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A TAXONOMIC REASSESSMENT OF LITHOTHAMNIUM (CORALLINACEAE, RHODOPHYTA) BASED ON STUDIES OF R. A. PHILIPPI'S ORIGINAL COLLECTIONS

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Critical studies of the original collections upon which Lithothamnium Philippi (Corallinaceae, Rhodophyta) is based have revealed that none of the five species included in the initial presentation conforms to any modern concept of the genus. Two species are referrable to Amphiroa and one each to Goniolithon, Lithophyllum and Pseudolithophyllum. Since 1897, the name Lithothamnium Philippi has been widely and persistently applied to a taxon not including its nomenclatural type and it therefore must be rejected under Article 69 of the International Code of Botanical Nomenclature. After considering various alternative solutions to the problem of a replacement for one of the more widely used algal names in the botanical and geological literature, it is proposed to conserve Lithothamnion Heydrich, based on the selected lectotype species L. muelleri Lenormand ex Rosanoff, against Lithothamnium Philippi. Detailed morphological-anatomical accounts of specimens in the type collections are presented along with relevant historical data on the genus and on the various species studied.

Philippi (1837) established the genus Lithothannium (Corallinaceae, Rhodophyta) for rigid calcareous plants possessing cylindrical or somewhat compressed axes and dichotomous branches; previously such organisms usually had been referred to as nullipores, and these were considered to be animals (see Lamarck, 1816, p. 203; Lamarck, 1836, p. 306). Based on collections from the coast of Sicily, Philippi assigned five species to the genus, four of which [L. crassum(?), L. gracilis, L. ramulosum, L. rubrum] were newly described. For the fifth species [L. byssoides], Philippi listed Nullipora byssoides Lamarck and Millepora polymorpha var. globosa Esper as probable synonyms. The Lamarck and Esper taxa originally had been described as animals. In 1953, Mason selected L. ramulosum Philippi as lectotype species. Schmitz' (1889) choice of L. fasciculatum (Lamarck) Areschoug as lectotype and Hamel & Lemoine's (1953) choice of L. calcareum (Pallas) Areschoug as lectotype are not tenable since they were not included in the initial presentation of Lithothannium Philippi.

The original concept of *Lithothamnium* has undergone considerable refinement since 1837, and in more recent botanical publications (e.g. Adey, 1966, 1970a; Bressan, 1974; Cabioch, 1972; Cabioch & Giraud, 1978; Hamel & Lemoine, 1953; Johansen, 1976, 1981; Kylin, 1956; Mason, 1953; Masaki, 1968) its delineation has been based primarily upon anatomical and reproductive attributes rather than upon thallus form. Presently, taxa of Corallinaceae may be referred to *Lithothamnium* (as defined by Adey, 1966 and Johansen, 1976) if all of the following attributes occur: (1) geniculae absent; (2) tetrasporangial con-

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ceptacles multiporate and containing sporangia with apical plugs; (3) epithallial cells non-photosynthetic as well as periclinally flattened and thus angular in cross section; (4) hypothallium non-coaxial and multilayered; and (5) perithallial meristem cells elongate with cellular elongation restricted to the meristem. Since



FIG. 1. L 943, 10... 34 containing Philippi's type collections of *Lithothamnium* (L) and collections of other taxa. (\times 0.43). FIG. 2. Contents of package in Fig. 1, showing Kuetzing's notes (K) and Philippi's identification labels (P). All specimens were wrapped in the top piece of paper on which Kuetzing acknowledged Philippi as the source of the material.

1837, at least 696 of the 1483 described taxa of nongeniculate Corallinaceae known to this author have been referred to *Lithothamnium*, including over 350 taxa which never have been placed in another genus. As such, *Lithothamnium* has become associated with more taxa of nongeniculate Corallinaceae by far than any other generic name.

The relationships between various changes in the circumscription of *Litho-thamnium* and Philippi's original collections never have been determined, and Kuetzing (1869, p. 35, pl. 99) appears to have been the only subsequent investigator to provide any information on Philippi's specimens. None of the attributes upon which *Lithothamnium* presently is delineated are known definitely to occur in the generic type specimens or in any of the other collections which Philippi (1837) assigned to the genus. This troublesome situation was recognized by Adey (1966, p. 321; 1970a, p. 19), who also noted that the location of Philippi's collections apparently had become obscure (see also Foslie, 1907a, p. 21).

During a visit to the Rijksherbarium (L) in Leiden in May 1980, the present author undertook a special search to determine whether Kuetzing had retained any of the Philippi collections which he (Kuetzing, 1869, p. 35) reportedly had seen. No Philippi material was discovered among the "named" collections of Corallinaceae at Leiden. While scrutinizing the "unnamed" collections of Corallinaceae, however, one box (L 943, 10...34) labelled *Lithothamnium* was opened to disclose a variety of material (Fig. 1) including all of Philippi's original *Lithothamnium* specimens!! Not only were the specimens acknowledged by Kuetzing (Figs 1, 2) to have come from Philippi, but most collections also contained a species identification label in Philippi's script (Fig. 2).

This paper presents results of studies on Philippi's collections of *Lithothamnium* and considers in detail the taxonomic implications of those findings. Brief historical accounts of the genus and of the five species also are included.

MATERIALS AND METHODS

Data was obtained from the type specimens and other collections which currently are housed at Laboratoire de Botanique, Faculté des Sciences, Université de Caen, Caen, France, (CN); Rijksherbarium, Leiden, Netherlands, (L); National Herbarium of Victoria, Royal Botanic Gardens, Melbourne, Victoria, Australia, (MEL), or Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris, France, (PC). Microtechnique procedures follow Woelkerling (1980) and a representative set of permanent slides from all collections examined has been retained at the Department of Botany, La Trobe University, Bundoora, Victoria, Australia, (LTB). Cellular measurements quoted include the decalcified cell walls as in most cases the protoplasts of the dried specimens were distorted. Scanning electron microscopy procedures are outlined by Woelkerling (1978) and herbarium abbreviations are taken from Holmgren, Keuken & Schofield (1981). Identification of hand writings was effected by comparison with samples on herbarium specimens in L and MEL, with correspondence lodged at L and MEL, and with data in Koster (1948).

HISTORICAL BACKGROUND

Prior to 1852, most authors (except Zanardini, 1843) did not recognize *Lithothamnium* Philippi (1837) as a distinct genus. Kuetzing (1841, p. 29) at first suggested that species placed in *Lithothamnium* by Philippi might best be divided into several genera, but subsequently he listed *Lithothamnium* as a subgenus of Spongites Kuetzing (Kuetzing 1843, 1845, 1849). Decaisne (1842a, p. 100; 1842b, p. 88) considered Lithothamnium to be the same as Amphiroa Lamouroux. Other investigators (e.g. Chauvin, 1842; Johnston, 1842; Endlicher, 1843; Lindley, 1846; Montagne, 1846, 1849; Ruprecht, 1851) omit mention of Lithothamnium entirely, although Harvey (1847, pl. 74; 1849a, 1849b) subsumed Lithothamnium into Melobesia sensu Decaisne (1842a, 1842b). Areschoug (1852, pp. 508-509, 520), however, resurrected Lithothamnium (as Lithothamnion; see Mason, 1953, p. 322 for othographic note), provided a more detailed description, and characterized the genus by the absence of geniculae. Geniculae were not mentioned by Philippi (1837) in the generic diagnosis, but he discussed the occurrence of "glieder" in the text, illustrated them for L. rubrum (Philippi, 1837, pp. 389, 390, pl. 9, fig. 5a), and noted that they were different from but analogous to those of Corallina officinalis L. [Philippi's "glieder" may be geniculae or more likely are just tiers of medullary cells]. Nevertheless, the absence of geniculae has been accepted as a generic criterion by all subsequent authors even though Areschoug did not examine Philippi's specimens.

The second major refinement to the generic concept occurred when Heydrich (1897b) restricted *Lithothamnium* to taxa which have a multilayered hypothallium and which produce zonate tetrasporangia within multiporate conceptacles. Prior to that time, reproductive features were not employed to delimit Lithothamnium as a genus (e.g. see Areschoug, 1852; Ardissone, 1883; Hauck, 1883; Schmitz and Hauptfleisch, 1897), although Solms-Laubach (1881, pp. 63–64) recognized differences between uniporate and multiporate tetrasporangial conceptacles, and Rothpletz (1891, p. 310) suggested that differences in sporangial conceptacle structure could be used to recognize three groups within Lithothamnium. Philippi (1837) did not mention reproductive structures in his generic diagnosis but he discussed the occurrence of uniporate conceptacles [contents not considered] in the text and provided an illustration for L. rubrum (Philippi, 1837, p. 390, pl. 9, Fig. 5a). Nevertheless the presence of multiporate tetrasporangial conceptacles has been accepted as a generic criterion for *Litho*thamnium by all subsequent authors even though Heydrich did not examine Philippi's specimens.

Since 1897, at least 15 other non-geniculate genera with multiporate tetrasporangial conceptacles [excluding Sporolithon Heydrich (1897a) and genera known only from fossils] have been recognized (Table I), and this has affected the circumscription of Lithothamnium in various ways. Heydrich (1900, 1911) segregated Eleutherospora, Paraspora, Sphaeranthera, and Squamolithon from Lithothamnium based on presumed differences in gametic reproduction and carposporophyte development. These four taxa have not been recognized by

TABLE I. Genera of non-geniculate Corallinaceae recognized since 1897 which have multiporate tetrasporangial conceptacles and include non-fossil taxa

-	
Antarcticophyllum Mendoza, 1976	Neopolyporolithon Adey & Johansen, 1972
Clathromorphum Foslie, 1898a	Paraspora Heydrich, 1900
Eleutherospora Heydrich, 1900	Phymatolithon Foslie, 1898a
Kvaleya Adey & Sperapani, 1971	Polyporolithon Mason, 1953
Leptophytum Adey, 1966	Sphaeranthera Heydrich, 1900
Mastophoropsis Woelkerling, 1978	Squamolithon Heydrich, 1911
Melobesia Lamouroux, 1812	Synarthrophyton Townsend, 1979
Mesophyllum Lemoine, 1928	

subsequent authors, and some of Heydrich's accounts of post-fertilization development have been questioned by Suneson (1937), Lebednik (1977b) and Turner & Woelkerling (1982).

Lemoine (1928) restricted (by implication) Lithothamnium to taxa with a "non-coaxial" hypothallium and referred taxa with a "coaxial" hypothallium to Mesophyllum. Mason (1953) established Polyporolithon to include three species formerly placed in *Lithothamnium* which possessed a "hemiparasitic" habit and a mushroom-like growth form. Adey (1964, 1965, 1966) refined a number of generic concepts (Clathromorphum Foslie, Leptophytum Adey, Lithothamnium Philippi, *Phymatolithon* Foslie) and restricted *Lithothamnium* to taxa with a non-coaxial hypothallium, with elongate perithallial meristem cells, with perithallial cell elongation confined largely to meristem cells, and with thick-walled epithallial cells which appear angular in section. Mendoza (1976) further limited *Lithothamnium* to taxa in which the hypothallium is composed of many layers of horizontal filaments and in which the perithallial filaments are not stratified, and established Antarcticophyllum for taxa with one to four layers of horizontal hypothallial filaments and stratified rows of perithallial filaments. Finally, Townsend (1979) established Synarthrophyton for S. patena (Hooker & Harvey) Townsend and regarded the genus as transitional between Lithothamnium and Mesophyllum based on vegetative and reproductive features.

These proposals have had a mixed response. Mason (1953) and Masaki (1968) have regarded *Mesophyllum* as congeneric with *Lithothamnium*. Kylin (1956) listed *Clathromorphum* as a synonym of *Lithothamnium* but maintained *Mesophyllum* and *Phymatolithon* as distinct genera. Cabioch (1972) and Bressan (1974) considered *Clathromorphum*, *Leptophytum* and *Phymatolithon* to be subgenera of *Lithothamnium* but maintained *Mesophyllum* as a distinct genera. In addition, the type species of *Polyporolithon* and of its segregate genus *Neopolyporolithon* (Adey and Johansen, 1972) have been referred to *Clathromorphum* (see Lebednik, 1977a and Johansen, 1981). Johansen (1981), however, recognized *Antarcticophyllum*, *Clathromorphum*, *Leptophytum*, *Mesophyllum*, *Phymatolithon* and *Synarthrophyton* as distinct from *Lithothamnium*.

The three remaining genera listed in Table I [Kvaleya, Mastophoropsis, Melobesia (syn. Epilithon Heydrich, 1897b), are based on species which are generically distinct from Lithothamnium regardless of which modern concept of Lithothamnium one chooses to accept. These three genera also are recognized by Johansen (1981).

At present, there is no consensus of opinion as to how *Lithothamnium* should be circumscribed, and one can choose from proposals put forth by a succession of authors from Kylin (1956) to Johansen (1981). In this account, the concept of *Lithothamnium* developed by Adey (1964, 1965, 1966) and outlined by Johansen (1976) will be used as a framework for discussion, recognizing of course that the choice is subjective.

Two final points require emphasis. Although the circumscription and concept of *Lithothamnium* appears to be in a state of flux, all authors since Areschoug (1852) have restricted *Lithothamnium* to non-geniculate taxa and all authors since Heydrich (1897b) also have restricted *Lithothamnium* to taxa with multiporate tetrasporangial conceptacles. Secondly, none of the authors have confirmed that their concept of *Lithothamnium* agrees with the generic type specimens or with specimens of any species originally included in the genus by Philippi (1837). Thus, as noted by Adey (1966, p. 321), all proposals concerning *Litho-thamnium* are attended by nomenclatural uncertainties and by assumptions regarding the type collections.

THE PHILIPPI COLLECTIONS

"Lithothamnium gracile Philippi"

NOMENCLATURAL HISTORY

Philippi (1837, p. 388) established *L. gracile* for plants which were whitish and possessed divergent, linear, subfiliform, compressed, straight branches. He also described the plants as forming bushes 2.5-5 cm tall with branches up to 0.7 mm thick.

Since 1837, no one apparently has recognized *L. gracile* unequivocally as a distinct species. Kuetzing (1841, 1843, 1849) and Zanardini (1843) omit mention of the taxon. Areschoug (1852, p. 524) treated *L. gracile* as a "species inquirendae", while Solms-Laubach (1881, p. 19) regarded it as a synonym of *L. ramulosum* Philippi. Foslie (1895, pp. 90, 95) considered *L. gracile* to be conspecific with *L. coralloides* Crouan & Crouan, and De Toni (1905, p. 1,745) listed *L. gracile* as a synonym of *L. calcareum* (Pallas) Areschoug. Mason (1953, p. 322) regarded the status of *L. gracile* to be uncertain but suggested that it possibly was conspecific with *L. calcareum*. Heydrich (1911, p. 30), in contrast, recognized *L. gracile* as a distinct variety of *L. rubrum* Philippi.

LECTOTYPE COLLECTION

The original collection of *L. gracile* consists only of fragments (Fig. 3) (Philippi, 1837, p. 388), two of which remain intact. These two, together with the associated sections on permanent microscope slides prepared from a third smaller fragment, are designated here as the lectotype element. Both intact fragments are inconspicuously geniculate and contain branch apices. The smaller is 11 mm long, unbranched, and is composed of two intergeniculae. The larger is 17 mm long, includes two dichotomies and contains six intergeniculae. The intergeniculae are heavily calcified, distinctly compressed, up to 0.8 mm broad and up to 4 mm long, and are devoid of intact conceptacles. The surface of one intergeniculum of the larger fragment, however, contains a single more or less circular abrasion which probably denotes the position of a once intact conceptacle.

The single intergeniculum examined anatomically (Fig. 4) consists of a number of branched, closely contiguous filaments. Each filament contains a single terminal more or less flattened epithallial cell (L, 3-6 μ m; D, 8-15 μ m; L/D, 0·2-0·6), two to four subtending cortical cells (L, 8-27 μ m; D, 8-14 μ m; L/D, 1-2·5) and an indefinite number of medullary cells. [Throughout the text, L denotes cell length, D denotes cell diameter, and L/D denotes the ratio of cell length to cell diameter]. Proximal portions of filaments, which contain most of the medullary cells, lie more or less parallel to the intergenicular axis, while more distal portions of filaments, which contain the cortical and epithallial cells,



FIGS 3-5. Lectotype of Amphiroa johanseni nom. nov. (L. gracile Philippi). FIG. 3. Lectotype collection with label in Philippi's script (\times 1·58). FIG. 4. L.S. of part of an intergeniculum showing alternating tiers of long (L) and short (S) cells (\times 132·5). FIG. 5. L.S. showing part of a geniculum (G). Distal tier of genicular cells (arrow) is severed. (\times 141·4).

arch outwards towards the intergenicular surface. Thus terminal epithallial cells lie more or less perpendicular to the intergenicular axis. Within the medulla, cells of contiguous filaments are arranged in regular, more or less distally arched tiers (Figs 4, 5); single tiers composed of longer cells (L, 120–150 μ m; D, 8–16) μ m; L/D, 8–16) alternate with single tiers composed of shorter cells (L, 63–88 μ m; D, 11–19 μ m; L/D, 5–8). At least 30 tiers of cells occurred in the intergeniculum examined. In both the medulla and cortex, cells of contiguous filaments are interconnected by secondary pits; cell fusions were not observed.

The fragment also contained part of one geniculum consisting of one intact tier of medullary cells and a second adjoining tier of distally severed medullary cells (Fig. 5). The genicular cells appear to be much thicker walled than the intergenicular medullary cells but were similar in size. Neither secondary pit connections nor cell fusions were seen between cells of contiguous filaments.

Reproductive structures did not occur.

TAXONOMIC DISPOSITION

The lectotype material of *L. gracile* Philippi clearly belongs to the genus *Amphiroa* Lamouroux (1812) as delineated by Johansen (1976, 1981), Cabioch (1972) and Ganesan (1968). Philippi's specimens are geniculate (with geniculae composed of several tiers of cells), dichotomously branched, possess cortical and medullary cells interconnected with secondary pits, have alternating tiers of medullary cells which vary greatly in length and appear (judging from one circular abrasion) to produce conceptacles along the intergenicular surface. Collectively these characteristics distinguish *Amphiroa* from other genera of geniculate Corallinaceae.

Transfer of L. gracile Philippi into Amphiroa necessitates use of a new specific epithet to avoid creation of a later homonym for A. gracilis Harvey (1855, p. 547); Ducker (1979, p. 96, fig. 15B) has shown that the Harvey taxon is a true Amphiroa rather than a species of Metagoniolithon. The new epithet (A. johansenii), honours Dr H. William Johansen and the numerous contributions he has made towards our understanding of the Corallinaceae. Nomenclatural details and related taxonomic data are summarized in Table II.

The relationships of A. johansenii to other species of Amphiroa remain uncertain. At least 210 other taxa have been referred to Amphiroa since Lamouroux established the genus in 1812, and the fragmentary nature of the type material of A. johansenii may make detailed comparisons difficult. Until proper comparative studies of relevant types can be made, it seems best to retain A. johansenii as a distinct species so as to avoid creating further potential nomenclatural and taxonomic confusion.

"Lithothamnium rubrum Philippi"

NOMENCLATURAL HISTORY

Philippi (1837, p. 388, pl. 9, fig. 5) established *L. rubrum* for plants which were reddish and possessed slender, filiform, terete, subflexuous branches. He also described the species as forming bushes up to 2.5 cm tall and as having branches up to 0.5 mm thick.

TABLE II. Nomenclatural changes and selected taxonomic data on taxa originally placed in the genus *Lithothamnium* by Philippi (1837)

 Amphiroa johanseni nom. nov. Replaced synonym: L. gracile Philippi (Beweiss dass die Nulliporen Pflanzen sind, Arch Naturgesch, vol. 3 1837, p. 388, non Amphiroa gracilis Harvey, 1855, p. 547) Other synonyms: L. rubrum Philippi f. gracilis (Philippi) Heydrich (1911, p. 30) Type locality: Sicily Lectotype specimen: L 943, 1034 (see fig. 3) with the attached label L. gracile Ph. in Philippi's script
 Amphiroa rubra (Philippi) comb. nov. Basionym: L. rubrum Philippi (Beweiss dass die Nulliporen Pflanzen sind, Arch. Naturgesch., vol. 3 1837, p. 388, pl. 9, fig. 5) Type locality: Sicily Lectotype specimen: L 943, 1034 (see Fig. 6) with the attached label L. rubrum Ph. in Philippi's script
 Goniolithon byssoides (Lamarck) Foslie, 1898a:5 Basionym: Nullipora byssoides Lamarck (1801:374) Other synonyms: Lithophyllum byssoides (Lamarck) Foslie (1900b:20) Lithothannium byssoides (Lamarck) Philippi (1837:388) Millepora byssoides (Lamarck) Lamarck (1816:203) Spongites byssoides (Lamarck) Kuetzing (1869:35) Type locality: Mediterranean Sea Neotype specimen: L 943, 1034 (see Fig. 12) with the attached label L. byssoides in Philippi's script.
 Lithophyllum duckeri nom. nov. Replaced synonym: L. crassum Philippi (Beweiss dass die Nulliporen Pflanzen sind, Arch. Naturgesch., vol. 3) 1837, p. 388 (non L. crassum Rosanoff, 1866, p. 93, pl. 7, figs 5, 7). Other synonyms: Lithophyllum crassum (Philippi) Heydrich (1897b, p. 411) (non Rosanoff) Lithophyllum racemus f. crassa (Philippi) Foslie (1898b, p. 9) Lithothamnium calcareum f. crassa (Philippi) Lemoine (1909, p. 552) Spongites crassa (Philippi) Kuetzing (1869, p. 35, pl. 99, fig. A) Stichospora crassa (Philippi) Heydrich (1900, p. 316) Type locality: Sicily Lectotype specimen: L 943, 1034 (see Fig. 17) with the associated label L. crassum Ph. in Philippi's script
 Pseudolithophyllum ramulosum (Philippi) comb. nov. Basionym: Lithothamnium ramulosum Philippi 1837:388 Other synonyms: Lithothamnium fruticulosum f. ramulosa (Philippi) Foslie (1900b:13) Paraspora ramulosa (Philippi) Heydrich [1908:55 (nom. prov.)] Paraspora fruticulosa f. ramulosa (Philippi) Heydrich (1908:53) Spongites ramulosa (Philippi) Kuetzing (1869:35) Type locality: Sicily Lectotype specimen: L 943, 10 34 (see Fig. 23) with the associated label L. ramulosum Ph. in Philippi's script

Lithothamnium rubrum subsequently has been recognized as a distinct species (e.g. Heydrich, 1911), treated as a "species inquirendae" (e.g. Areschoug, 1852; Mason, 1953, p. 322) and considered to be conspecific with *L. ramulosum* Philippi by Solms-Laubach (1881, p. 19), with *L. calcareum* (Pallas) Areschoug by De Toni (1905, p. 1,745) or with *L. coralloides* Crouan & Crouan by Foslie (1895, pp. 91, 95).

LECTOTYPE COLLECTION

The original collection of *L. rubrum* survives as two fragments (one 10 mm long; one 20 mm long) which, together with associated sections on permanent



FIGS 6–8. Lectotype of *A. rubra* (Philippi) comb. nov. (*L. rubrum* Philippi). FIG. 6. Lectotype collection with label in Philippi's script. (Scale numbers in cm). FIG. 7. SEM of geniculum and parts of two intergeniculae. (\times 84·2). FIG. 8. SEM of conceptacle near branch apex. (\times 134·2).

microscope slides prepared during this study, are designated as the lectotype element (Fig. 6). Both fragments are inconspicuously geniculate (Fig. 7), include branch apices, are dichotomously branched, and possess intact conceptacles along the surface of certain intergeniculae. The intergeniculae are heavily calcified, cylindrical to somewhat compressed, and are up to 450 μ m broad and 4 mm long. The conceptacles (Fig. 8; see also Philippi, 1837, pl. 9, fig. 5a) protrude above the surface, are up to 325 μ m in external diameter and possess more or less dome-shaped roofs which contain a single pore at the summit. Cells immediately surrounding the conceptacle pore seem markedly more calcified than other cells of the conceptacle roof (Fig. 8).

The internal structure and organization of the intergeniculae of L. rubrum Philippi (Figs 9, 10) closely resemble that found in A. johanseni nom. nov. (syn: L. gracilis Philippi). The unistratose epithallium is subtended by a cortex up to 78 μ m broad and a central medulla up to 300 μ m broad. Medullary cells are arranged in more or less convexly arched tiers. Tiers with longer cells (L, 120– 145 μ m; D, 8–13 μ m; L/D, 11–16) alternate with tiers with shorter cells (L, 65–84 μ m; D, 8–14 μ m; L/D, 5–9). Cortical cells are more or less cylindrical and 8–16 μ m long and 8–14 μ m in diameter (L/D, 0·7–2) while epithallial cells are compressed and 3–4 μ m long and 4–12 μ m in diameter (L/D, 0·3–0·8). Within the cortex and medulla, cells of contiguous filaments are interconnected by secondary pits; cell fusions were not observed. The dichotomous branching of cortical filaments noted by Philippi (1837, pl. 9, fig. 5b) occurred only occasionally in the material examined.

The partial geniculum (Fig. 9) observed anatomically is similar to that of A. *johansenii*; the thick walled medullary cells (L, 109–144 μ m; D, 7–9 μ m; L/D, 14–18) lack cell fusions or secondary pits. At least two tiers of medullary cells occur in each geniculum, as noted by Philippi (1837, pl. 9, fig. 5b).

The conceptacles examined arise from cortical tissue and contain remains of mature carposporophytes (Fig. 11). The conceptacle chambers were up to 250 μ m in diameter and 95 μ m in height; the pores were 20–30 μ m in diameter and 40–50 μ m long. The roof contained two to four layers of cortical cells interconnected by secondary pits (cell fusions not seen); these cells were overlain with a unistratose layer of epithallial cells. The pore channel appeared to be lined with unmodified cortical cells devoid of terminal epithallial cells. Details of the carposporophyte structure could not be interpreted in the material examined; however presumed carpospores were present (Fig. 11) and some resemblances between the appearance of the conceptacle contents and those mentioned in the accounts of Suneson (1937) for A. rigida and Ganesan (1968) for A. foliacea were evident.

TAXONOMIC DISPOSITION

The lectotype material of *L. rubrum* Philippi possesses all of the characteristics of *Amphiroa* Lamouroux (as discussed in the account of *L. gracile* Philippi); nomenclatural details and related taxonomic data on *A. rubra* (Philippi) comb. nov. are summarized in Table II.

The relationships of *A. rubra* to other species of *Amphiroa* remain uncertain. Prior to 1837, at least 20 taxa were referred to *Amphiroa*, of which five to seven



FIGS 9-11. Lectotype of A. rubra (Philippi) comb. nov. (L. rubrum Philippi). FIG. 9. L.S. of part of a geniculum (\times 300). FIG. 10. L.S. of part of an intergeniculum showing alternating tiers of long (L) and short (S) cells. (\times 83·1). FIG. 11. T.S. of intergeniculum with two conceptacles containing remnants of carposporophytes (\times 201).

are still retained in the genus. Until comparative studies of all relevant type collections are undertaken, the relationships of A. rubra to these earlier described taxa cannot be determined confidently. Amphiroa rubra (Philippi) comb. nov. appears to be specifically distinct from A. johansenii nom. nov. because of differences in intergenicular size and shape and differences in medullary cell dimensions. Norris & Johansen (1981) regard differences in intergenicular size and shape as important in delineating species.

"Lithothamnium byssoides (Lamarck) Philippi"

NOMENCLATURAL HISTORY

Philippi (1837, p. 388) applied the name L. byssoides to plants in hand from Sicily which were glomeruliferose and pulvinate and had short, cylindrical, subverrucose branches. Although Philippi provided no further data on his collection, he listed two "synonyms": firstly, Nullipora byssoides Lamarck (citing Lamarck, 1816, p. 203 as the reference [where Lamarck used the name Millepora byssoides (Lamarck) Lamarck] rather than Lamarck, 1801, p. 374 [where the name N. byssoides Lamarck is first used]) and secondly, M. polymorpha var., globosa (citing Esper, 1791, pl. 13 as a reference, probably because Lamarck 1816, p. 204 also had done so).

When Lamarck (1801, p. 374) established N. byssoides, he provided no diagnosis and referred only to a single figure (Seba, 1758 pl. 116, fig. 7) of the pre-Linnean polynomial "Gleba corallina alba..." without citing the text (Seba, 1758, p. 212). The Seba (1758) figure [which Pallas (1766, p. 265) lists in the synonomy of M. calcarea Pallas], however, does not show essential characteristics which would allow for proper generic placement in a modern context. The Seba text contains some general data, but Cuvier (1836, p. 497) has labelled Seba's descriptive accounts in general as "... of no authority whatever, being written without accuracy or judgement". Moreover, according to Y. Chamberlain (pers. comm.) a search of collections at PC has failed to locate any specimens which Lamarck identified as N. byssoides. Thus, N. byssoides of Lamarck appears to be based entirely on data provided by Seba (1758) which cannot be interpreted in a modern context.

When Esper (1791, p. 215) established *M. polymorpha* var. *globosa*, he specifically indicated that his taxon was equivalent to that of Seba (1758, pl. 116, fig. 7); Esper (1791, p. 213) also equated the same Seba figure with the specimen he (Esper, 1791, pl. 13) illustrated. Thus both the Esper and Lamarck taxa are linked to the same Seba (1758, pl. 116, Fig. 7) illustration, and in terms of nomenclature, the epithet "globosa" has priority at the varietal level while the epithet "byssoides" has priority at the species level.

Whether the specimens used by Philippi are conspecific with those upon which the accounts of Seba (1758), Esper (1791) and Lamarck (1801) are based remains uncertain because comparisons of the relevant types never have been undertaken, no Lamarck specimens have been found, and it is unknown whether the Seba specimens still exist. After 1837, however, the use of the specific epithet "byssoides" always has involved reference back to the account of Philippi (1837). Consequently, Philippi's specimens are chosen here to serve as neotype element for *N. byssoides* Lamarck (see Table II). The taxon in the sense of Philippi has been maintained as a distinct species of *Lithothamnium* (e.g. Areschoug, 1852; Hauck, 1883; Heydrich, 1897a), but Kuetzing (1869, p. 39, pl. 99, fig. e) ,who examined Philippi material, transferred it to *Spongites* as *S. byssoides* (Lamarck) Kuetzing. At first Foslie (1895, p. 146) used the name *Lithothamnium byssoides* (Lamarck) Philippi, but later Foslie (1898a, p. 5) placed the taxon in *Goniolithon* as *G. byssoides* (Lamarck) Foslie. Still later Foslie (1900b, p. 20) transferred it to *Lithophyllum* as *L. byssoides* (Lamarck) Foslie. De Toni (1905, 1924), Lemoine (1911) and Funk (1927, 1955) retained use of the name *Lithothamnium byssoides* but more recently, Cabioch (1972, p. 210, pl. 6, figs 1–3) and Bressan (1974, p. 104, fig. 29) have employed the name *G. byssoides* based on the Foslie 1898a concept of *Goniolithon* (see Setchell & Mason, 1943 and Johansen, 1981 for nomenclatural data on the generic name *Goniolithon*).

THE PHILIPPI COLLECTION

The Philippi collection of *Lithothamnium byssoides* survives as six fragments 5-11 mm in greatest dimension and a small number of fragments less than 3 mm long (Fig. 12). It appears as if the original intact specimen consisted of highly branched, more or less interlocked, cylindrical excrescences most of which were $1\cdot0-2\cdot5$ mm in diameter and had smooth to somewhat verrucose surfaces. Whether the drawing of Kuetzing (1869, p. 35, pl. 99, fig. e) accurately reflects the appearance of the intact Philippi specimen or represents an artistic reconstruction is uncertain, but the very regular dichotomy of excrescences depicted in the Kuetzing drawing is not evident in the remaining Philippi fragments. Geniculae do not occur and the thallus surface is heavily calcified and covered with diatoms (Fig. 13). The fragments appear to be sterile, but a few dome-shaped conceptacle-like bumps were evident on the surface (Figs 13, 14).

Anatomically, the excrescences consist of a group of closely contiguous filaments. In longitudinal sections of excrescences (Fig. 15) individual filaments are readily identifiable, but in transverse sections of excrescences (Fig. 14) the central region appears to be parenchyma-like. Individual filaments (as seen in L.S.) are composed of a small, single, terminal, transversely compressed, rounded, thin-walled epithallial cell (L, 4-6 μ m; D, 8-11 μ m; L/D, 0.4-0.8), a subterminal meristem cell, a short series of basipetal derivatives which become increasingly elongate, and an indefinite number of mature, elongate cells (L, 88-186 μ m; D, 14-20 μ m; L/D, 5-14). Individual filaments are arched in such a way that the epithallial and meristem cells lie perpendicular to the axis of the excrescence while the mature cells come to lie more or less parallel to the excrescence axis (Fig. 15). Moreover, cells of contiguous filaments are organized into distinct acropetally arched tiers (Fig. 15) and are interconnected by secondary pits (Fig. 16). Cell fusions and trichocytes were not observed. Hypothallial tissue, which does not occur in excrescences (see Cabioch, 1972) could not be identified with certainty among the fragments in Philippi's collection.

The absence of conceptacles has precluded anatomical studies of reproductive structures. Several conceptacle like bumps (Fig. 13) were examined in transverse section and found to represent excrescence primordia (Fig. 14). Developmental details remain somewhat uncertain, but excrescence branching may be initiated



FIGS 12–16. Neotype of G. byssoides (Lamarck) Foslie [Lithothamnium byssoides (Lamarck) Philippi]. FIG. 12. Neotype collection with label in Kuetzing's script. FIG. 13. SEM of excrescence primordia (\times 112). FIG. 14. T.S. of excrescence showing new branch primordium (B) and central parenchyma-like region (P). (\times 91). FIG. 15. L.S. of excrescence showing arched tiers of cells (\times 78). FIG. 16. L.S. showing epithallial cells (E), meristem cells (M) and secondary pits (arrows) between cells of contiguous perithallial filaments. (\times 690).

from divisions of the subepithallial meristem to produce cells which do not elongate markedly (L, 16-25 μ m; D, 11-14 μ m; L/D, 1.5-2.5) at least during early stages after formation. Details of subsequent development are unknown.

TAXONOMIC DISPOSITION

Proper generic placement of sterile specimens of most non-geniculate Corallinaceae usually is attended by considerable uncertainty. In the case of Philippi's collection of *L. byssoides*, however, the vegetative thallus possesses five characteristics of sufficient distinction to allow for proper generic assignment. These are: (1) the absence of geniculae; (2) the occurrence of secondary pit connections; (3) the absence of cell fusions; (4) the progressive elongation of cells behind the internal subepithallial meristem; (5) the alignment of perithallial cells into conspicuous tiers. The only currently recognized genus of Corallinaceae possessing the above combination of characters is *Goniolithon* Foslie [1898a, non *Goniolithon* Foslie (1900b)—see Setchell & Mason (1943) for nomenclatural details] as circumscribed by Cabioch (1972) and Johansen (1981). Consequently Philippi's specimens are referred to *G. byssoides* (Lamarck) Foslie; nomenclatural details and related taxonomic data are summarized in Table II.

Considerable confusion has attended the placement of taxa into Goniolithon (see Setchell & Mason, 1943), and it is uncertain, therefore, how many Corallinaceae are referable to Goniolithon Foslie 1898a as delineated by Cabioch (1972) and Johansen (1981). If one considers only taxa placed in the genus by the above authors, G. byssoides is the earliest described entity and therefore must be considered as a distinct species. Relationships to other taxa placed in the genus remain uncertain; accounts of G. papillosum (Zanardini ex Hauck) Foslie, the type species, are provided by Cabioch (1972) and Huve (1962).

The status of *Goniolithon* Foslie 1898a as a genus also has been a matter of uncertainty in recent times. Hamel & Lemoine (1953, p. 63) placed the type species (and thus the genus) into *Dermatolithon*. Johansen (1969, p. 46) first recognized *Goniolithon* as a distinct genus, but later Adey & Johansen (1972, p. 162) considered its taxonomic position uncertain and (Johansen, 1976) omitted mention of it altogether. Most recently, however, Johansen (1981, p. 11, 43, 44, 218) has followed Cabioch (1972) and again recognized *Goniolithon* as a distinct genus.

"Lithothamnium crassum Philippi"

NOMENCLATURAL HISTORY

Philippi (1837, p. 388) established L. crassum (with a query) for plants which were white, fasciculate and possessed short, thick, rounded, nodular branches. He also indicated that his plants formed nearly spherical masses with branches $3\cdot 2-4\cdot 2$ mm thick. Although Philippi listed Nullipora racemosa Goldfuss (1826, with a query) as a possible synonym, he treated the two taxa as distinct, using different specific epithets for each. [The Goldfuss taxon has been referred to Lithothamnium by Gumbel (1871) and Lemoine (1918) but neither has examined the original Goldfuss or Philippi specimens.]

Lithothamnium crassum Philippi subsequently has been placed as a distinct

species in three other genera, has been treated as a distinct variety of two other species, and has been considered conspecific with at least four other taxa. Kuetzing (1841, 1843, 1845, 1849) first regarded *L. crassum* as a probable synonym of *Spongites racemosa* Kuetzing, but later (Kuetzing, 1869, p. 35, pl. 99, fig. 1a-b) after studying Philippi's material, concluded that *Spongites crassa* (Philippi) Kuetzing and *S. racemosa* Kuetzing were distinct taxa. Harvey (1847) as well as Johnstone & Croall (1859, p. 105) in contrast, placed *L. crassum* in synonomy with *Melobesia fasciculata* (Lamarck) Harvey, while Areschoug (1852, p. 521) treated *L. crassum* as a synonym of *L. racemus* (Lamarck) Areschoug.

Heydrich (1897a, p. 62) initially used the name Lithothamnium crassum Philippi but then (Heydrich, 1897b, p. 411) transferred the taxon to Lithiphyllum. Subsequently Heydrich (1900, p. 316), established Stichospora, listing Stichospora crassa (Philippi) Heydrich as sole species. Next, Heydrich (1901a, p. 274) considered Stichospora crassa (Philippi) Heydrich to be conspecific with Spongites racemus (Lamarck) Heydrich, but then (Heydrich, 1901b, p. 536) followed Foslie (1898b, p. 9) and adopted the name Lithophyllum racemus (Lamarck) Foslie f. crassa (Philippi) Foslie. Lemoine (1909, p. 552), however, accepted none of Heydrich's opinions and instead concluded that Philippi's taxon was best referred to as Lithothamnium calcareum (Pallas) Areschoug f. crassa (Philippi) Lemoine. Later, however, Hamel & Lemoine (1953, p. 57) and Mason (1953) listed L. crassum Philippi as a synonym of Lithothamnium racemus (Lamarck) Foslie.

LECTOTYPE COLLECTION

The lectotype collection of *L. crassum* Philippi (Fig. 17) consists of a single, branched, more or less globular, nongeniculate specimen up to 43 mm long and 33 mm in diameter which apparently grew in a detached state. Nodulary excrescences arise on all sides from a central core, are irregularly furcate, have more or less rounded apices, 3-8 mm in diameter, and are up to 15 mm long. Uniporate conceptacles occur singly or in scattered groups at the tips of many excrescences (Fig. 18). Conceptacle roofs protrude only slightly above the thallus surface and calcification is so heavy that cellular detail is largely obscured. In most cases, the single pore is situated in a slight depression in the more or less flattened, dome-like roof.

Each excrescence consists of numerous closely contiguous filaments (Figs 19–21), which are organized into a unistratose epithallium, a subtending region usually five to 15 cell layers, and a broad central area of numerous cell layers. Transverse (Fig. 19) and longitudinal (Fig. 20) sections have a similar appearance; in both, the subepithallial tissues are permeated by numerous enclosed cavities which are circular to lenticular to irregular in outline. At least some of these cavities represent the remains of conceptacles which have been overgrown and become buried.

Cells of the epithallium appear to be transversely flattened and narrowly ovoid in outline (L, 3-6 μ m; D, 6-16 μ m; L/D, 0·2-0·7). Cells of both subtending regions are more or less isodiametric or somewhat elongate (L, 8-27 μ m; D, 6-14 μ m; L/D, 1-3·7), are not arranged in conspicuous tiers, and cannot be



FIGS 17–18. Lectotype of *Lithophyllum duckeri* nom. nov. (*Lithothamnium crassum* Philippi). FIG. 17. Lectotype collection with label in Philippi's script (P) and wrapper in Kuetzing's script (K). "Tab. ph" on wrapper refers to Kuetzing (1869, pl. 99). FIG. 18. SEM of tetrasporangial conceptacle. Note pore (arrow). (\times 140).

distinguished readily from each other on size, shape, or orientation. Cells in the subepithallial region, however, appear to contain chromoplast remnants and are devoid of floridean starch granules whereas cells in the broad central region lack chromoplast remnants but possess numerous floridean starch granules. Structurally both the subepithallial and central regions of these excrescences constitute perithallium (see Cabioch, 1972 for developmental details of excrescences). Perithallial growth results from a meristematic layer situated just beneath the epithallium; cell elongation is confined largely to the meristem, and cells of the meristem rarely are readily distinguishable from their immediate basipetal derivatives. Cells of contiguous filaments are interconnected by secondary pits (Fig. 21); cell fusions and trichocytes were not observed.



FIGS 19–22. Lectotype of Lithophyllum duckeri nom. nov. (Lithothamnium crassum Philippi). FIG. 19. T.S. of excrescence showing tissue organization, several empty conceptacles (CO) and cavities in tissues (\times 111). FIG. 20. L.S. of excrescence showing several buried conceptacles (CO) with remnants of a columella and with cavities (C) in tissues. (\times 108). FIG. 21. Secondary pit connections in perithallial tissues. (\times 440). FIG. 22. Remains of a tetrasporangium in a buried conceptacle. Note lines of division (arrows). (\times 496).

Anatomical studies of the hypothallial region from which the excrescences arise were not undertaken as this would have severely damaged the lectotype specimen.

Conceptacles (Figs 19, 20) presumably arise from subsurface perithallial tissue, possess more or less ovoid chambers up to 450 μ m in diameter and 225 μ m in height and are uniporate. Several tetrasporangia were observed in conceptacles which had become overgrown and buried, and remnants of a columella also were evident in several buried conceptacles (Figs 20, 22). The roofs of conceptacles near the surface contained up to seven layers of cells similar to those of the perithallium, and roof cells also were interconnected by secondary pits.

TAXONOMIC DISPOSITION

The lectotype material of *Lithothamnium crassum* Philippi clearly belongs to *Lithophyllum* Philippi (1837) as currently delineated by Johansen (1981) and Masaki (1968). The lectotype specimens are nongeniculate, possess uniporate conceptacles, and have perithallial cells which are interconnected by secondary pits (cell fusions absent) but which are not arranged in conspicuous tiers. Collectively these characteristics distinguish *Lithophyllum* from other genera of Corallinaceae. [The status of *Lithophyllum* as a genus is reassessed elsewhere (Woelkerling, 1983).]

Transfer of Lithothamnium crassum Philippi into Lithophyllum necessitates use of a new specific epithet to avoid use of a later homonym [Lithophyllum crassum (Philippi) Heydrich (1897b, p. 411)] for Lithophyllum crassum Rosanoff (1866, p. 93, pl. 7, figs 5, 7). Rosanoff's taxon is based on exsiccate material distributed by Lloyd (1860) under the nomen nudum Melobesia crassa Lloyd. The new epithet (Lithophyllum duckeri nom. nov.) honours Dr Sophie C. Ducker in recognition of her contributions to our understanding of southern Australian Corallinaceae. Nomenclatural details and related taxonomic data are summarized in Table II.

The relationships of *Lithophyllum duckeri* to other species of *Lithophyllum* remain uncertain. At least 525 other taxa have been referred to *Lithophyllum* since 1837, and until comparative studies of relevant type collections can be undertaken, it seems best to retain *Lithophyllum duckeri* as a distinct species to avoid making unsound taxonomic judgements and creating further potential nomenclatural and taxonomic confusion.

"Lithothamnium ramulosum Philippi"

NOMENCLATURAL HISTORY

Philippi (1837, p. 388) established *L. ramulosum* for plants which were white, loosely fasciculate-pulvinate and possessed more or less terete, slender, flexuous branches with sublobate apices. He also indicated that the branches were 0.7-1.1 mm thick and that the largest specimen was 3.8 cm long, 2.5 cm broad and 1.3 cm thick.

The subsequent use of Philippi's epithet "ramulosum" as well as the status and concept of the taxon Philippi described has varied considerably. Areschoug (1852, p. 524) relegated the taxon to the status of "species inquirendae", but Kuetzing (1869, p. 35, pl. 99, fig. c) who examined Philippi's material, recognized the taxon as a distinct species of Spongites [S. ramulosa (Philippi) Kuetzing]. Heydrich (1908, p. 53) placed Philippi's taxon in Paraspora as P. fruticulosa (Kuetzing) Heydrich f. ramulosa (Philippi) Heydrich; Heydrich (1908, p. 55) also used the provisional name P. ramulosa (Philippi) Heydrich. Although Kuetzing (1869) recognized his "fruticulosa" and Philippi's "ramulosa" as distinct species (of Spongites), Hauck (1883, p. 274) reduced them to a single entity [Lithothamnium fasciculatum (Lamarck) Areschoug β fruticulosum (Kuetzing) Hauck] using the Kuetzing (1841) epithet rather than the older Philippi (1837) epithet. Heydrich (1897b, p. 414), in contrast, maintained L. fasciculatum and L. fruticulosum (Kuetzing) Foslie as distinct species, and Foslie (1900b, p. 13) recognized L. fruticulosum f. ramulosa (Philippi) Foslie as a distinct form of the latter. Earlier Foslie (1895, p. 51) had treated L. ramulosum as a synonym of L. fruticulosum f. curvirostra Foslie. More recently, some authors (e.g. Hamel & Lemoine 1953, p. 87; Bressan, 1974, p. 68) have listed L. ramulosum as a synonym of L. fruticulosum even though, as noted by Adey (1970a, p. 19), the name "ramulosum" has priority and should be used. Funk (1955, p. 97), however, treated L. ramulosum as a synonym of L. fruticulosum f. crassiuscula Foslie (see also Funk, 1927, p. 429).

LECTOTYPE COLLECTION

The lectotype collection (Fig. 23) of *L. ramulosum* Philippi survives as a single, branched, more or less ovoid specimen 38 mm long and up to 31 mm broad. The plant apparently grew in a detached state, and possesses a number of simple or furcate, non-geniculate, excrescences which arise on all sides and are separated from one another by distances of (0-) 1–5 (–12) mm. The excrescences are mostly 2–4 mm in diameter, up to 10 mm long, are more or less cylindrical with rounded or somewhat tapered apices, and have a smooth to somewhat verrucose surface. Uniporate conceptacles occur singly or in groups near and at the apices of most excrescences (Fig. 24). Conceptacle roofs are more or less dome-like, protrude up to 500 μ m above the thallus surface, and are so heavily calcified that cellular detail at the thallus surface is largely obscured. Multiporate conceptacles do not occur.

Anatomically, each excrescence consists of numerous closely contiguous filaments (Figs 25, 26) which are united into a pseudoparenchymatous mass in which individual filaments commonly become diffcult to identify. Tissue organization resembles that found in *Lithophyllum duckeri* nom. nov. (Syn: *Lithothamnium crassum* Philippi). The unistratose epithallium (Fig. 26) is composed of rounded or transversely compressed to flattened thin walled cells (L, 3–6 μ m: D, 11–14 μ m; L/D, 0·3–0·5) rather than thick walled angular cells which have been said to characterize *Lithothamnium* as a genus (Adey, 1966; Johansen, 1976, 1981). The subtending perithallium includes a subepithallial region usually of five to 25 cell layers in which remnants of presumed chromoplasts occur and a broad central region of numerous layers in which the cells contain floridean starch granules. In both longitudinal and transverse sections of excrescences, perithallial cells (L, 11–28 μ m; D, 8–18 μ m; L/D, 1–2) vary in outline from



FIGS 23-24. Lectotype of *Pseudolithophyllum ramulosum* (Philippi) comb. nov. (*L. ramulosum* Philippi). FIG. 23. Lectotype collection with label in Philippi's script (P) and wrapper in Kuetzing's script (K). "Tab. ph." on wrapper refers to Kuetzing (1869, pl. 99). FIG. 24. SEM of tetrasporangial conceptacle. $(\times 92)$.

squarrulose to elongate to oval to somewhat irregular, and cells of contiguous filaments are interconnected by means of cell fusions (Fig. 26). Secondary pit connections were not observed.

Perithallial growth presumably results from a meristematic layer situated just beneath the epithallium (Fig. 26); cell elongation appears to be confined largely to the meristem, the cells of which resemble their immediate basipetal derivatives. Trichocytes were not observed. Perithallial tissues also contain cavities (Fig. 27), some of which represent remains of buried conceptacles and some of which result from unknown causes.

The hypothallial region was not examined anatomically as this would have



FIGS 25–28. Lectotype of *Pseudolithophyllum ramulosum* (Philippi) comb. nov. (*Litho-thamnium ramulosum* Philippi). FIG. 25. T.S. of excrescence showing conceptacle (CO). (\times 97). FIG. 26. L.S. of excrescence showing epithallial cells (E), subepithallial meristem cells (M) and fusions (F) between cells of contiguous perithallial filaments (\times 610). FIG. 27. L.S. showing buried conceptacle (CO) and cavities (C) in vegetative tissue (\times 104). FIG. 28. Remnants of a tetrasporangium in a buried conceptacle. Note lines of division (arrows). (\times 453).

resulted in severely damaging the lectotype specimen to obtain necessary tissues for embedding.

Conceptacles (Figs 25, 27) presumably arise from subsurface perithallial tissue, possess more or less ovoid chambers up to 520 μ m broad and 310 μ m in height, and are uniporate. Pores vary in diameter from 63–96 μ m at the surface and 111–163 μ m at the top of the chamber, and pores were up to 150 μ m long. up to 10 layers of perithallial cells have been observed in roofs of conceptacles which protruded above the surrounding thallus surface and fusions between cells of contiguous roof filaments were common. Eventually conceptacles become overgrown and buried but nevertheless remain recognizable (Fig. 27). Details of conceptacle roof formation are uncertain, but no evidence for the existence of a columella could be found. Remnants of tetrasporangia occurred in some of the buried conceptacles (Fig. 28).

TAXONOMIC DISPOSITION

The lectotype specimen of *L. ramulosum* Philippi does not conform to any modern concept of *Lithothamnium* but rather falls within the genus *Pseudo-lithophyllum* as delineated by Adey (1970a, 1970b) and Johansen (1976, 1981). Philippi's specimens are non-geniculate, possess uniporate tetrasporangial conceptacles, lack trichocytes, and have perithallial cells interconnected by cell fusions and not secondary pits. Collectively, these characteristics delineate *Pseudolithophyllum* from other genera of Corallinaceae. Nomenclatural details and related taxonomic data on *P. ramulosum* (Philippi) comb. nov. are summarized in Table II.

The relationships of *P. ramulosum* to other species of *Pseudolithophyllum* remain uncertain. Adey (1970a) included 22 species in the genus and, over all, at least 34 taxa have been referred to *Pseudolithophyllum* since Lemoine established the genus in 1913. Since, however, *P. ramulosum* predates all other species referred to the genus, the specific epithet "ramulosum" has priority within the genus.

The concept of *Pseudolithophyllum* as a genus also has been a matter of recent controversy (Adey 1970a, 1970b; Lemoine 1978). In this study, the Adey concept is followed since his conclusions are based on the examination of the type specimen (in **TRH**) of the type species [*P. discoideum* (Foslie) Lemoine]. It should be noted, however, that Adey (1970a, p. 12) did not study tetrasporangial conceptacles and that Foslie (1900a, p. 74) in the protologue of the type species (as *Lithophyllum discoideum* Foslie) stated that he never saw tetrasporangia and also indicated that he was unsure whether the empty conceptacles he saw were uniporate. Later, however, Foslie (1907b, p. 11) reported tetrasporangia and uniporate conceptacles in specimens from the sub-Antarctic.

TAXONOMIC IMPLICATIONS

STATUS OF Lithothamnium PHILIPPI

A major result to emerge from this study is that none of the original collections upon which Philippi based the genus *Lithothamnium* (Philippi, 1837) conforms to any of the modern concepts of the genus (e.g. Mason, 1953; Kylin, 1956; Masaki, 1968; Adey, 1966, 1970a; Cabioch, 1972; Johansen, 1976, 1981). Based on generic concepts outlined by Johansen (1981), the lectotype species of *Lithothamnium* is referable to *Pseudolithophyllum*, two other species are referrable to *Amphiroa*, and one each of the remaining two is referrable to *Goniolithon* and *Lithophyllum*. All these genera possess uniporate tetrasporangial conceptacles. Every circumscription of *Lithothamnium* published since 1897 however, characterizes the genus as having multiporate tetrasporangial conceptacles. Thus the name *Lithothamnium* Philippi 1837 has been used widely (for more species than any other genus of Corallinaceae) and persistently (ever since 1897) for a taxon not including its type (or any other species originally placed in the genus) and therefore must be rejected under Article 69 of the International Code of Botanical Nomenclature (Staffleu, 1978).

Rejection of *Lithothamnium* Philippi 1837 as a legitimate name necessitates consideration of a different generic name for taxa which have been associated with a modern concept (e.g. Adey, 1966; Johansen 1976) of the genus. Three alternative solutions seem possible. One is to propose a completely new generic name based on a type species and type specimen which conforms to a modern concept of "Lithothamnium". Then, as the type specimens of other taxa are re-examined, new nomenclatural combinations could be effected as necessary. Adoption of this alternative, however, could lead to several potentially undesirable consequences, including (1) the wholesale renaming of hundreds of taxa without examining relevant types (a procedure which, unfortunately, is permissible under the Code) and (2) the abandonment of a name (*Lithothamnium*) which has been used extensively for many decades in both the botanical and geological literature.

The second alternative solution is to replace *Lithothamnium* Philippi 1837 with *Apora* Gunnerus (1768), a possibility first mooted and rejected by Foslie (1898c, p. 6, 7). Use of the name *Apora*, even if permitted nomenclaturally, would lead to the same problems as proposing a new generic name. Moreover the specimens upon which Gunnerus based his genus reportedly (Foslie, 1895, p. 40) are sterile and represent more than one species. A search in May 1980 at **TRH** has failed to locate any Gunnerus material for confirming studies. Thus application of the name *Apora* would be attended by considerable uncertainty and therefore does not seem desirable.

The third solution is to conserve the name Lithothamnion Heydrich (1897b, p. 412) against the name Lithothamnium Philippi (1837, p. 387). Lithothamnion Heydrich is a later homonym (see Mason, 1953, p. 322 for note on orthography) of Lithothamnium Philippi (Art. 48.1, ICBN, Staffleu, 1978) because when Heydrich limited his genus to taxa with multiporate tetrasporangial conceptacles, L. ramulosum (the type species of Lithothamnium Philippi), which has uniporate tetrasporangial conceptacles, inadvertently was excluded. Heydrich was the first person to restrict Lithothamnium to taxa with multiporate tetrasporangial conceptacles, and virtually all subsequent investigators have done likewise. Thus the Heydrich concept has prevailed in all the post 1897 literature while the original Philippi concept has become obscure. Moreover, conservation of Lithothamnion Heydrich would obviate the need for making numerous new nomenclatural combinations and thus best serve the stability of botanical nomenclature (Art,

14.1, ICBN, Stafleu, 1978). For the above reasons, therefore, conservation appears to be the most acceptable solution.

Before effecting a proposal for conservation, however, the lectotypification of *Lithothamnion* Heydrich must be considered. Heydrich (1897b) included a heterogeneous assemblage of 71 species in his genus, at least eight of which (Table III) have been chosen subsequently as type species of other genera. Moreover, at least half of the species listed by Heydrich (1897b) were transferred into other genera by Adey (1970a). Selection of any of these taxa as lectotype species of *Lithothamnion* Heydrich or of other species with a long history of nomenclatural shunting seems unwise and could lead to further possible confusion.

 TABLE III. Species included in Lithothamnion by Heydrich (1897b) which subsequently have been selected as type species of other genera of Corallinaceae*

Lithothamnion compactum Kjellman (1883, p. 132), lectotype species of Clathromorphum Foslie (1898a)

Lithothamnion decussatum (Solms-Laubach) Foslie (1895, p. 205), type species of Sphaeranthera Heydrich (1900)

Lithothamnion fruiticulosum (Kuetzing) Foslie (1895, p. 46), type species of Paraspora Heydrich (1900)

Lithothamnion patena (Hooker & Harvey) Heydrich (1897b), type species of Synarthrophyton Townsend (1979)

* See Farr, Leussink and Stafleu (1979) for further nomenclatural data.

After detailed study of relevant material and a consideration of published information, L. muelleri Lenormand ex Rosanoff (1866) has been chosen as lectotype species of *Lithothamnion* Heydrich. Several reasons have prompted this selection. Firstly, this species appears always to have been retained within the genus Lithothamnion and appears never to have been regarded as conspecific with another, earlier described species. Secondly plants referable to this species occur commonly, at least in southern Australia, and thus specimens are fairly readily obtainable for comparative study. Thirdly, the morphological and anatomical characteristics of the type specimens (Fig. 29) of L. muelleri conforms to the circumscription of *Lithothamnion* used by Johansen (1976, 1981). Thus the type specimens possess multiporate tetrasporangial conceptacles (Figs 30, 31), have a multilayered, non-coaxial [as noted by Lemoine (1911, p. 7, footnote) and contrary to the appearance in Rosanoff (1866, pl. 6, figs 10, 11)] hypothallium (Fig. 32), have cell fusions occurring between contiguous cells of hypothallial and perithallial filaments (Fig. 32), have an epithallium composed of cells which appear more or less angular in section (Fig. 33), have a subepithallial meristem to which cellular elongation is largely confined (Fig. 33), and have a perithallium composed of numerous cell layers (Fig. 31). Trichocytes and secondary pit-connections were not observed.

The concept of *Lithothamnion* used by Johansen (1976, 1981) is based on the studies of Adey (1966) and of Adey & McKibbin (1970), and represents the most restricted of the various modern day circumscriptions of the genus (e.g. compare

Lithothamnion lenormandi (Areschoug) Foslie (1895, p. 178), type species of Squamolithon Heydrich (1911)

Lithothamnion lichenoides (Ellis & Solander) Foslie (1895, p. 206), type species of Mesophyllum Lemoine (1928)

Lithothamnion papillosum Zanardini ex Hauck (1883), lectotype species of Goniolithon Foslie (1898a)

Lithothamnion polymorphum (Linneaus) Areschoug (1852), type species of Eleutherospora Heydrich (1900) and type species of Phymatolithon Foslie (1898a).



FIG. 29. Lectotype collection of L. muelleri Lenormand ex Rosanoff from CN. (\times 0.62).

Hamel & Lemoine, 1953; Mason, 1953, Kylin, 1956; Adey, 1966; Masaki, 1968; Cabioch, 1972; Mendoza, 1976). Because *L. muelleri* falls within the comparatively restricted boundaries used by Johansen (1976, 1981), it can also serve as type species if the broader boundaries set by other investigators are shown from future study to more accurately reflect the limits of *Lithothamnion* as a genus. Relevant taxonomic data on *L. muelleri* are summarized in Table IV.



FIGS 30–33. Lectotype of *L. muelleri* Lenormand ex Rosanoff, FIG. 30. SEM of multiporate tetrasporangial conceptacle. (\times 157). FIG. 31. T.S. of thallus showing tissue organization and tetrasporangial conceptacles at the surface (SC) or buried (BC) within the perithallium. (\times 90). FIG. 32. Hypothallium (H) and lower layers of perithallium (P). Note cell fusions (arrows). (\times 315). FIG. 33. Angular epithallial cells (E) and subepithallial meristem cells (M). (\times 1235).

Taxon:	Lithothamnion muelleri Lenormand ex Rosanoff
Protologue:	Rosanoff (1866, p. 101, pl. 6, figs 8–11)
Type Locality:	Western Port (Bay), Victoria, Australia
Typification:	Lectotype-(CN, see Fig. 29); Isotype-MEL 588439
Recorded distribution:	Australia (South Australia, Victoria, Tasmania), New Zealand
	Tierra del Fuego (Picton Is), Madagascar
Selected references:	De Toni (1905, p. 1.759; 1924, p. 632)
	Foslie (1900b. p. 17;
	Hariot, 1895, p. 99)
	Heydrich (1897b, p. 413; 1901, p. 544)
	King et al. (1971, p. 121)
	Lemoine (1912, LIV; 1913; p. 24)
	Levring (1946, p. 220, fig. 4)
	Oltmans (1922, p. 268, fig. 488.2)
	Papenfuss (1964, p. 31)
	Printz (1929, p. 43, pl. 7, figs 1–10)
	Puials (1963, p. 31)
	Skottsberg (1941, p. 79)
	SROTISCES (19 11)

TABLE IV. Relevant taxonomic data on lectotype species of *Lithothamnion* Heydrich (non *Lithothamnium* Philippi)

CONSERVATION PROPOSAL

Proposal to conserve *Lithothamnion* Heydrich 1897b against *Lithothamnium* Philippi 1837 (Rhodophyta):

Lithothamnion Heydrich, Ber. dt. bot. Ges. 15: 412. 1897 (nom. cons. prop'). Lectotype species (vide this paper): L. muelleri Lenormand ex Rosanoff, Mem. Soc. Imp. Sc. Nat. Math. Cherbourg 12: 101, pl. 6, figs 8–11, 1866, Rhodophyta: Corallinaceae.

Lithothamnium R. A. Philippi, Arch. Naturgesch. 3: 387. 1837 (non. rejic. prop.). Lectotype species (vide Mason 1953: 322): L. ramulosum Philippi. Rhodophyta: Corallinaceae.

Lithothamnium Philippi (1837), as noted earlier in this paper, was established for five species and was circumscribed solely using characteristics of the vegetative thallus. Lithothamnion Heydrich (1897b), in contrast, was characterized in part by the occurrence of multiporate tetrasporangial conceptacles, a characterization which has been adopted by all subsequent authors. Heydrich (1897b) and subsequent investigators [including Mason (1953) who lectotypified Lithothamnium Philippi] all have presumed that the lectotype or at least one of the species originally included in Lithothamnium Philippi possessed multiporate tetrasporangial conceptacles. Results from this study, however, have shown this presumption to be erroneous; all of the taxa originally included in Lithothamnium Philippi possess uniporate tetrasporangial conceptacles. Thus Heydrich (1897b) unknowingly excluded all of Philippi's taxa from his genus, thereby (Art 48.1) creating a later homonym for Lithothamnium Philippi 1837.

Unless conserved (Art 48.2), the name *Lithothamnion* in the sense of Heydrich, cannot be retained. In this case, however, retention of *Lithothamnion* Heydrich appears highly desirable since the Heydrich concept or various modifications of it have been used widely and persistently in the botanical and geological literature ever since 1897 and the generic name has become associated with nearly 700 taxa of Corallinaceae. If *Lithothamnion* Heydrich (1897b) is not conserved against *Lithothamnium* Philippi (1837), the stability of nomenclature (Art 14.1) would be markedly and adversely affected, and considerable confusion would

result. Thus the name Lithothamnium Philippi (type species L. ramulosum) would have to be used (barring another conservation proposal) for taxa now referred to Pseudolithophyllum (sensu Adey, 1970a), a genus characterized by uniporate terasporangial conceptacles, and a new name would have to be employed for all taxa now referred to Lithothamnion Heydrich. The end result would necessitate hundreds of nomenclatural changes for taxa now referred to Lithothamnion Heydrich, thereby destabilizing the nomenclature of a name and concept entrenched in the botanical and geological literature since 1897. Further confusion would result, moreover, if the name Lithothamnium Philippi were retained and applied to a taxon with uniporate conceptacles because two quite different concepts and useages of a single generic name would become a part of the botanical and geological literature. To avoid these undesirable consequences, approval (Art 15.1) of the General Committee and the next International Botanical Congress is sought to conserve Lithothamnion Heydrich against Lithothamnium Philippi.

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