

## One-Nerved Paleas in *Cinna arundinacea* L. (Poaceae)<sup>1</sup>

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### ABSTRACT

Electron microscopic analysis of cross-sections of the 1-keeled paleas of *Cinna arundinacea* reveals a single vascular trace. *Cinna bolanderi* exhibits 2-keeled paleas, each keel with a single trace.

### INTRODUCTION

A spikelet, the basic unit of a grass inflorescence, consists of an axis (=rachilla) bearing 1 or more flowers and associated bracts. Each flower is subtended by a usually membranous bract, the palea, and the combined flower/palea is, in turn, subtended by a scale-like lemma. For the vast preponderance of non-bam- busoid grasses, the palea is 2-keeled (1), but Bews (2) noted that some grasses bear paleas that are apparently 1-nerved. Chase (3) concluded that in these grasses "... the nerves are so close together as to appear like a single one." In contrast, Pilger (4) postulated that the single keel is the result of connation of the 2 nerves. Both views are highly speculative. Pizzolato (5) showed that the 1-keeled palea of the fertile floret of *Anthoxanthum odoratum* has a single vascular trace. There is some controversy, however, concerning the homology of this structure (6, 7). If the unit is a palea, then the observation of Pizzolato clearly contradicts the generalization of Chase; however, it does not provide confirmation of the fusion of keels in the evolution of 1-keeled paleas.

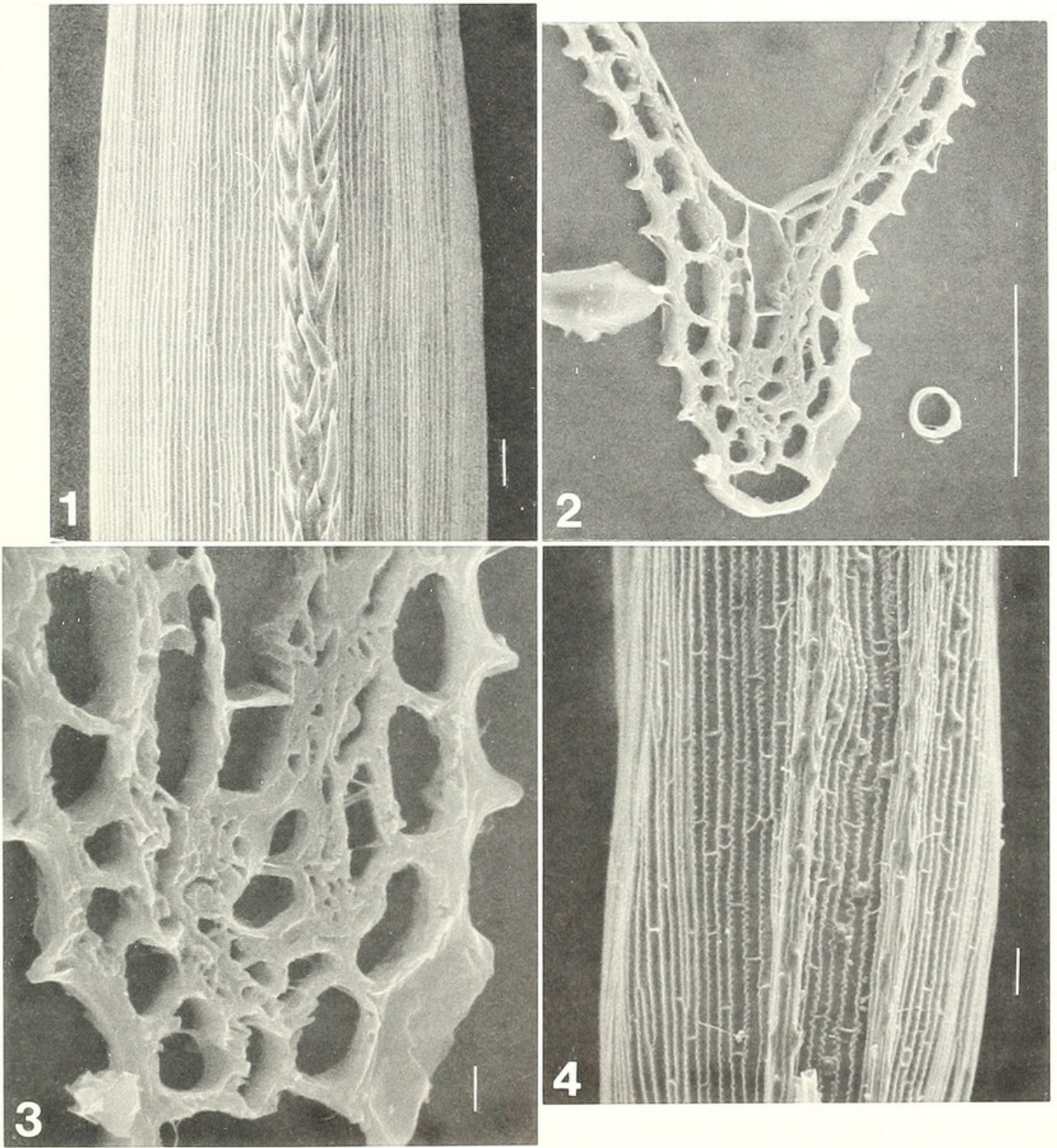
*Cinna arundinacea* also has a 1-keeled palea (8, 9), whereas the three other species in the

genus have paleas with 2 keels; there is no doubt that these paleas are homologous structures or that the single keel is the derived state. This species, therefore, provides an excellent opportunity to explore the morphology of 1-keeled paleas as a prologue to understanding their evolutionary origins. Accordingly, we studied the vasculature of the palea of *C. arundinacea* to determine whether there is a single keel or 2 closely placed ones and if the keel, or keels, has 1 or more vascular traces.

### MATERIALS AND METHODS

Spikelets to be sectioned were removed from dried herbarium specimens, soaked in Vatsol for 2 hr, dehydrated with an ethanol series (10%  $\gg$  100%), transferred to a mixture of Spurr's resin and propylene oxide (2:1), stored overnight, and transferred to a 2:1 mixture for 2 hr. Infiltration was completed in pure resin for 3 hr. Spikelets were then embedded in blocks of fresh resin and allowed to harden overnight in an oven at 60°C. Sections 5  $\mu$ m thick were cut with a glass knife on an ultramicrotome and mounted on glass slides by heating them over an alcohol flame. The sections were then subjected to a resin extraction procedure modified from Russell and Daghljan (10), outlined as follows: Acetone, benzene, and 0.5% KOH (1:1:2) (10 min)  $\gg$  1% acetic acid and 100% methanol (1:1) (2 min)  $\gg$  100%

<sup>1</sup> Reprint requests should be sent to JRE.



FIGS. 1-4. Paleas of *Cinna*, electron micrographs. 1. *C. arundinacea*, one-keeled palea. 2. *C. arundinacea*, cross-section of palea. 3. *C. arundinacea*, cross-section of palea. 4. *C. bolanderi*, two-keeled palea. Scale = 30  $\mu\text{m}$  (Figs. 1, 2, 4), 3  $\mu\text{m}$  (Fig. 3).

methanol (5 min)  $\gg$  100% methanol and 100% ethanol (1:1) (2 min)  $\gg$  air dry  $\gg$  mount on stubs  $\gg$  sputter coat with Au-Pd. Whole paleas were affixed to metal stubs by double-stick tape and coated with Au-Pd. Specimens were viewed with an ETEC Autoscan scanning electron microscope at a working distance of 15 mm.

## RESULTS

Paleas of *C. arundinacea* have a single keel, covered with trichomes (Fig. 1). Cross-sections through the palea reveal thick-walled parenchymatous cells on the outer surface, with a typical mesophyll (Fig. 2). A single vascular trace with 2 tracheary elements was observed

in this keel (Fig. 3). *Cinna bolanderi*, a 2-keeled species, clearly has 1 trace per keel (Fig. 4). Each trace is similar to that of *C. arundinacea*.

#### DISCUSSION

*Cinna arundinacea* was first described by Linnaeus (11), who made no mention of the 1-keeled palea. Cross-sections of paleas of this species, and of *C. latifolia*, were studied by Behrens (8), who concluded that the paleas of *C. arundinacea* are 1-nerved and those of *C. latifolia* 2-nerved. Primarily on the basis of this difference, he suggested the removal of the latter species from *Cinna*. Bentham and Hooker (12) indicated doubts about the number of traces present in the paleas of *Cinna*; they maintained the broader concept of the genus. None of the reports mentioning *Cinna* include an illustration of a cross-section of the palea (4, 8, 13), and Gould and Shaw (1) cautiously reported this condition as, "... apparently 1-nerved."

The present study clearly demonstrates that the palea of *C. arundinacea* (Fig. 1) has a single keel with 1 vascular trace (Figs. 1, 3). The morphology of the paleas of *Cinna* is almost identical to the 1-keeled structures reported by Pizzolato (5) for *Anthoxanthum odoratum*. There is no question that the 1-keeled palea of *C. arundinacea* arose from a 2-keeled ancestor—the outgroups including all other species of the genus and all phylogenetically related genera in Agrostideae have 2 keels. Therefore, Chase's supposition concerning the number of keels was incorrect, and Sharman's reluctance to employ the term "palea" for the subtending bract in *A. odoratum* was misplaced.

It is uncertain whether the single keel of *C. arundinacea* arose via fusion, as suggested by Pilger (4), or via the evolutionary loss of 1 of the 2 nerves. The close proximity of the 2 nerves in the other species of *Cinna* could be construed as an indication that the single keel resulted from connation of the 2 nerves. However, the vascularization of each of the 2 keels of *C. bolanderi* and the single keel of *C. arundinacea* is identical, whereas 2 traces might be expected if fusion had occurred. Clearly a rig-

orous phylogeny and detailed comparative developmental studies of all the species of the genus are necessary to test these 2 hypotheses. Comparative studies of other species of grasses with 1-keeled paleas also need to be accomplished to ascertain whether these observations are more general. We suggest, however, that all 1-nerved paleas can be traced to 2-keeled, 2-nerved ancestors.

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