

## **Terminology and Position of Reproductive Structures in Crustose Brown Algae: Misapplication, Confusion and Clarification<sup>1</sup>**

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**Abstract** — The different meanings and applications of the terms used to describe important taxonomic characters and to distinguish some species, genera, and families of Phaeophyceae are discussed. The position of reproductive structures on the thallus of crustose brown algae is considered a critical character but has been misapplied or interpreted differently by some investigators. The meaning of the terms “lateral” and “terminal” sometimes varies as used by different authors, as does the usage of “paraphyses” and “stalks.” For example, the position of the reproductive structure, lateral vs. terminal, and its relative position to the paraphyses, reproductive or vegetative filaments, and stalks have often not been clearly stated or defined. We propose restricted meanings and specific definitions for these terms in order to standardize their usage in algal systematics, and to simplify their use in comparative tables, numerical taxonomy, and morphological and phylogenetic analyses, etc. ...

**Crustose algae / morphology / Phaeophyceae / Ralfsiaceae / reproductive structures / taxonomy**

**Résumé** — Terminologie et position des structures de la reproduction des algues brunes encroûtantes : mauvais emploi, confusion et clarification. Les différentes significations et applications des termes utilisés pour décrire les caractères taxinomiques importants, ainsi que pour distinguer les espèces, les genres et les familles des Phaeophyceae, sont discutées. La position des structures de la reproduction sur le thalle des algues brunes encroûtantes est considérée comme un caractère discriminant mais il a été mal employé ou interprété différemment selon les investigateurs. La signification des termes “latéral” ou “terminal”, de même que l’emploi de “paraphyses” et de “pieds”, varient parfois selon les auteurs. Par exemple, la position des structures de reproduction, latérale vs terminale, et leur position relative vis-à-vis des paraphyses, des filaments fertiles ou végétatifs, et des pédicelles n’ont souvent pas été clairement établis ni définis. Nous proposons des significations restrictives et des définitions spécifiques pour ces termes afin de standardiser leur usage dans la systé-

1. In appreciation of her extensive phycological contributions, the authors are pleased to dedicate this paper to Prof. Isabella Aiona Abbott on the occasion of her 85<sup>th</sup> birthday.

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matique des algues, et pour simplifier leur usage dans les tableaux comparatifs, la taxinomie numérique, et les analyses morphologiques et phylogénétiques, etc.

**Algues encroûtantes / morphologie / organes reproducteurs / Phaeophyceae / Ralfsiaceae / taxonomie**

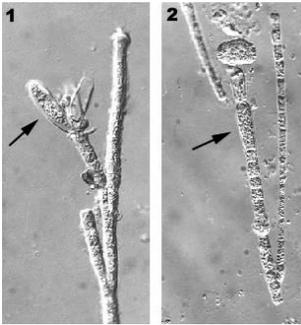
## INTRODUCTION

In the Class Phaeophyceae Kjellman (Heterokontophyta), a taxonomic character commonly used to distinguish species, genera and some families of these brown algae is the position of reproductive structures. “*Position*” is used in three different ways to state: 1) the ontogenetic relationship of a structure to the parent; 2) the spatial relationship of a mature structure to its parental filament or cell; and 3) the spatial relationship of a mature structure to its surroundings. To describe the position of reproductive structures in each of these three different situations, the same two main terms, “*lateral*” and “*terminal*,” have been used in the literature. Although the intended meaning may be clear for each taxon described, there has been ambiguity when the terms are used for comparisons among taxa. The result is that various authors interpret the anatomical morphologies differently. This fact is most obvious when using the reported position of the reproductive structures for comparisons, such as in trying to standardize comparative data for multiple uses, for instance, in generating keys, comparative morphological tables, numerical taxonomy, or phylogenies.

There are times when both “*lateral*” and “*terminal*” can be applied so that they mean the same thing. For example, we have observed some brown alga specimens in which the position of the reproductive structures (Figs 1, 2) may be considered terminal or lateral depending on whether one refers their position to the reproductive filament (terminal) or in relation to the paraphyses (lateral), and moreover, depending on whether one considers if paraphyses or stalks are present or absent. Since these terms are used relative to vegetative (=assimilatory) or reproductive filaments, or to paraphyses or stalks, the number of possible meanings or misapplications of these terms is high.

## DISCUSSION

**The different meanings.** Most authors use “*lateral*” to describe the position of reproductive structures in reference to the parent filament or cell, or another structure such as the paraphyses or surrounding filaments. In a proposed order, with the Ralfsiaceae Farlow (1881: 17) and other included families, Nakamura (1972: 153, as “*Ralfsiales*”) uses “*lateral*” as a character to distinguish it: “... the unilocular sporangia are lateral and the plurilocular sporangia are intercalary” [note: although this order was not accepted by Nelson (1982), nor was it validly published (Silva *et al.*, 1996: 572), it is in current use (Silva & de Reviere, 2000: 53)].



Figs 1-2. Both of the terms, “lateral” and “terminal,” can be used even to mean the same thing in interpreting the position of the reproductive structures (arrows).

For the context of this article it can be inferred that “lateral,” “intercalary,” and “terminal” all may refer to origin of reproductive initial. Fletcher (1987: 252, 257) says that in *Stragularia* Strömfelt (1886: 173) the sporangia are “... arising laterally at the base of paraphyses, [or] more rarely terminal on erect filaments ...,” and that *S. spongiocarpa* (Batters) Hamel (1939: XXXI) has unilocular sporangia “terminal on erect filament with or without associated paraphyses-like filaments, less frequently lateral at the base of the paraphyses-like filaments [which are] not markedly different from the erect vegetative filaments, sessile or on 1-2 celled pedicels, rarely reported terminally on paraphyses; ...” (Fletcher, 1987: 258). That is, the sporangia are lateral or terminal in origin, but lateral (to paraphysis-like filaments) or (ultimately) terminal in position (when stalks or pedicels are present) (Fletcher 1987: 260, fig. 72). Similarly, Feldmann (1937: 126, as ‘*Mesospora mediterranea*’) states that in *Hapalospongidion macrocarpa* (Feldman) León-Alvarez et González-González (1993: 474), “Les sporanges uniloculaires sont situés latéralement vers la base, ou plus fréquemment, vers la partie moyenne des filaments dressés.” While Feldmann (1937: fig. 41F) showed a unilocular reproductive structure arising from the reproductive filament, i.e. laterally, it becomes terminal in position on a stalk (see: Feldmann, 1937: Figs 40, 41E & G). He also mentioned the unilocular reproductive structures were medial in position on the erect filaments. Setchell & Gardner (1925: 497) described “zoosporangia” in *Ralfsia californica* Setchell et Gardner (1924: 2) as “borne laterally at the base of paraphyses”; however, pl. 36, fig. 22 of Setchell & Gardner (1925) shows the origin of reproductive structures at the same basal surface cell that produces the paraphyses [note: *R. californica* is considered to be the sporophyte of *Petalonia fascia* (O.F. Müller) O. Kuntze by Wynne (1969) and Kogame (1997)]. In describing *Mesospora mediterranea* Feldmann (1937: 266, Figs 40, 41E-G; now *Hapalospongidion macrocarpa* (Feldmann) León-Alvarez et González-González) states that in *Mesospora* Weber-van Bosse (1913: 143) the “Sporanges uniloculaires naissant latéralement à la base des filaments verticaux, ...,” i.e., the reproductive structures are lateral in origin and basal in position.

“Terminal” is used by most authors to describe the position of reproductive structures in reference to the parent filament or cell. Frequently “position” is also used in reference to reproductive or surrounding filaments. In the following examples, “terminal origin” is the same as “terminal in position.” In the Lithodermataceae Hauck (1883: 318), Nakamura (1972: 152) described the unilocular and plurilocular sporangia as “... terminally borne on the assimilating filament ...” Similarly *Petroderma* Kuckuck (1897: 382) was noted by Hollenberg (1969: 296) and Abbott & Hollenberg (1976: 174) to have “... unilocular sporangia terminal on the erect filaments.” Schiffner (1916: 158) in describing *Acrospongium*,

reported the position of sporangia in *A. ralfsioides* as: “Die uniloculären Sporangien sind an verkürzten Fäden terminal ... .”

The following examples describe the position of reproductive structures as “origin” and in reference to the surrounding filaments: Saunders (1899: 37) stated that *Hapalospongidion* has “unilocular sporangia arising from the transformation of the terminal cell or cells of the shorter vegetative filaments;” and, Tanaka & Chihara (1982: 388-389) in Mesosporaceae Tanaka *et* Chihara describe “... unilocular sporangium, without paraphyses, arising on stalk on erect filament, or arising terminally on erect filament ...;” however, *Mesospora* Weber-van Bosse, the type genus of Mesosporaceae, was described not with terminal, but with lateral unilocular reproductive structures [note: according to Womersley (1987: 74) and León-Alvarez & González-González (1990: 449) both *Mesospora* and *Basispora* John *et* Lawson (1974: 275) must be merged with *Hapalospongidion* Saunders].

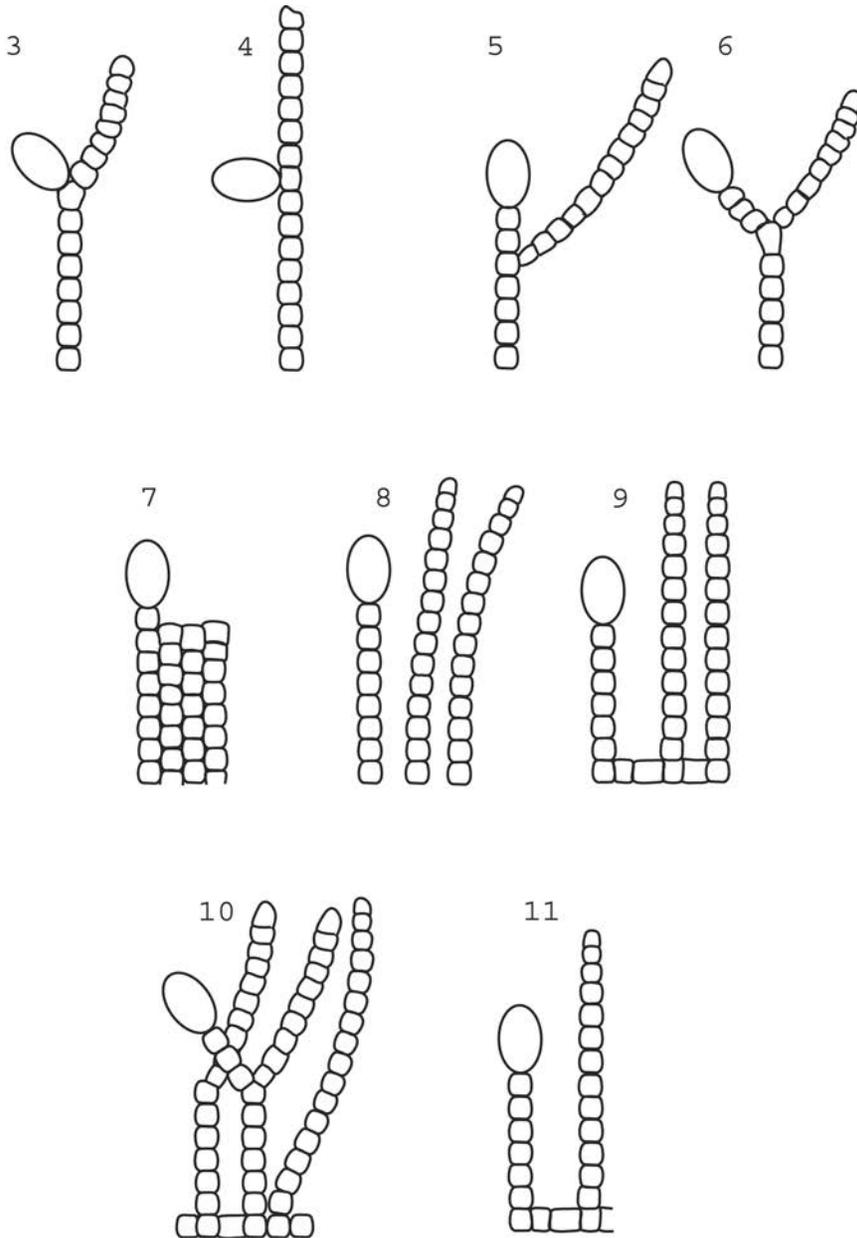
John & Lawson (1974: 285, as *Basispora*) mentioned that in *Hapalospongidion*, the “... unilocular sporangia arising from near base of erect vegetative filaments, terminal on distinct stalks which are usually several cells in length ... .” and their figure 4 shows one reproductive structure arising from a five-celled filament which is borne laterally from a vertical filament. Since they did not comment on the type of thallus development, we cannot infer from their study if the reproductive structure is terminal in origin or position, or if it is lateral in origin or position; however these structures are basal in position.

Some authors use the term “lateral” *sensu lato* without precisely stating its point of reference. Setchell (1924: 168, as *Ralfsia pangoensis*) said that in *Hapalospongidion pangoense* (Setchell) Hollenberg (1942: 532) “... the sporangia are not lateral but terminal, each on its own filament or stalk.” Similarly, Lindauer (1949: 346, as *Hapalospongidion durvilleae*) reported that in *Herpodiscus durvilleae* (Lindauer) South (1974: 457) the unilocular sporangia are “... terminal on short erect filaments.”

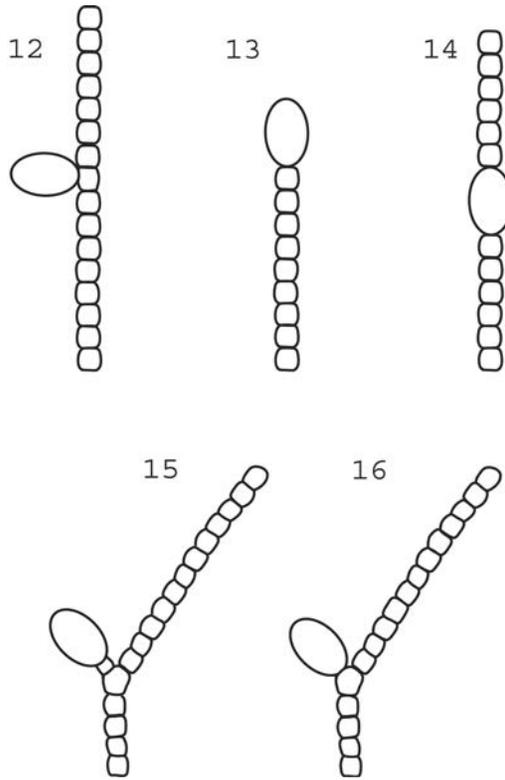
## RESULTS

In our review we found two different usages, *Cases 1* and *2*, of the term “**lateral**,” and two different usages, *Cases 3* and *4*, of the term “**terminal**.” Each case is an example of how these terms have been used differently by various authors, and is illustrated with diagrammatic figures that match the term as used in their published descriptions. *Case 1* (Figs 3, 4) shows reproductive structures in a “lateral” position. While *Case 2* (Figs 5, 6) illustrates reproductive structures borne “lateral to paraphyses.” *Case 3* (Figs 7-9) shows the reproductive structures as “terminal on erect filaments.” While in *Case 4* (Figs 10-11) the reproductive structures are: “terminal on their filaments or stalks” (Fig. 10), “terminal on erect short filaments (Fig. 11),” or “arising from near base of erect filaments, terminal on distinct stalks.”

In *Case 1*, “lateral” implicitly refers to the origin of the reproductive structures in reproductive filaments (whether there are paraphyses or not). In contrast, in *Case 2* “lateral” refers explicitly to the position of reproductive structures with respect to the paraphyses or other surrounding “paraphyses-like” filaments, so it depends on the presence or absence of paraphyses, and on the different interpretation and definitions given to such filaments. In general, a “paraphysis” is



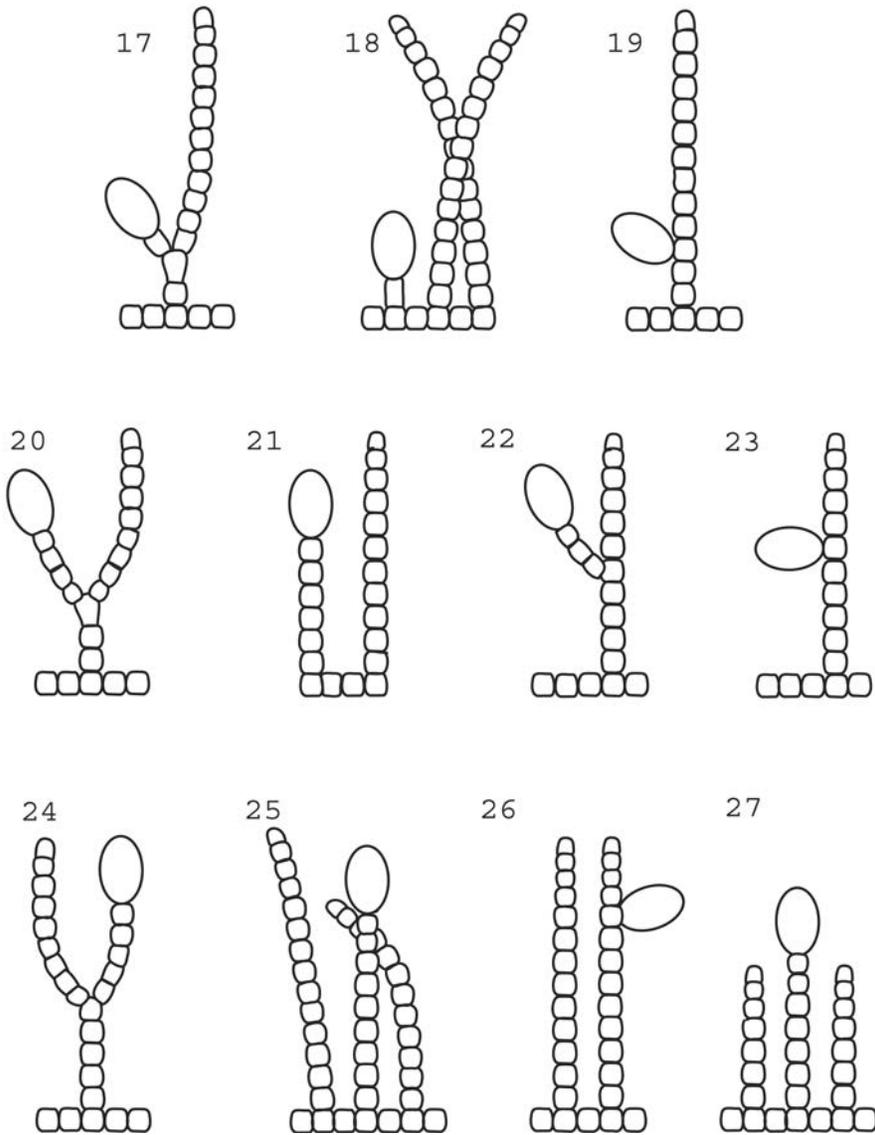
Figs 3-11. Position of the reproductive structure, diagrammatical drawn to show the “*lateral*” and “*terminal*” positions. **3-6.** Variations in the lateral positions, *Case 1* on reproductive filaments (3, 4); and *Case 2* lateral to a paraphysis (5, 6). **7-9.** *Case 3*, variations of the terminal position on reproductive filament [note: if not considered a paraphysis but a reproductive filament with a lateral branch, (as in 5) and the position would be “terminal;” or (as in 6 & 10) it could also be considered lateral on a reproductive filament, and therefore “terminal on a stalk”]. **10-11.** *Case 4*, examples of terminal position on “stalks” of a reproductive filament (6, 10; note paraphyses on both sides in Fig. 10), and “terminal” on a “short reproductive filament” (9, 11).



Figs 12-16. Position of the reproductive structure in the reproductive filament: **12**, lateral; **13**, terminal; and **14**, intercalary (not lateral). **15-16**. Use of the term “position” is arbitrary; for the character where insertion is on a unicellular stalk, we propose a “terminal position” (15); and when insertion is relative to a paraphysis, its position can only be “sessile” (without stalk) and lateral-basal to a paraphysis (16).

considered a filament or a cell arising from a vegetative or reproductive filament adjacent to the reproductive structures, and it probably protects them. Paraphyses can be morphologically differentiated from the supporting filament. In some species, e.g. *Stragularia spongiocharpa* (Batters) Hamel (1939: XXXI), the reproductive structures are borne laterally on an intercalary cell that divides the filament into two parts (Figs 3, 4), but the apical part is frequently not considered to be a paraphysis because it is morphologically undifferentiated, though its ascribed function is the same (Fig. 4). In *Case 2* (Figs 5, 6) the position of the reproductive structure is “lateral” with respect to the paraphysis; however the term is not applicable in reference to these *if* the apical part of the filament is not understood as such.

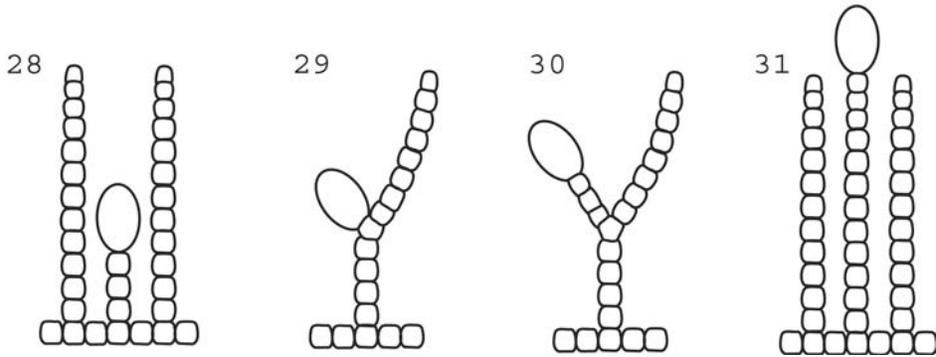
In *Cases 3* and *4* “terminal” explicitly refers to the reproductive filaments (whether on stalks or not) and *not* to the relative position with regard to paraphyses. Following this criterion, the situation for *Case 3* (Figs 5, 6) is not exclusive of *Case 4* (Figs 10, 11), and both groups of species have a terminal position. Following the same criterion of position on reproductive filaments, the reproductive structure’s position in species of *Cases 1* and *2*, is lateral only in the two left



Figs 17-27. Position of the reproductive structures relative to the height of surrounding filaments: **17-19**, basal; **20-23**, middle; **24-26**, sub-superficial; and **27**, superficial.

figures (Figs 3, 4) and terminal in the other two (Figs 5, 6). In *Case 3* (Figs 7-9) and *Case 4* (Figs 10, 11) two other criteria are used to distinguish them: 1) whether the “short” reproductive filament is considered a stalk (Fig. 10-11, 15) or not; and, 2) the position of reproductive structures with respect to the height of surrounding filaments (Figs 7-9).

Stalks are cells or short filaments from which the reproductive structures arise. They are morphologically differentiated from their generating filaments, but



Figs 28-31. **28-30.** Position of the reproductive structures with respect to the type of surrounding filaments is always *lateral*: i.e., 28, lateral to vegetative filaments; 29, lateral to paraphysis; and 30, lateral to reproductive filaments. **31.** Position of the reproductive structures is *not* lateral, if there are no filaments or paraphyses surrounding the reproductive structure (i.e., in this example it is above them).

neither differentiation nor generating filaments are always clearly recognized. For example, if a supporting filament is considered to be a stalk (Figs 1, 2, 10), then the position of the reproductive structure may be considered as lateral; otherwise it would be terminal. Following the second criterion, the reproductive structures are in the basal (Figs 17-19), medial (Figs 9, 20-23), sub-superficial (Figs 24-26), or superficial position (Fig. 27) relative to the height of the surrounding filaments.

Clearly one part of the problem in describing the reproductive structure's position is the use of several criteria for the same term; the other part is due to the different definitions given to "paraphyses" and "stalks." Presence or absence of paraphyses or stalks is dependent on stated definitions and consequently, so is the position of reproductive structures. Since there are many possible different interpretations of these characters, we propose criteria that may help simplify this problem.

First, we must distinguish between a reproductive structure's **origin** (= point-of-origin) and its **position**. We propose to restrict the term "**origin**" be used exclusively in relation to the origin of reproductive structures *on* the reproductive filaments, and we propose the use of "**position**" for the reproductive structure's position relative to its surrounding filaments and to the thallus as a whole. If we use the proposed "**origin**" criterion, the reproductive structures can arise in one of three ways (Figs 12-14): **lateral** (the reproductive structure arises laterally on an intercalary cell of the reproductive filament; Fig. 12); **terminal** (Fig. 13); and, **intercalary** (the whole reproductive structure originates between two vegetative cells of the reproductive filament, not laterally; Fig. 14).

Whenever there are no stalks, the *lateral origin* on the reproductive filament is equivalent to the *lateral position* of reproductive structures with respect to the reproductive filament. A reproductive structure is *terminal* in **origin** whenever it arises, and is developed by or is transformed from the apical cell of reproductive filaments or stalks, whether the stalks are unicellular (Fig. 15) or multicellular, and whether or not the position is lateral to whatever filament or paraphyses. The **origin** of reproductive structures can only be stated in relation to the paraphyses whenever these are on the same reproductive filament as the

reproductive structures (Fig. 16); otherwise in our proposal there would be no origin, only position. Tanaka & Chihara (1980: 338, as *R. bornetii*) mention that *Ralfsia clavata* (Harvey) P. et H. Crouan (1852: no. 52; note: considered by Fletcher, 1987: 254, to be *Stragularia clavata* (Harvey in J. Hooker) Hamel 1939: XXXI) has “paraphyses [are] arising terminally from an erect filament.” If we understood that paraphyses begin where the reproductive filament ends, then the origin of reproductive structures could be understood as terminal. But if we consider a paraphysis to be on the reproductive filament, then it is a part of it, in which case the origin of reproductive structure would always be lateral (sessile and basal to paraphyses) (Fig. 16).

Applying a criterion to the term **position**, we must observe the presence or absence of surrounding filaments, and if present, we can recognize three different positions of the reproductive structure (Table 1). In the first, its position relative to the height of surrounding filaments when they are present, the **position** of the reproductive structures on the thallus may be *basal* (Figs 17-19), *middle* (at mid-level) (Figs 20-23), and *sub-superficial* (Figs 24-26), or *superficial* (Fig. 27). In the second, regarding its position in relation to the surrounding filaments, the **position** can only be *lateral* to vegetative filaments (Fig. 28), paraphyses (Fig. 29), or reproductive filaments (Fig. 30). However “lateral” is not applicable if there are no surrounding filaments (Fig. 31), and in fact, it is important to also state this condition as a taxonomic character. In the third, its relation to the thallus as a whole, the **position** of the reproductive structures (a character often used in some species of *Ralfsia*) may be in the *center* of the thallus, on the *margins*, *intermedial* (between margin and center), or *irregularly* distributed.

## CONCLUSION

The origin of reproductive structures is essential to describe the reproductive structures, but unfortunately it is not always known. Whenever possible we should describe it using the proposed restricted meaning in combination with its position (Table 1). With the **origin** criterion we restrict the relativity of the repro-

Table 1. Proposed criteria for the application of the term “**position.**”

POSITION OF REPRODUCTIVE STRUCTURES			
	If Surrounding Filaments are Present		If Surrounding Filaments are Not Present <sup>1</sup>
Position is always <b>lateral</b> to the kind of filaments:	Position in relation to height of surrounding filaments:	Position in relation to whole thallus: <sup>2</sup>	<b>Not</b> applicable (Fig. 31)
<i>reproductive</i> ; <i>vegetative</i> ; or <i>paraphyses</i>	<i>basal</i> (Figs 17-19); <i>mid-level</i> (Figs 20-23); <i>sub-superficial</i> (Figs 24-26); or <i>superficial</i> (Fig. 27)	<i>center</i> ; <i>intermedial</i> ; <i>margin</i> ; or <i>irregular</i>	

1 It may be important to state as a character when there are no surrounding filaments.

2 This character is used in some species of *Ralfsia*.

Table 2. Proposed Terms for the Characters and Character States of the Position of Reproductive Structures in Crustose Algae.

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**I. Origin of Reproductive Structures:**

- a) *terminal* (whether on a stalk or a reproductive filament)
- b) *lateral* on the reproductive filament (always sessile)
- c) *intercalary* on the reproductive filament (not lateral)

**II. Position of Reproductive Structures:**

- 1. In relation to the height of surrounding filaments:
  - a) *basal* (near the hypothallus)
  - b) *mid-level* (in the middle of the perithallus)
  - c) *sub-superficial* (near the upper surface of the thallus)
  - d) *superficial* (on the upper surface of the thallus)
- 2. Type and presence or absence of filaments surrounding to the reproductive structures:
  - a) *reproductive filaments*
  - b) *vegetative filaments*
  - c) *paraphyses*
  - d) *no surrounding filaments*
- 3. If there is morphological differentiation of the surrounding filaments (i.e., whether they are paraphyses, or reproductive or vegetative filaments). If filaments are functional paraphyses that can be noted/coded apart as an independent character, either as:
  - a) *yes*; or b) *no*
- 4. In relation to the thallus as a whole:
  - a) *center*
  - b) *intermedial* (between margin and center)
  - c) *marginal*
  - d) *irregular*

**III. Morphological Differentiation of Supporting Filaments, as either:**

- a) *yes*, or b) *no*

**IV. Number of Cells of the Supporting Filament.**

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ductive structure's position *sensu lato* to the reproductive filament, and it is independent of different concepts of paraphyses or stalks and consequently of their presence or absence. In our proposal we do not intend to define the biological sense of the ambiguous terms "*paraphysis*" and "*stalk*" for which we think more work is needed, but we give criteria to describe them and in the case of the relative position of the reproductive structures they are referred to the "reproductive filaments," because they are easily recognized.

In order to more accurately describe the position of the reproductive structures and to facilitate the comparison of features, we propose a clarified use of terms and definitions (Table 2). We encourage their use to assist in the comparison of taxonomic characters and character states, including the type of surrounding filaments, the morphological differentiation of paraphyses (or surrounding filaments) and stalks, and the number of stalk cells.

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