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

Daniela GABRIEL,*, Tom SCHILS, Ana Isabel NETO, 
Luc PARAMIO & Suzanne FREDERICQ

*Departamento Biologia, Universidade dos Açores, Apartado 1422, 9501-801 Ponta Delgada, Açores, Portugal

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

*Marine 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 Nemastomataceae. P. feldmannii subsp. azorica shares with P. feldmannii subsp. feldmannii linear-oblong outer cortical cells, dichotomously branched cortical tasciales, 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 she-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


* Correspondence and reprint: danielagabriel@gmail.com
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INTRODUCTION

The red algal genus *Predaea* De Toni is unique among the nemastomataceae in having small clusters of nutritive cells flanking the creeping 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 carposporangial branch cells, number and arrangement of nutritive cells adjacent to auxiliary cells, and site of origin of the oospheroblast initial (Kraft & Abbott, 1971; Verlaque, 1990; Sansón et al., 1991; Gérég et al., 2004; Table 1).

Five species of *Predaea* are presently reported throughout the North Atlantic Ocean: *P. feldmannii* Borgesen from the Azores (Fredericq et al., 1992; Neto, 1994; Titly & Neto, 1994) and *P. huxleyi* Kraft (Lawsom et al., 1985; Haroun et al., 2002), *P. masonii* De Toni (Lawson et al., 1995; Haroun et al., 2002), *P. oltovieri* Feldmann (Haroun et al., 2002) and *P. pussila* Feldmann (Lawson et al., 1998; 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 *bonoa marginosa* (J. Agardh) Masuda & Guiry, are the only reported representatives of the Nemastomataceae in the Azores (Larkin, 1960; Fredericq et al., 1992, Neto, 1994; Titly & Neto, 1994).

One of the best studied Nemastomataceae is *P. feldmannii*, a species first described by Borgesen (1938) from St. Helena and subsequently reported from other locations worldwide, such as Atlantic Ocean and North Carolina, USA (Schneider & Searles, 1991), the Greater Antilles and Lesser Antilles (Littler & Littler, 2000), Venezuela (Ganesan, 1990), Brazil (Guanarés & Horta, 2004), the Azores (Fredericq et al., 1992; Neto, 1994; Titly & Neto, 1994), the Cape Verde Islands (John et al., 2004; Prudhomme van Reine et al., 2006), 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 strong component of cold water species together with some tropical and subtropical elements (Neto, 1997). While examining numerous collections obtained from multiple taxonomic surveys to clarify the classification of the Nemastomataceae in the Azores, some interesting morphological characteristics...
<table>
<thead>
<tr>
<th>Species</th>
<th>Habit</th>
<th>Outer cortical cell shape</th>
<th>Branching of cortical filaments</th>
<th>Secondary cortical filaments</th>
<th>Verticar (gland) cells</th>
<th>Site of origin of gonimoblasts</th>
<th>Carposporangial branch (number of cells)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. olivieri Feldmann</td>
<td>Subylindrical to flattened with irregular to subechiomatic branches</td>
<td>Linear-oblong</td>
<td>Dichotomous</td>
<td></td>
<td></td>
<td>Connecting filament</td>
<td>2</td>
</tr>
<tr>
<td>P. pusilla Feldmann</td>
<td>Subylindrical, subechiomatic</td>
<td>Linear-oblong</td>
<td>Dichotomous</td>
<td></td>
<td></td>
<td>Auxiliary cell terminally</td>
<td>3</td>
</tr>
<tr>
<td>P. subechiota Dauros</td>
<td>Infundibuliform to subechiota</td>
<td>Linear-oblong</td>
<td>Dichotomous</td>
<td></td>
<td></td>
<td>Connecting filament</td>
<td>2</td>
</tr>
<tr>
<td>P. solane Kajianu</td>
<td>Lobed blade</td>
<td>Spherical to ovad</td>
<td>Dichotomous</td>
<td></td>
<td></td>
<td>Connecting filament</td>
<td>3</td>
</tr>
<tr>
<td>P. sumebeni Kraft et G.W. Saunders</td>
<td>Compressed, irregular, radially lobed, the apex broadly rounded</td>
<td>Linear-oblong</td>
<td>Dichotomous</td>
<td></td>
<td></td>
<td>Auxiliary cell terminally</td>
<td>3</td>
</tr>
<tr>
<td>P. weldii Kraft et Abbott</td>
<td>Subylindrical, subechiomatic, with proliferations</td>
<td>Linear-oblong</td>
<td>Dichotomous</td>
<td></td>
<td></td>
<td>Auxiliary cell terminally</td>
<td>3</td>
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</tbody>
</table>

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<thead>
<tr>
<th>Species</th>
<th>Transverse division of fertilized carpogonium</th>
<th>Lateral cells on carpogonial branches</th>
<th>Number of nutritive cells</th>
<th>Placement of nutritive cells</th>
<th>Bisporangia</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. sumebeni Kraft et G.W. Saunders</td>
<td></td>
<td></td>
<td>Many</td>
<td>On one or two cells distant from auxiliary cells</td>
<td></td>
<td>Australia</td>
</tr>
<tr>
<td>P. bisporofera Kajianu</td>
<td></td>
<td></td>
<td>Many</td>
<td>On immediately adjacent cells to auxiliary cells</td>
<td>+</td>
<td>Japan</td>
</tr>
<tr>
<td>P. feldmanii Borssac</td>
<td></td>
<td></td>
<td>Many</td>
<td>On immediately adjacent cells to auxiliary cells</td>
<td></td>
<td>St. Helena L., Cape Verde Islands, Georgia, North Carolina, Venezuela, Caribbean Colomatta, Caribbean Greater Antilles, Caribbean Lesser Antilles, Guiana, South America (Indian Ocean), Rodrigues</td>
</tr>
<tr>
<td>P. feldmanii var. indica</td>
<td></td>
<td></td>
<td>Many</td>
<td>On immediately adjacent cells to auxiliary cells</td>
<td></td>
<td>India</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>Transverse division of fertilized carpogonium</th>
<th>Lateral cells on carpogonial branches</th>
<th>Number of nutritive cells</th>
<th>Placement of nutritive cells</th>
<th>Bisporangia</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. feldmanii subs. ecorica</td>
<td></td>
<td></td>
<td>Many</td>
<td>On immediately adjacent cells to auxiliary cells</td>
<td></td>
<td>Azores</td>
</tr>
<tr>
<td>P. griffithii Batunlote, Rue et Aponte</td>
<td></td>
<td></td>
<td>Few (2)</td>
<td>On immediately adjacent cells to auxiliary cells</td>
<td></td>
<td>Puerto Rico</td>
</tr>
<tr>
<td>P. haitatlanti Kraft</td>
<td></td>
<td></td>
<td>Few</td>
<td>On one or two cells distant from auxiliary cells</td>
<td></td>
<td>South and Western Australia, Canary Islands, Fiji, Tanzania</td>
</tr>
<tr>
<td>P. increpidae Kraft</td>
<td></td>
<td></td>
<td>Many</td>
<td>On one or two cells distant from auxiliary cells</td>
<td></td>
<td>Lord Howe Island (Australia)</td>
</tr>
<tr>
<td>P. japonica Yoshida</td>
<td></td>
<td></td>
<td>Many</td>
<td>On one or two cells distant from auxiliary cells</td>
<td></td>
<td>Japan</td>
</tr>
<tr>
<td>P. krafiaina Millar et Cauri</td>
<td></td>
<td></td>
<td>Few</td>
<td>On one or two cells distant from auxiliary cells</td>
<td></td>
<td>New South Wales (Australia)</td>
</tr>
<tr>
<td>P. leucoseriensis Kajianu</td>
<td></td>
<td></td>
<td>Few</td>
<td>On one or two cells distant from auxiliary cells</td>
<td></td>
<td>Japan</td>
</tr>
<tr>
<td>P. laciniosa Kraft</td>
<td></td>
<td></td>
<td>Many</td>
<td>On immediately adjacent cells to auxiliary cells</td>
<td></td>
<td>Australia, Fiji Islands, French Polynesia, Maia Hawaiian Islands, Northwestern Hawaiian Islands, New Caledonia, Oman, Papua New Guinea, Wallis &amp; Futuna Islands, Yemen (Socotra Island), Venezuela</td>
</tr>
<tr>
<td>P. navitia DeToni</td>
<td></td>
<td></td>
<td>Many</td>
<td>On immediately adjacent cells to auxiliary cells</td>
<td></td>
<td>Brazil, California, Canary Islands, Ghana, North Carolina, Pacific Mexico</td>
</tr>
<tr>
<td>P. olivieri Feldmann</td>
<td></td>
<td></td>
<td>Few</td>
<td>On immediately adjacent cells to auxiliary cells</td>
<td></td>
<td>Adriatic Sea, Canary Islands, Mediterranean Sea</td>
</tr>
<tr>
<td>P. pusilla Feldmann</td>
<td></td>
<td></td>
<td>Few</td>
<td>On one or two cells distant from auxiliary cells</td>
<td></td>
<td>Balaric Islands, Canary Islands, Mediterranean Sea, Venezuela</td>
</tr>
</tbody>
</table>
A new subspecies of *P. fedmannii* from the Azores.

**MATERIALS AND METHODS**

The studied *F. fedmannii* specimens were collected beginning in 1990 from various locations in the Archipelago of the Azores. *F. fedmannii* specimens 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 some representative specimens are given in the text.

Leica 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-E 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. Phylodendron *rbcL* was selected to infer a phylogeny of *P. fedmannii*. Protocols for DNA extraction, gene amplification and sequencing are described in Gavio & Fredericq (2002). PCR primers (F7, RFS3, F57-R557, F645-R1150, F903, R645, R557, R753, R1150), this study) 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 Nematostomataceae dataset, Schizymeniacae representatives were used as the outgroup. Outgroup species in the phylogenetic analyses were selected based on phylogenetic findings of a global analysis of Nematostomatae (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 (Swoford, 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 *Pseudos* are referred to as **sp. 1**, **sp. 2**, **sp. 3** (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Cell. id.</th>
<th>Collection locality and depth</th>
<th>Collection data</th>
<th>GenBank accession number</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pseudos</em> linnaeae Kraft</td>
<td>Hawaii-397</td>
<td>n.c.</td>
<td>Hawaii</td>
<td>FJ988210</td>
</tr>
<tr>
<td><em>Pseudos</em> pusilla (Berthold) Fiedmann</td>
<td>NSF-II-130-4</td>
<td>Campche Banco, Mexico (62-68 m depth), 22°03.6'N 92°27.6'W</td>
<td>S. Fredericia, D. Gabriel, F. Gergel &amp; T.O. Cho, 23 Jun 2005</td>
<td>FJ988211</td>
</tr>
<tr>
<td><em>Pseudos</em> pusilla (Berthold) Fiedmann</td>
<td>NSF-II-34-1</td>
<td>Campche Banco, Mexico (48-51 m depth), 22°07.5'N 91°23.7'W</td>
<td>S. Fredericia, D. Gabriel, F. Gergel &amp; T.O. Cho, 15 Nov 2005</td>
<td>FJ988212</td>
</tr>
<tr>
<td><em>Pseudos</em> sp.1</td>
<td>NSF-II-199-17</td>
<td>Campche Banco, Mexico (54-55 m depth), 22°15.6'N 90°42.8'W</td>
<td>S. Fredericia, D. Gabriel, F. Gergel &amp; T.O. Cho, 15 Dec 2005</td>
<td>FJ988213</td>
</tr>
<tr>
<td><em>Pseudos</em> sp.2</td>
<td>NSF-II-3-1</td>
<td>Campche Banco, Mexico (62-112 m depth), 28°06.1'N 91°02.4'W</td>
<td>S. Fredericia, D. Gabriel, F. Gergel &amp; T.O. Cho, 4 Jun 2005</td>
<td>FJ988224</td>
</tr>
<tr>
<td><em>Pseudos</em> sp.3</td>
<td>NSF-II-6-20-06.2.2</td>
<td>Fiorada Moralee Grond Banco, St. USA (65-65 m depth), 17°37,81'N 89°33.33'W</td>
<td>S. Fredericia, D. Gabriel, F. Gergel &amp; T.O. Cho, 6 Jun 2005</td>
<td>FJ988225</td>
</tr>
<tr>
<td><em>Pseudos</em> sp.4</td>
<td>NSF-II-11-20</td>
<td>Campche Banco, Mexico (43-45 m depth), 22°15.81'N 90°55.64'W</td>
<td>S. Fredericia, D. Gabriel, F. Gergel &amp; T.O. Cho, 6 Jun 2005</td>
<td>FJ988226</td>
</tr>
<tr>
<td><em>Pseudos</em> violans Kraft or L. Abbott Schizomeridae (Casoria ex Dario) J. Agnnih</td>
<td>Hawaii-338</td>
<td>n.c.</td>
<td>Jodogahama, Miyako, (water-ten, Japan)</td>
<td>AY94381</td>
</tr>
</tbody>
</table>

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*Note: The table continues with similar entries for other species.*
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 v3.6 (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 = 2.66, 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 = 3.3500. 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 20% of the trees were discarded as the "burn in" period to reach equilibrium. A 50% consensus tree (majority rule implementation by PAUP*) was bootstrapped from the trees saved after the "burn in" period, 18200 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 bulbate 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)

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

Pre- and early post-territization 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). Aborted carpogonial branches are recognized by septate trichogyne. 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-territization 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 gomphonema 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
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 involucral 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.
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. weddii* and *P. lactinosa* 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 *Prelarea* species in the *Nemastomataceae* using *Schierymanziaceae* 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 (Garvie 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 Burgess subsp. feliciana


Predaea feldmannii Burgess subsp. azoricus Gabriel, subsp. nov.

Diagnosis: Ut in Predaea feldmannii subsp. feliciana sed thallus lobato, interdum cellulis lateralis in filo carpogoniili.

As in Predaea feldmannii subsp. feliciana, 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 Alvaro, June 2006.

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

Etymology: The same refers to the Azores.

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


*P. feldmannii* subsp. azoricus shares with *P. feliciana* subsp. feliciana linear-oblong outer cortical cells, dichotomously branched cortical filaments, 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 to the Azorean subspecies, versus a subcylindrical, subdichotomous habit with marginal lobes and the lack of lateral cells on the carpogonial branch in *P. feliciana* subsp. feliciana (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 abortive carpogonial branches. Auxillary 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. feliciana* from the rather similar *Nematostella confluens* (Kraft & John, 1976).

The Azorean specimens may contain separate hair-like structures growing outwardly from the 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, bough 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 (Balakhshan & Chawla, 1984). Cells in the carpogonial branch of *P. feldmannii* var. *azoricus* are as in *P. feldmannii* var. *indica* (Balakhshan & 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 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 & Searies, 1991).

In *Predaea* the first gonimoblast initial is either apical and directed toward the thallus surface as in *P. veidilii* and *P. pusilla*; lateral as in *P. krautiana*, *P. adriatica*; and from the connecting filament as in *P. feldmannii*, *P. masonii*, and addition, the outer cortical cells of *P. masonii* are multiform 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 avoid mass of carpospores, whereas that of *P. feldmannii* is comprised of one-to-three pear-shaped gonimoblasts (Schneider & Searies, 1975). Berges (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 & Searies, 1975).
P. ollivieri and P. subphalata (Kraft & Abbott, 1971; Verlaque, 1990; Kajimura, 1995); Type of carposporangium germination has been reported as a diagnostic feature in Predorea; P. feldmannii (Lemus & Ganesan, 1977) belongs to the group that is composed of species whose carpospores form unipolar filaments (Vergès 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 (1980) 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 a small size, 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 in the carposporangial branch and the uniformity of their size and shape (see Table 1).

The life cycle of P. feldmannii never has been elucidated, but studies in other species of Nemastomaaceae suggest an alternative filiform-tetrasporophyte 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. krofta (Millar & Guiry, 1989), P. pusilla and P. ollivieri (Athanasiadis, 1988; Vergès 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 Predorea lacking nutritive cells (Gavio et al., 2005).

Most of the samples of P. feldmannii var. azoricus were collected by Kneip 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 groups 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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SHORT NOTE

Observations on the rare algae Arnodiella conchaphila V. Miller (Ulvophyceae: Cladophorales) from India

Jai Prakash KESHRI* & Ashis Ghosh HAZRA

CAS in Botany, The University of Burdwan, Golaprag, Burdwan-713104, West Bengal, India

Konagar High School, Konagar, Dist. - Hooghly, West Bengal, India

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Abstract - The rare alga Arnodiella conchaphila V. Miller has been recorded from India. It was found growing vigorously on shell deposits (Pila globosa Swansoon) in the Kangsabati, a small river in the Purulia district of West Bengal, India. The thallus morphology was investigated using light microscopy and compared with the known records for this species.

Arnodiella / Cladophorales / Distribution / Morphology

Résumé - Observations sur une algue rare trouvée en Inde: Arnodiella conchaphila V. Miller (Ulvophyceae: Cladophorales). L’algue rare Arnodiella conchaphila a été observée en Inde. Elle croissait vigoureusement sur des coquilles d’escargots (Pila globosa Swansoon) dans une petite rivière (Kangsabati) du district de Purulia au Bengale occidental (Inde). La morphologie de cette algue a été étudiée au microscope photonique et comparée avec les trouvailles antérieures.

Arnodiella / Cladophorales / Distribution / Morphologie

INTRODUCTION

The genus Arnodiella (Cladophorales) was established by Miller (1928) based exclusively on the type species, A. conchaphila V. Miller from lake Poresdawl in central Russia. The specimens observed by Miller were found growing on the surface of molluscan shells (Anodontinae and Unio) on which they formed dark green crusts. Miller gave a detailed description of the unusual morphology of the thallus, consisting in a one-layered creeping system formed by the connexione of prostrate threads from which densely apposed, little branched

* Correspondence and reprints: jpkeshri@indiatimes.com
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