Taxonomic composition of epiphytic diatoms (Bacillariophyta) from areas affected by invasive macroalgae Caulerpa Taxifolia (Vahl) C. Agardh and Caulerpa Racemosa (Forsskäl) J. Agardh (Adriatic sea, Croatia)

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DOCTORAL THESIS

Supervisors:
Prof. Andrzej Witkowski, PhD
Prof. Nenad Jasprica, PhD

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Morske bentoske dijatomeje u Jadranu su slabo poznate. Istraživanja u okviru disertacije su usmjerena na taksonomski sastav epifitskih dijatomeja u područjima invazivnih makroalgi roda *Caulerpa* uz istočnu obalu Jadrana. Materijal je sakupljan tijekom dvije godine (jesen 2008 – jesen 2010) u području s *Caulerpa taxifolia* u Starigradskom zaljevu na otoku Hvaru, te u područjima zahvaćenim makroalgom *Caulerpa racemosa* u Dubrovniku i u uvali Gonoturska na otoku Mljetu. Na istim su postajama istovremeno prikupljani uzorci autohtonih smeđih i zelenih algi radi analize odnosa epifitskih dijatomeja i domaćina. Pomoću svjetlosne i elektronske mikroskopije, po prvi se put u srednjem i južnom Jadranu odredio taksonomski sastav dijatomeja, opisala morfologija i ultrastruktura pojedinih vrsta te utvrdila sezonska na finoj vremenskoj skali. Dobivene spoznaje doprinjele su poznavanju bentoskih dijatomeja u Jadranu, ali i globalne biogeografske rasprostranjenosti dijatomeja (korologiji). Dobiveni rezultati omogućit će bolje razumijevanje funkcioniranja ekosustava u kojima dominiraju makroalge *Caulerpa* spp.. Saznanja o taksonomskom sastavu dijatomeja u područjima s *Caulerpa* spp. važna su za istraživanja toksičnog učinka domaćina.

(294 stranice, 113 slika, 42 tablica, 90 priloga, 142 literaturnih navoda, izvornik na engleskom jeziku)

Ključne riječi: morske epifitske dijatomeje, ‘alga ubojica’, *Caulerpa taxifolia, Caulerpa racemosa, Cocconeis caulerpacola*, Jadransko more, morfologija, taksonomija, ultrastruktura valvi, obraštaj, sukcesija

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TAXONOMIC COMPOSITION OF EPIPHYTIC DIATOMS (BACILLARIOPHYTA) FROM AREAS AFFECTED BY INVASIVE MACROALGAE *CAULERPA TAXIFOLIA* (VAHL) C. AGARDH AND *CAULERPA RACEMOSA* (FORSSKÅL) J. AGARDH (ADRIATIC SEA, CROATIA)

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There is a considerable lack of data on marine benthic diatoms in the Adriatic. In response to this fact the present study has been undertaken which focuses on the taxonomy of epiphytic diatoms in areas affected by invasive macroalgae representing the the genus of Caulerpa J.V. Lamouroux, 1809 on the eastern Adriatic Sea coast. Material for the study of epiphytic diatoms was collected during two years (autumn 2008 – autumn 2010) from an area influenced by *Caulerpa taxifolia* in the bay of Stari Grad (the Island of Hvar), and from areas influenced by *Caulerpa racemosa* in Dubrovnik and on the Island of Mljet (Gonoturska Bay). In order to compare epiphyte assemblages, sampling of coexisting autochthonous brown and green algae was conducted at the same stations. Light and electron microscopy examinations provide for the first time the information on the general morphology and ultrastructure of taxa, and enable a determination of the taxonomy of diatoms. The seasonal dynamics were described on a fine time scale. For the first time in the Central and Southern Adriatic Sea the composition of benthic diatoms and seasonal dynamics of taxa in areas affected by invasive macroalge *Caulerpa taxifolia* and *Caulerpa racemosa* were determined. The results of the presented PhD thesis contribute to the knowledge of benthic diatoms in the Adriatic, as well as of a global biogeographic distribution of diatoms (chorology). The results of this study will enable a better understanding of the functioning of ecosystems dominated by macroalgae *Caulerpa* spp. Knowledge of the diatom community structure in the areas impacted by *Caulerpa* spp. is important for studies of the toxic effects of the host.

(294 pages, 113 figures, 42 tables, 90 appendices, 142 references, original in English language)

Key words: marine epiphytic diatoms, ‘killer seaweed’, *Caulerpa taxifolia*, *Caulerpa racemosa*, *Cocconeis caulerpacola*, Adriatic Sea, biofouling, succession diatom morphology and taxonomy, valve ultrastructure,

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PROŠIRENI SAŽETAK

Dijatomeje (Bacillariophyta) su jednostanične eukariotske mikroalge odgovorne za oko 25% globalne primarne produkcije (Werner, 1977). Prisutne su na svim vlažnim mjestima, u moru, u bočatoj i slatkoj vodi. Građene su od „kućice“ (frustule) od opala (hidratizirani amorfni silicijev dioksid), a razmnožavaju se vegetativno uzastopnim diobama stanica. Poznato je i opisano tek oko 10 000 fosilnih I recentnih vrsta, ali se pretpostavlja da ih ima oko 100 000. Najveći broj vrsta dijatomeja su kozmopoliti, ali biogeografska klasifikacija dijatomeja na regionalne skupine ukazuje da postoje vrste karakteristične za određeno područje. S obzirom na ravninu simetrije razlikujemo dvije glavne skupine dijatomeja: centrice koje imaju radijalnu simetriju i pretežno su planktonski oblici, i penate koje imaju bilateralnu simetriju i prevladavaju u bentosu. Kod dijatomeja s bilateralnom simetrijom može se javljati uzdužni prorez (rapha), i to kroz jednu ili obje valve, te se stoga dijele na monorafidne i birafidne. Općenito, rafidne dijatomeje su među najranijim i najzastupljenijim primarnim kolonizatorima prirodnih i umjetnih podloga (Hoagland et al., 1986), a kontakt između citoplazme rafidne dijatomeje i podloge javlja se uz rafu (Round et al., 1990).

Bentoske mikroalge koloniziraju široki raspon supstrata te se javljaju pričvršćene na stijenama (epilitske), biljkama (epifitske), životinjama (epizoične) ili bilo kojem drugom supstratu, gdje mogu stvarati zajednice sa različitim udjelom pojedinih vrsta i time utjecati na bioraznolikost (Totti et al., 2007). Struktura epifitske zajednice može biti pod utjecajem različitih čimbenika okoliša, kao što je starost lista i sezonski ciklus biljke ili dubina vode (De Stefano et al., 2000).

Epifitske zajednice dijatomeja na morskoj cvjetnici *Posidonia oceanica* (L.) Delile su jedne od najtemeljitije istraženih. Na svim dubinama gdje se pojavljuje *Posidonia* dominiraju vrste roda *Cocconeis* tijekom svih godišnjih doba (Mazzella et al., 1994; De Stefano et al., 2000). De Stefano i sur. (2000) su našli osam vrsta roda *Cocconeis* na listovima *P. oceanica*. Neke od njih mogu stvarati gusti, gotovo monospecifični sloj (Mazzella et al., 1994). Iako postoje opsežne studije o epifitskim zajednicama na listovima *P. oceanica*, nedostaju studije o strukturi i sastavu zajednice dijatomeja vezane za morske zelene makroalge roda *Caulerpa* spp. (Bryopsidales, Chlorophyta), koje se u Mediteranu iznimno brzo šire istiskujući autohtone organizme, pa i sam endem *P. oceanica*, što ima za posljedicu narušavanje kompletnog ekosustava.

Caulerpa taxifolia i *Caulerpa racemosa* stvaraju guste jednolične populacije prekrivajući u potpunosti morsko dno, pri čemu se značajno mijenja sastav prirodnih zajednica te dolazi do gubitka biološke raznolikosti u Mediteranu. Međutim, iako se *Caulerpa taxifolia* smatra jednom od najvažnijih invazivnih vrsta u Mediteranu, ta je makroalga autohtona u tropskim i suptropskim morima diljem svijeta, uključujući i Australiju (Phillips & Price, 2002). *Caulerpa taxifolia* se uvelike koristila kao dekorativna alga u morskim akvarijima. Iz akvarija u Monaku slučajno je puštena 1984. godine (Meinesz & Hesse, 1991), te se potom brzo proširila prenošena sidrima i ribolovnim alatima, diljem zapadnog Sredozemlja (Meinesz et al., 2001). U Jadranu je zabilježena od 1994. godine u Starigradskom zaljevu na otoku Hvaru (Žuljević & Antolić, 2002). Brojne genetičke studije snažno podupiru hipotezu da je predak invazivnog tzv. “akvarijsko-mediteranskog" soja *C. taxifolia* donesen u europske akvarije iz zaljeva Moreton pored Brisbanea (Australija) (Wiedenmann et al., 2001; Famà et al., 2002). Osim genetskih sličnosti, "akvarijsko-mediteranski" soj dijeli i robusnu morfologiju sa populacijom iz zaljeva Moreton (Meinesz et al, 1995; Phillips i Price, 2002). *Caulerpa taxifolia* je bila prva makrofitska alga koji je radi svoje brze invazije Sredozemnog mora uspjela privući pozornost javnosti. Dodatno, došlo je do invazije i druge alge roda *Caulerpa*, *Caulerpa racemosa* var. *cylindracea* (Klein i Verlaque, 2008). Od pronalaska u Libiji 1990. godine (Nizamuddin, 1991), brzo se proširila cijelim Sredozemnim morem i Kanarskim otocima, razvijajući gusta i velika naselja sa svim značajkama invazivne vrste. Prvi nalaz alge *C. racemosa* u Jadranskom moru zabilježen je na Paklenim otocima kraj Hvara 2000. Broj zabilježenih nalazišta u hrvatskom podmorju od prvog nalaza iznimno brzo raste, a raspored nalazišta sugerira kako se alga primarno širi morskim strujama. Najveće naselje te alge zabilježeno je pored Sobre na Mljetu, a u Nacionalnom parku Mljet je pronađena na nekoliko područja, kao što su uvala Gonoturska i kanal Soline koji spaja otvoreno more s Velikim jezerom. Uvala Gonoturska je stalni "izvor" novih fragmenata alge, koje će struje unositi u kanal Soline i u Veliko jezero.

Alge *Caulerpa* spp. karakterizira prisutnost sekundarnih metabolita, kao što je kaulerpenin (CYN), čija je glavna funkcija kemijska obrana protiv biljojeda i epifita (Box et al., 2008; Sureda et al., 2009). Toksični učinci kaulerpenina su vidljivi posebice na ježincu *Paracentrotus lividus*. CYN utječe na regulaciju unutarstaničnog pH i ubija jaja ježinaca, te ima štetan utjecaj na razvoj ličinki, embriogenezu i metamorfozu (Lamée et al., 1993; Galgani et al., 1996; Pesando et al., 1998; Smit, 2004). Maksimalne koncentracije kaulerpenina u invazivnom "akvarijsko-mediteranskom" soju *C. taxifolia* su zabilježene u jesen, a minimalne u proljeće, s vrijednostima koje su mnogo veće od onih ustanovljenih kod ostalih vrsta *Caulerpa* (Dumay et al., 2002). Kao što rast i toksičnost *C. taxifolia* variraju unutar jedne godine (Amade i Lamée, 1998; Thibaut et al., 2004), tako i kemijska obrana *C. taxifolia* može smanjiti naseljavanje i razvoj epifitskih organizama različitim intenzitetom (Prado i Thibaut, 2008).

Bez obzira na potencijalno važnu ulogu epifitskih dijatomeja u funkcioniranju ekosustava pod utjecajem *C. taxifolia* i *C. racemosa*, specifičan sastav dijatomejskih zajednica nije ispitan. Analiza epifitskih dijatomeja na *C. racemosa* sa Pacifičke obale Japana nije dostatna jer se domaćin *C. racemosa* istraživao u područjima gdje alga nije invazivna vrsta. Dodatno, studija je prvenstveno fokusirana na morfologiju vrsta roda *Cocconeis* (Suzuki et al., 2001b). Informacije o sastavu dijatomejskih zajednica koje nedostaju su od osobite važnosti, naročito zbog prisutnosti toksina koji vjerojatno utječe i na sastav epifitskih dijatomeja, ali je i uzrok zbog čega glavni sredozemni makroherbivorni organizmi kao što su ježinci i ribe (npr. salpa) ne uspijevaju kontolirati širenje invazivnih *Caulerpa* sp. Radi mogućnosti usporedbe epifitskih dijatomeja na invazivnim *Caulerpa* sp. sa epifitskim dijatomejskim zajednicama na autohtonim makroalgama, potrebno je dodatno proučiti taksonomski sastav dijatomeja na smeđim i zelenim algama. Međutim, podaci o taksonomskom sastavu epifitskih dijatomeja na makroalgama *Padina pavonica, Halimeda tuna* i cvjetnici *Posidonia oceanica* u Mediteranu su oskudni (npr. Belegratis & Economou-Amilli, 2002). Općenito, bentoske dijatomeje u Jadranu su slabo poznate, a dosadašnja istraživanja provedena su u sjevernom Jadranu i estuarijima (npr. Totti et al., 2007; Caput Mihalić et al., 2008; Levkov et al., 2010).

Istraživanja u okviru disertacije su usmjerena na taksonomski sastav epifitskih dijatomeja u područjima invazivnih makroalgi roda *Caulerpa* uz istočnu obalu Jadrana. Materijal je sakupljan tijekom dvije godine (jesen 2008 – jesen 2010) u području s *Caulerpa taxifolia* u Starogradskom zaljevu na otoku Hvaru, te u područjima zahvaćenim makroalgom *Caulerpa racemosa* u Dubrovniku i u uvali Gonoturska na otoku Mljetu. Na istim su postajama istovremeno prikupljani uzorci autohtonih smeđih i zelenih algi radi analize odnosa epifitskih dijatomeja i domaćina.

Ciljevi doktorskog rada su bili odrediti taksonomski sastav epifitskih dijatomeja na invazivnim makroalgama *C. taxifolia* i *C. racemosa* u Jadranu; utvrditi taksonomski sastav sa dijatomejskim zajednicama na makroalgama; smeđoj algi (*Padina pavonica*) i zelenoj algi (*Halimeda tuna*), a u području koje obitava *Caulerpa* spp.; utvrditi sezonsku dinamiku dijatomeja na invazivnim makroalgama tijekom dvogodišnjeg uzorkovanja u mjesečnim intervalima, te usporediti strukturu dijatomeja na istraživanim makroalgama s podacima o zajednicama na algama iz drugih područja u Mediteranu i šire. Pretpostavlja se da postoji razlika u taksonomskom sastavu epifitskih dijatomeja između različitih vrsta invazivnih alga *Caulerpa* te između *Caulerpa* spp. i autohtonih smeđih i zelenih algi.

Za detaljnu analizu vrsta, trajni preparat se pripremao tretiranjem uzorka kloridnom kiselinom i vodikovim peroksidom. Uzorci su se kuhali i ispirali nekoliko puta sa deioniziranom vodom. Kao ljepilo u pripremi trajnih preparata koristio se Naphrax. Dijatomološke analize su uključivale svjetlosni (LM) i elektronski mikroskop (EM). Stanice dijatomeja su se analizirale i brojale pomoću svjetlosnog mikroskopa (Nikon Eclipse 600 i Zeiss Axioscope). Na svakom preparatu identificirano je minimalno 300 valvi, pod povećanjem 1000x. Detaljna analiza očišćenog materijala se odvijala pomoću transmisionog i skenirajućeg elektronskog mikroskopa (Hitachi SEM/STEM S-5500, S-3500, SU-70, SU-8000) u Poljskoj (Warsaw University of Technology, Faculty of Materials Science and Engineering). Zbirka visoko kvalitetnih fotografija omogućila je detaljna istraživanja morfologije i ultrastrukture dijatomeja te su se dobili potrebni podaci za detaljan opis vrsta. Za sortiranje podataka, izračunavanje statističkih pokazatelja i grafički prikaz koristili su se računalni paketi Microsoft Office i program Adobe Photoshop.

Po prvi se put u srednjem i južnom Jadranu utvrdio sastav bentoskih dijatomeja, opisala morfologija i ultrastruktura pojedinih vrsta i utvrdila sezonska dinamika vrsta u područjima zahvaćenim invazivnim makroalgama *C. taxifolia* i *C. racemosa*.

Utvrđeno je ukupno 631 dijatomeja u 80 rodova. Najzastupljeniji rodovi su *Cocconeis*, *Mastogloia*, *Nitzschia*, *Navicula*, *Amphora*, *Hyalosynedra*, *Licmophora*, *Grammatophora*, *Tabularia*, *Berkeleya*, *Fragilaria*, *Diploneis*, *Rhopalodia*, *Ardessonia* i *Toxarium*. Rodovi *Cocconeis* i *Navicula* zabilježeni su u svim uzorcima, dok su vrste rodova *Mastogloia, Nitzschia, Amphora, Hyalosyendra, Licmophora* i *Tabularia* nađene u više od 92% uzoraka. Rodovi s najvećim brojem svojti (više od 60) bili su *Mastogloia*, *Nitzschia* i *Amphora.* Rod *Cocconeis* se pojavljuje sa 29 svojti. Neke od njih, poput *Cocconeis scutellum* Ehrenberg var. *scutellum* i *Cocconeis molesta* var. *crucifera* Grunow u Van Heurck, zabilježene su u svim uzorcima. Najveću abundanciju imala je vrsta *Cocconeis scutellum* Ehrenberg var. *scutellum.* Osim svojti *Cocconeis scutellum* var. *scutellum* i *Cocconeis molesta* var. *crucifera*, najveću abudanciju i frekvenciju pojavljivanja, imale su: *Mastogloia crucicula* var. *alternans* Zanon, *Mastogloia crucicula* (Grunow) Cleve var. *crucicula* i *Mastogloia binotata* (Grunow) Cleve, *Cocconeis caulerpacola* Witkowski, Car & Dobosz, *Hyalosynedra laevigata* (Grunow) Williams & Round, *Navicula ramosissima* (Agardh) Cleve, *Nitzschia angularis* W. Smitha i *Nitzschia lanceolata* var. minima Grunow.

Sličan broj epifitskih svojti zabilježen je s jedne strane na autohtonoj smeđoj algi *Padina pavonica* i zelenoj algi *Halimeda tuna* (257), a na drugoj na invazivnim algama *Caulerpa racemosa* i *Caulerpa taxifolia* (370). Na invazivnoj algi *Caulerpa taxifolia* je pronađen ukupno najveći broj svojti (379), a na autohtonoj algi *Halimeda tuna* najmanji (243). Gledajući prosječan broj taxona po jednom uzorku, utvrđeno je da je zajednica epifitskih dijatomeja smeđe alge *Padina pavonica* najbogatija vrstama (64), dok je makroalge *Caulerpa racemosa* najsiromašnija (prosječno 50 svojti u jednom uzorku). Najmanji broj svojti na talusu makroalge *Caulerpa racemosa* na obje lokacije (Dubrovnik i Mljet) zabilježen je u veljači i ožujku, a najveći u rujnu.

Općenito, većina zabilježenih svojti dijatomeja pojavljuje se u različitim abudancijama tijekom godine. Manji broj svojti zabilježen je tijekom zime, dok ih je najviše utvrđeno tijekom ljetne sezone kada more dostigne godišnji temperaturni maksimum. Takav je slučaj i kod roda *Mastogloia* koji je vrlo bogat vrstama, te velikom abudancijom tijekom ljeta i jeseni značajno doprinosi bioraznolikosti što se vidi iz utvrđenih najviših vrijednosti Shannon-Wienerovog ideksa raznolikosti.

Multivarijantna analiza jasno je pokazala razliku u sastavu svojti ističući dvije različite skupine. Sličnost u epifitskom sastavu diatomeja između invazivne alge *Caulerpa taxifolia* i *Caulerpa racemosa* s jedne strane, i autohtonih makroalga, s druge strane, bio je manji od 20%. Nadalje, uočavaju se i dvije različite skupine unutar autohtonih algi, u jednoj prevladava zelena *Halimeda tuna* dok je u drugoj smeđa *Padina pavonica*.

U epifitskoj zajednici na smeđoj algi *Padina pavonica* dominiraju rodovi *Mastogloia, Nitzschia, Cocconeis, Navicula, Amphora, Hyalosynedra* i *Licmophora*. Od 25. dominantnih svojti koje imaju najveću abudanciju i frekvenciju pojavljivanja, 10 svojti pripada rodu *Mastogloia*. U epifitskoj zajednici na zelenoj algi *Halimeda tuna* dominiraju rodovi *Cocconeis, Mastogloia, Navicula, Nitzschia* i *Amphora*.

Na talusu makroalge *C. taxifolia* otkrvena je nova vrsta dijatomeje nazvana *Cocconeis caulerpacola* (Caulerpacola - na kaulerpi). Nova vrsta je po prvi put opisana na uzorcima kaulerpe s Hvara, ali je nađena i u uzorcima kaulerpa sakupljenim ispred grada Cannes (južna Francuska) te u zaljevu Moreton (istočna obala Australije). Dijatomeja je abundantna na talusu, što pokazuje da je *C. taxifolia* pogodan domaćin unatoč svojoj reputaciji „alge ubojice“. Nova dijatomeja je, također, utvrđena i na talusu *C. racemosa*, i to u uzorcima s otoka Mljeta i iz okolice Dubrovnika. Rezultati analiza zelenih i smeđih makroalgi prikupljenih u isto vrijeme s istih lokacija kao i invazivne kaulerpe pokazuju potpunu odsutnost ili prisutnost samo nekoliko primjeraka *C. caulerpacola.* i u skladu su sa pretpostavkom o postajanju razlike u taksonomskom sastavu epifitskih dijatomeja između istraživanih domaćina. Najveća abundancija dijatomeje *Cocconeis caulerpacola* na kaulerpama bila je u ljeto i jesen, istovremeno kad je i najveća koncentracija kaulerpenina, metaboličke tvari čija je glavna uloga kemijska obrana protiv predatora te kolonizatora poput te novoopisane vrste. Ostaje za ubuduće objasniti koji su to kemijski mehanizmi i specifičnosti koji omogućavaju novoj vrsti nesmetan rast i razmnožavanje na kaulerpama.

Rezultati istraživanja potvrdili su postojanje razlike između različitih vrsta invazivnih alga *Caulerpa*, te između *Caulerpa* spp. i autohtonih smeđih i zelenih algi. Dobivene spoznaje doprinjele su poznavanju bentoskih dijatomeja u Jadranu, ali i globalne biogeografske rasprostranjenosti dijatomeja (korologiji). Dobiveni rezultati omogućit će bolje razumijevanje funkcioniranja ekosustava u kojima dominiraju makroalge *Caulerpa* spp.. Saznanja o taksonomskom sastavu dijatomeja u područjima s *Caulerpa* spp. važna su za istraživanja toksičnog učinka domaćina.

SUMMARY

Diatoms (Bacillariophyta) are unicellular autotrophic microorganisms responsible for about 25 % of global primary production. They are widely distributed and highly abundant in all aquatic habitats occurring in the benthos and plankton of both marine and inland waters. The recent estimates of the number of diatom taxa range between ca. 10,000 and 100,000 taxa both fossil and recent. Their most recognizable feature is the presence of of an exoskeleton named “frustule”, which is composed of biogenic opal (amorphous hydrated silica). The largest number of species of diatoms are cosmopolitan, but there are species specific to particular geographic regions. With respect to the symmetry of the frustule there are two main groups of diatoms distinguished: centric forms having radial symmetry, which are mainly planktonic, and pennate ones having bilateral symmetry which are prevalent in the benthos. Benthic microalgae including diatoms colonize a wide range of substrates; occurring on rocks (epilithic communities), plants (epiphytic), animals (epizoic) or other substrata, where they may constitute communities with different individual abundances and thus affecting biodiversity (Totti et al., 2007). The structure of epiphytic communities can be influenced by various environmental factors, such as age of the plant and the seasonal cycle of plants or even the water depth (De Stefano et al., 2000). Epiphytic diatom communities of the seagrass *Posidonia oceanica* (L.) Delile are among the most thoroughly investigated. *Cocconeis* taxa are the most frequent and abundant diatoms on *P. oceanica* leaves throughout the seasons and throughout the depth range of the seagrass distribution (Mazzella et al., 1994; De Stefano et al., 2000). In contrast to the *Posidonia* communities, studies of the diatom communities associated with the marine, macroalga *Caulerpa* species (Bryopsidales, Chlorophyta) are lacking.

Caulerpa taxifolia and *Caulerpa racemosa* are outcompeting native seaweeds and seagrasses in the Mediterranean by forming dense carpets, leading to a loss of biodiversity. The invasive alga, *C. taxifolia*, was observed in Stari Grad Bay for the first time in 1994 on a hard, sandy and muddy substrate without vegetation or within meadows of *Posidonia oceanica* (Žuljević & Antolić, 2002). Numerous molecular studies strongly support the hypothesis that the invader is a descendant of the so-called ‘aquarium–Mediterranean’ strain of C. taxifolia from Moreton Bay, Australia (Wiedenmann et al., 2001; Famà et al., 2002). In addition, a further invasion event occurred and another species of the genus *Caulerpa*, *C. racemosa* var. *cylindracea*

(Klein and Verlaque, 2008) started its spread in the Mediterranea Sea. The number of locations with *Caulerpa racemosa* in the Croatian part of the Adriatic Sea after the first finding in 2000 at the Pakleni Islands near Hvar shows a dramatic increase. Locations of findings suggest that the alga is spread primarily by sea currents. The largest populations of *Caulerpa racemosa* heve been observed near the Sobra on the island of Mljet. In the Mljet National Park it was found in several areas such as Gonoturska Bay and Soline Channel, the channel that connects the Great Lakes with open sea. Gonoturska Bay is a constant "source" of new fragments of algae which are taken by currents through the Soline Channel in Big Lake. *Caulerpa* species are characterized by the presence of secondary metabolites such as caulerpenyne (CYN), the main function of which is a chemical defence against herbivores and epiphytes (Box et al., 2008; Sureda et al., 2009). Maximum concentrations of CYN for the ‘aquarium-Mediterranean’ strain of *C. taxifolia* were recorded in autumn while minimum ones were in spring, and concentrations levels are much higher than in in other *Caulerpa* species (Dumay et al., 2002). As the growth and toxicity of *C. taxifolia* vary greatly within a year (Amade & Lemée, 1998; Thibaut et al., 2004), the chemical defence of this species may affect the settlement and development of different sessile organisms in invaded systems with different intensities (Prado & Thibaut, 2008).

The composition of diatom communities of *C. taxifolia* has not been examined, in spite of the potentially important role of epiphytic diatoms in the functioning of the ecosystems influenced by *C. taxifolia* and by *C. racemosa*. This lack of information is of particular importance because of the existence of toxins, which probably affect the composition of epiphytic diatoms but are also the reason why the main predators, Mediterranean macroherbivores such as sea urchins and fish (eg. *Sarpa salpa*), can not control their spread. In order to facilitate comparison of epiphytic diatoms on invasive *Caulerpa* spp. with epiphytic diatom communities on autochthonous macroalgae, it is necessary to study the taxonomic composition of diatoms on brown and green algae. But the data on the taxonomic composition of epiphytic diatoms on macroalge *Padina pavonica* and *Halimeda tuna* in the Mediterranean are deficient (eg. Belegratis & Economou-Amilli, 2002). Generally, there is lack of information on benthic diatoms in the Adriatic. Previous studies have been conducted in the northern Adriatic and estuaries (eg. Totti et al., 2007; Caput Mihalić et al., 2008; Levkov et al., 2010).

The major goals of this study are the taxonomy and ecology of epiphytic diatoms in areas impacted by invasive macroalgae of the genus *Caulerpa* from the eastern coast of the Adriatic. Samples of invasive algae *C. taxifolia* and *C. racemosa*, along with coexisting autochthonous brown and green algae were collected in monthly intervals during the two year period (November 2008 - October 2010) in the Bay of Stari Grad, Island of Hvar (an area affected by *C. taxifolia*), in Gonoturska Bay (Island of Mljet) and at the location Orsula near Dubrovnik (areas affected by *C. racemosa*). For a detailed analysis of species composition permanent preparations were made. This was achieved by treating samples firstly with hydrochloric acid and secondly with hydrogen peroxide. After treatment with 10 % HCl samples were boiled in concentrated hydrogen peroxide and washed several times with deionized water. As a mounting medium of permanent preparations Naphrax® was used. Diatom analysis included light microscopy (LM) and electron microscopy (EM). Examination of slides in LM and EM provided the first information on the general morphology and ultrastructure of taxa, and enabled proper identification of the difficult (usually very small) diatom taxa. Diatoms were identified by means of a light microscope (Nikon Eclipse 600 and Zeiss Axioscope) equipped with x100 PLANapochromatic, immersion oil objective (numerical aperture – 1.40). In each sample a minimum of 300 valves were identified and counted, under magnification of 1000x. Detailed analysis of the cleaned samples was performed using transmission and scanning electron microscopes (Hitachi SEM/STEM S-5500, S-3500, SU-70 and SU-8000) in Poland (Warsaw University of Technology, Faculty of Materials Science and Engineering). A collection of high-quality photos allowed detailed studies of the morphology and ultrastructure of diatoms and supported detailed identification of diatom taxa. For sorting the data, calculation of statistical indicators and graphical representation computer packages Microsoft Office and Adobe Photoshop were used.

For the first time in the Central and Southern Adriatic Sea the composition of benthic diatoms and seasonal dynamics of taxa in areas affected by invasive macroalgae *Caulerpa taxifolia* and *Caulerpa racemosa* were determined. As a result it has been shown that both *C. taxifolia* and *C. racemosa* host a complex and diverse community of epiphytic diatoms. The influence of *Caulerpa* in the Mediterranean on diversity of diatoms was observed as well. The very abundant, newly-described species of

Cocconeis (*C. caulerpacola* Witkowski, Car et Dobosz) was observed as epiphyte with patchy distribution covering the surface of both non-indigenous and native *Caulerpa taxifolia* as well as *Caulerpa racemosa*. An absence of *Cocconeis caulerpacola* on green and brown macroalgae collected at the same time from the same localities as invasive *Caulerpa* spp. suggests a strong degree of host-specificity in this *Cocconeis* species. Mass occurrence of *Cocconeis caulerpacola* in both the Mediterranean and Australian coastal waters indicates that the substratum could be an important environmental factor in the structure of the epiphytic diatom community, regardless of geographic location. Results of the observations on thallus of *Caulerpa taxifolia* show that *C. taxifolia* as substrate could be favourable to particular growth forms, such as the strongly adherent prostrate species.

Epiphytic diatoms are important components of benthic communities, but the subject of their biodiversity and spatial and temporal distribution has been neglected. Knowledge of the subject has been improved by the data on the taxa observed in the present study. In addition the results of the research significantly enhance information about the biodiversity of the Mediterranean Sea diatom flora.

The results of this study will enable a better understanding of the functioning of ecosystems dominated by *Caulerpa* spp. Knowledge about the diatom community structure in the areas of *Caulerpa* spp. is important for studies of the toxic effects of the host plant.

1. INTRODUCTION

1.1. Diatoms

Diatoms are unicellular autotrophic microorganisms responsible for about 25 % of global primary production (Compton, 2011). They are widely distributed and highly abundant in all aquatic habitats from the polar to the tropical regions, occurring in benthos and plankton of both marine and fresh waters, as well as in terrestrial environments such as damp soils and moist surfaces of rocks and plants (Round et al., 1990).

Their most recognizable feature is the presence of an intricately structured siliceous exoskeleton, called a frustule. The frustule is composed of biogenic opal (amorphous hydrated silica, SiO_2 x nH_2O) with two overlapping parts called thecae; “epitheca” – upper/larger part and “hypotheca” – bottom/smaller part. Each of them is composed of a valve and a series of hoop-like or segmented girdle bands. Valvocopula is the first girdle band adjacent to the valve while other bands are referred as copulae. Regarding symmetry, there are two main groups of diatoms: “centric” (with radial symmetry of cells) and “pennate” (with bilateral symmetry of cells). Due to their unique frustule structure of two overlapping thecae and the division pattern in which new cell wall components are formed within the parental cell, diatoms gradually reduce their cell size in the course of the mitotic part of the life cycle, while restoring the original cell size in sexual reproduction (Round et al., 1990)

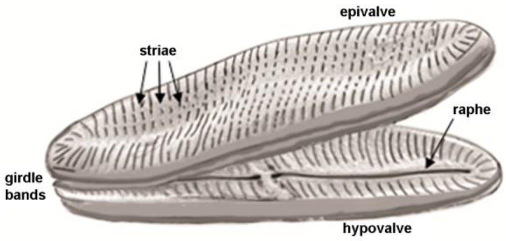

Figure 1 Schematic overview of the structure of a frustule showing the general features of pennate diatoms

The diatom frustules are characterized by various types of ornamentation composed of pores (areolae). In addition valves of a given frustule may possess ridges, various processes or spines protruding from the valve surface. The above ornamentation is species-specific and is the basis for LM and EM identification of diatoms. The most spectacular feature of diatoms, the amazingly different shapes and patterns of their frustule material, caused diatoms to create extraordinary interest not only with biologists but also with nanotechnologists who seek to produce new materials. As the pattern of siliceous components of the frustule is under the control of cell genetics, the taxa identification and taxonomy is based on the determination of the shape and structural specificities of frustule (Round et al., 1990).

The most recent inventories of daitom taxa point out to ca. 1200 genera and 100 000 taxa both fossil and recent (Fourtanier & Kociolek, 1999, Mann & Vanormelingen, 2013). Arguably most diatom diversity is not planktonic, but benthic and epiphytic (Sournia et al., 1991).

The evolution of diatoms is very complex and has been revealed only in recent years by analyzing the genome of a centric diatom *Thalassiosira pseudonana* and a pennate diatom *Phaeodactylum tricornutum*. New information about the evolutionary development of the metabolic adaptations explains the reasons for their exceptional ecological success.

Remains of diatoms occurring in lacustrine or oceanic deposits also have numerous applications. Accumulation of fossil remains of diatom frustules formed thick layers of diatomaceous earth or diatomite, which is used in industry to produce explosives, glass, fillers, filters, paints and toothpaste, and in the production of wine, beer, pesticides, etc. (Stoermer & Smol, 1999; Compton, 2011).

Diatoms are also a very useful tool in paleoecology, paleolimnology, paleooceanography and biostratigraphy extending back to the early Createceous age. This is due to the fact that numerous taxa have strict preferences in terms of environmental conditions, such as salinity, temperature or nutrients, and because many fossil genera are present today as well, it is possible to make accurate paleoecological reconstruction (Stoermer & Smol, 1999; Compton, 2011).

Occurrence of diatoms is influenced by a variety of physical and chemical factors such as salinity, temperature, pH and light and nutrients necessary for growth. Therefore, diatomaceous sediments are found in high latitudes, along the coasts, and especially in zones of upwelling of deep water masses enriched with nutrients. Based on estimates of total biomass and composition of the plankton community it is possible to assess the stability of the ecosystem and its sensitivity to natural and anthropogenic physical and chemical changes (Stoermer & Smol, 1999; Compton, 2011).

Although the largest numbers of diatoms are cosmopolitan taxa, biogeographical classification of diatoms in the regional group shows the existence of taxa characteristics for particular areas. This is used during forensic investigations of cases involving drowning.

1.1.1. Benthic diatoms

Benthic diatoms of coastal marine areas contribute to the dynamics of aquatic ecosystems in terms of primary production, sediment stabilisation, nutrient fluxes, and roles in the trophic web (MacIntyre et al., 1996; Totti, 2003; Underwood & Paterson, 2003). Communities of benthic diatoms can develop in association with different substrata, from the soft bottom, to rocks, macroalgae and seagrasses and animals. Establishment of different modes of contact with the substratum is a result of the development of well-differentiated growth forms of diatoms:

- **Adnate diatoms** (eg. *Cocconeis* Ehrenberg) strongly adhering horizontally to the substrate by means of the raphe valve and having limited motility. Due to their adhering mode on the host surface through the valve face, adnate taxa may easily benefit from the nutrient exchange with the host (Round, 1981; Sullivan, 1984; Romagnoli et al., 2014). Adnate diatoms grow close enough to the substrate to lie within low current-velocity boundary layers and thereby avoid the shear stress of severe currents and are the most resistant to grazing. However, they are easily overgrown by other organisms and may become light-limited by that overgrowth (McCormick & Stevenson, 1989).
- **Erect diatoms** (e.g. *Grammatophora* Ehrenberg, *Licmophora* C. Agardh, *Striatella* C. Agardh, *Ardissonea* De Notaris) adhering vertically through mucous pads or stalks/peduncles. Erect diatoms have better access to light, although they are more exposed to grazing pressure (Hillebrand et al., 2000) and their capability of regulating stalk lengths makes them competitors for light when dense benthic populations develop. Their decrease may be related to an effect of increased grazing pressure (Romagnoli et al., 2014).
- **Motile diatoms** (e.g. *Navicula* Bory de Saint-Vincent, *Nitzschia* Hassall) having movement capability enabling them to glide along the substratum (Round, 1971; Round et al., 1981; Romagnoli et al., 2014).
- **Tube-dwelling diatoms** (e.g. *Berkeleya rutilans* (Trentepohl) Grunow, *Parlibellus* spp. Cox, 1988). Species living in mucilage tubes of their own making. Diatom grows as an epiphyte on selected macroalgae, secreting a mucilage pad and a capsule, followed by a hollow cylindrical tube closed at the tip. As cell divisions proceed, the tubes may get elongated, or branches may be produced by daughter cells. This results in the development of a branched tube system usually with a single cell visible at the base of each tube.

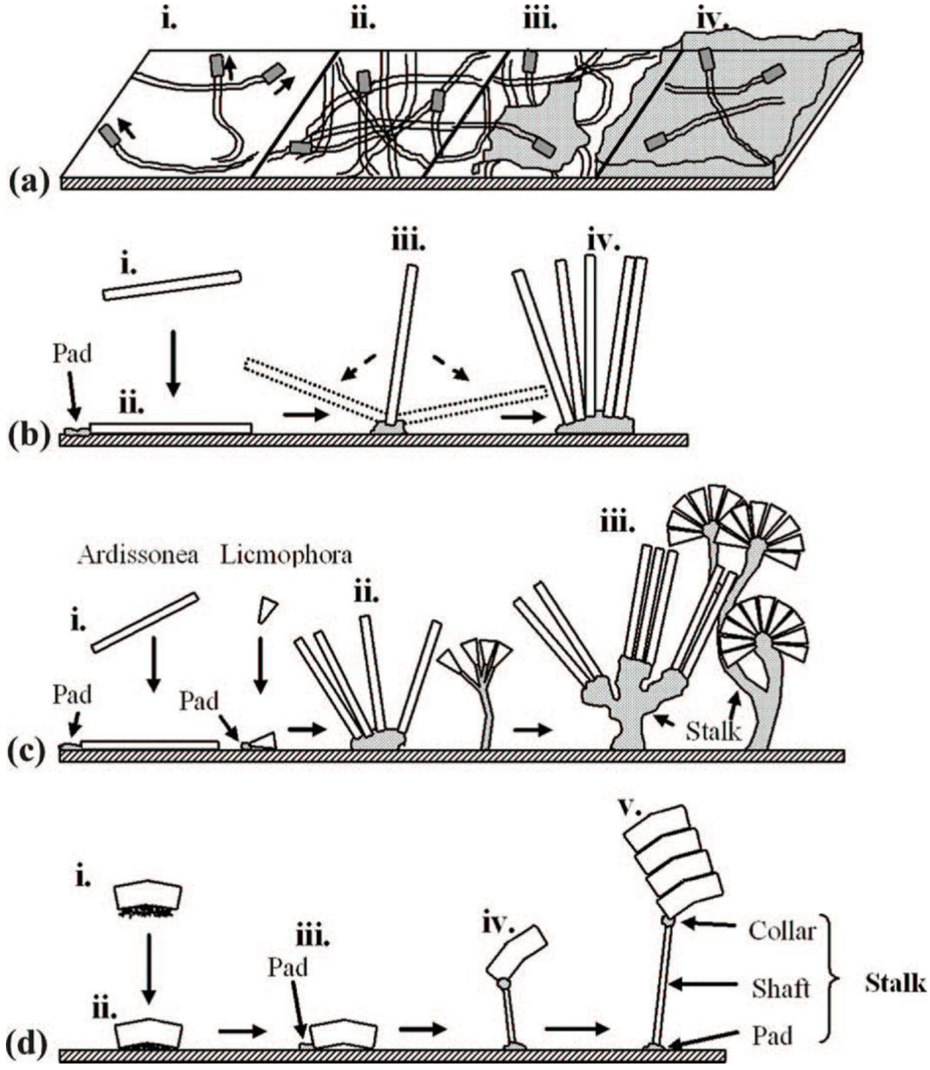

Figure 2. Scheme of adhesive structures produced by fouling benthic diatoms. (a) Film formation in *Amphora coffeaeformis.* (b) Pad formation in *Toxarium undulatum*. i–ii. Initial adhesion to the surface is via the girdle bands; thereafter a mucilaginous pad is secreted. iii. The cell eventually stands erect in the mucilaginous pad. Water currents have been observed to push the cells prostrate on the surface; however, the cells generally remain strongly adhered to the pad. iv. Cell division can produce large colonies of cells adhered to a single communal pad. (c) Stalk formation in *Ardissonea* and *Licmophora*. i. Initial adhesion via the girdle bands is followed by the secretion of an adhesive pad. ii. Cells of both species stand erect in large pad or early stalk structures; cell division increasing the number of cells attached to the adhesive structures. iii. Subsequent cell division and addition of mucilaginous material to the stalk structures produces branched stalks that elevate the cells several hundred microns from the substratum. (d) Stalk formation in *Achnanthes*. i–ii. Initial adhesion to the substrate, thereafter the cell may commence motility. iii. An adhesive pad is secreted, thereafter a stalk is secreted that is differentiated into three distinct sections (iv–v). Several cells may occupy a single stalk as a result of cell division of the primary cell from which the stalk is secreted (from Molino, P.J. & Wetherbee, R., 2008).

1.1.2. Genus *Cocconeis*

Species of *Cocconeis* are well known as components of the marine attached diatom community (e.g. Suzuki et al., 2001a), occurring on rocks (epilithic communities), plants (epiphytic), animals (epizoic) or other substrata, where they may constitute communities with very high individual abundances and contribute to taxa richness (Totti et al., 2007). The first taxon to be described (by Ehrenberg, 1837) was *C. scutellum*, which is the generitype (De Stefano et al., 2008; Jahn et al., 2009). *Cocconeis scutellum* and its varieties are still the most commonly reported taxa in taxonomic and ecological studies due to frequent occurrence, simple valvar morphology and ease of identification under the light microscope (De Stefano et al., 2008). Recent studies on the morphology of various marine *Cocconeis* taxa have revealed great morphological variability and the genus is among the most structurally complex of diatom genera. *Cocconeis* exhibits a heterovalvar morphology, each frustule being composed of a rapheless valve [exhibiting a sternum (=pseudoraphe)] and a raphe valve. This type of morphology is described as being 'monoraphid' (Kobayasi & Nagumo, 1985; Round et al., 1990; De Stefano & De Stefano, 2005; De Stefano & Romero, 2005; Molino & Wetherbee, 2008). One of the most important characteristics of *Cocconeis* and related genera is the structure of the cingulum (Holmes et al., 1982).

1.1.3. Genus *Mastogloia*

Mastogloia Thwaites ex W. Smith (1856: 63) is a large genus with some 410 taxa (Novarino, 1989). It is mainly recognized as a marine genus frequently occurring in tropical to temperate regions, and also extending its distribution to brackish and fresh water with a fairly high number of epilithic and epiphytic taxa. The genus has naviculoid valves, which are usually isopolar (Lobban & Pennesi, 2014). Morphologically it is mainly characterized by a modified valvocopula which consists of a series of adjacent partecta (i.e. chambers *sensu* Hustedt, 1933) running internally along each valve margin to form a partectal ring. Until 1975, when Ricard described for the first time the valve ultrastructure of several taxa of *Mastogloia* with the scanning electron microscope (SEM), the systematic of the genus *Mastogloia* was based on observations in light microscopy (Pennesi et al., 2011, 2012, 2013). Cells are usually solitary, although sometimes they form colonies in mucilage (Round et al, 1990, Lobban & Pennesi, 2014). Among key works on *Mastogloia* are those of Ricard (1975), Kemp & Paddock (1988), Simonsen (1990), Pennesi et al. (2011, 2012, 2013) and Lobban & Pennesi (2014).

1.2. Biofouling

Sessile marine organisms are continuously exposed to bacteria, diatoms, spores and larvae which may be ready to settle. The intensity of fouling pressure varies through time. Variation could be a result of different factors such as season, depth and local ecological factors, but despite all of that, any permanently exposed, non-defended surface will sooner or later become fouled (Wahl, 1989). In the case of two or more organisms being in a spatially close facultative association the phenomenon is known as epibiosis (Wahl, 1989). The colonisation of a living surface by epibionts, living organisms attached to the body surface of a basibiont (host or substrate organism), constitutes one of the most substantial modifications of the basibiont's body surface (Wahl, 2008). Small epibionts, although generally ignored in the description of marine organisms, may have profound effects on the basibiont by causing a multitude of beneficial or detrimental effects and must be taken into account when host ecology is studied (Gillan & Cadée, 2000).

Among the early settlers, microalgae play a key role in the biofilm development and are able to settle on even the most fouling resistant surfaces (Molino & Wetherbee, 2008). Raphid diatoms are generally among the earliest and most abundant primary colonizers of natural and artificial surfaces (Hoagland et al., 1986). Most aquatic vegetation, either saline or freshwater, hosts epiphytic forms of diatoms (Round et al., 1990).

Several stages have been recognized in the colonization of a new hard substrate. In the first stage, only bacteria and organic detritus settle on the substrate; afterwards, diatoms that lie flat on the substrate (i.e. adnate and motile forms) appear together with erect ‘rosette forming’ species; in the last stage, there is massive growth of erect stalked diatoms which create a complex three-dimensional community. These succeeding stages seem to be the same in all the microalgal communities that colonize hard substrates, i.e. epilithic, epiphytic and epizoic. Differences in species composition and growth form produce assorted three-dimensional structures of the attached algal biofilm (Tuji, 2000; Totti et al., 2007).

The availability of resources (space, nutrients, light) and level of disturbance are important growth factors for communities. The above factors influence the composition and development of the biofilm and its architecture (Lowe, 1996; Tuji, 2000). The structure of the epiphytic community on sea grasses can be influenced by several environmental factors, such as the age of the leaf, the seasonal cycle of the plant or water depth (De Stefano et al., 2000). Totti et al. (2009) suggested that both the architecture of the macroalgal thallus and the surface characteristics may have a role in affecting the abundance and taxonomic composition of the epiphytic diatom communities. Because the host effect on epiphytic communities may be explained by a number of reasons, such as chemical interactions, different life cycles of host and also the different environmental conditions that may have been experienced by the host, makes it difficult to choose a single major factor (Totti et al., 2009).

The epiphytic diatom communities of the endemic Mediterranean seagrass, *Posidonia oceanica* are some of the most thoroughly investigated (Mazzella et al., 1994; De Stefano et al., 2000). Mazzella et al. (1994) found that *Cocconeis* taxa are the most frequent and abundant diatoms on *P. oceanica* leaves throughout the seasons and all along the depth range of the seagrass distribution. De Stefano et al. (2000) documented eight taxa of *Cocconeis* on the leaves of *P. oceanica*. Some of these taxa can be very abundant and can constitute a continuous, almost monospecific layer on the colonized parts of the leaves (Mazzella et al., 1994). In contrast to the *Posidonia* communities, studies of the diatom communities associated with the marine, green macroalga *Caulerpa* spp. (Bryopsidales, Chlorophyta) are lacking.

1.3. *Caulerpa* J.V. Lamouroux, 1809

1.3.1. Caulerpa taxifolia

The marine, green macroalga *Caulerpa taxifolia* has pinnate, fern-like fronds (up to 25 cm long, 2 cm wide) that extend upwards from horizontal stolons (Meinesz et al., 1995) (Figure 3). This alga is outcompeting native seaweeds and seagrasses in the Mediterranean by forming dense carpets, leading to a loss of biodiversity. It is indigenous to tropical and subtropical seas worldwide, including Australia (Phillips & Price, 2002) and it has been used widely as a decorative plant in the marine aquarium trade. It was accidentally released from the Monaco Aquarium in 1984 (Meinesz & Hesse, 1991), rapidly spread across the western Mediterranean basin (Meinesz et al., 2001) and become one of the most invasive species. Numerous molecular studies strongly support the hypothesis that the invader is a descendant of the so-called 'aquarium–Mediterranean' strain of *C. taxifolia* originated from Moreton Bay, Australia (e.g. Wiedenmann et al., 2001; Famà et al., 2002). The 'aquarium–Mediterranean' strain also resembles the Moreton Bay population morphologically, both of these having more robust thalli than *C. taxifolia* found elsewhere (Meinesz et al., 1995; Komatsu et al., 1997; Phillips & Price, 2002). Moreton Bay experiences minimum winter temperatures similar to the Mediterranean Sea and the two populations of *C. taxifolia* thus exhibit similar cold tolerance thresholds (Komatsu et al., 1997; Chisholm et al., 2000; Phillips & Price, 2002; Burfeind & Udy, 2009).

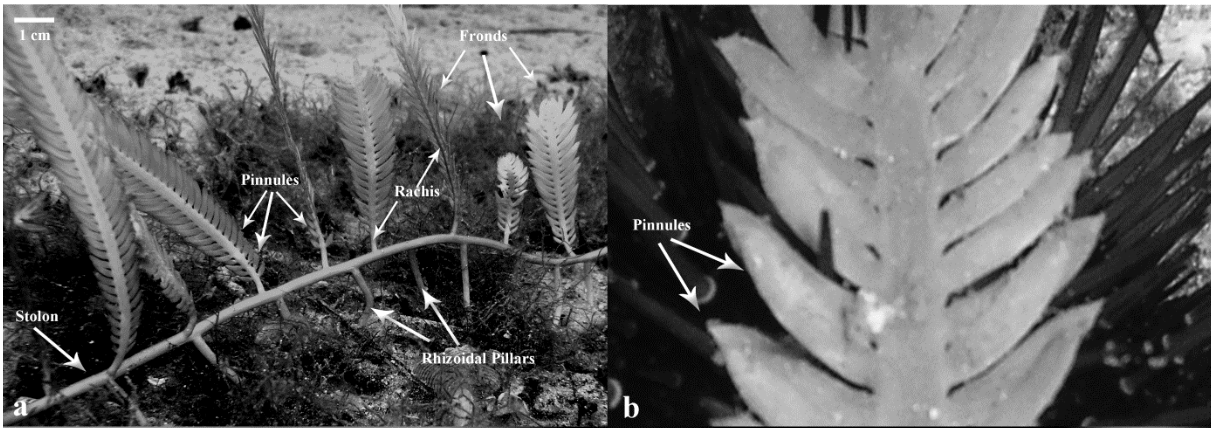

Figure 3. Morphology of *Caulerpa taxifolia*. (a) In situ morphology of *Caulerpa taxifolia*. (b) Detailed view of a frond. Pinnules (L. small feathers) grow out of the main axis of the frond [rachis (Gk. backbone)], to give each frond the characteristic feather-like appearance.

Caulerpa species are characterized by the presence of secondary metabolites, such as caulerpenyne (CYN), the main function of which is a chemical defence mechanism against herbivores and epiphytes (Box et al., 2008; Sureda et al., 2008, 2009).

A variety of toxic effects caused by CYN have been demonstrated, in particular on the sea urchin *Paracentrotus lividus* by e.g. killing sea urchin eggs (Lemée et al., 1993) (Figure 4) or affecting them via regulation of intracellular pH, and also having effects on embryogenesis, larval development and metamorphosis (Galgani et al., 1996; Pesando et al., 1996, 1998; Smit, 2004).

Figure 4. *Caulerpa taxifolia* on the sea urchin *Paracentrotus lividus*, the Bay of Stari Grad, Island of Hvar (Photo by Tonči Dulčić).

Recorded concentrations of CYN for the ‘aquarium-Mediterranean’ strain of *C. taxifolia* were maximum in autumn and minimum in spring, reaching values that are much higher than observed in other *Caulerpa* species (Dumay et al., 2002). As the growth and toxicity of *C. taxifolia* vary greatly within a year (Amade & Lemée, 1998; Thibaut et al., 2004), the chemical defence of this species may affect the settlement and development of different sessile organisms in invaded systems with different intensities (Prado & Thibaut, 2008). The specific composition of diatom communities of *C. taxifolia* has not been examined, in spite of the potentially important role of epiphytic diatoms in the functioning of the ecosystems influenced by *C. taxifolia*. This lack of information is of particular importance because of the existence of toxins, and because a new marine taxon of *Cocconeis*, *C. shikinensis*, has also been found growing on another species of *Caulerpa*, *C. racemosa* (Suzuki et al., 2001b).

1.3.2. Caulerpa racemosa

Caulerpa racemosa (Forsskål) J. Agardh *sensu lato* is one of the most widely distributed algae of tropical and warm-temperate seas. Three taxa of *Caulerpa racemosa* that differ morphologically and genetically have been reported in the Mediterranean Sea since the 1930s. Two of them, *C. racemosa* var. *turbinata–uvifera* (C. Agardh) J. Agardh and *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse f. *requienii* (Montagne) Weber-van Bosse, are typical non-aggressive Lessepsian immigrants and were observed only sporadically in the eastern Mediterranean (e.g. Lebanon, Egypt, Syria, Tunisia, Turkey and Israel). However, the situation changed in the early 1990s when a new form of the alga, the invasive *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque (Synonym: *Caulerpa cylindracea* Sonder) was found for the first time in the Mediterranean Sea in Libya (Nizamudin, 1991). *Caulerpa racemosa* var. *cylindracea* (in further text: *Caulerpa racemosa*) spreaded surprisingly quickly throughout the Mediterranean and the Canary Islands, developing a dense and large covers. Invasive alga *Caulerpa racemosa* have been reported from Italy (Alongi et al., 1993), Greece (Panayotidis & Montesanto, 1994), Albania (Di Martino & Giaccone, 1995), Cyprus (Hadjichristophorou et al., 1997) , France (Jousson et al., 1998), Turkey (Cirik, 1999), Malta (Stevens, 1999), Spain (Ballesteros et al., 1999), Tunisia (Belkhiria, 1999), Croatia (Žuljević et al., 2003) , and from Algeria (Ould-Ahmed & Meinesz, 2007).

First appearance of *Caulerpa racemosa* in the Adriatic Sea was observed on Pakleni Islands (islet Marinkovac) in the autumn 2000. By the end of 2005, it was found in Italian, Albanian and Montenegrin seabeds. Immediately after the first finding of alga *Caulerpa racemosa* in the Adriatic Sea, an attempt was made to remove its settlements by covering them with lime and black plastic film. Due to *C. racemosa*'s green colour and because it does not build dense settlements it is extremely difficult to notice it within well-developed settlements of indigenous algae. Because of this large numbers of small and hardly noticeable individual *Caulerpa racemosa* algae were overlooked and not covered. Due to difficulties in observation of individual fragments of alga, as well as an extremely successful and explosive growth of this species, the removal of *Caulerpa racemosa* is extremely demanding, and has almost no chance of success (http://jadran.izor.hr/kaulerpa/).

After the first findings the number of locations of *Caulerpa racemosa* in the Croatian part of the Adriatic Sea increased very fast. A small number of sites are the result of transfer of algae by fishing nets (e.g. ports where fishermen are cleaning their nets). Locations of finding suggest that the alga is spread primarily by sea currents. By the end of 2005, most of the sites in Croatia impacted by *C. racemosa* were from Cavtat to the island of Vis. North of the Vis Island only one finding, in Vrsar (Istria), was reported. Vrsar is the northernmost situated site of *Caulerpa racemosa* in the world, and this area was inhabited by algae probably around year 2001. In the northern Adriatic (Vrsar), *Caulerpa racemosa* survive low winter temperatures that decrease below 7°C. This shows that this species is very resistant to low temperature. By the end of 2008 there were 85 sites of *Caulerpa racemosa*, most of them located in the Central and Southern Adriatic Sea area from Cavtat to Šolta.

The largest settlement of *Caulerpa racemosa* was observed near the Sobra on the island of Mljet. In Mljet National Park it was found in seven areas. Its removal is carried out only in the Great Lake, Soline Channel (the channel that connects the Great Lakes with open sea) and Bay of Blace. In the Great Lake *Caulerpa racemosa* is found in the direct neighbourhood of the Mediterranean endemic coral stone *Cladocora caespitosa*. It appeared there in the fall of 2004 and immediately upon discovery its removal from this site was started (Kružić, P. & Požar-Domac, A., 2000). A large settlement has also been observed in Gonoturska Bay. (http://jadran.izor.hr/kaulerpa/).

Gonoturska Bay is a constant "source" of new fragments of algae which are taken by currents through the channel Soline in Big Lake (Figure 5).

Figure 5. *Caulerpa racemosa*, Gonoturska Bay, Island of Mljet (Photo A. Car).

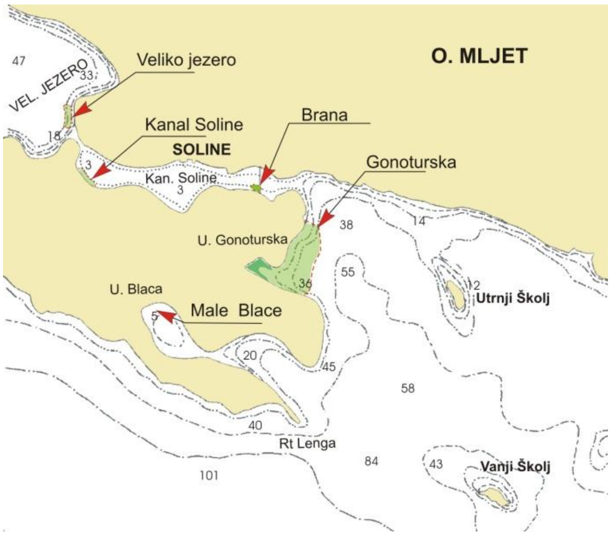

Figure 6. *Caulerpa racemosa* in. Mljet National Park in 2007. Green shading indicates area where alga was observed. (from: http://jadran.izor.hr/kaulerp; Institute of Oceanography and Fisheries)

1.4. The previous investigations of benthic diatoms in the Adriatic Sea

Regardless of the potentially important role of epiphytic diatoms in the functioning of ecosystems under the influence of *Caulerpa taxifolia* and *Caulerpa racemosa*, the specific composition of diatom communities has not been analysed. Analysis of epiphytic diatoms of *Caulerpa racemosa* on the Pacific coast of Japan is not sufficient because the investigated host *Caulerpa racemosa* was from areas where the alga is not an invasive species. In addition, the study was primarily focused on the morphology of taxa of genus *Cocconeis* (Suzuki et al., 2001b).

The missing information is of particular importance due to the presence of toxins, which probably affect the composition of epiphytic diatoms, but which are also the reason that the main predators, Mediterranean macroherbivore organisms such as sea urchins and fish (e.g. *Sarpa salpa*), cannot control the spread of the algae. In order to facilitate comparison of epiphytic diatoms on invasive *Caulerpa* sp. with epiphytic diatom communities on autochthonous macroalgae, a study of the taxonomic composition of diatoms on indigenous brown and green algae was needed. But the data of the taxonomic composition of epiphytic diatoms on macroalga *Padina pavonica* (Linnaeus) Thivy, *Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux and seagrass *Posidonia oceanica* in the Mediterranean are deficient (e.g. Belegratis & Economou-Amilli, 2002).

Generally, there is a lack of information on benthic diatoms in the Adriatic. Previous studies have been conducted in the northern Adriatic and estuaries (e.g. Burić et al., 2004; Totti et al., 2007; Caput Mihalić et al., 2008; Levkov et al., 2010).

Seasonal fouling by diatoms was studied on artificial substrates as in the heavily polluted and eutrophicated area near Piran in the Gulf of Trieste when concrete plates (50 x 50 cm) were placed at l m, 3 m and 7 m depths, with the fouling observed monthly from March to October during one year (Munda, 2005). In terms of depth distribution, maxima in the number of recorded taxa were found at 3 m in spring and at 7 m in autumn. The fouling populations were heterogeneous, including epilithic, epipsammic and epipelic taxa with different affinities (marine, brackish and even fresh water). Colonial forms belonging to the genera *Berkeleya*, *Navicula* and *Licmophora* were dominant and covered most of the experimental surfaces. Taxa belonging to *Achnanthes* were among the primary colonizers, while those belonging to *Nitzschia* first settled in autumn, along with several epipelic taxa (Munda, 2005).

The study of Totti et al. (2007) was also performed on artificial hard substrates. The colonization of epilithic diatoms on marble, quartzite and slate was investigated on a seasonal basis in a subtidal site of the northern Adriatic Sea to determine if substrate-dependent differences in colonization occur and to define the seasonal variations of microepilithic communities in terms of abundance, biomass and community structure. Artificial substrates were placed at a depth of 8 m in April and July 2003 and in January and February 2004 and collected after 6–7 weeks for counting and taxonomic identification of the diatoms. Diatom density showed a marked seasonal variability with lower density of diatom cells during winter. Abundance and biomass values did not present any significant differences for the three substrates examined. The community structure of epilithic diatoms showed a dominance of motile taxa over the entire study period, followed by erect, adnate and tube-dwelling diatoms.

Diatom composition and abundance in biofilm on artificial substrates exposed at several depths were investigated at two stations in the Zrmanja estuary in July 2000 (Caput Mihalić et al., 2008). Periphyton was composed mostly of *Amphora coffeaeformis* and *Navicula veneta* whose joint abundance exceeded 80 % at both stations. Shannon-Wiener Biodiversity Index ranged between 0.87 and 2.08 at the upper estuary station and between 1.1 and 2.7 at the other.

Also analysed was the abundance of periphytic pennate diatoms, particularly of *Cocconeis scutellum*, attached to artificial substrates in the karstic Zrmanja Estuary during summer 2000 (Burić et al., 2004). The latter authors focused on comparison of abundance of the attached *Cocconeis* cells and those suspended in plankton.

Although part of the material for taxonomical study of Levkov et al. (2010) was from the Ombla River near Dubrovnik, it was focused primarily on 15 species of genus *Rhoicosphenia* based on light and scanning electron microscopy. Information on seasonal distribution and succession of epiphytic diatoms on macroalgae is missing.

1.5. Aims of the study

The main objective of this thesis was to determine the taxonomic composition of epiphytic diatoms on invasive macroalgae *Caulerpa taxifolia* and *Caulerpa racemosa* and on autochthonous algae, brown (*Padina pavonica*) and green (*Halimeda tuna*), in an area inhabited by *Caulerpa* spp, in the Adriatic. It was expected that taxonomic composition of epiphytic diatoms on both species invasive *Caulerpa*, and between *Caulerpa* spp. and indigenous brown and green algae would be different.

Another aim is to describe the seasonal dynamics of diatoms on macroalgae during the monthly sampling over a two-year period and to compare the structure of the epiphytic diatom assemblages of investigated macroalgae with information about the algal communities from other areas in the Mediterranean and beyond, and also to describe taxa succession on invasive macroalgae on a fine time scale.

The framework of this research project included studies of the diatom flora epiphytic on *Caulerpa taxifolia*, focusing on the *Cocconeis* taxa which constitute the majority of the diatom population. The epiphytic diatom assemblage on thalli of *Caulerpa taxifolia* was found to be largely dominated by a taxon of the genus *Cocconeis* that could not be identified. The aim of the present study is to document the morphology of this taxon, based on light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM), and to describe it as new following a comparison with similar taxa, such as *Cocconeis diruptoides* Hustedt, *C. pseudodiruptoides* Foged and *C. borbonica* Riaux-Gobin & Compère.

A long term objective of this thesis is to facilitate correct taxa identification of the marine benthic diatoms on the local as well as global level which will provide the basis for further studies on the geographic distribution of diatoms. The data obtained within this research will also improve understanding of the impact of invasive *Caulerpa* spp. on an area which they inhabited.

2. MATERIALS AND METHODS

2.1. Study area

Samples for studies on benthic diatom assemblages hosted by invasive *Caulerpa* species and by co-occurring autochthonous brown and green algae from areas affected by *Caulerpa* spp. were taken monthly during the period of November 2008 – October 2010 by a SCUBA diver. They originated from:

1. An area affected by *Caulerpa taxifolia* at depths ranging from 5 to 8m*:*

- Central Adriatic, in the Bay of Stari Grad, Island of Hvar (43º 10′ 54″ N, 16º 35′ 00″ E). The invasive alga, *C. taxifolia*, was observed in Stari Grad Bay for the first time in 1994 on a hard, sandy and muddy substrate without vegetation or within meadows of *Posidonia oceanica* (Žuljević & Antolić, 2002).

2. Areas affected by *Caulerpa racemosa* at depths ranging from 10 m to 15 m:

- Southern Adriatic Sea, National Park Mljet, Gonoturska Bay (approximately 42° 45' N, 17° 23' E).

- Southern Adriatic Sea, location Orsula near Dubrovnik (42° 37' 50" N, 18° 8' 2" E).

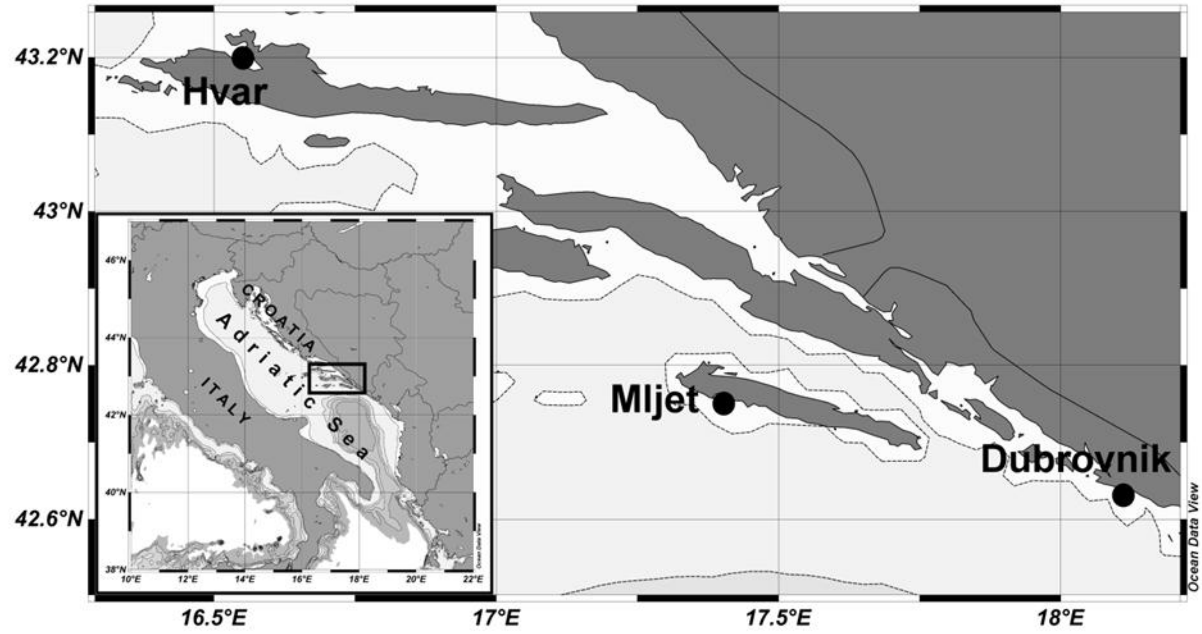

Figure 7. The study areas and the locations of sampling sites.

At all sampling sites of *Caulerpa* species in the Adriatic Sea over the research period of two years (autumn 2008-autumn 2010), water temperature ranged between 12°C during winter and 25°C during summer (Figure 8, Figure 89).

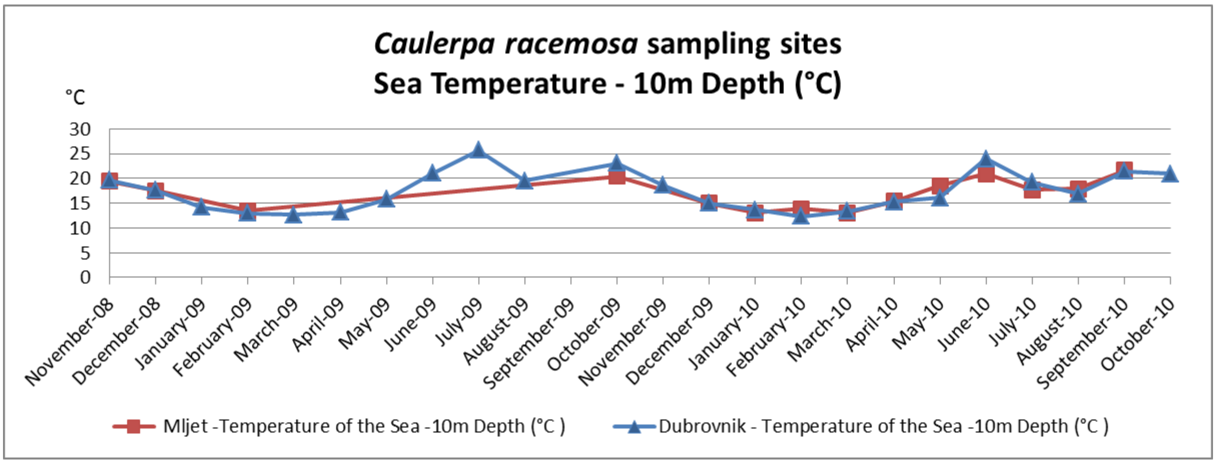

Figure 8. Temperature of the sea (°C) at the *Caulerpa racemosa* sampling sites from November 2008 till October 2010.

In order to compare the epiphytic diatom community on *Caulerpa* spp. with communities reported in previous studies and to provide information about host-dependence, particularly because of the existence of toxins characteristic for *Caulerpa* species, extensive sampling of the brown alga *Padina pavonica* (Linnaeus) Thivy and the green alga *Halimeda tuna* (J. Ellis & Solander) J.V. Lamouroux was conducted at the same time from the same localities.

Figure 9. *Padina pavonica* (arrow) in dense settlement of *Caulerpa taxifolia*, the Bay of Stari Grad, Island of Hvar, (Photo by Tonči Dulčić).

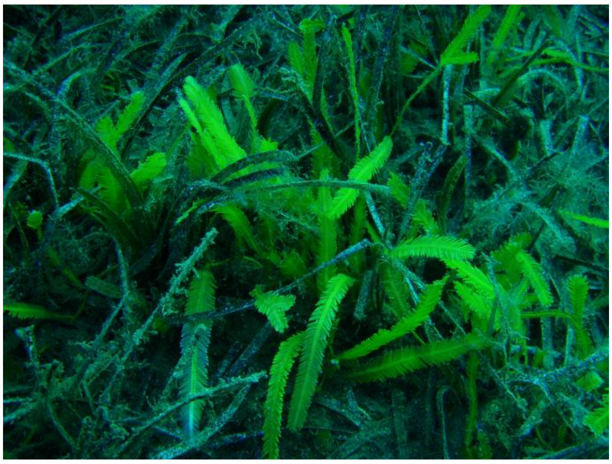

Figure 10. *Caulerpa taxifolia* and *Posidonia oceanica*, the Bay of Stari Grad, Island of Hvar, (Photo by Tonči Dulčić).

Samples of *Posidonia oceanica*, together with samples of the invasive *Caulerpa racemosa* were taken during autumn 2009 and 2010 by a SCUBA diver at depths of 10–15m in areas affected by *Caulerpa racemosa* near Dubrovnik. In addition samples of coexisting autochthonous seagrass *Posidonia oceanica* from seagrass beds affected by *C. taxifolia* in Stari Grad Bay were obtained in February 2012.

Caulerpa racemosa was chosen in order to compare the epiphytic diatom communities on two invasive *Caulerpa* species with different toxin contents. Finally, in order to compare and determine the epiphytic diatom community in areas affected by *Caulerpa racemosa*, *C. racemosa* and brown and green algae were also sampled from Mljet National Park.

Table 1. Schedule of sampling. A (Autumn). W (Winter) Sp (Spring) S (Summer).

SAMPLING SITE:			Dubrovnik				Mljet				Hvar				
SUBSTRAT:			Invasive algae		Autochthonous algae		Invasive algae		Autochthonous algae		Invasive algae			Autochthonous algae	
SEASON:	MONTH:	DATE:	*Caulerpa racemosa* - fronds	*Caulerpa racemosa*	*Padina pavonica*	*Halimeda tuna*	*Caulerpa racemosa* - fronds	*Caulerpa racemosa*	*Padina pavonica*	*Halimeda tuna*	*Caulerpa taxifolia* - fronds - top 2cm	*Caulerpa taxifolia* - fronds	*Caulerpa taxifolia*	*Padina pavonica*	*Halimeda tuna*
A	Nov-08	15.11.2008	X	X											
A		17.11.2008						X							
A		17.11.2008										X	X		
W	Dec-08	15.12.2008	X	X											
W		17.12.2008					X	X							
W		22.12.2008										X	X		
W	Jan-09	15.1.2009					X	X							
W		16.1.2009										X	X		
W	Feb-09	15.2.2009		X											
W		17.2.2009					X	X							
W		16.2.2009										X	X		
Sp	Mar-09	15.3.2009										X	X		
Sp		17.3.2009					X	X							
Sp	Apr-09	16.4.2009					X	X							
Sp		20.4.2009										X	X		
Sp	May-09	15.5.2009		X											
Sp		11.5.2009										X	X		
Sp		17.5.2009					X	X							
S	Jun-09	15.6.2009	X	X											
S		16.6.2009										X			
S		18.6.2009					X	X							
S	Jul-09	10.7.2009		X											
S		13.7.2009										X	X		
S		16.7.2009					X	X							
S	Aug-09	10.8.2009										X	X		
S		12.8.2009					X	X							
S		17.8.2009	X	X											
A	Sep-09	5.9.2009										X	X	X	X
A		9.9.2009					X	X							
A		11.9.2009			X	X									
A	Oct-09	12.10.2009										X	X	X	X
A		20.10.2009						X	X						
A		28.10.2009	X	X	X	X									
A	Nov-09	12.11.2009	X	X	X	X									
A		16.11.2009										X	X		X
A		20.11.2009						X	X						
W	Dec-09	17.12.2009		X		X									
W	Jan-10	11.1.2010										X	X	X	X
W		12.1.2010		X		X									
W		20.1.2010					X	X							
W	Feb-10	8.2.2010										X	X		X
W		15.2.2010								X					
Sp	Mar-10	10.3.2010				X									
Sp		13.3.2010										X	X	X	
Sp		17.3.2010						X							
Sp	Apr-10	12.4.2010										X	X	X	
Sp		21.4.2010						X		X					
Sp	May-10	18.5.2010										X		X	
Sp		19.5.2010				X									
Sp		25.5.2010					X	X		X					
S	Jun-10	15.6.2010									X	X	X	X	X
S		24.6.2010						X	X	X					
S	Jul-10	15.7.2010						X		X					
S		19.7.2010									X	X		X	X
S		21.7.2010			X										
S	Aug-10	15.8.2010									X	X		X	
S		17.8.2010								X					
S		24.8.2010		X	X	X									
A	Sep-10	14.9.2010					X	X	X	X					
A		16.9.2010									X	X	X	X	X
A		21.9.2010		X	X	X									
A	Oct-10	15.10.2010						X	X	X					
A		16.10.2010									X	X		X	
A		20.10.2010		X	X	X									

Table 2. Number of samples of each host at respective sampling sites.

Sampling site:	**Dubrovnik**	**Mljet**	**Hvar**	**TOTAL (No. of samples):**
Padina pavonica	7	5	11	23
Halimeda tuna	10	8	8	26
C. racemosa - fronds	6	13	0	19
Caulerpa racemosa	14	21	0	35
C. taxifolia -fronds - top 2cm	0	0	5	5
C. taxifolia - fronds	0	0	23	23
Caulerpa taxifolia	0	0	18	18
	37	47	65	149

Table 3. Sampling months throughout the seasons in 2008, 2009 and 2010.

Seasons:	**Winter**	**Spring**	**Summer**	**Autumn**
Months:	December 2008	March 2009	June 2009	November 2008
	January 2009	April 2009	July 2009	September 2009
	February 2009	May 2009	August 2009	October 2009
	December 2009	March 2010	June 2010	November 2009
	January 2010	April 2010	July 2010	September 2010
	February 2010	May 2010	August 2010	October 2010

Table 4. Number of samples of each host and during each season.

Season:	**Winter**	**Spring**	**Summer**	**Autumn**
Padina pavonica	1	3	6	13
Halimeda tuna	5	4	6	11
C. racemosa - fronds	5	4	5	5
Caulerpa racemosa	8	7	9	11
C. taxifolia -fronds - top 2cm	0	0	3	2
C. taxifolia - fronds	5	6	6	6
Caulerpa taxifolia	5	5	3	5
TOTAL (No. of samples):	29	29	38	53

Table 5. Number of samples on each sampling site during each season.

Season: Sampling site:	**Winter**	**Spring**	**Summer**	**Autumn**	**TOTAL (No. of samples):**
Dubrovnik	7	3	9	18	37
Mljet	9	12	12	14	47
Hvar	13	14	17	21	65
TOTAL (No. of samples):	29	29	38	53	149

Samples on which ultrastructural analysis of unidentified *Cocconeis*, described as *C. caulerpacola* was performed with SEM and TEM, were obtained from thalli of *Caulerpa taxifolia* collected during summer and autumn 2008 and in 2010 by SCUBA diving, in the Bay of Stari Grad (Island of Hvar), as well as at the following localities (Figure 11):

- The coast of the north-western Mediterranean Sea at Saint Raphaël, west of Cannes, France (approximately 43° 25' N, 6° 46' E). Sampling was performed during summer/autumn (August and September 2008). Non-native *C. taxifolia* is abundant (an established invader) at this location.

- The eastern coast of Australia in Moreton Bay, south-east Queensland (approximately 27.5° S, 153.3° E), where samples of native *C. taxifolia* were collected during February and March 2010 (Australian summer/autumn). Moreton Bay is a shallow subtropical bay with an average depth of 6.8 m, 45km from Brisbane.

The sampling sites of *C. taxifolia* in France and Australia were quite shallow (5–8m depth) and water temperature amounted to 19–25°C. *Caulerpa taxifolia* was carefully detached without damaging the fronds from the seafloor at depth of *c.* 5m.

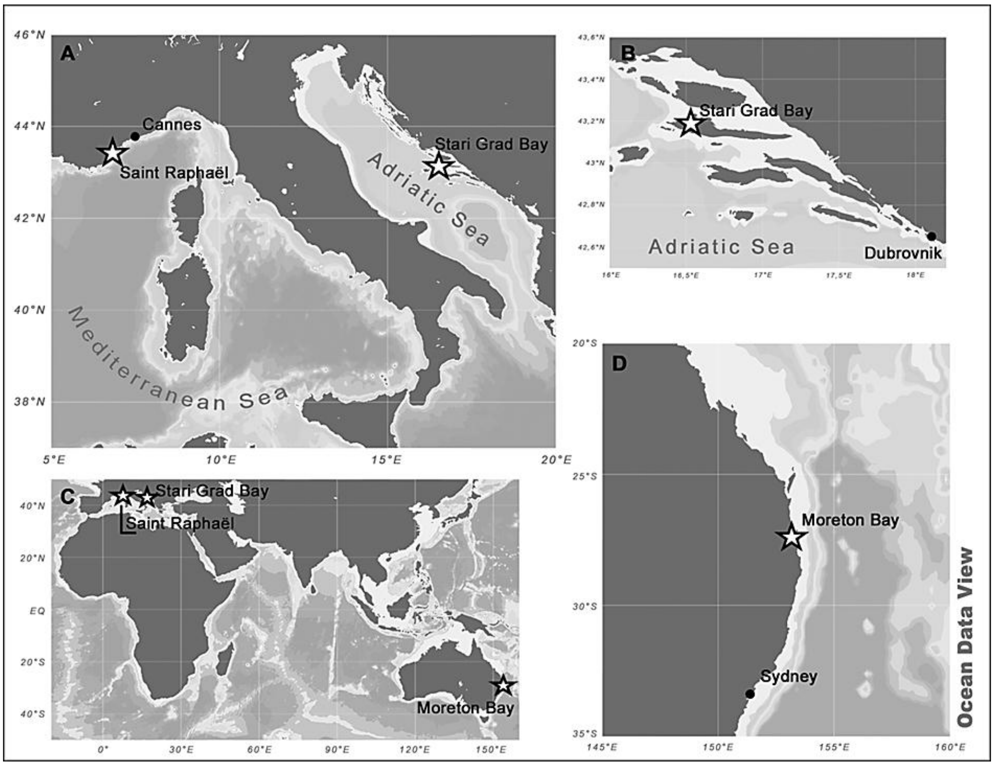

Figure 11. (a-b) Map of the Mediterranean Sea showing the position of the sampling sites of invasive *Caulerpa taxifolia* in France and Croatia. (c) Overview of the locations of sampling sites of *Caulerpa taxifolia*. (d) Location of sampling site of native populations of *Caulerpa taxifolia* in Australia.

Observations of *Cocconeis diruptoides* and *C. pseudodiruptoides* were made on samples from areas affected by *Caulerpa* spp. in Adriatic Sea, as well as on cleaned material obtained from the Hustedt Diatom Collection in Bremerhaven, Germany (material E 74, collected in July 1904 on Ravnik near the island of Vis, Adriatic Sea, Croatia). *Cocconeis borbonica* Riaux-Gobin & Compère was examined in a sample collected from the western Indian Ocean (Juan de Nova Island, collected by A. Witkowski in April 2009).

In order to make detailed analysis of epiphytic diatom assemblages of fronds of *Caulerpa taxifolia* and to describe their seasonal dynamics on a fine time scale, the top 2cm of *Caulerpa taxifolia* fronds from island of Hvar samples were cut and prepared for diatom analysis during summer and autumn 2010. (Figure 12).

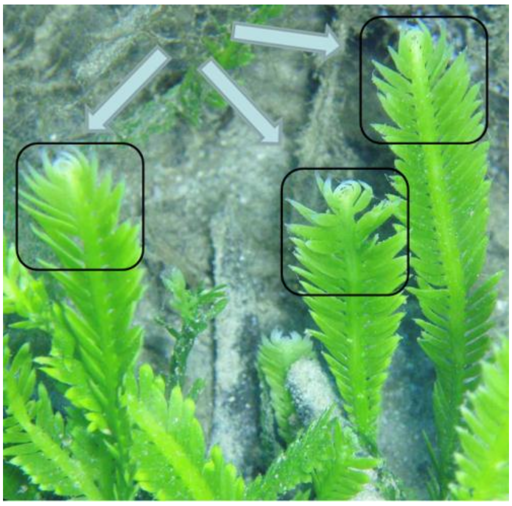

Figure 12. *Caulerpa taxifolia*, the Bay of Stari Grad, Island of Hvar, cut of top 2cm (Photo by Tonči Dulčić).

2.2. Laboratory methods

Samples were cleaned of organic material for LM and electron microscopy (EM) observations by boiling with 30% H_2O_2 and adding 10% HCl to remove $CaCO_3$.They were then rinsed with deionized water, pipetted onto ethanol-cleaned cover-slips and left to air dry, before mounting in Naphrax®.

2.2.1. Light microscopy

Specimens of *C. caulerpacola* were photographed with a Nikon Eclipse 600 light microscope (Nikon, Tokyo, Japan) equipped with differential interference contrast (DIC), and a Zeiss Axioskop (Phase Contrast and DIC) (Zeiss, Jena, Germany), in both cases using a 100x oil immersion planapochromatic objective (n.a. = 1.40). A few images were also taken from our material using advanced light photomicrography by ing. Wulf Herwig: for a detailed description of this method see:

http://www.microscopy-uk.org.uk/mag/artmar11/Advanced_Light_Photomicrography.pdf

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2.2.2. Electron microscopy

Ultrastructural analysis was performed with SEM and TEM. A drop of the cleaned sample was air-dried overnight on aluminium stubs and coated with gold–palladium or osmium. SEM observations were primarily made at the Warsaw University of Technology, Faculty of Materials Science and Engineering, using a Hitachi S-3500, SU-70 and SEM/ STEM S-5500. In the latter instrument the specimens can be observed either in in scanning or transmission mode. Further SEM observations were done at the University of Frankfurt using a Hitachi S-4500 (Hitachi, Tokyo, Japan). Selected parts of C. taxifolia thalli were dried in liquid carbon dioxide and sputter coated in order to observe diatom assemblages in situ in SEM, using the Hitachi S-4500.

2.3. Taxonomic references

Slides and prepared material have been deposited in the diatom collection (SZCZ) of the Institute of Marine Sciences, University of Szczecin, Szczecin (Poland). Terminology follows Round et al. (1990). The relative abundance of particular taxa and the taxa richness of the assemblages were estimated on the basis of at least 300 diatom valves counted per sample.

2.4. Statistical analysis

Cluster analysis (Legendre & Legendre, 1978) was used to analyse the variability in species composition over seasons and among sites and substrates. This was based on a matrix of 70 taxa over 76 samples. The dendrogram was based on standardized cell abundance data.

Table 6. MDS ordination was made on a base of 76 samples collected in parallel during the period of one year (autumn 2009 - autumn 2010) from three locations.

Sampling site:	**Dubrovnik**	**Mljet**	**Hvar**	**TOTAL (No. of samples):**
Padina pavonica	7	5	11	23
Halimeda tuna	10	8	8	26
Caulerpa racemosa	7	11	0	18
Caulerpa taxifolia	0	0	9	9
TOTAL (No. of samples):	24	24	28	76

Species richness was characterized by Shannon-Wiener Biodiversity Index (Krebs, 1999):

$$H = -\sum_{i=1}^{s} \rho_i \log_2 \rho_i$$

where H is the Shannon-Wiener diversity, s is the total number of species and p_i is the proportional abundance of i-th species.

Similarities in terms of microalgal abundance between two sampling sites with non-native *Caulerpa taxifolia* and among different parts of *Caulerpa taxifolia* were tested using the Bray-Curtis similarity. Analyses of similarity for the taxa were performed to identify a priori differences among the two sites with introduced *Caulerpa taxifolia* (France and Croatia). Macroalgal thalii were subdivided into four groups as follows: fronds, stolon with rhizoidal pillars and rhizoids, water in which *Caulerpa taxifolia* was washed, and water squeezed from specimens of *Caulerpa taxifolia*. Subsamples of fronds and stolon with rhizoids were used for analyses of differences in the abundance of the diatoms between apical and the basal parts of *Caulerpa taxifolia*.

Table 7. Samples used in Bray-Curtis similarity analyses (numbers in Table 7 refer to diatom collection of Palaeoceanology Unit, University of Szczecin (SZCZ).

Subsamples:	**France**	**Croatia**
stolon + rhizoidal pillars + rhizoides of *Caulerpa taxifolia*	12937	13085
fronds of *Caulerpa taxifolia*	12938	13084
H_2O	12939	/
H_2O (squeezed thalli of *Caulerpa taxifolia*)	12940	13081

ANOSIM randomization (Clarke & Warwick, 1994) was used to test for significant differences in diatom community structure between *Padina pavonica* and *Halimeda tuna* across seasons and sites. For this purpose, a matrix of 631 species and 49 samples was subjected to MDS (multivariate analysis) tools. The dissimilarity percentage programme (SIMPER, Clarke & Warwick, 1994) was used to identify the taxa making the greatest contribution to differences between clusters observed in the MDS plot.

All statistical analyses were performed using PRIMER v5 software (Clarke & Gorley, 2001; Wilkinson, 1986) and PRIMER v6 software (Clarke & Gorley, 2006).

3. RESULTS

A total of 61043 diatom valves were counted from 149 samples. From these samples, altogether 631 diatom taxa belonging to 80 genera were identified from three locations between autumn 2008 and 2010. The average number of taxa per sample was 54, while the maximum was 102 and the minimum 18.

The most abundant genera were *Cocconeis* Ehrenberg 1837, *Mastogloia* Thwaites ex Smith 1856, *Nitzschia* Hassall 1845, *Navicula* Bory de Saint-Vincent 1822, *Amphora* Ehrenberg ex Kützing 1844, *Hyalosynedra* Williams & Round 1986, *Licmophora* Agardh 1827, *Grammatophora* Ehrenberg 1840, *Tabularia* (Kützing) D.M.Williams & Round 1986, *Berkeleya* Greville 1827, *Pseudostaurosira* D.M.Williams & Round 1987, *Diploneis* Ehrenberg ex Cleve, 1894, *Rhopalodia* O. Müller 1895., *Ardissonea* De Notaris 1870 *and Toxarium* J.W. Bailey 1854. Together, these genera represented more than 85% of the total epiphytic diatoms.

Table 8. Dominant diatom genera with frequency of appearance (Freq.) > 50%. Avg. – average abundance. N = 149.

Genus:	**Freq. (%)**	**Avg. (%)**
Cocconeis	100.00%	37.25%
Mastogloia	97.32%	15.13%
Nitzschia	99.33%	8.17%
Navicula	100.00%	7.89%
Amphora	97.99%	6.36%
Hyalosynedra	99.33%	5.84%
Licmophora	93.29%	5.22%
Grammatophora	78.52%	3.05%
Tabularia	92.62%	1.96%
Berkeleya	68.46%	1.79%
Pseudostaurosira	79.19%	1.78%
Ardissonea	76.51%	1.52%
Toxarium	68.46%	1.41%
Diploneis	83.89%	1.34%
Rhopalodia	49.66%	1.15%

Genera *Cocconeis* and *Navicula* were recorded in all samples, while genera *Mastogloia*, *Nitzschia*, *Amphora*, *Hyalosyendra*, *Licmophora* and *Tabularia* occurred in more than 92% of the samples (Table 8).

Genera with the greatest number of taxa (more than 60) were *Mastogloia*, *Nitzschia* and *Amphora*. *Mastogloia crucicula* var. *alternans* Zanon, *Mastogloia crucicula* (Grunow) Cleve var. *crucicula* and *Mastogloia binotata* (Grunow) Cleve occurred in more than 84% of the samples. Genus *Cocconeis* occurred in 29 taxa (Table 14). Some of them, like *Cocconeis scutellum* Ehrenberg var. *scutellum* and *Cocconeis molesta* var. *crucifera* Grunow in Van Heurck, were recorded in all samples. Apart from these, the most frequently observed diatom taxa were *Cocconeis caulerpacola* Witkowski, Car & Dobosz, *Hyalosynedra laevigata*

(Grunow) Williams & Round, *Navicula ramosissima* (Agardh) Cleve, *Nitzschia angularis* W. Smith and *Nitzschia lanceolata* var. *minima* Grunow.

These mentioned 10 taxa (Table 9) were the most abundant group in the epiphytic diatom community dominating in terms of both frequency of appearance (> 45%) and abundance in total number of samples (>1%). Diatom taxa of *Cocconeis* and *Mastogloia* were considered dominant in the epiphytic assemblage with 60% of dominant 10 taxa belonging to these genera.

As genera *Cocconeis* and *Mastogloia* were two of the most frequently identified and were the most abundant, this study was focused particularly on these genera.

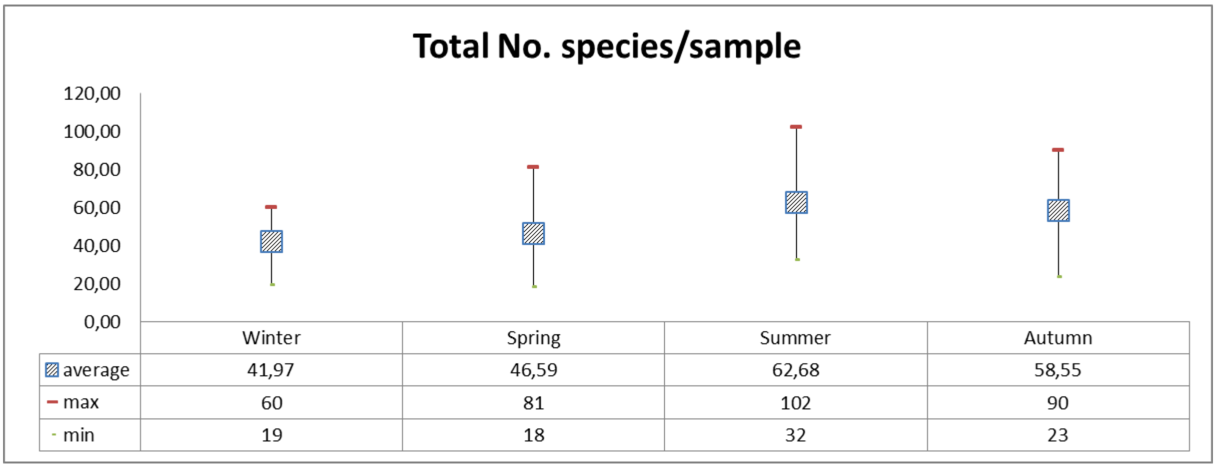
Table 9. Dominant diatom taxa with frequency of appearance (Freq.) > 45%. Avg. – average abundance (%). Max. - maximum abundance. N = 149.

Taxa:	**Freq. (%)**	**Avg.(%)**	**Max.(%)**
Cocconeis caulerpacola Witkowski, Car & Dobosz	45.64%	9.19%	62.99%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	100.00%	8.50%	32.60%
Cocconeis scutellum Ehrenberg var. *scutellum*	100.00%	20.41%	72.84%
Hyalosynedra laevigata (Grunow) Williams & Round	99.33%	5.84%	25.07%
Mastogloia binotata (Grunow) Cleve	84.56%	2.15%	21.47%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	90.60%	2.15%	10.67%
Mastogloia crucicula var. *alternans* Zanon	91.28%	2.34%	14.93%
Navicula ramosissima (Agardh) Cleve	91.28%	6.21%	18.72%
Nitzschia angularis W. Smith	92.62%	2.88%	15.16%
Nitzschia lanceolata var. *minima* Grunow	83.89%	2.50%	8.76%

3.1. Biodiversity - Seasonal aspect

Seasonal changes within diatom assemblages on particular substrates resulted from a presence of some genera which appeared only in particular seasons. Among such genera are e.g. *Rhaphoneis* Ehrenberg which occurred only in autumn and winter, and *Terpsinoë* Ehrenberg which was recorded only in spring (April/May 2010) in the Stari Grad Bay. Likewise seasonal variation was also influenced by occurrences of some rare taxa of abundant genera. Some taxa of genus *Mastogloia* appeared only in particular seasons and the highest number of these was recorded in autumn and summer on all sampling sites (Figure 23).

In summer season, considering all three locations (Dubrovnik, Mljet, Hvar) and all substrates of epiphytic diatoms (*Caulerpa* spp., *Padina pavonica*, *Halimeda tuna*) during the two year period (autumn 2008 – autumn 2010), the average number of taxa amounted to 63 per sample, with a maximum of 102 observed in August 2009 (Hvar, *Caulerpa taxifolia*) (Figure 13).



	Winter	Spring	Summer	Autumn
▨ average	41,97	46,59	62,68	58,55
— max	60	81	102	90
· min	19	18	32	23

Figure 13. Box and Whisker Plot of number of taxa considering all three locations (Dubrovnik, Mljet, Hvar) and all substrates of epiphytic diatoms (*Caulerpa* spp., *Padina pavonica*, *Halimeda tuna*) during two year period (autumn 2008 – autumn 2010). N = 149.

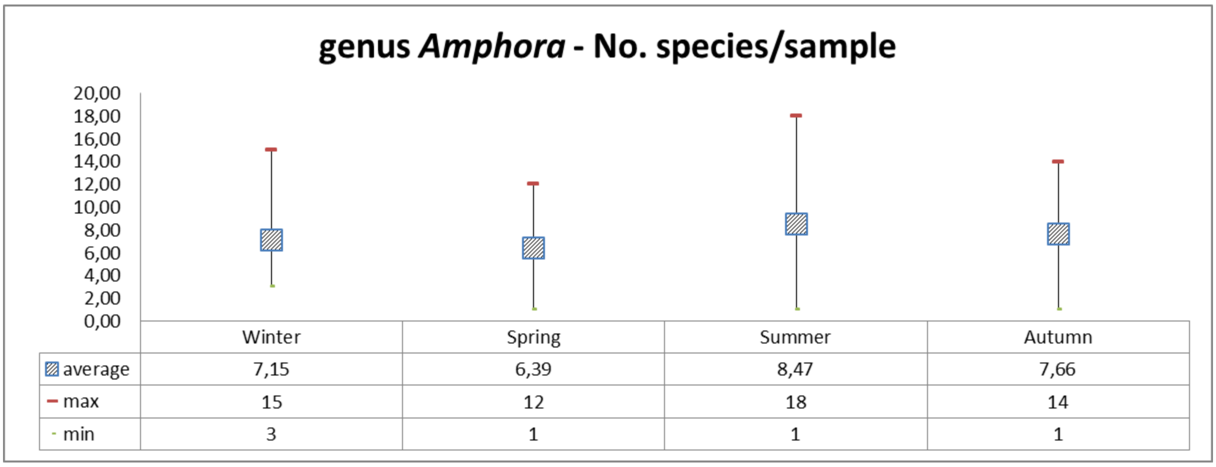
Distribution of dominant genera abundances over time showed that the majority of these genera reached high abundance during summer (Table 10).

Table 10. Average seasonal abundance of dominant genera. N = 149.

Genus:	**Average Seasonal Abundance (%):**			
	Winter	**Spring**	**Summer**	**Autumn**
Cocconeis	49.85%	32.81%	25.06%	32.28%
Mastogloia	8.61%	8.25%	17.82%	22.93%
Nitzschia	6.16%	6.56%	11.81%	9.42%
Navicula	6.70%	7.42%	9.87%	9.11%
Amphora	7.44%	7.48%	7.10%	5.95%
Hyalosynedra	5.32%	5.54%	7.40%	5.34%
Licmophora	4.68%	10.91%	3.60%	2.21%
Grammatophora	2.70%	4.36%	2.30%	2.33%
Tabularia	2.49%	2.97%	1.42%	1.17%
Berkeleya	0.60%	2.90%	2.17%	1.69%
Pseudostaurosira	2.48%	3.18%	1.06%	0.79%
Ardissonea	0.51%	1.88%	1.73%	1.07%
Toxarium	1.02%	1.08%	1.59%	1.35%
Diploneis	1.13%	1.13%	1.67%	1.47%
Rhopalodia	0.89%	0.51%	1.36%	1.27%

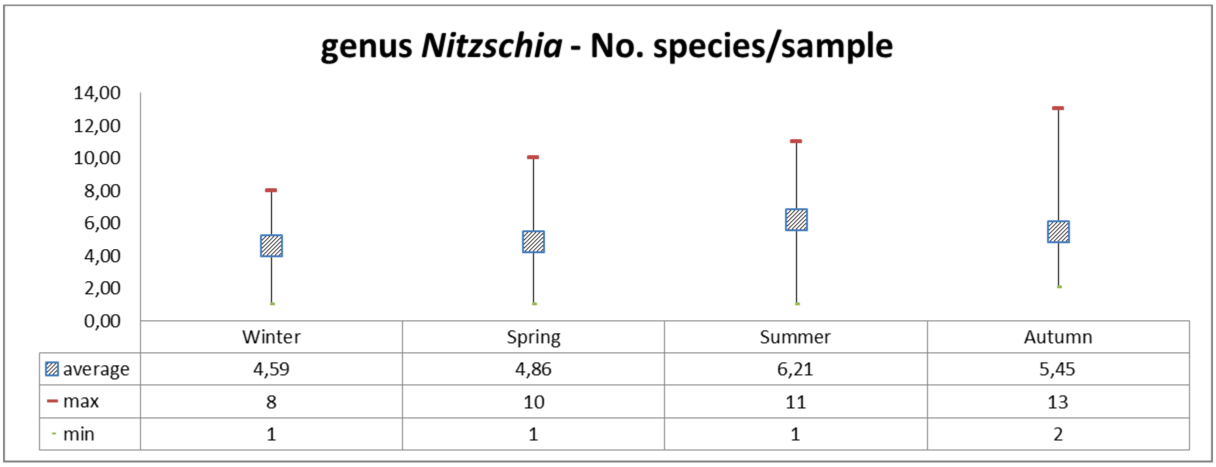
While genus *Mastogloia* reached high abundance during summer and autumn (17% and 22%, respectively), genus *Cocconeis* reached high abundance during winter (50%) and spring (33%). Genus *Licmophora* reached high abundance (11%) and occurred with highest number of taxa per sample during spring (Figure 17).

During the spring season a minimum number (18) of taxa in one sample (Mljet, *Caulerpa racemosa*, March 2009) was recorded. Genus *Amphora* occurred with the lowest number of taxa during spring (Figure 14). Considering all three locations (Dubrovnik, Mljet, Hvar) and all substrates (*Caulerpa* spp., *Padina pavonica*, *Halimeda tuna*), the average number of taxa of genus *Amphora* was only 6.39 per single sample during spring. Genus *Amphora* occurred throughout all seasons with average abundance of 7%. With average abundance of 7% genus *Hyalosynedra* occurred in summer while during other seasons abundance was around 5%. Genus *Grammatophora* reached higher abundance (4%) during spring, as did genus *Pseudostaurosira* (3%). Genera *Nitzschia* and *Navicula* occurred with higher abundances and higher number of taxa per sample during summer and autumn. No particular seasonality was observed for genus *Diploneis* (Figure 18).



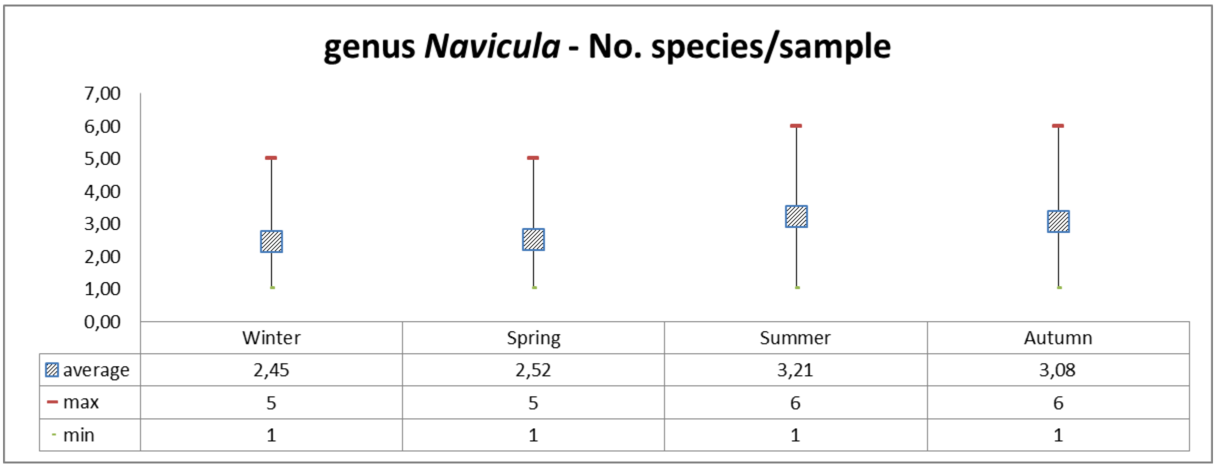
	Winter	Spring	Summer	Autumn
▨ average	7,15	6,39	8,47	7,66
− max	15	12	18	14
- min	3	1	1	1

Figure 14. Box and Whisker Plot of number of taxa of genus *Amphora*. N = 149.



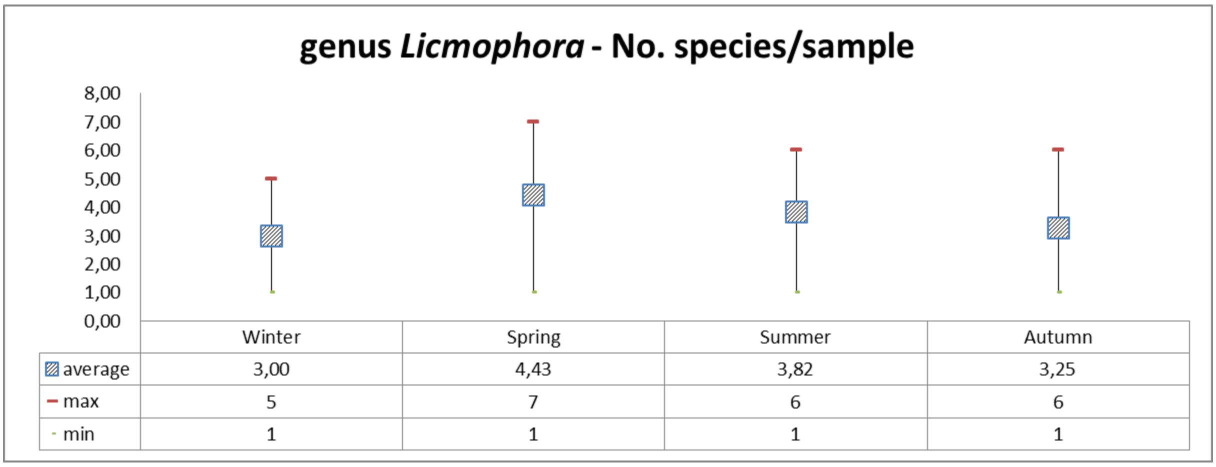
	Winter	Spring	Summer	Autumn
▨ average	4,59	4,86	6,21	5,45
− max	8	10	11	13
- min	1	1	1	2

Figure 15. Box and Whisker Plot of number of taxa of genus *Nitzschia*. N = 149.



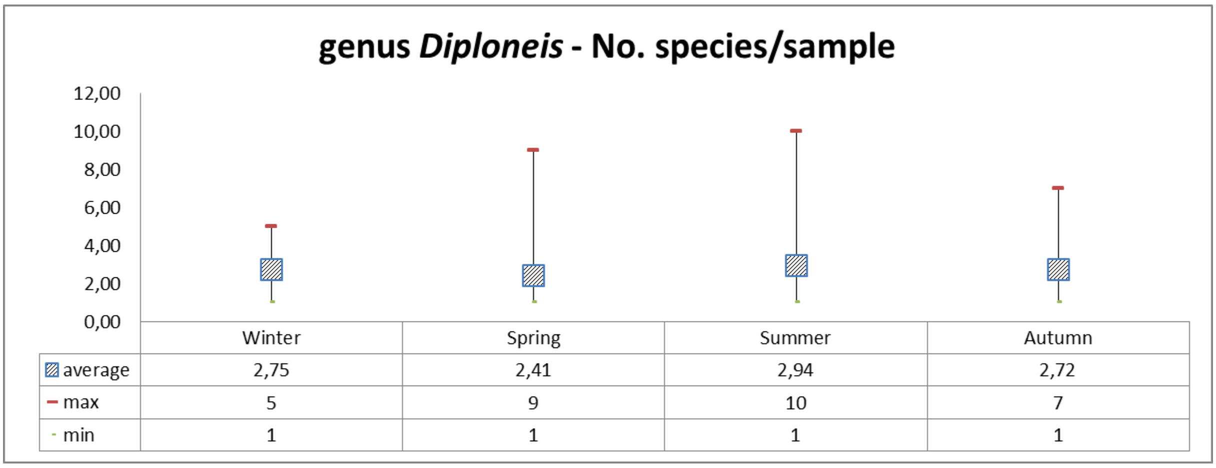
	Winter	Spring	Summer	Autumn
▨ average	2,45	2,52	3,21	3,08
− max	5	5	6	6
- min	1	1	1	1

Figure 16. Box and Whisker Plot of number of taxa of genus *Navicula*. N = 149.



	Winter	Spring	Summer	Autumn
▨ average	3,00	4,43	3,82	3,25
– max	5	7	6	6
- min	1	1	1	1

Figure 17. Box and Whisker Plot of number of taxa of genus *Licmophora*. N = 149.



	Winter	Spring	Summer	Autumn
▨ average	2,75	2,41	2,94	2,72
– max	5	9	10	7
- min	1	1	1	1

Figure 18. Box and Whisker Plot of number of taxa of genus *Diploneis*. N = 149.

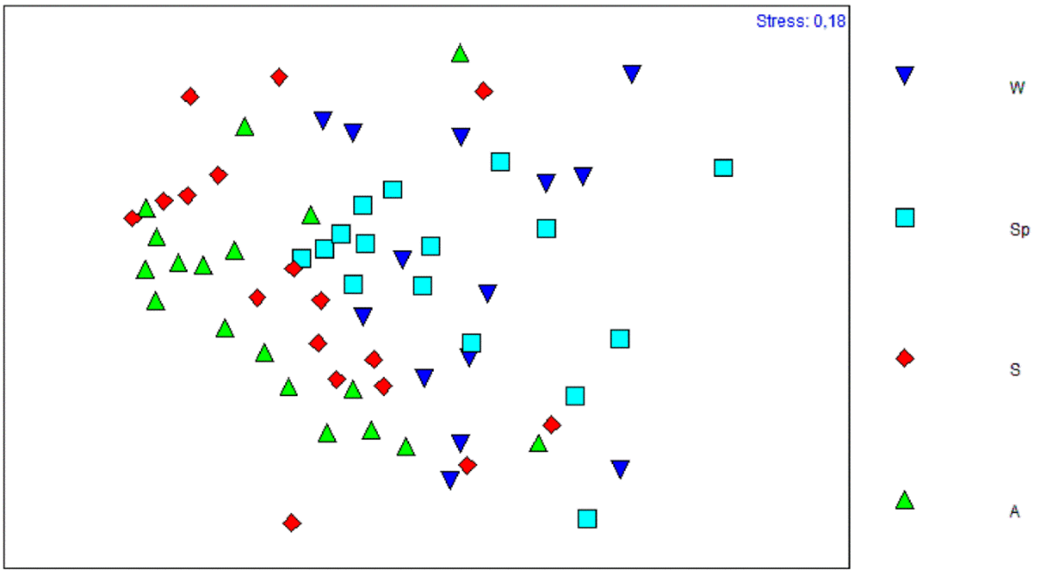


Figure 19. Two-dimensional configuration (non-metric multi-dimensional scaling ordination) of the epiphytic diatom assemblages on all substrates at all three sampling sites during the two year period (taxa abundance data, stress value = 0,18). For the ordination analysis, only the ten most common diatom taxa were used. Common taxa included those with a mean relative abundance >1% or a maximum relative abundance >8%. Symbols W (winter), Sp (spring), S (summer), A (autumn). N(W) = 14; N(Sp) = 16; N(S) = 17; N(A) = 18.

Distribution of dominant taxa abundances over time showed that the majority of these taxa except *Cocconeis scutellum* var. *scutellum* had their peaks in abundances in summer and autumn (Table 11). While *Cocconeis molesta* var. *crucifera* did not show particular seasonality, the other taxa of genus *Cocconeis*, *Cocconeis caulerpacola* showed strong seasonality and reached highest abundance during autumn.

Table 11. Average seasonal abundance of 10 dominant taxa. N = 149.

Taxa:	**Average Seasonal Abundance (%):**			
	Winter	**Spring**	**Summer**	**Autumn**
Cocconeis caulerpacola Witkowski, Car & Dobosz	4.01%	0.55%	5.06%	17.90%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	8.96%	9.42%	8.90%	7.42%
Cocconeis scutellum Ehrenberg var. *scutellum*	32.33%	26.13%	14.08%	15.19%
Hyalosynedra laevigata (Grunow) Williams & Round	5.59%	5.31%	7.29%	5.53%
Mastogloia binotata (Grunow) Cleve	0.93%	1.20%	2.52%	2.85%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.94%	1.63%	2.28%	2.40%
Mastogloia crucicula var. *alternans* Zanon	2.38%	1.30%	2.17%	2.90%
Navicula ramosissima (Agardh) Cleve	5.18%	6.00%	7.13%	6.18%
Nitzschia angularis W. Smith	2.51%	2.08%	3.64%	2.96%
Nitzschia lanceolata var. *minima* Grunow	1.65%	1.67%	2.42%	3.23%

Table 12. Comparison of average monthly abundances (%) of 10 dominant taxa. N = 149.

Taxa: **Season:**	**Winter**					
Months:	**Dec-08**	**Dec-09**	**Jan-09**	**Jan-10**	**Feb-09**	**Feb-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	10.42%	0.90%	0.95%	0.26%	0.76%	0.00%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	8.36%	6.30%	9.97%	7.26%	8.55%	14.11%
Cocconeis scutellum Ehrenberg var. *scutellum*	28.04%	38.32%	44.02%	34.96%	34.38%	16.23%
Hyalosynedra laevigata (Grunow) Williams & Round	4.43%	2.94%	9.77%	3.66%	9.12%	4.77%
Mastogloia binotata (Grunow) Cleve	1.40%	1.60%	0.51%	0.78%	0.37%	1.00%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.53%	3.92%	0.96%	2.15%	1.17%	2.17%
Mastogloia crucicula var. *alternans* Zanon	2.70%	3.49%	1.15%	3.45%	0.90%	1.82%
Navicula ramosissima (Agardh) Cleve	6.44%	6.47%	3.55%	4.71%	4.78%	5.72%
Nitzschia angularis W. Smith	3.29%	3.93%	0.47%	3.58%	1.24%	1.85%
Nitzschia lanceolata var. *minima* Grunow	2.94%	0.82%	1.21%	1.47%	0.55%	1.46%
Taxa: **Season:**	**Spring**					
Months:	**Mar-09**	**Mar-10**	**Apr-09**	**Apr-10**	**May-09**	**May-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	0.99%	0.79%	0.26%	0.00%	0.45%	0.47%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	10.72%	6.95%	11.69%	6.12%	15.16%	7.08%
Cocconeis scutellum Ehrenberg var. *scutellum*	44.22%	15.82%	35.33%	15.21%	36.22%	17.21%
Hyalosynedra laevigata (Grunow) Williams & Round	4.04%	4.89%	6.00%	5.81%	4.95%	5.93%
Mastogloia binotata (Grunow) Cleve	0.23%	0.56%	0.85%	0.48%	0.41%	3.35%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.60%	1.09%	1.05%	2.03%	1.63%	2.12%
Mastogloia crucicula var. *alternans* Zanon	0.86%	1.90%	0.73%	1.02%	2.14%	0.99%
Navicula ramosissima (Agardh) Cleve	3.88%	5.29%	6.63%	4.95%	6.16%	8.10%
Nitzschia angularis W. Smith	1.38%	2.22%	0.75%	2.20%	2.15%	3.23%
Nitzschia lanceolata var. *minima* Grunow	0.74%	2.55%	1.29%	1.35%	1.98%	1.59%
Taxa: **Season:**	**Summer**					
Months:	**Jun-09**	**Jun-10**	**Jul-09**	**Jul-10**	**Aug-09**	**Aug-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	1.75%	2.20%	1.90%	3.34%	8.27%	13.33%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	20.80%	9.60%	6.54%	5.84%	7.17%	5.86%
Cocconeis scutellum Ehrenberg var. *scutellum*	32.52%	12.20%	18.10%	10.19%	11.70%	6.10%
Hyalosynedra laevigata (Grunow) Williams & Round	4.20%	10.54%	10.28%	7.29%	6.34%	4.48%
Mastogloia binotata (Grunow) Cleve	1.30%	1.66%	2.40%	2.53%	2.11%	4.45%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.43%	2.35%	2.08%	3.79%	1.09%	2.46%
Mastogloia crucicula var. *alternans* Zanon	0.75%	2.19%	1.58%	3.61%	1.25%	2.86%
Navicula ramosissima (Agardh) Cleve	3.70%	13.34%	4.94%	8.34%	5.56%	6.31%
Nitzschia angularis W. Smith	1.36%	4.19%	1.05%	4.85%	2.26%	5.76%
Nitzschia lanceolata var. *minima* Grunow	2.25%	1.95%	2.18%	2.14%	3.01%	2.24%
Taxa: **Season:**	**Autumn**					
Months:	**Sep-09**	**Sep-10**	**Oct-09**	**Oct-10**	**Nov-08**	**Nov-09**
Cocconeis caulerpacola Witkowski, Car & Dobosz	12.60%	20.24%	18.31%	17.31%	18.73%	29.49%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	4.09%	5.06%	8.46%	8.00%	10.87%	9.86%
Cocconeis scutellum Ehrenberg var. *scutellum*	7.51%	6.53%	18.25%	9.53%	25.98%	29.83%
Hyalosynedra laevigata (Grunow) Williams & Round	5.84%	4.23%	5.00%	5.67%	10.51%	4.66%
Mastogloia binotata (Grunow) Cleve	3.09%	4.62%	3.09%	1.76%	1.02%	1.91%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.93%	1.67%	1.56%	5.02%	2.04%	2.02%
Mastogloia crucicula var. *alternans* Zanon	2.02%	2.06%	2.80%	5.33%	0.87%	3.51%
Navicula ramosissima (Agardh) Cleve	8.34%	5.46%	5.98%	7.63%	3.37%	5.58%
Nitzschia angularis W. Smith	2.89%	2.73%	2.32%	4.55%	1.86%	2.96%
Nitzschia lanceolata var. *minima* Grunow	4.57%	3.20%	2.69%	2.82%	2.07%	1.72%

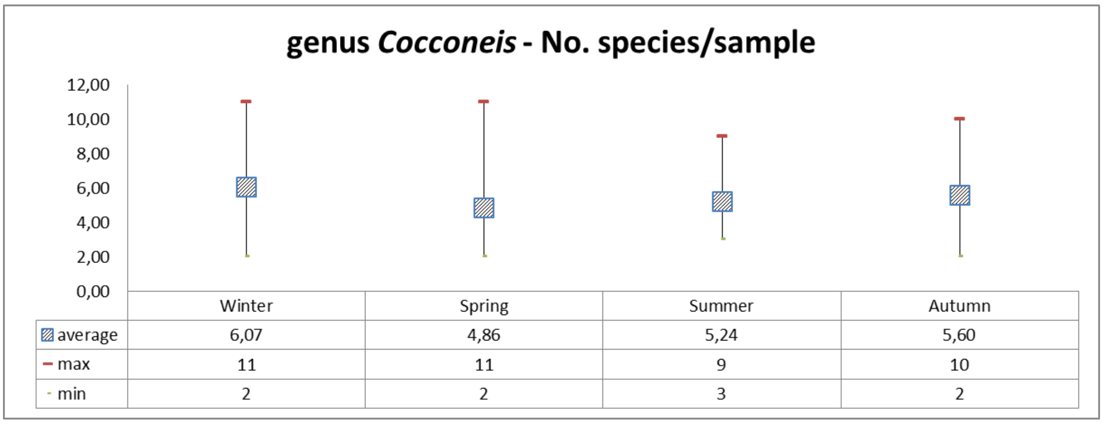


Figure 20. Box and Whisker Plot of number of taxa of genus *Cocconeis*. N = 149.

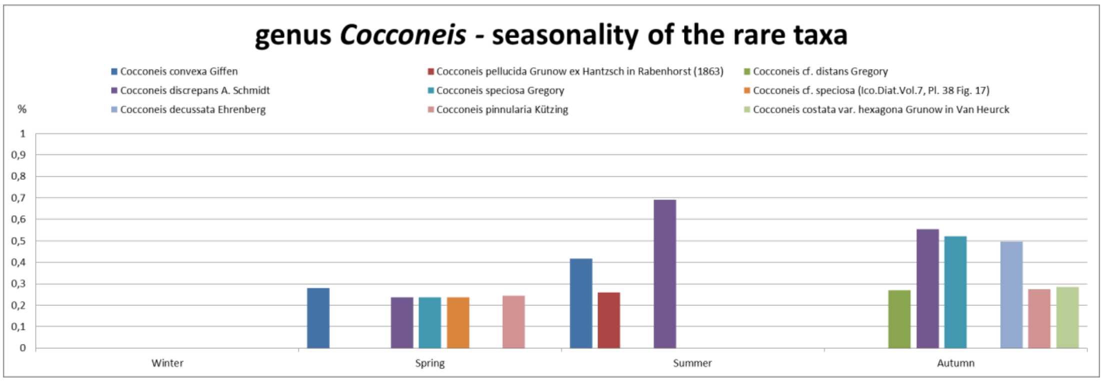


Figure 21. Seasonality of the 9 rare taxa of genus *Cocconeis* which abundance is less than 1%. N = 149.

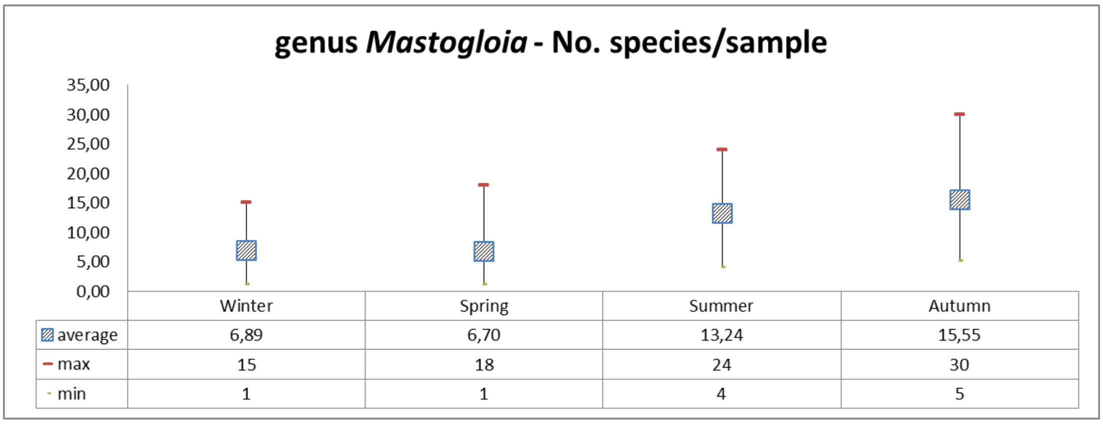


Figure 22. Box and Whisker Plot of number of taxa of genus *Mastogloia* during different seasons. N = 149.

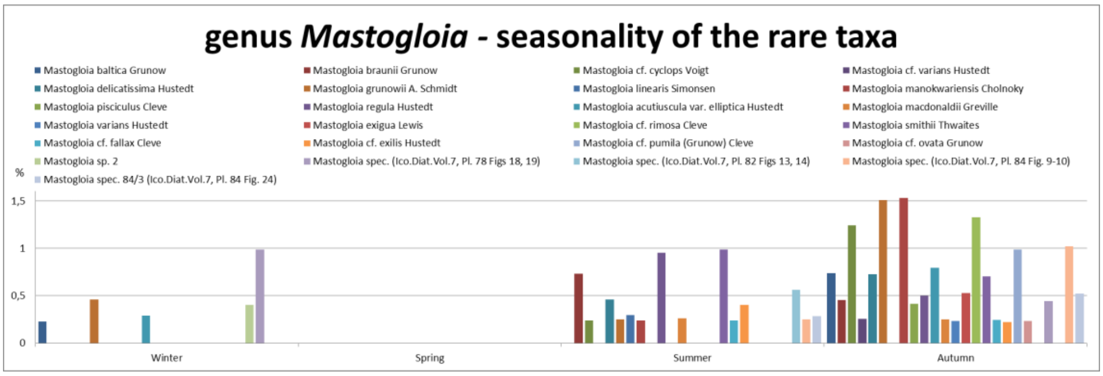


Figure 23. Seasonality of the 25 rare taxa of genus *Mastogloia* which abundance is less than 1.5%. N = 149.

3.2. Biodiversity - Comparison among sites

The species composition of epiphytes of Mljet was, in part, similar to diatom assemblages of the Bay of Stari Grad (island of Hvar) and also to that of the location Orsula near Dubrovnik.

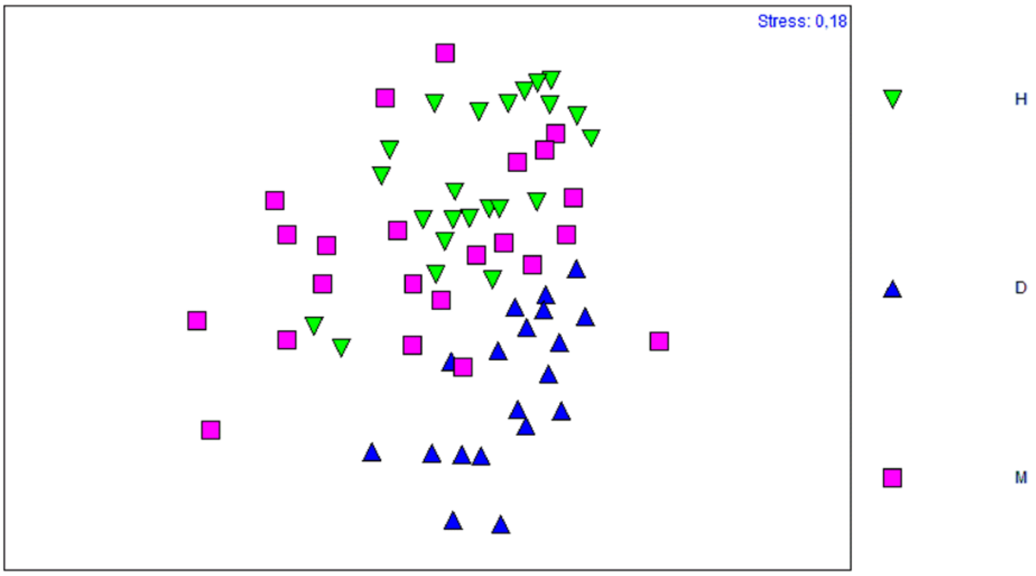


Figure 24. Two-dimensional configuration (non-metric multi-dimensional scaling ordination) of the epiphytic diatom assemblages of all taxa recorded on all substrates at all three sampling sites during the two year period (taxa abundance data, stress value = 0.18). Symbols H (Hvar), D (Dubrovnik), M (Mljet). N (Hvar) = 23; N (Dubrovnik) = 18; N (Mljet) = 23.

Some taxa which appeared specifically on some hosts like *Cocconeis caulerpacola* on invasive algae, particularly on *Caulerpa taxifolia*, had an impact on the difference between sampling sites.

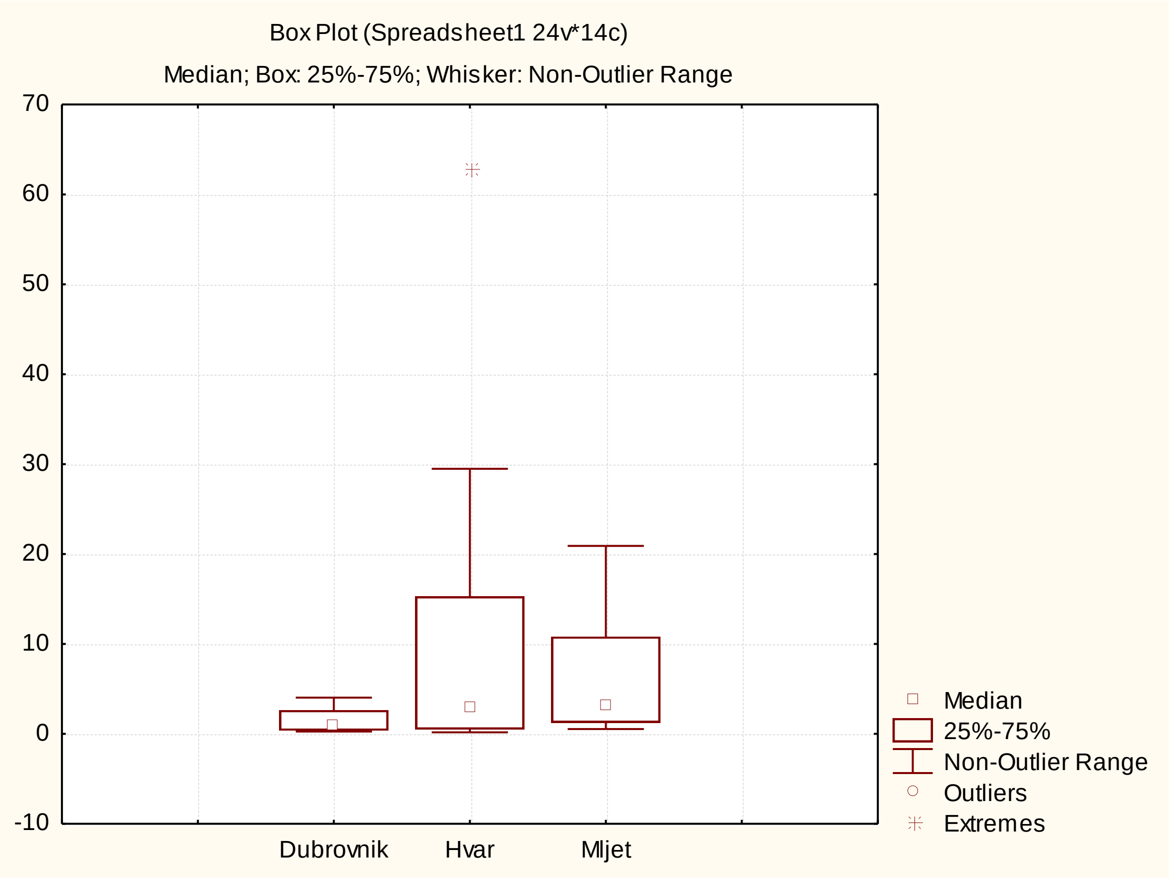


Figure 25. Box and Whisker Plot showing differences in abundance of *Cocconeis caulerpacola* on three sampling sites.

Considering all substrates (*Caulerpa* spp., *Padina pavonica*, *Halimeda tuna*) and epiphytic diatoms during the two year period (autumn 2008 – autumn 2010) the average abundances of 10 dominant taxa were computed for three sampling sites (Dubrovnik, Mljet, Hvar) (Table 13).

Table 13. Average site abundance of 10 dominant taxa. N = 149.

Taxa:	**Average Site Abundance (%):**		
	Dubrovnik	**Mljet**	**Hvar**
Cocconeis caulerpacola Witkowski, Car & Dobosz	1.04%	5.89%	12.81%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	11.75%	6.36%	8.17%
Cocconeis scutellum Ehrenberg var. *scutellum*	25.72%	25.49%	13.62%
Hyalosynedra laevigata (Grunow) Williams & Round	2.55%	4.68%	8.78%
Mastogloia binotata (Grunow) Cleve	3.36%	2.83%	0.94%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	2.58%	2.00%	2.01%
Mastogloia crucicula var. *alternans* Zanon	3.65%	1.89%	1.85%
Navicula ramosissima (Agardh) Cleve	6.83%	6.11%	5.84%
Nitzschia angularis W. Smith	4.08%	2.61%	2.33%
Nitzschia lanceolata var. *minima* Grunow	1.86%	2.78%	2.74%

A taxonomic list encompassing the whole investigated period at the Dubrovnik station includes altogether 235 taxa of which *Cocconeis scutellum* var. *scutellum* was commonly found throughout the whole study period with an average abundance of 26% (Table 13). The same average abundance for *Cocconeis scutellum* var. *scutellum* was computed for island of Mljet, while on the island of Hvar its abundance was lower (14%). The highest number of diatom taxa was observed in the Hvar sampling site. The taxonomic list from Hvar includes altogether 483 taxa. At the Mljet station, during the study period, 373 diatom taxa were counted. On the island of Hvar *Cocconeis caulerpacola* occurred with average abundance of 13%, which was much higher than on *Caulerpa racemosa* sampling sites. Also *Hyalosynedra laevigata* was found in greater abundance on *Caulerpa taxifolia* sampling sites than on *Caulerpa racemosa* sampling sites. *Mastogloia binotata* occurred in higher abundance on *Caulerpa racemosa* sampling sites. Some differences in abundance of *Navicula ramosissima* were observed in investigated sampling sites. On the island of Hvar *Navicula ramosissima* occurred with the lowest (5.84%) abundance while its abundance was higher on the island of Mljet (6.11%). and in Dubrovnik (6.83%). Average abundance of *Nitzschia angularis* was also the highest (4%) in Dubrovnik, followed by the Mljet sampling site (2.6%). The lowest abundance of *Nitzschia angularis* was on the island of Hvar (2.3%). In general, dominant taxa, except *Nitzschia lanceolata* var. *minima*, had extreme values of abundances in Dubrovnik and on the island of Hvar, while the values of abundances of taxa on the island of Mljet were in between.

To examine differences between diatom assemblages from three sampling sites, the taxa richness of diatom assemblages of epiphytic diatoms from the Dubrovnik, Mljet and Hvar sampling sites, *H'* (Shannon-Wiener Biodiversity Index), was compared. Generally, higher values of Shannon-Wiener Biodiversity Index were computed for August - October while they were lower for the January - March period (Figure 28). The highest value of Shannon-Wiener Biodiversity Index (3.71) was computed for the island of Hvar in August 2009. In August and September 2010 values of Shannon-Wiener Biodiversity Index were almost the same and amounted to ca. 3.5, for all sampling sites. In February 2009, values of Shannon-Wiener Biodiversity Index for both *Caulerpa racemosa* sampling sites were almost the same and amounted to 2.0. The lowest value (1.26) of Shannon-Wiener Biodiversity Index for the whole study period occurred in March 2009 on the island of Mljet. On the island of Hvar, the lowest value (2.23) was computed in November 2009. In November 2008 Shannon-Wiener Biodiversity Index on the island of Hvar was 2.5, almost the same as on the island of

Mljet (2.6), while in Dubrovnik it was slightly lower (2.2).

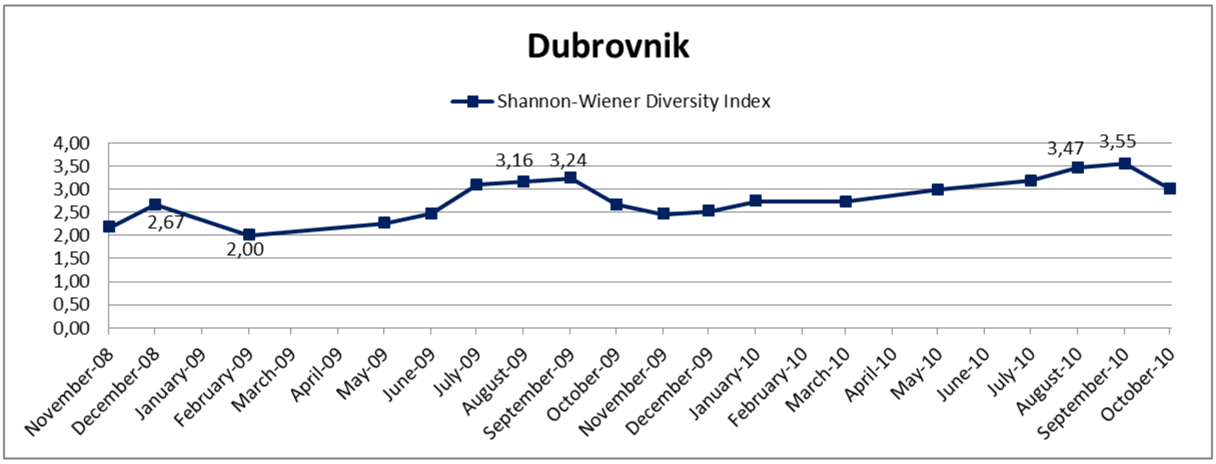


Figure 26. Changes in Shannon-Wiener Biodiversity Index of diatom community at the Dubrovnik sampling site through time. N = 149.

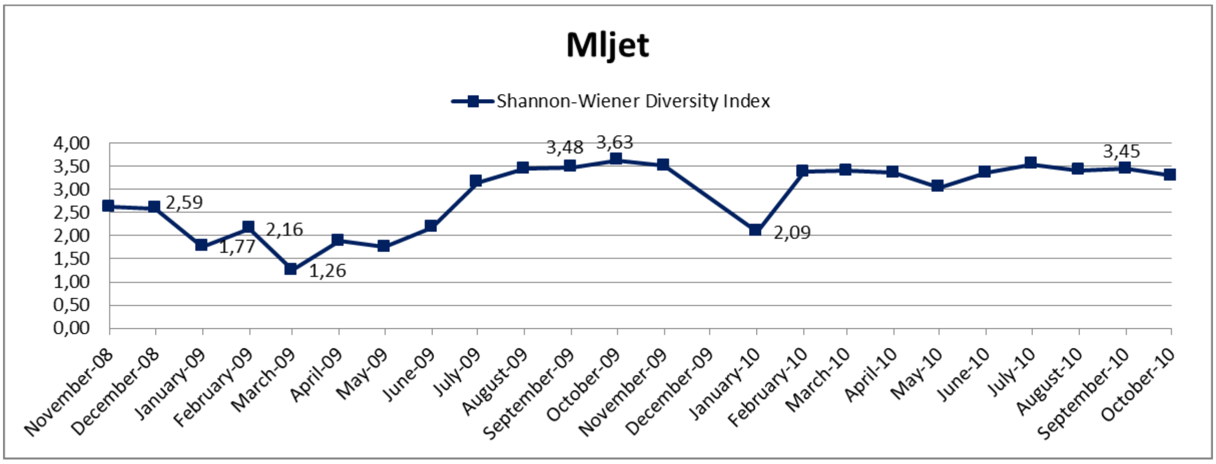


Figure 27. Changes in Shannon-Wiener Biodiversity Index of diatom community on the island of Mljet through time. N = 149.

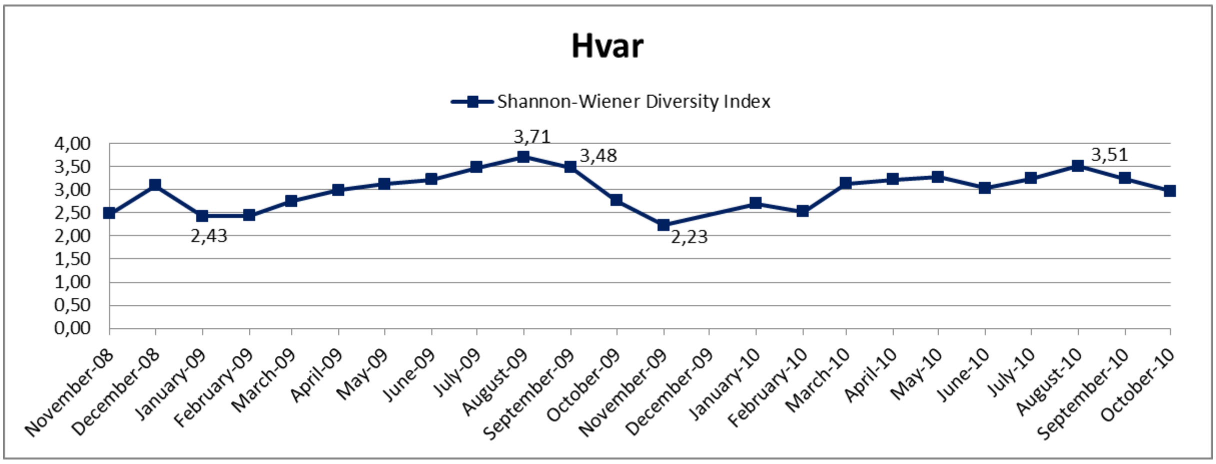


Figure 28. Changes in Shannon-Wiener Biodiversity Index of diatom community on the island of Hvar through time. N = 149.

Altogether, considering all sampling sites and all substrates (*Caulerpa* spp., *Padina pavonica*, *Halimeda tuna*) of epiphytic diatoms during the two year period, the total number of taxa of genus *Cocconeis* amounted to 29, with a maximum of 23 observed on the island of Mljet (Table 14). The highest frequency of appearance of *C. caulerpacola* was on the island of Hvar (87%), while the lowest was in Dubrovnik (33%).

Table 14. Frequency of appearance (%) of taxa of genus *Cocconeis.*

Species of genus *Cocconeis*:	**Frequency of appearance (%):**		
	Dubrovnik	**Mljet**	**Hvar**
Cocconeis britannica Naegeli in Kützing	77.78%	39.13%	17.39%
Cocconeis caulerpacola Witkowski, Car & Dobosz	33.33%	69.57%	86.96%
Cocconeis cf. *distans* Gregory	0.00%	4.35%	0.00%
Cocconeis cf. *distantula* Giffen	38.89%	69.57%	82.61%
Cocconeis cf. *krammeri* Lange-Bertalot & Metzeltin	0.00%	0.00%	4.35%
Cocconeis cf. *scutellum* Ehrenberg	0.00%	0.00%	39.13%
Cocconeis cf. *speciosa* (Ico.Diat.Vol.7, Pl. 38 Fig. 17)	0.00%	4.35%	0.00%
Cocconeis convexa Giffen	0.00%	4.35%	4.35%
Cocconeis costata Gregory var. *costata*	100.00%	60.87%	82.61%
Cocconeis costata var. *hexagona* Grunow in Van Heurck	0.00%	0.00%	4.35%
Cocconeis decussata Ehrenberg	5.56%	0.00%	0.00%
Cocconeis dirupta Gregory var. *dirupta*	11.11%	13.04%	17.39%
Cocconeis dirupta var. *flexella* (Janisch & Rabenhorst) Grunow	11.11%	13.04%	0.00%
Cocconeis diruptoides Hustedt	27.78%	8.70%	0.00%
Cocconeis discrepans A. Schmidt	0.00%	13.04%	8.70%
Cocconeis distans Gregory	44.44%	43.48%	21.74%
Cocconeis guttata Hustedt in Aleem & Hustedt	11.11%	13.04%	13.04%
Cocconeis krammeri Lange-Bertalot & Metzeltin	44.44%	13.04%	8.70%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	100.00%	100.00%	100.00%
Cocconeis pellucida Grunow ex Hantzsch in Rabenhorst (1863)	5.56%	0.00%	0.00%
Cocconeis pelta A. Schmidt	5.56%	52.17%	30.43%
Cocconeis peltoides Hustedt	33.33%	82.61%	86.96%
Cocconeis pinnata Gregory ex Greville	0.00%	21.74%	34.78%
Cocconeis pinnularia Kützing	0.00%	8.70%	0.00%
Cocconeis pseudodiruptoides Foged	22.22%	0.00%	4.35%
Cocconeis pseudomarginata Gregory	16.67%	17.39%	4.35%
Cocconeis scutellum Ehrenberg var. *scutellum*	100.00%	100.00%	100.00%
Cocconeis speciosa Gregory	5.56%	4.35%	0.00%
Cocconeis woodii Reyes	55.56%	13.04%	17.39%
TOTAL (No. species): 29	**20**	**23**	**21**

C. distans Gregory was observed in 22% of samples from Hvar and in more than 44% of samples from Mljet and Dubrovnik. A group of taxa including *C. pseudomarginata* Gregory and *C. speciosa* Gregory was also characteristic for *Caulerpa racemosa* sampling sites and occurred in 17% and 4.5% of samples respectively. *C. woodii* Reyes was found in

56% of samples from Dubrovnik, but only in 13% and 17% of samples from Mljet and Hvar respectively.

Considering all three locations (Dubrovnik, Mljet, Hvar) and all substrates of epiphytic diatoms in all the seasons during the two year period of study, the average number of taxa of genus *Cocconeis* was only 5.5 per single sample (Figure 29).

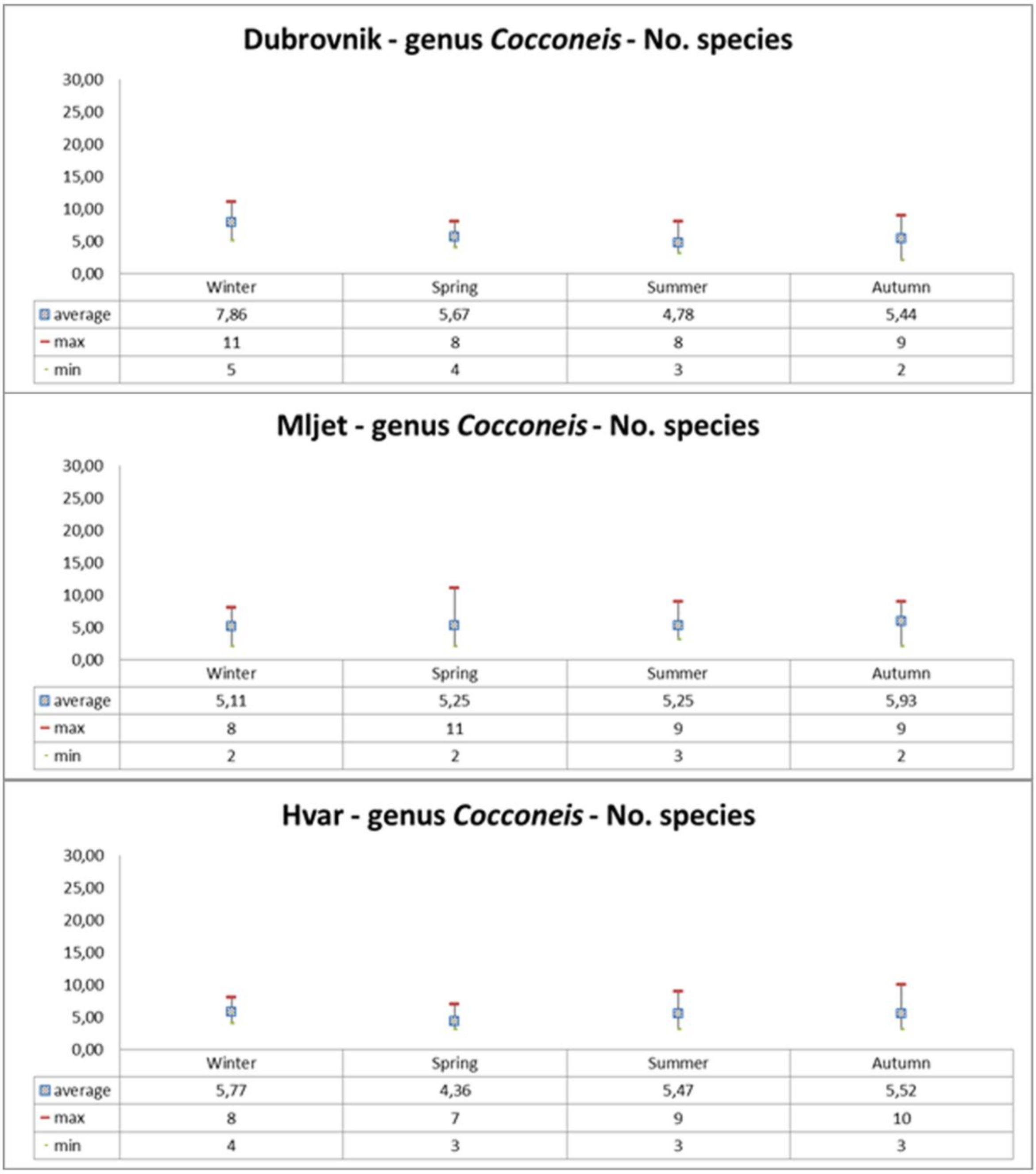
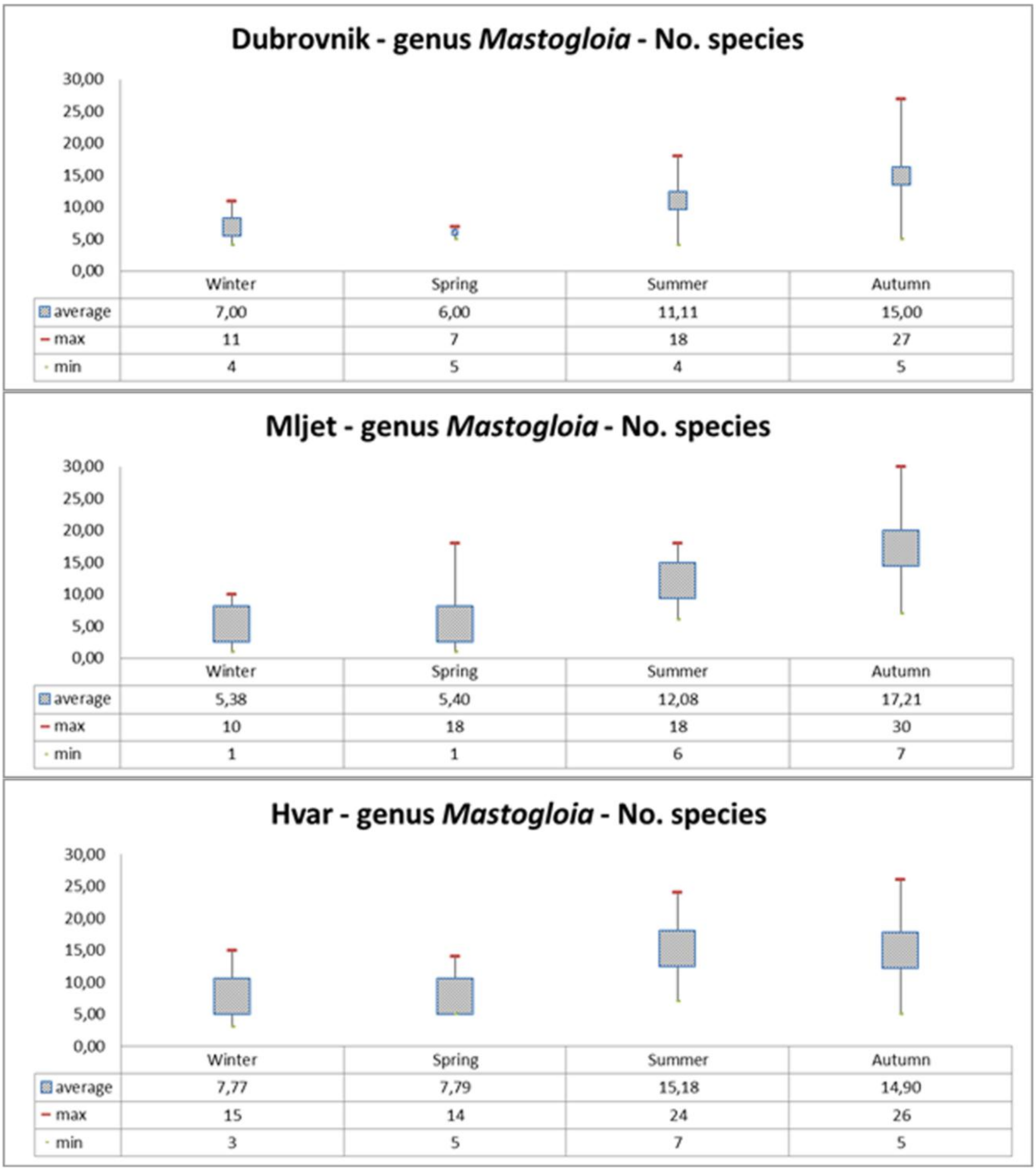


Figure 29. Box and Whisker Plots of number of taxa of genus *Cocconeis* during different seasons on different sampling sites.

The highest number of taxa of genus *Mastogloia* was observed during autumn (Figure 30). During winter the number of taxa did not exceed 50% of autumn values for Dubrovnik and Hvar. On the island of Mljet the most significant differences in the number of *Mastogloia* taxa were observed between winter (5) and autumn (17). The maximum number (30) of *Mastogloia* taxa in one sample was recorded on the island of Mljet (sample of *Caulerpa racemosa*, September 2009).



Dubrovnik - genus *Mastogloia* - No. species

	Winter	Spring	Summer	Autumn
▨ average	7,00	6,00	11,11	15,00
– max	11	7	18	27
· min	4	5	4	5

Mljet - genus *Mastogloia* - No. species

	Winter	Spring	Summer	Autumn
▨ average	5,38	5,40	12,08	17,21
– max	10	18	18	30
· min	1	1	6	7

Hvar - genus *Mastogloia* - No. species

	Winter	Spring	Summer	Autumn
▨ average	7,77	7,79	15,18	14,90
– max	15	14	24	26
· min	3	5	7	5

Figure 30. Box and Whisker Plots of number of taxa of genus *Mastogloia* during different seasons at different sampling sites. N = 149.

In the list of species from all three studied sites (Dubrovnik, Mljet, Hvar) and all substrates during the two year period, the total number of taxa representing *Mastogloia* amounted to 66, with a maximum of 61 observed on the island of Hvar (Table 15). *Mastogloia binotata* was observed in all samples from Dubrovnik, and in more than 91% and 96% of samples from Mljet and Hvar respectively. *Mastogloia crucicula* var. *crucicula* and *Mastogloia crucicula* var. *alternans* occurred in all samples from Hvar and in more than 87% of samples from Mljet. *Mastogloia crucicula* var. *alternans* was recorded in all samples from Dubrovnik, while *Mastogloia crucicula* var. *crucicula* occurred in more than 94%. *Mastogloia fimbriata* (Brightwell) Cleve was present in all samples from Dubrovnik and Hvar and in 83% of samples from Mljet. The highest frequency of appearance of *Mastogloia cuneata* (Meister) Simonsen was observed on the island of Hvar (95.65%), while in Dubrovnik and on the island of Mljet it amounted to 61% and 70% respectively. While *Mastogloia pseudolatecostata Yohn & Gibson* was recorded in all samples from island of Hvar, it was observed in 57% and 61% of samples on the island of Mljet and from Dubrovnik respectively. *Mastogloia decipiens* Hustedt was observed in 22% of samples from Dubrovnik and Mljet and in 52% of samples from Hvar. Also *Mastogloia ignorata* Hustedt was found in 52% of samples from Hvar, as well as from Mljet, and in 44% of Dubrovnik samples. A higher number of samples (48%) from Mljet and Hvar contained *Mastogloia corsicana* Grunow in Cleve & Möller than from Dubrovnik (28%). *Mastogloia splendida* (Gregory) Cleve was characteristic for *Caulerpa racemosa* sampling sites and occurred in more than 35% of samples. Also, *Mastogloia baltica* Grunow was characteristic for *Caulerpa racemosa* sampling sites and was recorded in 9-11% samples from Mljet and Dubrovnik. *Mastogloia adriatica* Voigt occurred equally at all three sampling sites with frequency of 22%. Also *Mastogloia ovalis* A. Schmidt was distributed equally at all three sampling sites with frequency of 60-67%. *Mastogloia ovulum* Hustedt was found in 33% of samples from Dubrovnik, but only in 9% and 13% of samples from Mljet and Hvar respectively.

Table 15. Frequency of appearance (%) of *Mastogloia* taxa. N = 149.

Species of genus *Mastogloia* :	**Frequency of appearance (%):**		
	Dubrovnik	**Mljet**	**Hvar**
Mastogloia acutiuscula var. *elliptica* Hustedt	0.00%	13.04%	0.00%
Mastogloia adriatica Voigt	22.22%	21.74%	21.74%
Mastogloia angulata Lewis	5.56%	17.39%	17.39%
Mastogloia baldjikiana Grunow	5.56%	13.04%	13.04%
Mastogloia baltica Grunow	11.11%	8.70%	0.00%
Mastogloia binotata (Grunow) Cleve	100.00%	91.30%	95.65%
Mastogloia biocellata (Grunow) Novarino & Muftah	33.33%	43.48%	43.48%
Mastogloia borneensis Hustedt in A. Schmidt, Atlas	0.00%	8.70%	43.48%
Mastogloia braunii Grunow	5.56%	8.70%	8.70%
Mastogloia cf. *cyclops* Voigt	0.00%	0.00%	13.04%
Mastogloia cf. *exilis* Hustedt	5.56%	4.35%	0.00%
Mastogloia cf. *fallax* Cleve	0.00%	4.35%	4.35%
Mastogloia cf. *laminaris* Grunow	38.89%	8.70%	21.74%
Mastogloia cf. *linearis* Simonsen	33.33%	13.04%	34.78%
Mastogloia cf. *ovata* Grunow	0.00%	0.00%	4.35%
Mastogloia cf. *pumila* (Grunow) Cleve	0.00%	8.70%	4.35%
Mastogloia cf. *rimosa* Cleve	0.00%	0.00%	17.39%
Mastogloia cf. *varians* Hustedt	0.00%	0.00%	4.35%
Mastogloia corsicana Grunow in Cleve & Möller	27.78%	47.83%	47.83%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	94.44%	86.96%	100.00%
Mastogloia crucicula var. *alternans* Zanon	100.00%	86.96%	100.00%
Mastogloia cuneata (Meister) Simonsen	61.11%	69.57%	95.65%
Mastogloia cyclops Voigt	22.22%	34.78%	52.17%
Mastogloia decipiens Hustedt	22.22%	21.74%	52.17%
Mastogloia delicatissima Hustedt	0.00%	4.35%	17.39%
Mastogloia emarginata Hustedt	66.67%	56.52%	86.96%
Mastogloia erythraea Grunow var. *erythraea*	27.78%	34.78%	34.78%
Mastogloia exigua Lewis	0.00%	8.70%	0.00%
Mastogloia exilis Hustedt	33.33%	17.39%	4.35%
Mastogloia fallax Cleve	16.67%	13.04%	8.70%
Mastogloia fimbriata (Brightwell) Cleve	100.00%	82.61%	100.00%
Mastogloia grunowii A. Schmidt	5.56%	13.04%	4.35%
Mastogloia hovarthiana Grunow	16.67%	26.09%	52.17%
Mastogloia ignorata Hustedt	44.44%	52.17%	52.17%
Mastogloia inaequalis Cleve	22.22%	43.48%	56.52%
Mastogloia lanceolata Thwaites in W. Smith	11.11%	30.43%	13.04%
Mastogloia laterostrata Hustedt	16.67%	17.39%	8.70%
Mastogloia linearis Simonsen	0.00%	0.00%	4.35%
Mastogloia macdonaldii Greville	5.56%	0.00%	4.35%
Mastogloia manokwariensis Cholnoky	0.00%	13.04%	8.70%
Mastogloia mauritiana Brun in A. Schmidt Atlas	11.11%	13.04%	8.70%
Mastogloia ovalis A. Schmidt	66.67%	60.87%	65.22%
Mastogloia ovulum Hustedt	33.33%	8.70%	13.04%
Mastogloia paradoxa Grunow in Cleve & Möller	11.11%	21.74%	17.39%
Mastogloia peragalli Cleve	16.67%	30.43%	13.04%
Mastogloia pisciculus Cleve	0.00%	0.00%	8.70%
Mastogloia pseudoexigua Cholnoky	16.67%	4.35%	13.04%

(*continued*)

Table 10. *Continued*

Species of genus *Mastogloia*:	**Frequency of appearance (%):**		
	Dubrovnik	**Mljet**	**Hvar**
Mastogloia pseudolatecostata Yohn & Gibson	61.11%	56.52%	100.00%
Mastogloia pumila (Grunow) Cleve	5.56%	8.70%	26.09%
Mastogloia pusilla (Grunow) Cleve var. *pusilla*	55.56%	52.17%	78.26%
Mastogloia quinquecostata Grunow	22.22%	21.74%	8.70%
Mastogloia regula Hustedt	11.11%	0.00%	13.04%
Mastogloia robusta Hustedt	22.22%	4.35%	13.04%
Mastogloia similis Hustedt	33.33%	26.09%	34.78%
Mastogloia smithii Thwaites	5.56%	4.35%	8.70%
Mastogloia sp. 1	22.22%	0.00%	13.04%
Mastogloia sp. 2	0.00%	0.00%	4.35%
Mastogloia spec. (Ico.Diat.Vol.7, Pl. 75 Figs 7-9)	61.11%	39.13%	82.61%
Mastogloia spec. (Ico.Diat.Vol.7, Pl. 78 Figs 18, 19)	0.00%	0.00%	8.70%
Mastogloia spec. (Ico.Diat.Vol.7, Pl. 82 Figs 13, 14)	0.00%	0.00%	4.35%
Mastogloia spec. (Ico.Diat.Vol.7, Pl. 84 Fig. 9-10)	11.11%	8.70%	0.00%
Mastogloia spec. 84/1 (Ico.Diatom.Vol.7, Pl.84 Figs 9-11)	0.00%	26.09%	17.39%
Mastogloia spec. 84/3 (Ico.Diat.Vol.7, Pl. 84 Fig. 24)	0.00%	4.35%	4.35%
Mastogloia splendida (Gregory) Cleve	38.89%	34.78%	4.35%
Mastogloia varians Hustedt	0.00%	0.00%	4.35%
Mastogloia vasta Hustedt	11.11%	8.70%	17.39%
TOTAL (No. species): 66	**47**	**53**	**61**

3.3. Biodiversity - Comparison between substrates

There is a wide range of epiphytic diatom taxa on autochthonous and invasive algae (Figure 31.). While the average number of taxa on autochthonous algae was slightly higher (59) than the number of taxa on invasive algae (52), the maximum number of taxa (102) was recorded on invasive algae (*C. taxifolia*). Likewise a minimum of 18 diatom taxa of epiphytes was also recorded on invasive algae. In general, however, the diatom community on brown alga *Padina pavonica* was the richest in number of taxa (64, Figure 32.). The number of taxa recorded as epiphytic diatoms on *Caulerpa racemosa* was the lowest (average 50 taxa in one sample). Although it happened that the richest in terms of species richness (102) was one of *Caulerpa taxifolia* samples, in general this invasive alga with 53 taxa per sample, hosted almost the same number of species as *Halimeda tuna* (54).

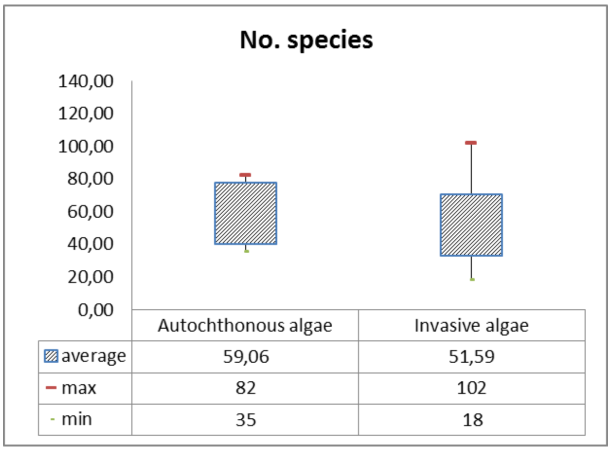


Figure 31. Number of taxa of epiphytic diatoms on autochthonous and invasive algae.

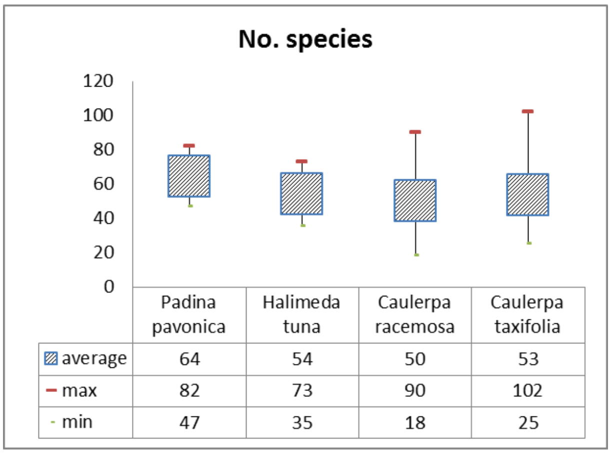


Figure 32. Number of taxa in diatom community on *Padina pavonica, Halimeda tuna, Caulerpa racemosa* and *Caulerpa taxifolia*.

Considering epiphytic diatoms from all three locations (Dubrovnik, Mljet, Hvar) studied during the two year period, the average abundance of *Cocconeis scutellum* var. *scutellum* on autocthonous algae amounted to 12.41% and on invasive algae to 24.32% (Table 16). On invasive algae, *C. scutellum* was followed by *Cocconeis caulerpacola* and *Cocconeis molesta* var. *crucifera*, both with an average abundance of 10%. On autocthonous algae, the average abundance of *Cocconeis caulerpacola* was less than 1%. The epiphytic diatoms fouling autochthonous algae were dominated by *Cocconeis scutellum* var. *scutellum* and *Navicula ramosissima*.

Table 16. Average substrate abundance of dominant 10 taxa. N = 149.

Taxa:	**Average Abundance (%):**	
	Autochthonous algae	***Invasive algae***
Cocconeis caulerpacola Witkowski, Car & Dobosz	0.67%	10.01%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	5.71%	9.87%
Cocconeis scutellum Ehrenberg var. *scutellum*	12.41%	24.32%
Hyalosynedra laevigata (Grunow) Williams & Round	4.24%	6.63%
Mastogloia binotata (Grunow) Cleve	3.46%	1.37%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	2.73%	1.84%
Mastogloia crucicula var. *alternans* Zanon	3.71%	1.59%
Navicula ramosissima (Agardh) Cleve	8.62%	4.85%
Nitzschia angularis W. Smith	4.79%	1.86%
Nitzschia lanceolata var. *minima* Grunow	2.42%	2.55%

Distribution of dominant taxa abundances during winter season (Figure 33.) showed similarity in abundances of 10 dominant taxa on autochthonous and invasive algae on the island of Hvar and in Dubrovnik. Differences in the abundances of 10 dominant taxa, especially of *Cocconeis caulerpacola*, between autochthonous and invasive algae were observed on the island of Mljet while on the island of Hvar *Cocconeis caulerpacola* was found only on invasive algae. During spring, *Cocconeis scutellum* var. *scutellum* was dominant on both autochthonous and invasive algae. On autochthonous algae, it was followed by *Hyalosynedra laevigata* on the island of Hvar and by *Navicula ramosissima* on the island of Mljet and in Dubrovnik. On invasive algae, it was followed by *Cocconeis molesta* var. *crucifera*.

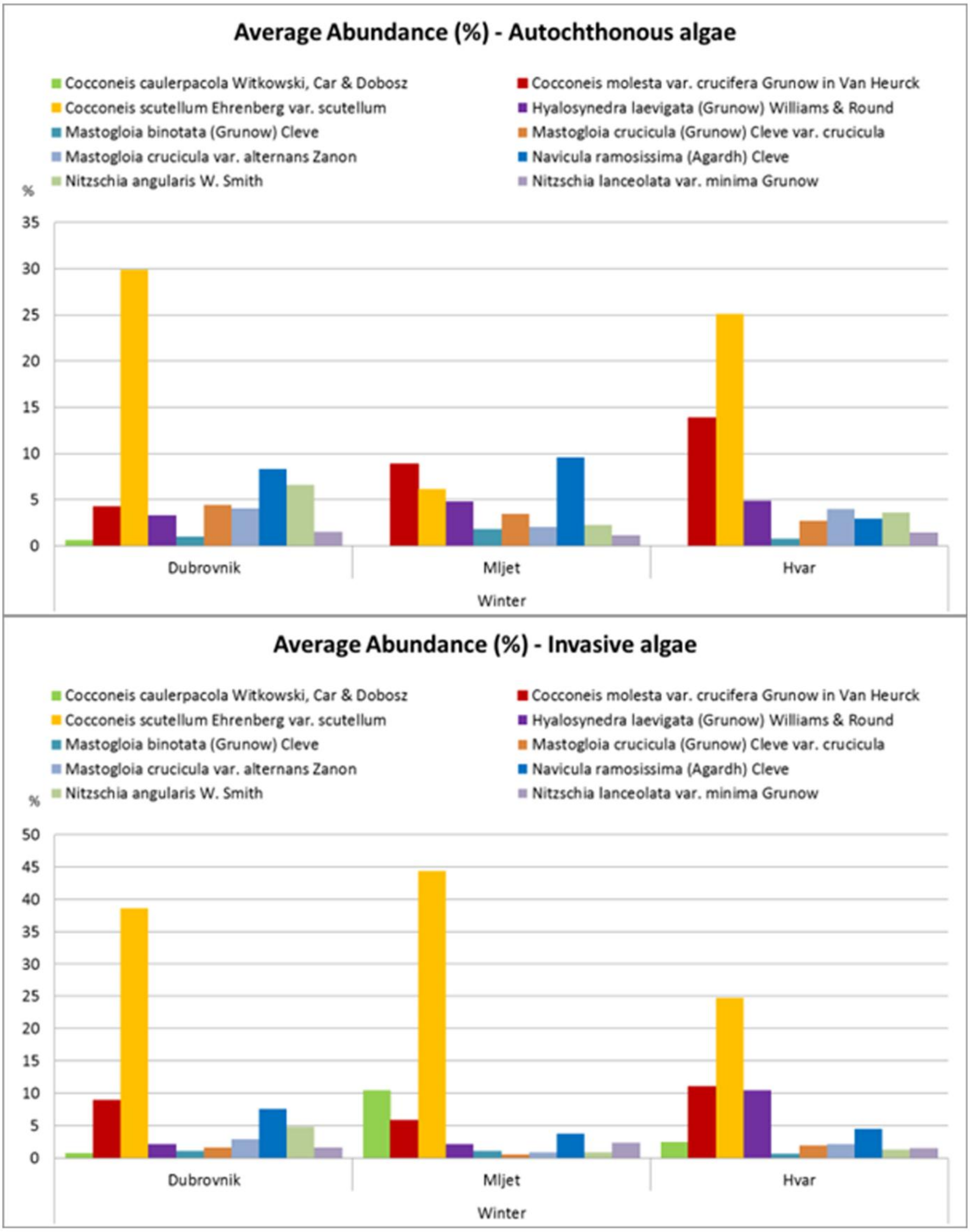


Figure 33. Average abundance of epiphytic diatoms on autochthonous and invasive algae during winter.

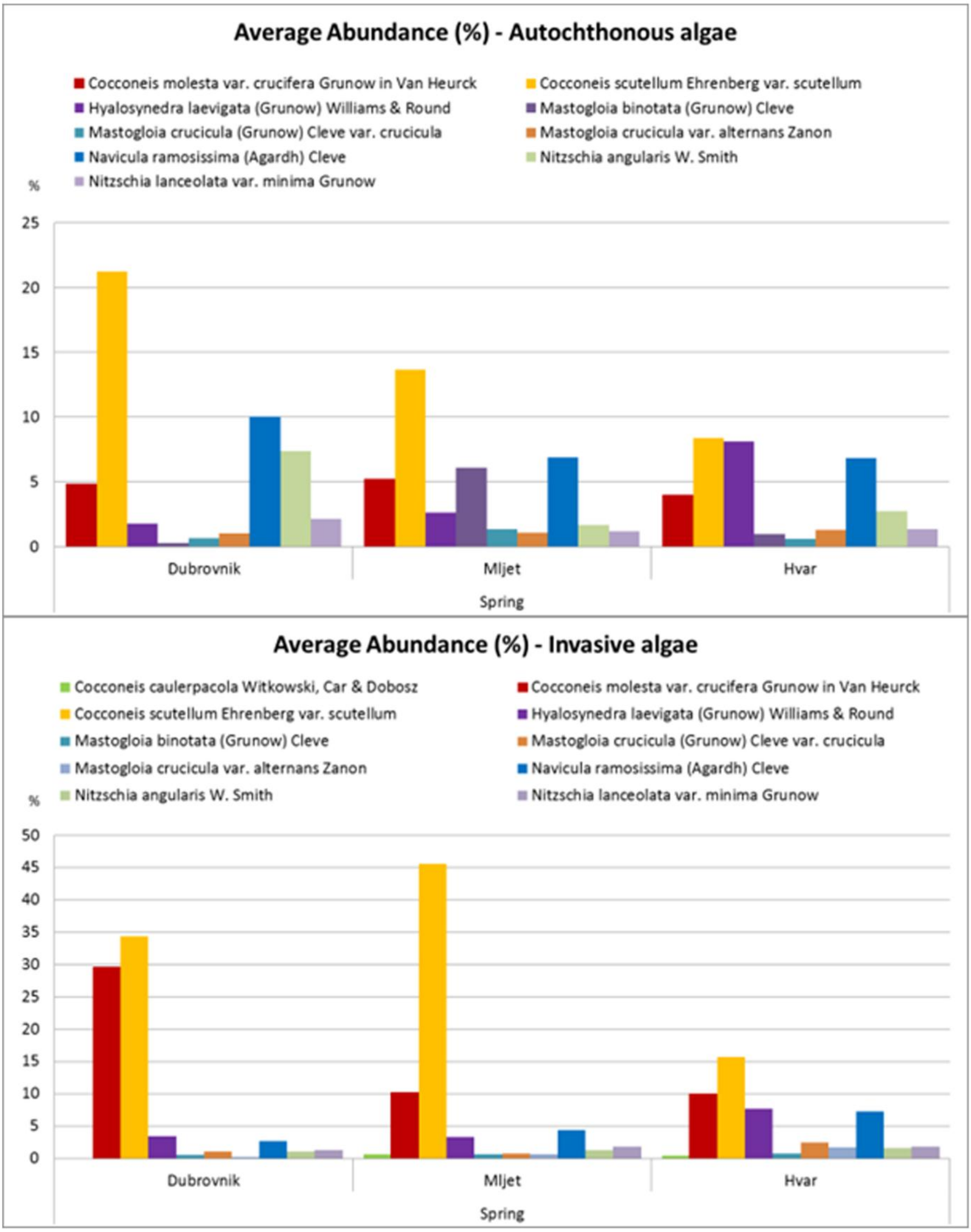


Figure 34. Average abundance of epiphytic diatoms on autochthonous and invasive algae during spring.

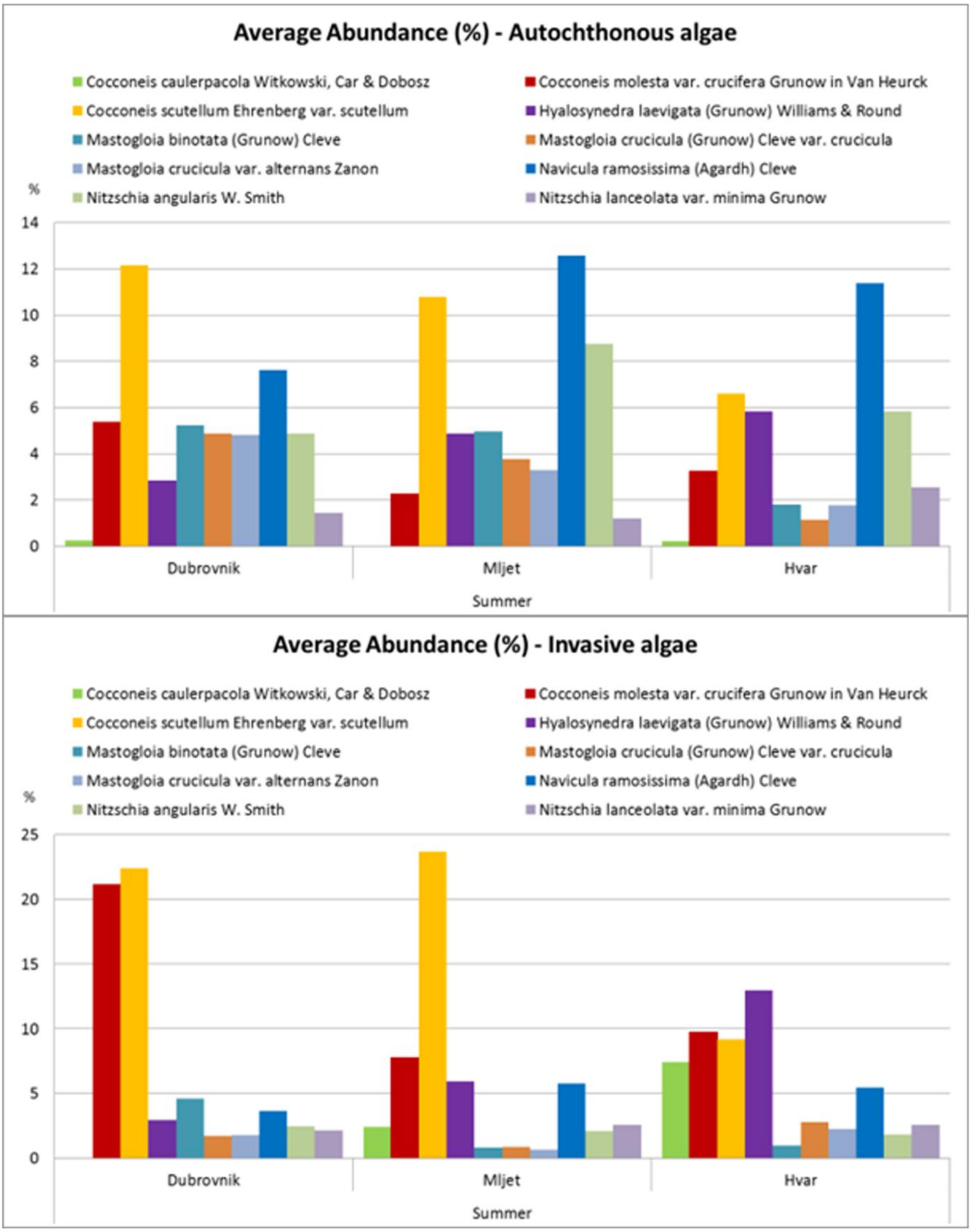


Figure 35. Average abundance of epiphytic diatoms on autochthonous and invasive algae during summer.

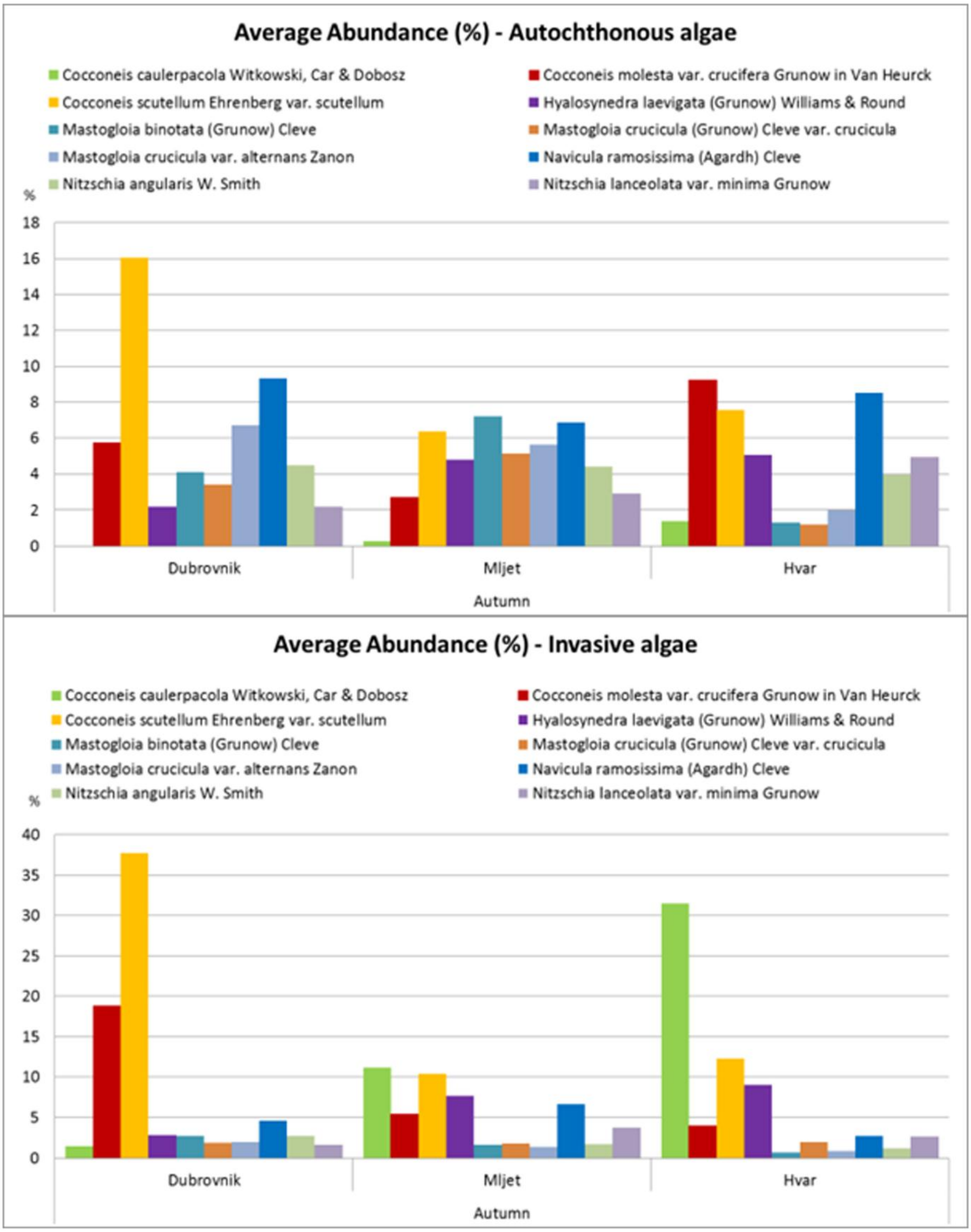


Figure 36. Average abundance of epiphytic diatoms on autochthonous and invasive algae during autumn.

On autochthonous algae, the majority of 10 dominant taxa, except *Cocconeis scutellum* var. *scutellum*, had their peaks of abundance during summer and autumn. During autumn *Cocconeis caulerpacola* showed strong host dependence and reached higher abundance on invasive algae on all three sampling sites.

Although generally *Cocconeis molesta* var. *crucifera* did not show particular seasonality, increased abundances were recorded on invasive algae in Dubrovnik during spring and summer. Abundance of *Navicula ramosissima* was higher during summer on autochthonous than on invasive algae.

3.3.1. Seasonal dynamics of epiphytic diatoms on autochthonous and invasive algae

In order to describe the seasonal dynamics of epiphytic diatom assemblages on autochthonous and invasive algae from Hvar, Mljet and from Dubrovnik on a fine time scale, detailed analyses of 10 dominant taxa during the second year of sampling from autumn 2009 till autumn 2010 were performed.

The maximum abundance of *Cocconeis scutellum* var. *scutellum* observed in winter 2009 both on autochthonous and invasive algae can be recognized as the first peak during the second year of sampling, while the second peak occurred in the end of spring for invasive and beginning of summer 2010 for autochthonous algae.

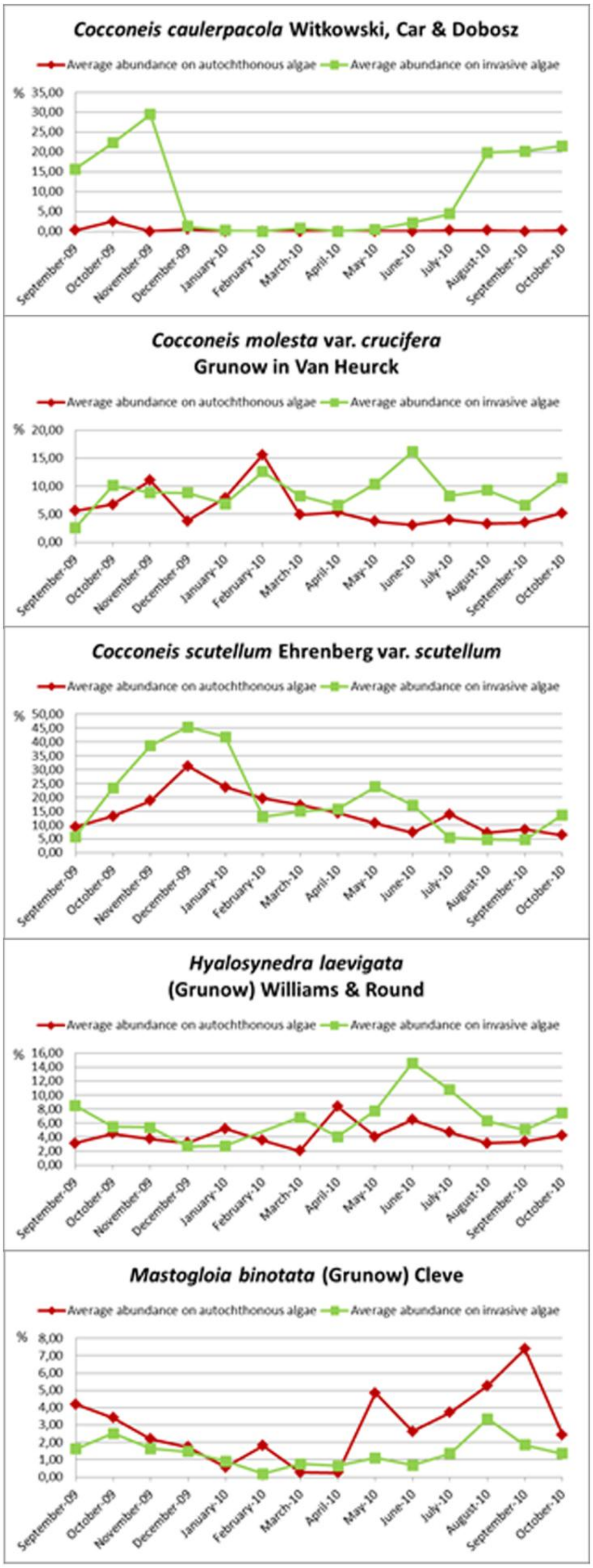
Cocconeis caulerpacola and *Cocconeis scutellum* var. *scutellum* colonies, which were the main fouling component during autumn 2009 occurring with average abundance of 22% in October 2009 on invasive algae, declined in February 2010, to be replaced by *Cocconeis molesta* var. *crucifera*. The latter taxon was dominant on invasive algae in June 2010 with average abundance of 15% and was accompanied by *Hyalosynedra laevigata* which occurred with average abundance of 16%.

Abundance of taxa of genus *Mastogloia* on both invasive and autochthonous algae did not exceed 10%. *Mastogloia crucicula* var. *alternans* reached its highest abundance on autochthonous algae during autumn 2009 and 2010, although not showing strong seasonal distribution on invasive algae.

Mastogloia binotata also did not show strong seasonality on invasive algae. On autochthonous algae, increased abundances (6%) were noticed in September 2009 and 2010 and in May 2010.

Average abundance of *Mastogloia crucicula* var. *alternans* as well as of *Mastogloia crucicula* var. *crucicula* during September amounted to 2%.

Abundance of *Navicula ramosissima* on invasive as well as on autochthonous algae was quite similar during all seasons with a higher abundance on autochthonous algae particularly in June 2010. While abundance on invasive algae was 9%, on autochthonous algae it reached 15.5%. During autumn its average abundance was 4.6% on invasive



(*continued*)

algae and 8.5% on autochthonous algae. Only exceptionally in December 2009 and in March 2010, average abundance of *Navicula ramosissima* was higher on invasive algae than on autochthonous.

Abundance of *Nitzschia angularis* was higher on autochthonous algae except in October 2009, July 2010 and September 2010 when average abundances for both types of algae were 2.34%, 4.81% and 2.73% respectively.

Abundance of *Nitzschia lanceolata* var. *minima* on invasive and on autochthonous algae was quite similar during all seasons with an exception during March 2010 when abundance on invasive algae reached 5% while it amounted to only 1.3% on autochthonous algae (Figure 37).

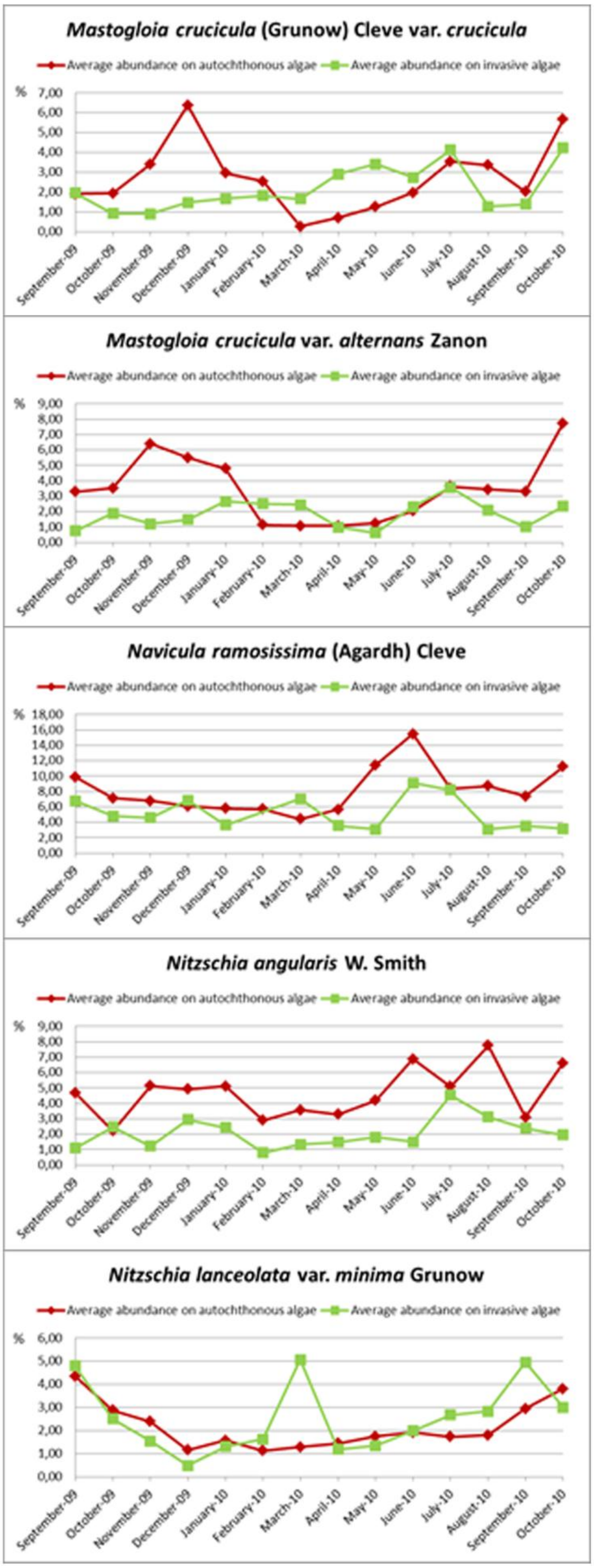


Figure 37. Seasonality of 10 dominant taxa on autochthonous and invasive algae from autumn 2009 till autumn 2010.

Results of analyses of epiphytic diatoms on green and brown macroalgae collected at the same time from the same localities as invasive *Caulerpa* species show a total absence, or the presence of just a few specimens, of *C. caulerpacola*. Average abundance of *Cocconeis caulerpacola* on *Padina pavonica* and *Halimeda tuna* did not exceed 1%. Average abundance of *Cocconeis caulerpacola* on *Caulerpa racemosa* amounted to 5%. The highest abundance (14%) of *C. caulerpacola* was observed on *Caulerpa taxifolia* (Table 17). The highest average abundance of *Cocconeis molesta* var. *crucifera* was seen on invasive *Caulerpa racemosa* with an average abundance of 11%. Abundance of *Cocconeis molesta* var. *crucifera* was similar on *Caulerpa taxifolia* and *Halimeda tuna* (7-8%). On *Padina pavonica* an abundance of *C. molesta* var. *crucifera* was the lowest (4%). The highest abundance of *Cocconeis scutellum* var. *scutellum* was observed on *Caulerpa racemosa* (32%), followed by abundances on *Halimeda tuna* (18%) and *Caulerpa taxifolia* (15%). Its lowest abundance was observed on *Padina pavonica* (6%).

Hyalosynedra laevigata occurred with an average abundance of 10% on *Caulerpa taxifolia,* while the abundances on other investigated algae was half that value and amounted to 4-5%. Higher abundances of *Navicula ramosissima* were determined on autochthonous algae. Average abundance on *Padina pavonica* and *Halimeda tuna* amounted to ca. 8.5% while on both investigated *Caulerpa* species to ca. 4.5-5%. Abundance of *Nitzschia angularis* was higher on *Halimeda tuna* (6.5%) than on other algae where its abundance amounted to ca. 2%. No differences were observed in abundance of *Nitzschia lanceolata* var. *minima* on investigated macroalgae.

It was observed that *Mastogloia binotata* was more typical for autochthonous algae where it occurred with an average abundance of 3.5%. The lowest abundance of this species occurred on *Caulerpa taxifolia* and did not exceed <1%. Average abundances of *Mastogloia crucicula* var. *crucicula* and of *Mastogloia crucicula* var. *alternans* were the highest on *Padina pavonica* and the lowest on *Caulerpa racemosa.* In general, regarding substrates, the largest number of taxa (55) of genus *Mastogloia* (

Table 18) was observed on *Padina pavonica*. Also on *Padina pavonica* the highest average number of *Mastogloia* taxa was observed in a single sample from the island of Mljet (22.4), followed by Dubrovnik (20.6) (Table 19).

Table 17. Abundance of 10 dominant taxa on different substrates.

Taxa:	**Average Substrate Abundance (%):**			
	Padina pavonica	***Halimeda tuna***	***Caulerpa racemosa***	***Caulerpa taxifolia***
Cocconeis caulerpacola Witkowski, Car & Dobosz	0.26%	0.76%	5.07%	13.82%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	3.90%	7.31%	11.06%	8.42%
Cocconeis scutellum Ehrenberg var. *scutellum*	6.41%	17.72%	32.14%	15.03%
Hyalosynedra laevigata (Grunow) Williams & Round	4.83%	3.71%	3.98%	10.04%
Mastogloia binotata (Grunow) Cleve	3.32%	3.60%	1.92%	0.78%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	3.29%	2.21%	1.36%	2.30%
Mastogloia crucicula var. *alternans* Zanon	4.73%	2.78%	1.44%	1.73%
Navicula ramosissima (Agardh) Cleve	8.07%	9.11%	5.04%	4.52%
Nitzschia angularis W. Smith	2.88%	6.55%	2.18%	1.51%
Nitzschia lanceolata var. *minima* Grunow	2.63%	2.19%	2.52%	2.58%

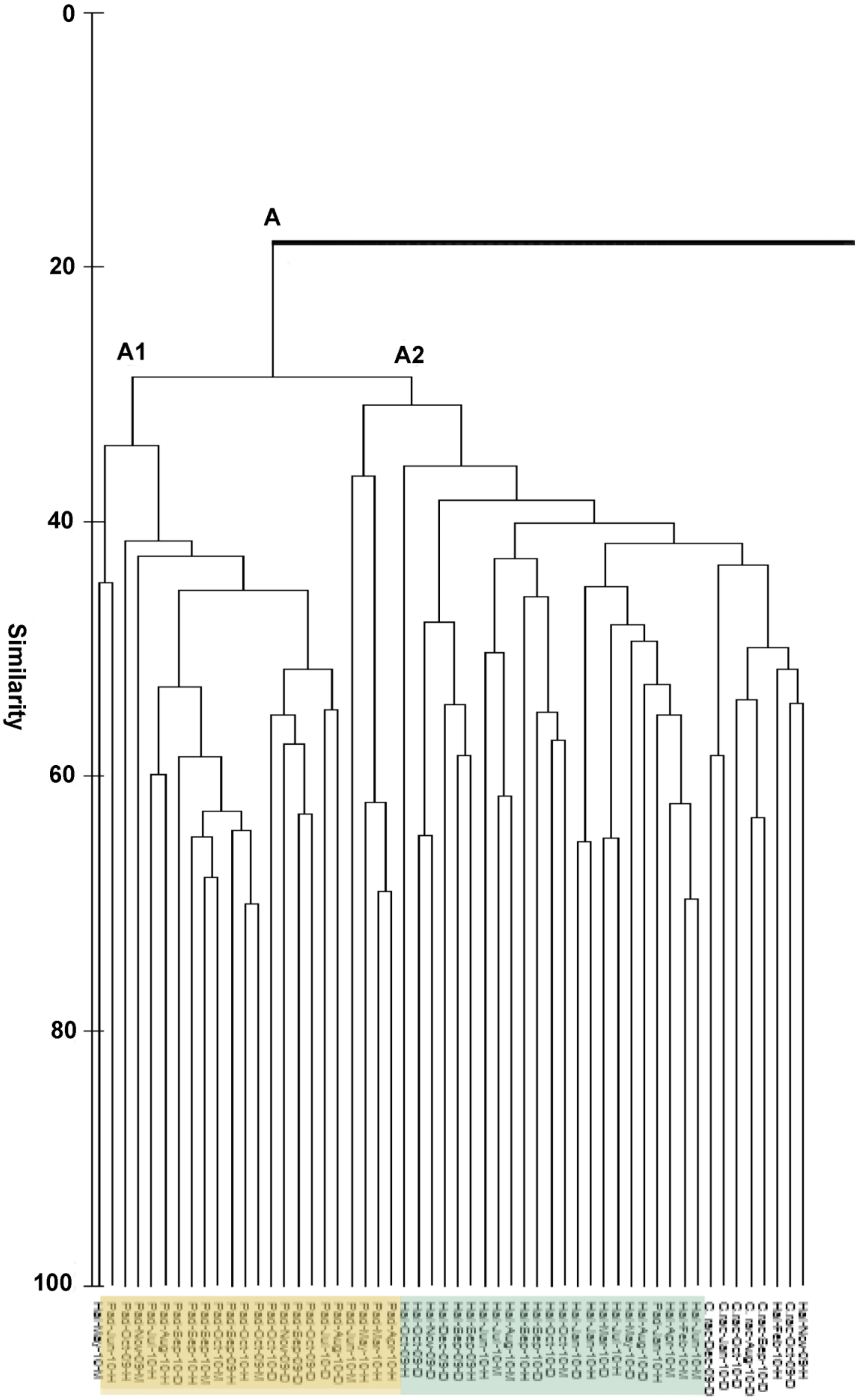
Table 18. Number of *Mastogloia* taxa on different substrates and sampling sites.

	No. species of genus *Mastogloia*			
Sampling site:	Dubrovnik	Mljet	Hvar	**TOTAL (No. species):**
Padina pavonica	41	41	46	**55**
Halimeda tuna	33	32	30	**43**
Caulerpa racemosa	29	39	0	**48**
Caulerpa taxifolia	0	0	43	**47**

Table 19. Average number of *Mastogloia* taxa per sample of different substrates and sampling sites.

	Avg. No. species of genus *Mastogloia* /sample:		
Sampling site:	Dubrovnik	Mljet	Hvar
Padina pavonica	20,6	22,4	18,6
Halimeda tuna	11,3	13,13	11,9
Caulerpa racemosa	9,11	8,58	0
Caulerpa taxifolia	0	0	10,46

The most striking differences in species composition of the epiphytic diatom community was observed between *C. taxifolia* and *C. racemosa* on the one hand, and green and brown macroalgae on the other (Figure 38). Cluster analysis revealed two groups of significantly different assemblages of epiphytic diatoms inhabiting different hosts. Similarity between two groups, a group A composed mostly of autochthonous algae and a group B including invasive *Caulerpa* spp., amounted to less than 20%. Group A contained subgroups A1 and A2 with similarity of 28%. Subgroup A1 contained almost exclusively an epiphytic diatom community of *Padina pavonica*, while subgroup A2 mostly contained epiphytes of *Halimeda tuna*.


0
20
40
60
80
100
Similarity
A
A1
A2

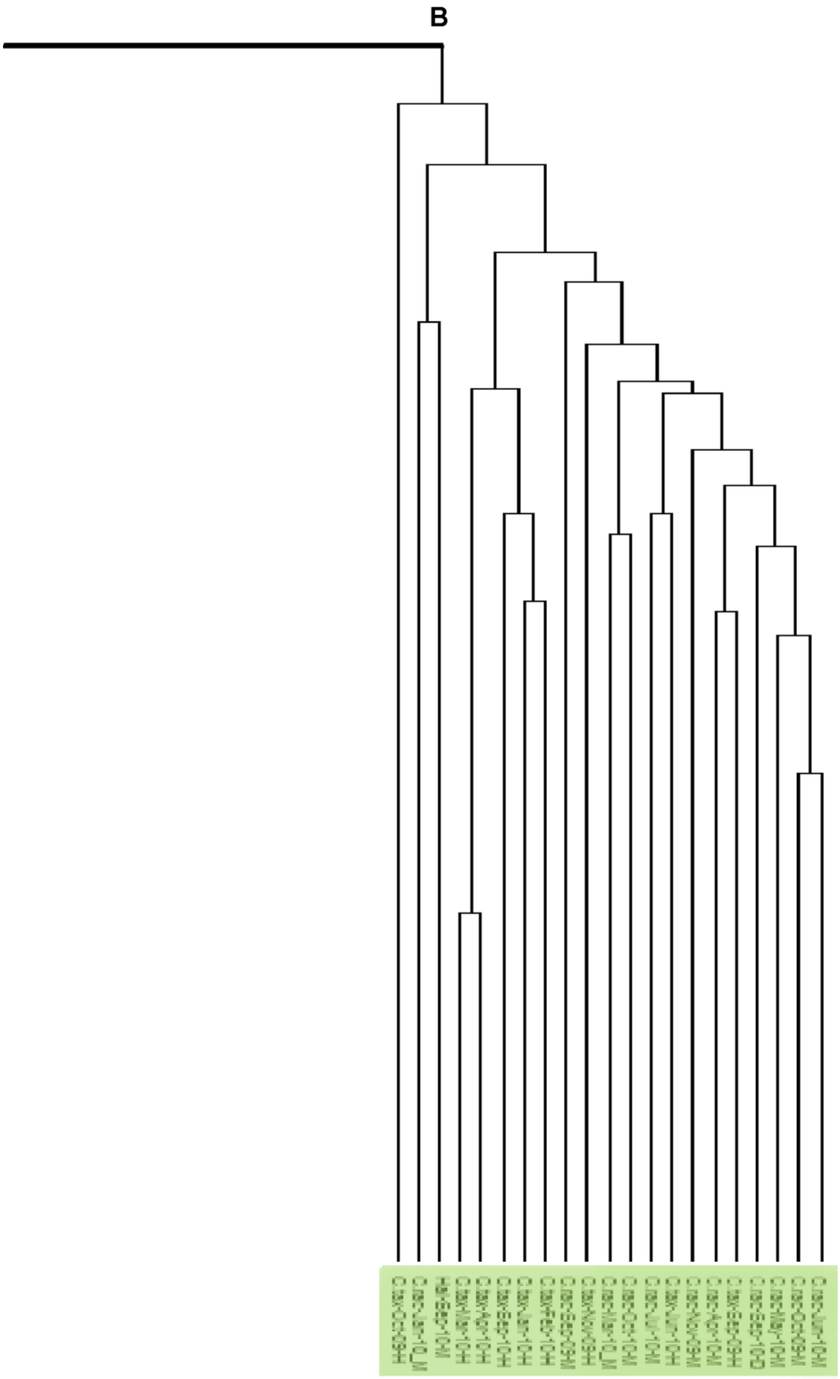


Figure 38. Similarity dendrogram based on average abundances of all recorded diatom taxa among different substrates (*Caulerpa racemosa*, *Caulerpa taxifolia*, *Padina pavonica*, *Halimeda tuna*) throughout the seasons over a time period from September 2009 to October 2010 (N = 76).

3.3.2. Epiphytic diatoms on *Padina pavonica*

Altogether, 271 taxa from 55 genera were identified as epiphytes on the investigated brown macroalga from three locations between September 2009 and October 2010. The diatom assemblage of brown alga *Padina pavonica* was characterized by high abundances of taxa belonging to *Mastogloia*, *Nitzschia*, *Cocconeis*, *Navicula*, *Amphora*, *Hyalosynedra* and *Licmophora*. In terms of taxa representing *Licmophora*, communities on *Padina* showed higher similarity to those on *Caulerpa taxifolia* than to another investigated autochthonous alga *Halimeda tuna* (Figure 39).

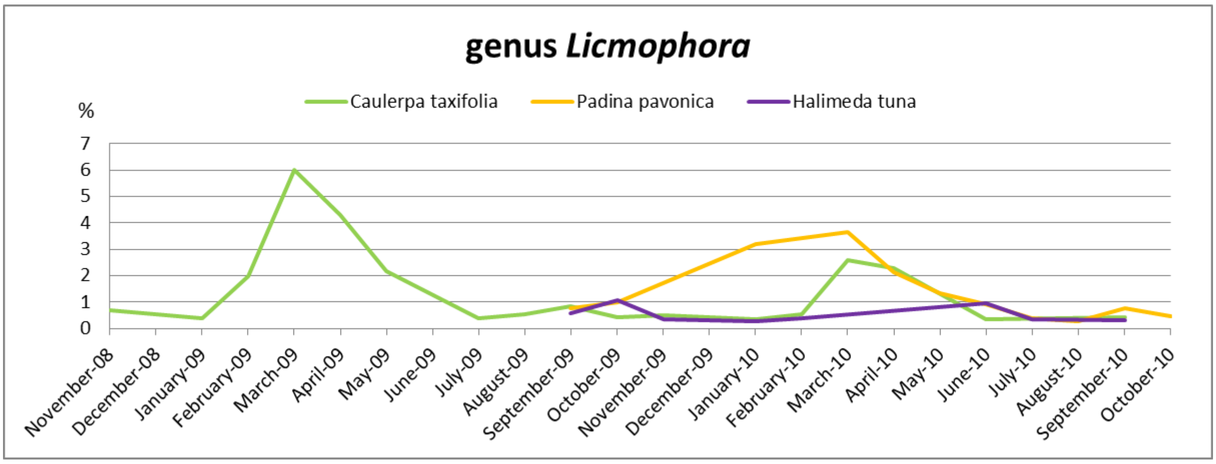


Figure 39. Seasonal distribution of *Licmophora* taxa on *Padina pavonica* in comparison to *Caulerpa taxifolia* and *Halimeda tuna*.

Table 20 lists 25 dominant taxa which were the most abundant at all three locations (Dubrovnik, Mljet, Hvar) during a one-year period (autumn 2009 – autumn 2010) on *Padina pavonica*. They were dominant in terms of both frequency of appearance (>1%) and abundance in total number of samples (>35%). When combined together in a single sample, these 25 dominant taxa contributed from 63 to 83% in the diatom community.

A group of listed taxa, i.e. *Amphora helenensis* Giffen, *Cocconeis molesta* var. *crucifera*, *Cocconeis scutellum* var. *scutellum*, *Hyalosynedra laevigata*, *Mastogloia binotata*, *Mastogloia crucicula* var. *crucicula*, *Mastogloia crucicula* var. *alternans*, *Navicula ramosissima*, *Nitzschia angularis* and *Nitzschia lanceolata* var. *minima* was present in all *Padina pavonica* samples studied.

Table 20. Dominant diatom taxa on *Padina pavonica* with an average abundance (Avg.) > 1% and frequency of appearance (Freq.) > 35%. N = 23.

***Padina pavonica* - 25 dominant taxa:**	**Freq. (%)**	**Avg. (%)**
Amphora acutiuscula Kützing	91.30%	1.76%
Amphora helenensis Giffen	100.00%	1.31%
Berkeleya rutilans (Trentepohl) Grunow	78.26%	3.37%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	100.00%	3.90%
Cocconeis scutellum Ehrenberg var. *scutellum*	100.00%	6.41%
Hyalosynedra laevigata (Grunow) Williams & Round	100.00%	4.83%
Licmophora paradoxa (Lyngbye) Agardh	82.61%	1.71%
Mastogloia binotata (Grunow) Cleve	100.00%	3.32%
Mastogloia crucicula (Grunow) Cleve var. crucicula	100.00%	3.29%
Mastogloia crucicula var. *alternans* Zanon	100.00%	4.73%
Mastogloia cuneata (Meister) Simonsen	86.96%	3.18%
Mastogloia decipiens Hustedt	43.48%	3.78%
Mastogloia fimbriata (Brightwell) Cleve	91.30%	1.62%
Mastogloia ignorata Hustedt	82.61%	2.95%
Mastogloia ovalis A. Schmidt	78.26%	3.53%
Mastogloia pseudolatecostata Yohn & Gibson	95.65%	2.46%
Mastogloia pusilla (Grunow) Cleve var. *pusilla*	91.30%	4.82%
Navicula ramosissima (Agardh) Cleve	100.00%	8.07%
Nitzschia angularis W. Smith	100.00%	2.88%
Nitzschia cf. *sigma* (Kützing) W. Smith	34.78%	4.23%
Nitzschia fusiformis Grunow	78.26%	4.37%
Nitzschia lanceolata var. *minima* Grunow	100.00%	2.63%
Nitzschia panduriformis Gregory var. *panduriformis*	91.30%	1.21%
Rhopalodia pacifica Krammer	86.96%	1.60%
Tabularia ktenoeoides Kuylenstierna	91.30%	1.29%

Of the 25 dominant taxa, 10 taxa represented *Mastogloia*. An average abundance of *Mastogloia binotata*, *Mastogloia crucicula* var. *crucicula*, *Mastogloia crucicula* var. *alternans*, *Mastogloia cuneata*, *Mastogloia decipiens*, *Mastogloia ignorata*, *Mastogloia ovalis*, *Mastogloia pseudolatecostata* and *Mastogloia pusilla* (Grunow) Cleve var. *pusilla* was 3.56%. *Mastogloia pusilla* var. *pusilla* showed strong seasonality and with abundance of 7% together with *Navicula ramosissima* it represented taxa characteristic for epiphytes on *Padina pavonica* during autumn. *Mastogloia decipiens* showed strong seasonality with 6% in summer, 3% during autumn, and absence during winter and spring. *Mastogloia fimbriata* occurred in 91% of samples with average abundance of 1.62% reaching up to 3% during winter.

Table 21. Seasonal distribution of the 25 taxa dominant on *Padina pavonica*. N = 23.

***Padina pavonica* - 25 dominant taxa:**	**Average Seasonal Abundance (%):**			
	Winter	**Spring**	**Summer**	**Autumn**
Amphora acutiuscula Kützing	2.82%	2.05%	1.51%	1.72%
Amphora helenensis Giffen	4.00%	0.97%	1.26%	1.20%
Berkeleya rutilans (Trentepohl) Grunow	0.00%	6.11%	1.97%	3.25%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	5.88%	3.96%	3.42%	3.96%
Cocconeis scutellum Ehrenberg var. *scutellum*	14.59%	8.36%	6.69%	5.21%
Hyalosynedra laevigata (Grunow) Williams & Round	7.06%	8.13%	4.75%	3.94%
Licmophora paradoxa (Lyngbye) Agardh	5.88%	5.18%	0.89%	0.70%
Mastogloia binotata (Grunow) Cleve	1.18%	0.98%	3.58%	3.90%
Mastogloia crucicula (Grunow) Cleve var. crucicula	4.94%	0.58%	3.29%	3.78%
Mastogloia crucicula var. *alternans* Zanon	7.06%	1.29%	3.18%	6.05%
Mastogloia cuneata (Meister) Simonsen	1.41%	3.66%	4.57%	2.49%
Mastogloia decipiens Hustedt	0.00%	0.00%	5.77%	3.28%
Mastogloia fimbriata (Brightwell) Cleve	3.06%	0.26%	1.09%	1.93%
Mastogloia ignorata Hustedt	0.24%	0.00%	1.48%	3.72%
Mastogloia ovalis A. Schmidt	1.88%	0.48%	3.31%	4.00%
Mastogloia pseudolatecostata Yohn & Gibson	5.18%	0.79%	2.84%	2.46%
Mastogloia pusilla (Grunow) Cleve var. *pusilla*	0.24%	0.72%	1.33%	7.10%
Navicula ramosissima (Agardh) Cleve	1.65%	6.85%	9.90%	7.99%
Nitzschia angularis W. Smith	3.76%	2.72%	4.06%	2.31%
Nitzschia cf. *sigma* (Kützing) W. Smith	0.24%	9.59%	1.53%	0.24%
Nitzschia fusiformis Grunow	1.65%	0.00%	9.69%	1.72%
Nitzschia lanceolata var. *minima* Grunow	2.12%	1.35%	1.80%	3.36%
Nitzschia panduriformis Gregory var. *panduriformis*	0.24%	0.38%	1.54%	1.27%
Rhopalodia pacifica Krammer	0.71%	0.24%	1.47%	1.82%
Tabularia ktenoeoides Kuylenstierna	2.82%	2.79%	1.23%	0.78%

Higher abundances of *Cocconeis scutellum* var. *scutellum* were observed during winter (15%) and spring (8%), while during other seasons its average abundance amounted to 5-7%. Likewise *Cocconeis molesta* var. *crucifera* reached higher abundance in winter (6%), whereas during remaining seasons it amounted to 3-4%. Apart from the taxa mentioned, during the winter the highest abundances occurred in *Hyalosynedra laevigata*, *Mastogloia crucicula* var. *alternans* and *Licmophora paradoxa* (Lyngbye) Agardh, all of which showed abundances of 6-7%. During the spring somewhat different taxa dominated on *Padina pavonica*. Dominant during spring were *Berkeleya rutilans* (Trentepohl) Grunow, *Cocconeis scutellum* var. *scutellum*, *Hyalosynedra laevigata*, *Licmophora paradoxa*, *Navicula ramosissima* and *Nitzschia* cf. *sigma* (Kützing) W. Smith. These differences were more significant when the summer epiphytic diatom community of *Padina pavonica* is considered. The summer assemblage was dominated by *Navicula ramosissima* and *Nitzschia fusiformis* Grunow both with abundance of 10%.

Considering all three locations (Dubrovnik, Mljet, Hvar), the diatom community on *Padina pavonica* was characterized by dominance of *Navicula ramosissima* which occurred with an average abundance of 8% (Table 22).

Table 22. Abundance of the 25 dominant taxa of *Padina pavonica* at different stations. N = 23.

***Padina pavonica* - 25 dominant taxa:**	**Average Site Abundance (%):**		
	Dubrovnik	**Mljet**	**Hvar**
Amphora acutiuscula Kützing	2.01%	1.23%	1.86%
Amphora helenensis Giffen	0.62%	1.27%	1.77%
Berkeleya rutilans (Trentepohl) Grunow	2.15%	2.16%	4.59%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	4.89%	2.55%	3.88%
Cocconeis scutellum Ehrenberg var. *scutellum*	9.22%	5.93%	4.85%
Hyalosynedra laevigata (Grunow) Williams & Round	2.69%	5.39%	5.94%
Licmophora paradoxa (Lyngbye) Agardh	1.05%	0.31%	2.77%
Mastogloia binotata (Grunow) Cleve	4.92%	4.58%	1.73%
Mastogloia crucicula (Grunow) Cleve var. crucicula	4.48%	5.39%	1.57%
Mastogloia crucicula var. *alternans* Zanon	7.84%	5.42%	2.43%
Mastogloia cuneata (Meister) Simonsen	4.41%	2.41%	2.75%
Mastogloia decipiens Hustedt	1.07%	4.41%	4.48%
Mastogloia fimbriata (Brightwell) Cleve	2.16%	1.58%	1.23%
Mastogloia ignorata Hustedt	2.63%	2.94%	3.19%
Mastogloia ovalis A. Schmidt	5.88%	2.91%	1.55%
Mastogloia pseudolatecostata Yohn & Gibson	2.75%	2.50%	2.24%
Mastogloia pusilla (Grunow) Cleve var. *pusilla*	4.51%	7.04%	3.83%
Navicula ramosissima (Agardh) Cleve	8.21%	9.31%	7.41%
Nitzschia angularis W. Smith	2.81%	2.31%	3.19%
Nitzschia cf. *sigma* (Kützing) W. Smith	2.89%	1.43%	4.92%
Nitzschia fusiformis Grunow	1.61%	2.42%	7.32%
Nitzschia lanceolata var. *minima* Grunow	1.69%	3.17%	2.99%
Nitzschia panduriformis Gregory var. *panduriformis*	0.70%	0.61%	1.81%
Rhopalodia pacifica Krammer	0.70%	2.02%	2.11%
Tabularia ktenoeoides Kuylenstierna	0.89%	1.16%	1.62%

A group of taxa belonging to *Mastogloia* i.e. *M. binotata*, *M. crucicula* var. *crucicula*, *M. crucicula* var. *alternans* and *M. pusilla* var. *pusilla* occurring with increased abundances (>4.5%) were rather characteristic for the *Caulerpa racemosa* epiphytic assemblage. On the contrary *Berkeleya rutilans* occurred with higher abundances (>4.5%) on *Caulerpa taxifolia* along with *Licmophora paradoxa*, *Nitzschia* cf. *sigma* and *Nitzschia fusiformis* with the latter three species showing higher abundances at the island of Hvar.

For all three study sites Shannon-Wiener Index was computed as a measure of the species diversity of the *Padina pavonica* epiphytic assemblages. Values of Shannon-Wiener index as shown in Figure 40 were the highest during autumn. The highest values of Shannon-Wiener Biodiversity Index for P. pavonica epiphytic diatoms were recorded on the island of Hvar in September 2010 (3.84), September 2009 (3.71) and in October 2010 (3.62). Likewise the lowest value of Shannon-Wiener Biodiversity Index (3.00) occurred in March 2010 at *Caulerpa taxifolia* sampling site. Low values of Shannon-Wiener Biodiversity Index were also computed in July 2010 for Island of Hvar and Dubrovnik sampling sites. In July 2010 in Dubrovnik this has corresponded with the minimum number of taxa (47) on *Padina pavonica* in one sample. Interestingly in October 2009 values of Shannon-Wiener Biodiversity Index were almost the same for all sampling sites and substrates, ranging from 3.46 to 3.58. In October 2010, values of Shannon-Wiener Biodiversity Index for *Padina pavonica* collected from Mljet and Dubrovnik sampling sites were almost the same (3.28).

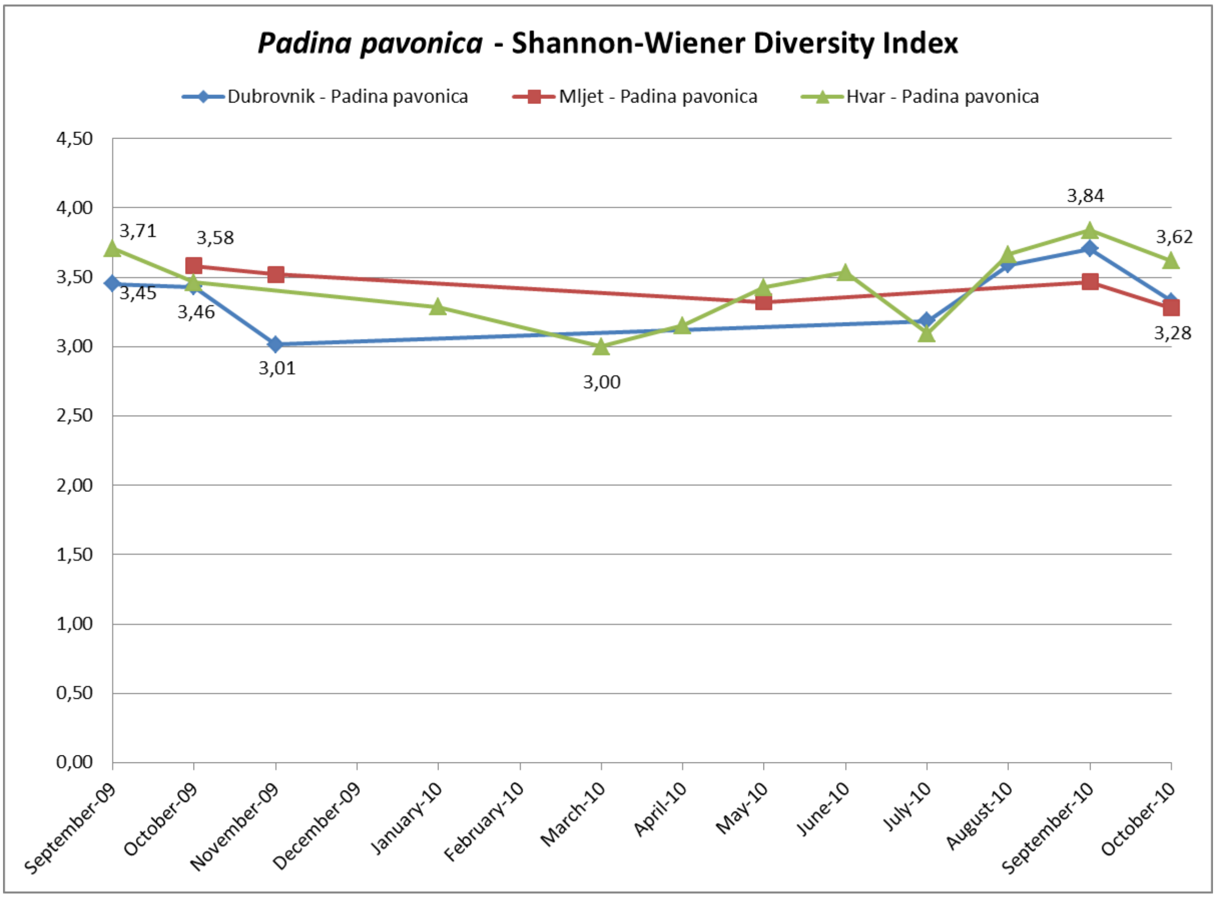
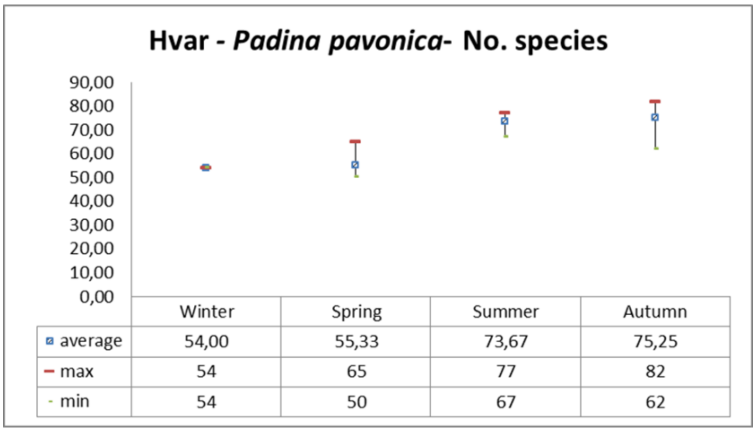


Figure 40. Shannon-Wiener Biodiversity Index of diatom epiphytic community on *Padina pavonica*. N = 23.

High values of Shannon-Wiener Index in autumn corresponded with high numbers of taxa. The maximum number of taxa in one sample on *P. pavonica* (82) was observed at the island of Hvar in September 2010.



	Winter	Spring	Summer	Autumn
◘ average	54,00	55,33	73,67	75,25
▬ max	54	65	77	82
- min	54	50	67	62

Figure 41. Number of taxa in diatom community on *Padina pavonica* (Island of Hvar).

This was not, however, an exceptional situation as the average number of taxa on the island of Hvar during autumn amounted to 75, with summer values only slightly lower (73.67) though a significant decrease in average number of taxa to 54.66 during winter and spring was observed (Figure 41).

Further analysis of *P. pavonica* epiphytic assemblages revealed significant correlation between the number of taxa and the sea temperature. Over the research period of one year (autumn 2009-autumn 2010), sea water temperature ranged between 12°C during in January to 25°C in August (Figure 42).

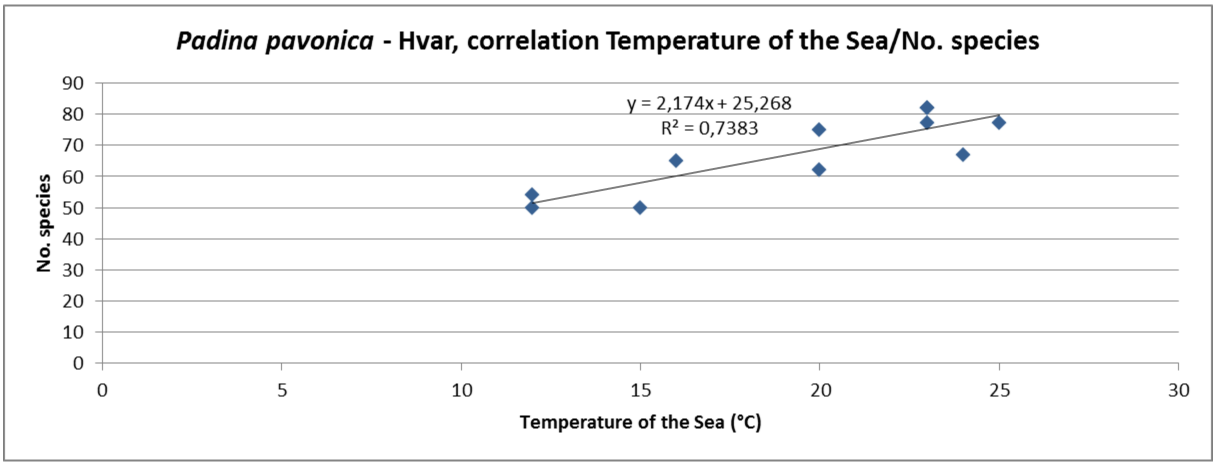


Figure 42. Correlation between number of diatom taxa on *Padina pavonica* and sea temperature on the island of Hvar (N = 10) (P < 0,01).

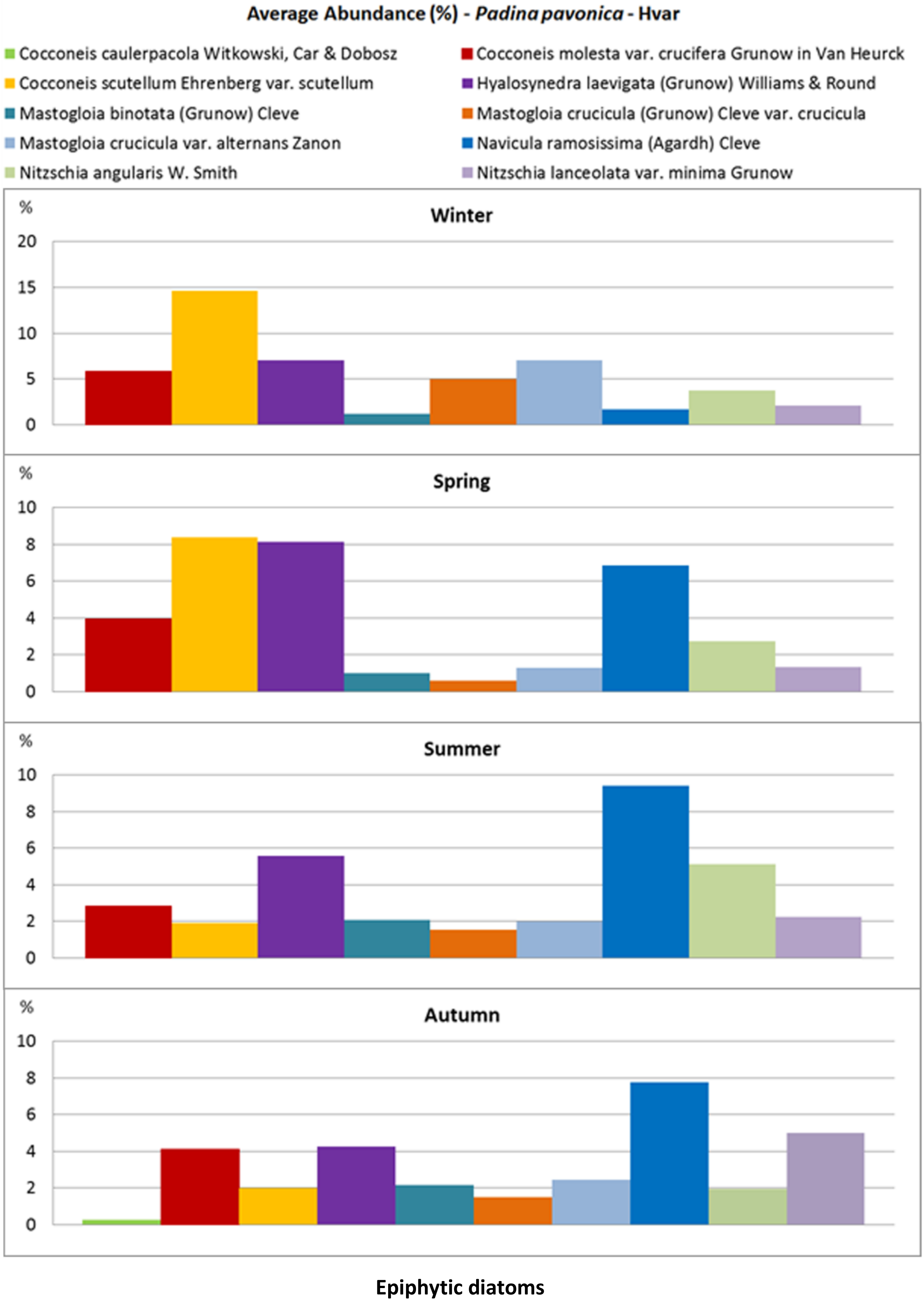


Figure 43. Average abundance of 10 dominant epiphytic diatoms on *Padina pavonica* on the island of Hvar.

3.3.3. Epiphytic diatoms on *Halimeda tuna*

Altogether, 243 diatom taxa representing 54 genera were recorded as epiphytes on *Halimeda tuna* from all three sampling sites. *Halimeda tuna* hosted diatom assemblages dominated by taxa belonging to *Cocconeis*, *Mastogloia*, *Navicula*, *Nitzschia* and *Amphora*. The group of 25 taxonomic entities listed below (Table 23) shows the most abundant epiphytic diatoms, which dominated in terms of both frequency of appearance (>15%) and abundance (>1%) in all samples. When combined together in a single sample, these 25 dominant taxa contributed 53-93% to the diatom community.

Table 23. Dominant diatom taxa on *Halimeda tuna* with average abundance (Avg.) >1% and frequency of appearance (Freq.) >15%. N = 26.

***Halimeda tuna* - 25 dominant taxa:**	**Freq. (%)**	**Avg. (%)**
Amphora acutiuscula Kützing	100.00%	3.29%
Amphora cf. *marina* W. Smith	84.62%	1.15%
Amphora helenensis Giffen	92.31%	1.79%
Amphora kolbei Aleem	76.92%	1.53%
Cocconeis costata Gregory var. *costata*	92.31%	2.31%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	100.00%	7.31%
Cocconeis scutellum Ehrenberg var. *scutellum*	100.00%	17.72%
Fragilaria investiens (W. Smith) Cleve-Euler	88.46%	1.91%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	73.08%	2.82%
Hyalosynedra laevigata (Grunow) Williams & Round	100.00%	3.71%
Licmophora paradoxa (Lyngbye) Agardh	69.23%	1.59%
Mastogloia binotata (Grunow) Cleve	92.31%	3.60%
Mastogloia crucicula (Grunow) Cleve var. crucicula	96.15%	2.21%
Mastogloia crucicula var. *alternans* Zanon	96.15%	2.78%
Mastogloia cuneata (Meister) Simonsen	53.85%	1.50%
Mastogloia fimbriata (Brightwell) Cleve	96.15%	1.88%
Navicula cf. *duerrenbergiana* Hustedt	15.38%	6.43%
Navicula ramosissima (Agardh) Cleve	100.00%	9.11%
Navicula sp.1	23.08%	4.92%
Navicula subagnita Proschkina-Lavrenko	88.46%	2.02%
Nitzschia angularis W. Smith	96.15%	6.55%
Nitzschia lanceolata var. *minima* Grunow	84.62%	2.19%
Rhopalodia pacifica Krammer	65.38%	1.20%
Tabularia ktenoeoides Kuylenstierna	100.00%	2.10%
Toxarium undulatum Bailey	61.54%	1.38%

A group of taxa including *Amphora acutiuscula* Kützing, *Cocconeis molesta* var. *crucifera*, *Cocconeis scutellum* var. *scutellum*, *Hyalosynedra laevigata*, *Navicula ramosissima* and *Tabularia ktenoeoides* Kuylenstierna was recorded in all samples. Less frequent (present in 92% of samples) were *Amphora helenensis*, *Cocconeis costata* var. *costata*, *Mastogloia binotata*, *Mastogloia crucicula* var. *crucicula*, *Mastogloia crucicula* var. *alternans*, *Mastogloia fimbriata* and *Nitzschia angularis* (Table 23).

Table 24. Seasonal distribution of 25 taxa dominant on *Halimeda tuna*. N = 26.

***Halimeda tuna* - 25 dominant taxa:**	**Average Seasonal Abundance (%):**			
	Winter	**Spring**	**Summer**	**Autumn**
Amphora acutiuscula Kützing	5.38%	3.32%	3.55%	2.20%
Amphora cf. *marina* W. Smith	0.69%	0.49%	1.64%	1.48%
Amphora helenensis Giffen	1.74%	2.24%	2.04%	1.47%
Amphora kolbei Aleem	1.11%	2.19%	1.82%	1.26%
Cocconeis costata Gregory var. *costata*	1.44%	6.96%	1.56%	1.80%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	10.60%	5.01%	3.47%	8.74%
Cocconeis scutellum Ehrenberg var. *scutellum*	25.34%	17.47%	12.08%	17.43%
Fragilaria investiens (W. Smith) Cleve-Euler	1.28%	7.11%	1.68%	0.68%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	2.97%	3.31%	1.52%	3.40%
Hyalosynedra laevigata (Grunow) Williams & Round	3.79%	2.17%	4.77%	3.67%
Licmophora paradoxa (Lyngbye) Agardh	1.91%	1.31%	2.52%	0.91%
Mastogloia binotata (Grunow) Cleve	1.02%	3.15%	4.26%	4.41%
Mastogloia crucicula (Grunow) Cleve var. crucicula	3.07%	0.99%	2.62%	2.02%
Mastogloia crucicula var. *alternans* Zanon	3.02%	1.03%	2.89%	3.28%
Mastogloia cuneata (Meister) Simonsen	0.00%	0.36%	2.26%	1.11%
Mastogloia fimbriata (Brightwell) Cleve	0.00%	2.80%	1.70%	1.79%
Navicula cf. *duerrenbergiana* Hustedt	11.01%	0.00%	0.00%	4.91%
Navicula ramosissima (Agardh) Cleve	6.65%	0.00%	0.00%	8.99%
Navicula sp.1	0.00%	0.74%	3.31%	6.37%
Navicula subagnita Proschkina-Lavrenko	0.00%	4.94%	2.35%	1.39%
Nitzschia angularis W. Smith	4.46%	4.52%	9.08%	6.88%
Nitzschia lanceolata var. *minima* Grunow	1.23%	1.66%	1.84%	3.20%
Rhopalodia pacifica Krammer	0.91%	1.29%	1.55%	1.16%
Tabularia ktenoeoides Kuylenstierna	3.15%	4.14%	2.21%	0.82%
Toxarium undulatum Bailey	0.91%	1.35%	1.91%	1.08%

Amphora acutiuscula, one of four *Amphora* taxa which belonged to 25 dominant epiphytic diatoms on *Halimeda tuna*, occurred with average abundance of 3.3% reaching higher (5.4%) abundance during winter. The second species *A. helenensis* was present with average abundance of 2% during all seasons, whereas *Amphora* cf. *marina* W. Smith occurred with increased abundance (1.6%) during summer and autumn while during winter and spring its average abundance was 0.6%.

The other species of epiphytes occurring on *H. tuna* was *Hyalosynedra laevigata* occurred with higher abundance on the island of Hvar. In general, at all three sampling sites, average abundance of *Hyalosynedra laevigata* on *Halimeda tuna* amounted to 4%. Its highest abundance was recorded during summer, while the lowest was during spring.

Cocconeis costata var. *costata*, one of three *Cocconeis* taxa which belonged in the group of 25 dominant taxa on *Halimeda tuna*, occurred with increased (7%) abundance in spring, while during other seasons its average abundance did not exceed 1.80%. *Cocconeis* *scutellum* var. *scutellum* and *Cocconeis molesta* var. *crucifera* reached higher abundances during winter and lower in summer. An opposite pattern of abundance was observed in case of *Navicula ramosissima* with higher (12%) abundances in summer, and lower (7%) in winter. *Navicula ramosissima* was one of four taxa of genus *Navicula* belonging to the 25 dominant epiphytic diatom taxa on *Halimeda tuna*.

Five of the 25 dominant taxa represented *Mastogloia*. All of them occurred on *H. tuna* with greater abundances in Mljet and Dubrovnik, where they were associated with *Caulerpa racemosa*, than on the island of Hvar where they were associated with *Caulerpa taxifolia*. *Mastogloia binotata* and *Mastogloia cuneata* occurred with decreased abundance during winter and spring. The abundance of *Mastogloia cuneata* was equal at all sampling sites. Increased (7%) abundance of *Mastogloia binotata* was observed on the island of Mljet. Average abundance of *Mastogloia fimbriata* amounted to 1.88% and in general was higher (2.8%) during spring on the island of Mljet (3.5%).

In samples collected at all three sites *Nitzschia angularis* occurred on *Halimeda tuna* with increased (9%) abundance in summer with a decrease (7%) in autumn. Winter and spring abundances of *N. angularis* were lower (4.5%). *Nitzschia lanceolata* var. *minima* occurred in 85% of the samples on *Halimeda tuna* with average abundance of 2%. During autumn its abundance showed a slight increase to 3.20%.

Fragilaria investiens (W. Smith) Cleve-Euler occurred with average abundance of 2% in 88% of samples on *Halimeda tuna*. Significantly higher abundance of *F. investiens* abundance was observed in spring (7%). In general this species tended to reach higher abundances at sites where it was associated with *Caulerpa racemosa*.

Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow was also more typical for *Caulerpa racemosa* sampling sites. Generally, it occurred in 73% of the samples from *Halimeda tuna* with average abundance of 3%. *Licmophora paradoxa* (Lyngbye) Agardh was found in 70% of samples with average abundance of 1.6%. Highest abundance occurred on the island of Mljet and the lowest on the island of Hvar. *Toxarium undulatum* Bailey which was found in 62% of samples occurred equally during all seasons and on all sampling sites with abundance of 1.38%.

Table 25. Average site abundance of the 25 dominant taxa on *Halimeda tuna*. N = 26.

***Halimeda tuna* - 25 dominant taxa:**	**Average Site Abundance (%):**		
	Dubrovnik	**Mljet**	**Hvar**
Amphora acutiuscula Kützing	2.71%	3.31%	4.01%
Amphora cf. *marina* W. Smith	1.31%	0.50%	1.37%
Amphora helenensis Giffen	2.27%	1.46%	1.53%
Amphora kolbei Aleem	1.60%	1.33%	1.60%
Cocconeis costata Gregory var. *costata*	3.82%	1.62%	0.84%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	5.75%	3.98%	12.59%
Cocconeis scutellum Ehrenberg var. *scutellum*	23.49%	10.65%	17.58%
Fragilaria investiens (W. Smith) Cleve-Euler	2.13%	2.32%	1.36%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	2.32%	3.76%	0.26%
Hyalosynedra laevigata (Grunow) Williams & Round	2.19%	3.91%	5.43%
Licmophora paradoxa (Lyngbye) Agardh	1.61%	2.38%	0.61%
Mastogloia binotata (Grunow) Cleve	2.91%	6.77%	0.53%
Mastogloia crucicula (Grunow) Cleve var. crucicula	2.73%	2.87%	0.99%
Mastogloia crucicula var. *alternans* Zanon	3.69%	2.64%	1.75%
Mastogloia cuneata (Meister) Simonsen	1.48%	1.64%	1.25%
Mastogloia fimbriata (Brightwell) Cleve	1.28%	3.53%	0.91%
Navicula cf. *duerrenbergiana* Hustedt	6.80%	0.00%	6.07%
Navicula ramosissima (Agardh) Cleve	9.55%	0.00%	9.12%
Navicula sp.1	3.62%	4.79%	6.96%
Navicula subagnita Proschkina-Lavrenko	2.33%	2.60%	1.27%
Nitzschia angularis W. Smith	6.79%	7.33%	5.56%
Nitzschia lanceolata var. *minima* Grunow	2.16%	1.43%	3.32%
Rhopalodia pacifica Krammer	0.83%	1.85%	0.72%
Tabularia ktenoeoides Kuylenstierna	1.34%	3.05%	2.10%
Toxarium undulatum Bailey	0.95%	1.84%	0.86%

To examine differences between diatom assemblages of *Halimeda tuna* from three sampling sites, the taxa richness of diatom assemblages of epiphytic diatoms at Dubrovnik, Mljet and Hvar sampling sites, *H'* (Shannon-Wiener Biodiversity Index), were compared (Figure 44). The highest values of Shannon-Wiener Biodiversity Index 3.39 and 3.45 of epiphytic assemblage on *H. tuna* were observed on the island of Hvar in September 2009 and in October 2009 respectively. The lowest value of Shannon-Wiener Biodiversity Index (2.24) occurred in November 2009 at the island of Hvar sampling site (associated with *Caulerpa taxifolia*). At Hvar a low value of H' of ca. 2.5 was also observed in February 2010. In January and March 2010, values of Shannon-Wiener Biodiversity Index for *Halimeda tuna* collected from Hvar and Dubrovnik (associated with *Caulerpa racemosa*) were almost the same (2.8). Interestingly in September and October 2010 values of Shannon-Wiener Biodiversity Index were almost the same for all sampling sites ranging from 3.15 to 3.38.

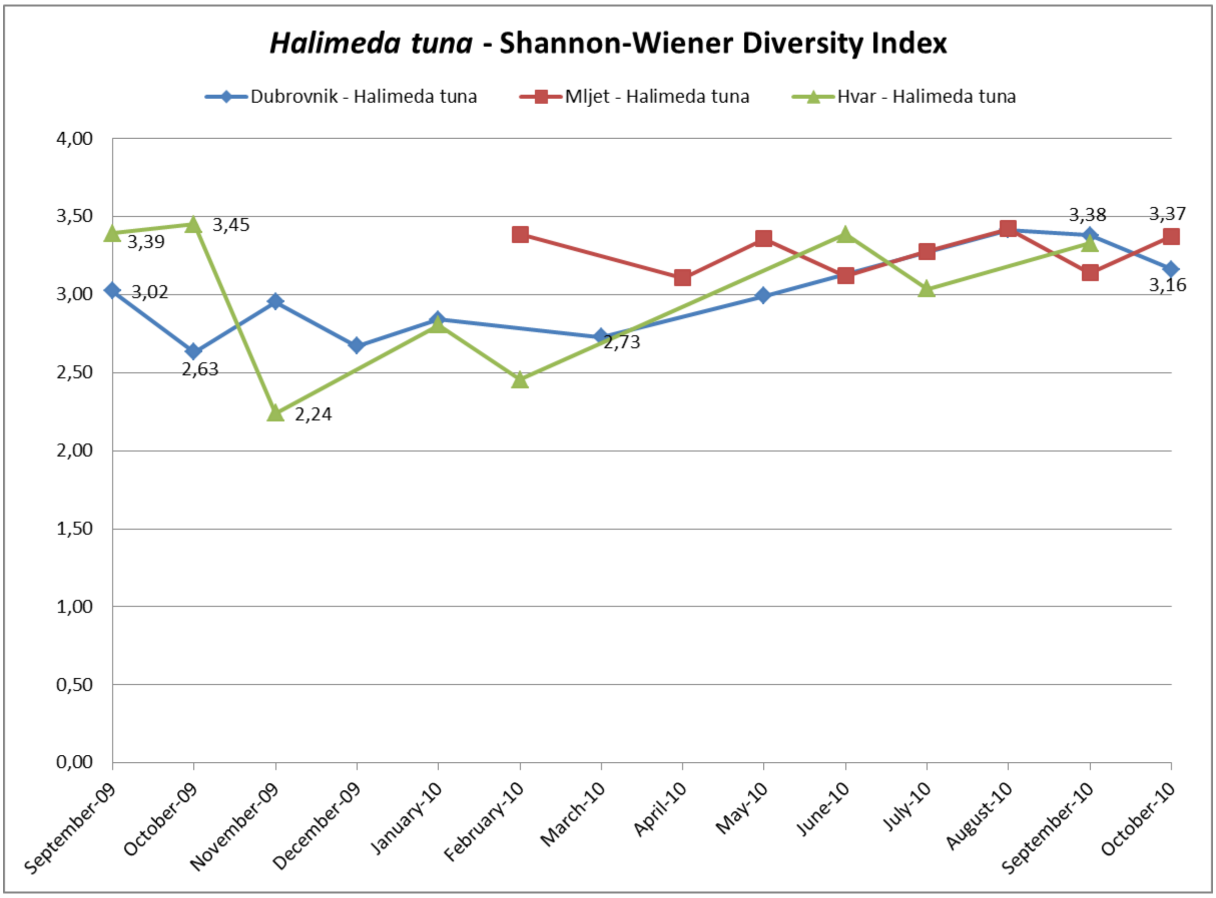
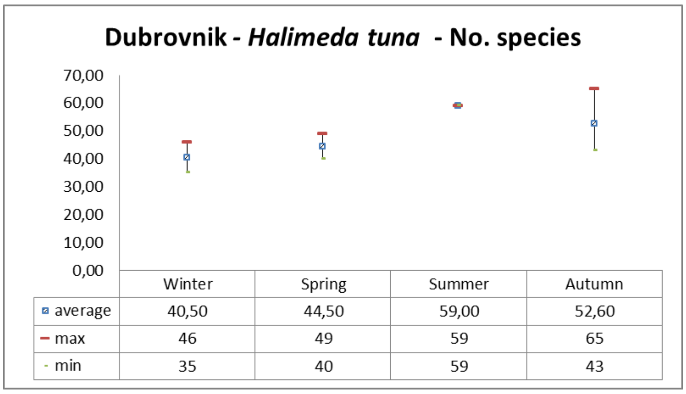


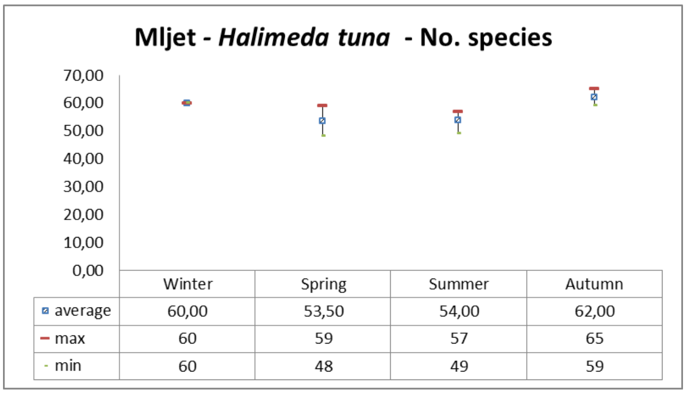
Figure 44. Shannon-Wiener Biodiversity Index of epiphytic diatom assemblage on *Halimeda tuna*. N = 26.

Generally, during summer and autumn assemblages of epiphytic diatoms from *Halimeda tuna* collected from Dubrovnik were composed of higher numbers of taxa ranging between ca. 59 and 65 (e.g. September 2010). The number of taxa in spring and winter was significantly lower and amounted to ca. 46 and 49 respectively. The minimum number of taxa (35) of epiphytic diatoms on *H. tuna* in one sample was recorded in Dubrovnik in December 2009. Interestingly from the sampling site at the Island of Mljet the sample richest in number of taxa was taken in December 2010 whereas spring and summer samples were characterized by significantly lower numbers of taxa. The maximum number of epiphytic diatom taxa amounting to 73 on *H. tuna* in one sample was recorded at the Island of Hvar in October 2009. During winter, assemblages of epiphytic diatoms on *H. tuna* from Hvar (area under the influence of *C. taxifolia*), contained an average of 50.5 taxa while during summer and autumn the number was significantly higher (61).



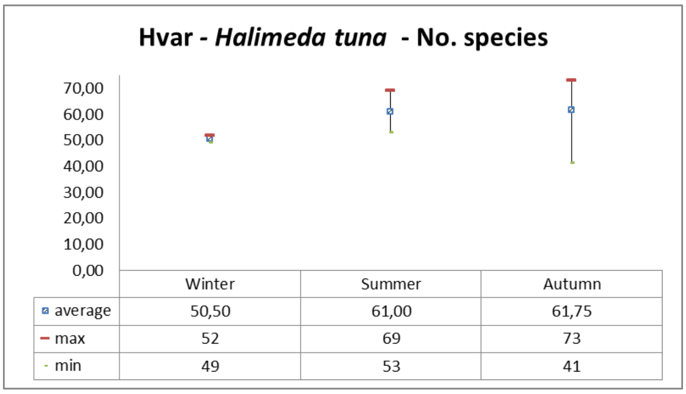
	Winter	Spring	Summer	Autumn
▫ average	40,50	44,50	59,00	52,60
− max	46	49	59	65
- min	35	40	59	43

Figure 45. Number of taxa in diatom community on *Halimeda tuna* collected from areas under the influence of *Caulerpa racemosa* in Dubrovnik. N=10.



	Winter	Spring	Summer	Autumn
▫ average	60,00	53,50	54,00	62,00
− max	60	59	57	65
- min	60	48	49	59

Figure 46. Number of taxa in diatom community on *Halimeda tuna* collected from areas under the influence of *Caulerpa racemosa* at the island of Mljet. N=8.



	Winter	Summer	Autumn
▫ average	50,50	61,00	61,75
− max	52	69	73
- min	49	53	41

Figure 47. Number of taxa in diatom community on *Halimeda tuna* collected from areas under the influence of *Caulerpa taxifolia* at the Island of Hvar. N=8.

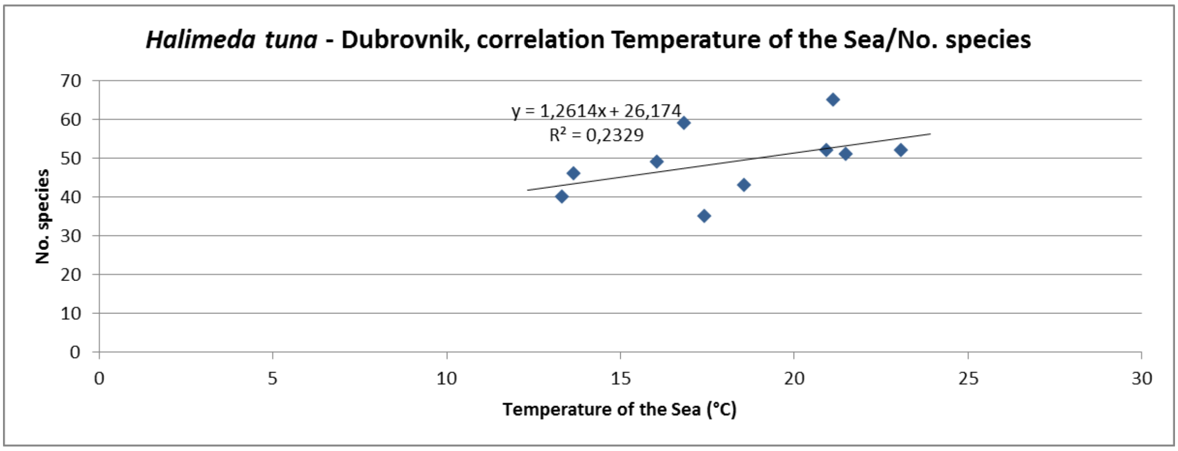


Figure 48. Correlation of number of taxa on *Halimeda tuna* and temperature of the sea water in Dubrovnik. (N=10).

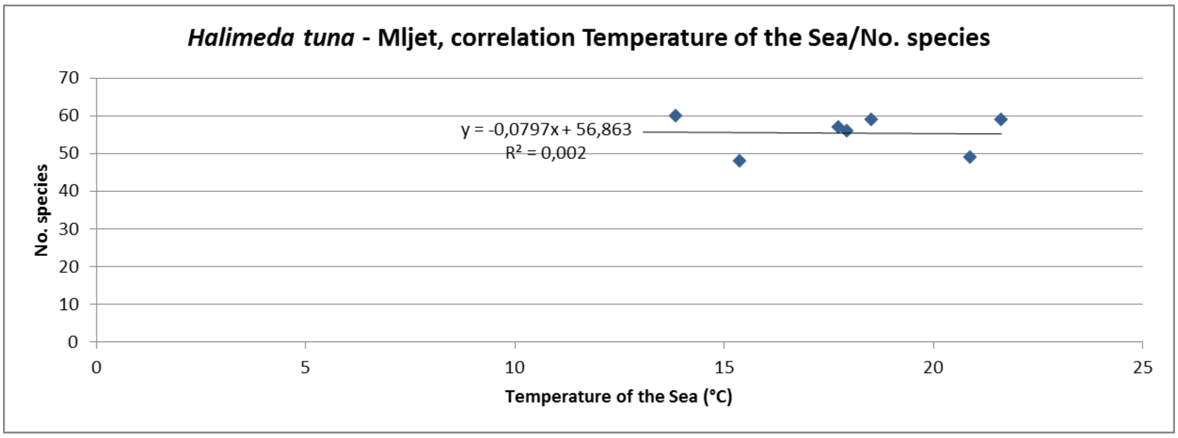


Figure 49. Correlation of number of taxa on *Halimeda tuna* and temperature of the sea water on the island of Mljet. (N=8).

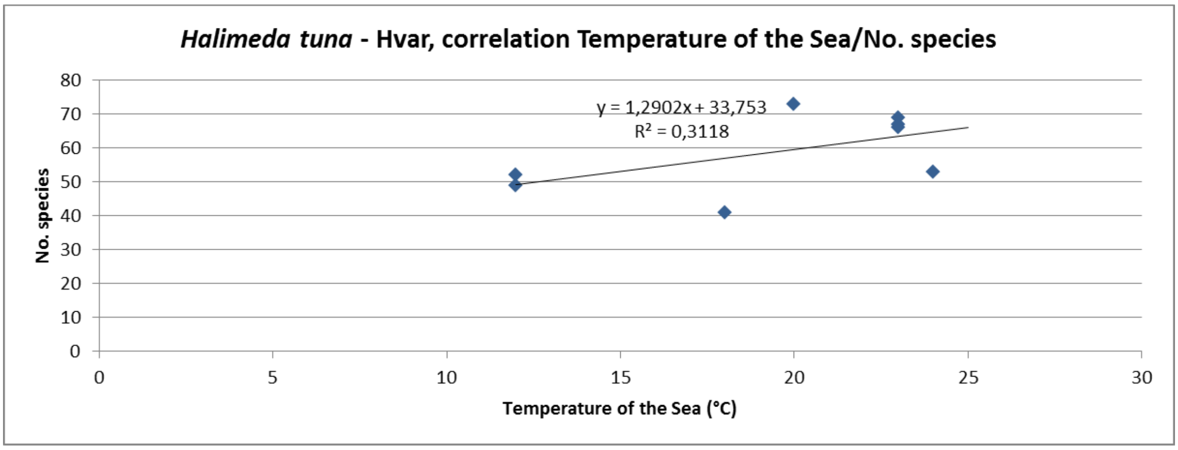


Figure 50. Correlation of number of taxa on *Halimeda tuna* and temperature of the sea water on the island of Hvar. (N=8).

The number of taxa in epiphytic diatom assemblages on *H. tuna* at all three sampling sites was plotted against the sea water temperature. The correlation between sea water temperature and the number epiphytic diatom of taxa on *Halimeda tuna* was very weak and the correlation coefficients low (Figure 48, Figure 49, Figure 50).

The largest number of diatom taxa (18) on *H. tuna* represented *Mastogloia*. Their occurrence was most abundant in September and October. In general during autumn *Mastogloia* representatives reached the highest abundance. Seven taxa of *Mastogloia* i.e. *M. binotata*, *M. crucicula* var. *alternans*, *M. crucicula* var. *crucicula*, *M. fimbriata*, *M. pusilla* var. *pusilla*, *M. cuneata* and *M. ovulum* together exceeded 60%, 40% and 20% of the whole of the epiphytic diatom assemblages on *Halimeda tuna* at Dubrovnik, Mljet and Hvar respectively.

A group of taxa which is second in terms of abundance included *Cocconeis scutellum* var. *scutellum*, *Navicula ramosissima* and *Cocconeis molesta* var. *crucifera*. Their joint contribution usually exceeded 25%. This was particularly observed during autumn at the island of Hvar. The above three taxa contributed 25-30% to the total abundance. Interestingly these three taxa were recorded as dominant on *Halimeda tuna* during all seasons at all three sites (Figure 51, Figure 52, Figure 53).

During winter average abundance of *Cocconeis scutellum* var. *scutellum* on the island of Hvar and at Dubrovnik amounted to 30%, while on the island of Mljet it was only 6%. *Navicula ramosissima* occurred during winter with similar abundance on sampling sites influenced by *C. racemosa* (9.5% on the island of Mljet and 8% at Dubrovnik), and only 3.5% on the island of Hvar which was influenced by *C.taxifolia*. During summer average abundance of *Cocconeis scutellum* var. *scutellum* on the island of Hvar amounted to 14%, on the island of Mljet to 12%, and in Dubrovnik to 10%. On the contrary abundance of *Navicula ramosissima* observed in summer was higher than in winter and amounted to 14% on the island of Hvar, 11% on the island of Mljet and 9% in Dubrovnik. *Cocconeis molesta* var. *crucifera* occurred with higher abundance on the island of Hvar than on sampling sites under the influence of *Caulerpa racemosa* during autumn and winter. During autumn its average abundance on the island of Hvar amounted to 14%, in Dubrovnik to 6% and only 3% on the island of Mljet. During winter average abundance of *Cocconeis molesta* var. *crucifera* on the island of Hvar was 18%, on the island of Mljet 9% and only 4% in Dubrovnik.

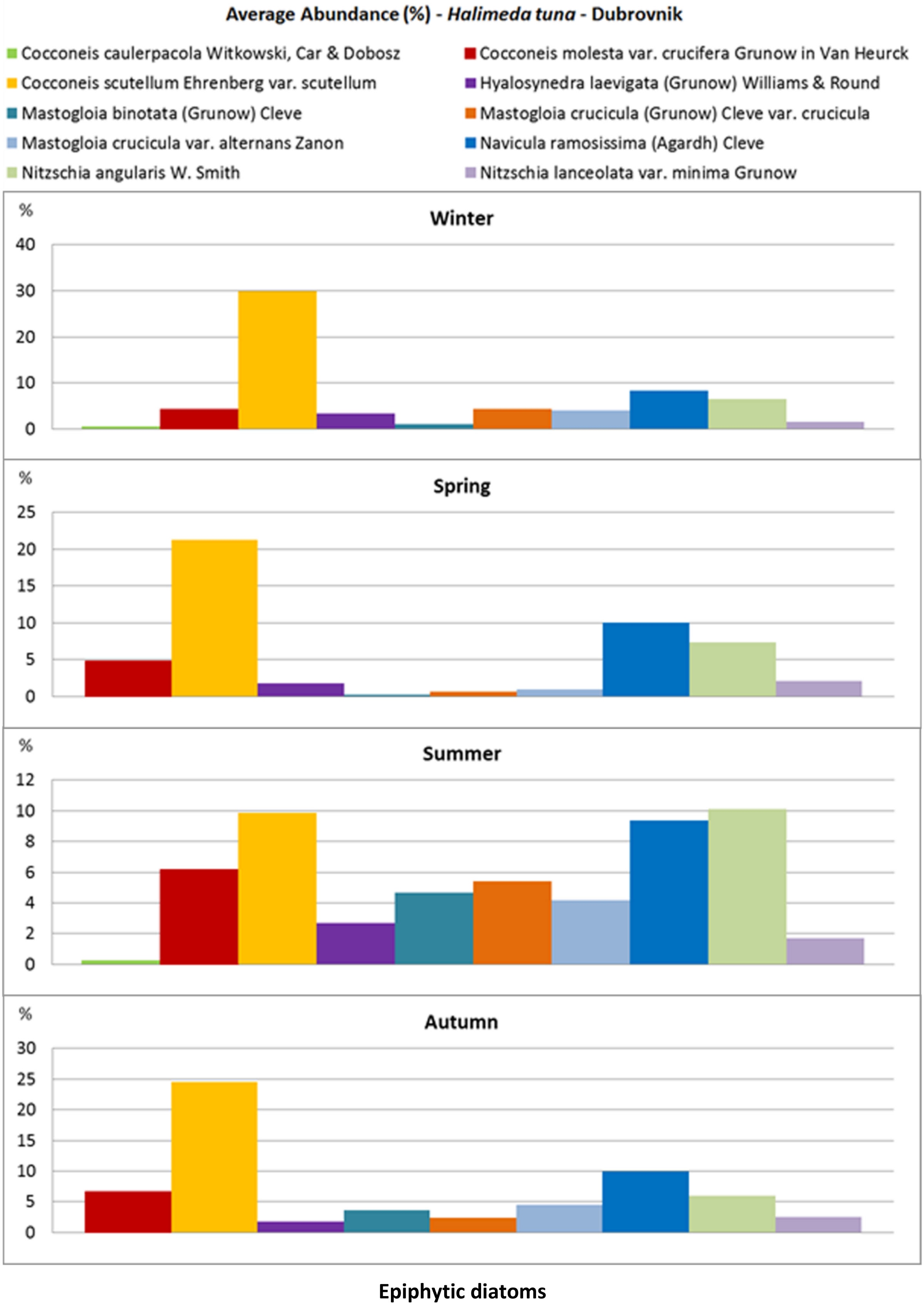


Figure 51. Average abundance of 10 dominant epiphytic diatoms on *Halimeda tuna* in Dubrovnik.

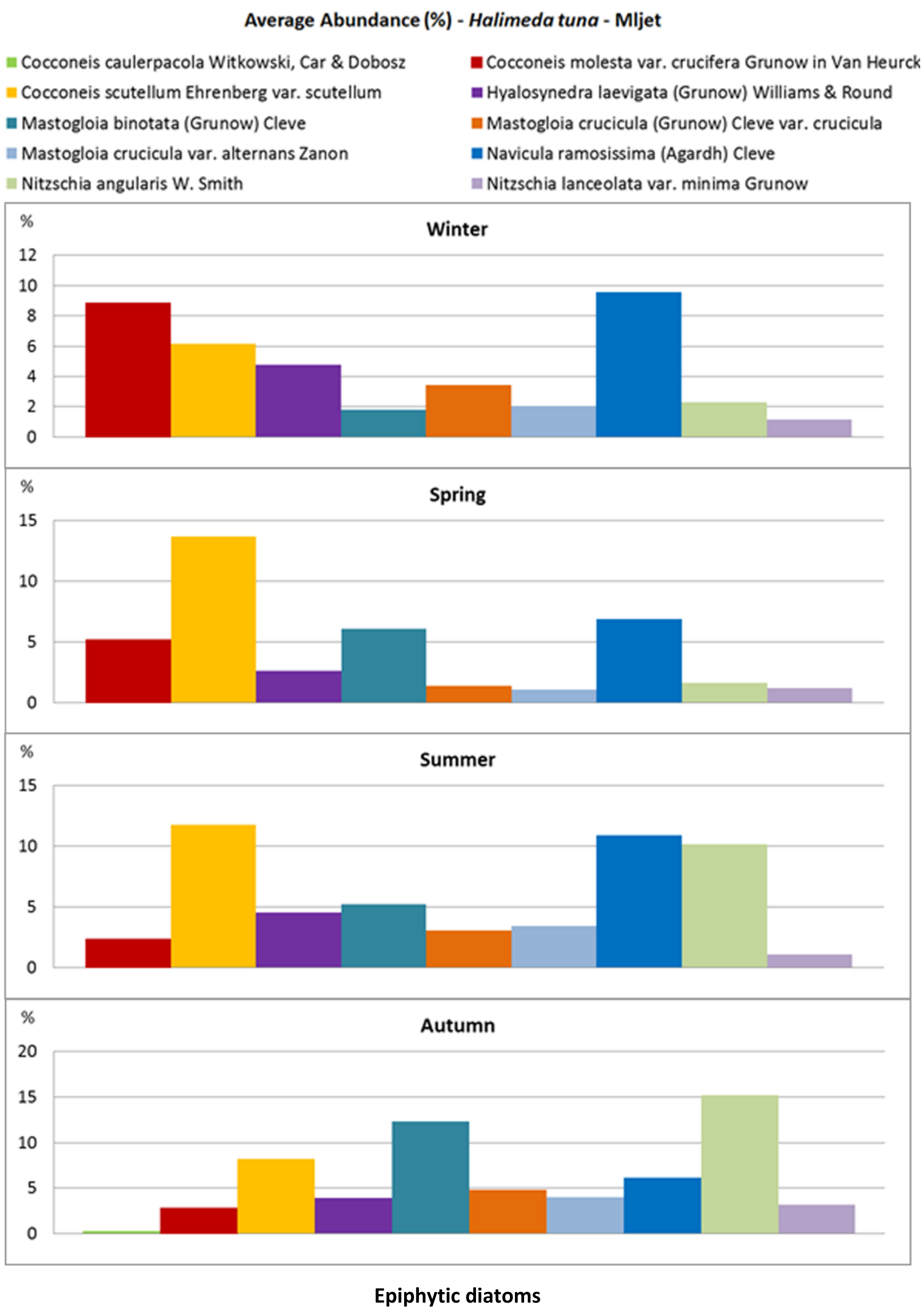


Figure 52. Average abundance of 10 dominant epiphytic diatoms on *Halimeda tuna* on the island of Mljet.

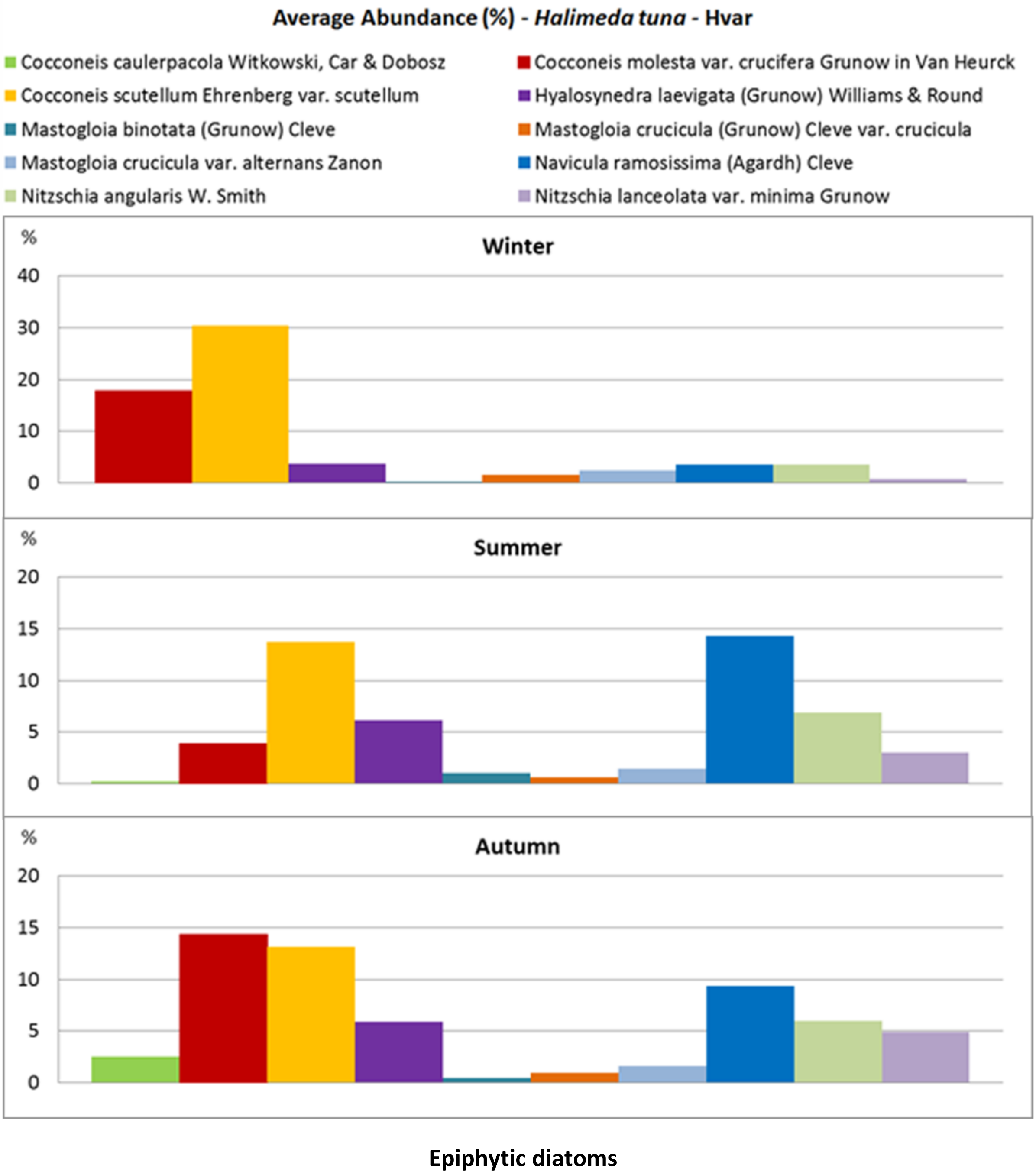


Figure 53. Average abundance of 10 dominant epiphytic diatoms on *Halimeda tuna* on the island of Hvar.

In general, epiphytic diatom assemblages of *Halimeda tuna* are different from those hosted by *Padina pavonica*. As revealed by SIMPER analyses, *Cocconeis scutellum* var. *scutellum*, *Navicula ramosissima*, *Nitzschia angularis*, *Cocconeis molesta* var. *crucifera*, *Mastogloia crucicula* var. *alternans*, *Mastogloia pusilla*, *Hyalosynedra laevigata*, *Mastogloia binotata*, *Berkeleya rutilans*, *Nitzschia fusiformis* and *Mastogloia ovalis* contributed the most (cumulatively 30%) to a variance among assemblages (Figure 54). Practically no differences were observed between diatom assemblages on *Halimeda tuna* from the islands of Mljet and Hvar. The group of taxa contributing the most to variance between *Halimeda tuna* from Dubrovnik on the one hand and *Halimeda tuna* from Mljet and Hvar on the other included *Cocconeis scutellum* var. *scutellum*, *Cocconeis molesta* var. *crucifera*, *Mastogloia binotata*, *Navicula ramosissima*, *Nitzschia angularis* and *Hyalosynedra laevigata.*

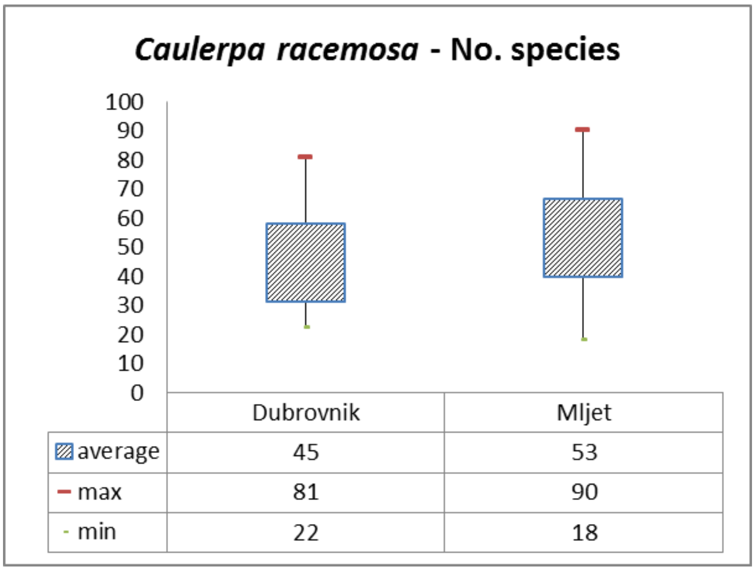
	PD	**PM**	**PH**	**HD**	**HM**
PM	.				
PH	.	.			
HD	*	*	*		
HM	*	.	*	*	
HH	*	*	*	*	.

Figure 54. Comparison of abundance of epiphytic diatoms among hosts at different sampling sites (PD=*Padina pavonica*, Dubrovnik; PM=*Padina pavonica*, Mljet; PH=*Padina pavonica*, Hvar; HD=*Halimeda tuna*, Dubrovnik; HM=*Halimeda tuna*, Mljet; HH=*Halimeda tuna*, Hvar). * P<0.05.

3.3.4. Epiphytic diatoms on *Caulerpa racemosa*

In samples collected from Mljet and Dubrovnik, altogether 360 taxa representing 55 genera were identified as epiphytic diatoms on *Caulerpa racemosa*. In Orsula near Dubrovnik 173 diatom taxa representing 39 genera were identified, whereas the number of epiphytic diatom taxa on *Caulerpa racemosa* found on Mljet was almost double amounting to a total of 312. They represented 54 genera.

The average number of diatom taxa on *Caulerpa racemosa* in Dubrovnik was 45 while on the island of Mljet it was 53 (Figure 55). At both sites, the highest number of taxa on *Caulerpa racemosa* was recorded in September, the lowest in February and March.



	Dubrovnik	Mljet
▨ average	45	53
– max	81	90
- min	22	18

Figure 55. Number of epiphytic diatom taxa on *Caulerpa racemosa* in Dubrovnik and on the island of Mljet.

The lowest number of 18 diatom taxa on *Caulerpa racemosa* was identified on the island of Mljet in March 2009. The highest number of taxa (90) in one sample was observed on *C. racemosa* from Island of Mljet.

The diatom assemblage of *Caulerpa racemosa* during February and March when the lowest number of taxa was recorded was characterized by high abundances of *Cocconeis* taxa. Two of them i.e. *Cocconeis scutellum* var. *scutellum* and *Cocconeis molesta* var. *crucifera*, contributed more than 63% and 81% to the total counts in samples with the lowest recorded number of taxa from Dubrovnik and Mljet respectively.

In Dubrovnik the maximum number of taxa occurred between August and September (Figure 56). Although no significant correlation was observed between number of taxa and salinity, the highest number of diatoms colonizing *C. racemosa* weakly correlated with the yearly temperature maxima (Figure 57, Figure 61).

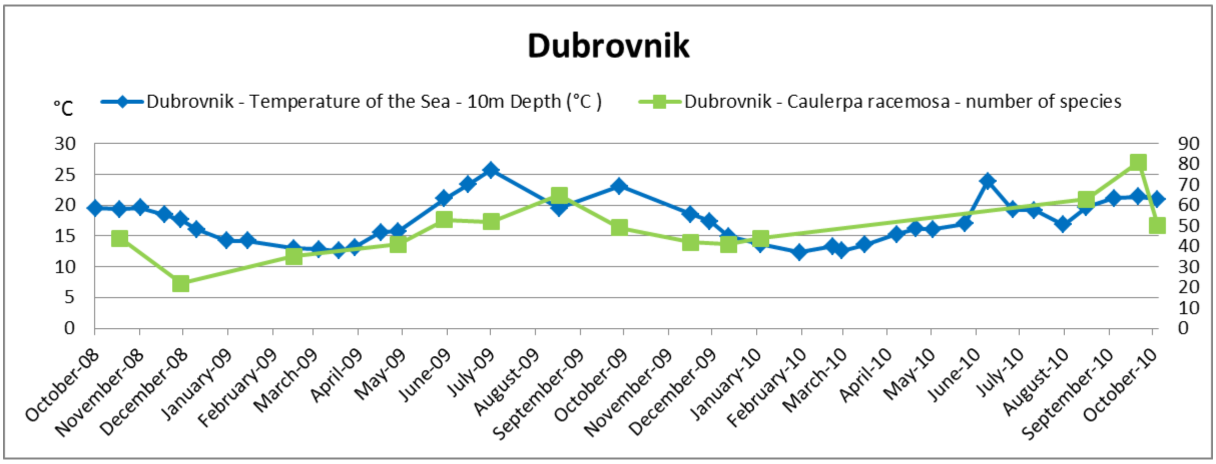


Figure 56. The number of taxa recorded on *Caulerpa racemosa* from Dubrovnik plotted against sea water temperatures. N = 14.

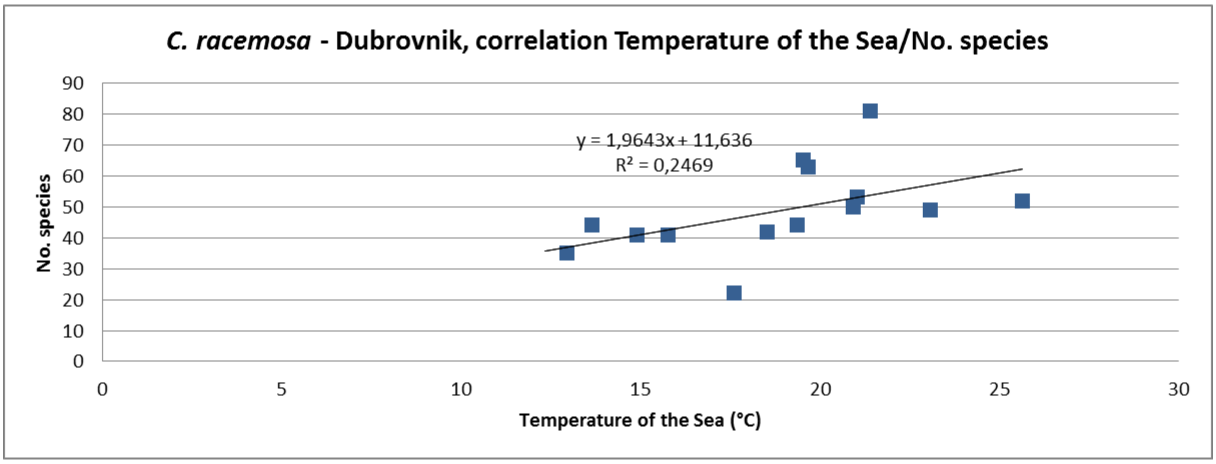


Figure 57. Correlation of sea water temperature and the number of taxa on *C. racemosa* samples from Dubrovnik.

The maximum number of taxa on *Caulerpa racemosa* in samples from Mljet Island appeared between July and October. The number of epiphytic diatom taxa showed no significant correlation with salinity or the yearly sea water temperature maxima (Figure 59, Figure 63).

The twelve most abundant taxa from samples with the highest recorded number of taxa (90) on *Caulerpa racemosa* (Mljet, September 2009) were *Navicula ramosissima*, *Mastogloia pusilla* var. *pusilla*, *Hyalosynedra laevigata*, *Nitzschia lanceolata* var. *minima*, *Cocconeis scutellum* var. *scutellum*, *Mastogloia fimbriata*, *Mastogloia crucicula* var. *crucicula*, *Nitzschia panduriformis* Gregory var. *panduriformis*, *Mastogloia binotata*, *Toxarium undulatum*, *Cocconeis molesta* var. *crucifera* and *Amphora acutiuscula*. These twelve taxa contributed more than 50% to the total count.

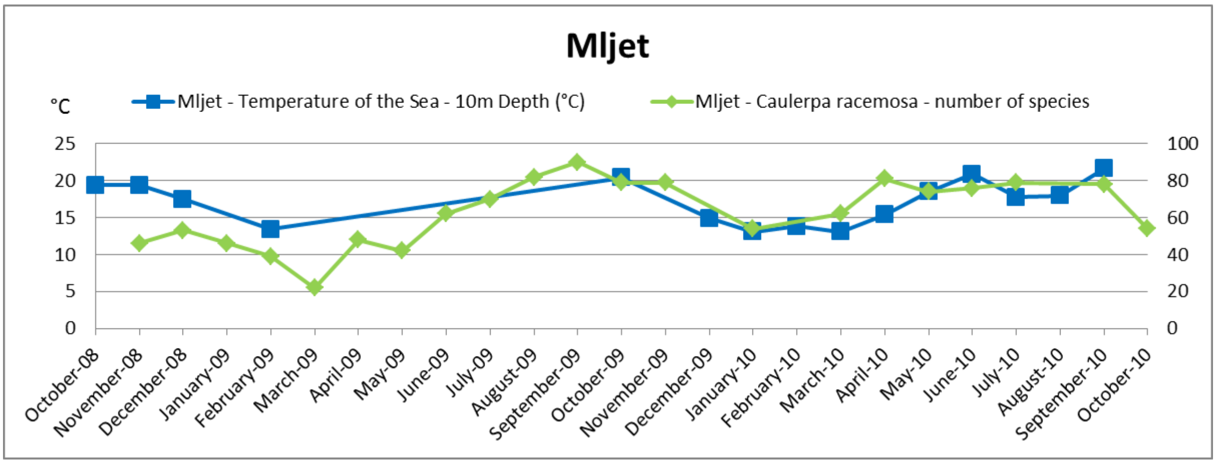


Figure 58. The number of recorded taxa on *C. racemosa* from island of Mljet is plotted against sea water temperatures. N = 21.

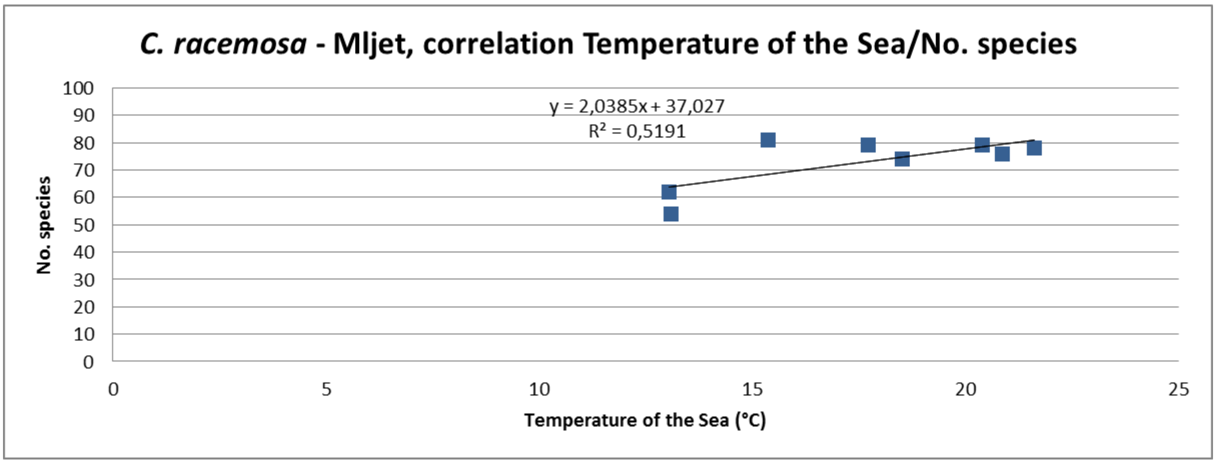


Figure 59. Correlation of sea water temperature and number of taxa on *C. racemosa* samples from island of Mljet.

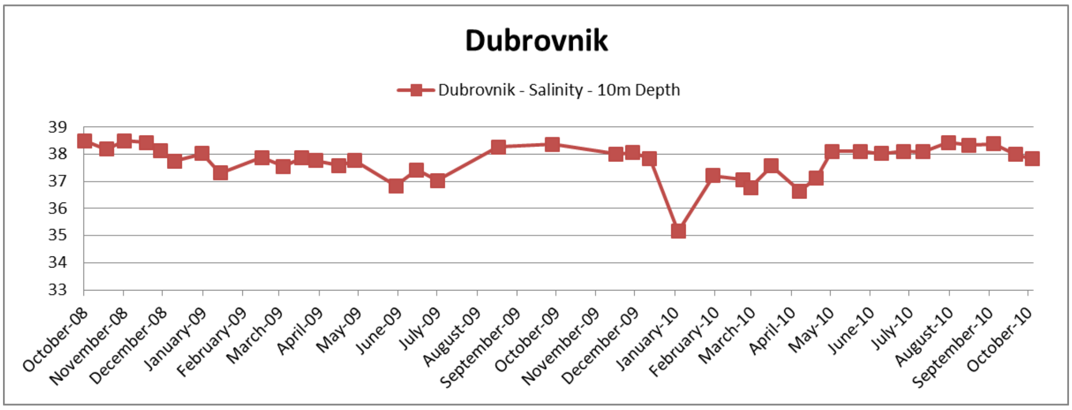


Figure 60. Temporal distribution of salinity at station Dubrovnik from October 2008 to October 2010.

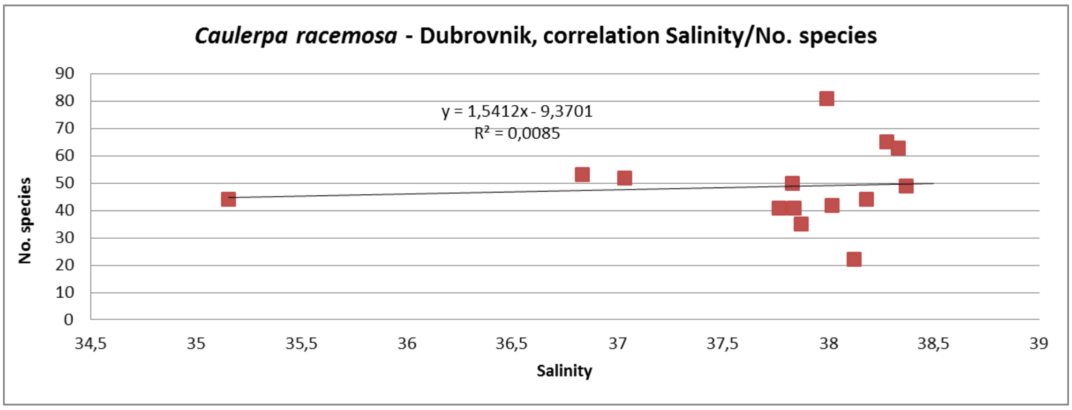


Figure 61. Correlation of salinity and number of taxa on *C. racemosa* samples from Dubrovnik.

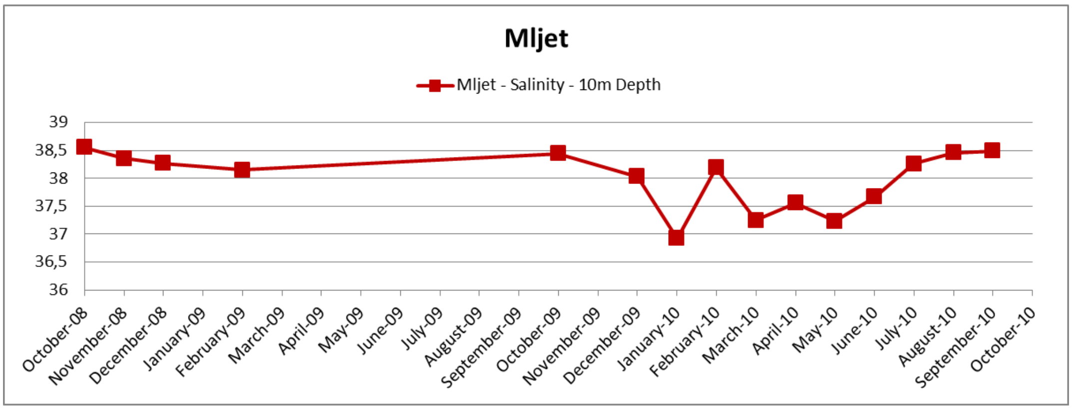


Figure 62. Temporal distribution of salinity at station Mljet from October 2008 to October 2010.

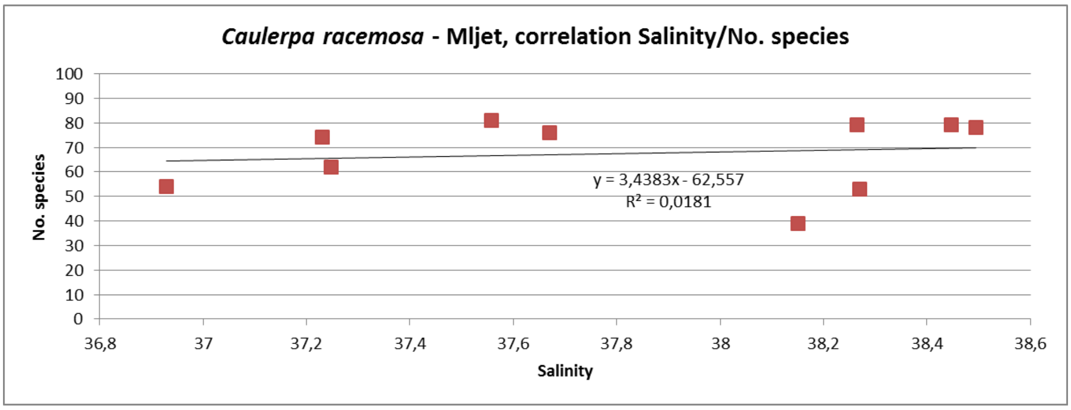


Figure 63. Correlation of salinity and number of taxa on *C. racemosa* samples from island of Mljet.

To compare diatom assemblages on *Caulerpa racemosa* the biodiversity measure, *H'* (Shannon-Wiener Biodiversity Index), was computed for the Dubrovnik and Mljet sampling sites (Figure 64, Figure 65). In general the values of *H'* ranged between 1.26 and 3.67. The highest values of Shannon-Wiener Biodiversity Index were observed on the island of Mljet in October 2009 and September 2010 amounting to 3.67 and 3.59 respectively. Values of Shannon-Wiener Biodiversity Index were almost the same for September 2010 for the Dubrovnik (3.57) and Mljet (3.59) sampling sites. The lowest value of Shannon-Wiener Biodiversity Index for *Caulerpa racemosa* amounted to 1.26 occurring in March 2009 on the island of Mljet. Likewise low values of Shannon-Wiener Biodiversity Index occurred in January 2009 and 2010 on the island of Mljet and in November 2008 and 2009 and in February 2009 in Dubrovnik.

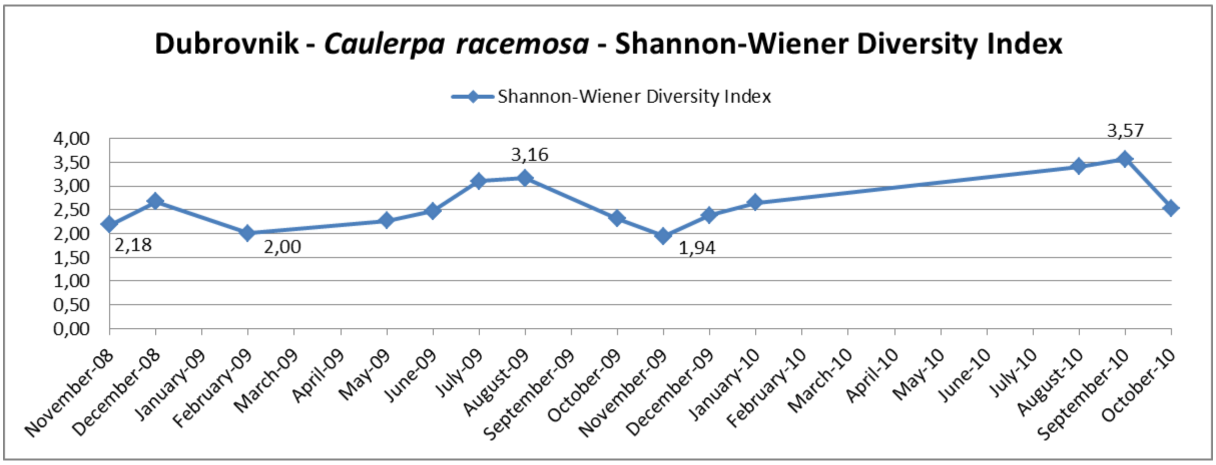


Figure 64. Shannon-Wiener Biodiversity Index of epiphytic diatom assemblage on *Caulerpa racemosa* collected from Dubrovnik area.

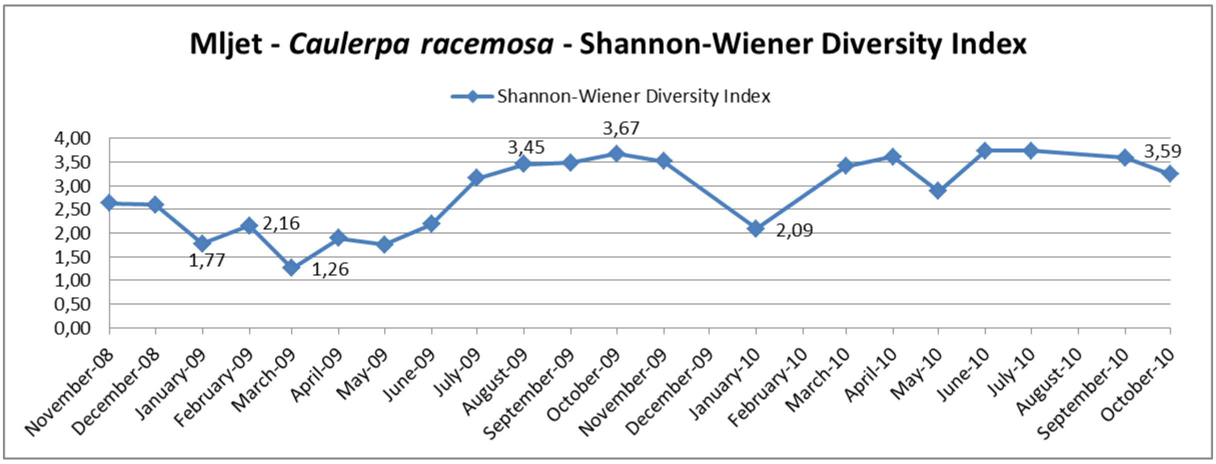


Figure 65. Shannon-Wiener Biodiversity Index of epiphytic diatom assemblage on *Caulerpa racemosa* collected from the island of Mljet.

Table 26 lists the most abundant 25 taxa of the epiphytic diatom assemblage on *Caulerpa racemosa*. They are dominant in terms of frequency of appearance (>46.30%) and abundance in total number of samples (>1.23 %). Combined together, they contribute in a single sample from 50.49 to 98.20% of the diatom community.

Table 26. Diatom taxa dominant on *Caulerpa racemosa* with an average abundance (Avg.) > 1% and frequency of appearance (Freq.) > 46%. N = 54.

***Caulerpa racemosa* - 25 dominant taxa:**	**Freq. (%)**	**Avg. (%)**
Amphora acutiuscula Kützing	81.48%	1.79%
Amphora helenensis Giffen	83.33%	1.49%
Ardissonea crystallina (C.A. Agardh) Grunow	50.00%	1.57%
Cocconeis caulerpacola Witkowski, Car & Dobosz	50.00%	5.07%
Cocconeis costata Gregory var. costata	59.26%	2.10%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	100.00%	11.06%
Cocconeis scutellum Ehrenberg var. *scutellum*	100.00%	32.14%
Fragilaria investiens (W. Smith) Cleve-Euler	75.93%	1.53%
Grammatophora marina (Lyngbye) Kützing	64.81%	1.23%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	90.74%	2.74%
Hyalosynedra laevigata (Grunow) Williams & Round	98.15%	3.98%
Licmophora gracilis (Ehrenberg) Grunow var. gracilis	74.07%	2.93%
Licmophora paradoxa (Lyngbye) Agardh	74.07%	1.46%
Licmophora remulus Grunow	46.30%	2.32%
Mastogloia binotata (Grunow) Cleve	75.93%	1.92%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	79.63%	1.36%
Mastogloia crucicula var. *alternans* Zanon	79.63%	1.44%
Mastogloia fimbriata (Brightwell) Cleve	75.93%	1.25%
Navicula lusoria Giffen	48.15%	1.65%
Navicula ramosissima (Agardh) Cleve	100.00%	5.04%
Nitzschia angularis W. Smith	87.04%	2.18%
Nitzschia lanceolata var. *minima* Grunow	81.48%	2.52%
Nitzschia panduriformis Gregory var. *panduriformis*	74.07%	1.26%
Tabularia ktenoeoides Kuylenstierna	96.30%	2.08%
Toxarium undulatum Bailey	61.11%	1.48%

The most common taxa occurring in almost all *Caulerpa racemosa* samples were *Cocconeis molesta* var. *crucifera*, *Cocconeis scutellum* var. *scutellum*, *Grammatophora oceanica*, *Hyalosynedra laevigata*, *Navicula ramosissima* and *Tabularia ktenoeoides*. Among these the highest abundance was reached by *Cocconeis scutellum* var. *scutellum* and *Cocconeis molesta* var. *crucifera*. Average abundance of *Cocconeis scutellum* var. *scutellum* amounted to 32.14% and of *Cocconeis molesta* var. *crucifera* to 11.06%. While *Cocconeis molesta* var. *crucifera* showed no particular seasonal distribution, *Cocconeis scutellum* var. *scutellum* reached higher abundances (almost twofold higher values) in winter and spring.

An opposite pattern of distribution was observed in the case of *Cocconeis caulerpacola* which showed higher abundances in autumn. Average abundance of *Cocconeis* *caulerpacola* on *C. racemosa* amounted to 5.07%. Almost the same abundance (5.04%) was reached by *Navicula ramosissima*. The highest abundance of *Cocconeis caulerpacola* on *C. racemosa* was observed in September 2009 and 2010 ranging from 9.33% to 12.44% (Table 28).

Hyalosynedra laevigata occurred in 98% of samples from *C. racemosa* with average abundance of 4%. During summer and autumn its abundance exceeded average values while during winter and spring it was lower than average. The highest abundance of *H. laevigata* on *C. racemosa* was observed in September 2009. The two above taxa i.e. *C. caulerpacola* and *H. laevigata* occurred more often on *Caulerpa racemosa* from the island of Mljet than from Dubrovnik. An opposite pattern of distribution was observed with *Cocconeis molesta* var. *crucifera* which occurred more frequently in Dubrovnik samples. In the case of *Cocconeis scutellum* var. *scutellum* no difference in frequency of occurrence between samples from these two sampling sites was observed (Table 29).

Of the 25 dominant taxa, three belonged in *Licmophora*. *Licmophora gracilis* (Ehrenberg) Grunow var. *gracilis* and *Licmophora paradoxa* occurred with the same frequency (74% samples). The highest abundance (9%) of *L. gracilis* var. *gracilis* was observed in winter. Generally it was found more often on the island of Mljet than in Dubrovnik. *L. remulus* Grunow was more abundant on the island of Mljet, however, with the highest abundance observed in summer. In general it occurred in 46% of *C. racemosa* samples. *Licmophora paradoxa* occurred with similar abundances during all seasons and from both sampling sites.

Mastogloia was represented by four taxa included in a group of dominant taxa on *Caulerpa racemosa*. *Mastogloia crucicula* var. *crucicula* and *M. crucicula* var. *alternans* occurred in 80% of samples and *Mastogloia binotata* and *Mastogloia fimbriata* occurred in 76%. Average abundance of the three taxa amounted to 1.6% and showed only slight seasonal changes. Amongst the 25 dominant taxa on *C. racemosa* were also *Nitzschia* representatives, namely *N. angularis*, *N. lanceolata* var. *minima* and *N. panduriformis* var. *panduriformis*. These occurred in more than 74% of samples, their abundance oscillating around 1%. *Ardissonea crystallina* (C.A. Agardh) Grunow occurred in 50% of samples with an average abundance of 1.6%. No particular seasonal changes in distribution or differences in its distribution between sampling sites were observed. *Fragilaria investiens* occurred with an average abundance of ca. 1.5% in 76% of samples of *Caulerpa racemosa*. Increased abundances (2.6%) were observed in spring. Generally its distribution was similar at both sampling sites.

Two taxa of genus *Grammatophora* were observed among dominant taxa on *C. racemosa*. *Grammatophora oceanica* occurred in 91% of the samples from *Caulerpa racemosa* with an average abundance of 3% while *Grammatophora marina* (Lyngbye) Kützing occurred in 65% of samples, with abundance of 1-2%. No special seasonal pattern or changes in distribution between sampling sites of *Grammatophora* taxa were observed. *Tabularia ktenoeoides* was observed in 96% of *C. racemosa* occurring with an average abundance of 2%. During summer and autumn slightly higher abundances of Grammatophora spp. were observed. *Toxarium undulatum* was found in 61% of samples occurring with an abundance of 1.48%. Both *Toxarium undulatum* and *Tabularia ktenoeoides* were found more often in samples from Dubrovnik.

Table 27. Seasonal distribution of 25 dominant taxa on *Caulerpa racemosa* from Dubrovnik and Mljet sampling sites combined together.

***Caulerpa racemosa* - 25 dominant taxa:**	**Average Seasonal Abundance (%):**			
	Winter	**Spring**	**Summer**	**Autumn**
Amphora acutiuscula Kützing	2.81%	2.08%	1.64%	1.14%
Amphora helenensis Giffen	1.39%	1.47%	1.42%	1.64%
Ardissonea crystallina (C.A. Agardh) Grunow	1.24%	1.96%	1.97%	1.26%
Cocconeis caulerpacola Witkowski, Car & Dobosz	6.60%	0.68%	2.40%	7.66%
Cocconeis costata Gregory var. costata	2.45%	1.30%	2.12%	2.08%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	7.00%	11.98%	12.88%	12.14%
Cocconeis scutellum Ehrenberg var. *scutellum*	42.17%	44.52%	22.30%	24.09%
Fragilaria investiens (W. Smith) Cleve-Euler	1.61%	2.56%	1.37%	0.59%
Grammatophora marina (Lyngbye) Kützing	1.43%	0.82%	1.76%	0.85%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	3.17%	3.29%	2.71%	1.98%
Hyalosynedra laevigata (Grunow) Williams & Round	2.13%	3.34%	4.61%	5.26%
Licmophora gracilis (Ehrenberg) Grunow var. gracilis	8.72%	1.38%	0.65%	1.15%
Licmophora paradoxa (Lyngbye) Agardh	1.30%	1.48%	1.97%	1.16%
Licmophora remulus Grunow	0.00%	0.81%	3.33%	1.36%
Mastogloia binotata (Grunow) Cleve	1.08%	0.65%	2.88%	2.23%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	0.92%	0.83%	1.27%	1.83%
Mastogloia crucicula var. *alternans* Zanon	1.77%	0.60%	1.30%	1.63%
Mastogloia fimbriata (Brightwell) Cleve	0.85%	0.42%	1.40%	1.71%
Navicula lusoria Giffen	1.35%	1.16%	1.44%	2.41%
Navicula ramosissima (Agardh) Cleve	5.21%	4.20%	4.90%	5.62%
Nitzschia angularis W. Smith	2.53%	1.22%	2.41%	2.23%
Nitzschia lanceolata var. *minima* Grunow	1.92%	1.72%	2.83%	2.92%
Nitzschia panduriformis Gregory var. *panduriformis*	1.03%	0.76%	1.45%	1.65%
Tabularia ktenoeoides Kuylenstierna	2.01%	3.90%	1.54%	1.37%
Toxarium undulatum Bailey	0.35%	1.07%	1.18%	2.72%

Table 28. Seasonal abundances (%) of dominant taxa epiphytic on *Caulerpa racemosa* from Dubrovnik and Mljet sampling sites. (/)-missing data.

Taxa: **Season:**	**Winter**					
Months:	**Dec-08**	**Dec-09**	**Jan-09**	**Jan-10**	**Feb-09**	**Feb-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	14,90%	1,23%	1,72%	0,26%	0,00%	/
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	7,23%	8,82%	6,88%	7,15%	6,02%	/
Cocconeis scutellum Ehrenberg var. *scutellum*	32,80%	45,34%	59,05%	47,22%	37,29%	/
Hyalosynedra laevigata (Grunow) Williams & Round	3,99%	2,70%	0,71%	1,04%	1,16%	/
Mastogloia binotata (Grunow) Cleve	1,53%	1,47%	0,00%	0,92%	0,45%	/
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	0,57%	1,47%	0,49%	1,24%	0,00%	/
Mastogloia crucicula var. *alternans* Zanon	2,67%	1,47%	0,00%	2,12%	0,91%	/
Navicula ramosissima (Agardh) Cleve	6,92%	6,86%	3,15%	3,63%	5,33%	/
Nitzschia angularis W. Smith	3,25%	2,94%	0,60%	4,47%	1,45%	/
Nitzschia lanceolata var. *minima* Grunow	2,54%	0,49%	2,46%	1,32%	0,90%	/
Taxa: **Season:**	**Spring**					
Months:	**Mar-09**	**Mar-10**	**Apr-09**	**Apr-10**	**May-09**	**May-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	0.00%	1.41%	0.28%	0.00%	0.28%	0.74%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	11.08%	7.04%	13.36%	5.21%	16.78%	10.16%
Cocconeis scutellum Ehrenberg var. *scutellum*	70.20%	14.65%	55.55%	19.43%	49.53%	27.75%
Hyalosynedra laevigata (Grunow) Williams & Round	1.17%	3.38%	1.60%	3.08%	2.79%	8.20%
Mastogloia binotata (Grunow) Cleve	0.23%	1.41%	0.00%	0.24%	0.40%	1.23%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	0.00%	1.41%	0.26%	0.95%	1.06%	0.49%
Mastogloia crucicula var. *alternans* Zanon	0.00%	1.97%	0.26%	0.24%	0.26%	0.25%
Navicula ramosissima (Agardh) Cleve	4.20%	7.04%	4.20%	3.55%	4.19%	3.11%
Nitzschia angularis W. Smith	0.45%	0.85%	0.40%	2.61%	0.92%	3.19%
Nitzschia lanceolata var. *minima* Grunow	0.00%	5.07%	1.29%	1.18%	0.92%	1.34%
Taxa: **Season:**	**Summer**					
Months:	**Jun-09**	**Jun-10**	**Jul-09**	**Jul-10**	**Aug-09**	**Aug-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	1.82%	3.87%	2.83%	3.18%	1.64%	0.00%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	22.94%	8.47%	8.21%	3.18%	9.50%	14.32%
Cocconeis scutellum Ehrenberg var. *scutellum*	37.00%	13.80%	23.18%	6.63%	15.95%	10.42%
Hyalosynedra laevigata (Grunow) Williams & Round	1.59%	6.54%	6.66%	2.12%	7.06%	1.30%
Mastogloia binotata (Grunow) Cleve	1.01%	1.45%	3.59%	1.33%	2.64%	9.11%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	0.39%	1.45%	1.67%	2.65%	1.26%	2.08%
Mastogloia crucicula var. *alternans* Zanon	0.73%	0.48%	1.65%	1.33%	1.42%	3.13%
Navicula ramosissima (Agardh) Cleve	2.96%	4.12%	4.67%	8.22%	5.97%	6.51%
Nitzschia angularis W. Smith	1.28%	2.91%	0.79%	5.57%	2.93%	5.99%
Nitzschia lanceolata var. *minima* Grunow	2.38%	2.42%	2.10%	2.65%	2.71%	2.60%
Taxa: **Season:**	**Autumn**					
Months:	**Sep-09**	**Sep-10**	**Oct-09**	**Oct-10**	**Nov-08**	**Nov-09**
Cocconeis caulerpacola Witkowski, Car & Dobosz	9.33%	12.44%	1.83%	5.65%	8.60%	0.00%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	3.74%	9.76%	15.53%	18.21%	14.40%	10.42%
Cocconeis scutellum Ehrenberg var. *scutellum*	7.47%	6.34%	24.90%	19.63%	38.49%	40.67%
Hyalosynedra laevigata (Grunow) Williams & Round	12.20%	3.80%	3.46%	6.52%	6.41%	1.90%
Mastogloia binotata (Grunow) Cleve	3.00%	3.42%	2.52%	2.35%	0.56%	2.10%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.91%	1.79%	0.92%	5.39%	1.33%	0.84%
Mastogloia crucicula var. *alternans* Zanon	0.82%	1.46%	2.44%	3.82%	0.80%	0.92%
Navicula ramosissima (Agardh) Cleve	6.45%	5.86%	7.18%	3.53%	3.08%	7.18%
Nitzschia angularis W. Smith	0.69%	2.84%	3.03%	2.75%	2.39%	1.35%
Nitzschia lanceolata var. *minima* Grunow	4.67%	3.49%	2.90%	1.94%	2.22%	1.37%

Table 29. Average site abundance of the 25 dominant taxa on *Caulerpa racemosa* from Dubrovnik and Mljet sampling site combined together.

Caulerpa racemosa **- 25 dominant taxa:**	**Average Site Abundance (%):**	
	Dubrovnik	**Mljet**
Amphora acutiuscula Kützing	1.95%	1.67%
Amphora helenensis Giffen	1.03%	1.83%
Ardissonea crystallina (C.A. Agardh) Grunow	1.73%	1.45%
Cocconeis caulerpacola Witkowski, Car & Dobosz	1.24%	6.16%
Cocconeis costata Gregory var. costata	2.89%	0.77%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	17.16%	7.48%
Cocconeis scutellum Ehrenberg var. *scutellum*	32.60%	31.86%
Fragilaria investiens (W. Smith) Cleve-Euler	1.33%	1.64%
Grammatophora marina (Lyngbye) Kützing	1.12%	1.28%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	2.58%	2.85%
Hyalosynedra laevigata (Grunow) Williams & Round	2.68%	4.76%
Licmophora gracilis (Ehrenberg) Grunow var. gracilis	0.52%	3.97%
Licmophora paradoxa (Lyngbye) Agardh	1.94%	1.14%
Licmophora remulus Grunow	1.41%	2.68%
Mastogloia binotata (Grunow) Cleve	3.01%	1.07%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.77%	1.07%
Mastogloia crucicula var. *alternans* Zanon	2.08%	0.93%
Mastogloia fimbriata (Brightwell) Cleve	1.26%	1.25%
Navicula lusoria Giffen	0.32%	1.82%
Navicula ramosissima (Agardh) Cleve	4.99%	5.07%
Nitzschia angularis W. Smith	3.17%	1.44%
Nitzschia lanceolata var. *minima* Grunow	1.77%	3.09%
Nitzschia panduriformis Gregory var. *panduriformis*	0.93%	1.44%
Tabularia ktenoeoides Kuylenstierna	1.62%	2.35%
Toxarium undulatum Bailey	0.83%	1.72%

During winter, the species composition of diatom assemblages on *C. racemosa* from two sampling sites showed slight differences (Figure 66, Figure 67). Though at both sites, *Cocconeis scutellum* var. *scutellum* dominated with abundance around 40%, the assemblages differed on account of *Cocconeis molesta* var. *crucifera* Grunow abundance in spring and summer. The latter taxon was observed with higher abundance (20-30%) in Dubrovnik than on the island of Mljet (less than 10%). However, the major difference between sampling sites was the frequency of occurrence and abundance of *Cocconeis caulerpacola* on *Caulerpa racemosa*. This was particularly pronounced in autumn when the abundance on the island of Mljet exceeded 10% while in Dubrovnik it amounted to only ca. 1%. Abundances of other taxa which belong to ten dominant taxa were quite low during all seasons (below 10%).

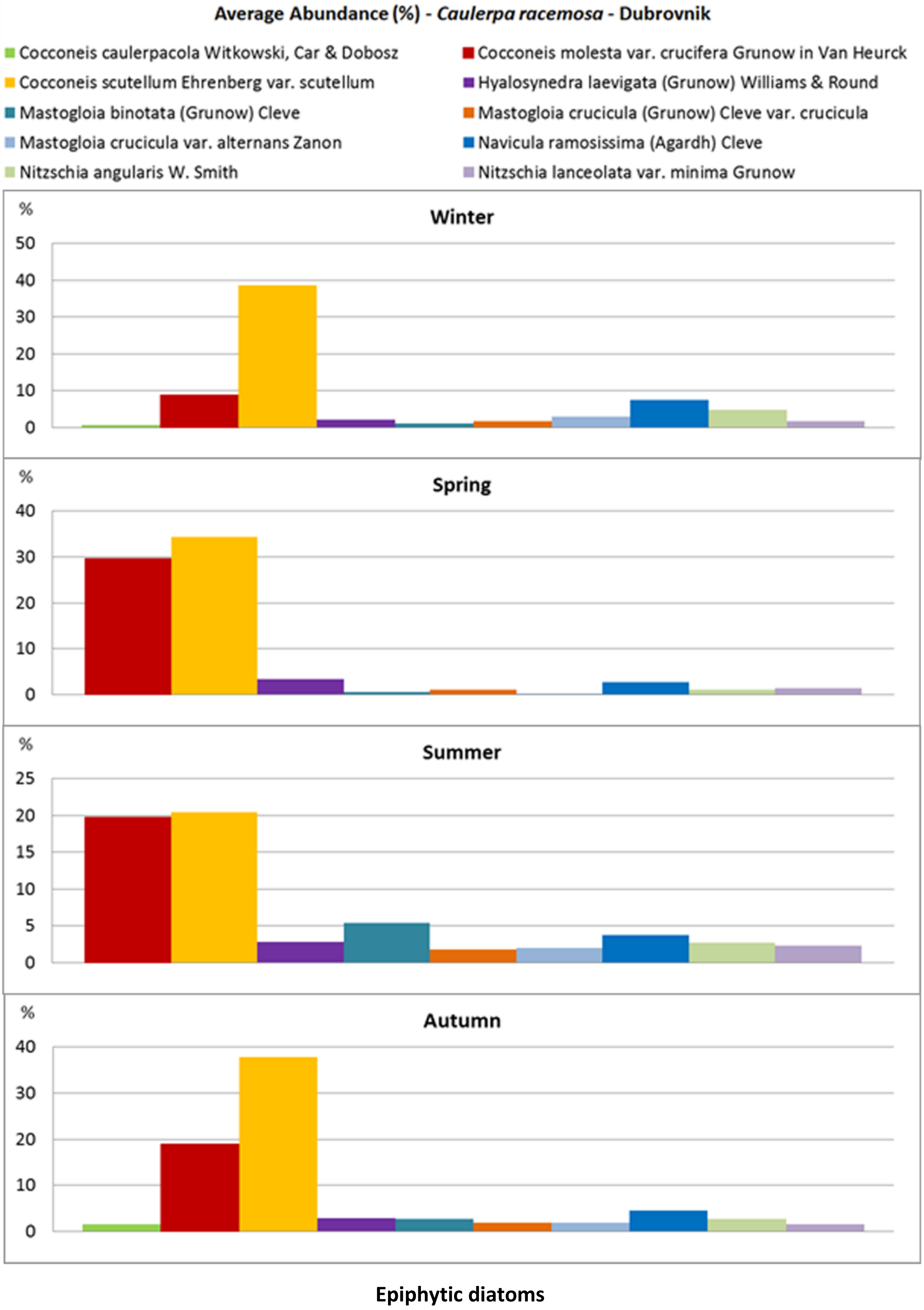


Figure 66. Seasonal distribution of 10 dominant taxa on *Caulerpa racemosa* from Dubrovnik.

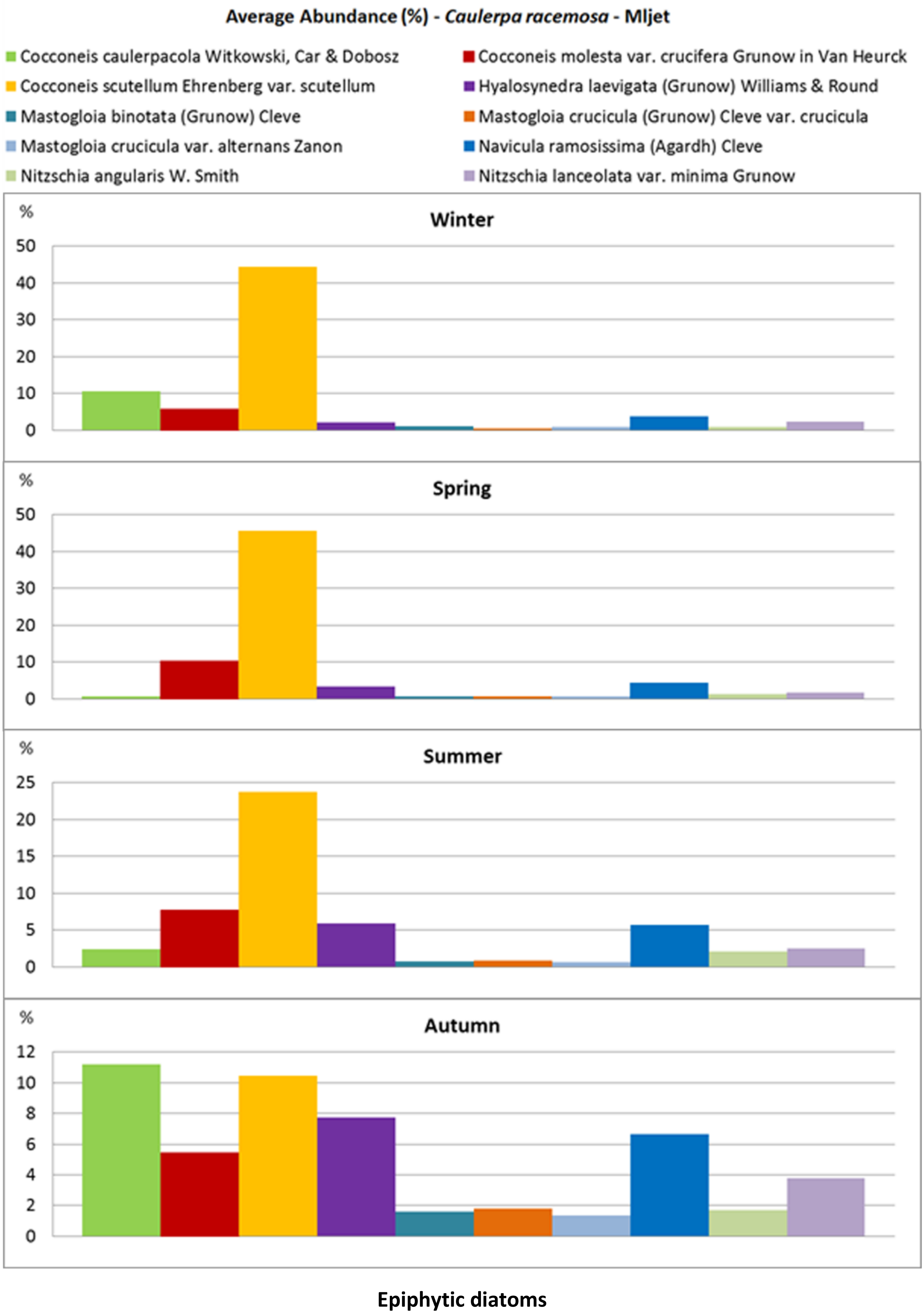


Figure 67. Seasonal distribution of 10 dominant taxa on *Caulerpa racemosa* from island of Mljet.

Table 30. Abundances of 10 dominant taxa on *C. racemosa* during particular seasons in 2009 and 2010.

Taxa:																**Average Abundance (%)**
	January				**May**				**July**				**October**			
	2009		**2010**		**2009**		**2010**		**2009**		**2010**		**2009**		**2010**	
	Dubrovnik	**Mljet**	**Dubrovnik**	**Mljet**	**Dubrovnik**	**Mljet**	**Dubrovnik**	**Mljet**	**Dubrovnik**	**Mljet**	**Dubrovnik**	**Mljet**	**Dubrovnik**	**Mljet**	**Dubrovnik**	**Mljet**
Cocconeis caulerpacola Witkowski, Car & Dobosz	/	1.72%	0.26%	0.00%	0.00%	0.28%	/	0.74%	0.00%	2.83%	/	3.18%	0.60%	3.06%	0.48%	10.82%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	/	6.88%	9.23%	6.11%	29.63%	10.35%	/	10.16%	14.55%	5.04%	/	3.18%	22.48%	1.65%	27.85%	8.57%
Cocconeis scutellum Ehrenberg var. *scutellum*	/	59.05%	34.30%	53.67%	34.39%	57.10%	/	27.75%	22.49%	23.53%	/	6.63%	35.00%	4.71%	29.06%	10.20%
Hyalosynedra laevigata (Grunow) Williams & Round	/	0.71%	0.26%	1.44%	3.44%	2.46%	/	8.20%	2.38%	8.80%	/	2.12%	2.01%	6.35%	2.42%	10.61%
Mastogloia binotata (Grunow) Cleve	/	0.00%	1.32%	0.72%	0.53%	0.28%	/	1.23%	6.61%	0.57%	/	1.33%	3.67%	0.24%	2.66%	2.04%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	/	0.49%	2.64%	0.54%	1.06%	0.00%	/	0.49%	3.97%	0.53%	/	2.65%	1.14%	0.47%	3.63%	7.14%
Mastogloia crucicula var. *alternans* Zanon	/	0.00%	4.22%	1.07%	0.26%	0.00%	/	0.25%	1.85%	1.46%	/	1.33%	3.07%	1.18%	3.15%	4.49%
Navicula ramosissima (Agardh) Cleve	/	3.15%	6.07%	2.42%	2.65%	4.96%	/	3.11%	3.44%	5.28%	/	8.22%	4.89%	11.76%	3.39%	3.67%
Nitzschia angularis W. Smith	/	0.60%	7.12%	1.82%	1.06%	0.78%	/	3.19%	1.59%	0.38%	/	5.57%	3.60%	1.88%	3.87%	1.63%
Nitzschia lanceolata var. *minima* Grunow	/	2.46%	1.32%	0.00%	1.32%	0.52%	/	1.34%	2.12%	2.09%	/	2.65%	0.82%	7.06%	2.66%	1.22%

3.3.4.1. Analyses of the epiphytic diatom community on *C. racemosa* fronds

Altogether 174 taxa representing 40 genera were identified in epiphytic diatom assemblages from Mljet and Dubrovnik *C. racemosa* fronds. In Dubrovnik (Orsula) only 73 diatom taxa belonging to 21 genera were identified, compared with 155 diatom taxa representing 36 genera on Mljet. The average number of taxa in one sample of epiphytic diatoms from fronds of *C. racemosa* was 35. Samples from Mljet contained a higher (38) number of taxa, whereas in samples from Dubrovnik the number of taxa on average did not exceed 30. Seasonal differences between the two sites were observed. During winter the number of taxa on fronds declined to an average of 28. The lowest number of taxa (18) was observed in spring, even though the average number of taxa observed in the Mljet and Dubrovnik sampling sites was 23.5. The average number of taxa on fronds of *Caulerpa racemosa* was the highest during summer and autumn (45 and 42, respectively). The difference in number of taxa in samples at two sampling sites partly resulted from a lack of samples from Dubrovnik area, from which just 6 samples were taken covering only the summer and autumn seasons compared with 13 samples from Mljet over all seasons.

Comparison of the list of 25 dominant taxa of epiphytic diatom community on *Caulerpa racemosa* (Table 26) with those most abundant on fronds of *C. aulerpa racemosa* (Table 31) revealed some differences in species composition. The group of taxa not included in the list of dominants on *C. racemosa* fronds but which were included in the general list of dominants on *Caulerpa racemosa* included *Amphora helenensis*, *Mastogloia crucicula* var. *crucicula*, *Mastogloia crucicula* var. *alternans* and *Nitzschia angularis*. On the contrary *Cocconeis britannica* Naegeli in Kützing, *Cocconeis krammeri* Lange-Bertalot & Metzeltin, *Cocconeis woodii*, *Cyclophora tenuis* Castracane 1878, *Licmophora* cf. *pfannkucheae* Giffen, *Licmophora flabellata* (Carmichael) Agardh, *Mastogloia cuneata*, *Mastogloia ovalis* and *Mastogloia* spec. 84/1 (Ico.Diatom.Vol.7, Pl.84 Figs 9-11) were not included in the general list of dominants on *C. racemosa*, but were included in the list of dominants on its fronds.

Table 31. Dominant diatom taxa on *Caulerpa racemosa* fronds with average abundance (Avg.) > 1% and frequency of appearance (Freq.) > 16%. N = 19.

Caulerpa racemosa **- fronds - dominant taxa:**	**Freq. (%)**	**Avg. (%)**
Amphora acutiuscula Kützing	25.58%	1.05%
Ardissonea crystallina (C.A. Agardh) Grunow	40.00%	2.32%
Cocconeis britannica Naegeli in Kützing	25.00%	1.30%
Cocconeis caulerpacola Witkowski, Car & Dobosz	70.83%	4.19%
Cocconeis costata Gregory var. *costata*	28.95%	1.37%
Cocconeis krammeri Lange-Bertalot & Metzeltin	28.13%	2.06%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	95.00%	12.56%
Cocconeis scutellum Ehrenberg var. *scutellum*	100.00%	43.90%
Cocconeis woodii Reyes	19.51%	1.21%
Cyclophora tenuis Castracane 1878	24.44%	1.01%
Fragilaria investiens (W. Smith) Cleve-Euler	34.29%	1.77%
Grammatophora marina (Lyngbye) Kützing	26.47%	1.89%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	50.00%	2.40%
Hyalosynedra laevigata (Grunow) Williams & Round	85.71%	5.43%
Licmophora cf. *pfannkucheae* Giffen	29.63%	2.42%
Licmophora flabellata (Carmichael) Agardh	34.48%	2.36%
Licmophora gracilis (Ehrenberg) Grunow var. *gracilis*	54.55%	4.62%
Licmophora paradoxa (Lyngbye) Agardh	24.32%	1.53%
Licmophora remulus Grunow	82.61%	4.41%
Mastogloia binotata (Grunow) Cleve	15.91%	1.04%
Mastogloia cuneata (Meister) Simonsen	30.77%	1.36%
Mastogloia fimbriata (Brightwell) Cleve	38.89%	1.64%
Mastogloia ovalis A. Schmidt	17.39%	1.00%
Mastogloia spec. 84/1 (Ico.Diatom.Vol.7, Pl.84 Figs 9-11)	23.81%	1.08%
Navicula ramosissima (Agardh) Cleve	72.00%	2.82%
Nitzschia lanceolata var. *minima* Grunow	36.36%	1.91%
Tabularia ktenoeoides Kuylenstierna	38.46%	2.73%
Toxarium undulatum Bailey	38.71%	2.16%

Whereas only three taxa of *Licmophora* were included in the list of general dominants on *Caulerpa racemosa*, five taxa were on the list of dominants on its fronds. In general, taxa belonging to *Licmophora* reached an abundance of 1.2%, but on fronds their average abundance increased to 2.1%. Seasonally, during spring the abundances of *Licmophora* taxa were lower on fronds than on *Caulerpa racemosa* thalli while during other seasons abundances on fronds were higher (Table 32).

Likewise *Cocconeis* taxa occurred with significantly higher abundance on fronds and this phenomenon was observed in all seasons. Other genera observed with increased abundances on fronds were *Hyalosynedra* and *Tabularia*. However, taxa belonging to *Navicula*, *Nitzschia*, *Amphora*, *Diploneis* and *Rhopalodia* showed an opposite pattern with lower abundances on fronds. No significant differences in abundances of *Mastogloia*, *Grammatophora*, *Berkeleya*, *Fragilaria*, *Ardissonea* and *Toxarium* for different parts of *Caulerpa racemosa* were observed.

Table 32. Seasonal abundance of taxa belonging in dominant genera on fronds and thallus of *Caulerpa racemosa*.

Genus:	**Average Seasonal Abundance (%):**							
	Winter		**Spring**		**Summer**		**Autumn**	
	***C. racemosa* fronds**	***Caulerpa racemosa* thallus**	***C. racemosa* fronds**	***Caulerpa racemosa* thallus**	***C. racemosa* fronds**	***Caulerpa racemosa* thallus**	***C. racemosa* fronds**	***Caulerpa racemosa* thallus**
Cocconeis	17.12%	7.76%	25.38%	12.27%	12.05%	6.39%	9.15%	6.24%
Mastogloia	0.45%	0.87%	0.25%	0.51%	0.89%	1.06%	0.78%	0.96%
Nitzschia	0.64%	1.70%	0.50%	0.79%	1.30%	1.40%	1.05%	1.65%
Navicula	2.14%	3.36%	1.51%	2.31%	1.25%	2.31%	2.01%	3.08%
Amphora	0.84%	0.92%	0.42%	1.00%	0.51%	0.82%	0.58%	0.73%
Hyalosynedra	3.22%	1.58%	3.85%	3.05%	6.60%	3.50%	7.31%	4.32%
Licmophora	2.96%	1.69%	0.81%	1.28%	2.09%	1.18%	2.35%	0.82%
Grammatophora	2.68%	2.14%	1.73%	3.08%	2.10%	2.21%	1.51%	1.52%
Tabularia	2.60%	1.79%	4.90%	3.33%	2.17%	1.18%	1.62%	1.25%
Berkeleya	0.53%	0.36%	0.35%	2.49%	0.41%	0.91%	0.61%	1.24%
Pseudostaurosira	1.75%	1.42%	2.85%	2.16%	0.46%	1.38%	0.57%	0.62%
Ardissonea	1.05%	0.45%	0.64%	0.84%	1.20%	0.93%	1.15%	0.82%
Toxarium	0.25%	0.38%	1.44%	0.92%	1.88%	0.87%	4.38%	2.25%
Diploneis	0.29%	0.33%	0.28%	0.53%	0.42%	0.51%	0.29%	0.47%
Rhopalodia	0.00%	0.87%	0.00%	0.38%	0.00%	0.99%	0.54%	0.69%

In general, at both sampling sites during all seasons, *Cocconeis* was represented by 26 taxa on *Caulerpa racemosa* thalli, while on fronds 18 taxa occurred of which *Cocconeis scutellum* var. *scutellum* achieved an abundance of 44% followed by *Cocconeis molesta* var. *crucifera* (13%), *Cocconeis caulerpacola* (4%) and *Cocconeis krammeri* (2%). Average abundance of *Cocconeis costata* var. *costata*, *Cocconeis britannica* and *Cocconeis woodii* amounted to ca. 1.3%. The remaining *Cocconeis* taxa were observed with very low abundances ranging from 0.2 to 0.6% (Table 33).

The abundances of *Cocconeis scutellum* var. *scutellum* and *Cocconeis molesta* var. *crucifera* were higher on fronds than on thalli during all seasons (Table 34).

Table 33. Average abundance (Avg.) of taxa of genus *Cocconeis* on fronds of *Caulerpa racemosa*.

***Caulerpa racemosa* fronds - species of genus *Cocconeis* :**	**Avg. (%)**
Cocconeis scutellum Ehrenberg var. *scutellum*	43.90%
Cocconeis molesta var. crucifera Grunow in Van Heurck	12.56%
Cocconeis caulerpacola Witkowski, Car & Dobosz	4.19%
Cocconeis krammeri Lange-Bertalot & Metzeltin	2.06%
Cocconeis costata Gregory var. *costata*	1.37%
Cocconeis britannica Naegeli in Kützing	1.30%
Cocconeis woodii Reyes	1.21%
Cocconeis dirupta Gregory var. *dirupta*	0.63%
Cocconeis cf. *distantula* Giffen	0.63%
Cocconeis discrepan s A. Schmidt	0.41%
Cocconeis diruptoides Hustedt	0.29%
Cocconeis convexa Giffen	0.28%
Cocconeis peltoides Hustedt	0.27%
Cocconeis cf. *distans* Gregory	0.27%
Cocconeis distans Gregory	0.27%
Cocconeis pelta A. Schmidt	0.27%
Cocconeis pseudomarginata Gregory	0.22%
Cocconeis dirupta var. *flexella* (Janisch & Rabenhorst) Grunow	0.18%

The abundance of *Cocconeis caulerpacola* was similar on fronds and thallus of *Caulerpa racemosa* during summer. During spring and autumn lower abundances were recorded on fronds while during winter a twofold higher abundance was observed on fronds than on the whole thallus.

Table 34. Seasonal distribution of *Cocconeis* taxa on *Caulerpa racemosa*.

Species of genus *Cocconeis* :	**Average Seasonal Abundance (%):**							
	Winter		**Spring**		**Summer**		**Autumn**	
	***C. racemosa* fronds**	***Caulerpa racemosa* thallus**	***C. racemosa* fronds**	***Caulerpa racemosa* thallus**	***C. racemosa* fronds**	***Caulerpa racemosa* thallus**	***C. racemosa* fronds**	***Caulerpa racemosa* thallus**
Cocconeis scutellum Ehrenberg var. *scutellum*	51.61%	36.27%	59.78%	35.79%	33.35%	16.16%	45.48%	19.56%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	5.81%	7.74%	14.18%	10.72%	14.70%	11.87%	15.12%	10.44%
Cocconeis caulerpacola Witkowski, Car & Dobosz	10.17%	5.71%	0.28%	1.07%	2.44%	2.37%	4.07%	8.63%
Cocconeis pseudodiruptoides Foged	0.00%	5.28%	0.00%	0.00%	0.00%	0.00%	0.00%	0.46%
Cocconeis costata Gregory var. *costata*	0.82%	3.27%	0.00%	1.30%	1.34%	2.51%	1.79%	2.21%
Cocconeis krammeri Lange-Bertalot & Metzeltin	4.95%	0.68%	0.00%	0.00%	0.00%	0.45%	0.62%	0.25%
Cocconeis britannica Naegeli in Kützing	1.93%	1.08%	0.36%	0.49%	0.71%	0.00%	1.28%	0.42%
Cocconeis woodii Reyes	2.97%	0.37%	0.00%	0.53%	0.32%	1.43%	0.92%	0.62%
Cocconeis guttata Hustedt in Aleem & Hustedt	0.00%	0.26%	0.00%	0.24%	0.00%	1.51%	0.00%	0.00%
Cocconeis peltoides Hustedt	0.00%	0.49%	0.00%	0.85%	0.00%	1.60%	0.27%	0.50%
Cocconeis cf. *distantula* Giffen	1.06%	0.46%	0.72%	1.05%	0.36%	1.10%	0.72%	0.81%
Cocconeis pelta A. Schmidt	0.29%	0.18%	0.00%	0.26%	0.25%	1.94%	0.00%	0.77%
Cocconeis decussata Ehrenberg	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.50%
Cocconeis distans Gregory	0.00%	0.37%	0.00%	0.87%	0.00%	0.32%	0.27%	0.71%
Cocconeis dirupta Gregory var. *dirupta*	0.99%	0.34%	0.00%	0.26%	0.00%	0.26%	0.27%	0.00%
Cocconeis discrepans A. Schmidt	0.00%	0.00%	0.00%	0.24%	0.41%	0.00%	0.00%	0.24%
Cocconeis convexa Giffen	0.00%	0.00%	0.28%	0.00%	0.00%	0.00%	0.28%	0.00%
Cocconeis pseudomarginata Gregory	0.18%	0.23%	0.00%	0.49%	0.00%	0.00%	0.27%	0.27%
Cocconeis cf. *distans* Gregory	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.27%	0.00%
Cocconeis diruptoides Hustedt	0.29%	0.23%	0.00%	0.28%	0.00%	0.00%	0.30%	0.24%
Cocconeis pinnularia Kützing	0.00%	0.00%	0.00%	0.25%	0.00%	0.00%	0.00%	0.27%
Cocconeis pellucida Grunow ex Hantzsch in Rabenhorst (1863)	0.00%	0.00%	0.00%	0.00%	0.00%	0.26%	0.00%	0.00%
Cocconeis speciosa Gregory	0.00%	0.00%	0.00%	0.24%	0.00%	0.00%	0.00%	0.00%
Cocconeis cf. *speciosa* (Ico.Diat.Vol.7, Pl. 38 Fig. 17)	0.00%	0.00%	0.00%	0.24%	0.00%	0.00%	0.00%	0.00%
Cocconeis pinnata Gregory ex Greville	0.00%	0.18%	0.00%	0.24%	0.00%	0.27%	0.00%	0.00%
Cocconeis dirupta var. *flexella* (Janisch & Rabenhorst) Grunow	0.18%	0.23%	0.00%	0.00%	0.00%	0.24%	0.00%	0.20%

3.3.5. Epiphytic diatoms on *Caulerpa taxifolia*

Altogether, on *Caulerpa taxifolia*, 379 taxa representing 65 genera were identified in light microscope (LM) preparations. An assemblage of epiphytic diatoms was characterized by high abundances of taxa representing *Cocconeis*, *Hyalosynedra*, *Mastogloia*, *Nitzschia*, *Navicula*, *Amphora* and *Licmophora*. The largest number of taxa belonged to *Mastogloia* (47), *Amphora* (44), *Nitzschia* (43), *Navicula* (25), *Diploneis* (24) and *Cocconeis* (19).

Caulerpa taxifolia hosted tube-dwelling *Mastogloia* spp. which were attached point-like to very small areas of the host plant. Observed taxa of *Mastogloia* included *M. crucicula* var. *crucicula*, *M. fimbriata*, *M. crucicula* var. *alternans*, *M. pseudolatecostata*, *M. cuneata*, *M. binotata*, *M. emarginata* Hustedt, *M. decipiens*, *M. inaequalis* Cleve, *M. ignorata*, *M. pusilla* var. *pusilla* and *M. cyclops Voigt*.

Unlike *Mastogloia*, the number of taxa representing *Cocconeis* was quite low. However, in terms of abundance *Cocconeis* taxa dominated the epiphytic diatom assemblage on *C. taxifolia*. *Cocconeis scutellum* var. *scutellum* was the most abundant with an average abundance of 15%. During winter, the abundance of *Cocconeis scutellum* var. *scutellum* was the highest reaching 25%, while during summer it decreased to 9%. The maximum abundance of *Cocconeis scutellum* var. *scutellum* on *C. taxifolia* was recorded in January 2010 and amounted to 33.63%. In general, for both years of sampling, January showed the maximum abundance of *Cocconeis scutellum* var. *scutellum* on *C. taxifolia*. During summer, the abundance of *Cocconeis caulerpacola* reached its highest values in August 2009 with 14.89% and August 2010 with 19.87%. However, the highest abundances of *C. caulerpacola* were observed in October 2009 with 42.71% and in October 2010 with 37.49%. The other two species i.e. *Cocconeis molesta* var. *crucifera* and *Cocconeis costata* var. *costata* followed the distribution pattern of *Cocconeis scutellum* var. *scutellum* with increased abundances of 11% and 7% respectively during winter.

Listed below are the 25 dominant taxa (Table 35) which were the most abundant group in the epiphytic diatom assemblage of *C. taxifolia*. They dominated both in terms of frequency of appearance (>39.13%) and abundance in the total number of samples (>1.34%). Combined together, they contributed in one sample from 56.35 to 97.77% of the diatom community.

Table 35. Dominant diatom taxa on *Caulerpa taxifolia* with average abundance (Avg.) > 1% and frequency of appearance (Freq.) > 39.13%. N = 46.

***Caulerpa taxifolia* - 25 dominant taxa:**	**Freq. (%)**	**Avg. (%)**
Amphora acutiuscula Kützing	60.87%	1.74%
Amphora helenensis Giffen	80.43%	1.49%
Ardissonea fulgens (Greville) Grunow	69.57%	1.47%
Berkeleya scopulorum (Brébisson) Cox	63.04%	1.37%
Cocconeis caulerpacola Witkowski, Car & Dobosz	76.09%	13.83%
Cocconeis cf. *scutellum* Ehrenberg	39.13%	9.89%
Cocconeis costata Gregory var. *costata*	67.39%	3.09%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	100.00%	8.47%
Cocconeis scutellum Ehrenberg var. *scutellum*	100.00%	15.15%
Fragilaria investiens (W. Smith) Cleve-Euler	67.39%	2.50%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	56.52%	1.49%
Hyalosynedra laevigata (Grunow) Williams & Round	100.00%	9.69%
Licmophora gracilis (Ehrenberg) Grunow var. *gracilis*	76.09%	3.45%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	95.65%	2.30%
Mastogloia crucicula var. *alternans* Zanon	97.83%	1.73%
Mastogloia cuneata (Meister) Simonsen	71.74%	1.34%
Mastogloia fimbriata (Brightwell) Cleve	89.13%	2.03%
Mastogloia pseudolatecostata Yohn & Gibson	89.13%	1.42%
Navicula arenaria Donkin var. arenaria	43.48%	2.77%
Navicula ramosissima (Agardh) Cleve	71.74%	4.54%
Nitzschia angularis W. Smith	93.48%	1.52%
Nitzschia lanceolata var. *minima* Grunow	78.26%	2.58%
Nitzschia panduriformis Gregory var. *panduriformis*	91.30%	1.92%
Tabularia ktenoeoides Kuylenstierna	84.78%	2.07%
Toxarium undulatum Bailey	71.74%	1.51%

Table 36. Seasonal distribution of the 25 most abundant taxa of *Caulerpa taxifolia*.

***Caulerpa taxifolia* - 25 dominant taxa:**	**Average Seasonal Abundance (%):**			
	Winter	**Spring**	**Summer**	**Autumn**
Amphora acutiuscula Kützing	1.81%	3.75%	0.81%	0.86%
Amphora helenensis Giffen	1.37%	1.22%	1.43%	1.79%
Ardissonea fulgens (Greville) Grunow	0.29%	1.75%	2.17%	0.78%
Berkeleya scopulorum (Brébisson) Cox	0.50%	2.06%	1.65%	0.38%
Cocconeis caulerpacola Witkowski, Car & Dobosz	2.44%	0.44%	7.41%	31.51%
Cocconeis cf. *scutellum* Ehrenberg	14.51%	1.73%	3.02%	9.64%
Cocconeis costata Gregory var. *costata*	6.58%	2.59%	0.85%	0.62%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	11.23%	9.96%	9.72%	3.94%
Cocconeis scutellum Ehrenberg var. *scutellum*	25.33%	15.74%	9.17%	12.32%
Fragilaria investiens (W. Smith) Cleve-Euler	3.84%	3.26%	0.55%	0.78%
Grammatophora oceanica (Ehrenberg 1854 pro parte) Grunow	0.45%	3.19%	0.56%	0.22%
Hyalosynedra laevigata (Grunow) Williams & Round	8.90%	7.65%	12.96%	9.02%
Licmophora gracilis (Ehrenberg) Grunow var. *gracilis*	1.38%	9.14%	0.71%	0.51%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.90%	2.51%	2.79%	1.93%
Mastogloia crucicula var. *alternans* Zanon	2.15%	1.72%	2.25%	0.86%
Mastogloia cuneata (Meister) Simonsen	0.36%	1.43%	2.22%	0.74%
Mastogloia fimbriata (Brightwell) Cleve	2.34%	2.71%	1.05%	1.99%
Mastogloia pseudolatecostata Yohn & Gibson	0.82%	0.95%	2.00%	1.61%
Navicula arenaria Donkin var. arenaria	2.38%	2.41%	3.72%	2.31%
Navicula ramosissima (Agardh) Cleve	4.60%	7.25%	5.47%	2.70%
Nitzschia angularis W. Smith	1.28%	1.64%	1.84%	1.24%
Nitzschia lanceolata var. *minima* Grunow	1.56%	1.86%	2.58%	3.53%
Nitzschia panduriformis Gregory var. *panduriformis*	1.00%	0.79%	2.78%	2.48%
Tabularia ktenoeoides Kuylenstierna	2.71%	2.37%	1.27%	1.89%
Toxarium undulatum Bailey	1.53%	0.89%	2.10%	1.45%

Average abundance of *Hyalosynedra laevigata* on *Caulerpa taxifolia* amounted to 10% with a winter seasonal average abundance of 8.90%. In 2009 the average and maximum (observed in January) abundances of *H. laevigata* were significantly higher amounting to 18% and 18.83% respectively. In 2010, the average abundances during January and February were similar at 5.61%, which was almost the same as in December 2008. If the above extreme values are excluded, the average seasonal abundance in winter amounted to 5.5%. Average abundance of *Hyalosynedra laevigata* in spring, summer and autumn amounted to 7.6%, 13% and 9% respectively.

Table 37. Seasonal average abundances (%) of dominant epiphytic taxa on *Caulerpa taxifolia* from Hvar sampling sites (/)-missing data.

Taxa: **Season:**	**Winter**					
Months:	**Dec-08**	**Dec-09**	**Jan-09**	**Jan-10**	**Feb-09**	**Feb-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	5.93%	/	0.56%	0.00%	0.83%	0.00%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	10.62%	/	13.06%	6.39%	13.51%	12.59%
Cocconeis scutellum Ehrenberg var. *scutellum*	18.54%	/	28.98%	33.63%	32.63%	12.88%
Hyalosynedra laevigata (Grunow) Williams & Round	5.32%	/	18.83%	5.24%	9.15%	5.97%
Mastogloia binotata (Grunow) Cleve	1.21%	/	0.51%	0.90%	0.32%	0.19%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	2.98%	/	1.20%	2.30%	1.21%	1.82%
Mastogloia crucicula var. *alternans* Zanon	2.74%	/	1.15%	3.45%	0.92%	2.50%
Navicula ramosissima (Agardh) Cleve	5.47%	/	3.95%	0.00%	4.39%	0.00%
Nitzschia angularis W. Smith	3.38%	/	0.20%	0.38%	1.07%	0.80%
Nitzschia lanceolata var. *minima* Grunow	3.74%	/	0.59%	1.28%	0.43%	1.63%
Taxa: **Season:**	**Spring**					
Months:	**Mar-09**	**Mar-10**	**Apr-09**	**Apr-10**	**May-09**	**May-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	0.99%	0.17%	0.24%	0.00%	0.61%	0.20%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	10.37%	8.92%	10.02%	7.28%	12.73%	10.89%
Cocconeis scutellum Ehrenberg var. *scutellum*	18.24%	15.06%	15.11%	13.96%	16.26%	15.84%
Hyalosynedra laevigata (Grunow) Williams & Round	6.91%	8.51%	10.39%	4.59%	8.19%	6.93%
Mastogloia binotata (Grunow) Cleve	0.00%	0.44%	0.85%	0.84%	0.41%	0.99%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.60%	1.77%	1.45%	3.89%	1.91%	6.34%
Mastogloia crucicula var. *alternans* Zanon	0.86%	2.69%	0.96%	1.37%	3.08%	0.99%
Navicula ramosissima (Agardh) Cleve	3.57%	0.00%	9.06%	0.00%	9.11%	0.00%
Nitzschia angularis W. Smith	1.85%	1.58%	1.09%	0.91%	3.38%	0.40%
Nitzschia lanceolata var. *minima* Grunow	0.74%	0.00%	0.00%	0.00%	4.09%	0.00%
Taxa: **Season:**	**Summer**					
Months:	**Jun-09**	**Jun-10**	**Jul-09**	**Jul-10**	**Aug-09**	**Aug-10**
Cocconeis caulerpacola Witkowski, Car & Dobosz	1.60%	1.64%	1.44%	4.98%	14.89%	19.87%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	12.23%	18.72%	4.03%	10.84%	2.50%	6.77%
Cocconeis scutellum Ehrenberg var. *scutellum*	14.63%	18.28%	10.46%	4.79%	3.19%	1.88%
Hyalosynedra laevigata (Grunow) Williams & Round	14.63%	17.31%	15.71%	15.07%	4.90%	8.79%
Mastogloia binotata (Grunow) Cleve	1.86%	0.43%	1.20%	1.36%	1.06%	0.49%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	5.59%	3.17%	2.70%	4.87%	0.75%	0.87%
Mastogloia crucicula var. *alternans* Zanon	0.80%	2.94%	1.50%	4.69%	0.91%	1.57%
Navicula ramosissima (Agardh) Cleve	6.65%	14.07%	5.35%	0.00%	4.75%	1.41%
Nitzschia angularis W. Smith	1.60%	1.03%	1.44%	4.01%	1.59%	1.67%
Nitzschia lanceolata var. *minima* Grunow	1.86%	1.84%	2.34%	2.69%	3.78%	2.96%
Taxa: **Season:**	**Autumn**					
Months:	**Sep-09**	**Sep-10**	**Oct-09**	**Oct-10**	**Nov-08**	**Nov-09**
Cocconeis caulerpacola Witkowski, Car & Dobosz	22.05%	25.45%	42.71%	37.49%	33.92%	29.49%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	1.40%	3.51%	2.08%	4.75%	5.56%	6.56%
Cocconeis scutellum Ehrenberg var. *scutellum*	3.98%	3.01%	21.12%	7.51%	7.22%	35.75%
Hyalosynedra laevigata (Grunow) Williams & Round	4.89%	6.35%	8.55%	8.40%	16.66%	10.61%
Mastogloia binotata (Grunow) Cleve	0.93%	0.29%	0.00%	0.37%	1.72%	0.26%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	1.98%	0.97%	0.00%	3.06%	3.10%	1.00%
Mastogloia crucicula var. *alternans* Zanon	0.70%	0.56%	0.26%	0.87%	0.98%	1.63%
Navicula ramosissima (Agardh) Cleve	7.14%	1.15%	1.30%	2.79%	3.81%	0.76%
Nitzschia angularis W. Smith	1.51%	1.67%	0.79%	1.16%	1.06%	1.01%
Nitzschia lanceolata var. *minima* Grunow	4.92%	3.16%	1.31%	2.04%	1.85%	1.79%

Mastogloia crucicula var. *crucicula* and *Mastogloia crucicula* var. *alternans* occurred in 96-98% of samples with an average abundance of 2% and a maximum of 5% in summer. *Mastogloia fimbriata* and *Mastogloia pseudolatecostata* occurred with the same frequency, but in 89% of samples. Average abundance of *Mastogloia fimbriata* was 2%, and of *M. pseudolatecostata* 1.5%. Both of these species showed a slight seasonal change. During winter and spring the abundance of *M. fimbriata* was higher than average (2.5%) while during summer and autumn it was lower (1.5%). *Mastogloia pseudolatecostata* showed an opposite tendency with higher abundance (1.8%) during summer and autumn and lower abundance (0.9%) in winter and spring.

During the study period, the average abundance of *Navicula ramosissima* was 5% with lower values were recorded in winter and autumn and a maximum abundance (14.07%) observed in June 2010. A second taxon of *Navicula* belonging to the 25 dominant taxa was *N. arenaria* Donkin var. *arenaria,* which, however has lower abundance (3%) and no specific seasonality.

The average abundance of *Nitzschia angularis* ,which occurred in 93% of samples, was 1.52% and no specific seasonality was observed. *Nitzschia lanceolata* var. *minima* was identified in 78% samples with an average abundance of 2.6%. In the 25 dominant taxa *Nitzschia panduriformis* var. *panduriformis* has been included, occurring in more than 91% of samples with an average abundance of 2%. *N. lanceolata* var. *minima* and *N. panduriformis* var. *panduriformis* achieved higher abundances during summer and autumn.

Amphora was represented by *A. acutiuscula* and *A. helenensis* and occurred in 61% and 80% of samples of epiphytic diatoms on *C. taxifolia* with an average abundance of ca. 1.6%. While *Amphora helenensis* showed no special seasonality, *Amphora acutiuscula* occurred with the highest abundance (4%) during spring.

A group of several taxa was observed with relatively low frequency and low average abundance. Included in this group were e.g. *Berkeleya scopulorum* (Brébisson) Cox , *Ardissonea fulgens* (Greville) Grunow, and *Grammatophora oceanica*. *Berkeleya scopulorum* occurred in 63% of samples of *C. taxifolia* with an average abundance of 1.4% and highest abundance (2%) in spring. *A. fulgens* (Greville) Grunow occurred in 70% of samples with an average abundance of 1.5%. *Grammatophora oceanica* was found in 57% samples of epiphytic diatoms on *Caulerpa taxifolia* with an average abundance of 1.5%, reaching its highest abundance (3.19%) during spring.

The least frequent component of the 25 epiphytic diatom taxa on *C. taxifolia* were *Licmophora gracilis* var. *gracilis*, *Tabularia ktenoeoides* and *Toxarium undulatum*. *Licmophora gracilis* var. *gracilis* showed strong seasonal distribution with a highest abundance of 9.14% in spring. Its maximum abundance of 22.93% was observed in March 2009. That value was very high compared to the average abundance which was generally low and reached only 2.98%. The average abundance of *Tabularia ktenoeoides* which occurred in 85% of *Caulerpa taxifolia* samples was 2%, being somewhat lower in summer and autumn. The abundance of *T. undulatum* which occurred in 72% of samples was 1.5%.

Figure 68. Differences in average abundance of dominant taxa on *Caulerpa racemosa*, *Caulerpa taxifolia*, *Halimeda tuna* and *Padina pavonica*.

3.3.5.1. *Cocconeis caulerpacola* Witkowski, Car & Dobosz

A taxon of *Cocconeis* new to science has been primarily identified on *C. taxifolia* from the island of Hvar where it was achieving the highest abundance. Its average abundance at Hvar amounted to 13%, whereas in samples from Island of Mljet and from Dubrovnik it averaged 6% and 1% respectively (Figure 69).

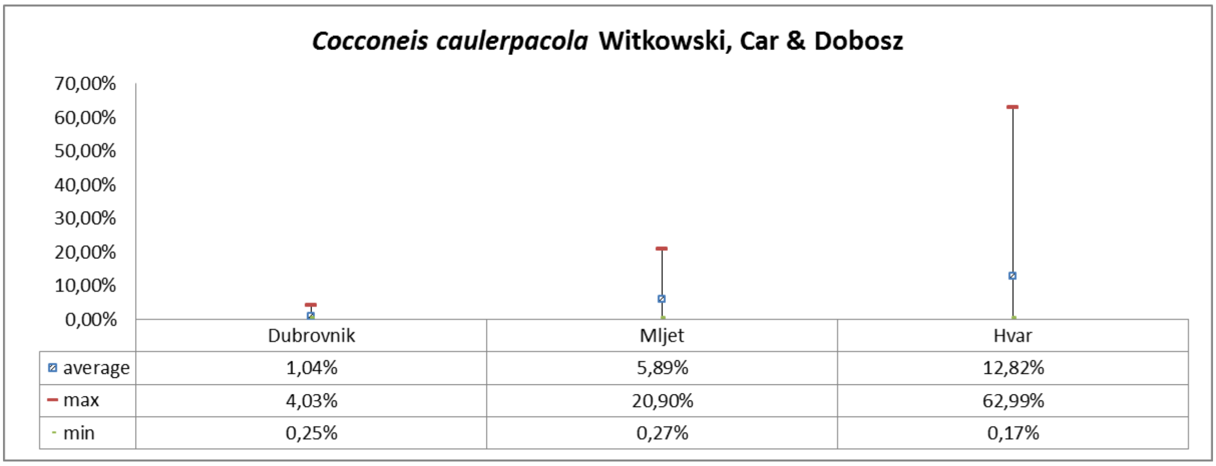


Figure 69. Box and Whisker Plot showing average, maximum and minimum abundance of *Cocconeis caulerpacola* at three sampling sites. N = 149.

Cocconeis caulerpacola was found almost exclusively on invasive algae and showed strong seasonality with its maximum during autumn (Figure 70). In general, over all three sampling sites during all seasons, the average abundance of *Cocconeis caulerpacola* on autochthonous algae amounted to 0.67%, while on invasive algae it was 10%.

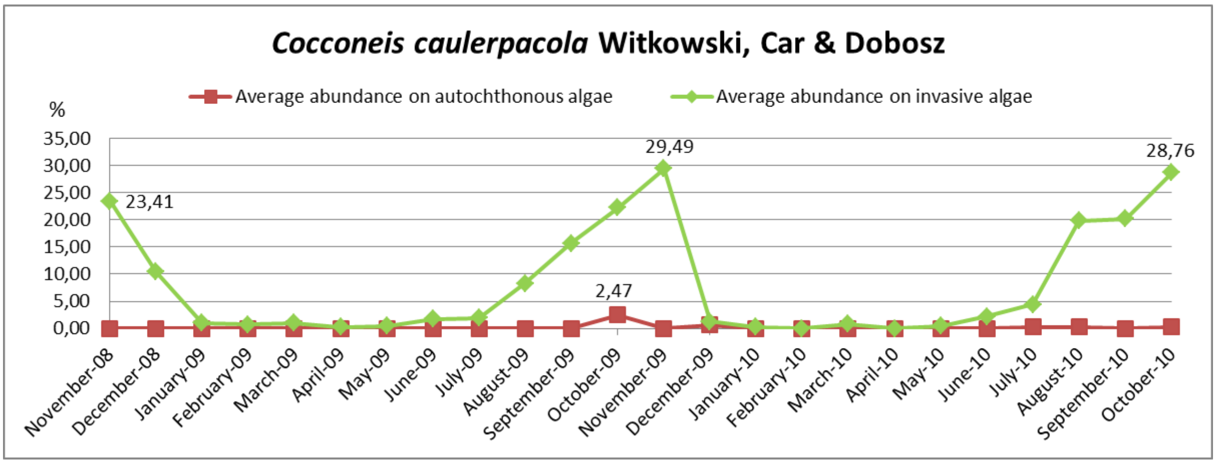


Figure 70. Average abundance of *Cocconeis caulerpacola* on autochthonous and invasive algae during two year period from November 2008 till October 2010. N = 149.

While both frequency of occurrence and average abundance of *Cocconeis caulerpacola* on autochthonous algae *Padina pavonica* and *Halimeda tuna* were around 1%, it was observed in more than 50% of samples from invasive algae with an average abundance of 5% on *Caulerpa racemosa* and of 14% on *Caulerpa taxifolia* (Table 38).

Table 38. Frequency of appearance (Freq.) and average abundance (Avg.) of *Cocconeis caulerpacola* on autochthonous and invasive algae studied.

Substrates:	***Cocconeis caulerpacola*** Witkowski, Car & Dobosz	
	Freq. (%)	**Avg. (%)**
Padina pavonica	0.04%	0.26%
Halimeda tuna	0.19%	0.76%
Caulerpa racemosa	50.00%	5.07%
Caulerpa taxifolia	76.09%	13.83%

It was observed that during autumn the frequency of occurrence and abundance of *Cocconeis caulerpacola* were higher than average. The new taxon of *Cocconeis* was found in all samples of invasive algae with an average abundance of 8% on *Caulerpa racemosa* and of 32% on *Caulerpa taxifolia*.

The maximum abundance of *Cocconeis caulerpacola*, 63%, was recorded on *C. taxifolia* in October 2009, while on *C. racemosa* its maximum was 21%. Minimum abundances (0.17-0.26%) of this new *Cocconeis* species were observed in spring both on *C. racemosa* and on *C. taxifolia*.

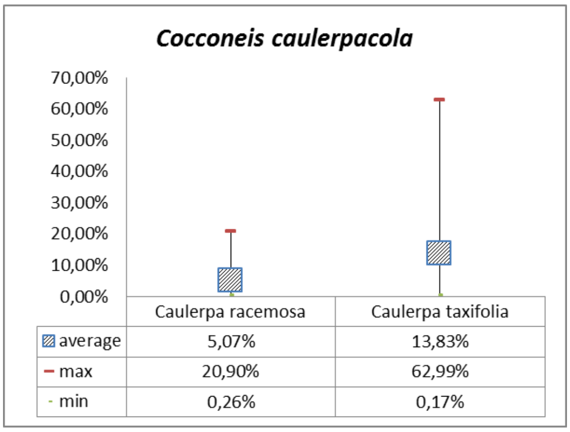


Figure 71. Box and Whisker Plot showing average, maximum and minimum abundances of *Cocconeis caulerpacola* on different invasive algae.

Cocconeis caulerpacola was found inhabiting both Mediterranean (invasive) and Australian (native) specimens of *C. taxifolia*, as well as invasive *C. racemosa*, while only a very few specimens, or none at all, were observed on coexisting indigenous algae and on native seagrass *Posidonia oceanica* (Table 39) (Car et al., 2012).

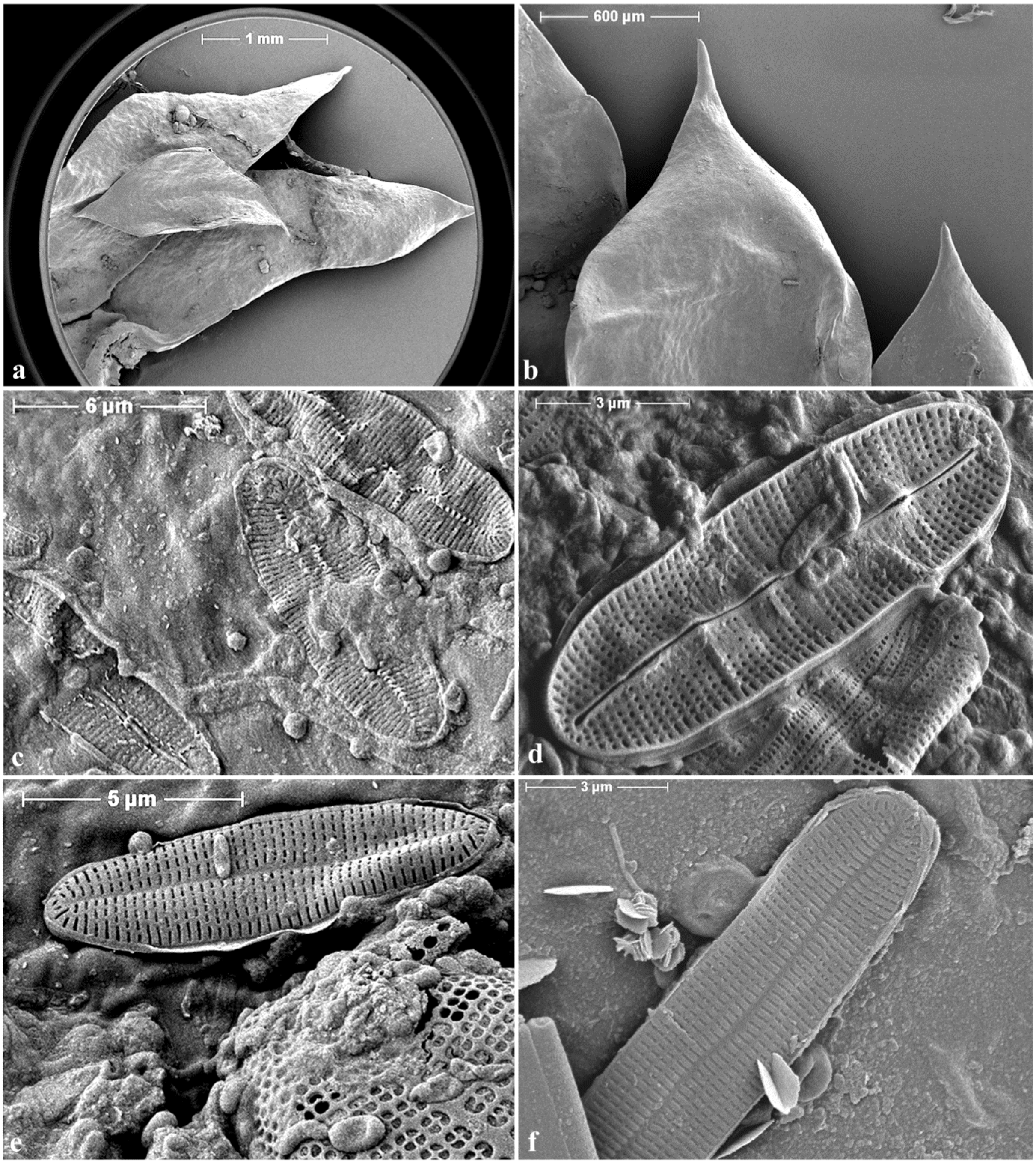
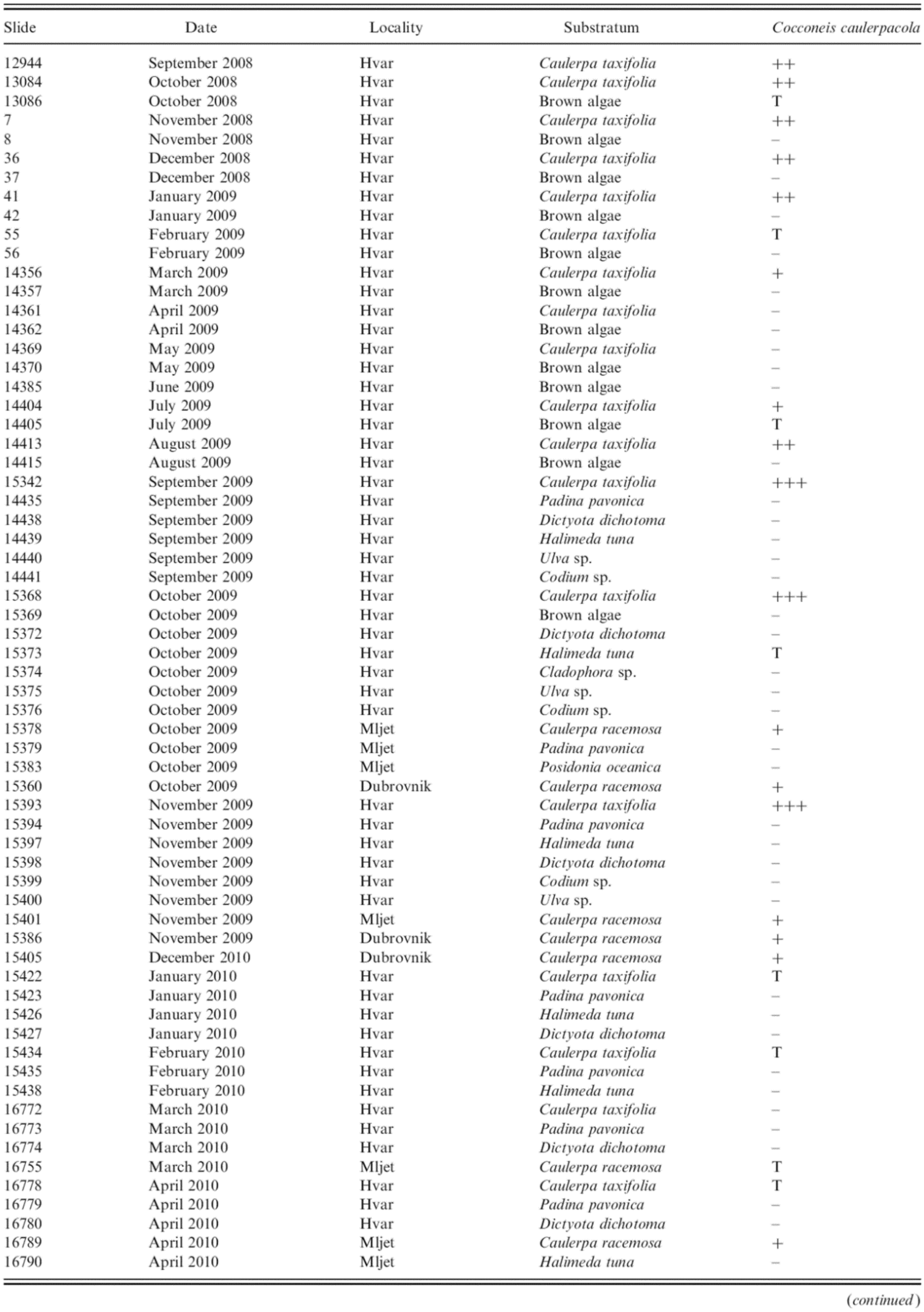


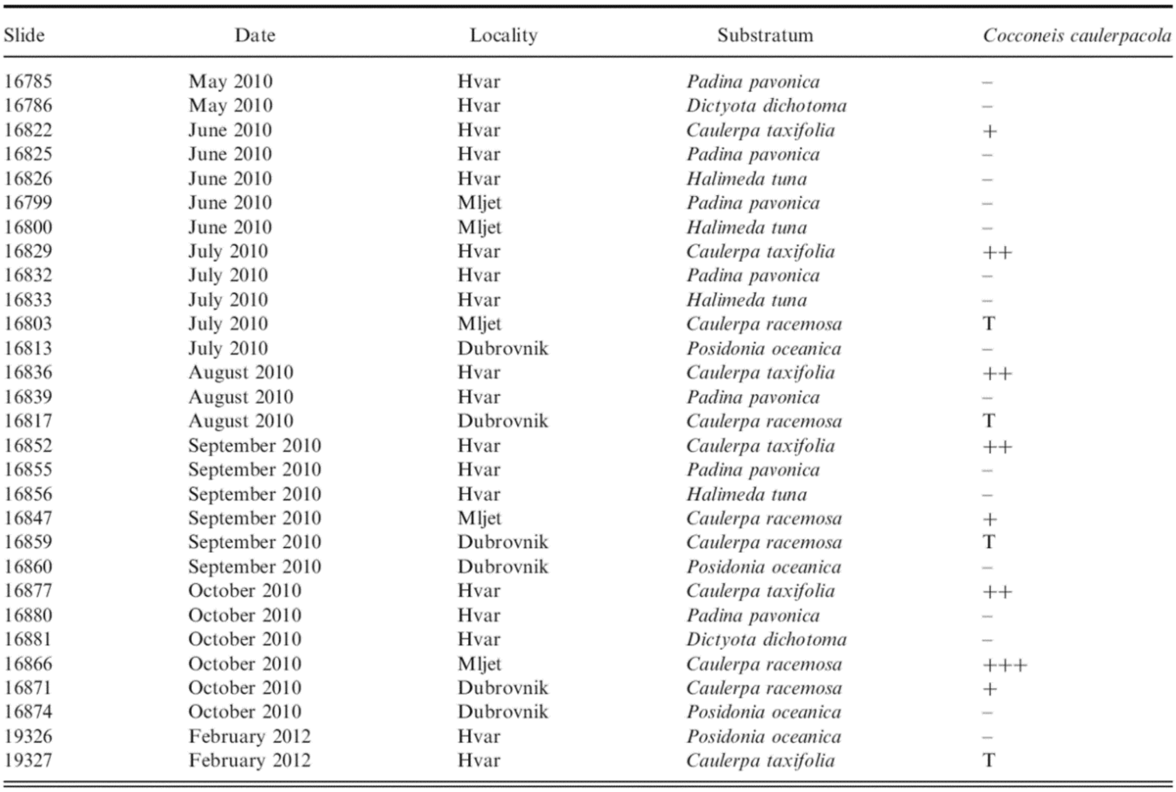
Figure 72. Examination of unprocessed material of invasive *Caulerpa taxifolia* from Croatia under low magnification with the SEM. Figures c, d, e and f valves of *Cocconeis caulerpacola* photographed in situ on *C. taxifolia* from Croatia. Figs c and d raphe valve interior. Figs e and f sternum valve showing generally convex surface along the margins then becoming flat with a slightly depressed sternum. Note the transapical striae parallel in the middle, becoming radiate towards the apices.

Table 39. List of samples from the Adriatic Sea examined for the presence of *Cocconeis caulerpacola*. Occurrence of *C. caulerpacola* estimated as + to +++ (+ present in moderate quantities, ++ abundant, +++ very abundant) or T (trace); – indicates that the taxon was not observed in the sample.



Slide	Date	Locality	Substratum	*Cocconeis caulerpacola*
12944	September 2008	Hvar	*Caulerpa taxifolia*	++
13084	October 2008	Hvar	*Caulerpa taxifolia*	++
13086	October 2008	Hvar	Brown algae	T
7	November 2008	Hvar	*Caulerpa taxifolia*	++
8	November 2008	Hvar	Brown algae	–
36	December 2008	Hvar	*Caulerpa taxifolia*	++
37	December 2008	Hvar	Brown algae	–
41	January 2009	Hvar	*Caulerpa taxifolia*	++
42	January 2009	Hvar	Brown algae	–
55	February 2009	Hvar	*Caulerpa taxifolia*	T
56	February 2009	Hvar	Brown algae	–
14356	March 2009	Hvar	*Caulerpa taxifolia*	+
14357	March 2009	Hvar	Brown algae	–
14361	April 2009	Hvar	*Caulerpa taxifolia*	–
14362	April 2009	Hvar	Brown algae	–
14369	May 2009	Hvar	*Caulerpa taxifolia*	–
14370	May 2009	Hvar	Brown algae	–
14385	June 2009	Hvar	Brown algae	–
14404	July 2009	Hvar	*Caulerpa taxifolia*	+
14405	July 2009	Hvar	Brown algae	T
14413	August 2009	Hvar	*Caulerpa taxifolia*	++
14415	August 2009	Hvar	Brown algae	–
15342	September 2009	Hvar	*Caulerpa taxifolia*	+++
14435	September 2009	Hvar	*Padina pavonica*	–
14438	September 2009	Hvar	*Dictyota dichotoma*	–
14439	September 2009	Hvar	*Halimeda tuna*	–
14440	September 2009	Hvar	*Ulva* sp.	–
14441	September 2009	Hvar	*Codium* sp.	–
15368	October 2009	Hvar	*Caulerpa taxifolia*	+++
15369	October 2009	Hvar	Brown algae	–
15372	October 2009	Hvar	*Dictyota dichotoma*	–
15373	October 2009	Hvar	*Halimeda tuna*	T
15374	October 2009	Hvar	*Cladophora* sp.	–
15375	October 2009	Hvar	*Ulva* sp.	–
15376	October 2009	Hvar	*Codium* sp.	–
15378	October 2009	Mljet	*Caulerpa racemosa*	+
15379	October 2009	Mljet	*Padina pavonica*	–
15383	October 2009	Mljet	*Posidonia oceanica*	–
15360	October 2009	Dubrovnik	*Caulerpa racemosa*	+
15393	November 2009	Hvar	*Caulerpa taxifolia*	+++
15394	November 2009	Hvar	*Padina pavonica*	–
15397	November 2009	Hvar	*Halimeda tuna*	–
15398	November 2009	Hvar	*Dictyota dichotoma*	–
15399	November 2009	Hvar	*Codium* sp.	–
15400	November 2009	Hvar	*Ulva* sp.	–
15401	November 2009	Mljet	*Caulerpa racemosa*	+
15386	November 2009	Dubrovnik	*Caulerpa racemosa*	+
15405	December 2010	Dubrovnik	*Caulerpa racemosa*	+
15422	January 2010	Hvar	*Caulerpa taxifolia*	T
15423	January 2010	Hvar	*Padina pavonica*	–
15426	January 2010	Hvar	*Halimeda tuna*	–
15427	January 2010	Hvar	*Dictyota dichotoma*	–
15434	February 2010	Hvar	*Caulerpa taxifolia*	T
15435	February 2010	Hvar	*Padina pavonica*	–
15438	February 2010	Hvar	*Halimeda tuna*	–
16772	March 2010	Hvar	*Caulerpa taxifolia*	–
16773	March 2010	Hvar	*Padina pavonica*	–
16774	March 2010	Hvar	*Dictyota dichotoma*	–
16755	March 2010	Mljet	*Caulerpa racemosa*	T
16778	April 2010	Hvar	*Caulerpa taxifolia*	T
16779	April 2010	Hvar	*Padina pavonica*	–
16780	April 2010	Hvar	*Dictyota dichotoma*	–
16789	April 2010	Mljet	*Caulerpa racemosa*	+
16790	April 2010	Mljet	*Halimeda tuna*	–

(*continued*)



Slide	Date	Locality	Substratum	*Cocconeis caulerpacola*
16785	May 2010	Hvar	*Padina pavonica*	–
16786	May 2010	Hvar	*Dictyota dichotoma*	–
16822	June 2010	Hvar	*Caulerpa taxifolia*	+
16825	June 2010	Hvar	*Padina pavonica*	–
16826	June 2010	Hvar	*Halimeda tuna*	–
16799	June 2010	Mljet	*Padina pavonica*	–
16800	June 2010	Mljet	*Halimeda tuna*	–
16829	July 2010	Hvar	*Caulerpa taxifolia*	++
16832	July 2010	Hvar	*Padina pavonica*	–
16833	July 2010	Hvar	*Halimeda tuna*	–
16803	July 2010	Mljet	*Caulerpa racemosa*	T
16813	July 2010	Dubrovnik	*Posidonia oceanica*	–
16836	August 2010	Hvar	*Caulerpa taxifolia*	++
16839	August 2010	Hvar	*Padina pavonica*	–
16817	August 2010	Dubrovnik	*Caulerpa racemosa*	T
16852	September 2010	Hvar	*Caulerpa taxifolia*	++
16855	September 2010	Hvar	*Padina pavonica*	–
16856	September 2010	Hvar	*Halimeda tuna*	–
16847	September 2010	Mljet	*Caulerpa racemosa*	+
16859	September 2010	Dubrovnik	*Caulerpa racemosa*	T
16860	September 2010	Dubrovnik	*Posidonia oceanica*	–
16877	October 2010	Hvar	*Caulerpa taxifolia*	++
16880	October 2010	Hvar	*Padina pavonica*	–
16881	October 2010	Hvar	*Dictyota dichotoma*	–
16866	October 2010	Mljet	*Caulerpa racemosa*	+++
16871	October 2010	Dubrovnik	*Caulerpa racemosa*	+
16874	October 2010	Dubrovnik	*Posidonia oceanica*	–
19326	February 2012	Hvar	*Posidonia oceanica*	–
19327	February 2012	Hvar	*Caulerpa taxifolia*	T

HOLOTYPE: Slide no. 16 822 in coll. A. Witkowski, Institute of Marine Sciences University of Szczecin, Poland (SZCZ). Leg. Ana Car, June 2010. Holotype specimen is illustrated in Figure 73 a.

TYPE HABITAT: On the invasive alga *C. taxifolia*, collected from sandy bottom of the sublittoral zone in Stari Grad Bay, 43° 10' 54" N, 16° 35' 00" E.

ETYMOLOGY: The specific epithet refers to generic name of a host plant (*Caulerpa taxifolia*) on which this taxa grows abundantly.

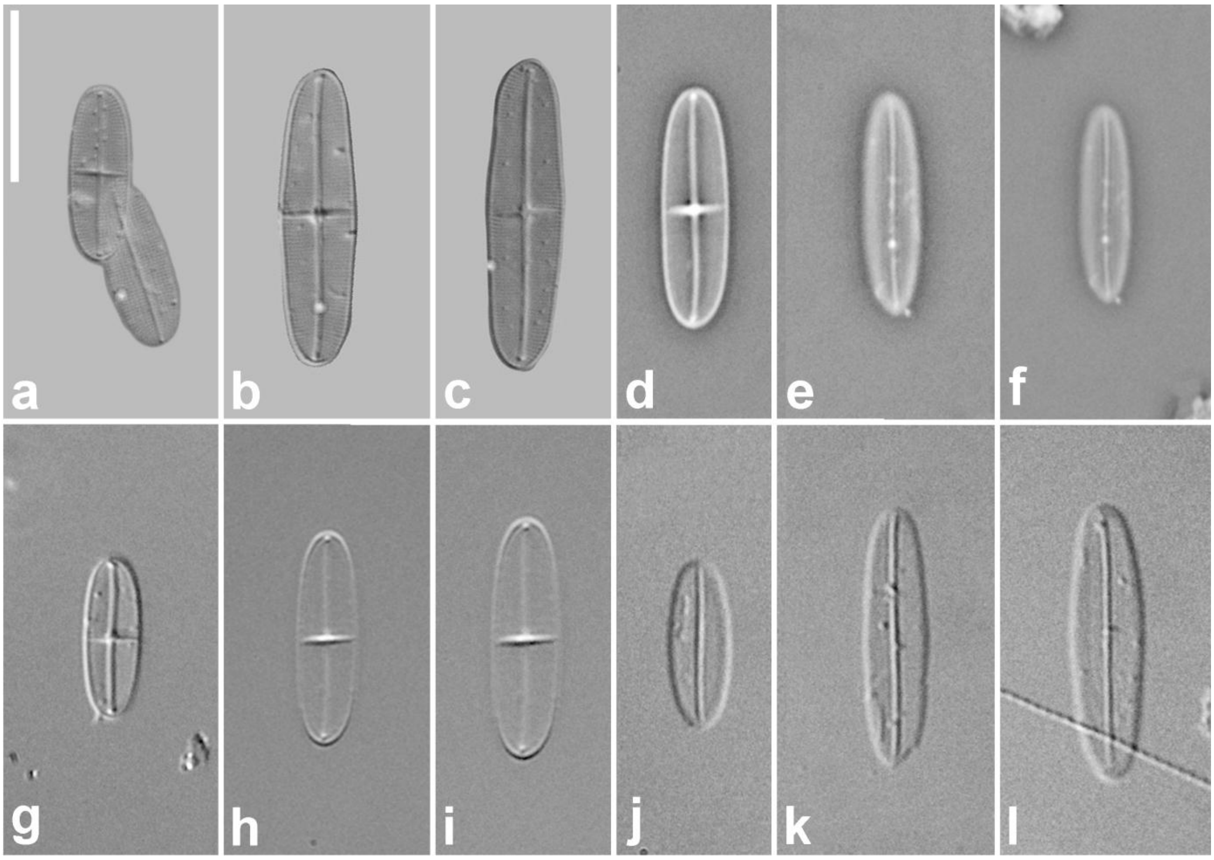


Figure 73. a-l. *Cocconeis caulerpacola*, LM. Specimens from the holotype slide. Figs a–c are micrographs taken by means of an advanced photomicrography method (kindly provided by Wulf Herwig); Figs d–f are phase contrast; Figs g–l are differential interference contrast. a. Holotype specimen, comprising raphe (left) and sternum (right) valves. b–l. Selected raphe (Figs b–d, g–i) and sternum (Figs e, f, j–l) valves. Scale bar = 10 µm.

Morphology.

The frustules are rectangular in girdle view (not shown). The valves are strictly linear-elliptical with broadly rounded apices, 10–18 μm long, 3–4 μm wide (Figure 73). The raphe valve (RV) has a sigmoid raphe sternum and raphe (Figure 73 b, c, d, g, h, i). The axial area is barely distinguishable in LM, whereas the central area is fairly distinct, taking the form of a transapically expanded fascia that usually extends almost to the valve margins (Figure 73 b, c, d, g, h, i). The sternum valve (SV) has a narrow, slightly sigmoid sternum, which is not noticeably enlarged at the centre (Figure 73 e, f, j, k, l). The transapical striae are not resolvable in LM, either on the RV or the SV, unless observed with special methods, such as advanced light photomicrography (Figure 73 a-c). Specimens of *Cocconeis caulerpacola* observed with TEM and SEM are illustrated in Figure 74 - Figure 80 including some in situ on *Caulerpa taxifolia* fronds (Figure 75 a-c, e, g; Figure 76 a, b; Figure 77 a, b). Cells are attached to *Caulerpa* by the whole of the valve face of the raphe valve (Figure 76a and Figure 76b at right). Supplementary SEM observations of *Cocconeis caulerpacola* are illustrated in Figure 80 a-h.

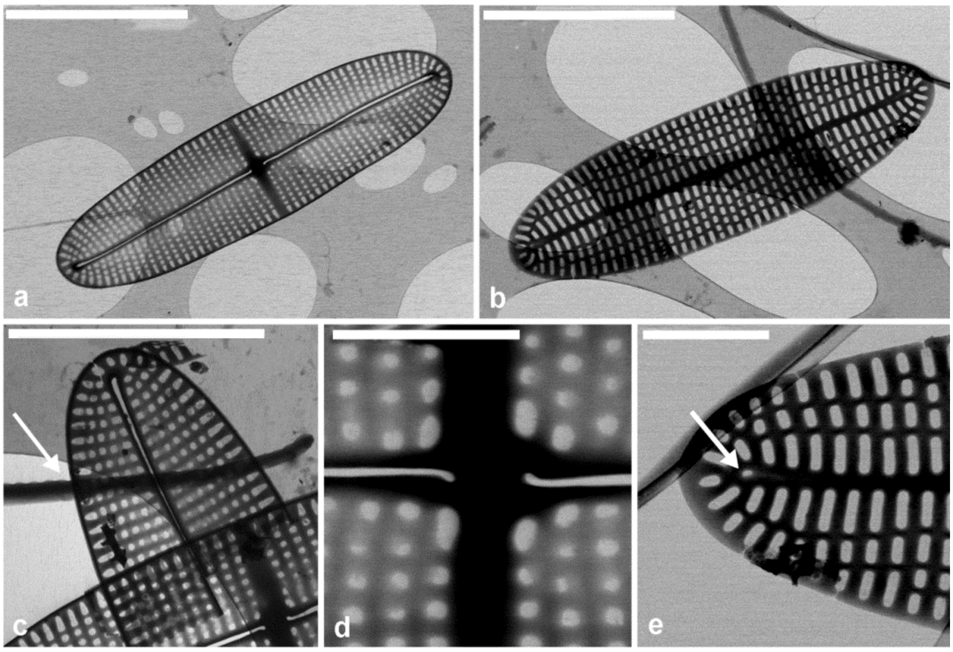


Figure 74. a-e *Cocconeis caulerpacola*, TEM. a. Raphe valve showing the striation and raphe branches with terminal and central endings. Note that the raphe endings are slightly bent towards opposite sides. b. Sternum valve with longitudinal ribs and transapically elongate areolae. c. Detail of raphe valve apex and part of valvocopula with very shallow undulations on one margin (arrow). d. Centre of raphe valve. e. Apex of sternum valve. Note the rudiment of a raphe (arrow). Scale bars = 5 μm (Fig. a), 4 μm (Figs b, c); and 1 μm (Figs d, e).

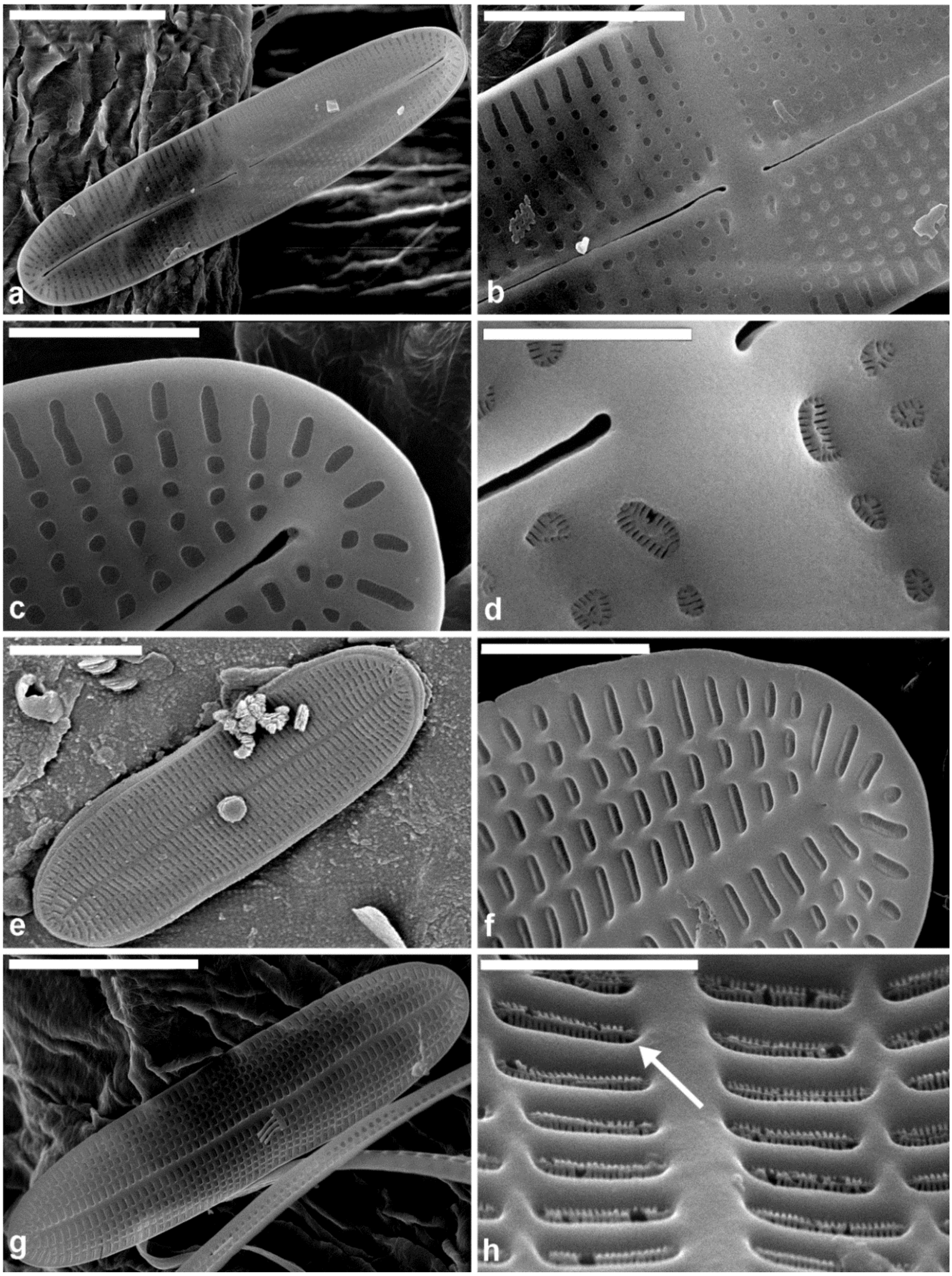


Figure 75. a-h. *Cocconeis caulerpacola*, SEM, from the holotype sample, Croatia. a, b. Raphe valve exterior, general view. Note sigmoid raphe with external central and terminal endings slightly expanded. c. Internal view of raphe valve apex. Note the terminal raphe ending. d. Close up of the centre of the interior of the raphe valve. e. Sternum valve, external view. f. Internal view of the sternum valve apex. g. Sternum valve interior. h. Close up of sternum valve interior. Note the areolae occlusions (arrow) containing apically oriented slits. Scale bars = 5 µm (Figs a and g); 3 µm (Fig. e); 2 µm (Fig. b); 1 µm (Figs c, f); and 500nm (Figs d, h).

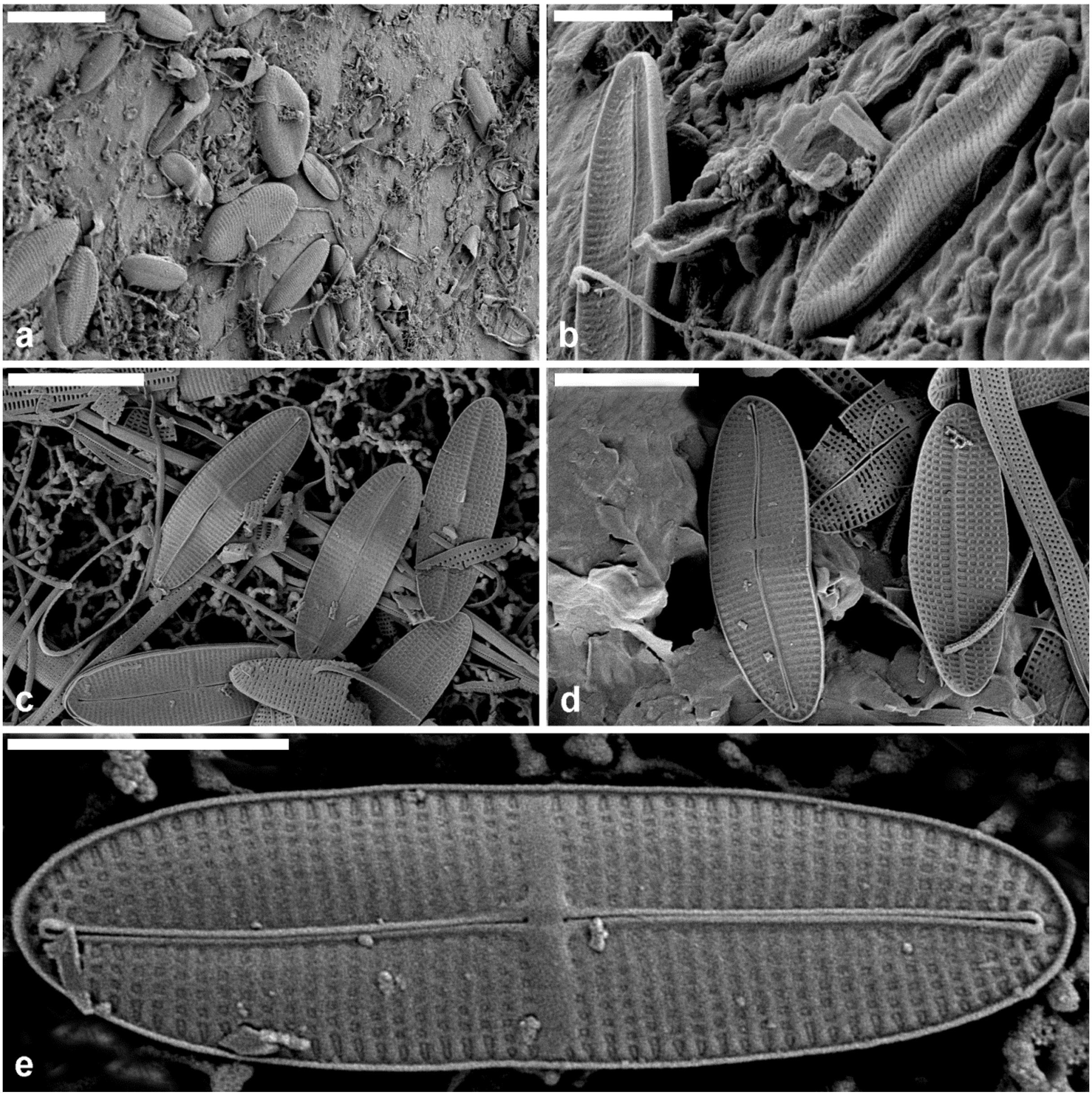


Figure 76. a-e. *Cocconeis caulerpacola*, SEM, from France. a, b. Specimens photographed in situ on Caulerpa taxifolia. c, d. External and internal views of cleaned sample. e. Raphe valves, internal view. Note the internal central and apical raphe endings. Scale bars = 10 µm (Fig. a); 6 µm (Fig. c); 4 µm (Fig. d); and 3 µm (Figs b, e).

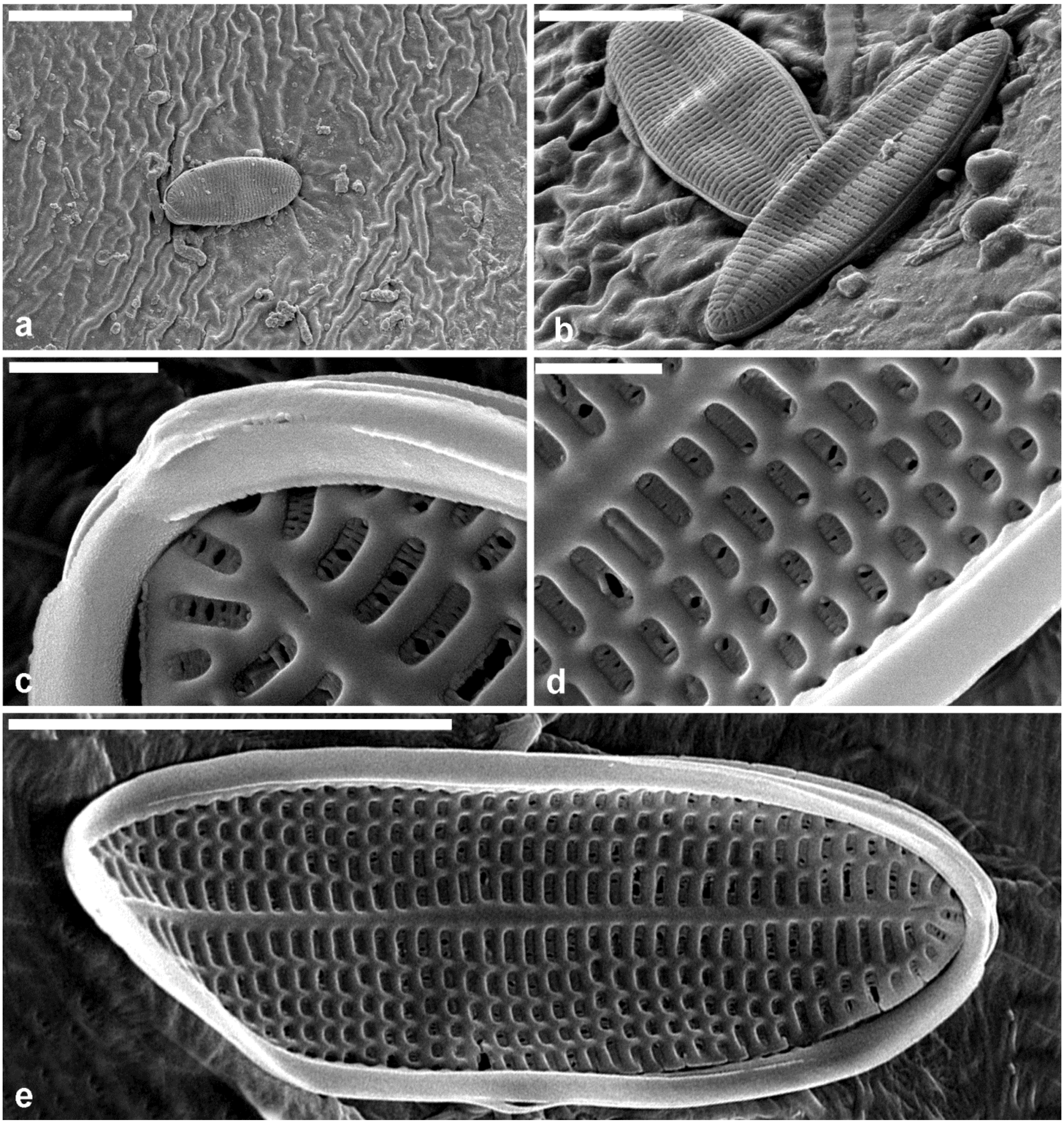


Figure 77. a-e. *Cocconeis caulerpacola* from France, SEM. Figs a, b show cells in situ on *Caulerpa taxifolia*. a, b. Cells with sternum valve uppermost, showing generally convex surface along the margins then becoming flat with a slightly depressed sternum. Note that the transapical striae are parallel in the middle, becoming radiate towards the apices. c–e. Close up and whole (Fig. e) of sternum valve interior showing transapically elongate areolae. The areolae contain the same type of hymenate occlusions as in the raphe valve. Scale bars = 6 µm (Fig. a); 4 µm (Fig. e); 3 µm (Fig. b); and 500nm (Figs c, d).

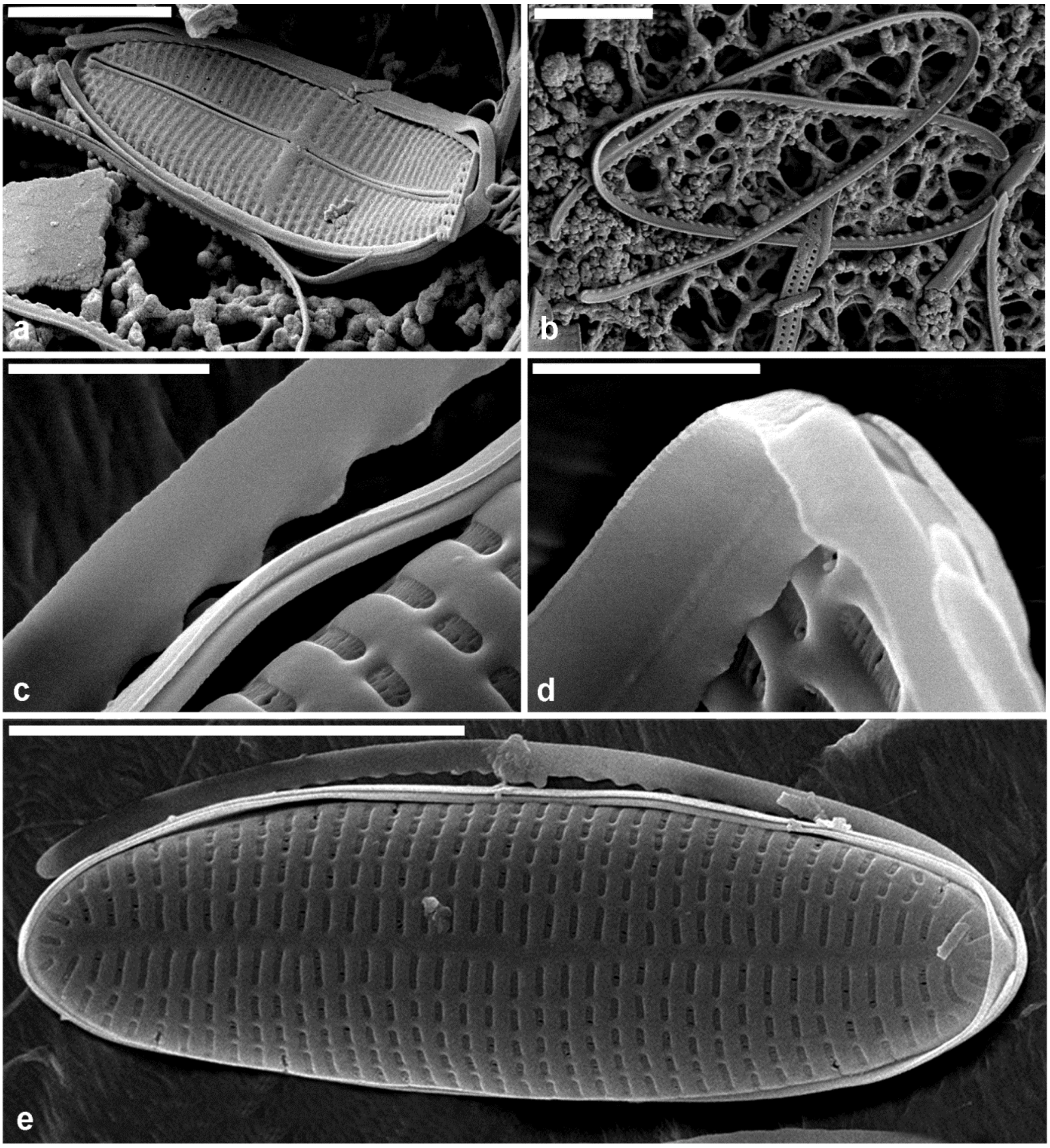


Figure 78. a-e. *Cocconeis caulerpacola* from France, SEM. a. Frustule in oblique view. b. Valvocopula detached from a frustule of *C. caulerpacola*. c, d. Close ups of valvocopula: the pars interior has an undulate margin fitting over the valve interstriae. e. Whole frustule with detached valvocopula. Scale bars = 4 µm (Fig. e); 3 µm (Figs a, b); and 500nm (Figs c, d).

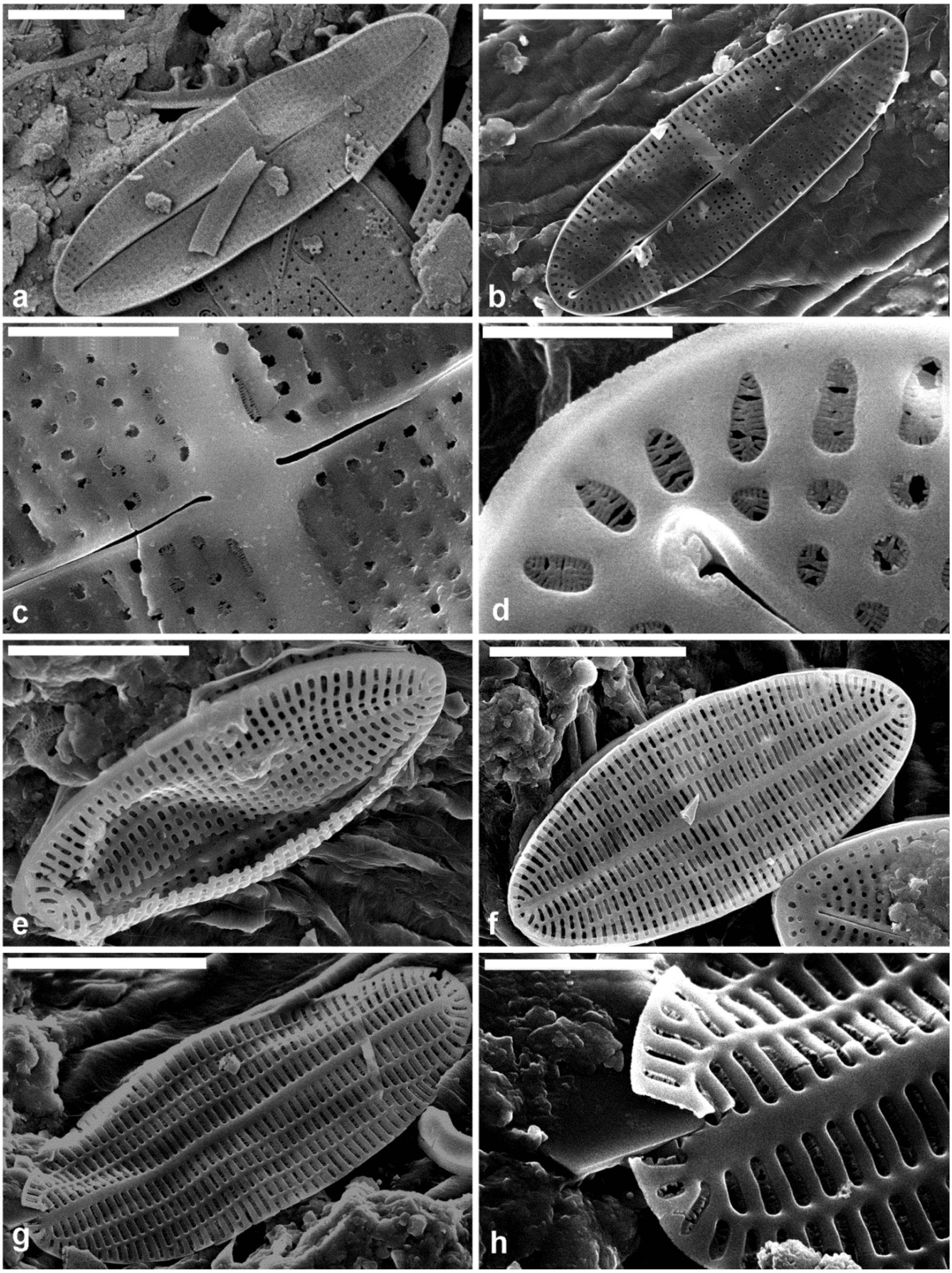


Figure 79. a-h. *Cocconeis caulerpacola* from Australia, SEM. a. Raphe valve, external view. Note the sigmoid raphe and the areola pattern typical for *C. caulerpacola* from the type habitat. b–d. Raphe valve internal view. Note the hymenate areolae occlusions. e, f. Sternum valve external view. g, h. Sternum valve internal view. Note the structure of the areolae hymenate occlusions. Scale bars = 5 µm (Fig. b); 4 µm (Figs e–g); 3 µm (Fig. a); 1 µm (Figs c, h); and 500nm (Fig. d).

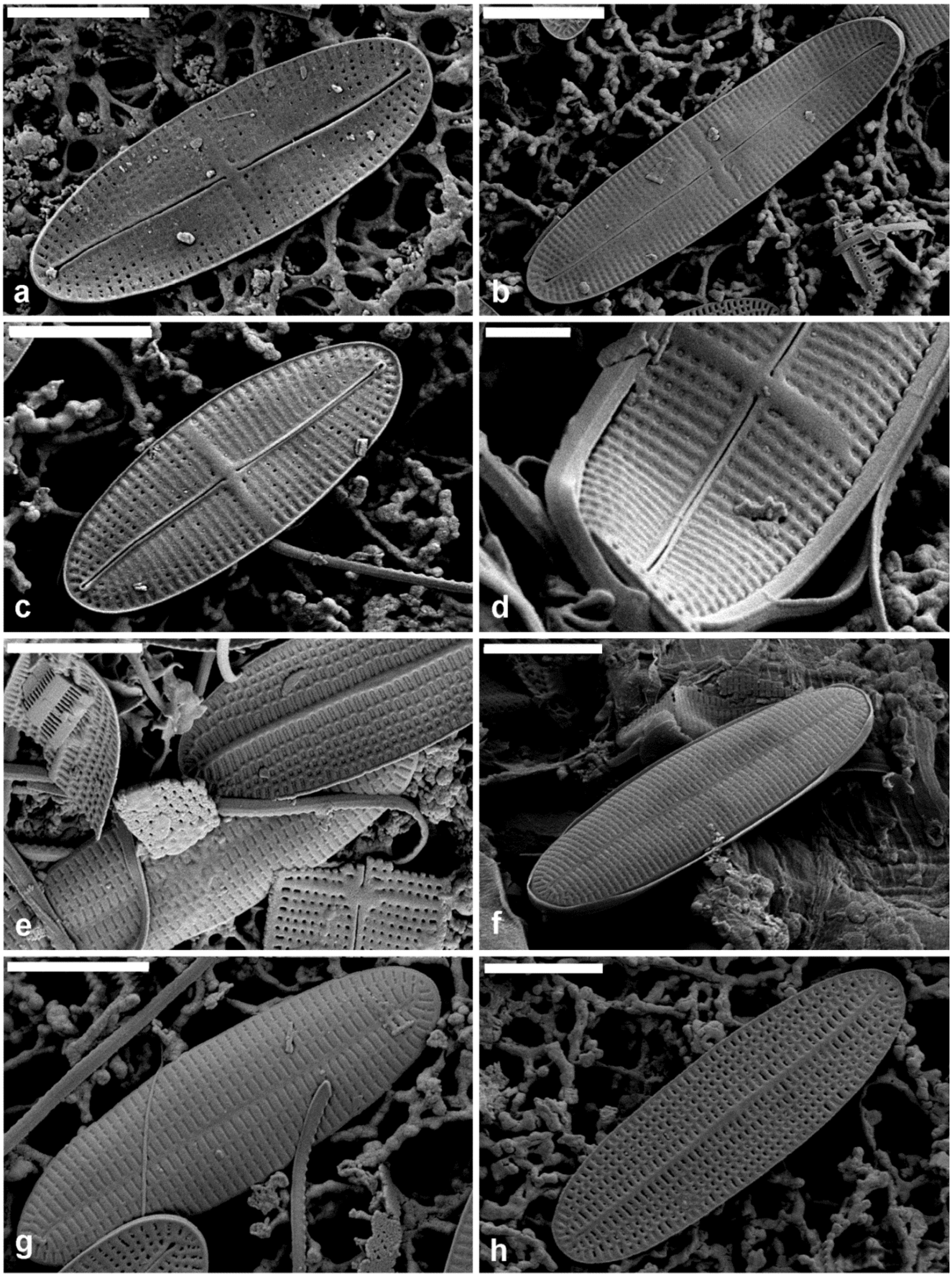


Figure 80. a-h. *Cocconeis caulerpacola*, SEM from sample from France. Figs a, b. External view of the selected raphe valves. Note the concave valve surface and the sigmoid raphe. Fig. c. Raphe valve internal view. Note the internal central and apical raphe endings. Fig. d. Frustule in oblique view. Fig. e. Valvocopulae detached from frustules of *C. caulerpacola*. Fig. f. Sternum valve photographed in situ on *Caulerpa taxifolia*. Fig. g. Sternum valve from prepared material showing generally convex surface along the margins then becoming flat with a slightly depressed sternum. Fig. h. Internal view of the sternum valve. Scale bars = 4 μm (Fig. b); 3 μm (Figs a, c, e–h); and 1 μm (Fig. d).

Raphe valve

The external surface is slightly concave with an elevated raphe sternum (Figure 75a, Figure 75b, Figure 79a). The axial area is very narrow and symmetrical, with a transapically extended central area in the form of a fascia, which reaches the valve margins (Figure 75a, Figure 75b, Figure 76c, Figure 76e). The fascia seems to be created by the absence of a single stria in the middle of the valve (Figure 74a, Figure 74d, Figure 75b). The raphe is sigmoid, with the external central endings usually very slightly expanded (Figure 74a, Figure 75b, Figure 76e but see Figure 75d). The external apical endings are slightly expanded, terminate at some distance from the apices (areolae are present between the raphe endings and the valve margin at the pole: Figure 74a, Figure 74c, Figure 75c), and are very slightly bent in opposite directions (Figure 74a, Figure 75a, Figure 79a, Figure 79b). The transapical striae are parallel in the middle, becoming radiate towards the apices, and number 40 in 10 μm. The striae are slightly depressed below the coarser interstriae (virgae). All of the valve face areolae are of approximately the same size and shape (square to rounded: Figure 74a, Figure 74c, Figure 75b), the only exceptions being a few larger areolae near the central raphe endings (Figure 75b, Figure 75d), and a row of areolae next to the valve margin: these latter are transapically elongate (Figure 74a, Figure 75b, Figure 79b). The areolae are occluded by hymenate occlusions containing apically oriented slits (Figure 75b–Figure 75d). The valve surface is flat internally and the raphe sternum is slightly elevated (Figure 76b, Figure 76d, Figure 76e). The internal central raphe endings are very slightly expanded and bent in opposite directions (Figure 74d, Figure 75d, Figure 76e, Figure 79c). The apical internal raphe endings terminate in small, simple helictoglossae which are slightly bent in opposite directions (Figure 75c, Figure 76d, Figure 76e, Figure 79d). Extra SEM observations of selected raphe valves of *C. caulerpacola* are illustrated in Figure 80.

Sternum valve

The valve external surface is slightly convex at the margin becoming flat in the middle (Figure 75e, Figure 76b, Figure 77b). The sternum is slightly sigmoid and depressed below the valve surface (Figure 75e, Figure 78e) and sometimes bears the remnants of a raphe (Figure 74e, Figure 77c). The transapical striae are parallel in the middle, becoming radiate towards the apices, and number 44–46 in 10 μm. The striae are crossed by a few longitudinal ribs, resulting in the development of rectangular, transapically elongate areolae (Figure 74b,

Figure 74e, Figure 77e). The areolae are occluded with the same type of hymenate occlusions as in the raphe valve (Figure 75f, Figure 75h, Figure 77c, Figure 77d, Figure 79h). The SV surface is concave internally along the margin becoming flat in the middle with the sternum elevated above the remainder of the valve interior. The girdle is composed of a few (at least four) plain, open copulae (Figure 77c–Figure 78e). The advalvar margin of the valvocopula possesses shallow undulations (Figure 74c, Figure 78b, Figure 78c, Figure 78e), which appear to match the valve interstriae in their spacing and fit around them in vivo (Figure 78d). Supplementary SEM observations of the selected sternum valves of *C. caulerpacola* are illustrated in Figure 80 e-h.

Differential diagnosis

The newly described taxa shows some resemblance, in terms of valve outline and the sigmoid raphe (see also Hustedt, 1933; Foged, 1975; Simonsen, 1987; Witkowski et al., 2000), to *C. diruptoides* (Figure 81) and *C. pseudodiruptoides* (Figure 82). These taxa differ, however, with respect to size range and stria density (Figure 83), *C. caulerpacola* being much smaller and more finely striated. *Cocconeis caulerpacola* also shows some similarities in terms of general valve outline and size to *C. borbonica* (Riaux-Gobin & Compère, 2008). However, they differ with respect to raphe characteristics and stria density. *Cocconeis borbonica* has a higher stria density, the raphe is not sigmoid but straight, and the fascia does not reach the margin of the raphe valve, in contrast to *C. caulerpacola* (Figure 84b, contrast Figure 84a).

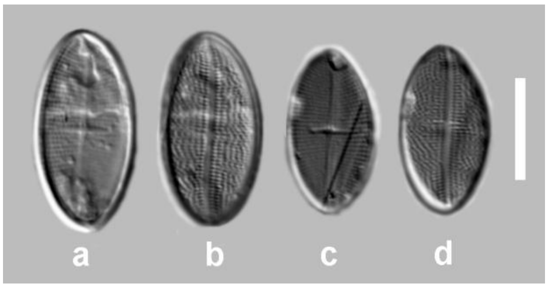


Figure 81. a-d. *Cocconeis diruptoides* from Vis (Hustedt Diatom Collection, E74), LM. Scale bar =10 µm.

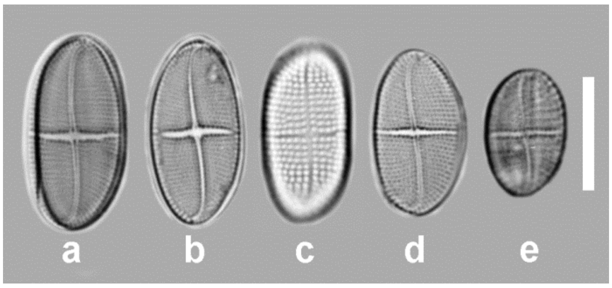


Figure 82. a-e. *Cocconeis pseudodiruptoides*, LM. Indian Ocean, Tanzania, Coll. Foged (1975), Holotype slide. Scale bar = 10 µm.

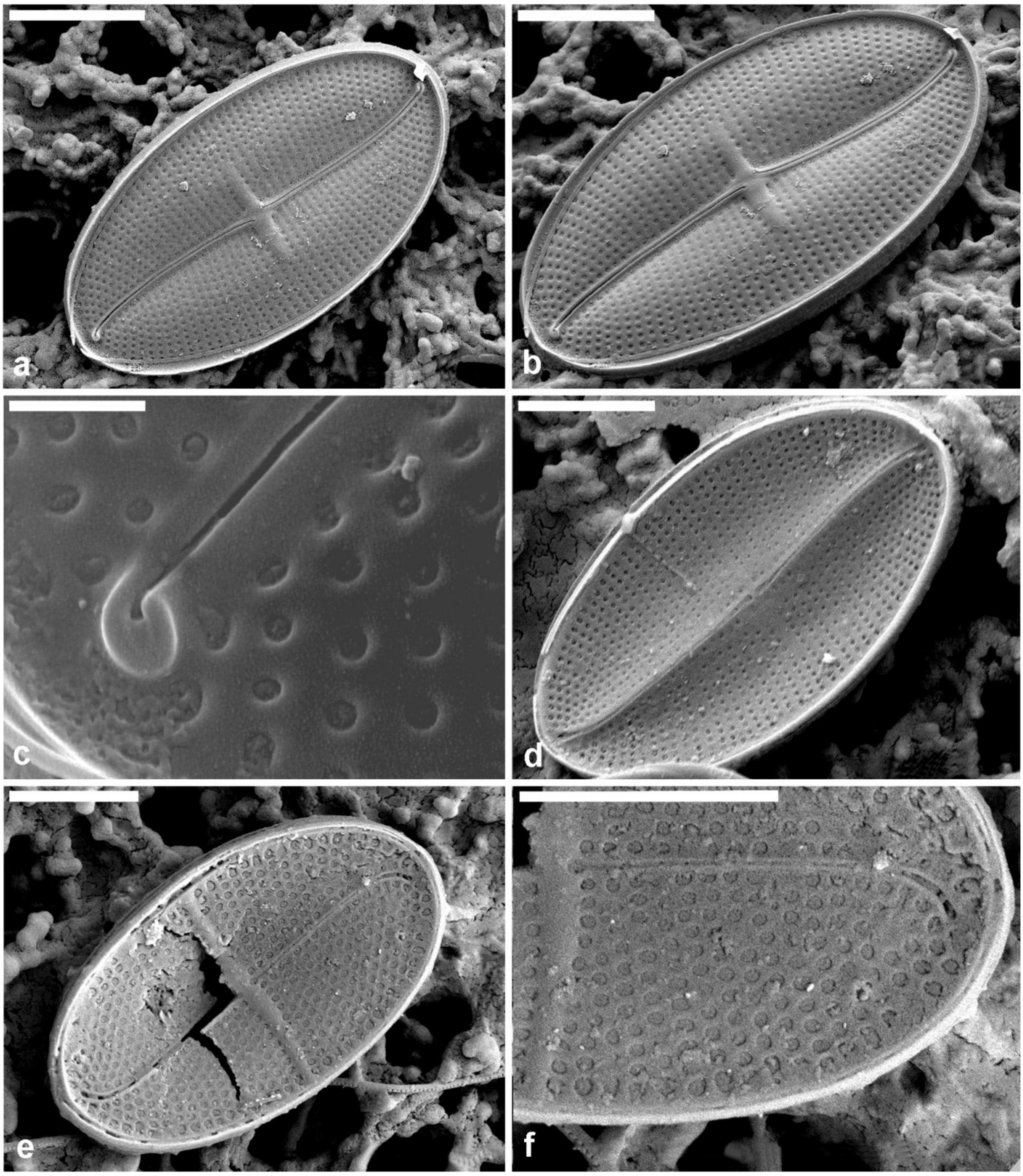


Figure 83. a-f. *Cocconeis diruptoides* and *Cocconeis pseudodiruptoides* from Vis (Hustedt Diatom Collection, E74), SEM. Figs a–c. *Cocconeis diruptoides*, type material. Raphe valves internal views. Note the internal central and apical raphe endings. Fig. d. External view of raphe valve. Note the concave valve surface and the sigmoid raphe. Figs e, f. *Cocconeis pseudodiruptoides*. External view of raphe valve. Scale bar = 6 mm (Fig. b); 5 mm (Figs a, d); 4 mm (Figs e, f); and 600 nm (Fig. c).

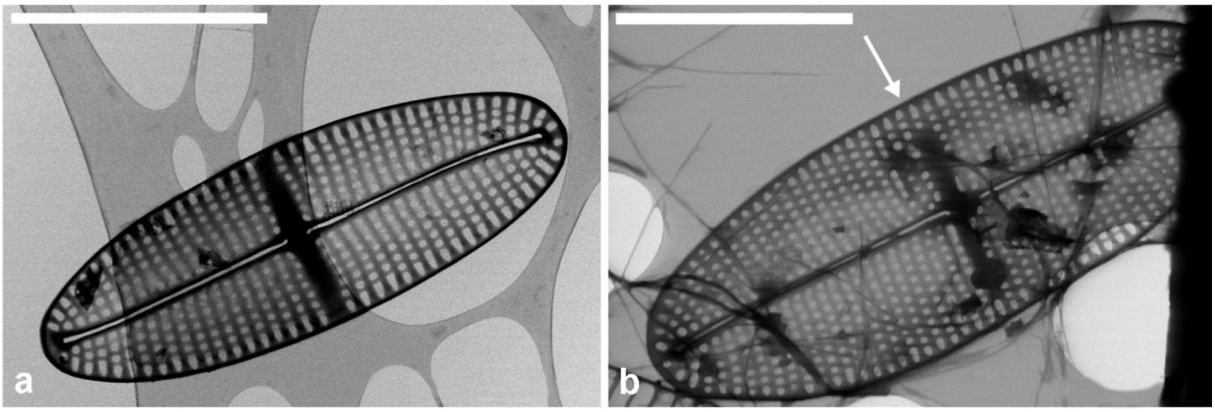


Figure 84. a-b. Comparison of *Cocconeis caulerpacola* (sample from France) and *C. borbonica* (sample from Western Indian Ocean, Juan de Nova Island), TEM. Fig. a. Raphe valve of *Cocconeis caulerpacola*. Note that both endings are slightly bent into opposite sides. Fig. b. Raphe valve of *Cocconeis borbonica*. Note the straight raphe and the presence of a fascia on the RV, which does not reach the valve margins (arrow). Scale bars = 4 µm.

Table 40. Major morphometric characteristics of *Cocconeis caulerpacola* and similar taxa, with diagnostic information.

	Length µm	Breadth µm	RV striae in 10 µm	SV striae in 10 µm	Diagnostic characters	Habitat and distribution	References
C. caulerpacola	10–18	3–4	40	44–46	RV: raphe sigmoid, fascia reaching the valve margins; SV striae radiate only at apex; transapical striae not resolvable in LM without special optics on either RV or SV	Epiphyte on *Caulerpa* sp.: Mediterranean Sea and E coast of Australia (Moreton Bay)	Present study
C. borbonica	8–12	3–4.2	42–60	50–62	RV: raphe straight, fascia (one shorter stria); SV striae radiate only at apex	Marine coral sands and brackish sediments: Réunion Island, western Indian Ocean	Riaux-Gobin & Compère, 2008
C. diruptoides	19–22	9–11	26–30	26–29 at the centre; 34 at the margin	RV: raphe sigmoid, the central area wide, stauros-like, variable but not exceeding half the valve width; several SV striae dichotomize at the valve face margin leading to an increase in stria density from the centre	Wide distribution in temperate and warm seas: Adriatic Sea at Rovinj and Vis (Hustedt Diatom Collection, E74)	De Stefano & Marino, 2001
C. pseudodiruptoides	15–22	8–12	26–28	18	RV: raphe strongly sigmoid, the central area stauros like reaching the valve margin. SV: sternum strongly sigmoid, central area very narrow, in the form of an indistinct stauros. The striae easily recognizable in LM on both valves	Indian Ocean, Tanzania, Coll. Foged (1975)	Witkowski *et al.*, 2000

3.3.5.2. Epiphytic diatoms on different parts of *Caulerpa taxifolia* thalli

Vertical distribution of epiphytic diatoms on macroalgal hosts has also been investigated in *Caulerpa taxifolia* from Croatia and France. Examination of unprocessed material under low SEM magnification demonstrated strong patchiness in the occurrence of the attached diatom flora. Aside from diatom-free patches, numerous spots with abundant diatoms were observed. The diatom abundance significantly varied between the different thallus parts, with the number of specimens in apical part significantly higher than in the basal one.

The abundance of new *Cocconeis caulerpacola* significantly differed between the various parts of fronds and pinnules (Figure 85, Figure 86, Figure 87). The number of *C. caulerpacola* specimens on basal part of pinnules and of rachis is significantly higher than in the apical one. Usually we have observed dispersed occurrence of *C. caulerpacola* along with either other *Cocconeis* taxa or *Mastogloia* spp. However, the mass development of *C. caulerpacola* observed on fronds shows that within such a dense cover this taxa occurs alone and the associated taxa are completely missing.

On the other hand, no correlation has been found between fouling diatom species composition of the *Caulerpa taxifolia* and the age of different parts of its thallus. The age gradient along the *Caulerpa* thallus does not seem to be the factor controlling the diatom community composition (Figure 112).

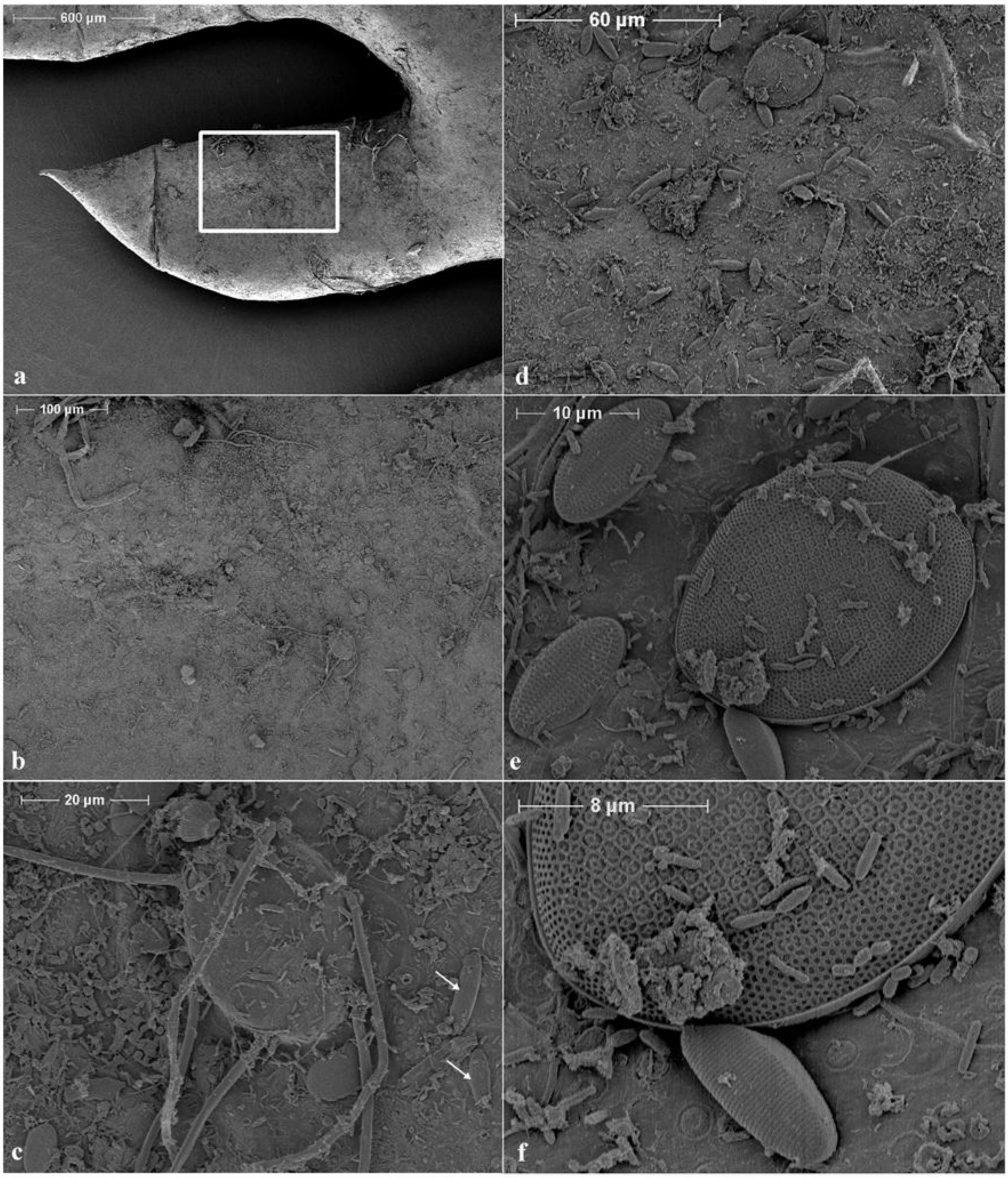


Figure 85. SEM images of a frond of *Caulerpa taxifolia* from France. (a) Area of pinnule observed in detail for epibiontic microalgal communities. (b) Close-up view of image (a). (c) Close-up view of image (b) showing a single large specimen of *Mastogloia* with characteristic mucilaginous outgrowth and solitary sternum valves of *C. caulerpacola* (arrows). (e) Close-up view of image (d) showing dominance of *Cocconeis* spp. (f) Sternum valve of tiny *Cocconeis caulerpacola* neighbouring sternum valve of *C. scutellum*.

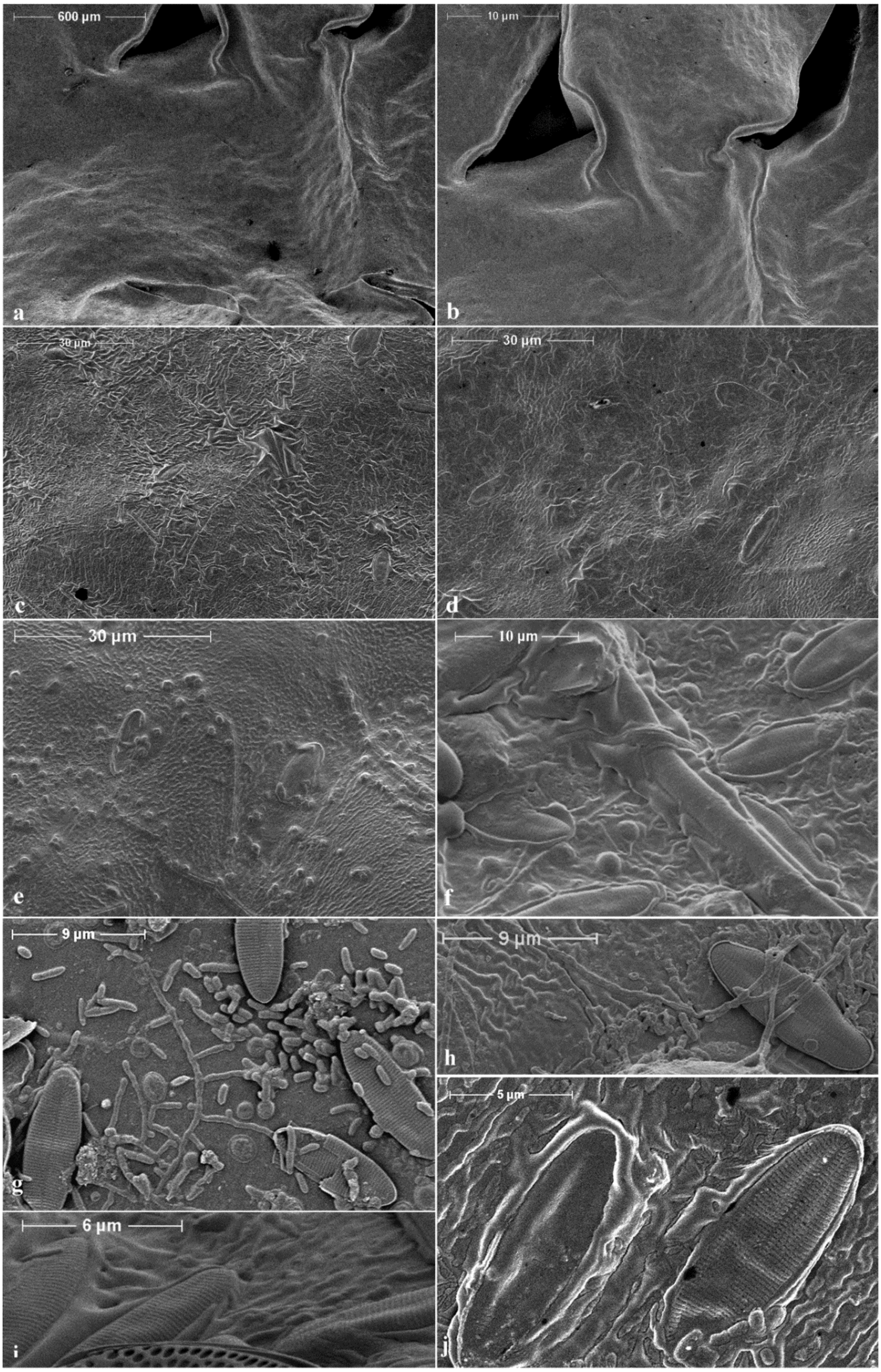


Figure 86. SEM images of epibiontic microalgal communities on basal part of pinnules of *Caulerpa taxifolia* from France (figs a and b and their close ups in the following figures). (c, d and e) The dominance of a tiny *Cocconeis caulerpacola* which was observed as epiphyte with patchy distribution covering the surface of basal part of pinnules. (f) Sternum valves of *Cocconeis caulerpacola*. (g, h, i and j) Valves of *Cocconeis caulerpacola* firmly attached to *Caulerpa taxifolia*

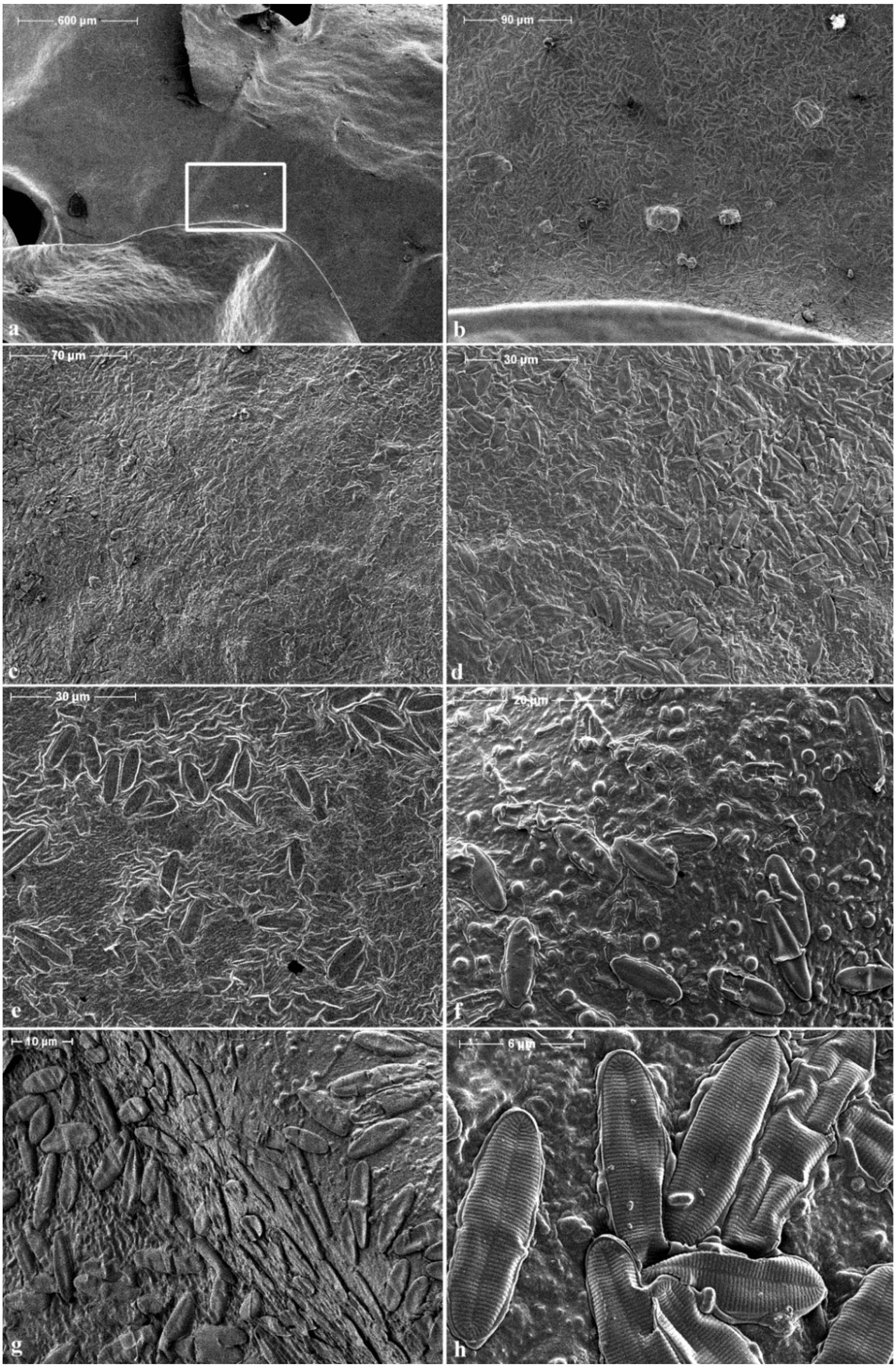


Figure 87. SEM images of epibiontic microalgal communities on the main axis of the frond of *Caulerpa taxifolia* from France. (b) Detail view of selected part of image (a). (c, d, e, f and g) Dense populations of *Cocconeis caulerpacola* observed under low magnification. (d and g) Areas with highest observed number of *Cocconeis caulerpacola*. (g) Dense population of *C. caulerpacola*. (h) External view of sternum valves of *C. caulerpacola*.

3.3.5.3. Seasonal dynamics of epiphytic diatoms on *Caulerpa taxifolia*

Seasonal distribution of the epiphytic diatom species on the “killer” seaweed *C. taxifolia* was analysed in the Bay of Stari Grad (the Island of Hvar, Croatia) over a time period exceeding 2 years (autumn 2008 – autumn 2010).

The average number of taxa during summer amounted to 77, with the highest recorded in August (102 in August 2009 and 88 in August 2010). The number of taxa decreased in September and there was a significant decrease in number of taxa (37) in winter months. The lowest number of taxa was recorded at the end of autumn/winter (e.g. 41 in November 2008, 38 in November 2009, 34 in January 2009 and 33 in January 2010, Figure 88). Several new taxa appeared in spring, but most appeared during summer, when the sea water reached its yearly temperature maximum (25°C, Figure 89).

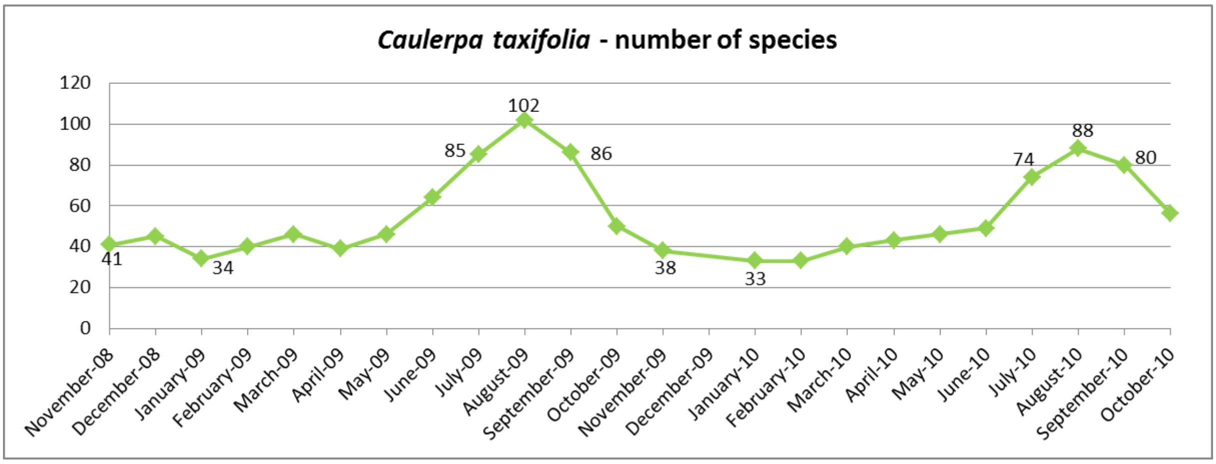


Figure 88. Number of epiphytic diatom taxa on *C. taxifolia* during the study period.

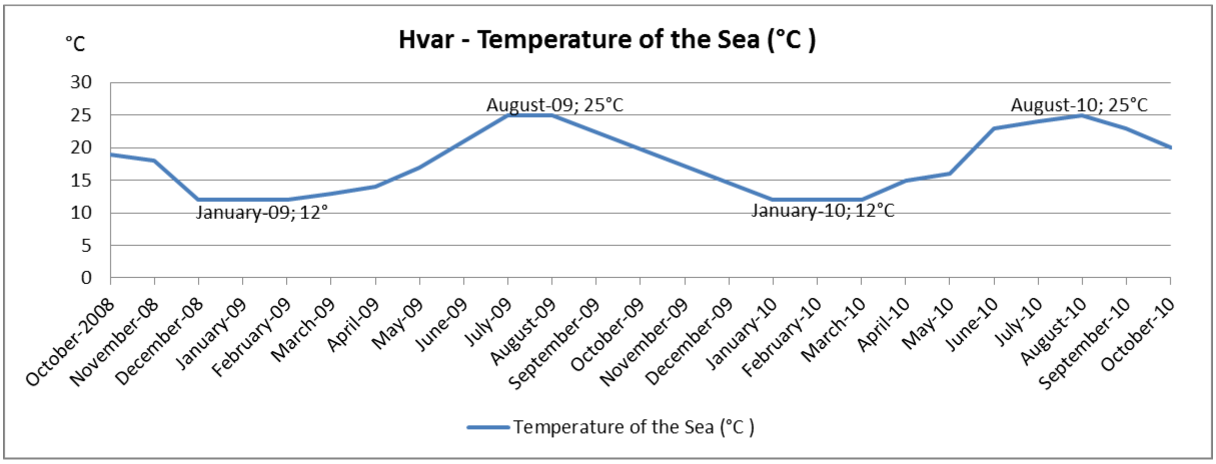


Figure 89. Temperature of the sea water (°C) at station Hvar from October 2008 to October 2010.

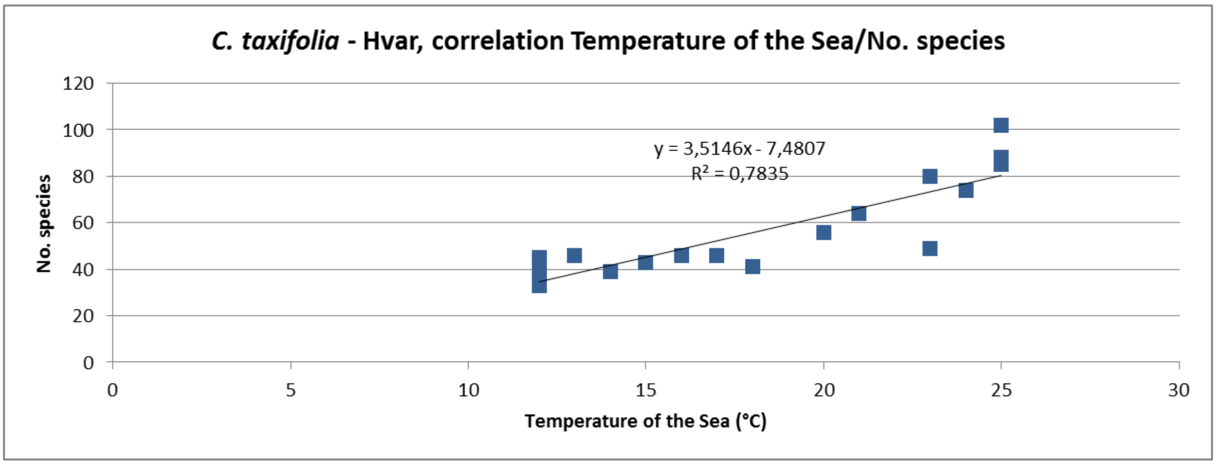


Figure 90. The number of taxa recorded on *C. taxifolia* from island of Hvar is presented in relation to sea water temperature.

Over the research period, sea water temperature showed no significant variation between years ranging from 12°C in January to 25°C in August. A strong and significant correlation between the number of epiphytic taxa on *C. taxifolia* and sea water temperature was observed (Figure 90).

Summer and autumn seasons in 2009 and 2010 showed similarities both in terms of high number of taxa and in species composition of epiphytic diatoms on *C. taxifolia*. The diatom assemblage was characterized by the abundance of a tiny *Cocconeis caulerpacola*, particularly during summer and autumn (e.g. up to 63% in October 2009 and 40% in October 2010). Although the number of *Cocconeis* taxa was quite small at 20, the genus itself comprised the dominant group of epiphytes on the investigated macroalga *C. taxifolia* particularly during summer and autumn with the significant contribution of *C. caulerpacola*.

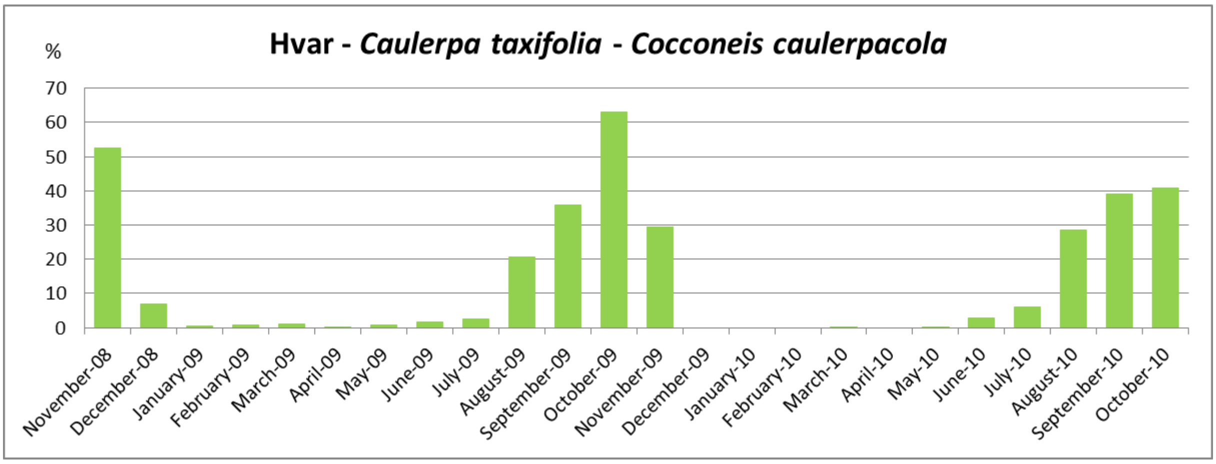


Figure 91. Seasonality of *Cocconeis caulerpacola*.

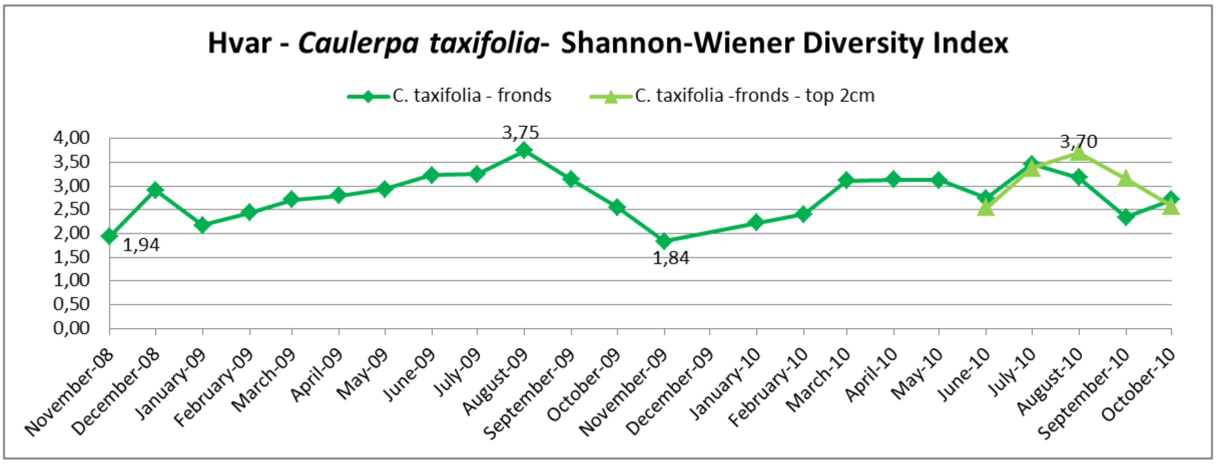


Figure 92. Shannon-Wiener Biodiversity Index of diatom community on Caulerpa taxifolia.

To examine the taxa richness of epiphytic diatom assemblages on *C. taxifolia* at the Hvar sampling site, *H'* (Shannon-Wiener Biodiversity Index) values were computed. The highest value of Shannon-Wiener Biodiversity Index of the epiphytic diatoms on C. taxifolia at the island of Hvar was recorded in August 2009 and amounted to 3.75. In August 2010 its value was almost the same at 3.70 for the upper 2 cm of *Caulerpa taxifolia* fronds, while for the rest of the *Caulerpa taxifolia* thallus its value was slightly lower. In June, July and October 2010 values of Shannon-Wiener Biodiversity Index for the upper 2 cm of *Caulerpa taxifolia* fronds were almost the same as for the rest of the thallus. In November 2009, the value of Shannon-Wiener Biodiversity Index for *Caulerpa taxifolia* was lowest at 1.84. A similarly low value (1.94) occurred in November 2008.

3.3.5.3.1. Seasonal distribution of epiphytic diatoms on *C. taxifolia* fronds

In order to perform a detailed analysis of epiphytic diatom assemblages of fronds of *Caulerpa taxifolia* and to describe the seasonal dynamics of epiphytic diatoms on *Caulerpa taxifolia* on a fine time scale, the top 2cm of *Caulerpa taxifolia* fronds from Island of Hvar were cut and prepared for diatom analysis for the summer and autumn seasons of 2010 (see Figure 12).

Scanning electron photomicrographs demonstrated the presence of diatoms adhering to the surface of the investigated macroalgae. Altogether, 137 diatom taxa belonging in 42 diatom genera were identified as epiphytes on the upper 2 cm of *C. taxifolia* fronds. The genus with the highest number of taxa was *Mastogloia* (29), followed by *Amphora* (18), *Nitzschia* (14), *Cocconeis* (9) and *Navicula* (7).

The number of taxa on the top 2cm of *Caulerpa taxifolia* fronds increased from June to August, with the lowest in June (41) and the highest in August (88). On the contrary, the highest numbers of taxa on *Padina pavonica* and *Halimeda tuna* were observed in September (82 and 67 respectively).

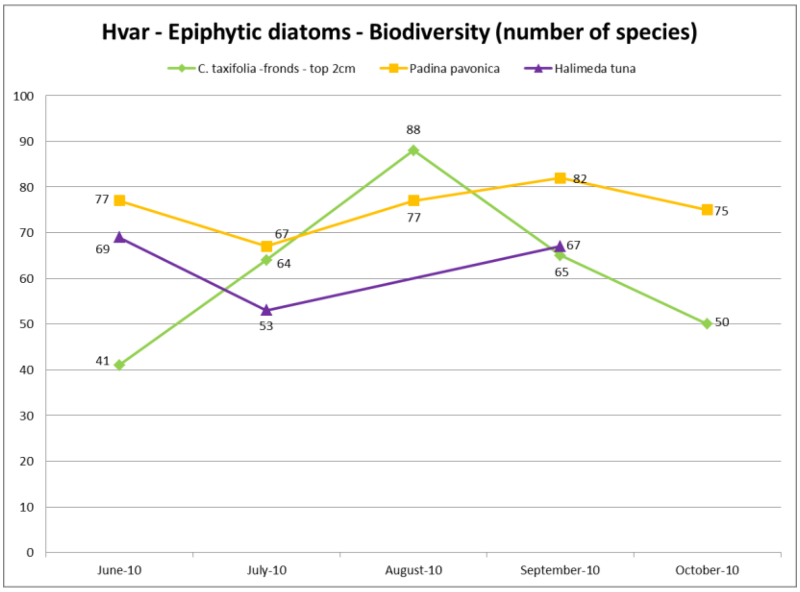


Figure 93. Number of diatom taxa epiphytic on young *Caulerpa taxifolia* fronds, *Padina pavonica* and *Halimeda tuna* from June to October 2010.

The widest (2.54–3.70) range of Shannon-Wiener Biodiversity Index was shown on *Caulerpa taxifolia*, with the minimum in June and maximum in August. Generally, there was no clear difference in taxa richness on *Padina pavonica* (3.10–3.84) and *Halimeda tuna* (3.04–3.39) from June till October.

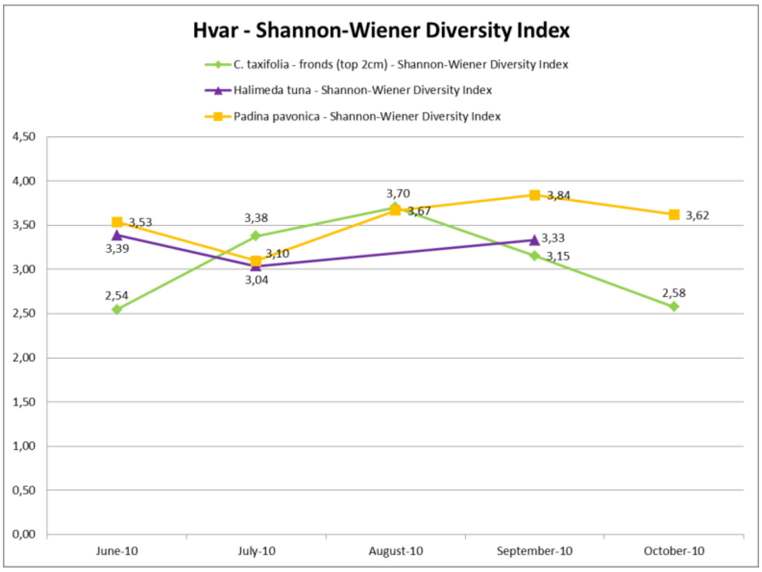


Figure 94. Values of Shannon-Wiener Biodiversity Index for epiphytic diatom samples on *Caulerpa taxifolia*, *Padina pavonica* and *Halimeda tuna* during summer and autumn 2010 on the island of Hvar.

The reason for a low Shannon-Wiener Biodiversity Index in June and October 2010 was the high abundance (>40%) of genus *Cocconeis* which occurred with a low number of taxa.

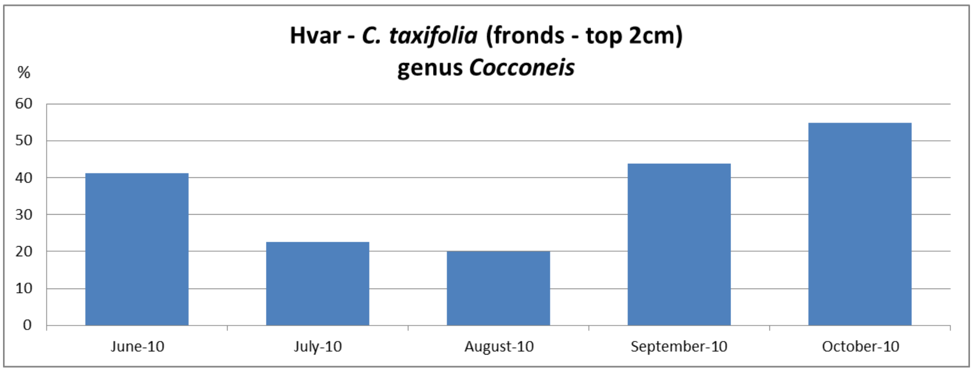


Figure 95. Abundance (%) of genus *Cocconeis* on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

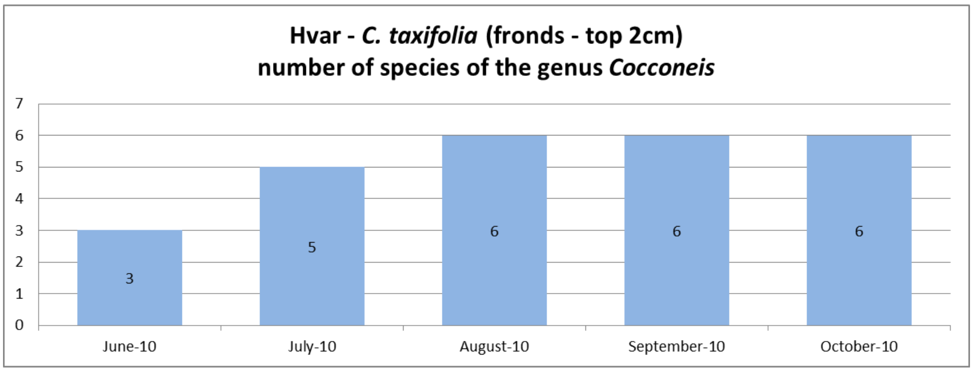


Figure 96. Number of *Cocconeis* taxa on young parts of *Caulerpa taxifolia* fronds.

Cocconeis molesta var. *crucifera* and *Cocconeis scutellum* var. *scutellum*, which were initially the main fouling component occurring as patches, declined in July, to be replaced by *Cocconeis caulerpacola*, the latter species being dominant during autumn.

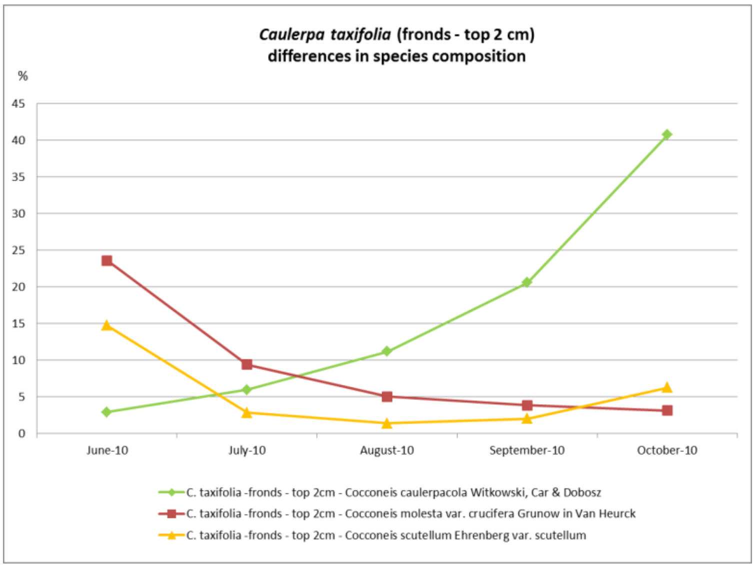


Figure 97. The contribution of particular *Cocconeis* taxa to the epiphytic diatom community on *Caulerpa taxifolia* investigated during summer and autumn 2010.

Due to high abundance of *Cocconeis caulerpacola* in September, maxima in the number of taxa observed in this month on *Caulerpa taxifolia* were replaced by those on *Padina pavonica*.

As illustrated in Figure 98, no correlation between abundance of *Cocconeis caulerpacola* and sea water temperature was confirmed.

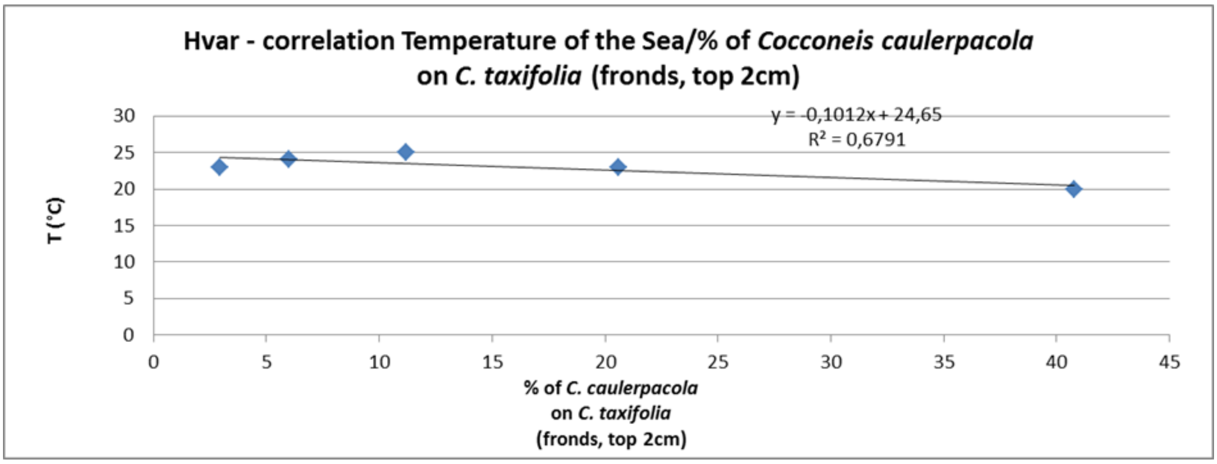


Figure 98. The average abundance of *Cocconeis caulerpacola* on *Caulerpa taxifolia* from island of Hvar is presented in relation to sea water temperature. N = 5.

Table 41 lists 22 dominant taxa which were the most abundant among the epiphytic diatom assemblage on *C. taxifolia* fronds. They dominated in terms of both frequency of appearance (>40%) and abundance in total number of samples (>1%). When combined together in a single sample, these 22 dominant taxa contribute from 70% to 87% in abundance.

Table 41. Dominant diatom taxa on upper 2cm of *Caulerpa taxifolia* fronds with an average abundance (Avg.) > 1 % and frequency of appearance (Freq.) > 40% in summer and autumn 2010. N = 5.

***Caulerpa taxifolia* - fronds (2cm) - dominant taxa:**	**Freq. (%)**	**Avg. (%)**
Amphora helenensis Giffen	60.00%	2.05%
Ardissonea fulgens (Greville) Grunow	100.00%	1.54%
Berkeleya scopulorum (Brébisson) Cox	80.00%	1.13%
Cocconeis caulerpacola Witkowski, Car & Dobosz	100.00%	16.31%
Cocconeis cf. *scutellum* Ehrenberg	80.00%	6.25%
Cocconeis molesta var. *crucifera* Grunow in Van Heurck	100.00%	9.01%
Cocconeis scutellum Ehrenberg var. *scutellum*	100.00%	5.47%
Hyalosynedra laevigata (Grunow) Williams & Round	100.00%	14.44%
Licmophora remulus Grunow	80.00%	1.88%
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	100.00%	2.59%
Mastogloia crucicula var. *alternans* Zanon	100.00%	2.02%
Mastogloia cuneata (Meister) Simonsen	80.00%	1.69%
Mastogloia pseudolatecostata Yohn & Gibson	80.00%	3.23%
Mastogloia spec. (Ico.Diat.Vol.7, Pl. 75 Figs 7-9)	80.00%	1.52%
Navicula arenaria Donkin var. *arenaria*	80.00%	3.38%
Navicula ramosissima (Agardh) Cleve	60.00%	1.55%
Navicula subagnita Proschkina-Lavrenko	40.00%	1.88%
Nitzschia angularis W. Smith	100.00%	1.37%
Nitzschia lanceolata var. *minima* Grunow	100.00%	2.96%
Nitzschia panduriformis Gregory var. *panduriformis*	100.00%	2.61%
Opephora cf. *pacifica* (Grunow) Petit	60.00%	1.57%
Toxarium undulatum Bailey	100.00%	1.57%

The following taxa, characteristic of summer and autumn on *C. taxifolia* fronds (2cm), occurred in all five samples with an average abundance >1%: *Cocconeis caulerpacola*, *Hyalosynedra laevigata*, *Cocconeis molesta* var. *crucifera*, *Cocconeis scutellum* var. *scutellum*, *Nitzschia lanceolata* var. *minima*, *Nitzschia panduriformis* var. *panduriformis*, *Mastogloia crucicula* var. *crucicula*, *Mastogloia crucicula* var. *alternans*, *Toxarium undulatum*, *Ardissonea fulgens* and *Nitzschia angularis*.

Comparison of the preceding list of 25 dominant taxa on *Caulerpa taxifolia* in general (Table 35) with the list above of the most abundant taxa on the upper 2cm i.e. the younger parts of *Caulerpa taxifolia* fronds (Table 41), revealed some differences in species composition. A group composed of *Amphora acutiuscula*, *Cocconeis costata* var. costata, *Fragilaria investiens*, *Grammatophora oceanica*, *Mastogloia fimbriata* and *Tabularia* *ktenoeoides* belonging to the dominants on *C. taxifolia* are absent from the dominants on young parts of *C. taxifolia*. Instead of *Licmophora gracilis* var. *gracilis* on young parts of *C. taxifolia* fronds another taxon of *Licmophora*, *L*. remulus was dominant. In addition, some taxa, like *Navicula subagnita* Proschkina-Lavrenko and *Opephora* cf. *pacifica* (Grunow) Petit, were dominant on young parts but were not among the dominants on *C. taxifolia*.

In the case of taxa which occurred on both lists of dominants some differences in frequency of appearance and abundance were observed. Frequency of occurrence of *Cocconeis scutellum* var. *scutellum* was equal on young and on other parts of *C. taxifolia*, but its abundance was subject to significant variation. While generally on *C. taxifolia*, *Cocconeis scutellum* var. *scutellum* achieved an abundance of 15%, on the young parts of the fronds its abundance was threefold lower at 5%. On the contrary *Cocconeis caulerpacola* occurred in all samples of young *Caulerpa taxifolia* fronds with an abundance of 16%, while in general on *Caulerpa taxifolia* it was observed with an abundance of 14% and with lower frequency of occurrence (76%).

In some cases frequency of occurrence was the same irrespective of the development stage of the host, but abundance was variable. For example *Hyalosynedra laevigata* reached higher abundance (14%) on young parts versus 10% in general abundance on *Caulerpa taxifolia*. Others e.g. *Navicula arenaria* var. *arenaria* were more often observed and with higher abundance on young parts of *Caulerpa taxifolia* than on *Caulerpa taxifolia* in general.

A very few taxa e.g. *Cocconeis molesta* var. *crucifera*, occurred with the same frequency of appearance and abundance on all parts of *Caulerpa taxifolia*. These taxa showed no significant difference in frequency of appearance and abundance between different parts of the *Caulerpa taxifolia* thallus. *Mastogloia crucicula* var. *crucicula*, *Mastogloia crucicula* var. *alternans* and *Mastogloia cuneata* were in this group. Generally *Mastogloia crucicula* var. *crucicula* and *Mastogloia crucicula* var. *alternans* occurred in 96-100% samples of *Caulerpa taxifolia* with an abundance of 2%. *Mastogloia cuneata* occurred in 72%-80% samples of *Caulerpa taxifolia* with an average abundance of 1.5%.

Diatom colonization on *Caulerpa taxiofolia* fronds during summer and autumn revealed, however, that colonial forms in mucilage tubes (genus *Mastogloia*) belong to the dominants in the fouling community. In July and August 2010, *Mastogloia* spp. occurred in high abundance (>20%) and with high numbers of taxa on young parts of *Caulerpa taxifolia* fronds thus contributing to high value of Shannon-Wiener Biodiversity Index (Figure 99,

Figure 100).

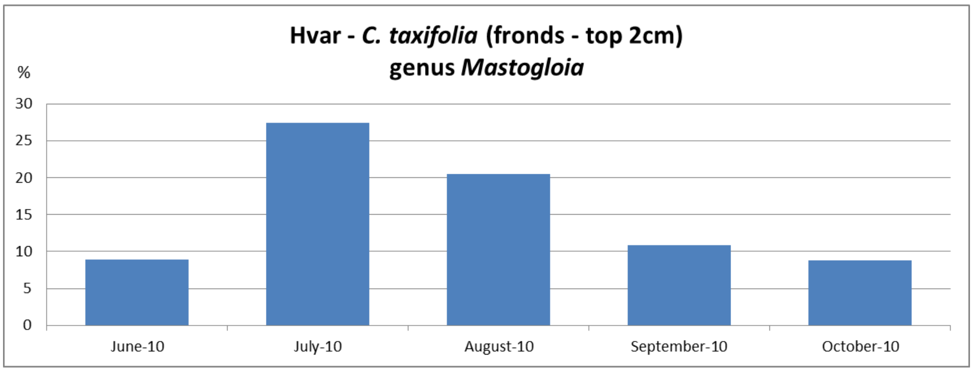


Figure 99. Abundance (%) of *Mastogloia* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

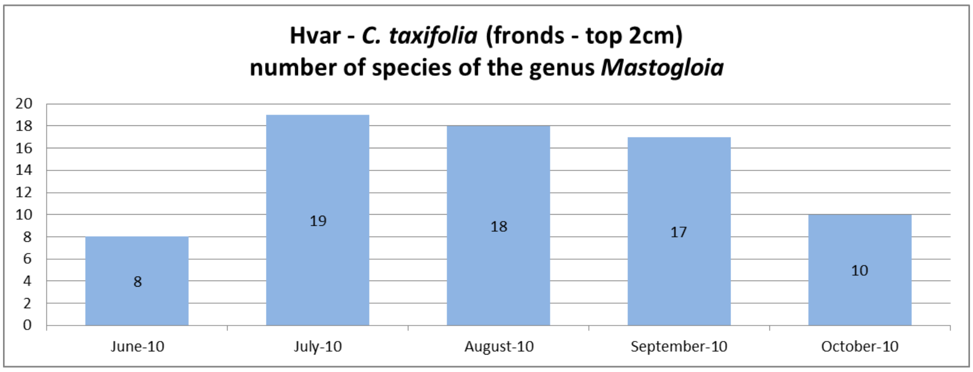


Figure 100. Number of *Mastogloia* taxa on young parts of *Caulerpa taxifolia* fronds.

Of 19 *Mastogloia* taxa identified in July 2010, the most abundant was *Mastogloia crucicula* var. *crucicula*, followed by *Mastogloia crucicula* var. *alternans* and *Mastogloia cuneata* (Figure 102). Although *Mastogloia binotata* occurred in all five samples of young parts of *Caulerpa taxifolia* fronds, with highest abundance (1%) observed in July, the average abundance amounted only to 0.6% and thus *Mastogloia binotata* is not included in the list of dominant taxa of young *Caulerpa taxifolia* fronds. In June 2010 on young parts of *Caulerpa taxifolia* fronds only three taxa of *Mastogloia*, i.e. *M. crucicula* var. *crucicula*, *M. crucicula* var. *alternans* and *M. cuneata*, together constituted 73% of the total abundance of *Mastogloia* taxa, thereby contributing to a low value of Shannon-Wiener Biodiversity Index (Figure 101).

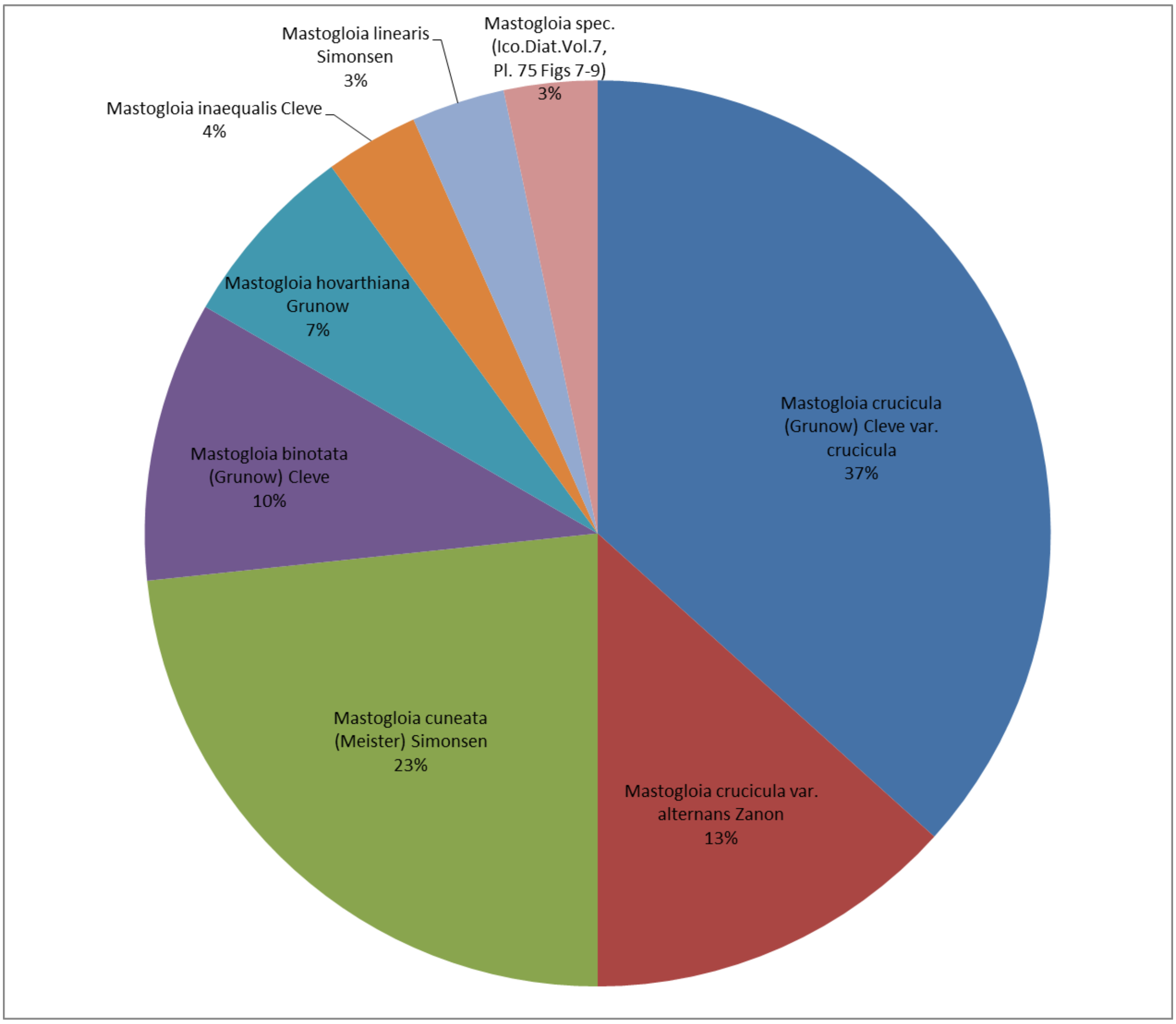


Figure 101. Relative percentage contribution of particular *Mastogloia* taxa on young parts of *Caulerpa taxifolia* fronds in June 2010.

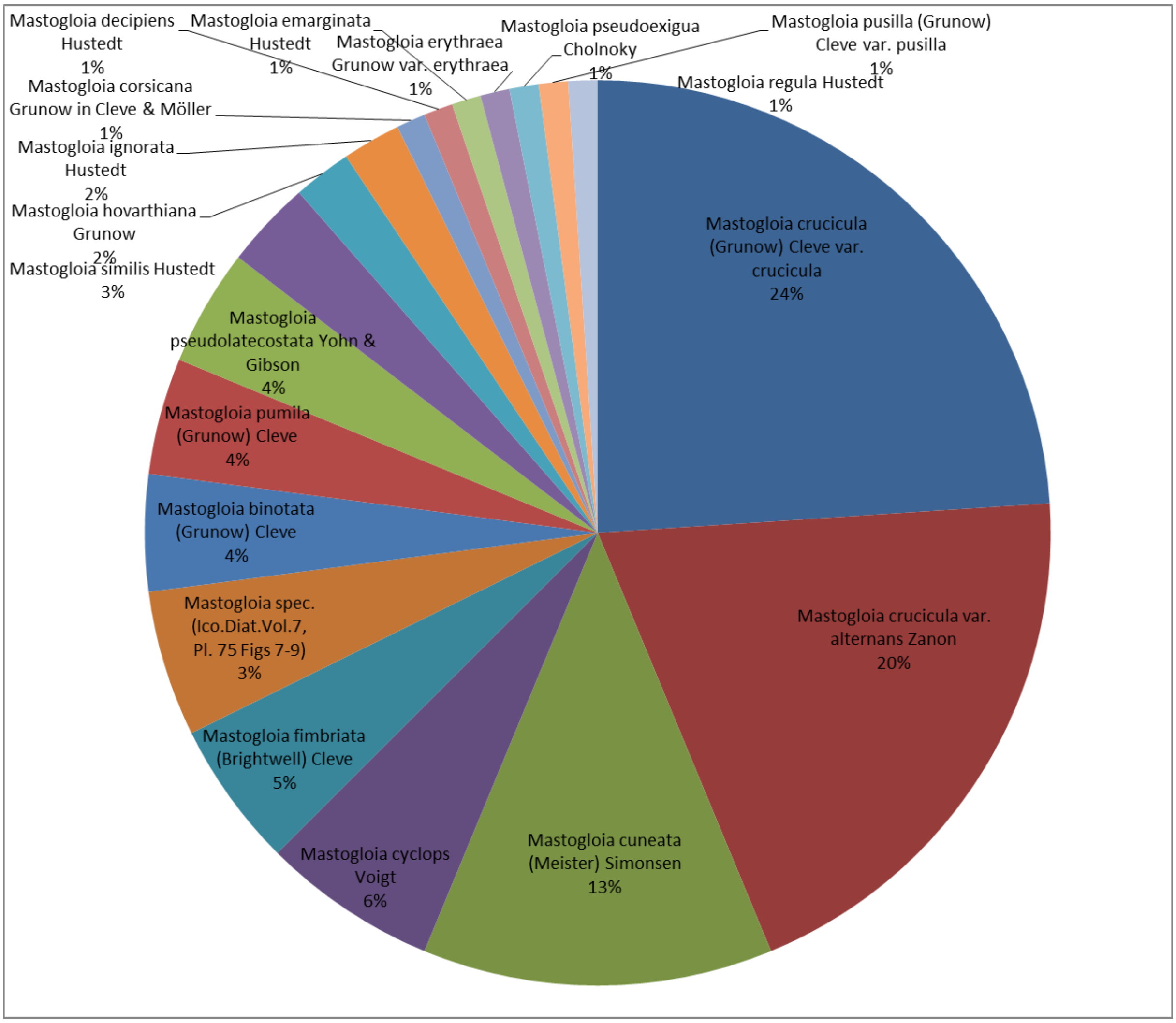


Figure 102. Relative percentage contribution of particular *Mastogloia* taxa on young parts of *Caulerpa taxifolia* fronds in July 2010.

Table 42. Occurrence of different taxa of genus *Mastogloia* on young parts of *Caulerpa taxifolia* fronds from June till October 2010 ("+" = present; " "=indicates that the taxon was not observed in the sample).

Species of genus *Mastogloia* :	**June-10**	**July-10**	**August-10**	**September-10**	**October-10**
Mastogloia (Pl. 75 Fig. 7-9)	+	+	+	+	
Mastogloia (Pl. 82 Fig. 13, 14)			+		
Mastogloia baldjikiana Grunow			+		
Mastogloia binotata (Grunow) Cleve	+	+	+	+	+
Mastogloia borneensis Hustedt			+	+	
Mastogloia cf. *cyclops* Voigt				+	
Mastogloia cf. *laminaris* Grunow				+	+
Mastogloia cf. *varians* Hustedt				+	
Mastogloia corsicana Grunow in Cleve & Möller		+	+		+
Mastogloia crucicula (Grunow) Cleve var. *crucicula*	+	+	+	+	+
Mastogloia crucicula var. *alternans* Zanon	+	+	+	+	+
Mastogloia cuneata (Meister) Simonsen	+	+	+		+
Mastogloia cyclops Voigt		+	+		+
Mastogloia decipiens Hustedt		+	+	+	
Mastogloia delicatissima Hustedt			+		
Mastogloia emarginata Hustedt		+		+	+
Mastogloia erythraea Grunow var. *erythraea*		+			
Mastogloia fimbriata (Brightwell) Cleve		+	+	+	
Mastogloia hovarthiana Grunow	+	+	+	+	
Mastogloia ignorata Hustedt		+	+	+	
Mastogloia inaequalis Cleve	+				
Mastogloia linearis Simonsen	+				
Mastogloia pisciculus Cleve				+	
Mastogloia pseudoexigua Cholnoky		+			
Mastogloia pseudolatecostata Yohn & Gibson		+	+	+	+
Mastogloia pumila (Grunow) Cleve		+			
Mastogloia pusilla (Grunow) Cleve var. *pusilla*		+	+	+	+
Mastogloia regula Hustedt		+			
Mastogloia similis Hustedt		+	+	+	
TOTAL :	**8**	**19**	**18**	**17**	**10**

The distribution of dominant genera abundances over time showed that the majority of these genera reached high abundances in July and in August (Figure 103 - Figure 109). An exception was *Cocconeis* with the lowest abundances in July and August and the highest in October. Average abundance of *Hyalosynedra* declined from 25% in June to 8% in October, whereas *Amphora* reached increased abundances at the beginning of autumn.

Analysis of the succession of diatoms during colonization of *Caulerpa taxiofolia* fronds during summer and autumn showed that colonial tube dwelling forms e.g. *Berkeleya* taxa and *Navicula ramosissima*, belonged to dominants of the fouling community. No significant difference in abundance of *Navicula* taxa was noted during this study period (Figure 104). In the case of *Berkeleya* taxa an interesting switch in species composition during August and September was observed (Figure 108). Abundance of *Berkeleya scopulorum*, initially the only fouling component of *Berkeleya* decreased in the end of summer and at the beginning of autumn was replaced by *Berkeleya rutilans.*

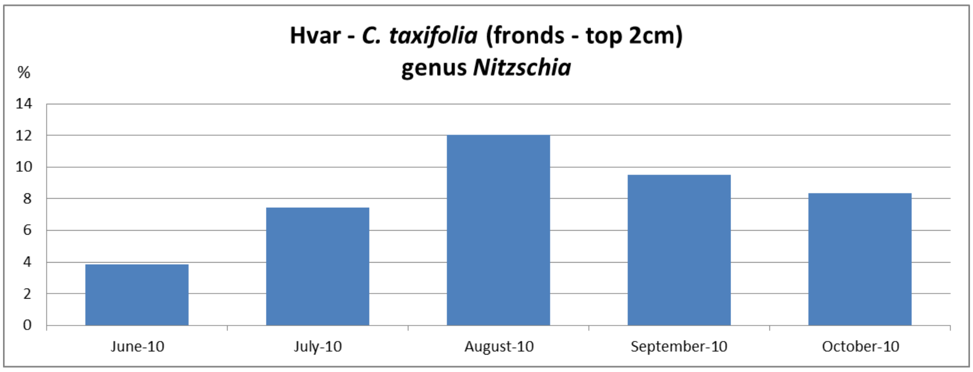


Figure 103. Abundance (%) of *Nitzschia* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

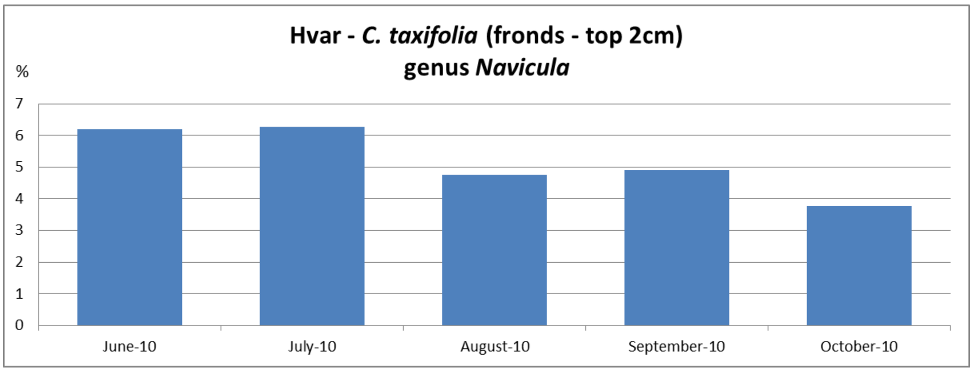


Figure 104. Abundance (%) of *Navicula* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

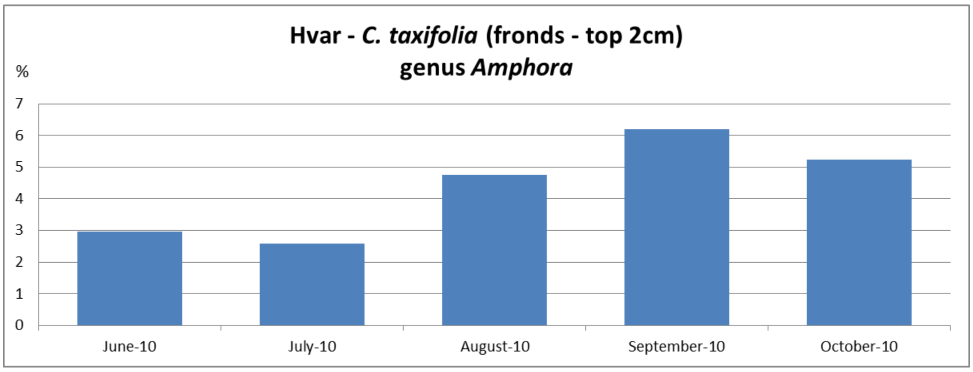


Figure 105. Abundance (%) of *Amphora* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

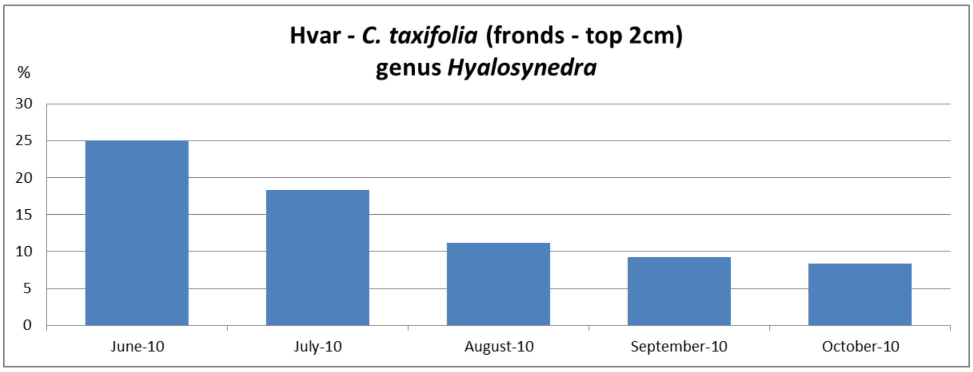


Figure 106. Abundance (%) of genus *Hyalosynedra* on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

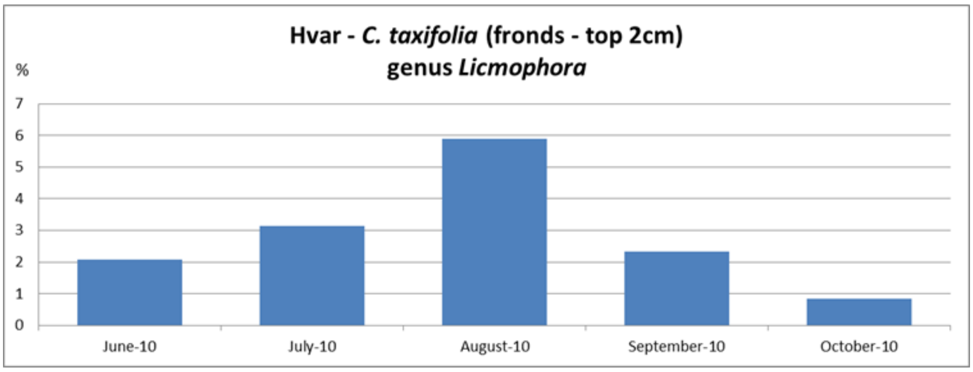


Figure 107. Abundance (%) of *Licmophora* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

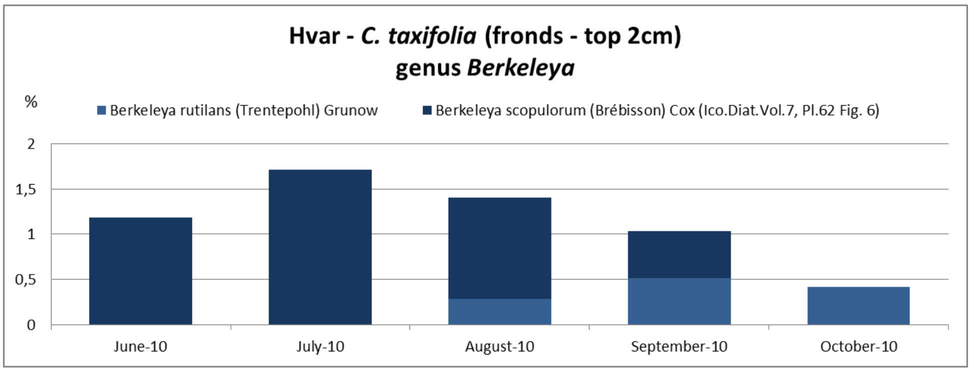


Figure 108. Abundance (%) of *Berkeleya* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

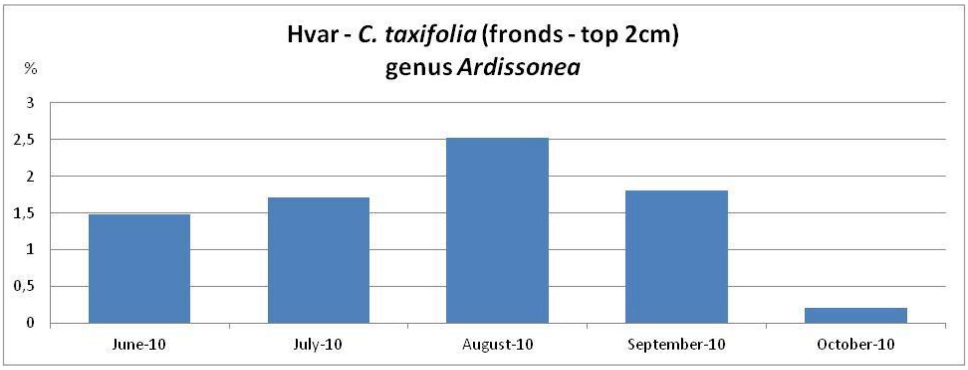


Figure 109. Abundance (%) of *Ardissonea* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

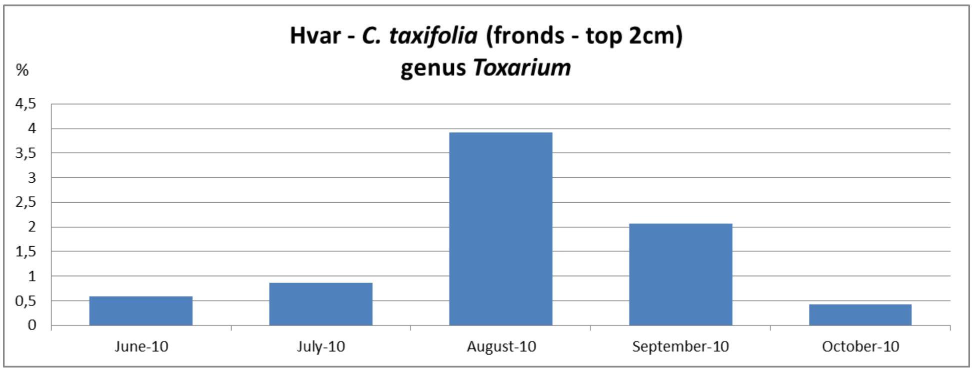


Figure 110. Abundance (%) of *Toxarium* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

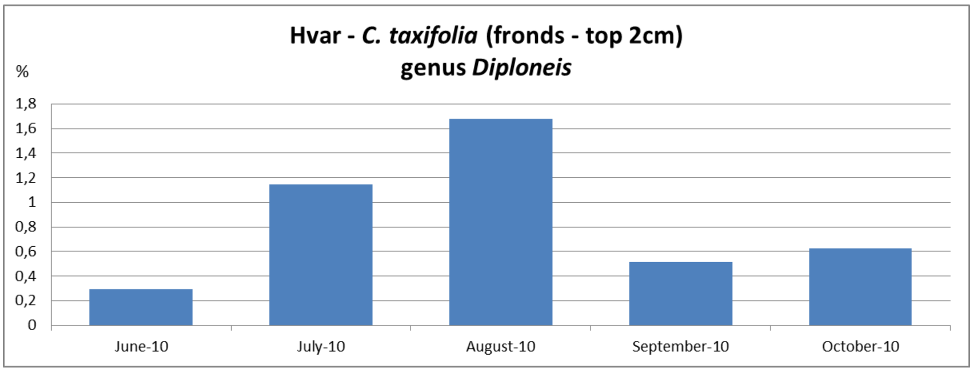


Figure 111. Abundance (%) of *Diploneis* taxa on young parts of *Caulerpa taxifolia* fronds from June till October 2010.

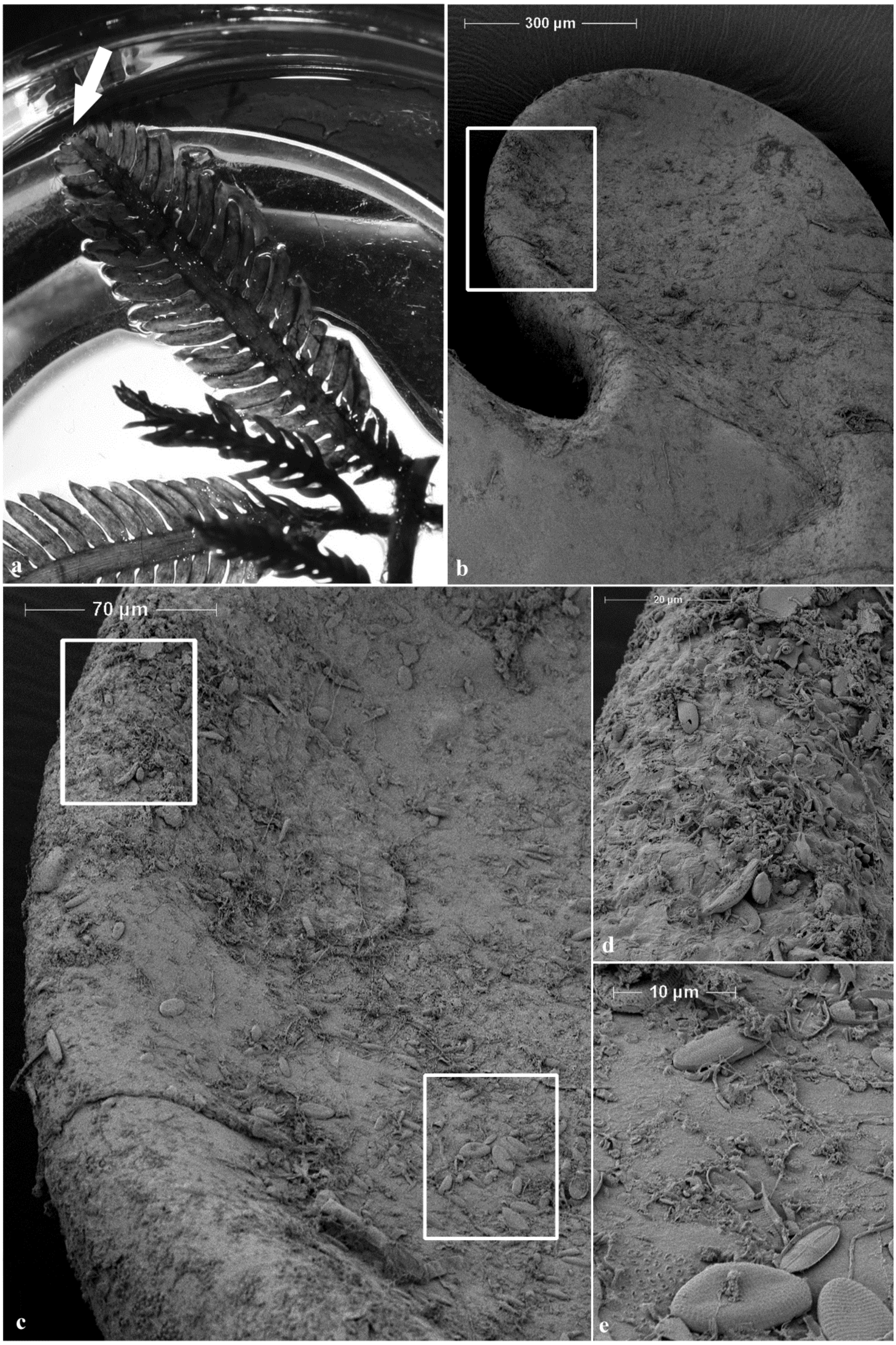


Figure 112. SEM images of the young part of thallus of *Caulerpa taxifolia*. (c) Close-up view of figure (b). (d) Specimens of *Amphora* sp. and *Cocconeis* sp. (e) A rich assemblage of small *Cocconeis caulerpacola* together with larger *Cocconeis* sp.

3.3.5.4. Analysis of the epiphytic diatom community on *C. taxifolia* from various localities

Epiphytic diatom communities on *Caulerpa* species from this study were compared with communities reported in earlier research. The major aim of the comparison was to provide information about host-dependence, particularly because of the existence of toxins characteristic for *Caulerpa* taxa. To perform the comparison the Bray-Curtis similarity method was applied to a diverse set of subsamples taken from France and Croatia. Subsamples originated from the fronds, stolons with rhizoids, water in which *Caulerpa taxifolia* specimens were washed and water squeezed from *Caulerpa taxifolia* samples. Bray-Curtis analysis of similarity prepared for both sites (France and Croatia) showed two distinct clusters, though the level of similarity amounted to only ca. 50%. The least degree of similarity was shown in subsamples from water squeezed from the thalli of French specimens.

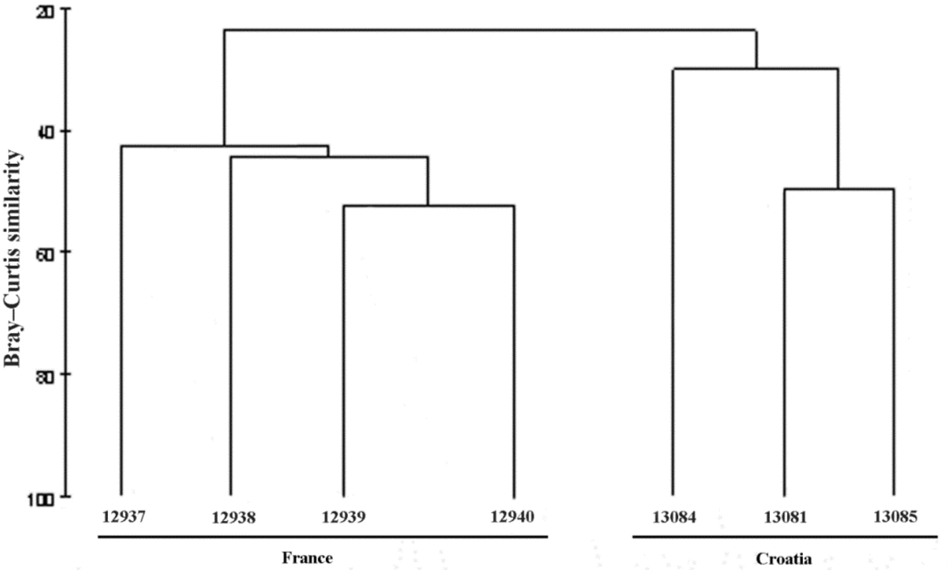


Figure 113. Similarity dendrogram based on abundance of diatom taxa between two sites with introduced *Caulerpa taxifolia* (France and Croatia, for details see Table 7).

The dominant taxon *Cocconeis caulerpacola* was found to be growing both on invasive Mediterranean and Croatian specimens of *Caulerpa taxifolia*. In general taxa belonging to *Cocconeis* comprised the dominant group of epiphytes on the investigated macroalga. Our estimates of its abundance indicated 2000-11000 specimens inhabiting 1 mm^2 on *Caulerpa taxifolia* from Croatia and 4000-11500 (with a maximum of 15000) in 1 mm^2 on *Caulerpa taxifolia* from France.

In *Caulerpa taxifolia* collected off the coast of France much higher diatom abundances were observed in which adnate forms (*Cocconeis* spp. and *Mastogloia* spp.) dominated. The genus *Cocconeis* in addition to strongly dominant *C. caulerpacola* was represented by some other taxa which, while of lower abundance, were easily observed either in samples processed with hydrogen peroxide or in situ dried in liquid carbon dioxide. Included in this group were *C. neothumensis* var. *marina* De Stefano, Marino et Mazilla, *C. scutellum* Ehrenberg var. *scutellum*, *Cocconeis molesta* Kutzing var. *molesta*, *C. molesta* var. *crucifera* Grunow in Van Heurck and *C. dirupta* Gregory var. *dirupta*. Interestingly *Cocconeis scutellum* var. *posidoniae* De Stefano, Marino & Mazzella was also observed (Figures 3d-f; 4 and 11e). This species was originally described from *Posidonia oceanica* leaves and occurred on *C. taxifolia* as well. This is interesting because *C. taxifolia* is competing for space with *Posidonia oceanica*. The relative abundance of other *Cocconeis* taxa did not exceed 2 %.

The second most abundant were taxa belonging to *Mastogloia* represented by e.g. *M. binotata* (Grunow) Cleve (Figure 6d), *M. fimbriata* (Brightwell) Cleve, *M. cuneata*, *M. crucicula* var. *alternans, M. crucicula* var. *crucicula, M. inaequalis* Cleve, *M. ovalis* A. Schmidt and *M. ovulum* Hustedt. In Croatia, the group of taxa with higher abundances also included *Berkeleya fennica* Juhlin-Dannfelt and *Berkeleya rutilans* (Trentepohl) Grunow. The latter taxon, at least, is well known as a tube dweller. However, in general the abundant taxa, with the exception of the recently described *Cocconeis caulerpacola* Witkowski, Car *et* Dobosz, are well known in diatomological literature as epiphytes. The relative abundance of particular *Mastogloia* taxa only rarely exceeded 2%. The third most abundant was genus *Navicula* with *N. ramosissima*, *N. subagnita* and some undetermined taxa. *Navicula ramosissima* achieved the highest relative abundance amongst them amounting to ca. 5 %.

The result of the similarity analysis shows that despite different geographic locations, *C. taxifolia* hosts similar diatom assemblages. This similarity results from the dominance of a small, previously unobserved *Cocconeis* taxon mentioned above as recently-described *C. caulerpacola* which in processed material accounted for 67% of the relative diatom abundance in France and 26.5% in Croatia (counted under LM). Our study also confirmed the occurrence of *C. caulerpacola* on *Caulerpa taxifolia* from Moreton Bay in East Australia. However, detailed comparisons of diatom assemblages which we have so far been able to perform for the two Mediterranean localities, i.e. France and Croatia, show two distinct clusters. The comparisons were based on LM countings of hydrogen peroxide processed samples.

4. DISCUSSION

The main objective of this thesis was to determine the taxonomic composition of epiphytic diatoms on invasive macroalgae (*Caulerpa taxifolia* and *Caulerpa racemosa*) and on autochthonous algae (*Padina pavonica* and *Halimeda tuna*) in an area inhabited by *Caulerpa* spp, in the Dalmatian coast of the Adriatic Sea. To have an idea about the specificity of the diatom assemblages on killer seaweed, *C. taxifolia* samples from St. Raphael in France and from Moreton Bay in Australia, presumably origin site of the so called aquarium strain were examined as well.

The present investigation of three locations in Adriatic Sea between autumn 2008 and autumn 2010 confirmed expected differences in taxonomic composition of epiphytic diatoms between selected autochthonous algae and invasive algae of *Caulerpa* and between *Caulerpa* species.

Similar numbers of taxa were recorded in epiphytic diatom community of the investigated autochthonous brown macroalga *Padina pavonica* and green alga *Halimeda tuna* on the one hand (257), and on the other on invasive *Caulerpa racemosa* and *Caulerpa taxifolia* (370). The largest number of taxa (379) was found on *Caulerpa taxifolia*, and the lowest (243) on *Halimeda tuna*. This seems to imply that invasive algae do not reduce biodiversity.

The MDS analysis of samples with epiphytic diatom abundances clearly showed differences in species composition. The epiphytic diatoms formed two distinct groups which were related to the two groups of substrates studied. In one group epiphytic diatoms clustered on invasive algae *Caulerpa taxifolia* and *Caulerpa racemosa*, whereas in the second one on autochthonous macroalgae, *Halimeda tuna* and *Padina pavonica*. The similarity between the two groups did not exceed 20%. The diatom assemblage on brown alga *Padina pavonica* was characterized by high abundances of taxa representing *Mastogloia*, *Nitzschia*, *Cocconeis*, *Navicula*, *Amphora*, *Hyalosynedra* and *Licmophora*. Epiphytic communities of genus *Licmophora* on *Padina* appeared to be more similar to those on *Caulerpa taxifolia* than to those on the other investigated autochthonous alga *Halimeda tuna*. *Halimeda tuna* hosts a diatom assemblage dominated by representatives of *Cocconeis*, *Mastogloia*, *Navicula*, *Nitzschia* and *Amphora*. The diatom assemblage on *Caulerpa taxifolia* was characterized by high abundances of *Cocconeis*, *Hyalosynedra*, *Mastogloia*, *Nitzschia*, *Navicula*, *Amphora* and *Licmophora*. The dominant genera were roughly similar between the two *Caulerpa* taxa. The epiphytic diatom assemblages on thalli of both *Caulerpa* spp. were found to be largely dominated by taxa of the genus *Cocconeis.*

A few of the diatom taxa recorded during the present experiments were found throughout the whole year, while most of them exhibited an uneven, scattered distribution pattern. During winter, fewer taxa were observed. Several taxa were found as initial colonizers during spring, but most taxa appeared during summer when the sea water reached annual temperature maxima. For example, some taxa of *Mastogloia* appeared only in particular seasons and the highest number of these was recorded in autumn and summer at all sampling sites. *Mastogloia* which is very rich in number of taxa (>60) and had a high frequency of appearance which contributed strongly to a high value of Shannon-Wiener Biodiversity. Whereas genus *Mastogloia* reached high abundances during summer and autumn, *Cocconeis*, the second most abundant genus in this study, was represented by a much lower number of taxa (29) and reached high abundances during winter and spring. Taxa reaching high abundance in spring also included *Licmophora*, represented in this study by only 13 taxa. A consequence of this was the fact that, at all three locations, generally, values of Shannon-Wiener Biodiversity Index were lower from January till March and higher from August till October. This is in agreement with study of seasonal fouling by diatoms on artificial substrata in the Gulf of Trieste in which the maximum number of colonizing diatom taxa was also found in autumn, between August and October, at 7 m depth (Munda, 2005). These studies are comparable because although the previous study was carried out on concrete plates the depths of both were almost the same.

The maximum number of taxa of genus *Mastogloia* was observed on the island of Hvar. The very high number of *Mastogloia* taxa on Hvar seems to be related to the much higher number of samples collected in this area (65) compared to other locations. The average number of *Mastogloia* taxa found in a sample of *Caulerpa taxifolia* amounted to 10.46. The abundance of *Mastogloia* taxa on *Caulerpa taxifolia* was quite low with only 5 species of this genus present among the 25 dominant taxa on *Caulerpa taxifolia.* On *Caulerpa racemosa* just 4 *Mastogloia* taxa are among the most dominant. On *Halimeda tuna* again five of 25 dominant taxa belonged to *Mastogloia*. In general all of them occurred with higher abundances at the Dubrovnik and island of Mljet (*Caulerpa racemosa*) sampling sites than on the island of Hvar (*Caulerpa taxifolia*). Although the maximum number of *Mastogloia* taxa in one sample was recorded in a sample of *Caulerpa racemosa,* further studies of this genus should not be focused on *Caulerpa racemosa* as a host because average number of taxa in one sample of *C. racemosa* amounted to only 8.58 on the island of Mljet and to 9.11 in

Dubrovnik. In contrast, on *Padina pavonica* 10 of 25 dominant taxa belonged to *Mastogloia*. Likewise the diversity of *Mastogloia* (with more than 40 taxa) on *Padina* was much higher than on any other macroalga studied here. Thus *Mastogloia* in this study could be considered as "typical *Padina*'s epiphytic genus". As *Mastogloia binotata*, *Mastogloia crucicula* var. *crucicula*, *Mastogloia crucicula* var. *alternans* and *Mastogloia pusilla* var. *pusilla* occurred in the epiphytic community of *Padina pavonica* with higher abundances (>4.5%) than at the *Caulerpa racemosa* sampling sites, the focus of further investigations should be on these areas. The average number of *Mastogloia* taxa per sample of *Padina pavonica* from the island of Mljet was 22.4, in Dubrovnik it was 20.6 and on Hvar 18.6. Generally, *Mastogloia* reached high abundance during summer and autumn. The maximum number (30) of *Mastogloia* taxa in one sample was recorded on the island of Mljet (sample of *Caulerpa racemosa*, September 2009). In *Halimeda tuna* samples the largest number of *Mastogloia* taxa (18) was observed in September and October. During autumn seven taxa (*Mastogloia binotata*, *Mastogloia crucicula* var. *alternans*, *Mastogloia crucicula* var. *crucicula*, *Mastogloia fimbriata*, *Mastogloia pusilla* var. *pusilla*, *Mastogloia cuneata*, *Mastogloia ovulum*) together contributed more than 60%, 40% and 20% to the total of epiphytic diatoms of *Halimeda tuna* at the Dubrovnik, Mljet and Hvar sampling sites respectively. Because the genus *Mastogloia* showed higher abundance and the highest number of taxa of during autumn, *Mastogloia* can be considered as an "autumn genus". These observations suggest that in a future investigation of genus *Mastogloia*, samples of *Padina pavonica* should be collected in areas under the influence of *Caulerpa racemosa,* particularly on the island of Mljet especially during summer and autumn.

For another of the investigated autochthonous macroalgae, *Halimeda tuna*, genus *Amphora* could be considered as common. *Amphora acutiuscula*, one of four *Amphora* taxa which are among 25 dominants on *Halimeda tuna*, occurred with average abundance of 3.3% reaching highest abundance of 5.4% during winter. *Amphora acutiuscula* occurred with highest abundances on the island of Hvar. *Amphora helenensis* occurred with average abundance of 2% during all seasons, whereas *Amphora* cf. *marina* W. Smith occurred with highest abundance during summer and autumn (1.6%) while during winter and spring its average abundance was 0.6%.

Of 25 taxa dominant on *C. racemosa*, three belong to *Licmophora*. *Licmophora gracilis* var. *gracilis* and *Licmophora paradoxa* occurred with the same frequency and both were identified in 74% of samples. The highest abundance of *Licmophora gracilis* var.

gracilis occurred during winter (9%). Generally it was found more often on the island of Mljet than in Dubrovnik. *Licmophora remulus* was also found on the island of Mljet but with its highest abundance during summer. Generally it was recorded in 46% of samples from *Caulerpa racemosa*. *Licmophora paradoxa* was found with equal abundances during all seasons and from both sampling sites. *Licmophora* cf. *pfannkucheae* and *Licmophora flabellata* were among the dominant taxa on fronds of *Caulerpa racemosa*. *Licmophora flabellata* is an erect form with typical fan-shaped colonies, attaching to the substrate through a single mucilaginous stalk extruded by the basal pole. This species has been recorded as one of the most abundant *Licmophora* taxa colonizing marine hydrozoid *Eudendrium racemosum*, occurring from autumn to spring, with higher density in spring, mainly in the upper part of colony under the polyp (Romagnoli et al., 2014).

While erect diatoms were represented mainly by *Licmophora* spp., *Grammatophora* spp. and *Tabularia ktenoeoides*, the most important adnate taxa observed on *Caulerpa* spp., *Padina pavonica* and *Halimeda tuna* belong to the genus *Cocconeis*. *Cocconeis scutellum* var. *scutellum* was generally the most abundant over all three locations (Dubrovnik, Mljet, Hvar) during the two year period (autumn 2008 – autumn 2010), with an average abundance of 12% on autochthonous and 25% on invasive seaweeds. Comparing the species composition of epiphytic diatoms on *Caulerpa* spp., *Padina pavonica* and *Halimeda tuna* with those in other studies of epiphytic (e.g. seaweeds, seagrasses, mangroves), epilithic (artificial hard substrata) and epizoic (marine invertebrates) diatoms (Romagnoli et al., 2014), the most common taxon on all substrata was *Cocconeis scutellum* with its varieties which seem to be the most ubiquitous and show no preference for either the geographic region or the type of substrate.

In addition to *Cocconeis scutellum* var. *scutellum*, the epiphytic diatoms fouling autochthonous algae were dominated by *Navicula ramosissima*. Average abundance of *N. ramosissima* on *Padina pavonica* and *Halimeda tuna* amounted to ca. 8.5% while on both investigated *Caulerpa* taxa it was ca. 4.5-5%. Because *Navicula ramosissima* showed higher abundance on autochthonous than on invasive algae, but showed no observed difference in abundance between investigated sampling sites, it is apparent that sampling sites had lower influence on the diatom assemblage composition than the characteristics of the host itself. *Navicula ramosissima* could be considered as a diatom typical for autochthonous macroalgae ("autochthonous taxon"). In general during all seasons abundance of *Navicula ramosissima* on invasive as well as on autochthonous algae was quite similar, with some higher abundances observed during spring and summer particularly on autochthonous algae. During summer, the epiphytic diatom assemblage on *Padina pavonica* was dominated by *Navicula ramosissima* and *Nitzschia fusiformis* with an abundance of 10% each. Likewise on *Halimeda tuna* its summer abundance was 12% with an average of 8% for remaining seasons. In general on *Halimeda tuna* during all seasons at all three sites *Navicula ramosissima*, *Cocconeis scutellum* var. *scutellum* and *Cocconeis molesta* var. *crucifera* were recorded as the most abundant taxa. No seasonal variation in abundance of *Navicula ramosissima* on *Caulerpa racemosa* was observed. On *Caulerpa taxifolia* higher abundance was noticed during spring. These observations suggest that *Navicula ramosissima* could be considered as diatom more typical for spring and summer ("spring/summer taxon") than for autumn and winter.

In addition to *Cocconeis scutellum* var. *scutellum*, dominant among the epiphytic diatoms fouling invasive algae were *Cocconeis molesta* var. *crucifera, Hyalosynedra laevigata* and *Cocconeis caulerpacola*. *Hyalosynedra laevigata* was found in greater abundance at the *Caulerpa taxifolia* sampling site than at *Caulerpa racemosa* sampling sites. On *Caulerpa taxifolia, Hyalosynedra laevigata* occurred with average abundance of 10%, while the abundances on all other investigated macroalgae were half of this (4-5%). On *Halimeda tuna* the highest abundance was recorded during summer and the lowest during spring. On another autochthonous algae *Padina pavonica* highest abundances were recorded during winter and spring (7-8%) and lower during summer and autumn. A value of 13% was calculated as a summer seasonal average abundance of *Hyalosynedra laevigata* on *Caulerpa taxifolia*. Generally higher abundances of *Hyalosynedra laevigata* on *Caulerpa taxifolia* were observed during summer and autumn with the highest value of 17% recorded in November 2008 and June 2010. While *Hyalosynedra laevigata* occurred in all samples of *Caulerpa taxifolia* with average abundance of 10%, it was found in 98% of samples of *Caulerpa racemosa* with average abundance of 4%. In *Caulerpa racemosa* samples its abundance was higher during summer and autumn and below average in winter and spring. The highest abundance on *Caulerpa racemosa* was observed in September 2009. The above observations may imply that *Hyalosynedra laevigata* can be described as "*Caulerpa taxifolia*'s taxon".

Cocconeis molesta var. *crucifera* was recorded in all 149 samples of this two year study. This species did not show particular seasonal distribution pattern and occurred with higher average abundance on invasive than on autochthonous algae. It was however the most common and most abundant taxon in *Caulerpa racemosa* samples. The abundance of *Cocconeis molesta* var. *crucifera* reached even higher values on fronds of *Caulerpa racemosa* than on thalli during all seasons. Therefore in this study *Cocconeis molesta* var. *crucifera* seems to be a “*Caulerpa racemosa* taxon*”*. The diatom assemblage of *Caulerpa racemosa* during February and March, when the lowest number of taxa was recorded, was characterized by high abundances of *Cocconeis scutellum* var. *scutellum and Cocconeis molesta* var. *crucifera*, together making up more than 63% and 81% of the total counts of samples with the lowest recorded number of taxa from Dubrovnik and Mljet respectively. Abundance of *Cocconeis molesta* var. *crucifera* on *Caulerpa taxifolia* and *Halimeda tuna* was similar, while on *Padina pavonica* its abundance was the lowest. On *Padina pavonica* and *Halimeda tuna Cocconeis molesta* var. *crucifera* reached highest abundance in winter. During autumn and winter on the island of Hvar, *Cocconeis molesta* var. *crucifera* occurred with higher abundance than on sampling sites under the influence of *Caulerpa racemosa*. During the winter *Cocconeis molesta* var. *crucifera* occurred with highest abundance on autochthonous *Padina pavonica* and *Halimeda tuna* and on thalli of *Caulerpa racemosa*. However, due to low sea water temperatures the number of *Caulerpa racemosa* specimens sampled was low. Therefore, higher abundances of the latter taxon were recorded on the island of Hvar although it was the *Caulerpa taxifolia* sampling site. With *Caulerpa racemosa* as a host, *Cocconeis molesta* var. *crucifera* was found more often in Dubrovnik samples. There is no clear explanation of the differences in abundance of this taxon between the two sampling sites in spring and summer and future study of environmental variables is necessary to explain this phenomenon.

In addition to *Cocconeis molesta* var. *crucifera*, the most common and the most abundant taxon occurring in all *Caulerpa racemosa* samples was *Cocconeis scutellum* var. *scutellum*. Average abundance of *Cocconeis scutellum* var. *scutellum* on *Caulerpa racemosa* amounted to 32.14 % reaching highest abundances (43%) during winter and spring. *Cocconeis* taxa also dominated the epiphytic diatom assemblage of *Caulerpa taxifolia*. *Cocconeis scutellum* var. *scutellum* was the most abundant with average abundance of 15%. During winter, the abundance of *Cocconeis scutellum* var. *scutellum* was the highest reaching 25%. *Cocconeis scutellum* var. *scutellum* on *Caulerpa taxifolia* reached its maximum abundance of 33.63% in January 2010. In general, for both sampling years, January can be regarded as the peak of abundances of *Cocconeis scutellum* var. *scutellum* on *Caulerpa taxifolia*. Highest abundances of *Cocconeis scutellum* var. *scutellum* on *Padina pavonica* and *Halimeda tuna* were also observed in winter. On the investigated macroalgae, both autochthonous and invasive, *Cocconeis scutellum* var. *scutellum* seems to be a “winter taxon” with abundances from 15% (*P. pavonica*), followed by 25% (*H. tuna* and *C. taxifolia*) and

43% (*C.racemosa*). The lowest average abundance of *Cocconeis scutellum* var. *scutellum* recorded on *Padina pavonica* (6.4%) is probably due to low number of winter samples (just 1!).

While on autocthonous algae the average abundance of another dominant *Cocconeis* species *C. caulerpacola* was less than 1%, on invasive algae it amounted to 10%. Results of analyses of green and brown macroalgae collected at the same time from the same localities as invasive *Caulerpa* spp. show either a complete absence or the presence of just a few specimens of *C. caulerpacola*. Average abundance of *Cocconeis caulerpacola* on *Caulerpa racemosa* amounted to 5%. The highest abundance (14%) was observed on *Caulerpa taxifolia*. Increased abundance of *Cocconeis caulerpacola* on *Caulerpa* spp. was responsible for clustering communities together into a group A despite different localities of sampling. Also, although a strong seasonality of *Cocconeis caulerpacola* was observed with higher abundances at the end of summer and in autumn and the lowest in spring, the relationship of epiphytic diatom and the host seems to be much more important. Group B1 encompassed the samples from *Padina pavonica* also regardless of the season and sampling sites. Group B2 is more heterogeneous containing mostly samples from autochthonous green algae *Halimeda tuna* but also a few samples of autochthonous *Padina pavonica* and invasive *Caulerpa racemosa*. No samples of invasive *Caulerpa taxifolia* were recorded in either of the groups B1 or B2. Apparently diatom communities of *Caulerpa taxifolia* showed less similarity to others than those of *Caulerpa racemosa*. This is primarily because of the high abundance of a new *Cocconeis* species, *C. caulerpacola* Witkowski, Car & Dobosz.

A thorough taxonomic survey of the relevant diatom literature (e.g. Hustedt, 1933; Foged, 1975; Montgomery, 1978; Simonsen, 1987; Witkowski et al., 2000) did not reveal any described taxa corresponding to *C. caulerpacola*. It resembles in some respects *C. diruptoides* and *C. pseudodiruptoides*, possessing a comparable valve outline and a similar sigmoid appearance of the raphe and the sternum. Like *C. caulerpacola*, *C. diruptoides* occurs in the Adriatic Sea as an epiphytic diatom on leaves of *Posidonia oceanica* (De Stefano & Marino, 2001), but *C. caulerpacola* is much smaller and has a much higher stria density. Similarly to *C. diruptoides*, *C. pseudodiruptoides* has much lower stria densities than *C. caulerpacola*, the striae being easily recognizable under LM on both valves (contrasting with *C. caulerpacola*), and the raphe and sternum are more strongly sigmoid. *Cocconeis caulerpacola* and *C. borbonica* resemble each other in shape and size (both are tiny) and the striation is hardly discernible in LM. However, other features permit them to be differentiated: fascia on the RV does not reach the valve margins in *C. borbonica* (contrast *C. caulerpacola*), and the raphe is straight in *C. borbonica* (sigmoid in *C. caulerpacola*).

Caulerpa taxifolia is apparently a suitable host for epiphytic diatoms because it tolerates some degree of microbial fouling, despite its common reputation as the ‘killer seaweed’. The major feature of the diatom microflora of *C. taxifolia* is that epiphytes are composed almost exclusively of diatoms from the genera *Cocconeis* and *Mastogloia*, as on the leaves of *Posidonia oceanica* growing in similar sandy habitats of the Mediterranean. It was therefore expected that the composition of the epiphytic diatom assemblage on *Caulerpa taxifolia* might be similar to that on *P. oceanica*. However, whereas the most abundant taxa on *Posidonia* are *C. scutellum* var. *posidoniae* and *C. neothumensis* var. *marina* (De Stefano et al., 2000), the most striking characteristic of the epiphytic flora of *C. taxifolia* – both in the Mediterranean, where it is an invader, and in Australia, where it is native – is the predominance of *Cocconeis caulerpacola*.

The distribution of *Cocconeis caulerpacola*, occurring on both *Caulerpa taxifolia* in Australian marine waters and on invasive *C. taxifolia* in the Mediterranean, is interesting and in accordance with DNA analyses showing the origin of *C. taxifolia* to be from Moreton Bay, Queensland, Australia. Allozyme surveys have suggested that populations with a robust form of *C. taxifolia* in eastern Australia may be genetically more similar to populations with similar morphology in the Mediterranean than to populations with a finer morphology on the central Great Barrier Reef in north-east Australia (Benzie et al., 2000). Furthermore, sequencing of the Internal Transcribed Spacer (ITS) region of ribosomal DNA have indicated an aquarium origin of the Mediterranean *C. taxifolia* and also a genetic similarity between the Mediterranean strain and Australian populations (Jousson et al., 1998, 2000, 2001; Meusnier et al., 2001; Famà et al., 2002). DNA signatures of *C. taxifolia* have also provided evidence for the introduction of an aquarium strain into the Mediterranean Sea and showed the close relationship of the ‘aquarium-Mediterranean’ strain to an Australian population from Moreton Bay (Wiedenmann et al., 2001). Finally, the presence or absence of a chloroplast intron in the rbcL gene supports the hypothesis that Mediterranean and Australian populations belong to the same lineage. Among natural populations, specimens that possess the intron are restricted to tropical areas (Caribbean, Red Sea, South-East Asia), whereas those that lack it are present in subtropical North-eastern Australia (Queensland) and in the temperate waters of South-eastern Australia (New South Wales, Famà et al., 2002). The rbcL intron is lacking in introduced populations from the Mediterranean, as well as in aquarium strains.

Despite different geographical locations and a great difference in CYN values between the two assayed taxa of *Caulerpa*, *C. taxifolia* and *C. racemosa*, there is a general similarity between their epiphytic diatom assemblages, including the occurrence of the new *Cocconeis* species. However, a higher number of specimens of *C. caulerpacola* were observed on *C. taxifolia* than on *C. racemosa*. Periods of higher abundance of *C. caulerpacola* appear to coincide with maximum toxicities observed for *C. taxifolia* in summer and autumn, while the minimum abundance is observed in winter and spring (Dumay et al., 2002). Further research is necessary to determine the influence of seasonal processes, such as the production of CYN and the growth rate of *Caulerpa* thalli on the occurrence of *Cocconeis caulerpacola*. The difference in epiphytic diatom community composition between *Caulerpa taxifolia* and *C. racemosa* on the one hand, and green and brown macroalgae and seagrass on the other, is striking. Although the same abundant genera are observed (*Cocconeis* spp. and *Mastogloia* spp.), different taxa are present on *Caulerpa* and *Posidonia oceanica*, with *Cocconeis scutellum* dominant on *Posidonia oceanica*. The latter observation is in accordance with previous examinations e.g. De Stefano et al., (2000) collected in areas influenced by invasive *Caulerpa* spp. (either *C. taxifolia* or *C. racemosa*, which is also invasive in the Mediterranean: Klein & Verlaque, 2008). Results of analyses of green and brown macroalgae collected at the same time from the same localities as invasive *Caulerpa* are consistent with a hypothesis of host-specificity of the new *Cocconeis* taxon by showing a total absence or the presence of just a few specimens of *C. caulerpacola*. A future study of the physiology of this new taxon is therefore justified, to examine why it is almost entirely restricted to colonizing members of the genus *Caulerpa* and how it is able to colonize *C. taxifolia* in such great abundance.

According to Totti et al. (2009) adnate diatoms, which include *Cocconeis* taxa, seem to be more affected by the structure of host surface, with increasing cell abundances in thalli which offer a more complex microarchitecture for colonization, while they were absent in soft thalli with smooth surface. This would explain dominance of the genus but not *Cocconeis caulerpacola* specificity. *Cocconeis caulerpacola* which covered a great amount of the surface of both non-indigenous and native *Caulerpa taxifolia*, seems to be unique to that macroalga. The reason for greatest abundance in France (up to 67% of the diatom abundance), is probably because of established invasion of *Caulerpa taxifolia* at that location. Since the launch of the invasion in 1984, *C. taxifolia* has colonized large areas of seafloor in Mediterranean. Aquarium-Mediterranean strain is capable of forming exceptionally dense meadows. The alga's spread can result in coverage of up to 100% between depths of 1m and 35m in the most affected benthic areas (Madl and Yip 2005). The alga, forming dense carpets, is outcompeting native seaweeds and leading to a loss of biodiversity. Apparently loss of biodiversity is not only affecting the macro-world but the micro-world as well. If *Cocconeis caulerpacola* is really host-specific for *Caulerpa*, it would be that omnipresence of *Cocconeis caulerpacola* at the French location is the reason for finding it in such a great amount in our samples. The ability of invasive taxa to defend against resident epibionts may substantially affect competitiveness and influence the success of their invasion (Wahl, 2008).

Activities of the host undoubtedly modulate the interactions among epibionts (Wahl, 2008). Studies of distribution of epiphytic community on the leaves of *Posidonia oceanica* showed that the community structure is influenced by several factors, including the seasonal cycle of the plant, the depth of the meadow, the age of the leaf, and the grazing pressure by herbivores (Mazzella et al. 1983; Mazzella and Spinoccia 1992; Mazzella et al. 1994; De Stefano et al. 2000).

Caulerpa taxifolia have a marked seasonal biomass cycle with higher biomass corresponding to higher water temperatures (Meinesz et al., 1995). In summer and autumn fronds of *Caulerpa taxifolia* reach their maximum length, while in winter the leaves of *Posidonia oceanica* are larger than fronds of *Caulerpa taxifolia* (Meinesz & Hesse, 1991; Meinesz et al., 1993, 1995). As biofouling by the diatom *Isthmia nervosa* is related to a decline in growth and reproduction of the red alga *Odonthalia floccosa* (Esper) Falkenberg (Ruesink, 1998), finding that the same pattern applies for *Caulerpa taxifolia* and its fouling diatoms would be significant. It is necessary to examine the macrophyte-epiphyte relation by comparing the seasonal changes in taxonomic composition and biomass of the epiphytes growing on *Caulerpa taxifolia* but also on native plants growing together in shallow bays. In Antarctic waters, Al-Handal and Wulff (2008) suggested the existence of a host effect because of differences in epiphytic diatom composition occurred on seaweed from the same area and depth. Likewise Sutherland (2008) reported that the epiphytic diatom communities differed in terms of dominant taxa on frondose and coralline red algae from the same area; and Snoeijs (1994, 1995) reported from the Baltic Sea that, although the microepiphytic community was more affected by season and salinity gradient than by host preference, the plant hosts somehow affected the epiphytic taxonomic composition because they supported different abundances of epiphytes. The reason for poor colonization of invasive taxa by resident epibionts could be epibiont-basibiont specificity (Dunn & Dick, 1998). Another explanation could be more powerful antifouling defence in the invasive taxa. The lack of any definite relationships between indigenous algae and epiphytes growing on them does not allow us to make definite conclusions about host and seasonal specificity.

Defence and epibiosis might vary among body parts. Jennings and Steinberg (1997) noticed greatest epiphyte densities on the oldest tissue and least on the youngest. They examined samples of a sublittoral kelp *Ecklonia radiata* where epiphyte abundance was strongly correlated with age of different parts of the thallus. In a case of *Caulerpa taxifolia* despite the fact that the stolon can grow by nearly 2 cm per day throughout the summer and autumn (Meinesz, 2002) it seems that there is no difference in epibiosis especially in case of *Cocconeis caulerpacola*. Investigation of development in epiphytic diatom communities on the fronds of *Caulerpa taxifolia* followed throughout the 2010 summer/autumn season, suggests that we can even conclude that *Caulerpa taxifolia* is growing together with *Cocconeis caulerpacola*.

Results of vertical distribution analyses of epiphytic diatoms on macroalgal host *Caulerpa taxifolia* agree with those of Tanaka (1986) who reported that diatom taxa having higher adhesive strength (*Cocconeis* and *Achnanthes* taxa) because they can tolerate adverse hydrodynamic conditions such as wave action, were more abundant on fronds than on stipes of various seaweeds. *Cocconeis* morphology is perfectly suited for the colonization of surfaces exposed to high shear stresses. *Cocconeis* cells are only ca. 2–3 μm thick, enabling the entire cell mass to be positioned prostrate and very close to the surface, allowing the cell to sit inside the boundary layer and avoid the shear forces that may be experienced by organisms that occupy a more elevated position off the surface or having cells with higher pervalvar axis.

Monoraphid *Cocconeis* spp. adhere tightly along their raphe, but as organisms capable of slow motility they are able to migrate to areas with greatest availability of light and nutrients or the least chance of desiccation due to tidal fluctuations (Mitbavkar & Anil, 2004), which are generally areas that provide the most suitable and productive environmental conditions (Edgar & Pickett-Heaps, 1984). Moreover, motility may allow cells to disperse their colonization over a large area of substrate to reduce the effect of grazers on the population (Harper, 1977; Hudon & Legendre, 1987). One of the explanations for the results of examination of unprocessed material of *Caulerpa taxifolia* under low magnification with the SEM which demonstrated strong patchiness in the occurrence of the attached diatom flora, with diatom-free patches and numerous spots with abundant diatoms, could be because *Cocconeis caulerpacola* avoids parts of thallus which are under high influence of toxins.

Chemical defence of *Caulerpa taxifolia* may decrease settlement and development of sessile organisms in invaded systems (Prado & Thibaut, 2008). Preliminary studies of secondary metabolites from seaweeds and algae have shown biological activity against epiphytes (Phillips & Towers, 1982; de Nys et al., 1991, 1995). Organisms can produce different types and rates of metabolites such as wastes, nutrients and toxins, depending on season, grazing pressure, developmental stage and biological cycles of the individual. Production and exudation may also vary among different organs of the same individual. Successful colonizers must either have a large tolerance range or settle during phases when – or on organs where – the composition and quantities of exudates are not harmful (Wahl, 1989). For the Mediterranean strain of *Caulerpa taxifolia* maximum concentrations of caulerpenyne contents were recorded in autumn (September/November) and minimum values occurred in spring (April/May) (Dumay et al. 2002). High summer and autumn values of toxic substances could be the reason for extraordinary taxa compositions in the investigated macroalgae which manifest decreased diversity of diatoms and dominance of *Cocconeis caulerpacola*. One explanation for this observation was the possibility of a targeted chemical defence against certain taxa, leading to a numerically similar but taxonomically different community profile in comparison to undefended substrates.

One of the greatest dangers in an epibiont's life is falling as victim to grazers of the substrate organism (Wahl, 1989). The current and predominant paradigm, based on the analysis of subtidal seagrass beds, asserts that diverse micro- or macro-algal epiphytes attached to seagrass blades can reach high biomass and may provide better quality nutrients compared to seagrasses itself, and thus are the main food source for macrofaunal invertebrates (Lebreton et al., 2011). Some herbivores selectively consume epiphytes, reducing epiphyte loads without directly affecting the macroalgal or seagrass host (Mazzella & Russo, 1989; Duffy, 1990; Dudley, 1992). According to Dudley (1992), without grazers macroalgal thalli would be heavily encrusted with a complex microalgal assemblage, while grazers tended to eliminate all epiphytes except small, adnate diatoms. Thus grazing may have an indirect positive effect on macrophytes. Previously, Sand-Jensen (1977) explored the epiphytes, mainly diatom *Cocconeis scutellum*, which formed a crust several layers thick on the older leaves of eelgrass. The epiphytes reduced the photosynthetic rate of the leaves by acting both as a barrier to carbon uptake and by reducing light intensity. Host plants potentially benefit from grazing activity of herbivores as they remove epiphytes and thereby alleviate competition for nutrients and light (Sand-Jensen, 1977). On the other hand, herbivores can have a negative direct effect on epiphytes in cases when grazers ingest macrophytic and epiphytic tissue, though it has not been fully explored whether epiphytes are consumed intentionally or incidentally (e.g. Nicotri, 1977, 1980; Lobel & Ogden, 1981; Shacklock & Croft, 1981; Norton & Benson, 1983; Shacklock & Doyle, 1983; D'Antonio, 1985; Duffy, 1990; Trowbridge, 1993; Fong, et al. 2000).

Previous investigations of feeding behaviour have shown that diatoms are the dominant components in the diet of Molluscs and amphipod Crustaceans (Mazzella & Russo, 1989; Scripione & Mazzella, 1992). However, only some Molluscs can feed on the strongly adherent *Cocconeis* spp., while the other grazers are able to remove the more motile taxa, such as *Amphora* sp. and *Navicula* sp. This indicates that *Cocconeis* spp., unless the most abundant, are not preferred. That selectivity could thus influence the abundance. On the other hand, taxa diversity seems to be very important both in patterns of substrate colonization and as a food source for grazers (Mazzella et al., 1994). The prostrate diatom growth taxa of genus *Cocconeis* form a continuous layer on *Posidonia oceanica* (Mazzella et al., 1994) which is comparable to that of macroalgal encrusting algae. The prostrate growth form could be considered as a survival strategy against grazing. The major characteristic of "killer seaweed" beds is that epiphytes are almost exclusively composed of diatoms of genus *Cocconeis*, dominated by *Cocconeis caulerpacola*, which could also be considered as a survival strategy against grazing. Sacoglossan molluscs of the genus *Elysia* are among the few organisms that graze *Caulerpa taxifolia*. *Elysia* sp. seems to be the best candidate as an agent of biological control of *Caulerpa taxifolia* not only because of high feeding rate on *Caulerpa taxifolia* (Thibaut et al., 1998) but also because it has a direct benthic development (Clark et al., 1979), which enables the rapid development of locally dense populations. However, little is known about their feeding ecology. Generally, epiphytes may have a positive effect by blocking herbivore access, a negative effect by facilitating herbivore attack, or no influence on the herbivore-seaweed association (neutral effects, respectively, Trowbridge, 1993). Epibionts interact not only with the host plant (basibiont) or with herbivores (consumers of the basibiont) but also among each other (Wahl, 2008). The intricacies of these types of herbivore-seaweed-epiphyte interactions have not yet been sufficiently explored.

5. CONCLUSIONS

Assemblages of epiphytic diatoms were studied on indigenous and invasive macroalgae from three sites in the Dalmatian coast of the Adriatic Sea. As invasive seaweeds *Caulepa taxifolia* ("killer seaweed") and *C. racemosa* were selected. Indigenous macroalgae were represented by *Padina pavonica* and *Halimeda tuna*. To have an idea about the specificity of the diatom assemblages on killer seaweed, *C. taxifolia* samples from St. Raphael in France and from Moreton Bay in Australia, the presumed origin site of the so called aquarium strain, were examined. The two year sampling and LM and EM examination of the samples collected from the study sites resulted in following conclusions:

- The epiphytic diatom communities on indigenous and invasive macroalagae from Dubrovnik, Mljet and Hvar sampling sites showed high diversity.

- Some of the diatom taxa, recorded during the present experiments were found throughout the whole year, while most at them exhibited an uneven, scattered pattern of distribution. During winter, fewer taxa were observed. Several taxa were found as initial colonizers during spring, but most of them appeared during summer, when the sea water reached its yearly temperature maximum (ca. 25°C).

- At all three locations (Dubrovnik, Mljet, Hvar), the highest biodiversity was observed during autumn.

- The species composition of epiphytes on the island of Mljet was, in part, similar to diatom assemblages in the Bay of Stari Grad (island of Hvar) and also to that of the location Orsula near Dubrovnik.

- The present investigation of three locations in Adriatic Sea between autumn 2008 and autumn 2010 confirmed expected differences in taxonomic composition of epiphytic diatoms between invasive algae of *Caulerpa* and between *Caulerpa* spp. and selected autochthonous algae. The diatom assemblages showed a predominant host-dependent difference at the species level. The type of substrata greatly influenced the occurrence of diatom taxa and their relative abundance.

- Similar numbers of taxa were recorded in the epiphytic diatom communities of the autochthonous brown macroalga *Padina pavonica* and green alga *Halimeda tuna* on the one hand (257), and on invasive *Caulerpa racemosa* and *Caulerpa taxifolia* (370) on the other. The largest number of taxa (379) was found on *Caulerpa taxifolia* and the lowest on *Halimeda tuna* (243).

- The diatom assemblage of *Padina pavonica* was characterized by high abundances of taxa belonging in *Mastogloia, Nitzschia, Cocconeis, Navicula, Amphora, Hyalosynedra* and *Licmophora.*

- The diversity of *Mastogloia* (with more than 40 taxa) on *Padina* was much higher than on any other studied macroalga.

- *Mastogloia*, which is very rich in number of taxa and had high frequency of appearance, contributed strongly to a high value of Shannon-Wiener Biodiversity Index.

- Epiphytic diatom assemblages of another investigated autochthonous macroalgae *Halimeda tuna* are different from those hosted by *Padina pavonica.* For *Halimeda tuna* the genus *Amphora* could be considered as common.

- The correlation between sea water temperature and the number epiphytic diatom of taxa on *Halimeda tuna* was very weak and the correlation coefficients low.

- The marine epiphytic diatom assemblages of invasive *C. racemosa* are rather different from the epiphytic diatom assemblages of brown and green indigenous macroalgae reported from the same locations. The following taxa occurred rather frequently on *C. racemosa*: *Cocconeis scutellum* Ehrenberg var. *scutellum, Cocconeis molesta* var. *crucifera* Grunow in Van Heurck, *Cocconeis caulerpacola* Witkowski, Car & Dobosz, *Navicula ramosissima* (Agardh) Cleve, *Hyalosynedra laevigata* (Grunow) Williams & Round and *Licmophora gracilis* (Ehrenberg) Grunow var. *gracilis.*

- Of 25 taxa dominant on *C. racomosa*, three belong to *Licmophora*. For *C. racemosa* genus *Licmophora* could be considered as common.

- On both sites (Dubrovnik and island of Mljet) the highest number of taxa on *Caulerpa racemosa* was recorded in September, while the lowest was in February and March.

- *Caulerpa taxifolia* is apparently a suitable host for epiphytic diatoms because it tolerates some degree of microbial fouling, despite its common reputation as the "killer seaweed".

- The dominant genera were roughly similar between *C. taxifolia* and *C. racemosa*. *Cocconeis* comprised the dominant group of epiphytes on the investigated macroalga *C. taxifolia* and *C. racemosa.* The diatom assemblages studied showed a distinct host-dependent differences at the level of taxa.

- The proportional contributions of individual species varied seasonally.

- During summer and autumn, the composition of epiphytic diatoms on *Caulerpa taxifolia* contained a high number of taxa.

- A strong and significant correlation between the number of taxa and temperature of the sea water was observed. Over the research period, temperature of the sea water did not significantly vary between years. The temperature ranged between 12°C in January and 25°C in August.

- A new *Cocconeis* species, *Cocconeis caulerpacola,* contributed to similarity of summer and autumn samples. The maximum abundance (63%) of *Cocconeis caulerpacola* was observed in autumn 2009. The new species occurred on both invasive Mediterranean and Australian native specimens of *Caulerpa taxifolia,* as well as on invasive *Caulerpa racemosa,* while only a very few specimens, or none at all, were observed on coexisting algae and on the seagrass *Posidonia oceanica.*

- Results of analyses of green and brown macroalgae collected at the same time from the same localities as invasive *Caulerpa* species are consistent with a hypothesis of host-specificity of the new *Cocconeis* by showing a total absence or the presence of just a few specimens of *C. caulerpacola.*

- A higher number of specimens of *C. caulerpacola* were observed on *C. taxifolia* than on *C. racemosa*. *Cocconeis caulerpacola* was occurred in 50% of samples of *Caulerpa racemosa* with average abundance of 5%, and in 76% of *Caulerpa taxifolia* samples with average abundance of 14%.

- Despite different geographical locations and a great difference in CYN values between the two assayed taxa of *Caulerpa*, *C. taxifolia* and *C. racemosa*, there is a general similarity between their diatom assemblages, including the occurrence of *Cocconeis caulerpacola*.

- Periods of higher abundance of *C. caulerpacola* appear to coincide with maximum toxicity observed for *C. taxifolia* in summer and autumn, while the minimum abundance is observed in winter and spring.

- Toxicity is assumed to be the most important factor implied in the heterogeneity of diatom communities.

- The diatom abundance significantly varied between the different thallus parts, with the number of epiphytic diatoms on the apical part significantly higher than on the basal part.

- The abundance of *Cocconeis caulerpacola* significantly differed between the various parts of fronds and pinnules. The number of *C. caulerpacola* on the basal part of pinnules and of rachis is significantly higher than on the apical part. Usually, dispersed occurrences of *C. caulerpacola* either with other *Cocconeis* taxa or with *Mastogloia* spp. were observed. However, the mass development of *C. caulerpacola* observed on fronds shows that within such a dense cover this taxon occurs alone and the associated taxa are absent.

- *Caulerpa taxifolia* hosts a diatom assemblage dominated by tube-dwelling *Mastogloia* spp. which are attached point-like to very small areas of host plant.

- More than 25 *Mastogloia* taxa were found, including: *M. binotata* (Grunow) Cleve, *M. fimbriata* (Brightwell) Cleve, *M. splendida* (Gregory) Cleve, *M. crucicula* (Grunow) Cleve, *M. erythraea* Grunow, *M. corsicana* Grunow, *M. inaequalis* Cleve, *M. cuneata* (Meister) Simonsen, *M. ovulum* Hustedt, *M. pusilla* Grunow, *M. ovata* Grunow, *M. paradoxa* Grunow, *M. decipiens* Hustedt, *M. ignorata* Hustedt, *M. cyclops* Voigt, *M. pseudolatecostata* Yohn & Gibson, and *M. pumila* (Grunow) Cleve.

- The results of this project will help fill the gap in our knowledge of communities and assemblages of *Mastogloia* taxa on Adriatic Sea coast.

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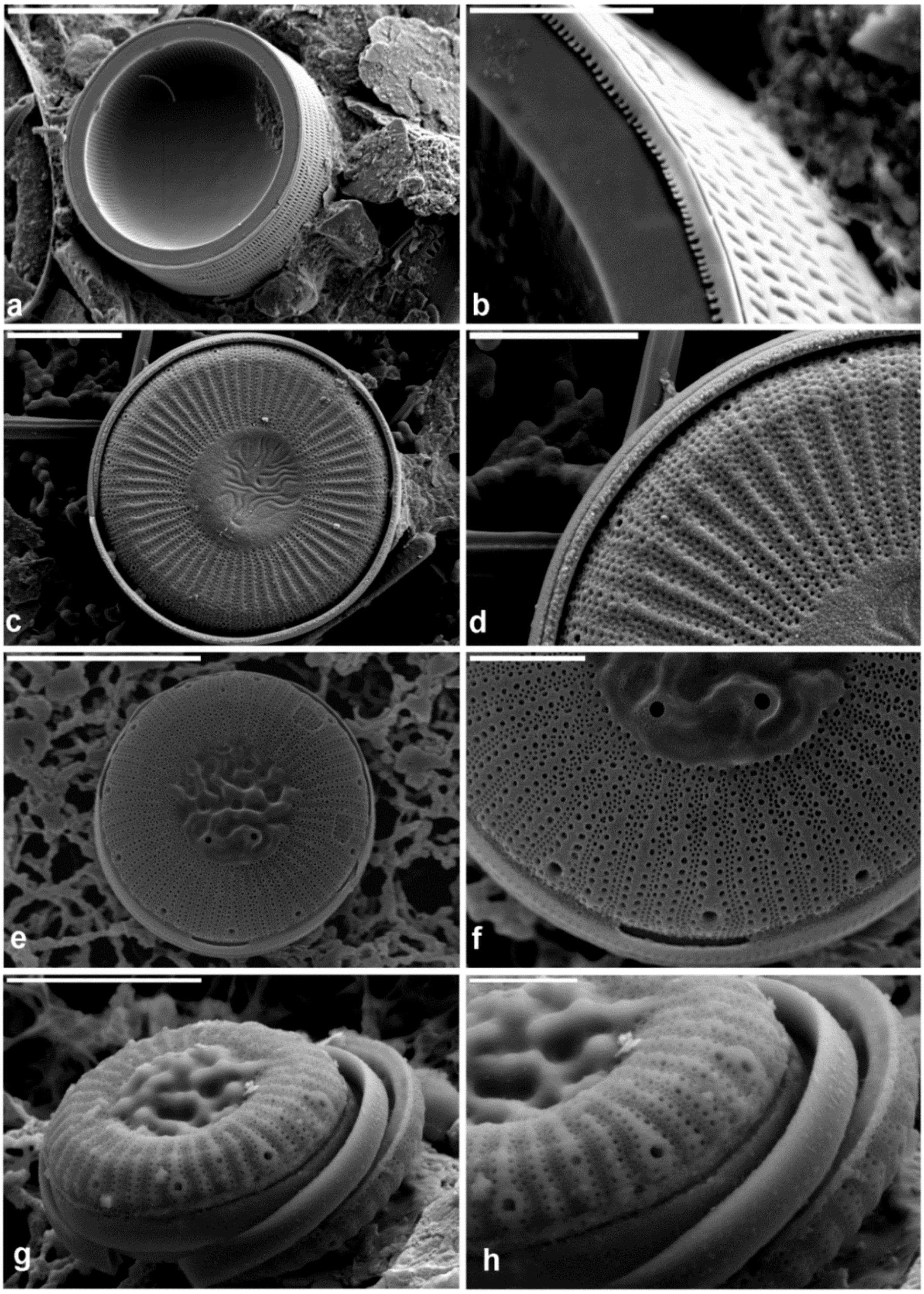
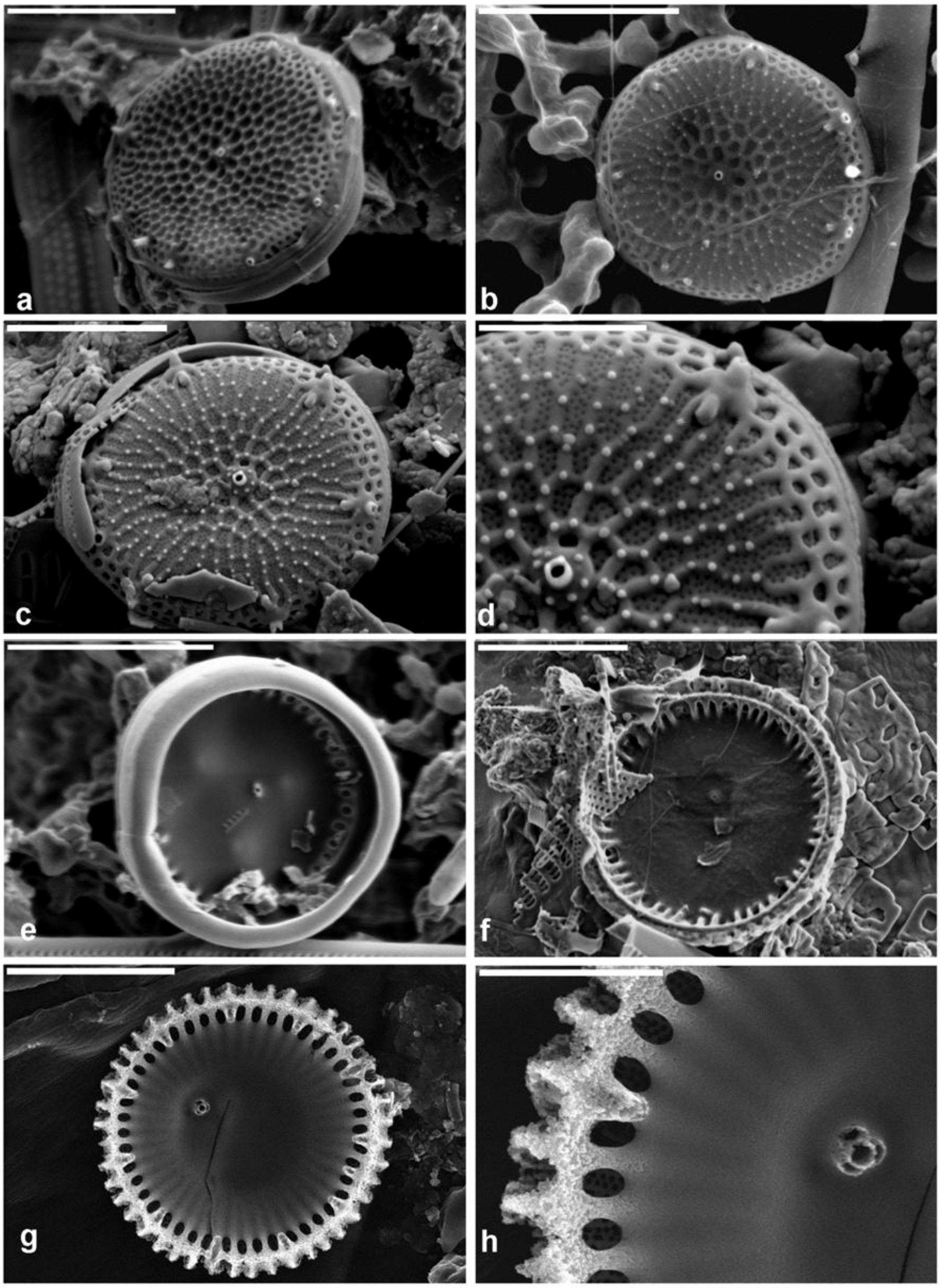
7. SUPPLEMENTS

Plate 1



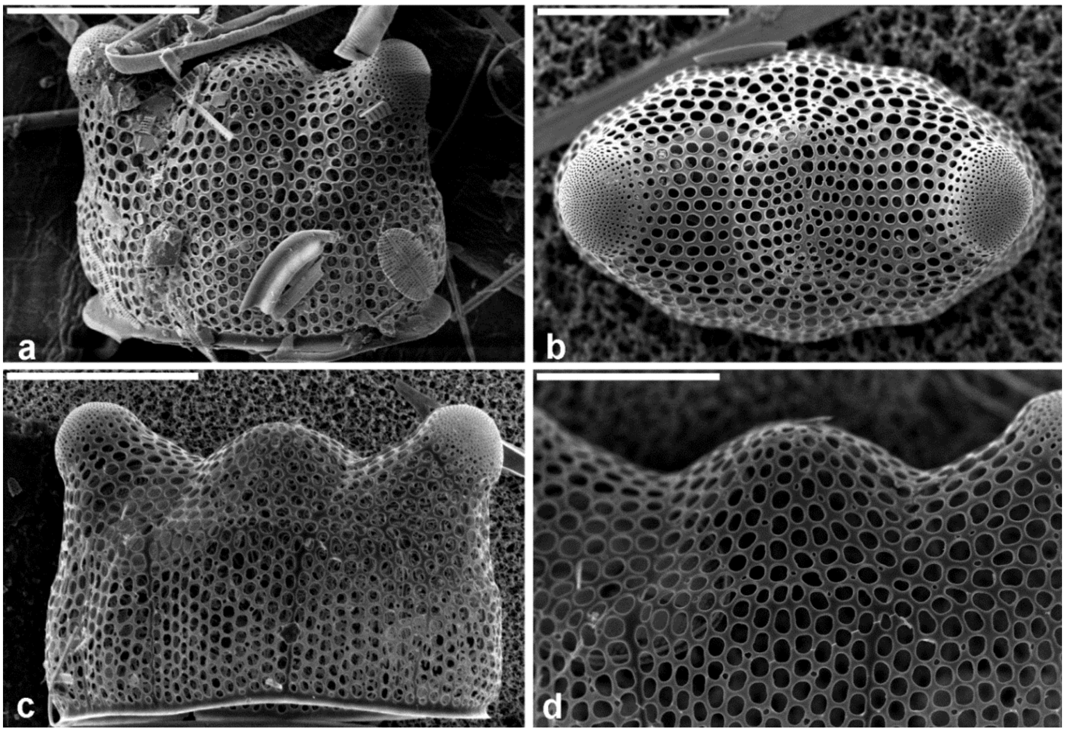
Figs a-b. *Paralia sulcata* (Ehrenberg) Cleve; Figs c-h. *Cyclotella meneghiniana* Kützing; Figs. e-h. Scale bars = 10 µm (Fig. a); 5 µm (Fig. c); 4 µm (Fig. e); 3 µm (Figs d, g); 2 µm (Fig. b); 1 µm (Figs f, h).

Plate 2



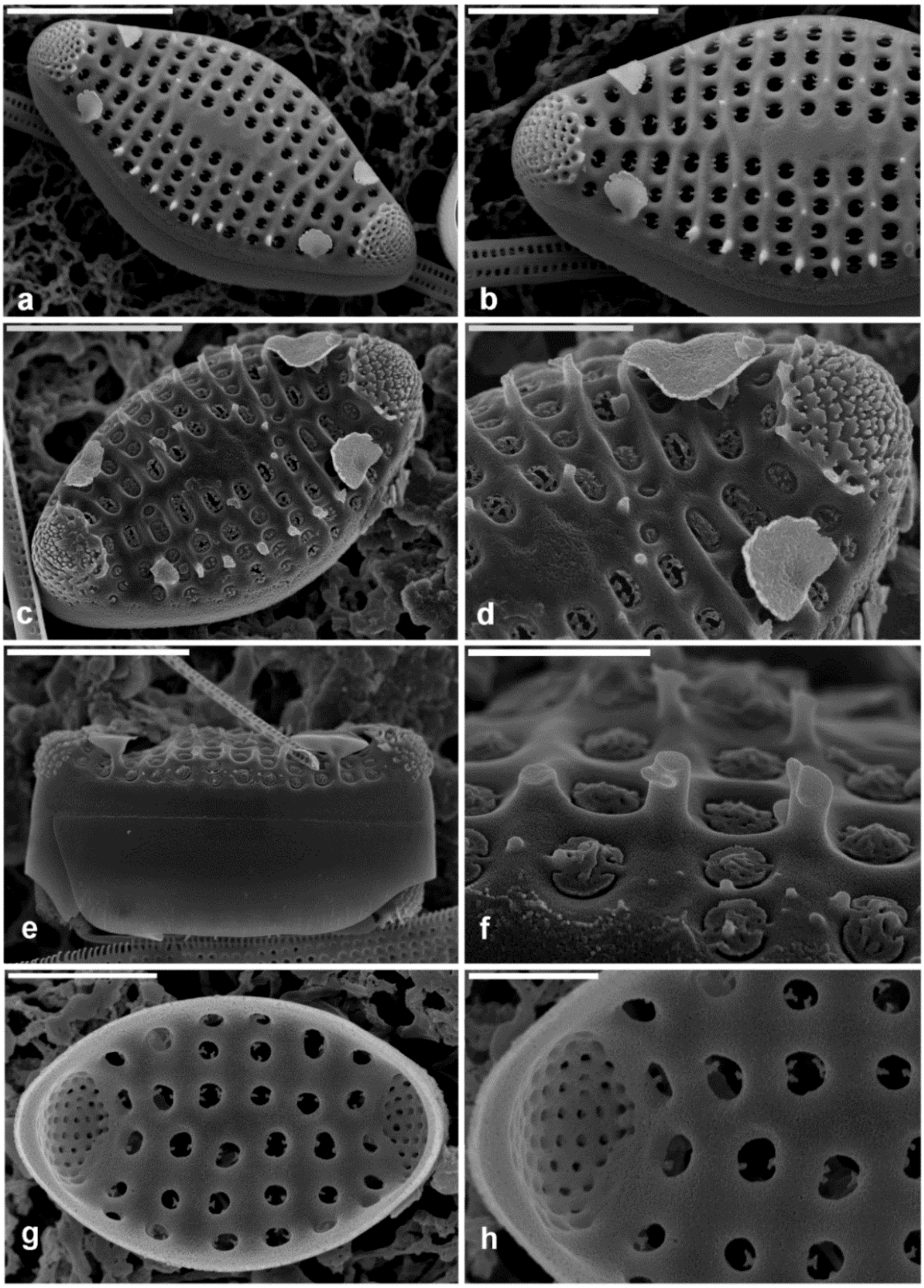
Figs a-h. *Thalassiosira* sp. Scale bars = 5 µm (Figs e, f); 3 µm (Figs a, b, g); 2 µm (Fig. c); 1 µm (Figs d, h).

Plate 3



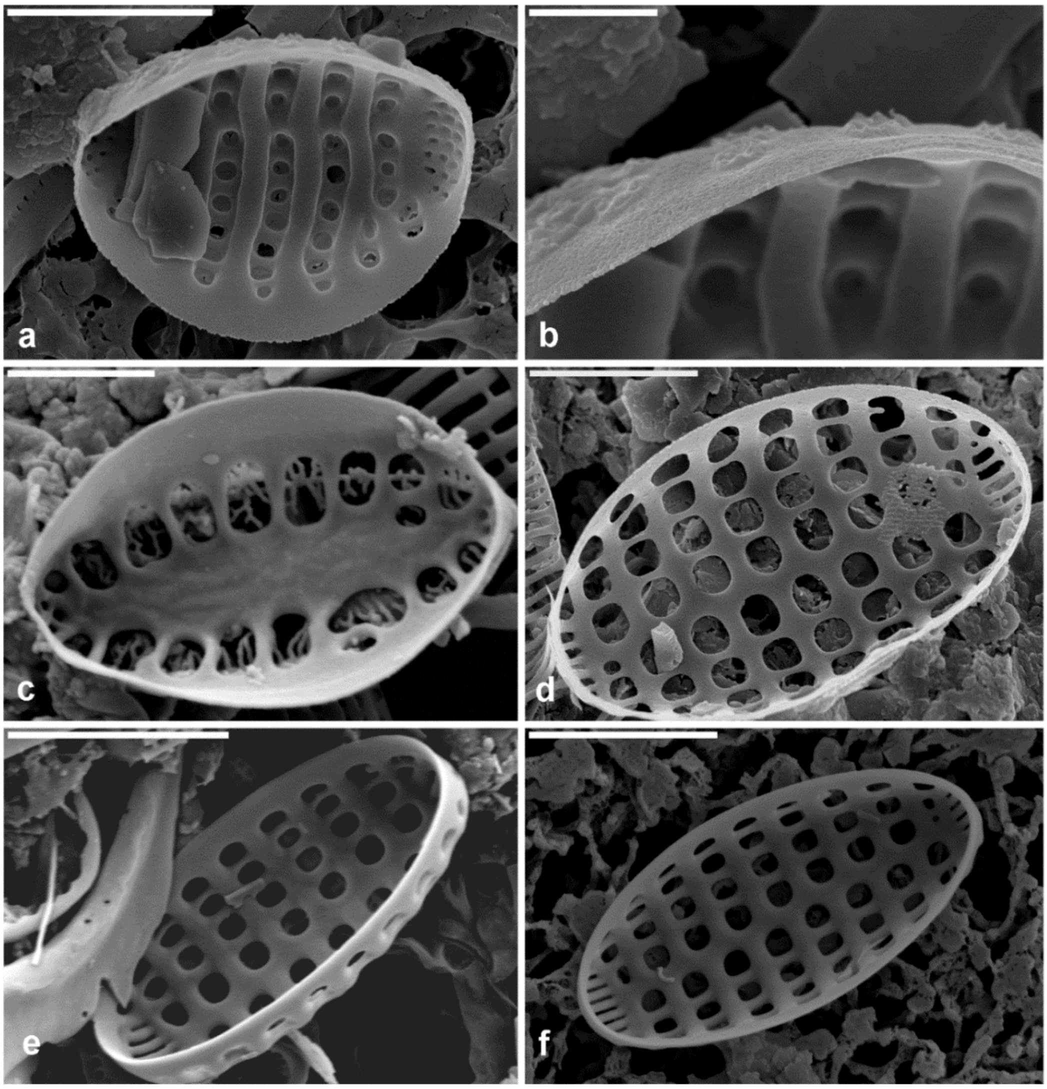
Figs a-d. *Biddulphia pulchella* Gray (SEM). External view. Scale bars = 30 µm (Figs a, b, c); 20 µm (Fig. d).

Plate 4



Figs a-h. *Dimeregramma minor* (Gregory) Ralfs in Pritchard (SEM). Figs. a-f. External view. Figs g-h. Internal view. Scale bars = 5 µm (Figs a, e); 4 µm (Figs b, c); 2 µm (Figs d, g); 1 µm (Figs f, h).

Plate 5

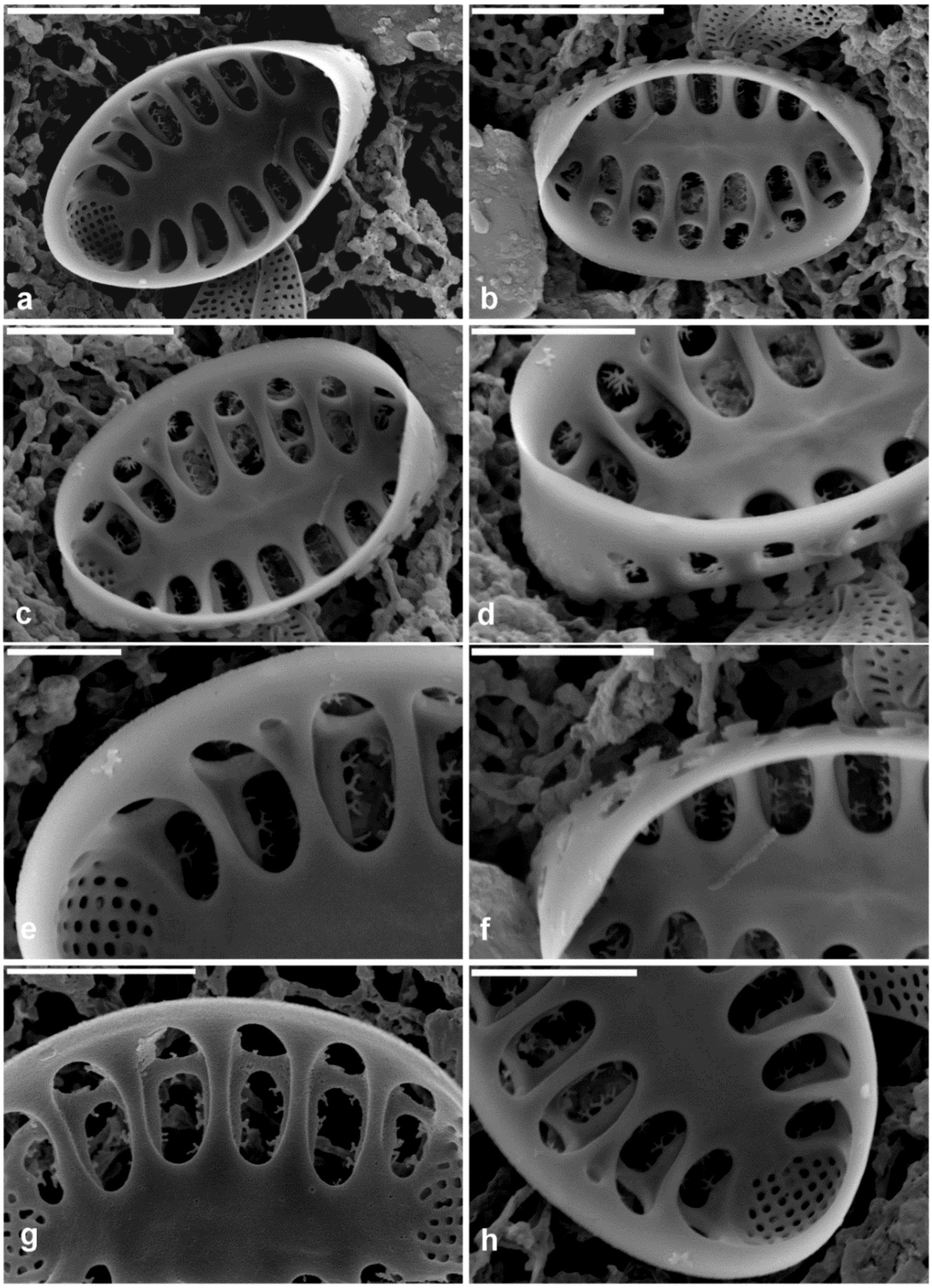


Figs a, b. *Psammogramma vigoensis* Sato & Medlin (SEM). Fig. c. *Cymatosiraceae*, gen et sp. nov. (SEM).

Figs d-f.

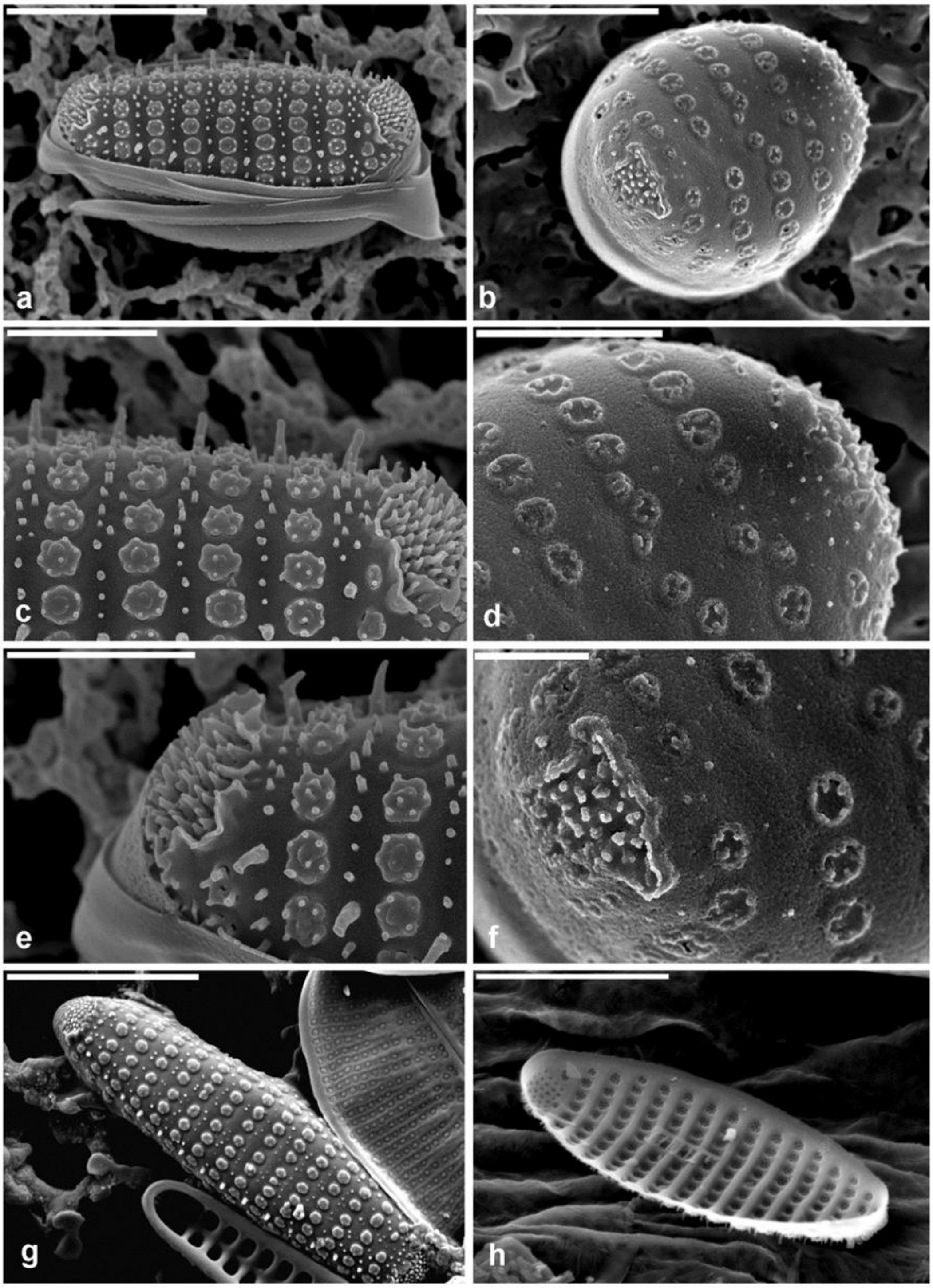
Scale bars = 3 µm (Figs e, f); 2 µm (Figs a, d); 1 µm (Fig. c); 500 nm (Fig. b).

Plate 6



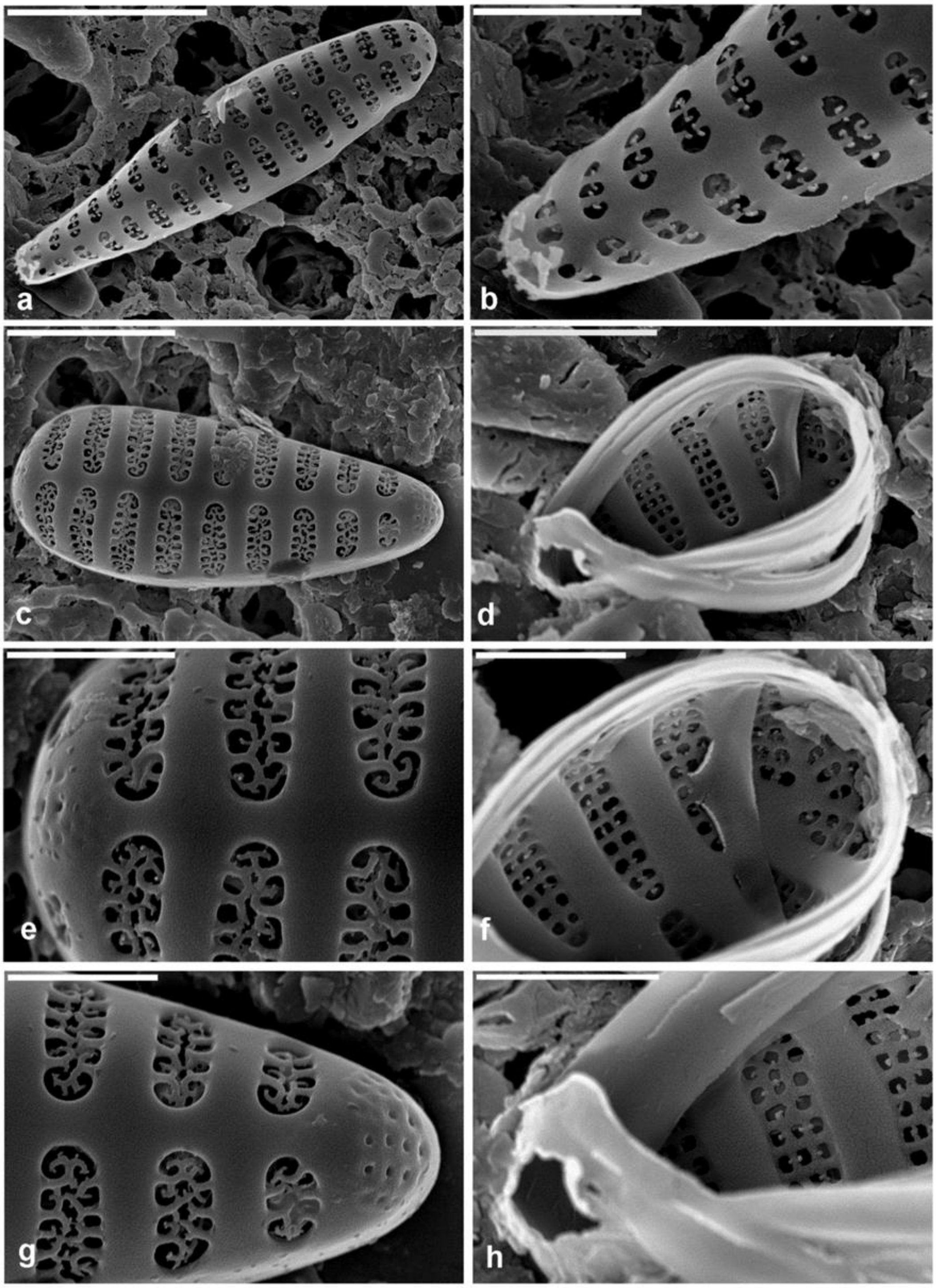
Figs a-h. *Plagiogrammaceae* gen. et sp. nov. Scale bars = 4 µm (Figs a, b); 3 µm (Fig. c); 2 µm (Figs d, f, g, h); 1 µm (Fig. e).

Plate 7



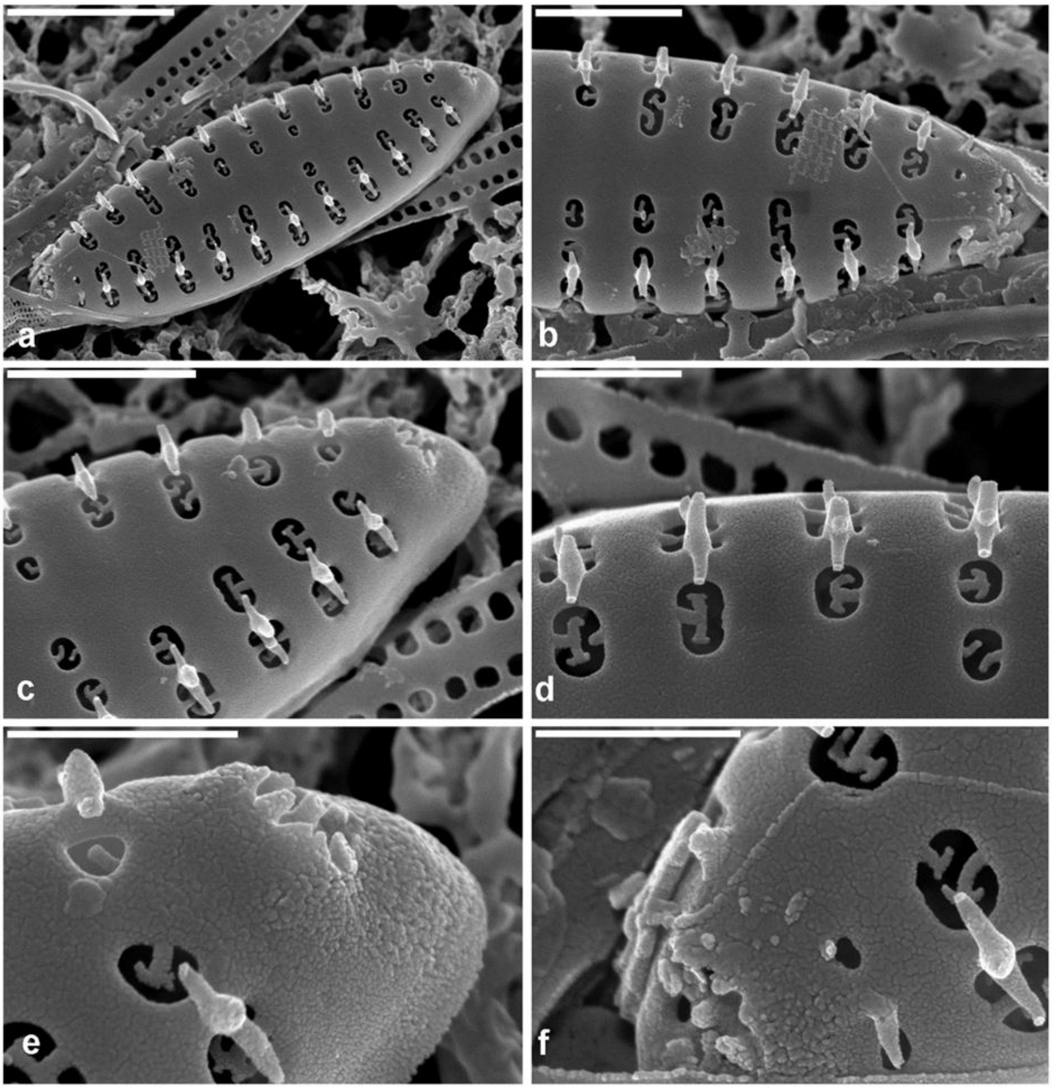
Figs a-h. *Plagiogrammaceae* gen. et sp. nov. Scale bars = 4 µm (Figs g, h); 3 µm (Fig. a); 2 µm (Fig. b); 1 µm (Figs c, d, e); 500 nm (Fig. f).

Plate 8



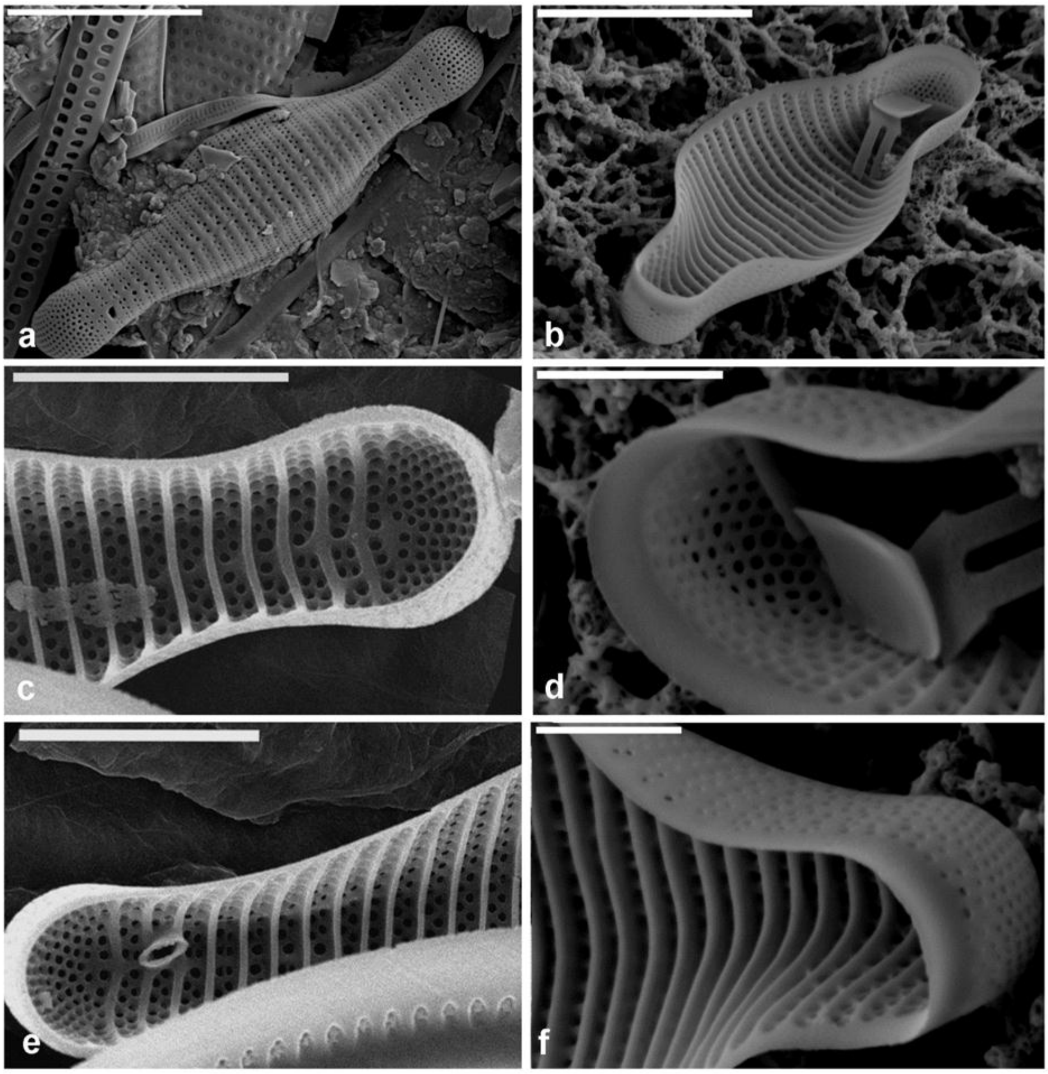
Figs a, b. *Pseudostaurosira* sp. (SEM). Figs c-h. *Opephora* sp. nov. (SEM). Scale bars = 3 µm (Figs a, c); 2 µm (Fig. d); 1 µm (Figs b, e, f, g, h).

Plate 9



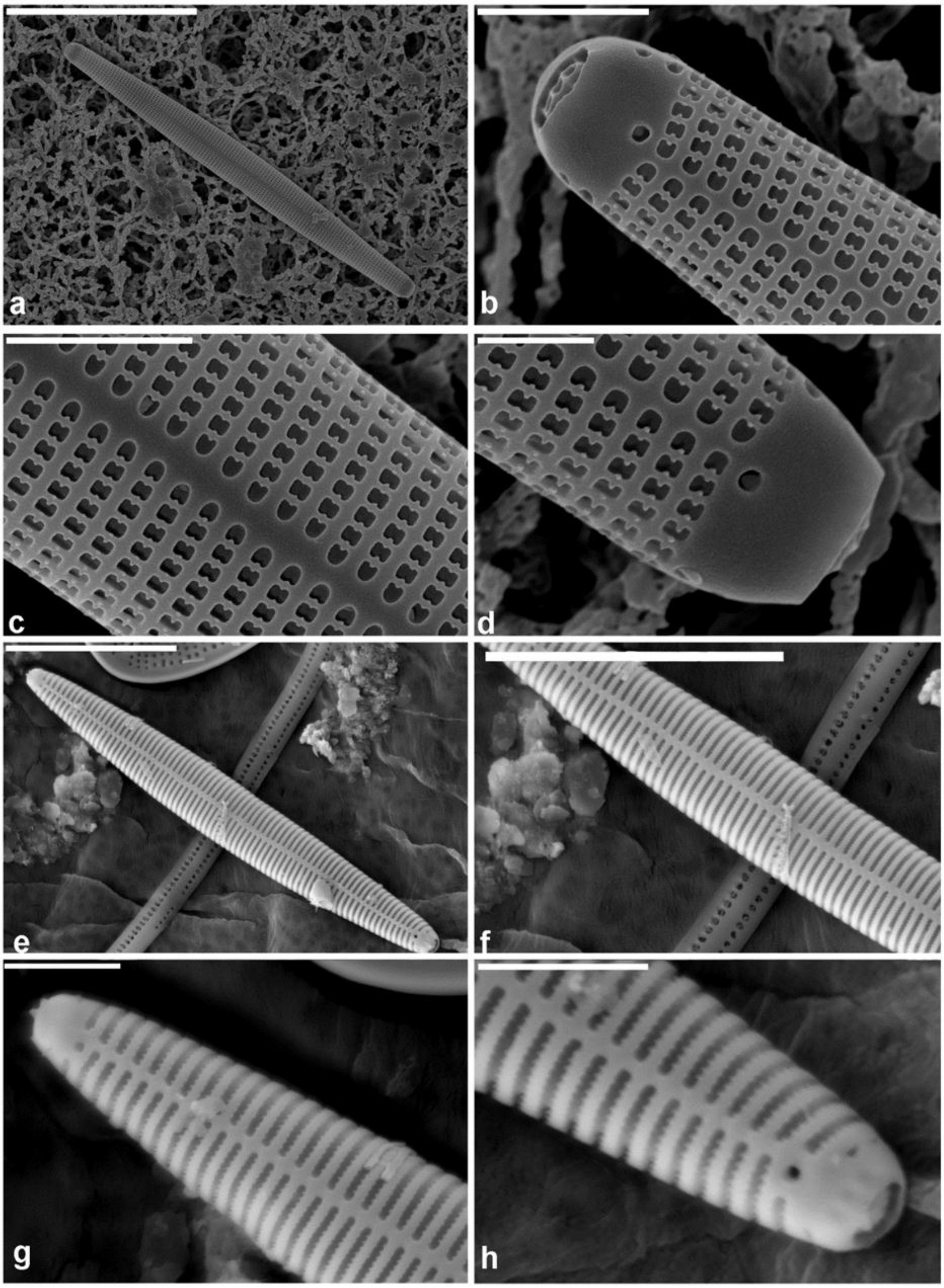
Figs a-f. *Psuedostaurosira* sp. nov. (SEM). Scale bars = 2 µm (Fig. a); 1 µm (Figs b, c); 500 nm (Figs d, e, f).

Plate 10



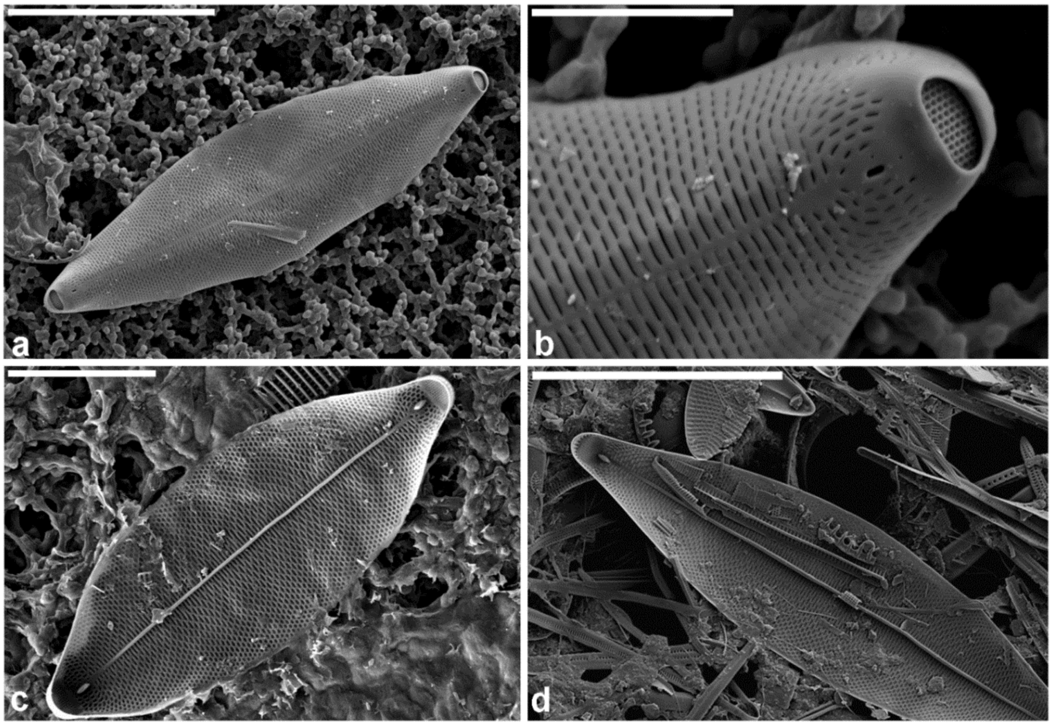
Figs a-f. *Hyalosira* sp. nov. (SEM). Scale bars = 4 µm (Figs a, b); 2 µm (Figs c, e); 1 µm (Figs d, f).

Plate 11



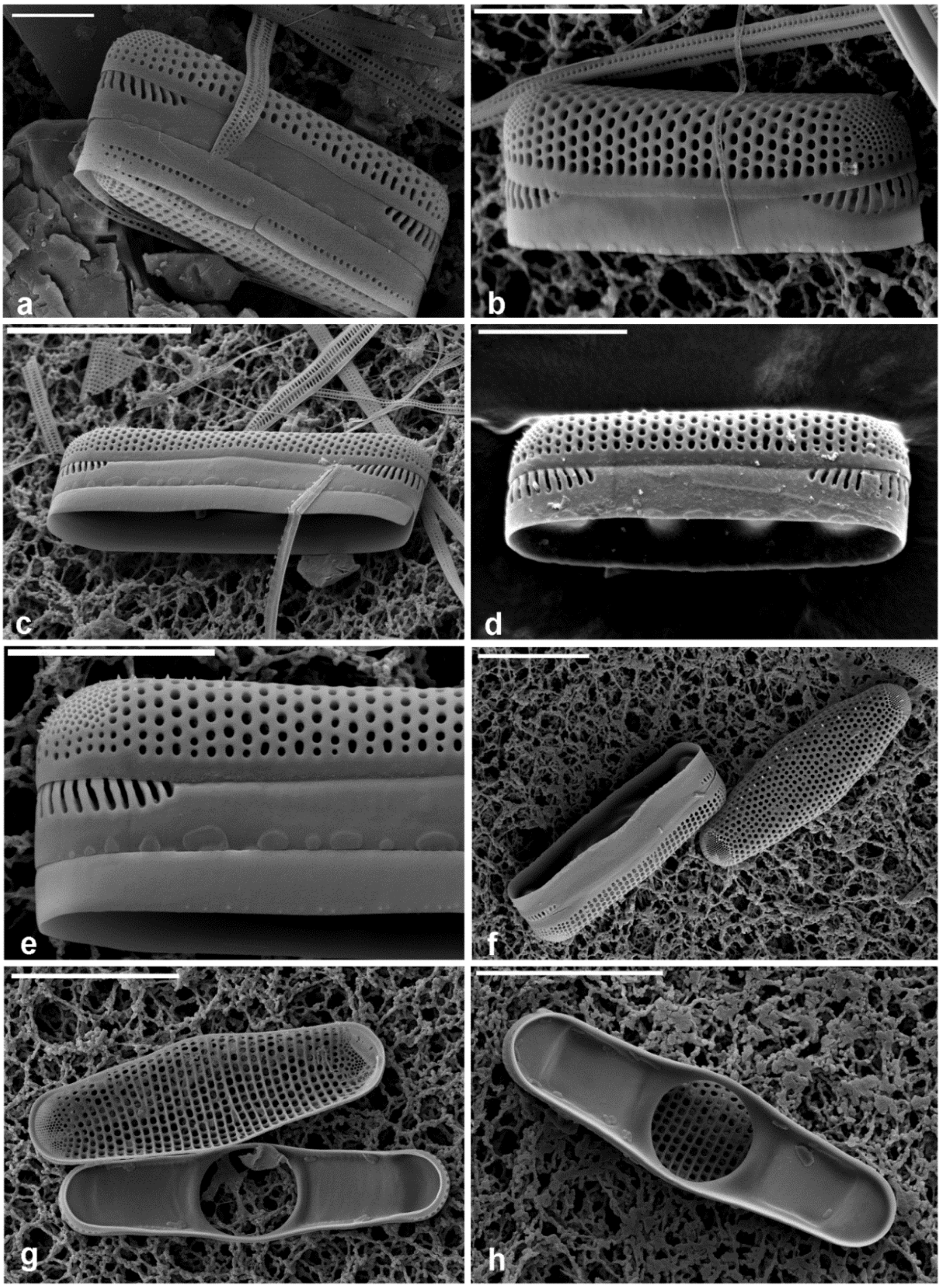
Figs a-h. *Hyalosynedra* cf. *laevigata* (SEM). Scale bars = 10 µm (Fig. a); 5 µm (Figs e, f); 1 µm (Figs b, c, g, h); 500 nm (Fig. d).

Plate 12



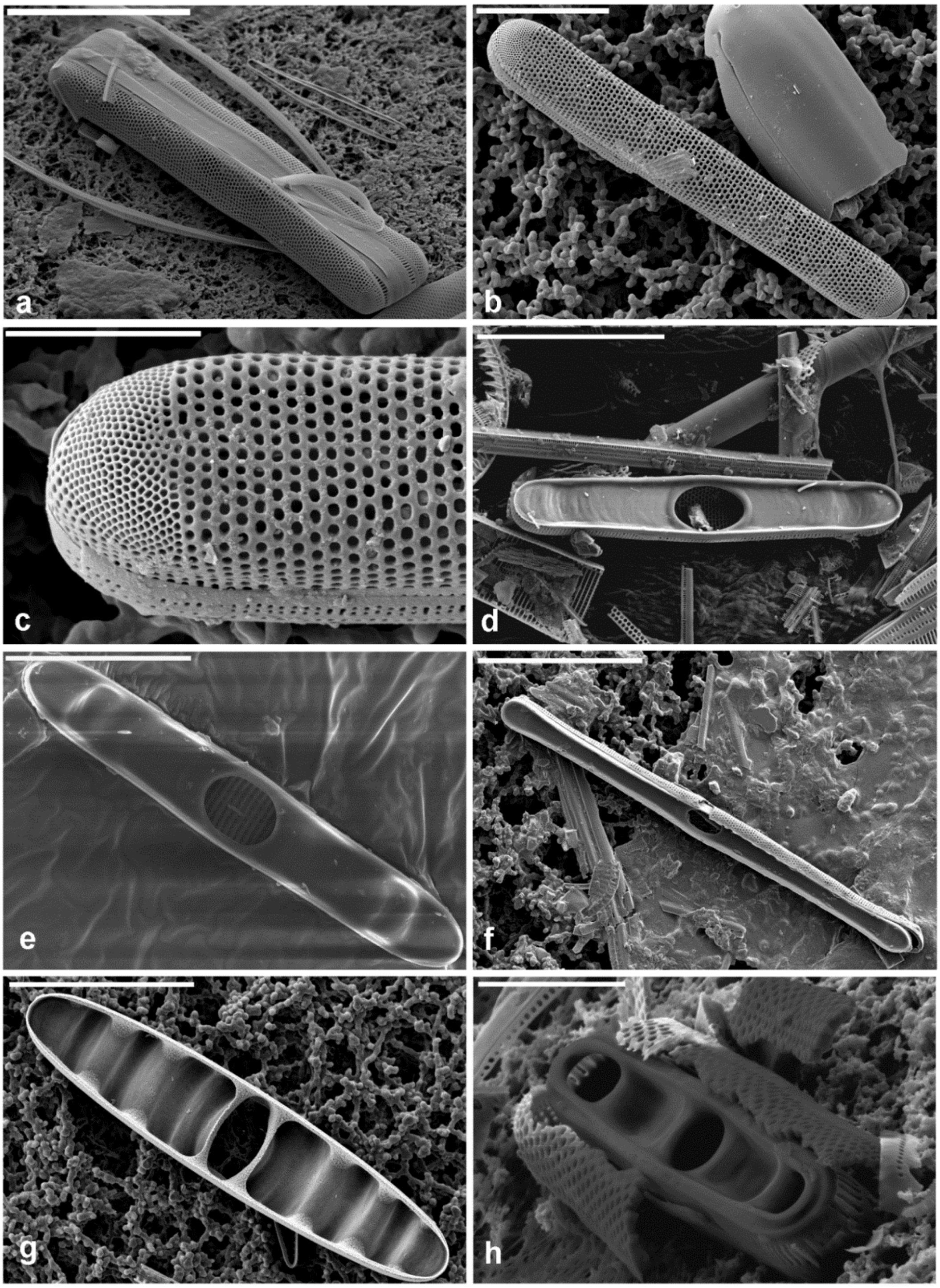
Figs a-d. *Striatella unipunctata* (Lyngbye) Agardh (SEM). Figs a, b. External view. Figs c, d. Internal view. Scale bars = 20 µm (Figs a, d); 10 µm (Fig. c); 4 µm (Fig. b).

Plate 13



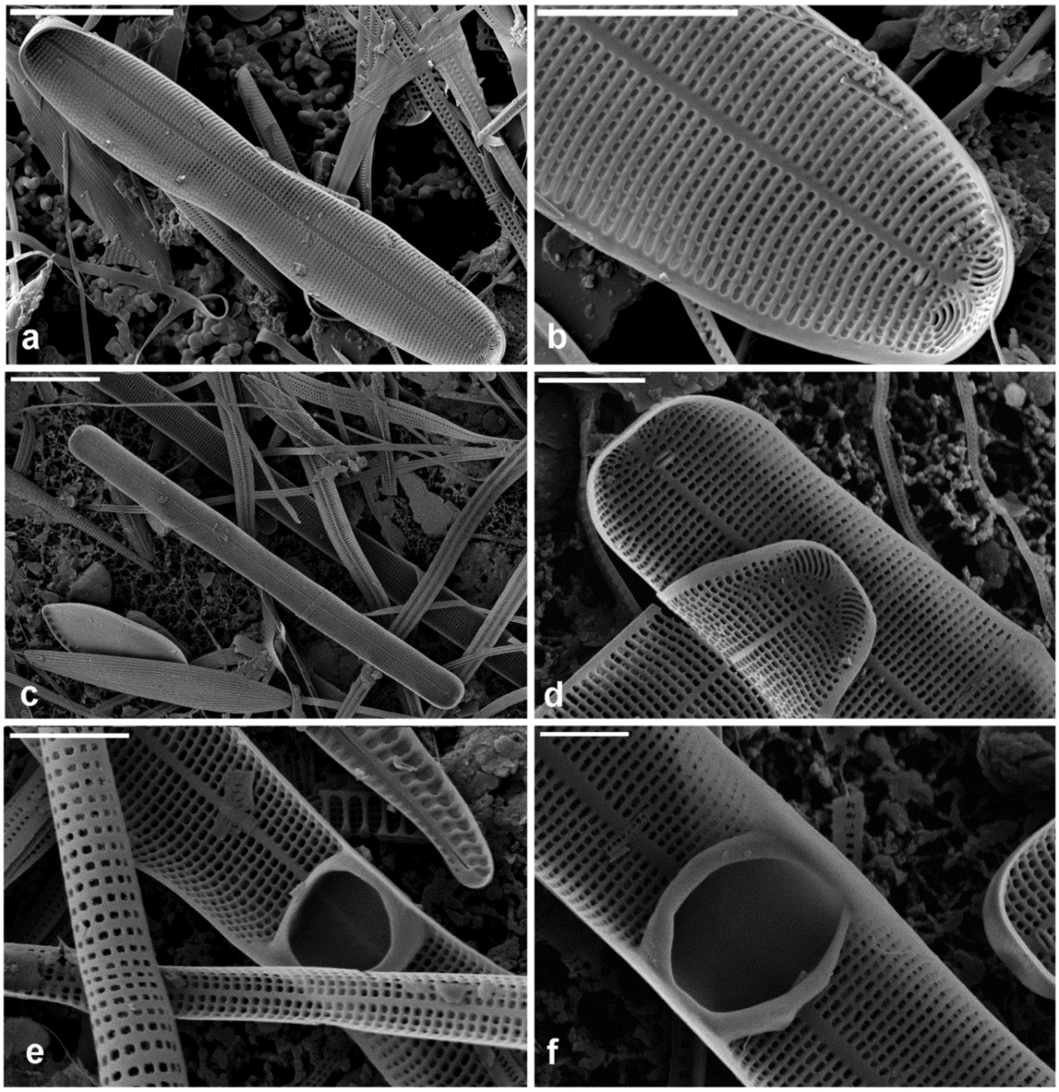
Figs a-f. *Grammatophora marina* (Lyngbye) Kützing (SEM). Figs a-e. External view. h. Internal view. Scale bars = 10 µm (Figs c, f, g, h); 5 µm (Figs b, d, e); 3 µm (Fig. a).

Plate 14



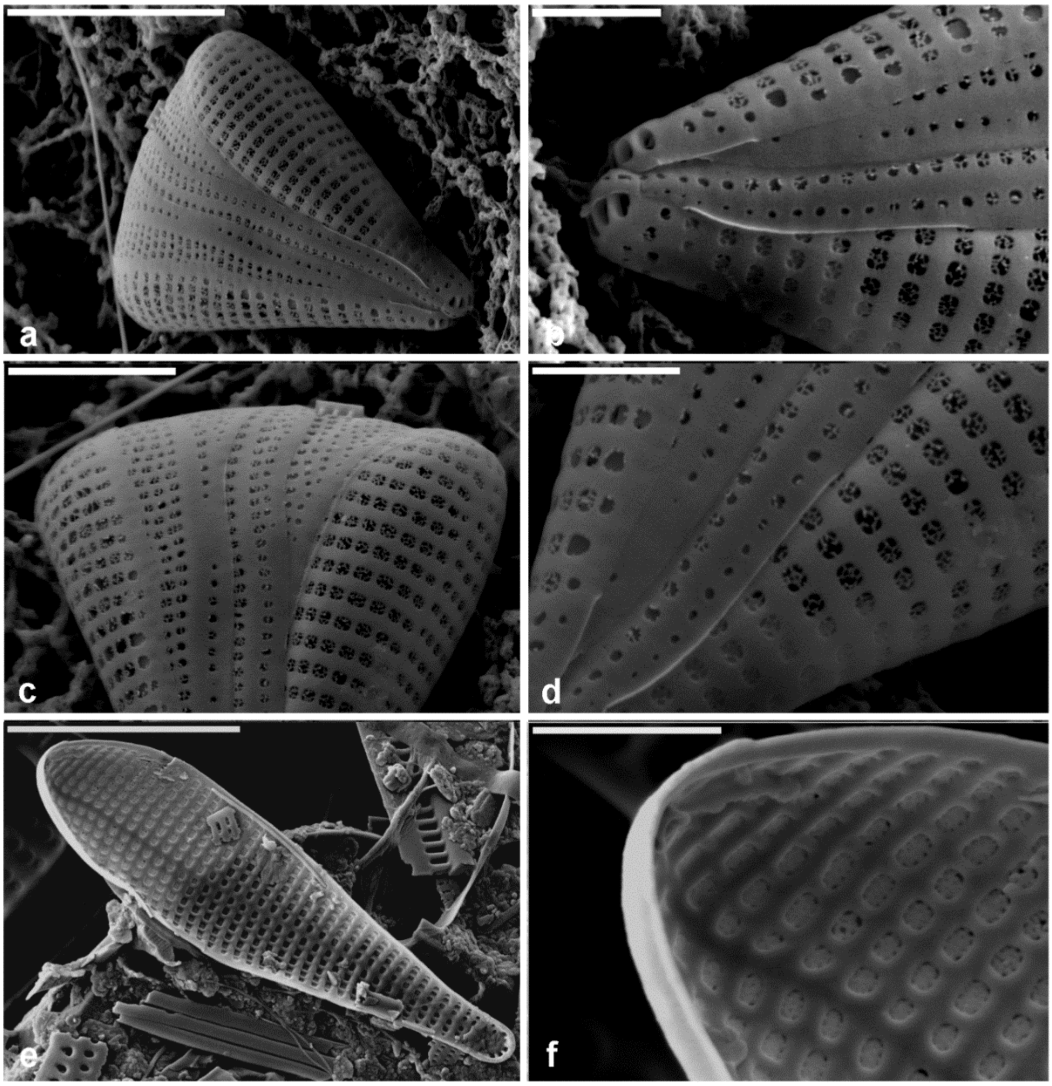
Figs a-f. SEMs of *Grammatophora* spp. Figs a-e. *Grammatophora oceanica* (Ehrenberg 1854 pro parte) Grunow. Figs a-c. External view. Figs d, e. Internal view. Fig. f. *Grammatophora macilenta* W. Smith. Internal view. Fig. g. *Grammatophora serpentina* (Ralfs) Ehrenberg. Internal view. Fig. h. *Grammatophora angulosa* var. *islandica* (Ehrenberg) Grunow. Scale bars = 20 µm (Figs a, d, f, g); 10 µm (Figs b, e); 5 µm (Fig. h); 4 µm (Fig. c).

Plate 15



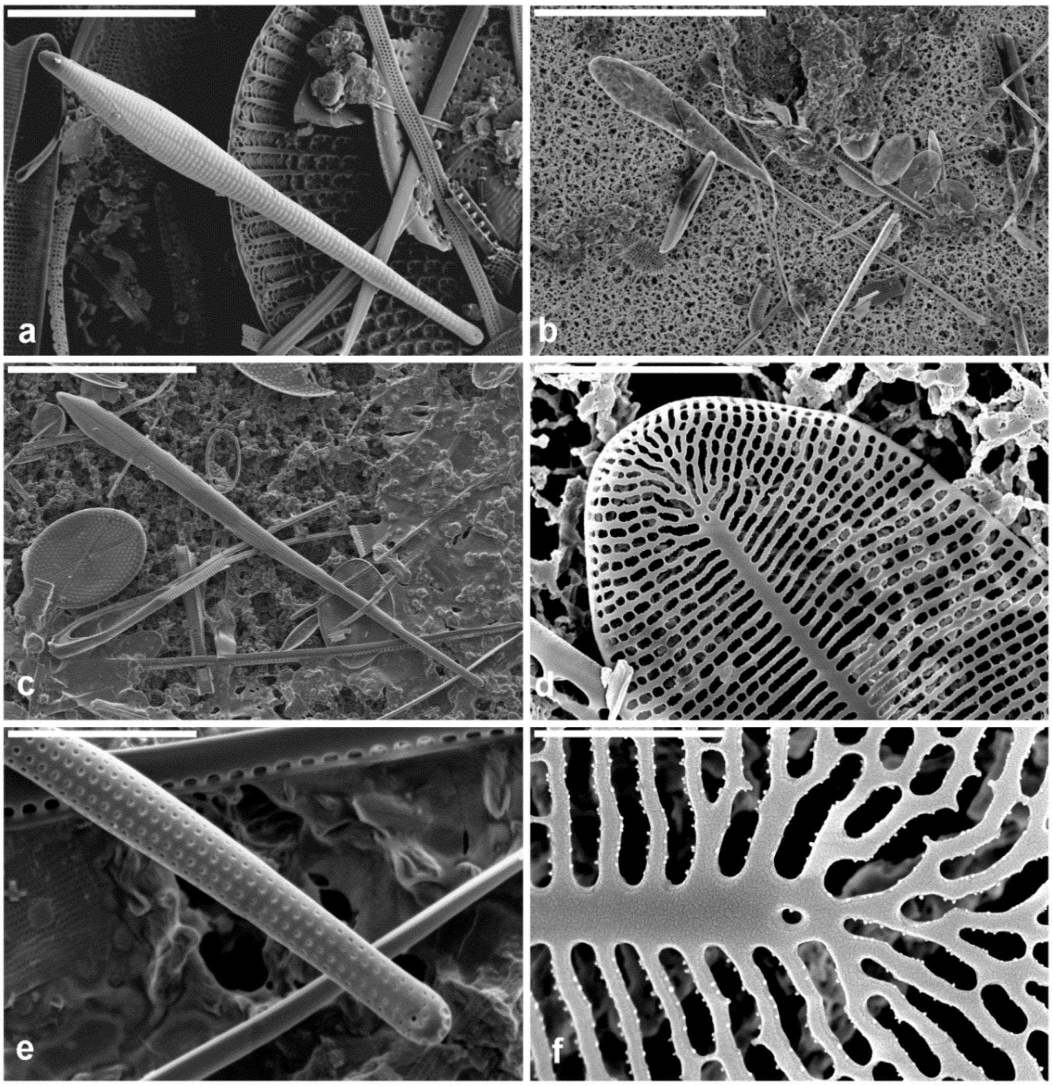
Figs a-f. SEMs of *Cyclophora* spp. Internal view. Scale bars = 10 μm (Figs a, c, d); 4 μm (Fig. b); 3 μm (Fig. e); 2 μm (Fig. f).

Plate 16



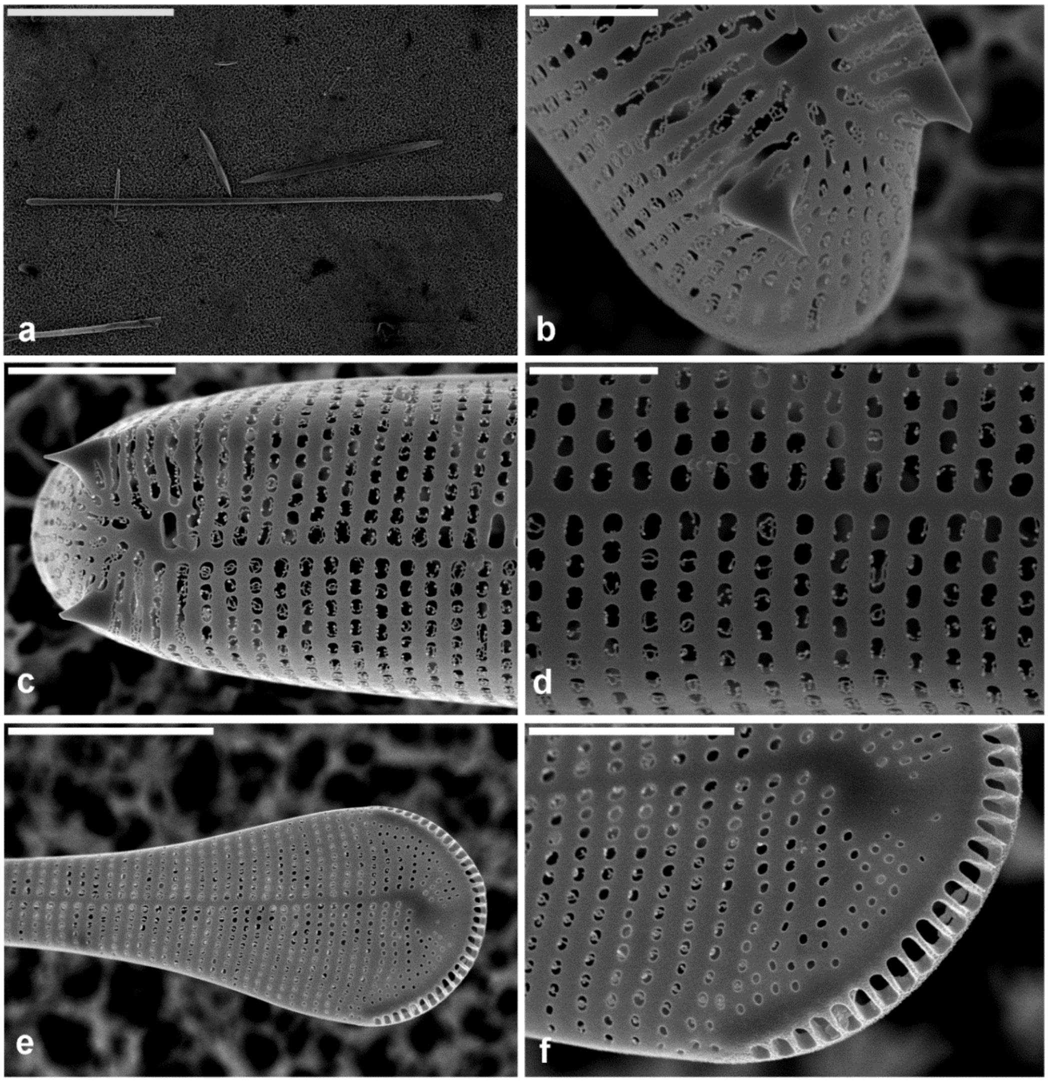
Figs a-f. *Licmophora* (SEM). Figs a-d. External view. Figs e-f. Internal view. Scale bars = 5 µm (Fig. e); 4 µm (Fig. a); 2 µm (Fig. c); 1 µm (Figs b, d, f).

Plate 17



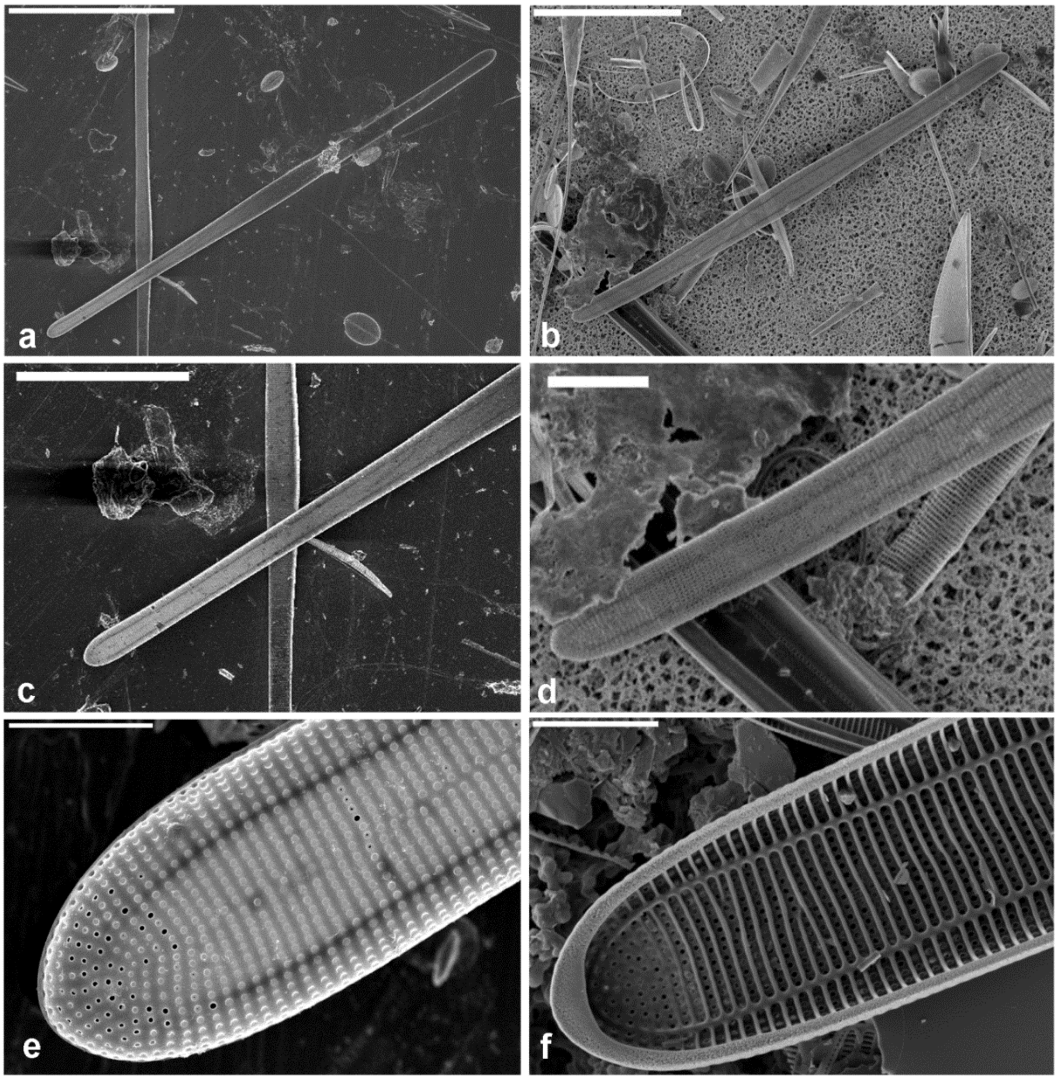
Figs a-f. SEMs of *Licmophora* spp.. Figs b, d, f. *Licmophora remulus* Grunow. Scale bars = 50 µm (Fig. b); 30 µm (Fig. c); 10 µm (Fig. a); 5 µm (Fig. e); 4 µm (Fig. d); 1 µm (Fig. f).

Plate 18



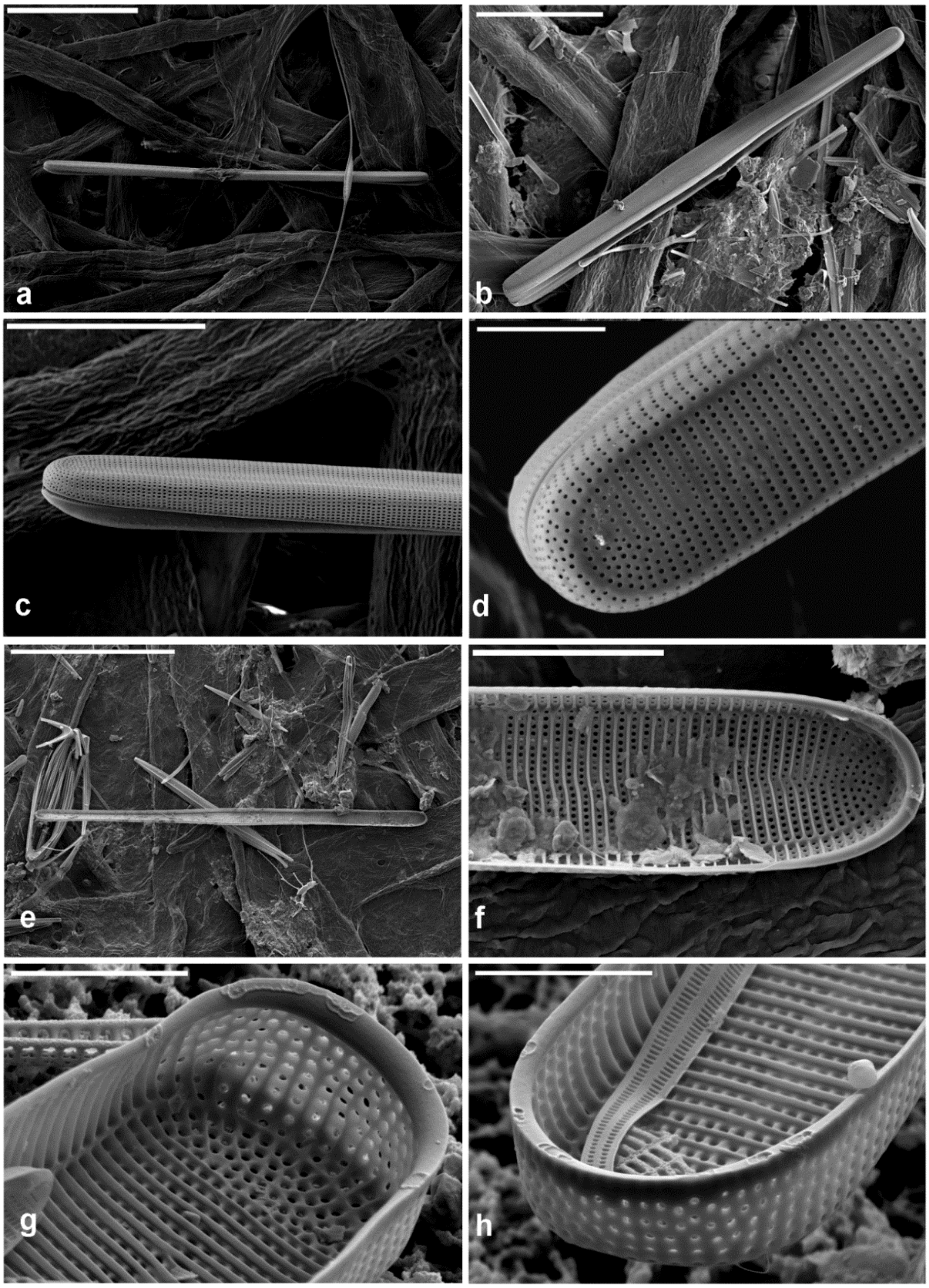
Figs a-f. *Licmophora* sp.(SEM). Scale bars = 100 µm (Fig. a); 5 µm (Fig. e); 2 µm (Figs c, f); 1 µm (Figs b, d).

Plate 19



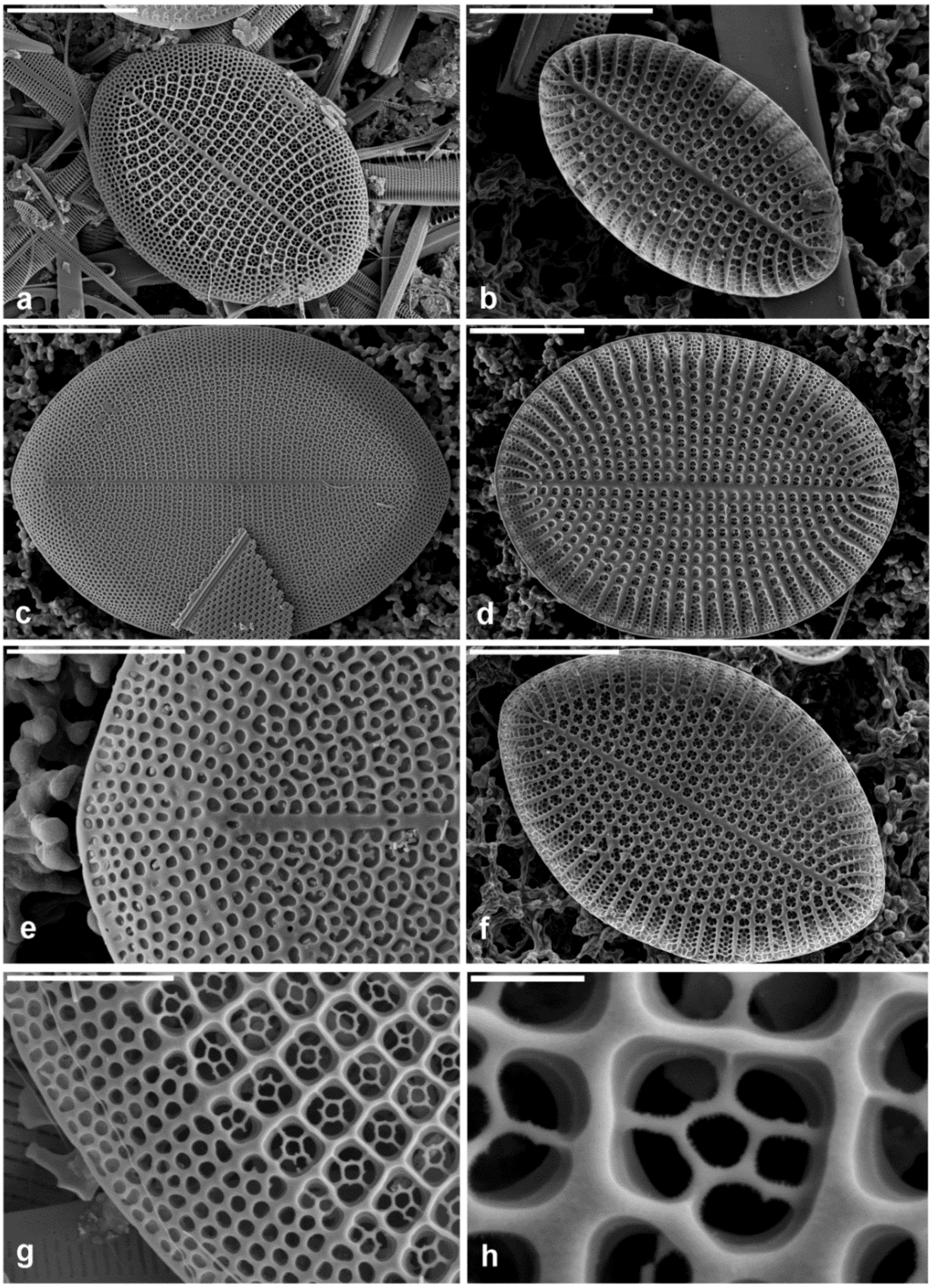
Figs a-h. *Ardessonia crystallina* (C.A. Agardh) Grunow (SEM). Figs a-e. External view. Fig. f. Internal view. Scale bars = 100 µm (Fig. a); 50 µm (Figs b, c); 10 µm (Fig. d); 5 µm (Figs e, f).

Plate 20



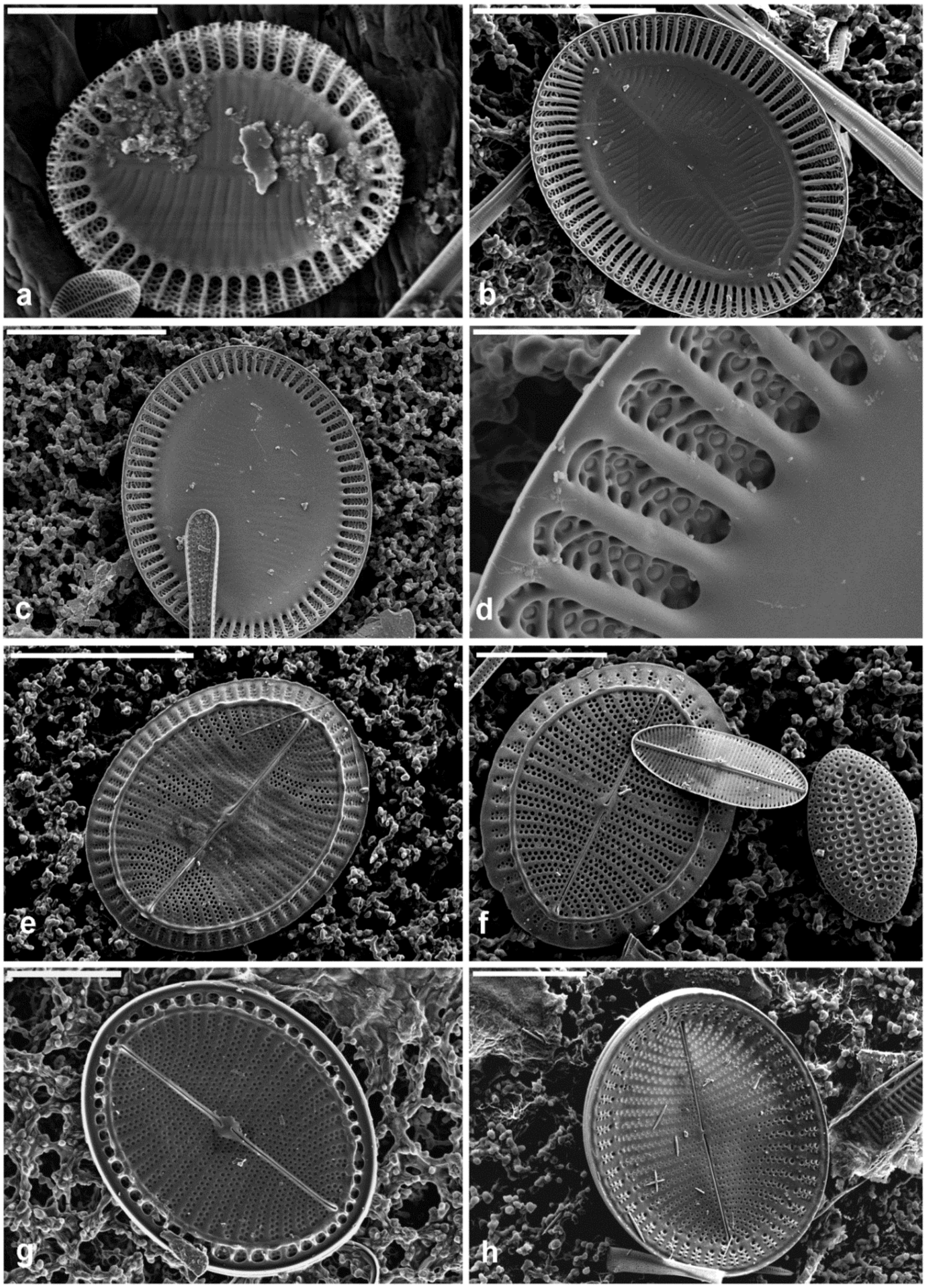
Figs a-h. *Ardessonia fulgens* (Greville) Grunow (SEM). Figs a-d. External views. Figs e-h. Internal views. Scale bars = 100 µm (Figs a, e); 50 µm (Fig. b); 30 µm (Fig. c); 10 µm (Fig. f); 5 µm (Figs d); 4 µm (Figs g, h).

Plate 21



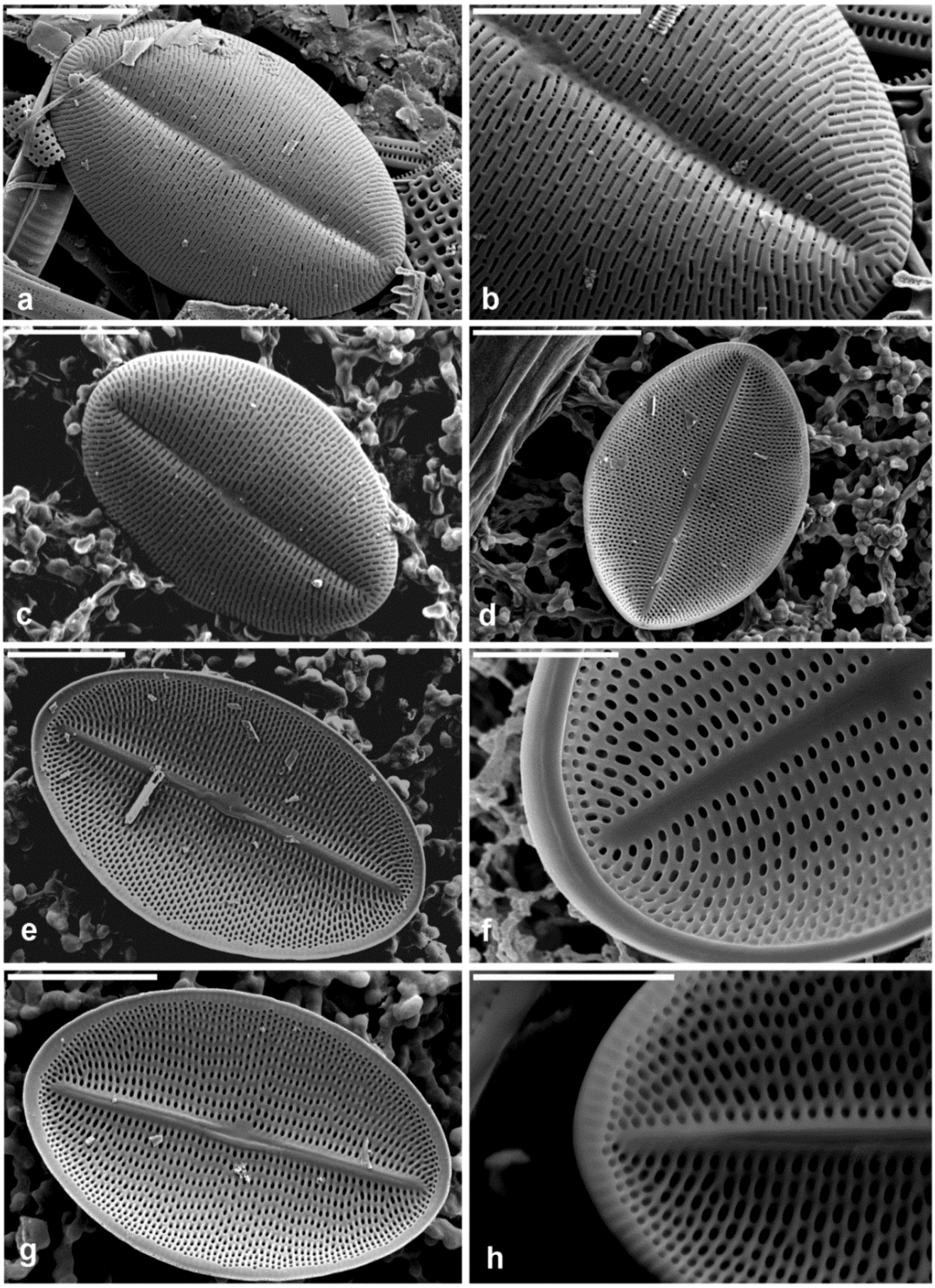
Figs a-h. *Cocconeis scutellum* Ehrenberg var. *scutellum* (SEM). Sternum valve. Figs a, c, e, g, h. External views. Figs b, d, f. Internal views. Scale bars = 10 µm (Figs a, b, c, d, f); 4 µm (Fig. e); 3 µm (Fig. g); 500 nm (Fig. h).

Plate 22



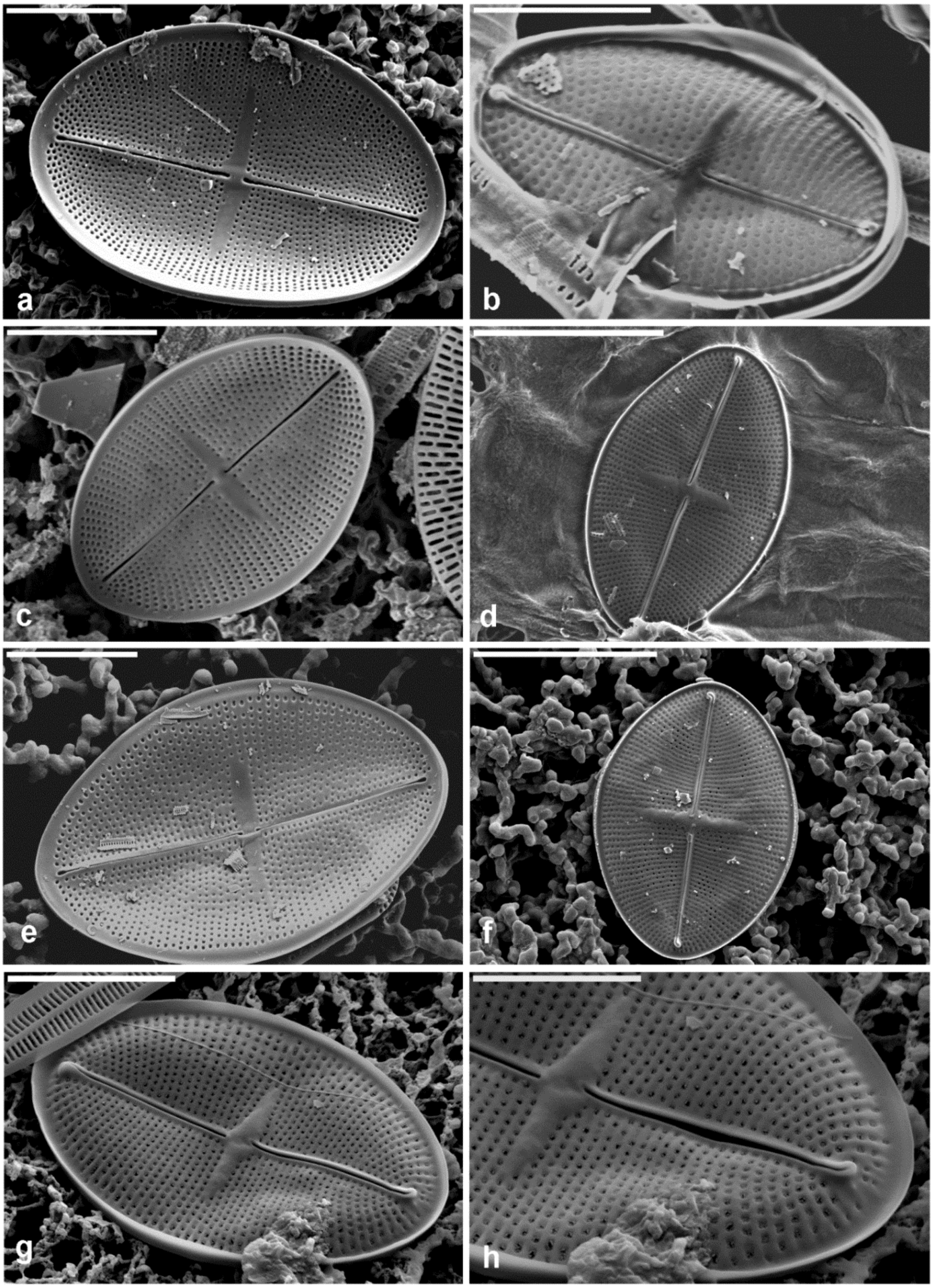
Figs a-h. SEMs of *Cocconeis* spp. Figs a-d. *Cocconeis*; sternum valves. Figs e-h. Raphe valves, internal view. Fig. h. Raphe valve, external view. Scale bars = 20 µm (Figs b, c, e, f); 10 µm (Figs a, g, h); 3 µm (Fig. d).

Plate 23



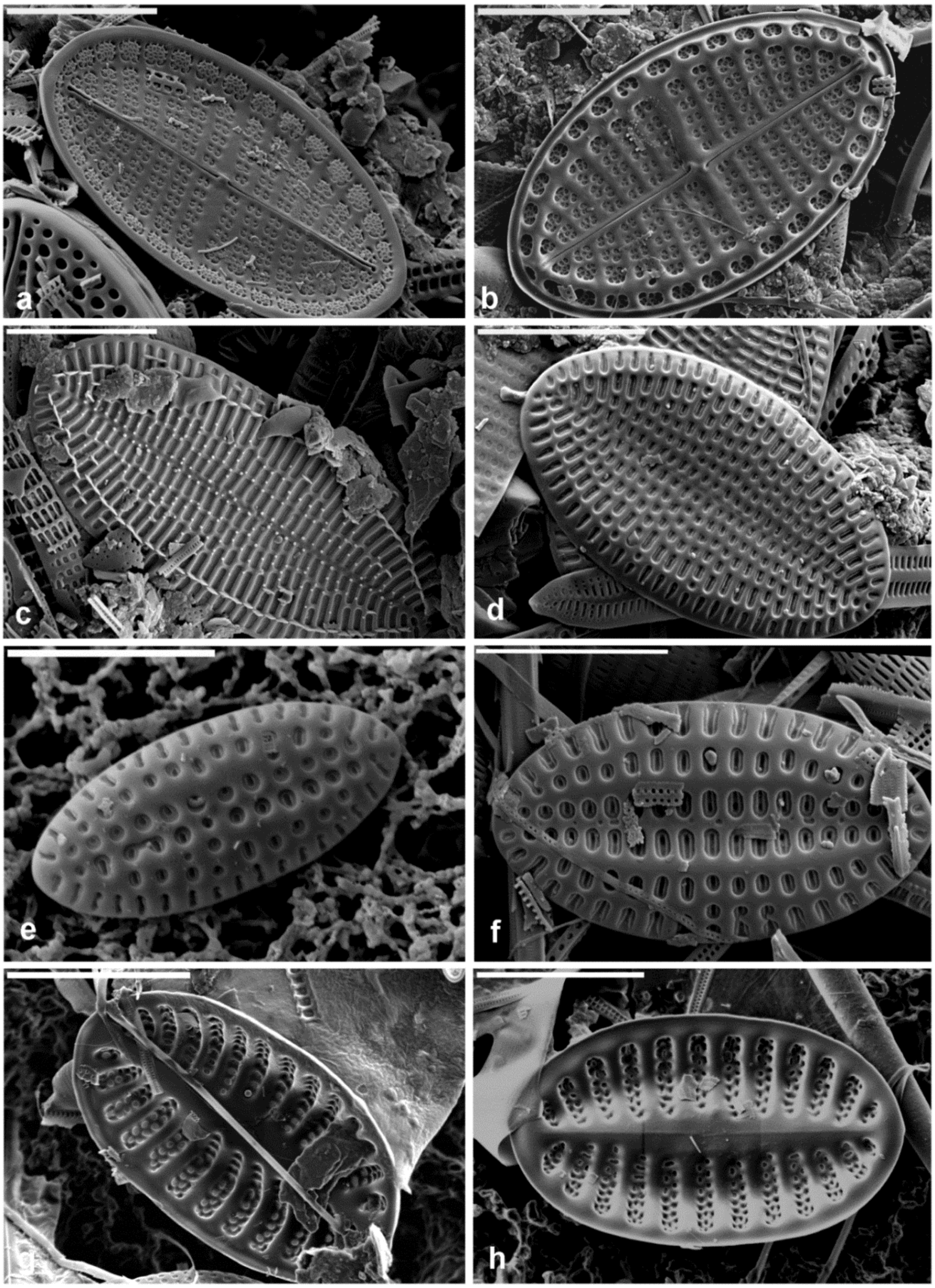
Figs a-h. *Cocconeis molesta* var. *crucifera* Greunow in Van Heurck (SEM). Figs a-c. Sternum valves, external view; Figs d-h. Sternum valves, internal view. Scale bars = 10 µm (Fig. d); 5 µm (Figs a, c, e, g); 3 µm (Figs b, h); 2 µm (Fig. f).

Plate 24



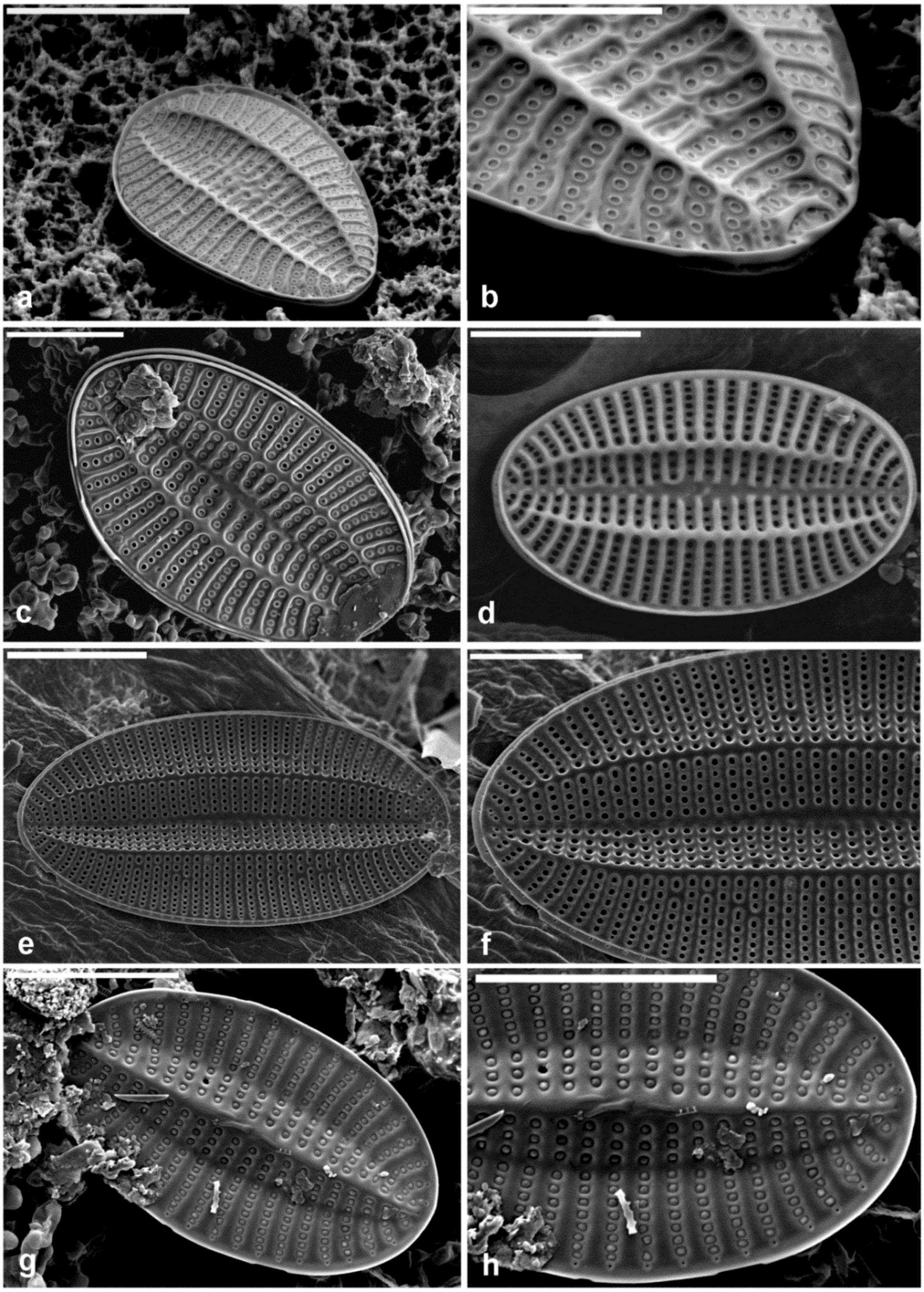
Figs a-e. *Cocconeis* (SEM). Raphe valves. Figs a, c, e. External view. Figs b, d, f, h. Internal view. Scale bars = 10 µm (Figs d, f); 5 µm (Figs a, c, e, g); 4 µm (Fig. b); 3 µm (Fig. h).

Plate 25



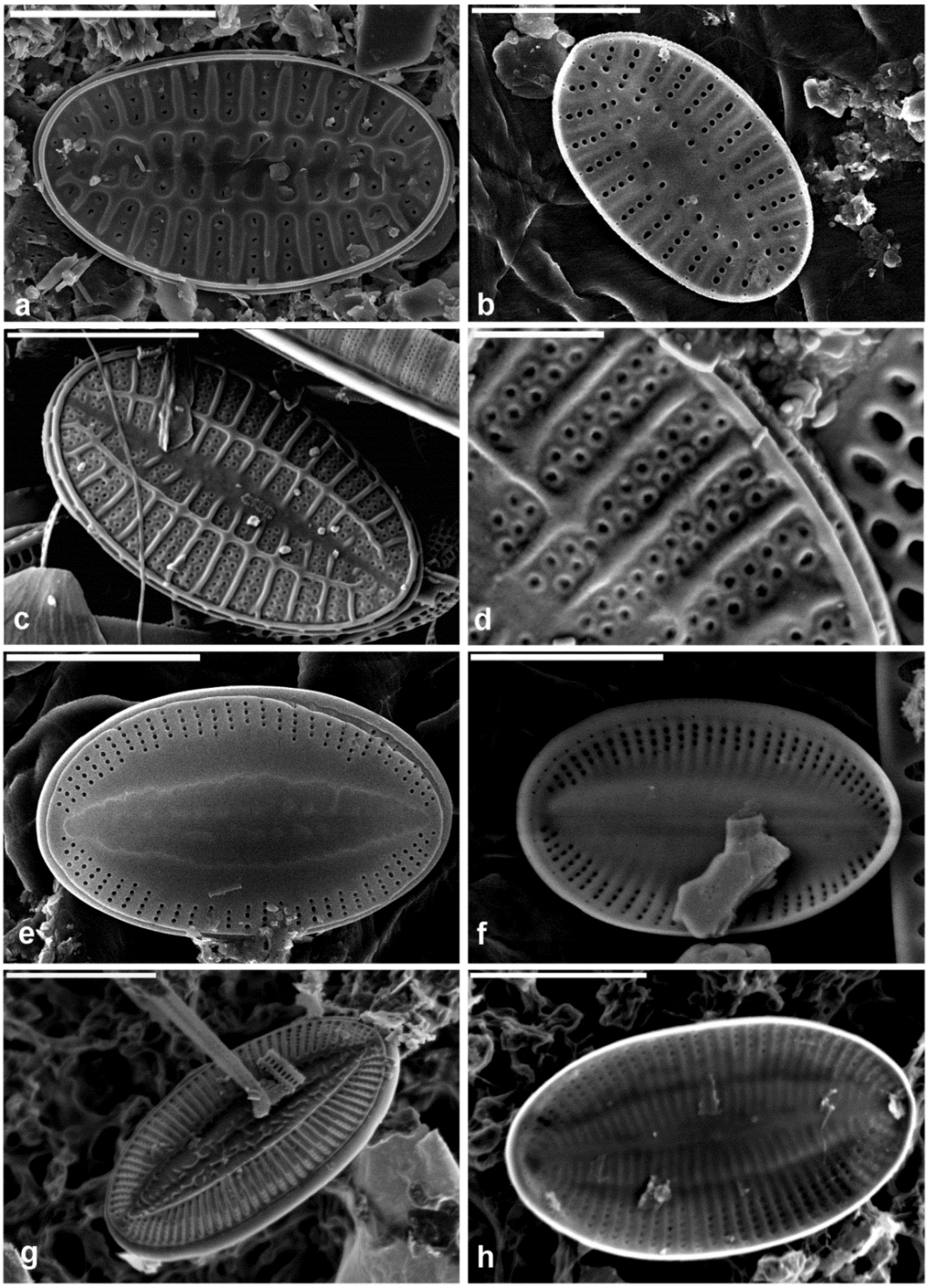
Figs a-h. SEMs of *Cocconeis* spp.. Fig. a. External views of raphe valve. Fig. b. Internal view of raphe valve. Figs g, h. *Cocconeis pinnata* Gregory ex Greville (SEM). Fig. g. External view. Fig. h. Internal view. Scale bars = 10 µm (Figs g, h); 5 µm (Figs a, b, c, d, e, f).

Plate 26



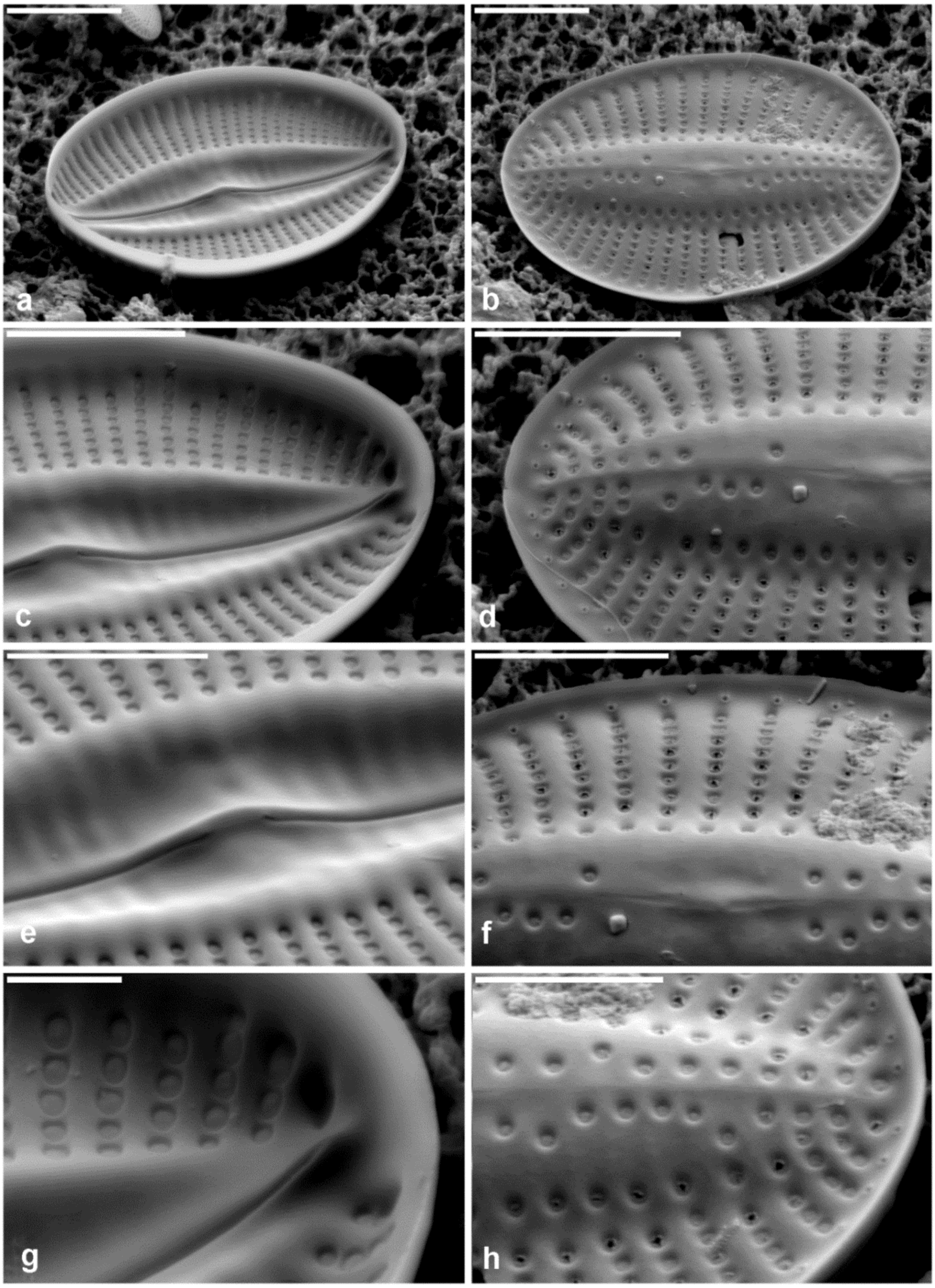
Figs a-f. *Cocconeis peltoides* Hustedt (SEM). Scale bars = 10 µm (Figs a, e); 5 µm (Figs c, d, g, f, h); 4 µm (Fig. b).

Plate 27



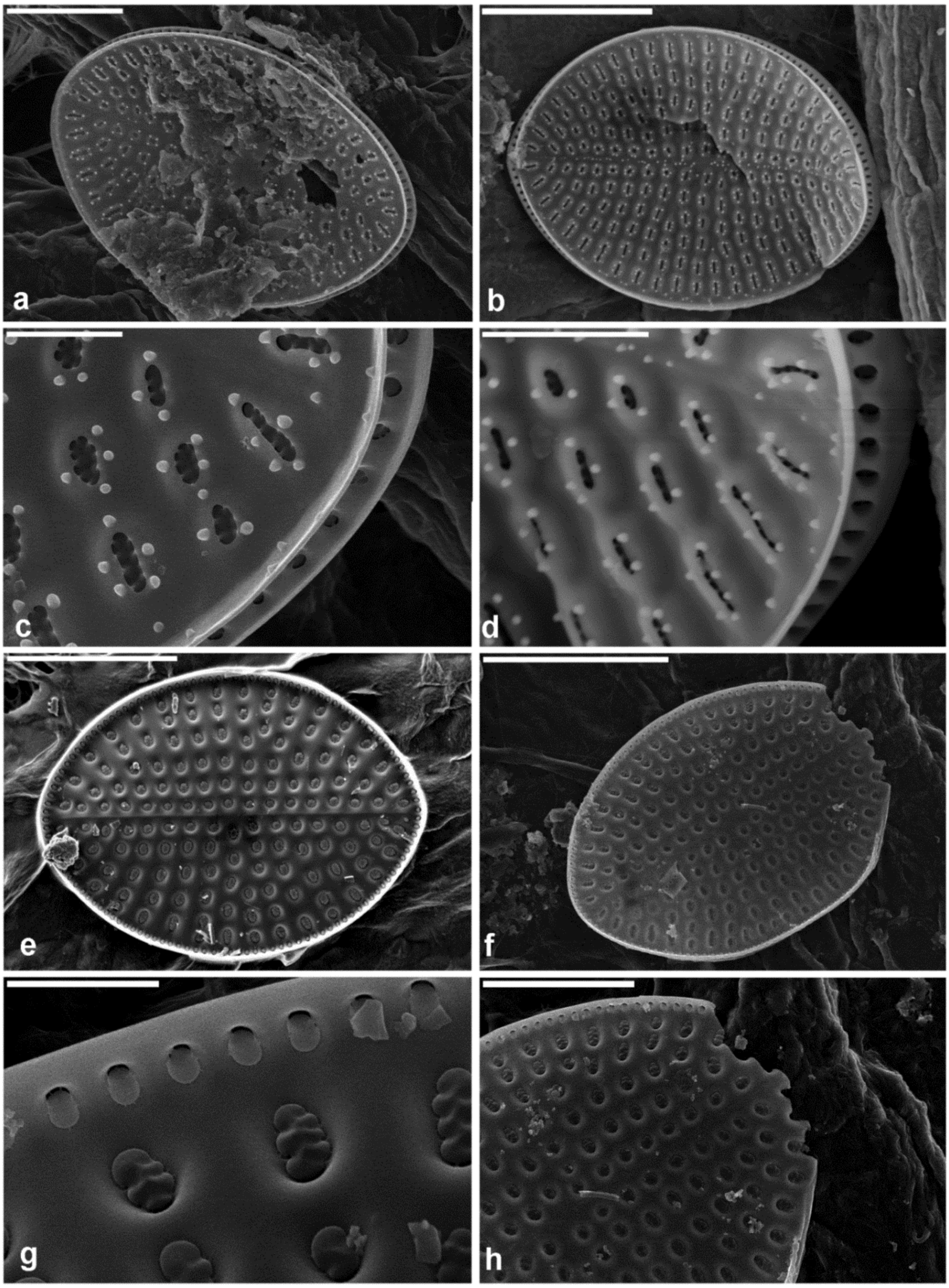
Figs a-h. SEMs of *Cocconeis* spp. Figs a-d. *Cocconeis peltoides* Hustedt (SEM). Scale bars = 5 µm (Figs a, b, g); 4 µm (Figs c, e, f, h); 1 µm (Fig. d).

Plate 28



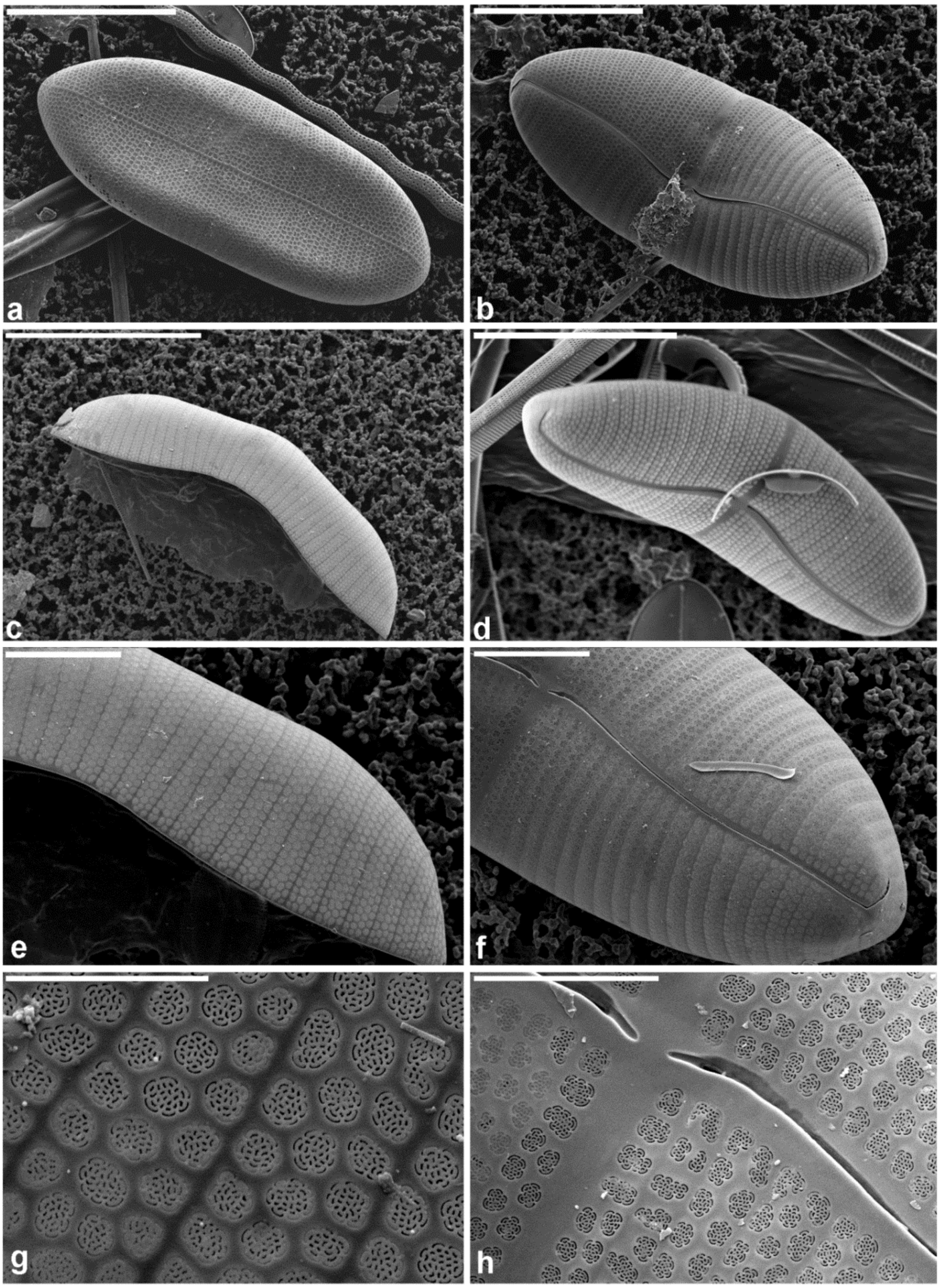
Figs a-h. *Cocconeis pelta* A. Schmidt. Figs a, c, e, g. Internal view. Figs b, d, f, h. External view. Scale bars = 5 µm (a, b, d); 4 µm (c, f); 3 µm (e, h); 1 µm (g).

Plate 29



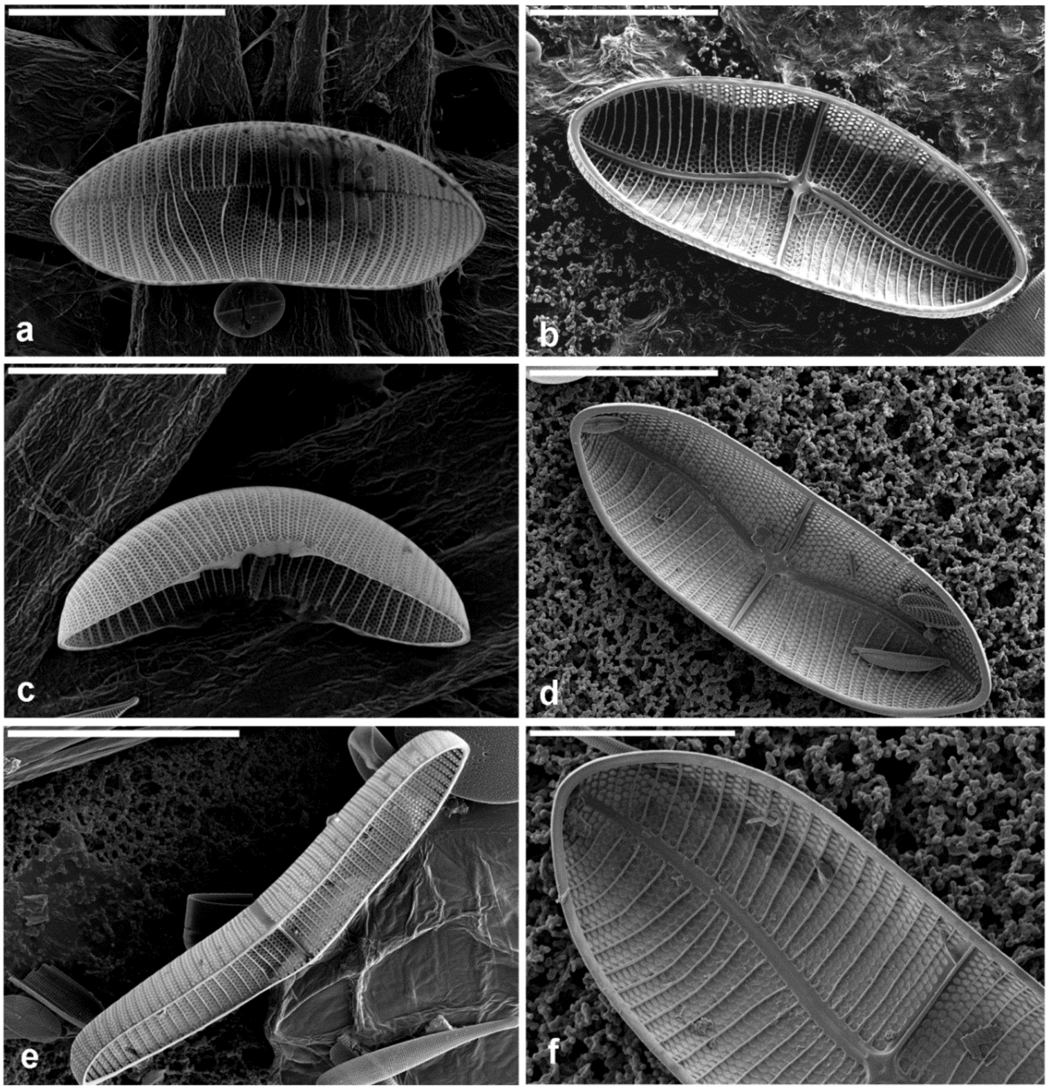
Figs a-d. *Cocconeis guttata* Hustedt in Aleem & Hustedt. Fig. e-h. *Cocconeis* sp. Scale bars = 10 µm (Figs b, e, f, h); 5 µm (Figs a); 2 µm (Fig. d); 1 µm (Figs c, g).

Plate 30



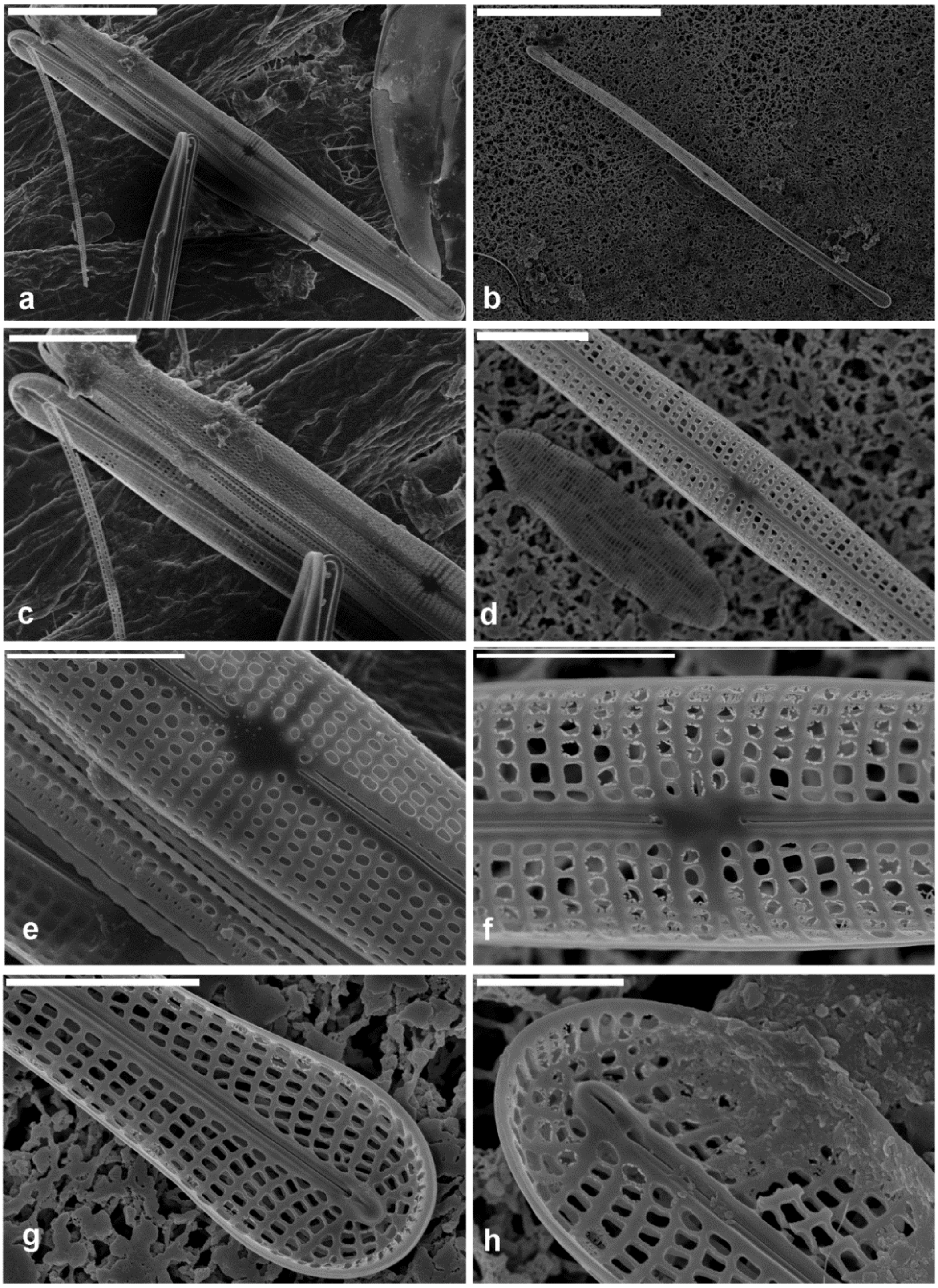
Figs a-h. *Achnanthes brevipes* C.A.A. Agardh var. *brevipes* (SEM). External view. Figs a, c, e, g. Sternum valves. Figs. b, d, f, g. Raphe valves. Scale bars = 40 µm (Fig. c); 30 µm (Figs a, b, d); 10 µm (Figs e, f); 5 µm (Fig. h); 3 µm (Fig. g).

Plate 31



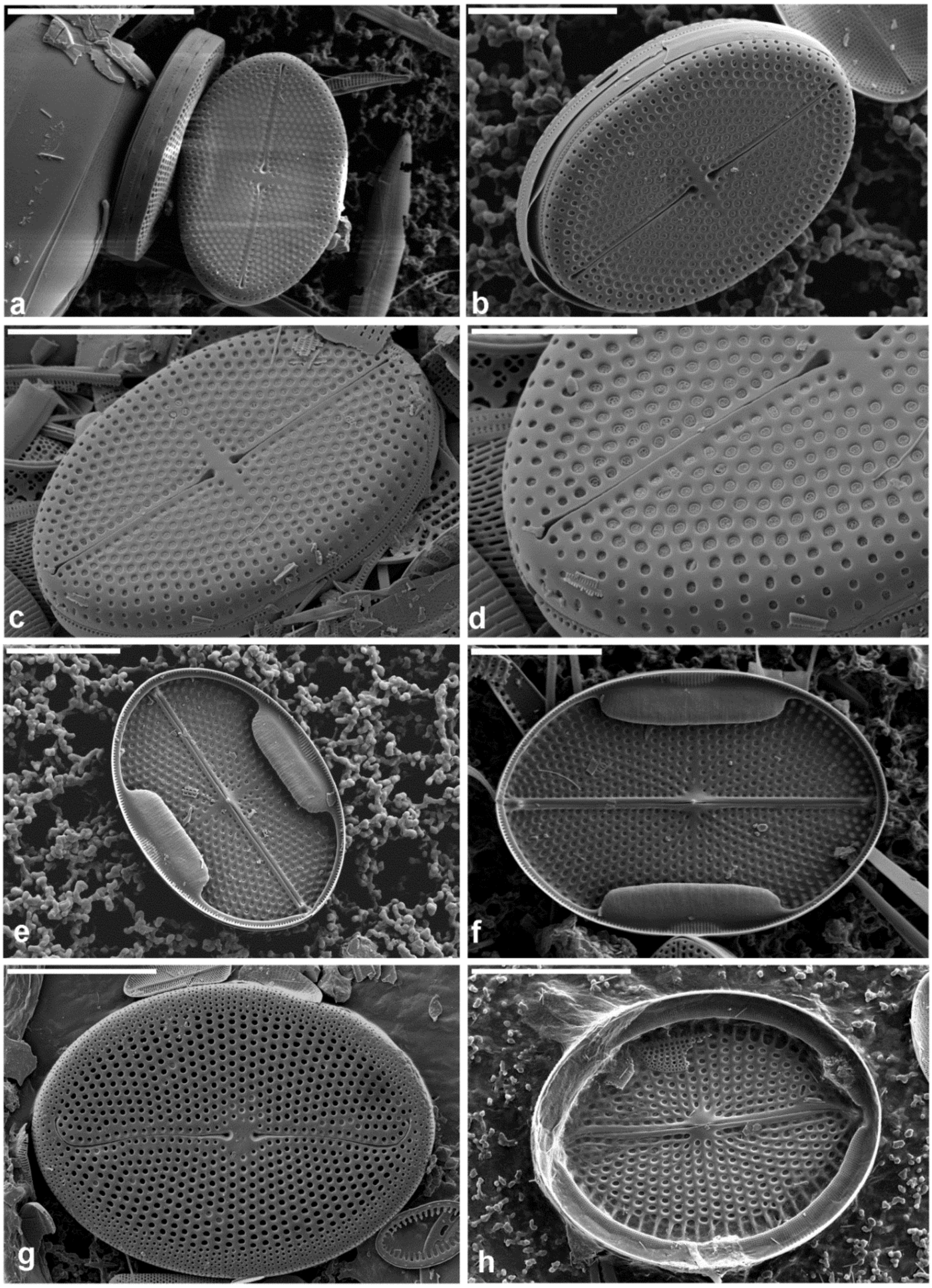
Figs a-f. *Achnanthes brevipes* C.A.A. Agardh var. *brevipes* (SEM). Figs a, c. Sternum valves. Figs b, d, f. Internal views of raphe valves. Scale bars = 50 µm (Fig. e); 40 µm (Figs a, c); 30 µm (Figs b, d); 20 µm (Fig. f).

Plate 32



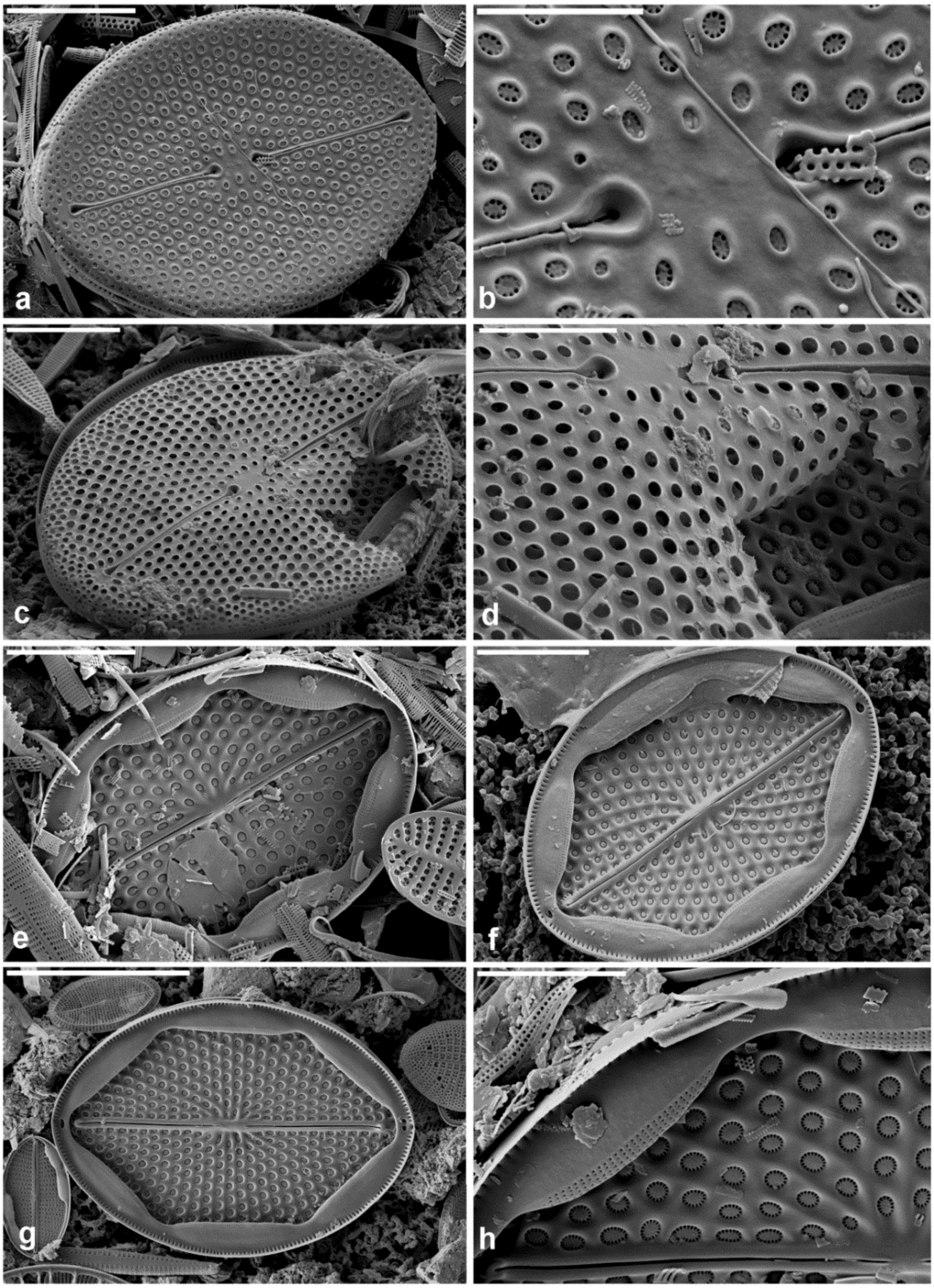
Figs a-h. *Berkeleya scopulorum* (Brébisson) Cox (SEM). Figs a, c&e. External view. Figs. b, d, f, g&h. Internal view. Scale bars = 50 µm (Fig. b); 20 µm (Fig. a); 10 µm (Fig. c); 5 µm (Fig. d); 4 µm (Fig. g); 3 µm (Fig. f); 2 µm (Fig. h):

Plate 33



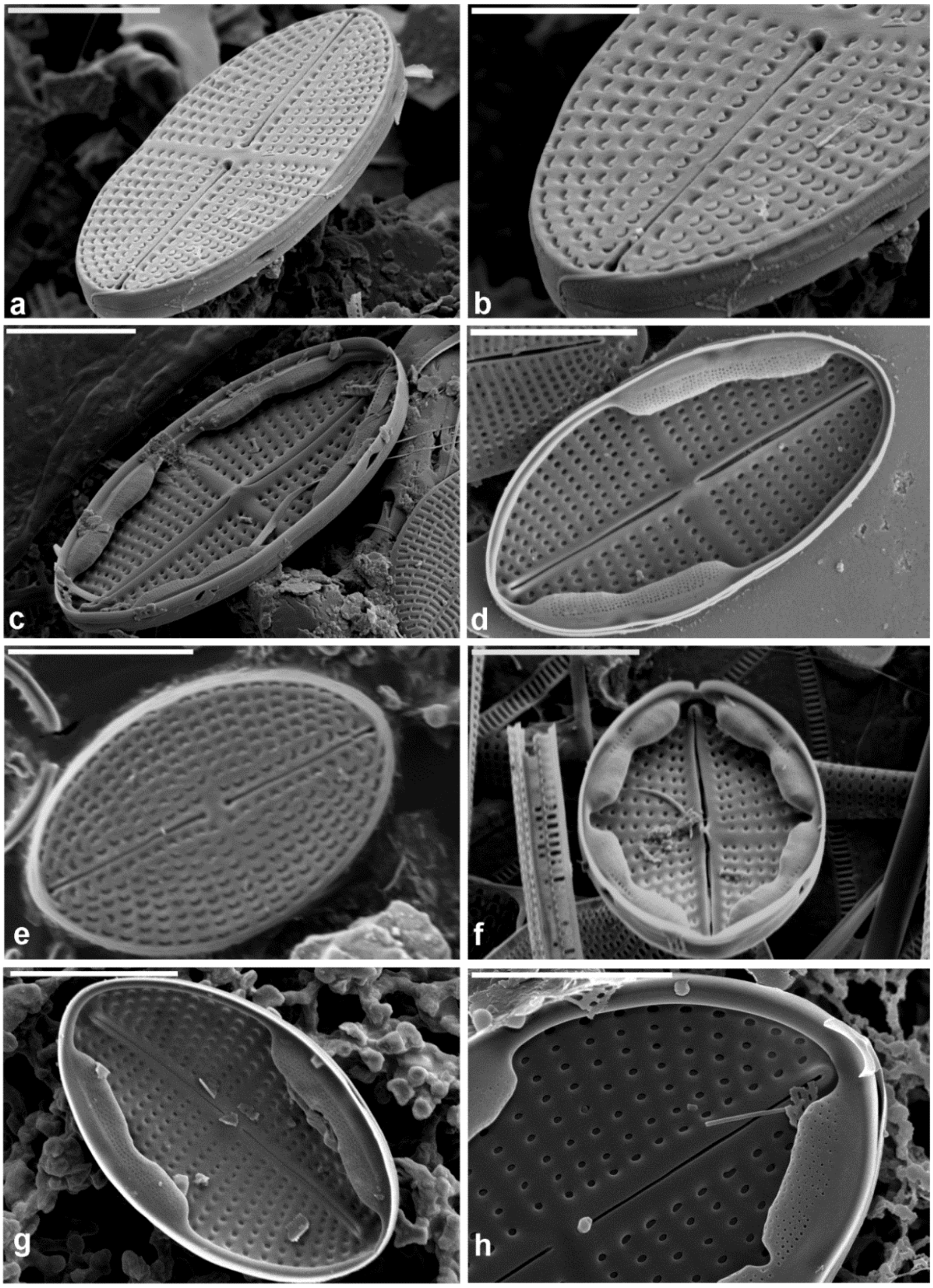
Figs a-f. *Mastogloia binotata* (Grunow) Cleve (SEM). Figs a-d. External view. Figs e&f. Internal view. Figs g&h. *Mastogloia splendida* (Gregory) Cleve (SEM). Fig. g. External valve view. Fig. h. Internal valve view. Scale bars = 20 µm (Figs a, g, h); 10 µm (Figs b, c, e, f); 5 µm (Fig d).

Plate 34



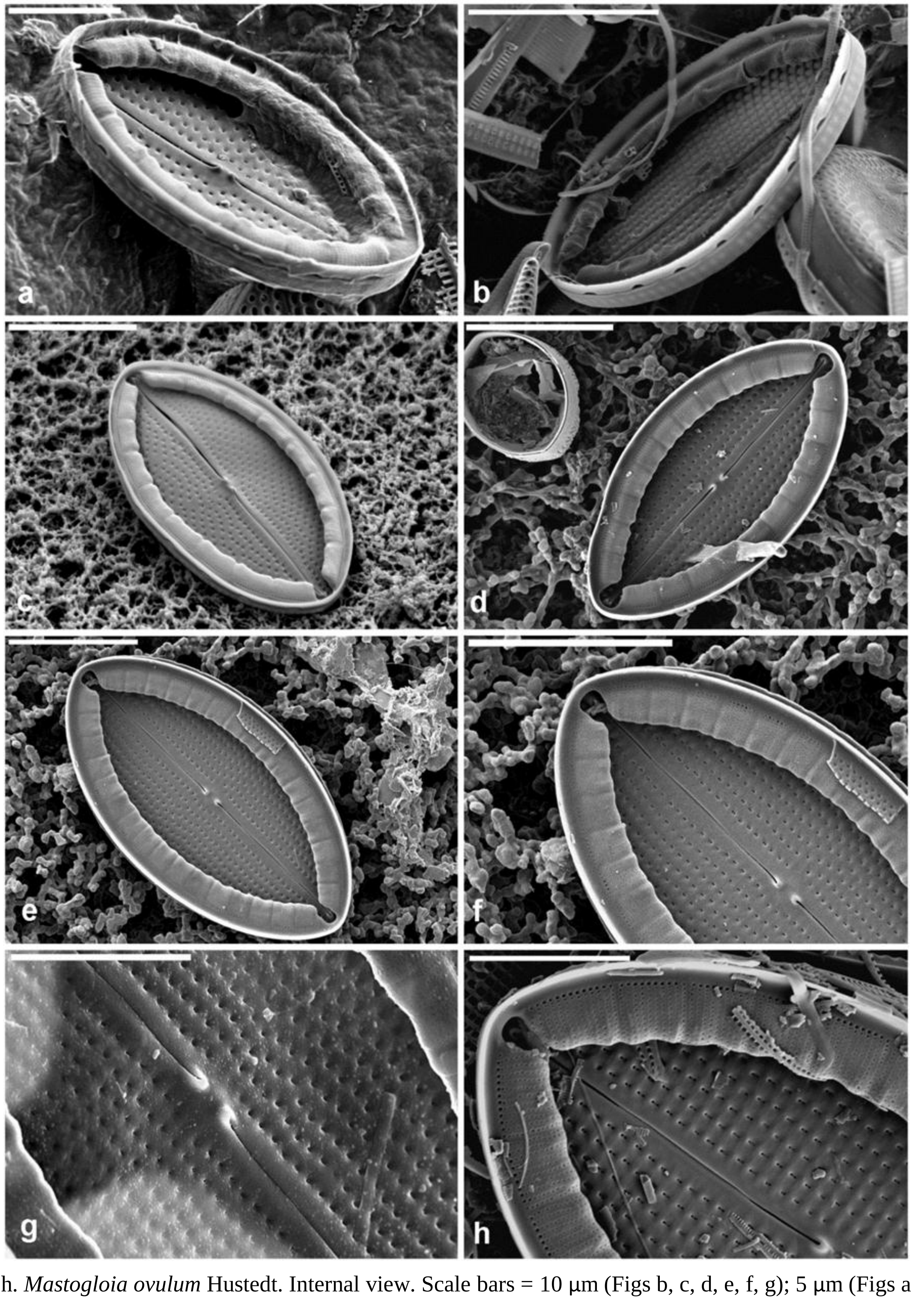
Figs a-h. *Mastogloia fimbriata* (Brightwell) Cleve (SEM). Figs a-d. External valve view. Fig. b. External detail of areolae. Figs e-h. Internal valve view. Note specialized valvocopula that develops into a series of hollow chambers or partecta attached to each other to form a well-developed partectal ring running along the inner side of the girdle band. Scale bars = 20 µm (Fig. g); 10 µm (Figs a, c, e, f); 5 µm (Figs d, h); 3 µm (Fig. b).

Plate 35



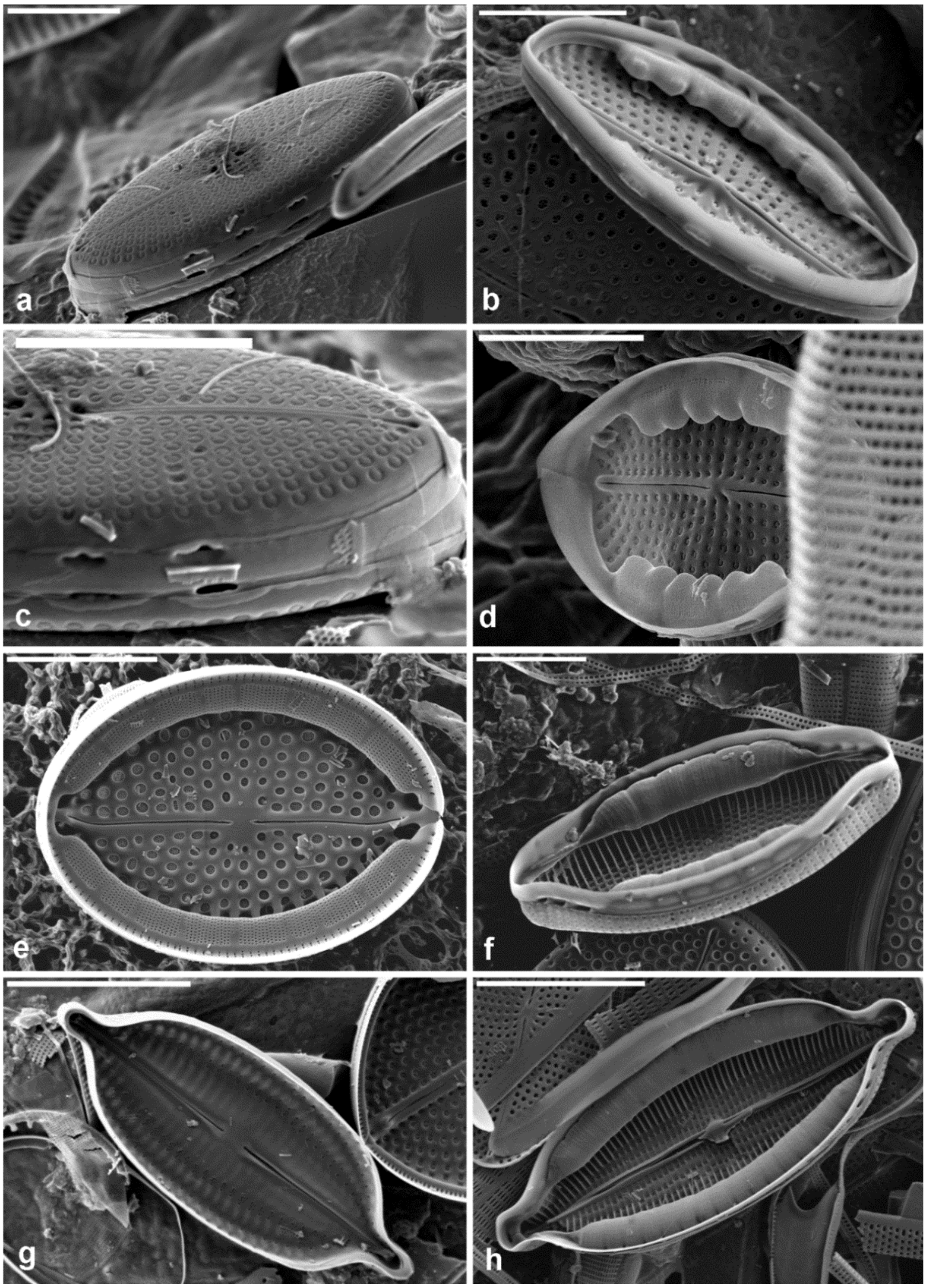
Figs a-h. SEMs of *Mastogloia* spp. Figs a-c. *Mastogloia crucicula* (Grunow) Cleve var. *crucicula*. Figs a&b. External view; Fig. c. Internal view. Fig. d. *Mastogloia crucicula* var. *alternans*; internal view. Fig. e. External view of *Mastogloia* sp. Figs g-h. *Mastogloia ovulum* Hustedt; internal view. Scale bars = 5 μm (Figs a, c, d, e, f, g); 3 μm (Figs b, h).

Plate 36



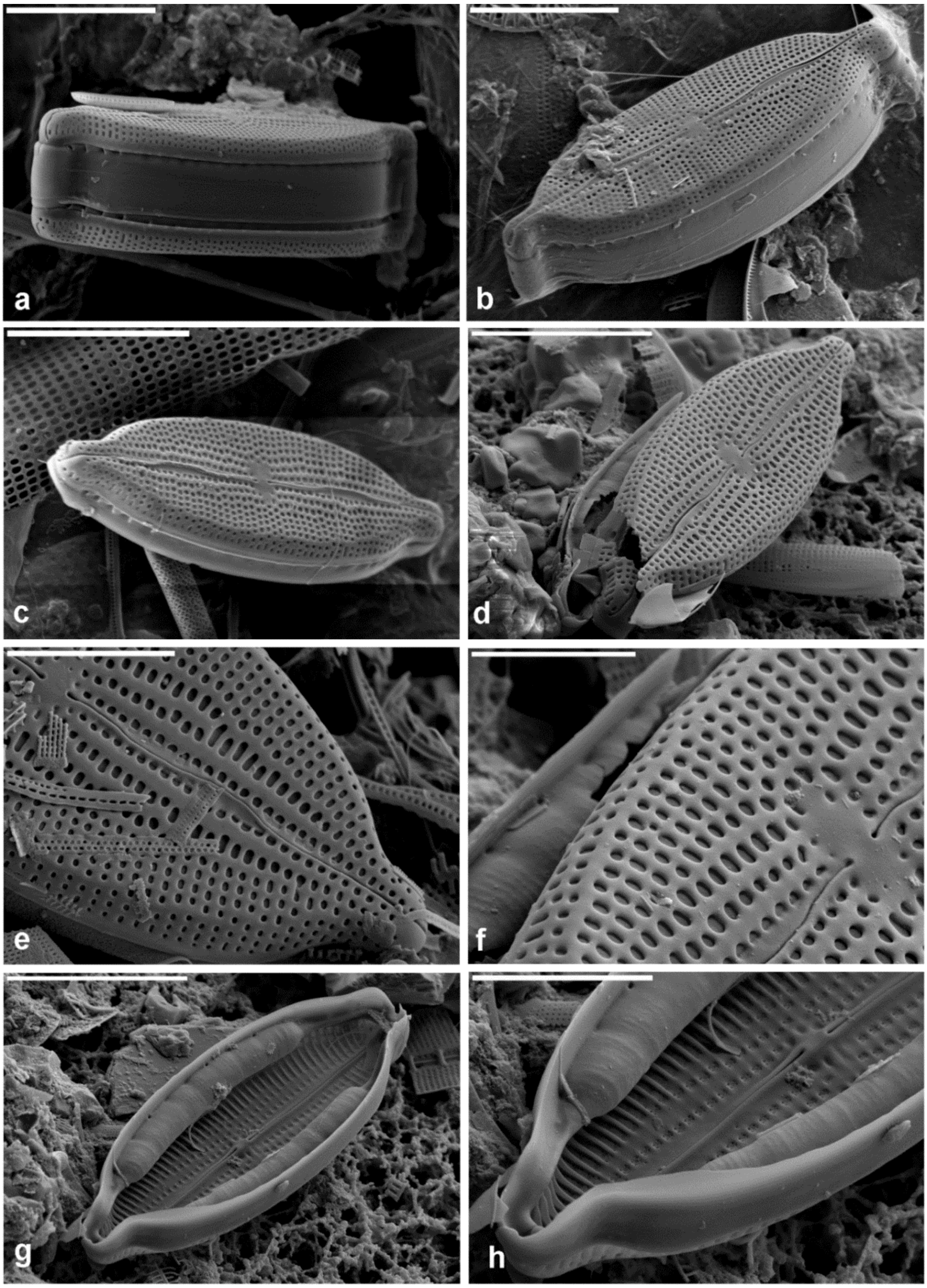
Figs a-h. *Mastogloia ovulum* Hustedt. Internal view. Scale bars = 10 µm (Figs b, c, d, e, f, g); 5 µm (Figs a, h).

Plate 37



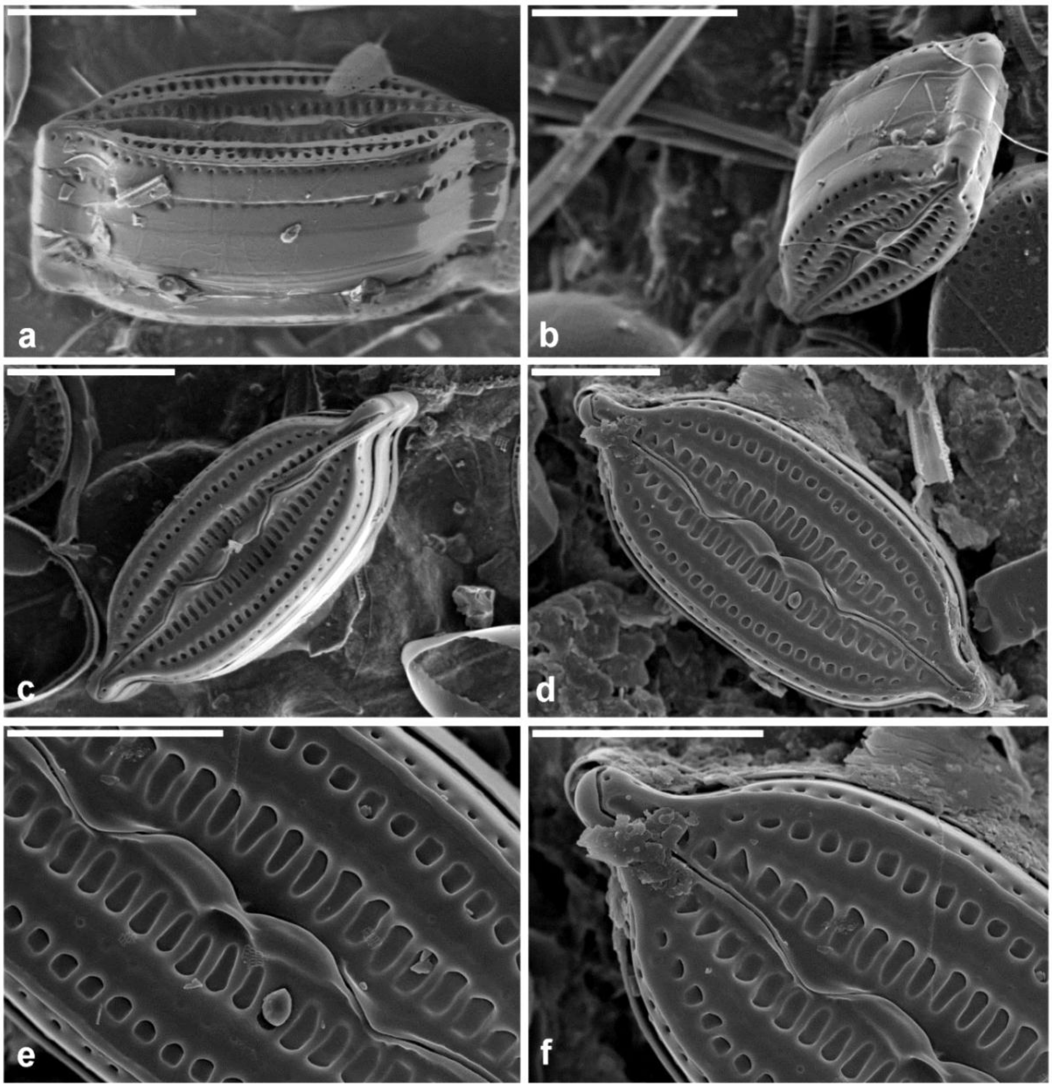
Figs a-h. SEMs of *Mastogloia* spp. Figs a-d. *Mastogloia ovalis*: a&c. External valve view: b&d. Internal valve view. Note partectal chambers on its valvocopulae. Fig. e. *Mastogloia*; Fig. f. *Mastogloia* ; Fig. g. *Mastogloia* ; Fig. h. *Mastogloia* (SEM). Scale bars = 10 µm (Figs e, g, h); 5 µm (Figs a, b, c, d, f).

Plate 38



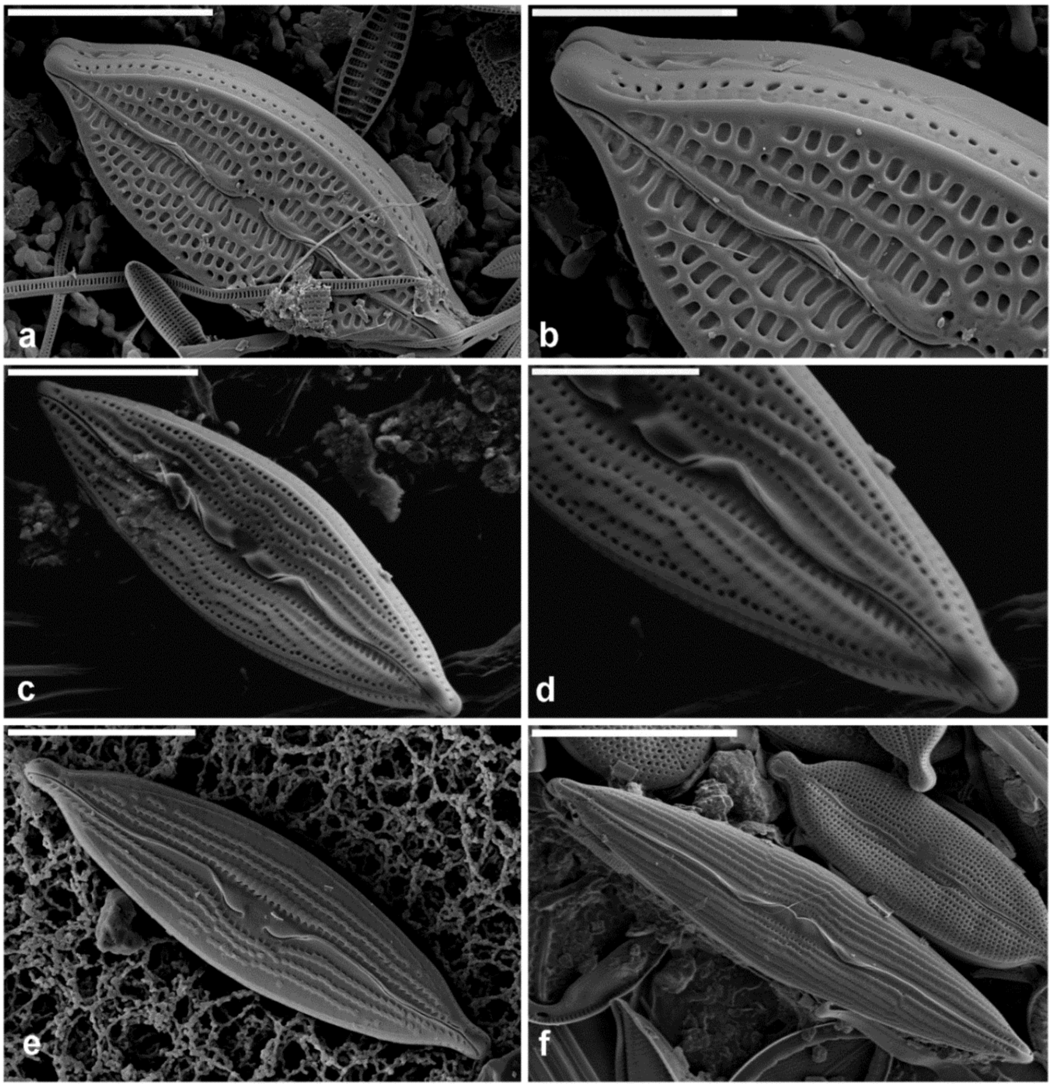
Figs a-h. *Mastogloia ignorata* Hustedt, Figs a-f. External valve view, Figs g-h. Internal valve view SEM. Scale bars = 10 µm (Figs a, b, c, d, g), 5 µm (Figs e, h), 3 µm (Fig. f).

Plate 39



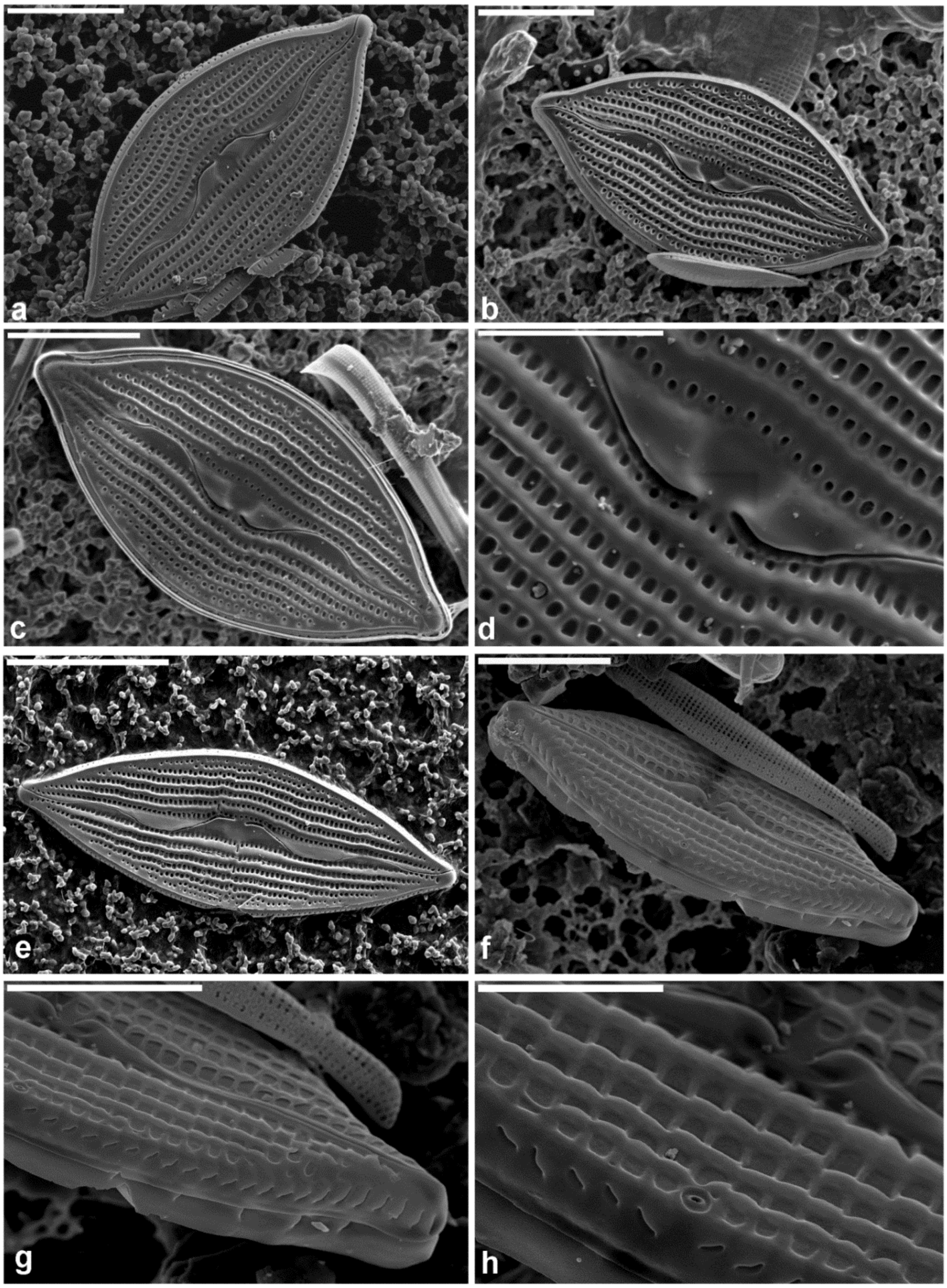
Figs a-f. *Mastogloia corsicana* Grunow in Cleve & Möller: External valve view, SEM. Scale bars = 10 µm (Figs a, b, c), 5 µm (Figs d, f), 4 µm (Fig. e).

Plate 40



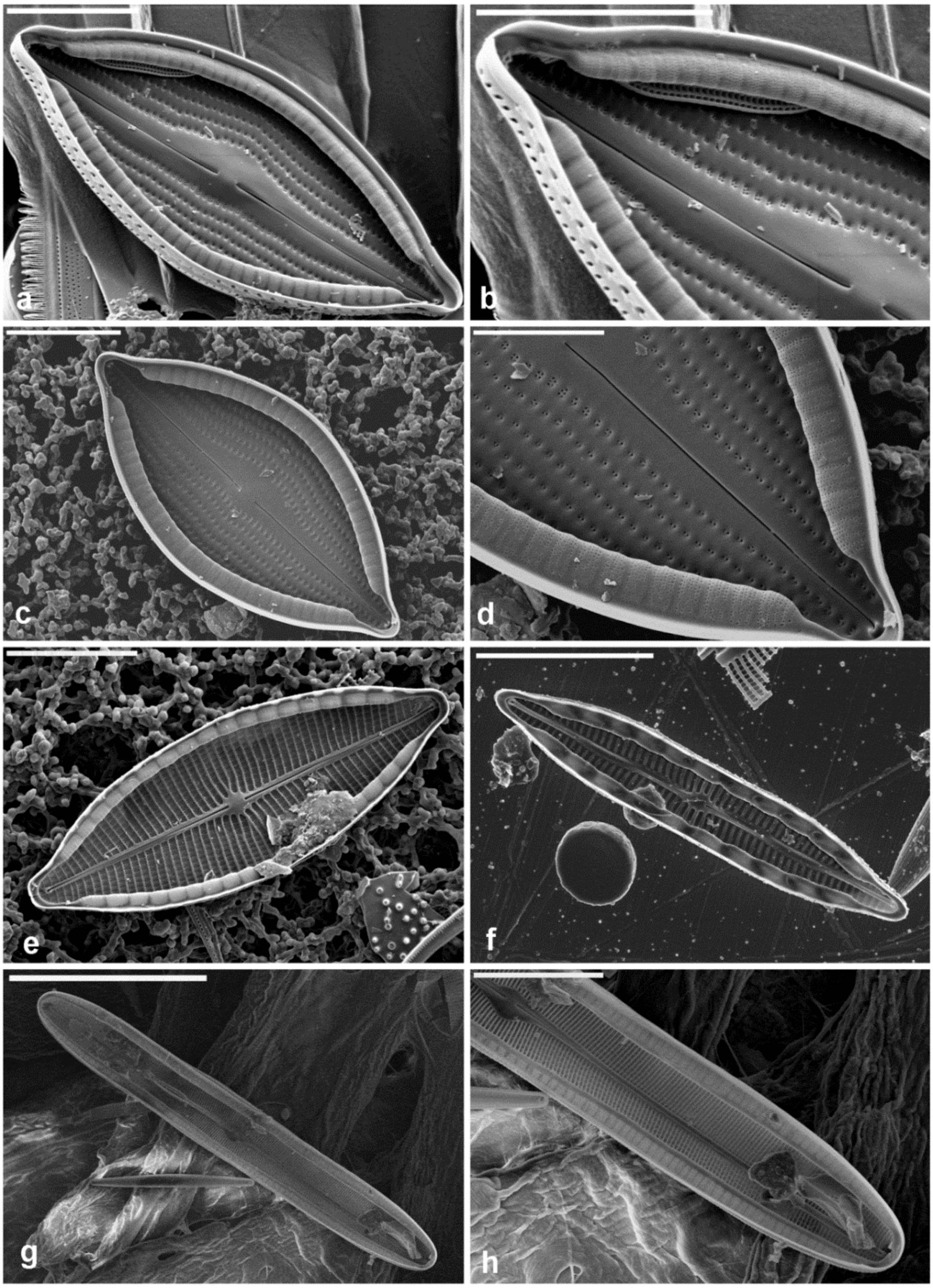
Figs a-h. SEMs of *Mastogloia* spp. External valve views. Figs c-f. *Mastogloia* cf. *erythraea* Grunow var. *erythraea* (SEM). External valve view, SEM. Scale bars = 20 µm (Fig. f); 10 µm (Fig. a, c, e); 5 µm (Figs b, d).

Plate 41



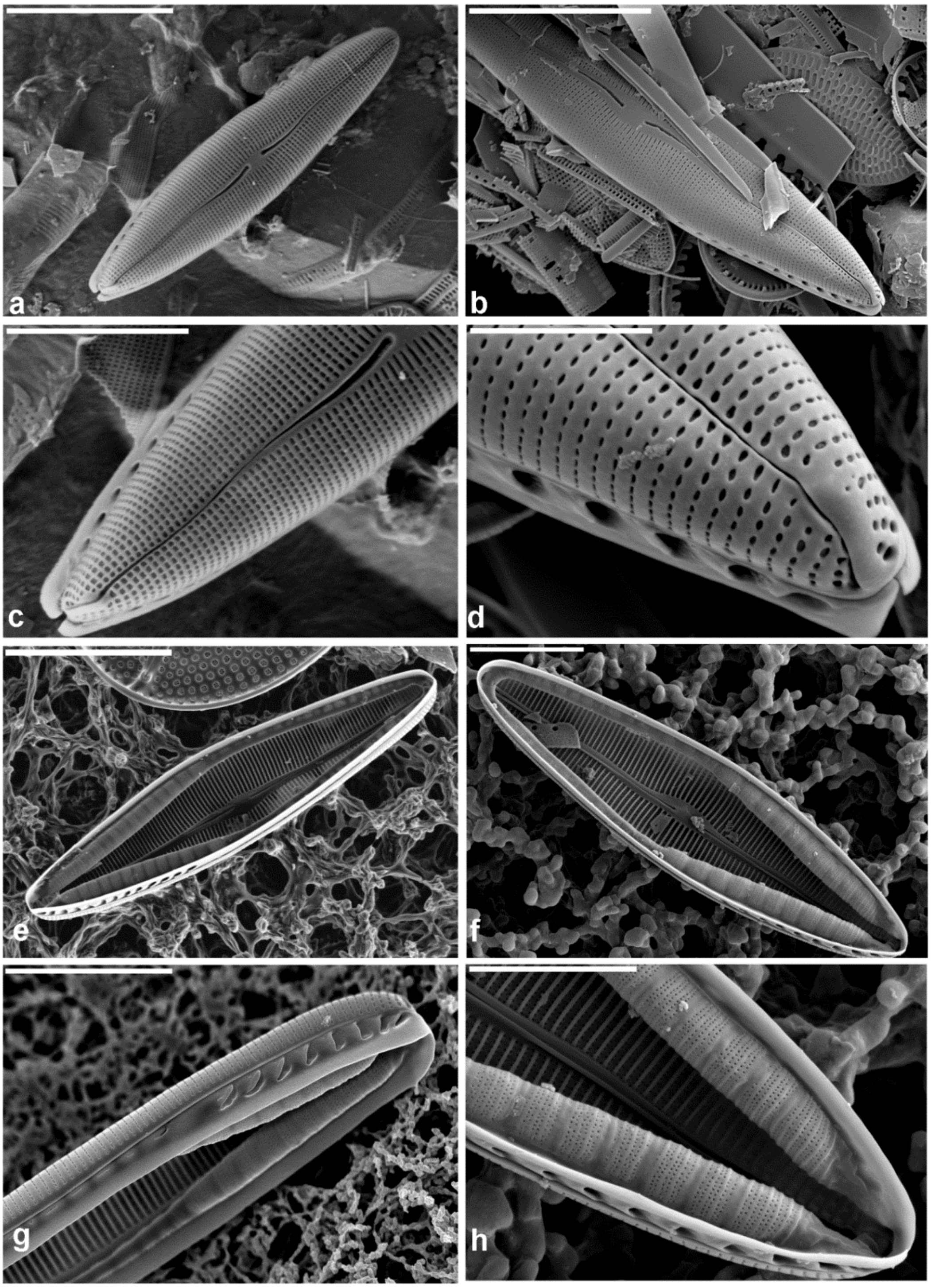
Figs a-h. SEMs of *Mastogloia* spp. External valve views. Scale bars = 20 µm (Fig. e); 10 µm (Figs a, b, c); 5 µm (Figs f, d); 4 µm (Fig. g); 2 µm (Fig. h).

Plate 42



Figs a-h. SEMs of *Mastogloia* spp. Figs a-d. *Mastogloia cyclops* Voigt; Fig. e. *Mastogloia*; Fig. f. *Mastogloia regula* Hustedt; Figs g-h. *Mastogloia*. Scale bars = 30µm (Fig. g); 10µm (Figs a, b, c, e, f, h); 5µm (Fig. d).

Plate 43



Figs a-h. *Mastogloia cuneata* (Meister) Simonsen. Figs a-d. External valve view. Figs e-h. Internal valve view. Scale bars = 10μm (Figs a, b, e); 5μm (Figs c, f, g); 3μm (Fig. h); 2μm (Fig. d).

Plate 44

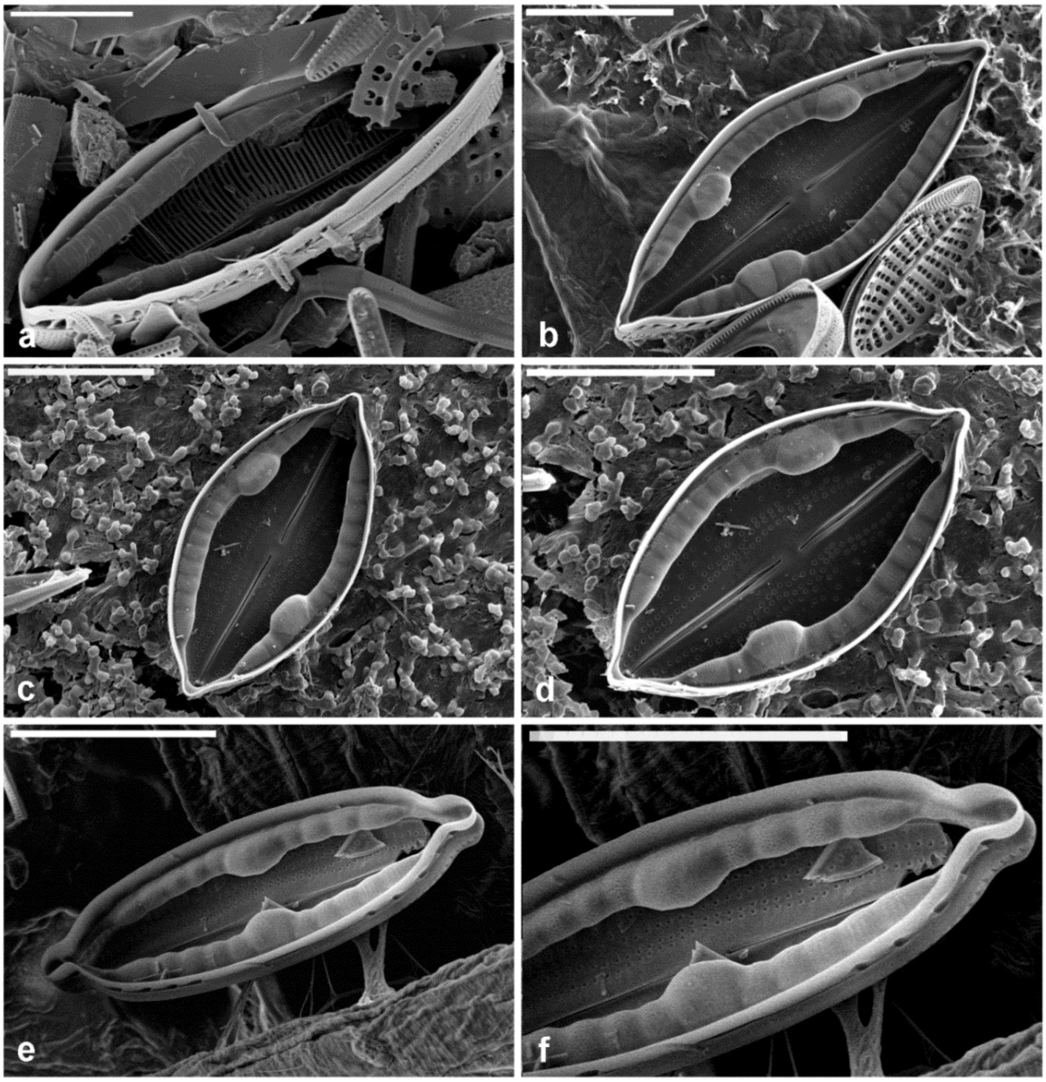


Fig. a. *Mastogloia inaequalis* Cleve. Internal view of frustule showing partectal ring. Figs b-d. *Mastogloia erythraea* var. *grunowii* Foged. Figs e-f. *Mastogloia biocellata* (Grunow) Novarino & Muftah. Figs a-f. Internal valve view. Scale bars = 10 µm (Figs b, c, d, e, f); 5 µm (Fig. a).

Plate 45

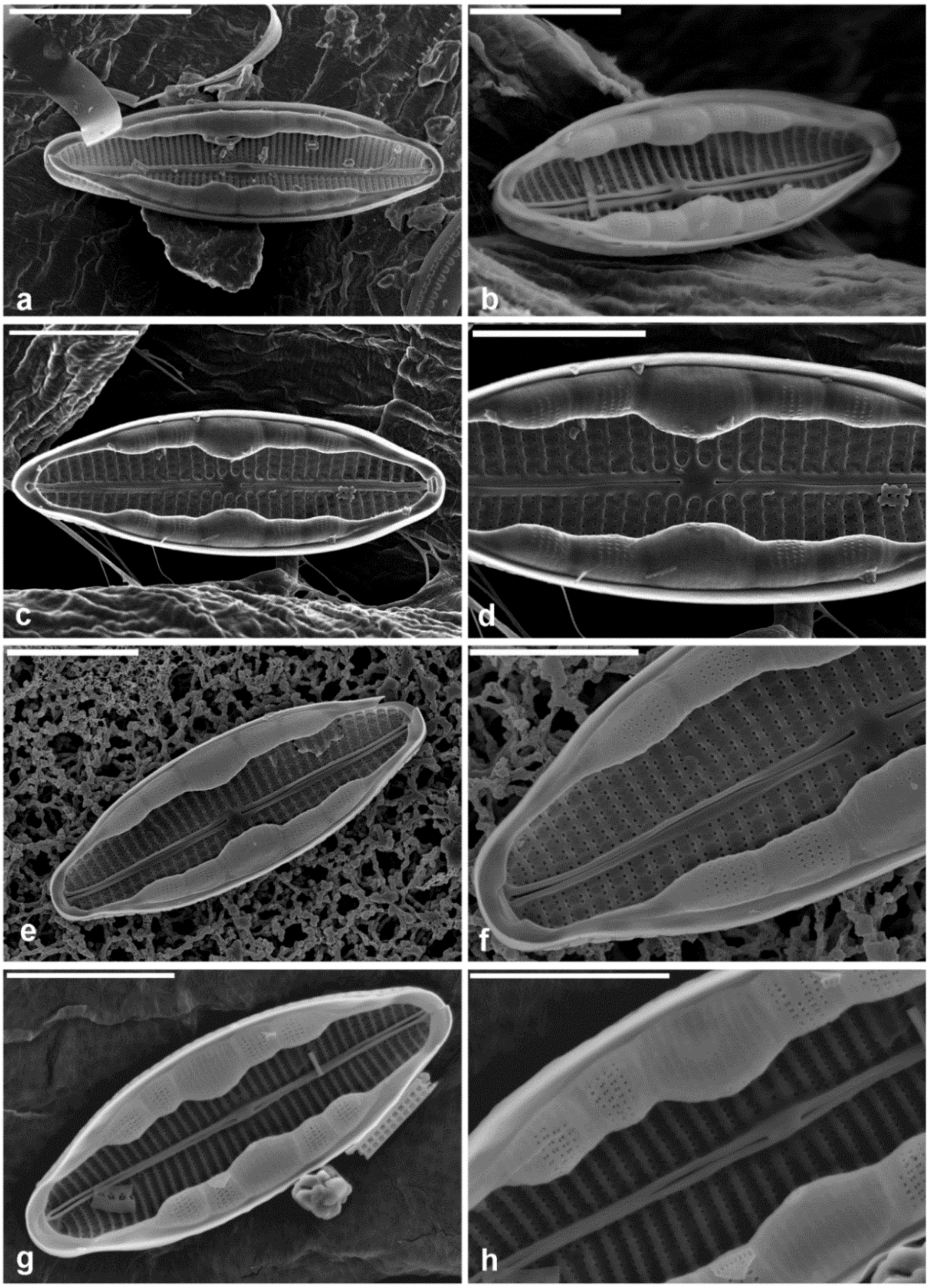
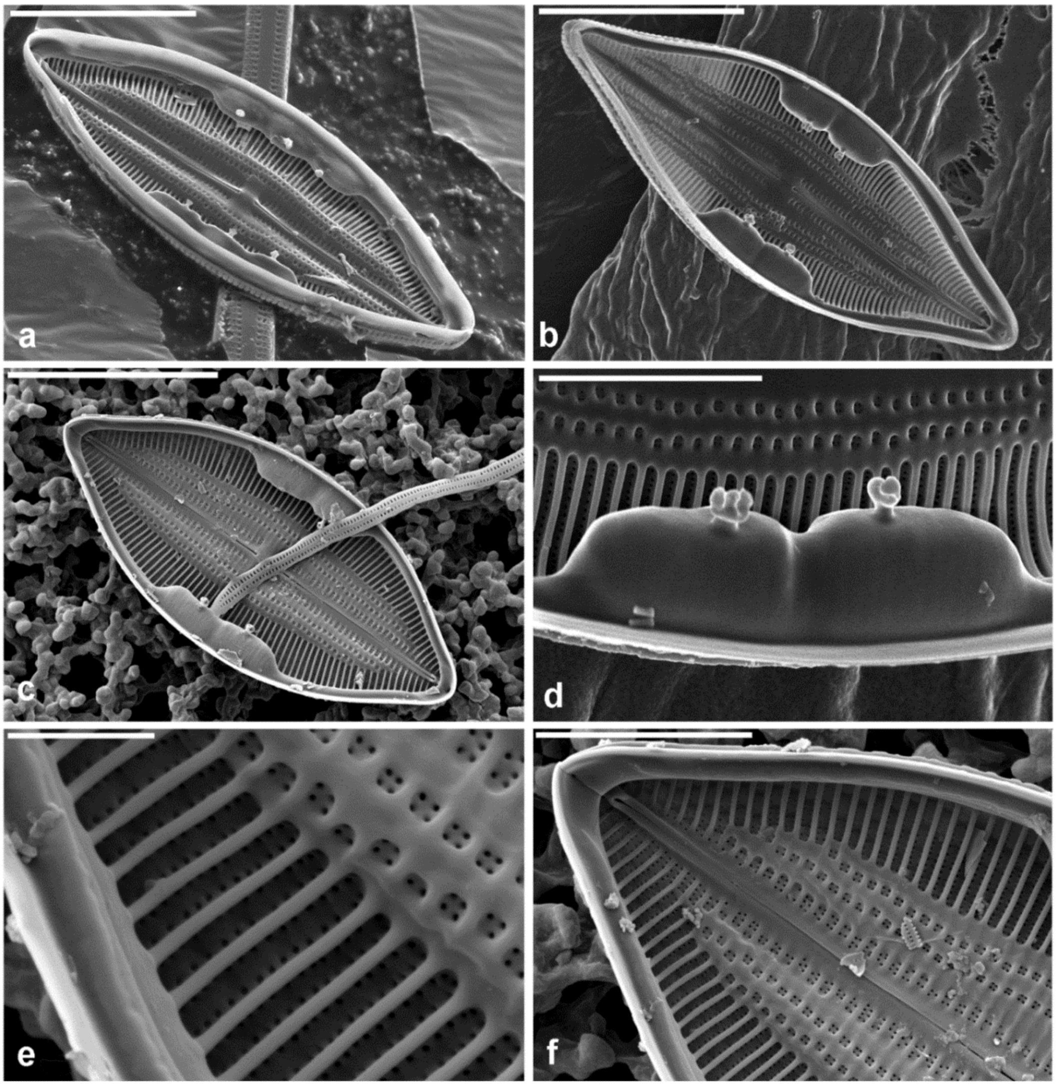


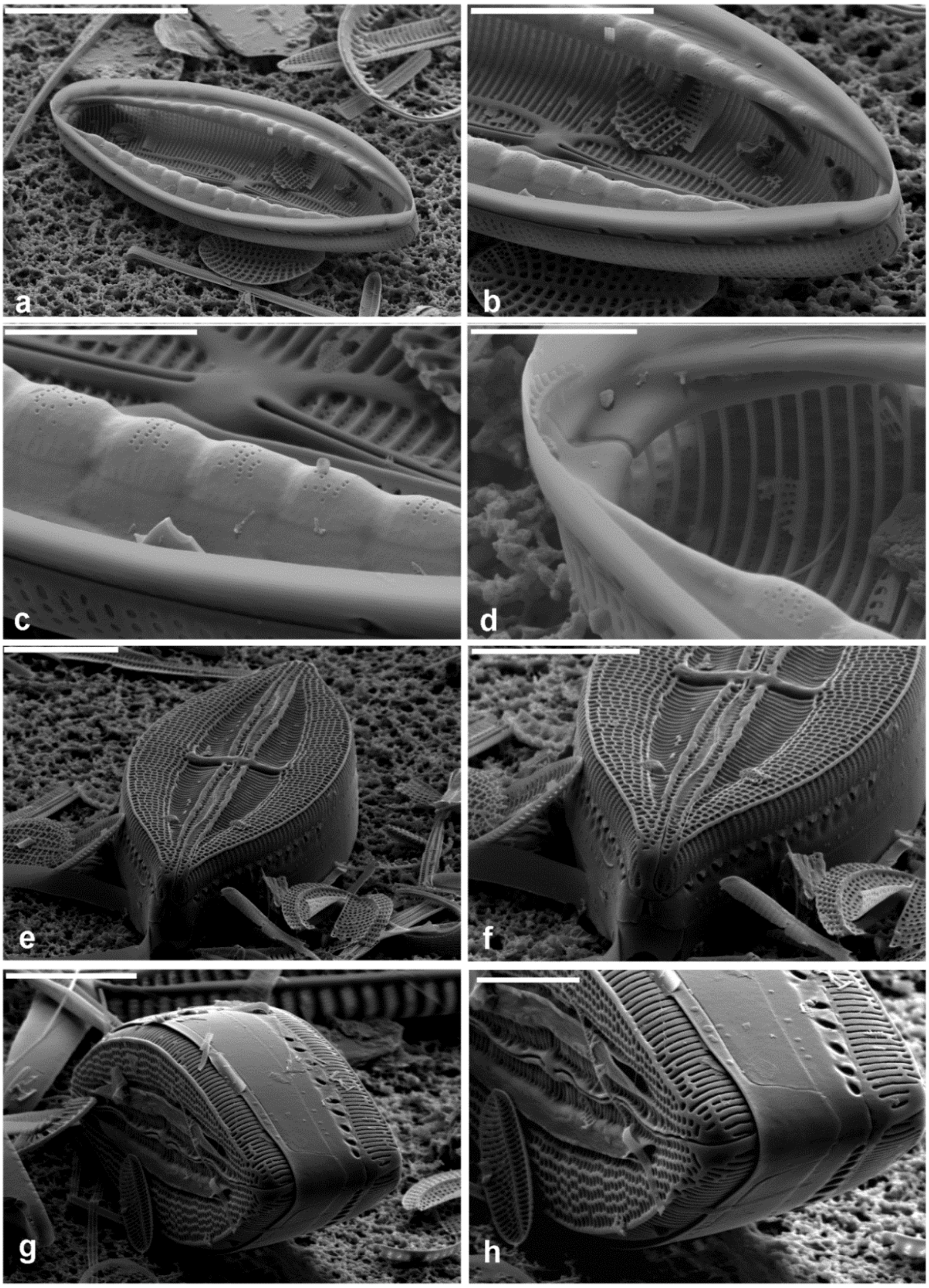
Fig. a *Mastogloia pusilla* (Grunow) Cleve) var. *pusilla*; Internal valve view, SEM. Figs b-h. *Mastogloia pumila* (Grunow) Cleve. Figs a-h. Internal valve view, SEM. Scale bars = 10 µm (Fig. a); 5 µm (Figs b, c, e, g); 4 µm (Fig. d); 3 µm (Figs f, h).

Plate 46



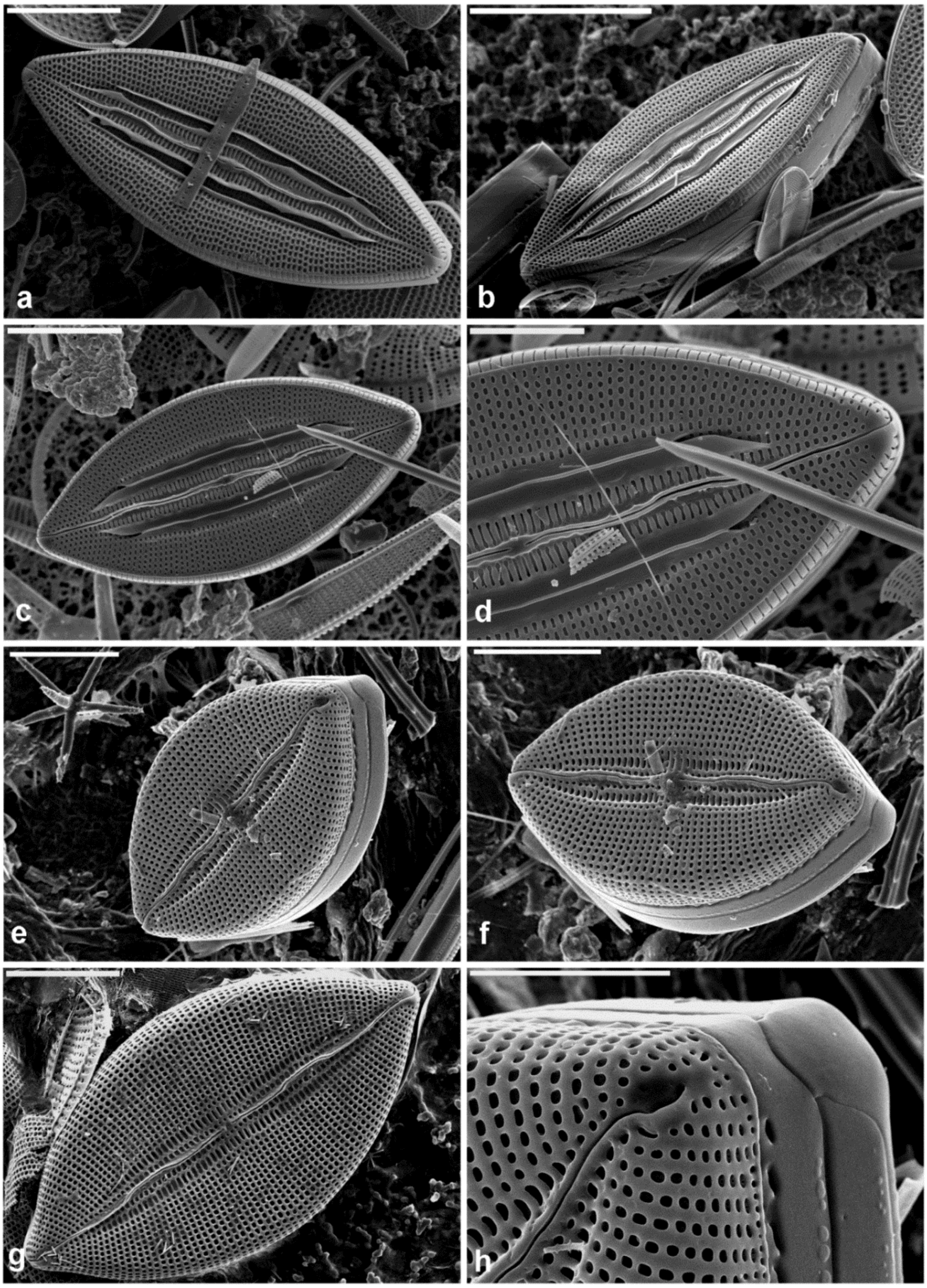
Figs a-f. *Mastogloia exilis* Hustedt, Internal valve view, SEM. Scale bars = 10 µm (Figs a, b, c); 4 µm (Fig. f); 3 µm (Fig. d); 1 µm (Fig. e).

Plate 47



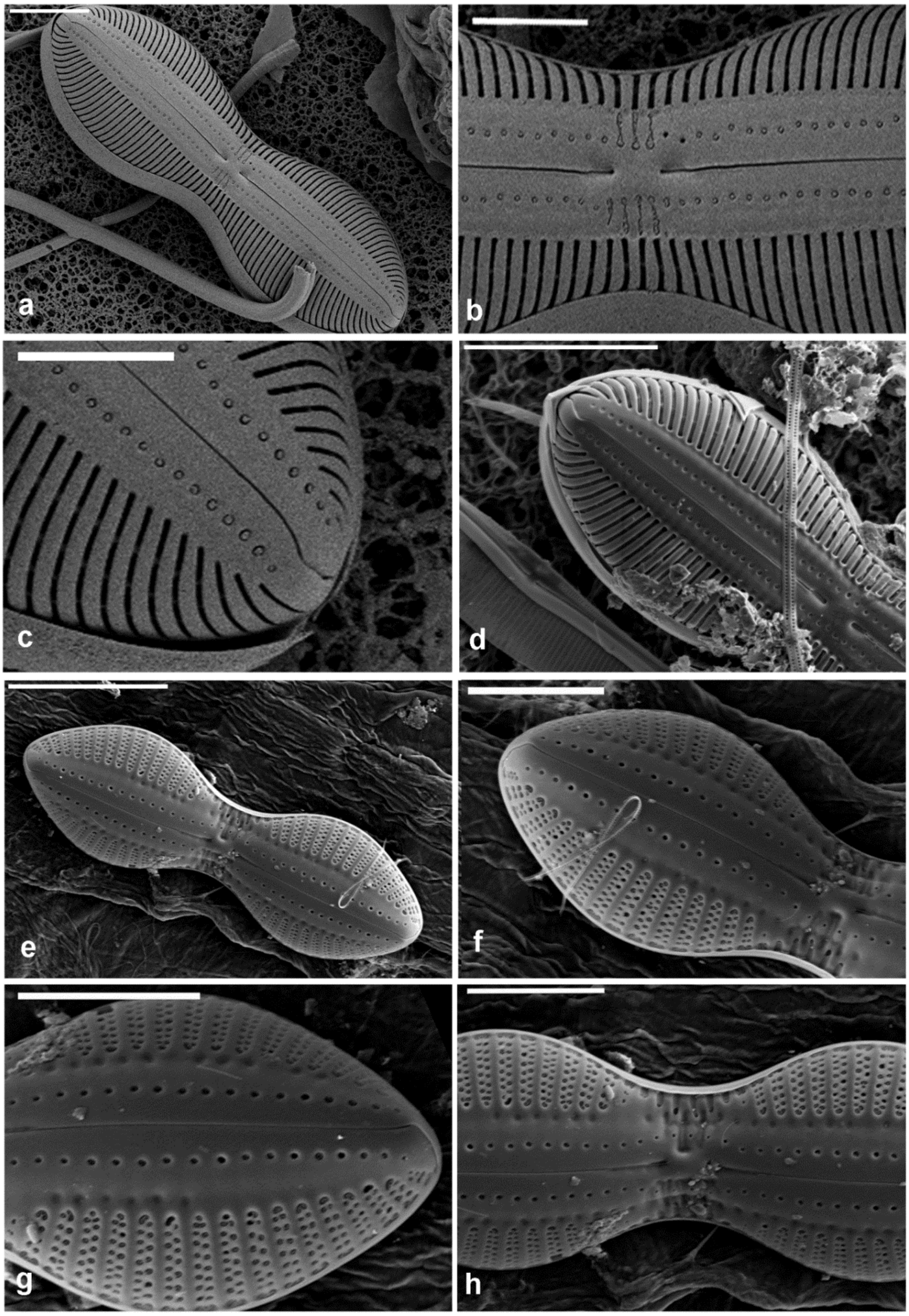
Figs a-d. SEMs of *Mastogloia* spp.Figs a-d. Internal view. Figs. e-h. External view. Scale bars = 20 µm (Fig. a); 10 µm (Figs b, e, f, g); 5 µm (Fig. h); 4 µm (Fig. c); 3 µm (Fig. d).

Plate 48



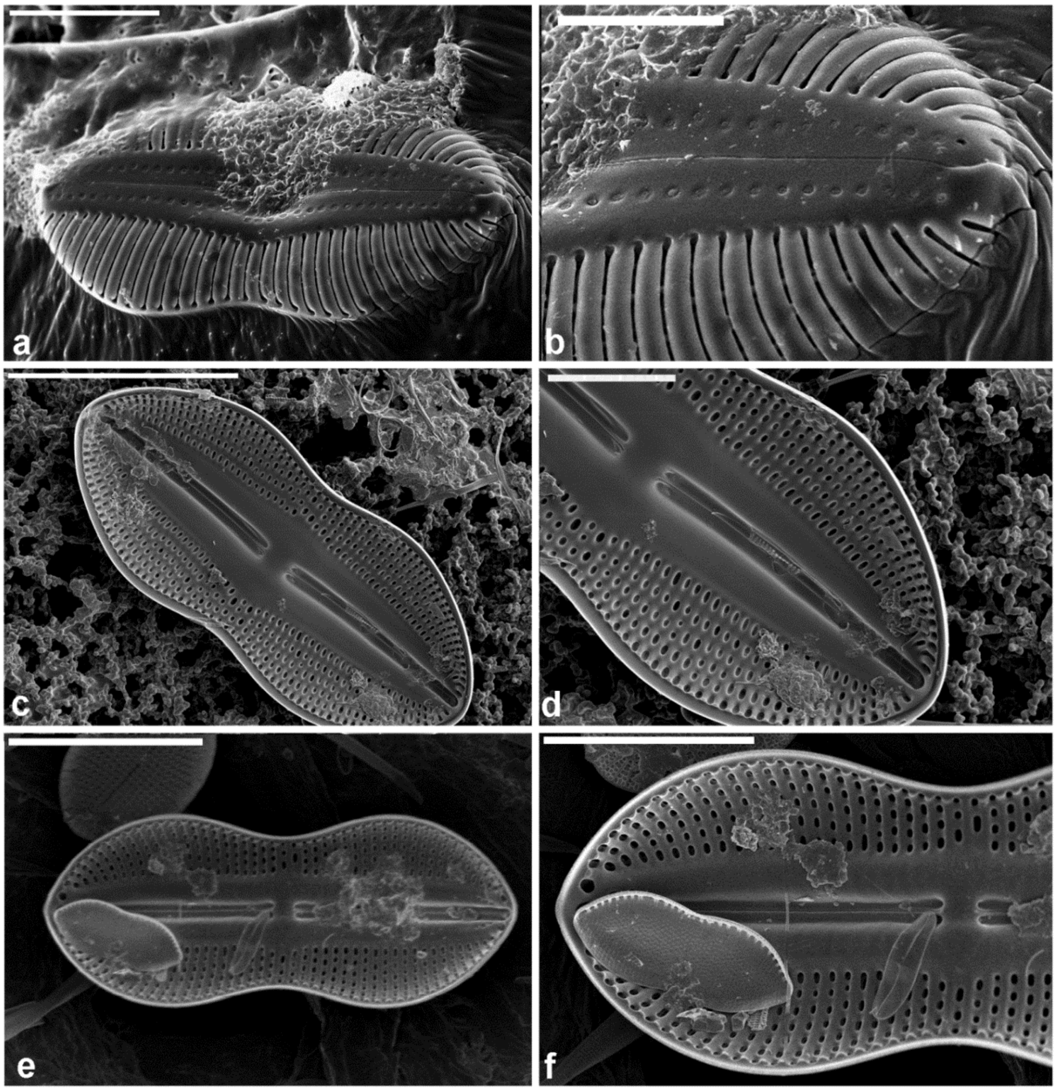
Figs a-h. SEMs of *Mastogloia* spp. External valve views.Figs a-d. *Mastogloia quinquecostata* Grunow. Scale bars = 20 µm (Fig. b); 10 µm (a, c, e, f, g); 5 µm (d, h).

Plate 49



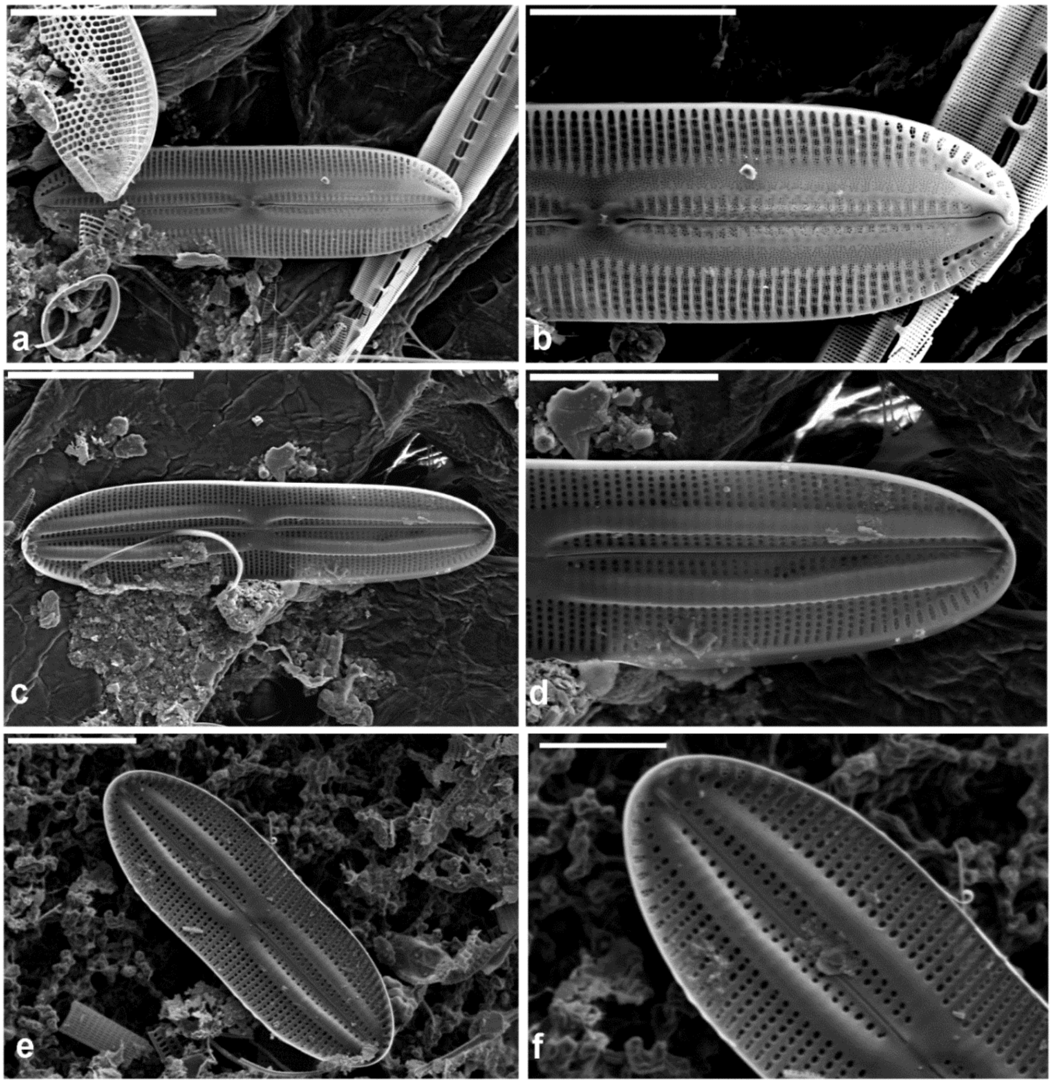
Figs a-h. SEMs of *Diploneis* spp. External view. Figs e-h. *Diploneis stoermii* Hustedt. Scale bars = 20 µm (Fig. e); 10 µm (Figs a, d, f, g, h); 5 µm (Figs b, c).

Plate 50



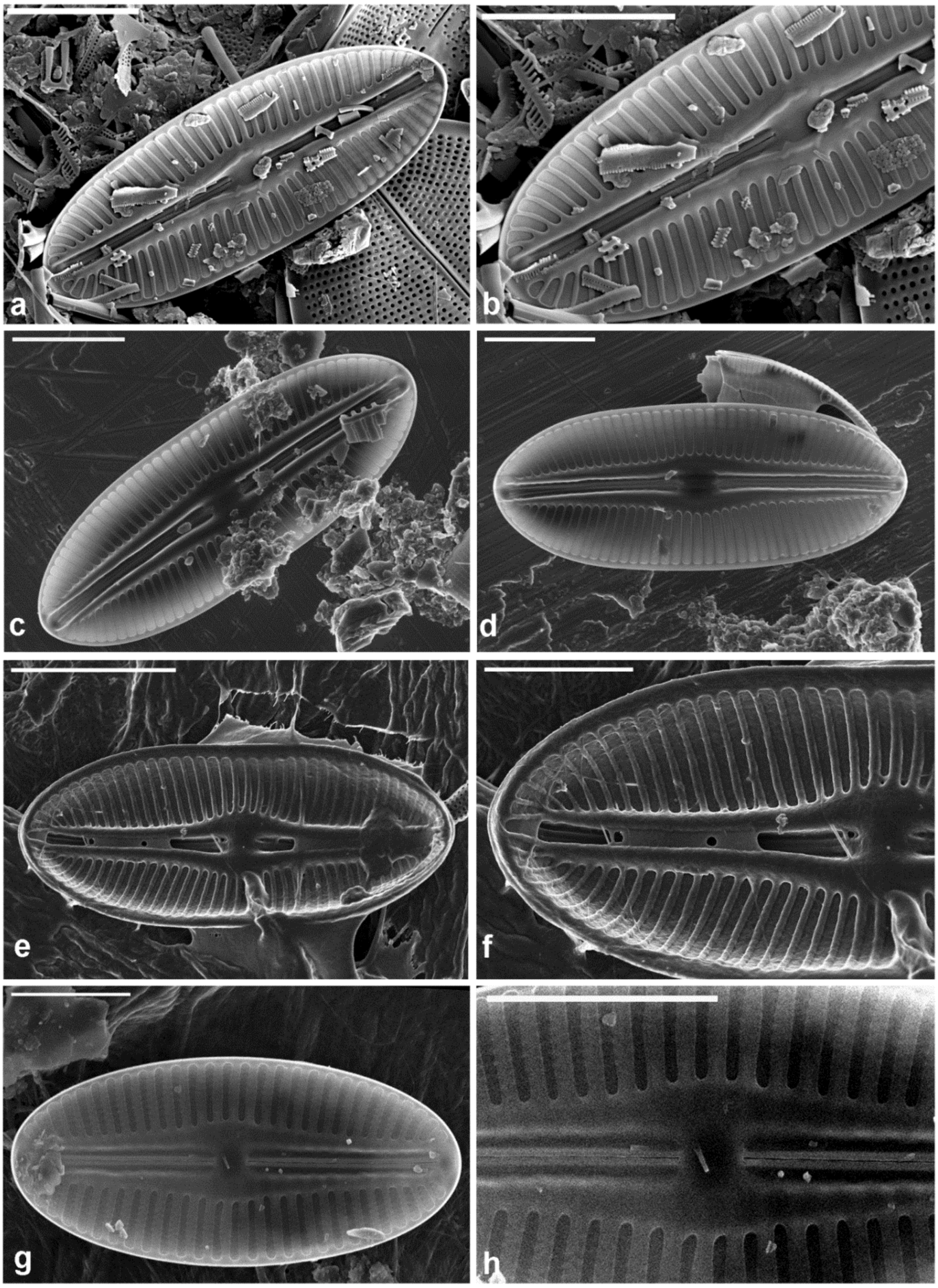
Figs a-h. SEMs of *Diploneis* spp. Figs a-b. External view. Figs c-f. *Diploneis bomboides* (A. Schmidt) Cleve. Internal view. Scale bars = 30 µm (Figs c, e); 20 µm (Fig. f); 10 µm (Figs a, d); 5 µm (Fig. b).

Plate 51



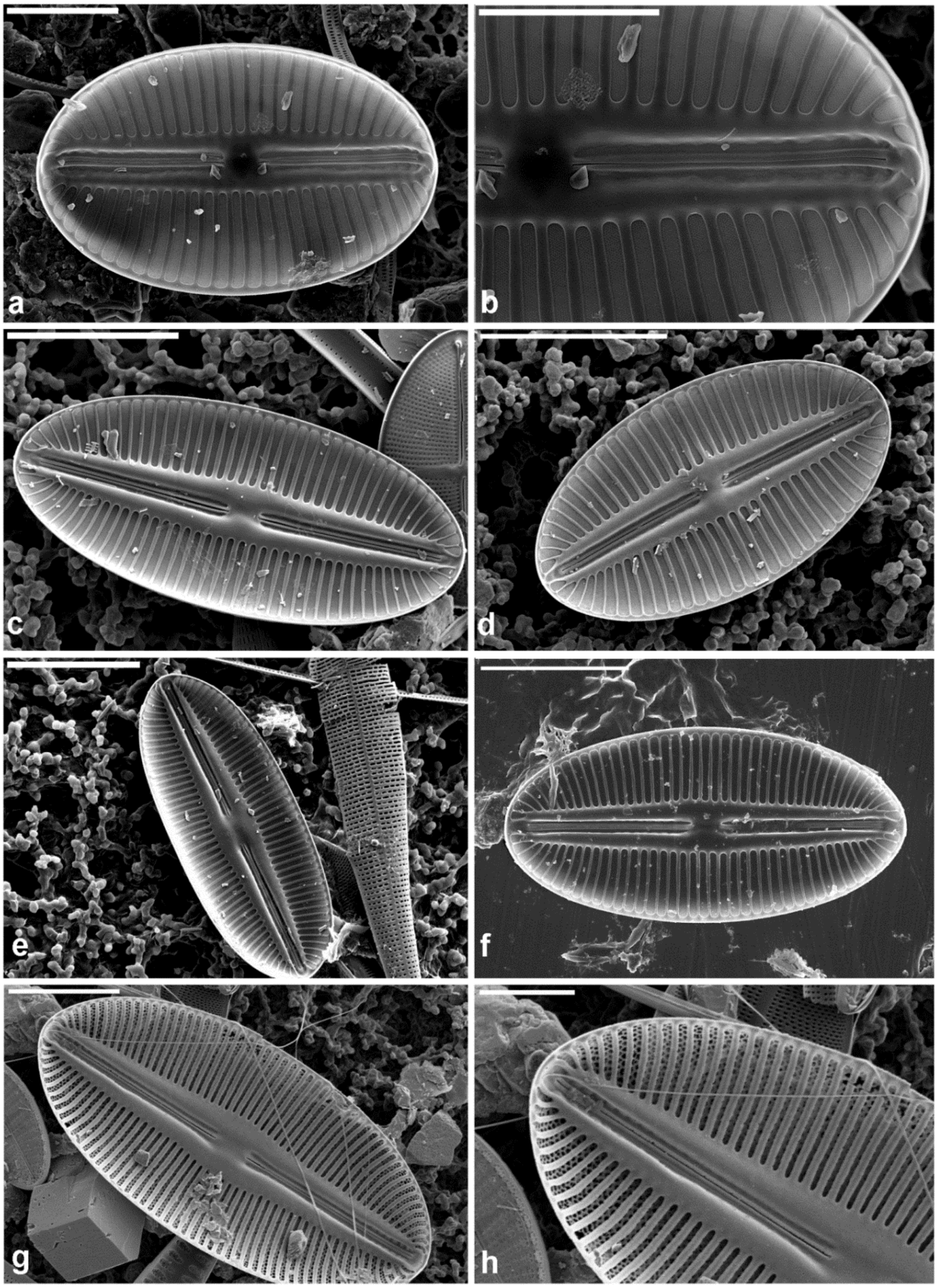
Figs a-f. *Diploneis incurvata* fo. *stricta* Hustedt. Figs a,b. External view. Figs c-f. Internal view. Scale bars = 20 µm (Figs a, c); 10 µm (Figs b, d, e); 5 µm (Fig. f).

Plate 52



Figs a-h. SEMs of *Diploneis vacillans* (A. Schmidt) Cleve var. *vacillans*. Scale bars = 10 µm (Figs); 5 µm (Figs a, b); 4 µm (Fig.).

Plate 53



Figs a-h. SEMs of *Diploneis* spp. .Figs a-b. *Diploneis litoralis* (Donkin) Cleve var. *litoralis*. Figs c-d. *Diploneis vacillans* var. *renitens* A. Schmidt. Fig. e. *Diploneis litoralis* var. *clathrata* Østrup. Scale bars = 10 µm (Figs c, d, e, f, g); 5 µm (Figs a, b, h).

Plate 54

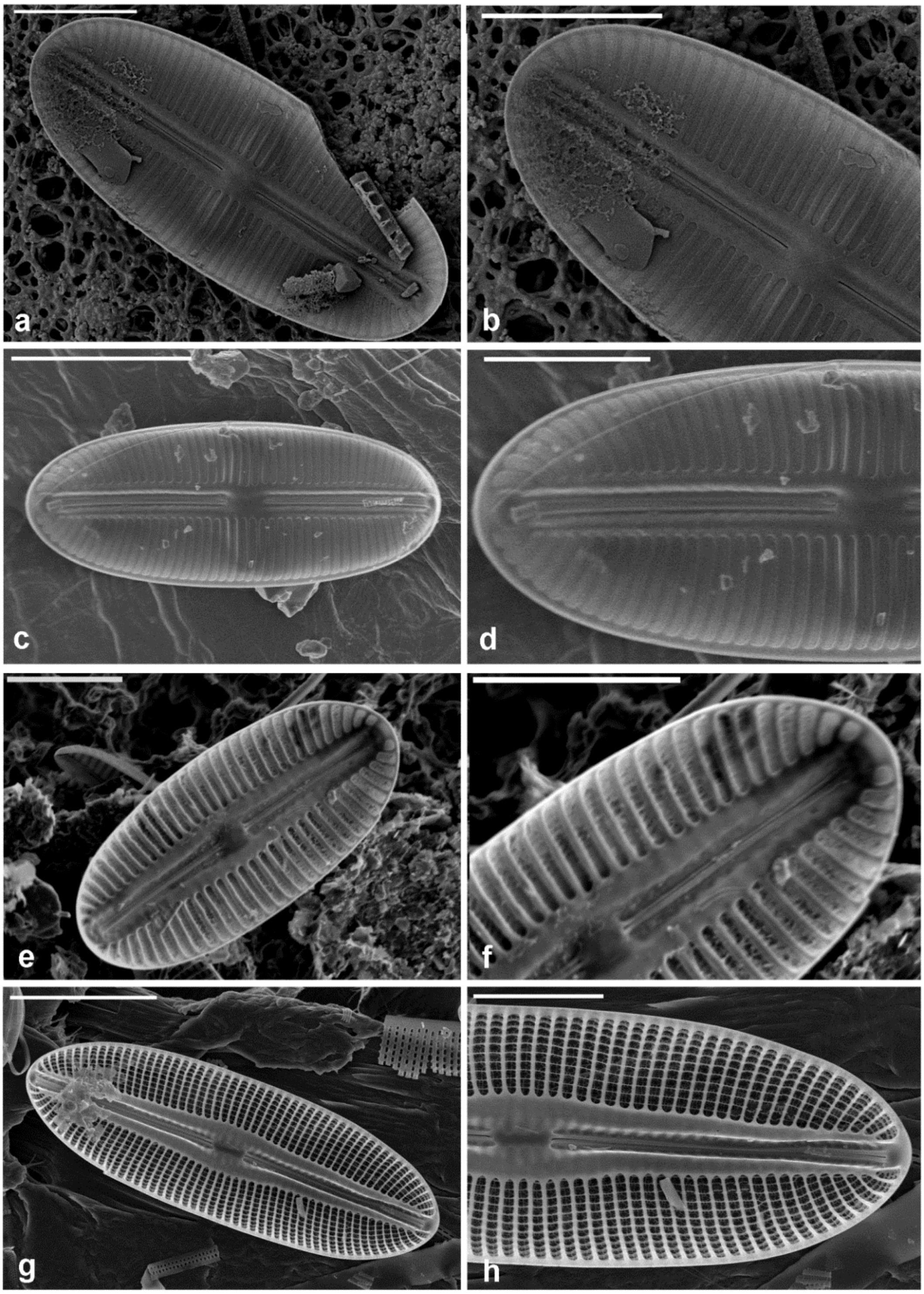


Fig. a-h. SEMs of *Diploneis* spp. Figs a-d. *Diploneis litoralis* var. *clathrata* Østrup. Scale bars = 10 µm (Figs c, g); 6 µm (Figs a, b); 5 µm (Figs d, e, f, h).

Plate 55

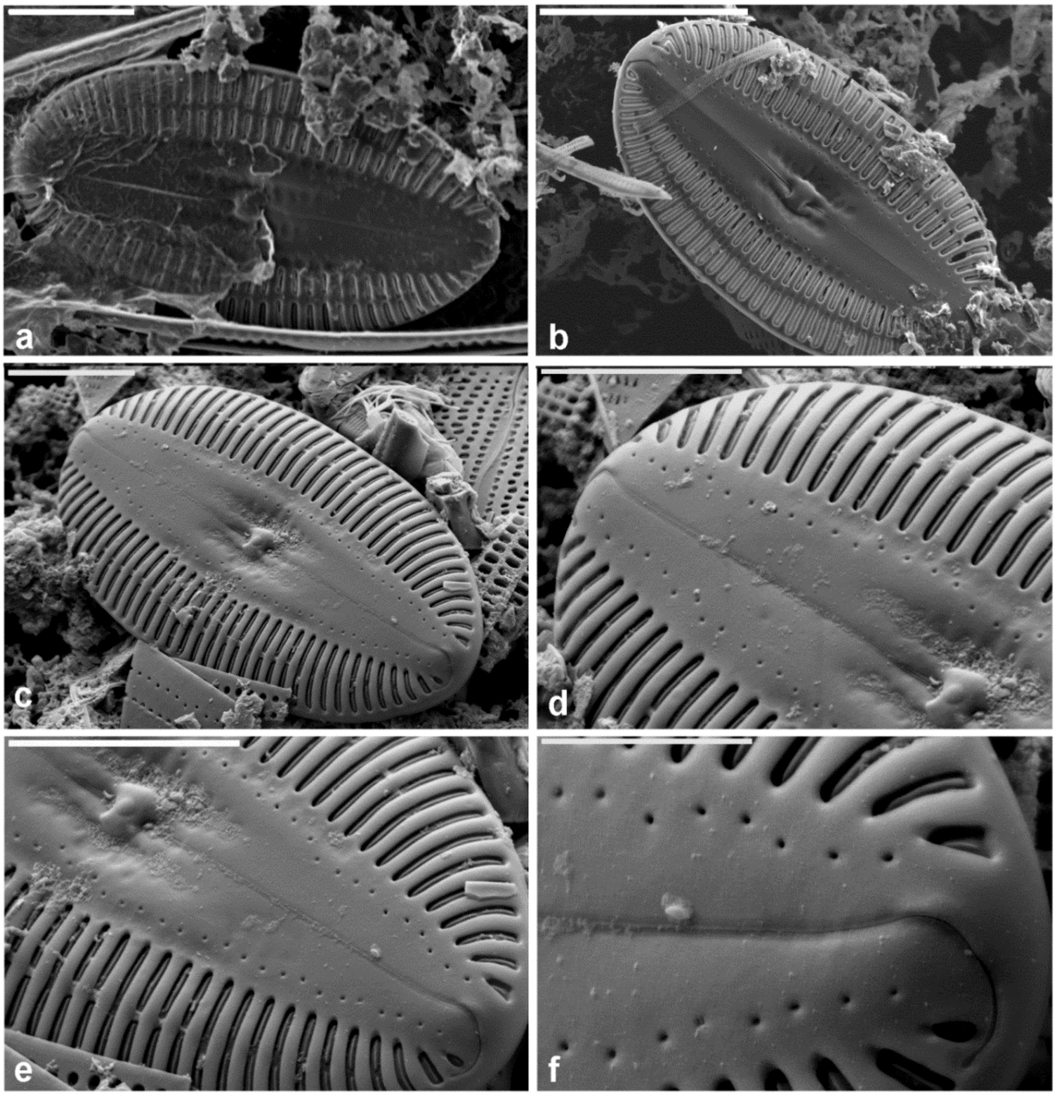
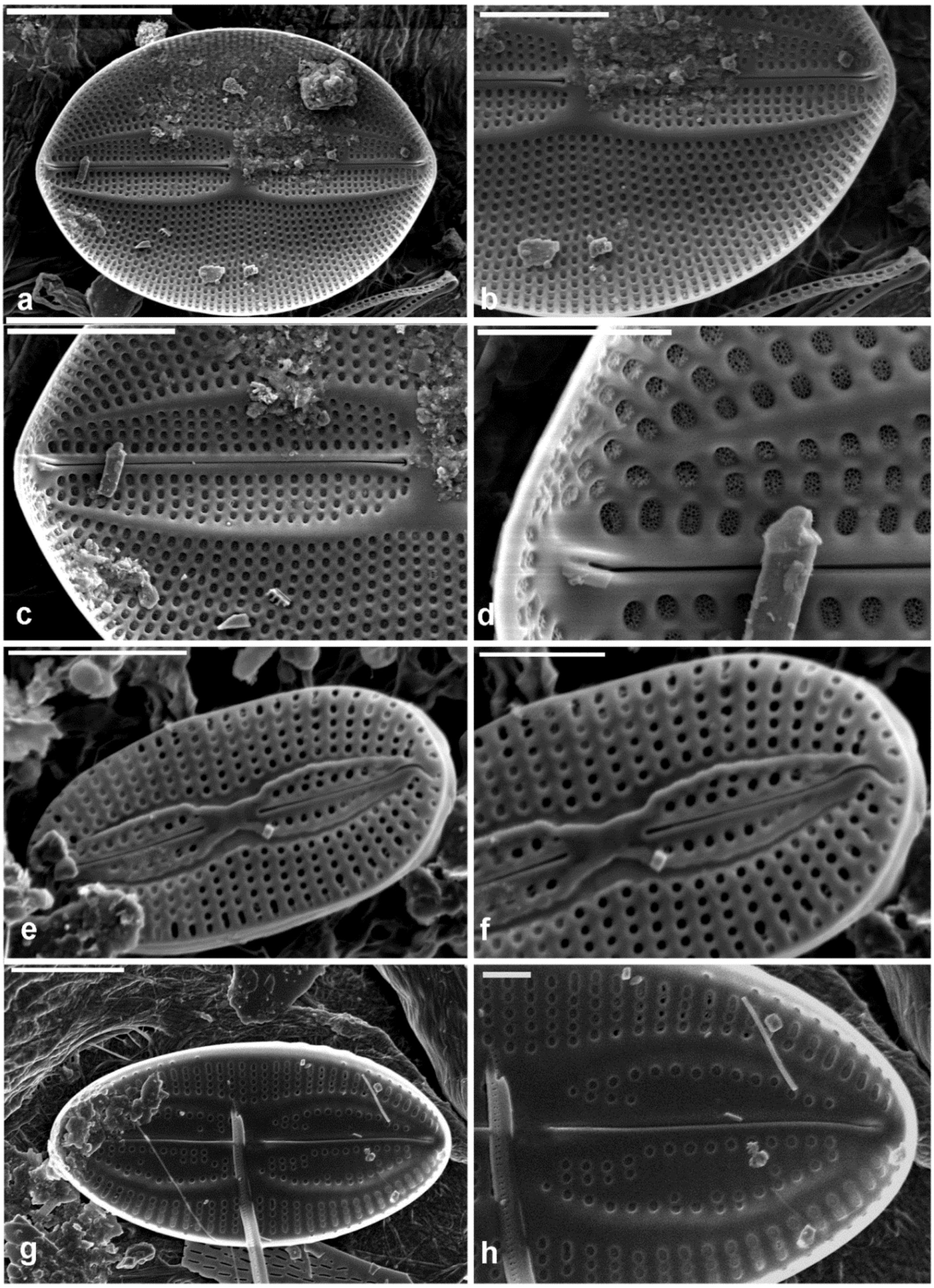


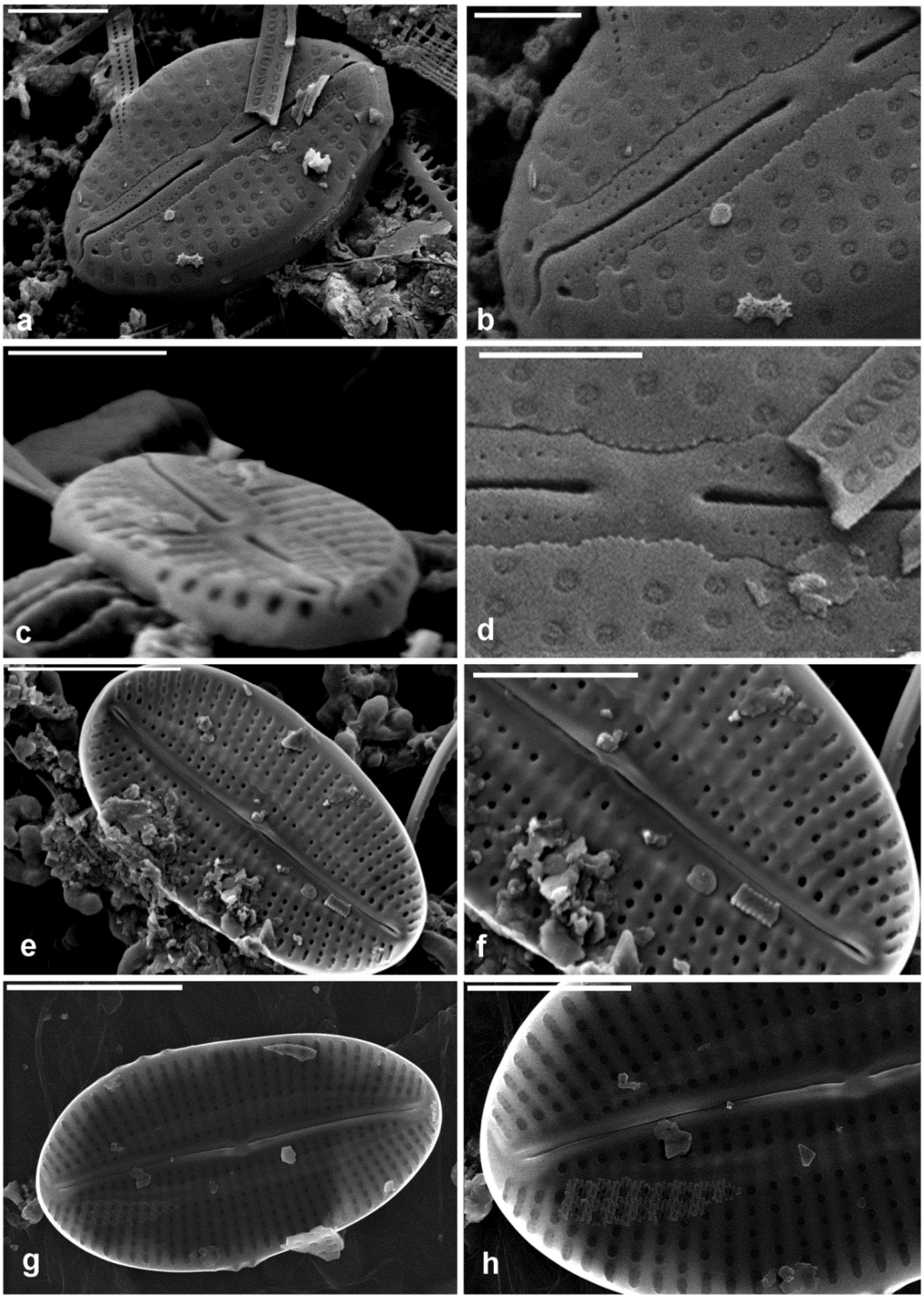
Fig. a-f. *Diploneis notabilis* (Greville) Cleve. External valve view, SEM. Scale bars = 10 µm (Fig. b); 5 µm (Figs a, c, e); 4 µm (Fig. d); 2 µm (Fig. f).

Plate 56



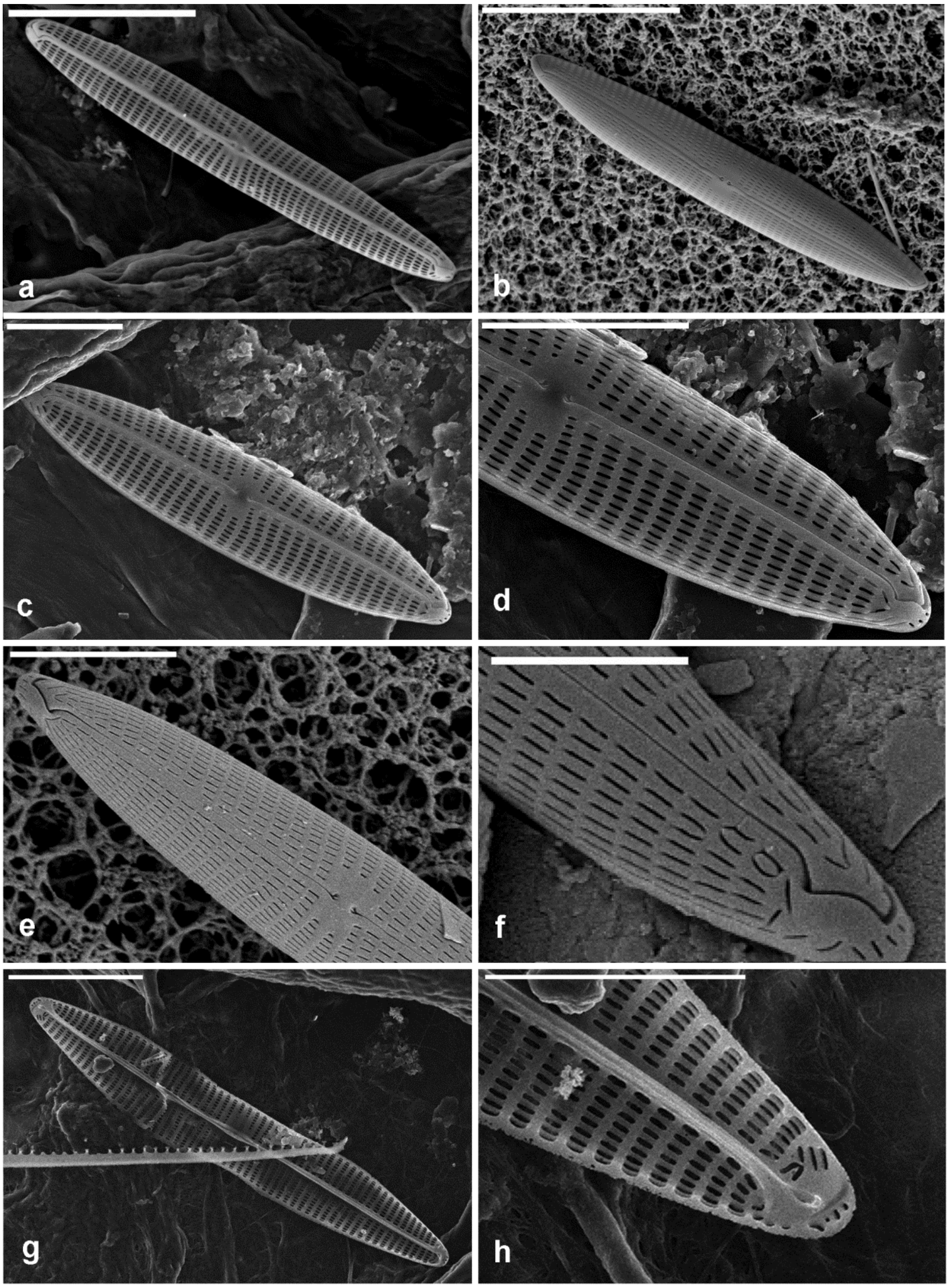
Figs a-d. SEMs of *Fallacia* spp. Fig. e-f. *Fallacia clepsidroides* Witkowski. Scale bars = 20 µm (Fig. a); 10 µm (Figs b, c); 5 µm (Fig. g); 4 µm (Figs d, e); 2 µm (Fig. f); 1 µm (Fig. h).

Plate 57



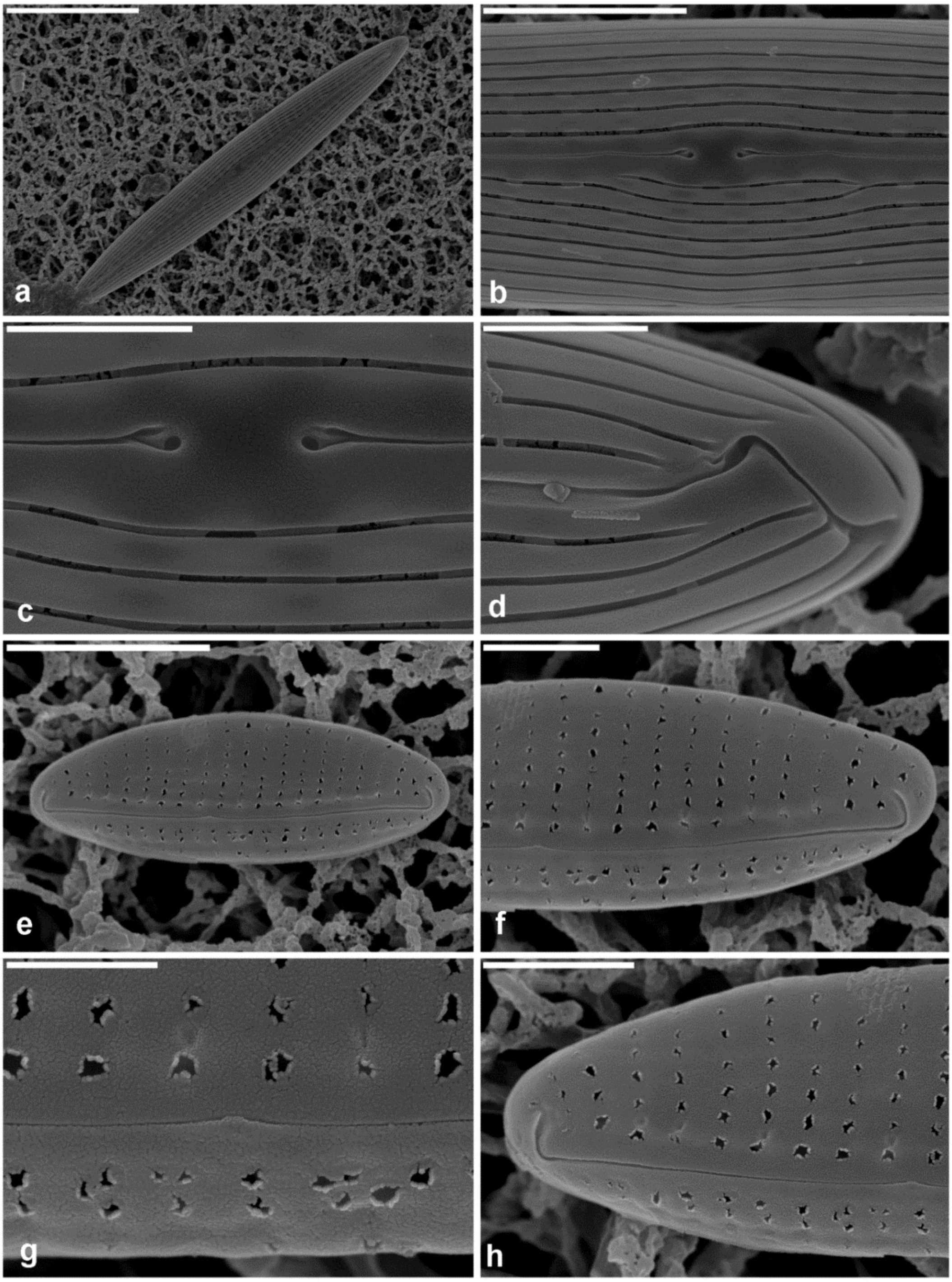
Figs a-d. SEMs of *Fallacia* spp. Scale bars = 4 µm (Figs e, g); 2 µm (Figs a, f, h); 1 µm (Fig. b);

Plate 58



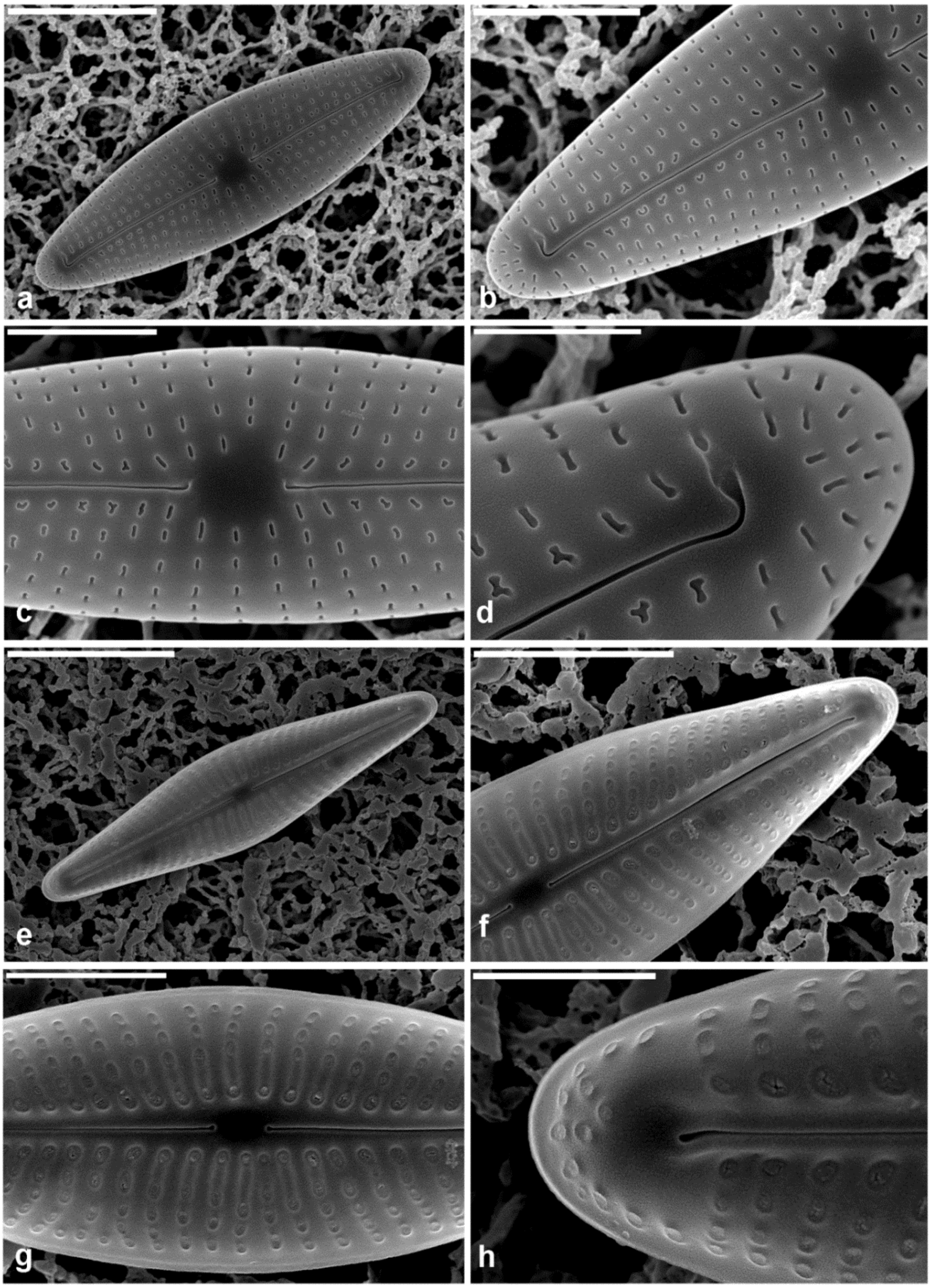
Figs a-h. SEMs of *Navicula* sp. Scale bars = 20 µm (Fig. b); 10 µm (Figs a, g,); 6 µm (Fig. e); 5 µm (Figs c, d, h); 3 µm (Fig. f).

Plate 59



Figs a-d. *Navicula subagnita* Proshkina-Lavrenko (SEM). Figs e-h. *Nitzschia* sp. (SEM). Scale bars = 10 µm (Fig. a); 3 µm (Figs b, e); 1 µm (Figs c, d, f, h); 500 nm (Fig. g).

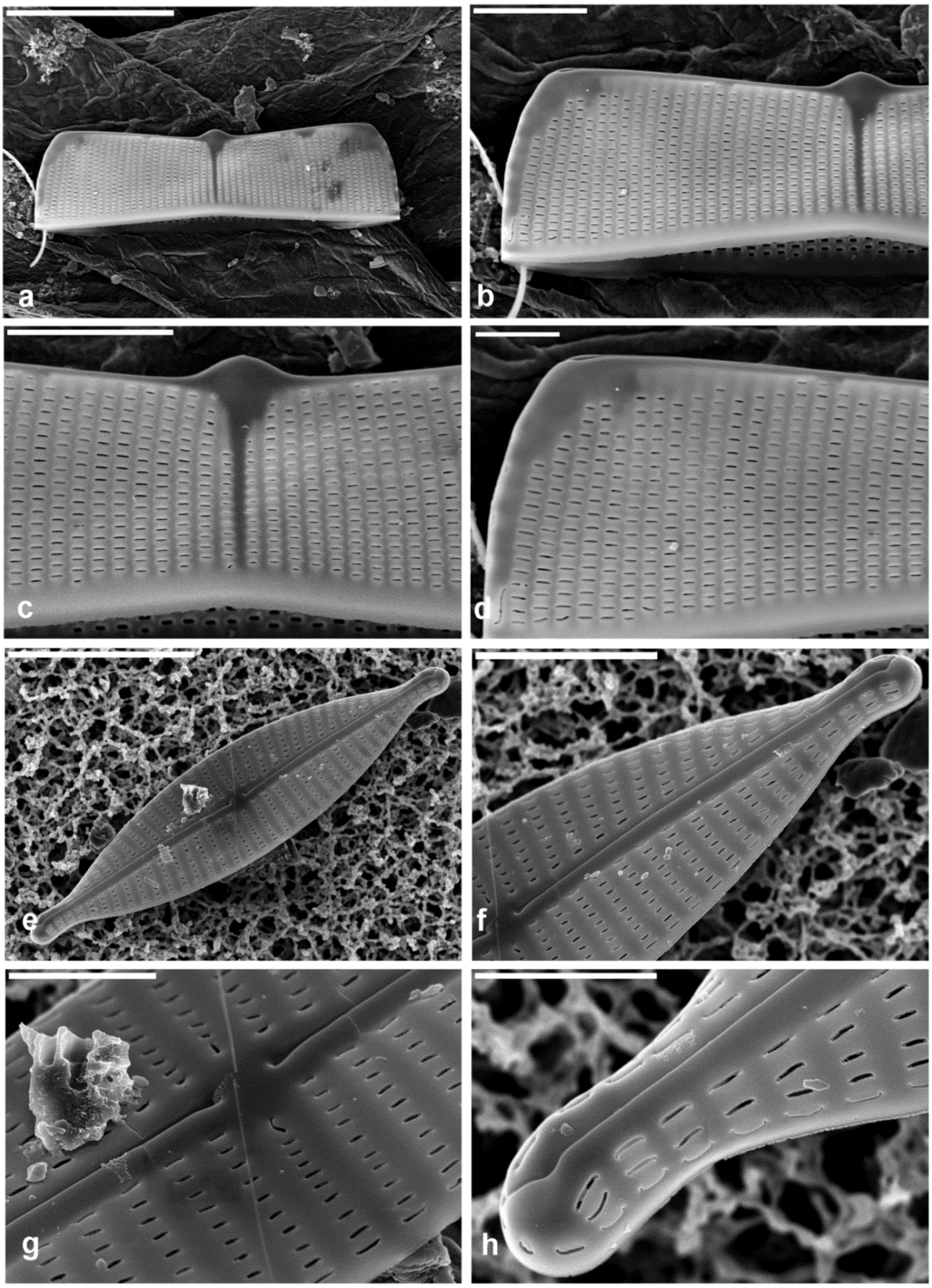
Plate 60



Figs a-d. *Navicula* sp. (SEM). Figs e-h. *Navicula* sp. (SEM).

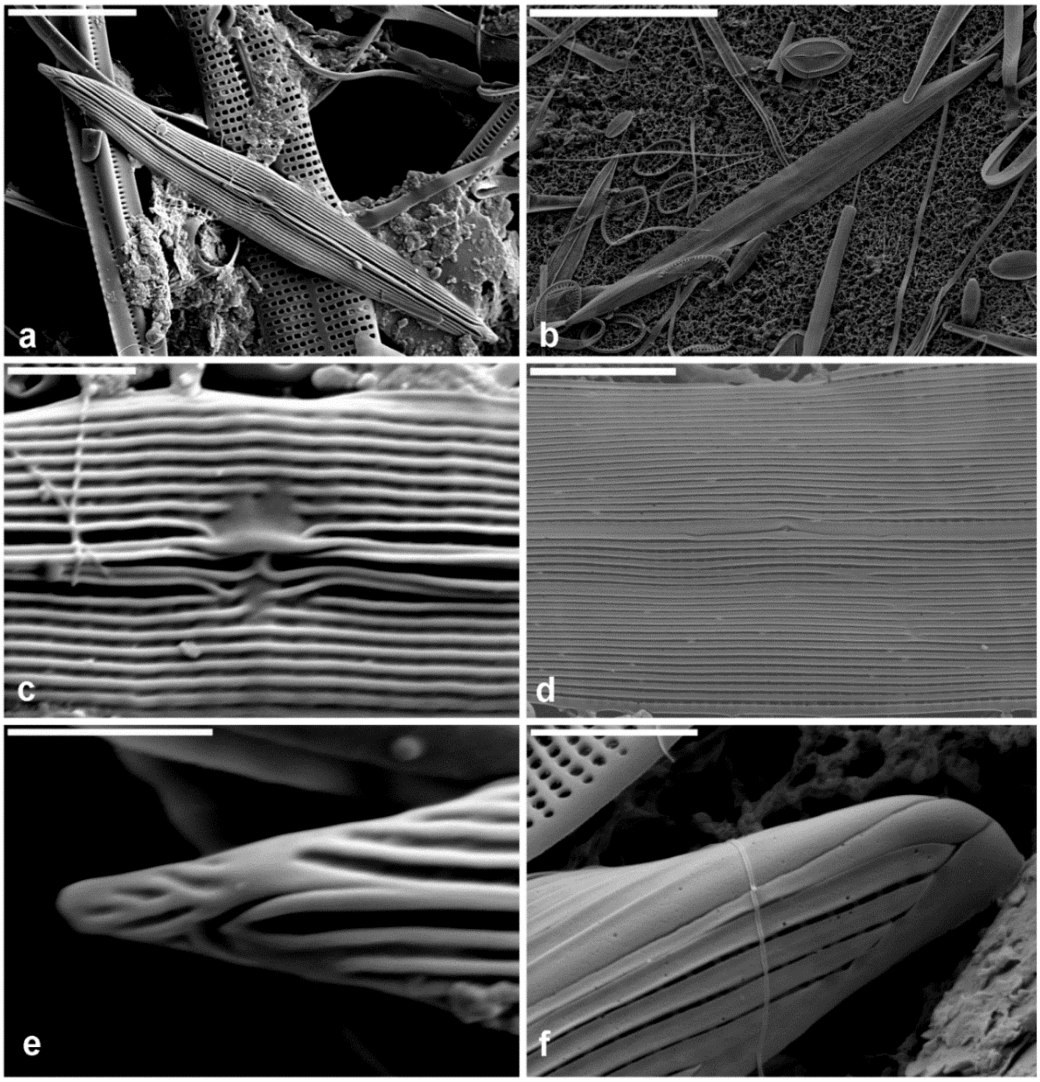
Scale bars = 5 µm (Figs a, e); 3 µm (Figs b, f); 2 µm (Figs c, g); 1 µm (Figs d, h).

Plate 61



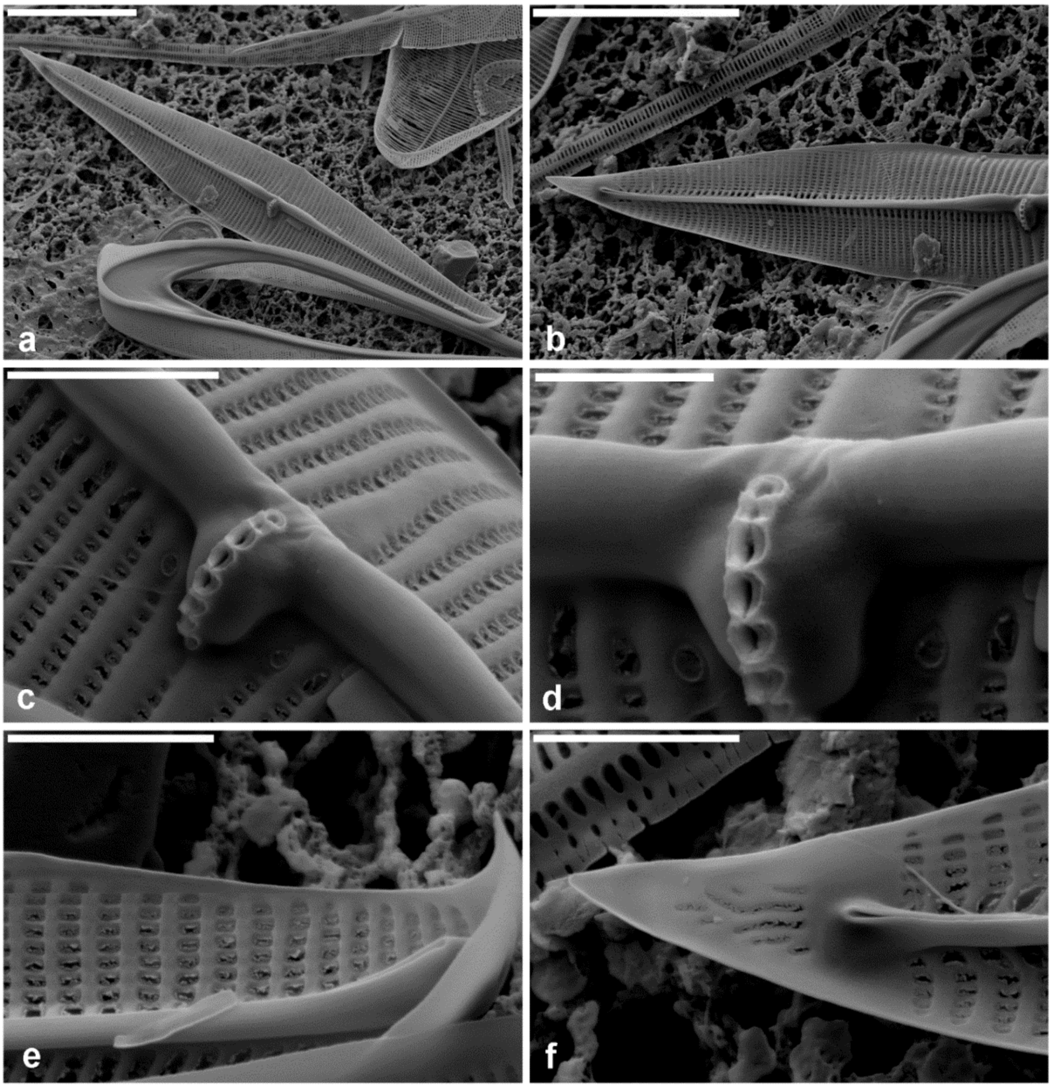
Figs a-d. SEMs of *Navicula northumbrica* Donkin. Figs e-h. SEMs of *Navicula* sp. Scale bars = 30 µm (Fig. a); 10 µm (Figs b, c, e); 5 µm (Figs d, f); 2 µm (Figs g, h).

Plate 62



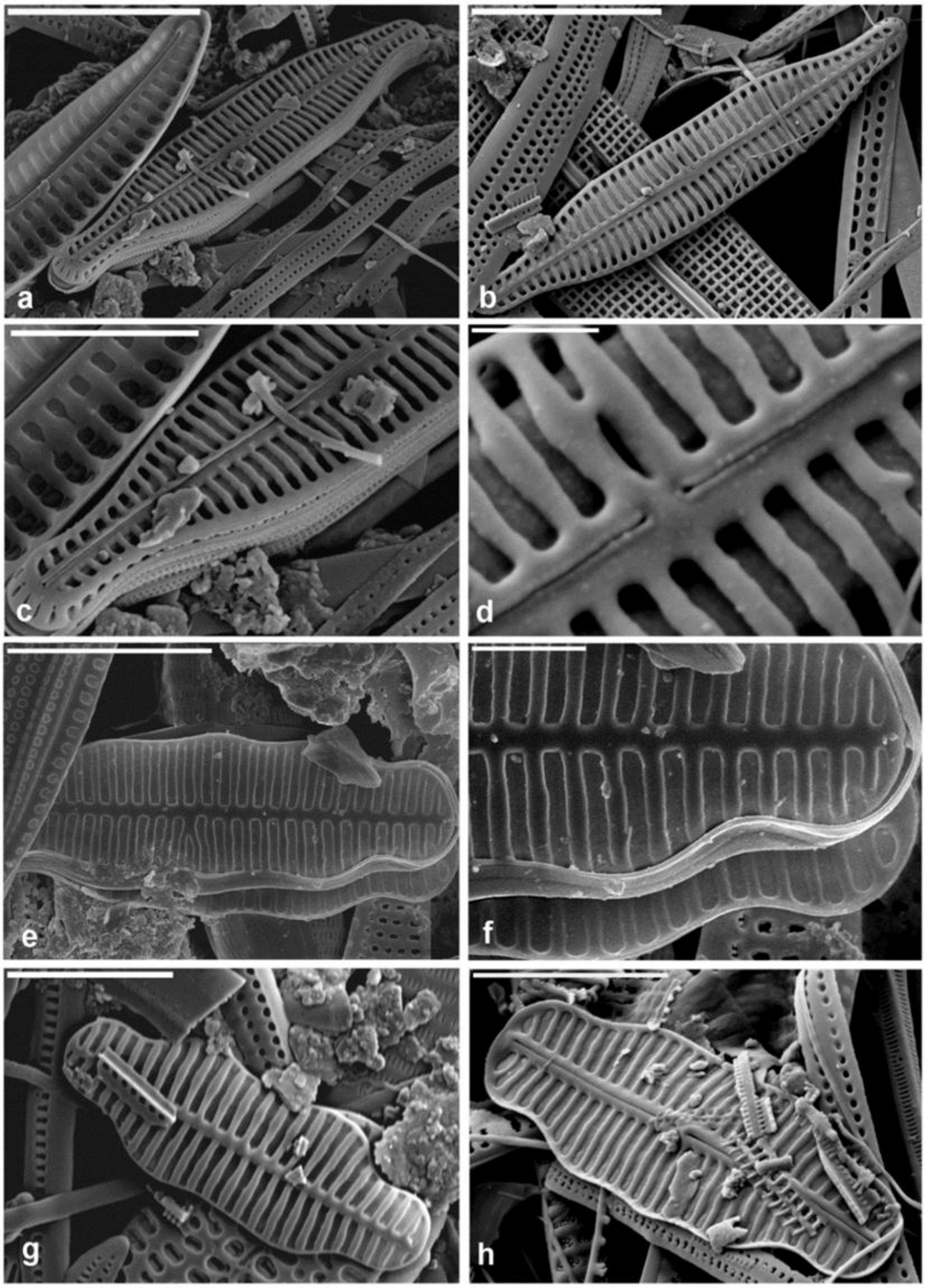
Figs a-f. SEMs of *Navicula* sp. Scale bars = 50 µm (Fig. b); 5 µm (Figs a, d); 2 µm (Fig. f); 1 µm (Figs c, e).

Plate 63



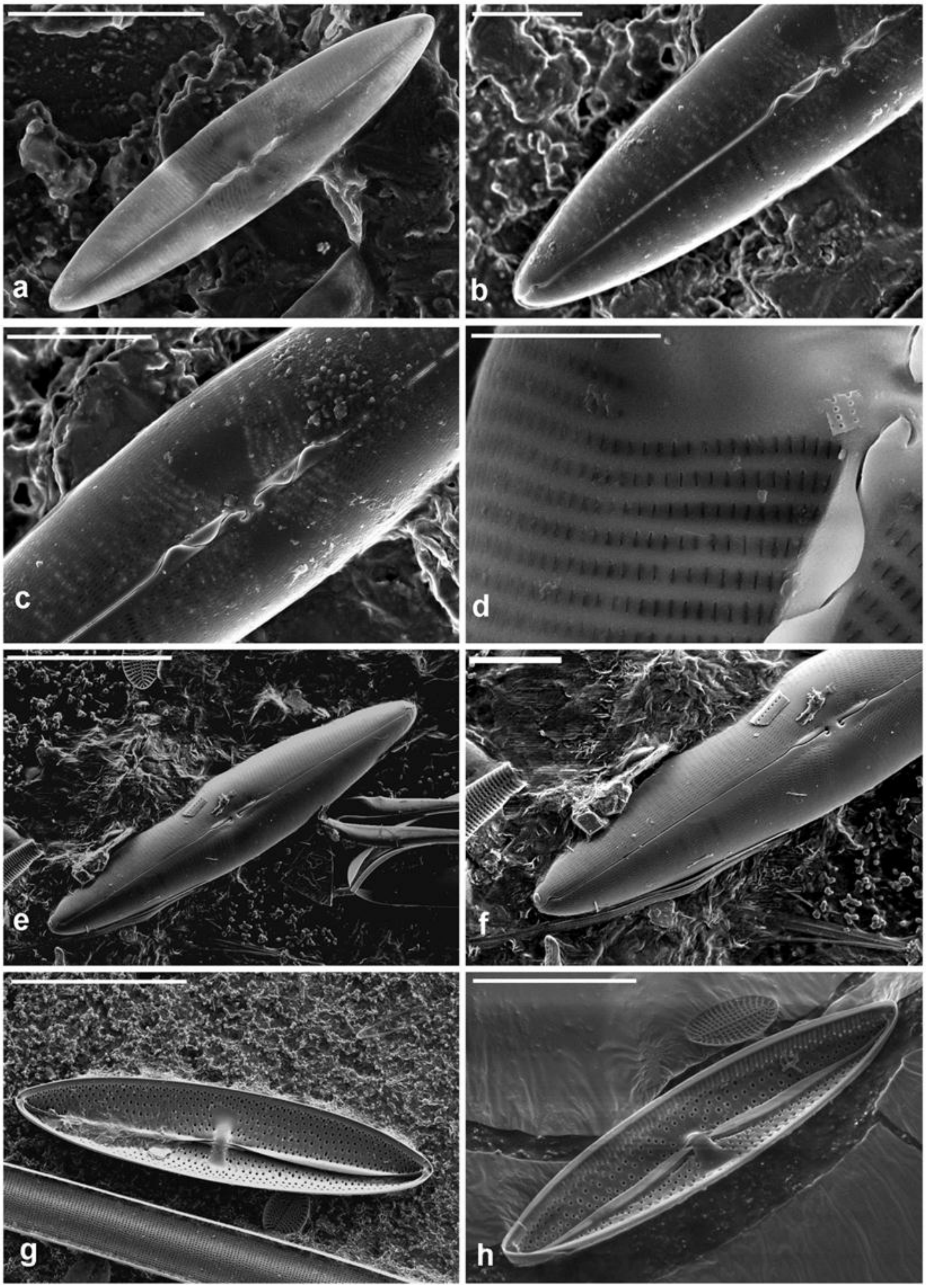
Figs a-f. SEMs of *Navicula* sp. Scale bars = 10 µm (Figs a, b); 2 µm (Figs c, e, f); 1 µm (Fig. d).

Plate 64



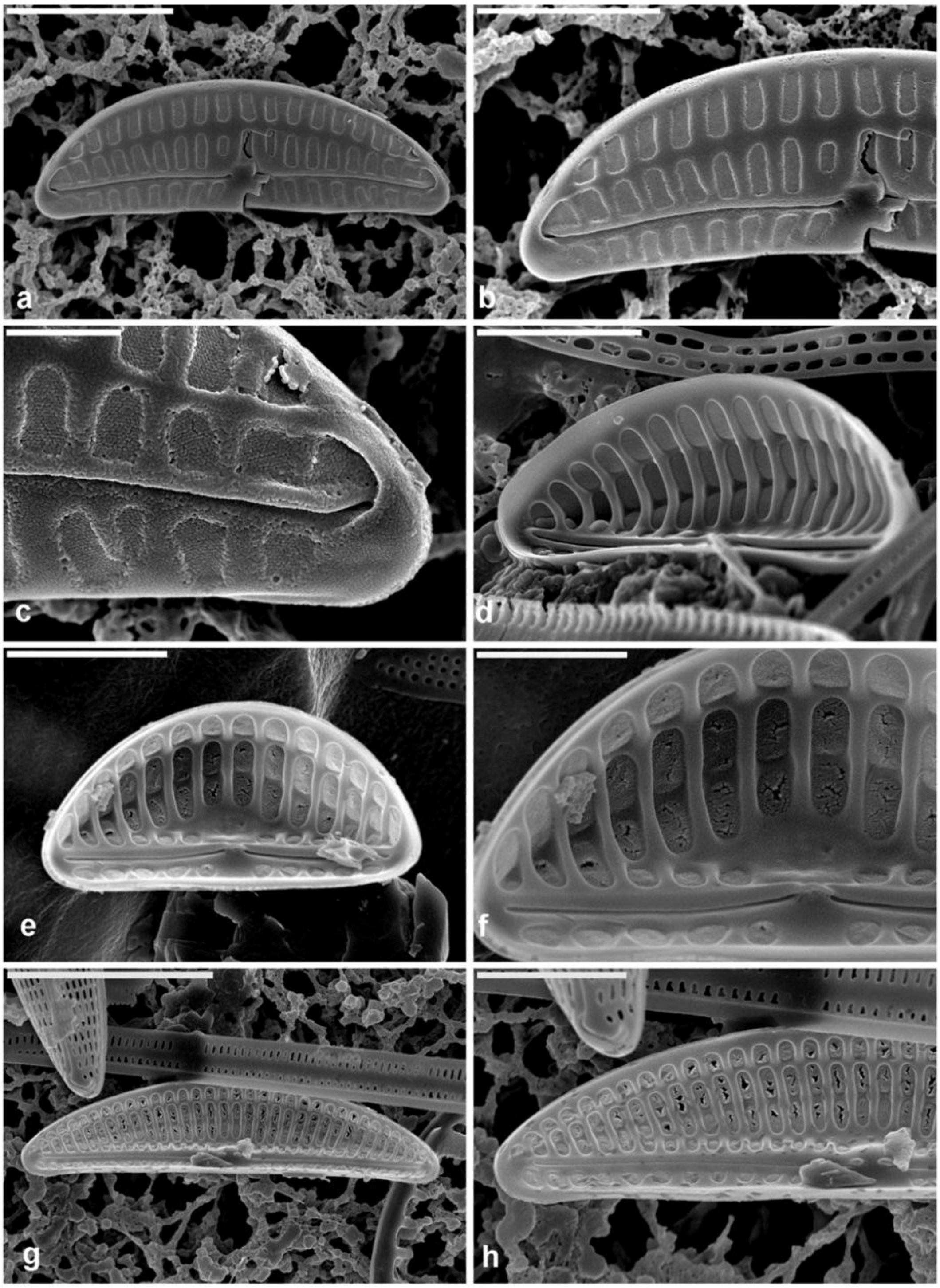
Figs a-d. *Olifantiella* sp. Figs e-h. *Madinithidium undulatum*. Scale bars = 4 µm (Figs a, b, e), 3 µm (Figs g, h), 2 µm (Fig. c), 1 µm (Fig. f); 500 nm (Fig. d).

Plate 65



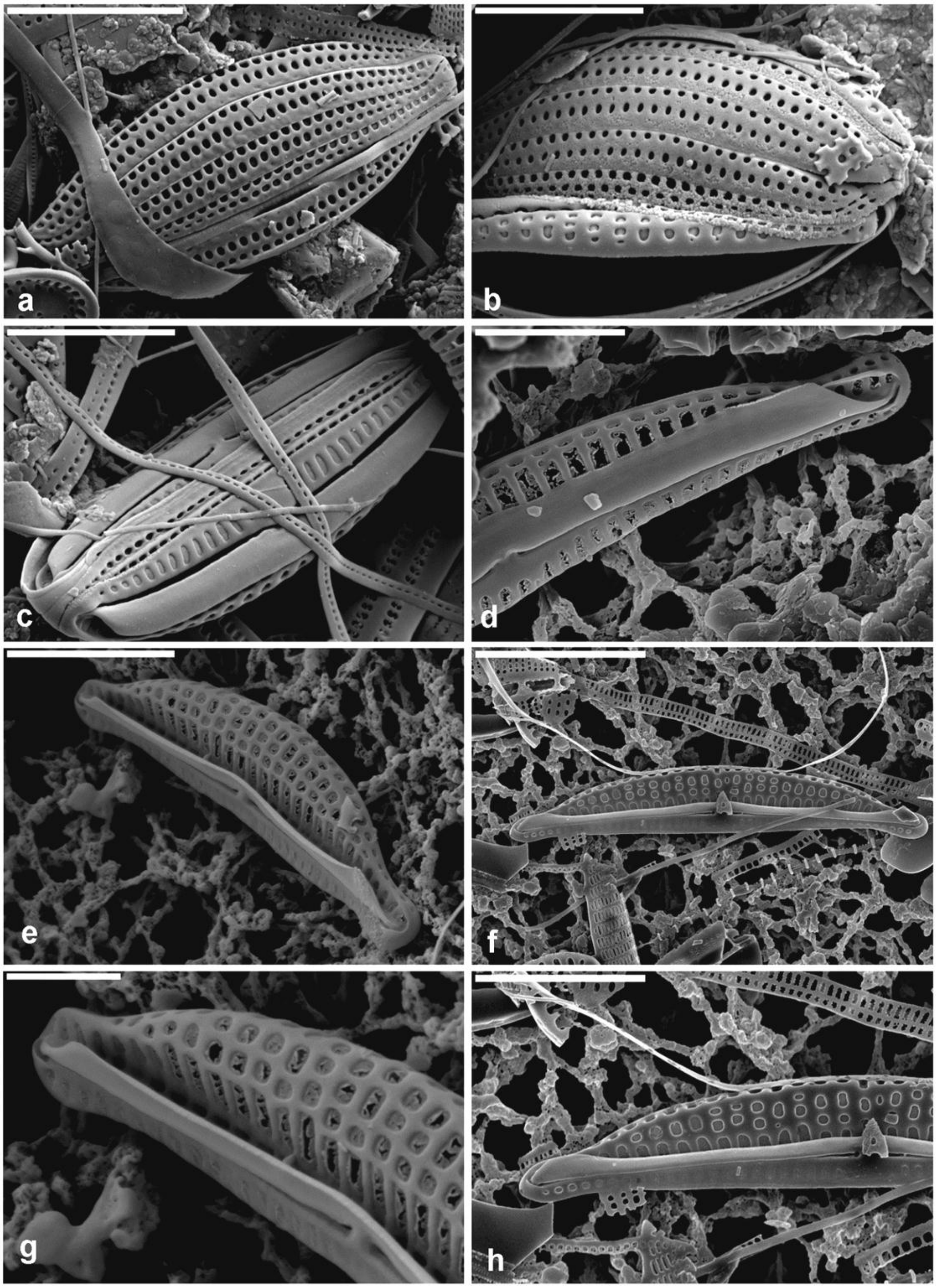
SEMs of *Trachyneis* spp. Scale bars = 40 µm (Fig. g); 30 µm (Figs a, e); 20 µm (Fig. h); 10 µm (Figs b, c, f); 4 µm (Fig. d).

Plate 66



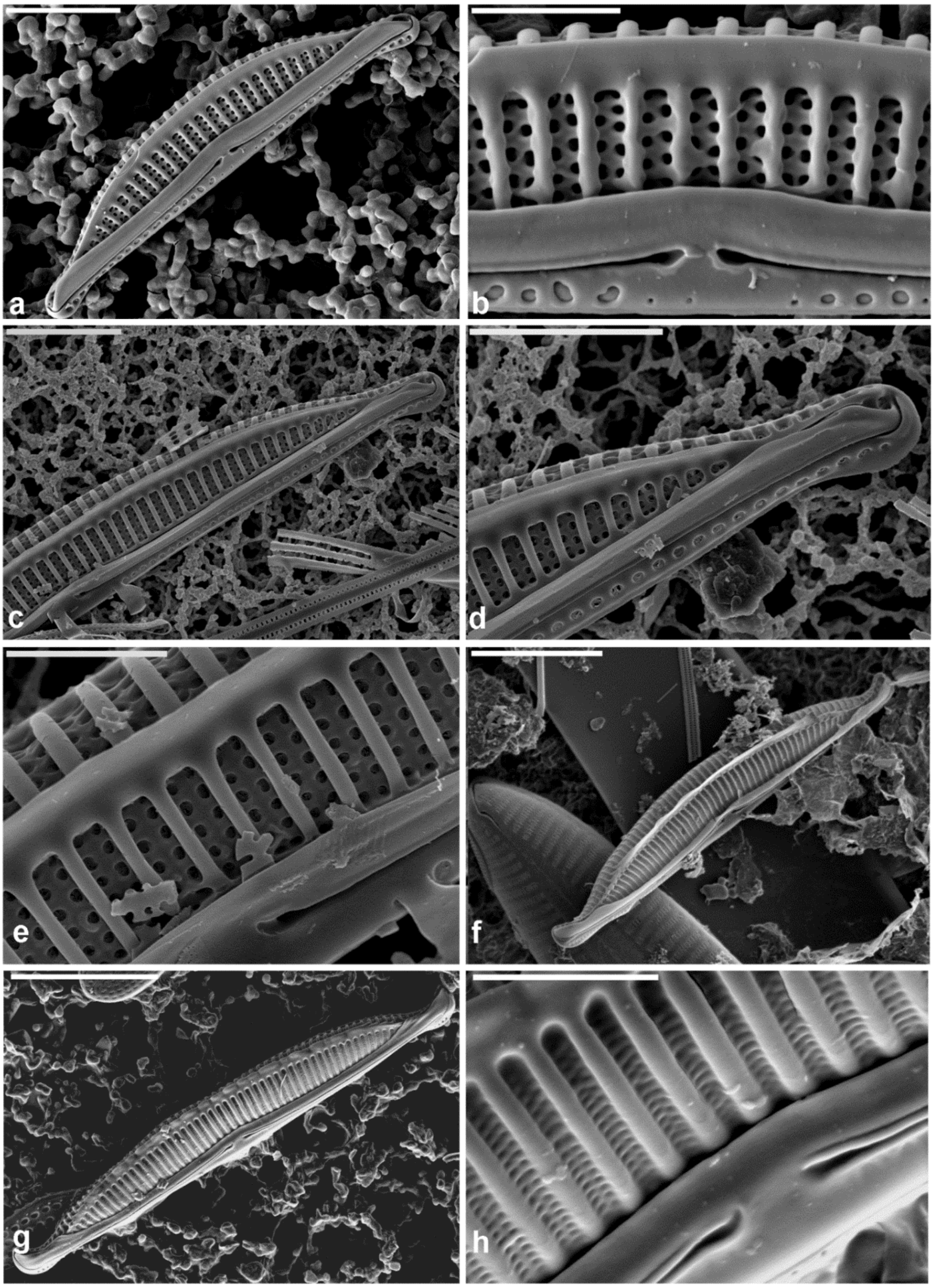
Figs a-h. SEMs of *Amphora* sp. Scale bars = 5 µm (Fig. g); 3 µm (Fig. a); 2 µm (Figs b, d, e, h); 1 µm (Fig. f); 500 nm (Fig. c).

Plate 67



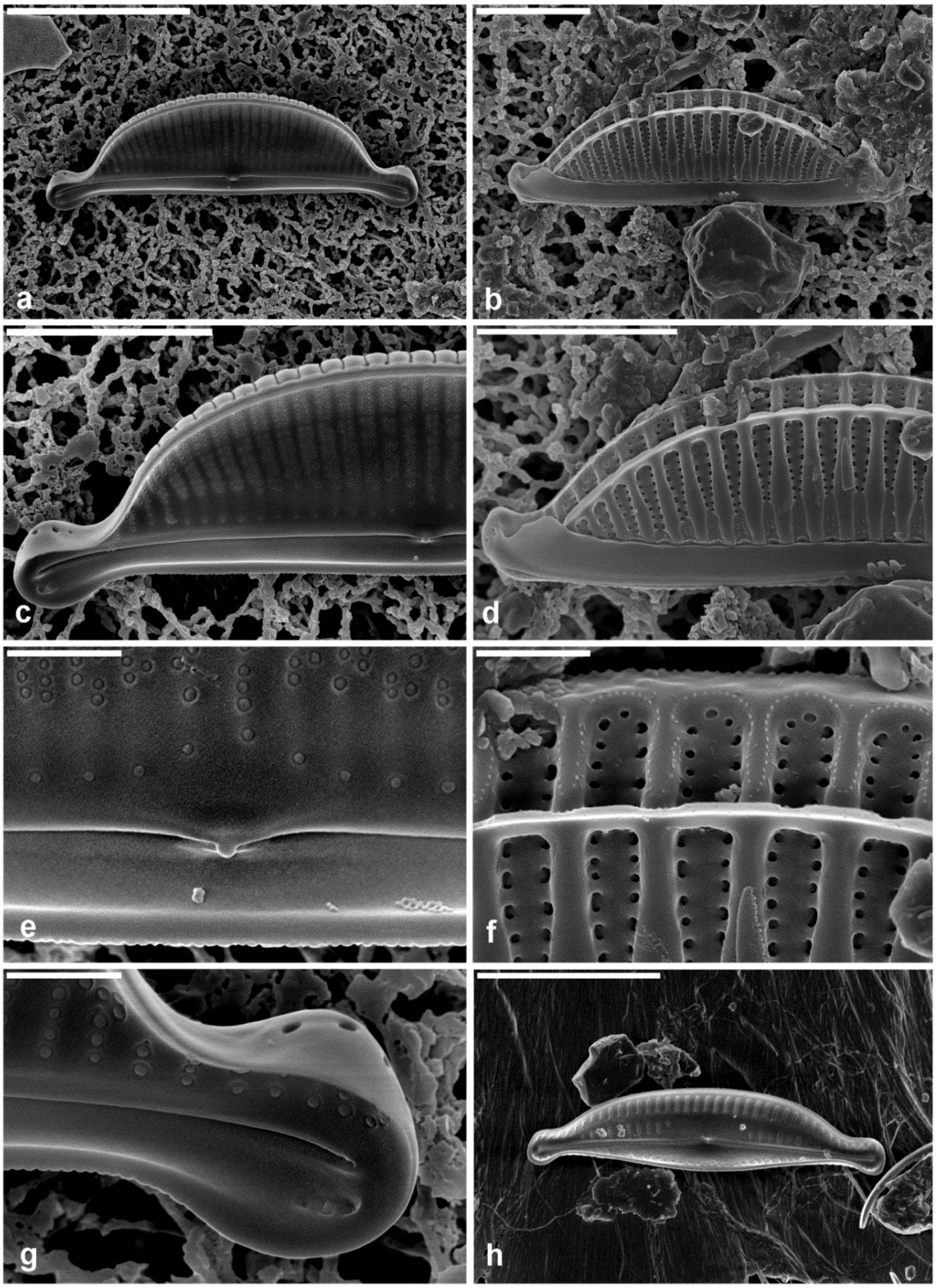
Figs a-h. *Amphora* sp. (SEM); (a and b) SEM image of the dorsal surface of *Amphora*, revealing the cell girdle band structures. (c) SEM image of the ventral surface of *Amphora*, including the two cell raphes.Figs e-h. *Amphora* (SEM). Scale bars = 5 µm (Fig. f); 4 µm (Fig. a), 3 µm (Figs b, c, e, h), 2 µm (Fig. d); 1 µm (Fig. g).

Plate 68



Figs a-h. SEMs of *Amphora* spp. Figs a-e. *Amphora* (SEM); Figs f-h. *Amphora* (SEM); Scale bars = 10 µm (Figs f, g), 5 µm (Figs a, c), 4 µm (Fig. d), 2 µm (Figs b, e, h).

Plate 69



Figs a-h. SEMs of *Amphora* spp. Figs a, c, e &-g. *Amphora* cf. *delicatissima* Krasske. Figs b, d, &-f. *Amphora turgida* Gregory var. *turgida*. Fig. h. *Amphora delicatissima* Krasske. Scale bars = 10 µm (Figs a, h); 5 µm (Figs b, c, d); 1 µm (Figs e, f, g).

Plate 70

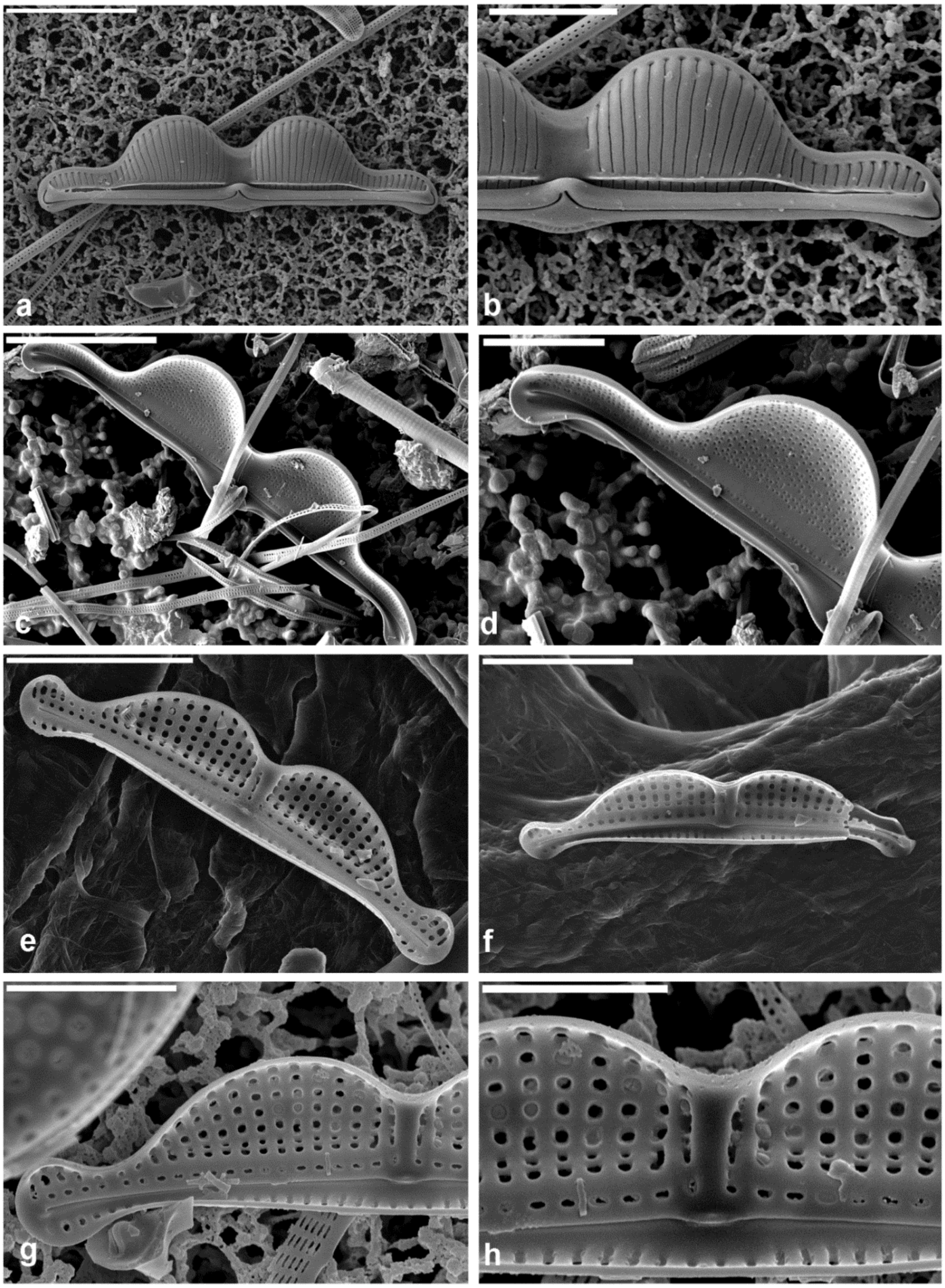
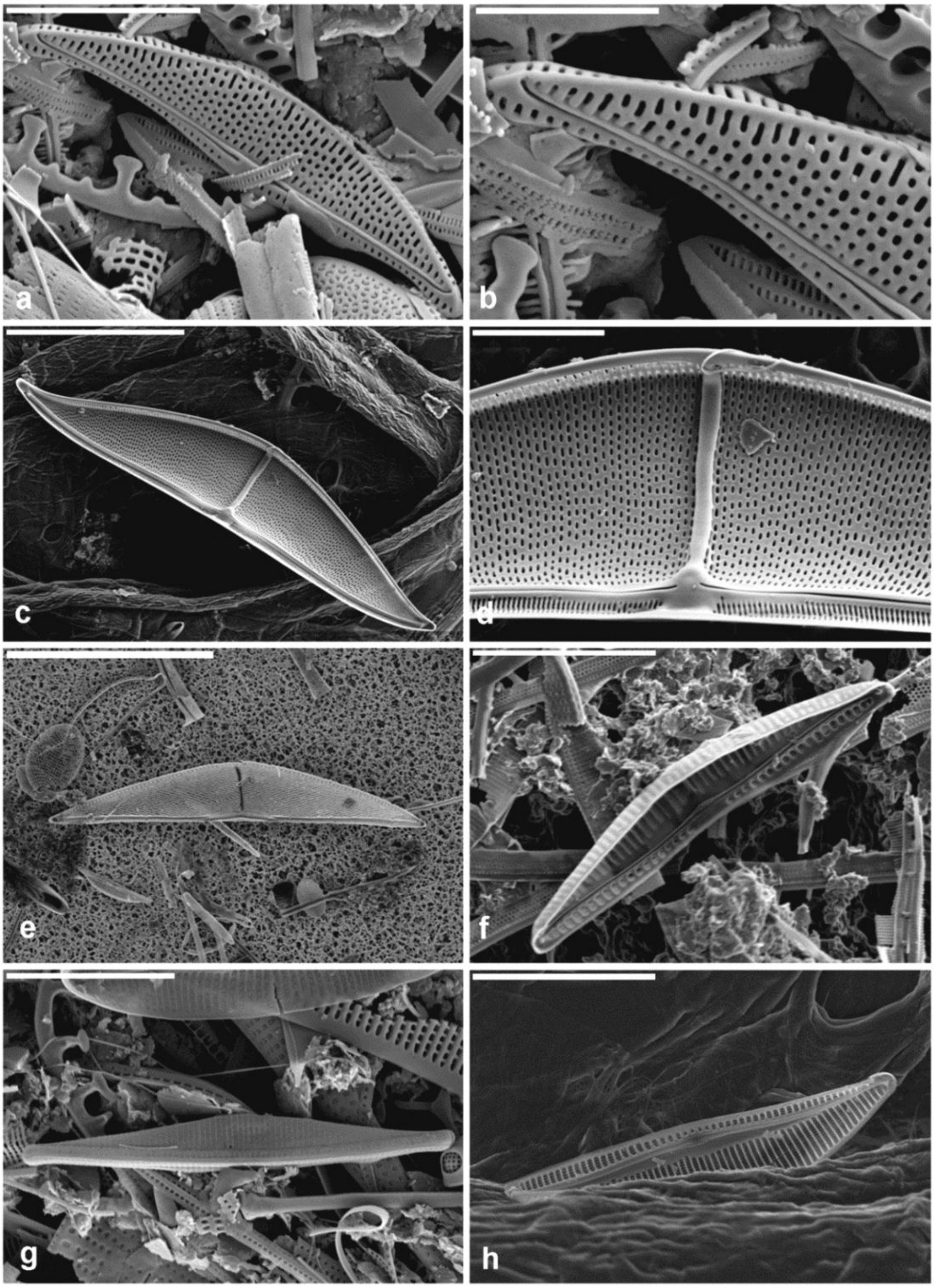


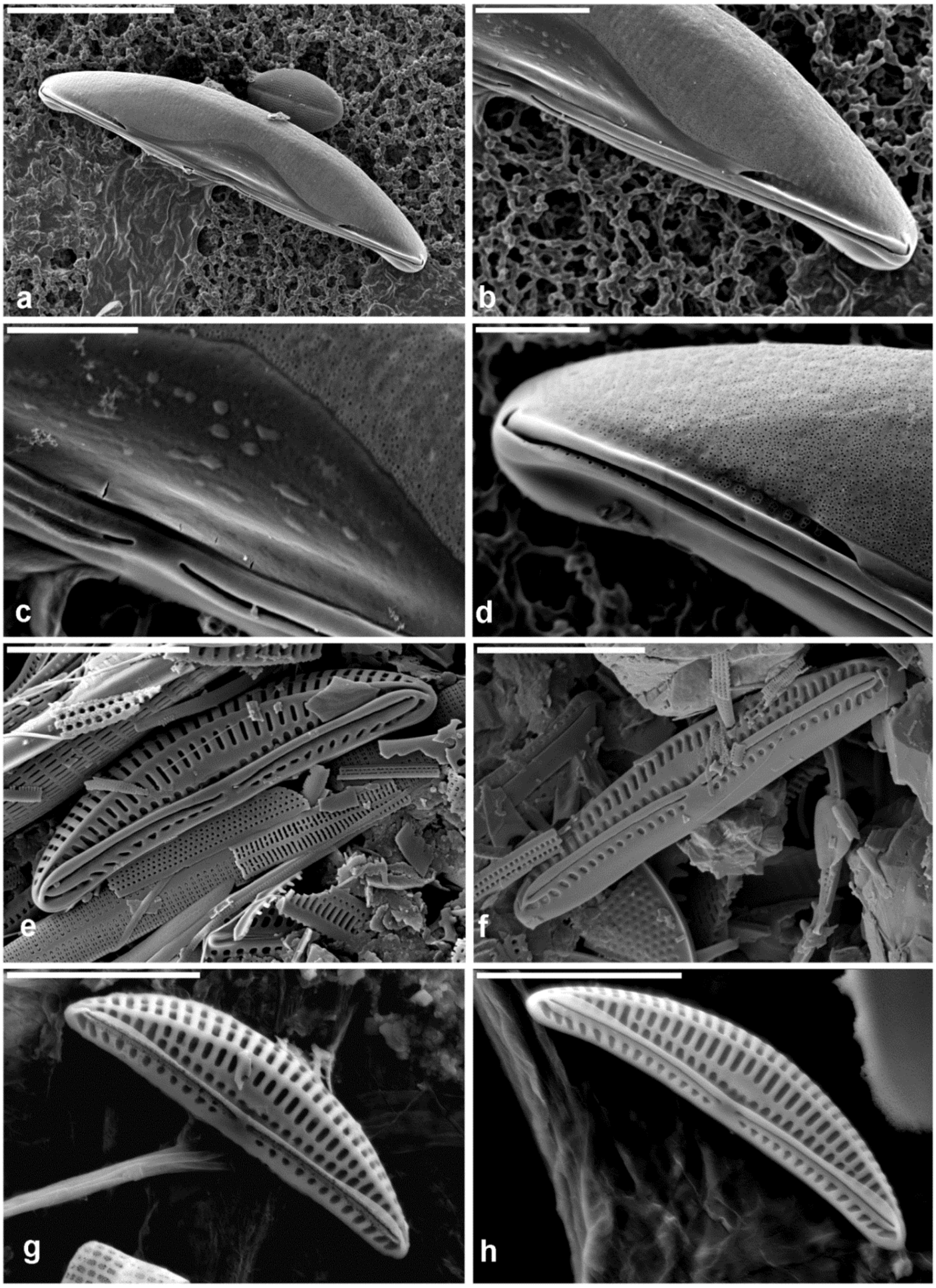
Fig. a-b. *Amphora bigibba* Grunow var. *interrupta* Grunow (SEM). External view. Figs b-d. *Amphora* cf. *bigibba* Grunow var. *interrupta* Grunow (SEM). Internal view. Figs e-h. *Amphora kolbei* Aleem (SEM). Internal view. Scale bars = 10 µm (Figs a, c); 5 µm (Figs b, d, e, f); 3 µm (Fig. g); 2 µm (Fig. h).

Plate 71



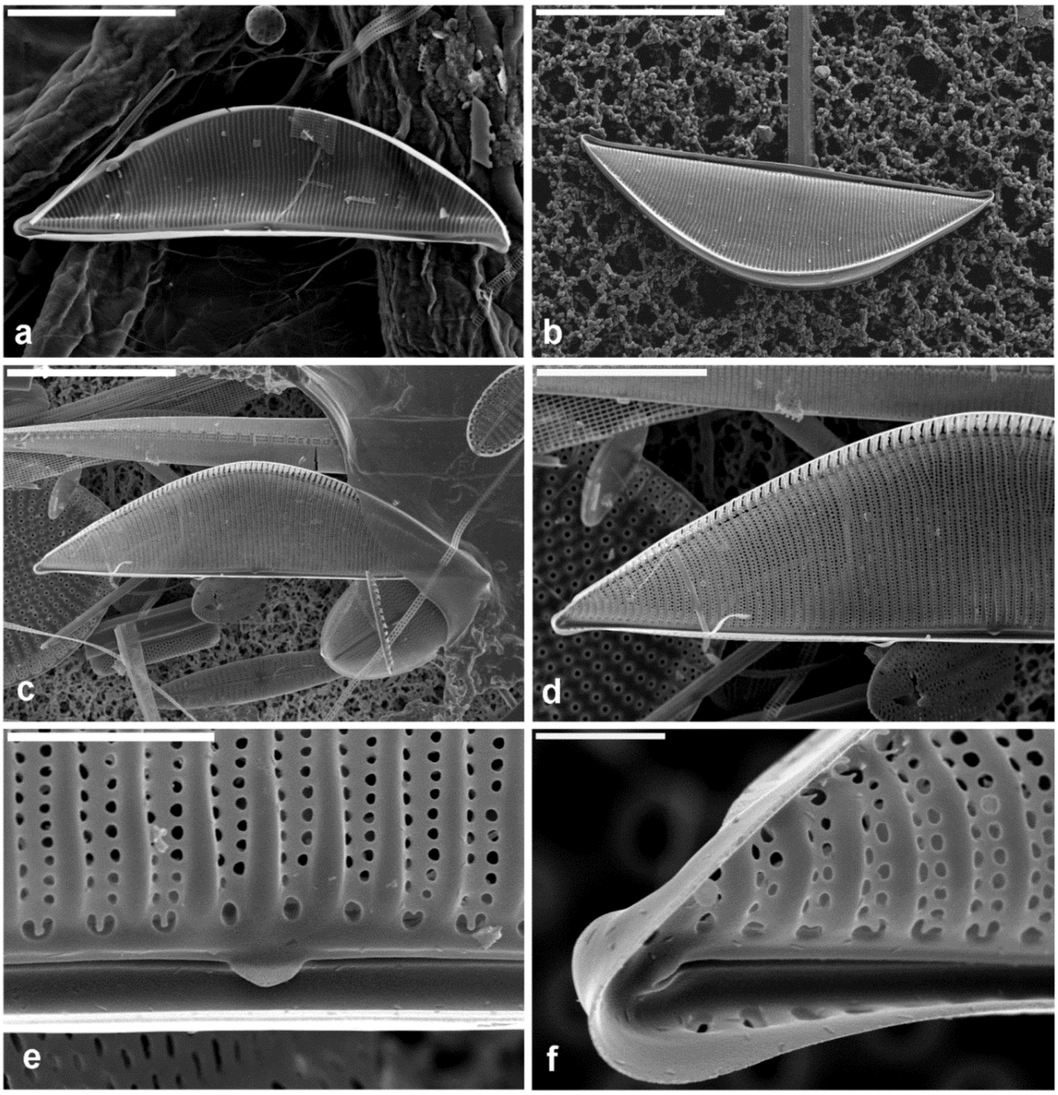
Figs a-f. *Amphora hyalina* Kützing. Fig. h. *Seminavis robusta* D.B.Danielidis & D.G.Mann (SEM). Scale bars = 50 µm (Fig. e); 40 µm (Fig. c); 10 µm (Figs d, f, h); 5 µm (Fig. g); 4 µm (Fig. a); 2 µm (Fig. b).

Plate 72



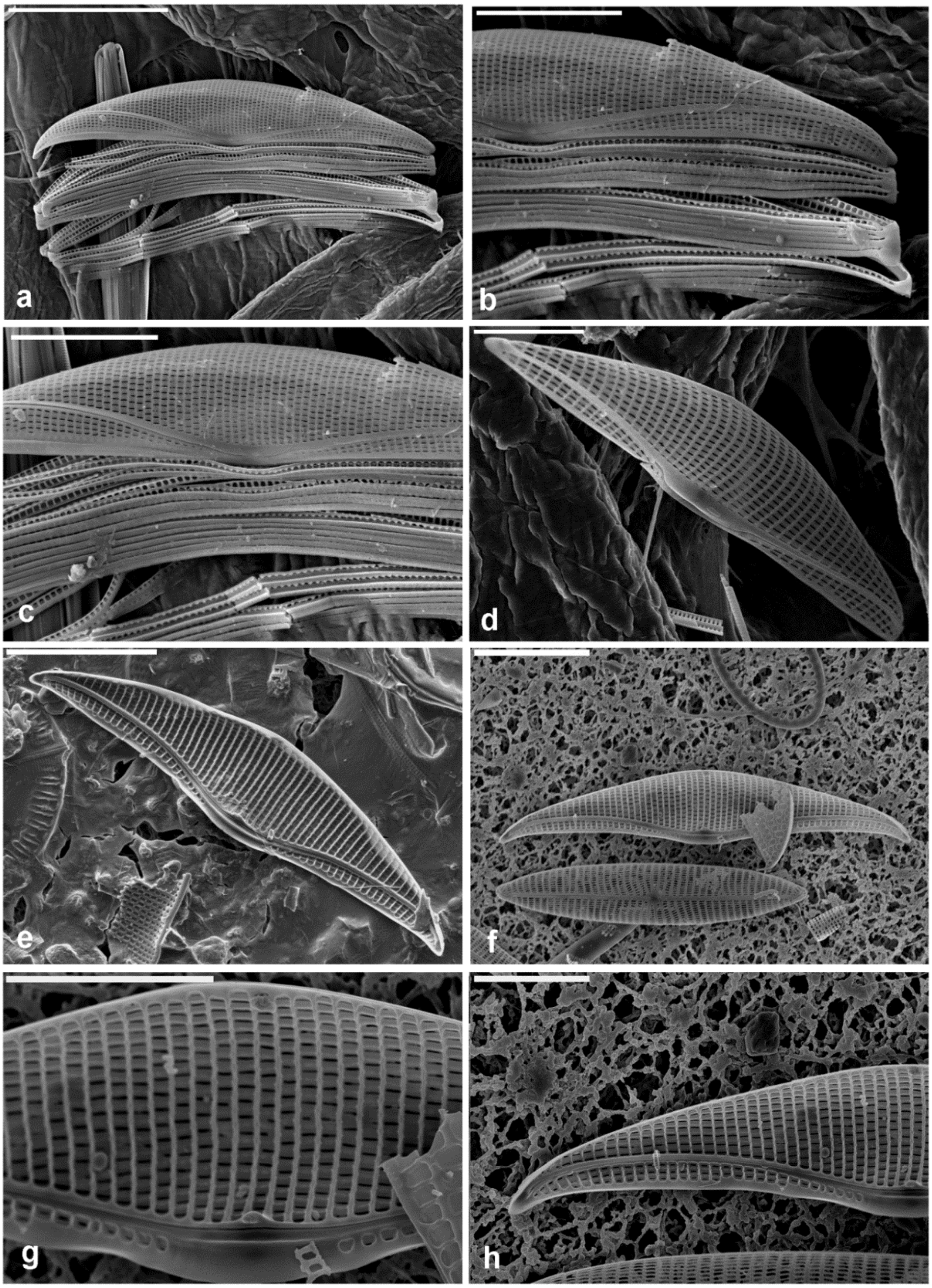
Figs a-d. *Amphora* cf. *laevissima* Gregory (SEM). Figs e-h. *Amphora gracialis* W. Smith (SEM). Scale bars = 30 µm (Fig. a); 10 µm (Fig. b); 5 µm (Figs c, d, e, f, h); 4 µm (Fig. g).

Plate 73



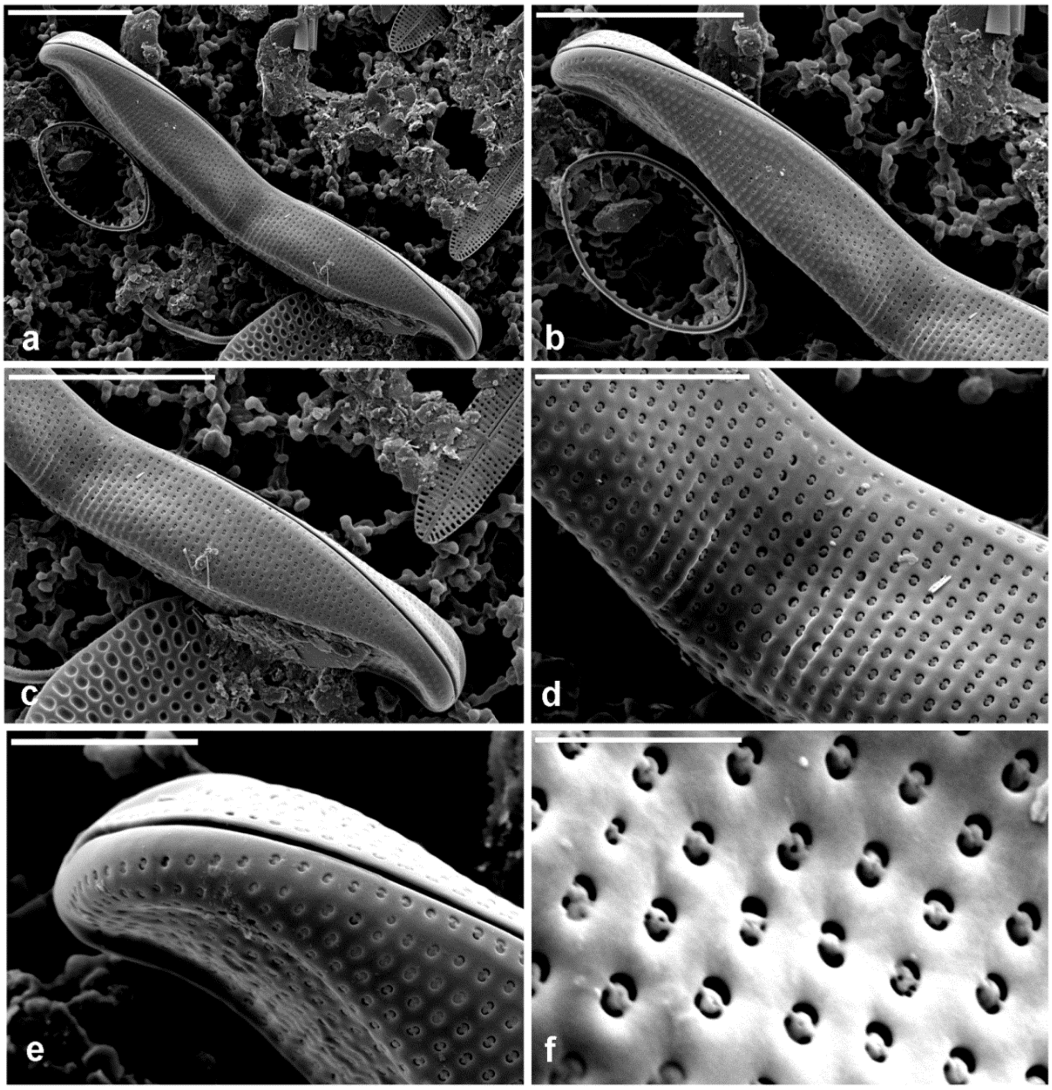
Figs a-f. *Amphora pseudohyalina* Simonsen (SEM). Scale bars = 30 µm (Fig. b); 20 µm (Fig. c); 10 µm (Figs a, d); 2 µm (Fig. e); 1 µm (Fig. f).

Plate 74



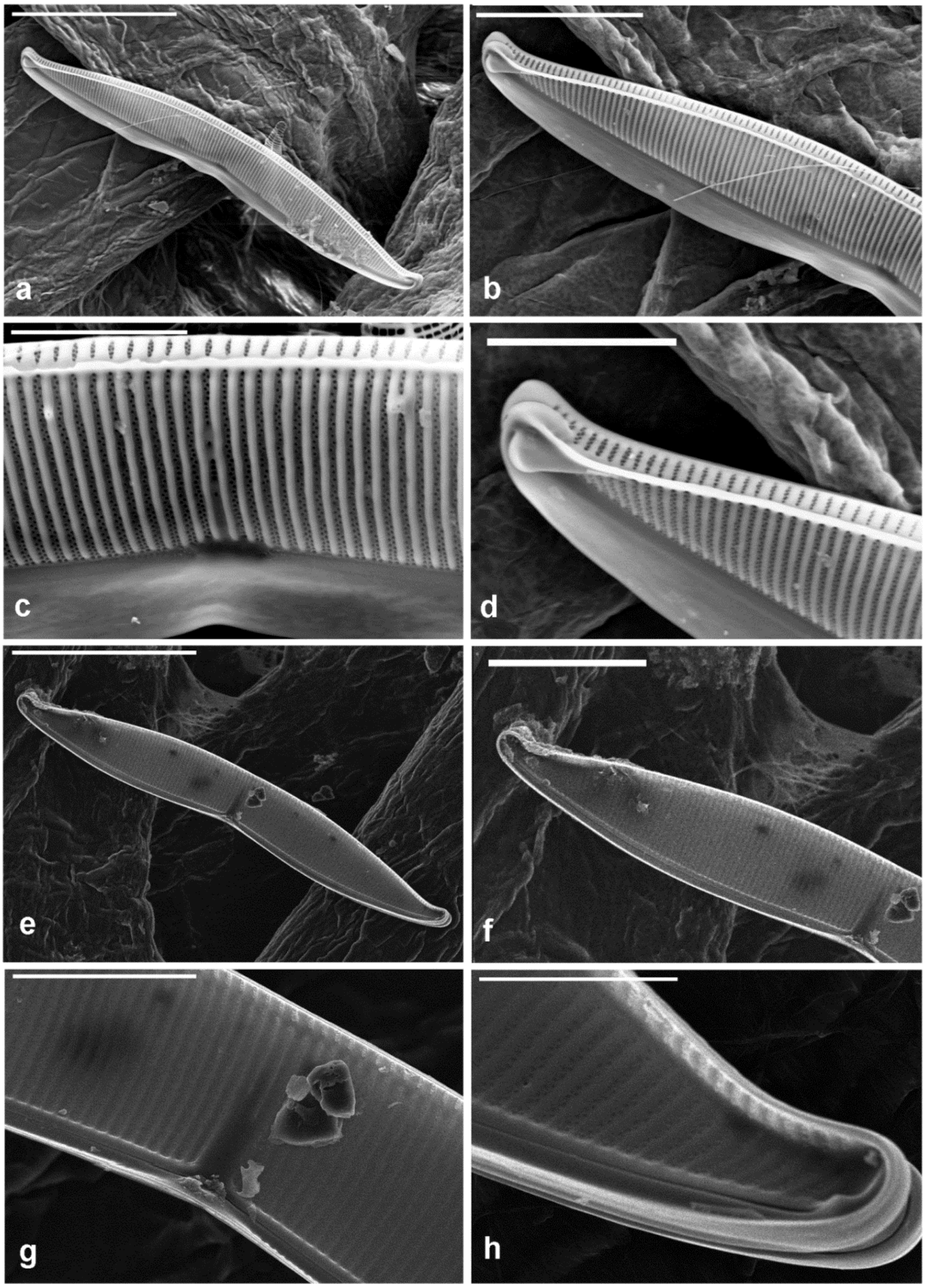
Figs a- h. *Amphora* aff. *securicula* Peragallo(SEM). Figs a-d. External view. Figs e-h. Internal view. Scale bars = 20 µm (Fig. a); 10 µm (Figs b, c, e, f); 5 µm (Figs d, g, h).

Plate 75



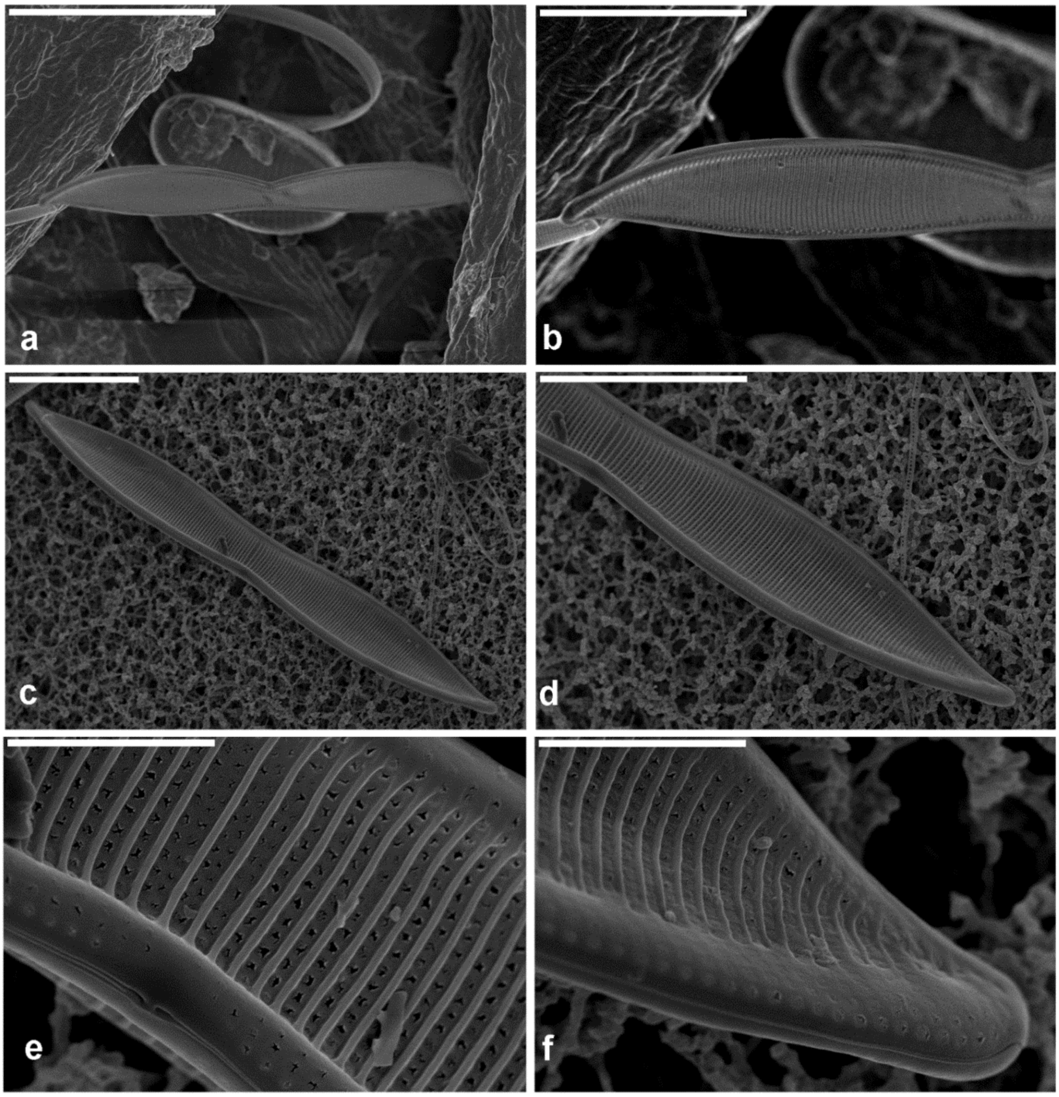
Figs a- f. *Amphora jostesorum*Witkowski, Metz. & Lange-B. (SEM). External view. Scale bars = 10 µm (Figs a, b, c); 4 µm (Fig. d); 3 µm (Fig. e); 1 µm (Fig. f).

Plate 76



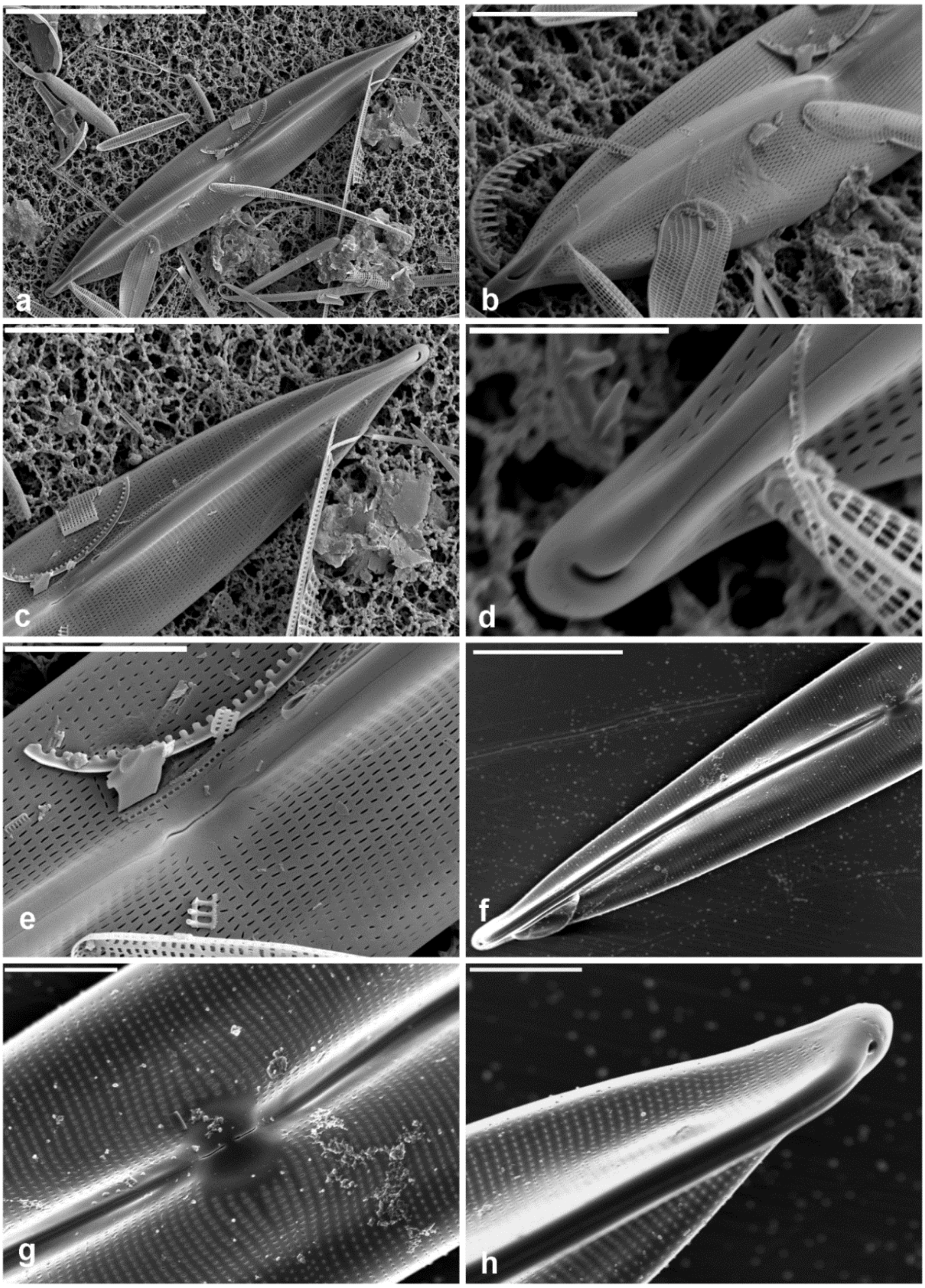
Figs a-h. SEMs of *Amphora* spp. Figs a-d. External view. Figs e-h. Internal view. Scale bars = 20 µm (Figs a, e); 10 µm (Figs b, f); 5 µm (Figs d, g); 4 µm (Fig. c); 3 µm (Fig. h).

Plate 77



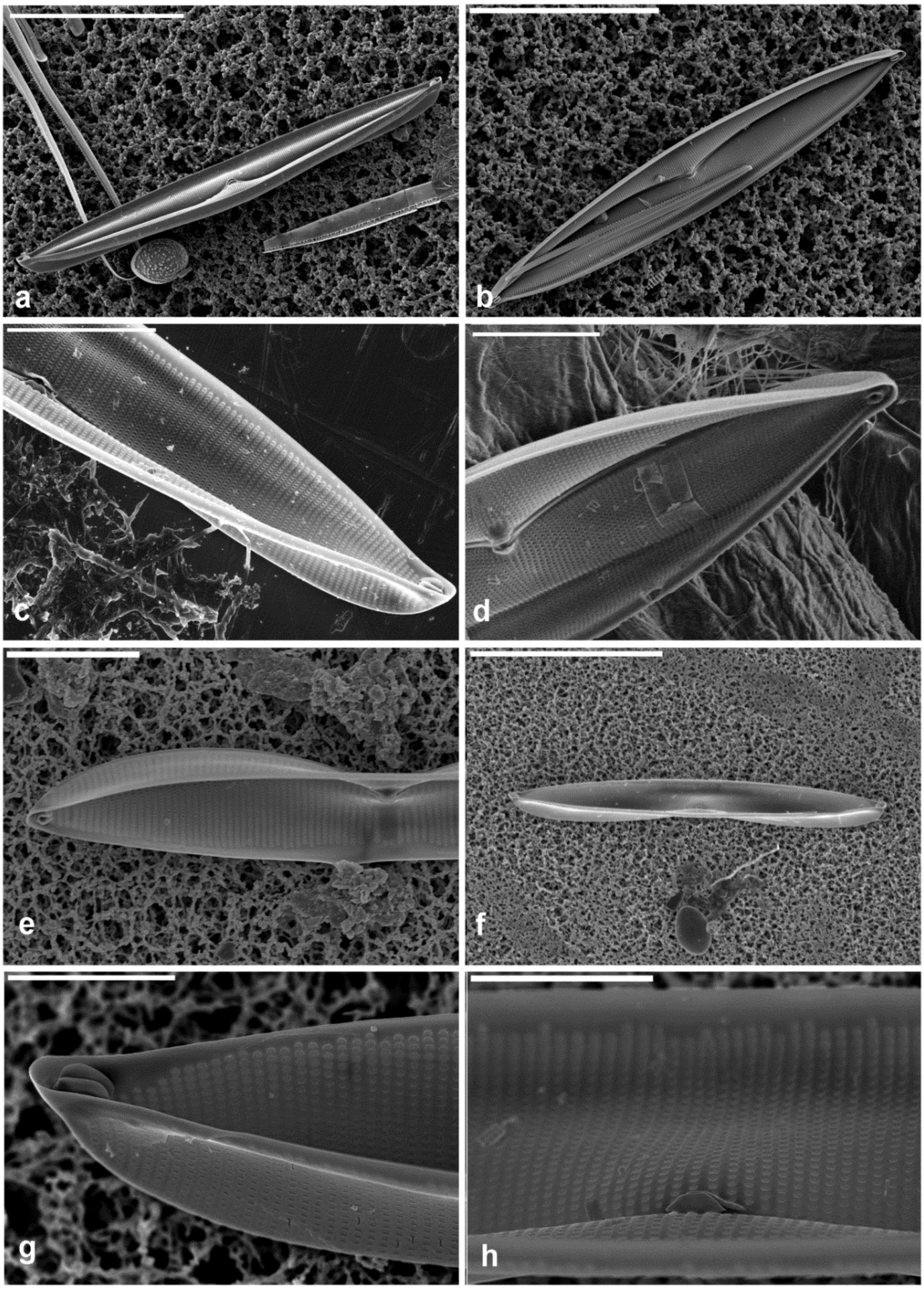
Figs a-h. SEMs of *Amphora* sp. Scale bars = 20 µm (Fig. a); 10 µm (Figs b, c, d); 2 µm (Figs e, f).

Plate 78



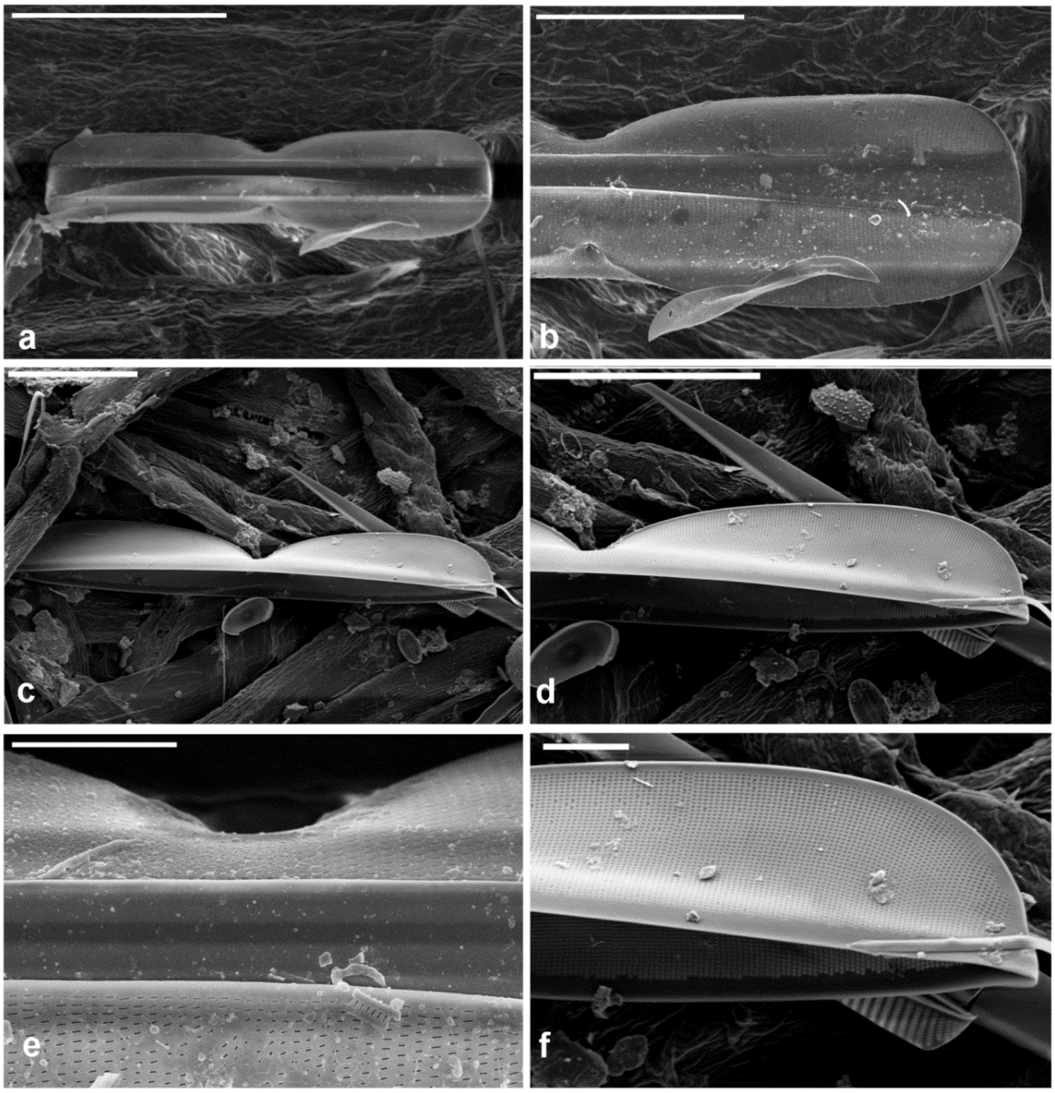
Figs a-h. SEMs of *Plagiotropis* spp. External view. Scale bars = 30 µm (Fig. a); 20 µm (Figs f); 10 µm (Figs b, c); 5 µm (Figs e, g, h); 3 µm (Fig. d).

Plate 79



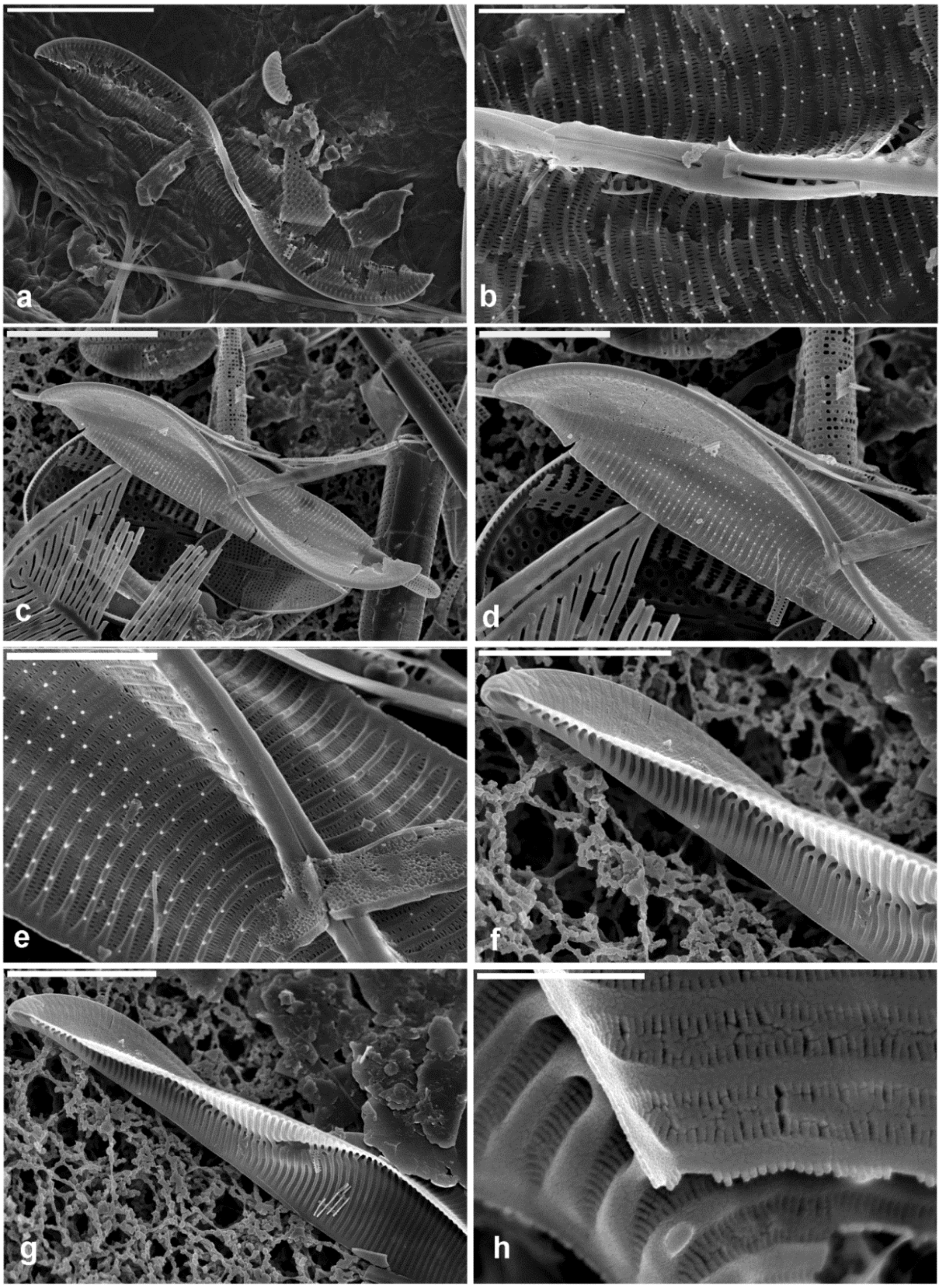
Figs a-h. SEMs of *Plagiotropis* spp. Internal view. Scale bars = 40 µm (Figs a, b, f); 10 µm (Figs c, d, e); 5 µm (Figs g, h).

Plate 80



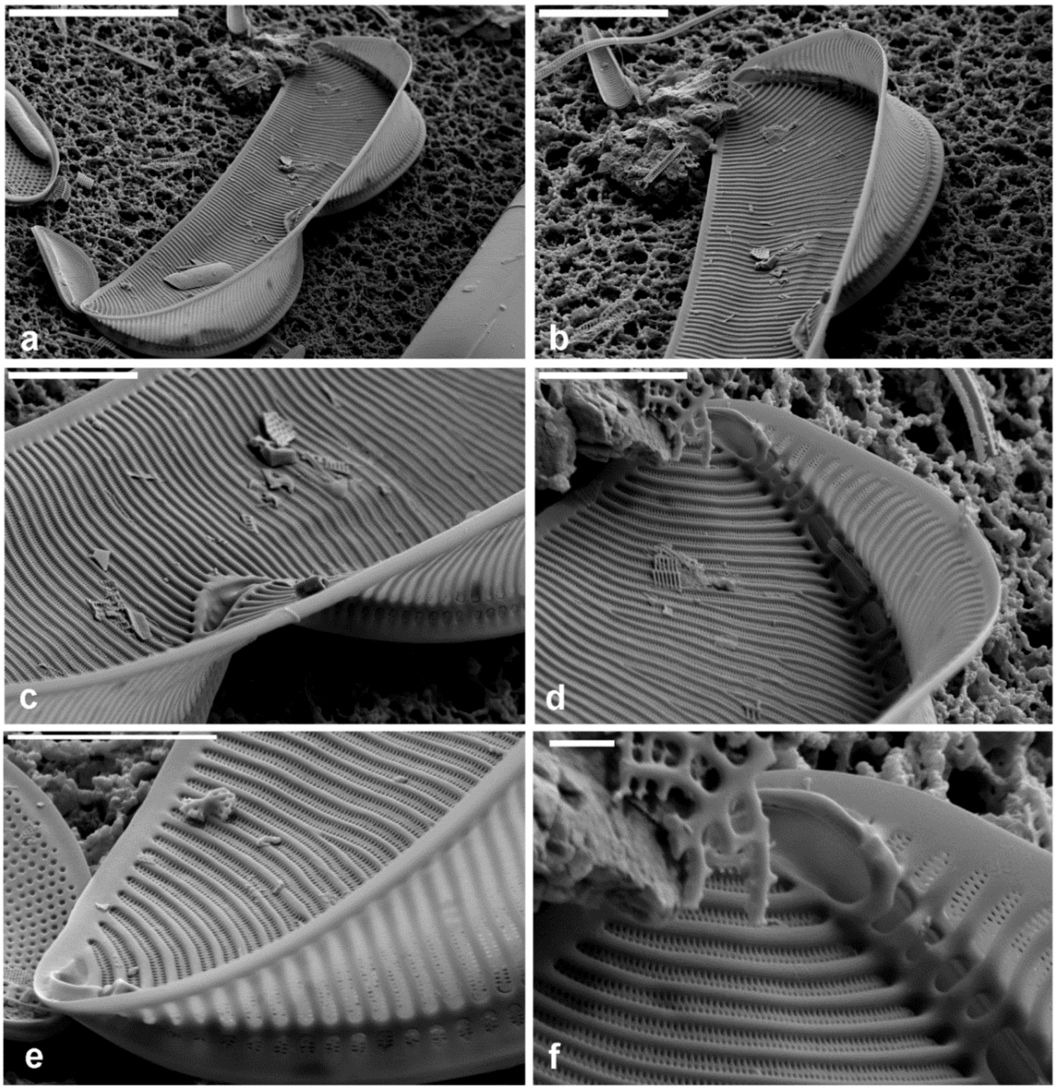
Figs a-h. SEMs of *Plagiotropis* spp. External view. Scale bars = 50 µm (Figs c, d); 40 µm (Fig. a); 20 µm (Fig. b); 10 µm (Fig. f); 5 µm (Fig. e).

Plate 81



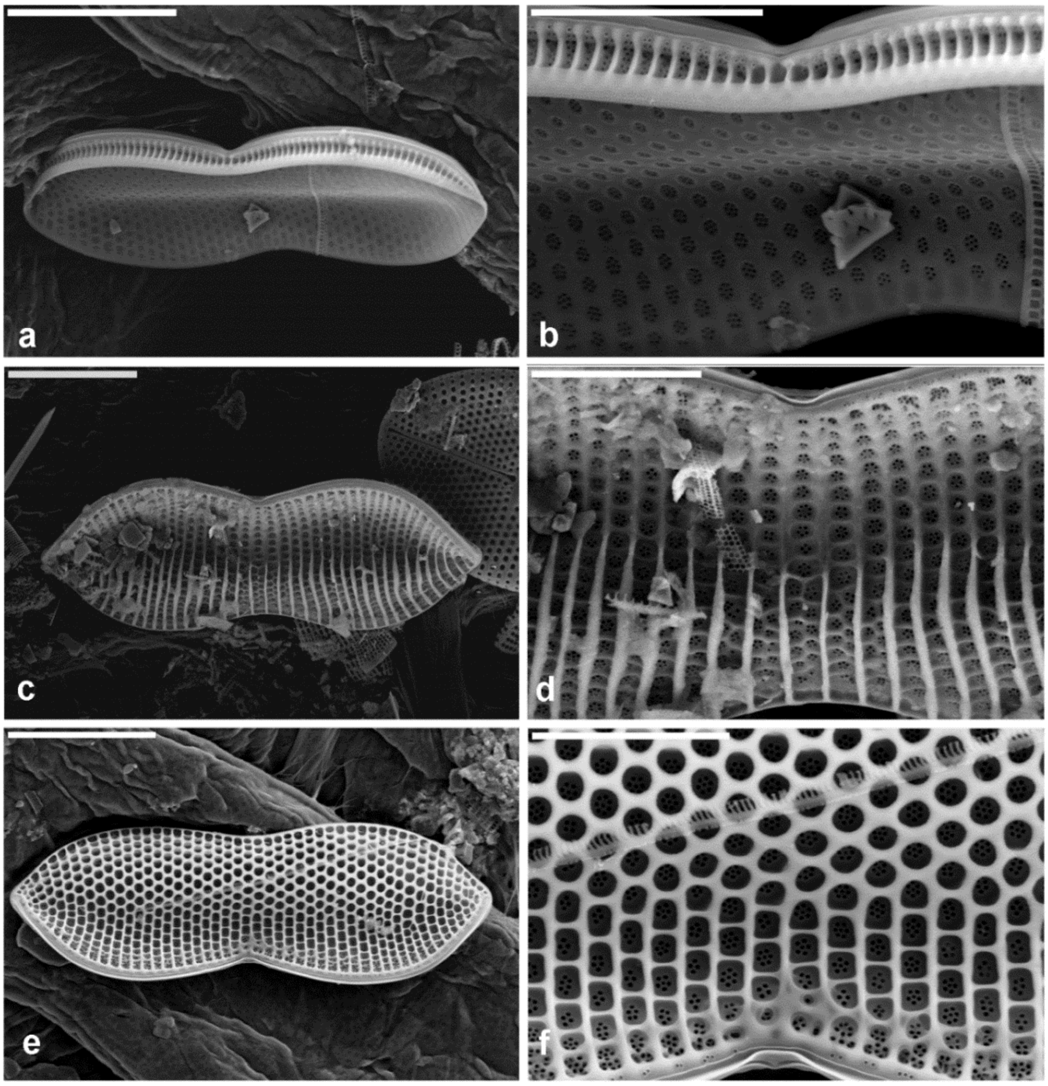
Figs a-h. SEMs of *Entomoneis* spp.. Scale bars = 10 µm (Figs a, c); 5 µm (Figs d, f); 4 µm (Fig. g); 2 µm (Figs b, e); 500 nm (Fig. h).

Plate 82



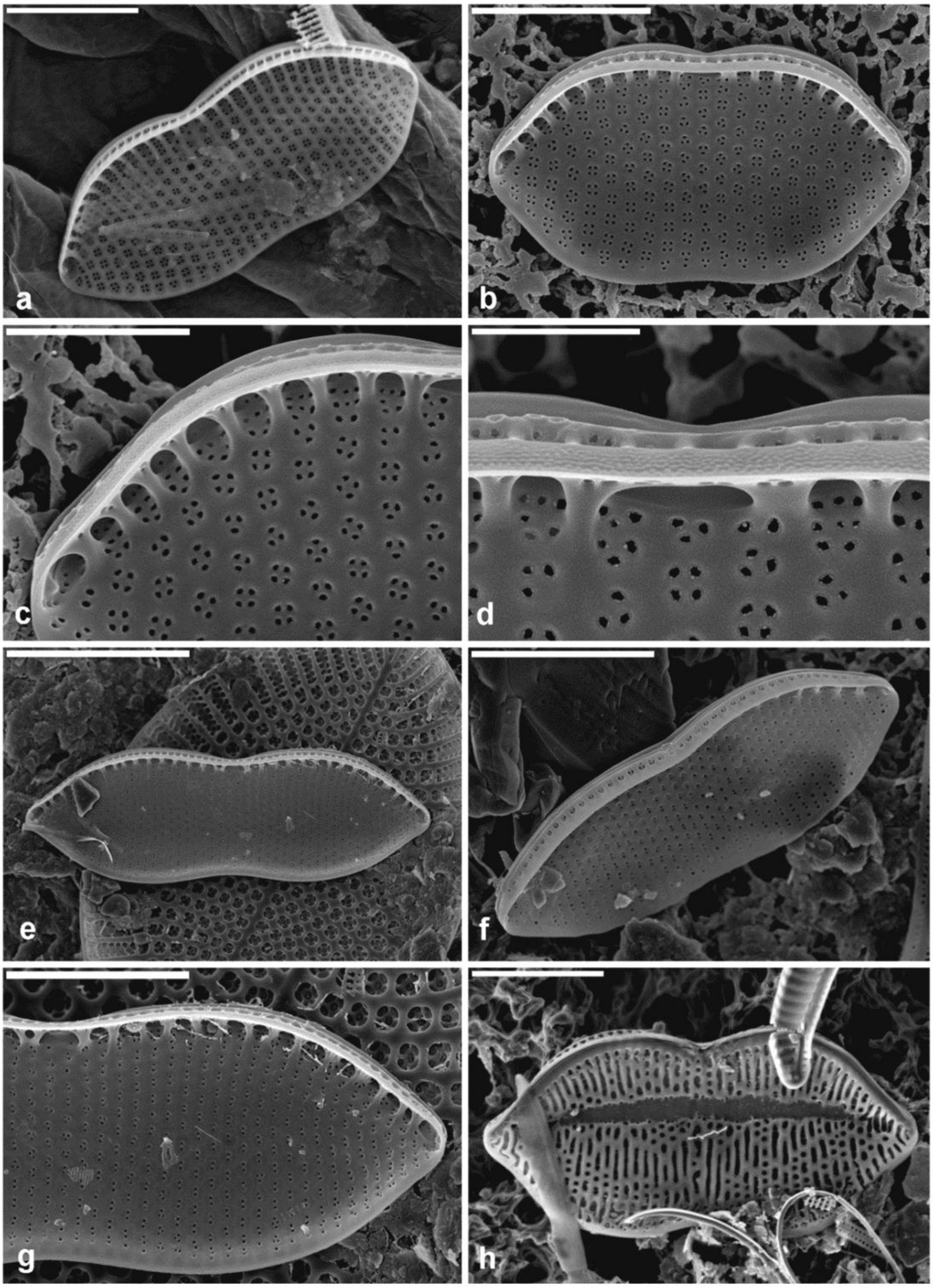
Figs a-h. SEMs of *Entomoneis* spp.. Scale bars = 20 µm (Fig. a); 10 µm (Fig. b); 5 µm (Figs c, d, e); 1 µm (Fig. f).

Plate 83



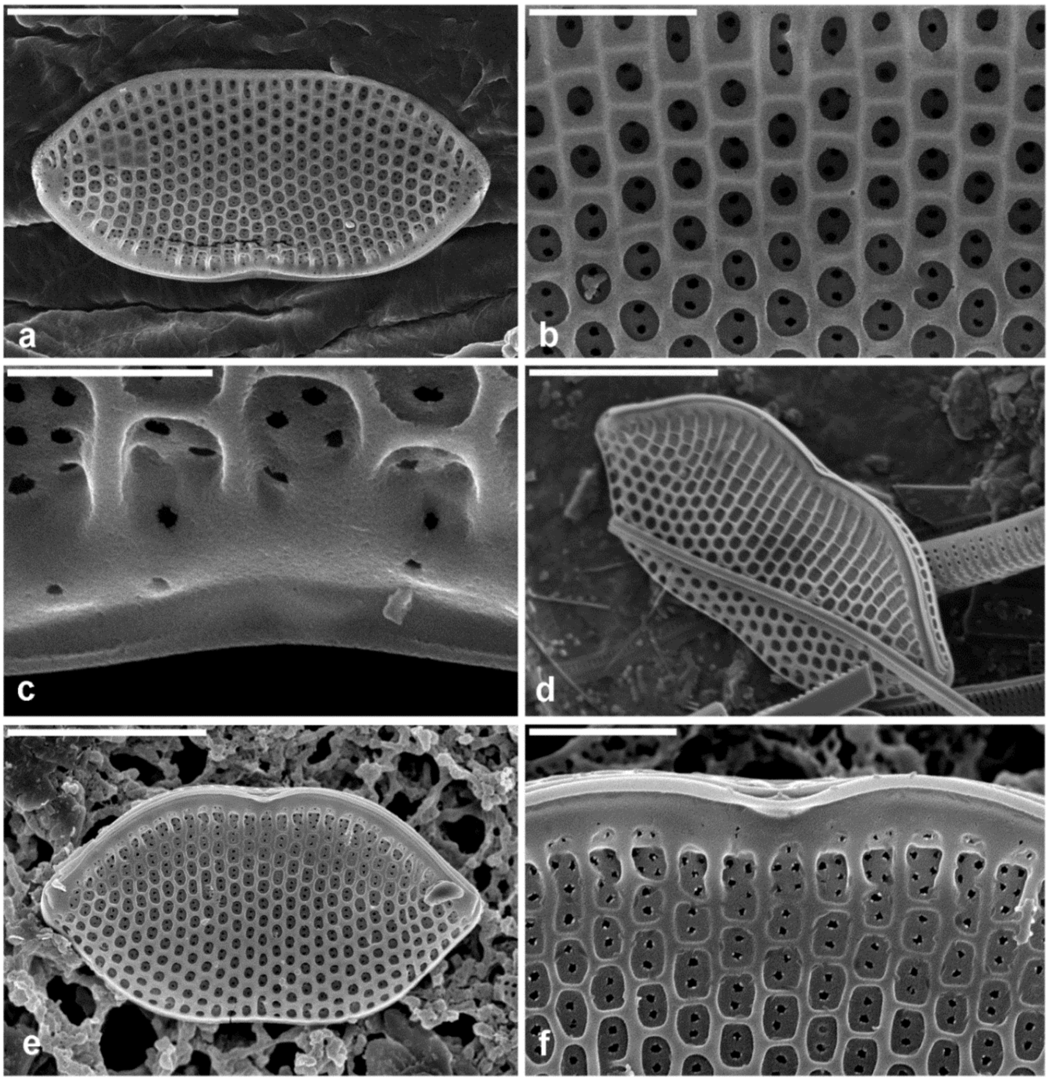
Figs a-f. SEMs of *Nitzschia* cf. *panduriformis* Gregory var. *panduriformis.* Scale bars = 10 µm (Figs a, c, e); 5 µm (Figs b, d); 4 µm (Fig. f).

Plate 84



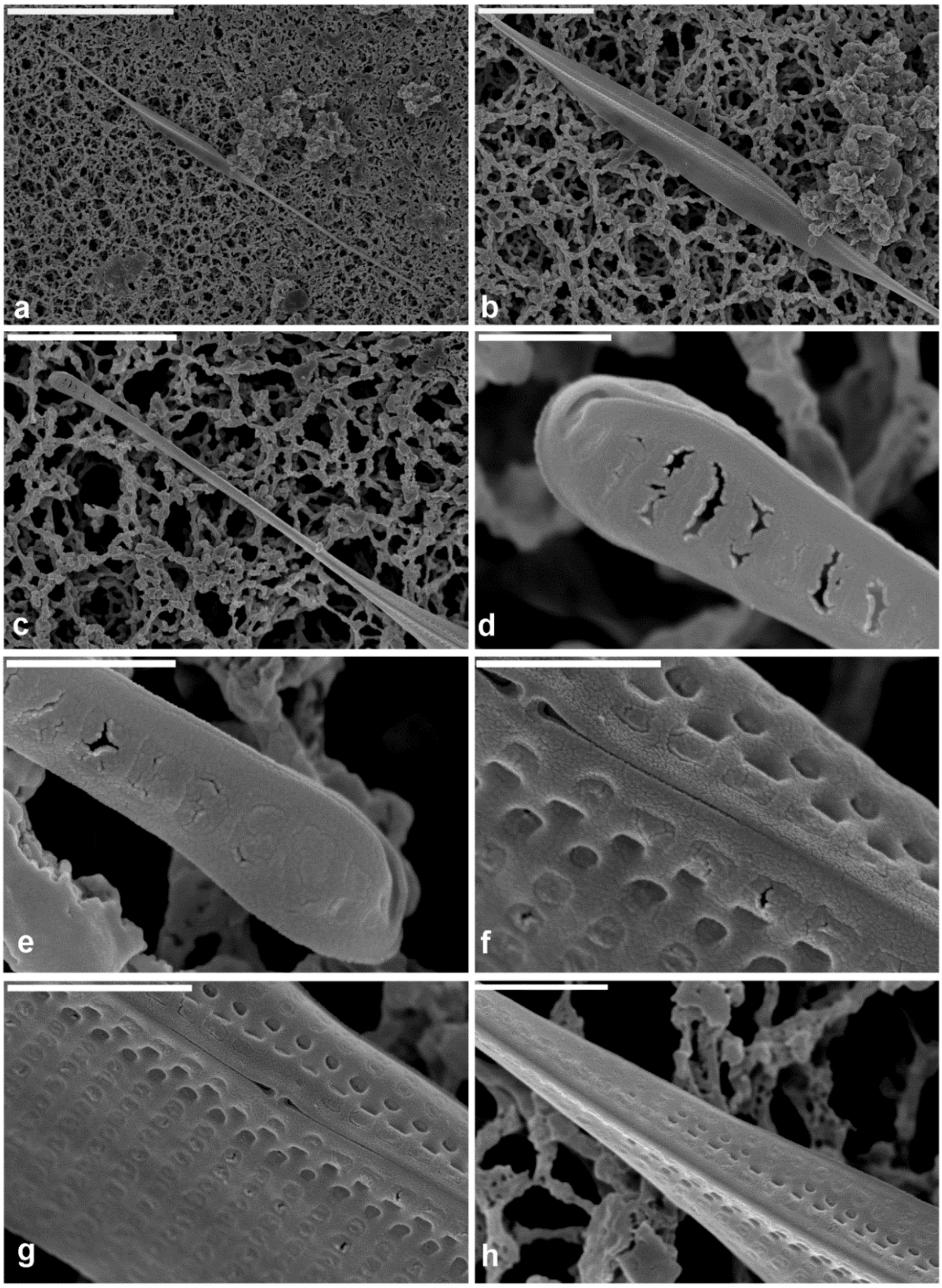
Figs a-h. SEMs of *Nitzschia* spp. Figs a-d. *Nitzschia* (SEM); Figs e-g. *Nitzschia coarctata* Grunow var. *continua*; Fig. h. *Nitzschia* cf. *coarctata Grunow*. Scale bars = 10 µm (Fig. e); 5 µm (Figs a, f, g, h); 4 µm (Fig. b); 2 µm (Fig. c); 1 µm (Fig. d).

Plate 85



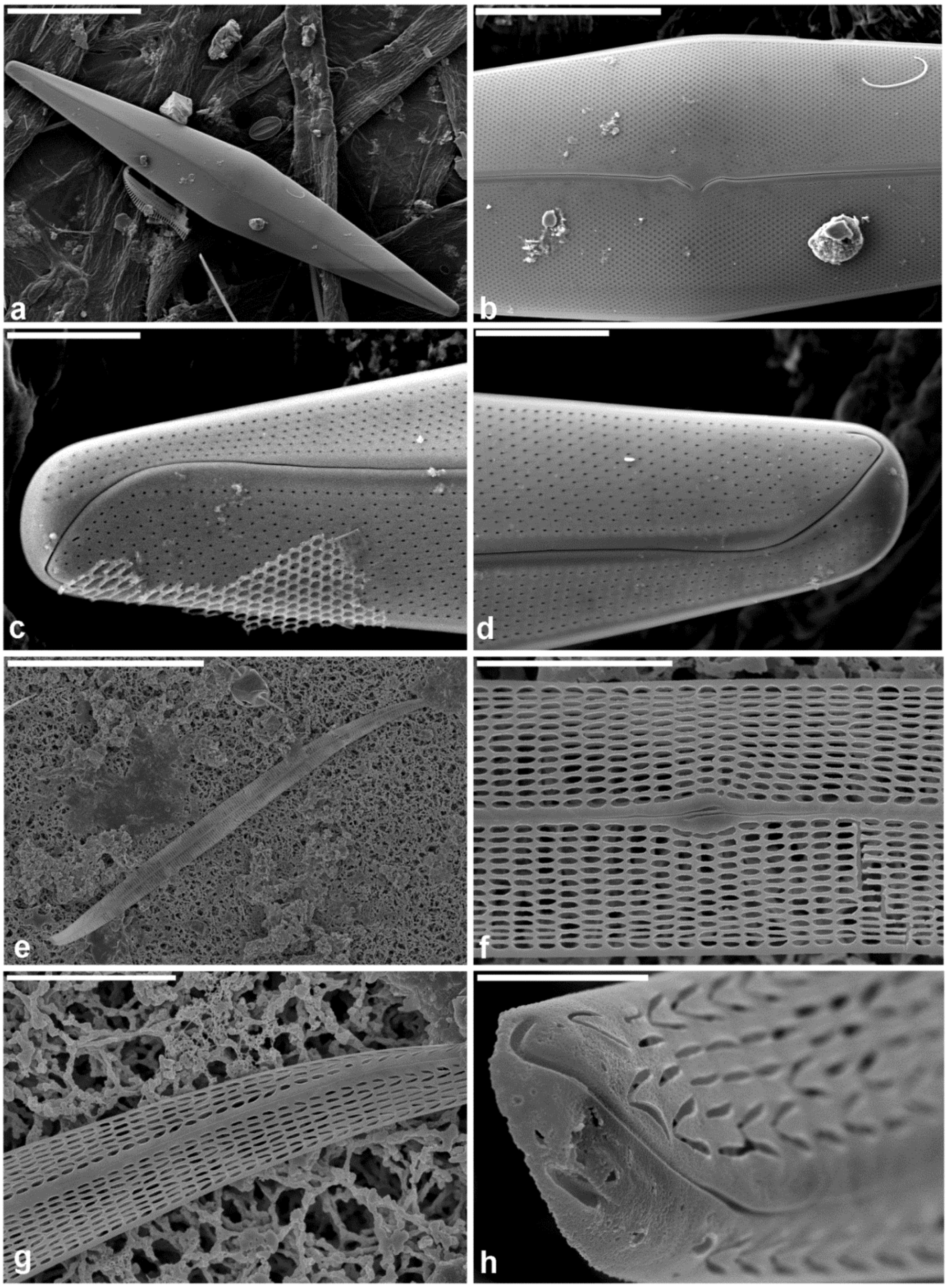
Figs a-f. SEMs of *Nitzschia* cf. *panduriformis* var. *continua* Grunow. Scale bars = 5 µm (Figs a, d); 4 µm (Fig. e); 1 µm (Figs b, f); 500 nm (Fig. c).

Plate 86



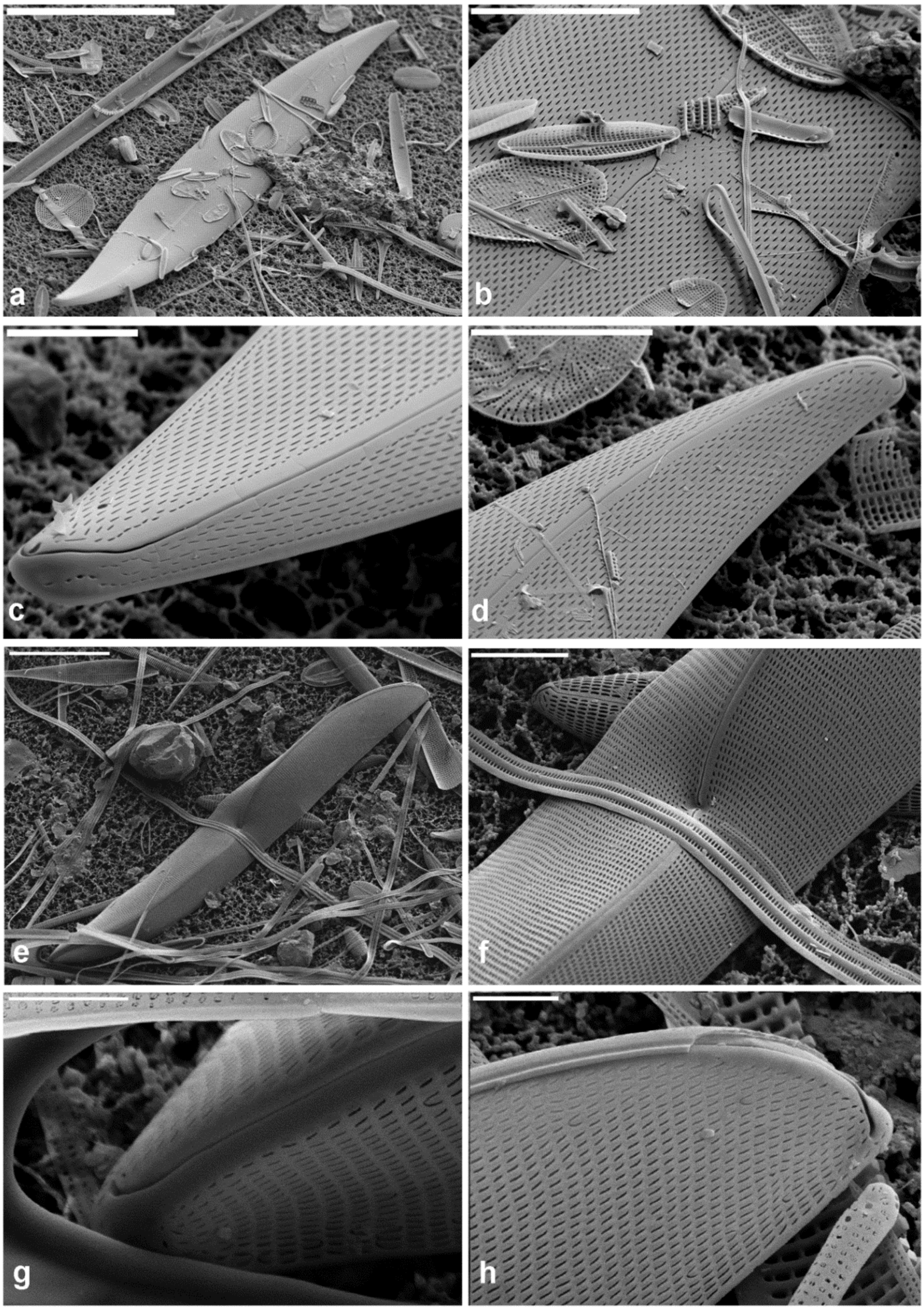
Figs a-h. SEMs of *Nitzschia* cf. *closterium* (Ehrenberg) W. Smith. Scale bars = 20 µm (Fig. a); 5 µm (Figs b, c); 1 µm (Figs g, h); 500 nm (Figs d, e, f).

Plate 87



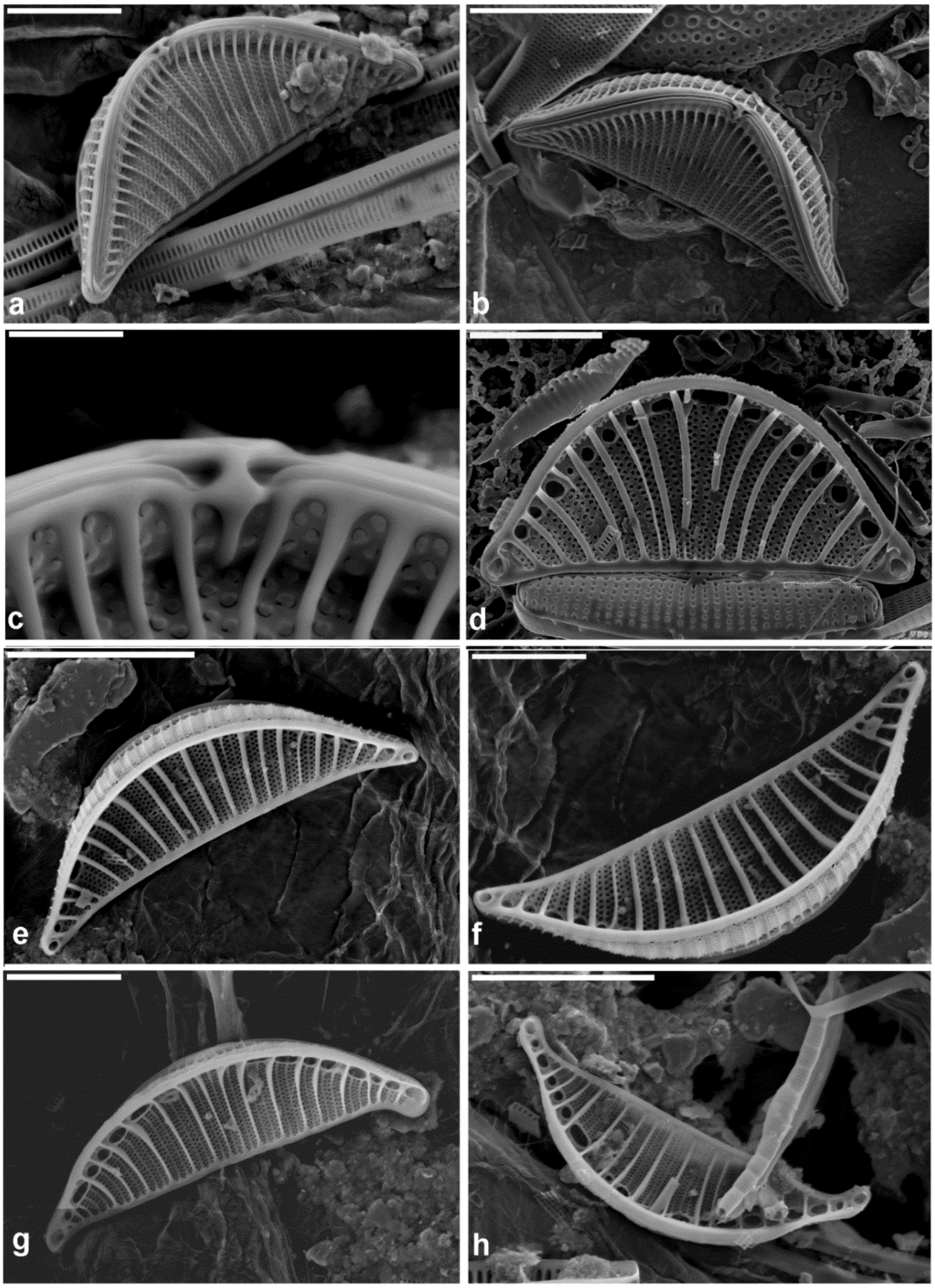
Figs a-h. *Pleurosigma* sp. (SEM); Figs e-h. *Gyrosigma tenuissimum* (W.Smith) Griffith & Henfrey 1856. Scale bars = 50 µm (Fig. a); 40 µm (Fig. e); 20 µm (Fig. b); 5 µm (Figs c, d, g); 4 µm (Fig. f); 1 µm (Fig. h).

Plate 88



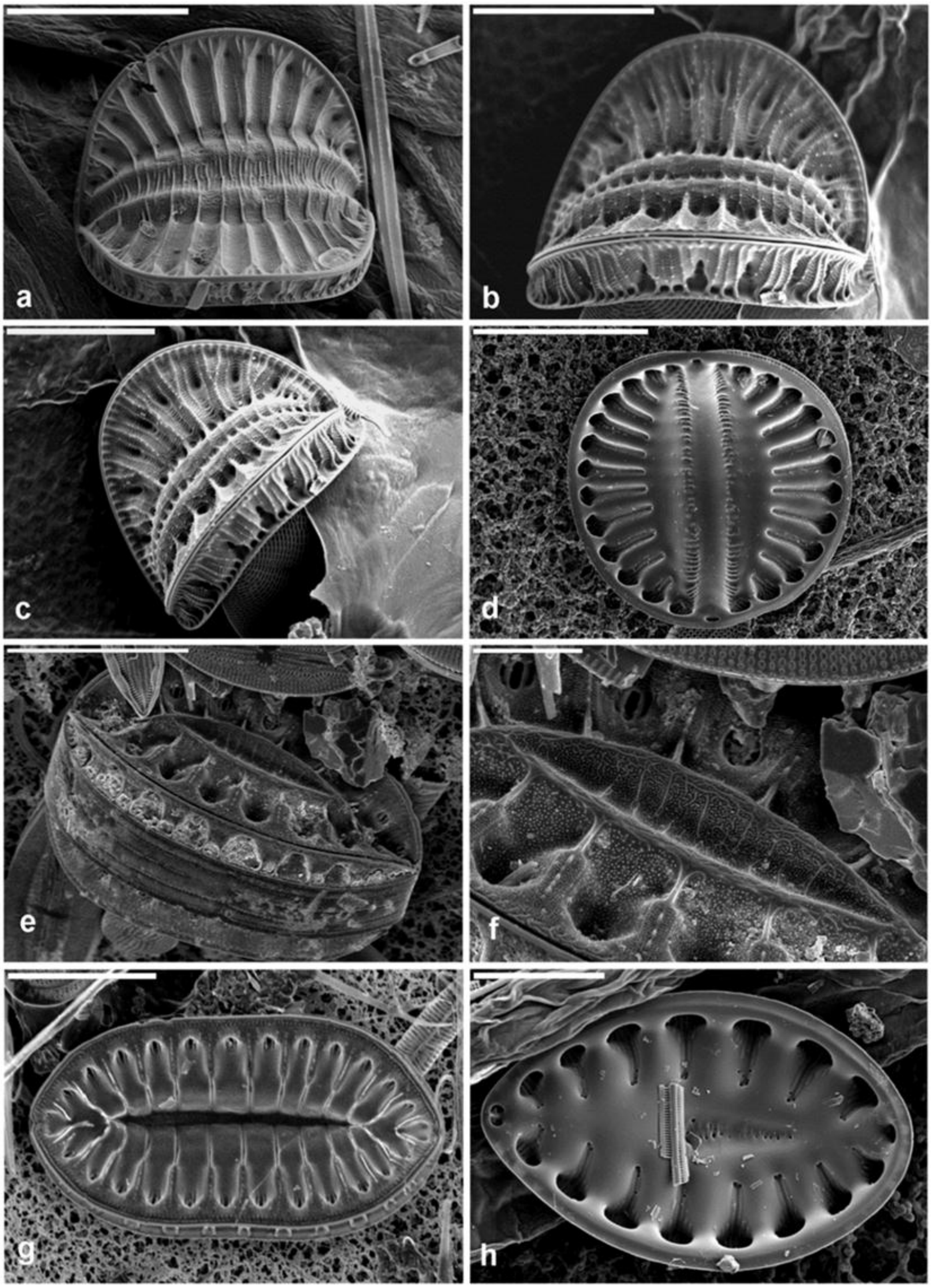
Figs a-h. SEMs of *Pleurosigma* spp. External valve views. Fig. a-d. *Pleurosigma* sp. Fig. e-h. *Pleurosigma* sp. Scale bars = 50 µm (Fig. a); 20 µm (Fig. e); 10 µm (Figs b, d); 5 µm (Figs c, f); 2 µm (Figs g, h).

Plate 89



Figs a-c & g-h. *Rhopalodia pacifica* Krammer(SEM); Fig. d. *Rhopalodia* cf. *musculus*. Scale bars = 10 µm (Figs b, e, h); 5 µm (Figs a, d, f, g); 1 µm (Fig. c).

Plate 90



Figs a-d. *Campylodiscus* sp. (SEM); Fig. e-f. *Surirella fastuosa* (Ehrenberg) Kützing (SEM); Fig. h. *Surirella brebissonii* Krammer & Lange-Bertalot (SEM); Scale bars = 50 µm (Fig. a); 40 µm (Fig. d); 20 µm (Figs e, g); 10 µm (Figs b, c, h); 5 µm (Fig. f).

8. CURRICULUM VITAE

Ana Car was born on 29th of October 1980 in Zagreb, Croatia where she completed primary and high school education (IX Gymnasium). In 1999 she enrolled the undergraduate engineering degree program of Molecular Biology, Department of Biology, Faculty of Science, University of Zagreb where she gradauated in 2007. Research for her diploma thesis entitled “Analysis of satellite DNA "library" in parthenogenetic nematode *Meloidogyne fallax* (Karssen, 1996)” was focused on rapidly evolving segments of eukaryotic genomes that may raise a genetic barrier that leads to speciation and conducted at Laboratory for Structure and Function of Heterochromatin, Division of Molecular Biology, Ruđer Bošković Institut, Zagreb under the supervision of Miroslav Plohl.

Since 2008 she has been employed as a research assistant at Institute for Marine and Coastal Research, University of Dubrovnik. In 2008 she enrolled the Interdisciplinary Doctoral study in Oceanology at the Faculty of Science, University of Zagreb with the research interest focused on taxonomy and ecology of marine benthic diatoms. During her work she participated in different national and international scientific projects; at the project ‘Jadran’ and project no. 275-0000000-3186 “Plankton Populatin Structure in the Trophic Gradient in the South Adriatic” lead by PhD Mirna Batistić, founded by the Croatian Ministry of Science, Education and Sports of Croatia and project (N306 468 538) founded by the Polish Ministry of Science and Higher Education. Since 2008 she had regular research visits in duration of one month to University of Szczecin, Poland where she has been working in an international laboratory lead by Prof. Andrzej Witkowski. Since 2013 she is a principal investigator of international project “Taxonomic composition of benthic diatom assemblages (Bacillariophyceae) from areas affected by invasive macroalgae *Caulerpa taxifolia* (Vahl) C. Agardh and *Caulerpa racemosa* (Forsskal) J. Agardh“ (Skład gatunkowy bentosowych zespołów okrzemkowych (Bacillariophyta) z regionów będących pod wpływem inwazyjnych makroglonów *Caulerpa taxifolia* (Vahl) C. Agardh oraz *C. racemosa* (Forsskal) J. Agardh) (2012/07/N/NZ8/02359) founded by The National Science Centre (Narodowe Centrum Nauki) in Poland.

She participated at 6 international and 4 national conferences as a first author and co-author of 19 presentations. She has published one scientific paper as a first author in journal cited in the *Current Content* base and one as a co-author in the journal cited by *Web of Science*. She is a member of various professional associations including International Society for Diatom Research, International Phycological Society and Croatian Botanical Society.

LIST OF PUBLICATIONS:

- **(CC base):**

  Car, Ana; Witkowski, Andrzej; Dobosz, Slawomir; Burfeind, Dana D.; Meinesz, Alexander; Jasprica, Nenad; Ruppel, Manfred; Kurzydlowski, Krzysztof J.; Plocinski, Tomasz (2012): Description of a new marine diatom, *Cocconeis caulerpacola* sp. nov. (Bacillariophyceae), epiphytic on invasive *Caulerpa* species. *European Journal of Phycology* 47:4,433-448. DOI: 10.1080/09670262.2012.735255 (Impact factor: 1.912)

- **(WoS):**

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