

***Predaea feldmannii* subsp. *azorica*
(Nemastomataceae, Nemastomatales),
a new subspecies of red algae (Rhodophyta)
from the Azores**

Daniela GABRIEL^{a, b*}, Tom SCHILS^c, Ana Isabel NETO^a,
Luz PARAMIO^a & Suzanne FREDERICQ^b

^aDepartamento Biologia, Universidade dos Açores, Apartado 1422,
9501-801 Ponta Delgada, Açores, Portugal

^bDepartment of Biology, University of Louisiana at Lafayette, Lafayette,
LA 70504-2451, USA

^cMarine Laboratory, University of Guam, Mangilao, GU 96923, USA

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Abstract – The red algal genus *Predaea* (Rhodophyta, Nemastomataceae, Nemastomatales) currently comprises 20 species found in tropical to temperate waters worldwide. The species going under the name *Predaea feldmannii* (Nemastomataceae, Nemastomatales) in the Azores is here reduced to subspecies rank as *P. feldmannii* subsp. *azorica* on the basis of comparative morphology and *rbcL* sequence analysis. The evidence presented here includes a phylogenetic tree inferred from chloroplast-encoded *rbcL* sequences of selected members of the Nemastomatales. *P. feldmannii* subsp. *azorica* shares with *P. feldmannii* subsp. *feldmannii* linear-oblong outer cortical cells, dichotomously branched cortical fascicles, a large number of auxiliary nutritive cells per cluster, and gonimoblast initiation from the incoming connecting filament near its point of fusion with the auxiliary cell. Differences include a sac-like, lobed thallus and occasional lateral cells on the carpogonial branch in the Azorean subspecies, *versus* a subcylindrical, subdichotomous habit with marginal lobes, and lack of lateral cells on the carpogonial branch in *P. feldmannii* subsp. *feldmannii*. The known distribution of *P. feldmannii* subsp. *feldmannii* is worldwide in tropical regions and so far *P. feldmannii* subsp. *azorica* is known only from the Azores.

Azores / Nemastomataceae / Nemastomatales / North Atlantic / *Predaea* / *rbcL* / Rhodophyta

Résumé – *Predaea feldmannii* subsp. *azorica* (Nemastomataceae, Nemastomatales), une nouvelle sous-espèce d'algues rouges (Rhodophyta) des Açores. Le genre d'algues rouges *Predaea* (Rhodophyta, Nemastomataceae, Nemastomatales) comporte actuellement 20 espèces habitant les mers tropicales et tempérées du monde entier. L'espèce connue sous le nom de *Predaea feldmannii* aux Açores est réduite ici au rang d'une sous-espèce, *P. feldmannii* subsp. *azorica*, sur la base de l'analyse morphologique comparative et le séquençage du gène *rbcL*. Les données présentées ici incluent un arbre phylogénétique des

* Correspondence and reprints: danielalgabriel@gmail.com
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séquences *rbcL*, qui montre la position évolutive de l'espèce des Açores par rapport à celles d'autres régions. *P. feldmannii* sous-espèce *azorica* est caractérisée, comme la sous-espèce *P. feldmannii* subsp. *feldmannii*, par des cellules corticales externes linéaires-oblongues, des fascicules corticaux dichotomes, un grand nombre de cellules nutritives auxiliaires, et le développement du gonimoblaste à partir du filament de connexion près du point de fusion avec la cellule auxiliaire. Les différences pour la sous-espèce açoréenne incluent un thalle lobé et en forme de sac, un rameau carpogonial occasionnellement portant des cellules latérales, vis-à-vis d'un thalle subcylindrique et subdichotome avec lobes marginaux ; pour *P. feldmannii* subsp. *feldmannii*, l'absence de cellules latérales sur la rameau carpogonial.

Atlantique nord / Les Açores / Nemastomataceae / Nemastomatales / Predaea / *rbcL* / Rhodophyta

INTRODUCTION

The red algal genus *Predaea* De Toni is unique among the Nemastomataceae in having small clusters of nutritive cells flanking the generative auxiliary cell (Feldmann, 1942; Womersley, 1994). Species of *Predaea* are distinguished by their habit, shape of outer cortical cells, presence or absence of gland cells, number and shape of carpogonial branch cells, number and arrangement of nutritive cells adjacent to auxiliary cells, and site of origin of the gonimoblast initial (Kraft & Abbott, 1971; Verlaque, 1990; Sansón *et al.*, 1991; Vergés *et al.*, 2004; Table 1).

Five species of *Predaea* are presently reported throughout the North Atlantic Ocean: *P. feldmannii* Børgesen from the Azores (Fredericq *et al.*, 1992; Neto, 1994; Tittley & Neto, 1994), and *P. huismanii* Kraft (Lawson *et al.*, 1995; Haroun *et al.*, 2002), *P. masonii* De Toni (Lawson *et al.*, 1995; Haroun *et al.*, 2002), *P. ollivieri* Feldmann (Haroun *et al.*, 2002) and *P. pusilla* Feldmann (Lawson *et al.*, 1995; Haroun *et al.*, 2002) from the Canary Islands. The latter species is also present in the Gulf of Mexico (Gavio *et al.*, 2005). *P. feldmannii*, together with *Nemastoma confusum* Kraft & John and *Itonoa marginifera* (J. Agardh) Masuda & Guiry, are the only reported representatives of the Nemastomataceae in the Azores (Larkum, 1960; Fredericq *et al.*, 1992; Neto, 1994; Tittley & Neto, 1994).

One of the best studied Nemastomataceae is *Predaea feldmannii*, a species first described by Børgesen (1950) from St Helena and subsequently reported from other locations worldwide, such as Atlantic Georgia and North Carolina, USA (Schneider & Searles, 1991), the Greater Antilles and Lesser Antilles (Littler & Littler, 2000), Venezuela (Ganesan, 1990), Brasil (Guimarães & Horta, 2004), the Azores (Fredericq *et al.*, 1992; Neto, 1994; Tittley & Neto, 1994), the Cape Verde Islands (John *et al.*, 2004; Prud'homme van Reine *et al.*, 2005), Ghana (Lawson & John, 1987; John *et al.*, 2004), and also along the Indian Ocean coast of South Africa (De Clerck *et al.*, 2005).

The archipelago of the Azores, located in the North Atlantic Ocean, is organized into three separate groups encompassing nine volcanic islands and several small islets (Neto, 2000). Floristic studies have revealed a mixed flora with a strong component of cold water species together with a few tropical and subtropical elements (Neto, 1997). While examining numerous collections obtained from multiple taxonomic surveys to clarify the classification of the Nemastomatales in the Azores, some interesting morphological characteristics

Table 1. Comparison of *Predaea* species. Adapted from Kraft & Abbott (1971) and Kajimura (1987, 1995)

Species	Habit	Outer cortical cell shape	Branching of cortical fascicles	Secondary cortical filaments	Vesicular (gland) cells	Site of origin of gonimoblast	Carpogonial branch (number of cells)
<i>P. aurora</i> Kraft et G.W. Saunders	Flattened, foliose, ovate to variously lobed and deeply incised	Linear-oblong	Dichotomous	?	+	Connecting filament	3
<i>P. bisporifera</i> Kajimura	Lobed blade	Linear-oblong	Dichotomous	–	–	Connecting filament	2
<i>P. feldmannii</i> Børgesen	Subcylindrical, subdichotomous with marginal lobes	Linear-oblong	Dichotomous	–	–	Connecting filament	3
<i>P. feldmannii</i> var. <i>indica</i> Balakrishnan et Chawla	Sac-like, irregularly lobed	Linear-oblong	Dichotomous	–	–	Connecting filament	2 (3-4)
<i>P. feldmannii</i> subsp. <i>azorica</i> Gabriel	Sac-like, lobed	Linear-oblong	Dichotomous	?	–	Connecting filament	3-4
<i>P. goffiana</i> Ballantine, Ruiz et Aponte	Compressed lobes which radiate to form a irregularly round shape	Linear-oblong	Dichotomous	?	–	Connecting filament	3
<i>P. huismannii</i> Kraft	Compressed, lobed, fringed by exerted cortical filaments	Linear-oblong	Simple	+	–	Connecting filament	3
<i>P. incraspeda</i> Kraft	Lobed blade, fringed by exerted cortical filaments	Linear-oblong	Simple	+	–	Connecting filament	2 (3)
<i>P. japonica</i> Yoshida	Lobed oval blade	Spherical to ovoid	Dichotomous	–	+	Connecting filament	2
<i>P. kraftiana</i> Millar et Guiry	Flabellate or lobed blade	Linear-oblong	Dichotomous	–	–	Auxiliary cell; laterally	3-4
<i>P. kuroshioensis</i> Kajimura	Orbicular, undulate blade often with bullate protuberances on surface	Linear-oblong	Dichotomous	–	–	Connecting filament	2-4
<i>P. laciniosa</i> Kraft	Compressed, irregularly branched with proliferations	Spherical to ovoid	Dichotomous	–	+	Connecting filament	3
<i>P. masonii</i> De Toni	Blade with veinlets	Linear-oblong	Dichotomous	–	–	Connecting filament	2

Table 1. Comparison of *Predaea* species. Adapted from Kraft & Abbott (1971) and Kajimura (1987, 1995) (continued)

Species	Habit	Outer cortical cell shape	Branching of cortical fascicles	Secondary cortical filaments	Vesicular (gland) cells	Site of origin of gonimoblast	Carpogonial branch (number of cells)
<i>P. ollivieri</i> Feldmann	Subcylindrical to flattened with irregular to subdichotomous branches	Linear-oblong	Dichotomous	–	–	Connecting filament	2
<i>P. pusilla</i> Feldmann	Subcylindrical, subdichotomous	Linear-oblong	Dichotomous	–	–	Auxiliary cell; terminally	3
<i>P. subpeltata</i> Dawson	Infundibuliform to subpeltate	Linear-oblong	Dichotomous	–	–	Connecting filament	2
<i>P. tokidae</i> Kajimura	Lobed blade	Spherical to ovoid	Dichotomous	–	+	Connecting filament	3
<i>P. tumescens</i> Kraft et G.W. Saunders	Compressed, irregularly radially lobed/branched, the apices broadly rounded	Spherical to ovoid	Dichotomous	?	–	Connecting filament	3
<i>P. weldii</i> Kraft et Abbott	Subcylindrical, subdichotomous, with proliferations	Linear-oblong	Dichotomous	–	–	Auxiliary cell; terminally	3

Species	Transverse division of fertilized carpogonium	Lateral cells on carpogonial branches	Number of nutritive cells	Placement of nutritive cells	Bisporangia	Distribution
<i>P. aurora</i> Kraft et G.W. Saunders	?	–	Many	On one or two cells distant from auxiliary cells	–	Australia
<i>P. bisporifera</i> Kajimura	–	–	Many	On immediately adjacent cells to auxiliary cells	+	Japan
<i>P. feldmannii</i> Børgesen	–	–	Many	On immediately adjacent cells to auxiliary cells	–	St. Helena I., Cape Verde Islands, Georgia, North Carolina, Venezuela, Caribbean Colombia, Caribbean Greater Antilles, Caribbean Lesser Antilles, Ghana, South Africa (Indian Ocean), Rodrigues
<i>P. feldmannii</i> var. <i>indica</i> Balakrishnan et Chawla	?	–	Many	On immediately adjacent cells to auxiliary cells	–	India

<i>Species</i>	<i>Transverse division of fertilized carpogonium</i>	<i>Lateral cells on carpogonial branches</i>	<i>Number of nutritive cells</i>	<i>Placement of nutritive cells</i>	<i>Bisporangia</i>	<i>Distribution</i>
<i>P. feldmannii</i> subsp. <i>azorica</i>	?	Occasional	Many	On immediately adjacent cells to auxiliary cells	-	Azores
<i>P. goffiana</i> Ballantine, Ruiz et Aponte	?	+ (rare)	Few 1 (2)	On immediately adjacent cells to auxiliary cells	-	Puerto Rico
<i>P. huismanii</i> Kraft	-	-	Few	On one or two cells distant from auxiliary cells	-	South and Western Australia, Canary Islands, Fiji, Tanzania
<i>P. incraspeda</i> Kraft	-	-	Many	On one or two cells distant from auxiliary cells	-	Lord Howe Island (Australia)
<i>P. japonica</i> Yoshida	-	-	Many	On one or two cells distant from auxiliary cells	-	Japan
<i>P. kraftiana</i> Millar et Guiry	+	+	Few	On one or two cells distant from auxiliary cells	-	New South Wales (Australia)
<i>P. kuroshioensis</i> Kajimura	-	Occasional	Few	On one or two cells distant from auxiliary cells	-	Japan
<i>P. laciniosa</i> Kraft	-	-	Many	On immediately adjacent cells to auxiliary cells	-	Australia, Fiji Islands, French Polynesia, Main Hawaiian Islands, Northwestern Hawaiian Islands, New Caledonia, Oman, Papua New Guinea, Wallis & Futuna Islands, Yemen (Socotra Island), Venezuela
<i>P. masonii</i> DeToni	-	-	Many	On immediately adjacent cells to auxiliary cells	-	Brazil, California, Canary Islands, Ghana, North Carolina, Pacific Mexico
<i>P. ollivieri</i> Feldmann	-	-	Few	On immediately adjacent cells to auxiliary cells	+	Adriatic Sea, Canary Islands, Mediterranean Sea
<i>P. pusilla</i> Feldmann	-	-	Few	On one or two cells distant from auxiliary cells	+	Balearic Islands, Canary Islands, Mediterranean Sea, Venezuela

Species	Transverse division of fertilized carpogonium	Lateral cells on carpogonial branches	Number of nutritive cells	Placement of nutritive cells	Bisporangia	Distribution
<i>P. subpeltata</i> Dawson	–	–	Few	On immediately adjacent cells to auxiliary cells	–	Pacific Mexico
<i>P. tokida</i> Kajimura	–	–	Many	On immediately adjacent cells to auxiliary cells	–	Japan
<i>P. tumescens</i> Kraft et G.W. Saunders	?	–	Few	On immediately adjacent cells to auxiliary cells	–	Australia, Guam
<i>P. weldii</i> Kraft et Abbott	–	–	Few	On immediately adjacent cells to auxiliary cells	–	Australia, Canary Islands, Easter Island, Micronesia, Fiji Islands, Main Hawaiian Islands, Northwestern Hawaiian Islands, New Caledonia, Oman, Papua New Guinea, Puerto Rico, South Africa (Indian Ocean), Venezuela, Wallis and Futuna Islands, Yemen

were observed in *P. feldmannii* specimens collected from two islands. The present paper assesses the status of morphological and ecological observations and the phylogeny of *P. feldmannii* from the Azores.

MATERIALS AND METHODS

The studied *Predaea* specimens were collected beginning in 1990 from various locations in the Archipelago of the Azores. *Predaea* species were observed and collected from May to September, in both intertidal and subtidal habitats (to a depth of 35 m). Additional samples from the Herbarium of the University of the Azores, Ghent University Herbarium (GENT) and the Herbarium of the University of Louisiana at Lafayette (LAF) were used for comparison.

Reference collections were made by preserving samples in a 5% formalin/seawater solution, pressing them on herbarium sheets or drying specimens in silica-gel. The collections are deposited in the Herbarium of the Department of Biology, University of the Azores. The code numbers of the more representative specimens are given in the text.

Leitz Diaplan and Olympus BX60 light-microscopes were used to observe vegetative and reproductive characters. Microscope slides of squash mounts were stained with 1% aniline blue with HCl acidification, and mounted in 50% Karo corn syrup-water solution containing a few drops of phenol. Photomicrographs were taken using Olympus DP50 and Polaroid DMC-IE digital cameras.

DNA samples were prepared using the DNeasy Plant Minikit (Qiagen, Valencia, CA). Silica gel dried specimens and extracted DNA samples are deposited at the University of Louisiana at Lafayette and stored at -20°C . Plastid-encoded *rbcL* was selected to infer a phylogeny of *Predaea*. Protocols for DNA extraction, gene amplification and sequencing are described in Gavio & Fredericq (2002). PCR primers (F7-R753, F57-R557, F645-R1150, F993-RrbcSstart) and sequencing primers (F7, F57, F645, F993, R376, R557, R753, R1150, RrbcSstart) are listed in Lin *et al.* (2001) and Gavio & Fredericq (2002).

A total of 25 *rbcL* sequences were used in this study, including 19 newly generated sequences and 6 sequences downloaded from Genbank. Newly generated DNA sequences are deposited in GenBank (Table 2). For the Nemastomataceae dataset, Schizymeniaceae representatives were used as the outgroup. Outgroup species in the phylogenetic analyses were selected based on phylogenetic findings of a global analysis of Nemastomatales (Gavio *et al.*, 2005). The information about taxa, collection sites and collectors is listed in Table 2.

The generated *rbcL* sequences were compiled, edited and aligned using Sequencher software (Gene Codes Corp., Ann Arbor, MI, USA) and exported for phylogenetic analysis in PAUP* v.4.0 beta 10 (Swofford, 2003) and MacClade v.4 (Maddison & Maddison, 2000). Because some *rbcL* sequences used in this study were incomplete at the 5' coding region of the gene, the dataset was restricted to the last 1360 bp of the 1467 *rbcL* coding region.

Phylogenetic analyses were conducted with the Maximum Parsimony (MP) and Maximum Likelihood (ML) algorithms as implemented in PAUP, and the Bayesian inference (BI) as implemented in MrBayes 3.0 (Huelsenbeck & Ronquist, 2001; Hall, 2001). Parsimony trees obtained under the Fitch criterion of equal weights for all substitutions (Fitch, 1971) were inferred from a heuristic search, excluding uninformative characters consisting of 1000 random sequence

Table 2. List of voucher information used in *rbcL* analysis, and GenBank accession number. New, undescribed species of *Predaea* are referred to as sp. 1, sp. 2, sp. 3

Species	Coll. id.	Collection locality and depth	Collection data	GenBank accession number
<i>Nemastoma canariense</i> (Kützing) Montagne		Canary Islands	R. Haroun, s.d.	AY294369
<i>Nemastoma canariense</i> (Kützing) Montagne		Canary Islands	R. Haroun, s.d.	AY294370
<i>Platoma cyclocolpum</i> (Montagne) Schmitz	SMG-04-202	Ponta Garça, Vila Franca, São Miguel, Azores (8 m depth)	D. Gabriel & P. Madeira, 20 Aug 2004	FJ868809
<i>Predaea feldmannii</i> Børgesen		Long Bay Point, Isla Colon, Caribbean Panama	B. Wyss, 17 Oct 1999	AY294366
<i>Predaea feldmannii</i> Børgesen		Puerto Rico, s.l.	D. Ballantine, s.d.	AY294383
<i>Predaea feldmannii</i> Børgesen	HEC15095	Balise Nord of Tulear, Madagascar (10 - 15 m depth)	E. Coppejans, D. Douterlungne & I. Razanakoto, s.d.	FJ868810
<i>Predaea feldmannii</i> subsp. <i>azorica</i>	GRW-06-804	Graciosa, Azores	N. Álvaro, Jun 2006	FJ868811
<i>Predaea feldmannii</i> subsp. <i>azorica</i>	SMG-03-151	Viteiro, São Miguel, Azores	7 Jul 2003	FJ868812
<i>Predaea feldmannii</i> subsp. <i>azorica</i>	SMG-06-103	Ribeirinha, São Miguel, Azores (34 m depth)	D. Gabriel, K. Leon-Cisneros & J. Brum, 18 Sep 2006	FJ868813
<i>Predaea goffiana</i> Ballantine, Ruiz et Aponte	NSF-II-17-1	Campeche Banks, Mexico (52-53 m depth), 22°15.15'N 90°43.29'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 7 Jun 2005	FJ868814
<i>Predaea goffiana</i> Ballantine, Ruiz et Aponte	NSF-II-78-13	Campeche Banks, Mexico (46-48 m depth), 22°10.42'N 91°09.55'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 14 Jun 2005	FJ868815
<i>Predaea goffiana</i> Ballantine, Ruiz et Aponte	NSF-II-79-10	Campeche Banks, Mexico (49-47 m depth), 22°10.39'N 91°09.69'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 14 Jun 2005	FJ868816
<i>Predaea goffiana</i> Ballantine, Ruiz et Aponte	NSF-II-95-12	Campeche Banks, Mexico (53-54 m depth), 22°08.56'N 91°22.91'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 17 Jun 2005	FJ868817
<i>Predaea goffiana</i> Ballantine, Ruiz et Aponte	NSF-II-97-1	Campeche Banks, Mexico (36-49 m depth), 22°07.43'N 91°22.85'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 17 Jun 2005	FJ868818
<i>Predaea goffiana</i> Ballantine, Ruiz et Aponte	NSF-II-100-14	Campeche Banks, Mexico (49-53 m depth), 22°11.33'N 91°08.71'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 17 Jun 2005	FJ868819

Table 2. List of voucher information used in *rbcL* analysis, and GenBank accession number. New, undescribed species of *Predaea* are referred to as sp. 1, sp. 2, sp. 3 (*continued*)

Species	Coll. id.	Collection locality and depth	Collection data	GenBank accession number
<i>Predaea laciniosa</i> Kraft	Hawaii-937	Hawaii	s.d.	FJ868820
<i>Predaea pusilla</i> (Berthold) Feldmann		Dredged offshore L.A., USA (66 m depth), 28°03.451'N 92°27.345'W	S. Fredericq, B. Gavio, C.F. Gurgel & J. Lopez-Bautista, 27 May 2000	AY294367
<i>Predaea pusilla</i> (Berthold) Feldmann	NSF-II-130-4	Campeche Banks, Mexico (62-68 m depth), 22°03.62'N 92°27.65'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 23 Jun 2005	FJ868821
<i>Predaea</i> sp.1	NSF-II-94-1	Campeche Banks, Mexico (48-51 m depth), 22°07.98'N 91°23.75'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 17 Jun 2005	FJ868822
<i>Predaea</i> sp.1	NSF-II-109-17	Campeche Banks, Mexico (54-56 m depth), 22°16.08'N 90°42.89'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 18 Jun 2005	FJ868823
<i>Predaea</i> sp.2	NSF-II-3-1	Campeche Banks, Mexico (62-112 m depth), 28°06.12'N 91°02.45'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 4 Jun 2005	FJ868824
<i>Predaea</i> sp.3	NSF-III-6,28,06,2,2	Florida Middle Ground Banks, FL, USA (63-65 m depth), 27°37.81'N 89°33.32'W	S. Fredericq, D. Krayesky, N. Arakaki, W. Schmidt, 28 Jun 2006	FJ868825
<i>Predaea</i> sp.4	NSF-II-11-20	Campeche Banks, Mexico (42-43 m depth), 22°15.88'N 90°35.64'W	S. Fredericq, D. Gabriel, F. Gurgel & T.O. Cho, 6 Jun 2005	FJ868826
<i>Predaea weldii</i> Kraft <i>et</i> L.A. Abbott	Hawaii-938	Hawaii	s.d.	FJ868827
<i>Schizymenia dubyi</i> (Chauvin <i>ex</i> Duby) J. Agardh		Jodogahama, Miyako, Iwate-ken, Japan	M.H. Hommersand & M. Yoshizaki, 10 Jul 1994	AY294388

additions holding 10 trees at each step, MULPARS and tree-bisection-reconnection (TBR) algorithms with the MULTREES (saving multiple trees) and STEEPEST DESCENT option. Consistency (CI) and retention (RI) indices were calculated (Kluge & Farris, 1989). Support for nodes in the MP and ML analyses were assessed by calculating bootstrap proportion (BP) values (Felsenstein, 1985) based on 1000 and 100 resamplings, respectively.

The optimal models of sequence evolution to fit the data alignment estimated by hierarchical likelihood ratio tests performed by Modeltest v.3.6 (Posada & Crandall, 1998) was the GTR + I + G (General Time Reversible model with a proportion of invariable sites and gamma distribution split into 4 categories) for the data set. The Akaike Information Criterion (AIC) parameters were as follows: assumed nucleotide frequencies A = 0.30; C = 0.15; G = 0.21; T = 0.34; substitution rate matrix A-C substitutions = 1.28, A-G = 4.29, A-T = 2.60, C-G = 1.29, C-T = 12.32, G-T = 1.0; proportion of sites assumed to be invariable = 0.6474 and rates for variable sites assumed to follow a gamma distribution with shape parameter = 3.5505. These likelihood parameters were also applied in the Bayesian analysis.

The ML phylogram was inferred in PAUP using the General Time Reversible model from trees generated by a heuristic using an "as is" sequence addition option.

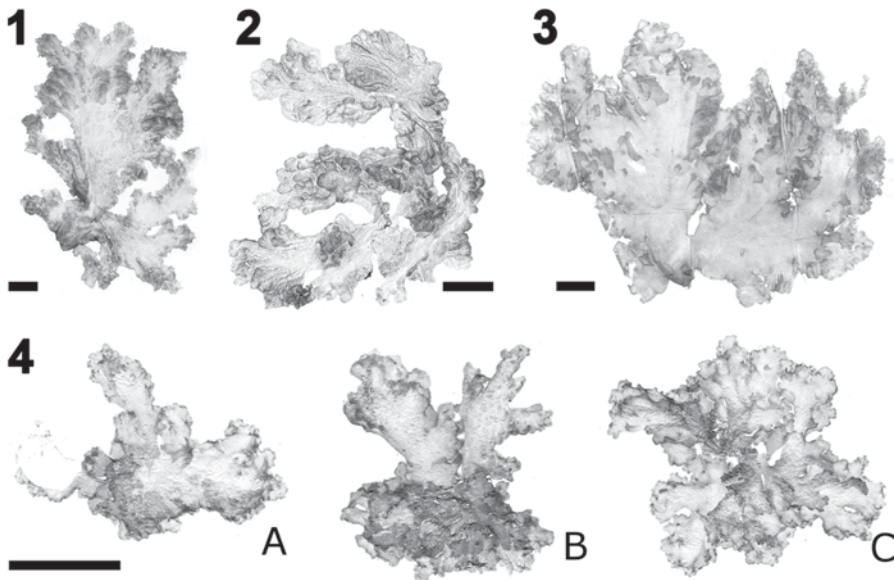
For the Bayesian analysis, four chains of the Markov chain Monte Carlo were run, sampling 1 tree every 100 generations for 2,000,000 generations starting with a random tree for the *rbcL* data sets. The first generations were discarded as the "burn in" period to reach equilibrium. A 50% consensus tree (majority rule as implemented by PAUP*) was computed from the trees saved after the "burn in" point, 18500 generations. Reliability of the Bayesian consensus tree is given by the frequency at which each node appears among all saved trees after the "burn in" generation. This frequency corresponds to the posterior probability of the clades (Hall, 2001).

RESULTS

Morphology of *Predaea feldmannii* from the Azores

Habit and vegetative structure. Erect plants of *Predaea feldmannii* from the Azores are up to 17 cm tall, light pink to rosy red, some with greenish patches, very gelatinous, slippery, soft, delicate and slippery sack-like masses, irregularly lobed in more than one plane, sub-cylindrical to broadly flattened, bearing few to many bullate projections (Figs 1-3). The thallus is epilithic, attached to the substratum by a small discoid holdfast without an obvious stipe (Figs 1-3). Plants of *P. feldmannii* from Madagascar (Figs 4a-c) superficially resemble specimens from the Azores.

The cortex is composed of radiating subdichotomously branched filaments of elongated, deeply pigmented cells (Figs 5-6). From the medulla to the surface, branching becomes more pronounced and cortical cells are gradually smaller in size (Figs 5-6, 10). Surface cells are linear-oblong, sometimes forming hair-like structures (Fig. 7). Gland cells were not observed. Medullary filaments are elongated and sparsely branched (Figs 5-6). Numerous X-shaped cells (Fig. 6)

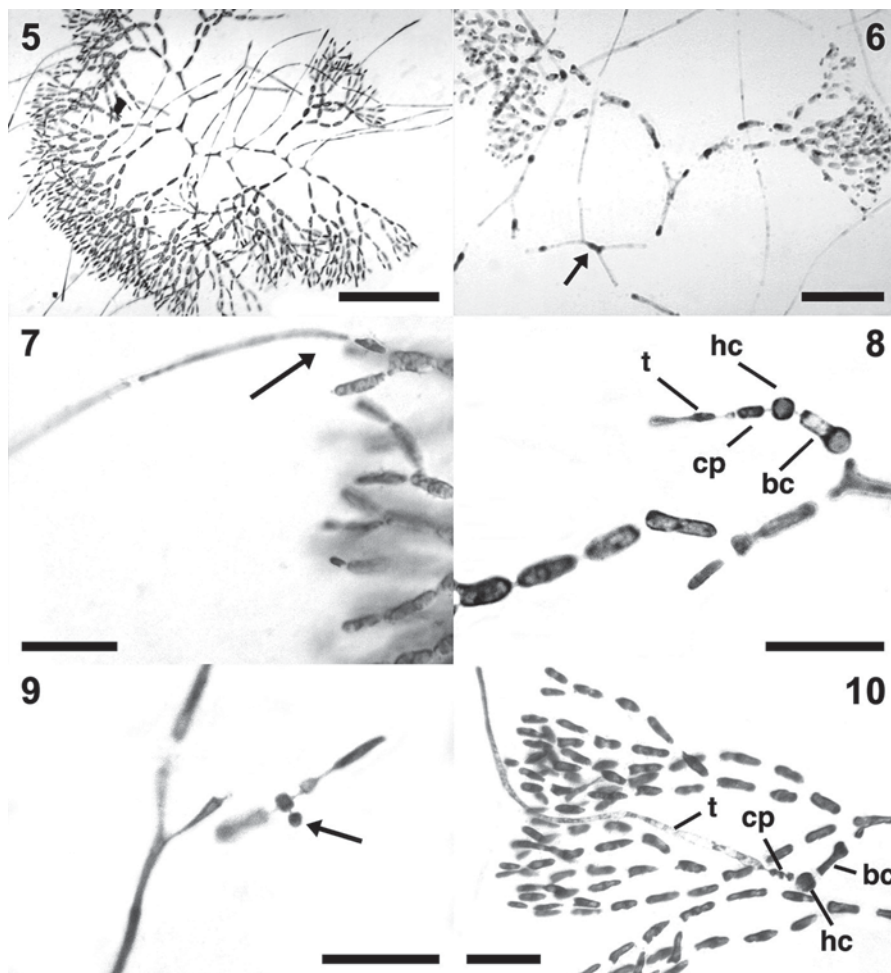


Figs 1-4. *Predaea feldmannii* subsp. *azorica*. Habits. **1.** Holotype, a female gametophyte from Graciosa Island, GRW-04-804, bar = 2 cm. **2.** Isotype, specimen from Graciosa, GRW-06-809, bar = 1 cm. **3.** Male gametophyte from São Miguel, SMG-94-141, bar = 1 cm. **4.** *Predaea feldmannii* from Madagascar, HEC15095a, b, c, bar = 1 cm

are present in the lax medulla. Cortical and medullar filaments are embedded in a gelatinous matrix.

Pre-and early post-fertilization structures. Plants are dioecious. Presumed functional carpogonial branches (darkly staining and thus protein-rich) are 3-celled, borne laterally and singly on inner cortical cells which serve as supporting cells (Figs 8-10). The basal cell is barrel-like with a bulbous-like base (Figs 8-10); the hypogynous cell is spherical (Figs 8-10) and may occasionally bear one lateral cell (Fig. 9), and the carpogonium is conical terminating in a rather straight trichogyne (Figs 8-10). Abortive carpogonial branches are recognized by septate trichogynes. After presumed fertilization, connecting filament formation from the carpogonium was not observed. Auxiliary cells (Figs 11-12) are transformed inner cortical cells spatially remote from carpogonial branches. Larger than ordinary cortical cells, an auxiliary cell is easily recognizable by the clusters of numerous globose nutritive cells flanking it (Figs 11-14). These nutritive cells are cut off by cortical cells connected to the auxiliary cell (Figs 11-16). Auxiliary cells are far more numerous than carpogonial branches.

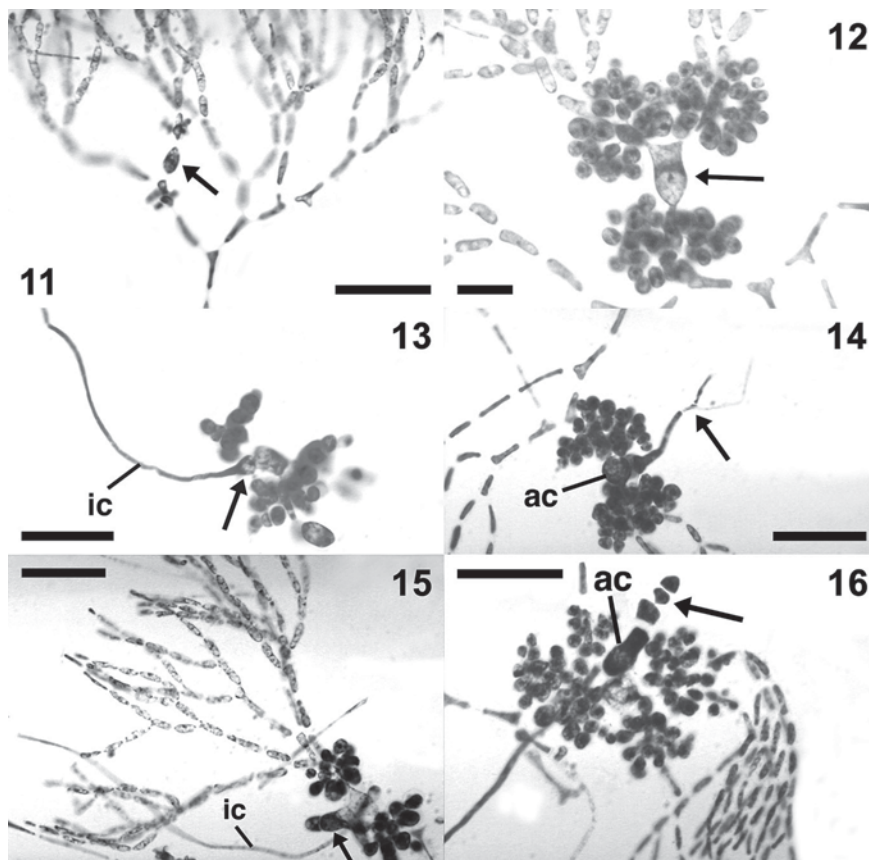
Post-fertilization structures. An incoming connecting filament may remain unbranched (Fig. 13) or may branch (Fig. 14) before fusing partly with an auxiliary cell. After the incoming connecting filament diploidizes an auxiliary cell, it continues its course as the outgoing connecting filament can diploidize other auxiliary cells. A portion of the non-septate connecting filament produces a bulge (Fig. 15) when approaching the auxiliary cell to transfer the diploid nucleus. Near the point of fusion, a gonimoblast initial is cut off from the auxiliary cell and develops outwardly into a linear filament of cells by transverse division (Fig. 16). Further longitudinal divisions of these cells (Fig. 17) lead to a pear-shaped mass



Figs 5-10. *Predaea feldmannii* subsp. *azorica*. Female gametophyte. **5.** Cortex and medulla, bar = 100 μ m. **6.** X-shaped medullary cells (arrow), bar = 40 μ m. **7.** Hair-like structure (arrow), originating from surface cell, bar = 25 μ m. **8.** Unfertilized 3-celled carpogonial branch, composed of basal cell (bc), hypogynous cell (hc) and carpogonium (cp) with trichogyne (t), bar = 25 μ m. **9.** Young carpogonial branch with lateral sterile cell (arrow) on hypogynous cell, bar = 25 μ m. **10.** Unfertilized 3-celled carpogonial branch, composed of basal cell (bc), hypogynous cell (hc) and carpogonium (cp) with trichogyne (t), bar = 25 μ m.

of gonimoblast cells, all of which mature into carposporangia. The mature carposporophyte (Fig. 18) is subspherical in shape and consists of 2 or more distinct lobes that mature sequentially. Mature carpospores are ovoid (Fig. 18). No pericarp or involucre filaments were observed. Carpospores are released through the cortex with no noticeable pore.

Spermatangia were found in patches scattered over the thallus, arising from surface cortical cells (Figs 19-20) with pairs of small, colorless rounded spermatia cut off from spermatangial parent cells (Fig. 20). Tetrasporangia were not seen.



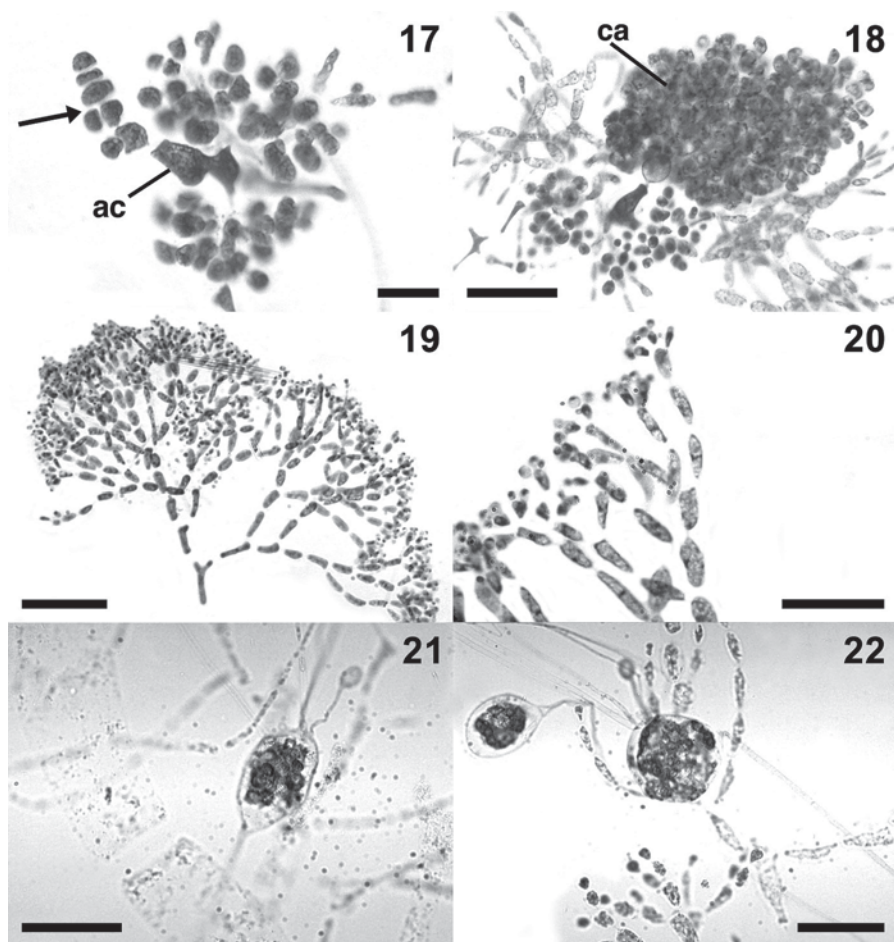
Figs 11-16. *Predaea feldmannii* subsp. *azorica*. **11.** Young auxiliary cell (arrow) flanked by young nutritive cells, bar = 40 µm. **12.** Mature auxiliary cell (arrow) and nutritive cells, bar = 20 µm. **13.** Incoming connecting filament (ic) making bulge (arrow) with auxiliary cell at point of fusion, bar = 40 µm. **14.** Branched connecting filament (arrow), auxiliary cell (ac) and nutritive cells, bar = 40 µm. **15.** Presumably diploidized auxiliary cell with bulge (arrow), incoming connecting filament (ic), and nutritive cells, bar = 40 µm. **16.** Three-celled gonimoblast filament (arrow) originating from auxiliary cell (ac), and nutritive cells, bar = 40 µm.

Ecology

P. feldmannii from the Azores is a rare alga growing on rocky platforms or in dense algal assemblages covering cobbles at depths of 10-27 m. Thalli were also found epizoically on empty carapaces of *Megabalanus* sp. *Blastophysa rhizopus* Reinke (Figs 21-22), a green algal endophyte is commonly found growing among cortical filaments, resulting in a green sheen of infested specimens (Bucher & Norris, 1992).

Molecular sequence data

Nine distinct species of *Predaea* worldwide were identified in this study on the basis of comparative *rbcL* sequence analysis (Fig. 23). *RbcL* sequences



Figs 17-22. *Predaea feldmannii* subsp. *azorica*. **17.** Carposporophyte. Branched gonimoblast filament (arrow) on auxiliary cell (ac), bar = 20 μ m. **18.** Carposporophyte. Mass of carposporangia (ca), bar = 50 μ m. **19.** Male gametophyte. Portion of male gametophyte, showing terminal spermatangial parent cells bearing terminal spermatangia, bar = 40 μ m. **20.** Male gametophyte. Parent cells bearing terminal spermatangia, bar = 100 μ m. **21, 22.** Thallus infestation with the green alga *Blastophysa rhizopus*, bar = 40 μ m.

between the *P. feldmannii* specimens of the Azores and the Caribbean samples showed 1.5-1.9% uncorrected sequence divergence. Sequences from samples from the Caribbean (Panama and Puerto Rico) and the Indian Ocean (Madagascar) revealed 0.8% sequence divergence among one another. The samples from the Azores are sister to both *P. feldmannii* from Caribbean Puerto Rico and Panama, and from Indian Ocean Madagascar. The *P. feldmannii* clade in turn is sister to an undescribed species from the Campeche Banks, Mexico, in the SW Gulf of Mexico (Fig. 23). In addition, three other undescribed species from the Gulf of Mexico are reported here, which are different from *P. weldii* and *P. laciniosa* from Hawaii, and from *P. feldmannii*. These species will be described in a separate paper.



Fig. 23. Single-most parsimonious tree inferred from chloroplast-encoded *rbcL* sequences showing the position of *Predaea* species in the Nemastomataceae using Schizymeniaceae as the outgroup. Number at nodes represent MP and ML bootstrap values and Bayesian posterior probabilities.

DISCUSSION

RbcL sequence divergence greater than 2% in representatives of the Nemastomatales has been referred to as separate species (Gavio *et al.*, 2005). Sequence divergence between *P. feldmannii* samples from the Azores, on the one hand, and the Caribbean (Panama and Puerto Rico) and the Indian Ocean (Madagascar), on the other hand, is large enough (0.8%) to identify distinct subspecies. The following two subspecies are proposed:

Predaea feldmannii* Børgesen subsp. *feldmannii

Børgesen F., *Dansk Botanisk Arkiv*, 14 (8), p. 7 (1950).

***Predaea feldmannii* Børgesen subsp. *azorica* Gabriel, subsp. nov.**

Diagnosis: *Ut in Predaea feldmannii* subsp. *feldmannii* sed thallo lobato, interdum cellulis lateralibus in filo carpogoniali.

As in *Predaea feldmannii* subsp. *feldmannii*, but with sac-like, lobed thallus, and occasional lateral cells on the carpogonial branch.

Type locality: Graciosa (Azores), approximately 30 m depth.

Holotype: Female gametophyte, Graciosa Island, GRW-06-804, deposited at the University of the Azores Herbarium, collector Nuno Álvaro, June 2006.

Isotype: University of Louisiana at Lafayette Herbarium, LAF-06-809.

Etymology: The name refers to the Azores.

Distribution: NE Atlantic: Azores (Fredericq *et al.*, 1992; Neto, 1994; Tittley & Neto, 1994, all reported as *P. feldmannii*).

Specimens examined: São Miguel: SMG-90-237, SMG-91-14, SMG-96-14, SMG-97-220, SMG-01-45, SMG-01-46, SMG-01-47, SMG-01-48, SMG-03-151, SMG-06-103. Graciosa: GRW-06-804, GRW-06-809, GRW-06-811, GRW-06-812, GRW-06-814, GRW-06-818, GRW-06-820. All specimens located in the University of the Azores Herbarium (see Table 3 for full details).

P. feldmannii subsp. *azorica* shares with *P. feldmannii* subsp. *feldmannii* linear-oblong outer cortical cells, dichotomously branched cortical fascicles, a large number of auxiliary nutritive cells per cluster, and gonimoblast initiation from the incoming connecting filament near the point of fusion with the auxiliary cell. Differences include a sac-like, lobed thallus and occasional lateral cells on the carpogonial branch in the Azorean subspecies, versus a subcylindrical, subdichotomous habit with marginal lobes and the lack of lateral cells on the carpogonial branch in *P. feldmannii* subsp. *feldmannii* (Kraft & John, 1976). The occasional presence of sterile cells in Azorean samples has not been described before for *P. feldmannii*; however, these structures could have been misidentified as aborted carpogonial branches. Auxiliary cells generally occur at a dichotomy in cortical filaments, but they have also been observed elsewhere in cortical filaments. The presence of nutritive cell clusters cut off from cells adjacent to the auxiliary cell separates *P. huismanii* from the rather similar *Nemastoma confusum* Kraft & John (Sanson *et al.*, 1991).

The Azorean specimens may contain septate hair-like structures growing outwardly from surface cells. These hairs could increase surface area for nutrient uptake as reported for other taxa (DeBoer and Whoriskey, 1983) or could function as the origin of a new filament system.

Carpogonial branches of *P. feldmannii* var. *indica* are mostly 2-celled, though 3- or 4-celled carpogonial branches were also observed. This differs from the Ghana individuals of this species in which Kraft & John (1976) observed the carpogonial branches to be invariably 3-celled (Balakrishnan & Chawla, 1984). Cells in the carpogonial branch of *P. feldmannii* var. *azorica* are as in *P. feldmannii* var. *indica* (Balakrishnan & Chawla, 1984), but show characteristic differences in shape or size with *P. feldmannii* from Ghana (Kraft & John, 1976). The only record of a carpogonial branch supporting cell serving as an auxiliary cell was reported by Kraft & John (1976).

P. feldmannii might be mistaken for *P. masonii*, a species comprised of a broad flat blade that reaches up to 8 cm in height; however, *P. feldmannii* is multilobate and at maturity reaches up to 30 cm (Schneider & Searles, 1991). In

Table 3. List of the Azorean specimens of *Predaea feldmannii* examined here.

<i>Coll. id.</i>	<i>Collection locality and depth</i>	<i>Collection data</i>
SMG-90-237	São Miguel, Azores	1990
SMG-91-14	São Roque, São Miguel, Azores (7-12 m depth)	6 Jul 1991
SMG-96-141	Moaçor, São Miguel, Azores (5-18 m depth)	12 Jul 1996
SMG-97-220	São Miguel, Azores	1997
SMG-01-45	Porto de Santa Iria, São Miguel, Azores (3-10 m depth)	28 Jun 2001
SMG-01-46	Porto de Santa Iria, São Miguel, Azores (3-10 m depth)	28 Jun 2001
SMG-01-47 SMG-01-47	Porto de Santa Iria, São Miguel, Azores (3-10 m depth)	28 Jun 2001
SMG-01-48 SMG-01-48	Porto de Santa Iria, São Miguel, Azores (3-10 m depth)	28 Jun 2001
SMG-03-151	Viteleiro, São Miguel, Azores	7 Jul 2003
SMG-06-103	Ribeirinha, São Miguel, Azores (34 m depth)	D. Gabriel, K. Leon-Cisneros & J. Brum, 18 Sep 2006
GRW-06-804	Graciosa, Azores	N. Álvaro, Jun 2006
GRW-06-809	Graciosa, Azores	N. Álvaro, Jun 2006
GRW-06-811	Graciosa, Azores	N. Álvaro, Jun 2006
GRW-06-812	Graciosa, Azores	N. Álvaro, Jun 2006
GRW-06-814	Graciosa, Azores	N. Álvaro, Jun 2006
GRW-06-818	Graciosa, Azores	N. Álvaro, Jun 2006
GRW-06-820	Graciosa, Azores	N. Álvaro, Jun 2006

addition, the outer cortical cells of *P. masonii* are moniliform and contain occasional gland cells (Kraft & John, 1976), whereas the outer cortex of *P. feldmannii* is composed of elongate and cylindrical cells lacking gland cells. The carposporophyte of *P. masonii* consists of a single ovoid mass of carpospores, whereas that of *P. feldmannii* is comprised of one-to-three pear-shaped gonimolobes (Schneider & Searles, 1975). Børgesen (1950) illustrates a connecting filament that connects to, but continues on from the auxiliary cell, and a continuation of the connecting filament is initiated by the auxiliary cell in North Carolina specimens referred to as *P. feldmannii* (Schneider & Searles, 1975).

In *Predaea* the first gonimoblast initial is either apical and directed toward the thallus surface as in *P. weldii* and *P. pusilla*; lateral as in *P. kraftiana*, *P. adriatica*; and from the connecting filament as in *P. feldmannii*, *P. masonii*,

P. ollivieri and *P. subpeltata* (Kraft & Abbott, 1971; Verlaque, 1990, Kajimura, 1995); Type of carpospore germination has been reported as a diagnostic feature in *Predaea*; *P. feldmannii* (Lemus & Ganesan, 1977) belongs to the group that is composed of species whose carpospores form unipolar filaments (Vergés *et al.*, 2003).

Although their habit similarities are striking, *P. weldii* and *P. feldmannii* have been distinguished by differences in nutritive cell number and the site of gonimoblast initiation (Kraft & Abbott, 1971; Kraft & John, 1976). As shown by Balakrishnan & Chawla (1984) in *P. feldmannii* var. *indica*, by Børgesen (1950) in the type from St Helena, and by Kraft & John (1976) in *P. feldmannii* from Ghana, the lateral production of the gonimoblast initial is from a typical swelling formed at the junction of the connecting filament with the auxiliary cell. Coupled with thallus shape, this post-fertilization feature is the main characteristic used to separate this species from others.

The Indian Ocean algal specimen represents a variety of this species, *P. feldmannii* var. *indica* Balakrishnan & Chawla (1984), a taxon described based on the variable number of cells on the carpogonial branch and the uniformity of their size and shape (see Table 1).

The life cycle of *P. feldmannii* never been elucidated, but studies in other species of Nemastomataceae suggest an alternative filiform tetrasporophytic phase. Culture studies are needed to confirm the life cycle phases of the genus. Filiform tetrasporophytes have been obtained in culture for *P. feldmannii* (Lemus & Ganesan, 1977), *P. kraftiana* (Millar & Guiry, 1989), *P. pusilla* and *P. ollivieri* (Athanasiadis, 1988; Vergés *et al.*, 2004).

Nemastoma confusum was thought to be the so-called “male” of *P. feldmannii* described by Børgesen from St Helena (Kraft & John, 1976). However, this taxon may be a species of *Predaea* lacking auxiliary nutritive cells (Gavio *et al.*, 2005).

Most of the samples of *P. feldmannii* var. *azorica* were collected by Scuba diving around the islands of São Miguel and Graciosa, usually at depths of less than 30 m on rocky platforms surrounded by sand. Its seasonal occurrence is from early spring (May) to late summer (September), when the water temperature is about 20°C and storms are less frequent. The species inhabits the central and eastern group of the Archipelago along the North or South Coast, showing a large but discontinuous distribution. The lack of reports for the western group is probably due to the paucity of relevant sampling.

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