

Vascular System of the
Male and Female Florets
of *Raddia brasiliensis*
(Poaceae: Bambusoideae: Olyreae)

Thompson Demetrio Pizzolato



SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

1990

A B S T R A C T

Pizzolato, Thompson Demetrio. Vascular System of the Male and Female Florets of *Raddia brasiliensis* (Poaceae: Bambusoideae: Olyreae). *Smithsonian Contributions to Botany*, number 78, 32 pages, 23 figures, 1 table, 1990.—The components of the vascular systems in the male floret and the female floret of *Raddia* are described from reconstructed serial, transverse sections. Squat tracheary elements, sieve elements, and intermediary cells comprise the systems. The male floret has six and the female floret three collateral bundles in the rachilla at the floret base that become interconnected into a lower sieve-element plexus with accompanying tracheary elements. Besides contributing to the lower plexus, the rachilla bundles serve as the traces for the lemma and palea. That bundle (bundle 3) which is the trace for the lemma median contributes most of the sieve and tracheary elements to the lower plexus. Supernumerary bundles are associated with bundle 3. Rising in the rachilla from the lower plexus is the upper plexus of sieve and tracheary elements. The circular form of the upper plexus of the male floret is influenced by the two traces from each of the anterior lodicules and by each trace from the three stamens. The trace from the posterior lodicule of the male and female florets does not influence the upper plexus. The bi-arcuate form of the upper plexus of the female floret is influenced by the two, more posterior traces from the anterior lodicules. The three staminodia in the female floret do not influence the upper plexus because they are avascular. At the pistil base is a massive amphicribal bundle, the pistil plexus, that sends down vascular prongs and lobes to merge with the upper and lower plexi. Two posterolateral (stylar) collateral bundles merge with the pistil plexus in a gynobasic manner. A placental bundle ascends from the posterior of the pistil plexus, merges with the chalaza, and exceeds the tip of the ovule before ending in a stylar core. Components of the floret vascular system of *Raddia* confirm the Olyreae as a tribe of the Bambusoideae that should not be placed in the subfamilies Festucoideae, Oryzoideae, or Panicoideae.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: Leaf clearing from the katsura tree *Cercidiphyllum japonicum* Siebold and Zuccarini.

Library of Congress Cataloging-in-Publication Data

Pizzolato, Thompson Demetrio

Vascular system of the male and female florets of *Raddia brasiliensis* (Poaceae: Bambusoideae: Olyreae) / Thompson Demetrio Pizzolato.

p. cm.—(Smithsonian contributions to botany ; no. 78)

Includes bibliographical references.

Supt. of Docs. no.: SI 1.29:78

1. *Raddia Brasiliensis*. 2. Flowers. 3. Vascular system of plants. I. Title. II. Series.

QK1.S2747 no. 78 [QK492.G74] 581 s-dc20 [584'.93] 90-10223

Contents

	<i>Page</i>
Introduction	1
Materials and Methods	7
Acknowledgments	7
Vascular Morphology of the Male Floret	7
Vascular Anatomy of the Male Floret	9
Vascular Morphology of the Female Floret	12
Vascular Anatomy of the Female Floret	14
Comparative and Phylogenetic Considerations	19
Components of the Floret Vascular System of <i>Raddia</i> Are Compared to Those Known in the Festucoideae and Oryzoideae	19
Floret Vascular Anatomy Suggests that <i>Raddia</i> Belongs to the Olyreae of the Bambusoideae	24
Floret Vascular Anatomy Suggests that <i>Raddia</i> and the Olyreae Are Not Panicoid Grasses	27
Floret Vascular Anatomy Suggests that <i>Brachyelytrum</i> Is Not an Olyroid Grass	29
Floret Vascular Anatomy Suggests that <i>Raddia</i> and the Olyreae Are Not Oryzoid Grasses	29
Literature Cited	31

Vascular System of the Male and Female Florets of *Raddia brasiliensis* (Poaceae: Bambusoideae: Olyreae)

Thompson Demetrio Pizzolato

Introduction

Early anatomists investigating the florets of grasses such as Arber (1934), Belk (1939), Chandra (1962), and Butzin (1965) were compelled by the lack of techniques to treat the vasculature of the floret axis as if it were a homogenous mass of tissue whose only variation was the number of branches or traces it sent into the appendages of the floret. However, techniques of light microscopy such as glutaraldehyde fixation, plastic embedding, and thin sectioning (not available to earlier workers) suggested to Zee and O'Brien (1970) that the vascular tissue of the grass floret, instead of being homogeneous, contained organized and discrete components with generic constancy or variability. The analyses of serial cross sections by Zimmermann and Tomlinson (1972) and Larson (1975) revealing three-dimensional vascular organization in large stems of other angiosperms indicated further that these newer techniques similarly should reveal the systems in the compact stems of grass florets. Zimmermann and Tomlinson (1972), Larson (1975), and Hitch and Sharman (1968, 1971) in their studies of the vegetative stems of grasses, also demonstrated that the components of a mature three-dimensional vascular system are delimited best after a developmental study shows how the components of the system are blended together. Aided by such techniques and ideas, a few anatomists have begun studying anew the vasculature of the grass floret at anthesis.

One or more florets are arranged distichously on the axis or rachilla of the spikelet, the basic unit of the grass inflorescence (Gould and Shaw, 1983). The floret consists of two alternate bracts, the proximal lemma and the distal palea, and the flower they subtend. The grass flower usually consists of two scales or

lodicules subtending a few stamens and a pistil. Because the axis of the floret is a continuation of the rachilla of the spikelet, the axis in the floret is designated the rachilla also (Robinson-Beers and Pizzolato, 1987a).

Means of studying the vascular system of a floret rachilla involve tracing with the aid of a microscope drawing tube the various vascular tissues from serial cross sections, transferring the tracings to plastic sheets, and reconstructing the various systems into a three-dimensional model or facsimile by superimposing the vascular tracings (Pizzolato, 1983, 1984, 1988; O'Brien et al., 1985). The components of the vascular systems are discerned through study of the facsimiles. Comparisons among the various rachillae continue and more features are revealed as more models are generated and studied. If there is interest in using the revealed components of the vascular systems to test phylogenetic relationships as French and Tomlinson (1983) have done concerning stems of the Araceae, natural systems of grass classification are found in the works of Soderstrom and Ellis (1987), Watson et al. (1985), Macfarlane and Watson (1982), and Hilu and Wright (1982).

The system of Hilu and Wright (1982) recognizes a large subfamily, the Festucoideae, to include genera previously assigned to triticoid, agrostoid, festucoid, avenoid, and phalaroid groups. In this discussion, festucoid and Festucoideae are used in the sense of Hilu and Wright (1982). Four of the festucoid genera analyzed for the floret vascular system are closely related according to their scheme: *Anthoxanthum* L., 1753, (Pizzolato, 1984; Pizzolato and Robinson-Beers, 1987; Robinson-Beers and Pizzolato, 1987a, b, c) *Alopecurus* L., 1753, (Pizzolato, 1987), *Phleum* L., 1753, (Pizzolato, 1988), and *Phalaris* L., 1753, (Pizzolato, 1989a). *Triticum* L., 1753, (Zee and O'Brien, 1970; O'Brien et al., 1985) is related more distantly to these four. *Leersia* Swartz, 1788, (Pizzolato, 1989b), which is placed into a distinct subfamily, the Oryzoideae, by Hilu and Wright (1982) is the least related of

Thompson Demetrio Pizzolato, Delaware Agricultural Experiment Station, Department of Plant and Soil Sciences, College of Agricultural Sciences, University of Delaware, Newark, Delaware 19717-1303.

the five genera sufficiently studied. Only one species of each of these six genera has been analyzed, so the systematic value of any component of the vascular system hardly can be appreciated. However, even this survey indicates that some components of the vascular system are more constant across the genera than others.

Before the components of the vascular system are enumerated, the tissues composing the vascular system are described primarily from the observations of *Triticum* (Zee and O'Brien, 1970; O'Brien et al., 1985) and *Anthoxanthum* (Pizzolato, 1984; Robinson-Beers and Pizzolato, 1987a, b, c; Frick and Pizzolato, 1987), which agree with the observations in the other genera studied. The sieve elements are enucleate at maturity and in every way normal except that they tend to be shorter and narrower than those in stems. Callosed pores often are clustered into sieve areas on walls serving as sieve plates, and sieve tubes composed of sieve-tube members are found. However, because sieve areas on sieve plates are not seen always, the less precise term "sieve element" (Esau, 1977) safely describes the conducting cell of the phloem.

Two kinds of tracheary elements occur. The normal ones are usually squat with scalariform secondary thickenings on cells devoid of contents at maturity. Simple perforations frequently are difficult to identify positively. Therefore, the less precise term tracheary element is preferable to vessel member to describe the normal conducting cells of the xylem (Esau, 1977). The abnormal conducting cells of the xylem of the floret are known as the cells of the xylem discontinuity (Zee and O'Brien, 1970; Pizzolato, 1984; Robinson-Beers and Pizzolato, 1987a, b, c; Frick and Pizzolato, 1987). At maturity, the cells comprising the xylem discontinuity resemble the normal tracheary elements except that their secondary walls often are thicker and their protoplasts are persistent; thus, these cells are likely poor conductors of sap (Zee and O'Brien, 1970; Frick and Pizzolato, 1987).

The tracheary elements and sieve elements are contained in a matrix of vascular parenchyma cells extending from the rachilla at the base of the floret into the ovule. The cells of the vascular parenchyma are densely cytoplasmic and, by anthesis, their primary walls usually lack ingrowths. Hence, these cells are intermediary cells (Esau, 1977). When the intermediary cells are adjacent to sieve or tracheary elements and have developed from the same mother cell, such intermediary cells also serve as companion cells or contact cells (Esau, 1977). The vascular parenchyma cells, sieve elements, and tracheary elements comprising the floret vascular system is a compact tissue with little intercellular space.

Before discussing the patterns in which the sieve elements and tracheary elements are arranged to form the various components of the floret vascular system, it is appropriate to mention the developmental principles underlying the formation of the segments of the vascular system. The vascular system in the vegetative shoot is initiated as isolated procambia that are the incipient traces for nearby leaf primordia. Those isolated procambial sites destined to become major traces are initiated

earlier in the stem and lower from their primordium; procambium to become lesser traces is initiated isolated later and closer to its primordium or even in it (Hitch and Sharman, 1968; Patrick, 1972). The vascular system in the rachilla is initiated similarly (Maze et al., 1971, 1972; Pizzolato and Robinson-Beers, 1987). Upon this basic pattern of isolated procambia formed in relation to the primordia on the rachilla, all the complexity of the floret vascular system is built.

The isolated procambia that initiate the vascular system develop in meristematic tissues of the young rachilla. The meristematic tissue in which the procambial traces develop are residual meristems, tissues retaining their meristematic features beyond the apical meristem (Esau, 1953, 1977). The major procambial traces are initiated when most of the young rachilla is composed of residual meristem (Pizzolato and Robinson-Beers, 1987). During subsequent development of the rachilla, most of the residual meristem disappears as it contributes cells to the traces of the primordia and differentiates into ground parenchyma (Esau, 1977; Pizzolato and Robinson-Beers, 1987; Robinson-Beers and Pizzolato, 1987a, b). However, two cores of residual meristem persist longer in the floret. One of these cores develops directly from the apical meristem of the developing floret as it becomes converted into the ovule primordium (Maze et al., 1971, 1972; Robinson-Beers and Pizzolato, 1987c). From this core of residual meristem will develop the several components of the vascular system related to the pistil. The second core of residual meristem persists lower in the rachilla, between the developing procambial trace related to the lemma primordium and the higher traces related to the stamen primordia (Pizzolato and Robinson-Beers, 1987). Sieve elements, which differentiate acropetally in procambium that developed from this residual meristem, connect the lemma trace with the stamen traces and form another component of the floret vascular system, the upper sieve-element plexus (Robinson-Beers and Pizzolato, 1987a, b; Pizzolato and Robinson-Beers, 1987).

Two developmental principles underlying the formation of the vascular system have just been discussed: (1) its initiation in the residual meristem as isolated procambial traces related to the primordial appendages of the floret; and (2) the extended persistence of two cores of residual meristem, one in the pistil primordium, and the other lower, where it will connect the principal lemma trace with the stamen traces. A third developmental principle is that all of the initially isolated procambial segments in the rachilla of the floret will become more or less interconnected in an orderly pattern by the continued growth of the early procambial sites related to the traces and by the formation of procambium in the persistent cores of residual meristem. Vascular tissues will differentiate along these procambial paths.

There are a number of ways in which the procambia, and the vascular tissues differentiating from them, grow and interconnect in the rachilla. Isolated procambial traces grow acropetally toward the apex of their appendage and basipetally in the rachilla until they merge with strands of a lower component of

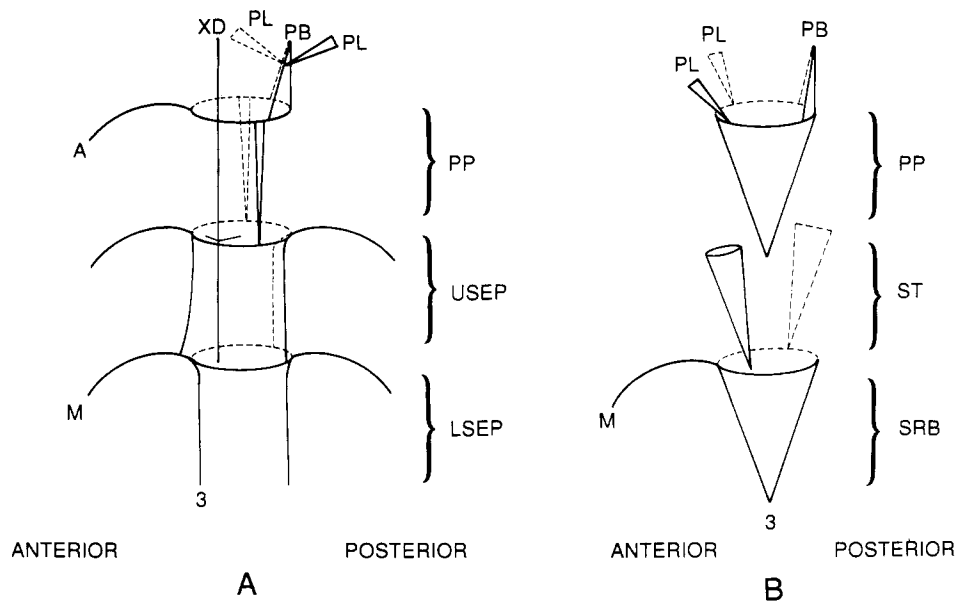


FIGURE 1.—Diagrams of major components of typical floret vascular systems. A. Festucoideae. At floret base one or several vascular bundles occur in the rachilla. These are traces to major veins of lemma and palea. The principal bundle is bundle 3, which is the trace for the lemma median (M). At the emergence of the bundles from rachilla to bracts, sieve elements from the bundles interconnect into the lower sieve-element plexus (LSEP). Sieve elements of the LSEP merge into the upper sieve-element plexus (USEP). Many of the sieve elements of the USEP come from the vicinity of M. Because the USEP is the vascular system of the stamens, it is bilobed with two stamens and trilobed with three. At the pistil base, below the ovule, is the pistil plexus (PP). It is connected by vascular bundles (prongs) to the USEP between the emergences of the stamen traces. If the USEP is bilobed, the pistil plexus connects with two prongs. If the USEP is trilobed, the pistil plexus connects with three. The anterior sieve tube (A) connects at the anterior of the pistil plexus. Only the sieve elements at the posterior of the pistil plexus ascend to contribute sieve elements to the placental bundle (PB), which develops between the attachments of the posterolateral sieve tubes (PL). The placental bundle supplies the ovule. The posterolaterals supply the styles. The xylem discontinuity (XD), a system of anomalous tracheary elements, replaces all normal tracheary elements above bundle 3. The xylem discontinuity complements the sieve elements in all other components except A and PL.

B. Oryzoideae. A xylem discontinuity does not occur; normal tracheary elements accompany all sieve elements. There is no lower sieve-element plexus because sieve and tracheary elements of the sole rachilla bundle (SRB) interconnect in becoming the median trace of the lemma (M). Hence, SRB is like bundle 3 in the Festucoideae. No upper sieve-element plexus occurs but only a system of stamen traces (ST), which weakly link horizontally before merging with the posterior of SRB. The pistil plexus (PP) connects weakly between the stamen traces by one vascular bundle (prong). The placental bundle (PB) is more narrow than that in the Festucoideae. The posterolaterals (PL) do not attach high at the PB but near the anterior of PP instead of an anterior bundle.

the system (Maze et al., 1971, 1972; Pizzolato and Robinson-Beers, 1987; Robinson-Beers and Pizzolato, 1987a, c). Horizontal interconnections or short circuits form between more axially arranged procambial strands by the differentiation of procambium from the intervening parenchyma or meristematic cells (Hitch and Sharman, 1971; Robinson-Beers and Pizzolato, 1987a). As the vascular tissues differentiate, they may shunt from one procambial strand through a procambial bridge to another procambial strand and use that strand for a further path of differentiation (Robinson-Beers and Pizzolato, 1987a). Interconnections can occur also as adjacent horizontal and vertical procambia increase in girth by converting surrounding parenchyma or meristematic cells into procambia, and thus grow together (Dengler et al., 1985; Robinson-Beers and

Pizzolato, 1987a). Vascular tissue differentiating in one of the strands can differentiate into the newly fused neighboring strand. This last means of interconnection is how one of the main components of many vascular systems, the lower sieve-element plexus, arises (Robinson-Beers and Pizzolato, 1987a).

Discussion of the developmental principles underlying the initiation and interconnection of the components of the floret vascular system is followed now by an introduction to the segments themselves. The components of the festucoid genera will be discussed first because they are more alike, and then they can be contrasted together with the components of oryzoid florets. Continual reference to the diagrams of the festucoid (Figure 1A) and oryzoid (Figure 1B) systems and to the figures

in the cited works will be helpful. The discussion begins with the number of vascular bundles in the rachilla at the base of the floret.

That bundle number is one to several. Three may be a frequent number (Arber, 1934; Pizzolato, 1984). The bundles are the basipetal portions of major traces for the lemma only or for the lemma and palea (Robinson-Beers and Pizzolato, 1987a; Pizzolato and Robinson-Beers, 1987; Pizzolato, 1987, 1988, 1989a). The solitary bundle or the principal bundle (bundle 3) is the basipetal portion of the median trace of the lemma (M). Bundle 3 is usually collateral with its tracheary elements between its sieve elements and the lemma; that is, the transverse axes of the xylem and the phloem in bundle 3 are perpendicular to the lemma. Some of the other bundles are composite bundles of two fused lemma or palea traces.

The significance to the vascular system of more than one bundle in the rachilla is that sieve elements from these separate bundles horizontally link higher in the rachilla forming the segment designated the lower sieve-element plexus. Therefore *Anthoxanthum*, *Phleum*, *Phalaris*, and *Triticum* have the lower sieve-element plexus in the rachilla above the separate rachilla bundles, but *Alopecurus* with one rachilla bundle does not (Pizzolato, 1984, 1987, 1988, 1989a; Robinson-Beers and Pizzolato, 1987a; O'Brien et al., 1985). The lower sieve-element plexus is a peripheral, horizontal network of sieve elements interconnecting the axial rachilla bundles as they bend toward the lemma and palea or toward the lemma alone to become the major traces of these appendages. As bundle 3 turns into the lemma median, it always extensively contributes sieve elements to the lower sieve-element plexus.

Higher in the rachilla, above the divergence of the lemma and palea traces, another sieve-element plexus occurs, the upper sieve-element plexus. The lower sieve-element plexus (or phloem from the solitary rachilla bundle of *Alopecurus*) merges in various patterns into the upper sieve-element plexus (Pizzolato, 1984, 1987, 1988, 1989a). The upper sieve-element plexus first serves as the phloem system of the stamens in the rachilla. Because it forms under the influence of the stamens (Pizzolato and Robinson-Beers, 1987; Robinson-Beers and Pizzolato, 1987b) from a residual meristem in the internode between the stamen insertions and the median trace to the lemma (M), the upper sieve-element plexus is a hollow, vasselike, bi- or trilobed network of sieve elements arising from the vicinity of M (Pizzolato, 1984, 1987, 1988, 1989a). When O'Brien et al. (1985) recognized this component of the floret vascular system in *Triticum*, they did not realize its initial function as the vascular system for the stamens. After anthesis the upper sieve-element plexus is the link between the lower sieve-element plexus and the next higher segment of the floret vascular system, the pistil plexus.

The pistil plexus is a horizontal ring of interconnected sieve elements at the base of the pistil (O'Brien et al., 1985; Robinson-Beers and Pizzolato, 1987c; Pizzolato, 1987, 1988, 1989a). All components of the floret vascular system related to

the pistil develop from procambium differentiating in a residual meristem persisting from the apical meristem (Holt, 1954; Sharman, 1960a, b; Maze et al., 1971, 1972; Robinson-Beers and Pizzolato, 1987c). The pistil plexus is connected to the upper rim of the upper sieve-element plexus by basipetally differentiating vascular bundles in the form of prongs that merge with the upper sieve-element plexus between the sites where the stamen traces diverge (Robinson-Beers and Pizzolato, 1987c). Therefore, a bistaminate upper plexus is linked to the pistil plexus by two prongs, and a tristaminate one by three prongs (Pizzolato, 1984, 1987, 1988, 1989a). At the anterior (the lemma side) of the pistil plexus, a single sieve tube develops and supplies the anterior of the pistil (Robinson-Beers and Pizzolato, 1987c). This sieve tube is recognized as a component of the floret vascular system, the anterior sieve tube (Aziz, 1978, 1981; Pizzolato, 1984, 1987, 1988, 1989a; Lingle and Chevalier, 1985). Because they did not recognize its segments, O'Brien et al. (1985) designated the continuum of lower sieve-element plexus, upper sieve-element plexus, and pistil plexus as a unit, or "phloem annulus."

The sieve elements at the posterior of the pistil plexus merge into the next component of the floret vascular system, the placental bundle. The placental bundle is the last segment of the floret vascular system to differentiate (Aziz, 1972, 1978, 1981; Lingle and Chevalier, 1985; Robinson-Beers and Pizzolato, 1987c). The sieve elements of the placental bundle differentiate in the posterior of the ovary between the sieve elements coming from the styles, the posterolaterals. The sieve elements of the placental bundle become united with the posterolaterals and the sieve elements in the posterior of the pistil plexus (Robinson-Beers and Pizzolato, 1987c). Rising from the pistil plexus, the sieve elements of the placental bundle fan out in the posterior of the pistil, diminish, and at anthesis, end about the base of the chalaza. The chalaza is that region of the ovule where its cells are continuous from the embryo sac to the posterior of the ovary without intervening epidermises of nucellus, inner integument, outer integument, and inner posterior ovary wall (Pizzolato, 1984). The placenta has a higher and broader area, includes the chalaza, and is the region of contact between the young seed and the inner posterior ovary wall.

Besides the sieve elements and the cells of the xylem discontinuity, the placental bundle has an abundance of intermediary cells continuous with those in the lower components. In the distal regions of the placental bundle, most of the intermediary cells are located horizontally between the ovule and diminishing sieve elements of the placental bundle (Pizzolato, 1984, 1987, 1988, 1989a). The intermediary cells continue distally beyond their associated sieve elements to blend with those at the chalazal end of the nucellus. Hence, by means of its intermediary cells, as the placental bundle ascends and departs the posterior ovary wall, it terminates by blending with the nucellus of the young seed (Pizzolato, 1984, 1987, 1988, 1989a). The distalmost intermediary cells of the placental bundle end in the chalaza by merging with the intermediary

cells of the nucellus because the placental bundle and nucellus, both in continuity, originate from the residual meristem that persists in the tip of the floret from the apical meristem (Robinson-Beers and Pizzolato, 1987c).

The most distal component of the floret vascular system is made of the sieve elements in or near each of the two styles, the posterolaterals. The attachments of the posterolaterals to the flanks of the placental bundle set a convenient, albeit imprecise, proximal limit to the placental bundle of festucoid grasses (Pizzolato, 1988, 1989a). The sieve elements of the posterolaterals mature before those of the placental bundle when they originate in isolation near the styles and differentiate basipetally (Aziz, 1978, 1981) toward the posterior of the pistil plexus.

Until now the phloem of the components of the floret vascular system has been discussed. The tracheary elements in the floret vascular system are of two types. The vascular bundles in the rachilla at the base of the floret contain normal tracheary elements. These do not continue up the rachilla beyond the lower sieve-element plexus because they leave the rachilla as they enter the lemma and palea traces (Pizzolato, 1984, 1987, 1988, 1989a). Just above the entrance of the median trace into the lemma from the rachilla, all normal tracheary elements in the rachilla are superseded by the abnormal tracheary elements of the xylem discontinuity. The base of the xylem discontinuity occurs in the rachilla in continuity with a few normal tracheary elements that continue in the rachilla for a few micrometers above the emergence of the lemma median; the xylem discontinuity now occurs instead of a system of normal tracheary elements. In other words, the xylem discontinuity begins in the rachilla immediately above the median lemma trace at the level where the lower sieve-element plexus is beginning to merge with the upper sieve-element plexus (Pizzolato, 1984, 1987, 1988, 1989a). The xylem discontinuity is thus surrounded by these peripheral sieve-element networks. Intermediary cells constitute the matrix of these three components. The xylem discontinuity at this level is differentiated from procambium developing from the core of residual meristem persisting in the rachilla above the emergence of M; this is the same core from which differentiated the upper sieve-element plexus (Robinson-Beers and Pizzolato, 1987b; Pizzolato and Robinson-Beers, 1987).

The xylem discontinuity is restricted to the center of the rachilla below the exits of the stamen traces from the upper sieve-element plexus into the stamens. At the level of the two or three stamen traces, the cells of the xylem discontinuity follow the phloem into the traces (Pizzolato, 1984, 1987, 1988, 1989a). However, the rachilla is not devoid of the xylem discontinuity above the exit of the stamen traces. The xylem discontinuity now occurs as the xylem complement of those two or three prongs of vascular tissues that develop from the pistil plexus and merge basipetally with the upper sieve-element plexus between its emerging stamen traces (Pizzolato,

1984, 1987, 1988, 1989a; Robinson-Beers and Pizzolato, 1987b).

The cells of the xylem discontinuity ascend from within the upper sieve-element plexus into each prong and then into the area within the enveloping sieve elements of the pistil plexus at the base of the pistil (Robinson-Beers and Pizzolato, 1987c; Pizzolato, 1984, 1987, 1988, 1989a). Surrounded by the pistil plexus, the xylem-discontinuity cells from the prongs coalesce toward the posterior of the pistil plexus. As the tracheary elements of the xylem discontinuity rise farther, they fan out in the same pattern as the sieve elements rising from the posterior of the pistil plexus. Therefore, the placental bundle comes to consist of an arc of the tracheary elements of the xylem discontinuity to the anterior of an arc of normal sieve elements in a matrix of intermediary cells. With farther ascent toward the base of the chalaza, the xylem discontinuity of the placental bundle diminishes and usually ends more proximally than its sieve elements. Although the xylem discontinuity becomes a part of the traces to the stamens, it does not enter the anterior bundle or the posterolateral first of the pistil. Although the component was designated first with the preferred "xylem discontinuity" by Zee and O'Brien (1970:789), it has more recently been designated "xylem block" in *Triticum* by O'Brien et al. (1985:507).

Although the above description summarizes the major components of the floret vascular system in the sampled festucoid species, a few minor components remain to be discussed. They are designated as minor because they do not appear to influence the formation of the other components (Pizzolato, 1989a). These minor components include the lesser traces for the lemma and palea and the trace system from the lodicules. Lodicule traces apparently differentiate from the lodicule into the rachilla and connect with the rest of the floret vascular system at the anterior of the lower sieve-element plexus (Pizzolato, 1989a). Although each lodicule often has only one trace, which lacks xylem, some genera differ in both features (Pissarek, 1971; Craig and O'Brien, 1975; Pizzolato, 1989a). Last are the short anterolateral sieve tubes that in a few genera connect to each flank of the placental bundle more proximally than the posterolaterals (Belk, 1939; Chandra, 1963; Pizzolato, 1989a).

Although there are generic variations among the floret vascular systems of the festucoid grasses, they share seven major components that have common ontogenies: (1) a lower sieve-element plexus joining multiple bundles in the rachilla at the base of the floret, (2) an upper sieve-element plexus related to the stamens, (3) a pistil plexus connected by prongs to the upper sieve-element plexus, (4) a sieve tube at the anterior of the pistil plexus, (5) a placental bundle rising from the posterior of the pistil plexus, (6) posterolaterals from the styles delimiting the placental bundle, and (7) a xylem discontinuity complementing all these components but the anterior and posterolateral bundles.

If these festucoid components are sought in the oryzoid

grasses *Leersia* (Belk, 1939; Pizzolato, 1989b) and *Oryza* L., 1753, (Zee, 1972; Kawahara et al., 1977), distinctions between the groups appear so striking that they favor more study to reveal the principal distinctions among the other great clusters of grasses. Therefore, the components of the vascular system, primarily of the floret of *Leersia* (Pizzolato, 1989b), will be enumerated and contrasted with those in the festucoid vascular system (Figure 1).

Leersia lacks a lower sieve-element plexus (Pizzolato, 1989b). Of the festucoid species analyzed, only *Alopecurus* (Pizzolato, 1987) agrees with *Leersia* in this regard. The reason is that *Leersia* and *Alopecurus* have only the rachilla bundle related to the median trace of the lemma in the floret base, thus avoiding the need as in other genera to link sieve elements from discrete bundles before farther ascent in the rachilla.

The arrangement of xylem and phloem in the rachilla bundle related to the lemma median at the floret base (bundle 3) also differs between the subfamilies. In the festucoids except *Alopecurus*, bundle 3 is collateral with xylem between the phloem and the lemma; that is, the vascular tissues are perpendicular to the floret's anterior-posterior plane (Pizzolato, 1984, 1988, 1989a). Bundle 3 is bicollateral in *Alopecurus* with phloem-xylem-phloem arranged parallel at the floret base to the anterior-posterior plane (Pizzolato, 1987). *Leersia* (Pizzolato, 1989b) and apparently the oryzoid *Luziola* (Arber, 1928) differ from the festucoid group. In the rachilla at the floret base, the oryzoids have a single collateral bundle whose phloem and xylem parallel the floret's anterior-posterior plane, and whose phloem envelops the xylem during ascent in the rachilla (Pizzolato, 1989b). In the other features to be discussed, *Alopecurus* is decidedly festucoid.

The festucoid grasses have an upper sieve-element plexus. Instead, *Leersia* has a stamen-trace system that is nearly independent of the rest of its floret vascular system (Pizzolato, 1989b). Upon entering the rachilla, the stamen traces descend its flanks with few horizontal interconnections between them. Their descent continues until they merge separately with the posterior of the solitary rachilla bundle, which blocks further descent. Compared to the upper sieve-element plexus of the festucoid grasses, the stamen traces of *Leersia* comprise a less integrated component in the floret vascular system (Pizzolato, 1989b). This tendency for the stamen traces to be more autonomous in the oryzoid grasses than in the festucoid grasses aids in understanding the variability of stamen number that is peculiar to rices (Hilu and Wright, 1982; Watson et al., 1985; Tucker, 1988).

Festucoid genera have a xylem discontinuity. Oryzoid genera lack one. Zee and O'Brien (1970) and Zee (1972) made these discoveries, and Pizzolato (1989b) has confirmed them. Only normal tracheary elements accompany each and all of the phloem components in the Oryzoideae.

Although the Oryzoideae and Festucoideae of Hilu and Wright (1982) are alike in having a pistil plexus, the plexus from each group is different in the number of vascular prongs

descending from it, and in the nature of the connection that the prongs make with the proximal segments. Two or three prongs of vascular tissue descend from the festucoid pistil plexus to merge, between the emerging stamen traces, with the sieve elements of the upper sieve-element plexus and the associated tracheary elements of the xylem discontinuity (Robinson-Beers and Pizzolato, 1987c; Pizzolato, 1987, 1988, 1989a). The single vascular bundle descending from the oryzoid pistil plexus cannot merge with an upper sieve-element plexus and, instead, inserts itself into the area circumscribed by the entering stamen traces and their tenuous, horizontal interconnections (Pizzolato, 1989b). The realization of this apparently less intimate connection correlates well with the experiments of Zee (1972) and Kawahara et al. (1977) showing that dyes introduced into the rachilla of *Oryza* move with difficulty into the pistil compared to movement into the lemma, despite the absence of a xylem discontinuity. On the other hand, despite the intimate interconnection between the festucoid pistil plexus and the upper sieve-element plexus, the xylem discontinuity prevents passage of sap through the xylem from the rachilla to pistil in *Anthoxanthum* (Frick and Pizzolato, 1987) and *Triticum* (Zee and O'Brien, 1970). As with the stamen components, the pistil components of the oryzoid grasses appear to be more nearly distinct in comparison with these components in the festucoid grasses.

The festucoid and oryzoid grasses of Hilu and Wright (1982) are alike in that the posterior of the pistil plexus merges into the placental bundle that merges and ends in the nucellus at the chalaza (Pizzolato, 1989b). However, the oryzoid placental bundle lacks the xylem discontinuity, is narrower than the festucoid placental bundle, and matures more slowly (Pizzolato, 1989b). A more significant distinction between the placental bundles involves the sites of attachment of the posterolaterals from the styles. In festucoid genera the posterolaterals merge with the rest of the floret system, high and posteriorly, at the placental bundle (Robinson-Beers and Pizzolato, 1987c; Pizzolato, 1987, 1988, 1989a). In oryzoid genera the posterolaterals merge, low and anteriorly, at the pistil plexus below the ovule (Belk, 1939; Kawahara et al., 1977; Pizzolato, 1989b). Pizzolato (1989b:600) called this type of posterolateral attachment "gynobasic." Apparently, the oryzoid tendency to keep its components somewhat distinct favors a longer independent basipetal course of differentiation before merger into the rest of the floret system.

Composition of the posterolaterals also varies between the groups: oryzoid posterolaterals contain both tracheary elements and sieve elements; festucoid genera contain only sieve elements in their posterolaterals (Pizzolato, 1989b). Related to the attachment of the posterolaterals near the anterior of the pistil plexus in the oryzoid grasses is another distinction between the subfamilies. Oryzoids lack an anterior bundle but festucoids have an anterior sieve tube attached at the anterior of the pistil plexus (Aziz, 1981; Lingle and Chevalier, 1985; Pizzolato, 1984, 1987, 1988, 1989a, b). A last readily apparent

distinction between the groups concerns one of the minor components, the lodicule traces. Because *Leersia* lacks a lower sieve-element plexus, the lodicule traces merge instead at the anterior and flanks of the descending stamen traces (Pizzolato, 1989b). Most festucoid grasses with lodicules have one trace per lodicule with only a phloem component (Pissarek, 1971; Pizzolato, 1988, 1989a). *Oryza* (Pissarek, 1971) and *Leersia* (Pizzolato, 1989b), however, have two traces per lodicule with tracheary elements as well as sieve elements.

Similarities within the Festucoideae and Oryzoideae of Hilu and Wright (1982) and the distinctions noted between them are a stimulus to continue looking for those characters of the floret vascular system that will reveal the natural system of classification. Components of the floret vascular system are "not intrinsic" to any of the current or older system of classification and, thus, should be valuable "external evidence" to check and improve the classification systems being developed (Macfarlane and Watson, 1982).

Now that some of the components of the floret vascular system are known to distinguish between genera of subfamilies unanimously recognized as distinct, a more controversial distinction might be attempted. The relative affinities of the Oryzoideae and the Bambusoideae are unsettled. Based on a synopsis of all readily available characters, Watson et al. (1985) and Tucker (1988) consider the Oryzoideae and Bambusoideae to be related much more closely to each other than to the Festucoideae, whereas, with nearly similar characters, Hilu and Wright (1982) consider the Oryzoideae more closely related to the Festucoideae than to the Bambusoideae. The Olyreae is a tribe of herbaceous Bambusoideae with uniflowered, unisexual spikelets (Soderstrom and Ellis, 1987) superficially similar to the spikelets in the Oryzoideae and Festucoideae, and, therefore, containing genera suitable for comparative anatomical studies. Living specimens of *Raddia* Bertoloni, 1819, of the Olyreae (Soderstrom and Zuloaga, 1985) enabled the continuation of the comparative, descriptive studies of the vascular anatomy of grass florets.

MATERIALS AND METHODS.—During anthesis in mid-November 1988, male and female spikelets with recently extruded stamens or stigmas were excised from their inflorescences on specimens of *Raddia brasiliensis* Bertoloni, 1819, originating from Rio de Janeiro, Brazil, and cultivated in the Smithsonian Institution Botany Department greenhouse. Vouchers prepared by E.J. Judziewicz (his no. 5417) were deposited in the United States National Herbarium (US). Preparation for microscopy and the construction of a plastic facsimile of the vascular system of one male floret and of one female floret was accomplished in a way previously detailed by Pizzolato (1983, 1988). Each spikelet is oriented in this way in the text and figures: anterior (left of page), posterior (right of page), right flank (top of page), left flank (bottom of page). The clusters of genera, festucoid, oryzoid, and bambusoid, are used in the sense of Hilu and Wright (1982) and Soderstrom and Ellis (1987).

ACKNOWLEDGMENTS.—Emmet Judziewicz suggested that this study be done and, in a generous and helpful manner, made the living specimens of *Raddia brasiliensis* from the Smithsonian greenhouse available to me for sampling. Eve Lucking photographed and printed the pictures of the plastic models. Barbara Broge and Karen Engeseth rendered the drawings. Siân Frick translated the study of Butzin (1965). Elaine Eiker typed the manuscript, which is published as Miscellaneous Paper No. 1295 of the Delaware Agricultural Experiment Station. My family was a source of encouragement during this study.

Vascular Morphology of the Male Floret

The male floret is not visibly subtended by glumes. However, subjacent to the base of the floret occurs a node with bumps that can be interpreted as one bearing aborted glumes (Figure 2, level -25). Above this region, the rachilla of the base of the floret contains six vascular bundles, in two rows of three on the anterior and posterior of the rachilla (Figure 2, level 5). The bundles are small except the middle one of the anterior row. At this level on the anterior occurs the lowest part of the lemma (Figure 2, level 5), but the lemma is not inserted on the rachilla until much higher (Figure 2, levels 185-245). At its insertion the lemma is pleated (Figure 2, level 245) so that the basal portion forms a pocket (Figure 2, levels 5-245). This pocket contained pollen grains. Below the traces to the lemma and palea, the six rachilla bundles appear to variously branch and merge during their ascent of the rachilla (Figure 2, levels 5-95). The first traces to become distinct are the lemma median and the two laterals (Figure 2, levels 95, 125). Higher, the median enters the insertion of the lemma (Figure 2, level 215) and continues up (Figure 2, level 245) then down and up the pocket formed by the central portion of the lemma (Figure 2, from level 245 back to level 35). The extreme lateral portions of the lemma, which are entered by the laterals at their insertions (Figure 2, levels 185, 215), do not descend like the middle; thus, the path of each lemma lateral trace is not tortuous like the path of the median trace. The two palea traces are discrete shortly above the appearance of the lemma traces (Figure 2, level 125) and ascend the rachilla to enter the palea near the flanks of its insertion on the rachilla (Figure 2, levels 155-341).

After the emergence of the lemma and palea traces, a large vascular bundle remains in the center of the rachilla or, synonymously at this level, the receptacle (Figure 2, levels 125, 155). The bundle appears to become hollow, then dissected, as the traces for the three lodicules and three stamens emerge (Figure 2, levels 185-275). Two traces enter each of the insertions of the anterior lodicules, but only one trace enters the smaller, posterior lodicule (Figure 2, levels 305, 341). Three traces remain around the center of the rachilla, and one apiece enters each of the three stamen insertions (Figure 2, levels 341, 380). There is no sign of an aborted pistil where the rachilla ends.

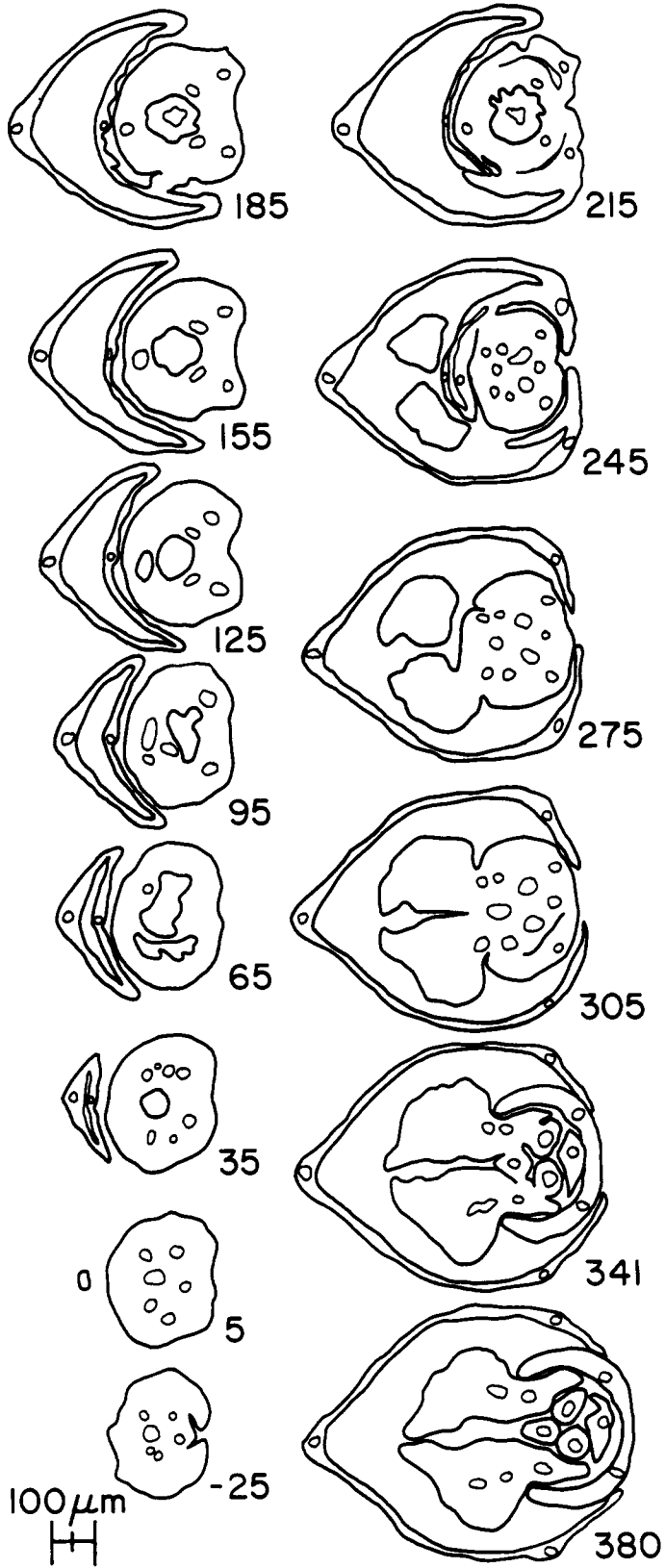


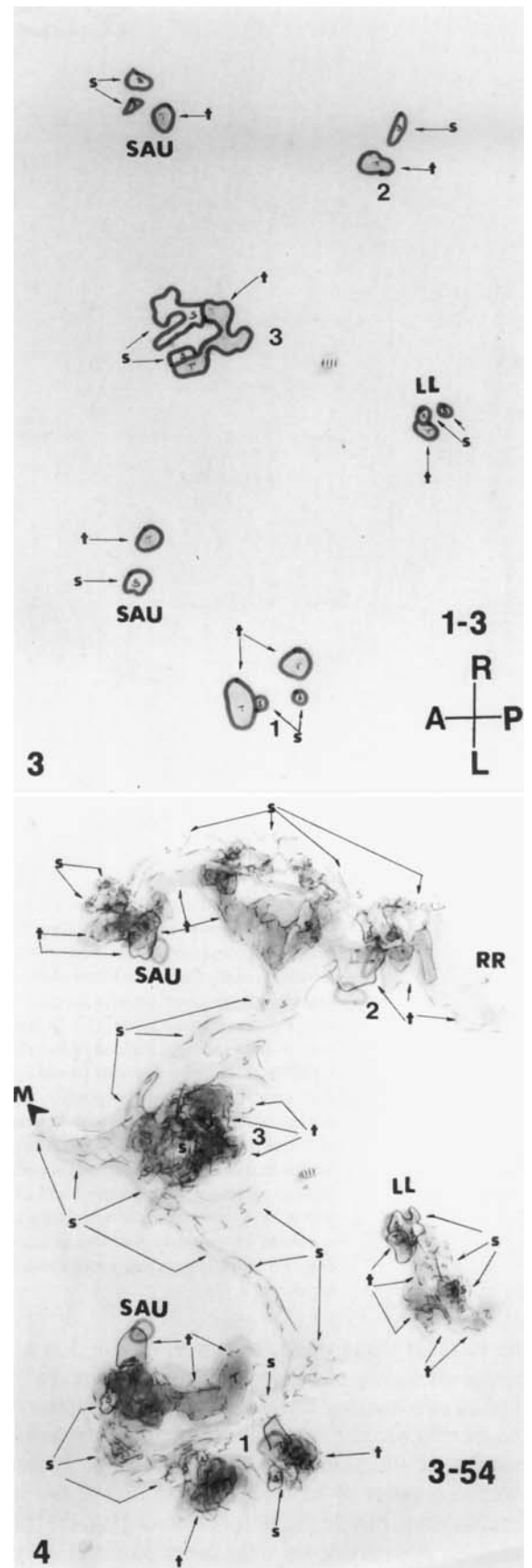
FIGURE 2 (left).—Tracings of serial transverse sections of the male floret arranged acropetally at intervals indicated in μm ($\times 55$). Left and right of page, respectively, is anterior and posterior of the floret. Top and bottom of page, respectively, is right and left of floret. Closed circular areas within the parts of the floret are vascular bundles including their intermediary cells. Level -25 is the rachilla below the floret base showing a node bearing the aborted glumes fully developed in the female floret of Figure 10. Level 5 is the rachilla at the floret base. The large anterior bundle is bundle 3. The posterior, flanking bundles are bundle 1 (left) and 2 (right). The segment anterior to the rachilla is the lowest part of the lemma. Levels 35 to 275 show that the middle of the lemma is a pleated pocket, which bundle 3 traverses after entering between levels 275 and 245 after ascending the rachilla from level 5. Bundles 1 and 2 are, respectively, the left and right laterals of the lemma. The palea traces are apparent in the posterior of the rachilla by level 95 but do not occur in the palea until between levels 305 and 341. Two traces for each of the anterior lodicules and the sole trace for the posterior lodicule appear about level 245. The three traces remaining in the center of the rachilla by level 275 are the traces of the stamens which are distinct from the rachilla by level 380.

Vascular Anatomy of the Male Floret

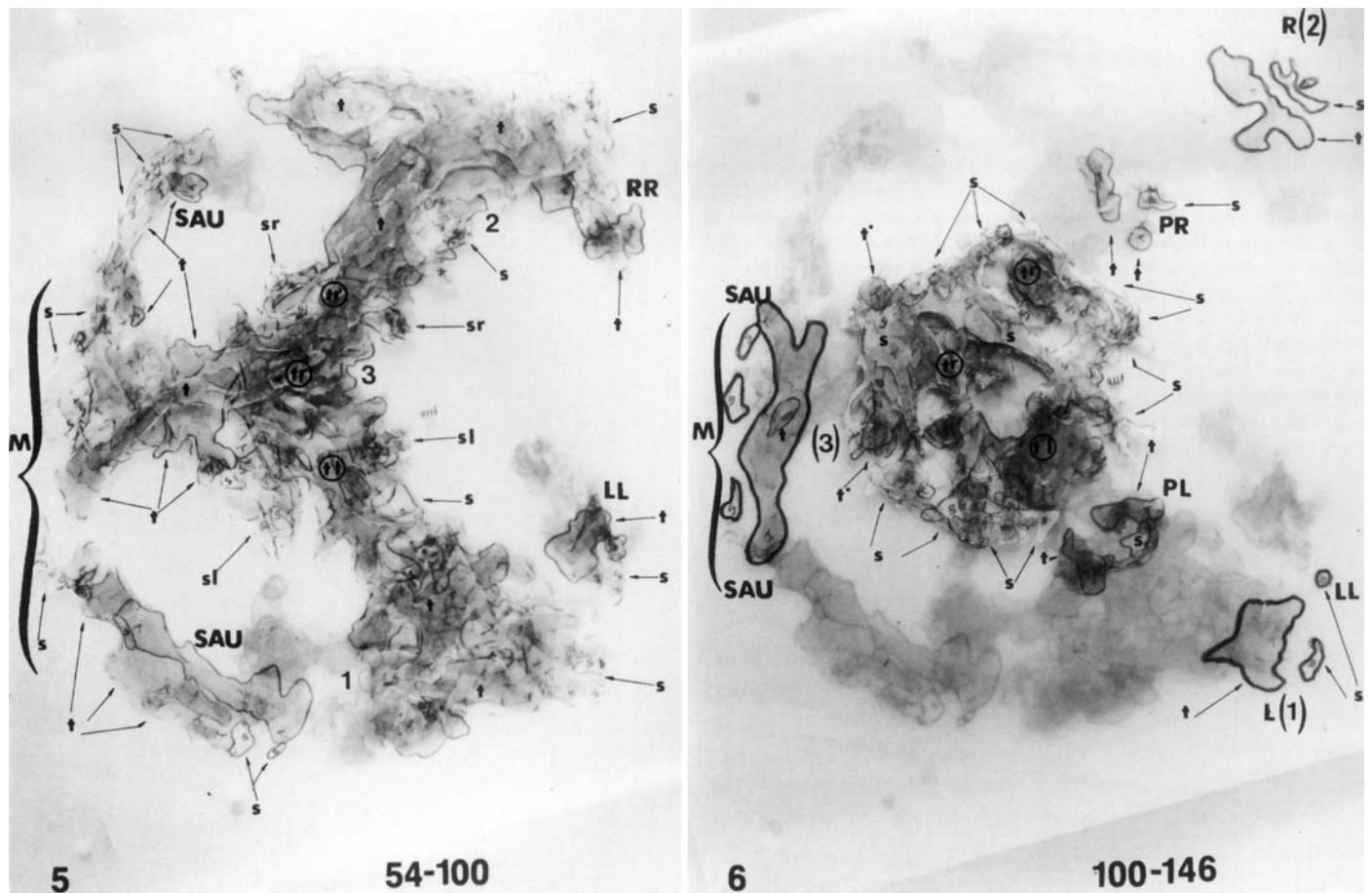
In the rachilla at the base of the floret about the level of Figure 2, level 5, six collateral bundles occur in two rows (Figure 3). The tracheary elements in each tend to be nearer the center of the rachilla, and the sieve elements are more peripheral. Throughout their courses in the rachilla, the tracheary and sieve elements tend to be squat and to be accompanied by a matrix of intermediary cells. The six bundles are small except the large central one of the anterior row. That is bundle 3, which probably was initiated first in the rachilla as the median trace of the lemma.

With ascent in the rachilla, the sieve elements from bundle 3 interconnect with sieve elements from all the other bundles as sieve elements horizontally traverse the intervening ground parenchyma of the rachilla (Figures 4, 5). This horizontal network of sieve elements connecting the phloem of rachilla bundles that were isolated at the rachilla base is the lower sieve-element plexus. A larger, accompanying horizontal system of tracheary elements overlies the lower sieve-element plexus (Figure 5). The sieve-element plexus is semicircular and open at the posterior because the ground parenchyma between rachilla bundles of the posterior row is not bridged by sieve and tracheary elements.

While the sieve and tracheary elements emanating from bundle 3 are contributing to the lower sieve-element plexus, some elements of bundle 3 ascend to become the median trace (M) of the lemma (Figures 4-6). Bundle 3 contributes most of



FIGURES 3, 4 (right).—Facsimiles of male floret vascular system at levels shown in micrometers ($\times 700$). Scale (3 μm in length) remains in parenchyma in the same relative position throughout all the levels of the male floret. Figure 3 identifies the six rachilla bundles at the floret base. Figure 4 shows the lower regions of the lower plexus containing most of the horizontally connecting sieve elements. (A = anterior of floret; L = left of floret; LL = bundle related to lemma extreme left lateral; M = bundle related to lemma median; P = posterior of floret; R = right of floret; RR = bundle related to lemma extreme right lateral; s = sieve elements; SAU = satellite, supernumerary, superposed, or subsidiary bundles associated with bundle 3; t = tracheary elements; 1, 2, 3 = bundles 1, 2, 3.)



FIGURES 5, 6.—Facsimiles of male floret vascular system at levels shown in micrometers ($\times 700$). As sieve and tracheary elements from bundle 3 form the lower parts of the lower plexus, sieve and tracheary elements also from bundle 3 become the lemma median. The satellite or subsidiary bundles separate from M as they enter the rachilla. Besides contributing to the lower plexus in Figure 5, bundles 1 and 2 form the principal lemma laterals. Minor, extreme laterals associate with the main laterals. One of the extreme laterals (LL) descends the rachilla without merging with its main lateral (L). In Figure 5, columns of tracheary elements flanked by sieve elements ascend over M from the right and left of bundle 3 and the lower plexus. In Figure 6, these sieve elements encircle the columns of tracheary elements to make the lower layers of the upper plexus. Scale ($3 \mu\text{m}$ in length) remains in parenchyma in same relative position throughout all the levels of the male floret. (L = bundle related to lemma left lateral; LL = bundle related to lemma extreme left lateral; M = bundle related to lemma median; PL = bundle of left of palea; PR = bundle of right of palea; R = bundle related to lemma right lateral; RR = bundle related to lemma extreme right lateral; s = sieve elements; SAU = satellite, supernumerary, superposed, or subsidiary bundles associated with bundle 3 and M; sl = sieve elements of the left lower parts of the upper sieve-element plexus; sr = sieve elements of the right lower parts of the upper sieve-element plexus; t = tracheary elements; tl = column of tracheary elements associated with the left lower parts of the upper sieve-element plexus; tr = columns of tracheary elements associated with the right lower parts of the upper sieve-element plexus; 1, 2, 3 = bundles 1, 2, 3.)

the vascular tissue of M. However, bundle 3 is a composite bundle consisting of the vascular tissue of bundle 3 accompanied by two flanking components, which in farther descending the rachilla become the smaller bundles in the anterior row of bundles at the floret base (Figures 6-3). Probably, these satellite bundles of M were initiated higher and later in the rachilla than bundle 3. Before descending the rachilla, the satellites also participate in the lower plexus (Figures 5, 4).

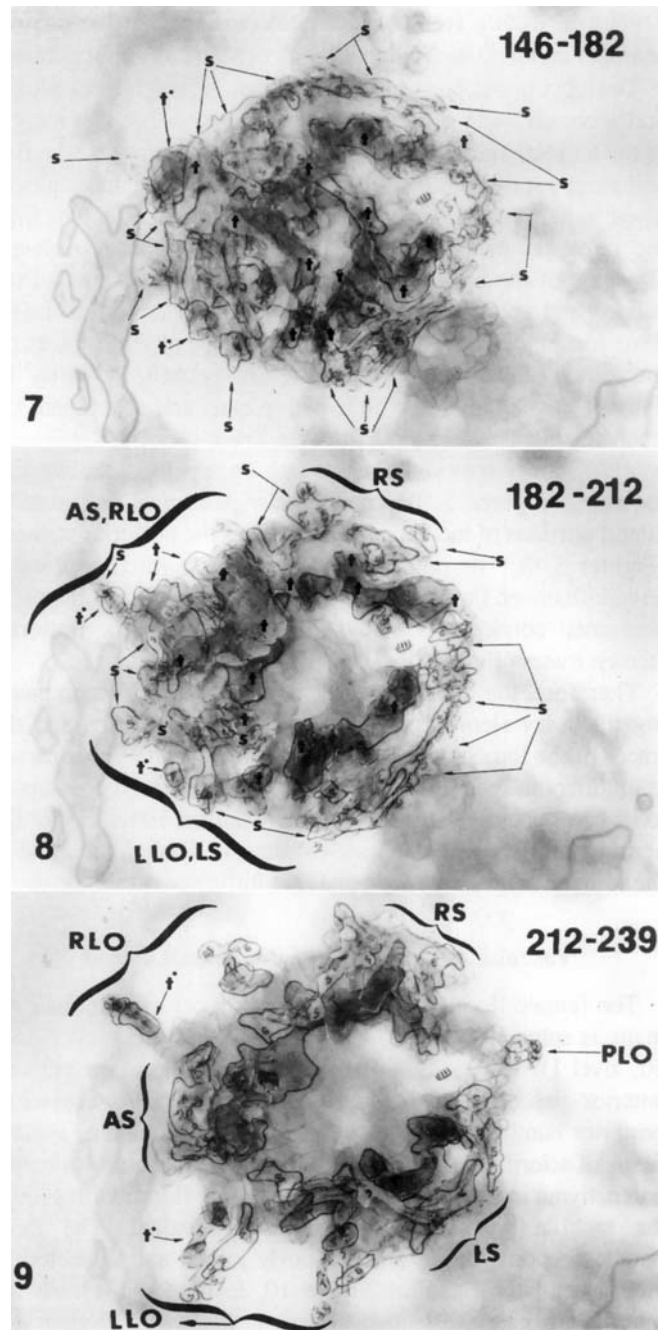
Also participating in the lower plexus are the flanking bundles from the posterior row of the rachilla (Figures 3-5). These are bundles 1 and 2. Like bundle 3, they probably were initiated isolated in the rachilla near the site of the lower sieve-element plexus and differentiated basipetally in the rachilla and acropetally into the lemma. Above the lower plexus, bundles 1 and 2 become the lemma laterals (Figures 5, 6).

FIGURES 7-9.—Facsimiles of the upper portions of the upper plexus of the male floret at levels shown in micrometers ($\times 700$). In Figure 7, the columns of tracheary elements from the lower upper plexus of Figure 6 become horizontally interconnected in the center of the plexus as the sieve elements interconnect around them. In Figure 8, the central region of parenchyma in the upper plexus becomes larger as portions of the plexus cluster under the influence of the traces of the anterior lodicules and the stamens. In Figure 9, the lodicule traces enter the upper plexus between the clusters related to the stamen traces. The posterior lodicule trace connects to the upper plexus in the gap between the clusters related to the right and left stamen traces. Tracheary elements of the inner traces of the right and left lodicule (t with dot) can be followed throughout the upper plexus (Figures 6-9). Scale (3 μm in length) remains in parenchyma in same relative position throughout all the levels of the male floret. (AS = anterior stamen trace; LS = left stamen trace; LLO = the two traces of the left lodicule; PLO = trace of the posterior lodicule; RLO = the two traces of the right lodicule; RS = right stamen trace; s = sieve elements; t = tracheary elements.)

Only two laterals ascend the lemma (Figure 2). However, in the rachilla in the vicinity of the lower sieve-element plexus, a smaller, inner bundle unites with each lateral before it ascends the lemma (LL and RR in Figures 5, 6). These poorly developed extreme laterals were probably initiated higher in the rachilla than the larger laterals and had a short acropetal course. The small, right, extreme lateral had a brief descent in the rachilla before merger with its larger partner; however, the small, left, extreme lateral missed fusing with its larger partner and descended far in the rachilla (Figures 5-3; Figure 2, level 5). Therefore, one should expect variation at the rachilla of the floret base in the bundle number due to the presence or absence of mergers of the satellites of bundles 1, 2, and 3.

The two palea traces were probably initiated higher and later in the rachilla than bundles 1, 2, and 3. In descending from the palea, the left trace of the palea (PL) merges where it is obstructed by bundle 1, which is proliferating to contribute to the lower sieve-element plexus (Figures 6, 5). In its descent from the palea, the right trace (PR) behaves like the left in merging with proliferating bundle 2 at the lower sieve-element plexus.

Sieve and tracheary elements rise from the center of the lower sieve-element plexus to form the lower portion of the upper sieve-element plexus and accompanying tracheary elements (Figures 5, 6). Bundle 3 contributes most of the sieve and tracheary elements to the lower levels of the upper plexus. The center of the lower plexus from which the upper plexus emanates is a triradiate ridge of tracheary elements around whose radii the sieve elements flow upward (Figure 5, note sr and sl). The tracheary elements accompanying the ascending sieve elements rise from each of the radii in three columns (Figure 5, note tr and tl). The two columns of tracheary elements that are more to the right and the accompanying sieve elements form the right leg of the upper plexus (Figure 5, note tr and sr), and the left column forms the left leg of the upper plexus (Figure 5, note tl and sl). The sieve elements of the plexus then cross horizontally among the three columns as well as around the whole unit, creating the lower levels of the upper



sieve-element plexus (Figures 5, 6). As the sieve elements create the encircling pattern of the upper sieve-element plexus, within it the columns of tracheary elements become horizontally interconnected (Figures 6, 7). The uppermost levels of the upper sieve-element plexus with accompanying tracheary elements resemble two concentric circles—an outer system of horizontal sieve elements and an inner system of horizontal tracheary elements—surrounding ground parenchyma devoid of conducting cells (Figures 7, 8). Probably the upper sieve-element plexus and accompanying tracheary elements

developed from a residual meristem persisting in the rachilla between bundle 3 and the insertions of stamens and lodicules.

The uppermost portions of the upper sieve-element plexus and accompanying tracheary elements are the levels of merger of the lodicule traces and stamen traces (Figures 8, 9). The five collateral traces from the three lodicules enter the upper plexus lower and more diagonally than the three collateral traces from the three stamens. The patterns of the sieve and tracheary elements of the upper plexus as they are directed toward the stamen and anterior lodicule traces—despite the interconnections just emphasized—reflect the influence of these traces on the formation of the upper plexus. The pattern, in which the anterior of the upper sieve-element plexus and accompanying tracheary elements emanate from the lower plexus, supplies the anterior stamen trace and the flanking trace pairs of the anterior lodicules (Figures 5–8). The vascular pattern of the posterolateral portions of the upper plexus serves the posterior stamens (Figures 5–8). The posterior lodicule trace, which appears to have influenced the pattern of the upper plexus least joins it at horizontal connections below the gap between the posterior stamen traces (Figures 9–7).

Therefore, the upper sieve-element plexus and accompanying tracheary elements axially link the lower plexus and the traces of the lodicules and stamens. Although the upper plexus is a horizontally interconnected vascular system, it consists of axial components formed from a residual meristem, under the acroflagal influence of the traces of the anterior lodicules and of the stamens, and under the basifugal influence of bundle 3.

Vascular Morphology of the Female Floret

The female floret, which is larger in most aspects than the male, is subtended by two large, vascularized glumes (Figure 10, level 1). The rachilla of the base of the floret contains an anterior vascular bundle and two flanking, but somewhat, posterior bundles. The three bundles are surrounded by ground tissue of sclerified parenchyma, in contrast with the thin-walled parenchyma in the same region of the male floret; with ascent, the rachilla parenchyma becomes thin-walled. The three bundles become larger and variously joined and dissected as they ascend the rachilla (Figure 10, levels 21–131). At the same levels near the lemma insertion, the lemma median and paired lemma laterals become discrete from the vascular system in the rachilla (Figure 10, levels 131–220). The central portion of the female lemma does not form a pleated anterior pocket as does the male lemma. From the same regions of the rachilla as the apparent emergences of each of the pairs of lemma laterals, the palea traces emerge (Figure 10, levels 131–161). However, they reach the palea more distally on the rachilla (Figure 10, levels 191–428).

Above the emergences of the palea traces, the rachilla is filled with a large bundle, from whose anterior flanks three traces emerge toward the anterior lodicule insertions (Figure 10, levels 250–398). The posterior lodicule insertion contains

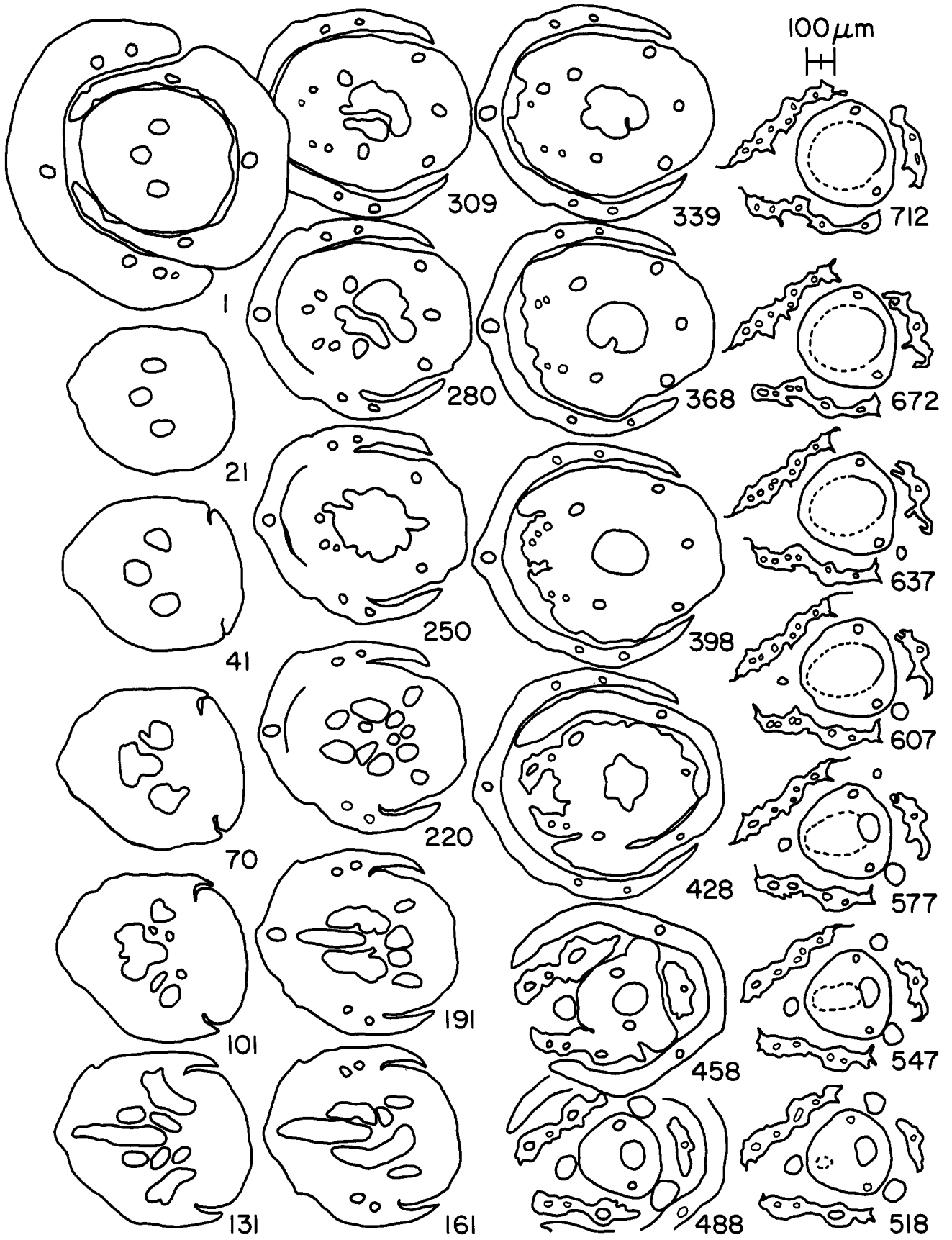
one trace (Figure 10, levels 428, 458) that emerges about the same levels as the traces of the anterior lodicules (Figure 10, levels 250, 280). Alternating with the lodicule insertions, three avascular, aborted stamens emerge from the rachilla or receptacle and ascend 100 μm (Figure 10, levels 428–607). The large bundle remaining in the rachilla or receptacle above the emergence of the lodicule traces is the lowest vascular tissue related to the pistil (Figure 10, levels 339–398), which is lacking in the male floret.

A vascular bundle merges at each flank of the vasculature of the base of the pistil (Figure 10, level 428), shortly below the locule, which is in the anterior of the ovary (Figure 10, level 518). Each bundle probably descended from a stigma, through a long style (Figure 11, levels 1152, 1112), and through the right and left flanks of the ovary (Figure 11, levels 1072–752; Figure 10, levels 518–428) before the merger. These stylar bundles are called “posterolateral bundles” to distinguish them from an anterior bundle that probably does not occur in any species of *Raddia*.

The large vascular bundle in the posterior of the ovary behind the locule is the placental bundle (Figure 10, levels 518–712). Proximally, the placental bundle merges with the vasculature of the pistil base (Figure 10, levels 518–428). Distally, the placental bundle supplies the ovule.

The ovule fills the locule but is free from the interior ovary wall except at the placenta. The placenta is the region of merger of one or both integuments of the ovule with the interior posterior wall of the ovary. Figure 10, level 547 is the lowest level of the placenta. The placenta ends between levels 992 and 1032 of Figure 11. The chalaza is that part of the ovule where the epidermises of the integuments and of the nucellus are not interposed between the internal posterior of the ovary and the

FIGURE 10.—Tracings of serial transverse sections of the female floret arranged acropetally at intervals indicated in μm ($\times 55$). Left and right of page, respectively, is anterior and posterior of the floret. Top and bottom of page, respectively, is right and left of the floret. Closed circular areas within the parts of the floret are vascular bundles including their intermediary cells. Level 1 is the floret base with the inner and outer glumes surrounding the rachilla containing bundles 3, 2, and 1. Bundle 3 is the more anterior one. Bundle 1 is at the rachilla left, and bundle 2 is at the right. Glumes are not drawn higher. In levels 131–191, the lemma median trace becomes distinct from bundle 3. The paired left and right laterals of the lemma become distinct from bundles 1 and 2, respectively. Also, the traces of the left and right of the palea become distinct from the lemma laterals. By level 309, the lemma is distinct from the anterior of the rachilla, and the three traces of each of the pair of anterior lodicules are distinct as is that of the posterior lodicule. By levels 458 and 488, the palea, three lodicules, and three staminodia are distinct from the rachilla. Lemma and palea are not drawn higher. By these levels, the posterolateral (stylar) bundles are fusing with the rachilla bundle related to the pistil. This fusion occurs below the level of the locule shown by the dashed circular areas of levels 518 and higher; the ovule fills the locule. The large bundle in the pistil posterior of levels 518–577 is the placental bundle. By level 607, as the tips of the staminodia are reached, the placental bundle joins the nucellus of the ovule forming the base of the chalaza. The solid line is the posterior of the placental bundle and the dashed line is the boundary between the inner ovary wall and the outer walls of the integuments.



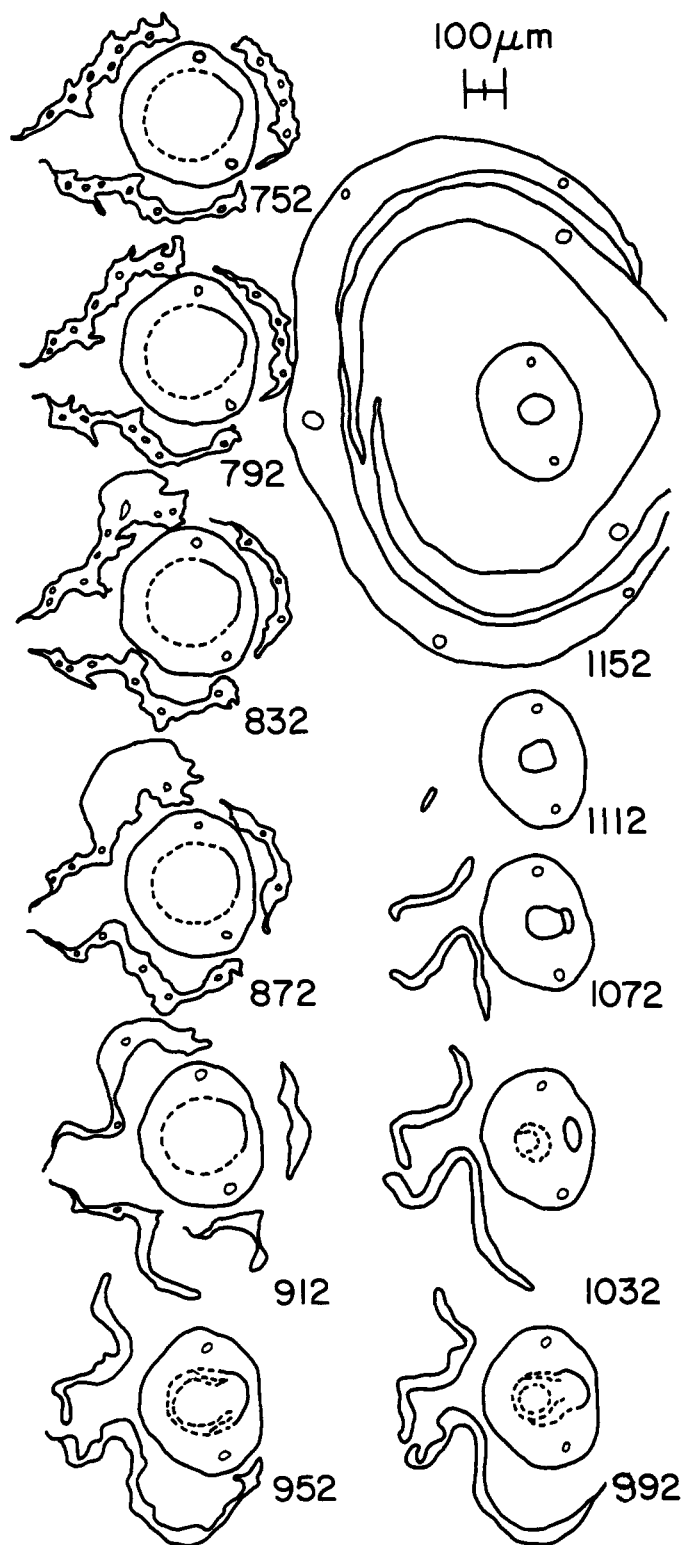


FIGURE 11.—Continuation of the floret in Figure 10 ($\times 55$). The right and left posterolaterals flank the ovule and continue beyond it into the style. From levels 752 to 992 the locule and ovule are shown by the dashed outer line (the boundary between the inner ovary wall and outer walls of the integuments) and a solid line (the posterior of the placental bundle). At levels 952 to 1032, the inner boundaries of the smaller, outer integument and of the larger, inner integument now are shown by the dashed lines enclosed by the dashed boundary between the inner ovary wall and the outer wall of the integuments previously indicated. By level 992, the chalaza ends as the nucellar epidermis (dashed circle) interposes between the nucellus and the placental bundle (solid line of ovule). By level 1032, the tip of the ovule is only the inner and outer integument filling the locule. The placental bundle no longer joins the ovule but is posterior to the ovule. By level 1072, the locule is passed and superseded by the stylar core (the large circle). The placental bundle contacts the posterior of the stylar core. By level 1112, the placental bundle ended and the stylar core ascends the style. Lemma and most of the palea are included with the tracing of the style in level 1152.

internal tissues of the nucellus. That is, the chalaza occurs where the nucellus and ovary wall are merged. The lowest level of the chalaza is between levels 577 and 607 of Figure 10; the highest level is between levels 952 and 992 of Figure 11. The placental bundle fills most of the placenta.

The placental bundle extends higher than the placenta (Figure 11, level 1032). The placental bundle fades out in contact with an avascular, parenchymatous cylinder of the style which supersedes the ovule and locule (Figure 11, levels 1072, 1112). This stylar core continues up the style, flanked by the posterolateral bundles.

Vascular Anatomy of the Female Floret

One anterior and two flanking posterior collateral bundles of large area occur in the rachilla at the floret base (Figure 12). Throughout their courses in the rachilla, the cytology of the tracheary elements, sieve elements, and intermediary cells from these bundles resembles their cytology in the male floret. The centripetal placement of the xylem of these bundles and their sequent courses in the rachilla and lemma indicate that the anterior bundle is the homologue of bundle 3 and that the posteriors are the homologues of bundles 1 and 2 in the male rachilla.

With ascent in the rachilla, bundles 3, 2, and 1 make the lower sieve-element plexus and accompanying tracheary elements. Most of the sieve and tracheary elements emanate from bundle 3. As the sieve elements ascend diagonally from a widening bundle 3 (Figures 12, 13) they form a V (Figures 14, 15). Tracheary elements emanating from those of bundle 3 accompany both sides of each phloic arm of the V (Figures 14, 15). The tips of the arms of the V then bend horizontally toward the flanks of the rachilla. Thus, bundle 3 forms wings of horizontal sieve elements sandwiched by the accompanying tracheary elements (Figures 15, 16). Merger of these derivatives of bundle 3 with a similar arrangement of sieve and tracheary elements from bundles 1 and 2 completes the semicircular lower sieve-element plexus and accompanying tracheary elements (Figure 16). Probably as occurs in the male

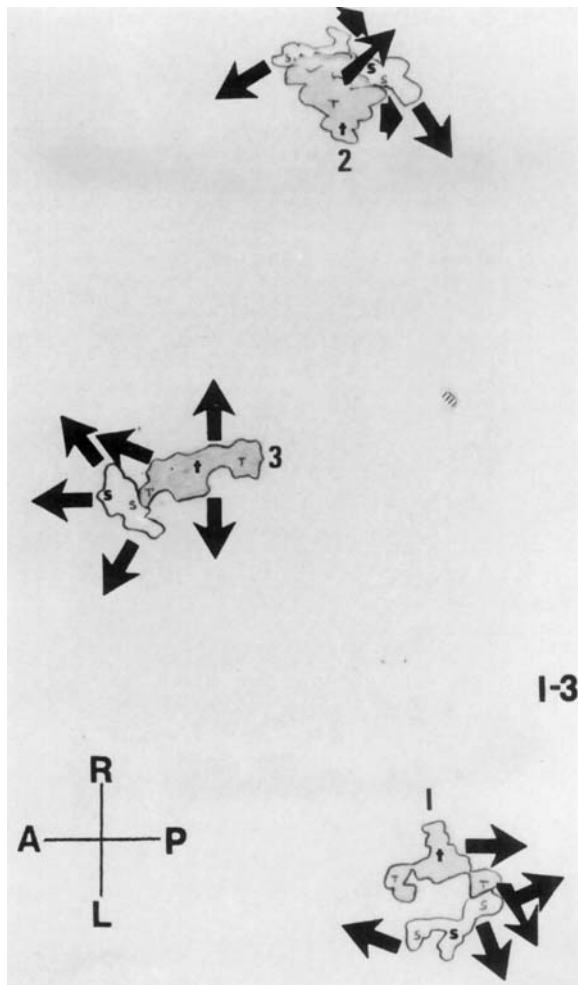


FIGURE 12.—Facsimile of female floret vascular system at 1–3 μ m above the base of the floret ($\times 700$). Note the three bundles in the rachilla at the floret base. Arrows indicate that while ascending to Figure 13, tracheary elements of bundles 1 and 2 spread centrifugally and posteriorly but tracheary elements of bundle 3 spread centrifugally and laterally. As sieve elements from bundles 1 and 2 ascend between Figures 12 and 13, they envelop the xylem except at the interior of the rachilla. The sieve elements of bundle 3 spread laterally without enveloping the xylem. Scale (3 μ m in length) remains in parenchyma in the same relative position throughout all the levels of the female floret. (A = anterior of floret; L = left of floret; P = posterior of floret; R = right of floret; s = sieve elements; t = tracheary elements; 1, 2, 3 = bundles 1, 2, 3.)

floret at this level, the lower sieve-element plexus arises as vascular shunts between bundle 3 and bundles 1 and 2. The view of the upper levels of the sieve-element plexus of the female floret shown in Figure 16 corresponds to the level of the male floret in Figure 5.

As in the male floret, the second role of bundle 3 is as median trace for the lemma (M). Bundle 3 becomes M in two levels. A few tracheary elements continuous with those from the lemma median connect at a low level to the inner xylem of both arms of the V of bundle 3 (Figure 15). Near this level, all of the sieve

elements from the lemma median connect to the sieve elements in the crotch of the V of bundle 3 (paired stars in Figures 16–14). The higher level of connection between bundle 3 and M involves only the tracheary elements. These have a thick, broad, horizontal course from M through the gap of intermediary cells between the ascending arms of the V of bundle 3 (Figures 17, 16). After passing horizontally through the gap of the V, the tracheary elements from M then descend vertically to end in intermediary cells in the posterior of bundle 3 (single stars in Figures 16–14).

Thus, there were probably two sites of initiation, which merged in development, for the creation of the lemma median trace: a lower one in the rachilla initiating bundle 3, and a superposed one nearer the insertion of the lemma that produced most of the xylem. There is likelihood that the two satellite bundles in the lemma median of the male floret, which consist largely of tracheary elements (Figures 5, 6), are moieties homologous to the superposed xylem bundle of the lemma median of the female floret. Because the center of the male rachilla, but not of the female, was obstructed by the developing lower sieve-element plexus and accompanying xylem, the developing satellite bundles of the male, unable to merge over bundle 3 and descend behind it, split around the rachilla (Figure 5).

Just as bundle 3 of the female floret contributes to the lower sieve-element plexus as well as to the lemma median, so do bundles 1 and 2 contribute to the lemma laterals, besides their roles in the formation of the lower sieve-element plexus. Bundle 1 forms in the rachilla as the trace for one of the left laterals (L or LL) of the lemma, and bundle 2 forms as the trace for one of the right laterals (R or RR; Figures 12–14). Because the mergers of the right and left laterals with their respective rachilla bundles are nearly equal, one cannot determine which of each lateral pair was the original bundle in the right and left of the rachilla (Figure 15). Using the male floret as a guide (Figure 6) suggests that the laterals closer to the median originated in the rachilla as bundles 1 and 2. The palea traces of the female floret behave the same as in the male floret, for each trace descends from the palea to merge, respectively, with bundles 1 or 2 as they proliferate in contributing to the lower sieve-element plexus and accompanying xylem (Figures 6, 15, 16).

From the semicircular, lower sieve-element plexus and accompanying xylem (Figure 16), the upper sieve-element plexus and its xylem rise uniformly (Figure 17). In the male floret, the formation of the upper plexus is influenced by the traces from the insertions of the anterior lodicules and stamens. Because the aborted stamens do not initiate traces, the anterior lodicules are the predominant influence on the shape of the upper plexus of the female floret. Accordingly, the posterior of the upper plexus remains open due to the absence of any influence from the posterior stamens (Figures 17, 18). At its middle levels, the upper sieve-element plexus and accompanying xylem consist of two opposed arcs open to the wide gap,

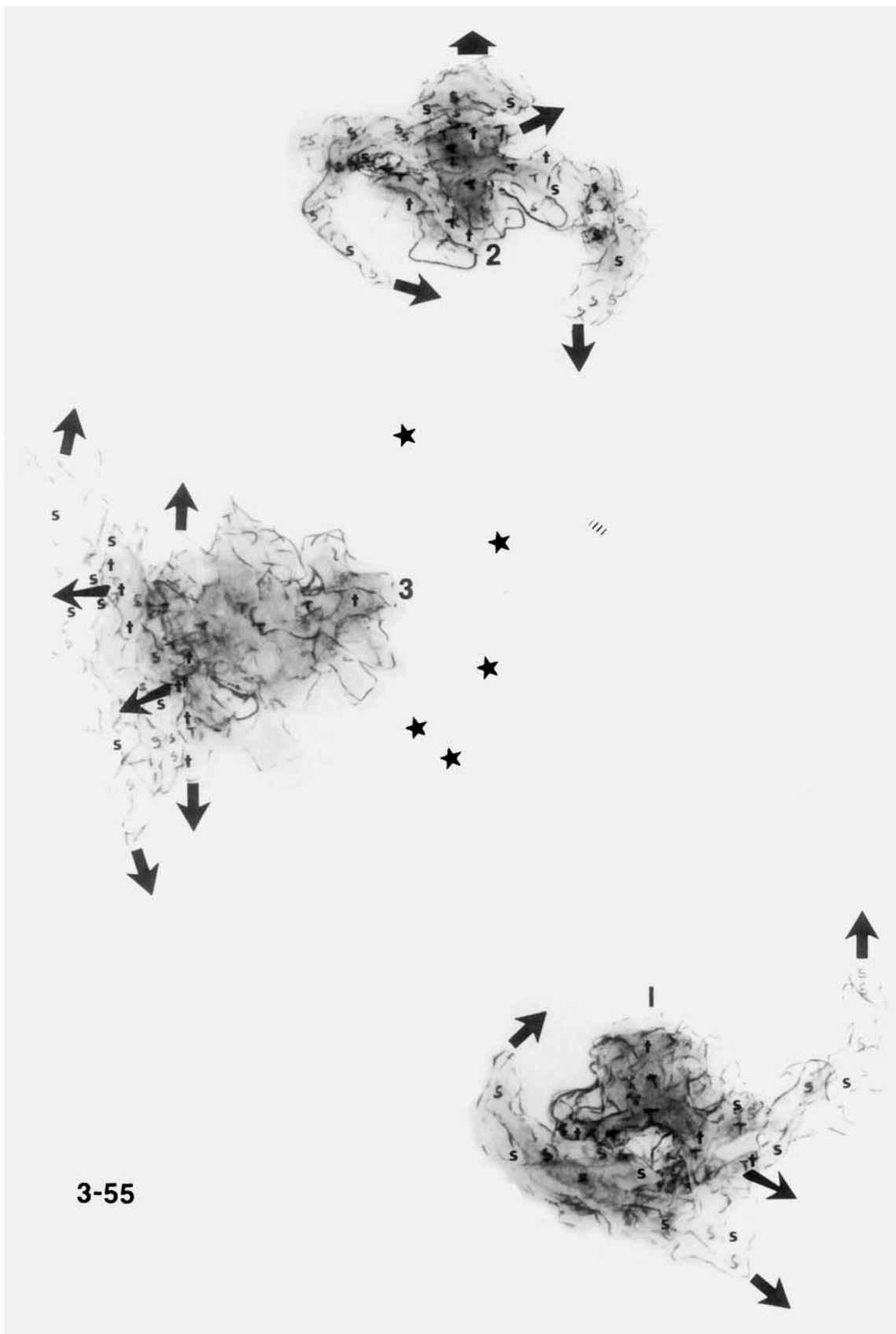


FIGURE 13.—Facsimile of female floret vascular system at 3–55 μm above the base of the floret ($\times 1000$). Arrows indicate the path of ascent of tracheary and sieve elements of bundles 1, 2, 3 to Figure 14. The position of the numbers identifying the bundles is in the same relative position in Figures 12 and 13 indicating that the tracheary elements do not rise centripetally. Stars are in a region of intermediary cells centripetal to bundle 3 below tracheary elements descending from Figure 16 through Figure 14. Scale (3 μm in length) remains in parenchyma in the same relative position throughout all the levels of the floret. (s = sieve elements; t = tracheary elements; 1, 2, 3 = bundles 1, 2, 3.)

which is over the superposed tracheary elements to M and which is continuous with the gap of the open posterior (Figure 17). At its middle levels, the anterior gap in the upper plexus persists over M because the anterior stamen trace is lacking. At the highest levels of the upper plexus, the anterior gap over M is bridged by horizontally shunting tracheary and sieve elements from the arcs (paired dots in Figure 18). The shape of each arc is influenced by the two peneposterior, collateral traces of the anterior lodicules (PEP) of the left and right (Figures 18, 17). The anterior trace from each of the anterior lodicules (Figure 18) appears to have joined the upper sieve-element plexus and accompanying xylem after its bi-arcuate shape was determined by the two major traces from each anterior lodicule.

Two massive lobes basipetally merge with the rest of the vascular system filling the posterior gap of the upper and lower plexi (Figures 18–16). These two broad prongs or lobes (POP) merge with the posterior of the open lower plexus (Figures 17, 16) after descending through the rachilla from the pistil plexus in the base of the pistil (Figure 10, level 398; Figure 20). During their basipetal course from the pistil plexus to the lower plexus, these lobes complement the bi-arcuate upper plexus to form a massive, hollow cylinder over the trace to the lemma median (Figure 18). The posterior of the right lobe from the pistil plexus is the site of merger of the solitary collateral trace from the posterior lodicule (Figure 18). Probably, there is variation among female florets in the linkage of this minor trace to the right or left lobe from the pistil plexus.

The pistil plexus, which sends down these lobes, is a large disk of tracheary elements virtually encircled by sieve elements in the rachilla (receptacle) at the pistil base (Figure 10, levels 368, 398; Figure 20). The pistil plexus sends down centrifugally three interconnected pairs of vascular prongs into the rachilla (AP, RPP, LPP in Figure 19). The anterior pair is of small, collateral bundles (AP in Figure 19), which soon merge with the anterior, horizontally shunting, tracheary and sieve elements of the upper plexus (Figure 18). The other two pairs of prongs descending from the pistil plexus are larger, less discrete, and more nearly amphivasal than the anterior pair (Figure 19). Each of the more posterior pairs continues descending the rachilla centrifugally (Figure 18) while merging to become the broad lobes that fuse anteriorly with the upper plexus to close the posterior gap of the lower plexus (Figures 17, 16).

The complex arrangement of the sieve and tracheary elements in these vascular components developing from the

pistil plexus beggars description. The pistil plexus is a vast reticulum of tracheary elements almost encircled by an enveloping reticulum of sieve elements (Figure 20). The two pairs of interconnected vascular prongs that descend from the pistil plexus to form the broad posterior lobes do so in a curious way. Segments descend from the sieve-element rim of the pistil plexus (darts in Figures 20, 19). Tracheary elements from the center of the pistil plexus penetrate centrifugally around the descending sieve elements and become interconnected on all sides of these clusters of sieve elements (Figures 19, 18). These events, which occur more precipitously at some sites than in others during the descent from the pistil plexus, eventually cause the right and left prong pairs to become the lobes. As the clusters of sieve elements in the lobes begin to become isolated by the encircling tracheary elements, the sieve elements from adjacent clusters reconnect within the encasing tracheary elements of a lobe (Figure 18). In this way, the descending lobes from the virtually amphicribal pistil plexus are an amphivasal weave of sieve and tracheary elements merging anteriorly with the upper plexus (Figure 17) and posteriorly with the lower plexus (Figure 16).

Now that the basipetal attachments of the pistil plexus to the upper and lower plexi in the rachilla are described, the two portions of the pistil vasculature attached at the upper pistil plexus can be detailed. First, the stylar or posterolateral, collateral bundles merge with the flanks of the pistil plexus (RPL and LPL in Figure 20), which occurs far below the ovule and the placental bundle (Figure 10, level 428). Second, the placental bundle emerges, without fanning out, above the posterior of the contracting pistil plexus (Figures 21, 22). The rim of sieve elements contracts by closing upon a small core of sieve elements—which is continuous with the rim—within the enclosed reticulum of tracheary elements (paired dots in Figures 20, 21). Since sieve and tracheary elements do not continue rising from the anterior of the contracting pistil plexus, the placental bundle becomes an arc of sieve elements opening toward the ovule and embracing the tracheary elements (Figure 22). Mature tracheary and sieve elements diminish and then end in immature elements in the placental bundle before it attains the level of the placenta (Figure 10, level 518). At the time of sampling, immature elements had developed into the placenta but not into the chalaza (Figure 10, level 577). Intermediary cells, which have accompanied the sieve and tracheary elements throughout their courses, continue the placental bundle beyond the placenta (Figure 11, level 1032), above the ovule into the base of the style. There the bundle ends after contacting the stylar core (Figure 11, levels 1072, 1112).

Figure 23 summarizes the basic pattern of the components of the male and female florets but neglects the subtleties of the system emphasized in the preceding descriptions of the facsimiles. Figure 23 emphasizes the similarities of the vasculature of the florets. Differences in the components of male and female florets are explained largely (1) by the absence

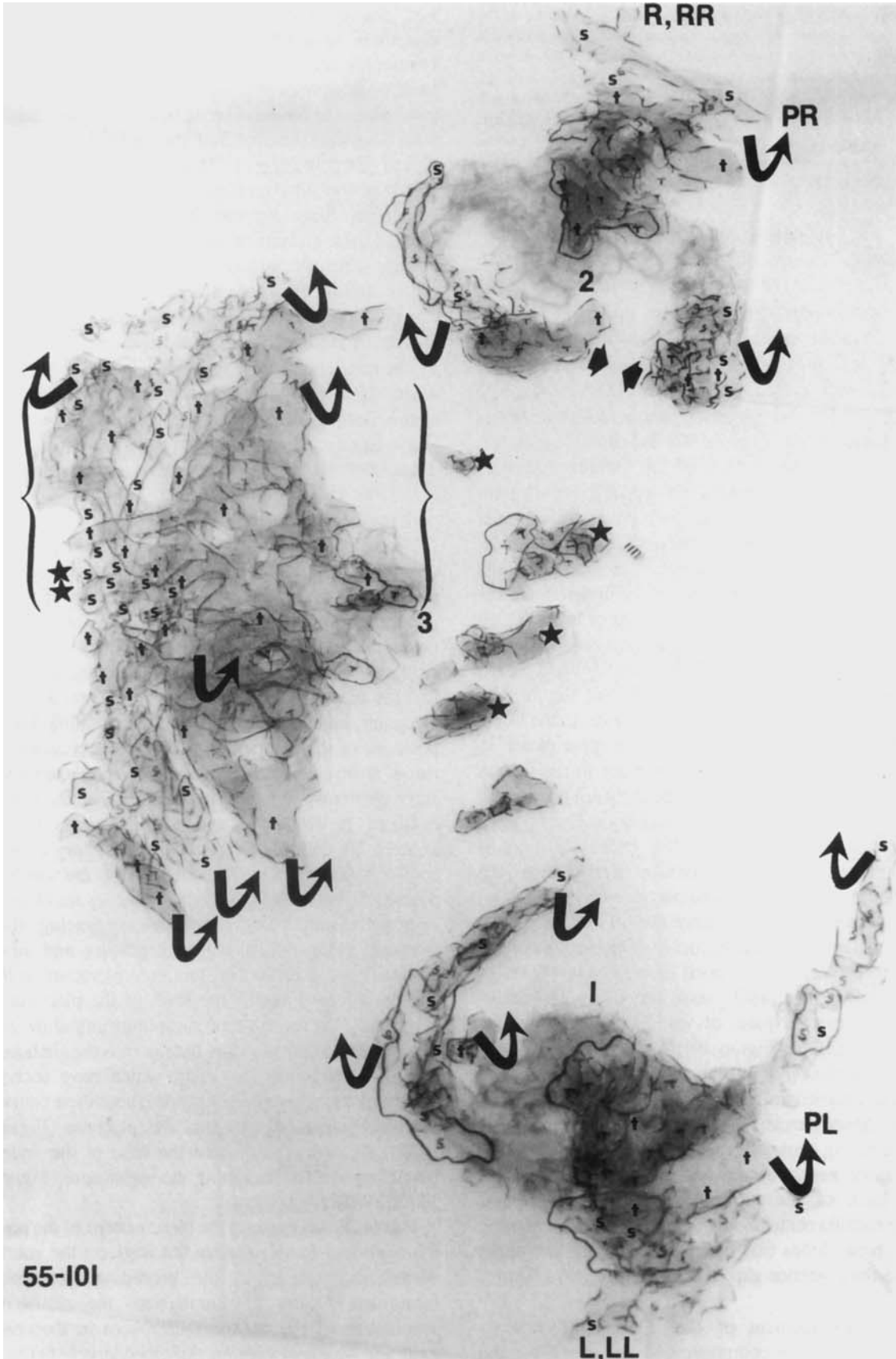


FIGURE 14.—Facsimile of female floret vascular system at 55–101 μm above the floret base ($\times 1000$). Position of numbers identifying bundles 1, 2, 3 are in same relative positions of Figure 13. Stars by tracheary elements show those descending into intermediary cells of the posterior of bundle 3 from Figure 16. Arrows indicate where regions of bundles 1, 2, 3 ascend to continue into Figure 15. Bundle 3 is at the level where it resembles the base of a V. No tracheary elements rise from those between the brackets, although tracheary elements and sieve elements ascend from outside the brackets. Paired stars indicate the attachment of the sieve elements so marked in Figure 15. Scale (3 μm in length) remains in parenchyma in the same relative position through all the levels of the floret. (L = lemma left lateral trace; LL = lemma extreme left lateral trace; PL = left trace of palea; PR = right trace of palea; R = lemma right lateral trace; RR = lemma extreme right lateral trace; s = sieve elements; t = tracheary elements; 1, 2, 3 = bundles 1, 2, 3.)

of gynoecial components compensated by an enhanced (relative to festucoid and oryzoid grasses) role of the lodicule components in the male floret, and (2) by elaborated gynoecial components compensating the loss of the androecial components in the female.

Comparative and Phylogenetic Considerations

COMPONENTS OF THE FLORET VASCULAR SYSTEM OF *Raddia* ARE COMPARED TO THOSE KNOWN IN THE FESTUCOIDEAE AND ORYZOIDEAE

The large anterior bundle in the rachilla at the base of both florets is the origin of the lemma median in *Raddia* and in all other investigated festucoid and oryzoid grasses (Pizzolato, 1989a, b). This bundle is designated bundle 3, and in *Raddia* and in most festucoid grasses, but not in oryzoid grasses, the xylem occurs between the phloem and the lemma (Figures 3, 12; Table 1, row 2). Besides bundle 3, several other bundles are in the rachilla at the floret base of *Raddia* and of most festucoid grasses (Table 1, row 1). These bundles are the origins of the lemma laterals and palea traces. Some of these bundles are actually composite bundles: the posterior ones of *Phalaris* and *Phleum* combine, respectively, the palea traces and the lemma extreme lateral traces (Pizzolato, 1988, 1989a); bundles 1 and 2 of the female floret of *Raddia* are composites of both lemma laterals on their respective sides.

The ground tissue of the rachilla surrounding the bundles of the floret base is usually of parenchyma, and in *Raddia* it is a particularly sclerified matrix for the thinly walled tissues of bundles 3, 2, and 1 of the female floret (Figure 10, level 21). This may create a brittle condition in the rachilla favorable to the violent dispersal of the mature female floret commented upon by Davidse (1987). Arber (1929) also mentions the extreme sclerification of the parenchyma around the bundles at the lemma and palea insertions of the olyroid ally, *Streptochaeta* Schrader ex Nees, 1829.

Pizzolato (1987, 1989a) has considered developmental explanations for the varying number of rachilla bundles at the base of the floret. He concluded that, in aggregate with other influences, rachilla amplitude increases rachilla bundle num-

ber. His conclusion cannot be totally correct because the smaller rachilla at the base of the male floret of *Raddia* contains twice as many bundles as does the big rachilla of the female floret (Figure 2, level 5; Figure 10, level 21).

After originating in the floret base as the traces for the lemma and palea, the rachilla bundles in most of the festucoid grasses and in *Raddia* become interconnected into the lower plexus (Figures 4, 5, 14–16; Table 1, row 4). In these genera, bundle 3 contributes most of the vascular tissue to the lower plexus. The lower plexi of both *Raddia* florets differ from those of the festucoid grasses, which are closed on the posterior. The lower plexi of the *Raddia* florets are open at the posterior because bundles 1 and 2 are farther apart with no intervening bundles (Figures 13, 14) or with only a descending small branch from bundle 1 (Figures 3, 4). Sieve elements dominate the lower plexi of the festucoid grasses except *Anthoxanthum* (Pizzolato, 1987, 1988, 1989a). In *Anthoxanthum* (Pizzolato, 1984) and *Raddia*, the lower sieve-element plexus is accompanied by a large volume of tracheary elements.

Besides contributing the most to the lower plexus, rachilla bundle 3 originates and serves as the lemma median in *Raddia*. Bundle 3 behaves so in all the non-panicoid genera studied (Table 1, row 2). However, *Raddia* differs markedly from these genera because it has multiple sites of origin in the rachilla. One is in the normal position in the rachilla (Figures 4, 5, 13, 14) and the other, smaller, sites are higher and nearer the lemma insertion (Figures 5, 16, 17). These satellite or supernumerary or superposed bundles of the median have only a brief horizontal course before merging with M distally and bundle 3 proximally. Thus, these superposed bundles of the lemma median were unnoticed until now (Table 1, row 3). However, Page (1947) noted them in the midribs of vegetative leaves of most of the genera of the Olyreae including *Raddia* and in midribs of olyroid allies such as *Streptochaeta*. Her findings in leaves were confirmed and extended by Metcalfe (1960), Calderón and Soderstrom (1973), and Renvoize (1985). Some of the variation in number and position of the satellites of midribs noted by Page (1947) and Metcalfe (1960) is similar to the variation in the positions of the superposed bundles relative to bundle 3 that occurs between the male and female floret lemma median of *Raddia*. The discovery of superposed bundles in the rachilla at the lemma median of *Raddia* supports the conclusions of Barnard (1957) and Sharman (1960a, b), from their developmental studies, that vegetative leaves and lemmas are homologous in all grasses including the bamboos. Apparently, the median trace of all bamboo leaves has multiple, isolated sites of procambial initiation in the rachilla near the insertion in contrast to the one isolated site of initiation of festucoid grasses (Hitch and Sharman, 1968; Patrick, 1972; Pizzolato and Robinson-Beers, 1987).

Of the investigated genera, *Raddia* is most like the festucoid genera in its producing an upper plexus (Table 1, row 8). The upper plexi of the festucoid grasses is different, however, because in them the stamen traces are the principal influence on

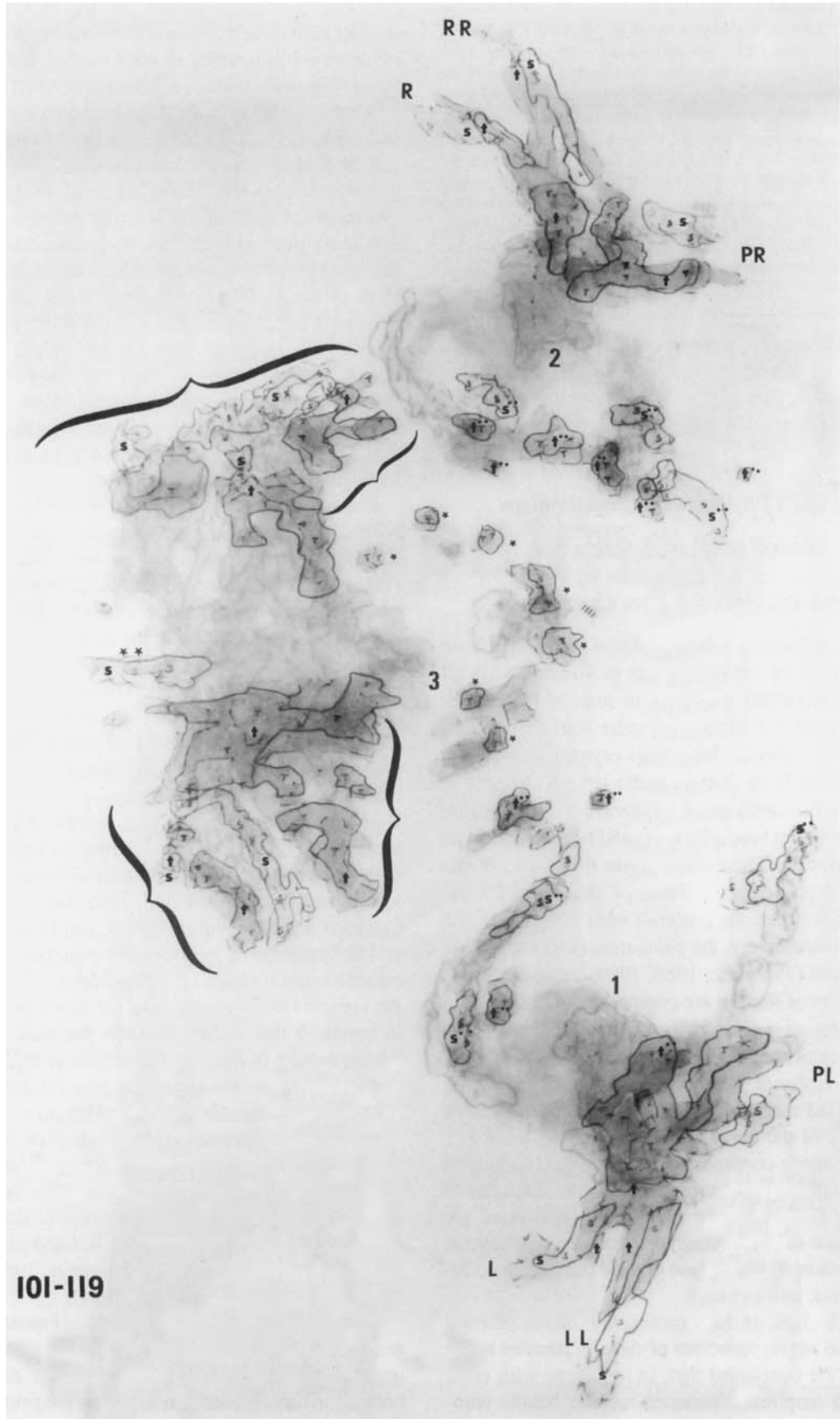


FIGURE 15.—Facsimile of female floret vascular system at 101–119 μm above the floret base ($\times 700$). Figures 14 and 15 show the lowest levels of the lower plexus. Positions of numbers identifying bundles 1, 2, 3 are in same relative positions of Figure 13. Stars by tracheary elements show those descending into intermediary cells of the posterior of bundle 3 from Figure 16. Bundle 3 is at the level where its phloem and xylem arms are rising from the base of the V shown in Figure 14. No tracheary elements rise from the crotch of the V (the out-of-focus view of Figure 14). Paired stars mark the attachment of the sieve elements from M so marked in Figure 14. The arms of the V of bundle 3 between the brackets flow into the parts of the lower plexus so marked in Figure 16. The tracheary and sieve elements from bundles 1 and 2 with paired dots connect at the regions of the lower plexus so marked in Figure 16. Scale (3 μm in length) remains in parenchyma in the same relative position throughout all the levels of the floret. (L = lemma left lateral trace; LL = lemma extreme left lateral trace; PL = left trace of palea; PR = right trace of palea; R = lemma right lateral trace; RR = lemma extreme right lateral trace; s = sieve elements; t = tracheary elements; 1, 2, 3 = bundles 1, 2, 3.)

the form of the plexus. In the male floret of *Raddia*, the influence of the three stamen traces is shared with the traces from the anterior lodicules. In the female floret of *Raddia*, the peneposterior traces from the anterior lodicules determine the form of the upper plexus. That is why the upper plexus is circular, not lobed, in the male floret (Figures 6–9) of *Raddia*, but is bi-arcuate in the female floret (Figures 17, 18). The trace of the posterior lodicule acts like a minor vein by not influencing the form of the upper plexi.

Of all the genera investigated three dimensionally, only *Raddia* has a posterior lodicule. Oryzoid lodicules are similar to those of *Raddia* because their traces contain tracheary and sieve elements, not just sieve elements as do the festucoid grasses (Table 1, row 7). The traces from the oryzoid lodicules and stamens are like that of the posterior lodicule of *Raddia*

TABLE 1.—Components of the floret vascular system useful in characterizing the Oryzoideae, Olyreae, and Festucoideae.

Components	Oryzoideae	Olyreae	Festucoideae
1. Rachilla bundles at floret base	one	few	few*
2. Rachilla bundle for lemma median	collateral, parallel tissues	collateral, perpendicular tissues	collateral*, perpendicular tissues
3. Rachilla bundle for lemma median with satellites	no	yes	no
4. Lower plexus	no	yes	yes*
5. Palea traces	median, laterals	laterals	laterals*†
6. Vascularized posterior lodicule	no	yes	no
7. Traces in lodicules	tracheary, sieve elements	tracheary, sieve elements	sieve elements
8. Upper plexus	no	yes	yes
9. Anterior lodicule traces and the vascular system	autonomous	integral	autonomous
10. Stamen traces and the vascular system	autonomous	integral	integral
11. Pistil plexus prongs to lower components	one, autonomous	few, integral	few, integral
12. Anterior bundle	no	no	yes
13. Posterolaterals	tracheary, sieve elements	tracheary, sieve elements	sieve elements
14. Posterolateral attachment	gynobasic, at pistil plexus	gynobasic, at pistil plexus	high, at placental bundle
15. Placental bundle maturity at anthesis	tardy	tardy	prompt
16. Placental bundle continues above ovule	no	yes	no
17. Xylem discontinuity	no	no	yes

* except *Alopecurus*

† except *Anthoxanthum*

Sources:

Oryzoideae data based specifically on *Leersia virginica* (Pizzolato, 1989b).

Olyreae data based specifically on *Raddia brasiliensis*.

Festucoideae data based specifically on *Alopecurus carolinianus* (Pizzolato, 1987), *Anthoxanthum odoratum* (Pizzolato, 1984), *Phalaris arundinacea* (Pizzolato, 1989a), *Phleum pratense* (Pizzolato, 1988), and *Triticum aestivum* (O'Brien et al., 1985).



FIGURE 16.—Facsimile of female floret vascular system at 119–164 μm above the floret base showing the upper levels of the lower plexus ($\times 500$). After the tracheary elements of M pass through the gap of the crotch of the V of bundle 3 shown in Figure 15, they descend into the posterior of bundle 3 shown by stars. There are a few contacts of the peripheral tracheary elements of M with the tracheary elements of the inside of the arms of the V from bundle 3. Sieve elements from M contact sieve elements of the V at the paired stars. Regions of the lower plexus marked by brackets and paired dots show mergers with the areas similarly shown in Figure 15. The regions between the arrows are the lowest levels of the pistil plexus filling the posterior gap of the lower plexus. Scale (3 μm in length) remains in parenchyma in the same relative position throughout all the levels of the floret. (M = lemma median trace including its superposed satellite bundle; PL = left trace of palea; PR = right trace of palea; s = sieve elements; t = tracheary elements.)

because these traces appear as minor traces by not influencing the formation of an upper plexus (Figures 8, 9, 18).

All the studied genera produce a pistil plexus at the base of the pistil from which descends one or more vascular prongs that connect to the lower components in the rachilla. The pistil plexus of the female floret of *Raddia* behaves like that of festucoid grasses by sending down multiple prongs to connect intimately with the lower components (Table 1, row 11). In the festucoid genera, the prongs from the pistil plexus merge with the upper plexus, which obstructs further descent (Pizzolato, 1984, 1987, 1988, 1989a). However, the female upper plexus of *Raddia* opens at the posterior. Therefore, the prongs from the pistil plexus of *Raddia* not only merge on the anterior with the

upper plexus (Figures 19, 18) but also on the posterior with the lower plexus (Figures 17, 16).

Although all festucoid grasses have an anterior bundle that attaches at the pistil plexus (Table 1, row 12), neither *Raddia* nor *Leersia* (Pizzolato, 1989b) has one. *Raddia* and *Leersia* are similar also in that the posterolaterals (stylar bundles) contain tracheary and sieve elements that merge with the pistil plexus below the ovule (Figure 20), not with the placental bundle at the level of the ovule typical of the festucoid grasses (Table 1, rows 13, 14).

The placental bundle emerges from the posterior of the pistil plexus in all grasses studied. The placental bundle of *Raddia* and *Leersia* is somewhat less mature by anthesis than that of

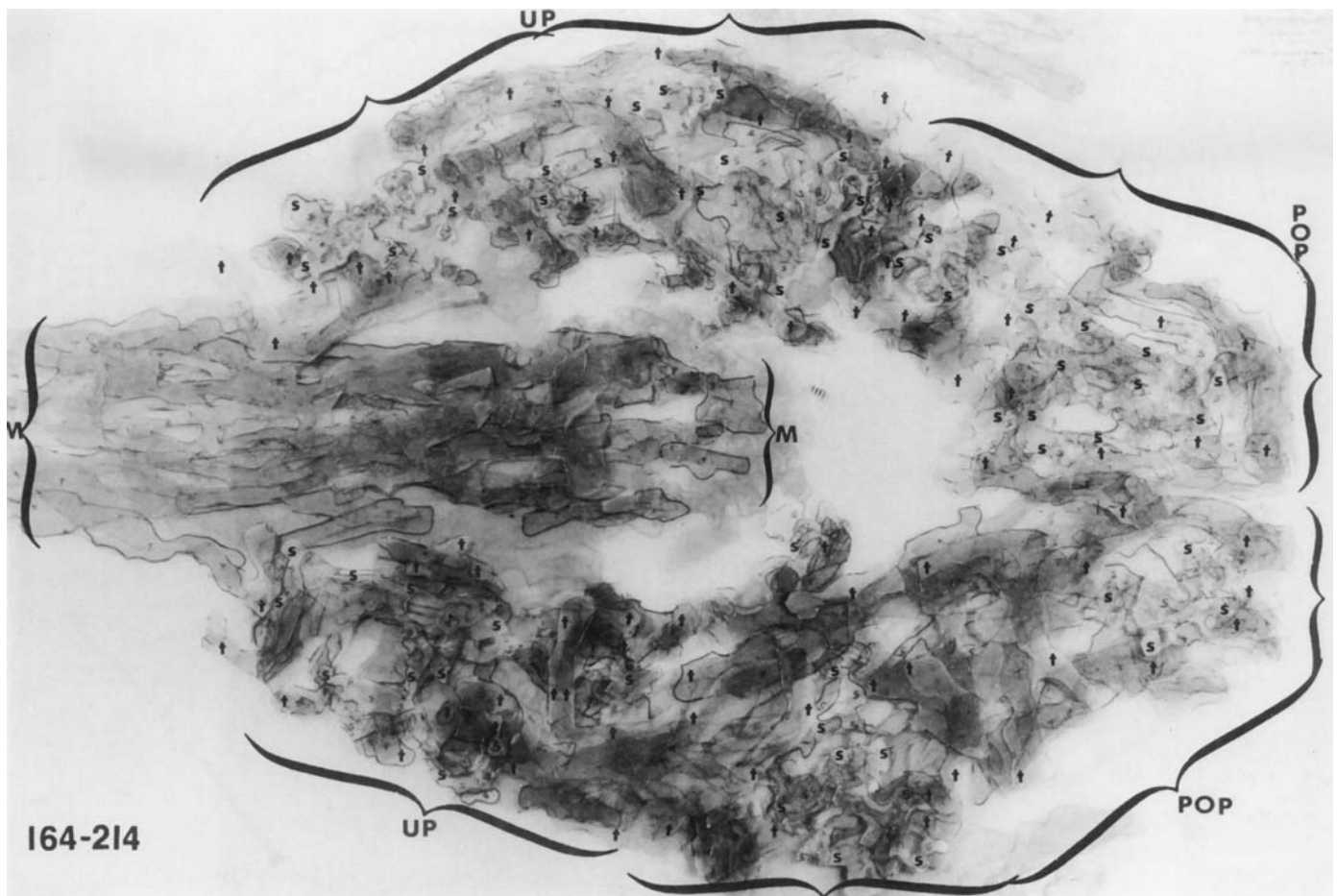


FIGURE 17.—Facsimile of female floret vascular system at 164–214 μm above the floret base showing the middle levels of the upper plexus and posterior prongs from pistil plexus ($\times 700$). Scale (3 μm long) remains in parenchyma in the same relative position throughout all of the levels of the floret. (M = upper portion of superposed or satellite bundle of lemma median consisting solely of tracheary elements; POP = lower segments of posterior prongs descended from right and left of pistil plexus in Figure 20; s = sieve elements; t = tracheary elements; UP = middle layers of right and left lobes of upper plexus rising uniformly from the lower plexus of Figure 16.)

festucoid grasses and does not widen to right and left after emerging from the placental bundle (Figure 22), as do festucoid grasses (Table 1, row 15). Despite these two similarities in the placental bundles of *Leersia* and *Raddia*, that of *Raddia* differs from that of *Leersia* and that of festucoid grasses because the placental bundle in *Raddia* exceeds the tip of the ovule (Table 1, row 16; Figure 10, level 1072).

The placental bundle and all major components of the vascular system of the festucoid grasses, except the lower plexus, contains the system of occluded, anomalous tracheary elements: the xylem discontinuity (Table 1, row 17). *Raddia* and the oryzoid grasses lack such a component, a fact that substantiates the diagnostic value of this component in delimiting the festucoid grasses from the rest of the family. Zee and O'Brien (1970) were prescient in their understanding of the significance of this component.

In considering the interconnection of the units of the vascular system of the festucoid and oryzoid grasses, Pizzolato (1989b) indicates that both groups bar the path of tracheary elements to the stamens and pistil. Festucoid grasses achieve this end with the xylem discontinuity. Oryzoid grasses do so without it but with a system of autonomous stamen and pistil components instead. On the other hand, *Raddia*, and presumably the Olyreae and bamboos in general, seem to have the most integrated, woven system of sieve and tracheary elements. Hence, there may exist fundamental differences in achieving anthesis and grain-filling between the bamboos and the rest of the grasses.

A succinct judgment of the similarities and differences in florets of *Raddia* of the Olyreae and those of the investigated festucoid and oryzoid grasses is that *Raddia* in its rachilla vascular components resembles the Festucoideae but in its

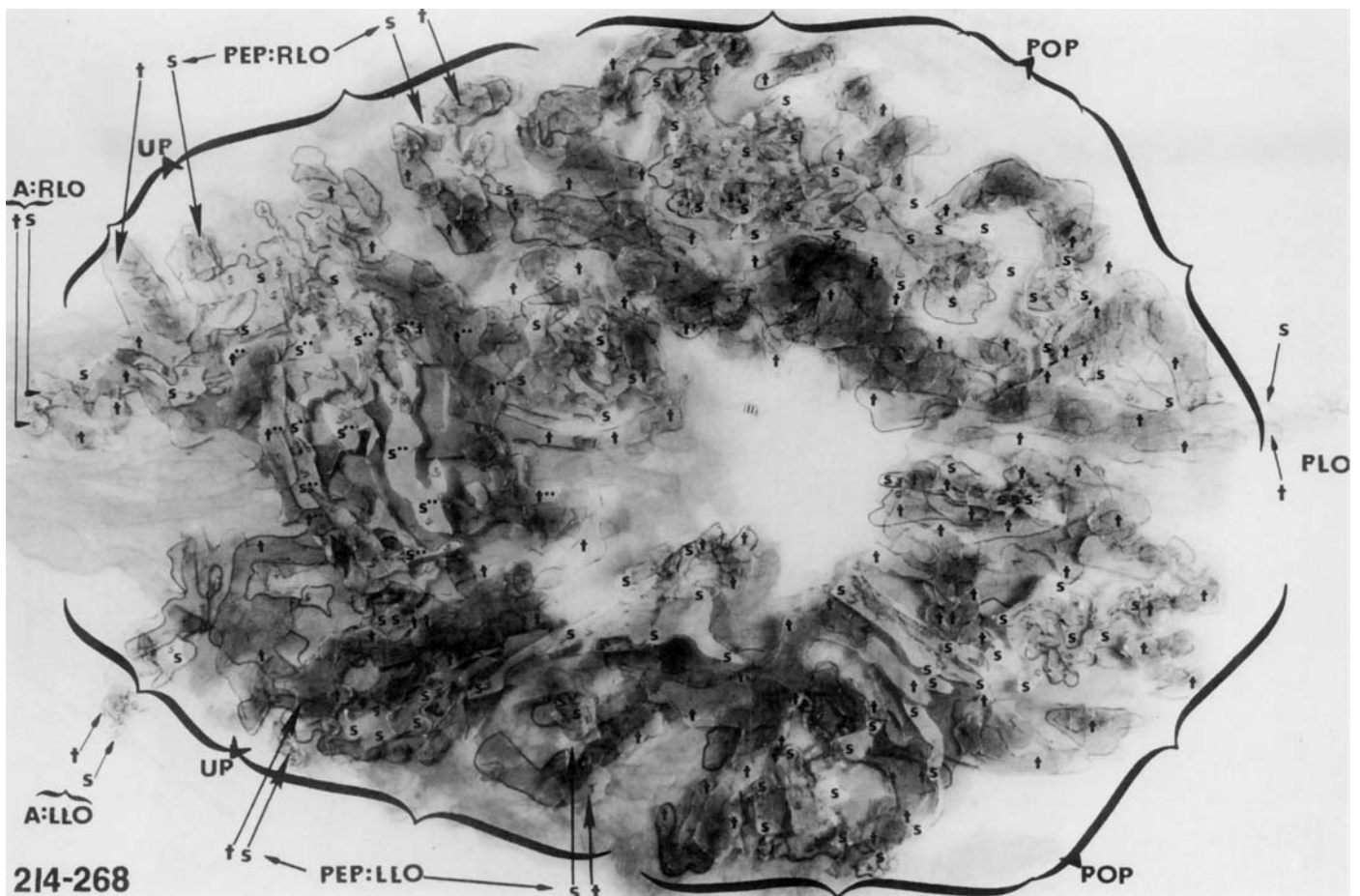


FIGURE 18.—Facsimile of female floret vascular system at 214–268 μm above floret base showing the upper levels of the upper plexus (UP), middle levels of the posterior prongs (POP) or lobes descending from the pistil plexus, and merger of lodicule traces ($\times 700$). Sieve and tracheary elements indicated by paired dots comprise the horizontal connection between the anterior segments of the upper plexus; this connection bridges the parenchyma gap over M of Figure 17. Scale (3 μm long) remains in parenchyma in same relative position throughout all of the levels of the floret. (A = anterior trace of anterior lodicules; LLO = all traces of the left anterior lodicule; PEP = peneposterior traces of both anterior lodicules; PLO = trace of posterior lodicule; RLO = all traces of right anterior lodicule; s = sieve elements; t = tracheary elements.)

pistil components resembles the Oryzoideae. However, in some of these upper and lower segments, *Raddia* differs from the group it more closely resembles. Thus, a fair statement is that, based on components of the floret vascular system, *Raddia* is no more oryzoid than it is festucoid.

FLORET VASCULAR ANATOMY SUGGESTS THAT *Raddia* BELONGS TO THE OLYREAE OF THE BAMBUSOIDEAE

Soderstrom and Zuloaga (1985) and Soderstrom and Ellis (1987) have summarized the characteristics of the spikelet that delimit the tribe Olyreae from the other bamboos. Based on these features, *Raddia* is a genus of the Olyreae. Features of the floret vascular system just enumerated were not used in this assignment. Now that the floret vascular system is known for *Raddia*, comparisons in its features can be made with the few

olyroid genera whose florets have been studied anatomically.

Calderón & Soderstrom (1973) studied the spikelets of *Maclurolyra* Calderón and Soderstrom, 1973, and Butzin (1965) studied the female spikelet of *Olyra* L., 1759. Both genera, like *Raddia*, belong to the Olyreae. In spikelet morphology and anatomy, they are similar. The male florets of *Maclurolyra* and *Olyra* are smaller than the females and lack glumes. There are two vascularized anterior lodicules, a vascularized posterior lodicule, and three vascularized stamens in the male floret of *Maclurolyra*. *Maclurolyra* differs slightly from the single studied spikelet of *Raddia* in that reduced glumes, three staminodia, and an aborted pistil may be present in the male. The female floret of *Maclurolyra* and *Olyra* has vascularized glumes, and three vascularized lodicules, and three avascular staminodia. Calderón and Soderstrom (1973) indicate that one trace joins each lodicule to the rest of the

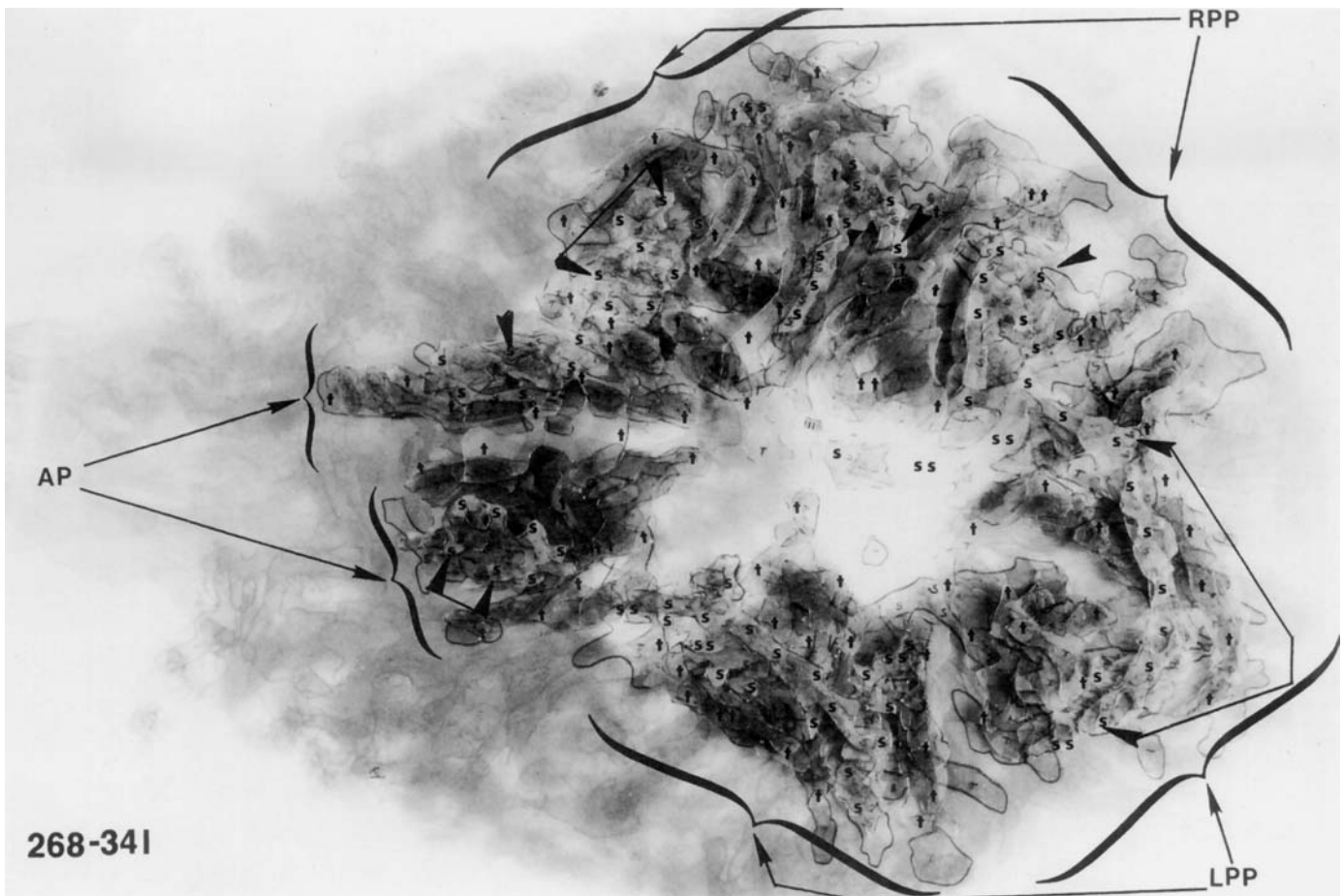


FIGURE 19.—Facsimile of female floret vascular system at 268–341 μm above floret base showing the vascular prongs descending from the pistil plexus of Figure 20 ($\times 700$). During descent, RPP and LPP become the posterior prongs of Figure 18. During descent, AP merges with the horizontal connection across the anterior of Figure 18. Darts show where clusters of sieve elements so marked in Figure 20 descended from the pistil plexus to contribute to AP, RPP, and LPP. Scale (3 μm long) remains in parenchyma in same relative position throughout all the levels of the floret. (AP = pair of anterior vascular prongs descending from anterior of pistil plexus of Figure 20; LPP = pair of vascular prongs descending on the left and posterior from the pistil plexus of Figure 20; RPP = pair of vascular prongs descending on the right and posterior from the pistil plexus of Figure 20; s = sieve elements; t = tracheary elements.)

system. However, their cleared unsectioned material did not show the two (male) or three (female) traces that merge into the rest of the system from the anterior lodicules of *Raddia*. In sectioned female florets of *Olyra*, Butzin (1965) saw the three traces from each anterior lodicule that occur in *Raddia*, as well as the solitary trace from the posterior lodicule. Calderón and Soderstrom (1973) and Butzin (1965) did not identify the vascular tissue of the lodicule traces of *Maclurolyra* and *Olyra*.

The cleared pistils of *Maclurolyra* revealed to Calderón and Soderstrom (1973) a placental bundle whose mature xylem and phloem ended at the base of the ovule, and two posterolateral (stylar) bundles of xylem and phloem. After examining several species of five genera in the Olyreae including *Maclurolyra* and *Olyra* but not *Raddia*, Calderón and Soderstrom (1973:24) concluded that a “gynoecium with three vascular traces seems

to be the general rule for the Olyreae,” a conclusion that the pistil of *Raddia* fully supports. The pistil vasculature of the Olyreae differs with that of the woody bamboos, which may have an anterior bundle as well as anterolaterals besides the placental bundle and two posterolaterals of the Olyreae (Arber, 1926; Chandra, 1963). The study of *Raddia* showed that the posterolaterals or stylar bundles attach to the pistil plexus, as occurs in the Oryzoideae, not to the placental bundle as occurs in the Festucoideae (Table 1). Although Calderón and Soderstrom (1973) were unaware of this character in the Olyreae when they studied *Maclurolyra*, their figure 13E of a cleared pistil shows this feature.

Although Calderón and Soderstrom (1973) are unclear if the placental bundle ascends beyond the ovule as happens in *Raddia*, their “connecting strand” likely is the region of merger

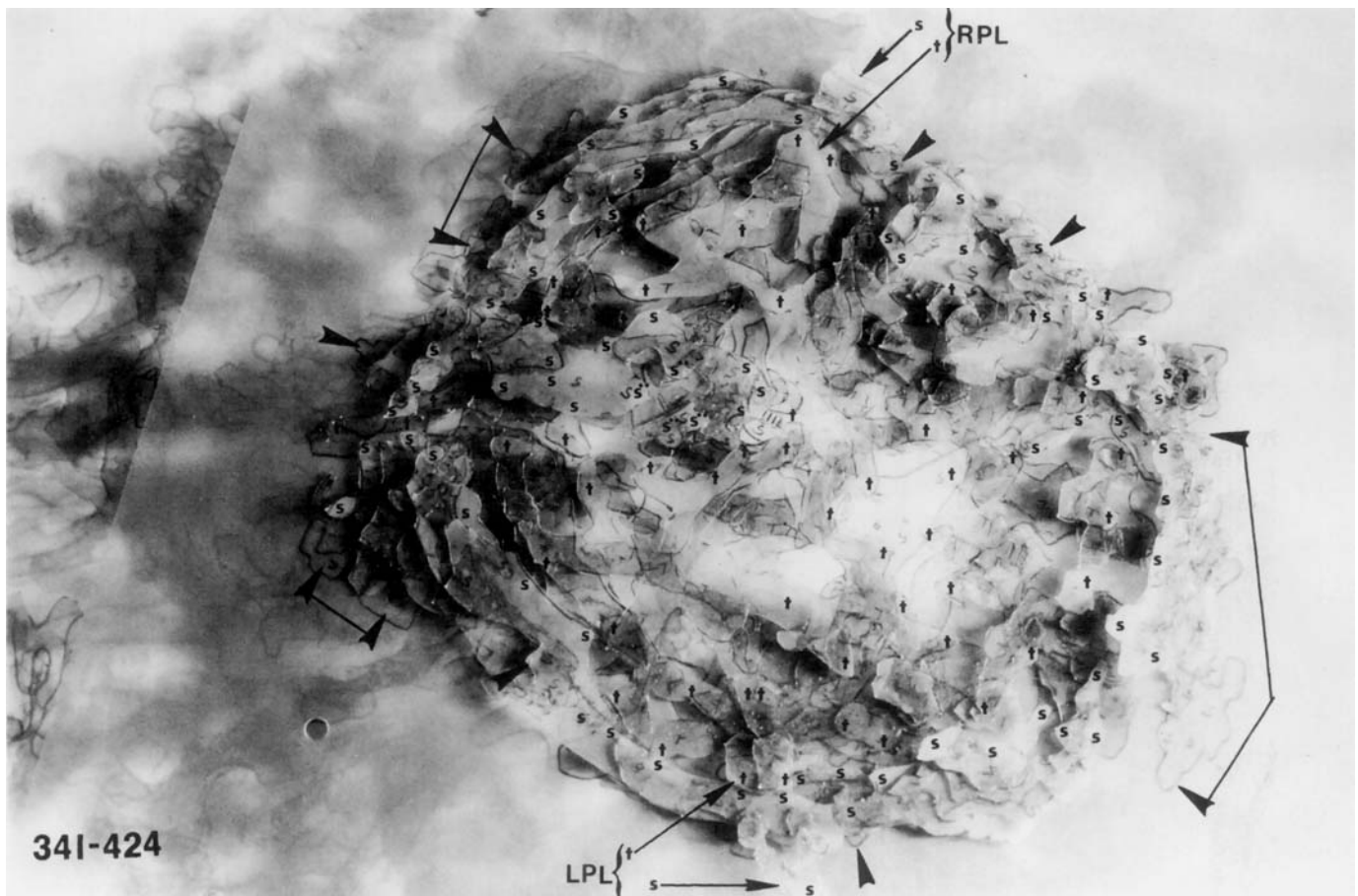


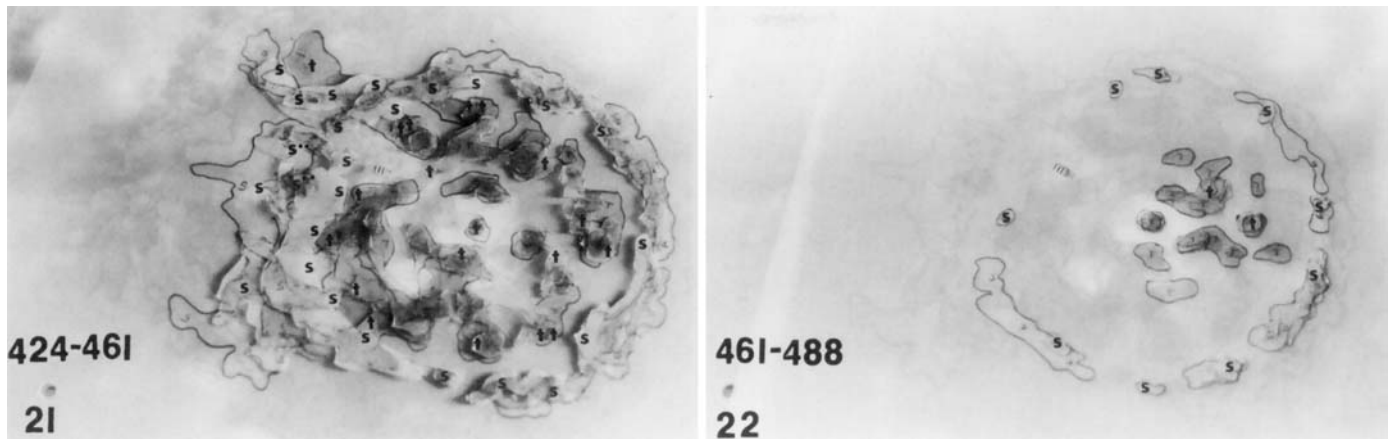
FIGURE 20.—Facsimile of female floret vascular system at 341–424 μm above floret base showing the pistil plexus ($\times 800$). Paired dots show core of sieve elements among tracheary elements but continuous with sieve elements of the periphery of the pistil plexus; as pistil plexus contracts to form the placental bundle of Figure 21, its anterior sieve elements (paired dots in Figure 21) connect at this sieve-element core. Darts show whence clusters of sieve elements descend to connect with those so marked in Figure 19. Scale (3 μm long) remains in parenchyma in same relative position throughout all the levels of the floret. (LPL = site of merger of left posterolateral (stylar) bundle with pistil plexus; RPL = site of merger of right posterolateral (stylar) bundle with pistil plexus; s = sieve elements; t = tracheary elements.)

of the placental bundle above the ovule with the stylar core as shown for *Raddia* in Figure 11, level 1072. The study of *Raddia* supported by Calderón and Soderstrom's (1973) study of the pistil of *Maclurolyra* indicates that the placental bundle ascends a little above the ovule before being superseded by the stylar core. Among the non-olyroid bamboos, there is variation in this character (Arber, 1926; Chandra, 1963).

Only two earlier studies exist in which florets from the Olyreae or its allied tribe, the Streptochaeteae of Soderstrom and Ellis (1987), were studied in sectioned material. When these papers are examined in light of the *Raddia* study, some pertinent similarities in the vascular systems of these olyroid bamboos are revealed. In Butzin's (1965) study of the female spikelet of *Olyra*, figure 5, is oriented so that the floret's posterior is to the left of the page. His figure 5E is nearly identical to Figure 10, level 1 of *Raddia* (herein) showing the

rachilla with bundles 3, 2, and 1 surrounded by the glumes. Butzin's (1965) figure 5F is virtually identical to Figures 14 and 15 of *Raddia* showing bundles 3, 2, and 1 simultaneously forming their respective traces to M and the lemma laterals while they form the lower plexus.

Butzin's (1965) comment that the lemma and palea lateral traces on each side of the rachilla connect closely with each other and the bundle of *Olyra* corresponding to bundles 1 (or 2) of *Raddia* relates well to the pertinent observations in *Raddia*. In *Raddia*, bundle 1 (or 2) occurs in the rachilla as a lemma left (or right) lateral. The other member of the lemma lateral pair merges so soon with bundle 1 (or 2) that it is difficult to be certain which one of the lateral pair was the original bundle 1 (or 2). Then the left (or right) lateral of the palea merges with the mergers of the paired lemma laterals as they are proliferating to form the flanks of the lower plexus of *Raddia*



FIGURES 21, 22.—Facsimile of female floret vascular system at 424–461 and 461–488 μm above floret base showing the upper levels of the pistil plexus and the lower levels of the placental bundle ($\times 700$). Sieve elements marked with paired dots are continuous with those so marked in Figure 20. With ascent from Figure 20, the pistil plexus contracts toward the posterior and opens at the anterior to become the placental bundle. Scale (3 μm long) remains in parenchyma in same relative position throughout all the levels of the floret. (s = sieve elements; t = tracheary elements.)

(Figures 13–16). “Deck- und Vorspelzennervatur stehen also in engem Konnex” [thus the lemma and palea traces are closely connected] in the rachilla of *Olyra* (Butzin, 1965:36) and *Raddia*.

Butzin’s (1965) figure 5G is like Figure 16 of *Raddia* because both show the top layers of the lower plexus and the superposed portion of the lemma median. Butzin’s (1965) figure 5L,M indicates that, as in *Raddia*, the posterolaterals are gynobasic. Although Calderón and Soderstrom (1973) also studied Butzin (1965), they were unable to make revealing comparisons with his figure 5 because they lacked comparative sectioned material of *Maclurolyra*. The posterolaterals merge at the flanks of the pistil plexus as they do in *Raddia*. As in *Raddia* there is no other bundle in the pistil besides the posterolaterals and the placental bundle (Butzin, 1965).

Arber’s (1929) study of the sectioned perfect floret of *Streptochaeta*, which she orients with the anterior to the bottom of the page, is also informative when compared with *Raddia*. Bundles 3, 2, and 1 are arranged in the rachilla at the floret base in Arber’s (1929) figure 4A2 of *Streptochaeta* just as they are in *Raddia* and *Olyra*. Arber’s (1929) figure 4A3–5 indicates that M from bundle 3 follows the same tortuous course below a lemma pocket as does M in the male floret of *Raddia*. Arber’s figure 4A5 is like a sketch of Figure 16 of *Raddia* showing the superposed portion of M between the upper levels of the lower plexus. Arber’s (1929) figure 4A6 of *Streptochaeta* suggests the gynobasic nature of the posterolateral attachment of *Raddia*, *Olyra*, and *Maclurolyra*. The anterior bundle of *Streptochaeta* distinguishes the Streptochaeteae from the Olyreae.

The similarities of the floret vascular system of *Raddia* with those revealed by the earlier studies of *Streptochaeta* (Arber, 1929), *Olyra* (Butzin, 1965) and *Maclurolyra* (Calderón and

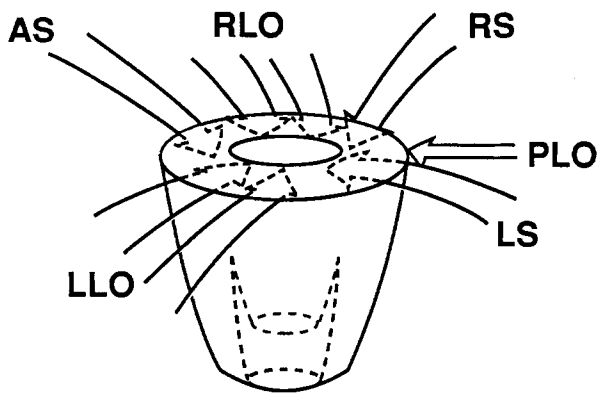
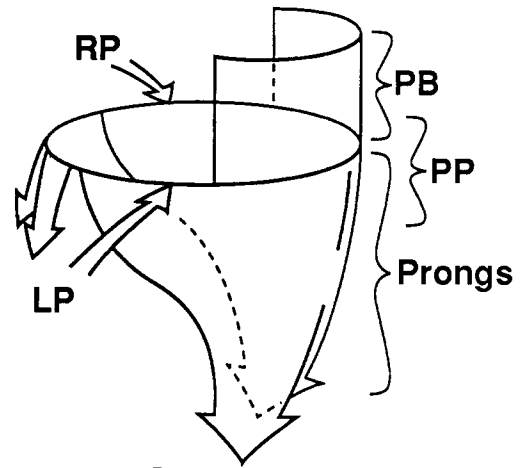
Soderstrom, 1973) indicate that the floret vascular system of *Raddia* typifies the Olyreae and the Streptochaeteae. Moreover, the similarities of the floret vascular system of these tribes with the corresponding characters recorded for the woody bamboos (Arber, 1926, 1929; Chandra, 1963; Butzin, 1965) support the inclusion of the Olyreae and Streptochaeteae among the bamboos by Soderstrom and Ellis (1987), who used a suite of other morphological and anatomical characters including the supernumerary midrib bundles of Page (1947), Metcalfe (1960), and Renvoize (1985).

FLORET VASCULAR ANATOMY SUGGESTS THAT *Raddia* AND THE OLYREAE ARE NOT PANICOID GRASSES

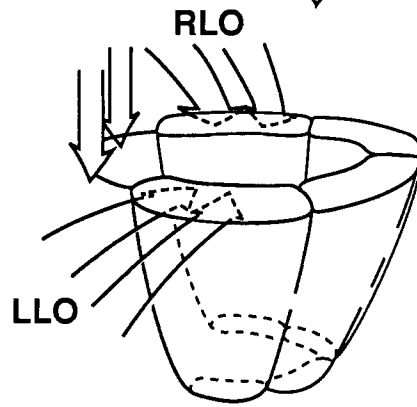
If the vascular system in both florets of *Raddia* and its allies is compared with that of *Panicum* L., 1753 (Pizzolato, 1983), *Raddia* is found strikingly different from *Panicum* and more like the genera whose florets have been analyzed three dimensionally (Table 1). The palea traces of these nonpanicoid grasses do not descend the rachilla beyond the floret base without linking with other traces of the rachilla (Pizzolato, 1984, 1987, 1988, 1989a, b). The palea traces must first be part of the lower plexus (*Phalaris*) or be obstructed by the lower plexus (*Raddia*, *Anthoxanthum*), or be obstructed by traces of the lemma median (*Leersia*, *Alopecurus*) or laterals (*Phleum*). In *Panicum*, the palea traces and lemma laterals do not interconnect with the rest of the floret system in the rachilla at the floret base. Apparently Chandra (1962) and Clifford (1987) attempt to make similar distinctions between panicoid and nonpanicoid grasses without having analyzed the floret vascular system three dimensionally.

In nonpanicoid florets, the components of the vascular

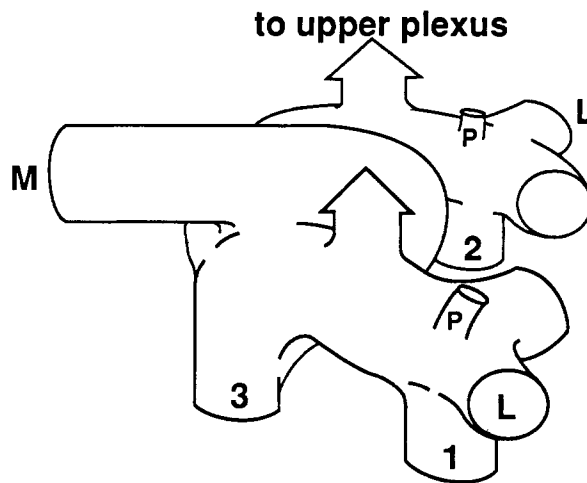
D. Pistil components



B. ♂ Upper plexus



C. ♀ Upper plexus with descending pistil plexus prongs



A. Lower plexus

FIGURE 23.—Diagrams of the components of the vascular system of the male floret and the female floret. In the lower plexus, the subsidiary bundles of M are shown united as they occur in the female floret, not discrete as they occur in the male floret. (AS = anterior stamen trace; L = lateral traces of the lemma; LLO = traces of left anterior lodicule; LP = left posterolateral bundle; LS = trace of left stamen; M = median trace of lemma; P = palea trace; PB = placental bundle; PLO = trace of posterior lodicule; PP = pistil plexus; RLO = traces of right anterior lodicule; RP = right posterolateral bundle; RS = trace of right stamen; 1, 2, 3 = bundles 1, 2, 3.)

system above the lemma median merge axially (directly) with bundle 3; but the higher components of *Panicum* merge with the lemma median diagonally, giving the system an unguil morphology (Pizzolato, 1983). The floret of *Panicum* lacks a lower plexus and an upper plexus in vivid contrast to the condition in *Raddia*. The stamen traces of *Panicum* appear autonomous as in *Leersia*; thus, there is a gap in the rachilla between the flanking stamens of *Panicum* not allowable by the stamen traces to the upper plexus of the male floret of *Raddia* or of a festucoid grass.

Additionally, there is a marked distinction between the course of the placental bundle between *Raddia* and the panicoid grasses. In *Raddia* and *Maclurolyra* (Calderón and Soderstrom, 1973), the placental bundle ascends the length of the ovary but in the Paniceae, the placental bundle merges with the ovule at the base of the ovary (Zee and O'Brien, 1971; Giles et al., 1975).

Therefore, anatomy of the floret vascular systems does not support placing the Olyreae among the Paniceae despite the fact that both groups host similar rust fungi (Savile, 1987). Floret vascular anatomy, certainly as esoteric (Macfarlane and Watson, 1982) as rust susceptibility, supports the schemes of natural classification of Hilu and Wright (1982) and Watson et al. (1985) that place the Olyreae away from the Panicoideae. Root anatomy supports this conclusion from floret vasculature, for Raechel and Curtis (1990) observe that certain genera of the Olyreae including *Raddia* have several features that vary from the panicoid type.

FLORET VASCULAR ANATOMY SUGGESTS THAT *Brachyelytrum* IS NOT AN OLYROID GRASS

The association of superposed bundles with the lemma median of male and female florets of *Raddia*, and the occurrence of these bundles in the midribs of genera of the Olyreae (Soderstrom and Zuloaga, 1985) including *Raddia* strongly support the inclusion of the Olyreae among the Bambusoideae as suggested by Page (1947), Metcalfe (1960), and Soderstrom and Ellis (1987). Therefore, the absence of superposed midrib bundles (Campbell et al., 1986) from the *Brachyelytrum* Palisot de Beauvois, 1812 of "chequered classificatory history" (Macfarlane and Watson, 1980:650) does not support its inclusion in the Olyreae.

That the pistil of *Raddia* lacks an anterior bundle but has two posterolaterals besides the placental bundle supports the

placement of *Raddia* among the Olyreae according to the conclusions of Calderón and Soderstrom (1973:24) that "gynoecium with three vascular traces seems to be the general rule for the Olyreae." The suggestion that *Brachyelytrum* be included with the Olyreae (Campbell et al., 1986) is not supported by Belk (1939:72) who noted that "three vascular strands in addition to the ovule supply bundle are present in the gynoecium." Moreover, Belk's (1939) figures 294–300 plainly show the anterior bundle in the pistil of *Brachyelytrum*. Furthermore, *Brachyelytrum* should be excluded from the Olyreae because Belk (1939) indicates that the ovule supply bundle (placental bundle) does not extend beyond the ovule, whereas the reverse is probably true of *Maclurolyra* and definitely of *Raddia* of the Olyreae. Belk (1939) shows that *Brachyelytrum* lacks the stylar core which supersedes the placental bundle of *Raddia* and *Maclurolyra* of the Olyreae and many other bamboos. Wherever the affinities of *Brachyelytrum* lie, they are probably not with the Olyreae.

FLORET VASCULAR ANATOMY SUGGESTS THAT *Raddia* AND THE OLYREAEE ARE NOT OLYROID GRASSES

Using a multitude of characters, character states, and genera, Watson et al. (1985) place olyroid grasses including *Raddia*, *Maclurolyra*, and *Olyra* together with oryzoid grasses including *Leersia*, *Luziola* Jussieu, 1789, and *Oryza* into a supertribe separate from another supertribe containing woody bamboos. By placing *Streptochaeta* into the supertribe of woody bamboos, away from the Olyreae, Watson et al. (1985) discount the olyroid affinity of *Streptochaeta*.

However, the floret vascular system of *Raddia* indicates that olyroid grasses should be classified separately from the oryzoid grasses. The olyroid grasses are no more similar to the oryzoid grasses in floret vasculature than the olyroid grasses are to the festucoid grasses (Table 1). Moreover, Table 1 indicates three features of floret vasculature in the Olyreae not found in either the Oryzoideae or Festucoideae of Hilu and Wright (1982). The floret vascular systems of *Raddia* and of the herbaceous bamboos *Streptochaeta* (Arber, 1929), *Olyra* (Butzin, 1965), and *Maclurolyra* (Calderón and Soderstrom, 1973) support the notion of a close affinity of the olyroid grasses—not encumbered by the oryzoid grasses—with the woody bamboos suggested by the anatomical and systematic studies of Page (1947), Metcalfe (1960), Soderstrom and Ellis (1987), and Hilu and Wright (1982). Although Hilu and Wright (1982) included fewer characters and genera in their scheme of classification, as summarized in their Figures 1 and 6, than did Watson et al. (1985), the former system is harmonious with the affinities deduced from floret vasculature for the Festucoideae, the Oryzoideae, and the Bambusoideae including *Olyra*. Connor (1979) and Stebbins (1987) overemphasize the importance of the frequently similar stamen number among bambusoid and oryzoid grasses as an indicator of their close affinity. The

autonomous connections of the stamen traces of *Leersia* (Pizzolato, 1989b) to the rachilla vascular system, without an upper plexus, is too different from the intimate connection of the stamen traces of the female floret of *Raddia*, via an upper plexus, to be obscured by similarity of stamen number.

Pertinent to these conclusions are four bits of data as esoteric (Macfarlane and Watson, 1982) as floret vascular systems. First, Savile (1987) observed that rusts that parasitize *Leersia* produce teliospores very different from those that parasitize *Oryza*. Second, Hamby and Zimmer (1988) were puzzled that nucleotide sequences of RNA's from *Oryza* and *Arundinaria*

Michaux, 1803, a woody bamboo (Tucker, 1988), were not as similar as the scheme of Watson et al. (1985) suggests the sequences should be. Third, Esen and Hilu (1989) indicate that the low immunological similarity of prolamin seed proteins from another woody bamboo and *Oryza* opposes the idea of the Oryzoideae as part of the Bambusoideae. Fourth, Bhanwra (1988) noted features in the microsporangia and ovule of *Oryza* which keep the genus apart from some species of woody bamboos. These sets of esoteric distinctions are consistent with the differences noted between vascular systems of florets in the Oryzoideae and in the Olyreae.

Literature Cited

- Arber, A.
 1926. Studies in the Gramineae, I: The Flowers of Certain Bambuseae. *Annals of Botany*, 40:447-469.
 1928. Studies in the Gramineae, V: 1, On *Luziola* and *Dactylis*; 2, On *Lygeum* and *Nardus*. *Annals of Botany*, 42:391-407.
 1929. Studies in the Gramineae, VI: 1, *Streptochaeta*; 2, *Anomochloa*; 3, *Ichnanthus*. *Annals of Botany*, 43:35-53.
 1934. *The Gramineae: A Study of Cereal, Bamboo, and Grass*. 480 pages. Cambridge: The University Press.
- Aziz, P.
 1972. Histogenesis of the Carpel in *Triticum aestivum* L. *Botanical Gazette*, 133:376-386.
 1978. Initiation of Procambial Strands in the Primordium of Stamens and Carpel of *Triticum aestivum* L. *Pakistan Journal of Scientific and Industrial Research*, 21:12-16.
 1981. Initiation of Primary Vascular Elements in the Stamens and Carpel of *Triticum aestivum* L. *Botanical Journal of the Linnean Society*, 82:69-79.
- Barnard, C.
 1957. Floral Histogenesis in the Monocotyledons, I: The Gramineae. *Australian Journal of Botany*, 5:1-20.
- Belk, E.
 1939. Studies in the Anatomy and Morphology of the Spikelet and Flower of Gramineae. 183 pages, 510 figures. Doctoral dissertation, Cornell University, Ithaca, New York.
- Bhanwra, R.K.
 1988. Embryology in Relation to Systematics of Gramineae. *Annals of Botany*, 62:215-233.
- Butzin, F.
 1965. Neue Untersuchungen über die Blüte der Gramineae. 183 pages, 35 figures, 8 plates. Doctoral dissertation. Freie Universität, Berlin.
- Calderón, C.E., and T.R. Soderstrom
 1973. Morphological and Anatomical Considerations of the Grass Subfamily Bambusoideae Based on the New Genus *Maclurolyra*. *Smithsonian Contributions to Botany*, 11:1-55.
- Campbell, C.S., P.E. Garwood, and L.P. Specht
 1986. Bambusoid Affinities of the North Temperate Genus *Brachyelytrum* (Gramineae). *Bulletin of the Torrey Botanical Club*, 113:135-141.
- Chandra, N.
 1962. Morphological Studies in the Gramineae, I: Vascular Anatomy of the Spikelet in the Pooideae. *Proceedings of the National Institute of Sciences of India*, 28B:545-562.
 1963. Morphological Studies in the Gramineae, III: On the Nature of the Gynoecium in the Gramineae. *Journal of the Indian Botanical Society*, 42:252-259.
- Clifford, H.T.
 1987. Spikelet and Floret Morphology. In T.R. Soderstrom et al., editors, *Grass Systematics and Evolution*, pages 21-30. Washington, D.C.: Smithsonian Institution Press.
- Connor, H.E.
 1979. Breeding Systems in the Grasses: A Survey. *New Zealand Journal of Botany*, 17:547-574.
- Craig, S., and T.P. O'Brien
 1975. The Lodicules of Wheat: Pre- and Post-Anthesis. *Australian Journal of Botany*, 23:451-458.
- Davidse, G.
 1987. Fruit Dispersal in the Poaceae. In T.R. Soderstrom et al., editors, *Grass Systematics and Evolution*, pages 143-155. Washington, D.C.: Smithsonian Institution Press.
- Dengler, N.G., R.E. Dengler, and P.W. Hattersley
 1985. Differing Ontogenetic Origins of PCR ("Kranz") Sheaths in Leaf Blades of C₄ Grasses (Poaceae). *American Journal of Botany*, 72:284-302.
- Esau, K.
 1953. Anatomical Differentiation in Shoot and Root Axes. In W.E. Loomis, editor, *Growth and Differentiation in Plants*, pages 69-100. Ames: Iowa State College Press.
 1977. *Anatomy of Seed Plants*. Second edition, 550 pages. New York: John Wiley and Sons.
- Esen, A., and K.W. Hilu
 1989. Immunological Affinities Among Subfamilies of the Poaceae. *American Journal of Botany*, 76:196-203.
- French, J.C., and P.B. Tomlinson
 1983. Vascular Patterns in Stems of Araceae: Subfamilies Colocasioideae, Aroideae and Pistioideae. *American Journal of Botany*, 70:756-771.
- Frick, H., and T.D. Pizzolato
 1987. Adaptive Value of the Xylem Discontinuity in Partitioning of Photoassimilate to the Grain. *Bulletin of the Torrey Botanical Club*, 114:252-259.
- Giles, K.L., H.C.M. Bassett, and J.D. Eastin
 1975. The Structure and Ontogeny of the Hilum Region in *Sorghum bicolor*. *Australian Journal of Botany*, 23:795-802.
- Gould, F.W., and R.B. Shaw
 1983. *Grass Systematics*. Second edition, 397 pages. College Station: Texas A & M University Press.
- Hamby, R.K., and E.A. Zimmer
 1988. Ribosomal RNA Sequences for Inferring Phylogeny within the Grass Family (Poaceae). *Plant Systematics and Evolution*, 160:29-37.
- Hilu, K.W., and K. Wright
 1982. Systematics of Gramineae: A Cluster Analysis Study. *Taxon*, 31:9-36.
- Hitch, P.A., and B.C. Sharman
 1968. Initiation of Procambial Strands in Leaf Primordia of *Dactylis glomerata* L. as an Example of a Temperate Herbage Grass. *Annals of Botany*, 32:153-164.
 1971. The Vascular Pattern of Festucoid Grass Axes with Particular Reference to Nodal Plexi. *Botanical Gazette*, 132:38-56.
- Holt, I.V.
 1954. Initiation and Development of the Inflorescences of *Phalaris arundinacea* L. and *Dactylis glomerata* L. *Iowa State College Journal of Science*, 28:603-621.
- Kawahara, H., T. Matsuda, and N. Chonan
 1977. Studies on Morphogenesis in Rice Plant, IX: On the Structure of Vascular Bundles and Phloem Transport in the Spikelet. *Japanese Journal of Crop Science*, 46:82-90.
- Larson, P.R.
 1975. Development and Organization of the Primary Vascular System in *Populus deltoides* according to Phyllotaxy. *American Journal of Botany*, 62:1084-1099.
- Lingle, S.E., and P. Chevalier
 1985. Development of the Vascular Tissue of the Wheat and Barley Caryopsis as Related to the Rate and Duration of Grain Filling. *Crop Science*, 25:123-128.

- Macfarlane, T.D., and L. Watson
 1980. The Circumscription of Poaceae Subfamily Pooideae, with Notes on Some Controversial Genera. *Taxon*, 29:645-666.
 1982. The Classification of Poaceae Subfamily Pooideae. *Taxon*, 31:178-203.
- Maze, J., L.R. Bohm, and C.E. Beil
 1972. Studies on the Relationships and Evolution of Supraspecific Taxa Utilizing Developmental Data, 1: *Stipa lemonii* (Gramineae). *Canadian Journal of Botany*, 50:2327-2352.
- Maze, J., N.G. Dengler, and L.R. Bohm
 1971. Comparative Floret Development in *Stipa tortillis* and *Oryzopsis miliacea* (Gramineae). *Botanical Gazette*, 132:273-298.
- Metcalf, C.R.
 1960. *Anatomy of the Monocotyledons, I: Gramineae*. 731 pages. Oxford: Clarendon Press.
- O'Brien, T.P., M.E. Sammut, J.W. Lee, and M.G. Smart
 1985. The Vascular System of the Wheat Spikelet. *Australian Journal of Plant Physiology*, 12:487-511.
- Page, V.M.
 1947. Leaf Anatomy of *Streptochaeta* and the Relation of this Genus to the Bamboos. *Bulletin of the Torrey Botanical Club*, 74:232-239.
- Patrick, J.W.
 1972. Vascular System of the Stem of the Wheat Plant, II: Development. *Australian Journal of Botany*, 20:65-78.
- Pissarek, H.-P.
 1971. Untersuchungen über Bau und Funktion der Gramineen-Lodiculae. *Beiträge zur Biologie der Pflanzen*, 47:313-370.
- Pizzolato, T.D.
 1983. A Three-Dimensional Reconstruction of the Vascular System to the Lodicules, Androecium, and Gynoecium of a Fertile Floret of *Panicum dichotomiflorum* (Gramineae). *American Journal of Botany*, 70:1173-1187.
 1984. Vascular System of the Fertile Floret of *Anthoxanthum odoratum* L. *Botanical Gazette*, 145:358-371.
 1987. Vascular System of the Floret of *Alopecurus carolinianus* (Gramineae). *Canadian Journal of Botany*, 65:2592-2600.
 1988. Vascular System of the Floret of *Phleum pratense*. *Canadian Journal of Botany*, 66:1818-1829.
 1989a. Vascular System of the Fertile Floret of *Phalaris arundinacea*. *Canadian Journal of Botany*, 67:1366-1380.
 1989b. Vascular System of the Floret of *Leersia virginica* (Gramineae-Oryzoideae). *American Journal of Botany*, 76:589-602.
- Pizzolato, T.D., and K. Robinson-Beers
 1987. Initiation of the Vascular System in the Fertile Floret of *Anthoxanthum odoratum* (Gramineae). *American Journal of Botany*, 74:463-470.
- Raechal, L.J., and J.D. Curtis
 1990. Root Anatomy of the Bambusoideae (Poaceae). *American Journal of Botany*, 77:475-482.
- Renvoize, S.A.
 1985. A Survey of Leaf-Blade Anatomy in Grasses, V: The Bamboo Allies. *Kew Bulletin*, 40:509-535.
- Robinson-Beers, K., and T.D. Pizzolato
 1987a. Development of the Vascular System in the Fertile Floret of *Anthoxanthum odoratum* L. (Gramineae), I: Traces to the Fertile Lemma and Palea. *Botanical Gazette*, 148:51-66.
 1987b. Development of the Vascular System in the Fertile Floret of *Anthoxanthum odoratum* L. (Gramineae), II: Sieve-Element Plexus, Stamen Traces, and the Xylem Discontinuity. *Botanical Gazette*, 148:209-220.
 1987c. Development of the Vascular System in the Fertile Floret of *Anthoxanthum odoratum* L. (Gramineae), III: Vasculature Supplying the Gynoecium. *Botanical Gazette*, 148:346-359.
- Savile, D.B.O.
 1987. Use of Rust Fungi (Uredinales) in Determining Ages and Relationships in Poaceae. In T. R. Soderstrom et al., editors, *Grass Systematics and Evolution*, pages 168-178. Washington, D. C.: Smithsonian Institution Press.
- Sharman, B.C.
 1960a. Development of the Inflorescence and Spikelets of *Anthoxanthum odoratum* L. *New Phytologist*, 59:60-64.
 1960b. Developmental Anatomy of the Stamen and Carpel Primordia in *Anthoxanthum odoratum*. *Botanical Gazette*, 121:192-198.
- Soderstrom, T.R., and R.P. Ellis
 1987. The Position of Bamboo Genera and Allies in a System of Grass Classification. In T. R. Soderstrom et al., editors, *Grass Systematics and Evolution*, pages 225-238. Washington, D.C.: Smithsonian Institution Press.
- Soderstrom, T.R., and F.O. Zuloaga
 1985. New Species of Grasses in *Arberella*, *Cryptochloa*, and *Raddia* (Poaceae: Bambusoideae: Olyreae). *Brittonia*, 37:22-35.
- Stebbins, G. L.
 1987. Grass Systematics and Evolution: Past, Present, and Future. In T. R. Soderstrom et al., editors, *Grass Systematics and Evolution*, pages 359-367. Washington, D.C.: Smithsonian Institution Press.
- Tucker, G.C.
 1988. The Genera of Bambusoideae (Gramineae) in the Southeastern United States. *Journal of the Arnold Arboretum*, 69:239-273.
- Watson, L., H.T. Clifford, and M.J. Dallwitz
 1985. The Classification of Poaceae: Subfamilies and Supertribes. *Australian Journal of Botany*, 33:433-484.
- Zee, S.-Y.
 1972. Vascular Tissue and Transfer Cell Distribution in the Rice Spikelet. *Australian Journal of Biological Sciences*, 25:411-414.
- Zee, S.-Y., and T.P. O'Brien
 1970. A Special Type of Tracheary Element Associated with "Xylem Discontinuity" in the Floral Axis of Wheat. *Australian Journal of Biological Sciences*, 23:783-791.
 1971. Aleurone Transfer Cells and Other Structural Features of the Spikelet of Millet. *Australian Journal of Biological Sciences*, 24:391-395.
- Zimmermann, M.H., and P.B. Tomlinson
 1972. The Vascular System of Monocotyledonous Stems. *Botanical Gazette*, 133:141-155.