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Review

Davidian, H. H. 1982. The *Rhododendron* species, Vol. 1 - Leptodes, Timber Press, Portland, Oregon. 431 pp.

When I started my work on rhododendrons about ten years ago, we had only one comprehensive manual: Stevenson's "The species of *Rhododendron*", a largely outdated work which was quite difficult in use, at least for a beginner, as it was partly without keys and had very few illustrations. Mr. Davidian has now produced the kind of book we all have longed for. As could be expected from a man whose knowledge of the genus is already legendary, the descriptions are most carefully phrased down to the smallest detail. The information on the introduction history of each species is particularly valuable. There are keys to the series, to species, and even to varieties, and a number of colour photographs (some blue/red and blue/green colours are not quite well reproduced), as well as line drawings.

In addition some data of importance for gardeners are included: awards, hardiness, flowering time etc. Davidian has been very cautious when assigning the hardiness - too cautious in my opinion. His values are at variance with those used by for example Peter Cox in his recent books, values which have proven reliable in Scandinavia. Since the book is published in the United States it is also quite surprising that so little information is given about the conditions there. Directly misleading are statements like: "Although hardy, some forms require a sheltered position particularly along the east coast and inland". One should observe that this refers to the British Isles (or Scotland?) only!

The book is evidently written by a man deeply in love with the genus, particularly as garden plants. This is of course a strength, but has also had some negative effects. As a taxonomist I react on statements like: "On the basis of these distinctions *R. hypenanthum* might well be regarded as a variety. However, the extremes of these plants are so dissimilar in

cultivation that it may be desirable to retain the name *hypenanthum*". It is also obvious that Davidian does not with recent revisions by Chamberlain, Cullen and Philcox taxonomic principles. He comments on these revisions, but as he mostly makes statements in the form of: so and so is 'acceptable', or 'defends the old system because gardeners found it useful. Taxonomy is a science and its results should not be influenced by any interest group. I have, however, to declare my sympathy with the gardeners, at least change like those proposed by e.g. Cullen & Chamberlain result in difficulties for them. Nevertheless, I see no reason the genus *Rhododendron* should not be 'brought in line' with other genera. Why should it not be divided in sub-sections and subsections, rather than in the informal creeping plant could belong in the same species as that. Certainly everyone, also gardeners, accepts that *(Juniperus communis)* varies in that way. Of course such practical differences can be taken care of in the nomenclature e.g. by giving cultivar names.

I am convinced that the principles of these new revisions, and should not be rejected. I think, however, that revisions have gone a little too far in their lumping, e.g. including few intraspecific taxa. The authors have certainly also some mistakes because they do not have as great experience with the genus as Davidian. I highly regret that he has been impossible to put his vast knowledge into a modern taxonomic system. It is nevertheless extremely valuable that Mr. Davidian has passed on to us his lifelong experience with the genus, which has undoubtedly produced a marvellous monument over Ballouan era.

Per M. Jørg

Taxonomy and phylogeny of the genus *Acalypha* (Euphorbiaceae) in the Galápagos Archipelago

Ole Seberg



Seberg, O. 1984. Taxonomy and phylogeny of the genus *Acalypha* (Euphorbiaceae) in the Galápagos Archipelago. - Nord. J. Bot. 4: 159-190. Copenhagen. ISSN 0107-055X.

A preliminary phylogeny of the Neotropical *Acalypha* is proposed, and previous infragenetic classifications commented upon. New views are presented on the floral morphology; the homology of the inflorescences and of the allomorphic female flower. The Galápagos *Acalypha* (Euphorbiaceae, Acalyphinae) are revised; the group is established as monophyletic and its relationships are shown. The sister-group is the Neotropical *A. cuspidata*-complex. Four species are recognized, viz. *A. baurii* Robinson & Greenman, *A. wiggenatii* Webster, *A. parvula* J. D. Hooker, and *A. abingdonii* sp. nov. *A. baurii* is shown to be the sister-group of *A. abingdonii* + *A. parvula*, and *A. abingdonii* the sister-group of *A. wiggenatii* + *A. parvula*. Brief accounts are given on nomenclatural history, aspects of morphology, chromosome numbers, geographical distribution (incl. the biogeography of the Galápagos Isles), ecology, pollination biology, and population structure.

Se propone una filogenia preliminar para la *Acalypha* neotropical y se comenta la clasificación infragenética anterior. Se presenta nuevos puntos de vista sobre la morfología floral, la homología de las inflorescencias y sobre las floras alomorfas femeninas. Se revisa nomenclatura y taxonomía de *Acalypha* de Galápagos (Euphorbiaceae, Acalyphinae); se establece el grupo como monofilético y se revelan sus relaciones: el grupo gemelo es el complejo *A. cuspidata* neotropical. Se reconocen cuatro especies en esta revisión: *A. baurii* Robinson & Greenman, *A. wiggenatii* Webster, *A. parvula* J. D. Hooker, y una nueva, *A. abingdonii* que se describe. *A. baurii* parece ser gemela de *A. abingdonii* + *A. parvula*, y *A. abingdonii* la gemela de *A. wiggenatii* + *A. parvula*. Se dan comentarios cortos sobre la historia de la nomenclatura, aspectos de morfología, número cromosómico, distribución geográfica (incluyendo la biogeografía de las Islas Galápagos), ecología, biología de polinización y estructura poblacional.

O. Seberg, Inst. of Systematic Botany, Univ. of Copenhagen, Gothersgade 140, DK-1123 Copenhagen K, Denmark.

Introduction

Webster's treatment (1970, 1971) of the genus *Acalypha* for the "Flora of the Galápagos Islands" has proved very difficult to use. It was based on rather scanty material, and did not include the very extensive collections of J. T. Howell. These, and a considerable number of specimens accumulated during the seventies, mainly due to the efforts of O. Hamann, H. Aderssen, and H. van der Werff, made it possible for me to undertake

the present taxonomic and nomenclatural revision of the Galápagos *Acalypha*.

Materials and methods

The revision is based on field studies, herbarium and to a less extent cultivated material. Specimens representing 400 collections were borrowed from the following herbaria (abbreviations according to Holmgren et al. 1981): AAU, BKL, C, CAS, CGE, DAV, DS, F, G,

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GB, GH, K, MO, NY, S, U, and US. A few specimens have been studied at CDS. Reference to herbaria having possessed the types of J. D. Hooker's taxa is in accordance with Porter (1980).

Sterile parts were measured directly on pressed material, floral parts on material soaked in 27% ammonia for 2-3 h before being transferred to 70% alcohol. Glands and floral parts, incl. seeds, were measured using a light microscope. As many specimens as possible were measured. Mean values and standard deviations were calculated and used to indicate the variation of the continuous variables in the descriptive part; extreme values are given in brackets for both continuous and discrete variables.

The terminology follows the recommendations given in Taxon 11, (Anon. 1962) and Stearn (1978), with the exception of syn- and inflorescence terminology which follows Troll (1964, 1969; see also Weberling 1965).

Information about ecology is based on field studies, collectors' notes, and literature mainly Hamann (1981). The names of formations and subformations are used in accordance with Hamann (1981), while the vegetation zones follow Wiggins & Porter (1971). The official Spanish names of the islands are used. A list of the corresponding English or other names in common use may be found in Bowman (1966).

Taxonomic and biogeographic concepts

The basic systematic principles of Hennig (1965, 1966) are adhered to; see also Nelson & Platnick (1981) or Wiley (1981). The quantitative characters investigated are highly variable and show extensive overlapping; they are consequently not applicable in the reconstruction of the phylogeny (Estabrook 1978).

The ancestors are defined character-wise, by the progressive extrapolation of plesiomorph character states into them, and are thus purely hypothetical constructions (Ross 1974).

The species concept used is morphological, and mostly in line with DuRoi (1930). The methodological problems encountered when using this approach on island populations has been treated by e.g. Eliasson (1974).

The biogeographic method is mainly in accordance with Platnick & Nelson (1978) and Nelson & Platnick (1980, 1981). However, historical geology does not affect or test the generality of biological area-cladograms (Patterson 1981, Rosen 1978), it merely provides guidelines for an explanation of process.

Systematic position of *Acalypha* L.

The genus *Acalypha* L. is included in Acalyphoideae, tribe Acalyphaceae, subtribe Acalyphinae. Of these taxa only the subtribe can be considered monophyletic. *Acalyphopsis* Pax & Hoffmann (1924) is probably best included in *Acalypha*, on account of its apomorph

anther- and inflorescence-morphology, character states shared with several species of *Acalypha*. Thus in the above circumscriptions *Acalypha* is characterized by 2 whorls of 4 bisporangiate anthers, with pendulous vermiciform thecae, opening extremely by longitudinal slits, coiling up in the shape of a corkscrew. This character state is considered an autapomorphy.

Infrageneric classification of *Acalypha*

The latest infrageneric classification of *Acalypha* exists. No recent exhaustive treatment, by Pax & Hoffmann (1924), is just a slightly altered version of an earlier classification by J. Müller of Aargau (1865, 1866), in which he relied heavily on a priori weighted inflorescence characters, and to a less extent on other characters (e.g. indumentum, stipules, leaf-venation). According to the classification is monothetic. Though artificial (see below) it has gained wide acceptance, see e.g. Engler & Prantl (1931) and Radcliffe-Smith (1973). A minor variation on the same framework can be found in Hurusawa (1954).

Preliminary phylogeny of the neotropical *Acalypha*

Though it is beyond the scope of the present paper to furnish an infrageneric classification of *Acalypha*, a preliminary investigation was made of the phylogeny of the Neotropical species. This was done in an attempt to establish whether the Galápagos species constitute a monophyletic group, and if so, to find their extant sister-group. The investigation was restricted to the Neotropical region, as the possibility that the Galápagos species have their sister-group anywhere else can be ignored.

Species representing all 'Series' (in Pax & Hoffmann (1924) the categories Series and Section are misapplied, as the Series are ascribed a higher rank than the Sections) known to occur in the Neotropical Region were initially selected (Tab. 1). 'Series' and species, except the Galápagos species, are circumscribed as in Pax & Hoffmann (1924), irrespective of several recent treatments which have, however, all been made on a regional scale (e.g. Standley & Steyermark 1949, McVaugh 1961, Webster & Burch 1967, Seymour 1979).

In the survey main emphasis has been given to a reconsideration of inflorescence characters. The biased approach has been followed mainly for two reasons; inflorescence characters have been extensively used previously and are fairly easy to observe. Due to the main scope of the present paper, characters constant in the Galápagos *Acalypha*, but known to vary within the genus have deliberately not been considered, viz. anatomy (Ritterhausen 1982), pollen-morphology (Patterson 1962), chromosome numbers (e.g. Miller & Webster

Tab. 1. Species used in constructing the preliminary phylogenetic tree of the Neotropical *Acalypha* (Fig. 3) and their systematic position according to Pax & Hoffmann (1924). Three pairs of taxa are excluded by superficial investigation considered conspecific. The Galápagos species are as circumscribed in the present paper. Concerning the position of the Galápagos species as accepted by Pax & Hoffmann, see the text.

Subgenus:	Series:	Species:	Number of specimens		
= <i>Linostachys</i>	= <i>(Elae-)Acalypha</i>	Acro = <i>Acrostachyae</i>	2, 2		
		Oligo = <i>Oligogyneae</i>	2, 2		
		Panto-Acro = <i>Pantogyneae-Acrogyneae</i>	2, 2		
		Panto-Pleuro = <i>Pantogyneae-Pleurogyneae</i>	2, 2		
		Poly-Acro = <i>Polygyneae-Acrogyneae</i>	2, 2		
		Poly-Dicho = <i>Polygyneae-Dichogyneae</i>	2, 2		
		Poly-Pleuro = <i>Polygyneae-Pleurogyneae</i>	2, 2		
		= <i>Linostachys</i>	= <i>(Elae-)Acalypha</i>	Acro = <i>Acrostachyae</i>	2, 2
				Oligo = <i>Oligogyneae</i>	2, 2
				Panto-Acro = <i>Pantogyneae-Acrogyneae</i>	2, 2
Panto-Pleuro = <i>Pantogyneae-Pleurogyneae</i>	2, 2				
Poly-Acro = <i>Polygyneae-Acrogyneae</i>	2, 2				
Poly-Dicho = <i>Polygyneae-Dichogyneae</i>	2, 2				
Poly-Pleuro = <i>Polygyneae-Pleurogyneae</i>	2, 2				
= <i>Linostachys</i>	= <i>(Elae-)Acalypha</i>			Acro = <i>Acrostachyae</i>	2, 2
				Oligo = <i>Oligogyneae</i>	2, 2
				Panto-Acro = <i>Pantogyneae-Acrogyneae</i>	2, 2
		Panto-Pleuro = <i>Pantogyneae-Pleurogyneae</i>	2, 2		
		Poly-Acro = <i>Polygyneae-Acrogyneae</i>	2, 2		
		Poly-Dicho = <i>Polygyneae-Dichogyneae</i>	2, 2		
		Poly-Pleuro = <i>Polygyneae-Pleurogyneae</i>	2, 2		
		= <i>Linostachys</i>	= <i>(Elae-)Acalypha</i>	Acro = <i>Acrostachyae</i>	2, 2
				Oligo = <i>Oligogyneae</i>	2, 2
				Panto-Acro = <i>Pantogyneae-Acrogyneae</i>	2, 2
Panto-Pleuro = <i>Pantogyneae-Pleurogyneae</i>	2, 2				
Poly-Acro = <i>Polygyneae-Acrogyneae</i>	2, 2				
Poly-Dicho = <i>Polygyneae-Dichogyneae</i>	2, 2				
Poly-Pleuro = <i>Polygyneae-Pleurogyneae</i>	2, 2				

Character-analysis
The following character-analysis is greatly hampered by the lack of a suitable out-group (Wattous & Wheeler 1981). This lack is due to the fact that the present classification of Euphorbiaceae is at all levels from family to genus, predominantly a classification of grades rather than cladés. Thus to avoid an almost infinite regress, a different, though not strictly phylogenetic, approach has been applied. This approach can, to some extent, be accused of being in-group comparison (Wattous & Wheeler 1981), but has, however, been chosen as the character polarities, and hence the resulting cladogram and phyletic tree, always may, and eventually will be, checked against a more general cladogram. The characters used in the present study appear from Tab. 2.

Inflorescence (Character L-III)
As all Euphorbiaceae, *Acalypha* have monotelic inflorescences (Troll 1969).

Inflorescence homology
Of utmost importance in elucidating the phylogeny of *Acalypha* is the establishment of a hypothesis concerning the homology of inflorescence-types. In this context the basic problem is the relationship between the lax, terminal thyrsopaniculate, female inflorescence of e.g. *A. costaricensis* (Fig. 2A) and the condensed, terminal spiciform male, androgynous or female thyrses of e.g. *A. multicaulis*, *A. chamaedrifolia* or *A. dicyonura* (Fig. 2C, E, G). Once a hypothesis on this relationship has been made the remaining inflorescence-types are easily arranged in morphoclines and their polarities disclosed (Fig. 2).

The below hypothesis rests upon two basic assumptions: *Acalypha* is monophyletic, and unisexual flowers are derived (Michaelis 1924).
Accepting the monophyly of the genus, the most parsimonious hypothesis on inflorescence homology is as follows: The terminal, male thyrses of e.g. *A. multicaulis* or the male part of the terminal, androgynous thyrses of e.g. *A. chamaedrifolia* are homologous with the whole terminal, female inflorescence of e.g. *A. costaricensis* (Fig. 1). Consequently, the minute, membranaceous male bracts and glomerules and the minute, membranaceous female bracts and the partial, thyrsopaniculate inflorescences, arising from these bracts, are homologous. The minute, membranaceous bracts on the female, partial inflorescences can be traced as bractoles between the male flowers in the glomerules. In accordance with the above interpretation the leaf-like, female bracts and glomerules found below the male thyrses in e.g. *A. chamaedrifolia* and the ordinary leaves and the axillary inflorescences found beneath the terminal, female inflorescence of e.g. *A. costaricensis* are homologous, too. Usually even the stipules of the ordinary leaves persist at the base of the leaf-like bracts.

Termination of primary stem:

C→F→E→G→I
A→I

First order paracladia:

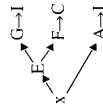
D→C→F→E→G→H
A/C→B/C

The crucial step is to disclose the polarities of these morphoclines. Troll (1964) has shown that the inflorescences of the paracladia replicate the inflorescence of the primary stem. Therefore the notion that the plesiomorph character state is the same in both inflorescence types provides the most parsimonious hypothesis. Accordingly the spiciform, androgynous thyse (character state E) and the thyse-paniculate inflorescence (character states A and A/C) are plesiomorph.

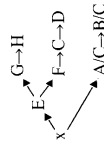
Postulating any other character states the plesiomorph state either requires that the plesiomorph character states are different for the primary stem and first order paracladia (otherwise dioecy would have to be plesiomorph), or will violate Dollo's Law (1893).

Apparently the correlation of character states A and C or B and C favours the hypothesis of different plesiomorph states for the primary stem and first order paracladia, however, these inflorescences are strictly homologous, which is not the case with any other relevant combination of inflorescences.

The relationship between the morphoclines has been commented on previously, the character state of the hypothetical ancestor will be designated x. To sum up, the following trends are hypothesized for the character states of the terminal part of the primary stem:



and for the first order paracladia:



The hypothesis, proposed by Rao (1971), that the thyse-paniculate inflorescence is the plesiomorph character state in the Euphorbiaceae, is founded on considerations of group trends (Ross 1974, Crisci & Stuessy 1980), and is thus of dubious value.

In addition to the character states just accounted for, a tenth state is encountered in the first order paracladia of several African *Acalypha* and in the genus *Acalypha* Pax & Hoffmann: The spiciform, gynaeandrous thyse, usually with minute, membranaceous bracts

throughout. This character state is apparently difficult to fit into the above character state tree, however, for a possible interpretation, see below.

Number of female flowers/leaf-like bract (character IV)

Three character states describe this character sufficiently (the minute, membranaceous bracts are homologous with the male bracteoles):

- A. dichasium, with 5-7 flowers and 8-10 minute, membranaceous bracts.
- A. monochasium, with 2-3 flowers and 4 minute, membranaceous bracts.
- A. single flower with 2 minute, membranaceous bracts.

The character states can be arranged in both an ascending and a descending morphocline, but as the above character is, in essence, the same character as character I the trend is easily established:

a→b→c

The trend chosen is thus preferred as compatible with the previously depicted trend in inflorescence character states (first order paracladia). It is worth mentioning that the acceptance of the reverse trend only adds additional support to the functional in-group (Watrous & Wheeler 1981) including the Galapagos species, by adding yet another synapomorphy to the group.

Allomorphic female flowers (character V)

The term allomorphic female flower is used in accordance with Radcliffe-Smith (1973). The presence of allomorphic female flowers is considered apomorphic as it is restricted to the genus *Acalypha* within the Euphorbiaceae (out-group comparison, Watrous & Wheeler 1981), and thus the replacement of a male flower terminating the androgynous first order paracladia with an allomorphic female flower is the apomorphic character state.

It is interesting that the allomorphic female flowers of the Neotropical *Acalypha* show limited morphological variation (the whole pattern being found in e.g. *A. baurei* or *A. parvula* (Fig. 5B-F). This contrasts markedly with the tremendous morphological variation seen between some African species (Radcliffe-Smith 1973).

In two Neotropical *Acalypha*, *A. setosa* A. Rich. and *A. subcastrata* A. Rich., not only the terminal male flower but even some of the subapical male glomerules of the first order paracladia may be replaced by allomorphic female flowers. As the allomorphic female flower may, though rarely, be secondarily replaced by a female flower, the character state gynaeandrous inflorescence is conveniently explained as being derived from character state C (character I). This hypothesis gains support by the female and male bracts usually

being similar in the gynaeandrous inflorescences. If the female bracts are enlarged, this is secondary.

The presented evidence does, together with another morphological, strongly favour the reduction of *Acalypha* to: Pax & Hoffmann to synonymy under *Acalypha*.

Female variant (character VI)

In agreement with Michaelis (1924) and with Rao & Ramaswami (1969) the 5-merous perianth is considered to be a plesiomorph character state.

Prophylls (character VII)

The lack of prophylls is doubtless a reductional phenomenon, and is as such to be considered as an apomorphy.

Phylogenetic hypothesis

The Phylogenetic hypothesis constructed from the characters in Tab. 2 is shown in Fig. 3. The distribution of character states within the species can be found in Tab. 3. Concerning the phylogeny of the Galapagos species: see below. However, one species *A. diversifolia* Jacq. requires additional comment. This species has been placed in the indicated position (Fig. 3) as the female leaf-like bracts "basally on the spiciform thy-

ses (first order paracladia) are not, as generally believed, homologous with the leaf-like, female bracts of the remaining species; the "bracts" of *A. diversifolia* are enlarged prophylls; and only one in a pair is enlarged. Evidence supporting this hypothesis is as follows: (1) when the first order paracladia are male, which is often the case, two prophylls are apparently present, when androgynous apparently only one, (2) the prophyll supporting female flowers is when young indistinguishable from the other prophyll, (3) the prophyll and the "bract" are precisely, transversely aligned, and (4) the "bract" is without stipules, as is usually found in the leaf-like, female bracts.

For obvious reasons no formal recognition of infrageneric taxa is attempted in the present paper. Still, certain problems inherited from the traditional classification (Pax & Hoffmann 1924) are evident (cf. Tab. 1 and Fig. 3): The subgenera *Linosyachys* and (*Eiolypha*) *Acalypha* are presumably monophyletic, but their exact genealogical relationship remains obscure, as their only synapomorphy is the peculiar anther-morphology.

The "Series" *Polygyne-Acrogyne*, *Pantogyne-Acrogyne*, and *Oligogyne* are all non-monophyletic. The artificial nature of the "Series" is unfortunate as the Galapagos *Acalypha* are thus widely separated in the classification, even though the present study shows that they constitute a monophyletic group. Webster (1970) has commented on this previously.

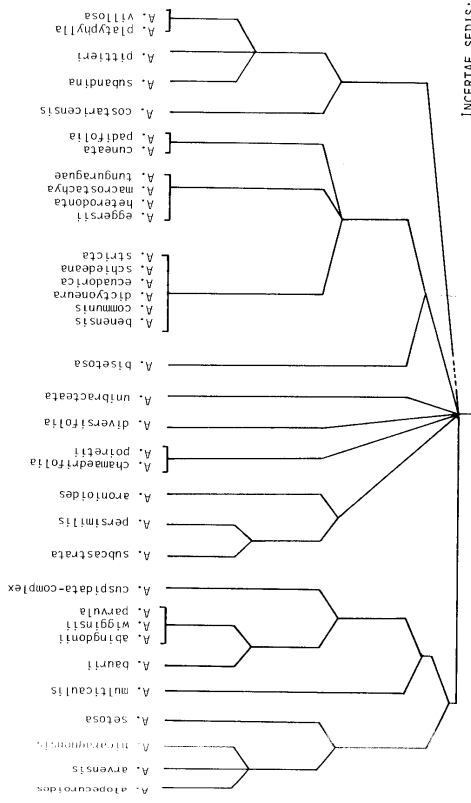


Fig. 3. Preliminary phylogenetic tree of the Neotropical *Acalypha*. Uncertainty is expressed as tri- or multifurcations. Species budding off in the same position thus have the same apomorphies. Some of the characters used to reconstruct the underlying cladogram are, however, without doubt homoplasious. Concerning the phylogeny of the Galapagos species, see Fig. 6.

Tab. 3. Character state-matrix for the species in Tab. 1. Characters and character states as in Tab. 2. - p and a: pleio- and apomorph character state of binary characters (III and V-VII); a': the allomorphic female flower was secondarily lost in androgynous Pests of the species; dash: the character in question could not be decided in the present material; blank: the character is irrelevant for the species. Character states of *Acalypha diversifolia*, see text.

Species	I	II	III	IV	V	VI	VII
<i>A. abingdonii</i>	E	E/F	p	b	a'	a	a
<i>A. alopecuroides</i>	E	D	a	b	a	a	a
<i>A. amblyodonta</i>	I	F	c	c	p	a	a
<i>A. aronioides</i>	I	E/C	p	c	p	a	a
<i>A. arvensis</i>	E	E/F	a	b	a	a	a
<i>A. baurii</i>	G	C	a	a	p	a	a
<i>A. benensis</i>	I	F	a	c	p	a	a
<i>A. biszosa</i>	I	E	p	c	p	a	a
<i>A. chamaedryfolia</i>	A	F	p	c	p	a	a
<i>A. canariensis</i>	G	C	a	c	p	a	a
<i>A. comaricensis</i>	G	C	a	c	p	a	a
<i>A. eunata</i>	G	G/C	p	b	a	a	a
<i>A. fidiata</i>	I	F	a	c	p	a	a
<i>A. dictyonera</i>	I	(F/C)	a	b	a	a	a
<i>A. diversifolia</i>	G	C	a	c	p	a	(a/p)
<i>A. ecuadorica</i>	I	C/G	a	c	p	a	a
<i>A. egypti</i>	I	F	a	b	a	a	a
<i>A. flabellifera</i>	I	C/G	a	c	p	a	a
<i>A. heterodonta</i>	-	E	-	-	-	-	-
<i>A. hispida</i>	-	-	-	-	-	-	-
<i>A. macrophylla</i>	-	-	-	-	-	-	-
<i>A. macrosaetosa</i>	-	C/G	a	c	p	a	a
<i>A. multicaulis</i>	C/F	F	a	a	a	a	a
<i>A. nicaraguensis</i>	E	G/C	p	c	a	a	a
<i>A. padifolia</i>	G	E	p	c	a	a	a
<i>A. parvula</i>	E	E/E	b	b	a	a	a
<i>A. persimilis</i>	E	E/C	p	c	p	a	a
<i>A. pittieri</i>	I	B/C	a	c	p	a	a
<i>A. plathyphlla</i>	I	I	p	c	p	a	a
<i>A. potretii</i>	E	-	-	-	-	-	-
<i>A. ruzizana</i>	E	-	-	-	-	-	-
<i>A. schiedana</i>	G	C	a	c	p	a	a
<i>A. setosa</i>	E	E/C	p	c	a	a	a
<i>A. stricta</i>	E	C	a	c	p	a	a
<i>A. subandina</i>	I	A/C	p	c	p	a	a
<i>A. subcastrata</i>	I	E/D	p	c	p	a	a
<i>A. tunguraguae</i>	G	-	-	-	-	-	-
<i>A. villosa</i>	I	B/C	a	b	a	a	a
<i>A. wigginsii</i>	E	E/F	a	a'	a	a	a
<i>A. unibractea</i>	-	H/-	-	-	-	-	-

Delimitation and sister-group relationship of the Galápagos *Acalypha*

The classification problems of Pax & Hoffmann (1924) are, however, easily explained, as a survey of the inflorescence types they used in separating infragenetic taxa in (*Eu*-)*Acalypha* reveals that 9 of 11 different types occur in the Galápagos species (viz. type a, b, c, e, f, g, h, i, and k; Pax & Hoffmann 1924: 3, Fig. 2). Additional examples could readily be found, e.g. the species-pair *A. dicyonera* and *A. stellipila*, which are doubtless conspecific (sharing an apomorph indumentum character state: setate hairs) yet due to the presence or absence of terminal inflorescence are ascribed to different "Series".

The lack of a consistent infragenetic classification has led to a vicious circle: It is at present far easier to describe a new taxon than to establish whether it has previously been described.

rain: these taxa are unreliable. Several species recognized by Pax & Hoffmann (1924) might eventually prove to belong to this group (e.g. *A. lagoensis* Müll. Arg., *A. santae-martae* Pax & Hoffmann), they have, however, not been available in the present study.

The above monophyletic group can be recognized on the following combination of characters: Propiyl-less, specific, m., androgynous first order paracladia, terminated by an allomorphic female flower (may be secondarily lost in some species) with few (1-4, rarely more) leaf-like bracts, each supporting 2-7 female flowers with a 3-merous perianth.

The Galápagos species are either subshrubs or have habits easily derived from a subshrubby habit. The *A. cuspidata*-complex are shrubs. Though this is not in agreement with Pax & Hoffmann (1924), the admittedly few specimens of *A. multicaulis* at my disposal were all clearly shrubs. Accordingly, out-group comparison reveals that within the smaller functional in-group (the *A. cuspidata*-complex + the Galápagos *Acalypha*), the character state of the Galápagos *Acalypha* is apomorphic. In addition to the above mentioned attributes, the Galápagos *Acalypha* may thus be separated from the *A. cuspidata*-complex by being subshrubs or "facultative" annuals.

Some plesiomorph character-states may also be useful in separating the Galápagos species from their closest relatives: the primary stem is terminated by an androgynous or female spiciform thyse, usually with many (more than three) leaf-like female bracts. The leaf-like bracts are lobed, lobes cut 1/2-2/3 to the base. The fruit has protruding tubercles.

Morphology of the Galápagos *Acalypha*

Some of the characters examined are of no taxonomic importance in the Galápagos *Acalypha*, but either they have not been discussed in detail previously or they have not been looked upon in the presented way before. Additionally some of the characters might prove valuable in the badly needed monographic treatment of the genus.

ference in degree of woodiness. The primary stem and main branches are in *A. abingdonii*, *A. wigginsii*, and to a less extent in *A. baurii*, extensively lignified in most of their length. When developed as a subshrub *A. parvula* is lignified at the base only.

Stems and branches are obtuse-angled when young, becoming terete, and more or less smooth white aging. Basally, the bark of older specimens of especially *A. baurii* is often covered with light-coloured lenticels. The colour of the plants varies from green to red; the variation being most pronounced in *A. parvula*.

Indumentum

There are three types of trichomes: (1) Coronulate, smooth-lobed papillae (Wilkinson 1979; the "Drüsenpapillen" of Ritterhausen 1892), (2) Simple, uniseriate, multicellular (usually 2-6 cells long hairs, and (3) Simple, multiseriate, stalked glandular hairs, with subglobose-turbinate heads.

The papillae are found on unligified organs. They vary considerably in prominence. The non-glandular indumentum falls into two categories; viz. puberulent and hirtellous. The puberulent indumentum on the axial organs is frequently recurved. The prevailing type of non-glandular indumentum differs between the species. *A. parvula* and *A. wigginsii* are mostly puberulent whereas in *A. baurii*, and to a less extent in *A. abingdonii* the hirtellous type dominates, but no sharp distinction can be made between the species.

All species are glandular. The principal vein of the teeth of the leaves and of the lobes of the female, leaf-like bracts are consistently terminated by a gland. The density of glands varies among the species. *A. wigginsii* is always densely glandular, *A. parvula* mostly so, while *A. baurii* and *A. abingdonii* appear eglandular, but overlapping occurs. The size and colour of the gland-heads are useful taxonomic characters. *A. abingdonii*, *A. baurii* and *A. parvula* all have small, colourless to red glands, and *A. wigginsii* large, bright yellow glands. Thus in the field, the glands of *A. wigginsii* are readily visible with the naked eye, whereas the glands of the other species are usually only visible with a hand lens.

Leaves

The leaves are all, except the first epicotyledonary pair, alternate. The stipules are free, entire, with indumentum confined to the abaxial surface, and the margins. Usually they are eglandular or with a few marginal glands basally. The petioles are obtuse-angled. The indumentum on the lamina is most dense on the veins. The leaf-margins are crenate-serrate; the basal teeth straight, otherwise convex (Hickey 1979). The venation of the lamina is invariably perfect, actinodromous (Hickey 1979) with 5 basal primary veins; the 2 lowest ones reduced. The prophylls are similar to but smaller than the stipules.

The first order paracladia (Pc^1) are all, except those developed from the cotyledons, very much reduced, composed of an apical, androgynous or above of a female inflorescence, and a second order paracladium only; the Pc^2 even lack prophylls. In *A. baarii* the androgynous inflorescences are terminated by an allomorphic female flower, in *A. abingdonii*, *A. parvula*, and *A. wigginsii* by a male flower. The female Pc^1 are invariably terminated by an allomorphic female flower. Development is mesotomic (Troll 1969). First order paracladia arising from the cotyledons (CoT) are similar to the primary stem, prostrate-ascending, with reduced basi- and mesopodium.

The second order paracladia (Pc^2) arising at the base of the epicotyledonary Pc^1 are either similar to the primary stem, suberect or the lowest pair occasionally ascending, or similar to the corresponding Pc^1 . Though fundamentally emerging from the Pc^1 , their development is basitonic with respect to the primary stem. The basi- and mesopodium are reduced.

When similar to the primary stem, the Pc^2 may under adverse conditions be reduced so much that only the apical inflorescence is present. The development of the Pc^2 on the CoT s depends on their position; from the axis of the prophylls they are similar to the primary stem, whereas from the axils of ordinary leaves they are similar to the epicotyledonary Pc^1 .

Likewise, third order paracladia (Pc^3) similar to the primary stem are occasionally developed from the axils of the prophylls on the Pc^2 , whereas the Pc^3 arising from the axils of ordinary leaves are similar to the epicotyledonary Pc^1 , or in *A. baarii* and *A. parvula*, especially basally on the plants, entirely female, consisting of 1-8 leaf-like bracts and a pedicellate allomorphic female flower.

Summing up, paracladia developed in the axils of prophylls, which, however may be entirely reduced, and cotyledons are usually similar to the primary stem (but see the Pc^2), whereas paracladia developed in the axils of ordinary leaves are reduced to inflorescences. Development and flowering may continue following this pattern as long as conditions are favourable; when conditions get severe growth either ceases or the plants die. Growth may be resumed from paracladia developing in the axils of prophylls. Plants having survived several growth-seasons, thus tend to become increasingly branched. This may be very pronounced in *A. parvula*.

An alternative interpretation, assuming that the branches arising from the nodes are accessory, is given by Champault (1970).

Inflorescence

Inflorescence structure

The inflorescences are monotelic, spiciform thyrse, but may be variously reduced, obscuring the basic pattern. Development is acropetal apart from the terminal

flowers which develop precociously. The terminal flowers are ebracteate, with inarticulate pedicels.

The bracteate, female thyrses apically on the primary stem are often well developed, but variable with respect to number and distance between the bracts. In *A. baarii* there are 14-25, in *A. parvula* usually 7-20 slightly spaced bracts. In *A. abingdonii* there are usually 24-44, strong condensed bracts. *A. wigginsii* is excluded from the present discussion; the single apical inflorescence is in line with the inflorescences of *A. baarii* and *A. parvula*. The terminal male thyrses are, when present, usually strongly reduced, occasionally only the terminal male flower persists, scarcely visible, hidden between the female bracts.

The majority of epicotyledonary Pc^1 are androgynous, but below the apical inflorescence often female; similar to, but smaller than, the apical inflorescence. A continuous change between the androgynous and female Pc^1 is frequently evident; the female Pc^1 , near the apical inflorescence, are terminated by allomorphic female flowers, which are replaced by male thyrses: increasing in length away from the apex, concomitant with a decrease in the number of female bracts. A stable configuration of the androgynous Pc^1 is reached after a few nodes (generally 1-4) from the apex. The below descriptions are drawn from these androgynous paracladia. The androgynous Pc^1 are sessile to long pedunculate, usually with 1-4 female bracts basally. The male thyrses are projecting above the female bracts on an often well developed rachis.

Male bracts and pedicels

The male bracts may or may not be evenly spaced along the rachis, making the thyrses contiguous or variously interrupted. The bracts are sessile, extremely variable in shape, even within a single thyrsis, rarely exceeding 1 mm in length, membranaceous. The indumentum is mostly found on the margins, occasionally on the abaxial surface, too. All bracts support a many-flowered glomerule. In homology with the structure of the female partial-inflorescences (Pl of Troll 1964) the glomerules are probably cymose, but further studies are needed. The bracteoles are filiform, minute, and transparent; their relationships to individual flowers obscure.

The pedicels are on all but the terminal flowers articulate. The articulation has been used in favour of the hypothesis that each flower is the sole survivor of a cyme (Rao 1971). No evidence supports this, on the contrary, the creation of this hypothesis seems superfluous. Therefore a less intricate and thus more parsimonious hypothesis is presented below:

The articulation is simply the external manifestation of an abscission-zone. There is a striking time difference in development among the flowers in a glomerule, and the flowers developed first would, if they were not shed, make it impossible for the later ones to develop and shed their pollen, by forming a dome-shaped shield enclosing them. That abscission does take place in this

zone can easily be seen either by manipulating older flowers or studying older inflorescences.

Female, leaf-like bracts

The female, leaf-like bracts are sessile and bistipulate. The stipules are narrowly triangular to subulate and inconspicuous. The margin is lobed or double-lobed. However, transitional types are not infrequent. The three primary lobes in the double-lobed bracts may be traced to the three major veins in the ordinary leaves. The indumentum is confined to the abaxial surface, the adaxial surface of the lobes, and the margin.

All bracts support a monochasium, with 2-3, very rarely 1-4 or 5 subsessile flowers. The oldest flower with both, the younger with only one prophyll (bracteoles). The prophylls are similar to the male bracts, but often smaller.

Flowers

No perfect flowers have been observed.

Male flowers

The male flowers are 4-, the terminal rarely 5-merous, depressed pyramidal. The perianth lobes are triangular, membranaceous, green-brown, and papillose. The lobes are glabrous in *A. wigginsii*, and usually more or less puberulent in the other species. The prominence of the papillae is variable, in *A. abingdonii* they protrude from the surface with a length comparable to their diameter, while in *A. baarii*, *A. parvula*, and *A. wigginsii* they are much shorter. Wilkinson (1979) has, however, recently questioned the taxonomic value of papilla characters.

The 8(-10) free stamens are arranged in 2 whorls. The filaments are simple, compressed cylindrical, dilated below, and annulate. The anthers are bisporangiate. The thecae are basifixed, pendulous, vermiform, and open extensively by a longitudinal slit, coiling up in the shape of a corkscrew. The connectives are obtrullate, with obtuse apex.

The pollen grains are spheroidal, tricolporate, and psilate (see also Punt 1962). The pollen grains are dispersed separately.

Female flowers

The female flowers are 3-merous. The perianth lobes are imbricate, decreasing in size in accordance with the age-sequence of the flowers and towards the bract. The indumentum is mostly found on the margins, occasionally on the abaxial surface.

The ovary is 3-carpellate and 3-loculed, with one ovule in each locule. The styles are free, cut into several filiform segments, rarely subtentire, often reddish basally. The fruit is capsular, with 3 elastically dehiscent cocci separating from a persistent columella.

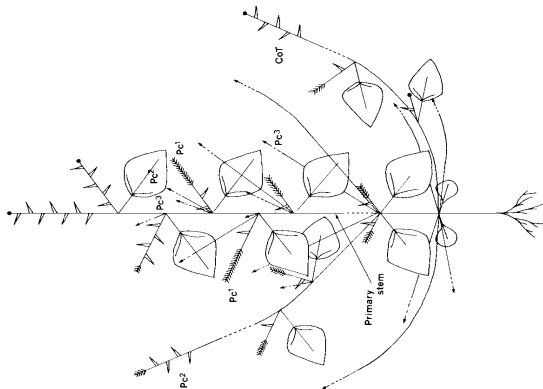


Fig. 4. Diagrammatic drawing of the symplorescence of *Acelypha parvula*. - CoT: Cotyledonary first order paracladia. - Pc^1 , Pc^2 , and Pc^3 : First, second, and third order paracladia. Symbols otherwise as in Fig. 2.

Symplorescence

All species are monoecious with the inflorescences arranged in a complex, monotelic symplorescence (Fig. 4). The primary stem is erect, either ending in an androgynous inflorescence, terminated by a male flower, or in a female inflorescence terminated by an allomorphic female flower. In *A. wigginsii* only a single specimen with an apical inflorescence (Werff 1669 in U) is known, probably due to the few collections (7) which are all but one from the same period of the year.

All leaves on the primary stem, including the cotyledons, are potentially capable of supporting paracladia. However, the field of inhibition (HZ of Troll 1964) varies between the species. In natural habitats only *A. parvula* develops paracladia from the two lowest nodes (the cotyledonary and first epicotyledonary nodes, respectively). Caution must, however, be taken when evaluating this character, as inhibition may be caused by environmental factors (Troll 1964). Under uniform greenhouse conditions the inhibition persists in *A. abingdonii* and *A. baarii*, but is broken in *A. wigginsii*. Thus the field of inhibition is probably genetically fixed in *A. abingdonii* and *A. baarii*. In both species inhibition may be broken if the primary stem is destroyed.

Tab. 5. Plesio- and apomorph character states employed in constructing the cladogram of the Galápagos *Acadlypha* (Fig. 6).

Character	Plesiomorph	Character states	Apomorph
a. Habit	Subshrub		"Facultative" annual
b. Ground-colour	Yellow		Colourless to red
c. Zones of inhibition (H. of Troll 1964)	Encompassing the 2 lowest nodes		No inhibition
d. Petiole in the axils of secondary leaves	Female-allomorphic female		Androgynous
e. Apical thyrse	With 7-20, slightly spaced, leaf-like bracts		With 24-44, strongly condensed, leaf-like bracts
f. Inflorescence on male perianths	Puberulent		Glabrous
g. Papillae on male perianths	Slightly protruding		Very prominent
h. Termination of androgynous Petiole	Allomorphic female flower		Male flower

5. The embryogeneses of the ovules of both types of female flowers are identical (Kapil 1960).
 6. The absence of a carunculus is probably due to the fact that the fruit is indehiscent.

Seeds and seedlings

There is one seed in each locule. The mature seeds are ovoid, reticulate-foveate. The seeds of the female flowers are carunculate, whereas the otherwise identical seeds of the allomorphic female flowers are scarunculate. The seedlings are epigeous. The cotyledons are more or less circular, 1-2 mm long; chartaceous, puberulent, and eglanular. Base decurrent, margins entire, and apex rounded.

Chromosome numbers

Chromosomes have been counted in 3 species, viz. *A. baurii*, *A. parvula*, and *A. abingdonii*. All have $2n = 20$ (Hart & Werff in Love 1977). This is compatible with $x = 10$ for the genus as proposed by Miller & Webster (1966).

Pollination biology and population structure

The population structure of the Galápagos *Acadlypha* shows striking differences. Thus *A. parvula* is very homogeneous within and quite heterogeneous between populations, whereas *A. abingdonii* and *A. wigginsii*, and to a less extent *A. baurii*, are rather homogeneous. A variation pattern similar to the one found in *A. parvula* has been reported from the predominantly self-pollinated Galápagos tomatoes (Rick 1963).

As the *Acadlypha* species are monoecious and adapted to wind-pollination, out-breeding is initially thought to prevail, and accordingly all species are expected to be

fairly homogeneous. However, if they are self-compatible as are some other Galápagos genera (*Lycopersicon*, Rick 1963; *Scatelia*, Rick 1966; Eliasson 1974), two circumstances may enhance their micro-geographic differentiation: (1) The male and female flowers are in close proximity, especially in the androgynous inflorescences, and as dichogamy is not pronounced, out-breeding is strongly reduced. (2) The populations often have a patchy distribution (pers. obs.; O. Hamann obs.), each population probably having descended from a single or a few propagules. Therefore genetic drift is supposed occasionally to play a decisive role in shaping individual populations, an effect that is enforced by in-breeding. As the fundamental assumption of the genetic drift hypothesis is not likely to be tenable (Endler 1977), every single population must be presumed to be closely adapted to the ecological conditions prevailing on the habitat.

For these reasons a possible explanation accounting for the observed differences in population structure could be that *A. parvula* occurs in the most varied, occasionally unstable, habitats, *A. baurii* in fairly homogeneous, stable habitats, and at least the present distribution of *A. abingdonii* is continuous, while *A. wigginsii* only consists of a single population.

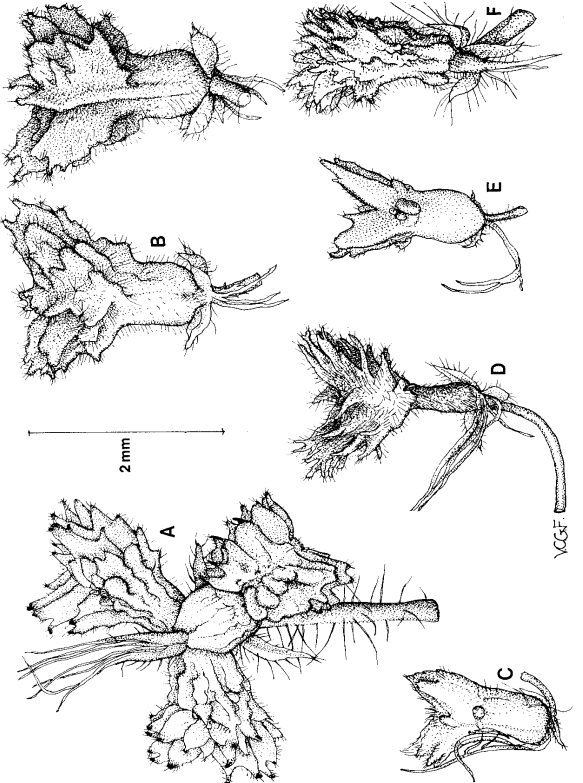


Fig. 5. Morphological variation of the allomorphic female flower. - A: *Acadlypha abingdonii*, three-carpellate, allomorphic female flower; - B-F: *A. parvula*, variations in the mono-carpellate, allomorphic female flower. B is the typical shape and A, C-F are occasional variations in all specimens. A: Hamann & Seberg 1790.3 (C); B: Howell 9893 (CAS); C: Wiggins 18400 (DS); D: Howell 9014 (CAS); E: Howell 9101 (CAS); F: A. & H. Adersen 1934 (C).

Allomorphic female flowers

Allomorphic female flowers have not previously been reported from Galápagos *Acadlypha*. The allomorphic female flowers are 3-4-merous. The perianth is similar to the perianth of the female flowers. The ovary is mono-carpellate, rarely 2- or 3-carpellate (Fig. 5). The carpel(s) is turbinately-clavate, divided into two equal halves by a suture, distally covered with tubercles arranged in two groups. Often the carpels are asymmetrical or the tubercles are more or less reduced. When a single carpel is present, it is situated in an oblique angle to the pedicel, and the style protrudes between the perianth lobes. When 2- or 3-carpellate, the carpels are in a right angle to the pedicel, and the styles are terminal (Fig. 5). Style as on the female flowers. The fruit is indehiscent. The function of this type of flower is unknown. It probably aids dispersal (indehiscent, long tubercles), and due to its precocious development increases the amount of out-breeding.

Homology of the allomorphic female flowers

Radcliffe-Smith (1973, 1975) expressed doubts as to the relationship of some of the structures of the allomorphic

female flower. However, I find no difficulties in establishing homology between the allomorphic female and the female flowers. Thus the appearance of the allomorphic female flower is to be viewed in line with the deviating apical flower found in genera of other families with monotelic inflorescences; e.g. *Menyanthes* and *Berberis* (Troll 1964). Evidence supporting this hypothesis is:

1. The allomorphic female flowers are when 3-carpellate essentially similar to the female flowers (Fig. 5A).
2. Rarely the carpel(s) of the allomorphic female flowers are replaced by carpels indistinguishable from the carpels of the female flowers.
3. The structure on the allomorphic female flowers variably described as sterile carpels (Müller 1865, Rao 1971) or, though with doubt, as bracts (Radcliffe-Smith 1973) are similar to the tubercles found on the fruits of the female flowers. Their epidermal nature is also obscured by their ontogeny (Kenover 1919).
4. The vascular supplies of the carpels of the allomorphic and the female flowers are identical, or at most so (Rao 1971).

Tab. 5. Character state-matrix for the Galápagos *Acadlypha*. Characters and character states as in Tab. 4. -p and a: plesio- and apomorph character state, respectively.

Species	Characters									
	a	b	c	d	e	f	g	h		
1. <i>A. baurii</i>	p	a	p	p	p	p	p	p	p	p
2. <i>A. abingdonii</i>	p	a	p	a	p	a	p	a	a	a
3. <i>A. wigginsii</i>	p	a	p	a	p	a	p	a	a	a
4. <i>A. parvula</i>	a	a	p	p	p	p	p	p	p	p

1966) making a decision of plesio- and apomorph states impossible.

Loss of the ability to produce female-allomorphic female inflorescences in the axis of ordinary leaves (P_2^c) is postulated to have occurred in parallel in *A. abingdonii* and *A. wigginsii* as a result of dominance of the primary stem growth, caused by different means. Thus *A. baurii* is to be regarded as the relatively most plesiomorph of the Galápagos species and the sister-group of the remaining species, whereas *A. abingdonii* is the sister-group of *A. wigginsii* + *A. parvula*.

Two tenets presently pervade any discussion on evolution of the endemic Galápagos vascular plants: (1) The flora has a "weedy" origin (Porter 1976, 1979, Hamann 1981), and (2) The vegetation of the mesic upland habitats has been populated recently (within the last 10,000 years) from adjacent South America (Johnson & Raven 1973, Porter 1979). Similar or slightly different ideas have a long standing in the literature. The "weedy" nature of the flora has been commented on by Darwin (1839), and a dual "origin" postulated by Hooker (1847b).

However, no unequivocal evidence supports the above tenets. Although "weediness" is a vague concept (Baker 1974) there cannot, following the schemes of Baker (1974:4; Ideal weed characteristics) or Panka (1974:90; Some of the correlates of r and K selection), be any doubt that *A. parvula* has more "weedy characteristics" or is more r-selected than *A. baurii*. Still, *A. baurii* has many "weedy" characteristics. However, the environmental conditions on the islands apparently favour evolution of "weediness".

The radiation of the Galápagos *Acalypha* occurred, using a crude division of the vegetation into zones (Johnson & Raven 1973), from mesic to arid, and secondarily back to mesic habitats (*A. wigginsii*).

Johnson & Raven (1973), and following them, Porter (1979) claim that the mesic habitats have been populated recently from the mainland. Porter (1979) even suggested that subsequently some taxa e.g. *Scaltesia* penetrated the mesic habitats, from the arid zone. However, both statements are unfounded. Colinvaux (1972) and Colinvaux & Schofield (1976a) stressed that even during periods of drought places persisted where a mesic vegetation could survive, and though not explicitly stated the postulated polarity of the radiation in *Scaltesia* is presumably founded on the center of origin concept (viz. largest species diversity = center of origin), which is of dubious value (Cain 1944, Croizat et al. 1974), and definitely not on rigorous phylogenetic analysis. It is additionally opposed by the adaptive radiation seen in e.g. *Peperomia* (Porter 1979).

Phytogeography of the Galápagos *Acalypha*

The Caribbean/South American-Galápagos relationship

The sister-group of the Galápagos *Acalypha*, the *A. cuspidata*-complex is widely distributed in the Neotrop-

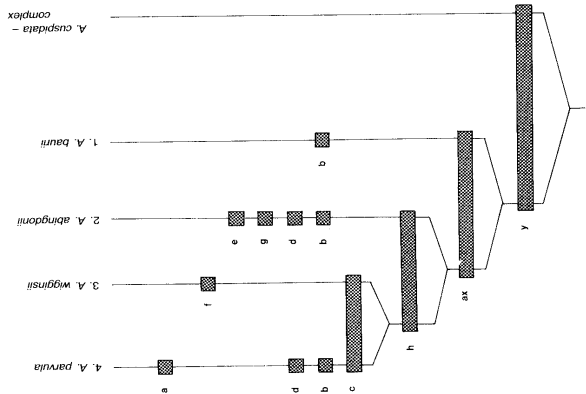


Fig. 6. Cladogram of the Galápagos *Acalypha*. Bars indicate synapomorphies. Letters correspond to characters in Tab. 4. - ax: subshrubs, or with a habit derived from substratum habit., - y: character state b of character IV, and the apomorph character state of character V in Tab. 2.

Phylogeny of the Galápagos *Acalypha*

The cladogram constructed from the characters in Tab. 4 is shown in Fig. 6. The sister-group of the Galápagos species is indicated by inclusion in the diagram of the *A. cuspidata*-complex. The distribution of character states within the species can be found in Tab. 5. Character trends were established by out-group comparison (Ross 1974, Watrous & Wheeler 1981) using the *A. cuspidata*-complex as functional out-group. When the character state was not found in the *A. cuspidata*-complex, the out-group was enlarged to encompass *A. multicaulis*. Examination of the depicted cladogram discloses that alternative cladograms could be drawn. However, the one presented here is preferred for the following reasons:

Gland-colour is the external manifestation of unknown chemical processes, and accordingly the postulation of a hypothesis on homology requires complete knowledge of the underlying reactions. Therefore the relationship between the yellow colour of the glands in the *A. cuspidata*-complex and *A. wigginsii* is better treated as unknown (paratologous, in the sense of Inglis

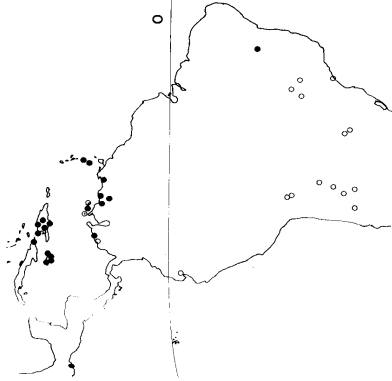


Fig. 7. Known distributional range of the *Acalypha cuspidata*-complex, as based on specimens from C. DAV., F. GH. NY., and S. dots) and on the traceable records in Pax & Hoffmann (1924); (circles). Though not exhaustive, the map covers the range of the complex. Several coincident individual tracks can be found in Svenson (1946), and a postulated generalized track in Rosen (1975).

cal region (Fig. 7). Unfortunately, it is unknown whether the deducible area-cladogram of this species group + the Galápagos *Acalypha* is general. Only one other area-cladogram, which is incongruent with the Galápagos *Acalypha* + *A. cuspidata*-complex pattern, may presently be constructed (*Tiquilia*, Richardson 1977). If both of these area-cladograms have any generality, this would have bearings on the question of the different relationships postulated for the arid and mesic vegetation (Johnson & Raven 1973, Porter 1979).

However, one fact is immediately apparent from a comparison between the distribution pattern and the phylogeny (see Figs 6 and 7): No "center of origin" of the Galápagos *Acalypha* exists. The search for the "center of origin" of e.g. the Galápagos vascular plants (see e.g. Porter 1976, 1979) rests in essence upon a general, unfounded belief in the center of origin/dispersal concept (Croizat et al. 1974, Nelson & Platnick 1981). Difficulties in using this concept have previously been stressed by Cain (1944).

Although previous work on the "origin" of the Galápagos flora and fauna (e.g. Wiggins 1966, Orr 1966, Vágvölgyi 1976, Porter 1979) falls within the realm of phenetic biogeography (Nelson & Platnick 1978) or quantitative biogeography (Crovell 1981) ample biotic evidence exists supporting a general pattern (Platnick & Nelson 1978, Nelson & Platnick 1980, 1981) connecting the Galápagos with the Neotropical region (e.g. van Balgooy 1971).

Recent geological evidence emphasizes the widely held notion of an "oceanic" origin of the Galápagos

Archipelago. Hey et al. (1977) and Hey (1977) have generated a model explaining the plate tectonic evolution of the eastern Pacific according to which the Galápagos islands are created over a fixed hot-spot, and the Cocos and Carnegie Ridges are nemataths emanating from this hot-spot. Substantial support for this hypothesis has been furnished by Lonsdale & Klitgaard (1978).

An alternative, less likely, hypothesis postulating that the Cocos and Carnegie Ridges were originally joined and later rifted apart has been advanced by Andel et al. (1971). For a discussion see Hey (1977). This hypothesis has a similar fixed position of the Archipelago, but allows a continental (l) origin of the ancestral Carnegie Ridge.

At present no unequivocal evidence supports the existence of guyots that may have acted as "stepping-stones" between the continent and the Galápagos as proposed by Holden & Dietz (1972) based on a hypothesis similar to Hey et al.'s (1977), and advocated by Croizat et al. (1974).

The strong evidence favouring an "oceanic" origin of the Galápagos Islands had caused several authors (e.g. Dawson 1966, Stebbins 1966, Porter 1979) to invoke or accept repeated (from 2 to 5) introductions to account for the phenetic dissimilarity between the species of particular genera (e.g. *Alternanthera*, *Cordia*, *Opuntia*). Admittedly recurring introductions are a possibility, but the acceptance of this hypothesis requires firm phy-

Tab. 6. Known distribution of the Galápagos *Acalypha*. Fosberg 44941 (C. US) from Isla Wolf is referred to *A. parvula* with doubt. An unidentified species of *Acalypha* was reported from Isla Champion near Isla Santa María by B. R. and P. R. Grant.

	1. <i>A. baurii</i>	2. <i>A. abingdonii</i>	3. <i>A. wigginsii</i>	4. <i>A. parvula</i>
Isla Baltra
Isla Bartolome
(near San Salvador)
Isla Daphne Mayor
Isla Española
Isla Fernandina
Isla Gardner
(near Española)
Isla Isabela
Isla Marchena
Isla Pinta
Isla Pinzón
Isla Rábida
Isla San Cristóbal
Isla San Cador
Isla Santa Cruz
Isla Santa Fe
Isla Santa María
Isla Venecia
(near Santa Cruz)

logenetic support, and not indefinable regress to considerations of variation patterns (Stebbins 1966) or the like.

Obviously only one dispersal event is necessary to account for the *Acadlypha*-species on the Galápagos as the group is monophyletic. *Acadlypha* is generally not suited to long-distance dispersal, and the Galápagos species are no exception. Though the possibility of endozooic dispersal of the seeds cannot be ignored, the fruit of the allomorphic female flower is a more likely prophyll in long-distance dispersal, as it is indehiscent and usually equipped with long protruding tubercles, and thus adapted to epizooic dispersal. Birds are by far the most probable vector.

Inter-island distribution pattern

A summary of the distribution can be found in Tab. 6. *A. baurii* is found on all higher islands in the Archipelago, except San Salvador and Santa María, but has only been reported once from San Cristóbal (collected by G. Baur in 1891). Additionally it is apparently missing from several volcanoes on Isabela (Ecuador, Wolf, Darwin and Cerro Azul) where it may eventually be found. Incidentally the two above-mentioned islands in which *A. baurii* is missing, and where suitable habitats are thought either to occur or have occurred (see e.g. Stewart 1915), have been heavily disturbed by humans or by impact of feral animals during the last 75 years or more (Wiggins & Porter 1971, Werff 1979). Presumably *A. baurii* is very vulnerable to habitat-disturbances and is exterminated on these islands, and maybe on San Cristóbal, too. In accordance with this, the majority of *Acadlypha*-pollen found in the cores from "El Junco" on San Cristóbal (Colinvaux & Schofield 1976a) is probably better referred to *A. baurii* than to *A. wigginsii*, which has never been collected on the island.

A. parvula is absent from Darwin, Genovesa, Seymour, and perhaps some minor islets. It is probably truly absent, at least from Genovesa, as it has neither been reported by botanists nor by P. Grant's students during their year-long stay on the island (pers. comm. O. Hamann). It is probably also truly absent from Seymour, which has a vegetation similar to Genovesa (pers. obs.).

The area-cladogram that can be deduced from the distribution pattern of the Galápagos *Acadlypha* is not congruent with any 3-, 4- or larger area pattern presently found among the endemic, vascular plants (see Porter 1979). (No search for congruent area-cladograms has been made in other groups, including animals, in the present study.)

The lack of congruent area-cladograms may be accounted for in one of two ways; either the distribution pattern of the Galápagos *Acadlypha* is unique, which would constitute direct proof of dispersal (Croizat et al. 1974, Platnick & Nelson 1978, Nelson & Platnick 1980, 1981, Wiley 1980), or alternatively, no pattern is likely

to emerge as a consistent phylogeny is only available for *Tiquilia* (Richardson 1977), and hence only one other reliable area-cladogram may be constructed for the areas involved. The question of uniqueness can only be decided in the light of a general pattern. However, even if recurring patterns can be found it does not necessarily mean that we are able to choose objectively between vicariance and dispersal hypotheses; the resolution of process ultimately hinges on historical geology (Platnick & Nelson 1978, Nelson & Platnick 1980, 1981). A priori acceptance of either vicariance or dispersal explanations leads to an overrating of the importance of either, as they are equally ad hoc projected against falsification (Platnick & Nelson 1978, Nelson & Platnick 1980, 1981).

The geological evolution of the Galápagos area is rather complicated. According to Hey (1977), Hey et al. (1977) and Lonsdale & Klitgord (1978) the Galápagos fracture zone has experienced several jumps with respect to the Galápagos hotspot, and volcanic material has intermittently been added to the Cocos and Nazca Plates. But if this is to have any significance for the evolution of the Galápagos Archipelago, a far greater age than 3 M yr, as determined by Bailey (1976), is to be demonstrated. Incidentally the age of the "Archipelago" is debatable. As pointed out by Bailey (1976) and Vagyolgyi (1976), the 3 M yr is a minimum estimate. Holden & Dietz (1972) argued for a possible age of 40 M yr, but as they anticipated, the estimate was based on an erroneous assumption of drift rate of the Pacific Plate (9.0 instead of 7.1 cm/yr), and thus the possible age is reduced to 20 M yr (Hey et al. 1977). This is consistent with a start of the hot-spot activity 20 m. B.P. as postulated by Lonsdale & Klitgord (1978).

Hey (1972) accepted 3 M yr as the probable age of the "Archipelago", and supported it by meager, biological information of evolutionary rates. At present the age of the "Archipelago" is estimated to be somewhere between 3 and 22 M yr, perhaps closest to the former.

Thus the possibility that the north-eastern islands (Genovesa, Marchena and Pinta) have a history different from the remaining islands exists; they may once have been in the process of being added to the Cocos Plate. Genovesa is clearly the summit of a large partially subsided volcano (McBirney & Williams 1969). The islands Darwin and Wolf might even have a different history yet as they are completely detached from the Galápagos Platform (McBirney & Williams 1969). For a different, but compatible explanation, see Morgan (1978). More recently, during the last glaciation, sea level dropped approx. 100 m (Flint 1971), which may have aided dispersal significantly (Simpson 1974).

Summing up, at the moment no evidence unequivocally discards vicariance as the explanation of at least some of the disjunction observed in the Galápagos taxa, however, circumstantial evidence presumably favours dispersal.

The distribution pattern of *A. wigginsii* and *A. parvula* might be caused by vicariance as well as dispersal. According to Colinvaux (1972) the Galápagos Islands were projected to a drought before the start of the Holocene, and the arid zone probably then reached the summit of San Cristóbal. Due to proximity, Santa Cruz, though slightly higher, must have experienced similar conditions. At this time the ancestor of *A. wigginsii* + *A. parvula* had the opportunity to enlarge its range. Later disjunction was brought about by the spread of the *Scaevola*-zone. This happened 10,000 yr ago when the mesic vegetation spread from isolated pockets, to give the vegetation its modern aspect (Colinvaux & Schofield 1976a, b).

Taxonomy of the Galápagos *Acadlypha*

Hitherto 15 binomials have been applied for the Galápagos *Acadlypha*, 2 of which are, however, illegitimate. One more binomial exists as a consequence of Kuntze's (1891) different generic concept. Eight varieties have been proposed in *A. parvula*, three in *A. sericea*, and two in *A. velutina*.

Webster (1970) in the last revision of the Galápagos *Acadlypha*, reduced the 13 species accepted by Robinson (1902) to 4: *A. flaccida* J. D. Hooker, *A. parvula* J. D. Hooker, *A. sericea* Andersson, and *A. velutina* J. D. Hooker, and described one species, *A. wigginsii*, as new. In *A. parvula* 3 varieties were recognized: *var. parvula* *var. reniformis* (J. D. Hooker) Müll. Arg., and *var. str. bilifera* (J. D. Hooker) Müll. Arg.; and one new combination was made: *var. chathamensis* (Robinson) Webster. In *A. sericea*, 3 varieties were recognized: *var. baurii* (Robinson & Greenman) Webster, *var. sericea*, and *var. indefessus* Webster. Webster's infra-specific inter-relationships have recently been challenged by Werff (1977).

In the present revision 4 species are recognized one of which is described as new.

Key to the Galápagos species of *Acadlypha*

1. Androgynous, first order paracladia (axillary inflorescences) terminated by a male flower
1. Androgynous, first order paracladia terminated by an allomorphic female flower*
 1. *A. baurii*
 - Plant very sparsely - densely covered with colourless - red glands. Male perianths more or less pubescent
 - Plant covered with conspicuous bright yellow glands. Male perianths glabrous
 - Plant usually not branched from the cotyledons (no GOTS). Bracteate female part of the apical thyrse, strongly congested, with (18-24-44) leaf-like bracts. Male perianths with prominent papillae
 - Plant usually branched from the cotyledons (well-developed GOTS). Bracteate, female part of the apical thyrse, slightly spaced, with (3-7-20) rarely more (to 42) and then the thyrse markedly elongated, leaf-like bracts. Male perianths with slightly protruding papillae
 1. *A. wigginsii*
 2. *A. wigginsii*
 3. *A. wigginsii*
 - Plant usually not branched from the cotyledons (no GOTS). Bracteate female part of the apical thyrse, strongly congested, with (18-24-44) leaf-like bracts. Male perianths with prominent papillae
 - Plant usually branched from the cotyledons (well-developed GOTS). Bracteate, female part of the apical thyrse, slightly spaced, with (3-7-20) rarely more (to 42) and then the thyrse markedly elongated, leaf-like bracts. Male perianths with slightly protruding papillae
 1. *A. parvula*

* The presence or absence of an allomorphic female flower is most easily decided in the upper part of the primary stem, as they are shed while ageing.

1. *Acadlypha baurii* Robinson & Greenman

Acadlypha baurii Robinson & Greenman 1895: 144; Robinson 1902: 163; Stewart 1911: 86; Pax & Hoffmann 1924: 132 - *Acadlypha sericea* Andersson var. *baurii* (Robinson & Greenman) Webster 1970: 261; Webster 1971: 573; Werff 1977: 97; Porter 1979: 241. - Types: Baur 285; Chatham Island, south-west end, middle region, common upon open places, June 1891 (GH lectotype, here selected; K isotype).
Acadlypha sericea Andersson var. *indefessus* Webster 1970: 261; Webster 1971: 573. - Type: Wiggins 18672: Isla Santa Cruz (Indefatigable), along "new road" from Bahía Academy to Bella Vista, transition zone, 9 Feb 1964 (DS holotype; CAS isotype).

Erect to straggling, hirtellous and occasionally sparsely pubescent, sparsely glandular, glabrescent subshrubby to 4 m high. Leaves with petiole (4.4-16.2-14.6(-24.3) cm long; stipules subulate - triangular, rarely narrowly ovate - ovate, (0.6-10.8-2.4(-3.9) mm long, 0.3-0.7(-0.8) mm wide, with acute - acuminate apex; lamina ovate, rarely broadly ovate, (3.1-14.1-9.3(-13.3) cm long, (1.9-2.6-6.0(-10.8) cm wide, chartaceous, opaque, and strigose; base obtuse - subcordate, rarely cuneate, attenuate or truncate; margins crenate-serrate, with (17-20-38(-42) teeth/side, and (0-1)(-2) glands/tooth; marginal glands colourless - slightly reddish (45-) 62-84(-135) µm long, head-diam (20-35-57(-60) µm; apex acute - acuminate. Primary stem terminated by a female, rarely androgynous inflorescence. Paracladia usually not developed from the cotyledonary and first epicotyledonary nodes. First order paracladia diverging, either androgynous, straight - slightly hanging at the apex, or, at the uppermost 1-4 or rarely more nodes, female, suberect, terminated by an allomorphic female flower. Second order paracladia similar to the primary stem, suberect, very rarely similar to the corresponding first order paracladia. Third order paracladia similar to the primary stem, suberect, often reduced. Third order paracladia basally on the second order paracladia, occasionally entirely female, composed of 1-4 female, leaf-like bracts and a pedicellate, allomorphic female flower. First epicotyledonary node ca. 1.8 cm long. Bracteate, female part of the apical, spiciform thyrse (0.9-)1.1-2.9 cm long, with 14-25 leaf-like bracts, terminated either by an allomorphic female flower on a (1-3-12) mm long, almost glabrous pedicel or rarely by a 1.3-1.8 cm long male thyrse on a 0.2-0.3 cm long, almost glabrous rachis. Androgynous, first order paracladia (1.4-2.3-6.3(-10.6) cm long, with 1-2(-6) female, leaf-like bracts; sessile or rarely on an up to 2.4(-4.0) mm long peduncle. The terminal, allomorphic female flower sessile or rarely on an up to 2.8(-8.0) mm long, almost glabrous pedicel. The spiciform, male thyrse (0.9-)1.5-3(-9.6) cm long, contiguous or interrupted below, born on a 0.3-1.1(-1.6) cm long rachis. The male thyrse constituting (53-68-86(-93) % of the whole paracladium.

Male bracts usually narrowly - broadly elliptic or narrowly - broadly ovate, 0.5-0.8(-1.2) mm long, 0.2-

Fig. 9. Correlation between number of teeth per side and lamina length in *Acalypha baerii*. The sample is random, but all islands where *A. baerii* occurs are represented.

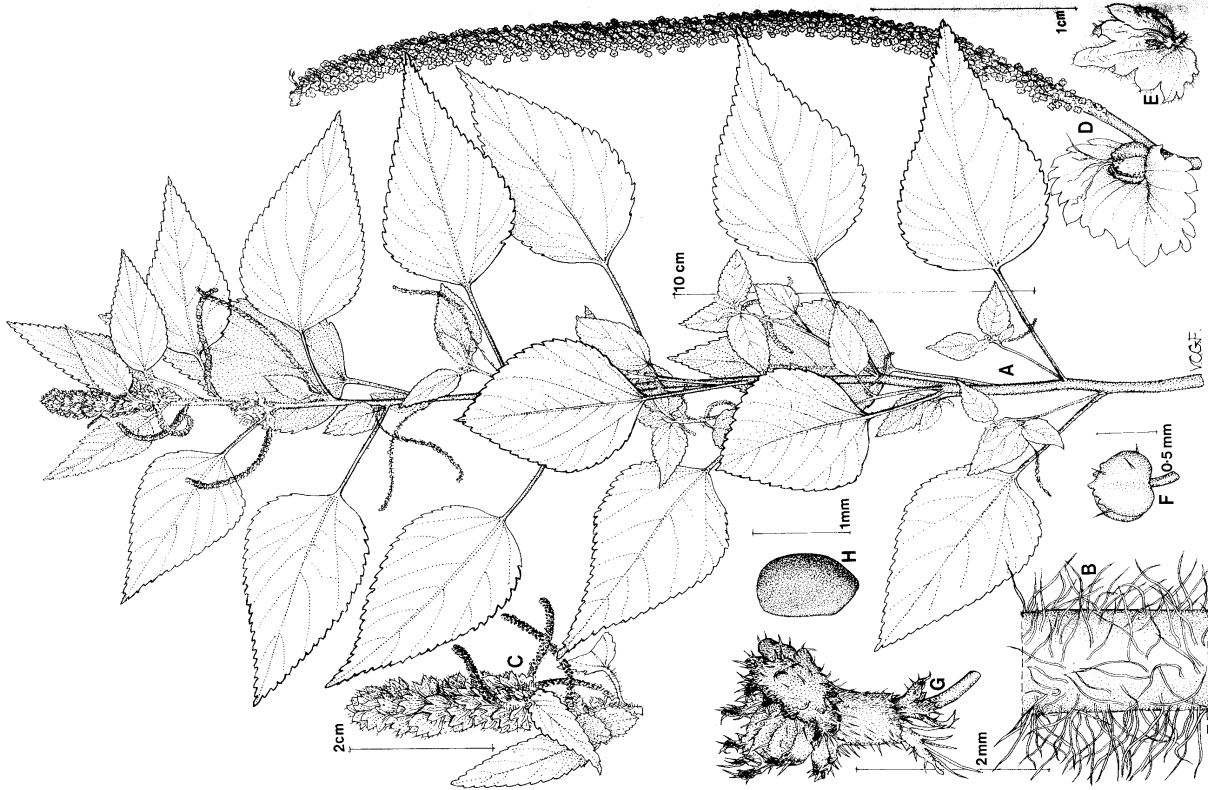
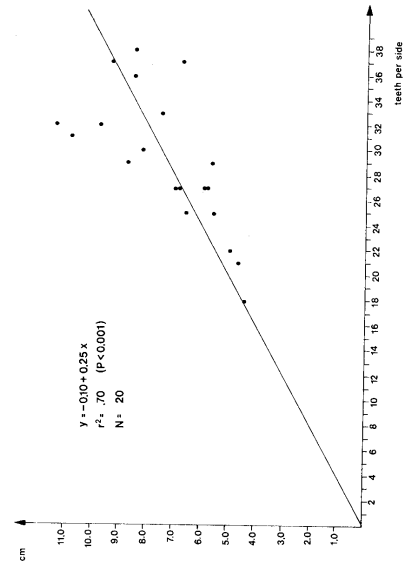


Fig. 8. *Acalypha baerii*. A: Habit. - B: Stem-indumentum. - C: Apical thyrse. - D: First order paracladium (Pe¹) and female flower. - E: Third order paracladium (Pe³) and leaf-like, female bract. - F: Male flower. - G: Allomorphic female flower. - H: Seed. - A. B. Werff 1414 (U); C. A. & H. Adersen 953 (C); D. F. A. & H. Adersen 997 (C); E. G. Werff 1417 (U); H. Hamann & Seberg 1783 (C).

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0.3(-0.4) mm wide, puberulent and/or sparsely hirtellous; margins usually with a few glands basally; apex usually: acute or obtuse. Female, leaf-like bracts very broad; depressed ovate, (2.9-4.0(-7.4(-12.2)) mm long, (1.3-3.6(-5.10(-13.5)) mm wide, hirtellous and occasionally puberulent, sparsely glandular; base obtuse or more or less cordate, amplexicaul; margin lobed, with 6-16(-21), usually \pm triangular or \pm ovate lobes, cut $\frac{1}{2}$ - $\frac{3}{4}$ to the base; apex of lobes acute or obtuse, rarely rounded. Male flowers (0.3-0.4(-0.5(-0.6)) mm wide, (glabrous) sparsely puberulent, papillose. Female flowers with narrowly - broadly triangular or narrowly - broadly ovate perianth-lobes, (0.5-0.6(-0.8(-0.9)) mm long, (0.3-0.4(-0.5(-0.7)) mm wide, glabrous, rarely puberulent; margins ciliate, often with a few glands basally; apex acute - slightly acuminate or obtuse. Capsule (1.2-1.3-1.7 mm high, (1.3-1.5-1.9(-2.0)) mm wide, tuberculate, hirtellous, and puberulent at the apex; styles (1.7-2.1-4.5(-5.8)) mm long, puberulent at the base. Allomorphic female flowers zygo-, rarely anisomorphic; perianth 3-4, very rarely 5-lobed. Lobes narrowly - broadly ovate, rarely triangular, (0.4-0.5-0.8(-1.0)) mm long, 0.2-0.4(-0.6) mm wide, puberulent, rarely glabrous; margins with a few glands basally, rarely glandular. Apex acute - slightly acuminate or obtuse. Carpel(s) more or less tuberculate and shortly puberulent; rarely sparsely glandular. Style(s) (0.9-1.2-2.4(-4.0)) mm long, glabrous or puberulent at the base. Seeds (1.06-1.13-1.29(-1.36)) mm long, (0.75-0.83-0.99(-1.09)) mm wide, finely reticulate-foveate, chestnut brown - black. - Fig. 8.

Distribution: Known from the higher islands in the Archipelago, except San Salvador and Santa María.

Habitat: *Scalésia*-zone. In mesophytic, evergreen forest and steppe forest. Recorded from southern Santa Cruz in xerophytic, dry season deciduous forest, along the "old trail" and the "new road" from Bahía Academy to Bella Vista, (100-3400-1350 m a.s.l. Very rare below 400 m, except on the southern slope of Santa Cruz, where it is found between 100 and 200 m.

The material examined is rather homogeneous. The density of glandular trichomes is variable, but the spe-

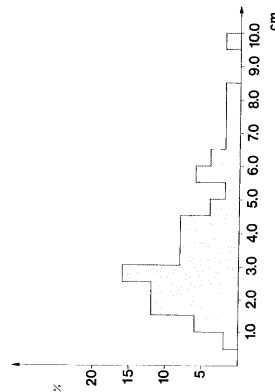


Fig. 10. Variation in the length of the male thyrse of the androgynous Pe¹ or Pe³ in *Acalypha baerii*. The total distribution area: N = 49.

cies appears essentially eglandular, as the glands are hidden in the dense non-glandular indumentum. The lamina-length, and the number of teeth/side which is correlated with lamina-length (Fig. 9) vary considerably, and there is a certain variation in the length of the male thyrses (Fig. 10) and seeds.

A. baurii as treated here includes only 1 taxonomical synonym; *A. sericea* var. *indefessus*. However, var. *indefessus* is based on the above-mentioned characters which vary continuously. A specimen from Santa Cruz (Schimpff 96 (DS)) is intermediate between *A. baurii* and *A. wigginsi*.

2. *Acalypha abingdonii* O. Seberg sp. nov.

Type: Hamann & Seberg 1774; Galápagos Islands: Isla Pinta. On the south slope between the highest point and Cabbio Ibberson. Close to the trail in dry season deciduous steppe forest. The dry season deciduous steppe forest dominated by *Bursera graveolens*, *Caselia galapagensis*, and *Strelitzia baurii*. Alt. 135 m, 25 Mar 1981 (C holotype; isotypes distributed to various herbaria).

Acalypha sericea auct. non Andersson; Robinson 1902: 164; Stewart 1911: 87; Pax & Hoffmann 1924: 30; Webster 1970: 260; Webster 1971: 573; Werff 1977: 97; Porter 1979: 241.

Acalypha abingdonii differt a *A. baurii* flore masculo terminante paracladia primus ordine, a *A. wigginsi* et *A. parvula*, paribus axialibus eglandulosis, sine paracladis e axillis cotyledonis emergentibus, parte bracteata feminea thyrsi apicalis, valde condensata, cum (18-)24-44 bracteis foliiformibus, et flore masculo cum papillis prominentibus. *A. abingdonii* differt usque a *A. wigginsi* glandibus incoloratibus et perianthis masculo pubescentibus.

Erect, hirtellous and puberulent, very sparsely glandular (axial parts eglandular), glabrescent subshrub to 60 cm high. Leaves with petiole (1.1-)2.0-6.0(-8.9) cm long; stipules narrowly triangular - triangular or ovate - broadly ovate, (0.4-)0.6-1.2(-1.9) mm long, (0.2-)0.3-0.5(-0.6) mm wide, with acute or rarely acuminate apex; lamina broadly ovate, rarely ovate, (0.8-)1.3-3.5(-5.3) cm long, (0.7-)1.1-2.7(-4.1) cm wide, chartaceous, rarely rugose; opaque and strigose; base obtuse - subcordate, rarely truncate or truncate; margins crenate-serrate, with 9-19 teeth/side, and (0-)1(-3) glands/tooth; marginal glands colourless, (40-)46-76(-83) µm long; head diam (25-)32-44(-54) µm; apex acute or obtuse. Primary stem terminated by an androgynous or female inflorescence. Apical male thyse, when present, strongly reduced, occasionally only a single male flower present, scarcely visible, hidden between the female, leaf-like bracts. Paracladia usually not de-

veloped from the cotyledonary and first epicotyledonary nodes. First order paracladia diverging, straight, either androgynous, terminated by a male flower or, at the uppermost 1-3, rarely up to 6, nodes, female, terminated by an allomorphic female flower. Second order paracladia similar to the primary stem, suberect, or very rarely and only apically similar to the corresponding first order paracladia. Third order paracladia similar to the primary stem, suberect, often well developed especially below. First epicotyledonary node 1.5-3.3 cm long. Bracteate, female part of the apical, spiciform thyse, strongly condensed, (0.7-)1.2-3.4(-4.8) cm long with (18-)24-44 leaf-like bracts, terminated either by an allomorphic female flower on an up to 4 mm long, sparsely puberulent pedicel, rarely subsessile or by an up to 0.1 cm long male thyse on an up to 0.2 cm long, puberulent rachis. Androgynous, first order paracladia 1.3-4.6(-6.5) cm long, with 1-(4-8) female, leaf-like bracts; on a peduncle up to 9.9(-14.0) mm long, rarely sessile. The spiciform male thyse 0.8-2.5(-3.4) cm long, contiguous - distantly interrupted, on a (0.2-)0.3-1.1(-1.8) cm long rachis. The male thyse constituting (22-)38-60(-65)% of the whole paracladium.

Male bracts usually narrowly elliptic - elliptic or narrowly ovate - ovate, 0.4-0.6(-0.8) mm long, (0.1-)0.2-0.4 mm wide, puberulent; margins rarely with a few glands basally; apex acute or obtuse. Female, leaf-like bracts very broadly-depressed ovate, (1.2-)3.2-6.0(-8.6) mm long, (2.1-)4.9-9.3(-12.4) mm wide, hirtellous and puberulent, eglandular - very sparsely glandular; base obtuse or more or less cordate, amplexicaul; margin lobed, with 6-10(-13) lobes or double-lobed, with 3 primary and (1-)3-7(-9) secondary lobes; lobes ± triangular or ± ovate, cut 1/2-1/2 to the base, with acute or obtuse, rarely rounded apices. Male flowers (0.3-)0.4-0.5 mm wide, (glabrous-)densely puberulent, prominently papillose. Female flowers with narrowly - broadly ovate perianth-lobes, (0.3-)0.5-0.7(-0.8) mm long, (0.1-)0.3-0.5 mm wide, glabrous, rarely puberulent; margins ciliate, rarely with a few glands basally; apex acute or obtuse. Capsule 1.2-1.6 mm high, 1.3-1.9(-2.0) mm wide, tuberculate, hirtellous and puberulent at the apex. Styles 2.3-4.4(-5.8) mm long, puberulent at base. Allomorphic female flowers zygomorphic actinomorphic; perianth 3-, rarely 4-lobed; lobes usually ovate - broadly ovate, 0.5-0.9(-1.4) mm long, 0.2-0.3(-0.7) mm wide, glabrous or puberulent; margins ciliate, rarely with a few glands basally; apex acute. Carpel(s) tuberculate, shortly puberulent and eglandular. Style(s) 2.3-5.8 mm long, glabrous or puberulent at the base. Seeds (0.94-)1.00-1.16(-1.21) mm long, (0.69-)0.72-0.80(-0.82) mm wide, reticulate-foveate, chestnut brown - black. - Fig. 11.

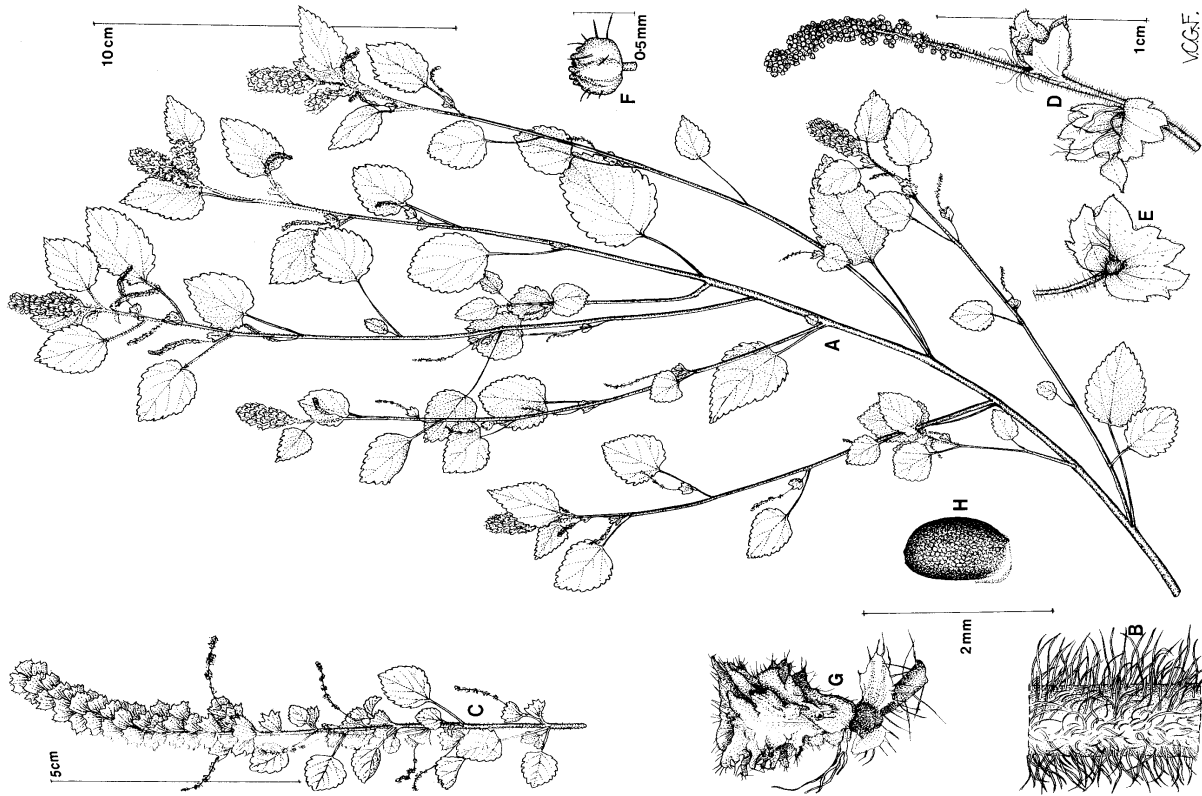


Fig. 11. *Acalypha abingdonii*. A: Habit. - B: Stem-indumentum. - C: Apical thyse. - D: First order paracladium (Pc.). - E: Leaf-like, female bract and female flower. - F: Male flower. - G: Allomorphic, female flower. - H: Seed. - A-B: Hamann & Seberg 1774a (C); C: Jeppesen 3059 (AAU); D, F: Hamann & Seberg 1790.1 (C); G: Hamann & Seberg 1709.4 (C); H: Hamann & Seberg 1774d (C).

Distribution: Only known from Isla Marchena and Isla Pinta.

Habitat: In arid and transition zone. In xerophytic, dry season deciduous steppe forest. Occasionally on barren lava, or in open, dry spots in \pm seasonal herb-grass meadow, but disappearing as the vegetation becomes closer. 0-350(-540) m a.s.l. Only a single record above 350 m, from Isla Pinta (1974), when the impact of feral goats was still heavy.

The material examined is remarkably homogeneous. The most pronounced variation being in the proportion of the two types of non-glandular indumentum, as every combination ranging from almost entirely hirtellous to almost entirely puberulent occurs. Additionally an un-interrupted variation can be seen between the rugose and the chartaceous leaves and between the lobed and the double-lobed, leaf-like female bracts.

3. *Acalypha wigginsii* Webster

Acalypha wigginsii Webster 1970: 261; Webster 1971: 574; Porter 1979: 241. - Type: Wiggins & Porter 663; Isla Santa Cruz (Indefatigable), north slope of Mt. Crocker, 18 Feb 1967, alt. 860 m (DS holotype; CAS isotype).

Erect, densely puberulent and occasionally hirtellous, densely glandular, glabrescent subshrub to 1 m high. Leaves with petiole (2.0-)2.7-6.1(-8.2) cm long; stipules narrowly triangular, rarely narrowly ovate - ovate, (1.7-)1.9-2.7(-3.4) mm long, (0.6-)0.8-1.1(-1.5) mm wide, with acute - acuminate apex; lamina broadly ovate, rarely ovate or very broadly ovate; (1.6-)2.0-3.8(-4.8) cm long, (1.2-)1.6-3.3(-4.5) cm wide, chartaceous, opaque - somewhat shining, strigose; base more or less cordate; margins crenate-serrate, with (10-)12-21(-23) teeth/side, and 1-4(-7) glands/tooth; marginal glands bright yellow, (101-)161-327(-462) μ m long; head-diam (40-)57-75(-94) μ m; apex acute. Primary stem indeterminate (?) or ending in a female (or androgynous ?) inflorescence. Paracladia usually not developed from the cotyledonary and first epicotyledonary nodes. First order paracladia diverging, straight, either androgynous, terminated by a male flower, or, at the uppermost 1-3 or rarely more, nodes, female, terminated by an allomorphic female flower. Second order paracladia similar to the primary stem, suberect. Third order paracladia similar to the primary stem, suberect, often reduced. Length of first epicotyledonary node unknown. Bracteate, female part of the apical spiciform thyrses 1.4 cm long, with about 10 female, leaf-like bracts. Androgynous, first order paracladia (0.5-)0.7-1.4(-2.2) cm long with (1-)3-4(-6)

female, leaf-like bracts; sessile. The spiciform, male thyrses (0.1-)0.2-0.6(-0.9) cm long, contiguous, rarely interrupted below, on a 0.1-0.5(-0.8) cm long rachis. The male thyrses constituting (20-)27-50(-67) of the whole paracladium.

Male bracts usually narrowly elliptic - elliptic-ovate - very broadly ovate, (0.5-)0.7-0.9(-1.0) mm long, (0.3-)0.4-0.7(-0.9) mm wide, glabrous or rarely sparsely puberulent; margins sparsely ciliate, rarely glabrous, and rarely with a few glands basally; apex acute, rarely obtuse - rounded or slightly acuminate. Female, leaf-like bracts very broadly-depressed ovate (3.6-)4.9-7.0(-7.8) mm long, (5.6-)7.3-9.7(-10.5) mm wide, puberulent, rarely sparsely hirtellous, densely glandular; base more or less cordate, amplexicaul, rarely obtuse; margins lobed, with 6-15(-18) usually triangular - broadly triangular or ovate - broadly ovate lobes, cut 1/3-1/2 to the base; apex of lobes acute. Male flowers (0.3-)0.4-0.5(-0.6) mm wide, glabrous, pillose. Female flowers with narrowly - broadly ovate-triangular perianth-lobes, 0.6-0.9(-1.0) mm long, (0.3-)0.4-0.7(-0.9) mm wide, glabrous, rarely puberulent; margins sparsely ciliate, eglandular, very rarely with a few glands basally; apex acute, rarely obtuse or acuminate. Capsule (1.2-)1.4-1.7(-1.8) mm high (1.8-)1.9-2.3(-2.5) mm wide, tuberculate, puberulent, very rarely hirtellous too, and/or glandular from the apex. Styles (2.0-)2.5-3.6(-4.2), glabrous or rarely puberulent at the base. Allomorphic female flower (only one seen!) zygomorphic; perianth 3-lobed; lobes broadly ovate, 0.7 mm long, 0.5 mm wide, glabrous; margins very sparsely ciliate, eglandular. Apex obtuse. Carpel tuberculate, puberulent. Style 2.0 mm long, glabrous. Seeds (1.24-)1.30-1.38(-1.42) mm long, (0.91-)0.95-1.00(-1.03) mm wide, reticulate-foveate, chestnut brown - black. - Fig. 12.

Distribution: Known only from the highest altitudes of Isla Santa Cruz.

Habitat: In the fern-sedge-zone. In mesophytic, \pm seasonal, fern meadow. 700-865 m a.s.l.

The material known of this species (7 collections; 26 specimens, 21 of which are collected within 100 m²) is too scanty to give a reliable impression of the morphological variation.

Specimens showing transition to *A. parvula* are though rarely, found on Santa Cruz.

4. *Acalypha parvula* J. D. Hooker

Acalypha parvula J. D. Hooker 1847a: 185; Andersson 1824: 240; Andersson 1861: 104; Müll. Arg. 1865: 48; Müll. Arg.

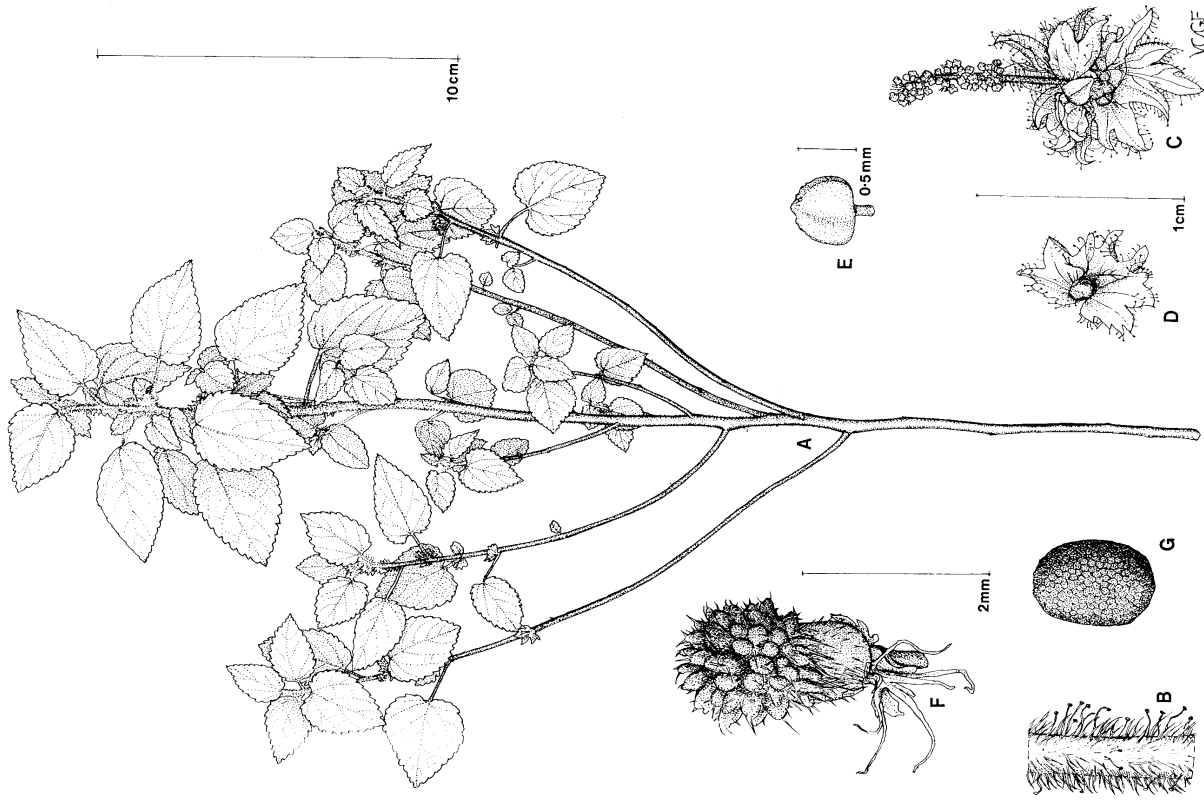


Fig. 12. *Acalypha wigginsii*. A: Habit. - B: Stem-indumentum. - C: First order paracladium (Pc). - D: Male flower. - E: Leaf-like female bract and female flower. - F: Allomorphic, female flower. - G: Seed. - A-B, E, G: Hamann & Seberg 1674 (C); G: Werff 1669 (U); F: Hamann & Seberg 1673.1 (C).

1866: 878; Robinson 1902: 164; Stewart 1911: 86; Pax & Hoffmann 1924: 133; Webster 1970: 261; Webster 1971: 570, f. 152; Werff 1979: 97; Porter 1979: 241; Porter 1980: 102-104. — *Ricnocarpus parvula* (J. D. Hooker) O. Kuntze 1891: 618. — Types: MacRae s.n.; Ins. Albemarle, Gallapagos, 1825 (K. Herb. Hook.) lectotype, selected by Porter 1980; K. (Herb. Benth.), CGE, and probably G (isolectotypes). See notes 1 and 2 below.

Acalypha adamsii Robinson 1902: 161-163; Stewart 1911: 86; Pax & Hoffmann 1924: 133. — Type: Baur 282; Chatham Island, southwest end, middle region, June 1891 (GH holotype; K isotype).

Acalypha albatrossensis Robinson 1902: 163; Stewart 1911: 86; Pax & Hoffmann 1924: 133. — Type: Snodgrass & Heller 885; Albemarle Isl., Tagus Cove, 15 Jun 1899, alt. 1220 m (GH holotype).

Acalypha chathamensis Robinson 1902: 163; Stewart 1911: 86; Pax & Hoffmann 1924: 133. — *Acalypha parvula* J. D. Hooker var. *chathamensis* (Robinson) Webster 1970: 263; Webster 1971: 572. — Types: Snodgrass & Heller 541; Chatham Isl., May 1899 (GH lectotype, selected by Webster 1970); DS isotype; Snodgrass & Heller 540; Chatham Isl., May 1899 (GH, DS).

Acalypha cordifolia J. D. Hooker 1847a: 186, nec Grisebach 1874; Anderson 1855: 238; Anderson 1861: 103; Robinson 1902: 163; Stewart 1911: 86; Pax & Hoffmann 1924: 132. — *Acalypha parvula* J. D. Hooker Mill. Arg. 1865: 47; Müll. Arg. 1866: 877. — *Acalypha hookeri* MacBride 1931: 26 (nom. illeg.) — Types: C. Darwin s.n.; Charles Island, Gallapagos Islands, end of Sept. 1835 (CGE lectotype, here selected; K isotype). See note 2 below.

Acalypha diffusa Anderson 1855: 240; Anderson 1861: 104, f. 4. — Robinson 1902: 163; Stewart 1911: 86; Pax & Hoffmann 1924: 133. — *Acalypha parvula* J. D. Hooker var. *procumbens* Müll. Arg. 1865: 48; Müll. Arg. 1866: 878. — *Acalypha parvula* J. D. Hooker var. *procumbens* Müll. Arg. f. *diffusa* (Anderson) Müll. Arg. 1866: 878. Types: N. J. Anderson s.n.; Hab. feces steccanis insulae Albemarle (Gallapagos), Maj 1852. (S isotype, here selected; the lectotype is mounted on the same sheet as *A. cordifolia* Hook. f.; GH, S isotype; the S isotype is wrongly annotated 1853).

Acalypha flaccida J. D. Hooker 1847a: 186; Anderson 1855: 238; Anderson 1861: 103; Robinson 1902: 164; Stewart 1911: 86; Pax & Hoffmann 1924: 132; Webster 1970: 261; Webster 1971: 570; Porter 1979: 240; Porter 1980: 103. — *Acalypha parvula* J. D. Hooker var. *flaccida* (J. D. Hooker) Müll. Arg. 1865: 48; Müll. Arg. 1866: 878-879. — Types: C. Darwin s.n.; James Islands, Gallapagos, begm. of Oct. 1835 (K lectotype, here selected; CGE isotype). See note 2 below.

Acalypha reniformis J. D. Hooker 1847a: 187-188; Anderson 1855: 240; Anderson 1861: 104; Robinson 1902: 164; Stewart 1911: 86; Pax & Hoffmann 1924: 31. — *Acalypha parvula* J. D. Hooker var. *reniformis* (J. D. Hooker) Müll. Arg. 1865: 48; Müll. Arg. 1866: 878; Webster 1970: 263; Webster 1971: 572. — Types: C. Darwin s.n.; Charles Island, Gallapagos Islands, end of Sept. 1835 (CGE (Mus. Henslow) lectotype, here selected; CGE (Herb. Babington), K isotype). — See note 2 below.

Acalypha sericea Anderson 1855: 238-239; Anderson 1861: 103-104, t. 14, fig. 1. — *Acalypha parvula* J. D. Hooker var. *pubescens* Müll. Arg. f. *sericea* (Anderson) Müll. Arg. 1865: 47-48. — Types: N. J. Anderson s.n.; Hab. lapidosis regionis inferioris insulae Albemarle (Gallapagos), Maj 1852. (S lectotype, here selected, mounted on the same sheet as *A. velutina* Hook. f.; S isotype, wrongly annotated 1853).

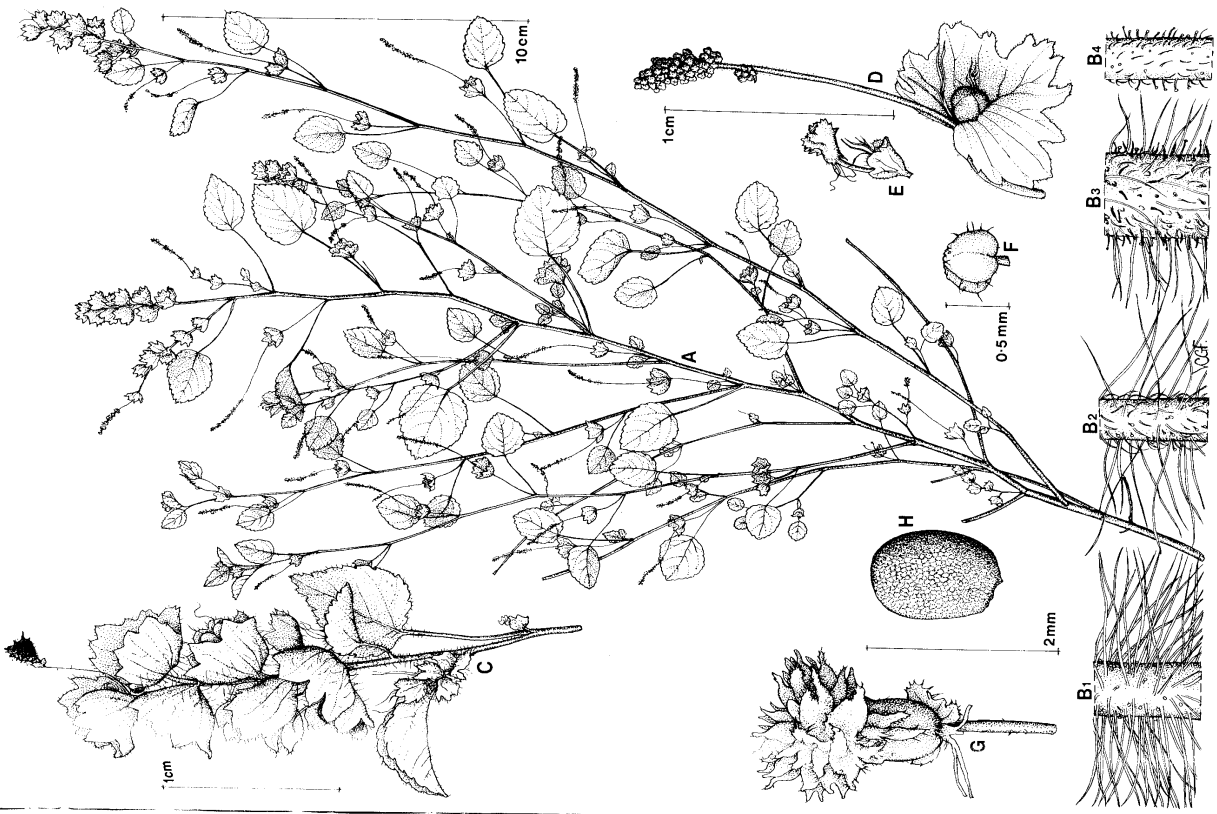


Fig. 13. *Acalypha parvula*. A: Habit. — B₁₋₄: Variation in stem-indumentum. — C: Apical thyrse. — D: First order paracarpel (Pc), leaf-like, female bract, and female flower. — E: Third order paracarpel (P₃). — F: Male flower. — G: Allomorphic, leaf-like flower. — H: Seed. — A: Howell 9855 (CAS); B₁: Werff 2147 (CAS); B₂: Werff 2275 (U); B₃: Howell 9855 (C); B₄: Howell 9855 (C); D, E, H: Hamann & Seberg 1773 (C); F: Fagerlin & Wibom 3433 (GB); G: Stewart 1785 (CAS).

Note 1. On the type collection of *A. parvula* J. D. Hooker: Müller (1865:48, 1866:878) refers to a specimen in Herb. Boiss. (G) identified by him as *A. parvula* var. *genuina* (= var. *parvula*) and collected by a Captain King. Only one specimen of Gallapagos *Acalypha* is found in G and not in Herb. Boiss. (A. Charpin, pers. comm.). This specimen has been studied by Müller, as indicated by the hand-writing on the annotation-label; it was ascribed to *A. parvula* var. *procumbens*, but never cited as such. However, the G-specimen is a very close match of the type collection of *A. parvula* J. D. Hooker (1847a), collected by MacRae and a label in Hooker's hand-writing is attached to it. Accordingly I suggest that the G-specimen is part of the type collection of *A. parvula*, and thus an isotype.

This interpretation requires that Müller has in some way confused the names of MacRae and King which, on the evidence available, is slightly probable: P. King, i.e. probably the Captain King referred to by Müller, was commander on the H.M.S. Adventure, which accompanied the H.M.S. Beagle. He made extensive collections from e.g. mainland South America, but the only other specimen from the Gallapagos Islands claimed to be collected by Captain King is also in Euphorbiaceae revised by Müller (1866); *Croton*

scouleri J. D. Hooker var. *macraei* Müll. Arg. (Robinson 1902). The type collection again being cited as made by King (sic) and MacRae. Thus there is a strong connection between the names MacRae and King in Müller's work, and I find it highly improbable that King should have secured only two specimens from the Islands, both belonging to the Euphorbiaceae.

Note 2. On lectotypification: According to Porter (1980) Webster (1970) lectotyped most of Hooker's taxa (1847a) of *Acalypha*. However, as Webster terminates his paper by saying (1970:263): "... since the specimens at Kew were not seen, no attempt was made to specify whether the collections at CGE are syntypes or isotypes", lectotypification of Hooker's taxa was clearly not intended. On the contrary, whenever a lectotype is selected, this is unambiguously indicated, for example, "*Acalypha parvula* Hook. f. var. *chathamensis* (Robins.) Webster, Snodgrass and Heller 541 (GH-lectotype, DS-isotype)" (Webster 1970:263). Porter was probably misled by Webster's addition of the word "type" to each citation of a type-collection. That Webster did not attempt to lectotypify Hooker's taxa is indicated also by the annotation-labels. In the case of *A. parvula* var. *chathamensis* the label reads "Holotype (sic) of ..." whereas in the case of e.g. *A. reniformis* it reads "Type collection of ...". Thus the only taxon in Hooker 1847a, which has been lectotypified is *A. parvula* (Porter 1980). According to article 8 in the IBCN (Stafleu et al. 1978) all the remaining lectotypifications can be ignored as they were done arbitrarily.

Having studied the CGE-specimens and photos of the K-specimens I proposed to lectotypify all taxa, except *A. flaccida*, in accordance with Porter (1980). In *A. flaccida*, the K-specimen has been preferred, as the syntype at CGE is a mere fragment.

Prostrate, ascending or erect, densely puberulent and occasionally more or less hirtellous, glandular, often reddish, annual or shortlived subshrub to 1 m high. Leaves with petiole (0.4-)1.9-5.3(-10.0) cm long; stipules narrowly - very broadly ovate or narrowly triangular - deltate, (0.2-)0.5-1.1(-2.7) mm long, (0.1-)0.2-0.8(-1.0) mm wide, with acute, rarely obtuse or slightly acuminate apex; lamina ovate - broadly ovate, rarely very broadly-depressed ovate, (0.3-)1.0-2.8(-5.5) cm long, (0.5-)1.0-2.6(-4.1) cm wide, chartaceous - slightly rugose, opaque, strigose; base obtuse or more or less cordate, rarely attenuate, cuneate or truncate; margins crenate-serrate, with 7-18(-22) teeth/side, and (0-)1-10(-18) glands/teeth; marginal glands colourless - red, very rarely faintly yellow, (27-)55-183(-456) µm long; head-diam (13-)20-56(-60) µm; apex acute or obtuse, rarely rounded. Primary stem terminated by an androgynous or a female inflorescence. Apical male thyrses, when present, often reduced, occasionally only a single male flower present, scarcely visible, hidden between the female, leaf-like bracts. Cytolodony para-

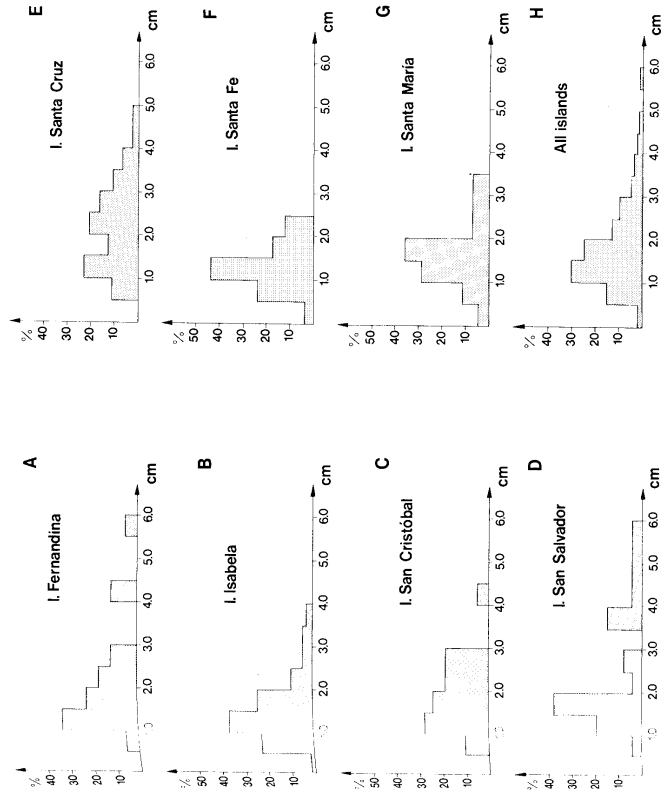


Fig. 14. Variation in lamina-length in *Acalypha parvula* in selected, different areas and in the total distribution area. A: N = 19, B: N = 75, C: N = 22, D: N = 27, E: N = 50, F: N = 25, G: N = 28, H: N = 275.

mm wide; glabrous or puberulent; margins ciliate, usually with a few glands basally; apex acute or obtuse, rarely rounded or slightly acuminate. Carpels) more or less tuberculate, usually shortly puberulent, eglandular or rarely glandular. Style(s) (0.3-)1.2-3.2(-4.3) mm long, glabrous or puberulent at the base. Seeds (0.81-)0.94-1.2(-1.39) mm long, (0.60-)0.66-0.90(-1.05) mm wide; finely - coarsely reticulate-foveate, chestnut brown - black. - Fig. 13.

Distribution: Known from all the major islands, except Darwin, Genovesa, and Seymour.

Habitat: In arid and transition zone. Recorded from evergreen forest, closed evergreen scrub with scattered trees, evergreen scrub, dry season deciduous and evergreen steppe forest, evergreen desert scrub, and broad-leaved seasonal herb-grass meadow. Probably also found in other xero- to mesophytic subformations. Also found on various types of barren substrates, 0-1450 m a.s.l. Generally well below 400 m. Only on Isla Fernan-

dina and Isabela regularly above this elevation in natural vegetation. On islands with heavy impact of feral animals occasionally above 400 m.

A. parvula is a remarkably variable species, especially concerning general habit, indumentum, leaves, branching pattern (symplochence structure), and dimensions of androgynous, first order paracodia. However, each character seems to vary continuously and quite at random. It has not been possible to demonstrate significant inter- or intra-island correlations with the variation of any character, nor does any of the taxa characters display discontinuity. The variation in some of the most variable characters is shown in diagrams (Figs 14-17). The inter-island variation patterns are essentially similar in all characters; the most extensive variation being found on the large, more heterogeneous islands (e.g. Santa Cruz), and a more limited variation on the smaller, more homogeneous islands (e.g. Santa Fe), for an example see Fig. 14.

As treated here, *A. parvula* includes 11 taxonomical

The chromosome number of *Heliconia* (Musaceae)

Lennart Andersson



Andersson, L. 1984. The chromosome number of *Heliconia* (Musaceae). - Nord. J. Bot. 4: 191-193. Copenhagen. ISSN 0107-055X.

The chromosome number $2n = 24$ was determined in 31 taxa of *Heliconia*, representing nearly the entire morphological spectrum of the genus. The karyotype is a graded series of rather small chromosomes ranging between 0.7 and 1.7 μ m. One pair has satellites. It is concluded that morphological chromosome differentiation played no great part in the diversification of the genus.

L. Andersson, Dept of Systematic Botany, Univ. of Gothenburg, Carl Skottsbergs Gata 22, S-413 19 Gothenburg, Sweden.

Introduction

Several chromosome numbers have been reported for species of *Heliconia*, most frequently $2n = 24$ (Cheesman & Larter 1935, Venkatasubban 1946, Simmonds 1954, Bisson et al. 1968, Mahanty 1970), but sometimes also $2n = 22$ (Cheesman & Larter 1935, Chakravorti 1960) and $2n = 26$ (Venkatasubban 1946). Agharkar & Bhaduri (1935) report the numbers $2n = 16, 18, 20$, and 22 for the same species, *H. metallica*. This report is readily dismissed from discussion, however, since miscounts are obvious even from the published photomicrographs illustrating the article. Chakravorti (1960), claims to have shown important structural differences between the karyotypes of different species. Common to all reports, except Simmonds', is that counts have been made on horticultural material of dubious origin and doubtful identity.

With all its shortcomings, literature seems to suggest the presence of at least three chromosome numbers in *Heliconia*, forming an aneuploid series $2n = 22, 24, 26$. Having a fair number of species in cultivation, representing most of the morphological spectrum of the genus, I decided to scan my material for cytological data that might be taxonomically useful.

Material and methods

All material used was collected from spontaneous populations and grown in the greenhouses of the Gothenburg Botanical Garden. Most plants were grown from seeds, but some of the slenderer species were grown from rhizomes. Since great homogeneity was found in the karyotype, and since hybridization is obviously quite rare in nature (Kress 1983; own obs.), no distinction is made between seed-grown and rhizome-grown material. Since no plants have yet flowered in cultivation, the counts are vouchered by collections made from the original, spontaneous populations. In some cases no material suited for pressing was found together with the fruiting plants, and in these cases a collection from the same general area is cited as illustrating my concept of the species. Such citations are indicated by a "cf."

Actively growing root-tips were cut as long as possible (usually 2-5 cm) and pretreated for 2-4 h at ca. 15°C in a solution of 0.1% colchicine in 1 mM 8-hydroxy-chinoline. Although the longer pretreatment increases the number of cells with mitoses, it also gives rise to increased stickiness. Fixation was made in a 1:3:6 mixture of acetic acid, chloroform, and absolute ethanol. The material was squashed (directly after fixation, or after storage at -20°C) and stained with aceto-orcinine. Stainability was found to differ somewhat between species, and much between different brands of stain.

Observations

All species and populations examined were found to have $2n = 24$ (Tab. 1). The chromosomes are small and

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