

FLORAL STRUCTURE OF *VALLISNERIA CAULESCENS* BAILEY & F. MUELLER

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ABSTRACT

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The previously unknown flowers of *Vallisneria caulescens* Bailey & F. Mueller are described. The female flowers differ from those of other species of *Vallisneria* in being bipartite as opposed to tripartite and having the stigma branches arranged above instead of between the sepals. Further notes are made about the pollen and male flowers, in which adjacent pollen grains may be linked by intine bridges. These results are compared with the floral structure of the closely related genera *Maidenia* and *Nechamandra*.

INTRODUCTION

The range of pollen dispersal mechanisms in the Hydrocharitaceae is one of the most diverse to be found in a single angiosperm family (Cook, 1982). The vectors used include insects and passive dispersal by wind and water. The conveyance of pollen by water is achieved by either shedding the pollen onto the water surface or into the water column. Several genera in this family, however, have specialised male flowers that are released from the parent plant and act as small boats to transport the pollen to the stigma held at the water surface. Within this group are three genera that can be distinguished from the others by having zygomorphic male flowers. These are *Vallisneria* L. and the two monotypic genera, *Nechamandra* Planchon and *Maidenia* Rendle. The floral structure of these latter two taxa has been examined by Cook and Löönd (1982) and McConchie (1983), respectively.

A recent study has synonymised many of the described species of *Vallisneria*

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into two species but did not treat the Australian representatives of the genus (Lowden, 1982). In the present paper we examine the floral structure of the Australian species *Vallisneria caulescens* Bailey & F. Mueller which was not known when the genus was first described. The results, which broaden the original generic concept, are compared with the floral structure of related species and genera.

MATERIALS AND METHODS

The observations reported here are based on dried and liquid collections held in the following herbaria: BRI, CANB, DAR, MEL, PERTH and SYD. Material used for scanning electron microscopy was preserved in 70% alcohol and was dehydrated further with alcohol treated with molecular sieve type 3A and critical-point dried using CO₂ as the transition fluid. The specimens were mounted on stubs using a conductive adhesive or double-sided adhesive tape prior to being sputter coated with gold. These preparations were examined on a Leitz scanning electron microscope.

After being embedded in Spurr's resin (Spurr, 1969), 1- μ m sections of flowers were cut, mounted on glass slides and stained with 0.05% crystal violet at 80°C, photographed and the cell wall outlines traced.

The distribution map is based on collectors notes from the specimens held in the above herbaria.

The terminology used in this paper was adopted from Tomlinson (1982) as a convenient format for comparison with other publications on related species. The use of Tomlinson's terminology should not be taken as support for his interpretation.

RESULTS

Description

Vallisneria caulescens Bailey & F. Mueller, Syn. Queensl. Fl. Sec. Suppl.: 56 (1888)

Type locality: Australia; Queensland M. Lagoon, about 60 miles west of Normanton, Dr. Thos. L. Bancroft.

Dioecious freshwater perennial. Roots many at base of vertical shoot, fibrous. Plants with or without stolons in axils of basal leaves. Axis elongate, 1.0–3.0 mm diameter, unbranched or branching irregularly. Leaves alternate, internodes 0.3–7.0 cm long; leaves 1.4–31.0 \times 0.2–1.6 cm, linear to lanceolate or narrowly elliptical, amplexicaulous at base, obtuse to acute at apex; leaf margin finely serrulate mainly near apex, mostly entire towards base; leaves with 3–5 major longitudinal veins, middle vein only slightly stronger than lateral veins;

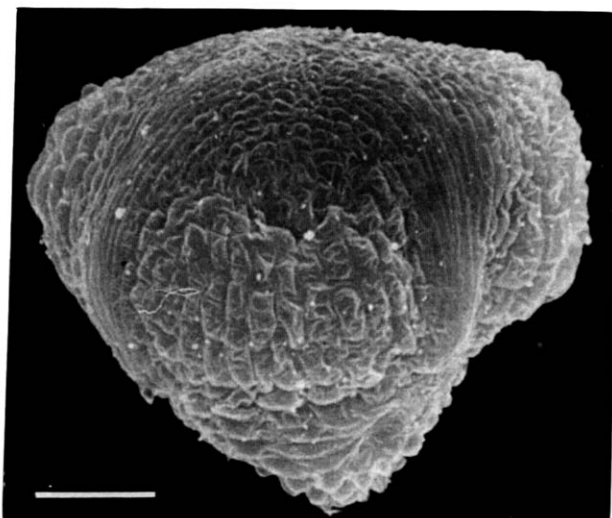


Fig. 1. Unopened male flower as released from pedicel. Scale bar = 100 μ m. $\times 160$.

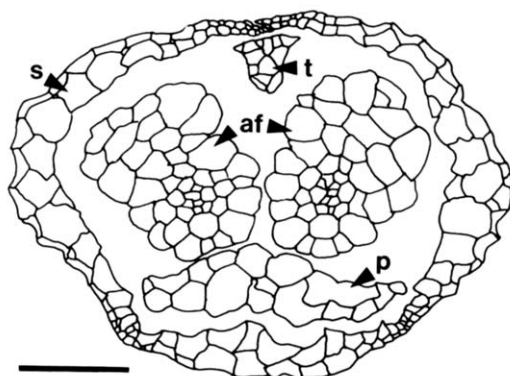


Fig. 2. Drawing of a basal transverse section of a male flower prior to anthesis. Note the arrangement of the free anther filaments (af), petal (p), staminode (t) and united sepals (s). Scale bar = 100 μ m. $\times 210$.

sometimes leaves with irregular weak transversal veins. Plants often with purple tinge.

Male plants with 1 to numerous inflorescences in leaf axils; individual inflorescence on short peduncle, peduncle elongating to up to 7.0 mm during anthesis; inflorescence ellipsoid to obovoid, dorsally compressed, up to 9.5 \times 5.0 mm; inflorescence composed of a single spathe enclosing numerous flowers borne on short pedicels densely arranged on an elongate axis; spathe rupturing irregularly near apex, releasing detached flowers (Fig. 1); flowers opening at water surface; flowers minute (< 0.5 mm), consisting of 3 zygomorphic sepals,

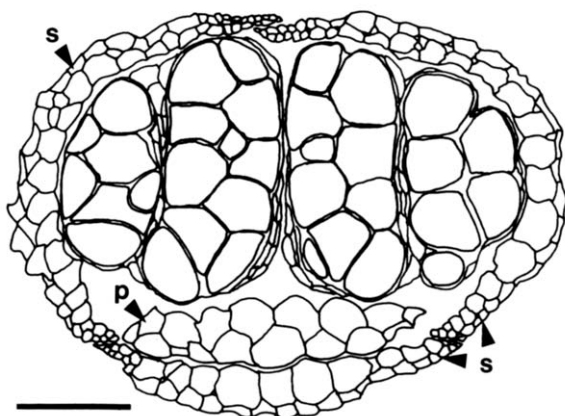


Fig. 3. Drawing of a transverse section of a more apical region of a male flower than shown in Fig. 2, showing the two bilocular anthers, broad two cell thick petal (p) and zygomorphic arrangement of the three sepals (s). Scale bar = 100 μ m. \times 150.

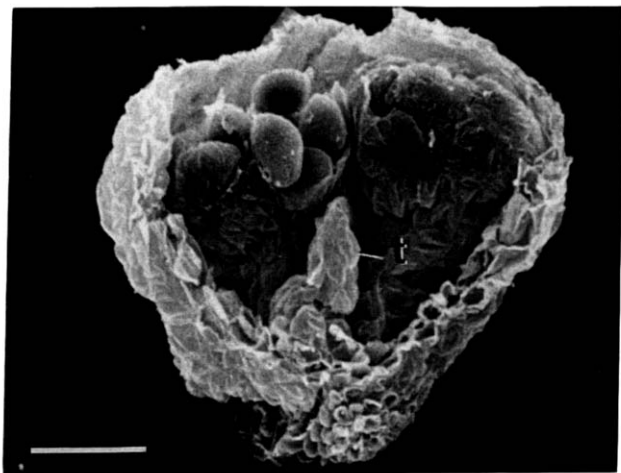


Fig. 4. Dissected male flower showing the minute staminode (t) between the fertile anthers. Scale bar = 100 μ m. \times 150.

a single petal, a single staminode and 2 bisporangiate anthers arranged as shown in Figs. 2–6. Pollen spherical, 60 μ m in diameter; omniaperturate exine consisting of irregularly spaced spinules, pollen occasionally united by bridges of intine (Fig. 7). Less than 40 pollen grains per anther.

Female plants with 1 to several inflorescences in leaf axils; individual inflorescence pedunculate, peduncle thin, elongating to up to 20.0 cm before anthesis; inflorescence clavate, up to 1.0 cm long prior to fertilization; spathe enclosing 1 sessile flower, rupturing at apex; flower opening at water surface; ovary inferior, unilocular with numerous parietal placentae; flower strongly compressed; perianth of 2 sepals, 2 short filiform minute petals, 2 short filiform minute staminodes and 2 deeply cleft bifid stigmas covered with unicellular

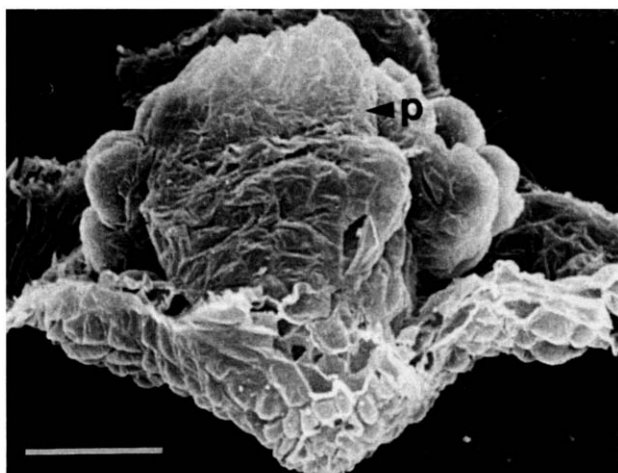


Fig. 5. Dissected male flower with broad petal (p) covering the anther filaments. Scale bar = 100 μm . $\times 180$.

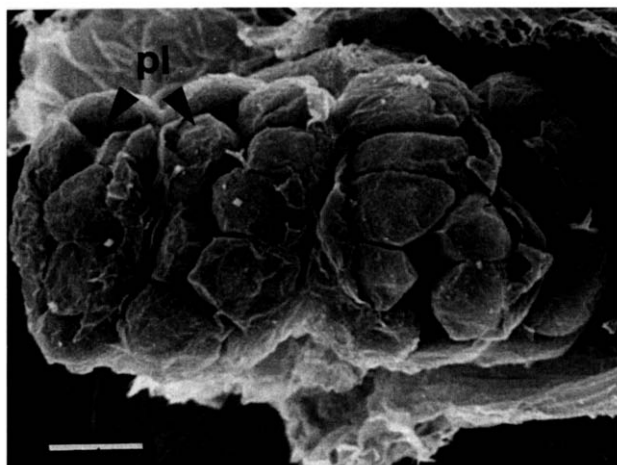


Fig. 6. Dissected male flower viewed from above. Note the clusters of pollen grains (pl) held within two loculi per anther. The walls of the loculi degenerate before anthesis. Scale bar = 50 μm . $\times 250$.

filiform papillae, whorls arranged decussately (Fig. 8–10); branches of stigmas widely separated, lying next to corresponding branch of other stigma above the sepals; open flowers up to 6.0 mm across. Fruit 5.5–7.0 \times 0.25–0.65 cm, two-winged, retracted below water surface by coiling peduncle. Seeds numerous, ellipsoid.

Distribution

V. caulescens is endemic to the tropical and subtropical rivers of north Western Australia, Queensland and the Northern Territory (Fig. 11). The type collection represents the southernmost locality known for this species.

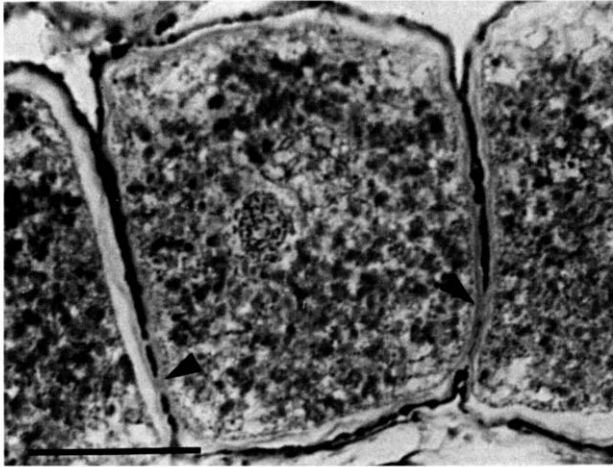


Fig. 7. Basal pollen grains within anther. The pollen has an incomplete exine (dark layer). The intine forms bridges (arrows) connecting adjacent pollen grains. Scale bar = 25 μm . $\times 1000$.

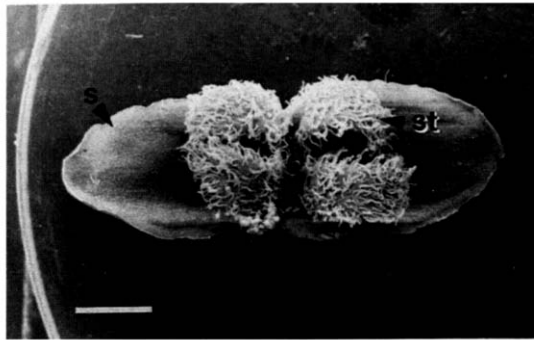


Fig. 8. Female flower showing the paired stigma branches (st) held above the two opposing sepals (s). Scale bar = 1 mm. $\times 10$.

DISCUSSION

In its flowers, *V. caulescens* shows both similarities and dissimilarities to *V. spiralis* L. and *V. americana* Michaux. The presence of sepals, petals, staminodes and bifid stigmata is a common feature of all three species. In contrast to the latter two species, however, in which the female flowers are tripartite, *V. caulescens* has only bipartite female flowers (Fig. 12). In addition to the absence of one member in each whorl, the stigmatic branches are orientated differently. In both *V. spiralis* and *V. americana* the two branches of one stigma remain close to each other and are epipetalous. The stigma branches of *V. caulescens* are widely separated, twisted 90° and paired with the corresponding branch of the other stigma. This may have a reproductive advantage insofar

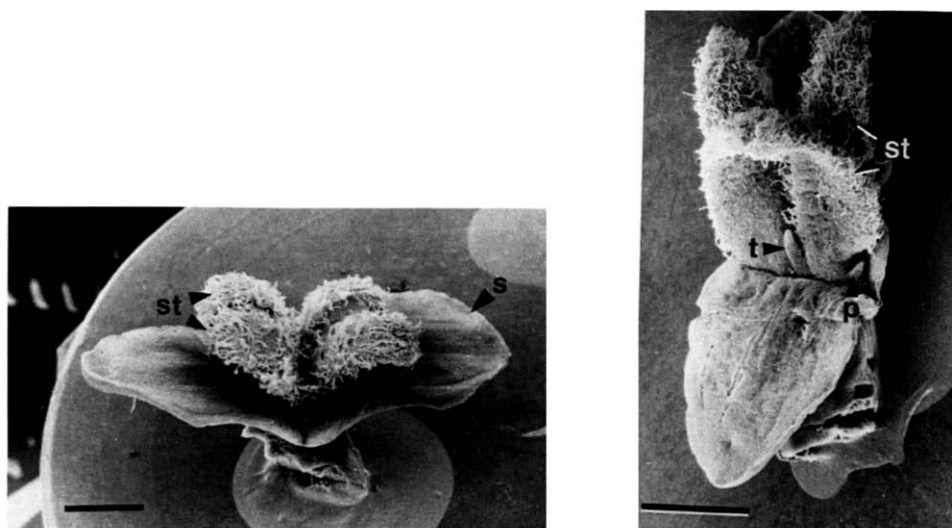


Fig. 9. Lateral view showing the arrangement of the stigma branches (st) above the sepals (s). Note the cluster of pollen grains attached to the base of the left-hand stigma branch. Scale bar = 1 mm. $\times 10$.

Fig. 10. Partially dissected female flower showing the position of the minute petal (p) between the basally united stigma branches (st) and a staminode (t) alternating with the stigmas. Scale bar = 1 mm. $\times 14$.

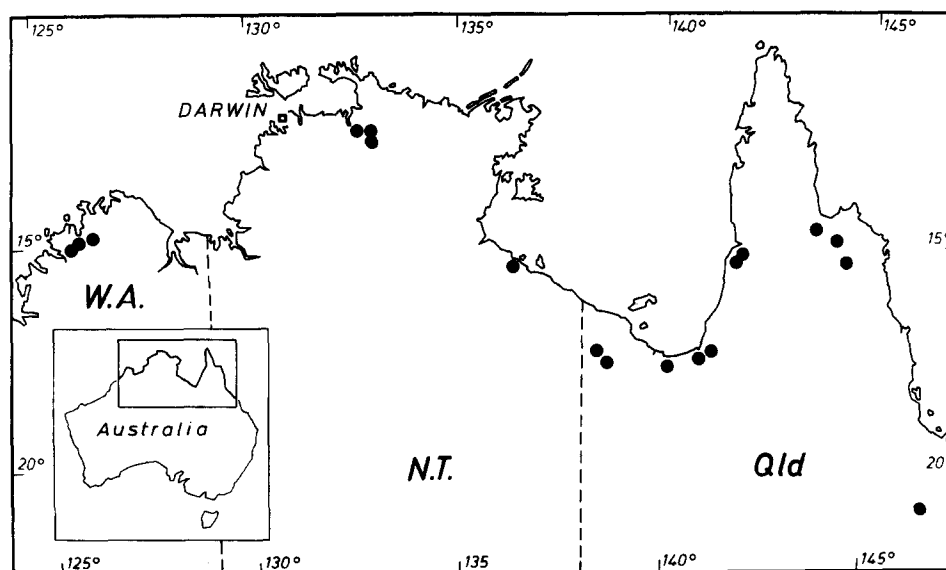


Fig. 11. Distribution of *V. caulescens* in northern Australia based on herbarium records. ● = collection site.

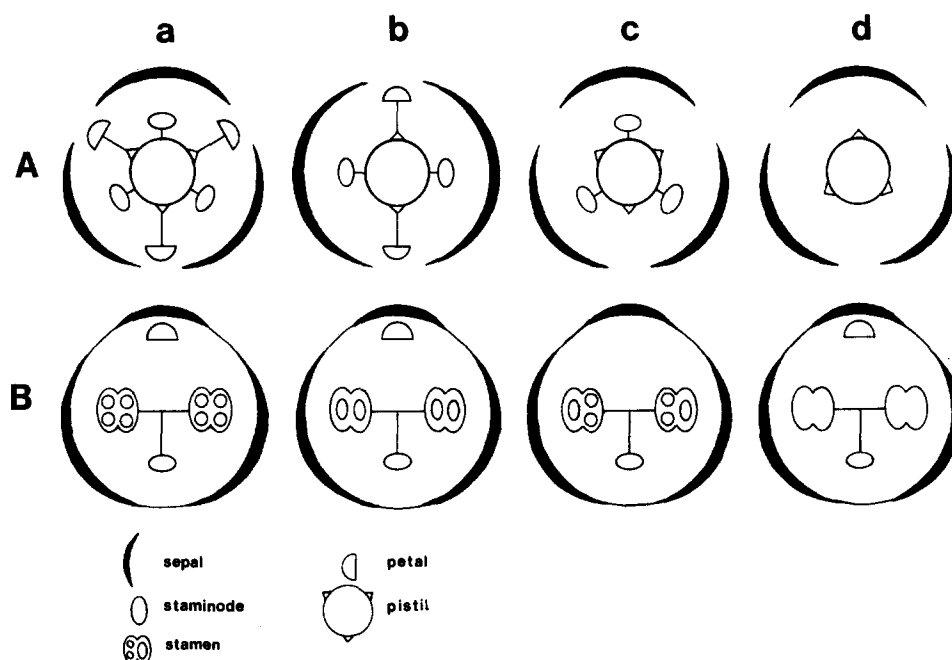


Fig. 12. Floral diagrams of (A) female flowers and (B) male flowers, of (a) *Vallisneria* (except *V. caulescens*), (b) *V. caulescens*, (c) *Maidenia* and (d) *Nechamandra*. Note that the number and position of the locules within the anther are represented by internal line (unknown for *Nechamandra*). The position of the stigmas is indicated by a triangle on the outer side of the circle indicating the pistil.

as the stigma branches may be better protected against contact with water in their position above the comparatively large sepals.

The female flowers of *Maidenia* and *Nechamandra* are tripartite as in *V. spiralis* and *V. americana*, but lack petals in the case of *Maidenia*, and petals and staminodes in *Nechamandra*. The transport of the stigmas to the water surface in *Nechamandra* is accomplished by the hypanthium, whereas in *Vallisneria* and *Maidenia* the peduncle elongates. Curiously, the stigma branches of *Nechamandra* are reported to be arranged opposite instead of alternate with the sepals (Cook and Löönd, 1982) (Fig. 12).

The male flowers of *Vallisneria caulescens* resemble those of the other species of *Vallisneria* in having three zygomorphic sepals, a petal, a staminode and two anthers (Fig. 12). The degree of connation of the two anther filaments forms a basis for taxonomic division in the genus (Lowden, 1982). There is a gradation ranging from *V. spiralis* var. *spiralis*, in which the filaments are distinctly separated, to *V. americana* var. *biwaensis* (Miki) Lowden where they are connate for almost their entire length. The male flowers of *Vallisneria caulescens* have not been observed at anthesis but the mature buds show that the filaments are almost entirely free. The male flowers of *V. caulescens* also

resemble those of *V. spiralis* in lacking the hairs at the base of the androecium that occur in *V. americana*. Filament connation and the presence of hairs at the base of the stamen are thought to be derived characters. The absence of these features in *Nechamandra* and *Maidenia* might support this conclusion.

Light microscope studies of pollen development in *V. spiralis* have shown that the number of loculi per anther may vary from one to four (Witmer, 1937). In *V. caulescens* there are consistently only two loculi per anther and the pollen has fewer spinules than shown for *V. spiralis*. The cohesion of the basal pollen grains by bridges between the intine layers has not previously been observed in this genus. Similar bridges have been recorded in the Winteraceae (Sampson, 1981) and in the pollinia of the Orchidaceae (Zavada, 1983). Dimorphism of this character among the pollen grains of an anther does not occur in the other two families. Compound pollen grains are found in other members of the Hydrocharitaceae, notably in *Elodea nuttallii* St. John (Cook, 1982) and *Halophila* Thouars (Pettitt, 1981). The structural details of these tetrads have only been studied in *Halophila*, where pollen grains are held in moniliform tubes composed of polysaccharide material (Pettitt, 1981). The cohesion of pollen in *V. caulescens* may serve to maintain sex ratios in the progeny. Populations with a disproportionately large number of pistillate plants are recorded in the other species of *Vallisneria* (Lowden, 1982).

Despite the fact that the type collection contains obviously bipartite female flowers and dorsally compressed winged fruits, little mention is made of floral characters in the original description of *V. caulescens*. This and a note accompanying the collection mainly stress that the species can be distinguished from *V. spiralis* on account of its elongate axis.

Vegetatively, *V. caulescens* deviates from the remaining members of the genus. Although the occasional occurrence of a set of enlarged basal leaves in *V. caulescens* is similar to *V. spiralis* and *V. americana*, in which the vertical axis is reduced to a rosette of mostly few leaves (< 50) and branching takes place only for stolon formation, the presence of an elongate axis with both stolons and leaf-bearing branches in *V. caulescens* makes it more similar to *Maidenia* and *Nechamandra*. In these latter genera there exists no basal rosette and the axis carries numerous small (< 8.0 cm) leaves. Except for *V. spiralis*, *V. americana* and the seagrass *Enhalus* Rich., all other species of Hydrocharitaceae that produce boat-like male flowers rely on an elongate axis to raise the leaves towards the water surface and light.

CONCLUSIONS

If *V. caulescens* is accepted as a member of the genus, on the basis of the presence of sepals, petals, staminodes and bifid stigmas in the female flowers of this species, the circumscription of this has to be changed both with regard to vegetative characters (*V. caulescens* has an elongate axis) and floral char-

acters (*V. caulescens* has bipartite female flowers). Although the delimitation of *Vallisneria* from *Maidenia* and *Nechamandra* is no longer possible with simple vegetative characters, and the increased variability of floral structure in this group may require the drawing of new boundaries, we have refrained from making any taxonomic changes because there still exist poorly known Australian species of *Vallisneria* that need to be collected and studied more intensively.

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