

# A Morphological, Anatomical and Cytological study of *Potamophila prehensilis* (Nees) Benth.

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## 1. INTRODUCTION.

*Potamophila prehensilis* (Nees) Benth. was first described by Nees in his Fl. Afr. Austr. (1841) under the name *Maltebrunia prehensilis*. Bentham in 1881 included the genus *Maltebrunia* Kunth under *Potamophila* R. Br.

Kuntze in his Rev. Gen. Plant. (1893) and Stapf in Dyer, Fl. Cap. VII (1900) described the uppermost florets of *Potamophila* as hermaphrodite or unisexual with the organs of one sex reduced. Phillips in his description of this genus in his S. Afr. Grasses (1931) makes no mention of this reduction. Moreover, when the descriptions of *P. prehensilis* and *P. parviflora* (type species for the genus *Potamophila* R. Brown) were compared, it appeared rather doubtful whether *P. prehensilis* should be included under this genus.

The present work is an attempt to clear up the doubtful points mentioned above, as well as to investigate the alleged relationship between the *Oryzaceae* and the *Bambuseae*,

## 2. DESCRIPTION OF THE GENUS.

### POTAMOPHILA R. Brown.

**Potamophila** R. Brown, Prodr. Fl. Nov. Holl., ed. 2, 1, 67 (1827); Steudel, Syn. Plant. Glum. 1, 4 (1854); Bentham, Fl. Austr. VII, p. 550 (1878); Bentham et Hooker, Gen. Plant. III, 2, p. 1116 (1883); Stapf in Dyer, Fl. Cap. VII, 658 (1900); Medley Wood, Natal, Plants, t. 444 cum descr. (1905); Stent in Bothalia, I, 4, 274 (1924); Phillips, Gen. S. Afr. Fl. Pl., 82 (1926); Bews, World's Grasses, t. 21, p. 75 (1929) in clavi p. 122; Phillips, S. Afr. Grasses, 169 (1931).

*Spikelets* laterally slightly compressed on short or rather long pedicels. Inflorescence a lax or contracted panicle. *Rhachilla* disarticulating above the rudimentary, basal glumes. *Florets* 3 in number only the uppermost fertile, the lower two reduced to

minute empty lemmas. Uppermost hermaphrodite or unisexual with the organs of one sex reduced. *Glumes* persistent, reduced to a minute entire or bi-lobed hyaline rim. *Empty lemmas* reduced, subulate, elliptic and rounded or lobed. *Fertile lemma* membranous, 5-nerved, nerves sometimes raised or even slightly winged. *Palea* more or less similar to the fertile lemma but slightly longer and 3-nerved. *Lodicules* 2, usually large, finely nerved. *Stamens* 6. *Styles* 2, distinct; stigmas plumose. *Caryopsis* obovate, compressed or terete, crowned by the thickened bases of the styles, enclosed by the unaltered lemma and palea, but free.

Tall aquatic or hygrophytic grasses; ligules membranous; panicle effuse or contracted.

A genus with four species; two in Africa (East Africa one, South Africa one); Madagascar one, New South Wales one.

### 3. DESCRIPTION OF THE SOUTH AFRICAN SPECIES.

#### *Potamophila prehensilis* (Nees) Benth.

in Journ. Linn. Soc. 19, 55 (1881); Medley Wood, Natal Plants, t. 444 cum descr. (1905); Stapf in Dyer, Fl. Cap. VII, 659 (1900); Stent in Bothalia 1, 4, 274 (1924) sphalm. *prehensiles*; Bews, World's Grasses, t. 21, 75 (1929); Phillips, S. Afr. Grasses, t. 48 (1931).

Synonymy. *Maltebrunia prehensilis* Nees, Fl. Afr. Austr., 194 (1841); Dur. et Schinz, Consp. Fl. Afr. V, 788 (1894) sphalm, *praehensilis*; *Oryza prehensilis* (Nees) Steud., Syn. Pl. Glum, 1, 3, (1854).

*Perennial*, rhizome horizontal, covered with cataphylls, in robust plants more or less strongly branched. *Culms* erect, climbing, up to 10 m. high or more, slender, many noded; innovations produced intravaginally; nodes swollen, annular, pallid to brownish, glabrous or sometimes minutely hairy; internodes hollow, exerted, terete to slightly laterally compressed, up to 13.5 cm. long, the lower grooved on one side, striate, pallid to greenish, sparsely villous below the nodes or glabrous. *Leaf-sheaths* tight or more or less lax; retrorsely ciliate along the thin margins, sometimes sparsely long-ciliate at the top or glabrous, slightly keeled, scabrous on the upper part of the keel, strongly striate, lighter in colour than the leaves, slightly auricled. *Ligule* up to 1 mm. long, membranous, usually truncate, at length becoming fimbriate. *Leaf-blades* heterophyllous, viz., the usual lanceolate vegetative type and a caudate prehensile linear type (fig. 2). There exists a gradual transition from the vegetative lanceolate type to the linear (caudate) prehensile type of blade, which besides possessing a normal assimilative function, also enables the plant to climb. The extremes, however, are very different in appearance. Lanceolate type, acuminate, up to 14.5 cm. long and 0.6 cm. broad, dark green in colour, flat, more or less flaccid, sparsely hairy, margins and keel usually spiny with minute sharp retrorse barbs; primary nerves 3-5 on each side of the mid-nerve; keel and nerves light yellow or white in colour. Caudate prehensile type, very narrowly linear and much longer than the usual lanceolate type, up to 23.0 cm. long and 0.4 cm. broad, tapering to form a capillary pendent apex; margins and keel very strongly spinous with minute retrorse barbs. Occurring mainly as the first few leaves on young sterile shoots. Flowering branches usually bearing only the lanceolate type of leaf. *Panicles* terminal on the main culm as well as on the lateral branches, ovate, open and lax, up to 14 cm. in length and 10 cm. wide, the spikelets opening successively from the apex towards the base of the panicle. Branches up to 10 cm. long, spreading, fine, stiff, the lower-most longest and sparingly branched; branchlets 3-4 spiculate; pedicels up to 2 cm. long. *Spikelets* up to 9 mm. long, broadly lanceolate, slightly twisted, usually glaucous (pallid when young), scabrous, slightly laterally compressed, pedicelled; rhachilla not produced, disarticulating above the rudimentary basal glumes. *Florets* 3, two represented by empty lemmas, the third hermaphrodite and well developed. *Glumes* persistent, much reduced, forming a small entire or

bilobed hyaline cup. *Sterile lemmas* subulate, armed with minute hyaline spines, variable in length. *Fertile floret* with a well-developed lemma and palea. *Lemma* about 8 mm. long, boat-shaped acuminate, coarsely covered with hyaline spines, coriaceous clasping the palea with the tough inflexed margins, nerves raised, set with curved hyaline hairs, at times nearly winged. *Palea* similar to the lemma with the exception that it is 3-nerved, narrower, and possesses hyaline margins. *Lodicules* 2, broadly ovate, obtuse, fleshy, up to 1.2 mm. long; nerves fine, indistinct. *Stamens* 6; anthers linear, pale yellow, 6 mm. long. *Ovary* subglobose; styles distinct; stigmas densely plumose up to 3 mm. long. *Caryopsis* 5-6 mm. long, brown, spindle-shaped, longitudinally finely ribbed, terete in transverse section. *Embryo* 1/6-1/7 the length of the grain; hilum linear, as long as the grain; epiblast present, about  $\frac{1}{3}$  the length of the plumule (small). *Starch grains* compound, more or less globose, each grain composed of about 14 polyhedral granules. Reaction of KI<sub>2</sub> with starch normal.

#### 4. ANATOMICAL FEATURES OF THE SOUTH AFRICAN SPECIES.

The abbreviations used in the text figures designate the following:—

|          |                        |         |                               |
|----------|------------------------|---------|-------------------------------|
| MVB..... | midvein bundle.        | C.....  | chlorenchyma.                 |
| IVB..... | first order bundle.    | BS..... | bundle sheath.                |
| 2VB..... | second order bundle.   | S.....  | mechanical tissue (stereome). |
| 3VB..... | third order bundle.    | LC..... | long ripplewalled cell.       |
| UE.....  | adaxial epidermis.     | SC..... | silicified cell.              |
| LE.....  | abaxial epidermis.     | CC..... | suberized cell.               |
| MC.....  | motor cells.           | TR..... | two-celled trichome.          |
| ST.....  | stomata.               | RB..... | retorse barbs.                |
| P.....   | colourless parenchyma. | PP..... | papillae.                     |

#### Shoot Characters. (Fig. 3D.)

Shoots circular or elliptic in transverse section. Leaves rolled in the bud, protected by the sheaths of the lowermost leaves.

#### Anatomy of the Leaf Blade. (Figs. 4, 5, 6, 7.)

The description of the anatomy is based on observations made from handcut transverse sections. The epidermi were studied by the aid of surface sections, and maceration of leaf material made it possible to study the shape and size of the cells. Sections were cut near the base of the leaf to bring out certain characteristics. Drawings were made with the aid of a Leitz "Panphot."

The lanceolate type of leaf has the following characteristics:

*Leaf blade* flat on both surfaces, extremely thin, about 0.055 mm. in cross-section, only about 4-6 cell-layers thick, including the epidermi. *Keel* prominent rounded, retrorsely barbed. *Adaxial epidermis* (fig. 6), with 2-3 rows of motor cells between the bundles, followed by 5-6 rows of ripple-walled cells; the rather narrow and constricted silicified cells adjacent to the bundles alternating with the broader suberized cells. *Stomata* occurring on both sides of the bundles; in a double row next to first and second order bundles, whereas in a single row next to third order bundles. *Papillae* present on the motor cells. *Ripple-walled cells* densely covered with papillae. *Narrow and shorter cells* slightly resembling silicified cells occur between the ripple-walled elements (e.g., long and short elements: Agnes Arber, *The Gramineae*). *Two-celled bulbous based hairs*, long, thin, acuminate, situated here and there above the vascular bundles (fig. 3B). *Epidermis* above the vascular bundles (especially the midrib) retrorsely barbed. *Shorter two-celled hairs* with thin-walled deciduous apices and occurring between the ripple-walled cells. *Motorcells* usually three in number occupying from one-third to one-half the leaf thickness. *Abaxial epidermis* (fig. 7) resembling the adaxial except for the absence of the motor cells and more abundant stomata.

*Vascular bundles*: First order bundles conspicuous, projecting slightly abaxially. Adaxial and abaxial stereome strand present; abaxial strand sometimes only consisting of a few fibres; outer bundle sheath present, consisting of 15–20 parenchyma cells, interrupted by the adaxial stereome strand, inner bundle sheath consisting of 20–22 lignified cells (mid-vein bundle without outer sheath); phloem surrounded by strongly lignified cells; lysigenous cavity and xylem surrounded by parenchyma. Second order bundles occurring infrequently, but constantly submarginally. Third order bundles small; outer sheath complete, consisting of up to 12 parenchyma cells; inner sheath weakly developed, not lignified. *Midrib* prominent, composed of a well-developed abaxial and a weakly developed adaxial stereome strand together with an abaxial first order bundle and a superposed adaxial amphivasal bundle of the third order; fundamental tissue composed for the larger part of colourless parenchymatous cells with a gradual transition to chlorenchymatous tissue adaxially. Margin rounded, with very little or no schlerenchyma, set with curved broadbased retrorse hairs 0.3 mm. long in the upper two-thirds of the leaf (fig. 3A). *Chlorenchyma* cells more or less regular in transverse section but with fairly deep invaginations of the cell walls (fig. 4D); in surface section the chlorenchyma also shows invaginations, thus appearing as rows of separate cells (elements). *Stereome* weakly developed; abaxially a few rows of schlerenchyma cells (fibres) present adjacent to the first and second order bundles; adaxially only a few fibres present. Third order bundles provided with 1–5 fibres both ad- and abaxially. Since there is a gradual transition from the lanceolate type of leaf to the prehensile type (the intermediate types not so frequent), a gradual transition in the anatomical structure from the one type to the other is also met with. The extreme types, however, show marked differences. The midrib of the caudate prehensile type (fig. 5) is much larger and trapezoid in section; except for the superposed amphivasal bundle (third order) and the median first order bundle, two pairs of amphivasal third order bundles are situated lateral to the two median bundles. Furthermore the leaf-blade is much narrower and thicker than the lanceolate type and is set with a greater number of retrorse barbs along the margins and on the keel. *Potamophila prehensilis* possesses two types of leaf-blade which differ both morphologically and also anatomically from each other; the prehensile leaves predominate on sterile main shoots and aid the plant in its climbing habit, whereas the lanceolate leaves are most frequently met with on the lateral shoots arising intravaginally on the main shoot and which eventually terminate in an inflorescence. *P. prehensilis* is therefore heterophyllous, a character worthy of note since true heterophylly is of rare occurrence in the *Gramineae*. The course of the Vascular bundles in the midrib (fig. 8).

Since superposed vascular bundles are rarely met with in the midrib of the leaves of the *Gramineae* (e.g. *Bambuseae*) and little is therefore known regarding their relative origin and course, a study in this direction was undertaken. This was done on basis of a series of handcut sections prepared from a caudate prehensile leaf in the vicinity just below and above the juncture of blade and sheath. Figure 8 (A-F) depict the origin and course of the finally superposed bundles of the midrib of the leaf-blade. In (A) the midnerve and two lateral third order bundles of the sheath are present. At a slightly higher level (B) the lateral bundles divide, one giving origin to two, the other to three smaller bundles; the third bundle of the latter group gradually moves inward towards the midnerve (C) and finally becomes superposed above the midnerve (D). The two remaining small bundles of the two groups also move apart to occupy respective adaxial and abaxial positions (E); higher up in the leaf adaxial bundles terminate (F).

In the lanceolate type of leaf something similar happens with the exception that only one of the lateral third order bundles divides into two; one of these branches gradually moves towards the midnerve finally taking in a superposed position above the midnerve. The two remaining bundles ultimately take in an abaxial position in the leaf-blade and hardly are included in the midrib.

Superposed vascular bundles have so far also been met with in the midrib of the leaf of the remaining South African representatives of the *Oryzae*, viz. *Leersia* and *Oryza*.

## 5. CYTOLOGICAL INVESTIGATION OF THE SOUTH AFRICAN SPECIES.

**Origin of the Material.**

Material for this study was collected by Dr. H. G. Schweickerdt at Magoebaskloof in the Northern Transvaal.

**Technique.**

(cf. "Technique" under *Pseudobromus* p. 142)

**Observations.**

*Potamophila prehensilis*  $2n=24$  (Fig. 9).

*P. prehensilis* has a complex of 24 somatic chromosomes. Owing to the smallness of the chromosomes (the length varying from  $1.5-3 \mu$ ) no morphological study of the somatic complement was undertaken. No satellites were found as is reported for *Oryza sativa* by Nandi (1936) (23). In some metaphase plates an indication of a double structure was found in the split ends of the chromosomes (fig. 9). The position of the constrictions could not be determined. Somatic pairing of chromosomes was found in a few instances. The same phenomenon was reported for the *Oryzae* by Ramanujam (1938) (24).

According to Hubbard in Hutchinson's Fam. of Flow. Plants (25) the tribe *Oryzae* is composed of two sections, the *Oryzinae* and *Zizaniinae*. Hitchcock in his Man. of Grasses of the U.S. (1935) (7) regards the *Zizaniinae* as a separate tribe. These facts are interesting from a cytological point of view.

Ramanujam (24) maintains that the primary basic number of the *Oryzae* is five, the section *Zizaniinae* having retained the original basic number, while the *Oryzinae* developed a secondary basic number, twelve. The cytological investigation of the tribe therefore seems to support Hitchcock's classification.

## 6. REMARKS AND DISCUSSION.

In 1827 the genus *Potamophila* was created by Robert Brown, based on the species *P. parviflora* R. Brown (1). Three years later Kunth in his Rev. Gram. (1830) (2) created the new genus *Maltebrunia* on basis of the species *M. Leersioides*. In 1841 a second species (South African) was described under this genus by Nees in his Fl. Afr. Austr. (3) namely, *M. prehensilis*. Bentham (4), however, regarded the two genera as congeneric and in 1881 included *Maltebrunia* under *Potamophila*, the two genera combined forming (according to his views) a natural genus of three species. There remained, however, certain points of difference between the species. Both Kuntze in his Rev. Gen. Pl. (1893) (5) and Stapf in Dyer, Fl. Cap VII (1900) (6) described the uppermost florets of *Potamophila* as hermaphrodite or unisexual with the organs of one sex reduced, so as to include the South African species, which has the fertile floret of the uppermost spikelets constantly bisexual. A comparison of the characteristics of *P. prehensilis* with those of the type species *P. parviflora* makes it very doubtful whether *P. prehensilis* should be included under the genus *Potamophila* R. Brown. The differences between the two species are given in the following tabulated form:—

**P. parviflora** R. Br.

1. Uppermost florets unisexual or bisexual.
2. Lemma and palea membranous, nerves not raised.
3. Lemma not clasping the palea.
4. Sterile lemmas more or less ovate.
5. A hydrophytic canelike grass 1-1½ m. high, leaves narrow and erect.

**P. prehensilis** (Nees) Benth.

- Florets all bisexual.
- Lemma and palea hardened, nerves raised.
- Lemma clasping the palea.
- Sterile lemmas subulate.
- A hydrophytic climbing grass, up to 10 m. high, leaves heterophyllous.

Taking the above differences into consideration and amplified by further cytological and anatomical study of the two species in question, it may result in the necessity of creating a new genus to accommodate the species *P. prehensilis* (Nees) Benth.

Mention should be made of the totally misleading representation of the habit of *Potamophila prehensilis* by Bews (20). Study of the species in its natural habitat has shown it to be a climber able to reach a height of  $\pm 10$  meters, aided in this respect by the caudate prehensile leaves; the numerous inflorescences are not only borne terminally on the main shoots but also on relatively short lateral branches.

The interpretation of the spikelet in the *Oryzae* has proved difficult mainly on account of the "palea" of the fertile floret not being two-keeled and two-nerved (as is usually the case in the *Gramineae*), but being dorsally keeled and three-nerved.

Much difference of opinion, however, still seems to exist in the interpretation of the lower part of the spikelet as well.

Hitchcock (7) interprets the spikelet of the *Oryzae* as follows: the glumes are small (sometimes much reduced) structures, followed by the three-nerved lemma subtending the fertile floret. The palea is three-nerved and similar in texture to the lemma. According to this interpretation the spikelet is one-flowered and disarticulates entire, i.e., with glumes attached.

Most authors, however, interpret the spikelet as being one- to three-flowered (fig. 10A). This interpretation was originally put forward by Stapf (8) and is supported by agrostologists of the front rank, i.e., Arber (9) and Hubbard (10A). The inconspicuous hyaline two-lipped cuplike structure (which may be reduced to a mere rim), present at the base of the spikelet, is interpreted as representing the reduced glumes; the successive structures (regarded as glumes by Hitchcock and others) represent two sterile lemmas (florets), whereas the third floret is terminal and hermaphrodite. According to this interpretation (fig. 10A) the tip of the rachis would be situated between the palea of the third lemma (F) and the sterile lemma (D) of the second floret.

Arber investigated the spikelet anatomically and by study of transverse sections of the spikelet, arrived at the conclusion that the two scales at the apex of the pedicel occupy a position corresponding to that of glumes.

Hubbard, in his description of *Oryza australiensis* Domin, pointed out that the basal bracts in this species, although small, are not only larger than in most of the other species of *Oryza*, but are two quite distinct structures. These represent the much-reduced glumes. By the discovery of rice spikelets bearing abnormal florets in the axils of the bracts below and preceding the fertile floret, by Michaud (11), the identity of these structures (sterile lemmas) has apparently finally become established. Despite all the arguments forwarded in favour of Stapf's interpretation of the rice spikelet, Backer (12) recently reverted to support the older interpretation of Hitchcock.

Chatterjee (13) after giving an outline of the history of the various interpretations concerning the structure of the rice spikelet, votes in favour of Stapf's interpretation; he furthermore proceeds to criticise the arguments forwarded by Backer against Stapf's interpretation. Comparing the tip of the pedicel of *Oryza* (i.e., glumes sensu Stapf), with the cupular structure occurring at the base of the spikelet in the genus *Asthenochloa*, Backer apparently considers these organs homologous. Since the genera *Oryza* and *Asthenochloa* belong to distinct tribes, these structures may equally well be considered analagous, and need not necessarily be homologous. Chatterjee furthermore points out that in certain species of *Oryza* the cupular structure occurring at the apex of the spikelet is distinctly bi-lobed; in fact these lobes are not attached to the axis on the same level, but on different levels, viz., one is attached slightly above the other (cf. *O. australiensis* Domin and *O. ridleyi* Hook fil.).

In the present investigation it was found that the pedicel tip of *Potamophila* also is distinctly bi-lobed, the lobes being attached to the axis on different levels. (cf. fig. 1B).

Moreover, either of the two sterile lemmas may at times subtend a very delicate hyaline and much reduced palea (fig. 1B). The presence of this palea had already been observed by Stapf, and was indicated by him in his drawings of a dissection of a spikelet taken from a Drege gathering, although no mention is made of this in his account of the species in the Fl. Cap. VII. Both drawing and sheet are deposited in the Herb. Benth. at Kew. The position of the lemma subtending the palea is such that the two lowermost hyaline bracts must undoubtedly be regarded as representing much reduced glumes (fig. 1B).

Two different hypotheses have been put forward to explain the presence of the dorsally keeled three-nerved "palea" of the *Oryzae*.

The generally accepted theory is that the fertile floret consists of a lemma subtending a true palea, which is three-nerved and similar in substance to the lemma. In an effort to prove this interpretation Rossberg (14) endeavoured to indicate that it is possible that a true palea may at times be more than two-nerved and dorsally keeled. It must be admitted that his arguments are quite plausible. Seen in the light of recent discoveries, however, his theory when applied to the *Oryzae*, is difficult to maintain.

A totally different interpretation of the upper part of the spikelet was advanced independently by Peterson (15), Pilger (16) and Parodi (17).

To explain the presence of the six stamens and three-nerved "palea" of the rice spikelet Peterson assumed the spikelet to be two-flowered, the lower flower being perfect and the upper staminate. The structure usually considered to be the "palea" is really the lemma of the staminate floret, while the pales of both are thus wanting.

Parodi's interpretation is essentially the same as Peterson's, but the former gives a more detailed exposition of his views, supported by morphological evidence (18).

Parodi regards the upper part of the spikelet as the result of the fusion of two florets, of which the pales of both and the pistil of one has disappeared, thus giving rise to a floret composed of a single ovary and six stamens (cf. fig. 11B). Subsequent to the publication of this theory a rice plant with abnormal spikelets containing two grains as well as two bi-nerved pales was actually found. These adorsed pales originating from the inner basal part of the spikelet, together with the two outer bracts, may thus be regarded to correspond with the two florets fused to form (together with the glumes and sterile lemmas) the typical spikelet of the *Oryzae*.

The unusual structure of the spikelet and the absence of evident affinity with other tribes of the *Gramineae*, induced Parodi to create the independent subfamily the *Oryzoideae* to accommodate the tribe *Oryzae*.

It may be mentioned here that a cross-section of a rice spikelet with two florets was illustrated by Schuster (19) in 1910.

In spite of the observations mentioned above, Chatterjee dismissed Parodi's theory as a bold assumption, without commenting on the morphological evidence in favour of such an interpretation. Moreover he remarks that he has no doubt that the dorsally-keeled three-nerved structure (occupying the position of a palea) is indeed a true palea, because in the mature caryopsis the hilum points towards this structure. It might be pointed out that according to Parodi's interpretation the hilum would in any case be turned towards the upper lemma ("palea" sensu Chatterjee).

Pilger's theory (fig. 10B and 11A) mainly agrees with that of Peterson and Parodi. Pilger, however, regards the spikelet as the product of the fusion of two florets of which the pales of both and the pistil stamens and lodicules of one have disappeared. This implies that Pilger regards the *Oryzae* as derived from ancestors with six stamens per floret, whereas Parodi regards the relatively high number of stamens, as the result of the combination of two sets of three stamens,\* i.e., originating from an ancestral stock with three stamens per floret.

\* One of the characteristics used by Parodi as a basis for his theory, is that the spikelet of the *Oryzae* contains six stamens (not three). From this one can conclude that the six stamens normally found in this tribe is regarded by Parodi as the result of the fusion of two sets of stamens originating from different florets.

It does seem more logical to accept Pilger's view of the sequence of reduction in the floret (Fig. 11A). According to Pilger the upper floret has disappeared through a downward reduction, while the consequence of Parodi's theory is that the reduction has taken place from above, as well as from below, leaving only the stamens intact (cf. fig. 11B). If it is assumed that the upper floret is male, one still has to account for the disappearance of the lodicules, which have not been included in the typical rice spikelet through fusion of the two florets (2 lodicules are typically present). Apart from this fact certain characters of the *Oryzeae* pointing to a phylogenetic relationship with the *Bambuseae*, a tribe where 6 stamens per spikelet is of common occurrence, seem to indicate Pilger's interpretation as the most acceptable one.

The *Oryzeae* on the whole form a well-defined group exhibiting no evident relationship to other tribes. The tribe nevertheless exhibits a number of characters which are indicative of a possible phylogenetic relationship to the *Bambuseae*; these characters are being put forward in the following tabulated form:—

| BAMBUSEAE  | ORYZEAE  |
|--|--|
| 1. Reduction of the florets in the spikelets has taken place in both an acropetal and basipetal direction. | Likewise.  |
| 2. The "palea" may be dorsally keeled and similar to the lemma ( <i>Melocanninae</i> ).                    | Likewise.  |
| 3. Stamens usually 6 per floret.   | Likewise.  |
| 4. Styles 2-3.   | Styles two, occasionally a third non-stylar process present.   |
| 5. Caryopsis with an elongated linear hilum.   | Likewise.  |
| 6. Epiblast large and broad.   | Likewise.  |
| 7. Starch grains compound.   | Likewise.  |
| 8. Chlorenchyma of the leaf possesses conspicuously invaginated cell walls.                                | Likewise.  |
| 9. Vascular bundles in the mid-rib of the leafblade are often superposed.                                  | In the S. African representatives of the above tribe likewise. |
| 10. Basic chromosome number $x=12$ .   | Likewise.  |

According to Bews (20) Camus furnishes the following information regarding the spikelet of the *Bambuseae*: the spikelets are usually several-flowered, but often only one floret per spikelet is fertile; moreover, the reduction of the floral parts in the spikelet has taken place both from above as well as below. The structure of the *Oryza* spikelet is thus very similar to that met with in the *Bambuseae*, that is, if Pilger's interpretation is accepted; reduction in the *Oryza* spikelet has, however, progressed much further.

The keelless "palea" and its similarity to the lemma as met with in the *Melocanninae* suggests a possible relationship to the "palea" of the *Oryzeae*. In *Dinocloa* this "palea" may be absent and reduction has here progressed to an extreme.

In the discussion of abnormal rice spikelets discovered, Michaud pointed out that in certain of the spikelets studied, an abnormal flower with an indurate three-nerved palea was found to be present in the axil of one of the usually reduced sterile lemmas.

Concluding her discussion she remarks that if Parodi's and Peterson's hypothesis is accepted, the presence of a flower in the axil of one of the usually sterile lemmas, similar in structure to the normal flower found in the *Oryzeae*, "is a strong indication that a branching system is involved," and that if this is actually the case, it "would lend strong support to Parodi's suggestion that the *Oryzeae* constitute a separate sub-family."

It is possible that the somewhat similar development found in certain members of the *Bambuseae* where inflorescences are known to develop in the axils of lemmas [as



indicated by Pilger (21) in the genus *Guadua*] may also be regarded as evidence of a relationship between the *Oryzeae* and *Bambuseae*.

Examination of the chlorenchyma of the leaf of all the South African representatives of the *Oryzeae* has revealed the presence of conspicuously invaginated cell-walls.

In this respect the *Oryzeae* strongly resemble various representatives of the *Bambuseae* cf. Haberlandt (22).

Superposed vascular bundles occur in the midrib of the leaf of all South African representatives of the *Oryzeae*, a character which is likewise met with in the *Bambuseae*, e.g., in the leaves of our native bamboo *Arundinaria tessellata*.

A more comprehensive anatomical study of the various genera of the two tribes concerned may possibly furnish additional evidence of a close phylogenetic relationship between the *Bambuseae* and the *Oryzeae*.

## 7. MATERIAL EXAMINED.

Abbreviations used for the various Herbaria are as follows:—

|            |   |
|------------|---|
| BOL.....   | Bolus Herbarium, Cape Town.                 |
| CTM.....   | South African Museum, Cape Town.            |
| GRA.....   | Albany Museum, Grahamstown.                 |
| NH.....    | Natal Herbarium, Durban.                    |
| NU.....    | Natal University College, Pietermaritzburg. |
| PRE.....   | National Herbarium, Pretoria.               |
| STELL..... | University of Stellenbosch.                 |
| UPR.....   | University of Pretoria.                     |

The following material was examined:..

CAPE PROVINCE.—Willowvale district: Neeyele Forest (also at Monubu), alt. 500', IV., 1906, Pegler 1338 (BOL, CTM, GRA, PRE). King Williamstown district: Perie bush, III., 1894, Schönland 856 (GRA). Do., Perie, XI., 1901, Sim 2809 (GRA, PRE). Lusikisiki district: Igosia Forest, Pondoland, IV., 1918, Mogg 362 (NU). Port St. Johns district: Port St. Johns River, IV., 1918, Pole Evans H. 18039 (PRE). Do., Port St. Johns, XII., 1943, Schelpe 367, (NU). Umzimkulu district: Insikini, Nlokolwana Forest, creeping grass, good fodder grass, IV., 1925, Miller 6045 (PRE).

NATAL PROVINCE.—Port Shepstone district: Oribi Gorge, IV., 1937, McClean 473 (NH). New Hanover district: Blinkwaterbos, II., 1944, Schweickerdt 1532 (NU, UPR). Lions River district: Karkloof Forest, III., 1940, Ryecroft 8 (PRE, NU). Pietermaritzburg district: Town Bush—Masais Farm, III., 1946, Clarkson 256 (NU). Do. Town Bush Valley, alt. 3,200', IV., 1946, Fisher 1018 (NU). Do., near Curryspos, VII., 1945, Acocks 11580 (PRE). Inanda district: Inanda, alt. 1,800', XII., 1886, Medley Wood 558 (CTM). Do., Inanda, X., 1881, Medley Wood 1305 (BOL, CTM). Do., Inanda Heights, III., 1940, Schweickerdt 1432 (NH, PRE). Do., about 10 miles from Verulam on road to N'dedwe, first record of fruiting material, IV., 1940, Schweickerdt 1441 (NH). Do., Verulam, near N'dedwe, IV. 1940, Schweickerdt 1450 (NH, PRE). Richmond district: in moist forests, climbing 30' or more up trees, IV. 1832, Galpin 11955 (PRE). Zululand, N'kandla district: Qudeni Forest, alt. 5,000', II., 1940, Fisher et Schweickerdt 82 (NU, PRE). Do., Qudeni Forest, alt. 5,000', II., 1940, Fisher et Schweickerdt 117 (NU, PRE). Eshowe district: Eshowe, IV, 1941, McClean 1002 (NH). Do., Eshowe Forest, tolerates a lot of shade, III. 1927, Kotze 248 (PRE). Between Ubombo Magistr. and Ugaza Mountains—Mkuzi Station, IV., 1944, Gerstner 4502 (PRE).

TRANSVAAL PROVINCE.—Pietersburg district: The Downs, Junod 4103 (TRV). Letaba district: De Hoek, Houtbosch, I., 1945, Schweickerdt 1557 (UPR, NU). Do., De Hoek, Houtbosch, I., 1945, Schweickerdt 1562 (UPR, NU). Do., De Hoek by Haenertsburg, VII., 1944, Enslin et Schweickerdt (UPR). Do., near Magoebaskloof

Hotel, IV., 1942, Codd and Muller 360 (PRE). Do., Magoebaskloof (Diepkloof), IV., 1946, de Winter 105 (UPR). Do., Magoebaskloof, Patattabos, IV., 1946, de Winter 107 (UPR). Zoutpansberg district: Louis Trichardt, Hangklip, I., 1945, Schweickerdt 1566 (UPR, NU).

FRAGMENTS EX. HERB. HORT. BOT. REG. KEW.—Natal: Umpumulo, common in bush, alt. 2,000' to down to the coast, XI., 1875, Buchanan (PRE). Natal, Dumisa, Ellesmere, im Unterholz shatt. Wälder, VI., 1912, Rudatis 1651 (PRE). Cape Province, Transkei, Kentani near Manubi, XII., 1911, Saxton 28 (PRE).

Authentic material, fragment of Drége 4352 (PRE) Isotype.

TYPE SPECIMEN (not seen).—The type specimen Drége s.n. is deposited in the Botanisches Museum, Berlin-Dahlem and does not bear any locality except that it comes from Natal. According to Dr. H. G. Schweickerdt this sheet is probably of the same gathering as Drége 4352, ex Herb. Lübeck, which was seen and identified by Stapf.

#### 8. ECONOMIC NOTES.

Collector's notes furnish information to the effect that this grass is heavily browsed upon by game and thus only reaches the flowering stage in less readily accessible situations. The species is furthermore reported to be a good fodder grass for stock.

#### Vernacular names.

Afr.: Klimgras; Klimopgras. Zulu: uBabe wehlathi.

#### 9. DISTRIBUTION OF THE SOUTH AFRICAN SPECIES (FIG. II).

The species occurs at an altitude from 500 ft. up to 6,000 ft. It is one of our most characteristic hygrophytic forest grasses and is an important component of the undergrowth of the low-lying riparian forests and at higher altitudes the more temperate mist belt forests of the eastern escarpment (see map). The species prefers shady, moist localities. As far as is known at present its northernmost limit appears to be the southern slopes of the Zoutpansberg.

#### 10. SUMMARY.

1. A detailed description of the morphology and anatomy of *Potamophila prehensilis* (Nees) Benth is given. It is pointed out that true heterophylly occurs in this plant; a rare occurrence in the *Gramineae*.

2. The chromosome number of *P. prehensilis* is  $2n=24$ .

3. A comparison of the characteristics of *P. prehensilis* with those of the type species of the genus *P. parviflora* makes it extremely doubtful whether the former should be included in the genus *Potamophila* R. Br. Further study of the two species in question may result in the necessity of creating a new genus to accommodate the species *P. prehensilis* (Nees) Benth.

4. A discussion concerning the interpretation of the rice spikelet in the light of recent discoveries is given. Pilger's interpretation is regarded as the most satisfactory explanation of the anomalies found in the rice spikelet. Pilger interprets the spikelet as being four-flowered with the two lowermost florets reduced, while the upper part of the spikelet is the result of the fusion of two florets of which the pales of both and the lodicules stamens and ovary of the upper have disappeared, thus giving rise to a floret composed of a single ovary and six stamens enclosed by two lemmas, the lower being 5-nerved and clasping the upper, which is 3-nerved and dorsally keeled.

5. The author has endeavoured to enlarge on the alleged phylogenetic relationship between the *Oryzaceae* and *Bambuseae*. Several morphological and anatomical similarities hitherto unknown have been recorded.

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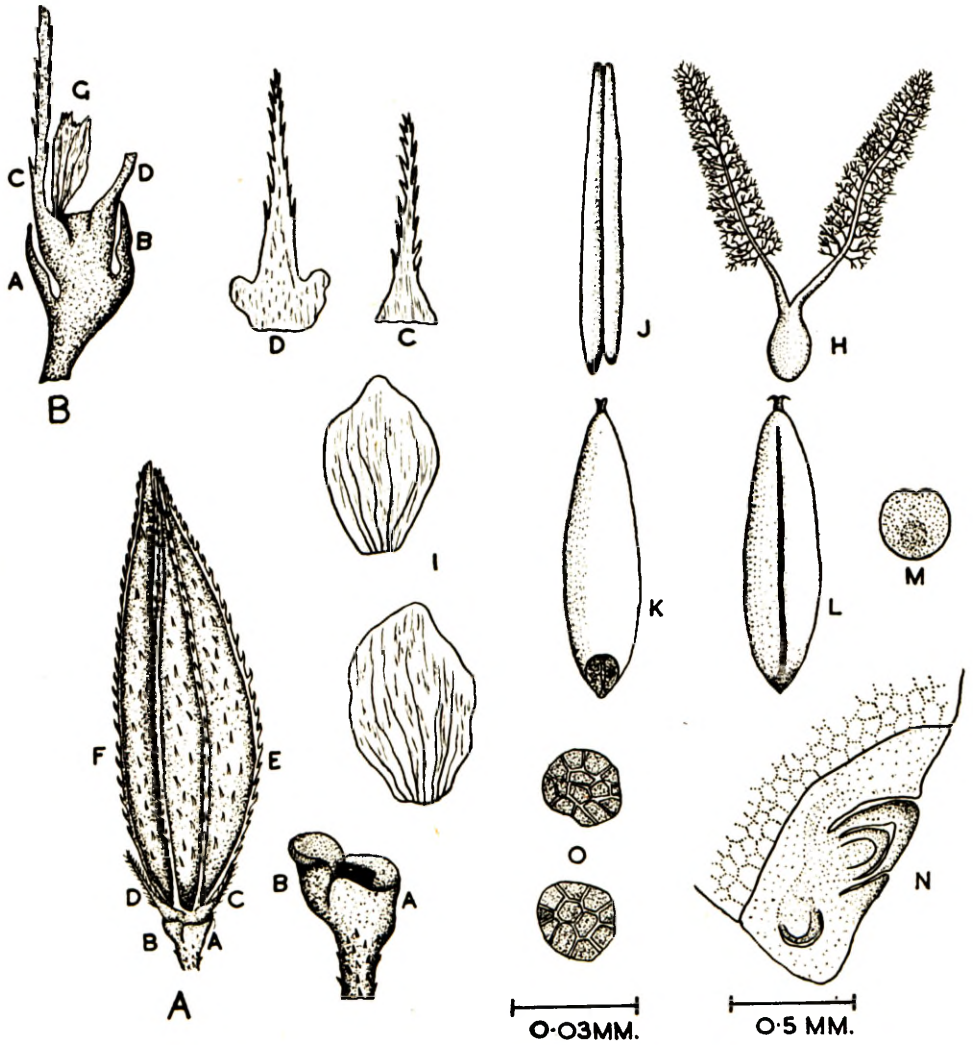


FIG. 1. *Potamophila prehensilis* (Nees) Benth.

A, Spikelet. B, Base of the spikelet. A, lower glume; B, upper glume; C, sterile lemma 1; D, sterile lemma 2; E, lemma; F, palea; G, reduced palea; H, pistil; I, lodicules; J, anther; K, caryopsis, dorsal view; L, caryopsis, ventral view; M, cross-section of the caryopsis; N, longitudinal section of the embryo; O, compound starch granule.—(Schweickerdt 1532).

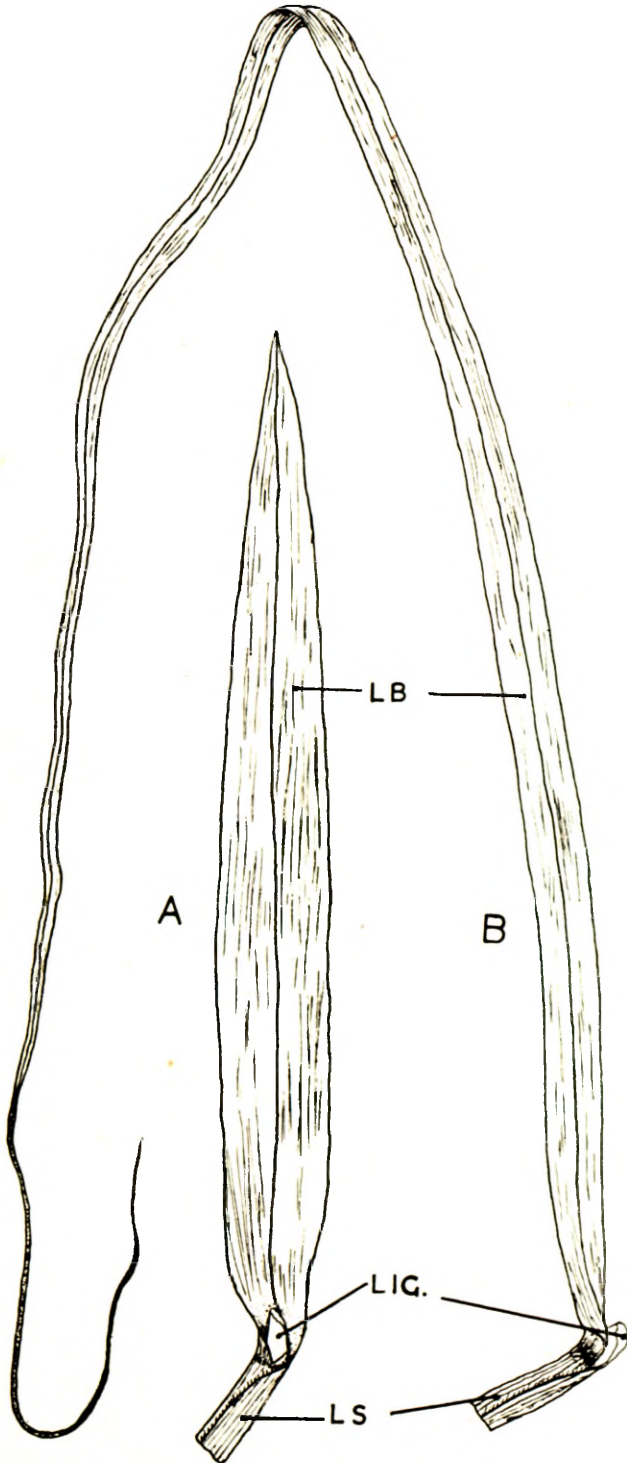


FIG. 2.—A, lanceolate type of leaf. B, caudate prehensile type of leaf.

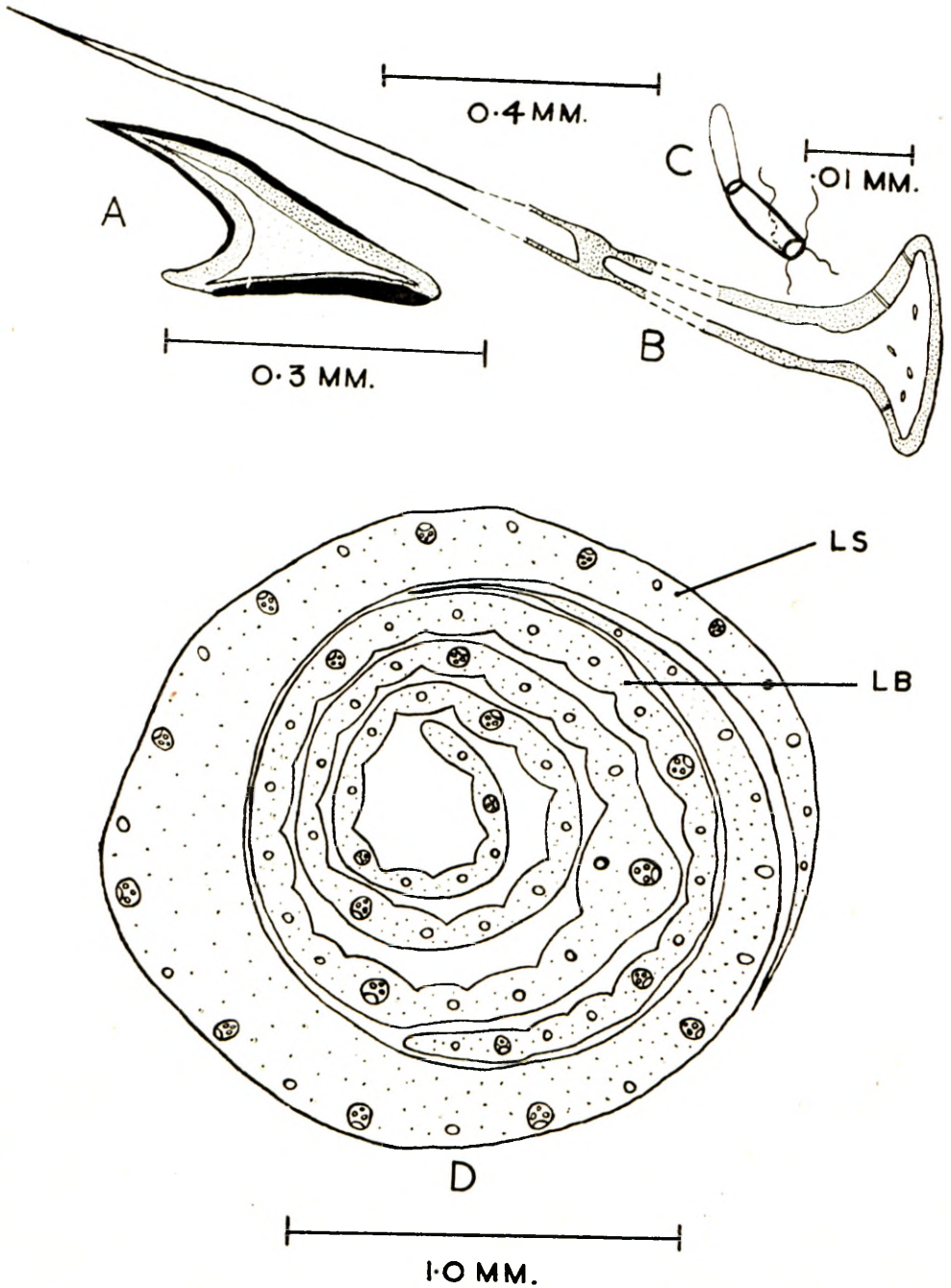


FIG. 3.—*A*—Broadbased retrorse barb. *B*—Long thin two-celled hair. *C*—Two-celled deciduous hair. *D*—Cross-section of the shoot.

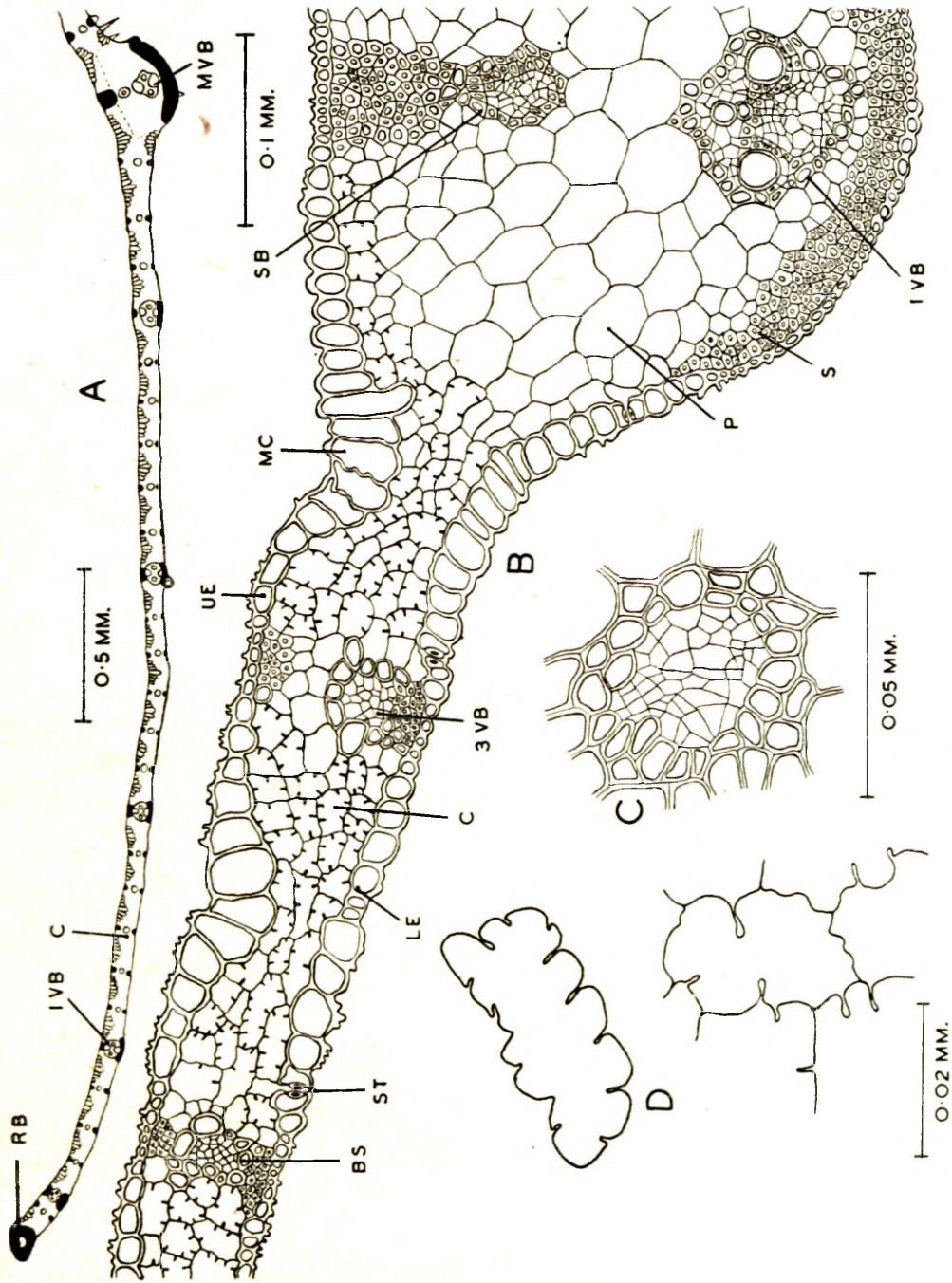


FIG. 4. Lanceolate type of leaf. *A*—Diagrammatic cross-section of the leaf-blade. *B*—Cross-section of a part of the leaf-blade, including the midrib enlarged. *C*—Amphivasal superposed bundle enlarged. *D*—Macerated chlorenchyma tissue. (Schweickerdt 1532).

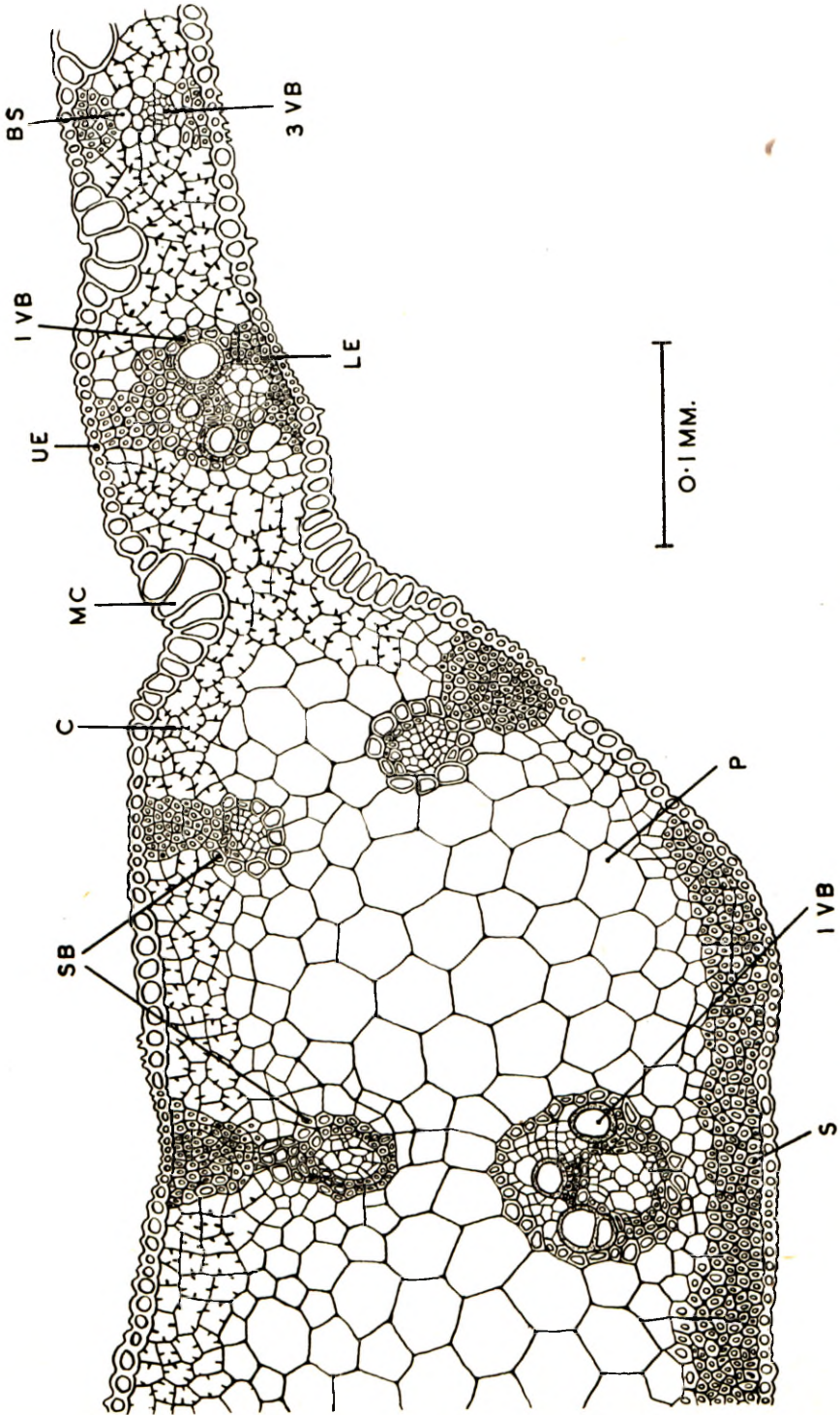


FIG. 5.—Cross-section of a part of a caudate prehensile type of leaf, including the midrib.—(Schweickerdt 1532.)



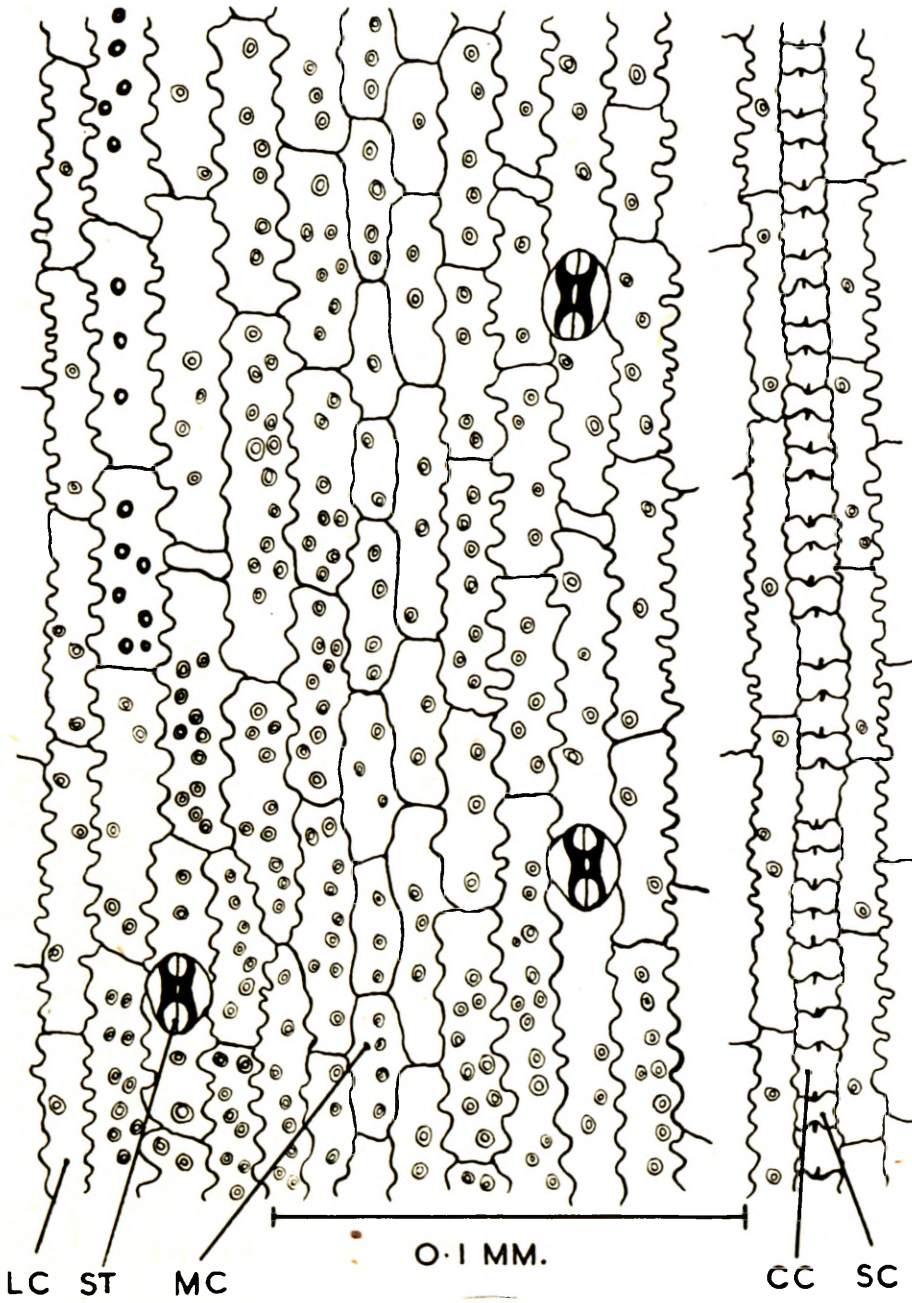


FIG. 6.—Adaxial epidermis of the leaf-blade.—(Schweickerdt 1532.)

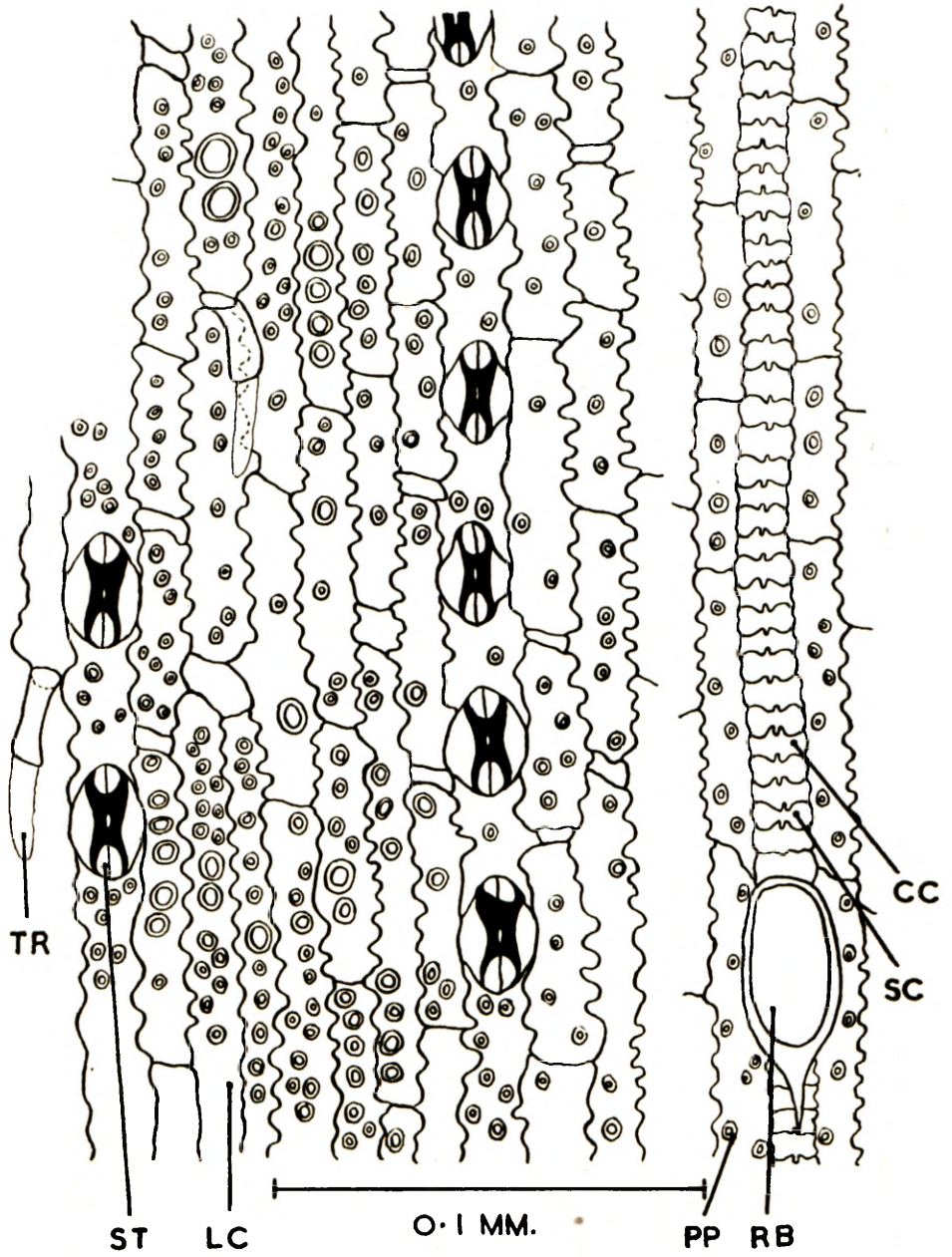


FIG. 7.—Abaxial epidermis of the leaf-blade.—(Schweickerdt 1532.)

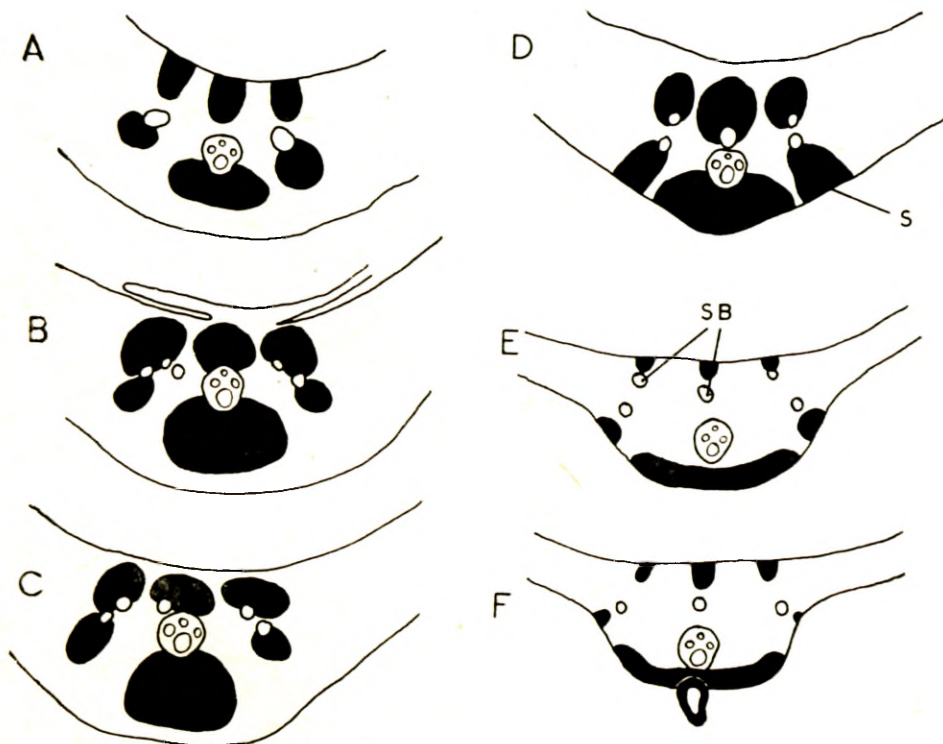


FIG. 8.—Diagrammatic drawing of the course of the vascular bundles in the midrib of a caudate prehensile type of leaf.—(Schweickerdt 1532.)



0.01 MM.

FIG. 9.—Polar view of a metaphase in a root-tip cell.

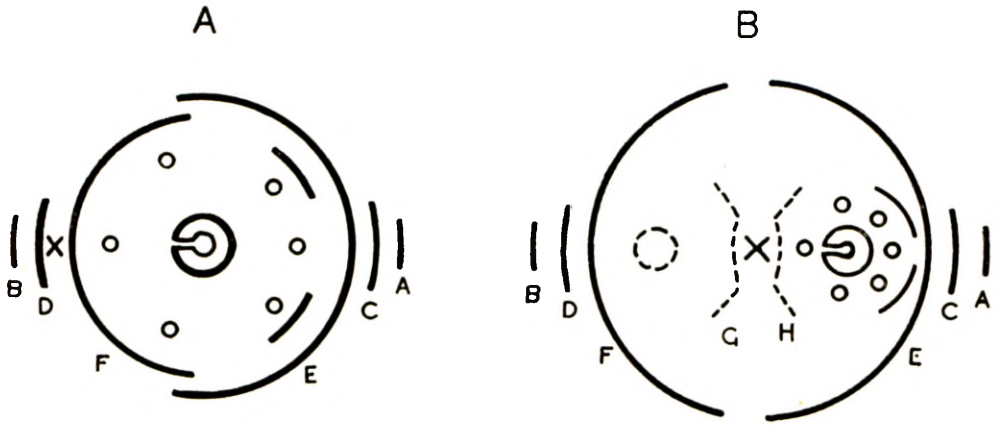


FIG. 10.—Diagrammatic drawing to illustrate the different interpretations of the spikelet of the *Oryzeae*.

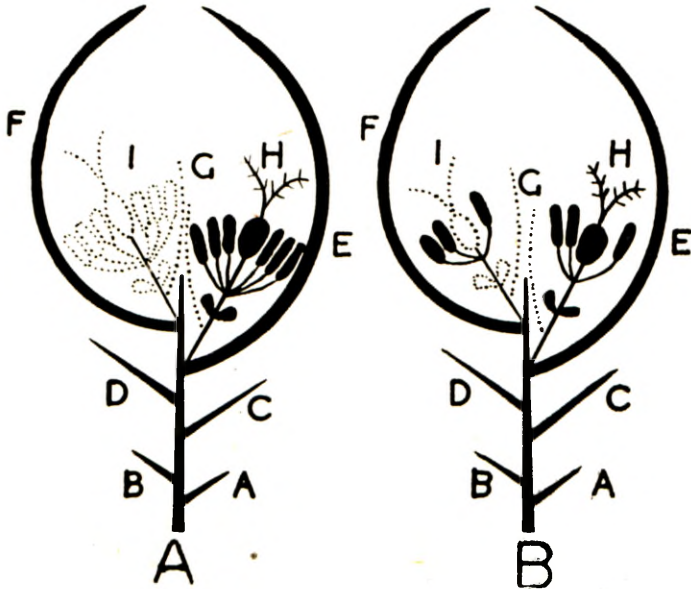


FIG. 11.—Diagrammatic drawing to illustrate the difference between the interpretations of the rice spikelet. *A*—According to Pilger. *B*—According to Parodi. *A*—lower glume. *B*—upper glume. *C*—first sterile lemma. *D*—second sterile lemma. *E*—lower lemma of fertile floret. *F*—upper lemma of fertile floret. *G*—pales. *H*—lower floret. *I*—upper floret. (The dotted lines indicate reduced structures.)

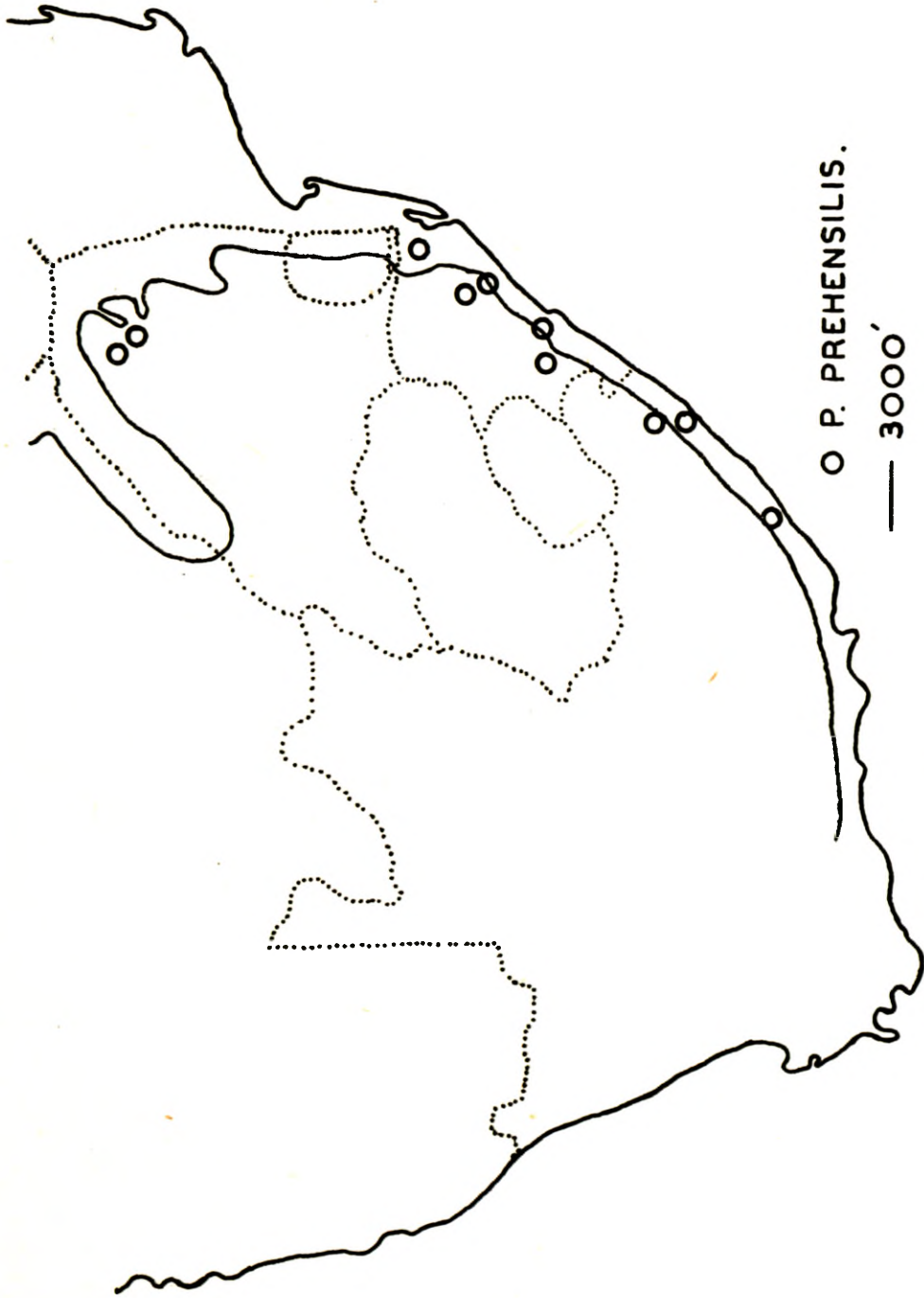


FIG. 12.—Distribution of *Potamophila prehensilis* in South Africa.

