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This monograph will serve as the primary reference for species of the crustose lichen genus *Rinodina* in North America. Ninety six species are included, approximately one third of the estimated number that occur worldwide. Thirty six species are endemic to the continent, five of which are described as being new to science. Nine species are reported from North America for the first time.

The contents are divided into ten chapters, including accounts of the limits to the genus, species descriptions, species groups within the genus and phytogeographic considerations. One hundred and eighty three figures are included, the majority of which are either photomicrographs of spore structure or dot maps of distributions. Seven line drawings comprise the remainder of the figures. Two color plates incorporate photographs of the thalli of sixteen representative species.

The book will be essential to scientists whose studies include the ecology of crustose lichens and to taxonomists interested in the lichenized Ascomycetes, to conservationists and to herbarium curators who have responsibility for collections of these groups. The monograph compliments other works on the saxicolous *Rinodina* species of Europe, the Old World, Australasia, and two others that include all species known from the Iberian Peninsula and Scandinavia. It makes *Rinodina* one of the better known of the large genera of crustose lichens. A potentially controversial hypothesis is that a few saxicolous species common to dry regions of western North America, southern Europe, North Africa and central Asia may date back 240 million years to the Middle Triassic.

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John W. Sheard

The Lichen Genus *Rinodina (Ach.) Gray*

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The Lichen Genus *Rinodina*

(Lecanoromycetidae, Physciaceae) in North America, North of Mexico

by John W. Sheard

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The Lichen Genus *Rinodina* (Ach.) Gray (Lecanoromycetidae, Physciaceae) in North America, North of Mexico

John W. Sheard

Department of Biology, University of Saskatchewan
112 Science Place, Saskatoon, SK S7N 5E2, Canada

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Front cover photo: *Rinodina ascociscana*, Hedgehog Mountain, northern Maine, on *Acer saccharum* bark. Photograph by Stephen Sharnoff.

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For Anne, with thanks for her encouragement and patience.

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Abstract

Ninety-six *Rinodina* species are recorded for North America, including five species new to science: *R. albertana*, *R. austroborealis*, *R. imshaugii*, *R. siouxiana*, and *R. wetmorei*. One new combination is made, *R. notabilis* (= *Buellia notabilis*) and ten species are recorded from the continent for the first time: *R. confragosula*, *R. fimbriata*, *R. freyi, R. intrusa*, *R. maculans*, *R. obnascens*, *R. notabilis*, *R. oleae*, *R. pycnocarpa*, and *R. sibirica*. *Rinodina* "*insularis*" is excluded from the genus on the basis of its lecideine apothecial characters and ascus type, but no formal recombination has been made.

Thirty species are placed into synonymy, including 13 North American taxa: *Lecanora exigua* f. *pruinosa* (= *R. hallii*), *R. annulata* (= *R. subminuta*), *R. applanata* (= *R. maculans*), *R. arctica* (= *R. olivaceobrunnea*), *R. constrictula* (= *R. straussii*), *R. glauca* (= *R. freyi*), *R. halei* (= *R. subminuta*), *R. hyperborea* (= *R. septentrionalis*), *R. iowensis* (= *R. cana*), *R. ochrocea* (= *R. destituta*), *R. subsophodes* (= *R. ascociscana*), *R. thomsonii* (= *R. santae-monicae*), and *R. vezdae* (= *R. destituta*). Other non-North American taxa placed into synonymy for the first time are *R. erumpens* (= *R. subminuta*); *R. erysiphaea* and *R. guianensis* (= *R. colobinoides*); *R. consocians*, *R. exigua* f. *lecideina*, and *R. phaeostigmella* (= *R. metaboliza*); *R. exiguella* and *R. jenisejensis* (= *R. septentrionalis*); *R. haplosporoides*, *R. metabolica* f. *leioplaca, R. neglecta*, and *R. prasina* (= *R. maculans*); *R. parvula* (= *R. notabilis*); *R. sibirica* f. *aggregata* and *R. sophodiodes* (= *R. sibirica*); *R. subfusca* (= *R. laevigata*); and *R. succedens* (= *R. turfacea*).

Thirty-six species are endemic to North America. These include the five new species listed above and *R. adirondackii*, *R. ascociscana*, *R. athallina*, *R. aurantiaca*, *R. badiexcipula*, *R. bolanderi*, *R. boulderensis*, *R. brouardii*, *R. californiensis*, *R. chrysomelaena*, *R. coloradiana*, *R. endospora*, *R. grandilocularis*, *R. granuligera*, *R. hallii*, *R. herrei*, *R. innata*, *R. juniperina*, *R. lobulata*, *R. macrospora*, *R. marysvillensis*, *R. oregana*, *R. pachysperma*, *R. pacifica*, *R. papillata*, *R. perreagens*, *R. populicola*, *R. riparia*, *R. santae-monicae*, *R. verruciformis*, and *R. willeyii*. All but six of these endemic species are exclusively corticolous. *Rinodina xanthomelana* is reported from Jamaica, the first record of this tropical species from the Western Hemisphere.

A full discussion of the characters upon which the taxonomy of the genus is based is given, together with accounts of the limits of the genus and natural groups of species within the genus. Thirteen groups of species are listed based on spore type. The *Physcia*- and *Physconia*-types represent a continuum of structure, as the *Physcia*-type is always a developmental stage of the *Physconia*-type. The *Milvina*-type spore may be ancestral to them. The *Pachysporaria*-type is divided into two types, based on spore size and structure. The two resulting species groups are also distinguished by chemistry and type of vegetative propagule.

Sixteen phytogeographic elements are recognized corresponding to phanerogam and other lichen distribution patterns in North America. Individual saxicolous species of all species groups have extensive distributions in other parts of the world, which may be indicative of an ancient origin. The calcareous *Bicincta*-type species group is of particular interest, since it is over-represented in the Colorado plateau floristic element. These species are also found in arid areas of southern Europe and China and may have a very ancient origin, dating back to the Middle Triassic (240–230 Ma). *Rinodina confragosula*, from southern California, is a remarkable Southern Hemisphere disjunct that may have rafted from eastern Gondwanaland during the breakup of that supercontinent 160–100 Ma.

Corticolous species generally have more restricted distributions, suggesting more recent origins. The majority of the *Physcia–Physconia*-group, the most common group of species, are corticolous and are most frequent in the temperate regions of the Northern Hemisphere. In contrast, the two *Pachysporaria*-groups, which are also primarily corticolous, have more southerly distributions, and some species are pantropical.

*Key words***:** lichenized Ascomycetes, new species, endemic species, taxonomy, phytogeography, paleogeography.

Résumé

En Amérique du Nord, on répertorie quatre-vingt-seize espèces du genre *Rinodina*, y compris cinq espèces nouvellement décrites : *R. albertana*, *R. austroborealis*, *R. imshaugii*, *R. siouxiana* et *R. wetmorei*. En plus d'établir une nouvelle combinaison, *R. notabilis* (= *Buellia notabilis*), on recense, pour la première fois sur le continent, dix espèces : *R. confragosula*, *R. fimbriata*, *R. freyi, R. intrusa*, *R. maculans*, *R. obnascens*, *R. notabilis*, *R. oleae*, *R. pycnocarpa* et *R. sibirica*. *Rinodina* « *insularis* » est exclue du genre en raison de ses apothécies lécidéines et de son type d'asque, mais aucune recombinaison officielle n'est proposée.

Trente espèces sont mises en synonymie, y compris13 taxons nord-américains : *Lecanora exigua* f. *pruinosa* (= *R. hallii*), *R. annulata* (= *R. subminuta*), *R. applanata* (= *R. maculans*), *R. arctica* (= *R. olivaceobrunnea*), *R. constrictula* (= *R. straussii*), *R. glauca* (= *R. freyi*), *R. halei* (= *R. subminuta*), *R. hyperborea* (= *R. septentrionalis*), *R. iowensis* (= *R. cana*), *R. ochrocea* (= *R. destituta*), *R. subsophodes* (= *R. ascociscana*), *R. thomsonii* (= *R. santae-monicae*) et *R. vezdae* (= *R. destituta*). Au nombre des autres taxons exotiques (de l'extérieur de l'Amérique du Nord) mis en synonymie pour la première fois figurent *R. erumpens* (= *R. subminuta*); *R. erysiphaea* and *R. guianensis* (= *R. colobinoides*); *R. consocians*, *R. exigua* f. *lecideina* et *R. phaeostigmella* (= *R. metaboliza*); *R. exiguella* et *R. jenisejensis* (= *R. septentrionalis*); *R. haplosporoides*, *R. metabolica* f. *leioplaca, R. neglecta* et *R. prasina* (= *R. maculans*); *R. parvula* (= *R. notabilis*); *R. sibirica* f. *aggregata* et *R. sophodiodes* (= *R. sibirica*); *R. subfusca* (= *R. laevigata*); *R. succedens* (= *R. turfacea*).

Trente-six espèces sont endémiques de l'Amérique du Nord. De ce nombre, cinq sont nouvelles (mentionnées ci-dessus) et les trente-et-une autres sont : *R. adirondackii*, *R. ascociscana*, *R. athallina*, *R. aurantiaca*, *R. badiexcipula*, *R. bolanderi*, *R. boulderensis*, *R. brouardii*, *R. californiensis*, *R. chrysomelaena*, *R. coloradiana*, *R. endospora*, *R. grandilocularis*, *R. granuligera*, *R. hallii*, *R. herrei*, *R. innata*, *R. juniperina*, *R. lobulata*, *R. macrospora*, *R. marysvillensis*, *R. oregana*, *R. pachysperma*, *R. pacifica*, *R. papillata*, *R. perreagens*, *R. populicola*, *R. riparia*, *R. santae-monicae*, *R. verruciformis* et *R. willeyii*. Toutes ces espèces endémiques sauf six sont exclusivement corticoles. *Rinodina xanthomelana* est signalée de la Jamaïque, le premier registre de cette espèce tropicale de l'hémisphère occidental.

On traite en détail des caractéristiques taxinomiques du genre, et on décrit ses limites ainsi que les groupes naturels des espèces qui le composent. Treize groupes d'espèces sont présentés en fonction de leur type de spores. Les types *Physcia* et *Physconia* constituent un continuum structural, puisque *Physcia* est toujours le stade de développement de *Physconia*. Les spores de type *Milvina* sont possiblement leur forme ancestrale. Le type *Pachysporaria* est divisé en deux groupes, selon la taille et la structure des spores. Ces deux groupes ainsi formés se distinguent également par leur chimie et leurs propagules.

Seize éléments phytogéographiques sont reconnus en relation avec la répartition des phanérogames et d'autres lichens nord-américains. Chacune des espèces saxicoles de tous les groupes d'espèces est caractérisée par une répartition géographie étendue dans d'autres parties du monde, ce qui dénote une origine ancienne possible. Le groupe d'espèces calcaires de type *Bicincta* est d'un intérêt particulier, car il est surreprésenté dans l'élément floristique du plateau du Colorado. Ces espèces sont également recensées dans les régions arides du sud de l'Europe et de la Chine et pourraient indiquer une origine ancienne, remontant jusqu'au Trias moyen (240–230 Ma). Du sud de la Californie et isolée de l'hémisphère Sud, *Rinodina confragosula* est digne de mention, car elle pourrait être issue de la partie est du continent du Gondwana transportée lors de la rupture de ce supercontinent (160–100 Ma).

Les espèces corticoles, de par leur répartition plus restreinte, ont probablement une origine plus récente. La plupart des espèces du groupe *Physcia–Physconia*, le groupe le plus commun, sont corticoles et abondamment signalées dans les régions tempérées de l'hémisphère Nord. En revanche, les deux groupes de *Pachysporaria*, qui sont aussi principalement corticoles, présentent une répartition plus méridionale, et quelques-unes des espèces sont pantropicales.

Mots-clés **:** Ascomycète lichénisé, nouvelle espèce, espèce endémique, taxinomie, phytogéographie, paléogéographie.

Introduction

The cosmopolitan lichenized Ascomycete genus *Rinodina* (Ach.) Gray comprises approximately 300 species (Sheard 2004). Despite major contributions to the understanding of the genus subsequent to the catalogues of Zahlbruckner (1931, 1940) and Lamb (1963), the genus remains poorly understood in the western hemisphere. An exception is the excellent treatment of *Rinodina* species from Brasil (Malme 1902). The present study is the first comprehensive attempt to understand the North American species that occur north of the Mexican border.

Nonsaxicolous species of *Rinodina* from Europe and Siberia were monographed by Magnusson (1947*b*) in a very detailed and valuable study, although it reflects the author's typological species concept. Saxicolous species have been well studied in recent years, starting with the European monograph of Mayrhofer and Poelt (1979) and continuing with a treatment of the old world (Mayrhofer 1984*a*). Regional studies include New Zealand (Mayrhofer 1983), Australia (Mayrhofer 1984*b*), the Mediterranean (Mayrhofer et al. 1993), the Southern Hemisphere (Matzer and Mayrhofer 1994), southern Africa (Matzer and Mayrhofer 1996), and Australasia (Kaschik 2006).

Many papers on corticolous species of *Rinodina*, mainly in southern Europe, have been published by Professor Mayrhofer (Graz, Austria) and his associates and students in recent years. Most important among these are Hinteregger et al. (1989), Hinteregger (1994) on alpine species found on *Rhododendron*, Ropin and Mayrhofer (1993) on species of the eastern Alps, Giralt and Mayrhofer (1994*a*) on species containing atranorin, Giralt and Mayrhofer (1994*b*) on species with polyspored asci, Giralt et al. (1994) on species containing pannarin, Giralt and Mayrhofer (1995) on species lacking secondary metabolites, Giralt et al. (1995) on species with vegetative propagules, and Ropin and Mayrhofer (1995) on species with a blue–grey epihymenium. Corticolous species of temperate Australia are documented by Mayrhofer et al. (1999).

Most recently three regional studies have been published for different parts of Europe, reflecting an increased level of confidence in the understanding of the genus. These are the comprehensive studies of Giralt et al. (1997) for the low countries of northern Europe, Giralt (2001) for the Iberian Peninsula, and Mayrhofer and Moberg (2002) for Scandinavia.

The first accounts of *Rinodina* in North America subsequent to Fink (1935) were those of Magnusson (1947*a*, 1952, 1953). Individual species were described by Sheard and Tønsberg (1995), Sheard (1995), and Sheard (1998). Sheard and Mayrhofer (2002) described 14 new species from western North America, the region with the greatest species diversity and where the genus was particularly poorly understood. Sheard (2004) provides a detailed account of the genus in the greater Sonoran Desert region, the first for any region of the continent.

A number of North American species have been moved to other genera (as summarized by Esslinger 2009*). Saxicolous species with lobate thallus margins and unthickened spore walls are now placed in *Dimelaena* (Sheard 1974; Sheard and Mayrhofer 1984; Mayrhofer and Sheard 2004*a*). Ground-dwelling species with squamulose thalli and brown rhizohyphae were moved to *Phaeorrhiza* by Mayrhofer and Poelt (1978*a*). Two southwestern saxicolous coastal species with broad conidia, strongly ornamented ascospores, and norstictic acid have been placed in *Mobergia* by Mayrhofer et al. 1992*b*; Mayrhofer and Sheard 2004*b*). Finally, species with filiform conidia were moved to *Amandinea* (Sheard and May 1997; Mayrhofer and Sheard 2002), but see Bungartz et al. (2004, 2007) for a different opinion. In addition, two calcicolous southern European species with very thin-walled, pale brown spores were placed in a new genus, *Rinodinella* H. Mayrhofer & Poelt (Mayrhofer and Poelt 1978*b*).

Finally, readers should be aware of the following words of caution. Although 96 species are covered in detail, a handful of other species, most of which are new to science, are known to occur but have not been described because they are poorly understood from only one or two small collections. It is likely that other species also will be discovered as the lichens of the western half of the continent become better known. Eastern North American species were studied initially because the flora of that region was the best known at that time. However, recent collections from the region have not been systematically examined, resulting in more complete coverage of the western and northern regions. Additional study of the eastern *Rinodina* flora should therefore be a priority, to fill gaps in the knowledge of the region and better define distribution boundaries. Another failing of this study is that it has not been possible to carry out more field work. Some outstanding problems will only be resolved in this way. Also, the findings regarding secondary metabolites should be regarded as preliminary only.

*Authorities for genera and species are omitted in the following account unless they are absent from this reference.

Materials and Methods

This study is based primarily on herbarium material borrowed from the institutional and private herbaria cited in the Acknowledgments section. Abbreviated collection information for the approximately 6300 specimens examined are available in dBASE IV format upon request.

Surface observations of specimens were made using a Wild M5 stereomicroscope and measurements were taken at 25× magnification and rounded to the nearest 0.05 mm. Internal ascomata tissue measurements were made on vertical sections (20–25 µm thick), cut with a Leitz freezing microtome, at 50× magnification to an accuracy of 5 mm using a Wild M20 compound microscope. All thallus and apothecial tissue measurements are quoted as ranges, and outlier measurements are presented in brackets.

Apothecial sections were mounted in Melzer's reagent (Hawksworth et al. 1995, under stains) or water and squashed to release the ascospores from their asci for measurement. Melzer's reagent is essential to clear the spores of freshly collected material in order to observe their wall structure. This treatment does not obscure wall pigmentation or change spore dimensions or the wall structure of spores in older herbarium specimens (ca. 2–3 years). Heating water-mounted slide preparations of sections over a methylated spirits burner (Wetmore 1994) clears ascospores more rapidly, but it is not yet known whether spore size and structure are left undistorted for all spore types. Dilute potassium hydroxide (K) and concentrated nitric acid (N) were used to test for certain tissue reactions, and the former was also used to reveal any swelling at the ascospore septum. Potassium hydroxide must never, therefore, be used in conjunction with spore measurements.

Ascospore and conidium measurements were taken at 500× magnification using a Wild vernier micrometer (scale of 0.1 µm) to an accuracy of 0.5 µm. Ascospore measurements are quoted using a convention similar to that used in Sheard (1973). Spore dimensions are given as a range within which the mean can be expected to fall with 95% confidence; the outer figures in parentheses represent the range in which 95% of the population is expected to occur. Spores with nonoverlapping confidence limits about their means indicate statistically significant differences. The coefficient of variation (CV) of spore measurements for most species was <10%. Observations of ascospore wall structure were made with an oil immersion lens at 1250× magnification. Spore photographs were taken with a stand-mounted Nikon Coolpix 950 digital camera using wide angle, aperture priority, macro, and highest quality picture settings. A remote monitor was necessary to assure adequate focus control.

Secondary compounds were characterized by thin-layer chromatography (TLC) according to the standardized methods for lichen products (Culberson and Kristinsson 1970; C.F. Culberson 1972; Elix and Ernst-Russell 1993). Distribution maps are produced by Versamap version 2.07 (Culberson 2000) using an azimuthal equal-area projection for the North American continent and equirectangular projection for regional maps. Dots may represent more than one sample.

Characters

Sixty-one characters were assessed for each specimen studied in detail. The characters' states for each species were assembled in a spreadsheet. Sorting by character allowed species to be compared conveniently and also was invaluable for key construction.

Thallus thickness

Thallus thickness was not quantified, owing to the difficulties of measuring thalli firmly fixed to their substrates. Thallus thickness is very variable, although a qualitative assessment (thick or thin) was attempted. One lichenicolous species, "*R. insularis*", lacks an independent thallus, at least in the North American material studied. The majority of species are considered to possess thin thalli. Seventeen species have mostly thick thalli, but the same number of species have thalli that vary between thin and thick. The only three species always categorized as possessing thick thalli are corticolous or lignicolous: *R. ascociscana*, *R. grandilocularis*, and *R. oregana*.

Thallus colour

Thalli are typically a shade of grey, brown, or more rarely citrine. Grey thalli vary from light grey to dark grey, grey–green (mostly when freshly collected), ochraceous, or grey–brown. Most of this variation appears to be associated with the degree of exposure to sunlight. Thalli with atranorin in the cortex are typically light grey, often gaining a "cream" tinge in the herbarium. Brown thalli also vary in intensity of colour, the darkest again being associated with exposed conditions. Species with darkly pigmented cortical cells may have grey thalli, owing to the presence of a well-developed epinecral layer masking the cortical pigment. *Rinodina septentrionalis* typically possesses a copper–brown thallus (sometimes referred to as red–brown in the literature), and the thallus of *R. freyi* H. Magn. may vary from dark grey to copper–brown in exposed habitats, leading to difficulties in separating these two species. The saxicolous species *R. chrysomelaena* and the corticolous *R. lepida*, *R. efflorescens*, and *R. flavosoralifera* have citrine thalli or yellowish-green soralia, owing to the presence of xanthone pigments in the cortex and (or) medulla.

Thallus morphology

Thalli may be composed of discrete units or areoles (particularly around their margins), but most frequently the units become contiguous to form a continuous, rimose, or areolate thallus. This contrasts with the genus *Buellia* De Not., in which some species with differentiating discrete marginal units become primarily areolate, often with a dark prothallus visible between the areoles, while other species with continuous margins (using the terminology of Sheard 1964 and Bungartz 2004*b*) become rimose or secondarily areolate (rimose-areolate). In *Rinodina* a minority of species become areolate directly, but there is never a dark prothallus showing between the areoles. If the discrete units are markedly convex, they are described as being verrucose. This morphology is most pronounced in the corticolous species *R. endospora* and *R. oregana* and in the saxicolous *R. tephraspis* and *R. verruciformis*. The most extreme form is found in the corticolous species *R. excrescens*, in which thallus units are relatively high and the condition is referred to as being bullate.

In a number of saxicolous species with areolate thalli, the areole margins tend to become elevated in moist environments, giving them a subsquamulose appearance. *Rinodina castanomela* has lobate or squamulose thallus margins free from the substrate, as does *R. castanomelodes*. Corticolous species that may develop subsquamulose margins are *R. ascociscana*, *R. dolichospora*, *R. excrescens*, and *R. herrei*. Only the maximum sizes of discrete thallus units and areoles of each specimen were measured. When present, they varied in size from 0.10–0.20 mm wide in *R. septentrionalis* to 1.20–1.60 mm wide in the saxicolous *R. castanomela*, *R. destituta* and *R. zwackhiana*.

Thallus rugosity

The great majority of species have a plane to rugose (rough) thallus. Poorly developed thalli with isolated, more or less erect, and very small units, termed scabrid, are found in the corticolous *R. albertana* Sheard, sometimes in the corticolous *R. colobina*, and in the saxicolous *R. fimbriata* Körb.

Thallus surface

The majority of species possess a matt surface, but some species with a relatively thick epinecral layer have a glossy (wax-like) surface. In other species the character is variable. *Rinodina roscida*, *R. terrestris*, and *R. castanomela* sometimes possess a pruinose thallus surface.

Thallus margin

Thalli are described as determinate if their margins are clearly defined or indeterminate if they are not. Thalli are always determinate if they are limited by a prothallus, but a prothallus is consistently present in only six species. Prothalli may be entire or fimbriate, even within the same species.

Vegetative propagules

Twenty-two species possess vegetative propagules, most of them consistently so, and all but three of these species are corticolous. The saxicolous, western inland species *R. zwackhiana* has mostly sexual or vegetative forms (Anderson 1962), although a minority of specimens have been shown to possess both apothecia and soredia (Sheard 1982). Only the saxicolous, western oceanic *R. aspersa* has not been observed to possess apothecia in North America, although it may sometimes do so in Europe (Mayrhofer and Moberg 2002). This form has previously been referred to as *R. fatiscens* (Th. Fr.) Vain. The third vegetatively reproducing species occurring on rock is *R. stictica*, although it is typically corticolous.

Three types of vegetative propagule occur in the study area: soredia, consoredia, and blastidia. Soredia in *Rinodina*, unless developed from consoredia, are produced in soralia and consist of one or a few algal cells surrounded by fungal hyphae and a cortex one cell deep, as illustrated by Tønsberg (1992*a*, Figs. 9 and 10, but note that in other works (e.g., Purvis et al. 1992) soredia are considered to be noncorticate). Soredia are found in *R. aspersa*, *R. degeliana*, *R. flavosoralifera*, *R. griseosoralifera*, *R. perreagens*, *R. sheardii*, *R. stictica*, *R. willeyii*, and *R. zwackhiana*.

Consoredia were defined by Tønsberg (1992*a*, Figs. 15–17) as aggregates of soredia. In *Rinodina* they are rounded or irregular aggregations of soredia and may or may not occur in soralia. They frequently breakdown into soredia. Consoredia have been recorded in *R. colobina*, *R. efflorescens*, *R. juniperina*, *R. obnascens* (Nyl.) Oliv., and *R. pachysperma*.

Blastidia were originally described as marginal, elongate structures budding in a yeast-like manner (Poelt 1980), but in *Rinodina* have come to include surficial vegetative structures (Matzer and Mayrhofer 1994; Giralt 2001) produced in a less regular manner. They might otherwise be described as proliferating consoredia. In *Rinodina* they sometimes produce consoredia or soredia terminally. The distinction between consoredia and blastidia is therefore not absolute, and the term blastidium is used here for structures that are rounded or elongate and larger than consoredia (>ca. 100 µm). Blastidia are found in *R. colobinoides*, *R. disjuncta*, *R. excrescens*, *R. herrei*, *R. papillata*, *R. poeltiana*, *R. santae-monicae*, and *R. wetmorei* Sheard. Isidia are not associated with any species in the study area, but *R. isidioides* (Borrer) H. Olivier was recently recorded from northern Mexico (Sheard 2004).

Apothecial attachment

Apothecia may be innate, broadly attached, or narrowly attached. Innate apothecia (cryptolecanorine or immersed; Giralt 2001) are more or less level with the thallus surface and therefore always lack a prominent thalline margin. Three saxicolous species possess this type of apothecium: *R. cana*, *R. innata*, and *R. straussii* J. Steiner. The difference between broadly attached and narrowly attached apothecia is illustrated in Fig. 1. Note that the attachment area of narrowly attached apothecia is smaller than their surface area. The resulting basal constriction may be very marked, as in *R. turfacea*, and in some forms of *R. sibirica* H. Magn. the apothecia are almost stipitate. Some apothecia are also described as being erumpent during early development, emerging from the thallus with the broken cortex or epinecral layer adhering to the circumference of the apothecium, producing a thalline margin with a flaking or halo-like appearance. The species that provides the best example of erumpent apothecia is the corticolous *R. subminuta*, in which most apothecia finally becoming broadly attached.

Apothecial abundance

Most species have abundant apothecia, and in some species they become contiguous in older parts of the thallus. Contiguous apothecia are often angular by compression. Only seven species have infrequent and widely scattered apothecia: *R. adirondackii*, *R. castanomela*, *R. degeliana*, *R. disjuncta*, *R. efflorescens*, *R. flavosoralifera*, and *R. griseosoralifera*. It is no coincidence that the last five species possess vegetative propagules. Such species may often have areas of the thallus that are strictly fertile and other areas where only vegetative propagules are found. This phenomenon is often associated with features of the substrate microtopography and hence

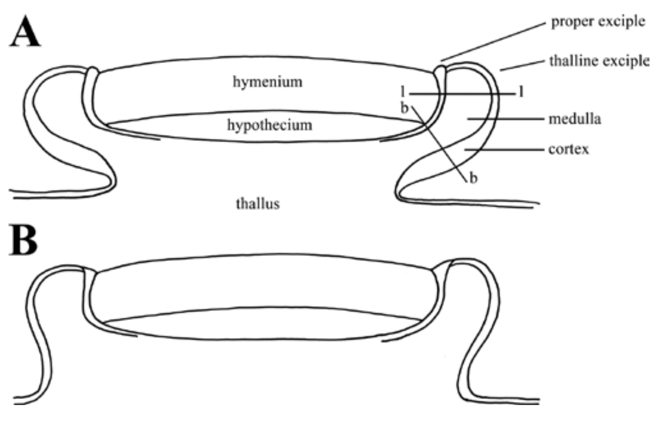

Fig. 1. Apothecial anatomy in median section. (A) Narrowly attached apothecium with raised proper exciple (excipular ring) and expanded lower cortex. (B) Broadly attached apothecium with confluent proper exciple and unexpanded cortex. Lines l—l and b—b represent direction of lateral and basal thalline exciple measurements, respectively.

with the microenvironment. Tønsberg (1992*a*) observed that it is energetically too expensive to consistently produce both vegetative propagules and apothecia.

Apothecial size

Apothecium maximum size, excluding deformed apothecia, was recorded and varies between 0.25 and 0.55 mm in diameter for *R. polyspora* and between 1.00 and 1.60 mm in diameter for *R. bolanderi*.

Apothecial disc

Disc colour is frequently brown when immature and changes to black at maturity. Four species typically retain brown discs throughout their life histories: *R. ascociscana*, *R. flavosoralifera*, *R. hallii*, and *R. polyspora*, dark brown for the last species and best seen when moist. The discs of *R. hallii* and *R. mniaraea* frequently become white pruinose due to the extrusion of hymenial gelatin, and this may rarely occur in other species. *Rinodina badiexcipula* is almost unique in possessing orange pruina when its discs become pruinose. The same phenomenon is also very rarely seen in *R. turfacea* and *R. disjuncta*. The discs of *R. roscida* are typically pruinose, owing to the presence of surface oxalate crystals, and the same phenomenon may occasionally be seen in other species growing on calcareous substrates. Another source of pruinosity is the presence of pannarin crystals, which may be found in five corticolous species: *R. aurantiaca*, *R. excrescens*, *R. granuligera*, *R. marysvillensis*, and *R. perreagens*. The crystals occur within the epihymenium in the first three species (forming an episamma).

Discs may be concave, plane, or convex. Six species have concave discs early in development, which all later become plane at maturity. Only one specimen of *R. flavosoralifera* with mature open apothecia has been seen; poriform immature apothecia are more typical. The majority of species have plane discs, but many become slightly convex with age. Only six species may have convex apothecia from a relatively early stage of development: *R. colobinoides*, *R. imshaugii* Sheard, *R. mniaraea*, *R. polyspora*, *R. pycnocarpa* H. Magn., and *R. pyrina*.

Apothecial margin

Typically thalline and entire in *Rinodina*, the margin may not be distinguishable from the confluent thallus in species with innate apothecia as noted previously. A thalline margin is absent in the saxicolous "*R. insularis*", the innate apothecium always being delimited by the darkly pigmented proper exciple. The corticolous *R. hallii* has quite prominent biatorine margins, which lack algal cells. A thalline margin may also be absent in *R. intrusa* (Nyl.) Malme and *R. maculans* Müll. Arg. In *R. maculans* the margin is sometimes incomplete as it grows upwards from the base of the apothecium, giving the margin a crenulate appearance. The same phenomenon also has been observed in *R. colobinoides*, *R. degeliana*, *R. dolichospora* and *R. tephraspis* but less frequently. All these species are corticolous except the last, which is saxicolous.

Species such as *R. macrospora* and *R. turfacea* with large, non-contiguous apothecia often possess flexuose margins. Apothecial margins also may sometimes become ± angular by compression in species in which they are contiguous at maturity. The thalline margin may become pigmented in the saxicolous *R. destituta*, *R. fimbriata*, and *R. oxydata*, which are all related species with *Mischoblastia*-type spores. Pigmentation progresses from the cortex inwards until, in extreme cases, no hyaline tissue or algal cells remain in the margin. Presumably, algal cells are not able to reproduce and die out due to shading. The margin is often excluded in other species that develop strongly convex discs at maturity. The apothecial margin varies from 0.05 mm wide in most species to 0.10–0.15 mm wide in species with prominent margins. The margins of *R. stictica* are particularly prominent in fertile thalli, measuring 0.10–0.20 mm wide.

Excipular ring

Viewed from the apothecium surface, the proper exciple may be visible as an excipular ring situated between the thalline margin and the disc (Fig. 1). It may be in the form of a raised ring or be flat and confluent with the thalline margin. In the latter case, the ring is usually more lightly pigmented than the disc. It is easily visible as an inner, darker ring to the thalline margin in species with lightly pigmented thalli. However, a confluent ring is consistently present in only five species: *R. ascociscana*, *R. endospora*, *R. macrospora*, *R. milvina*, and *R. roscida*. A confluent excipular ring is also very common in *R. freyi*, but is not visible in darkly pigmented thalli. There are only two species that always possess a raised ring: *R. colobinoides* and *R. olivaceobrunnea*. An excipular ring is absent in a small majority of species.

Thalline exciple

Measurements were taken according to Fig. 1. The dimensions of the thalline margin in different species with broadly attached apothecia vary laterally from 20–100 to 70–200 µm wide and basally from 25–40 to 100–180 µm wide. Comparable measurements for species with narrowly attached apothecia are from 40–60 to 55–155 µm laterally, and from 20–110 to 90–150 µm basally.

Cortex

Measurements are for the apothecial cortex, although the thalline cortex is very similar, if not identical.The cortex is 5–20 µm wide laterally, consisting of inflated, isodiametric terminal cells of medullary hyphae that are present in all species. Peripheral cells may be pigmented or not. The largest cortical cells were measured and varied from 3.0 to 8.5 µm wide. The cortex may therefore be only a single cell wide and is never more than a few cells in thickness. It is typically poorly organized and often poorly delimited from the medulla (Giralt 2001). The cortex of *R. exigua* is particularly indistinct as Giralt (2001) has noted. In many species with narrowly attached apothecia, the lower cortex is thickened, typically to double or more the size of the lateral cortex, and varies from 10–15 to 30–95 µm deep. Less commonly, cortical thickening may also occur at the base of the margins of broadly attached apothecia and most markedly (15–75 µm wide) in *R. bolanderi*. The structure of the apothecial lower cortex may be cellular or comprise elongated, columnar (vertical), or intricate hyphae. A reaction with iodine (I+ blue) is often associated with the thickened lower cortex (Magnusson 1947*b*; Giralt 2001), but this character is variable within species and also difficult to detect in thin section. It has not been found to be a useful character, since the reaction is consistently present in only a few species, such as *R. turfacea*, which are otherwise easily distinguished.

Epinecral layer

This tissue has previously been referred to as an epicortex (Mayrhofer and Sheard 1988). This outermost part of the thallus is often associated with saxicolous species that live in arctic and temperate deserts or near deserts. It is less frequent in corticolous species. The above authors speculated that the layer is composed of excreted polysaccharides and may therefore be similar to the pored epicortex of Hale (1981). The epinecral layer may serve to protect the thallus from heat stress by reflecting sunlight from the thallus surface and preventing dessication. Thalli of saxicolous lichens have been observed to exceed the ambient air temperature by 20 °C (Coxson and Kershaw 1983). An epinecral layer may be present in almost half the species studied, varying in width from 5 to 30 µm.

Algal cells

Algal cells are frequently ellipsoidal in shape, owing to compression by the radiating medullary hyphae of the margin. When not spherical, long axis measurements were taken and therefore recorded as lengths. The largest cells in the thalline exciple were measured and were very variable in size, the range being from 7.0 to 28.0 µm long. Variation of both cortical and algal cell size within species is too large to be helpful for identification of individual species. However, Giralt (2001) and Mayrhofer and Moberg (2002) have commented on the large size (20–30 µm wide) of the algal cells of *R. pyrina*. While certainly at the large end of the size range for corticolous species, the range appears to be smaller in North America and comparable to the oroarctic species *R. imshaugii* and also to *R. freyi*. Although the algal cells have not been cultured, they possess a central pyrenoid and lobed chloroplast and probably belong to the genus *Trebouxia* (Friedl and Büdel 1996).

Proper exciple

The proper exciple is the internal part of the excipular ring and forms a narrow tissue between the thalline exciple and hymenium (Fig. 1). In "*R. insularis*" it is darkly pigmented, forms a proper margin to the apothecium, and is relatively well developed, measuring 40–50 µm wide. *Rinodina hallii*, as previously noted, also lacks a thalline margin, but the proper exciple (70–100 µm wide) is hyaline except for some lightly pigmented bands, which suggest annual growth increments. Some other species, such as the corticolous *R. maculans* and saxicolous *R. tephraspis*, may lack or possess an incomplete thalline margin. In these situations, the proper exciple again forms a proper margin, is relatively well developed, and is lightly pigmented in comparison with the usual hyaline state when it is enclosed by the thalline exciple.

In most species of *Rinodina*, the proper exciple is a hyaline tissue of parallel hyphae that is not easily distinguished from the adjacent paraphyses of the hymenium but is often more obvious where it widens at the surface of the apothecium. Here its pigmentation is the same colour as the epihymenium, typically a shade of brown but sometimes blue–grey (see under epihymenium). The proper exciple is not typically easy to distinguish from the hypothecium either. In a few species, however, such as the oroarctic, ground-dwelling *R. turfacea* and the Pacific, corticolous species *R. badiexcipula*, *R. disjuncta*, and *R. macrospora*, the proper exciple is pigmented and its limits are then easily determined, often extending some way around the hypothecium. Probably the same relationship occurs between the hypothecium and the unpigmented proper exciple typical of most species. The exciple varies from 5–10 to 15–30 µm wide laterally in different species and from 10–20 to 40–90 µm wide peripherally.

Hypothecium

The hypothecum is typically hyaline but dark brown in "*R. insularis*" and a light to dark, reddish-brown in *R. sheardii*. *Rinodina perreagens* has a yellowish hypothecium and a few other species may sometimes show this pigmentation; others show a very light brown colour. The hypothecium often increases in size with the age of the apothecium and then is responsible for the disc becoming convex. Hypothecium measurements tend to be extremely variable for this reason. They vary from 15–50 µm deep in *R. turfacea* to 120–190 µm deep in *R. zwackhiana*. The hypothecium is inspersed with oil drops in *R. castanomela* and sometimes in *R. austroborealis* Sheard and *R. macrospora*, the only corticolous species with inspersion in either the hypothecium or hymenium.

Hymenium

Variation in size of the hymenium within species is less than that of the hypothecium, ranging from 55–80 µm in *R. pyrina* to 120–150 µm in *R. oregana*. There are only four species in which hymenium height is consistently less than hypothecium depth: "*R. insularis*", *R. rinodinoides*, *R. efflorescens*, and *R. granuligera*. At the other extreme, there are seven species in which the hymenium is consistently more than twice the size of the hypothecium: *R. griseosoralifera*, *R. olivaceobrunnea*, *R. perreagens*, *R. septentrionalis*, *R. stictica*, *R. terrestris*, and *R. turfacea*. Among these are the oroarctic species *R. turfacea* with large apothecia and *R. olivaceobrunnea* with small apothecia, suggesting that the relative size of the hypothecium and hymenium is independent from apothecial size. The hymenium is consistently inspersed with oil droplets in *R. calcigena*. Inspersion is present or absent in *R. bischoffii* and rarely present in *R. endophragmia*. These three species are all calcicoles.

Paraphyses

Mostly unbranched except near their apices, paraphyses vary in thickness from 1.5–2.0 to 2.5–3.5 µm in different species. They are conglutinate in about half the species studied and therefore not easily separated in squash slide preparations. Oil paraphyses (Poelt and Pelletier 1984; Giralt and Mayrhofer 1994*a*; Matzer and Mayrhofer 1994) have been observed in *R. macrocarpa*. Apices of the paraphyses are cellular and inflated, varying from 2.5–3.0 µm in *R. hallii* to 6.5–7.5 µm in *R. pycnocarpa*. The latter species has *Bicincta*-type spores and all five species with this spore type possess relatively broad paraphyses apices, with the exception of *R. zwackhiana*, for which there remains some doubt about its spore type.

Epihymenium

Pigmentation in the apical cells of the paraphyses is partly responsible for the colour of the epihymenium and has been recorded as light or dark. This pigmentation is deposited in an apical cap, which is typically black or more rarely dark brown. Sometimes the penultimate cells possess a thinner cap. Pigments dispersed in the epihymenial gelatin also influence the colour of the epihymenium. The most common of these is a red–brown pigment nearly always, but not exclusively, associated with species possessing *Physcia*- and *Physconia*-type spores. The other pigment is a grey–blue pigment reacting K+ and N+ violet. Saxicolous species with this epihymenium pigmentation, *R. athallina* and *R. zwackhiana* in North America, have been reviewed by Sheard (1982) and corticolous species by Ropin and Mayrhofer (1995). The pigment is lighter in the corticolous *R. colobina*, and the reaction is transient in the recently described *R. lobulata* (Sheard 2004). This pigment colour is referred to by Ropin and Mayrhofer (1995) as being grey. The combination of cap and diffuse pigmentation results in epihymenium pigmentation that varies from orange–brown to red–brown to light brown to dark brown, or from light to dark blue. Pannarin crystals may be found within the epihymenium of *R. aurantiaca*, *R. excrescens*, and *R. granuligera* and on the surface of the epihymenium of *R. marysvillensis* and *R. perreagens*.

Asci

Asci belong to the *Lecanora*-type, with the exception of "*R. insularis*", which possesses the *Bacidia*-type ascus (Rambold et al. 1994). The ascus is uniformly clavate in shape with the number of spores varying from 4–8 in *R. badiexcipula*, *R. macrospora,* and *R. oregana*, to 8 in most species, to 12–16 in *R. polyspora*, and to 16–32 in *R. populicola*. There is an obvious inverse relationship between number of spores per ascus and the size of the spores, both between and within species. Rarely, in individual asci, one or two spores will not develop past the single-cell stage, a phenomenon that has been observed in a number of species; for example, in *R. bischoffii* (Fig. 23A).

Asynchronous development of spores is frequent in *R. endospora* (Fig. 64A) and also occurs less frequently in some other species. It may represent a stage towards the reduced number of spores noted in the three species above. There may be an indication of seasonality in the production of spores for some species, apothecia being devoid of mature spores in some collections, while possessing mature or over-mature spores in others. This phenomenon has been reported for *Buellia molongolo* U. Grube and Elix (Grube et al. 2004).

Ascospores

Ascospores are primarily 1-septate and always pigmented. A number of spore types, defined by the number of septa, type of wall thickening, and degree of pigmentation, are found within the genus *Rinodina* (Poelt and Mayrhofer 1979; Mayrhofer 1984*a*; Matzer and Mayrhofer 1996; Sheard and Mayrhofer 2002). Recent electron microscope studies have done much to elucidate spore wall structure in the Physciaceae (Nordin 1997). Five wall layers have been defined (Nordin and Mattson 2001):

(1) The outermost layer is hyaline and gelatinous and is not easily distinguished under the light microscope. Spores released from the ascus sometimes appear to adhere where they touch each other, presumably a result of contact between their gelatinous layers.

(2) The perispore, which is typically darkly pigmented and often deeply fractured. These fractures may be visible as surface ornamentation with an oil objective lens under the light microscope and very rarely at a lower magnification.

(3) An intermediary layer occurs between the perispore and proper wall. The intermediary layer thins during spore development. It is most easily seen under the light microscope in spores in which the septal region swells after the application of KOH.

(4) The pigmented proper wall is usually the thickest part of the wall and is responsible for wall thickening at the spore apices and septum. The thickening pattern at maturity defines the shape of the spore lumina, a very important character for the recognition of the different spore types.

(5) The innermost layer is the thinner hyaline endospore wall.

The spore septum comprises the proper wall and endospore wall only (Nordin and Mattson 2001).

Two types of spore development are found within the genus *Rinodina* (Fig. 2). In Type A apical wall thickening takes place after the development of the septum; in contrast, Type B apical wall thickening occurs prior to the formation of the septum (Giralt and Mayrhofer 1995; Matzer and Mayrhofer 1996; Giralt 2001; Mayrhofer and Moberg 2002; Sheard 2004). Type B development has also been referred to as delayed septation by Scheidegger et al. (2001). These events occur before the appearance of wall pigmentation at the very earliest stage of development and are limited to spore types that display apical wall thickening during some stage of ontogeny subsequent to the appearance of wall pigmentation. Type B development is a transient phenomenon, which may easily be missed in some species. In such species, development has been described as belonging to Type A or B (Sheard and Mayrhofer 2002; Sheard 2004).

In some spores a refractive septal disc occurs between the two walls of the septum (Fig. 3A). This is usually a transient phenomenon, but it sometimes persists to maturity when the disc may appear to be pigmented. It is often associated with spores that are swollen at the septum and become more swollen upon the application of KOH (*Dirinaria*-type). The septal disc does not have a consistent enough presence in any species for it to be used as a diagnostic character. The European *R. ventricosa* Hinteregger and Giralt possesses spores swollen

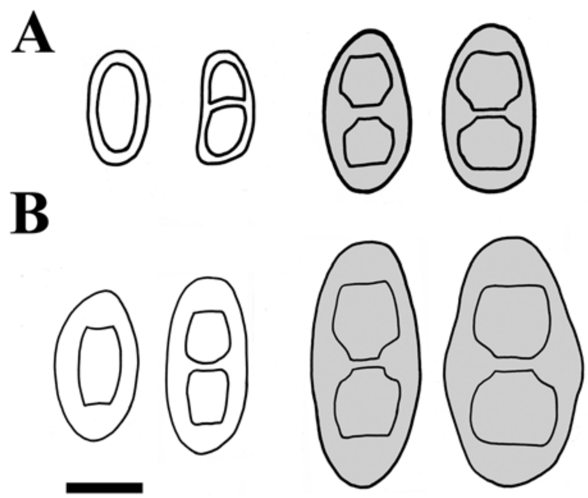

Fig. 2. Ascospore developmental types in *Rinodina*; shading represents pigmented walls of the more mature spores. (A) Type A development in the *Physcia*-type ascospore of *R. confragosa*, in which apical wall thickening occurs after septum formation. (B) Type B development in the *Dirinaria*-type ascospore of *R. oregana*, in which apical thickening precedes septum formation; also note the septal swelling in the most mature stage. Scale bar = 10 µm.

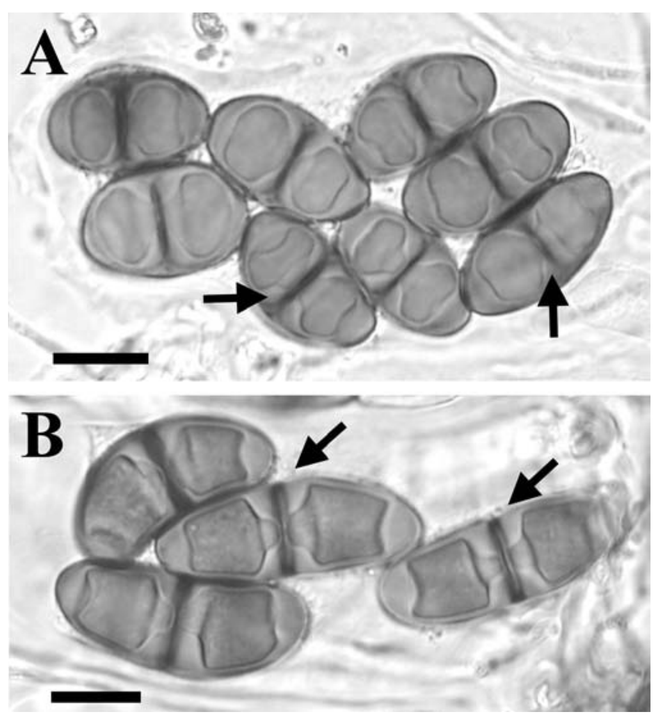

Fig. 3. Septal structures of the ascospore. (A) Septal disc in *Rinodina marysvillensis*; a refractive structure (arrows) in the centre of the septum between the two wall layers. (B) Torus in *R. turfacea*. Arrows indicate a pigmented band around the circumference of the septum. Its ring-shaped structure can be deduced from the darker pigmentation at the edge of the spore where it is seen in greater depth. Both scale bars = 10 µm.

at the septum, which do not respond to further treatment with KOH (Hinteregger 1994, Fig. 43). Some spores of the corticolous *R. exigua* and the saxicolous *R. pacifica* show very restricted septal swelling among North American species.

The presence or absence of a torus distinguished between two major groups of spore types and species in Mayrhofer (1982, 1983, 1984*a*, 1984*b*). The nature of this ring-shaped structure, which differentiates between the cells in the outer septal region, is not fully understood. "There is no support for the distinction of a torus as a structurally different part of the spore wall", although the torus has been shown to be electron dense in comparison with the adjacent intermediary and proper wall layers (Nordin 1997, Fig. 5). Partly because the torus is a developmental phenomenon, but also for other reasons cited by Scheidegger (1993) and Matzer and Mayrhofer (1996), it is no longer accepted as a basis for distinguishing different spore types.

The torus, nevertheless, often remains a good diagnostic character at the species level. The figures of Mayrhofer (1982, 1983, 1984*a*, 1984*b*) illustrate the torus at the septum edge only where the structure is at its thickest in optical section. In some recent publications, the torus is not included in spore illustrations (Giralt 2001; Mayrhofer and Moberg 2002). When developed, the torus is seen as a pigmented band in the middle of the septum (Fig. 3B), although it may or may not be prominent, depending both on the species and the stage of spore development.

A final spore character is the presence or absence of surface wall ornamentation, as seen under the oil immersion lens. As previously mentioned, it is caused by fractures in the perispore. It should be searched for at all stages of pigmentation development. It is typically best observed in mature spores, but it is occasionally hidden in the most mature and darkly pigmented spores. Ornamentation is found in many species but is often variably present. It is particularly well developed in *R. macrospora*, in which it is visible at 400× magnification, appearing as a ridged pattern at higher magnifications.

The following 13 (or 14, see below) spore types are found in North American species. It is important to note again that measurements and observations must be made on mature spores, since both immature and over-mature spores may be smaller and have different internal structures. Mature spores are those in which wall pigmentation is fully developed and in which the walls have not become buckled and (or) the lumina deformed or lost as occurs in over-mature spores. Bungartz (2004*b*) has correctly emphasized that spore ontogeny is a dynamic process that is overlooked by describing spore types based only on the static, mature stage of development.

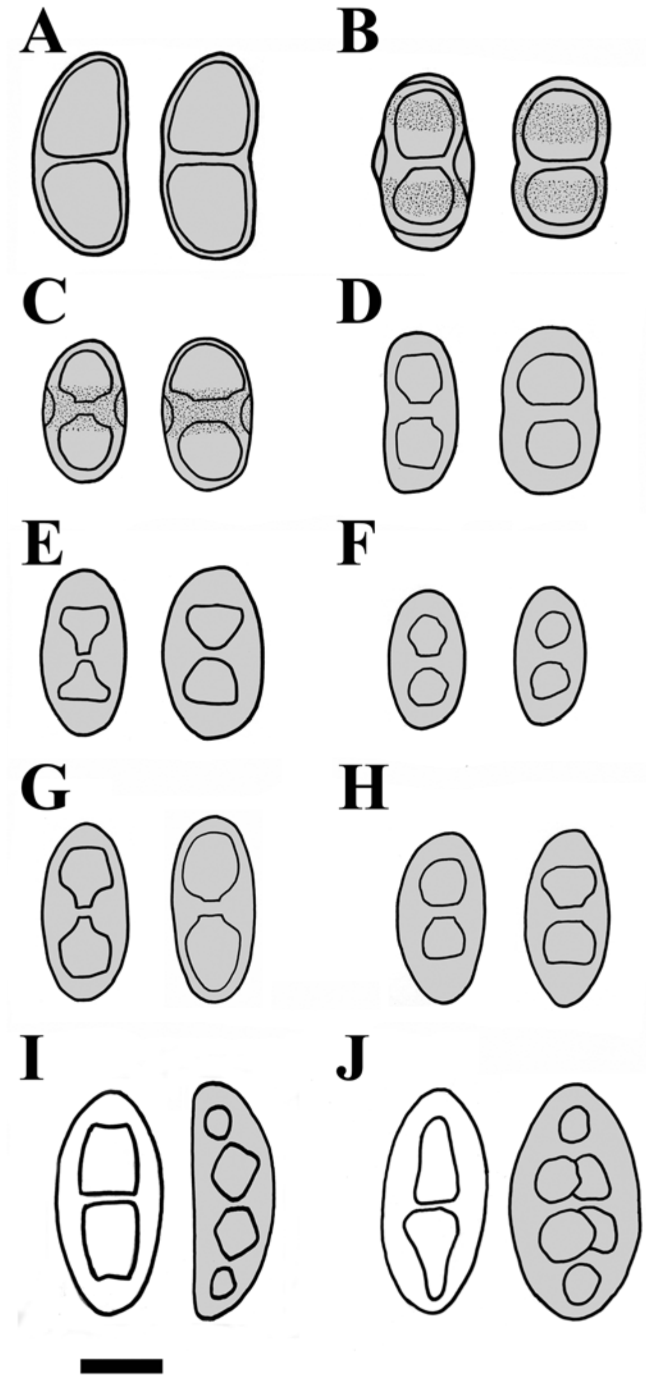

Fig. 4. Ascospore types of *Rinodina* species in the study area. (A–H) Mature stages with pigmented walls. (I and J) Immature and mature stages. (A) *Beltraminia*-type, *R. athallina*. (B) *Bicincta*-type, *R. castanomela*. (C) *Bischoffii*-type, *R. bischoffii*. (D) *Milvina*-type, *R. milvina*. (E) *Mischoblastia*-type, *R. destituta*. (F) *Pachysporaria*-type, *R. coloradiana*. (G) *Physconia*-type, *R. trevisanii*. (H) *Teichophila*-type, *R. herrei*. (I) *Conradia*-type with Type B development, *R. conradii*. (J) Submuriform-type with Type A development, *R. intermedia*. Scale bar = 10 µm. Note that *Dirinaria*- and *Physcia*-type ascospores are not included, since they are illustrated in Fig. 2.

BELTRAMINIA-type (Poelt 1965, including the *Buellia*-type of Mayrhofer and Poelt 1979 (Matzer and Mayrhofer 1996) and Giralt 2001) Fig. 4A. Spores lack wall thickenings at maturity and possess Type A development. Classically, this spore type was thought to be a character that separated the genus *Buellia* from *Rinodina*, until it was discovered in *Rinodina* by Mayrhofer and Poelt (1979). In addition, some spores in the genus *Buellia* are now known to have septal wall thickening in the earliest stages of development (Scheidegger 1993; Bungartz et al. 2004). They were referred to the *Physconia*-type by Scheidegger, although they lack apical wall thickening at all stages of development. The *Beltraminia*-type spore is found only in the corticolous *R. lobulata* (Fig. 97) and saxicolous *R. athallina* (Fig. 15) in the present study, and both show slight septal thickening at some stage of development. Spore sizes average 17.5–18.5 µm × 8.0–9.0 µm in *R. lobulata* and 22.5–24.5 µm × 9.5–10.5 µm in *R. athallina*, with average length/width (l/w) ratios of 2.0–2.2 and 2.2–2.5, respectively. The *Rinodinella*-type, characteristic of the genus *Rinodinella*, differs from the *Beltraminia*-type in the ascospores being very thin-walled and pale brown in colour (Mayrhofer and Poelt 1978*b*; Giralt 2001).

BICINCTA-type (Poelt and Mayrhofer 1979) Figs. 4B and 161 (*R. straussii*). A pigmented band is present around each cell but may be very faint in some species and is absent in *R. zwackhiana*. The spore type is further characterized by septal and apical wall thickenings and is often swollen around the septum when immature. Separate wall layers are visible at the margins of the septum, and sometimes at the spore apices at maturity. In North America these spores possess Type A development and the average spore size varies from 12.5–13.5 µm × 8.5–9.0 µm in *R. luridata* to 20.0–21.5 µm × 11.5–12.0 µm in *R. straussii*. The spores of all species are similarly broadly ellipsoid with an average l/w ratio <2.0. Other species characterized by this spore type are *R. castanomela, R. endophragmia*, and *R. pycnocarpa*. All species are saxicolous, although one corticolous species, *R. mayrhoferi* Crespo, is known from continental climates in southern Europe where it grows on *Juniperus* species (Crespo 1983). Giralt (2001) reports this last species as having either Type A or B ontogeny, which is unique among *Bicincta*-type spores.

BISCHOFFII-type (Sheard 1967) Figs. 4C and 23 (*R. bischoffii*). A pigmented band is present around the septal region and this spore type possesses septal wall thickening only. Separate wall layers are visible at the septum. These spores possess Type A development. Average spore size varies from 16.5–17.5 µm × 10.5–11.5 µm in *R. bischoffii* to 21.0–22.0 µm × 12.0–13.0 µm in *R. guzzinii*. Other species with this spore type are *R. calcigena* and *R. castanomelodes*. All species possess broadly ellipsoid spores (average l/w ratio < 2.0) and are saxicolous.

CONRADIA-type (Malme 1902) Fig. 4I. This spore type is 4-celled, possessing ± angularly rhombic lumina at first that become more rounded at maturity. The spores show Type B development and the spore type is only known in *R. conradii*. Average spore size is 26.0–27.5 µm × 11.5–12.0 µm and average l/w ratio is 2.2–2.4. This spore type is probably not closely related to the Submuriform-type or to other species with 4-celled spores (Krenn 1994) that possess Type A development.

DIRINARIA-type (Mayrhofer 1982) Figs. 2B and 9 (*R. albertana*). Septal and apical wall thickenings are well developed and similar to the *Physcia*-type, as noted by Giralt (2001), although the lumina are often less angular during development. At least some spores are swollen at the septum, and this swelling becomes more obvious upon treatment with KOH. Ontogeny mostly belongs to Type B (Giralt and Mayrhofer 1995; Matzer and Mayrhofer 1996), but this type of development may be very transient and easily missed, so some species are referred to as possessing Type A or B development. Type B development has not yet been observed in four species with this spore type: *R. brouardii*, *R. californiensis*, *R. granuligera*, and *R. marysvillensis*. Septal swelling upon treatment with KOH appears to be due to enlargement of the intermediate layer. Although Type B development is most typical of the *Dirinaria*-type, it is occasionally found in other spore types (Giralt and Mayrhofer 1995; Giralt 2001 and see below). There is a tendency for the endospore spore wall to become pigmented and (or) refractive when the spores of some species are over mature.

It should be noted that a number of species with other spore types sometimes display arrested spore development when septum formation does not take place. This may result in a single-celled spore with a fully pigmented wall and with apical thickenings mimicking Type B development. This phenomenon, however, can be distinguished from true Type B development, in which wall thickening takes place very early in development before wall pigmentation occurs.

Average spore size varies from 11.5–12.0 µm × 6.0–6.5 µm in "*R. insularis*" to 29.5–31.5 µm × 14.5–15.5 µm in *R. oregana*. Average l/w ratio varies from 1.7–1.9 in *R. californiensis* to 2.0–2.3 in *R. metaboliza*. *Dirinaria*-type spores are also found in *R. albertana*, *R. brouardii*, *R. colobina* (*Mischoblastia*-type (Giralt 2001), intermediate between *Pachysporaria*-, *Physcia*-, and *Mischoblastia*-types (Mayrhofer and Moberg 2002)), *R. endospora*, *R. gennarii*, *R. granuligera*, *R. marysvillensis*, *R. oleae* Bagl., *R. riparia*, and *R. santae-monicae*. The large spores of *R. oregana* provide the clearest expression of Type B development discovered to date.

MILVINA-type (Poelt and Mayrhofer 1979) Figs. 4D and 113 (*R. obnascens*). *Milvina*-type is similar to the *Physcia*-type, with less angular and less pronounced apical wall thickenings and more broadly ellipsoid spores, which are often constricted at the septum at maturity. This spore type possesses Type A ontogeny. Average spore size varies from 14.5–15.5 µm × 7.5–8.0 µm in *R. rinodinoides* to 18.5–19.5 µm × 10.5–11.0 µm in *R. milvina*. Average l/w ratio varies from 1.5–1.7 in *R. notabilis* (Lynge) Sheard to 1.8–2.0 in *R. rinodinoides*. Only one other species, *R. obnascens*, is known with this spore type in North America. All three species are saxicolous, although *R. crespoa* Giralt & H. Mayrhofer and *R. sophodes* (Ach.) Massal. of Europe are corticolous (Giralt 2001; Mayrhofer and Moberg 2002).

MISCHOBLASTIA-type (Malme 1902) Figs. 4E and 123 (*R. oxydata*). Both septal and apical wall thickenings are very pronounced, with lumina becoming ± triangular during development and often rounded later, and walls that are usually lightly pigmented. This spore type possesses Type A development. Average spore size varies from 18.5–19.0 µm × 10.5–11.5 µm in *R. oxydata* to 22.0–22.5 µm × 12.0–12.5 µm in *R. destituta*. Average l/w ratio is ≤2.0 for all species. Two other saxicolous species occur in the region, *R. cana* and *R. fimbriata*; a fifth species, *R. wetmorei*, is corticolous. Only one other corticolous species with this spore type is known, *R. euskadiensis* A. Crespo & M.B. Aguirre from Spain (Giralt 2001).

PACHYSPORARIA-type (Malme 1902) Fig. 4F. Wall thickening is strongly developed, including the lateral walls, forming ± rounded and small lumina relative to spore cell size. This spore type is reported to possess either Type A or B ontogeny (Giralt and Mayrhofer 1995; Giralt 2001; Kaschik 2006). It is proposed here that this spore type can be divided into two types based on size and developmental characteristics. *Pachysporaria*-type I has an average spore size of 24.0–25.5 µm × 13.0–14.0 µm with lumina that may be irregularly angular or polygonal during development, may develop satellite lumina at maturity (Fig. 5), and always possesses Type A development. *Pachysporaria*-type II possesses smaller spores with average spore size of 16.0–17.0 µm × 8.5–9.5 µm, which have small *Physcia*-like, lacrimiform, or irregularly rounded lumina in early development, always lacks satellite lumina (Fig. 6), and has Type A or B development.

Pachysporaria-type I, Fig. 59 (*R. perreagens*). The average spore size varies from 21.0–23.0 µm × 12.0–13.5 µm in *R. griseosoralifera* to 28.0–30.0 µm × 14.0–16.0 µm in *R. adirondackii*. Average l/w ratio varies from 1.5–1.9 to 2.0–2.1 in the same two species. Other species possessing this spore type are *R. dolichospora*, *R. flavosoralifera* (Fig. 5B), *R. lepida*, *R. perreagens*, *R. sheardii*, *R. stictica*, *R. verruciformis* (Fig. 5A), and *R. willeyii*. Also belonging to this group are *R. isidioides* and *R. roboris* (Duf. ex Nyl.) Arnold recently reported in northern Mexico (Sheard 2004), although the spores of the latter species are smaller (19.5–20.5 µm × 10.0–11.0 µm) than those reported above.

Pachysporaria-type II, Fig. 103 (*R. maculans*). Average spore size varies from 14.5–15.5 µm × 8.0–8.5 µm in

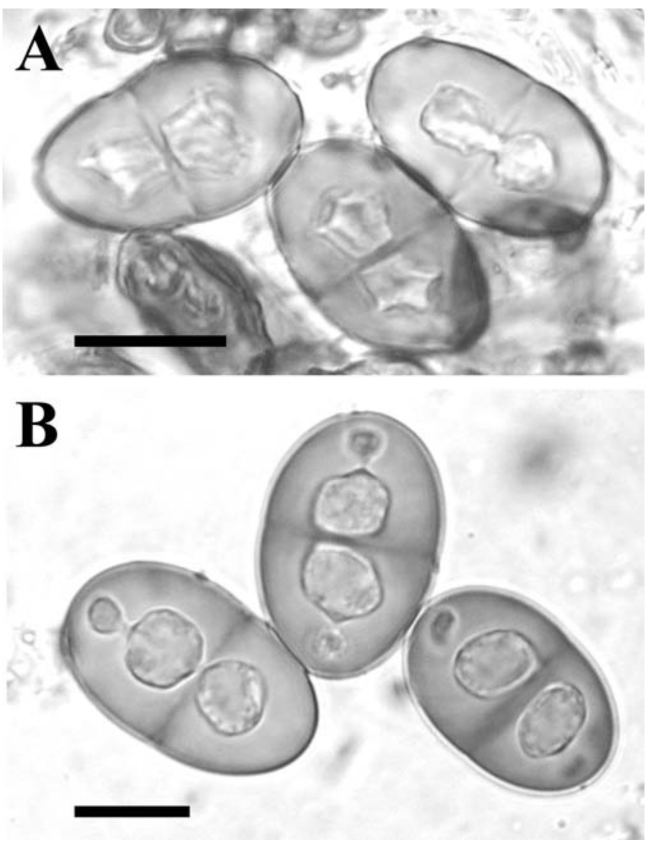

Fig. 5. *Pachysporaria*-type I ascospores. (A) *Rinodina verruciformis* spores at an intermediate stage of development with polygonal lumina. (B) *Rinodina flavosoralifera* spores with apical satellite lumina at maturity. Both scale bars = 10 µm.

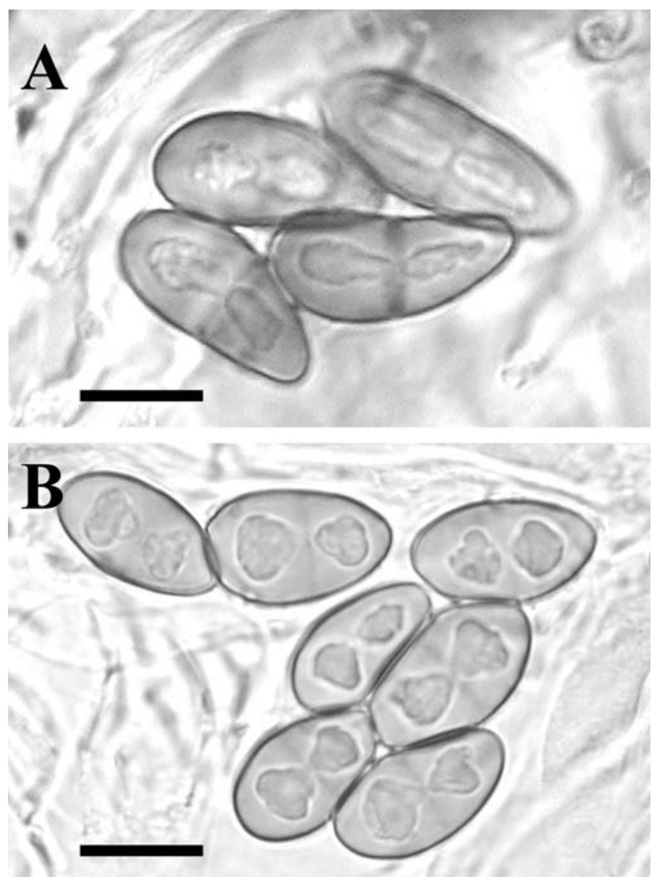

Fig. 6. *Pachysporaria*-type II ascospores. (A) *Rinodina colobinoides* spores with elongate (lacrimiform) lumina. (B) *Rinodina papillata* spores with irregularly rounded lumina. Both scale bars = 10 µm.

R. coloradiana to 17.5–18.5 µm × 9.5–10.0 µm in *R. papillata* (Fig. 6B). Average l/w ratio is 1.7–2.0 in both species but is as high as 2.0–2.3 in *R. maculans*. Other species possessing this spore type are *R. colobinoides* (Fig. 6A), *R. intrusa*, *R. pachysperma*, *R. poeltiana*, and *R. siouxiana* Sheard.

PHYSCIA-type (Poelt 1965) Figs. 2A and 101 (*R. macrospora*). Both septal and apical wall thickenings are well developed, usually resulting in lumina with concave or flat apices. Lumina are very symmetric and sharply angular during development, although less so at maturity. The group predominantly possesses Type A ontogeny. Average spore size varies from 15.0–16.0 µm × 7.5–8.0 µm in *R. freyi* to 30.0–32.5 µm × 14.5–15.5 µm in *R. macrospora*. Average l/w ratio varies from 1.7–1.9 in *R. degeliana* to 2.2–2.5 in *R. roscida*. *Physcia*-type spores are found in the largest number of species. In addition to the species mentioned above, this spore type is characteristic of *R. ascociscana*, *R. aurantiaca, R. badiexcipula*, *R. boulderensis*, *R. capensis*, *R. chrysomelaena*, *R. confragosa*, *R. disjuncta*, *R. efflorescens, R. excrescens*, *R. exigua*, *R. hallii*, *R. innata*, *R. juniperina*, *R. laevigata*, *R. mniaraea*, *R. olivaceobrunnea*, *R. orculata*, *R. parasitica*, *R. polyspora*, *R. septentrionalis*, *R. subminuta*, and *R. turfacea*.

Physcia-type spores with septal swellings have been described for *R. ventricosa* (Hinteregger 1994), but these spores do not become more swollen in KOH as do the *Dirinaria*-type. Mature spores of *R. pacifica* are frequently slightly swollen at the septum. Spores of *R. exigua* may also be slightly swollen but rarely so. The spores of *R. mniaraea* are frequently asymmetric with cells of different sizes (Fig. 111D). This phenomenon is seen in a few other species, but only rarely; for example, in *R. subminuta* (Fig. 163B). Spore development in *R. badiexcipula* is very unusual, in that apical wall thickening is delayed until after the walls have started to become pigmented (Fig. 21). Thus, *R. badiexcipula* spores start their developmental sequence with a *Physconia*-like appearance, their true *Physcia*-type nature only becoming apparent relatively late in their development. This is the reverse of the developmental sequence in the *Physconia*-type; *Physconia*-type spores typically begin their development with *Physcia*-like wall thickenings before losing their thick apical walls.

PHYSCONIA-type (Poelt 1965, including the *Dubyana*-type (Mayrhofer and Poelt 1979), *Sicula*-type (Mayrhofer 1982) Matzer and Mayrhofer 1996, and the *Orculariopsis*-type) Figs. 4G and 11 (*R. archaea*). This spore type is developmentally similar to the *Physcia*-type, except that the apical walls are thin or become thin (e.g., Fig. 127, *R. pacifica*), and it also possesses Type A development. Average spore size varies from 12.5–13.5 µm × 5.5–6.0 µm in *R. pyrina* to 20.5–22.0 µm × 10.5–11.0 µm in *R. pacifica*. Average l/w ratios vary from 1.7–1.9 in *R. grandilocularis* to 2.0–2.3 in *R. imshaugii*. Other species with *Physconia*-type spores are *R. archaea*, *R. populicola*, and *R. trevisanii*. Septal wall thickenings are limited to the earliest stages of development in *R. grandilocularis*, *R. populicola*, and *R. pyrina* and might therefore cause confusion with the *Beltraminia*-type.

The *Physconia*-type represents the final developmental stage of the *Physcia*-type spore in the genus *Rinodina*, and the spore type is maintained only because of its widespread use in the literature. It possesses Type A ontogeny. The difficulty of maintaining the separation of the *Physcia*- and *Physconia*-types of spore is exemplified by *R. terrestris*, which may possess either spore type in different collections. It has also been noted that both *R. archaea* and *R. trevisanii* spores, which typically belong to the *Physconia*-type, retain a higher proportion of spores in the *Physcia*-type developmental stage in the most mesic habitats that they occupy. Such specimens are often particularly well developed, suggestive of a high growth rate. *Rinodina austroborealis*, *R. disjuncta*, *R. obnascens*, and *R. sibirica* are other species with spores intermediate between the two types.

Other evidence for continuity between these two spores types is found in the literature. Mayrhofer and Moberg (2002) note that *R. interpolata* (Stirt.) Sheard of Europe has spores that are intermediate between the *Physcia*- and *Physconia*-types. Again, in the present work *R. orculata* is listed as possessing *Physcia*-type spores, whereas Giralt (2001) and Mayrhofer and Sheard (2007) regard it as belonging to the *Physconia*-type, further illustrating difficulties of separation. In North America its spores typically possess limited apical thickening, but short, broadly ellipsoid spores have mostly thin apical walls and these might be frequent in some samples.

Scheidegger (1993), Bungartz (2004*a*), and Bungartz and Nash (2004) have reported *Physconia*-type spores in the genus *Buellia*. However, none of these species show apical thickening at any stage of development and it is very doubtful that they can be considered to be homologous with the *Physconia*-type spores of *Rinodina* (Wedin et al. 2000; Helms et al. 2003).

Most interestingly, the spores of *R. roscida* and *R. terrestris* sometimes show very obvious Type B development, the first report of this developmental type occurring in species with either the *Physcia*-type or *Physconia*-type spore. It is possible that the spores of these two species have a relationship with *Dirinaria*-type, which also have *Physcia*-like locules, despite the difference in epihymenium pigmentation and the characteristic septal swelling in KOH of species with this spore type.

SUBMURIFORM-type (Giralt 2001; Mayrhofer et al. 2001) Fig. 4J. Spores of this type possess four or more cells, rounded lumina, and Type A development. This spore type is found only in *R. intermedia* and has an average size of 25.5–27.0 µm × 12.0–13.0 µm and an average l/w ratio of 2.0–2.2. It is probably not closely related to *R. conradii* as suggested by Malme (1902). Giralt (2001) noted that the lumina were surrounded by globular inclusions similar to some species with *Pachysporaria*-type spores, but Mayrhofer et al. (2001) did not find such inclusions. The spore type may possibly be related to *Pachysporaria*-type I and to *R. connectens* Malme and *R. homobola* (Nyl.) Vain., two 4-celled species placed in Sect. *Conradia* by Malme (1902).

TEICHOPHILA-type (Sheard and Mayrhofer 2002) Figs. 4H and 25 (*R. bolanderi*). The spores are characterized by septal and apical wall thickening with unusually variable locule shape and spore size during development and by Type A development in North American species. Septal swellings are present or absent, which in the former case may become more prominent upon application of KOH, as in the *Dirinaria*-type. Lumina are similar to the *Physcia*-, *Mischoblastia*-, or *Pachysporaria*-types at different stages of development, in contrast with the *Dirinaria*-type, in which the lumina are persistently *Physcia*-like and the spores are less variable in size. Spores of *R. teichophila* (Nyl.) Arnold were included under the *Mischoblastia*-type by Giralt (2001), who also stated that its spores show tendencies to the *Pachysporaria*-type at maturity. Both Type A and B development were reported for *R. teichophila* by Giralt (2001). Average spore size varies from 19.5–20.0 µm × 10.0–11.0 µm to *R. herrei* and 22.5–24.0 µm × 11.0–12.0 µm in *R. bolanderi*. Average l/w ratio varies from 1.7–2.0 in *R. tephraspis* to 1.9–2.1 in *R. bolanderi*.

TUNICATA-type (Poelt and Mayrhofer 1979; Giralt 2001; Kaschik 2006) Fig. 7 (*R. confragosula* (Nyl. in Cromb.) Müll. Arg. and *R. tunicata* H. Mayrhofer & Poelt). This spore type is characterized by a markedly thick outer wall and represented by *R. confragosula* alone in North America. In this species, lumina are *Pachysporaria*- or *Milvina*-like and development belongs to Type A, but Type B also has been reported in *R calcarea* (Arnold) Arnold (Giralt 2001). A torus develops late in *R. confragosula* and its walls are finely ornamented.

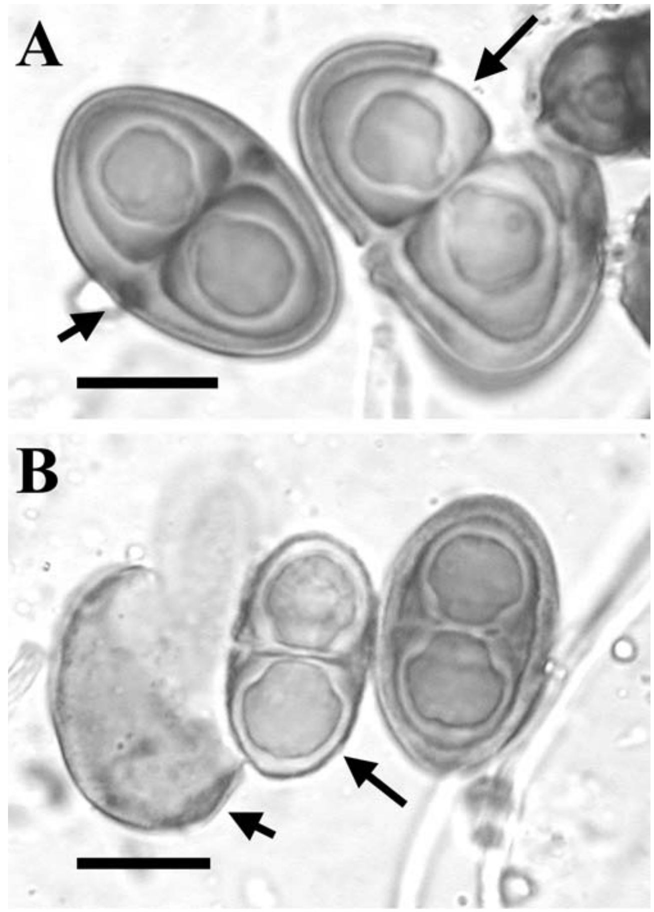

Fig. 7. *Tunicata*-type ascospores. (A) *Rinodina confragosula* ascospores in KOH. Inflated mature spore showing two wall layers. Short arrow indicates torus in vertical section at the septum periphery. Long arrow indicates wall layers broken away in part, in a spore that has been crushed. (B) *Rinodina tunicata* ascospores in water. The right-hand spore is intact, showing two wall layers. Short arrow indicates a spore with the outer wall entirely broken away. Large arrow indicates the inner wall layers and their two lumina. Both scale bars = 10 µm.

Pycnidia

Pycnidia are small and either partly immersed with protruding pigmented ostioles or deeply immersed in the thallus and found only by chance in thin sections. However, they have not been observed in the majority of species. A wide range of conidiophore types have been observed (Types I, II, V, and VI of Vobis 1980; Vobis and Hawksworth 1981). These results should be regarded as very preliminary, since the sample sizes were small. Giralt (2001) states that the conidiophores of Type VI are characteristic of *Rinodina*, but Type I has been found to be the most common in the present study. Conidia are bacilliform, ranging in size from 2.5–3.0 µm long in *R. santae-monicae* to 5.5–7.0 µm in *R. calcigena*, 5.5–7.5 µm in *R. sibirica*, and 6.0–7.0 µm in *R. lobulata*. Conidium breadth in these and the majority of species is ca. 1.0 µm. A few species have consistently broader conidia: *R. bischoffii*, 3.5–4.0 µm × 1.5 µm (4–5 µm × 1 µm; Mayrhofer and Moberg 2002); *R. milvina*, 4.0–5.0 µm × 1.5 µm (4–5 µm × 1 µm; Mayrhofer and Moberg 2002); *R. notabilis*, 5.0–6.0 µm × 1.5 µm; and *R. grandilocularis*, 5.0–6.5 µm × 1.5 µm.

Chemistry

The genus *Rinodina* is not known to be chemically diverse, although 45 species (46%) have been shown to contain secondary metabolites in the present study (Table 1). The terpenoid zeorin has been recorded in 27 species, although it is frequently present in trace amounts or is inconsistently present. The next most common substance is the cortical β-orcinol depside atranorin in 19 species. It is consistently present in all except 2 of these 19 species. The two substances occur together in eight species. Atranorin

Table 1. Secondary metabolites found in North American *Rinodina* species.

Species	Orcinol depsides and **β-orcinol depsides**	Orcinol depsidones and **β-orcinol depsidones**	Terpenoids	Anthraquinones and **xanthones**
R. adirondackii		**pannarin**		
R. archaea			± zeorin	
R. aspersa	**atranorin** gyrophoric acid[1]			
R. aurantiaca	**atranorin**	**pannarin** e	± zeorin	
R. badiexcipula	sphaerophorin[2]			
R. bolanderi	**atranorin**		zeorin	
R. boulderensis	**atranorin**			
R. calcigena			± zeorin	
R. californiensis	**atranorin**			
R. capensis	**atranorin**		zeorin	
R. castanomela			zeorin	
R. chrysomelaena	**atranorin**[3]			secalonic acid W[4]
R. confragosa	**atranorin**[3]		± zeorin	
R. degeliana	**atranorin**		zeorin	
R. destituta atranorin	**atranorin**			
R. disjuncta	sphaerophorin[2]			
R. efflorescens		**pannarin**	± zeorin	± secalonic acid A
R. endophragmia			± zeorin	
R. excrescens		**pannarin** + e		
R. exigua	**atranorin**			
R. flavosoralifera				**arthothelin, thiomelin**
R. granuligera	**atranorin**	**pannarin** e		
R. griseosoralifera	**atranorin**		zeorin	
R. hallii		± variolaric acid	± zeorin	
R. intermedia[a]		± **pannarin**		± graciliformin, ± skyrin
R. lepida			zeorin	**thiomelin**[5]
R. luridata			zeorin	
R. macrospora	**atranorin**		zeorin	
R. marysvillensis	**atranorin**	**pannarin** e		
R. mniaraea	± **atranorin**	± variolaric acid		± skyrin
R. olivaceobrunnea		± **pannarin**	± zeorin	
R. oxydata	**atranorin**			
R. perreagens		**pannarin**[6]	zeorin	
R. polyspora			± zeorin	
R. rinodinoides			zeorin	
R. roscida		± variolaric acid	± zeorin	
R. sheardii				secalonic acid A, **thiomelin**[7]
R. stictica	**atranorin**[3]	**stictic acid**[8]	zeorin	
R. subminuta			zeorin	
R. tephraspis	± ʹ5-*O*-methylhiascic acid[9]		zeorin	
R. terrestris			± zeorin	
R. trevisanii			± zeorin	
R. turfacea	sphaeorophorin[2] ± atranorin	± variolaric acid		
R. verruciformis	**atranorin**	± **stictic acid**	zeorin	
R. willeyii		**pannarin**	zeorin	

Note: β-Orcinol depsides, β-orcinol depsidones, and **xanthones** are shown in bold font. Accompanying biosynthetically related substances (superscript numbers in the table body refer to the following): [1], lecanoric, orsellenic, ovoic, umbilicaric, 5-*O*-methylhiascic acids; [2], isosphaeric acid; [3], chloroatranorin; [4], eumitryin Y, secalonic acid A; [5], 2-dechlorothiomelin 4-dechlorothiomelin, 5,7-dichloro-8-hydroxy-2-methoxy-1, 3-dimethylxanthone, 5,7-dichloro-2-8-hydroxy-1,3-dimethylxanthone; [6], dechloropannarin; [7], '5,7-dichloro-8-hydroxy-2-methoxy-1,3-dimethylxanthone; [8], cryptostictic, constictic, norstictic acids; [9], lecanoric acid; e, epihymenium only, + e, thallus and epihymenium.
[a]*R. intermedia* also contains the aliphatic compound deoxylichesterinic acid.

also appears to be present in the medulla of *R. granuligera*. The only other depside recorded is the orcinol compound sphaerophorin (in three species).

Of the remaining 11 secondary metabolites, the β-orcinol depsidone pannarin is the most frequent, occurring in nine species, including an association with the epihymenium of four species. The two other depsidones recorded are stictic acid (β-orcinol) in two species and variolaric acid (orcinol) in four species. They are not consistently present, except for the former in *R. stictica*. Two orcinol depsidones have been found: gyrophoric and lecanoric acids. Four anthraquinones are known in the North American *Rinodina* flora: secalonic acids A and W, graciliformin, and skyrin. Arthothelin and thiomelin are the only recorded xanthones. Deoxylichestrinic acid is the only known aliphatic substance (fatty acid). It consistently accompanies graciliformin in *R. intermedia*, creating a unique chemosyndrome in the genus (Mayrhofer et al. 2001). Biosynthetically related accessory compounds to these substances are listed in Table 1 for the different species whenever they have been recorded.

Species with high concentrations of atranorin typically possess a light grey or "cream" colour after storage in the herbarium. This cortical "pigment" is presumably too light in colour to be visible until photosynthetic pigments have at least partially degraded. Thallus colour is often a darker shade of grey when atranorin is present in low concentrations, as is sometimes the case for *R. exigua*, and may give ambiguous results with spot tests. In this state atranorin crystals are always detectable in low concentrations under polarizing light. Blanco et al. (2006) suggested that atranorin is of limited taxonomic value at the generic or suprageneric level in the parmelioid lichens. Its scattered distribution within 5 of the 13 spore types would also suggest that it is of little value at the subgeneric level in *Rinodina*. The same would also appear to be true of the other two relatively common secondary metabolites, pannarin and zeorin.

Limits of the Genus *Rinodina*

The genus has traditionally been placed in the Physciaceae, a family defined by its mostly 1-septate and brown spores, which included the crustose genera, *Buellia* and *Rinodina*, and also foliose and a few fruticose genera (Tehler 1996; Tehler and Wedin 2008). The classic distinction between the genus *Buellia* with its lecideine apothecial margin (proper exciple), lacking algae and darkly pigmented like the hypothecium, and *Rinodina* with its lecanorine margin (thalline exciple) containing algae, with a poorly developed and hyaline proper exciple like the hypothecium, still applies with some exceptions (Hafellner et al. 1979; Giralt 2001; Mayrhofer and Moberg 2002; Sheard 2004; Bungartz et al. 2007). These characters are usually associated with spores having unthickened walls (*Beltraminia*-type) in *Buellia* (but see Malme 1927; Sheard et al. 2008) and variously thickened walls in *Rinodina*. There are, nevertheless, species that deviate from this general concept and are difficult to place satisfactorily in either genus.

Scheidegger (1993), Bungartz et al. (2002), Bungartz (2004*a*), Bungartz and Nash (2004), and Bungartz et al. (2007) have shown the spores of some *Buellia* species to have septal wall thickenings, particularly during development, and they place such spores in the *Physconia*-type rather than in the *Beltraminia*-type. None of these spores, however, show *Physcia*-type apical wall thickening during their ontogeny, which is typical of the *Physconia*-type spore in *Rinodina*. In this author's opinion it is very doubtful that *Physconia*-type spores described for *Buellia* species are homologous with those of *Rinodina* and therefore should not be regarded as evidence for the monophyletic origin of the two genera. Grube et al. (2004) seem to be of the same opinion, as they describe the spores of *Buellia molongolo* as being "similar to the *Physconia*-type".

Rambold et al. (1994) surveyed ascus types in the Physciaceae (Poelt 1974), showing that *Buellia* is characterized by asci belonging to the *Bacidia*-type and *Rinodina* by asci belonging to the *Lecanora*-type, with a few exceptions in both genera. Giralt and Matzer (1994) considered corticolous species of *Rinodina* with biatorine or lecideine apothecia, observing that "The species treated ... can be included in *Buellia* or *Rinodina* depending on which character is given the most taxonomic weight". The characters under consideration were apothecial type, hypothecium pigmentation, ascus types, and spore types, with spore type taking precedence in their treatment. Giralt (2000) discussed the taxonomic position of *Buellia ericina* (Nyl.) Jatta and a related species, which have *Dirinaria*-type spores but otherwise possess lecideine characters including *Bacidia*-type asci. The saxicolous, lichenicolous species "*R. insularis*", one of the problem *Rinodina* species identified by Rambold et al. (1994), possesses similar characters and may be related. Giralt suggests that these species, together with *R. kalbii* Giralt & Matzer, may well belong in their own genus, but these relationships need testing with molecular studies. "*Rinodina insularis*" was excluded from the genus by Kaschik (2006), who confirmed its isolated position with molecular studies, showing it to be grouped with *Buellia* species. Based on the accumulated evidence it is also excluded from *Rinodina* in this study.

Cladistic studies of the Physciaceae based on morphological characters (Nordin and Mattson 2001; Scheidegger et al. 2001) show *Rinodina* to be a paraphyletic taxon and to possess the most complex intrageneric relations within the family. A similar result was found in the molecular study of Grube and Arup (2001), in which *Rinodina* species were found scattered among three of four major clades. Helms et al. (2003), using small subunit (SSU) rDNA, confirm the close relationship of the Caliciaceae and Physciaceae proposed by Wedin et al. (2000, 2002) and show the Caliciaceae to include *Buellia* and other buellioid genera. The classical separation of genera *Buellia* and *Rinodina* is therefore confirmed, but it is more fundamental than previously suspected. The idea that *Rinodina* evolved linearly from *Buellia* by loss of pigmentation and increased lichenization of apothecial tissues, as might be inferred from Sheard (1967, Fig. 3), is no longer tenable.

Internal transcribed spacer (ITS) rDNA analyses of a larger data set of Physciaceae species (Helms et al. 2003) proved both *Buellia* and *Rinodina* to be "clearly polyphyletic" and separated in two well supported clades, although the majority of other genera were monophyletic. Species of *Rinodina* were found in at least six independent lineages in Clade A. It is particularly surprising that three well understood, ground dwelling, oroarctic species (*R. mniaraea*, *R. olivaceobrunnea*, and *R. turfacea*) with *Physcia*-type spores in the strict sense rather than the wider sense of Helms et al. (2003), which includes the *Pachysporaria*- and *Polyblastidium*-types, are so widely separated from each other. This result is inexplicable and cannot be accepted without confirmation by other molecular studies based on additional genes. Nevertheless, it raises the possibility of a polyphyletic origin for species with *Physcia*-type spores.

The molecular studies of Grube and Arup (2001) and Helms et al. (2003) helped to resolve the relationships of two of the anomalous species discussed by Rambold et al. (1994). *Buellia lindingeri* Erichs., possessing a lecideine apothecium, colourless proper exciple, pigmented hypothecium, *Lecanora*-type asci, and *Physcia*-type spores, is shown to be most closely related to *R. lecanorina* (A. Massal.) A. Massal. and should therefore be regarded as a *Rinodina* species, contrary to the view of Giralt and Matzer (1994). Helms et al. (2003) also placed *R. cacuminum* (Th. Fr.) Malme, which has lecanorine apothecia, a hyaline to brownish hypothecium, *Bacidia*-type asci, and *Beltraminia*-type spores, together with