Int. J. Plant Sci. 180(9):1004–1015. 2019.

1058-5893/2019/18009-0009$15.00 DOI: 10.1086/705587

GAMETOPHYTES OF THE FERN GENERA *DRACOGLOSSUM* AND *LOMARIOPSIS* (LOMARIOPSIDACEAE) AND THEIR PHYLOGENETIC SIGNIFICANCE

James E. Watkins Jr.[1],* and Robbin C. Moran[1],†

*Department of Biology, Colgate University, 13 Oak Drive, Hamilton, New York 13346, USA; and †New York Botanical Garden, 2900 Southern Boulevard, Bronx, New York 10458-5126, USA

Editor: Gerhard Prenner

Premise of research. Molecular phylogenetic studies have resolved *Dracoglossum* and *Lomariopsis* as sister, even though their sporophytes are quite dissimilar morphologically. We wanted to examine the gametophytes of both genera to determine whether they supported the sister relationship.

Methodology. We studied wild populations of gametophytes of *Dracoglossum plantagineum* and three species of *Lomariopsis* (*L. japurensis*, *L. maxonii*, and *L. vestita*) at three locations in Costa Rica. We recorded gametophyte form, behavior upon maturation, and substrate occurrence (soil, rocks, or trees). Gametophytes were identified by finding young sporophyte leaves still attached and tracing them to successively larger leaves that were readily assignable to species.

Pivotal results. Morphologically, the gametophytes of the two genera were identical, being indistinguishable unless young sporophyte leaves were present. Both had gametophytes that were alike by being ribbon shaped, centrally thickened, notched apically with the meristem located within the notch, and attached to the substrate by apically branched rhizoids. Gametophytes of both also exhibited a distinctive behavior: when young, the thalli were appressed to the substrate, but as they matured, their lower edge lifted up and away from the substrate, leaving the gametophyte attached to the substrate only on the upper side. Gametangia occurred only on gametophytes with a shelflike form. In both genera, archegonia were common, but antheridia were not found in *Dracoglossum* and observed only twice in *Lomariopsis*. The main difference between the gametophytes of *Dracoglossum* and *Lomariopsis* is ecological: *Dracoglossum* grows on boulders in streams, whereas *Lomariopsis* grows as an epiphyte on the lower portions of trunks. Although the sporophytes of *Dracoglossum* and *Lomariopsis* are dissimilar, we found one likeness previously unreported: purplish petioles and rachises in the fiddlehead stage.

Conclusions. The gametophytes of *Dracoglossum* and *Lomariopsis* are identical morphologically and share several distinctive characters such as ribbon-shaped thalli, hairless surfaces and margins, and apically branched rhizoids. They also share an uncommon behavior upon maturation: gametophytes change from appressed against the substrate to a shelflike form with the lower margin lifted upward. These characters are derived and support the sister relationship of the two genera. *Dracoglossum* and *Lomariopsis* are unusual among ferns in that the sporophyte provides almost no evidence of a sister relationship, whereas the gametophytes strongly support it.

Keywords: ecology, growth habit, hemiepiphyte, systematics, ferns, gametophyte.

Introduction

Dracoglossum Christenh. (Lomariopsidaceae) is entirely Neotropical, occurring from southern Mexico to Bolivia and Puerto Rico and the Lesser Antilles to the Guianas and northern Brazil (Christenhusz 2007). It grows from 0 to 800 (–1000) m in wet shaded forests, typically on boulders in and along the sides of streams but to a lesser extent on muddy banks and forest floors. Nowadays, two species are recognized in the genus: *D. plantagineum* (Jacq.) Christenh. and *D. sinuatum* (Fée) Christenh. (Christenhusz 2007). Both are characterized by short-creeping rhizomes, polystichously arranged leaves, simple and entire or slightly sinuate laminae, a single bud present in an apical notch of the lamina, reticulate venation, and round sori (figs. 1, 2).

Because of its finely reticulate veins and round sori, *Dracoglossum* was for a long time classified in *Tectaria* Cav. It was construed as containing as a single species, *T. plantaginea* (Jacq.) Maxon, with two varieties: var. *plantaginea* and var. *macrocarpa* (Fée) C.V. Morton (= *D. sinuatum*). The latter has large circular-peltate indusia (var. *plantaginea* is nonindusiate) similar to those found in certain species of *Tectaria*, such as *T. acutiloba* (Hieron.) Maxon, *T. fimbriata* (Willd.) Proctor & Lourteig, and *T. heracleifolia* (Willd.) Underw.

---

[1] Authors for correspondence; email: jwatkins@colgate.edu; rmoran@nybg.org.

Manuscript received March 2019; revised manuscript received May 2019; electronically published September 25, 2019.

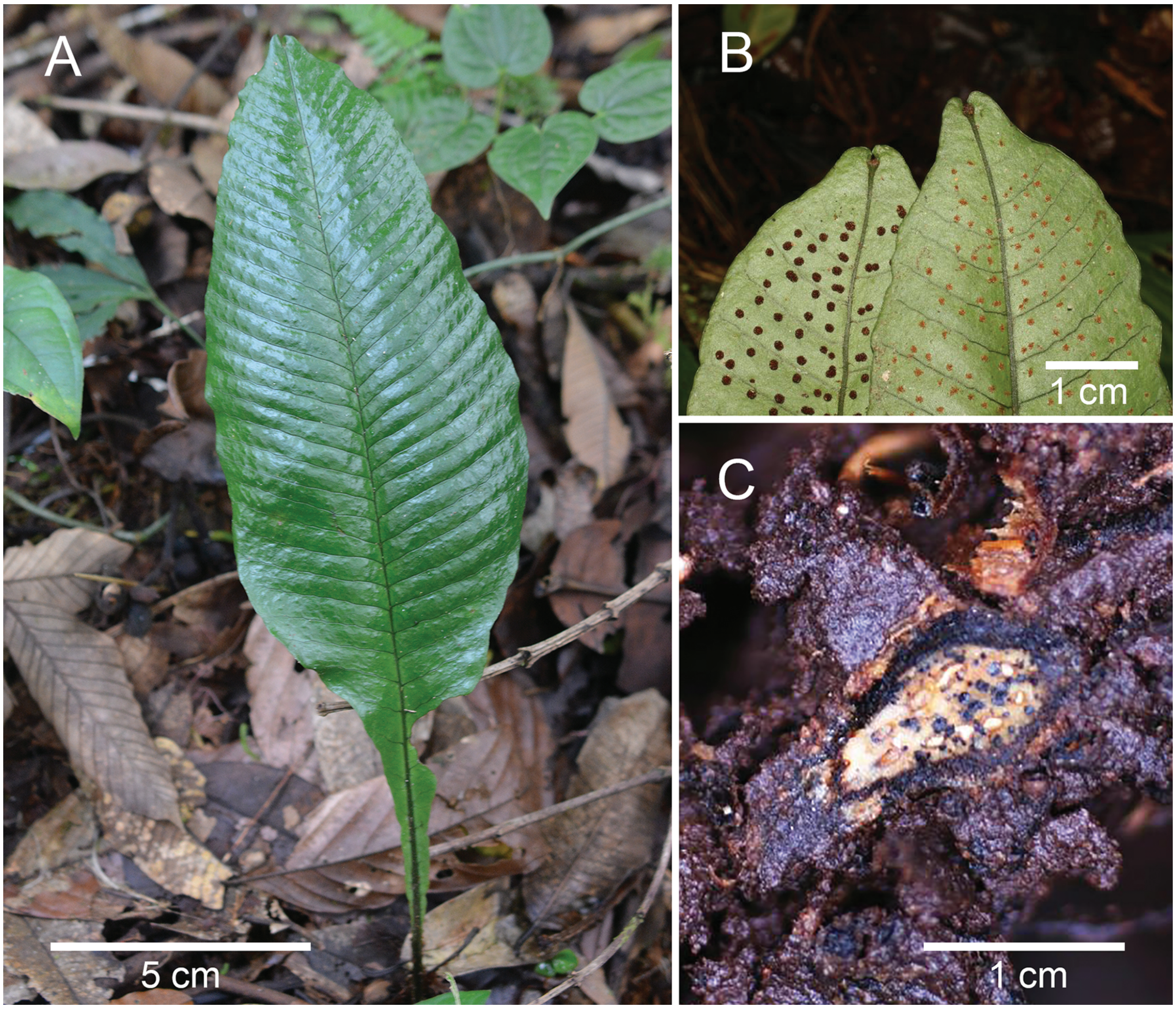

Fig. 1 *Dracoglossum*. *A*, Single leaf. *B*, Two lamina apexes showing sori and single terminal bud in an apical notch. *C*, Cross section of rhizome showing meristeles and dark patches of sclerenchyma scattered in the lighter-colored ground tissue. Dorsal side is oriented upward and slightly to the left.

This classification of *T. plantaginea* in *Tectaria* was eventually overturned by molecular phylogenetic analyses. A preliminary molecular study by Eric Schuettpelz (cited as personal communication in Christenhusz 2007) recovered *T. plantaginea* outside of *Tectaria*. On the basis of this evidence, Christenhusz (2007) published *Dracoglossum* as a new genus with two species, *D. plantagineum* and *D. sinuatum*. The family assignment of *Dracoglossum* was left open, awaiting a more comprehensive phylogenetic study. Later such studies recovered *Dracoglossum* as sister to *Lomariopsis* in the Lomariopsidaceae (Christenhusz et al. 2013; Zhang et al. 2016).

This sister relationship of *Dracoglossum* and *Lomariopsis* was surprising because the sporophytes of the two genera have little in common morphologically. The sporophytes of *Dracoglossum* are terrestrial or epipetric. The meristeles of the rhizomes are approximately the same size and shape when viewed in transverse section. Each meristele is surrounded by light-colored ground tissue, not by a black sclerenchymatous sheath, although blackish clusters of cells may be found scattered in the ground tissue (fig. 1*C*). The roots are produced on all sides of the rhizome. In contrast, the sporophytes of *Lomariopsis* are hemiepiphytic (sensu Zotz 2013, 2016) with long-creeping dorsiventral rhizomes (fig. 2). Its rhizome anatomy is strikingly different. As seen in cross section (fig. 2*D*), the ventral meristele is elongated and has a notch or indentation on the upper side, apparently a phylogenetic vestige of the fusion of two formerly separate meristeles. This ventral meristele gives rise to all the roots, so that roots are borne only along the ventral surface of the rhizome, not on all sides (Moran 2000). The dorsal meristeles are circular or nearly so in cross section. These and the ventral meristele are each individually surrounded by a black sclerenchymatous sheath that contrasts with the lighter-colored ground tissue. In short, the rhizomes of *Dracoglossum* and *Lomariopsis* share hardly any characters in common.

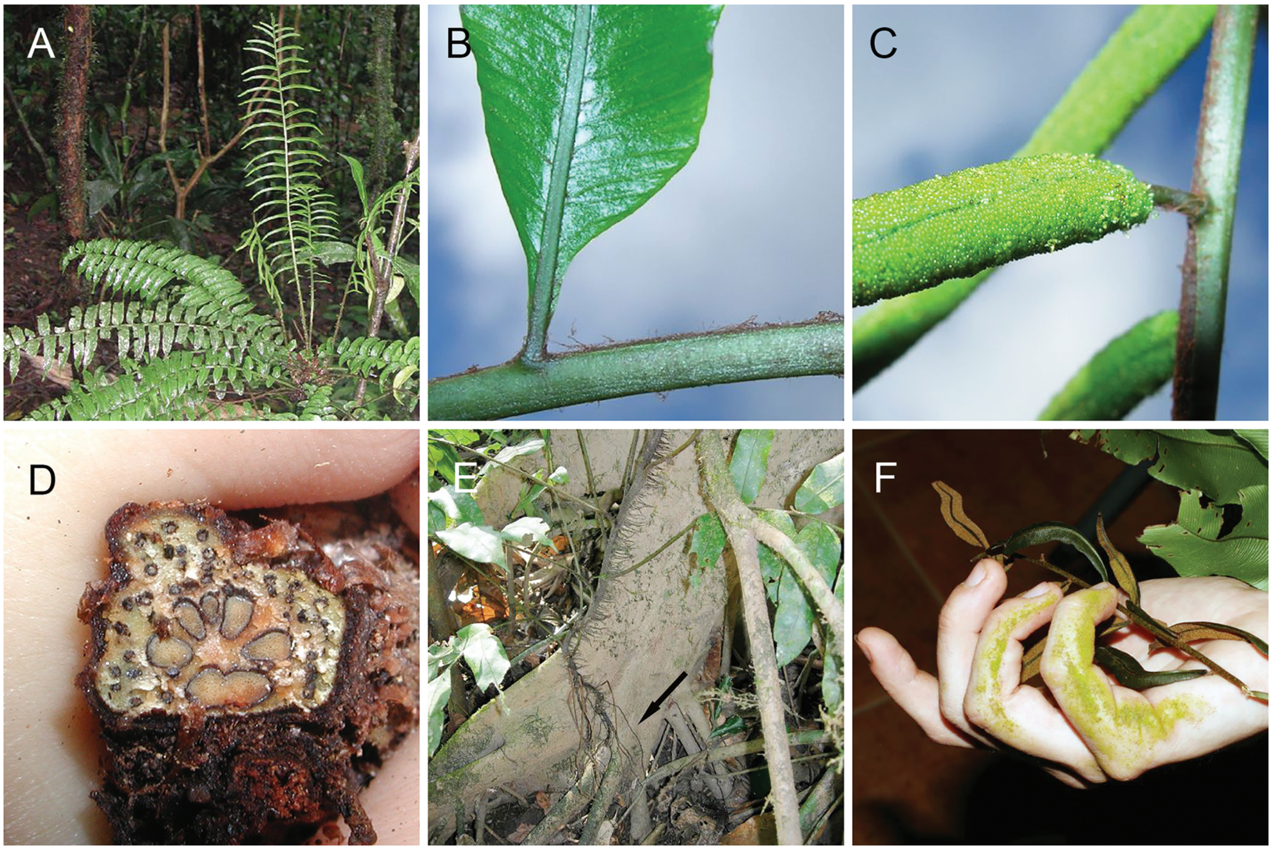

Fig. 2 *Lomariopsis*. *A*, Sterile-fertile leaf dimorphy. *B*, Pinna with free venation; note the faint dark line (articulation); pinna joins the rachis. *C*, Fertile pinnule with green spores. *D*, Rhizome cross section showing cat's-paw pattern of the meristeles; note the notch in the elongated ventral meristele. *E*, Hemiepiphytic climbing habit; note the long-creeping rhizome and the long clasping roots (2–3 cm) along its length, with the long feeder roots (arrow) extending into the soil. *F*, Green spores on hand, shed from *L. japurensis*.

Besides rhizomes, the two genera differ by their leaves. The sterile and fertile leaves of *Dracoglossum* are monomorphic, with laminae that vary from simple and entire to slightly sinuous (fig. 1*A*). Each leaf bears a single bud in an apical notch (fig. 1*B*). The veins, which are often obscured by the thickness of the laminae, are finely reticulate with included free veinlets in the areoles. In contrast, *Lomariopsis* exhibits strong sterile-fertile leaf dimorphy (fig. 2*A*–2*C*; Moran 2000; Moran and Watkins 2004). Its leaves are 1-pinnate throughout their length, ending in a conform terminal segment, that is, a segment similar in shape to the lateral pinnae. This terminal segment lacks a bud, and buds are not found elsewhere on the leaves. The veins are free and either simple or once forked (fig. 2*B*; Moran 2000). Thus, the two genera differ in sterile-fertile leaf dimorphism, lamina division, presence or absence of foliar buds, and venation.

Finally, the sori and spores of both genera differ greatly. The sori of *Dracoglossum* are mostly round but sometimes slightly elongate; those of *Lomariopsis* are acrostichoid, conforming to the shape of the pinnae (figs. 1*B*, 2*C*). The spores of *Dracoglossum* are brown (J. E. Watkins and R. C. Moran, personal observations), whereas those of *Lomariopsis* are chlorophyllous (fig. 1*C*, 1*F*; Lloyd and Klekowsky 1970; Sundue et al. 2011). Previous studies have examined the spores of both genera (Tryon and Tryon 1982; Tryon and Lugardon 1991; Rouhan et al. 2007). In general, the perines of *Dracoglossum* are less elaborate than those of *Lomariopsis* (fig. 3). Both have broad folds, but *Dracoglossum* has short sparse spines or spicular deposits, whereas *Lomariopsis* exhibits spines, wings, and spherical deposits (Rouhan et al. 2007). The greater diversity of perines in *Lomariopsis* (fig. 3*C*–3*F*) in part reflects its greater number of species, but none of its species have perines low and sparsely spiculate like those of *Dracoglossum* (fig. 3*A*, 3*B*).

In sum, few previously studied sporophytic characters lend support to the sister relationship of *Dracoglossum* and *Lomariopsis* as recovered by molecular phylogenetic studies. The purpose of this paper is to examine whether the gametophytes of these taxa provide such support.

Material and Methods

Fieldwork

Fieldwork was carried out in Costa Rica during January 2015, 2017, and 2019. Observations were made at three sites: the La Selva Biological Station, Quebrada Gonzalez in the Braulio Carrillo National Park, and the Las Alturas Biological Station. The La Selva Biological Station (50 m) is located in the Caribbean lowlands (lat. 10.4310°N, long. 84.0036°W) and consists of

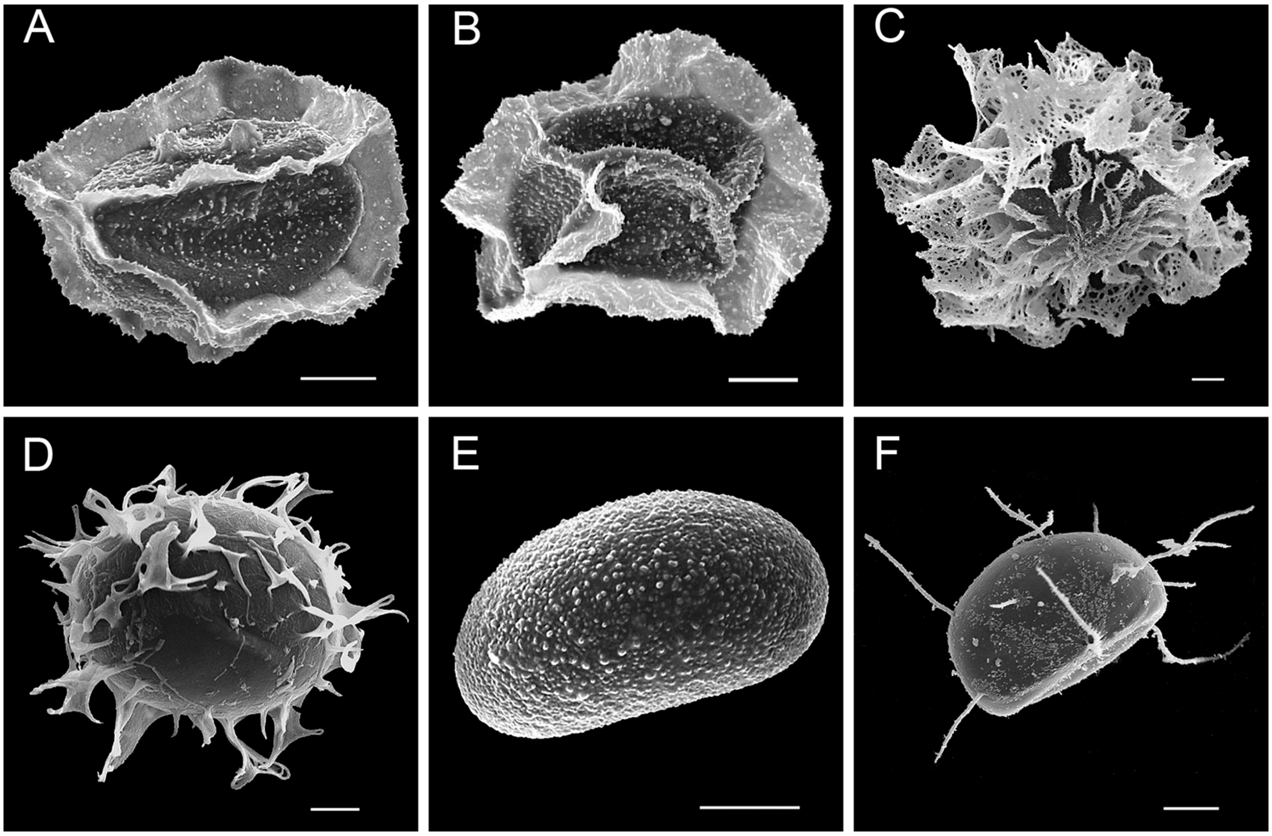

Fig. 3 Spores of the two species of *Dracoglossum* and several of *Lomariopsis*, showing the diversity that exists within that genus. *A*, *Dracoglossum plantagineum* (Costa Rica, Herrera 1033, NY). *B*, *Dracoglossum sinuatum* (French Guiana, Mori et al. 25928, NY). *C*, *Lomariopsis maxonii* (Panama, Croat 66314, NY). *D*, *Lomariopsis vestita* (Costa Rica, Folsom 9011, NY). *E*, *Lomariopsis japurensis* (Panama, Hayes 4, NY). *F*, *Lomariopsis guineensis* (Sierra Leone, Fay and Fay s.n., NY). Scale bars = 10 μm.

nearly aseasonal rainforest (McDade 1994). Quebrada Gonzalez (500 m) is located on the Caribbean side of the central mountains of Costa Rica (lat. 10.1599°N, long. 83.974425°W) and is covered by relatively aseasonal premontane rainforest (Sawyer and Lindsey 1971). The Las Alturas Biological Station (1500 m) is located on the western side of Talamanca Range (lat. 8.945°N, long. 82.833°W), north of the town of Las Alturas. This forest is classified as a premontane wet forest with a slight dry season during December and February (Holdridge 1967; Sawyer and Lindsey 1971). This station was visited only in January 2017.

In total, we studied three species of *Lomariopsis*. At the La Selva Biological Station, we studied hundreds of individuals of *L. japurensis* (Mart.) J. Sm. and *L. vestita* E. Fourn. At the Las Alturas Biological Station, we studied 10 populations of *L. maxonii* and at Quebrada Gonzalez 12 populations of *Dracoglossum plantagineum*.

Gametophytes were identified by finding young sporophyte leaves still attached and tracing them to successively larger leaves that were readily assignable to species. *Dracoglossum* sporeling leaves were distinguished from those of *Lomariopsis* by anastomosing veins (*Lomariopsis* has free veins) and often notched lamina apexes. Gametophytes and sporophytes were photographed in the field and subsequently taken to the laboratory at La Selva for microscopic and photographic documentation.

Spore Characters

Spores were transferred with dissecting needles from herbarium specimens to aluminum SEM stubs, where they were affixed with an asphalt adhesive and coated with a gold-palladium alloy in a sputtercoater for 3.5 min. Spores were digitally imaged using a JEOL JSM-5410LV SEM equipped with a JEOL Orion 5410 software interface at an accelerating voltage of 10 kV. Our spore images, including those of *Dracoglossum* and many species of *Lomariopsis* not shown in this article, are available at http://www.plantsystematics.org.

Results

Lomariopsis

The gametophytes of *Lomariopsis japurensis*, *L. maxonii*, and *L. vestita* were entirely epiphytic and most abundant on small-diameter trees. Only occasionally were they were found on the buttresses or low trunks of large-diameter trees. Nearly all occurred less than 3 m from the ground.

Lomariopsis gametophytes were relatively uniform and lacked characters to distinguish the three species. All were perennial, strap shaped, and apically notched with the meristem located in the notch (figs. 4, 5, 6*A*, 7). The surfaces and margins were glabrous, lacking capitate-glandular hairs (figs. 5–8). Two types of rhizoids were produced: unbranched and terminally branched (fig. 8*E*). Both types could be produced from either the surface or the margins of the thallus (fig. 8*F*). The branched ones appeared physically connected to the host bark. Both types of rhizoids lacked chloroplasts. The archegonia had four rows of neck cells projecting from the ventral surface of the central cushion

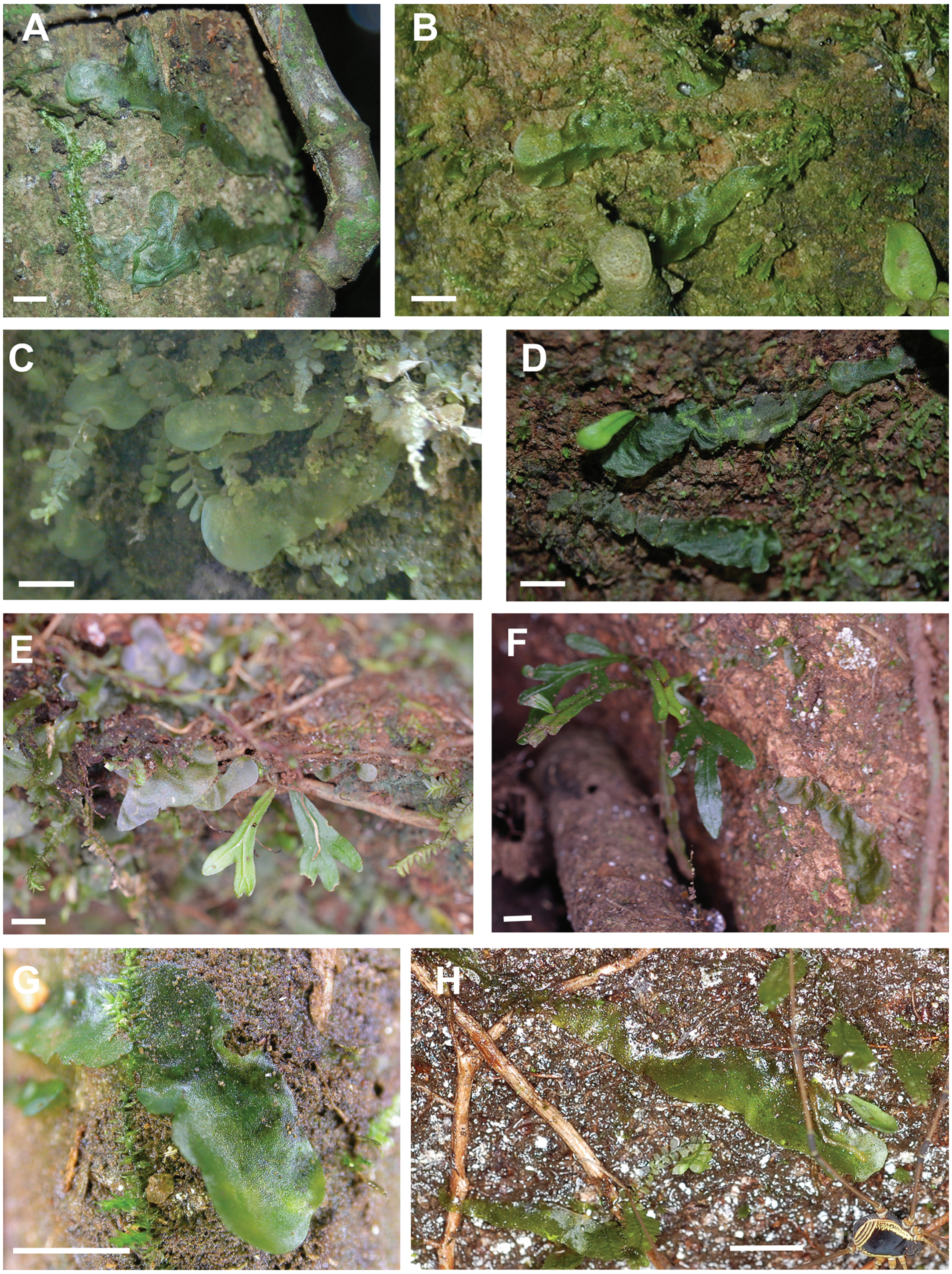

Fig. 4 *Lomariopsis* and *Dracoglossum* gametophytes in situ. *A*, *Lomariopsis vestita*, appressed form. *B*, *Lomariopsis vestita*, shelf form. *C*, *Lomariopsis japurensis*, shelf form. *D*, *Lomariopsis japurensis*, shelf form; note the sporeling leaf on gametophyte in upper left. *E*, *Lomariopsis maxonii*, shelf form, with two sporeling leaves at right. *F*, *Lomariopsis maxonii*, appressed form (right); at upper left are sporeling leaves. *G*, *H*, *Dracoglossum plantagineum*, shelf form. Scale bars = 1 mm.

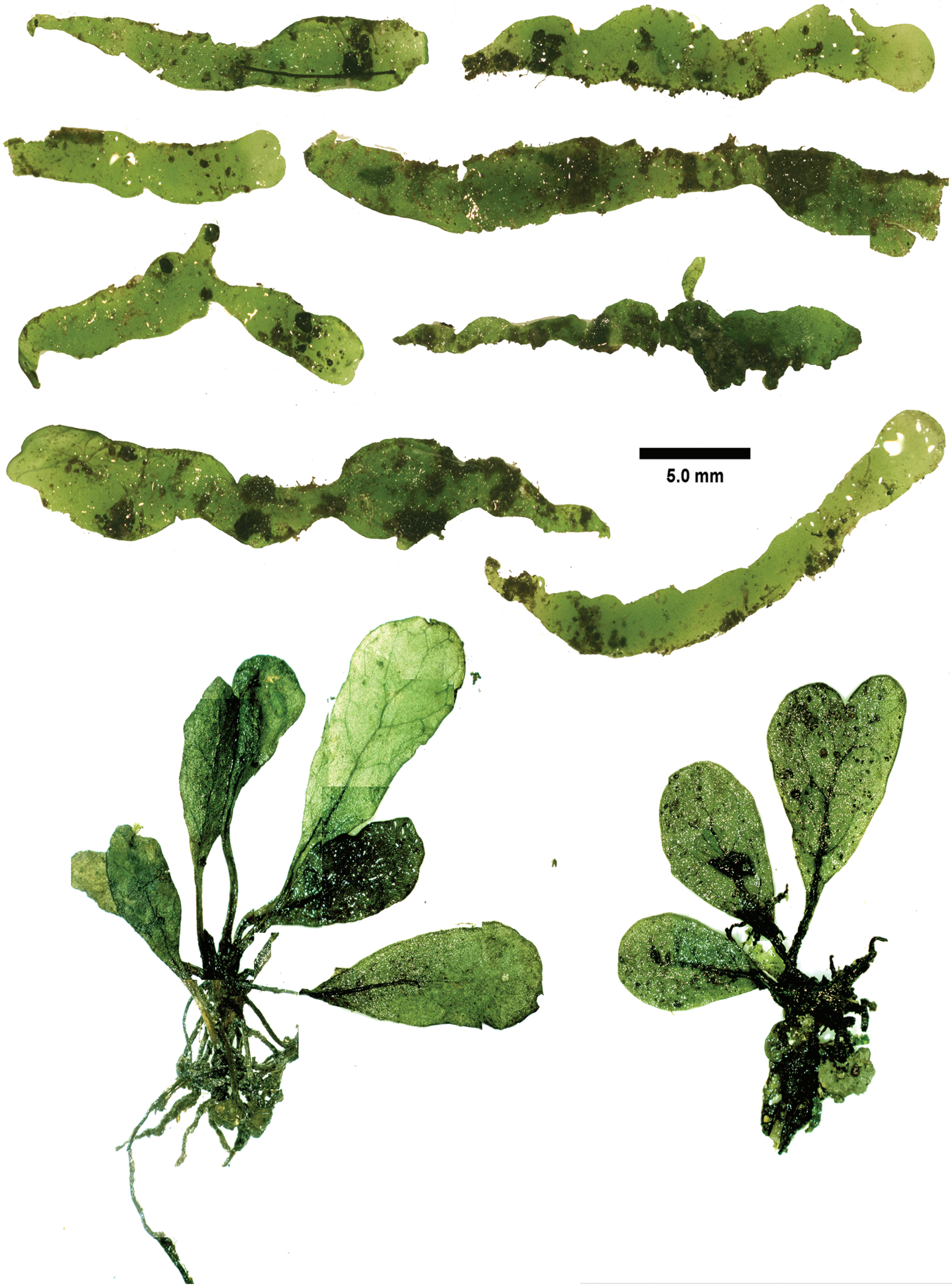

Fig. 5 Gametophytes of *Dracoglossum plantagineum* removed from substrate and photographed on a white background. The two gametophytes at the bottom bear sporeling leaves with anastomosing veins, and the one at right exhibits a notched lamina apex.

(fig. 8*A*, 8*B*). The antheridia were three celled, with a basal cell, donut-shaped ring cell, and operculum or cap cell.

The gametophytes exhibited a movement upon maturity. Initially, they were appressed to the substrate (fig. 4*A*), but as they matured, they shifted to a shelf form where the lower side (i.e., the side oriented toward the ground) lifted up and away from the substrate (fig. 4*B*). The appressed forms were always sterile; only the shelf form produced gametangia. Archegonia were nearly always present on the shelf form, whereas antheridia were rare, being found on only two gametophytes at the La Selva

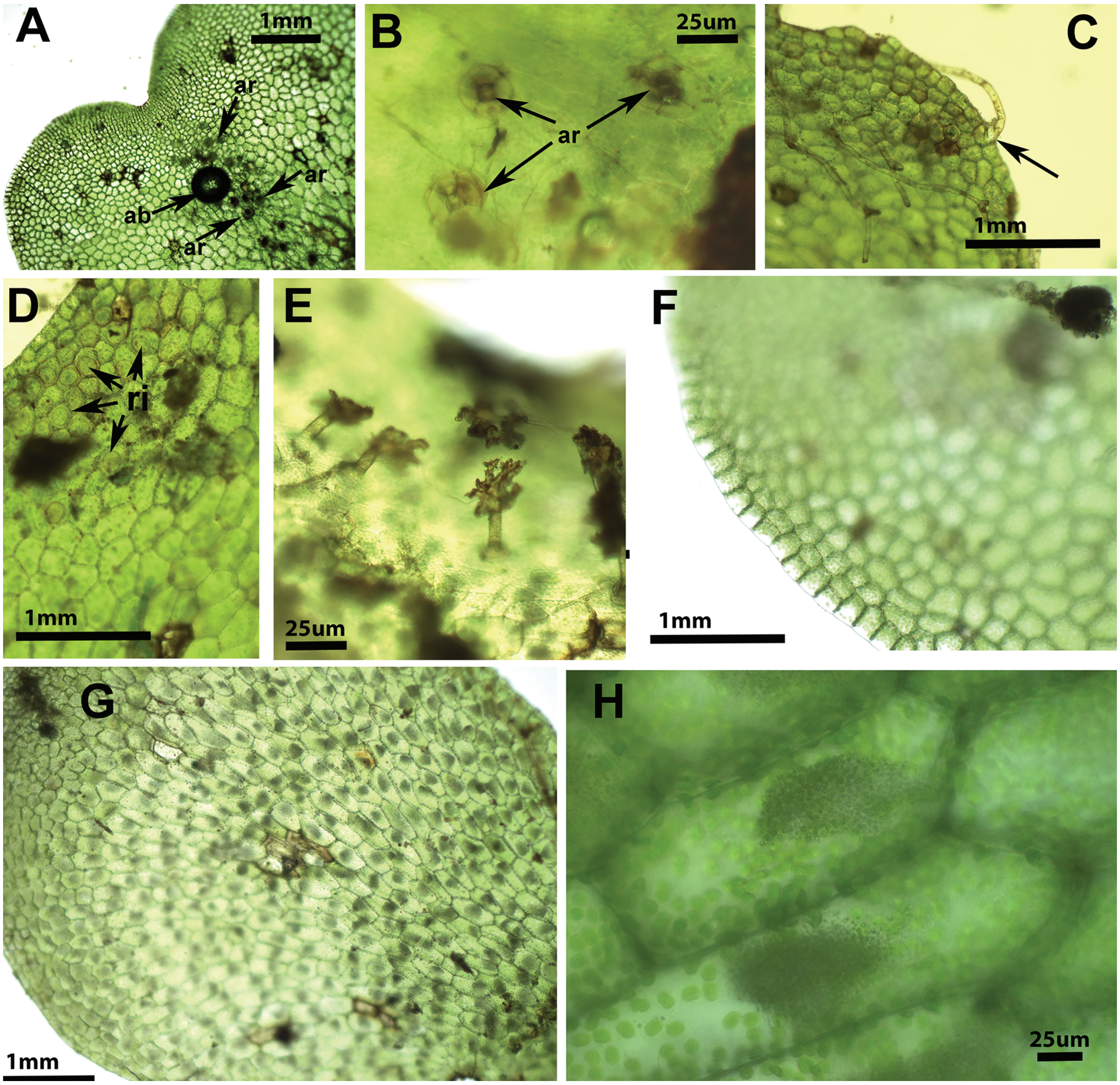

Fig. 6 Gametophytes of *Dracoglossum plantagineum A*, Region near the apical meristematic notch. *B*, Typical four-celled archegonia as seen from above. *C*, Marginal rhizoids. *D*, Rhizoid initials from the surface of the thallus. *E*, Branched rhizoids. *F*, Distinctive row of quadrate cells along the margins. *G*, Unidentified spots of unknown nature on the outer surface of each cell. *H*, Detail of spots showing their granular texture. ab = air bubble; ar = archegonia; ri = rhizoid initials.

Biological Station of either *L. japurensis* or *L. vestita* (fig. 8*C*, 8*D*). Antheridia were not found in *L. maxonii.* The two antheridiate gametophytes lacked archegonia. They were similar in size and shape to the mature archegoniate thalli.

Dracoglossum

Gametophytes and sporophytes of *Dracoglossum plantagineum* were always found growing on rocks in and around stream beds. None were found on trees.

The gametophytes of *D. plantagineum* were elongate strap shaped with the meristem located in an apical notch region. They consistently produced an ordered array of marginal cells that were smaller than the central cells of the thallus (fig. 6*A*). Archegonia were borne along a central cushion (fig. 6*A*, 6*B*). They were typical for leptosporangiate ferns, being composed of four tiers of neck cells that protrude from the surface of the thallus (fig. 6*A*, 6*B*; Atkinson and Stokey 1964; Nayar and Kaur 1971). All gametophytes collected were either asexual or archegoniate; no antheridia were found.

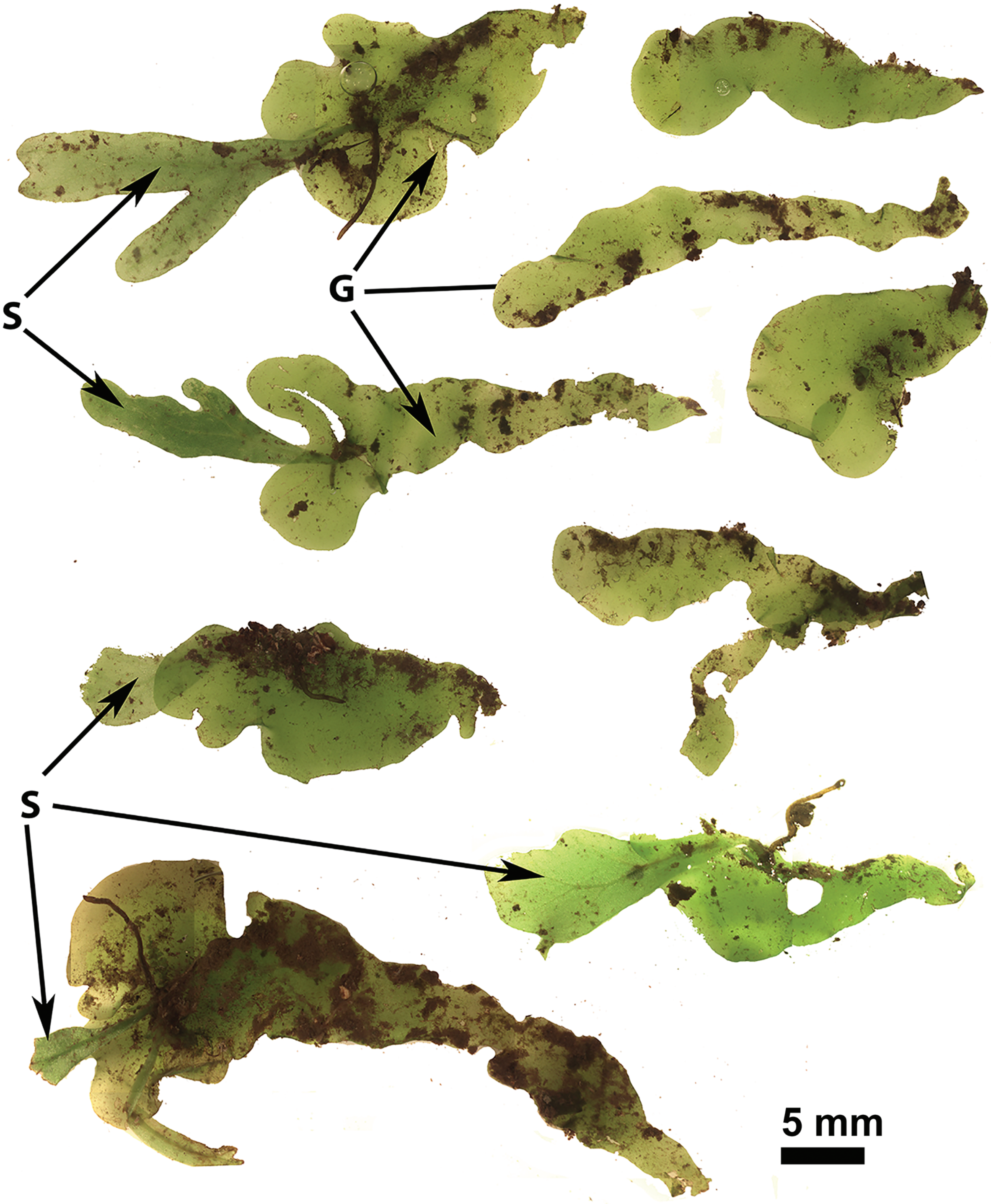

Fig. 7 *Lomariopsis vestita*. Gametophytes removed from substrate and photographed on a white background. The first leaves are typically undivided, strap shaped, or forked. G = gametophyte; S = first sporophyte leaves.

Two types of rhizoids, unbranched and apically branched, were produced along the margins and on the surfaces of the thallus (fig. 6*C*–6*E*). The branched rhizoids appeared physically connected to the substrate. All rhizoids lacked chloroplasts.

Curiously, we observed several gametophytes that had gray granular spots near the center of the outer surfaces of their cell walls (fig. 6*G*, 6*H*). These spots might be bacterial colonies, but their regular placement seems to contradict that idea. We were

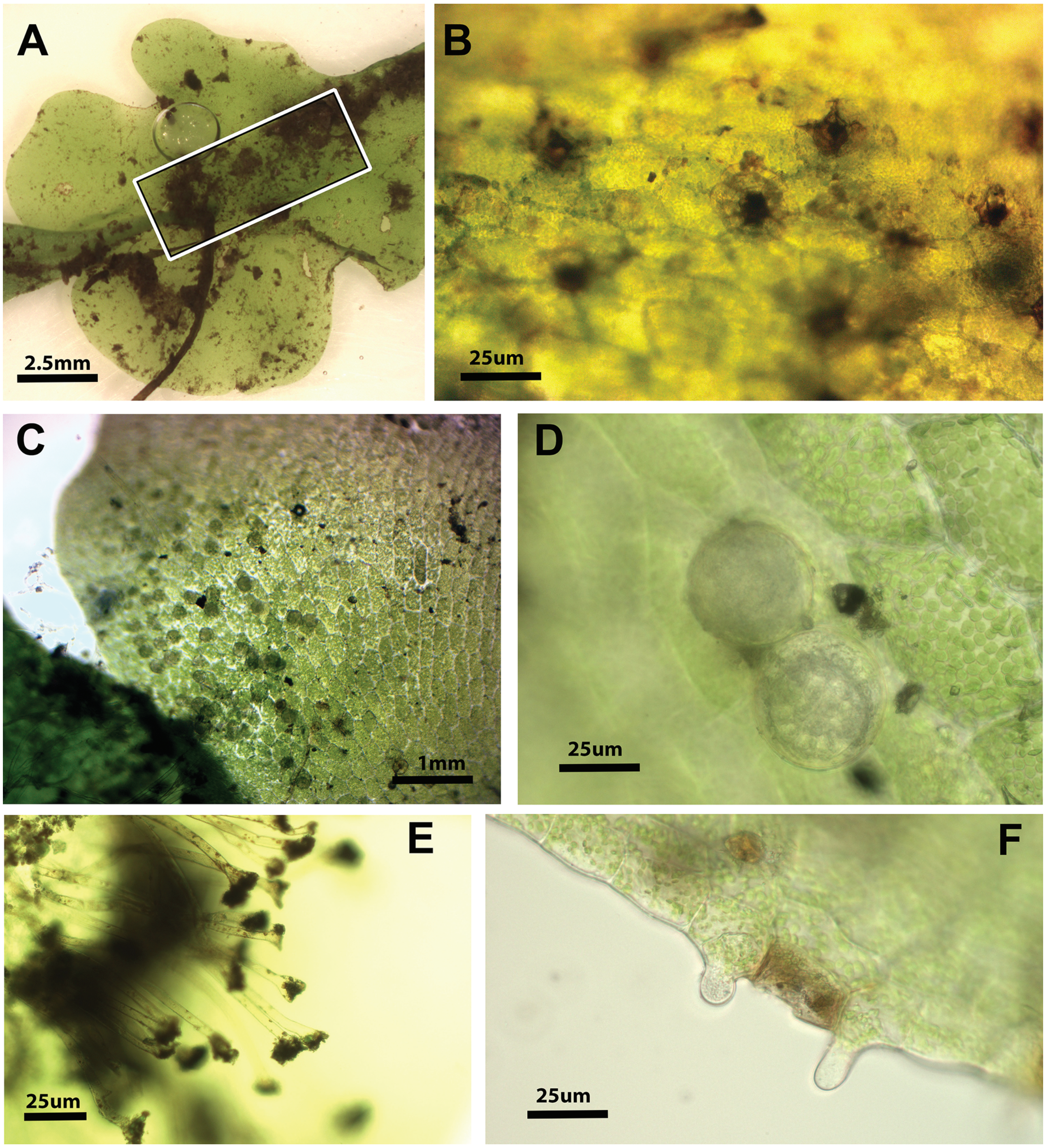

Fig. 8 Gametophytes of *Lomariopsis vestita*. *A*, Central cushion bearing archegonia, within the white box. *B*, Archegonia with four rows of neck cells. *C*, Antheridia on ventral surface. *D*, Detail of antheridia. *E*, Rhizoids, apically branched, that were in contact with the substrate. *F*, Marginal rhizoid initials.

unable to determine the nature of these spots and found no reports of similar spots in the literature.

In many cases, the first several leaves still attached to the gametophytes had a terminal leaf notch similar to that of more mature fronds (fig. 5). The presence of this notch and anastomosed veins helped identify small leaves of this species.

Discussion

Gametophyte Comparisons

The gametophytes of *Dracoglossum* and *Lomariopsis* were indistinguishable morphologically. Both were elongate strap shaped, slightly thickened centrally, and notched apically with the meristem located in the notch. This corresponds to the type II morphology of Farrar et al. (2008). The gametophytes of only two species of *Lomariopsis* have been described previously: *L. lineata* (C. Presl) Holttum vel aff., and *L. spectabilis* (Kunze) Mett. Those of the former are ribbon shaped but differ by being highly branched and aquatic (Li et al. 2009). The gametophytes are sold in the aquarium trade. They never produce sporophytes, even after planting on soil (Li et al. 2009). An in situ photo of *L. spectabilis* gametophytes from Taiwan was shown by Li et al. (2009). The gametophytes appear identical to those of the three species we encountered in Costa Rica.

The main difference between *Dracoglossum* and *Lomariopsis* gametophytes was ecological, with those of *Dracoglossum* occurring on rocks and those of *Lomariopsis* on lower trunks. The same is true of the sporophytes, but the rhizomes of *Lomariopsis* produced long feeding roots from the lower portions of the rhizome to the soil; that is, *Lomariopsis* was hemiepiphytic (sensu Zotz 2016).

How do the gametophytes of *Dracoglossum* and *Lomariopsis* compare with the other genera in their family? Currently, three other genera are recognized in Lomariopsidaceae: *Cyclopeltis* J. Sm., *Dryopolystichum* Copel., and *Thysanosoria* A. Gepp (PPG1 2016; Chen et al. 2017). Only the gametophytes of *Cyclopeltis* have been previously described in detail (Rincón-Barón et al. 2008). The description is based on material grown from spores of the American tropical *C. semicordatum* (Sw.) J. Sm. (Rincón-Barón et al. 2008). Its gametophytes differ from those of *Dracoglossum* and *Lomariopsis* in two main respects. First, they are cordate-spathulate, not greatly elongate, or shelflike. Second, they are beset with capitate-glandular hairs on the surfaces and margins, not glabrous. Stokey (1960) mentioned abundant septate hairs for two paleotropical species of *Cyclopeltis* [*C. crenata* (Fée) C. Chr. and *C. presliana* Berk.], but she did not describe other morphological aspects of the gametophytes of these species. Thus, the gametophytes of *Dracoglossum* and *Lomariopsis* differ from those of *Cyclopeltis* by being strap shaped and glabrous.

Is the strap-shaped form and glabrous condition of the thalli derived or ancestral? *Cyclopeltis* and two closely related outgroup families to the Lomariopsidaceae, the Nephrolepidiaceae and the Tectariaceae, have cordate gametophytes and hairs (Nayar and Kaur 1971; Kaur and Devi 1976; Pérez-García and Mendoza-Ruiz 2005). Thus, outgroup comparison suggests that the strap-shaped form and glabrous surfaces in the gametophytes of *Dracoglossum* and *Lomariopsis* represent a derived condition. As such, they support the sister relationship of the two genera.

Additional evidence of the relationship between *Dracoglossum* and *Lomariopsis* is the shelflike habit of their gametophytes. This habit has been reported in other taxa, where it is believed to be a phototropic response to low light (Farrar 1978; Dassler and Farrar 1997). Thalli growing in low light frequently orient themselves perpendicular to the incoming light. This presents the broadest photosynthetic surface toward light to maximize light capture. Phototropism, however, might not be responsible for the shelflike behavior in *Dracoglossum* and *Lomariopsis* for two reasons. First, these genera commonly have mixed shelf and appressed thalli in the same apparent light environments. This would not be expected if phototropism were responsible for the shelflike orientation. Second, only gametophytes with the shelf form had gametangia (when found); the appressed forms lacked gametangia. This suggests that the gametophytes change upon sexual maturity from appressed to shelflike. Such a behavior does not occur in the close outgroup genera and families (Nayar and Kaur 1971; Rincón-Barón et al. 2008). Therefore, the shelflike habit apparently represents another synapomorphy that supports the sister relationship of *Dracoglossum* and *Lomariopsis*.

Possible antheridiogen system. One mystery is why antheridia were not observed in *Dracoglossum* and found only twice, both times at the La Selva Biological Station, in *Lomariopsis*. Deepening this mystery is that most sporophytes of *L. vestita* at La Selva are heterozygous—a clear indication of outcrossing (J. E. Watkins, R C. Moran, and D. Farrar, unpublished data) and thus the existence of antheridiate gametophytes. Also suggestive of frequent outcrossing is that *L. japurensis* and *L. vestita* hybridize to produce *L.* × *farrarii* R. C. Moran & J. E. Watkins (Moran and Watkins 2004), which is common at La Selva and currently known from at least 16 plants along the Sura Trail (J. E. Watkins and R C. Moran, personal observations). How does outcrossing occur if antheridate gametophytes are rare? Although neither *Dracoglossum* nor *Lomariopsis* has been tested for the presence of an antheridiogen system, *Cyclopeltis* and the closely related outgroup Nephrolepidiaceae are known to produce antheridiogens (Näf et al. 1975; Rincón-Barón et al. 2008). This suggests that antheridiogens are present in *Dracoglossum* and *Lomariopsis*, making the near lack of antheridiate thalli all the more of a puzzle.

Assuming that an antheridiogen system is present, two hypotheses might explain why male gametophytes are rare in *Dracoglossum* and *Lomariopsis*. First, male gametophytes induced by an antheridiogen system might have been present but very small and thus overlooked by us. As a result, we did not find antheridia. Second, the antheridiogen system of both genera does not affect the size and shape of the male gametophytes as it does in other ferns. The evidence for this is that the two male gametophytes of *Lomariopsis* observed at La Selva appeared normally shaped, not stunted or filamentous. They were morphologically indistinguishable from mature archegoniate gametophytes. This suggests that the antheridiogen system, if present, does not alter gametophyte form and morphology as it does in many other taxa (Schneller 2008). A problem with this hypothesis is that it does not account for the rarity of male gametophytes.

Granular Spots on Gametophytes

Unclear is the nature of the dark gray granular spots observed in the center of the outer cell walls of two gametophytes of *Dicranoglossum plantagineum* (fig. 6*G*, 6*H*). These spots might be bacterial colonies, but their regular placement in the center of each cell wall surface seems to contradict that idea. We were unable to identify the spots and found no reports of similar occurrences in the literature.

Purple Fiddleheads

As explained in the introduction, the sporophytes of *Dracoglossum* and *Lomariopsis* are dissimilar morphologically. During fieldwork, however, we noted one similarity not previously reported: purple petioles and rachises on the fiddleheads (fig. 9).

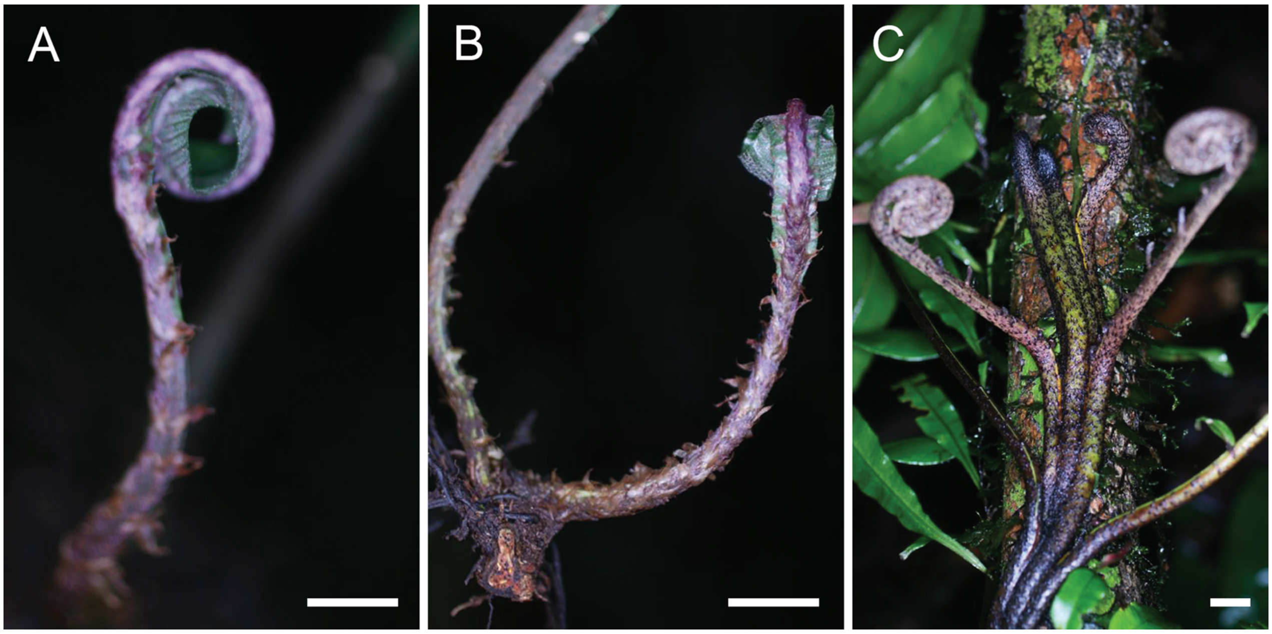

Fig. 9 Fiddleheads with purple rachises. *A*, *B*, *Dracoglossum plantagineum*. *C*, *Lomariopsis vestita*. Scale bars = 1 cm.

This character was not present in all individuals of the three species of *Lomariopsis*. Nevertheless, the ability of both genera to produce the color, even though inconsistently expressed in *Lomariopsis*, indicates a relationship. We do not know of any other eupolypod fern genus that produces similarly colored petioles and rachises in the fiddlehead stage. This is one character of the sporophyte that does support the sister relationship of the two genera.

Concluding Remarks

The use of gametophyte characters in fern classification remains in its infancy. This is largely because early work in the field was discouraged by Bower's remarks in the first volume of his monumental book, *The Ferns* (Bower 1923). He claimed that gametophyte characters were too limited and plastic to be useful in phylogenetic comparison. Nowadays, these views have changed considerably. Thanks to the pioneering work of Atkinson and Stokey (1964), Nayar and Kaur (1971), and others since, we have a greater appreciation of the utility of gametophytes in phyletic comparisons. Recently, studies of fern gametophytes have flourished (e.g., Perez Garcia and Riba 1998; Riba et al. 2000; Farrar et al. 2008), and comparative discussions of their results have often been incorporated into fern classification and systematics (e.g., Atkinson 1973; Pangua and Vega 1996; Nakazato and Gastony 2003). One wonders what Bower would have thought about our conclusions, namely, that in *Dracoglossum* and *Lomariopsis*, it is the gametophyte, not the sporophyte, that provides the main source of morphological evidence supporting the sister relationship as recovered by molecular phylogenetic studies.

Acknowledgments

Fieldwork for this study was done in Costa Rica during several courses that we cotaught of *Tropical Ferns and Lycophytes*, sponsored by the Organization for Tropical Studies (OTS). We thank OTS for making those courses possible. We also thank the Costa Rican government agencies SINAC (*Sistema Nacional de Áreas de Conservación*) and MINAE (*Ministerio de Ambiente y Energía*) for permission to study plants in Costa Rica in conjunction with our courses in 2015, 2017, and 2019. We are grateful for the insightful comments of Professor Donald R. Farrar and an anonymous reviewer on the manuscript.

Literature Cited

Atkinson LR 1973 The gametophyte and family relationships. Pages 73–90 *in* AC Jermy, JA Crabbe, BA Thomas, eds. The phylogeny and classification of ferns. Academic Press, New York.

Atkinson LR, AG Stokey 1964 Comparative morphology of the gametophytes of homosporous ferns. Phytomorphology 14:51–70.

Bower FO 1923 The ferns (Filicales) treated comparatively with a view to their natural classification, vol 1. Analytical examination of the criteria of comparison. Cambridge University Press, Cambridge.

Chen C, M Sundue, L Kuo, W Teng, Y Huang 2017 Phylogenetic analyses place the monotypic *Dryopolystichum* within Lomariopsidaceae. Phytokeys 78:83–107.

Christenhusz MJM 2007 *Dracoglossum*, a new Neotropical fern genus (Pteridophyta). Thaiszia 17:1–10.

Christenhusz MJM, M Jones, S Lehtonen 2013 Phylogenetic placement of the enigmatic fern genus *Dracoglossum*. Am Fern J 103:131–138.

Dassler CL, DR Farrar 1997 Significance of form in fern gametophytes: clonal, gemmiferous gametophytes of *Callistopteris baueriana* (Hymenophyllaceae). Int J Plant Sci 158:622–639.

Farrar DR 1978 Problems in the identity and origin of the Appalachian *Vittaria* gametophyte, a sporophyteless fern of the eastern United States. Am J Bot 65:1–12.

Farrar DR, C Dassler, JE Watkins Jr, C Skelton 2008 Gametophyte ecology. Pages 222–256 *in* TA Ranker, CH Haufler, eds. Biology and evolution of ferns and lycophytes. Cambridge University Press, Cambridge.

Holdridge L 1967 Life zone ecology. Tropical Science Center, San José, Costa Rica. 124 pp.

Kaur S, S Devi 1976 Prothallus morphology in some tectarioid ferns. Am Fern J 66:102–106.

Li FW, BC Tan, V Buchbender, RC Moran, G Rouhan, CN Wang, D Quandt 2009 Identifying a mysterious aquatic fern gametophyte. Plant Syst Evol 281:77–86.

Lloyd RM, EJ Klekowski 1970 Spore germination and viability in Pteridophyta: evolutionary significance of chlorophyllous spores. Biotropica 2:129–137.

McDade LA 1994 La Selva: ecology and natural history of a Neotropical rain forest. University of Chicago Press, Chicago.

Moran RC 2000 Monograph of the Neotropical species of *Lomariopsis* (Lomariopsidaceae). Brittonia 52:55–111.

Moran RC, JE Watkins 2004 *Lomariopsis* × *farrarii*, a new hybrid from Costa Rica between *L. japurensis* and *L. vestita* (Lompariopsidaceae). Brittonia 56:205–209.

Näf U, K Nakanishi, M Endo 1975 On the physiology and chemistry of fern antheridiogen. Bot Rev 41:315–359.

Nakazato T, GJ Gastony 2003 Molecular phylogenetics or *Anogramma* species and related genera (Pteridaceae: Taenitidoideae). Syst Bot 28:490–502.

Nayar BK, S Kaur 1971 Gametophytes of homosporous ferns. Bot Rev 37:295–396.

Pangua E, B Vega 1996 Comparative study of gametophyte development in *Consentinia* and *Anogramma* (Hemionitidaceae) and *Cheilanthes* (Sinopteridaceae). Pages 497–508 *in* JM Camus, M Gibby, RJ Johns, eds. Pteridology in perspective. Royal Botanic Gardens, Kew.

Pérez-García B, A Mendoza-Ruiz 2005 Comparative studies of the gametophytes of five New World species of *Tectaria* (Tectariaceae). Am Fern J 95:141–152.

Pérez-García B, R Riba 1998 Bibliografía sobre gametofitos de helechos y plantas afines, 1699–1996. Missouri Botanical Garden Press, St. Louis.

PPG (Pteridophyte Phylogeny Group) I 2016 A community-derived classification for extant lycophytes and ferns. J Syst Evol 54:563–603.

Riba R, B Pérez-García, A Mendoz, IR Jaramillo 2000 Morfología de gametofitos de helechos. Universidad Autónoma Metropolitana-Iztapalapa, Mexico City.

Rincón-Barón EJ, S Ortiz-Báez, N Rocha-Nuñez, M Mantilla-Martínez, O Torres-Montagut 2008 Fase sexual de *Cyclopeltis semicordata* (Lomariopsidaceae). Caldasia 30:289–299.

Rouhan G, J Garrison-Hanks, D McClelland, RC Moran 2007 Preliminary phylogenetic analysis of the fern genus *Lomariopsis* (Lomariopsidaceae). Brittonia 59:115–128.

Sawyer JO, AA Lindsey 1971 Vegetation of the life zones in Costa Rica. Indiana Academy of Science, Indianapolis.

Schneller J 2008 Antheridiogens. Pages 134–158 *in* TA Ranker, CH Haufler, eds. Biology and evolution of ferns and lycophytes. Cambridge University Press, Cambridge.

Stokey AG 1960 Multicellular and branched hairs on the fern gametophyte. Am Fern J 50:78–87.

Sundue M, A Vasco, RC Moran 2011 Cryptochlorophyllous spores in ferns: nongreen spores that contain chlorophyll. Int J Plant Sci 172:1110–1119.

Tryon AF, B Lugardon 1991 Spores of the Pteridophyta. Springer, New York.

Tryon RM, AF Tryon 1982 Ferns and allied plants with special reference to tropical America. Springer, New York.

Zhang L, E Schuettpelz, CJ Rothfels, X-M Zhou, X-F Gao, L-B Zhang 2016 Circumscription and phylogeny of the fern family Tectariaceae based on plastid and nuclear markers, with the description of two new genera: *Draconopteris* and *Malaifilix* (Tectariaceae). Taxon 65:723–738.

Zotz G 2013 “Hemiepiphyte”: a confusing term and its history. Ann Bot 111:1015–1020.

——— 2016 Plants on plants: the biology of vascular epiphytes. Springer, Berlin.