.1999, KZN 0541); Rabbit Rock, intertidal (leg. Coppejans *et al.*, 13.viii.1999, KZN 0539); Sodwana Bay, 2 Mile Reef, KwaZulu-Natal, subtidal, 12 m deep (leg. De Clerck & Leliaert, 10.ii.2001, KZN 2110); Sodwana Bay, KwaZulu-Natal, intertidal pools (leg. Coppejans *et al.*, 8.viii.1999, KZN 0215); St. Lucia, KwaZulu-Natal (unknown collector, BR); Wahlberg (unknown collector, S); KwaZulu-Natal (leg. Anderson, s.n.).

Chamaedoris peniculum (Ellis & Solander) Kuntze – **Atlantic Ocean: Brazil.** Pernambuco (unknown collector, 1844–1845, S); **Carribean Sea: Bahamas.** Cave Cays, under rock overhang at low tide mark (leg. Howe 4005, 28.iii.1903, NY); Stella Maris Estate, Long Island (leg. Coppejans, 20.viii.1982, HEC 5032); **Barbados.** Bath (leg. Vickers 34, 13.ii.1899, NY; leg. Vickers s.n., 24.i.1899, BR); Bathsheba, W coast of Barbados (leg. Diaz-Piferrer 17537, 26.x.1966, NY); Kendal Point (leg. Vickers s.n., ii.1899, BR); unknown locality (leg. Vickers 34, L 937 183 160; leg. Vickers s.n., ii.1899, L 937 183 163); **Curaçao.** Boca Ascension, low intertidal, under overhanging rock (leg. Vroman s.n., 23.iv.1958, L 7665); **Dominican Republic.** Puerto Plata, infralittoral fringe, epilithic (leg. Dargent & Bel, 8.ii.2002, HOD RD 2-02-45); Rio San Juan, Laguna Gri-Gri, infralittoral fringe, epilithic (leg. Dargent & Bel, 13.ii.2002, HOD RD 08-02-16); **Jamaica.** Marant Bay (leg. Pease & Butler s.n., vii.1894, NY); Port Antonio (leg. Pease & Butler s.n., vii.1894, NY); Pt. Morant, drift (leg. Howe 6154, 8.iii.1909, NY); **Puerto Rico.** E of Guanica Harbour, dredged 40–50 m deep (leg. Howe 7091, 28.iii.1903, NY); Guanica, epilithic, 4.5 m deep (leg. Almodovar 4454, 28.iii.1962, NY); Muertos Island (leg. Howe 7530, 8.vii.1915, BR); San Juan, drift (leg. Howe 2218, 28.iii.1903, NY; leg. Howe 4430, 25.iii.1906, NY); **Santo Domingo.** Bahia Escosesa, Nagua (leg. Almodovar 7481, 10.vi.1976, NY); **St. Croix**. The Beach of White Bay (leg. Børgesen 1575, 9.ii.1906, NY); White Bay (leg. Børgesen 1530, 7.ii.1906, L 937 183 187; leg. Børgesen 1575, L 937 183 180); **St. Jan**. Cruz Bay (leg. Børgesen 2155, 26.iii.1906, NY); **Gulf of Mexico: USA.** Key West, Florida (leg. Hall 626, v.1897, NY; leg. Hall 629, iv.1897, BR); Key West, Florida (leg. Howe 1650, 8.xi.1902, NY); Loggerhead Key, Dry Tortugas, Florida (leg. Taylor 83, 7.xii.1924, NY).

Struvea okamurae Leliaert (***Chamaedoris orientalis*** Okamura & Higashi) – **Pacific Ocean: Japan.** Yonakuni Island, Ryukyu (unknown collector, 15.iv.1935, NY); Yonakuni-jima, Ryukyu (leg. Yamada s.n., 15.iv.1935, S); **The Philippines.** Dancalan, Bulusan, Sorsogon Province (leg. Coppejans, 21.iv.1998, HEC 12289); Dapdap, Bulusan, Sorsogon Province, shallow subtidal, 6 m deep, epilithic on horizontal rock substratum of lagoon (leg. Coppejans, 22.iv.1998, HEC 12301); **Guam.** Pago Bay, 25–30 m deep, very abundant in reef gulleys (leg. T. Schils, 10.v.2007, GUAM 00102); Pago Bay, 4–15 m deep (leg. T. Schils, 10.v.2007, GUAM 00103).