AMPHIBROMUS SCABRIVALVIS (GRAMINEAE) IN LOUISIANA

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The South American grass *Amphibromus scabrivalvis* (Trin.) Swallen was reported in 1967 (Flinchum & Baker 1967) as an introduced weed in Louisiana strawberry fields (Tangipahoa Parish). Since then, the name of the species has appeared in some pertinent floristic accounts (Allen 1980; Kartesz & Kartesz 1980; Thieret 1972) but not in others that should have included it (Gould & Shaw 1983; Shetler & Skog 1978; Soil Conservation Service 1982). The purpose of our paper is to call attention to the continued occurrence of this grass in the United States and to present descriptive data on the species.

Amphibromus in Louisiana

The date of arrival and the method of introduction of *A. scabrivalvis* into Louisiana are uncertain, although the species is said to have been discovered in Tangipahoa Parish "in the late 1950's" (Flinchum & Baker 1967). One strawberry grower told us that he first noted *Amphibromus* the year after he had set out strawberry plants imported from Argentina. Whatever the source, the new weed was obviously "established and actively growing," increasing "the cost of production [of strawberries] . . . because of the extra labor and time needed to control it" (Flinchum 1966). In 1984, about a quarter of a century later, attempts are still being made to eliminate the grass, which apparently has not spread far from the original point of introduction.

In Louisiana, *A. scabrivalvis* is well adapted to the cultural practices used in the production of strawberries, which are grown there as annuals and are generally mulched with black plastic. When the soil is prepared in fall (late October or early November) to receive the strawberry transplants, the grass makes its appearance. The infestation may be from perennating buds left in the soil or from caryopses produced during the preceding season. The plant is more or less dormant during winter, but vigorous growth and tillering are resumed as soon as spring weather becomes favorable. Terminal panicles appear in April-June. Maturation of *Amphibromus* caryopses occurs just before the strawberry season is completed. After harvest, a non-selective,

SIDA 11(2): 207 – 214. 1985.

top-kill herbicide (e.g., Paraquat) is sprayed over the fields to eliminate strawberry plants and weeds (the grass, if not sprayed, may continue vegetative growth during the summer). A second crop (e.g., of peppers) is then set into the soil through existing holes in the plastic mulch.

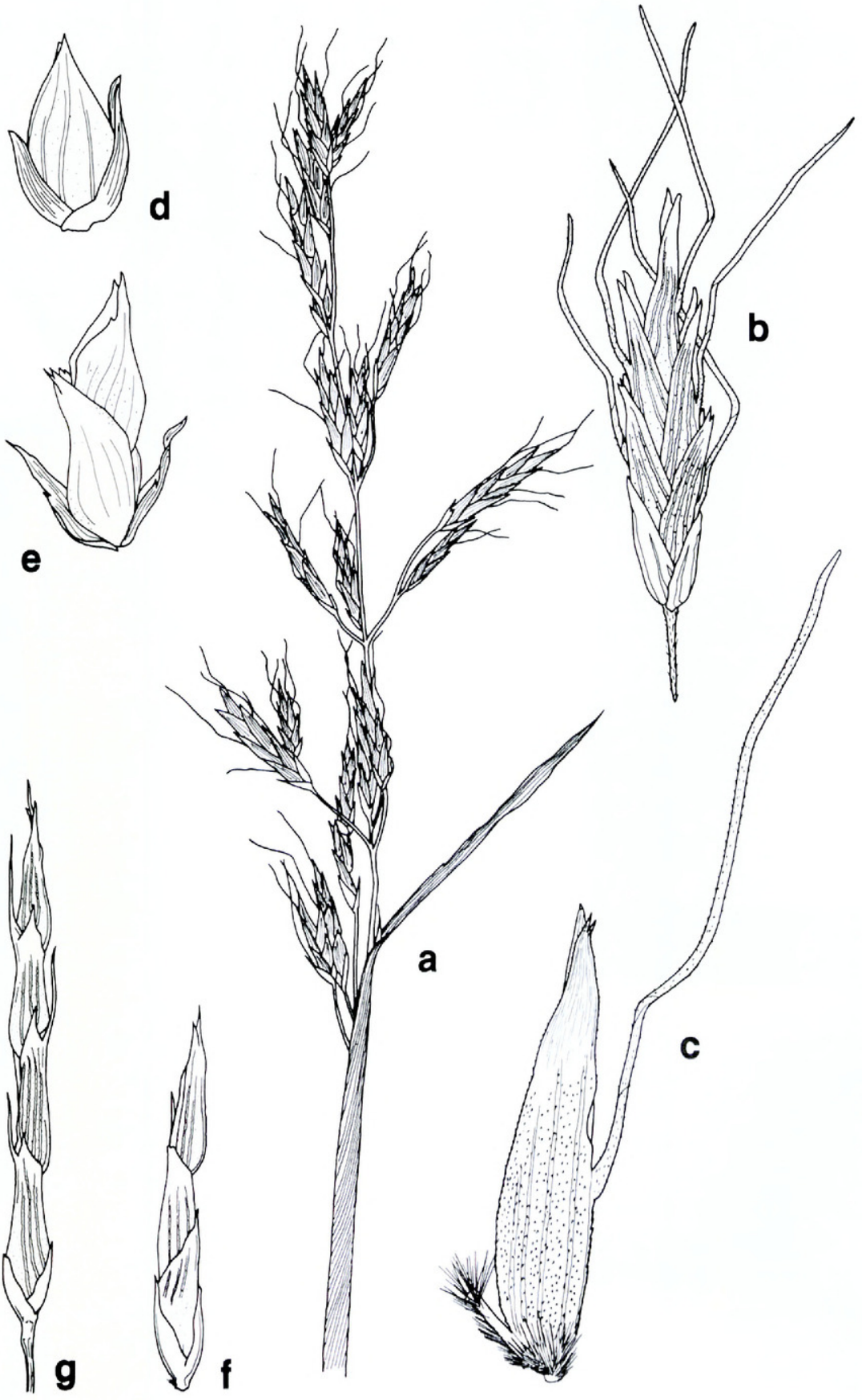
CLEISTOGAMY

According to Campbell et al. (1983), cleistogamy has been reported in 83 genera of grasses—about 19% of the total number of genera in the family. *Amphibromus* is one of these (Burkart 1969; Nicora 1978; Rosengurtt & Arrillaga de Maffei 1961; Rosengurtt et al. 1970; Stopp 1958; Torres 1970). In *A. scabrivalvis*, cleistogamous spikelets (Fig. 1d, e, f, g) are produced within the leaf sheaths at all nodes of the stem (the number of nodes may be as many as 10). Up to three or four of these nodes may, as often as not, be underground. The spikelets ("cleistogenes"; see Chase 1918) at the lowermost one or two nodes (Fig. 1d, e) are strikingly different from those of the terminal panicle (Fig. 1a, b, c), so different, indeed, that if their source were not known they would hardly be considered to belong to *A. scabrivalvis* at all. Floret number is one to three (spikelets of the terminal panicle produce three to nine); the apex of the lemma is but slightly notched, erose, or mucronulate (lemmas of terminal spikelets are deeply 2-lobed to or slightly below the middle and bear a long, dorsal awn); and the caryopses are 3 – 4.5 mm long and 1.5 – 2 mm wide (caryopses of terminal spikelets are 2 – 3 mm long and 1.2 – 1.3 mm wide).

At successively higher nodes the cleistogamous spikelets (Fig. 1f, g) become progressively more like those of the terminal panicle: floret number increases, lemma lobing is initiated and becomes deeper, awns appear and grow longer (although not more than about half the length of the awns of terminal spikelets), and caryopsis size decreases.

That *A. scabrivalvis* commonly produces its most reduced cleistogamous spikelets underground is a phenomenon matched, we believe, by few other grasses. Indeed, Campbell et al. (1983) listed only four genera—*Amphicarpum*, *Chloris*, *Eremitis*, and *Paspalum*—that have subterranean spikelets. The spikelets in these are "borne on specialized rhizomes" rather than at the base of the culms as in *A. scabrivalvis*. Such burial, resulting in the complete loss of dispersal from the parent plant, would seem to be an

Figure 1. *Amphibromus scabrivalvis*. a. panicle; b. chasmogamous spikelet from panicle; c. floret from chasmogamous spikelet; d, e. cleistogamous spikelets from lowest leaf sheath (underground); f, g. cleistogamous spikelets from 5th and 6th leaf sheaths. The vertical lines = 5 mm.


d
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example of atelochory, "the limitation of dispersal to the already occupied, obviously suitable spot" (van der Pijl 1972). The advantage of such an arrangement to *Amphibromus* is obscure.

Campbell et al. (1983) distinguished four types of cleistogamy in grasses. *Amphibromus scabrivalvis* does not fit convincingly into any of these, combining, as it does, features of types I and II. These are described as follows: "Type I. Sheath fertilization. Inflorescences or spikelets remain within the leaf sheaths of the middle or uppermost part of the stem" and "Type II. Unlike Type I . . . Type II occurs only within the lowermost sheaths and is usually associated with major inflorescence and spikelet modifications, with fruit dimorphism, and sometimes with specialized dispersal mechanisms." Certainly the lowermost cleistogamous spikelets of *A. scabrivalvis* can easily be referred to Type II, but the presence of cleistogamous spikelets in sheaths *all along* the stem would appear to be a connecting link to Type I.

ENLARGED BASAL INTERNODES

The first, second, third, and sometimes the fourth internodes of *A. scabrivalvis* may become swollen (Fig. 2). These enlarged internodes are generally underground but can occasionally appear above the soil surface. They are hollow (as are the more distal, normal internodes) and have scattered vascular bundles. Similar structures can be seen in other grasses, e.g., *Arrhenatherum elatius* var. *bulbosum*, some species of *Melica*, and *Phleum pratense*. Such structures have been described as "tuberous" or "bulblike," but we prefer to call them corms, which seems to be more in harmony with their morphology.

TAXONOMY

The genus *Amphibromus*, which belongs to the tribe Aveneae (Macfarlane & Watson 1982), was last studied in its entirety by Swallen (1931), who recognized five species—one of Australia, one of Tasmania, one of New Zealand, and two of South America. He ascribed *A. scabrivalvis* to "open grassland" in Peru, Bolivia, Uruguay, and Chile; the species also occurs in Argentina (Cabrera 1953) in "suelos inundables, zanjas, etc."

The Louisiana plants are *A. scabrivalvis* var. *scabrivalvis*, not var. *indigestus* Nicora (Nicora 1973).

The following description of *A. scabrivalvis*, based upon Louisiana specimens, largely follows the format drawn up by Brandenburg & Estes (pers. comm.) for the Poaceae in the *Vascular Flora of the Southeastern United States*.

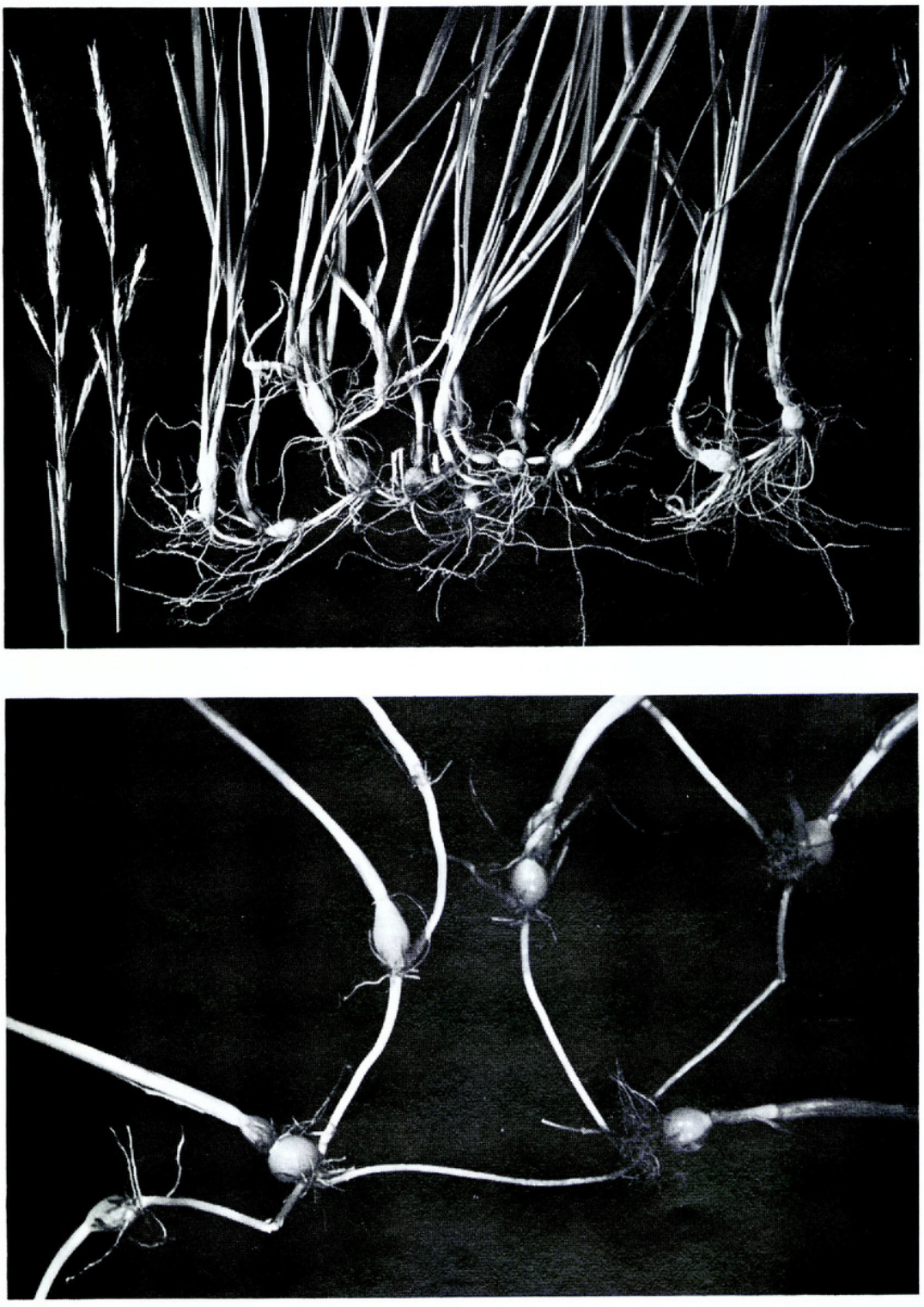

Figure 2. *Amphibromus scabrivalvis*. Plants (upper), X¼, and rhizome (lower), X½, showing enlarged basal internodes (from Flinchum 1966).

Rhizomatous perennial. Culms erect to decumbent, mostly unbranched, terete, 1.5 – 6.5 dm tall, glabrous or, just below the inflorescence, slightly scabrous, hollow at internodes, the lowest 1 – 3(4) internodes often swollen, the leaves mostly cauline. Sheaths open or, at base, closed, terete, mostly longer than internodes, glabrous, the margins scarious, auricles none. Ligules scarious, 5 – 16 mm tall, glabrous. Collars yellow, somewhat indurate, glabrous. Blades bluish-green, rolled in bud, linear, 5 – 25(40) cm long, 3 – 5 mm wide (uppermost blades reduced to as little as 1 cm long and 1.5 mm wide), chartaceous, scabrous above, especially proximally, glabrous or slightly scabrous below, the midrib not or but slightly more prominent than other veins; apex acute; margins smooth to scabrous; blade anatomy pooid; horizontally elongated silica bodies present over veins abaxially.

Inflorescence a terminal panicle (intravaginal, cleistogamous spikelets also present; see below), often basally included in uppermost sheath, ovate to narrowly ovate, 7 – 27 cm long, the branches flexuous, ascending to horizontally spreading, 2 – 8 cm long, 1 per node (sometimes appearing as 2 or 3, with 1 of them bearing spikelets nearly to its base).

Spikelets laterally compressed, disarticulating above the glumes and between the florets, each floret falling attached to the adjacent rachilla internode; reduction distal.

Chasmogamous spikelets (those of the terminal panicle) narrowly ovate, 12 – 25 mm long (excluding awns), 2 – 2.5 mm wide, 3 – 9 floreted, pedicels lacking or up to 10 mm long, scabrous; rachilla sometimes exposed in intact spikelets, prolonged to 1 mm beyond uppermost floret, the internodes 2.5 – 3 mm long, upwardly pilose on abaxial side, the trichomes longest (ca 1 mm) at internode apices. Glumes ½ – ⅔ as long as the lemmas above them, narrowly ovate, scarious (green only along nerves, if at all); first glume 4.7 – 6.5 mm long, 1 – 3 nerved, second glume 5 – 8 mm long, 3 – 5 nerved, nerves of both glumes scabrous, outermost 2 nerves much the shortest, sometimes obscure; internerves glabrous; apex acute, sometimes slightly notched or erose, nerveless; margins scabrous. Lemmas awned, pale green to stramineous, ovate to narrowly ovate, 5 – 11 mm long, chartaceous, 7 – 9 nerved, the nerves and internerves scabrous, with a small tuft of trichomes to 1 mm long on each side of callus; apex deeply 2-lobed to or slightly below the middle, the lobes scarious and often erose or slightly notched distally; margins scabrous; awn arising at or just below middle of lemma (0.5 – 1 mm below base of cleft), 8 – 17 mm long, geniculate at or somewhat below the middle, more or less twisted below the bend, scabrous; callus glabrous proximally, white pilose distally, the trichomes to 1 mm long. Paleas shorter than lemmas, bowed out basally,

4 – 6 mm long, chartaceous, 2 keeled, 2 nerved, the nerves scabrous, reaching the apex; apex scarious, often notched; margins scabrous to ciliolate distally. Lodicules 2, scarious, 1 – 1.5 mm long, not vasculated. Stamens 3, anthers 0.7 – 2 mm long, yellow. Caryopses narrowly ellipsoid to narrowly ovoid, yellow brown, 2 – 3 mm long, 1.2 – 1.3 mm wide, pubescent at apex, longitudinally and shallowly grooved, somewhat laterally compressed.

Cleistogamous spikelets (the most reduced ones, i.e., those in the lowermost sheath) ovate to broadly ovate, 6 – 10 mm long, 2.5 – 4.5 mm wide, 1 – 2(3) floreted, pedicels lacking; rachilla not exposed, prolonged to 2.5 mm beyond uppermost floret, the internodes 2.5 mm long, upwardly pilose on abaxial side, the trichomes longest (ca 0.5 mm) at internode apices. Glumes ½ – ¾ as long as the lemmas above them, nearly setaceous to narrowly ovate, scarious; first glume 4 – 4.5 mm long, 1 nerved, second glume 4.7 – 5.5 mm long, 3 nerved, nerves of both glumes scabrous, sometimes obscure; internerves glabrous; apex acute, sometimes notched or erose, nerveless; margins scabrous, sometimes denticulate. Lemmas awnless or mucronulate, stramineous, ovate to broadly ovate, 6 – 8.5 mm long, chartaceous, 7 – 13 nerved, the nerves scabrous to nearly smooth, obscure to obvious, the internerves scabrous or hispidulous, with a small tuft of trichomes to 0.5 mm long on each side of callus; apex erose, slightly notched, or mucronulate; margins scabrous distally; callus glabrous proximally, white pilose distally, the trichomes to 0.5 mm long. Paleas shorter than lemmas, bowed out basally, 5 – 6 mm long, chartaceous centrally, with a wide scarious margin and apex, 2 keeled, 2 nerved, the nerves scabrous, reaching the apex; apex often notched; margins scabrous to ciliolate distally. Lodicules scarious, 1 mm long, not vasculated. Stamens at least 1, anthers 0.7 mm long, yellow. Caryopses ellipsoid, yellow brown, 3 – 4.5 mm long, 1.5 – 2 mm wide, pubescent at apex, longitudinally and shallowly grooved, somewhat laterally compressed.

Specimens examined: Louisiana. Tangipahoa Parish: strawberry fields 2 – 2.5 mi N of Independence, 18 May 1960, *C. A. Brown s.n.* (US); 8 May 1967, *E. R. Wascom 562* (LSU); 24 Apr 1971, *J. W. Thieret 32968* (DUKE – 2 sheets, LAF, LSU, NCU – 2 sheets, SMU, VDB – 2 sheets); 9 May 1984, *M. L. Calaway 84-6* (GH, KNK, NCU, NY, US).

ACKNOWLEDGEMENTS

Thanks are due to the following individuals who gave aid during the preparation of this paper: David M. Brandenburg, Christopher S. Campbell, Wayne Flinchum, Frank Lopinto, Rahmona Thompson, and Wayne Wells.

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