Morphogenesis and generic concepts in coralline algae – a reappraisal*

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ABSTRACT: In coralline algae, anatomy has long been used for generic definition, in addition to reproductive structures. Coralline anatomy is here analysed according to its two main components: cell behaviour and morphogenesis. The meristems and their function are explained and the main types of organization are examined in an evolutionary context. Emphasis is given to ontogenetical data such as the occurrence of metamorphosis and progressive development in some species of the *Lithophyllum* complex, which have raised difficulties for generic definitions in the past. Consequently, a certain number of terms (epithallus, hypothallus, perithallus) are clarified and some of them restricted in relation to their morphogenetic significance. As a consequence of this clarification, evolutionary groups are defined and within them parallel phylogenetic lines appear as continuums along which genera are morphogenetic steps.

INTRODUCTION AND HISTORICAL BACKGROUND

Coralline algae have recently been raised to ordinal status as the Corallinales (Silva & Johansen, 1986). Their calcification creates a unifying character and this mineralization has acted as a frame for their evolution. However, within this frame they exhibit a wide range of biological adaptations (Fig. 1), including morphologically regressive and parasitic forms, highly developed crustose thalli and articulated or non-articulated erect thalli. Erect thalli always develop from a crustose stage whatever their final complexity.

As a general rule, perhaps because of their calcification (they often look like stones), coralline algae are difficult to identify. One species can show a wide range of morphological variability, while fundamentally different species can look remarkably similar. Perhaps this accounts for the fact that for many years the artificial but easily recognised distinction between articulated and non-articulated forms was used as a basis for classification (e.g. Areschoug, 1852; Hamel & Lemoine, 1953).

At the end of the last century anatomical studies were initiated. They were mainly based on ground section techniques, unadapted, and it is still not easy to take the results into account (see, for example, Weber van Bosse & Foslie, 1904). The situation was improved by the introduction of histological procedures (Lemoine, 1911) but still accompanied by highly static interpretations. Later, Suneson (1937, 1943) did more dynamic analyses mostly on the development of reproductive structures. More recently, some authors localized growth and defined meristems (Adey, 1964, 1965, 1966; Johnson & Adey, 1965; Masaki, 1968) but they did not emphasize their functional potentialities.

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* Dedicated to Dr. Dr. h. c. Peter Kornmann on the occasion of his eightieth birthday.
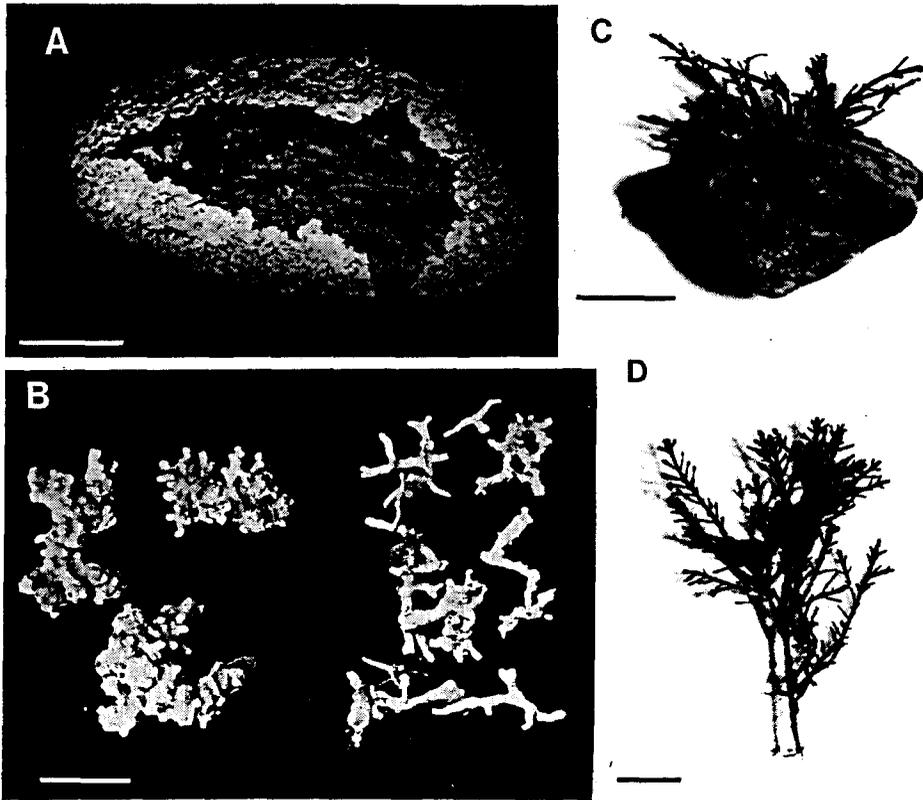
Fig. 1. Morphological diversity in coralline algae. A: *Lithothamnion lenormandii* (Areschoug) Foslie, a permanent crust; B: *Lithothamnion corallioides* Crouan, crustose forms with young branches on the left, free-living forms on the right; C and D: *Corallina elongata* Ellis & Solander, C: young erect branches attached to a pebble completely covered by a crust of *Lithophyllum incrustans* Philippi; D: normal aspect of an adult thallus. Scale bar: 1 cm

   Fifteen years ago, an attempt was made to improve generic definitions according to morphogenetic potentialities (Cabioch, 1972). Anatomy was analysed according to its two main components: cell behaviour and morphogenesis. Morphogenetic data were first obtained from ontogenetic observations on the progressive establishment of an adult organization from the spore. The function and behaviour of meristems during ageing, and repair phenomena were also taken into account. This study revealed unexpected affinities between the genera; for instance, close relationships between articulated and non-articulated forms. A new formulation of their phylogenetic position was proposed leading to a more natural classification of the group (Cabioch, 1971).

   The first observations with electron microscopy (Bailey & Bisalputra, 1970; Cabioch & Giraud, 1974) led to a general search for cytological peculiarities mainly in relation to mineralization. Some results emphasized the general features of ultrastructure in coralline algae (Giraud & Cabioch, 1977); others elucidated the precise steps of calcification (Borowitzka et al. 1974; Giraud & Cabioch, 1976a, 1979; Giraud & Hauswirth, 1979).

   Nowadays, interest in coralline algae is greatly increasing throughout the world.

They are important reef-builders and the need for their identification is required not only by systematicists, but also in the field of marine ecology. However, too many species have been described in the past (Woelkerling, 1984) so that many specialists must turn again to herbarium studies (Chamberlain, 1983; Mendoza & Cabioch, 1984, 1985, 1986; Woelkerling, 1985; Woelkerling et al. 1985, 1986a, b) often far removed from nature and sometimes difficult to rely on considering the biological complexity. Morphogenesis has therefore been somewhat neglected and it seems important to recall its systematical significance.

In addition, a certain number of terms which were introduced in the past for anatomical descriptions are still used. It now appears that they have been applied to structures completely different in origin and function. Their restricted and precise definition has also to be recalled.

CYTOLOGICAL PECULIARITIES – A REVIEW

Whatever their morphological complexity, coralline algae are all built according to the multiaxial type (Oltmanns, 1904; Kylin, 1956) or derived from it. The organized files of cells can easily be seen on sections after decalcification (Figs 2, 3, 4).

Under the electron microscope the cells show all the usual characters of rhodophycean cytology. Pueschel & Cole (1982) have described pit plugs of a special type, considered characteristic of the order. They have a disc-shaped plug core and a pair of globose plug caps, the functional significance of which should be discussed.

Mineralization

Mineralization has been the subject of many observations and review papers (Borowitzka, 1977, 1982a, b; Cabioch & Giraud, 1986; Littler, 1976; Pentecost, 1980). It occurs directly in the vegetative cell-wall as a deposition of calcite crystals. Two main features have so far been determined:

(1) Calcification involves two successive processes that can be observed in the young superficial zones (Giraud & Cabioch, 1979): at first, thin needles appear tangentially in the outer part of the wall; they remain localized in the interstitial matrix; then, crystallization develops radially in the cell-frame itself in contact with the plasmalemma;

(2) Calcification, in its development and maintenance, is strictly controlled by a polysacaridic and fibrillar matrix acting as a pattern. This results from the secretory activity of superficial cells (Giraud & Cabioch, 1976b) which also produces a general polysaccharidic external envelope typical of coralline organization (Fig. 2A, C). The chemical nature of these polysaccharides may be very close to alginic acid (Okazaki et al. 1982, 1984). Local decalcification occurs when reproductive structures are formed. Spores (carpo- or tetraspores) are always uncalcified. The first crystals appear just after settlement during the early divisions (Cabioch, 1968; Cabioch & Ciraud, 1986).

Cell ageing phenomena

Anastomoses between adjacent cell-files occur in many Rhodophyta. They are expecially significant in coralline algae. When ageing, neighbouring cells of adjacent

filaments connect after local cell-wall resorbtions. The resulting anastomoses are of two kinds: fusions or secondary pit connections. In the latter, a pit plug similar to the primary ones forms directly after wall resorbtion. The distribution of the two types of anastomoses in coralline algae is significant (Cabioch, 1970). They are never both present in a species or a genus, except in the genus *Sporolithon (Archaeo-lithothamnium)*. For example, anastomoses (Fig. 3) are the main but fundamental difference between *Pseudolithophyllum* and *Hydrolithon* – two genera otherwise similar in thallus organization and reproduction.

GENERAL PATTERNS OF MORPHOGENESIS

Growth localization – Definition of meristems

In spite of their mineralization, cell-files grow and ramify by means of i n i t i a l c e l l s always localized near the thallus surface in one of two positions: terminal or intercalary (Fig. 2).

1. When t e r m i n a l, the initial cells collectively form t e r m i n a l   m e r i s t e m s. Such examples are observed at the margin of crustose forms (Fig. 2A, D) or at the apex of some geniculate forms such as *Corallina* (Fig. 2C). In the case of crusts, terminal meristems can be uni- or multilayered.

2. When i n t e r c a l a r y, the initial cells build an i n t e r c a l a r y   m e r i s t e m covered by one or several layers of protecting cells called c o v e r   c e l l s or e p i t h a l - l i a l   c e l l s. Intercalary initials divide transversely to produce daughter cells both above and below: the distal are epithallial and the proximal normal vegetative cells (Fig. 2B, E, F, G, H). Such a position and function recalls what is well-known in Phaeophyta as t r i c h o t h a l l i c   g r o w t h. Epithallial cells have long been considered merely protective, but electron microscopy has revealed their intensive secretory contribution to the polysaccharidic external envelope (Giraud & Cabioch, 1976b).

Main types of organization

The different arrangements of meristems, combined with their permanent or temporary activity result in several types of functional organization and complexity. They must be observed in radial sections of crusts and axial sections of erect branches.

In spite of the existence of meristems, vegetative cell arrangements in multicellular algae cannot be considered exactly equivalent to what is commonly called t i s s u e in higher plants (with one exception, perhaps, in the more complex organization of

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Fig. 2. Different kinds of meristems in coralline algae (radial sections in crusts, axial sections in branches, stained with haematoxylin and acid fuchsin). A: *Mesophyllum lichenoides* (Ellis) Lemoine, multilayered terminal and marginal meristem; B: id., intercalary superficial meristem; C: *Corallina elongata*, terminal meristem at the apex of a branch; D: *Pseudolithophyllum expansum* (Philippi) Lemoine, unilayered terminal and marginal meristem; E: *Lithophyllum incrustans*, intercalary meristem; F: *Amphiroa* sp., id. at the apex of a branch; G and H: *Clathromorphum circumscriptum* (Strömfelt) Foslie, id. recalling the aspect of a trichothallic growth. ev: polysaccharidic envelope; arrows: meristems; scale bar: 50 μm
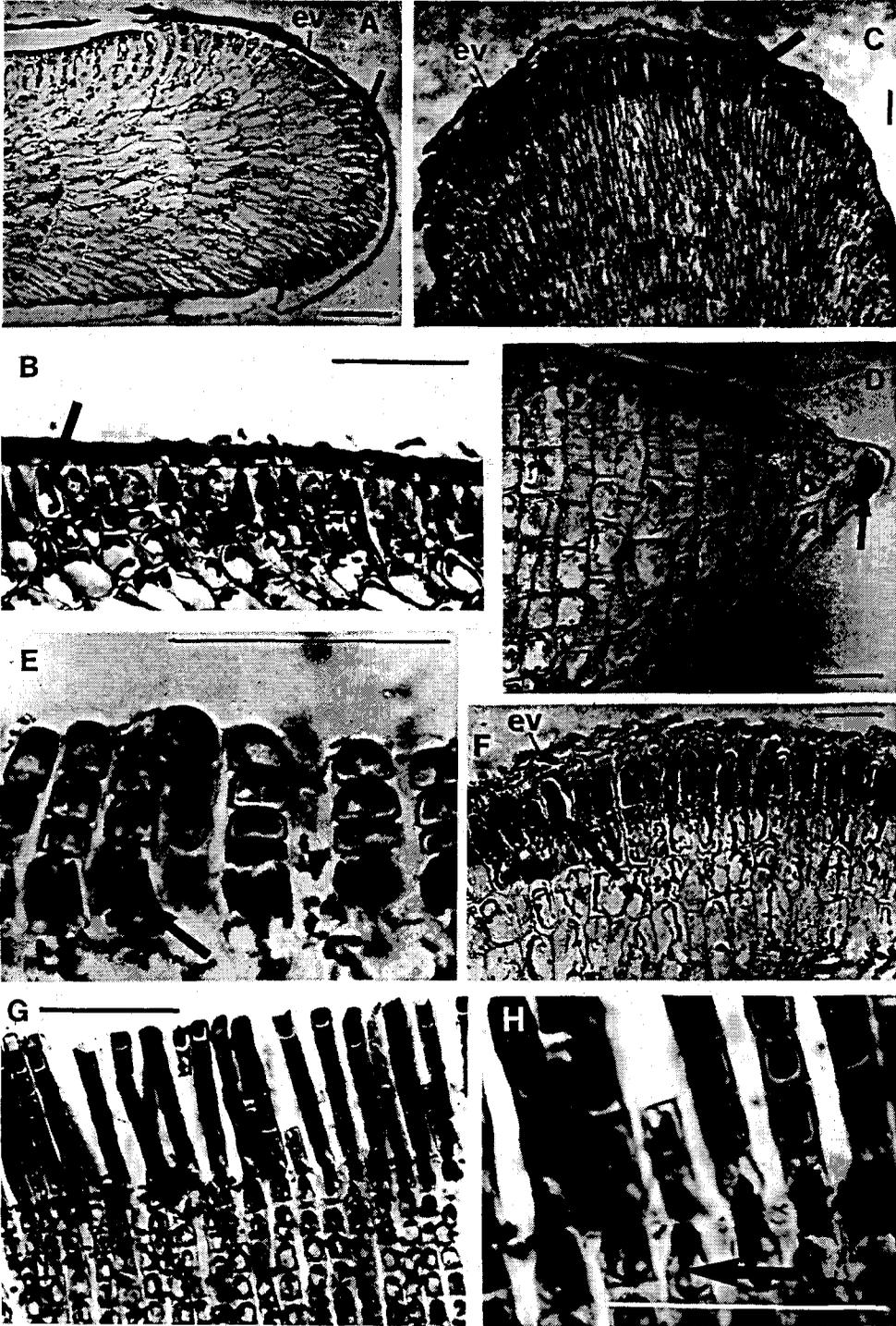
Laminariales). It thus seems better to delete this term in the case of Corallinales, in agreement with Fritsch (1945).

One of the most striking and important features of morphogenesis, common to most coralline algae (with the exception of some regressed, parasitic species), is the existence, during their life-cycle, of a crustose form, whatever its development and duration might be. Different kinds of complexity have been observed; these are summarized in Figure 5.

(1) Forms with medium complexity – the example of *Lithothamnion lenormandii* (Areschoug) Foslie – a permanent crust (Fig. 4A).

The thallus grows parallel to its substrate by means of a marginal terminal and multilayered meristem. By transverse divisions, the marginal initial cells produce a set of prostrate filaments usually called the h y p o t h a l l u s. Pseudodichotomous divisions of these initials give rise upwards to erect filaments, the initials of which very soon become intercalary in position. Thus, a set of erect filaments build what is termed a p e r i t h a l - l u s growing by means of an intercalary meristem and covered by an epithallus (multilayered in this case). Anastomoses in this example are exclusively cell fusions. Similar organization is met with in other genera *(Neogoniolithon, Porolithon, Clath-romorphum, Sporolithon)* sometimes with very different reproductive features.

A similar a n a t o m i c a l aspect is offered by sections of crusts of *Lithophyllum* species (Fig. 4C, E). However, the adult margin grows in this case by means of an intercalary meristem which is of a perithallial nature and origin as will be shown later. The basal multilayered prostrate system is not equivalent to the hypothallus of *Lithothamnion* and must be named differently.

(2) More simplified forms than that seen in *L. lenormandii* are found in several genera.

They are crustose, often very reduced or epiphytic but sometimes developed and saxicolous. They expand over the substrate by means of a u n i l a y e r e d m a r g i n a l and t e r m i n a l meristem thus producing a u n i l a y e r e d h y p o t h a l l u s. In some genera (e.g. *Hydrolithon, Pseudolithophyllum*) marginal initial cells give rise to a more or less developed perithallus with a typical intercalary meristem and a uni- or multilayered epithallus. In some more simplified examples (e.g. *Melobesia, Fosliella, Pneophyllum*) the perithallus is reduced or absent but epithallial cells are still present even in non-calcified examples (e.g. *Melobesia van Heurcki* [Heydrich] Cabioch in Cabioch, 1972). Anastomoses can be exclusively fusions or secondary pit connections and are observed in hypo- and perithallus.

(3) The most complicated forms are the erect thalli, whether articulated or not.

They always develop from crusts which are simple or of medium complexity. Whatever the nature of the crust, branches appear, as a general rule, as local prolifera-tions of the perithallus, and take form according to two fundamentally different pro-cesses:

(a) In most cases, perithallial proliferation generates a branch which permanently grows by means of an intercalary meristem easily observed at the apex. Such branches can be articulated (e.g. *Amphiroa*) or not (e.g. *Lithothamnion, Lithophyllum, Porolithon, Hydrolithon, Sporolithon* . . .). They can also detach from their basal crust and become free-living forms (maerl).

Even within a single genus, species may show a wide range of relative development between crustose and branched productions. This variability which is well-known in
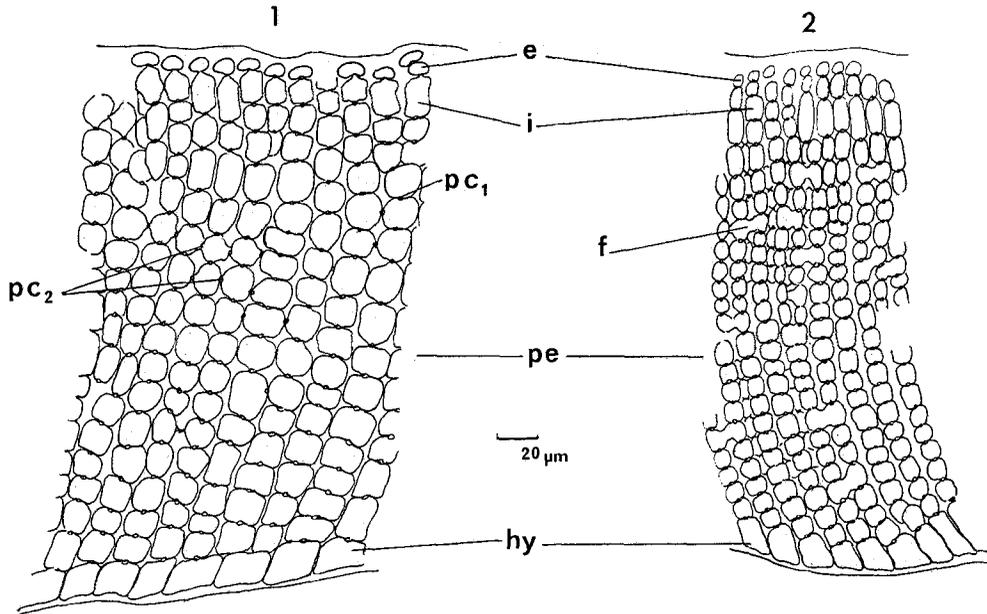
Fig. 3. Compared anatomical structures in *Pseudolithophyllum* and *Hydrolithon*. 1: *Pseudolithophyllum expansum*, 2: *Hydrolithon decipiens* (Foslie) Adey. Radial sections; e: epithallus; f: fusion; hy: unilayered hypothallus; pc1: primary pit connection; pc2: secondary pit connection; pe: perithallus

non-articulated species is also encountered in articulated'ones, as can be shown in the genus *Amphiroa*. Many *Amphiroa* species (Cabioch, 1969a, 1972; Srimanobhas & Masaki, 1987) have a juvenile endophytic filamentous stage followed by a reduced crust, then by erect branches. In contrast, *A. crustaeformis*, described by Dawson (1963) from the Galapagos, occurs as an extensive saxicolous crust bearing small articulated protuberances.

(b) A completely different situation occurs in *Corallina* and some related genera.

Basal crust organization is roughly similar to that of *Lithothamnion* (Cabioch, 1968; Johansen, 1969) whatever the variability of its development (Cabioch, 1966). When erect branches form locally, the intercalary meristem becomes terminal after sloughing off of the epithallus. A strand of elongated terminal initials is formed and internal organization of the branches is completely different from that of the perithallus of the crust.

In this context, the genus *Metamastophora* is quite unique. Erect thalli are borne on a small basal crust which has not been studied. They have a leafy habit and grow by means of a terminal meristem. Important cell ageing changes have been observed (Suneson, 1945). Among these, Woelkerling (1980) has shown what resembles secondary pit-connections in addition to prevailing cell-fusions. As in many foliose pseudoparenchymatous Rhodophyta, however, interpretation of such ageing phenomena is difficult and deserves new investigations.
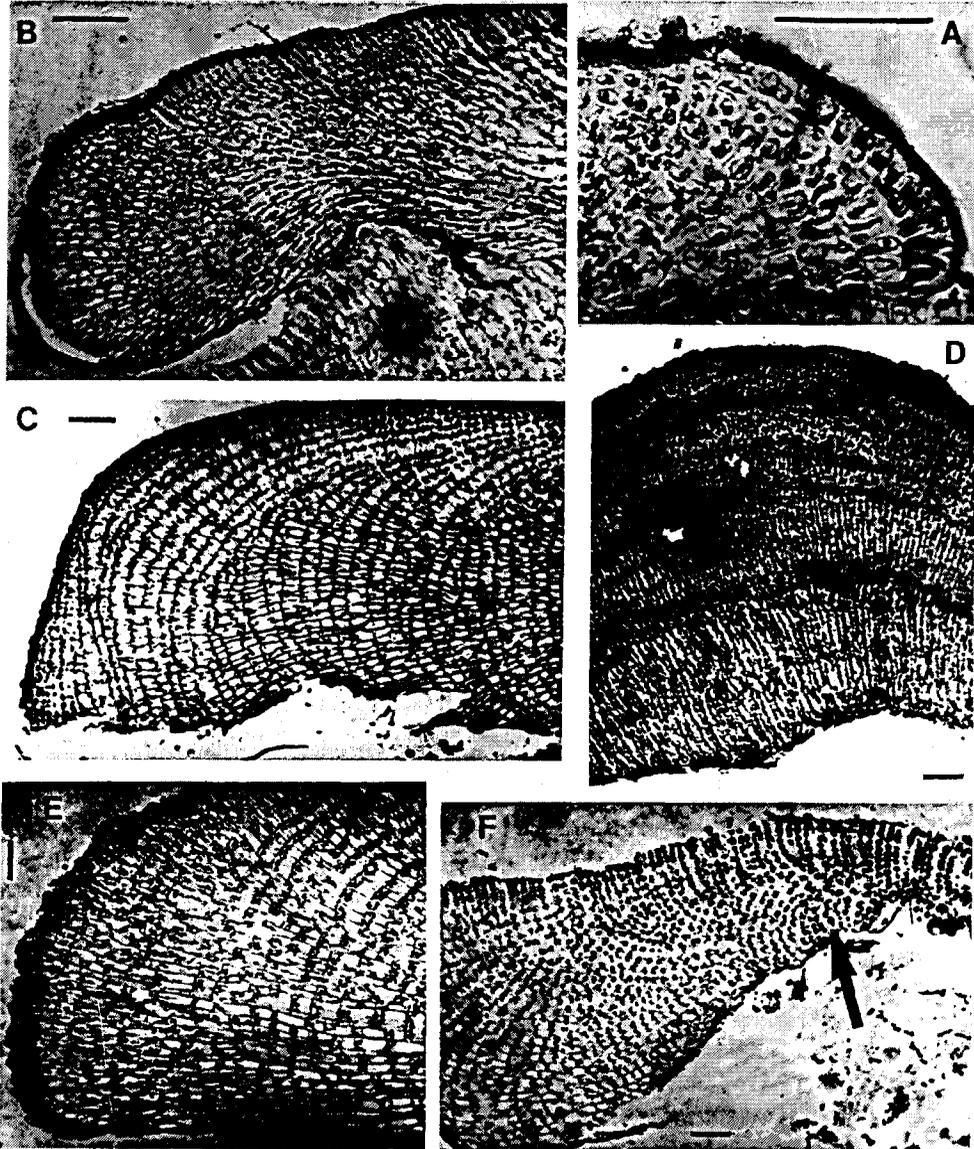
Fig. 4. Some types of organization in coralline algae. A: *Lithothamnion lenormandii*, margin of a crust; B: *Lithothamnion sp.*, general aspect of a crust; C: *Lithophyllum fasciculatum* (Lamarck) Foslie, id.; D: *Lithothamnion calcareum* (Pallas) Areschoug, first step of a branch development by local proliferation of the perithallus; E: *Lithophyllum incrustans*, margin of an adult thallus; F: id., metamorphosis, young juvenile stage on the right, adult organization on the left. Radial and axial sections, stained by haematoxylin and fuchsin; scale bar: 50 μm

Ontogenesis, metamorphosis and progressive development

Ontogenesis is a necessary complement to morphogenesis. Data are obtained from the cultivation of spores and by the observation of juvenile stages collected in nature. They give important precise information for generic definition. Despite the small number of sometimes contradictory observations reported in the literature (Bressan et al., 1977; Cabioch, 1972; Chamberlain, 1983; Chihara, 1974), two main ideas emerge:

(1) The spore develops directly (Fig. 6A, B) into a plant in parasitic (e.g. *Choreonema*) and endophytic (e.g. *Amphiroa*) forms; in all other known coralline algae, the spore transforms by segmentation into a germinative mass (Fig. 6C, D E) from which a plant develops.

(2) One type of adult organization can proceed from different kinds of development.

In most cases, such as in *Lithothamnion* (Fig. 6E), adult organization is initiated directly at the margin of the germinative mass (Cabioch, 1968, 1972).

But in some examples, encountered in the *Lithophyllum* complex, a juvenile stage is formed from the germinative mass; a more elaborate organization (Fig. 4F) appears later. In *L. incrustans* Philippi, the type species of the genus, a juvenile crust is observed in cultures; it has a simple organization (unilayered hypothallus) similar to an adult *Pseudolithophyllum*. Then, at the margin of this juvenile crust, a complete change of morphogenesis occurs (Cabioch, 1969b). The perithallial filaments generate a prostrate system still growing by means of an intercalary meristem which is not equivalent to a hypothallus either in origin or in organization. It has been named f a l s e h y p o t h a l - l u s (Cabioch, 1972). Such a complete change from one type of organization to another is usually called a m e t a m o r p h o s i s. This succession recalls what has been described in Sphacelariales (Sauvageau, 1909) and named p r o g r e s s i v e d e v e l o p m e n t (développement échelonné). Other similar cases, even if not general, are probably not rare in coralline algae.

Regeneration as a morphogenetical indicator

Despite their heavy mineralization, coralline algae have developed efficient survival strategies. Their internal cells remain alive for a long time and the thallus regenerates actively according to three main processes:

(1) In the case of internal destruction, regeneration is directly effected by closing reactions or surrounding living cells (Giraud & Cabioch, 1981).

(2) In the case of an external but superficial wound, one observes direct repair (Cabioch & Giraud, 1978a). Internal living cells recover meristematic and secretory activities and directly produce new cell files.

(3) In the case of greater destruction, regeneration is indirect. Surrounding living cells become meristematic and give rise to a crust with juvenile characters which covers the dead zone. The juvenile interpretation of this crust must, however, be inferred from ontogenetical data which are insufficiently available at present. A first attempt at applying such characters to generic definition has been proposed (Cabioch, 1972) but more investigations are needed before a generalization of results can be obtained.
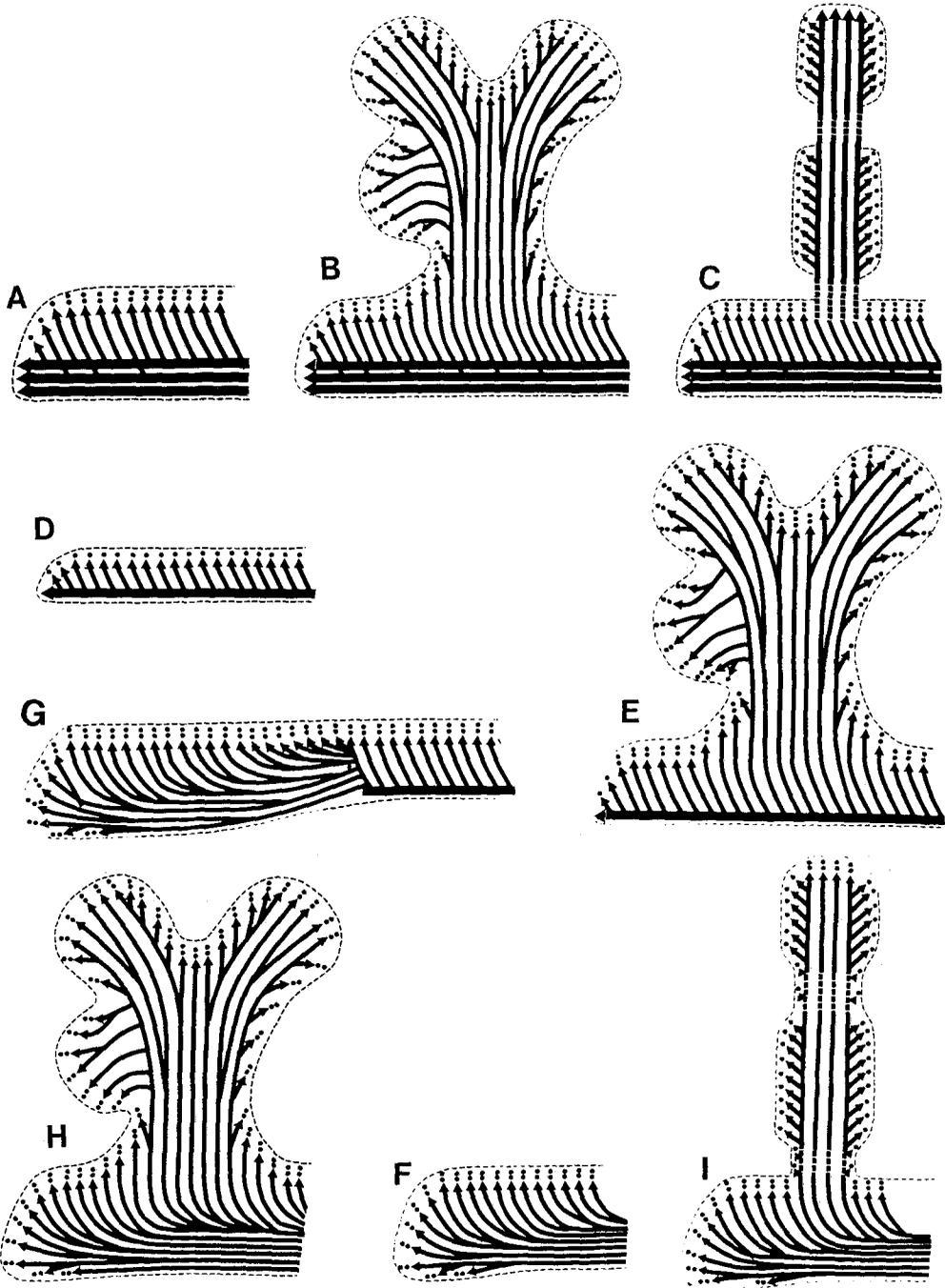
DISCUSSION

Some general features of morphogenesis can be pointed out and discussed in terms of their generic significance:

(1) The relative homogeneity of cell behaviour is markedly visible in a number of features such as the process of calcification, the constant presence of a secretory epithallus and the production of a polysaccharidic envelope which probably plays a more important role than is currently supposed. For example, special molecules involved in mollusc recruitment seem to be available at the surface of crustose forms (Morse & Morse, 1984); this is perhaps in relation with epithallial excretion.

(2) The main types of organization reflect different evolutionary steps comprising a whole range of possibilities from simple or regressed forms to more evolved erect and articulated ones.

(3) The constant presence of a crust in the life-cycle of all coralline algae, whatever its development and duration, seems highly significant for generic definition. It is crucial, however, to consider that crust at the maximum complexity it can reach, especially in the case of the *Lithophyllum* concept.

(4) Some classical anatomical terms must then be defined and somewhat restricted in relation to their real morphogenetical significance.

E p i t h a l l u s remains unchanged but has a very important functional significance. Correlatively some morphological criteria such as the shape of epithallial cells, still used by some authors for generic delineation *(Phymatolithon/Lithothamnion)*, have proved to be merely two aspects of the same process (Cabioch & Giraud, 1978b). They will probably be progressively deleted.

H y p o t h a l l u s currently designates the basal part of a crust, composed of horizontal filaments (uni- or multilayered) of crusts. When considering general features of morphogenesis throughout the Corallinales, the word must be restricted to prostrate filaments growing by means of a t e r m i n a l m e r i s t e m. The peculiar prostrate system in adult *Lithophyllum*, which is of a perithallial nature and origin, must be named differently: f a l s e h y p o t h a l l u s.

With the exception of this f a l s e h y p o t h a l l u s, p e r i t h a l l u s remains normally applied to all structures growing by means of an intercalary meristem.

Most branched forms (except *Corallina* and related genera) are of a purely perithallial nature even if some of them show morphological differentiation in cell arrangement. It must be recalled that some anatomical but confusing terms have formerly been introduced in the literature. In branches, articulated or not, one usually speaks of

Fig. 5. Characterization of the main genera by the different morphogenetic types encountered in coralline algae (radial and axial sections). A: crustose forms of *Lithothamnion, Clathromorphum, Neogoniolithon, Porolithon, Sporolithon;* B: branched forms of *Lithothamnion, Neogoniolithon, Porolithon, Sporolithon;* C: *Corallina* and related genera; D: simplified crustose forms: *Melobesia, Fosliella, Pneophyllum, Hydrolithon, Pseudolithophyllum, Titanoderma;* E: branched forms of *Hydrolithon, Pseudolithophyllum, Titanoderma* (= *Goniolithon*); F: adult *Lithophyllum;* G: crust of *Lithophyllum* with persistent juvenile characters; H: branched *Lithophyllum;* I: *Amphiroa.* Thick lines: hypothallus; thin lines: perithallus; arrows: meristems; dots: epithallus; dotted lines: uncalcified parts, general envelope or genicula
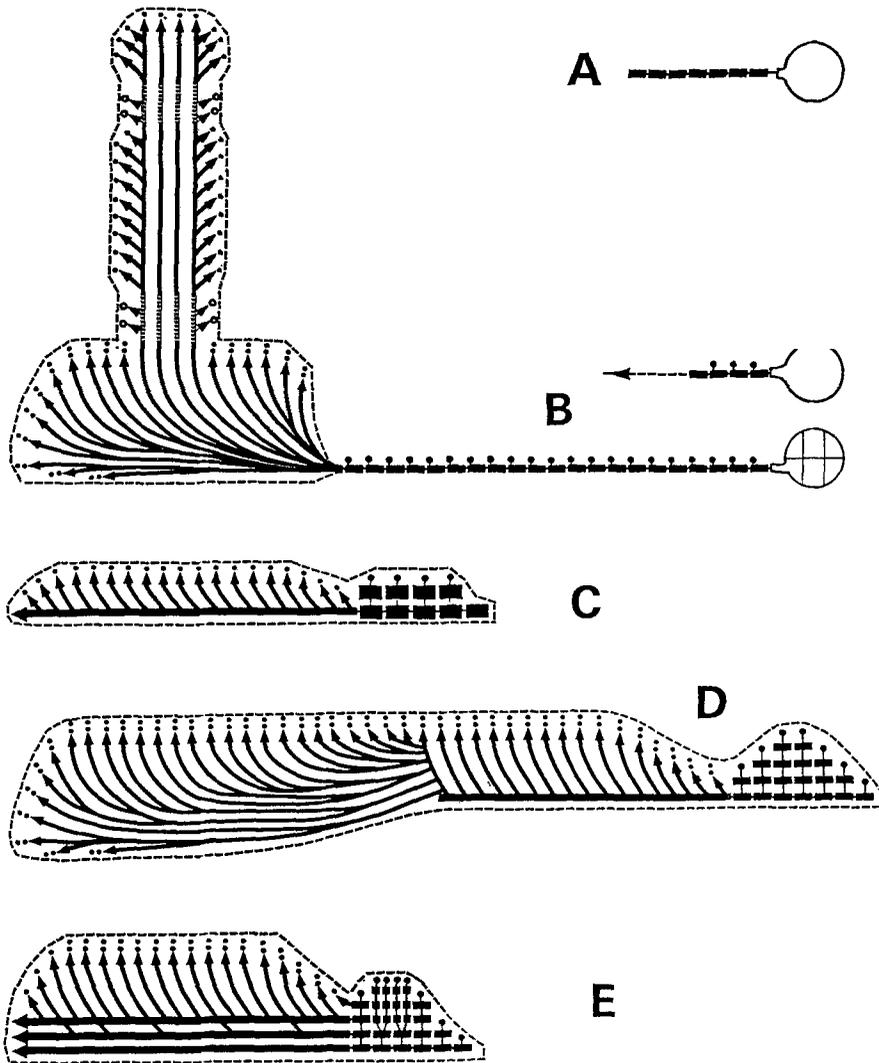
Fig. 6. Pattern of ontogenesis in coralline algae. A: *Choreonema*, B: *Amphiroa* – simple or direct development of the spore; C D E: the spore transforms first into a germinative mass; C: simplified crustose forms; D: progressive development in *Lithophyllum*; E: direct formation of a crust of a medium complexity. Same conventions as in Fig. 5. Reproduced from Cabioch, 1972

m e d u l l a and c o r t e x. This merely has topographical and not morphogenetical significance and can be maintained. In fact, these zones are the result of a physiological differentiation: the cortex being mainly photosynthetic (plastids predominant in cells), and the medulla more specialized for storage (starch grains predominant).

(5) Despite the lack of paleontological proof (Lemoine, 1977), a survey of ontogenesis and morphogenesis in coralline algae allows us to assume a general pattern of evolution
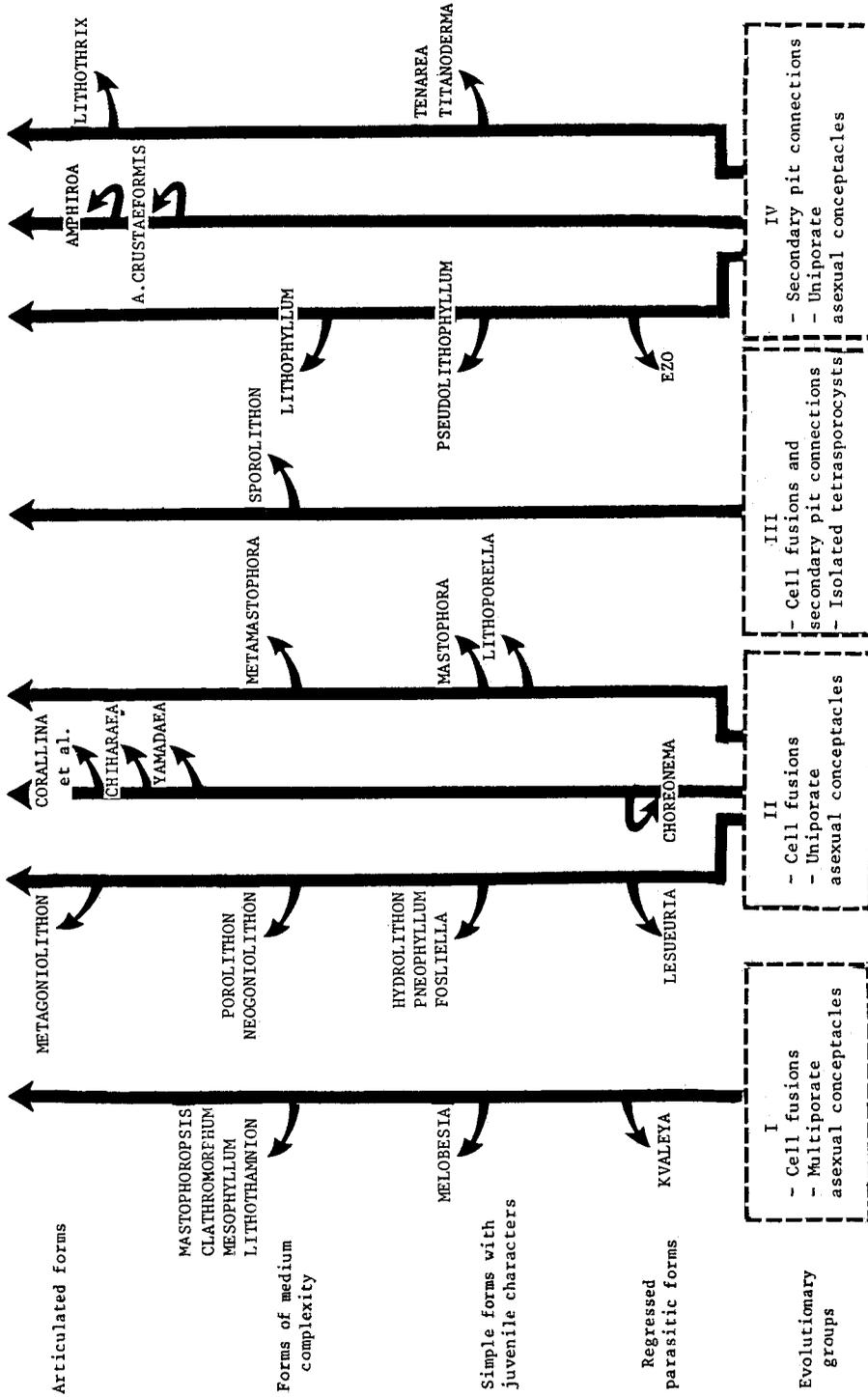
Fig. 7. Distribution of the main genera of coralline algae in evolutionary groups and phylogenetic lines according to their morphogenetic complexity. Modified from Cabioch, 1972

in coralline algae, marked by progressive realization of erect forms. Fundamental characters such as anastomoses and reproductive features (mainly asexual conceptacles) combine to form four natural groups (Fig. 7)*. Within them parallel evolutionary lines appear as continuums where genera are morphogenetical steps. This is emphasized by the frequent difficulty of their delineation. As an example, *Hydrolithon* and *Pneophyllum*, which are very close in organization and reproduction, differ mainly in their perithallial development. They are still undoubtedly separate entities. The delineation between *Pseudolithophyllum* and *Lithophyllum* is often more difficult because of the existence of a progressive development which is perhaps not general in *Lithophyllum*.

Such evolutionary groups have been assigned the value of subfamilies (Cabioch, 1972): group I: Lithothamnioideae; group II: Corallinoideae; group III: Sporolithoideae; group IV: Lithophylloideae.

CONCLUSION

Morphogenetical data can greatly improve generic definition but the following important facts should be kept in mind:

(1) Reproductive structures remain a strictly necessary complement (Johansen, 1976, 1981).

(2) Herbarium studies, even if strictly necessary, have to be considered cautiously. A type specimen in coralline algae is often just a stage in the life of an individual. In the case of progressive development, contestable conclusions can be obtained. Such cases emphasize the difficulty in obtaining sufficient knowledge of a taxon only by features of the type specimen. This knowledge must be completed by the study of freshly collected, well-preserved and abundant material at all stages of development.

(3) As a general rule, the morphogenetical potentialities of the p r i m a r y b a s a l c r u s t, considered at its m a x i m u m c o m p l e x i t y, seem to be a good generic characterization. (The term p r i m a r y is here applied to the adult crust developing directly or progressively from the spore, in opposition to possible s e c o n d a r y produc- tions such as repairs or discoid holdfasts . . .) New investigations should be undertaken along these lines.

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* Figure 7 does not take into account the recent proposal by Penrose & Woelkerling (1988) to merge *Hydrolithon*, *Neogoniolithon* and *Porolithon* into one genus: *Spongites* previously redefined (Woel- kerling, 1985). This proposal does not agree with our own observations (Mendoza & Cabioch, unpublished) on *H. reinboldii* (Weber van Bosse & Foslie) Foslie, type species of *Hydrolithon*, neither with those of Afonso-Carillo (1982) who emphasized the difference *Neogoniolithon/Porolithon* by the means of reproductive features; *Spongites* will perhaps partially replace *Neogoniolithon*, but the type species (*Spongites fruticulosa* Kützing) as recently redefined is still not fully relatable to any of the Mediterranean species known to date, not even to the species most closely resembling it: *N. mamillosum* (Hauck) Setchell et Mason.

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