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# A taxonomic reassessment of Rhodolith-forming species of *Lithophyllum* (Corallinales : Rhodophyta) in the Gulf of California, México

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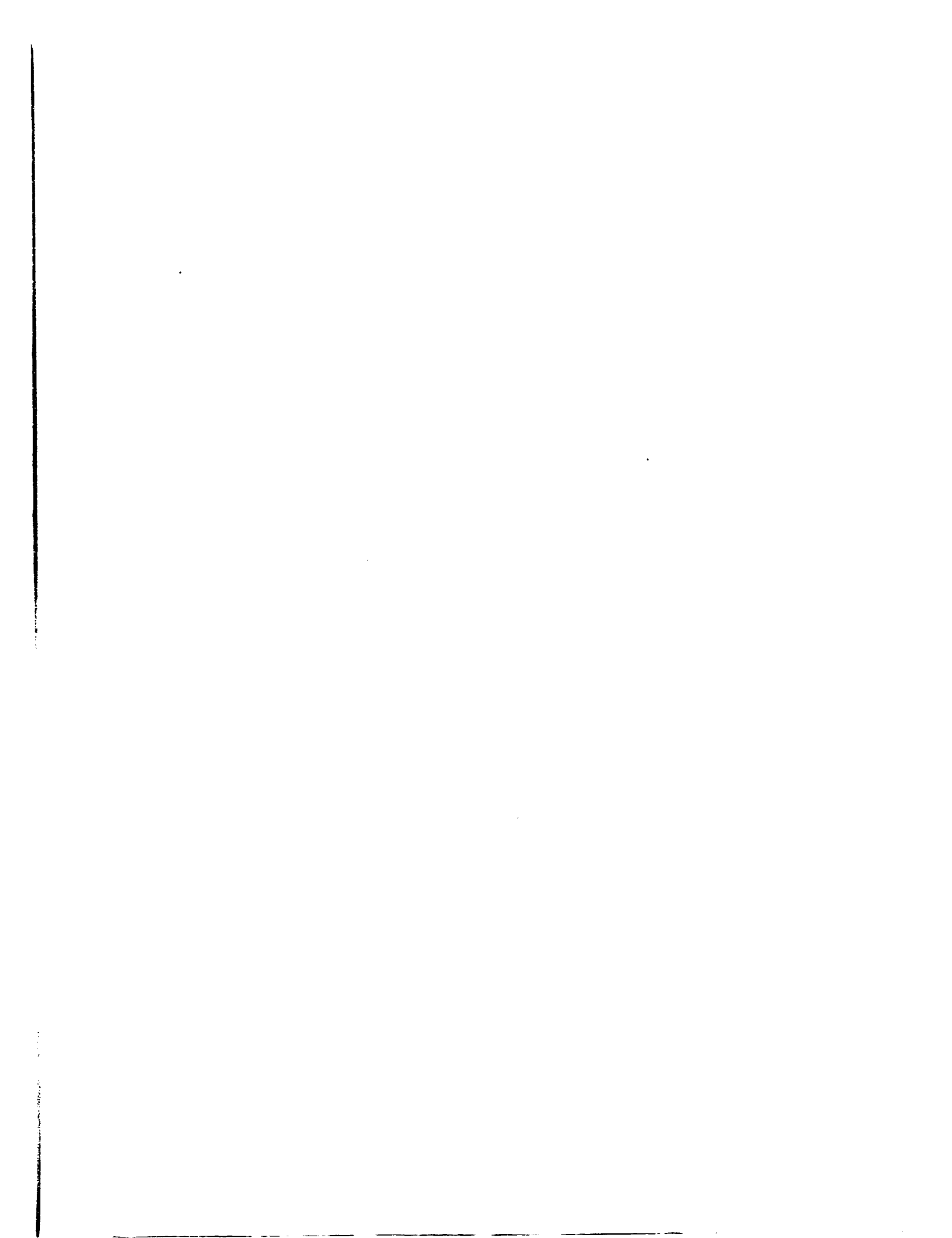
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**A TAXONOMIC REASSESSMENT OF RHODOLITH-FORMING SPECIES OF  
*Lithophyllum* (CORALLINALES: RHODOPHYTA) IN THE GULF OF  
CALIFORNIA, MÉXICO.**

A Thesis Presented to the Faculty

of

Moss Landing Marine Laboratories

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

By

Rafael Riosmena-Rodriguez.  
December 1997

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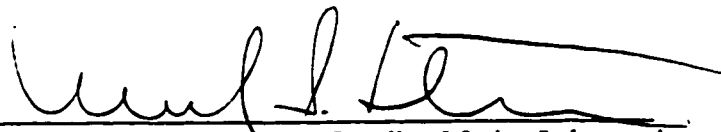
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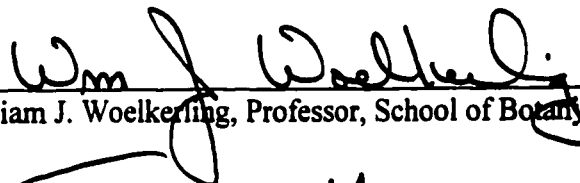
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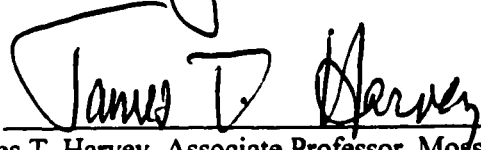
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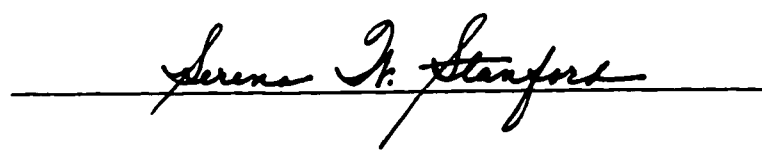


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## ABSTRACT

### A TAXONOMIC REASSESSMENT OF RHODOLITH-FORMING SPECIES OF *Lithophyllum* (CORALLINALES: RHODOPHYTA) IN THE GULF OF CALIFORNIA, MÉXICO

by Rafael Riosmena-Rodríguez.

Rhodolith beds in the Gulf of California, México are widespread and commonly dominated by specimens belonging to *Lithophyllum* (Corallinales, Rhodophyta). The number of rhodolith-forming species of *Lithophyllum* in these beds, however, has been uncertain. Five species have been recognized in the past. I examined over 700 specimens from 45 localities, and compared these to all relevant types to determine how many species are represented and how they might be distinguished. Two species, *L. californiense* and *L. brachiata* did not agree with the modern concept of the genus. An evaluation of characters used by Dawson (1960a) showed that they cannot be reliably used to separate species the remaining species. Modern characters related to tetrasporangial conceptacles, were similar among species. I therefore conclude that there is only one species, *Lithophyllum margaritae* (Hariot) Heydrich, whose growth form varies continuously from encrusting to foliose to fruticose to warty to lumpy within and between populations probably related to local environmental conditions.



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Tecomates; 14. El Cardon; 15. Requeson; 16. El Burro; 17. Correcaminos; 18. Punta El Coloradito; 19. La Hacienda; 20. Los Pocitos; 21. Channel in the western side of Coronado I.; 22. western side of Coronado I.; 23. eastern side of Coronado I.; 24, southwestern side of Carmen I.; 25. Puerto Escondido; 26. Danzante I.; 27. Moserrat I.; 28. Agua Verde; 29. Santa Cruz I.; 30. San Diego I.; 31. northwestern side of Isla San José; 32. western side of Isla San José; 33. southwestern side of I. San José; 34. Callo I.; 35. western side of Coyote I.; 36. eastern side of Coyote I.; 37. northwestern side of La Partida; 38. Ballena I.; 39. Gallo I.; 40. Gallina I.; 41. San Gabriel in Espiritu Santo Island; 42. Canal de San Lorenzo; 43. La Bonanza; 44. northwestern part of Cerralvo I.; 45. Punta Perico.

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## INTRODUCTION

Rhodoliths beds in the Gulf of California, Mexico have been recorded from the upper Gulf to the Revillagigedo Islands (Dawson 1961; Foster et al. 1997). They are particularly abundant in La Paz Bay (Dawson 1944, 1960) and Concepción Bay (Steller & Foster 1995). Dawson (1960) reported that rhodolith beds in the Gulf of California are composed of two species of *Lithothamnion* [*Lithothamnion australe* (Foslie) Foslie in Weber van Bosse and Foslie, *L. crassiusculum* Foslie] and five species of *Lithophyllum* [*L. diguetti* (Hariot) Heydrich, *L. lithophylloides* Heydrich, *L. margaritae* (Hariot) Heydrich, *L. pallescens* (Foslie) Heydrich and *L. veleroae* Dawson]. However, Dawson's (1960) concept of *Lithophyllum* does not conform to more recent concepts of the genus (Woelkerling 1983, 1988) and thus generic affinities of species placed by Dawson in this genus also require confirmation.

Knowledge of rhodoliths in the Gulf of California began with Hariot's (1895) description of two new species (*Lithothamnion diguetti* Hariot and *L. margaritae* Hariot) and a report of a third previously described (*L. racemus* Lamark). This material was re-examined by Foslie (1895, 1897, 1898, 1899, 1900, 1901, 1903, 1904, 1907a, 1907b, 1907c, 1908, 1909), Heydrich (1897a, 1897b, 1901), Lemoine (1911, 1929) and Printz (1929) and transferred to *Lithophyllum*. The specimens referred to *L. racemus* were redescribed as two new species: *L. lithophylloides* Heydrich and *L. pallescens* (Foslie) Heydrich. The types of the above species are housed in Paris (Heydrich, 1901; Woelkerling & Lamy 1997) and Trodheim (Woelkerling 1993). Dawson (1944) later



described *L. veleorae* based on a single collection housed in the Herbarium of the Natural History Museum of Los Angeles County (Anderson 1991). Finally, Dawson (1960a) reported 15 species and one variety in the genus *Lithophyllum* from the Pacific off Mexico; three of these formed rhodoliths exclusively, while two also grew attached (*L. pallescens* and *L. lithophylloides*).

Dawson (1960a:36, 44) separated the five species he recognized based on differences in branch morphology and general appearance, but suggested that only one extremely polymorphic species might be involved. Steller & Foster (1995) found that beds were composed primarily of two growth-form: foliose and fruticose. They determined that branch density, regardless of the taxonomic disposition of the taxa, varied with depth. Foster *et al.* (1997) described variability in the morphology of rhodoliths related to two kinds of environments: wave and current beds. This question, of species composition requires resolution, especially in view of recent monographic studies of *Lithophyllum* elsewhere (Chamberlain 1991; Chamberlain *et al.* 1991; ; Woelkerling & Campbell 1992; Irvine & Chamberlain 1994; Woelkerling 1996) which have been demonstrated that morphological characters used to delimit species in this genus are not reliable, but that characters related to tetrasporangial /bisporangial are.

All five species of *Lithophyllum* recognized by Dawson (1960a), the focus of the present study, are based on type collections from La Paz region. The taxonomic

disposition of the species of nongeniculates in the Pacific Mexico has not been formally reviewed since Dawson (1960a), and there is little evidence that Dawson reviewed the type material of most of the species. He only referred to the type of *L. digueti* (Dawson, 1944, plate 59-7; 1960a, plate 29-7) and *L. lithophylloides* (Dawson, 1944, p.269, plate 58-2&3) in the legends of a few plates. However, only in the first case did he cite as a "type" the material housed at Berkeley and in the second the original collections of Diguët. In this sense there is no evidence that he used the correct names for all his taxa. It is also necessary to review the types of most of the species assigned to this genus in the light of modern concepts of morphology and taxonomy (Woelkerling, 1988; Campbell and Woelkerling, 1990; Woelkerling and Campbell, 1992; Irvine and Chamberlain, 1994) to thoroughly evaluate species status and assign correct names.

The aims of the present study were to: 1) reassess the generic disposition of Gulf of California rhodolith-forming species referred to *Lithophyllum* by Dawson (1960a) through re-examination of relevant type collections; 2) re-evaluate the stability of characters used by Dawson (1960a) to delimit the species he recognized; 3) determine how many rhodolith-forming species of *Lithophyllum* occur in the Gulf and how they can be delimited from each other and; 4) provide accounts of the species recognized.

## **METHODS**

### **Field sampling**

Populations of rhodolith-forming *Lithophyllum* were collected at 45 localities in the Gulf of California (Fig. 1). Plants were collected using scuba and dredges (described in detail by Foster *et al.* 1997) in a haphazard manner within localities, but collection was stratified to include several depths spanning the known range of distribution. Scuba collections also included the range of forms occurring in each site. Material was fixed with 4% formalin in seawater, transported to the laboratory and then transferred to 70% alcohol-water solution with 5% glycerin.

### **Herbarium procedures**

Each date and locality sampled was listed and labeled by consecutive number in a spreadsheet with relevant data (collectors, depth, latitude and longitude). Each plant collected was then determined based on characters used by Dawson (1960a), and selected material processed for optical and electron microscopy. After the taxonomic evaluation, each taxa determined from representative populations was housed dry and fresh at the Phycological Herbarium of Universidad Autonoma de Baja California Sur [FBCS]. All material stored in FBCS was cataloged in the central database using DBASE-III Plus® program.

Additional data were obtained from material previously curated in several Herbaria: Herbarium of the Universidad Autonoma de Baja California Sur [FBCS],

Botany Section of Natural History Museum of Los Angeles County [LAM], Herbarium of the University of Michigan [Mich], Herbarium of the Natural History Museum, Smithsonian Institution [US], Herbarium of the University of California, Berkeley [UC], Foslie Herbarium at Trodheim [TRH] and the Museum National d'Histoire Naturelle Paris [PC]. Herbarium abbreviations follow Holmgren *et al.* (1990), anatomical terminology follows Woelkerling (1988), and growth-form terminology follows Woelkerling *et al.* (1993).

#### **Histological procedures**

Permanent slides for optical microscopy were prepared from selected (for vegetative or reproductive analysis) fragments decalcified in 0.6 M HNO<sub>3</sub>, stained in 5% aqueous KMnO<sub>4</sub> for 30 min., dehydrated through 30, 60, 90 and 100% ethanol, ethanol-butanol (50% each) and 100% butanol steps at 30 minute intervals and infiltrated and embedded in paraffin (Paraplast™). Embedding was done in 3 steps, the first and the third for 30 min. and the second overnight (12 hrs.). Sections 4-6 μm thick were cut with a disposable blade, placed on a warm bath with grenetin, mounted on slides and deparaffined with xilol and, finally, covered with Cytoseal as a mounting media. Fractured fragments for scanning electron microscopy were prepared following the procedures of Woelkerling (1988, p.34).

### **Taxonomic evaluation**

The first evaluation was the re-examination of the generic disposition of relevant type material. This was done through analysis of anatomic characters in the specimens. Those plants having secondary pit connections between filaments and uniporate tetra/bisporangial and gametangial conceptacles were recognized as *Lithophyllum* according with the generic concept Woelkerling (1983, 1988) and Irvine and Chamberlain (1994).

A comprehensive evaluation of the stability of the diagnostic characters used by Dawson (1960a) was then done to determinate the variability present within and among populations. The morphology and anatomy (vegetative and reproductive) of these populations was also evaluated using the 81 qualitative and quantitative characters compiled by Woelkerling and Campbell (1992) to segregate species and the diagnostic features presented in the recent accounts for species from the British Isles (Chamberlain 1991; Chamberlain *et al.* 1991; Irvine & Chamberlain, 1994), Spain (Reyes *et al.* 1988), southern Africa (Chamberlain, 1996) and southern Australia (Woelkerling 1996). Finally, type collections were analysed to select the appropriate name(s) for the phenetic units delineated in the previous analyses.

## RESULTS & DISCUSSION

### a) Generic Disposition

The examination of the type specimens of all species recognized by Dawson (1960a), and their synonyms, indicated that most of the material fit the generic concept of *Lithophyllum*, having only secondary pit connections between filaments (fig. 2) and uniporate tetrasporangial (figs. 4-5, 17-22) and gametangial (figs. 23-25) conceptacles. The specimens conformed to the modern concept of *Lithophyllum* as delimited by Woelkerling and Campbell (1992) and Woelkerling (1996). The types also fell within the narrower concept of *Lithophyllum* sensu Irvine and Chamberlain (1994) and Chamberlain (1996). However, the evaluation of the type material of *L. brachiata* and *L. californiense* treated by Dawson (1960a) as heterotypic synonyms of *L. lithophylloides* and *L. pallescens* indicated these species; do not belong to *Lithophyllum* or to the subfamily Lithophylloideae. Further information on these two taxa is included in the section on taxonomic accounts. No mixtures among genera were observed in the same rhodolith.

### b) Dawson's Species Characters

Dawson (1960a) used 9 morphological characters to differentiate species (Table 1). In the types and populations I examined, surface finish and the presence of regular/irregular surface texture were similar in most of the specimens analyzed (figs. 2, 6-11 & 14). The predominance of any particular morphology in the thallus (foliose,

cylindrical or knobby) was not consistent because of the presence of intermediate forms between any of them (fig. 2, 9 & 14). Dawson (1960a) also associated relative thickness and sharpness of the branches, or the presence of tapering branches with form. However, these features were observed to intergrade (fig. 14). The arrangement (density) of the excrescences has been previously invalidated because this varies related with depth (Steller and Foster 1995; Foster *et al.* 1997). Finally, the presence of channels and ridges, used by Dawson (1944) to delimit *L. veleroae*, was inconsistent even in the type collection (figs. 10-1). This is reflected in the anatomy, where channels correspond to a single, thick axis (figs. 12) from which simple, thin branches can form (fig. 13).

The plants from a range of localities (fig. 1) and depths (from 3 to 50 m) were examined, and *L. margariate* was found in several growth-forms: encrusting, foliose, fruticose and lumpy (figs. 2, 6-11, 14) with intergradations among them. Thus, none of the features used by Dawson (1960a) are reliable for species limitation and most previous collections only represent portions of the total phenotypic variability (fig. 14). Dawson's proposals for species are not supported by the present evidence and, thus, must be rejected. The rejection of Dawson's proposals leaves unanswered the questions of how many rhodolith-forming species might be present in the Gulf of California and how they are delimited. These questions are addressed below.

### c) Other Characters and Species Delimitation

The assessment of qualitative (two-state, multistate) and quantitative (measured or counted) characters, in approximately 1300 slides from 700 specimens from 45 localities and using the 81 characters of Woelkerling and Campbell (1992, Table 5) showed that 13 were not applicable to this species because it is free-living. From the 68 applicable to these plants, none could be reliably used because these characters showed either a continuous range of variation in the Gulf of California collections/populations or were invariant. Diagnostic characters and character states used in recent monographic accounts of *Lithophyllum* (Woelkerling & Campbell 1992, Irvine & Chamberlain 1994, Chamberlain 1996, Woelkerling 1996) were used (Table 2) to evaluate how many species were present in the area. This evaluation indicated that only features related to the anatomy of the tetrasporangial conceptacle could be used as discriminant characters to delimit the species and justify synonymization. These features were presence of a central columella (fig. 5), the number of peripheral cells that form the roof (fig.22-27) and the presence of senescent cells derived from the columella and their presence all over the roof in the tetrasporangial conceptacle (figs. 17-22).

Based on this evaluation, there is only a single rhodolith forming species of *Lithophyllum* in the Gulf of California. Among the available names, *L. margaritae* (Hariot) Heydrich is the available name and that *L. diguetii*, which was described in the same paper (and thus could be used) has not been chosen because the type material of *L. margaritae* is in better condition and shows the characteristics of the species more clearly



than the type material of *L. diguetii*. The examination of the type collections of *L. diguetii*, *L. lithophylloides* f. *lithophylloides*, *L. pallescens* and *L. veleroae* revealed that they are heterotypic synonyms. Most of the types of the above species were tetrasporangial plants (fig. 5) as were in recent collections (figs. 17-22). Only the type of *L. pallescens* was carposporangial, but the morphology of the conceptacle of these plants was the same as that in samples from other regions (fig.25). Furthermore, additional collections in the type locality (western side of Espiritu Santo Island) of the species included tetrasporic plants according as described for the species, but with the same type of conceptacle anatomy as the other types.

#### **d) Taxonomic Accounts**

##### *Recognised Species*

***Lithophyllum margaritae* (Hariot) Heydrich 1901: 530.**

Foslie 1901:19; De Toni 1905:1792; Dawson 1944: 266; Dawson 1946:190; 1953:134; 1960a:44; 1961: 416; Woelkerling 1984:76; Huerta-Múzquiz & Mendoza-González 1985:48; Dreckmann 1991:34; Steller 1993:16, fig.3; Mendoza-González & Mateo-Cid 1994:51; González-González *et al.* 1996:238 & 401; Paul-Chávez 1996:50; Riosmena-Rodríguez & Paul-Chávez 1997:in press; Woelkerling & Lamy 1997:in press.

##### **BASIONYM:**

*Lithothamnion margaritae* Hariot 1895: 167; Foslie 1900:20; 1901:28; 1909:27; Lemoine 1911: 173-5, Fig. 100 pl. 21 Fig. 2; Woelkerling 1984:76.

**HOMOTYPIC SYNONYMS:**

*Pseudolithophyllum margaritae* (Hariot) Lemoine 1913:46.

**HETEROTYPIC SYNONYMS:**

*Lithothamnion diguetii* Hariot 1895:168; Foslie 1909:26; Woelkerling 1984:50.

*Lithophyllum diguetii* (Hariot) Heydrich 1901:532; Foslie 1901: 13,21-2; De Toni 1905: 1783; Foslie 1909:26; Lemoine 1911:120; Printz 1929:33, pl.61 fig.8; Dawson 1944: 270, pl. 59, fig. 8, 11-16; 1946:190; 1953:133; 1960a:39; Dawson 1961:416; Adey & Lebednik 1967: 45; Woelkerling 1984:50; Huerta-Múzquiz & Mendoza-González 1985:48; Dreckmann 1991:34; Mateo-Cid *et al.* 1993:46; Steller 1993:16, fig. 3; Mendoza-González & Mateo-Cid 1994:51; Steller & Foster 1995: 205, fig. 2; González-González *et al.* 1996:237 & 400; Paul-Chávez 1996:50; Riosmena-Rodríguez & Paul-Chávez 1997:in press; Woelkerling & Lamy 1997:in press.

*Lithothamnion elegans* Foslie f. *angulata* Foslie 1895:6, 10; 1897a: 10, pl.1 figs. 9-10; Heydrich 1897b: 415; 1897c:64; Foslie 1929:27; Woelkerling 1984:52; 1993:83-4.

*Lithothamnion elegans* Foslie f. *complanata* Foslie 1895: 6, 10; 1897: 10, pl.1 figs. 9-10; Heydrich 1897b:415; 1897c:64; Foslie 1909:27; Woelkerling 1984: 52; 1993:83-4.

*Goniolithon elegans* Foslie 1899:8; Woelkerling 1984: 52; 1993:83-4.

*Lithophyllum elegans* Foslie 1900:20; De Toni 1905: Foslie1909:27; Printz 1929: 34, pl.63, figs.1-2; Setchell & Mason 1943:95; Woelkerling 1984:52; 1993:83-4.

*Lithothamnion lithophylloides* (Heydrich) Foslie 1907c:11; Woelkerling 1984:73; 1993:138.

*Lithophyllum lithophylloides* f. *lithophylloides* Heydrich 1901:531; Foslie 1901:21; De Toni 1905:1793; Foslie 1907:10; De Toni 1924: 685; Dawson 1944:269, pl. 55, fig. 3; pl. 58, fig. 2,3,7; pl. 59, fig. 9, 10; pl. 61, fig. 1; 1946:190; 1953:134; 1960a:43; 1961:416; Adey & Lebednik 1967:48; Norris 1975:265-6; Woelkerling 1984:73; Huerta-Múzquiz & Mendoza-González 1985:48; Dreckmann 1991:34; González-González 1992:48; León-Alvarez & González-González 1993: 461; León-Tejera & González-González 1993:497; Serviere-Zaragoza 1993:77; Serviere-Zaragoza *et al.* 1993:484; Woelkerling 1993:138; Mendoza-González & Mateo-Cid 1994:51; González-González 1996:238&401; León-Tejera *et al.* 1996:164; Riosmena-Rodríguez & Paul-Chávez 1997:in press; Woelkerling & Lamy 1997:in press.

*Lithothamnion pallescens* Foslie 1895:4, 10, pl.1 figs. 11-13; 1897:13-4; Heydrich 1897a:60; 1897b:413; Foslie 1909:36; Woelkerling 1984:85; 1993:167-8.

*Goniolithon pallescens* (Foslie) Foslie 1898:9; Woelkerling 1984:85; 1993:167-8.

*Lithophyllum pallescens* (Foslie) Foslie 1900:20; Foslie 1901:20; Heydrich 1901:531; Foslie 1903:467; 1904:33, 60; De Toni 1905: 1789; Foslie 1906: 134; 1907a:104; 1907b: 188; 1908:216; Lemoine 1911:156-8, figs. 87-91; Printz 1929:37, pl. 64, fig. 15-7; Dawson 1944:266, pl. 55, fig. 4; 1946:190; 1949:244; 1953:134; 1960a:46;1960b:50; 1961:416; 1962a:230; 1966:35; Adey & Lebednik 1967:42; Scwab 1969:189-193, figs. 1-14; Adey 1970:5; Adey 1979:461-2; Norris 1975:266-7; Townsend 1981: 408; Adey *et al* 1982:37-8, 40-42, figs. 23,26,27; Schmetter & Meyer 1982:126; Lewis 1984:16; Woelkerling 1984:85; Huerta-Múzquiz & Mendoza-González 1985:48; Mendoza-González & Mateo-Cid 1986:423; Silva *et al.* 1987:36; Dreckmann 1991:34; Mateo-Cid *et al.* 1993:46; Steller 1993:16, fig.3; Woelkerling 1993:167-8; Mendoza-González & Mateo-Cid 1994:51; Ballesteros & Afonso-Carrillo 1995:207, fig.4; Steller & Foster 1995: 205, fig. 2; González-González *et al.* 1996: 238 & 401; Silva *et al.* 1996:249; Riosmena-Rodríguez & Paul-Chávez 1997:in press; Woelkerling & Lamy 1997:in press.

*Lithophyllum veleroae* Dawson 1944:270, pl. 55, fig.5; pl. 56, fig. 1-4; 1953:134; 1946:190; 1960a: 52, pl. 47, fig. 1-4; 1961: 417; 1962:48; Huerta-Múzquiz & Mendoza-González 1985:48; Ortega *et al.*1986:103; Anderson 1991:32; Dreckman 1991:34; Mateo-Cid *et al.* 1993: 46; Steller 1993:16, fig.3; Mendoza-González &

Mateo-Cid 1994:51; Steller & Foster 1995:205, fig. 2; González-González *et al.* 1996: 239; Riosmena-Rodriguez & Paul-Chávez 1997:in press; Woelkerling & Lamy 1997: in press.

#### **MISAPPLIED NAMES:**

*Lithophyllum bracchiatum* auct.non. Taylor 1945:179; Dawson 1946:189; León-Alvarez & González-González 1993: 461; León-Tejera *et al.* 1996: 164.

*Lithothamnion crassum* f. *typica* auct.non. Foslie 1895:3, fig.14.

*Lithothamnion indicum* auct.non. Taylor 1945:173.

*Lithothamnion racemous* auct.non. Hariot 1895:168.

**HOLOTYPE:** La Paz Bay, collected by Diguët in 1894 and housed in PC as number 1. Along with the type material of the species, Diguët included three annotations and a map with San Juan Nepomuceno Island as the type locality (Woelkerling & Lamy 1997). As a part of the development of the Pichilingue harbour in the early 70's, the eastern side of the island was connected to the land using material from the western side. The intensive dredging activities around the western side may have destroyed the population observed by Diguët. In the surveys during this study no rhodoliths were found in the western side of San Juan Nepomuceno I. However, Diguët's map also included the western side of

Espiritu Santo Island as the type locality of *L. pallescens*, which is a heterotypic synonym of *L. margaritae*. Recent surveys have found several rhodolith beds with specimens like the type around the southern, eastern and northeast side of Espiritu Santo Island. The western side of Espiritu Santo Island should thus be considered as the type locality of the species.

**COMMON NAME:** Rhodoliths have several names in the Gulf of California, the most used is *Chicharron* (dry pork skin) and is related to the appearance of the beds in the bottom. In the northern part of the gulf the fishermen call them in two different ways: *Oreja de cochi* (pork ear) for the foliose growth-form and *Granola* for the fructicose growth form. The common names have been used by fisherman since the beginning of the century (Cuevas, J. pers. comm.<sup>1</sup>) because natural banks of pearl oyster were associated with these plants (Dawson 1960a). During the early days of pearl culture, "chicharrones" were also used as a substrate for oysters in San Gabriel Bay in Espiritu Santo Island (Cariño-Olvera & Cáceres-Matínez, 1990:5 photographs 6, 7 & 8).

**DESCRIPTION:** Thallus purple-reddish, free-living, 1-15 cm in diameter, irregular to regular in shape, branching varies in density, lamellar, subcylindrical or cylindrical in cross section. Growth-form from encrusting to foliose to fructicose to warty to lumpy (figs. 2, 6-11, 14). Thallus composed of a central core of filaments with contiguous secondary pit

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<sup>1</sup> Personal interview of Foster M.S. & Riosmena-Rodriguez R. with José Cuevas during September of 1994 in "El Pardito" (official known as Coyote I.).

connections (figs.3-4), cell fusions and trichocytes absent. Central filaments with cells 12-30  $\mu\text{m}$  long and 6-15  $\mu\text{m}$  wide; several layers of peripheral cells, each cell of 6-18  $\mu\text{m}$  long and 5-10  $\mu\text{m}$  wide; only one layer of epithallial cells and each cell of 2-4  $\mu\text{m}$  long and 6-10  $\mu\text{m}$  wide.

Tetrasporangial plants with abundant conceptacles in several layers, sometimes protruding through the pore above the epithallial cells (figs. 17-8, 21). Conceptacles oblong with a central columella ranging from slightly evident to conspicuous (figs. 5, 17-22). Collumella is associated with senescent filaments (fig. 18-9), that cover entire the roof filaments (figs. 219-21), leading to pore formation without occlusion (fig. 21). Roof of the conceptacle usually formed by 3-4 cells in horizontal subepithallial groups (figs. 17-22). Pore canals lined with somewhat projecting but not occluding cells. Conceptacle chambers 150-450  $\mu\text{m}$  across and 50-150  $\mu\text{m}$  tall; tetrasporangia scattered across the conceptacle chamber floor or more commonly occurring peripheral to a columella. Bisporangial plants not observed.

Gametangial plants dioecious, the pore in all stages occluded with two filaments that converge from the margins (figs. 23-25). Male conceptacle roofs non- or slightly protruding; chambers 100-150  $\mu\text{m}$  in diameter and 30-60  $\mu\text{m}$  tall; spermatangial branches confined to the floor, simple, with each initial bearing one or several elongate spermatangia (fig. 23). Female/carposporangial conceptacle roofs non- or slightly

protruding; chambers 100-250  $\mu\text{m}$  in diameter and 40-80  $\mu\text{m}$  tall; carpogonial filaments arising from chamber floor, usually 3-4 cells long and bearing 1-2 carpogonia terminally (fig. 24). Carposporophytes developing within female conceptacles after presumed karyogamy; each comprising a central more or less flattened fusion cell and some several-celled gonimoblast filaments with terminal (or possible catenate) carposporangia 30-45  $\mu\text{m}$  in diameter (fig. 25).

*Remarks on distribution and ecology.*

Widely distributed in the Gulf of California from 3 - 50 m depth. The populations in Mejia Island around 29.5°N represent the known northern distributional limit of the species; the southern boundary remains undetermined. The various growth-forms that this species have are not restricted to any depth or region. The dominance of particular growth forms within an area is currently in review (Yabur pers. com.) and appears linked to local environmental conditions (Foster et al. 1997). Papers cited in the synonymy section suggest this species is potentially distributed around the tropical Pacific and Indian Ocean, and has been present since the tertiary (Adey 1979).

*Comparisons with other species.*

*Lithophyllum margaritae* differs from other well known species in the genus based on the tetrasporangial anatomy (Table 4). The number of peripheral cells over the roof in *L. margaritae* (4-6) was very characteristic and slightly overlaps with *L. incrustans*. The



presence of a central columella associated with senescent filaments in pore formation results in the alignment of the former without occluding the pore is one of the features that *L. margaritae* has in common with some other species (*L. bermudense*, *L. pustulatum* (Lamouroux) Foslie and *L. incrustans* Phillipi). But, the distribution of these senescent filaments (as cells, figs. 17-22) over the roof is unique to *L. margaritae* (Table 4).

*Diagnostic features:*

1. The presence of a central columella associated with senescent filaments to form the pore.
2. Remaning cells from the senescent filaments restricted to the conceptacular roof and aligned without occluding the pore.
3. Roof of tetrasporangial conceptacle usually 3-4 (6) cells thick above the chamber.

*Comparisons with other rhodolith-forming species.*

The present study revealed that one highly polymorphic species, *L. margaritae*, is commonly distributed in the Gulf of California as one of the major components of rhodolith beds. The high phenetic variability of this species is shown in several growth-forms (figs. 2, 6-11, 14-19) and in the variation of branch density and sphericity with depth (Steller & Foster 1995; Foster *et al.* 1997). Similar variability in branch density and sphericity has been recorded for *Lithothamnion corallioides* (P. & H. Crouan) P. & H. Crouan 1867 and *Phymatolithon calcareum* (Pallas) Adey & McKibbin 1970

(Boscence 1976; Irvine & Chamberlain 1994), but these species only vary between fructicose and warty. Different growth-forms also occur within the species of *Lithophyllum* in Southern Australia (Woelkerling & Campbell 1992, Woelkerling 1996), the British Isles (Irvine & Chamberlain 1994), Malasia (Weber van Bosse & Foslie 1904) and *Lithophyllum frondosum* (Dufour) Furnari, Cormanci & Alogni 1996 from the Mediterranean (Furnari *et al.* 1996). However, none has the phenological extremes observed in *L. margaritae* in the Gulf of California.

#### *Excluded Species*

*Lithophyllum brachiata* (Heydrich) Lemoine 1929 p. 44, pl.4 fig. 5.

#### Basionym

*L. lithophylloides* f. *brachiata* Heydrich 1901 p.530.

#### Holotype

La Paz Bay, Baja California Sur, México collected by L. Diguet, 1894. PC, no. 14 in the General Herbarium box collection and holotype fragments housed in TRH no. 14, includes 1 slide 668; UC 790561 (Woelkerling & Lamy 1997).

#### Gulf of California Records as:

*L. lithophylloides* f. *brachiata* by Dawson 1944:269, pl. 58, fig. 2; Dawson 1960a:43;

Adey & Lebednik 1967:48; Woelkerling 1993:42.

*Lithophyllum brachiatum* (Heydrich) by Lemoine 1930:44, pl.4, fig.5; Dawson

1944:269; 1946:189; 1953:134; González-González 1992:48; Serviere-Zaragoza 1993:77.

**Remarks**

Dawson (1960) listed *L. brachiata* (Heydrich) Lemoine as a synonym of *L. lithophylloides*, but examination of the types showed that neither belongs to the subfamily Lithophylloideae. Generic placement is uncertain because the type of *L. brachiata* has only cell fusions, thus belonging to the subfamily Mastophoroideae.

*Lithophyllum californiense* Heydrich 1901 pag.530

**Holotype**

La Paz Bay, Baja California Sur, México collected by L. Diguët, 1894. PC, Heydrich No. 2 in the General Herbarium box collection and holotype fragments housed in TRH unnumbered, includes slide 664; UC 790561 (Woelkerling & Lamy 1997).

**Gulf of California Records as:**

Heydrich 1901:530; De Toni 1905: 1796; Dawson 1944:266; 1960:134; Adey *et al.* 1982:40.

**Remarks**

Dawson (1960) listed *L. brachiata* (Heydrich) Lemoine as a synonym of *L. pallescens*, but the type of *L. californiense* has empty multipored conceptacles and both cell fusions and secondary pit connections. It therefore belongs in the subfamily Melobesioideae.

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**Table 1.** Character and character states used by Dawson (1960a)

to delimit species of *Lithophyllum* that form rhodoliths.

CHARACTERS	SPECIES				
	<i>L. digueti</i>	<i>L. lithophylloides</i>	<i>L. margaritae</i>	<i>L. pallescens</i>	<i>L. veleroae</i>
Surface finish	Not indicated	Not indicated	Not indicated	Dull	Not indicated
Surface texture	Not indicated	Not indicated	Irregular	Regular	Not indicated
Thalli morphology	Blade-like	Not indicated	Not indicated	Not indicated	Not indicated
Relative thickness	Thin	Not indicated	Not indicated	Not indicated	Thick
Relative sharpness	Present	Absent	Present	Absent	Present
Tapering	Present	Absent	Present	Absent	Absent
Excrescences arrangement	Not indicated	Loose	Spreading	Compact	Not indicated
Form predominantly of excrescences	Flattened	Subcylindrical	Flattened to Subcylindrical	Subcylindrical	Flattened
Channels or ridges	Absent	Absent	Absent	Absent	Present

**Table 2.** Diagnostic characters and character states used in recent monographic accounts of *Lithophyllum* (Woelkerling & Campbell 1992; Irvine & Chamberlain 1994; Chamberlain 1996; Woelkerling 1996). T/b = tetrasporangial/bisporangial.

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**A. Characters related to thallus morphology and habit.**

1. Relative adherence to the substrate: unattached or attached.
2. Relative branch density: compact or loose.
3. Shape of the branches: knobby or lamellate.
4. Size of the branches.

**B. Characters related to vegetative anatomy**

1. Terracing of thallus surface: present or absent.
2. Origin of applanate branches from primigeneous or postigeneous filaments.
3. Ventral section with erect filament cells laterally aligned throughout: present or absent.
4. Cells laterally aligned to or sometimes arranged coaxially: present or absent.

**C. Characters related to reproductive anatomy.**

1. T/b pore canal anatomy: occluded or not.
  2. Position of t/b conceptacle chamber floor: near the margin of the thallus or not.
  3. T/b conceptacle roof elevated: above the thallus surface, prominently or not.
  4. T/b conceptacle diameter.
  5. Presence/ absence of a central columella.
  6. T/b conceptacles with or without a central columella
  7. Columella well developed or pronounced or not.
  8. Central columella calcified or not.
  9. Number of cells in the roof of the conceptacle.
  10. General morphology of the t/b conceptacle: conical, globular or not.
  11. Gametangial conceptacle morphology: flask shaped or other.
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**Table 3.** Herbarium material examined; including all the type collections and material from the south, central and northern parts of the Gulf of California (acronyms according to Holmgren *et al* 1990).

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**Type collections:** La Paz bay (*Diguet*, 1894, PC 1; UC 790592 as part of the TYPE collection of *L. margaritae*); (*Diguet*, 1894, PC 5 & 7; US 68664; TRH A-20; UC 790566 and UC 700554 as part of the TYPE collection of *L. pallescens*); (*Diguet*, 1894, PC 10 as part of the TYPE collection of *L. lithophylloides* f. *lithophylloides*); (*Diguet*, 1894, PC 13; TRH A-28 UC 790553 as part of the TYPE collection of *L. diguetii*); (*Diguet*, 1894, TRH A-23 as part of the TYPE of *L. elegans* f. *angulata* and *L. elegans* f. *complanata*). San Lorenzo channel dredged 12-26 m (*Dawson* 592, 14.ii.40, LAM; Mich as part of the TYPE collection of *L. veleroae*) and (*Dawson* 592, 14.ii.40, UC 700530 and UC 700545 as part of the ISOTYPE of *L. veleroae*).

**Southern Gulf:** Bonanza at Espiritu Santo Island dredge 10 m (*Foster*, 02.x.94, FBCS 5215). Cabeza de Ballena (*Dawson* 6827, 11.iii.49, AHF 1727 as *L. pallescens*). Callo I. 15 m (*Foster & R-R*, 09.x.94, 5237-39, FBCS 5137-9, 5241). Eastern side of Coyote I. at 12m (*Foster & R-R*, 07.x.94, FBCS 5225-8); (*Foster & Yabur-Pacheco*, 10.ii.95, FBCS 5306-8); (*Medina-López M.A.*, 29.ix.95, FBCS 5330); (*Rivera M.G.*, 11.iii.95, FBCS 5333-6) and (*Medina-López M.A.*, 25.viii.96, FBCS 5356). Estero Zacatecas (*R-R*, 26.v.90, FBCS 5261-2) and (*R-R*, 27.ix.92, FBCS 5263). Internal Lagoon, Southwestern

San José I. 5-7 m (*R-R, Foster & Yabur-Pacheco, 10.ii.95, FBCS 5312-3*). La Paz bay drifted in sandy area (*Dawson 3120, 31.x.46, US 8205 as L. lithophylloides*). La Paz bay (*Dawson 3416a, 10-11.xii.46, US 8209 as L. pallescens*). Mangrove channel at San José Island 4-5 m (*Foster & R-R, 09.x.94, FBCS 5240*). Northwestern side of Cerralvo I. 12 m (*Ochoa E., 06.xii.96, FBCS 5352-4*) and (*Cintra C., 06.iii.97, FBCS 5372*). Northwestern side of San José I. 12 m. (*Ochoa E., 26.vi.96, FBCS 5338-9*). Partida I. near La Paz at 6-40 ft. (*Neushul 20205, 22.viii.57, US 8147 as L. diguetii*). Punta Perico 20-50 m (*Ochoa E., 09.viii.96, FBCS 5343- 5347*). San Gabriel in Espiritu Santo I. (*Dawson 572, 13.ii.40, UC 700542 as L. pallescens*); (*Dawson 593, 14.ii.40, UC 700544 as L. pallescens*) and (*Dawson 591, 14.ii.40, UC 700550 as L. diguetii*); (*Dawson 7037, 14.iii.49, AHF as L. pallescens*); 10 m (*Foster & R-R, 14.x.94, FBCS 5242-4*). San José I. southwest 12 m (*Foster & R-R, 07.x.94, FBCS 5221-4*). San Lorenzo channel dredged (*Dawson 6943, 15.iii.49, AHF 1738 as L. diguetii*); (*Dawson 591, 14.ii.40, AHF 3585; US 8146 as L. diguetii*); (*Dawson 6942, 15.iii.49, AHF; US 8206 as L. margaritae*); (*Dawson 6940, 15.iii.49, AHF as L. veleroae*) and (*Dawson 6940c, 15.iii.49, US 8204 as L. lithophylloides*); 12 m (*Foster & R-R, 02.x.94, FBCS 5217-9*); (*Foster & Ochoa E., 11.xi.94, FBCS 5292-95*); (*Medina-López M.A. & Foster, 02.ii.95, FBCS 5302-4*) and (*Foster & Medina-López M.A., 03.iii.95, FBCS 5315-7*). Southwestern lagoon of San José I. at 5-7 m (*Foster & R-R, 08.x.94, FBCS 5233-5*). Western side of Coyote I. at 13 m (*Foster & R-R, 07.x.94, FBCS 5229-32*); 20 m (*Foster & Yabur-Pacheco, 11.ii.95, FBCS 5309-11, 5314*); (*Rivera M.G., 10.iii.96, FBCS 5332*) and (*Medina-López M.A.,*

25.viii.96, FBCS 5355). Western side of Isla San José 5 m (*Ketchum J.*, 05.ix.96, FBCS 5350).

**Central Gulf:** Agua Verde dredged (*Dawson*, 04.ii.11, US 32242 as *L. margariatae*). 13 km south of Santa Rosalia cast up (*Dawson* 2975, 24.x.46, AHF; US 8208 as *L. pallescens*) and (*Dawson* 2976, 24.x.46, US 8244; AHF as *L. veleroae*). Catalina I. 7-12 m (*Ochoa E.*, 28.vi.96, FBCS 5337). Coyote I. 3 m (*Steller & Foster*, 02.vi.91, FBCS 5204-5); 7 m (*Steller & Foster*, 02.vi.91, FBCS 5208-9) and 12 m (*Steller & Foster*, 02.vi.91, FBCS 5213). Cueva Island 3 m (*Steller & Foster*, 02.vi.91, FBCS 5167); 7 m (*Steller & Foster*, 02.vi.91, FBCS 5171) and 12 m (*Steller & Foster*, 02.vi.91, FBCS 5169-70). El Bajo 20 m (*Foster & Ochoa E.*, 22.03.95, FBCS 5322-25) and (*Foster & James*, 22.iii.97, FBCS 5357-8). La Hacienda (R-R, 04.iv.91, FBCS 5251-2). Los Pocitos 7 m (*Steller & Foster*, 30.v.91, FBCS 5168) and 12 m (*Steller & Foster*, 30.v.91, FBCS 5174-8). Montserrat I. (*Ochoa E.*, 29.vi.96, FBCS 5341). Morro Tecomán 3 m (*Steller & Foster*, 28.v.91, FBCS 5153-4); (*Steller & Foster*, 02.vi.91, FBCS 5207) and 7-12 m (*Steller & Foster*, 01.vi.91, FBCS 5161-2); (*Steller & Foster*, 09.x.91, FBCS 5157). Puerto Escondido (*Dawson* 513, 10.ii.40, AHF; UC700529 as *L. lithophylloides*). Punta el Coloradito 3 m (*Steller & Foster*, 30.v.91, FBCS 5172) and 12 m (*Steller & Foster*, 30.v.91, FBCS 5165). Requeson 3-4 m (*Riosmena-Rodriguez*, 20.ix.89, FBCS 5245); (R-R, 09.ix.90, FBCS 5258-9), (R-R, 03.iv.91, FBCS 5248-9); (*Steller & Foster*, 30.v.91, FBCS 5184-5); (*Rivera M.G. & Medina-López M.A.*, 20.i.95, FBCS 5278-81); (*Foster &*



*Ochoa E.*, 30.iii.95, FBCS 5319-5321); 5-7 m (*Steller & Foster*, 17.i.91, FBCS 5068-70, 5072-3); 10-12 m (*Steller & Foster*, 17.i.91, FBCS 5065-6); (*Foster & Ochoa E.*, 12.xii.94, FBCS 5298-5300); (*Rivera M.G. & Medina-López M.A.*, 19.i.95, FBCS 5283-5); site 1, 3 m (*Steller & Foster*, 14-15.i.91, FBCS 5074-5, 5077, 5079, 5131-4); (*Steller & Foster*, 28.v.91, FBCS 5135-6); (*Steller & Foster*, 7-9.x.91, FBCS 5163, 5186-7); site 1, 7 m (*Steller & Foster*, 14-15.i.91, FBCS 5081-84, 5129-30); (*Steller & Foster*, 28.v.91, FBCS 5137-39); (*Steller & Foster*, 7-9.x.91, FBCS 5155, 5193); site 1, 12 m (*Steller & Foster*, 14-15.i.91, FBCS 5086-7, 5128); site 1, 12 m (*Steller & Foster*, 7-9.x.91, FBCS 5159-60, 5188-89, 5201-2); site 2, 3 m (*Steller & Foster*, 14-15.i.91, FBCS 5089-90, 5126-27); (*Steller & Foster*, 28.v.91, FBCS 5133-4); site 2, 7 m (*Steller & Foster*, 14-15.i.91, FBCS 5092-93, 5123-25); (*Steller & Foster*, 28.v.91, FBCS 5144-5); site 2, 7 m (*Steller & Foster*, 7-9.x.91, FBCS 5196-8); site 2, 12 m (*Steller & Foster*, 14-15.i.91, FBCS 5095-96, 5121-2); (*Steller & Foster*, 28.v.91, FBCS 5141-2); site 2, 12 m (*Steller & Foster*, 7-9.x.91, FBCS 5190-1); site 3, 3m (*Steller & Foster*, 14-15.i.91, FBCS 5098-99, 5120); site 3, 7 m (*Steller & Foster*, 14-15.i.91, FBCS 5102-3, 5116-19); site 3, 12 m (*Steller & Foster*, 14-15.i.91, FBCS 5105-6, 5113-5); site 4, 3 m (*Steller & Foster*, 14-.i.91, FBCS 5112); (*Steller & Foster*, 28.v.91, FBCS 5146-7); site 4, 3 m (*Steller & Foster*, 7-9.x.91, FBCS 5199); site 4, 7 m (*Steller & Foster*, 14-15.i.91, FBCS 5110-1); (*Steller & Foster*, 28.v.91, FBCS 5148-50); site 4, 7 m (*Steller & Foster*, 7-9.x.91, FBCS 5195); site 4, 12 m (*Steller & Foster*, 14-15.i.91, FBCS 5108-9) and (*Steller & Foster*, 28.v.91, FBCS 5151-2). Santispac shallow (*R-R*, 24.v.90,

FBCS 5254-56). South bed 3 m (*Steller & Foster*, 01.vi.91, FBCS 5179) and 12 m (*Steller & Foster*, 01.vi.91, FBCS 5181). West of Coronados I. 4 m (*Medina-López M.A.*, 14.viii.95, FBCS 5326-28).

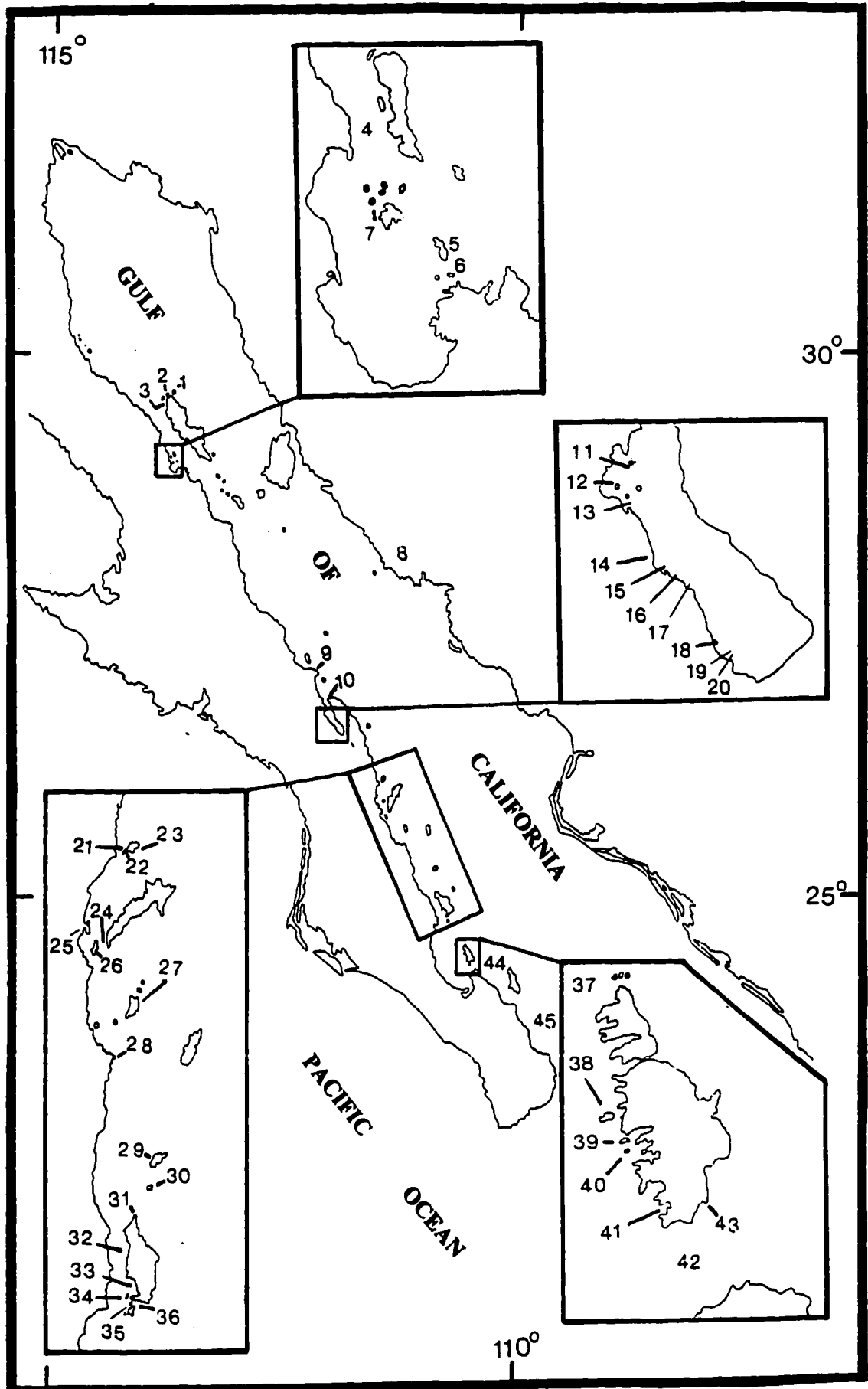
**Northern Gulf:** Angel de la Guarda I. 42 m (*Dawson 250*, 26.i.40, AHF 3645 as *L. lithophylloides*). Bocohibampo Bay (*Manriquez*, 06.ii.90, FBCS 5264). Coronados I. in Los Angeles Bay (*Foster & James*, 25.iii.97, FBCS 5359-60; 5370-1). El Piojo I. (*Foster & James*, 25.iii.97, FBCS 5331). In the channel in the western side of Coronados I. (*Foster & James*, 25.iii.97, FBCS 5365). Mejia channel dredged at Angel de la Guarda I. (*Dawson 278*, 26.i.40, UC 700546 as *L. lithophylloides*). Outside of Cabeza de Caballo I. (*Foster & James*, 25.iii.97, FBCS5366-7). Puerto Refugio at Angel de la Guarda I. 42 m (*Dawson 250-1*, 26.i.40, UC 700541 and 700551 as *L. lithophylloides*). Southern part of Cabeza de Caballo I. (*Foster & James*, 25.iii.97, FBCS5368-9).

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**Table 4.** A comparative summary of characteristics of *L. margaritae*, and closely related species and the type species of the genus *L. incrustans*.

Character\species	<i>L. margaritae</i>	<i>L. orbiculatum</i>	<i>L. bermudense</i>	<i>L. kotschyannum</i>	<i>L. pustulatum</i>	<i>L. incrustans</i>
Number of epithelial cells over the roof of tetrasporangial conceptacle.	1	4-6	1	1	(2-)3(-4)	> 4
Central columnella associated with senescent filaments.	Yes	No	Yes	No	Yes	Yes
Pore canals of tetrasporangial/bisporangial conceptacles lined with cells which may project somewhat into but do not completely occlude the entire canal.	Yes	No	Yes	No	Yes	Yes
Senescent filaments covering the roof of the conceptacle chamber.	Yes	No	No	No	No	No

**Fig. 1. Gulf of California localities where rhodolith forming species of *Lithophyllum* have been found:** 1. southern part of Mejía I.; 2. Channel around Mejía I.; 3. Puerto Refugio in the northwestern side of Angel de la Guarda I.; 4. Channel in the western side of Isla Coronados; 5. western side of Cabeza de Caballo I.; 6. southern side of Cabeza de Caballo I.; 7. El Piojo I.; 8. Bocochibampo Bay; 9. Punta Chivato; 10. Punta Aguja; 11. Cueva I.; 12. Coyote I.; 13. Morro Tecomates; 14. El Cardon; 15. Requeson; 16. El Burro; 17. Correcaminos; 18. Punta El Coloradito; 19. La Hacienda; 20. Los Pocitos; 21. Channel in the western side of Coronado I.; 22. western side of Coronado I.; 23. eastern side of Coronado I.; 24. southwestern side of Carmen I.; 25. Puerto Escondido; 26. Danzante I.; 27. Moserrat I.; 28. Agua Verde; 29. Santa Cruz I.; 30. San Diego I.; 31. northwestern side of Isla San José; 32. western side of Isla San José; 33. southwestern side of I. San José; 34. Callo I.; 35. western side of Coyote I.; 36. eastern side of Coyote I.; 37. northwestern side of La Partida; 38. Ballena I.; 39. Gallo I.; 40. Gallina I.; 41. San Gabriel in Espiritu Santo Island; 42. Canal de San Lorenzo; 43. La Bonanza; 44. northwestern part of Cerralvo I.; 45. Punta Perico.



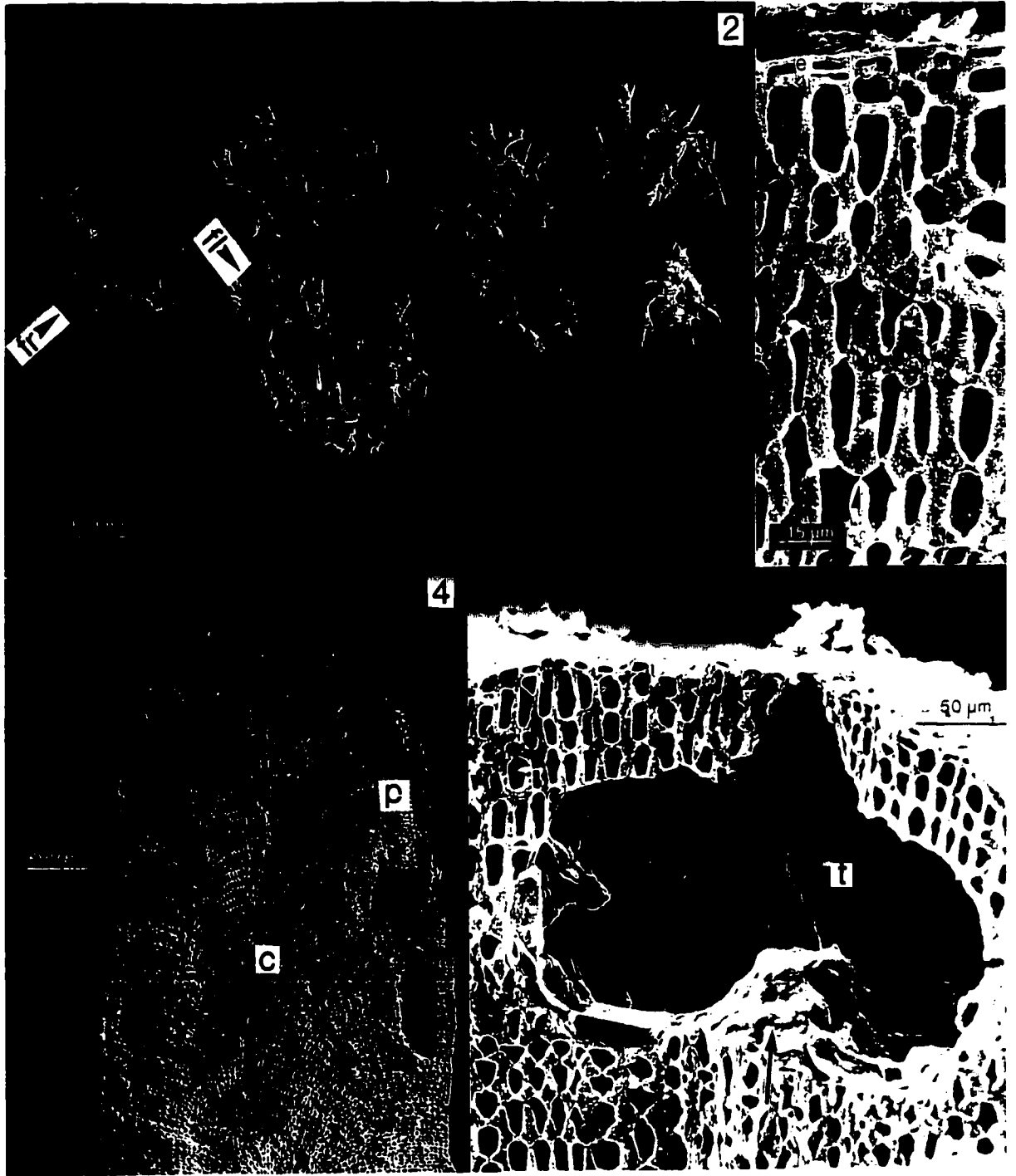
**Figs.2-5. *Lithophyllum margaritae*: holotype (PC 1)**

**Fig.2. Specimens from the holotype collection showing both foliose (**f**) and fruticose (**fr**) branches.**

**Fig.3. Fracture of the holotype material with secondary pit connections (arrows) and epithallial cells (**e**).**

**Fig.4. Longitudinal fracture of holotype material showing monomerous organization with a centrally located core of filaments (**c**) and peripheral regions (**p**) where portions of the filaments curve outwards toward the plant surface.**

**Fig.5. Tetrasporangial conceptacle with a central columella (arrow) and tetraspores (**t**).**



**Fig.6-9. *L.margariate*: variability in growth-forms represented in the types of heterotypic synonyms.**

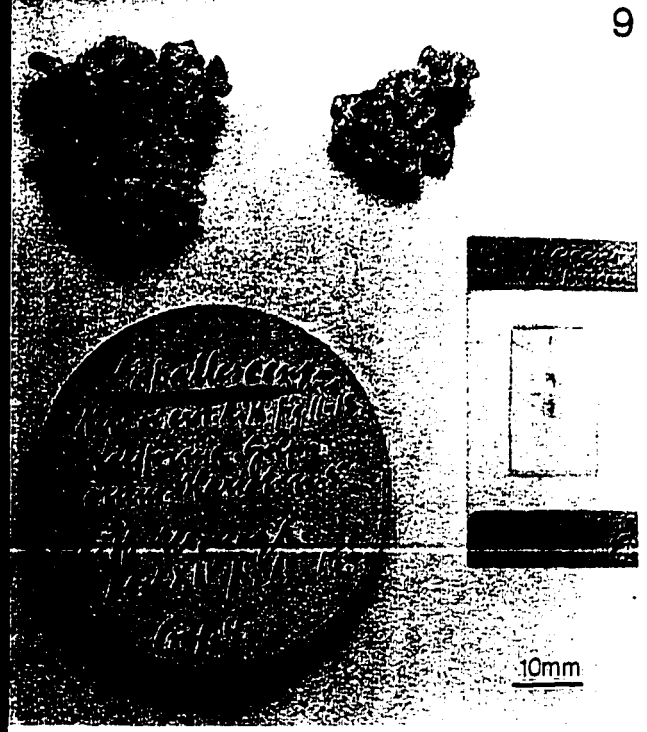
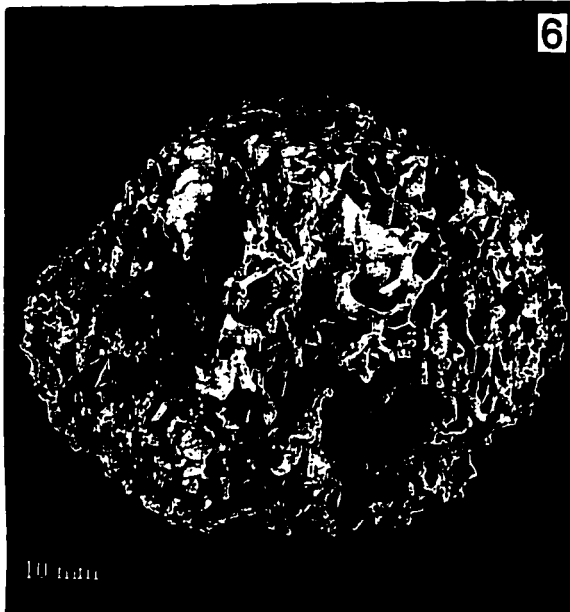
**Fig. 6. Densely branched, foliose plant represented by the lectotype of *L. diguetii* [PC 13].**

**Fig.7. Densely branched, warty plant represented by the holotype of *L.lithophylloides* [PC 10]**

**Fig.8. Sparsely branched, plant with foliose (fi) central region but fruticose branches (fr) represented by the holotype of *L. elegans* f. *complanata* (lower) and fruticose plant that is the holotype of *L. elegans* f. *angulata* (upper) [TRH A-23].**

**Fig.9. Sparsely branched, lumpy plant represented by the holotype of *L. pallescens* [TRH A-20].**





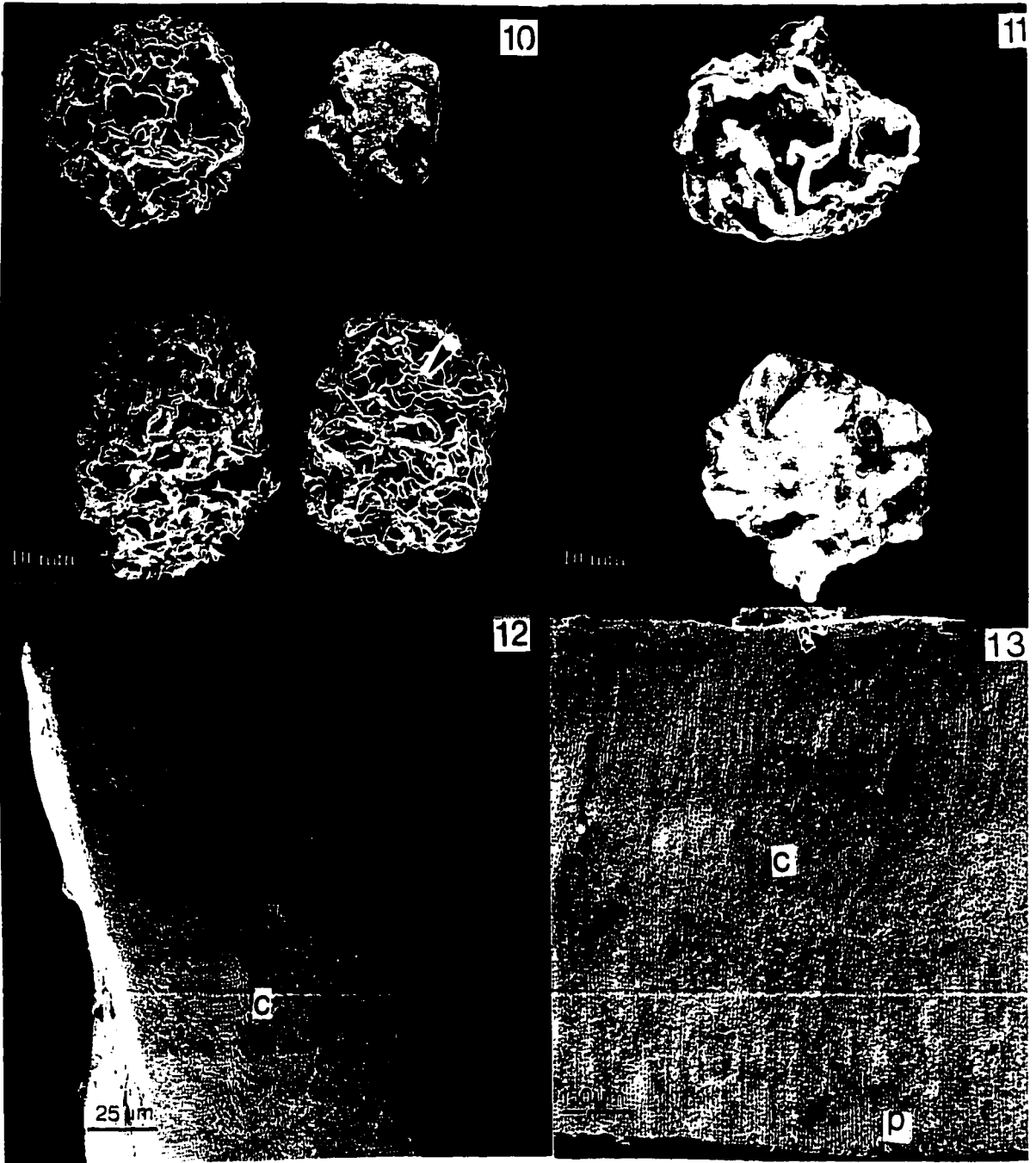
**Figs. 10-13. Holotype of *L. veleroae*: variability in morphology and anatomy [LAM 00357].**

**Fig. 10. Holotype material showing two growth-forms: densely branched foliose plants (both at bottom and top left) and an encrusting plant (upper right). The lower right plant has both foliose branches (arrow) and ridges on the same plant.**

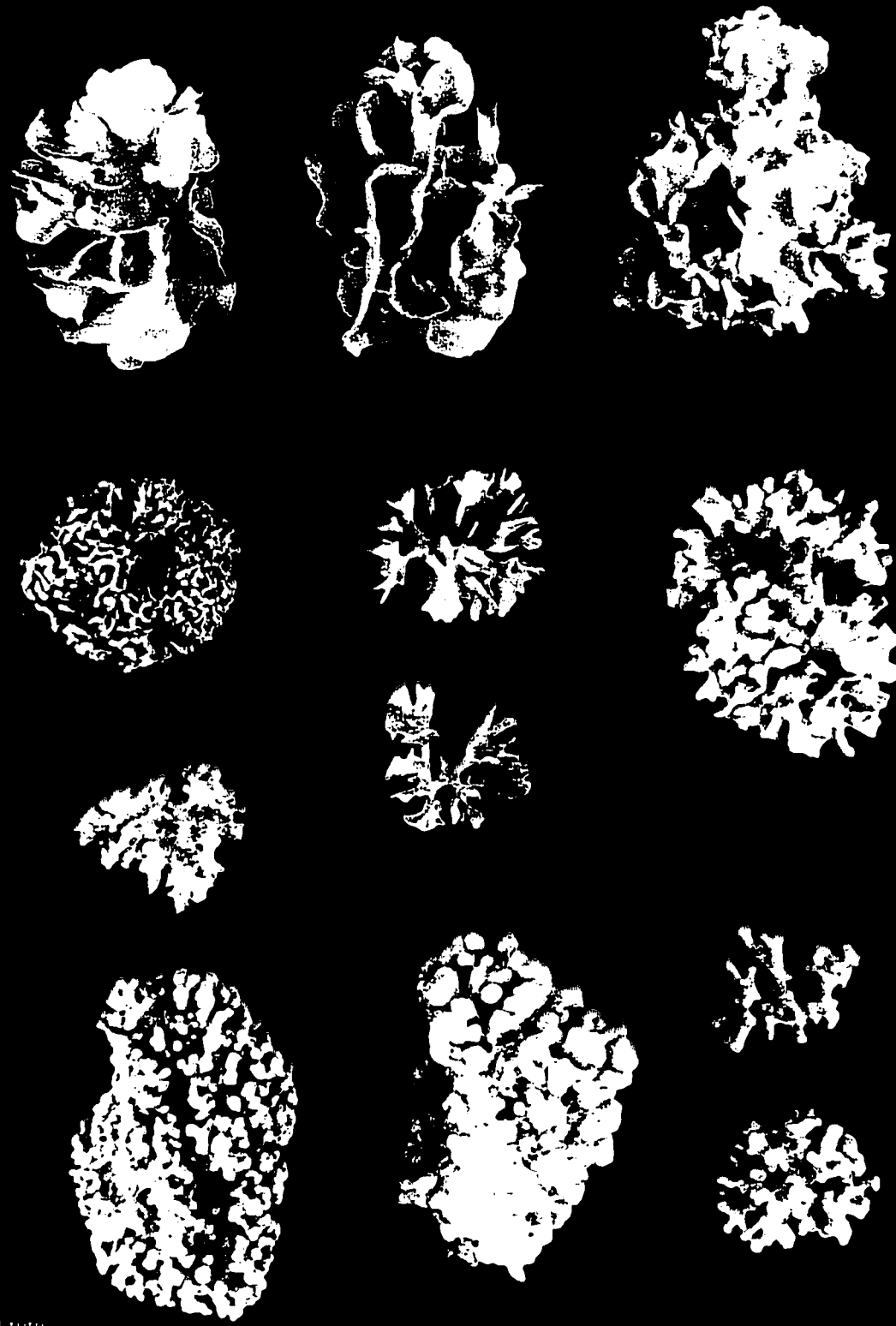
**Fig. 11. Part of the holotype with foliose (upper side) and encrusting (lower side) growth-form in the same plant.**

**Fig. 12. Apical portion of a longitudinal fracture showing that the peripheral region is composed of only one core of filaments (c).**

**Fig. 13. Longitudinal fracture with a core of filaments (c) and peripheral region (p).**



**Figs. 14.** Variability in growth-forms represented in recent collections of *L. margaritae* top row show the range in foliose growth-form [FBCS 5317 left, FBCS 5221 at center and FBCS 5239 at right]. Middle rows show transitional forms with foliose bases and fruticose branches (two at the center FBCS 5345 and the second at the left FBCS 5302) and fruticose bases with foliose tips (like the first in the left FBCS5082 and the right; FBCS 5314). The lower row shows how this species can range from fruticose [FBCS5204] to lumpy [FBCS 5216] and warty [FBCS 5273]



10 mm

**Figs. 15-16. *L. margaritae*: vegetative anatomy.**

**Fig. 15. Longitudinal section of thallus showing a fructicose (fr) branch that becomes foliose (fl) [FBCS 5345].**

**Fig. 16. Longitudinal section of a foliose (fl) branch that becomes fructicose (fr) [FBCS 5098]**

15

16

fr ▶

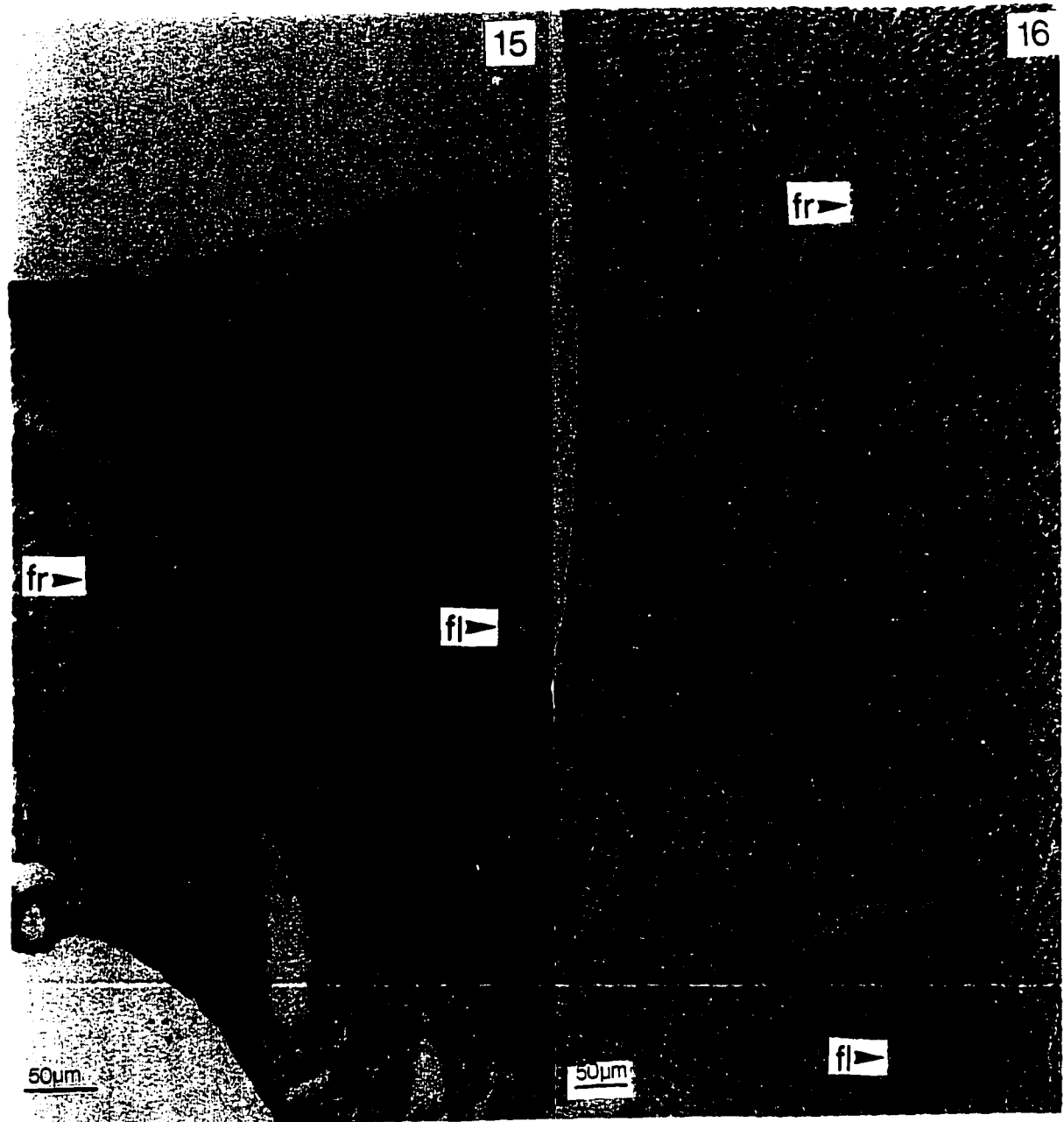
fr ▶

fl ▶

50µm

50µm

fl ▶



**Figs. 17-22. *L. margaritae*: anatomy of tetrasporangial conceptacles.**

**Fig. 17. Tetrasporangial conceptacle with a central columella (C) [FBCS 5238].**

**Fig. 18. Tetrasporangial conceptacle with senescent cells originally involved in roof formation (arrow) associated with the columella (C) in the process of pore (p) formation [FBCS 5279].**

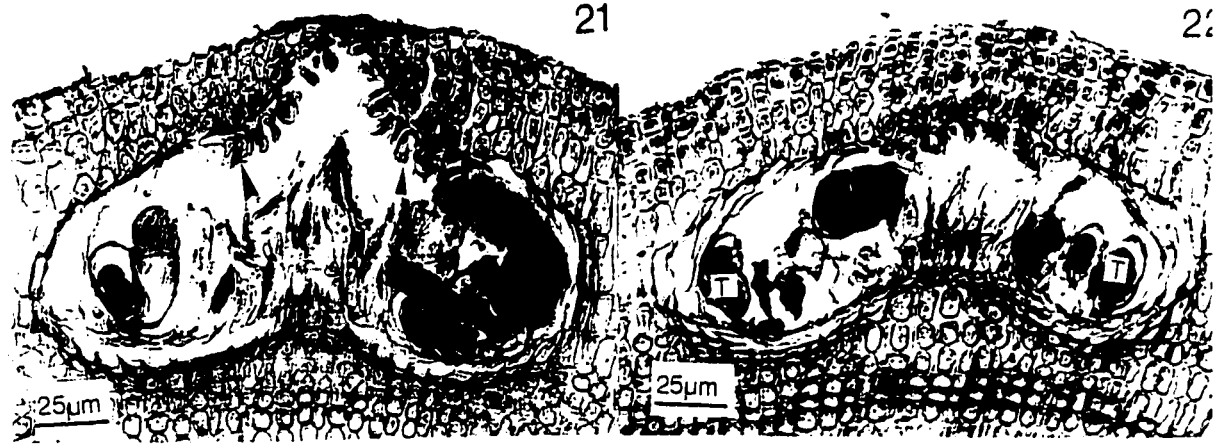
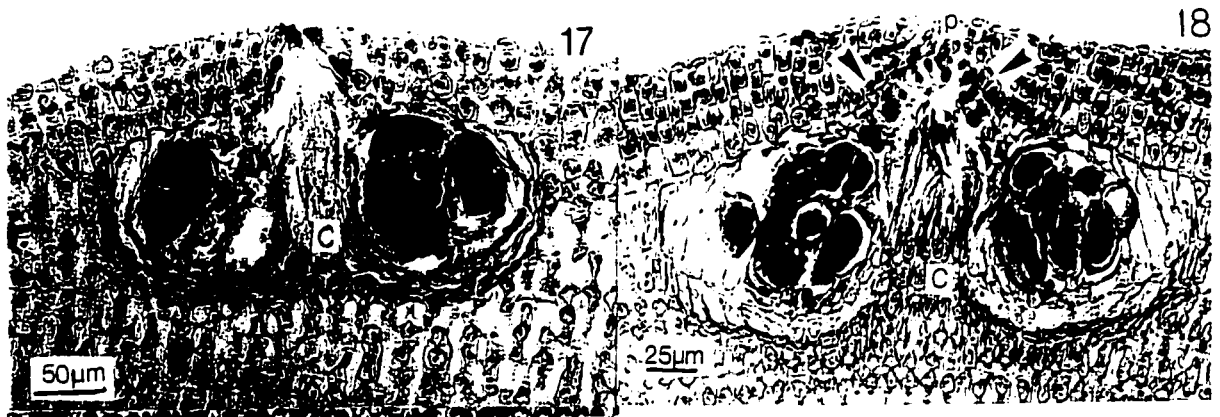
**Fig. 19. Young tetrasporangial conceptacles showing the close relationship (arrow) between the columella (C) and senescent cells (S) [FBCS 5473].**

**Fig. 20. Young tetrasporangial conceptacle with senescent cells (arrow) over the entire roof [FBCS 5280].**

**Fig. 21. Mature tetrasporangial conceptacle showing the senescent cells (arrow) spreading all over the roof [FBCS 5239].**

**Fig. 22. Young tetrasporangial conceptacle with young tetrasporocytes (T) [FBCS 5274].**





**Figs.23-25. *L. margaritae*: gametangial conceptacles.**

**Fig.23. Male conceptacle with simple spermatia (arrows) [FBCS 5272].**

**Fig.24. Female conceptacle [FBCS 5088].**

**Fig.25. Carposporangial conceptacle with fusion disc (fd), gonimoblast filaments (g) and carpospores (C) [FBCS 5088].**

