INTRODUCTION

All plants vary somewhat in morphological features such as leaf size, leaf shape, and amount of hairiness. However, some populations show greater degrees of variation. Botanists must decide if the extremes of variation can be described as separate species or if the whole range of variation can be expressed in one species. In the latter case, the cause of the variations may be genetic, related to environmental factors, or both.

For over 100 years, botanists have noticed the variability of *Waltheria* (Sterculiaceae) from the Galápagos Islands (Fig. 1). *Waltheria* are common shrubs of the dry forests on most of the major Islands. Hooker in 1847, when studying specimens collected by Darwin and others, described a new species, *W. reticulata* (Hooker 1847). Robinson (1902) recognized this species but divided it into four forms, based on leaf shape, size, and pubescence. In 1911, Stewart likewise maintained Hooker’s species, but described two forms (Stewart 1911). Not until Svenson’s study of Galápagos plants (Svenson 1935) was Hooker’s name placed in synonymy under the older epithet, *W. ovata* Cav. However, Svenson also tried to deal with the leaf variation by delineating four forms. In a later study, Svenson (1946) noted the similar variations in leaves of *Waltheria* growing near the coasts of Ecuador and Perú. In the *Flora of the Galápagos Islands*, Wiggins and Porter (1971) took a conservative approach by treating *W. ovata* as a variable species and placing all the previously described forms in synonymy.

This study was prompted by observations of two types of pollen, which were seen during the preparation of reference slides for a study of fossil pollen in the Galápagos (Colinvaux and Schofield 1976). Most plants have distinctive pollen grains, which can be preserved in soil for thousands of years. They are used to reconstruct the vegetation of previous times; and by comparing the past and present vegetation, changes in climate can be identified.

Some time later, herbarium specimens were obtained of *Waltheria* from Galápagos and South America. These, plus some field observations, were...
used to further investigate the dimorphic pollen, to
document the variations in leaf size and shape, and to
look for correlations that might clarify the taxonomic
interpretation of *W. ovata*.

**METHODS**

Pollen samples were removed from 81 herbarium
specimens (51 Galápagos and 30 South America,
Ecuador and Perú) and processed by the acetolysis
method (Faegri and Iversen 1975). Permanent slides
were made with glycerin jelly and examined under a
light microscope at 400X. Polar and equatorial
diameters of several grains per slide were measured
with a micrometer and averaged. Fossil pollen
samples were processed and measured in the same
way, but were mounted in liquid glycerine so they
could be moved for better observations.

Flowers were removed from 24 herbarium
specimens (9 Galápagos, 15 South America) and
softened in water. Petals and sepals were removed,
and the gynoecium and androecium (male and female
organs) were observed with a dissecting microscope
and measured with a millimeter ruler.

Leaf variations were recorded for 167 specimens
(73 Galápagos, 94 South America). For each
specimen, the largest and the smallest leaves were
measured with a millimeter ruler. The length of
blade along the midrib and width of blade at the
widest point were noted. Averages were calculated
for all specimens and for Galápagos and South
American specimens separately. The texture of dry
leaves, shape of leaf bases, and dentation of leaf
margins also were described for each specimen.

**RESULTS**

**Pollen.**—Among specimens from South America,
18 samples had reticulate pollen (netlike surface) and
12 had echinate pollen (spiny surface). Among
Galápagos specimens, 31 samples were reticulate
and 20 were echinate.

Within the Galápagos, both kinds of pollen
occurred on the eastern Islands (Santa Cruz and east);
only echinate occurred on two Islands (Pinta and
Santiago); and only reticulate on three Islands (Rábida,
Isabela, and Fernandina).

Echinate pollen grains were consistently larger,
with an average polar diameter of 68.1μ and an
average equatorial diameter of 67.9μ. Size of the
reticulate grains averaged 51.2μ for polar diameter
and 50.8μ for equatorial diameter.

Only two collections from South America showed
a clear difference in flower color. Reticulate pollen
was found in the orange flowers and echinate in the
yellow flowers.

In the fossil material from the Galápagos, there
were few *Waltheria* grains in any sample. However,
both kinds of pollen were present at three sites:
lagoons on Santiago, a crater lake on Genovesa, and
Beagle crater on Isabela. Echinate pollen was found
in 16 samples and reticulate pollen in 9 samples of
these postglacial deposits.

**Flowers.**—Two types of flowers were observed,
one with styles exserted (pin) and one with styles
inserted (thrum) (Fig. 2). Long styles averaged 4.5
mm, and stamens associated with them averaged 3.6
mm. Short styles averaged 1.1 mm, with associated
stamens averaging 5.5 mm. In short-style forms, the
stigma was longer in proportion to the style.

There were 5 long styles versus 4 short styles in
Galápagos specimens and 10 long versus 5 short
styles in South American material. All long styles
correlated with reticulate pollen, and all short styles
correlated with echinate pollen.

**Leaves.**—A “typical” leaf of *Waltheria ovata* and
the range of variations are shown in Fig. 3. The
average leaf size for 167 specimens was 3.0 cm long
× 2.5 cm wide. Overall, the largest leaf was 10.0 × 7.5
cm, and the smallest leaf measured 0.5 × 0.2 cm. The
average size for leaves from South America was 4.0
× 3.0 cm, whereas that for leaves from Galápagos was
2.9 × 2.0 cm.
Comparisons were made of several duplicates of individual collections from Perú and Galápagos. For Hutchinson and Wright 5419 (Perú), leaf size ranged from 8.0 x 7.2 cm to 0.5 x 0.4 cm, averaging 3.7 x 3.1 cm. For Schimpff 165 (Galápagos), the size varied from 3.7 x 2.4 cm to 0.6 x 0.3 cm, averaging 2.1 x 1.2 cm.

A separate analysis of 69 specimens from the Galápagos showed a size distribution from the largest leaf on Genovesa to the smallest average on Isabela. The largest individual leaf (6.5 x 7.0 cm) and the smallest individual leaf (0.5 x 0.2) also occurred on these respective Islands.

Leaf shape varied from nearly lanceolate, through ovate, to oval or cordate (occasionally three-lobed). The most common shape for both geographical areas was ovate, hence the specific epithet "ovata."

Leaves from Galápagos specimens tended to be more rugose (wrinkled) in texture, regardless of size. In South American specimens, only the smaller leaves appeared rugose.

In South American collections, there were 24 specimens with cordate bases and 70 without. Galápagos specimens included 27 with cordate bases and 46 with noncordate. The latter ranged from slightly rounded to nearly acute.

Among South American specimens, there were 69 with leaf margins having pointed teeth, 23 with intermediate, and 2 with rounded teeth. Galápagos specimens included 24 with pointed, 38 with
intermediate, and 11 with rounded teeth. Two shallow, basal lobes were apparent only on leaves of three specimens from South America.

**DISCUSSION**

**Pollen.**—Dimorphic pollen was not reported previously in *Waltheria* from the Galápagos Islands. Pollen of *M. ovata* from Chile was described by Heusser (1971) as having a reticulate surface. However, Köhler (1976) did describe two types of pollen in several specimens of *W. ovata* from Ecuador, Perú, and Brazil. Surface textures and dimensions were similar to those mentioned here.

The distribution of two types of extant pollen among the Islands does not clarify the taxonomic status of the species. A majority of the Islands have both types. Also, the fossil pollen samples indicated that both types were present in the past on Isabela (now only reticulate) and Santiago (now only echinate). Another consideration is the random nature of pollen preservation—not all pollen present in an area will be preserved.

Among the limited number of fossil pollen samples, the echinate type was more common. This does not agree with Köhler’s (1976) opinion that the reticulate type has more primitive characteristics.

**Flowers.**—Distyl y (two types of styles) in flowers of Galápagos *Waltheria* was overlooked by previous collectors. The detailed description of *W. ovata* in Wiggins and Porter (1971) did not give any measurements of styles and noted that stamens were “about equal” to the petals in length. However, distylly was known from the Sterculiaceae and several species of *Waltheria* (Köhler 1976). As in this study, his results showed that long styles were consistently associated with reticulate pollen and short styles with echinate pollen.

The occurrence of more than one style type is a system of self-incompatibility that favors outbreeding. Pollen dimorphism frequently is associated with the different flower types (Davis and Heywood 1963). In a survey of angiosperms, Vuilleumier (1967) found that heterostyly occurs sporadically and independently in different families. She further stated that morphological dimorphism of floral parts and diallelic incompatibility are independent breeding systems. When they occur together, they produce increased efficiency of cross-pollination and cross-fertilization.

Carlquist (1974) observed *Limonium*, a heterostylous genus distributed both on islands and continents, and concluded that outbreeding would be an advantage for the small island populations. The same conclusion could be drawn for *Waltheria* in the Galápagos, but insect pollinators are scarce. Further study is needed to determine if the genetics of *Waltheria* require some outbreeding, even with a limited supply of insects to facilitate cross-pollination.

**Leaves.**—The variations in leaf shapes of *W. ovata* have been noticed since the earliest collections were studied. Attempts to organize these variations into forms or subspecies were based on limited numbers of specimens. This study of a larger number of plants from a wider geographical range showed that the leaves vary even more than previously described.

For example, the “typical” leaf derived from my analysis was 3.0 x 2.5 cm and oval, with a noncordate base and small, pointed teeth (Fig. 3). A “typical” leaf described by Robinson (1902) was 2.5 x 1.5 cm with dentate margin and rounded (not cordate) base. Svenson (1935) described a “typical” leaf as 4 x 3 cm, broad, and cordate. Even the ranges for length, width, base, and margin published by Wiggins and Porter (1971) did not include all of the variations noted in this study.

Size varied widely in both geographic areas, but leaves of Galápagos specimens were generally smaller than those from South America. Svenson (1946) also observed that the small leaf sizes seen on Galápagos plants did not occur on the mainland. This difference might be due to climatic or ecological conditions, but no data have been compiled.

Not enough Galápagos collections are available to make any significant correlations between leaf variations and location. *Waltheria* grows from near the shore to mid-elevations on small and larger Islands but is most common in the Transition Zone forming a shrub layer under *Bursera* trees (Fig. 1). Further study is necessary to determine if there are sufficient differences in ecological factors to account for the morphological variability.

**CONCLUSIONS**

My preliminary study of leaves, flowers, and pollen of *Waltheria ovata* from the Galápagos Islands
and South America documented the presence of distyly, dimorphic pollen, and considerable diversity in leaf morphology. A detailed examination and comparison of these variations, an evaluation of environmental differences, and a study of genetics and pollination within populations of *Waltheria* in both areas are needed. Such analyses of a much larger data base might indicate useful taxonomic subdivisions of this variable species. Until such data are compiled, the plants in Galápagos and South America must be considered as belonging to a single species.

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**LITERATURE CITED**


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