

Guía para la identificación de rodolitos de algas rojas coralinas no geniculadas (Corallinales, Rhodophyta)

A guide to nongeniculate coralline red algal (Corallinales, Rhodophyta) rhodolith identification

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Resumen

Los rodolitos son estructuras libres compuestas principalmente de algas rojas coralinas no geniculadas. Por lo general no es posible identificar con certeza las especies que forman los rodolitos con base únicamente en la forma en que crecen u otras características morfológicas externas. Para una identificación precisa y confiable normalmente se requiere realizar cortes histológicos para examinar los caracteres vegetativos y reproductivos pertinentes. En este trabajo se presentan pasos simplificados para facilitar la identificación de rodolitos de algas rojas coralinas no geniculadas. El proceso de identificación se divide en dos etapas y consiste en identificar los especímenes a nivel de género, en primera instancia, y a nivel de especie, en segunda. Se han registrado aquí los géneros comunes de algas no geniculadas formadoras de rodolitos (*Hydrolithon*, *Neogoniolithon*, *Lithophyllum*, *Sporolithon*, *Lithothamnion*, *Phymatolithon*, *Mesophyllum* y *Spongites*), y se proporcionan ilustraciones y/o referencias de caracteres taxonómicos importantes de utilidad para la identificación de especímenes a nivel de género. También se proporciona bibliografía de publicaciones recientes sobre descripciones florísticas o estudios taxonómicos detallados de especies formadoras de rodolitos de estos ocho géneros para facilitar su identificación.

Palabras clave: rodolitos, algas coralinas, identificación, Corallinales.

Abstract

Rhodoliths are free-living structures composed mostly of nongeniculate coralline red algae. Species that form rhodoliths usually cannot be identified with certainty using only growth form or other external morphological features. Accurate and reliable identification usually requires sectioning for examination of pertinent vegetative and reproductive characters. Simplified steps to facilitate identification of nongeniculate coralline red algal rhodoliths are presented in this paper. Identification is a two-tiered process involving identification of specimens to genus followed by identification of specimens to species. We list the common nongeniculate rhodolith-forming genera (*Hydrolithon*, *Neogoniolithon*, *Lithophyllum*, *Sporolithon*, *Lithothamnion*, *Phymatolithon*, *Mesophyllum* and *Spongites*) and provide illustrations and/or references to important taxonomic characters useful for identifying specimens to genus level. We also provide references to recently published floristic descriptions or detailed taxonomic accounts to rhodolith-forming species in these eight genera to facilitate species identification.

Key words: rhodolith, coralline algae, identification, Corallinales.

Introducción

Las algas rojas coralinas (Corallinales, Rhodophyta) se encuentran en la mayoría de los hábitats marinos, desde las regiones tropicales hasta las polares y desde la zona intermareal hasta profundidades de por lo menos 268 m (Littler *et al.* 1985). Morfológicamente, estas algas son ya sea geniculadas (con ramas que consisten de segmentos no calcificados y calcificados alternados llamados genículos e intergenículos, respectivamente) o no geniculadas (sin segmentos no calcificados y calcificados alternados).

Los rodolitos son estructuras libres compuestas principalmente (>50%) de algas rojas coralinas no geniculadas (Foster 2001, p. 659). Un rodolito individual puede estar integrado por una o varias especies coralinas, además de contener otros organismos incrustantes como briozoarios, foraminíferos, gasterópodos, etc. Los mantos de rodolitos son agregaciones de

Introduction

Coralline red algae (Corallinales, Rhodophyta) are represented in most marine habitats from tropical to polar regions and from the intertidal to depths of at least 268 m (Littler *et al.* 1985). Morphologically, coralline red algae are either geniculate (with branches consisting of alternating uncalcified and calcified segments, respectively called genicula and intergenicula) or nongeniculate (lacking alternating uncalcified and calcified segments).

Rhodoliths are free-living structures composed mostly (>50%) of nongeniculate coralline red algae (Foster 2001, p. 659). An individual rhodolith may be composed of one or several coralline species and may also include other encrusting organisms such as bryozoans, foraminifers, gastropods, etc. Rhodolith beds are aggregations of rhodoliths, and such beds are found in many parts of the world (Foster 2001). While not

rodolitos y se encuentran en muchas partes del mundo (Foster 2001). Aunque no se incluyen en esta guía, es importante indicar que algunos corales geniculados (Foslie 1887) y otras algas rojas, tales como los miembros de la familia Peyssonneliaceae (Ballantine *et al.* 2000, Lund *et al.* 2000), también pueden formar estructuras libres llamadas “rodolitos”.

Se sabe que existen amplios registros fósiles de rodolitos diseminados en depósitos desde el norte de Noruega (Freiwald *et al.* 1991), en los trópicos (Foster *et al.* 1997), y hasta Nueva Zelanda (Burgess y Anderson 1983). No obstante que los rodolitos fósiles son componentes sedimentarios importantes en varios contextos, incluyendo las llamadas “litofacies rodoalgales” (Halfar y Mutti 2005), aún existen muchas preguntas por contestar sobre la taxonomía de estas estructuras y este trabajo ha tenido que limitarse a las algas rojas coralinas no fósiles.

Por lo general no es posible identificar con certeza a las especies formadoras de rodolitos con base únicamente en su forma de crecimiento u otras características morfológicas externas. Para una identificación precisa y confiable normalmente se requiere realizar cortes histológicos que permitan examinar los caracteres vegetativos y reproductivos pertinentes. El proceso de identificación se divide en dos etapas y consiste en identificar los especímenes a nivel de género, en primera instancia, y a nivel de especie, en segunda.

Este trabajo pretende ser una guía para facilitar la identificación de los géneros de algas coralinas no geniculadas que forman rodolitos, así como un compendio de la literatura publicada desde 1990 sobre las especies formadoras de rodolitos. No es un manual para “determinaciones rápidas”, sino más bien un intento de resumir la literatura taxonómica para que, con cierta práctica, se puedan identificar los especímenes rodolíticos. Por tanto, se han registrado los géneros comunes de algas no geniculadas que forman rodolitos y se proporcionan ilustraciones y/o referencias de caracteres taxonómicos importantes de utilidad para la identificación de especímenes a nivel de género. También se proporciona bibliografía de publicaciones recientes (desde 1990) sobre descripciones florísticas o estudios taxonómicos detallados de especies formadoras de rodolitos de los ocho géneros comunes para facilitar la posible identificación de especies.

Identificación a nivel de género

El orden Corallinales incluye tres familias con representantes de géneros vivientes (Harvey *et al.* 2003a). Taxonómicamente, dos familias (Sporolithaceae y Hapalidiaceae) incluyen sólo géneros no geniculados, mientras que el tercero (Corallinaceae) incluye tanto géneros no geniculados como geniculados. Este trabajo se enfoca exclusivamente en los taxones no geniculados.

De los 42 géneros coralinos actualmente reconocidos con representantes vivos (tabla 1), 26 son no geniculados; de éstos, 8 incluyen especies que se sabe forman rodolitos. El potencial de especies de otros géneros para formar rodolitos es incierto.

included in this guide, it should be noted that some geniculate corallines (Foslie 1887) and other red algae, such as members of the Peyssonneliaceae (Ballantine *et al.* 2000, Lund *et al.* 2000), can also form free-living structures termed “rhodoliths”.

Rhodoliths are also known to occur extensively in the fossil record, forming deposits as far north as northern Norway (Freiwald *et al.* 1991), through the tropics (Foster *et al.* 1997), down to New Zealand (Burgess and Anderson 1983). While fossil rhodoliths are major sedimentary components in several contexts, including so-called rhodalgal lithofacies (Halfar and Mutti 2005), there are many unanswered questions regarding the taxonomy of these structures and the current paper is necessarily restricted to non-fossil coralline red algae.

Species that form rhodoliths usually cannot be identified with certainty using only growth form or other external morphological features. Accurate and reliable identification usually requires sectioning for examination of pertinent vegetative and reproductive characters. Identification is a two-tiered process involving identification of specimens to genus followed by identification of specimens to species.

This paper is intended as a guide to help identify common nongeniculate coralline rhodolith-forming genera and as a resource to accounts of rhodolith-forming species published since 1990. It is not a “quick-fix” manual but rather an attempt to summarize the taxonomic literature so rhodolith specimens can, with some practice, be identified. In order to do this we list the common nongeniculate rhodolith-forming genera and provide illustrations and/or references to important taxonomic characters useful for identifying specimens to genus level. We also provide references to recently (since 1990) published floristic descriptions or detailed taxonomic accounts to rhodolith-forming species in these eight genera to facilitate possible species identification.

Identification to genus

The Corallinales includes three families with currently living genera (Harvey *et al.* 2003a). Taxonomically, two families (Sporolithaceae and Hapalidiaceae) include only nongeniculate genera, while the third (Corallinaceae) includes some nongeniculate genera and some geniculate genera. The present paper focuses exclusively on nongeniculate taxa.

Of the 42 currently recognized coralline genera with living representatives (table 1), 26 are nongeniculate; of these, 8 include species that are known to form rhodoliths. The potential of species in other genera to form rhodoliths is uncertain.

Generic characters for nongeniculate taxa have been studied in detail on a world scale and, with one-two exceptions, are reasonably stable. Thus, identifying most fertile specimens to genus is usually relatively straightforward.

Accurate and reliable identification of unknown specimens to genus usually requires embedding and sectioning for detailed examination of taxonomically important vegetative and reproductive characters (see table 2). If a plant is sterile, occasionally it can be provisionally identified using only

Tabla 1. Géneros reconocidos del orden Corallinales con representantes vivos. Se subrayan los géneros no geniculados. (Información tomada de Harvey *et al.* 2003a, tabla 4, y actualizada según Guiry y Selivanova 2007.)**Table 1.** Currently recognized Corallinales genera with living representatives. Nongeniculate genera are underlined. (Taken from Harvey *et al.* 2003a, table 4, updated as per Guiry and Selivanova 2007.)

Family and subfamily	Genera
Corallinaceae	
Metagoniolithoideae	<i>Metagoniolithon</i>
Corallinoideae	<i>Alatocladia</i> , <i>Arthrocardia</i> , <i>Bossiella</i> , <i>Calliarthron</i> , <i>Cheilosporum</i> , <i>Chiharaea</i> , <i>Corallina</i> , <i>Haliptilon</i> , <i>Jania</i> , <i>Marginosporum</i> , <i>Masakiella</i> , <i>Serraticardia</i> , <i>Yamadaea</i>
Mastophoroideae	<u><i>Hydrolithon</i></u> , <u><i>Lesueuria</i></u> , <u><i>Lithoporella</i></u> , <u><i>Mastophora</i></u> , <u><i>Metamastophora</i></u> , <u><i>Neogoniolithon</i></u> , <u><i>Pneophyllum</i></u> , <u><i>Spongites</i></u>
Lithophylloideae	<i>Amphiroa</i> , <u><i>Ezo</i></u> , <u><i>Lithophyllum</i></u> / <u><i>Titanoderma</i></u> , <i>Lithothrix</i> , <u><i>Paulsilvella</i></u> , <u><i>Tenarea</i></u>
Hapalidiaceae	
Austrolithoideae	<u><i>Austrolithon</i></u> , <u><i>Boreolithon</i></u>
Choreonematoideae	<u><i>Choreonema</i></u>
Melobesioideae	<u><i>Clathromorphum</i></u> , <u><i>Exilicrusta</i></u> , <u><i>Kvaleya</i></u> , <u><i>Lithothamnion</i></u> , <u><i>Mastophoropsis</i></u> , <u><i>Melobesia</i></u> , <u><i>Mesophyllum</i></u> , <u><i>Phymatolithon</i></u> , <u><i>Synarthrophyton</i></u>
Sporolithaceae	<u><i>Heydrichia</i></u> , <u><i>Sporolithon</i></u>

Los caracteres genéricos de los taxones no geniculados han sido estudiados en detalle a nivel mundial y, con uno o dos excepciones, son razonablemente estables. Por tanto, la identificación de la mayoría de los especímenes fértiles a nivel de género resulta relativamente directa.

La identificación precisa y confiable de especímenes desconocidos a nivel de género normalmente requiere de su inclusión y corte para observar detalladamente sus caracteres vegetativos y reproductivos de importancia taxonómica (ver tabla 2). Si una planta es estéril ocasionalmente puede ser identificada de manera provisional con base únicamente en los caracteres vegetativos, pero en general se requieren los caracteres reproductivos para confirmar cualquier identificación provisional.

Identificación a nivel de especie

La identificación a nivel de especie de especímenes de algas coralinas formadoras de rodolitos casi siempre resulta más compleja que la identificación genérica.

Se han descrito más de 1600 especies no geniculadas y taxones infraespecíficos (Woelkerling 1988, 1998a), pero un legado de trabajo taxonómico de mala calidad, particularmente entre 1890 y 1910, ha dejado muchos problemas sin resolver y el número real de especies aún queda por determinarse (Woelkerling 1998a). No existe ninguna monografía mundial del orden Corallinales, y la evaluación de los caracteres empleados en la delimitación de especies a nivel mundial es actualmente materia de investigación. Muchos especímenes típicos de especies formadoras de rodolitos requieren de un análisis moderno y, hasta que esto suceda, no hay ninguna certeza de que los nombres publicados han sido aplicados de forma correcta. En consecuencia, los nombres de especies que

vegetative characters, but reproductive characters are usually needed to confirm any provisional identifications.

Identification to species

The identification of rhodolith-forming specimens of coral-line algae to species almost always is more complicated than generic identification.

Over 1600 nongeniculate species and infraspecific taxa have been described (Woelkerling 1988, 1998a), but a legacy of poor quality taxonomic work, particularly from 1890 to 1910, has left many unresolved problems, and the true number of species has yet to be determined (Woelkerling 1998a). No world monograph of the Corallinales currently exists, and the assessment of characters used in delimiting species on a world basis is a focus of ongoing research. Many type specimens of rhodolith-forming species are in need of modern examination and, until this is done, there is no guarantee that published names have been correctly applied. As a result, species names in the literature must be treated with caution. For this reason tables 3–10 also include pertinent information on type material for each species.

There are two routes one can follow after placing a genus name on a specimen. The first is to place the specimen in the hands of an expert. The second is to use published taxonomic accounts to try to identify the species. It is not possible at present to provide a reliable worldwide key to rhodolith-forming species. Tables 3–10, however, contain a summary of accounts published since 1990 of rhodolith-forming species in each genus, and these can be used as a starting point for attempting to identify specimens. The fact that a specimen occurs as a rhodolith is of little significance from a taxonomic standpoint and the taxonomic and floristic accounts in

se manejan en la literatura deben ser usados con cautela. Por tal motivo en las tablas 3–10 también se incluye información pertinente de material típico para cada especie.

Después de identificar el género de un espécimen se puede proceder de dos formas. El primero es colocar el espécimen en manos de un experto. El segundo es tratar de identificar la especie con base en la literatura taxonómica existente. Actualmente no es posible proporcionar una clave universal confiable para las especies que forman rodolitos en todo el mundo; sin embargo, en las tablas 3–10 se presenta un resumen de trabajos publicados sobre tales especies en cada género desde 1990, los cuales pueden ser utilizados como punto de referencia para la identificación de especímenes. El hecho de que un espécimen se presente como rodolito tiene poca importancia desde un punto de vista taxonómico, y es posible que los listados taxonómicos y florísticos en dichas tablas no incluyan representantes vivos; más bien el objetivo principal ha sido proporcionar detalles e ilustraciones que resulten de utilidad para identificar las especies.

Para las regiones que cuentan con trabajo monográfico reciente o estudios detallados modernos de especies individuales, la identificación a nivel de especie probablemente resulte menos problemática, especialmente si se han estudiado los especímenes típicos.

Una revisión monográfica es un tratado sobre un taxón individual o un grupo de taxones relacionados (i.e., listado de un género, una familia o una subfamilia algal). En general es completa en sí misma y con frecuencia se presenta en forma de artículo que describe detalles de los géneros y las especies de una región en particular. Se han publicado estudios monográficos modernos sobre taxones coralinos no geniculados para el archipiélago de Spermonde en Indonesia (Verheij 1993a, 1993b, 1994), las Islas Británicas (resumidas en Irvine y Chamberlain 1994), el sur de Australia (resumidas en Womersley 1996), el sureste de Australia (Harvey *et al.* 2002, 2003b, 2006) y la zona central de Nueva Zelanda (Harvey *et al.* 2005).

Las revisiones detalladas de especies frecuentemente incluyen datos morfológicos y anatómicos, ilustraciones de los caracteres taxonómicos importantes, descripciones detalladas de las especies, discusiones taxonómicas y/o comparaciones con especies relacionadas. En contraste, las descripciones florísticas frecuentemente proporcionan ilustraciones de la morfología a grandes rasgos, breves descripciones de las especies y emplean terminología menos especializada.

Entre los estudios florísticos publicados desde 1990 que contienen descripciones ilustradas de los taxones coralinos no geniculados se encuentran las de Baba (1998, Japón); Bressan y Babbini (2003, Mediterráneo); Cabioch *et al.* (1992, Europa); Fragosa y Rodríguez (2002, costa tropical del Pacífico mexicano); Huisman (2000, Australia); Littler y Littler (1997, Cayos Pelican, Belice); Littler y Littler (2000, Caribe); Littler y Littler (2003, Pacífico Sur); Mendoza *et al.* (1996, Argentina); y Payri *et al.* (2000, Polinesia Francesa).

tables 3–10 may not include free-living specimens; rather, their primary purpose is to provide details and illustrations useful for species identification.

For regions where recent monographic work has been published, or detailed modern studies of single species exist, identification to species level is likely to be more straightforward, especially when studies of the types have been conducted.

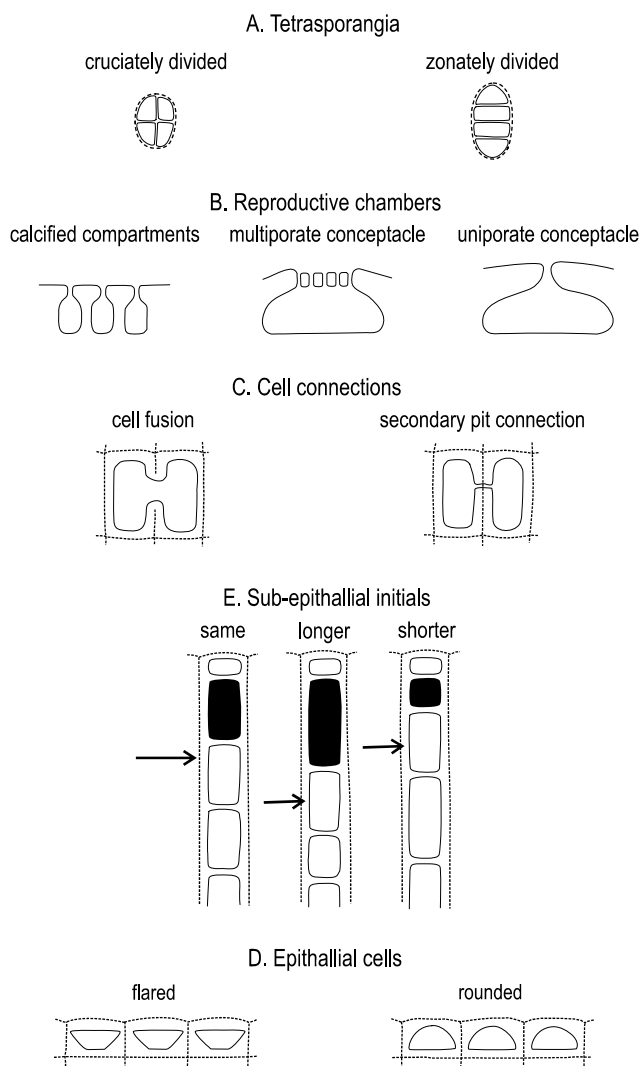


Figura 1. Caracteres taxonómicos importantes, simplificados, de utilidad para la identificación de los géneros de algas coralinas no geniculadas (ver tabla 2). A. Tetrasporangios divididos. B. Cámaras reproductivas. C. Conexiones celulares. D. Células epitalliales. E. Iniciales subepitalliales. Nota: las iniciales subepitalliales (sombreadas) pueden ser del mismo tamaño, más largas o más cortas que la célula inmediatamente debajo de ellas (flechas).

Figure 1. Simplified important taxonomic features useful for identifying nongeniculate coralline genera (as per table 2). A. Divided tetrasporangia. B. Reproductive chambers. C. Cell connections. D. Epithallial cells. E. Subepithallial initials. Note: subepithallial initials (shaded) may be the same size, longer or shorter than the cell immediately below them (arrows).

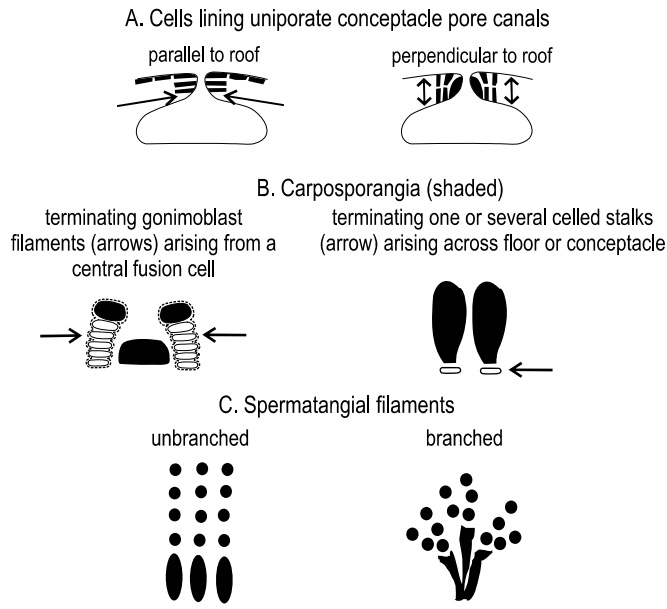


Figura 2. Caracteres taxonómicos importantes, simplificados, de utilidad para la identificación de los géneros de algas coralinas no geniculadas (ver tabla 2). A. Células que revisten el canal del poro de los conceptáculos uniporados. B. Carposporangios. C. Filamentos espermatangiales.

Figure 2. Simplified important taxonomic features useful for identifying nongeniculate coralline genera (as per table 2). A. Cells lining uniporate conceptacle pore canal. B. Carposporangia. C. Spermatangial filaments.

Las algas coralinas no geniculadas son muy variables en su morfología (Woelkerling *et al.* 1993a). Una sola especie puede mostrar una variedad de formas de crecimiento que pueden ser exhibidas por varias otras especies, lo cual dificulta una identificación visual (ver Womersley 1996, pp. 196, 206, 230). Mientras que las guías de campo o los listados florísticos tienden a ser más amenos para el usuario que las revisiones taxonómicas, la identificación se puede basar más bien en las características vegetativas y/o morfológicas más evidentes que en los caracteres reproductivos de importancia taxonómica. No obstante, las descripciones florísticas a menudo incluyen fotografías útiles e información importante, y con frecuencia resultan ser un buen punto de partida para la identificación de los especímenes. En las tablas sólo se incluyen las publicaciones que contienen descripciones ilustradas o estudios detallados de los taxones. No se presentan registros no confirmados de otras especies formadoras de rodolitos que aún tienen que ser analizados desde el punto de vista taxonómico.

Nuestro conocimiento de los caracteres para el diagnóstico de las especies coralinas no geniculadas recientemente ha cambiado de forma significativa. Los trabajos monográficos y los estudios detallados de géneros individuales han mostrado que varios de los rasgos utilizados anteriormente para diferenciar las especies no son confiables (Wilks y Woelkerling 1991, 1995; Woelkerling y Campbell 1992; Woelkerling y Harvey 1993, p. 601; Woelkerling 1997), y se requieren estudios adicionales de especímenes y material típicos para evaluar completamente los conceptos de especies a nivel mundial. Por

A monographic account is a treatise on a single taxon or group of related taxa (i.e., an account of an algal genus, family or subfamily). It is usually complete in itself, and can often take the form of a paper providing detailed studies of the genera and species from a particular region. Modern monographic studies covering nongeniculate coralline taxa have been published for the Spermonde Archipelago in Indonesia (Verheij 1993a, 1993b, 1994), the British Isles (summarized in Irvine and Chamberlain 1994), southern Australia (summarized in Womersley 1996), southeastern Australia (Harvey *et al.* 2002, 2003b, 2006) and central New Zealand (Harvey *et al.* 2005).

Detailed accounts of species often include pertinent morphological and anatomical data, illustrations of important taxonomic features, detailed species descriptions, taxonomic discussions and/or comparisons with related species. By comparison, floristic descriptions will often provide illustrations of gross morphology, short species descriptions and use less specialized terminology.

Floras published since 1990 that have illustrated descriptions of nongeniculate coralline taxa include Baba (1998, Japan); Bressan and Babbini (2003, the Mediterranean); Cabioch *et al.* (1992, Europe); Fragosa and Rodríguez (2002, Mexican tropical Pacific coast); Huisman (2000, Australia); Littler and Littler (1997, Pelican Cays, Belize); Littler and Littler (2000, the Caribbean); Littler and Littler (2003, the South Pacific); Mendoza *et al.* (1996, Argentina); and Payri *et al.* (2000, French Polynesia).

Nongeniculate coralline algae are highly morphologically variable (Woelkerling *et al.* 1993a). A single species may show a variety of growth forms that may also be displayed by numerous other species, thus making reliable sight recognition difficult (see Womersley 1996, pp. 196, 206, 230). While field guides or floras tend to be more “user-friendly” than taxonomic accounts, identifications may be based on more readily observable vegetative/morphological features rather than taxonomically important reproductive features. Nevertheless, floristic descriptions often include useful photographs, contain important information and are often a good starting point when identifying specimens. The tables only include accounts where there are illustrated descriptions or detailed studies of the taxa. Unconfirmed records of other rhodolith-forming species have not been included in the tables and need to be properly assessed from a taxonomic point of view.

Our knowledge of characters considered diagnostic of nongeniculate coralline species has changed significantly in recent times. Monographic work and detailed studies of single genera have meant many characters previously used to differentiate species have been found to be unreliable (Wilks and Woelkerling 1991, 1995; Woelkerling and Campbell 1992; Woelkerling and Harvey 1993, p. 601; Woelkerling 1997) and further studies of type material and specimens are required to fully evaluate species concepts on a world scale. As a result, more recent publications are apt to be more useful/accurate than older publications.

tanto, las publicaciones más recientes tienden a ser de mayor utilidad y precisión que las más viejas.

Como utilizar esta guía

1. Los rodolitos individuales pueden estar compuestos de una sola especie o ser multiespecíficos. Al principio del proceso de identificación es importante determinar si el rodolito está formado por una o más especies o géneros. En un rodolito multiespecífico es necesario buscar si existe más de una forma típica de crecimiento, más de un tipo de conceptáculo (órgano reproductivo), o uniones o traslapes evidentes de las partes vegetativas de las plantas.
2. Inclusión y corte de los especímenes para la determinación de los caracteres genéricos importantes.
 - (a) La tabla 2 muestra una clave tabular de los caracteres y sus respectivos estados para los ocho géneros no

How to use this guide

1. Individual rhodoliths may be composed of a single species or be multi-specific. It is important to determine if one or more than one species/genus is part of a given rhodolith at the beginning of the identification process. Things to look for in a multi-specific rhodolith include: more than one type of growth form, more than one type of conceptacle (reproductive organ) or obvious joining/overlapping of vegetative parts of plants.
2. Embed and section specimens for important generic characters.
 - (a) Table 2 contains a tabular key to the characters and character states of the eight common nongeniculate rhodolith-forming genera. Important taxonomic characters are illustrated in figures 1 and 2 (also see Womersely 1996, Harvey *et al.* 2005).

Tabla 2. Clave tabular que resume los estados de los caracteres diagnósticos para ocho géneros de algas rojas coralinas no geniculadas, formadoras de rodolitos.

Table 2. Tabular key summarizing diagnostic character states for eight common rhodolith-forming nongeniculate coralline red algal genera.

Characters and codes for character states as follows:

1. Tetrasporangia (fig. 1A): cruciately divided (A), or zonately divided (B).
2. Reproductive chambers (fig. 1B). Tetrasporangia borne in: calcified compartments (A), multiporate conceptacles (B), or uniporate conceptacles (C).
3. Cell connections (fig. 1C). Cells of adjacent filaments joined by: cell fusions only (A), secondary pit-connections only (B), or either cell fusions or secondary pit-connections or both (C).
4. Epithallial cells (fig. 1D): flared (A), or rounded or flattened (B).
5. Subepithallial initial length compared to cells immediately subtending (below) them (fig. 1E): same size (A), as short or shorter (B), or as long or longer (C).
6. Uniporate tetra/bisporangial conceptacle pore canals lined by cells orientated (fig. 2A): more-or-less perpendicularly to roof surface (A), or more-or-less parallel to roof surface (B).
7. Spermatangial filaments within a single conceptacle (fig. 2C): branched only (A), unbranched only (B), or both branched and unbranched (C); **and** spermatangia formation: only on floors of male conceptacle chambers (A), or on floors and roofs of male conceptacle chambers (B).
8. Mature carposporangia (fig. 2B): terminating several-celled gonimoblast filaments that arise from a central fusion cell (A), or terminating one- or several-celled stalks (that are the remains of modified carpogonial branches) occurring across the chamber floor and walls.

Genus (family)	1	2	3	4	5	6	7	8
<i>Sporolithon</i> (Sporolithaceae)	A	A	C	A	A	N/a	A and B	B
<i>Phymatolithon</i> (Hapalidiaceae)	B	B	A	B	B	N/a	C and B	A
<i>Mesophyllum</i> (Hapalidiaceae)	B	B	A	B	C	N/a	B and B	A
<i>Lithothamnion</i> (Hapalidiaceae)	B	B	A	A	C	N/a	C and B	A
<i>Lithophyllum</i> (Corallinaceae)	B	C	B	B	C	N/a	B and A	A
<i>Neogoniolithon</i> (Corallinaceae)	B	C	A	B	C	B	B and B	A
<i>Hydrolithon</i> (Corallinaceae)	B	C	A	B	C	A	B and A	A
<i>Spongites</i> (Corallinaceae)	B	C	A	B	C	B	B and A	A

Note: *Mastophora rosea* (Agardh) Setchell has also occasionally been reported to form rhodoliths (Verheij 1994, p. 112). This species has not been included in this guide but can be distinguished by its ribbon-like growth form (see Woelkerling *et al.* 1993a, fig. 5A; Littler and Littler 2000).

Generic concepts follow Harvey *et al.* (2002) for *Sporolithon*; Harvey *et al.* (2003b) for *Phymatolithon*, *Mesophyllum*, and *Lithothamnion*; Harvey *et al.* (2006) for *Neogoniolithon* and *Hydrolithon*; Penrose (1996c) for *Spongites*; and Woelkerling (1996b) for *Lithophyllum*. All characters listed above are illustrated in Womersley (1996) and Harvey *et al.* (2005). For generic characters of *Mastophora* see Woelkerling (1996a)

geniculados que forman rodolitos. En las figuras 1 y 2 se ilustran los caracteres taxonómicos importantes (ver también Womersely 1996, Harvey *et al.* 2005).

(b) Harvey *et al.* (2005) proporciona información detallada sobre cómo realizar la inclusión y el corte de las algas coralinas.

3. Inclusión y corte de los especímenes para la determinación de sus caracteres específicos importantes. En las tablas 3–10 se da la referencia de los estudios detallados y las descripciones florísticas de especies publicadas desde 1990. Alternativamente se puede pedir a un experto que identifique el espécimen.
4. Al publicar es necesario proporcionar la fuente utilizada en la identificación (e.g., *Lithophyllum margaritae* según la descripción en Riosmena-Rodríguez *et al.* 1999) o indicar el experto a cargo de la identificación.
5. Los ejemplares se deberán depositar en un herbario reconocido.

(b) Harvey *et al.* (2005) provides detailed information on how to embed and section coralline algae.

3. Embed and section specimens for important species characters. Tables 3–10 contain recent references to detailed species accounts and floristic descriptions. Alternatively ask an expert to identify the specimen.
4. In publication, give the source used in the identification (e.g., *Lithophyllum margaritae* as described in Riosmena-Rodríguez *et al.* 1999) or acknowledge the expert who identified the material.
5. Deposit voucher specimens in a recognized herbarium.

Concluding remarks

Ongoing coralline algal taxonomic research and stable generic characters have facilitated generic identification of

Tabla 3. Bibliografía de los estudios taxonómicos detallados o las descripciones florísticas recientes (desde 1990) de las especies formadoras de rodolitos de *Hydrolithon*. Los trabajos se listan cronológicamente. Para información pertinente sobre el material típico, ver notas abajo.

Table 3. Recent (since 1990) detailed taxonomic accounts or floristic descriptions of rhodolith-forming species of *Hydrolithon*. Accounts are listed chronologically. For pertinent information on type material see notes below.

Species	Detailed taxonomic accounts and floristic descriptions
¹ <i>Hydrolithon boergesenii</i> (Foslie) Foslie	Baba (1998) Littler and Littler (1997) Littler and Littler (2000)
² <i>Hydrolithon munitum</i> (Foslie and Howe) Penrose	Penrose (1996a) Harvey <i>et al.</i> (2006)
³ <i>Hydrolithon onkodes</i> (Heydrich) Penrose	Penrose and Woelkerling (1992) Verheij (1993b, 1994) Keats and Chamberlain (1994a) Penrose (1996a) Baba (1998) Payri <i>et al.</i> (2000) Fragosa and Rodríguez (2002) Littler and Littler (2003) – as <i>Porolithon onkodes</i> Harvey <i>et al.</i> (2006)
⁴ <i>Hydrolithon reinboldii</i> (Weber van Bosse and Foslie in Foslie) Foslie	Penrose and Woelkerling (1992) Verheij (1993b, 1994) Baba (1998) Huisman (2000) Payri <i>et al.</i> (2000) Ringeltaube and Harvey (2000) Littler and Littler (2003) Oliveira <i>et al.</i> (2005)

Note: not all records in the literature are confirmed identifications.

¹ For information on type material see Price *et al.* (1992), Woelkerling (1993, p. 40) and Woelkerling *et al.* (2005, p. 107).

² Published illustrations of holotype (Foslie and Howe 1906). For further information on holotype and isotype material see Woelkerling (1993, p. 153), Woelkerling and Verheij (1995, p. 66), Woelkerling (1998b, p. 319) and Woelkerling *et al.* (2005, p. 49).

³ Published illustrations of lectotype (Penrose and Woelkerling 1988, figs. 10–14). For further information on type material see Woelkerling (1993, p. 164).

⁴ Published illustrations of lectotype (Penrose and Woelkerling 1988, figs. 1–9; Penrose and Woelkerling 1992, fig. 3; Ringeltaube and Harvey 2000, fig. 17). For further information on type material see Verheij and Woelkerling (1992, pp. 284–285), Woelkerling (1993, p.188), Woelkerling and Verheij (1995, p. 73) and Woelkerling *et al.* (2005, p. 113).

Tabla 4. Bibliografía de los estudios taxonómicos detallados o las descripciones florísticas recientes (desde 1990) de las especies formadoras de rodolitos de *Lithophyllum*. Los trabajos se listan cronológicamente. Para información pertinente sobre el material típico, ver notas abajo.

Table 4. Recent (since 1990) detailed taxonomic accounts or floristic descriptions of rhodolith-forming species of *Lithophyllum*. Accounts are listed chronologically. For pertinent information on type material see notes below.

Species	Detailed taxonomic accounts and floristic descriptions
¹ <i>Lithophyllum dentatum</i> (Kützinger) Foslie	Chamberlain and Irvine (1994a), De Grave <i>et al.</i> (2000) Bressan and Babbini (2003)
² <i>Lithophyllum fasciculatum</i> (Lamarck) Foslie	See notes below
³ <i>Lithophyllum incrustans</i> Philippi	Cabioch <i>et al.</i> (1992), Chamberlain and Irvine (1994a) Chamberlain (1996), Bressan and Babbini (2003)
⁴ <i>Lithophyllum kotschyianum</i> Unger	Verheij (1993b, 1994), Cribb (1996) Piller and Rasser (1996), Baba (1998) Ringeltaube and Harvey (2000) – as <i>L. tamiense</i> Huisman (2000), Payri <i>et al.</i> (2000) Littler and Littler (2003), Oliveira <i>et al.</i> (2005)
⁵ <i>Lithophyllum margaritae</i> (Hartot) Heydrich	Riosmena-Rodríguez <i>et al.</i> (1999), Marrack (1999)
⁶ <i>Lithophyllum neoatalayense</i> Masaki	Chamberlain (1996), Baba (1998) Lluch (2002)
⁷ <i>Lithophyllum okamurai</i> Foslie	Verheij (1993b, 1994) Baba (1998) – as <i>L. okamurae</i> Littler and Littler (2003) – as <i>L. okamurae</i>
⁸ <i>Lithophyllum racemus</i> (Lamarck) Foslie	Chamberlain and Irvine (1994a) – as <i>L. duckeri</i> Basso <i>et al.</i> (1996) Bressan and Babbini (2003)
⁹ <i>Lithophyllum stictaeforme</i> (Areschoug in J. Agardh) Hauck	Woelkerling and Campbell (1992) – as <i>L. bermudense</i> Woelkerling (1996b) – as <i>L. frondosum</i> Furnari <i>et al.</i> (1996) – as <i>L. frondosum</i> Athanasiadis (1999) Ringeltaube and Harvey (2000) – as <i>L. frondosum</i> Huisman (2000) – as <i>L. frondosum</i> Fragosa and Rodríguez (2002) – as <i>L. frondosum</i> Bressan and Babbini (2003) Harvey <i>et al.</i> (2005) Oliveira <i>et al.</i> (2005) – as <i>L. frondosum</i>

Note: not all records in the literature are confirmed identifications.

¹ Woelkerling (1985, figs. 1–8) studied the holotype in detail. For information on type material see Woelkerling and Verheij (1995, p. 46) and Woelkerling *et al.* (2005, p. 194).

² While this species is reported to form rhodoliths in the British Isles and France (Brittany) (Chamberlain and Irvine 1994a, p. 73) all collections require reassessment. Basso *et al.* (2004, pp. 218–222) studied the type (*Millepora fasciculata* Lamarck) in detail and found no plants attributable to *Lithophyllum* in the type collection. The lectotype is attributable to a species of *Clathromorphum*.

³ Woelkerling (1983) studied type material but characters now known to be important in species delimitation were not included and the type requires further study (John *et al.* 1994, p. 62). For information on type material see Woelkerling and Verheij (1995, p. 58).

⁴ Ringeltaube and Harvey (2000, p. 437) found a continuum of specimens referable to either *Lithophyllum tamiense* (Heydrich) Foslie or *L. kotschyianum*. Published illustration of holotype (Verheij 1994, fig. 8). For further information on type material see Woelkerling (1993, p. 133).

⁵ Riosmena-Rodríguez *et al.* (1999) studied and illustrated the holotype. *Lithophyllum pallescens* (Foslie) Foslie and *Lithophyllum veleroae* Dawson (cited in Steller and Foster 1995) were found by Riosmena-Rodríguez *et al.* (1999) to be heterotypic synonyms of *Lithophyllum margaritae*.

⁶ Published illustrations of holotype (Chamberlain 1996, figs. 42, 54, 55).

⁷ For information on type material see Woelkerling (1993, p. 163) and Woelkerling *et al.* (2005, p. 176).

⁸ Published illustrations of neotype (Basso *et al.* 1996, figs. 64/3, 65/2). Also see Woelkerling (1998b, pp. 276–278) and Woelkerling *et al.* (2005, p. 182) for further type information on this species. Basso *et al.* (1996) considered *Lithophyllum duckeri* Woelkerling a heterotypic synonym of *Lithophyllum racemus*.

⁹ Athanasiadis (1999) studied the type of *Lithophyllum stictaeforme*. *Lithophyllum bermudense* Foslie and Howe and *Lithophyllum frondosum* (Dufour) Furnari, Cormaic and Alongi are considered heterotypic synonyms of *L. stictaeforme* (see Furnari *et al.* 1996; Woelkerling 1996b, p. 233).

Tabla 5. Bibliografía de los estudios taxonómicos detallados o las descripciones florísticas recientes (desde 1990) de las especies formadoras de rodolitos de *Lithothamnion*. Los trabajos se listan cronológicamente. Para información pertinente sobre el material típico, ver notas abajo.

Table 5. Recent (since 1990) detailed taxonomic accounts or floristic descriptions of rhodolith-forming species of *Lithothamnion*. Accounts are listed chronologically. For pertinent information on type material see notes below.

Species	Detailed taxonomic accounts and floristic descriptions
¹ <i>Lithothamnion australe</i> (Foslie) Foslie	See notes below
² <i>Lithothamnion corallioides</i> (P. and H. Crouan) P. and H. Crouan	Chamberlain and Irvine (1994b), Basso <i>et al.</i> (1996) Mendoza and Cabioch (1998), De Grave <i>et al.</i> (2000) Bressan and Babbini (2003)
³ <i>Lithothamnion crassiusculum</i> (Foslie) Mason	See notes below
⁴ <i>Lithothamnion crispatum</i> Hauck	Bressan and Babbini (2003)
⁵ <i>Lithothamnion glaciale</i> Kjellman	Chamberlain and Irvine (1994b), Freiwald (1995) Baba (1998)
⁶ <i>Lithothamnion minervae</i> Basso	Basso <i>et al.</i> (1996), Bressan and Babbini (2003) Basso <i>et al.</i> (2004)
⁷ <i>Lithothamnion muelleri</i> Lenormand ex Rosanoff	Wilks and Woelkerling (1995), Woelkerling (1996c)
⁸ <i>Lithothamnion philippii</i> Foslie	Basso <i>et al.</i> (1996), Bressan and Babbini (2003)
⁹ <i>Lithothamnion prolifer</i> Foslie	Verheij (1993b, 1994), Keats <i>et al.</i> (1996) Ringeltaube and Harvey (2000)
¹⁰ <i>Lithothamnion rugosum</i> Foslie	Mendoza <i>et al.</i> (1996)
¹¹ <i>Lithothamnion ruptile</i> (Foslie) Foslie	Littler and Littler (2000)
¹² <i>Lithothamnion superpositum</i> Foslie	Wilks and Woelkerling (1995) – as <i>L. indicum</i> Woelkerling (1996c) – as <i>L. indicum</i> Keats <i>et al.</i> (2000) Harvey <i>et al.</i> (2003b) Oliveira <i>et al.</i> (2005) – as <i>Lithothamnion</i> c.f. <i>indicum</i>
¹³ <i>Lithothamnion tophiforme</i> (Esper) Unger	Adey <i>et al.</i> (2005)
¹⁴ <i>Lithothamnion valens</i> Foslie	Basso <i>et al.</i> (1996), Bressan and Babbini (2003)

Note: not all records in the literature are confirmed identifications.

¹ Rhodolith-forming specimens of *Lithothamnion australe* (Foslie) Foslie from the Gulf of California, Mexico (Steller and Foster 1995, p. 205), await further examination in a modern context (Riosmena-Rodríguez *et al.* 1999, p. 401). For further information on type material see Woelkerling *et al.* (2005, p. 461).

² Chamberlain and Irvine (1994b, p. 183) selected and studied the neotype.

³ Rhodolith specimens of *Lithothamnion crassiusculum* have been cited in the Gulf of California (Rivera *et al.* 1998, Frantz *et al.* 2000, Halfar *et al.* 2000) but this material requires further examination in a modern context (Athanasiadis *et al.* 2004, p. 155).

⁴ Status and disposition of *Lithothamnion crispatum* uncertain (Woelkerling *et al.* 1998, p. 133).

⁵ For information on type material see Woelkerling (1993, p. 106).

⁶ For information on type material see Woelkerling (1998b, p. 272).

⁷ Wilks and Woelkerling (1995, figs. 1, 2) studied and published illustrations of type material.

⁸ Status and disposition of *Lithothamnion philippii* uncertain (Woelkerling *et al.* 1998, p. 139). For further information on type material see Woelkerling (1993, p. 171), Woelkerling and Verheij (1995, p. 69) and Woelkerling *et al.* (2005, p. 325).

⁹ For information on type material see Verheij and Woelkerling (1992, p. 282), Woelkerling (1993, p. 176), Woelkerling and Verheij (1995, p. 70) and Woelkerling *et al.* (2005, p. 335).

¹⁰ For information on type material see Woelkerling (1993, p. 192) and Woelkerling *et al.* (2005, p. 459).

¹¹ For information on type material see Woelkerling (1993, p. 193) and Woelkerling *et al.* (2005, p. 335).

¹² Keats *et al.* (2000) concluded that *Lithothamnion indicum* Foslie is a heterotypic synonym of *Lithothamnion superpositum* (see also Harvey *et al.* 2003b, pp. 656, 659). For information on type material see Woelkerling (1993, p. 218) and Woelkerling *et al.* (2005, p. 460).

¹³ Adey *et al.* (2005) studied the neotype.

¹⁴ For information on type material see Woelkerling (1993, p. 231; 1998b, p. 366) and Woelkerling *et al.* (2005, p. 406).

Tabla 6. Bibliografía de los estudios taxonómicos detallados o las descripciones florísticas recientes (desde 1990) de las especies formadoras de rodolitos de *Mesophyllum*. Los trabajos se listan cronológicamente. Para información pertinente sobre el material típico, ver notas abajo.

Table 6. Recent (since 1990) detailed taxonomic accounts or floristic descriptions of rhodolith-forming species of *Mesophyllum*. Accounts are listed chronologically. For pertinent information on type material see notes below.

Species	Detailed taxonomic accounts and floristic descriptions
¹ <i>Mesophyllum engelhartii</i> (Foslie) Adey	Woelkerling and Harvey (1993) Chamberlain and Keats (1995) Woelkerling (1996c) Harvey <i>et al.</i> (2005)
² <i>Mesophyllum erubescens</i> (Foslie) Lemoine	Woelkerling and Harvey (1992) – as <i>M. incisum</i> Woelkerling and Harvey (1993) – as <i>M. incisum</i> Verheij (1993b, 1994) Keats and Chamberlain (1994b) Woelkerling (1996c) – as <i>M. incisum</i> Keats and Maneveldt (1997) – as <i>M. incisum</i> Baba (1998) Huisman (2000) – as <i>M. incisum</i> Payri <i>et al.</i> (2000) Littler and Littler (2003) Ringeltaube and Harvey (2000) Harvey <i>et al.</i> (2003b) Harvey <i>et al.</i> (2005) Oliveira <i>et al.</i> (2005)
³ <i>Mesophyllum lichenoides</i> (Ellis) Lemoine	Cabioch <i>et al.</i> (1992) Chamberlain and Irvine (1994b) Cabioch and Mendoza (2003) Littler and Littler (2003) Bressan and Babbini (2003)
⁴ <i>Mesophyllum syrphetodes</i> Adey, Townsend and Boykins	Verheij (1993b, 1994)

Note: not all records in the literature are confirmed identifications.

¹ Published illustrations of lectotype (Woelkerling and Harvey 1993, figs. 1–2). For further information on type material see Woelkerling (1993, p. 84) and Woelkerling *et al.* (2005, p. 349).

² Published illustrations of holotype (Keats and Chamberlain 1994b; Harvey *et al.* 2003b, fig. 12). For further information on type material see Woelkerling (1993, p. 85) and Woelkerling *et al.* (2005, p. 446). Harvey *et al.* (2003b) concluded *Mesophyllum incisum* (Foslie) Adey is a heterotypic synonym of *Mesophyllum erubescens*.

³ Woelkerling and Irvine (1986a, figs. 1–24) provide details and illustrations of original neotype material. New lectotype material subsequently designated by Woelkerling and Irvine (2007) and the superseded neotype material designated as epitype. New lectotype material (as designated by Woelkerling and Irvine 2007) illustrated in Woelkerling and Irvine (1986a, p 381, fig. 2). New epitype material (as designated by Woelkerling and Irvine 2007) illustrated in Woelkerling and Irvine (1986a, figs. 1D, 3, 4), who also provide a detailed study of *Mesophyllum lichenoides*. Published illustrations of isoneotype (Woelkerling and Harvey 1993, fig. 30).

⁴ Adey *et al.* (1982, p. 63) designated and illustrated the type.

Comentarios finales

Los estudios taxonómicos recientes sobre las algas coralinas y sus caracteres genéricos estables han facilitado la identificación del género de los especímenes de rodolitos. Aunque la evaluación de los caracteres útiles para delimitar las especies es materia actual de investigación, la identificación a nivel de especie a escala mundial sigue siendo problemática. Por tanto, es importante que los ejemplares sean depositados en herbarios reconocidos para que estén disponibles en caso de que se requiera una reevaluación.

A nivel de género, al menos 8 de los 26 géneros coralinos no geniculados reconocidos tienen especies que forman rodolitos (*Hydrolithon*, *Lithophyllum*, *Lithothamnion*, *Mesophyllum*,

rhodolith specimens. While the assessment of characters useful in delimiting species is a focus of ongoing research, identification to species level on a world scale remains problematic. As a result, it is important that voucher specimens be deposited in a recognized herbarium so that they are available for reassessment if required.

At a generic level, at least 8 of the 26 currently recognized nongeniculate coralline genera contain species that commonly form rhodoliths. These eight genera (*Hydrolithon*, *Lithophyllum*, *Lithothamnion*, *Mesophyllum*, *Neogoniolithon*, *Phymatolithon*, *Spongites* and *Sporolithon*) represent all three Corallinales subfamilies (Hapalidiaceae, Corallinaceae and Sporolithaceae).

Tabla 7. Bibliografía de los estudios taxonómicos detallados o las descripciones florísticas recientes (desde 1990) de las especies formadoras de rodolitos de *Neogoniolithon*. Los trabajos se listan cronológicamente. Para información pertinente sobre el material típico, ver notas abajo.

Table 7. Recent (since 1990) detailed taxonomic accounts or floristic descriptions of rhodolith-forming species of *Neogoniolithon*. Accounts are listed chronologically. For pertinent information on type material see notes below.

Species	Detailed taxonomic accounts and floristic descriptions
¹ <i>Neogoniolithon brassica-florida</i> (Harvey) Setchell and Mason	Penrose (1992) – as <i>N. fosliei</i> Verheij (1993b, 1994) Iryu and Matsuda (1994) – as <i>N. fosliei</i> Cribb (1996) – as <i>N. fosliei</i> Penrose (1996b) Baba (1998) – as <i>N. fosliei</i> Baba (1998) – as <i>N. frutescens</i> Payri <i>et al.</i> (2000) – as <i>N. fosliei</i> Ringeltaube and Harvey (2000) Payri <i>et al.</i> (2000) – as <i>N. frutescens</i> Littler and Littler (2003) – as <i>N. fosliei</i> Littler and Littler (2003) – as <i>N. frutescens</i> Littler and Littler (2003) – as <i>N. laccadivicum</i> Bressan and Babbini (2003) Mateo-Cid and Pedroche (2004) – as <i>N. fosliei</i> Oliveira <i>et al.</i> (2005) Harvey <i>et al.</i> (2006)
² <i>Neogoniolithon spectabile</i> (Foslie) Setchell and Mason	Littler and Littler (1997) Littler and Littler (2000)
³ <i>Neogoniolithon strictum</i> (Foslie) Setchell and Mason	Littler and Littler (1997) Littler and Littler (2000)
⁴ <i>Neogoniolithon trichotomum</i> (Heydrich) Setchell and Mason	See notes below

Note: not all records in the literature are confirmed identifications.

¹ Published illustrations of lectotype (Woelkerling *et al.* 1993b, figs. 7–11). For further information on type material see Woelkerling (1993, p. 43). *Neogoniolithon fosliei* (Heydrich) Setchell and Mason, *N. frutescens* (Foslie) Setchell and Mason, and *N. laccadivicum* (Foslie) Setchell and Mason are heterotypic synonyms of *N. brassica-florida* (Harvey *et al.* 2006, p. 411).

² Published illustrations and information on lectotype (Woelkerling 1998b, p. 294, fig. 135). For further information on type material see Woelkerling (1993, p. 204).

³ For information on type material see Woelkerling (1993, p. 208).

⁴ While *Neogoniolithon trichotomum* is reported to commonly form rhodoliths in the Gulf of California (Hinojosa-Arango and Riosmena-Rodríguez 2004), there are apparently no recent published detailed taxonomic accounts or floristic descriptions of this species. For information on type material see Woelkerling (1998b, pp. 364–365).

Tabla 8. Bibliografía de los estudios taxonómicos detallados o las descripciones florísticas recientes (desde 1990) de las especies formadoras de rodolitos de *Phymatolithon*. Los trabajos se listan cronológicamente. Para información pertinente sobre el material típico, ver notas abajo.

Table 8. Recent (since 1990) detailed taxonomic accounts or floristic descriptions of rhodolith-forming species of *Phymatolithon*. Accounts are listed chronologically. For pertinent information on type material see notes below.

Species	Detailed taxonomic accounts and floristic descriptions
¹ <i>Phymatolithon calcareum</i> (Pallas) Adey and McKibbin	Cabioch <i>et al.</i> (1992) Chamberlain and Irvine (1994b) Mendoza and Cabioch (1998) De Grave <i>et al.</i> (2000) Bressan and Babbini (2003) Konar <i>et al.</i> (2006)
² <i>Phymatolithon repandum</i> (Foslie) Wilks and Woelkerling	Wilks and Woelkerling (1994) Woelkerling (1996c) Harvey <i>et al.</i> (2003b) Harvey <i>et al.</i> (2005)

Note: not all records in the literature are confirmed identifications.

¹ Woelkerling and Irvine (1986b) provide details and illustrations of neotype material. See also Lawson *et al.* (1995, p. 103) and Woelkerling (1998b, pp. 261–266) for further information on type material.

² Wilks and Woelkerling (1994) provide details and illustrations of lectotype material. See Woelkerling (1993, p. 189) and Woelkerling *et al.* (2005, p. 471) for further information on type material.

Tabla 9. Bibliografía de los estudios taxonómicos detallados o las descripciones florísticas recientes (desde 1990) de las especies formadoras de rodolitos de *Spongites*. Los trabajos se listan cronológicamente. Para información pertinente sobre el material típico, ver notas abajo.

Table 9. Recent (since 1990) detailed taxonomic accounts or floristic descriptions of rhodolith-forming species of *Spongites*. Accounts are listed chronologically. For pertinent information on type material see notes below.

Species	Detailed taxonomic accounts and floristic descriptions
¹ <i>Spongites fruticosus</i> Kützinger	Penrose (1991) Penrose and Woelkerling (1992) Penrose (1996c) Baba (1998) – as <i>S. fruticosum</i> Ringeltaube and Harvey (2000) Fragosa and Rodríguez (2002) Bressan and Babbini (2003) Basso and Rodondi (2006)
² <i>Spongites hyperellus</i> (Foslie) Penrose	Penrose (1996c)

Note: not all records in the literature are confirmed identifications.

¹ Published illustrations of holotype (Woelkerling 1985, figs. 23–32; Penrose 1991, figs. 1–3). For further information on type material see Woelkerling (1993, p. 99) and Woelkerling and Verheij (1995, p. 54).

² For information on type material see Woelkerling (1993, p. 119) and Woelkerling *et al.* (2005, p. 46), both under *Lithophyllum hyperellum*.

Table 10. Bibliografía de los estudios taxonómicos detallados o las descripciones florísticas recientes (desde 1990) de las especies formadoras de rodolitos de *Sporolithon*. Los trabajos se listan cronológicamente. Para información pertinente sobre el material típico, ver notas abajo.

Table 10. Recent (since 1990) detailed taxonomic accounts or floristic descriptions of rhodolith-forming species of *Sporolithon*. Accounts are listed chronologically. For pertinent information on type material see notes below.

Species	Detailed accounts and floristic descriptions
¹ <i>Sporolithon durum</i> (Foslie) R.A. Townsend and Woelkerling	Townsend <i>et al.</i> (1995) Woelkerling (1996d) Harvey <i>et al.</i> (2002) Harvey <i>et al.</i> (2005)
² <i>Sporolithon episoredion</i> (Adey, Townsend and Boykins) Verheij	Verheij (1992, 1993a, c) Payri <i>et al.</i> (2000) Littler and Littler (2003)
³ <i>Sporolithon epispurum</i> (M.A. Howe) E.Y. Dawson	Verheij (1993a) Keats and Chamberlain (1993) Littler and Littler (2000) Oliveira <i>et al.</i> (2005)
⁴ <i>Sporolithon molle</i> (Heydrich) Heydrich	Verheij (1993a) Lund <i>et al.</i> (2000)
⁵ <i>Sporolithon ptychoides</i> Heydrich	Alongi <i>et al.</i> (1996) Keats and Chamberlain (1993) Verheij (1993a) Payri <i>et al.</i> (2000) Littler and Littler (2003) Bressan and Babbini (2003) Oliveira <i>et al.</i> (2005)

Note: not all records in the literature are confirmed identifications.

¹ Published illustrations of lectotype (Townsend *et al.* 1995, figs. 1A, 2). For further information on type material see Woelkerling (1993, p. 81) and Woelkerling *et al.* (2005, p. 477).

² Adey *et al.* (1982, p. 51) designated and illustrated the type.

³ Published illustrations of holotype (Verheij 1993a, figs. 11, 12).

⁴ Published illustrations of lectotype (Verheij 1993a, figs. 13, 14).

⁵ Published illustrations of lectotype (Woelkerling 1988, figs. 239, 243, 245). For further information on type material see Woelkerling (1993, p. 183).

Neogoniolithon, *Phymatolithon*, *Spongites* y *Sporolithon*); éstos representan las tres subfamilias del orden Corallinales (Hapalidiaceae, Corallinaceae y Sporolithaceae).

Por lo menos 40 especies coralinas no geniculadas se listan en la literatura como formadoras de rodolitos; sin embargo, no todos los registros en la literatura son identificaciones confirmadas. Además, no se han publicado estudios detallados de material típico de todas las especies, y el estado y la disposición de algunas especies son aún inciertos. Con frecuencia se descubren y estudian nuevos mantos de rodolitos. Por tal motivo es probable que con el estudio taxonómico de nuevos mantos de rodolitos y la revisión de su material típico cambie el número de especies formadoras de rodolitos a nivel mundial.

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- At least 40 nongeniculate coralline species are listed in the literature as forming rhodoliths. Not all records in the literature, however, are confirmed identifications. Moreover, not all species have published detailed studies of type material and the status and disposition of some species remains uncertain. New rhodolith beds are also regularly being discovered and surveyed. The number of rhodolith-forming species worldwide, therefore, is likely to change with detailed taxonomic studies on additional rhodolith beds and study of type material.
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