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Growth-forms in Non-geniculate Coralline Red Algae (Corallinales, Rhodophyta)

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Abstract

Although differences in growth-form have been widely used in delimiting taxa of non-geniculate coralline red algae (Corallinales, Rhodophyta), there has been no consistent application of the more than 100 terms employed to describe the growth-forms present, and considerable confusion has resulted. This study of over 5000 populations of non-geniculate corallines from all parts of the world has shown that an intergrading network of growth-forms with 10 focal points is present: unconsolidated, encrusting, warty, lumpy, fruticose, discoid, layered, foliose, ribbon-like and arborescent. This focal point terminology can be used to describe any specimen or species of non-geniculate coralline in a consistent, easily interpretable manner. Details of the system are provided, the relationships of the system to past proposals are discussed, and the extent to which differences in growth-forms can be used as taxonomic characters in the non-geniculate Corallinales is reviewed.

Introduction

Differences in growth-form (i.e. external appearance) have been widely used to delimit and identify genera, species and infraspecific taxa of non-geniculate coralline algae (Corallinales, Rhodophyta) for over 200 years (e.g. Linnaeus 1767: 1282-1285; Lamouroux 1816: 313-316; Philippi 1837; Areschoug 1852; Solms-Laubach 1881; Lemoine 1911; Hamel and Lemoine 1953; Adey *et al.* 1982). Foslie, who described 428 species and infraspecific taxa of non-geniculate Corallinales during the period 1891–1909 (Woelkerling 1993), based many of his taxa on slight differences in growth-form (see Woelkerling 1984 for an analysis of Foslie's approach to taxon delimitation). Subsequently, various authors have used differences in growth-form for the delimitation of species and infraspecific taxa (e.g. see publications of Lemoine (lists provided by Ardré and Cabioch 1985 and Chamberlain 1985)). In addition, growth-form differences have been used in keys for identification (e.g. Lemoine 1917; Printz 1929; Newton 1931; Hamel and Lemoine 1953; Mason 1953; Taylor 1957; Dawson 1960; Taylor 1960; Lee 1967; Masaki 1968; Chapman and Parkinson 1974; Johansen 1976; Adey *et al.* 1982; Cribb 1983; Lawson and John 1987).

One major difficulty attending the use of growth-form differences for taxonomic delimitation and in keys is that there has been inconsistency in the application of terms used to describe the range of growth-forms present. By 1960 this situation had become so confusing that Taylor (1960: 376) concluded that '...both surface and histological characters 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 regarding measurements of critical structures, that it is practically impossible to glean from the literature balanced comparative accounts of related species at the present'. Although several proposals pertaining to the description of growth-forms (Bosence 1976, 1983; Johansen 1981: 44-52; Woelkerling and Irvine 1988: 5-7; Woelkerling and Campbell 1992: 3-5) have appeared subsequently, there has been no comprehensive analysis of growth-form terminology to date, and Taylor's comments still largely apply. Indeed, a survey of 29 (of the over 2000) publications on non-geniculate corallines has shown that at least 103 different terms have been used to describe growth-forms (Table 1).

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Table 1. A non-exhaustive list of terms used to describe the growth-forms of non-geniculate Corallinales (Rhodophyta)

Sources: Foslie 1895, Foslie 1904, Foslie 1905, Printz 1929, Newton 1931, Suneson 1943, Setchell and Mason 1943, Mason 1953, Dawson 1960, Taylor 1960, Adey 1964, Adey 1966, Masaki 1968, Adey and Adey 1973, Chapman and Parkinson 1974, Bosence 1976, Gordon *et al* 1976, Johansen 1976, Magruder and Hunt 1979, Johansen 1981, Adey *et al.* 1982, Bosence 1983, Woelkerling and Irvine 1986, Lawson and John 1987, Woelkerling and Irvine 1988, Littler *et al.* 1989, Schneider and Searles 1991, Cabioch *et al.* 1992, Woelkerling and Campbell 1992

arborescent
arbusculate
club-shaped
coalescent
columnar
compressed spherical
coralloid
crateriform
crust-like
crustaceous
crustose
cushion-like clumps
cushion-shaped
disc-shaped
discoid
discoidal
ellipsoidal
encrusting
erect clumps
erect, subglobose clumps
excrescent
fasciculate
fastigiate
flabellate
flabelliform
foliaceous
foliose
fruticose
fruticose-lamellate
fruticulose
granular
head-like
hemispherical
hemispherical-shaped heads
imbricate
inverted plate-shaped
irregular
knobbly
knobby
knobby crusts
knoblike bosses
lamelliform
laminar
layered
leaf-like
leafy
lichenoid
lithophylloid
lobate
lobate-lamellate
lobed
lumpy
mammillate
monostromatic
net-work of meandering filaments
nodular
nodulose
not elegant
oligostromatic
orbicular
overlapping shelves
papillate
partly spherical
plate-like
plurilamellate
polystromatic
proliferous
prostrate
protuberant
reniform
ribbon corallines
ribbon-like
rose-like
rounded clumps
rugose
semicircular
semiendophytic
simple
smooth crusts
spheroidal
spiniform
spreading plates
squamose
squamulose
stoutly branching
sub-leafy
subglobose
subhemispheric cushions
subhemispherical masses
suborbicular
subspherical
taeniform
thick crusts
thin crusts
trumpet-shaped
tuberculate
unattached
unconsolidated
unilamellate
verruciform
wart-like
warted crusts
warty

The absence of a uniform system for describing growth-forms of non-geniculate corallines also has made it difficult to compare published accounts of taxa and to determine from these the range of growth-forms that can occur within and amongst species and genera. Moreover, a number of studies (e.g. see Taylor 1945: 178, pls 39-42; Huvé 1962; Adey 1966; Lee 1967; Steneck and Adey 1976; Bosence 1983; Penrose 1991; Penrose and Woelkerling 1991; Penrose 1992*a*, 1992*b*; Woelkerling and Campbell 1992; Woelkerling and Harvey 1992) have shown that considerable variation in growth-form can occur within a species. Thus, as noted by Huvé (1962: 234-235), differences in growth-form may be of much more limited value in delimiting species and genera than has generally been realised. Irrespective of the taxonomic value of growth-form differences, however, it is highly desirable to have a more uniform system of terminology not only for strictly morphological purposes but also for use in producing descriptions of species and genera in monographic and floristic accounts.

The aims of the present study are to determine the range of growth-forms present amongst non-geniculate Corallinales, to devise a comprehensive system of terminology to describe them, and to determine the extent to which various growth-forms can intergrade with one another and the effects this has on producing descriptions of species.

Materials and Methods

An initial survey of southern Australian non-geniculate coralline populations at LTB (Department of Botany, La Trobe University, Bundoora, Victoria, Australia) was undertaken to assess the range in growth-forms present and construct a preliminary system for describing them. This preliminary system was then tested and modified as a result of studies of the extensive mondial collections of non-geniculate corallines at BM (The Natural History Museum, Cromwell Road, London, UK). The first revision was then subjected to testing by Dr Yvonne Chamberlain (Marine Laboratory, University of Portsmouth), Drs Eric Verheij (Rijksherbarium, University of Leiden) and Dr H. W. Johansen (Departmant of Biology, Clark University), and this resulted in further modifications. The second revison was then presented to the Second International Coralline Workshop at the Fourth International Phycological Congress (Duke University, North Carolina, USA, August 1991) for comment, after which further testing was undertaken on most collections in the Foslie herbarium at TRH (Department of Botany, Museum of Natural History and Archaeology, University of Trondheim, Trondheim, Norway) and on collections from C (Botanical Museum, University of Copenhagen, Copenhagen, Denmark), L (Rijksherbarium, University of Leiden, Leiden, Netherlands) and PC (Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, Paris, France). In total, over 5000 populations of non-geniculate corallines from various localities ranging from tropical to polar seas were examined. The extent to which intergrades occur between focal points in the growth-form network was also determined from these collections. In order to ensure complete objectivity, analyses were conducted independently of the taxonomic names attached to specimens (most of which require confirmation in the context of recent taxonomic studies).

In the results and discussion, examples cited from the literature are referred to by the names used in the relevant publications. The taxonomic status and disposition of some of the species mentioned therein requires critical review in a modern context (a task beyond the scope of the present paper), and it would be inappropriate to update their nomenclature until the necessary studies are carried out.

Results and Discussion

Growth-forms and Their Descriptions

It has not been possible to devise a comprehensive system of mutually exclusive groups to describe the spectrum of growth-forms occurring amongst the non-geniculate Corallinales. Our analysis of over 5000 populations suggests, however, that an intergrading network of growth-forms is present and that this network has 10 focal points (Table 2). The relationships between the 10 focal points within the network are depicted diagramatically in Fig. 1, and examples of plants representing each of the focal points are provided in Figs 2–5. While some specimens (and species) appear to have a growth-form that more or less coincides with a focal point, others vary more widely and span two or more focal points within the network. The recognition of focal points within a network, however, provides a powerful tool that can be universally applied in a consistent manner for describing the external appearance of plants and producing descriptions of species in taxonomic accounts. Comments on each focal point or group of focal points follow.

Table 2. A summary of data on focal points in the network of growth-forms of non-geniculate Corallinales (Rhodophyta)

Terms for focal points are indicated in bold

1.	**Unconsolidated** Plants composed partly or entirely of unconsolidated (free) filaments.
2.	**Encrusting** Plants crustose and flattened or sleeve-like, largely or entirely attached ventrally, and devoid of protuberances and lamellate branches.
3.	**Warty** Plants with warty (verrucose) protuberances[A] that are usually <3 mm long and unbranched.
4.	**Lumpy** Plants with lumpy, usually swollen protuberances[A] that may vary in length, are usually crowded and contiguous, and rarely may be branched.
5.	**Fruticose** Plants with cylindrical to compressed protuberances[A] that are mostly >3 mm long, do not look lumpy, are usually branched, and are free from one another or laterally coherent to varying degrees.
6.	**Discoid** Plants each consisting of an unbranched and largely unattached disc-like lamella[B] of varying shape.
7.	**Layered** Plants consisting of several to many flattened, lamellate[B] branches arranged in horizontally oriented layers. Such branches often give the plant a terraced appearance in surface view.
8.	**Foliose** Plants consisting of several to many lamellate[B] branches arranged at various angles to one another. Such branches may be simple or ramified, may be flattened or variously curved, and may be free from one another or interwoven and coherent to varying degrees.
9.	**Ribbon-like** Plants composed of flat, ribbon-like (taeniform) branches and lacking a distinct holdfast and stipe.
10.	**Arborescent** Plants more or less tree-like, composed of a distinct holdfast and stipe bearing flattened, ribbon-like to fan shaped branches.

[A] protuberance: a cylindrical to compressed or more irregularly shaped outgrowth or branch that usually has a radial organisation.

[B] lamella; lamellate: a more or less flattened or curved branch that usually has a dorsiventral internal organisation; lamella-like.

1. *Unconsolidated.* Plants composed partly or entirely of unconsolidated filaments (Fig. 2*A*) occur in relatively few non-geniculate corallines. The largely endophytic species *Choreonema thuretii* (Bornet) Schmitz (see Suneson 1937; Woelkerling 1987) and *Lesueuria minderiana* Woelkerling *et* Ducker (1987) normally produce unconsolidated thalli. Partly or largely unconsolidated thalli also have been reported in epiphytic plants ascribed to *Fosliella* (e.g. see Chamberlain 1983: 351-352; Coppejans 1983), *Melobesia* (e.g. see Chalon 1905: 207, as *Lithothamnion;* Hamel and Lemoine 1953: 114, as *Epilithon*) and *Pneophyllum* (e.g. see Chamberlain 1983: 392-395;

Woelkerling 1988). *Fosliella* is now considered to be a heterotypic synonym of *Hydrolithon* (Penrose and Chamberlain 1993), and the status and disposition of species with unconsolidated thalli that have been ascribed to *Melobesia* and *Pneophyllum* require re-evaluation. References to representative published figures of unconsolidated plants are provided in Table 3. Within the growth-form network, **unconsolidated** intergrades only with **encrusting**. **Unconsolidated** is also the only focal point in which the plants are not pseudoparenchymatous.

2. *Encrusting.* Encrusting plants are produced by many species of non-geniculate Corallinales. Such plants are fundamentally crustose and lack protuberances and lamellate branches. They are largely or entirely attached ventrally to the substratum by cell adhesion, and thallus shape often is influenced by the nature of the substratum. Thus, individuals growing on rocks, molluscs, seagrass leaves, etc. commonly form flattened expanses (Fig. 2*B*) whereas those growing on algae with small diameter branches and similar types of substrata follow the contours of the host and often have sleeve-like thalli (Fig. 2*C*). References to representative published figures of encrusting plants are provided in Table 3. Within the growth-form network, intergrades between **encrusting** and **warty**, **lumpy**, **discoid**, **layered**, or **foliose** are common.

3–5. *Warty, Lumpy, Fruticose.* Warty, lumpy and fruticose plants are widely known amongst non-geniculate Corallinales; all have cylindrical to compressed or more irregularly shaped outgrowths or branches that usually have a radial organisation. Such outgrowths or branches have commonly been termed protuberances (see Woelkerling 1988: 5, 7, 231). Warty plants have verrucose (warty) protuberances that are usually unbranched and less than 3 mm long (Fig. 3*A*). Lumpy plants, in contrast, have more or less swollen protuberances that may vary in length, are usually crowded and contiguous, and rarely may be branched (Fig. 3*B*). Fruticose plants have protuberances that are mostly over 3 mm long, do not look lumpy, are usually branched, and are free from one another or laterally coherent to varying degrees (Fig. 3*C*). Warty, lumpy and fruticose plants may be attached to a substratum or grow unattached, and in some cases, individuals are composed largely or entirely of protuberances. References to other representative figures are given in Table 3. Intergrades between **warty**, **lumpy** and **fruticose** are common as are intergrades between these and most other focal points in the growth-form network (Fig. 1)

6–8. *Discoid, Layered, Foliose.* Discoid, layered and foliose plants have flattened or curved lamellae (lamellate branches) that usually have a dorsiventral organisation. Both attached and unattached individuals occur. Discoid plants consist of an unbranched and largely unattached disc that may be applanate (horizontally expanded) or curved to varying degrees (Fig. 4*A*). Layered plants are composed of several to many flattened branches arranged in horizontally oriented layers (Fig. 4*B*). Foliose plants consist of several to many lamellate branches arranged at various angles to one another; such branches may be simple or ramified, may be flattened or variously curved, and may be free from one another or interwoven and coherent to varying degrees (Fig. 4*D*). Discoid, layered and foliose individuals were not encountered as frequently as warty, lumpy and fruticose individuals during the present study. References to other representative figures are provided in Table 3. Intergrades occur between **discoid**, **layered** and **foliose** as well as between these and most other focal points in the growth-form network (Figs 1, 4*D*).

9. *Ribbon-like.* Ribbon-like plants (Fig. 5*A*), in which the thallus is composed largely of ribbon-like (taeniform) branches, occur mainly in *Mastophora* and *Tenarea*. In *Tenarea tortuosa* (Esper) Lemoine (see Woelkerling *et al.* 1985), plants appear to be locally attached by cell adhesion, while in *Mastophora rosea* (C. Agardh) Setchell (see Turner and Woelkerling 1982*a*, 1982*b*; Woelkerling 1988: 129, figs 11, 15, 117-119), individuals may be unattached or attached locally by rhizoids or by cell adhesion. Ribbon-like plants differ from arborescent plants (see below) in lacking a distinct

holdfast and stipe. References to representative published figures of ribbon-like plants are provided in Table 3. Within the growth-form network, intergrades occur between **ribbon-like** and **arborescent**, **encrusting**, **layered**, and **foliose** (Fig. 1).

10. *Arborescent.* Arborescent plants (Fig. 5*B*,*C*) are tree-like; they are composed of a distinct holdfast and a stipe that bears flattened, ribbon-like to flabelliform (fan shaped), ramified branches. This growth-form is characteristic of *Metamastophora flabellata* (Sonder) Setchell (see Woelkerling 1980*a*, 1980*b*) and *Mastophoropsis canaliculata* (W. H. Harvey and J. D. Hooker) Woelkerling (see Woelkerling 1978, 1988: 180). References to additional representative figures are provided in Table 3. Within the growth-form network, **arborescent** is very distinctive with no obvious intergrades (Fig. 1). It is, however, most closely allied to **ribbon-like** on the basis of the form of branches present, at least in *Mastophoropsis*.

Table 3. A selected list of published illustrations of plants representing focal points in the network of growth-forms of non-geniculate Corallinales (Rhodophyta)

The examples cited can be described with a single term (warty, foliose, etc.) and are taken from monographc accounts and field guides

1. **Unconsolidated**
Suneson 1937: fig. 33A; Woelkerling and Ducker 1987: figs 7, 8; Woelkerling 1988: figs 99, 147.

2. **Encrusting**
Printz 1929: pl. 1, figs 2, 3, 7, 8, 13, 23; pl. 2, figs 6, 8, 10; pl. 7, figs 1, 5; Segawa 1956: figs 309, 311, 316; Masaki 1968: pl. 1, figs 1, 2; pl. 19, figs 1, 2; pl. 22, figs 4, 5; Furher *et al.* 1981, pls 13, 14; Tseng 1983, pl. 44, fig. 4, pl. 45, figs 1, 2; Woelkerling 1988: figs 5, 120, 135; Littler *et al.* 1989: 217 (lower); Cabioch *et al.* 1992: fig. 144.

3. **Warty**
Printz 1929: pl. 3, figs 19, 20; pl. 4, fig. 21; pl. 12, fig. 3; pl. 54, fig. 22, pl. 72, fig. 7; pl. 73, fig. 2; Masaki 1968: pl. 2, fig. 5; pl. 36, fig. 2; Furher *et al.* 1981, pl. 16; Tseng 1983, pl. 39, fig. 3; Woelkerling 1988: fig. 158; Littler *et al.* 1989: 223 (lower).

4. **Lumpy**
Printz 1929: pl. 12, figs 12, 18; pl. 42, figs 6, 11; pl. 44, fig. 14; pl. 52, figs 4, 6; pl. 56, figs 16, 17; pl. 63, fig. 17; Segawa 1956: figs 310, 317; Magruder and Hunt 1979: 76 (lower); Tseng 1983: pl. 42, fig. 3; Woelkerling 1988: figs 9, 70.

5. **Fruticose**
Printz 1929: pl. 13, figs 13, 14; pl. 19, figs 6-9; pl. 48, figs 6-8; pl. 49, fig. 12; Masaki 1968: pl. 7, figs 1-3; Tseng 1983, pl. 41, fig. 2, pl. 43, fig. 4; Woelkerling 1988: figs 8, 67, 153; Littler *et al.* 1989: 213 (upper), 215 (upper); Cabioch *et al.* 1992: figs 145, 230.

6. **Discoid**
Printz 1929: pl. 10, figs 1, 22; Woelkerling 1988: fig. 253; Cabioch *et al.* 1992: fig. 147.

7. **Layered**
Printz 1929: pl. 9, fig. 4; pl. 11, figs 5, 7; Magruder and Hunt 1979: 84 (lower), 94 (upper); Woelkerling 1988: fig. 88; Littler *et al.* 1989: 217 (upper), 219 (upper).

8. **Foliose**
Printz 1929: pl. 9, fig. 11; pl. 54, figs 6-8; pl. 61, fig. 1; Segawa 1956: fig. 318; Masaki 1968: pl. 24, figs 2, 3; Woelkerling 1988: figs 15, 65, 66, 222; Cabioch *et al.* 1992: fig. 231.

9. **Ribbon-like**
Printz 1929: pl. 74, figs 4, 5; Woelkerling 1988: figs 11, 79; Cabioch *et al.* 1992: fig. 229.

10. **Arborescent**
Printz 1929: pl. 73, figs 10-12; pl. 75, figs 2-5; Woelkerling 1988: figs 125, 201.

The network concept and use of the focal point terminology (Fig. 1) allows specimens to be described in a consistent, easily interpretable manner. Specimens whose growth-form corresponds to a focal point can be described with single terms such as **unconsolidated**, **lumpy**, **foliose**, etc. while specimens intergrading between focal points can be described with phrases such as **encrusting** to **warty** to **fruticose**, **layered** to **foliose** etc. All of the 5000+ populations examined during the present study could be readily described in this manner, and it is equally possible to apply this terminology to species as a whole.

Relationships to Other Recent Proposals

The system outlined in Table 2 constitutes a refinement or expansion of earlier proposals by Johansen (1981), Woelkerling and Irvine (1988), and Woelkerling and Campbell (1992). It is based solely on thallus morphology, can be applied to all non-geniculate corallines, and is compatible with the system devised by Bosence (1976, 1983) for describing rhodolith morphology.

The growth-form scheme outlined by Johansen (1981: 4, 44-55) (Table 4) has not been adopted by us because it is not based solely on morphological criteria and does not adequately portray the array of growth-forms present amongst non-geniculate corallines. Johansen (1981: 4) recognised eleven growth-forms (1–11 in Table 4), and, in the context of the subfamilies Mastophoroideae and Melobesioideae (Johansen 1981: 44-55), placed these into six groups (*A–F* in Table 4).

Table 4. A summary of the growth-forms (1–11) and growth-form groups (*A–F*) of non-geniculate Corallinales (Rhodophyta) recognised by Johansen (1981: 4, 44-55)

Terminology and descriptions are those of Johansen

A. Thin Crusts

Plants < 200 μm thick that can grow on rock or other plants; subdivided into:

1. **Thin, smooth crusts**
2. **Thin crusts repeatedly overgrowing one another**
3. **Thin, loosely overlapping crusts, margins free**

B. Ribbon Corallines

4. **Branched corallines**

Branched, ribbon-like crusts attached at one end.

C. Thick Crusts

Plants > 200 μm thick; subdivided into:

5. **Thick, smooth crusts**
6. **Thick knobby crusts**

D. Unattached Coralline Algae

7. **Unattached coralline algae**

Unattached branched forms called maerl.

E. Epiphytic Coralline Algae

8. **Epiphytic coralline algae**

Epiphytic crusts of determinate vegetative growth.

F. Parasitic Coralline Algae

Plants greatly modified for an existence that is dependent on specific hosts that serve as substrates; subdivided into:

9. **Unpigmented parasites, vegetative system reduced**
10. **Pigmented parasites, vegetative system endophytic**
11. **Pigmented, endophytic between cell wall layers in *Cladophora*.**

Only three of Johansen's groups (thin crusts, ribbon corallines, thick crusts) (Table 4, *A–C*) are based solely on morphological characters. The other three (unattached, epiphytic, parasitic) (Table 4, *D–F*), by contrast, concern habit and substrate relations and thus are ecologically based. Unattached, epiphytic and parasitic plants, however can be described in morphological terms and thus can be readily accommodated within a system based solely on morphology. The use of both morphological and ecologically based attributes in the same scheme can lead to confusion: plants classed as thick crusts or ribbon corallines in Johansen's scheme, for example, may grow attached or unattached, and they may be epiphytic or non-epiphytic.

One of Johansen's three strictly morphological groups, ribbon corallines, encompasses two focal points (**ribbon-like** and **arborescent**) in our scheme (Table 2). The other two (thin crusts and thick crusts) are considered too broad and general since they encompass seven of the 10 focal points outlined in Table 2 (**encrusting, warty, lumpy, fruticose, discoid, layered, foliose**). There is no exact counterpart in Johansen's scheme for **unconsolidated**; Johansen treats unconsolidated plants together with plants of other growth-forms as epiphytic or parasitic.

Woelkerling and Irvine (1988: 5-7) recognised four morphological growth-forms (unconsolidated, crustose, protuberant, taeniform) but placed these within three groups relating to habit and substrate (semi-endophytic, epigenous, unattached). In the system proposed in the present paper (Table 2), groups relating to habit and substrate have been abandoned for reasons already outlined, **unconsolidated** has been retained, 'taeniform' has been divided into **arborescent** and **ribbon-like**, and 'crustose' and 'protuberant' have been replaced by a series of seven focal points (**encrusting, warty, lumpy, fruticose, discoid, layered, foliose**) that allow for a more graphic portrayal of the morphological forms present.

In southern Australian species of *Lithophyllum,* Woelkerling and Campbell (1992: 3-4) encountered six growth-forms: encrusting (= **encrusting** in the present paper), **layered, warty**, protuberant (= **fruticose** in the present paper), **lumpy**, coalescent (included within **foliose** in the present paper). Their scheme has been expanded and refined here (see Table 2) to encompass all non-geniculate Corallinales.

Bosence (1976, 1983) proposed a scheme for describing rhodoliths (defined as unattached non-geniculate corallines that commonly are nodular and develop about a nucleus such as a sand grain or small stone) based on shape, size, structure, and taxonomic composition. Although Bosence's scheme is limited to unattached plants, it can be applied to both unispecific and multispecific rhodoliths, and it is completely compatible with the system outlined in Table 2. It is possible to describe the growth-form of any unispecific rhodolith or other unattached non-geniculate coralline using either the Bosence scheme or the system in Table 2. The system in Table 2, however, has the advantage of being applicable to attached as well as unattached plants and thus is better suited for use in taxonomic and floristic studies. The Bosence scheme has the advantage of having more quantitatively defined categories and thus within its scope is potentially more useful in ecological studies of unattached plants. It also can be used to describe rhodoliths composed of more than one species, whereas the system in Table 2 is designed for describing individual plants or species.

Growth-forms as Taxonomic Characters

The extent to which differences in growth-form can be used to delimit taxa and identify specimens is unresolved.

In a monographic account of non-geniculate genera, Woelkerling (1988: 64) suggested that growth-form may be one of several characters that are diagnostic of the genera *Choreonema* (subfamily Choreonematoideae), *Lesueuria* and *Metamastophora* (subfamily Mastophoroideae) and *Mastophoropsis* (subfamily Melobesioideae). Penrose and Chamberlain (1993: 303) also used growth-form to help delimit *Lesueuria* and *Metamastophora* from other genera of Mastophoroideae. Each genus, however, contains only one known species, and thus it is difficult to determine whether growth-form is truly diagnostic of the genus or merely characteristic (or diagnostic) of a particular species.

At species level, there is increasing evidence (see introduction) that considerable variation in growth-form can occur, and thus the use of differences in growth-form as the only

diagnostic character of a species or as a single character in keys for specimen identification must be treated with great caution. Unfortunately, a number of keys in floristic accounts (see references in introduction) make use of growth-form differences as sole characters in couplets. Differences in growth-form may be helpful in specimen identification in a particular geographic region, but unfortunately this does not imply that such differences are of diagnostic value. Woelkerling and Campbell (1992: 16), for example, suggested that thallus layering and the occurrence of protuberant branches could be useful as ancillary characters in species identification of southern Australian specimens of *Lithophyllum,* but they did not consider growth-form characters to be diagnostic of those species. The significance in keys of characters relating to growth-form differences, therefore, needs to be carefully explained.

The infraspecific taxonomy of non-geniculate corallines is replete with taxa delimited from one another on slight differences in growth-form, and this has led to a great proliferation of names in the literature. Growth-form variation in unattached plants of *Phymatolithon calcareum* (Pallas) Adey *et* McKibbin, for example, has been studied by Lemoine (1910, as *Lithothamnion*), Hamel and Lemoine (1953, as *Lithothamnion*), and Cabioch (1966, as *Lithothamnion*), all of whom recognised a formal series of taxonomic formae. Indeed, at least 20 formae and varieties of *Phymatolithon calcareum* have been described based on growth-form differences. Bosence (1976), however, has concluded that growth-form variation in *P. calcareum* results from various environmental gradients, and that this variation can be quantified and described in morphological terms, thus obviating the need for the use of a formal taxonomic system. Woelkerling and Irvine (1986: 77) supported Bosence's conclusions and noted that since similar series of variants occur in unattached plants of many species, the addition of separate form names for each variant of each species would be counterproductive.

Between 1891 and 1909, Foslie described 192 infraspecific taxa largely or solely on apparent differences in growth-form (see Woelkerling 1984, 1993). According to Chamberlain (1991: 4), applying formae to all variants became an accepted practice with Foslie and was to some extent followed in the works of Lemoine (see Ardré and Cabioch 1985 and Chamberlain 1985 for a list of Lemoine's publications), who is second only to Foslie (Woelkerling 1984: 7) in terms of the number of taxa of non-geniculate corallines described. This plethora of taxa, most of which are poorly delimited (Woelkerling 1984: 17; Chamberlain 1991: 4, 9) and based on single specimens or collections (Woelkerling 1984: 16; Woelkerling 1993), is badly in need of critical re-evaluation, and, as noted by Chamberlain (1991: 4), recent studies suggest that a considerable reduction in the number of such taxa will occur. The use of a standardised terminology for describing growth-forms (Table 2) should facilitate these re-evaluations.

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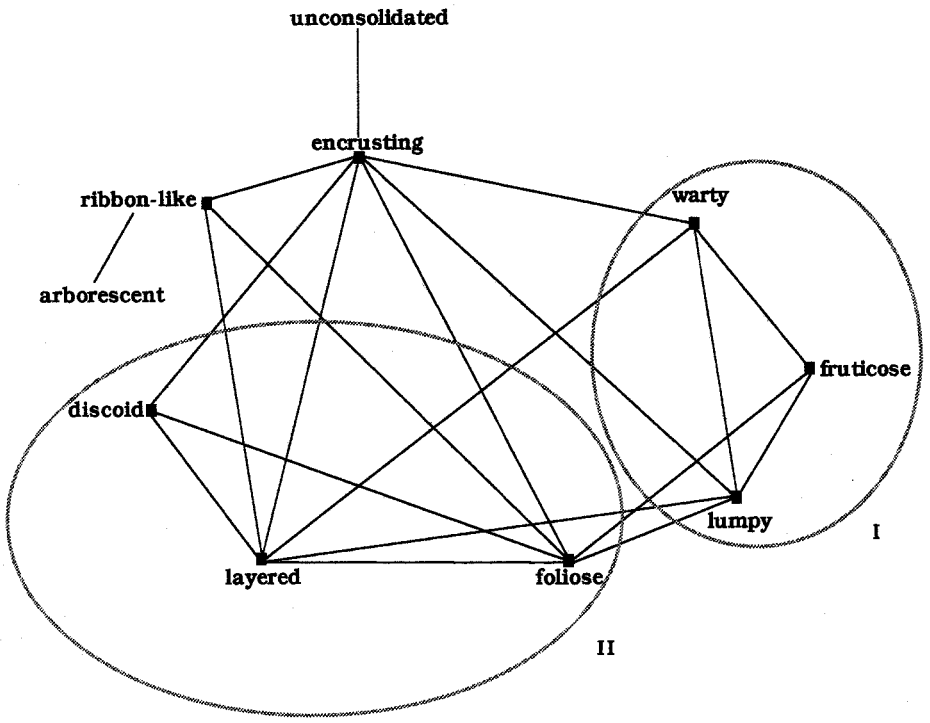

Fig. 1. Diagrammatic representation of the growth-form network showing the relationships between the 10 focal points. Lines connecting focal points indicate where known intergrades occur. Ellipse I encompasses those focal points involving plants with protuberances; ellipse II encompasses those focal points involving plants with lamellae.

Captions to Figures on Following Pages

Fig. 2. Examples of plants representing the focal points unconsolidated and encrusting. (*A*) Unconsolidated plants of *Pneophyllum* from southern Australia. (LTB 12937). (*B*) Rock from the Shetland Islands containing a mixture of encrusting plants of *Hydrolithon, Lithophyllum, Lithothamnion,* and *Phymatolithon.* (BM, material of David Irvine collected in August 1973). (*C*) Encrusting plants of *Synarthrophyton patena* (J.D. Hooker *et* W.H. Harvey) Townsend from southern Australia encircling branches of the green alga *Codium.* (LTB 12607).

Fig. 3. Examples of plants representing the focal points warty, lumpy and fruticose. (*A*) Warty plant of *Lithothamnion.* (BM, material of Linda Irvine collected 30 July 1975). (*B*) Lumpy plants of *Mesophyllum incisum* (Foslie) Adey from southern Australia growing on rock. (LTB 14413). (*C*) Fruticose plant of *Neogoniolithon* from Florida, USA. (BM, algal box collection 967).

Fig. 4. Examples of plants representing the focal points discoid, layered and foliose. (*A*) Discoid plants of *Synarthrophyton patena* (J.D. Hooker *et* W.H. Harvey) Townsend from southern Australia growing on the red alga *Ballia.* (LTB 16597). (*B*) Layered plant of *Lithophyllum prototypum* (Foslie) Foslie growing on an abalone shell from southern Australia. (*C*) Layered to foliose plant of *Mesophyllum incisum* (Foslie) Adey from southern Australia. (LTB 11719). (*D*) Foliose plant of *Lithophyllum lichenoides* Philippi from the Azores. (BM, algal box collection 1533).

Fig. 5. Examples of plants representing the focal points ribbon-like and arborescent. (*A*) Ribbon-like plants of *Mastophora rosea* (C. Agardh) Setchell from Guam. Note that plants are composed of flat, ribbon-like branches and lack a stipe and holdfast. (LTB 11824B). (*B*) Arborescent plant of *Mastophoropsis canaliculata* (W.H. Harvey in J.D. Hooker) Woelkerling from southern Australia. Arrow denotes position of holdfast. (LTB 12731). (*C*) Arborescent plant of *Metamastophora flabellata* (Sonder) Setchell from southern Australia. Arrow denotes position of holdfast. (LTB 10264).

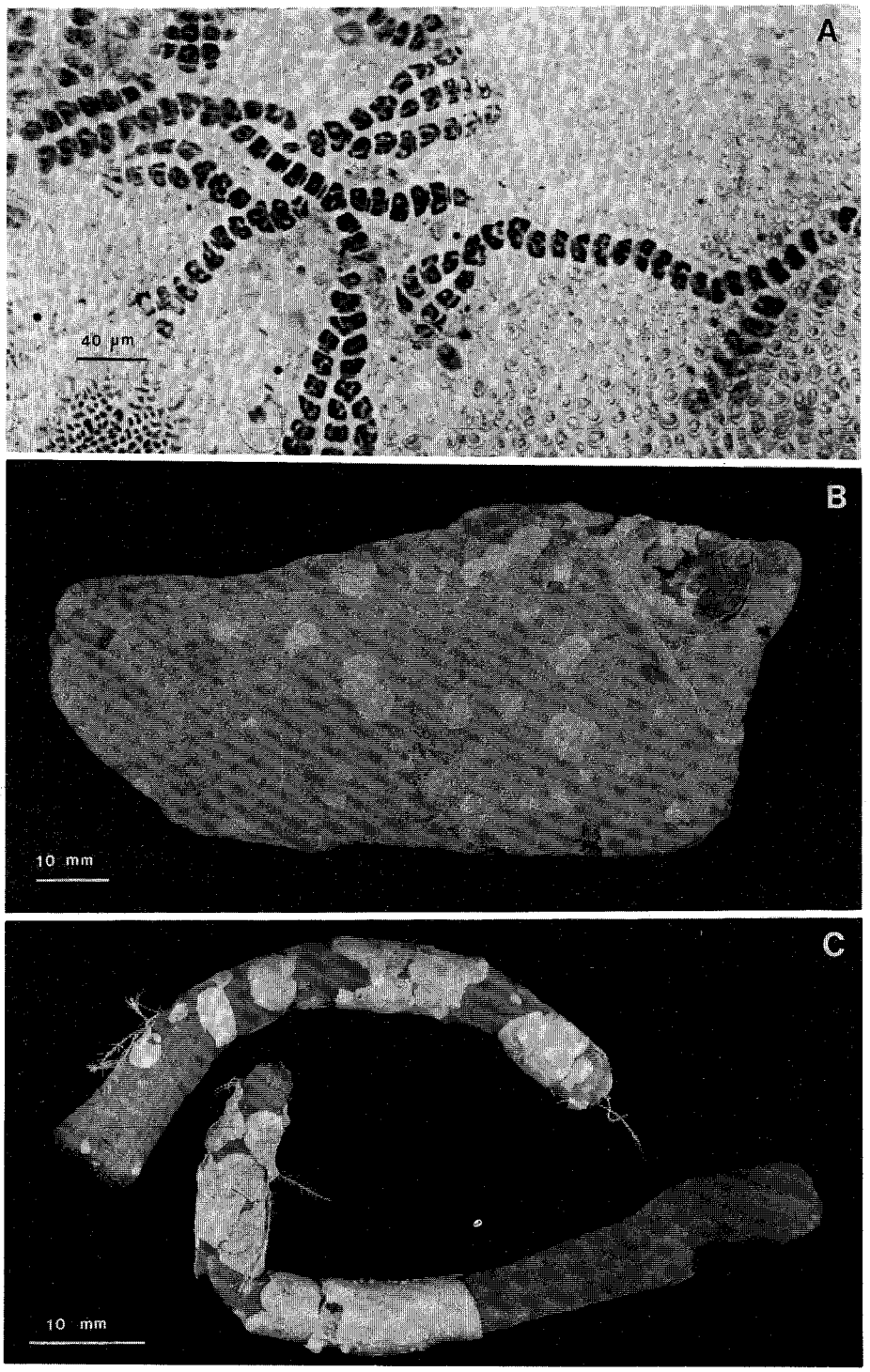

Fig 2.

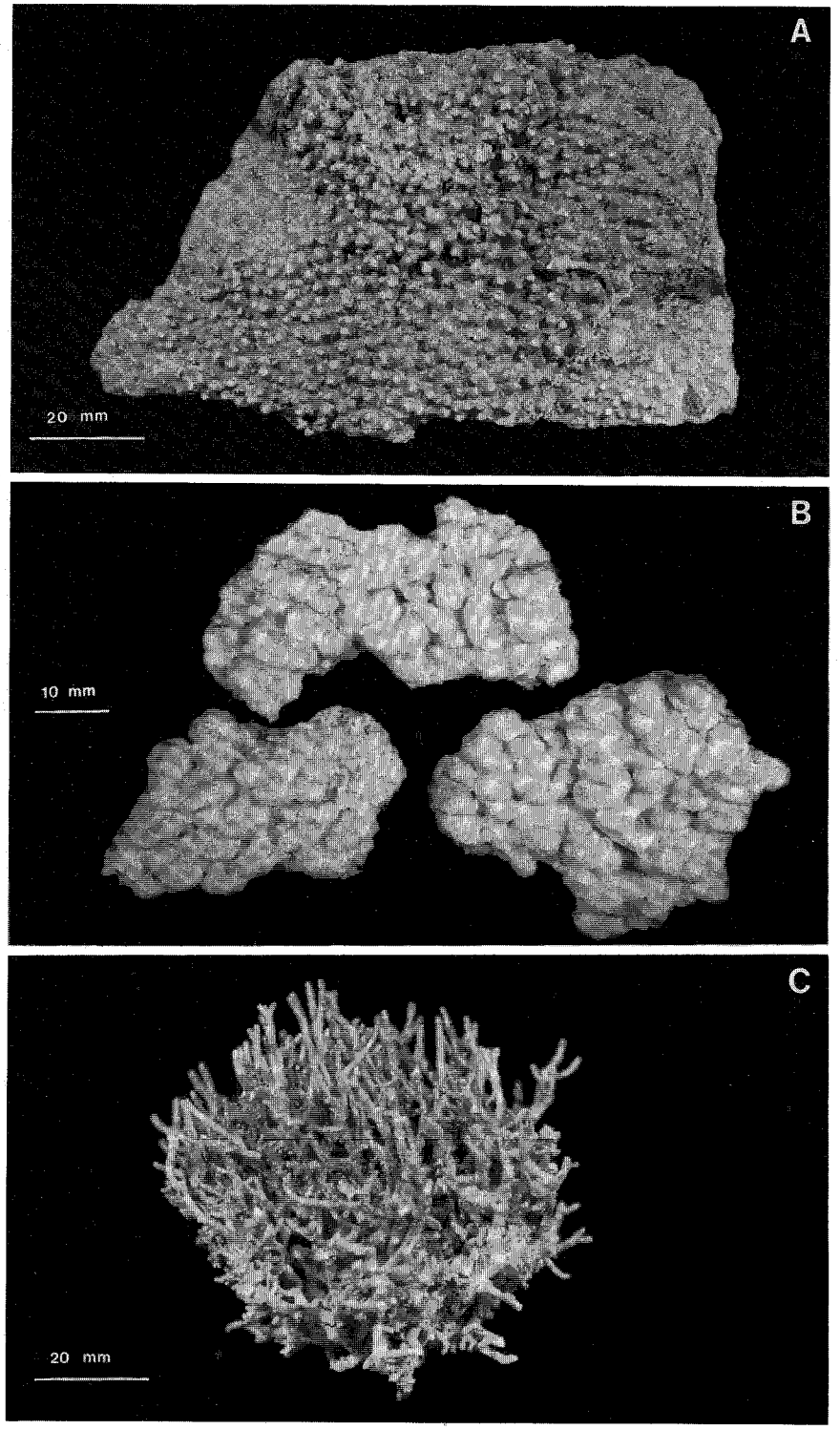

Fig 3.

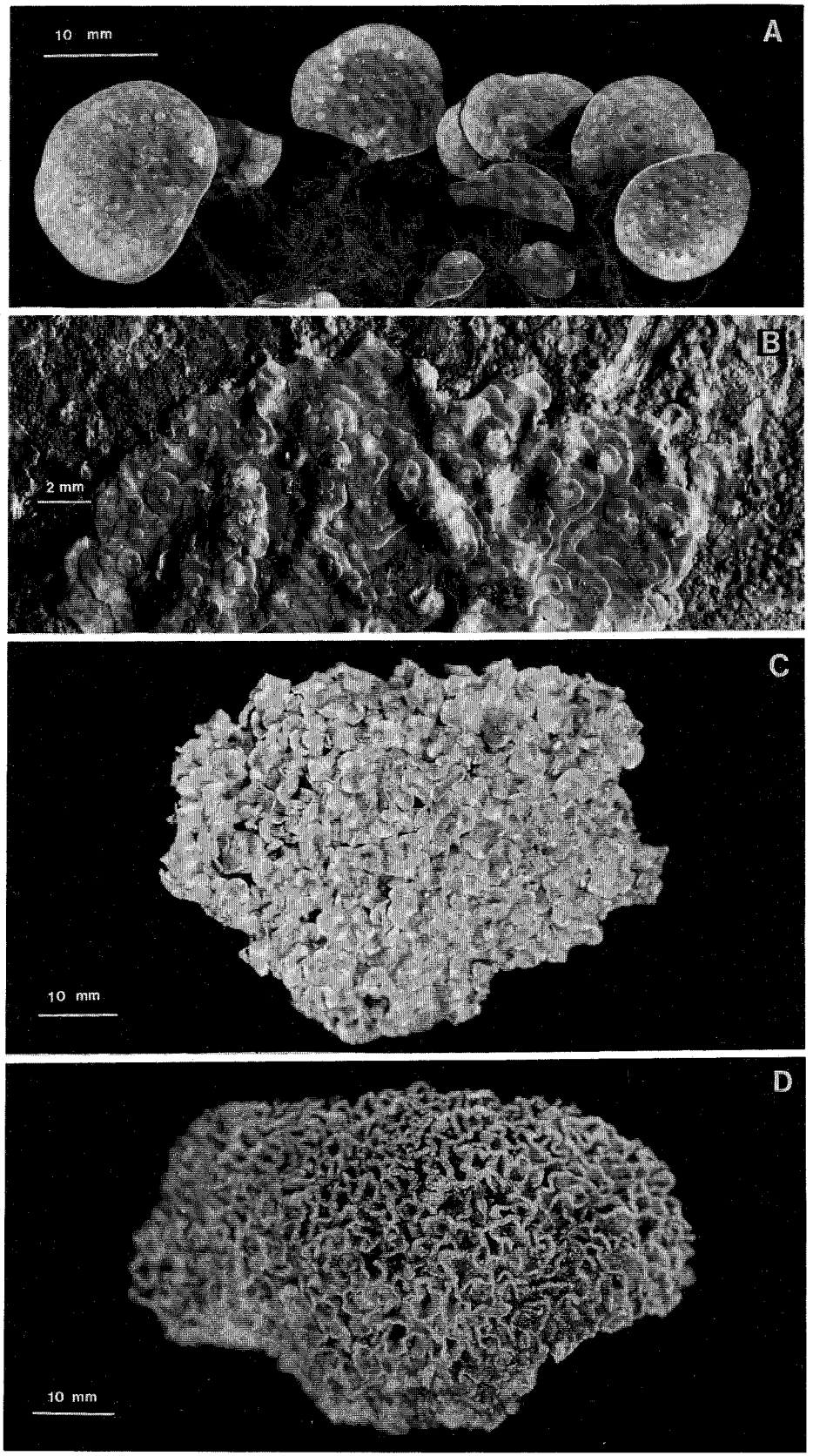

Fig 4.

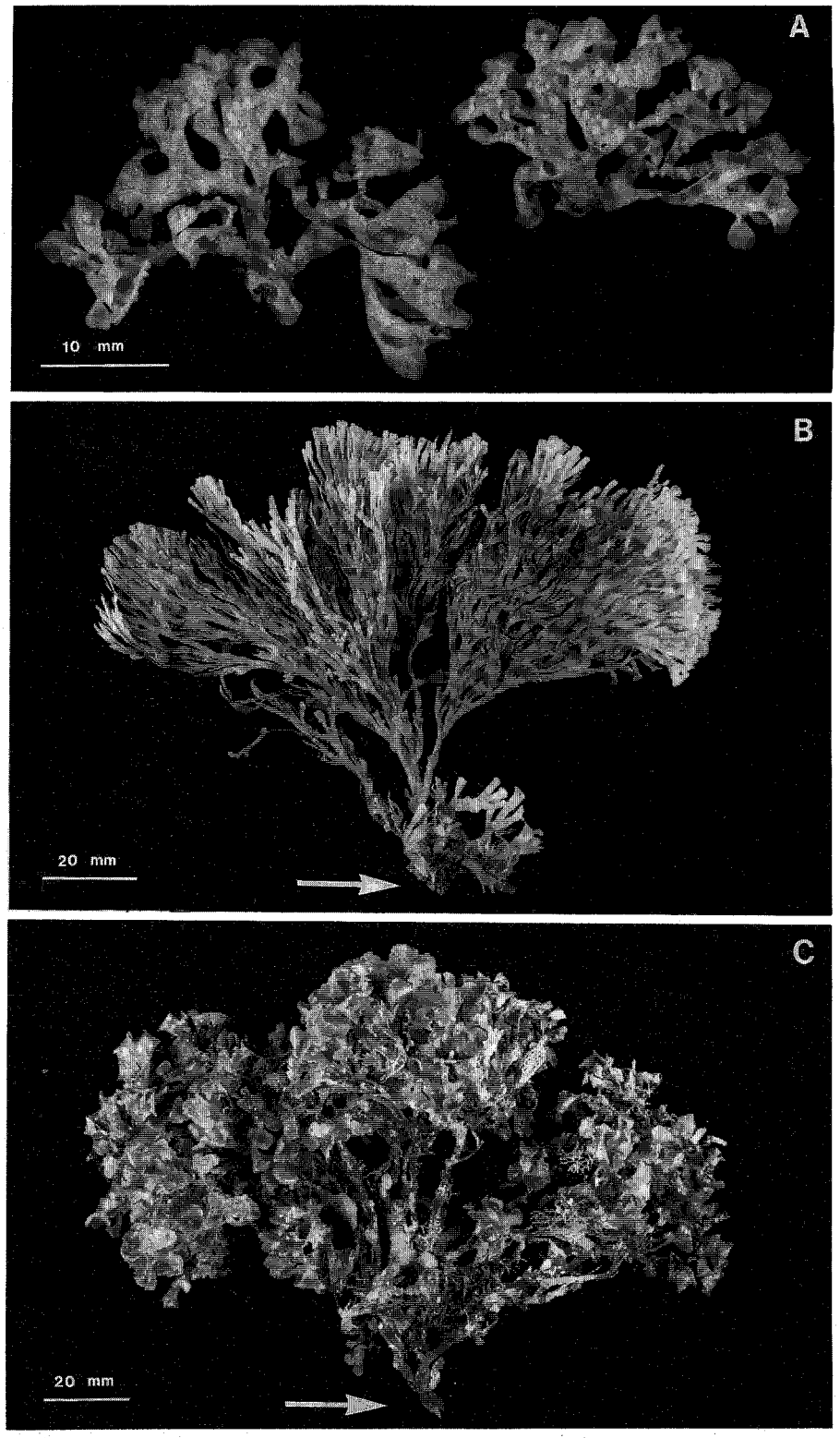

Fig 5.

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