Bulletin British Museum (Natural History)

Botany Series

VOLUME 22 NUMBER 1 25 JUNE 1992

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology.

The Botany Series is edited in the Museum's Department of Botany

---

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

A volume contains about 160 pages, made up by two numbers: published Spring and Autumn. Subscriptions may be placed for one or more of the series on an Annual basis. Individual numbers and back numbers can be purchased and a Bulletin catalogue, by series, is available. Orders and enquiries should be sent to:

Intercept Ltd.
P.O. Box 716
Andover
Hampshire SP10 1YG

Telephone: (0264) 334748
Fax: (0264) 334058

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Bot.)

ISSN 0068-2292

Botany Series
Vol. 22, No. 1, pp. 1–108

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 25 June 1992

Typeset by Ann Buchan (Typesetters), Middlesex
Printed in Great Britain by The Alden Press, Oxford

Bull. Br. Mus. nat. Hist. (Bot.) **22**(1): 1–107 Issued 25 June 1992

An account of southern Australian species of *Lithophyllum* (Corallinaceae, Rhodophyta)

WM. J. WOELKERLING & STUART J. CAMPBELL

Department of Botany, La Trobe University, Bundoora, Victoria, Australia 3083

CONTENTS

Synopsis. The Lithophylloideae (Corallinaceae, Rhodophyta) is represented in southern Australia by at least seven species, all belonging to the genus *Lithophyllum* (syn. *Dermatolithon, Titanoderma*). *Lithophyllumcorallinae* and *L. pustulatum* have been reported from this region previously, *L. bermudense* and *L. prototypum* are newly recorded, and *L. chamberlainianum, L. irvineanum*, and *L. johansenii*are newly described. Descriptions and detailed morphological/anatomical accounts are provided for each species along with information on etymology, nomenclature and synonymy, collections examined (including all relevant types), distribution and ecography, infraspecific taxonomy, and species relationships. Two further southern Australian collections, possibly representing additional species, are considered briefly.

Twelve additional entities have been recorded from southern Australia under the generic name *Lithophyllum. L. darwinii* and *L. okamurai* f. *contigua* are treated as taxa inquirendae because their type specimens cannot be found; *L. amplexifrons, L. hyperellum, L. mediocre* f. *tasmanica, L. patena, L. rupestre, L. tasmanicum, L. verrucosum*, and *L. zostericolum* f. *tasmanicum* have been excluded from *Lithophyllum* on the basis of type specimen examinations; and records of *L. tortuosum* and *L. tumidulum* have been found to be spurious.

As a prelude to the taxonomic accounts, a brief historical introduction is provided along with basic data on general morphological/anatomical attributes of species of *Lithophyllum*, a detailed analysis of diagnostic and ancillary characters used in species delimitation/identification, comments on specific and infraspecific delimitation, and dichotomous and tabular keys to species. Many of the over 80 characters used previously to delimit/identify species appear to have little or no diagnostic value for species occurring in southern Australia. Results from this study have led to the conclusion that species can be delimited mainly with qualitative characters, especially those associated with tetrasporangial/bisporangial conceptacle structure.

Brief concluding remarks, acknowledgments, and references follow the taxonomic accounts, and an index to taxa also is included.

INTRODUCTION

Published information on Holocene representatives of the subfamily Lithophylloideae (Corallinaceae, Rhodophyta) for southern Australia has been limited almost entirely to sporadic records of occurrence which have not been verified in a modern context (e.g. see Harvey, 1849, 1863; Rosanoff, 1866; Reinbold, 1898; Lucas, 1912; Printz, 1929; Lucas & Perrin, 1947; Guiler, 1952 et seq.; Cribb, 1954; Bennett & Pope, 1960; for general historical aspects of marine phycology for this region see Ducker, 1990 and Womersley, 1984).

In a mondial monograph of nongeniculate coralline genera, Woelkerling (1988) recognized four genera of Lithophylloideae: *Ezo* Adey, Masaki & Akioka (1974), with one species known only from Japan; *Tenarea* Bory (1832), with one species known only from the eastern Mediterranean; *Titanoderma* Nägeli (1858), for which at least 67 species and infraspecific taxa have been described; and *Lithophyllum* Philippi (1837), to which at least 661 species and infraspecific taxa have been ascribed. Subsequently Campbell & Woelkerling (1990) concluded that *Titanoderma* was not generically distinct from *Lithophyllum*, and they combined the two under the name *Lithophyllum*, thereby reducing the number of recognized genera of Lithophylloideae (sensu Woelkerling, 1988) to three. The status of *Goniolithon* Foslie (1898a) remains uncertain (see Woelkerling 1988: 216). Features collectively considered diagnostic of *Lithophyllum* sensu Campbell & Woelkerling (1990) are summarized in Table 1.

A world-wide monograph of *Lithophyllum* never has been published, and most species remain very poorly understood. Moreover, a number of species now referable to *Lithophyllum* have at various times in the recent pastbeen treated under *Titanoderma*, its homotypic synonym *Dermatolithon* Foslie (1898b), and/or *Tenarea*. Background information on the nomenclature and application of these four names has been summarized by Woelkerling (1983, 1988) and Woelkerling et al. (1985).

Table 1 Characters which collectively delimit *Lithophyllum* from other genera of Corallinaceae (Rhodophyta)

1. Thallus nongeniculate.
2. Crustose portions of thallus with a dorsiventral internal organization.
3. Haustoria absent.
4. Cells of contiguous vegetative filaments commonly joined by secondary pit-connections.
5. Fusions between vegetative cells absent or very rare.
6. Tetrasporangial/bisporangial conceptacles uniporate.
7. Tetrasporangia/bisporangia lacking apical plugs.

The keys of Abbott & Hollenberg (1976), Adey et al. (1982), Chamberlain (1991), Dawson (1955, 1960), Hamel & Lemoine (1953), Kylin (1944) Lemoine (1939), Masaki (1968), Mason (1953), Newton (1931), Okamura (1936) and Taylor (1945; 1957; 1960) provide some insight as to which characters have been used to delimit/identify species within the *Lithophyllum/Titanoderma/Dermatolithon* complex. Dawson (1955) and Woelkerling (1988: 105) have noted, however, that little is known about the stability of characters which supposedly distinguish the described species, and for many only scant data are available. Most species within the complex have been delimited on presumed differences in thallus appearance, vegetative anatomy, and conceptacle size. Chamberlain (1986), however, concluded from a study of several European species (which she referred to *Titanoderma*) that those species could not be identified solely on differences in cell size, cell number, and conceptacle size but certain features associated with conceptacle morphology and anatomy could be used. The situation for species occurring in southern Australia has not been assessed.

Since 1976, the first author has been engaged in a long-term research program on the taxonomy of nongeniculate Corallinaceae, one objective of which has been to produce monographic accounts of genera occurring in southern Australia (i.e. from Cape Naturaliste, Western Australia to the Victoria–New South Wales border and including Tasmania—see Womersley 1984: 13). In 1976, relatively few herbarium collections from this region were available, and nearly all were dried and unidentified, even at generic level. Consequently, an extensive program of field sampling was initiated, which to date has resulted in the acquisition of nearly 6000 new collections of plants comprising at least 35000 individuals (or over 500,000 if small, epiphytic individuals are counted). Preliminary analyses of these collections have revealed that plants of *Lithophyllum* grow throughout southern Australia (plants referable to *Ezo* and *Tenarea* have not been found). The present paper contains an account of the species found, an analysis of basicmorphological and anatomical features and their potential diagnostic significance, relevant historical data, and dichotomous and tabular keys.

This account constitutes a base-line study of southern Australian species of *Lithophyllum*. The area surveyed (which also includes the west coast of Western Australia as far north as Kalbarri) encompasses over 15000 km of coast of which about 200 localities, each less than 1 km long, have been visited. In other words, less than 1.3% of the region has been sampled, a minuscule proportion, even considering that long stretches of coast are inaccessible from land. Moreover, most localities have been sampled on only one occasion, collecting has been almost entirely restricted to depths of 10 m or less, and most specimens have been gathered with the disadvantage of not being able to recognize generic affinities in the field. It seems likely, therefore, that some species will have escaped detection.

MATERIALS AND METHODS

Most data were obtained from specimens gathered from a variety of intertidal and subtidal habitats in southern Australia and as far north as Kalbarri on the west coast (Maps 1–4). Collections are housed at LTB (Department of Botany, La Trobe University, Bundoora, Victoria, Australia) but will be transferred permanently to MEL. All species collected north of Cape Naturaliste , Western Australia also occur along the southern coast. Intensity of sampling at particular localities varied from thorough intertidal and subtidal surveys to the casual collection of a few plants. Field, herbarium processing and microtechnique procedures used at LTB are explained in detail by Woelkerling (1988). Collections housed at AD (State Herbarium of South Australia, Adelaide, South Australia), BM (British Museum (Natural History), London, England), CN (Laboratoire d'Algologie fondamentale et appliquée, Faculté des Sciences, Universitéde Caen, Caen, France), L (Rijksherbarium, Leiden, Netherlands), LD (Botanical Museum, The University, Lund, Sweden), MEL (National Herbarium of Victoria, Royal Botanic Gardens, South Yarra, Victoria, Australia), TCD (School of Botany, Trinity College, Dublin, Ireland) and TRH (Department of Botany, Museum of Natural History and Archaeology, University of Trondheim, Trondheim, Norway) also have been surveyed.

Some species of *Lithophyllum* may occur in considerable numbers on various substrates (most commonly other algae). Such species often grow intermixed with other nongeniculate corallines. In such collections, the various species are extremely difficult or impossible to separate from one another for purposes of herbarium processing. Consequently some LTB collections contain more than one species, and identification has been effected principally from permanent slides filed with each herbarium collection. In some mixed collections, plants of *Lithophyllum* clearly predominate, but in others only a few individuals may be present. Care must therefore be exercised not to assume that herbarium collections are monospecific or even contain a predominance of *Lithophyllum* plants. Chamberlain (1983) has found a similar situation with other nongeniculate Corallinaceae.

Herbarium abbreviations are taken from Holmgren et al. (1990), and except where noted, morphological and anatomical terminology follows Woelkerling (1988).

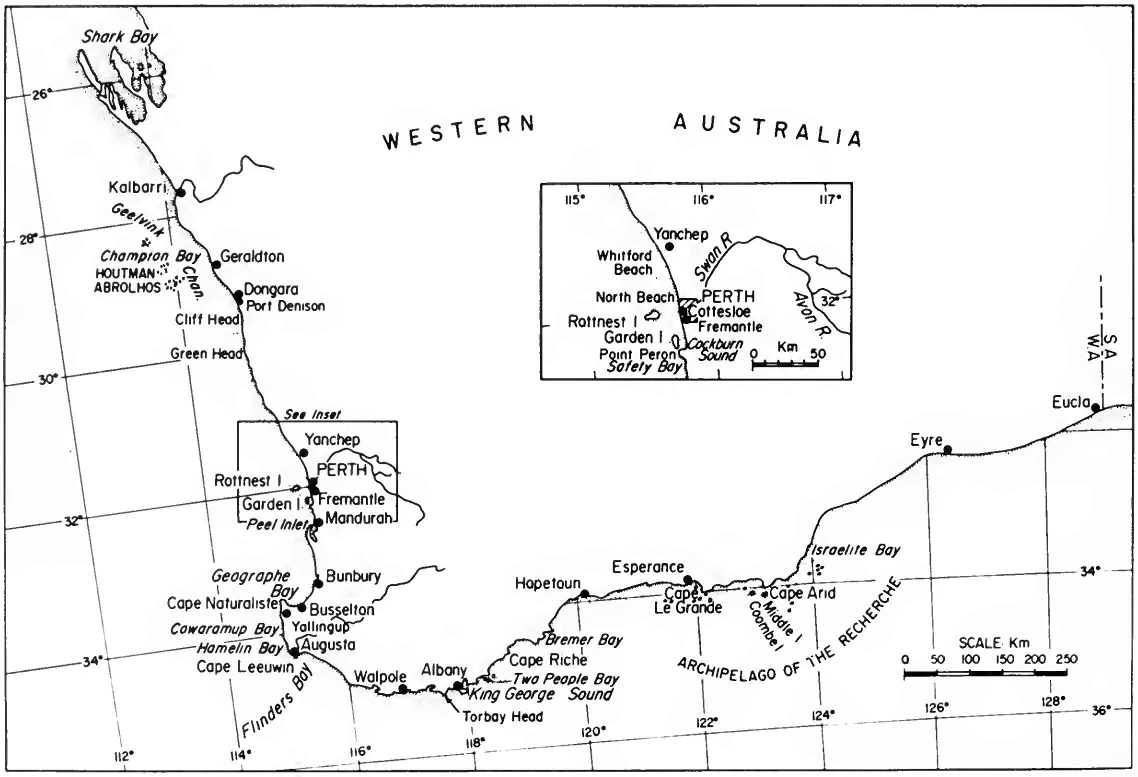
GENERAL MORPHOLOGICAL AND ANATOMICAL FEATURES

Vegetative Features

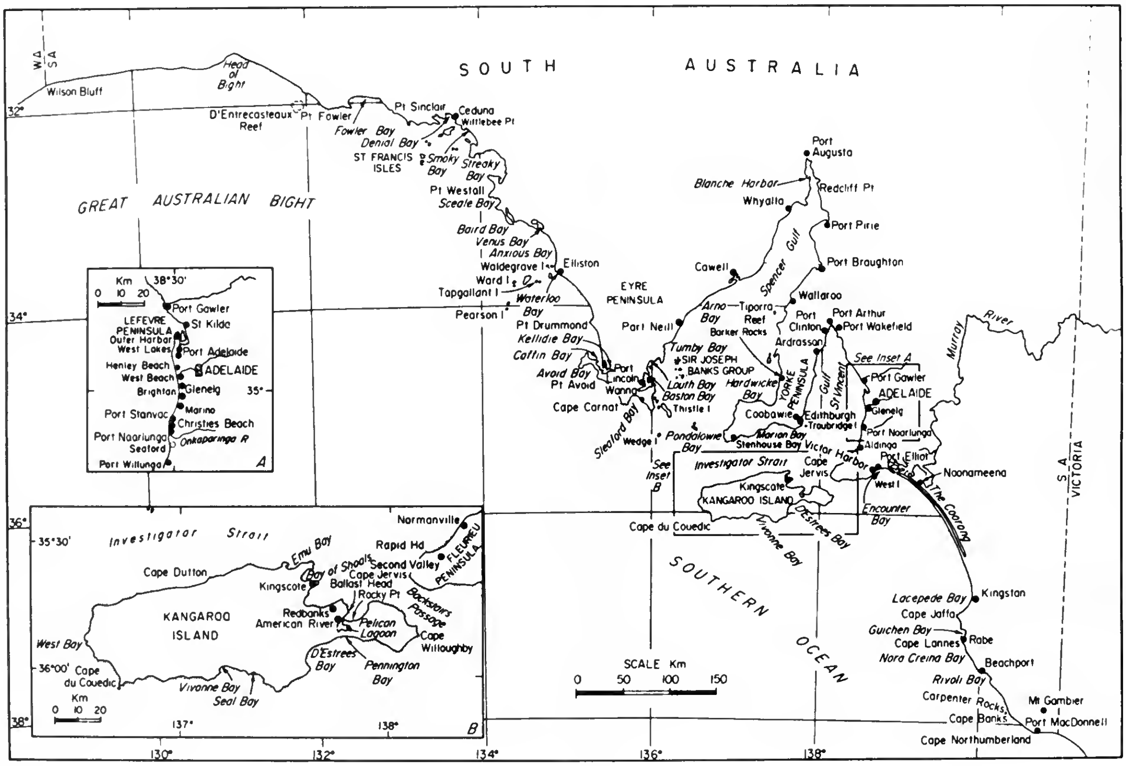
Plants of *Lithophyllum* are calcified and, on a world scale, range in form from crustose , flattened thalli less than 5mm in greatest dimension to thalli which are composed largely of branched, cylindrical to compressed, protuberant or coalescent branches or ridged, interlocked lamellae which canexceed 20cm in length, breadth or height. Thallus form varies considerably (e.g. Figs 4, 5, 16, 51), and the shape of individual thalli is commonly influenced by the substrate. Southern Australian plants have been found growing on other algae, angiosperms (seagrasses), molluscs, echinoderms and rock. Plants may grow on stationary substrates (e.g. rock), moving substrates (e.g. living molluscs), shifting substrates (e.g. small stones, dead mollusc shells), or are unattached. Because of variability in external appearance, it is usually extremely difficult to recognize plants at species or even genus level in the field.

Various terms have been used to describe external form and appearance of plants of crustose to protuberant morphology (see Woelkerling & Irvine 1988: 5–7 for a summary), and although Bosence (1983) has devised a system for characterizing growth-forms of unattached plants, no standardized system has emerged for attached plants. Amongst species of *Lithophyllum* in southern Australia, growth-form and appearance of crustose to protuberant plants are largely governed by the presence or absence of various types of branches or other outgrowths, and the following six categories have been devised to characterize these:

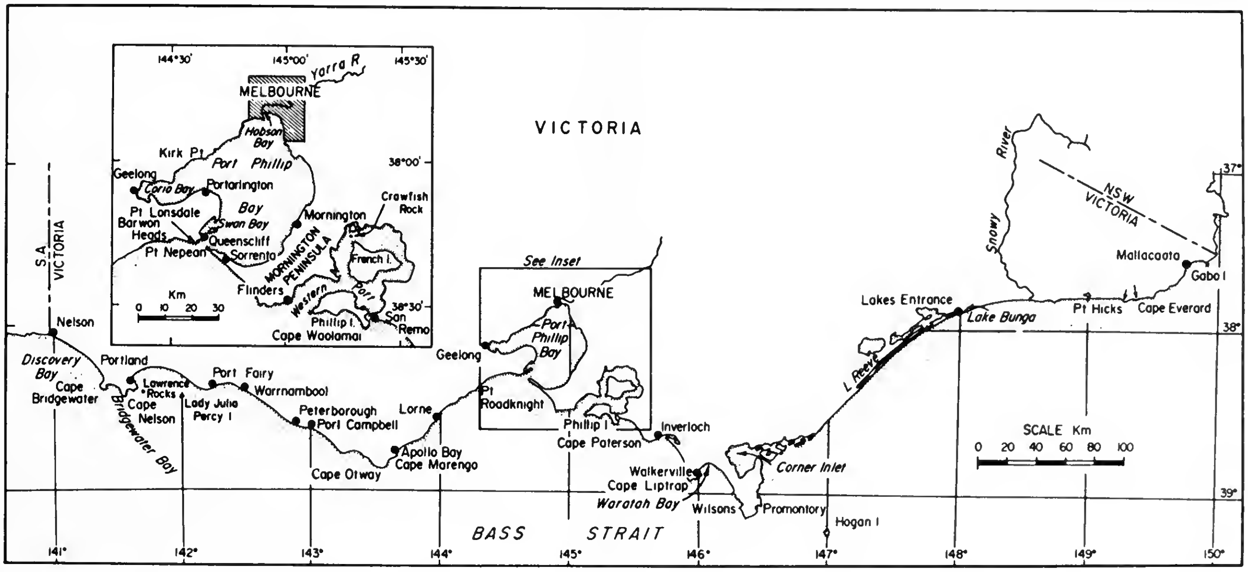
1. encrusting (complanate)—crustose, flattened with a more or less smooth surface devoid of lumps, furrows, outgrowths or branches (e.g. Figs 4B, 33A).
2. layered—crustose with flattened, more or less horizontally expanded (applanate) branches which can occur in successive vertical layers (e.g. Fig. 44A). Such branches may or may not give the thallus a conspicuous terraced appearance in surface view.
3. warty—with wart-like (verrucose) or tubercle-like (tuberculate) outgrowths forming small, unbranched bumps or humps (e.g. Fig. 23D). Such outgrowths form an intergrading continuum with protuberant branches (#5 below) (e.g. see Figs 5C, 5D); in general warty may be thought of as encompassing small (<3 mm tall) branches or outgrowths.
4. protuberant—with ascending, cylindrical to compressed



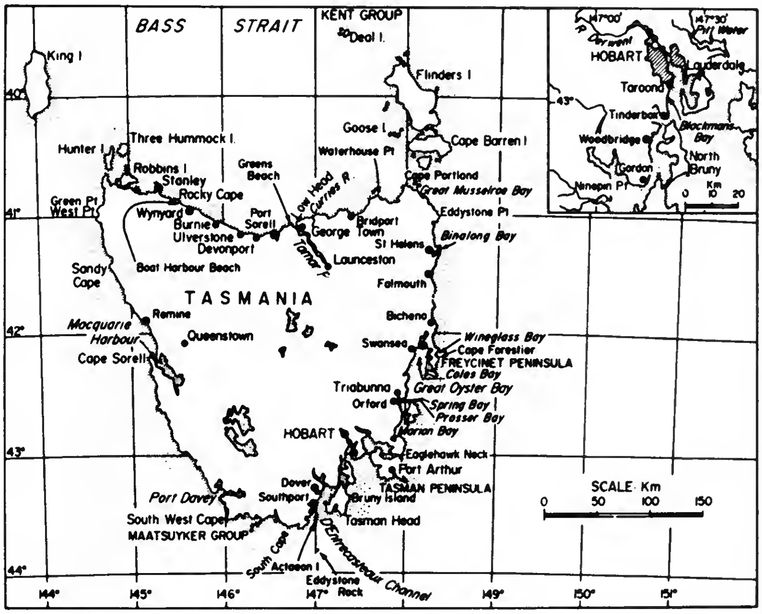
Map 1 Locality map: Western Australia. Reproduced from Womersley 1984 with permission of The Flora and Fauna of South Australia Handbooks Committee.



Map 2 Locality map: South Australia. Reproduced from Womersley 1984 with permission of The Flora and Fauna of South Australia Handbooks Committee.



Map 3 Locality map: Victoria. Reproduced from Womersley 1984 with permission of The Flora and Fauna of South Australia Handbooks Committee.



Map 4 Locality map: Tasmania. Reproduced from Womersley 1984 with permission of The Flora and Fauna of South Australia Handbooks Committee.

branches which may be simple or branched and free from one another or laterally coherent to varying degrees (e.g. Figs 5A, 5C, 23F).

5. lumpy—with swollen lumps and furrows; these may be small or large (e.g. Figs 4E, 5D), are usually crowded together, and can sometimes give the thallus a brain-like appearance. Thalli in which the tips of closely crowded protuberant branches have become abraded may look similar (e.g. Fig. 5C).
6. coalescent—with more or less vertical outgrowths of variable shape formed by coalesing, ascending, applanate branches (e.g. Figs 5E, 9).

In some species (e.g. *L. prototypum*), thallus appearance is more or less uniform, but in others (e.g. *L. bermudense*) all of the above growth-forms may occur. Thus differences in growth-form are of limited taxonomic significance. The above list applies to southern Australian species of *Lithophyllum*; other categories such as interlocking lamellate branches (see Woelkerling 1988, figs 65, 66) occur elsewhere, and a broader spectrum of crustose to protuberant corallines will have to be examined before a comprehensive, standardized system for characterizing growth-form and appearance can be produced.

All species of *Lithophyllum* are pseudoparenchymatous. Crustose portions of thalli that have a dorsiventral organization are either entirelydimerous or partly dimerous and partly monomerous (e.g. Figs 7, 25). Dimerous construction (Woelkerling & Irvine 1988) involves two distinct, successively produced groups of filaments termed primigenous and postigenous filaments (Figs 7A–7C). Primigenous filament form a unistratose layer which is ventralmost in a thallus or branch (Figs 7C, 25F, 53B). They may be composed of palisade cells [i.e. elongated cells in which the end walls (those possessing primary pit-connections) are much longer (usually 2–4 times) than the side walls and in which cell length is substantially less than cell height] (e.g. Figs 25A, 53A, 53C), or of nonpalisade cells [i.e. cells in which the side walls are usually less than twice as long as the end walls] (e.g. Fig. 25E) or of both (e.g. Fig. 37C).

Postigenous filaments arise from primigenous filaments at right angles. Sometimes postigenous filaments are unicellular, consisting only of epithallial cells (e.g. Figs 44C, 53A). In all coralline algae, epithallialcells occur only at the thallus surface; they normally are smaller in size than other cells, commonly have noncalcified outer cell walls, and are thought (see Johansen 1981: 30–31) to have specialized functions. Postigenous filaments may also be multicellular and include one or occasionally more terminal epithallial cells, a subterminal initial, and one or more additional subtending cells which arise inwardly from divisions of subterminal initials (e.g. Figs 7A, 7B, 25F, 53E). In some plants, extensive postigenous development occurs, and the thallus becomes increasingly thick (e.g. Figs 11B, 30C, 58C). Lemoine (1971: 551–552, as *Dermatolithon*), whose use of the term perithallial is equivalent to postigenous, has summarized literature records on the extent of postigenous development for a number of species. With the exceptions of some plants of *L. bermudense* and *L. corallinae*, crustose portions of southern Australian plants are entirely dimerous. All applanate branches are also dimerous.

Athanasiadis (1989) described a type of postigenous development involving coordinated divisions of groups of initials in Aegean plants of *Lithophyllum cystoseirae* (Hauck) Heydrich (as *Titanoderma*). This results in the production of successive horizontal rows of postigenous cells, giving the appearance of periclinal banding within the thallus (see Athanasiadis, 1989, fig. 9). This type of development also appears to occur in some but not all plants of *Lithophyllum bermudense* (Fig. 7C) and *L. pustulatum* (Fig. 53E).

Monomerous construction involves a single system of repeatedly branched filaments in which some derivatives contribute to a ventral or central core while other derivatives curve outwards, collectively forming a more peripheral region (Figs 7D, 8C, 25C). In contrast to crustose portions, protuberant branches are usually monomerous and radial (Figs 8E, 26A).

In some plants of *L. bermudense* and *L. corallinae*, monomerous as well as dimerous construction can occur in crustose portions of the same plant (Figs 7D, 8C, 25C). Monomerous growth appears to be secondary and arises when groups of postigenous filaments become orientated more or less parallel to the thallus surface, thereby forming a core. Some derivatives or the distal parts of core filaments again curve upwards towards the thallus surface. Primigenous filaments composed of palisade cells do not occur in monomerous portions of thalli.

Protuberances also are monomerous (Figs 8E, 26A); a central core of filaments occurs, and distal parts of core filaments or their derivatives curve outwards to form a peripheral region where each filament usually terminates in an epithallial cell at the thallus surface.

Throughout the thallus, cells of contiguous filaments are linked by secondary pit-connections (e.g. Figs 8F, 37F, 54). In addition, secondary pit-connections can occur between successive palisade cells of the same primigenous filament (Figs 26B, 44D), and in plants of *L. prototypum*, secondary pit-connections also can occur between cells of filaments belonging to two vertically contiguous branches (Fig. 44F). To distinguish between secondary pit-connections involving cells of the same filament or cells of adjacent filaments in the same applanate branch from those involving cells of noncontiguous filaments belonging to different branches, the terms contiguous and adjunctive have been adopted for the two respective types. This terminology parallels that used by Turner & Woelkerling (1982) for describing cell fusions. Secondary pit-connections have not been found between adjacent epithallial cells, and cell fusions have not been found during this study. Suneson (1943: 38, 44, 51, fig 20D), however, recorded cell fusions in two species of *Lithophyllum*, but he described these as very rare. Trichocytes have been detected in *L. corallinae* and *L. prototypum* (Figs 29B, 44B, 45A); they have also been found in European plants (see Lemoine 1971: 553 for records) and in specimens from the Caspian Sea (Woelkerling 1986).

Reproduction

Gametangia and sporangia develop within conceptacles (specialized structures consisting of a chamber, a floor, and a roof; e.g. Figs 55, 59, 60). The sexual cycle (Fig. 1), which has yet to be confirmed experimentally in *Lithophyllum*, presumably involves three successive phases:

(1) haploid, holotrophic, gametangial plants;
(2) a diploid carposporophyte (e.g. Figs 15B, 15D, 21F,

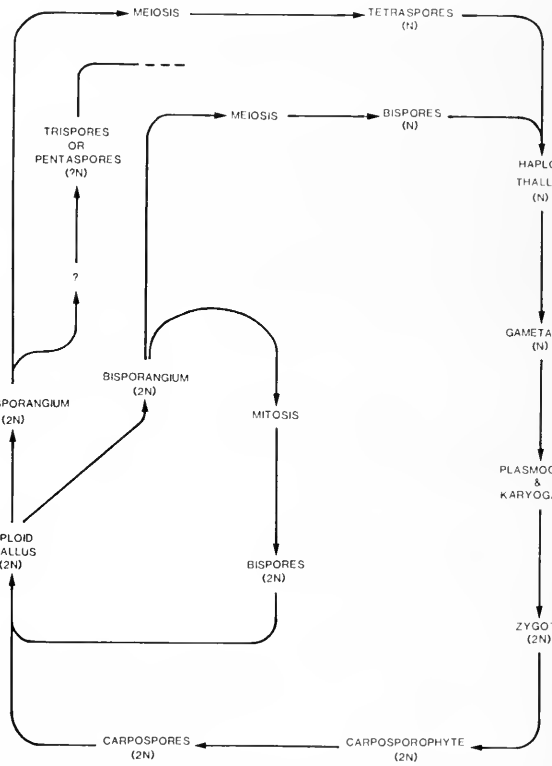


Fig. 1 Diagram of presumed life history of species of *Lithophyllum* based on hitherto published information. Details for the vast majority of included species are incomplete; the cytology and fate of trispores and pentaspores is unknown, and whether bispores are haploid or diploid is also unknown in nearly all species.

32C, 60C) of markedly different morphology which develops within female/carposporangial conceptacle after karyogamy, presumably is heterotrophic, and produces diploid carposporangia;

(3) a diploid, holotrophic tetrasporophyte (or possibly a bisporophyte; see below) which is morphologically and anatomically concordant with gametangial plants and in which meiosis presumably occurs during tetraspore (or sometimes bispore) formation.

In most species, male, female and/or carposporophytic plants have not been recorded; a summary of data on southern Australian plants is provided in Table 2. Where known, spermatangia (male gametes) and carpogonia (female gametes) develop in uniporate conceptacles which may be produced on the same, or in most species, on separate plants. Spermatangia are unbranched, arise only from the floors of conceptacle chambers (Figs 13A, 13B, 20, 31A, 31B) and are eventually released from the conceptacle. Carpogonia, which are never released, terminate several-celled branches (e.g. Figs 14B, 21C, 31D, 60A). Within most conceptacles, only carpogonia situated more or less beneath the pore canal reach full maturity and have elongated trichogynes (e.g. Figs 14B, 21C). After presumed karyogamy, which always occurs within female/carposporangial conceptacles, a carposporophyte comprising a large central fusion cell and short gonimoblast filaments bearing terminal carposporangia develops (e.g. Figs 21F, 32C, 60C). Eventually, carpospores are released and develop into tetrasporophytes (i.e. plants producing tetrasporangia).

Tetrasporangia are formed in uniporate conceptacles (e.g. Figs 12, 18, 46) which normally do not occur on the same plants as gametangial conceptacles.Tetrasporangia may be scattered across the conceptacle chamber floor (e.g. Fig. 11E), or they may occur around the periphery of the conceptacle chamber floor, with the central region occupied by a tuft of sterile cells or filaments, commonly called a columella (e.g. Fig. 12E). In older conceptacles, cells of the columella often appear senescent or completely degenerate (e.g. Figs 12D, 28B). Each sporangium contains four zonately arranged spores, presumably formed by meiosis. [Meiotic formation of tetraspores has yet to be confirmed cytologically; in some regions of the world, gametangial plants are unknown, and it is possible that tetraspores form apomeiotically and give rise directly to new tetrasporic individuals.] Sporangial plugs, such as those found in *Choreonema* (Woelkerling, 1987) do not occur. After release, meiotically formed tetraspores germinate and presumably give rise to new gametangial plants.

Some species of *Lithophyllum*, including six found in southern Australia (Table 2), also produce conceptacles containing bisporangia (e.g. Figs 19B, 29C, 35B). Although bisporangial conceptacles are morphologically and anatomically concordant with tetrasporangial conceptacles of the same species, bispores do not necessarily function like tetraspores (i.e. give rise to gametangial plants). In *L. corallinae* (P.-L. & H.-M. Crouan) Heydrich, for example, Suneson (1950) concluded that binucleate bispores give rise to gametangial plants whereas uninucleate bispores give rise to new bisporangial plants. Subsequently, Suneson (1982) demonstrated in culture that uninucleate bispores of *L. pustulatum* [as *Dermatolithon litorale* (Suneson) Hamel & Lemoine; see Chamberlain 1991: 29 concerning the identification of Suneson's material] give rise to new bisporangial plants. Thus bisporangial plants producing binucleate bispores form part of a sexual cycle whereas those with uninucleate bispores form part of an apomictic (asexual) cycle (Fig. 1). Chamberlain (1991) reported that most species she included in *Titanoderma* reproduced in British waters exclusively by means of uninucleate bispores and were presumably apomeiotic.

Suneson (1943: 41, figs 23A, 23B) also recorded aberrant bisporangia (e.g. bispores containing 3 nuclei) and a trisporangium in *Lithophyllum pustulatum*. Conceptacles containing both bisporangia and tetrasporangia have been found in '*Dermatolithon nodulosum*' Chamberlain (1965: 216, fig. 65), and conceptacles with mature bisporangia and carpogonia were reported by Suneson (1943: 39) in *Lithophyllum litorale* Suneson (= *L. pustulatum*). In southern Australia, trisporangia have been found mixed with tetrasporangia in *L. corallinae* (Fig. 30A) and *L. pustulatum* (Fig. 58A) and pentasporangia have been found mixed with tetrasporangia and bisporangia in *L. bermudense* (Fig. 11E). The functional significance of trispores and pentaspores is unknown.

DIAGNOSTIC AND ANCILLARY CHARACTERS

Historical aspects

In the protologue of *Lithophyllum*, Philippi (1837: 388, 389) included four species [*L. decussatum* (Ellis & Solander) Philippi, *L. expansum* Philippi, *L. incrustans* Philippi and *L. lichenoides* Philippi] which were delimited from one another on presumed differences in thallus thickness, relative size, colour, shape, margin morphology and growth-form. An account of Philippi's collections and a historical resumé of the changes in the concept of *Lithophyllum* between 1837 and

Table 2 Summary of reproductive structures found to date in southern Australian collections of *Lithophyllum*. + = known for southern Australian collections; – = not found to date in southern Australian collections.

Species	Spermatangia	Carpogonia	Carposporangia	Bisporangia	Tetrasporangia	Trisporangia
L. bermudense	+	+	+	+	+	–
L. chamberlainianum	+	+	+	+	+	–
L. corallinae	+	+	+	+	+	+
L. irvineanum	–	–	–	+	–	–
L. johansenii	+	–	–	+	+	–
L. prototypum	+	+	+	–	+	–
L. pustulatum	+	+	+	+	+	+

1983 are provided by Woelkerling (1983).

Since 1837, at least 661 specific and infraspecific taxa have been ascribed to *Lithophyllum* (Table 3), and at least 67 to *Dermatolithon* (Table 4), a heterotypic synonym of *Lithophyllum*. Many but not all species ascribed to *Dermatolithon* (and to *Tenarea* and *Titanoderma*, two other genera regarded as heterotypic synonyms) have at some stage also been placed in *Lithophyllum*; thus the total number of entities involved probably does not exceed 700. How many actual species are represented by these entities is uncertain, and how many of those belong to *Lithophyllum* as circumscribed in the present study is unknown.

During the first 53 years (1837–1889) following its establishment, 30 specific and infraspecific taxa were ascribed to *Lithophyllum* (Table 3). During the next 20 years (1890–1909), this number soared to 403; for every one entity of *Lithophyllum* existing in 1889, over 13 existed by 1909! Much of this phenomenal proliferation occurred in the publications of M.H. Foslie, who described far more genera and species of nongeniculate Corallinaceae than any person before or since. In a detailed analysis of Foslie's publications, Woelkerling (1984: 17) concluded that Foslie's concepts of species and infraspecific taxa are often vague, superficial, extremely difficult to evaluate and are attended by numerous uncertainties, confusions, and changes of mind. This conclusion certainly applies to most of the entities Foslie placed in *Lithophyllum*. Indeed, Foslie never provided keys or tables which summarized and/or compared characters he considered to be diagnostic, and statements in a majority of his protologues are so vague or cryptic that it is virtually impossible to determine precisely how species were being delimited.

In the 80 years (1910–1989) after Foslie's death in 1909, the number of entities ascribed to *Lithophyllum* rose from at least 403 to at least 661 (Table 3). Among the new entities were a number of fossil species described by Conti (e.g. 1943; 1946), Ishijima (e.g. 1954), Johnson (e.g. Johnson & Ferris 1948), Lemoine (e.g. 1939), Maslov (e.g. 1956) and Mastrorilli (e.g. 1968). Johnson (1965) has summarized many data on fossil species described up to that time.

Table 3 Numeric summary of taxa ascribed to *Lithophyllum* since 1837. Figures should be regarded as tentative and minimum, as further literature searching may uncover additional taxa.

Time period	No. of new taxa	No. of new combinations	Total	Cumulative total
1837–1839	3	1	4	4
1840–1849	8	–	8	12
1850–1859	1	–	1	13
1860–1869	1	4	5	18
1870–1879	1	1	2	20
1880–1889	6	4	10	30
1890–1899	14	42	56	86
1900–1909	137	80	217	403
1910–1919	8	24	42	45
1920–1929	43	17	60	505
1930–1939	36	8	44	549
1940–1949	29	2	31	580
1950–1959	29	–	29	609
1960–1969	42	1	43	652
1970–1979	5	–	5	657
1980–1989	4	–	4	661

Table 4 Numeric Summary of taxa ascribed to *Dermatolithon* since 1898. Figures should be regarded as tentative and minimum, as further literature searching may uncover additional taxa.

Time period	No. of new taxa	No. of new combinations	Total	Cumulative total
1898–1899	1	4	5	5
1900–1909	12	17	19	24
1910–1919	1	–	1	25
1920–1929	–	2	2	27
1930–1939	–	–	–	27
1940–1949	1	3	4	31
1950–1959	3	7	10	41
1960–1969	6	2	8	49
1970–1979	2	16	18	67
1980–1989	–	–	–	67

Philippi (1837) delimited the first four species of *Lithophyllum* entirely on presumed differences in thallus morphology. Such features have been used extensively ever since (e.g. see Adey et al., 1982). In addition, vegetative cell sizes and arrangements, and thallus thickness have been used widely for both fossil species and nonfossil species (e.g. Hamel & Lemoine, 1953; Lemoine, 1939). Indeed, a survey of publications containing regional accounts and/or protologues of species of *Lithophyllum* has revealed over 80 characters which have been used in species delimitation/identification (Table 5).

In compiling data for Table 5, extensive use has been made of taxonomic keys, since often these are the only sources of information about characters authors consider to be diagnostic. Adey et al. (1982), for example, described two new species of *Lithophyllum*, but neither species accountcontained any statements on diagnostic features or species delimitation. Their key, however, indicates which characters are presumed by the authors to be diagnostic, and how the species were delimited from one another. It could be argued that keys contain many characters which authors do not consider diagnostic (i.e. ancillary characters; see below), but in the absence of clear statements, one has little choice but to assume that all features used in keys are considered to be at least potentially diagnostic. The data in Table 5 are considered in more detail below.

Assessments of characters

Over 250 populations of *Lithophyllum* have been examined in evaluating the diagnostic potential of a range of qualitative (two-state, multistate) and quantitative (measured) characters. Of the 27 quantitative characters studied, 15 pertain to vegetative structures (Table 6) and 12 to reproductive structures (Table 7). The evaluation has led to four conclusions:

(1) most stable, diagnostically important species characters are qualitative;
(2) diagnostically important characters associated with conceptacles are more numerous than those associated with the vegetative thallus;
(3) some characters are generally diagnostic while others become diagnostic only for certain species and then only when used in conjunction with other diagnostic characters;

Table 5 Characters which have been used for species delimitation and identification in *Lithophyllum*. Data based on information in keys and/or species accounts of selected publications (cited after relevant character). Terminology updated where possible to conform to current usage. In cited references, data appear under one or more of the following names: *Lithophyllum, Dermatolithon, Tenarea, Titanoderma*. These names as used by cited authors including species now referable to *Lithophyllum*.

A. General thallus characteristics

1. Surface texture: smooth, irregular, flat, uneven, patched, papillate, mammillate, warty, terraced, tessellate. Adey et al. (1982), Dawson (1955, 1960), Lemoine (1930), Masaki (1968), Taylor (1960). Compare with characters 17, 18 below.
2. Thallus or thallus margin with/without grooves or ridges. Adey & Adey (1973), Garbary (1978), Masaki (1968).
3. Surface finish: dull, glossy, chalky, glazed, shiny. Abbott & Hollenberg (1976), Adey & Adey (1973), Adey et al. (1982), Dawson (1960), Mason (1953).
4. Colour of thallus. Adey & Adey (1973), Adey et al. (1982), Chamberlain (1991), Hamel & Lemoine (1953), Kylin (1944), Mason (1953).
5. Shape of thallus: orbicular, spherical, lamellate, crustaceous. Masaki (1968), Newton (1931).
6. Diameter of crustose thallus. Kylin (1944), Masaki (1968), Newton (1931).
7. Occurrence and extent of superimposed layers of crustose thallus (applanate branches). Dawson (1955; 1960), Lemoine (1917; 1929; 1939; 1971), Masaki (1968).
8. Width of terraces in thalli with superimposed branches. Adey et al. (1982: 35, 36).
9. Degree of vertical separation of successive superimposed branches. Lemoine (1929: 49; 1930: 69).
10. Degree of thallus calcification. Hamel & Lemoine (1953: 64).
11. Degree of thallus fragility. Hamel & Lemoine (1953: 64).

B. Characters pertaining to the substrate

12. Relative adherence to substrate: firmly attached, loosely attached, becoming free, unattached. Dawson (1955: 275; 1960), Hamel & Lemoine (1953: 64), Mason (1953), Taylor (1945).
13. Thallus margin adherent to substrate vs raised or bent back. Hamel & Lemoine (1953).
14. Nature of substrate relationship: epilithic, epiphytic, epizoic. Chamberlain (1991), Dawson (1955; 1960), Hamel & Lemoine (1953), Kylin (1944), Masaki (1968), Newton (1931).
15. Host specificity: growing on particular algal genera or groups of genera. Chamberlain (1991), Dawson (1955), Kylin (1944), Masaki (1968), Taylor (1957; 1960).
16. Host-epiphyte interaction: extent to which epiphyte encases host. Dawson (1955).

C. Morphological characters pertaining to outgrowths and protuberant branches

17. Presence or absence of outgrowths. Hamel & Lemoine (1953: 46). Compare with character 1 above.
18. Shape of outgrowths: mound-like, papillate, elongate, subspherical. Dawson (1960). Compare with character 1 above.
19. Diameter of outgrowths or proliferations. Hamel & Lemoine (1953).
20. Presence or absence of protuberant branches. Abbott & Hollenberg (1976), Adey et al. (1982), Dawson (1960), Hamel & Lemoine (1953), Lawson & John (1987), Masaki (1968), Mason (1953), Newton (1931), Taylor (1945; 1960).
21. Protuberant branches simple vs branched. Dawson (1960), Mason (1953), Taylor (1945).
22. Relative density and distribution of protuberant branches. Dawson (1960), Hamel & Lemoine (1953).
23. Shape of protuberant branches: terete, subcylindrical, flattened, blade-like, plate-like, mushroom-shaped, irregular. Adey et al. (1982), Dawson (1960), Gordon et al. (1976, Hamel & Lemoine (1953), Lawson & John (1987), Mason (1953), Taylor (1945).
24. Shape of branch tips: pointed, rounded, narrow, enlarged, flat-topped, swollen. Abbott & Hollenberg (1976), Dawson (1960), Gordon et al. (1976), Lawson & John (1987), Taylor (1945).
25. Length of protuberant branches. Abbott & Hollenberg (1976), Adey et al. (1982), Dawson (1960), Smith (1944), Taylor (1945).
26. Diameter/thickness of protuberant branches. Dawson (1960), Mason (1953), Taylor (1945).
27. Presence or absence of fused or anastomosed protuberant branches. Dawson (1960), Gordon et al. (1976), Hamel & Lemoine (1953), Mason (1953), Taylor (1945; 1960).
28. Degree of fusion/anastomosing of protuberant branches: lower parts only vs nearly to tips. Taylor (1960).
29. Presence or absence of channels or ridges on flattened protuberant branches. Dawson (1960).

D. General anatomical characteristics

30. Thallus thickness (in µm or mm). Abbott & Hollenberg (1976), Dawson (1955; 1960), Hamel & Lemoine (1953), Kylin (1944), Lemoine (1939), Masaki (1968), Mason (1953), Newton (1931), Taylor (1945; 1957; 1960).
31. Number of layers of cells in thallus. Dawson (1955), Hamel & Lemoine (1953), Taylor (1957).
32. Occurrence and extent of so-called monostromatic margins of crustose thalli (i.e. regions devoid of multicellular postigenous filaments). Dawson (1955; 1960), Hamel & Lemoine (1953), Kylin (1944), Lemoine (1971), Rosenvinge (1917: 268), Suneson (1943: 43, 44).
33. Filament initials (meristem cells): short vs long. Adey & Adey (1973).

E. Characters pertaining to primigenous cells

34. Cell height (commonly reported as length). Dawson (1955, 1960), Hamel & Lemoine (1953), Masaki (1968).
35. Variation in cell height: cells uniformly high vs cells variable in height. Dawson (1955), Masaki (1968).
36. Cell shape: very regular, variable, sinuous or not. Hamel & Lemoine (1953), Lemoine (1929: 48).

F. Characters pertaining to postigenous filaments

37. Presence or absence. Lemoine (1971; 1976).
38. Number of cells. Dawson (1955), Lemoine (1971).
39. Cell length. Dawson (1955), Hamel & Lemoine (1953), Taylor (1945).
40. Cell diameter. Hamel & Lemoine (1953).

G. General characters pertaining to cells and filaments

Note: Characters in this section may overlap some characters listed in sections D, E & F. Because authors involved have used the terms 'hypothallium', 'perithallium' and medulla in differing ways and have applied them to both monomerously and dimerously constructed thalli, care must be taken in interpreting these features. Proper interpretation can only be made on a species by species basis within each publication.

41. Degree of development of 'hypothallium': feeble, well developed, 1/8 or less vs 1/4 or more of thallus thickness. Dawson (1960), Mason (1953), Newton (1931).
42. Presence or absence of coaxial 'hypothallium'. Adey & Adey (1973).
43. Number of cell layers in 'hypothallium'. Adey & Adey (1973), Hamel & Lemoine (1953), Masaki (1968), Mason (1953).
44. Appearance of 'hypothallium': layered, concentric layers, tiers of cells, regular or irregular. Hamel & Lemoine (1953), Lemoine (1939).
45. 'Hypothallial' cell length. Hamel & Lemoine (1953), Lawson & John (1987), Lemoine (1939), Newton (1931).
46. 'Hypothallial' cell diameter. Hamel & Lemoine (1953), Lawson & John (1987), Lemoine (1939), Newton (1931), Taylor (1960).
47. Appearance of 'perithallium': layered, in tiers, a mix of rows and tiers. Adey & Adey (1973), Hamel & Lemoine (1953), Lemoine (1939).
48. 'Perithallial' cell length. Hamel & Lemoine (1953), Lawson & John (1987), Lemoine (1939).
49. 'Perithallial' cell diameter. Hamel & Lemoine (1953), Lawson & John (1987), Lemoine (1939).

50. 'Perithallial' cell length/diameter ratio: 2–10 vs less than 2. Adey & Adey (1973).
51. Arrangement of cells in protuberant branches: in rows or in tiers. Hamel & Lemoine (1953).
52. Length of 'medullary' cells. Taylor (1945).
53. Diameter of 'medullary' cells. Taylor (1945).
54. Presence or absence of alternating wide and narrow zones of 'medullary' cells. Taylor (1945).

H. CHARACTERS PERTAINING TO EPITHALLIAL CELLS AND SECONDARY PIT-CONNECTIONS

55. Epithallial cells: 1 vs several per filament. Adey & Adey (1973).
56. Epithallial cell shape: rectangular, triangular. Dawson (1955; 1960), Masaki (1968).
57. Epithallial cells: degree of periclinal flattening. Dawson (1955; 1960), Masaki (1968).
58. Relative abundance of secondary pit-connections. Hamel & Lemoine (1953).

I. TETRASPORANGIAL/BISPORANGIAL CONCEPTACLES: EXTERNAL CHARACTERS

59. Relative elevation above thallus surface: protruding, convex, elevated, flush, subprominent, depressed, immersed. Chamberlain (1991), Dawson (1955, 1960), Gabrielson et al. (1989), Kylin (1944), Mason (1953), Suneson (1943).
60. Outside diameter of conceptacle. Dawson (1955; 1960).
61. Roof surface: stepped, honeycomb-like. Chamberlain (1986: 195).
62. Size relative to female/carposporangial conceptacles. Dawson (1955).

J. TETRASPORANGIAL/BISPORANGIAL CONCEPTACLES: INTERNAL CHARACTERS

63. Conceptacle chamber diameter. Chamberlain (1991), Dawson (1955; 1960), Gordon et al. (1976), Suneson (1943).
64. Number of intact cells in roof filaments. Chamberlain (1986; 1991).
65. Orientation of epithallial cells: right angles to roof surface or in plane of roof surface. Chamberlain (1986).
66. Presence or absence of a columella. Nichols (1909: 355), Rosenvinge (1917: 268).
67. Relative length of cells in side walls of conceptacle. Suneson (1943).
68. Nature of sporangia present: tetrasporangia only, bisporangia only, both tetrasporangia and bisporangia. Dawson (1955), Rosenvinge (1917: 268), Taylor (1957).
69. Sporangium length. Taylor (1957).
70. Sporangium diameter. Taylor (1957).

K. MALE CONCEPTACLE CHARACTERS

71. Roof curvature: convex vs concave. Dawson (1960).

L. MISCELLANEOUS CONCEPTACLE CHARACTERS

Note: Authors do not specify whether characters apply to all types of conceptacles or only particular sorts.

72. Relative elevation above thallus surface: raised, sunken, etc. (see character 59). Adey & Adey (1973), Dawson (1955), Hamel & Lemoine (1953), Lemoine (1929: 69), Rosenvinge (1917: 268), Taylor (1945).
73. Conceptacle roof shape: concave, flat, convex, subconical, angular, hemisperical, deformed. Dawson (1955), Hamel & Lemoine (1953), Lemoine (1929: 48), Masaki (1968).
74. Shape of conceptacle in vertical section. Adey & Adey (1973).
75. Roof surface: stepped vs not stepped (see character 61). Garbary (1978: 214, 216).
76. Presence or absence of conceptacles buried within thallus. Rosenvinge (1917: 268).
77. Conceptacle height. Dawson (1955).
78. Outside diameter (see character 60). Adey et al. (1982), Taylor (1945).
79. Conceptacle chamber diameter. Kylin (1944), Taylor (1945, as inside diameter).
80. Relative thickness of roof near pore. Kylin (1944).
81. Diameter (inside/outside not specified). Taylor (1945; 1960).

(4) some species can be identified from a single diagnostic character, while the identification of other species involves a combination of diagnostic characters.

Of the 27 quantitative characters examined, only one (tetrasporangial/bisporangial conceptacle chamber diameter —see Table 7) appears to be of diagnostic importance amongst the species studied. Two others (female/carposporangial conceptacle chamber diameter—see Table 7; and primigenous cell height—see Table 6) may have limited diagnostic potential but require further evaluation. It has not been possible to assess fully the diagnostic potential of qualitative characters associated with gametangial conceptaclesbecause male conceptacles are unknown for one southern Australian species and female/carposporangial conceptacles are unknown for two species. Moreover, gametangial conceptacles occur in only a minority of available collections of the other five species. Thus the second of the four conclusions above involves only tetrasporangial/bisporangial conceptacles. Finally, all four conclusions are based on a regional data set involving seven particular species. These conclusions now need to be tested on data sets from different regions and on other groupings of species to determine what modifications are required.

Characters considered diagnostic of southern Australian species

Four characters associated with tetrasporangial/bisporangial conceptacles and three associated with the vegetative thallus have been found useful in delimiting species of *Lithophyllum*. In considering the seven diagnostic characters below, the abbreviation t/b used in headings refers totetrasporangial/ bisporangial conceptacles.

(1) T/b pore canal anatomy

Three distinct sorts of tetrasporangial/bisporangial pore canal anatomy occur. In *L. chamberlainianum* (Fig. 18D), the entire pore canal is completely occluded by a cluster of enlarged, more or less tubular and sometimes clasping or inflexed cells which terminate roof filaments flanking the canal and normally project beyond the surrounding roof surface. In *L. irvineanum* (Fig. 35A) and *L. johansenii* (Figs 39C, 39D), pore canals are completely occluded by 2–4 (as seen in vertical section) enlarged, angular cells which arise laterally from filaments flanking the canal and do not project beyond the surrounding roof surface. In *L. bermudense* (Fig. 10E), *L. corallinae* (Fig. 27E), *L. prototypum* (Fig. 46D), and *L. pustulatum* (Fig. 55E) pore canals may be lined with cells which project somewhat into the pore canal but without completely occluding it. Conceptacles in these species may also have the distal end of the canalcovered by mucilaginous plug-like material (e.g. Fig. 12D), but the entire length of the canal is not blocked by such material.

Differences in pore canal anatomy are readily observable and stable within and between the seven species studied. Indeed, plants of *L. chamberlainianum* are identifiable on the basis of pore canal anatomy alone. As far as can be determined, differences in pore canal anatomy have not been used previously to help delimit species of *Lithophyllum*.

Table 6 A comparative summary of data on measured characters relating to vegetative features in southern Australian specimens of *Lithophyllum*. Extreme values are given in parentheses. Characters not occurring in particular species are listed as 'absent'.

	Specific Epithet						
Character/unit	*bermudense*	*chamberlainianum*	*corallinae*	*irvineanum*	*johansenii*	*prototypum*	*pustulatum*
Thallus breadth (mm)	4–200+	0.05–2.5	10–20+	3–105	30–40	20–50+	6–100
Thallus thickness or height (mm)	0.1–60	0.04–0.5	0.2–1.0 (–3.0)	0.05–1.0	0.2–1.0	0.1–0.9	0.05–2.5
Lumpy outgrowth breadth (mm)	3–20	Absent	1–4	Absent	1–6	1–3	1–10
Protuberant branch length (mm)	5–60	Absent	1–5	Absent	Absent	Absent	Absent
Protuberant branch diameter (mm)	2–28	Absent	0.4–0.6	Absent	Absent	Absent	Absent
Coalescent outgrowth breadth (mm)	2–26	Absent	Absent	Absent	Absent	Absent	Absent
Coalescent outgrowth height (mm)	2–17	Absent	Absent	Absent	Absent	Absent	Absent
Primigenous cell length (μm)	5–18	5–15	5–20	5–12	8–12	5–14	(5–)8–18
Primigenous cell height (μm)	(16–)26–60 (–110)	(13–)20–75 (–90)	(13–)20–65 (–82)	(15–)25–70 (–80)	5–25	15–50–(–70)	(12–)25–75 (–100)
Postigenous cell length (μm)	(3–)8–50(–60)	Absent	5–40(–55)	Normally absent	8–30	Absent	(5–)16–55(–65)
Postigenous cell diameter (μm)	3–15	Absent	5–16	Normally absent	5–10	Absent	5–14
Monomerous cell diameter (μm)	5–50(–70)	Absent	5–35(–50)	Absent	Absent	Absent	Absent
Monomerous cell length (μm)	5–14	Absent	5–14	Absent	Absent	Absent	Absent
Epithallial cell length (μm)	2–6	2–7	2–6	2–6	4–6	2–6	2–6
Epithallial cell diameter (μm)	4–12	4–12	4–9	4–9	6–9	4–9	4–12

(2) *Position of t/b conceptacle chamber floor*

Relative to the surrounding thallus surface, the floor of a tetrasporangial/bisporangial conceptacle may occupy one of two positions. In *L. chamberlainianum* (Fig. 18D), *L. irvineanum* (Fig. 35A), *L. prototypum* (Fig. 46D), and *L. pustulatum* (Fig. 55E), the floors of functional conceptacles (those which are not buried or becoming buried) is usually situated one to three cell layers below the surrounding thallus surface. This contrasts with *L. bermudense* (Fig. 10E), *L. corallinae* (Fig. 27E), and *L. johansenii* (Fig. 39D) where the floor of functional conceptacles usually is situated six or more cell layers below the surrounding thallus surface. No intraspecific variation in these two character states has been detected, although rarely, a conceptacle chamber floor in *L. pustulatum* may be four or five cell layers below the thallus surface (probably indicative of imminent burial). Consequently, t/b conceptacle chamber floor position is considered to be diagnostic at species level.

In species where the floor is one to three layers below the surrounding thallus surface, most or all of the conceptacle chamber is normally emergent (i.e. above the level of the thallus surface). In species where the floor is six or more layers below the surrounding thallus surface, the chamber normally is largely or entirely submerged within the thallus. When identifying species, it generally is easier to determine the relative position of the chamber floor by noting the emergence/submergence of the chamber than by counting cell layers. Care must be taken with a few plants of *L. pustulatum*, however, as chambers can become more than half-submerged when surrounding postigenous filaments are composed of elongate cells.

(3) *T/b conceptacle roof elevation*

The relative elevation of tetrasporangial/bisporangial conceptacle roofs above the surrounding thallus surface has been used by a number of authors to help delimit or identify species of *Lithophyllum* (see Table 5, characters 59 & 72 and references cited there). In general, t/b conceptacle roofs have been categorized as either more or less prominently elevated or as more or less flush with the surrounding thallus surface.

Results from the present study generally support the use of relative t/b conceptacle roof elevation as a diagnostic character. Thus, in *L. chamberlainianum* (Fig. 18A), *L. irvineanum* (Fig. 33D), *L. prototypum* (Figs 42D, 46A), and *L. pustulatum* (Fig. 55A), roofs of tetrasporangial/bisporangial conceptacles normally protrude prominently above the surrounding thallus surface. In *L. bermudense* (Fig. 11A) and *L. corallinae* (Fig. 27A), t/b conceptacle roofs protrude inconspicuously above or are almost flush with the surrounding thallus surface, and in *L. johansenii* (Fig. 38A) roofs are completely flush with the thallus surface.

Relative roof elevation is related to but not linked with the position of the conceptacle chamber floor. In *L. chamberlai-*

Table 7 A comparative summary of data on measured characters relating to reproductive features in southern Australian specimens of *Lithophyllum*. Extreme values are given in parentheses. An entry of 'unknown' means that relevant structure has not been found in southern Ausralian material. T/b = tetrasporangial/bisporangial conceptacle; M = male conceptacle, F/c = female carposporangial conceptacle. Chamber height measurements exclude pore canal length.

	Specific Epithet						
Character/unit	*bermudense*	*chamberlainianum*	*corallinae*	*irvineanum*	*johansenii*	*prototypum*	*pustulatum*
T/b external roof diameter (µm)	390–475(–512)	370–520(–703)	235–330(–419)	370–519	163–205	440–670(–740)	390–690(–890)
T/b roof cell length (µm)	(5–)8–25(–30)	(5–)10–27(–35)	5–32(–43)	8–24	5–14	5–40(–55)	(8–)14–45
T/b roof cell diameter (µm)	2–10	2–15	2–9	4–12	4–6	5–8	4–11
T/b chamber diameter (µm)	(255–)320–410 (–440)	(145–)175–210 (–252)	(157–)190–235 (–280)	(180–)215–245 (–263)	130–155(–196)	375–425	(328–)390–500 (556)
T/b chamber height (µm)	(68–)90–125 (–160)	(60–)80–120 (–135)	68–105(–136)	82–125	65–108	125–140	110–180
T/b sporangium length (µm)	(55–)75–125 (–135)	(35–)55–95 (–118)	(37–)50–95 (–123)	68–88(–101)	45–70	(60–)71–103 (–110)	100–140
T/b sporangium diameter (µm)	25–45(–55)	(16–)20–35(–47)	(16–)27–55(–92)	(29–)40–55	27–35	30–45	55–82
M. chamber diameter (µm)	(100–)140–160	160–200	116–145	Unknown	80–100	133–185	222–444
M. chamber height (µm)	25–45(–100)	29–55(–90)	32–47(–82)	Unknown	32–47(–80)	(22–)37–60	50–90
F/c chamber diameter (µm)	(275–)300–375 (–385)	160–225(–259)	185–233(305)	Unknown	Unknown	405–497	220–300
F/c chamber height (µm)	(65–)85–115 (–125)	81–115	60–110(–140)	Unknown	Unknown	103–150	85–111
Carposporangium diameter (µm)	30–55	20–30(–52)	27–40(–57)	Unknown	Unknown	37–88?	30–75

nianum, *L. irvineanum*, *L. prototypum*, and *L. pustulatum* normally have both 'shallow' floors and more or less prominently protruding roofs. In *L. johansenii* the floor is always situated eight or more cell layers below the surface and roofs are flush with the surface. In *L. bermudense* and *L. corallinae*, however, floors are six or more cell layers deep but roofs can be elevated or protruding to some extent at least (e.g. Fig. 11A).

(4) T/b conceptacle chamber diameter

Tetrasporangial/bisporangial conceptacle chamber diameter has been used by various authors (see Table 5, characters 63 & 79 and associated references) to help delimit/identify species of *Lithophyllum*, and results from the present study (Table 7) suggest that differences in chamber diameter can be of diagnostic value when used in conjunction with other characters. Tetrasporangial/bisporangial conceptacle chambers are mostly 130–155 µm in diameter in L. *johansenii*, mostly 175–245 µm in diameter in *L. chamberlainianum*, *L. corallinae*, and *L. irvineanum* and mostly of 320–500 µm in diameter in *L. bermudense, L. prototypum*, and *L. pustulatum*. Slight overlap between these categories can occur in extreme cases (see Table 7), however, and judgments should not therefore be made on single measurements.

(5) Terracing of thallus surface

Plants of *Lithophyllum prototypum* are always composed of a number of imbricate layers of applanate branches which give the thallus a terraced appearance in surface view (Fig. 44A). Successively produced layers of branches are smaller in size than subtending ones and thus look like a series of stacked vertical terraces. These terraces are more or less visible to the unaided eye and become very obvious when viewed with a dissecting microscope . No other southern Australian coralline shows similar terracing.

(6) Origin of applanate branches

In *Lithophyllum chamberlainianum, L. irvineanum,* and *L. prototypum*, applanate branches arise (or are presumed to arise) directly from groups of primigenous cells (e.g. Figs 34B–34D). This contrasts with *L. bermudense, L. corallinae, L. johansenii,* and *L. pustulatum* in which applanate branches (when present) arise from groups of postigenous cells (e.g. Fig. 53C). This difference appears to be diagnostically important because applanate branches originating from both primigenous cells and from postigenous cells have not been detected within the same species. No southern Australian species can be recognized on the basis of this character alone, however, and further studies of *L. pustulatum* are required to determine whether in at least some plants, applanate branches can develop directly from groups of primigenous cells. In at least one plant of *L. pustulatum* (Fig. 53C), applanate branches had developed from two-celled postigenous filaments. Townsend & Adey (1990, p. 112) also have noted that applanate branches in species of Mastophoroideae arise from postigenous cells while those in *L. prototypym* (as *Titanoderma tesselatum*) arise from primigenous cells.

(7) Occurrence of multicellular postigenous filaments

Three patterns of multicellular postigenous filament occurrence are evident. Plants of *L. bermudense*, *L. corallinae*, and *L. johansenii* always possess multicellular postigenous filaments. In plants of *L. chamberlainianum*, *L. irvineanum* (one isolated exception known), and *L. prototypum* postigenous development is limited to production of epithallial cells. In *L. pustulatum*, some plants possess multicellular postigenous filaments while others do not. Thus the presence or absence of multicellular postigenous filaments is potentially diagnostic of some species, but not of others. In the species accounts below, this character has been included in the list of diagnostic features because it is so readily observable. It can never be considered as the final determinant of a species, however.

Ancillary characters

Seven ancillary characters (i.e. characters used to help confirm species identifications) have been employed in the dichotomous and tabular keys. None are considered diagnostic because particular character states can vary or do not occur in all specimens of relevant species. When present, however, these ancillary characters are useful aids in identification. Brief comments follow.

(1) Composition of t/b conceptacle chamber floor

The floors of tetrasporangial/bisporangial conceptacles may be composed of primigenous cells (e.g. Fig. 18D) or of cells of postigenous or monomerous filaments (e.g. Fig. 10E). In *L. chamberlainianum, L. irvineanum*, and *L. prototypum*, primigenous cells normally form conceptacle floors. In *L. bermudense* and *L. johansenii*, postigenous or monomerous cells normally form conceptacle floors. In *L. corallinae* and *L. pustulatum*, both character states can occur.

(2) Mode of conceptacle submergence

Older conceptacles may or may not become buried within a thallus. In *L. chamberlainianum, L. irvineanum*, and *L. prototypum* this usually occurs via overgrowth by applanate branches. In *L. bermudense, L. corallinae,* and *L. johansenii* submergence results from envelopment by surrounding vegetative filaments and sometimes by renewed growth of roof filaments. Either mode of submergence may occur in plants of *L. pustulatum*.

(3) Number of cells in t/b conceptacle roofs

This character has been used only to help identify certain specimens of *L. bermudense* and *L. corallinae*. In *L. bermudense*, roof filaments above conceptacle chambers commonly (but not always) have four to seven intact cells. In *L. corallinae*, two to four intact cells are most common.

(4) Occurrence of columnar cells in t/b conceptacle roofs

This character also has been used only to help identify certain specimens of *L. bermudense* and *L. corallinae*. In *L. corallinae*, t/b conceptacle roofs may have a subepithallial layer of columnar cells [i.e. elongated cells in which end walls (those possessing primary pit-connections) are much shorter than side walls and cell length is substantially greater (usually two to four times) than cell diameter; see Woelkerling 1988: 16, 66] above the chamber (e.g. Fig. 28A). Such columnar cells are very rare in plants of *L. bermudense*. Other species of *Lithophyllum* also may have columnar cells in tetraspoarangial/bisporangial conceptacle roofs, but their occurrence has not been considered diagnostic or used in an ancillary manner in this study.

(5) Occurrence of protuberant branches

Some specimens of *L. bermudense* and *L. corallinae* produce protuberant branches; such branches are unknown in other southern Australian species. Thus the presence (but not absence) of protuberant branches may be an aid in identifying *L. bermudense* and *L. corallinae* . The same applies to coalescent branches in *L. bermudense*.

Elsewhere, the presence or absence of protuberant branches has been widely used in a diagnostic sense (see Table 5, character 20 and associated references). However, given the variability present in *L. bermudense* and *L. corallinae* (see species accounts) this character requires critical re-evaluation.

(6) Thallus construction in crustose portions of plants

In *L. chamberlainianum, L. irvineanum, L. johansenii, L. prototypum*, and *L. pustulatum*, crustose portions of thalli normally are completely dimerous. Some specimens of *L. bermudense* and *L. corallinae* also are entirely dimerous, but in crustose parts of other specimens, both monomerous and dimerous construction can occur. Thus the presence (but not absence) of monomerous construction in crustose parts of thalli may be an aid for identifying plants of *L. bermudense* and *L. corallinae*. Further comments on dimerous/monomerous construction as a taxonomic character are provided by Woelkerling (1988: 9, 65).

(7) Occurrence of adjunctive secondary pit-connections

Some plants of *L. prototypum* possess adjunctive secondary pit-connections between cells of two vertically contiguous applanate branches (Fig. 44F). When present, adjunctive secondary pit-connections are of value in identifying specimens of *L. prototypum*; such connections have not been seen in other southern Australian species of *Lithophyllum*.

Characters used by other authors

Many characters used by previous authors (Table 5) have not been used in a diagnostic or ancillary capacity in this study. Of the general thallus characters in Table 5 (characters 1-11), terrace width (character 8) has been shown to be unreliable (see account of *Lithophyllum prototypum*). Considerable variation occurs in surface texture (character 1) in most species, and differences are apt to be of little or no diagnostic value. Character 2 occurred in all species examined and thus could not be properly evaluated. Surface finish (character 3) and thallus colour (character 4) may be of value in field identification (e.g. see Adey & Adey, 1973; Chamberlain 1991) but cannot be assessed in most herbarium material. Remaining thallus characters were not evaluated, but it seems likely that most of them have little diagnostic potential.

Considerable within-species variation occurs in all substrate-related characters (Table 5, characters 12–16).

Plants of *L. bermudense* may grow attached or unattached (character 12). Southern Australian plants of *L. corallinae* occur on a variety of substrates (character 14), none of which include other algae, whereas in the British Isles (Chamberlain 1991 as *Titanoderma*), this species has been found only as an epiphyte. Similarly, most characters associated with outgrowths and protuberances (Table 5, characters 17–29) are probably too variable to be of diagnostic value; many of these features show considerable variation in *Lithophyllum bermudense* (q.v.).

Amongst general anatomical features (Table 5, characters 30–33), no evaluations of thallus thickness or filament initials were made. The number of cell layers in a thallus and the extent of so-called 'monostromatic margins' vary greatly in plants of *L. pustulatum*, suggesting that these characters are at best of limited taxonomic value. No measured characters pertaining to vegetative cells (Table 5, characters 34–54) were found to be of diagnostic value (see data in Table 6). Epithallial cell and secondary pit-connection characters (Table 5, characters 55–58) have not been evaluated except to note that in some plants of *L. corallinae*, filaments within a thallus may terminate in one or in two epithallial cells (Fig. 26C).

Some characters relating to tetrasporangial/bisporangial conceptacles (Table 5, characters 59–70) have been commented on in previous sections. Of the remainder, outside diameter (character 60), columellar occurrence (character 66), the nature of sporangia present (character 68), and sporangial dimensions (characters 69, 70) were too variable to delimit species (see species accounts and Table 7 for details). Roof characters (characters 61, 65) used by Chamberlain (1986) at species level apply to entities which subsequently (Chamberlain, 1991) have been treated as varieties of a single species (*Lithophyllum pustulatum*; q.v. in species accounts).

The size of tetrasporangial/bisporangial conceptacles relative to those of female/carposporangial conceptacles (Table 5, character 62) and the roof curvature of male conceptacles (Table 5, character 71) have not been evaluated. Finally, miscellaneous conceptacle characters (Table 5, characters 72–81) cannot be properly evaluated because it is unclear exactly which sorts of conceptacles were being referred to by particular authors.

SPECIFIC AND INFRASPECIFIC DELIMITATION

Delimitation of species within most genera of nongeniculate Corallinaceae has been fraught with substantial difficulties which have stemmed principally from published work of questionable quality rather than from any intrinsic properties of the plants. The literature is replete with described species based on single, often fragmentary or sterile specimens (see additional comments in Woelkerling, 1984: 7–18), and as noted by Taylor (1960: 376), 'characters [of species] have been described by authors with such different standards of workmanship, with such different ideas of what characters should be described, using descriptive words with such different meanings and making such discordant statements, that it is practically impossible to glean from the literature balanced comparative accounts of related species at the present'. Within *Lithophyllum*, most species are poorly known (Dawson, 1955: 272, as *Dermatolithon*; Woelkerling, 1988: 115), and as noted by Chamberlain (1986; 1991), a number of published accounts are based on misidentified plants. Moreover, most authors have not included an explicit statement about their approach to species delimitation or about any assessments of variability in characters considered diagnostically important at species level.

In the present account, species delimitation is based on the morphological/anatomical species concept, a detailed account of which is given by Davis & Heywood (1963: 89–98). According to this concept, each species comprises an assemblage of individuals which has a common suite of morphological/anatomical characters and is separable from other such assemblages by clear morphological/anatomical discontinuities. It has not been possible to determine the extent to which the morphological-anatomical species of *Lithophyllum* recognized here coincide with biological species (i.e. assemblages of individuals which can actively or potentially interbreed but are reproductively isolated from other such assemblages) or with genetic species (i.e. gene pools which generate phenotypes which reproduce sexually or parasexually to produce new combinations of genes). Moreover it is unlikely that such determinations will be possible until techniques for routinely growing and manipulating these algae in the laboratory are improved, until all relevant stages in the sexual cycle of all species are found and can be grown, and until routine DNA sequencing studies can be done. In addition, current limitations associated with biological/genetic species concepts (see Davis & Heywood, 1963: 95–98; Levin, 1979) make it likely that morphological/anatomical concepts of species will continue to be the mainstay of coralline taxonomy for some years to come.

Delimiting morphological/anatomical species involves taxonomic judgments which to varying degrees are subjective and influenced by extrinsic factors relating both to the content of the work and to the taxonomist (see Davis & Heywood, 1963: Silva, 1984). The soundness and durability of taxonomic judgments are also influenced by the amount of material available for study, the extent to which assessments of character variability have been made, and the extent to which lumping or splitting (see Davis & Heywood 1963: 85–87) has occurred. Most hitherto described species and infraspecific entities of nongeniculate Corallinaceae, including those assignable to *Lithophyllum*, have been based on limited studies of single specimens. This has resulted in exceedingly narrowly and often incomprehensibly delimited species and infraspecific entities. As a result, our understanding of morphological/anatomical species and infraspecific entities in most genera is atrocious. In the present study, the degree of character variation within individuals, among individuals within populations and among populations from various localities has been determined to the extent permitted by available material. This has led to a broader concept for species within *Lithophyllum* and to the use of two state or multistate characters associated with tetrasporangial/bisporangial conceptacle anatomy as the principal means of delimiting species. Most measured characters, in contrast, have been avoided for diagnostic purposes because of their comparatively greater variability. Because considerable uncertainty has surrounded species delimitation within *Lithophyllum*, it has been necessary to elucidate species limits de novo and then to test resulting hypotheses on newly collected specimens.

Given the great uncertainty surrounding delimitation of species in *Lithophyllum* (and amongst nongeniculate Corallinaceae generally), it may seem dangerously adventurous to describe three species as new, as is done below. In the context of the current study, however, which includes an analysis of published accounts from which reasonably reliable data can be gleaned, recognition of these new species seems justifiable. Progress towards a better understanding of species concepts in *Lithophyllum* (and in other nongeniculate genera) would be impeded for decades if the type collections of all 600+ previously described nongeniculate corallines ascribed to *Lithophyllum* had to be located and reassessed as a prelude to the description of three new species in a regional monographic account. Indeed, the production of regional monographic accounts with detailed, reliable data on meaningfully delimited species is a necessary step towards the eventual production of a world monograph of the genus.

Among nongeniculate Corallinaceae, hundreds of infraspecific entities have been described, with the vast majority accorded the rank of form. Most of these forms lack significance, needlessly clutter the literature, and now make meaningful use of this rank extremely difficult within the Corallinaceae. In a coordinated attempt to bring stability and consistency to the application of infraspecific ranks to nongeniculate corallines, Y. Chamberlain and the present authors (see Chamberlain, 1991: 4) considered the matter in detail and came to three conclusions:

(1) The rank of form should be avoided at present as its continued use is likely to compound already existing confusion.

(2) The rank of variety should be employed in cases where it is desirable or advantageous formally to name particular morphological/anatomical focal points within a highly and continuously variable species without assuming or implying any geographic or genetic basis. As noted by Davis & Heywood (1963: 100) the rank of variety can be used '. . . for variations whose precise nature is not understood, a treatment often necessary in the pioneer phase of taxonomy.'

(3) The rank of subspecies should be employed in cases where available evidence suggests that two or more species may be represented but which at present cannot be separated unequivocally. Such subspecies should be delimited on morphological/anatomical grounds without consideration of geographic distribution (which usually is inadequately known) or of presumed genetic characters (which are presently unknown).

This approach to infraspecific delimitation reinforces the fundamental idea that the species is the central rank to be considered within genera and it also allows for flexibility and provides guidance in the recognition of infraspecific entities as seems warranted by regional circumstances and knowledge.

Finally, there is increasing evidence (e.g. see Chamberlain, 1986: 1991; Woelkerling, 1983a; 1983b; 1985; Woelkerling & Irvine, 1986) that a number of names have been misapplied to commonly occurring nongeniculate Corallinaceae, thereby casting doubt on the authenticity of published references to a number of entities. To avoid further difficulties and to foster greater nomenclatural stability, the application of all names to entities occurring in southern and southwestern Australia has been verified through examination of relevant type collections.

KEYS TO SOUTHERN AUSTRALIAN SPECIES OF *LITHOPHYLLUM*

General comments

Dichotomous and tabular keys are provided below. The dichotomous key is based on vegetative and reproductive characters in mature tetrasporangial/bisporangial plants. Anatomical characters relating to tetrasporangial/ bisporangial conceptacles, especially those associated with the pore canal, are best seen in vertical (i.e. anticlinal) sections cut along the centre of the pore canal. It is difficult or impossible to determine whether or not the pore canal is blocked by enlarged cells in sections cut obliquely through the pore canal or in sections cut along the periphery of the pore canal.

The tabular key is composed of two sections. Part A contains a list of characters and codes for character states; Part B contains the identification chart. To identify specimens using the tabular key, start with any feature listed in Part A and determine which species in Part B possess the character state found in the specimen. Then choose another character and repeat the process considering only those species possessing the first character shown by the specimen. Continue repeating this process until all but one of the species are eliminated.

Some specimens (hopefully less than 10%) may prove difficult or impossible to identify . These may represent species newly recorded for the region, specimens in poor condition, specimens which are poorly sectioned, or specimens possessing characteristics which fall outside the range currently known for a species. Specimens of the first and last categories may prove critically important to the refinement of species concepts in *Lithophyllum* and always should be properly annotated, calling attention to any apparent anomalies.

Dichotomous key

1a. Entire pore canals of mature tetrasporangial/bisporangial conceptacles completely occluded by enlarged cells (Figs 18D, 35A, 39C)
  2a. Floors of functional tetrasporangial/bisporangial conceptacles usually situated one to three cell layers below surrounding vegetative thallus surface (Figs 18D, 35A); conceptacle roofs commonly protruding prominently above surrounding thallus surface; postigenous filaments usually composed only of epithallial cells (rarely two or three cells long)
    3a. Entire pore canal occluded by a conglomerate cluster of overlapping, more or less tubular and sometimes clasping or inflexed cells which are derived from at least the first two rows of roof filaments flanking the pore canal and which usually project beyond the surrounding roof surface (Fig. 18D) .... ***L. chamberlainianum***
    3b. Entire pore canal occluded by two or four angular cells which are derived only from the row of roof filaments immediately flanking the pore canal and do not project beyond the surrounding roof surface (Fig 35A) .... ***L. irvineanum***
  2b. Floors of functional tetrasporangial/bisporangial conceptacles usually situated eight or more cell layers below surrounding

vegetative thallus surface (Fig 39D); conceptacle roofs usually more or less flush with surrounding thallus surface; postigenous filaments multicellular, commonly composed of ten or more cells .... ***L. johansenii***

1b. Pore canals of mature tetrasporangial/bisporangial conceptacles lined with cells which may project somewhat into but do not completely occlude the entire canal (Figs 10E, 27E, 46D, 55E)

4a. Floors of functional tetrasporangial/bisporangial conceptacles usually situated one to three (– to five) cell layers below surrounding vegetative thallus surface (Figs 46D, 55E)

5a. Thallus composed of a number of imbricate (overlapping like roof tiles) layers of applanate branches which give the thallus a terraced appearance in surface view (Fig. 44A); postigenous development limited to epithallial cells in vegetative parts of thallus. .... ***L. prototypum***

5b. Thallus lacking applanate branches or with sporadic branches which do not form numerous imbricate layers or give the thallus a terraced appearance in surface view; postigenous development commonly but not always involving multicellular filaments. .... ***L. pustulatum***

4b. Floors of functional tetrasporangial/bisporangial conceptacles usually situated six or more cell layers below surrounding vegetative thallus surface (Figs 10E, 27E)

6a. Tetrasporangial/bisporangial conceptacle chambers usually 190–235 µm (rarely to 280 µm) in diameter; conceptacle roofs commonly (but not always) two to four cells thick over the chamber and commonly with a single subepithallial layer of elongate, columnar cells (Figs 28A, 28B) .. ***L. corallinae***

6b. Tetrasporangial/bisporangial conceptacle chambers usually 320–440 µm (rarely down to 255 µm) in diameter; conceptacle roofs commonly (but not always) four to seven cells thick over chamber and only rarely with a subepithallial layer of elongate, columnar cells (Fig. 10E) .... ***L. bermudense***

Tabular key

Part A. List of characters and codes for character states listed in Part B. Characters are numbered in the sequence used in Part B.

I. Characters relating to vegetative morphology and anatomy.
  1. Terracing of thallus surface to unaided eye
    - O surface obviously and more or less completely terraced to unaided eye as a consequence of numerous (usually 6–30 or more) layers of applanate branches which commonly have swirled or scroll-like margins and which appear to form successively smaller tiers or terraces on top of one another (Fig. 44A)
    - N surface not obviously terraced to unaided eye; applanate branching absent or infrequent to common, but branches, when present, inconspicuous, without swirled margins, and not visible to unaided eye
  2. Presumed origin of applanate branches (when present)
    - PR from groups of primigenous cells
    - PO from groups of postigenous cells
  3. Protuberant or coalescent branches
    - A absent or unknown
    - P present in some but not all specimens
  4. Vegetative postigenous development
    - E limited to epithallial cells
    - MS multicellular postigenous filaments developing in some (but not all) specimens
    - MA multicellular postigenous filaments present in all thalli
  5. Thallus construction in crustose portions
    - D dimerous
    - DM dimerous in some plants but both dimerous and monomerous in other plants
  6. Adjunctive secondary pit-connections
    - U unknown
    - P present between applanate branches in some thalli

II. Characters relating to tetrasporangial/bisporangial conceptacles
  7. Conceptacle roof
    - P protruding above surrounding thallus surface (e.g. Fig. 18A)
    - F more or less flush with surrounding thallus surface (e.g. Fig. 38A)
    - PF either protruding (usually slightly) or flush with the surrounding thallus surface (e.g. Fig. 11A)
  8. Pore canal
    - C entire canal completely blocked by a conglomerate cluster of enlarged, elongate, more or less tubular and sometimes inflexed cells
    - A entire canal completely blocked by two or four enlarged more or less angular cells
    - O pore canal open or with cells which project into but do not completely obstruct the entire canal; top of canal sometimes covered by a mucilaginous 'plug'
  9. Position of conceptacle chamber floor
    - 1–3 usually situated one to three cell layers below surrounding thallus surface
    - 6+ usually situated six or more cell layers below surrounding thallus surface
  10. Composition of conceptacle chamber floor
    - PR always composed of primigenous cells
    - P composed of primigenous cells in thinner thalli or of postigenous cells in thicker thalli
    - PO composed of postigenous cells of or cells of monomerous filaments
  11. Mode of conceptacle submergence (when occurring)
    - O via overgrowth by applanate branches
    - E via envelopment by surrounding vegetative filaments and renewed growth of conceptacle roof filaments
    - EO either by overgrowth or by envelopment
  12. Diameter of tetrasporangial/bisporangial conceptacle chamber (small overlap of categories occurs in cases of extremely large or small conceptacles; see data in Table 7)
    - A mostly 130–155 µm in diameter
    - B mostly 175–245 µm in diameter
    - C mostly 320–500 µm in diameter

TAXONOMIC ACCOUNTS

I. LITHOPHYLLUM

Lithophyllum Philippi in *Arch. Naturgesch.* 3: 387 (1837).

LECTOTYPE SPECIES. *Lithophyllum incrustans* Philippi in *Arch. Naturgesch.* 3: 388 (1837); designated by Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(2): 6 (1898a).

HOLOTYPE. L 943, 10 . . . 34 (part of)(from Sicily; see Woelkerling, 1983b: 315, figs 15–23).

HOMOTYPIC SYNONYMS:

Melobesia Lamouroux sect. *Lithophyllum* (Philippi) Areschoug in J.G. Agardh, *Sp. Gen. Ord. Algarum* 2(2): 515 (1852).

Melobesia Lamouroux subg. *Lithophyllum* (Philippi) Ardissone in *Mem. Soc. Crittogam. Ital.* 1: 447 (1883).

Lithothamnium subg. *Lithophyllum* (Philippi) Foslie in *K. norske Vidensk. Selsk. Skr.* 1894: 178 (1895).

Hyperantherella Heydrich in *Ber. dt. Bot. Ges.* 18: 316 (1900).

Crodelia Heydrich in *Bibthca bot.* 18(75): 12 (1911).

Tabular key: Part B. Identification Chart. Characters and character codes are given in Part A.

Species	Thallus morphology and anatomy							Tetrasporangial/bisporangial conceptacles				
	1	2	3	4	5	6	7	8	9	10	11	12
L. bermudense	N	PO	P	MA	DM	U	PF	O	6+	PO	E	C
L. chamberlainianum	N	PR	A	E	D	U	P	C	1–3	PR	O	B
L. coralline	N	PO	P	MA	DM	U	PF	O	6+	PO[2]	E	B
L. irvineanum	N	PR	A	E[1]	D	U	P	A	1–3	PR	O	B
L. johansenni	N	PO	A	MA	D	U	F	A	6+	PO	E	A
L. prototypum	O	PR	A	E	D	P	P	O	1–3	PR	O	C
L. pustulatum	N	PO	A	MS	D	U	P	O	1–3	P	EO	C

1. Two-celled postigenous filaments found in one collection.
2. Rarely with floor composed of primigenous cells.

HETEROTYPIC SYNONYMS.

Titanoderma Nägeli, *Stärkekörner*: 532 (1858).

Melobesia Heydrich in *Ber. dt Bot. Ges.* 15: 408 (1897a) (non *Melobesia* Lamouroux in Nouv. *Bull. Sci. Soc. Philomat. Paris* 3: 186 (1812); nec *Melobesia* Foslie in *K. norske Vidnesk. Selsk. Skr.* 1898(3): 10 (1898b)).

Dermatolithon Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(3): 11 (1898b).

Perispermon Heydrich in *Ber. dt. bot. Ges.* 18: 316 (1900).

Stichospora Heydrich in *Ber. dt. bot. Ges.* 18: 316 (1900).

Litholepis Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(5): 5 (1905b).

Pseudolithophyllum Lemoine in *Deux. Exped. Ant. Fr.* 1(Bot.): 45 (1913).

Melobesia Foslie (non Lamouroux nec Heydrich) subg. *Litholepis* (Foslie) Lemoine in *Dansk bot. Ark.* 3: 176 (1917).

Fosliella Howe subg. *Litholepis* (Foslie) Cabioch in *Cah. Biol. mar.* 13: 182 (1972).

ETYMOLOGY. *Lithophyllum*, from the Greek *lithos* (stone) and the Latinized Greek word *phyllon* (leaf). See DeToni (1905: 1778); Philippi (1837) did not explain the etymology.

DESCRIPTION. Plants nongeniculate; varying in form from encrusting to fruticose thalli composed largely or entirely of protuberances or coalesced branches; plants anchored to the substrate by cell adhesion or growing unattached and forming thalli of various shapes; haustoria unknown.

Thallus pseudoparenchymatous. Crustose portions of plants dorsiventral and dimerous, monomerous, or both; protuberant branches, when present, more or less radial and monomerous. Dimerous parts of thallus consisting of: 1) a unistratose ventral layer of primigenous filaments which may be composed of palisade, nonpalisade cells or both; and 2) postigenous filaments which arise dorsally from cells of primigenous filaments and which may consist only of epithallial cells or become multicellular. Monomerous parts of thallus composed of a ventral or central core of coaxial or noncoaxial filaments and a peripheral region where distal portions of core filaments or their derivatives curve outwards towards the thallus surface. Thallus filaments each consisting of a terminal initial or a subterminal initial which can produce epithallial cells outwardly at the thallus surface and additional vegetative cells inwardly. Terminal epithallial cells with outer walls rounded or flattened but not flared. Cells of adjacent filaments commonly joined by contiguous secondary pit-connections; adjunctive secondary pit-connections sometimes present between cells belonging to two vertically adjacent applanate branches; cell fusions and trichocytes unknown in most species.

Tetrasporangial/bisporangial conceptacles uniporate; apparently arising from small groups of subepithallial initials. Conceptacle roof several cells thick, enclosing a spore-bearing chamber; roof filaments reaching outer surface each terminating in an epithallial cell. Cells of adjacent roof filaments sometimes joined by contiguous secondary pit-connections. Columella present or absent; conceptacles lacking persistent groups of calcified filaments interspersed amongst the sporangia. Tetrasporangia/bisporangia lacking apical plugs; restricted to the periphery or scattered across the conceptacle chamber floor; at maturity each sporangium containing four zonately arranged tetraspores or two bispores. Trisporangia and/or pentasporangia known in several species, usually occurring intermixed with tetrasporangia within conceptacles.

DIAGNOSTIC FEATURES. Diagnostic features are summarized in Table 1.

COMMENTS. The genus *Lithophyllum*, as delimited here, incorporates the recent conclusion of Campbell & Woelkerling (1990) that *Titanoderma* should be regarded as a heterotypic synonym. Chamberlain (1991, pp. 13, 23, 24) and Chamvberlain et al. (1991, pp. 164, 165) in contrast, have retained both genera based on presumed differences in the anatomy of dimerous portions of the thallus. Thus *Lithophyllum* includes species which 1) have a pedominance of squarish (nonpalisade) cells and 2) entirely lack a bistratose thallus margin (i.e. a margin which is only two cells thick), while *Titanoderma* includes species which 1) have a predominance of palisade primigenous cells and 2) have at least some bistratose margin. Chamberlain (1991, p. 13) also noted that some species of *Titanoderma* (citing *T. corallinae* as an example) have thalli that thicken (i.e. become multistratose) immediately behind the marginal initial as in *Lithophyllum* in addition to bistratose areas, and Chamberlain et al. (1991, p. 165) noted that in the type collection of *T. corallinae* ‘ . . . both plants with a thickened and plants with a bistratose margin occur’.

Unfortunately, attempts to apply the above concepts of *Lithophyllum* and titanoderma to southern Australian Lithophylloideae have not been successful. In *Lithophyllum bermudense*, *L. corallinae*, and *L. johansenii*, some specimens have a predominance of nonpalisade (squarish) cells whereas others have a predominance of palisade primigenous cells in dimerous portions of the thallus (Figs 7, 8A–d, 25, 37). On this basis, different specimens of the same species would be referable to different genera. Moreover, some specimens of *L. bermusense* and *L. corallinae* are almost entirely monomerous, thus making generic placement difficult.

Similar problems attend the use of the presence or absence of a bistratose thallus margin. A bistratose margin may occur in dimerous portions of some plants of *L. bermudense, L. corallinae*, and *L. johansenii*, but in other plants no bistratose margin has been detected even after extensive sectioning. This again means that different specimens of the same species could be referred to different genera. In addition. many specimens of *L. bermudense* that completely encircle stones or other objects or that grow unattached have no detectable margins of dimerous construction, thus making generic placement difficult or impossible to determine. It could be argued that the *potential* for a *species* to produce or not produce a bistratose thallus margin is taxonomically significant at generic level. However, providing direct evidence that a species lacks the potential to produce a bistratose margin is exceedingly difficult. Because particular plants of some species (e.g. *L. bermudense, L. corallinae*) have bistratose margins while others apparently do not and because some plants have both bistratose and multistratose margins on the same individual, it seems unlikely that the presence or absence of a bistratose margin is of fundamental taxonomic significance at generic level. At best such a character is more or less cryptic (see Davis and Heywood, 1963, p. 139) and thus highly inconvenient, and Davis & Heywood (op. cit.) suggest that such characters may be ignored in the delimitation of taxa.

Details relating to homotypic and heterotypic synonyms, other nomenclatural matters, infrageneric classification, etc. are provided by Woelkerling (1988: 97–105, 109–115) and Woelkerling (1991).

ACCOUNTS OF SPECIES

Unless otherwise indicated, the following accounts are based on studies of southern Australian specimens and type material. Consequently, statements in the descriptions and in the sections on ecography and on morphology & anatomy may not encompass the total variation present within each species on a world scale. This is especially true for measured characters mentioned in the descriptions and summarized in Tables 6 & 7. Indeed, morphological measurements (thallus breadth, thallus thickness, protuberant branch length, etc.—see Table 6) have been obtained from specimens processed for herbarium storage rather than in the field because, with the exception of *Lithophyllum prototypum*, it is not possible at present to identify unequivocally plants to species level in the field . It is highly likely, therefore, that size and length information for morphological features are understated.

Maps showing nearly all localities cited in 'Collections Examined' are provided as Maps 1–4; these have been reproduced with permission of The Flora and Fauna of South Australia Handbooks Committee from Womersley (1984, figs 2–5).

1. **Lithophyllum bermudense** Foslie & Howe in *Bull. N. Y. Bot. Gdn* 4(13): (132) (1906).

Figs 2–15

Holotype. TRH [Spanish Point, Bermuda, leg. *M.H. Howe*, 21 June 1900 (no. 199); on calcareous rock]. Figs 2, 3; see also Printz 1929: 32, pl.72, fig.19. Printz (op. cit.) incorrectly gives the plate number as 63.

Homotypic synonyms:

Dermatolithon bermudense (Foslie & Howe) Foslie & Howe in Foslie in *K. norske Vidensk. Selsk. Skr.* 1909(2): 58 (1909). *Tenarea bermudense* (Foslie & Howe) Adey in *K. norske Vidensk. Selsk. Skr.* 1970(1): 6 (1970). *Titanoderma bermudense* (Foslie & Howe) Woelkerling et al. in *Phycologia* 24: 333 (1985).

Misapplied names. No published misapplications of other names to southern Australian specimens were discovered during this study.

Etymology. The specific epithet refers to Bermuda, from which the type specimen was collected.

Previously published illustrations of Australian plants. Woelkerling, *Coralline Red Algae*: 12, fig. 17; 100 figs 70, 72, 73: 101, fig. 74; 102, fig. 77; 112, fig. 93 [specimens identified either as *Titanoderma* sp. (fig. 17) or *Lithophyllum* sp. (remaining figs)](1988).

Description. Plants mostly 4–200+ mm across and 0.1–60 mm thick or tall; variably flat (complanate), layered (without conspicuous terracing), warty, lumpy, protuberant and/or coalescent; completely or partially adherent or entirely unattached.

Thallus dimerous, dimerous and monomerous or largely monomerous; dimerous portions with primigenous filaments composed of palisade or occasionally nonpalisade cells 5–18 µm long and (16–)25–60(–100) µm tall and postigenous filaments composed of 5–30+ cells (3–)8–50(–60) µm long and 3–15 µm in diameter; monomerous portions with filaments usually composed of 20+ cells 5–50(–70) µm long and 5–14 µm in diameter; epithallial cells 2–6 µm long and 4–12 µm in diameter terminating postigenous and monomerous filaments. Contiguous secondary pit-connections common; adjunctive secondary pit-connections, cell fusions, and trichocytes not seen.

Tetrasporangial plants with scattered non- or slightly protruding conceptacles. Conceptacle roofs 390–475(–512) µm in external diameter; roof filaments above chamber usually 3–7 cells long, cells (5–)8–25(–30) µm long and 2–10 µm in diameter with columnar cells occurring sporadically or infrequently in horizontal subepithallial groups. Pore canals lined with somewhat projecting but not occluding cells . Conceptacle chambers (225–)320–410(–444) µm across and (68–)90–125(–160) µm tall; floor of mature chambers usually 7 or more cells below thallus surface; tetrasporangia (55–)75–125(–135) µm long and 25–45(–55) µm in diameter, scattered across the conceptacle chamber floor or more commonly occurring peripheral to a columella and/or pseudoparenchymatous hump.

Bisporangial plants not seen.

Gametangial plants dioecious. Male conceptacle roofs non- or slightly protruding; chambers (100–)140–160 µm in diameter and 25–45 µm tall; spermatangial branches confined to chamber floor, simple, with each initial bearing one or

Fig. 2. *Lithophyllum bermudense*: holotype collection. A. Holotype in Foslie herbarium (TRH, unnumbered). B. Section of part of vegetative thallus showing dimerous construction and one applanate branch (t) overgrowing another (b). Branch junction (large arrow) is at left. Note variation in height of primigenous cells which vary from palisade (p) to nonpalisade (n). Small arrows denote epithallial cells of lower branch.

several elongate spermatangia. Female/carposporangial conceptacle roofs non- or slightly protruding; chambers (275)300–375(–385) µm in diameter and (65–)85–115(–125) µm tall; carpogonial filaments arising from chamber floor, usually 2–3 cells long and bearing 1(–2) carpogonia terminally.

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 posssibly catenate) carposporangia 30–55 µm in diameter.

DIAGNOSTIC FEATURES. *L. bermudense* differs from other southern Australian species of *Lithophyllum* in having the

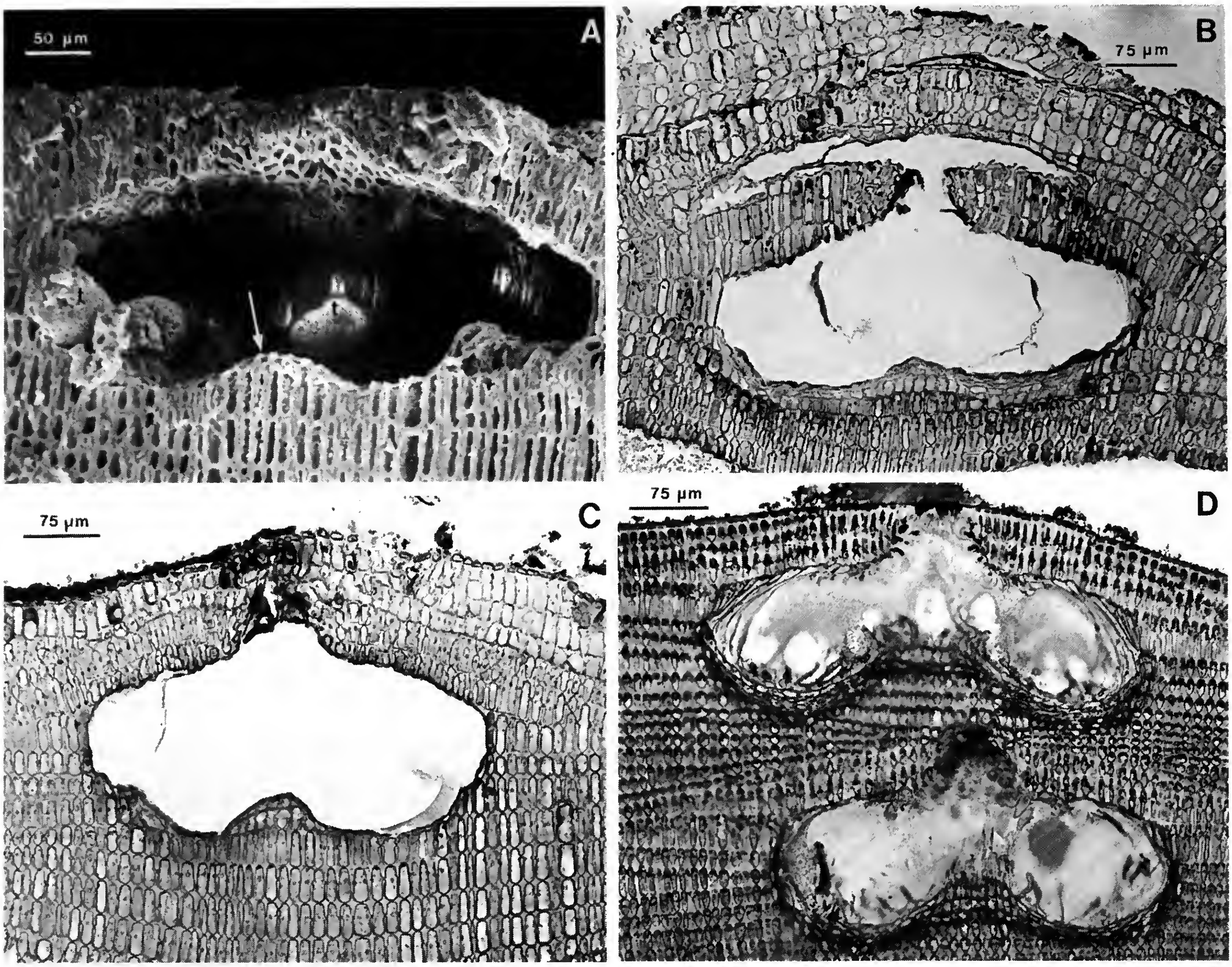


Fig. 3 *Lithophyllum bermudense*: holotype collection (TRH, unnumbered) and LTB 13365. A. Thallus fracture showing conceptacle with several tetrasporangia (t) and a central hump (arrow) on the conceptacle chamber floor (holotype). B,C Sections containing conceptacles showing roof structure and a small hump on each chamber floor (holotype). D. Tetrasporangial conceptacles in a Tasmanian population with a roof anatomy nearly identical to that of holotype conceptacles. (LTB 13365).

following combinationof features:

1. Pore canals of tetrasporangial conceptacles with cells which may project somewhat into but do not completely occlude the entire canal (Figs 10E, 11C–11E, 12).
2. Floors of functional tetrasporangial conceptacles usually situated seven or more (rarely five) cells below the thallus surface and conceptacle roofs more or less flush with or protruding somewhat above the thallus surface (Figs 10E, 11A, 11C–11E, 12).
3. Thallus surface not obviously and more or less completely terraced as a consequence of applanate branche development;
4. Postigenous filaments normally multicellular except in very young portions of thallus.
5. Roofs of tetrasporangial conceptacles usually three to seven cells thick above the chamber and only rarely with a subepithallial layer of columnar cells (Figs 3D, 10E, 11C–11E, 12A–12F).
6. Chambers of tetrasporangial conceptacles mostly 320–410 µm (rarely down to 255 µm) in diameter.

The extent to which this combination of features can be used to delimit *L. bermudense* as a species within *Lithophyllum* cannot be fully assessed in the absence of a world-wide monograph of the genus. Moreover, the putative differences between *L. bermudense* and *L. corallinae* as circumscribed in this study require clarification, as explained in the section on species relationships (p. 97).

TYPIFICATION. Foslie & Howe [1906: (132)] indicate that the original collection designated by them [op. cit, p.(132)] as the type was divided into two parts with one lodged at TRH and the other at NYBG. The TRH portion of the holotype collection (Fig. 2A), which contains two of the three pieces illustrated in the protologue [namely Foslie & Howe, 1906: pl. 81, fig. 3 (left-hand specimen) and pl. 85, fig. 3] has been examined during the present study.

COMMENTS ON HOLOTYPE MATERIAL. The original account of *Lithophyllum bermudense* (Foslie & Howe, 1906) is one of only several Foslie protologues accompanied by photographs of internal thallus structure. Plate 92 in the protologue shows a dimerously constructed part of a thallus in which the primigenous cells all appear palisade-like. Campbell &

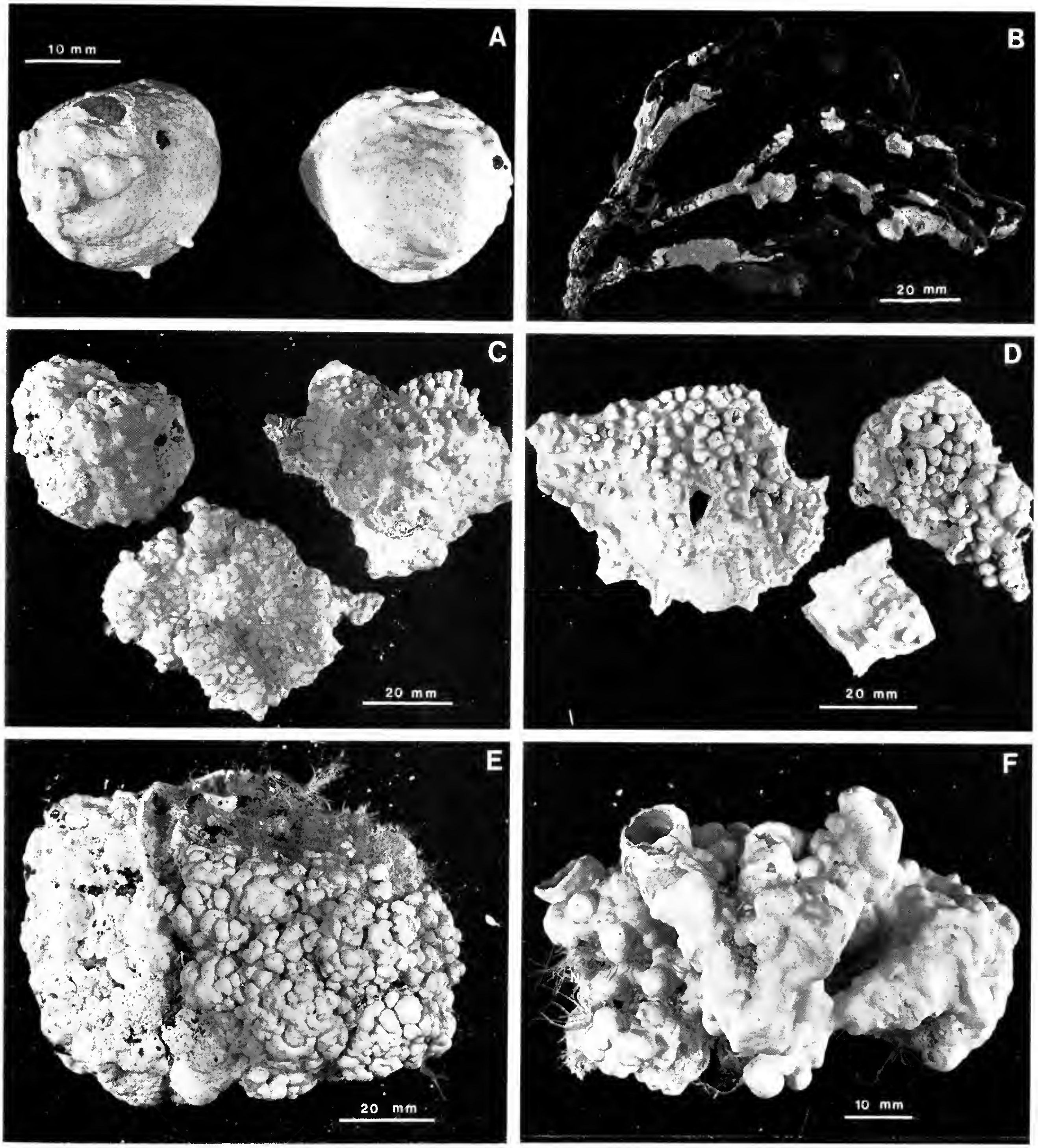


Fig. 4 *Lithophyllum bermudense*: growth-forms of southern Australian plants. A,B. Flat, smooth-surfaced thalli growing on snails [A] and on the red alga *Osmundaria* [B]. (A = LTB 13374; B = LTB 14061). C,D. Warty, epilithic plants with uneven surfaces or short, simple more or less cylindrical protuberances. (C = LTB 15682; D = LTB 15803). E,F. Lumpy plants. (E = LTB 10590; F = LTB 10623).

Woelkerling (1990: fig. 16), however, found both palisade and nonpalisade primigenous cells in type material, a situation also evident in present study (Fig. 2B). Thus in Fig. 2B, the bottom branch contains both palisade (left side) and nonpalisade (far right) cells whereas the top branch contains only nonpalisade cells. A number of holes/gaps also occur in this material, but the causes are uncertain. Monomerous construction has not been detected in type material. Foslie & Howe (1906) found only empty conceptacles, but during the present study several tetrasporangia were discovered in one conceptacle (Fig. 3A). Conceptacle roof structure (Figs. 3B, 3C) falls within the range present in southern Australian

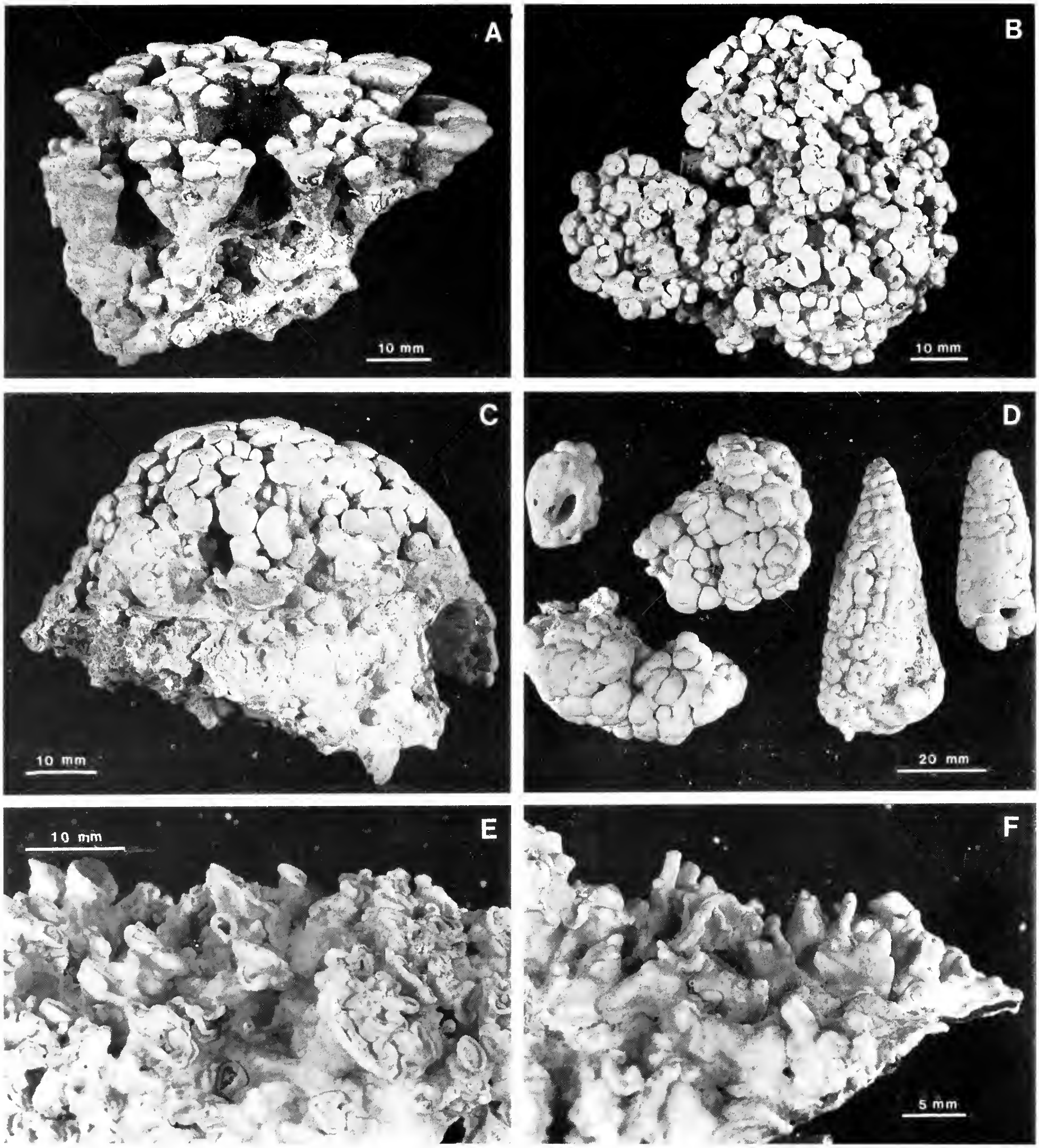


Fig. 5 *Lithophyllum bermudense*: growth-forms of southern Australian plants. A–C. Markedly branched protuberant specimens from reef edge. A. Side view; B. Top view; C. Surface view of plant in which protuberant branches have become more or less cohesive. (LTB 10668). D. Unattached plants enveloping mollusc shells and small stones. (LTB 15228). E, F. Portions of crustose specimens with highly irregular coalesced outgrowths (See also Figs 9–C). (E = LTB 13260; F = LTB 13056).

plants (e.g. Fig. 3D), although the roof of one buried conceptacle (Fig. 3B) contained more elongate cells than occur in most Australian specimens.

NOMENCLATURE AND SYNONYMY. No matters relating to nomenclature require comment. Foslie (1908a, p.219) suggested that *L. polycephalum* Foslie (1905c, p.16) was very closely related to *L. bermudense*. Comparisons of the type collections of these two entities have revealed that they are concordant in terms of vegetative anatomy. However, the structure of tetrasporangial conceptacles differs somewhat, and while specimens from southern Australia can be linked clearly to the type of *L. bermudense*, they cannot be linked to

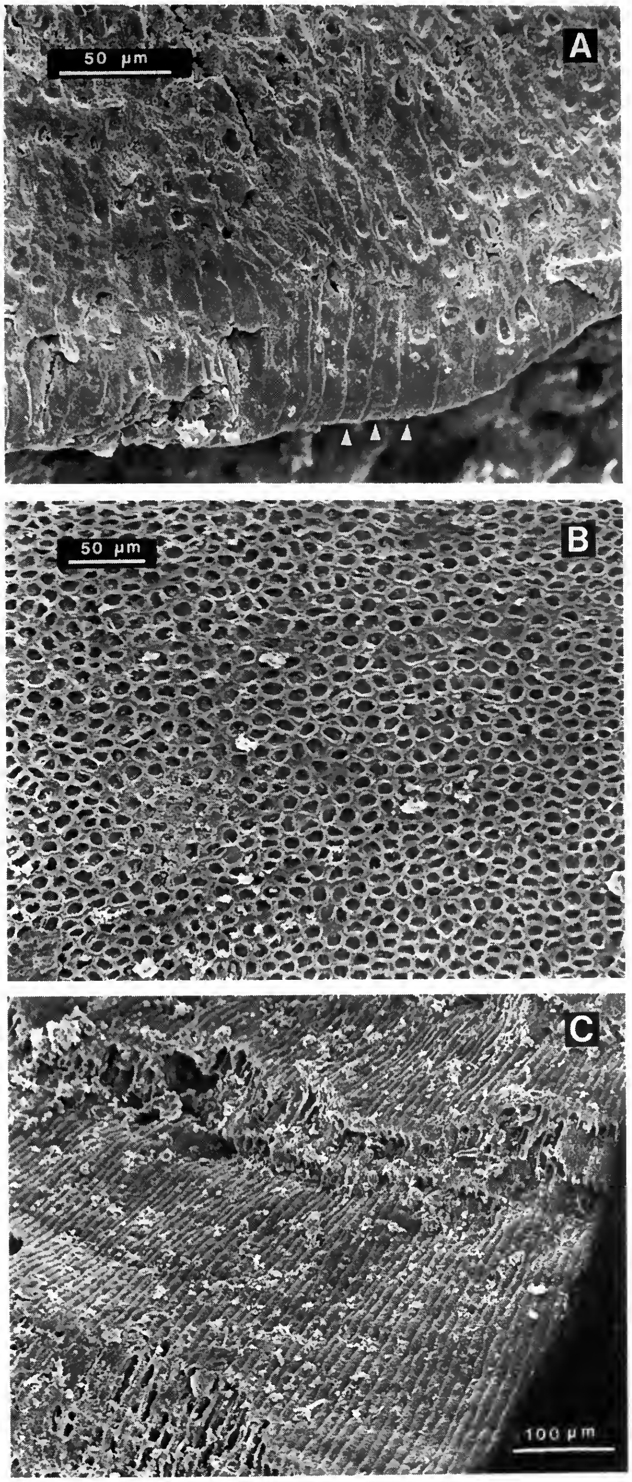


Fig. 6 *Lithophyllum bermudense*: surface features. A. Dorsal view of margin of dimerous portion of thallus in which apices of contiguous filaments (arrowheads) are evident. Arrows denote epithallial concavities. (LTB 13111). B. Portion of dorsal thallus surface with numerous epithallial concavities. (LTB 13111). C. Ventral surface of thallus showing alignment of primigenous filaments in distinct rows (cf. A above). (LTB 13111).

the type of *L. polycephalum* unequivocally. As a result, the two species are kept separate for the present.

DISTRIBUTION AND ECOGRAPHY. *Lithophyllum bermudense* has been found from Cape Vlaming, Rottnest Island, Western Australia eastwards to Walkerville South, Victoria and in northern and eastern Tasmania. One collection from New South Wales (LTB 14684) also has been seen. Specimens have been obtained from February through May and September through December. The species undoubtedly occurs year-round and is the most common species encountered during this study. Of the 91 collections examined, male plants were detected in three (LTB 13365, 15296, 13924) and female/carposporangial plants were detected in 15 (LTB 10675, 12924, 12977, 13115, 13130, 13172, 13187, 13220, 13253, 13573, 13574, 14031, 14381, 14650, 15295). Three of these collections (LTB 13187, 13220, 13365) also contained tetrasporangial individuals, but none apparently contained both male and female/carposporangial individuals.

Elsewhere (Table 8), *L. bermudense* has been reported from Bermuda, Florida, the Caribbean and Juan Fernandez Island. With the exception of the type collection , none of these records have been confirmed during this study. Consequently, nothing definitive can be said at present about the world distribution of *L. bermudense*, and the apparent range disjunction (Bermuda, southern Australia) almost certainly reflects a lack of meaningful data.

In southern Australia, *L. bermudense* has been found intertidally on rocky reefs (usually along reef edges in heavy surf) and in reef pools. Subtidal collections have been detected to depths of 13m on rock or infrequently on molluscs, algae or seagrass (*Amphibolis*) stems. In addition, some populations of unattached plants have been found subtidally at Rottnest Island, W. Australia (e.g. LTB 10589, 10590, 10596, 15228). The type collection (Fig. 2A) is said [Foslie & Howe, 1906: (132)] to occur on calcareous pebbles.

COLLECTIONS EXAMINED:

NEW SOUTH WALES: Newport (*Womersley*, 30 May 1950, LTB 14684, originated from AD A13077 as a gift).

SOUTH AUSTRALIA: Beachport (Post Office Rock) (*Campbell, Penrose & Woelkerling*, 1 December 1986, LTB 15510; *Woelkerling*, 6 November 1987, LTB 15822; *Campbell & Penrose*, 26 February 1988, LTB 15682). Cape Banks (*Cleland,* February–March 1945, LTB 13676, originated from AD A20716 as a gift). Cape Willoughby, Kangaroo Island (*Campbell & Penrose*, 6 April 1988, LTB 15588, 15589; *Woelkerling*, 25 February 1979, LTB 11611). Elliston (Waterloo Bay) (*Turner*, 28 October 1981, LTB 15360, 15363; 31 October 1981, LTB 15375). Head of Great Australian Bight (*Woelkerling, Platt, & Jones*, 13 February 1984, LTB 14381). Nora Creina (*Mitchell*, 26 May 1953, LTB 15895, originated from AD A26532 as a gift). Point Sinclair (Port Le Hunt) (*Woelkerling, Platt, & Jones,* 15 February 1984, LTB 14516; *Womersley*, 26 January 1951, LTB 13636, originated from AD A15212 as a gift). Port Lincoln (Boston Island) (*Woelkerling*, 14 May 1968, LTB 14683). Red Rock Bay, near Carpenter Rocks (*Shepherd*, 26 January 1978, LTB 12430, originated from AD A19647 as a gift). Sceale Bay (Point Westall) (*Platt & Jones*, 16 February 1984, LTB 14527, 14530, 14549). Southwest River (Hansen Bay), Kangaroo Island (*Woelkerling*, 21 February. 1979, LTB 11640).

TASMANIA: Bluestone Bay, Freycinet Peninsula (*Platt & Woelkerling*, 21 February 1983, LTB 13056, 13071). Clydes

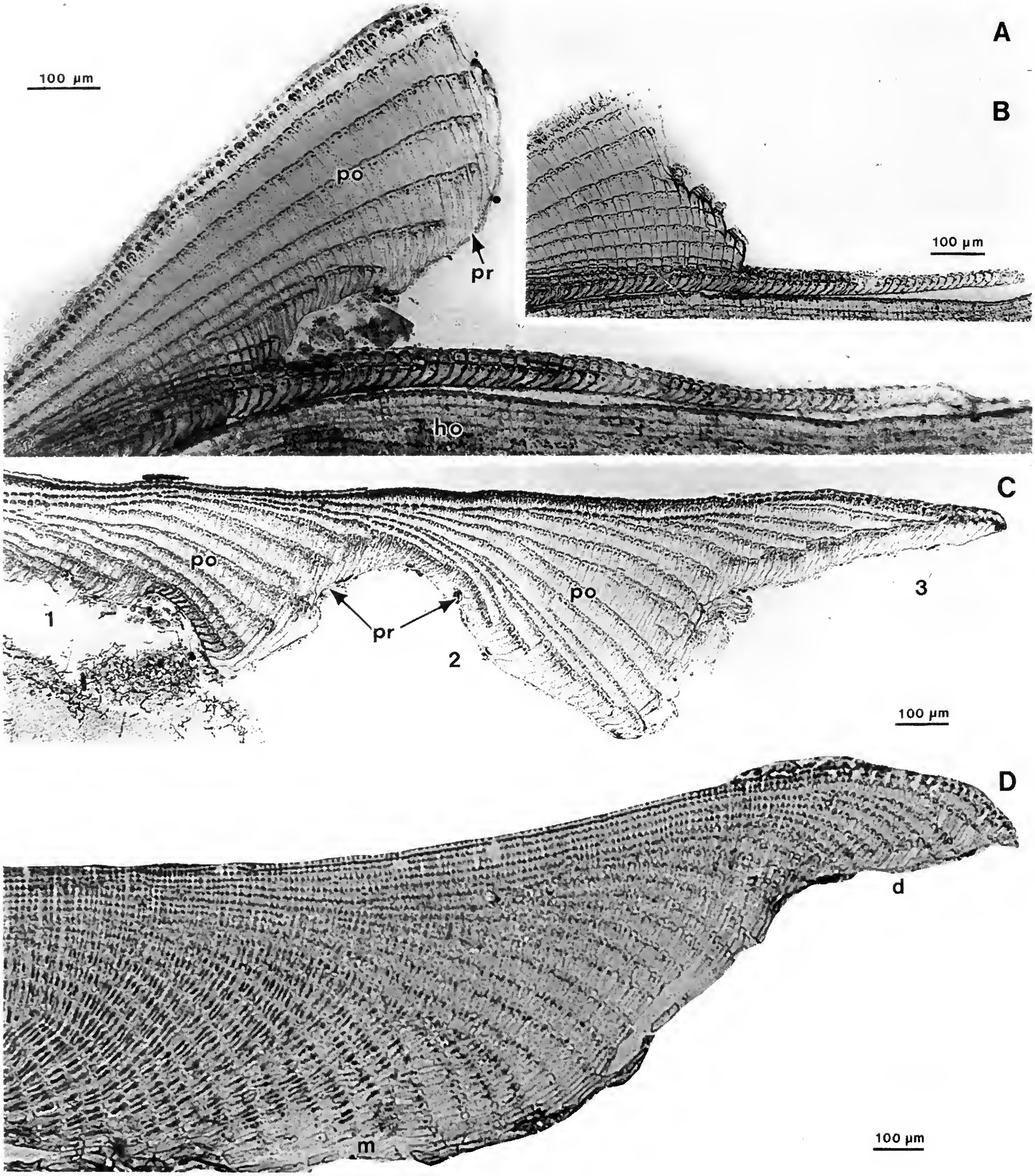


Fig. 7 *Lithophyllum bermudense*: vegetative anatomy (h = host; po = postigenous filaments; pr = primigenous filaments). A. Edge of dimerous thallus in which ventral-most crustose portion 2–3 cells thick is being overgrown by much thicker applanate branch of dimerous construction. (LTB 13188). B. Early stage of applanate branch formation behind the thallus margin. (LTB 13188). C. Margin of crustose portion of a thallus of dimerous construction in which three successive growth spurts (1,2,3) are evident. Note apparent coordinated development of groups of postigenous filaments and the periclinal to curving alignment of postigenous cells of contiguous filaments. (LTB 13130). D. Margin of crustose portion of a thallus in which the edge is of dimerous construction (d) and the remainder of monomerous construction (m). (LTB 12914).

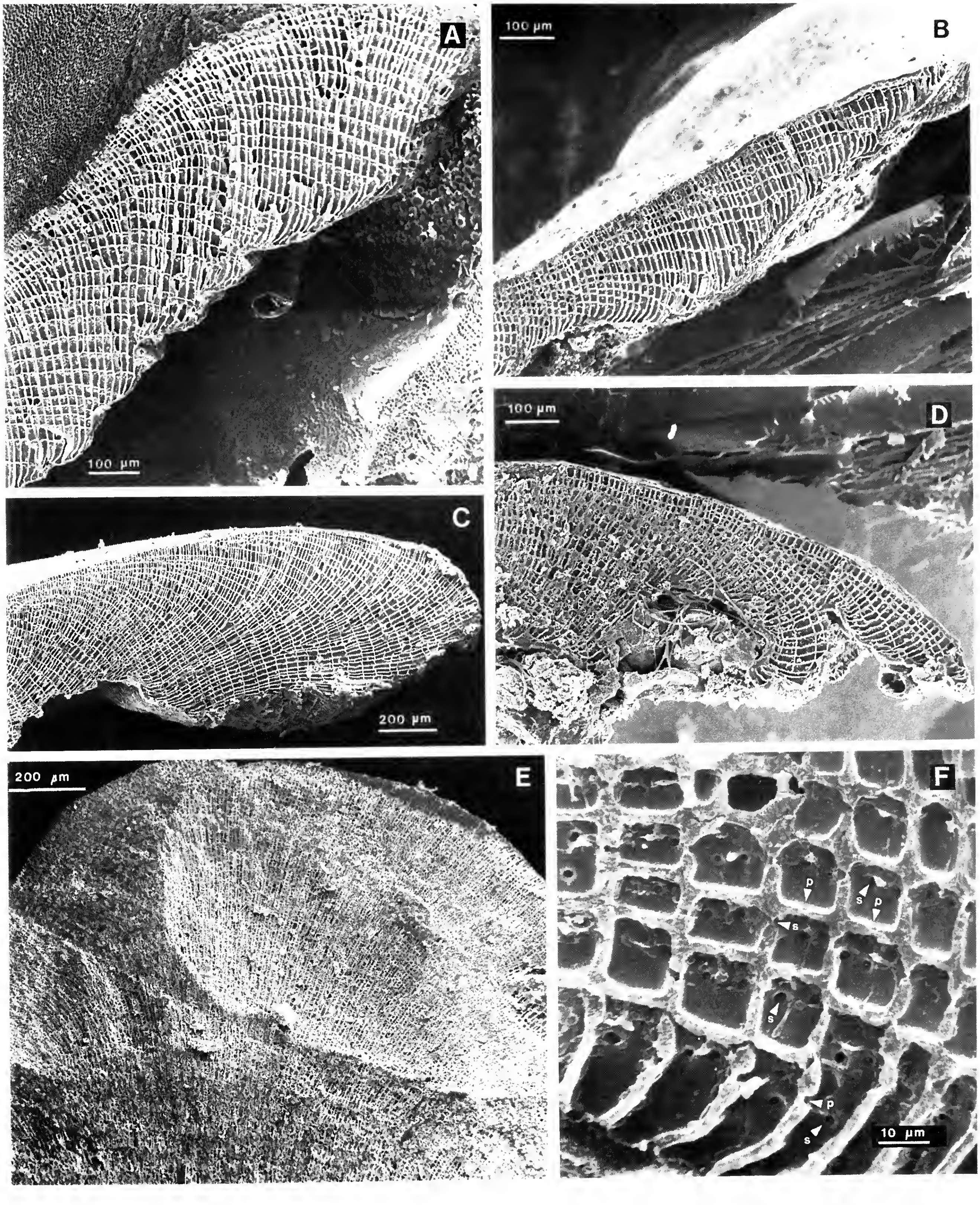


Fig. 8 *Lithophyllum bermudense*: vegetative anatomy. A–B. Margins of crustose portions of thalli showing dimerous construction with (Fig. A) or without (Fig. B) postigenous development at edge. (A = LTB 13111; B = LTB 13188). C. Margin of crustose portion of thallus which shows only monomerous construction. (LTB 13111). D. Margin of thallus in which one applanate branch has completely overtopped another. (LTB 13056). E. Longitudinal fracture of apex of a protuberant branch showing monomerous construction. (LTB 13056). F. Fracture of dimerous portion of thallus in which primary (p) and secondary (s) pits are evident. (LTB 13188).

Island, Eaglehawk Neck (Platt, 26 February 1983, LTB 13320; *Platt & Woelkerling*, 26 February 1983, LTB 13260). Coles Bay, Freycinet Peninsula (*Platt & Woelkerling*, 21 February 1983, LTB 13111, 13115, 13130, 13144). Eddystone Point (*Platt*, 23 February 1983, LTB 13187, 13188, 13189, 14648). Ramsgate, Recherche Bay (*Platt & Brown*, 28 February 1983, LTB 13365, 13370, 13374, 14640, 14650). Rocky Cape National Park (*Platt*, 2 March 1983, LTB 13435). Safety Cove, Port Arthur (*Platt & Woelkerling*, 25 February 1983, LTB 12803, 12817). Sister Bay (Convict Burial Ground) (*Platt*, 16 February 1983, LTB 12913, 12914, 12915, 12924, 14654). Tesselated Pavement, Eaglehawk Neck (*Platt & Woelkerling*, 26 February 1983, LTB 13241, 13243, 13253). Variety Bay, Bruny Island (*Platt, Woelkerling & Brown*, 17 February 1983, LTB 12975, 12977).

VICTORIA: Anglesea (Ingoldsby Reef) (*Beanland*, 6 Dec. 1982, LTB 13573, 13574; 13 Dec. 1982, LTB 15295, 15296). Blanket Bay, Otway National Park (*Campbell, Penrose, & May,* 14 November 1985, LTB 15251). Cape Paterson (Eagles Nest), (*Woelkerling*, 27 November 1976, LTB 12510). Sorrento (Ocean Beach) *(Woelkerling*, 5 December 1976, LTB 12427). Walkerville South (*Woelkerling, Platt, & Beanland*, 30 November 1983, LTB 13906, 13924).

WESTERN AUSTRALIA: Armstrong Point, Rottnest Island (*Woelkerling*, 12 February 1978, LTB 10675). Bunbury (*Woelkerling*, 5 February 1978, LTB 10746, 10747). Cape Vlaming, Rottnest Island (*Woelkerling,* 8 February 1978, LTB 10601, 10603, 10604, 10619). Eucla (*Woelkerling*, 26 January. 1978, LTB 10523). Eyre ('Nine Mile Reef‘) (*Woelkerling, Platt, & Jones,* 1 February 1984, LTB 13963). Green Island, off Rottnest Island (*Woelkerling*, 9 February 1978, LTB 10589, 10590, 10592, 10594, 10596; *Parsons*, 11 November 1968, LTB 15888, originated from AD A33340 as a gift; *Womersley*, 6 September 1979, LTB 13679, originated from AD A51046 as a gift). Jeannies Lookout, Rottnest Island (*Woelkerling*, 9 February 1978, LTB 10623, 10631). Mabel Cove, Rottnest Island (*Woelkerling*, 12 February 1978, LTB 10639, 10645). North Point Reef, Rottnest Island (*Woelkerling*, 10 February 1978, LTB 10664, 10668). North Point Reef, Rottnest Island (collector unknown, February. 1951, LTB 13660, originated from AD A16506 as a gift). Parker Point, Rottnest Island (*Walker*, 26 November 1985, LTB 15228). Point Valliant, Two People Bay, Albany (*Woelkerling*, 2 February 1978, LTB 10725). Radar Reef, Rottnest Island (*Woelkerling*, 9 February 1978, LTB 10652). Strickland Bay, Rottnest Island (*Marsh*, 8 February 1978, LTB 10678). Twilight Cove, Eyre (*Woelkerling, Platt, & Jones*, 2 February 1984, LTB 14031, 14038, 14043, 14061).

BERMUDA: Spanish Point (*Howe*, 21 June 1900, TRH, unnumbered). Holotype.

REMARKS ON MORPHOLOGY AND ANATOMY. *L. bermudense* shows the greatest morphological and anatomical variation of all species studied. External features provide no reliable clues regarding specific or generic affinity, and identification to species can be effected only from sections of tetrasporangial conceptacles in which the pore canal is obvious and clear.

Some plants (e.g. Fig. 4C) closely resemble specimens in the type collection (Fig. 2A) in external appearance. The overall spectrum of growth-forms, however, ranges from flat (complanate) (Figs 4A–4B) to warty (Figs 4D–4F) to protuberant [in which branches may or may not become coherent] (Figs 5A–5C) to lumpy (Fig. 5D) to coalesced (Figs 5E,5F). Plants belonging to all growth-forms are concordant repro-

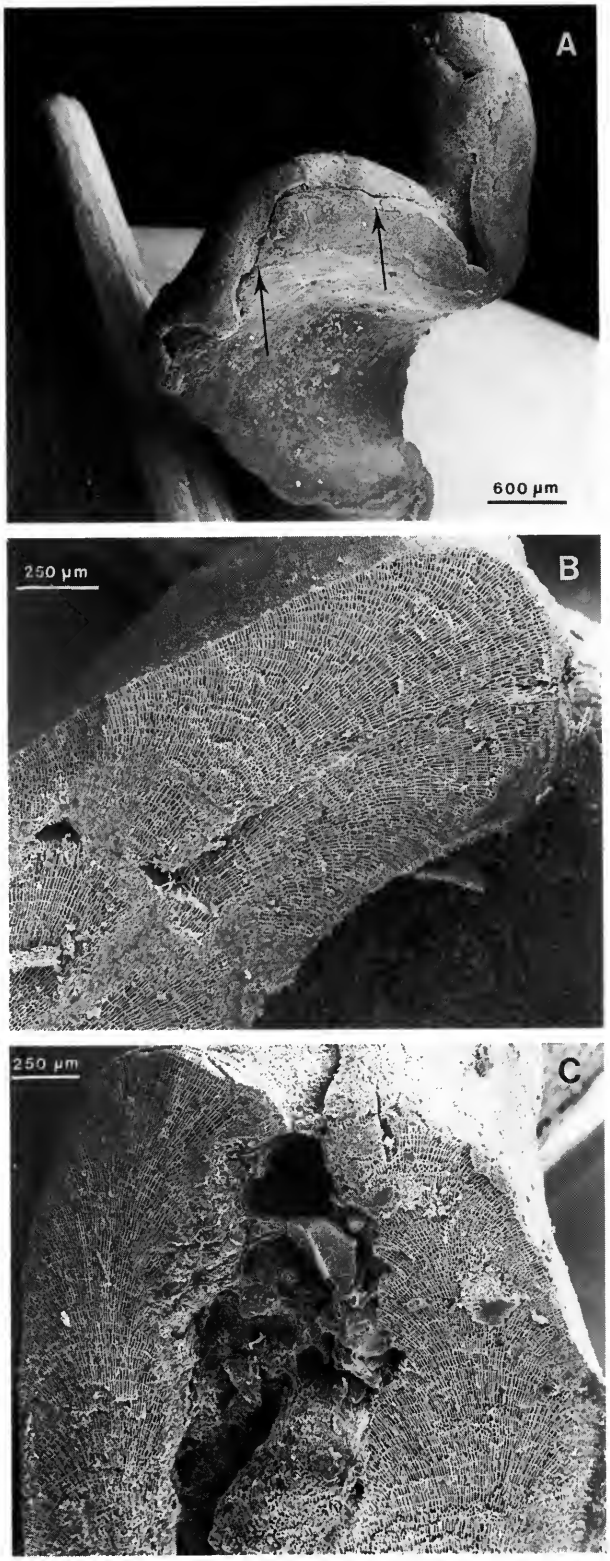


Fig. 9 Lithophyllum bermudense: Coalesced outgrowths formed from ascending, abutting, applanate branches. (LTB 13056). A. Surface view of a coalesced outgrowth showing line (arrows) of abutment of opposing branches. (Fig. 5F shows habit view of a group of these coalesced outgrowths). B,C. Fractures through coalesced outgrowths showing firm [B] and loose [C] abutment of opposing branches. Note monomerous construction.

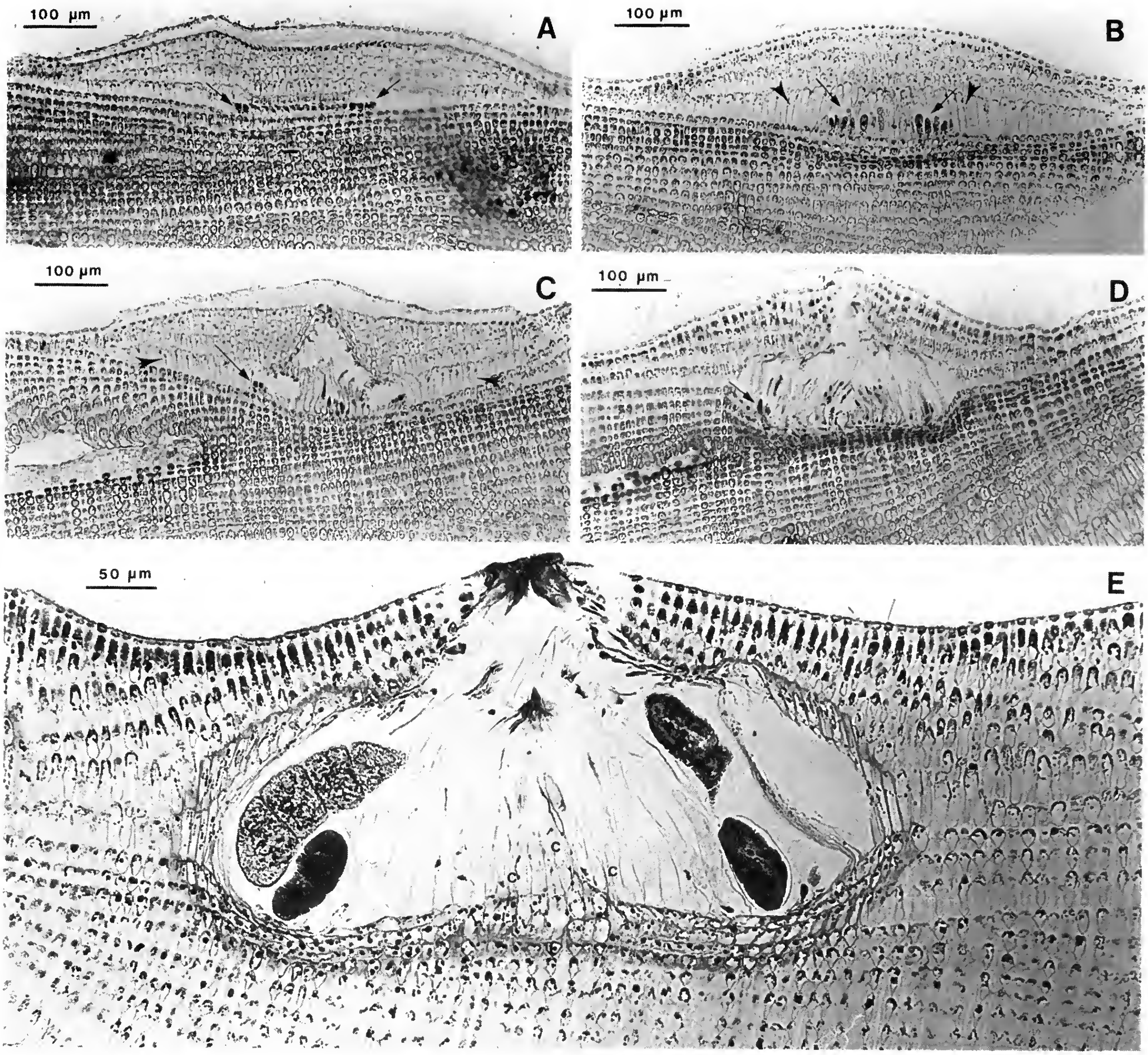


Fig. 10 *Lithophyllum bermudense*: tetrasporangial conceptacle ontogeny. A.–D. Stages in tetrasporangial conceptacle development. Note sporangial initials (arrows), a layer of cavity cells (arrow heads) which degenerate to form the conceptacle chamber, the remains of an old vegetative epithallial layer overlying the developing roof (Figs A,C), and how floor of conceptacle chamber gradually becomes immersed due to continued development of surrounding vegetative filaments. (LTB 13188). E. Mature tetrasporangial conceptacle with degenerate columella (c) and with numerous small cells appearing to line the chamber floor. (Compare with Figs 11 C–F and B12 A–F). (LTB 14654).

ductively. The multiplicity of growth-forms in *L. bermudense* is yet another example (e.g. see Adey, 1966; Bosence, 1983, 1985; Lee, 1967; Steneck & Adey, 1976) of the marked polymorphism which can occur within single species. Growth-forms of *L. bermudense* intergrade gradually into one another, thus proscribing any attempt to describe them in formal taxonomic terms.

Parallel ridges and grooves demarcating the positions of individual primigenous filaments are evident dorsally along the margins of dimerous portions of plants (Fig. 6A). As in *L. pustulatum* (Fig. 52B), more marked grooves and ridges outlining primigenous filaments can occur on ventral surfaces of thalli (Fig. 6C), and numerous epithallial concavities caused by the collapse of epithallial cell walls may be evident on dorsal thallus surfaces (compare Figs 6B & 52D). These features appear not to be taxonomically significant.

Both dimerous and monomerous construction occur, usually within single individuals. Crustose portions of plants may be dimerous, monomerous or both (Figs 7, 8A–8D). In protuberances, however, only monomerous construction has been found (Figs 8E, 9A–9C). *L. bermudense*, along with some plants of *L. corallinae*, are the only southern Australian species of *Lithophyllum* in which monomerous construction occurs.

Variation in the internal structure has been elucidated mainly from margins of crustose portions of plants (Figs 7,

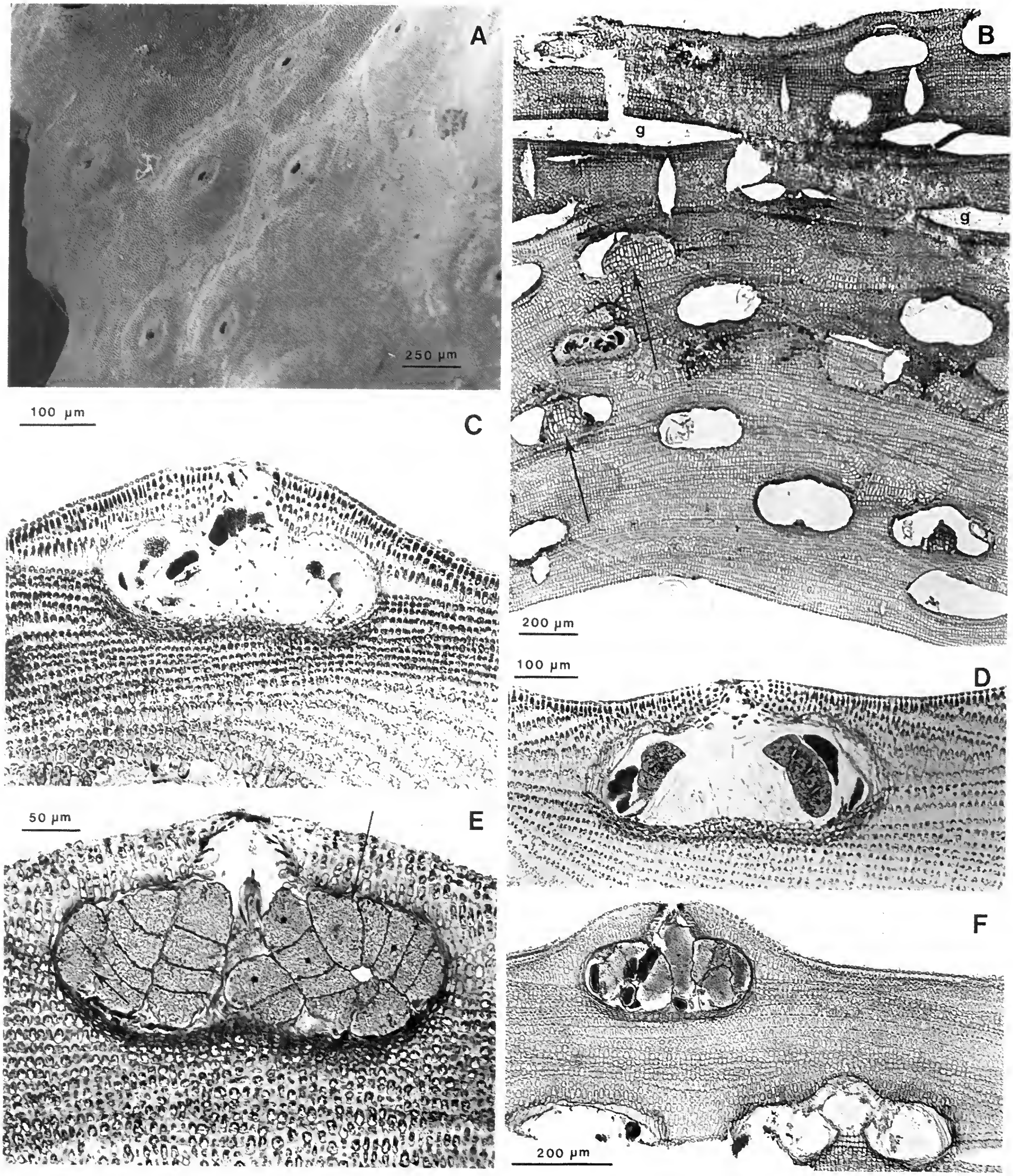


Fig. 11 *Lithophyllum bermudense*: tetrasporangial conceptacles. A. Surface view of a group of conceptacles. Note how roof may be flush with thallus surface or protrude somewhat above it. (LTB 13111). B. Section through portion of a thallus containing a number of buried conceptacles. Note how conceptacle may become infilled (arrows) and gaps (g) in vegetative tissue. (LTB 14684). C–E. Examples of conceptacles in which chamber floor lacks a central hump of pseudoparenchymatous filaments. Note variation in size of sporangia and that a columella may [D] or may not [E] be evident; also note bisporangia and pentasporangia (E, arrows). (C = LTB 13111; D = LTB 14654; E = LTB 10668). F. Plant in which adjacent conceptacles lack (left) or possess (right) a central pseudoparenchymatous hump on the chamber floor. (LTB 10631).

8A–8D). Where dimerous construction occurs, the extreme margin usually consists only of primigenous filaments or of primigenous filaments with dorsal epithallial cells (Figs 7A–7C). Nearly all primigenous cells appear palisade (Fig. 7C), and extensive rows of nonpalisade cells like those in parts of the holotype material (Fig. 2B) have not been detected.

Almost always, however, multicellular postigenous filaments develop immediately behind the margin. In one collection (LTB 13188), however, some portions of the thallus show more extensive primigenous margins (compare Figs 7A & 7B with 8B), while in another collection (LTB 13111) multicellular postigenous filaments occur right at the thallus margin (Fig 8A). Margins a number of cells thick also occur in cases where monomerous construction is present (Fig. 8C). Monomerous and dimerous construction can occur along different portions of the margin of the same plant (compare Figs 8A & 8C), or the margin may be dimerous while portions a short distance behind the margin are monomerous (Fig. 7D).

In dimerous portions of plants, cells of contiguous postigenous filaments are commonly aligned horizontally, giving the impression of periclinal banding within the thallus (e.g. Figs 7C, 8A, 8B). Such bands, which may be uniform or vary in height across portions of thallus, also have been found in *L. corallinae* and *L. pustulatum* and are considered in somewhat greater detail in the account of *L pustulatum* (q.v.).

Applanate branches have been found in some plants. In LTB 13188 (Figs 7A, 7B), applanate branches appear to originate at some distance behind the thallus margin, quickly develop multicellular postigenous filaments, and then begin to overgrow the subtending portion of thallus. In LTB 13056 (Fig. 8D), in contrast, applanate branches apparently form closer to the margin, contain (at least initially) comparatively short postigenous filaments, and quickly extend beyond the margin of the subtending branch. This latter pattern also has been found in some plants of *L. pustulatum* (Fig 53B) and is quite different from the situation in *L. prototypum* (Fig 44A) where younger applanate branches usually do not outgrow subtending branches.

Coalescent branches (Figs 5E, 5F, 9), in marked contrast, are formed from opposing, flattened (applanate) branches which have abutted and grown more or less upright. Longitudinal fractures of coalescent branches clearly show that at least two branches, each of monomerous construction and dorsiventral organization, are involved.

Both protuberant branches and coalescent branches may occur on the same thallus. Protuberant branches are single, homogeneous structures of monomerous construction and more or less radial organization. In longitudinal sections/fractures, they contain a central core of filaments and a more peripheral region where core filaments or their derivatives curve outwards to the surface (Fig. 8E). Protuberant branches occur commonly in other nongeniculate corallines (e.g. Penrose & Woelkerling, 1988: fig. 27; Woelkerling, 1988: figs 19, 90, 196; Woelkerling & Irvine, 1986: fig. 6) and are usually cylindrical or more or less compressed in form (e.g. Fig. 5A).

Throughout the thallus, successive cells of the same filament are linked by primary pit-connections, and cells of adjacent filaments are linked by contiguous secondary pit-connections (Fig. 8F). Adjunctive secondary pit-connections, cell fusions and trichocytes were not detected.

Tetrasporangial (Figs 3D, 10, 11, 12) and gametangial (Figs 13, 14) conceptacles occur; conceptacle roofs are more or less flush with the thallus surface or protrude only slightly above it.

Tetrasporangial conceptacle development (Figs 10A–10E) involves groups of sterile filaments interspersed amongst sporangial initials. In the youngest stages seen (Figs 10A, 10B), a small solid mound of filaments and sporangial initials were evident, but a conceptacle chamber had yet to form. Conceptacle primordia develop just beneath a layer of epithallial cells, the remains of which sometimes persist (Figs 10A, 10C) before degenerating completely and disappearing. As conceptacles develop further, surrounding vegetative filaments also develop further such that the chamber floors of mature conceptacles become situated seven or more cells (rarely five or six cells) below the surrounding thallus surface (compare Figs 10C, 10D, 10E).

The sterile filaments interspersed amongst sporangial initials are involved both in roof and chamber formation. At an early stage (Figs 10A, 10B), the basal-most cells of a number of filaments elongate to form cavity cells. Eventually, a number of cavity cells (presumably along with cells above some of them) degenerate, thereby resulting in formation of a conceptacle chamber and a pore canal (Figs 10C, 10D, 10E). In most conceptacles, entire cells or remnants of some of the more centrally situated cavity cells persist as a columella (Figs 10C–10E, 12C, 12D). Sterile filaments and portions thereof which do not degenerate contribute to formation of the conceptacle roof. Details of the development of sporangial initials (Fig. 10A, 10B) into mature sporangia remain unknown, although stalk cells were seen in one mature conceptacle (Fig. 12B).

Intact portions of filaments above the chamber collectively form a roof of characteristic but somewhat varying structure (Figs 10E, 11C–11F, 12A–12F). Pore canals are never completely occluded (filled) by enlarged cells as, for example, in *L. chamberlainianum* (e.g. Fig. 18D) and *L. irvineanum* (e.g. Fig. 35A). Sometimes, however, a mucilaginous plug of uncertain origin covers the pore (e.g. Figs 10E, 12C, 12D) without filling the entire canal.

Most roof filaments above the chamber contain three to seven intact cells including a terminal epithallial cell. Cells vary in length with short and long ones commonly intermixed (Figs 10E, 11C–11F, 12A–12F). Sometimes a few elongate, adjacent subepithallial cells occur within a roof (e.g. Figs 10E, 11C, 12B), but roofs containing a layer of subepithallial columnar cells were found only in some conceptacles of one Tasmanian collection (LTB 13365, Fig. 3D). In certain conceptacles (e.g. Fig. 12E), roof filaments close to the pore canal contained more intact cells than other parts of the roof, thus making the central roof area look thicker. In other conceptacles (e.g. Fig 12D) the roof was more uniformly thick and in still other conceptacles (e.g. Fig. 10E) the roof became thinner near the pore canal.

Some variability also occurs in other conceptacle features, but this is of no taxonomic significance. Thus, for example, adjacent conceptacles within the same thallus, may have or lack such a hump (Fig. 11F). Similarly, conceptacles may (e.g. Fig. 12B) or may not (e.g. Fig. 12A) have several layers of very small cells lining the chamber floor, and this difference can occur in adjacent conceptacles (Fig. 11F). Pore canals may or may not have cells of various shapes and sizes protruding into them from adjacent roof filaments (compare Figs 10E, 11C–11E, 12), but none of these protrusions occur in a constant or consistent manner. The floors of all concep-

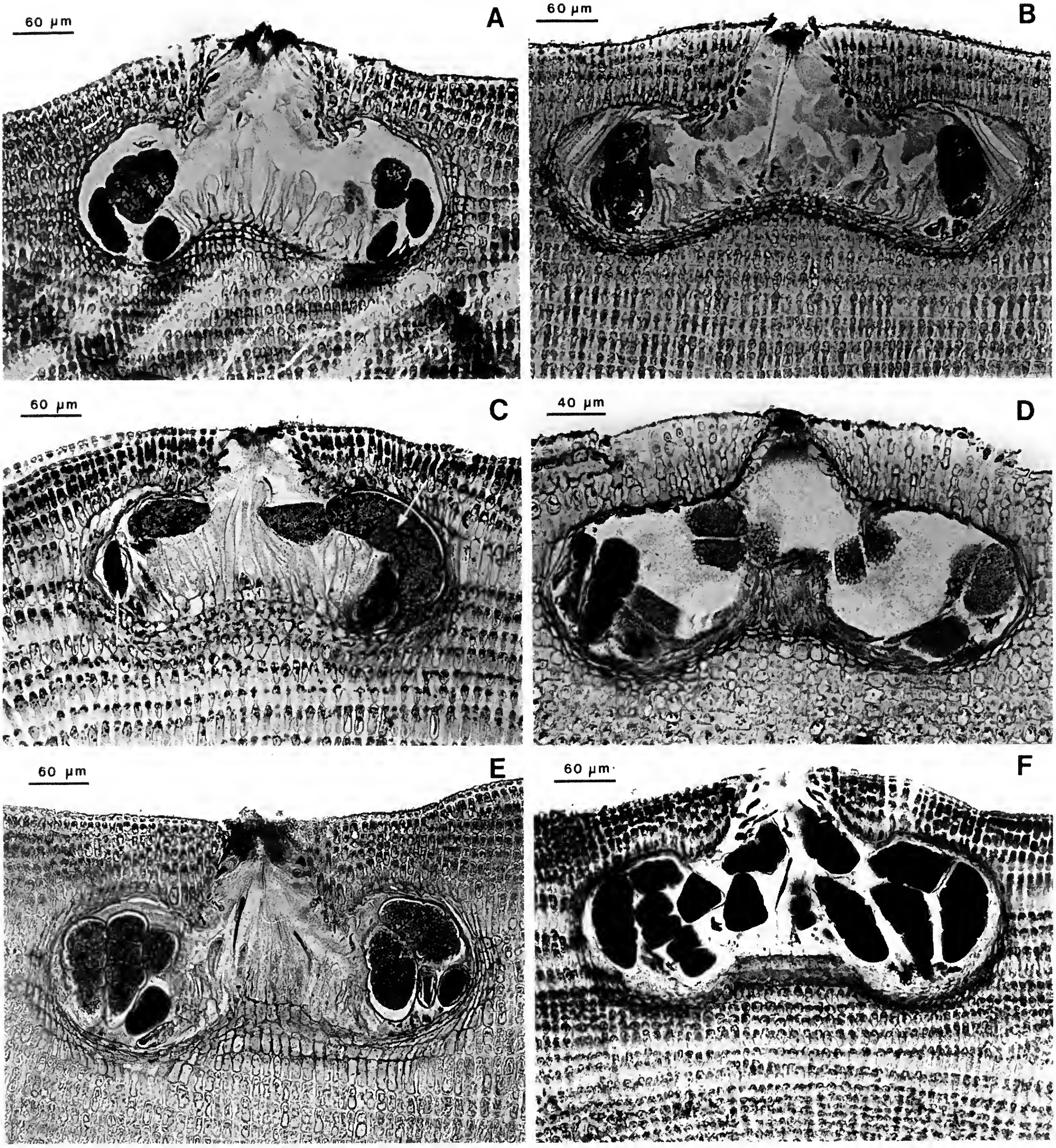


Fig. 12 *Lithophyllum bermudense*: tetrasporangial conceptacles. A–F. Examples of conceptacles in which chamber floor possesses a central hump of pseudoparenchymatous filaments. Note variation in extent of hump, in size of chamber, in size of sporangia within a single conceptacle (C, arrows), the extent of columella development, the occurrence and size of cells protruding into the pore canal, the number of intact cells in roof filaments above the chamber and the extent to which the chamber floor lacks (e.g. 12A) or possesses (e.g. 12B) a 'lining' of numerous small more or less compressed cells. (A = LTB 13260; B = LTB 13187; C= LTB 12803; D = LTB 10619; E = LTB 13056; F = LTB 12915).

tacles observed were subtended by multicellular filaments; in no case was a floor formed from primigenous cells.

In most conceptacles, tetrasporangia are situated peripherally within the conceptacle chamber and the central area is occupied by a hump or by a columella (e.g. Figs 12D–12F). Sometimes, however, sporangia can occur across the entire chamber floor and a columella appears absent (e.g. Figs 11E, 11F). Within a given conceptacle individual mature sporangia

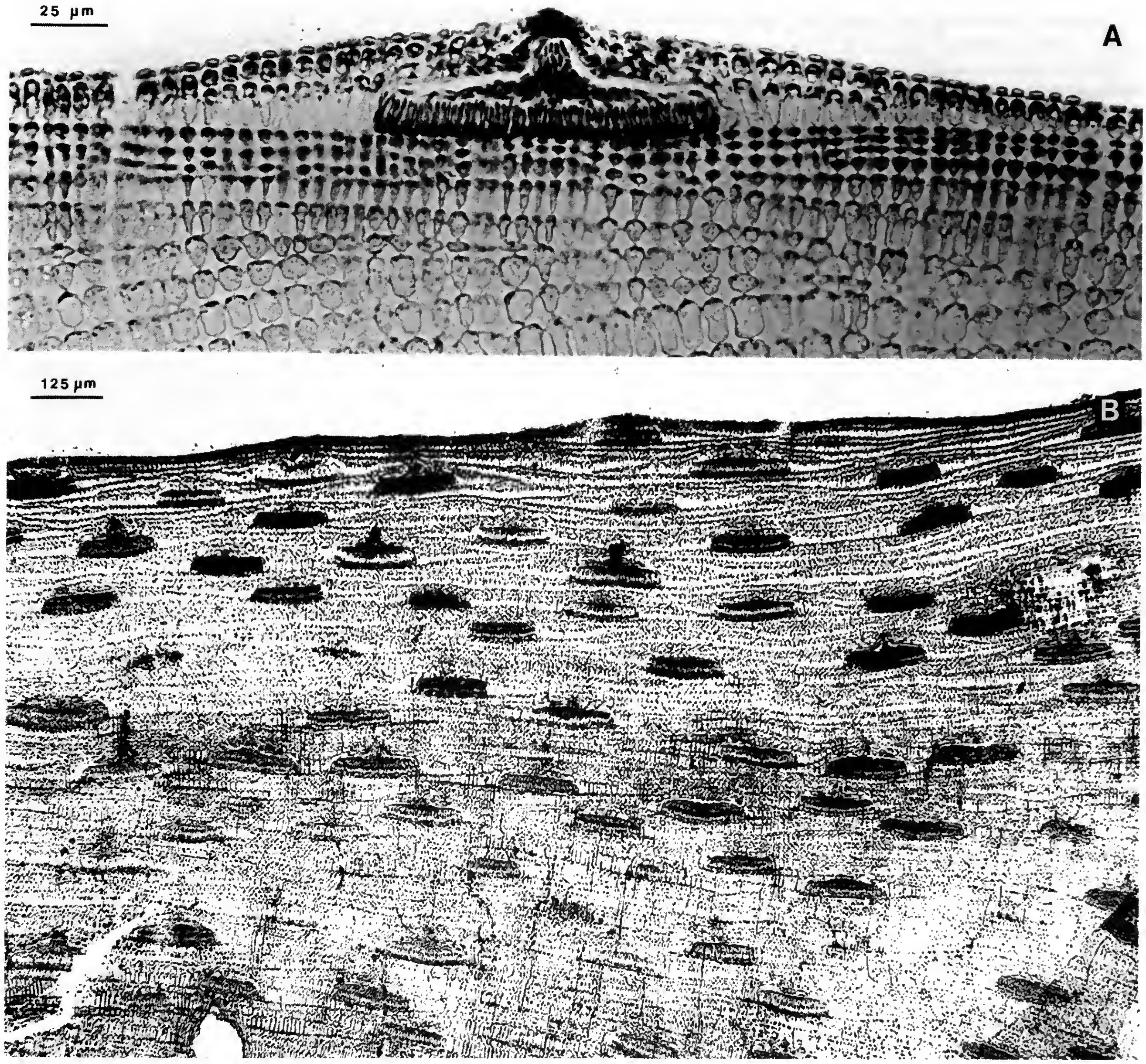


Fig. 13 *Lithophyllum bermudense*: male conceptacles. A. Mature male conceptacle with simple spermatangia on conceptacle chamber floor. (LTB 15296). B. Section of plant with numerous buried male conceptacles. (LTB 13365).

can vary enormously in size (e.g. Figs 10E, 12C) or be more uniformly large (e.g. Fig. 11E) or small (e.g. Fig. 12F). Older conceptacles commonly become buried as a result of continued vegetative development (Figs. 11B, 11F), and sometimes they become infilled by renewed growth of filaments beneath the conceptacle floor (Fig. 11B).

Two bisporangia and a single pentasporangium occurred intermixed with tetrasporangia in one conceptacle (Fig. 11E). Conceptacles containing both bisporangia and tetrasporangia have not been found in other southern Australian collections of *Lithophyllum* but are known in other nongeniculate corallines (e.g. see Woelkerling 1988: fig. 36). Pentasporangia appear not to have been recorded previously in nongeniculate corallines; whether such pentaspores are viable remains unknown.

Male conceptacles have not been reported previously. Only mature conceptacles have been found (Figs 13A, 13B); roofs contain two groups of filaments. Filaments immediately bordering the chamber are branched. Each consists of a main axis which curves over and encloses the chamber and of one to three celled laterals which arise secundly and collectively from the central part of the roof. Remaining roof filaments are unbranched; each consists of two or three cells including a terminal epithallial cell situated at the roof surface. The basal cell of each three-celled filament near the chamber may be distinctly more elongate than other cells but it does not senesce like cavity cells in tetrasporangial conceptacles. Spermatangia are simple and borne on initials across the entire chamber floor. Each initial can bear one to three more or less club-shaped spermatangia. In at least some plants (e.g. Fig.

13B), male conceptacle production can be prolific, and intact conceptacles containing spermatangia can readily become buried within a thallus.

Female/carposporangial conceptacles have not been reported previously. Only a few developmental stages have been found (Figs 14, 15). By the time mature carpogonial branches develop, the conceptacle roof appears to be completely formed (Figs 14A, 14B). Carpogonial branches occur across the entire floor and bear 1 (occasionally 2) terminal carpogonia; carpogonia beneath the pore are usually distally prolonged into trichogynes (Fig. 14B).

Roof filaments flanking the chamber and pore canal more or less overtop peripheral portions of the chamber and produce short branches which terminate in cells lining the pore canal. These cells can vary somewhat in shape and size and protrude to varying degrees into the canal (Figs 14B, 15). These filaments do not terminate in epithallial cells. Remaining roof filaments appear to be unbranched, usually contain four to ten cells and terminate in an epithallial cell (Figs 14A, 14B, 15). Basal cells of roof filaments may become elongate (i.e. become cavity cells) and senesce, thus increasing the size of the chamber (Figs 14B, 15A).

Carposporophytes arise within female/carposporangial conceptacles after presumed karyogamy. A fusion cell forms across the chamber floor (Fig. 15A), and remains of old carpogonial branches persist on the dorsal surface. Details of fusion cell ontogeny have not been elucidated. Eventually gonimoblast filaments are produced from the margin of the fusion cell, and these bear carposporangia (Figs 15B–15D). In some cases (Fig. 15C), only terminal carposporangia occur, but in other cases (Figs 15B, 15D) what appear to be catenate carposporangia were observed. Further study is required to determine whether sporangia really do form in chains.

Spore germination and very early thallus development have not been observed.

Published references to *L. bermudense* (and its synonyms) from outside Australian waters are summarized in Table 8. With exceptions of the protologue (Foslie & Howe 1906) and of Campbell & Woelkerling (1990), these reports contain few

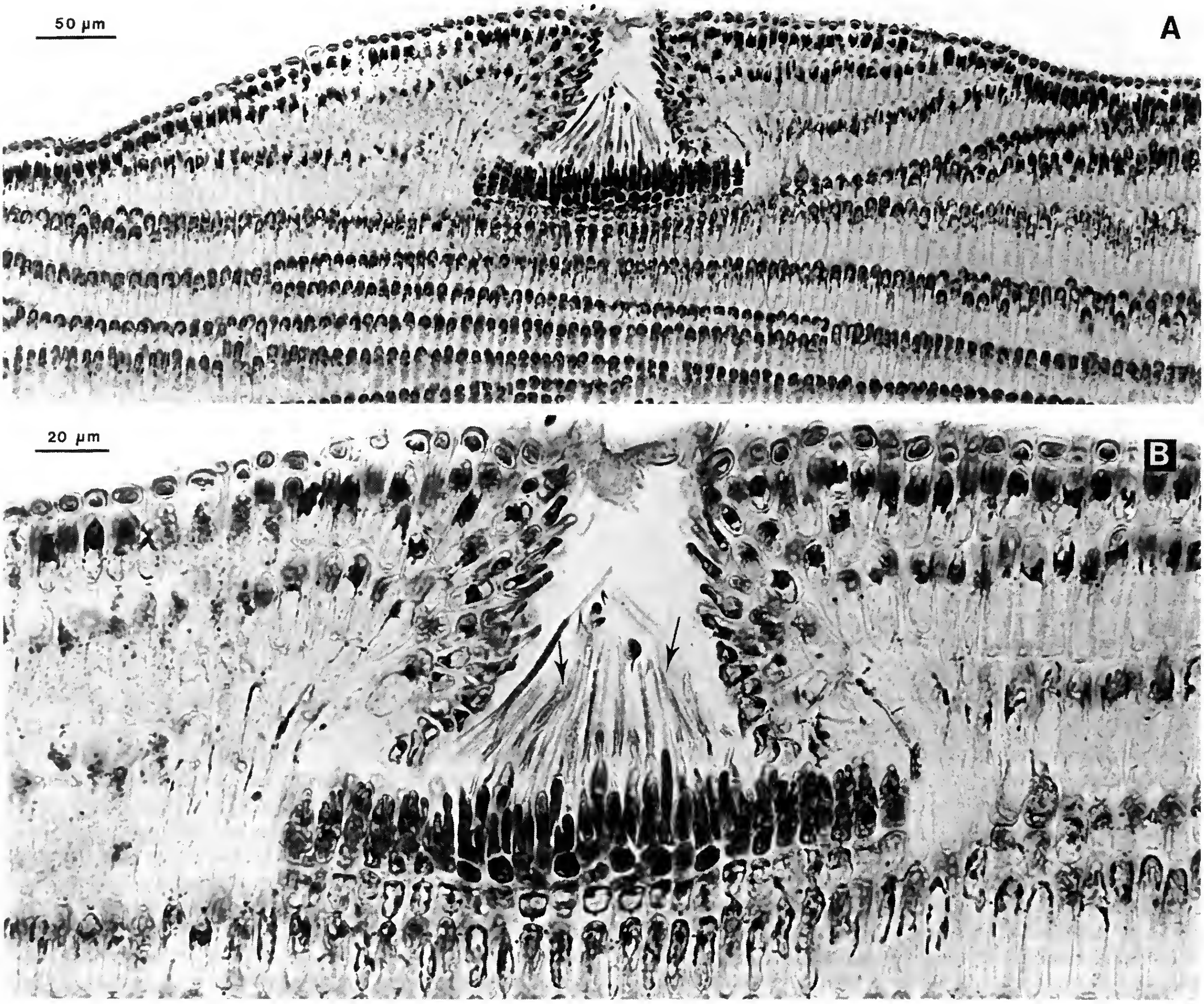


Fig. 14 *Lithophyllum bermudense*: female/carposporangial conceptacles. A. Habit of conceptacle. Note broad expanse of sterile roof filaments flanking conceptacle chamber. (LTB 13253). B. Mature carpogonial branches. Note trichogynes (arrows). (LTB 13253).

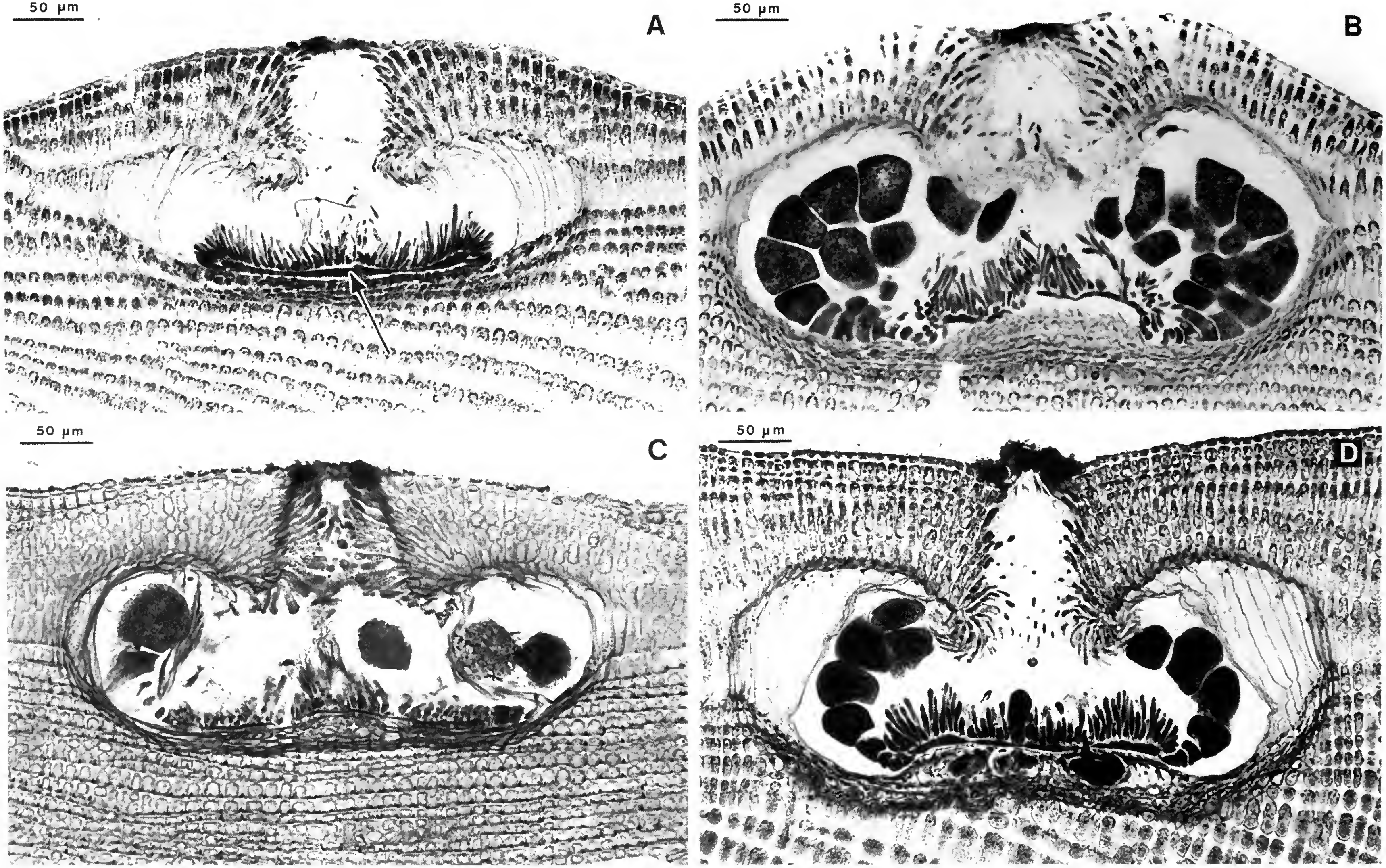


Fig. 15 *Lithophyllum bermudense*: carposporophytes. A. Fusion cell (arrow) prior to gonimoblast filament formation. Note remains of old carpogonial branches on dorsal surface of fusion cell. (LTB 13120). B–D. Mature carposporophytes. Note variation in conceptacle roof anatomy and how sporangia may [B, D] or may not [C] occur in apparent chains. (B = LTB 13320; C = LTB 10675; D= LTB 12924).

Table 8 Published records of *Lithophyllum bermudense* and its synonyms. Names used by authors are listed alphabetically. Localities are listed in parentheses; superscripts refer to notes at end of table. Authorities for names given in synonymy listings.

Dermatolithon bermudense

Dawson in *Essays Nat. Sci. Hon. A. Hancock:* 274 (1955) (Bermuda) [1]. De Toni, *Sylloge Algarum* 6: 668 (1924) (Bermuda, Florida) [1,2,3]. Foslie in *K. norske Vidensk. Selsk. Skr.* 1909(2): 58 (1909) [4]. Lemoine in *Bull. Soc. Bot. Fr.* 117: 550, 552 (1971) [1,4].

Lithophyllum bermudense

Adey & Lebednik, *Catalog Foslie Herbarium*: 41 (1967)(Bermuda, Florida) [3]. Campbell & Woelkerling in *Phycologia* 29: 119, fig. 13 (1990) (Bermuda) [16]. Etcheverry, D., *Alg. Mar. Benth. Chile*: 199 (1986) (Juan Fernandez) [5]. Foslie in *K. norske Vidensk. Selsk. Mus. Aarsbetetn*. 1904: 16 (1905c) [4,6]. Foslie in *Dt. Sudpol.-Exped*. B(VIII): 219 (1908a) [4,7]. Foslie & Howe in *Bull. N.Y. Bot. Gdn* 4(13): (132), pl.81, fig.3, pl85, fig.3, pl.92 (1906) (Bermuda, Florida) [3,8]. Howe in N.L. Britton, *Flora of Bermuda*: 538 (1918) (Bermuda) [1,2]. Levring in *Nat. Hist. Juan Fernandez & Easter Is*. 2(Bot.): 756, figs 1d,1e (1943) (Bermuda, Florida, Juan Fernandez) [3,9,10]. Printz, *M. Folsie Contr. Monogr. Lithothamnia*: 32, pl.72, fig.19 (1929) (Bermuda) [11]. Taylor, *Mar. Alg. East. Trop. Subtrop. Coasts Am.*: 393 (1960) (Bermuda, Florida) [2,3].

Tenarea bermudense

Adey in *K. norske Vidensk. Selsk. Skr*. 1970(1): 6 (1970) [4]. Adey in J. Gray & A.J. Boucot, *Hist. Biogeog. Pl. Tect. & Chg. Environ.*: 461, 462 (1979) (Caribbean) [12]. Bosellini & Ginsburg in *J. Geol*. 79: 676 (1971) (Bermuda) [12,13].

Titanoderma bermudense

D. Littler et al., *Mar. Pl. Caribb.*: 218 (1989) (Caribbean) [13,14,15]. Woelkerling et al. in *Phycologia* 24: 333 (1985) [4]

Notes on Table 8

[1] Data provided by author based only on studies of previous literature.
[2] Includes description of species.
[3] Record from Florida not confirmed during present study.
[4] Locality data not given.
[5] Record not confirmed during present study; probably based on report of Levring (1943).
[6] *Nomen nudum*.
[7] Incidental mention only.
[8] Protologue.
[9] Record from Juan Fernandez not confirmed during present study.
[10] Some new morphological/anatomical data provided.
[11] Includes photo of holotype specimen.
[12] Incidental ecographic data presented.
[13] Record not confirmed during present study.
[14] Includes new morphological and ecological information.
[15] Color photograph provided.
[16] Includes some anatomical data on lectotype specimen.

morphological/ anatomical data.

Relationships of *L. bermudense* to other species are considered below (p.97).

INFRASPECIFIC TAXONOMY. No infraspecific taxa of *L. bermudense* have been recognized.

2. **Lithophyllum chamberlainianum** Woelkerling et Campbell, sp. nov.

Figs 16–21

HOLOTYPE. LTB 14334 (Lucky Bay, Cape Le Grand National Park, Esperance, Western Australia, *Woelkerling, Platt, & Jones*, 9 February 1984; epiphytic on *Laurencia*). Fig. 16A.

MISAPPLIED NAMES. No published misapplications of other names to specimens of *L. chamberlainianum* were discovered during this study.

ETYMOLOGY. The specific epithet honours Dr. Yvonne M. Chamberlain for her numerous, significant contributions to nongeniculate coralline taxonomy.

PREVIOUSLY PUBLISHED ILLUSTRATIONS OF AUSTRALIAN PLANTS. Woelkerling 1988: 114, fig. 95 (as *Titanoderma* sp.).

LATIN DIAGNOSIS:

L. chamberlainianum characteribus generis *Lithophyllum*; differt de speciebus affinibus inter alia quod canalis pori conceptaculorum tetrasporangium a fasciculo cellulanum amplifactum tubularium superimpositorum obstructus est.

The characteristics of *Lithophyllum* are given in Table 1; features delimiting *L. chamberlainianum* as a species and its relationships to other species are considered below.

DESCRIPTION. Plants mostly 0.05–2.5 mm across and 0.04–0.5 mm thick; flat (complanate) to layered (without conspicuous terracing); completely or partially adherent.

Thallus dimerous; primigenous filaments usually composed of palisade cells 5–15 μm long and (13–)20–75(–90) μm tall; postigenous filaments composed only of epithallial cells 2–7 μm long and 4–12 μm in diameter. Contiguous secondary pit-connections common; adjunctive secondary pit-connections, cell fusions, and trichocytes not seen.

Tetrasporangial/bisporangial plants with scattered protruding conceptacles. Conceptacle roofs 370–520(–703) μm in external diameter; roof filaments above chamber usually 2–4(–5) cells long; cells (5–)10–27(–35) μm long and 2–15 μm in diameter, with columnar cells commonly occurring in subepithallial horizontal groups. Pore canals completely occluded by a conglomerate of enlarged, conspicuously elongate, more or less tubular and sometimes inflexed cells which usually project above surrounding roof surface. Conceptacle chambers (145–)175–210(–252) μm in diameter and (60–)80–120(–135) μm tall; floor of mature chambers usually 1 cell below thallus surface; tetrasporangia/bisporangia (35–)55–95(–118) μm long and (16–)20–35(47) μm in diameter, scattered across chamber floor or peripheral to a columella.

Gametangial plants dioecious. Male conceptacle roofs protruding; chambers 160–200 μm in diameter and 29–55 μm tall; spermatangial branches confined to chamber floor, simple, with each initial bearing one to several elongate spermatangia. Female/carposporangial conceptacle roofs protruding; chambers 160–225(–259) μm in diameter and 81–115 μm tall; carpogonial filaments arising from chamber floor, usually 2–3 cells long and bearing 1(–2) carpogonia terminally.

Carposporophytes developing within female conceptacles after presumed karyogamy; each comprising a central more or less flattened fusion cell and some several–celled gonimoblast filaments arising peripherally with terminal carposporangia 20–30(–52) μm in diameter.

DIAGNOSTIC FEATURES. *L. chamberlainianum* differs from other southern Australian species in having the following combination of features:

1. Entire pore canals of tetrasporangial/bisporangial concep-

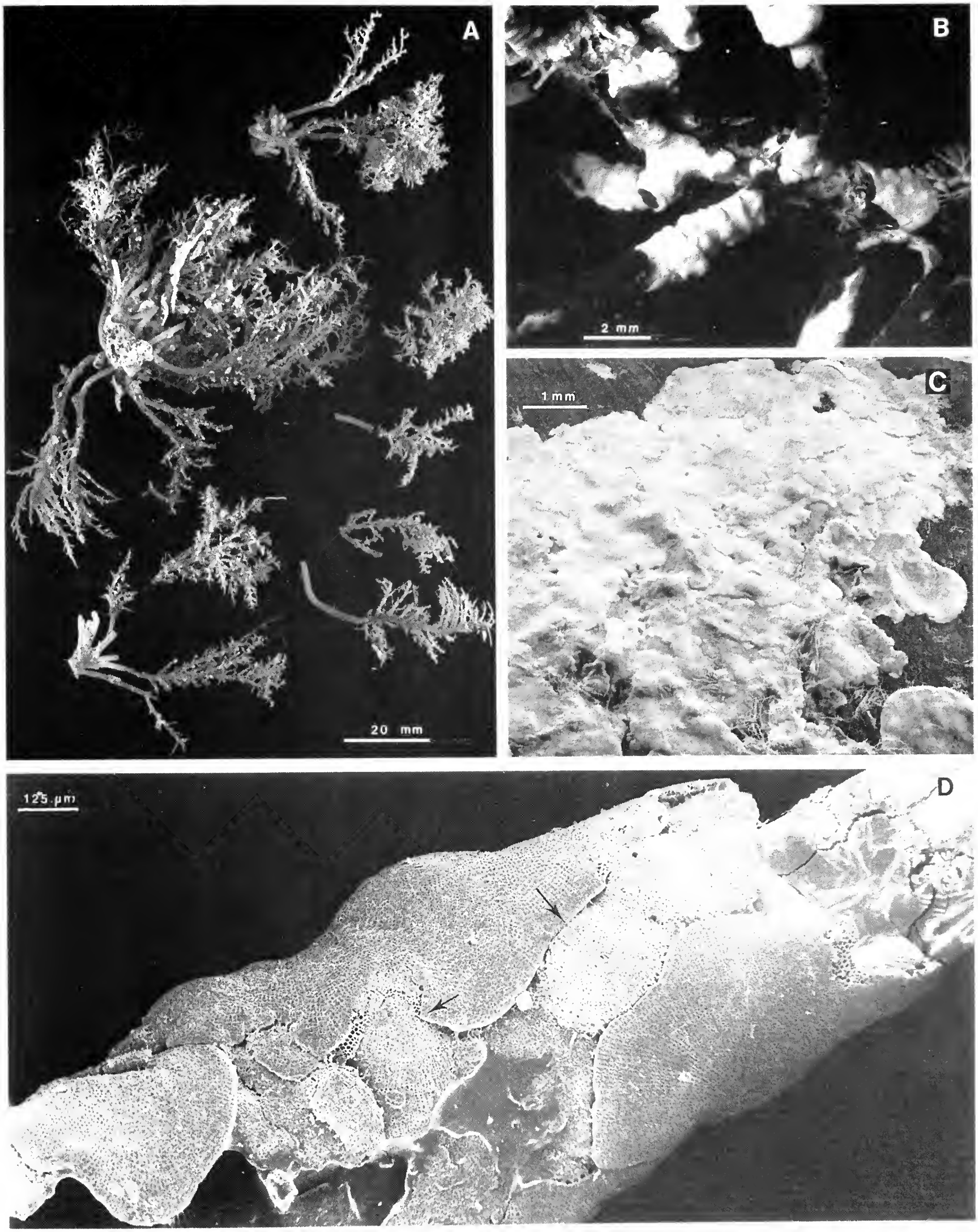


Fig. 16. *Lithophyllum chamberlainianum*: holotype and habit. A. Holotype collection. (LTB 14334). B. Group of conceptacle-bearing plants in holotype collection. (LTB 14334). C. Surface view of thallus with numerous, small applanate branches. (LTB 15851). D. Surface view of thallus encasing host branch showing onset of conceptacle overgrowth (arrows). (LTB 14328).

tacles normally completely occluded by a conglomerate of enlarged, conspicuously elongate, more or less tubular and sometimes inflexed cells which terminate roof filaments adjacent to the pore canal (Figs 18C, 18D, 19A). When conceptacles are viewed in vertical section through the pore canal, the derivation of these cells from at least the first two rows of roof filaments flanking the pore canal is clearly evident.

2. Floors of functional tetrasporangial/bisporangial conceptacle chambers usually situated only one cell below the thallus surface and conceptacle roofs protruding above the thallus surface (Figs 18D, 19A, 19B).
3. Thallus surface not obviously and more or less completely terraced as a consequence of applanate branch development (compare Figs 16C & 44A).
4. Applanate branches, when present, presumably arising from groups of primigenous cells.
5. Postigenous filaments normally composed only of epithallial cells.

In so far as known, no other described species of *Lithophyllum* possesses this combination of features. Over 650 entities have been ascribed to *Lithophyllum*, however, and a critical study of all relevant type collections (a task beyond the scope of this study) may eventually show that an earlier specific epithet is available.

NOMENCLATURE AND SYNONYMY. No matters relating to nomenclature and synonymy require comment.

DISTRIBUTION AND ECOGRAPHY. *L. chamberlainianum* has been recorded from Lucky Bay (east of Esperance), Western Australia eastwards to Flinders, Victoria and in northern and eastern Tasmania; collections were obtained from January through April and in December. The species is unknown outside southern Australia. Of the 28 collections examined, gametangial as well as tetrasporangial plants occurred in 14. Five of these (LTB 13444, 13940, 14315, 14328, 14334) apparently contained both male and female/carposporangial plants, two (LTB 13148, 14393) contained male but no female/carposporangial plants, and seven (LTB 13094, 13152, 13959, 14327, 14335, 14366, 15751) contained female/carposporangial but no male plants.

Plants have been found in intertidal rocky reef pools and subtidally at depths of 0.1–3m on a variety of algal hosts including species of *Apjohnia, Caulerpa* (Chlorophyta), *Acrocarpia, Sargassum, Scaberia* & *Zonaria* (Phaeophyta), and *Laurencia, Metamastophora* & *Osmundaria* (Rhodophyta); specimens also occur on limpets (LTB 15672), snails (LTB 15851) and abalone (LTB 15751). Dense aggregations sometimes cover hosts (Fig 16A), but in other collections only isolated individuals occur. The type collection (Fig.

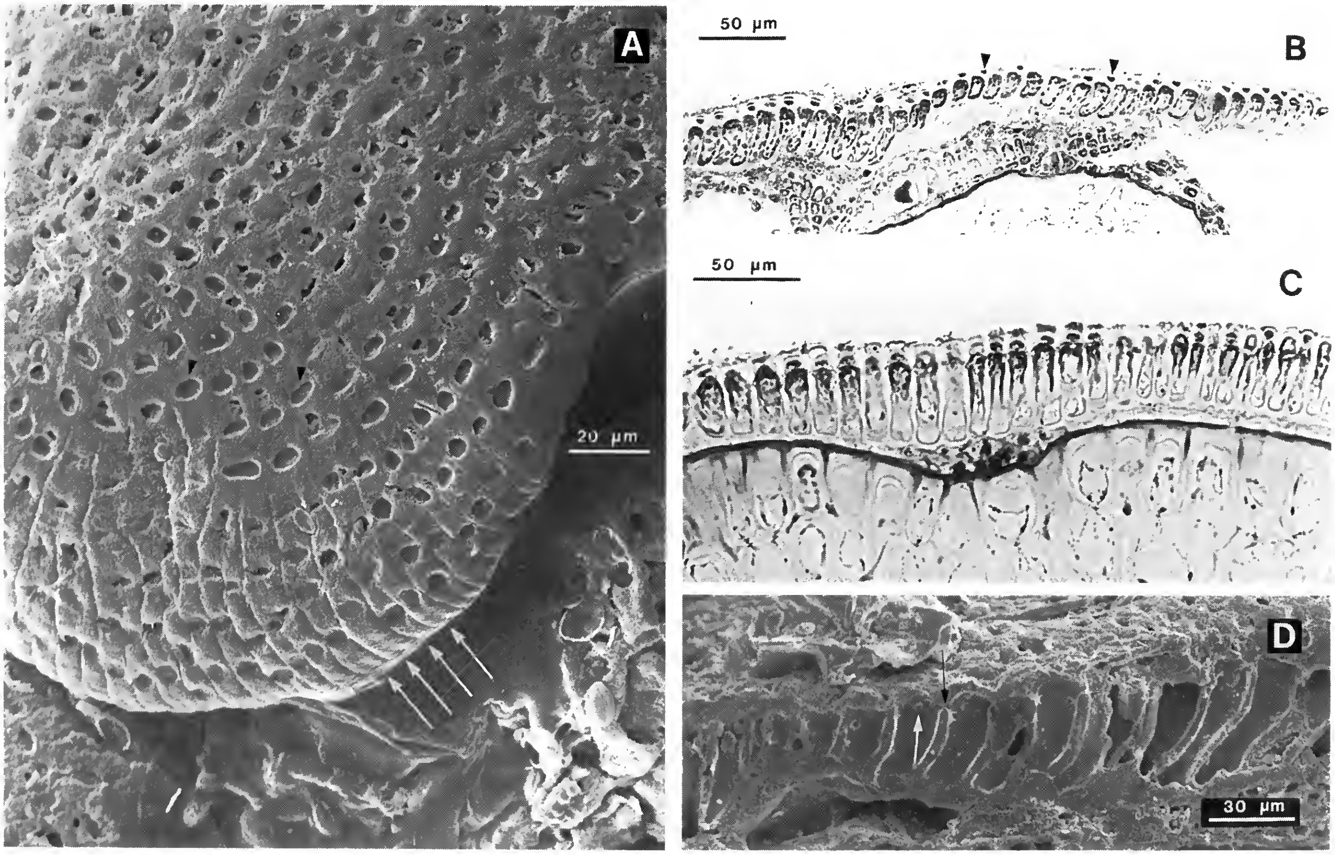


Fig. 17. *Lithophyllum chamberlainianum*: vegetative features. A. Margin of thallus in holotype collection. Note how contiguous filaments appear to be aligned in rows and epithallial concavities (arrows) resulting from the collapse of dried epithallial cells. (LTB 14334). B. Longitudinal section through margin of thallus showing obliquely oriented primigenous cells of varying height and small epithallial cells (arrowheads). (LTB 14334). C. Transverse section of thallus showing upright primigenous cells. (LTB 13148). D. Fracture of thallus showing primary (black arrow) and secondary (white arrows) pit-connections. (LTB 14334).

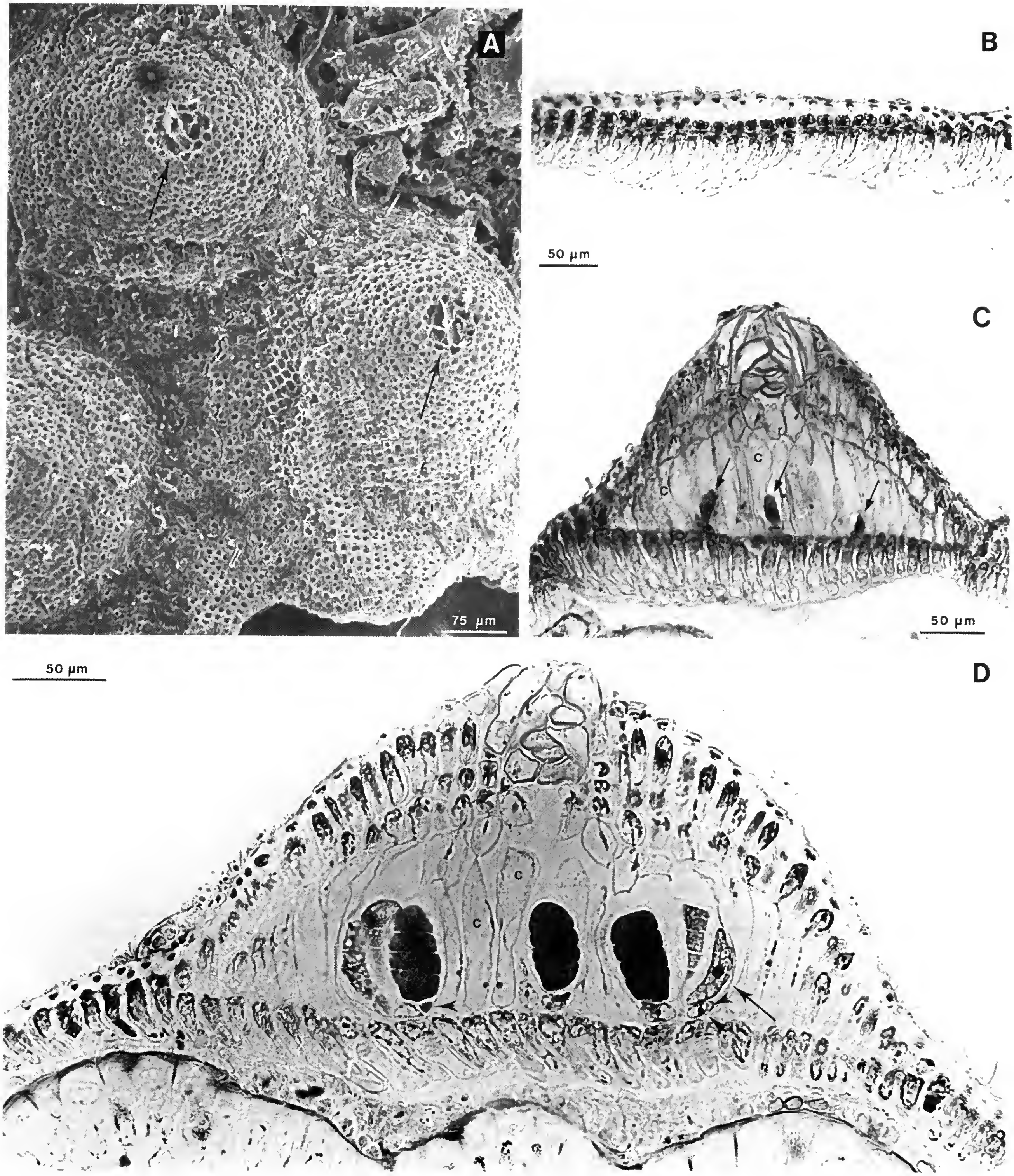


Fig. 18. *Lithophyllum chamberlainianum*: tetrasporangial conceptacles. A. Surface view of tetrasporangial conceptacles of thallus in type collection showing occluded pore canals (arrows). (LTB 14334). B. Tetrasporangial conceptacle primordium showing early stage in the collective detachment of the overlying epithallial cells. (LTB 13148). C. Developing tetrasporangial conceptacle showing three tetrasporocytes (arrows) interspersed amongst roof filaments, intact cavity cells (c) and fully developed cells occluding pore canal. (LTB 14334). D. Mature tetrasporangial conceptacle from type collection with persistent, scattered cavity cells (c) but no columella (cf. Fig. 19A). Note both mature and immature (arrow) sporangia and subtending stalk cells (arrowheads). See text for further details. (LTB 14334).

16A) contains a number of specimens epiphytic on *Laurencia*.

COLLECTIONS EXAMINED:

SOUTH AUSTRALIA: Beachport (*Campbell & Penrose*, 24 February 1988, LTB 15851; 26 February 1988, LTB 15751, 15762). Beachport (Post Office Rock) (*Campbell, Penrose, & Woelkerling*, 1 December 1986, LTB 15523). Cape Cassini, Kangaroo Island (*Penrose*, 3 April 1988, LTB 15613). Chinaman's Hat Island Bay, Yorke Peninsula (*Woelkerling*, 30 December 1976, LTB 11266). Hansen Bay, Kangaroo Island (*Campbell & Penrose*, 9 April 1988, LTB 15705). Penneshaw, Kangaroo Island (*Campbell & Penrose*, 13 April 1988, LTB 15672). Point Fowler, Fowlers Bay (*Woelkerling, Platt, & Jones*, 14 February 1984, LTB 14393).

TASMANIA: Coles Bay, Freycinet Peninsula (Platt & *Woelkerling*, 21 February 1983, LTB 13094). Eddystone Point (*Platt & Woelkerling*, 23 February 1983, LTB 13148, 13152, 13158). Greens Beach (North Coast) (*Platt*, 2 March 1983, LTB 13398). Rocky Cape National Park (*Platt*, 2 March 1983, LTB 13444).

VICTORIA: Flinders (*Woelkerling*, 15 February 1985, LTB 15269). Port Fairy (*Woelkerling*, 4 January 1979, LTB 11708, 11717).

WESTERN AUSTRALIA: Lucky Bay, Cape Le Grand National Park, Esperance (*Woelkerling, Platt, & Jones*, 9 February 1984, LTB 14315, 14327, 14328, 14334 [holotype], 14335, 14366). Eyre ('Nine Mile Reef'), (*Woelkerling, Platt, & Jones*, 1 February 1984, LTB 13940, 13944, 13945, 13959).

REMARKS ON MORPHOLOGY AND ANATOMY. Unequivocal identification can be made only from sections of mature tetrasporangial/bisporangial conceptacles in which pore canal and roof characters are obvious and clear. External features provide no reliable clues as to specific or generic identity because some or all southern Australian species belonging to *Fosliella, Lithoporella, Mastophora, Melobesia, Pneophyllum*, and *Spongites* (concepts for these genera follow Woelkerling 1988) as well as other species of *Lithophyllum* may have thalli of similar size and appearance.

All plants of *L. chamberlainianum* were flat (complanate) or layered. Individual thalli were contoured to the substrate, and both horizontally expanded and sleeve-like thalli were encountered (Figs 16C, 16D). Applanate branching occurs fairly commonly in plants in the type collection (LTB 14334) (Figs 16C, 16D); in other collections, however, very few or no applanate branches were observed, and in no case were more than three layers of branches seen. All branches were more or less horizontally expanded and difficult to detect with the unaided eye. At the dorsal margins of branches or thalli, the positions of individual filaments are usually demarcated by a series of parallel grooves and ridges (Fig. 17A). Epithallial cells normally collapse on drying, leaving numerous oval or rounded concavities on the dorsal surface (Figs 16D, 17A).

Dimerous construction and dorsiventral organization occurred in all thalli examined (Figs 17B–17D). Primigenous filaments are composed of palisade cells which can vary in height over short distances in some thalli but be more uniform in others (Figs 17B–17D). Lateral expansion of thallus margins and of applanate branches occurs from apical initials which produce new primigenous cells inwardly (Fig. 17A). Postigenous development is limited to the production of epithallial cells (Figs 17A–17C).

The mode of applanate branch formation has not been determined. It is probable, however, that it occurs in the same ways as in *L. irvineanum* (q.v.), i.e. directly from groups of primigenous cells. While applanate branching of the sort found in *Lithoporella melobesioides* (Foslie) Foslie (see Turner & Woelkerling 1982) cannot be ruled out, it seems unlikely because it involves development of multicellular postigenous filaments, and these have not been detected in *Lithophyllum chamberlainianum*.

Throughout the thallus, successive cells of the same filament are linked by primary pit-connections while cells of adjacent filaments are linked by contiguous secondary pit-connections. Adjunctive secondary pit-connections, cell fusions, and trichocytes were not observed.

Both tetrasporangial/bisporangial conceptacles (Figs 18, 19A) and gametangial conceptacles (Figs 20, 21) occur; roofs of all conceptacles protrude above the thallus surface. Tetrasporangial/bisporangial conceptacles (Fig. 18A) can be distinguished in surface view from female/carposporangial conceptacles (Fig. 21A) because pores of the former are occluded while those of the latter are not; and they can be distinguished from male conceptacles (Fig. 20A) which are smaller, have a different roof structure, and sometimes bear a spout.

Tetrasporangial/bisporangial conceptacle primordia arise when groups of initials are cut off dorsally from primigenous palisade cells (Fig. 18B). Concurrently, the overlying epithallial cells, which have become detatched from the palisade cells, collectively form a temporary protective cover which soon degenerates. Subsequently, these initials give rise either to sterile filaments which contribute to roof formation or to tetrasporocytes and subtending stalk cells which are interspersed amongst the roof filaments (Fig. 18C). By the time tetrasporocytes become clearly visible, developing conceptacles already protrude markedly above the thallus surface, and roof filaments associated with the pore canal terminate in greatly enlarged, often somewhat swollen and inflexed cells which occlude the developing pore canal (Fig. 18C). Remaining roof filaments terminate in small, more or less compressed or rounded epithallial cells. During conceptacle formation, the basal cells of most sterile filaments become markedly elongate to form cavity cells (Fig. 18C). Cavity cells undergo varying degrees of senescence and degeneration, thereby resulting in formation of the conceptacle chamber. Scattered cavity cells may or may not persist in more mature conceptacles, and sometimes a central columella forms (Figs 18D, 19A). The chamber floor is usually situated one cell beneath the surrounding thallus surface.

Intact portions of filaments above the chamber collectively form a roof of characteristic structure (Figs 18D, 19A). Enlarged cells which occlude the pore canal develop terminally from two (or even three) rows of filaments immediately flanking the canal, and they appear collectively to form a conglomerate cluster of overlapping cells within the canal (Figs 18D, 19A). These enlarged cells appear to be largely devoid of contents, but signs of degeneration were not observed, and it is not certain how spores are eventually released. In addition to enlarged terminal cells, filaments flanking the pore canal contain 1–2(–3) much smaller, often more or less isodiametric or slightly elongate subtending cells (Fig. 18D).

Remaining roof filaments above the chamber each usually consist of a terminal epithallial cell, a subterminal cell which is normally more elongate than other cells, and one (rarely

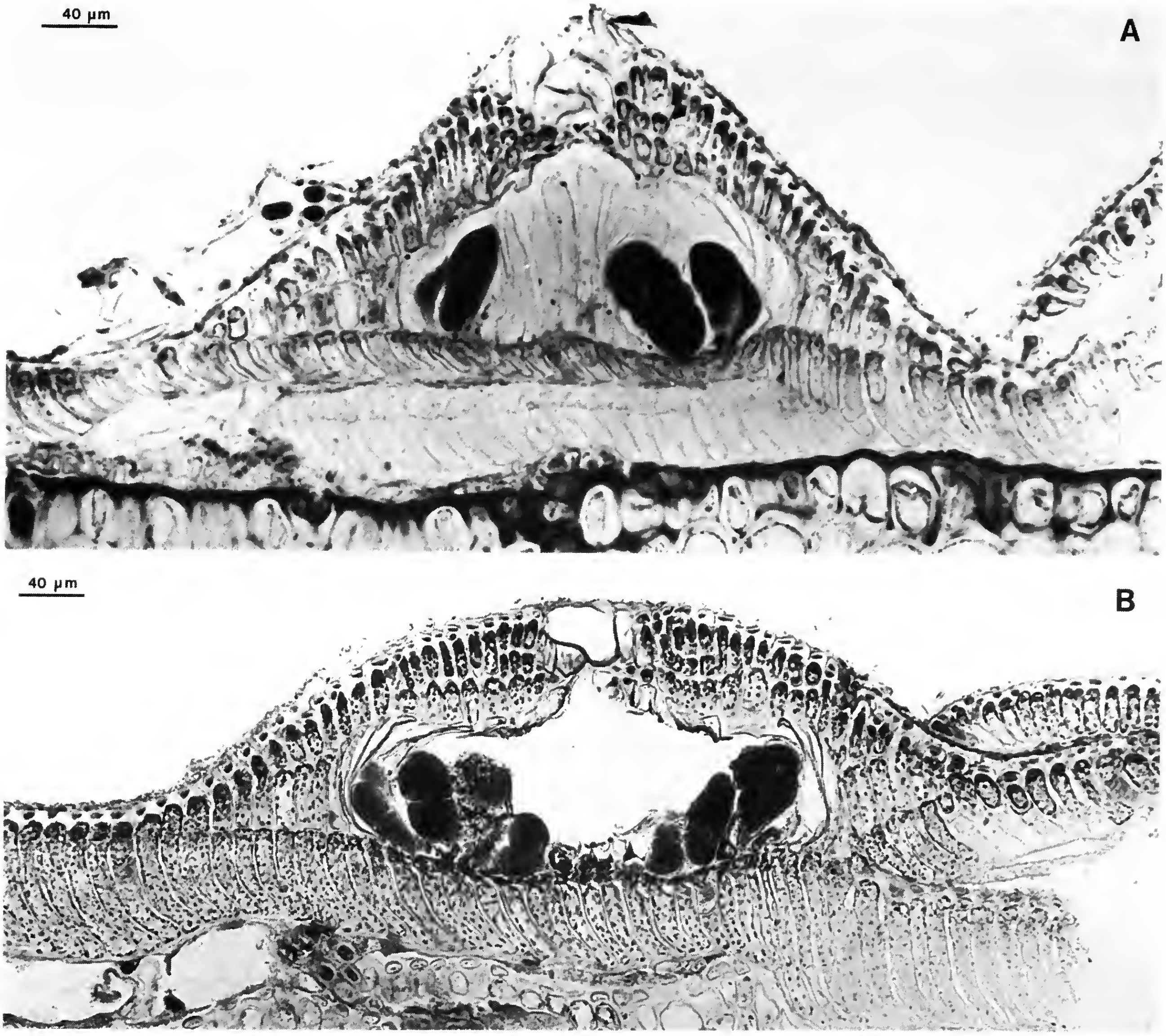


Fig. 19. *Lithophyllum chamberlainianum*: tetrasporangial/bisporangial conceptacles. A. Another (cf Fig. CH3D) tetrasporangial conceptacle from type collection, this with a distinct columella beneath pore canal. (LTB 14434). B. Bisporangial conceptacle in LTB 15751 with somewhat less elongate cells occluding the pore canal.

two) shorter subtending cells (Figs 18D, 19A). At the margins of conceptacles , roof filaments remain completely intact. Each contains a terminal epithallial cell and one or two subtending, more or less elongate cells, the ventral-most of which is situated upon a primigenous cell (Fig. 18D). Tetrasporangia may arise from any area of the chamber floor (Figs 18C, 18D, 19A). Subtending stalk cells often remain evident beneath mature tetrasporangia. Each sporangium contains four zonately arranged spores (Fig. 18D). Both mature and immature tetrasporangia may occur within a conceptacle (Fig. 18D). Although older conceptacles may become overgrown by new applanate branches (Fig. 16D), they never become enveloped and buried by development of postigenous filaments.

One specimen (LTB 15751) contained a bisporangial conceptacle (Fig. 19B). Structurally, bisporangial and tetrasporangial conceptacles appear concordant although the enlarged cells blocking the pore canal were not as elongate as some of their tetrasporangial counterparts. The bispores were uninucleate, possibly suggesting (see Suneson, 1950; 1982) that they were formed apomeiotically.

Male conceptacle primordia (Fig. 20B) arise in the same manner as those of tetrasporangial conceptacles, but reproductive and non-reproductive initials are not interspersed. Instead, two distinct groups occur: a large central group destined to produce spermatangia and a small circumferential group destined to produce roof filaments (Fig. 20C). Each spermatangial initial cuts off several more or less clavate spermatangia directly (no dendroid branching occurs), and these mature to form a dense carpet across the conceptacle chamber floor (Figs 20D, 20E). At the margin of the fertile disc, a single ring of initials produces a group of filaments which arch over the developing spermatangia (Fig. 20C); these eventually coalesce to form the conceptacle roof (Figs

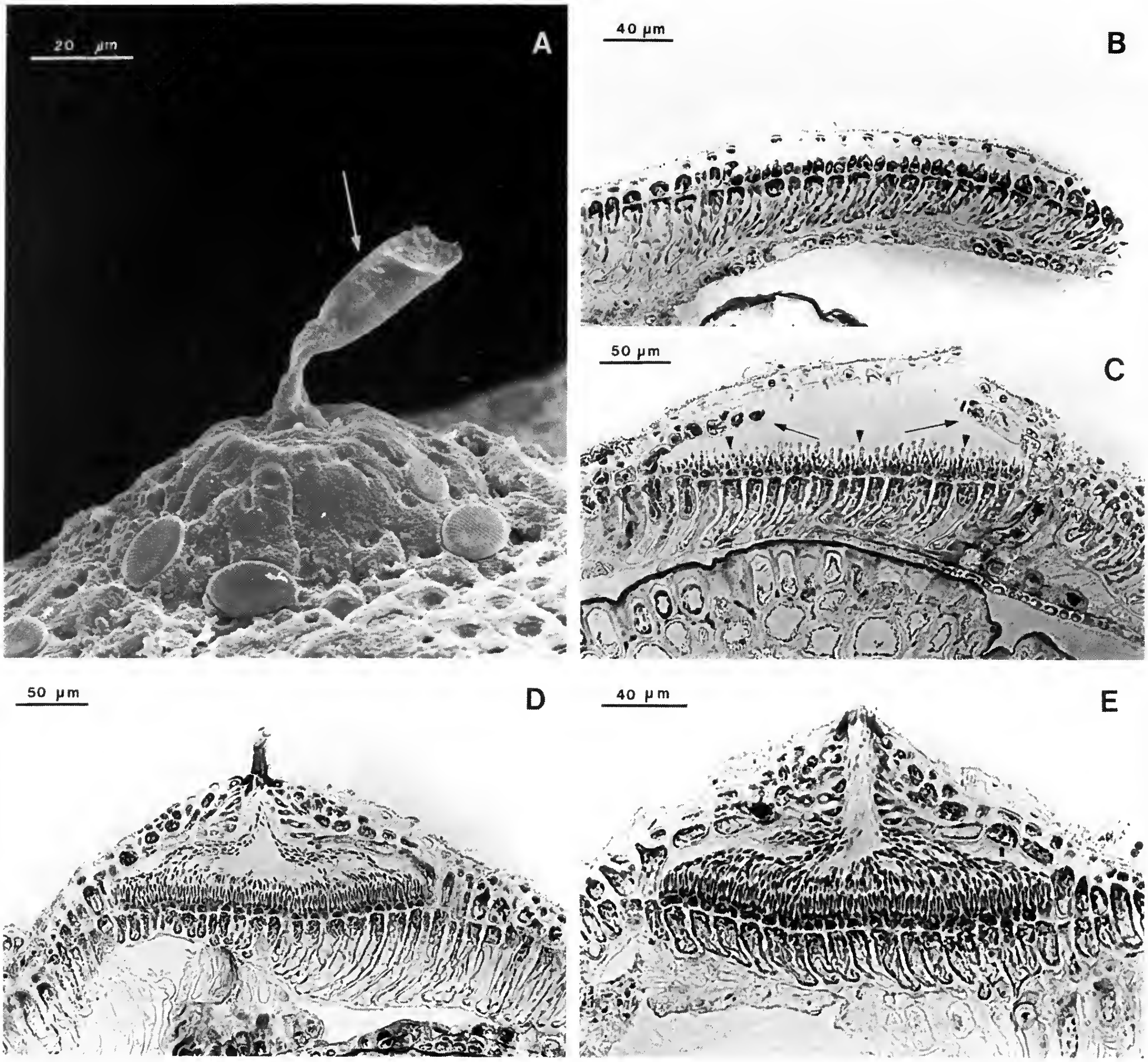


Fig. 20. *Lithophyllum chamberlainianum:* spermatangial conceptacles. A. Surface view of male conceptacle in type collection. Note spout-like extension (arrow) of pore canal. (LTB 14334). B. Male conceptacle primordium with overlying epithallial cells. (LTB 14334). C. Developing male conceptacle showing roof formation (arrows), young spermatangia (arrowheads) and degenerating dome of epithallial cells (e). (LTB 14334). D, E. Mature male conceptacles with and without spouts. (LTB 14334).

20D, 20E). Each roof filament consists of a main axis and a small number of one- to several-celled laterals which arise obliquely and more or less secundly from the outer side of cells of the main axis. Laterals either terminate in epithallial cells along the outer surface of the roof or in ordinary vegetative cells which flank the pore canal (Figs 20D, 20E). The canal of some conceptacles (Figs 20A, 20D) is extended into a mucilaginous spout.

Female/carposporangial conceptacle ontogeny involves a central group of initials destined to produce carpogonial branches and eight or more rings of surrounding, peripheral initials destined to produce roof filaments (Fig. 21B). Carpogonial branches begin to develop on most initials in the central group, but only the centre-most ones normally become fully mature (Figs 21B–21D). Each branch consists of a terminal carpogonium (with a distal, elongate trichogyne) and one or two subtending cells (Fig. 21D). Sometimes two carpogonia develop terminally on the same branch, but only one produces a trichogyne (Fig. 21D).

Roofs of female/carposporangial conceptacles usually do not reach full maturity until after karyogamy (Figs 21C–21F). Completely developed roofs consist of: 1) a pore and pore canal surrounded by distal remnants of filaments which lack epithallial cells, usually contain cells different in shape and/or size to those of other roof filaments, and terminate in cells which more or less protrude into but do not occlude the pore canal; 2) the remaining region above the chamber in which intact portions of filaments each consist of a terminal epithallial cell, a subterminal columnar cell and in some cases another usually shorter subtending cell and/or the remnants of a cavity cell; and 3) a region flanking the chamber in which roof filaments remain more or less intact and each contains a terminal epithallial cell, one (rarely two) subterminal elongate cells and in some cases a more or less senescent and sometimes somewhat crushed cavity cell.

Carposporophytes arise within female/carposporangial conceptacles after presumed karyogamy (Figs 21D–21F). A large more or less flattened fusion cell forms (Figs 21D–21F). Some fusion cells appear discontinuous; this suggests that such cells are more or less irregular in shape (see Adey, 1966: fig. 77) and that the sections have been cut through several arms of the one fusion cell. Eventually, short unbranched gonimoblast filaments bearing terminal carposporangia are produced around the periphery of the fusion cell (Figs 21E, 21F). Remains of unfertilized carpogonia are usually evident on the dorsal surface of the fusion cell (Figs 21E, 21F).

Spore germination and very early thallus development have not been observed.

Relationships of *L. chamberlainianum* to other species are considered below (p.97).

INFRASPECIFIC TAXONOMY. No infraspecific taxa of *Lithophyllum chamberlainianum* are being recognized.

3. **Lithophyllum corallinae** (P. & H. Crouan) Heydrich in *Ber. dt. Bot. Ges.* 15: 47 (1897b).

Figs 22–32

BASIONYM. *Melobesia corallinae* P. & H. Crouan, *Florule du Finistere*: 150, 252, pl. 20, gen. 133 bis, figs 6–11 (1867).

LECTOTYPE. CO (Brest, France; epiphytic on *Corallina officinalis* Linnaeus), designated by Chamberlain (1991). Fig. 22. Additional figures and a detailed account of the lectotype collection are provided by Chamberlain (1991).

HOMOTYPIC SYNONYMS:

> *Dermatolithon corallinae* (P. & H. Crouan) Foslie in Boergesen, *Mar. Alg. Faeroes*: 402 (1902). *Dermatolithon pustulatum* var. *corallinae* Foslie ex Belsher et al. in *Trav. sci. Parc. natn. Port-Cros.* 2: 51 (1976) (comb. invalid as full citation of basionym not given in accordance with ICBN Art. 33.2). *Lithophyllum macrocarpum* f. *corallinae* (P. & H. Crouan) Foslie in *K. norske Vidensk. Skr.* 1909 (2): 47 (1909). *Lithophyllum pustulatum* f. *corallinae* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 118, 127 (1905a). *Lithophyllum pustulatum* var. *corallinae* (P. & H. Crouan) Lemoine in *Deux. Exped. Ant. Fr. Sci. nat.* 1(Bot): 138 (1913b). *Tenarea corallinae* (P. & H. Crouan) Notoya in *Bull. Jap. Soc. Phycol.* 22: 47 (1974) (comb. invalid as full citation of basionym not given in accordance with ICBN Art. 33.2). *Tenarea corallinae* (P. & H. Crouan) Masaki ex Park in *Bull Nat. Fish. Univ. Busan* 20(1): 15 (1980). (comb. invalid as full citation of basionym not given in accordance with ICBN Art. 33.2). *Titanoderma corallinae* (P. & H. Crouan) Woelkerling et al. in *Phycologia* 24: 333 (1985).

MISAPPLIED NAMES. No published misapplications of names to southern Australian specimens were uncovered during the present study.

ETYMOLOGY. The specific epithet *corallinae* almost certainly refers to the host *Corallina* plant on which the type material occurs, but Crouan & Crouan (1867) did not provide an explicit etymological statement.

PREVIOUSLY PUBLISHED ILLUSTRATIONS OF AUSTRALIAN PLANTS. Campbell & Woelkerling in *Phycologia* 29: figs 2, 10, 11 (1990) (as *Lithophyllum corallinae*). Woelkerling, *Coralline Red Algae*: p.25, fig. 33 (as *Titanoderma* sp.); p. 101 fig. 75 (as *Lithophyllum* sp.); p. 112, fig. 92 (as *Titanoderma* sp.)(1988).

DESCRIPTION. Plants mostly 10–50+ mm across and 0.2–1.0(–5.0) mm tall; variably flat (complanate) to layered (without conspicuous terracing), warty, lumpy and/or protuberant; completely or partially adherent.

Thallus dimerous, dimerous and monomerous or largely monomerous; dimerous portions with primigenous filaments composed of palisade and/or nonpalisade cells 5–20 μm long and (13–)20–65(–82) μm tall and postigenous filaments usually composed of 5–20+ cells 5–40(–55) μm long and 5–16 μm in diameter; monomerous portions with filaments usually composed of 20+ cells 5–35(–55) μm long and 5–14 μm in diameter; epithallial cells 2–6 μm long and 4–9 μm in diameter terminating postigenous and monomerous filaments. Contiguous secondary pit-connections common; adjunctive secondary pit-connections and cell fusions not seen; trichocytes apparently rare.

Tetrasporangial/bisporangial plants with scattered non- or slightly protruding conceptacles. Conceptacle roofs 235–330(–419) μm in external diameter; roof filaments above chamber usually 2–4 cells long; cells 5–32(–43) μm long and 2–9 μm in diameter with columnar cells occurring in horizontal subepithallial groups or more isolated. Pore canals lined with somewhat projecting but not completely occluding cells. Conceptacle chambers (157–)190–235(–280) μm in diameter and 68–105(–136) μm tall; floor of maturechambers usually 6 or more cells below thallus surface; tetrasporangia/bisporangia (37–)50–95(–123) μm long and (16–)25–55(–92) μm in diameter, scattered across chamber floor or peripheral to a columella.

Gametangial plants dioecious. Male conceptacle roofs non- or slightly protruding; chambers 116–145 μm in diameter and 32–47 μm tall; spermatangial branches confined to chamber floor, simple with each initial bearing one to several elongate spermatangia. Female/carposporangial conceptacle roofs non- or somewhat protruding; chambers 185–233(–305) μm in diameter and 60–110(–140) μm tall; carpogonial filaments arising from chamber floor, usually 2–3 cells long and bearing 1(–2) carpogonia terminally.

Carposporangia developing within female conceptacles after presumed karyogamy; each comprising a central more or less flattened fusion cell and some several-celled gonimoblast filaments arising peripherally with terminal carposporangia 27–40(–57) μm in diameter.

DIAGNOSTIC FEATURES. *L. corallinae* differs from other southern Australian species of *Lithophyllum* in having the following combinationof features:

1. Pore canals of tetrasporangial/bisporangial conceptacles lined with cells which may project somewhat into but do not completely occlude the entire canal (Figs 27E, 28, 29).
2. Floors of functional tetrasporangial/bisporangial conceptacles usually six or more cells below the thallus surface and conceptacle roofs more or less flush with or protruding

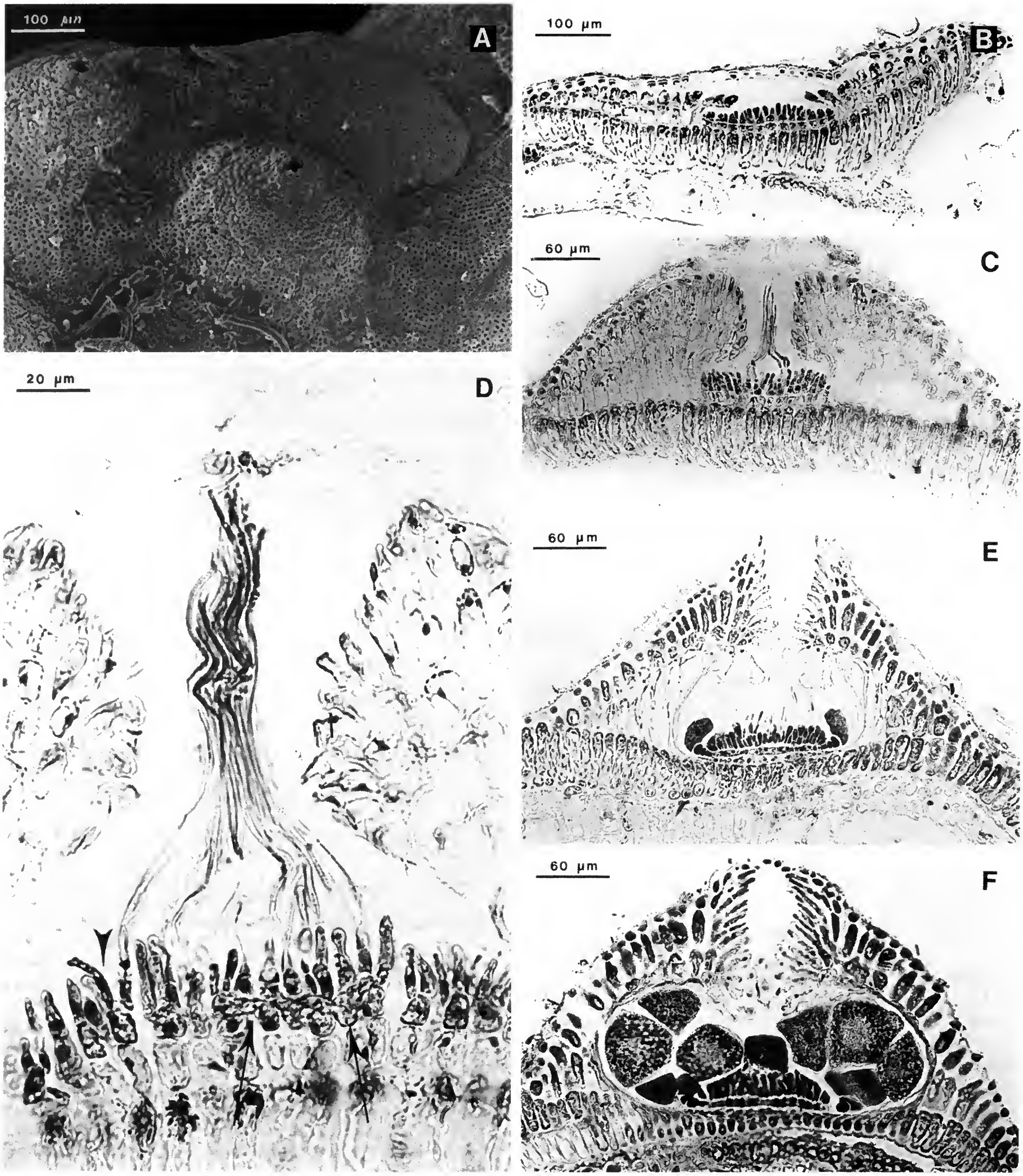


Fig. 21. *Lithophyllum chamberlainianum*: female/carposporangial conceptacles. A. Surface view of female/carposporangial conceptacles in type collection. Note that pore canals are not obstructed. (LTB 14334). B. Very young female/carposporangial conceptacle with overlying dome of epithallial cells still intact (LTB 14334). C. Female/carpogonial conceptacle with mature carpogonial branches. Note elongate trichogynes. (LTB 14335). D. Fusion cell formation (arrows) and details of carpogonial branch structure (arrowhead). (LTB 14334). E. Developing carposporophyte with young carposporangia and remains of unfertilized carpogonia on dorsal surface of fusion cell. (LTB 14334). F. Mature carposporophyte. (LTB 13049).

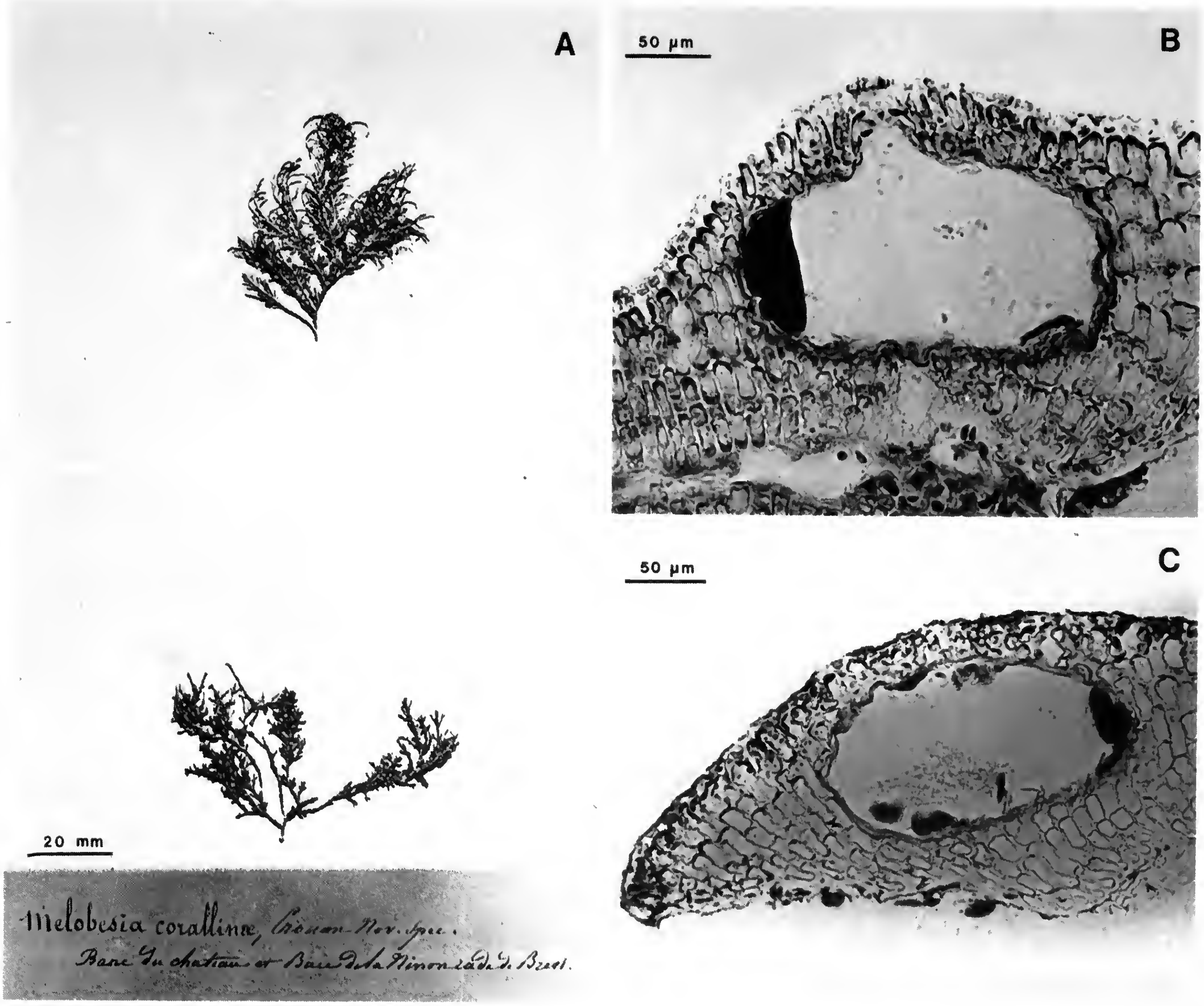


Fig. 22. *Lithophyllum corallinae:* lectotype (CO, unnumbered). A. Lectotype sheet. B. Section through tetrasporangial conceptacle showing roof structure and dimerous construction. C. Margin of portion of thallus in which thallus construction appears more or less monomerous.

somewhat above the thallus surface (Figs 27A, 27E, 28, 29).

3. Thallus surface not obviously and more or less completely terraced as a consequence of applanate branch development.
4. Postigenous filaments normally multicellular except in very young portions of thallus.
5. Roofs of tetrasporangial/bisporangial conceptacles usually two to four cells thick above the chamber and with or without a subepithallial layer of columnar cells (Figs 27E, 28, 29).
6. Chambers of tetrasporangial/bisporangial conceptacles mostly 190–235 µm (rarely up to 280 µm) across.

The extent to which this combination of features delimits *L. corallinae* as a species within *Lithophyllum* cannot be fully assessed in the absence of a world monograph of the genus. Presumptive differences between *L. corallinae* and *L. bermudense* (q.v.) also require clarification.

NOMENCLATURE AND SYNONYMY. No matters relating to nomenclature and synonymy require comment.

DISTRIBUTION AND ECOGRAPHY. *Lithophyllum corallinae* has been found in southern Australia from Eyre, Western Australia eastwards to Anglesea, Victoria and from four localities on the east coast of Tasmania. Specimens have been obtained in January, February, April, August, October, November and December, suggesting that the species occurs year-round. Of the 37 collections examined, male plants were found in three (LTB 13171, 13174, 13673) and female/carposporangial plants were detected in six (LTB 13171, 13174, 13176, 13306, 13621, 13673). All but two of these (LTB 13621, 13673) also containedtetrasporangial/bisporangial individuals.

Elsewhere, plants identified as *L. corallinae* have been reported from Africa, Asia, Europe, North America and various Atlantic and Pacific Islands(Table 9). Levring (1974, as *Dermatolithon*) and Chamberlain (1991, as *Titanoderma*)

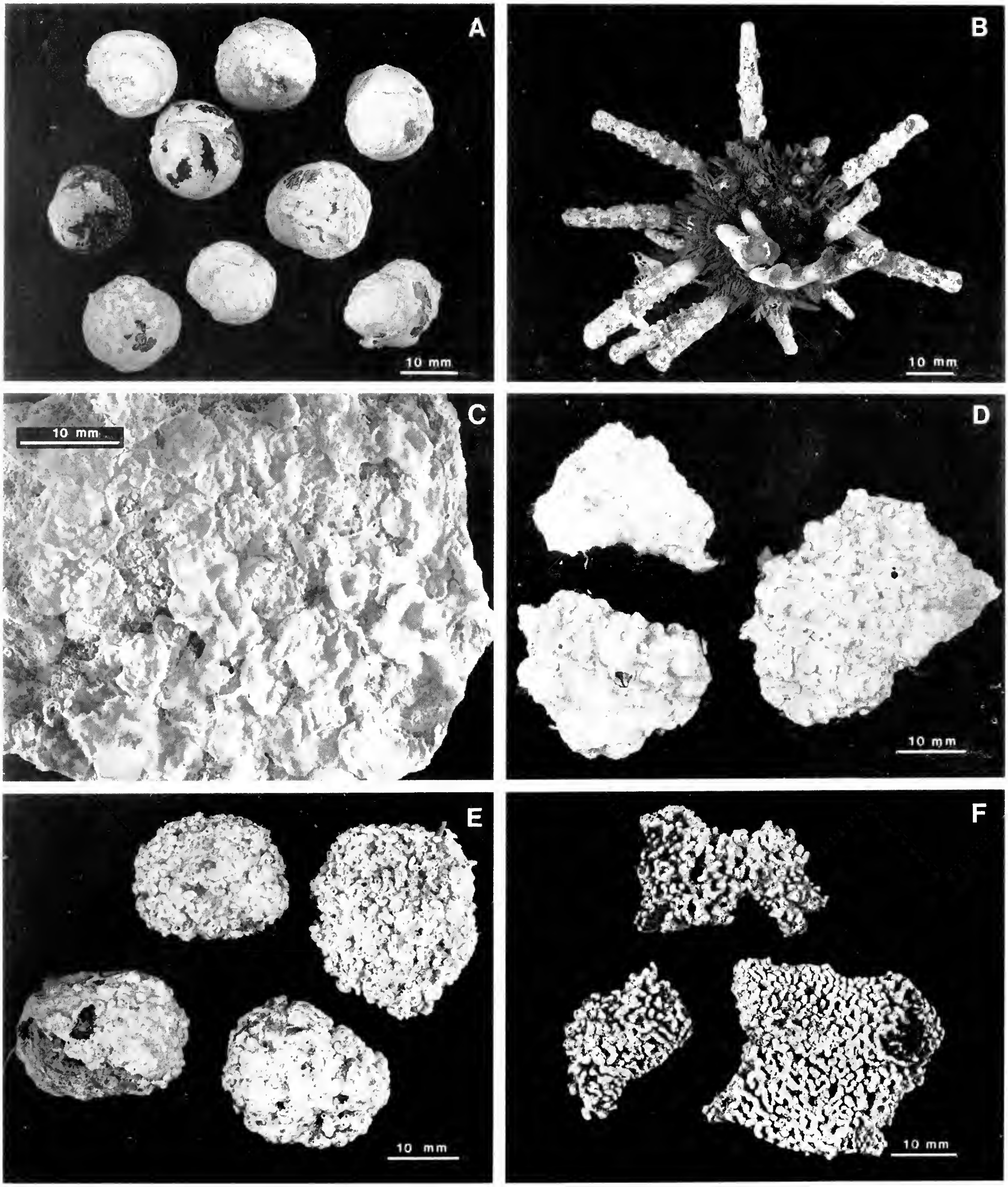


Fig. 23. *Lithophyllum corallinae*: growth-forms of southern Australian plants. A. Part of a collection of flat (complanate) or slightly warty plants on snails. (LTB 15578). B. Collection of flat (complanate) plants on a spiny sea urchin. (LTB 13176). C. Group of plants on part of an abalone shell. (LTB 13306). D. Warty, epilithic specimens. (LTB 13236). E. Warty to lumpy specimens on limpet shells or (upper left) on worm tubes attached to limpet shells. (LTB 15243). F. Protuberant epilithic plants with numerous short branches. (LTB 13621).

comment that the species is probably cosmopolitan. With the exception of the European specimens identified or confirmed by Chamberlain (1991), however, all of these reports require verification.

Within southern Australia, *L. corallinae* has been found intertidally on rocky reefs (near edges) and in reef pools. Subtidal collections have been obtained from depths of 0–9m on rock, snails, limpets, abalone shells and sea urchins. Epiphytic collections have not been encountered during this study, a marked contrast to the situation in the British Isles where Chamberlain (1991) found only epiphytic specimens. Specimens in the type collection from France are epiphytic on *Corallina*.

COLLECTIONS EXAMINED:

SOUTH AUSTRALIA: Beachport (Post Office Rock) (*Woelkerling*, 6 November 1987, LTB 15824; *Campbell & Penrose*, 6 November 1987, LTB 15841, 15842; *Campbell & Penrose*, 24 February 1988, LTB 15853). Cape Willoughby, Kangaroo Island (*Womersley*, 8 January 1950, LTB 13585, originated from AD A12984 as a gift). Elliston (Waterloo Bay) (*Turner*, 28 October 1981, LTB 15360; *Turner*, 31 October 1981, LTB 15377; *Turner*, 1 November 1981, LTB 15398, 15409; *Turner*, 2 November 1981, LTB 15423). Nora Creina, *Woelkerling*, 6 November 1987, LTB 15578; *Campbell & Penrose*, 21 November 1987, LTB 15879). Penneshaw, Kangaroo Island (*Campbell & Penrose* 13 April 1988, LTB 15669). Pennington Bay, Kangaroo Island (*Womersley*, 22 January 1948, LTB 13696, originated as a gift from AD, A7908). Point Sinclair (Port Le Hunt) (*Woelkerling, Platt, & Jones*, 15 February 1984, LTB 14507). Sceale Bay (Point Westall) (*Platt & Jones*, 16 February 1984, LTB 14550, 14585). Vivonne Bay, Kangaroo Island (*Womersley*, 14 January 1947, LTB 13587, originated from AD A12978 as a gift; *Womersley*, 29 January 1957, LTB 13622, originated from AD A21021 as a gift; *Campbell & Penrose*, 8 April 1988, LTB 15884).

TASMANIA: Clydes Island, Eaglehawk Neck (*Platt*, 26 February 1983, LTB 13306). Eddystone Point (*Platt & Woelkerling*, 23 February 1983, LTB 13171, 13172, 13174, 13176). Sisters Bay (Convict Burial Ground) (*Platt*, 16 February 1983, LTB 12926). Tesselated Pavement, Eaglehawk Neck (*Platt & Woelkerling*, 26 February 1983, LTB 13236, 13240).

VICTORIA: Anglesea (Potato Patch Reef) (*Beanland*, 31 August 1982, LTB 12721). Apollo Bay (Haylings Reef) (*Pope & Bennett*, 17January 1949, LTB 13703, originated from AD A15243 as a gift). Bridgewater Bay, Portland (*Womersley*, 21 August, 1953, LTB 13646, originated from AD A19053 as a gift; *Womersley* 14 April 1959, LTB 13621, originated from AD A22633 as a gift). Lawrence Rock, Portland (*Beauglehole*, 13 January 1954, LTB 13680, originated from AD A20547 as a gift; *Beauglehole*, 15 January 1960, LTB 13673, 13675, originated from AD A24017 and AD A24761 as gifts; *Beauglehole*, 26 December 1965, LTB 13698, originated from AD A29772 as a gift).

WESTERN AUSTRALIA: Eyre ('Nine Mile Reef') (*Woelkerling, Platt, & Jones*, 1 February 1984, LTB 13974).

FRANCE: Brest (Lectotype; see details above).

REMARKS ON MORPHOLOGY AND ANATOMY. External features of *Lithophyllum corallinae* provide no reliable clues as to specific or generic affinity. Unequivocal identification requires sections of tetrasporangial/bisporangial conceptacles in which the pore canal is obvious and clear.

Plants of *L. corallinae* vary from flat (complanate), more or less smooth-surfaced or somewhat wrinkled individuals (Figs 23A–23C) to crustose individuals with lumpy or knobby outgrowths (Figs 23D, 23E) to individuals composed mainly of short, cylindrical or somewhat compressed protuberant branches which may be simple or branched (Fig. 23F). All growth-forms are reproductively concordant. The greater range in form in southern Australian specimens as compared to British specimens (see Chamberlain, 1991) may be a reflection of the greater range in substrates upon which southern Australian plants have been found. As with the even more polymorphic *L. bermudense* (q.v.), intergrades occur between most growth-forms of *L. corallinae*, and thus there is little value in describing them in formal taxonomic terms.

Additional surface features become apparent in scanning electron micrographs of *L. corallinae* (Figs 24A–24D), but none seem to be diagnostically important. Inconspicuous, horizontally expanded applanate branches were detected in some specimens (Fig. 24A), but these never resulted either in obvious terracing as occurs in *L. prototypum* (Fig. 44A) or in coalesced branches as found in *L. bermudense* (Figs 5E, 5F, 9A–9C). Parallel ridges and grooves demarcating the positions of individual filaments are evident at the extreme margins of dimerous applanate branches (Fig. 24B), and numerous small rounded to angular concavities resulting from collapsed epithallial cells are common on dorsal surfaces of thalli (Fig. 24C). The ventral surface of a thallus growing on a mollusc was striated, but positions of individual primigenous filaments were not obvious (compare with *L. pustulatum*, Fig. 52B).

Both dimerous and monomerous construction can occur (Figs 25, 26A). British specimens examined by Chamberlain (1991), in contrast, were all dimerous. Inlectotype material from France, however, both dimerous and apparent monomerous construction are evident (Figs 22B, 22C). Crustose portions of all thalli are dorsiventrally organized; radial organization occurred only in protuberant branches.

Crustose portions of most thalli are dimerous. Young portions of some plants or applanate branches consist only of primigenous palisade cells and unicellular postigenous filaments (i.e. epithallial cells) (Fig. 25A). In most plants, however, multicellular postigenous filaments develop almost immediately behind the thallus/branch margin (Fig. 25B), and quickly become five to twenty or more cells long. Normally, edges of thalli or branches are thinner than older portions of thallus. When plants occur on snails, however, edges along the lip of the snail mantle often become thicker than older parts of the thallus (Fig. 25D). Postigenous filaments of such edges not only may contain more cells, but these tend to be distinctly columnar. It is likely that such thicker thallus margins result from some as yet unknown chemical or other defensive action initiated by the snail which prevents the coralline thallus from completely enveloping and thus killing the snail.

In dimerous portions of most thalli, primigenous cells are palisade (Figs 25A, 25B, 25F), but in some plants most primigenous cells are nonpalisade (Fig. 25E; see also Campbell & Woelkerling, 1990: figs 10, 11). Cells of postigenous filaments may or may not be columnar (Figs 25B, 25D–25F, 26C) and mixtures can occur. In some plants, cells of contiguous postigenous filaments become more or less horizontally aligned, and periclinal banding (Figs 25F, 26C) comparable to that found in *L. bermudense* (e.g. Fig. 7C) and *L. pustulatum* (Fig. 53E) results. Each postigenous filament

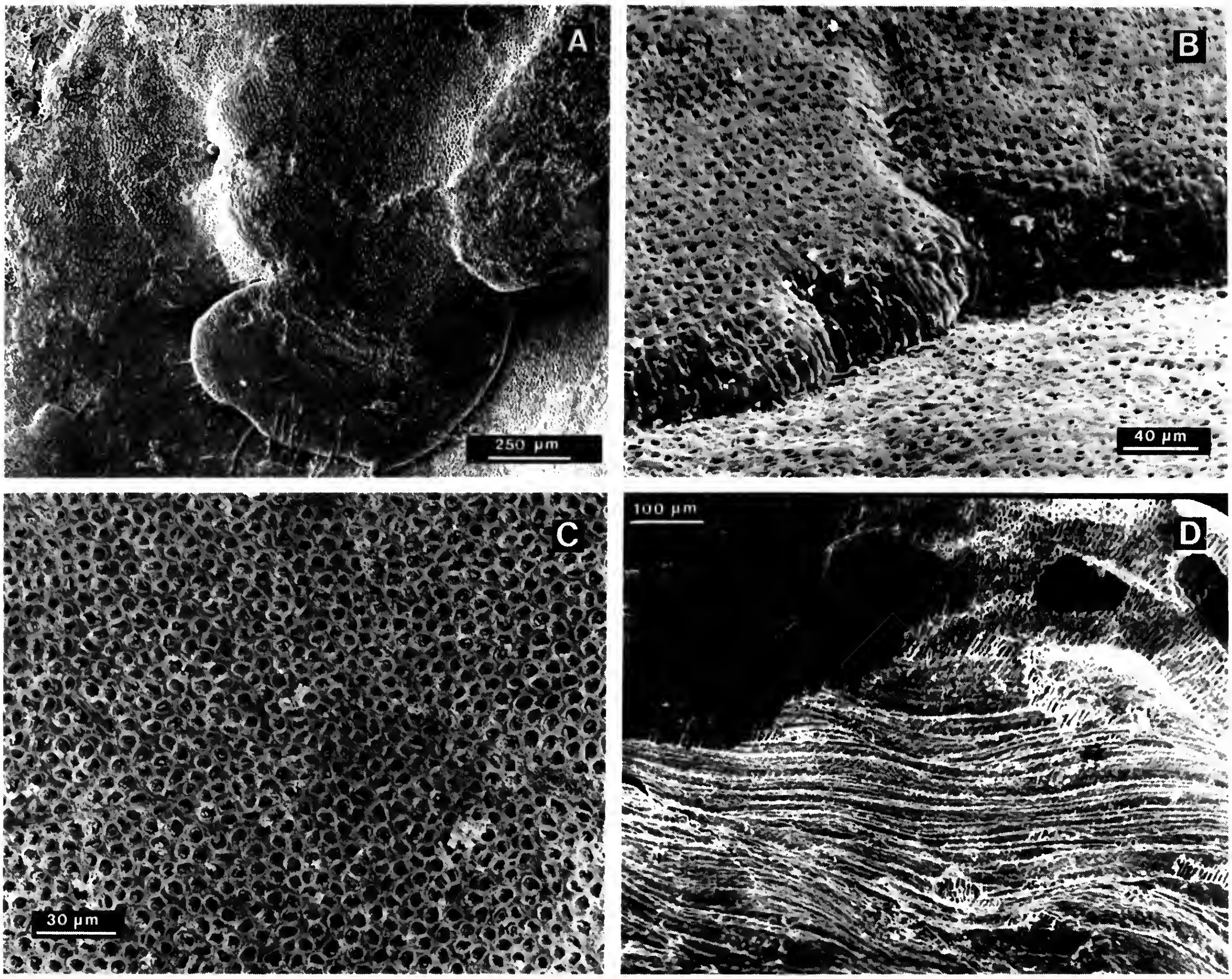


Fig. 24. *Lithophyllum corallinae*: surface features. A. Applanate branches in surface view. Note very young branch (arrow). (LTB 15578). B. Margin of applanate branch with grooves delimiting the positions of the apices of contiguous filaments. (LTB 15578). C. Dorsal thallus surface with numerous epithallial concavities. (LTB 13174). D. Thallus fracture showing portion of ventral surface of applanate branch. Position of individual filaments is not evident. (LTB 13174).

normally terminates at the thallus surface in one or sometimes two epithallial cells (Fig. 26C).

Monomerous construction is uncommon in crustose portions of thalli (Fig. 25C) but occurs in all protuberant branches (Fig. 26A). In crustose portions(Fig. 25C), a broad ventral core of filaments can occur, and terminal portions of these filaments or their derivatives curve more or less upwards to the dorsal surface and terminate in epithallial cells. Protuberant branches (Fig. 26A) contain a central core of filaments, and terminal portions or their derivatives curve outwards towards the thallus surface and terminate in epithallial cells. Whereas crustose thalli of monomerous construction are dorsiventral in organization, protuberant branches are more or less radial.

Throughout the thallus, successive cells of the same filament are linked by primary pit-connections and cells of adjacent filaments are linked by contiguous secondary pit-connections (Fig. 26B). Adjunctive secondary pit-connections and cell fusions were not detected, and the only trichocyte seen occurred in the roof of a tetrasporangial conceptacle (Fig. 29B). Details of applanate branch ontogeny have not been elucidated.

Both tetrasporangial/bisporangial (Figs 27–30) and gametangial (Figs 31, 32) conceptacles occur in southern Australian material. Roofs of tetrasporangial/bisporangial conceptacles may be flush with or project slightly above the thallus surface (Fig. 27A) but, pores are usually detectable in surface view. Tetrasporangial/bisporangial conceptacle development involves groups of sterile filaments interspersed amongst sporangial initials (Fig. 27B). It is presumed from Fig. 27B that conceptacle primordia (not seen) arise from groups of initials cut off from subepithallial cells and that early stages of development occur beneath an uplifted dome of epithallial cells. This dome (Fig. 27B) apparently degenerates and disappears as conceptacles develop further (Figs 27C, 27E). Although conceptacle primordia presumably are formed just beneath epithallial cells, surrounding vegetative filaments continue to produce new cells as conceptacles develop (compare Figs 27B & 27C), and consequently the conceptacle

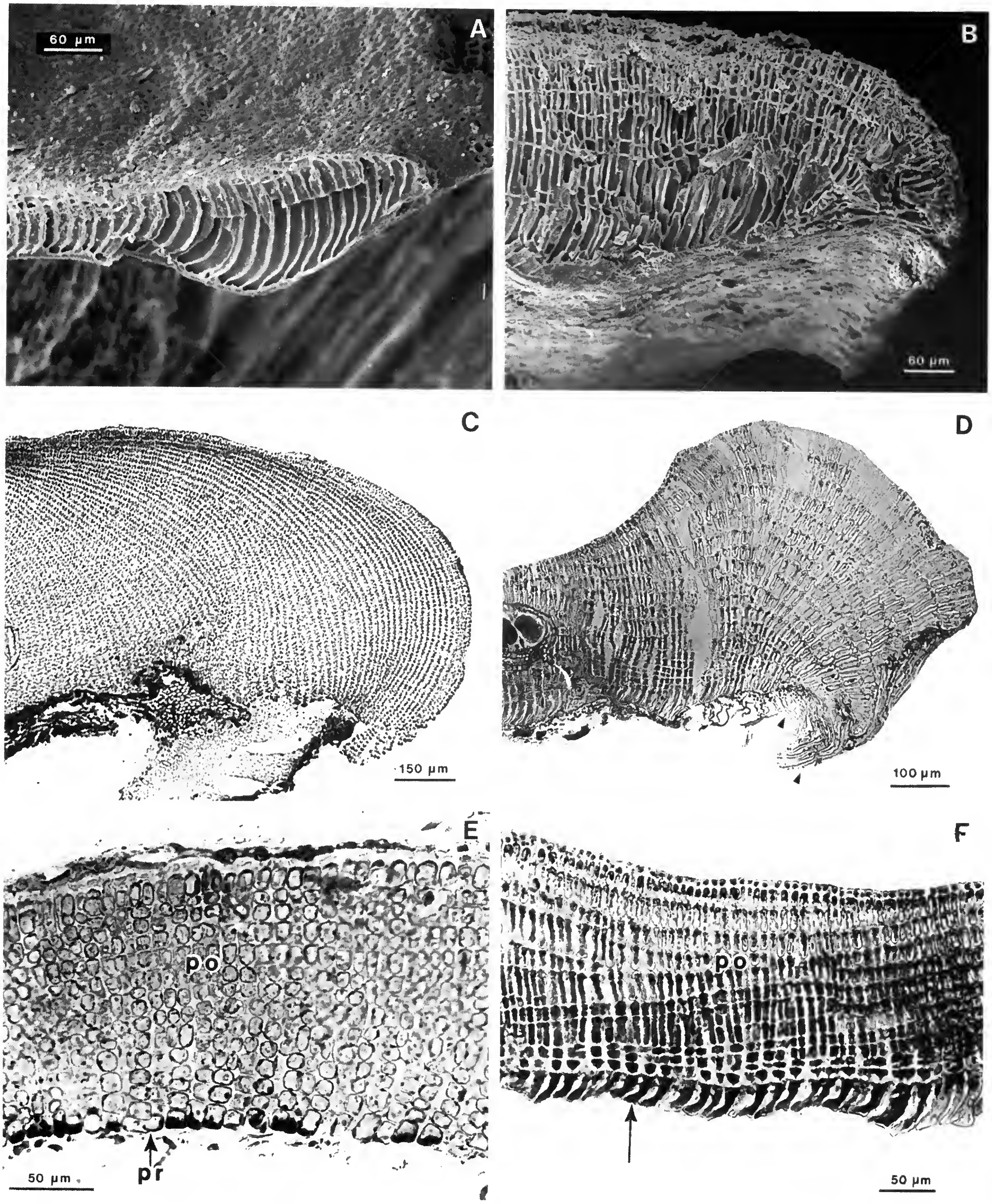


Fig. 25. *Lithophyllum corallinae*: vegetative anatomy (po = postigenous filaments; pr = primigenous filaments). A. Margin of dimerous branch with postigenous development limited to epithallial cells. (LTB 15578). B. Margin of dimerous branch with multicellular postigenous filaments occurring to extreme margin. (LTB 15578). C. Margin of monomerous portion of a crustose part of a thallus. (LTB 13621). D. Margin of primary crustose thallus along the lip of a snail shell. Note extended postigenous development at margin and distorted cells (arrow heads) along edge of thallus. (LTB 15578). E. Older portion of dimerously constructed crustose thallus in which primigenous cells are nonpalisade. (LTB 13587). F. Older portion of dimerously constructed crustose thallus in which primigenous cells are palisade. (LTB 15578).

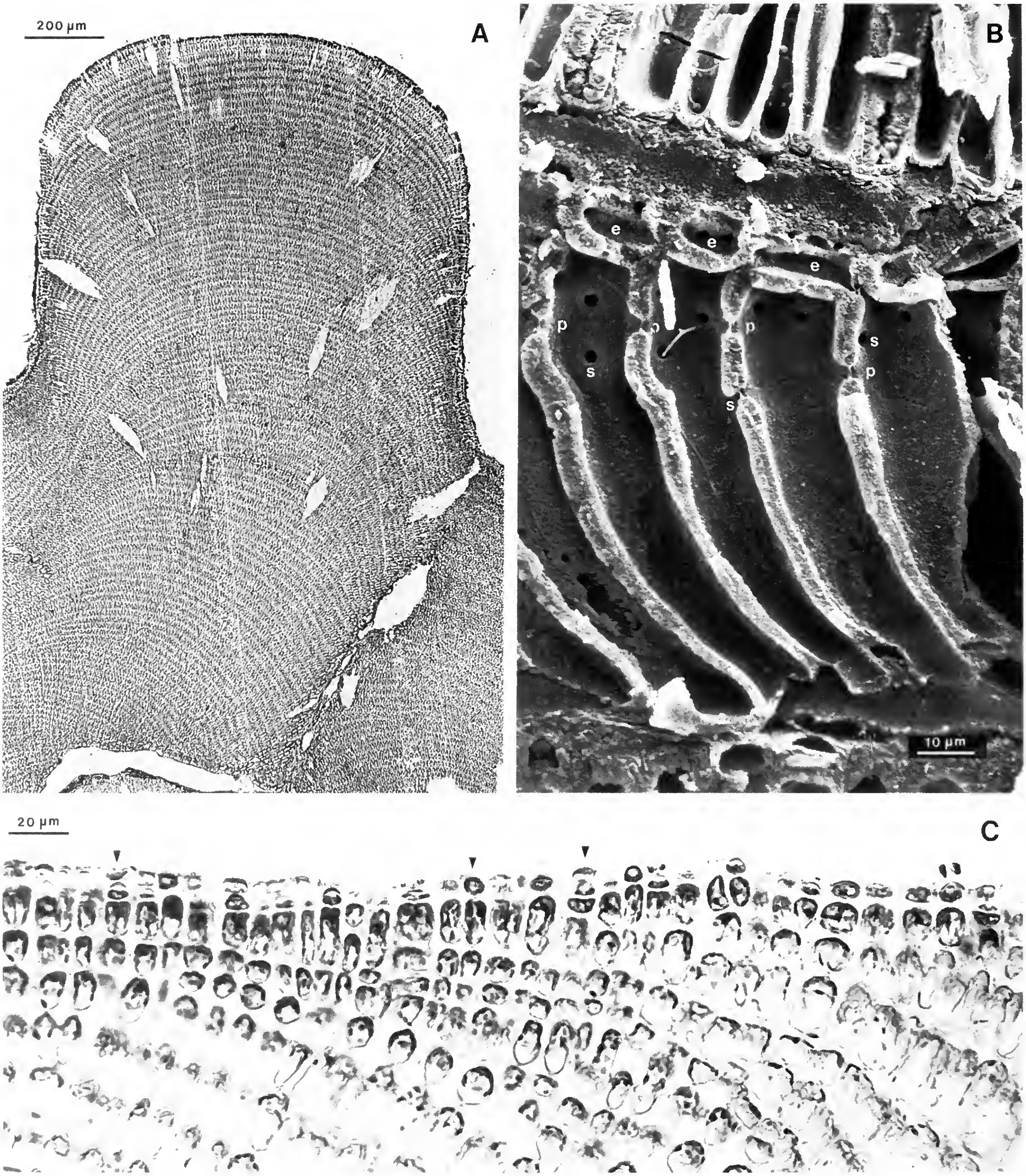


Fig. 26. *Lithophyllum corallinae*: vegetative anatomy. A. Section through young protuberant branch showing monomerous construction. (LTB 13703). B. Fracture of portion of thallus showing primary (p) and secondary (s) pit-connections in primigenous cells. e = epithallial cell. (LTB 15578). C. Section of thallus in which filaments terminate in one or several epithallial cells (arrow heads). (LTB 13171).

chamber floor becomes situated six or more cells below the thallus surface (Fig. 27E).

Three distinct groups of cells/filaments are associated with conceptacle development (Fig. 27B): (1) central sterile filaments/cells not directly involved in roof formation; (2) sporangial initials; and (3) sterile roof-forming filaments. Central filaments stop growing after becoming one or two cells long, and a columella forms. This creates a gap in the developing roof which is destined to become a pore canal (Figs 27B, 27C, 27E). As conceptacles mature, columellar

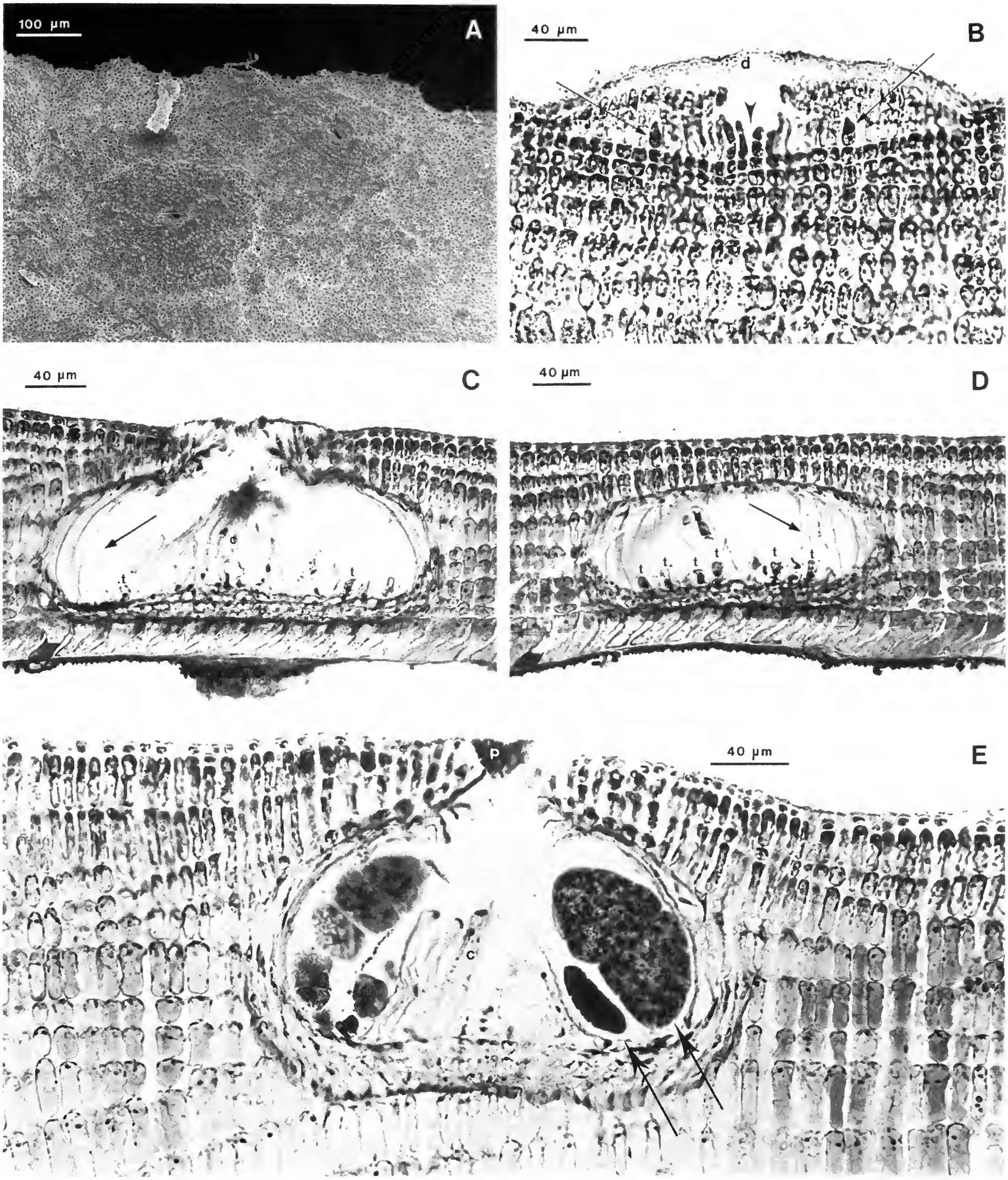


Fig. 27. *Lithophyllum corallinae:* tetrasporangial conceptacle appearance and ontogeny (LTB 15578). A. Surface view of conceptacles. B. Early stage of development. Note ephemeral dome (d) created by remains of old vegetative epithallial cells overlying developing conceptacle, several sporangial initials (arrows) and a group of central filaments (arrowhead) beneath the developing pore and pore canal which are destined to form a columella. C,D. Sections through the pore [C] and more peripheral [D] regions of a developing conceptacle containing tetrasporocytes (t) a degenerating columella (c) and remains of cavity cells (arrows) which have degenerated, resulting in development of a conceptacle chamber. E. Mature tetrasporangial conceptacle. Note sporangia (arrows) of greatly differing size, a degenerate columella (c), and a pore which has a plug (p) but a pore canal which is not completely obstructed by enlarged cells.

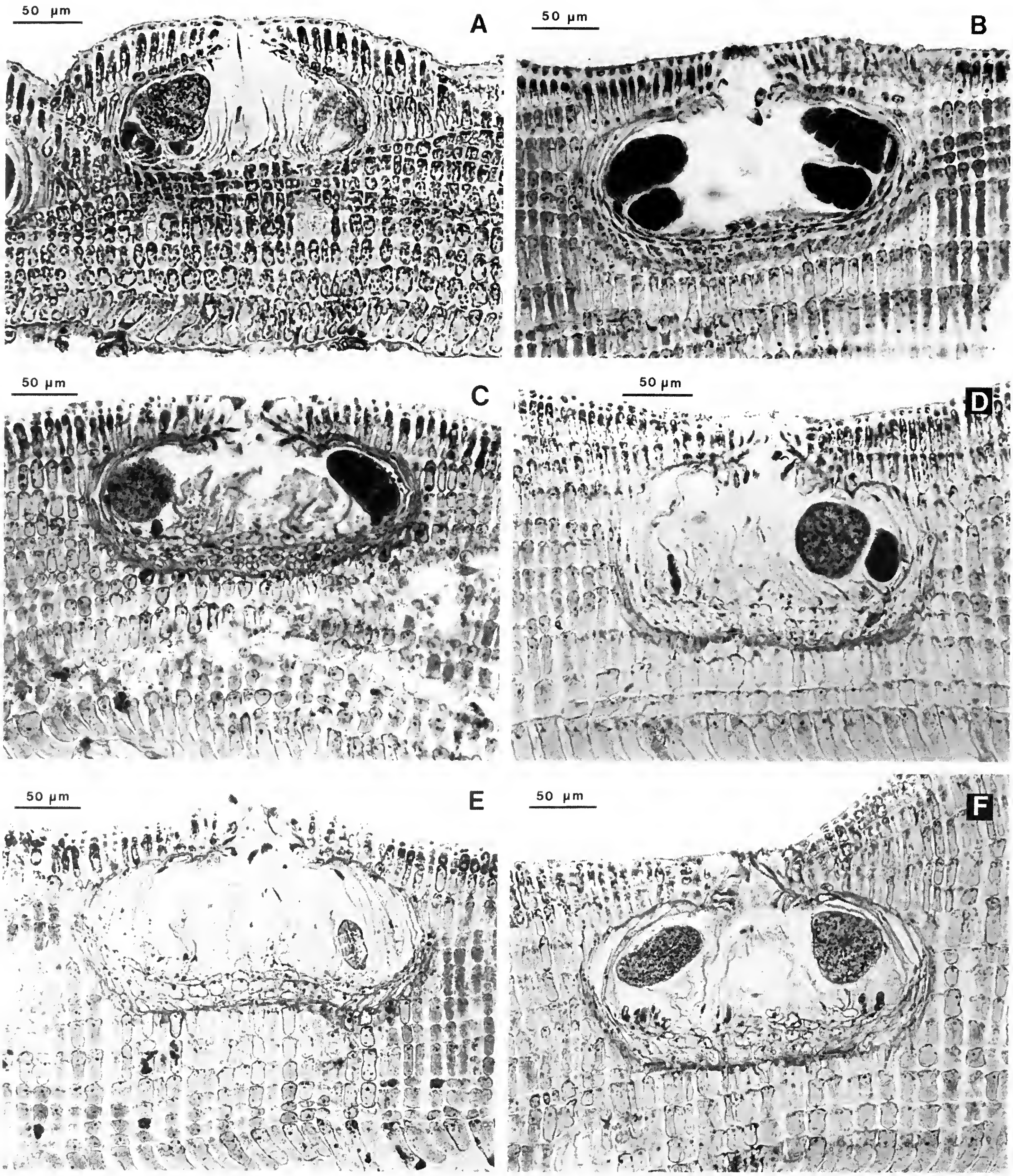


Fig. 28. *Lithophyllum corallinae*: tetrasporangial/bisporangial conceptacles. A–F. Examples of conceptacles within and among populations (See also Fig. 29). Note variability in number of intact cells in roof filaments above the chamber, the occurrence of elongate subepithallial cells in roof filaments, the presence or absence of a columella and the presence or absence of one or several layers of small cells along the conceptacle chamber floor. (A = LTB 15669; B = LTB 13171; C–F = LTB 15578).

cells become more or less elongate and degenerate to varying degrees. A columella is evident in most conceptacles (e.g. Figs 27E, 28C, 29A, 29C), but sometimes it is not evident (e.g. Figs 28B, 29E), and sporangia occur both centrally and

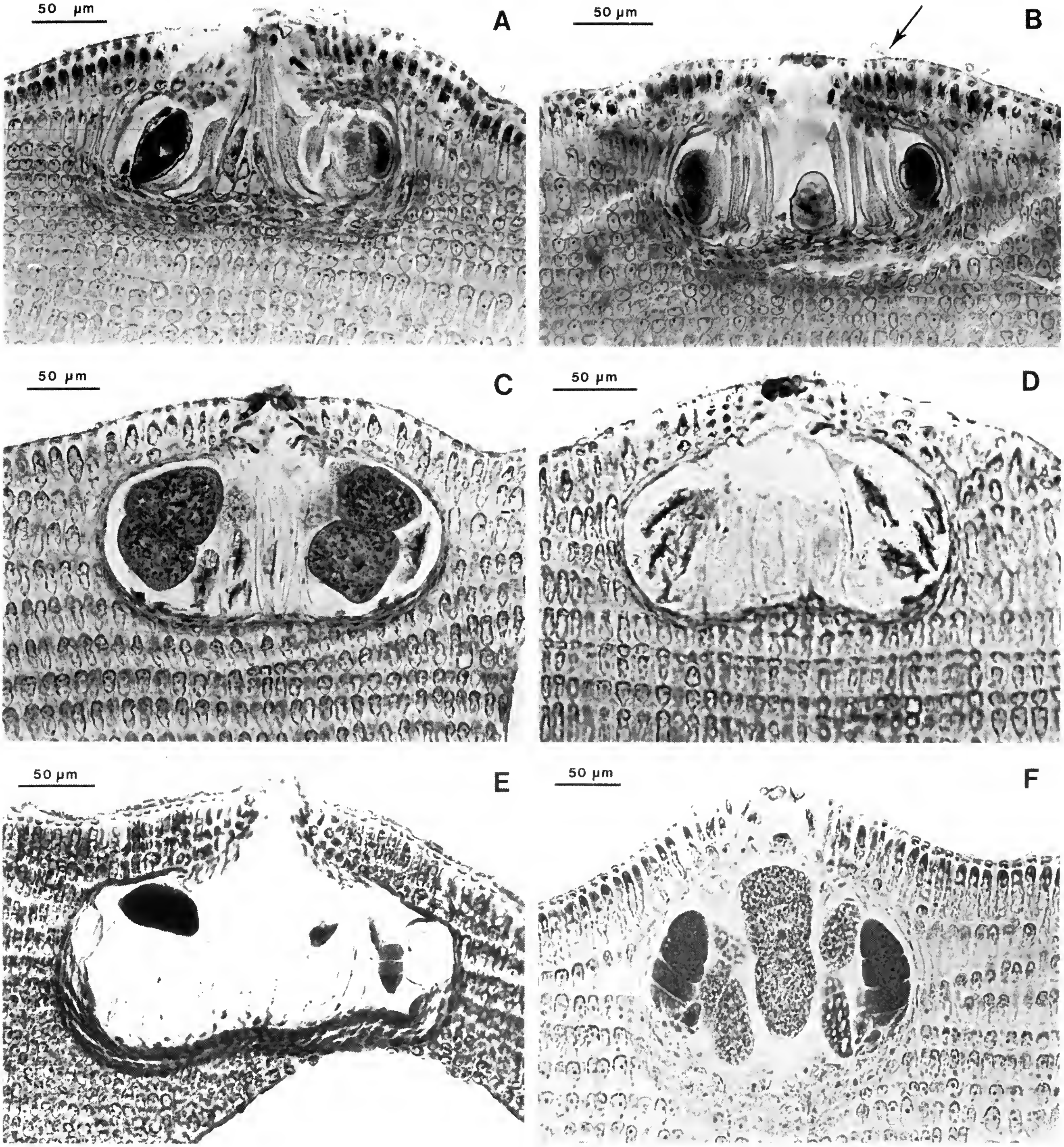


Fig. 29. *Lithophyllum corallinae*: tetrasporangial/bisporangial conceptacles. A–F. Additional examples of conceptacles within and among populations (see also Fig. 28). Note variability in number of intact cells in roof filaments above the chamber, the occurrence of elongate subepithallial cells in roof filaments, the presence or absence of a columella, whether sporangia are peripheral only or occur across the chamber floor, and the presence or absence of small cells along the conceptacle chamber floor. An isolated trichocyte occurs in one roof (Fig. 29B, arrow). (A, B = LTB 13171; C, D = LTB 13974; E = LTB 13703; F = LTB 13174).

peripherally within the chamber (e.g. Figs 29B, 29E). It is possible that either a columella never developed or that complete degeneration has occurred. In either case, however, sporangial initials and sporangia could develop in the central part of the conceptacle chamber, as is evident in Figs 29B and 29E. In British specimens, Chamberlain (1991) reports that a well-defined columella is usually present.

Sporangial initials and sterile roof-forming filaments occur intermixed during early stages of conceptacle development (Fig. 27B). Sporangial initials (Figs 27B–27D) eventually

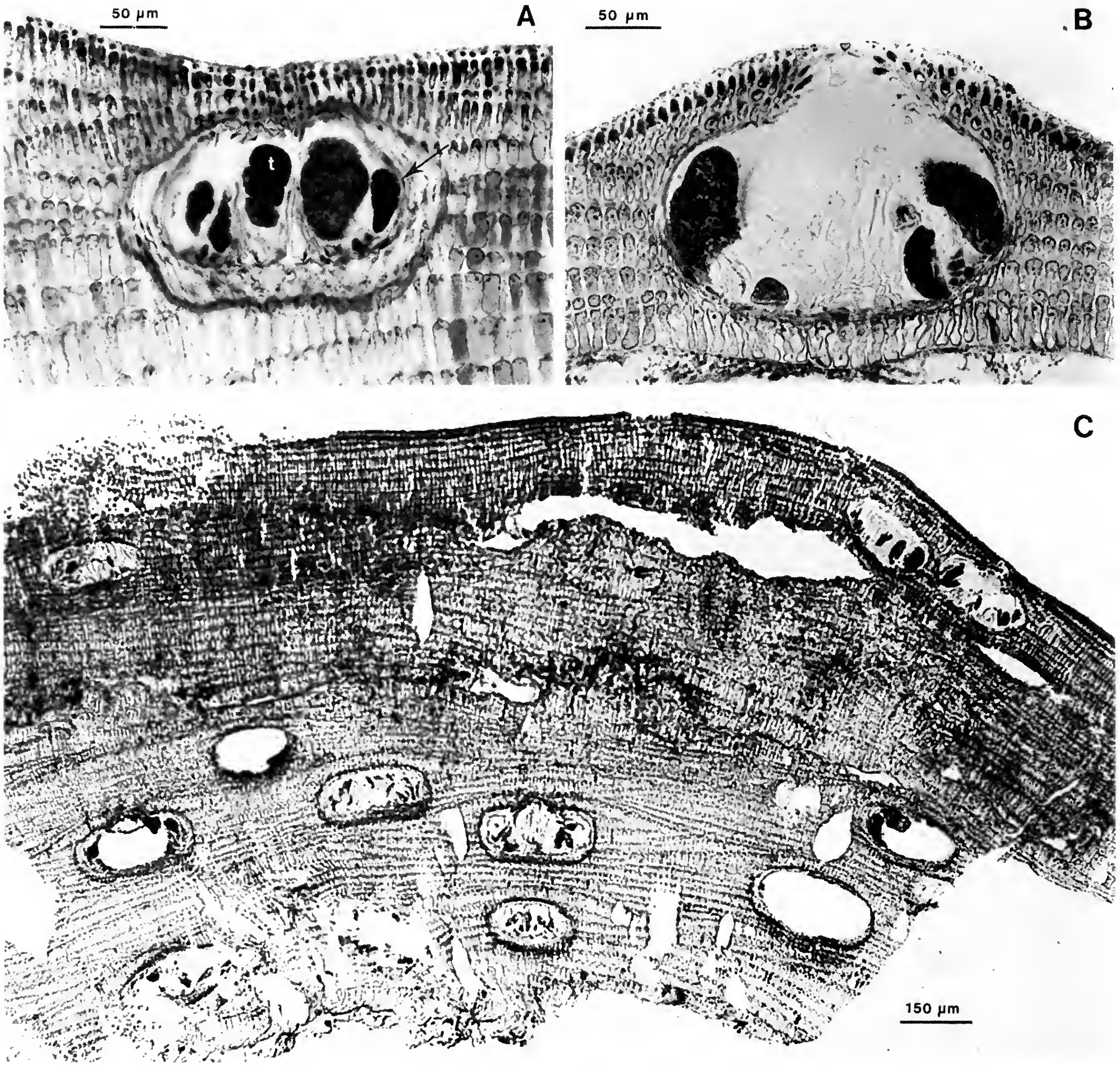


Fig. 30. *Lithophyllum corallinae*: conceptacles. A. Conceptacle containing both trisporangia (t) and tetrasporangia (arrow). (LTB 15578). B. Conceptacle with chamber floor composed of primigenous cells. (LTB 13176). C. Section of thicker thallus containing a number of buried conceptacles. (LTB 12926).

divide to form a sporocyte and a subtending stalk cell (Fig. 27B), and the sporocyte ultimately matures into a tetrasporangium or bisporangium. In some conceptacles (e.g. Fig. 28F), sporocytes continue to be produced after mature sporangia have formed. Roof-forming filaments usually become four to seven cells long, and the chamber forms when the lowermost cells elongate (e.g. Fig. 29B) and degenerate (Figs 27C, 27D). Such cavity cells sometimes persist either more or less intact (Fig. 29B) or more or less crushed against the chamber wall (e.g. Figs 28E, 28F, 29E).

Intact portions of roof filaments above the chamber collectively form a roof of characteristic but somewhat variable structure (Figs 27E, 28, 29). The entire pore canal is never completely occluded by enlarged cells as in *L. chamberlainianum* (Fig. 18D) or *L. irvineanum* (Fig. 35A). Sometimes,however, what appears to be a mucilaginous plug covers the pore (Fig. 27E), or occasionally the top of the pore canal is apparently blocked by protruding, inflated tips of cells adjacent to the pore canal (Figs 28F, 29C). It is important when examining pore canal structure to ensure that sections are cut vertically through the centre of the canal; sections cut near the periphery or cut off-angle can give the erroneous impression that the pore canal is completely occluded.

Roof filaments immediately flanking the pore canal usually terminate in cells which differ in size and shape from other roof cells, which may be very small or somewhat inflated in

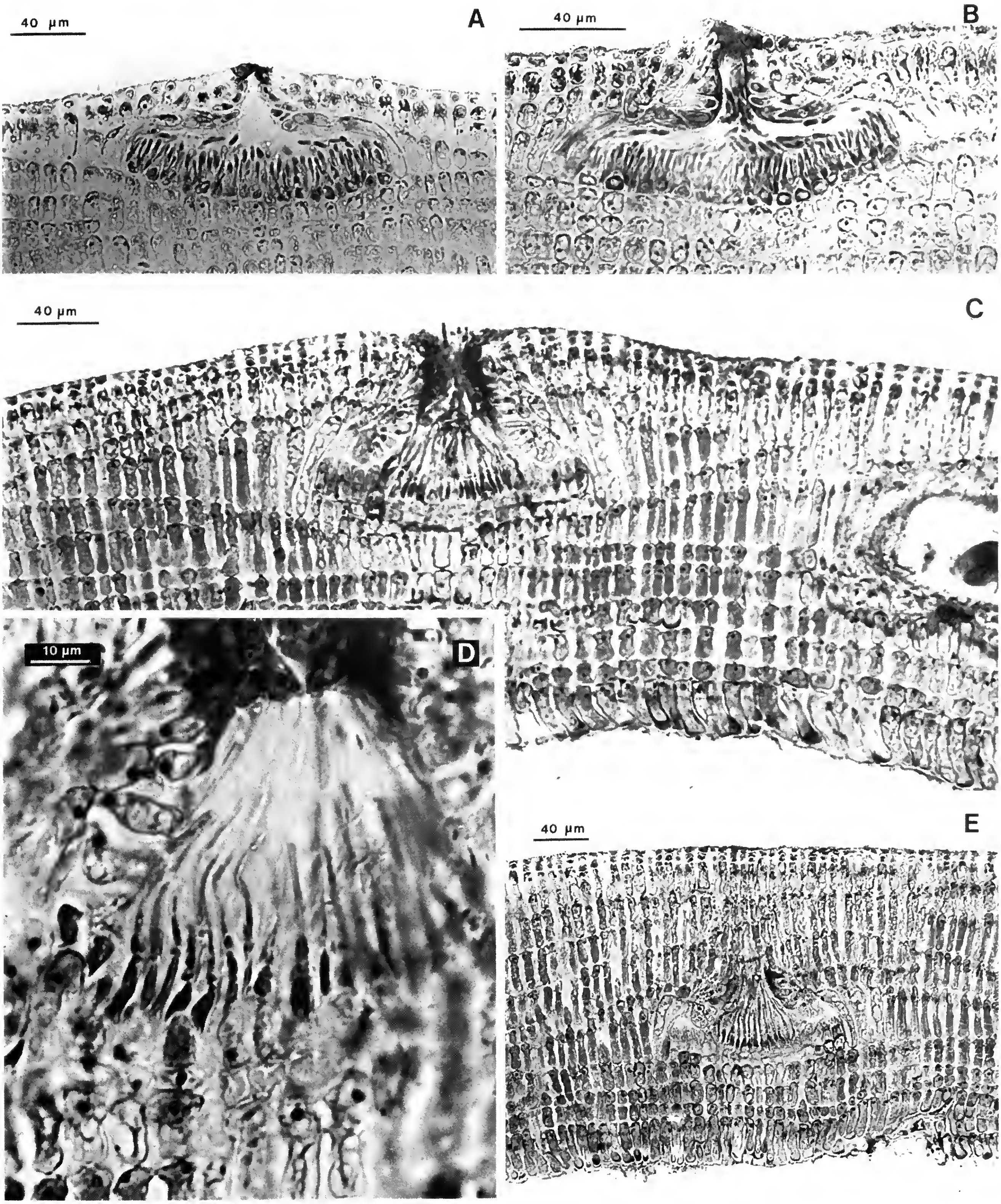


Fig. 31. *Lithophyllum corallinae*: gametangial conceptacles. A, B. Male conceptacles. Note variation in roof anatomy. (A = LTB 13174; B = LTB13171). C. Female conceptacle at thallus surface. (LTB 15578). D. Carpogonia and carpogonial branches within female conceptacle. (LTB 15578). E. Buried female conceptacle containing unfertilized carpogonia. (LTB 15578).

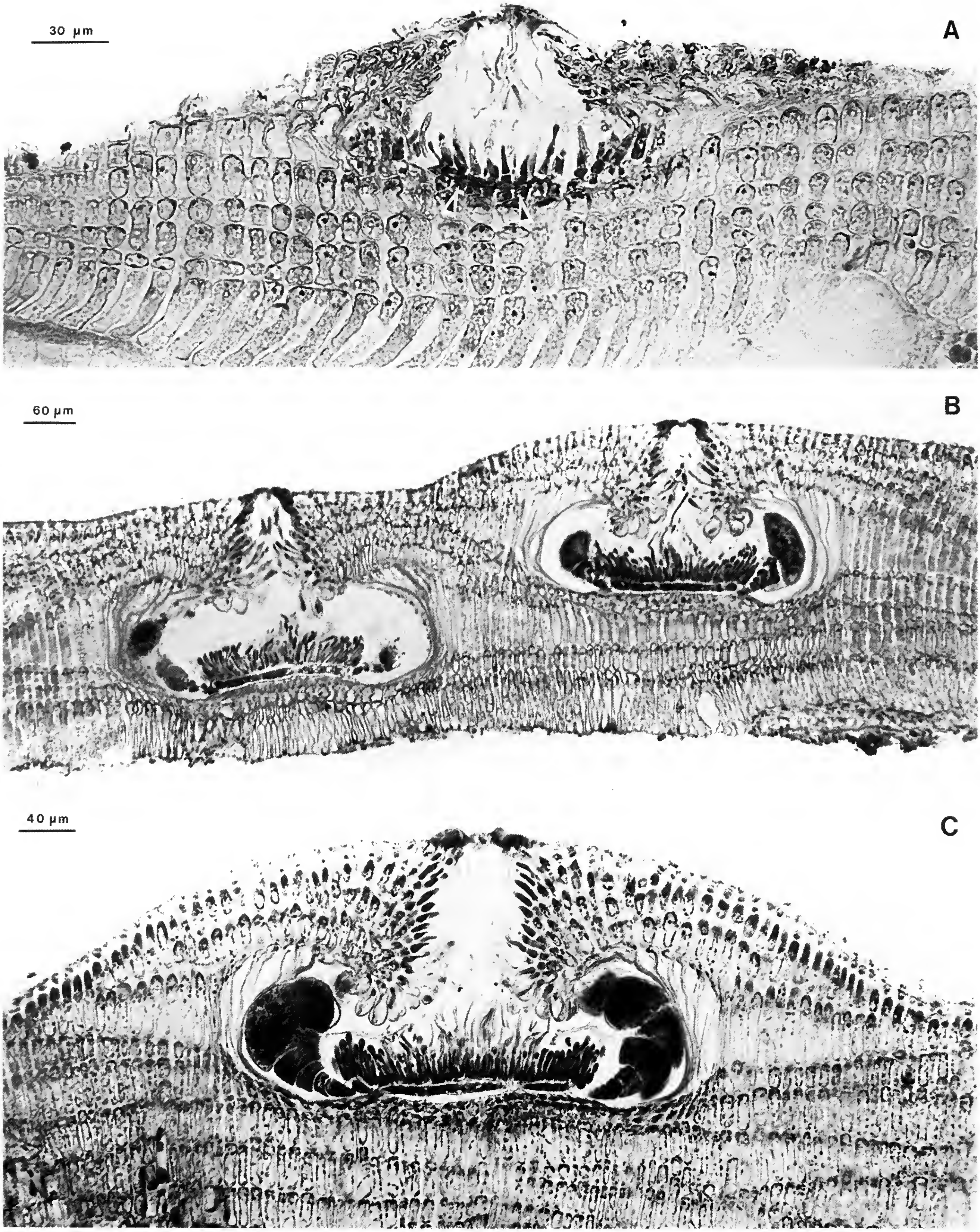


Fig. 32. *Lithophyllum corallinae*: carposporophytes. A. Developing fusion cell (arrowheads) after presumed karyogamy. Conceptacle roof is damaged. (LTB 13176). B. Female/carposporangial conceptacles containing fully developed fusion cells and developing gonimoblast filaments. (LTB 15578). C. Mature carposporophyte within female/carposporangial conceptacle. Note structure of conceptacle roof and gonimoblast filaments with mature carposporangia (C). (LTB 15578).

Table 9 Representative published records of specimens attributed to *Lithophyllum corallinae* and its synonyms. Names of taxa are listed alphabetically by specific epithet. Localities are given in parentheses; superscripts refer to notes at end of table. Unless otherwise indicated, records have not been verified during the present study.

Dermatolithon corallinae
Boergesen, *Bot. Faeroes*: 402 (1902) (Faeroes Is.). Cabioch in *C. R. hebd. Seanc. Acad. Sci. Paris* 288D: 1522 et. seq., text figs A-D, pl. 1 (1979) (France)[1]. Cinelli et al. in *Mem. Biol. mar. Oceanogr.* n.s. 6(5): 164 (1976) (Italy). Dawson in *Pacif. Nat.* 2: 35, pl. 25, figs 6,7 (1960) (Mexico)[2]. Gallardo et al., *Prel. Checklist Iberian Benth. Mar. Algae*: 56 (1985) (Spain). Guiry, *Concensus Bibliog. Irish Seaweeds*: 33 (1978) (Ireland). Hamel & Lemoine in *Archs Mus. Hist. nat. Paris* ser 7, 1: 64, text fig. 27, pl. f, fig. 6 (1953) (France) [2]. Levring in *Bolm. Mus. munic. Funchal* 28: 66 (1974) (Madeira). Masaki in *Mem. Fac. Fish. Hokkaido Univ.* 16: 50 (1968) (Japan)[2]. Masaki & Tokida in *Bull. Fac. Fish. Hokkaido Univ.* 10(4): 285, pls 1,2,4,5 (1960) (Japan)[2]. Tseng, *Common Seaweeds of China*: 76, pl. 41, fig. 1 (1983) (China)[2]. Zinova, *Red Brown Green Algal Fl. Stn Seas USSR*: 228 (1967) (Black Sea)[2].
Lithophyllum corallinae
Heydrich in *Ber. dt. Bot. Ges.* 15: 47 (1897b) (Mediterranean & Adriatic)[2]. Rosenvinge in *K. Dansk Vidensk. Selsk. Skr.* ser 7(Nat. og Math. Afd.) 7: 265, figs 186-190 (1917) (Denmark)[3]. Suneson in *Acta Univ. lund.* N.F. Avd. 2, 39(9): 43, text figs 24-26, pl. 6, fig. 28, pl. 8, fig. 38 (1943) (Sweden)[3]. Suneson in *Bot. Notiser* 1950: 436, figs 4-8 (1950) (Sweden)[4]. Taylor, *Mar. Algae Neast. Coast N. Am.*: 251 (1957) (Atlantic Canada & USA)[2]. Taylor, *Mar. Algae East. Trop. Subtrop. Coasts Americas*: 391 (1960) (Atlantic USA)[2].
Melobesia corallinae
Bornet in *Mem. Soc. natn. Sci. nat. math. Cherbourg* 28: 348 (1892) (Algeria, Morocco). Crouan & Crouan in *Bull. Soc. bot. Fr.* 7: 370 (1860) (France)[5]. Crouan & Crouan, *Florule Finistère*: 150, 252, pl. 20 (133 bis), figs 6-11 (1867) (France)[6]. De Toni, *Sylloge Algarum* 4: 1768 (1905)[2, 7]. Funk in *Publ. Staz. zool. Napoli* 7(suppl): 432, pl. 9, fig. 9 (1927) (Adriatic). Hauck, *Meeresalg. Dt. Österr.*: 266 (1883) (Adriatic)[2]. Lemoine in *Bull. Soc. bot. Fr.* 58: LXI (1912)[8]. Newton, *Handb. Br. Seaweeds*: 302 (1931)(British Isles)[2]. Preda, *Fl. Ital. Crypt.* (Pt. II Algae): 32 (1908) (Mediterranean)[2]. Solms-Laubach in *Fauna Flora Golf. Neapel.* 4: 9, pl. 2, fig. 25, pl. 3, figs 21-24 (1881) (Adriatic)[3].
Tenarea corallinae
Park in *Bull. Nat. Fish. Univ. Busan* 20(1): 15, pl. 2, fig. 4 (1980) (Korea)[2].
Titanoderma corallinae
Chamberlain in *Bull. Br. Mus. Nat. Hist.(Bot. Ser.)* 20(2): (1991) (British Isles)[9]. South & Tittley, *Checklist Dist. Index Benth. Mar. Algae. N. Atlantic Ocean*: 45 (1986) (North Atlantic)[7].
Lithophyllum pustulatum f. corallinae
Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 118 (1905a) 118[10].

Notes on Table 9.
[1] Describes effects of *Lithophyllum corallinae* on host *Corallina* plants.
[2] Includes description.
[3] Contains a detailed morphological/anatomical account.
[4] Contains cytological data on bispores and tetraspores.
[5] *Nomen nudum.*
[6] Protologue.
[7] Data summarized from previous literature.
[8] Contains list of specimens in Thuret herbarium, most of which are vouchers for earlier published records.
[9] Provides an in depth account of the species, including the type collection; cites southern Australia in distribution records.
[10] Provides considerable data, all of which requires verification.

appearance and which may or may not project into the pore canal (Figs 28, 29). Remaining roof filaments above the chamber normally terminate in an epithallial cell and contain two or three intact subtending cells. In some roofs (e.g. Figs 28A, 29F), all subepithallial cells tend to be elongate; in others (e.g. Fig. 29D), all subepithallial cells are short; and in still others (e.g. Figs 27E, 29A), mixtures of short and elongate subepithallial cells occur. When a series of conceptacles are compared (e.g. Figs 27E, 28, 29), it becomes obvious that a continuous spectrum of variation in roof structure occurs, and that it would be counterproductive to recognize each variant as a distinct taxonomic form or variety.

The margins of tetrasporangial/bisporangial conceptacles, when seen in sectional view, are not usually clearly delimited from the surrounding thallus because roof filaments immediately flanking the conceptacle chamber look more or less identical to ordinary vegetative filaments. With several exceptions (Figs 27C, 30B), the floors of all tetrasporangial/bisporangial conceptacles examined were subtended by multicellular filaments; in the exceptions, the conceptacle floor was subtended by primigenous palisade cells.

Tetrasporangia/bisporangia may occur across the conceptacle chamber floor (Figs 29B, 29F), but more commonly they occur peripheral to a central, oftendegenerate columella (e.g. Figs 28B, 29D). Stalk cells subtending sporangia seldom remain apparent (Fig. 27E), and individual sporangia within a conceptacle can vary considerably in size (Fig. 27E). In some conceptacles, chamber floors may contain a number of small cells (e.g. Figs 28C–28F), but in other conceptacles in the same collection (Fig. 3OB) such cells are lacking. It appears that these small cells may give rise (secondarily?) to sporangial initials (Fig. 28F), but initials also can arise in the absence of such cells (Fig. 27B). In more robust plants, older conceptacles can become buried within the thallus (Fig. 30C).

In one conceptacle (Fig. 30A), both trisporangia and tetrasporangia were found. Whether such trispores are viable, however, is unknown.

Only mature male conceptacles (Figs 31A, 31B) have been seen. The conceptacle roof above the chamber is formed from a ring of peripheral filaments which arch over and enclose a central fertile region on the chamber floor. Each filament consists of a main axis of larger cells which border the chamber and a few smaller-celled laterals which arise secundly, are usually two to four cells long, and either terminate at the roof surface in an epithallial cell or help to line the pore canal. Filaments flanking main filaments are difficult to distinguish from ordinary vegetative filaments and appear to represent little more than extensions of them. Spermatangia are more or less club-shaped and are borne in groups of one to three on initials which occur across the entire chamber floor.

The youngest female/carposporangial conceptacles detected already were fully formed and contained mature carpogonial branches (Figs 31C–31E). Carpogonial branches occurred across the entire chamber floor, and all terminated in carpogonia with elongate trichogynes (Fig. 31C). One or sometimes two carpogonia occurred per branch (Fig. 31D). In one collection (Fig. 31E), conceptacles containing carpogonial branches became buried in the thallus, apparently precluding karyogamy.

Roofs of female/carposporangial conceptacles may be more or less flush with (Figs 31C, 32B) or protrude above (Fig. 32C) the surrounding thallus surface, and they may reach full maturity prior to karyogamy. Filaments flanking the pore canal contain cells differing in size and/or shape from other roof filaments and they terminate in cells which project somewhat into the pore canal (Figs. 32B, 32C). Remaining roof filaments above the chamber each contain a terminal epithallial cell and two to four intact subtending cells. Peripheral cavity cells comparable to those found in tetrasporangial/bisporangial conceptacles also occur (Figs 31C, 32B, 32C); these senesce and degenerate to varying degrees, resulting in the enlargement of the conceptacle chamber. Remains of cavity cells are common in conceptacles containing mature carposporophytes (Fig. 32C).

Carposporophytes arise within female/carposporangial conceptacles after presumed karyogamy. A fusion cell forms across the chamber floor, and remains of old carpogonial branches persist on the dorsal surface (Figs 32A–32C). Although one early stage of fusion cell development was seen (Fig. 32A), details of its ontogeny have not been elucidated. Eventually, gonimoblast filaments arise peripherally and produce terminal carposporangia (Figs 32B, 32C).

Spore germination and very early thallus development have not been observed.

There are a number of published accounts of plants ascribed to *L. corallinae* or its homotypic synonyms from outside Australian waters (Table 9). The most detailed recent account is that of Chamberlain (1991, as *Titanoderma*) who provides data on British specimens and summarizes data from earlier studies including Cabioch (1979), Hamel & Lemoine (1953), Masaki (1968), Masaki & Tokida (1960), Rosenvinge (1917) and Suneson (1943; 1950).

Relationships of *L. corallinae* to other species are considered below (p.97).

INFRASPECIFIC TAXONOMY. No infraspecific taxa of *Lithophyllum corallinae* have been recognized.

4. **Lithophyllum irvineanum** Woelkerling et Campbell, sp. nov.

Figs 33–35

HOLOTYPE. LTB 15676 ('The Midden', Three Mile Rocks, ca. 5 km west of Beachport, South Australia, *Campbell & Penrose,* 26 February 1988; 3–6 m deep on snail shells). Fig. 33A.

Note: Several additional species of nongeniculate Corallinaceae (subf. Mastophoroideae) occur on the same mollusc shells; identification of plants of *L. irvineanum* has been effected from permanent microscope slides made from fragments removed from the substrate.

MISAPPLIED NAMES. No published misapplications of other names to specimens of *L. irvineanum* were discovered during this study.

ETYMOLOGY. The specific epithet honours Linda M. Irvine for her long-term interest in and her valuable contributions to nongeniculate coralline taxonomy.

LATIN DIAGNOSIS:
L. irvineanum characteribus generis *Lithophyllum*; differt de speciebus affinibus inter alia quod solum conceptaculorum bisporangium 1–3 cellulosis stratis immersis et canalis pori conceptaculorum bisporangium a 2–4 cellulis amplifactis angularibus non superimposit obstructus est.

The characteristics of *Lithophyllum* are given in Table 1; features delimiting *L. irvineanum* as a species and its relationships to other species of *Lithophyllum* are considered in greater detail below.

DESCRIPTION. Plants mostly 3–10.5 mm across and 0.05–1.0 mm thick or tall; flat (complanate) to layered (without conspicuous terracing); completely adherent.

Thallus dimerous; primigenous filaments usually composed of palisade cells 5–12 μm long and (15–)25–70(–80) μm tall; postigenous filaments composed only of epithallial cells 2–6 μm long and 4–9 μm in diameter, or rarely becoming 2 cells long. Contiguous secondary pit-connections common; adjunctive secondary pit-connections, cell fusions and trichocytes not seen.

Bisporangial plants with scattered, protruding conceptacles. Conceptacle roofs 370–519 μm in external diameter; roof filaments above chamber usually (2–)3–4 cells long; cells 8–24 μm long and 4–12 μm in diameter with columnar cells sometimes occurring singly, in pairs, or in horizontal subepithallial groups. Pore canals completely occluded by 2 or 4 enlarged angular cells which do not project above the surrounding roof surface. Conceptacle chambers (180–)215–245(–263) μm in diameter and 82–125 μm tall; floor of mature chambers 1(–3) cells below thallus surface; bisporangia 68–88(–101) μm long and (29–)40–55 μm in diameter, scattered across chamber floor or peripheral to a columella.

Tetrasporangial plants, gametangial plants and carposporophytes not seen.

DIAGNOSTIC FEATURES. *Lithophyllum irvineanum* differs from other southern Australian species in having the following combination of features:

1. Entire pore canals of bisporangial (and presumably tetrasporangial) conceptacles normally completely occluded by enlarged angular cells which line the canal (Figs 35A, 35B, 35D). When conceptacles are viewed in vertical section through the pore canal, two or four such cells usually are evident and these do not project above surrounding roof filaments.
2. Floors of functional bisporangial (and presumably tetrasporangial) conceptacles usually situated one (rarely two) cells below the thallus surface and conceptacle roofs protruding above the thallus surface (Figs 33D, 35A, 35B).
3. Thallus surface not obviously and more or less completely terraced as a consequence of applanate branch development.
4. Applanate branches, when present, arising from groups of primigenous cells (Figs 34B–34D).
5. Postigenous filaments normally unicellular (composed only of epithallial cells) in vegetative parts of thallus (one collection with two-celled postigenous filaments has been seen).

In so far as known, no other described species of *Lithophyllum* possesses this combination of features. A comparative analysis of the type collections of the over 650 entities ascribed to *Lithophyllum* may, however, uncover an earlier specific epithet for *L. irvineanum*, but such an analysis is beyond the scope of the present study.

NOMENCLATURE AND SYNONYMY. No matters relating to nomenclature and synonymy require comment.

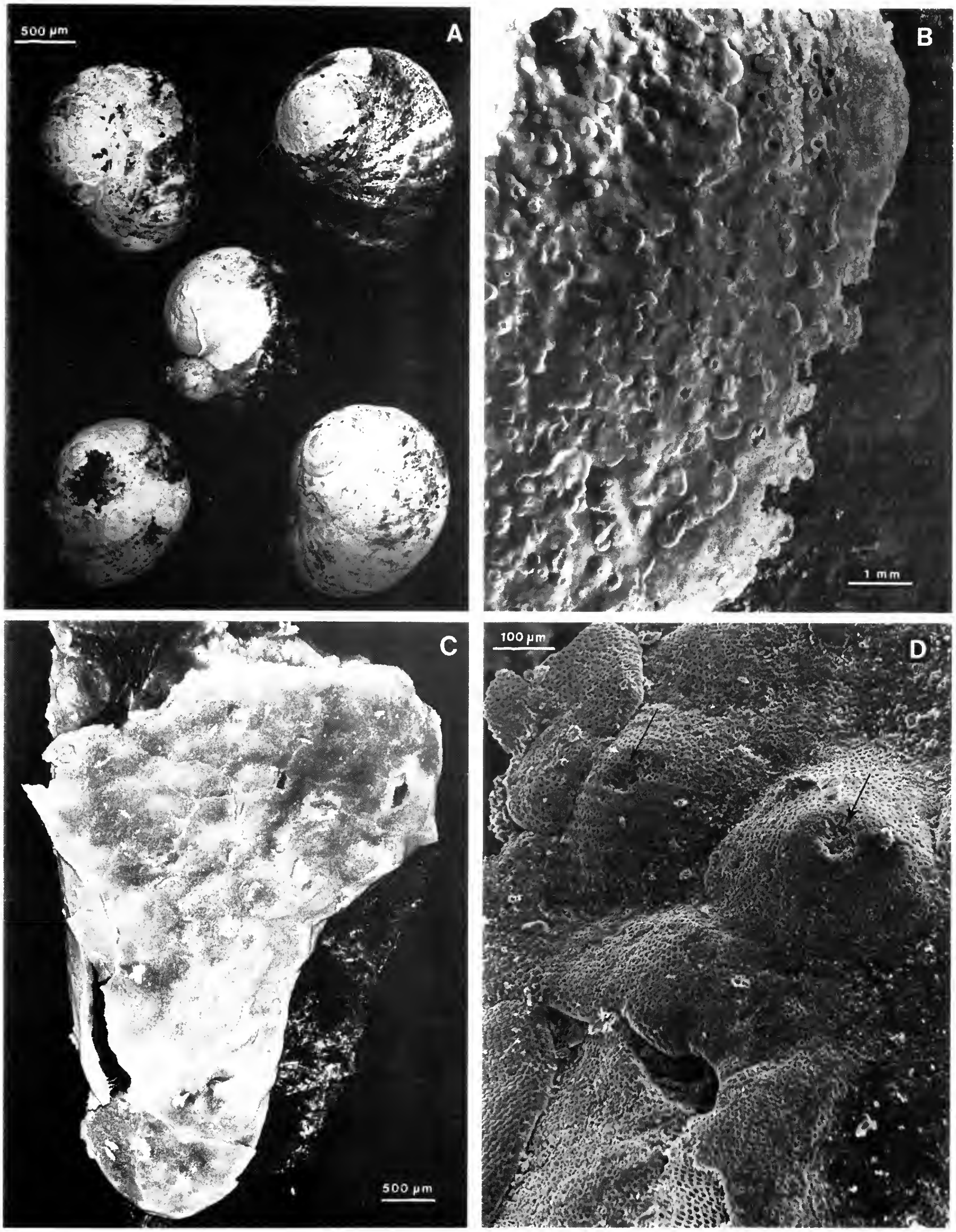


Fig. 33. *Lithophyllum irvineanum*: holotype and surface features. A. Holotype collection on snails. (LTB 15676). B. Surface view of layered specimen in holotype collection showing small branches near thallus margin. (LTB 15676). C. Surface view of specimen on *Osmundaria* with little apparent applanate branching. Thallus, however, consists of numerous layers of applanate branches (see Fig. 34A). (LTB 14247). D. Surface view of specimen in holotype collection showing two bisporangial conceptacles. Thallus surface is pitted by numerous concavities resulting from the collapse of epithallial cells during drying. Note that conceptacle pores (arrows) are obstructed (see text for details). (LTB 15676).

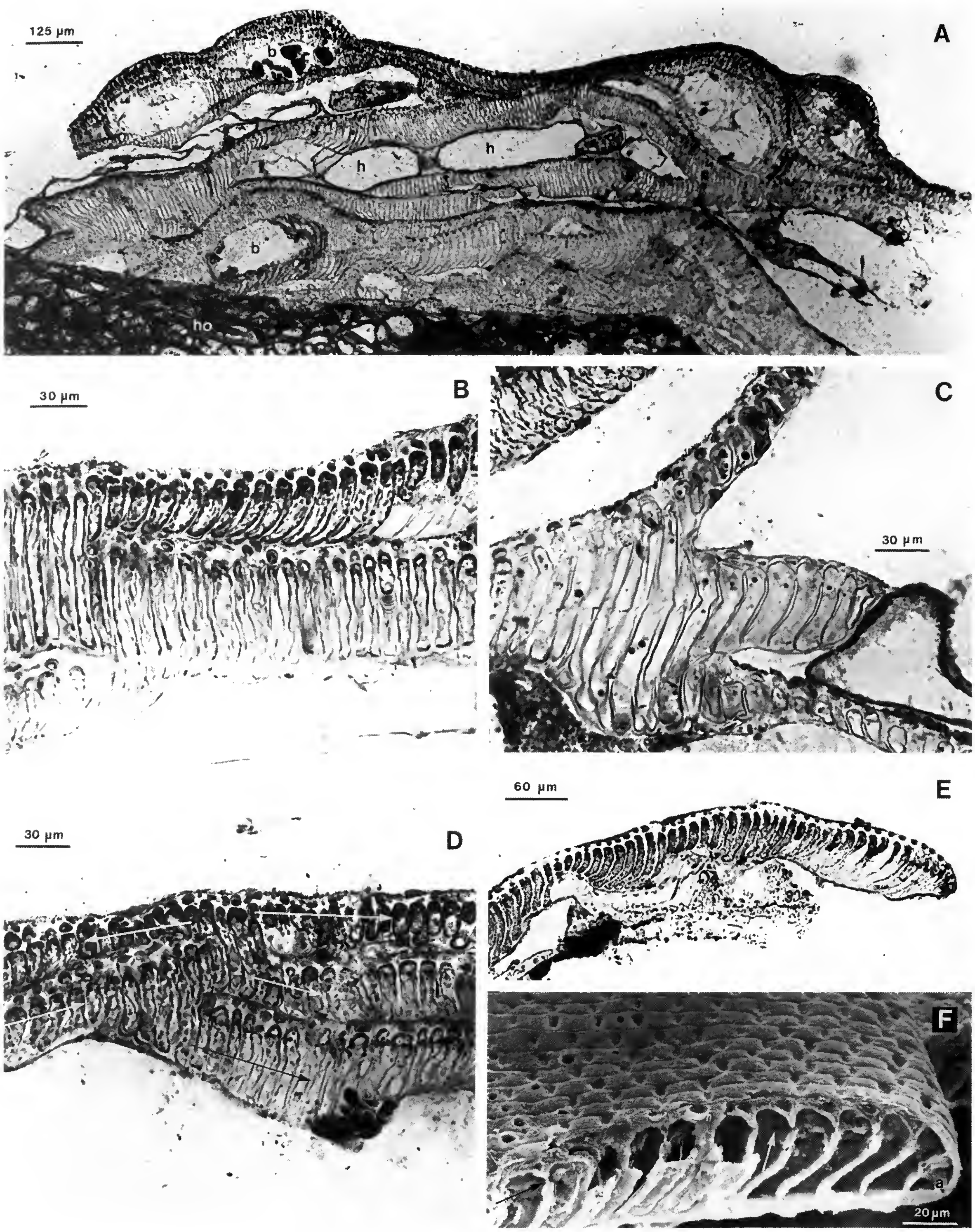


Fig. 34 *Lithophyllum irvineanum*: vegetative anatomy. A. Section through thallus composed of a number of layers of applanate branches. Note variation in height of primigenous cells, bisporangial conceptacles (b) both at the surface of and immersed within the thallus, and hollows (h) within the thallus where successive layers of branches are not touching one another. ho = host. (LTB 14247). B.-D. Sections showing points of origin of applanate branches in plants from LTB 14247. See text for detailed explanation. Note variation in height of primigenous cells. In Fig. 34D note how only two primigenous cells separate the points of origin of two branches. Arrows indicate direction of filament growth. E. Section through thallus margin of plant in holotype collection. Note variation in height of primigenous cells. (LTB 15676). F. Combined surface view/fracture of margin of a specimen in the holotype collection. Note apical initial (a), primary (black arrow) and secondary (white arrow) pit-connections, epithallial concavities on thallus surface and the alignment of contiguous filaments in rows. (LTB 15676).

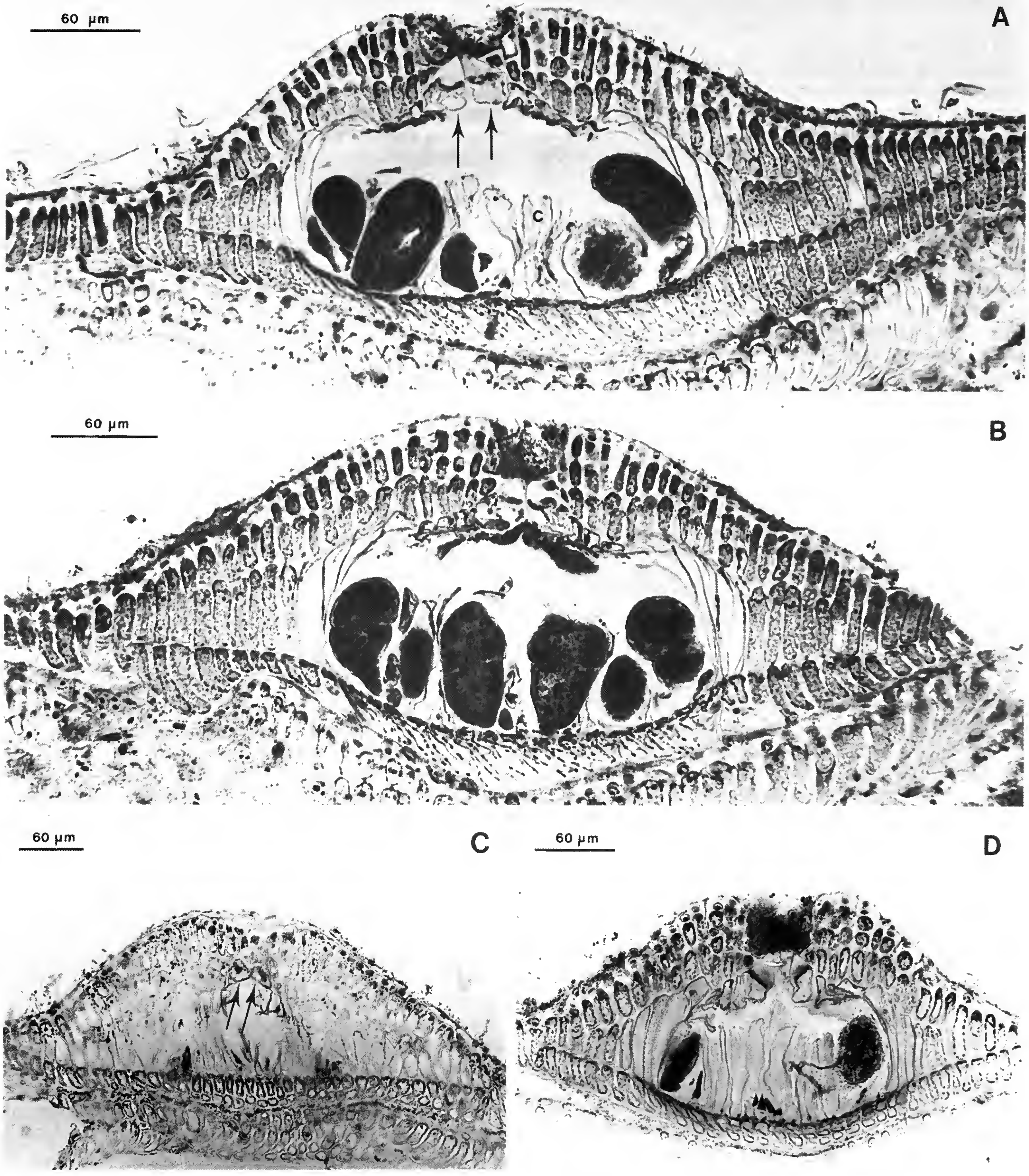


Fig. 35 *Lithophyllum irvineanum*: bisporangial conceptacles. A, B. Mature bisporangial conceptacles from holotype collection (LTB 15676), one with (35A) and one without (35B) a columella (c). Note large, angular cells (arrows) occluding pore canal, and bisporangia. Further details given in text. C. Young bisporangial conceptacle showing bisporangial initials and enlarged cells (arrows) destined to block the pore canal. (LTB 14607). D. Nearly mature bisporangial conceptacle with sporangia at a stage just (?) prior to bispore formation. (LTB 14607).

Distribution and ecography. *Lithophyllum irvineanum* has been recorded from three localities in South Australia and one in Western Australia; collections were made in February and October. The species is unknown elsewhere.

Plants have been found subtidally at depths of 1–11m on rock, on the red alga *Osmundaria* (Fig. 33C) and on snails (Fig. 33A). In all known collections, *Lithophyllum irvineanum* occurs intermixed with other nongeniculate corallines and usually is not dominant. The type collection consists of plants growing on the snail *Turbo undulatum* (Solander) (Fig. 33A).

COLLECTIONS EXAMINED:

SOUTH AUSTRALIA: Beachport (The Midden, Three Mile Rocks)(*Campbell & Penrose*, 26 February 1988, LTB 15676). Holotype. Elliston (Waterloo Bay) (*Turner*, 28 October 1981, LTB 15446; 31 October 1981, LTB 15390). Sceale Bay (Point Westall) (*Platt & Jones*, 16 February 1984, LTB 14580, 14607).

WESTERN AUSTRALIA: Dempster Point, Israelite Bay (*Woelkerling, Platt, & Jones*, 8 February 1984, LTB 14247).

REMARKS ON MORPHOLOGY AND ANATOMY. Specimens of *Lithophyllum irvineanum* cannot be identified from external features for reasons outlined in the account of *L. chamberlainianum* (q.v.). Unequivocal identification requires sections of mature bisporangial conceptacles in which the pore canal is clearly shown (Figs 35A–35D).

All plants of *L. irvineanum* examined were flat (complanate) or layered. Individual thalli were more or less contoured to the substrate, and both horizontally expanded and sleeve-like specimens have been observed (Figs. 33A–33C).

Applanate branches are common, inconspicuous, and horizontally expanded (Fig. 33B), but the thallus never appears conspicuously terraced to the unaided eye as in *L. prototypum* (Fig. 44A). At thallus margins, the positions of individual filaments are demarcated by parallel ridges and grooves, and concavities resulting from the collapse of dried epithallial cells are evident on the dorsal thallus surface (Fig. 34F).

Thalli are dimerous and dorsiventral (Figs 34A–34F). Primigenous filaments are usually composed of palisade cells which can vary considerably in height over short distances-(Figs 34A, 34C, 34E). Lateral expansion of thallus margins and of applanate branches occurs when apical initials divide and produce new primigenous cells inwardly (Figs 34E, 34F). In most plants, postigenous development is limited to the production of epithallial cells (Figs 34B, 34E, 34F), although two-celled postigenous filaments were seen once in LTB 14247.

Thallus thickness varies depending upon the extent of applanate branching and the relative height of primigenous cells. Most specimens in the type collection contain four or fewer layers of applanate branches and have more or less uniformly tall primigenous cells. In LTB 14247 (Figs 33C, 34A–34D), in contrast, more than four layers of branching can occur, and primigenous palisade cells vary more in height (Figs 34A–34C).

Applanate branches arise directly from groups of primigenous cells (Figs 34B–34D) in two apparently different ways. Primordial stages, unfortunately, have not been found. One mode of formation almost certainly involves periclinal, coaxial divisions (see Turner & Woelkerling 1982: 203) of groups of apical initials (Figs 34E, 34F). Each initial presumably divides into two (not observed) such that one lies on top of the other. Subsequently, both new initials cut off primigenous cells inwardly such that the filament produced by the top initial lies over the one produced by the bottom initial (Fig. 34B). On one occasion, three branches appeared to originate from virtually the same point of the parent thallus (Fig. 34C).

Another mode of branch formation appears to involve secondary elongation of small groups of primigenous palisade cells above the surrounding thallus surface (primordial stages not seen). Peripheral cells in this group then presumably divide transversely, and the top cells produce new initials (details uncertain). These subsequently give rise to new filaments which collectively form a new applanate branch (Fig 34D). The lower cell resulting from the transverse division of each original, secondarily elongated palisade cell remains part of the underlying branch. This interpretation is based on observations of sectioned thalli (Fig 34D) in which secondarily elongated groups of primigenous cells occur and in which new filaments emanate from cells at the margin of the group.

Both modes of branch formation may be present within a single thallus (Fig 34D). Some thalli contain numerous small branches (Fig 33B) and appear somewhat roughened in close surface view. Other thalli have more expansive branches giving the thallus surface a smoother appearance in surface view (Fig 33C). Terracing and swirling of the sort present in *L. prototypum* (q.v.) does not occur.

Throughout the thallus, successive cells of the same filament are linked by primary pit-connections while cells of adjacent filaments are linked by contiguous secondary pit-connections (Fig. 34F). Adjunctive secondary pit-connections, cell fusions and trichocytes were not detected.

Only bisporangial conceptacles have been found (Figs 33D, 35). In the earliest stage of conceptacle development encountered (Fig 35C), bisporangial initials were present, the roof was mostly formed, the large angular cells destined to occlude the pore canal were clearly evident, and the conceptacle protruded conspicuously above the surrounding thallus surface. One can surmise from this and from observations of more mature conceptacles (Figs 35A, 35B, 35D) that roof formation is effected from filaments interspersed amongst developing sporangia. As conceptacles develop, the lowermost cells of a number of filaments become markedly elongate, forming cavity cells which later degenerate to varying degrees, thereby resulting in a chamber for developing sporangia. Relatively intact cavity cells persist around the periphery of the chamber, while more degenerate ones may persist amongst the sporangia or occasionally form a central columella (Figs 35A, 35D). The chamber floor normally is situated one cell (rarely two or three) beneath the surrounding thallus surface.

Intact portions of filaments above the chamber collectively form a roof (Figs 35A, 35B, 35D). The single ring of roof filaments immediately adjacent to the pore can produce large, usually angular cells which completely occlude the pore canal. These enlarged cells appear to develop as unicellular lateral branches from the adjacent roof filaments. When conceptacles are sectioned vertically through the exact centre of the pore canal, at least two enlargedcells, one on either side, are evident in the lower part of the pore canal. A second pair of enlarged cells also occurs in the upper part of the pore canal, but in mature conceptacles, these appeared to be partially degenerate and/or become obscured by densely staining mucilagenous particles (Figs 33D, 35A, 35B, 35D).

Roof filaments from which the enlarged cells arise may or may not terminate in epithallial cells. Remaining roof filaments above the chamber, however, normally consist of a terminal epithallial cell and (1–)2–3 intact subtending cells of variable length but usually more or less elongate. At conceptacle margins, roof filaments remain completely intact; each consists of a terminal epithallial cell and 1–2(–3) elongate subtending cells, the ventral-most of which is connected to a primigenous cell (Figs 35A, 35B, 35D). The conceptacle chamber floor contains a single layer of primigenous cells (Figs 35A, 35B).

Bisporangia can arise from any area of the conceptacle chamber floor (Figs 35A–35D). Sporangia are borne on small stalk cells which may or may not be evident in mature conceptacles. Both mature and immature sporangia may be present within a single conceptacle, and older conceptacles eventually may be overgrown by new applanate branches.

Gametangial plants have not been encountered, and only uninucleate bispores (Fig. 35B) have been seen. If uninucleate bispores of *L. irvineanum* are cytologically like those of *L. pustulatum* (see p. ; also see Suneson, 1950, 1982), then they are likely to be apomeiotic and would give rise to new bisporangial plants in an apomictic manner. Confirming culture studies have yet to be undertaken.

Spore germination and very early thallus development have not been observed.

Relationships of *L. irvineanum* to other species are considered below (p.97).

INFRASPECIFIC TAXONOMY. No infraspecific taxa of *Lithophyllum irvineanum* are being recognized.

5. **Lithophyllum johansenii** Woelkerling et Campbell, sp. nov.

Figs 36–41

HOLOTYPE. LTB 11724 (Port Fairy, Victoria, *Woelkerling*, 4 January 1979; on rock, 0–1m deep, west of boat slip entrance). Figs 36A, 36C–36F, 37A–37F, 38A–38C, 39D, 40B.

MISAPPLIED NAMES. No published misapplications of other names to specimens of *Lithophyllum johansenii* were discovered during this study.

ETYMOLOGY. The specific epithet honours H. William Johansen for his numerous, important contributions to the morphology, anatomy and systematics of the Corallinaceae.

PREVIOUSLY PUBLISHED ILLUSTRATIONS OF AUSTRALIAN PLANTS. Campbell & Woelkerling in *Phycologia* 29: figs 5–9 (as *Lithophyllum* sp.) (1990). Woelkerling, *Coralline Red Algae*: 102, fig. 78 (as *Lithophyllum* sp.) (1988).

LATIN DIAGNOSIS:

L. johansenii characteribus generis *Lithophyllum*; differt de speciebus affinibus inter alia quod sola conceptaculorum tetrasporangium sub 5–10 cellulosis stratis immersa sunt et canales porosi conceptaculorum tetrasporangium a 2–4 cellulis, amplifactis, angularibus, et non superimpositis obstructi sunt.

The characteristics of *Lithophyllum* are given in Table 1; features delimiting *L. johansenii* as a species and its relationships to other species of *Lithophyllum* are considered in greater detail below.

DESCRIPTION. Plants mostly 30–40 mm across and 0.2–1.0 mm thick or tall; variably flat (complanate) to layered (without conspicuous terracing), warty and/or lumpy; completely adherent.

Thallus dimerous; primigenous filaments composed of palisade and/or nonpalisade cells 8–12 µm long and 5–25 µm tall; postigenous filaments composed of 5–30+ cells 8–30 µm long and 5–10 µm in diameter with each filament terminating in an epithallial cell 4–6 µm long and 6–9 µm in diameter. Contiguous secondary pit-connections common; adjunctive secondary pit-connections, cell fusions and trichocytes not seen.

Tetrasporangial/bisporangial plants with scattered nonprotruding conceptacles. Conceptacle roofs 163–205 µm in external diameter; roof filaments above chamber 2–4 cells long; cells 5–14 µm long and 4–6 µm in diameter with isolated columnar cells sometimes present. Pore canals completely occluded by 2 or 4 enlarged, angular cells which do not project above the surrounding roof surface. Conceptacle chambers 130–155(–196) µm in diameter and 65–108 µm tall; floor of mature chambers usually 8 or more cells below thallus surface; tetrasporangia/bisporangia 45–70 µm long and 27–35 µm in diameter, scattered across chamber floor; columella not seen.

Gametangial plants apparently dioecious. Male conceptacle roofs non- or slightly protruding; chambers 80–100 µm in diameter and 32–47 µm tall; spermatangial branches confined to chamber floor, simple, with each initial bearing one to several elongate spermatangia. Female/carposporangial conceptacles not seen.

Carposporophytes not seen.

DIAGNOSTIC FEATURES. *L. johansenii* differs from other southern Australian species of *Lithophyllum* in having the following combination of features:

1. Entire pore canals of tetrasporangial/bisporangial conceptacles normally completely occluded by enlarged angular cells which line the canal (Figs 39C, 39D). When conceptacles are viewed in vertical section through the pore canal two or four enlarged cells normally are evident but do not project above surrounding roof filaments, and those nearest the bottom of the canal look more or less rectangular.
2. Floors of functional tetrasporangial/bisporangial conceptacles usually situated eight or more cells below the surrounding vegetative thallus surface and conceptacle roofs nearly flush with the surrounding vegetative thallus surface (Figs 38A, 39D).
3. Thallus surface not obviously and more or less completely terraced as a consequence of applanate branch development.
4. Applanate branches, when present, arising from groups of postigenous cells.
5. Postigenous filaments normally multicellular except in very young portions of thallus.

In so far as known, no other described species of *Lithophyllum* possesses this combination of features.

NOMENCLATURE AND SYNONYMY. No matters relating to nomenclature and synonymy require comment.

DISTRIBUTION AND ECOGRAPHY. *Lithophyllum johansenii* has been recorded from two localities in South Australia and one each in Tasmania and Victoria; collections were made in January and February. The species is unknown elsewhere.

Both male and tetrasporangial conceptacles occur in LTB 12446; two collections (LTB 12459, LTB 13134) contain bisporangial specimens; and two (LTB 11724, LTB 11576) contain tetrasporangial plants. Plants have been found in intertidal rocky reef pools and at depths of up to 2.5 m on rock or on the holdfast of the brown alga *Ecklonia*. The type collection (Fig. 36A) occurs on rock. The size of epilithic specimens (Figs 36A, 36B) indicates that plants are probably perennial.

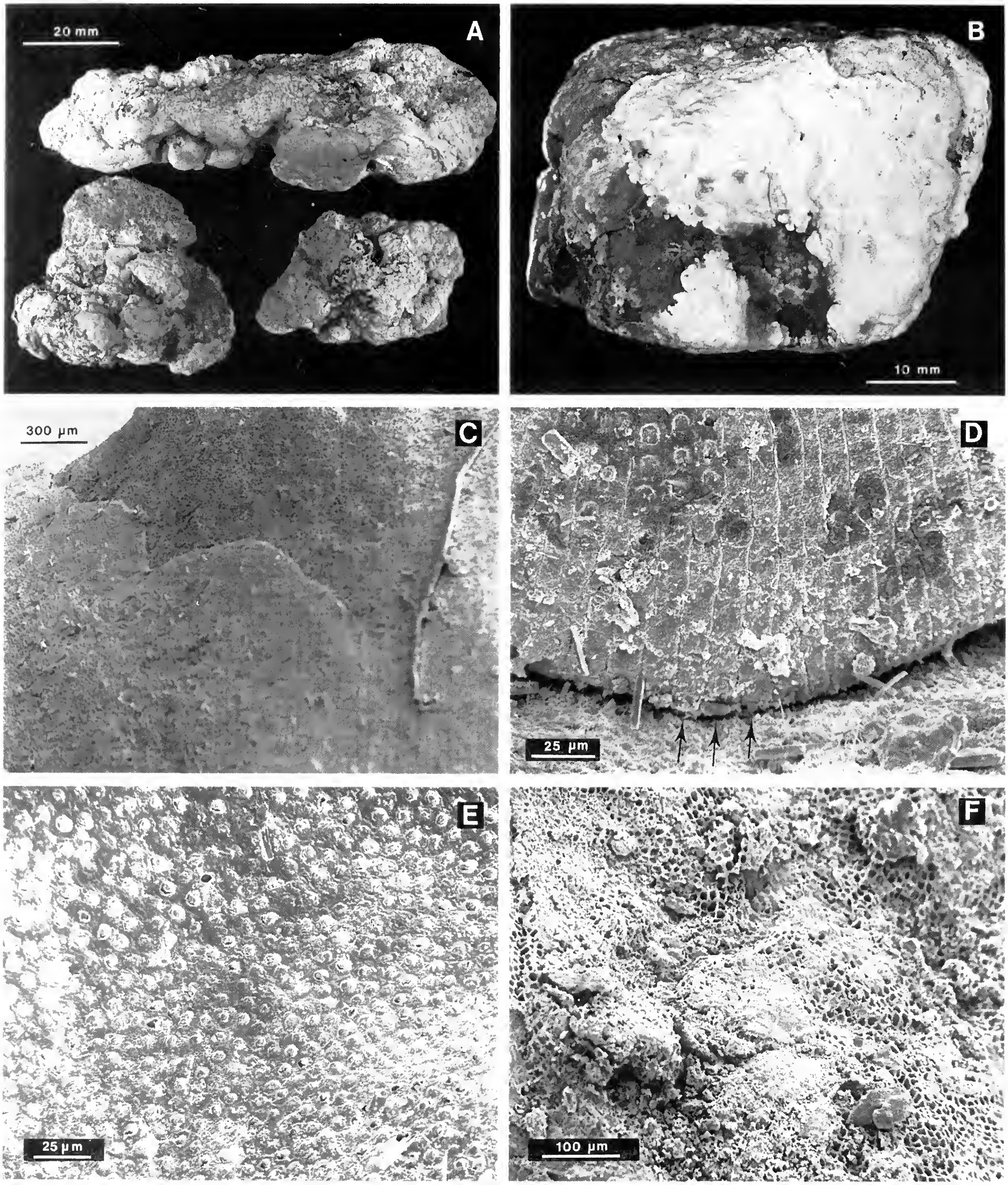


Fig. 36 *Lithophyllum johansenii*: holotype and surface features. A. Holotype collection. (LTB 11724). B. Habit of a flat (complanate) specimen from Tasmania. (LTB 13134). C-F. Holotype collection. (LTB 11724). C. Surface of thallus showing applanate branch. D. Margin of applanate branch in which positions of contiguous filaments (arrows) are evident. E. Dorsal thallus surface showing positions of epithallial cells which have not collapsed. F. Ventral surface of thallus detached from rock.

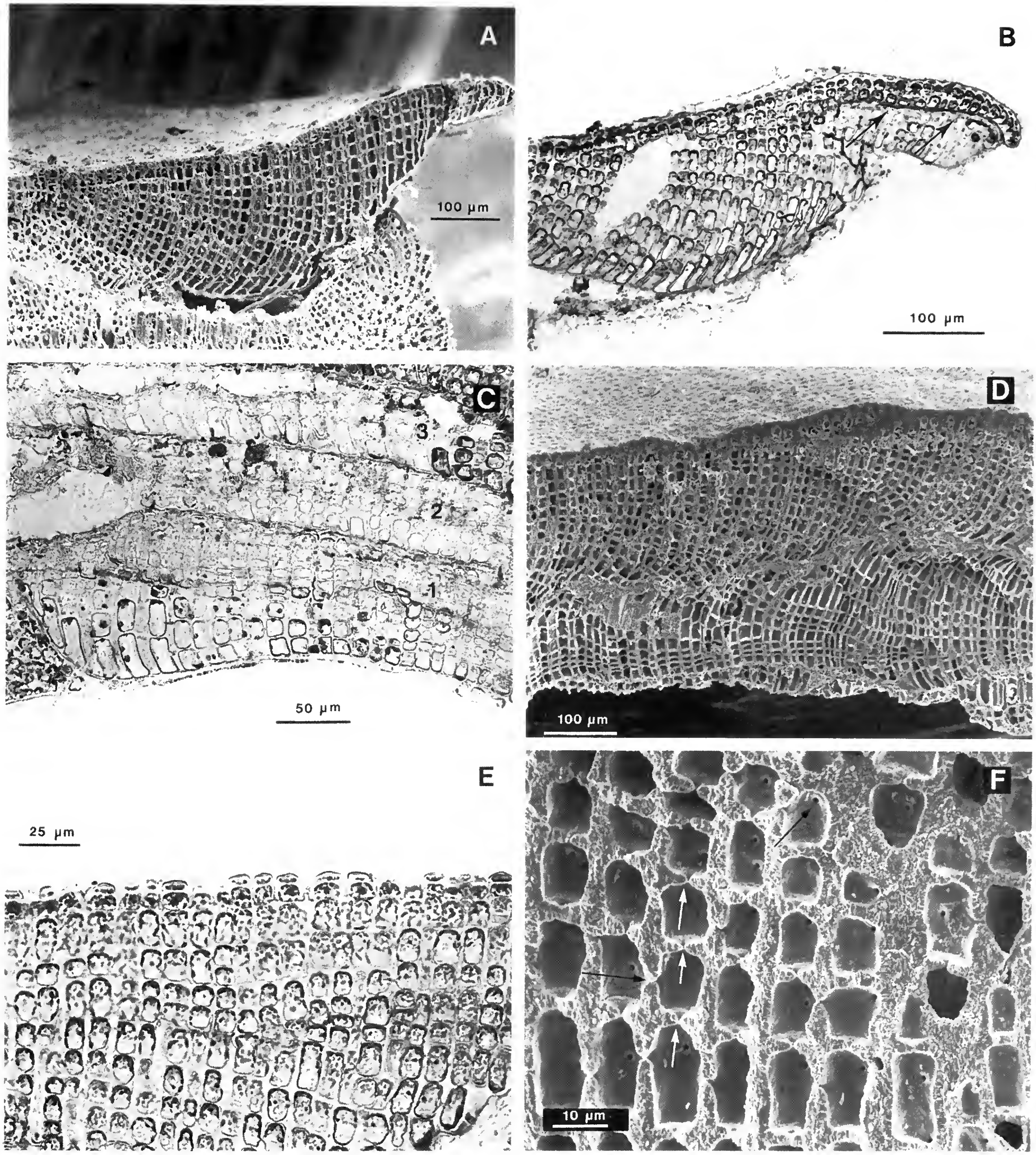


Fig. 37 *Lithophyllum johansenii*: vegetative anatomy of holotype (LTB 11724). A. Portion of thallus margin of dimerous construction in which all primigenous cells are palisade. B. Thallus margin with developing applanate branch (arrows) overgrowing subtending portion of thallus. Note that primigenous cells of new branch are nonpalisade while those of subtending thallus are palisade. C. Portion of thallus with three layers (1,2,3) of applanate branching in which primigenous filaments contain a mixture of palisade and nonpalisade cells. D. Fracture of thallus showing both palisade and nonpalisade cells and heavy calcification of dorsal surface. E. Section of thallus showing epithallial cells. Note how most vegetative cells look small and are noncolumnar (see also Figs 2A–D,F). F. Thallus fracture showing primary (white arrows) and secondary (black arrows) pit-connections.

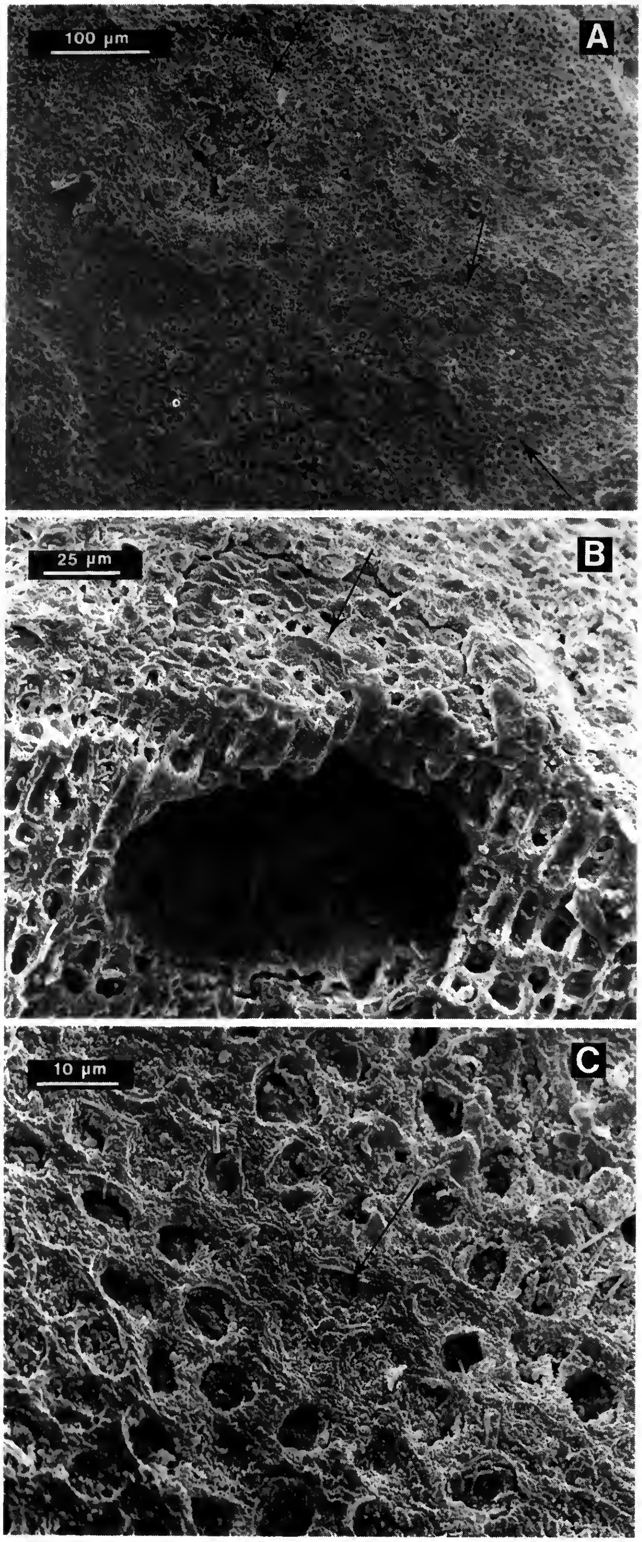


Fig. 38 *Lithophyllum johansenii*: surface features of tetrasporangial conceptacles of holotype. (LTB 11724). A. View showing how conceptacles (arrows) are inconspicuous and difficult to detect in surface view. B. Fracture through conceptacle. Note occluded pore (arrow) and how roof blends into vegetative thallus surface. C. Central portion of conceptacle roof with a completely obstructed pore (arrow).

COLLECTIONS EXAMINED:

SOUTH AUSTRALIA: Cape Willoughby, Kangaroo Island (*Woelkerling*, 25 February 1979, LTB 11576). Port Macdonnell (*Woelkerling*, 6 January 1977, LTB 12446; LTB 12459).

TASMANIA: Coles Bay (near jetty) (*Platt & Woelkerling*, 21 February 1983, LTB 13134).

VICTORIA: Port Fairy (*Woelkerling*, 4 January 1979, LTB 11724). Holotype.

REMARKS ON MORPHOLOGY AND ANATOMY. The crustose to irregularly lumpy thalli of *Lithophyllum johansenii* (Figs 36A, 36B) resemble those of many other Southern Australian nongeniculate corallines, none of which can be identified to species or genus using external features. Unequivocal identification to species is possible only from sections of tetrasporangial/bisporangial conceptacles in which pore canal anatomy is clearly shown (Figs 39C, 39D).

Although the thallus surface may be somewhat lumpy (Fig 36A), well-defined protuberant branches have not been found. Inconspicuous, horizontally expanded applanate branches occur, however(Figs 36C, 37C), and the positions of individual filaments are evident along dorsal margins of branches (Fig. 36D). Epithallial cells may either collapse, leaving concavities, or, if calcified, remain turgid, causing minute bulges in the thallus surface (Figs 36E, 38A). Ventral surfaces detached from rock (Fig. 36F) look roughened and have no evident filamentous arrangement such as that in *L. bermudense* (Fig. 6C) and *L. pustulatum* (Fig. 52B).

Dimerous construction and dorsiventral organization occur throughout. Cells of particular primigenous filaments were all palisade, nearly all nonpalisade or a mixture of both palisade and nonpalisade (Figs 37A–37D; see also Campbell & Woelkerling, 1990: figs 5–9).

Multicellular postigenous filaments arise almost immediately behind the margins of thalli/applanate branches and commonly become 5–30 (sometimes more) cells long (Figs 37A–37E). Few if any postigenous cells are columnar. As a result, such sections/fractures can look quite different to most comparable sections/fractures of *L. bermudense* (Figs 7A–7C), *L. pustulatum* (Figs 53C, 53D, 58C) and to a somewhat lesser extent *L. corallinae* (Figs 25B, 25D). Similarly, periclinal banding of the sort found in *L. bermudense* (Fig. 7C) and *L. pustulatum* (Fig. 53D) was not detected in *L. johansenii*. Postigenous filaments in *L. johansenii* each terminate in an epithallial cell at the thallus surface (Fig. 37E).

Applanate branches (Figs 36C, 37B) ostensibly form from groups of postigenous filaments, but details of their ontogeny are unknown. Successive layers of branches appear to become firmly adherent to subtending ones (Figs 37C, 37D).

Throughout the thallus, successive cells of the same filament are linked by primary pit-connections and cells of adjacent filaments are linked by contiguous secondary pit-connections (Fig. 37F). Adjunctive secondary pit-connections, cell fusions and trichocytes were not encountered.

Tetrasporangial/bisporangial conceptacles (Figs 38A–38C, 39A–39D, 40A–C) are difficult to detect in surface view not only because roofs are flush with the thallus surface but also because pore canals are completely occluded by cells which do not project above the roof (Figs 38A–38C). Often, the only way of locating conceptacles is to look for those in which roofs are cracked or broken (Fig. 38A). Male conceptacles (Figs 41A, 41B) have not been detected in surface view.

Few details of tetrasporangial/bisporangial conceptacle

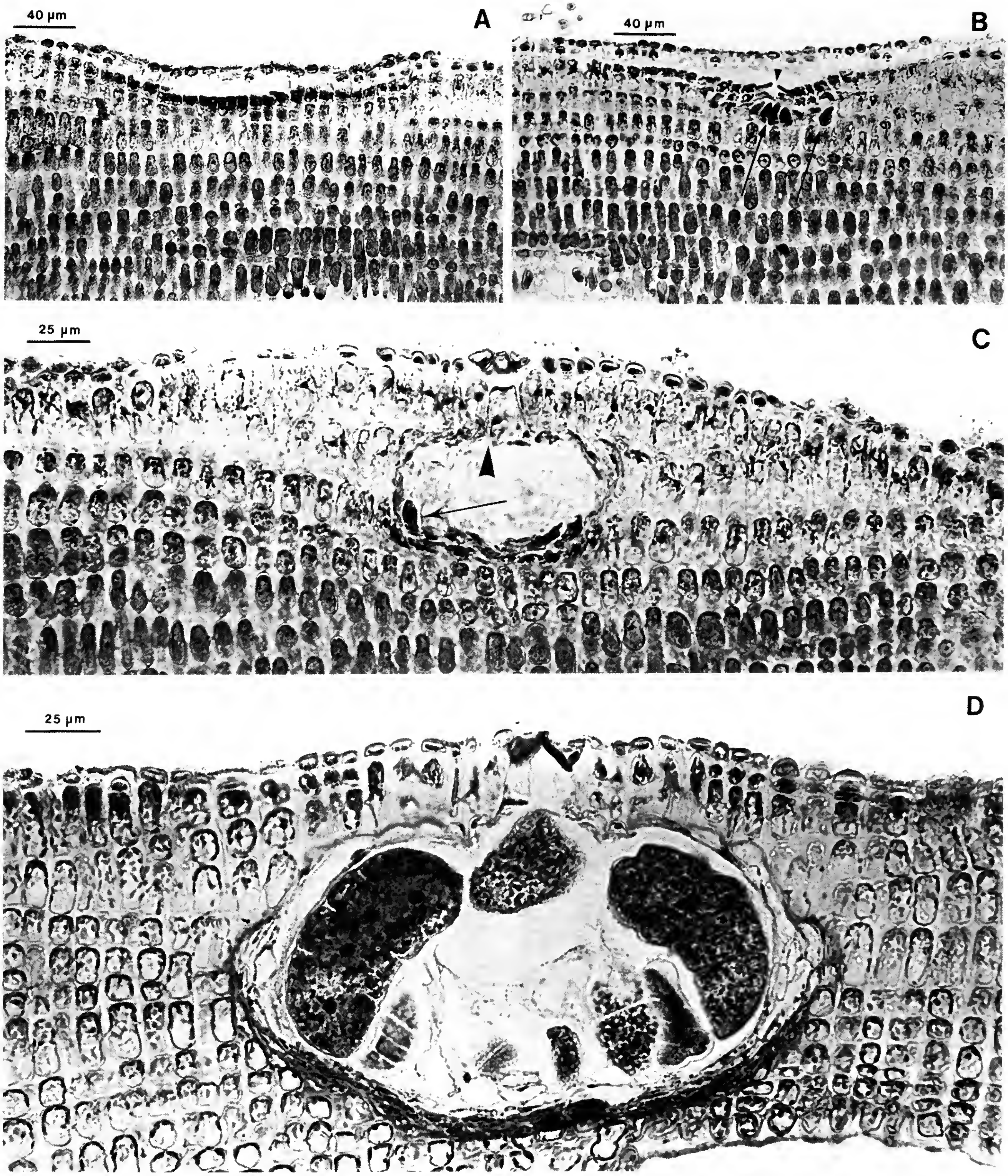


Fig. 39 *Lithophyllum johansenii*: tetrasporangial conceptacle ontogeny. A. Primordial stage showing a group of darkly stained initials and the detachment of overlying epithallial cells. (LTB 13134). B. Slightly later stage in which tetrasporangial initials have become evident (arrows) and roof formation has begun (arrowhead). (LTB 13134). C. Later stage of development showing completely occluded pore canal (arrowhead) and a tetrasporocyte (arrow). (LTB 13134). D. Mature conceptacle from holotype collection. Note occluded pore canal and anatomy of roof above conceptacle chamber. (LTB 11724).

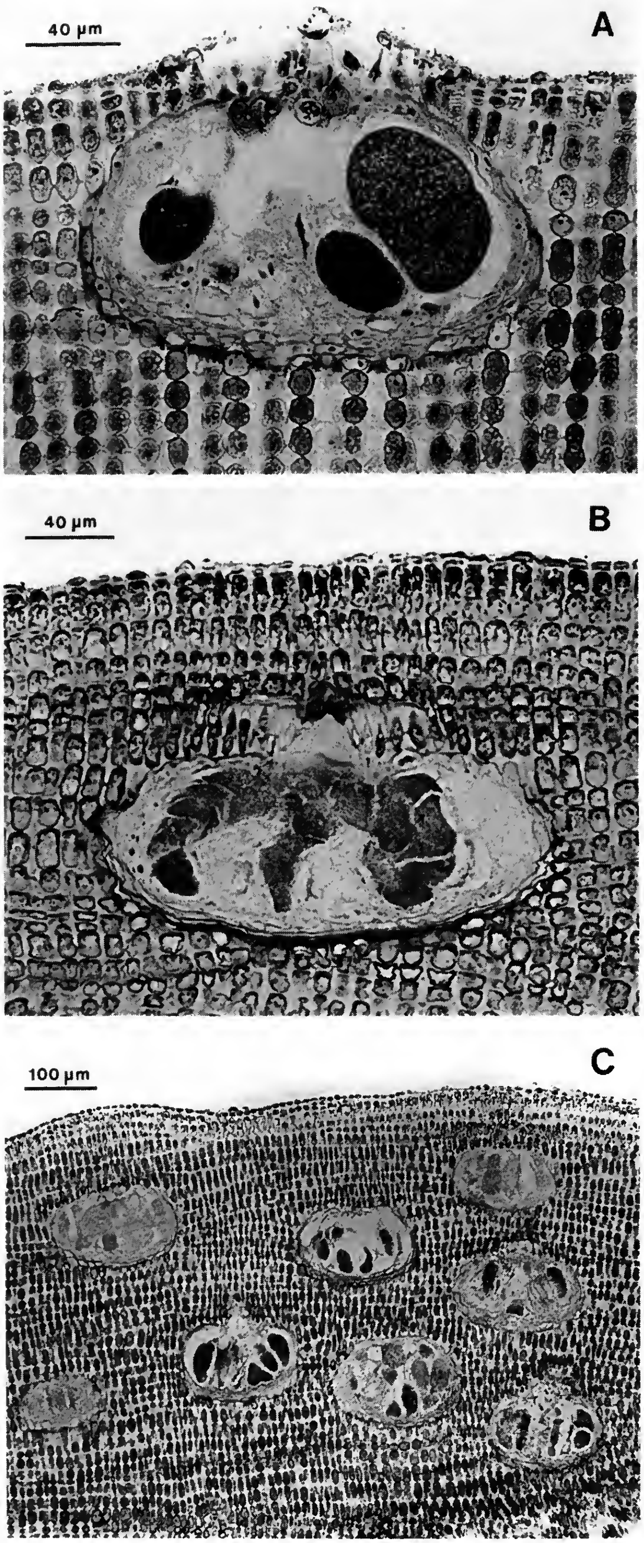


Fig. 40 *Lithophyllum johansenii*: bisporangial and buried conceptacles. A. Conceptacle with bisporangia. (LTB 13134). B. Recently buried conceptacle in holotype collection resulting from renewed growth of roof and surrounding vegetative filaments. (LTB 11724). C. Portion of thallus with a number of buried conceptacles. (LTB 13134).

development have been elucidated. Conceptacle primordia arise when groups of initials are cut off from subepithallial cells of postigenous filaments (Figs 39A, 39B). Concurrently, the epithallial cells become detached and form a temporary protective cover (Figs 39A, 39B) which presumably degenerates as conceptacle development proceeds. It is not clear how the conceptacle roof forms from the conceptacle primordium. What appears to be a group of tetrasporocytes was seen in one older primordium (Fig. 39B), and initials flanking these seemed to show signs of producing cells which eventually would surround and enclose the developing sporangia. This possible mode of development, which is different from that found in the other southern Australian species of *Lithophyllum*, could not be confirmed, however.

The enlarged angular cells which obstruct the pore canal form at an early stage (Fig. 39C) and cells resembling enlarged epithallial cells occur above the main cells in the canal. It is possible, judging from one mature conceptacle (Fig. 39D) that these obstructing cells eventually begin to degenerate, ultimately leaving an opening through which spores can escape. It also is clear from Fig. 39C that by the time conceptacle chamber formation occurs, vegetative filaments adjacent to the conceptacle have continued to produce new cells. As a result, the developing conceptacle roof always (?) remains flush with the surrounding thallus surface and the chamber becomes embedded within the thallus. In mature conceptacles, the chamber floor normally is situated eight or more cells below the surrounding thallus surface (Fig. 39D).

Within the chamber in Fig. 39C, only one tetrasporocyte is evident, and no degenerate cavity cells connecting the floor and roof occur. Their presence in the central part of the chamber may suggest that conceptacle roofs of *L. johansenii* form in the same 'interspersed' way as in other southern Australian species of *Lithophyllum*, but their absence in one conceptacle cannot be taken as unequivocal evidence of a 'surround and enclose' mode of development because such cavity cells may have completely degenerated in this instance.

Intact portions of filaments above the chambers of mature tetrasporangial/bisporangial conceptacles (Figs 39D, 40A) collectively form a roof of characteristic structure. The entire pore canal normally is occludedby two or four enlarged cells which are presumed to originate laterally from roof filaments flanking the pore canal. Remaining filaments above the chamber consist of a terminal epithallial cell and one to three subtending cells which may be more or less isodiametric or somewhat elongate (Figs 39D, 40A). A distinct subepithallial layer of elongate cells such as occurs in *L. prototypum* (Fig. 46C) was not found. Cells in roof filaments at the margin of the chamber (Fig. 39D) are more or less identical to those immediately flanking the chamber, and the latter are identical in appearance to other vegetative filaments. Coneptacle chamber floors are subtended by multicellular filaments.

Tetrasporangia/bisporangia apparently can arise from any part of the conceptacle chamber floor (Figs 39D, 40A–40C). In most conceptacles, several layers of small cells (Fig. 40A) or their remains (Figs 39D, 40B, 40C) occurred along the chamber floor. Similar cells also occur in some conceptacles of *L. corallinae* (e.g. Figs 27E, 28C), but their morphological and taxonomic significance remain uncertain. Older conceptacles commonly become buried within the thallus (Figs 40B, 40C). Most buried conceptacles contained a number of unreleased spores with intact sporangia.

Male conceptacles were found only in one dried specimen (Figs 41A, 41B). The conceptacles seemed to be mature,

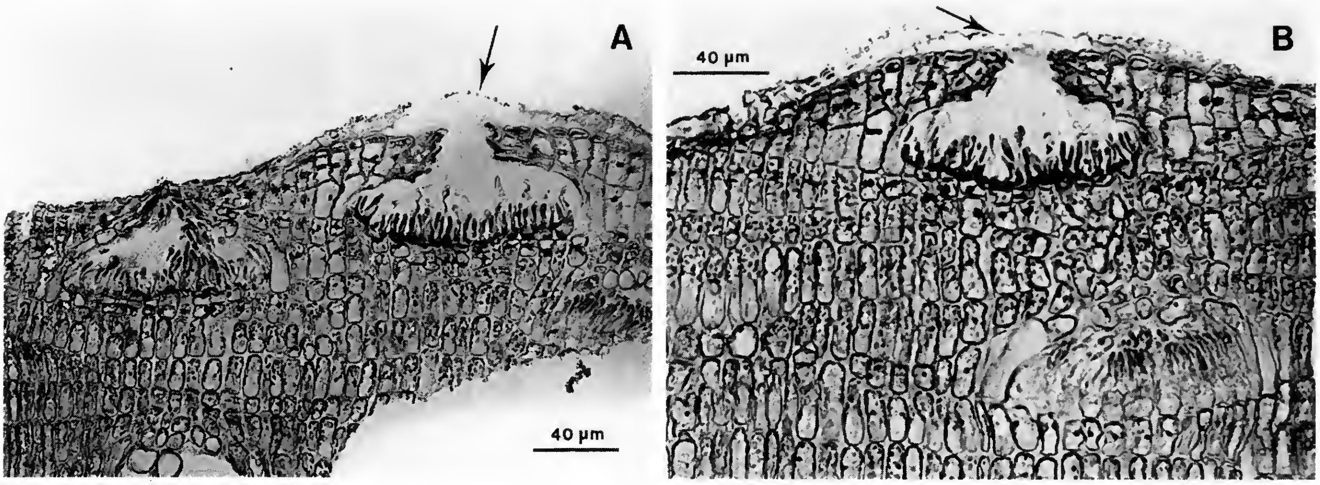


Fig. 41 *Lithophyllum johansenii:* male conceptacles. A–B. Male conceptacles at and beneath surface of a dried specimen. Note remains of old vegetative epithallial cells overlying several roofs (arrows). (LTB 12446).

although remnants of old, vegetative, overlying epithallial cells were still evident. Conceptacle roofs appear to be formed by a group of peripheral filaments which arch over and enclose a central fertile region on the conceptacle chamber floor. Early stages of development remain unknown, however. Spermatangia are simple and confined to the floor, and conceptacles with intact spermatangia can readily become buried within the thallus (Fig. 41B).

Female/carposporangial conceptacles have not been found, and spore germination and very early thallus development have not been observed.

Relationships of *L. johansenii* to other species are considered below (p.97).

INFRASPECIFIC TAXONOMY. No infraspecific taxa of *L. johansenii* are being recognized.

6. **Lithophyllum prototypum** (Foslie) Foslie in *K. norske Vidensk.Selsk. Skr.* 1905(3): 129 (1905a)./ Figs 42–49

BASIONYM. *Lithothamnion prototypum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1897(1): 18 (1897).

HOLOTYPE. TRH [St. Croix Is., U.S. Virgin Islands (West Indies), leg. *F. Boergesen*, 1892; on a razor clam shell]. Figs 42A, 42B, 43A, 43B; see also Printz, 1929: pl. 72, fig. 8. Foslie (1897: 19) mistakenly lists the type locality as St. Croix, West India.

HOMOTYPIC SYNONYMS:

Dermatolithon prototypum (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1900(5): 22 (1900) (as *prototypus*). *Goniolithon prototypum* (Foslie) Setchell & Mason in *Proc. Natn. Acad. Sci. Wash.* 29: 89 (1943). *Melobesia prototypa* (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(3): 11 (1898). *Tenarea prototypa* (Foslie) Adey in *K. norske Vidensk. Selsk. Skr.* 1970(1): 7 (1970). *Titanoderma prototypum* (Foslie) Woelkerling et al. in *Phycologia* 24: 333 (1985).

HETEROTYPIC SYNONYMS:

Lithophyllum tessellatum Lemoine in *Archs Mus. Hist. Nat. Paris*, Ser. 6, 4: 68 (1930). *Dermatolithon tessellatum* (Lemoine) Lemoine in *Bull. Soc. Bot. Fr.* 117: 556 (1971). *Goniolithon tessellatum* (Lemoine) Setchell & Mason in *Proc. Natn. Acad. Sci. Wash.* 29: 89 (1943). *Tenarea tessellata* (Lemoine) Littler in *Phycologia* 10: 355 (1971). (Combination invalid as full citation of basionym not given in accordance with ICBN Art. 33.2). *Tenarea tessellata* (Lemoine) Littler ex Adey et al. in *Smithson. Contr. mar. Sci.* 15: 35 (1982). *Titanoderma tessellatum* (Lemoine) Woelkerling et al. in *Phycologia* 24: 333 (1985).

MISAPPLIED NAMES. No published misapplications of other names to southern Australian specimens of *Lithophyllum prototypum* were discovered duringthis study; see, however, comments in the section on infraspecific taxonomy below.

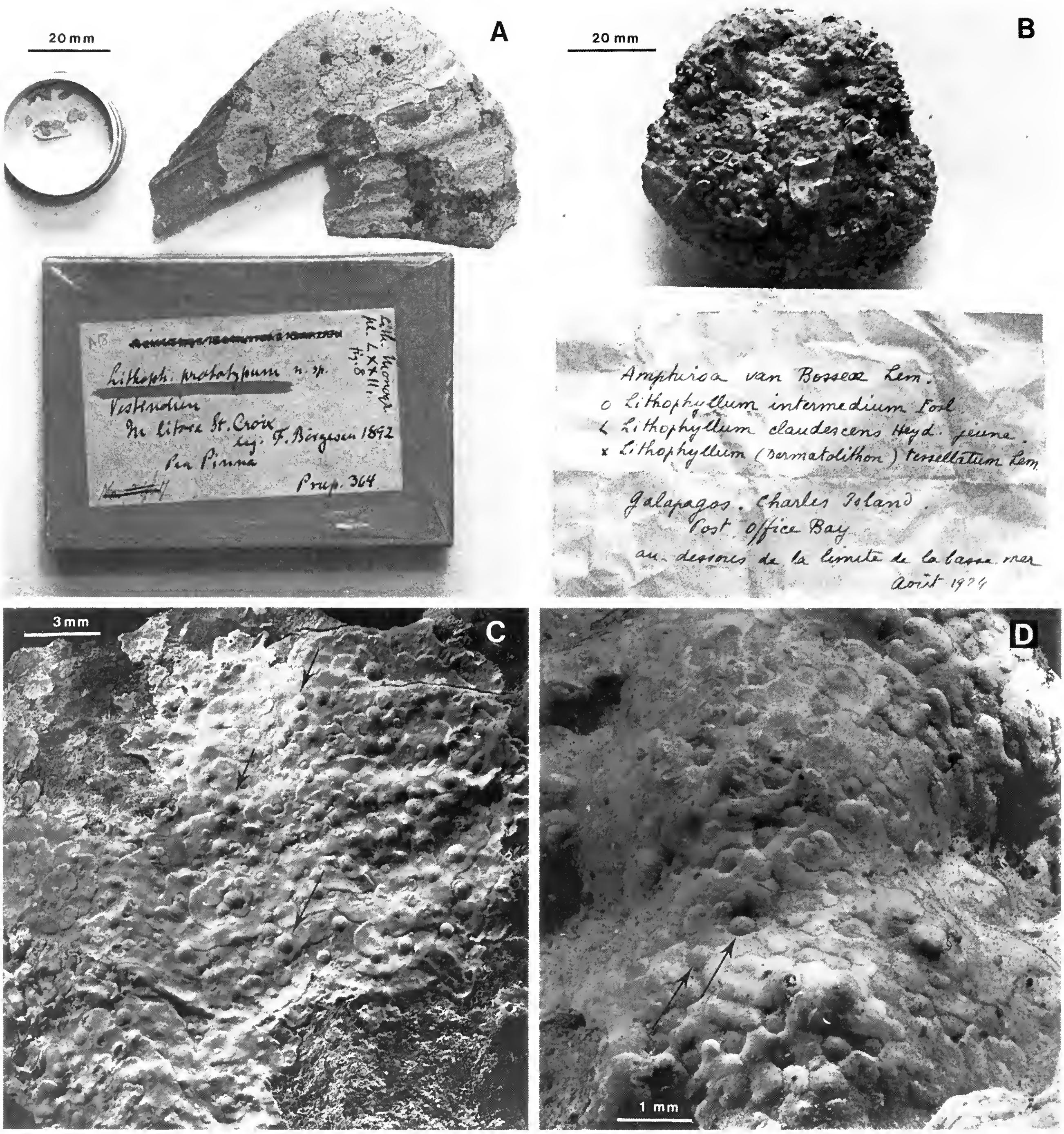
ETYMOLOGY. The basis of the specific epithet is uncertain and was not explained in the protologue (Foslie 1897).

PREVIOUSLY PUBLISHED ILLUSTRATIONS OF AUSTRALIAN PLANTS. Campbell & Woelkerling in *Phycologia* 29: fig. 3 (as *Lithophyllum prototypum*)(1990). Woelkerling, *Coralline Red Algae:* 110, fig. 88 (as *Titanoderma tessellatum*); 114, figs 94, 96 (as *Titanoderma* sp.)(1988). [A colour plate of *Lithophyllum prototypum* appears in D. Littler et al. (1989, p. 218).]

DESCRIPTION. Plants mostly 20–50+ mm in diameter and 0.1–0.9 mm thick; layered with conspicuous terracing, rarely(?) with isolated lumpy outgrowths; completely or partially adherent.

Thallus dimerous; primigenous filaments usually composed of palisade cells 5–14 µm long and 15–50(–70) µm tall; postigenous filaments composed only of epithallial cells 2–6 µm long and 4–9 µm in diameter. Contiguous secondary pit–connections common; adjunctive secondary pit–connections occasional to common in some plants; cell fusions not seen; trichocytes rare, occurring singly or in groups.

Tetrasporangial plants with scattered, protruding concepta-



NB

Lithoph. prototypum n. sp.
Vestindien
In litore St. Croix
leg. F. Børgesen 1892
Per Pinna
Prep. 364
Lith. Monogr. Pl. LXXII, fig. 8

Amphiroa van Bosseae Lem.
o Lithophyllum intermedium Fosl
L Lithophyllum claudescens Heyd. jeune
x Lithophyllum (Dermatolithon) tessellatum Lem
Galapagos. Charles Island
Post Office Bay
au-dessous de la limite de la basse mer
Août 1924

Fig. 42 *Lithophyllum prototypum*: type collections. A. Holotype collection (Foslie herbarium, TRH, unnumbered). B. Lectotype collection of *L. tessellatum* (BM, Algal box collection 999). C. Surface view of holotype of *L. prototypum* showing applanate branches and conceptacles (arrows). D. Surface view of lectotype of *L. tessellatum* showing applanate branching and conceptacles (arrows).

cles. Conceptacle roofs 440–670(–740) μm in external diameter; roof filaments above chamber 2–3 cells long; cells 5–40(–55) μm long and 5–8 μm in diameter with nearly all subepithallial cells columnar. Pore canal lined with non– or slightly projecting, non–occluding cells. Conceptacle chambers 375–425 μm in diameter and 125–140 μm tall; floor of mature chambers usually 1 cell below thallus surface; tetrasporangia (60–)71–103(–110) μm long and 30–45 μm in diameter, usually peripheral to a central columella on chamber floor.

Bisporangial plants not seen.

Gametangial plants dioecious. Male conceptacle roofs protruding; chambers 133–185 μm in diameter and (22–)37–60 μm tall; spermatangial branches confined to chamber floor, simple, with each initial bearing one to several elongate spermatangia. Female/ carposporangial conceptacle roofs

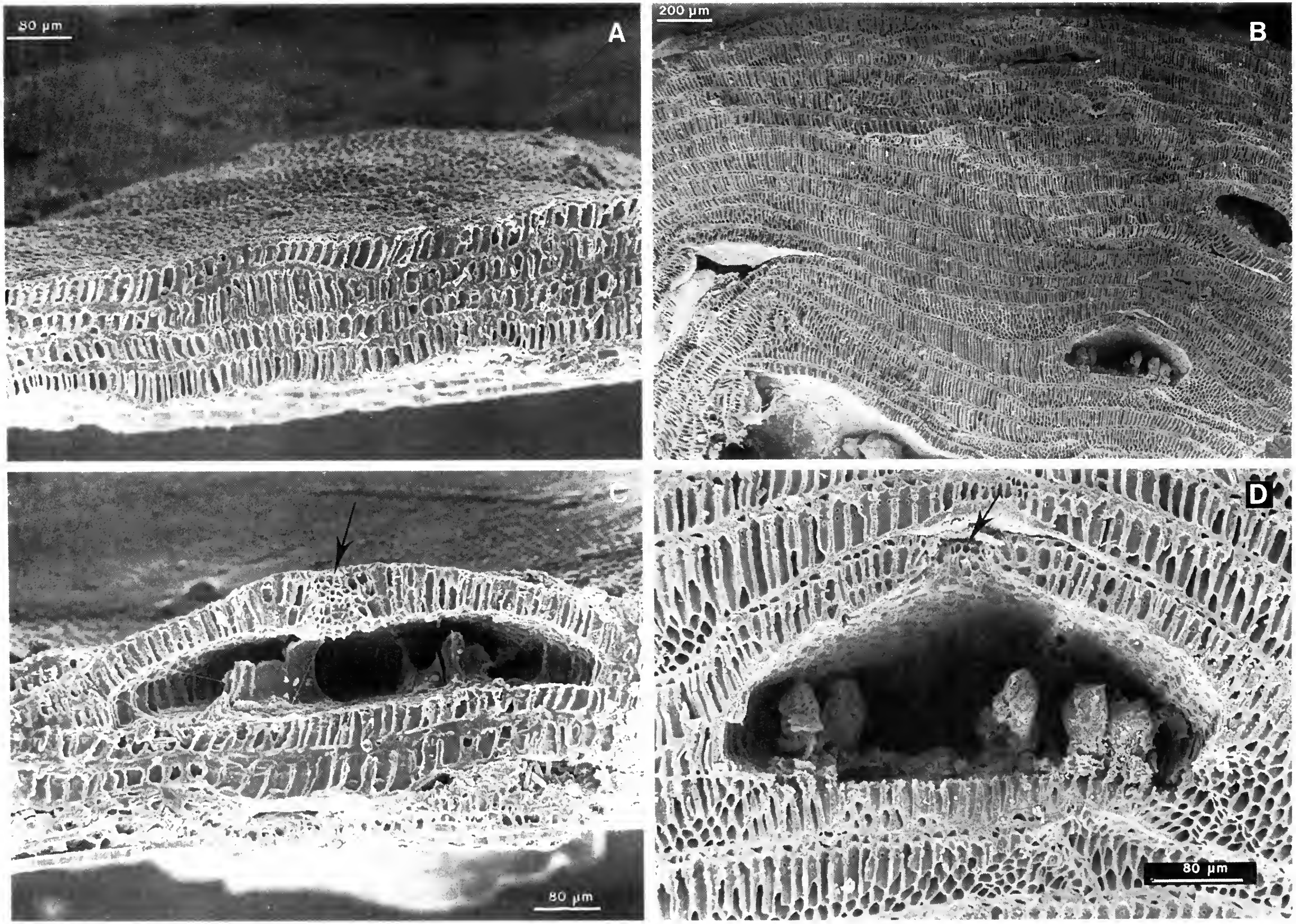


Fig. 43 *Lithophyllum prototypum*: type collections. A. Fracture of thallus from holotype collection (Foslie herbarium, TRH, unnumbered) showing four layers of applanate branches. B. Fracture of lectotype of *L. tessellatum* (BM, Algal box collection 999) showing numerous layers of applanate branches. C. Fracture of tetrasporangial conceptacle on surface of specimen in holotype collection showing roof and pore canal (arrow) structure. D. Fracture of immersed tetrasporangial conceptacles from lectotype of *L. tessellatum* showing roof and pore canal (arrow) structure and remains of tetrasporangia.

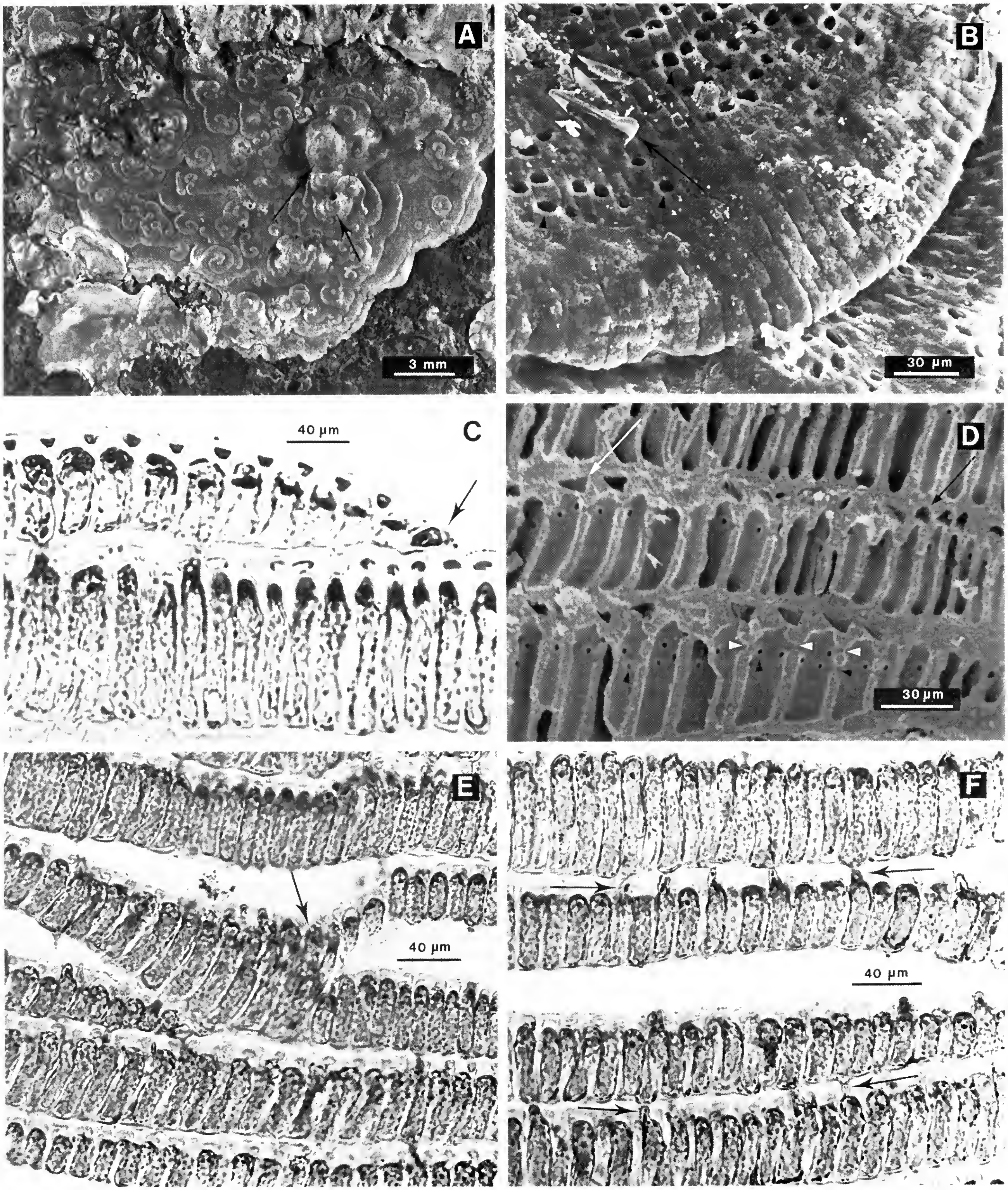


Fig. 44 *Lithophyllum prototypum*: surface features and vegetative anatomy. A. Surface view of thallus in LTB 15444. Note several small protuberances (arrows), how some young applanate branches have swirled margins while others do not, and how width of 'terraces' varies. B. Surface view of thallus margin in LTB 15444. Note how contiguous filaments appear to be aligned in rows, epithallial concavities (arrow heads) resulting from the collapse of dried epithallial cells, and the hair (arrow) of a trichocyte. C. Longitudinal section of applanate branch showing apical initial (arrow). Note difference in height of primigenous cells in top and bottom branches. (LTB 14494). D. Fracture of thallus showing primary (white arrowheads) and secondary (black arrowheads) pit-connections and epithallial cells which appear triangular (white arrow) and rounded (black arrow) along a single filament. (BM, Algal Box Collection 310). E. Section of thallus showing probable branch formation (arrow). Also note great variation in height of primigenous cells. (LTB 14494). F. Section through thallus showing adjunctive secondary pit-connections (arrows) between cells of different applanate branches. (LTB 14494).

protruding; chambers 405–497 µm in diameter and 103–150 µm tall; carpogonial filaments arising from chamber floor, usually 2–3 cells long and bearing 1(–2) carpogonia terminally.

Carposporophytes developing within female conceptacles after presumed karyogamy; each comprising a central more or less flattened fusion cell and some several–celled gonimoblast filaments peripheral with terminal carposporangia 37–88 µm in diameter.

DIAGNOSTIC FEATURES. *L. prototypum* differs from other southern Australian species of *Lithophyllum* in having the following combinationof features:

1. Pore canals of tetrasporangial conceptacles lined with cells which may project slightly into but never completely occlude the entire canal (Figs 46C, 46D).
2. Floors of functional tetrasporangial conceptacle chambers usually situated only one cell below the thallus surface and conceptacle roofs protruding above the thallus surface (Figs 46C, 46D).
3. Thallus surface obviously and more or less completely terraced as a consequence of numerous layers of imbricate, applanate branches whose margins commonly look swirled or scroll–like (Fig. 44A).
4. Applanate branches presumably arising from groups of primigenous cells.
5. Postigenous filaments normally unicellular (composed only of epithallial cells) in vegetative parts of thallus.

In the absence of a world monograph of *Lithophyllum* the extent to which the above combination of features delimits *L. prototypum* as a species within the genus remains uncertain.

TYPIFICATION. The Foslie herbarium (TRH) contains a single pre–1897 collection of *Lithophyllum prototypum* from the locality stated in the protologue (see Adey & Lebednik, 1967: 40). In accordance with ICBN Art. 7.3, Note 1, this collection must be accepted as the holotype, as is indicated by Adey (1970: 7, as *Tenarea*).

NOMENCLATURE AND SYNONYMY. In the protologue of *Lithophyllum prototypum*, Foslie (1897: 18) listed the species as '*L. prototypum*' without explicitly indicating whether the '*L.*' stood for *Lithophyllum* or *Lithothamnion*. Some authors (e.g. Adey, 1970: 7; Chapman, 1963: 94; Howe, 1920: 586) have assumed that '*L.*' signified *Lithophyllum* while others (e.g. De Toni, 1905: 1773; Taylor, 1960: 392) have assumed that '*L.*' signified *Lithothamnion*. Woelkerling (1984: 25) has pointed out, however, that Foslie (1895) reduced *Lithophyllum* to subgeneric status within *Lithothamnion* and did not resurrect *Lithophyllum* as a distinct genus until 1898 (Foslie, 1898a), the year after publication of '*L. prototypum*'. Consequently the basionym is considered here to be *Lithothamnion prototypum* and not *Lithophyllum prototypum*.

Lemoine (1930: 689, pl.1, figs 3,6; pl.4, fig. 7) established *Lithophyllum tessellatum* Lemoine for specimens collected by C. Crossland at Post Office Bay (Charles Is.) and Tagus Cove (Albemarle Is.) in the Galapagos Islands, but without designating a type. Much of the protologue is devoted to comparing *L. tessellatum* with *L. prototypum*, and it culminates in a list of four features which supposedly separate the two taxa:

1. Palisade cell height in *L. tessellatum* is said to be 30–110µm but in *L. prototypum* the maximum is said to be 65(–85)µm;
2. In decalcified preparations, applanate branches of *L. tessellatum* are said to remain adherent to one another whereas in *L. prototypum* they are said to become completely separate;
3. Conceptacles of the two taxa are said to be of the same size and form, but those of *L. tessellatum* are more sunken in the thallus;
4. The terraced appearance of the thallus is much more evident in and characteristic of *L. tessellatum* than of *L. prototypum*.

Lemoine's protologue lacks information on and illustrations of tetrasporangial conceptacle roof anatomy, and nothing is said about the contents of the conceptacles which were present.

Adey et al. (1982: 36, as *Tenarea)* list the type locality of *Lithophyllum tessellatum* as Post Office Bay and indicate that the 'holotype' is unnumbered and is in PC, but they do not state explicitly that any of the original material had been examined during their study. Because Lemoine cited collections from two localities and did not specify a type, the Adey et al. (1982) citation of a holotype specimen is incorrect (see ICBN, Arts 7.3 & 7.4). Moreover, none of the material cited by Lemoine was found during a thorough search at PC (F. Ardré, personal communication), contrary to the statement of Adey et al. (1982, p.36). It appears, therefore, that the typification by Adey et al. (1982) was done in a mechanical manner (see ICBN, Art 8.1) and also is technically in error in stating the nature of the type.

Although not explicitly indicated in her publication, Lemoine (1930a) returned all of the Galapagos collections to C. Crossland; most of these are now on deposit at BM (see Tittley et al., 1984: 59), and they include annotation slips in

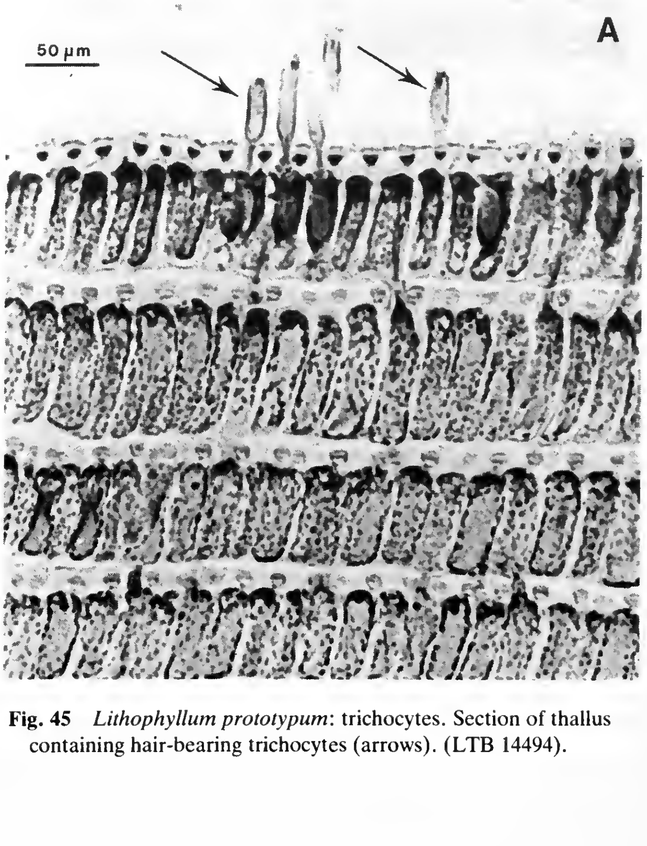


Fig. 45 *Lithophyllum prototypum*: trichocytes. Section of thallus containing hair-bearing trichocytes (arrows). (LTB 14494).

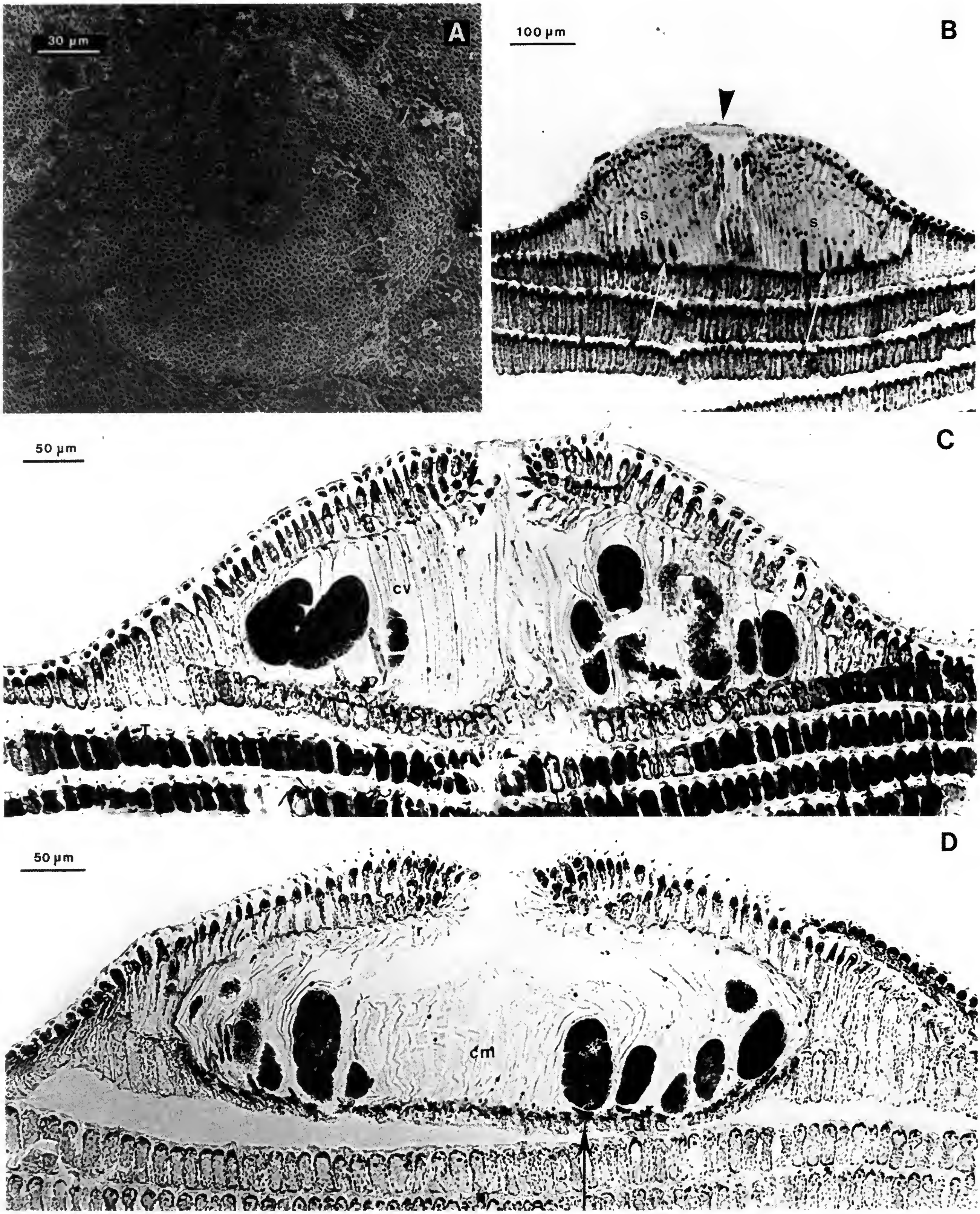


Fig. 46 *Lithophyllum prototypum*: tetrasporangial conceptacles. A. Surface view of tetrasporangial conceptacle in type collection of *L. prototypum. Note how pore canal is not obstructed by cells (cf. L. chamberlainianum* and *L. irvineanum*). (TRH, Foslie herbarium, unnumbered; holotype). B. Developing tetrasporangial conceptacle showing tetrasporocytes (white arrows), sterile filaments involved in roof formation and remains of old epithallial layer above developing pore canal (black arrowhead). (LTB 14494). C,D. Representative mature tetrasporangial conceptacles (see text for detailed comments). cm = columella; cv = cavity cells or remnants thereof; r = remnants of cavity cells attached to conceptacle roof; arrow = stalk cell subtending tetrasporangium. (C : LTB 14459; D : LTB 14494).

Lemoine's handwriting. For *L. tessellatum*, the collections from both Post Office Bay (BM, Algal Box Collection No. 999) andTagus Cove (BM, Algal Box Collection No. 310) are present and numbered, and in both cases, the collections contain a mixture of species (including *L. tessellatum*) which are clearly marked by Lemoine. Of the two collections, the one from Post Office Bay is considered here to be the lectotype, in line with the choice of Adey et al. (1982).

Plants in the lectotype collection of *L. tessellatum* (Figs 42B, 42D, 43C, 43D) are vegetatively and reproductively concordant with those in the holotype collection of *L. prototypum* (Figs 42A, 42C, 43A, 43B). Cell and conceptacle sizes overlap considerably, terracing resulting from applanate branch production is equally evident (Figs 42C. 42D) and conceptacle roof anatomy (Figs 43C, 43D) is fundamentally the same. The degree of branch adherence in decalcified thalli and the extent to which conceptacles are 'sunken' in the thallus almost certainly vary from plant to plant and are not considered of diagnostic significance here. This also applies to the width of 'terraces' on the thallus surface (see Adey 1979: 463 & Adey et al. 1982: 36). Indeed Adey et al. (1982: 35, 36) state that terraces in *L. tessellatum* are 200–2000 µm wide, thus completely overlapping their figure (up to 1mm wide) for *L. prototypum*. As no other reliable criteria could be found to separate these two entities, they are considered conspecific and*L. tessellatum* thus becomes a heterotypic synonym of *L. prototypum*.

DISTRIBUTION AND ECOGRAPHY. *Lithophyllum prototypum* has been found from Green Island Bay, Rottnest Island, Western Australia, eastwards to Encounter Bay, South Australia. Specimens have been obtained in February, April, October and December. *L. prototypum* has not been reported previously from this region. Six of the 12 collections examined contained tetrasporangial plants, three (LTB 14179, 14378, 14494) had male plants, two (LTB 15443, 15649) had female/carposporangial plants, and two (LTB 11318, 14168) were sterile.

Elsewhere (Table 10), records from the U.S. Virgin Islands (Foslie, 1897), the Galapagos Islands [Lemoine, 1930, as *L. tessellatum* (see nomenclature and synonymy below)] and Hawaii (Littler, 1971, as *Tenarea tessellata*) have been confirmed from herbarium specimen studies. Records from the Bahamas, Bermuda, Cuba, Florida, Jamaica, Mexico, Midway Island, Panama and Puerto Rico however, have not been confirmed during the present study, and thus some uncertainty surrounds the world distribution of *Lithophyllum prototypum*.

Adey (1979: 459) commented that over half of the coralline species of the Caribbean and Indo-Pacific can be characterized as 'species pairs', citing (pp 461–463) *L. prototypum* and *L. tessellatum* (both as *Tenarea*) as an example. Adey (1979: 459) also noted that some of these 'species pairs' are indistinguishable, and subsequently Adey et al. (1982: 2) concluded that insufficient data were available to determine whether such pair species were identical or evolutionarily divergent. Comparisons of relevant types have now shown (see nomenclature and synonymy section above) that *L. prototypum* and *L. tessellatum* are conspecific. As a consequence, the status of the species pairs hypothesis (especially in relation to biogeographic patterns) cannot be properly evaluated until all relevant types of such pair species can be re-examined and their status as distinct taxa determined.

Within southern and southwestern Australia, *L. prototypum* has been found subtidally at depths of 1–20m on rock, abalone shells, snails, sponges and bottles. In contrast, M. Littler (1971: 355) reported that *L. prototypum* (as *Tenarea tessellata*) grew only on consolidated calcareous substrata in Hawaii. Foslie (1909b: 49), however, reported that *L. prototypum* occurs on the green algae *Avrainvillea* and *Udotea* and on mussels, shells, corals and stones, while D. Littler et al. (1989: 218) report plants growing on dead shells or rubble fragments in the Caribbean. In a study of two deeper water areas off Oahu, Hawaii, M. Littler (1973) found *Lithophyllum prototypum* (as *Tenarea tessellata*) to be one of the three most abundant nongeniculate corallines at depths of 8–28m in terms of cover, relative density and frequency, and he considered it to be an important reef builder. Earlier, M. Littler (1971: 355, as *T. tessellata*) reported that this species

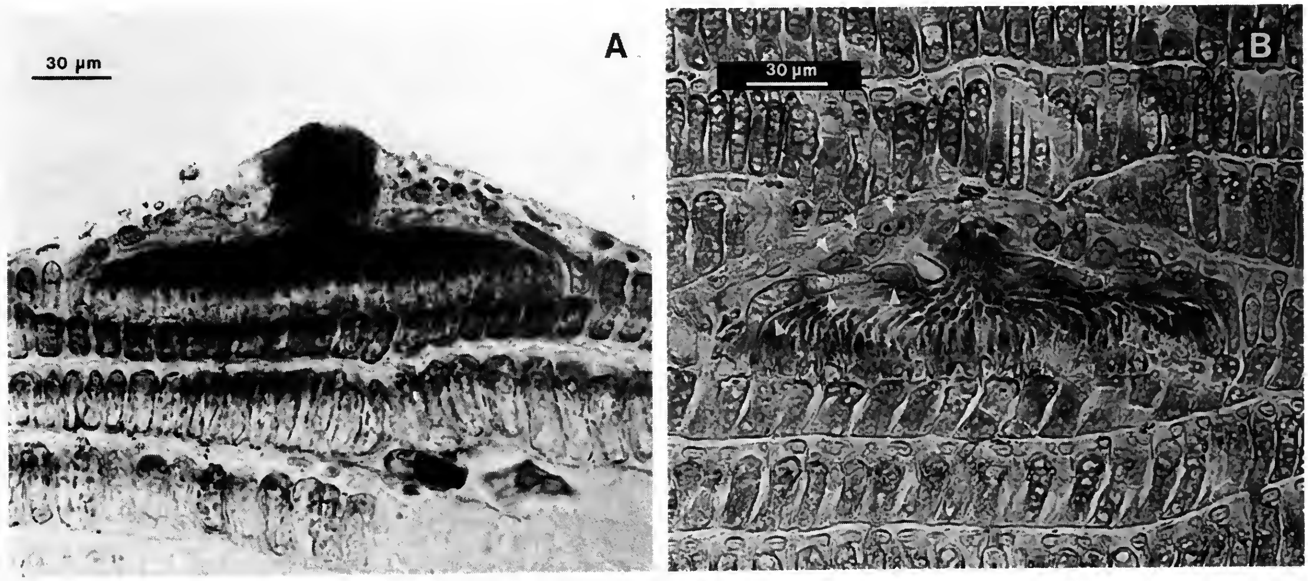


Fig. 47 *Lithophyllum prototypum*: male conceptacles. A. Male conceptacle at thallus surface. (LTB 14179). B. Male conceptacle immersed within a thallus. Cells of roof filaments are indicated by white arrowheads. (LTB 14179).

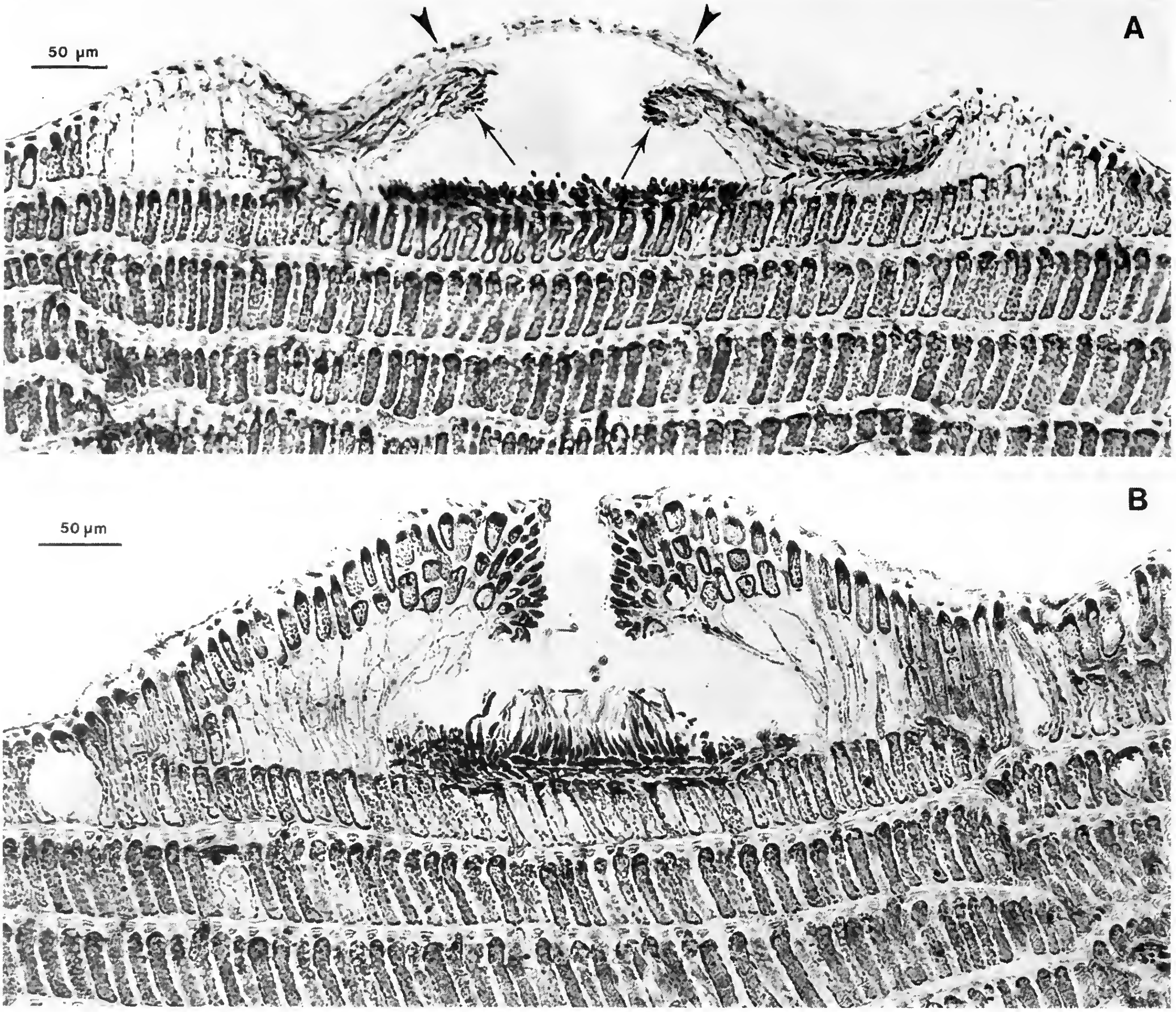


Fig. 48 *Lithophyllum prototypum*: female/carposporangial conceptacles. A. Stage in development of female/carposporangial conceptacle showing initials destined to produce carpogonial branches developing roof (arrows) and ephemeral protective dome (arrowheads) formed by uplifted group of epithallial cells. (LTB 15649). B. Female/carposporangial conceptacle containing fully developed carpogonial branches and a fully developed roof. See text for details of roof anatomy. (LTB 15649).

grew only below 10m and that it became increasingly abundant down to 30m, the maximum depth where collections were made. In subsequent studies of Hawaiian nongeniculate corallines, Adey et al. (1982: 36) stated that plants of *Lithophyllum prototypum* (as *Tenarea tessellata*) were fairly common in their collections from the intertidal to a depth of 40m, while Magruder & Hunt (1979: 95, as *T. tessellata*) remarked that plants were most common at about 10m deep but occurred occasionally on reef flats. In the Caribbean, D. Littler et al. (1989: 218, as *Titanoderma*) indicate that the species often occurs in water less than 5m deep, while van den Hoek et al. (1978: 35, as Tenarea) report the species at depths of 55–60m off of Curaçao, Netherlands Antilles.

COLLECTIONS EXAMINED:

SOUTH AUSTRALIA: Beachport (Post Office Rock) (*May*, 1 December 1986, LTB 15910). Elliston (Waterloo Bay) (*Turner*, 31 October 1981, LTB 15388); Encounter Bay (*Littler*, 31 December 1975, LTB 13885; originated as a gift from AD A47021). Head of Great Australian Bight (*Woelkerling, Platt, & Jones*, 13 February 1984, LTB 14378). Point Fowler, Fowlers Bay (*Platt & Jones*, 14 February 1984, LTB 14459). Point Sinclair (Port Le Hunt) (*Woelkerling, Platt, & Jones*, 15 February 1984, LTB 14494). Searcy Bay (comm. S. Shepherd, October 1981, LTB 15444); Snug Cove, Kangaroo Island (*Campbell & Penrose*, 12 April 1988, LTB 15629, 15649). Speed Point (comm. S. Shepherd, October 1981, LTB 15443).

WESTERN AUSTRALIA: Esperance (Observatory Point) (*Woelkerling, Platt, & Jones*, 5 February 1984, LTB 14168, 14179, 14184). Green Island, off Rottnest Island (*Woelkerling*, 12 February 1978, LTB 11318).

GALAPAGOS ISLANDS: Post Office Bay, Charles Island (*D.C. Crossland*, August 1924, BM, Algal Box collection 999; lectotype of *Lithophyllum tessellatum*). Tagus Cove,

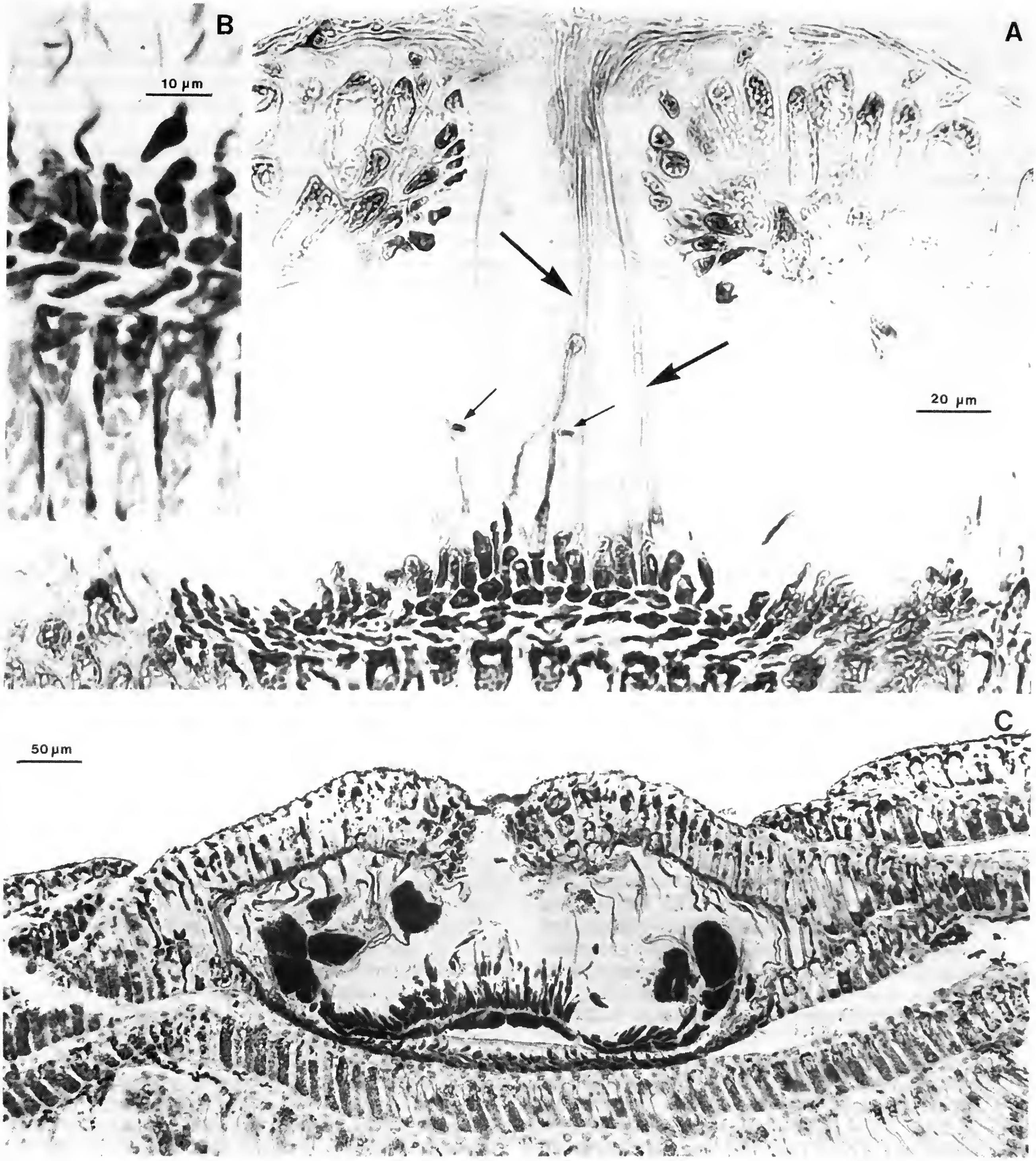


Fig. 49 *Lithophyllum prototypum*: female/carposporangial conceptacles. A. Nearly mature carpogonial branch system. (LTB 15649). B. Group of fully mature carpogonia with elongated trichogynes (large arrows) extending through the pore canal. Several trichogynes have spermatia (small arrows) attached. (LTB 15649). C. Developing carposporophyte from a dried collection. Central part of fusion cell has become detatched from chamber floor (probably an artefact of drying). (LTB 15443).

Albemarle Is. (*D.C. Crossland*, August 1924, BM, Algal Box Collection 310).

HAWAII: Makua, Oahu Is. (*M.M. Littler*, 29 March 1970, US, ML1082). A portion of this collection also is at BM (Algal Box Collection 1338).

VIRGIN ISLANDS (West Indies): Little Princess, St. Croix Is. (*Boergesen*, 1 March 1892, TRH, unnumbered). Type of *Goniolithon udoteae* Foslie. St Croix Is. (*Boergesen*, 1892, TRH, unnumbered). Holotype.

REMARKS ON MORPHOLOGY AND ANATOMY. *L. prototypum* is the only southern Australian species of *Lithophyllum* which can be readily recognized from external appearance (Figs 42C, 42D, 44A). During thallus development, a succession of dorsally produced, imbricate, closely coherent, thin, applanate branches arise; these commonly but not invariably have swirled margins (especially when young) (Fig. 44A), and they almost always give the thallus a distinctive terraced look in surface view. Preliminary identification from external appearance, however, should always be confirmed microscopically.

With one exception (LTB 15444, Fig. 44A), all collections contained crustose thalli which lacked knobby or lumpy outgrowths. Littler (1971), in contrast, found specimens with small knob-like outgrowths. Littler (1971b: 358) attributed outgrowth formation to the '. . . spiral piling-up of thalli . . .'. This hypothesis, however, requires review in light of the fact that terracing in southern Australian plants is a consequence of the applanate branching within individuals and not of the overgrowth of a succession of thalli. To avoid destruction of the few outgrowths found so far in southern Australian material, sections were not prepared. At the margins of branches, the positions of primigenous filaments are evident from a series of parallel grooves and ridges(Fig. 44B), and epithallial concavities occur over the dorsal thallus surface.

Dimerous construction and dorsiventral organization occurred in all thalli examined (Figs 43A–43D, 44C–44F). Primigenous filaments are composed of cells which are normally palisade (Figs 43A, 43B, 44E); the only nonpalisade primigenous cells encountered occurred at the margins of several applanate branches (Figs 44C, 44E). Postigenous development in vegetative parts of the thallus is limited to the production of epithallial cells (Fig. 44C).

Lateral expansion of all branches occurs from apical initials which divide to produce new primigenous cells inwardly (Figs 44B, 44C). Lateral expansion of most branches appears to be sequential and ongoing. As a consequence, the older lower branches of thalli are usually largest and the relatively newer superimposing branches smaller, with the end result that thalli look terraced in surface view (Fig. 44A). The only exception occurred in a female plant (LTB 15649) where terracing was not evident because all applanate branches had attained roughly the same size, giving the surface a relatively smooth appearance. The width of terraces depends on the relative growth of applanate branches in successive layers, and considerable variation can occur within single thalli (Figs 44A).

Precise details of applanate branch formation in *L. prototypum* remain uncertain, but it seems clear that specimens are composed of single applanately branched individuals rather than a series of superimposed thalli (see Littler, 1971: 358). Based on sections of older thalli (Fig. 44E), it appears that branches arise directly from primigenous palisade cells as occurs in *L. irvineanum* (q.v.). Townsend & Adey (1990, p. 112, as *Titanoderma tesselatum*) report similar results from their preliminary studies.

The margins of new branches commonly appear swirled (Fig. 44A), and as noted by Littler (1971), such swirling can occur in a clockwise or a counterclockwise (anticlockwise) manner. Swirls seldom turn through 360° or more in southern Australian plants, however, and thus it seems inappropriate to describe this phenomenon as spiraling (see Littler, 1971, Magruder & Hunt, 1979; Adey et al., 1982). Littler (1971) explained how such swirled margins develop, but this has not been confirmed during the present study. As branches continue to expand, the swirling becomes less evident (Figs 42C, 42D, 44A), and in older branches near the thallus edge, all traces of swirling usually disappear. Not all young branches show evidence of swirling; some develop in a more circular or irregular manner (Fig. 44A).

Throughout the thallus, successive cells of the same filament are linked by primary pit-connections (Fig. 44D). Secondary pit-connections can occur between primigenous palisade cells of contiguous filaments within an applanate branch (Fig. 44D) but not between epithallial cells. Secondary pit-connections also may form between successive cells of the same filament (Fig. 44D). In some plants, secondary pit-connections also develop between cells of vertically adjacent branches (Fig. 44F). Commonly, papilla-like protrusions develop from the dorsal surface of palisade cells in the lower branch, and a secondary pit-connection then forms between this papillate extension and the ventral surface of the cell in the upper branch (Fig. 44F). This is the first known report in the Corallinales of secondary pit-connections developing between different branches of the same thallus. Such connections are here termed adjunctive secondary pit-connections as they are considered analagous with the adjunctive cell fusions in *Lithoporella melobesioides* (Turner & Woelkerling, 1982). Adjunctive secondary pit-connections are not considered diagnostic of *Lithophyllum prototypum* because they have not been found in all specimens.

In Hawaiian plants of *L. prototypum*, Littler (1971, figs 4,5) described epithallial cells as triangular in 'side view' but rectangular in 'face view'. A similar situation sometimes occurs in southern Australian plants, but some variation in epithallial cell shape can occur regardless of the plane of sectioning or fracture (Fig. 44D), and thus epithallial cell shape can serve only as a rough guide in determining the plane in which a particular portion of thallus is being viewed.

Trichocytes (Figs 44B, 45A) were seen in two collections, one (LTB 14494) from a depth of 0.2m and the other (LTB 15444) from a depth of 20m. As far as could be determined, these trichocytes are transformed primigenous cells which have produced hairs; they are not distinct cells which arise from the division of primigenous cells.

Tetrasporangial (Fig. 46) and gametangial conceptacles (Figs 47, 48, 49A, 49B) both occur, and the roofs of all conceptacles protrude above the surrounding thallus surface. In the youngest tetrasporangial conceptacle seen (Fig. 46B), tetrasporocytes had already become clearly visible, the conceptacle roof protruded markedly above the surrounding thallus surface, the developing pore canal was identifiable, and two distinct groups of filaments (additional to tetrasporocytes) were evident. One group of filaments is associated indirectly with pore canal formation and occurs centrally. These filaments rarely contain more than 1–2 cells which undergo elongation but become senescent, thereby leaving a gap in the developing roof which ultimately becomes the pore and pore canal (Fig. 46B). Remnants of these central filaments usually persist in mature conceptacles, forming a more or less degenerate columella (Figs 46C, 46D). A much larger group of more parietal filaments contributes to roof formation (Fig. 46B). These may become up to 6 cells long and each terminates in an epithallial cell. As development proceeds, the lowermost cells become elongate, undergo varying degrees of degeneration, thereby forming a chamber for maturing sporangia. Remnants of cavity cells may persist amongst mature sporangia (Figs 46C, 46D). Tetrasporocytes (Fig. 46B) develop amongst the parietal filaments; each is subtended by a small stalk cell which in turn is anchored to a primigenous palisade cell. Vegetative cells surrounding conceptacles do not produce postigenous filaments; as a result the conceptacle chamber floor is usually situated only one cell beneath the surrounding thallus surface.

Intact portions of filaments above the chamber collectively form a roof of characteristic structure (Figs 46C,46D). Filaments immediately flanking the pore canal usually lack epithallial cells and are composed of comparatively small cells which may be narrow and somewhat elongate, short and rounded, ormore variable in shape. Cells of these filaments never completely occlude or markedly protrude into the pore canal. Sometimes, however, remnants of degenerate cells persist at the base of intact portions of these filaments and protrude somewhat into the bottom of the pore canal (Figs 46C, 46D). Two other groups of filaments occur above the chamber. In the group immediately lateral to the pore canal filaments, the intact portion of each filament contains a terminal epithallial cell and two subtending cells which are elongate to varying degrees. The subterminal cell almost always is the longer of the two (Figs 46C, 46D). In the other group, which encompasses a majority of the filaments above the chamber, the intact portion of each filament consists only of a terminal epithallial cell and one subtending columnar cell. At the margins of conceptacles (i.e. portions flanking the chamber), roof filaments remain completely intact. Each consists of a terminal epithallial cell and one or two subtending elongate cells, the lowermost of which is connected to a primigenous palisade cell by a primary pit. The floor beneath the chamber consists only of primigenous cells.

Tetrasporangia arise peripheral to a columella (Figs 46B–46D). Small stalk cells subtending sporangia occasionally were evident (Fig. 46D). Older conceptacles commonly become overgrown by new applanate branches (Figs 43B, 43D). Tetrasporangial conceptacle development and structure in southern Australian plants of *Lithophyllum prototypum* differs in some respects from that described by Littler (1971: 358, fig. 10) for Hawaiian plants. Thus in Hawaiian plants, conceptacles were said to originate in branches one to five layers below the surface whereas in southern Australian plants they originate in the surface branch. The pore canal in Hawaiian plants is blocked by a plug even after sporangia have matured; only young southern Australian conceptacles had pore canals blocked by epithallial cell remnants rather than a plug. The conceptacle in Littler's (1971: fig. 10) diagram also shows the structure of the roof tangential to the pore canal rather than through the pore canal. Conceptacle ontogeny in Hawaiian material has not been reinvestigated during the present study.

The only previous record of male conceptacles in *L. prototypum* is the doubtful report of Foslie (1909) which was subsequently repeated by Lemoine (1917), Taylor (1928) and Chapman (1963). Only mature male conceptacles have been found in southern Australian material. The structure of these (Figs 47A, 47B) is similar to those of *L. chamberlainianum* (see Figs 20A–20E). The roof is formed by a single ring of coalesced filaments which arise from primigenous palisade cells and arch over developing spermatangia to form a roof. Each filament consists of a main axis and in some cases a small number of one- to several-celled laterals (Fig. 47B). Epithallial cells are borne terminally or laterally on roof filaments (Fig. 47B). The structure adjacent to the pore canal has not been fully elucidated. Spermatangia are simple, elongate and are borne in small groups on spermatangial initials which arise directly from subtending primigenous palisade cells on the conceptacle chamber floor (Fig. 47B). Male conceptacles, like tetrasporangial ones, may be overgrown by new applanate branches and thus become immersed within a thallus (Fig. 47B).

The only previous report of female/carposporangial conceptacles in *L. prototypum* appears to be that of Adey et al. (1982: 36, as *Tenarea tessellata*) who provide data on conceptacle dimensions and fusion cell and carpospore sizes but no accompanying figures. Female/carposporangial conceptacles have been found in two collections (LTB 15443, 15649), the former consisting only of dried plants, but conceptacle primordia have not been observed. Based on the youngest stage encountered, (Fig. 48A), female/carposporangial conceptacle ontogeny in *Lithophyllum prototypum* appears to be similar to that in *L. chamberlainianum* (q.v.). Thus a group of initials is produced from primigenous cells and the overlying layer of epithallial cells becomes arched upwards to form a temporary protective dome (Fig. 48A) which degenerates and is lost as the conceptacle matures. Centrally situated initials give rise to carpogonia (Figs 48B, 49A, 49B) while a surrounding group of more peripheral initials give rise to filaments which become coalesced and overtop the developing gametangia to produced theconceptacle roof (Figs 48A, 48B). Of those initials involved in carpogonial branch formation, only those directly beneath the pore canal normally reach full maturity (Fig. 49B). Each branch consists of a terminal carpogonium (with a distal, elongate trichogyne), and one or two subtending cells (Fig. 49A). Sometimes two carpogonia are produced on the same branch, but only one develops fully. In one conceptacle (Fig. 49A), spermatia had become attached to several trichogynes, but karyogamy and stages associated with fusion cell formation were not observed.

Roofs of female/carposporangial conceptacles reach full maturity by the time trichogyne-bearing carpogonia are evident (Fig. 48B). Distal remnants of filaments flanking the pore canal lack epithallial cells and contain cells different in size and shape to those of other roof filaments. Remaining roof filaments above the chamber can be divided into two groups: (1) a group lateral to the pore canal in which the intact portion of each filament consists of an epithallial cell and two or three (rarely four) subtending cells which may be more or less isodiametric or somewhat elongate; and (2) a more peripheralgroup in which the intact portion of each filament contains only a terminal epithallial cell and one subtending elongate cell. Lower cells of filaments above the chamber usually become senescent and eventually degenerate, thereby creating a larger chamber for developing carposporophytes (Fig. 48B). At themargin of conceptacles, roof filaments remain intact, each containing a terminal epithallial cell and one or two subtending elongate cells (Figs 48B, 49C).

Only one carposporophyte has been encountered, and this probably was not fully mature (Fig. 49C). In this carposporophyte, a flattened fusion cell spans most of the conceptacle chamber floor, remains of unfertilized carpogonia are evident on the dorsal surface of the fusion cell, and gonimoblast filaments emanate from the periphery. One nearly mature but dried carposporangium was found (Fig. 49C); this was 43 µm long and 30 µm in diameter, more or less comparable to that mentioned by Adey et al. (1982: 36). Spore germination and very early thallus development have not been observed.

References to *L. prototypum* and its synonyms from out-

Table 10 Published records of *Lithophyllum prototypum* and its synonyms. Names used by authors are listed alphabetically first by specific epithet and then by genus. Localities are listed in parentheses; superscripts refer to notes at end of table. Authorities for names are given in the synonymy listings.

Dermatolithon prototypum

Dawson, *Essays Nat. Sci. Honor Capt. A. Hancock*: 273 (1955) (West Indies) [1]. De Toni, *Sylloge Algarum* 4: 1773 (1905) (US Virgin Islands) [1,2]. De Toni, *Sylloge Algarum* 6: 666 (1924) [1]. Foslie in *K. norske Vidensk Selsk. Skr.* 1900(5): 22 (1905e) [3]. Foslie in *K. norske Vidensk. Selsk. Skr.* 1909(2): 58 (1909) [3]. Lemoine in *Bull. Soc. bot. Fr.* 117: 556 (1971) [3,4].

Goniolithon prototypum

Setchell & Mason in *Proc. Natn. Acad. Sci. Wash.* 29: 89 (1943) (West Indies) [1].

Lithophyllum prototypum

Adey & Lebednik, *Catalog Foslie Herbarium*: 40 (1967) (Bahamas, Florida, Jamaica, Puerto Rico, US Virgin Islands) [5]. Chapman in *Bull. Inst. Jamaica Sci. Ser.* 12(2): 94, fig. 27 (1963) (Jamaica, West Indies) [2,6]. Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(5): 8 (1905b) [3]. Foslie in *K. norske Vidensk. Selsk. Skr.* 1909(2): 49 (1909) (West Indies) [7]. Howe in N.L. Britton & C.F. Millspaugh, *The Bahama Flora:* 586 (1920) (Bahamas, Florida, Jamaica, Puerto Rico, US Virgin Islands) [5]. Lemoine in *Dansk bot. Ark.* 3: 167, figs 163, 164 (1917) (Florida, West Indies) [4,5,7]. Lemoine in *Dansk bot. Ark.* 4(7): 36 (1924) (Beta Island (Cuba), Florida, West Indies) [6]. Printz, *M. Foslie Contr. Monogr. Lithothamnia:* 37, pl.72, fig. 8 (1929) (West Indies) [16]. Taylor in *Pap. Tortugas Lab.* 25: 209, pl. 37, fig. 6 (1928) (Bahamas, Bermuda, Florida, US Virgin Islands) [2,6]. Taylor, *Mar. Algae Eastn Trop. Subtrop. Coasts Americas*: 392 (1960) (Bahamas, Florida, Jamaica, Puerto Rico, US Virgin Islands) [1(in part), 2,6].

Lithothamnion prototypum

Foslie in *K. norske Vidensk. Selsk. Skr.* 1897(1): 18 (1897) (US Virgin Islands) [7,8].

Tenarea prototypa

Adey in *K. norske Vidensk. Selsk. Skr.* 1970(1): 7 (1970) [3]. Adey in J. Gray & A.J. Boucot, *Hist. Biogeog. Pl. Tectonics Changing Environ.*: 461 (1979) (Caribbean) [9]. Hoek et al. in *Aquatic Bot.* 5: 16, 35 (1978) (Curacao) [13]. Townsend in *Phycologia* 20: 408 (1981) [3,10].

Titanoderma prototypum

D. Littler, et al., *Mar. Pl. Caribbean*: 218 (1989) (Caribbean) [6,14]. Woelkerling et al. in *Phycologia* 24: 333 (1985) [3]. Wynne in *Can. J. Bot.* 64: 2243 (1986) (tropical and subtropical western Atlantic) [1].

Dermatolithon tessellatum

Lemoine in *Bull. Soc. bot. Fr.* 117: 556 (1971) [3].

Goniolithon tessellatum

Dawson in *Pacif. Nat.* 2: 43 (1960) (Mexico, Panama) [6]. Dawson in *Pacif. Sci.* 15: 415 (1961) (Galapagos Islands) [7,8]. Taylor in *Allan Hancock Pacif. Exped.* 12: 183 (1945) (Galapagos Islands)[1].

Tenarea tessellata

Adey in J. Gray & A.J. Boucot, *Hist. Biogeog. Plate Tectonics Changing Environ.*: 461 (1979) (Indo-Pacific) [9]. Adey et al. in *Smithson. Contr. mar. Sci.* 15: 35, figs 21,22 (1982) (Galapagos Islands, Hawaii, Midway Island, Panama) [7,11]. Littler in *Phycologia* 10: 355-9, figs 1-10 (Hawaii) [7,12]. Littler in *Pacif. Sci.* 27: 281 et seq. (1973) (Hawaii) [13]. Magruder & Hunt, *Seaweeds of Hawaii*: 95 (1979) (Hawaii) [14].Townsend in *Phycologia* 20: 408 (1981) [3,10].

Titanoderma tessellatum

Woelkerling, *Coralline Red Algae*: 110, 114, figs 88,94,96 (1988) [15]. Woelkerling et al. in *Phycologia* 24: 333 (1985)[3].

Notes on Table 10.

[1] Data provided by author based only on studies of previous literature.
[2] Includes description of species.
[3] Locality data not given.
[4] Excluding var. *udoteae*.
[5] Records other than that for type collection not confirmed during present study.
[6] Record(s) not confirmed during present study.

Table 10 *cont.*

[7] Includes detailed morphological/anatomical information.
[8] Protologue.
[9] Source of locality information uncertain.
[10] Limited data on conceptacle anatomy provided.
[11] Records not confirmed by specimen examination but figures without doubt pertain to this species.
[12] Includes specimen ML1082 examined during present study.
[13] Contains ecological data only.
[14] Includes color photograph.
[15] Figures are southern Australian plants; figs 94, 96 not identified to species in figure legends.
[16] Includes photo of holotype specimen.

side Australian waters are summarized in Table 10. The most detailed morphological/anatomical account is that of Littler (1971, as *Tenarea*) who studied specimens from Hawaii.

Relationships of *Lithophylum prototypum* to other species are considered below (p.97).

INFRASPECIFIC TAXONOMY. Within *L. prototypum*, one infraspecific entity has been established: *L. prototypum* var. *udoteae* (Foslie) Lemoine (1917: 167). This entity was originally described as *Goniolithon udoteae* Foslie (1901a: 21) and is based on a specimen from St. Croix (U.S. Virgin Islands) collected by F. Boergesen. Subsequently, De Toni (1924: 666, as *Dermatolithon*) treated Foslie's entity as a heterotypic synonym of *Lithophyllum prototypum* without according it varietal status, a course of action also adopted by Taylor (1960: 392). Dawson (1955: 274) and Lemoine (1971: 556), in contrast, retained the variety under the name *Dermatolithon prototypum* var. *udoteae* (Foslie) Lemoine. [Dawson's combination is invalid because the full citation of the basionym is not provided in accordance with ICBN Art. 33.2 (see Greuter, 1988).]

The Foslie herbarium at TRH contains a single Boergesen collection labelled *Goniolithon udoteae* from St. Croix. This collection must therefore be regarded as the holotype even though it is not so designated by Adey & Lebednik (1967: 26) or mentioned by Adey (1970). The holotype, which is figured in Printz (1929: pl. 45, fig. 1), contains a host *Udotea* plant (found in two pieces when re-examined in 1989) to which thalli of two conspicuous but distinctly different nongeniculate corallines are attached: *Lithophyllum prototypum*, which covers a greater portion of the host and is characteristically terraced in surface view; and secondly plants of *Neogoniolithon* (sensu Penrose, 1992), which cover a lesser portion of the host and are not terraced in surface view. It is clear from the protologue of *Goniolithon udoteae* (Foslie, 1901a) as well as from the re-examination of the type collection that Foslie's description pertains to the plants of *Neogoniolithon* and not to the plants of Lithophyllum *prototypum*. This conclusion has been confirmed from an examination of the single slide (prep. 367) which Foslie had made from material in the type collection. Prep. 367 contains only fragments of *Neogoniolithon* and no material of *Lithophyllum prototypum*. Consequently, *Goniolithon udoteae* is neither a variety nor a heterotypic synonym of *Lithophyllum prototypum*; its status within *Neogoniolithon*, however, has yet to be clarified.

7. **Lithophyllum pustulatum** (Lamouroux) Foslie in *K. norske Vidensk. Selsk. Skr.* 1904(2): 8 (1904).

Figs 50–60

BASIONYM. *Melobesia pustulata* Lamouroux, *Hist. Polypiers*

Coralligenes Flexibles: 315 (1816).

LECTOTYPE. CN (France; no further details given in protologue). Fig. 50.

HOMOTYPIC SYNONYMS:

> *Dermatolithon pustulatum* (Lamouroux) Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(3): 11 (1898b). *Epilithon pustulatum* (Lamouroux) Lemoine in *Bull. Soc. linn. Provence* 3: 10 (1921). *Tenarea pustulata* (Lamouroux) Adey in *Colo. Sch. Mines Q.* 60(2): 88 (1965) (combination invalid as full citation of basionym not given in accordance with ICBN Art. 33.2).. *Titanoderma pustulatum* (Lamouroux) Nägeli, Stärkekörner: 532 (1858).

Note: For additional synonomy involving infraspecific names, see sections A & B of Table 13 and comments in the section on infraspecific taxonomy below.

HETEROTYPIC SYNONYMS:

> *Lithothamnion adplicitum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1897(1): 17 (1897). *Dermatolithon adplicitum* (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1900(5): 22 (1900e). *Lithophyllum adplicitum* (Foslie) Newton, *Handbook Br. Seaweeds*: 306 (1931). *Melobesia caspica* Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(9): 131 (1900). *Dermatolithon caspicum* (Foslie) Zaberzhinskaya ex Zinova, *Red, Brown and Green Algal Flora of the Southern Seas of the USSR*: 227 (1967). *Litholepis caspica* (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(5): 6 (1905b). *Tenarea caspica* (Foslie) Adey in *K. norske Vidnesk. Selsk. Skr.* 1970(1): 7 (1970). *Titanoderma caspica* (Foslie) Woelkerling in *Phycologia* 25: 257 (1986). *Melobesia confinis* P. & H. Crouan, *Florule du Finistere*: 150 (1867). *Dermatolithon confinis* (P. & H. Crouan) W. & P. Adey ex Parke & Dixon in *J. mar. biol. Ass. UK* 56: 534 (1976) (comb. invalid as full citation of basionym not given in accordance with ICBN Art. 33.2). *Dermatolithon confinis* (P. & H. Crouan) Boudouresque et al. in *Vie Milieu* 34: 46 (1984) *Tenarea confinis* (P. & H. Crouan) W. & P. Adey in *Br. phycol. J.* 8: 393 (1973). *Titanoderma confinis* (P. & H. Crouan) Price et al. *Bull. Br. Mus. nat. Hist. Bot.* 15: 86 (1986). *Dermatolithon hapalidioides* f. *confinis* (P. & H. Crouan) Foslie in *K. norske Vidnesk. Selsk. Skr.* 1899(7): 12 (1900). *Lithophyllum hapalidioides* f. *confinis* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905a). *Lithophyllum hapalidioides* var. *confinis* (P. & H. Crouan) Lemoine in *Bull. Soc. Linn. Provence* 3: 12 (1921). *Titanoderma pustulatum* var. *confine* (P. & H. Crouan) Chamberlain in *Bull. Br. Mus. nat. Hist. Bot.* 21(1):50: (1991). *Melobesia hapalidioides* P. & H. Crouan, *Florule du Finistere*: 150 (1867). *Dermatolithon hapalidioides* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(3): 11 (1898b).[Ortho. var. & lapsus calami: *D. nepalidioides* (P. & H. Crouan) Foslie; see Price et al. in *Bull. Br. Mus. nat. Hist. Bot.* 15: 86 (1986)]. *Lithophyllum hapalidioides* (P. & H. Crouan) Hariot, *Mission Sci. Cap Horn* 5(Bot): 84 (1889). *Tenarea hapalidioides* (P. & H. Crouan) W. & P. Adey in *Br. phycol. J.* 8: 294 (1973). *Titanoderma hapalidioides* (P. & H. Crouan) Price et al. in *Bull. Br. Mus. nat. Hist. Bot.* 15: 86 (1986).

Note: For additional names involving infraspecific autonyms, see Section E of Table 13 and comments in the section on infraspecific taxonomy below.

> *Lithophyllum litorale* Suneson in *Acta Univ. lund.* N.F. Avd 2, 39(9): 39 (1943). *Dermatolithon litorale* (Suneson) Hamel & Lemoine in *Archs Mus. Hist. nat. Paris*, Ser. 7, 1: 66 (1953). *Melobesia macrocarpa* Rosanoff in *Mem. Soc. Imp. Sc. Nat. Math. Cherbourg* 12: 74 (1866) *Dermatolithon macrocarpum* (Rosanoff) Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 14 (1900b). *Lithophyllummacrocarpum* (Rosanoff) Foslie in *Wissenschaft. Meeresunters. Abt. Helgoland*, n.s. 7(1): 29 (1904b). *Nelobesia macrocarpa* (Rosanoff) Kleen ex Kjellman in *K. svenska Vetensk. Akad. Handl.* 20(5): 105 (1883). [*Nelobesia* is an orthographic variant of *Melobesia*; see Woelkerling, *Coralline Red Algae:* 186 (1988).] *Titanoderma macrocarpum* (Rosanoff) Chamberlain in *Cryptogamie algol.* 7: 203 (1986). *Dermatolithon pustulatum* f. *macrocarpum* (Rosanoff) Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(3): 11 (1898b). *Lithophyllum pustulatum* f. *macrocarpum* (Rosanoff) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 117 (1905a). *Lithophyllum pustulatum* var. *macrocarpum* (Rosanoff) Lemoine in *Nouv. Arch. Mus. Hist. Nat. Paris.*, ser. 5, 5: 142 (1913b). *Titanoderma pustulatum* var. *macrocarpum* (Rosanoff) Chamberlain in *Bull. Br. Mus. Nat. Hist. Bot.* 21(1):33 (1991).

Note: For additional names involving infraspecific autonyms, see Section F of Table 13 and comments in the section on infraspecific taxonomy below.

> *Dermatolithon macrocarpum* f. *faeroensis* Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 15 (1900b). *Lithophyllum macrocarpum* f. *faeroensis* (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 *Lithophyllum pustulatum* f. *ascripticium* Foslie in *K. norske Vidensk. Selsk. Skr.* 1906(8): 34 (1907a). *Dermatolithon pustulatum* f. *ascripticium* (Foslie) Foslie ex De Toni, *Sylloge Algarum* 6: 665 (1924) *Lithophyllum pustulatum* f. *intermedium* Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 117 (1905a). *Dermatolithon macrocarpum* f. *intermedium* (Foslie) Foslie ex De Toni, *Sylloge Algarum* 6: 666 (1924). *Lithophyllum macrocarpum* f. *intermedium* (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905). *Melobesia pustulata* β *canellata* Kützing, *Species Algarum*: 696 (1849). *Titanoderma pustulatum* var. *canellatum* (Kützing) Chamberlain in *Bull. Br. Mus. Nat. Hist. Bot.* 21(1):61 (1991). *Melobesia simulans* P. & H. Crouan, *Florule du Finistere*: 149 (1867). *Melobesia verrucata* Lamouroux, Hist. *Polypiers Coralligenes Flexibles*: 316 (1816). *Titanoderma verrucatum* (Lamouroux) Chamberlain in *Cryptogamie algol.* 7: 201 (1986).

ORTHOGRAPHIC VARIANTS:

> *Melobesia postulata* Lamouroux. Coupin 1920, *Album General des Cryptogames, Algae* Vol. 4: 281, pl. 281, fig. c. Citation error for *pustulata. Melobesia pustulosa* Lamouroux. Frauenfeld in *Verh. Zool-bot. Ver. Wien* 4:340 (1854). Citation error for *pustulata*.

MISAPPLIED NAMES. No published misapplications of other names to southern Australian specimens of *Lithophyllum pustulatum* were found during the present study. Chamberlain (1986, 1991), however, has recorded a number of such misapplications involving British and other European collections, and caution therefore must be exercised in accepting previously published records without confirming herbarium studies. Problems involving use of the name *Melobesia pustulata* and its homotypic synonyms in past publications are considered below in the section on distribution and ecography.

ETYMOLOGY. The specific epithet *pustulatum* possibly refers to the pustulose appearance of the conceptacles on the surface of the thallus; Lamouroux (1816: 315), however, did not explain his choice of epithet.

PREVIOUSLY PUBLISHED ILLUSTRATIONS OF AUSTRALIAN PLANTS. Campbell & Woelkerling in *Phycologia* 29: figs 1, 4 (as *Lithophyllum pustulatum*) (1990). Woelkerling, *Coralline Red Algae*: 110, fig. 89 (as *Titanoderma* sp.) (1990).

DESCRIPTION. Plants mostly 1–100 mm across and 0.05–2.5

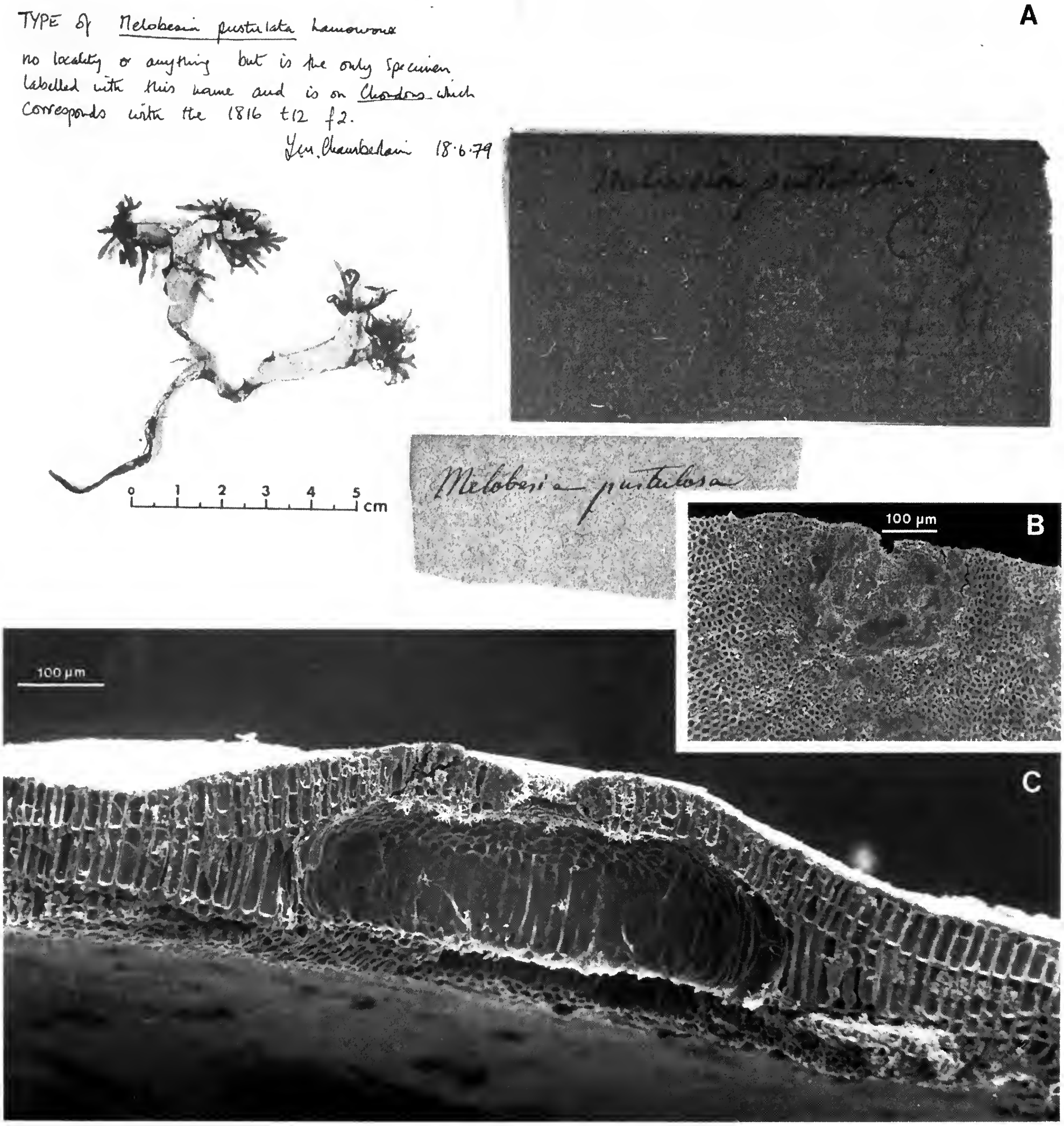


Fig. 50 *Lithophyllum pustulatum*: type collection. A. Lectotype specimen. (CN, unnumbered). B. Surface view of conceptacle shown in Fig. 50C. Note heavy calcification of roof. C. Fracture of conceptacle showing roof and chamber anatomy.

mm thick or tall; variably flat (complanate) to layered (without conspicuous terracing) to randomly warty or lumpy; completely or partially adherent.

Thallus dimerous; primigenous filaments usually composed of palisade cells (5–)8–18 µm long and (12–)25–75(–100) µm tall; postigenous filaments composed only of epithallial cells 2–6 µm long and 4–12 µm in diameter or more commonly of 2–30+ additional subtending cells (5–)16–55(–65) µm long and 5–14 µm in diameter. Contiguous secondary pit-connections common; adjunctive secondary pit-connections, cell fusions and trichocytes not seen.

Tetrasporangial/bisporangial plants with scattered protruding conceptacles. Conceptacle roofs 390–690(–890) µm in external diameter; roof filaments above chamber usually (2–)3(–4) cells long in some but 3–7 cells long in other conceptacles; cells (8–)14–45 µm long and 4–11 µm in diameter with columnar cells occurring in an isolated or sporadic manner or in subepithallial horizontal groups. Pore canals lined with non- or somewhat projecting, non-occluding cells. Conceptacle chambers (328–)390–500(–556) µm in diameter and 110–180 µm tall; floor of mature chambers usually 1–3(–5) cells below thallus surface; tetrasporangia/bisporangia 100–140 µm long and 55–82 µm in diameter, scattered across the chamber floor or more commonly peripheral to a columella. Gametangial plants dioecious. Male conceptacle roofs protruding; chambers 220–450 µm in diameter and 50–90 µm tall; spermatangial branches confined to chamber floor, simple, with each initial bearing one to several elongate spermatangia. Female/carposporangial conceptacle roofs protruding; chambers 220–300 µm in diameter and 85–110 µm tall; carpogonial filaments arising from chamber floor, usually 2–3 cells long and bearing 1(–2) carpogonia terminally.

Carposporophytes developing within female conceptacles after presumed karyogamy; each comprising a more or less flattened fusion cell and some several-celled gonimoblast filaments arising peripherally with terminal carposporangia 30–75 µm in diameter.

DIAGNOSTIC FEATURES. *Lithophyllum pustulatum* differs from other southern Australian species of *Lithophyllum* in having the following combination of features:

1. Pore canals of tetrasporangial/bisporangial conceptacles lined with cells which may project somewhat into but do not completely occlude the entire canal (Figs 55E, 56A–56F, 57A–57H).
2. Floors of functional tetrasporangial/bisporangial conceptacle chambers usually situated one to three cells below the thallus surface, and conceptacle roofs protruding above the thallus surface (Figs 55A, 55E, 58C).
3. Thallus surface not obviously and more or less completely terraced as a consequence of applanate branch development.
4. Applanate branches, when present, arising from groups of postigenous cells.
5. Postigenous filaments multicellular in vegetative parts of most but not all thalli.

Whether this combination of features can be used to distinguish *L. pustulatum* from all other species of *Lithophyllum* cannot be determined until monographic studies of the genus are carried out on a world scale.

TYPIFICATION. Woelkerling et al. (1985: 325 & figs 29–39) designated the lectotype specimen for *Melobesia pustulata* and provided a detailedaccount of material in the type collection. *Melobesia pustulata* is also type species of *Titanoderma* Nägeli (1858: 532) and its later homotypic synonyms *Melobesia* Heydrich (1897: 408) and *Dermatolithon* (Foslie 1898b: 11). In addition, *Melobesia pustulata* is type species of *Lithophyllum* subg. *Dermatolithon* (Foslie, 1904: 3). Woelkerling (1988: 111, 113) provides a fuller explanation of matters relating to the typification of these genera and subgenera.

NOMENCLATURE AND SYNONYMY. Chamberlain (1986, 1991) has concluded from comparative studies of type and other European collections that at least 11 other described entities are heterotypic synonyms of *Lithophyllum pustulatum*. In the list of heterotypic synonyms above, these include all but *Melobesia caspica* and its derivative combinations. After studying the type and other collections of *Litholepis*, Woelkerling (1986) concluded that the genus was a heterotypic synonym of *Titanoderma* (which now is regarded to be a heterotypic synonym of *Lithophyllum*—see Campbell & Woelkerling, 1990). Woelkerling (1986: 260) also concluded from evidence then available that the type species of *Litholepis* [i.e. *L. caspica* (Foslie) Foslie] was specifically distinct from *Lithophyllum pustulatum* (both as *Titanoderma*). Subsequent studies by Chamberlain (1991) and of southern Australian populations of *Lithophyllum pustulatum*, however, have shown that *L. pustulatum* encompasses a considerably broader spectrum of form and structure than realized in 1986. As a result, the criteria used by Woelkerling (1986: 260) to distinguish *Litholepis caspica* from *Lithophyllum pustulatum* (both as *Titanoderma*) can no longer be applied (see remarks on morphology and anatomy below), and the twoentities are considered conspecific.

DISTRIBUTION AND ECOGRAPHY. *L. pustulatum* has been found from Cape Vlaming, Rottnest Island, Western Australia eastwards to Point Lonsdale, Victoria, and from Bluestone Bay on the east coast of Tasmania. A single collection from southern New South Wales (LTB 12635) also has been seen. Specimens have been obtained in January, February, April, August and October through December. Except for Campbell & Woelkerling (1990) and Chamberlain (1991), previously published records from southern and southwestern Australia (Table 11) have not been verified. Similarly, the records of Bailey (1913: 829, as *Dermatolithon*), Barton (1893: 202, as *Melobesia)*, Chapman (1977: 162, as *Dermatolithon*), De Toni (1905: 1772, as *Dermatolithon*), Dickie (1875: 32 as *Melobesia*), Foslie (1905a; 127, as *Lithophyllum*), Harvey (1849: 110, as *Melobesia*), Laing (1901: 300, as *Melobesia*), Lewis (1984: 13, as *Dermatolithon*), Lucas (1909: 55, as *Melobesia*; 1912: 163, as *Dermatolithon*), Reinbold (1900: 153, as *Melobesia*), Rosanoff (1866: 72, as *Melobesia*) and Sonder (1880–1881: 20, as *Melobesia*) of *Lithophyllum pustulatum* from unspecified Australian localities or from localities elsewhere in Australia require confirmation.

Of the 29 collections examined, one (LTB 143390) contained male and female/carposporangial as well as tetrasporangial plants, one (LTB 14365) contained both male and female/carposporangial plants, one (LTB 12667) contained only female/carposporangial plants, and two (LTB 14396, 15596) contained male but no female/carposporangial plants.

An authoritative account of the world distribution of *L. pustulatum* is not presently possible. There are hundreds published reports of *L. pustulatum* (including those involving

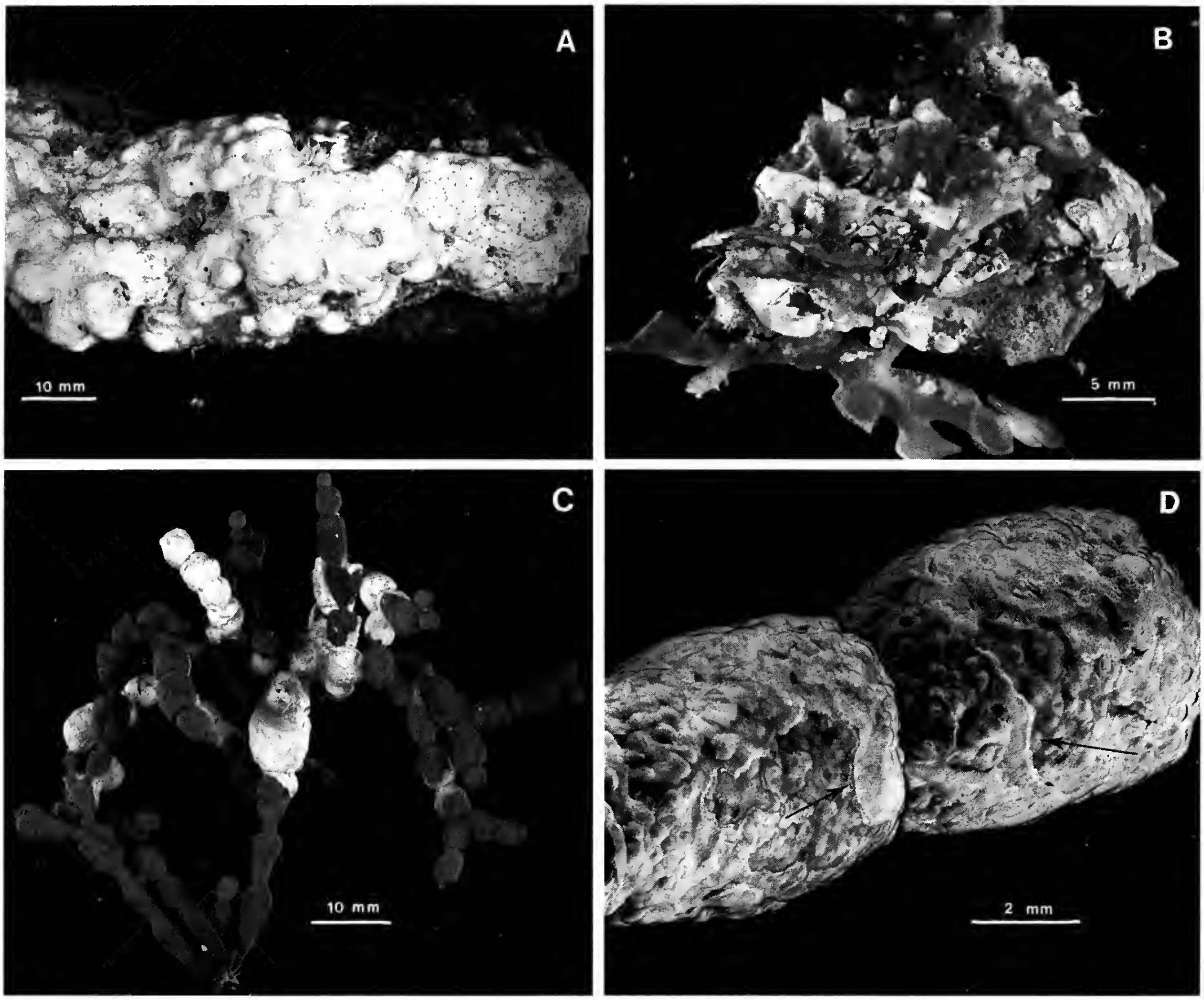


Fig. 51 *Lithophyllum pustulatum*: habit of southern Australian specimens. A. Surface view of a specimen with lumpy outgrowths (LTB 14581). B. Surface view of thin, flat (complanate) plants growing on (LTB 14365). C.D. Layered specimens encasing receptacles of *Hormosira*. Note (D, arrows) overgrowing applanate branches. (LTB 13054).

homotypic and heterotypic synonyms) encompassing all continents. Most of these records require verification in the context of our present understanding of *L. pustulatum*. Chamberlain (1991) has confirmed from direct study of specimens that *L. pustulatum* (as *Titanoderma*) occurs along the coasts of the British Isles, Denmark, northern and western France, Germany (Helgoland), Norway, and Sweden in Europe; the Mediterranean (including the Aegean and Adriatic seas); the Faeroes and the Canary Islands in the North Atlantic Ocean; California (North Pacific) and India (Indian Ocean) as well as southern Australia. Chamberlain (1991) also has uncovered a number of specimens wrongly identified as *L. pustulatum* during her studies, clearly reinforcing the need to recheck all specimens upon which published reports are based.

Within southern and southwestern Australia, *Lithophyllum pustulatum* has been found in intertidal rocky reef pools and at depths of 0–5m on rock, sponges, abalone shells, snails, and on various brown and red algae including *Ecklonia, Hormosira, Scaberia, Callophyllis* and *Pterocladia*. The absence at present of collections from depths greater than 5m probably reflects the limited sampling from deeper waters and does not imply that *Lithophyllum pustulatum* is restricted to shallow water.

COLLECTIONS EXAMINED:

NEW SOUTH WALES: Green Cape (*Platt*, 31 December 1982, LTB 12635).

SOUTH AUSTRALIA: Aldinga Beach (*Woelkerling*, 3 January 1977, LTB 12487). Beachport (Post Office Rock) (*Campbell & Penrose*, 6 November 1987, LTB 15843). Cape du Coudeic, Kangaroo Island (*Woelkerling*, 22 February 1979, LTB 15843). Cape Willoughby, Kangaroo Island (*Campbell & Penrose*, 6 April 1988, LTB 15596). Elliston (Waterloo Bay) (*Turner*, 28 October 1981, LTB 15361). Head of Great Australian Bight (*Woelkerling, Platt, & Jones*, 13 February 1984, LTB 14377, 14380). Penneshaw, Kangaroo Island (*Campbell & Penrose*, 13 April 1988, LTB 15673). Point

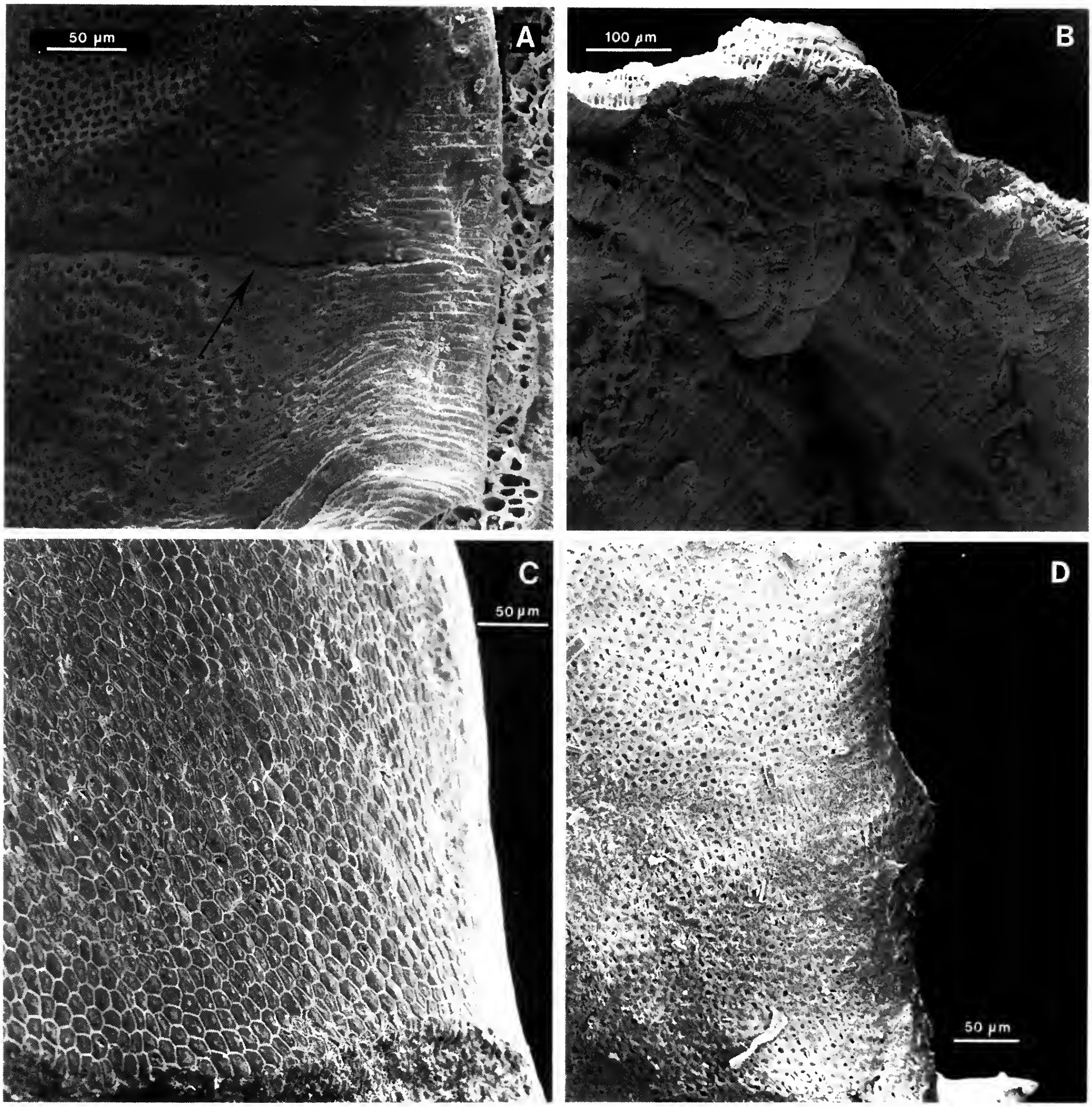


Fig. 52 *Lithophyllum pustulatum*: surface features. A. Dorsal surface and margin (arrow) of two abutting thallus branches (LTB 11670). B. Ventral surface of thallus showing several layers of applanate branching and the alignment of primigenous filaments into distinct rows. (LTB 11670). C. Dorsal surface of thallus in which no epithallial concavities are evident and in which the polygonal outlines of postigenous cells are visible. (LTB 14464). D. Dorsal view of thallus with numerous epithallial concavities present. (LTB 14390).

Fowler, Fowlers Bay (*Woelkerling, Platt, & Jones*, 14 February 1984, LTB 14464, 14390, 14396, 14398). Pondalowie Bay, Yorke Peninsula (*Woelkerling*, 31 December 1976, LTB 12473). Sceale Bay (Point Westall) (*Platt & Jones*, 16 February 1984, LTB 14581). Vivonne Bay, Kangaroo Island (*Womersley*, 17 January 1948, LTB 13594 collection originated as a gift from AD A7907).

TASMANIA: Bluestone Bay, Freycinet Peninsula (*Platt & Woelkerling,* 21 February 1983, LTB 13054, 13055).

VICTORIA: Point Lonsdale (*Turner*, 6 January 1979, LTB 11542). Warrnambool (*Pope & Bennett*, 16 Aug 1948, LTB 13700; collection originated as a gift from AD A12125).

WESTERN AUSTRALIA: Cape Vlaming, Rottnest Island (*Woelkerling*, 8 February 1978, LTB 12667). Eyre ('Nine Mile Reef') (*Woelkerling, Platt, & Jones,* 1 February 1984, LTB 13953, 13956). Frenchman Bay, Albany (*Woelkerling*, 2 February 1978, LTB 10732). Lucky Bay, Cape Le Grand National Park, Esperance (*Woelkerling, Platt, & Jones,* 9 February 1984, LTB 14301, 14361, 14365, 14367).

FRANCE: Lectotype; collection details not given in protologue or on specimen; see Fig. 50.

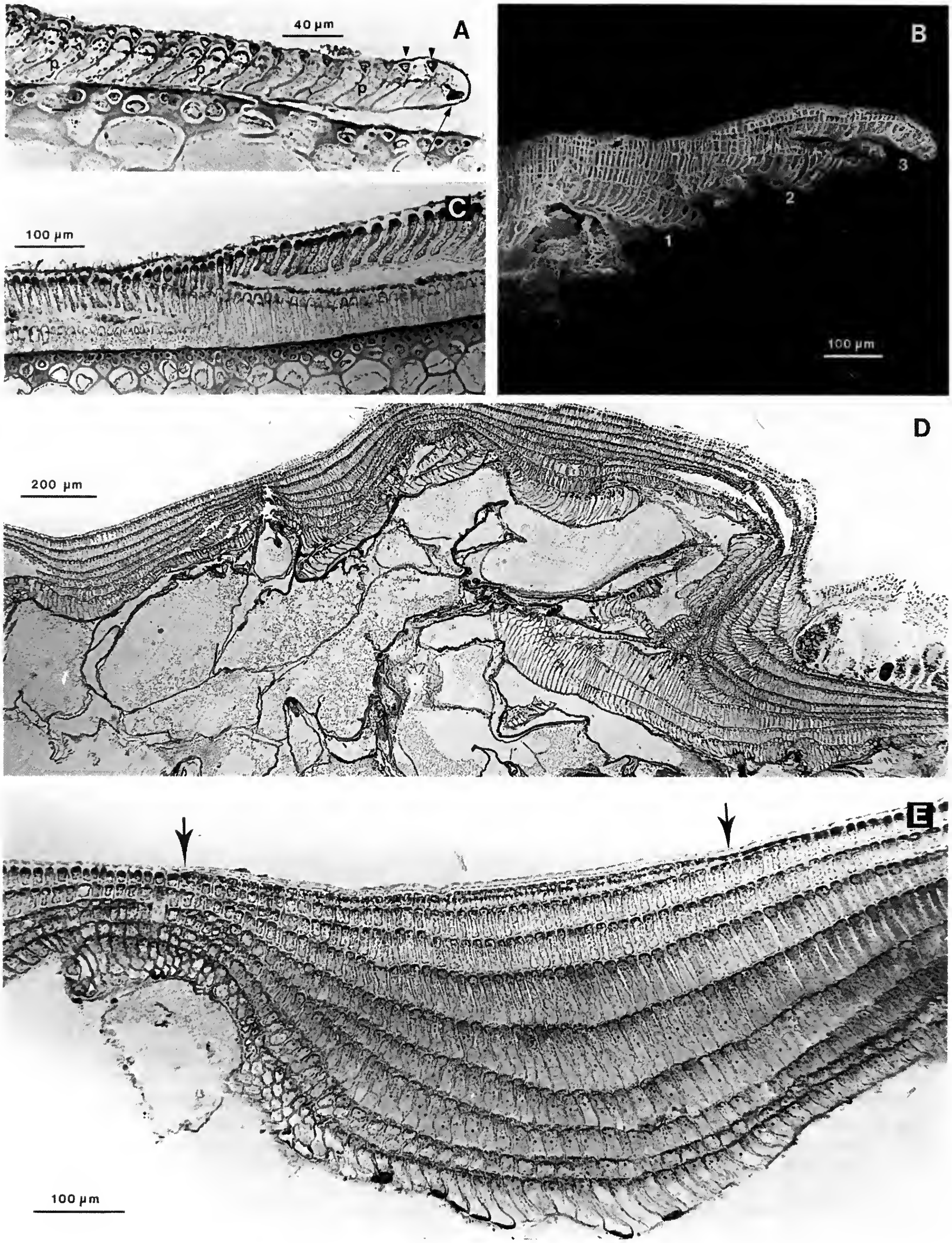


Fig. 53 *Lithophyllum pustulatum*: vegetative anatomy. A. Longitudinal section through thallus margin showing apical cell (arrow), palisade primigenous cells (p) and epithallial cells (arrowheads). (LTB 14365). B. Fracture of thallus margin showing three successive, overtopping applanate branches (1, 2, 3) which originated from groups of postigenous filaments. (LTB 11670). C. Section showing applanate branch which originated indirectly from a subtending layer of primigenous filaments. (LTB 14365). D. Section through portion of a somewhat twisting thallus. Note great variation in height of primigenous palisade cells and how thallus closely conforms to irregularities in the substrate. (LTB 14464). E. Section through portion of thallus showing coordinated development of groups of postigenous filaments and periclinal banding within the thallus. Note coordinated formation of a new group of postigenous cells in region between arrows. (LTB 14581).

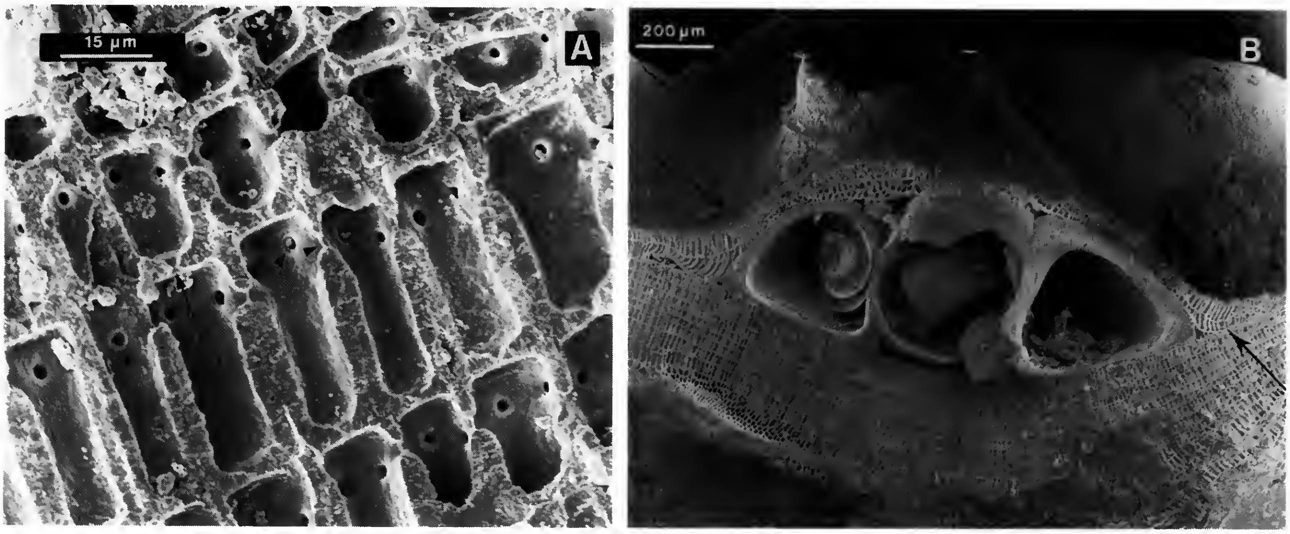


Fig. 54 *Lithophyllum pustulatum*: vegetative anatomy. A. Fracture showing primary (arrow) and secondary (arrowheads) pit-connections in cells of contiguous postigenous filaments. (LTB 14464). B. Fracture showing part of thallus in which several applanate branches (arrows) have engulfed a probable bryozoan fragment. (LTB 14464).

REMARKS ON MORPHOLOGY AND ANATOMY. Southern Australian specimens of *Lithophyllum pustulatum* cannot be identified to species or genus using external features for reasons outlined in the account of *L. chamberlainianum* (q.v.). Unequivocal identification only can be made from sections of tetrasporangial/bisporangial conceptacles in which the pore canal is obvious and clear (Figs 55E, 56, 57).

Thallus appearance varies and depends upon size of the individual and physiognomy of the substrate. Plants in most collections are flat (complanate) or layered (Figs 51B–51D) and commonly form horizontal expanses (Fig. 51B) or occasionally encircle branches of host thalli (Figs 51C, 51D; see also Woelkerling 1988, fig. 89 for a lower magnification of material in Fig. 51D), and they appear to be smooth-surfaced or slightly rugose to the unaided eye. This contrasts with one robust specimen (Fig 51A) which had distinct lumpy outgrowths. Chamberlain (1991) did not record specimens with lumpy outgrowths from the British Isles.

Dorsal margins of thalli commonly possess numerous small parallel ridges and grooves (Fig. 52A) which demarcate the position of individual primigenous filaments. Comparable but more marked ridges and grooves can occur on the ventral surface of thalli (Fig. 52B). While some applanate branches clearly overgrow one another (Fig 52B; see also Figs 51D, 53B, 53C), others abut along a common margin (Fig. 52A). Chamberlain (1991, as *Titanoderma*) used the term ‘imbricate’ to describe thallus overgrowth and suggested that such imbricating possibly could involve parts of the same or different individuals.

In portions of thalli where postigenous filaments have developed, the dorsal thallus surface sometimes remains smooth and the polygonal boundaries of surface cells of individual postigenous filaments are clearly evident (Fig. 52C). The distal walls of epithallial cells terminating such filaments appear calcified, and the position of these is demarcated by small bumps on each underlying postigenous cell (Fig. 52C). In most plants, however, the distal walls of epithallial cells are not calcified and consequently collapse when specimens are dried. This leaves a series of concavities on the thallus surface (Fig. 52D). Epithallial cells associated with primigenous cells also normally collapse on drying and leave distinct concavities (Fig. 52A).

Dimerous construction and dorsiventral organization occurred in all thalli examined. Lateral expansion of thallus margins and of applanate branches occurs from apical initials which produce new primigenous palisade cells inwardly (Fig. 53A). Each primigenous cell soon produces an epithallial cell dorsally. In most specimens, all primigenous cells are palisade.

In the vast majority of plants, multicellular postigenous filaments occur and are 4–15 cells long (e.g. Figs 53D, 53E, 54B. In LTB 14581 (Fig. 58C); occasionally,however, postigenous filaments more than 30 cells long occur and wart-like outgrowths are present. Rarely, postigenous development was limited to epithallial cell production except near conceptacles. Chamberlain (1991) reports such plants to be more common in European and Mediterranean waters and refers them to a distinct variety [as *Titanoderma pustulatum* var. *verrucatum* (Lamouroux) Chamberlain].

Applanate branches arise directly from groups of postigenous cells (Figs 53B, 53C), possibly in the same manner as in *Lithoporella melobesioides* (see Turner & Woelkerling, 1982). Primordial stages, however, have not been found. It is apparent from one section (Fig. 53C) that branches can arise from postigenous filaments which are only two cells long. After formation of a group of subepithallial postigenous cells, some of these presumably divide anticlinally to produce new initials laterally (not seen) which then give rise to primigenous filaments of new applanate branch. In one specimen (Fig. 53B), a series of applanate branches was produced with each new one expanding beyond the margin of the subtending branch, thereby resulting in a series of overhanging ‘shelves’. Applanate branch formation directly from primigenous cells [as occurs in *L. chamberlainianum*, *L. irvineanum* and *L. prototypum*, (q.v.)] was not observed. In LTB 14464 (Fig. 54B) several applanate branches had engulfed fragments of a probable bryozoan and then became coalesced to form a chimney-like structure.

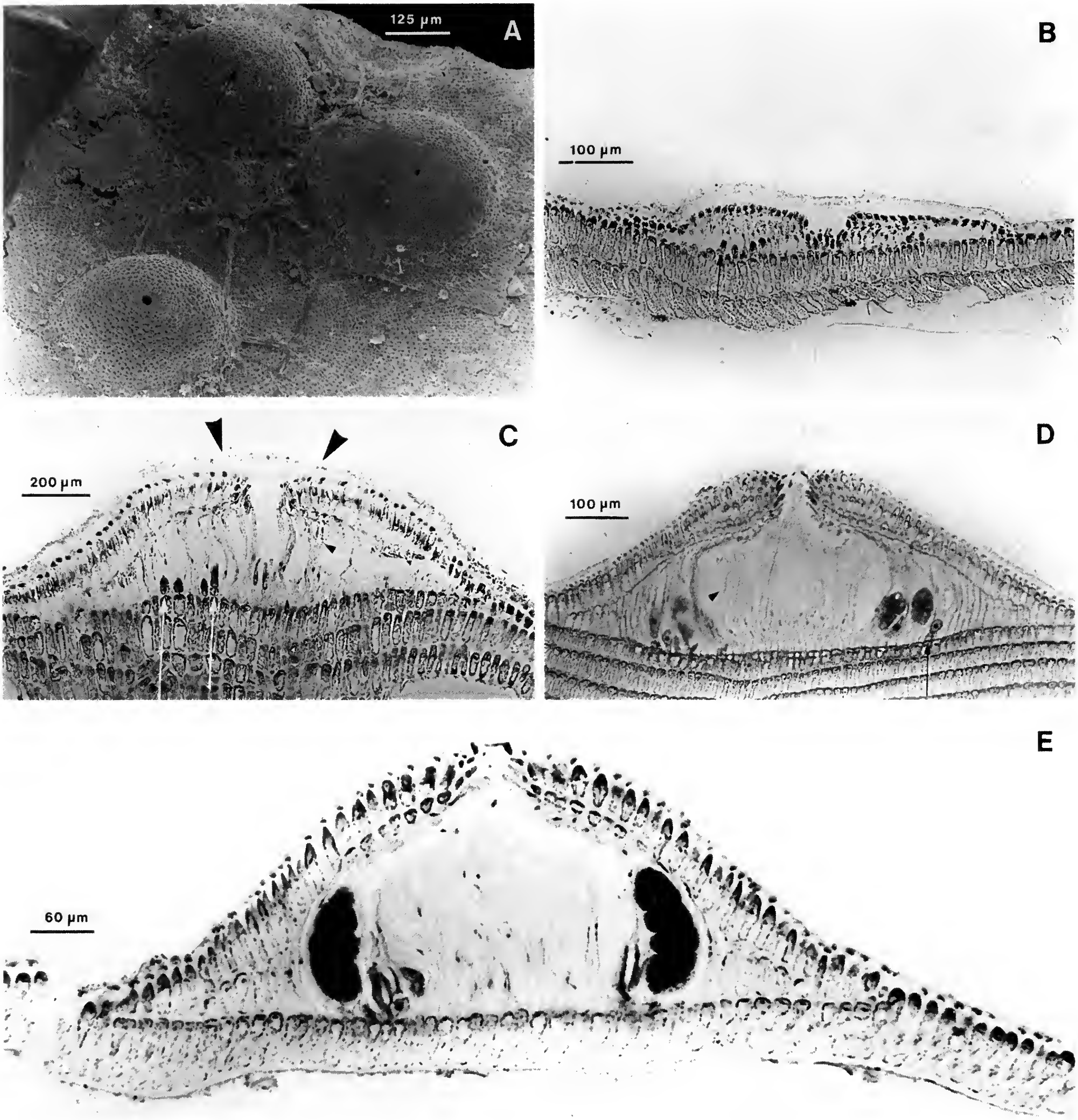


Fig. 55 *Lithophyllum pustulatum*: tetrasporangial conceptacle appearance and ontogeny. A. Surface view of a group of tetrasporangial conceptacles. Note mucilaginous plug (arrow) covering one pore. (LTB 13054). B–D. Stages in the development of tetrasporangial conceptacles. Note sporangial initials (arrows), a central group of filaments which is not involved in roof formation and is destined in these conceptacles to form a columella, degenerating cavity cells (C, D: small arrowheads) and remains of overlying epithallial layer (B, C: large arrowheads) which degenerates as conceptacle develops. (C: LTB 14396; D: LTB 13055; E: LTB 14464). E. Mature tetrasporangial conceptacle in which the chamber floor is composed of primigenous cells (compare with Figs 6A–F, 7A–H). (LTB 14365).

Throughout the thallus, cells of adjacent filaments were interlinked by one or more contiguous secondary pit-connections (Fig. 54A). Adjunctive secondary pit-connections and cell fusions were not seen. Suneson (1943: 38, figs 30D,21), however, recorded cell fusions in conceptacle roofs of several specimens he identified as *L. litorale*; Chamberlain (1991) has examined Suneson's collections (housed at LD) and found *L. litorale* to be conspecific with *L. pustulatum* (as *Titanoderma*). Similarly, trichocytes have not been seen in specimens during the present study, but Chamberlain (1991) reports that occasional trichocytes occur in British collections.

Table 11 Earlier published records of *Lithophyllum pustulatum* and its synonyms from southern and southwestern Australia. Names used by authors are listed alphabetically by specific epithet and then by genus. Superscripts refer to notes at end of table. Except for Chamberlain (1991), records have not been verified through herbarium specimen studies. See distribution and ecography section for references citing Australia without specifying a particular region or locality.

Dermatolithon pustulatum
De Toni & Forti in *Mem. R. Ist. Veneto Sci.* 29(3): 60 (1923)[1] Lucas in *Trans. R. Soc. S. Aust.* 53: 53 (1929) (as *Dermalithon*)[2]. May in *Contr. NSW Natn. Herb.* 3(6): 355 (1965)[3].
Lithophyllum pustulatum
Campbell & Woelkerling in *Phycologia* 29: Table 1, figs 1, 4 (1990)[4]. Lemoine in *Rep. Dan. oceanogr. Exped. Mediterr.* 2(K1): 26 (1915)[5]. Levring in *Acta Horti gothoburg.* 16: 220 (1946)[6].
Melobesia pustulata
Harvey in J.D. Hooker, *Bot. Ant. Voy. III Fl. Tasm.* 2: 311 (1860)[7]. Reinbold in *Nuova Notarisia* 9: 54[8]. Reinbold in *Hedwigia* 38: 51 (1899)[9].
Titanoderma pustulatum var. confine
Chamberlain in *Bull. Br. Mus. Nat. Hist. (Bot. Ser.)* 20(2): 50 (1991)[10].
Titanoderma pustulatum var. *mecrocarpum*
Chamberlain in *Bull. Br. Mus. Nat. Hist. (Bot. Ser.)* 20(2): 33 (1991)[10].
Melobesia verrucata
Dickie in *J. Linn. Soc. Bot.* 15: 45 (1876)[11]. Harvey in J.D. Hooker, *Bot. Ant. Voyage III Fl. Tasm.* 2: 311 (1860)[12].

Notes on Table 11

[1] Recorded from Gearldton, Western Australia as an epiphyte on the seagrass *Amphibolis* (as *Cymodocea*).

[2] Said to occur in Investigator Strait and the eastern bays of South Australia but not subsequently included in a flora of the region (Lucas & Perrin 1947).

[3] Said to occur on all Australian coasts and Norfolk Island but specific localities not cited.

[4] Lists collections from South Australia and Tasmania and illustrates vegetative thalli.

[5] Said to occur on the south and east coasts but explicit localities not given.

[6] Said to occur on *Amphibolis* (as *Cymodocea*) at Flinders, South Australia (Flinders is in Victoria). A search of Levring's collections at the University of Göteborg in October 1988 by WJW failed to locate any material.

[7] Infers occurrence in Tasmania, but subsequently (Harvey 1863, p.xxx) records species only from Norfolk Island.

[8] Said to occur in Lacepede and Guichen Bays South Australia.

[9] Said to occur in Investigator Strait, South Australia.

[10] Record based on the examination of light microscope sections of conceptacles of southern Australian specimens supplied by the present authors.

[11] Said to occur in Tasmania.

[12] Infers occurrence in Tasmania, but subsequently (Harvey 1863, p.xxx) does not include this entity in his list of Australian algae.

Tetrasporangial/bisporangial conceptacle development involves groups of sterile filaments interspersed amongst sporangial initials (Figs 55B–55D). Very early stages of development occur beneath an uplifted dome of epithallial cells (Fig. 55B) which becomes detached from the thallus during conceptacle primordium formation (not seen). This epithallial dome eventually degenerates and disappears (Figs 55C–55E).

Three distinct groups of cells/filaments may be involved in conceptacle development. The first is a central group of sterile cells situated beneath what will become the pore canal and pore (Figs 55B, 55C). These cells eventually become more or less elongate, undergo senescence to varying degrees and collectively form a central columella (Figs 55D, 55E, 56A). A columella is not always evident, and in some mature conceptacles (e.g. Figs 57B–57D, 57H) sporangia occur centrally. This suggests that either a columella never developed or that it has disintegrated totally. Chamberlain (1991) reported that a columella occurred in most British specimens of *Lithophyllum pustulatum* (as *Titanoderma*).

The two other groups of cells/filaments involved in conceptacle development occur intermixed and originate directly from cells on the conceptacle floor. One group, the sporangial initials (Figs 55B–55D), eventually divide, and each initial gives rise to a stalk cell and a sporocyte which subsequently matures into a bisporangium or tetrasporangium (Fig. 55E). The other group of cells is sterile and collectively gives rise to the conceptacle roof (Figs 55B–55D). The lowermost cells filaments become markedly elongate to form cavity cells (Figs 55C. 55D) which eventually senesce and degenerate thereby resulting in formation of a conceptacle chamber. Scattered cavity cells may or may not persist in more mature conceptacles. During conceptacle development, vegetative cells/filaments surrounding conceptacles show little or usually no growth. As a consequence, the conceptacle chamber floor becomes situated 1–3(–5) cell layers below the surrounding thallus surface.

Intact portions of filaments above the chamber collectively form a roof of characteristic but nevertheless varying structure (Figs 55E, 56, 57). The pore canal is never completely occluded (filled) by enlarged cells such as those found in *Lithophyllum chamberlainianum* (Figs 18C, 18D), *L. irvineanum* (Figs 35A, 35B) or *L. johansenii* (Figs 39C, 39D). Care must be taken, however, not to wrongly interpret sections cut near the periphery of the pore canal (e.g. Fig 57E) as showing occluded pore canals. Occasionally, a mucilaginous plug can cover the pore (Figs 55A, 55E, 56D, 56E, 57A, 57D).

Variation in roof structure occurs principally in the number of intact cells present in filaments above the chamber, in whether subepithallial cells are elongate or not, and in the morphology and orientation of cells lining the pore canal. The number of intact cells in roof filaments above the chamber is mostly three (rarely two or four) in some conceptacles (e.g. Figs 55E, 56) but commonly four to seven in other conceptacles (e.g. Figs 57B–57H). Very small epithallial cells always terminate roof filaments except for those associated with the pore canal. Subepithallial cells all may be comparatively elongate (e.g. Figs 55E, 56A–56C) or comparatively short (e.g. Figs 56F, 57D, 57H), or there may be a mixture of comparatively elongate and comparatively short cells (e.g. Figs 56E, 57B, 57C). Similarly, cells terminating filaments which immediately flank the pore canal may be narrow-elongate (e.g. Fig 55E), or more or less wedge-shaped (e.g. Fig 56B), or more or less club-shaped (e.g. Fig 56D). The canal can also vary, looking like a truncate cone in some conceptacles (e.g. Fig. 56A) or appearing more or less cylindrical in others (e.g. Fig. 57H). A continuum of variation occurs across the range of all the above attributes. While it is possible to clearly see particular differences when comparing isolated conceptacles (e.g. compare Figs 55E, 56F and 57H), it is not possible meaningfully to superimpose a formal taxonomic framework on this variation because many specimens could not be readily assigned to any one of a series of the infraspecific taxa which might be recognized.

Roof filaments flanking the chamber remain completely intact; each consists of a terminal epithallial cell and two or three (rarely four) subtending cells which in most conceptacles are more or less elongate (Figs 55E, 56, 57). The chamber floor may be composed of postigenous cells (e.g.

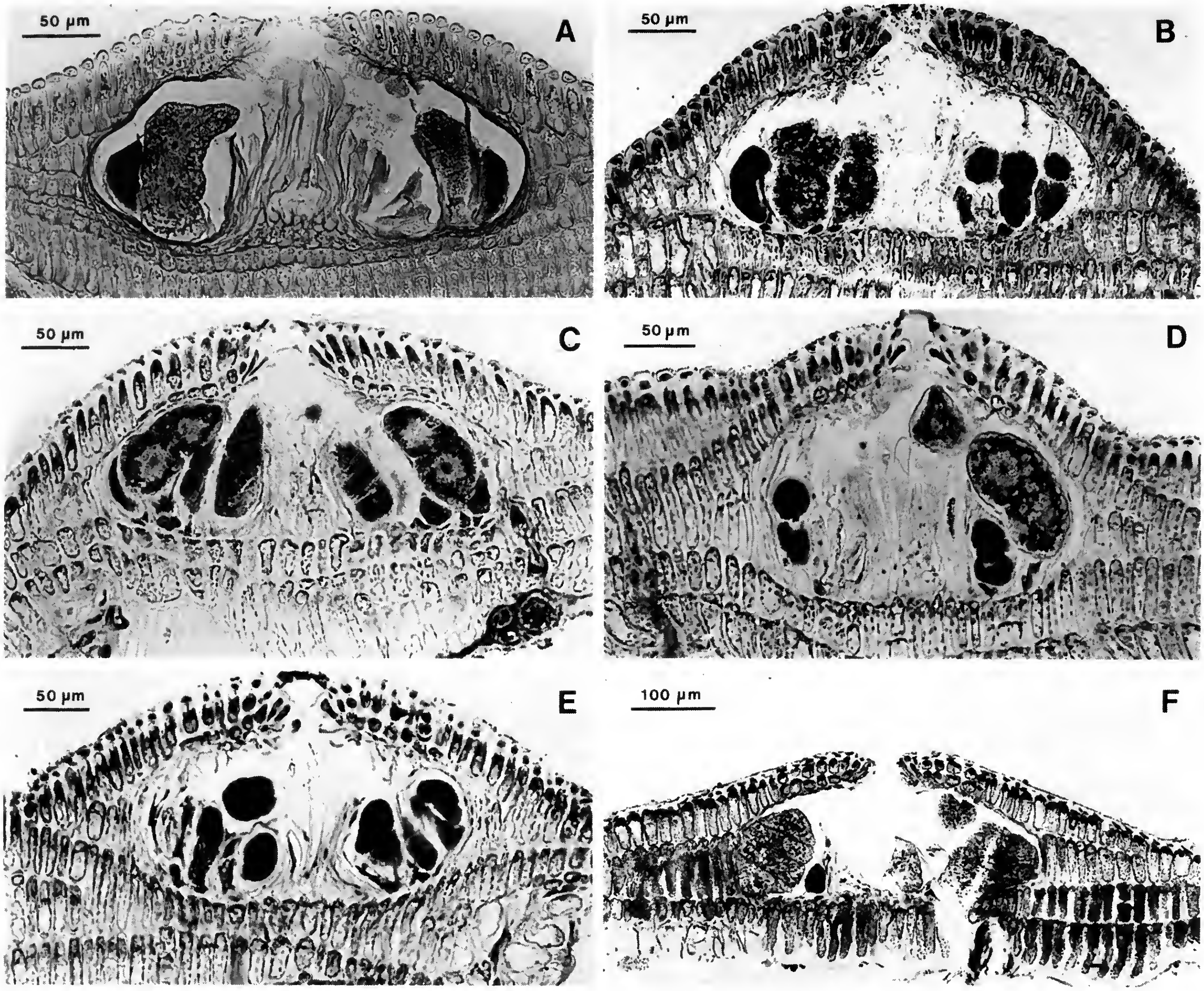


Fig. 56 *Lithophyllum pustulatum*: tetrasporangial/bisporangial conceptacles. A–F. Anatomical variation in tetrasporangial/bisporangial conceptacles in which roof filaments above chamber contain 2–3(–4– intact cells. See text for details. (A: LTB 11670; B: LTB 14396; C: LTB 13054; D: LTB 14398; E: 13055; F: 12473).

Figs 57C, 57G) or occasionally of primigenous cells (e.g. Fig. 55E). Where conceptacles overlay postigenous cells, roof filaments flanking the chamber constitute continuations of vegetative filaments. Tetrasporangia/bisporangia may arise from any part of the conceptacle chamber floor (e.g. Figs 57B, 57D) or may be peripheral to a columella (e.g. Figs 57F, 57G). Subtending stalk cells may or may not be evident, and both mature and immature sporangia may be present (e.g. Fig. 57E). Individual sporangia also can vary considerably in size within a conceptacle (e.g. Fig. 57G), a phenomenon also occurring in some British specimens of *L. pustulatum* (Chamberlain, 1991) and in southern Australian plants of *L. bermudense* (q.v.). In thalli with considerable postigenous development, older conceptacles commonly become buried as a result of renewed growth of roof filaments above the chamber and of surrounding vegetative filaments (Figs 58B, 58C). Infilling of buried conceptacle chambers (see Chamberlain, 1991) was not seen, however. In one collection (LTB 14396; Fig. 57A), trisporangia as well as tetrasporangia developed within a single conceptacle.

Only mature male conceptacles (Fig. 59) have been seen. The roof consists of a group of peripheral filaments which arch over and enclose a central fertile region on the conceptacle chamber floor. Each filament above the chamber is branched and consists of a main axis bordering the chamber and one to three-celled branches which arise secundly and collectively help form the roof (Figs 59A, 59B). Branches ending at the pore canal terminate in cells which differ in size and shape from other roof cells and may protrude somewhat into the canal. Remaining branches terminate in epithallial cells at the roof surface. Conceptacle roofs may appear more cone-like (Fig. 59A) or dome-like (Fig 59B), depending on the extent of roof filament branching and on whether cells are shorter or more elongate. At the extreme periphery of the conceptacle, roof filaments may remain unbranched and consist only of a terminal epithallial cell and a subterminal more or less elongate cell. Spermatangial branches form across the entire floor of the conceptacle chamber; these are

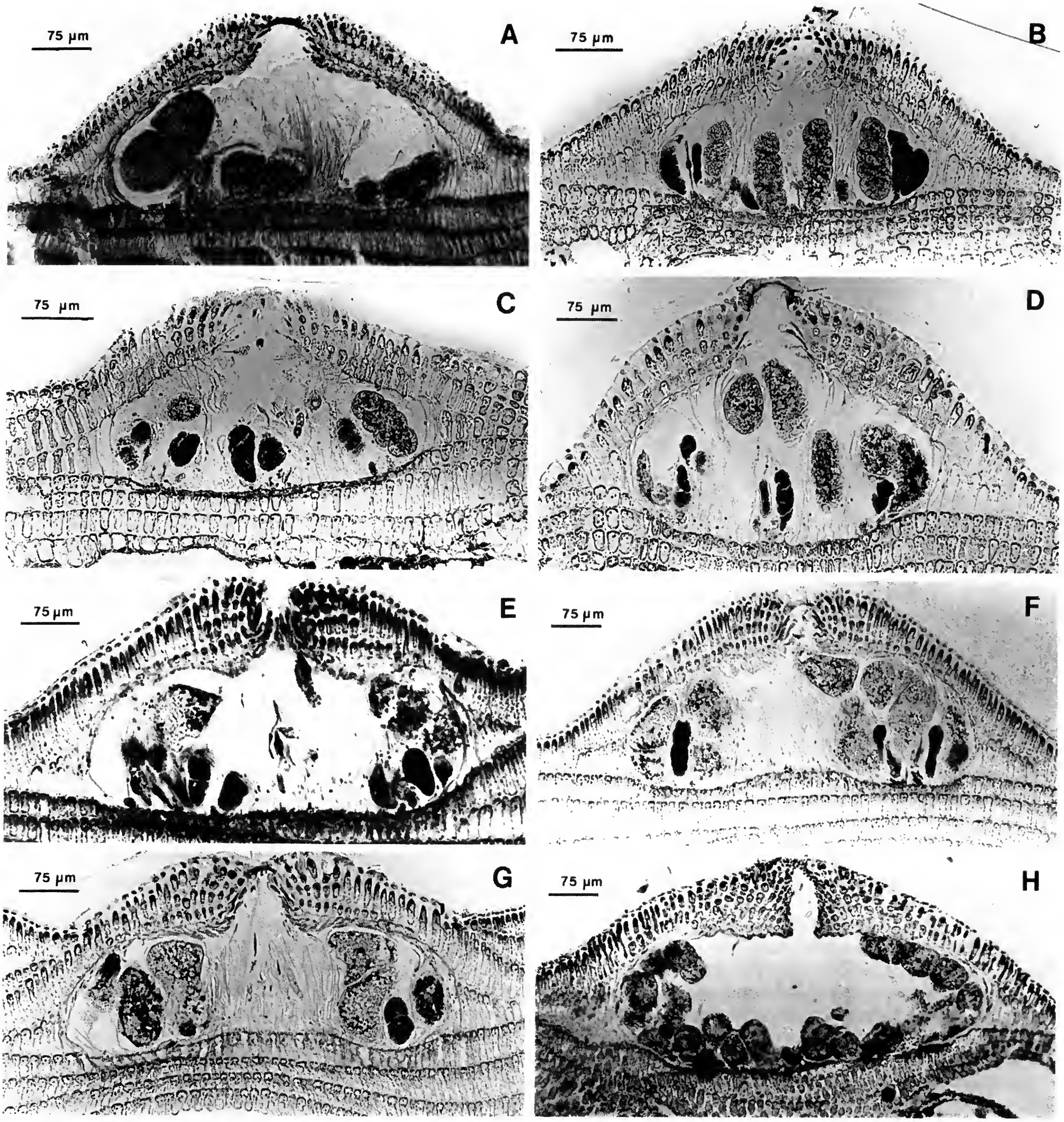


Fig. 57 *Lithophyllum pustulatum*: tetrasporangial/bisporangial conceptacles. A–H. Anatomical variation in tetrasporangial/bisoporangial conceptacles in which roof filaments above chamber contain up to 7 intact cells. See text for details. (A: LTB 14361; B: LTB 14396; C: LTB 14396; D: LTB 14390; E: LTB 14581; F: LTB 14581; G: LTB 14581; H: LTB 12487).

simple and each bears one or several elongate spermatangia (Figs 59A, 59B).

Only several stages of female/carposporangial conceptacles have been found (Fig. 60). Carpogonial branches arise across the entire chamber floor, but only those beneath the developing pore canal reach full maturity with a terminal carpogonium with an elongate trichogyne (Fig. 60A). A second undeveloped carpogonium occasionally occurs on the same branch as a more mature one.

Roofs of female/carposporangial conceptacles appear not to reach full maturity until after karyogamy. Filaments surrounding the pore canal contain cells differing in size and/or shape from those of other roof filaments. Remaining roof filaments above the chamber terminate in an epithallial cell

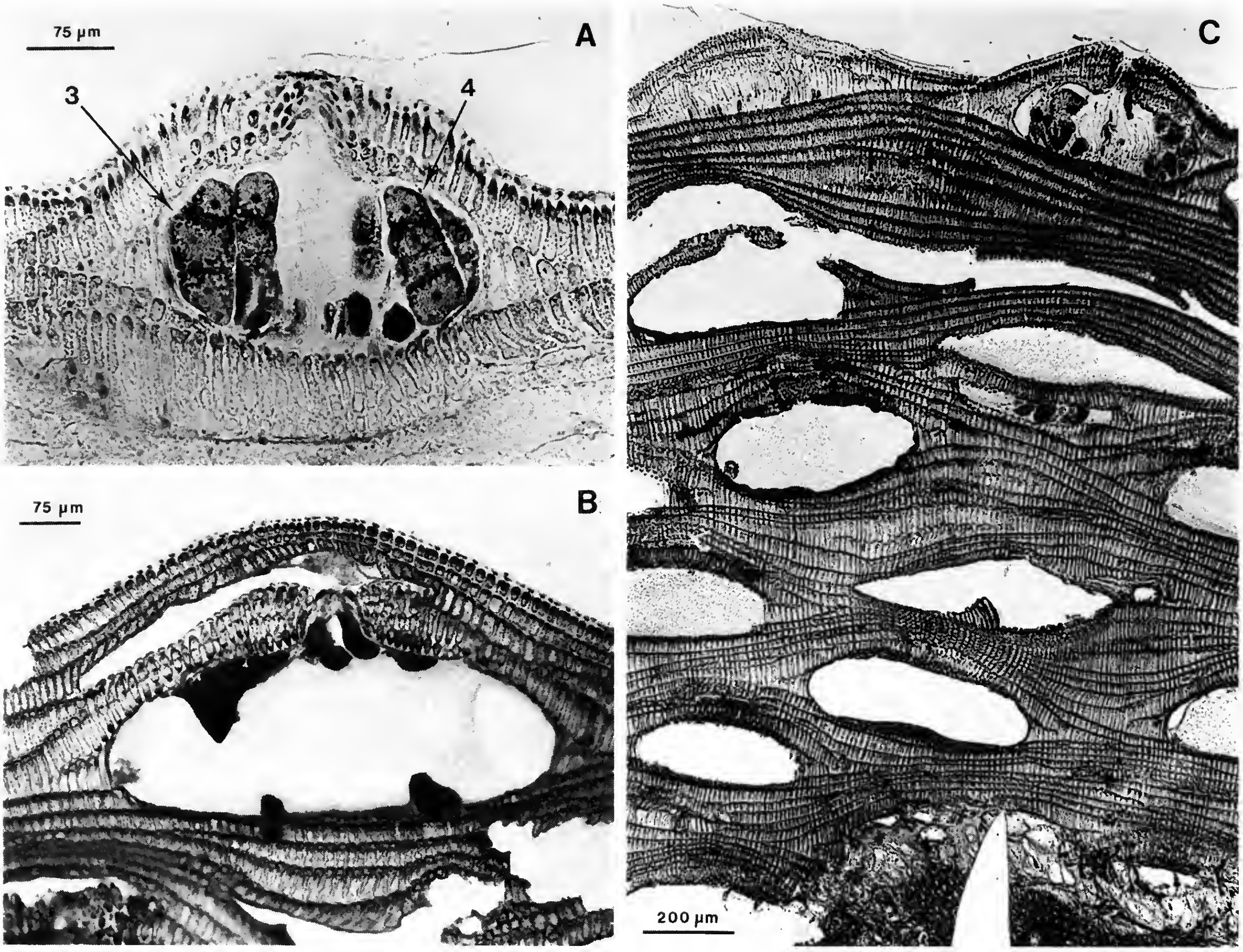


Fig. 58 *Lithophyllum pustulatum*: sporangial conceptacles. A. Conceptacle containing both trisporangia (3-arrow) and tetrasporangia (4-arrow). (LTB 14396). B. Older tetrasporangial/bisporangial conceptacle becoming buried in thallus by continued growth of surrounding vegetative filaments and renewed growth of some roof filaments. (LTB 14581). C. Section of more robust thallus containing numerous buried tetrasporangial/bisporangial conceptacles. (LTB 14581).

and contain one to three subtending intact cells which may or may not be comparatively elongate. Cavity cells similar to those found in tetrasporangial/bisporangial conceptacles undergo varying degrees of senescence and degeneration, resulting in the enlargement of the conceptacle chamber (Fig 60C).

Carposporophytes arise within female/carposporangial conceptacles after presumed karyogamy (Figs 60B, 60C). A fusion cell forms across the chamber floor and is anchored by the lowermost cells of the old carpogonial branches which appear to have become more elongate. Remains of the distal portion of carpogonial branches persist on the dorsal surface of the fusion cell. Eventually gonimoblast filaments up to six cells long develop around the periphery of the fusion cell, and each produces a terminal carposporangium (Fig. 60C).

Spore germination and very early thallus development have not been observed.

A selection of published accounts of plants referred to *L. pustulatum* or its synonyms from outside Australian waters and containing descriptions or detailed morphological/anatomical accounts is provided in Table 12 together with relevant notes. The most detailed recent accounts are those of Chamberlain (1986, 1991), Woelkerling (1986) and Woelkerling et al. (1985). The identifications of specimens used for most studies listed in Table 12 have not been verified.

The relationships of *L. pustulatum* to other species are considered below (p.97).

INFRASPECIFIC TAXONOMY. The matters of whether and which infraspecific taxa of *Lithophyllum pustulatum* merit recognition need to be considered in the context of an analysis of already established names for such entities. At least 51 infraspecific names (Table 13) are directly or indirectly associated with *L. pustulatum*. Thirty-nine of these pertain to forms, eleven pertain to varieties, and one pertains to an infraspecific entity of unspecified rank. In Table 13, the names have been arranged in 10 groups to provide a logical framework for comment.

All nine names comprising groups A and B in Table 13 are typified by the lectotype specimen which also typifies *Melobesia pustulata* Lamouroux (see Woelkerling et al., 1985: 325–327, figs 29–39 for an account of this specimen). The

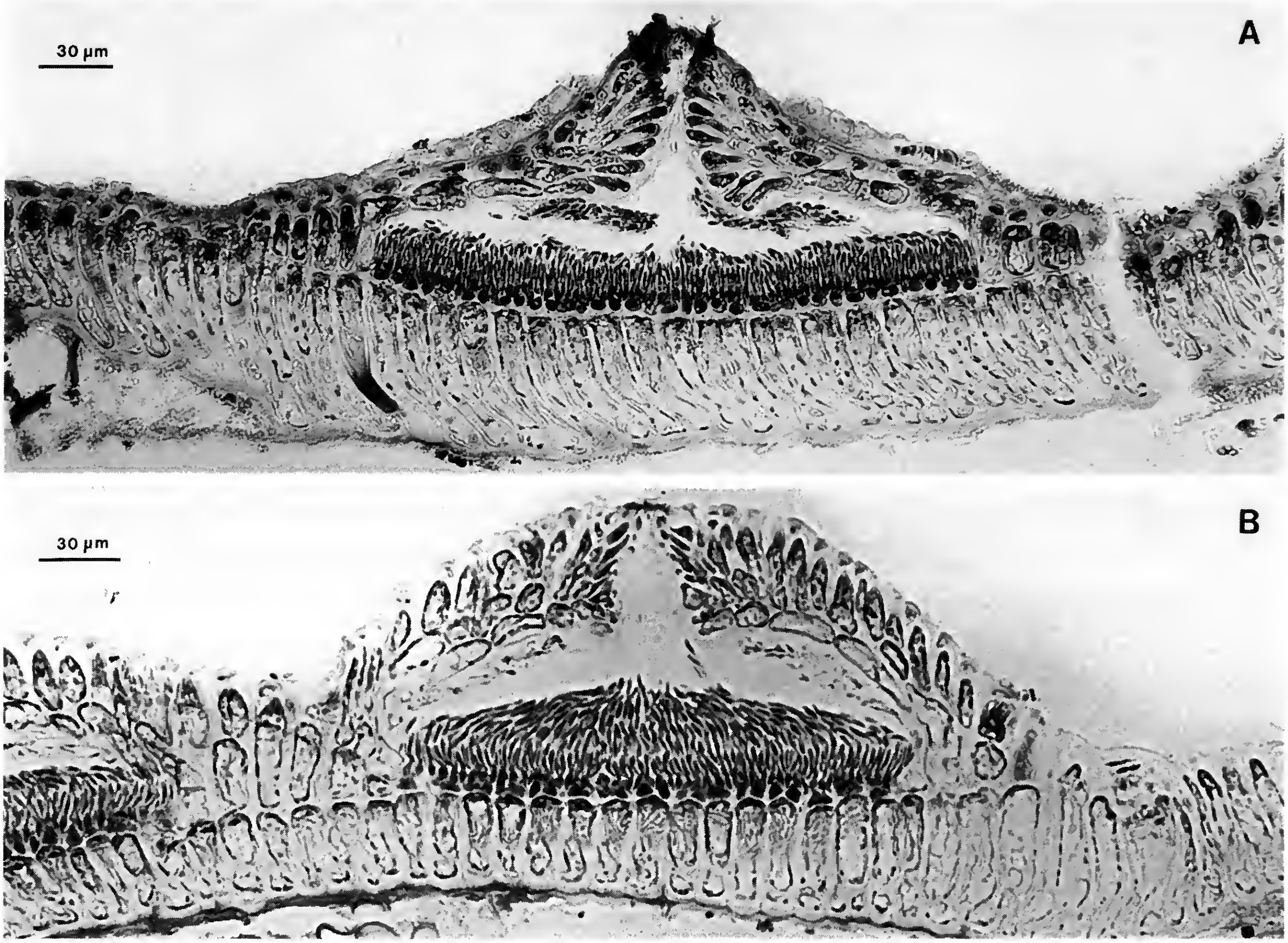


Fig. 59 *Lithophyllum pustulatum*: male conceptacles. A, B. Mature male conceptacles from two collections showing variation in roof structure. (See text for details). (A: LTB 15596; B: LTB 12667).

placement of Lamouroux's species in *Lithophyllum*, as is done in the present account, means that of names 1–9, only 2 and/or 3 are in full accord with the Rules of the International Code of Botanical Nomenclature (see Greuter, 1988) and are thus available for use if forms and/or varieties of *L. pustulatum* are to be recognized.

The thirteen names in group C of Table 13 involve six different entities. Chamberlain (1991) concluded that the type specimens of f. *ascripticium* (names 11,12), S *canellata* (name 14) and f. *intermedium* (names 17–19) are conspecific with the type specimen of *Lithophyllum pustulatum* (as *Titanoderma*). She (op. cit.) also concluded that the first and third names are heterotypic synonyms of other infraspecific taxa of *L. pustulatum*. In contrast, the type specimens of f. *australis* (names 12,13), f. *crinita* (names 15,16) and f. *similis* (names 20,21) have not been re-examined in a contemporary context, and thus the relationships between them and *L. pustulatum* are uncertain.

The five specimens which respectively typify the four names in group D, the seven names in group E, the seven names in group F, the two names in group G and the one name in group H in Table 13 have been examined by Chamberlain (1986, 1991) who concluded that all are conspecific with the type specimen of *L. pustulatum*.

Chamberlain (1991) also examined the type specimens of *Melobesia corallinae* and *M. laminariae* upon which names 44–46 (Group I) and names 47–51 (Group J) in Table 13 are based and concluded that they represent species of *Lithophyllum* (as *Titanoderma*) which are distinct both from *L. pustulatum* and from one another. Her conclusion regarding the type specimen of *Melobesia corallinae* has been confirmed during the present study (see account of *Lithophyllum corallinae* above). The type of *Melobesia laminariae*, however, has not been examined .

To summarize the above, 37 of the 51 names listed in Table 13 (i.e. names 1–11, 14, 17–19, 22–43) are typified by specimens which are considered conspecific with the specimen which lectotypifies *Lithophyllum pustulatum*. Of the remainder, eight (i.e. names 44–51) are typified by specimens which belong to *Lithophyllum* but which are not conspecific with the specimen which lectotypifies *L. pustulatum,* and six (i.e. names 12,13,15,16, 20, 21) are typified by specimens which have not been re-examined in the current context and thus are of uncertain status.

The only contemporary assessment of infraspecific delimitation within *Lithophyllum pustulatum* is that of Chamberlain (1991) which is based on studies of British specimens and a number of relevant type collections. Using the generic name

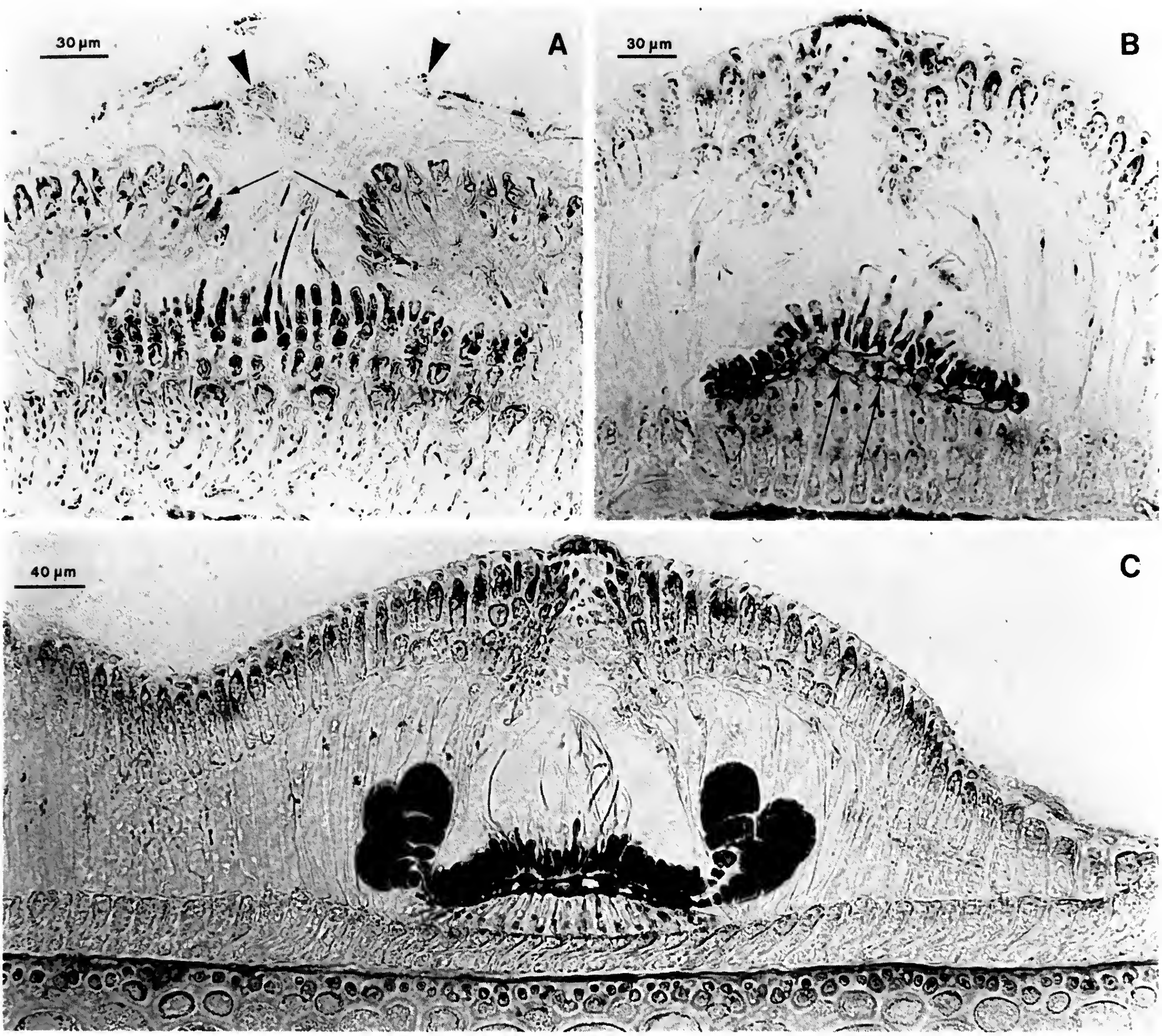


Fig. 60 *Lithophyllum pustulatum*: female/carposporangial conceptacles. A. Developing female/carposporangial conceptacle with nearly mature carpogonial branches. Note several elongate trichogynes, surrounding roof filaments (arrows) which are not as yet fully developed and remains of degenerating vegetative epithallial cells (arrowheads) above developing roof. (LTB 14365). B. Fusion cell (arrows) prior to gonimoblast filament formation. Note elongate supporting cells beneath fusion cell. (LTB 14365). C. Mature carposporophyte with fusion cell and gonimoblast filaments bearing terminal carposporangia. Note remains of old carpogonial branches on dorsal surface of fusion cell. (LTB 14365).

Titanoderma, Chamberlain (1991) recognized four varieties:

1. *T. pustulatum* var. *pustulatum* [with f. *faeroënsis* (see names 40, 41 in Table 13) listed as a heterotypic synonym];
2. *T. pustulatum* var. *confine* [with f. *ascripticium* (see names 10,11 in Table 13) and f. *intermedium* (see names 17–19 in Table 13) listed as heterotypic synonyms];
3. *T. pustulatum* var. *macrocarpum* [with *Melobesia hapalidioides, Melobesia simulans* and *Lithothamnion adplicitum* listed as heterotypic synonyms];
4. *T. pustulatum* var. *canellatum.*

Chamberlain (1991: Table 1) also summarized comparatively the characteristics of the four varieties and provided a key for identification. Moreover, var. *confine* and var. *macrocarpum* were said to occur in southern Australia on the basis of an examination of sections of conceptacles of certain collections supplied by the present authors.

While Chamberlain (1991) has found it possible to recognize four varieties amongst British collections of *Lithophyllum pustulatum* on the bases of external, anatomical and ecological parameters, the variability present amongst southern Australian plants is such that it has not been possible to identify clear-cut focal points with which all specimens could be readily associated in a formal taxonomic framework. While some specimens could be referred to one of the varieties recognized by Chamberlain (1991), many were intermediate, and as a result, it seemed neither desirable nor

Table 12 A selection of published records involving the name *Lithophyllum pustulatum* or its synonyms from outside Australia which include descriptions or morphological/anatomical accounts. Names of taxa are listed alphabetically by specific epithet. Localities are given in parentheses; superscripts refer to notes at end of table. Unless otherwise indicated, records have not been verified during the present study. Australian records are given in Table 11.

Titanoderma caspica
Woelkerling in *Phycologia* 25: 253 et seq., figs 1–12 (1990) (Caspian Sea)[1,2,8].

Tenarea confinis
Adey & Adey in *Br. phycol. J.* 8: 393 (1973) (British Isles)[3,4].

Dermatolithon hapalidioides
Bressan in *Boll. Soc. Adriat. Sci. nat.* 59: 97, fig. 39 (1974) (Italy)[5]. Hamel & Lemoine in *Archs Mus. Hist. nat. Paris*, ser.7, 1: 61, text fig. 23, pl. 8, fig. 7 (1953) (Algeria, France, Morocco)[3]. Newton, *Handbook Br. Seaweeds*: 306 (1931) (British Isles)[3].

Tenarea hapalidioides
Adey & Adey in *Br. phycol. J.* 8: 394 (1973) (British Isles)[3,4].

Dermatolithon litorale
Chamberlain in *Phycologia* 17: 396 et seq., figs 1–8 (British Isles)[2,4]. Hamel & Lemoine in *Archs Mus. Hist. nat. Paris*, ser. 7, 1: 66, text figs 28,29, pl. 9, fig. 3 (1953) (France)[3]. Suneson in *Br. phycol. J.* 17: 107 et seq., figs 1–15 (1982) (Sweden)[2,6].

Lithophyllum litorale
Suneson in *Acta Univ. lund.* N.F. Avd 2, 39(9): 36, text figs 20,21, pl. 6, fig. 25, pl. 8, fig. 39 (1943) (Sweden)[2].

Lithophyllum macrocarpum
Rosenvinge in *K. danske Vidensk. Selsk. Skr.*, Ser. 7 (Natur Math. Afd) 7: 263, figs 184,185 (1917) (Denmark)[2].

Melobesia macrocarpa
Rosanoff in *Mem. Soc. Imp. Sc. Nat. Math. Cherbourg* 12: 74, pl. 4, figs 2–8, 11–20 (1866) (France)[7].

Titanoderma macrocarpum
Chamberlain in *Cryptogamie algol.* 7: 203, figs 12–22. (1986)[2,8].

Dermatolithon pustulatum
Bauch in *Planta* 26: 379, fig. 8 (1937)[9]. Bressan in *Boll. Soc. Adriat. Sci. nat.* 59: 98, fig. 38 (1974) (Italy)[5]. Hamel & Lemoine in *Archs Mus. Hist. nat. Paris,* Ser. 7, 1: 59, text fig. 22, pl. 9, figs 1,2 (1953) (Algeria, France, Morocco, Mediterranean Islands)[3,10]. Kornmann & Sahling in *Helgolander wiss Meeresunters.* 29: 206, pl. 115 (Federal Republic of Germany).[3]. Pham-Hoang Ho, *Mar. Algae S. Vietnam*: 152, fig. 2.82 (1969) (Vietnam)[3]. Zinova, *Red Brown Green Algal Fl. Stn Seas USSR*: 228 (1967) (USSR—southern seas)[3].

Lithophyllum pustulatum
Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 117 (1905a)[2,14]. Newton, *Handbook Br. Seaweeds*: 305, figs 188A–C (1931) (British Isles)[3,11]. Suneson in *Acta Univ. lund.* N.F. Avd. 2, 39(9): 39, text figs 22,23, pl. 6, figs 26,27 (1943) (Sweden)[2]. Taylor, *Mar. Algae Neastn Coast N. Am.*: 251 (1957) (Atlantic USA)[3]. Taylor, *Mar. Algae Eastn Trop. Subtrop. Coasts Am.*: 392 (1960) (Tropical Atlantic North and South America)[3].

Melobesia pustulata
Hauck, *Meeresalgen Dt. Öster.*: 265, fig. 109 (1883) (North Sea and Adriatic Sea)[3]. Rosanoff in *Mem. Soc. Imp. Sc. Nat. Math. Cherbourg* 12: 72, pl. 4, figs 2–8 (1866)[2,12].

Titanoderma pustulatum
Chamberlain in *Bull. Br. Mus. Nat. Hist. (Bot. Ser.)* 20(2): (1991) (British Isles)[2,4,13]. Woelkerling et al. in *Phycologia* 24: 329, figs 29–39 (1985)[2,8].

Titanoderma verrucatum
Chamberlain in *Cryptogamie algol.* 7: 197, figs 4–11 (1986)[2,8].

Notes on Table 12

[1] See section on nomenclature and synonymy regarding the conspecificity of this entity and *Lithophyllum pustulatum*.

[2] Contains a detailed morphological/anatomical account.

[3] Includes a description

[4] Includes ecographic data.

Table 12 *cont*

[5] Provides morphological/anatomical data in point-form.

[6] Includes life history data based on culture studies.

[7] Protologue.

[8] Publication focuses on study of type collection.

[9] Provides data on bispores from culture studies.

[10] Includes delimitation of forms *laminariae, macrocarpa, similis.*

[11] Includes recognition of vars. *corallinae* and *laminariae.*

[12] Distribution listed as Mediterranean and Atlantic Europe, New Caledonia, the Antilles, Australia.

[13] Separate accounts are presented for each of the four recognized varieties: *confinis, macrocarpum, pustulatum, verrucatum.*

[14] Including forms *australis, corallinae, intermedia, laminariae, macrocarpa*. See also Foslie 1909: 46 where f. *ascripticia* and f. *similis* are recognized.

Table 13 Infraspecific names associated directly or indirectly with *Lithophyllum pustulatum* and its heterotypic synonyms. Names are grouped in relation to basionyms from which they are derived. Listing within groups is alphabetical; names are numbered to facilitate cross-referencing to text.

A. Automatically established autonyms (ICBN Art 26.2) derived from *Melobesia pustulata* Lamouroux and its homotypic synonyms. Autonyms are cited without authorities (Art. 26.1); dates of establishment are given in parentheses as determined form Art 32.6.

1. *Dermatolithon pustulatum* f. *pustulatum*. Established without explicit mention by Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(3): 11 (1898b) in conjunction with several other forms.
2. *Lithophyllum pustulatum* f. *pustulatum*. Established without explicit mention by Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 117 (1905a) in conjunction with several other forms.
3. *Lithophyllum pustulatum* var. *pustulatum*. Established without explicit mention by Lemoine in *Nouv. Archs Mus. Hist. Nat. Paris* Ser. 5, 5: 138 (1913b) in conjunction with several other varieties.
4. *Melobesia pustulata* f. *pustulata*. Established without explicit mention by Möbius in *Notarisia* 7: 1441 (1892) in conjunction with several other forms.
5. *Titanoderma pustulatum* var. *pustulatum*. Established explicitly by Chamberlain in *Bull. Br. Mus. Nat. Hist. Bot. Ser.* 21(1): 26 (1991).

B. Infraspecific taxa typified by the type of *Melobesia pustulata* which are invalid under ICBN Art 24.3 or illegitimate under Art. 63.1.

6. *Dermatolithon pustulatum* f. *bispora* Foslie in *K. norske Vidensk. Selsk. Skr. 1898(3): 11 (1898b). Superfluous for f. pustulatum* and thus illegitimate under Art. 63.1.
7. *Dermatolithon pustulatum* f. *typicum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1900(5): 21 (1900e). Invalid under Art 24.3.
8. *Lithophyllum pustulatum* f. *typicum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1909(2): 46 (1909). Invalid under Art. 24.3.
9. *Melobesia pustulata* f. *genuina* Möbius in *Notarisia* 7: 1441 (1892). Invalid under Art. 24.3.

C. Names linked to basionyms originally treated as infraspecific taxa of *Melobesia pustulata* and its derivatives. Infraspecific epithets listed alphabetically with basionym followed by any additional combinations.

10. *Lithophyllum pustulatum* f. *ascripticium* Foslie in *K. norske Vidensk. Selsk. Skr.* 1906(8): 34 (1907a).
11. *Dermatolithon pustulatum* f. *ascripticium* (Foslie) Foslie ex De Toni, *Sylloge Algarum* 6: 665 (1924).
12. *Lithophyllum pustulatum* f. *australis* Foslie in *K. norske Vidensk Selsk. Skr.* 1905(3): 117 (1905a).
13. *Dermatolithon pustulatum* f. *australis* (Foslie) Foslie ex De Toni, *Sylloge Algarum* 6: 665 (1924).
14. *Melobesia pustulata* β *canellata* Kützing, *Species Algarum*: 696 (1849).

Table 13 *cont.*

15. *Titanoderma pustulatum* var. *canellatum* (Kützing) Y. Chamberlain in *Bull. Br. Mus. nat. Hist. Bot. Ser.* 21(1): 61 (1991).
16. *Melobesia pustulata* f. *crinita* Möbius in *Notarisia* 7: 1441 (1892).
17. *Dermatolithon pustulatum* f. *crinita* (Möbius) Möbius ex Foslie in *K. norske Vidensk. Selsk. Skr.* 1900(5): 21 (1900e).
18. *Lithophyllum pustulatum* f. *intermedium* Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 117 (1905a).
19. *Dermatolithon macrocarpum* f. *intermedium* (Foslie) Foslie ex De Toni, *Sylloge Algarum* 6: 666 (1924).
20. *Lithophyllum macrocarpum* f. *intermedium* (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905a).
21. *Lithophyllum pustulatum* f. *similis* Foslie in *K. norske Vidensk. Selsk. Skr.* 1909(2): 47 (1909).
22. *Dermatolithon pustulatum* f. *similis* (Foslie) Foslie ex Hamel & Lemoine in *Archs Mus. Hist. Nat. Paris Ser.* 7, 1: 60 (1953).

D. Names of infraspecific taxa typified by the type of *Melobesia confinis* P. & H. Crouan (1867: 150). *M. confinis* is a heterotypic synonym of *M. pustulata* (see section on nomenclature and synonymy).

23. *Dermatolithon hapalidioides* f. *confinis* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 12 (1900b).
24. *Lithophyllum hapalidioides* f. *confinis* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905a).
25. *Lithophyllum hapalidioides* var. *confinis* (P. & H. Crouan) Lemoine in *Nouv. Archs Mus. Hist. Nat. Paris* Ser 5, 5:136 (1913b).
26. *Titanoderma pustulatum* var. *confine* (P. & H. Crouan) Chamberlain in *Bull. Br. Mus. nat. Hist. (Bot. Ser.)* 21(1): 50 (1991).

E. Names of infraspecific taxa typified by the type of *Melobesia hapalidioides* P. & H. Crouan (1867: 150). *M. hapalidioides* is a heterotypic synonym of *M. pustulata* (see section on nomenclature and synonymy).

27. *Dermatolithon hapalidioides* f. *hapalidioides*. An autonym automatically established (but without mention) by Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 12 (1900b) in conjunction with another form (No. 22 above).
28. *Dermatolithon hapalidioides* f. *typicum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 12 (1900b). Invalid under ICBN Art. 24.3.
29. *Lithophyllum hapalidioides f. hapalidioides. An autonym automatically established (but without mention) by Foslie in K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905a) in conjunction with another form (No. 23 above).
30. *Lithophyllum hapalidioides* var. *hapalidioides*. An autonym automatically established (but without mention) by Lemoine in *Nouv. Archs Mus. Hist. Nat. Paris,* Ser. 5, 5: 136 (1913b) in conjunction with another variety (No. 24 above).
31. *Lithophyllum hapalidioides* f. *typicum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905a). Invalid under ICBN Art. 24.3
32. *Melobesia hapalidioides* f. *hapalidioides*. An autonym automatically established (but without mention) by Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 10 (1900b) in conjunction with another form (No. 32 below).
33. *Melobesia hapalidioides* f. *typica* Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 10 (1900b). Invalid under ICBN Art. 24.3.

F. Names of infraspecific taxa typified by the type of *Melobesia macrocarpa* Rosanoff (1866: 74). *M. macrocarpa* is a heterotypic synonym of *M. pustulata* (see section on nomenclature and synonymy).

34. *Dermatolithon macrocarpum* f. *macrocarpum*. An autonym automatically established (but without mention) by Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 15 (1900b) in conjunction with another form (No. 40 below).
35. *Lithophyllum macrocarpum* f. *macrocarpum*. An autonym automatically established (but without mention) by Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905a) in conjunction with several other forms.

Table 13 *cont.*

36. *Lithophyllum macrocarpum* f. *typica* Foslie in *K. norske Vidensk. Selsk. Skr.* 1909(2): 47 (1909). Invalid under ICBN Art. 24.3.
37. *Dermatolithon pustulatum* f. *macrocarpum* (Rosanoff) Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(3): 11 (1898b).
38. *Lithophyllum pustulatum* f. *macrocarpum* (Rosanoff) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 117 (1905a).
39. *Lithophyllum pustulatum* var. *macrocarpum* (Rosanoff) Lemoine in *Nouv. Archs Mus. Hist. Nat. Paris,* Ser 5, 5: 142 (1913b).
40. *Titanoderma pustulatum* var. *macrocarpum* (Rosanoff) Chamberlain in *Bull. Br. Mus. nat. Hist. (Bot. Ser.)* 21(1): 33 (1991).

G. Names linked to basionyms originally treated as infraspecific taxa of *Melobesia macrocarpa* and its derivatives.

41. *Dermatolithon macrocarpum* f. *faeroensis* Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(7): 15 (1900b).
42. *Lithophyllum macrocarpum* f. *faeroensis* (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905a).

H. Names of infraspecific taxa typified by the type of *Melobesia verrucata* Lamouroux (1816: 316). *M. verrucata* is a heterotypic *M. pustulata* (see section on nomenclature and synonymy).

43. *Melobesia verrucata* var. *verrucata*. An autonym automatically established (but without mention) by W.H. Harvey & J.D. Hooker in J.D. Hooker, *Bot. Ant. Voyage. I Fl. Ant.*: 482 (1847) in conjunction with *M. verrucata* var. *antarctica*. The latter is now regarded as a heterotypic synonym of *Synarthrophyton patena* (J.D. Hooker & W.H. Harvey) Townsend (see May & Woelkerling, 1988: 68).

I. Names of infraspecific taxa typified by the type of *Melobesia corallinae* P.& H. Crouan (1867: 370) but at some stage linked with *Melobesia pustulata* or its synonyms. See text for comments on status of *M. corallinae*.

44. *Lithophyllum macrocarpum* f. *corallinae* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1909(2): 47 (1909).
45. *Lithophyllum pustulatum* f. *corallinae* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 118 (1905a).
46. *Lithophyllum pustulatum* var. *corallinae* (P. & H. Crouan) Lemoine in *Nouv. Archs Mus. Hist. Nat. Paris* Ser 5, 5: 138 (1913b).

J. Names of infraspecific taxa typified by the type of *Melobesia laminariae* P. & H. Crouan (1867: 150) but at some stage linked with *Melobesia pustulata* or its synonyms. See text for comments on status of *M. laminariae*.

47. *Dermatolithon macrocarpum* f. *laminariae* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1900(5): 22 (1900e).
48. *Dermatolithon pustulatum* f. *laminariae* (P. & H. Crouan) Foslie ex Hamel & Lemoine in *Archs Mus. Hist. Nat. Paris* Ser 7, 1: 60 (1953).
49. *Lithophyllum macrocarpum* f. *laminariae* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 128 (1905a).
50. *Lithophyllum pustulatum* f. *laminariae* (P. & H. Crouan) Foslie in *K. norske Vidensk. Selsk. Skr.* 1905(3): 118 (1905a).
51. *Lithophyllum pustulatum* var. *laminariae* (P. & H. Crouan) Lemoine in *Nouv. Archs Hist. Nat. Paris*. Ser 5, 5: 138 (1913b).

---

advantageous to recognize varieties of *L. pustulatum* in southern Australia. Instead, the range in infraspecific variation has been recorded outside a formal taxonomic framework, an approach used successfully by Bosence (1983) for other species of nongeniculate corallines.

It is possible that varieties are more readily identifiable in British material because only bisporangial plants of *L. pustulatum* have been found there. This implies that reproduction in British populations is probably largely or entirely apomictic and (Chamberlain 1991:2) that a greater morphological/anatomical uniformity occurs within particular populations. By contrast, gametangial, tetrasporangial and bisporangial plants are all found in southern Australia. The occurrence of sexual reproduction could result in a more complete spectrum of expressed variation and consequently in greater difficulty in identifying clear-cut focal points for use in a formal taxonomic framework.

COLLECTIONS OF POSSIBLE ADDITIONAL SPECIES

Two collections contained plants of *Lithophyllum* which could not readily be assigned to a species. Whether these plants represent extreme variants of one of the other seven species or are distinct species could not be determined from material presently available. Inclusion of brief accounts of these collections seems justified not only to emphasize the occurrence of possible additional species of *Lithophyllum* in this region but also to record what appear to be distinct sorts of tetrasporangial/bisporangial conceptacle morphology/anatomy, thereby providing a more complete data base for future assessment.

1. LTB 12981. (Fig. 61).

COLLECTION DATA.

TASMANIA: Variety Bay, Bruny Island (*Platt*, *Woelkerling*, & *Brown*, 17 February 1983, LTB 12981).

COMMENTS. This collection contains a single stone obtained from a depth of 2–4m which is dominated by a crustose thallus of *Lithophyllum* 55 mm in greatest breadth. The thallus is flat (complanate) to slightly bumpy but lacks applanate or protuberant branches. Thallus construction is dimerous (Fig. 61A), with a single layer of primigenous cells which are palisade. Postigenous filaments are mostly 10–20+ cells long and terminate at the thallus surface in epithallial cells.

Bisporangial conceptacles (Figs 61A, 61B) differed anatomically from other southern Australian species. Mature bisporangial conceptacles (Figs 61A, 61B) are more or less flush with the thallus surface, have chambers which are 240–270 μm in diameter and 93–112 μm tall, and have a chamber floor situated at least seven layers below the thallus surface. The external diameter of the roof is difficult to determine because marginal roof filaments are little more than extensions of ordinary vegetative filaments. Bisporangia are mostly 65–75 μm long and 28–42 μm in diameter and appear to occur peripheral to a small, central columella.

The conceptacle roof anatomy is quite distinct. The pore canal is occluded by a group of branched filaments which flank the canal and produce enlarged, clavate to elongate cells which do not protrude beyond the roof surface (Fig. 61B). Remaining filaments above the chamber mostly contain three to four intact cells including a terminal epithallial cell and two or three subtending cells which can vary in length but are usually more or less elongate. Roof filaments flanking the chamber look like ordinary vegetative filaments.

Three southern Australian species of *Lithophyllum* have tetrasporangial/bisporangial conceptacles with pore canals completely occluded by enlarged cells. *L. chamberlainianum* (Fig. 18D) and *L. irvineanum* (Fig. 35A) differ from the plant in LTB 12981 not only in pore canal anatomy, but also in having conceptacles in which the floors are only one or two cell layers below the thallus surface. In addition, neither *L. chamberlainianum* nor *L. irvineanum* produces multicellular postigenous filaments.

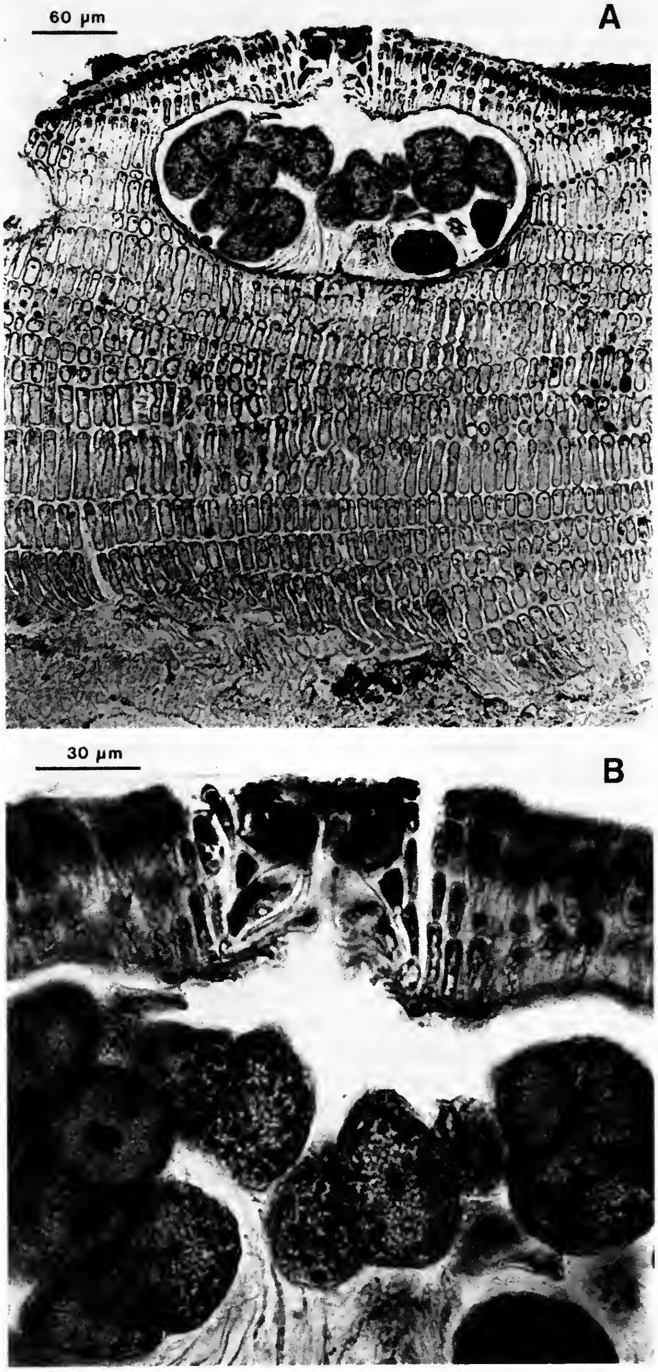


Fig. 61 *Lithophyllum* sp.: LTB 12981. A. Mature bisporangial conceptacle. B. Details of pore canal anatomy of bisporangial conceptacle. Note that canal is completely obstructed by enlarged cells.

The specimen in LTB 12981 most closely resembles *L.*

johansenii; both entities have multicellular postigenous development and conceptacles whose chamber floor are situated seven or more cells below the thallus surface. Conceptacle roof anatomy, however, differs in the two (compare Figs 39C & 39D with 61A & 61B), especially in the nature of the cells which obstruct the pore canal.

It is possible that the plant in LTB 12981 is a variant of *L. johansenii*, but no plants with conceptacle roofs intermediate between LTB 12981 and collections of *L. johansenii* have been found. It is also possible that LTB 12981 represents a distinct species (for which no name could be found in the existing literature). Pending the availability of new, additional collections, it seems best to treat LTB 12981 as an anomalous collection rather than arbitrarily assigning it to *L. johansenii* or describing it as a distinct species on the basis of a single collection.

2. LTB 15845. (Fig. 62)

COLLECTION DATA.

SOUTH AUSTRALIA: Beachport (Post Office Rock) (*Campbell & Penrose*, 24 February 1988, LTB 15845).

COMMENTS. The above material was collected on abalone shells obtained from a depth of about 1m and contains a mixture of nongeniculate corallines including at least one plant of *Lithophyllum* whose tetrasporangial conceptacles (Fig. 62A) differed from those of all other plants of *Lithophyllum* examined. These conceptacles occur on plants which are dimerous. Primigenous cells are distinctly palisade and postigenous development is limited to the production of epithallial cells.

Mature tetrasporangial conceptacles protrude above the thallus surface, have roofs which are 519–741 µm in external diameter, have chambers which are 195–442 µm across and 56–93 µm tall, contain tetrasporangia which are 65–85 µm long and 28–42 µm in diameter, and have a chamber floor composed of primigenous palisade cells. Tetrasporangia occur peripheral to a central more or less degenerate columella.

The conceptacle roof anatomy appears to be quite distinct (Fig. 62A). The pore canal, which is quite elongate, is not occluded by enlarged cells such as those in *L. chamberlainianum* (Fig. 18D) or in *L. irvineanum* (Fig. 35A). The roof above the chamber is composed of two distinct groups of filaments. One group occurs near the canal and contains branched filaments up to nine cells long. Those filaments reaching the roof surface terminate in epithallial cells while those lining the pore canal terminate in narrow, usually elongate cells which project slightly in an ascending manner into the canal. The other group of filaments, occurring over more peripheral parts of the chamber, is unbranched. Each consists of two intact cells: a terminal epithallial cell and a subtending columnar cell. Roof filaments flanking the chamber remain intact; each arises from a palisade primigenous cell and consists of a terminal epithallial cell and one or two subtending elongate cells.

It is possible that the plant represented in Fig. 62A is an extreme variant of *L. pustulatum*, but no intermediates between this variant and the many variants of *L. pustulatum* (see particularly Figs 57E, 57H) have been found. Moreover, material in Fig. 62A could not be matched with figures of any other described species of *Lithophyllum* (or *Dermatolithon* or *Titanoderma*, which are synonyms of *Lithophyllum*). Consequently it is equally possible that the plants represented by Fig. 62A are an undescribed species. Unfortunately, attempts to find additional individuals of this material in LTB 15845 have not been successful (although other nongeniculate corallines occur) thus its taxonomic status is best not formally assessed until additional material becomes available.

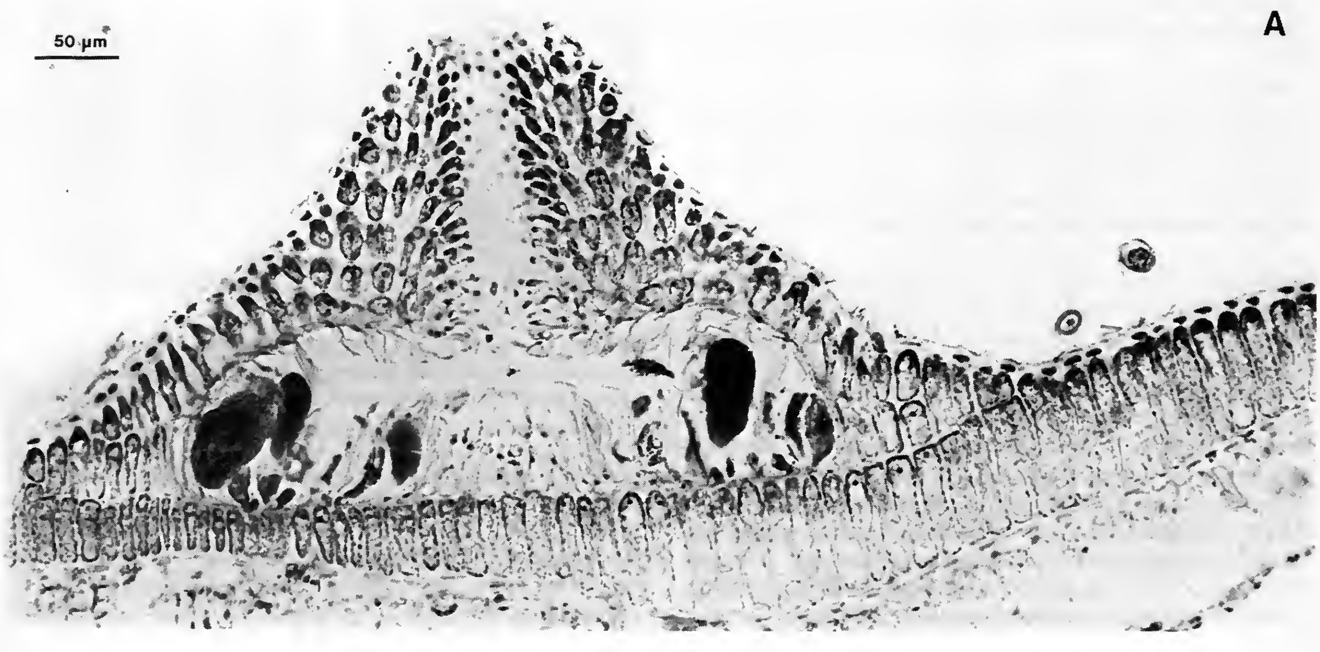


Fig. 62 *Lithophyllum* sp.: LTB 15845. A. Mature tetrasporangial conceptacle. See text for details.

INDETERMINATE COLLECTIONS

Of the 258 collections examined, 48 (or 18.6%) could be identified to genus but not to species. Generic identification was possible because *Lithophyllum* is the only genus in southern Australia in which thalli possess secondary pit-connections and lack cell fusions. Twelve of the 48 samples contained only male plants; the remainder contained sterile plants or plants whose conceptacles were in such poor condition that species placement could not be confidently effected.

SPECIES RELATIONSHIPS

The plethora of current problems surrounding species delimitation in *Lithophyllum* coupled with the absence of a world monograph (or a series of regional monographs) and the presence of numerous poorly and incompletely defined species from amongst the 650 + ascribed to the genus make it impossible to meaningfully consider phylogenetic relationships at present. The origin of *Lithophyllum* as a genus is obscure, and because complete, modern studies of vegetative and reproductive morphology/anatomy are available for so few species, few clues have emerged as to how and in which directions speciation may have proceeded. Until an adequate data base is available, only restricted phenetic comparisons can be made, and in the context of this study, these have been limited to those species dealt with in detail.

Basic similarities and differences amongst the seven southern Australain species are summarized in the tabular key, in Table 6 and in Table 7. In addition, features considered diagnostic are listed in each species account. An analysis of these data, taken together with the conclusion that characters associated with tetrasporangial/bisporangial conceptacles are significant in determining species limits, suggests that the seven species fall into two groups: one (containing *L. chamberlainianum, L. irvineanum* and *L. johansenii*) in which pore canals are completely occluded by enlarged cells; and a second (containing *L. bermudense, L. corallinae, L. prototypum* and *L. pustulatum*) in which pore canals are not completely occluded. Within each group, there are species in which the conceptacle chamber floor is 1–3(–5) cell layers below the thallus surface (*L. chamberlainianum, L. irvineanum, L. prototypum, L.pustulatum*) and species in which the floor is 6 or more cell layers below the thallus surface (*L. bermudense, L. corallinae, L. johansenii*). There is no clear evidence presently to suggest that pore canal characters are of any greater or lesser evolutionary significance than conceptacle floor characters, but in the dichotomous key , greater importance has been arbitrarily accorded pore canal characters.

Amongst species in which the pore canal is completely occluded by enlarged cells, *L. irvineanum* and *L. johansenii* both have two or four enlarged angular cells in the pore canal (Figs 35A, 39D). The former, however, has a chamber floor 1–2 cell layers below the thallus surface whereas the latter has a chamber floor 8 or more cell layers below the thallus surface. *L. chamberlainianum* differs from both in having a conglomerate of tubular, more or less inflexed cells occluding the pore canal (Figs 18C, 18D).

Amongst species in which the pore canal is not completely occluded, *L. prototypum* and *L. pustulatum* have conceptacle chamber floors 1–3(–5) cell layers below the thallus surface whereas *L. bermudense* and *L. corallinae* have floors 6 or more cell layers below the thallus surface. *L. prototypum* always differs from *L. pustulatum* in the nature and extent of applanate branching. In *L. prototypum*, numerous layers of applanate branching always occur, each branch arises from a group of primigenous cells, many branches at least when young have swirled margins, and the thallus surface becomes conspicuously terraced as a consequence of younger branches not completely overgrowing older ones. In *L. pustulatum*, in contrast, applanate branching (if present at all) is sporadic; each branch develops from a group of postigenous cells; branches lack swirled margins; and the thallus never becomes conspicuously terraced because new branches commonly completely overgrow older ones. All plants of *L. prototypum* lack multicellular postigenous filaments and have applanate branches whereas those plants of *L. pustulatum* lacking multicellular postigenous filaments also lack applanate branches.

Lithophyllum bermudense and *L. corallinae* have been delimited from one another mainly on differences in tetrasporangial/bisporangial conceptacle roof anatomy and chamber diameter. In *L. bermudense*, roofs are usually 3–7 cells thick above the chamber and only rarely have a subepithallial layer of columnar cells (Figs 3D, 10E, 11C–11E, 12), whereas in *L. corallinae*, roofs are usually 2–4 cells thick and commonly contain a layer of columnar cells (Figs 27E, 28, 29). *L. bermudense* chambers are mostly 320–410 µm in diameter whereas *L. corallinae* chambers are mostly 190–235 µm in diameter. While these differences are clear-cut in most specimens, a few plants placed in *L. bermudense* on roof characters have chambers as small as 255 µm in diameter and a few plants placed in *L. corallinae* on roof characters have chambers as large as 280 µm in diameter. The occurrence of isolated specimens of a seemingly intermediate nature suggests that the two species may hybridize or that other as yet undetermined characters may better serve to delimit them. Alternatively, what is here interpreted to be two quite variable species in reality may be a single extremely variable species. On the basis of present evidence, the second possibility seems less likely because of probable differences in gametangial conceptacles. Male conceptacles of *L. bermudense* have a larger and somewhat differing roof than those of *L. corallinae* (compare Figs 13A & 31A, 31B), and the same seems to be the case with young female/carposporangial conceptacles (compare Figs 14A, 14B & 31C, 31E). Further studies are required, however, before firm conclusions can be reached.

Relationships between southern Australian species of *Lithophyllum* and those occurring elsewhere remain obscure and will continue to do so until a series of regional monographs are available and until current ideas on species delimitation are further tested and refined. Only then can a meaningful phylogenetic analysis occur.

REPORTS OF OTHER TAXA FROM SOUTHERN AUSTRALIA ASCRIBED TO *LITHOPHYLLUM*

Twelve additional entities have been reported to occur in southern Australia or in the Perth region of the west coast under the generic name *Lithophyllum*. These fall into three categories: taxa inquirendae excluded taxa, and spurious records.

Taxa inquirenda

Taxa in this category are based on type collections from Southern Australia which appear to be missing.

1. **Lithophyllum darwinii** (Harvey) Foslie in *K. norske Vidensk. Selsk. Skr.* 1900(5): 18 (1900e).

BASIONYM. *Melobesia darwinii* Harvey, *Nereis Australis*: 109 (1849)

TYPE. Apparently missing.

SOUTHERN AUSTRALIAN RECORDS AS:

> *Goniolithon darwinii* (Harvey) Foslie in *K. norske Vidensk. Selsk. Skr.* 1898(3): 9 (1898b). *Lithophyllum darwinii* (Harvey) *Foslie in K. norske Vidensk. Skr.* 1900(5): 18 (1900e). De Toni, *Sylloge Algarum* 4: 1780 (1905). *Lucas in Proc. Linn. Soc. NSW* 37: 163 (1912). *Lithothamnion darwinii* (Harvey) Areschoug in J.G. Agardh, *Sp. Gen. Ord. Algarum* 2(2): 523 (1852). Foslie *in K. norske Vidensk. Selsk. Skr.* 1897(1): 15 (1897). Harvey, *Phyc. Aust.* 5: xxx (1863). Heydrich in *Ber. dt. Bot. Ges.* 15: 64 (1897b); 415 (1897a). Lucas in *Proc. Linn. Soc. NSW* 34: 55 (1909). Sonder in F. Mueller, *Frag. Phytogr. Aust.* 11(suppl 1): 20 (1880–1881). *Melobesia darwinii* Harvey, *Nereis Australis:* 109 (1849). Porter in *Bull. Br. Mus. Nat. Hist. (Hist. ser.)* 14: (1987).

REMARKS. Harvey (1849: 109, 110) based this species on a specimen received from Charles Darwin which was, according to statements in the protologue, lodged in TCD. The specimen was collected from King Georges Sound, Western Australia and was said to form large masses built up of cylindrical branching stony fronds soldered together with all branches very erect and the ultimate ones free and mammilliform. Plants also were said to be 5–7.5 cm in height and to look like a mass of stalagmites. Harvey did not mention reproductive structures.

The subsequent transfers of *Melobesia darwinii* to *Lithothamnion*, then *Goniolithon* Foslie, 1898a (non *Goniolithon* Foslie, 1900e; see Setchell & Mason, 1943 and Woelkerling, 1988: 216 for comments on these two names) and finally *Lithophyllum* were effected without examining material of the species. Thorough searches by the first author at TCD and at BM (where a number of Harvey collections also reside) have failed to locate any plants identified by Harvey as *Melobesia darwinii* or any specimens from King Georges Sound fitting Harvey's description of *M. darwinii*. Similarly, Porter (1987: 198) failed to find any material, but he speculated that it may have been sent to Foslie and not returned. However, no specimen with the specific epithet '*darwinii*' was listed for the Foslie herbarium by Adey & Lebednik (1967) and the first author has not found such material in TRH during visits in 1980, 1985 and 1988.

It is possible that the Darwin specimen Harvey called *Melobesia darwinii* belongs to either *Lithophyllum bermudense* or *Sporolithon* since plants of these entities can have thalli like that described by Harvey and do occur along the southern coast of Western Australia. The true status of *Melobesia darwinii* cannot be determined, however, until the original specimen is relocated and examined.

2. **Lithophyllum okamurai f. contigua** Foslie in *K. norske Vidensk. Selsk. Skr.* 1904(2): 7 (1904a).

TYPE. Apparently missing.

SOUTHERN AUSTRALIAN RECORDS AS:

> *Lithophyllum okamurai* f. *contigua* De Toni, *Sylloge Algarum* 6: 685 (1924). Foslie in *K. norske Vidensk. Selsk. Skr.* 1904(2): 7 (1904a).

REMARKS. Foslie (1904a: 7) based f. *contigua* on several specimens from Cape Jaffa, South Australia which were sent by Dr August Engelhart. Some specimens were said to be attached to 'hard objects' and to produce crustose thalli from which short, subdichotomous closely spaced branches arose. Others were said to form free-growing masses up to 7cm in diameter and to be composed of short radiating somewhat gnarled branches 5–8 mm thick. A few overgrown conceptacles 120–200µm in diameter were seen, but Foslie said nothing about their contents.

The fate of the specimens upon which Foslie based *Lithophyllum okamurai* f. *contigua* is a mystery. Adey & Lebednik (1967) do not mention this form and do not list (op. cit.: 42) any Australian collections under the entry for the species. Similarly Printz (1929) contains no reference to the form or to Australian collections of the species, and several searches by the first author at TRH have failed to locate any collections of f. *contigua* or any Australian collections of Engelhart labelled with the specific epithet *okamurai.* Until the relevant Foslie collections are found and analyzed, the status and disposition of *L. okamurai* f. *contigua* will remain unresolved.

Excluded taxa

The following entities, for which southern Australian records exist under the name *Lithophyllum*, have been excluded from that genus based on examination of relevant types.

1. **Lithophyllum amplexifrons** (Harvey) Heydrich in *Bot. Jb.* 28: 536 (1901).

BASIONYM. *Melobesia amplexifrons* Harvey, *Nereis Australis*: 110 (1849).

LECTOTYYPE. TCD (Port Natal, South Africa, *Guienzius*, no date); designated here (Fig. 63A; see below).

SOUTHERN AUSTRALIAN RECORDS AS:

> *Lithophyllum amplexifrons* (Harvey) Heydrich. De Toni, *Sylloge Algarum* 4: 1788 (1905). Foslie in *K. norske Vidensk. Selsk. Skr.* 1901(3): 6. Lemoine in *Bull. Soc. Bot. Fr.* 58: LVIII (1912). Lucas in *Trans. R. Soc. S. Aust.* 53: 53 (1929). Lucas & Perrin, *Seaweeds of South Ausatralia* 2: 393 (1947). Masaki in *Mem. Fac. Fish. Hokkaido Univ.* 16: 30, pls14 (figs 4–6), 16, 55, 56 (1968). Tittley et al., *Catalogue of Type Specimens and Geographical Index to the Collections of Rhodophyta (Red Algae) at the British Museum Natural History*: 29, 62 (1984). *Melobesia amplexifrons* Harvey (Reinbold) in *Nuova Notarisia* 9: 54 (1898). Rosanoff in *Mem. Imp. Sc. Nat. Math. Cherbourg* 12: 75, pl.7, figs 2, 3 (1866).

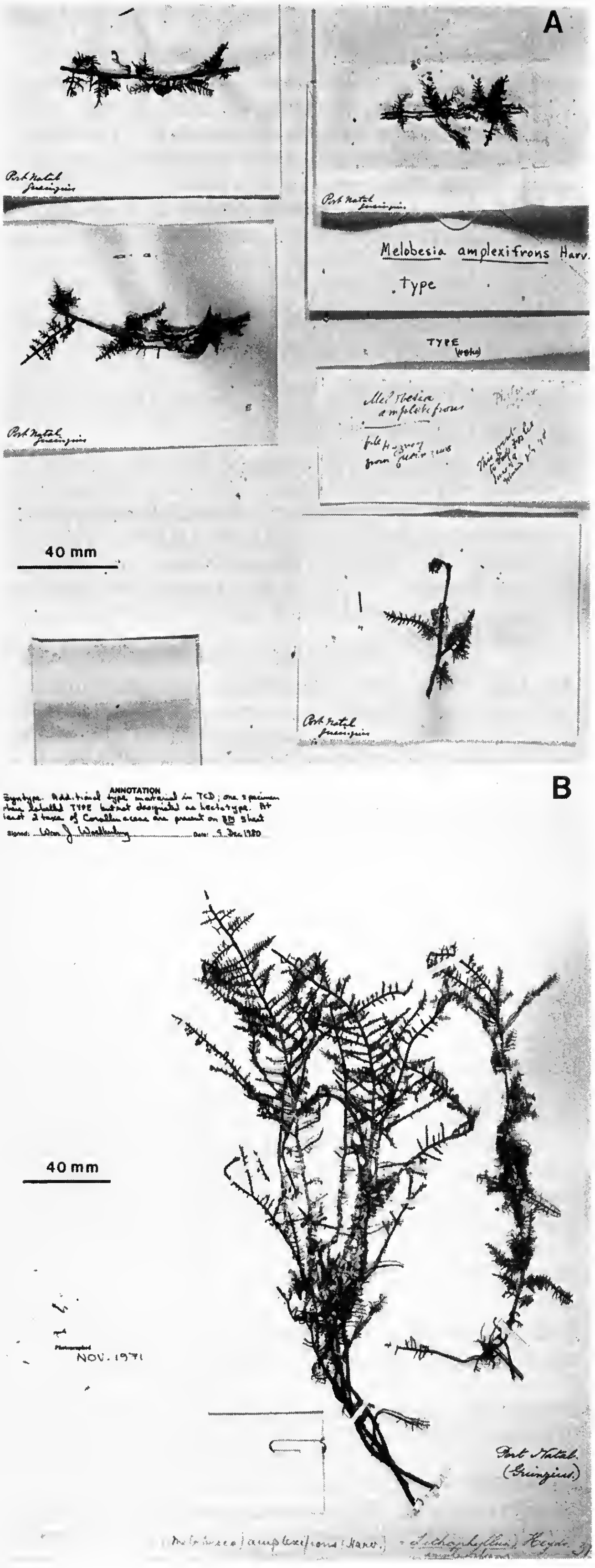


Fig. 63 *Melobesia amplexifrons*. A. Lectotype collection (TCD). B. Isotype collection (BM).

TYPIFICATION AND REMARKS. The protologue of *Melobesia amplexifrons* (Harvey 1849: 110) contains a two-line description of the appearance of the plants, lists *Gelidium* as the host, and states that the material seen is in TCD. A single unnumbered sheet (Fig. 63A) containing four attached specimens is presently housed at TCD; one of these specimens has been annotated as type by H.B.S. Womersley, but this herbarium designation has not been published. Of the four specimens attached to the sheet, the one annotated by Womersley is the best and is here chosen to serve as lectotype of the species. The remaining three specimens on the sheet are considered to be isolectotypes. A further isolectotype exists as an unnumbered sheet in BM (Fig. 63B): this is a much larger host specimen and contains at least two different species of nongeniculate corallines.

Fragments of the TCD lectotype examined during this study contained plants with uniporate tetrasporangial conceptacles and plants with female/carposporangial conceptacles, all of which are referable to *Pneophyllum* (subf. Mastophoroideae) (see Penrose & Woelkerling 1991). The status of Harvey's species within *Pneophyllum* requires further study. The BM isolectotype contains plants identical to those of the designated lectotype but in addition contains specimens of what appears to be *Lithophyllum corallinae*. Judging from the protologue, Harvey (1849: 110, 111) did not realize that at least two species were present in his material, especially since they look the same externally. The choice of the *Pneophyllum* material to serve as lectotype is based on its prevalence in the TCD portion of the collection.

With two exceptions, specimens on which Australian records of *Lithophyllum amplexifrons* are based have not been available for examination. Lemoine's (1912) record is based on specimens identified by Foslie. Foslie (1907a: 33), however, used the TRH portion of this collection as the basis for a distinct entity (*Lithophyllum zostericolum* f. *tasmanicum*) which he (Foslie 1908b: 16) raised to the rank of species [i.e. *Lithophyllum tasmanicum* (Foslie) Foslie]. This TRH collection almost certainly is also the basis of Foslie's (1901b: 6) earlier report of *L. amplexifrons* from Tasmania. *L. tasmanicum* has now been excluded from *Lithophyllum* (see below).

The Foslie herbarium also contains a Rosanoff collection originally labelled as *Melobesia amplexifrons* from southern Australia. Foslie (1908b: 5) used this collection as the basis for his new species *Lithothamnion rosanoffii* Foslie. After examining the type of *Lithothamnion rosanoffii,* Wilks & Woelkerling (1991) concluded that it represented a distinct species of *Melobesia.*

2. **Lithophyllum hyperellum** Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(5): 27 (1900a).

LECTOTYPE. See remarks.

SOUTHERN AUSTRALIAN RECORDS AS:

Lithophyllum hyperellum Foslie Adey & Lebednik, *Catalog Foslie Herbarium:* 19 (1967). Bennett & Pope in *Aust. J. mar. freshwat. Res.* 11: 195, 207, 212, 215, fig. 2 (1960). Cribb in *Pap. Proc. R. Soc. Tasm.* 88: 25, 31, 37 (1954). De Toni, *Sylloge Algarum* 4: 1780 (1905). Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(5): 27 (1900a); 1900(5): 17, 18 (1900e); 1909(2): 16 (1909). Guiler in *Pap. Proc. R. Soc. Tasm.* 86: 17 (1952a); 86: 32, 38 (1952b); 86: 87 (1952c); 88: 108, 115 (1954); 92: 180

(1958); 94: 60, 61; J. Ecol. 48: 20 (1960a). Lucas in *Proc. Linn. Soc. NSW* 37: 163 (1912). Lucas & Perrin, *Seaweeds of South Australia* 2: 393 (1947). Printz, *M. Foslie Contr. Monog. Lithothamnia*: 35, pl.55, figs 7–13 (1929). Saenger in *Pap. Proc. R. Soc. Tasm.* 107: 80 (1974). Stephenson & Stephenson, *Life Between Tide Marks on Rocky Shores*: 297, fig. 11.14 (1972). Tittley et al., *Catalogue of Type Specimens and Geographical Index to the Collections of Rhodophyta (Red Algae) at the British Museum (Natural History)*: 30, 62 (1984). Womersley in *Bot. rev.* 25: 584 (1959). Womersley in N.M. Clayton & R.J. King, *Marine Botany, An Australasian Perspective:* 227, 229 (1981) Womersley, *Mar. Benthic Fl. Sthn Aust.*: 47, 48, pl. 9, fig. 2 (1984). Womersley & King in N.M. Clayton & R.J. King, *Biology of Marine Plants*: 285, 288. *Pseudolithophyllum hyperellum* (Foslie) Adey in *K. norske Vidensk Selsk. Skr.* 1970(1): 13 (1970). King in *Proc. R. Soc. Vict.* 85: 156, 157 (1973).

REMARKS. The protologue of *Lithophyllum hyperellum* (Foslie, 1900a: 27) contains accounts of two forms (f. *fastigiata* and f. *heteroidea*) based on a series of specimens collected by J. Gabriel from Port Phillip Bay [?] and Western Port, Victoria, Australia.

Foslie (op. cit) did not, however, provide separate descriptions for the species (as opposed to the two forms), did not indicate which form he regarded to be the 'typical' one, and did not designate types for either of the forms or for the species. The Foslie herbarium (TRH) contains four pre-1900 collections of *Lithophyllum hyperellum* from localities cited in the protologue; each of these encompasses a number of plants. Adey in Adey & Lebednik (1967: 19) lectotypified the species with an 1899 Gabriel collection which is marked *Lithophyllum hyperellum* f. *fastigiata*. This means that f. *fastigiata* must be taken as the typical form of the species and that *Lithophyllum hyperellum* f. *fastigiata* must be known as *Lithophyllum hyperellum* f. *hyperellum* in accordance with ICBN Article 26.1 (see Greuter 1988). The plants in this collection belong to *Spongites* (see Penrose & Woelkerling 1991) within the subfamily Mastophoroideae (sensu Woelkerling 1988: 115). The status of this species within *Spongites* is currently being assessed (Penrose, personal communication).

3. **Lithophyllum mediocre f. tasmanica** (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1907(6): 27 (1907b).

REMARKS. See account of *Lithophyllum tasmanica* below.

4. **Lithophyllum patena** (J.D. Hooker & W.H. Harvey) Rosanoff in *Mem. Imp. Sc. Nat. Math. Cherbourg* 12: 88 (1866).

BASIONYM. *Melobesia patena* J.D. Hooker & W.H. Harvey in Harvey, *Nereis Australis*: 11, pl. XL, M. patena (1849).

LECTOTYPE. TCD, *Colenso* 1331 (Flat Point, near Castlepoint, New Zealand, no date given); designated by Chapman & Parkinson (1974, pl.72).

SOUTHERN AUSTRALIAN RECORDS AS:

Lithophyllum patena (J.D. Hooker & W.H. Harvey) Rosanoff. Barton in *J. Bot. Lond.* 31: 202 (1893). Rosanoff in *Mem. Soc. Imp. Sc. Nat. Math. Cherbourg* 12: 88, pl.5, figs 7, 15 (1866). Records under other names are summarized by Townsend (1979: 252) and by May & Woelkerling (1988: 52, 69).

REMARKS. This entity is the type species of *Synarthrophyton* Townsend (1979: 252) within the subfamily Melobesioideae (sensu Woelkerling 1988: 158). Townsend (1979) and May & Woelkerling (1988) have provided detailed accounts of *S. patena*; Woelkerling (1988: 210) has summarized data on the genus; and Woelkerling & Foster (1989) have described a second species based on collections from the Chatham Islands.

5. **Lithophyllum rupestre** Foslie in *K. norske Vidensk. Selsk. Skr.* 1906(8): 26 (1907a).

HOLOTYPE. TRH (Ocean Beach, Phillip Island, Victoria, Australia, *J. Gabriel*, iv.1905).

SOUTHERN AUSTRALIAN RECORDS AS:

Lithophyllum rupestre Foslie De Toni, *Sylloge Algarum* 6: 686 (1924). Foslie in *K. norske Vidensk. Selsk. Skr.* 1906(8): 26 (1907a). Printz, *M. Foslie Contr. Monogr. Lithothamnia*: 37, pl. 54, fig. 1 (1929). *Mesophyllum rupestre* (Foslie) Adey in *K. norske Vidensk. Selsk. Skr.* 1970(1): 26 (1970).

REMARKS. Foslie (1907a) based the protologue of this species on a single specimen, and although he mentioned that conceptacles occurred in rather large numbers and were 100 µm in median vertical section, he provided no information on their contents. Adey (1970: 26) transferred the species to *Mesophyllum* with the comment 'Asexual conceptacles not studied'. Fragments of the type sectioned during this study contained male conceptacles in which spermatangia developed only on the conceptacle chamber floor. In addition, cells of contiguous filaments were linked by cell fusions; secondary pit-connections were not found. In view of Lebednik's (1978) studies of non-geniculate coralline spermatangia (see also comments of Woelkerling 1988: 75), the present species almost certainly does not belong to *Mesophyllum* or to the subfamily Melobesioideae, both of which, according to Lebednik, produce spermatangia both on the floor and the roof of the conceptacle chamber. The presence of cell fusions and the absence of secondary pit-connections precludes placement in either *Lithophyllum* or the subfamily Lithophylloideae. All features evident in the type are consistent with placement in *Hydrolithon* (subf. Mastophoroideae) (see Penrose & Woelkerling 1992); the status of '*rupestre*' within *Hydrolithon* is under current study (Penrose, personal communication).

6. **Lithophyllum tasmanicum** (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1980(7): 16 (1908b).

BASIONYM. *Lithophyllum zostericolum* f. *tasmanicum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1906(8): 33 (1907a).

LECTOTYPE. TRH (Georgetown Heads, Tasmania, no collector or date given, ex herb. Bornet); designated by Adey & Lebednik (1967: 17); see also Adey, 1970: 14 (as *Pseudolithophyllum*). Lemoine (1912: p. LVIII) lists the PC portion of this collection under *Lithophyllum amplexifons* (Harvey) Heydrich with F. von Mueller as collector.

SOUTHERN AUSTRALIAN RECORDS AS:

Lithophyllum tasmanicum (Foslie) Foslie. Adey & Lebednik, *Catalog of the Foslie Herbarium: 17* (1967). Foslie in *K. norske Vidensk. Selsk. Skr.* 1908(7): 16 (1908b); 1908(11): 7 (1908c). *Lithophyllum mediocre* f. *tasmanica* (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1907(6): 27 (1907b). *Lithophyllum zostericolum* f. *tasmanicum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1906(8):33 (1907a). *Melobesia tasmanica* (Foslie) De Toni, *Sylloge Algarum* 6: 650 (1924). Guiler in *Pap. Proc. R. Soc. Tasm.* 86: 86 (1952c). *Pseudolithophyllum tasmanicum* (Foslie) Adey in *K. norske Vidensk. Selsk. Skr.* 1970(1): 14 (1970).

REMARKS. Foslie (1907a) based this entity on specimens from Georgetown Heads, Tasmania and Cape Jaffa, South Australia. The designated lectotype is epiphytic on a small brown algal fragment (identity uncertain) and contains several coralline plants. The fragments examined belong to *Pneophyllum* (see Penrose & Woelkerling 1991) within the subfamily Mastophoroideae (sensu Woelkerling 1988: 115). Its status as a distinct species is presently being assessed (Penrose, personal communication).

7. **Lithophyllum verrucosum** (Foslie) Foslie in *K. norske Vidensk. Selsk. Skr.* 1900(6): 21 (1901a).

BASIONYM. *Goniolithon verrucosum* Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(5): 24 (1900a).

LECTOTYPE. TRH (Cape Jaffa, South Australia, A. Engelhart, 1899); designated by Adey & Lebednik (1967: 18); see also Adey, 1970: 10.

SOUTHERN AUSTRALIAN RECORDS AS:

Lithophyllum verrucosum (Foslie) Foslie. Adey & Lebednik, *Catalog of the Foslie Herbarium*: 18 (1967). De Toni, *Sylloge Algarum* 6: 675 (1924). Foslie in *K. norske Vidensk. Selsk. Skr.* 1900(6): 21 (1901a); 1905(5): 3 (1905b); 1906(8): 28 (1907a); 1909(2): 14 (1909). Printz, *M. Foslie Contr. Monogr. Lithothamnia*: 38, pl. 54, figs 27–30 (1929). *Lithophyllum verruculosum* Foslie (ortho. var.). Okamura, *Jap. Mar. Algae*: 103 (1936). *Goniolithon verrucosum* Foslie. De Toni, *Sylloge Algarum* 4: 1799 (1905). Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(5): 24 (1900a); 1900(5): 16 (1900e). Lucas in *Proc. Linn. Soc. NSW* 37: 163 (1912). Lucas & Perrin, *Seaweeds of South Australia* 2: 393 (1947). *Neogoniolithon verrucosum* (Foslie) Adey in *K. norske Vidensk. Selsk. Skr.* 1970(1): 10 (1970). Tittley et al., *Catalogue of Type Specimens and Geographical Index to the Collections of Rhodophyta (Red Algae) at the British Museum (Natural History)*: 36, 62 (1984).

REMARKS. This species is based on a series of specimens (see Adey & Lebednik, 1967: 18) collected by A. Engelhart at Cape Jaffa, South Australia. The designated lectotype is referable to *Spongites* (see Penrose 1991; Penrose & Woelkerling 1991, 1992) within the subfamily Mastophoroideae (sensu Woelkerling 1988: 115). Its status as a distinct species is under current investigation (Penrose, personal communication).

8. **Lithophyllum zostericolum f. tasmanicum** Foslie in *K. norske Vidensk. Selsk. Skr.* 1906(8): 33 (1907a).

REMARKS. See account of *Lithophyllum tasmanicum* above.

Spurious records

The following records are considered erroneous:

1. **Lithophyllum tortuosum** (Esper) Foslie in *K. norske Vidensk. Selsk. Skr.* 1899(5): 20 (1900a).

BASIONYM. *Millepora tortuosa* Esper, *Fortsetzungen der Pflanzenthiere* 1(5–6): 118, *Millepora* Tab. XXII.

LECTOTYPE. FR (Mediterranean Sea; precise locality, collector and date not given); designated by Woelkerling et al. (1985: 322).

SOUTHERN AUSTRALIAN RECORDS AS:

Lithophyllum tortuosum (Esper) Foslie. Tittley et al., *Catalogue of Type Specimens and Geographical Index to the Collections of Rhodophyta (Red Algae) at the British Museum (Natural History)*: 31, 62 (1984)

REMARKS. This record is based on the specimen in BM (Algal Box Collection No.9) which contains one annotation slip attributing identification to M. Foslie and a second note giving the locality only as Swan River (no mention of Western Australia) and indicating that the specimen was purchased from Mr. Cuming. Re-examination of this specimen by the first author has shown that the plant belongs to *Lithophyllum lichenoides* Philippi (1837: 389), the type of which has been the subject of a previous study (Woelkerling, 1983: 317–322, figs 24–32). *Lithophyllum lichenoides* is known only from the western Mediterranean and adjacent areas of the North Atlantic Ocean; no specimens of this species have been found growing in southern Australia. The conclusion reached by Tittley et al. (1984) that the Swan River referred to on the annotation slip is the one in Western Australia is almost certainly incorrect as applied to the specimen in question, and the associated record is treated here as spurious. It is possible, of course, that the label with Swan River on it was wrongly placed in the box at some stage. The species upon which the name *Lithophyllum tortuosum* is based is now correctly known as *Tenarea tortuosa* (Esper) Lemoine. The genus *Tenarea* (see Woelkerling et al., 1985 and Woelkerling, 1988: 106 for detailed accounts) is monotypic and is known only from areas of the eastern Mediterranean Sea.

2. **Lithophyllum tumidulum** Foslie in *K. norske Vidensk. Selsk. Skr.* 1901(3): 5 (1901b).

REMARKS. In the protologue of *Lithophyllum tumidulum*, Foslie (1901b: 6) makes comparisons with *L. amplexifrons*, citing a specimen of the latter from Tasmania. Comments on the Tasmanian specimen are written in such a manner, however, that it is possible to interpret them as applying to *L. tumidulum* and not *L. amplexifrons*. This was not Foslie's intention as he states explicitly that *L. tumidulum* is known only from Japan, thereby indirectly making it clear that he regarded the Tasmanian specimen to belong to *L. amplexifrons*. Further comments on *L. amplexifrons* appear earlier in the section on excluded taxa.

CONCLUDING REMARKS

Prior to the present study, 14 species and infraspecific taxa ascribed at some stage to *Lithophyllum* had been reported from southern Australia. Of these, only two (*L. corallinae, L. pustulatum*) have now been verified to belong to *Lithophyllum* and to occur in this region. Eight have been removed from *Lithophyllum* after studying relevant type collections, two represent spurious records, and two are now considered to be taxa inquirenda. However, five species additional to *L. corallinae* and *L. pustulatum* are now known to occur in southern Australia, including three which are newly described. Two possible additional species also may be present.

These data clearly demonstrate that a largely inaccurate understanding of *Lithophyllum* in southern Australia had built up in the published literature and that a new, broad-based study has provided an almost totally different but much more accurate awareness of the real situation. Such inaccurate perceptions are probably wide-spread on a world scale not only for *Lithophyllum* but also for a number of other genera of nongeniculate Corallinaceae. Not only are comparable studies needed for other nongeniculate genera occurring in southern Australia, but they are also needed for most other regions of the world as a prelude to production of world monographs of genera and as a prelude to any assessments of a biogeographic nature. The use of older, often fragmentary published data (as opposed to newer, more comprehensive and trustworthy data) in generating floristic compilations and suggesting patterns of biogeographic distributions is highly likely to continue to give false or misleading results, create more confusion and apprehension than already occurs, and perpetuate and compound existing inaccuracies in the literature.

Results from the present study also clearly show that many criteria previously used to delimit species of *Lithophyllum* are too variable to be reliable, that new characters relating to conceptacle anatomy are important in species delimitation, and that studies comparable to this one are needed elsewhere to help elucidate a more meaningful and reliable understanding of species limits and species relationships within the genus. Until considerably more work is done and trustworthy data generated, any attempts to elucidate phylogenetic relationships would be little more than a 'garbage in, garbage out' routine (see Pimentel & Riggins, 1987).

In their reports on this manuscript, both (anonymous) reviewers disagreed with the subsuming of *Titanoderma* into *Lithophyllum* (see Introduction). One reviewer felt that they are two separate entities, well-defined by their morphogenesis; the other felt recognition of one vs two genera was a matter of personal judgment and that recognition of one genus was a tenable point of view. Neither reviewer, however, provided any firm evidence or published references to data which might override the conclusions reached by Campbell & Woelkerling (1990), and thus the single genus concept has been retained. As noted in the Introduction, this account constitutes a base-line study. While some past incaccuracies have been corrected, additional studies are needed, and these almost certainly will lead to refinements of the conclusions reached here. As with work at generic level (see Woelkerling, 198: 224), this study is much more a starting-point for future research than an end-point of past research.

ACKNOWLEDGEMENTS. Sincere thanks are due Dr Yvonne Chamberlain for providing copies of her manuscript on British species of *Lithophyllum* (*Titanoderma*) prior to publication, for examining various slides of southern Australian collections and confirming their relationships to British species and for valuable discussions concerning the taxonomy of *Lithophyllum* and the Lithophylloideae during her visits to Australia and the visits of the first author to England. Thanks are also due to Linda Irvine for ensuring that visits of the first author to the British Museum (Natural History) to examine specimens and use facilities were highly successful, to Dr Deborah Penrose for information on taxa referable to the Mastophoroideae, to Dr Françoise Ardré for information concerning the type of *Lithophyllum prototypum*, to Dr Scoresby Shepherd for polishing the Latin diagnoses of new species, to Dr Mark Littler for providing specimens of *Lithophyllum prototypum* from Hawaii, to Dr Athanasios Athanasiadis for providing a prepublication copy of his paper on *Titanoderma cystoseirae,* to Dr Murray Parsons for providing a photocopy of an obscure publication relating to New Zealand corallines, to Brett Light for assistance with the preparation of specimens for optical and scanning electron microscopy during the latter stages of this study, to the two anonymous reviewers who provided many valuable suggestions, to Ken Wong Hee for preparing Figure 1, and to the curators at AD, BM, CN, L, LD, MEL, TCD, TRH, and US for the loan of specimens. Financial support provided by the Australian Marine Sciences and Technologies Grants Scheme and by the Australian Research Council is gratefully acknowledged.

REFERENCES

Abbott, I.A. & Hollenberg, G.J. 1976. *Marine Algae of California*. Stanford University Press, Stanford, California. xii + 827 pp.

Adey, W.H. 1965. The algal tribe Lithophylleae and its included genera. pp. 67–102 *In*: J.H. Johnson & W.H. Adey, Studies of *Lithophyllum* and related algal genera. *Colo. Sch. Mines Q*. 60(2): 1–105.

——. 1966. The genera *Lithothamnium, Leptophytum* (nov. gen.) and *Phymatolithon* in the Gulf of Maine. *Hydrobiologia* 28: 321–370.

——. 1970. A revision of the Foslie crustose coralline herbarium *K. norske Vidensk. Selsk. Skr*. 1970 (1): 1–46.

——. 1979. Crustose coralline algae as microenvironmental indicators for the Tertiary. *In*: J. Gray & A.J. Boucot (Eds), *Historical Biogeography, Plate Tectonics, and the Changing Environment*, pp. 459–464. Oregon State Univ. Press, Corvallis, Oregon.

——**& Adey, P.J.** 1973. Studies on the biosystematics and ecology of the epilithic crustose Corallinaceae of the British Isles. *Br. phycol. J*. 8: 343–407.

——**& Lebednik, P.A.** 1967. *Catalog of the Foslie Herbarium*. Det Kongelige Norske Videnskabers Selskab Museet, Trondheim, Norway. 92 pp.

——**, Masaki, T. & Akioka, H.** 1974. *Ezo epiyessoense*, a new parasitic genus and species of Corallinaceae (Rhodophyta, Cryptonemiales). *Phycologia* 13: 329–344.

——, *Townsend, R.A., & Boykins,* W.T. 1982. The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. *Smithson. Contr. mar. Sci*. 15: i–iv, 1–74.

Ardissone, F. 1883. Phycologia mediterranea. Part 1. Floridee. *Mem. Soc. Crittogam. Ital*. 1: 1–516.

Areschoug, J.E. 1852. Ordo XII. Corallinaceae. Pages 506–576 In: Agardh, J. *Species, Genera, et Ordines Algarum*. Vol. 2, Part 2 C.W.K. Gleerup, Lund.

Athanasiadis, A. 1989. North Aegean marine algae. III. Structure and development of the encrusting coralline *Titanoderma cystoseirae* (Rhodophyta, Lithophylloideae). *Nord. J. Bot*. 9: 435–441.

Bailey, F.M. 1913. *Comprehensive Catalogue of Queensland Plants*. Government Printer, Brisbane. 879 pp., 16 pl.

Barton, E.S. 1893. A provisional list of the marine algae of the Cape of Good Hope. *J. Bot., Lond*. 31: 53–56, 81–84, 110–114, 138–144, 171–177, 202–210.

Bauch, R. 1937. Die Entwicklung der bisporen der Corallinaceen. *Planta* 26: 365–390.

Belsher, TH., Augier, H., Boudouresque, C.F. & Coppejans, E. 1976. Inventaire des algues marines benthiques de la rade et des iles d'Hyeres. *Trav. sci. Parc. natn. Port-Cros*. 2: 39–89.

Bennett, I. & Pope, E.C. 1960. Intertidal zonation of the exposed rocky shores of Tasmania and its relationship with the rest of Australia. *Aust. J. mar. Freshwat. Res*. 11: 182–221, pl. 1–7.

Boergesen, F. 1902. *The marine algae of the Faeroes.* H.H. Tiele, Copenhagen. Reprinted without change in pagination from Botany of the Faeroes, Part II, pp. 339–532 (Det Nordiske Forlag, Copenhagen).

Bornet, E. 1892. Les Algues de P.K.A. Schousboe. *Mém. Soc. natn. Sci. nat. Math. Cherbourg* 28: 165–376, pls 1–3.

Bory, J.B. 1832. Notice sur les polypiers de la Grece. *Expéd. Sci. Moree (Sect. Sci. Phys.)* 3(1): 204–209, pl. 54.

Bosellini, A. & Ginsburg, R.N. 1971. Form and internal structure of recent algal nodules (Rhodolites) from Bermuda. *J. Geol.* 79: 669–682.

Bosence, D.W.J. 1983. Description and classification of rhodoliths (rhodoids, rhodolites). *In*: T.M. Peryt (Ed.), *Coated Grains*, pp. 225–242. Springer-Verlag, Berlin.

——. 1985. The morphology and ecology of a mound-building coralline alga (Neogoniolithon strictum) from the Florida Keys. *Palaeontology* 28: 189–206, pl. 21–23.

Boudouresque, C.F., Perret-Boudouresque, M. & Knoepffler-Peguy, M. 1984. Inventaire des algues marines benthiques dans les les Pyrenees-Orientales (Méditerranée, France). *Vie Milieu* 34: 41–59.

Bressan, G. 1974. Rodoficee calcaree dei mari Italiani. *Boll. Soc. adriat.* Sci. nat. 59: 1–132, Figs. 1–43.

Cabioch, J. 1972. Étude sur les Corallinacées. II. La morphogenèse; consequences systématiques et phylogénétiques. *Cah. Biol. mar.* 13: 137–288. pl. 1–13.

——. 1979. Sur un nouveau cas de semi-parasitisme chez les Corallinacées (Rhodophycées): *Dermatolithon corallinae* (Crouan) Foslie. *C.r. hebd. Séanc. Acad. Sci., Paris* 288D: 1533–1535.

Campbell, S.J. & Woelkerling, Wm J. 1990. Are *Titanoderma* and *Lithophyllum* (Corallinaceae, Rhodophyta) distinct genera? *Phycologia* 29: 114–125.

Chamberlain, Y. 1965. Marine aglae of Gough Island. *Bull. Br. Mus. nat. Hist. (Bot. ser.)* 3: 173–232, pl. 16–19.

——. 1978. *Dermatolithon litorale* (Suneson) Hamel & Lemoine (Rhodophyta, Corallinaceae) in the British Isles. *Phycologia* 17: 396–402.

——. 1983. Studies in the Corallinaceae with special reference to *Fosliella* and *Pneophyllum* in the British Isles. *Bull. Br. Mus. nat. Hist. (Bot. ser.)* 11: 291–463.

——. 1986. A reassessment of the type specimens of *Titanoderma verrucatum* and *T. macrocarpum* (Rhodophyta, Corallinaceae). *Cryptogamie algol.* 7: 193–213.

——. 1991. Historical and taxonomic studies on the genus *Titanoderma* (Rhodophyta, Corallinaceae) in the British Isles. *Bull. Br. Mus. nat. Hist. (Bot. ser.)* 21 (1): 1–80.

——**, Irvine, L.M. & Walker, R.** 1991. A redescription of *Lithophyllum orbiculatum* (Rhodophyta) Corallinales in the British Isles and a reassessment of generic delimitation in the *Lithophylloideae. Br. phycol. J.* 26: 149–167.

Chapman, V.J. 1963. The marine algae of Jamaica. Part 2. Phaeophyceae and Rhodophyceae. *Bull. Inst. Jamaica Sci. Ser.* 12(2): 1–201.

——. 1977. Marine algae of Norfolk Island and the Cook Islands. *Bot. mar.* 20: 161–165.

Cinelli, F., Drago, D., Furnari, G., Giaconne, G., Scammacca, B., Solazzi, A., Sortino, M., & Tolomio, C. 1976. Flora marina dell' Isola di Linosa (Arcipelago delle Pelagie). *Memorie Biol. mar. Oceanogr.* N.S. 6(5): 141–174.

Conti, S. 1943. Contributo allo studio delle corallinacee del terziaro italiano. *Paleontogr. ital.* 41: 38–61, pl. 5–8.

——. 1946. Le Corallinacee del calcare miocenico (Leithakalk) del bacino di Vienna. *Publ. Ist. Geol. Univ. Genova* 1–2 (Ser. A–Paleont): 31–68, pl. 1–9.

Coupin, H. 1920. *Album General des Cryptogames*. Algae. Vo. 4. [Plates 238–284]. Paris (Privately published).

Cribb, A.B. 1954. The algal vegetation of Port Arthur, Tasmania. *Pap. Proc. R. Soc. Tasm.* 88: 1–44.

Crouan, P.L. & Crouan, H.M. 1860. Liste des algues marines decouvertes dons le Finistère depuis la publication des algues ce de ce departement en 1852. *Bull. Soc. bot. Fr.* 7: 367–373.

——& . 1867. *Florule du Finistère*. F. Klincksieck, Paris. x + 262 pp., 32 pl.

Davis, P.H. & Heywood, V.H. 1963. *Principles of Angiosperm Taxonomy.* D. van Nostrand, Princeton, N.J. xx + 556 pp.

Dawson, E.Y. 1955. A preliminary working key to the living species of *Dermatolithon*. Pages. 271–277 In *Essays in the Natural Sciences in honor of Captain Allan Hancock*. U.So. Calif. Press, Los Angeles.

——. 1960. Marine red algae of Pacific Mexico. Part 3. Cryptonemiales, Corallinaceae, subf. Melobesioideae. *Pacif. Nat. 2: 3–125.*

Dawson, E.Y. 1961. A guide to the literature and distributions of Pacific benthic algae from Alaska to the Galapagos Islands. *Pacif. Sci.* 15: 370–461.

De Toni, G.B. 1905. *Sylloge Algarum Omnium Hucusque Cognitarum* Vol. 4. *Sylloge Floridearum*. Sec. 4. pp. 1523–1973. Privately published, Padova.

——. 1924. *Sylloge Algarum Omnium Hucusque Cognitarum* Vol. 6. Privately published, Padova.

——**& Forti, A. 1923.** Alghe di Australia, Tasmania e Nuova Zelanda. *Memorie R. Ist. veneto Sci.* 29(3): 1–183, pl. 1–10.

Dickie, G. 1875. Notes on algae from the Island of Mangaia, South Pacific. *J. Linn. Soc., Bot.* 15: 30–33.

——. 1876. Marine algae collected by Mr. Moseley at the Island of Kerguelen. *J. Linn. Soc., Bot.* 15: 43–47.

Ducker, S.C. 1990. History of Australian marine phycology. *In*: M.N. Clayton & R.J. King (Eds), *Biology of Marine Plants*, pp. 415–430. Longman Cheshire, Melbourne.

Esper, E.G.C. 1796. *Fortsetzungen der Pflanzenthiere*. Vol. 1, Parts 5–6 (pages 117–168). Raspe, Nurnberg.

Etcheverry, H. 1986. *Algas Marinas Bentonicas de Chile*. UNESCO (Regional office of Science and Technology for Latin America and the Caribbean), Montevideo, Uruguay. [i] + 379pp.

Foslie, M. 1895. The Norwegian forms of *Lithothamnion*. *K. norske Vidensk. Selsk. Skr.* 1894: 29–208, 23 pl.

——. 1897. On some Lithothamnia. *K. norske Vidensk. Selsk. Skr.* 1897(1): 1–20.

——. 1898a. Systematical survey of the lithothamnia. *K. norske Vidensk. Selsk. Skr.* 1898(2): 1–7.

——. 1898b. List of species of the lithothamnia. *K. norske Vidensk. Selsk. Skr.* 1898(3): 1–11.

——. 1900a. New or critical calcareous algae. *K. norske Vidensk. Selsk. Skr.* 1899(5): 1–34.

——. 1900b. Remarks on Melobesieae in Herbarium Crouan. *K. norske Vidensk. Selsk. Skr.* 1899(7): 1–16.

——. 1900c. *Melobesia caspica*, a new alga, *Ofvers. K. svenska Vetensk Akad. Förh.*. 1899(9): 131–133.

——. 1900d. Five new calcareous algae. *K. norske Vidensk. Selsk. Skr.* 1900(3): 1–6.

——. 1900e. Revised systematical survey of the Melobesieae. *K. norske Vidensk. Selsk. Skr.* 1900(5): 1–22.

——. 1901a. New melobesieae. *K. norske Vidensk. Selsk. Skr.* 1900(6): 1–24.

——. 1901b. New forms of lithothamnia. *K. norske Vidensk. Selsk.* Skr. 1901(3): 1–6.

——. 1904a. Algologiske notiser. *K. norske Vidensk. Selsk. Skr.* 1904(2): 1–9.

——. 1904b. Die Lithothamnien des Adriatischen Meeres und Marokkos. *Wissenschaft. Meeresunters. (Abt.) Helgoland*, new ser.., 7(1): 1–44, pl. I–3.

——. 1905a. Remarks on northern lithothamnia. *K. norske Vidensk. Selsk. Skr.* 1905(3): 1–138.

——. 1905b. New lithothamnia and systematical remarks. *K. norske Vidensk. Selsk. Skr.* 1905(5): 1–9.

——. 1905c. Den botaniske samling. *K. norske Vidensk. Selsk. Mus. Arsberetn.* 1904: 15–18.

——. 1907a. Algologiske notiser. III. *K. norske Vidensk. Selsk. Skr. 1906*(8): 1–34.

——. 1907b. Algologiske notiser. IV. *K. norske Vidensk. Selsk. Skr.* 1907(6): 1–30.

——. 1908a. Die lithothamnien der deutschen sudpolar-expedition 1901–1903. *Dt. Südpol.-Exped.* (B) VIII: 205–219.

——. 1908b. Algologiske notiser. V. *K. norske Vidensk. Selsk. Skr.* 1908(7): 1–20.

——. 1908c. Pliostroma, a new subgenus of Melobesia. *K. norske Vidensk. Selsk. Skr.* 1908(11): 1–7.

——. 1909. Algologiske notiser. VI. *K. norske Vidensk. Selsk. Skr.* 1909(2): 1–63.

——**& Howe, M.A.** 1906. New American coralline algae. *Bull. N.Y. bot. Gdn.* 4(13): 128–136, pls. 80–93.

Frauenfeld, G. 1854. Aufzahlung der Algen der Dalmatinischen Küste. *Verh. zool-bot. Ver. Wien.* 4: 317–350.

Funk, G. 1927. Die Algenvegetation des Golfes von Neapel. *Publ. Staz. zool. Napoli* 7(suppl): 1–507, pl. 1–20.

Gabrielson, P.W., Scagel, R.F. & Widdowson, T.B. 1989. *Keys to the Benthic Marine Algae and Seagrasses of British Columbia, Southeast Alaska, Washington, and Oregon.* Phycological Contribution Number 4. Department of Botany, University of British Columbia, Vancouver. vi + 187 pp.

Gallardo, T., Gomez-Garreta, A., Ribera, M.A., Alvarez M. & Conde, F. 1985. *A Preliminary Checklist of Iberian Benthic Marine Algae.* Real Jardin Botanico, Madrid. 83pp.

Garbary, D.J. 1978. An introduction to the scanning electron microscopy of red algae. *In*: D.E.G. Irvine & J.H. Price (Eds), *Modern approaches to the Taxonomy of Red and Brown Algae*, pp. 205–222. Academic Press, London.

Gordon, G.D., Masaki, T. & Akioka, H. 1976. Floristic and distributional account of the common crustose coralline algae of Guam. *Micronesica*, 12: 247–277.

Greuter, W. (Chm) 1988. I*nternational Code of Botanical Nomenclature Adopted by the Fourteenth International Botanical Congress, Berlin, July–August 1987.* Koeltz Scientific Books, Königstein, Federal Republic of Germany. xiv + 328 pp.

Guiler, E.R. 1952a. The intertidal ecology of the Eaglehawk Neck area. *Pap.*

Proc. R. Soc. Tasm. 86: 13–29, pl. 1–5.

——. 1952b. The nature of intertidal zonation in Tasmania. *Pap. Proc. R. Soc. Tasm.* 86: 31–61.

——. 1952c. The marine algae of Tasmania: check list with localities. *Pap. Proc. R. Soc. Tasm.* 86: 71–106.

——. 1954. The intertidal zonation at two places in southern Tasmania. *Pap. Proc. R. Soc. Tasm.* 88: 105–118, pl. 1.

——. 1958. Intertidal ecology of Fisher Island. *Pap. Proc. R. Soc. Tasm.* 92: 175–183, pl. 2.

——. 1960a. The intertidal zone-forming species on rocky shores of the east Australian coast. *J. Ecol.* 48: 1–28.

——. 1960b. Notes on the intertidal ecology of Trial Harbour, Tasmania. *Pap. Proc. R. Soc. Tasm.* 94: 57–62, pl. 1–3.

Guiry, M.D. 1978. *A Concensus and Bibliography of Irish Seaweeds.* J. Cramer, Vaduz. 287 pp. (Bibliotheca Phycologica, Vol. 44).

Hamel, G. & Lemoine, M. 1953. Corallinacées de France et d'Afrique du Nord. *Archs Mus. Hist. nat. Paris.* Ser. 7. 1: 15–136.

Hariot, P. 1889. Algues. *Mission Sci. Cap Horn* 5(Bot): 3–109, pl. 1–9.

Harvey, W.H. 1849. *Nereis Australis.* Part II. Pages 65–124 (plates 26–50). Reeve, London. Note: For data on publication date, see Taxon 17: 82, 725 (1968). A notice of Part I also appears in Lond. J. Bot. 7: 49–52 (1848).

——. 1860. Algae. *In*: J.D. Hooker, *The Botany of the Antarctic Voyage, Part III. Flora Tasmaniae* Vol. 2, pp. 242–383, pls 185–196. L. Reeve, London.

——. 1863. *Phycologia Australica.* Vol. 5. L. Reeve, London.

Harvey, W.H. & Hooker, J.D. 1847 Algae. *In*: J.D. Hooker, The *Botany of the Antarctic Voyage, Part I. Flora Antarctica*, pp. 175–193; 454–502.

Hauck, F. 1883. *Die Meeresalgen Deutschlands und Osterreichs.* Part 5 (pp. 225–272); Part 6 (pp. 273–320), pl. 1–5. E. Kummer, Leipzig.

Heydrich, F. 1897a. Melobesieae. *Ber. dt. bot. Ges.* 15: 403–420, pl. 18.

——. 1897b. Corallinaceae, insbesondere Melobesieae. *Ber. dt. bot. Ges.* 15: 34–71, Taf. 3.

——. 1900. Weitere Ausbau des Corallineensystems. *Ber. dt. bot. Ges.* 18: 310–317.

——. 1901. Die Lithothamnien des Museum d'Histoire Naturelle in Paris. *Bot. Jb.* 28: 529–545, Taf. XI.

——. 1911. *Lithophyllum incrustans* Phil. mit einem Nachtrag über *Paraspora fruticulosa* (Ktz.) Heydrich. *Biblthca bot.* 18(75): 1–24, pl. 1–2.

Hoek, C. van den, Breeman, A.M., Bak, R.P.M. & van Buurt, G. 1978. The distribution of algae, corals, gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing coral reef of Curacao, Netherlands Antilles. *Aquat. Bot.* 5: 1–46.

Holmgren, P., Holmgren, N.H. and Bartlett, L.C. 1990. *Index Herbariorum, Pt. 1. The Herbaria of the World.* Ed. 8. Koeltz Scientific Books, Königstein. x + 693 pp. [*Regnum Vegetabile* Vol. 120].

Hooker, J.D. See Harvey 1860 and Harvey & Hooker 1847.

Howe, M.A. 1918. Class 3. Algae. Pages 489–540 *In*: Britton, N.L., *Flora of Bermuda.* C. Scribner's Sons, New York.

——. 1920. Class 2. Algae. Pages 553–631 *In*: Britton, N.L. and Millspaugh, C.F. *The Bahama flora.* Privately published, New York.

Ishijima, W. 1954. *Cenozoic Coralline Algae from the Western Pacific* 87 pgs. 49 pls. Privately Published, Tokyo.

Johansen, H.W. 1981. *Coralline Algae, a First Synthesis.* CRC Press, Boca Raton, Florida. [vii] + 239 pp.

Johnson, J.H. 1965. The genus *Lithophyllum* and its fossil representatives. Pages 1–65 *In*: J.H. Johnson & W.H. Adey, Studies of Lithophyllum and related algal genera. *Colo. Sch. Mines Q.* 60(2): 1–105.

—— & Ferris, B.J. 1948. Eocene algae from Florida. *J. Paleont.* 22: 762–766, pl. 116–117.

King, R.J. 1973. The distribution and zonation of intertidal organisms in Bass Strait. *Proc. R. Soc. Vict.* 85: 145–162, pl. 10.

Kjellman, F.R. 1883. The algae of the Arctic Sea. *K. svenska Vetensk. Akad. Handl.* 20(5): 1–351, pls. 1–31.

Kornmann, P. & Sahling, P.H. 1977. Meeresalgen von Helgoland. *Helgolander wiss. Meeresunters.* 29: 1–289.

Kützing, F.T. 1849. *Species Algarum.* F.A. Brockhaus, Lipsiae. vi + 922 pp.

Kylin, H. 1944. Die Rhodophyceen der Schwedischen Westkueste. *Acta Univ. lund.* N.F., Avd. 2. 40(2): 1–104, pl. 1–32.

Laing, R.M. 1901. A list of the seaweeds of Norfold Island. *Trans. Proc. N.Z. Inst.* 33: 299–301.

Lamouroux, J.V.F. 1812. Extrait d'un mémoire sur la classification des polypiers coralligènes non entièrement pierreux. *Nouv. Bull. Sci. Soc. philom.* Paris 3: 181–188.

——. 1816. *Histoire des Polypiers Coralligènes Flexibles, Vulgairement Nommés Zoophytes.* F. Poisson, Caen. lxxxiv + chart + 559 pp., 19 pl.

Lawson, G.W. & John D.M. 1987. The marine algae and coastal environment of tropical West Africa (second edition). *Beih. nov. Hedwigia* 93: i–vi, 1–415.

Lebednik, P.A. 1978. Development of male conceptacles in *Mesophyllum* Lemoine and other genera of the Corallinaceae (Rhodophyta). *Phycologia* 17: 388–395.

Lee, R.K.S. 1967. Taxonomy and distribution of the melobesioid algae of Rongelap Attol, Marshall Islands. *Can. J. Bot.* 45: 985–1001, pl. 1–9.

Lemoine, MME. P. 1912. Catalogue des mélobésiées de l'Herbier Thuret (Muséum National d'Histoire Naturelle à Paris). *Bull. Soc. bot. Fr.* 58: LI–LXV. (Journal volume is dated 1911, but last portion appeared in 1912.)

——. 1913a. Mélobésiées. Revision des mélobésiées Antarctiques. *In*: Charcot, J., *Deuxième Expedition Antarctique Française (1908–1910). Sciences Naturelles, Vol. 1. Botanique.* 67 pgs. + 2 pls. Masson, Paris.

——. 1913b. Mélobésiées de l'ouest de l'Irlande (Clew Bay). *Nouv. Archs Mus. Hist. nat., Paris* Ser. 5, 5: 121–145.

——. 1915. Calcareous algae. *Rep. Dan. oceanogr. Exped. Mediterr.* 2(KI): 1–30, 1 pl.

——. 1917. Corallinaceae. Subfam. 1 Melobesieae. Pages 147–182 *In*: F. Boergesen, The marine algae of the Danish West Indies III Rhodophyceae, part c. *Dansk. bot. Ark.* 3: 145–240.

——. 1921. Note sur les algues calcaires recueillies par MM. A. et L. Joleaud et catalogue des mélobésiées des côtes françaises de la méditerranée. *Bull. Soc. linn. Provence* 3: 5–15.

——. 1924. Melobesieae. Page 36 *In*: C.H. Ostenfeld, Plants from Beta Island, St. Domingo. *Dansk bot. Ark.* 4(7): 1–36.

——. 1929. Fam 6—Corallinaceae. Subfam. 1. Melobesieae. Pages 19–68 *In*: F. Boergesen, Marine algae from the Canary Islands. III Rhodophyceae. Part II Cryptonemiales, Gigartinales, and Rhodymeniales. *Biol. Meddr.* 8(1): 1–97.

——. 1930. Les Corallinacées de l'archipel des Galapagos et du Golfe de Panama. *Archs Mus. Hist. nat. Paris.* Ser. 6, 4: 37–88, pls. 1–4.

——. 1939. Les algues calcaires fossiles de l'Algerie. *Mater. Carte geol. Alger (Ser. 1, paleont.)* 9: 1–131, pl. 1–3.

——. 1971. Apparition de la structure monostromatique dans un thalle epais de *Dermatolithon* (Mélobésiées, Corallinacées). *Bull. Soc. bot. Fr.* 117: 547–562.

——. 1976. Le genre *Lithoporella* Foslie (Algue Rhodophycée Corallinacée) au Tertiaire et au Quaternaire. *Bull. Soc. geol. Fr.* Ser. 7, 18: 773–787.

Levin, D.A. 1979. The nature of plant species. *Science* 204: 381–384.

Levring, T. 1943. Die Corallinaceen der Juan Fernandez-Inseln. *In*: C. Skottsberg (Ed.), *The Natural History of Juan Fernandez and Easter Island.* Vol. 2 (Botany), pp. 753–757. Almquist & Wiksells, Uppsala.

——. 1946. A list of marine algae from Australia and Tasmania *Acta Horti gothoburg.* 16: 215–227.

——. 1974. The marine algae of the archipelago of Madeira. *Bolm. Mus. munic. Funchal* 28: 5–111.

Lewis, J.A. 1984. *Checklist and Bibliography of Benthic Marine Macroalgae Recorded from Northern Australia. I. Rhodophyta.* Materials Research Laboratories, Department of Defence, Melbourne, Victoria. Report MRL–R–912. [i] + 97 pp., 1 Fig.

Littler, D.S., Littler, M.M., Bucher, K.E. & Norris, J.E. 1989. *Marine Plants of the Caribbean. A Field Guide from Florida to Brazil.* Smithsonian Institution Press, Washington, D.C. viii + 263 pp.

Littler, M.M. 1971. *Tenarea tesselatum* (Lemoine) Littler, comb. nov., an unusual crustose coralline (Rhodophyceae, Cryptonemiales) from Hawaii. *Phycologia* 10: 355–359.

——. 1973. The distribution, abundance and communities of deepwater Hawaiian crustose Corallinaceae (Rhodophyta, Cryptonemiales) *Pacif. Sci.* 27: 281–289.

Lucas, A.H.S. 1909. Revised list of Fucoideae and Florideae of Australia. *Proc. Linn. Soc. N.S.W.* 34: 9–60.

——. 1912. Supplementary list of the marine algae of Australia. *Proc. Linn. Soc. N.S.W.* 37: 157–171.

——. 1929. A census of the marine algae of South Australia *Trans. R. Soc. S. Aust.* 53: 45–53.

——. & Perrin, F. 1947. *The Seaweeds of South Australia. Part II. The Red Seaweeds.* Government Printer, Adelaide. pp. 11–458.

Magruder, W.H. & Hunt, J.W. 1979. *Seaweeds of Hawaii.* Oriental Publishing Co, Honolulu, Hawaii. 116 pp.

Masaki, T. 1968. Studies on the Melobesioideae of Japan. *Mem. Fac. Fish. Hokkaido Univ.* 16: 1–80, pls. 1–79.

& Tokida, J. 1960. Studies on the Melobesioideae of Japan. II. *Bull. Fac. Fish. Hokkaido Univ.* 10(4): 285–290, pl. 1–8.

Maslov, V.P. 1956. Fossil calcareous algae of the U.S.S.R. *Trudy Inst. geol. Nauk. Mosk.* 160: 1–301, pl. 1–86. (In Russian).

Mason, L.R. 1953. The crustaceous coralline algae of the Pacific Coast of the United States, Canada and Alaska. *Univ. Calif. Publs Bot.* 26: 313–390, pls. 27–46.

Mastrorilli, V.I. 1968. Nuovo Contributo allo studio delle Corallinacee Dell'oligocene ligure-piemontese: I reperti della Tav. TTA Pozone. *Atti Ist. geol. Univ. Genova* 5: 153–406, pl. 1–42.

May, D.I. & Woelkerling, Wm. J. 1988. Studies on the genus *Synarthrophyton* (Corallinaceae, Rhodophyta) and its type species, *S. patena.* (J.D. Hooker et W.H. Harvey) Townsend. *Phycologia* 27: 50–71.

May, V. 1965. A census and key to the species of Rhodophyceae (Red Algae) recorded from Australia. *Contr. N.S.W. natn. Herb.* 3(6): 349–429.

Möbius, M. 1892. Enumeratio algarum ad insulam Maltam collectarum. *Notarisia* 7: 1436–1449.

Nägeli, C. 1858. *Die Stärkekörner*. Vol. 2 of Naegeli, C. & Cramer, C., Pflanzenphysiologische Untersuchenungen. Friedrich Schulthess, Zurich. x + 624 pp., 10 pl.

Newton, L. 1931. *A Handbook of the British Seaweeds*. British Museum [Natural History], London. xiii + 478 pp.

Nichols, M.B. 1909. Contributions to the knowledge of the California species of crustaceous corallines II. *Univ. Calif. Publs Bot.* 3: 349–370, pl. 10–13.

Notoya, M. 1974. Spore germination in crustose coralline *Tenarea corallinae, T. dispar*, and *T. tumidula. Bull. Jap. Soc. Phycol.* 22: 47–51.

Okamura, K. 1936. *Japanese Marine Algae*. Uchidarokakuko, Tokyo. [11] + 964 + [11] pp., 427 Figs.

Park, C.H. 1980. The crustose coralline algae (Rhodophyta, Cryptonemiales) in Korea. *Bull. nat. Fish. Univ. Busan* 20(1): 1–30.

Parke, M. & Dixon, P.S. 1976. Check-list of British marine algae—third revision. *J. mar. biol. Ass. U.K.* 56: 527–594.

Penrose, D. 1991. *Spongites fruticulosus* (Corallinaceae, Rhodophyta), the type species of *Spongites,* in southern Australia. *Phycologia* 30: 438–448.

Penrose, D. 1992. *Neogoniolithon fosliei* (Corallinaceae, Rhodophyta) the type species of *Neogoniolithon*, in southern Australia. *Phyclogia* 31(3/4): in press.

Penrose, D. & Woelkerling, Wm. J. 1988. A taxonomic reassessment of *Hydrolithon,* Foslie, *Porolithon* Foslie and *Pseudolithophyllum* Lemoine emend. Adey (Corallinaceae, Rhodophyta) and their relationships to *Spongites* Kützing. *Phycologia* 27: 159–176.

Penrose, D. & Woelkerling, Wm. J. 1991. *Pneophyllum fragile* in southern Australia: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). *Phycologia* 30: 495–506.

Penrose, D. & Woelkerling, Wm J. 1992. A reappraisal of *Hydrolithon* (Corallinaceae, Rhodophyta) and its relationship to *Spongites. Phycologia* 31: 81–88.

Pham-Hoang Ho. 1969. *Marine Algae of South Vietnam*. Trung-tam Hoc-Lieu, Saigon. [iv] + 558 pp.

Philippi, R. 1837. Beweis dass die Nulliporen Pflanzen sind. *Arch. Naturgesch.* 3: 387–393, pl. 9, fig 2–6.

Pimentel, R.A. & Riggins, R. 1987. The nature of cladistic data. *Cladistics* 3: 201–209.

Preda, A. 1908. *Florideae. Flora Italica Cryptogamia Part II Algae. Vol. 1, Fasc. 2.* Societa botanica italiana, Florence. 459 pgs.

Porter, D.M. (Ed.) 1987. Darwin notes on Beagle plants. *Bull. Br. Mus. nat. Hist. (Hist. ser.)* 14: 145–233.

Price, J.H., John, D.M., & Lawson, G.W.. 1986. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. IV. Rhodophyta (Florideae) 1. Genera A–F. *Bull. Br. Mus. nat. Hist. (Bot. ser.)* 15: 1–122.

Printz, H. (Ed.) 1929. M. Foslie—Contributions to a Monograph of the Lithothamnia. *K. Norske Vidensk. Selsk. Museet, Trondhjem.* 60 pgs + 75 pls.

Reinbold, T. 1898. Die Algen der Lacepede und Guichen Bay (Süd Australien) und deren naherer Umgebung, gasammelt von Dr. A. Engelhart-Kingston, bestimmt durch Th. Reinbold-Itzehoe. II. *Nuova Notarisia.* 9: 33–54.

——. 1899. Meeresalgen von Investigator Street (Süd-Australien) ... *Hedwigia* 38: 39–51.

—— . 1900. Meeresalgen von den Norfolk Inseln. *Nuova Notarisia* 11: 147–153.

Rosanoff, S. 1866. Recherches anatomiques sur les Melobesiees. *Mém. Soc. Imp. Sc. nat. Math. Cherbourg.* 12: 5–112, pls. 1–7.

Rosenvinge, L.K. 1917. The marine algae of Denmark. Part I. Rhodophyceae II. (Cryptonemiales). *K. danske Vidensk. Selsk. Skr.*, Ser. 7 (Natur. og Math. Afd.) 7: 155–283, pl. 3–4.

Saenger, P. 1974. Natural history of the Hogan Group. 2. Some marine algae from Hogan Island, Bass Strait, with an account of the marine zonation. *Pap. Proc. R. Soc. Tasm.* 107: 73–81.

Setchell, W.A. & Mason, L.R. 1943. *Goniolithon* and *Neogoniolithon:* Two genera of crustaceous coralline algae. *Proc. Natn. Acad. Sci. Wash.* 29: 87–92.

Silva, P.C. 1984. The role of extrinsic factors in the past and future of green algal systematics. *In* D.E.G. Irvine & D.M. John (Eds), *Systematics of the Green Algae*, pp. 419–433. Academic Press, London.

Smith, G.M. 1944. *Marine Algae of the Monterey Peninsula California* Stanford University Press, Stanford, Calif. vii + 622 pp.

Solms-Laubach, H. 1881. Die Corallinenalgen des Golfes von Neapel und der angrenzenden meeres-abschnitte. *Fauna Flora Golf. Neapel* 4: 1–64, pl. 1–3.

Sonder, O.G. 1880. Algae australianae hactenus cognitae. *In*: F. Meuller (Ed.), *Fragmenta Phytographiae Australiae. Supplementum ad Volumen undecinum I*, pp. 1–42. Government Printer, Melbourne.

South, G.R. & Tittley, I. 1986. *A Checklist and Distributional Index of the Benthic Marine Algae of the North Atlantic Ocean.* Huntsman Marine Laboratory [St. Andrews, New Brunswick, Canada] & British Museum (Natural History) [London]. 76pp.

Steneck, R.S. & Adey, W.H. 1976. The role of environment in control of morphology in Lithophyllum congestum, a Caribbean algal ridge builder. *Bot. mar.* 19: 197–215.

Stephenson, T.A. & Stephenson, A. 1972. *Life Between Tidemarks on Rocky Shores*. W.H. Freeman & Co., San Francisco. xiii + 425 pp.

Suneson, S. 1943. The structure, life-history, and taxonomy of the Swedish Corallinaceae. *Acta Univ. lund.* N.F. Avd. 2, 39(9): 1–66, pl. 1–9.

——. 1950. The cytology of the bispore formation in two species of *Lithophyllum* and the significance of the bispores in the Corallinaceae. *Bot. Notiser* 1950: 429–450.

——. 1982. The culture of bisporangial plants of *Dermatolithon litorale* (Suneson) Hamel et Lemoine (Corallinaceae, Rhodophyta). *Br. phycol. J.* 17: 107–116.

Taylor, W.R. 1928. The marine algae of Florida with special reference to the Dry Tortugas. *Pap. Tortugas Lab.* 25: 1–219, pl. 1–37.

——. 1945. Pacific marine algae of the Allan Hancock expeditions to the Galapagos Islands. *Allan Hancock Pacif. Exped.* 12: 1–528.

——. 1957. *Marine Algae of the Northeastern Coast of North America.* 2 ed. 3 printing (1966) with corrections. (U. Michigan Press: Ann Arbor, Michigan. ix + 509 pp.

——. 1960. *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas.* U. Michigan Press, Ann Arbor, Michigan. ix + 860 pages.

Tittley, I., Irivne, L. & Kartawick, T. 1984. *Catalogue of Type Specimens and Geographical Index to the Collections of Rhodophyta (red algae) at the British Museum (Natural History).* British Museum (Natural History), London. 64pp.

Townsend, R.A. 1979. *Synarthrophyton*, a new genus of Corallinaceae (Cryptonemiales, Rhodophyta) from the southern Hemisphere. *J. Phycol.* 15: 251–259.

——. 1981. Tetrasporangial conceptacle development as a taxonomic character in the Mastophoroideae and Lithophylloideae (Rhodophyta). *Phycologia* 20: 407–414.

Townsend, R.A. & Adey, W.H. 1990. Morphology of the Caribbean alga: *Goniolithon improcerum* Foslie et Howe in Foslie (Corallinaceae, Rhodophyta). *Bot. mar.* 33: 99–116.

Tseng, C.K. 1983. *Common Seaweeds of China*. Science Press, Beijing, China. x + 316pp.

Turner, J.A. & Woelkerling, W.J. 1982. Studies on the *Mastophora*–*Lithoporella* complex (Corallinaceae, Rhodophyta). I. Meristems and thallus structure and development. *Phycologia* 21: 201–217.

Wilks, K. M. & Woelkerling, Wm J. 1991. Southern Australian species of *Melobesia* (Corallinaceae, Rhodophyta). *Phycologia* 30: 507–533.

Woelkerling, Wm. J. 1983a. A taxonomic reassessment of *Lithothamnium* (Corallinaceae, Rhodophyta) based on studies of R.A. Philippi's original collections. *Br. phycol. J.* 18: 165–197.

——. 1983b. A taxonomic reassessment of *Lithophyllum* Philippi (Corallinaceae, Rhodophyta) based on studes of R.A. Philippi's original collections. *Br. phycol. J.* 18: 299–328.

——. 1984. *Foslie and the Corallinaceae: an Analysis and Indexes.* J. Cramer, Vaduz. 142pp. (Bibliotheca Phycologica Vol. 69).

——. 1985. A taxonomic reassessment of *Spongites* (Corallinaceae, Rhodophyta) based on studies of Kützing's original collections. *Br. phycol. J.* 20: 123–153.

——. 1986. The genus *Litholepis* (Corallinaceae, Rhodophyta): Taxonomic status and disposition. *Phycologia* 25: 253–261.

——. 1987. The genus *Choreonema* in southern Australia and its subfamilial classification within the Corallinaceae (Rhodophyta). *Phycologia* 26: 111–127

——. 1988. *The Coralline Red Algae: An Analysis of the Genera and Subfamilies of Nongeniculate Corallinaceae.* British Museum (Natural History), London and Oxford University Press, Oxford. xi + 268 pp.

——. 1991. The status and disposition of *Perispermon* (Corallinaceae, Rhodophyta). *Phycologia* 30: 135–144.

——**, Chamberlain, Y.M. & Silva, P.C.** 1985. A taxonomic and nomenclatural reassessment of *Tenarea, Titanoderma* and *Dermatolithon* (Corallinaceae, Rhodophyta) based on studies of type and other critical specimens. *Phycologia* 24: 317–337.

——**& Foster, M.S. 1989**. A systematic and ecographic account of *Synarthrophyton schielianum* sp.nov. (Corallinaceae, Rhodophyta) from the Chatham Islands. *Phycologia* 28: 39–60.

——**& Irvine, L.M.** 1986. The typification and status of *Phymatolithon* (Corallinaceae, Rhodophyta). *Br. phycol. J.* 21: 55–80.

——&——. 1988. General characteristics of nongeniculate Corallinaceae. *In*: Wm. J. Woelkerling, *The Coralline Red Algae: An Analysis of the Genera and Subfamilies of Nongeniculate Corallinaceae*, pp. 4–28. British Museum (Natural History), London and Oxford University Press, Oxford.

——& **Penrose, D.** 1988. *Spongites* Kützing. *In*: Wm. J. Woelkerling, *The Coralline Red Algae: An Analysis of the Genera and Subfamilies of the Nongeniculate Corallinaceae*, pp. 150–157. British Museum (Natural History), London and Oxford University Press, Oxford.

Womersley, H.B.S. 1959. The marine algae of Australia. *Bot. Rev.* 25: 545–614.

——. 1981. Marine ecology and zonation of temperate coasts. *In*: N.M. Clayton & R.J. King (Eds), *Marine Botany: An Australasian Perspective*, pp. 211–240. Longman Cheshire, Melbourne.

——. 1984. *The Marine Benthic Flora of Southern Australia. Part I.* Government Printer, Adelaide, S. Australia. 329 pp.

——& **King, R.J.** 1990. Ecology of temperate rocky shores. *In*: N.M. Clayton & R.J. King (Eds), *Biology of Marine Plants*, pp.267–295. Longman Cheshire, Melbourne.

Wynne, M.J. 1986. A checklist of benthic marine algae of the tropical and subtropical western Atlantic. *Can. J. Bot.* 64: 2239–2281.

Zinova, A.D. 1967. *The Red, Brown, and Green Algal Flora of the Southern Seas of the U.S.S.R.* Academy of Sciences U.S.S.R., Moscow. (In Russian). 397 + [4] pp.

TAXONOMIC INDEX

British Museum (Natural History) Publications

THE CORALLINE RED ALGAE
An analysis of the genera and subfamilies of the nongeniculate Corrallinaceae

W.J. Woelkerling

Nongeniculate coralline red algae (Corallinales, Rhodophyta) are both abundant in and vital to coral reefs, cementing the coral animal skeletons into a durable reef framework. In colder waters they form pavements of many square kilometres on the sea bed. It is one of the aims of this study to help resolve outstanding difficulties relating to taxonomy of the group. Extremely well illustrated with over 60 pages of scanning electron micrographs.

1988, 245 × 176 mm, 268 pp, 82 scanning electron micrographs, 259 figs, 19 tables.
Co-published with Oxford University Press.
0 198 54249 6 Hardback **£40.00**

TAXONOMY AND BIOGEOGRAPHY OF MACQUARIE ISLANDS SEAWEEDS

R.W. Ricker
1987, 175 × 250 mm, 344 pp, 126 figs.
0 565 00998 2 Hardback **£40.00**

SEAWEEDS OF THE BRITISH ISLES

Vol. 1. Part 1. Rhodophyta. Introduction, Nemaliales, Gigartinales. *P.S. Dixon & L.M. Irvine.*
1977, xi + 252 pp, 90 figs.
0 565 00781 5 Paperback **£15.00**

Vol. 1. Part 2A. Cryptonemiales (*sensu stricto*), Palmariales, Rhodymeniales. *L.M. Irvine.*
1983, xii + 115 pp, 28 figs.
0 565 00871 4 Paperback **£15.00**

Vol. 2. Chlorophyta. *E.M. Burrows.*
1991, 256 pp.
0 565 00981 8 Paperback **£27.00**

Vol. 3. Part 1. Fucophyceae (Phaeophyceae). *R.L. Fletcher.*
1987, 145 × 210 mm, 359 pp, 90 figs, 15 plates.
0 565 00992 3 Paperback **£30.00**

Vol. 4. Tribophyceae (Xanthophyceae). *T. Christensen.*
1987, 145 × 210 mm, 36 pp, 8 figs.
0 565 00980 X Paperback **£7.50**

CONTENTS

Bulletin British Museum (Natural History)
BOTANY SERIES
Vol. 22, No. 1, June 1992